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NUMERIC ANALYSIS OF THE LIZARD GENUS *SCELOPORUS* WITH SPECIAL REFERENCE TO CRANIAL OSTEOLOGY

Kenneth R. Larsen[1,2] and Wilmer W. Tanner[1]

Abstract.— Numerical statistical methods were used to analyze the species in the genus *Sceloporus* using cranial osteology, external meristic and numeric characters, karyology, display behavior, and geographic distribution.

A new classification for the genus is proposed with three major branches or groups. Group I contains 7 species in 3 species groups. Group II contains approximately 19 species in 5 species groups. Group III contains approximately 32 species in 5 species groups. This classification is supported by the cluster analysis of several different sets of data. Cranial osteology, zoogeography, behavior, and karyology are shown to be taxonomically significant as numeric characters. Stepwise discriminate analysis shows that this classification of the species of *Sceloporus* into 3 major groups and 13 species groups is significant at the .999 confidence level: It is concluded that the 3 major groups should be given taxonomic recognition.

Cope (1900) stated, "The distinction of many of the species of this genus [*Sceloporus*] is not accomplished without difficulty. I recommend it as an excellent *pièce de résistance* for those persons who do not believe in the doctrine of derivation of species." This statement was endorsed by Hobart Smith (1938:548-49):

> *Sceloporus* is one of the most nearly ideal of living genera of reptiles for the study of speciation and related phenomena. The characteristics which it possesses and which are essential to an ideal genus for such studies are:
>
> 1. *A large number of living forms.* . . .
> 2. *Prolificity.* Where *Sceloporus* occurs, usually it is the most common of all reptiles, or for that matter, of all vertebrates.
> 3. *A large range, entirely contiguous.* The genus occupies practically all of the United States, and occurs as far south as Panama.
> 4. *Great adaptability.* Species in this genus have adapted themselves to considerable range of elevation—from below sea level (Death Valley) to about 13,500 feet above sea level. They occur in almost every conceivable terrestrial habitat—deserts, sand dunes, forests, on rocks, trees, or ground in grassy plains or heavy brush, and even on houses, fences and other man-made structures.
> 5. *Lack of obvious distinctive specific characters.* Subspecies are numerous and species not so well defined as in many other genera of animals, and for this reason relationships may more definitely be postulated.
>
> These characters are indicative of a group of relatively recent development.

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[1] Department of Zoology, Brigham Young University, Provo, Utah 84602.
[2] Present address: E.P.O. Biology, University of Colorado, Boulder, Colorado 84302.

Smith would probably have added a sixth and seventh characteristic if karyological and behavioral information had been available.

It is only proper, in consideration of the foregoing, that *Sceloporus* should be considered a suitable candidate for the application of recently developed statistical methods.

The study here reported was undertaken with several questions in mind: (1) What is the most natural arrangement of species within the genus? (2) Can satisfactory results be obtained with modern statistical methods? (3) Can significant intrageneric taxonomic information be obtained from the cranial osteology of *Sceloporus*? (4) Will different sets of characters (scale counts, external morphology, karyotypes, behavior, osteology, etc.) produce similar results? (5) Is *Sceloporus* a single genus?

We extend our deepest gratitude to the following persons and institutions for loans, exchanges, and gifts of specimens and for critical assistance in the preparation of the manuscript: Ticul Alvarez (University of Mexico), Charles C. Carpenter and James Richard Purdue (University of Oklahoma), Charles J. Cole (American Museum of Natural History, AMNH), William E. Duellman (University of Kansas), William P. Hall (University of Puerto Rico), Hymen Marx (Field Museum of Natural History, FMNH), Hobart M. Smith (University of Colorado), and Ernest E. Williams (Museum of Comparative Zoology, Harvard).

We thank the departments of Zoology, Geology, and Computer Science at Brigham Young University (BYU) for use of their facilities and for valuable assistance rendered by numerous staff and faculty members.

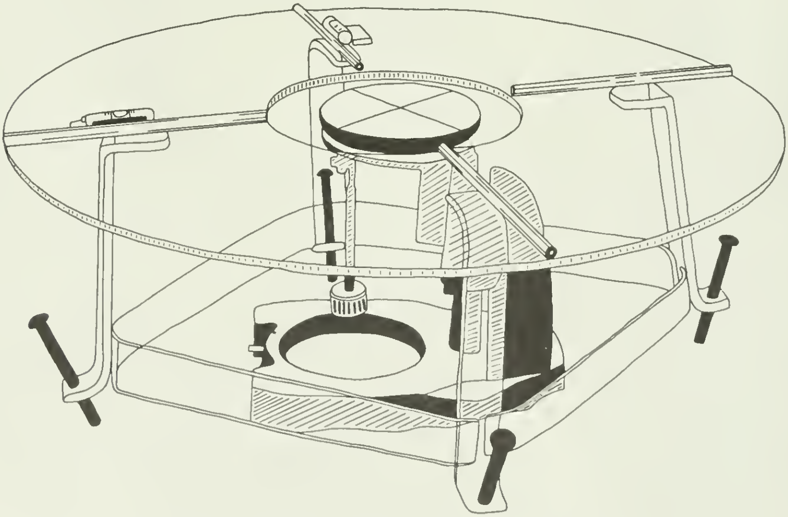

Fig. 1. Platform for constant angle photography of skulls.

This study was supported by a National Defense Education Act title IV fellowship to the senior author from 1966 to 1970.

REVIEW OF LITERATURE

Taxonomy

The term *Sceloporus* was coined by Weigmann (1828:369-70) from the Greek words *scelos* (leg) and *porus* (hole). Our translation of Weigmann's original description follows:

> Furthermore, there is a Mexican genus with many species which is similar to *Tropidurus* in body shape, head shape, placement of nostrils and ears, formation of teeth, and form and placement of dorsal and caudal scales.
>
> But it differs in that it has femoral pores and the dorsals are enlarged. Both genera have a peculiar dermal pocket on the side of the neck. This dermal pocket is crescent shaped in the new genus. It is formed by a fold in the skin

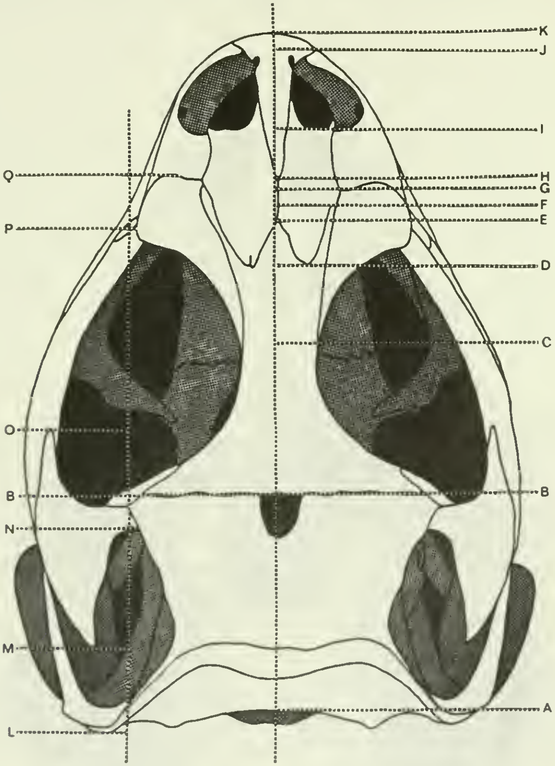

Fig. 2. Characters 41 to 50 on dorsal view of skull.

$41=\frac{A\text{-}B}{B\text{-}E}$ $42=\frac{E\text{-}H}{B\text{-}E}$ $43=\frac{H\text{-}K}{B\text{-}E}$ $44=\frac{D\text{-}F}{F\text{-}G}$ $45=\frac{G\text{-}I}{B\text{-}E}$ $46=\frac{I\text{-}J}{B\text{-}E}$ $47=\frac{B\text{-}P}{B\text{-}E}$

$48=\frac{L\text{-}N}{A\text{-}B}$ $49=\frac{M\text{-}O}{N\text{-}B}$ $50=\frac{C\text{-}G}{P\text{-}Q}$

and the inner surface is lined with shagreen-like scales. I usually found a population of 6-legged orange-colored epizoa in the dermal pocket in which case the scales would be missing.

His Highness, the Prince of Neuwied observed the same thing in his description of *Tropidurus torquatus* (Beitrage zur Naturgeschichte Brasiliens I. p. 148).

Hernandez has already mentioned 2 of the species of this genus. He reports that the species which can reasonably be considered typical is a crevice-dweller and eats worms. Because of the large femoral pores, I name this genus *Sceloporus*. The following is a short provisional description of the species.

Weigmann (1828) then gave a short description of the genus and six species: *torquatus*, *spinosus*, *grammicus*, *pleurostictus*, *aeneus*, and *scalaris*. In the heading, he provided the common name *Stone Lizard*, which name he explained in a footnote: "I have chosen this German name (Stone Lizard) because Hernandez says that the common species of this genus are called Tecoixin in Mexico. Tecoixin means Saxorum Lacerta [*Saxorum lacerta* = stone lizard]."

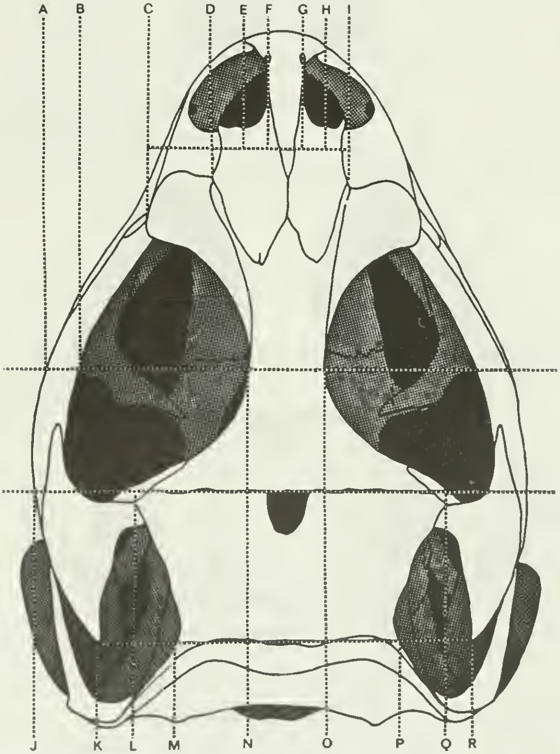

Fig. 3. Characters 51 to 56 on dorsal view of skull.

$51=\frac{N\text{-}O}{L\text{-}Q}$ $52=\frac{J\text{-}L}{L\text{-}Q}$ $53=\frac{M\text{-}P}{L\text{-}Q}$ $54=\frac{K\text{-}M}{L\text{-}Q}$ $55=\frac{D\text{-}C}{D\text{-}I}$ $56=\frac{F\text{-}G}{E\text{-}H}$

Hobart Smith (1938:547-48) provided an excellent history of the revisions of this genus which is paraphrased as follows:

> Weigmann (1834) recognized nine species—*torquatus, formosus, spinosus, horridus, grammicus, microlepidotus, variabilis, aeneus* and *scalaris*. Dumeril and Bibron (1837) recognized 10 species, adding *undulatus* Latreille. Bocourt (1834) recognized 22 species. Cope (1885) published a synopsis of *Sceloporus*, in which he recognized 36 species and subspecies.
>
> Boulenger (1885) recognized 33 species and subspecies and Gunther (1890) recognized 30 species and listed 7 other described forms without comment as to validity.
>
> Boulenger (1897) presented his conclusions with regard to the species of *Sceloporus* in his revision of the genus and recognized 36 species and subspecies. . . .
>
> In the last monograph of the genus is that of Cope (1900) published in 1900, in "The Crocodilians, Lizards, and Snakes of North America." Forty species and subspecies are recognized.

Smith (1939:29) added, "Of the 127 names proposed in the genus, I consider 95 valid. These have been segregated into 15 groups of approximately equivalent morphological value."

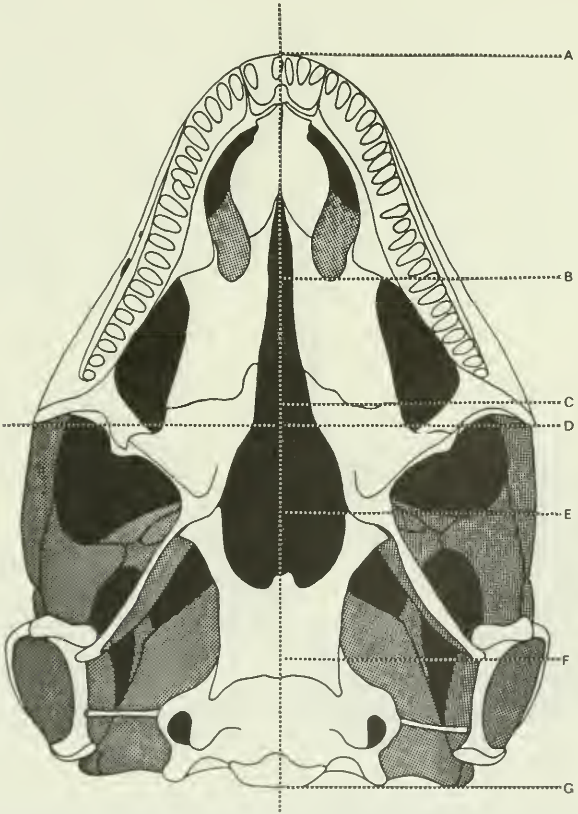

Fig. 4. Characters 57 to 60 on ventral view of skull.

$57=\frac{G\text{-}E}{A\text{-}D}$ $59=\frac{C\text{-}B}{A\text{-}D}$ $58=\frac{E\text{-}D}{A\text{-}D}$ $59=\frac{C\text{-}B}{A\text{-}D}$ $60=\frac{F\text{-}D}{A\text{-}D}$

Smith and Taylor (1950) provide the following list of groups and species (15 groups, 54 species; in each, the first species is the group name): (1) *formosus, malachiticus, asper, stejnegeri, presygous, lunaei;* (2) *spinosus, lundelli, edwardtaylori, melanorhinus, clarki, orcutti, magister, horridus, olivaceus;* (3) *undulatus, cautus, occidentalis, woodi;* (4) *graciosus;* (5) *grammicus, heterolepsis;* (6) *megalepidurus, pictus;* (7) *torquatus, serrifer, mucronatus poinsetti, cyanogenys, bulleri, lineolateralis, ornatus, dugesi, jarrovi;* (8) *variabilis, cozumelae, teapensis, parvus, couchi;* (9) *merriami;* (10) *maculosus;* (11) *chrysostictus;* (12) *siniferus, squamosus, carinatus, ochoterenai;* (13) *utiformis;* (14) *scalaris, jalapae, aeneus, goldmani;* (15) *pyrocephalus, gadoviae, nelsoni.*

Later, Smith and Taylor (1966) added four new species to their checklist: *macdougalli, shannonorum, subpictus,* and *virgatus.* Hall (1971) increased the number of species in this genus to 61 by recog-

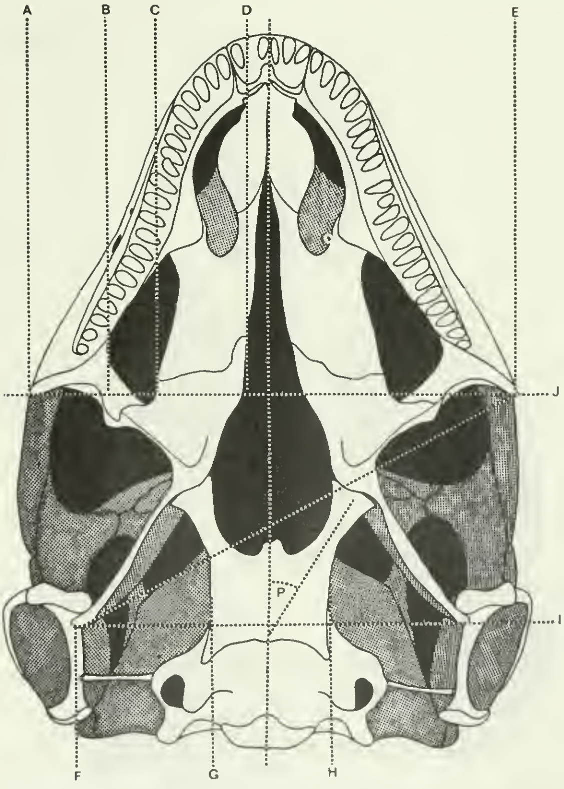

Fig. 5. Characters 61 to 66 on ventral view of skull.

$$61 = \frac{\text{A-B}}{\text{A-E}} \quad 62 = \frac{\text{B-C}}{\text{A-E}} \quad 63 = \frac{\text{C-D}}{\text{A-E}} \quad 64 = \frac{\text{G-H}}{\text{A-E}} \quad 65 = \frac{\text{E-F}}{\text{I-J}} \quad 66 = \frac{\text{(diagonal)}}{5\text{(Tangent P)}}$$

nizing *acanthinus* and by adding *exsul* and *insignis*. Hall (pers. comm.) has called attention to a new species in Baja California and has suggested the elevation of *magister zosteromus* and *orcutti licki* to specific rank. He has also proposed that *grammicus* contains at least six cryptic species. Hobart Smith (pers. comm.) also has a manuscript species. A second manuscript species described by Smith and Larsen is in press. If these new species are included, the total number in this genus would exceed seventy.

Osteology. Avery and Tanner (1971) presented a review of lizard osteology to which the reader is referred. On page 6 they stated:

> In summary the literature dealing with anterior osteology and myology of lizards is scattered and varied. Descriptions of skulls representing almost all families can be found. With the exception of such papers as Camp (1923), McDowell and Bogert (1954), Savage (1958), Etheridge (1964), and Presch (1969), little has been done, utilizing osteology, to analyze the evolutionary lines within families.

Of the above listed papers, only Savage, Etheridge, and Presch considered Sceloporine relationships, and none of these reported on species relationships within the genus *Sceloporus*.

Cope (1900:330-31) described the cranial osteology of *Sceloporus* on the basis of two specimens of *undulatus* and one specimen of *spinosus*. He described the following 35 characteristics:

> [1] Premaxillary bone has a long superior spine and is [2] truncate on the palatal face, and [3] has the button-like process. [4] The nostrils are partially vertical, so that the [5] nasals are a little shortened in front. [6] The latter are rather large and are distinct. [7] The frontal is simple and narrow and is [8] strongly grooved on the middle line below. [9] The parietal is short and wide, and [10] is perforated by a large pineal foramen, [11] which touches the

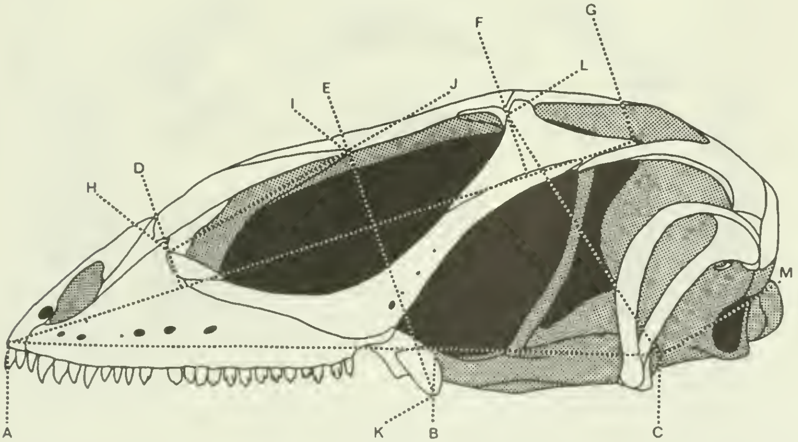

Fig. 6. Characters 67 to 73 on lateral view of skull.

$67=\frac{\text{A-B}}{\text{A-G}}$ $68=\frac{\text{B-C}}{\text{A-G}}$ $69=\frac{\text{A-D}}{\text{A-G}}$ $70=\frac{\text{D-E}}{\text{A-G}}$ $71=\frac{\text{E-F}}{\text{A-G}}$ $72=\frac{\text{H-I}}{\text{D-E}}$ $73=\frac{\text{J-K}}{\text{L-M}}$

coronal suture. [12] Parietoquadrate arch distinct. [13] Supraoccipital broadly but loosely attached [14] confluent with exoccipitals. [15] Prefrontals large, not reaching postfrontals above. [16] Lachrymal small and joining jugal. [17] Postfrontal a small splint. [18] Postorbital large, extensively in contact with jugal and supratemporal. [19] Paroccipital small. [20] Vomers short, divaricate, and separated by a deep notch behind. [21] Palatine with the vomerine process longer than maxillary; [22] Palatine foramen large. [23] Palatines and pterygoids well separated from each other on the middle line; [24] ectopterygoid deflected at its internal extremity. [25] Basipterygoids developed. [26] Quadrate with two conchs [27] the internal the narrower. [28] Presphenoid rudimental; [29] sphenoid and basioccipital coossified; [30] descending lateral processes of the latter strongly developed. [31] The supraforaminal part of the petrosal is very short; [32] the infraforaminal portion is produced beyond it and is nearly horizontal in position. [33] The foramen of the eighth nerve is at the bottom of a fossa. [34] Epipterygoid resting on pterygoid much posterior to ectopterygoid and reaching parietal without touching petrosal. [35] Occipital condyle not subdivided by grooves.

(We disagree with the last characteristic as most of our specimens exhibit a conspicuous pair of grooves that subdivide the occipital condyle.)

Lundelius (1957) produced the only computerized statistical analysis of *Sceloporus* cranial osteology to date. On pages 67 and 68, he listed 32 cranial measurements used in his analysis:

(1) midline length of premaxillary, (2) midline length of nasal, (3) midline length of frontal, (4) midline length of pineal, (5) midline length of parietal, (6) total length of skull roof from snout to posterior edge of parietal, (7) internarial width, (8) width anterior to orbit, (9) interorbital width, (10) anterior width of parietal, (11) width of pineal, (12) interfenestral width, (13) maximum width of temporal fenestra (diagonal), (14) distance from basicranial tubera to

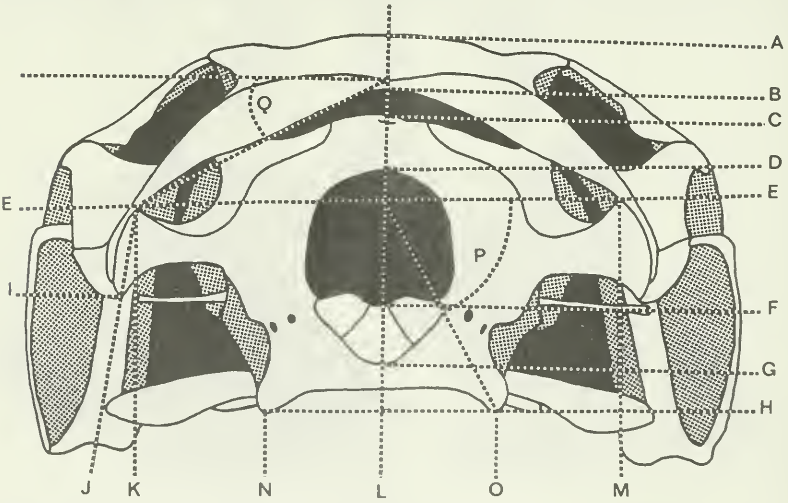

Fig. 7. Characters 74 to 80 on posterior view of skull.

$74=\frac{\text{C-D}}{\text{A-B}}$ $75=\frac{\text{D-F}}{\text{A-B}}$ $76=\frac{\text{F-G}}{\text{A-B}}$ $77=\frac{\text{E-I}}{\text{A-B}}$ (along diagonal J) $78=\frac{\text{K-M}}{\text{N-O}}$

79=5(Tangent P) 80=5(Tangent Q)

basipterygoid process, (15) length of palatine ramus of pterygoid, (16) length of palatine, (17) length of prevomer, (18) length of quadrate ramus of pterygoid, (19) width across basicranial tubera, (20) width across basipterygoid processes, (21) width across posterior ends of maxillaries, (22) width across descending processes of pterygoid, (23) width across anterior part of palate, (24) tooth row width of premaxillaries, (25) length of maxillary, (26) distance from the posterior end of maxillary to posterior edge of quadrate, (27) length of quadrate, (28) total width of skull across exoccipitals, (29) length of exoccipital, (30) medial end of exoccipital to lateral edge of foramen magnum, (31) width of foramen magnum, (32) width of occipital condyle.

Our analysis utilitzed all the above measurements, or functions of them, with the exception of numbers 4, 11, 13, 14, and 23. Numbers 4 and 11 were omitted because the thin bone around the parietal foramen is easily dissolved in bleach and because we suspect that the dimensions of the parietal foramen may be affected by the time spent in bleach during preparation. Number 13 was omitted because it is a diagonal with no definite points of origin. We measured the width of the temporal fenestra at right angles to the midline. Numbers 14 and 23 were omitted because they are difficult to define on a photograph (see material and methods below).

Karyology

The karyology of *Sceloporus* has attracted much interest because of the high level of intrageneric variation. Gorman, Atkins, and Holzinger (1967) published karyotypic data on 15 genera. On page 287 they reviewed a manuscript presented by William P. Hall:

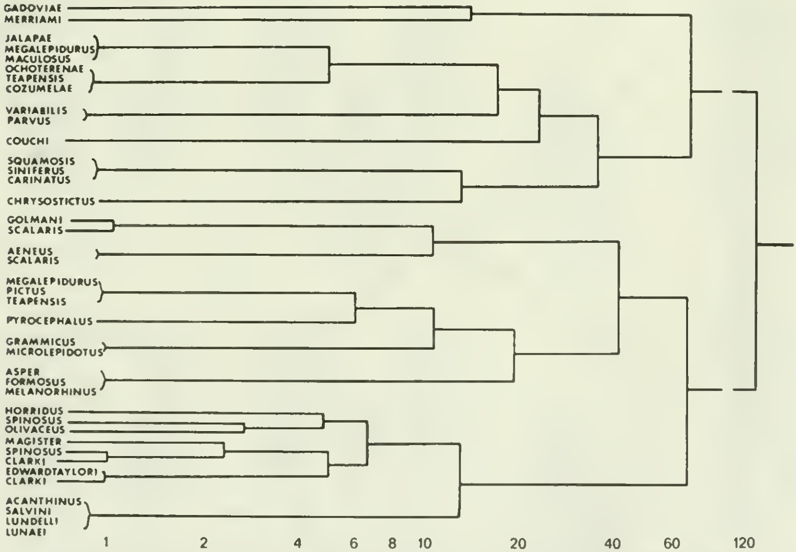

Fig. 8. Dendrogram produced by Ward's cluster analysis of Smith's (1939) data for *Sceloporus*.

> Hall (1965) has summarized all available information on iguanid karyotypes. He listed the formula 12 metacentric Macrochromosomes and 24 microchromosomes for the following genera: *Anolis*, *Crotaphytus*, *Dipsosaurus*, and *Phrynosoma*. Hall characterized the genera termed 'sceloporine' . . . as having 12 metacentric Macrochromosomes and a reduced number of microchromosomes, ranging from 10 to 22. Hall's data include members of the genera *Holbrookia*, *Callisaurus*, *Urosaurus*, *Uta* and *Sceloporus*.

Gorman et al. (1967) established that a formula of 12 metacentric macrochromosomes and 24 microchromosomes is primitive among many lizards. They concluded: "Chromosome loss would be of a specialized, advanced character, and this correlates with the phylogenetic position of the sceloporines."

Lowe, Cole, and Patton (1967) proposed that karyotypical evolution can be a matter of Robertsonian fusion, but they did not allow for Robertsonian fission. Cole (1970, 1971a, 1971b) published the karyotypes of the *spinosus* group, the *pyrocephalus* group, and the five monotypic groups (Smith's groups above). He proposed phylogenies of the two polytypic groups and discussed relationships among the others.

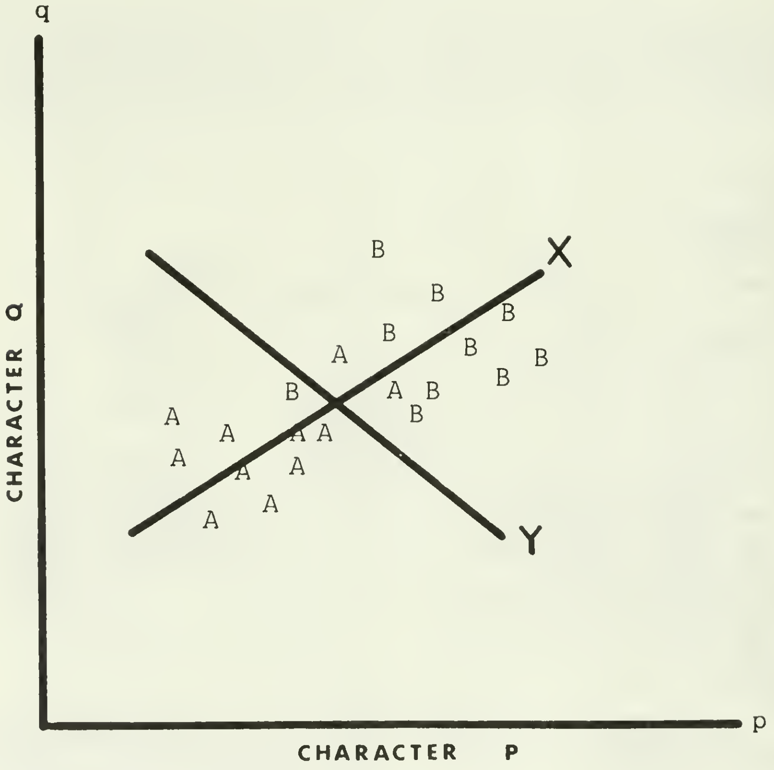

Fig. 9. Theory of canonical analysis.

See page 14 for caption

See page 14 for caption

See page 14 for caption

Fig. 10. Dorsal, ventral, lateral, and posterior views of 13 species of *Sceloporus*, representing the major groups within the genus: A, *Sceloporus gadoviae;* B, *S. couchi;* C, *S. maculosus;* D, *S. grammicus microlepidotus;* E, *S. pyrocephalus;* F, *S. scalaris scalaris;* G, *S. siniferus cupreus;* H, *S. variabilis variabilis;* I, *S. spinous caeruleopunctatus;* J, *S. formosus formosus;* K, *S. undulatus elongatus;* L, *S. jarrovi jarrovi;* M, *S. torquatus melanogaster.*

Hall (1970, 1973) has also attempted to establish a phylogeny of *Sceloporus* with major emphasis on karyology. With almost no disagreement concerning the karyotypes of different species, Hall and Cole have produced quite different phylogenies. Hall accepts fission as well as fusion. The occurrence of fission was shown in *Anolis* by Webster, Hall, and Williams (1972).

Ethology

In 1960 Hunsaker showed that different species of *Sceloporus* have specific display patterns. He showed that females can distinguish between the display patterns of closely related forms. In one part of his study, Hunsaker offered females a choice of males of closely related species. His results show that the females seemed to discern which male was most similar to their own species. This preference by females could be a valid systematic tool. For example, Hunsaker mixed female *jarrovi* with males of *jarrovi*, *dugesii*, and *ornatus*. He found that female *jarrovi* prefer to associate with male *dugesii* over *ornatus* 16 to 11 (61 observations): "These data reflect an apparent tendency of a female *jarrovi* to associate with male *dugesii* more frequently than with a male *ornatus*" (p. 67). Hunsaker also found that female *jarrovi* preferred male *dugesii* over male *jarrovi* 22 to 11 (70 observations) and *ornatus* over *jarrovi* 47 to 12 (47 observations). Possibly the females were not receptive and preferred to avoid their own species. As a result, it may be concluded that *ornatus* is closer to *jarrovi* than is *dugesi* (the *ornatus* males looked more like *jarrovi* to the female *jarrovi* who chose to avoid males). The results do not agree with Smith (1939), and Hunsaker's work is hardly sufficient for systematic conclusions at this point. However, this method may have future prospects.

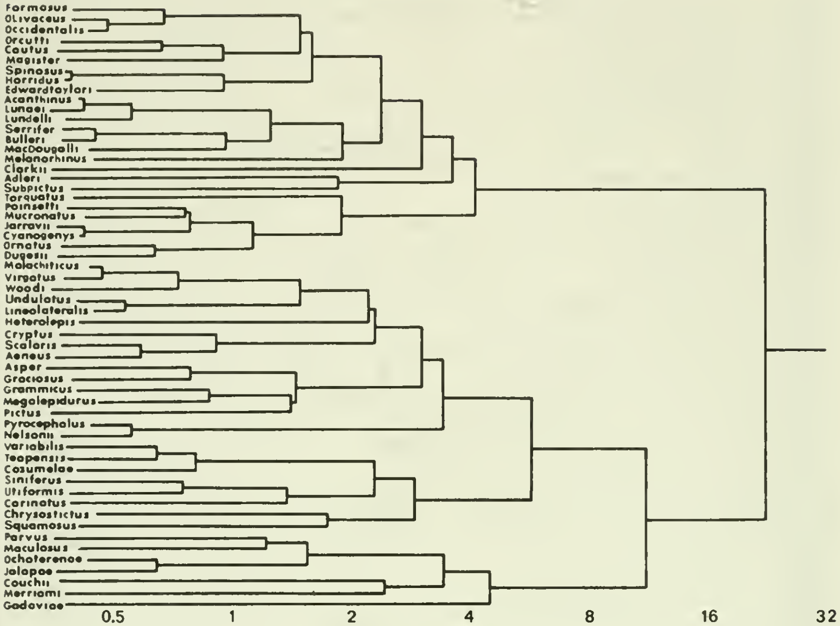

Fig. 11. Dendrogram generated by external characters (1 to 40).

A more promising aspect of lizard behavior is the analysis of "display action patterns." Carpenter (1962) reported on the display action patterns of *Uta*, *Streptosaurus*, and *Urosaurus* and concluded that *Urosaurus* is a valid genus because its patterns diverge significantly from those of *Uta*.

Purdue and Carpenter (1972a) compared one species of *Petrosaurus*, five species of *Uta*, and five species of *Urosaurus* to 22 species of *Sceloporus*. In their examination of displaying males, they found that the ratio of hip movement to eye movement is a valuable taxonomic character. They have also shown (1972b) that the ratio of shoulder movement to eye movement is a valid species-specific character. Both ratios have been included in our analysis.

Hematology

Guttman (1970) analyzed the hemoglobin of 12 species of *Sceloporus* using gel electrophoresis. His evidence gives ample support to the proposition that relative movement within the gel is indeed determined by genetic factors. His data also support the arrangement of *cyanogenys* and *torquatus* in one part and *jarrovi* in the other part of a distinct group.

Although some relationships can be shown with electrophoresis, there are problems that make this method suspect. If a heterozygous individual produces two bands, which band is representative of

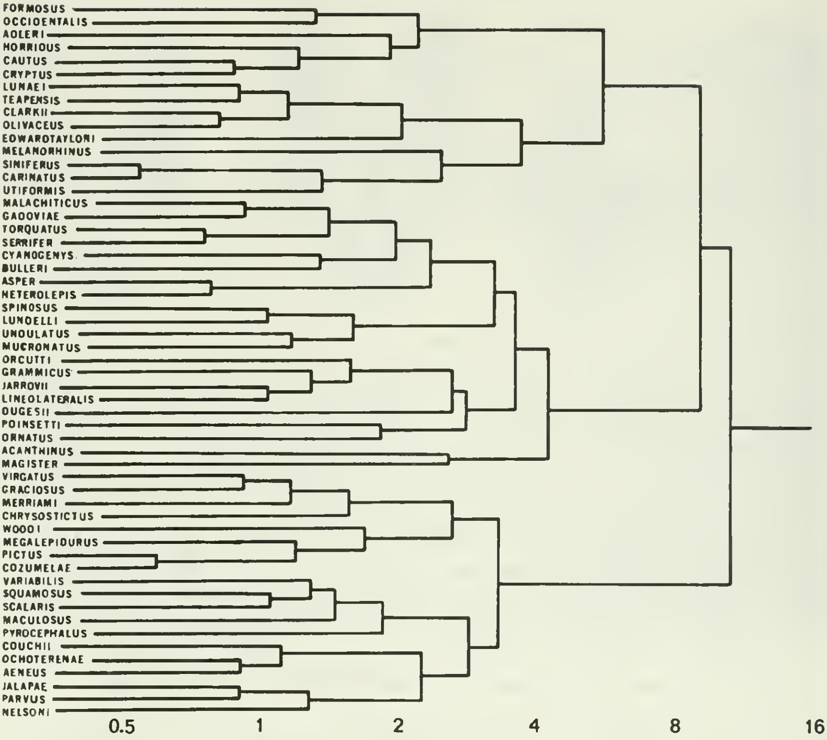

Fig. 12. Dendrogram generated by skull characters (41 to 80).

the position of the species? Sometimes the separation between two bands in a single individual is greater than the distance between single bands of widely divergent species. For example, the total range of relative movement reported by Guttman in the gel is from .11 to .50. *S. undulatus* and *cyanogenys* together cover almost the entire range (.16 to .50). Yet they have a nearly identical band (*cyanogenys* .30; *undulatus* .28 to .33). The relative movement of hemoglobin in an electrophoretic gel is obviously not an indication of degree of relationship. Such a number cannot be used as a numeric character, and the interpretation of electrophoresis must remain subjective and qualitative—which does not rule out its value in systematics. It would be a mistake, however, to consider *variabilis* (.16) and *merriami* (.17) as more closely related than *magister* (.20) and *orcutti* (.41). The members of each pair differ from each other, and further conclusions from electrophoresis may be misleading.

Temperature

Bogert (1949) computed average body temperatures of 10 forms of *Sceloporus* (Table 1). Two closely related forms (*v. variabilis*

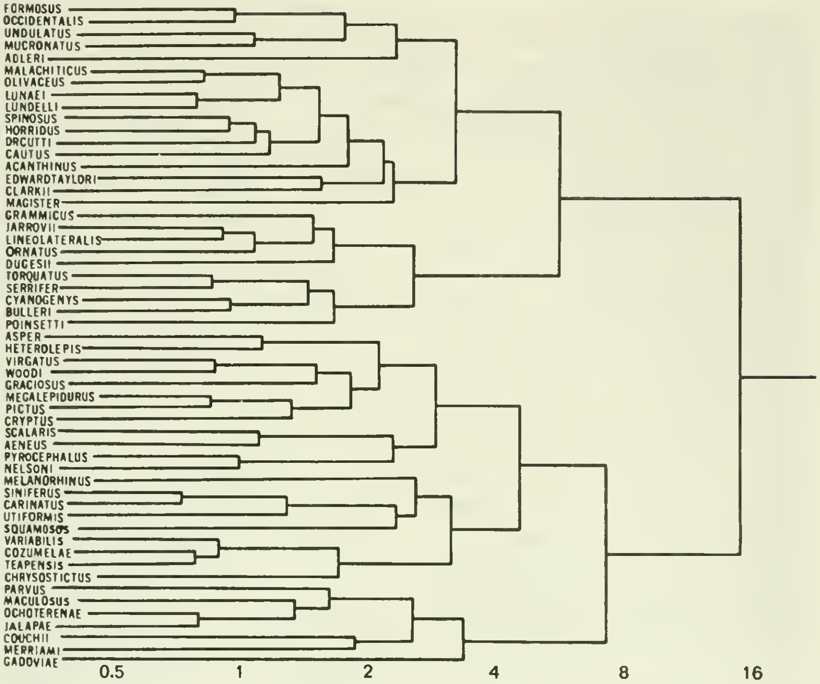

Fig. 13. Dendrogram generated by external and skull characters (1 to 80).

and *v. olloporus*) are separated by 1.4 degrees. However, a span of 1.3 degrees includes five widely divergent species (*magister*, *undulatus*, *poinsetti*, *grammicus*, and *merriami*). In fact, *grammicus* and *merriami* prefer the same temperature. It is doubtful that these data have any systematic value. Futher studies, however, may show that temperature preference or optimum temperature for enzyme systems can be useful.

Paleontology

Brattstrom (1955) reported some thoracic vertebrae, which he identified as *Sceloporus jarrovi*, in Late Pleistocene deposits in Zumpango, Mexico. However, Cole (1970:27) has found that, "The fossil record of *Sceloporus* is practically nonexistent."

Femoral Pore Secretions

Hunsaker (1960:72) suggested that lizards can identify femoral pore secretions by olfaction or taste:

> In *poinsetti* and *cyanogenys* there is a marked disposition of the members of each species to separate when put together. The lizards of one species would establish common territories to the exclusion of the other species. When the secretions of each species were transposed, a reversal of the associative patterns

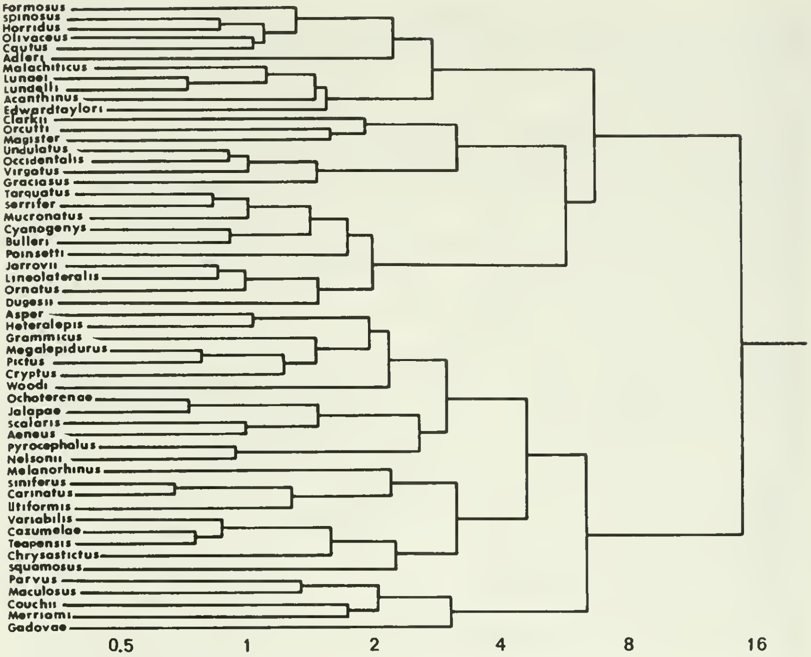

Fig. 14. Dendrogram generated by external, skull, and distribution characters (1 to 82).

occurred, and the members of one species associated with the other and excluded members of their own species.

If femoral pore secretions represent a species-specific territorial marker, then perhaps chemical analysis of these secretions will provide another valuable taxonomic character for future workers.

Myology

Secoy (1971) examined the myology of eight species of *Sceloporus*, including an extensive examination of *c. clarki*. She concluded that intrageneric myological variation is slight and that speciation in this genus is therefore recent. Although myology may be significant, and even diagnostic, at higher levels or with different taxa, its usefulness within the genus *Sceloporus* must yet be demonstrated.

MATERIALS AND METHODS

Specimens for this study were acquired from several museum collections and through extensive field collecting by the authors. Most specimens were collected by noosing or shooting with .22 dust shot.

The museum and locality data for specimens from the United States, Mexico, and Central America are as follows: *gadoviae*, BYU 36148 (skull), 45

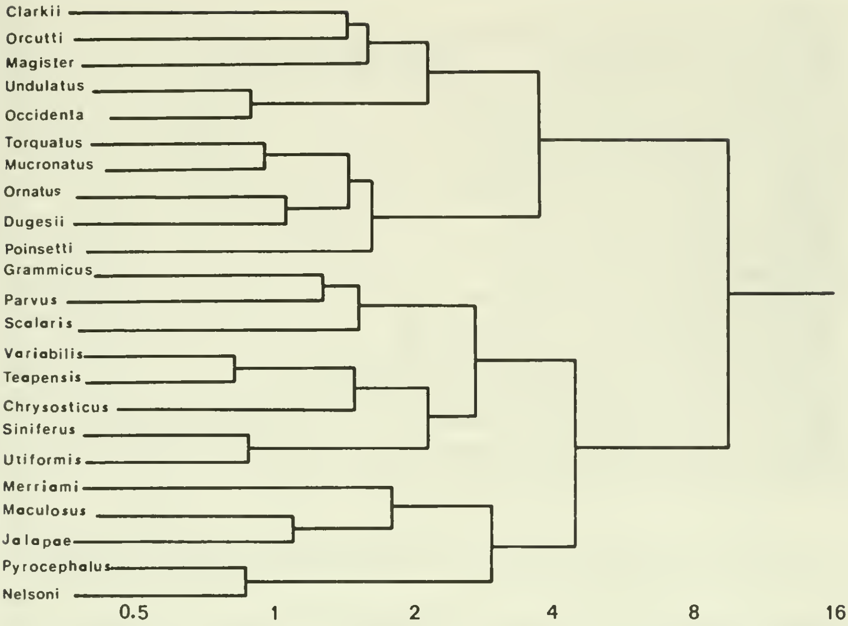

Fig. 15. Dendrogram generated by external, skull, distribution, and display characters (1 to 84).

km S Neuva Italia, Michoacan; *couchi* BYU 36418 (skull), 36417, Huestaca Canon, 18 km W Monterrey, Nuevo Leon; *merriami merriami* BYU 36389 (skull), 13 km S Shumla (Hwy 90 and Pecos River), Val Verde Co., Texas; *parvus scutulatus* BYU 36125 (skull), 4 km N Zimapan, Hidalgo; *parvus parvus* BYU 36126, 36127, 7 km W 3 km N Santiago Anaya, Hidalgo; *jalapae* BYU 36423 (skull) 13 km SE Nochixtlan, Oaxaca, BYU 36422 near Tehuacen (Cacoalepam), Puebla; *ochoterenae* BYU 36004 (skull), 36003, 36005, 36006, Chilpancingo, Guerrero; *maculosus* FMNH 33548 (skull), 32007, 23 km NE Pedricena, Durango; *grammicus microlepidotus* BYU 36300 (skull), 36015, 36017, 36021, Puebla, Puebla, east side of Orizaba, Veracruz; *pictus* BYU 36419 (skull), summit Mt. Acultzingo, Veracruz; *megalepidurus* BYU 36421 (skull), Lake El Chico, Hidalgo, BYU 36094, 36095, 3 km W Limon, Veracruz; *cryptus* AMNH 65835 (skull), Cerro de Humo, Oaxaca; *heterolepis* BYU 36420 (skull), Rancho Primarera, near Guadalajara, Jalisco; *asper* FMNH 32041 (skull), 32043 Uropan, Michoacan; *pyrocephalus* BYU 36268 (skull), 36264, 36265, 36266, 24 km N Colima, Colima; *nelsoni barrancorum* BYU 14316 (skull), 14317, 14318, 14319, 14320, Urique, Chihuahua; *scalaris scalaris* BYU 36132 (skull), Zumpango, Mexico, BYU 36132, Yuridin, Guanajuato, BYU 36133, 2 km S 4 km E Villa Victoria, Mexico; *aeneus aeneus* BYU 36137 (skull), 3 km S Atlacomulco, Mexico, BYU 36136, 4 km S Mexicaltzingo, Mexico, BYU 36138, Salazar, Mexico, BYU 36139, Lagunas Zempoala, Morelos; *siniferus cupreus* BYU 36228 (skull), 36225, 26336, 26229, 74-108 km SE Oaxaca, Oaxaca; *carinatus* BYU 36424 (skull), Rancho Meyapac, Ocozocoautla, Chiapas; *utiformis* BYU 36400 (skull), 36401, 36402, 36403. 262 km S Guadalajara (Hwy 80), Jalisco; *squamosus* BYU 36044 (skull), Chinandega Nicaragua; *variabilis variabilis* BYU 36018 (skull), 36163, 36164, 36172, 39 km E Jalapa, Veracruz; *cozumelae* BYU 36428 (skull), 36425, 36426, 36427, 8 km W Progreso, Yucatan; *teapensis* BYU 36121 (skull), 36122, 20 km N Randales, Chiapas, BYU 36123, Montepio, Veracruz, BYU 36124, Catemaco, Veracruz; *chrysostictus* BYU 36129 (skull), Piste 10 m Yucatan,

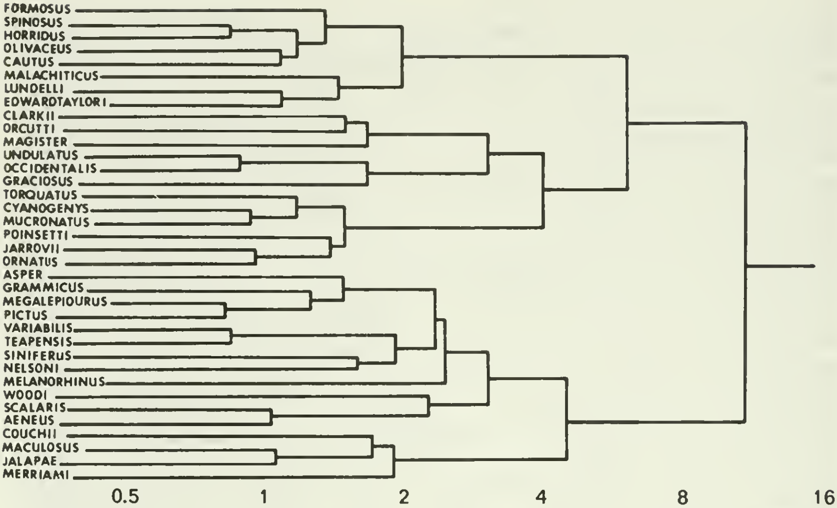

Fig. 16. Dendrogram generated by external, skull, distribution, and chromosome characters (1 to 83).

Yucatan, BYU 36128, Isla mujeres, Quintana Roo; *spinosus caeruleopunctatus* BYU 36213 (skull), 36205, 36212, 36219, 16 km S. Oaxaca, Oaxaca; *orcutti orcutti* BYU 32321 (skull), mountains S of Cabazoh, Riverside Co., California, BYU 30080, 30081, Canyon Guadalupe, Juarez Mountains, Baja California; *clarki clarki* BYU 36056 (skull), 36053, 36054, 36055, San Rafael Trail, Arizona; *melanorhinus calligaster* BYU 14640 (skull), Puerto Vallarta, Jalisco; *magister magister* BYU 8848 (skull), Panoche, San Benito Co., California, BYU 9850, 26 km W Caliente, Lincoln Co., Nevada, BYU 23666, Leeds, Washington Co., Utah, BYU 12886, Hole in the Rock, Kane Co., Utah; *olivaceus* BYU 13048 (skull), Camp Bullis, Texas, BYU 36397, 36398, Laredo, Texas; *cautus* BYU 36250 (skull), 36251, 24 km SE Saltillo, Coahuila; *horridus horridus* BYU 36387 (skull), 36384, Iguala (185 km S Mexico City), Guerrero, BYU 36024, 36025, Chilpancingo, Guerrero, BYU 36231, 132 km S Mexico City Morelos; *edwardtaylori* BYU 36080 (skull), 8 km NW Salina Cruz, Oaxaca; *formosus formosus* BYU 36074 (skull), 36075, 36076, Llano de las Flores, Chiapas; *lunaei* FMNH 64687 (skull), 64691, Santa Clara, Sierra de las Minas, Guatemala; *lundelli lundelli* FMNH 32123 (skull), 32088, 30261, Balchacaj, Campeche; *malachiticus malachiticus* BYU 36032 (skull), 36029, 36030, 36031, Cerro de la Muerte, 95 km S San Jose, Costa Rica; *acanthinus* FMNH 20156 (skull), Tiquisata, Guatemala, FMNH 167111, Santa Clara, Sierra de las Minas, Guatemala, FMNH 10991, Hacienda Chileta, Sonsonate, El Salvador; *undulatus elongatus* BYU 20642 (skull), 20632, 20633, 20635, Yellow Cat Mining District, Grand Co., Utah; *virgatus* BYU 17031 (skull), 15487, 15488, 17030, 16 km SW San Pedro, Chihuahua; *woodi* BYU 8370 (skull), Englewood, Florida; *occidentalis biseriatus* BYU 30097 (skull), 30094, 23873, 23875, 23878, Rainier Mesa, Nevada Test Site, Mercury, Nye Co., Nevada; *graciosus graciosus* BYU 16700 (skull), 33024, 33049, 21 km NE Provo, Wasatch Co., Utah, BYU 33057, 33058, 5 km E Spanish Fork, Utah Co., Utah; *jarrovi jarrovi* BYU 36007 (skull), 36008, 36010, Huachuca Mountains, Arizona, BYU 36072, Saddle Mountain Trail, Arizona; *lineolateralis* FMNH 100174 (skull), 32030, 10 km NE Pedrecena, Durango; *ornatus caeruleus* BYU 36262 (skull), 36263, 68 km E Torreon, Coahuila; *dugesi dugesi* BYU 36369 (skull), 36342, 36343, 36367, 36370, 165 km S Guadalajara, Jalisco; *torquatus melanogaster* BYU 36309 (skull), 36302, 36303, 36304, 36306, Morelia, Michoacan; *cyanogenys* BYU 36011 (skull), Rancho Santa Anna (13 km SE Padilla), Tamaulipas, BYU

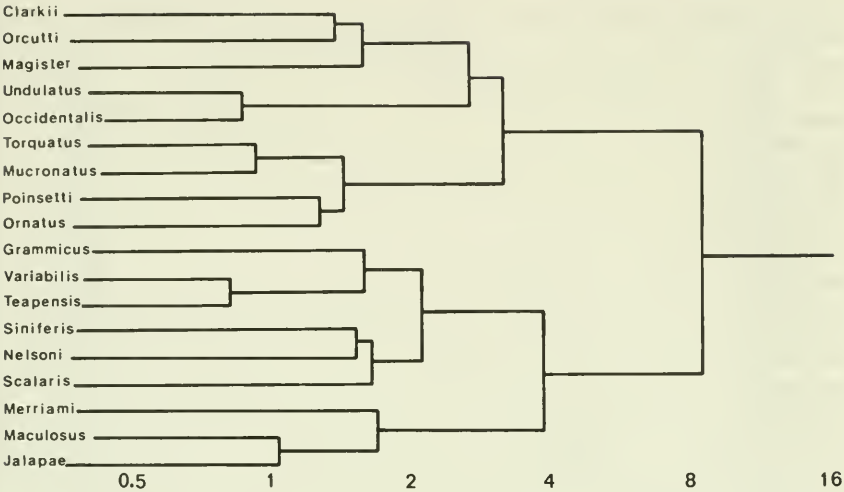

Fig. 17. Dendrogram generated by external, skull, distribution, display, and chromosome characters (1 to 85).

11402, 11404, 11405, Arroyo Vaqueriso, Nuevo Leon; *bulleri* BYU 40082 (skull), 36381, Autlan (185 km S Guadalajara), Jalisco; *macdougalli* FMNH 71661, AM 76119, Isthmus of Tehuantepec, Oaxaca; *mucronatus omiltemanus* BYU 36190 (skull), 36188, 36189, 105 km S Oaxaca, Oaxaca, BYU 36035, Omiltome, Guerrero; *serrifer plioporus* BYU 36182 (skull), 36183, 36149, 36185, 16 km E Jalapa, Veracruz; *poinsetti poinsetti* BYU 13812 (skull), 13814, 13815, 13820, 80 km W Chihuahua City, Chihuahua.

External Characters

The external characters used were chosen because of their suitability for numerical analysis. Keys and checklists (Smith and Taylor, 1950; Boulenger, 1885; Cope 1900; Van Denburgh, 1922) were examined and all quantitative characteristics were included. Color patterns were omitted because of variations caused by preservatives. The forty external characters utilized are:

(1) Snout–vent length (mm). (2) Snout–vent/snout–parietal eye. (3) Humerus (from ventral midline to outside of elbow)/snout–vent. (4) Femur (from ventral midline to outside of knee)/snout–vent. (5) Outside length of tibia/snout–parietal eye. (6) Length of fourth toe/femur. (7) Height-to-width ratio of tail at point one head length from vent. (8) Snout–parietal eye (mm). (9) Width of head at parietal eye/snout–parietal eye. (10) Vertical height of head at parietal eye/snout–parietal eye. (11) Width of head anterior to orbit/snout–parietal eye. (12) Distance between nares/snout–parietal eye. (13) Length of frontal scale(s)/snout–parietal eye. (14) Length of frontal scale(s)/snout–parietal eye. (14) Length of frontal scale(s)/smallest width of frontal. (15) Largest linear measurement on internasal scale/snout–parietal eye. (16) Length of interparietal/width of same (through parietal eye). (17) Width of widest supraocular/snout–parietal eye. (18) Width of widest supraocular/length of same. (19) Parietal eye to posterior edge of interparietal/length of interparietal. (20) Length of median frontonasal/width of same. (21) Length of median frontonasal/snout–parietal eye. (22) Dorsals from interparietal to posterior margin of thigh. (24) Dorsals equal to

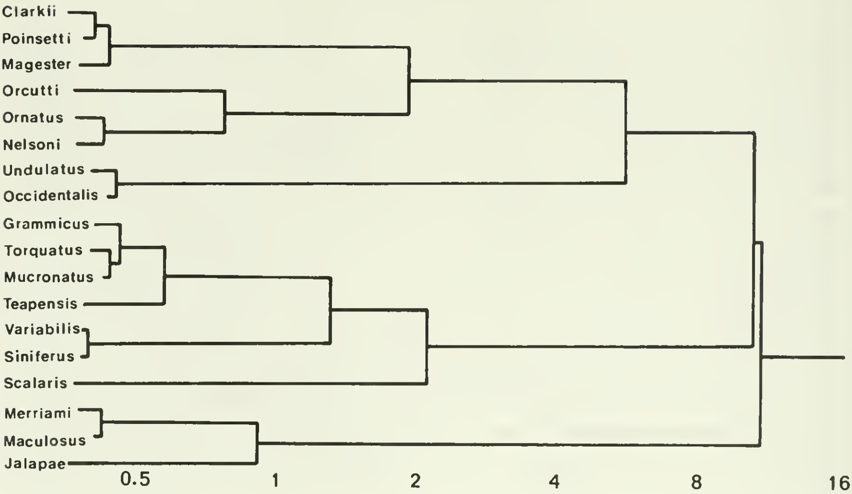

Fig. 18. Dendrogram generated by distribution, display, and chromosome characters (81 to 85).

one head length (between points 2 and 3 head lengths posterior to interparietal). (25) Laterals equal to one head length midway between limbs. (26) Ventrals equal to one head length (between points 2 and 3 head lengths posterior of snout). (27) Dorsals equal to ½ head length (counting laterally from midline at a point 2 head lengths from interparietal). (28) Ventrals equal to ½ head length (counting laterally from midline at a point 3 head lengths from snout). (29) Total femoral pores (both sides). (30) Ventrals between medial limits of femoral pores. (31) Ventrals from vent to a line connecting femoral pore series. (32) Caudals equal to one head length (between points 1 and 2 head lengths from vent). (33) Supralabials (total both sides and rostral). (34) Infralabials (total both sides and mental). (35) Sublabials (total both sides and mental). (36) Caudals around tail one head length from vent. (37) Dorsals equal to one interparietal (counting posterior from interparietal). (38) Ventrals equal to one interparietal (counting anterior from vent). (39) Head shields in contact with interparietal. (40) Fourth toe lamellae.

Skulls

Preparation. Skulls were prepared by boiling 15-20 minutes in 50 ml water with a few drops of detergent and NH_4OH. After boiling, they were allowed to dry until the muscles were easily removed with forceps. This procedure was repeated several times and the last remains of muscle were removed by dipping the skull in Clorox bleach.

Whitening of skulls. Kier, Grant, and Yochelson (1965:453-56) described a technique widely used in paleontological preparations but possibly new to investigators of herpetological osteology. The skull was first blackened by dipping in ink. (Shafer's permanent blue-black is excellent because it stains the skulls effectively and is easily removed by dipping the skull in a mild solution of NH_4OH.) The blackened skull was then highlighted with a thin layer of NH_4Cl. The dry NH_4Cl was placed in the chamber of a

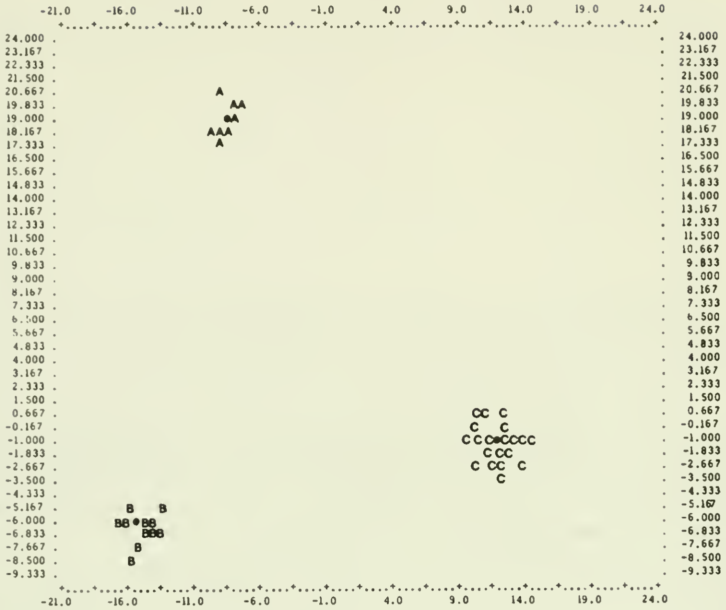

Fig. 19. Canonical display of three groups: I(A), II(B), and III(C).

100 ml pipette, and the open end of the pipette was attached with rubber tubing to a squeeze bulb. To vaporize the NH_4Cl, the pipette was heated over a flame. With careful pressure on the squeeze bulb, the skull was then highlighted with NH_4Cl vapor. This technique enhances the suture lines in black contrast and facilitates the study of photographs.

Skull photography. Several workers have taken measurements directly from skulls with calipers (Weiner and Smith, 1965; Jenkins and Tanner, 1968; Avery and Tanner, 1971). However, the small size of some species makes it virtually impossible to take precise measurements directly from the skulls. Weiner and Smith (1965) made some of their skull measurements with the aid of an ocular micrometer and a microscope. But measurements through a microscope or on a photograph are subject to error caused by variation in angle of view. Such measurements would be acceptable, however, if the angle of view were kept constant. Lewis (1944) studied the determination of dress patterns from photographs and found that if the subjects were properly oriented, correct three-dimensional dress patterns could be determined. To minimize the problem of distortion and provide constant orientation of skulls, special equipment was constructed. The apparatus (Fig. 1) was constructed to minimize variations in angle of view. This structure consists of a circular outer platform that can be leveled with spirit levels. The skull is placed on a second platform in the center. The inner plat-

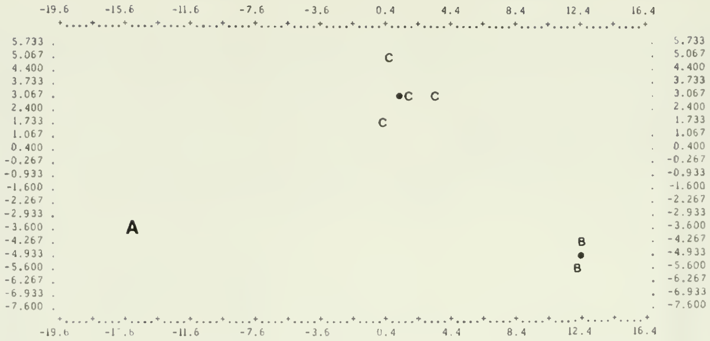

Fig. 20. Canonical display of the three subgroups of group I.

form can be tilted along two planes as well as adjusted vertically until specific reference lines on the skull are parallel with the outside platform. A camera (Nikon FTN with Kodak plus X film) was placed over the skull with spirit levels attached to the camera back so that the reference lines through the skull and the film in the camera were always as nearly parallel as possible.

A line through the tip of the premaxilla and the center of the foramen magnum was the first reference for dorsal, ventral, and lateral views. The second reference line for the dorsal view passed through the anterolateral corners of the parietals. The second reference line for the ventral view passed through the lateral tips of the ectopterygoids. The second reference line for the lateral view was the surface of the frontoparietal suture, which was oriented at right angles to the outer platform. The posterior view was arranged so that the surface of the parietal bone was at right angles to the outer platform and a line through the lateral tips of the exoccipitals was parallel to the outer platform.

Further to minimize possible error caused by variation in angle of view, all skull measurements were converted to ratios between two distances measured in the same direction on the same photograph. Although this technique reduces the effects of distortion, it unfortunately eliminates most of the traditional skull characters (width and length ratios of skull members).

Illustrations were prepared by projecting and tracing the photographs with a Saltzman Projector. Detail was added to the tracings with the aid of a binocular microscope (Presch, 1969; Nash and Tanner, 1970).

Skull Characters

The following 40 characters (numbers 41-80) were computed for each skull:

(41) Posterior extent of supraoccipital on midline to anterior border of parietal foramen/parietal foramen to suture between nasals (Fig. 2). (42) Length of suture between nasals/parietal foramen to suture between nasals (Fig. 2). (43)

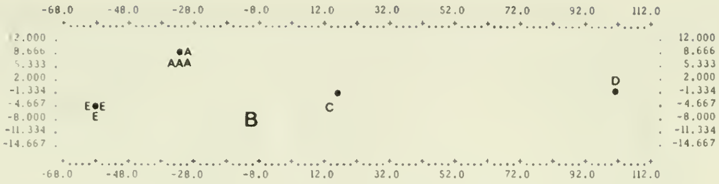

Fig. 21. Canonical display of the five subgroups of group II.

Length of premaxilla/parietal foramen to suture between nasals (Fig. 2). (44) Posterior tip of suture between frontal and nasal to posterior end of suture between prefrontal and nasal/posterior end of suture between prefrontal and nasal to anterior end of suture between prefrontal and nasal (Fig. 2). (45) Anterior end of suture between prefrontal and nasal to anterior end of suture between maxillary and nasal/parietal foramen to suture between nasals (Fig. 2). (46) Anterior end of suture between maxillary and nasal to anterior end of suture between maxillary and premaxillary/parietal foramen to suture between nasals (Fig. 2). (47) Pineal foramen to posterior end of suture between prefrontal and lacrimal/parietal foramen to suture between nasals (Fig. 2). (48) Posterior extent of lateral wing of parietal to posterior end of suture between parietal and postorbital/posterior extent of supraoccipital on midline to anterior border of parietal foramen (Fig. 2). (49) Length of postorbital/posterior end of suture between parietal and postorbital to anterior edge of parietal foramen (Fig. 2). (50) Posterior tip of prefrontal to anterior end of suture between prefrontal and nasal/posterior end of suture between prefrontal and lachrymal to anterior tip of prefrontal (Fig. 2). (51) Most narrow width of frontal/anterior width of parietal (along suture with postorbital) (Fig. 3). (52) Lateral side of jugal on transverse line through anterior border of parietal foramen to lateral extent of suture between postorbital and parietal/anterior width of parietal (Fig. 3). (53) Interfenestral width (on line passing through posterior tips of both postorbitals)/anterior width of parietal (Fig. 3). (54) Lateral edge of parietal on line passing through posterior tips of both postorbitals to posterior tip of postorbital on same side/anterior width of parietal (Fig. 3). (55) Anterior end of suture between prefrontal and nasal to posterior end of suture between prefrontal and lacrimal distance between left and right anterior ends of suture between prefrontal and nasal (Fig. 3.) (56) Internarial width/distance between left and right anterior ends of suture between maxillary and premaxillary (Fig. 3). (57) Posterior tip of occipital condyle to medial corner of tip of basipterygoid process of the basisphenoid/lateral tip of ectopterygoid to anterior tip of premaxilla (Fig. 4). (58) Medial corner of tip of basiterygoid process to lateral tip of ectopterygoid/lateral tip of extopterygoid to anterior tip of premaxilla (Fig. 4). (59) Posterior corner of lateral side of palatine to lateral limit of suture between palatine and maxilla/lateral tip of ectopterygoid to anterior tip of premaxilla (Fig. 4). (60) Posterior

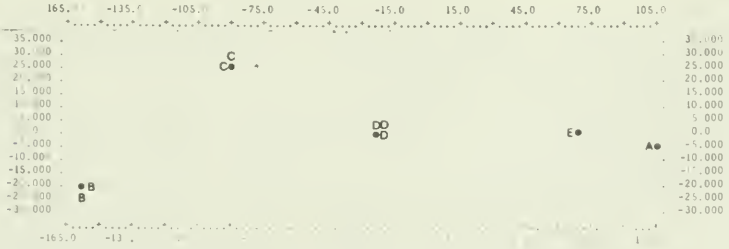

Fig. 22. Canonical display of the five subgroups of group III.

TABLE 1. Average body temperature of some *Sceloporus* as reported by Bogert (1949).

Temperature C	Species
36.9	*variabilis variabilis*
36.2	*woodi*
35.4	*variabilis olloporus*
35.3	*squamosus*
34.9	*magister*
34.8	*undulatus consobrinus*
34.2	*poinsetti*
33.6	*grammicus disparilis*
33.6	*merriami*
32.9	*formosus malachiticus*

tip of quadrate ramus of pterygoid to lateral tip of ectopterygoid/lateral tip of ectopterygoid to anterior tip of premaxilla (Fig. 4). (61) Lateral tip of ectopterygoid to medial limit of suture between maxilla and ectopterygoid/distance between lateral tips of ectopterygoid (Fig. 5). (62) Medial limit of suture between maxilla and ectopterygoid to posterior corner of lateral side of palatine/distance between lateral tips of the ectopterygoid (Fig. 5). (63) Posterior corner of lateral side of palatine to medial limit of suture between palatine and pterygoid/distance between lateral tips of ectopterygoids (Fig. 5). (64) Smallest width of basisphenoid/distance between lateral tips of ectopterygoids (Fig. 5). (65) Diagonal distance from lateral tip of ectopterygoid on one side to posterior tip of quadrate ramus of pterygoid on other side/length between the same points on one side (Fig. 5). (66) Five times the tangent of the angle between the midline and the extended line that passes through the midpoint on the tip of the basipterygoid process and the midpoint on the most narrow part of the neck of the basipterygoid process (Fig. 5). (67) Tip of premaxilla to most ventral extent of ectopterygoid projected onto a line from the tip of premaxilla to tip of quadrate ramus of pterygoid/tip of premaxilla to posterior tip of postorbital (Fig. 6). (68) Most ventral extent of ectopterygoid to tip of quadrate ramus of pterygoid projected onto a line from the tip of premaxilla to tip of quadrate ramus of pterygoid/tip of premaxilla to posterior tip of postorbital (Fig. 6). (69) Tip of premaxilla to anterior end of suture between prefrontal and lacrimal (parallel to denominator)/tip of premaxilla to posterior tip of postorbital (Fig. 6). (70) Anterior end of suture between prefrontal and lacrimal to posterior tip of prefrontal (parallel with denominator)/tip of premaxilla to posterior tip of postorbital (Fig. 6). (71) Posterior tip of prefrontal to anterior end of suture between postfrontal and parietal (parallel with denominator)/tip of premaxilla to posterior tip of postorbital (Fig. 6). (72) Anterior end of suture between prefrontal and lacrimal to posterior tip of prefrontal (direct)/same as numerator projected onto the line between the tip of the premaxilla and the posterior tip of postorbital (Fig. 6). (73) Posterior tip of prefrontal to most ventral extent of ectopterygoid/anterior end of suture between postfrontal and parietal to tip of quadrate ramus of pterygoid (Fig. 6). (74) Dorsal ridge of supraoccipital to dorsal edge of foramen magnum/top of parietal at midline (passes vertically through medial ridge of supraoccipital and through center of occipital condyle) to ventral edge of parietal at midline (Fig. 7). (75) Height of foramen magnum along midline/top of parietal to ventral edge of parietal (Fig. 7). (76) Ventral edge of foramen magnum on midline to ventral edge of condyle/dorsal-ventral height of parietal (Fig. 7). (77) Dorsal corner of lateral process of exoccipital to ventral corner of lateral process of exoccipital/dorsal-ventral height of parietal (Fig. 7). (78) Distance between right and left dorsal corners of lateral process of exoccipital/distance between right and left ventral corners of basioccipital tubercles (Fig. 7). (79) Five times the tangent of the angle formed by the dorsal corner of the lateral process of the exoccipital and its intersection with the midline (at right angles) and the ventral corner of the basioccipital tubercle (all points on one side) (Fig. 7). (80) Five times the tangent of the angle formed

TABLE 2. Groups and subgroups in the genus *Sceloporus*.

Group I	Group II	Group III
Subgroup A *gadoviae*	Subgroup A *grammicus* *pictus* *megalepidurus* *cryptus* _shannonorum_* *heterolepsis* *asper*	Subgroup A *spinosus* *orcutti* *clarki* *melanorhinus* *magister* *olivaceus* *cautus* *horridus* *edwardtaylori*
Subgroup B *couchi* *merriami*	Subgroup B *pyrocephalus* *nelsoni*	Subgroup B *formosus* *lunaei* *malachiticus* *acanthinus*
Subgroup C *maculosus* *parvus* *jalapae* *ochoterenae*	Subgroup C *scalaris* _goldmani_* *aeneus*	Subgroup C *undulatus* *virgatus* *woodi* *occidentalis* *graciosus*
	Subgroup D *siniferus* *carinatus* *utiformis* *squamosus*	Subgroup D *jarrovi* *lineolateralis* *ornatus* *dugesi*
	Subgroup E *variabilis* *cozumelae* *teapensis* *chrysostictus*	Subgroup E *torquatus* *cyanogenys* *bulleri* _insignis_* *macdougalli* *mucronatus* *serrifer* *poinsetti*

*Species not examined in this study.

by the shortest width of the parietal, its intersection with the midline, and the line from that intersection to the dorsal corner of the lateral process of the exoccipital (all points on one side) (Fig. 7).

Other Characters

Karyology. Extensive karyological data are available for most species of *Sceloporus* (see Literature Review—Karyology). Although many characters can be described for each species, the only karyological character included in this study is the number of microchromosomes. A change in microchromosomal number is theoretically a single karyotic event, and such events may indicate relationships. Hopefully, additional characters will soon be available for numeric analysis.

Display-action patterns. Although display-action patterns involve a complex of activities, only two measurements were considered: the ratio of vertical movement of the shoulder to the vertical movement of the eye and the ratio of vertical movement of the hip to the vertical movement of the eye (Purdue and Carpenter, 1972b).

Zoogeography. The approximate latitude and longitude of the center of distribution for each species were included as additional characters. Of course, a simple measure of latitude and longitude does not allow for altitude, climate, habitat preference, or natural barriers such as mountains and rivers. However, differences in latitude and longitude are a measurement of horizontal distance and represent a crude measure of natural resistance to gene flow. Latitude is also somewhat correlated with climatic gradients.

Data Analysis

Justification. Hennig (1966:74) defined species relationships as follows: "A species 'x' is more closely related to another species 'y' than it is to a third species 'z' if and only if it has at least one stem species in common with species 'y' that is not also a stem species of 'z'." Hennig proposed that classification be based on phylogenetic kinship and not form similarity because frogs and tadpoles should not be different taxa. Bigelow (1958) said that the measure of phylogenetic relationship is the "relative recency of common ancestry." These definitions of relationship seem to be circular. Phylogenies are based on circumstantial evidence, so it is impossible for Hennig to prove whether or not "x" and "y" have a stem species that is not an ancestor of "z." We believe that phylogenetic relationships are manufactured in the mind of the taxonomist from phenetic data and form similarities. We therefore reject Hennig's and Bigelow's proposals and suggest that the best phenotypic dendrogram (containing representatives of all populations of the group under consideration and including a sufficient number of characters manipulated in the best numeric manner) is also the best source for the most probable phylogeny. Sokal and Sneath (1963) suggested that at least 60 characters are necessary for highly significant results. Our study has

TABLE 4. Means and standard deviations for the eight diagnostic characters in groups I, II, and III.

	Groups					
	Group I		Group II		Group III	
Character	Mean	S.D.	Mean	S.D.	Mean	S.D.
32	13.97	1.00	9.90	1.55	7.90	0.72
7	10.02	0.88	10.98	1.23	9.45	0.63
27	9.08	1.72	6.59	1.65	4.39	1.03
13	4.05	0.17	3.84	0.22	3.71	0.21
30	4.71	4.55	9.49	5.64	9.04	3.06
6	10.15	3.01	10.93	1.14	9.32	1.00
39	7.19	1.94	7.48	1.57	5.70	1.04
70	2.56	0.19	2.34	0.24	2.55	0.19

TABLE 3. Results of stepwise discriminate analysis of the three groups.

Step	Variable Added	Group I	Group II	Group III	Percent Correctly Identified	F-Ratio This Variable	Degrees of Freedom	Approximate F-Value (U-statistic)	Degrees of Freedom
1	32	8	10	26	80	98.3	2, 52	98.3	2, 52
2	7	8	13	28	89	13.4	2, 51	43.3	4, 102
3	27	8	15	28	93	7.75	2, 50	34.9	6, 100
4	13	8	17	28	96	7.55	2, 49	31.1	8, 98
5	30	8	18	28	98	7.17	2, 48	29.1	10, 96
6	6	8	18	28	98	7.81	2, 47	28.6	12, 94
7	39	8	18	28	98	6.04	2, 46	27.8	14, 92
8	70	8	18	29	100	6.38	2, 45	27.7	16, 90

TABLE 5. Results of stepwise discriminate analysis of the three subgroups of Group I.

Step	Variable Added	Part A	Part B	Part C	Percent Correctly Identified	F-Ratio This Variable	Degrees of Freedom	Approximate F-Value (U-statistic)	Degrees of Freedom
1	7	2	1	5	89	86.62	2, 6	86.6	2, 6
2	23	2	2	5	100	51.71	2, 5	61.1	4, 10

TABLE 6. Means and standard deviations of the two diagnostic characters in the three subgroups of Group I.

	Parts					
	Part A		Part B		Part C	
Character	Mean	S.D.	Mean	S.D.	Mean	S.D.
7	12.04	0.00	9.33	0.48	9.90	0.13
23	81.00	0.00	75.00	5.66	55.43	2.67

TABLE 7. Results of stepwise discriminate analysis of the five subgroups of group II.

Step	Variable Added	Part A	Part B	Part C	Part D	Part E	Percent Correctly Identified	F-Ratio This Variable	Degrees of Freedom	Approximate F-Value (U-statistic)	Degrees of Freedom
1	17	5	1	2	3	2	72	24.4	4, 13	24.38	4, 13
2	40	5	2	2	3	4	89	11.9	4, 12	16.49	8, 24
3	7	5	2	2	4	4	94	6.3	4, 11	13.39	12, 29
4	64	6	2	2	4	4	100	6.9	4, 10	13.21	16, 31
5	21	5	2	2	4	4	94	6.5	4, 9	13.82	20, 30
6	75	5	2	2	4	4	94	6.4	4, 8	15.14	24, 29
7	20	6	2	2	4	4	100	7.3	4, 7	17.69	28, 26

TABLE 8. Means and standard deviations of the seven diagnostic characters in the five subgroups of Group II.

	Parts									
	Part A		Part B		Part C		Part D		Part E	
Character	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
17	1.57	0.12	2.23	0.04	1.38	0.02	2.01	0.23	2.23	0.08
40	21.13	1.36	16.75	0.71	19.04	0.41	23.06	1.48	21.94	0.63
7	10.48	0.34	13.72	1.36	10.45	0.49	11.45	0.79	10.18	0.53
64	23.22	2.14	23.00	3.84	23.80	0.95	23.61	2.13	24.19	1.76
21	1.91	0.19	1.73	0.01	1.55	0.01	1.52	0.19	1.40	0.17
75	4.83	0.33	5.37	0.16	4.87	0.17	4.85	0.44	4.80	0.27

TABLE 9. Stepwise discriminate analysis of Group II. Number of pairs separated at .95, .99, and .999 confidence levels for each step.

	Confidence Level		
Step	.95	.99	.999
1	7	6	6
2	9	8	7
3	9	8	8
4	9	8	8
5	8	8	8
6	8	8	8
7	8	8	8
8	9	8	8
9	9	9	8
10	10	10	9
11	10	10	10
12	10	10	8
13	10	8	8

utilized over 80 characters with the hope that at least 60 are significantly independent.

Cluster analysis. All past statistical studies of this genus have utilized some form of univariate analysis (except Lundelius, 1957, who considered only two species). That is, relationships were determined by combining the indications presented by each individual character. The problems with univariate analysis and the advantages of multivariate analysis were discussed at length by Ingram and Tanner (1971). They stated (pp. 25-26):

> Another more compelling reason for using multivariate analysis of data concerns what is actually being analyzed. Taxonomists are classifying whole organisms, not any one scale count (Mayr, 1969; Sokal and Sneath, 1963). Univariate methods consider only one variable at a time as completely unrelated to all other variables. Multivariate methods consider groups of characters, as a unit, and their relationships with each other. This is a better approximation of the organisms with which taxonomists are concerned.

The arrangement of species into phenetic clusters was accomplished with Ward's Cluster Analysis. This procedure was used because (1) it is available as a packaged computer program (Wishart, 1968), (2) it has been used with success by other workers in herpetological systematics (Ingram and Tanner, 1971; Smith and Tanner 1974), (3) it is theoretically sound, and (4) it produces satisfactory results.

Ingram and Tanner (1971:26) explained the theory of Ward's Cluster Analysis:

> *Cluster Analysis.* When a taxonomic study is made taking two measurements on each individual, the specimens studied could be represented as points on a two-dimensional space. The resulting graph would illustrate the phenotypic interrelations of the individuals. Expanding this to 90 measurements on each individual, the specimens could be represented as points in a hypothetical 90 (or p)-dimensional hyperspace. The representation of individuals on a 90-dimensional graph is best grasped by visualizing many points in space grouped in clusters of varying size. The number of dimensions in the hyperspace is equal to the number of variables measured. This concept of individuals being repre-

TABLE 10. Results of stepwise discriminate analysis of the five subgroups of group III.

Step	Variable Added	Part A	Part B	Part C	Part D	Part E	Percent Correctly Identified	F-Ratio This Variable	Degrees of Freedom	Approximate F-Value (U-statistic)	Degrees of Freedom
1	31	6	3	2	0	3	48	19.02	4, 24	19.02	4, 24
2	81	8	4	5	1	4	76	11.16	4, 23	14.38	8, 46
3	24	8	4	5	4	6	93	9.61	4, 22	13.5	12, 58
4	7	8	5	5	4	6	97	7.31	4, 21	12.99	16, 64
5	37	8	5	5	4	6	97	5.47	4, 20	12.42	20, 67
6	61	9	5	5	4	6	100	5.25	4, 19	12.33	24, 67

TABLE 11. Means and standard deviations of the six diagnostic characters used to classify the five subgroups of group III.

	Parts									
	Part A		Part B		Part C		Part D		Part E	
Character	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
31	4.76	0.68	5.38	0.54	6.85	0.76	7.63	1.20	7.67	0.74
81	24.14	6.58	15.50	3.84	34.60	5.18	24.75	3.40	22.50	5.17
24	6.15	1.20	7.55	0.83	9.35	1.11	10.25	0.98	6.65	1.33
7	9.39	0.46	10.16	0.41	9.58	0.27	8.51	0.42	9.47	0.55
37	3.71	0.80	3.98	0.70	5.53	0.36	4.60	0.75	3.67	0.38
61	14.55	1.43	16.41	0.87	14.92	1.37	14.00	0.89	14.55	1.38

TABLE 12. Stepwise discriminate analysis of group III. Number of pairs separated at .95, .99 and .999 confidence levels for each step.

	Confidence Level		
Step	.95	.99	.999
1	6	6	5
2	9	9	8
3	10	10	8
4	10	10	9
5	10	10	8
6	10	10	10
7	10	10	10
8	10	10	9
9	10	10	99
10	10	10	9

sented as points in a p-dimensional space is essential to cluster and discriminant analyses.

Ward's method of cluster analysis forms spherical clusters of individuals in the hyperspace. New clusters are formed by measuring the distance from each individual in the original cluster to the center of the cluster, called the centroid. These distances are summed to form the error sum of squares for the cluster. The individuals to be added to the cluster are conditionally added, and the new centroid formed. An error sum of squares for the newly formed cluster is calculated. This procedure is done for all possible entries to the original cluster (possible entries include other clusters as well as individuals). The entry that causes the least increase in the error sum of squares is joined to the original cluster. Each new cluster is formed by joining those individuals that move the centroid the smallest distance. In other words, each cluster is composed of those individuals located closest to each other in the hyperspace. Thus, it is seen that this method unites individuals of the highest morphological similarity first (Wishart, 1969).

Besides producing a phenetic dendrogram. Wishart's program (1968) provides other useful information, including (1) raw-data listing (numeric and binary), (2) maxima and minima for numeric data, (3) standard scores for numeric data, (4) means and standard deviations, (5) product-moment correlation coefficients, (6) principle components eigenvalues, (7) percentage and cumulative variances. (8) eigenvectors, (9) binary attribute frequencies, (10) binary attribute percentage occurrences, (11) similarity matrix, (12) "normalized" classification array. (13) listing of sample numbers for each cluster, (14) cluster means, standard deviations, F-ratios and T-values for continuous variable in each cluster, (15) cluster frequencies for binary attributes, (16) cluster percentage occurrences for binary attributes, (17) binary attribute percentage ratios.

The F-ratios printed for each character in each cluster are computed as the variation within that cluster divided by the variation in the total population. It must be remembered that this is not the traditional F-ratio (variance within clusters/variance between clusters). A character with a low F-ratio in one cluster is not necessarily a diagnostic character. The high total variance may be caused by variance within another cluster rather than variance between clus-

TABLE 13. X and Y canonical coordinates of the species in groups I, II, and III.

Species	X	Y	Species	X	Y
Group I			Group III		
gadoviae	–8.8	18.4	*spinosus*	12.5	–1.7
merriami	–7.8	19.6	*edwardtaylori*	11.9	–1.8
couchi	–8.5	18.1	*melanorhinus*	10.1	–0.4
parvus	–7.7	20.1	*clarki*	12.7	–1.1
maculosus	–8.2	18.7	*orcutti*	13.7	–0.8
ochoterenae	–8.8	17.5	*magister*	11.4	–1.2
jalapae	–8.8	20.9	*horridus*	11.0	0.6
			olivaceus	11.9	–3.3
			cautus	11.3	–1.1
Group II			*formosus*	11.3	–0.9
asper	–14.9	–6.5	*malachiticus*	12.9	–1.4
grammicus	–15.3	–6.0	*lunaei*	11.7	–2.7
heterolepis	–15.4	–5.7	*lundelli*	12.7	–1.1
megalepidurus	–16.2	–5.2	*undulatus*	10.1	–2.5
pictus	–14.6	–6.6	*virgatus*	11.3	–1.1
cryptus	–15.2	–7.1	*occidentalis*	12.2	–1.5
pyrocephalus	–16.2	–5.1	*woodi*	12.7	–0.4
nelsoni	–15.5	–7.2	*graciosus*	11.7	–1.2
scalaris	–15.8	–5.4	*lineolateralis*	10.7	1.0
aeneus	–13.5	–5.2	*ornatus*	12.0	–2.4
siniferus	–14.1	–6.6	*dugesi*	9.4	–1.3
squamosus	–15.4	–7.8	*jarrovi*	13.6	–2.7
carinatus	–16.1	–8.5	*torquatus*	11.9	–2.7
utiformis	–15.0	–5.7	*poinsetti*	12.5	–1.0
variabilis	–14.3	–5.6	*cyanogenys*	10.9	–1.5
cozumelae	–14.5	–6.4	*serrifer*	10.4	–1.2
teapensis	–17.2	–6.2	*mucronatus*	12.7	0.3
chrysostictus	–13.3	–6.3	*bulleri*	14.2	–1.3

ters. With this limitation in mind, Wishart's program is extremely valuable.

As an independent check on this system, Ward's Cluster Analysis was applied to some of the data used by Smith in 1939 (pers. comm.). Because of the nature of Smith's data, only 12 characters were used: (1) snout–vent length (mm), (2) snout–occiput/snout–vent, (3) snout–ear/snout–vent, (4) length of hind leg/snout–vent, (5) length of tibia/snout–vent, (6) length of fourth toe/snout–vent, (7) length of fourth toe/length of fifth toe, (8) lamellae on fourth toe, (9) femoral pores (total both sides), (10) dorsal scales from occiput to back of thigh, (11) ventral scales from front of arm to vent, and (12) scale rows around body.

The resulting dendrogram is illustrated in Figure 8. The strong similarity between Figure 8 and Smith's phylogeny (1939) suggests that there is a similar mechanism in Ward's Cluster Analysis and the subjective thinking of classical taxonomy. This supports the conclusion that a person capable of considering 60 to 80 characters on 50 to 60 species simultaneously, would arrive subjectively at results similar to those produced by Ward's Cluster Analysis.

Stepwise Discriminate Analysis. The purposes of stepwise discriminate analysis are (1) to determine the validity of proposed

TABLE 14. X and Y canonical coordinates for the species in the three subgroups in Group I.

Species	X	Y	Species	X	Y
	Subgroup A			Subgroup C	
gadoviae	–15.3	–3.3	*parvus*	1.4	3.1
			maculosus	1.2	3.3
	Subgroup B		*ochoterenae*	0.5	5.1
merriami	12.1	–5.7	*jalapae*	–0.2	2.0
couchi	12.3	–4.2			

groups, (2) to determine the relative diagnostic value of each character, and (3) to classify individuals according to the proposed groups. The stepwise discriminate analysis computer program published by Dixon (1967) considers one character at a time according to F-ratios (variation between groups/variation within groups). Each step "includes" the remaining character with the highest F-ratio. At each step the species are classified according to all the included characters. As more characters are included, the differences between group means become more significant (as indicated by a U-statistic and an approximate F-value), and more individuals are properly classified.

Dixon's program produces (1) means for each group and overall means for each character, (2) standard deviations for each character in each group, (3) within-group covariance matrix, (4) within-group correlation matrix, (5) detailed results for each "step."

At each step a new variable is included and the program prints the F-ratios (and degrees of freedom) for all variables included and not included. The program also prints a U-statistic with degrees of freedom for an estimate of the significance of group separation. Since the U-statistic becomes extremely small and exceeds the capacity of most charts, the program computes an approximate F that, with its degrees of freedom, can show the confidence level for overall group separations.

Dixon's program also produces an F-matrix in which F-ratios are computed for every possible combination of two groups. If the characters included provide good overall separation but fail to distinguish between two groups, this matrix will quickly show which pairs are not separated at .9, .99, and .999 levels of significance. (F tables are not included in the printout.)

This program also produces canonical functions for each step. These functions are then used to classify all species according to the information in the included characters. As more characters are included, the percent of species properly classified increases if the original groupings are valid. At the end of the printout the "distance" is computed from each species to the center (centroid) of each group. Posterior probability for inclusion in each group is also computed for each species. The computer was instructed to "include" characters only if their F-ratio exceeded 1.0 and to "remove" characters if their F-ratio fell below 0.5. A summary of variables "in-

TABLE 15. X and Y canonical coordinates for the species in the five subgroups in Group II.

Species	X	Y	Species	X	Y
	Subgroup A			Subgroup D	
asper	–30.0	7.5	*siniferus*	101.7	–1.2
grammicus	–32.2	5.6	*squamosus*	102.2	–0.1
heterolepis	–31.0	7.6	*carinatus*	101.7	0.1
megalepidurus	–32.1	9.0	*utiformis*	101.1	0.5
pictus	–30.0	6.1			
cryptus	–33.0	6.7		Subgroup E	
			variabilis	–57.3	–6.5
	Subgroup B		*cozumelae*	–57.3	–6.0
pyrocephalus	–9.3	–6.5	*teapensis*	–59.1	–4.8
nelsoni	–9.7	–7.4	*chrysostictus*	–56.8	–5.9
	Subgroup C				
scalarus	14.6	–3.3			
aeneus	16.1	–1.2			

cluded" or "removed" including F-ratios and U-statistics is printed near the end of the printout. Then the program tabulates (1) eigenvalues, (2) cumulative proportion of total dispersion, (3) canonical correlations, (4) coefficients for canonical variables, (5) canonical variables evaluated at group means, and (6) graph coordinates for the first and second canonical variables for each species in each group. The program terminates with a graphic representation of all species on the first two canonical variables.

Canonical Analysis. The canonical analysis (a part of Dixon's program) computes a pair of linear coefficients for each character so that the greatest separation of groups can be displayed on a two-dimensional graph. For example, Figure 9 shows groups A and B plotted on characters p and q. To reduce the illustration from two dimensions to one, all points must be projected onto a single line. Line X would show more information about groups A and B than would line Y. In accordance with this idea, the canonical analysis rotates an imaginary plane through a multidimensional hyperspace until the best separation of groups is displayed. The lists of canonical functions are used to classify additional individuals according to the originally proposed classification and the "best" characters.

RESULTS

Skulls. Skulls of 13 species of the genus *Sceloporus* are illustrated in Figure 10.

Cluster Analysis. Ward's cluster analysis was applied to the following sets of variables:

1. External characters 1-40 (Fig. 11).
2. Skull characters 41-80 (Fig. 12).
3. External and skull characters 1-80 (Fig. 13).
4. External, skull, and distribution characters 1-82 (Fig. 14).
5. External, skull, distribution, and display characters (Fig. 15).
6. External, skull, distribution, and karyological characters (Fig. 16).

TABLE 16. X and Y canonical coordinates for the species in the five subgroups of Group III.

Species	X	Y	Species	X	Y
Subgroup A			Subgroup C		
spinosus	103.9	–3.9	*undulatus*	–90.4	25.2
edwardtaylori	104.6	–5.3	*virgatus*	–90.7	26.3
melcinorhinus	103.1	–5.8	*occidentalis*	–91.7	27.0
clarki	102.5	–4.2	*woodi*	–92.1	26.9
orcutti	102.4	–5.6	*graciosus*	–91.3	28.1
magister	104.9	–5.8			
horridus	104.3	–4.4	Subgroup D		
olivaceus	102.2	–4.6	*jarrovi*	–22.5	0.32
cautus	104.7	–3.7	*ornatus*	–23.8	2.6
			dugesi	–23.9	0.2
Subgroup B			*lineolateralis*	–22.5	3.1
formosus	–158.3	–21.0			
malachiticus	–158.4	–19.7	Subgroup E		
lunaei	–158.4	–22.5	*torquatus*	67.5	1.6
lundelli	–157.1	–19.5	*poinsetti*	68.7	1.7
			cyanogenys	67.0	0.8
			serrifer	69.9	0.6
			mucronatus	66.1	1.0
			bulleri	68.0	1.1

7. External, skull, distribution, display, and karyological characters (Fig. 17).
8. Distribution, display, and karyological characters (Fig. 18).

ANALYSIS AND CONCLUSIONS

Species Groups. The minor differences among these eight dendrograms were resolved subjectively to produce three major divisions and 13 species groups (Table 2). Careful examination will reveal the similar patterns generated by different sets of data. Figure 18 shows that distribution, display, and chromosome characters produce results similar to those produced by external and osteological characters. This increases our confidence in Table 2 and demonstrates the taxonomic value of zoogeography, behavior, and karyology.

Stepwise Discriminate Analysis. Dixon's stepwise discriminate analysis program cannot consider as many as 82 characters in one run. It was therefore used with external characters alone (1-40) and skull characters alone (41-80). For both studies the program was run four times to consider the three groups and their subgroups. The number of characters in the data set was reduced by eliminating those characters with consistently small F-ratios. The characters removed were numbers 2, 5, 15, 18, 19, 25, 42, 45, 46, 51, 65, 68, 73, 76, and 78. With the inclusion of latitude and longitude, this program then evaluated 66 characters.

Table 3 shows the results of stepwise discriminate analysis of the three groups in the genus *Sceloporus.* This table shows that when characters are considered according to F-ratios, eight characters are sufficient for correct classification of all species: (1) size of caudal scales, (2) degree of compression of tail, (3) width of dorsal scales, (4) length of frontal scale, (5) ventrals between medial limits of femoral pores, (6) length of fourth toe, (7) head shields in contact with interparietal, and (8) length of prefrontal bone. The first eight characters contribute variation significant at the .99 level. Of the 39 most diagnostic characters (F-ratio greater than 1.0), 10 are osteological, 1 is geographical (longitude), and 28 are external. The null hypothesis that the three groups are not different is rejected at the .999 level after consideration of the first character (number of caudal scales equal to one head length). The same hypothesis is rejected at the .999 level with respect to any combination of two groups. The eight diagnostic characters with means and standard deviations are shown in Table 4.

Table 5 shows the results of stepwise discriminate analysis for the three subgroups of group I. Two characters are sufficient to classify the species into their subgroups. Both characters contribute variation significant at the .999 level. The first is a measure of the degree of compression of the tail, and the second is the number of ventrals. At every step, the separation of means is significant at the .999 level after inclusion of the second character. Of the six most diagnostic characters (F-ratio greater than 1.0), two are osteological and four are external. Table 6 shows the means and standard deviations of the first two characters.

Tables 7, 8, and 9 show the results of stepwise discriminate analysis of the five subgroups of group II. Four characters are sufficient for 100-percent correct classification of all species: (1) the relative width of the supraoculars, (2) the number of lamellae on the fourth toe, (3) the degree of compression in the tail, and (4) a measure of the relative width of the basisphenoid bone. Of the 13 most diagnostic characters (F-ratio greater than 1.0) 4 are osteological, 1 is geographical (latitude), and 8 are external. The approximate F (U-statistic) for overall separation of means is significant at the .999 level for every step.

Tables 10, 11, and 12 show the results of stepwise discriminate analysis of the five subgroups within group III. Six characters are sufficient for correct classification: (1) the size of ventral scales in the vent region, (2) latitude, (3) the number of dorsals equal to the length of the head, (4) the compression of the tail, (5) the size of dorsals near the interparietal scale, and (6) the shape of the ectopterygoid bone. The separation of the subgroups of group III is as significant as is the separation in group II. Of the 24 most diagnostic characters (F-ratio greater than 1.0) 8 are osteological, 1 is geographical (latitude), and 15 are external.

Tables 3 to 12 show that the groups and subgroups proposed in Table 2 are distinct at the .999 level of confidence according to the characters used in this study. These tables also show which characters are most diagnostic among the groups.

Canonical Analysis. Figure 19 shows the first two canonical dimensions for the species in each major group. Table 13 gives the x and y coordinates for each species. This canonical separation gives strong support to the conclusion that each of the three groups is monophyletic and should be given taxonomic recognition.

Figures 20, 21, and 22 and Tables 14, 15, and 16 indicate that the subgroups of each major group are also distinct phenetic units with no overlap.

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THE GENERIC NAME OF THE NORTH AMERICAN MUSK TURTLES

Hobart M. Smith[1] and Kenneth R. Larsen[1]

Abstract.— Although several recent workers have used the name *Sternothaerus* for the North American musk turtles, the rules of priority render *Sternotherus* the correct name for them. The generic type fixation by Stejneger of *S. odoratus* is accepted.

A number of recent regional as well as more general works (e.g., Cochran and Goin, 1970:137-139) use the generic name *Sternothaerus* for the North American musk turtles commonly bearing the name *Sternotherus*. Use of the former generic name in recent years stems from the excellent revision by Tinkle (1958) of the *S. carinatus* complex, wherein (p. 51) the generic name *Sternotherus* is held to be a misspelling that should be replaced by *Sternothaerus*. As pointed out by Albrecht (1967:82), the latter spelling actually does not supersede *Sternotherus*.

It is true that Bell is credited ("*Sternotherus*, Bell, Mss.") by Gray (1825:211) as the source of *Sternotherus* in the first appearance of either name and that accordingly perhaps Bell should now be regarded as the author of the name. The wording of the description is, however, completely different from that of Bell's subsequently published *Sternothaerus* (Bell, 1826:305), and Gray employs the first person form in commenting on the genus: "Cuvier describes the anterior and posterior lobes of the sternum of these species to be moveable; but the hinder was fixed on the specimens which I have examined, which were all dry." Thus the description appears to be in Gray's words, even though he clearly may have drawn the idea for the genus from Bell's MS.

The International Code of Zoological Nomenclature (1964), Article 50, specifies, in this context, that "The author . . . of a scientific name is . . . the person . . . who first publishes it . . . in a way that satisfies the criteria of availability . . . , unless it is clear from the contents of the publication that . . . some other person . . . is alone responsible both for the name and the conditions that make it available." Clearly Gray's account is not a copy of Bell's, and accordingly it can only be concluded that Bell did not provide the description in the form in which it appeared in Gray's work, even though he may have provided the name or a basis for the name. Reluctantly, but seemingly incontrovertibly, the conclusion is that, by present rules, Gray must be regarded as the author of *Sternotherus*. Bell remains author of his name *Sternothaerus*, based upon a different array of taxa, including one African, one Asian, and two North American nominal species.

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[1] Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder 80302.

The name appearing in 1825 cannot be rendered as *Sternothaerus* even if attributed to Bell. Although it is true that incorrect original spellings are to be replaced by correct spellings, as pointed out by Tinkle (1958:51), the code severely limits the concept of "incorrect original spellings." In this case, only an inadvertent error could be called incorrect, whereas there is no evidence whatever that Gray did not use the spelling *Sternotherus* quite deliberately. Article 32 of the code makes it clear that even if Gray did err in transliteration, such an error is not itself "inadvertent." Again there is no escape from the conclusion that *Sternotherus* is the correct spelling for the 1825 name. Indeed, Gray repeated this spelling in his subsequent works, giving no indication of occurrence of error therein.

In turn, Article 56 expressly provides that "even if the difference between two genus-group names is due to only one letter, these two names are not to be considered homonyms." Accordingly *Sternothaerus* of 1826 must be judged on its own merits, as it were, as a name completely independent of and different from *Sternotherus* of 1825.

Although Gray (1825) included a species of *Kinosternon* in his *Sternotherus* ("*S. pensylvanica*" = *K. subrubrum*), as well as a species we now recognize in *Sternotherus* ("*S. odorata*"), the name *Sternotherus* has long been accepted as fixed with its type as *S. odoratus*, although the earliest selection of this species as type is questionable. It was not selected either directly or indirectly by Bell, as Stejneger (1902:236) maintained. Gray's name could never be applied properly to an African group, since among the originally included species (to which type selection is limited) there were no African representatives. Stejneger's (1902:237) restriction of type is explicit and acceptable. The alternative would merely make *Sternotherus* a synonym of *Kinosternon* Spix, 1824 by fixation with *K. subrubrum*.

The type of *Sternothaerus* Bell could have been restricted subsequently to any of the four species included by Bell: *trifasciatus sp. n.* (=*Cuora trifasciata*), *leachianus sp. n.* (=*Pelusios subniger* Lacépède, 1789), *odoratus* (=*S. odoratus* Latreille, 1801), and *boscii* (Merrem, 1820) (=*S.odoratus*). Stejneger (1902:237) explicitly designated *S. odoratus* as the type, although by specious reasoning (in modern contexts), since he regarded Bell's *Sternothaerus* as merely a deviant spelling of Gray's *Sternotherus* and since he regarded Bell's inclusion in *Sternothaerus* of but one (*S. odoratus*) of the species Gray included in *Sternotherus* as fixing the type of both genera as *S. odoratus*. This is not admissible under the present code, but at this date no reassignment would be useful. Other workers have long accepted Stejneger's explicit type restrictions, and we recommend that this policy be perpetuated.

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STUDIES ON THE TOLERANCE OF AQUATIC INSECTS TO LOW OXYGEN CONCENTRATIONS[1]

Arden R. Gaufin[2], Robert Clubb[3], and Robert Newell[4]

ABSTRACT.— Acute, short-term (96-hour) tests were conducted to determine the relative sensitivity of low oxygen concentrations to 20 species of aquatic insects. In addition, the longer-term effects of low oxygen levels on the survival, molting, growth, and emergence of 21 species were studied. This paper encompasses work conducted at the University of Montana Biological Station from 1968 to 1970 and at the University of Utah from 1966 to 1972.

An evaluation of the average minimum dissolved-oxygen requirements of the different groups of aquatic insects tested indicates that the mayflies are the most sensitive, that the stoneflies are next, and that the caddis flies, freshwater shrimp, true flies, and damselflies follow, in that order. While two species of mayfly could tolerate as low a dissolved-oxygen concentration as 3.3 mg/l for 10 days, a level of 4.6 mg/l was required for 50-percent survival at 30 days. Fifty percent of the true flies and damselflies tested were able to survive at levels ranging from 2.2 to 2.8 mg/l for periods ranging from 20 to 92 days.

Oxygen is a basic need of aquatic insects, yet information concerning exact oxygen requirements is known for but a very few species. Gaufin and Tarzwell (1956) pointed out that if the oxygen requirements of different species of aquatic insects were better known, it should be possible to estimate in retrospect, with considerable accuracy, what oxygen levels have existed in a given aquatic environment during the life history of the organisms. Thus, aquatic insects could be used as an excellent index of water quality.

The literature is extensive on oxygen consumption by various animals, yet such values are meaningful only for the particular conditions of measurement. The conditions under which such measurements were made are important because the rate of oxygen consumption is influenced by several internal and external variables: activity, temperature, nutrition, body size, stage in life cycle, season, time of day, and previous oxygen experience and genetic background (Prosser and Brown, 1961). The highest respiratory rates usually occur in the small, very active forms, whereas the lowest occur in the large, relatively sedentary forms.

Wigglesworth (1950) and Edwards (1946) summarized much of the work done on respiration rates of insects. The majority of the publications on immature aquatic insects has been on European species. Extensive work on individual, immature aquatic insects was done by Balke (1957) on European species of the orders Neuroptera, Odonata, Plecoptera, and Trichoptera. The difficulty in selecting a suitable and adequate method for the measurement of the respiratory rate in a particular species of aquatic insect was evaluated by Kam-

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[2] Professor of Zoology, University of Utah and Montana Biological Station.

[3] Graduate Assistant, University of Utah, Salt Lake City, Utah.

[4] Graduate Assistant, University of Montana, Biological Station, Bigfork, Montana.

ler (1969). An analysis of the various factors that influence the oxygen requirements and respiratory rates of benthic invertebrates is presented by Hynes (1970). The oxygen consumption of 10 of the most common species of stonefly of the western United States and the factors that modify their metabolic rate are discussed by Knight and Gaufin (1966). The oxygen requirements of immature aquatic insects in relation to their classification as index organisms are thoroughly evaluated by Olson and Rueger (1968). Their statistical analyses of oxygen-consumption rates by 12 representative species of aquatic insects of the upper Great Lakes Region constitute very valuable data for establishing water-quality criteria for the protection of aquatic life.

The principal objectives of the studies presented in this report were to determine the oxygen requirements of representative species of aquatic insects of the Intermountain Region and to determine their relative sensitivity to low oxygen concentrations. Oxygen levels necessary for survival and the long-term effects of low oxygen concentrations on molting, growth rates, times of emergence, and behavior patterns were investigated.

This report summarizes the results of acute, short-term (96-hour) tests (TLm^{96}) used in screening 20 species of aquatic insects to determine their relative sensitivity to low oxygen concentrations. In addition, the longer-term effects of low oxygen levels on the survival, molting, growth, time of emergence, and behavior patterns of 21 species are considered. The 96-hour TLm (Standard Methods, 1965) was used as a measure of survival in the tests. This report encompasses work conducted at the University of Montana Biological Station from 1968 to 1970 and at the University of Utah from 1966 to 1972.

Materials and Methods

The organisms used in the tests were all insects, except for one species of Amphipoda. All organisms were collected from streams and ponds in northwestern Montana and northern Utah. The organisms for a test were all collected from the same area at the same time. The specimens were kept in well oxygenated holding tanks for three days prior to testing. Only specimens of the same age group were utilized. These were generally of the oldest year class present. Test procedures were those outlined in Standard Methods (1965).

Deoxygenated water was obtained from degassing equipment as described by Mount (1964). Modifications included a cooling system and an oxygen "ladder." The ladder is constructed of single pane glass cemented with silicone. The ladder is 5 1/2 feet long, 7 inches wide, and 7 inches deep. It is divided into 15 compartments, each separated by a glass partition 2 inches high. The remainder of the divider is composed of fiberglass screen with a 1 mm mesh opening.

The deoxygenated water comes from the degasser through plastic tubing, passes through the cooler and then enters the elevated end of the ladder. As the water flows over the 2-inch compartment dividers toward the lower end, its oxygen content increases. Rates of increase are dependent upon rate of inflow and angle of inclination of the ladder. At an inclination of 40 degrees from the horizontal and at a flow rate of 1000 cc/min, the oxygen increase per chamber is about 0.5 mg/1 at 10 C.

Ten organisms were placed in each of seven test chambers and observed twice daily. Point of death was determined by lack of response when stimulated. Small rocks were placed in the test chambers to which the organisms could cling.

The flow rate was checked weekly and was found to vary ±25 cc/min. The temperature was taken daily with a pocket thermometer and was found to vary ±0.5 C. Oxygen concentration was taken daily using the modified Winkler method, utilizing a 50 ml sample. Variations of plus or minus 0.2 mg/l occurred.

Water used in the tests at the Biological Station was unchlorinated well water with the following chemical composition: pH 7.8; total hardness, 135 mg/l; temperature, 6.4 C; turbidity, 0-5 J. T. U.; carbon dioxide, 1-2 mg/l.

Short-term (Acute) Bioassays Conducted at University of Montana Biological Station

Results

Nineteen species of aquatic insect and one species of Amphipoda were studied to determine their 96-hour median tolerance limit (TLm). Eight species of Plecoptera were tested. The mean TLm for this group was 3.04 mg/l of oxygen. *Acroneuria pacifica* Banks had the lowest TLm, 1.6 mg/l at a flow rate of 1000 cc/min (Table 1). The highest TLm was obtained with *Pteronarcys californica* Newport (3.9 mg/l) at a rate of 500 cc/min. The TLm for this species decreased to 3.2 mg/l at a flow of 1000 cc/min. All of the specimens of *Arcynopteryx parallela* Frison survived at oxygen concentrations of from 2 to 5 mg/l at a flow of 1000 cc/min. All of the test species were stream forms.

Four species of mayfly (Ephemeroptera) were examined. Two species were lotic forms, *Hexagenia limbata* Guerin and *Callibaetis montanus* (Eaton). Their TLm's were 1.8 mg/l and 4.4 mg/l respectively. The lentic forms tested were *Ephemerella doddsi* Needham and *Ephemerella grandis* Eaton, with D. O. values of 5.2 mg/l and 3.0 mg/l respectively. The mean for the group was 3.6 mg/l.

Seven species of Trichoptera were tested, and all were from lentic environments. Several of these organisms could not be identified to the species level. Ninety percent of the specimens of *Brachycentrus occidentalis* Banks survived at oxygen concentrations of 2-4 mg/l and at a flow rate of 500 cc/min. *Neothremma alicia* Banks, a small species (5 mm), had the lowest TLm of 1.7 mg/l. *Neophylax* sp. had the highest TLm of 3.8 mg/l. The mean for the entire group was 2.86 mg/l.

One Dipteran was tested (*Simulium vittatum* Zetterstadt) and had a TLm of 3.2 mg/l. One Amphipoda was examined (*Gammarus*

TABLE 1. Test organisms, TLm in mg/l, percent saturation and water flow in cc/min.

Organisms	TLm	Saturation	Flow
PLECOPTERA			
Acroneuria pacifica Banks	1.6	14	1000
Arcynopteryx aurea Smith	3.3	29	1000
Arcynopteryx parallela Frison	100*	2-5 mg/l	1000
Diura knowltoni (Frison)	3.6	32	500
Nemoura cinctipes Banks	3.3	29	1000
Pteronarcys californica Newport	3.9	34	500
Pteronarcys californica Newport	3.2	28	1000
Pteronarcella badia (Hagen)	2.4	21	1000
EPHEMEROPTERA			
Callibaetis montanus Eaton	4.4	38	500
Ephemerella doddsi Needham	5.2	46	500
Ephemerella grandis Eaton	3.0	27	1000
Hexagenia limbata Guerin	1.8	15	1000
TRICHOPTERA			
Brachycentrus occidentalis Banks	90*	2-4 mg/l	500
Drusinus sp.	1.8	15	1000
Hydropsyche sp.	3.6	32	500
Lepidostoma sp.	80*	3-4 mg/l	1000
Limnephilus ornatus Banks	3.4	30	500
Neophylax sp.	3.8	33	500
Neothremma alicia Banks	1.7	14	500
DIPTERA			
Simulium vittatum Zetterstadt	3.2	28	500
AMPHIPODA			
Gammarus limnaeus Smith	80*	3 mg/l	500

*Percentage of survival

limnaeus Smith) with a survival of 80 percent at 3 mg/l of oxygen and at a flow rate of 500 mg/l.

The mean TLm for all organisms tested was 3.1 mg/l. The mean for all organisms tested at a flow of 1000 cc/min was 2.55 mg/l and 3.64 mg/l at a flow of 500 cc/min. The lowest TLm recorded was 1.6 mg/l for *Acroneuria pacifica*, or 14-percent oxygen saturation. The highest TLm was 5.2 mg/l for *Ephemerella doddsi*, or 46-percent oxygen saturation.

Discussion

Of the organisms tested, the group most tolerant to low dissolved-oxygen (D.O.) values was the Trichoptera (2.86 mg/l). All of the Trichoptera tested, except *Hydropsyche*, were cased forms, and all came from lentic environments. All the organisms except *Drusinus* sp. were tested at a flow rate of 500 cc/min. Higher flow rates would probably reduce the TLm of many of the forms.

Acroneuria pacifica, a predacious stonefly, was the most resistant form tested with a TLm of 1.6 mg/l (14-percent saturation). The largest organism tested, *Pteronarcys californica*, showed a decrease in TLm as the flow rate increased (3.9 mg/l to 3.2 mg/l).

The mayfly, *Ephemerella doddsi*, had the highest TLm of 5.2 mg/l (46-percent saturation) at 500 cc/min. This species is found attached to rocks in fast streams.

It has been shown by Knight and Gaufin (1963, 1964) that rate of water flow is very important in determining tolerance limits. And that conclusion is supported by the flow-rate ranges and means for *Pteronarcys californica* observed in this study. The TLm range for 11 species tested at 500 cc/min was 1.7 mg/l to 5.2 mg/l, with a mean of 3.64 mg/l. At 1000 cc/min, the range for 10 species was 1.6 mg/l to 3.3 mg/l with a mean of 2.55 mg/l, a substantially lower value.

Behavior of organisms during testing was of interest. All of the Plecoptera initiated "push-up" movements upon introduction to the test chambers. Most species ceased this motion after several hours but *Pteronarcys californica* continued these movements periodically throughout the test. *Pteronarcys californica* also assumed a position half out of the water in the low oxygen chambers. *Nemoura cinctipes* assumed a stilted position upon death.

Number of gill beats per unit time was indicative of oxygen concentration. Gill beats in *Ephemerella grandis* were counted after 12 hours in the test chambers and results are given in Table 2. Each value is the mean number of beats for the ten organisms in each chamber.

Except at the lowest D.O. concentration, the gill beat decreased as the oxygen increased. The rhythm of gill beats also became erratic as the oxygen increased.

The high TLm of the pond mayfly, *Callibaetis montanus*, was surprising. It had the second highest TLm of all species tested (4.4 mg/l). Another lotic species *Hexagenia limbata* had a low TLm of 1.8 mg/l. This could probably be explained by its acclimation to lower oxygen concentrations in its normal environment.

In response to low oxygen values, the Trichoptera undulated their abdomens in their cases. *Simulium vittatum* congregated on the chamber walls where the flow was the greatest. *Gammarus limnaeus* showed no behavioral response to the low oxygen values.

LONG-TERM BIOASSAYS CONDUCTED AT THE UNIVERSITY OF MONTANA BIOLOGICAL STATION AND THE UNIVERSITY OF UTAH

Results

Eight species of aquatic insects from northwestern Montana were studied to determine their tolerance levels and behavior patterns when exposed to low oxygen levels over periods of time longer than 96 hours. Five of these species, and an additional 13 species from northern Utah, were also tested for periods of time ranging from 4 to 104 days to determine their long-term reactions (Tables 3, 4, 5).

The results of the longer-term bioassays clearly indicate increased sensitivity and mortality of test specimens with increased length

TABLE 2. Gill beats/minute for *Ephemerella grandis* Eaton.

Oxygen conc. (mg/l)	Beats	Rhythm
2.4	176	steady
3.0	192	steady
3.6	192	steady
4.6	184	erratic
5.0	160	erratic
6.0	100	erratic

TABLE 3. Long-term dissolved-oxygen bioassays conducted at University of Montana Biological Station.

Species	Minimum D.O. level (mg/l)	Percentage of Survival	Survival time (days)
PLECOPTERA			
Pteronarcella badia (Hagen)	4.4	50	69
Pteronarcys californica Newport	4.8	40	97
Arcynopteryx aurea Smith	4.8	30	12
Acroneuria pacifica Banks	5.8	50	111
EPHEMEROPTERA			
Ephemerella grandis Eaton	4.6	30	30
TRICHOPTERA			
Brachycentrus occidentalis Banks	3.2	50	120
Hydropsyche sp.	4.8	30	50
DIPTERA			
Atherix variegata Walker	2.4	90	40
AMPHIPODA			
Gammarus limnaeus Smith Flow rate of 1000 cc/min	2.8	50	20

of exposure to low oxygen levels. For example, while 50 percent of the specimens of *Acroneuria pacifica* in Montana survived an oxygen concentration of 1.6 mg/l for 4 days, the minimal dissolved-oxygen level for 50-percent survival at 111 days was 5.8 mg/l. Similarly, 50 percent of the specimens of *Arcynopteryx aurea* survived in an oxygen concentration of 3.3 mg/l for 4 days, but only 30 percent survived at a dissolved-oxygen level of 4.8 mg/l for 12 days. This increased sensitivity can be explained partly on the basis of fungus infection and debilitation caused by lack of food. For example, 60 percent of the larvae of the crane fly, *Holorusia* sp., survived for 86 days at a dissolved oxygen level of only 2.0 mg/l. Infection with fungus and shrinkage of the larvae bodies owing to starvation caused a rapid die-off after 86 days.

Of the eight species of aquatic insects tested at the Biological Station, the carnivorous stonefly, *Acroneuria pacifica*, had the highest TLm, with a 50-percent death rate at an oxygen level of 5.8 mg/l for 111 days. The most tolerant species was the Dipteran, *Atherix variegata*, with 90 percent of the specimens surviving for 40 days at

TABLE 4. Long-term dissolved-oxygen bioassays conducted at the University of Utah (50-percent-plus survival).

Species	Minimum D.O. level (mg/l)	Percentage of Survival	Survival time (days)
PLECOPTERA			
Acroneuria pacifica Banks	3.0	50	24
Brachyptera nigripennis (Banks)	2.3	60	4
Isoperla fulva Claassen	2.3	50	13
EPHEMEROPTERA			
Ephemerella grandis Eaton	3.3	50	18
Rhithrogena robusta Dodds	3.3	50	7
	3.3	50	4
TRICHOPTERA			
Brachycentrus occidentalis Banks	2.6	80	91
Rhyacophila sp.	1.4	50	45
Arctopsyche grandis (Banks)	3.4	50	26
Parapsyche elsis Milne	5.2	60	30
DIPTERA			
Atherix variegata Walker	2.4	90	97
Holorusia sp.	2.0	60	86
ODONATA			
Argia vivida Hagen	3.0	50	56
Enallagma anna Williamson	1.4	50	21
Flow rate of 1000 cc/min			

TABLE 5. Long-term dissolved-oxygen bioassays conducted at the University of Utah (minimum D.O. with survival).

Species	Minimum D.O. level (mg/l)	Percentage of Survival	Survival time (days)
PLECOPTERA			
Acroneuria pacifica Banks	3.0	20	41
Arcynopteryx parallela Frison	3.4	10	8
	4.2	20	28
Brachyptera nigripennis (Banks)	3.7	20	9
Isoperla fulva Claassen	2.1	10	27
Pteronarcella badia (Hagen)	2.0	30	30
EPHEMEROPTERA			
Baetis bicaudatus Dodds	3.8	10	3
Ephemerella grandis Eaton	3.5	50	21
TRICHOPTERA			
Parapsyche elsis Milne	4.8	40	16
DIPTERA			
Atherix variegata Walker	1.7	70	90
Bibiocephala sp.	3.4	40	21
ODONATA			
Argia vivida Hagen	1.7	10	100
Enallagma anna Williamson	1.1	20	35
Flow rate of 1000 cc/min			

Table 6. Average minimum dissolved-oxygen requirements of different groups of aquatic invertebrates*.

	Montana species	Average survival (days)	Utah species	Average survival (days)
Plecoptera	4.9 mg/l	62	2.8 mg/l	14
Ephemeroptera	4.6 mg/l	30	3.3 mg/l	10
Trichoptera	4.0 mg/l	85	3.1 mg/l	48
Diptera	2.4 mg/l	40	2.2 mg/l	92
Odonata			2.2 mg/l	39
Amphipoda	2.8 mg/l	20		

*Averages based on 50-percent-plus survival for time indicated.

an oxygen concentration of 2.4 mg/l. This species was also the most tolerant of the Utah forms listed, 90 percent of the specimens surviving at the same oxygen level for 97 days. The higher oxygen requirement of *Acroneuria pacifica* under long-term conditions may be partially owing to its food requirements. Inasmuch as this species is carnivorous, lack of a varied animal diet may have reduced its ability to tolerate low oxygen levels for extended periods of time.

A comparison of the long-term median tolerance limits of the same species of aquatic insects from Montana and Utah shows considerable variation. Fifty percent of the specimens of the stonefly, *Acroneuria pacifica*, from Montana died at a dissolved-oxygen level of 4.4 mg/l in 69 days. The same percentage of Utah specimens survived at a much lower dissolved-oxygen concentration, 3.0 mg/l, but for only 24 days. A mayfly, *Ephemerella grandis*, was tested from both Montana and Utah with similar results. Thirty percent of the Montana specimens survived at a dissolved-oxygen level of 4.6 mg/l for 30 days, while 50 percent of the Utah specimens survived at a dissolved-oxygen concentration of 3.3 mg/l, but for only 18 days. The differences in tolerance limits between the same species may have been much less if the tests had been conducted under exactly the same conditions in the two locations. Time did not permit this, so the Utah tests were run at lower oxygen levels to determine maximum survival rates at these much lower oxygen limits.

An evaluation of the average minimum dissolved-oxygen requirements of the different groups of aquatic invertebrates tested shows that the mayflies are the most sensitive, that the stoneflies are next, and that the caddis flies, freshwater shrimp, true flies, and damselflies follow, in that order. While two species of mayfly could tolerate as low a dissolved-oxygen concentration as 3.3 mg/l for 10 days, a level of 4.6 mg/l was required for 50-percent survival at 30 days. Three species of stonefly from Utah survived at a dissolved-oxygen concentration of 2.8 mg/l for 14 days with 50 percent surviving, but an average oxygen concentration of 4.9 mg/l was required for 30- to 50-percent survival for 62 days. Tests on caddis flies also indicated that higher oxygen levels were necessary with longer exposure, a minimum of 4.0 mg/l being required for 50-percent survival for 84 days.

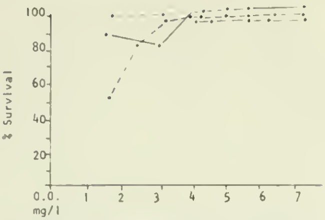

Fig. 1. *Acroneuria pacifica*: 1000 cc/min, 96-hour TLm results, oxygen.

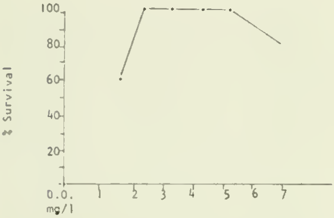

Fig. 3. *Arcynopteryx parallela*: 1000 cc/min, 96-hour TLm results, oxygen.

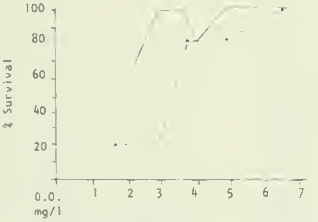

Fig. 5. *Pteronarcys californica*: 1000 cc/min, 96-hour TLm results, oxygen.

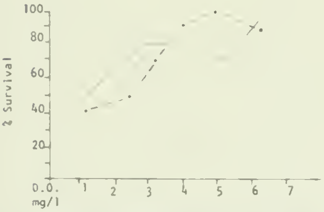

Fig. 7. *Hexagenia limbata*: 1000 cc/min, 96-hour TLm results, oxygen.

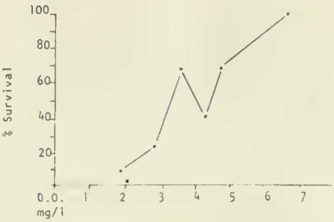

Fig. 2. *Arcynopteryx aurea*: 1000 cc/min, 96-hour TLm results, oxygen.

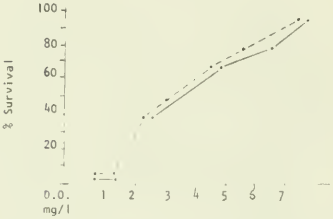

Fig. 4. *Pteronarcella badia*: 1000 cc/min, 96-hour TLm results, oxygen.

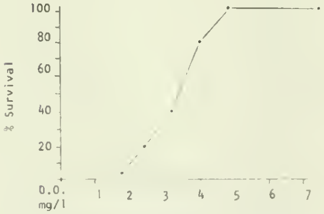

Fig. 6. *Nemoura cinctipes*: 1000 cc/min, 96-hour TLm results, oxygen.

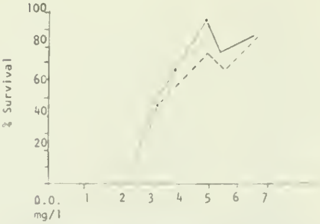

Fig. 8. *Ephemerella grandis*: 1000 cc/min, 96-hour TLm results, oxygen.

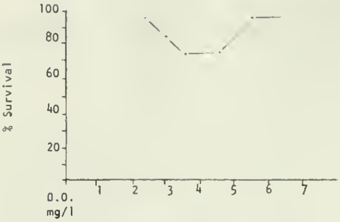

Fig. 9. *Lepidostoma* sp.: 1000 cc/min, 96-hour TLm results, oxygen.

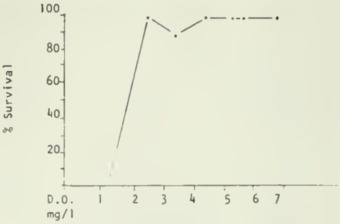

Fig. 10. *Drusinus* sp.: 1000 cc/min. 96-hour TLm results, oxygen.

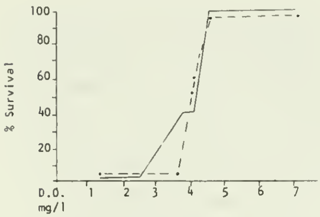

Fig. 11. *Pteronarcys californica*: 500 cc/min, 96-hour TLm results, oxygen.

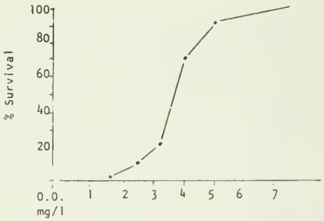

Fig. 12. *Diura knowltoni*: 500 cc/min, 96-hour TLm results, oxygen.

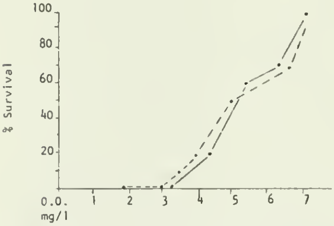

Fig. 13. *Ephemerella doddsi*: 500 cc/min, 96-hour TLm results, oxygen.

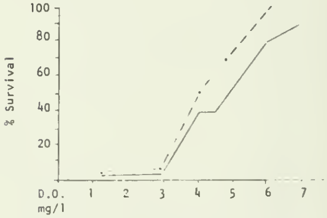

Fig. 14. *Callibaetis montanus*: 500 cc/min, 96-hour TLm results, oxygen.

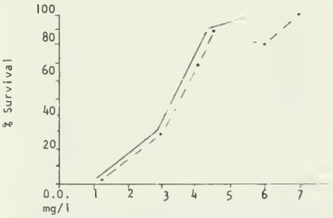

Fig. 15. *Limnephilus* sp.: 500 cc/min, 96-hour TLm results, oxygen.

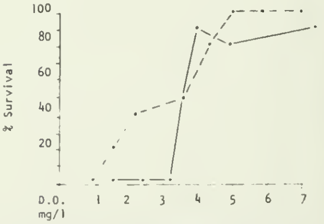

Fig. 16. *Hydropsyche* sp.: 500 cc/min, 96-hour TLm results, oxygen.

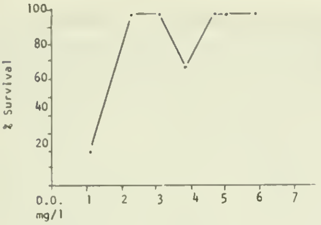

Fig. 17. *Neothremma* sp.: 500 cc/min. 96-hour TLm results, oxygen.

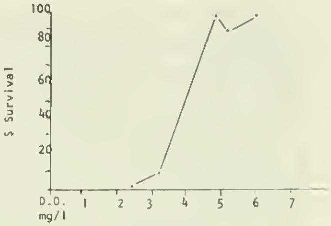

Fig. 18. *Neophylax* sp.: 500 cc/min, 96-hour TLm results, oxygen.

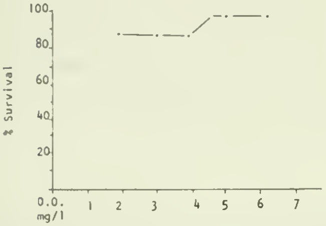

Fig. 19. *Brachycentrus occidentalis*: 500 cc/min, 96-hour TLm results, oxygen.

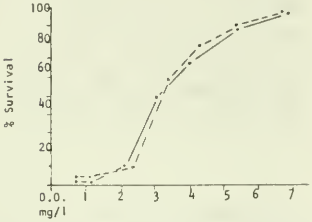

Fig. 20. *Simulium vittatum*: 500/cc min, 96-hour TLm results, oxygen.

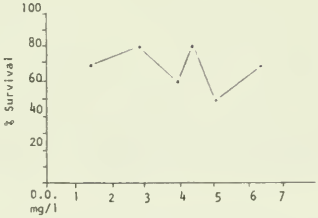

Fig. 21. *Gammarus limnaeus*: 500 cc/min, 96-hour TLm results, oxygen.

The true flies, freshwater shrimp, and damselflies displayed a much greater tolerance to low oxygen levels than did the previous three groups. Fifty percent of the specimens of these three groups were able to survive for periods ranging from 20 to 92 days at dissolved-oxygen levels ranging from 2.2 to 2.8 mg/l.

While the principal objective of this project was to determine the minimal dissolved-oxygen levels required for both short- and long-term exposure, survival without growth and metamorphosis would eventually eliminate a species of aquatic insect. While not all of the species tested molted or emerged during the study, many species did. All of the species on which bioassays were run for over 30 days molted one or more times at the oxygen levels required for 50-percent survival. Species such as the stoneflies *Brachyptera nigripennis*, *Pteronarcys californica*, and *Pteronarcella badia*, the mayfly *Ephemerella grandis*, and the damselfly *Enallagma anna* emerged during the tests at oxygen concentrations of 4.8 mg/l or less. None of the caddis flies or Dipterans emerged, inasmuch as only larvae and not pupae were used for testing purposes.

Discussion

Aquatic environments in which dissolved oxygen is available in excess at all times are rare. Many aquatic animals possess varied adaptations that facilitate the acquisition of oxygen when it becomes scarce. In stoneflies, diffusion, along with special ventilation mechanisms, provides extensive absorbing surfaces for the absorption of oxygen from the environment. An adaption utilized by the nymphs of *Pteronarcys californica* when environmental oxygen becomes reduced is undulating the body—to destroy the oxygen gradient that develops around the body and gills. Of particular interest is the variation in rate of undulation according to year class. In studies conducted at the University of Utah from 1963 to 1965, the undulations of the smaller nymphs of this species (year I, 17-18 mm long) were more rapid than those of the larger (year II, 30 mm long).

The respiratory mechanism possessed by different species of aquatic insects greatly influences their ability to withstand low oxygen concentrations. In work conducted by Knight and Gaufin (1966) at the University of Utah, the value of gills in enabling some species to better withstand low dissolved-oxygen levels was demonstrated clearly. The nymphs of *Pteronarcella badia*, *Isoperla fulva*, and *Acroneuria pacifica* were all exposed to an environment of reduced dissolved oxygen of 1.0 cc/l and water flow of 0.004 feet/second, at 10 C. The forms possessing gills exhibited quite similar mortalities during the exposure period. *Pteronarcella badia* nymphs exhibited a 13-percent mortality after 24 hours and 48 hours of exposure, and 29-percent at the end of 72 hours, with no further mortality for the remainder of the exposure period. *Acroneuria pacifica* showed the same mortality as did *Pteronarcella badia* after 72 hours of exposure. After 96 hours exposure, *Acroneuria pacifica* displayed a 25-percent mortality. No further mortality was noted for the remainder of the experimental period. Eighty percent of the *Isoperla fulva* nymphs, a species without gills, died within 24 hours. After 144 hours of exposure, all had succumbed. The increased mortality shown by the *Isoperla fulva* nymphs may have been owing to their smaller size and the fact that they were year class I, as opposed to year class II in the gilled forms. *Isoperla fulva* has only a one-year life cycle, so it was impossible to compare nymphs of similar size.

In view of the above, a second evaluation was carried out comparing nymphs of *Acroneuria pacifica* (gills) to those of *Arcynopteryx parallela* (no thoracic gills). The nymphs were tested at a temperature of 15.6 C with a water flow of 0.25 feet/second and a dissolved-oxygen concentration of 1.0 cc/l. The nymphs of both species were between 25 and 30 mm in length. In general, the results of this test—like those of the previous one—indicated that forms lacking gills are more sensitive to reduced dissolved oxygen than are forms possessing gills. No mortality of *Acroneuria pacifica* nymphs occurred during the experimental period, while nymphs of *Arcynopteryx parallela* showed 82-percent mortality after 10 hours of exposure, 88.5-percent mortality at the end of 24 hours, and 100-percent mortality after 34 hours.

The metabolism of poikilotherms rises with temperature about two and one-half times per 10 C change in temperature (Prosser and Brown, 1961). This metabolic increase in response to increased environmental temperature produces increased oxygen consumption. The increase in oxygen consumption with increased water temperature would cause an aquatic insect subjected to the higher temperature (15.6 C) to incur an oxygen debt at a higher dissolved-oxygen concentration than one subjected to a situation similar except for a reduced temperature (10 C). Stoneflies, mayflies, and caddis flies do not have an apparent ability to get along without oxygen for an extended period. They do survive for a short period in greatly reduced oxygen by greatly reducing their activity, and they use energy apparently produced by the anaerobic phase of glycolysis. If the oxygen supply is not restored within a certain time, the specimens die from asphyxiation.

In the work conducted to date by the author and his colleagues, there has been a great difference in the dissolved-oxygen concentration at which initial mortality of test organisms was recorded. This difference was greatly influenced by the temperature difference in the experimental environment. In a natural situation in which the dissolved oxygen is gradually reduced for short periods of time (for example, by intermittent discharges of organic oxygen-demanding wastes), the onset of stonefly mortality would be influenced by the existing water temperature. Provided that the water flow and other variables remained constant, one could expect the aquatic insects subjected to an environmental temperature of 10 C to withstand reduced oxygen concentrations about 2.4 times lower than would the same specimens exposed to similarly reduced oxygen concentrations at a water temperature of 15.6 C. In a hypothetical situation based on the work of Knight and Gaufin (1966), a stream possessing a temperature of 15.6 C and a dissolved-oxygen concentration of 0.6 cc/l would have a stonefly mortality of 18 percent while a stream similar in all respects except that its water temperature was 10 C would exhibit 100-percent survival. Thus, the water temperature of a stream is a very important factor in the survival of aquatic insects when they are subjected to a reduction in dissolved oxygen over a short period of time.

The rate of water flow in a stream also is a very important factor in the survival of aquatic insects exposed to low oxygen concentrations. Knight and Gaufin (1966) showed that a gradual reduction of dissolved oxygen with water flow of 0.06 ft/sec produced approximately 50-percent stonefly mortality and that a similar situation provided with a water flow of 0.25 ft/sec resulted in 100-percent survival.

In the present study the mean oxygen concentration required for 50-percent survival by 11 species of aquatic insects at a flow rate of 500 cc/min was 3.64 mg/l. The mean for 10 species at a flow rate of 1000 cc/min was considerably lower or 2.55 mg/l.

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SUBSTRATE COLOR MATCHING IN THE GRASSHOPPER, *CIRCOTETTIX RABULA* (ORTHOPTERA: ACRIDIDAE)

George W. Cox[1] and Darla G. Cox[2]

Abstract.— Mechanisms important in maintaining substrate color matching in the grasshopper, *Circotettix rabula*, were studied near Aspen, Colorado, during the summers of 1968-70. Studies concentrated on populations on gray shale and red sandstone substrates. In both areas, collections revealed appreciable numbers of mismatched phenotypes among all age groups. The possibility of developmental homochromy was examined by observation of nymphs held in rearing boxes on matching and contrasting soil colors. The behavioral selection of matching substrate colors was tested by preference experiments. While not negating the possibility of these mechanisms, results suggested that they were of minor importance. Predation experiments, using *Sceloporus* lizards, demonstrated significant levels of selective predation on mismatched nymphs on both red and gray substrates. Experiments with bird and mammal predators, using adult grasshoppers, gave similar results. Release-recapture experiments with marked adults in areas of red and gray substrates showed markedly higher disappearance rates for mismatched animals. These results are interpreted to indicate that selective predation on mismatched animals is a major factor in maintaining substrate color matching in this species.

Over the past 25 years, students of ecological genetics have documented several major cases of rapid evolutionary response by animal populations subjected to strong selective pressures. The most thoroughly investigated of these concern industrial melanism in moths (Kettlewell, 1961), pesticide resistance in a wide variety of animals (Crow, 1966), and the coloration and banding patterns of various land snails (Cain and Sheppard, 1954). For the Peppered Moth, *Biston betularia*, an industrial melanic, and for the land snail, *Cepaea nemoralis*, selective predation by vertebrates has been demonstrated (by experimentation and direct observation) to be an important factor in the observed evolutionary response (Kettlewell, 1955, 1956; Sheppard, 1951; Cain and Sheppard, 1954; Cain and Currey, 1968).

The phenomenon of substrate color matching has been recorded for many species of animals of open habitats and is especially common in Acridid grasshoppers (Rowell, 1971). For these animals, the mechanisms involved appear to be complex and varied, including—at least for different species—predator selection for crypsis, behavioral preference for color-matching substrates, and homochromic responses during individual development (ibid.). Acridid species showing spatial or temporal variation in substrate color matching may therefore be of major value in the study of evolutionary processes operating on organisms capable of behavioral or developmental modification of genetically based characteristics.

In the Roaring Fork Valley near Aspen, Colorado, populations of many animals of open habitats show differences in general body coloration correlated with soil and rock substrate color. The sub-

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[1] Department of Biology, San Diego State University, San Diego, California 92115.
[2] Biology Department, La Jolla Country Day School, La Jolla, California 92037.

strates involved vary strikingly in color as a result of the variety of geological formations exposed in the valley. The most extensive exposures near Aspen consist of red sandstones of the Maroon Formation, dark gray shales of the Mancos Formation, and Precambrian granites on which yellow to brown clay soils are developed. Smaller areas of dark basaltic lavas and white shales also occur in the lower part of the valley. Although sharp changes in substrate color sometimes exist at contacts between different parent materials, the presence of a variety of other bedrock formations and the mixing of various parental materials in glacial and alluvial deposits produce an additional variety of substrates of intermediate colors in different parts of the valley.

Correlation of general body color with substrate color has been observed in the lizards *Sceloporus undulatus* and *S. graciosus* (Coleman, 1968), and, by the authors, in various species of Acridid grasshoppers, including *Arphia conspersa* Scudder, *Circotettix rabula* Rehn and Hebert, *Cratypedes neglectus* (Thomas), and *Trimerotropis suffusa* (Scudder).

During the summers of 1968-70, the authors conducted studies of the role of various factors in the maintenance of substrate color matching in populations of the grasshopper *Circotettix rabula*, an Acridid of the subfamily Oedipodinae, in the vicinity of Aspen. These studies concentrated on populations on exposures of Mancos Shale (gray) and Maroon Sandstone (red). The Mancos Shale population was studied at a location 6 miles west of Aspen on Colorado State Highway 82 at Brush Creek. The Maroon Sandstone population was studied at an area of cliffs on the north side of the Roaring Fork River opposite the community of Snowmass, about 15 miles west of Aspen. Both study areas consisted of relatively open, dry habitats on hilly terrain, with the dominant vegetation being a complex mixture of sagebrush, oak-serviceberry, pinyon-juniper, and riparian elements.

PROCEDURE

At the outset, three major mechanisms that, separately or in combination, might account for the pattern of substrate color matching were recognized:

1. Homochromy (the adoption, through developmental process in the nymphs, of a body color matching that of the substrate upon which they are living). This mechanism has been demonstrated in many Acridid grasshoppers (Rowell, 1971).
2. Behavioral preference by individuals for substrates of matching color. Such preferences have been recorded for some Oedipodine grasshoppers (Rowell, 1971). This preference could presumably act in conjunction with either 1 (above) or 3 (below) to enhance the degree of color matching achieved by these mechanisms.
3. Predator selection favoring individuals closely matching the substrate in body color. This mechanism might operate in conjunction with 1 or 2 (above) by selection against individuals in which the mechanisms of homochromy or behavioral preference are imperfectly developed. Alternatively, selection may relate to matched and mismatched color pheno-

types resulting directly from genotypic differences in processes of pigment production.

The present studies were designed to investigate the relative importance of these possible mechanisms.

The hypothesis of developmental adoption of environmental color was tested by a combination of field and experimental studies. Nymphs were collected in both study areas during the period 22-25 June 1968. Total body length and color phenotype were recorded for each of these animals. These animals were visually assigned to four color phenotype classes: gray, yellow brown, brown, and red. These collections were made to determine the presence and general frequency of mismatched phenotypes in the two areas.

In addition, during the June and July of 1968, live nymphs from each study area were divided into two groups of equal size, and placed in separate rearing boxes with red and gray soils and correspondingly painted walls. Totals of 54 gray and 52 red nymphs were used in this experiment. Food and water were provided in each box. Although it proved impossible to rear many of these nymphs to adulthood, many completed one or more molts and were maintained for periods of up to four weeks. This experiment was performed to determine if changes in body color could be induced in nymphs of the size classes for which data on frequency of various color phenotypes had been obtained in the field observations.

To investigate hypothesis 2, that of possible behavior preferences for matching substrates, four substrate-color preference tests were conducted during the summer of 1968. Preferences were tested separately for nymphs and adults from the two study areas. Tests were conducted outdoors in 4′x8′ boxes covered with gray fiberglass screening, in which equal areas of red and gray soils from the study areas were presented. These tests consisted of a series of 1-hour runs, with the position of the boxes being reversed between successive runs. Experimental animals were introduced at the boundary of the two substrate types at the start of each run, and their positions were noted at the end of the one-hour period.

Several laboratory and field experiments were conducted to evaluate the intensity of predation on animals of matched and mismatched body color. The most extensive series was conducted using the lizards *Sceloporus undulatus* and *S. graciosus* as predators on nymphs. These experiments were carried out in the covered 4′x8′ boxes described above. A layer of red or gray soil was placed in the bottom of the box, and several piles of flat stones of matching color constructed near the center of the box to allow shelter for both lizards and grasshopper nymphs. This was necessary to minimize the tendency for animals to climb onto the walls and covers of the boxes (which were of different color). Equal numbers of red and gray nymphs were then placed in the box and lizards introduced so that a ratio of 6-8 nymphs per lizard was obtained. These experiments were terminated when approximately one half of the nymphs had been eaten. During the summer of 1968 experiments were conducted on gray substrates. Experiments on red substrates were performed during all three summers to obtain an adequate number of observations. Experiments were carried out in a shaded, outdoor area during 1968, with the duration of each run being 24 hours. In 1969 and 1970, experiments were done indoors under artificial lights. The duration of runs in these experiments varied from 6-12 hours.

During the summer of 1969 two series of experiments were conducted using the least chipmunk, *Eutamias minimus*, and the American robin, *Turdus migratorius*, as predators. For these experiments, adult grasshoppers were used. Experiments using the least chipmunk (Hobbs, 1969) were conducted in the 4′x8′ box described above. The flight wings and hind legs of the grasshoppers used in these tests were removed to minimize the effects of flight and rapid movement in attracting attention of the predators. Two grasshoppers, one red and one gray, were placed in the box on a given substrate color, and the predator introduced. The grasshopper first captured was then noted. A total of 25 such tests were performed on each substrate color. A similar procedure was followed in experiments using the American robin (Coate, 1969), except that tests were performed in a cage 6′x6′x6′ in size.

Two field experiments were also conducted to compare the rates of disappearance of red and gray adults following their release in an area of one substrate color. The animals used in these experiments were captured in the two study areas at locations about one-half mile from the locations at which releases were subsequently made. Animals were marked with a spot of colored airplane dope on the ventral side of the thorax and were released on the same date on which they were captured.

During the summer of 1968 two releases were made on a Mancos Shale (gray) area. On 24-26 July, 37 males and 34 females from the Mancos Shale population and 54 males and 50 females from the Maroon Sandstone population were released. The second release, made on 6 August, consisted of 14 males and 13 females from the Mancos Shale population and 15 males and 30 females from the Maroon Sandstone population. Recapture samples were taken on 1-3 August, 15-16 August, and 21 August.

During the summer of 1969, releases were made on an area of Maroon Sandstone (red) substrate. On 16-17 July, 65 males and 53 females from the red sandstone population and 62 males and 55 females from the gray shale population were released. Recapture samples were obtained on 24 July, 29-31 July, and 7-8 August.

RESULTS

Totals of 48 nymphs from the Mancos Shale population and 70 nymphs from the Maroon Sandstone population were obtained in the field collections made in June 1968 (Table 1). The distribution of these animals among the four color phenotype classes was summarized separately for animals less than 12 mm and for those 12 mm or over in total length. These data indicate that an appreciable frequency of mismatched color phenotypes exists, especially among

TABLE 1. Frequencies of nymphs of different color in collections from Mancos Shale (gray) and Maroon Sandstone (red) areas, 22-25 June 1968.

		Color Phenotype Class (Visual Groupings)				
Substrate	Size Class	Gray	Yellow Brown	Light-Dark Brown	Red	Total
Mancos Shale	<12 mm	18	1	2	5	26
	>12 mm	21	0	0	1	22
	Total	39	1	2	6	48
Maroon Sandstone	<12 mm	0	0	16	12	28
	>12 mm	0	2	9	31	42
	Total	0	2	25	43	70

the smaller nymphs, in both populations. In the Mancos Shale area, for example, 5 of the 25 nymphs less than 12 mm in total length were red. When analyzed by a 2x2 contingency test, the frequencies of matched and totally mismatched phenotypes in the two size groups were found to be significantly different, or nearly so. For the Mancos Shale population the calculated chi square value of 3.80 was nearly significant at the 5 percent level; for the Maroon Sandstone population, the value of 5.55 was significant at the 5 percent level (5 percent critical chi square, with 1 d.f., equals 3.841). In both cases, the frequency of mismatched individuals was lower among the larger nymphs.

The nymphs maintained in rearing boxes on substrates of contrasting color, however, showed no visually detectable changes in body color, as compared with those kept on matching substrates.

In the four experiments designed to test for substrate-color preference by nymphs and adults, the total numbers of preference responses obtained per experiment varied from 58 to 96. However, chi square goodness-of-fit tests, comparing observed results and an expectation of equal numbers selecting each substrate, showed no significant preferences for substrate color by nymphs or adults from either population.

Results of the predation experiments with the lizards *Sceloporus undulatus* and *S. graciosus* demonstrated selective predation on nymphs of mismatched color (Table 2). On the gray substrate a 2x2 contingency test of the experimental results showed that the numbers of nymphs eaten and not eaten were significantly influenced by body color (1 percent level); a similar test for the red substrate showed significance at the 5 percent level.

Fewer data were obtained for the experiments using the American robin and least chipmunk as predators (Table 3). Except for the results of the tests with the least chipmunk on the gray substrate (significant at the 5 percent level) these results do not show significantly different preferences for matched and mismatched grasshoppers. However, the pattern shown by these data is similar to that obtained for the lizard predation experiments. A common feature of experiments with all of the predators used was a higher intensity of

Table 2. Results of experiments involving predation by *Sceloporus undulatus* and *S. graciosus* on nymphs of *Circotettix rabula* from Mancos Shale (gray) and Maroon Sandstone (red) populations.

	Gray substrate			Red substrate		
	Eaten	Not eaten	Total	Eaten	Not eaten	Total
Red nymphs	41	9	50	46	48	94
Gray nymphs	20	30	50	61	32	93
Total	61	39	100	107	80	187
Chi square		16.81 (1 d.f.)			4.65 (1 d.f.)	

Table 3. Results of experiments involving predation by the American robin and the least chipmunk on adults of *Circotettix rabula* from Mancos Shale (gray) and Maroon Sandstone (red) populations.

	Gray substrate			Red substrate		
	Eaten	Not eaten	Total	Eaten	Not eaten	Total
American robin						
Red adults	17	8	25	12	13	25
Gray adults	8	17	25	13	12	25
Total	25	25	50	25	25	50
Chi square		3.17 (1 d.f.)			0.05 (1 d.f.)	
Least chipmunk						
Red adults	18	7	25	9	16	25
Gray adults	7	18	25	16	9	25
Total	25	25	50	25	25	50
Chi square		4.00 (1 d.f.)			1.44 (1 d.f.)	

predation on mismatched animals on the gray substrate than on the red.

Data from the release and recapture experiments with marked adults on both substrates showed rapid decline in the ratio of mismatched to matched animals with time (Figs. 1, 2). To evaluate the significance of this change, Chi Square tests were performed on the observed frequencies of red and gray animals in the first recapture sample obtained after each release, using the release ratio of red and gray animals to provide the expected frequencies. For the 24-26 July release and the 1-3 August recapture samples on the Mancos Shale area (1968), the calculated Chi Square value was 8.74. For the 6 August release and the 15-16 August recapture sample, the calculated Chi Square value was 8.78. Both of these tests indicate a highly significant (1 percent level) change in the ratio of red to gray animals. For the 16-17 July release and the 24 July recapture sample on the Maroon Sandstone area (1969), the calculated Chi Square value was 4.66 (significant at the 5 percent level).

The ratio of mismatched to matched animals (Figs. 1, 2) declined exponentially, according to the formula

$$R_t = R_o e^{bt}$$

Where: R_o = Ratio on date of release
R_t = Ratio t days after release
b = Rate of change in mismatched/matched ratio per day.

A rough estimate of the average rate of change, b, in this ratio was

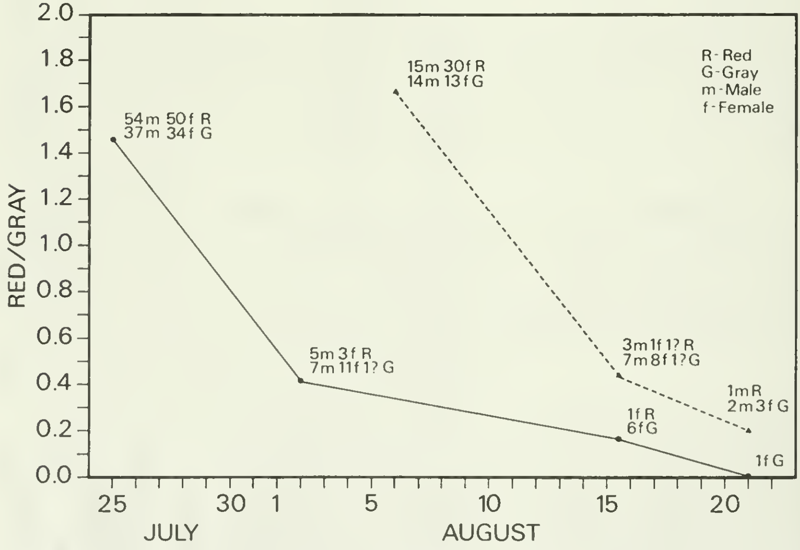

Fig. 1. Ratios of red (Maroon Sandstone) to gray (Mancos Shale) adults in the release-recapture experiment on the Mancos Shale study area.

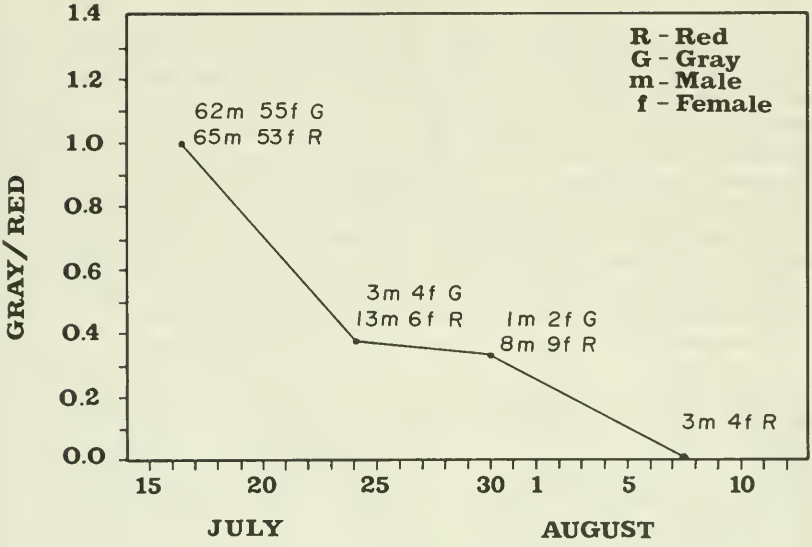

Fig. 2. Ratios of gray (Mancos Shale) to red (Maroon Sandstone) adults in the release-recapture experiment on the Maroon Sandstone study area.

obtained by calculating the least square linear regression of ln R on t. The slope of this relationship is a measure of b. Values for the rate of change in the red-gray ratio during the experiments initiated in July and August of 1968 on the Mancos Shale area were -0.10 and -0.14, respectively. These values indicate that the disappearance rate of the red animals was of the order of 10 to 14 individuals per 100 individuals per day greater than that of the gray animals. On the Maroon Sandstone area, the differential rate of disappearance of the gray animals, calculated in a similar manner, was -0.09, or 9 individuals per day greater than that of the red animals.

Recapture data from the field experiments were also analyzed with respect to frequencies of recapture of individuals of different sex. For the experiment on the Maroon Sandstone area, and for red animals in the Mancos Shale experiment no significant differences were noted between the sex ratios of animals released and those recaptured. However, for gray animals used in the Mancos Shale experiment, the sex ratio of the combined groups of released animals (24-26 July and 6 August 1968) was significantly different (Chi Square = 4.26, 5 percent critical value = 3.841) from that of the combined recapture samples for these releases. Males were less frequently recaptured than expected in this case. The males of this species perform a conspicuous aerial display, consisting of a prolonged dancing flight accompanied by a loud crackling call. This display is attractive to predators, and several observations of actual or attempted predation involved attempts by birds to capture such animals in flight.

Discussion

Although the phenomenon of substrate color matching is well developed in *Circotettix rabula*, variation in body coloration exists in both nymphal (Table 1) and adult (Trent, 1968) populations in the areas examined in this study. Both of the study areas were adjacent to alluvial terraces of the Roaring Fork River and, thus, to substrates of somewhat different color. Furthermore, the adults are strong fliers, and in such situations it is likely that considerable dispersal occurs between areas differing in substrate color. During the summers of 1969 and 1970, direct observations of such dispersal were made near Aspen at a locality in which a whitish gray shale formation sharply contacts an exposure of Maroon Sandstone.

The specific locations from which collections of nymphs (Table 1) were made in 1968, however, were at least 100 m from areas of strongly differing substrate color. The occurrence of strongly mismatched forms among these nymphs, together with the failure of nymphs of comparable size to show modification of body color in the red and gray rearing boxes, suggests that any homochromic developmental response is relatively weak and that body color is to a large extent under direct genetic control. The possibility that artificial light conditions may have been unfavorable for homochromic response cannot be entirely dismissed, however. Because of the low mobility of the nymphs, it is probable that the existence of mismatched nymphs in the study areas is the result of dispersal of adults into the areas from other substrate types.

No evidence of behavioral selection of matching substrates was obtained in the laboratory preference tests. This evidence is further supported by the direct observations, cited above, of dispersal of adults between substrates of sharply differing color. Nevertheless, it is still possible that behavioral selection of matching substrates does occur to some degree, but was inhibited, especially for adults, by the artificial conditions of the test boxes.

Evidence of selective predation is strong. Field observations indicate that a variety of vertebrates prey on this species. Observations of either attempted or successful predation in the field were obtained for the sagebrush lizard, *Sceloporus graciosus*, the least chipmunk, *Eutamias minimus*, the western tanager, *Piranga ludoviciana*, the Steller's jay, *Cyanocitta stelleri*, the mountain bluebird, *Sialia cucurroides*, and the red-winged blackbird, *Agelaius phoeniceus*.

Results of the predator selection experiments (Tables 2, 3) indicate that differential predation is of major importance in the maintenance of substrate color matching. These observations correlate with the significantly lower frequency of mismatched nymphs in the larger size classes in the field (Table 1) and with the significantly greater rate of disappearance of mismatched adults in the release-recapture experiments.

In the release-recapture experiments, as conducted, it is impossible to rule out entirely the possibility of differential dispersal away from the release point by matched and mismatched animals. But, the absence, or at least the weakness, of behavioral preferences for matching substrate color suggests that this is unlikely. The recapture data for males and females are also most consistent with the conclusion that predation is the primary factor in the differential disappearance rates of matched and mismatched adults. Males, which perform frequent and extensive aerial displays, should be both the most vulnerable to aerial predators and the most prone to dispersal from the release site. Mismatched males should then have the greatest opportunity for encountering and selecting more appropriate substrates. However, the only instance in which the disappearance rate for males significantly exceeded that for females was for gray adults on the gray substrate. If dispersal, combined with behavioral selection of matching substrates, had been of major importance, differences in male and female disappearance rates should have been greatest for mismatched animals.

In addition, the experimental predation studies and the release-recapture experiments share the common feature that mismatched animals are removed, or disappear more rapidly, from the gray shale than from the red sandstone substrate. This observation is difficult to interpret in the absence of detailed measurements of spectral reflectance of the substrates and animals. However, it may be that gray animals on the red substrate, while sharply contrasted in color, approximate in appearance spots of shadow produced by small objects, or perhaps dead twigs, and are thus not as easily recognized by predators.

These observations lead us to conclude that predator selection against mismatched animals is the major mechanism for maintaining substrate color matching in this species.

ACKNOWLEDGMENTS

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EFFECTS OF CHEMICALS ON THE GERMINATION OF POLLEN GRAINS OF *TORENIA ASIATICA* LINN.

E. M. V. Nambudiri[1] and M. K. Thomas[2]

Abstract.— Germination studies of the pollen grains of a Scrophulariaceae plant, *Torenia asiatica* Linn. have revealed that the maximum percentage of germination and longer tubes were attained in 15 percent sucrose solution. Among the chemicals tried, calcium and boron enhanced germination. Less germination occurred among grains treated with potassium or magnesium salts. Abnormalities such as branched tubes with or without vesicles were found in chemically treated pollen grains.

Torenia asiatica Linn., a common garden plant belonging to the tribe Gratioleae of the Scrophulariaceae family is cultivated as an ornamental plant in and around Bombay, India. This small herbaceous plant produces bright violet flowers. Pollen morphology of Scrophulariaceae plants has been described by Risch (1939), Erdtman (1952), Ikuse (1952), Natarajan (1957), and others. Varghese (1968) described the morphology of pollen grains of *Torenia cordifolia* Roxb., along with certain other plants of this family.

Successful germination of pollen is a prerequisite for success in fertilization; therefore, many workers have studied the effect of different chemicals on the germination of pollen from various plants. Compounds of boron, calcium, potassium, and magnesium were selected for the study of their effects on the germination of the pollen of *T. asiatica*. Although the effects of these chemicals on germination of pollen grains of certain other plants have already been studied by previous workers, in this paper the authors are concerned with the study of various concentrations (20, 40, 60, 80, and 100 ppm) of boric acid (H_3BO_3), calcium nitrate ($Ca[NO_3]_2 \cdot 4H_2O$), potassium nitrate (KNO_3) and magnesium sulphate ($MgSO_4 \cdot 7H_2O$) on the germination and tube growth of *T. asiatica* pollen.

Materials and Methods

Pollen grains used in the experiments were collected from flowers just prior to their opening to ensure that the material used was fresh and uncontaminated. Pollen grains of *T. asiatica* (Fig. 4b) show three colpae. Chemicals employed in the experiments were of AR-BDH. Culture media of sucrose (5, 10, 15, and 20 percent) were prepared in double-distilled water. After the sucrose concentration was standarized at 15 percent, different concentrations of four chemicals were added separately to the 15 percent sucrose solution. Concentrations of chemicals chosen were 20, 40, 60, 80, and 100 ppm. One drop of each of these solutions was then placed on a clean sterilized microslide, and pollen grains were dusted on these media. The microslides were then transferred to a moist filter chamber

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[1] P.O. Box 21563, Dar-es-Salaam, Tanzania.

[2] Botany Department, Wilson College, Bombay 400007, India.

where pollen grains were allowed to germinate and grow for two hours. Experiments were conducted at a pH of 6.5 and a temperature of 26 to 28 C. Percentage germination was calculated by counting 100-200 pollen grains from different fields of the microslide. Mean tube length was calculated from 50 pollen tubes selected at random. All experiments were repeated until concurrent results were available.

Results

During initial experiments, it was noticed that grains did not germinate in water but readily germinated in a sugar solution. Therefore, further germination tests were carried out with different types of sugars; namely, glucose, fructose, and sucrose. Sucrose gave maximum germination percentage and higher mean tube length. Hence, for further experiments with different chemicals, sucrose was selected as the basic medium.

Pollen germination in sucrose medium. Pollen grains were allowed to germinate in 5, 10, 15, and 20 percent sucrose solutions. The percentages of germination and tube growth in these media were recorded. Maximum germination percentage and tube growth were observed in 15 percent sucrose solution (Table 1, Fig. 1). A minimum percentage germination (10 percent) along with a lower mean tube length (222.5μ) were observed in 20 percent sucrose solution. A comparatively low germination percentage and shorter tubes were also found in 5 and 10 percent sucrose solutions (Table 1). It is therefore evident that 15 percent sucrose medium can be used for further experiments with different chemicals. Another benefit in selecting this sucrose concentration is that the bursting of pollen tubes in this medium is lower than in other concentrations. Bursting of pollen tubes before attaining required lengths is undesirable since such tubes cannot effect fertilization.

Pollen germination in different chemicals. Keeping 15 percent sucrose solution as the basic medium, different concentrations of the four chemicals were prepared separately. A comparative account of the results obtained is given in Table 2 and in Figure 2. The major effects of different chemicals on germination are given below:

1. *Boric acid* (Fig. 3b). A minimum concentration of boric acid enhanced pollen germination and tube length. Eighty-nine percent

Table 1. Percentage germination and mean tube length of pollen grains of *Torenia asiatica* Linn.

Percentage concentration of sucrose	Percentage germination	Mean tube length in microns after two hours
5	43	290.0
10	55	351.0
15	73	443.5
20	10	222.5

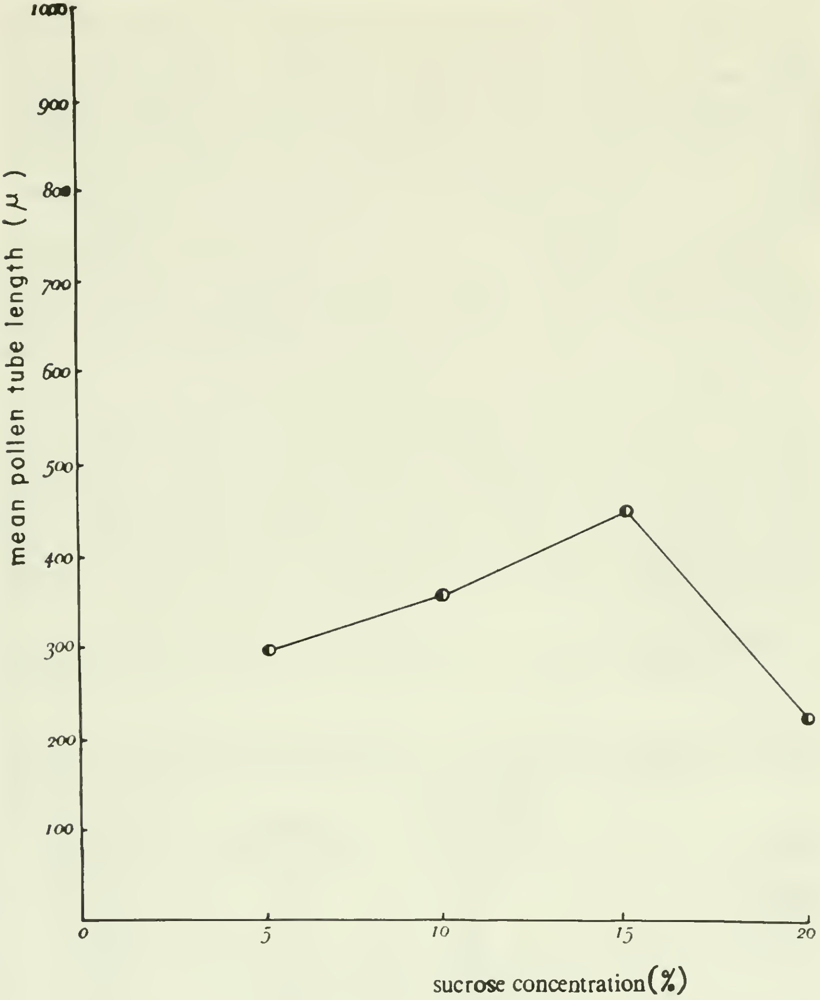

Fig. 1. *Torenia asiatica.* Graph showing mean tube length for pollen grains in control sucrose medium.

of the germinated pollen grains had a mean tube length of 755μ in 20 ppm of boric acid. Since the present work was confined to studying fixed concentrations of different chemicals, and not determining which concentration gave maximum tube length, the concentration of boric acid below 20 ppm was not tried. With an increase in the concentration of the chemical, percentages gradually declined—to a minimum of 70 percent germination and mean tube length to 403μ—in 100 ppm of boric acid.

2. *Calcium nitrate* (Fig. 3a). A condition the reverse of that for boric acid (as described above) was obtained when pollen grains were treated with calcium nitrate solution. A high germination percentage and longer tubes were noticed in the maximum concentration of this chemical (100 ppm), as can be observed in Table 2. Mean tube length gradually increased from 418μ in 20 ppm to 813μ in 100 ppm. Similarly, percentage germination progressed upwards from 66 percent in 20 ppm to 91 percent in 100 ppm.

3. *Magnesium sulphate.* A 40 ppm concentration of magnesium sulphate gave the highest germination percentage (88 percent) and the longest pollen tubes (mean length 556μ) of any of the concentrations of this chemical used. Higher concentrations, like 100 ppm, were toxic, and they produced minimum germination percentages (69 percent) and shorter pollen tubes (323.5μ).

4. *Potassium nitrate.* Potassium nitrate produced many abnormalities. The most favorable concentration of this chemical for pollen germination was 60 ppm. This concentration gave 74 percent germination with pollen tubes of 444μ mean length. At 20 ppm concentration of potassium nitrate, 4 percent of the pollen tubes were branched at their tips. However, rate of branching declined as the chemical concentration increased. Many of the branched pollen tubes had vesicles at the tip of one of their branches.

Morphology of pollen tubes: Pollen tubes in different media were studied for an understanding of the morphological variations,

TABLE 2. Percentage germination and mean tube length of *Torenia asiatica* pollen germinated in 15 percent sucrose solution mixed with different chemicals.

Chemical	Concentration of chemical (ppm)	Percentage germination	Mean tube length in microns after 2 hrs.
Boric acid	20	89	755.0
(H_3BO_3)	40	86	587.5
	60	78	492.7
	80	75	429.5
	100	70	403.0
Calcium nitrate	20	66	418.0
$(CA[NO_3]_2.4H_2O)$	40	68	484.0
	60	80	591.0
	80	83	707.5
	100	91	813.5
Magnesium sulphate	20	86	439.5
$(MgSO_4 \ . \ 7 \ H_2O)$	40	88	556.0
	60	75	499.5
	80	75	379.5
	100	69	323.5
Potassium nitrate	20	70	346.0
(KNO_3)	40	72	354.5
	60	74	444.0
	80	66	302.0
	100	62	240.0

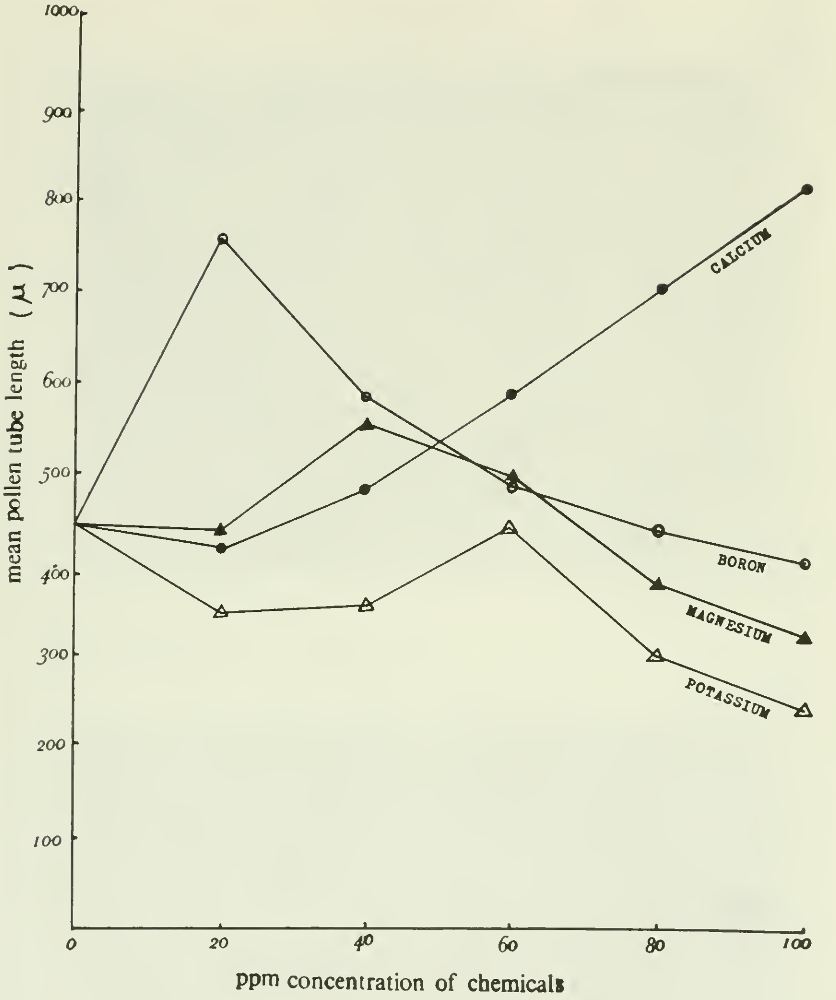

Fig. 2. Graph to show comparative effects of different chemicals on the mean pollen tube length for *Torenia asiatica*.

if any, shown by the growing tubes. Although pollen grains of *T. asiatica* consist of three germinal pores, only a single tube resulted. The protoplasm migrated into this tube. In the control sucrose medium and in the four chemicals, the pollen tube developed in either a coiled or a zig-zag manner (Fig. 4c). A combination of these growth characteristics also occurred in the same tube. Occasionally, tubes showed callose plugs (Fig. 4a). After its initiation into potassium nitrate, a pollen tube developed normally for a time and then branched. One of these branches had a vesicle at its tip.

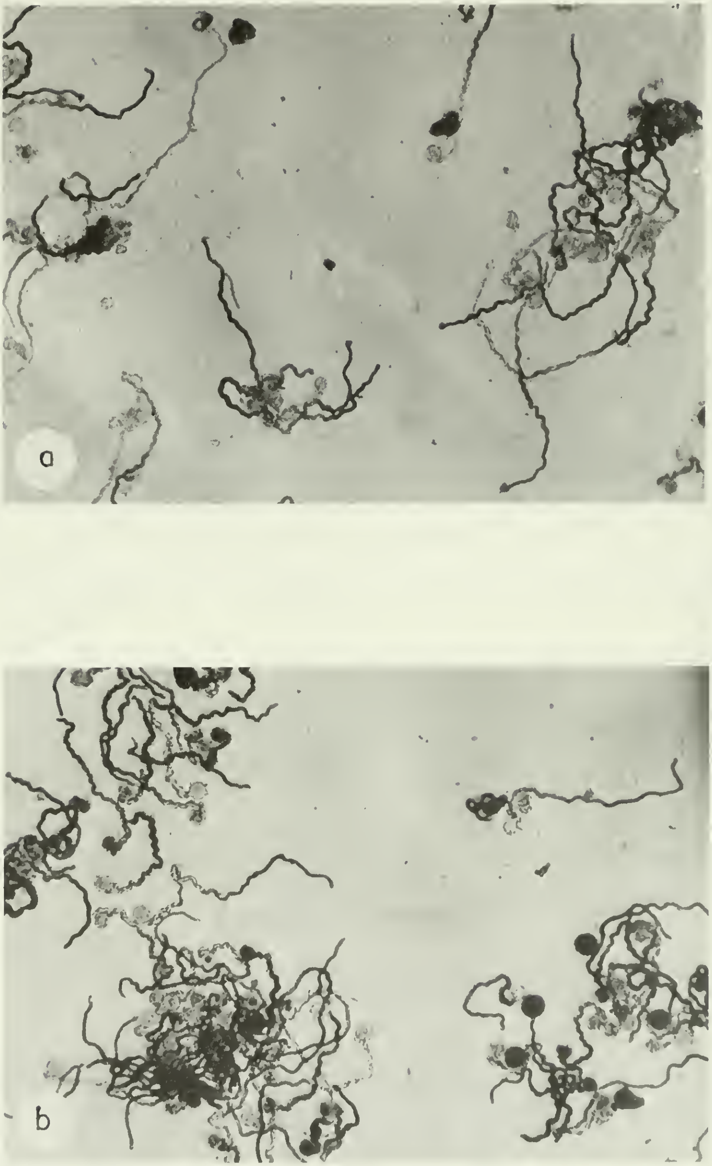

Fig. 3. *Torenia asiatica*: (a) germination of pollen grains in calcium nitrate-sucrose medium (60 X); (b) germinating grains in boric acid-sucrose medium (60 X).

Discussion

Johri and Vasil (1961) noted that germinating media give varied results when used with pollen grains of different species. This study revealed that sucrose is the best sugar for germination of the pollen grains of *T. asiatica* and that maximum germination occurs in a 15 percent concentration. This conclusion is in accord with that of Goss (1962) who attained maximum germination in 10-15 percent sucrose medium for *Ornithogalum caudatum* pollen and Nair and Deshpande (1968) for pollen of *Luffa cylindrica.* Sucrose medium was also used for germination of pollen grains of various plants by Vasil (1961), Biswas and Datta (1964), Cook and Walden (1965), Premnath and Purohit (1969), and others. Linskens (1964) suggested that sucrose was better than any other organic compound as a medium for pollen germination. However, Premnath and Purohit (1969) found no pollen germination in sucrose concentrations below 40 percent for spinach beet pollen they studied. Biswas and Datta (1964) and Datta and Neogy (1965) observed maximum germination in 4 percent sucrose solution, while Singh (1957) reached a maximum in 10 percent sucrose solution, for *Crotalaria* pollen. However, as stated above, we determined that a 15 percent concentration of sucrose was the most suitable for pollen germination of *T. asiatica.* We consider this to be a specific difference depending upon the osmotic pressure of the cell which again may be dependent upon the locality.

The role of boron on germinating pollen was described by Stanley and Loewus (1964), Vasil (1964), and others as associated with sugar metabolism, as an inducer of oxygen absorption, and as a requirement for pectin synthesis. The effects of various compounds of boron on the germinating pollen have been reported by Stanley and Lichtenberg (1963). In the present experiments a lower concentration of boron (20 ppm) promoted a high percentage germination and longer pollen tubes. In higher concentrations of this chemical, germination was retarded. Higher germination percentage and longer tubes with boron have been reported by Thompson and Batjar (1950), Young (1958), and Bamzai and Randhawa (1969). Young (1958) found that effective germination was possible when pollen grains were allowed to germinate in boric acid concentrations of up to 50 ppm. However, experiments of Bamzai and Randhawa (1969) showed that higher percentage germination and tube length could be achieved with concentrations of up to 20 ppm. The results of the present investigation are in general agreement with those of Bamzai and Randhawa (1969) regarding the effect of boric acid. Therefore, we agree that the reduction in the germination percentages and a lower mean tube length in higher concentrations of boric acid may be caused by the toxic effect of this chemical in these higher concentrations.

Cook and Walden (1965) reported that the presence of a calcium ion is required for pollen germination. In the present work germination increased with an increase in concentration of calcium

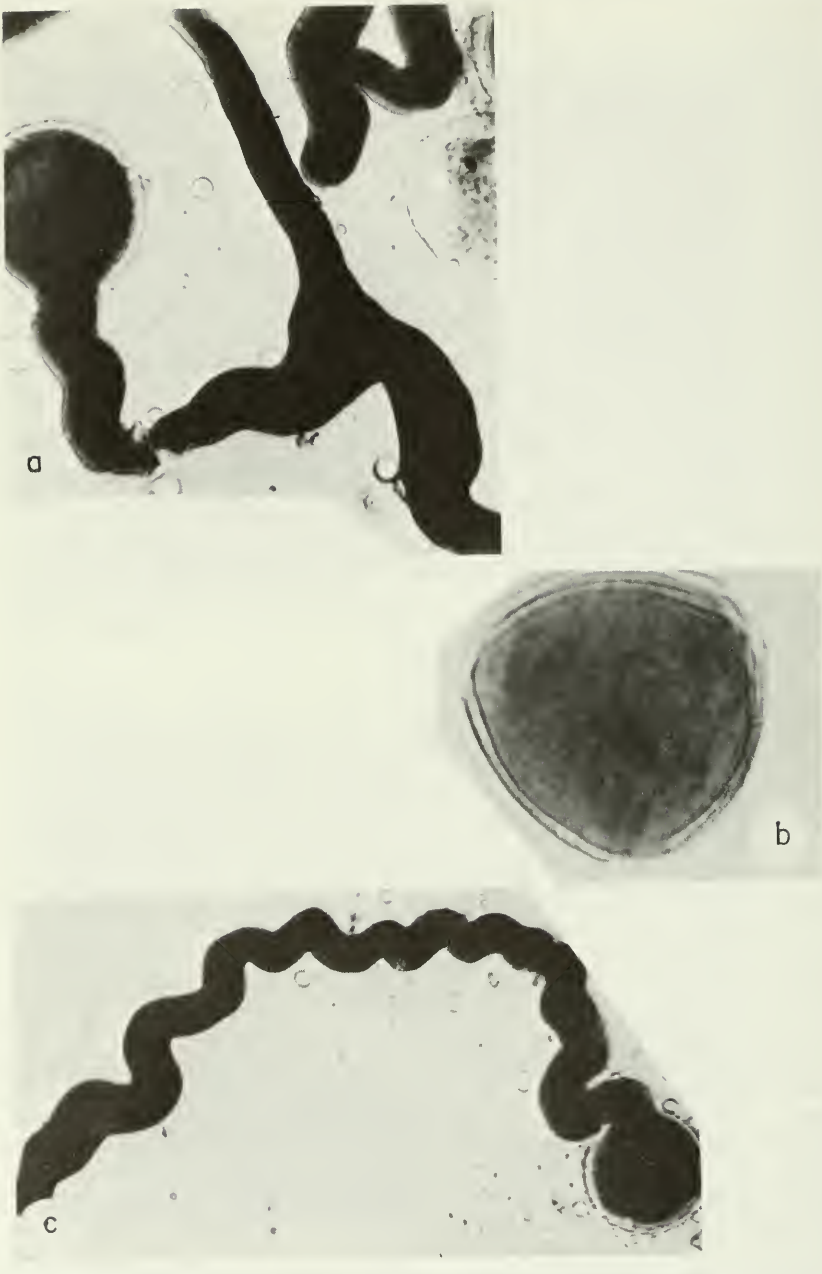

Fig. 4. *Torenia asiatica*: (a) branched pollen tube, showing callose plugs (150 X); (b) pollen grain of *Torenia asiatica*, showing tricolpate condition (250 X); (c) germinating pollen tube, showing the zig-zag nature (150 X).

nitrate (Table 2). Thus, in 100 ppm of calcium nitrate maximum germination was noted. The present experiments were intended to demonstrate only the effect of the known range of concentrations of different chemicals on pollen germination. Whether or not a higher concentration of calcium nitrate than 100 ppm would have enhanced pollen germination further was not within the scope of the present study; nevertheless, the study does provide a basis for further research. Cook and Walden (1967) also noted that concentrations of calcium higher than 100 ppm produced long pollen tubes and that germination does not occur in the absence of this chemical. Importance of calcium to the germinating pollen was given in detail by Faull (1955), Knawck and Brewbaker (1961), and Linskens (1964). Pfahler (1968) noted increased germination when calcium was added to pollen of some hybrid maize. As in experiments of Cook and Walden (1967), so in the present experiment: a relatively higher concentration of calcium gave better results. Most of the resulting pollen tubes did not rupture. This decreased incidence of rupture among the pollen tubes has been attributed to the capacity of calcium to give more rigidity to the cell wall (Brewbaker and Knawck, 1964).

Compared with the control medium, potassium and magnesium do not improve germination percentage or mean tube length of pollen grains. However, potassium nitrate induced certain abnormalities, such as branched pollen tubes and vesicles.

In the pollen tubes that grew in a coiled or zig-zag manner, the wall was not straight as in many other plants. Such coiled or zigzag tubes have been observed by Loo and Hwang (1944) and Vasil (1960). Loo and Hwang (1944) observed that when pollen grains of *Antirrhinum majus*, *Thea sinensis*, *Brassica juncea*, *Triticum vulgare*, and *Hordeum vulgare* were germinated in the presence of colchicine, the resultant tubes became either zig-zag or coiled. Loo and Hwang (1944) considered such an abnormality to be the direct effect of the treatment of colchicine, not of a change in the osmotic pressure, as had been suggested by earlier workers. Abnormal tubes were recorded by Brink (1924) and Vasil (1960) also. Vasil (1960) found in certain cucurbitas abnormal pollen tubes having branched or swollen tips. Vasil attributed these modifications to hypo- or hypernutrition, high humidity, high temperature and/or stale pollen. However, Nair and Deshpande (1968), working on *Luffa cylindrica* pollen, noted that apparently there was no significant correlation between germination results and meteorological data. Because the coiled tubes are found in both the control and the chemically induced pollen, there might be some other hitherto unexplored factor that regulates the morphology of the developing tube of the pollen of *T. asiatica*.

Branched pollen tubes having a vesicle on one of their tips were also found by Loo and Hwang (1944), Vasil (1960), Nair *et al.* (1964), and Nair and Deshpande (1968). Loo and Hwang suggested that these swellings were the result of germination in a medium containing indole-3-acetic acid and that the abnormality was the direct effect of this chemical. The branching of the tube and the subsequent swelling of one of these branches in the present experiments is observed only when the pollen grains are germinated in a potassium nitrate-sucrose medium. It is noteworthy that in lower concentrations of the above mixture there was a lower percentage of branching than in higher concentrations. Whether the abnormalities are a direct result of the addition of KNO_3 or an expression of certain other physiological phenomena in the plant cannot be ascertained until more pollen grains belonging to different taxa are studied responding to KNO_3 in the germinating medium.

Acknowledgment

The authors are grateful to Dr. D. Kumar, Department of Botany, University of Dar-es-Salaam, Tanzania, for critically reviewing the manuscript.

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AN UNUSUAL SPIDER BITE

Dorald M. Allred[1]

Abstract.— The bite of a male blackwidow spider on a Utah woman is described.

On 24 October 1973 a woman in Provo, Utah was bitten by a spider which I subsequently identified as a subadult blackwidow, *Latrodectus hesperus* Chamberlin and Ivie. As she arose in the morning she slipped her bare feet into a pair of solid-toe loafers, and walked into the kitchen. Her right foot immediately began to hurt, and as she removed her shoe she noted a crushed spider on her foot. Pain was localized in her big toe where she noticed a red spot and puncture marks on the top about one-half inch from the base.

The pain soon extended to her thigh where it remained for about the first hour. During this time her leg ached and throbbed, occasionally with sharp pains. After an hour the pain in her thigh subsided, but remained prominent in her foot. The pain in her foot gradually subsided until the third day after the bite when it completely disappeared. She did not consciously detect other symptoms of arachnidism (rigid abdomen, tightness in the chest, difficulty in breathing, nausea, and sweating, etc.), most likely because she was in her fifth month of pregnancy and was experiencing "morning sickness."

The site of the bite remained red during the whole period of pain, although no scab or necrosis occurred. One month after the bite the site remained red, although no pain or tenderness was present.

The bedroom of the victim was in a semi-basement apartment. It had two windows, one of which had been open for several days prior to the biting incident. The spider likely moved into the apartment through the open window with the advent of cold weather.

According to Dr. Willis J. Gertsch, bites by male blackwidows are unusual, and such incidences apparently have not been previously recorded. The male likely has venom similar to that of the female, but is not inclined to bite. The entrapment of the spider in the shoe was undoubtedly the stimulus that resulted in the bite.

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[1] Department of Zoology, Brigham Young University, Provo, Utah 84602.

GREAT BASIN NATURALIST

Special Notice

Commencing with volume 35 (March 1975) The Great Basin Naturalist will be combined with the Brigham Young University Science Bulletin, Biological Series under the title of The Great Basin Naturalist. The format will be changed from the present 6x9 inch single column page to a 7x10 inch double column page. The journal will continue to be published quarterly, but the number of pages per volume will increase to approximately 500. Manuscripts up to 100 printed pages (about 200 manuscript pages) in length will be acceptable. Publication and reprint charges will be adjusted to the new format, but will not be significantly different from that indicated below. The subscription rate will be increased to $9.00 per year (outside the United States, $10.00).

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THE SPECIES OF *CALINEURIA* AND *DORONEURIA* (PLECOPTERA: PERLIDAE)[1]

Bill P. Stark[2] and Arden R. Gaufin[2]

Abstract.— The genus *Doroneuria* is reviewed, and characters necessary for recognition of its two included species are figured. *Doroneuria baumanni*, sp. nov., is described for the male, female, and nymph, and a male holotype and female allotype are designated. *Calineuria* is removed from the synonymy of *Doroneuria*, and the genus is characterized in detail. Distributional data are presented for species in both genera.

Doroneuria was proposed as a subgenus of *Acroneuria* by Needham and Claassen (1922) with the newly described *theodora* as the type species. This subgenus was omitted from the systematic list in the Needham and Claassen monograph (1925). Ricker (1954), apparently unaware of the former paper, proposed a new subgenus, *Calineuria*, for the species *Acroneuria californica* (Banks) and *A. theodora* Needham and Claassen with *californica* (Banks) as type species. Illies (1966) gave *Doroneuria* generic status and considered *Calineuria* a synonym.

A detailed study of these species has indicated clearly that two genera are involved and has led to the discovery of a new species of *Doroneuria*.

Calineuria Ricker

Acroneuria (*Calineuria*) Ricker (1954:39). Type species *Perla californica* Banks.
Doroneuria: Illies (1966:330). In part.
Doroneuria: Zwick (1973:274). In part.

The genus *Calineuria* may be characterized in the adult male by (1) a longitudinally rectangular hammer on abdominal sternum 9, (2) a median, heavily sclerotized tergite on tergum 10 (Fig. 1), and (3) the aedeagus (Figs. 1, 2) bearing on the basal portion 4 prominent patches of long golden-brown spinules (2 lateral, 1 ventral, and 1 apical). Adult females are characterized by (1) the unproduced, shallowly notched posterior margin of sternum 8 with an unsclerotized, U-shaped border around the notch (Fig. 3) and (2) a membranous vagina that extends forward to near the anterior margin of sternum 7 and is not lined internally by spinulae.

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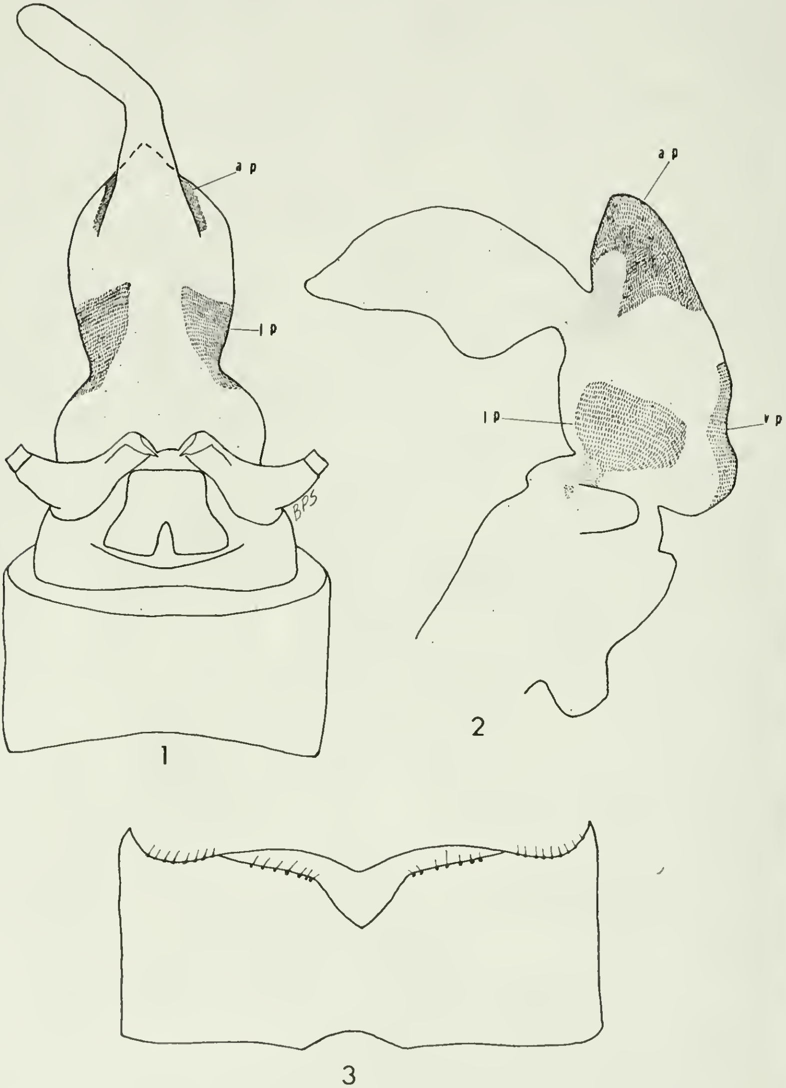
[1] Study supported by EPA Contract, Univ. of Montana #881 1
[2] Biology Dept., Univ. of Utah, Salt Lake City, Utah 84112

Mature nymphs are characterized by (1) an incomplete, irregularly spaced row of spines across the occiput, (2) numerous prominent spines on each abdominal tergum in addition to the posterior fringe, (3) a dense fringe of long silky hairs along the mesal surface of the cerci originating in the whorl of spines on each cercal segment (Fig. 14), and (4) usually a complete posterior fringe of spines across



Figs. 1-3. *Calineuria californica*: 1, Male terminalia with aedeagus extruded, dorsal; 2, Aedeagus, lateral; 3. Female abdominal sternum 8. (ap=apical patch, lp=lateral patch, vp=ventral patch).

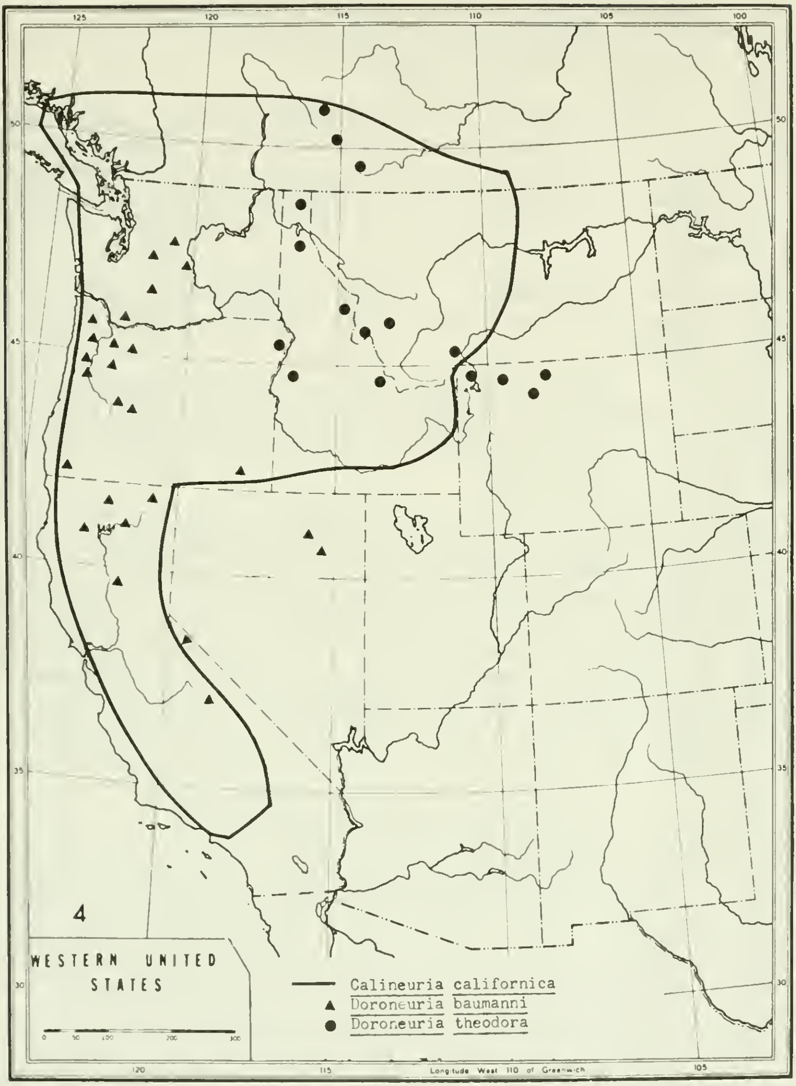


Fig. 4. Distribution map of *C. californica*, *D. baumanni*, and *D. theodora*.

abdominal sternum 7 (Fig. 14). This monotypic genus is known only from western North America.

Calineuria californica (Banks)

Perla californica Banks (1905:87). Holotype ♀; Claremont, California. (MCZ #11318).

Perla concolor Banks (1908:255). Syn. Needham and Claassen, 1922.
Acroneuria californica: Needham and Claassen (1925:192).
Acroneuria (*Calineuria*) *californica*: Ricker (1954:39).
Doroneuria californica: Illies (1966:330).

Male.— Macropterous. Length of forewings 19-21 mm; length of body 18-20 mm. General color yellow brown. Wings hyaline, veins brown. Paraprocts sclerotized, fingerlike, with a small terminal acute spine. Aedeagus (Figs. 1, 2) as described above. Occasional specimens with ventral patch of aedeagal spinules variously reduced in size.

Female.— Macropterous. Length of forewings 24-27 mm; length of body 22-23 mm. Subgenital plate (Fig. 3) and vagina as described above.

Nymph.— Length of mature male 17-18 mm; mature female 22-23 mm. General color yellow and brown. Head with distinctive large yellow spot covering ocellar area. Abdominal sterna and cerci (Fig. 14) as described above.

Calineuria californica is a species of the Pacific coast and northern Rocky Mountains (Fig. 4). Previous studies (Gaufin et al., 1966; Baumann, 1973; Stark et al., 1973) have recorded the species from Colorado and Utah, but an examination of all this material in the University of Utah collection previously determined as *californica* has shown these records are of a presently undetermined species of *Acroneuria* (possibly *depressa* Needham and Claassen).

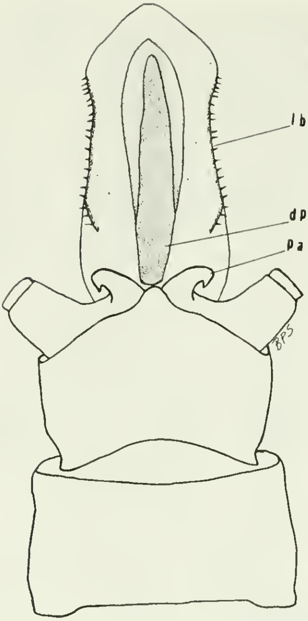
Specimens examined in this study: CALIFORNIA: *Alameda Co.*, Oakland, 15-V-10, E. C. Van Dyke, 1♀ (CAS); Oakland, 9-V-09, E. C. Van Dyke, 1♂ (CAS). *Alpine Co.*, Markleeville, 7-VII-49, Allen, 1♀ (CAS). *Butte Co.*, Big Chico Creek, 18-XI-71, M. Kainu, nymphs (UU). *Eldorado Co.*, 3 mi S Camino, 26-VI-48, MacNeil, 1♂ (CAS). *Humboldt Co.*, Prairie Creek, 9-VI-36, E. C. Van Dyke, 1♂ 1♀ (CAS); North Fk. Yager Creek, 8-VIII-66, R. E. Leech, 1♀ (CAS). *Lake Co.*, Anderson Springs, 20-III-55, Leuschner, 1♂ (INHS); 6 mi S Middletown, 12-V-26, 4♂ 5♀ (CAS). *Los Angeles Co.*, Arroyo Seco Canyon, 23-VI-18, E. C. Van Dyke, 1♀ (CAS); East Fk. San Gabriel River, 16-VI-59, nymphs (UU). *Marin Co.*, Muir Woods, 25-IV-64, D. G. Denning, 1♂ (ROM); Cascade Creek, 13-V-52, R. E. Leech, 1♂ (CAS); Bear Valley, 25-V-19, 1♂ (CAS); Ross, 25-IV-18, Van Duzee, 1♀ (CAS); Lagunitas, 14-IV-08, Van Duzee, 1♀ (CAS); Lagunitas, 30-V-38, Nast, 4♀ (CAS). *Mendocino Co.*, Camptche, 7-IV-36, E. C. Van Dyke, 1♂ (CAS); Yorkville, 30-IV-24, Van Duzee, 1♂ (CAS). *Mono Co.*, Convict Creek, VI-63, 1♂ (UU); Sonora Bridge, 28-VII-62, Rentz and MacNeil, 1♂ (CAS). *Placer Co.*, Truckee River, 1-VIII-68, R. W. Baumann, 6♂ 2♀ (USNM). *Plumas Co.*, Mohawk, 12-VII-57, Rentz, 1♂ (CAS); Quincy, 26-VI-73, D. R. Givens and S. D. Smith, 1♂ (CWSC). *San Bernardino Co.*, Lytle Creek, 7-VI-28, E. C. Van Dyke, 7♂ 4♀ (CAS). *Santa Clara Co.*, San Jose, 13-X-81, Van Duzee, 1♀ (CAS); Alum Rock Park, 29-VI-55, Ribble, 1♂ (KAN); 29-VI-69, Cobb, 1♂ (USNM). *Shasta Co.*, 26-VI-21, J. A. Kuscho, 1♀ (CAS); Burney Falls, 29-VI-47, H. P. Chandler, 1♀ (CAS); Castle Crags St. Pk., 20-VI-64, D. G. Denning, 1♂ (ROM). *Siskiyou Co.*, Sacramento River, 8-VII-53, H. P. Chandler, 3♂ (CAS). *Sonoma Co.*, Guerneville, 31-V-36, E. C. Van Dyke, 1♂ (CAS); 19-VI-10, J. Kuscho, 1♂ 1♀ (CAS). *Trinity Co.*, Trinity Center, 6-VI-64, J. Pinto, 2♂ 4♀ (UCR); Coffee Creek, 7-VI-34, E. C. Van Dyke, 1♂ 1♀ (CAS); Butter Creek, 21-VII-68, R. E. Leech, 1♀ (CAS). *Tuolume Co.*, Dana Fk. Tuolume River, 15-VII-36, Rayner 1♂ (INHS). IDAHO: *Boise Co.*, Boise River, 12-VI-31, Ivie, nymphs (UU). *Boundary Co.*, Moyie River, 26-III-65, A. V. Nebeker, nymphs (UU). *Kootenai Co.*, Hayden Creek, 7-VI-69, R. W. Baumann, 2♂

2♀ (USNM). *Lemhi Co.*, Salmon River, 28-VI-73, M. and E. Cather, 2♂ 2♀ (UU); Salmon River, 6-VII-64, A. R. Gaufin, 1♂ (UU); Salmon River, 11-VII-67, G. F. Edmunds, 1♂ 4♀ (USNM). *Shoshone Co.*, Coeur d'Alene River, 11-VI-69, A. R. Gaufin, 2♂ 2♀ (USNM). MONTANA: *Camas Co.*, Glacier Park, 7-VII-67, A. R. Gaufin, 1♂ (UU). *Flathead Co.*, Swan River, 29-VI-65, A. V. Nebeker and R. K. Allen, 41♂ 13♀ (UU) (USNM); Swan River, 1-VII-67, P. Milam, 6♂ 4♀ (UU); McGregor Creek, 1-VII-67, A. R. Gaufin, 1♂ 3♀ (UU); Camas Creek, 7-VII-67, A. R. Gaufin, 1♂ 1♀ (UU). *Lake Co.*, Swan River, 23-VI-67, P. Milam, 11♂ 6♀ (UU); Swan River, 10-VI-67, A. R. Gaufin, 9♂ 2♀ (UU). *Lincoln Co.*, Yaak River, 21-VI-69, R. W. Baumann, 7♂ (UU). *Missoula Co.*, Blackfoot River, 28-VI-67, A. R. Gaufin, 10♂ 7♀ (UU). *Pondera Co.*, Dupuyer, 24-VI-65, A. V. Nebeker, 1♂ (UU). *Ravalli Co.*, Bitterroot River, 28-VII-65, J. R. Grierson, 2♂ (UU). OREGON: *Benton Co.*, Corvallis, 22-V-34, R. E. Dimick, 1♂ (CAS); Corvallis, 8-V-34, Bali, 1♂ (INHS); Alsea, 27-V-34, J. Schuh, 2♂ 7♀ (CAS) (INHS). *Clatsop Co.*, Cannon Beach, 15-VI-27, E. C. Van Dyke, 1♂ (CAS); Big Creek, 28-V-49, S. G. Jewett, Jr., 5♂ 3♀ (CAS); Nehalem River, 11-VII-64, S. G. Jewett, Jr., 5♂ 1♀ (SGJ). *Columbia Co.*, Clatskanie, 19-V-36, J. Schuh, 1♂ (CAS); Scappoose, 20-VI-36, Rieder, 3♂ 3♀ (INHS). *Jackson Co.*, Rogue River, 17-VI-49, S. G. Jewett, Jr., 1♂ (CAS). *Lake Co.*, Paisley, 28-VI-51, B. Malkin, 2♂ 1♀ (CAS) (FMNH). *Lane Co.*, Bob Creek, 13-VIII-32, R. E. Dimick, 1♂ (CAS). *Lincoln Co.*, Siletz River, 24-V-34, R. E. Dimick, 3♂ (CAS). *Linn Co.*, Santiam, 26-VII-60, D. G. Denning, 1♀ (USNM). *Marion Co.*, Breitenbush, 11-VII-68, E. Evans, 1♂ (USNM). *Multnomah Co.*, Eagle Creek, 19-V-40, S. G. Jewett, Jr., 1♂ (CAS). *Washington Co.*, Gales Creek, 14-V-47, S. G. Jewett, Jr., 1♂ (CAS). WASHINGTON: *Clallam Co.*, Crescent Lake, 21-VI-40, S. G. Jewett, Jr., 1♂ (CAS); Forks, 2-VII-20, Van Duzee, 1♂ (CAS); Bogachiel River, 18-VI-67, R. W. Baumann, 2♂ 4♀ (USNM); Soleduck River, 23-VII-60, D. G. Denning, 1♀ (USNM). *Grays Harbor Co.*, East Fk. Humptulips River, 2-IX-58, nymphs (UU); Donkey Creek, 18-VI-67, R. W. Baumann, nymphs (USNM). *Jefferson Co.*, Hoh River, 3-IX-58, nymphs (UU). *King Co.*, Rex River, 20-VII-72, C. Baker, 1♂ (UU); Rex River, 5-X-73, A. R. Gaufin, nymphs (UU). *Kittitas Co.*, Liberty, 27-VII-49, White, 1♀ (KAN). *Spokane Co.*, Little Spokane River, 13-VI-55, nymphs (UU). *Thurston Co.*, Deschutes River, 15-VI-67, R. W. Baumann, 10♂ 5♀ (USNM). *Yakima Co.*, Toppenish, 9-VII-35, Beamer, 2♀ (KAN); Naches River, 5-IX-58, nymphs (UU).

Doroneuria Needham and Claassen

Acroneuria (*Doroneuria*) Needham and Claassen (1922:249). Type species *Acroneuria theodora* Needham and Claassen by original designation.
Acroneuria (*Calineuria*) Ricker (1954:39). In part.
Doroneuria: Illies (1966:330). In part.
Doroneuria: Zwick (1973:274). In part.

The genus *Doroneuria* may be characterized in the adult male by (1) a longitudinally rectangular hammer on abdominal sternum 9 (Fig. 11), (2) tergum 10 without a median tergite, and (3) the aedeagus bearing a spatulate sclerotized plate dorsally and two elongate, narrow, sclerotized lateral bars (Figs. 5, 6). Adult females are characterized by (1) the almost straight (sometimes slightly produced mesally) posterior margin of sternum 8 (Fig. 7) and (2) a membranous vagina that extends forward to the posterior margin of sternum 7 and is lined with numerous small golden brown spinulae (Figs. 7, 8). Mature nymphs are characterized by (1) an incomplete, irregularly spaced row of spines across the occiput (Fig. 12), (2) numerous prominent spines on each abdominal tergum in addition to the posterior fringe, (3) a dense fringe of long silky hairs along the mesal surface of the cerci (Fig. 13), and (4) an



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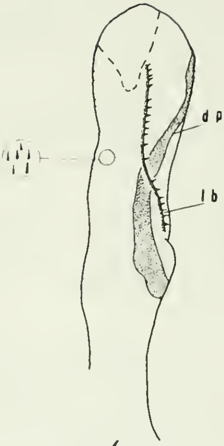

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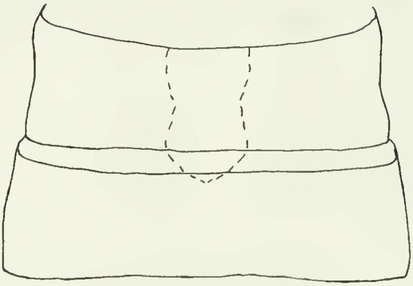

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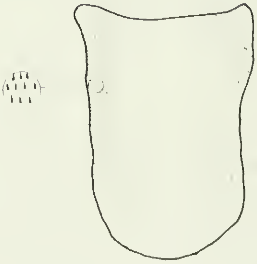

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Figs. 5-8. *Doroneuria baumanni*: 5, Male terminalia with aedeagus extruded, dorsal; 6, Aedeagus, lateral; 7, Female abdominal sterna 7 and 8, vagina shown in outline; 8, Vagina. (pa=paraproct, dp=dorsal plate, lb=lateral bar).

incomplete posterior fringe of spines on abdominal sternum 7 (Fig. 13). The genus is presently known only from western North America.

Doroneuria baumanni, sp. nov.

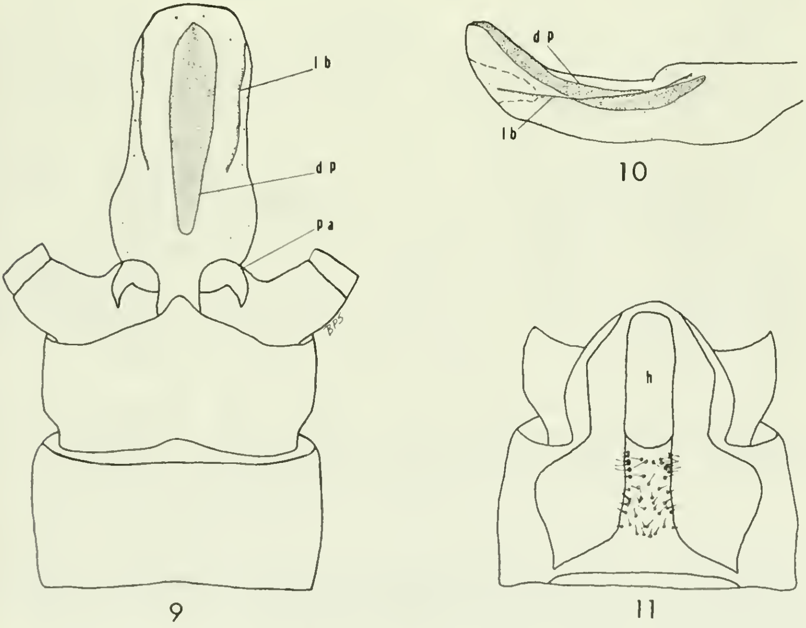
Acroneuria theodora: Frison (1942:284-285). In part.
Acroneuria (*Calineuria*) *theodora*: Jewett (1959:89). In part.
Doroneuria theodora: Illies (1966:331). In part.

Male.— Brachypterous to macropterous. Length of forewings 18-27 mm; length of body 22-25 mm. General color dark brown. Wings hyaline, veins black. Paraprocts similar to *D. theodora*, sclerotized and fingerlike. Aedeagus (Figs. 5, 6) with 12-22 prominent spines on the lateral sclerotized bars; ventral and lateral surfaces of aedeagus with numerous minute spinulae.

Female.— Macropterous. Length of forewings 31-33 mm; length of body 27-30 mm. Subgenital plate (Fig. 7) unproduced. Vagina (Figs. 7, 8) lined with minute golden brown spinulae.

Nymph.— Length of mature male 20-22 mm; mature female 31-34 mm. Similar to *D. theodora* in coloration and general morphology. Occiput with a transverse row of long silky hairs between the postfrontal suture and the row of spines. Frons with a single long seta near each antennal base. Dorsum of thorax and abdomen with a median longitudinal row of long silky hairs.

Doroneuria baumanni is a species of the Cascade and Sierra Nevada Mountains of western North America (Fig. 4) with relict populations in Nevada and southeastern Oregon. The lack of records for *Doroneuria* in Ricker's (1943) study of southwestern British Columbia indicates that the species survived the Pleistocene glacia-



Figs. 9-11. *Doroneuria theodora*: 9, Male terminalia with aedeagus extruded, dorsal; 10, Aedeagus, lateral; 11, Male abdominal sterna 9 and 10. (h = hammer, pa = paraproct, dp = dorsal plate, lb = lateral bar)

tions in a coastal refuge and has been unable to recolonize severely glaciated areas.

Types.— Male holotype, female allotype, and 5 male and 1 female paratypes from Burney Falls State Park, Shasta Co., California, 8-X-72, D. G. Denning. Holotype male No. 73022 and allotype female deposited at the United States National Museum, Washington, D.C. Additional paratypes as follows: CALIFORNIA: *Siskiyou Co.*, Tate Creek, 8-IX-54, H. P. Chandler, 2♂ (SGJ) (CAS); *Trinity Co.*, Grizzly Meadows, 10-15-IX-64, Buxton and Gurney, 3♂ 1♀ (USNM); 10 mi W Thompson Peak, 16-IX-64, Buxton, 2♀ (USNM). OREGON: *Benton Co.*, Marys Peak, 3-VI-68, T. Yamamoto and S. D. Smith, 1♀ (ROM). *Curry Co.*, Fork Creek, 19-VII-67, E. Evans, 1♂ (USNM). *Harney Co.*, Fish Creek, Steens Mts., 20-VII-69, S. G. Jewett, Jr., 2♂ (USNM). *Lane Co.*, McKenzie Bridge, 21-IX-34, R. E. Dimick, 3♂ (INHS) (UU); McKenzie River, 21-IX-34, R. E. Dimick, 2♂ (OSU). *Lincoln Co.*, Tidewater, 6-VI-68, T. Yamamoto and S. D. Smith, 1♂ (ROM). *Linn Co.*, Marion Forks, 28-VIII-68, Goeden and Gurney, 1♀ (USNM). *Tillamook Co.*, Neskowin, 11-VII-63, G. Wiggins, 1♂ (ROM). *Yamhill Co.*, McMinnville, 4-V-47, K. M. Fender, 1♂ (CAS). WASHINGTON: Anderson Creek, Stevens Pass, 29-IX-59, 1♂ (INHS). *Chelan Co.*, Icicle Creek 9-X-71, L. Whyte, 1♂ (CWSC). *Clark Co.*, Lewis River, 15-IX-57, H. Hacker, 1♂ (USNM).

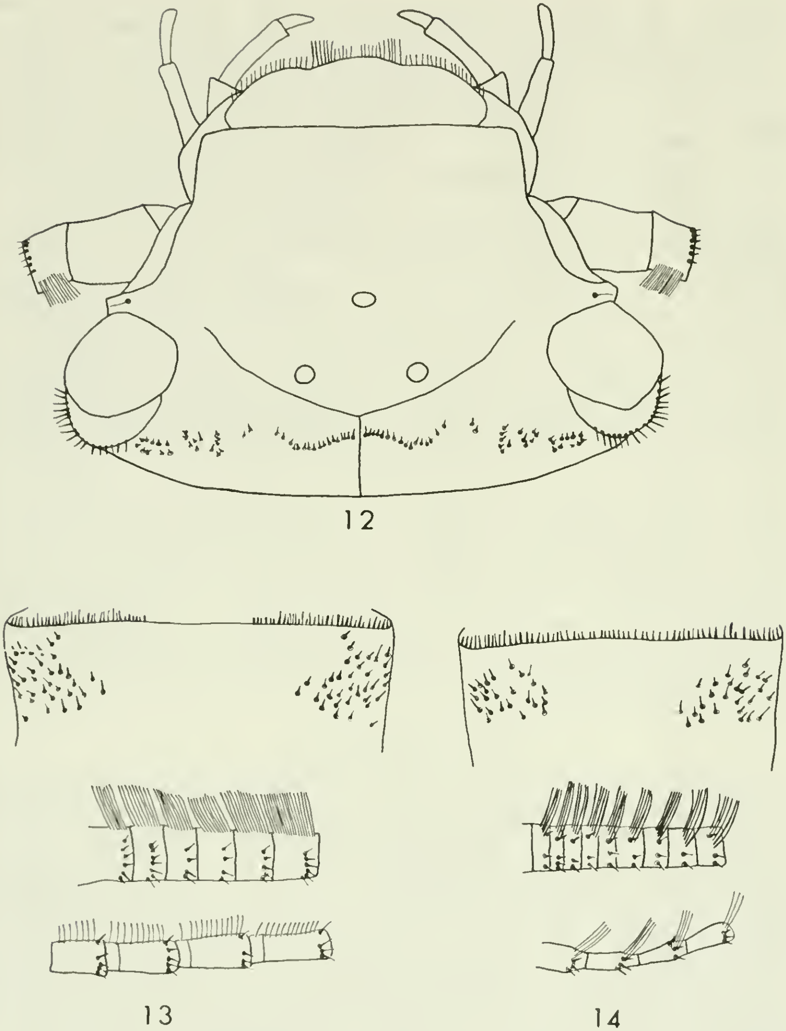
Additional specimens examined: CALIFORNIA: *Butte Co.*, Big Chico Creek, 26-XII-72, M. Kainu, nymphs (UU). *Fresno Co.*, South Fk. King River, 6-VII-10, E. C. Van Dyke, 1♂ (CAS). *Modoc Co.*, 20-VII-22, Lindsey, 1♂ (INHS). *Mono Co.*, Mono Lake, 31-VII-40, Lipovsky, 1♂ (KAN). *Tuolume Co.*, Kennedy Creek, 18-VII-73, D. R. Givens and S. D. Smith, nymphs (CWSC). NEVADA: *Elko Co.*, near Midas, 20-IX-57, G. F. Edmunds and R. K. Allen, nymphs (UU); Franklin River, 19-IX-57, G. F. Edmunds and R. K. Allen, nymphs (UU). OREGON: *Benton Co.*, Philomath, 4-VII-63, G. Wiggins, 1♀ (ROM); Corvallis, 27-VII-62, G. C. Eickwort, 1♀ (MSU). *Hood River Co.*, Mt. Hood, 24-VI-25, E. C. Van Dyke, 1♂ (CAS). *Lane Co.*, McKenzie Bridge, 21-IX-34, R. E. Dimick, 1♂ 1♀ (INHS) (CAS); South Fk. McKenzie River, 4-IX-32, R. E. Dimick, 1♂ (INHS); McKenzie River, 21-IX-34, R. E. Dimick, 2♂ 2♀ (INHS). *Multnomah Co.*, Wahkeenah Falls, 15-VII-63, G. Wiggins, 1♀ 2 nymphs (ROM). WASHINGTON: *King Co.*, Rex River 5-X-73, A. R. Gaufin, nymphs (UU). *Lewis Co.*, Nickle Creek, 1-IX-58, nymphs (UU). *Pierce Co.*, Slippery Creek, 5-IX-58, nymphs (UU). *Yakima Co.*, Chapparal Creek, 2-IX-54, B. Malkin, 1♂ (CAS).

This species is named for Dr. Richard W. Baumann of the Smithsonian Institution who has assisted in obtaining material and by making suggestions for this and other studies in progress.

Doroneuria theodora (Needham and Claassen)

Acroneuria (*Doroneuria*) *theodora* Needham and Claassen (1922:254). Holotype ♀, allotype ♂; Yellowstone Nat'l Pk., Wyoming. (Cornell Univ. #1180).
Acroneuria theodora: Frison (1942:284-285). In part.
Acroneuria (*Calineuria*) *theodora*: Ricker (1954:39).
Doroneuria theodora: Illies (1966:331). In part.

Male.— Brachypterous to macropterous. Length of forewings 7-17 mm; length of body 19-22 mm. Similar to *D. baumanni* in



Figs. 12-14. *Calineuria* and *Doroneuria* nymphal structures: 12, *Doroneuria*, dorsum of head; 13, *Doroneuria* abdominal sternum 7 (mature ♂ nymph) and cercal segments basal and apical; 14, *Calineuria* abdominal sternum 7 (mature ♂ nymph) and cercal segments basal and apical.

coloration and general features. Aedeagus (Figs. 9, 10) without spines on the lateral sclerotized bars; ventral and lateral surfaces of aedeagus with numerous minute spinulae.

Female.— Brachypterous to macropterous. Length of forewings 15-25 mm; length of body 29-31 mm. Subgenital plate and vagina similar to *D. baumanni*.

Nymph.— Length of mature male 20-22 mm; mature female 31-34 mm. Presently indistinguishable from *D. baumanni*.

Doroneuria theodora is a species of the northern Rocky Mountains (Fig. 4). Records are presently from north of the Wind River range in Wyoming into southern Canada and west through Idaho to eastern Oregon. Published records of *theodora* from Utah and Colorado are based on the same species of *Acroneuria* nymph discussed under *Calineuria californica* above and should be disregarded.

Specimens examined in addition to the holotype and allotype: ALBERTA: Banff Nat'l Pk., above Bow Falls, 19-VII-69, C. M. Yarmoloy, 1♂ (USNM); Spray River, Banff Nat'l Pk., 15-VI-69, C. M. Yarmoloy, nymphs (UU); Crows Nest River, Crows Nest, 13-IX-73, R. Beck, nymphs (UU). IDAHO: *Adams Co.*, Little Goose Creek, 21-VI-64, A. R. Gaufin, nymphs (UU). *Bonneville Co.*, West Fk. Pine Creek, 21-VI-64, J. W. Richardson and S. L. Jensen, nymphs (UU). *Boundary Co.*, Canyon Creek, 12-VIII-63, M. Brusven, 1♀ 4 nymphs (USNM). *Idaho Co.*, Lochsa River, 19-VI-64, A. R. Gaufin, nymphs (UU). *Kootenai Co.*, Beauty Bay Creek, 4-VII-64, A. R. Gaufin, nymphs (UU). *Lemhi Co.*, Pine Creek, 28-VI-64, J. K. Adams, nymphs (UU). MONTANA: *Gallatin Co.*, Hyalite Creek, 17-VIII-52, R. A. Hays, 1♂ (UU); Hyalite Creek, 16-VIII-52, R. A. Hays, 4♂ 1♀ (USNM). *Granite Co.*, Ranch Creek, 23-VII-66, M. L. Miner, 1♂ (USNM). *Ravalli Co.*, Burnt Fk. Bitterroot River, 16-VIII-65, J. R. Grierson, 2♂ 1♀ (USNM). OREGON: *Wallowa Co.*, French Camp, Lostine Valley, 18-VIII-52, G. F. Edmunds, 1♀ 1 nymph (UU). WYOMING: *Park Co.*, Beartooth Creek, 9-VIII-52, R. A. Hays, 1♂ (UU); Beartooth Creek, 31-VIII-51, R. A. Hays, 1♀ (UU); Beartooth Creek, 31-VIII-51, R. A. Hays, 5♂ (UU); Tower Creek, Yellowstone Nat'l Pk., 17-VIII-59, W. L. Peters and G. F. Edmunds, nymphs (UU). *Sheridan Co.*, Tongue River, 20-VII-40, T. H. Frison, 1♂ (INHS); Tongue River, 28-VII-40, T. H. Frison, 1♂ (INHS); Big Horn Mts., 30-VII-40, T. H. Frison and T. H. Frison, Jr., 1♂ (INHS); South Fk. Camp, Big Horn Nat'l Forest, 4-VIII-52, B. Malkin, 1♂ (CAS).

Acknowledgments

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THE NAME OF THE BAJA CALIFORNIA CAPE WORMSNAKE

Hobart M. Smith[1] and Kenneth R. Larsen[1]

Abstract.— The type-specimen of *Glauconia boettgeri* Werner, 1899, is consubspecific with *L. h. slevini* Klauber, 1931. The valid name of the Baja California Cape wormsnake accordingly is *Leptatyphlops humilis boettgeri* (Werner).

The allocation of a snake described 75 years ago (Werner, 1899:-116) as *Glauconia boettgeri* has long been uncertain, largely because of its unknown type locality. The original description is reasonably good, and the species was stated to be related to *Leptotyphlops humilis;* but no subsequent reviewer has placed it definitively with any known species. Werner (1917:198) later reviewed the whole family but added nothing except the speculation that *boettgeri* might be grouped with certain African species. He had earlier placed it as a synonym of the African *Leptotyphlops labialis,* but that species differs in numerous ways (e.g., no preocular supralabial, rostral extending posterior to eye level), as he noted in 1917. He concluded that *L. boettgeri* might be related to *L. latifrons* and *L. scutifrons,* both African species, but is distinct from them. Indeed it is distinct, since *L. scutifrons* has no preocular labial and *L. latifrons* has a very large rostral. His final thoughts, seemingly, placed *L. boettgeri* with African species rather than with *L. humilis,* his first impression; and perhaps for this reason Klauber (1940) made no attempt to allocate *L. boettgeri,* although he cited Werner's 1917 monograph.

In an attempt to fix the allocation of Werner's name, Dr. Josef Eiselt of the Vienna Museum very kindly loaned us the holotype of Werner's species for more careful examination. Although too faded to reveal the pattern of pigmentation, in other respects the specimen, now No. 15455 in the herpetological collection of the Natural History Museum of Vienna, is a typical representative of the population now known as *Leptotyphlops humilis slevini* Klauber (1931:338). It has 254 dorsals; 17 subcaudals; 12 scale rows around tail, 14 around body; and median scales on head all about equally wide and little, if any, narrower than the scales in the median row on the neck and trunk. The body length is 203 mm, the tail 10.8 mm. The body-length/diameter ratio is 58, the body-length/tail-length ratio 18.4. For *L. humilis slevini,* Klauber (1940) records 253 as the mean (range 244-269) for the dorsals; 15 (range 12-18) for the subcaudals; scalerow counts and median head scales as in *L. boettgeri;* body-length/diameter ratio mean 49; body-length/tail-length ratio mean 23.

These characters clearly place Werner's *G. boettgeri* with *L. humilis slevini.* The latter is the only *L. humilis* subspecies with

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[1] Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder, 80302.

equal-sized median head scales, and only one other (*L. humilis dugesi*) has as few as 254 dorsals (and its maximum is 257). Only one other (*L. humilis cahuilae*) has only five pigmented dorsal scalerows, but unfortunately this character cannot be determined; however, the general tone ("light brown') is matched. Direct comparisons of the holotype with all available specimens of *L. humilis* (unfortunately none of *L. humilis slevini*) reveal a complete agreement in all external features of scutellation, except for the median head scales being equally broad and as large as the median scales of the trunk. This feature Klauber emphasized, however, as distinctive of *L. humilis slevini*. There is a minor deviation of the holotype from the mean body proportions of *L. humilis slevini*, but the range of variation in these features is considerable. Klauber did not record the variation for *L. humilis slevini* but noted (1940:99) that in a homogeneous series of 52 *L. humilis humilis* the range of body-length/diameter ratios varied from "under 45" (1) to "over 70" (1) and that in 54 of the same subspecies from the same area the body-length/tail-length ratios varied from "under 16" (1) to "over 24" (3). Thus the ratios of the holotype of *G. boettgeri* respectively of 58 and 18.4 presumably fall well within the expected range for *L. humilis slevini* about the means respectively of 49 and 23. Indeed, the slightly shrunken holotype of *G. boettgeri* was originally measured at 214 mm in body length, tail 11 mm, diameter 3 mm. The latter measurement apparently was an error, for even now the diameter differs in various parts of the body, between extremes of 3 and 4 mm, with 3.5 mm being an approximate mean. In a less dehydrated condition 4 mm would be likely. The length of the body has clearly diminished in the interim. The body-length/diameter ratio of 75 given by Werner (1899:116) is, however, clearly too high; the most reasonable figure (based upon Werner's 214 mm body length and our 4 mm estimate for diameter in the fresh specimen) is 54, quite in line with that of *L. humilis slevini*.

The name *Leptotyphlops boettgeri* has not been used frequently, and therefore the possibility arises of appealing to the International Commission on Zoological Nomenclature for conservation of *L. humilis slevini*, 33 years a junior of *G. boettgeri*. However, the name *L. humilis slevini* itself has not been in use for 50 years; nor is it a widely cited name. The case does not justify an appeal, even under the terms of the 1972 decisions of the ICZN (Corliss, 1972:1120).

Accordingly, it is necessary to accept as valid the name *Leptotyphlops humilis boettgeri* (Werner, 1899) in replacement of *L. humilis slevini* Klauber (Klauber, 1931) as a subjective senior synonym of the latter name.

The Cape region of Baja California was visited by boat so frequently before 1900 that it is not at all strange that a specimen of *Leptotyphlops* from there should have reached a European museum before 1899. The most frequently visited port was La Paz, whence records for *L. humilis boettgeri* are already available. We accordingly here propose that the type locality of *G. boettgeri* be restricted to La Paz, Baja California, Mexico.

ACKNOWLEDGMENTS

We are much indebted to Dr. Josef Eiselt for the loan of the holotype of *G. boettgeri*, and to Dr. T. Paul Maslin for use of comparative material in the University of Colorado Museum.

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CONTRIBUTIONS TO THE CONCEPTS OF REPRODUCTIVE CYCLES AND THE SYSTEMATICS OF THE *SCALARIS* GROUP OF THE LIZARD GENUS *SCELOPORUS*

Hobart M. Smith and William P. Hall[1]

Abstract.— The concept of parity type is proposed as a criterion of relationship among members of the *Sceloporus aeneus-scalaris* complex, with members of *S. aeneus* being regarded as viviparous and those of *S. scalaris*, as oviparous. The viviparous *S. goldmani* is regarded as a relative of *S. aeneus*, and *S. a. subniger* is not regarded as intermediate between *S. scalaris* and *S. aeneus*. The proposal by Davis and Smith that *S. a. aeneus* is oviparous and specifically distinct (as *S. aeneus*) *from S. a. bicanthalis* (as *S. bicanthalis*) is rejected. *S. aeneus* is hypothesized to have a biennial reproductive cycle. *S. scalaris slevini* auctorum is segregated into two subspecies: *S. s. samcolemani* subsp. nov. in the Sierra Oriental (northern end), and *S. s. slevini sensu stricto* in the Sierra Occidental (also northern end) of Mexico and of the adjacent United States.

The systematics and phylogenetic history of the *scalaris* group of *Sceloporus* has long been viewed as enigmatic, beginning with the statement of the quandary by Smith (1939: 347-348) in explanation of the allocation of the northwestern member, *slevini*, to the species *scalaris* despite some contrary evidence. However, Smith and Poglayen (1958: 13-15) allocated *slevini* to the species *aeneus* after another population exhibiting certain features of intermediacy between the two polytypic species *scalaris* and *aeneus* was described (*S. a. subniger*).

Neither of the preceding accounts placed any overt emphasis upon parity types. Smith (1939: 332) made a passing comment that both oviparous and "ovoviviparous" species occur in the group. Evidence now available makes it certain that members of the *scalaris* complex are oviparous, and we here postulate that members of the *aeneus* complex are viviparous (a broader term, more certainly applicable than ovoviviparity, which has come to imply absence of placental structures, whereas "euviviparity" implies their presence; both conditions exist in viviparous reptiles and only by microscopic techniques can they be determined). Anderson (1962) has demonstrated that *slevini* is oviparous, and accordingly its allocation with the *scalaris* complex is correct.

The most critical doubt cast upon this hypothesis is the proposition by Davis and Smith (1953: 102) that *S. a. aeneus* is oviparous, whereas *S. a. bicanthalis* is incontrovertibly viviparous (Smith, 1939: 356, and personal data). On this basis these taxa were elevated to specific status (*S. aeneus, S. bicanthalis*). The data provided in Davis and Smith, however, strongly suggest that in *S. a. aeneus* viviparity does occur, but on a two-year cycle. Ten of 28 females collected from 25 July to 15 August "contained from 3 to 5 (average 4) large ova, the largest measuring 6 x 12 mm. . . . In none . . . was there any recognizable evidence of embryonic development. . . . Many of these

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[1] Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder, 80302; and Departamento de Biología, Universidad de Puerto Rico, Río Piedras, Puerto Rico, 00931.

specimens were taken at an elevation of 10,000 feet. . . ." Obviously these eggs could not be laid, at that elevation, and hatch before winter or survive the winter without hatching. Almost certainly they would be carried *in utero* through the winter, the embryos developing and the young being born in the spring. Indeed, further observations in Davis and Smith support this contention: "12 of the others appeared to have oviposited and in the others (6) the ova were minute, less than 1 mm. in diameter." The logical inference is that after the young are born in spring or early summer, ova start to develop but do not reach large size until the following year, and the embryos are not ready for birth until the spring or summer after that.

We are not aware of any previous record of occurrence of a biennial reproductive cycle in lizards, although Fitch (1970) records the occurrence of biennial or triennial cycles (his opinion being that they are sometimes more properly interpreted as irregular cycles, their length being determined by environmental variables) in several species of northern snakes (*e.g., Crotalus viridis, Vipera aspis*, and *V. berus*). Drs. Frank N. and Frieda C. Blanchard thought (personal communication) that a biennial cycle occurs in northern Michigan populations of *Thamnophis sirtalis* (Oliver, 1955: 244), and there is considerable evidence (obtained by Dr. Althea Gerrard of the Laboratory of Comparative Reproduction of the University of Colorado, under the direction of Dr. Richard Jones) that a biennial cycle occurs in populations of *Thamnophis radix* occurring at the extreme periphery of the range of the species in the foothill area near Boulder, Colorado. Reproductive cycles exceeding one year in length require, as a rule, considerable longevity, which is not ordinarily attributed to small lizards such as *Sceloporus aeneus*. Regardless of the apparent improbability of relative longevity in *S. aeneus*, a biennial viviparity does appear to occur in both subspecies of the species. Definitive investigation of this apparently unique phenomenon is of high priority.

It should be noted that although small size and probable short life (assumed on the basis of longevity records for related species: no records are available for members of the *scalaris* group of *Sceloporus*) mitigate against a biennial reproductive cycle (which might not be productive enough to offset the mortality rate), the very short season of activity and the perpetual coolness have the effect of increasing longevity. It has been amply documented that in squamatan reptiles and anurans, the members of subpolar or high-altitude populations of any species or group, subjected to cold-induced inactivity much of the year, are longer-lived and have more protracted reproductive cycles than do their more temperate or subtropical relatives, which are active most of the year and have shorter reproductive cycles. Indeed, if other lizards with biennial reproductive cycles exist, they are almost certainly high-altitude or subpolar in distribution. Andean lizards would be particularly suspect, since the reproductive cycles of the northern temperate lizards are well known and are consistently annual. However, *S. aeneus* and its viviparous relatives may truly be unique in this respect: whereas most, if not all, other high-altitude lizards are conspicuously heliotherm arboreals or saxicoles, *aeneus* is secretively terrestrial and graminicolous. *S. scalaris* is equally terrestrial and graminicolous but occurs at lower altitudes and is less secretive. *S. microlepidotus* occurs at altitudes as great as *aeneus*, but it lengthens its activity period conspicuously by insolation above ground, usually on trees; and insolation on rocks would have the same effect. Thus *S. microlepidotus* and other high-altitude species of arboreal or saxicolous habits may, through extreme heliophily, so protract their activity that an annual reproductive cycle may be maintained, whereas the terrestrial, seemingly much less heliophilous, *S. aeneus* has been forced to adopt a biennial reproductive cycle to survive. Even if it were known to have a lower optimum activity temperature (not yet established) than do other sympatric species, it would not thereby necessarily escape the need for a biennial cycle; *Sphenodon*, with the lowest optimum activity temperature of any living reptile, has a protracted reproductive cycle (± 13 months), although its freedom from temperatures in the freezing range permits a more rapid development of embryos than would be possible in the strongly seasonal weather to which *S. aeneus* is exposed. *Sphenodon* in the habitat of *S. aeneus* would undoubtedly also require two years for completion of one reproductive cycle.

Although *subniger* was interpreted when described as occupying an ancestral position relative to the *scalaris* and *aeneus* complexes (Smith and Poglayen, 1958: 14), the clear evidence of intergradation between *subniger* and *a. aeneus* (and absence of such evidence for *subniger* and *scalaris*) leads to the assumption that viviparity occurs in *subniger*, conclusive evidence that it is not an ancestral member of the *scalaris* complex.

An important link in considerations of relationship and phylogeny in the *scalaris* group is *goldmani*, which possesses a mixture of derived and primitive characters. Its viviparity—indicated by the occurrence of 9 well-developed young in the uteri of the holotype and one paratype of the species (Univ. Michigan Mus. Zool. 80896 and 77266, respectively, both from Charcas, San Luis Potosí)—is critical. Obviously *goldmani* falls with the *aeneus* complex, not with the *scalaris* complex, and it seemingly constitutes the northernmost member of its complex. However, the species is known from only the hypodigm (Charcas, S. L. P.; Carneros, Coah.) localities and Ojo de Agua, Pablillo, Nuevo León (Liner and Olson, 1973: 54). One of us (Hall) has surmised that the species is a grassland inhabitant whose existence has been critically attenuated by destruction of habitat through grazing by goats. A character progression from minimal derived states in northern populations (*goldmani*) to maximal derived states in southern populations (*a. aeneus*), through the intermediate populations of *subniger* and *bicanthalis*, supports Larsen's (1973) hypothesis of a northern origin for the group.

Sympatry of the *scalaris* and *aeneus* complexes is extensive in central parts of the Mexican plateau, although to the west the *sca-*

laris complex occurs without the other. A puzzling area of overlap occurs in the northern part of the Sierra Oriental, where populations referred to *slevini* are reported from areas occupied also by *goldmani*. It appears that the *scalaris*-complex representatives of that area are isolated from their closest relatives (*scalaris slevini*) in the western Sierra Occidental, Arizona, and New Mexico (Dixon and Medica, 1965: 73). Re-examination of material from the isolated northeastern populations reveals the existence of constant differences from paratopotypic *scalaris slevini* that justify recognition of a distinct taxon we here name:

Sceloporus scalaris samcolemani, subsp. nov.

Holotype.—University of Michigan Museum of Zoology (UMMZ) 124670, an adult female taken between Providencia and La Paz, Nuevo León, Mexico, by P. H. Litchfield, on 16 July 1960.

Paratypes.—Seventeen, including the Museum of Comparative Zoology (MCZ) 133167-73, 19 mi. S junction of roads to Doctor Arroyo and San Roberto, Nuevo León, 2250 m; and MCZ field nos. Y-25063 - Y-25071, 12 mi. SSE General Cepeda, 2250 m, Coahuila. All paratypes were slit the full length of the abdomen and rather distorted in preservation, but have retained their color and pattern with little change from life. *Hypoparatypes.* Seven, including UMMZ 95220(7), from Galeana, Nuevo León (all extremely discolored, two juveniles 23 and 23.5 mm s-v), taken 12-17 July 1945, by Hellmuth Wagner.

Diagnosis.—A short-legged (tibia 76-89 percent of snout-occiput length), oviparous member of the *scalaris* group of *Sceloporus* (of Smith, 1939), with essentially parallel rows of lateral scales, and two postrostrals; unique in the combination of usually (90 percent) a single canthal, dorsals 44-50, femoral pores 14-19 (66 percent 16 or more), maximum snout-vent length 51 mm, gular region barred or mottled (prominently in males, variable in females), and a consistently multicolored and patterned dorsum.

Description of holotype.—Smaller dorsal head scales moderately keeled, larger ones smooth or weakly rugose; two postrostrals; four scales between nasals, two between median frontonasal and postrostrals; median and lateral frontonasals broadly in contact with each other, median narrowly separating prefrontals and contacting frontal; frontal divided, broadly contacting interparietal; two frontoparietals on each side; three enlarged supraoculars on each side, separated from median head scales by one row of small scales, from superciliaries by two rows (except rear supraocular, separated by one row); one large subnasal and one canthal on each side; two loreals; one preocular; one subocular; 2-3 large keeled lower postoculars, three small upper ones; two rows of lorilabials ventral to loreals, one ventral to anterior half of subnasal, two ventral to posterior half; lorilabials reduced to one row over a length of 1-2 scales between subocular and labials; 3½ supralabials to below middle of eye.

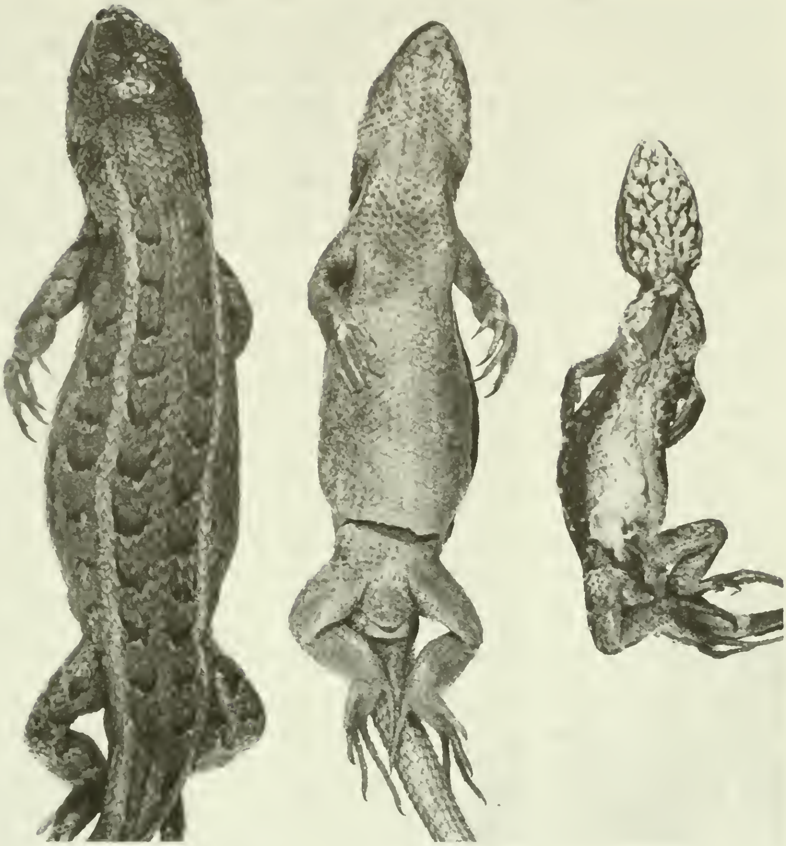

Fig. 1. Dorsal (left) and ventral (center) views of the holotype of *Sceloporus scalaris samcolemani*, UMMZ 124670, 51 mm SVL. Right, ventral view of a male paratype of same, MCZ Y-25066, 41 mm SVL.

Five infralabials; 3-4 pairs of chinshields, scales of anterior pair in medial contact, 2 scales between those of 2nd pair; labiomentals not reaching mental; one large medial auricular lobule; 6 scales between upper enlarged postocular and ear opening.

Dorsal scales 47 from interparietal to base of tail; 44 ventrals from shoulder level to anus; 44 scales around middle of body; 17-17 femoral pores, the two series in medial contact; dorsal scales straight sided, with a strong medial keel, a short medial mucrone, one or no denticule/scale, no lateral mucrones. All ventral scales smooth; lamellar formula for toes 7-11-13-18-12 (7-11-14-18-13).

Snout-vent length 51 mm; tail 62 mm; snout to occiput, 10.2 mm; hind leg 25 mm; tibia 8.6 mm.

Color a brownish slate gray above, browner on head; a dorsolateral light line on each side, largely on one scale row, separated by nine scale rows; ten U-shaped markings between shoulders and base of tail, dark-edged and light bordered to the rear, in each of two rows between dorsolateral light lines, separated medially by a space half as wide as markings; a row of similar marks lateral to dorsolateral light line, bordered laterally by a very faint lateral line; a row of dark dots corresponding in position to the other dark markings, lateral to lateral light line. Ventral surfaces whitish, with scattered gray pigment near chin, on chest, in preanal area and on ventral surfaces of the thigh.

Large, well-developed eggs in the uteri, with no evidence of developing young.

Variation.—In the entire hypodigm, the dorsals vary from 44 to 50 (22: 44, six; 45, three; 46, four; 47, six; 48, two; 50, one), mean 46.1; ventrals 36-49 (14: 39, one; 40, one; 42, one; 43, two; 44, five; 45, two; 48, one; 49, one), mean 43.9; scales around midbody 38-49 (17: 38, one; 39, one; 41, one; 42, three; 43, two; 44, five; 45, two; 47, one; 49, one), mean 43.3; femoral pores 14-19 (41: 14, eight; 15, six; 16, seven; 17, sixteen; 18, two; 19, two), mean 16.2. Scales between femoral pore series 0-1 (none, 11; one, 8); scales between second pair of postmentals 1-3 (1, four; 2, nineteen; 3, one); canthals 1-2 (1, forty-three; 2, five); snout-vent lengths 23-51 mm (23, 23.5, 36, 37(2), 38(2), 40(2), 41(2), 42(4), 43, 44, 45, 45.5, 47(3), 49, 51); tibia/snout-occiput ratio 76-88.8, mean (22) 81.25.

The dorsal pattern in all paratypes is much like that of the holotype, but the ventral markings are more prominent in some females and are conspicuous in males. In males the sides of the abdomen are dark blue, with no darker medial border but with scattered scales and white and irregular borders of scales black. No dark streaks traverse the blue patches. The gular region is conspicuously black-mottled or barred. Some females possess a vestige of the lateral abdominal patches, even with scattered light scales, but the color is gray rather than blue. The gular region is also weakly barred or mottled in some females.

Comparisons.—*Sceloporus scalaris slevini* is clearly the taxon that resembles *S. s. colemani* most closely—and indeed is the one with which the latter has long been united. *S. s. samcolemani* is markedly different, however, in having gular bars, in being consistently multicolored above, and in having dorsals 44 or more (100 percent in 22), femoral pores usually (66 percent in 41) 16 or more, and s-v length not exceeding 51 mm. In *S. s. slevini* no gular markings are present, the dorsal pattern is frequently unicolor, the dorsals are usually 43 or fewer (84 percent in 44), the femoral pores usually 15 or fewer (92 percent in 88), and the s-v length frequently exceeds 51 mm (13 in a total of 44 measured), reaching 61 mm. The complete absence of the unicolor phase in *S. s. samcolemani* is of course not a certainty, but that phase is so common in *S. s. slevini* and *S. s. scalaris* (no precise figures available) that the frequency in *S. s. samcolemani* is assuredly of a much lesser order, since 24 do not exhibit it.

The single canthal character-state of *S. s. samcolemani* is shared with *S. s. unicanthalis* as well as with *S. s. slevini*, but *S. s. unicanthalis* is distinctive in usually having the scales of the second pair of postmentals in contact, whereas they are separated by one to three small scales in the other two subspecies. In addition, *S. s. unicanthalis* has a longer tibia and larger dorsals and reaches a larger size than either *S. s. slevini* or *S. s. samcolemani*.

REMARKS.—The southern limit of the range of *S. s. samcolemani* does not reach as far as 12 mi. SW Ahuacatlán, or Ciudad Maíz, both in San Luis Potosí, whence specimens typical of *S. s. scalaris* (UMMZ 126228, Univ. Illinois Mus. Nat. Hist. 21512, respectively) are available. These have 2-2 canthals; 44 and 35 dorsals, 16-19 and

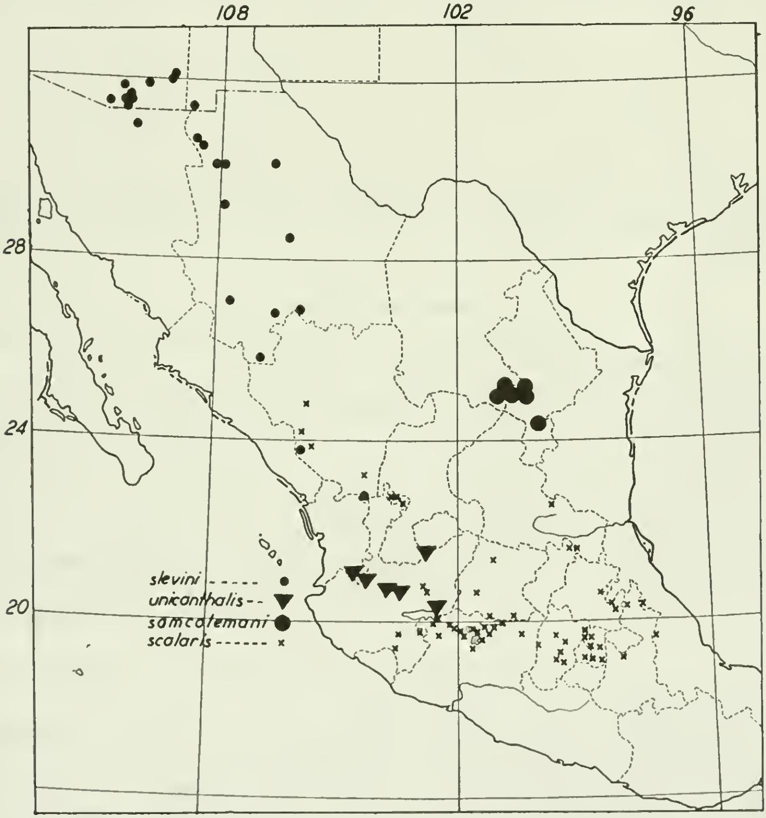

Fig. 2. Distribution of the subspecies of *Sceloporus scalaris*. Localities as given in text for *S. c. samcolemani*, from the literature and museum lists for others: especially Duellman (1961) for Michoacán, Dixon et al. (1972) for Querétaro, and Drake (1950) for Durango records of *S. s. scalaris*, and Grant and Smith (1960: 40) for an Jalisco record of *S. s. unicanthalis*.

14-15 femoral pores, respectively; and s-v measurements of 58 ♂ and 53 ♀ mm, respectively. The female is unicolor above; the male has faint dark gular bars. The female has the smallest dorsal count of any recorded specimen; Smith (1939:347) records counts no lower than 37.

The type series of 24 specimens includes 16 adult females, all with large eggs in the uteri, none showing evidence of embryonic development. In view of the lower altitude and longer season for activity than in *S. aeneus*, the early-middle July dates suggest ample time for egg deposition and hatching later the same year. Apparently, therefore, the population is oviparous and on that basis as well as pattern seems properly allocated with *S. scalaris* rather than with *S. aeneus*.

Localities other than those represented by the hypodigm include Hda. Pablillo, above Galeana, Nuevo León (Smith, 1939:349), the Gomez Farias region, Tamaulipas (Martin, 1955: 173); and Cedritos, Coah. (Amer. Mus. Nat. Hist. 77245).

The subspecies is named for Dr. Sam Coleman, who wrote the programs for processing the enormous quantity of data pertaining to the herpetology of Mexico and who thereby has contributed far more to a synopsis of Mexican herpetology than he realizes.

ACKNOWLEDGMENTS.—We are much indebted to Dr. Arnold Kluge, Dr. D. F. Hoffmeister, and Dr. Ernest E. Williams for the privilege of studying material under their care in their respective institutions.

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GROWTH AND DEVELOPMENT OF THE WESTERN HARVEST MOUSE, *REITHRODONTOMYS MEGALOTIS MEGALOTIS*

Gary H. Richins[1,2], H. Duane Smith[1], and Clive D. Jorgensen[1]

Abstract.— Growth rates, gestation period, litter size, reproductive age, sex ratios, and development were studied on 198 litters of *Reithrodontomys megalotis megalotis* (Baird). Growth was characterized by several standard skull and body measurements and was partitioned into four phases of 1-3, 4-12, 13-22, and 23-70 days. Growth was best described by measurements of tail length, ear length, and dried eye-lens weight.

Reproductive activity began as early as 38 days for females and 59 days for males. The gestation period was 22 days, and the mean litter size was 3.83 (range 1-7). Sex ratio was 53.49 percent males to 46.51 percent females. Reproductive efficiency was 53.53 percent. The development of *R. m. megalotis* was very similar to that of *R. m. dychei.*

Early breeding, postpartum estrous, year-round breeding, high reproductive efficiency, and a short gestation period contribute to a high reproductive potential in *R. m. megalotis.*

Small mammals occupy vital positions in the bioenergetics of North American deserts because they are important primary consumers, but many of their interactions within the ecosystem are not understood. Productivity estimates of rodent populations seldom take into account the biomass and biotic potential of young animals, especially when these estimates are made solely on the basis of trappable animals with disregard for such dynamic variables as litter size, gestation period, reproductive age, sex ratios, and biomass.

Because this type of data is difficult to obtain in the field, it is usually provided by laboratory studies. This study will define the growth and development of *Reithrodontomys megalotis megalotis* (Baird), a small cricetine found throughout much of North America.

The objectives of this study are (1) to characterize growth from birth to maturity by measurements of various body and skull parameters, (2) to determine gestation period, litter size, reproductive age, sex ratios, and development of behavioral sequences, and (3) to correlate these data, where possible, with similar studies on related species.

Literature Review

Growth rates have been studied for several small mammals (e.g., Meyer and Meyer, 1944; Pournelle, 1952; Chew and Butterworth, 1959; Layne, 1960; Goertz, 1965; Hayden and Gambino, 1966; Jones, 1967; Horner and Taylor, 1968), but *Reithrodontomys*, particularly *R. megalotis*, remains basically unstudied. Life histories of *R. humulis* (Holding and Royal, 1952; Layne, 1959; Kaye, 1961), *R. montanus* (Leraas, 1939), *R. fulvescens* (Svihla, 1950), and

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[1] Department of Zoology, Brigham Young University, Provo, Utah 84602

[2] Currently Wildlife Biologist, Dames and Moore, Cincinnati, Ohio

R. megalotis (Svihla, 1931; Smith, 1939; Brummel, 1961) have been partially studied. Bancroft (1966) completed an intensive study of reproduction, development, and behavior of *R. megalotis dychei* from Kansas, but no correlation of age with growth was attempted, nor has Bancroft's (1966) information been published.

Materials and Methods

Animals used in this study were reared from 20 pairs of *R. m. megalotis* captured approximately 19 km SE of Benmore Guard Station, Tooele Co., Utah, from 1-9 September 1971 and subsequently housed in a laboratory at Brigham Young University. The animals were caged in standard small-mammal cages with wood shavings provided as substrate and cotton as nesting material. Free water and Purina mouse breeder chow were available continuously. Laboratory temperature was held at 22 ± 2 C with a photoperiod of 12 hr. light and 12 hr. dark; varying intensities simulated dawn and dusk. Animals brought into the laboratory were sexed, paired, and checked daily for food, water, and presence of a litter.

When a litter was born, each litter member was marked by sequential toe clipping. The following measurements were taken daily from days 1-22 and then weekly for 7 additional weeks on a sample of 100 animals: (1) body weight, (2) total length, (3) tail length, (4) ear length from notch, and (5) hind-foot length. Daily observations on development and behavior were recorded for each litter. Body weight was determined to the nearest 0.05 g; total and tail lengths, to the nearest 0.5 mm; and ear and hind-foot lengths, to the nearest 0.01 mm. After the eyes had opened and the individuals had become more active (about 10 days of age), they were anesthetized with Penthrane.[3]

Ten individuals were killed daily from 1 to 22 days and weekly from 4 to 10 weeks for additional studies on skull measurements and eye lens weights to correlate age with the external measurements. On the day that an animal was to be killed, it was removed from the nest and administered a lethal dose of Penthrane. Standard body measurements were taken and the carcass placed in a 10-percent formalin solution to fix the eye lenses. After four days the carcass was taken from the formalin solution; the head was removed and skinned; and the lenses were extracted with a curved forceps after a slit had been made in the cornea. The lenses were stored in vials of 10-percent formalin, after which they were dried at 100 C for one week before weighing to the nearest .0001 g.

After the lenses had been extracted, the skull was stained and the (1) total length, (2) zygomatic breadth, (3) foramen magnum height, (4) mastoidal breadth, (5) nasal length, and (6) cranium width were measured to the nearest 0.01 mm with dial calipers. Staining followed the methods described by Humason (1967), except that the concentration of alizarine stock solution used was increased 10 times.

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[3] Abbott Laboratories, North Chicago, Illinois.

The instantaneous relative growth rate (IGR) described by Brody (1945) and Lackey (1967) was calculated to express growth as a rate between times of measurement and percentage of adult size. The IGR is expressed as $dW/dt/W$, where W is the parameter measured at the instant the rate of change of dW/dt is measured. Because it is not entirely possible to develop the "instantaneous" rate of growth, it was necessary to integrate the infinite number of growth rates to derive $W = Ae^{kt}$. This is conveniently written as $\ln W = \ln A + kt$ where: lnW is the natural logarithm of the variable measured (W) at $t = 0$, lnA is the natural logarithm of a theoretical constant based on the value of W at $t = 0$, k represents the instantaneous relative growth rate (when multiplied by 100, k = percentage growth rate), and t is time (age in days). For comparative purposes, the IGR (k) is determined with

$$k_n = \frac{\ln W_n - \ln W_{n-1}}{t_n - t_{n-1}}$$

Thus k is definite and can be used to compare differences in rates of growth.

Reproductive efficiency, defined as the weight of the litter multiplied by 100 and divided by the weight of the mother (Kaye, 1961) was determined for 19 adult female *R. m. megalotis.* In all instances both measurements were taken immediately after birth.

RESULTS AND DISCUSSION

Growth Rates

The instantaneous relative growth rates k for body weight, total length, tail length, ear length, and hind-foot length that were determined each day for 100 *R. m. megalotis* from 1 to 22 days and then weekly for the next 7 weeks are reported in Table 1. Growth rates (k) were also calculated for dried eye-lens weight, skull total length, zygomatic breadth, foramen magnum height, mastoidal breadth, nasal length, and cranium width on 10 animals each day from 1 to 22 days and then weekly for the next 7 weeks. This reduction in sample size from 100 to 10 per day was necessary, owing to the time required to raise animals to the proper age and to prepare the skulls and lenses.

Previous studies (Smith and Jorgensen, 1972) involving computer analyses of growth data using linear, quadratic, cubic, combined linear-quadratic, and combined linear-quadratic-cubic distributions with different time intervals were conducted to characterize species growth curves. Since the growth curves turned out to be curvilinear, none of the time intervals used with the above distributions and combinations of distributions adequately described the entire growth curve for any parameter. Brody's (1945) logarithmic approach adopted in this paper and used by Smith and Jorgensen (1973), however, does accurately describe the growth of *R. m.*

TABLE 1. Growth Data Analyses for *Reithrodontomys megalotis megalotis*, n=10 and n=100.

Parameter	Age in Days ($t=t$-1)	lnA n=10	lnA n=100	*k* n=10	*k* n=100	R^2 n=10	R^2 n=100
Body Weight	1-3	0.4087	0.2482	.1300	.1271	.3195	.2813
	4-12	0.6668	0.4029	.0848	.0845	.6079	.4963
	13-22	0.9555	0.8676	.0487	.0411	.4854	.2555
	23-70	1.9007	1.8053	.0084	.0157	.2799	.2092
Total Length	1-3	3.7444	3.7609	.0862	.0647	.6732	.3550
	4-12	3.8684	3.7895	.0614	.0537	.8251	.6862
	13-22	4.1701	4.0837	.0329	.0303	.7061	.5089
	23-70	4.8253	4.7579	.0020	.0044	.2392	.2299
Tail Length	1-3	2.3621	2.3960	.1329	.1055	.5156	.4327
	4-12	2.5983	2.4496	.1051	.0945	.8171	.7285
	13-22	3.2106	3.0958	.0467	.0414	.7109	.5220
	23-70	4.1493	4.0245	.0015	.0038	.6780	.1931
Ear Length	1-3	0.3022	0.3730	.3401	.2835	.5496	.4612
	4-12	1.1064	1.0368	.0888	.0837	.8458	.7426
	13-22	1.5477	1.4669	.0539	.0530	.7394	.6001
	23-70	2.6303	2.5732	.0010	.0030	.9162	.1970
Hind-Foot Length	1-3	1.8138	1.8136	.0929	.0887	.5784	.4904
	4-12	2.0453	1.9031	.0577	.0638	.7914	.7205
	13-22	2.4590	2.4023	.0194	.0194	.6268	.4368
	23-70	2.8773	2.8252	.0004	.0009	.1776	.0453
Dried Eye-Lens Weight	1-3	-9.6263		.4867		.4323	
	4-12	-8.6041		.1820		.9822	
	13-22	-6.9336		.0337		.6200	
	23-70	-6.7643		.0159		.9804	

Table 1 (Continued)

Skull Total Length	1-3	2.2411	.0683	.2656
	4-12	2.3662	.0371	.6839
	13-22	2.6658	.0113	.1985
	23-70	2.8731	.0017	.2810
Zygomatic Breadth	1-3	1.6980	.0496	.1116
	4-12	1.8599	.0266	.5816
	13-22	2.0332	.0106	.1004
	23-70	2.2512	.0006	.0293
Foramen Magnum Height	1-3	0.7337	.0570	.0517
	4-12	0.8292	.0297	.4024
	13-22	1.0644	.0090	.0835
	23-70	1.2950	.0008	.0136
Mastodial Breadth	1-3	1.5132	.0326	.0457
	4-12	1.7198	.0346	.5563
	13-22	2.0563	.0033	.0454
	23-70	2.1200	.0002	.0040
Nasal Length	1-3	0.8588	.0994	.4501
	4-12	1.0450	.0572	.7338
	13-22	1.4497	.0216	.6049
	23-70	1.8263	.0033	.1613
Cranium Width	1-3	1.7787	.0461	.2434
	4-12	1.9281	.0268	.6096
	13-22	2.1876	.0044	.1397
	23-70	2.2845	.0001	.0014

megalotis for the time intervals (growth phases) 1-3, 4-12, 13-22, and 23-70 days.

Not only is growth characterized by these four time intervals, but developmental sequences also tend to correspond to them. From 1 to 3 days the young harvest mouse is adjusting to the rigors of life outside the uterus. Because there is a rapid elongation of the extremities and a constant gain in weight (Figures 1-4), but little visible external development, there is probably considerable internal change taking place. During the 4-12–day growth phase, however, a great deal of external change is manifest. The extremities and body continue to elongate, and the animal increases in weight—although at a slower rate (Figures 1-4). The ears unfold, and the pinnae begin to develop. The toes separate and become functional. Pelage develops, and the teeth erupt from the gums. The eyes open, and there is increased activity about the nest. The external auditory meatus opens, and the sense of hearing develops. Little external change other than a continued elongation of the extremities (Figures 1-4) characterizes the 13-22–day growth phase. Near the beginning of this period the young animals begin to take solid food, and by 22 days of age they are completely weaned. From 23 to 70 days the growth of extremities all but ceases, and body weight is stabilized (Figures 1-4). Sexual development proceeds, and by 70 days both sexes have reached maturity.

The R^2 values (Table 1) indicate the amount of variation accounted for by growth of the parameter during a particular time interval. When R^2 values are converted to r, they indicate statistical significance. When time is partitioned into growth phases, a significant r indicates correlation between lnW and age and is used to establish confidence in k.

Tail length, ear length, and dried eye-lens weight provided the best correlations of relative growth with age (Table 1), r being significant during all four growth phases ($n = 10$). Although dried eye-lens weight was the best indicator of growth—and, ultimately, of age—in the laboratory, tail length or ear length would be the best parameter to measure in the field because these measurements are easily taken and do not involve killing the animal. Significance was spotty among the other parameters for the various growth phases, but all of the parameters were significantly correlated with age during the 4-12 day interval when the majority of growth and development occurred.

Graphic representations of means, standard errors, and instantaneous relative rates (k) were prepared for the three most significant growth parameters—tail length (Fig. 1), ear length (Fig. 2), and dried eye-lens weight (Fig. 3) as well as for body weight (Fig. 4). The close correlation of k with the actual data means indicates that the k values for each of the four growth phases characterize the growth of *R. m. megalotis.* If a detailed growth analysis as is presented here is unfeasible, a workable growth curve could be presented using the means and standard errors; but it is imperative that these be plotted on a logarithmic scale for the curve to be meaningful.

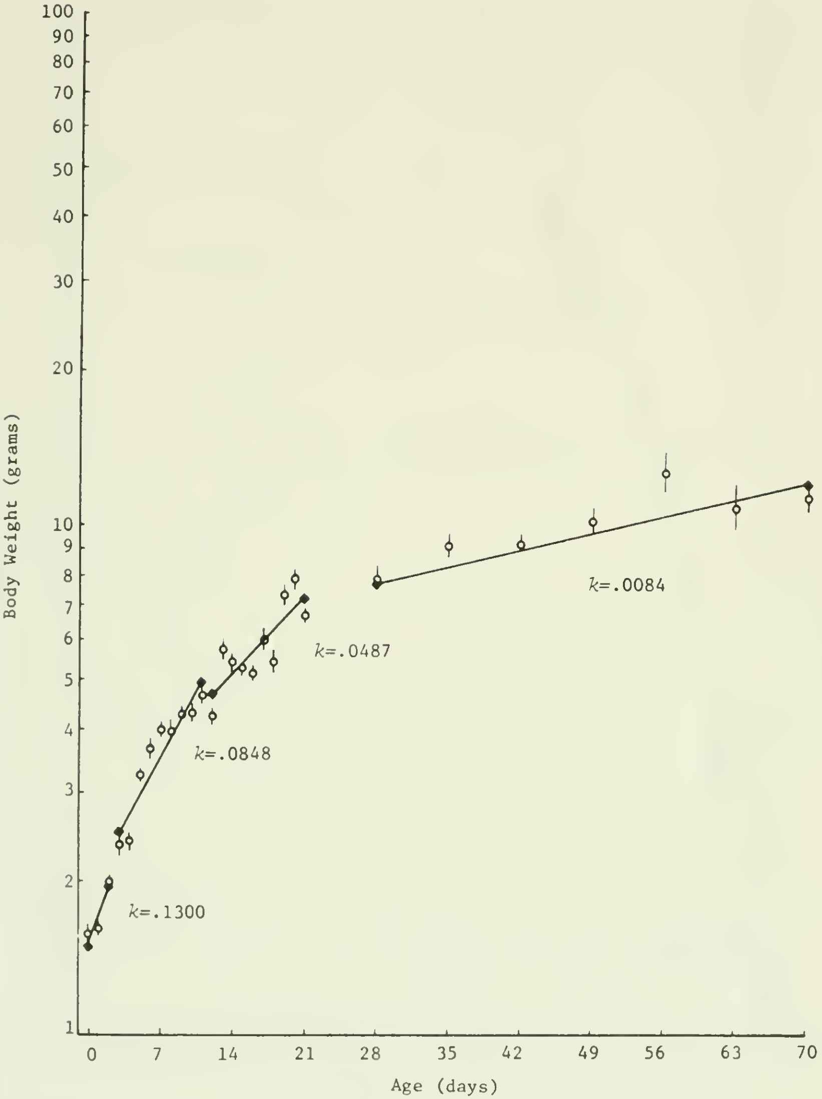

Fig. 1. Means, standard errors ($p = .95$), and instantaneous relative growth rates for tail length of *Reithrodontomys megalotis megalotis*.

The presence of four growth phases (1-3, 4-12, 13-22, and 23-70 days) in *R. m. megalotis* differs from the results of other workers. Layne (1959) found two growth phases in *R. humulis*: 0-3 weeks and 3-7 weeks. Bancroft (1966) found three growth phases in *R. m. dychei*: 0-3 weeks, 3-7 weeks, and 7-10 weeks.

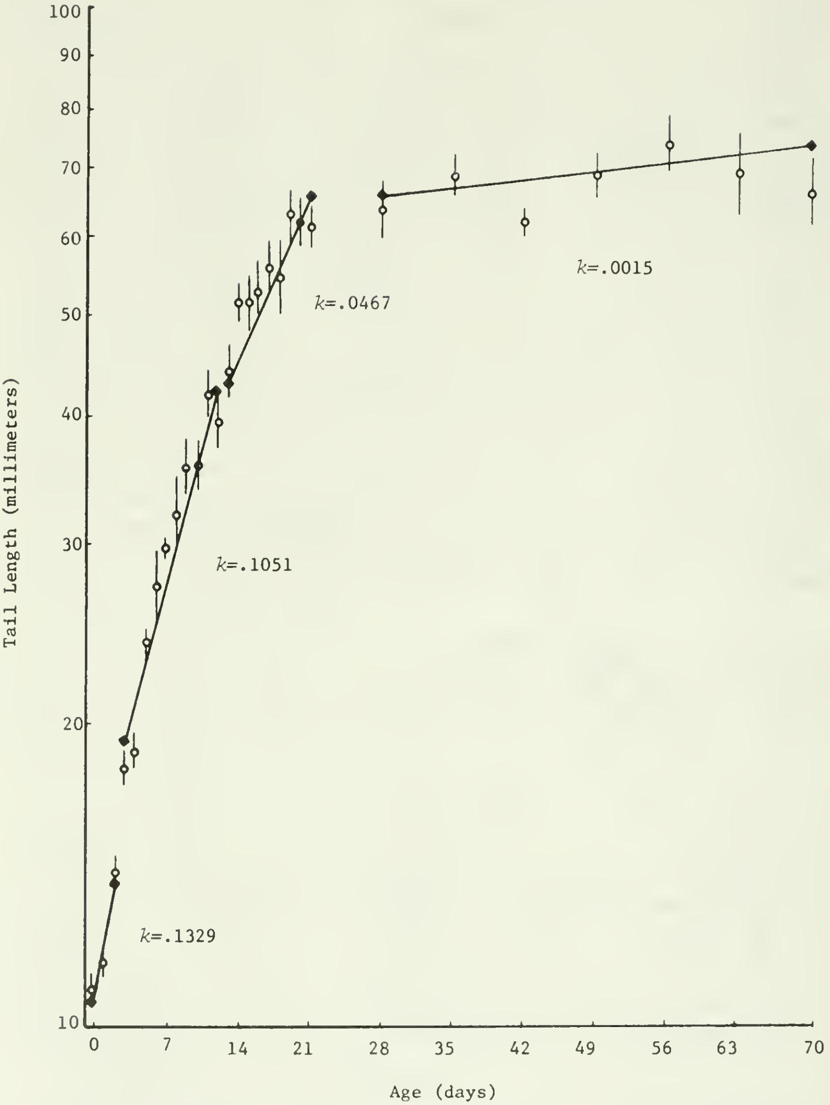

Fig. 2. Means, standard errors ($p = .95$), and instantaneous relative growth rates for ear length of *Reithrodontomys megalotis megalotis.*

Age prediction

Because the correlation of some growth parameters with age is significant, one might consider using these parameters to predict age. Although the process seems evident at first (it would involve simply reading the predicted age from a graph), the results cannot

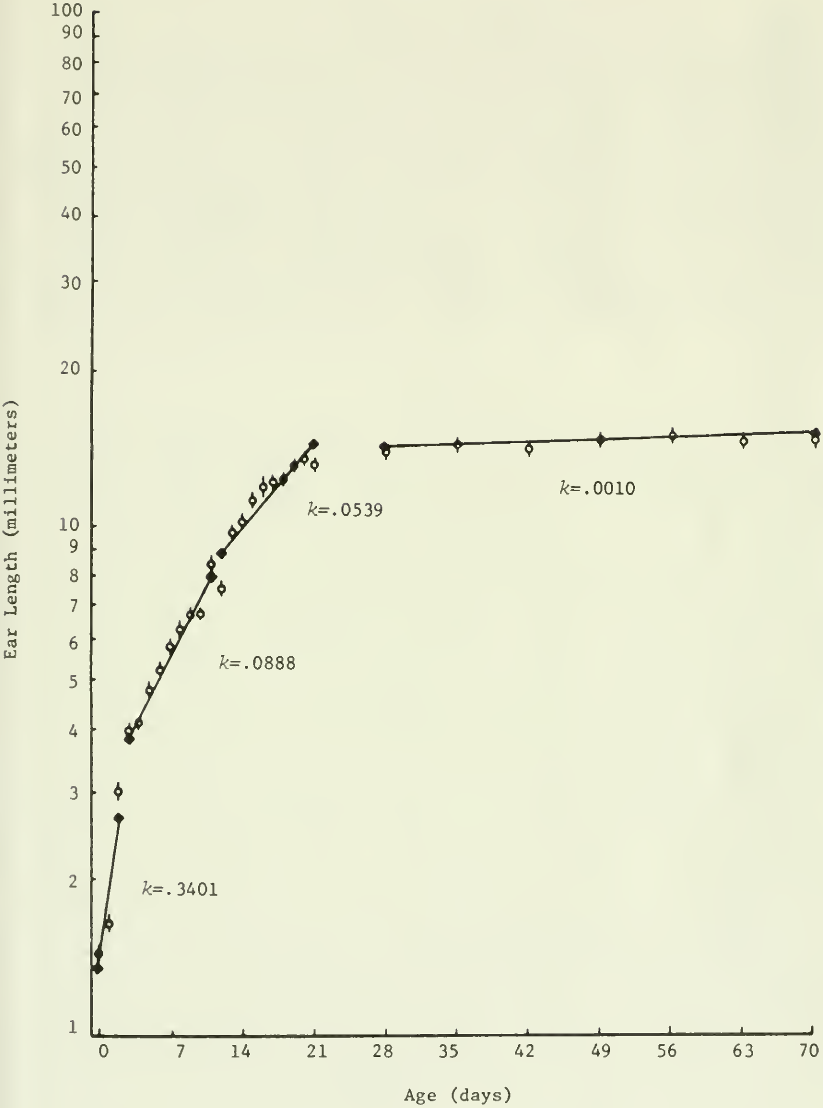

Fig. 3. Means, standard errors ($p=.95$), and instantaneous relative growth rates for dried eye-lens weight of *Reithrodontomys megalotis megalotis.*

be interpreted with statistical confidence because of the lack of variation among days. Calculation of confidence limits about the regression line presents special problems, because the X axis (age) is a non-random variable, selected arbitrarily by the investigator; thus, only the regression of Y on X can be estimated with confidence.

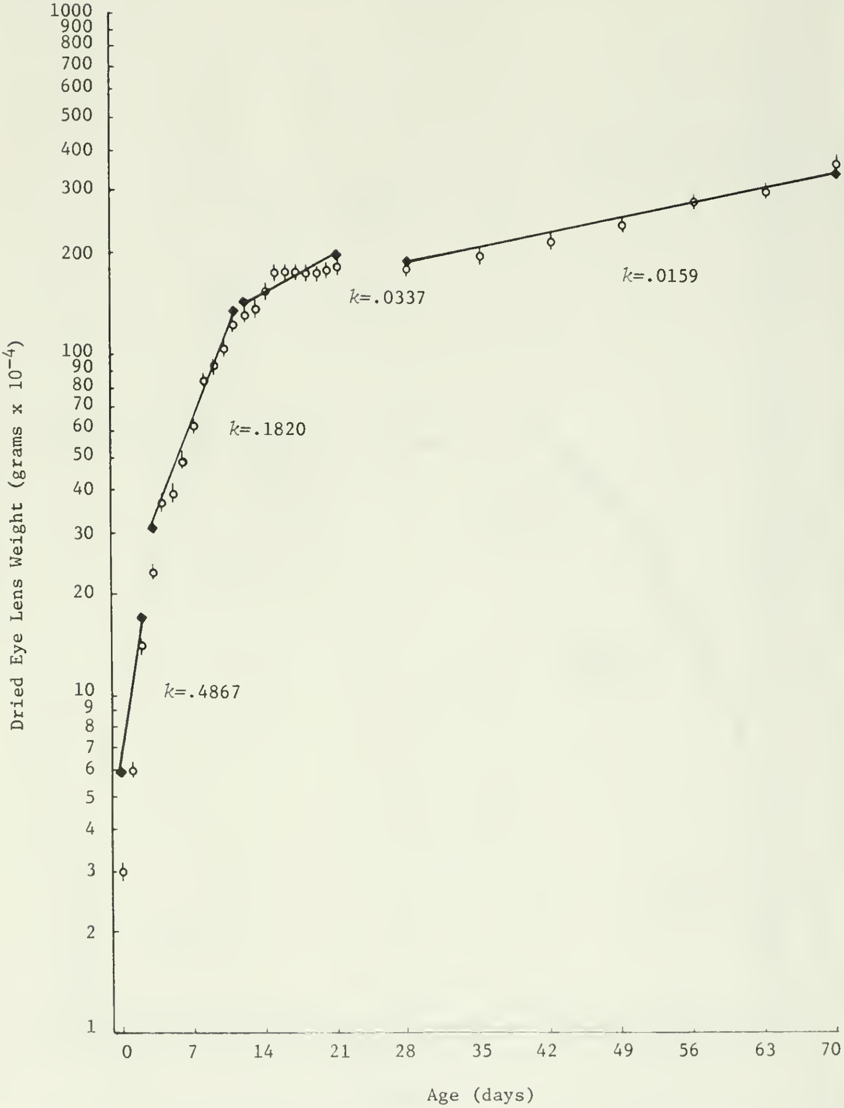

Fig. 4. Means, standard errors ($p = .95$), and instantaneous relative growth rates for body weight of *Reithrodontomys megalotis megalotis*.

When a least squares regression equation is used to predict ages of unknown animals, age becomes a random variable (Dapson and Irland, 1972; Smith and Jorgensen, 1972); consequently, the analyses of these data to provide age determinations await nonparametric procedures.

Gestation Period

The minimum gestation period of 22 days, as determined by the minimum interval between successive litters, was shorter than previously reported: Svihla (1931) reported 23 days and EcoDynamics (1971) reported 25-28 days as the gestation period for *R. m. megalotis*. One litter was born after only 20 days, but because all four young died within a few hours, the litter was assumed to be premature. Our results are similar to those of other workers. Bancroft (1967) reported 23 days as the gestation period for *R. m. dychei*, while Layne (1950) listed 24 days for *R. humulis*, although later Kaye (1961) reported 21 days. Leraas (1938) reported 21 days as the gestation period for *R. montanus*.

Litter Size

Litter size had a mean of 3.83 and ranged from 1 to 7 (Table 2), which is comparable to Bancroft's (1966) reporting of 3.84 and a range of 1-7 for *R. m. dychei*, although litter size had been stated earlier by Long (1962) to include up to nine. Svihla (1931) listed an average litter size of 2.60, ranging from 1 to 7, for *R. m. nigrescens* and *R. m. megalotis*. Other findings on litter size of *R. megalotis* vary somewhat, although always within the ranges previously stated: 4-6 in Oregon (Bailey, 1936); 1-4 and a mean of 2.0 in South Dakota (Zukerman, 1935); 1-7 for captive bred, with a mean of 4.27, and up to eight for laboratory bred (Egoscue, Bittmenn and Petrovich, 1970; Egoscue, 1972). Egoscue (1972) further reported an average litter size of 5.64 for wild caught females, ranging from 3 to 6, based on embryo counts of 56 placenta examinations.

Litter size varied with the number of litters females had already produced. The mean litter size (3.29) of 69 first litters of *R. m. megalotis* increased to 4.71 for 17 fourth litters before decreasing to 3.60 for five ninth litters (Table 2). Bancroft (1966) stated that mean litter size of three *R. m. dychei* was 4.30 for first litters, increased to a maximum of 6.00 for fifth litters, and decreased to a low of 3.30 for eleventh litters. This would indicate that female *R. m. megalotis* reach their maximum reproductive capabilities from 20-25 weeks of age—assuming that most are bred by 10 weeks and produce a new litter approximately every 3-3.5 weeks. While this reproductive rate is possible under laboratory conditions, it is likely to proceed more slowly in a field situation in which successful male-female encounters are logistically reduced.

Sex Ratio

The sex ratios of newly born *R. m. megalotis* resulted in 53.5 percent males and 46.5 percent females (Table 2). This sex ratio varies from those previously reported. Egoscue (1972) lists a sex ratio of 50.99 percent males to 49.01 percent females for 901 *R. m. megalotis*, whereas Bancroft (1966) reports a sex ratio at birth of 51 percent males to 49 percent females for 438 *R. m. dychei*. Layne

TABLE 2. Mean Number of Young *Reithrodontomys megalotis megalotis* Born in the Laboratory per Successive Litter.

Successive Litter Number	Number of Litters	Average			Percentage	
		Litter Size	Males	Females	Males	Females
1	69	3.29	1.90	1.39	52.7	42.3
2	37	3.86	2.24	1.62	58.0	42.0
3	30	4.23	1.90	2.33	44.9	55.1
4	17	4.71	2.76	1.94	58.8	41.2
5	12	4.25	2.17	2.08	50.9	49.1
6	10	4.10	1.80	2.30	43.9	56.1
7	9	4.00	2.00	2.00	50.0	50.0
8	8	3.88	2.00	1.88	51.6	48.4
9	5	3.60	1.60	2.00	44.4	55.6
10	1	5.00	2.00	3.00	40.0	60.0
1-10	198	3.83	2.05	1.78	53.49	46.51

(1959) found an even sex ratio at birth in *R. humulis*, but Kaye (1961) reported a ratio of 33.4 percent males to 66.6 percent females for 27 *R. humulis*.

Reproductive Age

Svihla (1931) reported 128 days as the youngest age at which a male or female *R. m. megalotis* had been found to breed. Leraas (1938) found that female *R. montanus albescens* gave birth as early as 90 days. Layne (1959) reported that one female *R. humulis humulis* became pregnant at 77 days and that males had enlarged testes as early as 49-50 days. Bancroft (1966) listed one female *R. megalotis dychei* as giving birth at 72 days and males as reaching sexual maturity at from 56 to 70 days.

During this study of *R. m. megalotis*, a female 29 days old was paired with a male 50 days old. This pairing resulted in a litter of four young born when the female and male parents were 62 and 83 days of age respectively. Granting a 22-day gestation period, *R. m. megalotis* can become reproductively active as early as 38 days and 59 days for females and males respectively, which supports the 35 days reported but unpublished by EcoDynamics (1971) but which supplants previously published data.

Reproductive Efficiency

R. megalotis has the highest reproductive efficiency reported for any mammal (Bancroft, 1966). Reproductive efficiency was calculated for 19 adult female *R. m. megalotis* resulting in a high of 53.33 percent for a litter of six. The mean reproductive efficiency of the 19 animals was 43.44 ± 2.91 percent (31.5-53.3 percent). Frank (1956) listed *Microtus arvalis* as having the highest reproductive efficiency of any mammal, the litter weight amounting to 53.2 percent of the mother's weight, but Bancroft (1966) reported 62.5 percent for a litter of five *R. m. dychei*. Kaye (1961) listed a high 50.5 percent for *R. humulis*. Dunaway (1962) listed 77.7 percent as the reproductive efficiency of a litter of eight *R. humulis*, but because the measurements were taken some 10-15 hours after birth, it is probably erroneous.

Reproductive Potential

Several of the foregoing factors contribute to the high reproductive potential of *R. megalotis*: early breeding, postpartum estrous, year-round breeding, high reproductive efficiency, and a short gestation period.

Early breeding allows for a longer reproductive life. Postpartum estrous which was evidenced during this study enables *R. m. megalotis* to maximize the number of litters born during a single season. In Utah the breeding season runs from mid-May to early September. Therefore, a harvest mouse born in early June could have as many as two litters its first year. A mature harvest mouse could have 4-5 litters during this time and could contribute 15-20 individuals to the population in a single year.

A high reproductive efficiency allows a greater percentage of energy intake to go for reproduction, thus maximizing reproductive potential. A short gestation period in concert with postpartum estrous is also advantageous because it tends to minimize the time between successive litters.

Reproductive potential for any species is clearly a function of litter rapidity and the length of time reproductive activity occupies in the life span of females. Under laboratory conditions, these factors can be maximized, although field conditions obviously impose yet another constraint—environmental limits, including population interactions. Bancroft (1966) reported postpartum estrous in *R. m. dychei;* and, although they can breed year-round in the laboratory, he doubts this would persist in nature, except perhaps in the southern part of their range.

Development

Condition at birth. Neonatal *R. m. megalotis* are similar in appearance to *R. m. dychei* (Bancroft, 1966) in that they are smooth and pink and are naked except for natal vibrissae. Eyes are closed and covered with a transparent membrane, including the crease marking the persisting fusion of upper and lower eyelids. Pupils are clear, with the exception of coloration in the iris. Ear pinnae are folded and appressed against the head. Toes are still fused, and nails are not yet present. The young vocalized faintly when handled.

One day. There is little morphological change, although the ear pinnae are sometimes unfolded. A gray dorsal stripe is visible, and the skin has lost its newborn transparency. Hair is not evident, although Bancroft (1966) reported fine hair visible upon close examination of the dorsum in *R. m. dychei.* Layne (1959) also noted abundant short and long hair on the dorsum of day-old *R. humulis.*

Two days. Ear pinnae have unfolded, and the dorsal pigmentation is darker, with dorsal hairs visible when held to the light. Toes are about one-third separated and claws are visible. Young move their feet rapidly and vocalize sharply when handled.

Three days. The young cling to the female's nipples and are often dragged around the cage several times before falling off when disturbed. Vocalization is a high-pitched squeak, 2-8/second. The toes are about one-half separated. Eyelid slits are visible. The dorsal pigmentation is almost black, and a white, scaly epidermal material observed by Bancroft (1966) in *R. m. dychei* and by Layne (1959) in *R. humulis* is present on the dorsum.

Four days. The toes are almost separated. The hair on the head is thicker and colored a pale gray brown. Bancroft (1966) stated that at this age *R. m. dychei* had claws approximately 5 mm long and that the ears were only fleshy lobes.

Five days. Dorsal furring extends about one-third of the way along the back, and the upper and lower incisors have erupted in some. Bancroft (1966) stated that the lower incisors had erupted in *R. m. dychei.* Layne (1959) also reported that the lower incisors were visible in *R. m. megalotis* on the fifth day.

Six days. There is little external change evident, although Bancroft (1966) reported that hair had appeared on the dorsal side of the tail in *R. m. dychei.*

Seven days. The dorsum is completely furred, and ventral hair is more pronounced. Mammae are visible in females.

Eight days. The external auditory meatus is open, and the young are very active and vocal. Opening of the external auditory meatus almost always precedes the opening of the eyes by one day.

Nine days. The venter, feet, and pinnae are completely furred, and the eyes are beginning to open. Smith (1936) reported that the eyes first opened at six days but were of little use for 48 hours. Bancroft (1966) found that the eyes were beginning to open in *R. m. dychei* at seven days but were not yet fully functional. Svihla (1931) found that the eyes opened on days 11-12 in *R. m. megalotis*, as did Brummel (1961). Leraas (1938) observed that the eyes opened on the eighth day in *R. montanus.* Layne (1959) reported that the eyes opened at from 7 to 10 days in *R. humulis.* In the present study, the eyes of *R. megalotis megalotis* opened at from 9 to 13 days.

Ten days. The eyes are open and fully functional in the majority of the young.

Fourteen days. Face washing is observed. There is very little vocalization. Observations of the feces suggest that the young have started eating solid food.

Sixteen days. Although nursing is observed until the sixteenth day, the majority of the young are completely weaned. There is no detectable change in appearance or behavior on days 11, 12, 13, and 15.

Summary and Conclusions

The growth date of *R. m. megalotis* can be divided into four distinct phases: 1-3, 4-12, 13-22, and 23-70 days; whereas *R. m.*

dychei and *R. humulis humulis* have three and two growth phases respectively (Bancroft, 1966; Layne, 1959). Growth of *R. m. megalotis* through all four phases is most accurately characterized by tail length, ear length, and dried eye-lens weight measurements.

R. m. megalotis had a 22-day gestation period, one day shorter than previously reported. Litter size varied from 1 to 7, and sex ratios at birth were approximately even.

Western harvest mice became reproductively active earlier than previously reported. One *R. m. megalotis* became pregnant at 38 days of age.

A high reproductive efficiency, 53.33 percent in this study and 62.5 percent (Bancroft, 1966), has been evidenced in *R. m. megalotis.*

R. m. megalotis has a high reproductive potential because of early breeding, postpartum estrous, year-round breeding, high reproductive efficiency, and a short gestation period.

The development of R. m. megalotis closely followed that of *R. m. dychei* as reported by Bancroft (1966), but differed slightly in that the eyes opened at from 9 to 13 days in *R. m. megalotis* while in *R. m. dychei* the eyes opened at from 7 to 11 days.

In the laboratory *R. m. megalotis* grows faster, has a shorter gestation period, has larger litters, breeds earlier, and has a higher reproductive efficiency than previously reported for this genus.

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BODY SIZE, BODY COMPOSITION, AND BEHAVIOR OF JUVENILE BELDING GROUND SQUIRRELS

Martin L. Morton[1], Catherine S. Maxwell[1], and Charles E. Wade[1,2]

Abstract.— Juvenile Belding ground squirrels were studied in the Sierra Nevada. Females were more trappable, had smaller home ranges, and tended to enter hibernation earlier than males. The primary sex ratio was 1:1. Individuals first emerged from the natal burrow at three to four weeks of age and a body weight of 35 g. Body weight and linear dimensions increased thereafter until hibernation began. Maximum prehibernatory weight of 200 to 260 g was attained at about 12 weeks of age. Prehibernatory fattening began at about six weeks of age. Maximum lipid stores attained weighed about 80 percent of the lean, dry body compartment. Seasonal changes occurred in weight of white and brown fat depots, adrenal glands, spleen, heart, kidneys, liver, and testes. Annual variations in snowpack and emergence schedule caused the reproductive period, and thus phenology of juveniles, to vary by as much as three weeks. The last animals to immerge were unusually small, being from late litters. Nonetheless, they may have had lipid stores sufficient for surviving hibernation.

In natural history studies of ground squirrels (*Spermophilus* sp.), juvenile members of the population are often ignored or examined only casually. Yet these young, inexperienced animals are logical subjects if one is trying to uncover fundamental adaptations of species to environments, such as high altitude, that are only seasonally accessible. Spermophiles survive in such environments through hibernation, and there is evidence that mechanisms favoring the success of juvenile hibernators, such as an accelerated ontogeny, are particularly important to the species as a whole (Mayer and Roche, 1954; Clark, 1970; Morton and Tung, 1971a).

In this article we present the biology of juvenile Belding ground squirrels, *Spermophilus beldingi beldingi*, from a population residing at high altitude in the Sierra Nevada of central California. Parameters of growth, behavior, prehibernatory fattening, and effects of annual variations in snowpack on the schedule of juveniles are discussed.

Methods

Data were gathered during a five-year period (1969–1973) on *S. b. beldingi* living on the eastern slope of the Sierra at the upper edge of the Mono Basin near Tioga Pass, Mono County, California. In this area there are subalpine meadows at elevations of 2926 to 3048 m (9600 to 10,000 ft) that are occupied by substantial numbers of *S. b. beldingi*.

Squirrels were live-trapped in Tomahawk wire mesh traps baited with peanut butter. Those to be released were toe-clipped for later identification, and those kept for dissection were etherized. Linear measurements were taken with calipers. Body weights were measured to the nearest 0.1 g on a Welch triple-beam pan balance. Fat pads,

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[1] Department of Biology, Occidental College, Los Angeles, California 90041

[2] Department of Physical Education, University of California, Davis, California 95616

kidneys, heart, spleen, and liver were weighed to the nearest 0.01 g on an Ohaus analytical pan balance. Gonads and adrenals were weighed to the nearest 0.01 mg on a Federal Pacific torsion balance. Carcasses, including dissected portions, were kept frozen for later laboratory analysis of water and lipid content. Water content was determined by drying carcasses to a constant weight in a vacuum oven at 55C. They were then homogenized and extracted for lipid with petroleum ether in a soxhlet apparatus (Morton and Tung 1971b). Data on snow depth at Tioga Pass and predictions of snowmelt runoff from the Mono Basin were taken from Bulletins 120 and 129 of the California Department of Water Resources.

Results and Discussion

Seasonal Schedule of Events and Behavior.— Juvenile *S. b. beldingi* usually appeared above ground in mid-July. During the rest of the summer they gained in body size, deposited fat, and began entering hibernation in September at about three months of age. The last animals disappeared from the surface in the final ten days of September (1970) and the first ten days in October (1969, 1971, 1972, and 1973).

Differences were noted in the behavior of males and females in terms of trappability, size of home range, and onset of hibernation. In 1971 a grid of 64 traps with 20 m spacing was set and centered on a burrow system containing a group of newly born litters. Fifty-five juveniles (30 females, 25 males) born in this burrow system were captured. During the course of the summer, females were captured an average of 9.53 times (range, 1-30), significantly ($P<0.05$) more often than males, 5.32 times (range, 1-21). This difference in number of recaptures may be due to sex-specific differences in home range and dispersal. Thirteen juveniles were always trapped within the outer rows of traps. Six were males trapped an average of 14.2 times, and seven were females trapped an average of 22.3 times. The mean home range of these animals, calculated by the "halfway to the next trap" method (Hayne, 1949), was 6408 m^2 for males and 4434 m^2 for females. The home range of males was significantly larger ($P<0.05$).

There are indications that males tended to remain active later in the season than did females. In 1973 juveniles were consistently trapped and released at burrow systems on a section of meadow roughly 300 m x 300 m. Each trapping session was conducted for about four hours with about 40 traps. Traps were checked once per hour. The daily catch increased from late July through August (Fig. 1). During that time, males and females were captured in about equal numbers during each trapping session, and 93 different individuals were handled: 47 males and 46 females. Beyond the first week in September, however, more males than females were captured during every trapping session except the final one, on 5 October. During September 10 individuals were trapped that had not been handled previously; nine were males, and only one was a

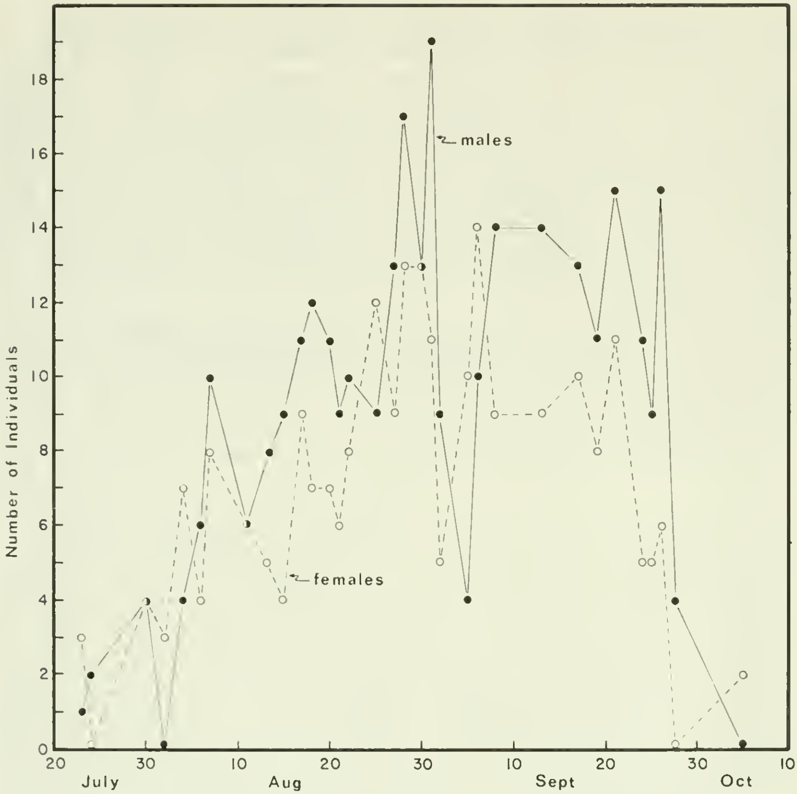


Fig. 1. Number of juvenile *Spermophilus beldingi beldingi* captured per trapping session during the 1973 season.

female. The four males captured on 28 September and the two females captured on 5 October were the last squirrels trapped or observed in the 1973 season, and all six were kept as specimens.

The larger home ranges of males, their lower rate of recapture, and their tendency to enter hibernation later than females are probably all indicators of greater dispersal of males from the natal area. Sex-specific emigration is common among young mammals and has been noted many times in ground squirrels (Quanstrom, 1971; Turner, 1972; Yeaton, 1972). One might predict that the hazards associated with dispersal would lead to greater mortality among juvenile males (Murray, 1967) and that an unbalanced sex ratio in favor of females would exist among those members of the population exceeding one year of age.

These data raise a question concerning the sex ratio in young squirrels. During the five years of this study, juveniles were captured or shot throughout the habitat at Tioga Pass known to harbor

S. b. beldingi. In all, 672 different individuals were handled: 336 males and 336 females. Clearly the sex ratio in juveniles was 1:1.

Seasonal Changes in Body Size.— Growth of young squirrels was evident in terms of their linear dimensions and body weights, as the season progressed. Both body length and hind-foot length increased throughout the summer (Fig. 2). There was considerable variance in foot length, however, and it would seem to be a poor indicator of age. Body length was a more reliable indicator and has been used to show that maximum body size is not achieved in *S. b. beldingi* until the end of the second season of life or beyond (Morton and Tung, 1971a).

In mid-September the oldest, largest juveniles began to enter hibernation, whereas the smallest, most immature individuals tended to remain active. This resulted in a decreased mean body size in late September samples.

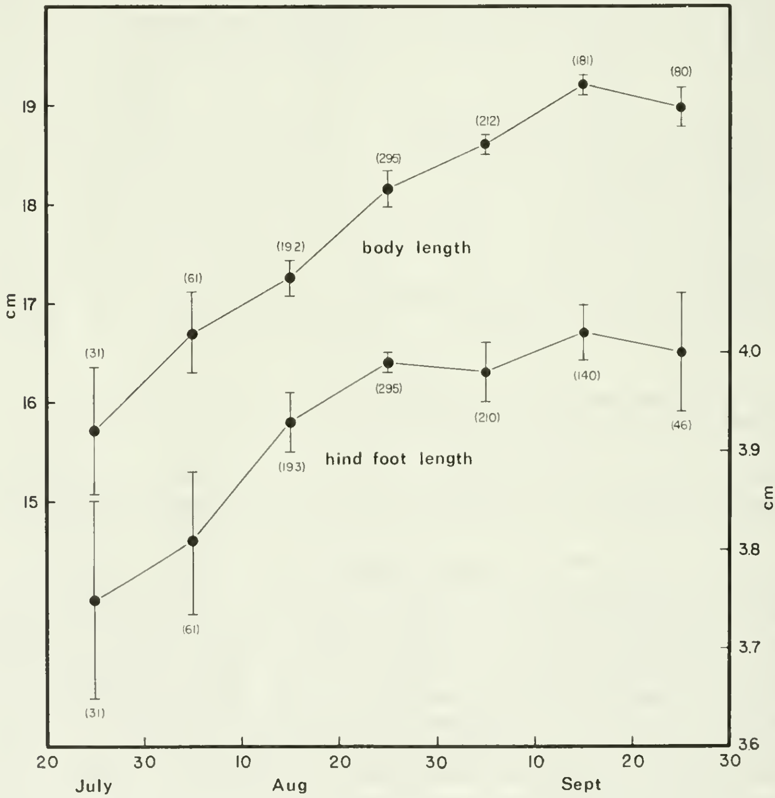
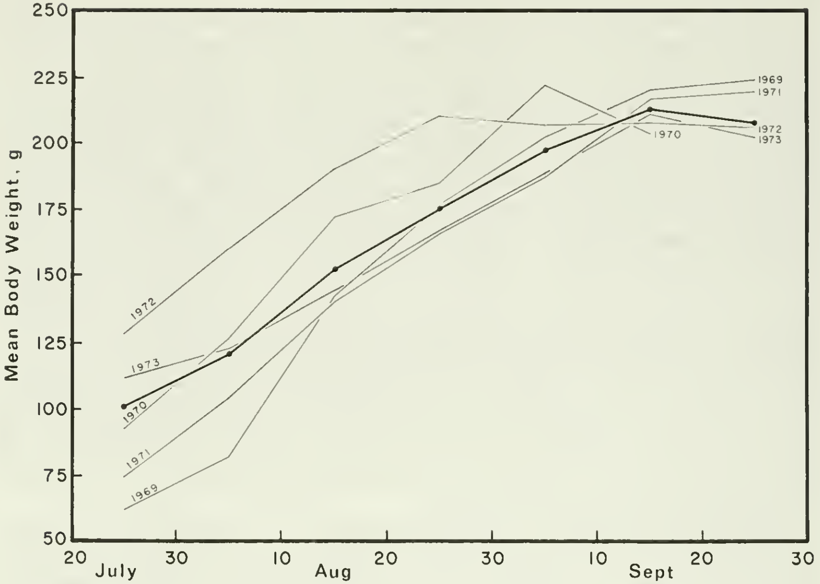


Fig. 2. Seasonal changes in mean body length and hind-foot length in juvenile *Spermophilus beldingi beldingi* at 10-day intervals. Data were pooled from five seasons, 1969-1973. Vertical lines indicate two S.E. Sample size shown in parentheses.

When they first emerged from the natal burrow, juveniles weighed about 35 g. For example, on 15 July 1970, members of one litter of six that were probably venturing out for the first time were observed for 40 minutes, then hand-captured and weighed. They paid no attention to an observer seated one m from them, and they did not go more than 1 m from the burrow entrance. Nevertheless, they sat erect, trilled, nibbled on grass, and when handled everted their anal glands. Coupling this information with that from captives of known age (Morton and Tung, 1971a), we estimate that these juveniles emerged at an age of three to four weeks. Their mean body weight was 36.4 g (range, 33.5-41.2 g), only one-half of what captives weigh at the same age (Morton and Tung, 1971a). Clearly, captives are precocious in comparison to wild juveniles, but the degree of precocity is difficult to determine. Turner (1972) has observed that *S. b. oregonus* juveniles attempt to nurse for the first few days after emerging from the natal burrow. Apparently the same behavior occurs in *S. b. beldingi*. Morhardt (1971) suggests that juvenile *S. b. beldingi* experience maternal care for about the first week following emergence.

Mean body weight increased steadily each season of the study, from about 100 g in late July to about 215 g in mid-September, where it leveled off as the fatter individuals began hibernating and were no longer sampled by us (Fig. 3). Because of the inability of the live traps to retain small juveniles and because of our preoccupation with other projects, no useful sample sizes were obtained until late July each year. As the season progressed thereafter, trapping success increased as the juveniles became larger and more active. During the final portion of September, trapping success decreased as the number of active squirrels decreased. There was considerable variation in mean body weight of the juvenile population from year to year. For example, 15 individuals weighed between 20 and 30 July 1973 were twice as heavy as 10 that were weighed during the same interval in 1969. There was a disparity of as much as three weeks in the dates at which specific mean body weights were reached. Obviously, young squirrels were not born within a certain very limited time year after year. These annual differences in growth schedules indicate that there is considerable variation in the timing of reproduction. Within a given season, variation occurred because females, even on the same meadow, emerged over a span of about a month, with adults tending to emerge ahead of yearlings. Furthermore, small yearling females often did not come into estrous until several weeks after emergence. Their offspring tended to be the ones that were active at the very end of the season.

There was also variation in the schedule of reproduction that could be attributed to annual differences in snowpack. Snow depth at the study area was measured every year in February and April, and in May 1969, by the State of California (Fig. 4, upper panel). Snowmelt runoff for the watershed of our study area (Mono Basin) was also forecast by them each month from February through May (Fig. 4, lower). Both of these measurements show that 1969 was



1969	10	12	43	17	39	51	21
1970	10	16	45	50	58	21	0
1971	12	19	41	102	87	78	43
1972	18	20	22	52	26	30	9
1973	15	42	95	131	103	72	67
Total	65	109	246	352	313	252	140

Fig. 3. Seasonal changes in mean body weight of juvenile *Spermophilus beldingi beldingi* at 10-day intervals. Heavy line shows means when data were pooled for all five seasons. Sample sizes are below each class interval.

the heaviest snow year during the study and that 1972 was the lightest. In fact, snowpack in 1969 was the heaviest recorded during the 44 years that the surveys have been taken, and snow was present on the study area for about a month longer than usual. In 1972 runoff was unusually early because of lack of precipitation and hot weather in March. These extremes in snow conditions strongly affected the timing of reproduction. As a result, juveniles reached prehibernatory weights several weeks earlier than usual in 1972, and they were larger early in the season than at comparable dates of other years. It is interesting that, despite their late start, the 1969 juveniles attained prehibernatory weight levels at about the same calendar time as in other years (Fig. 3). The basis for their increased growth rate is not known, but the wet, green phase of the meadow environment persisted much later than usual in 1969. This could have provided a highly favorable nutritional situation for young squirrels.

The data on mean body weights tend to obscure some rather important facets of growth and fattening as it actually occurred in individuals. Our records show that frequently captured, toe-clipped

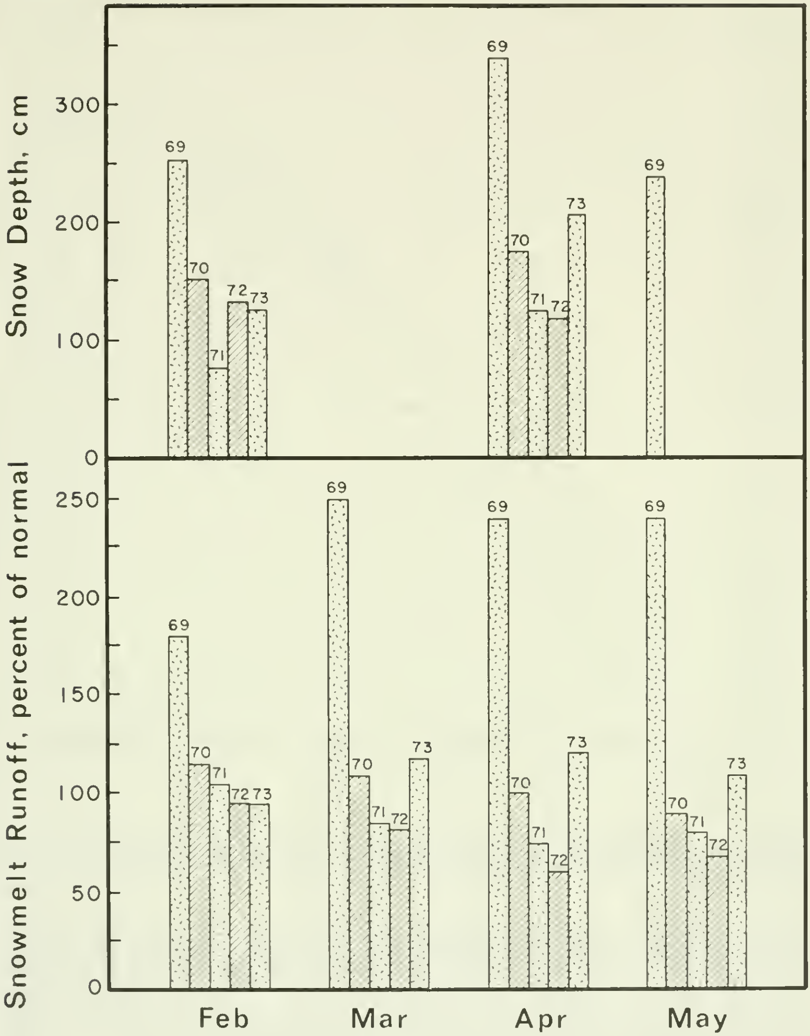


Fig. 4. Snow depth at Tioga Pass (upper) and snowmelt runoff predicted for Mono Basin (lower) from 1969 through 1973.

individuals gained body weight steadily throughout the season (Fig. 5). There often seemed to be a pause, however, in the rate of gain at midseason, followed by another rapid period of gain. The latter may have been caused primarily by prehibernatory fat deposition. Individuals entered hibernation shortly after maximum body weight (200-260 g) was obtained. A practical effect of this was that mean body weights leveled off or even declined as the oldest, fattest juveniles were no longer being trapped.

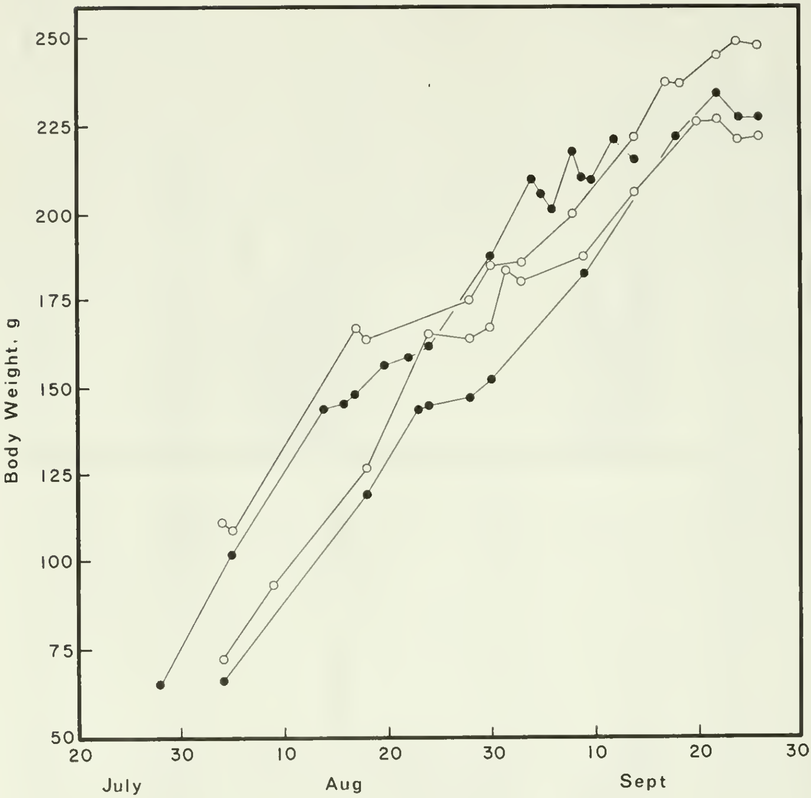


Fig. 5. Seasonal changes in body weight of four frequently recaptured juvenile *Spermophilus beldingi beldingi*. Open symbols represent females, closed symbols males.

To distinguish the prehibernatory fattening response from ordinary growth of nonlipid components, body composition of juveniles was analyzed throughout the season in 1973. These data show that juveniles began depositing significant quantities of lipid in mid-August (Fig. 6) and that the lipid compartment increased in weight for the next month. On the other hand, the lean, dry compartment of body mass increased only through late August then remained constant. Maximum lipid stores in juveniles occurred in mid-September. At that time lipid weighed 80 percent of the lean, dry compartment. In adult *S. b. beldingi*, lipid weighs about 125 percent of the lean, dry compartment at the time of hibernation (Morton, M.S.).

Morton and Tung (1971b) have shown that wet weight of both brown and white fat depots is correlated with total lipid stores in adult *S. b. beldingi*. In juveniles there was a seasonal increase in both absolute and relative mass of these depots (Fig. 7). This was

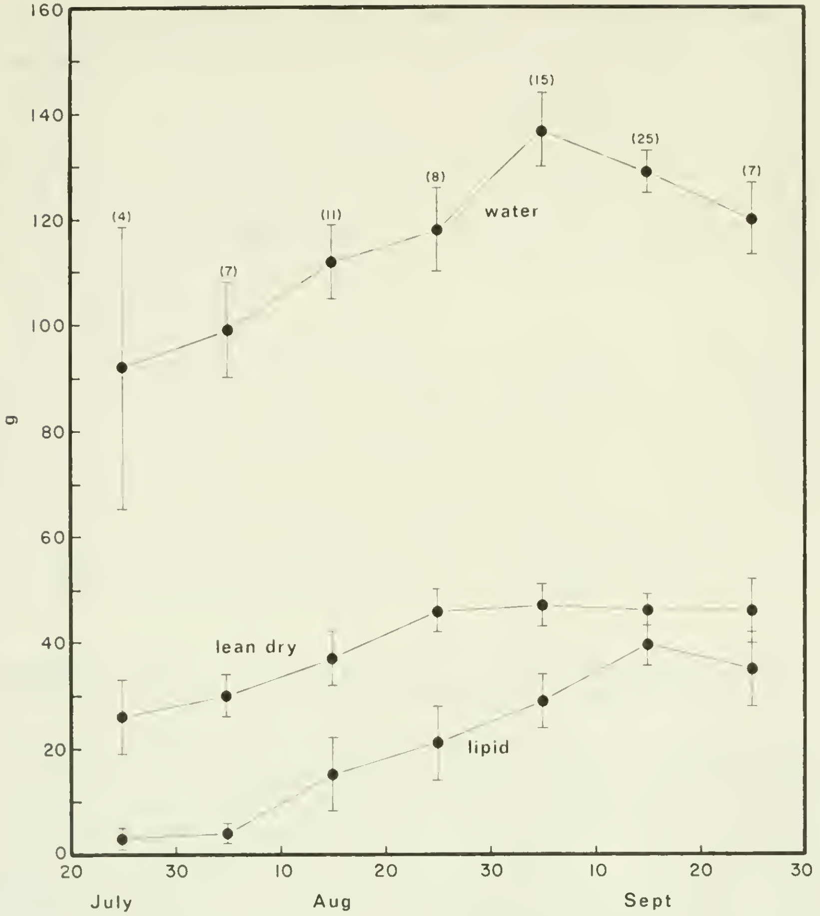


Fig. 6. Seasonal changes in mean weight of body components of juvenile *Spermophilus beldingi beldingi*. Vertical lines indicate two S.E. Sample size shown in parentheses.

expected for white fat because it is the primary form of intracorporeal energy storage in hibernators. Despite their comparatively limited mass, brown fat depots also show marked seasonal changes in size and may also be accurate indicators of general lipogenic activity.

It seems likely that *S. b. beldingi* do not hoard food; thus, all of the energy used during hibernation must come from catabolism of their own body tissues, principally fat. In juveniles it appears that fattening and overall growth were concurrent at first, but that caloric intake was then diverted primarily toward lipid synthesis and storage. This final phase was seen in a slowing of the increase in linear dimensions, in the leveling off of lean, dry body weight, and in the

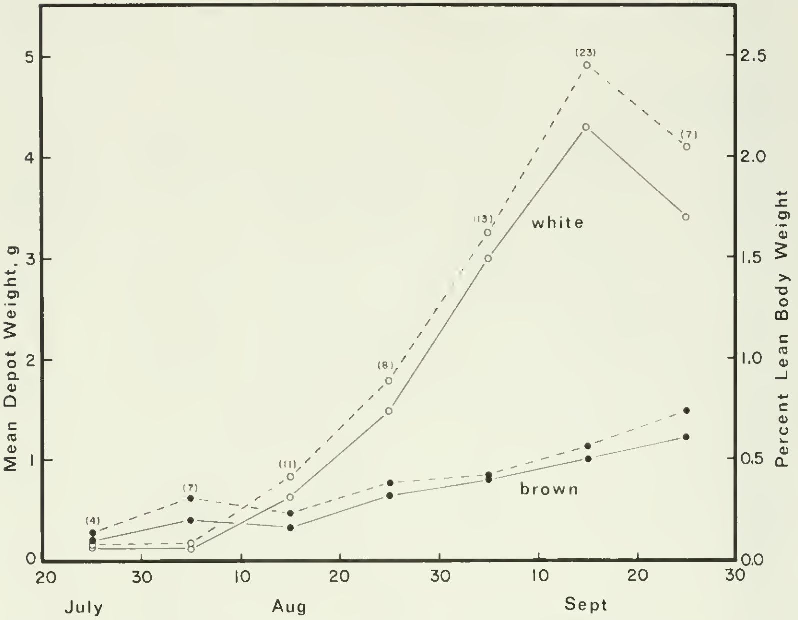


Fig. 7. Seasonal changes in mean absolute and relative weight of fat depots in juvenile *Spermophilus beldingi beldingi*. Sample size shown in parentheses.

mid-season pause in weight gain of individuals. The final relative stage of obesity attained was not as great as that observed in adults; however, the duration of hibernation may be about a month less in juveniles than in adults. A similar relationship was seen in *S. lateralis* (Jameson and Mead, 1964). The last juveniles to enter hibernation were from late litters and were excessively immature. Hock (1960) noticed the same phenomenon in *S. undulatus*. The ability of these immature individuals to survive a prolonged period of dormancy seems questionable, but we have some information suggesting otherwise. Consider, for example, the two females collected on 5 October. They were quite small, weighing only 137.5 and 150.1 g. Nevertheless, they had 19.7 and 30.0 g, respectively, of extractable carcass lipid. This was 61 and 88 percent of the lean, dry weight. In proportion, then, they had fat reserves comparable to those of normal-sized juveniles at the time of immergence. Perhaps the shift from general growth to lipogenesis occurs at an exceptionally small body size in juveniles from very late litters. This could be an important strategy for survival, particularly in populations existing in highly periodic environments. Mrosovsky (1971) has suggested that peak weight of hibernators at immergence is highly variable and will be determined by prevailing environmental conditions. Perhaps some of this variability in weight would seem less critical if the actual fat stores of the animals were known. It is not known how well the smaller juveniles survive hibernation, but we have observed every year that some very lean yearlings were among the first *S. b. beldingi* to emerge at Tioga Pass. This also underscores the difficulty of comparing our data with those of other workers. We have found that three functionally different age groups exist in *S. b. beldingi* at Tioga Pass: adults, yearlings, and juveniles. This can cause considerable confusion and distortion of data, particularly at the beginning and end of the active season, unless animals of known age are being dealt with. For example, in the fall, many of the smallest yearlings were active well into September and, on the basis of body weight, could not be distinguished from the largest juveniles at that time.

Seasonal Changes in Organ Size.— Various easily excised organs are often weighed in wild populations as indicators of growth and environmental adaptation. Our measurements of organs in juveniles are shown in absolute (Fig. 8) and relative terms (Fig. 9). The last sample in September consisted of four animals (all males) that were among the very last juveniles still active. They were smaller in body, kidney, liver, and spleen weight than animals sampled previously in the month and probably were from the last litters born that season. On the other hand, the adrenals of this last group weighed an average of 37 mg and were significantly heavier than those collected from the previous group in mid-September ($P<0.05$).

At one time it seemed that involution and hypofunction of all endocrines might be essential to normal hibernation. However, it eventually became clear that considerable variation existed in the functional status of endocrines, particularly the adrenal glands, at the onset of dormancy (Popovic, 1960). Within the last decade seasonal changes in adrenal size have been determined in several species of juvenile *Spermophilus*. There is considerable variation. For example, adrenal weights decreased seasonally in *S. b. oregonus* (McKeever, 1963), *S. tereticaudus* (Lyman and Chatfield, 1955; Neal, 1965) but increased in *S. beecheyi* (Tomich, 1962) and *S. richardsonii* (Clark, 1970). There are numerous problems associated with interpreting data of this type. Although adrenocortical secretion rate is probably a function of adrenal gland weight (Christian, 1962; Christian and Davis, 1964; Adams and Finn, 1972), there is no real assurance that this is true. The problem is exacerbated in juvenile hibernators in that normal growth and prehibernatory fattening may confuse the relationship between size and secretion rate when either absolute or relative weight changes are considered.

Increased adrenal weight has been most clearly linked to stress caused by increased social interaction (Christian, 1962); however, interplay among a multitude of factors is probably responsible for adrenal hypertrophy in many cases (Sheppard, 1968). In *S. b. beldingi* juveniles active at the very end of the season, for example, stress associated with difficulties in obtaining food and increased threat of predation might affect adrenal function.

Spleen size increased throughout the season. The same trend was

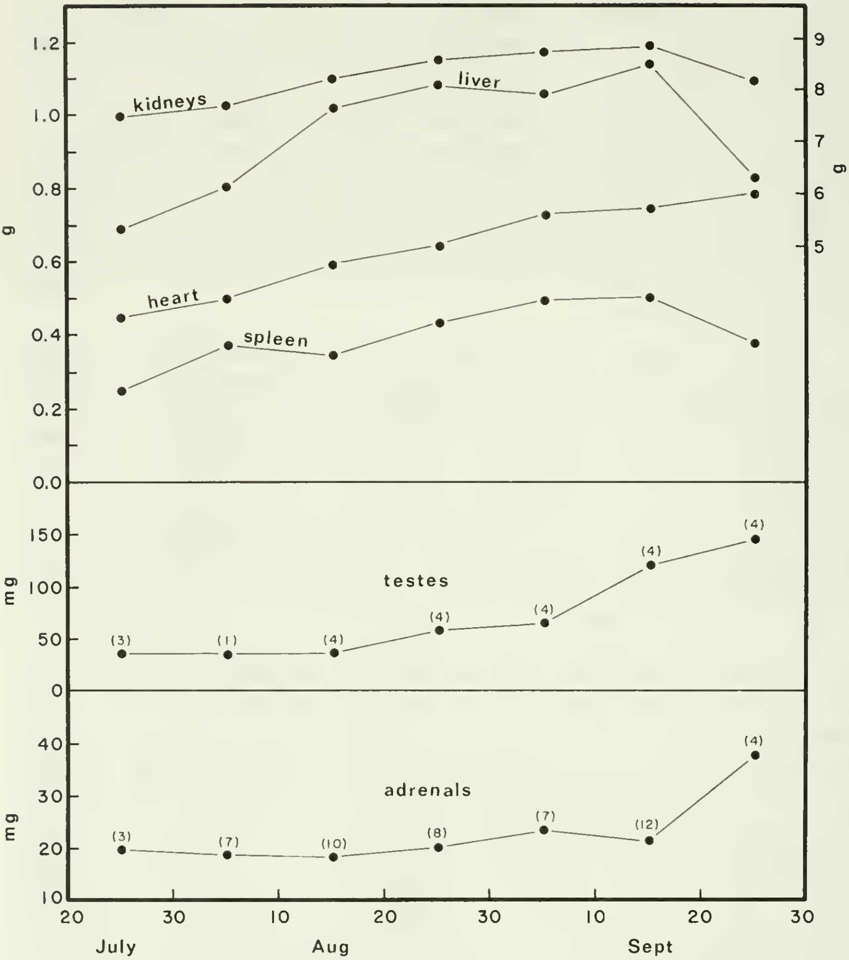


Fig. 8. Seasonal changes in mean organ weights of juvenile *Spermophilus beldingi beldingi*. Sample size shown for adrenals applies to other organs except testes.

observed in *S. b. oregonus* (McKeever, 1963), but, despite their similar body sizes, the spleens of juvenile *S. b. oregonus* were approximately twice as heavy as those of *S. b. beldingi*. The functional significance of this dramatic difference awaits investigation.

Kidneys enlarged slightly, in absolute terms, as the season progressed. Relative weight decreased, however. Heart weight increased in both absolute and relative terms. It is tempting to relate the size of these organs, particularly the heart, at the end of the season to their probable functional roles during torpor. The heart has a major role in the circulatory adjustments made during the

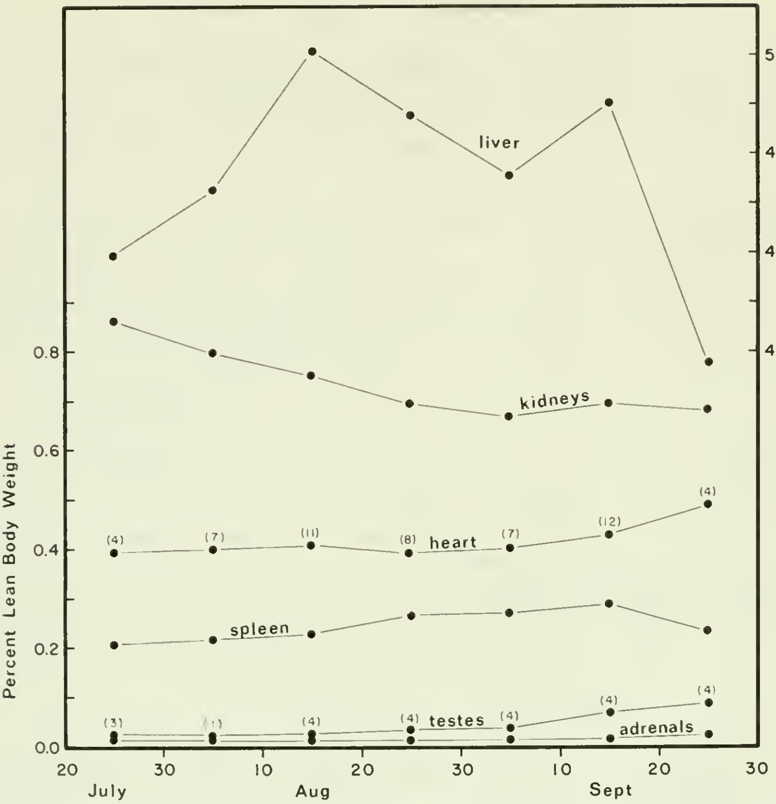


Fig. 9. Seasonal changes in organ size as a percentage of lean body weight in *Spermophilus beldingi beldingi*. Sample size shown for heart applies to other organs except testes.

arousals that occur regularly throughout the hibernation period. It may also be a source of heat that supplements the heat production of brown fat during arousals (Burlington et al., 1972). A small increase in heart weight was detected even during hibernation in the hedgehog, *Erincaeus europaeus* (Johansson and Senturia, 1972). Pretorpor and intratorpor hypertrophy of cardiac muscle could facilitate cardiac efficiency during arousals.

Livers reached maximum size early in the season then decreased significantly between our last two samples in September ($P<0.05$). This final decrease is difficult to understand but may be related to the unusual immaturity of animals active at the very end of the season.

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NEW SPECIES OF AMERICAN CORTHYLINI (COLEOPTERA: SCOLYTIDAE)[1]

Stephen L. Wood[2]

Abstract.— The following species are described as new to science: *Monarthrum cordicticum, M. tetradontium, M. conversum, M. bidentatum* (Mexico), *M. subgranulatum* (Honduras), *M. morsum, M. carinatum, M. adustum, M. insignatum, M. fastigiorum, M. limulum, M. carinulum, M. infradentatum, M. corculum, M. posticum, M. proximum* (Costa Rica), *M. proprium, M. notatum* (Costa Rica, Panama), *M. bifoveatum* (Costa Rica, Venezuela), *Corthycyclon caliginis, C. furvus, C. morulus* (Costa Rica), *C. tardus* (Costa Rica, Panama), *Corthylocurus debilis* (Costa Rica, Panama).

The 24 species of ambrosia beetles described below as new to science were discovered during the preparation of my monograph of the Scolytidae of North and Central America. They are named here in order to avoid nomenclatural confusion and to facilitate identification in the interim before publication of the monograph. The species treated below are in the tribe Corthylini and represent the genera *Monarthrum* (19), *Corthycyclon* (4), and *Corthylocurus* (1). As indicated in the above abstract, they are from the following countries: Mexico (4), Honduras (1), Costa Rica (13), Costa Rica and Panama (4), Costa Rica and Venezuela (1).

Monarthrum cordicticum, n. sp.

This species is distinguished from *cordatum* (Blandford) in the male by the more gradual elytral declivity, by the less strongly, less abruptly elevated lateral margin of the declivity, and by the larger, acutely pointed declivital spine 1 and smaller spine 2. The female is indistinguishable from *cordatum*.

Male.— Length 2.3 mm (paratypes 2.0-2.4 mm), 3.1 times as long as wide; color yellowish brown, except anterior half of pronotum and elytral declivity dark brown.

Frons and pronotum as in *bispinum* (Blandford).

Elytra 1.8 times as long as wide, 1.4 times as long as pronotum; sides straight and parallel almost to apex, then broadly rounded, rather deeply, subacutely emarginate on median third behind; surface subreticulate, except almost smooth near declivity, punctures obscure. Declivity steep; concavely truncate; margin abrupt; spine 1 almost at suture, rather small, sharply pointed, 2 in line with striae 3, twice as long as 1, pointed, curved very slightly mesad, lateral margin from spine 2 to suture subacute, rather strongly elevated, descending gradually on its inner margin; rather deeply, subacutely emarginate at suture; excavated area rugose-reticulate, rather numerous, confused punctures on median third, a conical

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[1] The research that resulted in the discovery of these insects was sponsored by the National Science Foundation.

[2] Department of Zoology, Brigham Young University, Provo, Utah 84602. Scolytidae contribution No. 52

spine just below middle in line with discal interstriae 3, this denticle about as large as spine 1. Subglabrous.

Female.— Similar to male, except posterior face of antennal club without long hair; anterior margin of pronotum feebly serrate; declivity flat on lower half, more nearly convex and shallowly sulcate from suture to interstriae 2 above, small, pointed denticles on interstriae 3 at base and also slightly above middle.

Type Locality.— Thirty km or 19 miles E Tulancingo, Hidalgo, Mexico.

Type Material.— The male holotype, female allotype, and 20 paratypes were collected at the type locality on 12-VI-67, at 2300 m, No. 15, from a *Quercus* log, by me.

The holotype, allotype, and paratypes are in my collection.

Monarthrum proprium, n. sp.

This species is distinguished from *dimidiatum* (Ferrari) by the smaller size, by the smoother, more brightly shining frons, by the more narrowly oval antennal club, and by the shorter, less strongly explanate elytral declivity.

Male.— Length 1.9 mm (paratypes 1.6-2.1 mm), 3.2 times as long as wide; color yellowish brown to dark reddish brown.

Frons convex, lower area, sides and vertex rugose-reticulate, large central area smooth, shining, punctures rather coarse, close; vestiture sparse, inconspicuous. Antennal club oval, 1.3 times as long as wide, sutures feebly procurved.

Pronotum 1.4 times as long as wide; sides almost straight and parallel on basal two-thirds, rather broadly rounded in front; anterior margin armed by about 10 serrations; summit on anterior third; anterior slope very steep, rather finely asperate; posterior areas reticulate, punctures minute. Glabrous.

Elytra 1.8 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on basal half, very slightly converging to level of sutural apex, then broadly rounded, rather deeply, obtusely emarginate on median fourth behind; surface reticulate, punctures obscure. Declivity rather steep, rather shallowly, broadly concave; margins rounded except acute near apex and at margins of emargination; lateral margins with spine 1 one-third and spine 2 two-thirds of declivital length from base, both on inner margin of lateral margin, each moderately small, conical, pointed, subequal in size; excavated area rugose-reticulate, except smooth and shining on median third, punctures on shining area small, sparse. Subglabrous.

Female.— Similar to male except antennal club 1.0 times as long as wide, ornamented on posterior face by long hair; anterior margin of pronotum more finely serrate; elytral declivity slightly less strongly impressed, spines smaller.

Type Locality.— Cerro Punta, Chiriqui, Panama.

Type Material.— The male holotype, female allotype, and 10 paratypes were taken at the type locality (labeled Volcan Chiriqui) on 11-I-64, 1800 m, Nos. 371, 398 (type), in a tree limb, No. 404, *Inga*, by me. Three paratypes were taken 15 km SE Cartago, Cartago, Costa Rica, 24-IX-63, 1800 m, No. 249, tree bole, S. L. Wood; one paratype bears identical data except No. 17B from *Conostegia oerstediana.*

The holotype, allotype, and paratypes are in my collection.

Monarthrum bifoveatum, n. sp.

The male of this species is rather similar to *proprium* Wood except for the frons which is as in *dentigerum* (LeConte); the female frons is radically different and suggests a relationship to *fimbriacorne* (Blandford).

Male (allotype).— Length of paratypes 1.8-2.0 mm, 3.0 times as long as wide; color light brown, anterior half of pronotum and posterior third of declivity often darker.

Frons about as in *dentigerum* except reticulation and punctures finer. Pronotum, elytral outline, and sculpture of elytral disc about as in *dentigerum* except elytral disc entirely reticulate, punctures much finer, rather obscure. Elytral declivity very similar to *proprium* except much less strongly explanate, emargination at suture much narrower, not as deep, floor of excavated area slightly wider.

Female (holotype).— Length 1.9 mm; similar to male except frons divided into thirds by two shallow, parallel grooves from epistomal margin to upper level of eyes, each groove with a row of short, stout bristles, median third smooth, shining, lateral thirds mostly reticulate, with lower area at inner margin of eye rather strongly, subfoveately impressed; a few setae along epistomal margin; posterior face of antennal club ornamented by long hair; anterior margin of pronotum unarmed; elytral declivity less strongly impressed, much as in female *proprium.*

Type Locality.— San José, San José, Costa Rica.

Type Material.— The female holotype and two paratypes were taken at the type locality on 12-XI-63, 1300 m, No. 187, from a tree limb, by me; the male allotype and seven paratypes should bear identical data except they were erroneously dated 22-X-63. Six paratypes are from Escasu, San José, Costa Rica, 2-X-63, 1300 m, No. 216, *Spondias purpurea*, S. L. Wood; 26 paratypes are from El Laurel experiment station, 12 km SW Caracas, Venezuela, 1-V-70, 1300 m, No. 474, tree bole, S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Monarthrum tetradontium, n. sp.

This species is distinguished from *exornatum* (Schedl) by the smoother, much more deeply punctured elytral disc and by the larger, much stouter declivital spines.

Male.— Length 2.4 mm, 3.3 times as long as wide; color dark brown, basal half of elytra slightly lighter.

Frons convex, reticulate, becoming rugose-reticulate toward epistoma, punctures moderately coarse, close; vestiture inconspicuous.

Pronotum 1.4 times as long as wide; sides straight and parallel on basal two-thirds, broadly rounded in front; anterior margin subserrate; otherwise as in *scutellare* (LeConte).

Elytra 1.9 times as long as wide, 1.3 times as long as pronotum; sides straight and parallel on basal half, distinctly tapered on posterior half, rather narrowly rounded behind, deeply emarginate on median sixth; surface almost smooth, obscurely reticulate in some areas, punctures rather small, moderately deep, confused except strial and interstrial punctures almost in rows near declivity. Declivity rather steep, flattened, lateral margins rounded, not elevated, apex moderately explanate; interstriae 2 (actually displaced interstriae 3) armed one-third and two-thirds distance from base by spines; spine 1 conical, pointed, about as high as its basal width; spine 2 slightly higher, very stout, blunt; surface near base of spine 2 rugose-reticulate, remaining area almost smooth and deeply punctured. Vestiture sparse, confined to declivity.

Type Locality.— Mt. Colima, Jalisco, Mexico.

Type Material.— The male holotype was taken at the type locality on 2-XII-48.

The holotype is in my collection.

Monarthrum conversum, n. sp.

This species is distinguished from *exornatum* (Schedl) by the larger, stouter size and by the very different elytral declivity.

Male.— Length 3.6 mm (paratypes 3.1-3.6), 3.0 times as long as wide; color very dark reddish brown, basal half of pronotum lighter.

Frons essentially as in *exornatum*, except upper areas almost smooth and with minute, impressed points.

Pronotum 1.3 times as long as wide; sides straight and parallel on basal half, rather narrowly rounded in front; anterior margin armed by about 10 coarse serrations; about as in *scutellare* (LeConte), except punctures on posterior areas slightly larger, those near base of disc transversely elongate. Glabrous.

Elytra 1.5 times as long as wide, 1.2 times as long as pronotum; outline about as *exornatum* except stouter; surface shining, with rather numerous fine, irregular lines, numerous impressed points, punctures rather small, moderately deep, confused. Declivity steep, broadly, concavely excavated; lateral margins moderately elevated, rounded except on apical fifth of declivital length; spine 1 on interstriae 3 at basal margin, as high as its basal width, subconical; spine 2 two-thirds declivital length from base, displaced less than its basal width from margin, subcylindrical, very slightly longer than its basal width, its apex subtruncate, its dorsal angle subacute; excavated area mostly shining, with numerous minute, impressed points, punctures moderately coarse, rather deep, lateral areas near margins rugose-reticulate. Subglabrous.

Female.— Similar to male except antennal scape with fine, short hair; anterior margin of pronotum obscurely serrate; elytral disc reticulate, punctures somewhat obscure; declivity mostly broadly convex, moderately sulcate on upper half, subconcave below; spine 1 much smaller; spine 2 at middle of declivity midway between lateral margin and suture, similar to spine 1 in size and shape; declivital surface rugose-reticulate, punctures small, obscure.

Type Locality.— Four miles or 6 km W Tepic, Nayarit, Mexico.

Type Material.— The male holotype and female allotype were taken at the type locality on 13-VII-65, 1000 m, No. 240, from a tree limb, by me. One paratype is from Volcan Colima, Jalisco, 23-VI-65, 2500 m, in flight, S. L. Wood.

The holotype, allotype, and paratype are in my collection.

Monarthrum morsum, n. sp.

This species is distinguished from *exornatum* (Schedl) by the smaller size, and by the steeper, narrower elytral declivity with different sculpture and arrangement of the spines.

Male.— Length 1.5 mm, 2.8 times as long as wide; color yellowish brown, posterior half of elytra darker.

Frons and pronotum as in *exornatum*, except pronotum 1.15 times as long as wide.

Elytra 1.5 times as long as wide, 1.3 times as long as pronotum; outline as in *conversum* Wood, except more strongly tapered on posterior third; disc obscurely reticulate on basal third, smooth and shining elsewhere, numerous impressed points present, punctures fine, distinct, in strial rows on posterior half. Declivity moderately steep, rather broadly, strongly sulcate; spine 1 on interstriae 2 near base, rather small, pointed, its upper margin feebly subcostate; spine 2 small, conical, two-thirds declivital length from base, displaced fron lateral margin one-third distance toward suture; feebly explanate below; surface of impressed area shining, numerous impressed points present, punctures evident only near suture. Vestiture confined to declivity, of short moderately abundant hair.

Type Locality.— Pandora, Limon, Costa Rica.

Type Material.— The male holotype was taken at the type locality on 23-VIII-63, 50 m, No. 135, from a limb 8 cm in diameter, by me.

The holotype is in my collection.

Monarthrum carinatum, n. sp.

This species is distinguished from *exornatum* (Schedl) by the larger size, by the fine, median, frontal carina, and by the steeper, more strongly impressed, more weakly explanate elytral declivity.

Male.— Length 2.7 mm (paratypes 2.5-2.8 mm), 3.0 times as long as wide; color dark brown.

Frons convex, a fine, acute, low carina from epistoma almost to upper level of eyes; surface on lower half etched by minute, subaciculate lines, more nearly smooth and shining above, punctures fine but superficially appearing large, indistinct, obscurely subaciculate; obscure vestiture confined to epistomal margin. Antennal club broadly oval, 1.3 times as long as wide.

Pronotum 1.3 times as long as wide, about as in *exornatum*, except anterior margin rather coarsely serrate.

Elytra 2.0 times as long as wide, 1.5 times as long as pronotum; outline more broadly rounded behind than *exornatum;* disc as in *exornatum*, declivity steeper, more deeply, more broadly impressed; spines 1 and 2 small, conical, pointed, 1 one-third declivital length from base, on rounded margin, 2 two-thirds declivital length from base, slightly mesad of margin; surface of impressed area finely rugose-reticulate, except almost smooth and very finely punctured near suture on lower half; apical margin acute, weakly explanate. A few setae on or near margins of declivity.

Female.— Similar to male except frontal carina longer; posterior face of antennal club ornamented by longer hair; elytral declivity less strongly impressed, denticles slightly smaller.

Type Locality.— Cerro de la Muerte, San José, Costa Rica.

Type Material.—The male holotype, female allotype, and 12 male paratypes were taken at the type locality on 6-VIII-63, 2600 m, No. 113, 30 cm bole of Melastomaceae(?) tree, by me.

The holotype, allotype, and paratypes are in my collection.

Monarthrum adustum, n. sp.

This species is distinguished from *punctifrons* (Blandford) by the larger size and by the very different elytral declivity in both sexes.

Male.— Length 3.1 mm (paratypes 2.8-3.4 mm), 3.1 times as long as wide; color dark brown, bases of pronotum and elytra often of lighter color.

Frons, pronotum, and elytral disc as in *punctifrons*. Elytral declivity similar to *punctifrons* but must more narrowly impressed, deeply sulcate on basal half; tubercle at base on interstriae 1 almost obsolete; spines 1 and 2 subequal in size, small, conical, 2 at middle of declivity; surface reticulate. Vestiture largely confined to declivity, of short, moderately abundant hair.

Female.— Similar to male, except posterior face of antennal club ornamented by long hair; anterior margin of pronotum weakly serrate; elytral declivity less strongly, more narrowly impressed; space between members of first pair of denticles equal to distance between members of second pair.

Type Locality.— Cerro de la Muerte, San José, Costa Rica.

Type Material.— The male holotype and 29 paratypes were taken at the type locality on 6-VIII-63, 2800 m, No. 110, *Quercus costaricensis*, by me; the allotype and 19 paratypes bear identical data except 1-VIII-66, Nos. 44 and 45, *Quercus*. Ten paratypes are from Volcan Irazu, Cartago, Costa Rica, 13-VII-63, 2300 m, No. 4, *Quercus*, S. L. Wood; and five paratypes are from Volcan Poas, Heredia, Costa Rica, 19-VII-66, 2600 m, No. 4, *Quercus*, S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Monarthrum insignatum, n. sp.

This species is distinguished from *hoegi* (Blandford) by having the median third of the elytral declivity smooth, with numerous minute, impressed points, and by the minute features of the frons as described below.

Male (allotype).— Length 2.4-2.6 mm, 2.9 times as long as wide; color dark brown.

Frons as in *hoegi*, except punctures slightly coarser, deeper, median carina slightly sharper. Pronotum and elytra as in *hoegi*, except median third of declivital excavation smooth, with numerous minute, impressed points.

Female (holotype).— Length 1.6 mm; similar to female *hoegi*, except transverse impression above epistoma deeper, its upper margin on median line rising very abruptly to conspicuous median tubercle, tubercle much larger than in *hoegi*, frons protruding slightly toward tubercle; elytral declivity smooth, with points.

Type Locality.— Volcan Poas, Heredia, Costa Rica.

Type Material.— The female holotype, male allotype, and two paratypes were taken at the type locality on 14-VII-63, 1500 m, No. 44, tree branch, S. L. Wood. Five paratypes bear similar data except 19-VI-66, 2600 m, No. 4, shrub branch.

The holotype, allotype, and paratypes are in my collection.

Monarthrum fastigiorum, n. sp.

This species is distinguished from *insignatum* Wood by the smaller size, by the more protuberant female frons with a subcarinate dorsal continuation of the median tubercle, and by the different male declivity.

Male (allotype).— Length 2.0 mm, 2.7 times as long as wide; color brown, somewhat bicolored.

Frons as in *insignatum*, except with a fine, low, median carina.

Pronotum and elytral disc as in *insignatum*. Elytral declivity similar to *insignatum*, except steeper, more widely, more shallowly impressed, about one-third of impressed area lateral to a line drawn from spine 1 to spine 2, spine 2 equal distance from suture and lateral margin.

Female (holotype).— Length 2.3 mm; similar to female *insig-*

natum, except frons more protuberant, median tubercle larger, with weak carina extending from its summit to upper level of eyes, surface more coarsely, more uniformly reticulate; declivital spine 2 almost as close to suture as to lateral margin.

Type Locality.— Tapanti, Cartago, Costa Rica.

Type Material.— The female holotype, male allotype, and one male paratype were taken at the type locality on 24-X-63, 1300 m, No. 245, from a woody vine, by me.

The holotype, allotype, and paratype are in my collection.

Monarthrum bidentatum, n. sp.

This species is distinguished from *bidens* (Blandford) by the smaller size, by the more finely punctured frons, and by other differences on the female frons and on the male declivity.

Male.— Length 2.3 mm (paratype 2.3-2.5 mm), 2.8 times as long as wide; color dark brown.

Frons broadly convex, a distinct, transverse impression just above epistoma; surface almost smooth, except rugose-reticulate in impressed area, upper areas with impressed points and a few fine punctures; vestiture inconspicuous.

Pronotum 1.2 times as long as wide; as in *punctifrons* (Blandford) and other allied species.

Elytra 1.5 times as long as wide, 1.3 times as long as pronotum; sides straight and parallel on basal two-thirds, converging very slightly to level of sutural apex, then abruptly rounded behind, except moderately emarginate on median fourth; surface reticulate, punctures minute, confused. Declivity rather abrupt, steep, broadly sulcate; sulcus widest between spines 1 and 2; spine 1 at base on interstriae 3, very small; spine 2 closer to suture than spine 1, or to lateral margin, its lower margin at level of sutural apex; spine 2 laterally compressed, not as high as length of its longitudinal basal axis, its summit emarginate and bituberculate; surface reticulate. Vestiture sparse, confined to declivity.

Female.— Similar to male, except transverse frontal impression very deep, deepest on its median third, occupying lower two-thirds of area below upper level of eyes, punctures in lateral areas larger, deeper; posterior face of antennal club ornamented by long hair; anterior margin of pronotum unarmed; declivity much more shallowly, more narrowly sulcate, lateral margins more evenly rounded, spines 1 and 2 of similar size and conical shape, equally spaced from suture.

Type Locality.— Six miles or 9 km NE Teziutlan, Puebla, Mexico.

Type Material.— The male holotype, female allotype, and 31 paratypes were taken at the type locality on 2-VII-67, 1600 m, Nos. 135 and 145 (type), in *Alnus*, No. 140, in a tree limb, by me.

The holotype, allotype, and paratypes are in my collection.

Monarthrum notatum, n. sp.

This species is distinguished from *bidentatum* Wood by the color, by the conical spine 2 on the male declivity, and by the deeper, narrower declivital impression.

Male.— Length 2.5 mm (paratypes 2.2-2.5 mm), 3.2 times as long as wide; color dark brown, most specimens with elytral disc yellowish brown.

Frons as in *bidentatum*, except punctures larger. Pronotum and elytra disc as in *bidentatum;* elytral declivity much more deeply impressed than in *bidentatum*, lateral margins more narrowly rounded, spine 2 conical, much larger than 1, its height equal to its basal width, much closer to lateral margin than to suture, surface reticulate, except smooth on interstriae 2. Vestiture confined to declivity, sparse.

Female.— Similar to female *dentatum*, except frons more evenly convex, deepest part of transverse impression rugose-reticulate (smooth in *bidentatum*); declivital sulcus much deeper, narrower, sutural emargination deeper, narrower, its margins distinctly elevated.

Type Locality.— Volcan Poas, Heredia, Costa Rica.

Type Material.— The male holotype, female allotype, and 11 paratypes were taken at the type locality on 14-VII-63, 2500 m, No. 50, from a large log; one paratype is from the same locality 19-VI-66, 2600 m, No. 7, leguminose shrub; and two paratypes are from Cerro Punta (labeled Volcan Chiriqui), Panama, 11-I-64, 1800 m, No. 371, *Inga;* all taken by me.

The holotype, allotype, and paratypes are in my collection.

Monarthrum limulum, n. sp.

This species is distinguished from *robustum* (Schedl) by the smoother pronotal disc, by the minute declivital granules which have replaced the punctures, and by having spine 2 strongly displaced toward the suture.

Male.— Length 2.4 mm (paratypes 2.2-2.6 mm), 2.5 times as long as wide; color brown.

Frons essentially as in *robustum.*

Pronotum as in *robustum* except disc smooth, minutely reticulate, punctures very minute.

Elytra with basic contours about as in *robustum*, with declivity commencing at middle, except lower half steeper; disc reticulate, punctures very fine, confused; declivital punctures anterior to spine 1 replaced by minute granules, granules on middle third almost obsolete, granules below spine 2 rather coarse; spine 1 conical, without ridge extending cephaled from its summit; spine 2 slightly closer to lateral margin than to suture, not connected to lateral margin, conical, slightly larger than in *robustum;* declivital surfaces reticulate, almost rugose in some areas. Vestiture confined to declivity, of fine, short, moderately abundant hair.

Female.— Similar to female *robustum*, except frons more coarsely punctured; pronotal disc more finely punctured; declivity reticulate, punctures minute with most of them accompanied by a very fine granule; declivital spine 2 almost as close to suture as to lateral margin.

Type Locality.— Tapanti, Cartago, Costa Rica.

Type Material.— The male holotype, female allotype, and 12 paratypes were taken at the type locality on 17-IX-63, 1300 m, No. 178, from a woody vine, by me.

The holotype, allotype, and paratypes are in my collection.

Monarthrum carinulum, n. sp.

This species is distinguished from *vittatum* (Blandford) by the absence of a transverse frontal groove and the presence of a median frontal carina in both sexes, and by the different male declivity.

Male.— Length 2.6 mm (paratypes 2.3-2.6 mm), 2.7 times as long as wide; color brown.

Frons broadly convex, a low, subacute median carina extending from epistoma almost to upper level of eyes; surface strongly reticulate, punctures fine, moderately abundant; glabrous.

Pronotum, elytral disc, and declivity as in *insignatum* Wood.

Female.—Similar to male except frontal carina higher and longer; posterior face of antennal club ornamented by a tuft of hair; declivity less strongly impressed, slightly narrower, spines 1 and 2 slightly smaller, tubercle at apex of striae 1 entirely absent.

Type Locality.— Tapanti, Cartago, Costa Rica.

Type Material.— The male holotype, female allotype, and eight paratypes were taken on 26-XI-63, 1300 m, No. 265, in *Phoebe mexicana* branches, by me; six paratypes bear similar data except 17-IX-63, No. 184 in *Miconia caudata*, and No. 178 in a woody vine.

The holotype, allotype, and paratypes are in my collection.

Monarthrum subgranulatum, n. sp.

This species is distinguished from *granulatum* Bright by the frontal and declivital characters described below.

Male.— Length 2.7 mm (paratypes 2.4-2.8 mm), 2.7 times as long as wide; color dark reddish brown.

Frons broadly convex, a weak transverse impression just above epistomal margin; lower half of area below upper level of eyes strongly rugose-reticulate, upper area smooth, with moderately abundant impressed points and rather small punctures; transition between areas rather abrupt; rugose area sparsely, finely pubescent.

Pronotum and elytral disc essentially as in *punctifrons* (Blandford). Elytral declivity steep, strongly sulcate, more broadly flattened below spine 2; sulcus occupying median half on upper two-thirds, sutural interstriae feebly elevated, gradually ascending to broadly rounded, rather strongly elevated lateral margins; spine 1 very small, at middle on margin; spine 2 one-fourth declivital length from apex, slightly closer to lateral margin than to suture, moderately large, conical, about as high as its basal width; inner margin of middle third of sulcus, just mesad of spine 1, armed by a row of about four to six small granules all smaller than spine 1; surface reticulate. Vestiture very sparse, confined to margins of declivity.

Female.— Similar to male, except rugose area on frons slightly larger and with much more abundant, fine, hairlike pubescence; posterior face of antennal club ornamented by a tuft of long hair; anterior margin of pronotum unarmed; declivity less strongly impressed, lateral margins more broadly rounded, spine 2 smaller, granules absent near summit of inner margin.

Type Locality.— Cerro Peña Blanca, Honduras.

Type Material.— The male holotype, female allotype, and 26 paratypes were taken at the type locality on 23-IV-64, 1900 m, No. 531, from *Persea popenoi*, by me.

The holotype, allotype, and paratypes are in my collection.

Monarthrum infradentatum, n. sp.

This species is distinguished from all preceding species by the obliquely truncate elytral declivity, with the ventrolateral margin acutely elevated from the sutural emargination to the level of spine 1 and by the absence of spine 2. It is distinguished from the three following species by the presence of a large spine on the margin of the apical emargination of the elytra.

Male.— Length 1.4 mm, about 3.0 times as long as wide (elytra spread); color dark reddish brown, base of pronotum pale.

Frons broadly convex, a weak transverse impression just above epistoma; surface reticulate, small punctures obscurely indicated.

Pronotum 1.3 times as long as wide; about as in *punctifrons* (Blandford) except anterior margin armed by eight serrations.

Elytra about 1.7 times as long as wide, about 1.3 times as long as pronotum, sides almost straight and parallel to level of sutural apex, very broadly rounded to apical denticles and emargination; surface reticulate, minute punctures apparently in rows, except confused near base. Declivity very steep, truncate, shallowly concave; basal margin rather abruptly rounded to striae 3, acutely margined from there to apical emargination; spine 1 small, conical, situated just below margin on interstriae 3; face of declivity smooth, shining, with minute points and small punctures, except somewhat rugulose near margins; sutural emargination rather narrow, deep, its margin extended perpendicular to declivital surface forming a large denticle on its basal half, denticle height equal to its greatest basal width. Vestiture confined to declivity near margins, sparse, mostly short.

Female.— Similar to male, except posterior face of antennal club ornamented by long hair; anterior margin of pronotum unarmed; declivity weakly convex, lateral margin acutely raised on lower third, margin of emargination weakly elevated, denticle not evident.

Type Locality.— Rincon de Osa, Puntarenas, Costa Rica.

Type Material.— The male holotype, female allotype, and one male paratype were taken at the type locality on 11-VIII-66, 30 m, No. 86, from a tree limb, by me.

The holotype, allotype, and paratype are in my collection.

Monarthrum corculum, n. sp.

This species is distinguished from *infradentatum* Wood by the larger size and by characters of the elytral declivity.

Male.— Length 1.8 mm (paratypes 1.7-1.9 mm), 2.8 times as long as wide; color dark reddish brown, except base of pronotum pale.

Frons, pronotum, and elytral disc as in *infradentatum*. Elytral declivity similar to *infradentatum*, except declivital outline heart-shaped, spine 1 on basal margin at interstriae 3, spine 2 two-thirds declivital length from base equal distances from suture and lateral margin; sutural emargination strongly obtuse, shallow, its margin moderately elevated but not forming a tooth; declivital surface shining, finely, rather closely punctured. Vestiture confined to declivity, consisting of moderately abundant, short hair.

Female.— Similar to male, except frons with a rather strong, transverse impression just above epistoma; posterior face of antennal club ornamented by a tuft of long hair; anterior margin of pronotum unarmed; declivity with acute margin only on lower third, apical margin less strongly elevated.

Type Locality.— Turrialba, Cartago, Costa Rica.

Type Material.— The male holotype, female allotype, and 42 paratypes were taken at the type locality on 9-III-64, 700 m, No. 497B, from a woody vine, by me. One paratype is from Finca La Lola, Limon, Costa Rica, 22-VI-63, *Theobroma cacao*, J. L. Saunders.

The holotype, allotype, and paratypes are in my collection.

Monarthrum posticum, n. sp.

This species is distinguished from *corculum* Wood by the much more coarsely punctured frons, by the smooth elytra, and by the different declivity.

Male.— Length 1.9 mm (paratypes 1.7-2.1 mm), 2.6 times as long as wide; color dark reddish brown, except base of pronotum usually pale.

Frons as in *corculum*, except surface smooth, with rather dense impressed points and rather coarse punctures.

Pronotum and elytra similar to *corculum*, except slightly stouter; elytral disc smooth and shining, except obscurely reticulate near base, strial punctures minute, in rows. Elytral declivity as in *corculum*, except much less strongly impressed, posterolateral angles much more abrupt, surface smoother, brightly shining, punctures much larger.

Female.— Similar to male, except frons more nearly subgranulate; posterior face of antennal club ornamented by a tuft of long hair; anterior margin of pronotum unarmed; declivity with lateral margin on basal third more broadly rounded, lateral two-thirds more nearly convex.

Type Locality.— Santa Ana, San José, Costa Rica.

Type Material.— The male holotype, female allotype, and 17 paratypes were taken at the type locality on 4-X-63, 1300 m, No. 222, from a tree limb; 14 paratypes are from Finca Gromaco on Río Coto Brus, Puntarenas, 4-VII-63, 500 m, Nos. 57, 68, 80, woody vines and tree seedlings; 19 paratypes are from Rincón de Osa, Puntarenas, 11-VIII-66, 30 m, No. 85, tree limb; 1 paratype is from Tapanti, Cartago, 24-X-63, 1300 m, No. 268, tree limb; all were taken in Costa Rica by me.

The holotype, allotype, and paratypes are in my collection.

Monarthrum proximum, n. sp.

This species is distinguished from *posticum* Wood by the larger average size and by characters of the frons and declivity as described below.

Male.— Length 2.3 mm (paratypes 1.9-2.3 mm), 2.4 times as long as wide. As in *posticum*, except frons more finely punctured, reticulate on lower half; posterolateral angles of elytral declivity abrupt (narrowly rounded in *posticum*), distance between apical and subapical margins greater.

Female.— Similar to female *posticum*, except transverse impression above epistoma deeper, more abrupt, frons almost entirely reticulate.

Type Locality.—San Isidro del General, Puntarenas, Costa Rica.

Type Material.— The male holotype, female allotype, and seven paratypes were taken at the type locality on 5-XII-63, 1000 m, No. 284, from *Miconia pubescens;* two paratypes are from Finca Gromaco on Río Coto Brus, Puntarenas, 14-VII-63, 500 m, No. 57, log; 20 paratypes are from Rincón de Osa, Puntarenas, 11-VIII-66, 30 m, No. 85, limb; and one paratype is from Río Damitas, Dota Mts., San José, 22-VIII-63, 250 m; all were taken in Costa Rica by me.

The holotype, allotype, and paratypes are in my collection.

Corthycyclon caliginis, n. sp.

This species is distinguished from others in the genus by the size, by the rather strongly, continuously elevated declivital interstriae 1, with 2 moderately impressed, and by the absence of punctures and tubercles on the declivity.

Female.— Length 2.1 mm (paratypes 2.0-2.1 mm), 2.3 times as long as wide; color almost black.

Frons feebly concave from eye to eye from epistoma to vertex, surface reticulate, except almost smooth on lower median area, punctures small to minute, shallow, not clearly impressed; vestiture of very fine, moderately long hair of uniform distribution, slightly longer at margins. Antennal club 1.5 times as long as wide; a small tuft of hair at apex.

Pronotum 1.04 times as long as wide; sides almost straight and parallel on basal half, rather narrowly rounded in front; anterior margin armed by a pair of slender, median teeth; summit indefinite, slightly behind middle; anterior half closely asperate; posterior half reticulate, reticulation also extending between asperities on anterior half, punctures small, moderately abundant, those near base of disc finely tuberculate on their posterior margins. Pubescence of fine, short, moderately abundant hair.

Elytra 1.4 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; disc subshining, surface with obscurely impressed lines and other minute irregularities; punctures obsolete on posterior half, very small and confused on basal half. Declivity steep, convex, except moderately sulcate on interstriae 2, 1 uniformly elevated from base to near apex; surface reticulate, punctures and granules obsolete. Vestiture largely confined to posterior third of elytra, of fine, short, confused hair.

Male.— Similar to female, except frons moderately convex, strongly reticulate, with fine punctures, subglabrous; antennal club without apical tuft of hair.

Type Locality.— Sixteen km SE Cartago, Cartago, Costa Rica.

Type Material.— The female holotype, male allotype, and two paratypes were taken at the type locality on 24-IX-63, 1800 m, Nos. 195, from a tree seedling, and 196 (type) from a woody vine, by me.

The holotype, allotype, and paratypes are in my collection.

Corthycyclon furvus, n. sp.

This species is distinguished from *caliginis* Wood by the smaller size, by the stouter body form, by the more deeply concave female frons, and by the row of subgranulate punctures on declivital interstriae 3.

Female.— Length 1.4 mm (paratypes 1.3-1.6 mm), 2.1 times as long as wide; color almost black.

Frons as in *caliginis*, except rather deeply concave, rather strongly reticulate over entire surface, punctures moderately coarse, most of them distinctly impressed. Pronotum and elytra as in *caliginis*, except declivity more finely, more uniformly reticulate, and interstriae 3 with a row of subreticulate punctures.

Male.— Similar to female, except sexual differences as in *caliginis*.

Type Locality.— Peralta, Cartago, Costa Rica.

Type Material.— The female holotype, male allotype, and two paratypes were taken at the type locality on 10-III-64, 500 m, No. 461, from a woody vine, by me. One paratype is from Tapanti, Cartago, Costa Rica, 24-X-63, 1300 m, woody vine, S. L. Wood.
The holotype, allotype and paratypes are in my collection.

Corthycyclon morulus, n. sp.

This species is distinguished by the compact antennal club and by the characters of the elytral declivity indicated below.

Female.— Length 2.1 mm, 2.5 times as long as wide; color almost black.

Frons essentially as in *furvus* Wood, except surface subreticulate, punctures rather fine, abundant, distinct, vestiture of very fine hair. Antennal club 1.2 times as long as wide.

Pronotum and elytra essentially as in *caliginis* Wood, except pronotal disc more coarsely punctured and interstriae 2 rather weakly impressed and without granules, 1 distinctly, moderately elevated, 1 and 3 each armed by a row of small, rounded, rather widely spaced granules. Vestiture sparse, confined to odd-numbered declivital interstriae, fine, rather short.

Type Locality.— Sixteen km SE Cartago, Cartago, Costa Rica.

Type Material.— The female holotype was taken at the type locality on 3-VIII-63, 1800 m, No. 18, from a small branch of *Conostegia oerstediana*, by me.
The holotype is in my collection.

Corthycyclon tardus, n. sp.

This species is distinguished from *aztecus* Bright by the smaller size, by the smaller declivital granules, by the more abundant short and sparse long declivital hair, and by the female antennal club.

Female.— Length 1.7 mm (paratypes 1.5-1.7 mm), 2.5 times as long as wide; color dark brown.

Frons about as in *morulus* Wood, except obscurely reticulate, punctures smaller, median half of epistomal margin transversely carinate. Antennal club 2.5 times as long as wide, tapered from basal third to apex; apex ornamented by a tuft of about two or three long hairs.

Pronotum and elytral disc as in *morulus*, except pronotal disc with punctures minute, almost obsolete. Elytral declivity steep, convex; interstriae 1 feebly if at all elevated, strial punctures minute to obsolete; surface shining; with numerous very minute, confused punctures, those bearing short hair often minutely granulate, particularly near base of declivity, interstriae 1 and 3 each bearing a few slightly larger granules at bases of longest setae. Vestiture confined to declivity, of moderately abundant fine, short hair and sparse rows of long hair on odd-numbered interstriae.

Male.— Similar to female, except frons convex, reticulate, sparsely punctured, subglabrous; antennal club less than twice as long as wide, without long hair.

Type Locality.— Sixteen km SE Cartago, Cartago, Costa Rica.

Type Material.— The female holotype, male allotype, and four paratypes were taken at the type locality on 24-IX-63, 1800 m, No. 197, from *Siparuna nicaraguensis*, by me. One paratype is from Volcan Poas, Heredia, Costa Rica, 6-IX-63, 2500 m, No. 169, *Vaccinium consanguineum*, S. L. Wood. Two paratypes are from Cerro Campana, Panama, 26-VII-66, 1000 m, No. 33, *Cecropia* petiole, S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Corthylocurus debilis, n. sp.

This species is distinguished from *aguacatensis* (Schedl) by the characters of the female frons and elytral declivity as indicated below.

Female.— Length 1.5 mm, 2.4 times as long as wide; color yellowish brown.

Frontal area narrow for this genus, 1.3 times as wide as long, somewhat shallowly, biconcavely impressed on quadrate area from epistoma to about three-fourths distance to upper level of eyes; narrow median line sharply impressed, its lateral margins shining, weakly elevated, lateral impressed areas covered by rather dense, very short, stout setae, those near median line apparently on a spongy area; upper areas convex, reticulate, glabrous. Antennal club large, broadly obovate, 1.2 times as long as wide; tuft of hair on posterior face very poorly developed.

Pronotum and elytra as in *aguacatensis*, except elytral declivity more brightly shining, very feebly sulcate, and granules on interstriae 3 obsolete.

Male.— Similar to female, except frons convex, reticulate, sparsely punctured, subglabrous; anterior margin of pronotum armed by six serrations, median pair much larger.

Type Locality.— Beverley, Limón, Costa Rica.

Type Material.— The female holotype was taken at the type locality on 26-VIII-63, 7 m, No. 154, from a woody vine, by me. The male allotype was taken at Ft. Clayton, Canal Zone, Panama, 22-XII-63, 30 m, No. 319, from *Serjania*, by me.

The holotype and allotype are in my collection.

THE ANATOMY AND TAXONOMY OF *VANCLEVEA* (ASTERACEAE)[1]

Loran C. Anderson[2] and Phillip S. Weberg[2]

Abstract.— Wood, leaf, and floral anatomy of *Vanclevea stylosa* is compared with that of several possibly related species in the genera *Acamptopappus*, *Eastwoodia*, *Grindelia*, *Haplopappus*, and *Petradoria*. Although *V. stylosa* was originally described as a *Grindelia*, it is clearly distinct from that genus. Of the taxa studied, it is most closely allied to *Haplopappus salincinus* and *H. scopulorum*. The taxonomy, morphology, and distribution of the monotypic *Vanclevea* are detailed, and known exsiccatae are listed.

Eastwood (1896) published the species *Grindelia stylosa* and noted, "It differs from typical *Grindeliae* in having entire leaves, turbinate involucres, and more numerous persistent pappus bristles. The long, conspicuous styles give to the flower its chief beauty, hence the name." A few years later, Greene (1899) made the species the basis of his genus *Vanclevea*. Steyermark (1937) stated,

> *Vanclevea* is closely related to *Grindelia* by its resinous involucres and pappus of comparatively few (12 or so) bristles, but differs in having a persistent pappus of more numerous bristles, very elongated exserted style branches and appendages, leaves of entirely different insertion and position, as well as a peculiar shedding epidermis of the stem. *Vanclevea* appears to be more closely related to *Acamptopappus* and is also related to *Chrysothamnus*.

The senior author's interest in the latter genus and related Astereae prompted the present study of this little-known monotypic genus. One of the closest morphotypes is *Petradoria discoidea*, formerly known as *Chrysothamnus gramineus* (cf. Anderson, 1963).

Methods and Materials

Fresh and dried materials were processed for anatomical study as in earlier studies (Anderson, 1963, 1970a). Generally, the basal portion of the central stem was used for study of wood features, but in *Grindelia decumbens* a portion of the upper root was used. Five heads from personal collections, along with two heads from other collections, were measured (as in Anderson, 1964) for involucral and floral data.

Taxa morphologically similar to *Vanclevea* plus some taxa previously considered related to that genus are included in the study. Specific voucher specimens are: *Acamptopappus schockleyi* Gray, *Anderson 2120* (ksc); *A. sphaerocephalus* (Harv. & Gray) Gray, *Anderson 2110, 2112* (ksc); *Eastwoodia elegans* Bdg., *Eastwood 5838* (ksc); *Grindelia columbiana* (Piper) Rydb., *Anderson 3591* (ksc); *G. decumbens* Greene, *Anderson 2678* (ksc); *G. squarrosa*

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[1] Contribution no. 1124, Division of Biology, Kansas Agr. Expt. Station, Manhattan, Kansas 66506. This study supported by National Science Foundation Grant GB 31996X.

[2] Division of Biology, Kansas State University, Manhattan, Kansas 66506.

(Pursh) Dunal., *Anderson 3117, 3529* (KSC); *G. squarrosa* var. *nuda* (Wood) Gray, *Anderson 2986* (KSC); *Haplopappus salicinus* Blake, *Eastwood 10* (US); *H. scopulorum* (Jones) Blake, *Anderson 2145* (KSC); and *Vanclevea stylosa* (Eastw.) Greene, *Anderson 1976, 3156, 3337* (KSC).

Anatomy

Seedling data are limited. *Vanclevea* seedlings have opposite leaves, a feature shared with *Chrysothamnus* and woody *Haplopappus* such as *H. scopulorum;* those of *Grindelia* are alternate.

Adult leaves of *Vanclevea* are isolateral with massive sclerenchymatous bundle sheaths and heavy cuticle (10-13μ). The leaves are essentially glabrous; however, a few small glandular trichomes occur at the leaf base. The most similar leaves (isolateral with massive sclerenchyma bundle sheaths) are found in *H. salicinus* and *H. scopulorum;* but the former has glandular hairs sparsely distributed on both leaf surfaces, and the latter has nonglandular hairs adaxially. Leaves of *Petradoria* (Anderson, 1963) are also somewhat similar to those of *Vanclevea. Acamptopappus* leaves are isolateral but have little or no sclerenchyma in the bundle sheaths; *A. shockleyi* leaves have uniseriate, nonglandular trichomes, whereas those of *A. sphaerocephalus* are glabrous. Leaves of *Eastwoodia* are isolateral, have glandular hairs along the midvein adaxially, and lack sclerenchyma in the bundle sheaths. Leaf anatomy in our *Grindelia* agrees with that of earlier studies (Dalbey, 1914; Giroux and Susplugas, 1935). *Grindelia* is unlike the other genera in that the leaves have prominent bundle-sheath extensions with little or no sclerenchyma associated with the veins. The epidermis is glandular-pitted with short multiseriate trichomes, and the mesophyll is isolateral to weakly bifacial.

Stems of *Vanclevea* are weakly pentagonal in transection just below the nodes but tend to be cylindrical farther below the nodes. The cortex has large collenchyma strands associated with the five ridges of the stem. The collenchyma strands are separated by zones of parenchyma. The endodermis does not contain casparian strip and is poorly defined in young stems; it becomes more prominent with age as the cork cambium is initiated deep in the cortex next to the endodermis. The endodermis is the only row of cells separating the cork and cork cambium from the extensive phloem fibers that cap the vascular bundles. The cork cambium is precocious, being activated simultaneously with the vascular cambium. The deep-seated origin of the periderm in *Vanclevea* stems accounts for the "peculiar shedding epidermis" noted by Steyermark (1937). Cells of the pith become thick-walled through secondary sclerosis.

Collenchyma distribution in stems of the other taxa studied is basically similar to that of *Vanclevea*, although it is not so extensive. Furthermore, in *Acamptopappus* species, the collenchyma forms a continuous band, two to three cells thick, around the stem rather than being separated by groups of parenchyma. Cork initiation in *Eastwoodia* and *H. scopulorum* is also deep in the cortex; however, four to five cell layers of parenchyma separate the cork cambium from the phloem fibers. Also, the periderm formation lags well behind the secondary vascular growth.

Vanclevea is the woodiest shrub of the taxa studied, with stems occasionally measuring up to 8 cm in diameter; the *Grindelia* species are the least woody. Selected features of woody anatomy are listed in Table 1. For comparisons with other related members of the Astereae, consult Carlquist (1960) and Anderson (1963, 1972). Measurements taken from a twig of *Eastwoodia elegans* were too limited to include in the table; the species has narrow vessel elements (about 30μ wide and 136μ long) and small wood rays about 0.7 mm tall.

The largest vessel elements and libriform fibers occur in the *Haplopappus*, followed closely by *Acamptopappus* and *Vanclevea* with *Grindelia* having relatively narrower and shorter xylem cells. The pattern of vessel grouping varies. In *Grindelia*, vessels are in single files (radial chains); those of *Vanclevea* are in groups a few cells wide but still somewhat radially aligned. Vessels in *Acamptopappus* and *H. scopulorum* are in larger, tangentially clustered groups. All woods tend to be diffuse-porous, but in *Vanclevea* they are semi-ring-porous. Although most woods tend to have wider vessels in the springwood and narrower ones in the summerwood, vessels in *A. sphaerocephalus* are widest in the mid-season wood of each ring, as in *H. acaulis* (Anderson, 1963).

Vascular tracheids are present but not common in *Vanclevea* woods. They are abundant and storied in wood of *H. scopulorum*. Axial parenchyma is paratracheal and scanty in most samples; in *Grindelia* species, paratracheal parenchyma is more abundant. That plus the taller, wider wood rays probably relate to the herbaceous nature of *Grindelia*. *Eastwoodia* and *Grindelia* also have a few uniseriate rays in their woods.

Paedomorphosis is clearly demonstrated in the patterns of change in vessel-element length during growth in the *Grindelia* taxa; the other taxa have a "normal or woody" growth curve (see Anderson, 1972).

Floral development in *Vanclevea* follows a common pattern in Astereae (Martin, 1892; Anderson, 1970a); floral organs are initiated in the sequence: corolla, stamens, pappus, and carpels. The species develops a Polygonum-type embryo sac. Mature embryo sacs (310-360μ long and 22-25μ wide) have three antipodals. There are no multinucleate antipodals, nor is there the increase in antipodal number beyond three that frequently occurs in related Astereae. The long, narrow embryo sacs resemble those in certain *Chrysothamnus* taxa (Anderson, 1970b). Embryo sacs seen in *Haplopappus scopulorum* were 160μ long and also contain three antipodals. Embryo sacs in *Grindelia squarrosa* have only two antipodals, with one or both developing prominent lateral haustoria (Howe, 1926). Embryo sacs in our material of *G. decumbens* and *G. squarrosa* var. *nuda* also have two antipodals with lateral haustoria, apparently the basic pattern in *Grindelia*.

TABLE 1. Comparative xylary features of *Vanclevea* and other Astereae.

	Vessel elements			Libriform fibers		Multiseriate rays			
Taxon and collection	Widest diameter, μ	Average diameter, μ	Average length, μ	Average diameter, μ	Average length, μ	Average height, mm	Average cell number at maximum width	Cells isodiametric to procumbent*	Cells isodiametric to erect
Acamptopappus sphaerocephalus, Anderson 2112	90.8	50.7	147.9	17.4	212.2	2.09	3.4	+	–
Grindelia decumbens, Anderson 2678	56.8	34.2	120.0	12.6	201.6	2.11	12.6	0	+
G. squarrosa, Anderson 3117	64.0	38.7	112.0	12.8	159.7	1.58	10.2	+	+
G. squarrosa var. *nuda, Anderson 2986*	78.4	40.9	127.3	14.6	212.0	1.19	4.7	–	+
Haplopappus scopulorum, Anderson 2145	97.6	69.5	156.1	17.2	249.7	1.13	3.1	+	–
Vanclevea stylosa, Anderson 1976	84.8	47.2	142.9	15.3	224.3	1.31	4.6	+	+
Anderson 3156	87.4	43.6	151.2	15.4	212.4	1.90	4.4	+	–

* + = frequent, – = infrequent, 0 = absent

Aspects of *Vanclevea* floral morphology are listed in Table 2. The heads are always discoid. Flower numbers (from single head counts) in our other taxa include: *Acamptopappus schockleyi*, 12 ray and 54 disc flowers; *A. sphaerocephalus*, 22 disc; *Eastwoodia elegans*, 50 disc; *Grindelia decumbens*, 12 ray and 59 disc; *G. squarrosa*, 38 ray and 270 disc; *G. squarrosa* var. *nuda*, 222 disc; *Haplopappus salicinus*, 12 disc; and *H. scopulorum*, 9 disc in ours and 24 in *Eastwood & Howell 7111* (RSA).

Differences in pappus are frequently considered characteristics for distinguishing genera in the Asteraceae. Among species under study, extremes are seen between *Grindelia* and *Haplopappus*. The former has two to eight deciduous, paleacous awns, whereas the latter has numerous persistent, capillary bristles. Pappus of *Vanclevea* is somewhat intermediate, though more like the *Grindelia* in having 15-18 tardily deciduous, paleacous awns. However, one *Vanclevea* flower from *Holmgren & Hansen 3801* was found with a small gall (chalcid-fly induced) arising from the top of the achene beside the corolla. (The senior author has found similar galls occasionally in *Chrysothamnus* and *Haplopappus*.) The pappus adjacent to the gall is composed of numerous capillary bristles 6 mm long, whereas the pappus adjacent to the corolla is typical, consisting of eight paleacous awns each about 2.5 mm long. Perhaps too much significance is attached to pappus differences in the Asteraceae. Shinners (1949) certainly thought so.

Data on floral anatomy are presented in Table 3; the format follows that in Anderson (1970a). Frequency classes are: ++, abundant; +, frequent; –, rare; and 0, absent. Zones I and II are the proximal and distal areas of the achene, respectively; zones III - V are from the corolla; and VI and VII, from the style. Trichome types d, n, and g are duplex (the nonglandular twin-hairs characteristic of achenes), uniseriate nonglandular, and biseriate glandular, respectively. Corolla thickness (cell number) was determined at

TABLE 2. Features of floral morphology in *Vanclevea stylosa*

Collection	Bract number	Involucral length, mm	Involucral width, mm	Flower number	Flower length, mm	Corolla lobe length, mm	Style length, mm	Stigmatic area—total style branch, %
Anderson 3156	55.6	12.0	6.9	44.2	7.8	1.0	13.5	42.2
Anderson 3337	51.0	10.5	7.5	43.6	7.3	1.0	11.6	41.8
Eastwood & Howell 6660	46.5	12.4	6.9	34.0	8.2	0.9	13.6	43.5
Cutler 3155	66.0	10.0	7.5	36.5	8.0	1.2	13.2	45.8
Holmgren & Hansen 3801	45.5	11.9	7.2	32.0	7.4	1.2	11.4	35.9

TABLE 3. Selected features of floral anatomy in *Vanclevea* and other Astereae.

Taxon	Ovarian bundle number		Secretory canal distribution							Trichomes						Disc corolla thickness (cell number)		
			Achene		Corolla			Style		Achene			Corolla tube					
	Average	Range	I	II	III	IV	V	VI	VII	Type	Frequency	Length, μ	Type	Frequency	Length, μ	A	B	C
Acamptopappus schokleyi	8.6	8-10	++	++	0	0	0	0	0	d	++	1000	g	+	100	8	5	2
										n	++	1000						
A. sphaerocephalus	9.0	8-10	++	++	0	0	0	0	0	d	++	1100	g	++	200	10	6	2
										n	++	1200						
Eastwoodia elegans	5.0	5	0	0	0	0	0	0	0	d	+	300	0			8	6	2
Grindelia decumbens	2.0	2	0	0	-	++	++	++	++	0			0			8	6	2
G. squarrosa	2.0	2	0	0	++	++	++	++	++	g	-	40	0			9	6	2
G. squarrosa var. *nuda*	2.0	2	0	0	+	++	++	++	++	0			0			9	6	2
Haplopappus salicinus	5.2	5-6	+	++	0	-	+	0	0	d	+	400	0			8	6	2
H. scopulorum	8.3	7-9	0	+	+	++	++	0	0	d	++	400	0			9	6	2
Vanclevea stylosa																		
Anderson 1976	6.2	5-7	-	+	0	+	+	0	0	d	+	400	0			11	5	2
Anderson 3156	6.9	6-8	-	+	+	++	++	0	0	d	-	380	0			12	6	2
Anderson 3337	5.8	5-7	0	+	0	+	++	0	0	d	-	270	0			11	6	2

three levels; those levels (A-C) and the seven zones studied for secretory canals are diagrammatically shown in Fig. 24 of Anderson (1970a).

Data relating to ray flowers are not included in Table 3 because several of the taxa are eradiate. Ray flowers of *Grindelia decumbens* have short (90μ), biseriate glandular trichomes, though none are found on the disc flowers. Trichomes in *Acamptopappus* are distinctive. Long isotropic, nonglandular trichomes (shag hairs) are found abundantly with the anisotropic duplex hairs on the achene walls. Duplex hairs were found only distally on *Vanclevea* achenes, and in *Grindelia squarrosa* the rare glandular hairs are restricted to the very top of the otherwise glabrous achenes.

Ovarian vascular bundle number and the pattern of secretory canal distribution (present in achenes and corollas but absent in styles) are similar in the *Haplopappus* and *Vanclevea*. At least a few flowers of all samples from those two genera have additional corolla vasculature (midveins); the other taxa had only five veins in their disc corollas. *Grindelia* is set apart from the other taxa by its highly reduced vasculature in the achenes.

Xeromorphy in *Vanclevea* flowers is evidenced in the thickness of its corollas and the massive sclerenchyma sheaths that surround the veins in the achenes.

TAXONOMY

Although *Vanclevea stylosa* was first described as a *Grindelia*, that relationship apparently is not close. In addition to having features of habit, morphology, and anatomy presented here, the two groups are distinguishable chromosomally. In *Grindelia*, $x = 6$, whereas the single documented count for *Vanclevea* is $n = 9$ (*Anderson 1976* in Solbrig et al., 1964). The remaining taxa studied here are also $n = 9$ or chromosomally unknown, as in *H. salicinus*.

The purported relationships of *Vanclevea* to *Acamptopappus* and *Chrysothamnus* (Styermark, 1937) now do not appear close. The genus has many features in common with *Haplopappus salicinus* and *H. scopulorum*. It is with that section of *Haplopappus* (*Hesperodoria*) that *Vanclevea* is most closely allied. Although pappus in *H. ciliatus* (section *Prionopsis*) more than in any other *Haplopappus* resembles that of *Vanclevea*, *H. ciliatus* differs from *Vanclevea* in most other features of morphology, anatomy, and cytology. *Haplopappus* (*sens. lat.*) is badly in need of revision, but we believe that after such a study, *Vanclevea* will still be considered a separate genus in the Astereae.

Vanclevea Greene, Pittonia 4:50. 1899.

E. L. Greene dedicated this monotypic genus to a Mr. J. W. Van Cleve of Dayton, Ohio.

Vanclevea stylosa (Eastw.) Greene, Pittonia 4:51. 1899.

BASIONYM: *Grindelia stylosa* Eastw., Proc. Calif. Acad. Sci. II 6:293. 1896.

Type: [Epsom Creek] Barton's Range, San Juan Co., Utah, 13 July 1895, *A. Eastwood* 36. CAS (holotype) US!, photo - KSC!

Slender branching shrubs (4) 6-7 (10) dm tall, older stems with shedding epidermis or dull white bark, often with axillary fascicles of small leaves, younger stems greenish white, glutinous, glabrous; leaves alternate, linear lanceolate, rigid, spreading to falcate and recurved, occasionally conduplicate, entire, (2.5) 3-3.5 (4.5) cm long and (2.5) 3-4 (5) mm wide; inflorescence cymose or a solitary head, discoid, viscous; involucres broadly turbinate, (9.5) 10-12 (12.5) mm tall, bracts graduated, subulate to broadly linear, acute to acuminate, often squarrose; flowers (31) 35-45 (48); corollas yellow, 7-8.5 mm long, lobes usually 1 mm long; styles well exerted, appendages longer than stigmatic lines; pappus of (12) 15-18 paleacous awns, stramineous, 2.5-3 mm long, often exceeding the involucre at anthesis; achenes narrowly cylindric, 4-5 mm long, nearly glabrous. $n = 9$.

Variation within the species is not great, and no subspecific taxa are recognized. In most plants the bracts are squarrose and acuminate to apiculate, but some are ascending and only acute. The degree to which the pappus is visible at anthesis also varies.

Distribution: Sandy washes and sand hills; from Emery and Grand counties south through the Canyonlands Section of Utah to Coconino and Navajo counties in Arizona (Fig. 1).

Phenology: Primarily blooming July through September, but occasionally later in the autumn and in March.

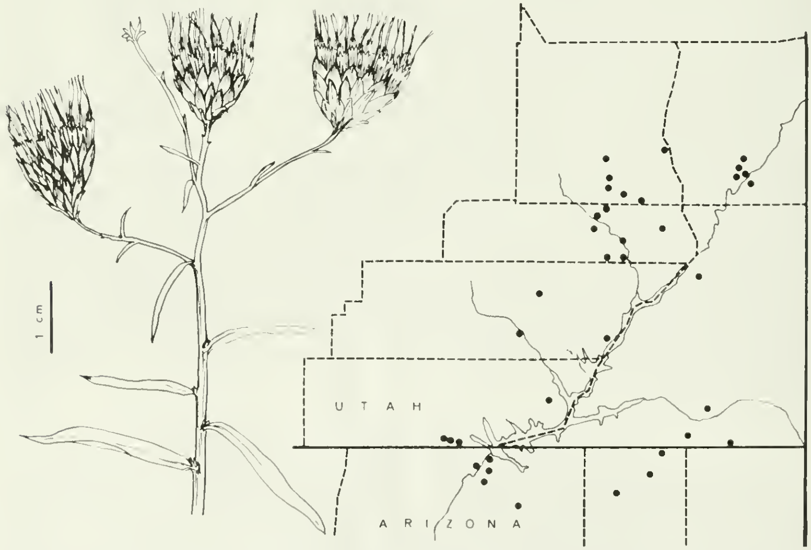

Fig. 1. Flowering twig of *Vanclevea stylosa* and the known distribution of the species.

EXSICCATAE: ARIZONA. Coconino Co.: Page, elev. 4300 ft, *L. C. Anderson 1976* (KSC); 11 mi SSW Page, elev. 5100 ft, *L. C. Anderson 1715* (UC, NY, RSA), *2619* (KSC); 9.3 mi SSW Page, *N. D. Atwood, S. L. Welsh, & B. Wood 3339* (BRY); 6 mi SW Page, elev. 4500 ft, *J. Daney* in 1971 (ASC), *R. H. Hevly & J. States* in 1972 (ASC); 1.5 mi below Lee's Ferry, *H. C. Cutler 3155* (MO, NY, US, SMU); Kaibito Plateau, elev. 6000 ft, *L. D. Love* in 1934 (ARIZ). Navaja Co.: Monument Valley, *A. Eastwood & J. T. Howell 6660* (CAS, UC, US), *J. T. Howell & G. True 44882* (CAS), *E. McClintock* in 1963 (CAS), *M. Blas 38* (CAS); 7 mi SW Utah line toward Kayenta, elev. 5400 ft, *J. T. Howell & G. True 45018* (CAS, NY); Tsegi Canyon, *L. C. Whitehead* in 1916 (ARIZ). UTAH. Emery Co.: Temple Wash, T25S, R11E NW¼ Sec 12, *L. C. Anderson 3337* (KSC); 2 mi E Gilson Butte, Green River Desert, elev. 4800 ft. *A. Baker* 5 (US); Andy Moore North Spring [T26S, R15E], San Rafael Desert, elev. 5000 ft, *Bryan & Read* in 1938 (UTC); 5 mi E Jeffrey Well, Green River Desert, elev. 4500 ft, *W. P. Cottam 17761* (COLO, UT); W Robber's Roost, *L. A. Stoddart* in 1943 (UTC); Dry Lake Wash, ca. 15 mi S Green River, *S. L. Welsh, N. D. Atwood, & G. Moore 10833a* (BRY, NY). Garfield Co.: 18 mi E Boulder vic. Circle Cliffs, *B. Maquire* in 1940 (NY); Baker's Ranch [T37S, R7E], *B. Markham* in 1940 (UTC); *Ticebo Mesa*, T36S, R12E, *J. C. Pederson 26* (BRY). Grand Co.: S Double Arch, Arches Nat'l Monument, *L. C. Anderson 66* (UTC); Courthouse Towers, Arches Nat'l Monument, *S. L. Welsh, B. F. Harrison, & G. Moore 2268* (BRY); S Turnbow Cabin, Salt Wash, Arches Nat'l Monument, *S. L. Welsh & G. Moore 2717* (BRY, NY); Little Sand Flats, E Moab, elev. 4500 ft, *K. Goodspeed* in 1968 (UTC). Kane Co.: 2.5 mi W Glen Canyon City, *L. C. Anderson 3156* (KSC); 2 mi E Glen Canyon City, *N. D. Atwood 3095* (BRY); 6 mi E Glen Canyon City, *N. D. Atwood & D. Kaneko* (UT); Fiftymile spring S Escalante [T40S, R8E], *J. R. Murdock 375* (BRY); 55 mi E Kanab, *S. L. Welsh 9418* (BRY). San Juan Co.: Forbidding Canyon, Rainbow Bridge area, elev. 3600 ft, *R. A. Darrow 2806* (ARIZ); Monument Valley, *A. Eastwood & J. T. Howell 6675* (CAS, K, NY, UC); S. Needle Rock, Monument Valley, *A. H. Holmgren & S. Hansen 3801* (NY, UC, US, UTC); Lower Beef Basin [T32S, R8E], NW Monticello, *W. A. Shands 140* (US); N Mexican Water, elev. 4900 ft, *B. Smith* in 1966 (UTC). Wayne Co.: 20 mi N Hanksville, *R. Jensen* in 1941 (UTC); Burr Point [T30S, R13E], *B. Markham* in 1940 (UTC); SSE Hanksville near county line, *W. A. Shands 124* (US); 2 mi E Wadlerman Home, S Hanksville, *W. A. Shands 140* (UT); San Rafael Desert, elev. 4500 ft, *W. D. Stanton 1068* (UT); Barrier (Horseshoe) Canyon, *S. L. Welsh, N. D. Atwood, & G. Moore 10867* (BRY, NY); 5 mi N Hanksville, *S. L. Welsh & G. Moore 3614* (BRY).

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A REVISION OF THE *ECHIDIOCARYA* SECTION OF *PLAGIOBOTHRYS* (BORAGINACEAE)

Larry C. Higgins[1]

Abstract.— This revision discusses two closely related species of *Plagiobothrys* (Boraginaceae) found in the southwestern United States and central Chile. One of the two species, *P. collinus*, is composed of five varieties that range from southern California and western Arizona to central Chile in South America. The following new combinations are proposed: *P. collinus* var. *californicus*, *P. collinus* var. *gracilis*, *P. collinus* var. *ursinus*, and *P. collinus* var. *fulvescens*. Detailed keys, synonymy, and descriptions are given for each entity.

The section *Echidiocarya*, as here defined, includes those species of the genus that are annuals with opposite or alternate lower leaves and that have the nutlet scar elevated on the end of a conspicuous stipe. The section *Allocarya* (to be treated in a later paper) differs mainly in that the nutlets lack the cylindrical stipe and the leaves are nearly always oppositely arranged.

The section *Echidiocarya* (Gray) Johnston is composed of two species and five varieties that are confined to the western half of the American continent, ranging from central California to central Arizona and southward to northern Sonora and northern Baja California, Mexico, with an outlying population in central Chile. The habitats of the various entities occur from sea level to steep mountain slopes and are characterized by scanty rainfall, warm temperatures, and high evaporation.

In 1857 R. A. Phillipi described the first species in the section when he published *Eritrichium collinum*. In 1908 K. Reiche transferred the species to *Cryptantha* in his treatment of the Boraginaceae published serially in the *Anales de la Universidad de Chile* and in 1910 as part of his *Flora de Chile*. In 1895 Phillipi described *E. inconspicuum*, which falls into synonymy with *E. collinum*.

Asa Gray (1876) proposed the genus *Echidiocarya* for *Echidiocarya arizonica* (*Plagiobothrys pringlei* Greene). It was characterized by the long-stiped nutlets. Gray (1877) added *E. californica* and (1883) *E. ursina* to the genus. Gray (1885), commenting on the very close relationship of his genus to *Plagiobothrys*, said, "The comparatively recent discovery of the preceding species [*P. ursina*] of this section has made it clear that both of them should fall in *Plagiobothrys*." He then transferred *E. californica* and *ursina* to *Plagiobothrys*, leaving the original species by iteslf.

Greene (1887) disposed of *Echidiocarya*, stating that it had "every aspect and every character of *Plagiobothrys*, except that there is a stipe between the scar, or point of attachment to the gynobase, and the body of the nutlet."

Johnston (1923) placed *Echidiocarya* as one of his sections under *Plagiobothrys*. He also described two additional varieties of *P. cali-*

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[1] Department of Biology and Killgore Research Center, West Texas State University, Canyon, Texas 79015.

fornicus. Since Johnston's treatment only Brand (1931) and Abrams (1951) have accepted *Echidiocarya* as a distinct genus.

During my research—which led ultimately to a complete revision of *Plagiobothrys*—a realignment of the members of this section became apparent because the South American *P. collinus* is conspecific with *P. californicus* of the southwestern United States and Mexico. Johnston (1927) was aware of the close relationship even though he never made any nomenclatural changes. He said, "the relationship between the Californian and Chilean plants is very clear and strong, so incontrovertible in fact, that some changes in the classification of the North American forms will probably be made." Those changes are the primary basis of this paper.

Special thanks are extended to the curators of the following herbaria for their loan of material for this study: BRY, CAS, GH, ND, ND-G, NY, UC, US. I also wish to thank West Texas State University and the Killgore Research Center for their support both physical and monetary.

TAXONOMY

Plagiobothrys Fisch. and Mey. Sect. *Echidiocarya* (Gray) Johnston, in Contr. Gray Herb. 68:65, 1923. *Echidiocarya* Gray, in Benth. and Hook. Genera Pl. 2:854, 1876; Proc. Amer. Acad. Arts 11:89, 1876. Species Holotypus: (*E. arizonica*) *P. pringlei* Greene.

Annual, usually diffusely branched, herb with the lowest leaves opposite or sometimes alternate; flowers in slender spikes, usually bracteate, calyx lobes linear-lanceolate, corolla white, the throad not crested; nutlets 4, incurved, conspicuously rugulose dorsally, conspicuously keeled ventrally; scar on a slightly to prominently elevated stipe.

1\. Stipe of nutlet elongate, approximating the body in length; nutlets commonly united in pairs; distribution in southern Arizona and northern Sonora .... 1. *P. pringlei*

1′. Stipe of nutlet short, 0.5 mm long or less, much shorter than the body of the nutlet .... 2. *P. collinus*

2\. Corolla 4-7 mm broad; pubescence fine, appressed, usually somewhat silky; California, Arizona, and northern Mexico .... 2A. var. *californicus*

2′. Corolla 1-3 mm broad; pubescence usually spreading; coarse, setulose 3

3\. Leaves narrowly linear, 2-2.5 mm broad 4

3′. Leaves oblanceolate, 3-5 mm broad 5

4\. Pubescence fine, nutlets rounded-rugulose; California and Baja California, Mexico .... 2B. var. *gracilis*

4′. Pubescence coarse, nutlets sharply rugose; Chile. .... 2C. var. *collinus*

5\. Racemes dense, hidden among leaves; San Bernardino Mountains, San Jacinto Mountains .... 2D. var. *ursinus*

5′. Racemes elongate, projecting from among the leaves and evident; southern California and Baja California, Mexico .... 2E. var. *fulvescens*

1. *Plagiobothrys pringlei* Greene

Echidiocarya arizonica Gray, in Benth. and Hook. Genera Pl. 2:854, 1876; Proc. Amer. Acad. Arts 11:89, 1876. Not *P. arizonicus* (Gray) Greene; *Plagiobothrys pringlei* Greene, in Pittonia 1:21, 1887. Mesa Verde, Arizona, Dr. Smart sn. Holotype GH!

Stems several to many branched from near the base, prostrate or decumbent to nearly erect, slender, 1-4 dm long, spreading setose; leaves numerous below, less so above, narrowly oblanceolate, 2-4 cm long, 2-5 mm broad, rounded or obtuse to nearly acute at apex, appressed strigose or canescent to conspicuously setose; floral bracts lanceolate to narrowly oblong, 1-2 cm long; spikes elongating in age, bractless near the apices; calyx segments lance-linear, about 3 mm long in fruit, hirsute; corolla 2-3 mm broad, inconspicuous; nutlets 4, the lowermost commonly joined in pairs, the upper separate, ovate, the apex acute, 1.8-2 mm long, dorsal keel evident above fading to rather distinct tuberculations below, dorsal surface rugulose with short ridges also conspicuously tuberculate; scar elevated on a prominent stipe at least 1.3 mm long and usually as long as the nutlet, ventral keel evident; style shorter than the stipe of nutlet.—Representative collections: J. J. Thornber sn. (CAS, NY); F. R. Fosberg 10663 (CAS, GH); V. L. Cory 3398 (GH); Pultz and Phillips 1572 (GH, NY); I. L. Wiggins 8689, 8190 (GH); L. C. Higgins 2822 (BRY, WTSU).

Distribution

Common in Cochise, Maricopa, Pima, and Pinal counties of Arizona and in northern Sonora, Mexico. Growing on sandy desert flats and mesas.

The most remarkable characteristic of Pringle's *Plagiobothrys* is the long-stiped nutlets, unique among the borages. This species is very closely related to *P. collinus* var. *fulvescens*, which it resembles in most details, except that the former has stalked nutlets and slightly longer calyx segments.

2a. *Plagiobothrys collinus* var. *californicus* (Gray) Higgins

Plagiobothrys collinus (Ph.) Johnston var. *californicus* (Gray) Higgins comb. nov., based on *Echidiocarya californica* Gray, in Proc. Amer. Acad. Arts 12:164, 1877. *Plagiobothrys californicus* (Gray) Greene, in Bull. Calif. Acad. Sci. 2:407, 1887. *Plagiobothrys cooperi* Gray, in Proc. Amer. Acad. Arts 20:285, 1885. *Allocaryastrum californicum* (Gray) Brand, in Pflanzenr. 4^{252}:100, 1931. Southeastern California in San Bernardino County, 1876, Parry and Lemmon 278. Holotype GH!

Leaves numerous below, oblanceolate, 1-3 cm long, 2-5 mm broad, rounded or obtuse at apex, thinly hirsute with ascending hairs or sometimes canescent with appressed pubescence; spikes slender, at maturity elongate and remotely flowered; calyx segments 3 mm long in fruit, linear-lanceolate, hirsute to hispid; corolla 4-6 mm broad; nutlets about 1.5 mm long, scar with a short stipe near base. —Representative collections: J. T. Howell 3935 (GH, CAS); T. S. Brandegee 1637 (GH); L. Abrams 3276 (GH); I. M. Johnston 1839 (GH).

Distribution

San Benito County, California, southward to northern Baja California, Mexico.

P. collinus var. *californicus* is most easily recognized by its large corollas, 4-7 mm broad and the more canescent pubescence; even at this, it intergrades with varieties *gracilis* and *fulvescens*.

2b. *Plagiobothrys collinus* var. *gracilis* (Johnston) Higgins

Plagiobothrys collinus (Ph.) Johnston var. *gracilis* (Johnston) Higgins comb. nov., based on *Plagiobothrys californicus* var. *gracilis* Johnston, in Contr. Gray Herb. 68:73, 1923. *Allocaryastrum gracile* Brand, in Pflanzenr. 4^{252}:100, 1931. *Echidiocarya californica* subsp. *gracilis* (Brand) Abrams, in Ill. Fl. Pacific Stat. 3:571, 1951. San Diego, San Diego County, California, on the mesas. 10 April 1902. T. S. Brandegee 1658. Holotype GH!

Stems slender, with spreading hispid pubescence; leaves linear-lanceolate, sparsely pubescent, with spreading setose hairs, 2-2.5 mm broad, acute or acutish; calyx segments linear, ca 2 mm long, very slender, hirsute; corolla 1.5-2 mm broad; nutlets 1-1.5 mm long, inconspicuously rugulose.—Representative collections: F. R. Fosberg 7681 (CAS, GH); I. L. Wiggins 4462 (GH); F. F. Gander 4955 (GH); Raven & Mathias 12520 (GH).

Distribution.

San Diego County, California, southward to northern Baja California, Mexico, and on the islands of Santa Cruz, Santa Catalina, and San Clemente.

The variety *gracilis* is differentiated from the other varieties by the sparse spreading hirsute pubescence, narrower leaves, and smaller corollas. Its closest relatives are to be found in the varieties *fulvescens* and *collinus*. Intermediates are not uncommon with variety *fulvescens* and are very difficult to separate from true *gracilis*.

2c. *Plagiobothrys collinus* var. *collinus*

Eritrichium collinum Ph. Linnaea 29:17, 1857. *Cryptantha collina* Reiche, in Anales Univ. Chile 121:828, 1908; Fl. Chile 5:233, 1910. *Plagiobothrys collinus* (Ph.) Johnston, in Contr. Gray Herb. 78:81-82, 1927. Hills, Huanta, August 1836, Gay 1623. Holotype MS! Isotype fragment and photograph GH!

Eritrichium inconspicum Ph. Anales Univ. Chile 90:534, 1895.

Cryptantha inconspicua Reiche, in Anales Univ. Chile 121:820. 1908; Fl. Chile 5:225, 1910. Coquimbo: La Serena, October 1878. Philippi s.n. Holotype MS! Fragment and photograph GH!

Stems several, mostly erect, 3-15 cm long, hispidulous-villous; leaves linear to oblance-linear, obtusish, conspicuously hispidulous, 2-4 mm broad; calyx segments 1.5-2.5 mm long, fulvescent; corolla 1-1.5 mm broad, inconspicuous; nutlets 1.2-1.5 mm long, reticulately rugose with sharp ridges; style approximating nutlets.—Representative collections: C. O. Skottsberg 1371, 723 (NY, GH); G. Montero

1895 (GH); E. Barros 6316, 6361 (GH); Worth & Morrison 16340 (GH).

Distribution

Chile, in the providence of Coquimbo. Apparently restricted to the area around Coquimbo.

This variety is most closely related to the varieties *gracilis* and *fulvescens*. It differs from the former in being coarser and in having broader obtusish more densely pubescent leaves and sharper and more prominently rugulose nutlets. From *fulvescens* it differs in having narrower leaves that are not so harshly pubescent, a more erect habit, and more prominently rugulose nutlets.

2d. *Plagiobothrys collinus* var. *ursinus* (Gray) Higgins

Plagiobothrys collinus (Ph.) Johnston var. *ursinus* (Gray) Higgins comb. nov., based on *Echidiocarya ursina* Gray, in Proc. Amer. Acad. Arts 19:90, 1883. *Plagiobothrys ursinus* Gray, in Proc. Amer. Acad. Arts 20:285, 1885. *Plagiobothrys californicus* var. *ursinus* (Gray) Johnston, in Contr. Gray Herb. 68:74, 1923. *Echidiocarya californica* var. *ursina* (Gray) Jepson, in Fl. Calif. 3:370, 1943. California, San Bernardino Mountains, S. B. Parish 927. Lectotype GH!

Stems much branched, dense, compact, 2-8 cm long; spikes short; flowers concealed by the hispidulous leaves and bracts which are 1-2.5 cm long; corolla 1-2 mm broad; nutlets weakly rugulose.—Representative collections: S. B. Parish 3247 (NY); P. A. Munz 5725 (GH); Munz & Johnston 4550 (GH); C. R. Orcutt 908 (GH).

Distribution

California, in the San Bernardino and the San Jacinto Mountains, growing in sandy to gravelly soils.

The caespitose, compact habit of variety *ursinus* serves best to distinguish it from all the other varieties. It also grows at a higher, more montane elevation.

2e. *Plagiobothrys collinus* var. *fulvescens* (Johnston) Higgins

Plagiobothrys collinus (Ph.) Johnston var. *fulvescens* (Johnston) Higgins comb. nov., based on *Plagiobothrys californicus* var. *fulvescens* Johnston, in Contr. Gray Herb. 68:74, 1923. *Allocaryastrum ursinum* var. *fulvescens* (Johnston) Brand, in Pflanzenr. 4^{252}:101, 1931. *Echidiocarya californica* subsp. *fulvescens* (Brand) Abrams, in Ill. Fl. Pacific Stat. 3:571-572, 1951. California, Santa Barbara, 1888, T. S. Brandegee s.n. Holotype GH!

Plagiobothrys micranthus A. Nels., in Amer. J. Bot. 25:115, 1938. Arizona, Prescott, moist creek banks, 28 April 1925. A. Nelson 10232, Holotype RM! Isotype GH!

Stems slender, elongate, prostrate, hispid-pubescent, leaves oblanceolate, obtusish to acutish, hispidulous 3-5 mm broad; spikes very slender at maturity, remotely flowered; corolla about 2 mm broad.—Representative collections: Eastwood and Howell 3914, 4156 (CAS, GH); F. R. Fosberg 10706 (CAS, GH); J. T. Howell 31075 (CAS); L. Abrams 3315 (NY); T. H. Kearney s.n. (CAS); C. B. Hardham 3049, 5602, 10048 (CAS).

Distribution

Santa Barbara County, California, southward to northern Baja California, Mexico, eastward to central Arizona. Also on the islands of Santa Rosa, Santa Catalina, and Anacapa.

Most closely related to the varieties *collinus* and *gracilis* as discussed under *collinus*. Variety *fulvescens* also introgresses considerably with varieties *californicus* and *gracilis*.

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GREAT BASIN NATURALIST

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GREAT BASIN NATURALIST

The *Great Basin Naturalist* was founded in 1939 by Vasco M. Tanner. It has been continuously published from one to four times a year since then by Brigham Young University, Provo, Utah. In general, only original, previously unpublished manuscripts pertaining to the biological natural history of the Great Basin and western North America will be accepted. Manuscripts are subject to the approval of the editor.

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STUDIES ON THE BIOLOGY AND ECOLOGY OF THE NORTHERN SCORPION, *PARUROCTONUS BOREUS* (GIRARD)[1]

Gregory Ira Tourtlotte[2]

Abstract.— An investigation to elucidate some facets of the biology and ecology of *Paruroctonus boreus* (Girard), in southeast Idaho, was conducted from 21 March to 13 October 1972. Three hundred and eighty-five observations were made on 202 scorpions captured in covered pitfalls and by ultraviolet light.

The greatest activity occurred at 2130 hours. Surface activity was not observed when ambient temperature was below 10 C, and, as ambient temperature increased, an increase in surface activity was noted. Male scorpions frequently moved as much as 30 m between observations, while females seldom moved more than five m.

Sex ratios varied considerably depending on time of year and method of sampling. Of 142 scorpions observed by blacklight, 92 were males, and 50 were females (1.84 males/female). Limited data suggest a mean litter size of 34 ± 11.

Paruroctonus boreus (Girard), the northern scorpion (Williams, 1972), is best known for its wide distribution and range northward into southern British Columbia and Alberta. In the United States, it has been reported from Arizona, California, Colorado, Idaho, Montana, Nevada, North Dakota, Oregon, Utah, Washington, and Wyoming (Gertsch and Soleglad, 1966).

P. boreus has been found in numerous localities throughout southern Idaho (Fig. 1). Some individuals have also been reported from central Idaho, near Challis, and from an area in eastern Washington across the Snake River from Lewiston, Idaho (Anderson, 1972). Individuals have been collected in a variety of habitats throughout the state, but most commonly on arid hillsides where the soil is dry and cracked or very rocky. Cracks and rocks provide shelter for the scorpions during daylight.

Descriptions of the species have been provided by Ewing (1928), Gertsch and Allred (1965), and Gertsch and Soleglad (1966). It is a medium-sized scorpion of conventional pale color, with a V-shaped black marking centered on the median eyes, and dusky transverse bands on the segments of the preabdomen.

Several recent studies regarding the biology and ecology of various species of Vaejovidae have been published, but a paucity of

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[1] This manuscript was prepared in partial fulfillment of the requirements for the degree of Master of Science in Zoology at Idaho State University, Pocatello, Idaho.

[2] Department of Biology, Idaho State University, Pocatello, Idaho 83201.

Fig. 1. Distribution of *P. boreus* in Idaho (after Anderson, 1972).

information regarding *P. boreus* still exists. Some aspects of the behavior of *Centruroides sculpturatus* Ewing, *Vaejovis spinigerus* (Wood), and *Hadrurus arizonensis* Ewing were described by Stahnke (1966). McDaniel (1968) studied the ecology of two species of scorpions in California; he compared an errant species, *Paru-*

roctonus sylvestrii Borelli, to a burrowing species, *Anuroctonus phaeodactylus* (Wood). Hadley and Williams (1968) described the nocturnal surface activities and feeding behavior of two species of Vaejovidae and one species of Buthidae. Williams (1966) described several aspects of scorpion biology, including the burrowing activities of *A. phaeodactylus*, birth activities of several species of scorpions, and (1970) the influence of various habitat types on the abundance, distribution, and community structure of *Vaejovis confusis* Stahnke, *V. spinigerus*, and *H. arizonensis*.

The present study was undertaken to elucidate some aspects of the biology and ecology of *P. boreus*, specifically: (1) daily and seasonal surface activity periods of a population of *P. boreus* in southeast Idaho, (2) frequency of surface activity for individual scorpions, (3) movement patterns, (4) sex-ratio characteristics, and (5) other facets relating to the biology and ecology of the species.

I thank Dr. Robert C. Anderson and Dr. Barry Keller for their help in organizing this investigation and in reviewing the manuscript. Thanks are also due Dr. Terry Ulrich and Eli Oboler for critically reviewing this manuscript.

METHODS AND MATERIALS

The study site was one mile southeast of Pocatello, Idaho, near the base of Chinks Peak, at an elevation of approximately 5000 ft. The predominant plant species on the site was Utah juniper, *Juniperus osteosperma* (Torr.). Other plant species present included big sagebrush, *Artemisia tridentata* Nutt.. cheat grass, *Bromus tectorum L.*, and Great Basin wildrye, *Elymus cynereus* Scribn & Merr. The site was characterized by dry cracked soil, with some rocky areas, and was selected following preliminary sampling of many areas the previous year because it contained numerous scorpions and was relatively free from human disturbance. Due to the large number of junipers on the site (Fig. 3), the sampling area (approximately 420 m²) was kept minimal to insure that the entire area could be adequately and thoroughly examined on each sampling occasion.

Scorpions were captured for marking and releasing by two methods: (1) the blacklight technique of Honetschlager (1965) and (2) covered pitfalls. The blacklight detection method incorporates the phenomenon whereby a substance in the scorpion cuticle converts shortwave ultraviolet radiation into visible light. A Burgess Safari-Lite® was used as a source of UV. Twenty-three pitfall traps were arranged in two lines, crisscrossing the study area (Fig. 4). The traps were covered with 25 X 25 cm masonite squares, as described by Williams (1968). Pitfall traps were checked twice each day, at dawn and at dusk.

To maintain uniformity in sampling, the study area was divided into seven line transects. The transects were approximately five meters apart, and each transect was marked with reference points every 5 m (Fig 4). Uniformity between samples was maintained

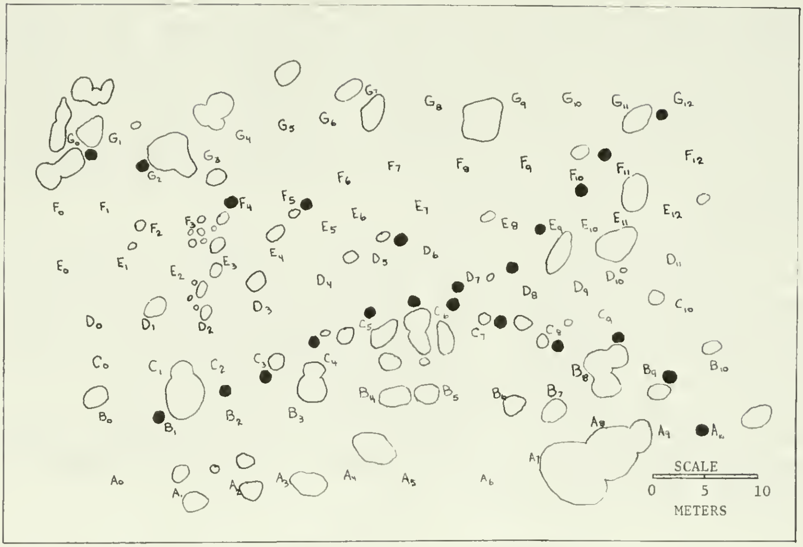

Fig. 2. Diagram of study area, indicating location of Utah juniper, *Juniperus osteosperma* (enclosures), pitfall traps (solid dots), and reference points (X_n).

by walking each transect at the same rate, while moving the light source from side to side. During periods of illumination from more than a quarter moon, the distance between transects was cut in half and the light source was held closer to the ground. By these pro-

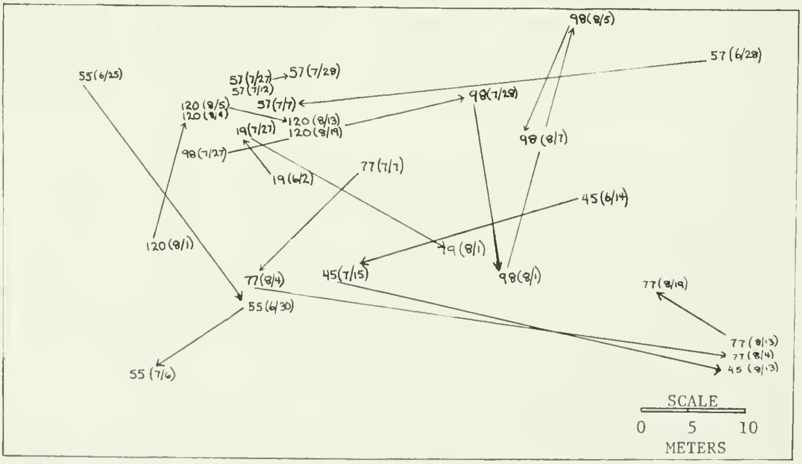

Fig. 3. Movement patterns of male *P. boreus* between 2 June and 17 August 1972 as determined by blacklight and pitfall.

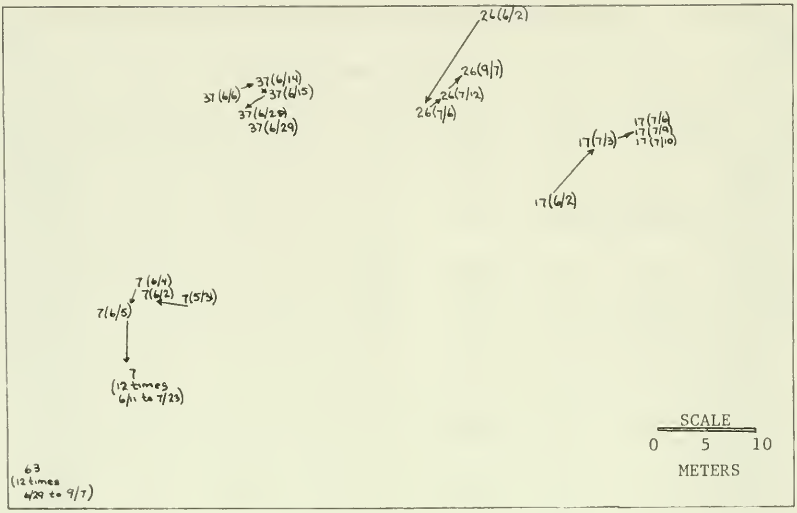

Fig. 4. Movement patterns of female *P. boreus* between 31 May and 7 September 1972 as determined by blacklight and pitfall.

cedures, active scorpions could be observed anywhere within the study site.

A map resembling that in Figure 3 was carried during each sampling occasion with blacklight. Reference points were used for recording the exact location of all scorpions observed. Scorpions larger than 30 mm total length were marked with a coded number system (Tourtlotte, 1973) by applying Testor's Pla Enamel®. Loss of marks due to molting was not evidenced, although some marks may have rubbed off as scorpions crawled into burrows and under debris. Sex, behavior, and location were recorded for all scorpions observed. Several gravid females were examined in the laboratory to obtain information on fertility.

By early fall several burrow locations were found and marked. During the first two weeks of March 1973, six burrows were excavated in an attempt to disclose the nature of the overwintering characteristics for the species.

Weather information recorded at the site included precipitation, air temperature at ground level, and soil temperature. Precipitation was measured with a Victor Rain-Gage®. A Taylor maximum-minimum thermometer was used to determine air temperature at ground level. Soil temperature was measured with a standard mercury bulb glass thermometer enclosed in a metal sleeve and placed at a depth of 15 cm.

RESULTS

MENSURATION OF BIOTYPE.— Taxonomic characteristics of four female and six male *P. boreus* from Pocatello were measured (Tables 1, 2) following the criteria of Gertsch and Soleglad (1966). Length

Table 1. Measurements (in mm) of adult female *P. boreus* from Pocatello, Idaho.

	Scorpion Number				Mean
Characteristics	1	2	3	4	± S.E.
Total length	40.1	38.5	38.4	38.6	38.9 ± 0.4
Carapace					
Length	6.1	5.8	3.6	5.7	5.8 ± 0.1
Width at side eyes	4.1	3.8	3.6	3.7	3.8 ± 0.1
Width at caudal edge	6.3	5.4	6.2	6.3	6.1 ± 0.2
Preabdomen					
Length	12.8	12.2	11.1	11.5	11.9 ± 0.4
Width	7.3	5.8	6.5	7.1	6.7 ± 0.4
Postabdomen, length	21.4	20.9	20.9	20.5	20.9 ± 0.2
Segment I					
Length	3.2	2.9	2.8	2.5	2.9 ± 0.2
Width	3.2	2.9	3.0	3.0	3.0 ± 0.1
Segment II					
Length	3.6	3.6	3.2	3.5	3.6 ± 0
Width	2.9	2.8	3.0	2.8	2.9 ± 0.1
Segment III					
Length	3.6	3.6	3.6	3.5	3.6 ± 0
Width	3.1	2.4	2.8	2.8	2.8 ± 0.2
Segment IV					
Length	4.4	4.2	4.4	4.4	4.4 ± 0
Width	2.8	2.6	2.7	2.6	2.7 ± 0
Segment V					
Length	6.6	6.6	6.9	6.6	6.7 ± 0.1
Width	2.8	2.5	2.5	2.6	2.6 ± 0.1
Telson, length	6.2	5.9	6.6	6.6	6.3 ± 0.2
Pedipalp	18.6	17.3	19.5	18.5	18.5 ± 0.4
Femur					
Length	4.8	4.2	5.1	4.4	4.6 ± 0.2
Depth	1.3	1.0	1.4	1.2	1.2 ± 0
Tibia					
Length	5.3	4.8	5.2	4.8	4.5 ± 0.1
Depth	2.0	1.6	1.9	1.8	1.8 ± 0
Hand					
Length	8.5	8.3	9.2	9.3	8.8 ± 0.2
Width	3.8	3.5	3.7	3.8	3.7 ± 0.1
Depth	2.7	2.7	2.6	2.8	2.7 ± 0
Palm length	5.1	4.7	4.5	5.0	4.8 ± 0.2
Moveable finger length	6.1	5.7	5.9	5.9	5.9 ± 0.2
Pectines					
Number of teeth					
Right	21	22	20	20	21 ± 0.5
Left	21	22	20	21	21 ± 0.5

and width of the carapace and preabdomen were consistently larger in females than in males, but the number of pectine teeth in females was considerably less than in males. Females possessed 20-22 pectine teeth, while males possessed 27-32. Although the number of teeth on the two pectines of one female and each of three males was not consistent, these differences appeared to be due to physical damage rather than of congenital origin. Two individuals observed in the field each had one pectine missing entirely.

Surface activity.— Surface activity was not indicated during the daylight period, as no scorpions were captured in pitfalls between

TABLE 2. Measurements (in mm) of adult male *P. boreus* from Pocatello, Idaho.

Characteristics	Scorpion Number 1	2	3	4	5	6	Mean ± S.E.
Total length	38.5	34.0	35.5	36.0	36.3	32.9	35.5 ± 1.7
Carapace							
Length	4.9	5.2	5.2	5.2	4.8	5.1	5.1 ± 0.1
Width at side eyes	3.2	3.5	3.1	3.1	3.6	3.6	3.4 ± 0.1
Width at caudal edge	4.8	5.2	4.9	5.4	5.1	4.8	5.0 ± 0.1
Preabdomen							
Length	13.2	9.4	10.2	10.6	10.9	9.0	9.8 ± 0.4
Width	5.2	5.7	5.1	6.0	5.6	5.5	5.5 ± 0.2
Postabdomen, length	20.3	20.0	20.1	20.8	20.3	19.4	20.2 ± 0.2
Segment I							
Length	2.7	2.7	3.1	2.8	2.8	2.6	2.8 ± 0.1
Width	2.5	2.5	2.4	2.6	2.7	2.7	2.6 ± 0.1
Segment II							
Length	3.4	3.1	3.3	3.4	3.1	3.1	3.2 ± 0.1
Width	2.4	2.6	2.4	2.6	2.7	2.7	2.6 ± 0.1
Segment III							
Length	3.6	3.7	3.6	3.8	3.8	3.4	3.7 ± 0.1
Width	2.5	2.4	2.4	2.2	2.6	2.5	2.4 ± 0.1
Segment IV							
Length	4.6	4.4	4.1	4.5	4.2	4.0	4.3 ± 0.1
Width	2.5	2.4	2.4	2.2	2.6	2.3	2.4 ± 0.1
Segment V							
Length	6.0	6.1	6.0	6.3	6.4	6.3	6.2 ± 0.1
Width	2.0	2.0	2.1	2.0	2.4	2.2	2.1 ± 0.1
Telson, length	5.8	5.7	6.1	6.5	6.0	5.5	5.9 ± 0.2
Pedipalp	16.1	17.1	18.8	17.4	17.0	16.3	17.1 ± 1.0
Femur							
Length	4.4	4.4	4.5	4.6	4.2	4.0	4.4 ± 0.2
Depth	1.1	1.4	1.1	1.2	1.1	1.1	1.2 ± 0.1
Tibia							
Length	4.2	4.5	4.4	4.4	4.7	4.5	4.5 ± 0.1
Depth	1.6	1.7	1.5	1.6	1.4	1.4	1.5 ± 0.1
Hand							
Length	7.5	8.2	7.9	8.2	8.1	7.8	7.8 ± 0.1
Width	3.7	3.6	3.4	3.6	3.6	3.3	3.5 ± 0.1
Depth	2.7	2.5	2.5	2.5	2.5	2.3	2.5 ± 0.1
Palm Length	4.8	4.8	5.0	4.6	4.8	4.6	4.8 ± 0.1
Moveable finger length	4.8	5.2	4.8	5.2	5.5	4.8	5.1 ± 0.2
Pectines							
Number of teeth							
Right	29	33	31	30	28	29	30 ± 0.8
Left	31	33	33	30	29	29	31 ± 0.8

dawn and dusk. Several scorpions were observed leaving their burrows shortly after sunset, apparently to spend the nocturnal hours on the ground surface. Surface activity was most intense during the first two hours of darkness, diminishing until dawn.

Observations were made at intervals between 2130 and 0330 hours to determine if scorpion activity was equally distributed throughout the nocturnal hours. Samples of surface activity were made at 2130, 0030, and 0330 hours on 7 and 12 July, and on 7 and 9 August 1972. Activity was highest at 2130 hours and lowest at 0330 hours on all sampling periods (Table 3). The number of scorpions observed at different times was compared by a chi-square test of homogeneity and goodness of fit. Heterogeneity was not detected, but analysis of the pooled data gave a significant ($P < 0.05$) chi-square value of 14.71, indicating that surface activity was not equally distributed throughout the night.

Surface activity was first observed on the study area 22 March 1972, and last observed on 13 October 1972. Surface activity may have occurred before and after these dates but was not evidenced. On 15 sampling periods in June, 89 scorpions were observed (5.93 scorpions/night); 98 scorpions were observed for 16 sampling periods in July (6.13 scorpions/night); 97 scorpions were observed for eight sampling periods in August (12.13 scorpions/night); and 18 scorpions were observed for six sampling periods in September (3 scorpions/night). Surface activity was greatest between 27 July and 9 August when 109 scorpions were observed on seven nights sampled (15.57 scorpions/night).

FREQUENCY OF SURFACE ACTIVITY FOR INDIVIDUAL SCORPIONS.— The frequency of surface activity varied greatly among individual scorpions. Many were observed only once throughout the study, while others were seen repeatedly. One female (#7) was observed 16 times, including 10 of the 15 nights sampled in June. Another female (#63) was observed on 11 of 17 sampling periods between 29 June and 1 August, and again on 7 September. No individual male scorpion was observed more than five times. Four males (#'s 57, 77, 98, and 120) were observed five times, and two males (#'s 82 and 125) were observed four times during the course of this study.

A total of 224 observations were made on 142 different scorpions by the blacklight technique. Fifty females were observed on 101 occasions (2.02 observations/female), and 92 males were observed on 123 occasions (1.33 observations/male). The observed frequency of surface activity was considerably higher for females than for males.

MOVEMENT PATTERNS.— Movements of individuals within the study area were assessed by noting the location of each scorpion

TABLE 3. Number of *P. boreus* observed by blacklight at three different times of night.

Date	Number of scorpions observed at different times 2130	0030	0330
July 7	5	3	2
July 12	7	4	1
August 7	21	13	9
August 9	14	9	5
Total	47	29	17
Mean ± S.E.	11.7 ± 3.6	7.2 ± 2.3	4.2 ± 1.8

observed. These data are summarized in Figures 3 and 4. It was not uncommon for males to move 30 meters or more between observations, while females seldom moved more than 5 meters. Two females (#'s 7 and 63) were each observed 12 times within the same square decimeter. Data from the pitfall traps further substantiated that males were more mobile than females. Of 161 scorpions captured in pitfall traps only 10 were females. Williams (1966) reported a similar differentiation in movement patterns with regard to sex in *Anuroctonus phaeodactylus*. In a pitfall study conducted for one year, he captured 33 scorpions, all mature males.

Several scorpions were marked and released on and around the study site during the previous summer (July 1971). During this study 11 of these individuals were recaptured, indicating that *P. boreus* will remain in the same general area for at least two seasons.

Sex ratio.— The sex ratio of *P. boreus* was extremely variable throughout the study (Fig. 5). Since pitfall data tended to drastically underestimate the number of females in the population, only blacklight data was used for sex ratio determinations. Of the 224 blacklight observations, 123 were of males and 101 were of females (1.22 males/female), and of the 142 individuals observed, 92 were males and 50 were females (1.84 males/female). The ratio of males to females was 24:67 (0.36 males/female) in June, 39:22 (1.77 males/female) in July, 91:6 (15.7 males/female) in August, and 11:6 (1.83 males/female) for the month of September.

During the period 29 June to 27 July, 12 of 17 females observed possessed a swollen mesosoma, indicating a gravid condition. Very few females were observed following this period. Williams (1969) reports that species of *Vaejovis*, *Anuroctonus*, and *Hadrurus* give

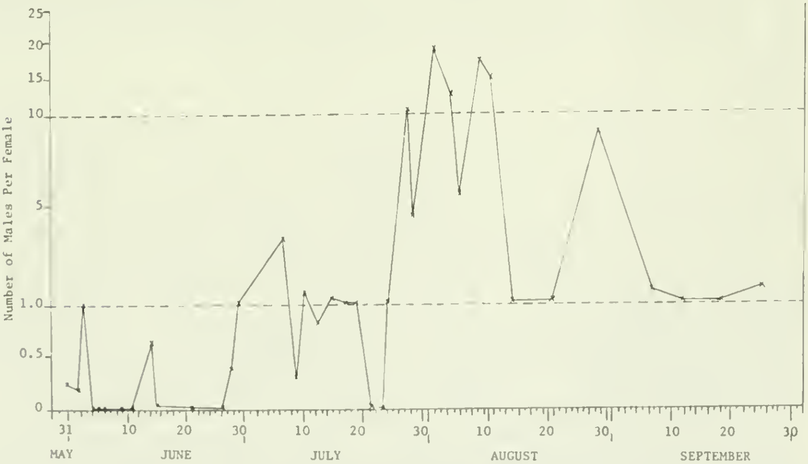

Fig. 5. Number of male *P. boreus* observed per female, between 31 May and 25 September 1972.

birth during the late summer and early fall, and that females usually remain in their burrows or other shelters while carrying young on their dorsum. The tendency of vaejovids to remain in seclusion following parturition would probably account for the paucity of females observed beyond 27 July.

Environmental influence.— Despite the fact that a multitude of factors probably interact to regulate the surface activity of terrestrial organisms, some interesting relationships between surface activity of *P. boreus* and temperature and rainfall were identified. Surface activity was not observed when the air temperature was below 10 C. As temperature increased, an increase in surface activity was noted (Fig. 6), except for the period between 29 June and 21 July, when there was no measurable precipitation (Fig. 6). The dry conditions during this period may have been responsible for the decrease in scorpion surface activity. Following the rainfall of 19 and 21 July, the original relationship of activity versus temperature was resumed.

Any measurable precipitation was immediately followed by a decrease in surface activity (Fig. 6). This decreased activity was followed within three to five days by a period of increased activity. Surface activity was not observed during periods of rainfall.

Reproduction.— No courtship activity was observed during this study. However, several gravid individuals were observed from 29 June to 27 July. During this period five gravid females were transported to the laboratory to determine fertility. Only two of the scorpions gave birth. A third died prior to parturition and was dissected. A female with only one pedipalp and a normal female each gave birth on 17 August 1972. The female with one pedipalp delivered 13 young, 10 of which she consumed before their first molt. The normal female delivered 39 young, all of which lived beyond their first instar. The dissected female contained 51 nearly mature embryos.

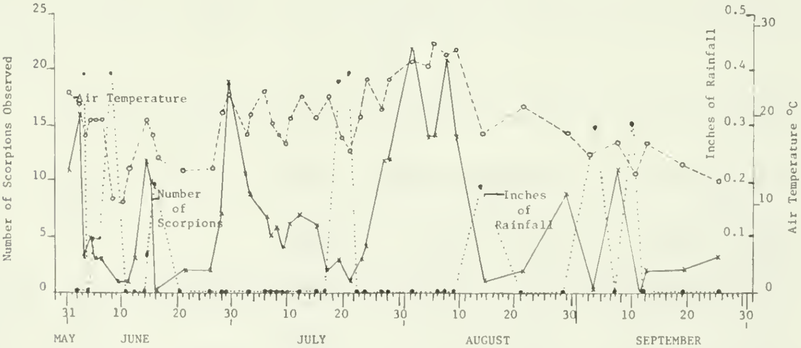

Fig. 6. Relationship between scorpion activity, air temperature, and rainfall, between 31 May and 25 September 1972.

Both females observed assumed a stilting position during parturition. The young, completely encased in a transparent birth membrane, passed through the genital aperture one by one. Within 10 to 20 minutes the young had freed themselves from the birth membrane and had climbed up the mother's walking legs to occupy a nonrandom position on her dorsum. The young scorpions first molted 12 days following birth, and within the next week they began to move from the mother's dorsum to assume an independent existence. The birth process and subsequent development of the young were similar to those described by Williams (1969). The mean litter size for the three observations was 34 ± 11.

MISCELLANEOUS OBSERVATIONS.— With few exceptions, all scorpions observed by blacklight were stationary. Similar behavior was reported by Hadley and Williams (1968) for other vaejovids. Most scorpions were observed sitting directly on the ground surface; however, several were seen on vegetation, as high as 50 cm above the ground.

Although scorpions were not observed in the act of capturing prey, feeding behavior was observed seven times during the study. Prey organisms included one grasshopper, two spiders, one scorpion (in a pitfall trap), two pentatomids, and one unidentified arthropod.

One adult female was uncovered by excavation on 10 March 1973. She was in a cavity approximately 30 mm long, 15 mm wide, and 10 mm high, at a depth of 25 cm. The air temperature at the time of capture was –1 C, and the ground temperature was approximately 8 C.

No organisms were observed to prey upon *P. boreus*, although several scorpions were killed in pitfall traps by Jerusalem crickets, *Stenopelmatus* sp. Cannibalism was observed only once in the field, but again in a pitfall.

DISCUSSION AND CONCLUSIONS

P. boreus was active on the surface only during the nocturnal hours. Nocturnal surface activity was not equally distributed throughout the night but was more intense shortly after sunset, diminishing until dawn. Hadley and Williams (1968) reported similar activity patterns for *V. confusis* and *P. mesaensis*. Decreased surface activity throughout the night might be attributed to decreasing air and soil temperatures during this period.

Surface activity of *P. boreus* was not evidenced until 22 March 1972, after which time it seemed to be contingent upon a minimum air temperature of 10 C. Surface activity was observed throughout the summer but diminished in the fall and was not evidenced after 13 October 1972. Causes for the variation in surface activity were not determined, but a relationship between activity, temperature, and rainfall seemed apparent. Many other factors, such as photoperiod, relative humidity, and soil moisture probably influence surface activity as well as temperature and rainfall, but these were not considered in this investigation.

Frequency of surface activity varied considerably among individuals. This variability might be explained by examination of such biologically necessary activities as feeding, mating, and population-dispersal. Nocturnal surface activity could provide a means of satisfying these necessities, after which the scorpion could remain in its burrow. Hadley and Williams (1968) suspected that nocturnal surface activity might be a means of maintaining water balance in a dry environment.

The high frequency of surface activity for females would permit a higher probability of mating encounters with the more mobile males. Once she has located a suitable shelter, the female appears to limit her surface activity to this vicinity. Williams (1966) suggested that the differentiation of movement patterns in male and female *A. phaeodactylus* might relate to the mate-seeking activity of males.

Sex ratios for *P. boreus* varied greatly, depending on time of year and sampling method. Allred (1973) assumed that males wander more extensively than females and are therefore more apt to fall into the pitfall traps. Because of the differentiation in mobility between males and females, data from pitfall studies were misleading in sex-ratio determinations. And because female vaejovids become less active on the surface in late summer and early fall, even blacklight data from this period tended to underestimate the number of females in the population. Probably the best method to determine sex ratio would involve comparison of the total number of males observed to the total number of females observed over the entire study period.

On the basis of the three litters examined, the variation in litter size for *P. boreus* is considerable. The smallest litter recorded (13) may have been a result of the female's handicapped condition, while the largest litter (51) may represent only the potential fecundity, since parturition had not yet occurred. The observed range in litter size is well within the range described by Baerg (1954) for several species of Scorpionida.

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NOTES ON THREE VARIETIES OF *ASTRAGALUS LENTIGINOSUS* (LEGUMINOSAE)

Carol S. Schoener[1]

Abstract.— A taxonomic review of the *Astragalus lentiginosus* complex in Utah indicates that the epithet var. *albiflorus*, antecedes and therefore should replace var. *diphysus.* The range of var. *vitreus* has been extended to include Kane and Garfield cos., Utah, and var. *fremontii* has now been identified from the state.

In a taxonomic review of the *Astragalus lentiginosus* complex in Utah, it was found that the name, var. *diphysus*, is anteceded by the name *A. diphysus* var. *albiflorus* Gray. The varietal name *diphysus* is more commonly used due to its previous status as a species. It also appears to be a misnomer to refer to this bright purple flowered plant by the epithet *albiflorus.* Barneby (1964, Mem. N. Y. Bot. Gard. 13:941) discusses this problem. According to the rules of botanical nomenclature (*International Code of Botanical Nomenclature*, Article 11, 1972), the older name in the same rank has precedence. Because the oldest name at varietal rank is *albiflorus*, I propose the new combination, to wit: *Astragalus lentiginosus* var. *albiflorus* (Gray) Schoener stat. nov. based on *Astragalus diphysus* var. *albiflorus* Gray in Memoirs of the American Academy II, 4 (Pl. Fendl.):34, 1894.

Herbarium specimens of *Astragalus lentiginosus* var. *fremontii* were collected in the vicinity of Terry's Ranch, at Beaver Dam Wash in Washington Co., Utah: Barnum 997 (BRY); Higgins 411 (BRY, NY) and 878 (BRY); Welsh 5265 (BRY, NY). This establishes a new state record: previously its distribution had been thought to be limited to the desert areas of southern Nevada and the northern and eastern Mohave Desert in California. The var. *fremontii* is quite distinctive with its small purple flowers (banner 9.4-11.5 [13.8] mm long, keel 6.3-7.9 mm long) and loose racemes which elongate as the flowers mature.

Astragalus lentiginosus var. *vitreus* has now been identified in Utah from Kane and Garfield cos. Kane Co.: Four Mile Bench, Atwood 4064 (BRY); Nipple Springs Road, Atwood and Allen 2820 (BRY); north end of Brigham Plain, Atwood and Allen 02791A (BRY); northeast slope of Smoky Mt., Cronquist 10022 (BRY, NY, RM, UTC). Garfield Co.: Star Spring, Henry Mts., Welsh 3942 (BRY, NY). Previous collection localities were in northern Mohave Co. and northwestern Coconino Co., Arizona, and in Washington Co., Utah. The variety can be characterized by its lax racemes (3.4) 4.0-9.0 (13.4) cm long and its inflated, papery-membranous, glabrous pods which become lustrous with maturity. Pods on two Kane Co. collections (Atwood and Allen, 02791A; Cronquist, 10022) are atypically mottled.

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[1] Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

NEW SPECIES OF AMERICAN *CORTHYLUS* (COLEOPTERA: SCOLYTIDAE)[1]

Stephen L. Wood[2]

Abstract.— The following species are described as new to science: *Corthylus nolenae*, *C. spinosus* (Mexico), *C. diligens* (Guatemala), *C. minimus* (Honduras), *C. granulifer*, *C. retusus*, *C. retusifer*, *C. oculatus*, *C. calamarius*, *C. cannularius*, *C. simplex*, *C. comosus*, *C. brunneus*, *C. calmicolens*, *C. zelus*, *C. trucis*, *C. pygamaeus*, *C. sobrinus*, *C. subserratus* (Costa Rica), *C. pumilus* (Panama), *C. donaticus*, *C. additus*, *C. cirritus* (Venezuela), *C. insignis*, (Colombia), *C. consimilis* (Mexico and Guatemala), *C. concisus* (Mexico, Costa Rica, and Panama), *C. sentus* (Guatemala and Costa Rica), *C. villifer*, *C. strigilis*, *C. trunculus*, *C. serratus* (Costa Rica and Panama). A lectotype is designated for *C. compressicornis* (Fabricius).

The 31 species of ambrosia beetles of the genus *Corthylus* described below as new to science were discovered during the preparation of my monograph of the Scolytidae of North and Central America. They are named here in order to avoid nomenclatural confusion and to facilitate identification in the interim period before publication of the monograph. The species described here are from Mexico (2), Guatemala (1), Honduras (1), Costa Rica (15), Panama (1), Colombia (1), Venezuela (3), Mexico and Guatemala (1), Mexico, Costa Rica, and Panama (1), Guatemala and Costa Rica (1), Costa Rica and Panama (4). *Corthylus compressicornis* (Fabricius) is redescribed, and a lectotype is designated.

Corthylus granulifer, n. sp.

This species is distinguished from *retusus* Wood by the smaller size, by much smaller tubercles on the elytral declivity, by the uniformly convex declivity lateral from striae 1, and by the more slender body form.

Male.— Length 2.0 mm, 2.5 times as long as wide; color dark brown.

Frons broadly convex, ascending slightly toward epistomal margin; surface shining at epistoma, reticulate above, reticulate area with sparse, rather fine punctures; vestiture sparse, inconspicuous. Antennal club as in *retusus*.

Pronotum 1.0 times as long as wide; anterior margin with median pair of serrations much larger, otherwise as in *retusus* female.

Elytra 1.5 times as long as wide, 1.5 times as long as pronotum; similar to *retusus*, except elytral surface smoother, strial punctures near declivity almost in rows, declivital interstriae 2 not impressed, 3 not elevated, tubercles much smaller, declivital vestiture apparently longer and slightly more abundant.

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[1] The research that resulted in the discovery of these insects was sponsored by the National Science Foundation.

[2] Department of Zoology, Brigham Young University, Provo, Utah 84602. Scolytidae contribution No. 53.

Type Locality.— Volcan Poas, Heredia, Costa Rica.

Type Material.— The male holotype was taken at the type locality on 9-XI-63, at 2500 m, No. 261, from a tree branch, by me. One male paratype is from 15 km SE Cartago, 24-IX-63, 1800 m, No. 200, *Myrica pubescens,* S. L. Wood.

The holotype and paratype are in my collection.

Corthylus retusus, n. sp.

This species is distinguished from *granulifer* Wood by characters summarized in the diagnosis of that species.

Female.— Length 2.3 mm (paratypes 2.2-2.4 mm), 3.3 times as long as wide; color very dark brown.

Frons deeply concave from eye to eye, from epistoma to vertex, lateral margin carinate from eye to lateral part of vertex; surface of lower half reticulate, upper half shining, slightly irregular, minutely, rather closely punctured, glabrous; a pair of widely spaced, slender, hornlike denticles near upper margin of concave area. Antennal club asymmetrically subquadrate, 1.4 times as long as wide; anterior surface minutely pubescent; suture 1 indicated by an obscure septum, 2 marked by an obscure groove; posterior face with a small tuft of hair extending slightly beyond apex of club.

Pronotum 0.93 times as long as wide; sides almost straight and parallel on basal half, abruptly converging to rather broadly rounded anterior margin; anterior margin with about 10 low serrations (viewed from cephalic aspect); summit indefinite, slightly anterior to middle; anterior slope coarsely asperate; posterior areas subshining, weakly reticulate, punctures minute, moderately abundant. Glabrous.

Elytra 1.3 times as long as wide, 1.5 times as long as pronotum; sides very feebly arcuate and subparallel on basal two-thirds, rather broadly rounded behind; disc smooth, shining, with obscure, irregular lines indicated, punctures small, confused, moderately abundant. Declivity convex, steep; interstriae 1 uniformly abruptly elevated from near base to near apex, about as high as wide on middle half, its summit smooth, shining, with sparse punctures; interstriae 2 moderately, broadly impressed, 3 convex, slightly elevated, 2-5 each bearing a row of conspicuous, closely spaced, pointed tubercles. Vestiture confined to declivity, of fine, long, interstrial hair.

Protibia with posterior face subrugulose, unarmed.

Male.— Similar to female, except frons and anterior margin of pronotum as in male *granulifer;* antennal club smaller, less strongly asymmetrical, tuft of hair absent.

Type Locality.— Tapanti, Cartago, Costa Rica.

Type Material.— The female holotype and one paratype were taken at the type locality on 26-XI-63, at 1300 m, No. 265, from *Phoebe mexicana* branches. The male allotype and one paratype are from the same locality, taken 2-VII-63, No. 9, *Miconia.* Eight paratypes are from 15 km SE Cartago, Cartago, Costa Rica, 24-IX-63, 1800 m, No. 198, *Solanum torvum*; one paratype bears this same data except it is from No. 195, tree seedling. All specimens were taken by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus retusifer, n. sp.

This species is distinguished from *retusus* Wood by the characters of the antennal club and elytral declivity as cited below.

Female.— Length 2.0 mm (paratypes 1.7-2.0 mm), 2.3 times as long as wide; color very dark brown (holotype not fully darkened).

Frons as in *retusus;* antennal club more nearly subcircular, sutures 1 and 2 entirely obsolete except for a very small piece of septum of 1 on lateral margin. Pronotum and elytra as in *retusus*, except declivital interstriae 2 impressed, very strongly narrowed, almost obsolete, unarmed, 3 weakly convex, 3-5 armed by small granules about as in *granulifer* Wood.

Male.— Similar to female, except frons, antenna, and anterior margin of pronotum as in male *granulifer.*

Type Locality.— Tapanti, Cartago, Costa Rica.

Type Material.— The female holotype and two paratypes were taken on 26-XI-63, at 1300 m, No. 265, *Phoebe mexicana.* The male allotype and two paratypes are from the same locality, 24-X-63, No. 266, *Cecropia* branch. One paratype bears data identical to the type except it is No. 271, *Werklia insignis;* two paratypes are from the same locality, one taken 2-VII-63, No. 7, woody vine, and one 17-IX-63, No. 176, tree branch. All were taken by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus villifer, n. sp.

This unique species is distinguished from all others in the genus by the small, slender form, by the abundant, minute setae on the posterior half of the elytra, by the female antennal club and frons, and by other characters.

Female.— Length 1.5 mm (paratypes 1.4-1.7 mm), 2.5 times as long as wide; color brown.

Frons rather shallowly concave from eye to eye from epistoma to upper level of eyes, a median, shining callus on epistoma; surface shining, punctures coarse, close, deep; vestiture of fine, long, uniformly distributed hair. Antennal scape rather strongly flattened; club large, asymmetrical, 1.3 times as long as wide, sutures obsolete except 1 at mesal margin, uniformly, finely pubescent.

Pronotum 1.05 times as long as wide; sides almost straight and parallel on basal half, rather broadly rounded in front; anterior margin unarmed; summit indefinite, slightly in front of middle; rather finely asperate on anterior slope; posterior areas reticulate, punctures small, obscure, moderately abundant; lateral margins rounded, not marked by a raised line. Subglabrous.

Elytra 1.6 times as long as wide, 1.6 times as long as pronotum; sides straight and parallel on more than basal two-thirds, broadly rounded behind; disc smooth and shining at base, becoming strongly reticulate toward declivity, punctures sparse, small, confused. Declivity steep, shallowly, subconcavely impressed on median half, lateral and basal margins broadly rounded; surface minutely, closely punctured; impressed area extending from suture to position of interstriae 3. Vestiture largely confined to posterior fourth, of dense, minute hair, a few longer setae on marginal areas.

Protibiae subinflated on posterior face, a few very minute granules indicated.

Male.— Similar to female, except frons convex, reticulate, punctures sparse, obscure, subglabrous; anterior margin armed by one median pair of large, slender teeth.

Type Locality.— Fifteen km SE Cartago, Cartago, Costa Rica.

Type Material.— The female holotype, male allotype, and 37 paratypes were taken at the type locality on 24-IX-63, 1800 m, Nos. 187, 199 (type), and 248, *Siparuna nicaraguensis.* Fourteen paratypes bear identical data except No. 201, woody vine. Three paratypes are from Tapanti, Cartago, Costa Rica, 2-VII-63, 1300 m, No. 177, woody vine. Twenty-six paratypes are from Cerro Punta (labeled Volcan Chiriqui), Chiriqui, Panama, 11-I-64, 1800 m, No. 385, woody vine. All were taken by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus oculatus Wood

This species is distinguished from *villifer* Wood by the smaller size, by the very large eyes, by the narrower, less strongly impressed female frons, and by the strongly elevated declivital interstriae 1.

Female.— Length 1.2 mm (paratypes 1.0-1.2 mm), 2.3 times as long as wide; color brown.

Frons narrow, shallowly concave from eye to eye, from epistoma to slightly below upper level of eyes; surface smooth and shining on upper half, reticulate below, punctures sparse, fine; vestiture rather sparse, moderately long. Eye very large, coarsely faceted. Antennal club similar to *villifer* but slightly smaller.

Pronotum and elytra about as in *villifer*, except elytral disc strongly reticulate to base, declivity more nearly convex, declivital interstriae 1 strongly, acutely elevated from base to near apex, punctures not evident, a few minute granules on interstriae 3; vestiture confined to declivity, consisting of very short, moderately abundant hair, a few long, slender bristles on declivital interstriae 1, 3, and lateral areas.

Male.— Similar to female, except frons convex, reticulate, punctures obscure; anterior margin of pronotum armed by a median pair of slender teeth.

Type Locality.— Pandora, Limon, Costa Rica.

Type Material.— The female holotype, male allotype, and eight paratypes were taken at the type locality on 23-VIII-63, at 50 m, No. 142, in a tree branch, by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus calamarius, n. sp.

This species is distinguished from *cannularius* Wood by the distinct strial punctures that are in rows, by the larger, regularly placed interstrial granules on the declivity, and by the more coarsely punctured female frons.

Female.— Length 2.9 mm (paratypes 2.5-2.9 mm), 2.6 times as long as wide; color yellowish brown, with anterior third of pronotum and elytral declivity dark brown to black.

Frons deeply concave from eye to eye, from epistoma to vertex; surface reticulate, punctures rather close, moderately coarse; vestiture of moderately abundant, fine, rather long hair, uniformly distributed except absent on a small median area at epistoma. Antennal club subreniform, 1.2 times as long as wide; suture 1 represented by septum on lateral third, 2 and 3 represented by arcuate grooves (secondary strengthening features, not true sutures); a small tuft of hair on posterior face not reaching apex.

Pronotum 1.02 times as long as wide; widest near base, sides weakly arcuate and converging very slightly on basal half, rather narrowly rounded in front; anterior margin serrate; summit indefinite, slightly in front of middle; anterior slope moderately steep, coarsely asperate; posterior areas finely reticulate, punctures very small, rather sparse; lateral margin rounded. Glabrous.

Elytra 1.6 times as long as wide, 1.6 times as long as pronotum; sides straight and parallel on basal two-thirds, rather broadly rounded behind; disc reticulate, punctures near base minute, obscure, confused, those on posterior third distinct and in definite strial rows. Declivity convex, steep; striae 1 and 2 with punctures minute; interstriae 2 broadly, very weakly impressed, 1-4 each with a row of small, regularly spaced granules. Vestiture confined to declivity, consisting of interstrial rows of moderately long, slender bristles.

Male.— Similar to female, except frons convex, reticulate sparsely punctured, subglabrous, antennal club smaller, less irregular in shape; median pair of serrations on anterior margin of pronotum much larger than others.

Type Locality.— Volcan Poas, Heredia, Costa Rica.

Type Material.— The female holotype, male allotype, and nine paratypes were taken at the type locality on 19-XI-63, near 2000 m elevation, from recently cut native bamboo, by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus cannularius, n. sp.

This species is distinguished from *calamarius* Wood by the confused, obscure to obsolete punctures near the elytral declivity, by the very minute to obsolete, irregularly placed interstrial granules on the declivity, and by the more finely punctured female frons.

Female.— Length 2.5 mm (paratypes 2.5-2.8 mm), 2.5 times as long as wide; color yellowish brown, anterior third of pronotum and elytral declivity darker.

Frons as in *calamarius*, except surface almost smooth, punctures minute. Pronotum as in *calamarius*, except anterior margin more coarsely serrate (somewhat variable). Elytra as in *calamarius*, except punctures near declivity confused or obsolete, strial punctures on declivity obsolete, interstrial granules on declivity much smaller and more widely, less regularly spaced, declivital vestiture finer and less abundant.

Male.— Similar to female, except frons convex, reticulate, sparsely punctured, subglabrous; antennal club smaller, less irregular in shape; anterior margin of pronotum armed by only two coarse teeth.

Type Locality.— Cerro de la Muerte, San José, Costa Rica.

Type Material.— The female holotype, male allotype, and 38 paratypes were taken at the type locality on 6-VIII-63, at 3200 m, No. 46, in native bamboo, by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus comosus, n. sp.

This species is distinguished from the very closely related *villosus* Eggers by the smaller pale area on the lower fifth of the female frons, by the smaller punctures on the elytral disc, by the more closely punctured elytral declivity, by the much more abundant declivital vestiture, and by the larger size (*villosus* 2.0-2.5 mm).

Female.— Length 2.6 mm (paratypes 2.5-2.8 mm), 2.1 times as long as wide; color dark brown.

Frons deeply, uniformly concave from eye to eye, from epistoma, to vertex; almost half of concave area above eyes; surface reticulate, finely, closely, uniformly punctured, lower one-sixth yellow and with punctures finer and much closer; vestiture of rather abundant, uniformly distributed, short, fine hair, slightly longer on upper margin. Antennal club large, reniform; tuft of hair on posterior face ending before apex of club.

Pronotum 0.90 times as long as wide; widest near bases, sides weakly arcuate and subparallel on basal third, broadly rounded in front; anterior margin armed by about 14 low serrations; summit indefinite, anterior slope moderately steep; asperities commence slightly behind middle and continue to anterior margin; posterior area reticulate, punctures minute. Minute, hairlike pubescence moderately abundant, but usually abraded.

Elytra 1.2 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on basal half, broadly rounded behind; disc smooth, a few very obscure irregular lines evident, punctures very fine, moderately abundant, confused. Declivity occupying posterior third, steep, evenly, broadly convex; surface smooth, shining, punctures very fine, close, confused, much closer than in *villosus.* Vestiture sparse on disc, abundant on entire declivity, of fine, moderately long hair, more abundant than in *villosus.*

Male.— Similar to female, except frons convex, reticulate, rather finely punctured, vestiture sparse; anterior margin of pronotum armed by two median teeth.

Type Locality.— Tapanti, Cartago, Costa Rica.

Type Material.— The female holotype, male allotype, and 30 paratypes were taken on 26-XI-63, at 1300 m, No. 264, from *Piper*, by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus simplex, n. sp.

This species is distinguished from *rubricollis* Blandford by the characters of the elytral declivity and of the female frons as indicated below.

Female.— Length 2.9 mm (paratypes 2.7-3.0 mm), 2.4 times as long as wide; color black.

Frons as in *rubricollis*, except punctures larger, vestiture coarser, slightly less abundant, slightly longer, broad median line on upper third impunctate and glabrous. Antennal club 1.3 times as long as wide; sutures 1 and 2 slightly procurved, parallel, clearly marked; tuft of hair on posterior face extending about half club length beyond apex.

Pronotum and elytra as in *rubricollis* except upper two thirds of declivity more gradual, declivital interstriae 2 less strongly impressed, strial punctures much smaller, declivital bristles (when present) about twice as long.

Male.— Similar to female, except frons convex, reticulate, punctures fine, sparse, subglabrous.

Type Locality.— Cerro de la Muerte, San José, Costa Rica.

Type Material.— The female holotype and male allotype were taken at the type locality on 6-VIII-63, at 3100 m. No. 111, from a tree seedling. Six paratypes are from Volcan Poas, Heredia, Costa Rica, three on 14-VII-63, 2500 m, No. 46, *Podocarpus oleifolius*, and three 19-XI-63, 2500 m, No. 262, tree branch. All were taken by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus consimilis, n. sp.

This species is distinguished from *panamensis* Blandford by the larger elytral punctures, by the feebly impressed interstriae 2, and by the larger elevated callus on the female vertex.

Female.— Length 2.8 mm (paratypes 2.5-2.8 mm), 2.2 times as long as wide; color very dark brown.

As in *panamensis*, except frontal callus larger, extending from vertex to slightly below upper level of eyes; elytral punctures distinctly larger, particularly on declivity; declivital interstriae 2 feebly impressed; declivital tubercles slightly larger and more widely distributed.

Male.— Similar to female, except differing as in *panamensis.*

Type Locality.— Nine km NE Teziutlan, Puebla, Mexico.

Type Material.— The female holotype, male allotype, and 22 paratypes were taken at the type locality on 2-VII-67, 1600 m, Nos. 136, 140 (type), from tree boles, or an unnumbered sample from *Alnus*. One paratype is from the same locality, taken 27-VI-53. Five paratypes are from Volcan Pacaya, Esquintla, Guatemala, 1-VI-64, 1300 m, No. 668, tree branch. Four paratypes are from Volcan de Agua, Guatemala, 19-V-64, 1000 m, No. 615, *Acacia*. All were taken by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus brunneus, n. sp.

This species is distinguished from *calmicolens* Wood by the smaller size, by the more slender body form, by the much more coarsely serrate anterior margin of the pronotum, and by the setal characters indicated below.

Female.— Length 3.2 mm (paratypes 3.0-3.3 mm), 2.4 times as long as wide; color dark brown, discal area of elytra lighter.

Frons as in *punctatissimus* (Zimmermann), except vestiture more abundant and slightly longer on margins of lower half. Antennal club very large, strongly subreniform, suture 1 weakly, 2 moderately procurved; tuft of hair on posterior face large, its tip reaching apex.

Pronotum as in *punctatissimus*, except anterior margin very coarsely serrate, median serrations larger.

Elytra as in *punctatissimus*, except punctures slightly smaller, declivity not as steep, more broadly convex, punctures much less numerous, very fine, confused except on striae 1, about four minute granules on interstriae 1; ventrolateral margin of declivity with a low, short, subacute carina extending from costal margin toward interstriae 8. Vestiture fine, hairlike, sparse, not confined to declivity, mostly confined to odd-numbered interstriae except on sides, rather sparse on interstriae 8 and 9 and not longer than elsewhere.

Male.— Similar to female, except frons convex, subshining, sparsely, coarsely punctured; median pair of serrations on anterior margin of pronotum larger.

Type Locality.— Volcan Barba, Heredia, Costa Rica.

Type Material.— The female holotype, male allotype, and 13 paratypes were taken on 19-XI-63, at 2500 m, No. 258, from native bamboo, by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus calmicolens, n. sp.

This species is distinguished from *brunneus* Wood by the larger size, by the stouter body form, by the much more finely serrate anterior margin of the pronotum, and by the setal characters indicated below.

Female.— Length 4.0 mm (paratypes 3.7-4.0 mm), 2.3 times as long as wide; as in *brunneus*, except anterior margin of pronotum finely serrate, elytral declivity more broadly convex, and vestiture along sides of elytra much more abundant and longer.

Male.— Similar to female, except differing as in male *brunneus*.

Type Locality.— South slope Volcan Barba, Heredia, Costa Rica.

Type Material.— The female holotype, male allotype, and 11 paratypes were taken at the type locality at Finca Vota Steinworth, on 8-II-65, from native bamboo, by J. B. Karren. One paratype is from Volcan Poas, 19-XI-63, 2500 m, No. 258, native bamboo, by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus strigilis, n. sp.

This species is distinguished from *comatus* Blandford by the more deeply impressed declivital interstriae 2, by the much less closely, more coarsely punctured female frons, by the very small tuft of hair on the posterior face of the female antennal club, and by the finely serrate apical margin of the female antennal club.

Female.— Length 2.7 mm (paratypes 2.7-3.1 mm), 2.3 times as long as wide; color dark brown.

Frons as in *comatus*, except less deeply concave, sparsely, less uniformly punctured, an indistinct median callus on upper third, vestiture much more sparse, very fine, absent on callus. Antennal club 2.8 times as long as wide, large, rather strongly asymmetrical: sutures 1 and 2 indicated by grooves, weakly procurved; tuft of hair on posterior face very small, ending remote from apex.

Pronotum and elytral disc as in *comatus*. Elytral declivity as in *comatus*, except interstriae 2 more strongly impressed, 1 more strongly elevated, half as high as wide, lateral convexities more narrowly rounded.

Male.— Similar to female, except differing as in *comatus*.

Type Locality.— Sixteen km SE Cartago, Cartago, Costa Rica.

Type Material.— The female holotype, male allotype, and three paratypes were taken at the type locality on 24-IX-63, at 1800 m, No. 205, in *Myrica pubescens*, by me; five paratypes bear identical data except No. 204 from *Miconia globuliflora*. Thirty-nine paratypes are from Tapanti, Cartago, Costa Rica, 2-VII-63, No. 9, *Miconia*, 17-IX-63, No. 176, tree limb, 24-X-63, No. 241, *Phoebe mexicana*, 26-XI-63, No. 265 on *Phoebe mexicana* and 270 on *Werklia insignis*. Two paratypes are from Escasu, San José, Costa Rica, 2-X-63, 1300 m, No. 217, *Ficus*. Fifteen paratypes are from Cerro Punta (labeled Volcan Chiriqui), Chiriqui, Panama, 11-I-64, 1800 m, No. 393 in a tree branch, No. 407 in a tree seedling. All were taken by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus diligens, n. sp.

This species is distinguished from *comatus* Blandford by the much more deeply impressed declivital interstriae 2 and by characters of the female frons and antennal club as indicated below.

Female.— Length 2.5 mm (paratypes 2.5-2.6 mm), 2.4 times as long as wide; color brown.

Frons as in *comatus*, except concave area more broadly oval, 1.2 times as long as wide (1.4 times in *comatus*); tuft of hair on posterior face of antennal club with tip ending remote from apex. Pronotum as in *comatus*, except anterior margin more coarsely serrate; punctures on disc minutely, obscurely granulate. Elytra as in *comatus*, except declivity more strongly impressed on interstriae 2, suture not as high, lateral convexities higher and more narrowly rounded.

Male.— Similar to female, except sexual differences as in *comatus*.

Type Locality.— Volcan de Agua, Esquintla, Guatemala.

Type Material.— The female holotype and five paratypes were taken at the type locality on 19-V-64, 1000 m, Nos. 593 in *Clusia*, 600 (type) in *Alnus*. The male allotype and one paratype are from Palin, Esquintla, Guatemala, 19-V-64, 300 m, No. 687, *Ficus*. Two paratypes are from Lago Amatitlan, 10-VI-64, 700 m, tree branch. All were taken by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus zelus, n. sp.

This species is distinguished from *diligens* Wood by the larger size and by characters of the female frons and antennal club as indicated below.

Female.— Length 3.5 mm (paratypes 3.4-3.5 mm), 2.5 times as long as wide; color very dark brown.

Frons similar to *diligens*, except concave area less strongly impressed, upper margin not clearly delimited; frontal vestiture longer. Tuft of hair on antennal club with its tip almost attaining apex. Anterior margin of pronotum less coarsely serrate. Elytral declivity with punctures on striae 1 in a row, shallow, of moderate size; lateral punctures much smaller.

Male.— Similar to female, except sexual differences as in *comatus*.

Type Locality.— Cerro de la Muerte, San José, Costa Rica.

Type Material.— The female holotype, male allotype, and one male paratype were taken at the type locality on 6-VIII-63, at 2500 m, No. 114, in *Brunellia costaricensis*, by me.

The holotype, allotype, and paratype are in my collection.

Corthylus trunculus, n. sp.

This unique species is distinguished from all other representatives of the genus by the small size, by the truncate elytral declivity that is armed at its base by a pair of denticles on interstriae 3, by the convex female frons, and by the strongly procurved sutures on the female antennal club.

Female.— Length 1.4 mm (paratypes 1.3-1.4 mm), 2.2 times as long as wide; color brown.

Frons weakly convex, except somewhat flattened on lower fifth; surface subreticulate, punctures small, obscure, moderately abundant; vestiture of uniformly distributed moderately long hair from epistoma almost to vertex. Antennal club subtriangular, more nearly symmetrical than normal for this genus, 1.1 times as long as wide; sutures 1 and 2 strongly procurved, 1 apparently partly septate but not showing on posterior face; posterior face with tip of small tuft of hair reaching apex.

Pronotum 1.1 times as long as wide; basically as in *comatus* Blandford, except sculpture much finer, posterior areas strongly reticulate.

Elytra 1.2 times as long as wide; 1.1 times as long as pronotum; sides almost straight on basal five-sixths, very slightly narrower behind, abruptly, very broadly rounded behind; disc almost smooth, subshining, points, lines, and punctures small, confused, somewhat obscure. Declivity truncate, very steep, margin from base to apex abruptly rounded, slightly elevated (not acutely margined); basal margin armed by a pair of small pointed spines at interstriae 3; sutural interstriae uniformly, subacutely, rather weakly elevated; surface strongly reticulate, punctures abundant, confused, shallow, very obscure. Vestiture sparse, short, confined to sides and margins of declivity.

Posterior margin of protibia subinflated and armed by four to six confused, minute denticles.

Male.— Similar to female, except frons more strongly convex, subglabrous; antennal club normal, sutures weakly procurved, tuft of hair absent; anterior margin of pronotum armed by two or more coarse teeth.

Type Locality.— Thirteen km or 8 miles S El Hato del Volcan, Chiriqui, Panama.

Type Material.— The female holotype, male allotype, and six paratypes were taken by me at the type locality on 7-I-64, 1000 m, No. 371, from a tree seedling, by me. One paratype is from Beverley, Limon, Costa Rica, 26-VIII-63, 7 m, No. 154, woody vine, by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus minimus, n. sp.

This species is distinguished from *minutissimus* Schedl by the characters of the head and elytral declivity as indicated below.

Female.— Length 1.3 mm (paratypes 1.3-1.4 mm), 2.3 times as long as wide; color brown.

Frons very narrow, very shallowly concave on central half, impressed area not attaining upper level of eyes; surface shining, obscurely reticulate, a few punctures in marginal areas; subglabrous. Eyes very large, coarsely faceted. Antennal club 1.5 times as long as wide, moderately asymmetrical; sutures almost straight, 1 partly septate, 2 very obscure; posterior face without a tuft of hair.

Pronotum and elytra essentially as in *minutissimus*, except elytral declivity with interstriae 2 narrowed, moderately impressed, 1 carinate, more strongly elevated, 3 distinctly elevated and armed by about four minute tubercles, 2 without setae.

Male.— Similar to female, except frons convex, rugose-reticulate, punctures more uniformly distributed; eyes of normal size; antennal club smaller, less elongate; anterior margin of pronotum armed by a pair of coarse, median teeth.

Type Locality.— La Ceiba, Atlantida, Honduras.

Type Material.— The female holotype, male allotype, and 15 paratypes were taken at the type locality from 20-V to 26-VIII-49 (type 1-VI-49), at light, by E. C. Becker.

The holotype, allotype, and paratypes are in my collection.

Corthylus pumilus, n. sp.

This species is distinguished from *minutissimus* Schedl by characters of the frons and elytral declivity as indicated below.

Female.— Length 1.7 mm (paratypes 1.5-1.8 mm), 2.2 times as long as wide; color brown.

Frons broadly, deeply concave from epistoma to vertex; surface evidently minutely, densely punctured and finely, densely, uniformly pubescent except smooth and glabrous on narrow median area on upper fourth; vestiture rather short, of uniform length. Antennal club 1.4 times as long as wide; strongly reniform, with grooved sutures, and with a small tuft of hair on posterior face as in *minutissimus*.

Pronotum and elytra as in *minutissimus*, except elytral declivity with interstriae 1 more strongly elevated, 2 weakly impressed, entirely unarmed, and devoid of setae, 4 feebly elevated and armed by about four minute tubercles. Vestiture as in *minutissimus*, except more slender, slightly longer, absent on interstriae 2.

Male.— Similar to female, except frons convex, reticulate, subglabrous; antennal club normal, anterior margin of pronotum armed by a pair of coarse, median teeth.

Type Locality.— Madden Forest, Canal Zone, Panama.

Type Material.— The female holotype, male allotype, and eight paratypes were taken at the type locality on 2-I-64, at 70 m, No. 366, in tree branch, by me. Eight paratypes are from Ft. Clayton, Canal Zone, Panama, 22-XII-63, 30 m, No. 363, tree branch, by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus trucis, n. sp.

This species is distinguished from *uniseptis* Schedl by the larger size, by the armed declivial interstriae 2, and apparently by other characteristics.

Female.— Length 3.0 mm (paratypes 2.9-3.1 mm), 2.3 times as long as wide; color dark brown, almost black.

Frons deeply concave from eye to eye, from epistoma to vertex; surface smooth, shining, finely, closely punctured, except narrowly impunctate on entire median line; vestiture of fine, erect moderately long hair of uniform length, except a few longer setae on lateral margins. Antennal club large, strongly asymmetrical, 1.25 times as long as wide, with three rather strongly procurved sutures, median half of 1 septate, cirrus extending slightly beyond apex.

Pronotum and elytral disc essentially as in *comatus* Blandford. Elytral declivity broadly convex, steep; posterolateral margin subacutely elevated from costal margin to interstriae 8; surface shining, impressed points rather numerous, strial punctures only slightly larger than points, mostly in rows; interstriae 1 distinctly elevated, subcostate, 2 distinctly, rather shallowly impressed, 1-3 each armed by about four to six moderately large tubercles, usually less numerous on 2. Vestiture mostly confined to declivity, of fine, long, interstrial hair of moderate abundance.

Male.— Similar to female, except frons convex, reticulate, sparsely punctured, subglabrous; antennal club much smaller, more nearly symmetrical, with only two sutures; anterior margin of pronotum more strongly serrate, median pair larger.

Type Locality.— Sixteen km SE Cartago, Cartago, Costa Rica.

Type Material.— The female holotype, male allotype, and three paratypes were taken at the type locality on 24-IX-63, at 1800 m, No. 204, in *Miconia globuliflora*, by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus nolenae, n. sp.

This species is distinguished from *detrimentosus* Schedl by the smaller size, by the female frons, and by the elytral declivity as noted below.

Female.— Length 2.3 mm (paratypes 2.0-2.3 mm), 2.3 times as long as wide; color reddish brown, elytra black.

Frons as in *detrimentosus*, except spongy area smaller, ending well below upper level of eyes, dorsal half of excavated area with a strongly elevated median carina, marginal setae slightly longer, cirrus on antennal club smaller, shorter.

Pronotum much as in *detrimentosus*, except pronotal disc with several broad subasperate crenulations, and elytral disc with strial punctures much larger and mostly in definite rows. Elytral declivity similar to *detrimentosus* but not as steep and more narrowly convex; strial punctures rather coarse, deep; interstriae 1 distinctly elevated, 3 feebly elevated on basal half, 1 and 3 each with about four to six small tubercles; ventrolateral margin as in *detrimentosus*.

Male.— Similar to female, except sexual differences as in *detrimentosus*.

Type Locality.— Huajuapan, 21 km or 13 miles SE Oaxaca, Oaxaca, Mexico.

Type Material.— The female holotype, male allotype, and 49 paratypes were taken at the type locality on 4-VII-53, in a *Nolena* fruiting stalk, by me.

The holotype, allotype, and paratypes are in my collection.

Corythylus spinosus, n. sp.

This species is distinguished in the male by the stouter body and by the very different elytral declivity.

Male.— Length 2.0 mm, about 2.0 times as long as wide; color very dark brown.

Frons, antenna, pronotum, and elytral disc as in *uniseptis* Schedl, except pronotum with summit nearer base, its disc with rather numerous low, rather broad, transverse crenulations. Elytral declivity much as in *uniseptis*, except wider, strial punctures slightly larger, interstriae 2 narrower and slightly deeper, 1 and 3 each bearing about four very coarse, sharply pointed tubercles, each higher than wide (unusually large for this genus), several smaller tubercles in lateral areas. Vestiture slightly longer and more abundant than in *uniseptis*.

Type Locality.— Fortin de las Flores-Sumidero, Veracruz, Mexico.

Type Material.— The male holotype was taken at the type locality on 27-IV-65, 900 m, at blacklight, by H. V. Weems, Jr. The holotype is in my collection.

Corthylus sentus, n. sp.

This species is distinguished from *minutus* Bright by the larger size and by the characters of the female frons.

Female.— Length 2.0 mm (paratypes 2.0-2.4 mm), 2.3 times as long as wide (2.4 times in Guatemalan specimens); color brown. Frons strongly concave from eye to eye, from epistoma to vertex; surface of upper half almost smooth, evidently with a few minute punctures, lower half from epistoma to upper level of eyes entirely occupied by a pair of oval, yellow, spongy areas, separated by a fine, low, acute, median carina, margins of spongy areas without a row of hair in most specimens, an irregular row in others. Antennal club strongly asymmetrical, apex subacute, sutures 1 and 2 moderately procurved, both partly septate at median end, a feeble suture 3 suggested; cirrus entirely absent.

Pronotum as in *uniseptis* Schedl, except discal areas with numerous weak, broad crenulations. Elytral disc as in *uniseptis*, except punctures more obscure; declivity about as in *spinosus*, except punctures obsolete, interstriae 1 weakly elevated, unarmed, 2 impressed, strongly narrowed, essentially obsolete, 3 and lateral areas convex, 3 armed by about three coarse spines (larger than in *spinosus*), usually with one to two smaller spines at base, lateral areas with about four to eight pointed tubercles. Vestiture confined to declivity, of sparse hair.

Male.— Similar to female, except frons convex, reticulate, sparse punctures obscure, antennal club smaller, less strongly asymmetrical; anterior margin of pronotum armed by one pair of median teeth.

Type Locality.— Two km SE Cartago, Cartago, Costa Rica.

Type Material.— The female holotype, male allotype, and 39 paratypes were taken at the type locality on 2-VIII-63, at 1300 m, No. 98, from a tree branch. Ten paratypes are from Cerro Peña Blanca, Honduras, 23-IV-64, 2000 m, No. 529, *Miconia schlechtendalii.* Five paratypes are from Guatemala City, Guatemala, 30-V-64, 1300 m, No. 644 in leguminous vine, or 643 in a shrub branch. One paratype is from Quezaltenango, Guatemala, 26-V-64, No. 623, tree branch. All were taken by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus pygmaeus, n. sp.

This species is distinguished from *spinifer* Schwarz by the smaller size and by the numerous minor features indicated below.

Female.— Length 1.8 mm (paratypes 1.5-1.8 mm), 2.0 times as long as wide; color brown.

Frons as in *spinifer*, except more shallowly impressed (transversely flat at upper level of eyes), punctures averaging smaller, longest setae on upper third less numerous. Cirrus on antennal club shorter, its length from insertion of last hair to its apex less than length of club.

Pronotum and elytra as in *spinifer*, except declivital sulcus not quite as deep, punctures slightly finer, impressed points largely obsolete, posterolateral margin more abruptly, less strongly elevated.

Male.— Similar to female, except sexual differences as in *spinifer*.

Type Locality.— Finca La Lola, Limon, Costa Rica.

Type Material.— The female holotype, male allotype, and four paratypes were taken at the type locality on 17-I-63, from *Theobroma cacao* branches, by J. L. Saunders. Eight paratypes are from Pandora, Limón, Costa Rica, 23-VIII-63, 50 m, No. 149, tree branch, by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus sobrinus, n. sp.

This species is distinguished from *flagellifer* Blandford by the larger size and by characters of the frons and elytral declivity mentioned below.

Female.— Length 3.0 mm (paratypes 3.0-3.4 mm), 2.1 times as long as wide; color very dark brown.

Frons as in *flagellifer*, except much more strongly impressed, particularly on upper half; lower fifth with a pair of rather widely separated, oval, yellow spongy areas (vestiture not interrupted by their presence); vestiture similar to *flagellifer*, except most setae strongly flattened, less abundant at upper margin. Antennal cirrus much more poorly developed but only slightly shorter.

Pronotum and elytra as in *flagellifer*, except punctures on elytral disc larger but very shallow, and elytral declivity somewhat more strongly, more broadly impressed.

Male.— Similar to female, except sexual differences as in *spinifer*.

Type Locality.— Turrialba, Cartago, Costa Rica.

Type Material.— The female holotype, male allotype, and 14 paratypes were taken at the type locality on 7-I-63, in *Theobroma cacao*, by J. L. Saunders. Two paratypes are from the same locality taken 9-III-64, 700 m, No. 468B, from a fence post, by me.

The holotype, allotype, and paratype are in my collection.

Corthylus subserratus, n. sp.

This species is distinguished from *serrulatus* Eggers (from Bolivia and Peru) by the larger size and by conspicuous differences on the head and elytral declivity as indicated below.

Female.— Length 2.5 mm (paratypes 2.3-2.5 mm), 2.4 times as long as wide; color black, with one-third to two-thirds of elytra yellowish brown (area and color intensity of pale portion variable).

Frons deeply concave from eye to eye, from epistoma to vertex, much deeper than in *serrulatus;* entire lower third occupied by yellow spongy area, upper areas dull, coarsely punctured; vestiture absent at center of concavity, increasing in size and density toward margins above eyes; margins above eyes ornamented by a dense brush of long, yellow, strongly plumose setae (as in *serrulatus*). Antennal club as in *serrulatus,* with suture 1 partly septate, 2 and 3 weakly impressed; cirrus entirely absent.

Pronotum as in *serrulatus,* except posterior areas more strongly reticulate, weak transverse crenulations on disc much narrower. Elytra as in *serrulatus*, except surface of disc less shining; declivity less convex, posterolateral margin ending slightly below middle of declivity, surface strongly reticulate, punctures mostly obscure, interstriae 1 slightly less strongly elevated, its summit conspicuously undulating, forming about six rounded serrations (summit an almost uniform costa in *serrulatus*). Vestiture confined to declivity, of rows of erect interstrial hair on interstriae 1 and 3 and base of 2, a few setae in lateral areas.

Male.— Similar to female, except frons convex, reticulate, sparsely punctured, vestiture sparse, inconspicuous; antennal club smaller, more nearly symmetrical; anterior margin of pronotum armed by one median pair of teeth.

Type Locality.— Volcan Poas, Heredia, Costa Rica.

Type Material.— The female holotype, male allotype, and 65 paratypes were taken at the type locality on 19-XI-63, 2500 m, Nos. 260, 261 (type), from tree branches. Twenty-eight paratypes were taken 14-VII-63, No. 44B, 12 paratypes were taken 6-IX-63, No. 169 from *Vaccinium consanguineum*, and four paratypes were taken 19-VII-66, at 1300 m, from the same locality. Three paratypes are from Guapiles, Limón, Costa Rica, 22-VIII-66, 100 m. All were taken by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus serratus, n. sp.

This species is distinguished from *serrulatus* Eggers and *subserratus* Wood by the smaller size and by conspicuous differences on the head and elytral declivity as noted below.

Female.— Length 2.0 mm (paratypes 2.0-2.3 mm), 2.5 times as long as wide; color dark brown.

Frons basically shallowly concave as in *serrulatus*, and with oval area on median half from near epistoma to near vertex abruptly, much more strongly concave; central concavity smooth, with a few punctures and hairlike setae; lateral areas minutely, densely punctured, becoming spongy and yellowish above on median margins, this area very minutely, densely pubescent; plumose vestiture on upper margin as in *subserratus*. Antenna as in *serrulatus*, except cirrus smaller, slightly shorter.

Pronotum and elytral disc as in *serrulatus*, except punctures on elytral disc slightly larger. Elytral declivity with margins abruptly angled, except rounded on basal fifth, face much more weakly convex than *serrulatus*, its surface shining and punctured about as in *serrulatus*, interstraie 1 more strongly elevated than in *serrulatus*, its crest with about four to six coarse crenulations, some of them acutely pointed. Interstriae 1, 3, and 4 with very long hairlike setae.

Male.— Similar to female, except sexual differences as in *subserratus*.

Type Locality.— Tapanti, Cartago, Costa Rica.

Type Material.— The female holotype was taken at the type locality on 24-X-63, 1300 m, No. 241, in *Phoebe mexicana;* two paratypes are from the same locality, one taken 2-VII-63, No. 9, *Miconia*, and one 24-XI-63, No. 271, *Werklia insignis.* Three paratypes are from 16 km SE Cartago, Cartago, Costa Rica, 24-IX-63, 1800 m, No. 204, *Miconia globuliflora.* The male allotype and 11 paratypes were taken from Cerro Punta (labeled Volcan Chiriqui), Chiriqui, Panama, 11-I-64, 1800 m, No. 371 in *Inga* (allotype), Nos. 388, 399, in tree branches; four paratypes from the same locality were taken 19-XII-63, No. 315, *Inga.* All were taken by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus donaticus, n. sp.

This species is distinguished from *serratus* Wood by the larger size, by the less strongly elevated declivital interstriae 1, by the abrupt, angulate margins being restricted to the lower half of the elytral declivity, and by the different female frons as described below.

Female.— Length 2.4 mm (paratypes 2.4-2.6 mm), 2.2 times as long as wide; color very dark brown.

Frons rather deeply concave from eye to eye from epistoma to vertex, a feeble median carina on floor of upper half of concave area; lateral area just mesad of lateral margin with an elongate, elevated, yellow spongy area from upper level of eyes to vertex, dorsal ends of these spongy areas separated from one another by a distance slightly less than half distance between eyes; spongy areas with minute pile, their lateral margins marked by a dense row of long yellow hair very similar to but shorter than in *serratus*.

Pronotum and elytral disc as in *serratus*. Elytral declivity as in *serratus*, except lateral margin subacutely angulate only on lower half and interstriae 1 less strongly elevated, crest almost as high as wide at highest point; setae on interstriae 1 short to obsolete.

Male.— Similar to female, except sexual differences as in *serratus.*

Type Locality.— Colonia Tovar, Aragua, Venezuela.

Type Material.— The female holotype, male allotype, and 28 paratypes were taken at the type locality on 4-V-70, 1700 m, Nos. 478 (1), 484 (8), 487 (1), 493 (2), 496 (holotype and 3 paratypes), 497 (allotype and 9 paratypes), 502 (2), 509 (2), from various hosts, by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus additus, n. sp.

This species is distinguished from *serratus* Wood by the larger size, by the more slender body form, and by the female frons as described below.

Female.— Length 2.7 mm (paratypes 2.3-2.7 mm), 2.8 times as long as wide; color very dark brown.

Frons similar to *serratus*, except lower half of excavated area as strongly impressed as dorsal half; lateral margins of impressed area narrowly, more strongly elevated, spongy and with very short pile-like pubescence from upper level of eye to upper level of ocular emargination, these spongy areas of yellow color; pubescence about as in *serratus* except slightly more abundant, a row of longer hair along lateral margins of spongy area to epistoma. Antenna as in *serratus*, with sutures 1 and 2 clearly marked, 1 septate.

Pronotum and elytra as in *serratus*.

Male.— Similar to female, except sexes differing as in *serratus*.

Type Locality.— La Carbonera experimental forest, about 50 km (airline) NW Merida, Merida, Venezuela.

Type Material.— The female holotype, male allotype, and 19 paratypes were taken at the type locality on 14-X-69, 2500 m, No. 50 (12) and 51 (1) in *Clusia*, 53 (2) and 61 (holotype, allotype, 2 paratypes), and 62 (1) in *Nectandra*, 66 (1). Other paratypes from the same locality were taken 10-X-69, No. 121 (1) in *Rubus*, 122 (2) and 123 (1) in a woody vine, 125 (2) in *Nectandra*, 128 (10) in a tree seedling; 9-XII-69, No. 171 (2) in a small log, 174 (2) in *Nectandra*. Three paratypes are from La Mucuy, Merida, Venezuela, 20-X-69, 2500 m, No. 74 (1) in *Nectandra*, and 12-XI-69, No. 131 (1) and 132 (1) in tree branches. Two paratypes are from Merida, Merida, Venezuela, 22-IX-69, 1700 m, No. 8 in *Ficus* and 12 in *Vismia*. All were taken by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus cirritus, n. sp.

This species is distinguished from *additus* Wood by the stouter body form, by the subangulate margin of the elytral declivity extending from the apex to the base, and by the conspicuous differences in the female frons and antenna as described below.

Female.— Length 2.3 mm (paratypes 2.2-2.4 mm), 2.3 times as long as wide; color very dark brown.

Frons similar to *additus*, except dorsal half more broadly impressed, spongy areas less strongly elevated, slightly wider; hair on lateral margins more abundant, extending to level of antennal insertion, a separate tuft of plumose hair on lateral areas of epistoma. Antennal club similar in shape to *additus* but sutures replaced by three arcuate calluses; cirrus slender, exceedingly long, more than four times length of club.

Pronotum and elytral disc as in *additus*. Declivity similar to *additus*, except margin subacutely elevated on a complete circle, interstriae 1 less strongly elevated, tubercles on interstriae 3 almost obsolete.

Male.— Similar to female, except sexual differences as in *serratus* Wood.

Type Locality.— La Carbonera experimental forest, about 50 km (airline) NW Merida, Merida, Venezuela.

Type Material.— The female holotype, male allotype, and 23 paratypes were taken at the type locality on 9-IV-70, 1100 m, Nos. 404 (1), 412 (11), 413 (holotype, allotype, 6 paratypes), 419 from *Piper* (1), 431 from *Nectandra* (2), 433 (1), 445 (1), by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus insignis, n. sp.

This species is distinguished from *schaufussi* Schedl by the smaller size and by characters of the frons and elytra as described below. Eggers erroneously considered this species to be *compressicornis* (Fabricius), as indicated by his specimens "mit type vergleichen."

Female.— Length 1.8 mm (paratypes 1.8-2.1 mm), 2.2 times as long as wide; color very dark brown.

Frons as in *schaufussi*, except short, pale setae in central area more strongly flattened, and more strongly plumose, marginal reddish, long setae much more densely placed, particularly on vertex and toward bases of mandibles. Antennal club as in *schaufussi*.

Pronotum as in *schaufussi*, except disc more strongly reticulate and with minute, transverse crenulations much more obscure, almost obsolete. Elytral declivity as in *schaufussi* except steeper, interstriae 1 less strongly elevated, with its crest smooth, without indications of serration; lateral areas more evenly convex, denticles on interstriae 3 much smaller.

Type Locality.— Twenty-four km E Barbosa, Antioquia, Colombia.

Type Material.— The female holotype, male allotype, and 26 paratypes were taken at the type locality on 18-VII-70, at 1200 m, No. 699, in *Inga*, by me.

The holotype, allotype, and paratypes are in my collection.

This species was reported by Schedl from Brazil and Peru as *praeustus* Schedl; *praeustus* apparently is restricted in its distribution to Central America.

Corthylus concisus, n. sp.

This species is distinguished from *praeustus* Schedl by the larger size and by the characters on the head mentioned below.

Female.— Length 2.2 mm (paratypes 2.0-2.3 mm), 2.1 times as long as wide; color dark brown to almost black.

Frons flat, a weak transverse callus at level of antennal insertion; large central area smooth, glabrous, impunctate, marginal areas with fine punctures; lateral, submarginal areas with a tuft of hair from level of antennal insertion to upper level of eyes, margin above upper level of eyes ornamented by a dense row of very long plumose setae. Antennal club very broad, 1.4 times wider than long, cirrus at least three times longer than club (club longer than wide and cirrus shorter than club in *praeustus*).

Pronotum and elytral disc essentially as in *petilus* Wood, except pronotal disc with minute, transverse crenulations and punctures on elytral disc minute, confused. Elytral declivity truncate, subvertical, margin abruptly, subacutely elevated on a complete circle from apex to base; face slightly convex, strongly reticulate, punctures small, confused; interstriae 1 strongly costate, as high as wide on middle half, middle area of 2 distinctly impressed, 3 weakly elevated on upper half and armed by about two to four small, pointed tubercles. Glabrous except for a few setae on declivital interstriae 1 and 3.

Male.— Similar to female, except sexual differences as in *petilus*.

Type Locality.— Tapanti, Cartago, Costa Rica.

Type Material.— The female holotype, male allotype, and 15 paratypes were taken at the type locality on 17-VIII-63, 1300 m, No. 106, from a woody vine; two paratypes are from the same locality taken 24-X-63, Nos. 224, 245, and one paratype 2-VII-63, No. 10, *Conostegia oerstediana*. Other paratypes include 20 from Turrialba, Cartago, Costa Rica, 7-I-63, *Theobroma cacao*, J. L. Saunders; 1 from 16 km SE Cartago, Cartago, Costa Rica, 3-VII-63, No. 11, woody vine; 6 from Peralta, Cartago, Costa Rica, 10-III-64, 500 m, Nos. 461, 462, woody vines; 2 from Puerto Viejo, Heredia, Costa Rica, 12-III-63, 70 m, No. 480, woody vine; 2 from Volcan, Puntarenas, Costa Rica, 11-XII-63, 1000 m, No. 304, tree branch; 4 from Escasu, San José, Costa Rica, 2-X-63, No. 215 in *Guazuma ulmifolia*, No. 216 in *Spondias purpurea*, No. 218 in a tree seedling;

10 from Santa Ana, San José 4-X-63, 1300 m, No. 223, tree branch, and 5 on 9-X-63, No. 229, tree branch; 2 from Río Damitas, Dota Mts., San José, 18-II-64, 250 m, No. 436, tree seedling; 4 from 13 km or 8 miles S El Hato del Volcan, Panama, 7-I-64, 1000 m, No. 371, tree seedling; 3 from Cerro Campana, Panama, 26-VII-66, 1000 m, No. 32, tree branch. All were taken by me except as noted.

The holotype, allotype, and paratypes are in my collection.

This species was treated as *Corthylus compressicornis* by Blandford (1904, Biol. Centr. Amer. Coleopt. 4(6):255).

Corthylus compressicornis (Fabricius)

Bostrichus compressicornis Fabricius, 1801, Systema Eleutheratorum 2:388 (Lectotype, female; Essequibo, British Guiana; Copenhagen Mus., present designation)

Two female type specimens of this species are in the Fabricius collection. The pin of each specimen bears a small green label without writing, and a red label with the printed word "Type". In addition, the first specimen bears a handwritten label, "Essequibo. Schmidt. Mus. J. Lund. Bostrichus compressicornis Fabr." The first specimen is here designated as the lectotype of *Bostrichus compressicornis* Fabricius and now bears my red lectotype label.

Female lectotype.— Length 2.2 mm, 2.1 times as long as wide; color dark brown.

Frons visible to upper level of eyes; flat to feebly concave, lateral margins along inner margin of eye subacutely elevated, ending ventrally in a small denticle just below upper limits of ocular emargination; epistomal margin weakly elevated; surface of subconcave area smooth and shining except for two large, contiguous, longitudinally oval, spongy areas occupying middle half from level of antennal insertion to a point well below upper level of eye; spongy areas yellow, almost smooth, their margins acutely elevated well above surfaces of frons or spongy areas; surface of spongy areas elevated slightly above surface of remainder of frons; areas of frons dorsad from spongy areas bearing fine, long, yellow hair over entire surface. Antennal club strongly asymmetrical much as in *concisus* Wood, and bearing a cirrus twice as long as width of club.

Pronotum as in *schaufussi* Schedl, except less strongly reticulate and transverse discal rugosites much more obscure. Elytra as in *schaufussi*, except disc less shining, declivity dull. Pronotum 1.2 times as long as elytral disc.

Notes.— This species has been reported from various parts of Central and South America; however, except for the two females in the Fabricius collection, it is unknown to me. At least two Central American species, *concisus* Wood and *praeustus* Schedl, have been reported as this species. The confusion of South American forms with this species is much more complex.

NOTES ON *VISCAINOPELMATUS DAVEWERNERI* (ORTHOPTERA: GRYLLACRIDIDAE; STENOPELMATINAE) FROM THE VISCAINO DESERT, BAJA CALIFORNIA SUR, MEXICO

Ernest R. Tinkham,[1] Clark R. Mahrdt,[2] and Benjamin H. Banta[3]

Abstract.— A male nymph in stadium 3 of *Viscainopelmatus davewerneri* Tinkham is reported and illustrated. The specimen was taken near Laguna Scammon, Baja California Sur, Mexico.

Tinkham (1970) described *Viscainopelmatus davewerneri* on the basis of a single specimen of undetermined sex (lacking an abdomen) from the coastal dunes at Laguna Manuela, approximately 25 km NE of Guerrero Negro, Baja California Norte, Mexico. The holotype was found while excavating a rodent burrow on 5 July 1965. We report a second specimen obtained from a rodent burrow by Banta on 30 December 1971. The specimen, deposited at California Academy of Sciences (CAS), was taken on the southwest side of Laguna Scammon, approximately 4 km east of the lagoon entrance, Baja California Sur, Mexico. The site is located at 114° 20′ W long., 27° 45′ N lat, near sea level. The dominant vegetation in this area of predominantly coastal sand dunes includes *Abronia maritima*, *Lycium* sp., *Seauvium verrucosum*.

Despite numerous visits in this area by scientists of diverse disciplines, only two specimens have been obtained. Tinkham and Mahrdt visited the area on two separate occasions (June 1968 and January 1971, respectively) but failed to obtain additional stenopelmatids.

The second specimen, a male, is apparently in the third stadium of nymphal development, and is significantly smaller than the type (Table 1). Size variation cannot be attributed to sexual dimorphism, because male and female stenopelmatids are usually consistent in their morphological features (Tinkham, 1970). The main difference between the two specimens, other than size, is that in the nymph the dorsal outline of the pronotum is rather quadrate

Table 1. Morphometric data (in millimeters) of *Viscainopelmatus davewerneri.*

Source	Body Length	Head + Thorax	Pronotum	Caudal Femur	Caudal Tibia
Type (Tinkham, 1970)	ca. 30-35 mm	11.3	7.2 x 8.8	10.0 x 4.1	10.8 x 3.5
CAS	26.8	9.5	4.2 x 5.4	6.7 x 2.4	7.2 x 2.0

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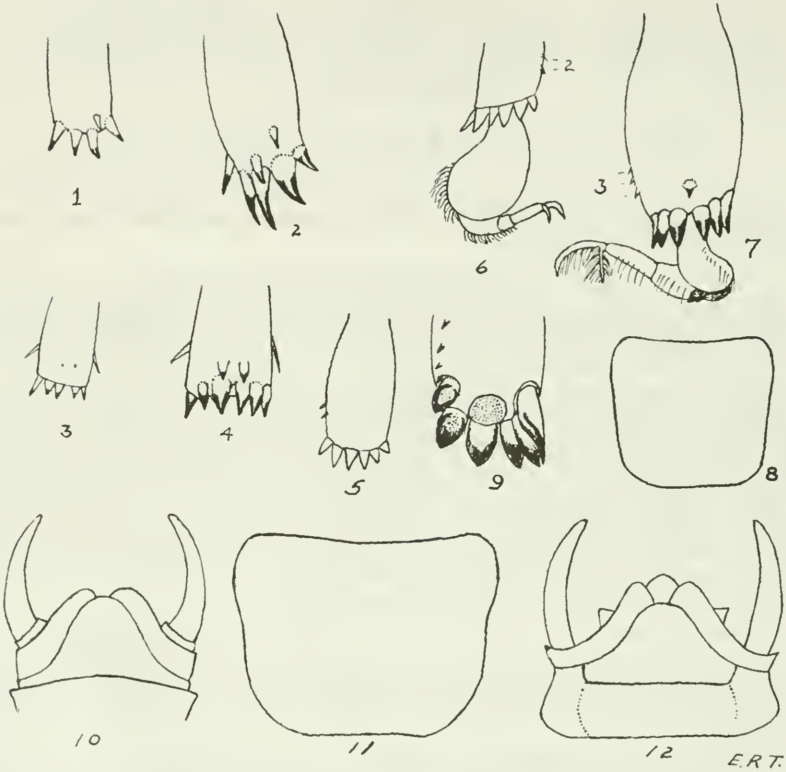
[1] 81-441 Date Palm, Indio, California 92201.
[2] San Diego Natural History Museum, P.O. Box 1390, San Diego, California 92112.
[3] Department of Biology, United States International University, San Diego, California 94131.



Figs. 1-12. *Viscainopelmatus davewerneri*: comparison of the holotype to the male stadium 3 nymph taken near Scammon Lagoon. 1, Apical chaetotaxy of right foretibia, ventral aspect, nymph; 2, same for holotype; 3, ventral aspect of right mesotibia of nymph; 4, same for holotype; 5, apical chaetotaxy of metatibia of nymph, dorsal aspect; 6, left metathoracic tarsus, showing plantar surface from ventromesal aspect, nymph; 7, same from right tibia of holotype; 8, outline of pronotum of nymph from dorsal aspect; 9, apical chaetotaxy of left metathoracic tibia of holotype, dorsal aspect; 10, apical terminalia of nymph, dorsal aspect; 11, outline of pronotum of holotype; 12, same, ventral aspect. All drawn with the aid of a stereoscopic microscope at 15 X magnification.

(Fig. 8), whereas in the type the pronotum is ampliate forward with all angles well rounded (Fig. 9). The supra-anal and subgenital plates of the nymph are roundly triangular and rather similar (Figs. 10, 11).

Leg Spination: Figures 1 and 2 show that the foretibiae, exclusive of size, are similar. Figures 3 and 4 depict identical chaetotaxy in the calcars, but the two dorsal subapical teeth are the merest black dots in the nymph. The dorsal subapical teeth are of important taxonomic value in Stenopelmatidae. Figures 5, 6, and 7 show relative sizes of the caudal tibia and tarsus and reveal that the peculiar feature of having a laterally flattened and twisted caudal tarsus, characteristic of *Viscainopelmatus*, is evident in the third stadium nymph. The nymph differs from the type in possessing only two minute, subapical, vestigial, external dorsal teeth instead of three. In Tinkham's (1970:174) key the sixth line should be amended to read, "only 2 or 3 very small, vestigial, external, dorsal, subapical teeth."

The coloration of the head, thorax, and abdomen in alcohol is brown pink to tan, 91-L in Maerz and Paul (1950). The abdomen is unicolor without alternating black and white bands.

Viscainopelmatus davewerneri, previously known only from the type locality, occupies a coastal sand dune habitat. Our specimen

Fig. 13. *Viscainopelmatus davewerneri* male nymph in stadium 3: 1, dorsal aspect; 2, ventral aspect; 3, ventral aspect showing black-edged spathulate calcars of metathoracic tibiae and twisted tarsi; 4, ventral aspect of protibial calcars.

was taken in ecological conditions like those of the type; its occurrence 60 km southwest on the south side of Scammon Lagoon further indicates a distribution confined to coastal sand dunes of the Viscaino Desert. Indeed, the salient features show an adaptation to such an arenicolous environment. However, there is still a need for more intensive sampling in the Viscaino Desert to discern the distributional parameters and extent of variation in this species.

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THE *AUSTRINA* GROUP OF THE GENUS *MICROVELIA* (HEMIPTERA; VELIIDAE)

John T. Polhemus[1]

Abstract.— Six new species of *Microvelia* are described from North and Central America: *depressus, glabrosulcata, leavipleura, paura, psilonota,* and *reflexus*. These species are compared to *Microvelia austrina* Bueno, and the *austrina* group is designated to hold them. The habitats and phoresy of the group are discussed.

Microvelia austrina Bueno is a widespread species, occurring from the southeastern United States into Central Mexico. No closely related species have been previously described. Through extensive collecting from the United States to Panama, I have been able to secure series of *Microvelia* containing a complex of closely related species which I here designate as the *austrina* group.

In the *austrina* group the males offer little in the way of diagnostic characters, but the apterous females exhibit various modifications to facilitate the males' riding astride or "piggyback," and these features provide excellent specific characters. Many of the small microvelias exhibit such modifications in the female, but they have rarely been used as key characters (Polhemus, 1970). The late Carl Drake described many *Microvelia*, including some with obvious female modification, but did not use the character in discrimination, which may explain why several of the species described below stand in his collection under *M. austrina*. (Loans from the Drake collection are not permitted, so those specimens are not included in this study).

All of the species of the *austrina* group are found in cryptic habitats during daylight hours as they are apparently strongly negatively phototropic. Only once were members of this group observed running on open water; this was in the early morning in canopy jungle, where *M. paura* n. sp. could be seen in the dim light as dark specks moving slowly over a pool in the small stream. The most successful method of collecting is violent sweeping and splashing in dark caverns or under overhanging banks adjoining slow clear water streams. Many specimens collected were paired even after being dashed about, but no mating pairs were observed; Esaki (1937) noted a similar phoresy in *M. notophora* Esaki.

The modifications to facilitate the male's riding "piggyback" would seem to serve two purposes. First, a male would be readily available at the time of mating; second, the specialized modification exhibited by each species would be a premating reproductive isolating mechanism. At this time it is not known whether or not there are strong postmating reproductive isolating mechanisms in the group, but several species are sympatric, and as Littlejohn (1969) has pointed out, premating isolation would permit the most efficient use of gametes.

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[1] 3115 S. York, Englewood, Colorado 80110

The *austrina* group will be described first, giving the generalized characters; the species descriptions will follow, providing additional detail and key characters. For all measurements 60 units equals 1 mm. Females are intentionally named as holotypes: those types being retained in the Polhemus collection are irrevocably committed to later placement in a designated type repository.

Much of the material reported here is in the Polhemus collection (JTP). Most of the remaining specimens belong to the University of Colorado Museum (CU), and I am indebted to Dr. Peter Robinson for the opportunity to study them. The latter were collected by Martin S. Polhemus and myself during a Mexican Expedition partly financed by a grant from the University of Colorado. I am indebted to the late Robert L. Usinger for permitting me to study specimens from the University of California at Berkeley (UCB), to the late Jean L. Lafoon for the exchange specimens from the Iowa State University Collection, to Harold C. Chapman for the gift of specimens from his collection, and to Peter D. Ashlock for the loan of recently collected specimens from the University of Kansas (KU).

Microvelia austrina Group

DESCRIPTION.— Small (1.2 to 2.2 mm), stout (see Figs. 1, 2). Head short, broad, recessed into anterior margin of pronotum; ground color blackish brown with fine greyish pubescence. Pronotum long, covering mesonotum. Legs short, stout. Antenna short, stout, fourth segment fusiform. Hemelytral markings and veins inconspicuous. Body of male somewhat depressed dorsoventrally.

Male parameres small, inconspicuous; male genital segment not prominent (Fig. 1E, F). Male foretibial comb prominent, extending beyond distal end of tibia.

Key to the *Microvelia austrina* Group

1. Humeri depressed in both sexes .... *depressus* n. sp.
   Humeri not depressed 2

2. Anterior lobe of pronotum with transverse orange brown band extending laterally onto episternum; body length at least 1.95 mm in male, 2.15 mm in female .... *reflexus* n. sp.
   Anterior lobe of pronotum with shorter transverse orange brown band, usually not extending past lateral margins; if transverse band extends onto episternum (*paura*), then body length not more than 1.3 mm in male, 1.75 mm in female 3

3. Distal segment of middle tarsi either shorter or longer than proximal segment by about 20 percent; coxae yellowish or dark brown 4
   Distal segment of middle tarsi subequal to proximal segment; coxae yellowish 5

4. Distal segment of middle tarsi longer than proximal segment (7:9); coxae dark brown .... *glabrosulcuta* n. sp.
   Distal segment of middle tarsi shorter than proximal segment (11:9); coxae yellowish .... *paura* n. sp.

5. Proepisternum yellowish or light orange brown with very obvious but tiny black conical setae .... *psilonota* n. sp.
   Venter unicolorous or proepisternum dark orange brown; proepisternum not light colored and black conical setae not obvious 6

6. Posterior acetabula with glabrous area .... *laevepleura* n. sp.
   Posterior acetabula without glabrous area .... *austrina* Bueno

Microvelia austrina Bueno 1924

Microvelia austrina Bueno 1924. Bull. Brooklyn Ent. Soc. 19(5):191 (North Carolina)

Drake and Hussey (1955) gave the distribution of this species as Indiana, Maryland, Mississippi, North Carolina, Tennessee, Virginia, and Mexico.

DESCRIPTION.— Female body shape elongate, quite similar to

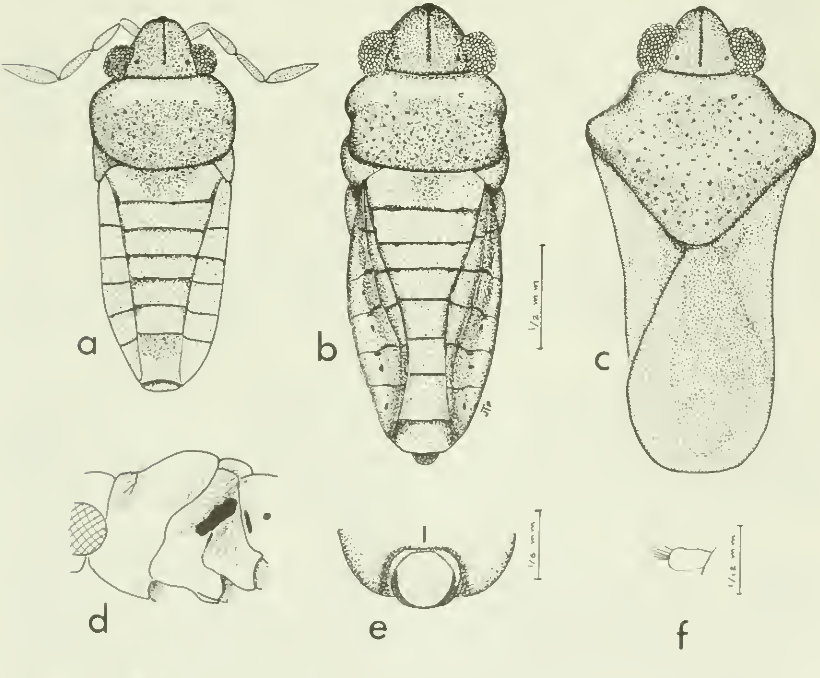

Fig. 1. *Microvelia leavipleura n.* sp.: a, Apterous male: b, Apterous female: c. Macropterous female; d. Pronotum and pleura. apterous female, side view; e. Genital segments, male; f. Male paramere.

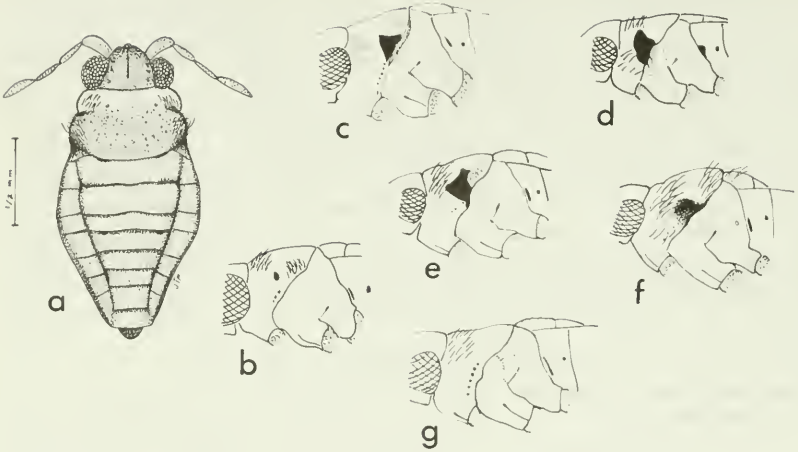

Fig. 2. *Microvelia* spp.: a, *paura* n. sp., apterous female; b-g, Pronotum and pleura, apterous females, side view; b, *paura* n. sp.; c, *depressus* n. sp.; d, *psilonota* n. sp.; e, *glabrosulcata* n. sp., f, *reflexus* n. sp., g, *austrina* Bueno.

Figure 1B; male body shape elongate, tapering caudad, very similar to Figure 1A.

Anterior lobe of pronotum with yellowish to dark orange brown band, continuous or weakly interrupted on midline, extending almost to lateral margins in some females, shorter and darker in males. Anterior lobe of pronotum, humeri, and pleura of apterous female with long stiff setae (Fig. 2G); alate females with a patch of stiff setae on anterolateral margins of pronotum; apterous and alate males with shorter scattered setae on pronotum and elytra. Apterous female without glabrous areas on pronotum or pleura, but with semiglabrous depressed area on propleura and mesopleura.

Connexiva slightly raised in male, almost flat to vertical in apterous females. Dorsum of abdomen covered with short inconspicuous pubescence.

Venter uniformly dark, except dark orange brown next to eyes on proepisternum, anterior and middle acetabula; venter of abdomen with semilong decumbent setae in female, shorter in male. Rostrum basally, coxae, trochanters, femora basally and legs beneath yellowish to testaceous, remainder of extremities brown. Legs with the following proportions (apterous female plesiotype):

	Femur	Tibia	Tarsal 1	Tarsal 2
Anterior	28	20	13	—
Middle	32	26	13	13
Posterior	33	36	8	12

Antennal proportions I; II; III; IV: 9; 10; 12; 14.

Body measurements:
Mean length of 10 apterous ♂♂: 1.59 mm (max. 1.70, min. 1.47).
Mean width of 10 apterous ♂♂: 0.60 mm (max. 0.68, min. 0.55).

Mean length of 10 apterous ♀♀ : 1.87 mm (max. 2.00, min. 1.80).
Mean width of 10 apterous ♀♀ : 0.74 mm (max. 0.80, min. 0.70).
Plesiotype: Length 1.88 mm, width 0.72 mm (apterous ♀).

Material examined.—MEXICO: San Luis Potosi; 1 ♂ apterous, 25 ♂♂, 23 ♀♀ macropterous, Ciudad del Maiz. CL528, 9-I-1971, J. T. & M.S. Polhemus (JTP): Veracruz; 1 ♂, 1 ♀ apterous, 8 ♂♂, 2 ♀♀ macropterous, Tantoyuca, CL523, 8-I-1971, J. T. & M. S. Polhemus (JTP). UNITED STATES; Georgia; Calhoun, 8-VIII-1958, H. C. Chapman, 22 ♂♂, 17 ♀♀, all apterous (JTP). Tennessee; Knoxville, 27-VI-1891 to 2-VII-1891, H. E. Summers Collection, 1♂, 4 ♀♀, all macropterous (JTP).

Discussion.— The description of *austrina* by Torre-Bueno (1924) is quite adequate but is given here for consistency. Curiously, Torre-Bueno chose a female for the type of *austrina*, but undoubtedly with a different motivation than mine in describing additional members of the group.

Austrina can be separated from the other group species by the key characters and by the small degree of modification in the apterous female.

Microvelia depressus, n. sp.

Female body shape elongate oval, widest across metapleura; male body shape similar to female but slightly narrower.

Anterior lobe of pronotum with orange brown band reaching inner margin of eyes, often weakly interrupted medially. Female pronotum with two groups of stiff but slender, long setae, most noticeable from side (Fig. 2C); male with shorter scattered setae; humeri depressed in both sexes, pronotum narrowed laterally, and entire dorsum depressed below level of first visible abdominal tergite; female with glabrous area on lateral margin.

Connexiva moderately raised in males, usually vertical in females or reflexed over last three tergites.

Venter uniformly dark except small brown spot on proepisternum cephalad of anterior coxae; jugum of head and entire venter covered with minute black conical setae, most noticeable on brown area of proepisternum. Legs, rostrum, and antennae brown; basal part of femora and trochanters yellowish. Posterior acetabula with glabrous spot. Legs with following proportions:

	Femur	Tibia	Tarsal 1	Tarsal 2
Anterior	21	17	10	—
Middle	27	22	8	11
Posterior	30	30	5	8

Antennal proportions I; II; III; IV: 10; 8; 7; 13.

Body measurements:
Mean length of 9 apterous ♂♂ : 1.74 mm (max. 1.78, min. 1.53).
Mean width of 9 apterous ♂♂ : 0.75 mm (max. 0.77, min. 0.72).
Mean length of 10 apterous ♀♀ : 167 mm (max. 1.72, min. 1.60).
Mean width of 10 apterous ♀♀ : 0.78 mm (max. 0.80, min. 0.73).
Holotype: Length 1.67 mm, width 0.78 mm.

Material examined.— Holotype, apterous ♀, 10 mi. N Chapala, Jalisco. Mexico, 22-IV-1964, J. T. & M. S. Polhemus (CU). Paratypes as follows;

MEXICO: Jalisco; 9 ♂♂, 18 ♀♀ apterous, 10 mi. N Chapala, 22-IV-1964, J. T. & M. S. Polhemus (CU, JTP).

Discussion.— The strongly depressed humeri in both sexes are characteristic of this species and set it off from the remainder of the group.

Microvelia glabrosulcata, n. sp.

Female body shape elongate, abdomen slightly wider than thorax, not as robust as *psilonota;* male body shape elongate, tapering caudad, similar to Figure 1A.

Anterior lobe of pronotum with orange brown uninterrupted band reaching inner eye margin, rarely beyond. Anterior lobe of alate and apterous females with long stiff setae, apterous females also with stiff setae on humeri directed cephalad (Fig. 2E), thinner long setae on propleura of females; males with shorter scattered setae, not prominent. Apterous and alate females with a shallow glabrous sulcus on lateral margin of pronotum cephalad of humeri.

Connexiva almost flat in males and some females, strongly raised in most females, rarely almost vertical.

Venter uniformly dark, except proepisternum dark grey brown; entire venter set with minute black conical setae, most noticeable on episternum. Legs, rostrum, and antennae brown, anterior femora lighter beneath. Acetabula with prominent glabrous areas. Legs with following proportions:

	Femora	Tibia	Tarsal 1	Tarsal 2
Anterior	24	17	10	—
Middle	25	22	7	9
Posterior	26	26	6	9

Antennal proportions I; II; III; IV: 8; 7; 6; 10.

Body measurements:
Mean length of 10 apterous ♂♂ : 1.34 mm (max. 1.38, min. 1.28).
Mean width of 10 apterous ♂♂ : 0.58 mm (max. 0.60, min. 0.55).
Mean length of 10 apterous ♀♀ : 1.66 mm (max. 1.72, min. 1.58).
Mean width of 10 apterous ♀♀ : 0.79 mm (max. 0.82, min. 0.72).

Holotype: Length 1.62 mm, width 0.73 mm.

Material examined.— Holotype, apterous ♀, Ciudad del Maiz, San Luis Potosi, Mexico, 9-I-1971, CL528, J. T. & M. S. Polhemus (in Polhemus Collection). Paratypes as follows; MEXICO: San Luis Potosi; 10 ♂♂, 22 ♀♀ apterous, 14 ♂♂, 21 ♀♀ macropterous, Ciudad del Maiz, 9-I-1971, CL528, J. T. & M. S. Polhemus (JTP). Jalisco; 1 ♂, 1 ♀ apterous, 10 mi. N Chapala, 22-IV-1964, CL1031, J. T. & M. S. Polhemus (CU). UNITED STATES: Arizona; 2 ♂♂, 11 ♀♀ apterous, 1 ♀ macropterous, Superior, 7-X-1964, CL313, J. T. Polhemus (JTP); 3 ♂♂, 7 ♀♀ apterous, Sabino Canyon, 27-XI-1970, CL497, J. T. Polhemus (JTP).

Discussion.— This species is widely distributed, but its known range is restricted to northern Mexico and Arizona. At Ciudad del Maiz, San Luis Potosi, it was taken with *austrina.*

The glabrous sulcus on the female pronotum, the dark coxae, and the long distal segment of the middle tarsi are diagnostic. The body shape is compact and somewhat resembles *depressus.*

Microvelia leavipleura, n. sp.

Female body shape elongate (Fig. 1B); male body shape elongate, tapering caudad (Fig. 1A).

Anterior lobe of pronotum with yellowish to dark orange brown band, continuous or weakly interrupted on mid-line, not extending to lateral margins. Anterior lobe of pronotum, humeri, and pleura of apterous female with long stiff setae (Fig. 1D); anterior lobe of pronotum and corium of hemelytra in alate female with long stiff setae; apterous and alate males with shorter scattered setae on pronotum and elytra. Apterous female with a glabrous sulcus on the metapleura (Fig. 1D); alate female with shallow sulcus in same position, not glabrous.

Connexiva slightly raised in male, reflexed over abdomen in female. Dorsum of abdomen covered with semilong decumbent setae, shorter in male.

Venter uniformly dark, covered with semilong decumbent setae in female, much shorter in male. Femora yellowish basally and beneath, remainder of femora and tibia deep brown. Coxae, trochanters, and beak yellowish, antennae deep brown. Legs with the following proportions (holotype):

	Femur	Tibia	Tarsal 1	Tarsal 2
Anterior	39	27	14	—
Middle	40	33	13	13
Posterior	42	42	10	13

Antennal proportions I; II; III; IV: 12; 15; 14; 17.

Body measurements:
Mean length of 10 apterous ♂♂ : 1.77 mm (max. 1.80, min. 1.72).
Mean width of 10 apterous ♂♂ : 0.68 mm (max. 0.70, min. 0.67).
Mean length of 10 apterous ♀♀ : 2.17 mm (max. 2.38, min. 2.05).
Mean width of 10 apterous ♀♀ : 0.78 mm (max. 0.83, min. 0.72).

Holotype: Length 2.20 mm, width 0.83 mm.

Genital segment and paramere of male as in Figure 1E and F respectively.

MATERIAL EXAMINED.— Holotype, apterous ♀, Rincon Chamula, Chis., Mexico, 6-I-1974, CL671, J. T. Polhemus (in Polhemus Collection). Paratypes as follows; MEXICO: CHIAPAS; 21 ♂♂, 17 ♀♀ apterous, Rincon Chamula, CL671, 6-I-1974, J. T. Polhemus (JTP); 13 ♂♂, 13 ♀♀ apterous, 2 ♂♂, 3 ♀♀ macropterous, 1 nymph, 12 mi. N Bochil, CL1091, 4 May 1964, J. T. and M. S. Polhemus (CU).

DISCUSSION.— This is the only member of the group in which the apterous female has an obvious glabrous sulcus on the metapleura. In general body shape, *leavipleura* resembles *austrina*, but the glabrous area on the posterior acetabula, lacking in *austrina*, will separate them.

The collections of this species were made over a rather restricted area in northern Chiapas.

Microvelia paura, n. sp.

Female body shape robust (Fig. 2A); male body shape similar to figure 1A.

Anterior lobe of pronotum with orange brown band extending to lateral margins in females, evanescent laterally in males; episternum orange brown. Dense area of bristly setae on each humerus of apterous females (Figs. 2A, B), absent in alate female; bristly setae sparsely set laterally on anterior pronotal lobe; males without long hairs on pronotum. Small glabrous spot, sometimes absent, on lateral margin of pronotum of apterous female (Figs. 2A, B); metapleura with a shallow transverse, faintly shining depression. Elongate glabrous area on pronotum in a shallow transverse sulcus cephalad of humeri, reaching lateral margin, and irregular glabrous spot on mesopleura of alate female.

Connexiva slightly raised, sometimes almost vertical in female. Dorsum of abdomen covered with semilong decumbent setae, shorter in male.

Venter uniformly dark except episternum; thickly set with minute black conical setae, sparser posteriorly, very noticeable on episternum. Femora yellowish, tibia yellow brown, knees embrowned in females; males slightly darker. Legs with following proportions (holotype):

	Femur	Tibia	Tarsal 1	Tarsal 2
Anterior	25	19	10	—
Middle	26	21	11	9
Posterior	30	30	7	9

Antennal proportions I; II; III; IV: 9; 10; 9; 12.

Body measurements:
Mean length of 7 apterous ♂♂ : 1.11 mm (max. 1.14, min. 1.07).
Mean width of 7 apterous ♂♂ : 0.44 mm (max. 0.44, min. 0.43).
Mean length of 10 apterous ♀♀ : 1.63 mm (max. 1.72, min. 1.57).
Mean width of 10 apterous ♀♀ : 0.74 mm (max. 0.83, min. 0.68).
Holotype: Length 1.58 mm, width 0.68 mm.

Material examined.— Holotype, apterous ♀, Palenque, Chis., Mexico, 13-XII-1973, CL608, J. T. Polhemus (in Polhemus Collection). Paratypes as follows; EL SALVADOR: 3 ♂♂, 13 ♀♀ apterous, 11 ♂♂, 33 ♀♀ macropterous, La Majadita, CL1256, 12-XII-1970, J. T. Polhemus (JTP). MEXICO: Chiapas; 5 ♂♂, 10 ♀♀ apterous, 4 ♂♂, 2 ♀♀ macropterous, Palenque, CL608, 13-XII-1973, J. T. Polhemus (JTP); 1♀ apterous, Rincon Chamula, CL671, 6-I-1974, J. T. Polhemus (JTP); 1 ♀ apterous, 2 ♂♂, 2 ♀♀ macropterous, Rizo de Oro, CL1331, 14-I-1970, J. T. Polhemus (JTP); 2 ♀♀ apterous, Simojovel, 22-VII- to 19-VIII-1958, J. A. Chermak (UCB). PANAMA: 3 ♂♂, 2 ♀♀ macropterous, Cerro Campana, 7-V-1973, P. D. Ashlock (JTP, KU).

Discussion.— The female body shape in *paura* is quite robust, and the transverse orange brown band on the anterior lobe of the pronotum reaches the lateral margins or extends onto the propleura; these characteristics give the females a rather distinctive appearance. The males, on the other hand, are very difficult to separate from the other species. The dense field of minute black conical setae on the venter, the orange brown episternum, and the long proximal segment of the middle tarsi are helpful.

Paura occurs throughout Central America.

Microvelia psilonota, n. sp.

Female body shape robust, similar to *paura* (Fig. 2A); male body shape elongate, tapering caudad, similar to Figure 1A.

Anterior lobe of pronotum with uninterrupted light to dark orange brown band not reaching lateral margins, rarely extending laterally to behind middle of eye. Anterior lobe of pronotum and propleura of alate and apterous females with long stiff setae (Fig. 2D); apterous and alate males with shorter scattered setae, not prominent. Apterous and alate females with a shallow glabrous sulcus of somewhat variable shape on lateral margin of pronotum (Fig. 2D). Pronotal disc of apterous female broadly feebly depressed.

Connexiva almost flat to feebly raised in males and most females, strongly raised and almost vertical in some females.

Venter uniformly dark, except proepisternum light orange brown; jugum of head, inner portion of anterior coxae, proepisternum behind eyes, lateral margins of metapleura and abdominal ventrites above spiracles with a field of minute black conical setae. Legs yellowish, embrowned dorsally on tarsi, tibia, and distal part of femora. Acetabula brown, posterior acetabula with glabrous area. Trochanters, coxae, rostrum and ventral part of first three antennal segments yellowish to yellowish brown; remainder of antennae brown. Legs with following proportions (holotype):

	Femora	Tibia	Tarsal 1	Tarsal 2
Anterior	23	18	11	—
Middle	24	21	9	9
Posterior	25	27	5	8

Antennal proportions I; II; III; IV: 8; 10; 7; 12.

Body measurements:
Mean length of 10 apterous ♂♂: 1.28 mm (max. 1.32, min. 1.21).
Mean width of 10 apterous ♂♂: 0.53 mm (max. 0.55, min. 0.52).
Mean length of 10 apterous ♀♀: 1.70 mm (max. 1.77, min. 1.62).
Mean width of 10 apterous ♀♀: 0.89 mm (max. 0.95, min. 0.80).
Mean length of 10 alate ♂♂: 1.55 mm (max. 1.62, min. 1.50).
Mean width of 10 alate ♂♂: 0.72 mm (max. 0.75, min. 0.70).
Mean length of 10 alate ♀♀: 1.85 mm (max. 1.95, min. 1.72).
Mean width of 10 alate ♀♀: 0.87 mm (max. 0.95, min. 0.83).

Holotype: Length 1.62 mm, width 0.83 mm.

MATERIAL EXAMINED.— Holotype, apterous ♀, 20 mi. SE Acatlan, Puebla, Mexico, 16-XII-1969, CL1243, J. T. Polhemus (in Polhemus Collection). Paratypes as follows: MEXICO: PUEBLA; 6 ♂♂, 15 ♀♀ apterous, 13 ♂♂, 15 ♀♀ macropterous, 20 mi. SE Acatlan, 16-XII-1969, CL1243, J. T. Polhemus (JTP); 27 ♂♂, 33 ♀♀, 3 nymphs apterous, 4 ♂♂, 2 ♀♀ macropterous, same place, 28-IV-1964, J. T. & M. S. Polhemus (CU, JTP); 1 ♂ macropterous, Izucar de Matamoros, 27-IV-1964, CL1050, J. T. & M. S. Polhemus (CU). DURANGO; 1 ♂ macropterous, La Palmita, 20-IV-1964; CL1018, J. T. & M. S. Polhemus (CU). SINALOA; 2 ♀♀ macropterous, Santa Lucia, 20-IV-1964, CL1019, J. T. & M. S. Polhemus (CU, JTP).

DISCUSSION.— The robust body shape, nature of the glabrous pronotal sulcus, and setae pattern make separation of *psilonota* females a simple matter, but the males are very difficult to separate. The combination of body size, yellowish proepisternum with the field of tiny conical black setae, and subequal middle tarsal segments are helpful, but for certain identification, associated females are desirable.

Microvelia reflexus, n. sp.

Female body shape elongate, similar to Figure 1B. Male body shape elongate, similar to Figure 1A, but with pronotum narrower than metanotum and lateral margins sinuate.

Anterior lobe of pronotum with orange brown band extending laterally onto episternum in both sexes. Sparsely set areas of long setae on anterior lobe of pronotum, humeri, and metanotum of apterous female (Fig. 2F); anterior lobe of pronotum and corium of hemelytra with similar setae in alate female; apterous and alate males with much shorter pubescence. Lateral pronotal margin of apterous female with a depressed area, feebly shining but not glabrous (Fig. 1F), absent in alate female.

Connexiva raised in male, but not vertical; vertical in female, abruptly reflexed over abdominal tergite 4 then diverging posteriorly and less strongly reflexed on segments 5 and 6, strongly hirsute on segment 6. Abdominal dorsum clothed with very fine pubescence; female with long decumbent setae on last abdominal tergite.

Venter uniformly dark, except episternum and genital segments orange brown; episternum thickly set with minute conical black setae and a few long setae. Male with last ventrite depressed, forming a broad transverse sulcus. Legs yellowish, embrowned dorsally on tibia, tarsi, and distal part of femora. Coxae, trochanters, beak, and ventral part of first antennal segment yellowish; remainder of antennae brown. Legs with following proportions (holotype):

	Femur	Tibia	Tarsal 1	Tarsal 2
Anterior	29	20	12	—
Middle	32	27	12	12
Posterior	35	38	7	10

Antennal proportions I; II; III; IV: 10; 10; 10; 14.

Body measurements:
Apterous male, length 1.95 mm, width 0.78 mm.
Macropterous male, length 2.14 mm, width 0.88 mm.
Apterous female (holotype), length 2.15 mm, width 0.88 mm.
Macropterous female, length 2.22 mm, width 0.97 mm.

MATERIAL EXAMINED.— Holotype, apterous ♀, San Vito de Java, Costa Rica, CL1287, 30-XII-1968, J. T. Polhemus (in Polhemus Collection). Paratypes, same data as holotype, 2 ♂♂ apterous, 4 ♂♂, 2 ♀♀ macropterous.

DISCUSSION.— The relatively larger size and the transverse orange brown band on the anterior lobe of the pronotum, extending onto the episternum, set *reflexus* apart from other members of the group.

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ADDITIONAL RECORDS OF COLEOPTERA COLLECTED AT THE NEVADA TEST SITE, MERCURY, NEVADA

Vasco M. Tanner[1] and Wilmer W. Tanner[1]

Abstract.— Thirty-nine species of Coleoptera not previously reported for the Nevada Test Site are listed.

Several reports dealing with the Coleoptera collected at the Nevada Test Site were based on collections taken from can pit-traps placed in various sites throughout the area (Allred, Beck, and Jorgensen, 1963; Allred and Beck, 1965; Tanner and Packham, 1965; and Tanner, 1963, 1966). Very few specimens have been reported other than those taken from traps. This has resulted in the sampling of insects that move about on the ground. There are many forms, however, that rarely would be taken by such methods. From 1965 to 1969 the following list of Coleoptera were taken by means of insect nets and from the vegetation of the Test Site area. Only species not reported previously are contained in this list. From the experience gained in our collecting, we are quite certain that many interesting species from this desert area have not yet been reported. Since the area is still being studied, this list may be of interest to workers in the area.

The present study was a part of the ecological research done under the Atomic Energy Commission Contract No. At(11-1)1946 awarded to the junior author and Brigham Young University. Most of the specimens were collected by the authors; however, J. M. Hopkin and R. Walker aided in the field work.

Family Carabidae

Rhadine jejuna Lec.
20 specimens, Mercury, N.T. Site, July 1967. An abundant species around Cane Springs.
Rhadine myrmecodes Horn
1 specimen, Pahute Mesa, 27-VII-67.

Family Melyridae

Collops punctulatus utahensis Schffr.
2 specimens, Pahute Mesa, 27-VII-67.
Trichochrous varius Csy.
5 specimens, Rainier Mesa, July 1967.
Eutrichopleurus concinnus Blais.
1 specimen, Nevada Test Site, 1969.
Attalus futilis Fall
1 specimen, 3 miles W area 12, Nevada Test Site, 29-VII-67.

Family Buprestidae

Acmaeodera sp.
1 specimen, Frenchman Flat, on Mesquite bush, 29-VIII-67.

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[1] Department of Zoology, Brigham Young University, Provo, Utah 84602.

Family Cucujidae

Oryzaephilus surinamensis L.
3 specimens, 10-X-66.

Family Phalacridae

Phalacrus sp.
25 specimens, Pahute Mesa, 27-VII-67.
5 specimens, Rainier Mesa, 29-VII-67.

Family Coccinellidae

Hippodamia apicalis Csy.
3 specimens, Pahute Mesa, 29-VII-67.
Hippodamia convergens Guer.
4 specimens, Pahute Mesa, 27-VII-67.
Hippodamia ambigua Lec.
1 specimen, Pahute Mesa, 27-VII-67.
Hippodamia convergens uteana Csy.
1 specimen, Rainier Mesa, 28-VII-67.
Hyperaspis quadrivittata Lec.
1 specimen, Pahute Mesa, 27-VII-67.
1 specimen Frenchman Flat, 29-VII-67.
Hyperaspis taeniata taeniata Lec.
2 ♀ 1 Rainier Mesa and 13 miles W area 12, 27-VII-67.
Hyperaspis taeniata nevadica Csy.
1 specimen, Frenchman Flat, 29-VII-67.
Hyperaspis pleuralis Csy.
1 specimen, 3 miles W area 12, 27-VII-67.
Scymnus pallens Lec.
1 specimen, Rainier Mesa, 28-VII-67.
Scymnus aridus Csy.
3 specimens, Pahute Mesa, 27-VII-67.

Family Alleculidae

Hymenorus prolixus Csy.
3 specimens, Nevada Test Site, 22-VII-65.

Family Tenebrionidae

Zopherodes uteanus Csy.
6 specimens, Rainier Mesa, 10-IX-69.
Eleodes cognata Hald.
2 specimens, Nevada Test Site, 1965.
Eleodes concinna Blais.
7 specimens, Rainier Mesa, 29-VII-69.
Eleodes nevadensis Blais.
2 specimens, Nevada Test Site, 27-VI-65.
Eleodes pimelioides subsp. *patruelis* Blais.
2 specimens, Rainier Mesa, Aug. 1968.
Eleodes carbonaria subsp. *interstitialis* Blais.
5 specimens, Nevada Test Site, 3-IX-65.
Eleodes omissa subsp. *pygmaea* Blais.
1 specimen, Pahute Mesa, 27-VII-69.
Trogloderus tuberculatus Blais.
2 specimens, Rainier Mesa, 8-IX-67.
Eusattus oblongulus Csy.
4 specimens, Nevada Test Site, collected in the Grayia-Lycium community, 5-V-63.

Family Cerambycidae

Prionus californicus subsp.
1 specimen, Rainier Mesa, 31-VII-67.

Moneilema gigas Lec.
1 specimen, Rainier Mesa, 31-VII-67.

Family Chrysomelidae

Chlamys memnonia Lac.
22 specimens, Frenchman Flat, 29-VII-67, abundant on *Larrea divaricata.*

Family Curculionidae

Crocidema californica Van Dyke
23 specimens, can trap, Rainier Mesa, 10 to 15-IX-67.
1 specimen, Rainier Mesa, 1969.
1 specimen, Rainier Mesa, 1970.

Anthonomus ochreopilosus Dietz
5 specimens, area 12, 27 to 29-VII-67.

Ceutorhynchus tescorum Fall
2 specimens, near Pahute Mesa, 1969.

Anthonomus near *juniperilius* Dietz
Pahute Mesa, 1967.

Anthonomus inermis Boh.
2 specimens, Nevada Test Site, 1969.

Tychius (Sibinia) setosus Lec.
1 specimen, on mesquite, Nevada Test Site, 1969.

Cleonus quadrilineatus (Chev.)
Nevada Test Site, 1971.

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A SUMMARY OF BIOLOGICAL INVESTIGATIONS CONCERNING THE GREAT SALT LAKE, UTAH (1861-1973)

Doyle W. Stephens[1]

Abstract.— The early stages in the history of biological investigation of the Great Salt Lake involved the identification and establishment of taxonomic relationships of the indigenous flora and fauna. A result of advancements in systematic biology is that many of the earlier names of organisms have been placed in synonomy. Recent interest in the lake has centered on biological productivity and interactions of components of the ecosystem. The creation of two ecologically distinct lakes by the construction of a railroad causeway has further enhanced the biological complexity of what was originally believed to be a lifeless body of brine.

Because of the late settlement of the Bonneville Basin, scientific investigation into the biological composition and biotic mechanisms of the Great Salt Lake was nonexistent before the latter half of the nineteenth century. An 1861 issue of *Scientific American* reported, "No living thing of any kind exists in the lake," ignoring Captain B. L. E. Bonneville's note of small animals in the water during his 1831-1833 explorations. By 1889 three species of algae (Farlow, 1879, cited in Kirkpatrick, 1934), a brine fly (Packard, 1871), and brine shrimp (Verrill, 1869) had been named from the lake, yet Jordan (1889) stated that no life could exist in the lake with the exception of brine shrimp. Schwarz (1891) investigated various forms of insect life adjacent to the lake and concluded that the brine fly, *Ephydra cinerea* Jones (as *Ephydra gracilis* Packard), was the only insect inhabitant of the lake. He made note of the adult flies' habits regarding oviposition and feeding in the water. Tilden (1898) reported five species of algae from the lake: *Aphanothece Utahensis* Tilden, *Polycystis packardii* Farlow, *Dichothrix utahensis* Tilden, *Enteromorpha tubulosa* (Kützing) Reinbold, and *Chara contraria* Braun.

It was now evident that the Great Salt Lake could support life and that additional biological inquiry was needed. Considerable interest and speculation centered around the introduction of marine organisms to the estuaries formed where fresh water entered the lake. Moore (1899) examined the chemical and physical characteristics of the lake and concluded that even with dilution, the waters would not support any introduced crustaceans or fish. The possibility of introducing oysters into the estuaries was considered, but he concluded that a self-replenishing colony could not exist from year to year, and commercial exploitation was not feasible.

Aldrich (1912) reported on the morphology and ecology of the brine flies *Ephydra cinerea* and *Hydropyrus* (as *E.*) *hians* (Say) from the lake, stating that a pulpy alga of the *Nostoc* group was the probable food of the *Ephydra* larvae. In his collection of notes on

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[1] Department of Biology, University of Utah, Salt Lake City, Utah 84112.

fauna in the lake, Vorhies (1917) stated that this *Nostoc* form was probably the alga *Alphanothece packardii* Setchell. He also commented on the viability of *Artemia* and *Ephydra* in various densities of lake water. Vorhies noted several protozoans in his culture flasks including an amoeba (similar to *Amoeba flowersi* Jones), a ciliate protozoan (similar to *Uroleptus*), and a species of *Euglena*. The alga *Chlamydomonas* (reported in Daines, 1917) appeared regularly and in great numbers in his cultures. He noted that the brine shrimp was never collected from the lake when the water temperature was below 9C. Complete absence of predators was suggested as an explanation for the great abundance of shrimp and brine flies.

In repudiation of Vorhies's (1917) comment that brine shrimp and brine flies were abundant due to lack of predators, Wetmore (1917) noted that a wide variety of waterfowl fed heavily on the animals in the lake. He stated massive production of offspring to be the most likely explanation for the abundance of *Artemia* and *Ephydra*.

A companion paper on the flora by Daines (1917, cited in error as Daniels) appeared with the observations of Vorhies on the fauna. Daines briefly mentioned Tilden's (1898) description of six algae and added a new one, *Chlamydomonas* sp. to the list. Two genera of diatoms (*Navicula* and *Cymbella*) were observed in the estuaries around the lake, and Daines concluded that they were adapted to dilute brines. He noted five bacteria, three being chromogenic, but offered no identifications. Daines noted a considerable size variation between the *Chlamydomonas* cells but through his experimentation concluded that it was not induced by differences in salinity.

The brine shrimp, *Artemia gracilis* Verrill was further observed and its general morphology described in some detail by Jensen (1918). He reported the optimum density for hatching and growth of *Artemia* to be between specific gravities of 1.044 and 1.089. The eggs would not hatch in a saturated brine solution.

Pack (1919) described a new species of protozoan, *Prorodon utahensis* Pack and studied the effects of brine dilution upon this species and another ciliate, *Uroleptus packii* Calkins. In less dense media, the animals increased in size, became more active, and developed more flexible and contractile bodies. Pack also believed that by "slowing down the rate of dilution, some of these Great Salt Lake forms may be transformed into fresh water animals."

Seville Flowers (1934), in his monograph on the vegetation of the Salt Lake area, reported the following algae as endogenous to the lake:

Aphanothece utahensis Tilden
Microcystis packardii Farlow (Tilden)
Oscillatoria tenuis var. *tergestina* (Kützing)
Oscillatoria tenuis var. *natans* (Kützing)
Chlamydomonas sp.
Tetraspora lubrica var. *lacunosa* Chauv.

The work of Flowers was followed by that of Kirkpatrick (1934) on the algal forms within the lake. Her conclusions touched upon the variety of organisms reported by earlier workers and are reproduced with added comments by this author:

1. There are five colonial forms of blue-green algae of the Great Salt Lake. Most of these forms did not thrive under laboratory conditions.
2. There are two species of *Chlamydomonas* in the Great Salt Lake. This form thrived at all densities (1.0145 to saturation).
3. Two species of diatoms. resembling *Navicula*, are present. They did not thrive in the weakest (sp. grav. 1.0145) nor the strongest (saturated) concentrations present.
4. A species of *Chroococcus* and one of *Gleocapsa* developed in the lower concentrations (sp. grav. 1.0225). They cannot be considered native lake forms.
5. A filament of *Oscillatoria* was seen twice. It is possible that this form exists in small quantities in the lake. It is very abundant in the hot springs along the shore and could readily be washed into the main body of water.
6. A great number of the species listed by former workers did not develop in the cultures, nor were they observed in examination of fresh material. It is possible that many of these forms came from extraneous sources, or were not able to survive the increased density of the lake water at its present low level.
7. The fauna observed in this experiment consists of three ciliates (*Uroleptus packii* Calkins, *Prorodon utahensis* Pack, and an unidentified species), one amoeba, one crustacean (*Artemia*) and one fly larvae (*Ephydra*).

The reported occurrence of diatoms by Daines (1917) and Kirkpatrick (1934) was further investigated by Ruth Patrick (1936). She found a variety of diatoms in the sediments of the lake, presumably originating from the Lake Bonneville era, but did not find any evidence of their currently living in the Great Salt Lake.

The bacterial composition within the lake was first investigated by Frederick (1924). Through the use of colonial morphology and several media, she isolated eleven forms, which she identified as the following:

Serratia salinaria (Harrison and Kennedy) Bergey
Cellulomonas subcreta (McBeth and Scales) Bergey
Bacillus freudenreichii (Miguel) Chester
Achromobacter solitarium (Ravenel) Bergey
Bacillus cohaerens Meyer and Gottheil
Flavobacterium arborescens (Frankland and Frankland) Bergey
Micrococcus sulflavus Chester
Achromobacter hartlebii (Jensen) Bergey
Bacteriodes rigidus (Dista) Bergey
Bacillus mycoides Flügge
Achromobacter album (Pagliani) Bergey

A brief mention of the brine shrimp, *Artemia fertilis* Verrill (*Artemia salina* Leach), *larval Ephldra*, the blue-green alga, *Aphanothece utahensis* as *Aphanothica packardii*, diatoms, and the green alga *Chlamydomonas* is made by Allee (1926). An observation of water bugs of the family Corixidae is also noted, probably referring to a similar observation by Schwarz (1891).

Woodbury (1936) provided the first comprehensive analysis of the lake ecosystem. His description of the aquatic system is brief, mentioning the apparent interspecific competition between two closely related species of *Ephydra* and *Artemia*. Several historical notes made by Fremont and Stansbury during early surveys were cited.

The bacterial composition within the lake was further investigated by Smith (1936). The majority of his results and conclusions are published in Smith and ZoBell (1937). Their conclusions, while not definitive, are of interest and are reproduced here:

> The attachment of bacteria to sterile glass slides submerged in Great Salt Lake indicates the presence of abundant and varied bacterial flora. Controlled experiments demonstrate that only living bacteria attach themselves to slides in appreciable numbers. This, together with the fact that micro-colonies develop on slides in the lake, indicates that the bacteria are multiplying in the lake and are not merely passive inhabitants. The inability of soil, sewage or marine bacteria to attach to slides in lake water supplies further proof for the latter contention. Most of the lake bacteria are small gram-negative rods besides other morphological varieties which do not fit into any conventional classification. The direct microscopic procedure offers possibilities for studying the seasonal and geographic distribution of bacteria in the lake.

A summary of research on the brine shrimp, *Artemia*, prior to 1936 is given in Relyea (1937), but no new data are presented.

An excellent compilation of research on the physiology of *Artemia salina* Leach appeared in the work of Quinn (1940). Magnesium ion concentrations of twice that in the lake did not appreciably change the time of nauplius emergence from the egg but did inversely affect the time of egg hatching. The time of emergence was found to vary inversely with the temperature, and effects of magnesium ion concentration on nauplii were restricted to the earliest developmental stages. A complete bibliography including many European articles is given.

A short paper presented by Rees (1942) presents a popular view of animal life within the lake. It is followed by an article by Behle (1942) listing four species of colonial nesting birds found on islands in the Great Salt Lake. Distribution and general ecology is presented for: American white pelican (*Pelecanus erythrorhynchos* Gmelin), double-crested cormorant (*Phalacrocorax auritus auritus* Lesson), Treganza great blue heron (*Ardea herodias* Treganza), and the California gull (*Larus californicus* Lawrence).

The amoeba noted by previous workers (Vorhies, 1917; Kirkpatrick, 1934; Woodbury, 1936) was described as *Amoeba flowersi* Jones by Jones (1944). He also described the Euglena seen by Vorhies (1917) and Kirkpatrick (1934), naming it *Euglena chamberlini* Jones.

Woodbury (1948) briefly mentioned the work of Quinn (1940) concerning salinity effects on *Artemia*. No new data are given. The Ephydridae of Utah (Jorgensen, 1956) lists *Ephydra cinerea* Jones as the most common brine fly from the lake, with *E. auripes* Aldrich, *E. riparia* Fallen (as *E. subopaca*) and *Hydropyrus* (as *E.*) *hians* (Say) also being reported by various other collectors.

Evans and Thompson (1964) list a new genus of ciliate protozoan, *Pseudocohnilembus*, occurring in the lake. Only one species, *P. persalinus* Evans and Thompson, was collected. Further work by Professor Evans and his students has resulted in the isolation of an additional ciliate, *Euplotes parsalinus* Reddy from the lake (Reddy, 1971).

Population pressures and its problems were becoming evident when McDonald (1956) investigated the effects of pollution upon lake organisms. Dissolved oxygen concentrations were found to be below 3.3 mg/liter with localized decomposition of brine organisms being primarily responsible for the oxygen demand. He reported that an experimental mixture of 2 percent commercial oil and gasoline added to lake water containing the alga *Chlamydomonas* resulted in complete elimination of cells within 45 hours.

A comprehensive study of the bird life associated with the lake was authored by Behle (1958). As the lake lies within the Pacific Flyway, there are numerous local and transient birds associated with its marshes, constituting the major predatory source for the macrofauna.

Evans (1960) listed five new genera of protozoa and three unidentified types from the lake. *Crystigera*, *Cyclidium*, *Euplotes*, and *Oikomonas* were believed to be bacterial feeders. *Podophyra* was predaceous upon *Euplotes*. An amoeba and two unidentified ciliates were also observed. *Cristigera* exhibited optimum growth in salt concentrations of 1 to 18 percent; its growth completely declined at 23 percent salt. Cysts of *Cristigera*, however, could survive long periods in a saturated salt solution. Preliminary tests on other protoza indicated that growth is inhibited at 15-18 percent salt concentration. Evans concluded that *Cristigera* and the amoeba were specialized halophilic protozoa and that certain of the other species of protozoa may be salt-tolerant, freshwater forms.

The occurrence of algal biostromes or tufa precipitated from the brine as a result of the action of blue-green algae was mentioned by Flowers (1934). Carozzi (1962) reported *Aphanothece packardii* to be the most predominant blue-green, forming the biostromes in distinct morphological zones. He concluded that the algae have no characteristic growth pattern of their own, but have developed on raised areas separating a system of erosional channels extending at right angles to the shoreline.

A fairly complete summary of plant and animal species found in and around the Great Salt Lake appeared in Flowers and Evans (1966). Their work lists two species of blue-green algae, *Coccochloris elabens* Drouet and Daily and *Entophysalis rivularis* (Kützing) Drouet, and two undescribed species of green algae, *Chlamydomonas*, as inhabiting the lake proper. The listing of bacteria follows that of Frederick (1924) with several forms listed in synonomy. The brine shrimp, *Artemia salina* is mentioned as the most conspicuous animal. The brine flies *Ephydra cinerea* Jones and *E. hians* Say are the only insects reported within the lake. The list of protozoa appearing in Evans (1960) was revised and expanded, listing the following ciliates:

Uroleptus packii Calkins
Chilophyra utahensis (Pack)
Podophyra sp.

Euplotes sp.
Pseudocohnilembus sp.
Cothurnia sp.

Two unidentified amoeba were noted as common, and several species of flagellates including *Tetramitus*, *Oikomonas* and at least two others were seen in large numbers from the lake and nearby salt ponds. Mention is made concerning the deposition of carbonate tufa by blue-greens, but the exact mechanism is unknown. Vegetation surrounding the lake is well described and its distribution noted.

Gaskill (1970) reported on waterfowl commonly associated with the southeastern shore of the Great Salt Lake concluding that coots were the most prevalent of nesting birds (39 percent of total), with cinnamon teal, redhead, mallard, and pintails of considerable importance.

The report of a National Science Foundation student-originated studies program (Carter, 1971) considered ecological relationships within the Farmington Bay Estuary of the Great Salt Lake, and the general terrestrial ecology of Antelope Island State Park. Portions of the aquatic study are relevant to the lake biology and are presented here.

> The estuary is less polluted now (1971) by coliform bacteria than it was in 1965. The coliforms are more heavily distributed on the estuary bottom than in the upper layers of water. Most coliforms are killed or fail to multiply in NaCl concentrations greater than 5.5 percent, with some of the bacteria being sensitive to concentrations of as little as 1.8 percent. The freshening of Farmington Bay could cause a definite increase in the coliform population.
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> There are large numbers and many species of protozoans living in the estuary resulting from freshening of the lake due to construction of the causeway from Syracuse to Antelope Island. Because of the increase in the protozoan population, it is reasonable to expect an increase in the overall biological productivity as protozoans are an important food and energy source.
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> The distribution, number, and species diversity of zooplankton and phytoplankton were established. Through comparison with the water chemistry of samples taken at the same locations, it was found that the distributions of *Artemia salina*, *Diaptomus*, sp., a Corixid, *Daphnia* sp., and *Nodularia* sp. are dependent on the salinity. A predator-prey relationship between the Corixid and *Artemia salnia* was suggested, and it is concluded that the introduction of marine game fish or fresh water fish to the area for sport fishing is not feasible.

The construction of a rock-filled railroad causeway between Little Mountain and Lakeside in 1957 resulted in the creation of two ecologically distinct lakes due to salinity imbalances. Its effect on the biota was reported by Gillespie, Wirick, and Stephens (1971). They concluded that the saline waters of the Great Salt Lake provided an extremely rigorous, and therefore relatively simple ecosystem. The northern basin contains saturated brine with a depauperate biota consisting of *Dunaliella salina* Teodoresco plus unidentified protozoa and bacteria. In the southern basin, two major energy-flow sequences dominate the system: a planktonic sequence consisting of (*Dunaliella*) → (*Artemia*) and a benthic sequence consisting of (blue-green algae + detritus) → (*Ephydra*). There is some crossover in that much of the detritus consists of dead *Artemia*, and *Artemia* will feed on benthic algae and detritus when *Dunaliella* are scarce.

Further work by Wirick (1972) demonstrated that the main phytoplankter, *Dunaliella viridis* Teodoresco (previously reported as a *Chlamydomonas*) exhibited one bloom per year in April. The zooplankter, *Artemia salina* is present and grazing *Dunaliella* only when the water temperature is above 6C. Construction of a mathematical simulation model suggested that the growth rate of the *Dunaliella* population is light limited and density dependent at high algal concentrations.

Porcella and Holman (1972) concluded that inorganic nitrogen is apparently the limiting factor for growth of phytoplankton in the Great Salt Lake water. Carbon may also be limiting. Phosphorus, iron, and other trace elements seem to be in abundant supply. Their observations were confirmed by algal bioassays. Growth and reproduction of the brine shrimp on *Dunaliella* alone was superior to yeast alone as a food source. The optimum utilization by the brine shrimp was about 1,000 algal cells per brine shrimp per day. Different concentrations and ages of added algae had no apparent effect on whether the mature brine shrimp produced live young (nauplii) or resistant cysts. It was their belief that a feasible aquaculture based on*Dunaliella* sp. and *Artemia* sp. could be developed for brine shrimp isolated from the Great Salt Lake. Production of algae and brine shrimp in lake enclosures may be increased by addition of specific nutrients.

Basic schemes for energy flow within the north and south lake basins were presented by Stephens and Gillespie (1972). They found that the northern basin supports a depauperate biota consisting primarily of an alga, *Dunaliella salina*, several protozoa, and bacteria. The southern basin exhibits two energy-flow systems with only minor interactions: the planktonic system with a dominant phytoplankter, (*Dunaliella viridis*), and a single zooplankter, (*Artemia salina*); and a benthic system of blue-green alga (*Coccochloris elabens*), detritis, and brine fly larvae (*Ephydra*). The only outflow from either system occurs when birds feed upon the shrimp or fly larvae. The *Dunaliella* population seems to be limited early in the calendar year by temperature and light. *Dunaliella viridis* reaches its peak population density (24 x 10^6/liter) in April and its decline to less than 1 x 10^6 cells/liter) occurs in May and June as a consequence of the rapidly expanding *Artemia salina* population. The availability of the nutrients nitrogen and phosphorous does not seem to be a limiting factor for *Dunaliella*.

The apparent conflict of the Porcella-Holman study (1972) and that of Stephens-Gillespie (1972) regarding limiting factors to phytoplankton growth is currently under investigation by Stephens (1973). Initial conclusions indicate that *Dunaliella* is (1) light limited during the April-May bloom and (2) nitrogen, carbon, and possibly vitamin limited later in the year. Grazing by *Artemia* could prevent additional algal blooms even if necessary nutrients were available.

Most recently, Van Auken and McNulty (1973) published on the factors limiting growth in laboratory cultures of *Dunaliella* sp.

isolated from the Great Salt Lake. Optimum growth was obtained under the following conditions: (1) temperature 32 C, (2) NaCl 19.2 percent (w/v), (3) CO_2 1-2 percent at a rate of 2.2 ml/min/ml of culture media, (4) light intensity of 25-35 klux, (5) pH 5.8-6.5. The K^+/Na^+ ratio should not be more than 0.1. The specific growth constant for this halophyte under the above conditions was 0.069 hrs^{-1}, which is equal to a doubling time of 10 hours.

Chemical control of the massive swarms of *Ephydra* in the beach areas was reported by Nabrotzky, Rosay, and Sadler (1973). Control lasting several hours to several days was obtained using both malathion and Dowco 214 insecticides. At the concentrations applied, no damage to *Artemia* or water bugs (Corixidae) was evident. An indigenous wasp parasite of *Ephydra* larvae collected near the lake indicates biological control of the brine flies may be possible.

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A NEW VARIETY OF *PENSTEMON THURBERI* (SCROPHULARIACEAE)

James L. Reveal[1] and Janice C. Beatley[2]

The Thurber Beard-tongue, *Penstemon thurberi* Torr. is currently known from the sandy desert regions of southwestern United States and northern Mexico ranging from the Sierra San Pedro Mártir in Baja California northward to the Providence Mountains of San Bernardino County, California, hence eastward into southern Mohave and Yavapai counties, Arizona, and across the southern tier of Arizona counties into western New Mexico. The recent discovery of a northern, disjunct population of *P. thurberi* from extreme northwestern Clark County, Nevada, in the near vicinity of the Nevada Test Site, has now been studied in detail and has proved to represent a distinct variant of the species which we hereby name.

Penstemon thurberi Torr. var. *anestius* Reveal & Beatley, var. nov. A var. *thurberi* floribus 8-9 mm longis (nec 10-15 mm longis) cum inferior labiis (1) 2-3 (3.5) mm longis (non 4-6 mm longis) et tubis (4) 6-7 mm longis (non 7-10 mm longis), capsulis 4-5 mm longis differt. Typus: NEVADA: Clark Co.: In deep volcanic sands on the upper bajada below the southwest end of the Buried Hills, east of Frenchman Flat dry lake, associated with *Larrea* and *Ambrosia*, at about 3800 feet elevation, 20 June 1973, *Beatley & Ackerman 13460*. Holotypus, US! Isotypi, 30 duplicates will be distributed from US.

Other Specimens Examined: All from the type area: 22 June 1971, *Beatley & Bamberg 12843* (MARY, NTS, US).

The var. *anestius* (from the Greek *anestios*, meaning homeless, alluding to its disjunct distribution) differs from var. *thurberi* primarily in the features of the flowers, which are smaller and less obvious than the flowers of the typical form. In var. *anestius* the flowers are 8-9 mm in length; those of var. *thurberi* are (10) 12-15 mm. The lower lip of var. *thurberi* is up to twice the length of that of var. *anestius*, whereas the tube of the Nevada plants is shorter than that of var. *thurberi*. The mature capsules of var. *anestius* are 4-5 mm long; those of var. *thurberi* are 6-9 (10) mm. Both forms occur in similar habitats and have the same general habit of growth, although the Nevada plants rarely exceed 5 dm in height. These features, coupled with the disjunct distribution pattern, have led us to recognize the Nevada variant as distinct.

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[1] Department of Botany, University of Maryland, College Park 20742, and National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. Research supported by National Science Foundation Grant GB-22645.

[2] Department of Biological Sciences, University of Cincinnati, Cincinnati, Ohio 45221. The work reported here was conducted in part under U.S. Atomic Energy Commission contracts No. AT (04-1) Gen-12 and AT (11-1) 2307.

A NEW SCELOPORINE LIZARD FROM OAXACA, MEXICO

Marlene M. Dasmann[1] and Hobart M. Smith[1]

Abstract.— *Sceloporus megalepidurus halli*, subsp. nov., is described from San José Lachiguiri, Oaxaca, Mexico, from one adult male.

Among specimens recently collected for the University of Colorado Museum by the late Thomas B. MacDougall in a remote sector of the Sierra Madre del Sur of Oaxaca, Mexico, is a single specimen of a distinct, unnamed race of *Sceloporus megalepidurus*. Despite an appeal for search for more material before his death, he was unable to secure it. The senior author attempted to reach the locality with directions provided by Mr. MacDougall only a week before his death but was unable to do so. Since additional material is not now likely to be acquired for at least several years, we here describe and name

Sceloporus megalepidurus halli, subsp. nov.

Holotype.— University of Colorado Museum 41137, adult male, collected by Thomas MacDougall in October 1967 at San José Lachiguiri, Oaxaca, Mexico.

Diagnosis.— A *Sceloporus megalepidurus* of small size, maximum snout-vent measurement 47 mm; dorsal scales 46 from occiput to base of tail; no ventral coloration.

Description of holotype.— Head scales above (Fig. 1) smooth, weakly pitted on frontonasals and prefrontals; interparietal about 3 mm wide, broader posteriorly than anteriorly, posterior edge fairly straight; parietals divided in two, each about one-sixth size of interparietal; a moderately large scale posterior to parietal, considered to be a secondary parietal; a pair of moderate-sized rectangular frontoparietals, separated medially by broad contact of frontal and interparietal; frontal transversely divided, posterior section three-fourths as large as anterior section; prefrontals moderate in size, narrowly contacting each other medially; median frontonasal somewhat larger than either lateral frontonasal; a pair of square scales in front of median frontonasals, preceded by another, similar pair of scales; four postrostrals; four enlarged supraoculars on each side, separated from median head scales by a complete row of small scales; one complete and another incomplete row of scales separating supraoculars from superciliaries; six superciliaries on each side, normal; one canthal on each side; subnasal present, about same size as loreal; preocular not divided; subocular long, single, followed posteriorly around margin of orbit by two postoculars; two incomplete rows of lorilabials (Fig. 2), reduced to one row below subocular; one row of

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[1] Department of Environmental, Population and Organismic Biology. University of Colorado, Boulder, Colorado 80302.

Fig. 1. Dorsal head scales of the holotype of *S. m. halli.*

lorilabials continuous around end of snout; five supralabials to a point at posterior margin of eye.

Mental pentagonal, with a labial border about half that of rostral; outer row of labiomentals separated from mental by narrow contact of first postmental and first infralabial; four pairs of well-differentiated postmentals, followed by several scales not well differentiated from adjoining gular scales; first pair of postmentals in contact

Fig. 2. Lateral head scales of the holotype of *S. m. halli.*

medially; gular scales all nearly equal in size, somewhat smaller than scales on chest, smallest below ear and between postmentals.

Auricular lobules three-four; about six scales between auricular lobules and postoculars; temporal scales keeled, larger than scales between ear and lateral nuchal fold, smaller than largest auricular lobule; scales between ear and lateral nuchal fold keeled, mucronate.

Dorsal scales 46 from occiput to base of tail, not reduced in size on nape, weakly keeled, weakly mucronate; lateral scales about one-third smaller than dorsals, not abruptly differentiated from them; lateral scales in oblique rows converging posterodorsally; most ventral scales with a single apical notch; scales in axilla and groin imbricate, some notched; scales on chest slightly larger than midventral scales; preanal scales somewhat smaller than lateral abdominal scales, subequal in size to smallest midventral scales; dorsal scales on rump somewhat reduced; dorsal caudal scales at least twice as large as scales on rump; scales around middle of body 54.

Dorsal scales of upper foreleg keeled, mucronate, equal in size to dorsal scales on body, slightly larger than largest dorsals on lower foreleg; scales on ventral surface of upper foreleg very small, keeled, weakly mucronate, those of lower foreleg larger, keeled, mucronate; lamellar formula for fingers 8-12-16-19-12 (9-11-16-18-12).

Dorsal scales of shank keeled, mucronate, equal in size to median dorsal scales, those of thigh slightly smaller; scales on anterodorsal surface of shank near tibiometatarsal joint greatly reduced in size; ventral scales of shank smooth, smaller than dorsal scales of same member, decreasing in size on ventral surface near femoral pores; scales preceding femoral pores subequal to preanal scales; median scales on posterior surface of thigh keeled, mucronate, subequal to scales in preanal region, decreasing toward series of femoral pores;

femoral pores 13-14, the two series separated by four scales; no postfemoral dermal pocket; enlarged postanals present, broader than long, separated narrowly by two small scales; lamellar formula for toes 9-13-17-20-13 (10-14-16-20-13).

Color and Pattern (Fig. 3). Dorsal surface brown gray; a broad, clove brown band from posterior margin of orbit to rump, bordered on each edge by a light line; below this, irregular spots of clove brown, absent toward ventral surface; black area on shoulder; limbs with narrow clove brown bands; posterior surface of thigh irregularly reticulated with clove brown; tail with narrow clove brown bands.

Male with immaculate ventral surface; gular scales brown gray, appearing banded toward throat.

Discussion.— The present specimen is placed in the *megalepidurus* group of Smith (1939). Its only major physical distinction in comparison with *Sceloporus pictus* is its lack of ventral color. This characteristic is also found in *Sceloporus megalepidurus*, a close relative of *S. pictus*. However, the specimen has fewer scales from occiput to base of tail (46) than does *S. megalepidurus* (52-63). Indeed the new taxon probably will prove to have a lower mean dorsal scale count than even *pictus*, perhaps even diagnostically lower. Comparisons are given in Table 1, from our own counts. The differences between the present type and both *megalepidurus* and *pictus* are such that we believe its accorded rank should be subspecific despite the extensive isolation presently indicated. There is no particular resemblance to either *S. subpictus* or *S. cryptus*, the only other taxa of the *megalepidurus* group; each has distinct lateral belly patches, dorsals no more than 37 from occiput to base of tail, and other distinctions.

If *S. pictus* were regarded as specifically distinct from *S. megalepidurus*, the taxon here described would most reasonably be regarded as a subspecies of the former (*S. pictus halli*). However,

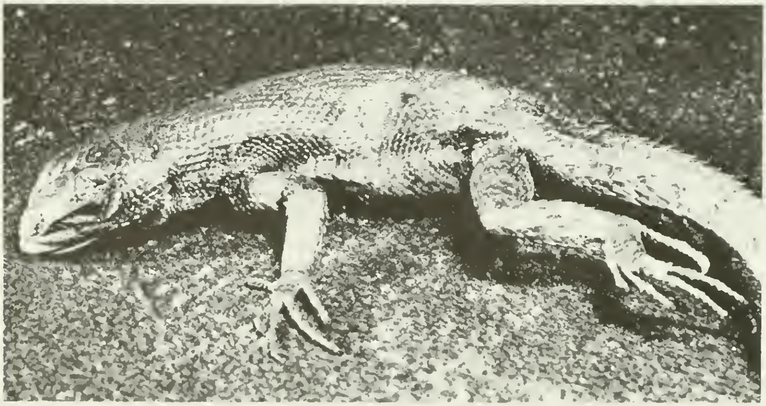

Fig. 3. Dorsolateral view of the holotype of *S. m. halli*.

TABLE 1. Selected scale counts (means and ranges) in *S. megalepidurus*.

Name	Sample size	Dorsal scales	Ventral scales	Scales around midbody	Femoral pores	Scales between femoral pores
Sceloporus m. pictus	13	50.6	49.4	56.9	15.0	4.8
		46-54	45-54	53-61	12-18	3-7
S. m. megalepidurus	45	56.7	56.2	57.4	14.7	5.7
		52-63	45-69	46-68	13-17	4-7
Hybrids (*pictus megalepidurus*)	51	57.8	53.6	55.2	14.5	5.9
		52-63	46-70	45-65	12-18	4-8
S. m. halli	1	46	50	54	13-14	4

recently Dr. William P. Hall discovered an apparent intergradation zone between the ranges of *S. pictus* and *S. megalepidurus*. The specimens collected from this area are quite similar to *megalepidurus* in numbers of dorsal scales, ventral scales, scales around the midbelly, femoral pores, and scales between the femoral pore series. However, the males have distinct blue belly patches, much as in *pictus*, although they are not as clearly defined as is typical of the latter race. Some of the hybrid males have thin black lines outlining these blue belly patches. We thus conclude that indeed *megalepidurus* and *pictus* do intergrade and should be ranked as conspecific subspecies; accordingly our new taxon must fall as a subspecies of *S. megalepidurus*.

Sceloporus m. pictus and *S. m. megalepidurus* probably evolved from the same ancestral race, and, due to geographic isolation, became phenotypically (and presumably genetically) distinct. The present zone of intergradation appears to be secondary, with reunion of the populations occurring after a number of differences between them had evolved. Because the specimens from this intergradation zone have the *S. m. pictus* ventral coloration and *S. m. megalepidurus* scale counts, we assume that *S. m. halli* was not of a similar origin (i.e., not a result of interbreeding between *pictus* and *megalepidurus*). It appears more likely that the new taxon is an offshoot of a common ancestral population. *S. m. halli* occurs in southern Oaxaca far removed from the present ranges of *S. m. pictus* or *S. m. megalepidurus* and far from the intergradation zone (Fig. 4). A founder population could conceivably have been displaced this far from its natural range by human agency, but it seems unlikely. Probably the range of the common ancestral population once maintained continuity from northern Oaxaca into this area, and has since contracted, leaving this population isolated to evolve on its own. Since all of the present subspecies of *megalepidurus* are so closely related, they probably carry many of the same genes. It would appear that *S. m. halli* has paralleled some of the mutations or combinations phenotypically expressed in *S. m. megalepidurus*, becoming like it in being immaculate ventrally but otherwise remaining similar to *S. m. pictus*, which presumably is more like the ancestral population than is either of the peripheral subspecies. Unfortunately, only one

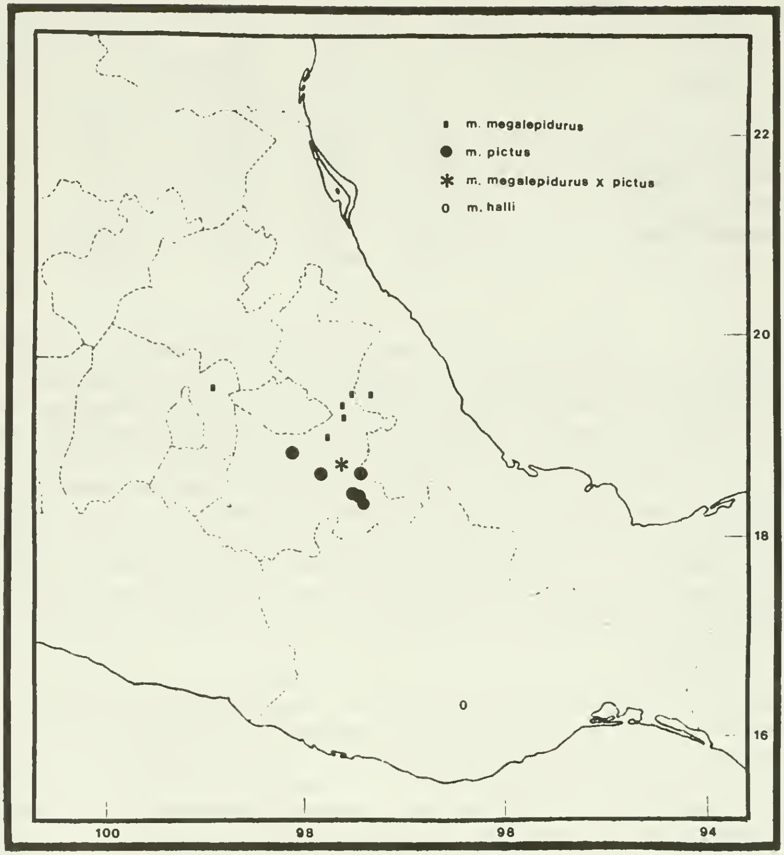

Fig. 4. Distribution of the subspecies of *S. megalepidurus.*

specimen of *S. m. halli* is available; it is hoped that future collecting efforts will concentrate on the area where the holotype was found.

The area around San José Lachiguiri, Distrito Miahuatlán, Oaxaca, is unusual in several ways other than serving as the habitat of *S. m. halli.* Unexpected taxa of the genera *Phrynosoma* and *Barisia* are also found here, all far removed from their close relatives. At one time the ranges of these and other species could have extended in continuity to this area. Due to climatic change, or some other limiting factor, their ranges contracted, leaving relic populations isolated in this area, where they became to some degree differentiated from their parental stock. Why this area appears to contain so many relictual populations is not yet understood. Whatever the reason, it constitutes an unusually distinctive faunal district.

Specimens Examined.— Specimens have been examined in the Museum of Comparative Zoology (MCZ), University of Colorado

Museum (CUM), the private collection of Edward H. Taylor (EHT) (now in part in the University of Illinois Museum of Natural History) and the private collection of Earl Olson (EO), as follows:

S. m. megalepidurus - VERACRUZ: Mt. Orizaba (MCZ 14157); Mal Paiz (CUM 50383). PUEBLA: Lago Alchichica (CUM 29111-21, 29123-39);4 mi. NE Entronque Zacatepec (MCZ 133158-65); 32 km SE Perote (MCZ 122162-3); 6 mi ESE San Salvador el Seco (MCZ 133155-7). MEXICO: Teotihuacan Valley (MCZ 133166).

S. m. pictus - VERACRUZ: Acultzingo (EHT 7623, 7629A); Cumbres de Acultzingo (CUM 48372-6; EO 764, 1191). PUEBLA: near Alseseca (EHT 7620A, 7620-2); 20 km N Tehuacán (EHT 7624-5, 7625A, 7626-9); Tehuacán (MCZ 42140-1); 15 km SSE Amozoc de Mota (MCZ 121885-8).

S. m. megalepidurus X *S. m. pictus* - PUEBLA: 5 km SE Ciudad Serdán (MCZ 133123-54); 8 km SE Ciudad Serdán (MCZ Y-25591, 122164-81).

S. m. halli - OAXACA: San José Lachiguiri (CUM 41137).

ACKNOWLEDGMENTS.— We are especially indebted to Dr. William P. Hall for calling our attention to the intergrade specimens and for permission to study them: the new taxon bears his name in recognition of these courtesies and of his numerous contributions to the systematics of this complex genus. In addition, we are grateful for the loan of comparative material by Dr. T. Paul Maslin, Dr. Ernest E. Williams, Dr. D. F. Hoffmeister, and Earl Olson, from CUM, MCZ, the University of Illinois Museum of Natural History, and the Earl Olson private collection, respectively. Finally, we are very grateful to Neal Burstein for the photographs.

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RANGE EXTENSION OF THE LONG-NOSED SNAKE, *RHINOCHEILUS L. LECONTEI*, INTO EAST-CENTRAL UTAH

William L. Grogan, Jr.[1] and Wilmer W. Tanner[2]

Abstract.— A review of the distribution of *Rhinocheilus l. lecontei*, in Utah, with a northward extension of its range in the Upper Colorado River Basin.

The long-nosed snake, *Rhinocheilus l. lecontei*, was previously thought to inhabit only the southwestern part of Utah (Tanner, 1935. Its range in Utah included only the Lower Sonoran life zone in the Virgin River Valley of Washington County. Tanner (1941) reported it for the Great Basin (Millard Co.), and Tanner and Heinrichs (1964) extended its range into southeastern Kane County. Stebbins (1966) reported a specimen from San Juan County, Utah (northeast of Page, Arizona), extending its range into the Colorado Plateau of southeastern Utah.

On 29 May 1970 at Dragerton, Carbon County, Utah, a specimen of *Rhinocheilus l. lecontei* was collected by William Ingram from under a rock. This specimen extends the range of *Rhinocheilus* well

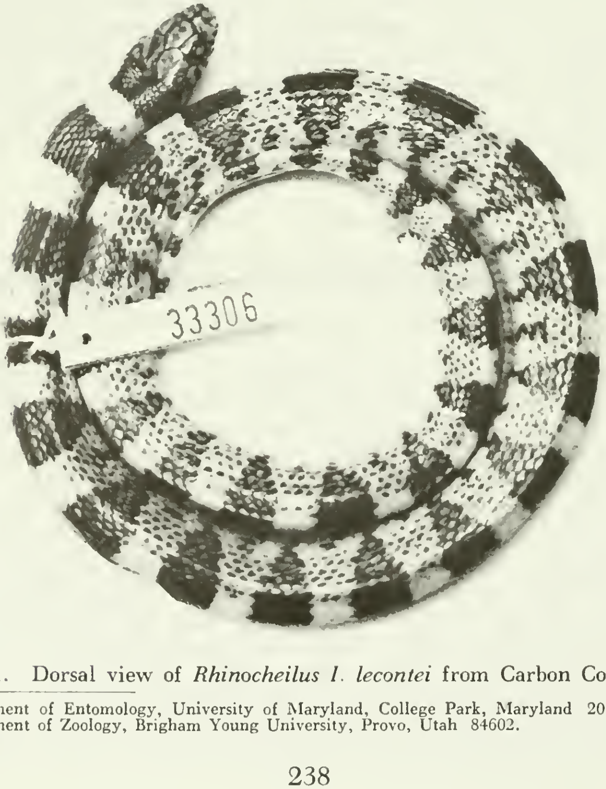

Fig. 1. Dorsal view of *Rhinocheilus l. lecontei* from Carbon County, Utah.

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[1] Department of Entomology, University of Maryland, College Park, Maryland 20742.
[2] Department of Zoology, Brigham Young University, Provo, Utah 84602.

into the Upper Colorado River Basin and is the first specimen taken in Utah east of the Wasatch mountains. It represents a range extension of approximately 175 miles north of previous records for southeastern Utah. Known locality records for Utah are plotted in Fig. 2.

The above specimen, a female, from Carbon County (Fig. 1), is now at Brigham Young University, Provo, Utah (BYU 33306). It is an example of the *lecontei* phase of this species as defined by Shannon and Humphery (1963) and Tanner and Jorgensen (1963). The pattern in alcohol is 35 dark slate-gray saddles and 35 cream-

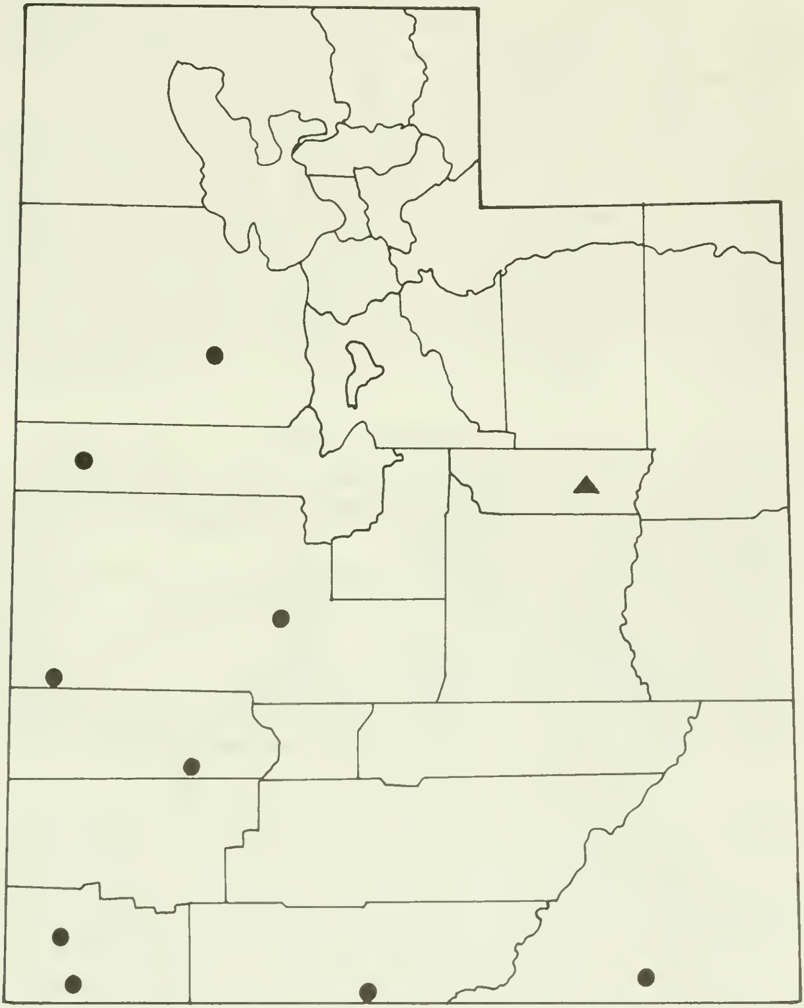

Fig. 2. Locality records of *Rhinocheilus l. lecontei* in Utah (solid circles). The Carbon County specimen is represented by the solid triangle.

colored saddles. The following scale counts were noted: ventrals 205; caudals 34; scales in 25-23-19 rows; upper labials 8; lower labials 9; preoculars 1; postoculars 2; loreals 1; prefrontals 1; internasals 1; right temporals 1+3+2; left temporals 2+3+2. The caudal number of 34 is apparently the lowest ever recorded for this species: Wright and Wright (1957) record a low of 41, and the lowest number reported by Tanner (1941) in specimens from Utah was 43. Additional specimens are needed from eastern Utah to determine the significance of this low ventral count.

The senior author visited the Dragerton locality during August 1972 in an attempt to obtain additional specimens. Four days were spent in the area driving roads at night and turning rocks, without success. Few other reptiles were seen, perhaps because of the extreme dryness of the area and the time of the year.

The significance of the Dragerton specimen is to again indicate the importance of the Upper Colorado Basin as a distribution route for many species. Western species (*Sauromalus obesus*, *Phrynosoma platyrhinos*, *Xantusia vigilis*, *Lampropeltis getulus californiae*, *Tantilla planiceps*, and others) and eastern species (*Eumeces multivirgatus gaigei*, *Lampropeltis triangulum taylori*, and *Elaple guttata*) have entered the basin from the south and moved northward. Because of the isolation factor for populations established in the Upper Basin, many distinct subspecies have evolved. Unfortunately, many populations are widespread and individuals are difficult to obtain, which leaves us with many unanswered systematic problems.

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DESCRIPTION OF A *PHYLLORHYNCHUS* FROM CERRALVO ISLAND, GULF OF CALIFORNIA, MEXICO

Arnold L. Powers[1] and Benjamin H. Banta[2]

Abstract.— *Phyllorhynchus decurtatus porelli* ssp. nov. is described from a single specimen from Cerralvo Island, Gulf of California, Mexico, and is regarded as different from *P. d. decuratus* on the basis of an increased number of dorsal blotches (41 as compared to 18-33) and an increased number of supralabials (7 as compared to 6), combined with geographical isolation and the high degree of endemism found in other reptiles on Cerralvo Island.

Among the herpetological specimens secured from Cerralvo Island, Gulf of California, Mexico, in January 1973 is an example of *Phyllorhynchus decurtatus* (Cope). It constitutes the first record of this species for Cerralvo Island. The specimen resembles a specimen of *P. decurtatus* (SDSNH 44682) reported by Soulé and Sloan (1966) from San José Island, located approximately 90 kilometers to the northwest (Fig. 1). When compared with the published meristic and morphological data provided by Klauber (1940) and Smith and Langebartel (1951), a number of distinctive features were found (Table 1). These data combined with the geographical isolation from the most similar populations on the Baja California peninsula and the high degree of endemism found in other reptiles occurring on Cerralvo Island merit the recognition of a distinct geographic race.

Table 1. Summary of selected morphometric and meristic characteristics of nominal forms of *Phyllorhynchus* adapted from Klauber (1935. 1940); Soulè and Sloan (1966); Savage and Cliff (1954); Smith and Langebartel (1951).

Species	Ventrals	Sub-caudals	Supra-labials	Dorsal blotches
decurtatus	157-167	33-36	6	18-33
*decurtatus**	153	33	6	28
porelli	160	33	7	41
arenicola	164	39	6	30-32
norrisi	151-156	31-34	6	28-48
perkinsi	168-182	32-41	6	26-57

*from San José Island

Phyllorhynchus decurtatus porelli, ssp. nov.

Holotype.— Subadult male; Natural History Society of Maryland number R1800 NHSM collected by Ismael Avilés from southwest Cerralvo Island, Gulf of California, 15 January 1973.

Diagnosis.— A new geographic race of *Phyllorhynchus decurtatus* closely related to peninsula populations of *P. decurtatus* in

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[1] Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder, Colorado 80302.

[2] Department of Biology, United States International University, San Diego, California 92131.

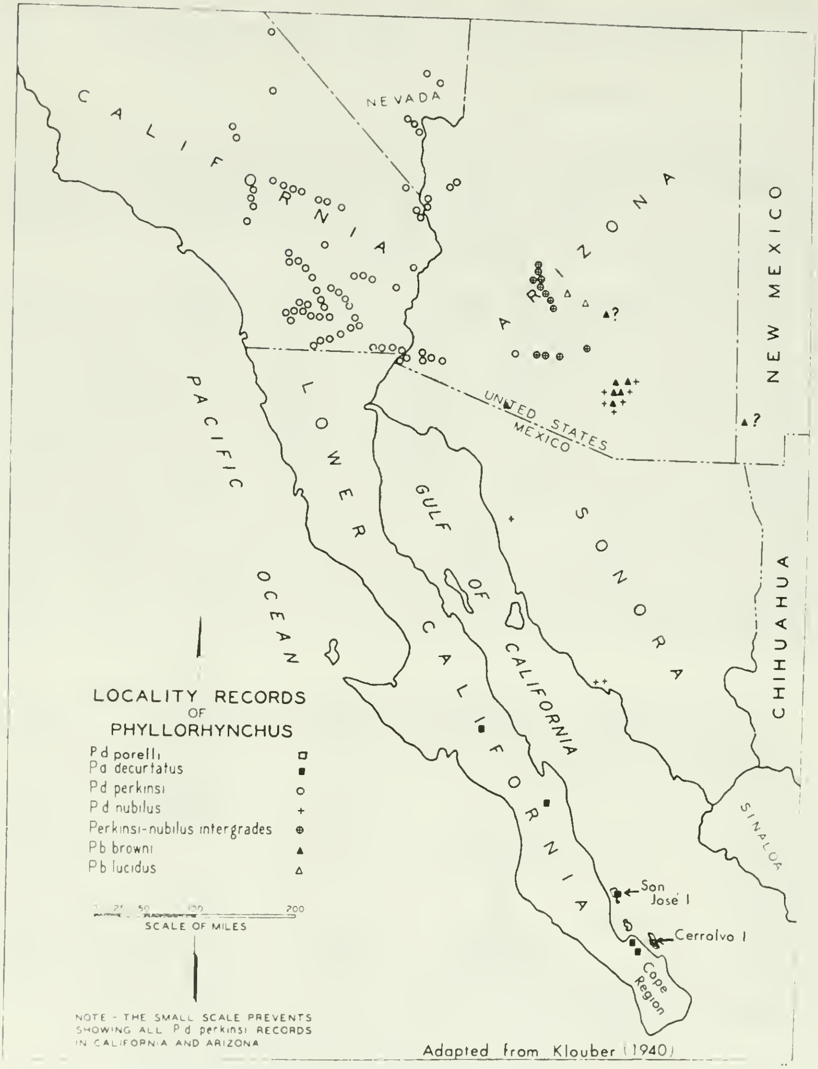

Fig. 1. Distribution of the genus *Phyllorhyncus*.

having an increased number of dorsal blotches (41 as compared to 18-33) and an increased number of supralabials (7 as compared to 6, Table 1).

Description.— Rostral large, truncate in dorsal profile, edges protruding and striated; internasals triangular, separated by rostral, in contact with upper loreal and both sections of nasal. Body moderately stout, slightly flattened below but cylindrical. Tail relatively

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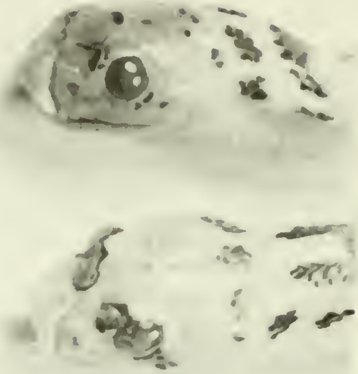

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Fig. 2. Head of *P. d. porelli*, dorsal (a), ventral (b), and anterior (c) views.
Fig. 3. Head views of *P. d. porelli* from Cerralvo Island (top) and *P. d. decurtatus* from San José Island (bottom).

short, decreasing rapidly in girth posteriorly. Head only slightly distinct from body, short with a blunt snout; not as broad at trunk as at mid-body. Scale rows 21-19-16; apical scale pits single; ventrals 160; anal single; subcaudals 33, all paired. The primary dorsal pattern is a series of 41 irregular brown blotches with a cream-white

Fig. 4. Dorsal views of *P. d. decurtatus* from San José Island and *P. d. porelli* from Cerralvo Island.

background. On the sides are auxiliary series of spots, irregular in form (Figs. 1-3).

REMARKS.— Geographically, *porelli* is most closely related to *decurtatus*, which occurs on the adjacent Cape Region to midcentral Baja California. A relationship of *porelli*, as with the San José specimen of *decurtatus*, can also be deduced with the western Mexico mainland *norrisi*, found approximately 500 kilometers northward across the Gulf of California in Sonora. The Monserrate Island species *arenicola*, can also be readily related to *porelli* based on comparable ventral counts. A better appraisal of the systematic status of this insular form can be obtained only if and when additional material becomes available for study.

ACKNOWLEDGMENTS

The expedition was partially sponsored by the Natural History Society of Maryland, Inc., through the generosities of Mr. Herbert S. Harris, Jr., and Dr. Robert S. Simmons. Mr. Clark R. Mahrdt, San Diego Society of Natural History (SDSNH) provided access to the society's extensive collections. Dr. Hobart M. Smith, EPO Biology Department, University of Colorado, provided editorial suggestions. Photographs were provided by Mr. Roy Porello, for whom the new race is named in appreciation of his many photographic contributions to the authors.

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TWO NEW VARIETIES OF *ERIOGONUM* (POLYGONACEAE) FROM THE INTERMOUNTAIN REGION

James L. Reveal[1]

Abstract.—Two new variants of *Eriogonum* are proposed: *E. brevicaule* var *atwoodii* from near Fredonia, Mohave Co., Arizona and *E. pharnaceoides* var. *cervinum* from southwestern Utah and adjacent northern Arizona and southeastern Nevada.

After a detailed review of the genus *Eriogonum* (Polygonaceae) for the state of Utah was published (Reveal, 1973a, b), material representing two undescribed varieties was discovered, and these are hereby proposed as new.

Eriogonum thompsonae S. Wats. var. *atwoodii* Reveal, var. nov. A var. *thompsonae* floribus albis et a var. *albifloro* foliis linearis differt. Typus: Arizona: Mohave Co.: Along Arizona Highway 389, 4.3 miles west of the junction of U.S. Highway 89A at Fredonia, on rolling reddish clay hills, associated with *Atriplex*, *Ephedra*, *Stanleya*, and *Eriogonum mortonianum*, at about 4700 feet elevation, 15 August 1973, *Reveal & Reveal 3211*. Holotypus, US! Isotypi, 15 duplicates to be distributed from US.

Low spreading herbaceous perennials (1) 1.5-3 dm high and 2-5 dm across; leaves sheathing up the stems 1-3 cm, linear, 3-8 (10) cm long including the petiole, 2-4 (6) mm wide, thinly to moderately tomentose below, usually glabrous above, infrequently glabrous on both surfaces, the margin inrolled or at least thickened, the nearly indistinguishable petiole about 1/5 the length of the leaf-blade; stems erect, 5-10 (12) cm long, glabrous; inflorescences open, cymose, (5) 8-15 cm long, glabrous; involucres turbinate, 2.5-4 mm long, 1.5-2 mm wide, glabrous, the 5 acute teeth 0.3-0.5 mm long; flowers white, 3-3.5 mm long, glabrous, the tepals oblong; achenes light brown, 2.5-3 mm long.

Other Specimens Examined: From the type area: 21 Jul 1973, *Atwood 5584* (bry, us).

This variety differs from typical var. *thompsonae* in having white flowers. The var. *thompsonae* occurs nearby on the steep slopes near Kanab westward to beyond Pipe Springs, but neither Atwood nor I found var. *thompsonae* in the vicinity of var. *atwoodii*. The var. *albiflorum* Reveal is similar in that it too has white flowers, but var. *atwoodii* differs from it (and var. *thompsonae* as well) in having long, narrowly linear leaves. The discovery of var. *atwoodii* confirms the seemingly close association I have assumed *Eriogonum thompsonae* has had with the more northerly *E. brevicaule* Nutt. and the more easterly *E. lonchophyllum* Torr. & Gray, both of which generally have narrow leaf-blades.

The variant is named for N. Duane Atwood, a former fellow

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[1] Department of Botany, University of Maryland, College Park 20742, and National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. Research supported by National Science Foundaton Grant GB-22645.

graduate student at Brigham Young University, and an outstanding plant collector.

Eriogonum pharnaceoides Torr. in Sitgr. var. *cervinum* Reveal, var. nov. A var. *pharnaceoides* floribus flavis differt. Typus: Utah: Washington Co.: Foothills south of Pinto on the north slope of the Pine Valley Mountains, associated with pinyon-juniper and other shrubs, 18 August 1973, *Atwood & Higgins 5895*. Holotypus, US! Isotypi, 20 duplicates to be distributed by US.

Erect herbaceous annuals 1-3 dm high; leaves basal and cauline, the basal ones linear-lanceolate to linear-oblanceolate, 1-3 (4) cm long, 1-2.5 (4) mm wide, lanate below, villous and greenish above, the petiole 1-3 (5) mm long, the cauline ones linear, 0.5-2 (2.5) cm long, 0.5-2 (3) mm wide, tomentose to lanate below, thinly villous to infrequently glabrous above, sessile or on petioles less than 2 mm long; stems erect, villous, leafy; inflorescences open, 0.5-2.5 dm long and up to 2 dm wide, the branches villous throughout; peduncles slender, erect or nearly so, (1) 2-5 cm long, villous to glabrous; involucres campanulate, the tube 1-2 mm long with 5 ± erect, lanceolate lobes 1-2 (3) mm long, villous; flowers yellow, 1-3 mm long, glabrous, the tepals dimorphic, those of the outer whorl oblong-ovate with a large saccate base on each side of the truncate to cordate base, those of the inner whorl linear-oblong and erect, usually far exceeding the length of the outer tepals; achenes brown, 1.8-2.3 mm long.

Other Specimens Examined: Arizona: Mohave Co.: Upper Trumbull Mountain, 6500 ft elev, 8 Sep 1953, *Merkle & Merkle 930* (GCNP). Nevada: Lincoln Co.: Deer Lodge, 15 Aug 1935, *Hall s.n.* (BRY); Deer Lodge, 7200 ft elev, 1 Sep 1935, *Hall s.n.* (BRY). Utah: Millard Co.: Cane Springs, 6000-7000 ft elev, 1898, *Purpus 6229* (K, UC, US). Washington Co.: Pine Valley Mountains, 22 Jul 1973, *Atwood 5418* (BRY, MARY, US); near Grass Valley Reservoir, 22 Jul 1973, *Higgins 7921* (US); Mountain Meadows, 15 Aug 1935, *Stanton 6583* (SD).

The var. *cervinum* differs from var. *pharnaceoides* in having yellow instead of white flowers and occupying a geographical area north and west of the typical variant. The flowers of var. *cervinum* are also a bit smaller, but the measurements overlap.

As I indicated before (Reveal, 1973a), the problem with this variety has been the paucity of material for critical evaluation and use as a type. In 1973, Atwood and Larry C. Higgins obtained specimens of this variant for me, and they succeed rather well. In addition, a visit to the Grand Canyon National Park resulted in the discovery of var. *cervinum* in northern Arizona, and thus the known range can be expanded to include this state for the variety.

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GREAT BASIN NATURALIST

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FIELD BEHAVIOR AND SEASONAL ACTIVITY OF THE RODENT BOT FLY, *CUTEREBRA TENEBROSA*, IN CENTRAL WASHINGTON (DIPTERA: CUTEREBRIDAE)[1]

Craig R. Baird[2]

ABSTRACT.— Behavior and activity of the rodent bot fly, *Cuterebra tenebrosa* Coquillett, was studied at a natural aggregation site in central Washington. Daily flight activity extended from 1700 hr to 2030 hr (PDT) beginning in mid-July of 1970 and 1971. The peak of flight activity, in August, was followed by a decline in activity through September. Male flies aggregated on the vertical faces of basalt cliffs, where they awaited females. Daily activity reached a peak at temperatures of 30-35 C. Eggs were laid in rock crevices without regard to the proximity of *Neotoma* wood rat hosts. Developing fly pupae were found in litter in wood rat tunnels in basalt cliffs.

Adult bot flies are rarely encountered in nature, and their general behavior was little known until recent years. Most early information was gathered from scattered accounts of one or two flies captured during the warm months, and specific identification was often impossible due to lack of adequate keys. The first in-depth study of adult *Cuterebra* activity and behavior was by Catts (1967), who worked with *C. latifrons* Coquillett in California. Adult *C. polita* Coquillett activity at aggregation sites in Utah was studied by Graham and Capelle (1970) and Capelle (1970). Recently, Hunter and Webster (1973) reported behavioral studies of *Cuterebra grisea* Coquillett and *C. tenebrosa* Coquillett in British Columbia.

Very little additional information is available on the activity of *Cuterebra tenebrosa*, a large black cuterebrid whose larvae parasitize *Neotoma* wood rats in the western United States and western Canada. Parker and Wells (1919) obtained a female in September in Montana, and Moilliet (1950) reported the capture of a female in British Columbia in August.

During 1970 and 1971, adult *C. tenebrosa* were studied at natural aggregation sites in central Washington. The purpose of this paper is to describe: (1) seasonal and diurnal occurrence of adult *C. tenebrosa* at aggregation sites, (2) flight activity and mating behavior, and (3) oviposition activity and sites.

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[2] Department of Entomology, Washington State University, Pullman, Washington 99163. Current address: University of Idaho Extension Service, P. O. Box 1058, Caldwell, Idaho 83605.

Materials and Methods

Field observations were conducted at the Columbia National Wildlife Refuge, Othello, Washington. The area is largely composed of rock slides and 15-35 m high basalt cliffs (Fig. 1A) with sagebrush and dry land grasses the main vegetation. Despite the overall dryness, a number of small streams and lakes exist in the lower areas (Fig. 1B).

Observations were made intermittently during all months of the year; however, the main attempts to study fly activity were between April and October of 1970 and 1971. Searches for aggregation sites

Fig. 1. General view of area where *Cuterebra tenebrosa* is active in central Washington. A. Male flies station themselves on the vertical cliff faces (arrows) to await females. B. Several aggregation sites (arrows) are visible in this view of the Columbia National Wildlife Refuge near Othello, Washington.

covered approximately 41 square kilometers (16 square miles) of the refuge. Intensive observations were confined to three aggregation sites, and nine additional sites were used for comparison.

Because of difficulty in collecting wild flies for release and resighting, only laboratory-reared flies were used for this purpose. They were marked on the mesonotum with white ink and released within two days of emergence. Marked flies were released under favorable weather conditions between late July and mid-August of 1971. Flies were released in shaded areas at the base of cliffs. Resighting and identification of individuals was possible with field binoculars (7x) from a distance of 10 m or less.

RESULTS

AGGREGATION SITES.— Adult *C. tenebrosa* were found on the vertical faces of basalt cliffs (Fig. 1A), rarely on top. Twenty-five different cliffs or rock formations were examined for activity during 1970 and 1971, and all had active *C. tenebrosa* on them at one time or another. As might be expected, some sites were better than others, as indicated by greater numbers of flies. The best sites were the east- and southeast-facing cliffs. These supported the greatest number of flies, whereas north- and west-facing cliffs were as a rule without *Cuterebra* activity. Smooth, brush-covered hilltops equal in elevation to the basalt cliffs were examined for fly activity, but no flies were found. Apparently they preferred the rocky, vertical sites.

During inclement weather and periods of inactivity, adult flies crawled into protected crevices in the vertical rock walls where they remained immobile until favorable conditions existed.

LONGEVITY OF ADULT FLIES.— Based on the release of marked flies, longevity in the wild is estimated at 5-9 days. In the laboratory, flies lived 8-13 days at room temperature (22 C) but were kept alive as long as 37 days at 4-6 C.

Resighting of marked male flies occurred as late as the ninth day after release, but for most flies 6-7 days was the maximum. Fourteen of 25 marked flies were resighted on subsequent days but only at the site where release took place. Although the three release sites were about 100-150 m apart, no interchange of marked males between sites was observed.

Only two of eight marked females were resighted. One was sighted on the sixth post-release day approximately 75 m from the release site as it investigated rock crevices in an apparent search for oviposition sites. The other female was seen on the fourth day as it rested beneath a rock overhang. It was within a few meters of the original release site.

SEASONAL AND DIURNAL ACTIVITY.— *C. tenebrosa* adults were active in the wild from July through September. In spite of regular searches of the study area beginning in April 1970, flies were not observed until 23 July 1970. In 1971, flies were first observed on 10 July. Following the first sighting in each year, adult flies were active on favorable days into late September. The last fly to be sighted in either year was on 8 October 1971.

Dr. Charles L. Graham, who has examined *Cuterebra* specimens and label data from major United States collections, reported that *C. tenebrosa* activity begins in mid-July and reaches a peak in August. Activity declines in September, but a few *C. tenebrosa* have been captured in California as late as October (personal communication, 1972).

In July and August of 1970 and 1971, fly activity at aggregation sites extended from 1700 hr to 2030 hr Pacific Daylight Time (PDT). More flies were seen on days when the air temperature was 30-35 C, although some activity was observed at temperatures as low as 24 C. Flies remained in protected areas at temperatures below 21 C and were reluctant to fly. Weather conditions strongly influenced activity. During cold or wet periods flies were inactive. Heavy wind even on hot days curtailed flight activity, whereas light wind 16-25 km/hr (10-15 mph) had no apparent effect. On days of peak fly activity, the air temperature changed little from midafternoon until after flight activity ceased.

Male flies appeared at aggregation sites earlier (1700 hr PDT) in the day than females (1800 hr) and in greater numbers. Five to seven males were active at each site on favorable evenings, whereas only an occasional virgin female was sighted. Since the sexes are similar, they were distinguishable from a distance only by behavioral differences. Males usually perched on vertical rock faces in a head-up or a head-down attitude and pursued other insects including other *C. tenebrosa* males. Marked laboratory-reared flies were resighted many times but were never observed to dislodge a resident male. Numerous pursuits lasting from 3 to 10 sec always resulted in the resident male's returning to his perch. Pursuit occasionally took place above the cliffs but was usually confined to the top one-third of the cliff within 1-3 m of the rock wall.

Virgin females did not linger at aggregation sites for more than a few minutes. Their flight was direct without apparent searching behavior characteristic of gravid females. Virgin females were readily pursued by waiting males. Males overtook and coupled with females and then fell to earth, where copulation was completed. Mating was observed on two occasions in the wild, and in both cases it was completed in 10-15 min. Laboratory-reared flies that were handheld or confined to petri dishes averaged 32 min per mating (30 matings).

Oviposition.— Gravid females were recognizable by their short flights from one crevice to another in search of oviposition sites. The earliest a gravid female was sighted was 1700 hr PDT in July; the latest was at 2115 hr or about 45 min after the last male was observed at the site.

After alighting near an opening and walking in, females remained inside for 5-10 min and then emerged to continue their investigative behavior. The flies seemed to prefer dark openings.

Most crevices and dark openings in the rocks were visited by ovipositing females, often by more than one fly. Preference was not shown for crevices and tunnels with active wood rat nests. Close examination of several crevices revealed *Cuterebra* eggs about 30-40 cm in from the entrance. These were laid without regard for the presence or location of a wood rat nest. Eggs were usually located on vertical surfaces singly or in groups of four to eight and were apparently laid as the fly entered. *Cuterebra* eggs were not found on nest materials or within 30 cm of any of 30 wood rat nests that were carefully dismantled and examined.

Egg capacity of 18 laboratory-reared *C. tenebrosa* females averaged 1870 (1462-2137), whereas gravid females captured in the wild averaged only 1270 (450-1460). This is probably a result of the flies' having already laid part of their eggs.

FLY PUPARIA IN WOOD RAT NESTS.— Twenty-two of 30 wood rat nests examined between May and August 1971 contained *C. tenebrosa* puparia. Twelve had viable pupae, 17 had empty puparia, and one nest had both. Puparia were found in the nest litter 5-20 cm below the nest proper. Gregson (1950) reported finding "shells of cuterebrid puparia" around wood rat nests.

DISCUSSION

AGGREGATION AND FLIGHT BEHAVIOR.— The occurrence of *C. tenebrosa* flies at elevated aggregation sites further points out the tendency for bot flies to concentrate at such locations. *Cuterebra tenebrosa* males utilized the vertical cliff walls for waiting sites rather than the actual cliff top. Townsend (1935) captured males of several *Cuterebra* species on bare hilltops and at upper end of ravines, although he made no mention of these sites as being for aggregation or mating purposes. Catts (1967) found male *C. latifrons* at hilltop sites between 0700 hr and 1200 hr (PST) from June to October in California's coastal mountains. Capelle (1970) and Graham and Capelle (1970) studied *C. polita* on south-facing hillsides in Utah where 30-40 flies (90%+ males) were active between 0930 hr and 1230 hr (MDT) on a given day. The *C. polita* flight season lasted only from late July to late August. Observations by Hunter and Webster (1973) concerning *C. tenebrosa* contrast with the present study in two ways: (1) The flies utilized the base of west-facing cliffs in British Columbia, whereas the same species aggregated near the upper portions of south- and east-facing cliffs in Washington. (2) The daily activity period was during late morning in British Columbia; in Washington, flies were active only in late afternoon.

Near Tucson, Arizona (Sabino Canyon), I observed an unidentified *Cuterebra* species active on 19-21 April 1969 on cactus-covered hilltops. We captured 11 males as they perched on prominent plants or rocks in an apparent watchful attitude, but the females were never sighted. Two days later, five males of the same species were taken from a rock-and-brush-covered hilltop near Congress, Arizona.

In these instances, all Cuterebrid activity was observed between 0800 hr and 1230 hr (MDT).

The abundance of *Cuterebra* males in relation to females is probably due to the females' being present at the site only long enough to be mated and the males' spending their entire lifetime there.

Marked fly release.— Marked flies were released to determine their longevity in the wild and to determine the extent of their travels. The longevity of 5-9 days is similar to the 10-day lifetime for *C. latifrons* (Catts 1967). Catts reported that only 1-2 percent of released flies moved from their original hilltop, an indication that males tend to occupy one aggregation site for their entire life. *C. tenebrosa* also tended to stay at one aggregation site.

Since resident *C. tenebrosa* males were not marked, identification of individuals was not possible. Therefore, territorial activity cannot be positively attributed to this species. On the basis of many observations, however, I believe the males do defend an area or territory against intruders as was described by Catts (1967). Marked laboratory reared flies were pursued by a resident male when they entered the primary activity area; at no time was a marked fly the established defender. Hunter and Webster (1973) observed *C. tenebrosa* males flying in an oval or figure-eight pattern over a 10-15 m long territory. Capelle (personal communication, 1973) offered an alternative opinion of male pursuit activity, suggesting that it is investigative mating behavior.

Diurnal activity.— *Cuterebra tenebrosa* appears exceptional in its late-afternoon and evening flight period. Other cuterebrids are morning or midday fliers (Catts, 1967; Capelle, 1970). Only one *C. tenebrosa* specimen was observed during morning hours. It was sighted at the base of a cliff at 0900 hr and probably had emerged that morning. Grunin (1959) indicates that members of Oestridae, Hypodermatidae, and Gastrophilidae generally are active during morning hours.

The intense heat of summer afternoons and evenings was not a deterrent to *C. tenebrosa* activity as it appears to be with morning-flying species. The stimulus to flight activity was not determined. Light intensity may be a factor, because at onset of fly activity (1700 hr) the east-facing cliffs were shaded although the air temperature remained at 30-35 C. Approaching darkness was the apparent terminating stimulus, although ovipositing females were active on windless evenings until complete darkness.

Oviposition.— For many years it was assumed that *Cuterebra* flies oviposited on their host. Dalmat (1943) disagreed and suggested they lay eggs in the immediate host environment. Findings of Beamer et al. (1943) supported Dalmat's suggestion when *C. beameri* Hall eggs were found at the entrance of wood rat houses. Beamer (1950) observed *C. buccata* (Fabricius) females ovipositing on grass stems along rabbit runs. Catts (1967) found *C. latifrons* eggs on sticks around the entrances to wood rat houses. Graham and

Capelle (1970) observed female *C. polita* investigating pocket gopher burrows whether the burrows were actively being used or not. They suggested the stimulus for egg laying may be visual rather than olfactory. Capelle (1970) carefully excavated gopher burrows from which *C. polita* had just emerged and found eggs on the fine roots hanging from the ceiling. Although most *Cuterebra* have not developed host finding to this degree, it appears that oviposition in the immediate area of the host is the general pattern. *C. tenebrosa* females laid eggs in almost any site involving a dark hole or crevice. The visual stimulus seemed to be important. Host activity was not evident except in a few oviposition sites.

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NOTES ON THE SPOTTED BAT (*EUDERMA MACULATUM*) FROM SOUTHWEST UTAH

Richard M. Poché[1] and Geoffrey L. Bailie[1]

Abstract.— In May 1974 four male spotted bats were netted near St. George, Utah. Contrary to published speculation on *Euderma*, indications are that the spotted bat in southwest Utah (1) is not a late flyer, (2) does not feed solely on moths, (3) may drop to the ground on occasion to forage, (4) is not a rapid flyer, and (5) appears to utilize crevices as roosting sites.

The spotted bat (*Euderma maculatum*) has been reported from the southwestern United States by several biologists. Easterla (1970) collected *Euderma* in Big Bend National Park, Texas. Durant (1935), Hardy (1941), Benson (1954), and Easterla (1965) discussed the spotted bat in Utah. A specimen from Las Vegas, Nevada, was reported by Hall (1935). Jones (1961), Constantine (1961), Rodeck (1961), and Findley and Jones (1965) gave accounts of the spotted bat from New Mexico, while Vorhies (1935) noted it from Arizona. Little natural history information on *Euderma* is available, leaving the field open to much speculation.

Four spotted bats were netted between 21 and 23 May 1974 in Fort Pierce Wash, approximately eight miles southeast of St. George, Washington County, Utah (113° 25′ W, 37° 00′ N). All were captured over scattered pools averaging only 25 cm in depth and 3-5 m in width.

This locality is in the Lower Sonoran Life Zone, with an average rainfall of 150 mm. Vegetation consists primarily of creosote bush (*Larrea tridentata*), snakeweed (*Gutierrezia microcephala*), blackbrush (*Coleogyne ramosissima*), bursage (*Franseria dumosa*), and scattered *Yucca*. Riparian vegetation in the wash is mainly salt cedar (*Tamarix pentandra*), creosote bush, and desert willow (*Chilopsis linearis*).

All spotted bats obtained were males, none with scrotal testes. On 21 May two *Euderma maculatum* were netted between 2215 hr and 2230 hr. The following night another was captured at precisely 2230 hr, and the fourth was netted on 23 May at 2228 hr. Preliminary indications are that the spotted bat is not a late flyer in southwestern Utah. This conflicts with reports by Easterla (1965), who suggests that *Euderma* is a late flyer and that most can therefore be captured after midnight.

The first spotted bat obtained was marked with *Pelikan*, black water-resistant ink, near the base of the tail on the uropatagium, and the remaining three were marked by perforating the plagiopatigum with small holes, 3 mm in diameter. No recaptures were obtained. Measurements of one live male were taken: total length, 120 mm; tail length, 60 mm; hindfoot, 11 mm; and ear, 35 mm.

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[1] Stearns-Roger, Inc. P.O. Box 5888, Denver, Colorado 80217.

One individual was placed in a cardboard box containing a damp towel and several unidentified moths and retained until the following evening. None of the food was consumed by the bat. But prior to release the bat was in excellent physical condition and its behavior was assumed to be normal. On 22 May the *Euderma* was released near Fort Pierce Wash at 2020, approximately 55 minutes before dark. We were positioned to follow its flight, hoping to locate a nearby roost.

The *Euderma* flew slowly and directly southward, toward the sloping valley wall (Fig. 1). (Having observed a high rate of injury among captured specimens, Easterla [1965] concluded that the spotted bat was probably a rapid flyer.)

While in flight, the *Euderma* appeared to be feeding on small insects within two meters of the ground. Suddenly it dropped to the ground and seized and ate a grasshopper; and within ten seconds it was again in flight. A second plunge to the rocky terrain was observed. (Prior to this observation, reports on food habits of the

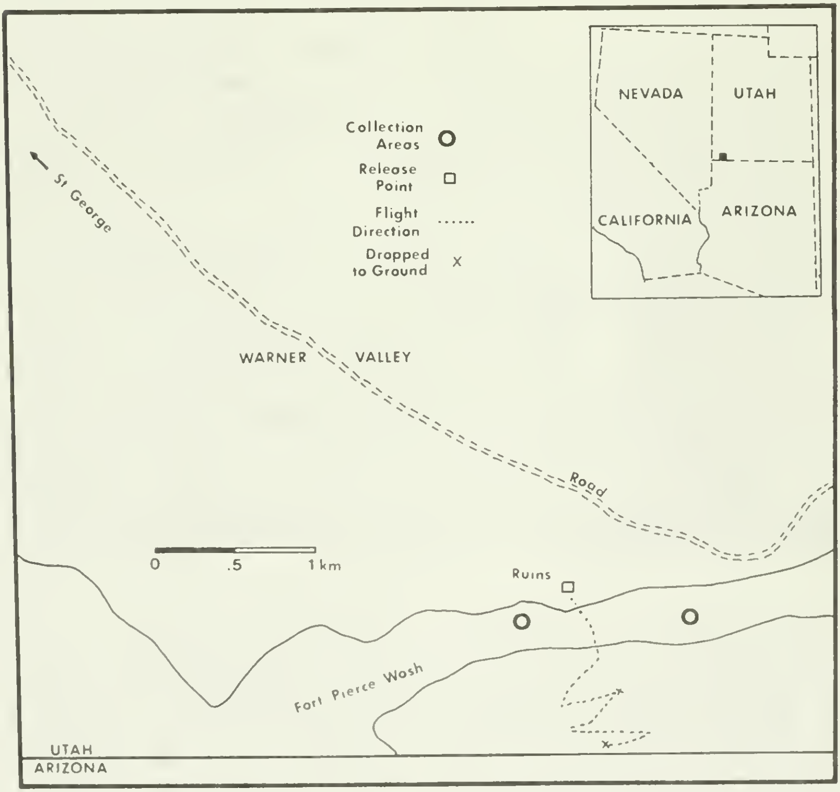

Fig. 1. The Washington Co., Utah, study site where spotted bat flight and behavior was observed.

spotted bat indicated that the diet was highly selective, consisting only of moths [Ross, 1961; Easterla, 1965; and Barbour and Davis, 1969a]. Easterla [1965] went so far as to speculate that the bat ate only moths of the family *Noctuidae*.) The descents to the ground were preceded by split-second hovering.

After four minutes of cruising and feeding over the low-lying vegetation, the spotted bat disappeared near a crevice only 300 m from the point of release. We were unable to approach the apparent roost before nightfall due to the rough terrain.

More detailed studies are currently under way. We feel that the population in the region is high as compared with estimates in previous reports on the spotted bats. Indications are that density may be higher in Mohave County, Arizona, where a similar habitat exists in close proximity to Fort Pierce Wash.

We would like to thank the Nevada Power Company, of Las Vegas, Nevada, for funding this project and for the continuation of natural history studies of the bat. Our appreciation is extended to Clyde Jones for critically reviewing this note.

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THE SIGNIFICANCE OF SCALE CHARACTERS IN EVALUATION OF THE LIZARD GENERA *GERRHONOTUS*, *ELGARIA*, AND *BARISIA*

James W. Waddick[1] and Hobart M. Smith[2]

Abstract.— Data taken on external scale characters of 1003 specimens representing nine of the sixteen species of *Gerrhonotus* sensu Stebbins, 1958, strongly indicate that Tihen's 1949 arrangement of those species in three genera (*Gerrhonotus*, *Elgaria*, *Barisia*) is valid. Misinterpretation of the identity of the head scales in various species of this group has led erroneously to disregard of them as indicators of relationships. Actually the scales are as constant as in most other lizards and seemingly provide firm clues to natural associations.

The proper generic allocation of species of "gerrhonotine" lizards, defined as those appropriately referred to *Gerrhonotus* Wiegmann (*sensu lato*) as understood before 1942 (Smith, 1942) has remained enigmatic despite the documentation provided by the most recent review of the group by Tihen (1949), based upon osteology and external scutellation. The primary doubt was cast upon the validity of Tihen's groupings by Stebbins (1958), who proposed an alternative grouping based upon reproductive habits, color patterns, and habitat.

Haunted by the impression that external scutellation provides more reliable clues to relationships in this group than was thought by Stebbins, we initiated a re-examination of this particular aspect, utilizing materials in the University of Illinois Museum of Natural History (UIMNH), University of California Museum of Vertebrate Zoology (MVZ), University of Kansas Museum of Natural History (KUMNH), University of Michigan Museum of Zoology (UMMZ), United States National Museum (USNM), Brigham Young University Museum of Natural History (BYU), University of Colorado Museum (CUM) and University of Texas Natural History Collection (TNHC). We are much indebted to authorities at these institutions for the privilege of borrowing material from them; particularly instrumental were Dr. Donald F. Hoffmeister, Dr. Robert C. Stebbins, Dr. E. Raymond Hall, the late Dr. Norman Hartweg, the late Dr. Doris Cochran, Dr. Wilmer W. Tanner, Dr. T. Paul Maslin, and Dr. W. F. Blair. As is apparent from this list, the work here reported was completed more than a decade ago. Its results remain valid and of current interest.

Descriptive Terminology

The definition of the genera of gerrhonotine lizards requires a definitive identification of the head and body scales involved. Uniformity of terminology has not existed in the past. Indeed, misidentification of scales was important in Stebbins' (1958) rejection of scutellation as a reliable indicator of relationship. The nomenclature

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[1] Curator of Education, New York Zoological Society, 185th & Southern Blvd., Bronx, New York, 10460.

[2] Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder.

here adopted is based on the work of Tihen (1949) and Smith (1942), and was depicted first, for *Elgaria*, by Woodbury (1945).

Nasal.— The nasal scale is an unmistakable point of reference, being the anterior lateral head scale through which the external naris is pierced. It is present universally in all Gerrhonotinae, is easily found, and is difficult to misinterpret (Figs. 1, 3).

Rostral.— Except for the nasal, the rostral is the easiest to identify with certainty, being the anteriormost scale on the upper jaw. It is median and unpaired. In no specimen has it been observed split (Fig. 1).

Internasals.— Gross misinterpretations have occurred in the past simply by regarding any scales occurring between the anterior and posterior boundaries of the nasals as internasals. Unfortunately, this is not correct; such an interpretation embraces several scales in addition to the true internasals. For that reason it is best to define anterior and posterior internasals separately.

Anterior internasals.— The scales bordering the nasal anteriorly and preventing contact of the nasals with the rostral are anterior internasals. When present they occur along the posterior boundary of the rostral and may occur in one (Fig. 2) or two pairs. The anterior internasals are absent when the nasal contacts the rostral scale (Fig. 1).

Posterior internasals.— These are scales located behind the anterior internasals, or their equivalent, and along the posterior boundary of the nasals. They always are limited to the dorsal surface of the head. They too may be absent or may occur in one or two pairs (Figs. 1, 2).

Supranasals.— Scales that have as their lateral boundaries the dorsal edge of the nasals are supranasals (Fig. 2, 3, 5). They are paired or absent and take the place in some groups of the anterior internasals (Fig. 1). They may also be accompanied by both anterior and posterior internasals (Fig. 2); if so, the supranasals are posterior to the anterior internasals and anterior to the posterior internasals.

Postnasals.— The scales forming a direct posterior border with the nasal scale are postnasals (Figs. 1, 3). They are always present and occur two to a side with few exceptions. They may be designated as the upper and lower postnasals. Occasionally the upper postnasal may be in a position to be confused with the supranasal, but it can always be identified by counting the scales posterior to the nasal dorsad from their contact with the supralabials (Fig. 3).

Supralabials.— The scales bordering the upper edge of the mouth, except for the rostral. are the supralabials; they always occur in a single row in contact with the lip (Fig. 1).

Postrostrals.— One (Fig. 2) or two (Fig. 4) small azygous scales bordering the rostral at its posterior median edge are postrostrals. When two are present they form a longitudinal series.

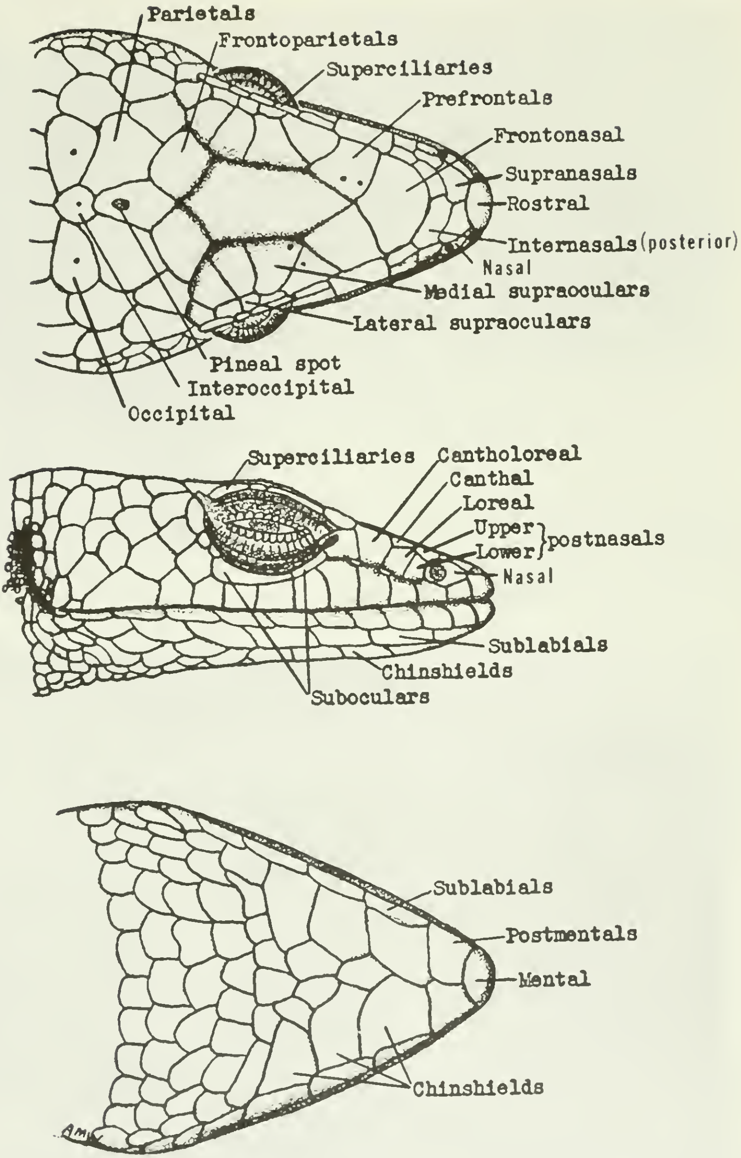

Fig. 1. Dorsal, lateral, and ventral head scales of *Elgaria coerulea shastensis* Fitch, from Woodbury (1945:10, fig 2), depicting the type of *Gerrhonotus coeruleus utahensis* Woodbury (synonymy *fide* Tanner, 1959).

Loreals.— The loreals form a series bordering the supralabials, the postnasals, the eye, and the canthals (Fig. 3). One to three may occur. They are frequently fused with the canthals, forming cantho-

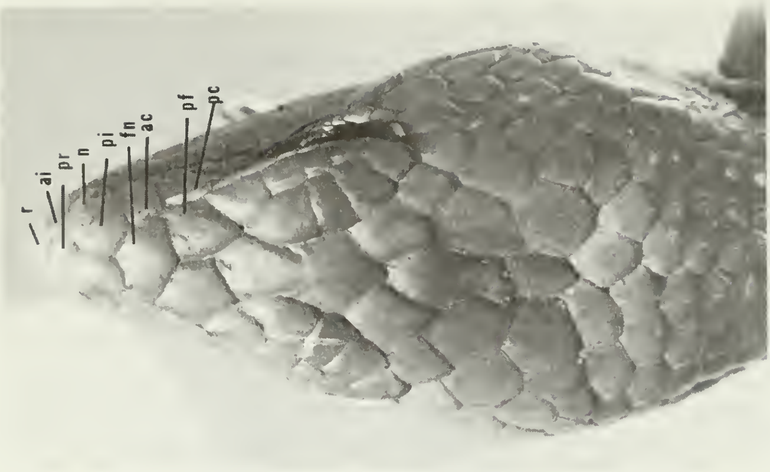

Fig. 2. Dorsal head scales of *Gerrhonotus liocephalus infernalis*, CUM 14552, Juniper Flat Road, nr. cabin area, Chisos Mts., Big Bend National Park, Brewster Co., Texas. Symbols: ac, anterior canthal; ai, anterior internasal; fn, frontonasal; n, nasal; pc, posterior canthal; pf, prefrontal; pi, posterior internasal; pr, postrostral; r, rostral.

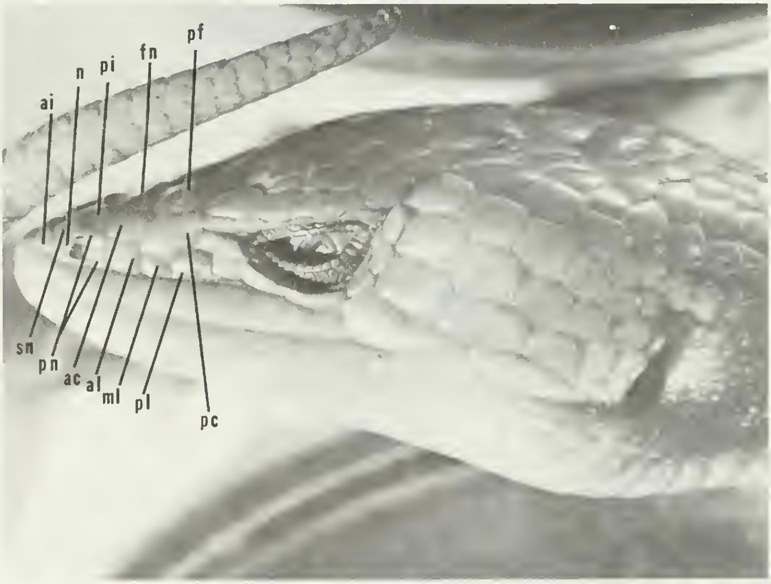

Fig. 3. Lateral head scales of *Gerrhonotus liocephalus infernalis*, CUM 14552, data as in Fig. 2. Symbols: ac, anterior canthal; ai, anterior internasal; al, anterior loreal; fn, frontonasal; ml, median loreal; n, nasal; pc, posterior canthal; pf, prefrontal; pi, posterior internasal; pl, posterior loreal; pn, postnasals; sn, supranasal.

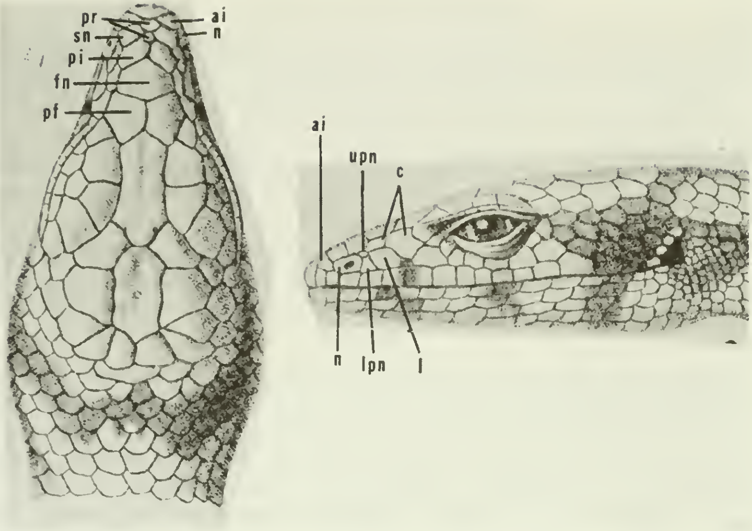

Fig. 4. Dorsal and lateral head scales of *Coloptychon rhombifer* (from Bocourt, Mission Scientifique au Mexique, Reptiles, 1878, pl. 21B, figs. 4, 4a). Symbols: ai, anterior internasal: c, canthals; fn, frontonasal; l, loreal; lpn, lower postnasal; n. nasal; pf, prefrontal; pi, posterior internasal; pr, postrostrals; sn, supranasal.

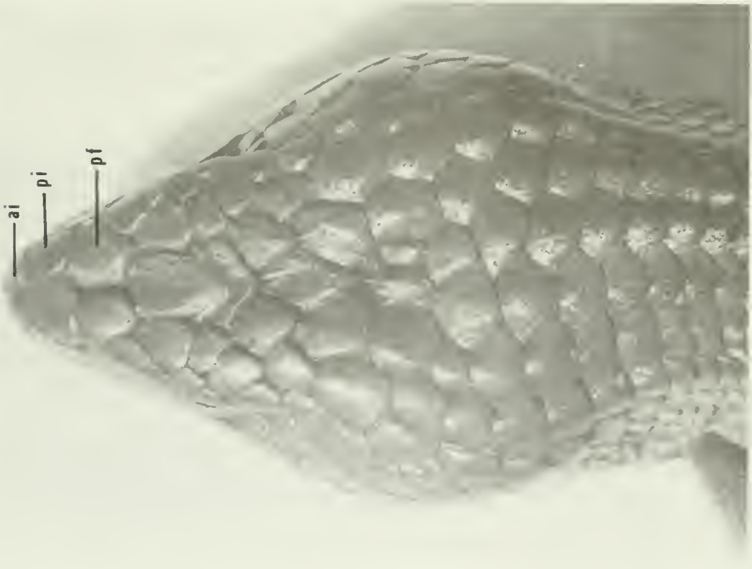

Fig. 5. Dorsal head scales of *Barisia imbricata*. CUM 48325, 21 mi. NW Galeana, Cerro Potosí, Nuovo León, Mexico. Symbols: ai, anterior internasal; pf, prefrontal; pi, posterior internasal.

loreals (Fig. 1). They are the only large scales on the sides of the snout.

Canthals.— The canthals form the peak of a ridge (the canthal ridge) separating the sides of the snout from the dorsal surface of the head (Figs. 2, 3). The scales usually occur in series with the loreals and may be fused with them (Figs. 1, 5) as cantholoreals.

Frontonasal.— The dorsal azygous scale between the canthals and posterior to the internasals is the frontonasal. It may be present (Fig. 1) or absent (Fig. 4).

Dorsal scale rows.— Counted along middorsal line from the scale behind the interparietal to the rear margins of the thigh. The number of scale rows is inversely proportional to the size of the scales.

Mental.—Directly comparable to the rostral, the mental is the anteriormost scale on the lower jaw. It too is unpaired (Fig. 1).

Chinshields.— All paired scales forming a diverging series posterior to the mental are chinshields (Fig. 1). There may be four or more pairs. The anteriormost pair cannot be mistaken for a postmental, which is always single and is not present in gerrhonotine lizards. When the anterior chinshields are anomalously fused to form a large single scale, they have a characteristic shape indicating their origin.

Gulars.— All scales noticeably smaller than chinshields and directly posterior and/or median to the chinshields are gulars (Fig. 1).

Others.— Other cephalic scales are commonly recognized and not readily subject to misinterpretation; some are illustrated and labelled on the accompanying figures.

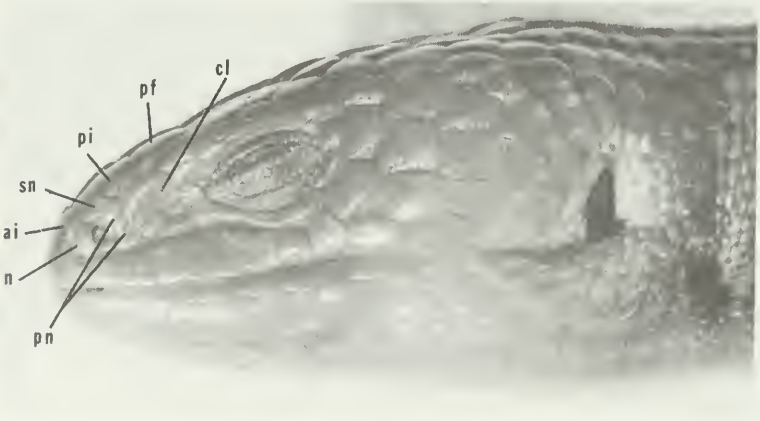

Fig. 6. Lateral head scales of *Barisia imbricata*, CUM 48325, data as in Fig. 5. Symbols: ai, anterior internasal; cl, cantholoreal; n, nasal; pf, prefrontal; pi, posterior internasal; pn, postnasals; sn, supranasal.

MATERIALS AND METHODS

Utilizing over 1300 specimens that represent 33 of the species and subspecies recognized in all but the first of Tihen's five genera (*Coloptychon*, *Abronia*, *Gerrhonotus*, *Elgaria*, *Barisia*), the following data were recorded on each: postrostral(presence, absence); frontonasal (presence, absence); nasal (contacting rostral or not); loreals (number, fusion); canthals (number, fusion); anterior internasals (number, presence, absence, dorsal contact or not); posterior internasals (number, presence, absence, dorsal contact or not); supranasals (presence, absence, dorsal contact or not); dorsal scale rows (number); chinshields (single or paired); and gulars (first one single or paired).

RESULTS

Coloptychon is a uniquely distinctive genus the validity of which is questioned by few (e.g., Wermuth, 1969). We have examined no specimens and therefore can shed no further light upon it. We call attention, however, to its unique character: two postrostrals, one following the other (Fig. 4). The genus presents no problem in an evaluation of the five gerrhonotine genera recognized by Tihen (1949).

Abronia likewise is recognized by most authorities following Tihen (1949), although not by Wermuth (1969). Although it thus constitutes no problem in the present context, we secured data on the 50 specimens of the genus available to us (Table 1). These data, and those published for the species no specimens of which we examined (*aurita*, *bogerti*, *fimbriata*, *fuscolabialis*, *matudai*, *mixteca*, *reidi*, *vasconcelosi*) may be summarized as follows: postrostral invariably absent; frontonasal usually present; nasal invariably separated from rostral; cantholoreals usually present; anterior internasals rarely not in contact; posterior internasals invariably in contact;

TABLE 1. Selected Data on Species of *Abronia*

Species and number of specimens examined	deppei (6)	lythrochila (2)	oaxacae (5)	ochoterenai (3)	taeniata (34)
Posterior internasals contact (%)	100	100	100	100	100
Frontonasal present (%)	100	100	40	100	85
Nasal separated from rostral (%)	100	100	100	100	100
Cantholoreal present (%)	0	100	100	100	85
Anterior internasals contact (%)	100	100	100	100	94
Supranasals present (%)	100	100	100	100	97
First chinshield paired (%)	100	0	100	100	100
First gular single (%)	100	100	100	100	85
Postrostral absent (%)	100	100	100	100	100
Dorsal scale rows range	27-30	33-36	28	28-33	24-29
Dorsal scale rows mean	28.4	34.5	28	30.6	26.9

supranasals rarely not present; first chinshields usually paired; first gular usually single; dorsal scale rows 24-36 (means 28-34).

The critical groups, whose validity of segregation has been widely questioned, are those designated by Tihen (1949) as the genera *Gerrhonotus*, *Elgaria*, and *Barisia*. Variation in the 1003 specimens from which complete data could be taken, representing nine species referable to these genera as of Tihen, is summarized in Table 2. These data clearly support Tihen's arrangement, which appears to reflect natural relationships. It is quite apparent that, far from being so variable as to be irrelevant, cephalic scutellation is constant within recognizable parameters in each natural group and provides vital clues to relationship. Extensive variation does exist, but it is not totally haphazard; clearly recognizable limits do exist, permitting ready recognition of natural groups.

Although we examined no specimens of four species of *Barisia* (*antauges*, *lugoi*, *modesta*, *rudicollis*) or of three of *Elgaria* (*cedrosensis*, *panamintinus*, *paucicarinatus*), the published descriptions of these taxa fall well within the range of the species we have examined. The generalizations evident from Table 3 are therefore valid for all species of these groups, although derived from the specimens we examined, representing the monotypic *Gerrhonotus*, 3 of the 6 species of *Elgaria*, and 5 of the 9 species of *Barisia*. Our series are sufficiently large to secure the validity of the indicated generalizations. Thus, *Gerrhonotus* differs trenchantly from *Elgaria* in six characters (1, 2, 3, 4, 6, 7); *Elgaria* from *Barisia* in three characters (2, 5, 6); and *Barisia* from *Gerrhonotus* in four characters (1, 3, 5, 7). Few of the individual differing character-states are absolute, but in combination they are.

We are confident that the three groups into which these 13 species fall on the basis of external scutellation are natural. The habitus of each group is also distinctive. Although Criley (1968) found no cranial distinctions, we are convinced that osteological distinctions correlated with differences in habitus will be found. Stebbins (1958), to be sure, interpreted *coeruleus* of the *Elgaria* group as a member of the *Barisia* group (subgenus *Barisia* of *Gerrhonotus*) and placed *liocephalus* with the rest of the *Elgaria* group (subgenus *Gerrhonotus*). That proposal, however, completely disregarded the scale characters here emphasized and the general habitus; it was predicated essentially upon reproductive and behavorial similarities. Those criteria, as he noted, are poorly known, and we point out that they are notoriously misleading unless fully documented. We regard Stebbins's subgenera *Barisia* and *Gerrhonotus* as artificial (through inclusion of *coeruleus* with *Barisia* and all other *Elgaria* with *Gerrhonotus*) and therefore untenable.

The scutellation data are incontrovertible in supporting the association Tihen originally proposed, and habitus is confirmatory. At the present time we are aware of no significant evidence that Tihen's five genera are not natural.

Even if admitted as natural, the validity of generic as opposed to subgeneric status of the *Gerrhonotus-Elgaria-Barisia* groups is open

Table 2. Variation in selected characters in species of *Gerrhonotus*, *Elgaria*, and *Barisia*

Species and number of specimens examined	liocephalus (131)	coerulea (421)	kingi (47)	multicarinata (78)	gadovi (62)	imbricata (104)	monticola (56)	moreleti (93)	viridiflava (11)
Postrostral (%)	95	7	4	5	35.5	1	0	4	9
Frontonasal (%)	98	99	98	100	100	6	100	99	55
Nasal-rostral (%)	1	98	94	100	0	0	3	1	0
Cantholoreal (%)	8	99	100	99	99	91	100	30	91
Ant. Intern. (%)	100	1	0	0	100	100	100	100	91
Ant. Intern. Cont. (%)	0	0	0	0	58	100	100	95	91
Post. Intern. (%)	100	100	100	100	100	100	100	100	100
Post. Intern. Cont. (%)	93	90	90	83	99	99	90	98	100
Supranasals (%)	100	100	100	100	100	0	73	99	100
Supranasals Cont. (%)	0	98	98	86	0	0	0	1	9
One ant. chinsh. (%)	0	0	0	0	0	0	98	98	100
Two ant. chinsh. (%)	100	100	100	100	100	100	2	2	0
One ant. gular (%)	29	97	100	100	100	95	90	87	100
Two ant. gulars (%)	71	3	0	0	0	5	10	13	0
Scale Rows	44-64	40-55	47-63	42-53	44-57	35-52	40-52	47-59	47-56
Mean Sc. R.	51	47.9	55.5	48.2	48.2	40.6	44.7	52.8	51.7

Table 3. Contrasts between the genera *Gerrhonotus*, *Elgario*, and *Barisia*.

Genera	GERRHONOTUS	ELGARIA	BARISIA
1. Postrostral absent	Seldom	Rarely not	Usually
2. Nasal-rostral contact	Rarely	Rarely not	Rarely
3. Cantholoreal present	Seldom	Rarely not	Usually
4. Ant. intern. present	Always	Rarely	Rarely not
5. Ant. intern. cont.	Never	Never	Usually
6. Supranasals cont.	Never	Rarely not	Rarely
7. Two ant. gulars	Usually	Rarely	Rarely

to question. The differential characters, however (even though each separately overlaps at least slightly), collectively indicate a long history of independent evolution that we regard as being consistent with separate generic status. We anticipate that ethological, serological, osteological, and karyological work in the future will substantiate these groupings and their generic rank.

It is quite evident that *Barisia* is the more variable and plastic of the three more closely related gerrhonotine genera, and it is presumably the most primitive of them. *Elgaria* and *Gerrhonotus* appear to be almost equally specialized derivatives from ancestral forms of *Barisia*, although the *imbricata* series of the latter genus is almost as specialized as the genera *Elgaria* and *Gerrhonotus*. Intermediates link all members of *Barisia*, however, whereas the members of both *Elgaria* and *Gerrhonotus* are trenchantly distinctive.

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REVEGETATION OF GOPHER MOUNDS ON ASPEN RANGE IN UTAH

W. T. McDonough[1]

Abstract.— The colonization of the pocket-gopher (*Thomomys talpoides*) mounds by annual and perennial species of the understory of aspen woodland was observed over a four-year period. New and old gopher mounds exist as a mosaic of sites in one of three surface conditions: bare, dominated by annuals with a few seedlings of perennials, and dominated by perennials with annuals in peripheral areas. The regular creation of these new sites for plant colonization appears to favor the maintenance of aggressive perennials at high densities in the understory vegetation.

On mountain rangeland in the western United States, foraging and soil-displacement activities of pocket gophers (*Thomomys talpoides*) have important effects on vegetation (Julander et al., 1969; Turner, 1969). The mounds and casts created by runway and cavity excavation present a new surface for plant colonization—seedbed conditions that may favor the establishment of particular species (Laycock, 1958). The purpose of this study was to describe the colonization of gopher mounds over a four-year period (1969 through 1972) on aspen (*Populus tremuloides* Michx.) range in Utah.

The aspen woodland of the study area (Fig. 1) occupies approximately 2 ha on a 19-degree south-facing slope at an elevation of 1900 m in Tony Grove Canyon on the Cache National Forest in northern Utah. Density of aspen (DBH greater than 5 cm) averages 2900/ha, and there is a dense understory vegetation of shrubs and annual and perennial forbs and grasses. Florez (1971) described the soil, climate, and vegetation of the site.

Methods

In early July 1968, 80 new gopher mounds were identified and numbered. In July 1969, the 50 mounds with the lowest assigned numbers and no previously established perennials emerging from them were designated for study. Percentage canopy cover of individual colonizing species was estimated visually in early July and early September of each year.

To determine the density, frequency, and distribution of new mounds each year, two belt transects, each 128 m long and consisting of 128 quadrats (each 1 m^2), were established 30 m apart near midslope where mound counts had indicated high mound-building activity. The transects were examined in early July of each year for new mounds. A mound was counted if any part of it was found within a quadrat. The distribution of mounds was estimated by use of variance-mean ratios (Greig-Smith 1964). In mid-June and mid-July of 1970, plant species in each of the quadrats of the transects

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[1] Plant physiologist, Intermountain Forest and Range Experiment Station, Ogden, Utah 84401; stationed in Logan, Utah, at the Forestry Sciences Laboratory in cooperation with Utah State University.

Fig. 1. The aspen woodland study area.

were noted. Dimensions and other characteristics of mounds were taken from 43 new mounds found in the transects in 1969. Frequency percentages of species on mounds over the four years of colonization were taken from the 50 mounds selected in 1969; quadrat frequencies were based on the transect data collected in 1970.

Soil samples of equal volume were taken from five new mounds and adjacent, undisturbed topsoil in late September of each year for standard fertility analysis—texture, pH, conductivity (total salts), organic matter, P, K, Ca, and NO_3-N. Subsamples from these collections were used to determine seed content by sieving and flotation on water. Additional collections of mound and adjacent topsoil were used in pot culture of two common annual (*Collomia linearis*, *Veronica biloba*) and two perennial (*Rudbeckia occidentalis*, *Senecio serra*) species with high densities in the study area. The purpose was to determine whether the soils affected plant growth. There were six 20-liter containers per species and four plants per container. After two months' growth in the greenhouse, shoots were harvested for oven-dry weight determinations. The statistical significance of differences was evaluated at the 5 percent level.

Results

Plants.— Based on quadrat frequency percentages, the most prevalent species were *Nemophila breviflora* and *Polygonum douglasii* among the annuals and *Bromus carinatus* and *Rudbeckia occidentalis* among the perennials (Table 1). Seed dispersal occurs

TABLE 1. Species frequencies in the quadrats of belt transects in 1970 and on gopher mounds during four years of colonization.

Species	Frequency (%) Quadrat	Frequency (%) Mound
Annual		
Chenopodium album L.	40	26
Collomia linearis Nutt.	43	38
Galium bifolium S. Wats.	34	46
Nemophila breviflora A. Gray	87	82
Polygonum douglasii Greene	68	56
Veronica biloba L.	57	64
Perennial		
Achillea millefolium L.	15	12
Agastache urticifolia (Benth.) Kuntze	13	18
Agropyron trachycaulum (Link) Malte	42	52
Bromus carinatus Hook. & Arn.	83	74
Delphinium occidentale (S. Wats.) S. Wats.	19	20
Elymus glaucus Buckl.	21	34
Phacelia utahensis J. Voss	30	22
Rudbeckia occidentalis Nutt.	95	82
Senecio serra Hook.	40	56
Stellaria jamesiana Torr.	18	34

among the annuals from late June and early July (*N. breviflora*, *V. biloba*) through September (*P. douglasii*, *Chenopodium album*), and toward the end of summer in most of the perennials. Seeds of the species listed in Table 1 are gravity dispersed, except for *S. serra* (wind dispersed) and *Galium bifolium* (adhesive).

GOPHER MOUNDS.— The outline of mounds varied from nearly circular to elliptic, with mean dimensions of 46 by 38 by 9 cm depth. Density of mounds per m^2 ranged from 0.06 to 0.22 and frequency percentages from 5 to 17 in the transects over the four-year period (Table 2). Variance-mean ratios were significantly greater than unity in four samples, indicating clustered distributions, and did not differ significantly in three samples, indicating random distributions (Greig-Smith 1964). Mound clusters were observed in some locations (Fig. 2), usually in midsummer. New mounds occurred in

TABLE 2. Density, frequency, and variance-mean distribution ratios of new mounds in the quadrats of belt transects.

Year	Transect	Density (m^2)	Frequency (%)	Variance-mean ratio
1969	1	0.17	13	1.41*
	2	.16	12	1.44*
1970	1	.06	5	1.50*
	2	.15	12	1.13
1971	1	.12	10	1.08
	2	.22	17	1.27*
1972	1	.09	8	1.11
	2	.19	16	1.05

*Differs significantly from unity.

Fig. 2. Clustered mounds were observed in some locations, usually in midsummer (30 cm ruler in foreground).

different quadrats from year to year, and 40 percent of the quadrats were occupied one or more times over the four-year period.

SOIL.— The soil of new mounds was higher in conductivity and lower in NO_3-N than was adjacent topsoil (Table 3). Since the soil of the mounds had been reworked by gopher action, it was uncompacted and friable as compared with the undisturbed topsoil. However, these chemical and physical differences did not affect the dry weight of shoots of annuals (*C. linearis*, *V. biloba*) or perennials (*R. occidentalis*, *S. serra*) after two months' growth in the greenhouse.

SEEDS.— No seeds were found in new mounds constructed before seed dispersal began; equivalent volumes of adjacent topsoil contained a mean of 36 seeds from nine species. Their weathered appearance suggested that most of these seeds were ungerminated from previous years and probably were not viable. By the end of September when seed dispersal had ceased, the mean count per mound was 37, significantly higher than the 23-seed mean for equivalent columns of adjacent topsoil. Mounds appeared to act as catchment areas; dispersed seeds were often buried in the loose mound soil. Four species (*N. breviflora*, *P. douglasii*, *B. carinatus*, and *R. occidentalis*) accounted for 64 percent of all seeds recovered.

COLONIZATION.— By October of the first year, 8 percent of the new mounds had been colonized by seedlings of three species: *Agastache urticifolia*, *R. occidentalis*, and *V. biloba*. By early summer of the second year, 94 percent of the mounds had been colonized by seedlings; and 100 percent colonization was attained by late spring of the third year. For species occurring on both quadrats and mounds, quadrat frequencies (greater than 10 percent) in transects in the summer of 1970 and frequencies on 50 mounds over the four-year period are given in Table 1. Photographs of representative mounds in various stages of colonization are shown in Figures 3 through 6. Of the 8 annual and 14 perennial species that colonized mounds, *N. breviflora* was the best represented annual and *R. occidentalis* the most prevalent perennial. The correlation coefficients between mound and quadrat frequencies were significant for both annuals

TABLE 3. Results of soil analysis from gopher mounds and adjacent undisturbed topsoil.

Factor	Mound soil	Undisturbed topsoil
Texture	Silt loam	Silt loam
pH	6.2	6.3
Conductivity (mmhos/cm)*	.33	.25
Organic matter (%)	4.7	4.9
P (ppm)	56	65
K (ppm)	466	480
Ca	0	0
NO_3-N (ppm)*	7.2	8.0

*Results differ significantly.

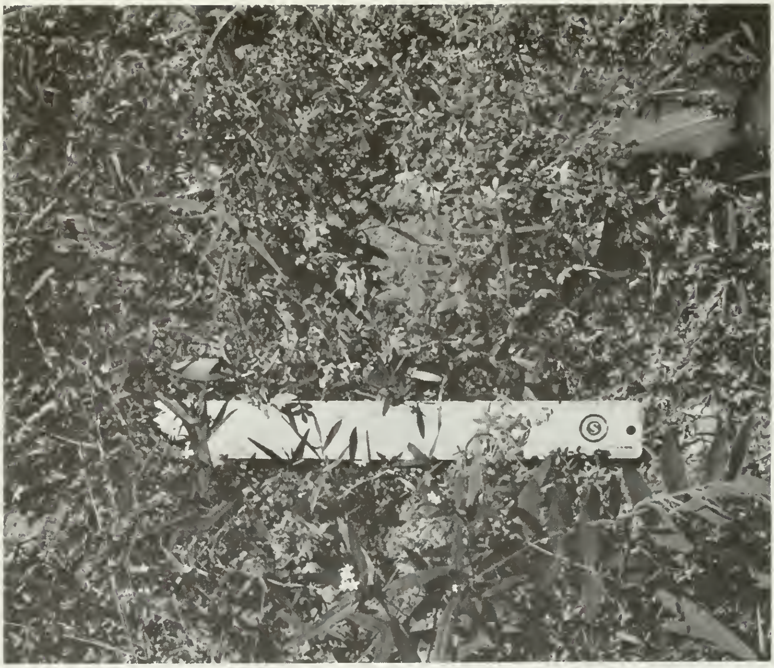

Fig. 3. First-year colonization by *C. linearis*, *N. breviflora*, and *S. jamesiana*.

Fig. 4. Second-year colonization by *N. breviflora*.

Fig. 5. Third-year colonization by *R. occidentalis.*

Fig. 6. Fourth-year colonization by *S. serra.*

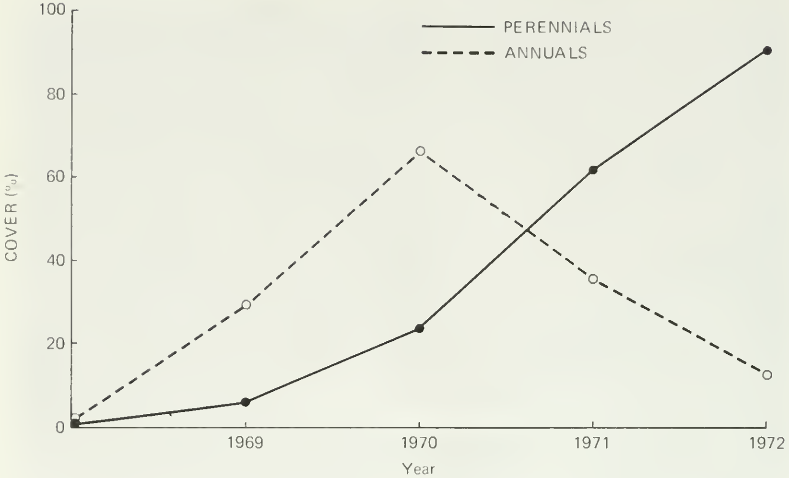

Fig. 7. Percentage of annual and perennial species cover during four years of colonization.

(r = 0.85) and perennials (r = 0.94). This reflects gravity dispersal of seeds to the mounds from adjacent plants, with higher probabilities for colonization by the more widely distributed species in the area.

The revegetation of mounds progressed from an initial dominance by annuals to dominance by perennials—a displacement largely completed within the four-year period (Fig. 7). The annuals reached maximum cover values in the second year and declined thereafter, while cover by perennials rose steadily through the period.

Conclusions

Soil disturbance by gophers creates small and constantly shifting new sites for colonization by plant species in the vicinity. Because new mounds appeared in 40 percent of the quadrats in the sample transects over the four-year period, it seems probable that a large portion of the woodland soil is overturned and laid bare over longer periods. Gopher mounds thus represent a mosaic of sites, constantly shifting in time and space, that individually exist in one of three soil-surface conditions—bare, invaded and dominated by annuals with a few seedlings of perennials, and dominated by perennials with a few persistent annuals in peripheral areas.

In aspen vegetation in Wyoming, Laycock (1958) found that 95 percent of all individual plants growing on gopher mounds during one summer were annuals. He concluded that the persistence and spread of annuals in the community were related to the level of mound-building activity. The constant renewal of bare surfaces keeps the aspen understory open to annuals that otherwise might be eliminated or persist only in low densities.

The constant renewal of bare surfaces also appears to work to the advantage of aggressive perennials, such as *R. occidentalis*, which is known to be an increaser species on aspen range. *Rudbeckia* produces an abundance of seed of high and rapid germinability over a wide temperature range, and there is vigorous seedling growth with relatively low mortality (Florez 1971; Florez and McDonough 1973). *Rudbeckia* appears, along with *B. carinatus*, to take advantage of gopher mounds to increase its importance in the aspen understory vegetation. However, the presence of aggressive species does not negate the effect of gopher activity in maintaining diversity in the species composition of the understory vegetation.

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OBSERVATION OF VOICE IN THE WESTERN COLLARED LIZARD *CROTAPHYTUS COLLARIS BICINCTORES*

Nathan M. Smith[1]

Abstract.— A noosed female *Crotophytus collaris bicinctores* Smith and Tanner voiced an alarm similar to that of *C. wislizeni*.

Lizards, with the exception of the geckos, are considered voiceless (Smith, 1946; Stebbins, 1954). The gecko voice, which can be heard up to one hundred meters, is believed to serve to threaten or warn (Goin & Goin, 1971). Apparently some members of Iguanidae possess a weak voice that also serves to threaten when provoked. Jorgensen, Orton, and Tanner (1963) noted under laboratory conditions that the leopard lizard *Crotaphytus wislizeni* Baird and Girard changes its usual hissing to a high-pitched squeal before a vicious attack of its agitator. They concluded that the voice was characteristic of the Nevada Test-Site population. In late July 1970, a noosed male lizard and a noosed female *wislizeni* squealed and attempted to bite as they were removed from the noose. They were captured approximately six miles north of Wendell, Gooding County, Idaho, just off state highway 46.

On the same collecting trip, a few days later, a captured young female western collared lizard, *Crotaphytus collaris bicinctores* Smith and Tanner (BYU 3113), made a squealing sound while being released from the noose. The squeal resembled that of the *C. wislizeni*. To my knowledge this is the first record of a distinct voice for this species. The capture was made on a hot afternoon about eight miles south of Bruneau, Owyhee County, Idaho, on the east side of the Bruneau River.

At this time a comparative study of several members of the family Iguanidae and *Coleonyx variegatus* Baird is underway to describe anatomical voice mechanisms in these taxa.

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[1] Graduate Department of Library and Information Sciences, Brigham Young University, Provo, Utah 84602.

NEW SYNONYMY AND RECORDS OF AMERICAN BARK BEETLES (COLEOPTERA: SCOLYTIDAE)

Stephen L. Wood[1]

ABSTRACT.— New synonymy affecting American Scolytidae is proposed as follows: *Acanthotomicus granulatus* (Ferrari), n. comb. (= *Mimips uncinatus* Wood), *Araptus deyrollei* (Blandford), new comb. (= *Araptus insinuatus* Wood), *Cnesinus adustus* Schedl (= *Cnesinus atrodeclivis* Wood), *Corthylocurus mexicanus* (Schedl), n. comb. (= *Corthylus cylindricus* Schedl), *Corthylus collaris* Blandford (= *Corthylus splendens* Wood), *Corthylus comatus* Blandford (= *Corthylus spendidus* Bright), *Corthylus uniseptis* Schedl (= *Corthylus reburrus* Bright.) *Dendrocranulus carbonarius* (Ferrari), n. comb. (= *Xylocleptes floridensis* Hopkins, *Xylocleptes anonae* Hopkins), *Dendrocranulus maurus* (Blandford), n. comb. (= *Dendrocranulus huehuetanus* Schedl), *Dendroctonus valens* LeConte (= *Dendroctonus rhizophagus* Thomas and Bright), *Gymnochilus consocius* (Blandford), n. comb. (= *Problechilus trimaculatus* Schedl), *Gymnochilus minor* (Blandford), n. comb. (= *Problechilus varius* Schedl), *Gymnochilus zonatus* Eichhoff (= *Problechilus freyi* Schedl), *Hypothenemus areccae* (Hornung) (= *Hypothenemus vafer* Blandford), *Hypothenemus eruditus* Westwood (= *Cryphalus obscurus* Ferrari), *Micracis grandis* Schedl (= *Micracis costaricensis* Wood), *Micracis swainei* Blackman (= *Micracis robustus* Schedl, *Micracis pygmaeus* Schedl), *Microcorthylus parvulus* Ferrari (= *Pterocyclon exile* Eichhoff), *Monarthrum bicolor* (Ferrari), n. comb. (= *Corthylus signatus* Ferrari, *Phthorius edentatus* Hagedorn), *Monarthrum consimile* (Blandford), n. comb. (= *Pterocyclon pseudosulcatum* Schedl), *Monarthrum egenum* (Blandford), n. comb. (= *Brachyspartus bisetosus* Schedl), *Monarthrum fimbraticorne* (Blandford) (= *Pterocyclon turbinatum* Schedl), *Monarthrum gnarum* (Schedl), n. comb. (= *Amphicranus spinatus* Bright), *Monarthrum validum* (Ferrari), n. comb. (= *Amphicranus mexicanus* Eggers, *Pterocyclon jalapae* Schedl), *Phloeoborus scaber* Erichson (= *Phloeoborus opacithorax* Schedl), *Phloeosinus serratus* (LeConte) (= *Phloeosinus rugosus* Swaine), *Phloeotribus setulosus* Eichhoff (= *Phloeotribus rudis* Eichhoff, *Phloeotribus sodalis* Blandford, *Phloeotribus bolivianus* Eggers), *Pycnarthrum reticulatum* Schedl (= *Pycnarthrum fici* Wood), *Scolytodes rugicollis* (Schedl), n. comb. (= *Scolytodes plicatus* Wood), *Xylosandrus morigerus* (Blandford) (= *Xyleborus luzonicus* Eggers). New names are proposed as follows: *Araptus decorulus* for *Araptus decorus* Wood, *Cnemonyx nigrellus* for *Loganius niger* Wood, *Monarthrum bicoloratum* for *Monarthrum bicolor* Wood. *Araptus sobrinus*, n. sp. (Mexico), and *Dendroctonus vitei*, n. sp. (Guatemala), are named as new to science. *Dendroctonus mexicanus* Hopkins is removed from synonymy.

During the preparation of a taxonomic monograph of the Scolytidae of North and Central America, the unpublished synonymy summarized in the above abstract and treated on the following pages was encountered. In order to stabilize nomenclature and fix established names, several lectotypes are designated.

Specimens or series referred to in the discussion are in my collection unless a definite statement indicates otherwise. The species are arranged in alphabetical order except that those described as new to science are presented at the end of the article.

Acanthomicus granulatus (Ferrari), n. comb.

Xylocleptes granulatus Ferrari, 1867, Die Forst- und Baumzuchtschädlichen

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[1] Department of Zoology, Brigham Young University, Provo, Utah 84602. Scolytidae contribution No. 54

Borkenkäfer, p. 40 (Lectotype, male; Venezuela, probably at Colonia Tovar; Vienna Mus., present designation).

Mimips uncinatus Wood, 1971, Brigham Young Univ. Sci. Bull., Biol. Ser. 15(3):41 (Holotype, male; Colonia Tovar, Aragua, Venezuela; Wood Coll.). *New synonymy*

The type series of four specimens of *Xylocleptes granulatus* Ferrari collected by Moritz in 1858 was compared directly to the type series of *Mimips uncinatus* Wood. They are identical in every respect. It is a common species in the vicinity of the Moritz home at Colonia Tovar; it was not found in the Caracas area where Moritz lived at an earlier date.

Araptus decorulus, n. n.

Araptus decorus Wood, 1974 (nec. Bright, 1972), Brigham Young Univ. Sci. Bull., Biol. Ser. 19(1):47 (Holotype, male; Rincon de Osa, Puntarenas, Costa Rica; Wood Coll.).

Araptus decorus Wood is a junior homonym of *Neodryocoetes decorus* Bright (1972, Bull. Inst. Jamaica, Sci. Ser. 21:96), because the genera to which they belong have been synonymized. The new name *Araptus decorulus* is proposed as a replacement for *decorus* Wood.

Araptus deyrollei (Blandford), n. comb.

Pityophthorus deyrollei Blandford, 1904, Biol. Centr. Amer., Coleopt. 4(6):245 (Lectotype, male; Mexico; British Mus. Nat. Hist., present designation).

Araptus insinuatus Wood, 1974, Brigham Young Univ. Sci. Bull., Biol. Ser. 19(1):43 (Holotype, male; Guatemala; Wood Coll.). *New synonymy*

Blandford named *Pityophthorus deyrollei* from two syntypic specimens taken in Mexico. Unfortunately these specimens were not available for loan at the time my study of this genus was made for the monograph, and I depended on specimens identified by other authors for my concept of Blandford's species. When the types were studied it was found that *deyrollei* is identical to *Araptus insinuatus* Wood. The first specimen in Blandford's series, a male, is here designated as the lectotype of *deyrollei*.

Cnemonyx nigrellus, n. n.

Loganius niger Wood, 1961 (nec. Eggers, 1933), Great Basin Nat. 21:95 (Holotype, female; 26 km W Tehuantepec, Oaxaca, Mexico; Wood Coll.).

Both *Ceratolepsis niger* Eggers (1933, Trav. Lab. Ent. Paris, Mem. 1:13) and *Loganius niger* Wood have been transferred to the genus *Cnemonyx* (Wood, 1972, Bull. Ent. Res. 62:344), thus creating homonymy. The new name *nigrellus* is proposed to replace the junior name, *niger* (Wood).

Schedl (1962, Beitr. Ent. 12:486) previously transferred *Ceratolepsis niger* Eggers to the genus *Camptocerus* and thus created secondary homonymy with *Camptocerus niger* (Fabricius). He then renamed Eggers's species *Camptocerus nigricans* Schedl. However, the type of the Eggers species is not congeneric with the type of the Fabricius species; consequently, the replacement name *nigricans* must be rejected and Eggers name restored to its original position.

Cnesinus adustus Schedl

Cnesinus adustus Schedl, 1949, Rev. Brasil. Biol. 9:266 (Lectotype, female; Turrialba, Costa Rica; Schedl Coll., present designation).

Cnesinus atrodeclivis Wood, 1968, Great Basin Nat. 28:108 (Holotype, female; Zamorano, Morazan, Honduras: Wood Coll.). *New synonymy*

Schedl named *adustus* from a syntypic series of females. The specimen in his collection labeled "Holotype" is here designated as the lectotype of the species. This lectotype was compared directly to the holotype of *atrodeclivis* Wood; only one species is represented by this material.

Corthylocurus mexicanus (Schedl), n. comb.

Brachyspartus mexicanus Schedl, 1950. Dusenia 1:163 (Holotype, male; Comitan, Chiapas, Mexico; Schedl Coll.).

Corthylus cylindricus Schedl, 1963, Ent. Arb. Mus. Frey 14:164 (Holotype, female; Jalapa, Veracruz, Mexico; Schedl Coll.). *New synonymy*

Several long series of this species were taken in Mexico, Guatemala, Costa Rica, and Panama. A male and a female in my collection taken with a series from the same branch were compared directly to the holotypes of *Brachyspartus mexicanus* Schedl and *Corthylus cylindricus* Schedl and were identical in all respects. Since these two names apply only to the opposite sexes of the same species, the name *cylindricus* must be placed in synonymy.

Corthylus collaris Blandford

Corthylus collaris Blandford, 1904, Biol. Centr. Amer. Coleopt. 4(6):261 (Holotype, male; Cerro Zunil, Guatemala; British Mus. Nat. Hist.).

Corthylus splendens Wood, 1967. Great Basin Nat. 27:138 (Holotype, female; 16 km SE Cartago, Cartago, Costa Rica; Wood Coll.). *New synonymy*

The holotypes of *collaris* Blandford and *splendens* Wood were examined. In addition, 43 specimens from Guatemala and 109 specimens from Costa Rica were studied. The northern and southern material can be distinguished by the small differences outlined in the description of *splendens*. However, in the absence of material from intermediate areas, it appears advisable to place *splendens* in synonymy until the existence of geographical races can be more conclusively demonstrated.

Corthylus comatus Blandford

Corthylus comatus Blandford, 1904, Biol. Centr. Amer., Coleopt. 4(6):258 (Holotype, female; Cerro Zunil, Guatemala: British Mus. Nat. Hist.).

Corthylus splendidus Bright, 1972. Canadian Ent. 104:1371 (Holotype, female; 5.6 km or 3.5 miles S Suchixtepec, Oaxaca, Mexico; Canadian Nat. Coll.). *New synonymy*

The holotypes of *comatus* Blandford and *splendidus* Bright were compared to my material from Mexico, Guatemala, Costa Rica, and Panama. I am unable to find any character that provides a means of subdividing this common species; consequently, the name *splendidus* is placed in synonymy.

Corthylus uniseptis Schedl

Corthylus uniseptis Schedl, 1961, Pan Pacific Ent. 34:229 (Holotype, male; Cordoba, Veracruz, Mexico; California Acad. Sci.).

Corthylus reburrus Bright, 1972, Canadian Ent. 104:1375 (Holotype, female; Palenque Ruins, Chiapas, Mexico; Canadian Nat. Coll.). *New synonymy*

The male holotype of *uniseptis* Schedl was compared directly to a topotypic male paratype of *reburrus* Bright. Except for the slightly lighter color of the dark brown *uniseptis* type I see no difference between the two specimens. Since the slight degree of color difference has no taxonomic value in this section of the genus, only one species is represented by these names.

Dendrocranulus carbonarius (Ferrari), n. comb.

Xylocleptes carbonarius Ferrari, 1867, Die Forst- und Baumzuchtschädlichen Borkenkäter. p. 41 (Holotype, male; Cuba; Vienna Mus.).

Xylocleptes floridensis Hopkins, 1915, U.S. Dept. Agric. Rept. 99:43 (Holotype, female; Biscayne Bay, Florida; U.S. Nat. Mus.). *New synonymy*

Xylocleptes anonae Hopkins, 1915, U.S. Dept. Agric. Rept. 99:43 (Holotype, female; Florida; U.S. Nat. Mus.). *New synonymy*

The holotypes of *carbonarius* (Ferrari), *floridensis* (Hopkins), and *anonae* Hopkins were compared directly to my series from Cuba. Only one species is represented by these names.

Dendrocranulus maurus (Blandford)

Dryocoetes maurus Blandford, 1898, Biol. Centr. Amer., Coleopt. 4(6):191 (Holotype, female; El Tumbador, San Marcos, Guatemala; British Mus. Nat. Hist.).

Dendrocranulus huehuetanus Schedl, 1940, An. Esc. Nac. Cienc. Biol., Mexico 1:344 (Lectotype, male; Huehuetán, Chiapas, Mexico; Schedl Coll., present designation). *New synonymy*

The male syntype from Huehuetán that was labeled by Schedl as the male "type" is here designated as the lectotype of *Dendrocranulus huehuetanus* Schedl. That lectotype was compared directly to my series of *maurus* (Blandford) which was compared directly to the holotype of this species in 1965. Since they represent the same species, Schedl's name must be placed in synonymy.

Dendroctonus valens LeConte

Dendroctonus valens LeConte, 1860, Pacific R. R. Expl. 5(2):59 (Holotype, male; San Francisco, California; Mus. Comp. Zool.).

Dendroctonus rhizophagus Thomas and Bright, 1970, Canadian Ent. 102:479 (Holotype, male; 16 km or 10 miles SW El Salto, Durango, Mexico; Canadian Nat. Coll.). *New synonymy*

The name *rhizophagus* Thomas and Bright was proposed for a long series of small specimens taken from the roots of pine seedlings during a severe drought near El Salto, Durango, in 1964. In 1965, I was unable to find specimens in seedlings at the same locality. All of the *Dendroctonus* taken in the area by me were *valens* LeConte of normal or near normal size. As with other Mexican *valens*, the El Salto specimens may construct parental tunnels that are linear, of the cave type, or a combination of these, and the frontal area of the head may be quite different from that seen in specimens from the United States and Canada. After examining the holotype and several paratypes of *rhizophagus*, the holotype and several thousand other specimens of *valens*, including several hundred from Mexico, Guatemala, and Honduras, I am able to recognize only one species. There is a certain amount of variability in the frons in all areas, but these intergrade to such a degree that geographical races are difficult if not impossible to characterize.

Gymnochilus consocius (Blandford), n. comb.

Problechilus consocius Blandford, 1897, Biol. Centr. Amer., Coleopt. 4(6):171 (Holotype, male; Cerro Zunil, Guatemala; British Mus. Nat. Hist.).

Problechilus trimaculatus Schedl, 1935, Arch. Instit. Biol. Veget. 2:91 (Holotype, female; Venezuela, probably Colonia Tovar; Schedl Coll.). *New synonymy*

The holotypes of *consocius* Blandford and *trimaculatus* Schedl were compared to 102 specimens of this species from Venezuela. Approximately 90 percent of the specimens match the characters of *consocius* very well. In the type of *trimaculatus* the discal striae are not at all impressed and the strial punctures are much smaller and less strongly impressed than expected and the color is more nearly reddish brown. About 10 percent of my Venezuelan material exhibits variations that completely bridge the gap in characters between the extremes. For this reason, Schedl's name must be placed in synonymy.

Gymnochilus minor (Blandford), n. comb.

Problechilus minor Blandford, 1897, Biol. Centr. Amer. Coleopt. 4(6):172 (Syntypes; Guatemala City, Guatemala; British Mus. Nat. Hist.).

Problechilus varius Schedl, 1951, Dusenia 2:86 (Holotype, female; Mexico; Schedl Coll.). *New synonymy*

Eight syntypes of *minor* (Blandford) and the holotype of *varius* Schedl were examined and compared to several series in my collection. The holotype of *varius* is a typical female of this species.

Gymnochilus zonatus Eichhoff

Gymnochilus zonatus Eichhoff, 1867, Berliner Ent. Zeitschr. 11:399 (Holotype, sex?; Colombia; lost with Hamburg Mus.).

Meringopalpus fallax Hagedorn, 1905, Bull. Mus. Paris 10:547 (Holotype, male; Venezuela, by Moritz, presumably Caracus or Colonia Tovar; Paris Mus.); Eggers, 1932, Wiener Ent. Zeit. 49:226. *Synonymy*

Problechilus freyi Schedl, 1966, Ent. Arb. Mus. Frey 17:103 (Holotype, female; Rancho Grande near Maracay, Aragua, Venezuela; Frey Mus.). *New synonymy*

Eggers compared the holotypes of *Gymnochilus zonatus* Eichhoff and *Meringopalpus fallax* Hagedorn and concluded that they were synonymous. Since the type of *zonatus* (3.3 mm) was subsequently lost in the destruction of the Hamburg Museum, Eggers's observation is accepted as correct. The male holotype of *fallax* (3.2 mm) and the female holotype of *freyi* (Schedl) (2.8 mm) were examined and were found to represent the same species. This species is almost identical to *consocius* (Blandford), but it is distinguished by the slightly larger size, by the less strongly impressed male frons, by the more strongly convex female frons, by the reticulate surface among the asperities on the anterior half of the pronotum, by the more coarsely punctured basal fourth of the pronotum, and by the slightly longer elytral vestiture.

Hypothenemus areccae (Hornung)

Bostrichus areccae Hornung, 1842, Stett. Ent. Zeit. (Lectotype, female; in Betel palm nuts presumably of East Indian origin; Berlin Zool. Mus., present designation).

Hypothenemus vafer: Wood, 1972. Great Basin Nat. 32:52.

As indicated in the above reference to my recent partial review of the synonymy of this species, there has been much confusion concerning the identity of *areccae* Hornung. The confusion was created by Eggers when he labeled specimens of both *areccae* and *eruditus* Westwood as having been compared to the "type." Two syntypes of of *areccae* in the Berlin Zoologisches Museum are of the species I have referred to as *areccae* (=*vafer* Blandford, *fungicola* Eggers, *hispidus* Eggers, etc.). The first of those syntypes has the impressed frons partly obscured by frass; therefore, the second syntype is here designated as the lectotype of *areccae* Hornung, as indicated above.

This species is common in seeds and fruits, although it is also able to breed in twigs, bark, and other materials. Apparently it is native to the Indo-Malayan region; *eruditus* is less common in seeds and fruits and was not introduced into the Indo-Malayan region until about a half century after *areccae* was described.

Hypothenemus eruditus Westwood

Hypothenemus eruditus Westwood, 1836, Trans. Ent. Soc. London 1(1):34 (Syntypes; England).

Cryphalus obscurus Ferrari, 1867, Die Forst- und Baumzuchtschädlichen Borkenkäfer, p. 17 (Holotype, female; Cuba; Vienna Mus.). *New synonymy*

Although *Cryphalus obscurus* Ferrari has been considered a junior homonym of a Fabricius species, the species has never been clarified. The female holotype was examined. It has the entire frontal area immersed in glue, but other features clearly indicate that it is a normal specimen of *eruditus* Westwood.

Micracis grandis Schedl

Micracis grandis Schedl, 1948, Rev. de Ent. 19:575 (Holotype, female; San José de Ixtepec, Chiapas, Mexico; Schedl Coll.).

Micracis costaricensis Wood, 1969, Brigham Young Univ. Sci. Bull., Biol. Ser. 10(2):39 (Holotype, female; Volcan Poas, Heredia, Costa Rica; Wood Coll.). *New synonymy*

The female holotypes of *grandis* Schedl and *costaricensis* Wood were compared directly to one another and to series from Honduras and Costa Rica. Only one species is represented by this material.

Micracis swainei Blackman

Micracis swainei Blackman, 1920. Mississippi Agric. Expt. Sta. Tech. Bull. 9:32 (Lectotype, female; Iuka, Mississippi; U.S. Nat. Mus., designated by Wood, 1963, Great Basin Nat. 33:178).

Micracis robustus Schedl, 1948. Rev. de Ent. 19:576 (Holotype, male; Esmeralda, Chiapas, Mexico; Schedl Coll.). *New synonymy*

Micracis pygamaeus Schedl, 1948, Rev. de Ent. 19:577 (Holotype, male; Huehuetán, Chiapas, Mexico; Schedl Coll.). *New synonymy*

The male holotypes of *robustus* Schedl and *pygamaeus* Schedl were compared directly to male specimens from the same series as my homotypes of *swainei* Blackman; they are of the same species. More than 500 specimens of this species from New York to Honduras were examined. The holotype of *robustus* is of normal size (1.8 mm) and is badly rubbed; the holotype of *pygamaeus* is near the lower limits of size (1.4 mm) and has the vestiture in good condition. The "second specimen" of *pygamaeus*, mentioned in the original description, is a female with the epistomal brush of setae that is characteristic of this species.

Microcorthylus parvulus Ferrari

Microcorthylus parvulus Ferrari, 1867, Die Forst- und Baumzuchtschädlichen Borkenkäfer, p. 58 (Holotype, male; Venezuela, probably Colonia Tovar; Vienna Mus.).

Pterocyclon exile Eichhoff, 1878, Mém. Soc. Roy. Sci. Liége (2) 8:451 (Holotype, male; Nova Grenada; Brussels Mus.). *New synonymy*

The male holotypes of *parvulus* Ferrari and *exile* (Eichhoff) were examined and compared directly to my material. In all, 159 specimens from Costa Rica to Colombia and Venezuela were examined. Following a detailed study of the genus from these and neighboring area, it was concluded that only one species was represented by this material. Minute variation occurs on the frons; other characters are constant.

Monarthrum bicolor (Ferrari), n. comb.

Corthylus bicolor Ferrari, 1867. Die Forst- und Baumzuchtschädlichen Borkenkäfer, p. 56 (Holotype, female; Venezuela, probably Colonia Tovar; Vienna Mus.).

Corthylus signatus Ferrari, 1867. Die Forst- und Baumzuchtschädlichen Borkenkäfer, p. 56 (Syntypes, male; Venezuela, probably Colonia Tovar; Vienna Mus.). *New synonymy*

Pthorius edentatus Hagedorn, 1905, Bull. Mus. Paris 10:549 (Holotype, male; Colonia Tovar, Venezuela; Paris Mus.). *New synonymy*

The holotypes of *bicolor* (Ferrari) and *edentatus* (Hagedorn) and the two male syntypes of *signatus* Ferrari were examined and compared directly to my material. The female frons is very distinctive, thus making this species easily identified. It is common at high elevations in Colombia and Venezuela. Since *bicolor* and *signatus* were taken in Venezuela in 1858 by Moritz, the type localities apparently are at or near the Moritz home at Colonia Tovar, Aragua, Venezuela. The male declivity varies slightly in certain series in its steepness and in the abruptness of the basal and lateral margins. Blandford's label on the syntypes of *signatus* erroneously identified them as *Monarthrum chapuisii* Kirsch.

Monarthrum bicoloratum, n. n.

Monarthrum bicolor Wood, 1968 (nec. Ferrari, 1867), Great Basin Nat. 28:4 (Holotype, male; Mile 10 on the Bartica-Potaro Road, British Guiana; British Mus. Nat. Hist.).

The transfer of *Corthylus bicolor* Ferrari to *Monarthrum* (above) made a junior homonym of *Monarthrum bicolor* Wood. The new name *bicoloratum* is proposed as a replacement name for *bicolor* Wood.

Monarthrum consimile (Blandford), n. comb.

Pterocyclon consimile Blandford, 1904, Biol. Centr. Amer., Coleopt. 4(6):275 (Holotype, female; Volcan de Chiriqui, Panama; British Mus. Nat. Hist.).

Pterocyclon pseudosulcatum Schedl, 1935, Rev. de Ent. 5:348 (Holotype, male; Vara Blanca, Heredia, Costa Rica; Schedl Coll.). *New synonymy*

Series of specimens containing both males and females from the type localities of both *consimile* (Blandford) and *pseudosulcatum* (Schedl) were collected and compared to the holotypes of these species. The holotype of *consimile* is the female, and *pseudosulcatum* is the male of the same biological species; consequently, Schedl's name is placed in synonymy.

Monarthrum egenum (Blandford), n. comb.

Pterocyclon egenum Blandford, 1904, Biol. Central Amer., Coleopt. 4(6):280 (Holotype, female; San Juan, Verapaz, Guatemala; British Mus. Nat. Hist.).

Brachyspartus bisetosus Schedl, 1954, Dusenia 5:38 (Syntypes, female; Rio Caraguata, Matto Grosso, Brazil; Schedl Coll., etc.). *New synonymy*

This species is common in *Inga* and other leguminous trees from Guatemala to Brazil. Females from Costa Rica were compared to the holotype of *egenum* (Blandford), to two topotypic female syntypes of *bisetosus* (Schedl), and to several series from Costa Rica, Colombia, and Brazil. Only one species is represented by this material. Schedl's males of *bisetosus* actually are females with frontal setae; his females lack part or all of these setae.

Monarthrum fimbraticorne (Blandford)

Pterocyclon fimbraticorne Blandford, 1904, Biol. Centr. Amer. Coleopt. 4(6):285 (Holotype, female; Purula, Verapaz, Guatemala; British Mus. Nat. Hist.).

Pterocyclon turbinatum Schedl, 1961, Pan Pacific Ent. 37:230 (Holotype, male; Cordoba, Veracruz, Mexico; California Acad. Sci.). *New synonymy*

The female holotype of *fimbraticorne* (Blandford) was compared to representatives of several series of this species from Costa Rica. Additional long series have been taken in Venezuela and one additional specimen was seen from Guatemala. Males of these series were compared directly to the male holotype of *turbinatum* (Schedl). The type of *turbinatum* is rather small for this species, but males of similar small size occur throughout the range of this species.

Monarthrum gnarum (Schedl), n. comb.

Pterocyclon gnarum Schedl, 1950, Dusenia 1:169 (Holotype, female; Mexico; Schedl Coll.).

Amphicranus spinatus Bright, 1972, Canadian Ent. 104:1383 (Holotype, male; 15 km or 32 miles S Valle Nacional, Oaxaca, Mexico; Canadian Nat. Coll.). *New synonymy*

The holotype of *Pterocyclon gnarum* Schedl is a female, not a male as stated in the original description. This holotype was compared to a topotypic female paratype of *Amphicranus spinatus* Bright and to another female from Hidalgo. The holotype, allotype, and other paratypes of *spinatus* were also examined. It is now clear that all represent one species that is very closely related to *praeruptum* (Blandford).

Monarthrum validum (Ferrari), n. comb.

Corthylus validus Ferrari, 1867, Die Forst- und Baumzuchtschädlichen Borkenkäfer, p. 55 (Lectotype, male; Mexico; Vienna Mus., present designation).

Amphicranus mexicanus Eggers, 1931, Ent. Blätt. 27:18 (Holotype, male; Mexico; Berlin Zool. Mus.). *New synonymy*

Pterocyclon jalapae Schedl, 1939, Mitt. Münchn. Ent. Ges. 29:584 (Holotype, male; Jalapa, Veracruz, Mexico; Schedl Coll.). *New synonymy*

The name *Corthylus validus* Ferrari was based on a male from Mexico, and a female from Venezuela. Blandford (1904, Biol. Centr. Amer., Coleopt. 4(6):271) transferred the female to another species. The male is here designated as the lectotype of *validus*. This lectotype and the male holotype of *Amphicranus mexicanus* Eggers were compared directly to my series from Costa Rica. Only one species is represented by this material; it occurs from Mexico to Panama. Later, my Costa Rican specimens were compared directly to the holotype of *Pterocyclon jalapae* Schedl and were also found to be identical.

Phloeoborus scaber Erichson

Phloeoborus scaber Erichson, 1836, Archiv. Naturgesch. 2(1):55 (Syntypes; Brazil; Berlin Zool. Mus.).

Phloeoborus opacithorax Schedl, 1940, Arb. Morph. Taxon. Ent. Berlin-Dahlem

7:205 (Syntypes; Panzos, Guatemala; Institut für Pflanzenschutzforschung Kleinmachnow). *New synonymy*

The female syntypes of *opacithorax* Schedl have the eyes slightly more narrowly spaced and the elytral vestiture stouter than do the types of *scaber* Erichson. The spacing of the eyes varies throughout the range of this species. The elytral vestiture becomes longer and stouter over a gradual cline from northern South America to southern Mexico, although there is considerable variation within series; and the elytral crenulations also become narrower, more numerous, and confused over the same cline. While Brazilian and Guatemalan specimens may be rather strikingly different, intergradation is such that distinctive races cannot be separated.

Phloeosinus serratus (LeConte)

Hylesinus serratus LeConte, 1868, Trans. Amer. Ent. Soc. 2:170 (Holotype, male; Middle States; Mus. Comp. Zool.).

Phloeosinus rugosus Swaine, 1917, Dom. Canada Dept. Agric. Ent. Br. Tech. Bull. 14(1):9 (Lectotype, female; Scaffold Meadow, Sequoia N.F., California; Canadian Nat. Coll., 9259, designated by Bright, 1967, Canadian Ent. 99:677). *New synonymy*

The female lectotype of *rugosus* Swaine lacks tubercles on declivital interstriae 2; it is also rather small (2.6 mm). The two female paratypes in the Canadian National Collection both have tubercles on declivital interstriae 2. It is clearly evident that all three specimens fall within the range of variation of *serratus* (LeConte); consequently, *rugosus* must be placed in synonymy under the older name.

Phloeotribus setulosus Eichhoff

Phloeotribus setulosus Eichhoff, 1868, Berliner Ent. Zeitschr. 12:149 (Lectotype, male; Colombia; Brussels Mus., designated by Wood, 1973, Great Basin Nat. 33:182).

Phloeetribus rudis Eichhoff, 1868, Berliner Ent. Zeitschr. 12:149 (Syntypes?: male; Brazil; lost with Hamburg Mus.?). *New synonymy*

Phloeotribus sodalis Blandford, 1897, Biol. Centr. Amer., Coleopt. 4(6):168 (Lectotype, male; Cerro Zunil, Guatemala; British Mus. Nat. Hist., present designation). *New synonymy*

Phloeotribus bolivianus Eggers, 1933, Trav. Lab. d'Ent. Mus. Nat. d'Hist. Nat. Paris, Mem. 1:5 (Holotype, male; Cochabamba, Bolivia; U.S. Nat. Mus.). *New synonymy*

The holotypes of *setulosus* Eichhoff and *bolivianus* Eggers, the lectotype of *sodalis* Blandford, and two specimens of *rudis* Eichhoff that were identified by Eichhoff and deposited in the Chapuis collection were all compared directly to series of this species in my collection and were found to represent one species. The two specimens of *rudis* probably are unmarked syntypes and evidently represent the only reasonably authentic representatives of *rudis* in existence. The first specimen in Blandford's series, a male from Cerro Zunil, is here designated as the lectotype of *sodalis* Blandford. This specimen was previously labeled as the type, but it was never so designated.

Pycnarthrum reticulatum Schedl

Pycnarthrum reticulatus Schedl, 1940, An. Esc. Nac. Cienc. Biol., Mexico 1:355 (Lectotype, female; Tonalá, Chiapas, Mexico; Schedl Coll., present designation).

Pycnarthrum fici Wood, 1971, Brigham Young Univ. Sci. Bull., Biol. Ser. 15(3): 11 (Holotype, male; 5 km W El Pino, Merida, Venezuela; Wood Coll.). *New synonymy*

A female of *reticulatus* [sic] Schedl in the Schedl collection, from Tonalá, Chiapas, has been labeled as the "Type" of this species by its author, although it has never been so designated. I here designate that female as the lectotype of *reticulatus.* This lectotype was compared directly to the holotype of *fici* Wood. Only one species is represented by this material.

Scolytodes rugicollis (Schedl), n. comb.

Hexacolus rugicollis Schedl, 1940, Arb. Morph. Taxon. Ent. Berlin-Dahlem 7:205 (Lectotype, female; Hamburgfarm on Río Reventazon, Limón, Costa Rica; Schedl Coll., present designation).

Scolytodes plicatus Wood, 1969, Brigham Young Univ. Sci. Bull., Biol. Ser. 10(2):21 (Holotype, female; 25 km SE Guapiles, Limón, Costa Rica; Wood Coll.). *New synonymy*

Schedl named *Hexacolus rugicollis* from a syntypic male and a female mounted together on the same microcard. In the original description the sexes were reversed. I designate the female syntype, marked on the microcard by a male symbol, as the lectotype of Schedl's species. This lectotype was compared directly to the holotype of *Scolytodes plicatus* Wood and was found to represent the same species.

Xylosandrus morigerus (Blandford)

Xyleborus morigerus Blandford, 1894, Insect Life 6:264 (Syntypes; intercepted in England from *Dendrobium* orchids imported from New Guinea; British Mus. Nat. Hist.).

Xyleborus luzonicus Eggers, 1923, Zool. Meded. 7:174 (Lectotype, female; Mt. Makiling, Insel Luzon, Philippinen; U.S. Nat. Mus.; designated by Anderson and Anderson, 1971, Smithsonian Contrib. Zool. 94:18). *New synonymy*

Six syntypes of *morigerus* (Blandford) were compared directly to my specimens; these were later compared directly to the lectotype of *luzonicus* Eggers. Only one species is represented by this material.

Araptus sobrinus, n. sp.

This species is distinguished from *schwarzi* (Blackman) by the weakly convex, more sparsely punctured female frons, by the different elytral vestiture, and by the more deeply, more broadly sulcate declivity.

FEMALE.— Length 2.3 mm (paratypes 1.9-2.3 mm), 2.5 times as long as wide; color reddish brown.

Frons weakly convex; surface almost smooth, punctures fine, moderately abundant; vestiture of fine, short, moderately abundant hair; frons about as in male *schwarzi* except for epistomal area.

Pronotum about as in *schwarzi*, except disc with more numerous impressed points and punctures slightly larger and more nearly circular (punctures in *schwarzi* oval to crescent-shaped).

Elytra as in *schwarzi* except with abundant impressed points (usually absent in *schwarzi*), declivity more deeply, more broadly impressed, and vestiture greatly reduced. Strial setae entirely absent, interstrial setae rare on disc, sparse on declivity except at sides. (In *schwarzi* interstrial rows of erect setae usually extend to elytral base and small strial hairs occur on disc and declivity.)

MALE.— Similar to female, except frons more strongly convex above, slightly impressed on lower half; epistoma broadly, shallowly emarginate about as in male *schwarzi*.

TYPE LOCALITY.— Siguatepec, Honduras.

TYPE MATERIAL.— The female holotype, male allotype, and 10 paratypes were taken at the type locality on 25-V-1972, in rust cones on *Pinus oocarpa*, by R. Billings.

The holotype, allotype, and paratypes are in my collection.

Dendroctonus mexicanus Hopkins

This species was placed in synonymy (Wood, 1963, Great Basin Nat. 23:41) under *Dendroctonus frontalis* Zimmermann, because series of this species from the southwestern United States could not be distinguished from variable series from Honduras. When it was recently noticed that two separate emergences took place in Honduras from the same logs, it became apparent that two distinct biological species occur in Honduras and that both were responsible for the epidemic of 1964. Once this event was apparent, and pure samples from each emergence were studied, the variable Honduras material was easily sorted into two groups, one having poorly developed to obsolete interstrial crenulations (*frontalis*) and a slightly larger, darker form with moderate to rather coarse interstrial crenulations. The former, *frontalis*, tends to occur at low elevations, less than 700 m, the latter at elevations above 700 m. They may occur in the same trees in the area of altitudinal overlap. The latter form appears to be of the same species as occurs throughout Mexico; consequently, the name *mexicanus* is removed from synonymy to designate it. Specimens from Arizona and New Mexico appear to be intermediate but are tentatively grouped with *frontalis*. Ultimately it may be necessary to reduce *mexicanus* to subspecific rank, due to intergradation in the northern area, even though the two populations behave as valid species in Honduras.

In 1970 I received specimens of an additional Guatemalan species in the *frontalis* complex, from E. W. Clark. Since then Dr. J. P. Vité and his associates have investigated Mexican and Central American *Dendroctonus* more thoroughly. Their results are being published elsewhere. It appears that *mexicanus* originally extended only as far south as Chiapas and was replaced in Guatemala by *vitei*, described below. Both *mexicanus* and *frontalis* appear to have been introduced into Honduras at a comparatively recent date, where they jointly caused epidemic losses of pine a decade ago. Apparently neither species has penetrated the range of *vitei*.

Dendroctonus vitei, n. sp.

This species is distinguished from *mexicanus* Hopkins by the slightly larger average size, by the much darker color, and by other differences cited below. The most reliable characters for distinguishing it are the pronotal granulation, the declivital characters, the frons, and the seminal rod.

Male.— Length 3.4 mm (paratypes 2.6-4.1 mm) (exclusive of head), 2.2 times as long as wide; color almost black.

Frons similar to *mexicanus*, except epistomal process wider (67 percent of epistomal width, 58 percent in *mexicanus*), its lateral arms much more strongly elevated; area from epistomal process to lateral summits on frons more strongly, more broadly impressed (often subconcave), more finely sculptured; largest tubercles at and near lateral summits less numerous, smaller than in *mexicanus*.

Pronotum similar to that of *mexicanus*, except punctures averaging much smaller, closer, interspaces averaging less than half diameter of a puncture; interspaces over most of surface minutely granular, subshining, smooth shining areas usually restricted to less than one-fifth of total surface (in *mexicanus* interspaces average more than half diameter of a puncture, their surface smooth, brightly shining over almost entire surface, granulation rare and restricted; small tubercles sometimes occur in lateral areas). Vestiture more uniformly distributed, slightly coarser and longer than in *mexicanus*.

Elytra similar to those of *mexicanus*, except discal striae less strongly impressed, punctures averaging smaller, obscurely impressed to obsolete in most specimens (larger and rather distinctly impressed in most specimens of *mexicanus*); interstrial crenulations narrower, lower, more numerous, rarely as much as one-third width of an interstriae (in *mexicanus* about one-third of crenulations at least half as wide as an interstriae, a few extend entire width of an interstriae). Declivity with striae feebly if at all impressed, punctures usually obsolete (striae and punctures rather strongly impressed in *mexicanus*); interstriae feebly if at all convex, crenulations less numerous and much smaller than in *mexicanus*. Vestiture slightly more abundant and coarser than in *mexicanus*, particularly at sides.

Female.— Similar to male, except epistomal process narrower, not as high, frontal summits more poorly developed, usually not tuberculate; pronotal callus more poorly developed than in female *mexicanus*.

Type Locality.— Patzun, Guatemala.

Type Material.— The male holotype, female allotype, and 26 paratypes were collected at the type locality on 19-IX-1974, from

Pinus tenuifolia, by J. P. Vité. Two hundred and sixty paratypes all with their abdomens dissected bear the same data except they were taken 22-V-1974; 50 paratypes are from the same locality taken 9-X-1974 from "*P. maximinoi*" by R. Lühl. Ten paratypes are from the same locality, taken on 12-III-1974, and four paratypes are from the same locality, taken on 14-X-1973, by J. P. Vité (all dissected). Three paratypes are from Puente Tzantzir, Sololá, Guatemala, 2-II-1972, from *Pinus montezuma*, by E. W. Clark.

Vité and his associates are studying the biology and behavior of the *frontalis* complex and adding significant information about these species (Vité, Islas, Renwick, Hughes, and Kliefoth, 1974, Zeit. Angew. Ent. 75:422-435). They will report additional biological and biochemical characters of this species. Their illustration of the male seminal rod (Fig. 2E on p. 426) is significant.

In June 1974 it was discovered that both Vité and I had independently prepared a description of this species. He kindly consented to withdraw his manuscript. This species is named in recognition of his numerous contributions to our understanding of these important insects and for the independent discovery of this species.

DESCRIPTION OF NEW SPECIES OF *MILODERES CASEY*, WITH COMMENTS ON OTHER SPECIES OF THE GENUS (COLEOPTERA: CURCULIONIDAE)

Vasco M. Tanner[1]

Abstract.— *Miloderes allredi*, from Utah, and *M. tingi*, from California, are described as new to science.

Miloderes allredi, n. sp.

Figs. 1-5

Derm black, clothed with bluish-green, iridescent, densely placed scales; side of prothorax and elytra with long brownish setae, disc of prothorax and elytra with sparse shorter setae. *Rostrum* continuous, with no transverse impression; apex one-half width base of head. Origin of scrobes near apex of rostrum, well developed and extending to lower base of eye. Antenna brown, with setae and scales; scape reaching to middle of eye; segments 1 and 2 of funicle elongate, as as long as segments 3-6 combined. Segment 7 asymmetrical, cuplike widest on outer margin, clavate at apex. Mentum large, flat, wider than long, filling entire gular cavity. Eyes small, vertical; row of scales between eye and vibrissae of prothorax. *Prothorax* widest at anterior third, sides arcuate, strongly convergent toward base; base well separated from elytra; postocular lobes small, with developed vibrissae; sides and disc punctate, scales compact, setae short and sparse on disc; apex slightly constricted. *Scutellum* obscure. *Elytra* widest at basal fourth; sides feebly arcuate, rounded behind, posterior declivity perpendicular; disc punctate, with sparse short brown setae, a mixture of compact blue, green, and iridescent scales. *Abdomen*, ventrites and legs clothed with scales and setae similar to those on dorsal areas of body; ventrite 1 at midline as long as 2 and 3 combined. Metathoracic tibia with corbel open, margin with amber-colored row of short spines. Prothoracic tibia corbel open and with an outward projection of the distal portion of tibia. Male spermatheca and female genitalia distinctive; related to *setosus* Ting, 1940.

Length.— 5.0-5.8 mm; breadth: 2.5-3.0 mm.

Type locality.— Cotton Bench, Glen Canyon City, Kane County, Utah.

Type specimens.— Male holotype and female allotype in the entomological type collection at Brigham Young University; one paratype in the entomological collection, U.S. Natural Museum.

Specimens of this species were collected by Dr. Dorald M. Allred and assistants in May and June 1973, while collecting plant and animal species of the Lake Powell area in connection with the En-

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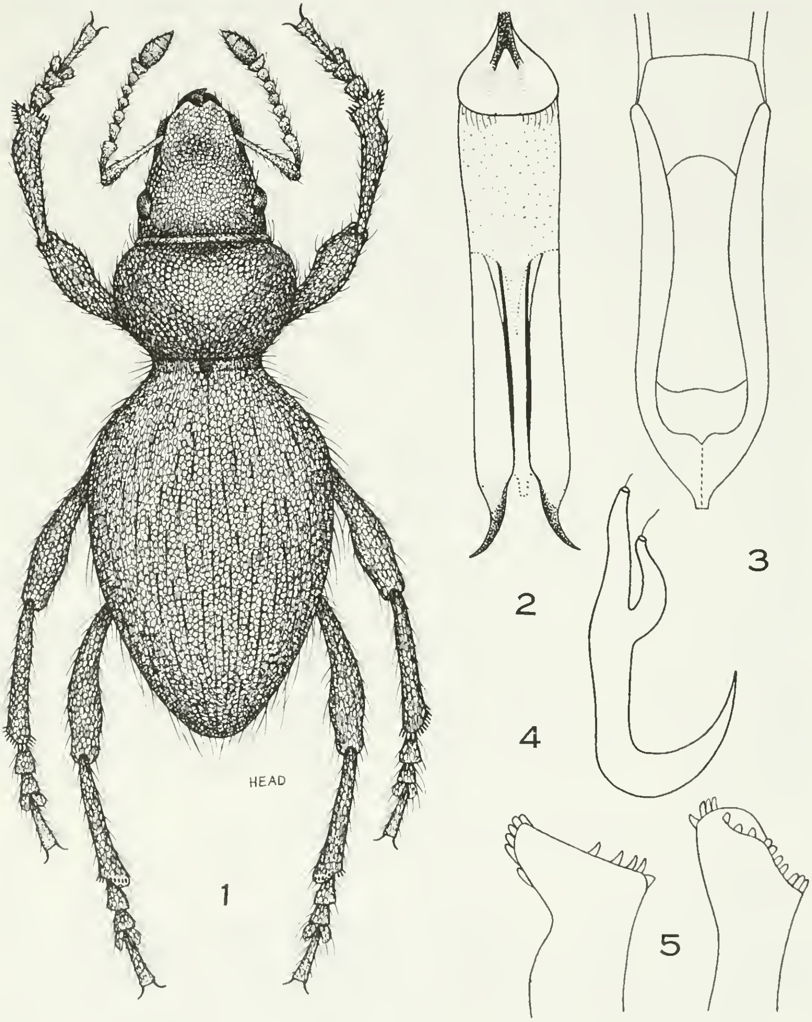
[1] Department of Zoology, Brigham Young University, Provo, Utah 84602.

vironmental Monitoring Project in relationship to Navajo Power Plant Project. Specimens dealt with above were collected on the sand dunes, in an association of *Ephedra viridis* Coville and *Yucca baileyi* Woot. Standl.

I am pleased to name this striking species in honor of Dr. Dorald M. Allred, Professor of Zoology at Brigham Young University. Dr. Allred is a capable field worker who has devised many means of collecting arthropods and is a leader in environmental studies.



Figs. 1-5. *Miloderes allredi*: 1, dorsal view of adult female; 2-3, ♀ and ♂ genitalia; 4, spermatheca; 5, front and hind tibia.

In making this study, the genitalia of several of the species of *Miloderes* have been compared. Drawings of tibia, male, female genitalia, and spermatheca of five species are included in this study.

Miloderes tingi, n. sp.

Fig. 6-9

Derm dark chestnut brown to black, with small, irregular-shaped, rather compact, ash-grey scales that clothe legs, head, prothorax, and dorsal and ventral parts of body, each scale with central puncture; long grey setae on sides of prothorax, sides and posterior dorsal sides of elytra. *Rostrum* continuous with head, with slight transverse impression, apex one-half width base of head. Scrobes shallow, extending to well below base of eye. *Antennae* reddish brown, scape slender, first segment of funicle enlarged, as long as segments 2 and 3 combined, club large and setiferous; prementum wider than long, with few short setae; eye ovate. *Prothorax* slightly wider than long; widest at middle, sides arcuate, weakly convergent toward base, moderately convex; sides covered with dense whitish scales and long setae; dorsally tuberculate, punctate, with few scales. *Scutellum* and postocular well developed; postocular lobes small, with well-developed vibrissae, apex slightly constricted. *Elytra* widest at anterior fourth, sides feebly arcuate, rounded behind, posterior declivity perpendicular; disc punctate, scales covering surface, with scattered long setae on posterior half of disc, scales with a center puncture. Ventrites covered with scales and setae; ventrite 1 as long as 2 and 3 combined, 2 as long as 3 and 4 combined. Metathorracic tibia open, with a row of eleven amber-colored spines. Size, shape, and number of tibial spines and tibia distinctive. Prothoracic tibia with distal portion spatulate, 10 spines (Fig. 7). Spermatheca and genitalia distinctive (Fig. 8-9).

LENGTH.— 7 mm; breadth: 3.6 mm.

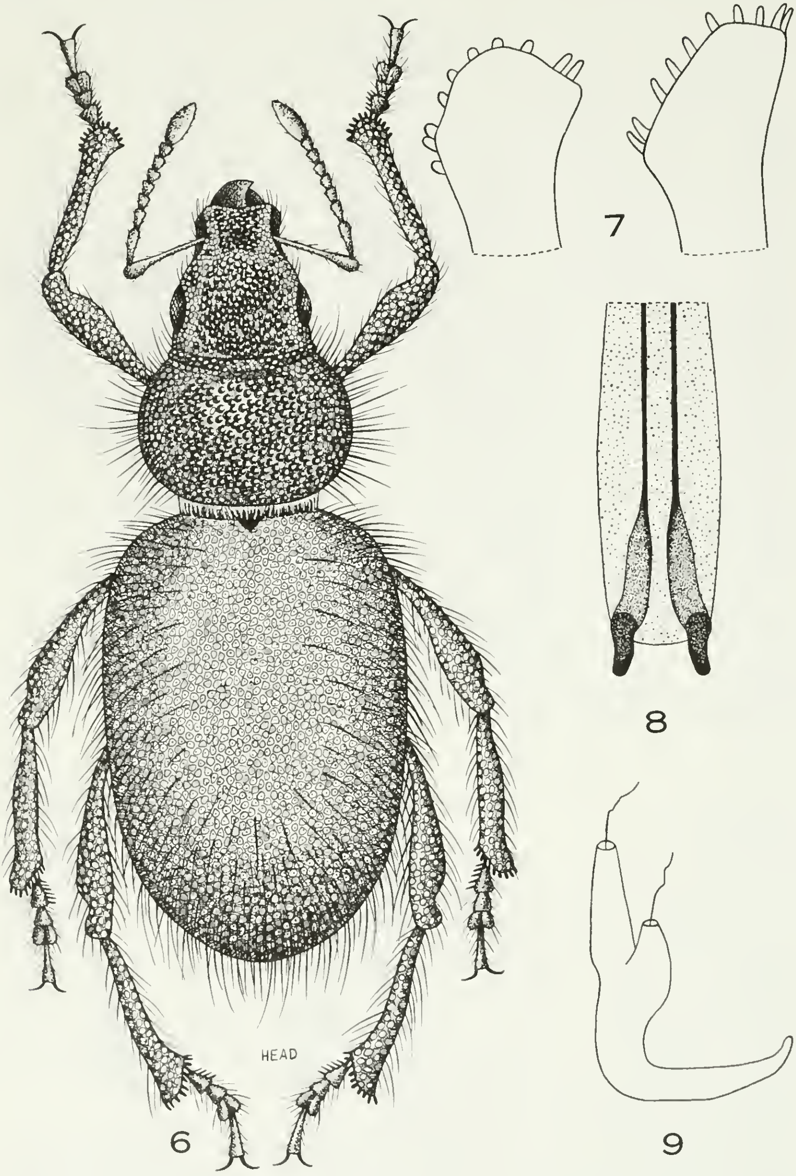
HOLOTYPE.— Female, deposited in type collection, Brigham Young University.

TYPE LOCALITY.— Essex, San Bernardino Co., California. 29-IV-1937, Collectors: P. T. Ting, M. Cazier.

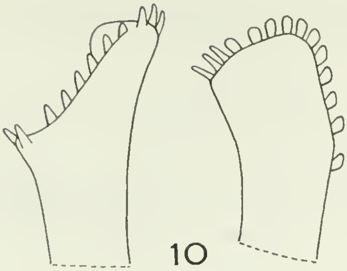
M. tingi is uniformly a dark brownish species, clothed with small dense greyish scales; head and prothorax tuberculate, no traces of striation on elytra, and devoid of setae on the central areas of prothorax and elytra. The female genitalia and spermatheca differ from similar structures of other species of this genus. This species is closely related to *M. setosa* Csy; however, it is more robust with smaller scale punctation on prothorax, and the female genitalia and spermatheca are different (Figs. 8-9).

I am pleased to name this species in honor of Peter T. Ting who contributed much to our knowledge of this group of Brachyrhininae weevils (1940). Edwin C. Van Dyke and David G. Kissinger have done much to bring about an orderly arrangement and understanding of this interesting western-American weevil fauna.

The keys to the genera and species of this group as contained in Ting's paper (1940) will be useful, in combination with the description and illustrations of this paper, in separating the species of



Figs. 6-9. *Miloderes tingi*: 6, dorsal view adult female; 7, front and hind tibia; 8, ♀ genitalia; 9, spermatheca.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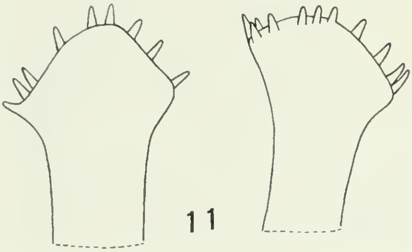
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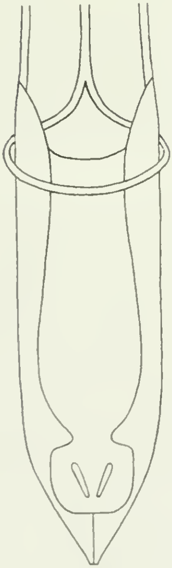
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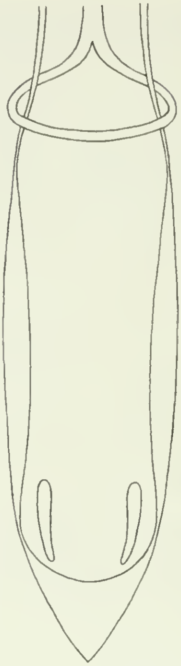
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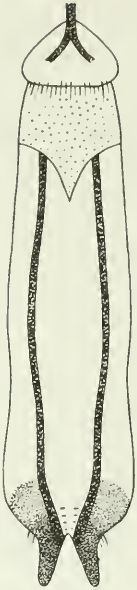
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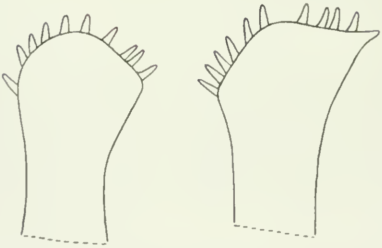
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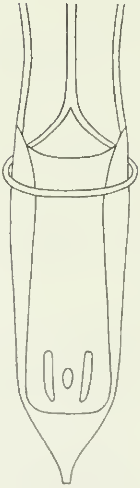
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Fig. 10: *Miloderes nelsoni* Kissinger, front and hind tibia. Fig. 11: *M. setosus* Casey. Fig. 12: *M. nelsoni*, ♂ genitalia. Fig. 13: *M. mercuryensis* Tanner, ♂ genitalia. Fig. 14: *M. setosus* Csy., ♀ genitalia. Fig. 15: *mercuryensis* Tanner, front and hind tibia. Fig. 16: *M. setosus* Csy. ♂ genitalia.

Miloderes. I have had the privilege of examining specimens of all six of the species now included in *Miloderes.* Unfortunately, I did not make drawings of the tibia of *M. viridis* Pierce.

Dr. Elbert L. Sleeper has made a study of some species of *Miloderes,* but I do not have access to his writings dealing with the species of this genus. He kindly contributed specimens of *M. nelsoni* Kissinger which I have reported on.

I wish to express my thanks to Dr. Rose Ella Warner for her aid in this study and for loan of specimens of *M. viridis* and *M. setosus* from the U.S. National Museum and courtesies extended while I studied at the museum.

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REVISION OF THE PLANT GENUS *GERANIUM* IN UTAH

Glen T. Nebeker[1]

Abstract.— Within the state of Utah are seven species of *Geranium*, two of which are annual. The nature of the caudex and the growth habit have been used to separate the perennial species. These characters are inadequate for separating the species. Better morphological characters, keys, and descriptions are presented.

Two characters used to separate various species of *Geranium* are not effective. One of these characters is "plants somewhat caespitose." Use of this character in keys would lead to plants which are sometimes three feet tall and with the same growth habit of plants considered not caespitose. The other character is the branching or simple nature of the caudex. In herbarium specimens it is usually impossible to see the caudex. In addition, authors vary in the description of the caudex; for example, *G. richardsonii* is described as: "caudex often slightly branched" (Hanks and Small, 1907), "the usually simple caudex" (Jones and Jones, 1943), "plants . . . erect from a simple caudex" (Harrington, 1959). The caudex actually varies from simple to very branched. (VanCott, 1969). These characters illustrate a need for a revision of the genus.

Hanks and Small (1907) treated the known species of North America *Geranium*. In Knuth's (1912) worldwide monograph of the genus the treatment of the North American species was more or less copied from Hanks and Small's work. Jones and Jones (1943) treated the perennial species north of Mexico, and Moore (1943) included one Utah species in his coverage of the Mexican species.

Taxonomic Characters

As mentioned above, the nature of the caudex and the growth habit are poor taxonomic characters. Six taxonomically significant characters are described below. The variations of each of them were measured, assigned numbers, then averaged for each character and plotted on polygonal graphs. (Fig. 1) All observations were made under a dissecting microscope.

Stylodia: These are the branches at the tip of the style column which bear the stigmatic surface. These were first soaked with Pohlstoffe then measured with a standard mm ruler. Only mature flowers were measured. For each species the length was averaged.

Petal pilosity: This is the pubescence on the upper surface of the petals. Three degrees of pilosity were recognized and assigned numbers for comparison. The degree and corresponding numbers are: ¼ of the petal covered = 1; ⅓ of the petal covered = 2; and ½ of the petal covered = 3.

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[1] Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

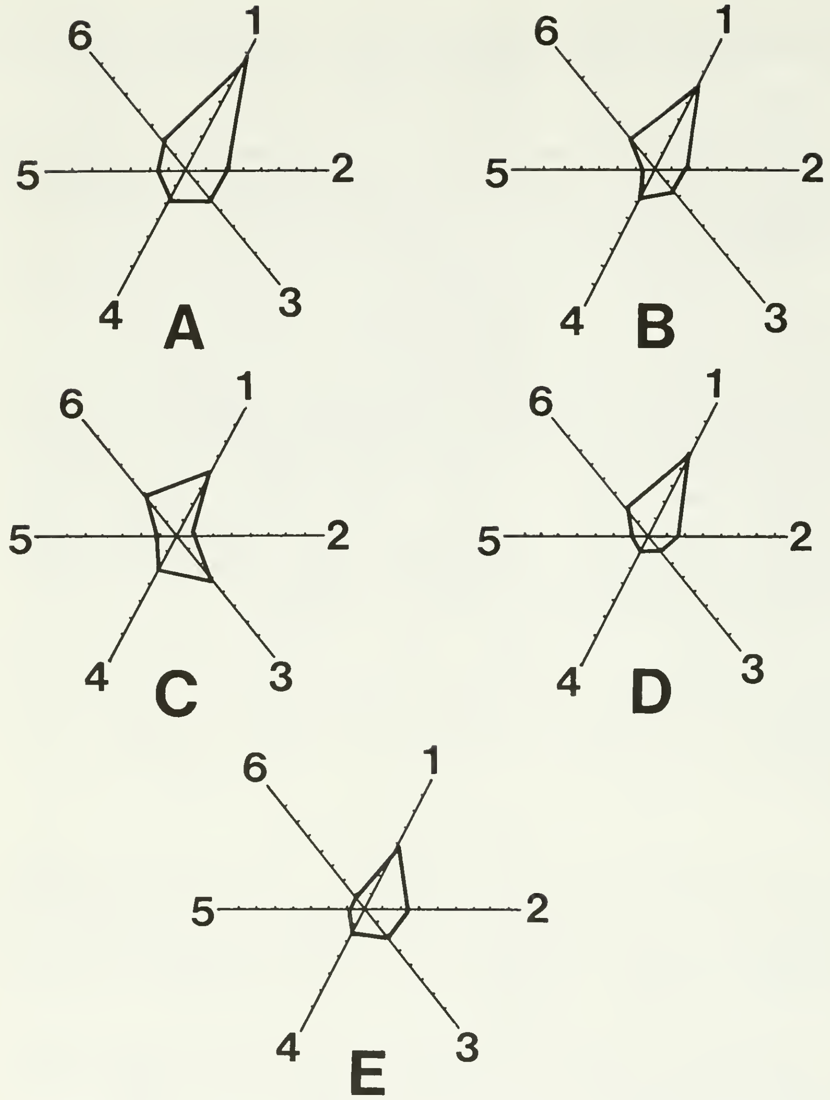

Fig. 1: 1, stylodia; 2, petal pilosity; 3, pubescence of pedicels; 4, pubescence of stems; 5, petals recurving or not; 6, petal color; A. *G. atropurpureum;* B, *G. fremontii;* C, *G. marginale;* D, *G. parryi;* E, *G. richardsonii.*

Pubescence of the pedicels: The pedicels of some species are glandular pubescent, while others are pubescent but not glandular. The color (purple or not) of the glands was also noted. The numbers given these characters are: glandular = 1; purple glands = 2; and nonglandular = 3.

Pubescence of the stems: Pubescence on the stems varied from very glandular to glabrous. The only significant difference in pubescence was glandular = 1; nonglandular = 2.

Petals recurving or not: The petals of most species extend out flat or curve upward slightly. One species has petals that curve downward abruptly. Numbers assigned to these are: petals not recurving = 1; petals recurving = 2.

Petal color: White petals = 1; varying shades of pink to purple = 2.

The above characters have been applied to the five perennial species that occur in the state. The characteristics used to separate the annual species are the number of fertile stamens and awned or nonawned sepals.

Shaw (1952) has worked out the cytology of four species that occur in Utah. The chromosome numbers that he reported are as follows: *G. carolinianum* 2n = 52; *G. pusillum* 2n = 26; *G. richardsonii n* = 26; *G. fremontii* (which he called *G. nervosum*) n = 26. Other cytological work should be done because there are indications of hybridization betweeen *G. richardsonii* and *G. fremontii.*

The probable phylogenetic relationships of the perennial species within the state are outlined on Figure 2 and their distributions are plotted on Figure 3.

TAXONOMY

Geranium L. Sp. Pl. 676 (1753)

Annual or perennial herbs, often with a woody caudex; stems glabrous to glandular-villous; leaves palmately lobed, cleft or parted, basal leaves generally larger than the cauline ones; inflorescence compact to spreading; flowers complete, actinomorphic; sepals 5 usually awn tipped; petals 5, deciduous, purple to white, usually pubescent toward the base; ovary 5 lobed, 5 loculed with 2 ovules per locule becoming 1 seeded, elastically recoiling at maturity but not twisting.

KEY TO THE SPECIES

1.	Plants annual, petals less than 1 cm long	2
	Plants perennial, petals more than 1 cm long	3
2(1).	Sepals awnless, fertile stamens 5	1. *G. pusillum*
	Sepals awned, fertile stamens 10	2. *G. carolinianum*
3(1).	Plants nonglandular (sometimes nonglandular in *G. richardsonii*)	4
	Portions of the plant glandular	5
4(3).	Petals reflexing at maturity, pilose on the petals ⅓-½ their length	3. *G. atropurpureum*
	Petals not reflexing at maturity, pilose on the petals ¼ their length	4. *G. marginale*

5(3). Pedicels and lower portions of the plant glandular .... 5. *G. parryi*
Lower portions of the plant nonglandular, pedicels glandular 6

6(5). Petals white, petals pilose ⅓-½ their length .... 6. *G. richardsonii*
Petals purple, petals pilose ¼ their length .... 7. *G. fremontii*

1. *G. pusillum* Burm. f. Sp. Bot. Geran. 27 (1759)

Annual; stems 10-60 cm long, decumbent or prostrate, puberulent; leaves reniform to orbicular, 1-6 cm broad, 3-7 parted; sepals 2.5-5 mm long, awnless; petals purple to violet; 5 fertile stamens; style column 6-9 mm long, glandular puberulent; carpel bodies 2 mm long; seeds smooth. A weed of fields and waste places. Type locality, England and France. Provo Bench near Pleasantview, Utah Co.,

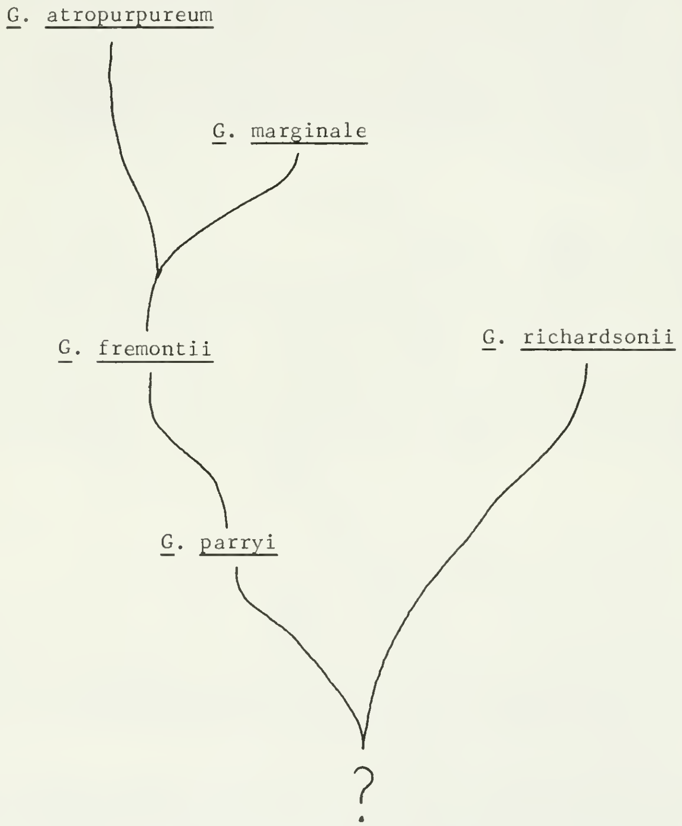

Fig. 2. The probable phylogenetic relationships of the perennial species of Utah *Geranium*.

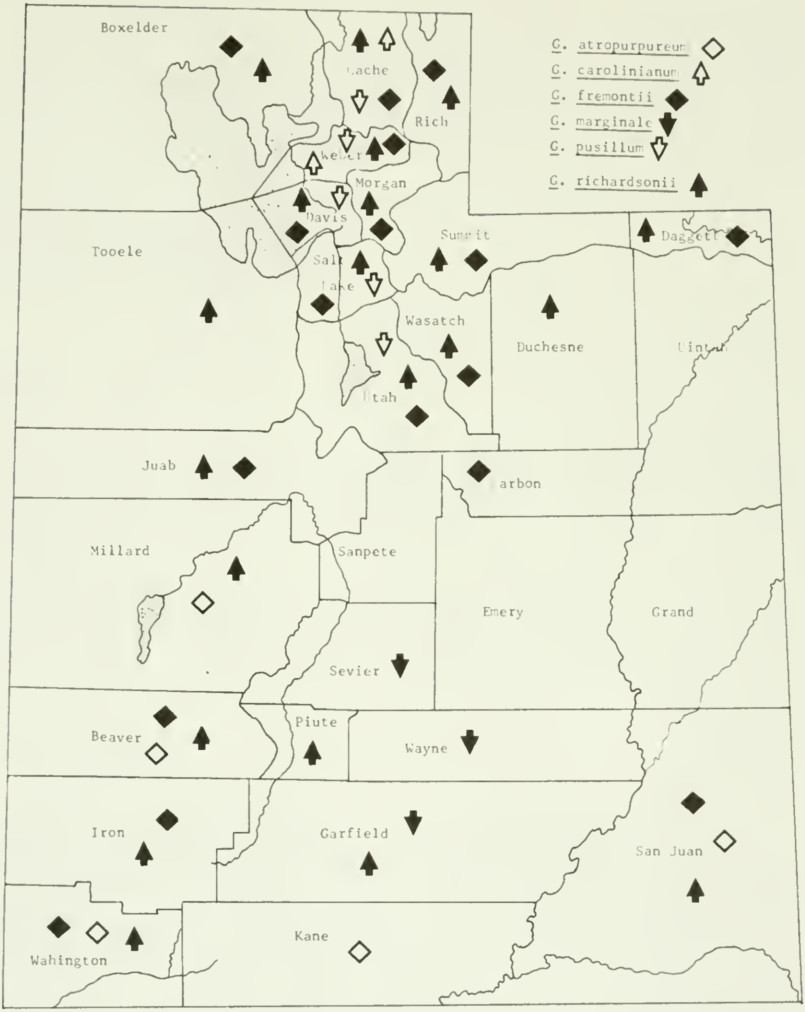

Fig. 3. Distribution of *Geranium* in Utah.

Harrison 7543 (BRY). Univ. St. and 1st. So., Salt Lake Co., WSF 729 (UT). Along Provo River, Utah Co., Sanders sn (UT). Near Salt Lake City, Salt Lake Co., Garrett 1766 (UT). Above Pelican Pond, Cache Co., Thieret 149 (UTC). Green Canyon, Cache Co., Shaw 36 (UTC). Logan, Cache Co., Smith 17669 (UTC).

2. *G. carolinianum* L. Sp. Pl. 682 (1753)

G. bicknellii Britt. var. longipes (Wats.) Fern.

Annual; stems 17-40 cm long, erect or branching at the base, short pubescence; leaf blades 2.5-7 cm wide, orbicular to reniform, 5-7 palmately parted; inflorescence very compact; sepals 6-8 mm long, tipped with awn 1-2 mm long; petals about as long as sepals, pink to whitish; 10 fertile stamens; style column 12-18 mm long with glandular hairs; carpel bodies 3-3.5 mm long; seeds reticulate. Open places and fields throughout North America. Type locality, Carolina. Antelope Island, Howard sn. (UT) Fern Hollow near Ogden, Weber Co., Cardon 313 (UTC)

"*Geranium carolinianum* has been confused with *G. bicknellii* Britt., the latter having been included in the Wasatch region by at least two authors. Inclusion of *G. bicknellii* in the flora might possibly have been based upon a collection from Logan Canyon in 1910 (C. P. Smith 2164). The stage of the plant's development makes it impossible to determine its true identity." (Shaw, 1952)

3. *G. atropurpureum* Heller Bull. Torr. Bot. Club 25:195 (1898)
G. caespitosum James ex Torr. apud Gray

Perennial; stems 10-90 cm long, erect sometimes becoming decumbent with age, retrorsely pubescent; basal leaves 2-6 cm wide, reniform to orbiculate, divided nearly to the base into 3-5 lobes, generally larger than the cauline leaves; inflorescence open and spreading; pedicels retrorsely pubescent but not glandular; sepals 9-11 mm long, awned; petals 10-15 mm long, pink to purple, pilose on petals ⅓-½ the petals' length, petals recurving; stylodia average 6.55 mm long. Often found growing in association with oak. Type from Santa Fe Creek, New Mexico (Heller 2723). (34 seen) Pine Valley, Wash. Co., Cottam 8905 (UT). Beaver Canyon, Beaver Co., Warnock sn (UT). Devils Canyon Campground, San Juan Co., Cottam 9523 (UT). Long Canyon above Orderville, Kane Co., Cottam 4279 (UT). 4 miles north of Glendale, Kane Co., VanCott 1002 (BRY). Sheba mine, Millard Co., Cottam and Biddulph 3200 (BRY).

"It was to this species that Gray assigned the name *G. caespitosum* (Gray 1849) believing it to be the species described by James. Material in the Gray Herbarium shows *G. atropurpureum* extending northward into the southern and southwestern counties of Colorado but not into the northeastern region where James is supposed to have collected his "caespitose" *Geranium* as pointed out by Heller (1898). Lacking collections from the general region or actual specimen collected by James, it seems advisable to follow Heller in calling this distinctly southern species *G. atropurpureum* and to consider *G. caespitosum* James ex Torr. a nomen dubium." (Moore, 1943)

4. *G. marginale* Rydb. ex Hanks and Small. N. Am. Fl. xxv 16 (1907)

Perennial; stems 10-30 cm long, retrorsely pubescent, slightly exceeding the basal leaves; leaves 2-3.5 cm wide, 5 parted; inflorescence not compact; pedicels retrorsely pubescent, not glandular; sepals 7-9 mm long, puberulent to nearly glabrous; petals purple, pilose ¼ the petal length; style column 1.5-2 cm long, stylodia average 4.33 mm long; carpel bodies 4 mm long; seeds 3 mm long, faintly reticulate. Type locality is the Aquarius Plateau at the head of Poison Creek, Utah, Rydberg and E. C. Carlton 7401. (Hanks and Small, 1907).

This is probably the smallest of the perennial species found in Utah. Aquarius Plateau, 35 miles north of Escalante in Wayne Co. Holmgren, Reveal, and LaFrance 2080 (BRY). Aquarius Plateau, Garfield Co., VanCott 1196a (BRY). 2 miles north of Fishlake, Sevier Co., VanCott 933 (BRY). Bryce Canyon, Weight B-31/26 (UT). Wildcat Ranger Station, Garfield Co., Cottam 14130 (UT). Aquarius Plateau, Garfield Co., Cottam 9113 (UT).

5. *G. parryi* (Engelm.) Heller. Cat. N. Amer. Pl. ed. 2. 7 (1900)

G. pattersonii Rydb., *G. fremontii* var. *parryi* Engelm.

Perennial; stems 10-45 cm tall, glandular-pubescent throughout; petioles glandular; leaves 2-7 cm wide, deeply 3-5 parted; inflorescence open and spreading; pedicels glandular-pubescent; sepals 6-10 mm long; petals 12-15 mm long, purple, pilose on petals ¼-⅓ their length; style column 1.5-3 cm long, glandular, stylodia average 5.23 mm long; carpels 4-5 mm long; seeds 3-3.5 mm long, reticulate. No specimens of this plant have been seen from the state, but it should be looked for in the Uinta Mountains and in other parts of eastern Utah.

Another completely glandular species with which this species may be confused is *G. viscosissimum*. The distinctive characteristic separating them is the compact inflorescence of *G. viscosissimum*.

6. *G. richardsonii* Fisch. & Trautv. Ind. Sem. Hort. Petrop. 4:37 (1837)

G. gracilentum Greene, *G. albiflorum* sensu Hooker, *G. pentagynum* Engelm., *G. loloense* St. John.

Perennial; stems 30-90 cm tall, glabrous to pubescent; petioles long; leaves 3-15 cm wide, deeply 3-5 parted; inflorescence open; pedicels glandular-pubescent, glands usually purple; sepals 6-12 mm long; petals 1.5-2 cm long, white sometimes bluish, pilose ⅓-½ the petals' length; style column 2-2.5 cm long, glandular, stylodia average 4.06 mm long; carpel bodies 2.5-4.5 mm long. Found in partial shade or in rather moist ground.

(36 seen) 3 miles north of Roosevelt, Duchesne Co., Hardy 113 (BRY). Pine Valley Campground, Pine Valley Mts., Washington Co., Higgins 3454 (BRY). Cedar Mountain near Navajo Lake, Iron Co., Higgins 4666 (BRY). East of Kamas 1 mile above Upper Falls, Summit Co., VanCott 967 (BRY). ¾ mile west of Puffer Lake, Beaver Co., VanCott 904 (BRY). 10 miles west of Monte Cristo, Cache Co., VanCott 898 (BRY). Aspen Grove, Utah Co., Hardy 87 (BRY). Vernon, Tooele Co., Frischknecht 106 (BRY). Skyline drive east of Sterling, Sanpete Co., VanCott 943 (BRY). Kigalia Ranger Station, San Juan Co., WDS sn (UT). Deep Creek Mts., Juab Co., Lindsay 265 (UT).

7. *G. fremontii* Torr. ex Gray. Pl. Fendl. 26 (1849)

G. caespitosum sensu Rydb., *G. furcatum* sensu Hanks & Small

Perennial; stems 20-70 cm long, glabrous to pubescent, not glandular; petioles long on northern plants shorter in southern specimens; leaves 3-10 cm wide, 5-7 parted, cauline leaves much smaller; inflorescence open, spreading; pedicels glandular-pubescent; sepals 7-12 mm long; petals 1-1.5 cm long, purple, pilose ¼-⅓ their length; style column 2.5-3 cm long, stylodia average 5.23 mm long; carpel bodies 4-5 mm long. Open areas of the foothills and mountains.

(49 seen) 4 miles east of Logan, Cache Co., VanCott 886 (BRY). Alpine Loop, Wasatch Co., Mullins 17 (BRY). South shore of Pineview, Weber Co., VanCott 896 (BRY). 4 miles west of Garden City, Rich Co., VanCott 885 (BRY). Near Cedar Breaks, Iron Co., Higgins 4643 (BRY). Pole Canyon, Utah Co., Hartman 127 (BRY). Tanners Flat, Little Cottonwood Canyon, Salt Lake Co., Day 30 (BRY). 13 air miles south of Wah Wah summit, Beaver Co., Holmgren and Bethers 3824 (BRY). Devils Canyon Campground, San Juan Co., Cottam 9523 (UT). Pine Valley, Washington Co., Cottam 8905 (UT). Beaver Canyon, Beaver Co., Warnock sn (UT). 15 miles NW of Orderville, Kane Co., Maguire 18821 (UTC).

This species is often confused with *G. nervosum*, which grows north of Utah. The difference between the two is in the inflorescence: *G. nervosum* has a compact inflorescence, and *G. fremontii* has a spreading inflorescence.

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UTAH PLANT NOVELTIES IN *ASTRAGALUS* AND *YUCCA*

Stanley L. Welsh[1]

Abstract.— *Astragalus iselyi* and *A. stocksii* are described as new species. The former is from the La Sal Mountains of Grand and San Juan counties in eastern Utah, and the latter is from the Henry Mountains in eastern Garfield County, Utah. *Yucca toftiae* is described as new from materials collected along Glen Canyon in San Juan and Kane counties, Utah.

Studies of plant collections taken from previously unexplored or little-known regions of Utah have demonstrated the presence of taxa not included in the known descriptions of plant species of the state. Two species of *Astragalus* and one of *Yucca* are included in the new entities. The La Sal Mountains and the Henry Mountains yielded the *Astragalus* species. The *Yucca* is from the margin of Glen Canyon.

Astragalus iselyi Welsh sp. nov.

Fig. 1

A Astragalo sabuloso Jones differt floribus parvioribus et petalis albidioribus carina immaculata et leguminibus parvioribus.

Herba perennis radice palari forti et caudice ramificanti; caules 8-25 cm alti recti aut ascendentes; stipulae 3-9 mm longae firmae purpurascentes amplectentes sed non connatae; folia 3.2-8.5 cm longa; foliola (3) 5-11 (13), 7-23 mm longa, 3-9 mm lata elliptica ad rhombica strigosa pilis simplicibus utrinque glabrescens; pedunculi 1.7-10 cm longi; racemi 1.2-3 cm longi, floribus 7 ad multus; bracteolae nullae; calyx strigulosus tubo cyclindrico 5.5-6.3 mm longi dentibus 1.8-3.1 mm longis; subulatis; flores 17-18 mm longi, petalis ochroleucis, carina apice immaculato; legumina 25-32 (38) mm longa stricta subcylindrica unilocularia coriacea strigosa.

Utah: San Juan Co., La Sal Mts., Brumley Ridge, ca. 1.5 miles north of Pack Creek Ranch, on Morrison formation, in pinyon-juniper community, S. L. Welsh 10970, 5 May 1971 (Holotypus bry; Isotypi isc, and many others); same locality, J. Pederson 23, 29 March 1967 (bry); S. Daines 39, 5 May 1971 (bry); C. Schoener 75, 11 June 1971 (bry). Grand Co., Paradox formation, gypsiferous clay, Onion Creek, Fisher Valley, S. L. Welsh 11929, 11929a, 30 May 1973 (bry).

Astragalus iselyi is a near congener of *A. sabulosus* Jones. It is similar in habit, leaflet shape and number, and pod features. The flowers are consistently smaller in all parts. Even the average pod size seems smaller than in *A. sabulosus*. The flowers of *A. iselyi* are only 17-18 mm long, whereas those of *A. sabulosus* are 28-31 mm long. Both of these entities complete flowering during early springtime, and it seems probable that the existence of *A. iselyi* has been

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[1] Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

Fig. 1. *Astragalus iselyi*. A, Habit sketch; B, Detail of pods.

obscured by the fact that most previous specimens were collected in fruit only.

It seems certain that the phase of the sabulosus-iselyi complex with massive flowers is that known as *A. sabulosus*. The measurements set forth in the original description (Jones, 1891) and in the Revision of North American Species of *Astragalus* (Jones, 1923:156-157) are those of the phase including the type of *A. sabulosus*. Materials collected on the La Sal Mountains by Rydberg and Garrett (9088, 19 July 1911 UT) and by Maguire et al. (16536, 14 July 1933 UTC) are almost assuredly *A. iselyi*. From the present information, it seems that *A. sabulosus* is a plant of bajadas and drainages over Mancos Shale in the Thompson-Cisco region of Grand County. *A. iselyi* is also a selenophyte, but grows on the Paradox and Morrison formations on the foothills of the La Sal Mountains.

This species is named in honor of Duane Isely, legume specialist, teacher, colleague, and philosopher.

Astragalus stocksii Welsh sp. nov.

Fig. 2

Species habitu cum Astragalo musiniensi Jones differt foliolis plus numerosis floribus parvioribus ochroleucis et leguminibus strigosis.

Herba perennis acaulis, caudice ligneo ramificanti, ferenti petiolis marcescentibus; stipulae lanceolatae 3-5 mm longae strigosae librae: folia 2.7-10.6 cm longa; foliola 7-13 mm longa obovata oblong-lanceolata vel elliptica, plumbea aut argentea, supra viridia saepe, strigosa utrinque, truncata ad mucronata aut acuta ad apicem; pedunculus 1.1-4 cm longus; racemus (2) 3-8 floribus, compactus: bracteae lanci-subulatae, strigulosae; flores ascendentes, 15-16 mm longi; calyx strigulosus, tubo cylindrico, 9-9.2 mm longo, dentibus lanci-subulatis 2-2.8 mm longis; corolla ochroleuca, venis purpurescentibus, carina-apice maculata; alis apicibus purpurescentibus; legumina unilocularia, compressa lateralle, lanci-ovoidea, rostro elongato tenui contracto, stricta aut arcuata, strigosa.

UTAH: Garfield Co., Henry Mountains, Penellen Pass, S. L. Welsh 11740, 30 May 1972 (Holotypus BRY; Isotypi US, LSC). Near same locality, S. L. Welsh 9817, 16 May 1970 (BRY, distributed as *A. newberryi* Gray); S. L. Welsh 11739, 11751, 30 May 1972 (BRY, Paratypes).

Astragalus stocksii is compared to the distinctive *A. musiniensis* Jones in the above description. It is indeed similar to that entity both in having a persistent thatch of petioles and in shape and texture of the pods. Habitually it is apparently nearer to *A. newberryi* Gray and to *A. eurekensis* Jones. From the former, *A. stocksii* differs in the smaller, paler flowers and merely strigose pods, and from the latter it differs in having smaller flowers and merely strigose pods.

The species is named in honor of the late Dayna L. Stocks, botanist, teacher, and extraordinary human being.

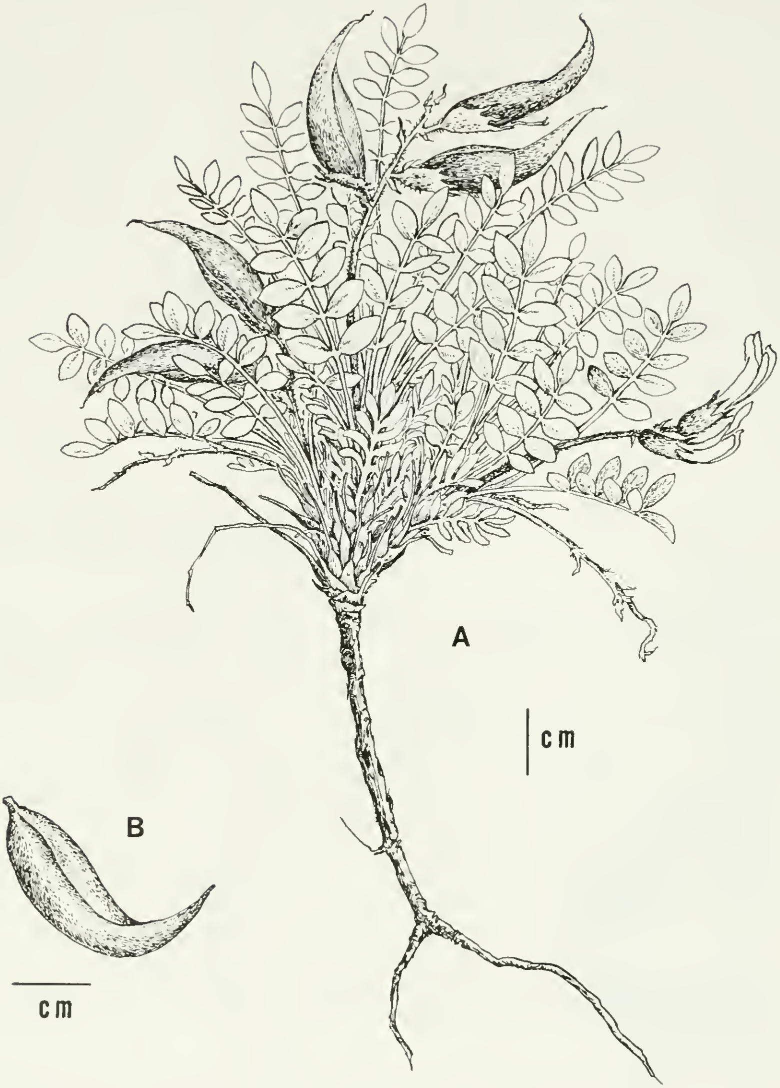

Fig. 2. *Astragalus stocksii.* A, Habit sketch; B, Detail of pod.

Yucca toftiae Welsh sp. nov.

Fig. 3

Differt haec species a Yucca angustissima in uterque amplitudine et habitu.

Planta acaulescens vel brevicaulescens, solitaria vel caespitosa; caules 0-7 (10) dm alti; folia 2-7.5 dm longa, 0.4-1.7 cm lata linearia

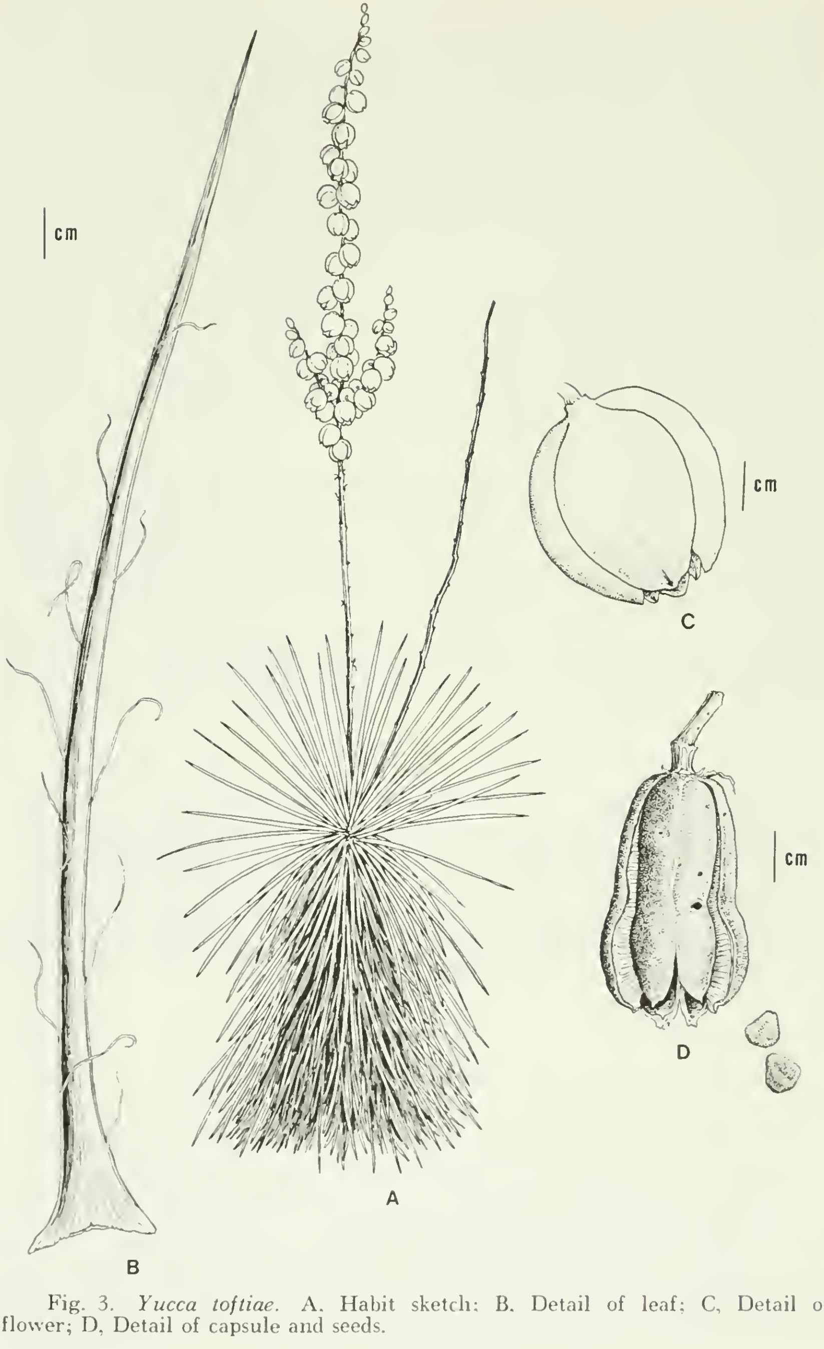

Fig. 3. *Yucca toftiae*. A, Habit sketch; B, Detail of leaf; C, Detail of flower; D, Detail of capsule and seeds.

plano-convexa vel concavo-convexa ad plano-carinata effusa rigide, viridia vel flavo-viridia, margo filifer; inflorescentiae 1.2-3.4 m altae, scapi folia 2-vel 6-plo longior; paniculae lineares vel ovoidae, 2.5-20 dm longae, ramulis 0-12 (23); flores numerosi globosi vel campanulati albi, cremei, vel viriduli plerumque exti rubro-purpurei suffusi, segmenta elliptica vel lanc-ovata, acuta; sepala 2.5-4.6 cm longa; petala 31-52 mm longa; filamenti staminale 7-24 mm longa; pistila 15-32 mm longa; styli (3) 7-11 mm longi; capsulae erectae, 3.5-5.5 (6) cm longae, cylindricae, plurumque constrictae, ligneae et persistentes.

UTAH: San Juan Co., Three Gardens, ca. 1 mile north of confluence of San Juan and Colorado rivers, Lake Powell, S. L. Welsh 11935a, 4 June 1973 (Holotypus BRY; Isotypi US, NY). Ribbon Canyon garden, east side of Lake Powell at ca. mile 66, N. D. Atwood 4112, 10 June 1972 (BRY). Kane Co., tributary of Dry Rock Creek, Lake Powell, S. L. Welsh and G. Moore 11779, 4 June 1972 (BRY).

This entity grows on sandy alluvium and on sandstone outcrops along the shores of Lake Powell in Glen Canyon of eastern Kane and western San Juan counties, Utah. The affinities of *Y. toftiae* are with *Y. angustissima* Englem ex Trel, from which it differs in both size and habit. Habitually, *Y. toftiae* is similar to *Y. utahensis* Mckelvy and *Y. verdiensis* Mckelvy. From the former it differs in the inflorescence which branches only near the base (or not at all), and from the latter in the short pistils and longer woody capsules.

This striking taxon is named in honor of Catherine Ann Toft, botanist.

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MCKELVY, S. D. 1938. Yuccas of the southwestern United States. Part 1. Arnold Arboretum, Harvard Univ. 150 pp.

———. 1947. Yuccas of the southwestern United States. Part 2. Arnold Arboretum, Harvard Univ. 197 pp.

A NEW COMBINATION IN *PENSTEMON* (SCROPHULARIACEAE)

James L. Reveal[1]

One of the more distinctive beard-tongues found in the sandy portions of northern Arizona, southern and western Utah, and southeastern Nevada is *Penstemon angustifolius* ssp. *venosus*. The pinkish-lavender to pinkish flowers of ssp. *venosus* mark it as one of the more readily recognized of the penstemons found in this part of the western United States. The typical subspecies is found far to the east on the high plains of the central United States. The ssp. *angustifolius* generally has narrower, more sharply acute foliage, typical blue flowers that are shorter, and mature capsules that are shorter and narrower than those found in ssp. *venosus*. The bracts in the inflorescences of ssp. *angustifolius* are not venose on both sides as in ssp. *venosus*, and the former has the unfortunate feature of blackening upon drying. As a result of its green, glaucous foliage, bright pinkish to lavender flowers, and general rareness, the ssp. *venosus* is often collected preferentially by even the most seasoned collector.

Many collectors have noted their dissatisfaction with Keck's placement of this plant with *Penstemon angustifolius*, but as yet no one has proposed a specific name for the taxon. So that a specific name might be available to Janice C. Beatley for her floristic work on the Nevada Test Site, the following combination is proposed:

Penstemon venosus (Keck) Reveal, stat. et comb. nov., based on *P. angustifolius* Nutt. ex Pursh ssp. *venosus* Keck in Kearney and Peebles, J. Wash. Acad. Sci. 29:490. 1939.

As a distinct species, *Penstemon venosus* may be distinguished by its flower color, leaf size and shape, the nature of the floral bracts, and its disjunct distribution.

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[1] Department of Botany, University of Maryland, College Park 20742, and National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. Research supported by National Science Foundation Grant GB-22645.

DOMINANCE RELATIONSHIPS OF THE DARK KANGAROO MOUSE (*MICRODIPODOPS MEGACEPHALUS*) AND THE LITTLE POCKET MOUSE (*PEROGNATHUS LONGIMEMBRIS*) IN CAPTIVITY

Andrew R. Blaustein[1] and Arthur C. Risser, Jr.[1]

Abstract.—Interspecific interactions between the little pocket mouse (*Perognathus longimembris*) and the dark kangaroo mouse (*Microdipodops megacephalus*) were tested in the laboratory. *P. longimembris* was statistically dominant over *M. megacephalus*. The dominant-subordinate relationships shown by our laboratory results indicate that interspecific aggression may be one mechanism involved in keeping these sympatric species ecologically separated.

In certain areas of northern Nevada, the dark kangaroo mouse (*Microdipodops megacephalus*) and the little pocket mouse (*Perognathus longimembris*) are sympatric (Hall and Kelson, 1959). These species are similar in size and, being primarily granivorous (Hall, 1946), probably have similar feeding habits. As compared with what is known about other members of their family (Heteromyidae), little is known about the ecology of these species. This study investigates the possibility that interspecific agonistic behavior may be a mechanism by which ecological isolation occurs between these two species in the field. To assess this possibility we observed interspecific interactions between pairs of captive *M. megacephalus* and *P. longimembris*. The possible role of interspecific agonistic behavior in the habitat segregation of small mammals has been reviewed by Grant (1972).

Three *Microdipodops* (two females and one male) and four *Perognathus* (two females and two males) were trapped in Warm Springs Valley, Washoe Co., Nevada. The animals were caged individually in steel cages measuring 34 x 24 x 24 cm. The front of each cage was covered with 1 x 1.25-inch hardware mesh. Sand one centimeter deep was placed in each cage. The cages were cleaned periodically. A mixture of sunflower seeds, rolled oats, and millet was given to the animals daily. Lettuce was provided once a week. No water was provided. The housing cages were placed under a 12-hour light—12-hour dark controlled photoperiod. The light and dark periods were reversed, allowing these normally nocturnal animals to be observed during convenient daytime sessions. The light phase was illuminated by two incandescent 60-watt white light bulbs, and the dark phase was slightly illuminated by two incandescent 25-watt red light bulbs.

Encounters took place in a cage measuring 34.5 x 45.7 x 122 cm. Three sides of the cage were aluminum, and the front was plexiglas. The top was covered with .25-inch hardware cloth, and an aluminum partition divided the cage into two equal sections, each

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[1] Andrew R. Blaustein and Arthur C. Risser, Jr., Department of Biology, University of Nevada, Reno 89507. Present address of Blaustein: Department of Biological Sciences, University of California, Santa Barbara 93106.

containing a nesting area and a food dish. Two cm of sand covered the floor of the cage and was replaced after each interaction.

To begin an interaction, one rodent was placed on each side of the central partition. The cage was subjected to the same reversed photoperiod as the housing cages. The animals were left alone for at least 24 hours as an adjustment period. Then the partition was removed, and the behavior and interrelationships of the rodents were recorded for 15 minutes. Interactions with the same two individuals were not repeated. At least two days were allowed to elapse before an individual was used again. All trials were conducted between 1000 hr and 1500 hr.

Any overt interaction between two animals was called an encounter. Agonistic encounters usually ended when one animal took the dominant role by attacking and chasing its opponent and the other became subordinate by escaping or trying to defend its nest area from attack.

The behavioral patterns and postures observed between the mice were classified into five major categories. These have been modified from Eisenberg (1963).

Upright posture.— The animal assumes a posture with the long axis of the body at an angle greater than 45 degrees to the substrate.

Rushing.— The animal usually has an elongated posture. The ears are erect and the eyes are wide open. When the opponent is reached, the animal may strike at it with its forepaws. This is the major aggressive movement.

Chase.— The animal runs after the opponent and tries to bite its rump.

Nest defense.— This usually involves an upright posture in defending a nest area from an opponent. It may involve short elongate rushes whereby the defender rushes in short spurts, not straying far from its nest area.

Escape leap.— Wild erratic jumps are used to escape a rush or subsequent chase.

Fighting usually began within the first two minutes after the partition was lifted and was initiated by *P. longimembris* in 11 of 12 interactions. The predominant patterns during interactions were rushing by *Perognathus* and escape leaping by *Microdipodops*. *Perognathus* was usually deliberate in rushing *Microdipodops* and when moving away it assumed a slow quadrupedal gait. *Microdipodops* defended its nest area vigorously during interactions but was usually driven away by *Perognathus*. Rushing by *Perognathus* also induced *Microdipodops* to defend its nest area via an upright stance or via a partial rush; that is, *Microdipodops* started to rush *Perognathus* but stopped short, not advancing far from its nest area. If *Microdipodops* escape leaped, *Perognathus* usually moved away or, rarely, chased *Microdipodops*. If *Microdipodops* defended its nest area, *Perognathus* would usually move away only to return several seconds later, rush *Microdipodops* and take over its nest area. *Microdipodops* only entered the *Perognathus* half of the cage after they were rushed or chased. Although Eisenberg (1963) noted chasing and locking fight (two animals meet and lock together by gripping with all four limbs) to be quite common between pocket mice intraspecifically, chasing was not frequent and locking fight did not occur in the present study. During interactions both species squealed in high-pitched tones. However, *Microdipodops* vocalized more often and this usually occurred when defending a nest area.

During 12 interactions of all combinations of sex pairings between *Microdipodops* and *Perognathus*, *P. longimembris* was dominant 11 times (Table 1). In one interaction involving a female of each species, neither individual was clearly dominant over the other. In all other cases, *Perognathus* was clearly dominant regardless of sex. *Perognathus* was equally dominant in both halves of the cage. Since each individual was used in more than one trial, the Mann-Whitney U test (Wilcoxon's two-sample test) was utilized to determine whether *P. longimembris* is significantly dominant over *M. megacephalus*. The Mann-Whitney U test in this case can be computed as the number of times a *P. longimembris* was dominant over *M. megacephalus* out of the 12 possible combinations (see Sokal and Rohlf, 1969). In this case, the "U" of the Mann-Whitney U test is either 0 or 1; the probability of this occurring if there is no difference between the species is either $\frac{1}{35}$ or $\frac{2}{35}$ ($\frac{1}{35} < P < \frac{2}{35}$). Thus, *P. longimembris* is significantly dominant over *M. megacephalus*. How does this compare with Grant's (1972) generalization that larger species are usually dominant over smaller species? We decided to compare differences in weights between the two species by utilizing Student's t test for the difference between mean weights and found that *P. longimembris*, the dominant species, was significantly lighter ($P < 0.05$; $N=4$, $\bar{X}=7.38$g, SE±0.69) than *Microdipodops* ($N=3$, $\bar{X}=10.5$g, SE±0.88).

The dominant-subordinate relationships between these two species may be a mechanism by which these species are ecologically separated in the field. O'Farrell's (1973) population study of the desert rodents in the same area where we collected our experimental ani-

TABLE 1. Dominance relationships in *Microdipodops megacephalus* (Mm)—*Perognathus longimembris* (Pl) interactions. Percentages are in parentheses. dom = dominant

Combination	Number of interactions	Mm-dom	Pl-dom	None-dom
Male Mm-Female Pl	2	0	2	0
Male Mm-Male Pl	2	0	2	0
Female Mm-Male Pl	4	0	4	0
Female Mm-Female Pl	4	0	3	1
Totals	12	0	11 (91.7)	1 (8.3)

mals lends credence to this idea. His data show that on a 2.7 hectare grid *M. megacephalus* emerged in early March and steadily increased until the middle of April. Towards the end of April, a steady decline of *Microdipodops* corresponded with the emergence and increase in numbers of *P. longimembris.* During the summer very few *Microdipodops* were captured and *Perognathus* covered the entire grid. In September *Perognathus* activity declined and *Microdipodops* activity again increased. Throughout the spring and fall, the centers of activity of the two species did not overlap. Thus, they were spatially isolated. O'Farrell (1973) believes that *P. longimembris* is the more general species and occupies a broader niche than *Microdipodops* because it was found on all habitat types on the grid while *Microdipodops* was generally restricted to areas of fine, loose sand. Furthermore, O'Farrell (1973) believes that *M. megacephalus* probably occupies an included niche within the fundamental niche of *P. longimembris* (see Miller, 1967, for terminology). An interesting situation may exist in Warm Springs Valley because the more general species (*P. longimembris*) appears to be competitively superior to the specialized species (*M. megacephalus*). This is not common, according to Miller (1967). He stated that if there are two sympatric species one of which occupies a smaller included niche within the broader niche of the other, then for coexistence to continue, the species occupying the smaller niche must be the superior competitor.

How, then, has *Microdipodops* avoided extinction? The answer to this question lies in the temporal aspects of the niches of the two species. As stated above, O'Farrell (1973) found that *P. longimembris* is active primarily during the summer while *M. megacephalus* is active primarily during the spring and the fall. Thus, temporally, *P. longimembris*, the superior competitor, has the narrower niche; and if a time axis were included in *Microdipodops*'s fundamental niche, this species niche would not be totally within the fundamental niche of *P. longimembris.* Presumably, *M. megacephalus* would not show decreased summer activity if *P. longimembris* were absent. When the temporal components of the niche are taken into account, it is seen that this system may conform to Miller's (1967) generalization. The dominant-subordinate relationships shown by our laboratory results and the fact that *M. megacephalus* apparently becomes rare as *Perognathus* increases in summer may indicate that interspecific aggression is one mechanism by which ecological isolation is maintained between *P. longimembris* and *M. megacephalus* in the field.

We would like to thank Drs. Fred A Ryser, Jr., and Beatrice Gardner (University of Nevada, Reno) for critically reviewing early drafts of the manuscript. Dr. Michael J. O'Farrell (Savannah River Ecology Laboratory) critically reviewed an earlier draft of the manuscript and allowed us access to some of his unpublished data. For this we wish to express our appreciation. Dr. Allan Oaten (University of California, Santa Barbara) helped with the statistical analysis of the data. Special thanks go to Dr. Stephen I. Rothstein

(University of California, Santa Barbara) for critically reviewing the manuscript and offering many helpful suggestions.

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LIST OF INSECT TYPE SPECIMENS IN THE ENTOMOLOGICAL COLLECTION OF BRIGHAM YOUNG UNIVERSITY, PROVO, UTAH, NO. V.

Vasco M. Tanner[1]

Abstract.— Type material added to the Brigham Young University Life Sciences Museum insect collection includes 6 holotypes, 5 allotypes, 106 paratypes, 78 cotypes, 48 homotypes, 1 metatype, and 1 androtype.

Since the previous lists (I-IV)[2] were published, the following type specimens have been added to the University Type Collections. Thousands of specimens have also been added to the research collection. The pinned collection now consists of more than 900,000 specimens. These are arranged in cabinets, catalogued as to orders, families, genera and species. Fortunately, rather intensive collecting was conducted in many areas of this region prior to the changes that have been made in the lands, watersheds, and drainage of the Great Basin. The biota of one hundred years ago is now greatly changed. Introduced plants and animals, along with killing and poisoning activities, have reduced and may have exterminated some species.

In 1974, Mrs. Lucile Maughan Johnson, wife of the late D. Elmer Johnson, contributed their bee-fly (Bombyliidae) collection to the Life Sciences Museum at Brigham Young University. This collection consisted of 6,400 pinned specimens. Included in it are many type specimens.

Order Hemiptera

Family Belostomatidae

Abedus herberti utahensis Menke
Univ. Calif. Publ. Ent. 16(8):423-424. 1960.
3 paratypes: St. George, Utah; V-1917. V. M. Tanner.

Order Homoptera

Family Hydrometridae

Hydrometra becki Drake
Bull. So. Calif. Acad. Sci. 50(2):103. 1951.
3 paratypes: Solomon Islands; Guadalcanal: VI-30-1944. D. E. Beck.

Order Coleoptera

Family Cantharidae

Malthodes thedae Fender
Northwest Sci. 42(3):108-110.
Holotype (male): Hat Creek, Lassen National Forest, California; VI-24-1961, S. L. Wood, J. B. Karren, and D. E. Bright.

Family Elateridae

Megopenthes apacheorum Becker
Canadian Ent. 103(2):157-160. 1971.

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[1] Department of Zoology, Brigham Young University, Provo, Utah 84602

[2] List I. Proc. Ut. Acad. Sci., Arts, and Letters 12:181-193. 1935. List II. Proc. Ut. Acad. Sci., Arts, and Letters 13:147-152. 1936. List III. Great Basin Nat. 29:150-164. 1969. List IV. Great Basin Nat. 29:183-205. 1969.

2 paratypes: 1 mi. south of Prescott, Yavapai Co., Arizona; VIII-1-1962, S. L. Wood, J. B. Karren, H. Shurtleff.

Family Tenebrionidae

Edrotes leechi Doyen
Pan. Pacific Ent. 44(3):218, 1968.
2 paratypes: Arches National Monument, Grand Co., Utah; VII-25-1965, J. Doyen, on sand dunes at night.

Family Curculionidae

Tychius badius Clark
Brigham Young Univ. Sci. Bull. Biol. Ser. 13(3):25-26, 1971.
4 paratypes (two males, two females):La Plata Co., Mancos, Colorado, W. E. Clark, V-1969; sweeping *Astragalus scopulorum*.

Tychius phalarus Clark
Brigham Young Univ. Sci. Bull. Biol. Ser. 13(3):31-33, 1971.
2 paratypes (one female, one male):Organ Pipe Cactus National Monument, Dripping Springs, Arizona; IV-1969, W. E. Clark.

Protostrophus peninsularis Mshl.
Ann. Mag. Nat. Hist. (12)6:323.
6 cotypes: South Africa, Cap Penin. Ralk Bay; XI-1950, G. A. K. Marshall.

Stenoscelis lefevrei Mshl.
Ann. Mus. Congo Belge (Ser. 8) Sci. Zool. 25:23.
5 cotypes: 5 Mulimgu. P. C. Lefevre. 1951. P.C.L. 586. Coll. R. Mayne, Com. Et. Bois. Congo, R. 2354.

Celetes bondari (Mshl.)
Rev. Ent. Rio de J. 14, 1943.
5 cotypes (2 male, 3 female):Brazil. Bahia, 1939, Dr. G. Bondar, #2625.

Conotrachelus leucophrys Mshl.
Rev. Ent. Rio de J. 11:646, 1940.
3 cotypes (1 male, 1 female):Brazil, Bahia, G. Bondar, #1519; (1 female): Brazil, Bahia, 1935 Dr. G. Bondar, #1880. In fruit of *Bacuparymirim*.

Opterus waigeensis Mshl.
The Otiorrhynchine Curculionidae of the Tribe Celeuthetini (Col.) British Museum, p. 93, 1956.
1 cotype (female): Waigen, Browning 63-47.

Cyrionyx pipesis Mshl.
Ent. Mon. Mag. 76:176, 1940.
6 cotypes (male): British West Indies, St. Lucia, 1000 ft. XI-20-1939, R. G. Gennah, #324, on *Pipes* sp.

Aspidomycter lunatus Mshl.
Ann. Mag. Nat. Hist. (11)10:109, 1943.
2 cotypes (female): Gopaldhora, Rungbong Vall., Sikkim, H. Stevens, 1916-218.

Macrocorynus inermipeo Voss
Rev. Ent. Rio de J. 18:57, 1947.
3 paratypes: L. edoardo. Ecydor. V-22-1938.

ORDER DIPTERA

Family Bombyliidae

Parabombylius subflavus Painter
Ent. News 37:76, 1926.
1 homotype: Arivaca, Arizona; III-12-1940, L. C. Knitert.

Heterostylum crocrum Painter
Kans. Ent. Soc. Jour. 3:6, 1930.
1 homotype: Gidding, Texas; V-5-1954, R. H. Beamer.

Heterostylum robustum Osten Sacken
(U.S. Dept. Int.) U.S. Geol. Geog. Survey Ter. Bull. 3:257, 1877.
1 homotype: Texas, Belfrage.

Lordotus apiculus Coq.
Ent. Amer. 3:116. 1887.
1 homotype: Dugway Proving Grounds, Tooele Co. IV-23-1956., D. E. Johnson.

Lordotus bucerus Coq.
Amer. Ent. Soc. Trans. 21:110, 1894.
1 homotype, Ehrenberg, Arizona; IV-16-1934. F. H. Parker.

Lordotus junceus Coq.
West Amer. Sci. 7:198, 1891.
2 homotypes: Amortajada Bay, Isla San José, Gulf of California, Mexico; III-25-1953.

Lordotus m. miscellus Coq.
Ent. Amer. 3:116, 1887.
2 homotypes: Walker Pass, California; IX-16-1945, D. E. Johnson.

Lordotus perplexus Johnson and Johnson
Great Basin Nat. 19(1):16, 1959.
4 paratypes: San Diego, California.
2 paratypes: Sabino Canyon, Arizona.

Lordotus ermae Hall
Pan-Pacific Ent. 28:49, 1952.
2 paratypes: Tanbark Flat, Los Angeles Co., California; VI-20-1950, J. C. Hall.
1 paratype: Johnston Point, Los Angeles Co., California; VII-14-1950, R. Schuster.

Lordotus lutescens Johnson and Johnson
Great Basin Nat. 19(1):15, 1959.
Holotype and Allotype: Las Cruces, New Mexico; IV-25-1954, R. H. Beamer.

Geminaria canalis Coq.
Ent. Amer. 3:115, 1887.
1 homotype: Tucson, Arizona: IV-23-1937, O. Bryant.

Aldrichia ehrmani Coq.
Amer. Ent. Soc. Trans. 21:94, 1894.
1 homotype: Robertson, Carlinville, Illinois.

Toxophora pellucida Coq.
Ent. Amer. 1:222, 1886.
1 homotype: Patagonia, Santa Cruz Co., Arizona; VIII-25-1955, F. G. Werner and G. D. Butler.

Toxophora vista Coq.
West Amer. Sci. 7:199, 1891.
1 homotype: Skull Valley, Tooele Co., Utah; VI-14-1956, D. E. Johnson.

Toxophora maxima Coq.
Ent. Amer. 1:222, 1886.
2 homotypes: Geddings, Texas; V-10-1954, L. D. Beamer.
1 homotype: Tucson, Arizona; VII-14-1954, G. D. Butler.

Aphoebantus borealis Cole
Calif. Acad. Sci. Proc., Ser. 4.11:251, 1921.
1 homotype: San Antonio, R. S. Santa Clara Co., California: VI-27-1953, R. A. Schuster.

Aphoebantus tardus Coq.
West Amer. Sci. 7:10, 1891.
2 homtypes: Dateland, Arizona; IV-2-1955, Butler and Wernest.

Dicranoclista vandykei Coq.
Amer. Ent. Soc. Trans. 21:94, 1894a.
1 homotype: Davis Mountains, Texas; IV-17-1954, L. D. Harmer.

Villa syrtis (Coq.)
Amer. Ent. Soc. Trans. and Acad. Nat. Sci. Phila., Ent. Sect. Proc. 14:173, 1887a.
1 homotype: San Bernardino Co., California, May.

Villa cinerea Cole
Calif. Acad. Sci. Proc., Ser. 4,12:299, 1923.
1 homotype: Inyokern Co., California; V-21-1945, D. E. Johnson.
2 homtypes: Sabino Canyon, Arizona; IV-30-1956, G. D. Butler.
1 homotype: Mesa, Arizona; IV-10-1952, D. E. Johnson.

Villa flavipilosa Cole
Calif. Acad. Sci., Ser. 4,12:303, 1923.
3 homtypes: Sabino Canyon, Pima Co., Arizona; V-5-1955, G. D. Butler.

Villa meridionalis Cole
Calif. Acad. Sci. Proc., Ser. 4,12:292, 1923.
1 homotype: Oracle Junction, Pima Co., Arizona; VII-1948, F. Werner.

Villa vigilans (Coq.)
Amer. Ent. Soc. Trans. and Acad. Nat. Sci. Phila., Ent. Sect. Proc. 14:176, 1887.
3 homotypes: Walker's Pass, California; VIII-16-1945, D. E. Johnson.

Villa crocina (Coq.)
Amer. Ent. Soc. Trans. 19:183, 1892.
1 homotype: Roll, Arizona; VI-13-1957, G. D. Butler.

Lepidanthrax inauratus (Coq.)
Amer. Ent. Soc. Trans. and Acad. Nat. Sci. Phila. Ent. Sect. Proc. 14:170, 1887a.
4 cotypes: San Diego and Sacramento, California.
1 homotype: San Francisco, California; V-21-1922; San Dunes, C. L. Fox.

Lepidanthrax hyalinipennis Cole
Calif. Acad. Sci. Proc., Ser. 4, 12:307, 1923.
3 homotypes: Inyokern, California; VIII-4-1945. D. E. Johnson.
1 paratype: Sanford, Arizona; IX-24-1956, G. D. Butler.
1 paratype: San Francisquito Bay, Gulf of California.
3 paratypes: Tortuga Island, Gulf, California; V-11-1921, E. P. Van Duzee.
1 paratype: Angeles Bay, Gulf, California; VI-23-1921, E. P. Van Duzee.

Lepidanthrax angulus O. S.
Biologia Centrali-Americana, Diptera 1:111, 1886.
1 homotype: Superior, Arizona; V-2-1938, E. C. Crumb.

Lepidanthrax agrestis (Coq.)
Amer. Ent. Soc. Trans. and Acad. Nat. Sci. Phila. Ent. Sect. Proc. 14:171, 1887.
1 cotype: California, Coq.
1 homotype: Delta, Utah; VII-4, D. E. Johnson.

Lepidanthrax painteri Maughan
Kans. Ent. Soc. Jour. 8:56, 1935.
1 metatype: Wendell, Idaho; VI-26-1953, A. R. Gittins, sweeping *Artemisia*.

Poecilanthax tanbarkensis Painter and Hall
Kans. Agr. Expt. Sta. Tech. Bull. 21, 1960.
1 paratype: Tanbark Flat, Los Angeles Co., California; VII-14-1956, R. W. Bushing.

Poecilanthrax vexativus Painter and Hall
Kans. Agr. Expt. Sta. Tech. Bull. 119, 1960.
1 paratype: Trinidad, Colorado; VIII-7-1925, C. J. Drake.

Poecilanthrax butleri Johnson and Johnson
Great Basin Nat. 17(1-2):11, 1957.
12 paratypes: Tucson, Arizona; V-1955, G. D. Butler.

Poecilanthrax marginatus Johnson and Johnson
Great Basin Nat. 17(1-2):14, 1957.
4 paratypes: Zion National Park, Utah, and Juab Co., Utah, A. M. Woodbury.

Poecilanthrax eremicus Painter and Hall
Kans. Agri. Expt. Sta. Tech. Bull. 106:51, 1960.

1 paratype: Near Kingman, Arizona; VII-1952, Beamer, La Berge, Liang.

Poecilanthrax moffitti Painter and Hall
Kans. Agri. Expt. Sta. Tech. Bull. 106:78, 1960.
2 paratypes: Walker Pass, Kern Co., California; IX-26-1957, J. C. Hall.

Poecilanthrax montanus Painter and Hall
Kans. Agri. Expt. Sta. Tech. Bull. 106:82, 1960.
1 paratype: Sheep Lake, Yakima Co., Washington; VIII-6-1940. J. F. O. Clark.

Poecilanthrax sackenii monticola Johnson and Johnson
Great Basin Nat. 17(1-2):23, 1957.
2 paratypes: Emerald Lake, Mt. Timpanogos, Utah Co., Utah; VIII-4, 1950, D. E. Johnson.
1 paratype: Pebble Basin, Idaho; VII-24-1948, D. E. Johnson.

Poecilanthrax fasciatus Johnson and Johnson
Great Basin Nat. 17(1-2):11, 1957.
1 paratype: Cronley, Colorado; IV-2-1939, M. T. James.

Poecilanthrax robustus Johnson and Johnson
Great Basin Nat. 17(1-2):20, 1957.
7 paratypes: Walker Pass, California; IX-29-1945, D. E. Johnson.

Pantarbes pusio Osten Sacken
Biologia Centrali-Americana, Diptera 1:153, 1886.
4 homotypes: Inyokern, California; Ribbonwood, California; Baboquivari Mts., Arizona; and Alpine, Utah Co., Utah.

Pantarbes willistoni Osten Sacken
Biologia Centrali-Americana, Diptera 1:153.
1 androtype: Orgen, New Mexico; IV-20-

Pantarbes capito Osten Sacken
(U.S. Dept. Int.) U.S. Geol. Geog. Survey Ter. Bull. 3:256, 1877.
3 homotypes: California.

Exoprosopa doris Osten Sacken
(U.S. Dept. Int.). U.S. Geol. Geog. Survey Ter. Bull. 3:235, 1877.
1 homotype: Inyokern, California; VIII-5-1945, D. E. Johnson.

Exoprosopa arenicola Johnson and Johnson
Great Basin Nat. 18(3-4):71. 1958.
13 paratypes: Little Granite Mt., Tooele Co., Utah; VII-24-1956, D.E. Johnson.

Exoprosopa butleri Johnson and Johnson
Great Basin Nat. 17(1-2):11, 1957.
4 paratypes: Mesa, Sycamore Canyon and Sacaton, Arizona.

Exoprosopa tiburonensis Cole
Calif. Acad. Sci. Proc. Ser. 4. 12:291, 1923.
2 homotypes: Inyokern, California; VIII-4-1945, D. E. Johnson.

Bombrylius lassenensis Johnson and Johnson, new name
Pallescens is preoccupied. Hesse. 1938. California.
1 holotype, 1 allotype, 5 paratypes: Herlong, California; V-7-14-16-1944, D. E. Johnson.

Conophorus sackeni Johnson and Maughan
Great Basin Nat. 13(1-2):22, 1953.
1 holotype, 1 allotype, 4 paratypes: Herlong, California; V-14-1944, D. E. Johnson.

Oestranthrax farinosus Johnson and Maughan
Great Basin Nat. 13:18, 1953.
1 holotype, 1 allotype, 9 paratypes: Delta, Utah; VII-1943, D. E. Johnson.

Exoprosopa sharonae Johnson and Johnson
  Great Basin Nat. 18(3-4):78, 1958.
  1 holotype: Little Granite Mountain(Tooele Co., Utah.
  1 allotype: Cedar Mountains, Tooele Co., Utah.
  paratypes: Delta, Millard County; Simpron Springs, Tooele Co., Utah, IX-1955, D. E. Johnson.

ORDER HYMENOPTERA
Family Formicidae

Pogonomyrmex guatemaltecus Wheeler
  Psyche 21:149-151, 1914.
  3 cotypes: Zacapa, Guatemala; XII-12-1911, Wm. M. Wheeler, all 3 specimens tipped on one pin.

Pogonomyrmex occidentalis var. utahensis, Olsen
  Harvard Univ. Mus. Compar. Zool. Bull. 77:498, 509, 1934.
  6 cotypes: Zion National Park, Utah; VII-18-1932, W. S. Creighton, all 6 specimens tipped on two pins.

Pogonomyrmex wheeleri Olsen
  Harvard Univ. Mus. Compar. Zool. Bull. 77:496, 511, 1934.
  3 cotypes: Escuinapa, Sinaloa, Mexico, J. H. Batty, all 3 specimens tipped on one pin.

Pogonomyrmex desertorum Wheeler
  Psyche 9:387-388, 1902.
  3 cotypes: Alamito, Presidio Co.; XII-19-1901, all 3 specimens tipped on one pin.

Pogonomyrmex (E.) saucius Wheeler and Mann
  Bull. Am. Mus. Hist. 33:29-31, 1914.
  7 cotypes: Mannesville, Haiti, W. M. Mann, all 7 specimens on tips, on two pins.

Pogonomyrmex desertorum var. ferrugineus Olsen
  Harvard Univ. Mus. Compar. Zool. Bull. 77:496, 506, 1934.
  3 cotypes: College Peak, Tucson, Arizona, P. Klingentery, all 3 specimens on tips.

Pogonomyrmex huachucanus Wheeler
  Psyche 21:151-152, 1914.
  4 cotypes: Miller Canyon, Huachuca Mountains, 5600 feet; XI-11-1910, W. M. Wheeler, all 4 specimens tipped on one pin.

Pogonomyrex similis Olsen
  Harvard Univ. Mus. Compar. Zool. Bull. 77:497, 512, 1934.
  Cotypes: Oracle, Arizona; III-13-1919; North Slope Mount Lemon, at 4500 feet, W. M. Wheeler.

Pogonomyrmex comanche Wheeler
  Psyche 9:392, 1902.
  4 cotypes: Milano, Sabine Co., Texas; V-23-1902, all 4 specimens tipped on one pin.

Pogonomyrmex californicus subsp. *sinaloanus* Olsen.
  Harvard Univ. Mus. Compar. Zool. Bull. 77:55, 504, 1934.
  6 cotypes: Sinaloa, Mexico, Case, all 6 specimens tipped on two pins.

Pogonomyrmex apache Wheeler
  Psyche 9:392, 1902.
  3 cotypes: Fort Davis, Texas, W. M. Wheeler, June, 1902, all 3 specimens tipped on one pin.

Aphaenogastee (Attomyrma)boulderensis M. R. Smith
  Great Basin Nat. 2:120-121, 1941.
  4 paratypes: Boulder Dam, Arizona; V-2-1941, 55661, Vasco M. Tanner.

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The genera and species described as new to science in this volume appear in bold type in this index.

GREAT BASIN NATURALIST

Special Notice

Commencing with volume 35 (March 1975) The Great Basin Naturalist will be combined with the Brigham Young University Science Bulletin, Biological Series under the title of The Great Basin Naturalist. The format will be changed from the present 6x9 inch single column page to a 7x10 inch double column page. The journal will continue to be published quarterly, but the number of pages per volume will increase to approximately 500. Manuscripts up to 100 printed pages (about 200 manuscript pages) in length will be acceptable. Publication and reprint charges will be adjusted to the new format, but will not be significantly different from that indicated below. The subscription rate will be increased to $9.00 per year (outside the United States, $10.00).

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