FIELDIANA
Zoology

Published by Field Museum of Natural History

Volume 65, No. 6 August 25, 1975

Philippine Zoological Expedition, 1946-1947
Millipeds of the Genus *Polydesmorhachis* Pocock (Polydesmida: Platyrhacidae)

RICHARD L. HOFFMAN
RADFORD COLLEGE, RADFORD, VIRGINIA

Until recently, only three species of Diplopoda were known from the large and biogeographically important island of Palawan. Two of them were described by R. I. Pocock over 75 years ago: one, a sphaeropoeid, *Castanotherium hirsutellum* (1895), the other a platyrhacid, *Polydesmorhachis atratus* (1897). Much later, in 1961, J.-M. Demange recorded the harpagophorid *Thyropygus segmentatus* from "Paragua," the old name for the island.[1]

To the best of my knowledge no deliberate collections of diplopods were made on Palawan until 1947, when a party under the leadership of Floyd G. Werner spent 11 weeks there and obtained a fair representation of at least the larger species.[2] An interesting new cryptodesmoid from this material was named by me in 1973, and a new species of *Salpidobolus* (1974a) and two new species of *Spissustreptus* (1975) in the following year.

Regrettably, the Field Museum collections do not appear to contain either of the early Pocock species, but do include three

[1]The recent examination of the "Paragua" specimens in the U. S. National Museum revealed that they are in fact referable to the recently-described *Spissustreptus wallacei* Hoffman. *S. segmentatus* is without much doubt confined to Mindanao and some immediately adjacent islands.

[2]A detailed account of the 1946-1947 collections is given by H. Hoogstraal, 1951, Philippine Zoological Expedition 1946-1947, Narrative and Itinerary, in: *Fieldiana: Zoology*, vol. 33, no. 1, pp. 5-86, pls. 1-7. Details on the collection site at Mount Balabag, type locality of the new species named in the present paper, appear on page 78. The Philippine material, along with much other, was placed in my hands for identification by my colleague, Dr. John Kethley of the Field Museum, to whom I here express my thanks.

US ISSN 0015-0754

Library of Congress Catalog Card No.: 75-20776

Publication 1207

undescribed platyrhacids unquestionably congeneric with *P. atratus*. I take this occasion to validate names for these taxa to augment the known Palawan fauna, as well as to establish the systematic position of *Polydesmorhachis* within its family (hitherto impossible without knowledge of the male genitalia). The genus is an interestingly disjunct taxon endemic to Palawan, having no close affinities with platyrhacids on either Luzon or Borneo.

Polydesmorhachis Pocock

Polydesmorhachis Pocock, 1897, Ann. Mag. Nat. Hist., ser. 6, **8**, p. 445.

Type species.—*Polydesmorhachis atratus* Pocock, 1897, by monotypy.

Diagnosis.—A genus of small to moderate-sized platyrhacids of variable form and coloration; antennae short, moniliform, articles 2 and 3 larger than usual in the family; collum ellipsoidal, widest across its midlength, the lateral ends often tuberculiform; anterior segments not appreciably wider than those following, body profile in general parallel-sided; ornamentation suppressed, metaterga nearly or entirely smooth or coriaceous; epiproct basally quadrate, apically semi-circular. Sterna smooth, elevated, moderately setose, without trace of subcoxal spines. Dorsal coxal condyles large, projecting. Anterior stigmata large, overlapping onto condyle, their dorsal apex projecting laterad.

Gonopod aperture small, rounded-oval, sometimes with high marginal rim; gonopods relatively small, slender, projecting forward onto sternum of 6th segment; no true sclerotized sternum between coxae, latter of normal shape, with a small field of unmodified macrosetae on dorsal side; telopodite ending apically in two branches (A and C) of which the smaller, median branch is the solenomerite; prostatic groove running up median face of telopodite, but distally curving over to the ventral side (an unusual feature in the family) to attain entry onto the solenomerite.

Distribution.—So far as known, endemic to Palawan.

Species.—Four are known, three of them apparently syntopic at one locality (!), probably as many as 10 to 20 species actually exist.

Relationships.—In the present state of our knowledge, I am unable to ally this genus with any so far known. The course of the prostatic groove appears not to be duplicated elsewhere in the family.

Remarks.—Pocock based this genus upon a single female from Palawan Island, without precise locality. His generic diagnosis was not comparative, and the only thing mentioned that does not apply to most platyrhacids is the formation of the collum (". . . broadest across the middle, where on each side it is furnished with a conspicuous tuberculiform keel"). Still the species could not be referred, due to its overall appearance, to any of the groups then

known to Pocock, and he was no doubt justified in suspecting that the male sex would present supplementary characters in the gonopods.

The four species known at present are relatively small platyrhacids, and quite slender for the family (W/L ratio about 14-18 per cent). It is moreover interesting that specific characters are manifest not only in gonopod structure, but also in peripheral features as size, color, shape of collum and of paranota, relative positioning of the paranota, location of ozopores, form of gonopod socket, and details of surface decor such as supra-coxal tubercules and the presence or absence of facial setation. It is easy to distinguish species by the unaided eye, from either males or females, so that the following key relies entirely on external characters.

There is appreciable plasticity in the structure of the collum. In one species (*P. macropogon*) the end is "normal" in shape; in *P. werneri* there is an indication of apical modification beginning, in *P. atratus* a definite tuberculiform projection occurs, finally in *P. pococki* the lateral end appears as a distinctly set-off lobe itself studded with small tubercules and like nothing else known in the Platyrhacidae.

In most species the antennae are abruptly broadened beyond the first article, the second and third antennomeres in particular seeming disproportionately massive and fully as wide as the fifth or sixth. The degree to which the anterior stigmata are carried up onto the anterior coxal condyle and thence project laterad from its surface also seems to reach an extreme among members of this genus.

Finally, it may be noted that the roster of apparent evolutionary specializations of this group includes pronounced sexual dimorphism, the females being appreciably longer and more massive than males of the same species; again to a greater extent than I have observed elsewhere in this family.

KEY TO THE KNOWN SPECIES OF POLYDESMORHACHIS

1. Collum of normal platyrhacid form, its lateral ends rounded, not set off; body form broad, the W/L ratio ± 18 per cent; paranota depressed in both sexes, continuing slope of middorsum; genae tuberculate, with long pale silky hairs. *macropogon.*

Collum modified, its lateral ends more or less constricted and set off as a tuberculate lobe or process (fig. 1); body form slender, the W/L ratio ± 14 per cent; paranota horizontal or slightly elevated on at least some segments in both sexes; genae without trace of setae 2

2. Dorsum uniformly brown; anterior paranota of females elevated above the horizontal ..... *atratus.*

   Dorsum with dorsal side of paranota and a median longitudinal band of yellow or white; anterior paranota of females at most horizontal 3

3. Paranota relatively small, tending to be widest across the anterior corners, noticeably emarginate laterally near their midlength, pores opening laterally at base of the emargination (fig. 2) or on the undersides of the marginal thickening on posterior segments ..... *pococki.*

   Paranota larger, widest near their midlength, the lateral edges evenly convex and continuous, not indented, the ozopores opening dorsally on all segments, at some distance from the edge (fig. 9) ..... *werneri.*

Polydesmorhachis atratus Pocock.

Polydesmorhachis atratus Pocock, 1897, Ann. Mag. Nat. Hist., ser. 6, **20,** p. 446.

Type material.—Female holotype, Brit. Mus. (Nat. Hist.) from Palawan Island, without precise locality (A. Everett, leg.).

Diagnosis.—A large species of the genus, length of holotype 61 mm., width 8.5 mm., uniformly piceus dorsally, paranota of anterior segments elevated above the horizontal in the female sex; stricture costulate; metaterga with three transverse rows of tubercules of which the posterior two are very small.

Description (adapted from Pocock, 1897).—Dorsum uniformly brownish black, lateral edges of paranota vaguely yellowish; legs and antennae brown; sterna light brown to testaceous.

Antennae short and robust, their length less than width of second segment.

Collum much narrower than second segment, widest across middle, the lateral ends produced outward into a tuberculiform knob, middorsum medially depressed, a postero-lateral tuberculate convexity on each side. Paranota of anterior and midbody segments broad, turned forward, dorsal surface granular, middorsum of metaterga with three transverse rows of small tubercules, of which only those in the first row are prominent. Ozopores completely marginal in a lateral indentation, directed outward.

Remarks.—The holotype was examined at the British Museum in 1973: I can add nothing to the original statements given by Pocock. Many of the features stated by him in the generic diagnosis apply only to the type species, and have so been combined in the above description.

In the majority of its characters, this species appears to be most closely related to *P. pococki,* in particular the modification of the collum ends and emargination of the paranotal lateral edge. *P. atratus* is perhaps to be sought in lowland forests, but I have no knowledge of the collector's travels on Palawan to suggest where he might have picked up the type specimen.

Polydesmorhachis pococki, new species. Figures 1-3.

Type material.—Male holotype, one male and one female paratype (Field Museum) from south slope of Mount Balabag, 4200 ft., Mantalingajan Range, Palawan, P. I.; May 10-14, 1947 (F. G. Werner).

Diagnosis.—The smallest and slenderest member of the genus (males less than 6.5 mm. wide); dorsum brownish with a narrow median whitish longitudinal stripe; paranota small, subquadrate, slightly elevated above the horizontal, the lateral edges thickened, pores opening laterally or sublaterally at the base of a broad emargination; metaterga virtually smooth except on first two or three and posteriormost five or six segments where three rows of about equally distinct small tubercules occur. Lateral ends of collum strongly modified, abruptly tuberculiform. Process C of gonopod relatively short, elongate-triangular.

Holotype.—Adult male, ca. 46 mm. in length, 6.2 mm. in width at midbody, W/L ratio 13.6 per cent. Body form elongate and slender, the paranota widely separated by the only slightly telescoped segments, imparting a loosely-articulated facies. Segment 2 the widest (but its paranota depressed), segments 3 and 4 slightly narrower, segments 5-17 about the same width, 18 and 19 abruptly narrower, epiproct large, elongate-hemispheric in outline.

Coloration altered by preservation and obscured by covering of dirt, but in general light brown overall, the prozona darker, each with a yellowish subtrapezoidal middorsal spot; middorsal area of each metatergum with a poorly- defined light area, giving effect of a continuous middorsal light stripe about one- fourth as wide as metatergal width. Ventral side of segments and bases of legs pale yellowish-brown.

Head finely granular, flattened in front, encrusted with dirt except for labrum; genae apically strongly convex and tuberculate. Antennal sockets separated by space about half the diameter of one socket; antennae massive, short, articles 2 and 3 as large the others and distinctly larger than 1.

Collum small, slightly wider than long, dorsally flattened with two low convexities toward the posterior-lateral corners, lateral ends constricted and abruptly set off as prominent large tubercules; a row of eight tubercules along the anterior margin, each paramedian convexity with three large and a number of smaller tubercules (fig. 1).

Paranota of second segment large, elevated, strongly convex and thickened, directed forward at about a 30° angle, with dorsolateral submarginal tubercules showing through the dirt-incrustation, and about three irregular transverse series of middorsal tubercules, those along posterior margin the largest.

Body segments 3 through 19 generally similar in form, the paranota of the shape shown in Figure 2, except for becoming slightly caudally directed on posteriormost segments, with the ozopores shifting position to open ventrolaterally almost at the caudal angle of paranota on segments 18 and 19. Surface of prozona densely set with minute elongate tubercules; stricture not sharply defined, its surface smooth. Sides of segments smooth. Dorsal coxal condyles enlarged and projecting laterally. Anterior stigmal opening large, a vertically-elongated slit on an elevated ridge above and in front of the coxal condyle, and projecting forward over the stricture; posterior stigma similar in size and shape but set on a smaller ridge located between the two condyles.

Sternal areas elevated, about as wide as combined length of coxa and prefemur, without trace of subcoxal spines but with two prominent transverse rows of large setae. Legs robust, without peculiarities, the relative lengths of podomeres: $3 > 6 > 2 > 5 = 4 = 1$, the femur by far the longest segment. Ventral sides of segments invested with fairly long setae, dorsal sides with much shorter and usually curved setae. Tarsal claw short, nearly straight, unmodified.

Sternum of segment 6 excavated medially to receive tips of gonopods, this excavation resulting in large, densely setose, rounded subcoxal sternal lobes at base of each leg. Gonopod aperture of normal form, ovoid in shape, with elevated posterior margin and with a low projecting knob on each side in front of the stigmal opening. Gonopod coxae flattened as usual, with a small field of unmodified macrosetae on the dorsal side. Telopodite relatively short, only slightly curved dorsad, terminating in a moderately small, elongate-triangular tibiotarsus (C), from the base of which on the median side projects the slender arcuate solenomerite (A) as represented in Figure 3.

Topoparatype.—Adult female, 55 mm. in length, 7.8 mm. in width at midbody; W/L ratio 14.6 per cent. Generally similar to male in appearance except tuberculation more prominent (12 tubercules in anterior series on collum, 5 major tubercules in each paramedian convexity), middorsal stripe somewhat wider than in male, and lateral edges of paranota nearly straight, not emarginate adjacent to the ozopores.

Etymology.-The species is named in honor of Reginald Innes Pocock, an outstanding early student of Diplopoda and other arthropods, Keeper in the British Museum and later Director of the London Zoological Garden in Regent's Park.

Polydesmorhachis macropogon, new species. Figures 4-7.

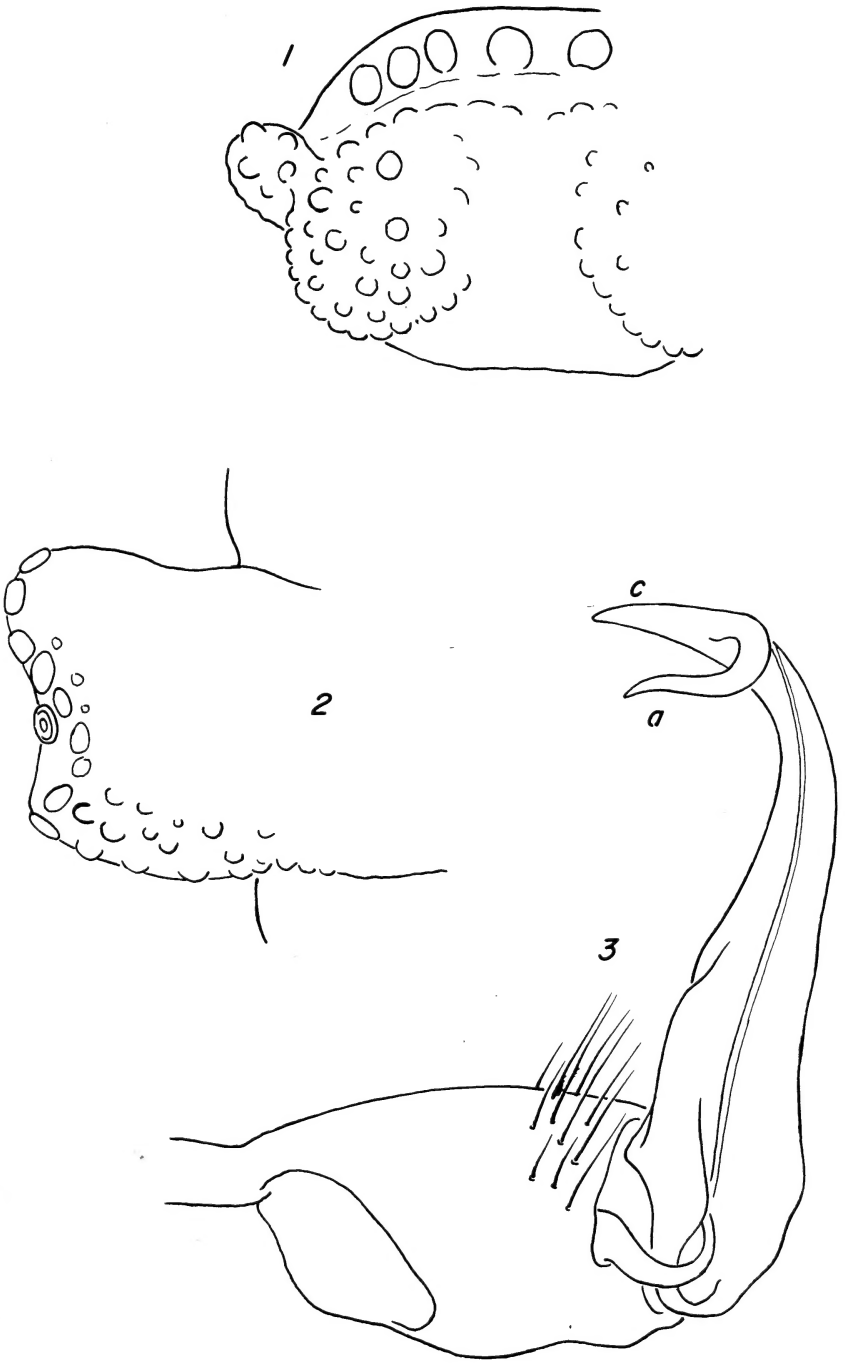
Type material.—Male holotype, eight male and six female paratypes (Field Museum) from south slope of Mount Balabag, 4200 ft., Mantalingajan Range, Palawan Island, P. I.; May 10-14, 1947 (Floyd G. Werner).

Diagnosis.—A moderately large and unusually broad member of the genus (W/L ratio 18-19 per cent), characterized in particular by the setose genae; normal outline of the collum; smooth and depressed paranota; and presence of an elongate projecting tubercule (or cluster of smaller ones) above the posterior coxal condyle. Dorsum uniformly black with outer half of the paranota yellow. Process C of gonopod short, uncinate, recurved mesad; process A curved mesad and dorsad, more slender than in the other two species in which males are known.

Holotype.—Adult male, length ca. 47 mm., maximum width 8.8 mm. at midbody; W/L ratio 18.7 per cent. Body widest at segment 7, thence tapering very gradually posteriad; 2nd segment actually the widest but its paranota strongly depressed ventrad. Segments relatively compact, the paranota nearly in contact.

Opposite.

FIGS. 1-3. *Polydesmorhachis pococki,* new species. **1.** Left side of collum, dorsal aspect. **2.** Left paranotum of 10th segment, dorsal aspect. **3.** Left gonopod, mesal aspect. *a,* solenomerite; *c,* tibiotarsal process.


1
2
c
c
a
3

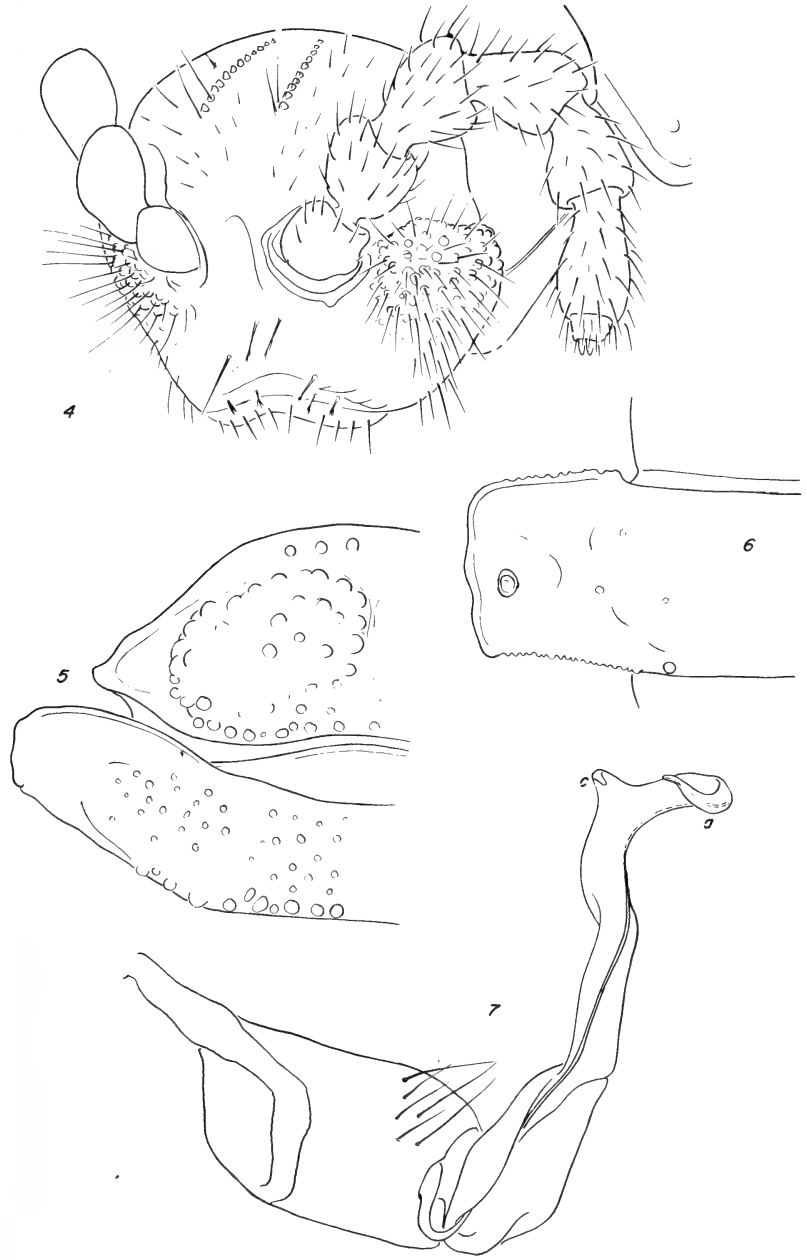
Coloration altered by preservation, but giving impression of originally uniform black dorsally with outer half of paranota yellow, this color extending inward along anterior margin nearly to base; legs also apparently yellow in life.

Head (fig. 4) flattened in front, labrum, clypeus, and frons smooth and polished, epicranium and genae tuberculate and dirt-incrusted, the former sparsely set with large stiff macrosetae, the latter with numerous long pale silky hairs. Epicranium with median depression, each side of which occurs a paramedian, anteriorly divergent low ridge composed of a series of small blackened tubercules. Interantennal space about equal to length of 1st antennomere, deeply depressed, the adjacent margins of antennal sockets with prominent elevated smooth rims. Antennae short, massive, the articles almost as wide as long, all sparsely setose, none with sensory areas.

Collum (fig. 5) transversely oval, slightly wider than head across genae (6.0 mm.), the lateral ends depressed, subacuminate, apically rounded, no trace of modification as in the other species, dorsal surface coriaceous, front and rear edges with traces of low rounded tubercules; a very shallow submarginal groove across middle behind front edge. Paranota of second segment long, slender, directed forward and downward, subtending ends of collum; those of third and fourth segments similar but not so wide and less depressed, margins of all set off by a narrow rim; posterior edge of metaterga with a single row of small round tubercules, largest near posterior edge of paranota but not continuing thereonto. Segments 5-16 subsimilar in appearance, the paranota almost directly transverse (fig. 6), nearly quadrate in dorsal aspect, those of 5th segment nearly twice as long as those of 4th, making a sharp transition in anterior end of body; anterior and posterior finely denticulate-serrate, lateral edge smooth, very slightly sinuous. Ozopores located slightly posterior to midlength, about the diameter of a peritreme from lateral edge, latter entire, smooth and with a distinct margin. Dorsum of metaterga appearing smooth to the eye, but finely microcoriaceous-granulate with a few scattered tubercules; stricture shallow, poorly defined. Podosterna prominent, not impressed, without trace of subcoxal spines, surface moderately beset with long pale stiff setae. Stigmata elongate vertical slits, the anterior larger, curving up and onto the coxal condyle and projecting laterad free from the surface; posterior smaller, less modified, located just behind anterior condyle and widely separated from posterior condyle. Sides of body with a few scattered, tiny tubercules and, just above posterior coxal condyle, either a single, large, elongate, digitiform tubercule or a cluster of three to six smaller tubercules in the same position.

Paranota of posteriormost segments directed caudad and bluntly acute at their corners; dorsum of the metaterga with three more or less regular transverse series of 8 to 10 widely spaced low, polished, tubercules. Epiproct nearly flat with the sides subparallel near the base, distal margin evenly hemispherical in outline.

Gonopod aperture small, rounded-oval, its edges strongly produced into prominent elevated marginal flange giving the effect of a partial sleeve surrounding bases of gonopods. Latter proportionately larger than in the other two species, lying parallel to each other but bowed outward near their midlength, the apices again in contact and broadly interlocked. Telopodite (fig. 7) bisinuate as seen in median aspect, the setose prefemur less than half telopodite length; process C small, subtriangular, its apex slightly recurved mesad, process A curved dominantly mesad except its termination which is curved dorsad in the direction of process C.



FIGS. 4-7. *Polydesmorhachis macropogon*, new species. **4.** Head, oblique anterior-lateral aspect, setation omitted from right antenna. **5.** Left side of collum and left paranotum of 2nd segment, dorsal aspect. **6.** Left paranotum of 10th segment, dorsal aspect. **7.** Left gonopod, mesal aspect.

Topoparatype.—Adult female, 57 mm. in length, 10.2 mm. in greatest width, W/L ratio 17.9 per cent. Aside from greater size agreeing closely with the male except that dorsal tuberculation is slightly more conspicuous and sterna relatively a little wider.

Etymology.—From the two Greek words, *macros* (long) + *pogon* (beard), in allusion to the genal setation. Masculine gender.

Polydesmorhachis werneri, new species. Figures 8-11.

Type material.—Male holotype, five male and two female paratypes, Field Museum, from south slope of Mount Balabag, 4200 ft., Mantalingajan Range, Palawan Island, P. I.; May 10-14, 1947 (Floyd G. Werner).

Diagnosis.—Easily recognized by the combination of middorsal light stripe; partly modified collum; high-set, nearly horizontal paranota which are widest across anterior corners; distally broadened epiproct; absence of strongly elevated rim around gonopod socket; absence of genal setae and of tubercules on the sides. Processes A and C of gonopod similar in shape, C slightly larger, both apically attenuated and curved anteriodorsad.

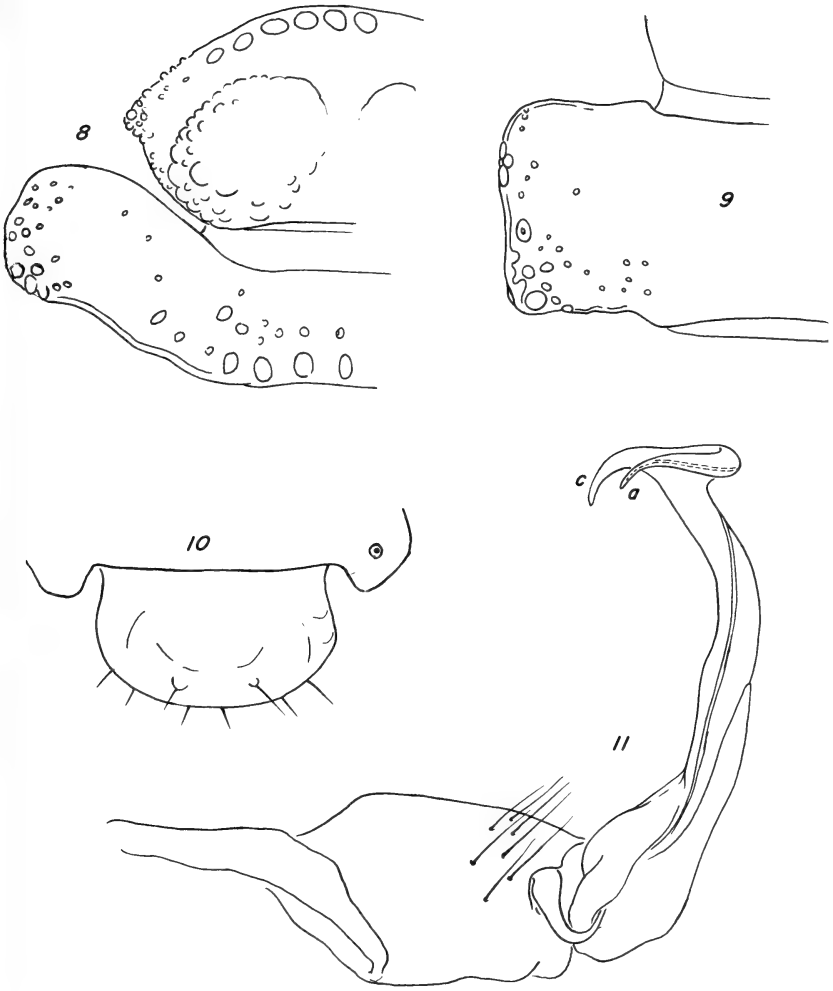
Holotype.—Adult male, length of body ca. 47 mm., 6.8 mm. in width at midbody, W/L ratio 14.5 per cent. Body slender, parallel-sided for most of its length, segments fairly compact and paranota almost in contact. Paranota of segment 2 not notably depressed, giving a width of 7.0 mm., somewhat wider than segments 3 and 4, but segment 5 and several following are equal in width to segment 2.

Dorsum at present light brown, partly obscured by earth incrustation, upper side of paranota lighter, the tubercules testaceous; prozona distinctly darker brown; a narrow (± 1.2 mm.) light middorsal stripe from segment 2 to the penultimate, its edges straight and parallel on prozona, more diffuse and wider on metazona; sterna and legs yellowish-brown, ventrum of prozona nearly white.

Front of head, except labrum and clypeus, roughened and granular, epicranium and especially genae set with prominent rounded tubercules; interantennal space concave, about 1.5 times length of 1st antennomere; socket with prominent polished rim on inner and dorsal sides. Paramedian epicranial ridges obsolete.

Collum (fig. 8) relatively small (4.2 mm. wide), distal surface nearly flattened, with lateral ends projecting at a much lower plane, giving impression of elevated posterior hemisphere sloping down toward front edge; latter with tubercules but without evident submarginal transverse groove.

Paranota of second segment moderately deflexed (fig. 8), tuberculate near the lateral ends but not thickened, distinctly broader than collum and the third segment but being deflexed preserves the approximately parallel-sided profile of the body. Segments 3-19 generally similar, the metazona coriaceously wrinkled middorsally, tuberculation nearly obsolete, but dorsal surface of paranota moderately granulate-tuberculate. Paranota set high on segments, virtually horizontal, the dorsum thus appearing nearly plane; widest across anterior corners and of the form shown in Figure 9; peritreme small, removed from lateral edge by a space equal to its diameter. Sides of segments vertically wrinkled, with scattered microtubercules. Posterior stigmal lobe as large as anterior, extending further dorsad and turned outward



FIGS. 8-11. *Polydesmorhachis werneri*, new species. **8**. Left side of collum and left paranotum of 2nd segment, dorsal aspect. **9**. Left paranotum of 10th segment, dorsal aspect. **10**. Epiproct, dorsal aspect. **11**. Left gonopod, mesal aspect.

apically. Epiproct (fig. 10) constricted at base, broadened distally. Other segmental details about as described for the other species.

Gonopod socket with low, indistinctly elevated posterior rim. Gonopods (fig. 11) elongated, the apical branches interlocked when at rest. Distal processes A and C long, slender, subparallel to each other, curved dorsomesad.

Female topoparatype:—Length ca. 50 mm., greatest width, 8.3 mm., W/L ratio 16.6 per cent. Generally similar to male except paramedian ridges of epicranium distinct; paranota appreciably narrower and depressed so that the dorsum is evenly convex;

dorsal tuberculation more profuse and prominent; sterna broader; middorsal stripe about 50 per cent broader relative to total width of segments.

Etymology:—The species is named for its collector, specialist in Coleoptera and the first person to assemble zoological collections in the interior of southern Palawan.

REFERENCES

DEMANGE, J.-M.

1961. Materiaux pour servir à une revision des Harpagophoridae (Myriapodes-Diplopodes). Mem. Mus. Nat. Hist. natur., n.s., ser. A, **24**, pp. 1-274, figs. 1-386.

HOFFMAN, RICHARD L.

1973. A pterodesmid milliped from the Philippine Islands. Fieldiana: Zool., **62**, no. 2, pp. 21-27, figs. 1-7.

1974. Studies on spiroboloid millipeds. X. Commentary on the status of *Salpidobolus* and some related rhinocricid genera. Rev. suisse Zool., **81**, fasc. 1, pp. 189-203, figs. 1-12.

1975. Studies on spirostreptoid millipeds. XI. A review of some Indonesian genera of the family Harpagophoridae. Jour. Nat. Hist., **9**, pp. 121-152, figs. 1-24.

POCOCK, R. I.

1895. Descriptions of new genera of Zephroniidae, with brief preliminary diagnoses of some new species. Ann. Mag. Nat. Hist., ser. 6, **18**, pp. 409-415.

1897. New genera and species of Millipedes of the family Platyrrhacidae from the Indo- and Austro-Malayan Subregions, contained in the Collection of the British Museum. Ann. Mag. Nat. Hist., ser. 6, **20**, pp. 427-446, figs. 1-191.

FIELDIANA
Zoology

Published by Field Museum of Natural History

Volume 65, No. 7 October 17, 1975

An Additional New *Stenus* from Australia (Coleoptera, Staphylinidae)

100th contribution to the knowledge of Steninae[1]

VOLKER PUTHZ[2]

In my "Revision of the Australian species of the genus *Stenus* Latreille" (1970) I listed one female with doubt under the species *S. maculatus* Macleay. Recently, I found in the Bernhauer collection the corresponding male, thus adding a new species to the *maculatus*-group represented in Australia.

My thanks are due to Mr. H. Dybas, Field Museum of Natural History, for the loan of the material in which the new insect was found.

Stenus (Parastenus) praedictus new species. Figure 1.

Closely related to and resembling *S. maculatus* Macleay and *S. pustulifer* Fauvel.

Description.—Black, moderately shiny, elytra brownish, each elytron with a very large orange-yellow spot. Head coarsely and rather densely punctate; pronotum coarsely punctate; the punctures coalescent in places; elytra with tortuous punctation; abdomen finely and sparsely punctate. Antennae reddish. Palpi entirely reddish-yellow. Legs reddish, bases of femora and tarsi slightly paler, knees infuscate or brownish. Clypeus moderately densely pubescent, anterior margin brownish-yellow. Labrum dark brown, anterior margin paler.

Length : 6.5-8.0 mm.

Head distinctly narrower than elytra (2000:2421μ; measurements given from holotype); frons very broad (average distance between eyes:1082μ), concavely excavated, with two distinct longitudinal furrows; median portion as broad as each of the side portions, distinctly but shallowly elevated, slightly higher than level of inner

[1]Manuscript submitted for publication in August, 1974.

[2]Limnologische Fluss-Station des Max-Planck-Instituts für Limnologie, Schlitż/Hessen, Germany.

US ISSN 0015-0754

Library of Congress Catalog Card Number: 75-18217

eye margins. Punctation coarse and dense; diameter of a puncture about as large as basal cross-section of third antennal segment; antennal tubercles smooth; interstices in narrow median longitudinal area of frons about as wide as diameters of punctures, those alongside middle distinctly smaller than half the diameter of a puncture; a very small smooth area present posteriorly near inner eye margins.

Antennae (paratype) moderately slender, when reflexed extending to about the posterior margin of the pronotum, penultimate segments about twice as long as broad.

Pronotum slightly longer than broad (1635:1588μ), broadest behind middle, sides convex toward anterior margin (see below), distinctly concavely narrowed toward posterior margin. Surface with several deep impressions:one moderately deep, transverse, behind anterior margin; one deep, latero-transverse, somewhat behind middle; one shallow, transverse, near posterior margin; and a deep longitudinal impression medially, which is abbreviated in anterior and posterior fifth. Punctation very coarse, coalescent near posterior third of longitudinal furrow. Diameter of a puncture about as large as largest x-section of 3rd antennal segment, interstices mostly narrower than one-half the diameter of a puncture, those in longitudinal furrow and alongside it sometimes larger, in places fully as large as the punctures.

Elytra distinctly broader than head (2421:2000μ), distinctly broader than long (2421:2064μ), shoulders prominent, sides distinctly divergent posteriorly, restricted in posterior quarter, posterior margin of each elytron separately emarginate in lateral third, inner two-thirds of elytra together deeply emarginate (sutural length:1553μ). Each elytron with a very large yellowish spot (color deepens to orange at outer limits of the spot), rest of elytron dark brown. Spot as shown in Puthz, 1970, fig. 34, or slightly larger, separated from the suture by a distance of about 1½ diameters of a parasutural puncture, laterally extending toward the side margin. Punctation of elytra very coarse, deep, and irregular, more or less distinctly separated near shoulders, at base of elytra, and near suture; rest of elytra with the punctation confluent and on the light-colored portions completely tortuous.

Abdomen broad, moderately narrowed toward apex; paratergites broad with the posterior half depressed, only a few punctures basally; basal furrows of first tergites deep, with a distinct callus beside paratergital suture; 7th tergite with a membranous fringe at posterior margin (the insect is winged). Punctation sparse, about equal from 3rd to 7th tergites, diameter of a puncture nearly as large as one inner eye facet, slightly coarser on last tergites; sides of first tergites with the punctation somewhat denser than in middle, interstices laterally smaller than twice the diameter of punctures, larger medially; 7th and 8th tergites with a denser punctation.

Legs moderately robust, posterior tarsi about three-fifths as long as posterior tibiae, first segment nearly as long as the following four segments together (834-294-200-329-423μ), fourth segment deeply bilobed.

Entire body with a very fine but visible reticulation.

MALE : Trochanters without any spine or tooth. Femora enlarged, posterior femora conspicuously enlarged in about middle, curved in posterior third. Posterior margin of mesotibiae tooth-like, produced; metatibiae with a large preapical tooth. Metasternum shallowly impressed, finely and sparsely punctate, interstices very shallowly reticulated, shiny. Except the 9th, all sternites medially with the punctation finer and denser than laterally and with a dense pubescence; in the

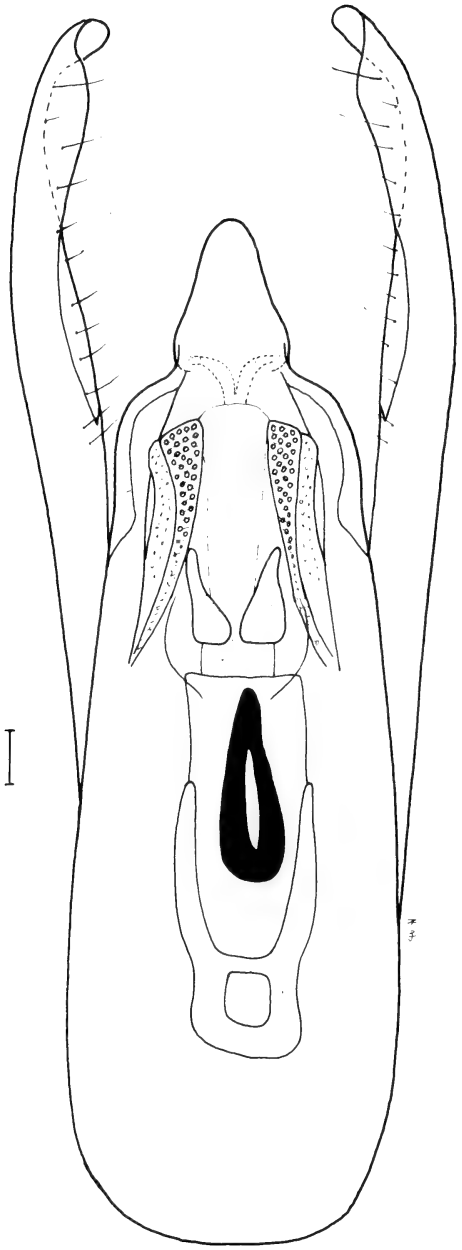


FIG. 1. *Stenus* (*Parastenus*) *praedictus* n. sp. Ventral aspect of aedeagus. Scale = 0.1 mm.

middle of sternites 3 and 4 the pubescence is conspicuously close, short, brush-like. 8th sternite with a nearly parallel-sided notch in about posterior quarter, apex rounded; 9th sternite broadly rounded apicolaterally, shallowly emarginate apicomedially; 10th tergite broadly rounded. Aedeagus (fig. 1): median lobe broad, the apical portion curved, rounded and lancet-like in shape; inside there are longitudinal expulsion bands and three different strongly sclerotized structures (two expulsion mechanisms and the internal sac); parameres much longer than median lobe, with wrinkles and few fine setae.

FEMALE : 8th sternite rounded at posterior margin, slightly produced apicomedially. Valvifers apicolaterally roundly produced. 10th tergite broadly rounded. Spermatheca distinctly sclerotized and spindle-shaped.

VARIABILITY : In the female paratype the punctation of the frons is not as close as in the holotype. Also the pronotum has a different side-outline, being more parallel-sided in the middle, and has a small lateral callus behind anterior 6th. Because this callus is more distinct on the right side than on the left, I am sure that these differences from the holotype reflect intra-specific variation in this new species.

Discussion.—Stenus praedictus n.sp. can be distinguished from *S. maculatus* Macleay and *S. pustulifer* Fauvel by its narrower pronotum, denser and completely tortuous punctation of the elytral spot, and sexual characters.

Because of genital structures, *S. praedictus* must be regarded as a sister species (*sensu* Hennig) of *S. maculatus* and *S. pustulifer.* The new species belongs to a monophyletic group which is derived from the Oriental stock. Other species of that group live in New Guinea (*gigas*-group : see Puthz,1971).

Male holotype: Australia, Queensland, Evelyne, August, Mjöberg leg. (Bernhauer Coll., Field Museum of Natural History, Chicago).

Female paratype: Queensland, Maranda, Hill leg (coll. Puthz).

REFERENCES

HENNIG, W.
1965. Phylogenetic systematics. Ann. Rev. Entomol., **10,** pp. 97-116.

PUTHZ, V.
1970. Revision of the Australian species of the genus *Stenus* Latreille (Coleoptera:Staphylinidae). Mem. Natn. Mus. Vic., **31,** pp. 55-80.

1971. Revision of the Stenus-Species of New Guinea. Part I. (Coleoptera: Staphylinidae). Pacific Insects., **13,** pp. 447-469.

FIELDIANA
Zoology

Published by Field Museum of Natural History

Volume 65, No. 8 October 23, 1975

Notes On Rodents of the Genus *Gerbillus* (Mammalia: Muridae: Gerbillinae) from Morocco

DOUGLAS M. LAY
DEPARTMENT OF ANATOMY
UNIVERSITY OF NORTH CAROLINA AT CHAPEL HILL

The current systematics of rodents of the genus *Gerbillus* from Morocco and adjacent areas of Algeria are based upon the works of Cabrera (1932), Ellerman and Morrison-Scott (1951), and St. Girons and Petter (1965). Much remains to be learned of the distribution, ecology, evolution, and systematics of these rodents in North Africa. Africa.

Species of *Gerbillus* have the plantar surface of the hindfeet either covered with hair or naked and classification reflects this dichotomy at either the generic or subgeneric levels (e.g., Allen, 1939; Ellerman and Morrison-Scott, 1951; Petter, 1959; Wassif et al., 1969; Harrison, 1972; Schlitter and Setzer, 1972). Generally, hairy-footed *Gerbillus* inhabit areas of sand or light sandy soils and naked-footed *Gerbillus* occur on compact substrates containing much rock. This study concerns only hairy-footed species of *Gerbillus.*

During 1971 and 1972, I obtained specimens of *Gerbillus* from several localities in Morocco for cytogenetic study. I visited Morocco in 1973 and collected additional specimens, karyotypes, and data on the environmental and physiographic characteristics of specimen localities. Analysis of this material suggests that at least three medium-sized species of hairy-footed *Gerbillus* occur in Morocco, two of which are described as new.

MATERIALS AND METHODS

Chromosomes were analyzed from cell suspensions of femoral bone marrow (Nadler and Lay, 1967). Karyotypes were arranged in

Library of Congress Catalog Card No.: 75-18214
US ISSN 0015-0754

pairs according to size and centromere position (metacentric, submetacentric, acrocentric). The fundamental number of chromosome arms (FN) is computed by counting biarmed autosomes as two arms and acrocentric autosomes as one arm.

Voucher specimens of karyotyped animals and other specimens were prepared (usually as skins and skeletons) and deposited in the collections of the University of Michigan, Museum of Zoology (UMZ) and Field Museum of Natural History (FMNH). Other specimens and cytogenetic preparations remain in my personal collection (DML), but will ultimately be deposited in the FMNH collection. Specimens in the collections of the British Museum (Natural History) (BM) were used in comparisons.

The following cranial dimensions, useful in distinguishing the taxa treated herein, were taken with dial calipers and rounded to the nearest 0.1 mm.: greatest breadth across the posterior mastoid bullae; greatest breadth across squamous portion of temporal bones; the width of the anterior process of the basioccipital at its articulation with the sphenoid was recorded indirectly as the least width between the medial walls of the tympanic bullae at the level of the above articulation; narrowest point of the interorbital constriction; height from base of tympanic bulla to superiormost point of suprameatal triangle (measured with ventral parts of tympanic bullae and incisors placed on glass slide and then subtracting slide thickness); greatest length of skull; length of nasals from distal tip to frontal articulation; greatest breadth between the lateral tips of the zygomatic process of the temporal bones. The anatomical terminology of middle ear structures follows that of Lay (1972). Color references are based on the color guide of Palmer (1962).

Gerbillus hoogstraali sp. nov.

Holotype. – Adult female, in fluid, skull removed, FMNH, no. 114647, from 7 km. S. Taroudannt, Morocco, elevation about 116 m.; taken on July 16, 1973 by D. M. Lay. This locality lies about 1 km. south of the Sous river.

Description. – A middle-sized species, mean and extremes of standard external measurements of seven specimens are (in mm.): total length, 208.1 (190-221); tail length, 113.8 (103-123); hind foot length, 27.3 (26-28); pinna length, 16.6 (16-17). Dorsal hair color is intermediate to cinnamon and buffy brown and is clearly delimited from the white ventral fur. A whitish postauricular spot exists, but its prominence is reduced due to a buffy suffusion. The posterior borders of the nasal bones at the articulations with frontal bones are either squared off or concave

TABLE 1. Statistical Comparisons of selected cranial variables of *Gerbillus hoogstraali* (H) and *G. occiduus* (O).

Measurements	Species	Number	Range	Mean	Standard Deviation	T values	2-tail probabilities
Greatest breadth across temporals	H	8	13.5-14.0	13.66	0.15	-2.29	.036
	O	10	13.6-14.3	13.91	0.27		
Breadth between tympanic bullae at basioccipital-sphenoid suture	H	8	0.8-1.0	0.90	0.05	6.42	.001
	O	10	1.0-1.7	1.37	0.20		
Breadth of interorbital constriction	H	8	5.2-5.7	5.49	0.05	6.98	.001
	O	10	5.9-6.4	6.03	0.20		
Height of tympanic bulla and suprameatal triangle	H	8	7.2-7.7	7.41	0.16	-2.10	.052
	O	10	6.3-7.4	7.10	0.39		
Length of nasals	H	7	10.5-11.5	11.07	0.32	2.19	.045
	O	10	10.8-11.8	11.42	0.33		

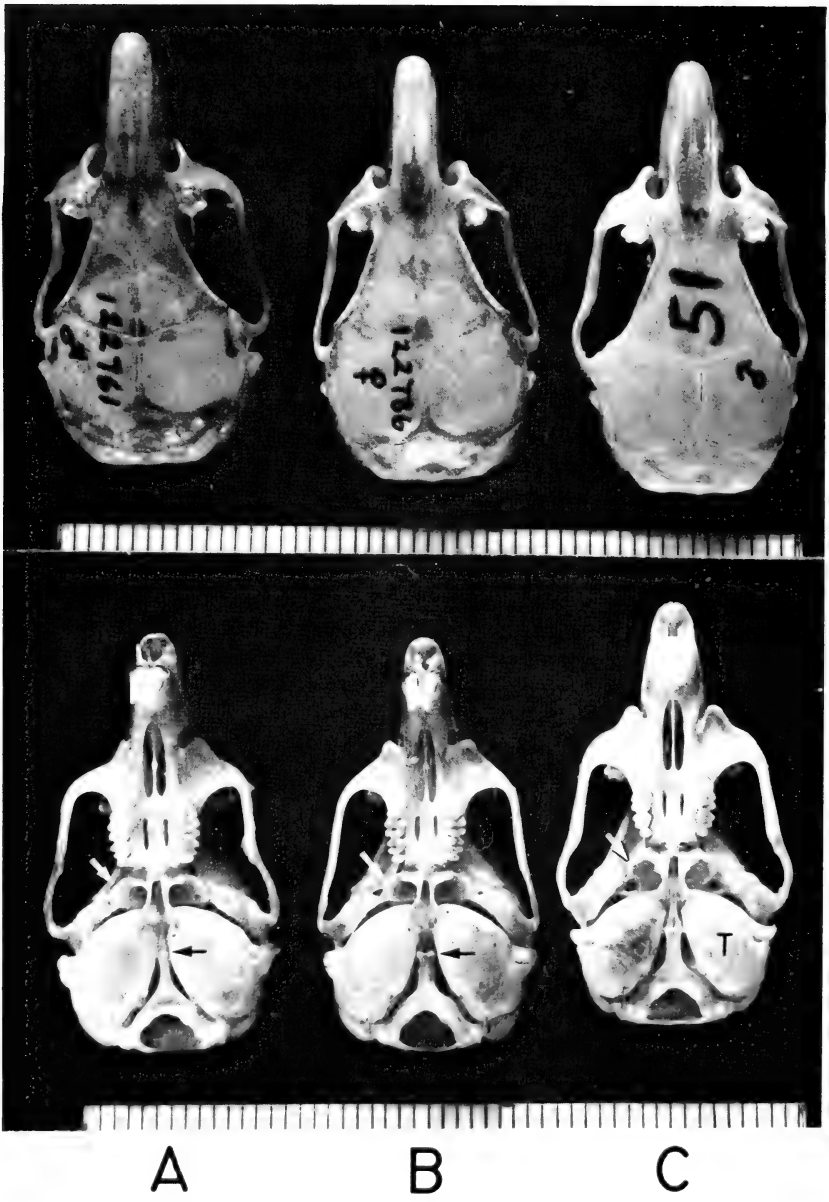


FIG. 1. Dorsal and ventral views of skulls of: **A**, *Gerbillus hoogstraali*; **B**, *G. occiduus*; **C**, *G. hesperinus*. White arrows denote lateral pterygoid processes. Black arrows mark the anterior end of the basioccipital at its suture with the basisphenoid. The letter T is on the ventral surface of the tympanic bulla. Scale units in millimeters.

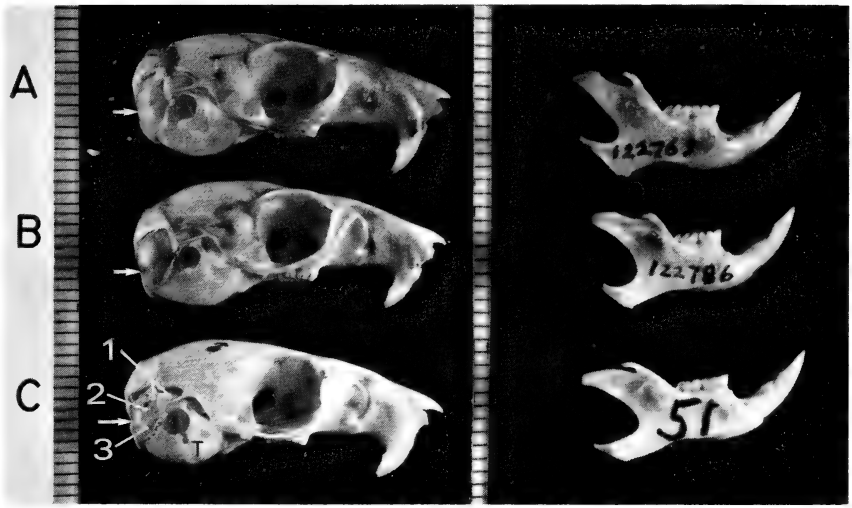


FIG. 2. Lateral view of skulls and mandibles. Black dots mark the extent of the posterior mastoid chambers of the bulla. **1**, Anterior mastoid chamber, **2**, posterior superior mastoid chamber, **3**, posterior inferior mastoid chamber. White arrows denote posterior inferior end of the external line of the septum separating the superior and inferior posterior mastoid chambers. Other symbols as in Figure 1.

anteriorly. The anterior end of the basioccipital bone and the interorbital constriction are relatively narrow (table 1). Diploid number of chromosomes is 72 (fig. 3).

Measurements. – Selected measurements of the holotype are: total length 211; tail length, 121; hind foot length, 28; ear length, 17; greatest length of skull, 29.3; length of nasals, 10.9; breadth across temporals, 13.7; breadth between tympanic bullae at basioccipital-sphenoid suture, 0.9; interorbital constriction, 5.5; height of tympanic bulla and suprameatal triangle, 7.4.

Distribution. – Presently known only from type locality, but likely occurs in suitable sandy habitat within the lower Sous valley.

Habitat-Natural History Miscellanea. – The type locality extends approximately 7 km. in both east-west and north-south directions and is characterized by areas of low sand dunes (3.5-4.5 m. above level ground) and intervening level ground of hard-packed sandy clay. Fine reddish sand forms a light cover on the hard alluvial surface. During the days of July 16 and 17, 1973 a strong westerly wind shifted loose sand over the entire area.

The principal vegetation consisted of thorny *Zizyphus* shrubs which varied in density but seldom exceeded 1.5 m. in height. Six specimens were trapped at burrow entrances located at the bases of *Zizyphus* stands. No animals were caught elsewhere, but fresh

tracks and diggings indicated activity throughout the area. One large rodent, possibly *Meriones grandis*, was observed in the area at dawn one morning. Shed snakeskins were very numerous in the area but no snakes were observed during night (6 hours) or day (8 hours) observations. One female trapped July 16 showed six placental scars and two subadults (total length 190, 191) were trapped at the same time, indicating a breeding period in the late spring or early summer.

Specimens examined. — Total of 10: 114567 FMNH (type); 117632, 122760-2 UM; 4572-3, 4575-7 DML. Karyotypes are available for three of these specimens.

Remarks. — I take great pleasure in naming this species for Dr. Harry Hoogstraal in recognition of his significant contributions to knowledge of the fauna and medical zoology of North African mammals.

Comparisons. — Pertinent comparisons are provided in the following species account.

Gerbillus occiduus sp. nov.

Holotype. — Adult female, skin and skeleton, FMNH no. 114648 from Aoreora (80 km. WSW Goulimine), Morocco, elevation about 43 m.; taken on January 16-17, 1971 by L. Robbins and J. Gruwell.

Description. — A middle-sized species, mean and extremes of standard external measurements of eight specimens are total length 207.1 (202-213); tail length, 111.0 (103-119); length hind foot, 29.1 (28-30); length pinna, 13.9 (12-16). Dorsal hair color is intermediate to cinnamon and buffy brown and is clearly delimited from the white ventral fur. A prominent white postauricular spot exists. The posterior border of the nasal bones is wedge-shaped or truncated (fig. 1). The anterior end of the basioccipital bone and the interorbital constriction are relatively wide (fig. 1, table 1). Diploid number of chromosomes is 40 (fig. 4).

Measurements. — Selected measurements of the holotype are: total length, 209; tail length, 111; hindfoot length, 29; pinna length, 15; greatest length of skull, 30.7; length of nasals, 12.7; breadth across temporals, 14.2; breadth between tympanic bullae at basioccipital-sphenoid suture, 1.5; interorbital constriction, 6.0; height of tympanic bulla and suprameatal triangle, 7.6.

Distribution. — Presently known from only the type locality.

Habitat-Natural History Miscellanea. — The type locality is an area of sparsely vegetated sand dunes but no other information is available (E.T. Hopper, *in litt.*).

Two pairs of animals trapped wild on January 16-17, 1971 bred beginning in June 1971. One female gave birth to ten litters of the following sizes (dates in parentheses): 3 (June 14), 4 (July 14), 3

(Aug. 22), 5 (Sept. 22), 5 (Nov. 2), 3 (Dec. 10), 5 (Feb. 5, 1973), 1 (Aug. 6, 1972). Another female produced a single litter of four on June 15, 1971. Mean litter size is 3.45. At least four of the litters of the first female totalling 16 progeny, contained six partial albinos: the fur was entirely white but the eyes were black. The ratio of 16 wild: 6 partial albinos suggests that both parents were heterozygous for a simple mendelian recessive locus for partial albinism. All other progeny had wild type coat color. Causes for the failure of these albinos to breed were not determined.

Specimens examined. – Total of 18; FMNH(type) 114648; UMZ 122765-6, 122773-86; DML 4392. Karyotypes are available for nine of these.

Remarks. – The name *occiduus* is Latin for western.

Comparisons. – *G. hoogstraali, G. occiduus,* and *G. hesperinus* Cabrera, 1906 are distinguished by the following cytogenetic, cranial, and pelage characteristics.

Karyotypes of the species differ significantly. *G. hoogstraali* has a diploid complement (2N) of 72, and FN = 80. The karyotype contains six submetacentric and 64 acrocentric autosomes. The sex chromosomes are a large submetacentric and a medium-sized metacentric (fig. 3). *G. occiduus* shows a 2N = 40 and FN = 76. The karyotype shows eight metacentric and 30 submetacentric autosomes. The sex chromosomes are medium-sized metacentrics (fig. 4). *G. hesperinus* Cabrera possesses 2N = 58 and FN = 76. The karyotype reveals 20 submetacentric and 36 acrocentric autosomes. The sex chromosomes are large and medium-sized metacentrics (fig. 5).

The diagnostic cranial features of *G. hesperinus* that distinguish it from both *G. hoogstraali* and *G. occiduus* are: less voluminous auditory bullae with smaller tympanic and posterior mastoid chambers; short and constricted posterior palatine foraminae; narrow lateral pterygoid processes, which produce smaller fossae for the medial pterygoid muscles; small posterior inferior mastoid chamber (about one-half as voluminous as in either of the other two species) (figs. 1, 2).

The crania of *G. hoogstraali* and *G. occiduus* can always be identified by the anterior process of the basioccipital that is broad in the latter and narrow in the former and the least interorbital breadth which varies in the same manner (fig. 1, table 1). This difference in basioccipital width is also constant between subadult

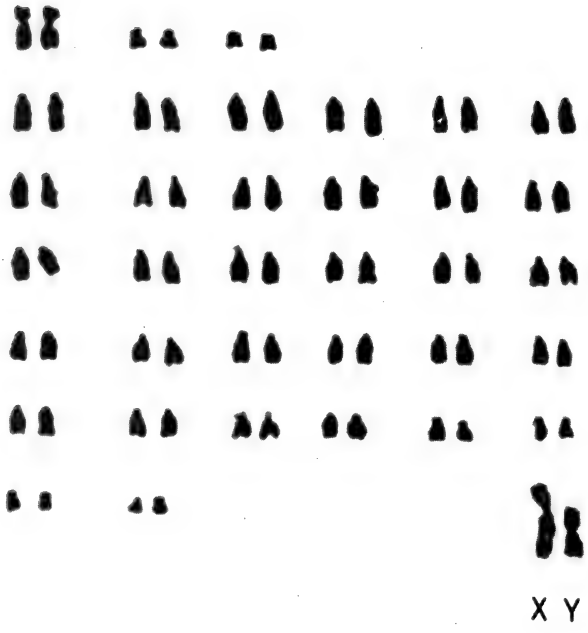


FIG. 3. Karyotype of *G. hoogstraali* with 2N = 72. It is not possible to distinguish between the X and Y chromosomes until female specimens are studied.

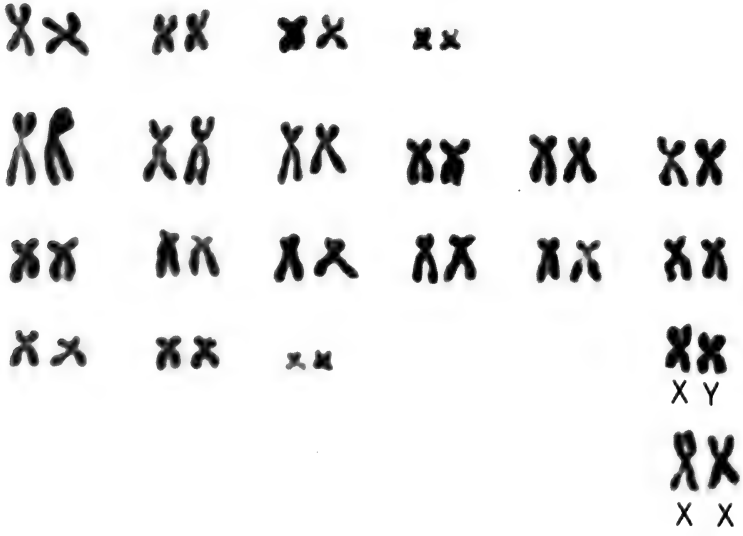


FIG. 4. Karyotype of *G. occiduus* with 2N = 40.

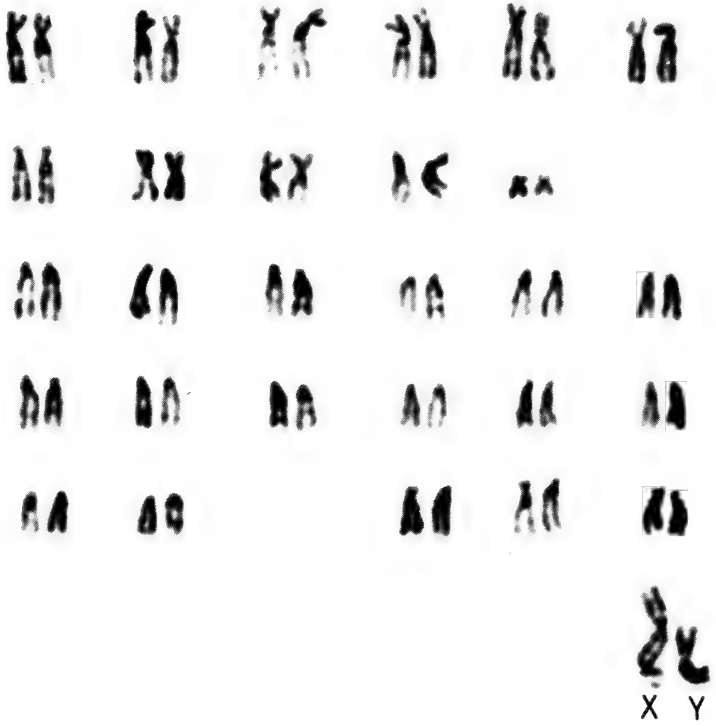


FIG. 5. Karyotype of *G. hesperinus* with 2N = 58. It is not possible to distinguish between the X and Y chromosomes until female specimens are studied.

specimens of both species. The nasal bones (at the articulation with the frontal bones) are truncated into a posteriorly directed wedge in *G. occiduus* but are broader and squared off or are concave anteriorly in *G. hoogstraali* (fig. 1). Beading of the supraoribital ridge is usually more prominent in *G. occiduus* particularly along the posterior third of the ridge (figs. 1, 2). The external orifices of both hypoglossal canals are readily visible when the inferior surface of the skull is viewed from the anterior in *G. occiduus*, but the laterally broadened occipital condyles obscure these canals in *G. hoogstraali*. The portion of the tympanic bullae anterior to the external auditory meatus is more inflated in all dimensions in *G. occiduus* than in *G. hoogstraali* (figs. 1, 2). Further, these two species differ significantly in at least five cranial dimensions (table 1).

These species differ in a number of pelage features. A narrow but distinct dark eye ring characterizes *G. occiduus* but is less prominent than that in *G. hoogstraali*, in which a distinct ring of

dark hairs surrounds the eye. The eye ring of *G. hesperinus* is very similar to that of *G. occiduus*, but lacks the clear white band of hair between the eye and base of pinna that characterizes the latter. The pinnae of *G. occiduus* show a slight, dark pigmentation around the distal free edge while the distal one-half to two-thirds are darkly pigmented in *G. hoogstraali* and *G. hesperinus*. Pinna length of *G. occiduus* averages shorter than in the other two species. Mean pinna length, range, and sample sizes are: *G. hoogstraali* (16.3, 14-17, n = 9); *G. hesperinus* (16.1, 14-19, n = 12); *G. occiduus* (13.8, 12-16, n = 8).

Prominent black terminal rings on the fresh dorsal pelage of *G. hoogstraali* and *hesperinus* give this region a much darker appearance than in *G. occiduus*. Further, the subterminal rings are more cinnamon colored in the former two species; the latter tends toward buffy brown.

Other Specimens Examined. — *G. hesperinus*, total of 14 from Morocco: 5 km. NE-5 km S Essouira (= Mogador), UM 122755-57, 22.5.30.24-31, (BM) 7.6.17.3, DML 4582; Cape Tefelney, (BM) 66.6067.

Discussion. — The ranges of *G. hesperinus*, *G. hoogstraali*, and *G. occiduus* are allopatric, each is apparently limited to a relatively small area of sand, and all lie near or along the Atlantic coast west of the High Atlas and Antiatlas mountains.

The High Atlas extend to the ocean north of Agadir and separate the sandy lowlands inhabited by *G. hesperinus* and *G. hoogstraali*. Similarly, an extension of the Antiatlas reaches the sea south of Tiznit forming a barrier between the ranges of *G. hoogstraali* and *G. occiduus*.

To my knowledge, hairy-footed *Gerbillus* are known to occur only in and around places of abundant, loose sand. Thus, the availability of loose sand seemingly constitutes an ecological constraint on the distribution of these gerbils and particularly the three above-mentioned species. The intervening mountain ranges are formidable barriers. Not only are they almost exclusively rock, but the higher regions support(ed) extensive forests, which could also form a significant barrier to dispersal.

If the distributions of these three species are to be interpreted on the basis of the present geomorphology and ecology of southwestern Morocco, one could conclude that *G. hesperinus* and *G. hoogstraali* dispersed across two and one mountain range,

respectively, to reach their present ranges. Another explanation seems more likely.

The crustal orogeny that produced the present elevations of the High Atlas and Antiatlas mountains began in the late Miocene and continued into the middle Pliocene (Choubert, 1945). The Sous valley, a broad syncline, was formed during the initial uplift of the High and Antiatlas ranges.

Pliocene and Early Pleistocene eustatic sea levels were high (200-300 m. above present MSL), but fluctuated, and most or all of the areas now inhabited by *G. hesperinus, G. hoogstraali,* and *G. occiduus* were inundated (Choubert, 1950). Sea levels for the period between 1,000,000 and 400,000 BP are insufficiently known, but were considerably higher than at present during most of this time (Lecointre, 1952); but, levels during the period from the latter date to the present are known with considerable accuracy (Fairbridge, 1961; Kassler, 1973). Mean sea level varied between 20 and 100 m. above the present level from 400,000 until about 120,000 BP, the beginning of the Riss-Illinoian glacial. The Riss and Wurm glacial, interstadial and interglacial sea level changes are well documented and averaged much lower than present levels (Fairbridge, 1961; Kassler, 1973). The Riss marine regression exposed a corridor along the present continental shelf that at maximum was 9 - 23 km. wide between Aoreora and Essouira. The corridor was open for about 20,000 years and closed during the Monastrian (Sangamon) interglacial. Bottom profiles and contour maps reveal that the continental shelf off Morocco slopes gently seaward from the coast to the 100 m. contour (Heezen et al., 1959). The Wurm regression reopened this corridor for a period of more than 40,000 years, and maximum exposure and width (12-30 km.) occurred about 20-17,000 BP. By 6000 BP, the Flandrian transgression reached present sea levels (Fairbridge, 1961; Kassler, 1973).

On the basis of the known geological record it is unlikely that *G. hesperinus* or *G. hoogstraali* could have spread into south-western Morocco during the Pliocene or early Pleisotcene, assuming that either/both existed then. There is a distinct possibility that hairy-footed *Gerbillus* dispersed northward from the Spanish Sahara region during either or both the Riss and Wurm low stands or possibly at some as yet unknown earlier Pleistocene low stand(s).

The discovery by Tchernov (1968) of fossils of the extant *G. dasyrus* in deposits dated as ± 125,000 BP suggests that other

modern species such as *G. hesperinus* and *G. hoogstraali* could have existed then. In any event, the Flandrian transgression onto the continental shelf seems likely to have isolated the latter two species or their ancestors about 6000 BP.

Additional study of these rodents is necessary to clarify the details of their origin and evolution. Fortunately, what is known of their distribution and affinities offers encouraging prospects for estimating rates of differentiation and speciation within *Gerbillus*.

ACKNOWLEDGEMENTS

I thank E. T. Hooper, H. Setzer, and L. Robbins for specimens. Alan Feduccia kindly criticized the manuscript. Kirk Agerson rendered valuable technical assistance. Funds for part of this research were provided by William and Janice Street and the Medical Foundation of North Carolina.

REFERENCES

ALLEN, G.M.
1939. A checklist of African mammals. Bull. Mus. Comp. Zool., **83**, 763 pp.

CABRERA, A.
1932. Los mamiferos de Marruecos. Trab. Mus. Nac. Cien. Nat., Ser. Zool. no. 57, 361 pp.

CHOUBERT, G.
1945. Note preliminaire sur le Pontien au Maroc (Essai de synthese orogenique du Moroc Atlasique). Bull. Soc. Geol. France, ser. 5, **15**, pp. 677-764.

1950. La limite du Pliocene et du Quaternaire au Maroc. Proc. Int. Geol. Cong., Part IX, section H, pp. 11-18.

ELLERMAN, J.R. and T.C.S. MORRISON-SCOTT
1951. Checklist of Palaearctic and Indian mammals. Brit. Mus. Nat. Hist., London, 810 pp.

FAIRBRIDGE, R.W.
1961. Eustatic changes in sea level, pp. 99-185 *in* Ahrens, L.H., F. Press, K. Rankama, and S.K. Runcorn, eds., Physics and Chemistry of the Earth, vol. 4, New York.

HARRISON, D.L.
1972. The mammals of Arabia, vol. 3. E. Benn Ltd. London, pp. 385-670.

HEEZEN, B.C., M. THARP, and M. EWING
1959. The floors of the oceans. Geol. Soc. America, Spec. Paper, **65**, 122 pp.

KASSLER, P.
1973. The structural and geomorphic evolution of the Persian Gulf, pp. 11-32. *in* Purser, B.H., ed., The Persian Gulf, New York.

LAY, D.M.
1972. The anatomy, physiology, functional significance and evolution of specialized hearing organs of Gerbilline rodents. Jour. Morphol., no. 138, pp. 41-120.

LECOINTRE, G.
1952. Recherches sur le Neogene et le Quaternaire marins de la cote Atlantique du Maroc, Part 1 Stratigraphy. Notes Memoires Service Geol. Maroc, no. 99, 198 pp., 8 pl.

NADLER, C.F. and D.M. LAY
1967. Chromosomes of some species of *Meriones*. Z. Saugetierk, no. 32, pp. 285-291.

PALMER, RALPH S.
1962. Handbook of North American Birds, Vol. 1, Yale Univ. Press, New Haven, 567 pp.

PETTER, F.
1959. Evolution du dessin de la surface d'usure des molaires des gerbillides. Mammalia, no. 23, pp. 304-315.

SAINT GIRONS, M. and F. PETTER
1965. Les rongeurs du Maroc. Trav. Inst. Sci. Cherifien., Zool. Ser., no. 31, 58 pp.

SCHLITTER, D.A. and H.W. SETZER
1972. A new species of short-tailed gerbil (*Dipodillus*) from Morocco (Mammalia: Cricetidae: Gerbillinae). Proc. Biol. Soc. Washington, no. 84, pp. 385-392.

TCHERNOV, E.
1968. Succession of rodent faunas during the upper Pleistocene of Israel. Berlin.

WASSIF, K., R. G. LUTFY, and S. WASSIF
1969. Morphological, cytological and taxonomical studies of the rodent genera *Gerbillus* and *Dipodillus* from Egypt. Proc. Egypt Acad. Sci., no. 22, pp. 77-97.