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THE HETRODINAE (ORTHOPTERA: ENSIFERA: BRADYPORIDAE)
OF SOUTHERN AFRICA: SYSTEMATICS AND PHYLOGENY

by

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(with 29 figures)

ABSTRACT

The Hetrodinae (Orthoptera: Ensifera: Bradyporidae) of Southern Africa: Systematics and Phylogeny. Navors. nas. Mus., Bloemfontein 8(8): 393-434. Five genera of Hetrodinae are present in southern Africa: *Hetrodes* Fischer von Waldheim (one species), *Acanthoplus* Stål (six spp.), *Hemihetrodes* Pictet (one sp.), *Acanthoproctus* Karsch (three spp.), and the recently revised *Enyaliopsis* Karsch that is not treated here. The first four genera are revised, their distributions mapped and their intrageneric phylogenies discussed. The four existing *Hetrodes* spp. are reduced to subspecies of *H. pupus* L. A new species of *Acanthoplus* is described from southwestern Angola. *Acanthoproctus elaphos* Weidner is synonymised with *A. cervinus* de Haan. The name *capreolus* Pictet is revived as a subspecies of *Acanthoproctus vittatus* Walker. Extensive geographical intraspecific morphological variation in several species is documented. (Orthoptera, Bradyporidae, Hetrodinae, systematics).

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CONTENTS

INTRODUCTION.....	394
SYSTEMATICS.....	395
PHYLOGENETIC DISCUSSION.....	426
OPSOMMING.....	431
ACKNOWLEDGEMENTS.....	431
REFERENCES.....	432

INTRODUCTION

Hetrodinae occur throughout Africa and adjacent parts of Arabia. In southern Africa, particularly in the drier western areas, they are conspicuously abundant in seasons of good rainfall. Thousands of *Acanthoplus discoidalis* may then be killed on any stretch of road by passing vehicles. The carcasses attract their scavenging peers, who are often themselves killed in like manner. Scavenging individuals often start devouring injured but alive members of their own species, and this cannibalistic trait, along with the habit of injured individuals to feed on themselves, earns them the fear and loathing of many. Their environmental impact as primary consumers has never been assessed, but, judging by their size and abundance, it must be significant.

Because they are such large and striking insects, many species have long been known, and most have been described more than once. Through the work of especially Weidner (1955) the bulk of nomenclatural problems were sorted out. However, distributional data on southern African Hetrodinae remained inadequate, with many species known from single or indeterminate localities only. The main objective of the present work was to expand our distributional knowledge of the Hetrodinae by examining the more abundant and better labelled material that has since become available. While examining large numbers of specimens, some cases of geographical variation became apparent, which resulted in some concurrent nomenclatural progress.

It was learnt through bitter experience that hetrodines do not travel well in the post, however well they may be packed. I was therefore limited to studying only those collections I could visit myself or from which I could receive material by hand. Consequently no types from European museums could be studied at first hand.

Weidner (1955) summarised our knowledge of hetrodine biology, which is largely based on studies of north African species. The biology and ecology of southern African species remains a virgin field for research.

Institutional abbreviations are according to Arnett & Samuelson (1986), with the addition of LRU (Locust Research Unit, a division of SANC which is housed and accessed separately) and UOVS (Department of Zoology and Entomology, University of the

Orange Free State, Bloemfontein, South Africa).

SYSTEMATICS

Only original or otherwise relevant literature references have been listed below. Full citations for all taxa, as well as full lists of synonymy, may be found in the catalogue of Beier (1964). The only subsequent papers treating the present taxa are Weidner (1968) and La Greca & Messina (1989).

KEY TO THE GENERA OF SOUTHERN AFRICAN HETRODINAE

(Weidner 1955 includes a key to all hetrodine genera)

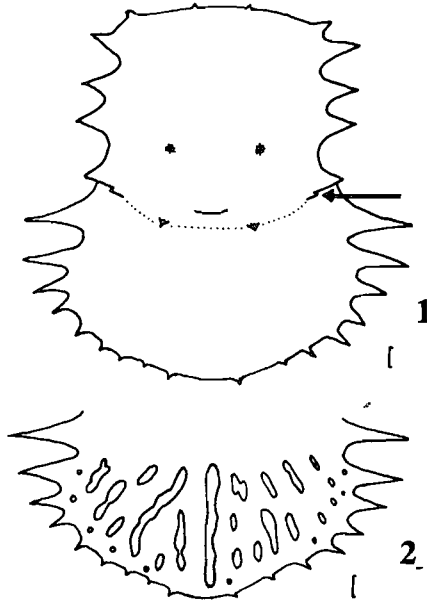
1. Anterolateral angle of pronotum bearing a projection (Figures 18, 21-25) 2
- Anterolateral angles of pronotum not so produced (Figures 1, 5-8, 17) 3
2. Protibial tympanum open, oval (Figure 20); anterolateral pronotal processes usually relatively shorter (Figure 18)..... *Enyaliopsis*
- Protibial tympanum partially covered, slit-like (Figure 19); anterolateral pronotal processes usually relatively longer, may also be short (Figures 21-25).....
..... *Acanthoproctus*
3. Anterior plane of pronotum with two submedian discal spines, which, together with two spines on the posterior margin, are arranged in a distinctive rectangular pattern (Figure 1); each procoxa with two spines *Hetrodes*
- Anterior plane of pronotum lacking submedian discal spines arranged as above (Figures 5-8, 17); each procoxa with one spine only 4
4. Metafemur dorsally spinose; pronotal spines usually apically curved (Figure 17).....
..... *Hemihetrodes*
- Metafemur dorsally unspined; pronotal spines always straight (Figures 5-8).....
..... *Acanthoplus*

HETRODES

Hetrodes Fischer von Waldheim 1833: 318.

Type species: *Hetrodes pupus* L., type by original designation.

Interantennal spine about as long as antennal scapus. Pronotum (Figure 1) divided into anterior and posterior planes by a transverse depression. Anterior plane: anterior margin with two small submedian spines; anterolateral angles each with a single small spine; lateral margins each with four larger spines, the posteriad pair of which may often carry a basally fused accessory spine each; posterior margin with two submedian spines; posteromedial disc with two spines that, together with the posterior marginal spines, are arranged in a distinctive quadrangular pattern. Posterior plane: posterior margin with 12-16 spines that decrease in size medially.



Figures 1-2: Pronota of *Hetrodes pupus*, dorsal aspect. Figure 1. *Hetrodes pupus namaqua*. Arrow indicates accessory pronotal spine. Figure 2. *Hetrodes pupus marginatus*, posterior plane only. Scale bar = 1 mm.

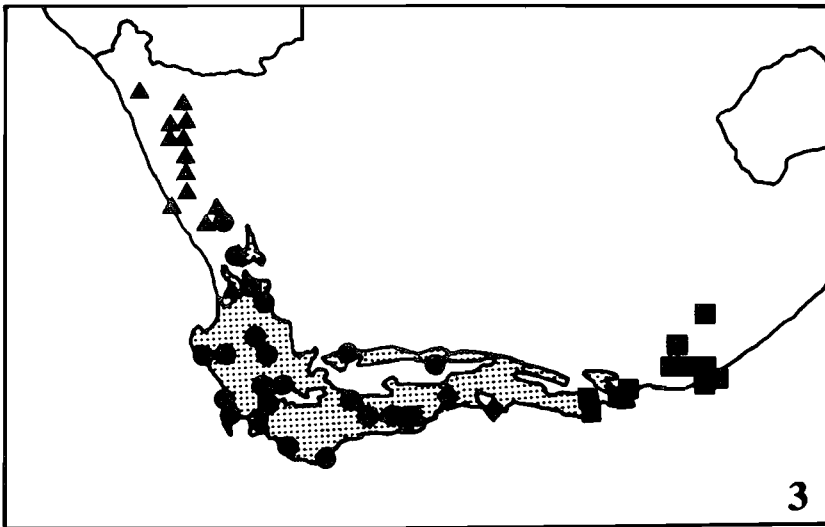


Figure 3: Distribution of *Hetrodes pupus*. Triangles: *H. p. namaqua*. Dots: *H. p. pupus*. Lozenges: *H. p. marginatus*. Squares: *H. p. abbreviatus*. Shaded area denotes limits of Fynbos Biome.

Posterior margin of metanotum with 0-8 blunt submedian spines. Procoxae with two spines each. Tibial tympanum open, oval. Most abdominal terga with three longitudinal rows of large spines; these are often interspersed with accessory rows of smaller spines, up to a total of 7-8 distinct spinal rows, besides additional lateral blunt spinal traces. Ovipositor robust, about as long as or longer than abdomen. Male cerci angled and acute.

Discussion

Previous workers have remarked on the variability of *Hetrodes* spp., and the difficulty of distinguishing between them. By the time of Weidner (1955), the nine nominate taxa had been reduced to only four clearly recognisable forms. The latter author suspected that these four may be conspecific, but continued to treat them as distinct species because he was disinclined to act on the basis of the limited material available to him. Examination of present material has shown that the four forms occupy geographically distinct areas, but most characters display overlapping or intermediate character states at the form's distributional boundaries (Figure 4). The presence of intermediate states, and the fact that actual differences are often slight or relative, argue against full specific status for the forms. Lumping them as one undifferentiated species will tend to obscure very real geographical variation. Keeping in mind that the variation is not continuous, but rather suggests a step-cline, I decided to treat the forms as subspecies of the genotype. The pre-existence of names for the taxa concerned allowed me to do so without adding to the group's nomenclatural burden. My conclusions are based on the evidence of external morphology. Presently unavailable biochemical data may test the alternative hypothesis that these are full species interfacing in hybrid zones.

Analysis of label data indicate similar annual occurrence patterns for all subspecies. Nymphs are commonest in September and October. Populations peak from December to February, and decline till June. They are generally absent in July and August.

Hetrodes pupus (L.)

Gryllus (Tettigonia) pupus Linnaeus 1758: 431.

Leg I, femur, dorsally unspined, ventrally with two tiny inner apical spinelets; tibia, dorsally unspined, ventrally with 5-6 inner and five outer spines. Leg II, femur, dorsally unspined, ventrally with two apical anterior spines and 0-1 small apical posterior spines (see also subspecies); tibia, dorsally with 0-3 small medial anterior spines (see subspecies) and two (occasionally three) proximal posterior spines, tibia ventrally with 4-6 small anterior and five (occasionally four) small distal posterior spines. Leg III, femur, dorsally with 2-5 (usually three) proximal inwardly directed spines, ventrally with two (occasionally one) distal inner spines (and often also with incipient traces of additional proximal spines), and 2-3 distal outer spines; tibia dorsally with 5-7 inner and 4-7 outer spines, ventrally with 4-6 inner and 5-7 outer spines (see also subspecies). Spination and coloration of abdominal terga varies, see subspecies. Length of ovipositor variable, see subspecies.

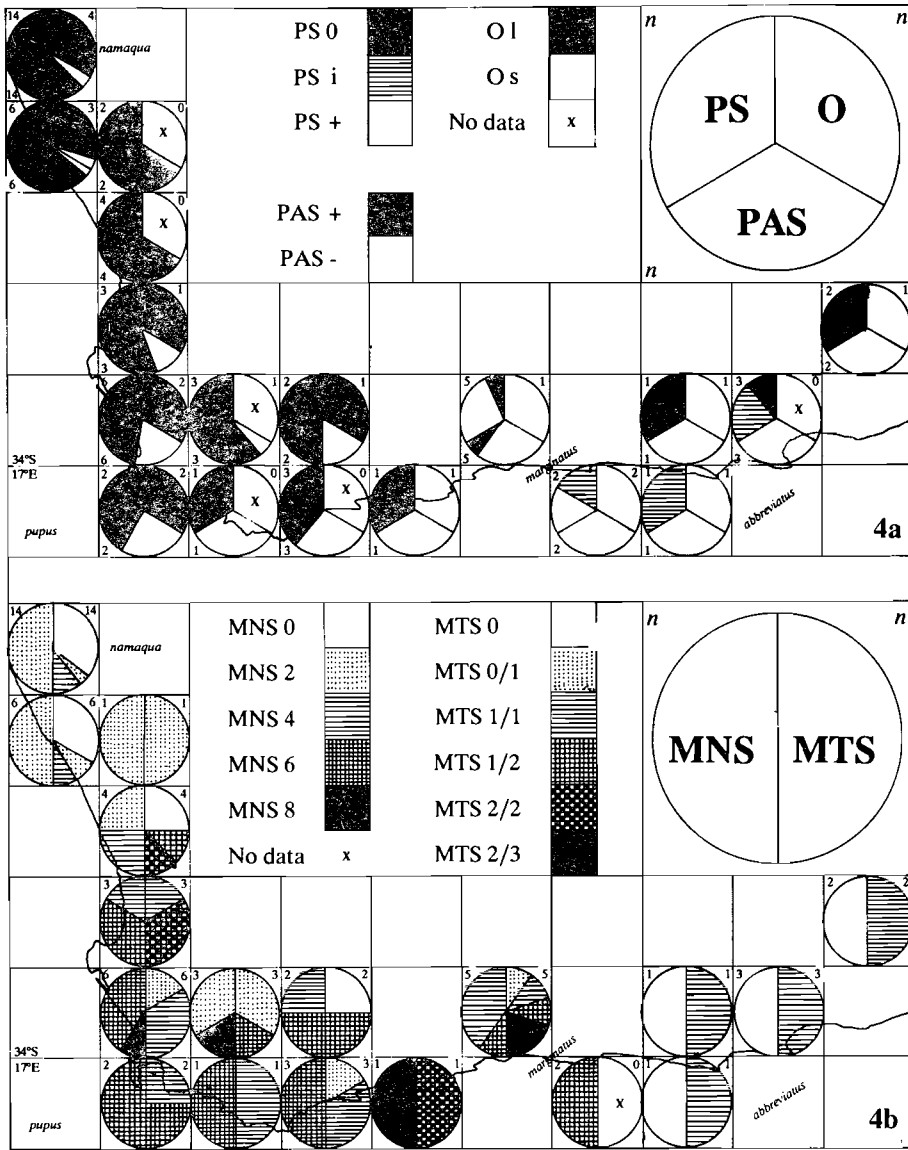


Figure 4: Morphological variation in the subspecies of *Hetrodes pupus*. Each square represents 1° x 1° geographical (compare Figure 3), and the pie diagram in the square represents morphological data for all examined specimens from that square. The large circle at top right indicates the sector of each smaller circle representing each of 2 or 3 characters. Different shades represent different character states for each character, according to the key. The number of specimens examined for each character in each square is indicated by the small numbers next to their corresponding sectors (*n*). Key: a) PS: Posterior pronotal striations, PS 0 = absent, PS i = incipiently present, PS + = well-developed; O: ovipositor length, O l = long (longer than the length of abdomen), O s = short, x = no data (males); PAS: Pronotal accessory spines, PAS + = present, PAS - = absent. b) MNS: Metanotal spines, total number present; MTS: Dorsal anterior mesotibial spines, number present, MTS 0 = no spines, MTS 0/1 = one spine on one leg, none on other, MTS 1/1 = one spine on each leg, etc.

KEY TO SUBSPECIES OF *Hetrodes pupus*

1. Metanotum with 2-8 small spines on the posterior margin..... 2
 - Metanotum completely unspined..... *H. p. abbreviatus*
2. Posterior metanotum with 4-8 spines; dorsal anterior margin of mesotibia with 1-3 spines 3
 - Posterior metanotum with two spines only; dorsal anterior margin of mesotibia usually unspined..... *H. p. namaqua*
3. Posterior plane of pronotum with raised subparallel striae (Figure 2) *H. p. marginatus*
 - Posterior plane of pronotum with granular sculpture..... *H. p. pupus*

Hetrodes pupus pupus (L.)

Hetrodes pupus L., *ut supra*.

Hetrodes variolus Fieber 1853: 259. *syn. nov.*

Hetrodes depressicollis Chopard 1955: 282. *syn. nov.*

Hetrodes pupus forma *gigantea* Weidner 1955: 127. *syn. nov.*

Posterior plane of pronotum with granular sculpture; accessory pronotal spines generally present in western populations, but absent in eastern populations. Metanotum generally with six small spines, occasionally eight. Leg II, femur, ventrally, often with a posterior spine; tibia, dorsally with 1-2 anterior spines. Leg III, tibia, with moderate numbers of spines. Abdominal terga generally heavily spinose. Abdomen generally with a longitudinally striate colour pattern. Ovipositor relatively long.

Material examined. 36 exx. (16 females, 10 males, 10 nymphs): SAMC (21); TMSA (8); LRU (3); SANC (2); DMSA (1); UPSA (1).

Distribution (Figure 3): Southwestern Cape Province.

LOCALITIES, LITERATURE: Karsch 1887. RSA, CAPE PROVINCE: Troe-Troe.

Weidner 1941. RSA, CAPE PROVINCE: Saldanha Bay.

Weidner 1955 (as *H. variolus*). RSA, CAPE PROVINCE: DuToitskloof; Hopefield; Troe-Troe.

Chopard 1955. RSA, CAPE PROVINCE: Cape Agulhas (type locality of *H. depressicollis*); Clanwilliam Cederberg; Platberg, Swartbergpas.

Weidner 1968. RSA, CAPE PROVINCE: Camps Bay; Paarl and Franshoek, between; Wemmershoek; Witsands [probably Witsandbaai], western Cape Peninsula.

PRESENT MATERIAL: RSA, CAPE PROVINCE: Albertinia; Bloubergstrand; Cape Town; Clanwilliam, 8 km W; Claremont; Grootvadersbos; Groot Winterhoek, Tulbagh, 1200m; Matjiesfontein; Nuwerus, 2 km S; Oudebosch [=Oubos, SE 3419Cb]; Piketberg; Riversdale; Somerset West; Tradouw Pass; Vanrhynsdorp, 6 km W; Worcester.

UNTRACED LOCALITY: Klipfontein (many possibilities). **DOUBTFUL LOCALITIES:** RSA, CAPE PROVINCE: Douglas. RSA, TRANSVAAL: Pretoria.

Discussion

The reasons for synonymising *H. variolus* here, are discussed under *H. pupus marginatus* below.

I have not seen the type of Weidner's infraspecific taxon *gigantea*. It was distinguished from typical *H. pupus* mainly by the possession of eight metanotal spines rather than the usual six. The character is neither constant, nor significant, enough to merit distinction at what now becomes the infrasubspecific level, therefore I sank the name *gigantea* in synonymy. Figure 4 indicates that individuals with eight metanotal spines were found only within the area inhabited by *H. pupus pupus*.

I have not seen the type of Chopard's *H. depressicollis* either. The basis on which it was granted specific status, namely the general shape and punctuation of the pronotum, falls well within the range of variation for *H. pupus pupus*, and there is nothing in the very detailed description and illustration that disagrees with this interpretation.

Hetrodes pupus marginatus Walker stat. nov.

Hetrodes marginatus Walker 1869: 226.

Hetrodes knysna Péringuey 1916: 429.

In view of the very small sample available, the following descriptive notes probably do not represent the full spectrum of variation in the taxon. Posterior plane of pronotum with raised striae (Figure 2); accessory pronotal spines generally absent. Metanotum generally with six small spines. Leg II, femur, ventrally, generally without a posterior spine; tibia, dorsally with 2-3 anterior spines. Leg III, tibia, with relatively larger numbers of spines compared to other subspecies. Abdominal terga moderately spinose. Abdomen generally unicolourous. Ovipositor moderately long.

Material examined. Lectotype male (designated by Uvarov 1928) and paralectotype female of *H. knysna*: *Hetrodes knysna*, typ, Py., Miss Wilman, George, 99. (SAMC)

Other material: 4 exx. (1 female, 3 males), all SAMC.

Distribution (Figure 3): Known from a limited area in the southern Cape Province only.

LOCALITIES, LITERATURE: Péringuey 1916 (as *H. knysna*). RSA, CAPE PROVINCE: George; Knysna.

Discussion

There has been some confusion of *H. marginatus* with *H. variolus* in the past. Weidner (1955) distinguished *H. variolus* chiefly on the basis of its relatively shorter ovipositor, at the same time expressing difficulty with separating it from *H. pupus* s.s. I found ovipositor length, though intrasubspecifically broadly similar, to be subject to considerable age-related and individual variation. There are no other significant differences between *H. pupus* s.s. and *H. variolus* apparent from the original description of *H. variolus*, the redescription by Ebner (1939), or the works of Weidner, therefore I have synonymised *H.*

variolus under *H. pupus pupus*.

Weidner further synonymised both *H. marginatus* and *H. knysna* with *H. variolus*, also on the basis of their shorter ovipositors. However, both former nominate taxa differ from all other *Hetrodes* by their very distinctive posterior pronotal sculpture. This character state has only been mentioned for *H. knysna* by Péringuey (1916), but I have had its presence on the type of *H. marginatus* and its absence from the type of *H. variolus* confirmed by Mrs. J. Marshall of the British Museum (Natural History) and Dr. A. Kaltenbach of the Naturhistorisches Museum, Wien, respectively. Uvarov (1928) previously synonymised *H. marginatus* and *H. knysna* after comparing the types.

Chopard (1955) recorded *H. marginatus* from Swartbergpas, and mentioned that the posterior pronotum of his specimen was 'wrinkled'. I have not seen this specimen, and it is unclear whether Chopard was referring to striate tuberculosities or not. Chopard also recorded *H. pupus* from the same locality, while present material from Swartbergpas is typical *H. pupus pupus*.

Hetrodes pupus abbreviatus Walker stat. nov.

Hetrodes abbreviatus Walker 1869: 227

The most distinctive subspecies of *H. pupus*. Posterior plane of pronotum with granular sculpture, though specimens from the far western part of the range may have incipient striae similar to that of *H. pupus marginatus*; accessory pronotal spines absent. Metanotum unspined. Leg II, femur, ventrally, generally with a posterior spine, but this is often very indistinct; tibia, dorsally with only one anterior spine. Leg III, tibia, with moderate numbers of spines. Abdominal terga generally lightly spinose only, with the three major spinal rows well developed, but only indications of the accessory rows. Abdominal colour pattern distinctive: posterior margins of terga raised and light coloured; each tergite with a dark median trapezoidal mark flanked by lighter lateral marks. Ovipositor relatively short, the shortest of all the subspecies of *H. pupus*.

Material examined. 26 exx. (15 females, 9 males, 2 nymphs): AMGS (18); SAMC (4); LRU (3); TMSA (1).

Distribution (Figure 3): Eastern Cape Province.

LOCALITIES, LITERATURE: Péringuey 1916. RSA, CAPE PROVINCE: Seymour.

Weidner 1955. RSA, CAPE PROVINCE: Grahamstown; Heligebirge [locality untraced]; Port Elizabeth.

PRESENT MATERIAL: RSA, CAPE PROVINCE: Atherstone; Bathurst; Blaauw Krantz; Brak Kloof; Governor's Kop, Grahamstown; Jeffrey's Bay; Kleinmond; Martindale; Mosslands; Patensie; Stone's Hill, Grahamstown; Uitenhage; Witteklip, Uitenhage.

UNTRACED LOCALITY: Paradise Kloof.

Hetrodes pupus namaqua Péringuey stat. nov.

Hetrodes namaqua Péringuey 1916: 430.

Hetrodes namaqua ab. *maculipes* Ebner 1939: 209. syn. nov.

Posterior plane of pronotum with granular sculpture only; accessory pronotal spines always present. Metanotum with 1+1 laterally situated spines only, but more towards the south of the range. Leg II, femur, ventrally, generally with a posterior spine; tibia, dorsally without anterior spines. Leg III, tibia, with relatively smaller numbers of spines than in other subspecies. Abdominal terga generally moderately spinose. Abdominal terga generally unicolourous, distal femora ('knees') usually black. Ovipositor relatively long.

Material examined. Lectotype male (designated by Uvarov 1928) and paralectotype female: *Hetrodes namaqua*, typ, Py., O'Okiep, L. Peringuey, 1884. (SAMC)

Other material: 25 exx. (10 females, 10 males, 5 nymphs): SAMC (9); LRU (7); TMSA (5); UPSA (2); AMGS (1); SMWH (1).

Distribution (Figure 3): Northwestern Cape Province.

LOCALITIES, LITERATURE: Péringuey 1916. RSA, CAPE PROVINCE: Okiep; Springbok; Uitenhage [locality doubtful].

Uvarov 1928. NAMIBIA: Windhoek [locality doubtful].

Weidner 1941. RSA, CAPE PROVINCE: Heligebirge [locality untraced].

Weidner 1968. RSA, CAPE PROVINCE: Mesklip.

PRESENT MATERIAL: RSA, CAPE PROVINCE: Bitterfontein, 5 km N; Buffelsrivier at 29°55'S, 17°39'E; Garies; Groenriviermond; Kamieskroon; Lamberts Bay and Graafwater, between; Lekkersing; Nuwerus, 2 km S; Okiep; Ratelfontein; Springbok, and 29 Km W, and 82-86 km S; Steinkopf, 13 km E. UNTRACED LOCALITY: Klipfontein [many possibilities].

Discussion

Ebner's infraspecific taxon *maculipes*, distinguished primarily by the dark coloration of the distal femora, represents the normal state for well-preserved material of this taxon, and a distinctive name is unnecessary.

ACANTHOPLUS Stål

Acanthoplus Stål 1873: 39.

Type species: *Hetrodes longipes* de Charpentier, type by original designation.

Interantennal spine less than half as long as antennal scapus, at most a blunt knob. Pronotum (Figures 5-8) divided into anterior and posterior planes by a transverse depression, which may be very shallow. Anterior plane: anterior margin with or without a

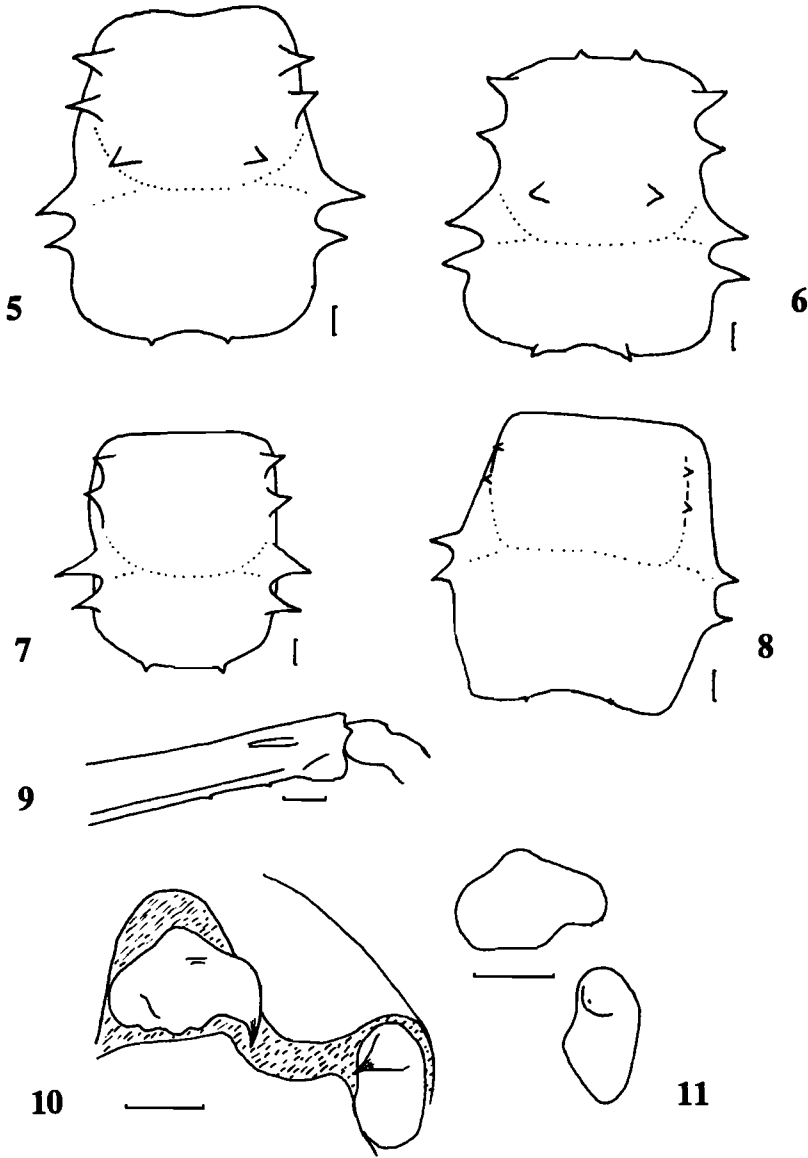
pair of submedian spines; anterolateral angles unspined; lateral margins each with two spines; posterior margin with or without two submedian spines; disc of anterior plane unspined. Posterior plane: posterior margin with four lateral and two posteromedial spines.

Metanotum unspined. Procoxae with one spine each. Tibial tympanum open, oval. All dorsal femora unspined, ventrally usually also unspined, but spinose in one species. Tibia I dorsally unspined, ventrally with 6-10 inner and 6-9 outer spines. Tibia II dorsally spinose or not, ventrally with 5-9 anterior and 5-8 posterior spines. Tibia III with varying numbers of inner and outer dorsal and ventral spines. Abdomen varies from well spinose to unspined. Ovipositor very short. Male cerci angled with apex acute (Figure 10), or flattened and lobe-like (Figure 11).

Analysis of label data indicate similar monthly occurrence patterns for all species. Though nymphs are occasionally found as early as September, most date from January to April. Adults are also common from January onwards, peaking in April-May and declining towards July. Single individuals may be encountered in all months, suggesting that some may persist into the following season.

KEY TO *ACANTHOPLUS* SPECIES

1. Posterior margin of anterior plane of pronotum with two submedian spines (Figures 5-6) 2
- Posterior margin of anterior plane of pronotum completely unspined (Figures 7-8) 5
2. Anterior margin of pronotum with two submedian spines (Figure 6) 3
- Anterior margin of pronotum without submedian spines (Figure 5) 4
3. Posterior margins of at least abdominal tergites I-IV each with a median spine as well as 1+1 lateral spines *A. armativentris*
- Posterior margins of at least abdominal tergites I-IV each with a median spine only *A. jallae*
4. Metafemur almost always with a few small subapical ventral spines (Figure 9); male cerci lobe-like as in Figure 11 *A. longipes*
- Metafemur always completely unspined; male cerci angled and apically acute as in Figure 10 *A. discoidalis*
5. Pronotum posteriorly rounded, spines well developed (Figure 7); metatibia with 3-4 dorsal outer spines *A. speiseri*
- Pronotum posteriorly truncate, spines small (Figure 8); metatibia lacking dorsal outer spines *A. weidneri* nov.



Figures 5-11: *Acanthoplus* spp. Figures 5-8. Pronota, dorsal aspect. Figure 5. *A. longipes*. Figure 6. *A. armativentris*. Figure 7. *A. speiseri*. Figure 8. *A. weidneri*. Figure 9. Apical inner metafemur of *A. longipes*. Figures 10-11. Male cerci, oblique ventral aspect. Figure 10. *A. discoidalis*. Figure 11. *A. longipes*. Scale bar = 1 mm.

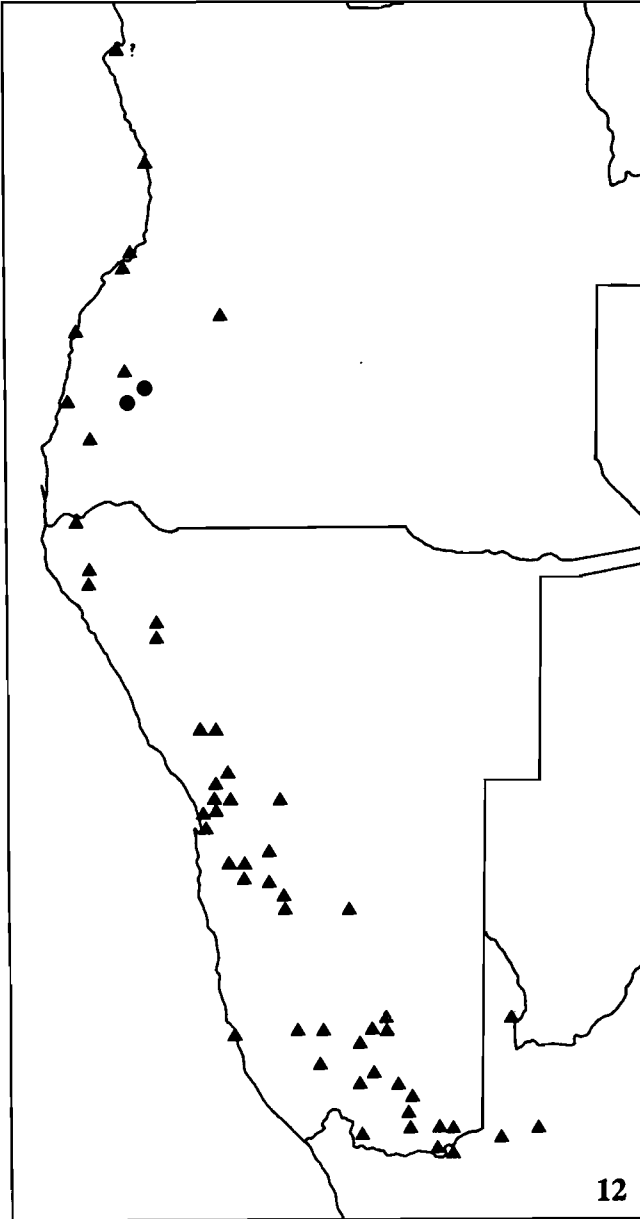


Figure 12: Distribution of *Acanthopulus longipes* (triangles) and *A. weidneri* (dots).

Acanthopplus longipes (de Charpentier)

Hetrodes longipes de Charpentier 1841-1845: Tab. 45.

Acanthopplus stratiotes Brancsik 1895: 259 *syn. nov.*

Acanthopplus loandae Péringuey 1916: 433.

Pronotum (Figure 5), anterior plane, anterior margin unspined; posterior margin with two submedian spines. Though subject to considerable individual variation, northern populations generally have the legs more spinose than southern populations (Figure 13). Leg I, femur, ventrally with 0-2 inner and 0 (occasionally one) outer spines; tibia ventrally with 7-10 inner and 7-9 outer spines. Leg II, femur, ventrally usually unspined, occasionally with up to two anterior and one posterior spines; tibia dorsally with 0-5 anterior and 1-6 posterior spines, and ventrally with 6-9 anterior and 6-8 posterior spines. Leg III, femur, ventrally usually with up to three inner and four outer spines, seldom unspined (Figure 9); tibia dorsally with 8-14 inner and 8-13 outer spines, and ventrally with 7-10 inner and 6-12 outer spines. Abdomen usually unspined, although some northern specimens may have sparsely spinose anterior abdominal terga. Male cerci (Figure 11) flattened and lobe-like, apically with 0-2, usually one, blunt spinules each.

Material examined. Types of *Acanthopplus loandae*: male and female, labelled: W. Africa, Loanda, 12.90, *Acanthopplus loandae* typ. Py. (SAMC)

Other material: 122 exx. (45 females, 55 males, 22 nymphs): SMWH (52); LRU (26); TMSA (20); SAMC (8); UPSA (6); SANC (5); GRSW (2); BMSA (1); DMSA (1); UOVS (1).

Distribution (Figure 12): Namib Desert and adjacent arid areas.

LOCALITIES, LITERATURE: de Charpentier 1841-45. ANGOLA: Benguella (type locality).

Stål 1874. RSA, CAPE PROVINCE: Walfish Bay.

Karsch 1887. ANGOLA: Benguela; Chinchoxo.

Bolivar 1890. ANGOLA: Biballa; Caconda (possibly not *A. longipes*, according to notes in original).

Karny 1910. NAMIBIA: Keetmanshoop; Walfischbai; Warmbad.

Péringuey 1916. ANGOLA: "Labelled Loanda, but probably from Mossamedes" (types of *A. loandae*). NAMIBIA: Angra Pequena; Lower Swakop.

Uvarov 1928. ANGOLA: R. Hinamangando, south of Cape St. Martha.

Weidner 1941. ANGOLA: Katumbella. NAMIBIA: Otjimbingwe.

Weidner 1955. ANGOLA: Hinamangando. As *A. stratiotes*: ANGOLA: [Porto] Amboim; Benguella; Catumbela.

Chopard 1955 (as *A. stratiotes*). NAMIBIA: Orupembe; Sanitatas.

Weidner 1968. NAMIBIA: Keetmanshoop; Okahandja [locality doubtful].

La Greca & Messina 1989. NAMIBIA: Husakos [= Usakos] - Karibib; Khorixas; Khorixas - Uis; Mariental.

PRESENT MATERIAL: ANGOLA: Mossamedes; Virei, 21 km W. BOTSWANA?: Bechuanaland [probably refers to the northern Cape Province, historically called 'British Bechuanaland']. NAMIBIA: Arandis, 6 km N; Aus; Brandberg; Coenbult, 7 km SW; Fish

River Canyon, 10 km W; Goageb, 30 km E; Gobabeb; Greylingshof 107; Grünau, 4 km W; Hamrivier at 28°22'S, 19°21'E; Holoog; Kalkrand, 26 km SSW; Karasburg, and 11 km NW, and 50 km SSE; Keetmanshoop, and 15 km W; Keimas 99; Khabus 146; Khwarib Schlucht; Kliphoek 72; Kuibis; Kuiseb Canyon; Lower Dome Gorge; Lower Hope Mine Wash; Lower Ostrich Gorge; Lower Swakop River; Naukluft; Otjinungwa; Rössing Mine; Solitaire, 10 km SSW; Spitzkoppe; Tsondabvlei; Uis; Upper Ostrich Gorge; Warmquelle; Zais 6. RSA, CAPE PROVINCE: Aughrabies Falls N.P.; Paul se Puts 143; Twee Rivieren; Upington; Vioolsdrif. DOUBTFUL LOCALITIES: RSA, ORANGE FREE STATE: Farm Maghaleen, Zastron. RSA, TRANSVAAL: Pongola.

Discussion

A. loandae was previously synonymised with *A. longipes* by Uvarov (1928). It differs only in the slight development of abdominal spines. Uvarov based his actions on the unreliability of the character in other species of the genus, and reported individual variation in other Angolan material at his disposal. None of my material, except the types of *A. loandae*, possessed abdominal spination, but in view of the clinal variation in this character in other *Acanthoplus* spp., strengthened by similar variation in leg spination in *A. longipes* and my assessment of the types, I agree with the proposed synonymy.

Weidner (1955) studied the type of *A. stratiotes* and distinguished it from *A. longipes* primarily on the shape of the male cerci and the presence of two spinules on its apex. I found minor details of shape in the male cerci to be influenced by mode of preservation, and that depicted in Weidner's figure falls well within the range of variation for *A. longipes*. In 37 adult males examined, 20 had one spinule on each cercus, six had one spinule on one cercus and none on the other, and nine had no spinules at all. All three character states were found in specimens from throughout the distribution range of the species. Two further specimens, one from the doubtful locality Maghaleen and the other from the Fish River Canyon in southern Namibia, had one spinule on the one cercus and two on the other. I saw no specimens with two spinules on both cerci, but the character is clearly subject to considerable, non-geographical, variation. In the absence of further concrete distinguishing characters, I conclude that *A. stratiotes* is synonymous with *A. longipes*. In this regard it may be noted that Uvarov (1928) already recorded the occasional presence of two spinules on male cerci of *A. longipes*.

On distributional grounds, the material of Krauss (1901) is probably *A. discoidalis* rather than *A. longipes*. Karny (1910), confused by the extent of variation in ventral femoral spination in his material, treated both *A. discoidalis* and *A. longipes* as one. His variety *pallascens*, said to lack ventral femoral spines, must therefore be referred to *A. discoidalis*.

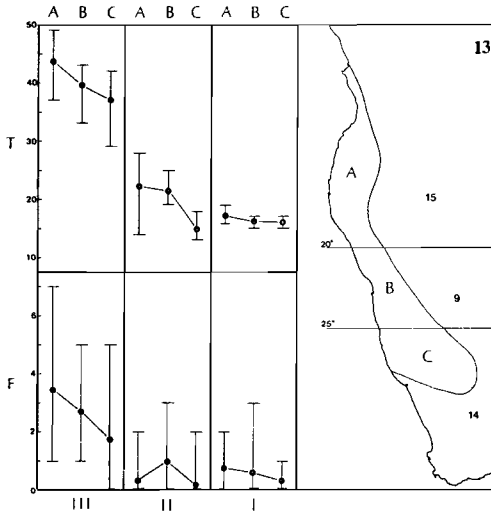


Figure 13: Geographical variation in leg spination in *Acanthoplus longipes*. Map on right indicates three arbitrarily chosen areas, A, B and C (compare Figure 12), with the number of specimens examined from each. Graphs on the left indicate the number of spines on each femur (F) and tibia (T) of legs I, II and III, in specimens from regions A, B and C respectively. Dots indicate average total spines per leg, and vertical lines the maximum and minimum numbers observed.

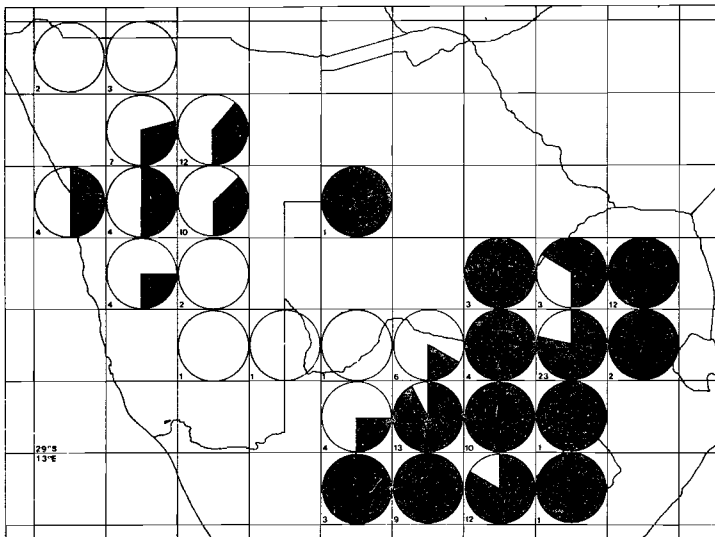


Figure 14: Morphological variation in *Acanthoplus discoidalis*. Squares represent 2° x 2° geographical (compare Figure 15). Pie diagrams represent the proportion of specimens from each square with any form of abdominal spination (black) or without (white). Small numbers in the left bottom of each square denote the number of specimens examined from that square.

Acanthopplus discoidalis (Walker)

- Hetrodes discoidalis* Walker 1869: 230.
Hetrodes pallidus Walker 1869: 231.
Acanthopplus desertorum Kirby 1899: 142.
Acanthopplus serratus Kirby 1899: 143.
Acanthopplus germanus Kirby 1899: 143.
Acanthopplus longipes var. *pallescens* Karny 1910: 46.
Acanthopplus bechuanus Péringuey 1916: 433.

Pronotum similar to Figure 5, anterior plane, anterior margin unspined; posterior margin with two submedian spines. All femora unspined. Tibia I ventrally with 7-8 inner and 6-8 outer spines. Tibia II dorsally with 0-2 anterior and 1-4 posterior spines, and ventrally with 4-7 anterior and 5-6 posterior spines. Tibia III dorsally with 7-11 inner and 5-8 outer spines, and ventrally with 6-7 inner and 8-9 outer spines. Abdominal spination variable, from 4-5 well-developed median spines and numbers of smaller lateral spines, to completely unspined; intermediate forms may have median spines but lateral traces only, or lateral spines without median spines, or a median carina only; unspined individuals are relatively more common in the north and west, and spined individuals in the south and east of the range (Figure 14). Male cerci angled, with apex acute (Figure 10).

Material examined: Types of *Acanthopplus bechuanus*: female, Free State, 1905, *Acanthopplus bechuanus* Typ, Py. (SAMC); male, *Acanthopplus bechuanus* typ., Py. (SAMC).

Other material: 278 exx. (127 females, 103 males, 48 nymphs): UPSA (73); SMWH (51); BMSA (30); LRU (30); SANC (23); TMSA (23); SAMC (20); UOVS (14); AMGS (8); AMMM (3); DMSA (2).

Distribution (Figure 15): Most of southern Africa.

LOCALITIES, LITERATURE: Kirby 1899. RSA, CAPE PROVINCE: King William's Town (types of *A. serratus* and *A. germanus*).

Krauss 1901 (as *A. longipes*, listed here on distributional grounds). NAMIBIA: Omapyu; Windhoek.

Karny 1910 (as *A. longipes*, listed here on distributional grounds). BOTSWANA: Lehututu-Kgokong. NAMIBIA: Okahandja; Windhuk; Windhuk-Waterberg.

Péringuey 1916. NAMIBIA: Luderitzburg [locality untraced]; Windhoek. RSA, CAPE PROVINCE: Douglas; Grahamstown; Kimberley (types of *A. bechuanus*); Walfish Bay. RSA, TRANSVAAL: Potchefstroom (types of *A. bechuanus*).

Bigalke 1922 (as *A. bechuanus*): RSA, ORANGE FREE STATE: Glen.

Weidner 1941. ANGOLA: Capelongo. NAMIBIA: Abbabis; Karibib; Neudamm; Okahandja; Okapehuri, nr. Okasise; Otjiwarongo; Voigtsland. ZIMBABWE: Bulawayo.

Weidner 1955. BOTSWANA: Schoschong. NAMIBIA: Gababis [locality untraced]; Oas [locality untraced, several possibilities]; Okonjati; Okowakuatjiwi.

Chopard 1955. NAMIBIA: Ohopoho; Omutati, 18 km E. RSA, CAPE PROVINCE: Haarlem (as *A. bechuanus*); Steenkampspuuts.

Weidner 1968. BOTSWANA: Sekuma Pan. NAMIBIA: Keetmanshoop. ZIMBABWE: Nyamandhlovu, NW of Bulawayo.

La Greca & Messina 1989. NAMIBIA: Karibib; Karkland [=Kalkrand]; Khorixas; Mariental; Okahandja; Otjiwarongo; Otjosondou; Outjo; Vitvley [=Witvlei]; Windhoek.

PRESENT MATERIAL: BOTSWANA: Gaborone; Ghanzi; Lobatsi; 10 km N Serowe. NAMIBIA: Arnhem 222; Changans; Claratal 18; Dorsland, Etosha; Elizabeth Hill, Okahandja; Etosha Pan at 18°36'S, 16°14'E; Gobabis; Göllschau 20; Goreangab Dam; Grootfontein; Hoffnung 66; Kamaseb, Etosha; Kos 28; Kupferberg 33; Leeubron-Adamax-Okaukuejo; Mooirivier, Maltahöhe Dist.; Oshakati, and 21 km NW; Otjansasema, Kaokoland; Otjiwarongo, 64 km S; Otjovasandu, Etosha; Rasputin 137; Rodenstein 307; "SE2217Aa"; Sebraskop 410; Tweekoppies, Etosha; Uis; Windhoek, 80 km S. RSA, CAPE PROVINCE: Bitterpan, Kalahari Gemsbok Park; Britstown; Douglas, and 67 km SW; Campbell & Schmidtsdrift, between; Farm Slypsteen, Hopetown; Grahamstad; Griekwastad; Heuningneskloof; Hopetown, 96 km W; Kenhardt; Langeberg 138, Kimberley; Magogong; Nossob Rest Camp; Petrusville; Prieska; Severn; Upington; Vaalbos N.P.; Vaalharts; Vryburg. RSA, ORANGE FREE STATE: Bethlehem; Bloemfontein; Glen; Kroonstad; Krugersdriftdam; Petrusburg; Rondebult, Kroonstad; "SE2927Aa"; Soutpan, OVS; Theunissen; Vredefort. RSA, TRANSVAAL: Bandolier Kop; Boksburg; Coligny; De Wildt; Edelweiss, Pretoria; Fort Klipsdam, Zoutpansberg [locality untraced]; Grasmere; Haenertsburg; Hammanskraal; Hartbeespoort; Langjan; Louis Trichardt; Marikana; Mooifontein, Pietersburg [locality untraced]; Nelspruit; Pietersburg; Pietersburg - Bandolier Kop, halfway; Potgietersrus; Pretoria; Rustenburg; Standerton; Swartruggens; Thabazimbi; Tzaneen; Vivo; Warmbad, 21 km ENE; Winternest. UNTRACED LOCALITIES: Excelsior [many possibilities]; Vergeleë [many possibilities]; Witrand [many possibilities].

Discussion

I have not seen the types of *A. discoidalis*, nor those of *A. pallidus*, *A. desertorum*, *A. serratus* or *A. germanus*, but find no reason to disagree with earlier workers who have synonymised all these.

A. bechuanus was distinguished from *A. discoidalis* mainly by the presence of abdominal spination. Predictably, it was described from the eastern part of the range where individuals with abdominal spination predominate.

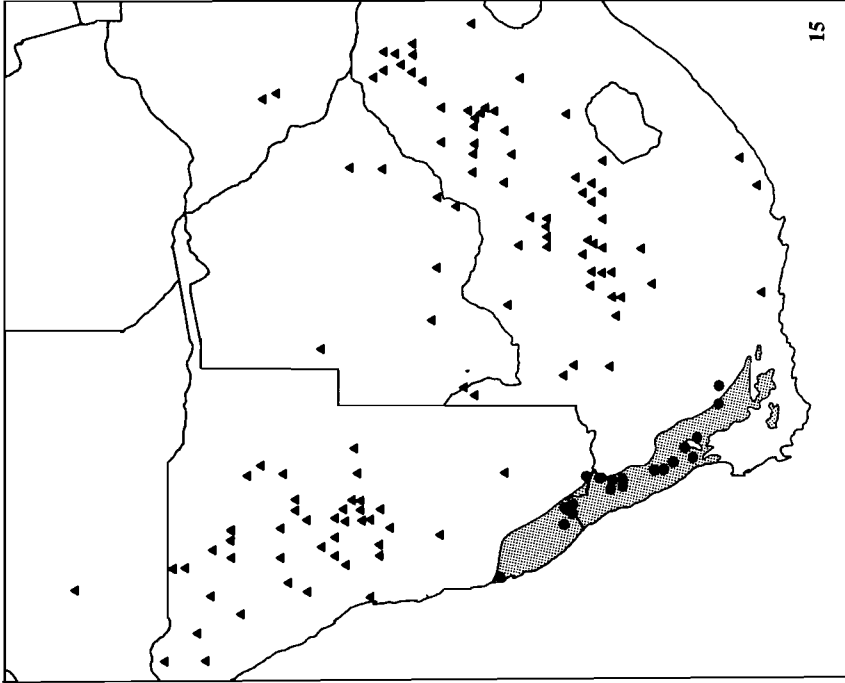


Figure 15: Distribution of *Acanthopius discoidalis* (triangles) and *Hemihetrodes bachmanni* (dots). Shaded area denotes extent of Succulent Karoo Biome.

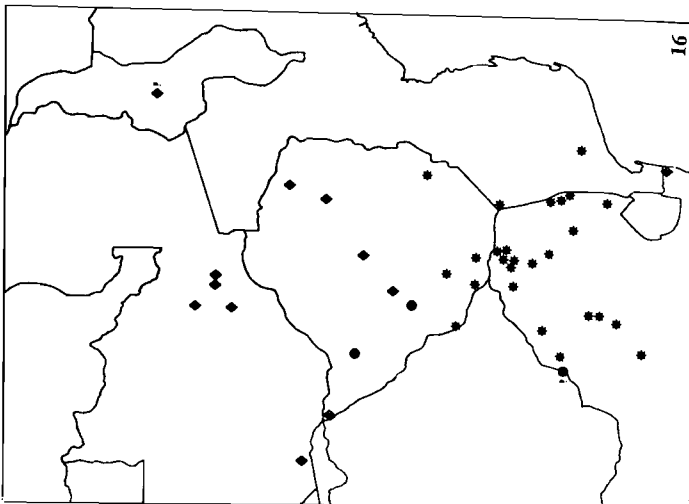


Figure 16: Distribution of *Acanthopius armativentris* (asterisks), *A. jallae* (dots), and *A. speiseri* (lozenges).

Acanthoplus speiseri Brancsik

Acanthoplus speiseri Brancsik 1895: 258.

Acanthoplus varicornis Péringuey 1916: 435.

Pronotum (Figure 7), anterior plane, with both anterior and posterior margins unspined. All femora unspined. Due to the small sample size, the following tibial spinations probably do not reflect the full spectrum of intraspecific variation. Tibia I ventrally with 6-7 inner and six outer spines. Tibia II dorsally unspined and ventrally with six anterior and six posterior spines. Tibia III dorsally with eight inner and 3-4 outer spines, and ventrally with 6-7 inner and seven outer spines. Abdomen unspined. Male cerci angled, with apex acute (illustrations of cerci in Uvarov 1928 and Weidner 1955 are derived from the holotype of *A. varicornis*, a nymph; adult male *A. speiseri* have cerci similar to that of e.g. *A. discoidalis*). The adult cerci of *A. speiseri* were illustrated by La Greca & Messina, 1989, Figure 7).

Material examined: Holotype of *Acanthoplus varicornis*: male nymph, N. Rhodesia (H. Dolman), Apr. 1915, *Acanthoplus varicornis* typ, Py. (SAMC)

Other material: 17 exx. (8 females, 5 males, 4 nymphs): SAMC (10); TMSA (5); SANC (2).

Distribution (Figure 16): Southeastern Africa, from northern Natal to Malawi. Previously known from Zambia and Zimbabwe only.

LOCALITIES, LITERATURE: Brancsik 1895. ZAMBIA: Boroma (type locality).

Giglio-Tos 1907. ZAMBIA?: Upper Zambesi.

Péringuey 1916. ZAMBIA: N. Rhodesia (types of *A. varicornis*). ZIMBABWE: Queque; Salisbury.

Weidner 1941. ZAMBIA: Broken Hill.

Weidner 1955. ZAMBIA: Luano Valley, Chisorwe; Muchina Depot [locality untraced]; Musongo [locality untraced, several possibilities]; NW Rhodesia, River Formoshi.

Weidner 1968. ZAMBIA: Lusaka. ZIMBABWE: Turk Mine, Matabeleland.

PRESENT MATERIAL: MALAWI: unspecified locality. RSA, NATAL: Kosi Bay.

ZAMBIA: Pembe [locality untraced, several possibilities]; Sesheke Dist. ZIMBABWE: Arcturus, Salisbury; Chishawasha; Darwin.

Acanthoplus jallae Griffini

Acanthoplus jallae Griffini 1897: 3.

Pronotum (similar to Figure 6), anterior plane, anterior margin with two submedian spines; posterior margin with two spines. All femora unspined. Due to the small sample size, the following tibial spinations probably do not reflect the full spectrum of intraspecific variation. Tibia I ventrally with 6-8 inner and 6-9 outer spines. Tibia II dorsally with 0-2 anterior, and 2-3 posterior spines, and ventrally with 6-7 anterior and 5-6 posterior spines.

Tibia III dorsally with 11 inner and eight outer spines, and ventrally with 7-8 inner and nine outer spines. Abdomen with median spines on tergites I-V or VI; lateral spines, if at all present, tiny and confined to tergites I-II. Male cerci angled, with apex acute.

Material examined: 4 exx. (3 males, 1 nymph): AMGS (3); SAMC (1).

Distribution (Figure 16): Good localities restricted to northwestern Zimbabwe.

LOCALITIES, LITERATURE: Griffini 1897. ZIMBABWE?: Road Kazungula - Bulawayo (type locality).

Giglio-Tos 1907. ZAMBIA?: Upper Zambesi.

Sjöstedt 1913. ZIMBABWE: 'Matabele'.

Weidner 1968. ZIMBABWE: Bulawayo.

PRESENT MATERIAL: RSA, TRANSVAAL: Junction Crocodile - Marico Rivers [identity in doubt, cf. below]. ZIMBABWE: Bulawayo.

Discussion

The only apparent difference between *A. jallae* and *A. armativentris* is in the presence of well-developed lateral abdominal spination in the latter, and its depletion or absence in the former. The two taxa occur in allopatry. In view of the range of variation in abdominal spination in e.g. *A. discoidalis*, it is highly probable that *A. jallae* and *A. armativentris* are simply the opposite ends of geographical variation in the same species. The single nymph from the western Transvaal, listed above, though from an area where one would expect typical *A. armativentris*, answers to *A. jallae* instead, implying that the apparent geographical isolation of the two taxa may not be absolute either. I refrain from synonymising them only because I have seen too few specimens answering to typical *A. jallae* to do this with complete confidence.

La Greca & Messina (1989) synonymised both *A. jallae* and *A. armativentris* with *A. discoidalis*. (Though their paper is dated 1989, the journal carries a printing date of December 1990, and was only distributed in early 1992. I first saw it after my manuscript had already been submitted. Our conclusions were reached independantly). La Greca & Messina's analysis of spinal variation in Namibian *A. discoidalis* agrees with my results, as does their reasoning that this implies synonymy of *A. jallae* and *A. armativentris*. However, I do not agree with their synonymising both the latter with *A. discoidalis*. In doing so, they minimise the importance of the presence of anterior pronotal spines in both *A. jallae* and *A. armativentris*. The only specimen of either of the two latter taxa they appear to have examined, is the holotype of *A. jallae*. My assessment of large samples of both *A. discoidalis* and *A. armativentris* is that they are distinct. Improved knowledge of *A. jallae*, and other *Acanthoplus* spp. in its area, is a prerequisite for resolving this case.

Acanthopplus armativentris Péringuey

Acanthopplus armativentris Péringuey 1916: 435.

Pronotum (Figure 6), anterior plane, anterior margin with two submedian spines; posterior margin with two spines. All femora unspined. Tibia I ventrally with 7-8 inner and 6-8 outer spines. Tibia II dorsally with 0-3 posterior spines, and ventrally with 5-7 anterior and 5-7 posterior spines. Tibia III dorsally with 7-8 inner and 4-8 outer spines, and ventrally with 6-8 inner and 8-9 outer spines. Abdomen with median spines on tergites I-IV or V, and 1+1 lateral spines on I-IV. Male cerci angled, with apex acute.

Material examined: Types, male and female: Tuli, South Rhodesia, C.R. Lounsbury, *Acanthopplus armativentris*, Type, Py. (SAMC)

Other material: 80 exx. (39 females, 35 males, 6 nymphs): TMSA (29); UPSA (25); LRU (10); DMSA (6); SAMC (5); SANC (4); UOVS (1).

Distribution (Figure 16): Transvaal, southern Zimbabwe and Moçambique.

LOCALITIES, LITERATURE: Péringuey 1916. ZIMBABWE: Tuli (type locality).

Cardoso 1935. MOÇAMBIQUE: Guijá.

Chopard 1955. ZIMBABWE: Beitbridge, 48 km N; Jessie.

Weidner 1968. BOTSWANA: Matjemloeti. ZIMBABWE: Dotts Drift, Lower Sabi; Nuanetsi, 154 km SE.

PRESENT MATERIAL: RSA, TRANSVAAL: Bandolier Kop; Bangu Gorge, Kruger N.P.; Bedford, 13 km NW [locality untraced, more than one possibility]; Carletonville; Derry Farm, Vivo; D'Nyala Nat. Res., Ellisras District; Grootpan; Hoedspruit; Langjan Nat. Res.; Letaba Region, Kruger N.P.; Louis Trichardt, 25 km NW; Malelane; Mara; Messina, and 8 km E; Mopane; Olifants Camp, Kruger N.P.; Pafuri; Phalaborwa; Pienaarsrivier; Pretoria; Satara Region, Kruger N.P.; Soutpansberg; Tshipise, and 2 km E; Tzaneen; Vivo; Warmbad; Waterpoort. DOUBTFUL LOCALITIES: NAMIBIA: Spitzkoppe, Central Namib; RSA, ORANGE FREE STATE?: Wesselsb.[ron?].

Acanthopplus weidneri sp. nov.

Acanthopplus sp. Weidner 1955: 135.

Only a single (male) specimen was examined. Transverse median furrow of pronotum (Figure 8) very shallow, almost non-existent; all pronotal spines small. Pronotum, anterior plane, anterior and posterior margins unspined. All femora unspined. Tibia I ventrally with six inner and six outer spines. Tibia II dorsally unspined, ventrally with five anterior and five posterior spines. Tibia III dorsally with seven inner and no (*sic!*) outer spines, and ventrally with five inner and 7-8 outer spines. Abdomen unspined. Male cerci angled, with apex acute.

Material examined: Holotype, male, pronotal length 10mm, total body length 24 mm, posterior femoral length 15 mm: Sa da Bandeira, Huila, ANGOLA, SE 1413Dc, 6-8 May 1974, H 18702. (SMWH)

Distribution (Figure 12): Known only from a limited area in the highlands of southwestern Angola.

LOCALITIES, LITERATURE: Weidner 1955. ANGOLA: Humpat(r)a.

PRESENT MATERIAL: ANGOLA: Sa. da Bandeira (type locality).

Discussion

The species is named after Dr. Herbert Weidner of Hamburg, who first recognised it as undescribed in Weidner (1955), but declined to describe it because of damage to his material. Though I have not seen Weidner's material, the present specimen conforms to his descriptive notes, and comes from the same area, therefore I believe them to represent the same taxon. In pronotal spination, it resembles *A. speiseri*, but differs in pronotal shape. The present differences in tibial spination between *A. speiseri* and *A. weidneri* may become less apparent when more material becomes available.

HEMIHETRODES Pictet

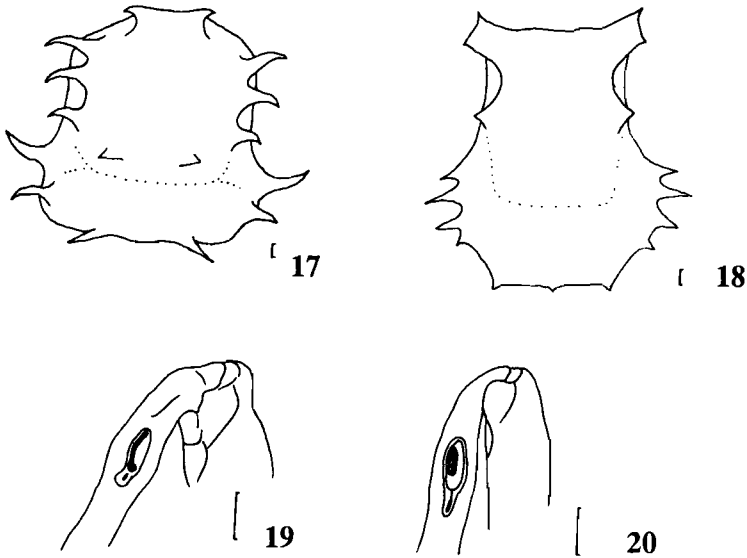
Hemihetrodes Pictet 1888: 74.

Type species: *Hemihetrodes peringueyi* Pictet, type by original designation.

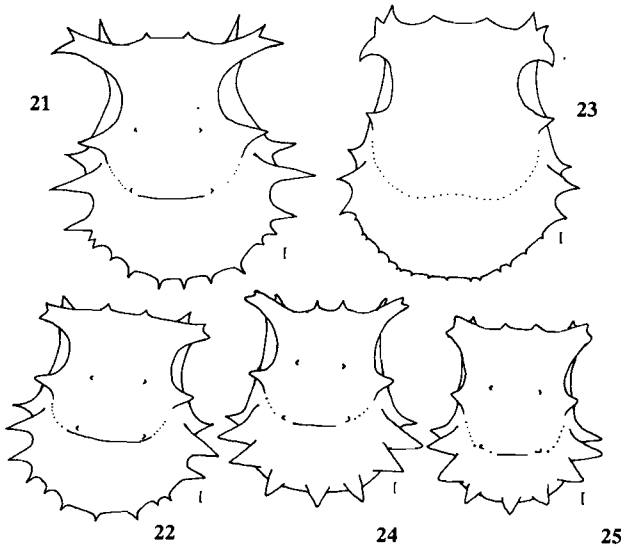
Interantennal spine at most a blunt knob. Pronotum (Figure 17) divided into anterior and posterior planes by a transverse depression. Anterior plane: anterior margin with two basally joined spines; anterolateral angles lacking marginal spines; lateral margins each with three apically downcurved spines; posterior margin with two spines, occasionally none; disc of anterior plane unspined. Posterior plane: posterior margin with four lateral and two posteromedial spines.

Metanotum unspined. Procoxae with one spine each. Tibial tympanum open, oval. Abdomen with both median and lateral spines on tergites I-VI; males have only 1+1 lateral spinal rows, but females have many more, usually about 4+4 on tergite I and decreasing in numbers posteriorly. Ovipositor short. Male cerci short and very sharply angled, with apex acute.

The genus is monospecific.



Figures 17-20: Figures 17-18. Pronota, dorsal aspect. Figure 17. *Hemihetrodes bachmanni*. Figure 18. *Enyaliopsis* sp. Figures 19-20. Proximal inner right protibiae, showing tibial tympana. Figure 19. *Acanthoproctus cervinus*. Figure 20. *Enyaliopsis* sp. Scale bar = 1 mm.



Figures 21-25: Pronota of *Acanthoproctus* spp., dorsal aspect. Figure 21. *A. cervinus*, shape typical for southern populations. Figure 22. *A. cervinus*, shape typical for northern populations. Figure 23. *A. diadematus*. Figure 24. *A. vittatus vittatus*. Figure 25. *A. vittatus capreolus*. Scale bar = 1 mm.

Hemihetrodes bachmanni (Karsch)

Hetrodes bachmanni Karsch 1887: 57.

Hemihetrodes peringueyi Pictet 1888: 74.

Leg I, femur, dorsally with 0-2 inner and 0-2 outer spines and ventrally with 0-2 inner and 0-2 outer spines; tibia dorsally unspined, ventrally with 5-6 inner and 4-5 outer spines. Leg II, femur, dorsally with 0-2 anterior and 0-1 posterior spines, and ventrally with 1-3 anterior and 0-1 posterior spines; tibia dorsally with 0-2 spines, ventrally with 3-5 anterior and 4-5 posterior spines. Leg III, femur, dorsally with 2-4 large spines, ventrally with 1-2 inner and four outer spines; tibia dorsally with 4-8 inner and 2-6 outer spines, and ventrally with 4-7 inner and 5-8 outer spines.

Intraspecific geographical variation in this species, though real, is poorly understood at present. Material from the same or proximate localities generally display similar character states, which remain the same in series collected decades apart, but the differences noted between different localities do not quite fit recognisable patterns at present. Possibly more abundant material will allow a more thorough analysis in future.

The two posterior marginal spines on the anterior plane of the pronotum are present and well developed in all specimens from throughout the range, but in two samples collected two days apart at "20 miles N Steinkopf" and "20 miles S Violsdrif" (virtually the same place) they are completely absent.

Dorsal spines on the pro- and mesofemora may be present or absent. Presence of spines appears to be more common in specimens from localities at lower altitudes nearer to the coast, while specimens from higher altitudes further from the coast usually lack such spines. The relationship is not absolute, though (Figure 26).

Label data suggests that *H. bachmanni* hatches from August onwards, populations peak in September and October, and decline towards December. There are no records between January and July.

Material examined. 83 exx. (35 females, 44 males, 4 nymphs): LRU (33); TMSA (22); SAMC (9); BMSA (6); UPSA (6); AMGS (3); SMWH (3); SANC (1).

Distribution (Figure 15): Northwestern Cape Province and southwestern Namibia.

LOCALITIES, LITERATURE: Karsch 1887. RSA, CAPE PROVINCE: Troe-Troe (type locality).

Weidner 1968. RSA, CAPE PROVINCE: Okiep; Springbok; Vanrhynsdorp.

PRESENT MATERIAL: NAMIBIA: Lüderitz, 24 km N; Obib dunes. RSA, CAPE PROVINCE: Annisfontein, and 13 km W; Bitterfontein, 14 km W; Blouheuvel, 5 km NW; Cornellskop, Richtersveld; 2 km NW Die Koei, Richtersveld; Doorn Riv, 32 km NW [*sic!* = NE] Wuppertal; Garies, 5 km SE; Hotnotsgeluk, Richtersveld; Kuboos, 18 km SW; Nuwerus, and 2 km S; Okiep, 2 km NE; Paradyskloof, Richtersveld; Ratelpoort, 30 km S Steinkopf; Rosyntjieberg, Richtersveld; Spektakel Pass, 29 km W Springbok; Springbok;

Steinkopf, 2 km N, and 32 km N; Sutherland; Vanrhynsdorp, 6 km W, and 20 km NE; Vioolsdrif, 32 km S.

ENYALIOPSIS

Enyaliopsis Karsch 1887: 60.

Enyaliopsis (Figures 18, 20) was recently revised by Glenn (1991) and is not treated further here. The 13 known species are distributed throughout East, South Central and Southeastern Africa. In southern Africa, at least four species occur in Moçambique, Zimbabwe, Transvaal and northern Natal.

ACANTHOPROCTUS Karsch

Acanthoproctus Karsch 1887: 65.

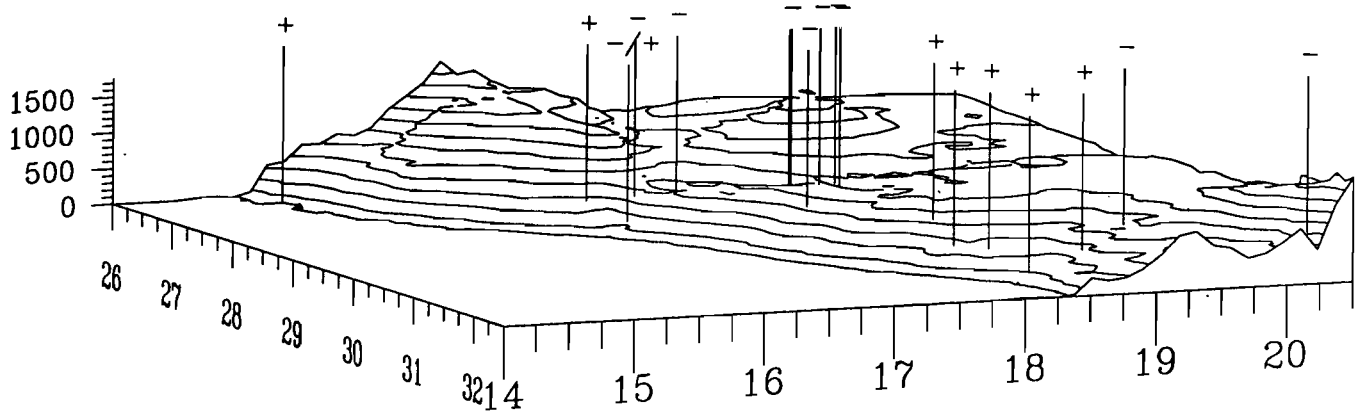
Type species: *Locusta cervinus* de Haan, type by original designation.

Interantennal spine as long as or longer than antennal scapus. Pronotum (Figures 21-25) divided into anterior and posterior planes by a transverse depression that may be very shallow. Anterior plane: anterior margin with two small, widely separated spines; anterolateral angles each with a bifurcate process, bearing a ventrally directed anterior spine; lateral margins each with a single spine; posterior margin unspined, but may have two blunt raised knobs in the usual spinal positions; posteromedial disc of anterior plane essentially unspined, but may have two blunt knobs that are connected by a raised mass to the knobs on the posterior margin. Posterior plane: posterior margin with 9-23 spines, generally decreasing in size medially.

Metanotum unspined. Procoxae with two spines each. Tibial tympanum elongate, slit-like. All femora totally unspined. Tibiae I and II dorsally unspined, III dorsally unspined or not. Tibiae ventrally each with 2-4 (usually three) inner and 3-6 (usually three) outer spines. Abdominal terga spined or not. Ovipositor short. Male cerci angled, with apex acute.

KEY TO ACANTHOPROCTUS SPECIES

1. Posterior margin of pronotum with a corona of very many (up to 23) tiny spines (Figure 23) *A. diadematus*
 Posterior margin of pronotum with fewer (9-16), larger spines 2
2. Posterior margin of pronotum with only nine large and very robust spines (Figures 24-25) *A. vittatus*
 Posterior margin of pronotum with about 16 less robust spines (Figures 21-22) *A. cervinus*



26

Figure 26: Morphological variation in *Hemihetrodes bachmanni*, plotted on a three-dimensional view of the west coast of southern Africa, between 26-32° S and 14-20.5°E (compare Figure 15). Heights in meters. Character state of specimens at each collecting locality indicated by + (dorsal pro- and mesofemoral spines present) and - (the same absent).

Acanthoproctus cervinus (de Haan)

Locusta (*Hetrodes*) *cervina* de Haan 1842: 183.

Hetrodes militaris White 1846: 316.

Hetrodes fortis Walker 1869: 229.

Acanthoproctus elaphos Weidner 1941: 294. *syn. nov.*

Interantennal spine at least twice longer than antennal scapus. Anterolateral pronotal processes shorter and stouter in individuals from the north of the range (Figure 22) than in those from the south (Figure 21); posterior apical bifurcation directed laterally. Pronotum, posterior plane, posterior margin with up to 16 irregular spines, decreasing in size medially. Tibiae I and II ventrally each with three inner and three outer spines. Tibia III dorsally with 1-2 inner spines in individuals from the south of the range, but unspined in northern individuals (Figure 27); ventrally with four inner and three (in the north of the range) to four (in the south) outer spines. Abdominal spination varies from five spinal rows on tergites I-VI in some individuals from the south of the range, to totally unspined in northern individuals (Figure 27).

Material examined: 177 exx. (76 females, 60 males, 41 nymphs): LRU (32); SMWH (30); SAMC (26); TMSA (22); AMGS (19); SANC (15); UPSA (15); UOVS (10); BMSA (5); AMMM (2); DMSA (1).

Distribution (Figure 28): Arid areas of southwestern Africa.

LOCALITIES, LITERATURE: Kirby 1906. RSA, CAPE PROVINCE: Deelfontein.

Weidner 1941. NAMIBIA: Keetmanshoop, N of [locality untraceable]; Rehoboth; Windhoek (type locality of *A. elaphos*).

Weidner 1955. UNTRACED LOCALITIES: Ondoga; Provinz Albert.

Chopard 1955. RSA, CAPE PROVINCE: Cradock, 16 km S; Haarlem; Prins Albert, 16 km W; Ratelkraal, NE Springbok.

Weidner 1968. NAMIBIA: Hardapdam.

PRESENT MATERIAL: NAMIBIA: Aar 16; Arandis, 6 km N; Areb [locality untraced, more than one possibility]; Betlehem 27; Brukkaros Mtn, 10 km E; Churutabis 108; Daan Viljoen Wildtuin; Gamsberg, foot, E; Kaapkruis, 16 km N; Khabus 146; Kliphhoek 72; Kochena 74; Koës, 20 km NE; Kub; Lichtenstein; Naukluft; Nauzerus 11; Noachabeb 97; Oberndorf 42; Otjikoko Süd 61; Pieterskloof 370; "SE2315Ca"; Torraabaai; Ubussis 1; Upper Ostrich Gorge; Wilderness (=Lekkerwater) 144; Zaris Waterhole. RSA, CAPE PROVINCE: Aberdeen, and 14 km S; Beaufort West; Bonnivale [locality untraced, several possibilities]; Brandvlei, 5 km NW; Britstown; Carnarvon; Colesberg; Cradock; Douglas; Fraserburg, 6 km NW; Groblershoop; Halesowen, nr. Cradock; Hantamsberg; Helskloof; Richtersveld; Kendrew; Koup Station, 2 km N; Kuruman; Laingsburg, 22 km S; Leeudrink, Kalahari G. Park [locality untraced]; Merweville, 3 km S; Nelspoort; Olifantshoek; Paradysberg, Richtersveld; Petrusville; Pofadder; Prince Albert; Reuning Myn, Richtersveld; Rooispruit; Rosyntjiesberg, Richtersveld; Teekloofpas; Toeslaan; Twee Rivieren; Upington; Victoria West; Williston, 16 km SE; Willowmore. RSA, ORANGE FREE STATE: Bainsvlei; Bloemfontein; Fauresmith; Jacobsdal; Oranjekrag; Philippolis.

INDETERMINATE LOCALITY: Found in box of watermelons from Hopetown, purchased in Durban Market. **DOUBTFUL LOCALITY:** RSA, TRANSVAAL: Warmbad.

Discussion

I have not seen the types of either *H. militaris* or *H. fortis*, but find no reason to differ from previous workers who have synonymised both these with *A. cervinus*. The distinguishing characters given for *A. elaphos* (Weidner 1941) all fall within the range of variation of *A. cervinus*, moreover, are typical for the northern end of clinal variation within the species (Figure 27), hence the proposed new synonymy.

Label data indicates that *A. cervinus* nymphs are commonest in September and October, and adults in January to April, but single nymphs and adults from most months are recorded.

Acanthoproctus diadematus (Stål)

Hetrodes diademata Stål 1858: 308.

Hetrodes crassipes Walker 1869: 231.

Acanthoproctus ibex Pictet 1888: 72.

Acanthoproctus coronatus Karny 1910: 48.

Interantennal spine shorter than in other species, about as long as antennal scapus. Anterolateral pronotal process with all spines short (Figure 23); posterior apical bifurcation directed posteriorly. Pronotum, posterior plane, posterior margin laterally with six small spines, posteriorly with a corona of 14-17 tiny spines. Tibia I ventrally with 2-4 inner and 3-4 outer spines. Tibia II ventrally with 3-4 anterior and three posterior spines. Tibia III dorsally bare, ventrally with 3-4 inner and 4-6 outer spines. Abdomen unspined.

Material examined: 29 exx. (9 females, 8 males, 12 nymphs): GRSW (13); SAMC (7); SMWH (5); TMSA (3); LRU (1).

Distribution (Figure 29): Restricted to the main southern Namib dune sea.

LOCALITIES, LITERATURE: Stål 1858, 1874, 1876. **NAMIBIA:** Kuiseb River (type locality).

Karny 1910. **RSA, CAPE PROVINCE:** Rooibank.

Péringuey 1916. **NAMIBIA:** Angra Pequena [= Lüderitz]. **RSA, CAPE PROVINCE:** Walfish Bay.

Weidner 1941. **NAMIBIA:** Between Okahandja and Waterberg [locality highly unlikely]. **RSA, CAPE PROVINCE:** Rooibank.

PRESENT MATERIAL: **NAMIBIA:** Elephant Valley; Far East dunes; Gobabeb; Homeb; Khoichab Pan; Nara Valley; Noctivaga dune; Swakop Riv. [probably near Swakopmund]; 23°43'S, 15°19'E.

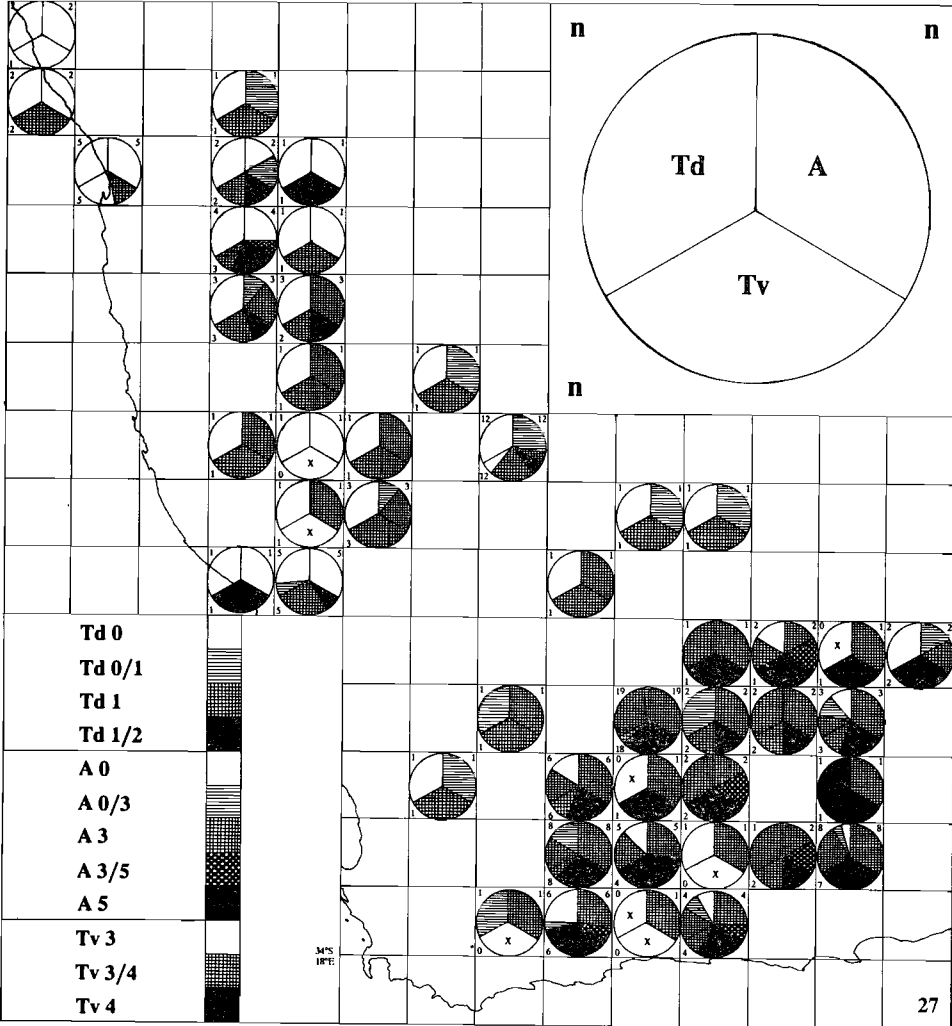


Figure 27: Morphological variation in *Acanthoproctus cervinus*. Squares represent 1° x 1° geographical (compare Figure 28). Key: Td: Inner dorsal metatibial spines, Td 0 = no spines on either leg, Td 0/1 = no spines on one leg, one spine on the other, Td 1 = one spine on each leg, etc.; A: Abdominal spination, A 0 = no spines, A 0/3 = median spinal row with lateral spinal traces, A 3 = 3 well developed spinal rows, A 3/5 = 3 well developed spinal rows with additional lateral spinal traces, A 5 = 5 well developed spinal rows; Tv: outer ventral metatibial spination, Tv 3 = 3 spines on either leg, Tv 3/4 = 3 spines on one leg, 4 spines on the other, Tv 4 = 4 spines on each leg.

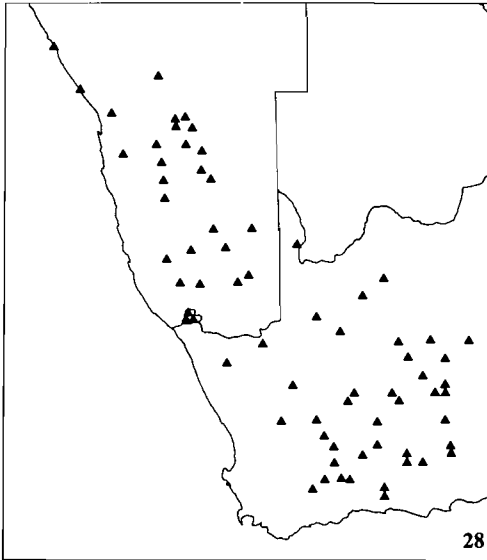


Figure 28: Distribution of *Acanthoproctus cervinus*.

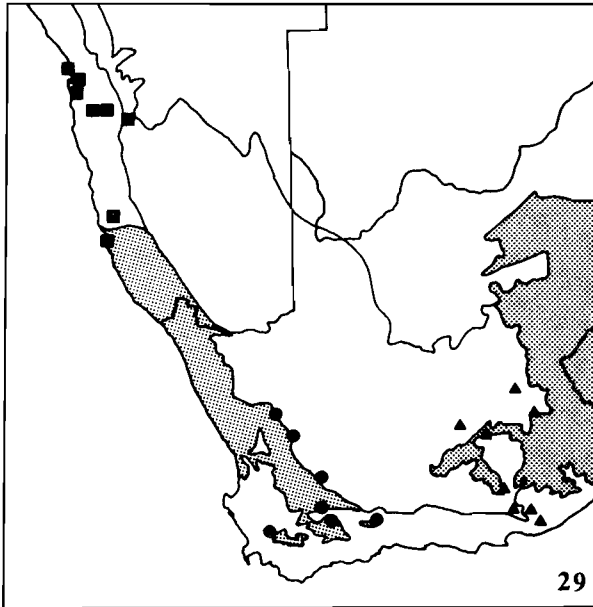


Figure 29: Distribution of *Acanthoproctus diadematus* (squares), *A. vittatus vittatus* (dots) and *A. v. capreolus* (triangles). Shaded areas denote the extent of the Succulent Karoo (west) and the Grassland (east) Biomes respectively, separated by the unshaded Nama-Karoo Biome.

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Discussion

I have not seen the type of *A. diadematus*, or any of its synonyms, but the photograph of the type in Sjöstedt (1934) allowed a positive identification to be made.

The sparse label data indicates that *A. diadematus* is present throughout the year, but no clear seasonal pattern emerges.

Acanthoproctus vittatus (Walker)

Hetrodes vittatus Walker 1869: 229.

Interantennal spine at least twice longer than antennal scapus. Anterolateral pronotal process with posterior apical bifurcation directed laterally. Pronotum (Figures 24-25), posterior plane, posterior margin with nine very robust spines. Tibia I ventrally with three inner and 3-4 outer spines. Tibia II ventrally with 3-4 anterior and three posterior spines. Tibia II dorsally spined or not, see subspecies; ventrally with 3-4 inner and four outer spines. Tergites spined, see subspecies.

The species can be divided into two subspecies, for one of which I have revived a name previously sunk in synonymy.

KEY TO SUBSPECIES OF *ACANTHOPROCTUS VITTATUS*

1. Each metatibia with a single dorsal spine; anterolateral pronotal processes longer and more slender (Figure 24); dorsal abdomen with more than three longitudinal spinal rows..... *A. vittatus vittatus*
- Metatibiae dorsally unspined; anterolateral pronotal processes shorter and more robust (Figure 25); dorsal abdomen generally with three well-developed longitudinal spinal rows only..... *A. vittatus capreolus*

Acanthoproctus vittatus vittatus Walker

Hetrodes vittatus Walker, *ut supra*.

Anterolateral pronotal processes relatively longer, causing the pronotum as a whole to appear shorter and wider (Figure 24). Abdominal terga each with three large medial spines, laterally with spinal traces or incipient spines only. Tibia III, dorsally, with two large inner spines.

Material examined: 6 exx. (2 females, 2 males, 2 nymphs): SAMC (2); TMSA (2); BMSA (1); LRU (1).

Distribution (Figure 29): Interior of southwestern Cape Province.

LOCALITIES, LITERATURE: Weidner 1968: RSA, CAPE PROVINCE: Calvinia (not seen, listed here on distributional grounds).

PRESENT MATERIAL: RSA, CAPE PROVINCE: Laingsburg, 22 km S; Loeriesfontein, 10 km NW; Matjiesfontein; Sutherland; Swartberg Pass; Witteberg, Worcester District.

Discussion

I have not seen the type of *H. vittatus*, but based on especially the number of posterior pronotal spines and the presence of dorsal metatibial spines as mentioned in the original description, there can be little doubt as to its identity.

Label data: the two nymphs are dated August and October, while the adults are dated from September to November.

Acanthoproctus vittatus capreolus Pictet stat. nov.

Acanthoproctus capreolus Pictet 1888: 69.

Acanthoproctus howarthae Kirby 1899: 145.

Anterolateral pronotal processes relatively shorter, causing the pronotum as a whole to appear longer and narrower. (Figure 25). Abdominal terga each with five or more well-developed medial spines. Tibia III dorsally unspined.

Material examined: 22 exx. (11 females, 7 males, 4 nymphs): AMGS (11); SAMC (9); SANC (1); TMSA (1).

Distribution (Figure 29): Eastern Cape Province.

LOCALITIES, LITERATURE: Kirby 1899 (as *A. howarthae*). RSA, CAPE PROVINCE: Brak Kloof, near Grahamstown; E. Karoo (type locality).

Kirby 1906. RSA, CAPE PROVINCE: Burghersdorp (as *A. vittatus*, listed here on distributional grounds).

Weidner 1955. RSA, CAPE PROVINCE: Grahamstown (as *A. vittatus*, listed here on distributional grounds).

Beier 1964 and Weidner 1968. The listing of the species from Botswana in the preceding two works is unsupported by material, and highly unlikely. It appears to stem from the mention of "Bechuanaland" in Péringuey (1916), where the distributions of *A. vittatus* and *A. cervinus* are lumped. *A. cervinus* may occur in southwestern Botswana.

PRESENT MATERIAL: RSA, CAPE PROVINCE: Kommadagga; Hanover; Middelburg; Somerset East. RSA, ORANGE FREE STATE: Bethulie. UNTRACED LOCALITY: Middleberg Road. DOUBTFUL LOCALITY: Namaqualand.

Discussion

I have not seen the types of either *A. capreolus* or *A. howarthae*, but the very detailed original descriptions and illustrations, especially with regard to posterior pronotal and dorsal metatibial spination, leave no doubt as to their identities. Both have been

synonymised with *A. vittatus* by previous workers.

Label data: all nymphs dated September to November. Adults recorded from all months, except January and February, with no discernable peak at any time, probably due to lack of sufficient data.

PHYLOGENETIC DISCUSSION

In attempting to reconstruct hetrodine phylogeny, the unsuitability of presently utilised characters becomes apparent. Most available characters have to do with spination, and most spination character states simply represent stages in the gradual loss of spines in an ancestrally more spinose group. Such apomorphic loss is not necessarily synapomorphic. There appear to be less autochthonous synapomorphies than genera in the group. As a consequence, the generic phylogram of Weidner (1955), though based on sound observations and probably a good approximation of the true state of affairs, does not bear up to critical Hennigian examination. For example, the tribe Eugastrini is well characterised by synapomorphic slit-like tympana, but it is united with the tribe Enyaliopsini by a 'loss'-character, namely ovipositors of Weidner's type three. As a result one of the few other good synapomorphic characters in the group, possession of a stigmal spine, is found to unite genera across the tribal boundaries in irreconcilable combinations. For this reason I did not follow Weidner's tribal system here, and I further suspect that some currently accepted genera may represent paraphyletic assemblages. While most of the genera concerned remain known to me from the literature only, I cannot address the problem further, and therefore limit my investigation to the intrageneric phylogeny of the genera treated here. At infrageneric level, being paucispecific apparent monophyletic lineages, reductionistic characters could be used with reasonable confidence. Outgroup comparisons could still be made, because, while the position of some of my genera in Weidner's phylogram was open to doubt, their positions relative to each other were much clearer. While an element of doubt remains, however, formal phylograms are not provided.

Additional comparison with sister-groups outside the Hetrodinae would have been preferred, particularly for *Hetrodes*, but this proved impractical. Considering the state of flux in the higher systematics of Ensifera, the identification of a suitable outgroup is difficult. I have followed Kevan (1982) in considering the Hetrodinae to belong to the Bradyporidae, rather than the more traditional views of including them in the Tettigoniidae or Ehippigeridae (Caudell 1916). Inability to procure adequate comparative material of the other (mainly southern Palaearctic) bradyporid subfamilies, inhibited my ability to use any of them as an outgroup.

Lists of utilised characters and character states for each genus follow. In each case, character states are listed in order of increasing apomorphy. Letters in brackets are abbreviations of the preceding character states, as used in the character matrices (Tables 1-3). Additional characters that may prove useful in future (and which have already been

utilised by Glenn 1991 for *Enyaliopsis*) include internal genitalia, the morphology of the male stridulatory apparatus, and sonograms. Working with dried museum material only, all these were inaccessible to me, though a wet collection has been started with the view of investigating them in future. Comparison of dried and wet male internal genitalia for the same species indicated that desiccation distorts them to a degree which renders identification with the wet structure difficult (neither examined *Hemihetrodes*, *Acanthoplus* nor *Acanthoproctus* specimens possess titillators comparable to that of *Enyaliopsis*). There is some variation in the dorsal sculpture of the tegmina, but little in the morphology of the stridulatory files. This information is available for so few species at present, that it has been omitted here.

Hetrodes

1. Number of metanotal spines. 10; 8; 6; 2; 0.
2. Abdominal spination. More; intermediate; less (m, i, l).
3. Accessory pronotal spines. Present; absent (+, -).
4. Ovipositor length. Long; intermediate; short (l, i, s).
5. Leg II, femur, ventral posterior spine. 1; 0.
6. Posterior pronotal striae. Absent; present (-, +).
7. Leg II, tibia, dorsal anterior spines. More; less (m, l).
8. Leg III, tibia, total number of spines. More; less (m, l).

Acanthoplus

1. Pronotum, anterior marginal spines. 2; 0.
2. Pronotum, anterior plane, posterior marginal spines. 2; 0.
3. Abdominal spination. Present; absent (+, -).
4. Male cerci. Acutely angular; flattened lobe-like (a, f).
5. Femoral spination. Present; absent (+, -).
6. Tibia I, ventral spines, average total number per leg. 19; 15; 14; 13; 12.
7. Tibia II, dorsal spines, average total number per leg. 11; 4; 2; 1; 0.
8. Tibia II, ventral spines, average total number per leg. 17; 13; 12; 10.
9. Tibia III, dorsal spines, average total number per leg. 27; 19; 16; 14; 12; 7.
10. Tibia III, ventral spines, average total number per leg. 22; 17; 16; 14; 13.

Acanthoproctus:

1. Interantennal spine. Long; short (l, s).
2. Pronotal processes. Long; short (l, s).
3. Posterolateral apical bifurcation of pronotal process. Directed laterally; directed posteriorly (l, p).
4. Number of posterior pronotal spines. 16; 9 or 23.
5. Tibia I, ventral outer spines. 4; 3.
6. Tibia II, ventral inner spines. 4; 3.
7. Tibia III, dorsal inner spines. 2; 0.
8. Tibia III, ventral outer spines. 5; 4; 3.
9. Abdominal spinal rows. 5; 3; 0.

Considering *Hetrodes* (Table 1), *Hetrodes pupus* exhibits bimodal clinal variation. The most plesiomorphic populations, judging by characters one and two, occur in the southwestern Cape Province. Within this population (*H. pupus pupus*) east-west variation in character three (presence or absence of accessory pronotal spines) occurs. These spines are found only in western populations of *H. pupus pupus* and in the allopatric *H. pupus namaqua*. Although accessory spines may possibly be an apomorphic clinal development in *H. pupus namaqua*, I consider them more likely to represent the retention of a plesiomorphic state. Throughout the Hetrodinae, more spines usually imply more plesiomorphic character states. Despite variation in this one character, it was not possible to base further subdivision of *H. pupus pupus* on it, because there is no line at which one character state becomes replaced by another. Rather, towards the north and west of the range of *H. pupus pupus*, the proportion of individuals possessing accessory spines (but conforming to typical *H. pupus pupus* in all other respects) gradually increases.

TABLE 1: Character matrix for *Hetrodes pupus* subspecies.

Characters:	1	2	3	4	5	6	7	8
<i>H. pupus namaqua</i>	2+	i	+	l	1	-	0	l
<i>H. p. pupus</i> (west)	6-8	m	+	l	0-1	-	1-2	i
<i>H. p. pupus</i> (east)	6-8	m	-	l	0-1	-	1-2	i
<i>H. p. marginatus</i>	6	i	-	i	0	+	2-3	m
<i>H. p. abbreviatus</i>	0	l	-	s	0-1	-	1	i

H. pupus namaqua retains additional plesiomorphic states for characters four and five, all of which indicate it to be directly related to *H. pupus pupus*. It is however, apomorphic in characters seven and eight. *H. pupus marginatus* retains plesiomorphic states in characters seven and eight, but is apomorphic for characters two, four and five. On holomorphic grounds, it is then an apomorphic descendant of *H. pupus pupus*. Character six is probably autapomorphic for *H. p. marginatus*, but there is no external evidence for this. *H. pupus abbreviatus* is the most apomorphic taxon, with apomorphic states for almost all characters, notably numbers one and four.

The relatively more plesiomorphic *H. pupus pupus* and *H. p. marginatus* are largely restricted to the Fynbos Biome (Rutherford & Westfall 1986). The distributional borders between the previous two taxa and the apomorphic endlines *H. p. namaqua* and *H. p. abbreviatus*, coincide with the limits of the fynbos (Figure 3). The implication is that *H. pupus* originated in the Fynbos Biome, from whence the latter two taxa spread. While the existence of the Cape Flora predates the breakup of Gondwana (viz. the distribution of the Proteaceae), the distribution of the Hetrodinae indicates that they postdate breakup.

Given the status of *Hetrodes* as the most plesiomorphic hetrodine (Weidner 1955), and its association with an ancient biome, the assumption of a high relative age for *Hetrodes*, and hence Hetrodinae, may be justified.

Turning to *Acanthoplus* (Table 2), it is seen that character four is autapomorphic for *A. longipes*, and the very plesiomorphic states for characters 5-10 indicate that *A. longipes* diverged from the rest of the genus at a very early stage. Present *A. longipes* populations in the north of its range retain relatively more plesiomorphic states for characters three and 6-10 than southern populations, indicating a northern origin for the species. In keeping with its isolated phylogenetic position, *A. longipes* is the only species in the genus that is largely restricted to the Desert and Nama-Karoo biomes, while all the other species are predominantly Savanna taxa. Northern *A. longipes* populations inhabit or border on the Savanna Biome, indicating a Savanna Biome origin for the genus.

TABLE 2: Character matrix for *Acanthoplus* species. Abbreviations of species names self-evident; capital letters refer to northern, southern, eastern or western populations of the respective species.

Ch.	<i>jalla</i>	<i>armat</i>	<i>longN</i>	<i>longS</i>	<i>discE</i>	<i>discW</i>	<i>speis</i>	<i>weidn</i>
1	2	2	0	0	0	0	0	0
2	2	2	2	2	2	2	0	0
3	+	+	+	-	+	-	-	-
4	a	a	f	f	a	a	a	a
5	-	-	+	+	-	-	-	-
6	15	15	19	14	15	15	13	12
7	4	2	11	1	4	4	0	0
8	13	12	17	12	12	12	12	10
9	19	14	27	16	16	16	12	7
10	17	16	22	13	16	16	14	13

Character one indicates that *A. jallae* and *A. armativentris* are the most plesiomorphic of the remaining *Acanthoplus* species. By its reduced abdominal spination, *A. jallae* would be the relatively more apomorphic, but in characters 7-10 it displays generally more plesiomorphic states. The relationship of these two taxa are still not clear. Assuming allopatric speciation to be the norm, the large gap in distribution between *A. longipes* and *A. jallae* / *armativentris* is unexpected. *A. jallae* probably ranges beyond that indicated in Figure 16 into western Zambia (e.g. the unmappable locality "Alto Zambese" in Giglio-Tos

1907). *Cloanthella clypeata* Bolivar 1890 ranges across Central Angola, from the Upper Zambezi to the Bihé Plateau, and neatly bridges the distributional gap between the aforementioned *Acanthopplus* spp. *C. clypeata* is the only representative of its genus, and was considered by Weidner (1955) to be the sister-group to *Acanthopplus*. It retains some plesiomorphic character states, i.a. the possession of two procoxal spines, and appears to have male cerci resembling those of *A. longipes*. Pending improved knowledge of *C. clypeata*, the generic position of *A. longipes* may need to be re-assessed. For the time being, the intrageneric biogeography and phylogeny of *Acanthopplus* tends to confirm Weidner's (1955) views.

A. discoidalis clearly shares an ancestor with *A. jallae* / *armativentris* (cf. character two, and the trends in characters 6-10). Eastern populations of *A. discoidalis* (nearest to the ranges of *A. jallae* and *A. armativentris*) are more plesiomorphic (character three).

A. speiseri and *A. weidneri* are related (character two), with *A. weidneri* being the relatively more apomorphic (characters 6-10). However, it is not at all clear where they diverged from the main lineage.

Hemihetrodes bachmanni is largely confined to the Succulent Karoo Biome. Its intraspecific variation is not yet understood.

In *Acanthoproctus* (Table 3), *A. cervinus* retains the plesiomorphic state for character four, and is probably nearest the ancestral species. It is also relatively plesiomorphic for all other characters except character five. Southern populations of *A. cervinus* are more plesiomorphic than northern ones (characters two and 7-9), indicating a southern origin for the species. Character nine indicates that *A. vittatus* evolved from southern *A. cervinus* populations. *A. vittatus capreolus* is the relatively more apomorphic, with two apomorphs (characters two and seven) compared to the one (character nine) of *A. vittatus* s.s. *A. diadematus* probably evolved from northern populations of *A. cervinus* (characters seven and nine), and is very apomorphic in almost all respects.

Biogeographically, *A. cervinus* is largely confined to the Nama-Karoo Biome, and *A. diadematus* to the adjacent Desert Biome. In view of the limited information available, the position of *A. vittatus* is not clear. Both subspecies seem to be restricted to marginal areas of the Nama-Karoo Biome: *A. vittatus vittatus* in the west on the borders with the Succulent Karoo, and *A. vittatus capreolus* is the east in the interface area between the Nama-Karoo and Grassland biomes. The gap in distribution between the two subspecies coincides with the area where the Nama-Karoo biome interfaces with the Fynbos Biome, and lack of suitable habitat may explain the gap. The gap is inhabited by *A. cervinus*. The Nama-Karoo / Grassland interface is a region of oscillating environmental conditions (Avery 1991), and the area vegetated by Fynbos is also known to have fluctuated (Endrödy-Younga 1988). *A. vittatus* possibly dates from a previous fluctuation when the habitats to which it is specific were more widespread and confluent.

TABLE 3: Character matrix for *Acanthoproctus* species and subspecies.

Ch.	<i>vil. v.</i>	<i>vil. c.</i>	<i>cerv. S</i>	<i>cerv. N</i>	<i>diadem.</i>
1	1	1	1	1	s
2	1	s	1	s	s
3	1	1	1	1	p
4	9	9	16	16	23
5	4	4	3	3	4
6	4	4	3	3	4
7	2	0	2	0	0
8	4	4	4	3	5
9	3	5	5	0	0

OPSOMMING

Daar is vyf genera van Hetrodinae (koringkriek) in suidelike Afrika. *Eryaliopsis* Karsch is onlangs hersien en word nie hier behandel nie. Die vier oorblywende genera word hersien, hulle verspreidings word gekarteer en hulle intrageneriese filogenie word bespreek.

Hetrodes Fischer von Waldheim sluit een spesie met vier subspecies in: *H. pupus pupus* (L.), *H. p. namaqua* Péringuey, *H. p. marginatus* Walker en *H. p. abbreviatus* Walker. *Acanthoplius* Stål sluit ses spesies in: *A. longipes* (de Charpentier), *A. discoidalis* (Walker), *A. jallae* Griffini, *A. armativentris* Péringuey, *A. speiseri* Brancsik, en *A. weidneri* sp. nov. *Hemihetrodes* Pictet is monospesief met *H. bachmanni* (Karsch). *Acanthoproctus* Karsch het drie spesies, waarvan een twee subspecies het: *A. cervinus* (de Haan), *A. diadematus* (Stål), *A. vittatus vittatus* (Walker) en *A. vittatus capreolus* Pictet.

Hetrodes is waarskynlik die mees plesiomorfe genus in die groep. Die verspreiding is grootliks tot die Fynbos Bioom beperk, met apomorfe subspecies wat in die noorde en ooste in aangrensende biotope inbeweeg het. *Acanthoplius* is merendeels beperk tot die Savanne Bioom. *A. longipes*, wat 'n geïsoleerde posisie in die genus beklee, bewoon die Woestyn en Nama-Karoo Biome. *Hemihetrodes* kom uitsluitlik in die Sukkulente Karoo Bioom voor. *Acanthoproctus* is gekonsentreerd in die Nama-Karoo en Woestyn Biome.

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