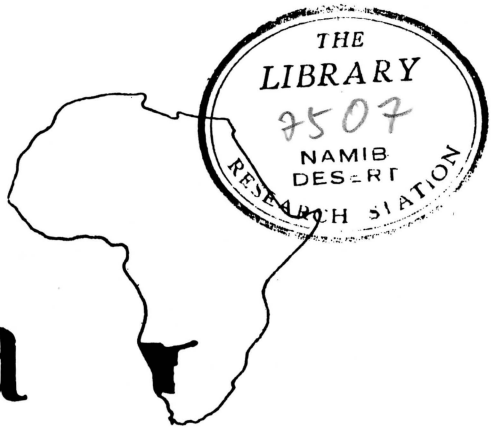

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Ser. A - Vol. 4 - No. 1
10 February 1975

THE STENINAE (COLEOPTERA, STAPHYLINIDAE) OF SOUTH-WESTERN AFRICA WITH SPECIAL REFERENCE TO THE ARID AND SEMI-ARID ZONES

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(With 13 figures)

(Manuscript received 27 February 1974)

ABSTRACT

New data concerning the occurrence of Steninae in south-western Africa and adjacent regions are presented. The distribution, ecology and taxonomy of the group in southern Africa are discussed, with special reference to the species of arid and semi-arid zones and with the aid of maps and tables. One species is resurrected from synonymy, one new subspecies is described and two new specific synonymies are proposed. The species and countries from which they are known in southern Africa are tabulated.

CONTENTS

I. INTRODUCTION

A recent monographic revision (Puthz, 1971*a*) has provided a sound basis upon which further studies of the taxonomy, phylogeny, zoogeography and ecology of African Steninae may proceed. In view of the generally scant attention paid to small Staphylinidae, in comparison with many groups of organisms, this monograph is inevitably in some measure preliminary. However, it deals comprehensively with available data and represents one of the very few substantial contributions to knowledge of Staphylinidae in which the recognition and classification of species is derived explicitly from considerations of phylogeny.

The present paper is intended to supplement the work of Puthz (1971*a*) with regard to a limited area: the semi-arid, arid and extremely arid regions of south-western Africa (Kalahari — Karroos — Namib — Namaqualand) and neighbouring areas in Angola, Botswana, South Africa and South West Africa. A body of new data which was unavailable to Puthz (1971*a*) is presented here and used as a basis for discussion of the Steninae of south-western Africa in the context of what is known of their ecology and in terms of the zoogeography of species-groups. Knowledge of the circumstances in which largely hygrophilous species are able to colonize certain parts of areas which are essentially arid may provide information relevant to various aspects of arid zone research. Data concerning the differential tolerance of species to the conditions in present-day arid zones may contribute to interpretations of historical movements of these species and thus to a knowledge of their phylogeny.

In relation to their numbers and diversity Staphylinidae from many parts of the world are poorly represented in collections. Although gleaned from most possible sources only approximately 4 300 specimens of African Steninae were available to Puthz (1971*a*) for his monographic studies. A relatively low number of species of Steninae in the African fauna is undoubtedly one factor contributing to the small amount of available material; the 255 species and subspecies included by Puthz are likely to represent the majority of those extant. The usual habitats and habits of Steninae in Africa also influence the numbers of specimens available for study; wholesale methods are generally unsuited to their collection. In particular, unlike many tropical Staphylinidae, Steninae are virtually absent from light-trap catches. Specimens are frequently collected in only ones or twos. Entomological expeditions of a "general" type are notable for the small numbers of specimens of Steninae collected. For example, that of Jordan (1936) to South West Africa and Angola, obtained no Steninae. However, small contributions to the collection of African Steninae have been made by numerous expeditions and individuals, as may be seen from a perusal of the collection data and extensive bibliography included in Puthz's (1971*a*) monograph.

Only some 450 of the specimens studied by Puthz (1971*a*) originated from the area which is the concern of the present paper — Angola, Botswana, Rhodesia, South Africa and South West Africa. As a result of recent expeditions rather more than 600 further specimens, from these same areas, have been made available for study.

Insects were collected by the Swedish Expedition to Southern Africa (1950–1951) in 356 localities, almost all of them in South Africa and South West Africa (Brinck & Rudebeck, 1955). Investigation by experienced entomologists of many aquatic and other habitats which might have been suitable for Steninae resulted in the collection of some 60 specimens of this subfamily. On the basis of data from the annotated itinerary provided by Brinck & Rudebeck (1955) I estimate that habitats *possibly* suitable for Steninae were investigated in approximately 180 of the 356 localities visited. Of these, Steninae were collected in 15. The Staphylinidae collected by the Swedish Expedition have, as noted by Puthz (1971*a*), until recently been mostly unavailable for study, but an account of these collections has now appeared (Scheerpeltz, 1974). I have been able to re-examine 42 of the specimens collected.

The expedition to southern Africa (1954) by Mr. J. Balfour-Browne, then of the British Museum (Natural History), covered much of the same ground as the Swedish expedition. Collections, principally of aquatic and semi-aquatic Coleoptera, were made between February and August, mostly in South Africa. Parts of southern Angola and northern South West Africa were also investigated. Specimens were obtained from 355 'collecting-stations' which, as separately numbered stations were frequently in close proximity, may be regarded as representing approximately 119 localities. On the basis of Mr. Balfour-Browne's unpublished notes I estimate that habitats possibly suitable for Steninae were investigated in approximately 88. Of these, Steninae were collected in 12. The 42 specimens of this group collected by Balfour-Browne are all in the British Museum (Natural History) and have been studied by me.

The British Museum (Natural History) Entomological Expedition to Southern Africa (1971–1972) provided the opportunity for a variety of specialized collecting of insects in (entomologically) poorly known areas of southern and south-western Africa. The team of five entomologists (including the present writer) investigated a total of 151 localities in Angola, Botswana, South Africa and South West Africa. As Steninae were one of the several groups of insects especially sought out by this expedition, data regarding their collection is relatively meaningful. Some 45 localities which may have contained suit-

able habitats were not investigated for Steninae as they were visited only to enable special samples to be taken (e.g. night-time stops for light-trapping). At each of the other 106 sites the type of habitat favoured by Steninae and other ripicolous and humicolous Staphylinidae was sought and, if found, investigated. In many cases, especially in South West Africa, surface water and humus were totally absent. In some other cases the only surface water was the result of human activity; naturally occurring water was frequently of a temporary nature. At all sites where surface water or moist humus was found Staphylinidae were collected by searching, sieving humus or moist plant debris, or by washing them out of mud, sand or gravel. Habitats regarded as possibly suitable for Steninae were investigated in 57 localities (see table 2), in 18 of which Steninae were found. The total of 513 specimens of this subfamily collected, all in the British Museum (Natural History), have been studied.

In the course of the three expeditions referred to above habitats possibly suitable for Steninae were investigated in 325 localities (see fig. 10). The location of the 45 sites where Steninae were found is given in figure 11.

II. NEW RECORDS AND TAXONOMIC NOTES

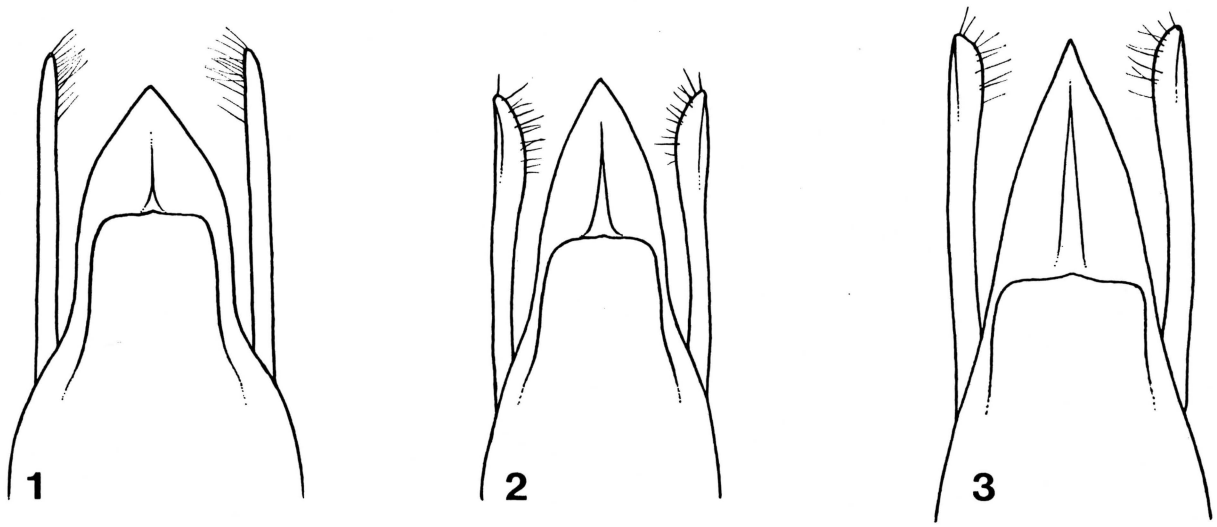
In the following list, records of specimens collected by J. Balfour-Browne include the appropriate 'collecting-station' number from his list ('St. N. –') while those collected by the BMNH expedition in 1971–1972 include the 'locality number' ('A 2', etc.). Collectors' names are given in each case, except for the 1971–1972 expedition, the bulk of the material, which was mostly collected by the present writer. A little additional material from the collections of the British Museum (Natural History) (= BMNH) and those of the Laboratório de Biologia, Museo do Dundo, Angola (= LB, Dundo) is included. Notes on specimens originating from the Swedish Expedition, already studied by Scheerpeltz (1974) but restudied by the present writer, are appended; this material is now in the Zoological Museum, University of Lund, Sweden. Taxonomic commentary is included in the list where appropriate discussion of ecology is largely deferred to the following section.

Stenus mendicus senegalensis Bernhauer
Figs 3 & 4.

ANGOLA: 3, Chianga (A 21), c. 8 mi. NE. Nova Lisboa, c. 5 200 ft, on mud among plant roots beside slow-flowing stream, 6.III.1972 (BMNH);

BOTSWANA: 3, Moremi Game Reserve (B 11), c. 2 700 ft, on mud among grass at edge of shallow reedy pool, 19.IV. 1972 (BMNH); 1, nr. Moremi Game Reserve, c. 2 700 ft, on mud among plant roots at edge of small water-hole, 20.IV. 1972 (BMNH); MALI: 1 ♀, 6 mi. E. Bamako (Clarke) (BMNH).

These specimens may be assigned without reservation to *S. mendicus senegalensis* as delimited by Puthz (1971*a*). Males from both Chianga and Botswana agree well in sexual characters with a male from "Léopoldville — Coquilhatville" (BMNH) studied by Puthz and in each case the structure of the lateral lobes and apical portion of the median lobe of the male genitalia are much as illustrated here (fig. 3). Although specimens from Botswana are a little smaller (see table 1) and more shining than those from further north, individuals from western



Figures 1–3. Lateral lobes and apical portion of median lobe of ♂ genitalia in ventral view: 1, *Stenus mendicus* cf. *senegalensis* Bernhauer (Roçadas); 2, *S. mendicus* cf. *protector* Fauvel (Cachoeiras); 3, *S. mendicus senegalensis* Bernhauer (Chianga).

Congo, Angola and Botswana all agree well in relative proportions of fore-parts and in puncturation. They do not, however, agree so well in these respects with females from Mali and Chad (see further discussion below).

S. mendicus cf. senegalensis Bernhauer
Figs 1 & 6.

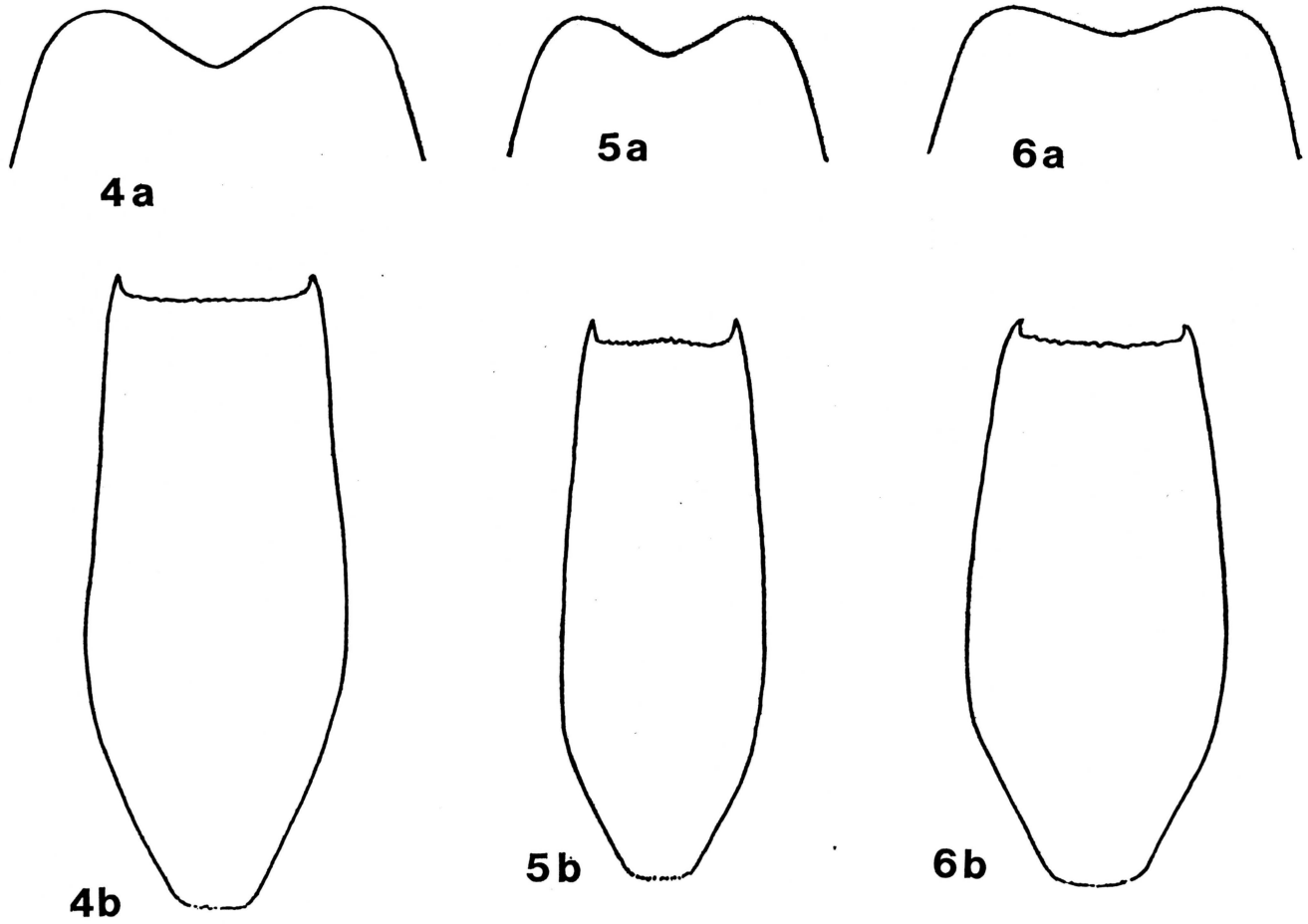
ANGOLA: 7, Roçadas (A 2), c. 3 600 ft, in wet vegetable debris on black mud beside temporary pool near the River Cunene, 20.II.1972 (BMNH).

These specimens differ from those of "typical" *S. m. senegalensis* from Angola in several respects: average smaller size and shorter elytra (see table 1), stronger and closer puncturation of the abdominal tergites, much shorter apical portion of the median lobe and much narrower lateral lobes of the male genitalia (fig. 1). Each of the four males from the small Roçadas sample exhibit more or less identical sexual characters which are rather markedly different from those of "typical" *S. m. senegalensis*. However, in puncturation and most other external features, they closely resemble specimens from Mali and Chad. No males from these latter countries have been available for examination although the genitalia of a male from Chad figured by Puthz (1971*a*, fig. 52) appears to be a little more similar to those of Roçadas specimens than are "typical" *S. m. senegalensis*.

S. mendicus cf. protector Fauvel
Figs 2 & 5.

ANGOLA: 57, Parque das Cachoeiras (A 32), c. 20 mi. SW. Gabela, c. 1 200 ft, on sand banks by small pools below small waterfall, 18.III.1972 (BMNH).

Specimens from this sample differ from those of *S. m. senegalensis* in average smaller size, slightly different proportions of the fore-parts (table 1) as well as in surface sculpture and sexual characteristics. The intervals between punctures are much less evidently micro-reticulate in Cachoeiras specimens, and therefore more shining than in *S. m. senegalensis* (or individuals from Roçadas); the puncturation is also slightly less close and, at least on the pronotum, slightly larger. The apex of the sternite of the ninth abdominal segment of males (fig. 5) is narrow-



Figures 4–6. Apical outline of sternite of 8th abdominal segment (a) and sternite of 9th abdominal segment (b) of ♂♂: 4, *Stenus mendicus senegalensis* Bernhauer (Chianga); 5, *S. mendicus* cf. *protector* Fauvel (Cachoeiras); 6, *S. mendicus* cf. *senegalensis* Bernhauer (Roçadas).

er than in *S. m. senegalensis* and the male genitalia, which appear to be of very constant form within the Cachoeiras sample, also differ in several respects, particularly in the shorter and more parallel-sided apical portion of the median lobe (fig. 2).

Most of these characteristics of the Cachoeiras population, except the form of the male genitalia, are shared to a considerable degree by members of five other races: *S. mendicus arens* Peyer., *S. m. orientis* Puthz, *S. m. protector* Fauvel, *S. m. pretoriensis* Puthz and *S. m. separatus* Benick. A female of *S. m. protector* examined (BMNH), except in slightly finer and closer puncturation, agrees particularly well with specimens from Cachoeiras.

S. mendicus pretoriensis Puthz

Two of the three specimens recorded by Scheerpeltz (1974) as *Stenus mendicus* var. *pretoriensis* have been examined. One of these, from Barberspan, Transvaal, appears to fall within the subspecies *S. m. pretoriensis* as delimited by Puthz (1971*a*). This specimen, a female, resembles the female from Warmbad discussed by Puthz and also has much in common with specimens from Botswana (*S. m. senegalensis*) and Roçadas (*S. m. cf. senegalensis*) in general appearance. The fore-parts are, however, somewhat narrower than in these and the puncturation is a little larger. Although slightly more shining than Roçadas specimens the Barberspan female is much less shining than specimens of *S. m. protector*. The female from Livingstone (Zambia) recorded by Scheerpeltz (1974) as *S. m.* var. *pretoriensis* closely resembles larger specimens from Botswana in size, proportions and surface sculpture and should be referred to subspecies *S. m. senegalensis*.

The status of geographical races in the *mendicus*-complex

As noted above, it has not been found possible to assign specimens of all recently collected samples to any of the eleven subspecies (of one species) into which the *mendicus*-complex was divided by Puthz (1971*a*). An approach consistent with the methodology of that author would be to describe specimens from the distinctive Roçadas and Cachoeiras populations as representatives of two new subspecies of *Stenus mendicus*. However, this approach is considered here to be inappropriate and possibly misleading.

Attempts to evaluate the likely status of these populations have involved a partial re-examination of the classification of the *mendicus*-complex provided by Puthz (1971*a*). Based on the published results of Puthz (1971*a*: 46–66, and previous works), some of the material forming the basis of those studies, and newly collected material, a brief discussion and some tentative conclusions are presented here.

Puthz (1967, 1971*a*) has well demonstrated how differences in morphology between the three most northerly forms (*S. mendicus* Erichson *f. typ.* — circum-Mediterranean in distribution, *S. m. arens* Peyer. — Saharan, and *S. m. orientis* Puthz — Iranian) correlate with three discrete but adjoining geographical ranges. Although the nature of the interfaces between these three forms requires further investigation their status as morphologically distinct allopatric forms is not in question. The status of forms from regions further to the south (including eight named subspecies of *Stenus mendicus* in the classification provided by Puthz), is more problematical. The significance of geographical variation of structural features is here more difficult to assess. In particular, local variations in structure of male genitalia are not easily interpreted on the basis of material presently available for study. Interpretations have also been hindered by lack of ecological data.

However, it is possible on morphological grounds to distinguish between two principal types among the members of the *mendicus*-complex occuring south of the Sahara. The (generally) more northerly populations are characterized by individuals of relatively larger size (table 1), mostly with closer puncturation of the upper surface, more evident micro-reticulation and therefore less shining appearance, larger male genitalia and broader sternite of the ninth abdominal segment. These larger (and generally more northerly) forms include five of the subspecies listed by Puthz (1971*a*), *Stenus mendicus senegalensis* Bernhauer, *S. m. azeganus* Fauvel, *S. m. naivashensis* Puthz, *S. m. collarti* Cameron and *S. m. decellei* Puthz, as well as the specimens from Roçadas (Angola) referred to above as *S. m. cf. senegalensis*. The more southerly, smaller and more shining type is represented by three of the subspecies included by Puthz (1971*a*), *S. m. protector* Fauvel, *S. m. pretoriensis* Puthz and *S. m. separatus* Benick, as well as by the population from Cachoeiras (Angola) referred to above as *S. m. cf. protector*. Although most specimens may be referred on both geographical and morphological grounds to one of these types, individuals from some areas (*S. m. cf. senegalensis* from southern Angola, *S. m. decellei* from southern Congo, *S. m. senegalensis* from Botswana and some *S. m. pretoriensis* from Transvaal) may be considered somewhat transitional between the two.

Within the area occupied by populations of the "northern" type Puthz (1971*a*) recognises one particularly widespread (and also variable) subspecies, *S. m. senegalensis* Bernhauer, distributed through much of tropical Africa, from Senegal to Zambia. Records referred to this form in the present paper extend its known range south to Botswana. Although closely resembling *S. m. senegalensis* in many features, two of the other subspecies recognised by Puthz among these northern populations exhibit some apparently fairly constant morphological dif-

ferences. The most notable are in size and proportions of parts (see table 1), surface sculpture and form of male genitalia (see Puthz, 1971*a*). As both forms (*S. m. collarti* Cameron at high altitude in Eastern Congo and the Rift Valley area, *S. m. azeganus* in Ethiopia) are known from several localities and occupy well-defined geographical areas adjoining the range of *S. m. senegalensis*, it would seem reasonable to regard all three as distinct, if somewhat weekly differentiated, subspecies. Individuals intermediate between *S. m. collarti* and *S. m. senegalensis* have been found in an apparently fairly narrow transition zone in Eastern Congo. As the known ranges of *S. m. azeganus* and *S. m. senegalensis* are separated by some five-hundred miles at their nearest points little can be said about the nature of the interface between these two races. The extent to which morphological differences between the three races are an expression of climatic and other environmental differences in the areas in which they occur can not be estimated. However, it may be noted that the relatively large size of *S. m. azeganus* and *S. m. collarti* as compared with *S. m. senegalensis* is paralleled by some other species of Staphylinidae in which individuals taken at high altitude in Eastern Congo and neighbouring areas are of larger size than those from West Africa or the Congo basin.

The two other "northern" forms, *S. m. naivashensis* Puthz (from Kenya) and *S. m. decellei* Puthz (from southern Congo) are both known from single localities and only one male is known of each. The male holotype of *S. m. naivashensis* has been examined (see table 1) and, apart from slightly longer elytra, it fits well within the usual range of variation of *senegalensis* as delimited by Puthz (1971*a*). The apex of the median lobe of the male genitalia is slightly unusual but, although *S. m. naivashensis* is somewhat transitional to *S. m. azeganus*, it would seem likely on both geographical and morphological grounds, that further evidence will show it to be more suitably included within the bounds of *S. m. senegalensis*. The description of *S. m. decellei* makes it clear that the single individual so far known differs little from *S. m. senegalensis* except in the form of the apical portion of the median lobe of the male genitalia. The type locality of *S. m. decellei* is shown by new records in the present paper to be included in the geographical range of *S. m. senegalensis*, and it would seem unlikely that *S. m. decellei* will prove to represent a distinct geographical race.

The status of populations of the *mendicus*-complex found beyond the known limit of the range of *S. m. senegalensis* in Angola, southern Africa and Madagascar is difficult to assess. The present availability of samples additional to those studied by Puthz (1971*a*) from seven localities in these areas and of some additional ecological data does little to clarify the situation. One newly available sample from Roçadas (Angola) indicates that the population there is more or less of "northern" type but marked differences with "typical" *S. m. senegalensis*, including those from less than 300 miles away at Chianga, in form of male genitalia are not easy to explain. However, as Roçadas represents the known limit of the *mendicus*-complex towards the south-west, specimens from this locality probably represent a peripheral population which is isolated to some degree from the main body of *S. m. senegalensis*. The distribution of members of the *mendicus*-complex, particularly those attributed to *S. m. senegalensis*, appears to be much more linked to the major African river systems (see Puthz, 1971*a*, fig. 73) than are the distributions of other widespread African species of *Stenus*. Watersheds between river-systems may play a role in the formation of local races, particularly in areas at the periphery of the range of *S. m. senegalensis*. The Roçadas population were taken from the Cunene valley while specimens from Chianga were found beside a stream feeding the Cubango, a river running south-east to the Okavango basin. However, without further data concerning the area between Roçadas and Chianga the widespread occurrence in the Cunene system of a well-defined race of "Roçadas-type" must remain uncertain.

The three races of "southern" type recognised by Puthz (1971*a*), *S. m. pretoriensis* Puthz in Transvaal, *S. m. separatus* Benick in Cape Province and *S. m. protector* Fauvel in Madagascar, all exhibit some distinctive morphological features, are known from more than one locality each, and occur in well-defined geographical areas. Although intergrades may prove to occur, subspecific status for these forms does not seem unreasonable in the light of present knowledge. Specimens of *S. m. senegalensis* from the southern part of its range appear to be somewhat transitional to *S. m. pretoriensis*, while the latter is intermediate between *S. m. senegalensis* and *S. m. separatus* in many respects. A simple geographical relationship between these races seems likely. The great similarity of the Madagascan race (*S. m. protector*) to *S. m. pretoriensis* may indicate, as suggested by Puthz (1971*a*), a genuine connection between the two and a relatively recent invasion of Madagascar by members of the *mendicus*-complex.

The occurrence of a population of "southern" type at Cachoeiras (Angola), some thirteen-hundred miles from the nearest known locality for *S. m. pretoriensis*, is perplexing. Cachoeiras lies on the periphery of the known range of *S. m. senegalensis*, for which the nearest known record is less than two hundred miles distant at Chianga, but a genuine connection with the other "southern" races, despite an apparently disjunct distribution, can not be ruled out. Importation from far afield, even from Madagascar, is possible as the Cachoeiras population appears to most closely resemble the Madagascan race *S. m. protector*. In this connection it may be noted that the *S. m. protector*-like population was found at Ca-

choeiras in company with *Stenus irroreus* Fauvel, a species known from Madagascar and Aldabra as well as having a scattered distribution in Africa and which may have spread to at least some areas by anthropochorous means. However, similarities with the Madagascan and South African races may have been produced in the Cachoeiras population by similar responses to environmental conditions. The Cachoeiras record relates to a different river system to those at both Chianga and Roçadâs. Although differing from *S. m. senegalensis* in several features, the *S. m. protector*-like population at Cachoeiras may have originated from a peripherally isolated population of *S. m. senegalensis* type.

As many of the problematical populations of the *mendicus*-complex occur at the periphery of the range of *S. m. senegalensis*, the nature of variation within that widespread race is of interest. Considerable variation in external morphology and at least some variation in form of the male genitalia does seem to occur in specimens referable to *S. m. senegalensis*. Some such variation, especially that of the male genitalia, may be very local while other variation is probably of a gradual clinal type over broad geographical areas. For example, specimens from the southern part of the range of *S. m. senegalensis* (Botswana, Angola, Western Congo) approach the "southern" group of races (*S. m. pretoriensis*, etc.) more closely in external morphology than do specimens which I have examined from Senegal, Chad and Mali, where the range of *S. m. senegalensis* abuts directly onto that of *S. m. arens*. Although the present discussion is concerned primarily with the races of the *mendicus* complex found south of the Sahara, a comment on the nature of the interface between *S. m. arens* and *S. m. senegalensis* is appropriate. No specific mention of the relationship between these two races is made by Puthz (1971*a*) although he notes that, in general, the subspecies of *S. mendicus* which he recognises intergrade. However, both *S. m. arens* and *S. m. senegalensis* are recorded by Puthz (1971*a*) from two localities in Chad and in these localities the two forms may have actually occurred together. I have not examined *S. m. senegalensis* and *S. m. arens* from the same locality but specimens of *S. m. senegalensis* from Chad and Mali which I have seen exhibit a greater difference with *S. m. arens* in external morphology than do *S. m. senegalensis* from further south. If, as is likely, the variation of *S. m. senegalensis* from north to south is clinal, then in relation to the interface with *S. m. arens* this variation may represent a reverse cline. It is thus possible that at the point where their ranges meet *S. m. arens* and *S. m. senegalensis* are behaving as distinct species. The "southern" races (*S. m. pretoriensis*, etc.) appear to share many more features in common with *S. m. arens* than do those races (*senegalensis* and *azeganus*) whose ranges meet or closely approach that of *S. m. arens* and an originally continuous cline, in which connections between *S. m. arens* and races of the "southern" type are now broken is possible. Based on environmental differences in the areas occupied by the various races of the complex today a palaeoecological explanation conforming with this hypothesis could be attempted.

However, the extent to which races sharing certain common features of external morphology are historically linked in the *mendicus*-complex is difficult to assess on the basis of evidence presently available. Present day regional or local differences may, at least in part, be an expression of very recent or existing differences in environmental conditions. Similarities between widely separated populations from Mali and Roçadas (Angola), which are unlikely to be linked historically, have already been noted. Relatively small size and shiny body surface are exhibited by most populations found in particularly arid areas and, perhaps, in more exposed or temporary habitats. Apparent differences between the habitats in which "typical" *S. m. senegalensis* and those in which other forms were found were noted by the present writer during the course of the BMNH 1971–1972 Expedition. The *S. m. senegalensis* habitats (see table 2) were characterised by mud or muddy sand, presence of permanent water and a degree of plant cover. In fact, specimens were taken in each case from among the roots of waterside plants. Roçadas specimens (*S. m. cf. senegalensis*) were taken from a rather more exposed situation, on mud without waterside plants but with a certain amount of plant debris, mostly dead leaves from two nearby trees. The habitat at Cachoeiras, where specimens (*S. m. cf. protector*) were taken in number running on sand banks, is a completely exposed one, devoid of plant cover and some one hundred feet from vegetation of any kind.

Whatever the historical or ecological explanation for the diverse forms of the *mendicus*-complex occurring south of the Sahara it is difficult to accept any interpretation in which differences in form of the male genitalia are regarded as sufficient grounds for the naming of subspecies. The precise form of the apex of the median lobe and the form of the lateral lobes of the male genitalia do appear to be very constant within a sample from one locality but differences in these respects between samples from different localities may be marked even at a fairly local level. Populations apparently isolated at the periphery of (or even within: *S. m. decellei*?) the range of the widespread and variable race *S. m. senegalensis* differ markedly in form of male genitalia from "typical" *S. m. senegalensis* and between themselves. As such populations are likely to be numerous and differences between them in form of male genitalia may be relatively uncorrelated with differences in external morphology or historical origin, the advantages of naming them are dubious. Members of the *mendicus*-complex appear to exhibit a broadly continuous distribution throughout their African

range. Only in the case of those geographical forms which are unlikely to be connected by an even clinal variation in characteristics with other forms, and which can be shown to occupy a substantial or particularly well demarcated area is there a practical need for separate names.

Although no formal changes in the classification of the *mendicus*-complex are necessitated by the foregoing discussion it is clear that some of the eleven presently recognised subspecies may be dispensed with when the complex is re-examined on the basis of more study material. In summary it may be noted that the formal naming of further subspecies in this complex is unlikely to serve any practical need although further studies of morphological and ecological variation may contribute considerably to an understanding of the historical and genetical relationships between the races. A clarification of the relationship between the Saharan race *S. m. arens* and those occurring to its south, *S. m. senegalensis* and *S. m. azeganus* would be particularly useful.

Stenus jovino jovino Eichelbaum

ANGOLA: 1, 10 mi. NE. Cacula (A 20), (Sá da Bandeira/Nova Lisboa road), c. 5 000 ft, on yellow mud at roots of reeds in hollow in *Brachystegia* woodland, 5.III.1972 (BMNH); 1, Chianga (A 32), c. 8 mi. NE. Nova Lisboa, c. 5 200 ft, sieved from heap of cut grass on banks of reservoir, 22.III. 1972 (BMNH); 1, Tundavala (A 40), c. 9 mi. NW. Sá da Bandeira, c. 6 600 ft, sieved from heap of cut grass and weeds by roadside, 28.III.1972 (BMNH); 1, R. Quê Gallery-forest, Caconda-Ngola road (c. 14°00'S; 14°30'E), vegetable debris, 7.XI.1969 (Reis) (LB, Dundo).

These specimens are indistinguishable from others of the type-form of *S. jovino* from various parts of Africa (BMNH) and run readily to this form in the key given by Puthz (1971*a*: 112). The bionomic data given above tends to confirm the assessment of the species made by Puthz (1971*a*: 90, 115–119). All of the localities listed are in the *Brachystegia* woodland zone and are at the top of the escarpment in central-south Angola.

Stenus jovino magnopunctatus n. subsp.

HOLOTYPE ♀ : SOUTH AFRICA, Cape Province, Du Toits Kloof (S 11), in dead leaves among thick reeds beside small, fast stream, at about ½ mi. below top of pass, c. 2 400 ft, 5.I.1972 (BMNH).

Length 4,25 mm. Agreeing in most respects with the diagnosis of *S. jovino jovino* Eich. given by Puthz (1971*a*: 91–92). Maximum breadth of head: 0,85 mm; maximum breadth of pronotum: 0,69 mm; maximum length of pronotum: 0,69 mm; maximum breadth of elytra together: 1,07 mm; length of elytra at shoulder: 1,00 mm. Fully-winged.

Puncturation of pronotum and elytra slightly stronger and distinctly more confluent than in the nominate form. Puncturation of the upper surface of the abdomen very different to that of the nominate form, very much stronger and deeper and also a little closer. Punctures much broader than the intervals, even on the tergite of the seventh abdominal segment. Intervals between punctures shining, with weak micro-reticulation which is scarcely visible in places.

The specimen from Du Toits Kloof agrees so closely with specimens of *S. jovino jovino* in size, colouration, proportions of parts and most other features, while differing in these respects from other members of the *jovino*-group of species, that it is here regarded as representing sister populations of the nominate form of *S. jovino*. The difference in surface sculpture, notably that of the abdomen, between the South African specimen and specimens of the nominate form examined, from Angola, Kenya and Rwanda, is striking. This difference, in a feature which appears to very constant within the nominate form, along with the great geographical separation of the South African locality from the limit of the known range of *S. jovino jovino*, would seem to justify the naming of a new subspecies. It is of some interest to record a member of the *jovino*-group, all members of which exhibit a classic montane distribution in Africa (see Puthz, 1971*a*, fig. 109), from the southermost portion of the continent. The most southerly previous records of the *jovino*-group are for the nominate form of *S. jovino*, from Angola and Rhodesia, in each case at least thirteen hundred miles from Du Toits Kloof. Populations linking those in Rhodesia and Western Cape Province may occur in other parts of South Africa. Although representatives of otherwise montane species or species-groups frequently descend to much lower altitudes in the most southern parts of Africa, this is not necessarily the case with the *jovino*-group as Du Toits Kloof is at a fairly high altitude.

S. jovino magnopunctatus will not fit readily into the key to the *jovino*-group provided by Puthz (1971*a*: 112–113) as, although sharing most features in common with *S. jovino jovino*, its abdominal puncturation is stronger even than in *S. umbrosus* Benick.

Stenus cameratus Benick
Fig. 8.

ANGOLA: 234, Roçadas (A 2), c. 3 600 ft, banks of temporary pools near the River Cunene, 20.II.1972 (BMNH); 1, at light near River Cunene, 21.II.1972 (BMNH); 1, Roçadas (A 42), at light by temporary pool near River Cunene, 30.III.1972 (BMNH).

These records extend the known range of *S. cameratus* several hundred miles to the west. The specimens from Roçadas agree with those of *S. cameratus* from other parts of Africa in structure of the male genitalia, secondary sexual features of males, puncturation and pubescence, but differ slightly in proportions of the elytra and fore-parts and in colouration of the appendages. In specimens from the Roçadas population both femora and tibiae are more or less black and the antennae are largely black, with the middle segments, somewhat variably, a little lighter.

Stenus machadoi Cameron

ANGOLA: 1, Duque de Bragança Falls (A 27), c. 3 000 ft, on gravelly bank of river just below falls, 12.III.1972 (BMNH); 1, Caungula, R. Cambonde (8°05′S, 18°13′E), c. 750 m, affl. rive droite Uamba, 20.VII.1962 (Machado) (LB, Dundo); 1, Lóvua, détritus végétaux de la forêt-galerie de la rivière Camuanga (7°19′S, 20°09′E), 779 m, affl. rive droite de Lóvua, 5.VIII.1956 (Machado) (LB, Dundo).

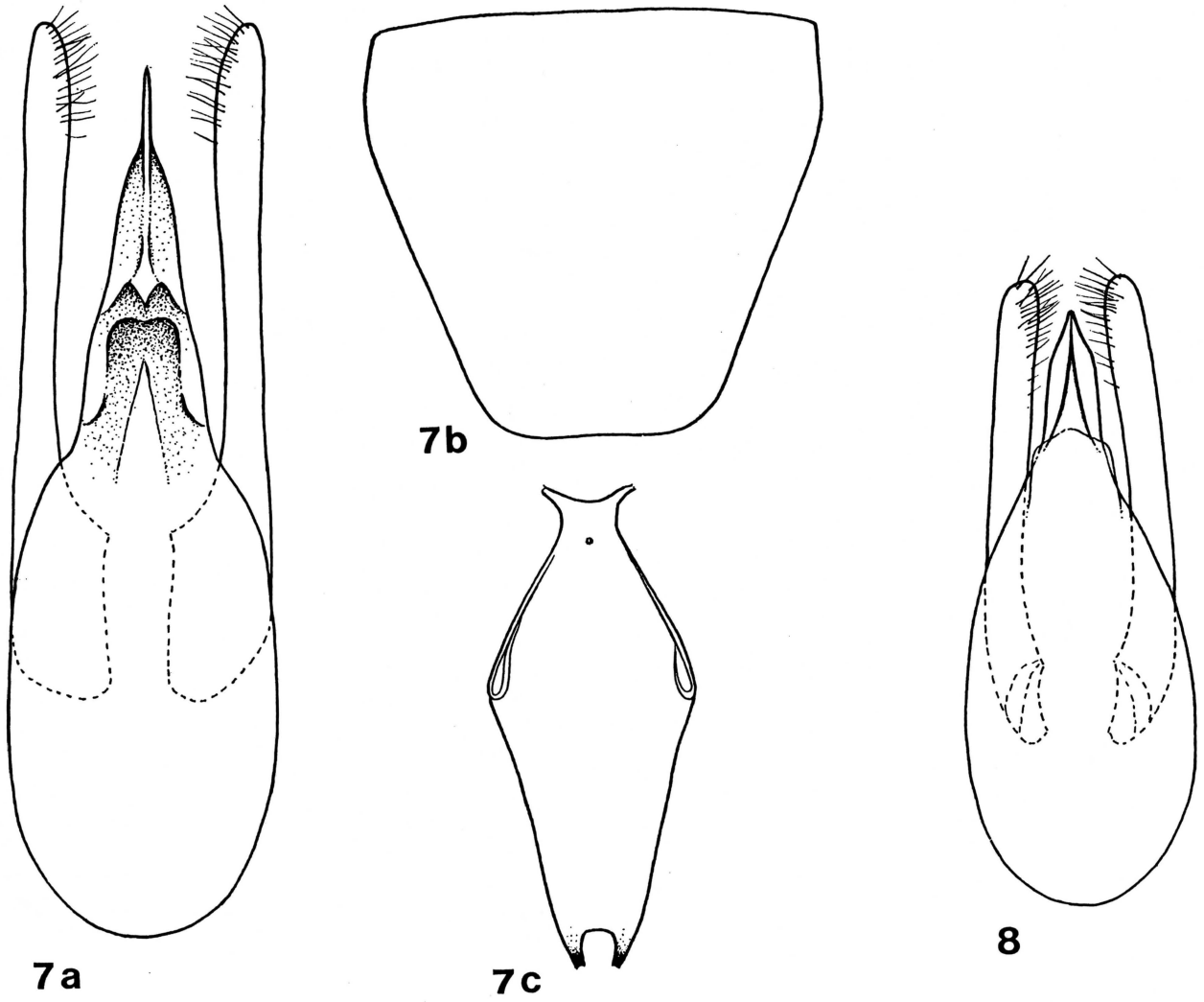
These records double the number of known specimens and known localities for *S. machadoi* and extend its known range to the west. Despite the comment of Puthz (1971*a*: 134) *both* of the original specimens mentioned by Cameron (1950) are in the collections of the BMNH. The full data of these specimens (previously unpublished) is as follows:— holotype: Angola: Dundo, forêt galerie de la Luachimo, dans les détritus végétaux accumulées au bord de l'eau par le courant du fleuve, VII.1948 (Machado); paratype ♂ : Angola: rive du fleuve Tchikapa (50 km SW. of Dundo), dans les détritus végétaux accumulées au bord de l'eau par le courant du fleuve (forêt-galerie), VII.1948 (Machado).

Stenus peringueyi Benick

SOUTH WEST AFRICA: 1, Windhoek (W 32), c. 5 500 ft, on mud by reservoir at night, 6.II.1972 (BMNH); 14, Hoffnung Farm (W 33), 10 mi. NE. Windhoek, c. 5 800 ft, on mud by reservoir, 7.II.1972 (BMNH);

BOTSWANA: 1 ♂, Kuke Pan (B 7), c. 3 100 ft, on mud by small pool, 16.IV.1972 (BMNH).

Although a number of problems regarding the delimitation of species in the *cameratus*-group clearly remain to be solved I have little doubt as to the identity of these specimens. The single male from Botswana, although agreeing closely with South African and South West African specimens in sexual characters, has darker legs and antennae than these. The habitats where the specimens recorded above



Figures 7–8. 7, *Stenus humidulus* Cameron: (a) ♂ genitalia in ventral view; (b) sternite of 8th abdominal segment of ♂; (c) tergite of 9th abdominal segment of ♂. *Stenus cameratus* Benick f.typ. (Roçadas), ♂ genitalia in ventral view.

were taken were all (subjectively) rather similar: open, muddy banks of still, permanent or more or less permanent water, with little or no vegetation and little vegetable debris.

The four specimens recorded by Puthz (1971*a*: 137) from Vila Arriaga (Angola) as *S. peringueyi* are all likely to be referable to *S. humidulus* Cam. (see below); I have examined the single male (in which the apex of the median lobe of the male genitalia appears to be broken) from this series and regard it as conspecific with other specimens of *humidulus* from nearby localities in south-west Angola. The specimen recorded for Salisbury (Rhodesia, *not* South Africa) as *S. kaguruensis* Bernh. by Puthz (1971*a*: 151) (in BMNH) appears to be referable to *S. peringueyi* (♀).

Stenus humidulus Cameron **sp. rev.**
Fig. 7a–c.

ANGOLA: 62, Bruco (A 11), c. 25 mi. SW. Sá da Bandeira, c. 3 000 ft, in wet leaf litter beside stream, 1.III.1972 (BMNH); 1 ♀, Tundavala (A 18), c. 8 mi. NW. Sá da Bandeira, c. 6 500 ft, in wet moss on rocks above waterfall, 4.III.1972 (BMNH); 1 ♀, 7 mi. W. Gabela (A 30), c. 3 600 ft, in damp leaf litter near stream in coffee forest, 18.III.1972 (BMNH); 1 ♀, Tundavala (A 40), c. 8 mi. NW. Sá da Bandeira, c. 6 500 ft, in wet moss on the face of small waterfall, 28.III.1972 (BMNH); 1 ♀, Huila dist., Ongueria (St.N. 266), in fine sand at side of stream above cataracts, 13.VI.1954 (Balfour-Browne) (BMNH).

Puthz (1971*a*: 151) placed *S. humidulus* in the synonymy of *S. kaguruensis* Bernhauer, but examination of a long series of specimens collected near the type locality of *S. humidulus*, including males (unavailable in the type series), enables a re-assessment of the status of Cameron's species.

The specimens listed above as *S. humidulus* (except in some measure one of the females from Tundavala — A 18) and Cameron's two original specimens of *S. humidulus* differ from specimens of *S. kaguruensis* examined in the following features:— smaller size, legs less robust, basal segment of the antennae very dark, usually black, darker than the second segment, puncturation of the upper surface slightly less close. Males differ from those of *S. kaguruensis* in additional features:— legs similarly developed to those of females, sternite of eighth abdominal segment (fig. 7b) more or less truncate apically, sternite of ninth abdominal segment with relatively shallow incision, genitalia (although apical portion of median lobe a little variable in length) characteristic (fig. 7a).

The legs of *S. humidulus* (except large female from Tundavala) are relatively light in colouration, femora and tibiae light to medium-brown, tarsi pale brown, legs sometimes a little darker around the knees. The proportions of parts of the holotype ♀, which resembles slightly larger than average females from Bruco, are:— maximum breadth of head: 0,78 mm; maximum breadth of pronotum: 0,64 mm; maximum length of pronotum: 0,70 mm; maximum breadth of elytra together: 0,94 mm; length of elytra at shoulder: 0,88 mm. Males are generally a little smaller than females and the proportions of an average male from the Bruco population are:— maximum breadth of head: 0,75 mm; maximum breadth of pronotum: 0,60 mm; maximum length of pronotum: 0,65 mm; maximum breadth of elytra together: 0,91 mm; length of elytra at shoulder: 0,82 mm.

Particularly in view of the markedly different sexual characters of the male *S. humidulus* should be regarded as a species distinct from *S. kaguruensis*. Apart from *S. habropedilus* Puthz, to which specimens of *S. humidulus* would run in the key provided by Puthz (1971*a*: 158–160), *S. humidulus* appears to be readily separated from all other species of the *cameratus*-group. On the basis of the single female paratype of *S. habropedilus* examined and the description given by Puthz (1971*a*: 150) few differences between *S. habropedilus* (known to date only from Kenya and Tanzania) and *S. humidulus* have been observed. *S. humidulus* is very similar to *S. habropedilus* in size, proportions of parts, surface sculpture, the form of the legs in both sexes and the form of the sternite of the eighth abdominal segment in males. The male genitalia of *S. humidulus* (fig. 7a) and of *S. habropedilus* (Puthz, 1971*a*, fig. 132) also appear to exhibit many similarities. Specimens of *S. humidulus* differ from the single specimen of *S. habropedilus* examined in puncturation of the pronotum and elytra which is a little larger and (on average) less close, and that of the abdomen which, especially on the more apical tergites, is not so strong and close as in *S. habropedilus*. In the paratype of *S. habropedilus* examined the first two antennal segments are unicolorous brown and not contrasting as in *S. humidulus* (see above). Both *S. humidulus* and *S. habropedilus* are known only from high altitude, the former from Angola and the latter from East Africa. It is possible that both forms are to be referred to a single species with a disjunct, montane distribution, in which case the species, or at least the nominate form, would take the older name *S. humidulus*.

The identity of females recorded above which are unassociated with males must remain somewhat doubtful. One of the females from Tundavala is larger than average specimens from Bruco and exhibits much closer puncturation than any other *S. humidulus* examined, resembling that of *S. kaguruensis*. The tibiae and femora of this specimen are very dark brown. Proportions of parts:— maximum breadth of head: 0,78 mm; maximum breadth of pronotum: 0;65 mm; maximum length of pronotum: 0,72 mm; maximum breadth of the elytra together: 0,96 mm; length of elytra at shoulder: 0,88 mm. The smaller female from Tundavala is of about the same size as a male from Bruco, the appendages are slightly darker than in Bruco specimens and the eyes are

unusual in that they are less bulbous and narrower in dorsal view. The female from Gabela is the smallest individual seen but, apart from its size, closely resembles specimens from Bruco. The proportions of this specimen are:— maximum breadth of head: 0,68 mm; maximum breadth of pronotum: 0,56 mm; maximum length of pronotum: 0,62 mm; maximum breadth of elytra together: 0,85 mm; length of elytra at shoulder: 0,76 mm. One of the females from Ongueria (Balfour-Browne) is small, pale-coloured and with irregular and atypical puncturation but these features are probably due to malformation; the left antenna of this specimen is nine-segmented while the right is ten-segmented.

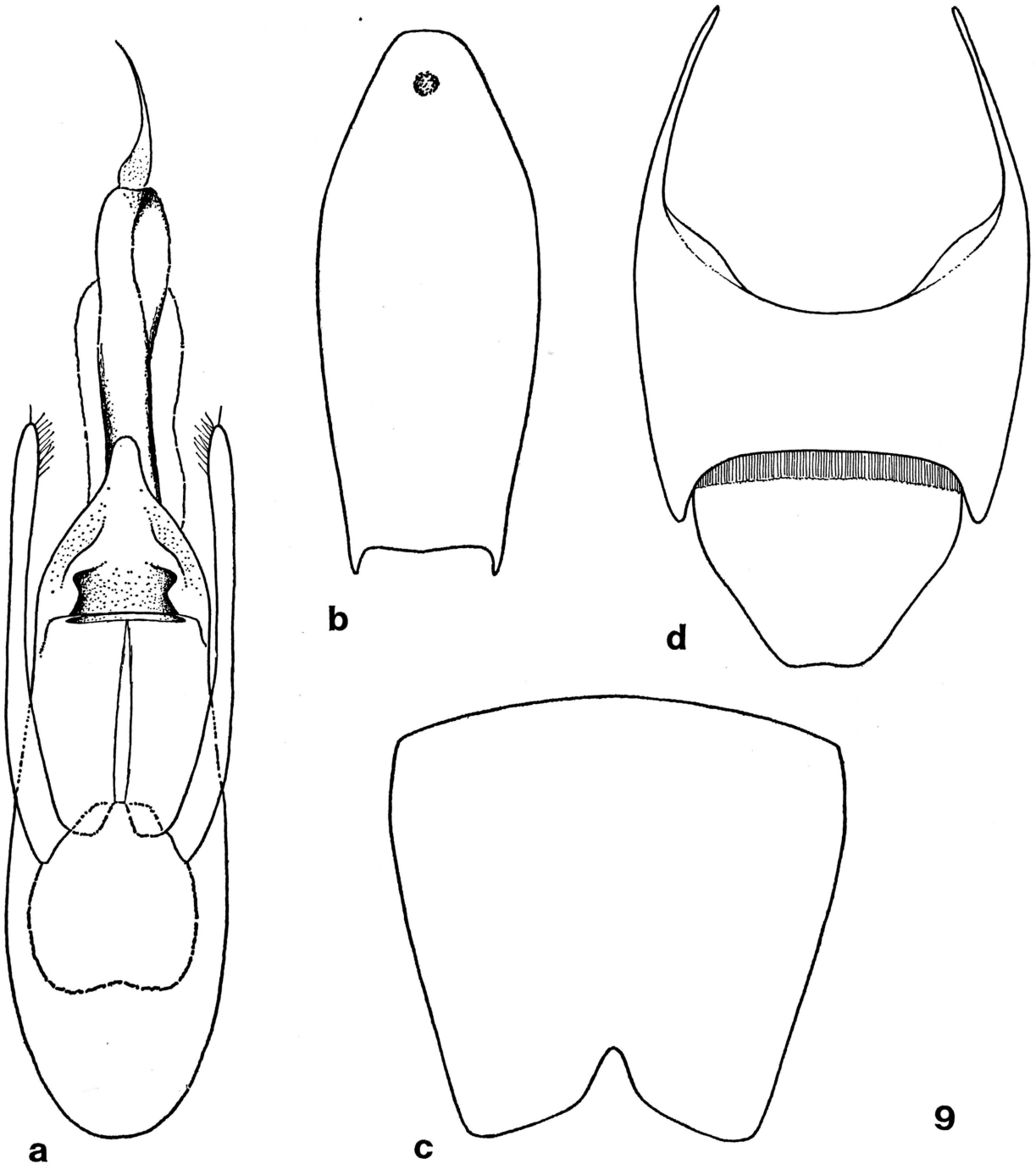


Figure 9. *Stenus levivestis* Scheerpeltz: (a) ♂ genitalia; (b) sternite of 9th abdominal segment of ♂; (c) sternite of 8th abdominal segment of ♂; (d) tergites of 9th and 10th abdominal segments of ♂.

As noted above, specimens recorded from Vila Arriaga as *S. peringueyi* by Puthz (1971*a*: 137) should be referred to *S. humidulus*. Vila Arriaga, like Bruco and Tundavala, is within forty miles of the type locality of *S. humidulus*. All four localities and the locality of the single known paratype are at the top, on the side or near the foot of the escarpment in the Sá da Bandeira district. The full data (previously unpublished) of the two original specimens of *S. humidulus* mentioned by Cameron (1951) is as follows:— holotype (without abdomen): Angola: ruisseau qui traverse la route Chibia-Jau à la bifurcation Jau-Ongueria, 45 km au SE. de Sá da Bandeira, c. 1 500 m, sous des pierres, 25.X.1949 (Machado) (BMNH); paratype ♀ : Angola: Cascade de Ongueria, 55 km au SSE. de Sá da Bandeira, c. 1 500 m, dans les détritus végétaux du sol (très humides), 25.IX.1949 (Machado) (BMNH).

Although probably restricted to the vicinity of streams and rivers, the bionomic data contained in the various records for *S. humidulus* suggest that this species may be regarded as humicolous to a degree.

(*Stenus kaguruensis* Bernhauer)

As noted above, records from Angola are to be referred to *S. humidulus* Cameron, while the record for Salisbury (Rhodesia) given by Puthz (1971*a*) probably refers to *S. peringueyi* Benick.

Stenus linearis Puthz

SOUTH AFRICA: 2 ♂, 2 ♀, Cape Province, Silvermine Nature Reserve (S 6), 12 mi. S. Cape Town, c. 1 200 ft, damp leaf litter on banks of stream in gulley, 2.I.1972 (BMNH).

Previously known only from Table Mountain.

S. linearis exsectior Puthz

Specimens from Bloukrans River, Cape Province (Loc. No. 139), which I have examined, recorded by Scheerpeltz (1974: 49) as *S. deplanatus* Benick, are to be referred to this subspecies of *S. linearis*.

(*Stenus depsarius* Benick)

See under *S. capensis* Puthz, below.

Stenus capensis Puthz

Specimens from Table Mountain (Loc. No. 84), which I have examined, recorded by Scheerpeltz (1974: 49) as *S. depsarius* Benick, are to be referred to *S. capensis*.

(*Stenus deplanatus* Benick)

Scheerpeltz (1974: 49) records this species from three localities in Cape Province. Those from Bloukrans River (see above) are to be referred to *S. linearis exsectior* Puthz, while those from near Bredasdorp and near Swellendam, which I have examined, appear to be *S. deplanatus*.

Stenus amaniensis Eichelbaum

ANGOLA: 1, 7 mi. W. Gabela (A 30), c. 3 600 ft, swept by stream in coffee forest, 18.III.1972 (BMNH).

Stenus levivestis Scheerpeltz

Figs. 9a–d.

S. levivestis proves to be a member of the *bifrons-nairobiensis*-group of species but the key to this group given by Puthz (1971*a*: 240–241) can not readily be modified to include this species. *S. levivestis* is probably most similar to narrow examples of *S. bifrons* Waterhouse in general appearance. The shape of the head and eyes and colouration of the appendages are almost identical in the two species. However, specimens of *S. levivestis* may be distinguished from any seen of the variable *S. bifrons* by the proportions of the fore-parts and slightly larger puncturation of the pronotum and elytra as well as by the sexual characters. Although the breadth of the head is similar in both species, *S. levivestis* is generally less robustly built than *S. bifrons*; in the former species the pronotum is narrower and the elytra much narrower and also shorter. The ratio of maximum breadth of head to maximum breadth of elytra together is from 80 : 100 to 86 : 100 in specimens of *S. levivestis*, and between 66 : 100 and 77 : 100 in specimens of *S. bifrons* examined. Although the apical segments of the abdomen are broader than in *S. bifrons* the form of these segments in males of *S. levivestis* (fig. 9 b–d) is of similar type to that in *S. bifrons*. The male genitalia, however, are markedly different (fig. 9 a); the median lobe is longer, more robust and differently formed apically while the lateral lobes are shorter than in *S. bifrons*.

The female specimen from Cape Province referred to (but not named) by Puthz (1971*a*: 241) may belong to *S. levivestis* as this, apart from *S. nairobiensis* Fauvel, is the only species of the group so far known from Cape Province. The type series of *S. levivestis* were taken at about 2 500 ft in the vicinity of a mountain torrent and the species may prove to be endemic to the mountainous areas of Western Cape Province.

Stenus nairobiensis Fauvel

SOUTH AFRICA: 2, Cape Province, Kingwilliamstown (St.N. 94), Maden Dam, along edge of lake, 25.III.1954 (Balfour-Browne) (BMNH);

ANGOLA: 1, Huila dist., Ongueria (St.N. 260), 5 300 ft, under stones near river, 11.VI.1954 (Balfour-Browne) (BMNH).

Stenus cooperi Bernhauer

TANZANIA: Mwanza, near Lake Victoria, 1 ♂, 1 ♀, in sweet potato channels, 1 ♂, marginal pools and ditches (Walton) (BMNH).

Although these specimens are smaller than those belonging to the type series from Ethiopia, males from the two countries agree very well in form of the genitalia and secondary sexual characters of males.

Stenus obconicus cf. damarensis Puthz

BOTSWANA: 1 ♀, Kuke Pan (B 7), c. 3 100 ft, on mud by small pool, 16.IV.1972 (BMNH).

This specimen agrees fairly well with the single known male of this subspecies but unassociated females of the *fulgidus*-group can not be identified with any certainty.

S. obconicus malawianus Puthz

MALAWI: 1 ♂, swampy pool near Lake Nyasa (no further locality data), 9.IV.1946 (Lowe) (BMNH).

(*S. obconicus obconicus* Fauvel)

See under *S. sybaris* Puthz below.

Stenus sybaris Puthz

= *S. (Hypostenus) pseudobconicus* Scheerpeltz, 1974:50, **syn. nov.**

SOUTH AFRICA: 5 ♂, 1 ♀, Natal, Lions River district, between Lidgetton & Balgowan (St.N. 134), 4 000 ft, on marshy edges of river, 1.IV.1954 (Balfour-Browne) (BMNH).

Stenus sybaris was described, on the basis of one male and one female, by Puthz (1971*a*: 250) from 'Ernelo, Tanzania' but there would appear to have been some confusion regarding the type locality. I have been unable to locate any locality by the name of 'Ernelo' and circumstantial evidence makes it almost certain that the locality in question is Ermelo in south-eastern Transvaal, South Africa. The holotype of *S. melanostolus* Puthz is also reported (Puthz, 1971*a*: 307) from 'Ernelo', although, in this case, the locality is regarded as being in South Africa and is included in the map of the *spinifer*-group (fig. 209), with a query, in the eastern part of Cape Province. The date of capture (7.XII.1948) and the collector (J. Omer-Cooper) are the same for both the holotype of *S. melanostolus* and the original specimens of *S. sybaris*. The known distribution of *S. melanostolus* (see below under *S. grandipennis* Benick) and other records of *S. sybaris* presented here, as well as the known collecting itineraries of Dr. Omer-Cooper, all confirm that the type localities for both species are in Transvaal.

Specimens from the Lions River district agree very well with the description of *S. sybaris*, particularly in the highly distinctive secondary sexual features of males. The holotype and a number of paratypes of *S. pseudobconicus* Scheerpeltz have been examined and prove to be indistinguishable from specimens of *S. sybaris* from Natal. The single female from Frere, Natal (BMNH) referred, with reservations to *S. obconicus obconicus* Fauvel by Puthz (1971*a*: 245) has been examined carefully and, although dirty and almost lacking in pubescence, proves to agree well with the female of *S. sybaris* from the Lions River district. It agrees particularly well in size and is considerably larger than females of the nominate form from Madagascar which I have examined. It is very likely, in view of the location of other records of *S. sybaris*, that this female is to be referred to this, the largest species of the *fulgidus*-group.

Stenus trepidus Waterhouse

SOUTH AFRICA: 1 ♂, 15 mi. SW. Johannesburg, c. 5 400 ft (S 3), damp litter in large reed bed, 28.XII.1972 (BMNH).

This record extends the known range of the species considerably to the south. Although the male genitalia of this South African specimen are indistinguishable from those of a male paratype of *S. trepidus* from "Zambesi" (BMNH) and the sternite of the ninth abdominal segment is much as figured by Puthz (1965, fig. 65b) the foreparts of this individual are slightly less robust and the elytra are slightly narrower than in the holotype and paratype male. The antennae of the South African specimen are darkened apically, segments nine to eleven are more or less black; the apical third to one-half of each femur is more or less black and the tibiae are slightly infuscate in the middle portion.

Stenus ravus Puthz

ANGOLA: 1 ♂, Cuango, Lusamba (9°03′S, 18°07′E), at black light, 11–21.V.1971 (Peles) (LB, Dundo).

Although not previously recorded from Angola this record does not materially extend the known range of *S. ravus*.

Stenus kisantuanus Bernhauer

ANGOLA: 1 ♀, Parque das Cachoeiras (A 32), c. 1 200 ft, on sand banks by small temporary pools at the base of small waterfall, 18.III.1972 (BMNH).

This specimen agrees well with the female from Vila Luso referred (with a query) by Puthz (1971*a*: 290) to this species, but some doubt concerning the determination must remain.

S. torrentum Cameron

ANGOLA: 38, Bruco (A 11), c. 25 mi. SW. Sá da Bandeira, c. 3 000 ft, in wet leaf litter beside stream, 1.III.1972 (BMNH); 1, Huila dist., Ongueria (St.N. 266), c. 5 400 ft, in fine sand at side of stream above cataracts, 13.VI.1954 (Balfour-Browne) (BMNH).

The specimens from Bruco (only 20 miles or so from the type locality of *S. torrentum*) are all rather uniform in size, proportion of parts and puncturation and closely resemble Cameron's original specimens from Ongueria. I have little doubt as to the conspecificity of specimens from the Sá da Bandeira district but for further discussion concerning the specific limits of *S. torrentum* see under *S. ruandae* Bernhauer below.

As noted by Puthz (1967: 227) the single male paratype of *S. torrentum* is not conspecific with the holotype and is to be referred to *S. jovino* Eich. (= *borodanus* Bernh.). This male paratype is from Tchivinguiro but the single female paratype is from Ongueria (not Tchivinguiro as it is labelled and as reported by Puthz (1967, 1971*a*); it should bear the same collection data as the holotype. The full data for

both holotype and female paratype of *S. torrentum* should read as follows:— Angola: Cascade de Ongueria, 55 km au SSE. de Sá da Bandeira, 1 500 m, dans les détritus végétaux du sol (très humides), 25.IX.1949 (Machado) (BMNH).

Stenus ruandae Bernhauer

ANGOLA: 4, Caungula, R. Cambonde (8°05′S, 18°13′E), 20.VII.1962 (Machado); 1, Lóvua, gallery-forest of R. Camuanga (7°19′S, 20°09′E), 5.VIII.1956 (Machado); 1 teneral, Nordeste, gallery-forest of R. Cassai (7°22′S, 18°03′E), 24.IX. 1956 (Machado); 1, Cuango, gallery forest of R. Cambamba (8°41′S, 18°03′E), 2.X.1969 (Machado); 1, R. Capulumba, gallery-forest (8°47′S, 18°00′E), 4.III.1970 (Peles) (all LB, Dundo). All specimens with bionomic data taken in "détritus végétaux du sol".

All of these specimens agree well with the holotype of *S. dundoanus* Cameron (currently placed in the synonymy of *S. ruandae*) and other specimens from the north-east of Angola. It would seem likely, as

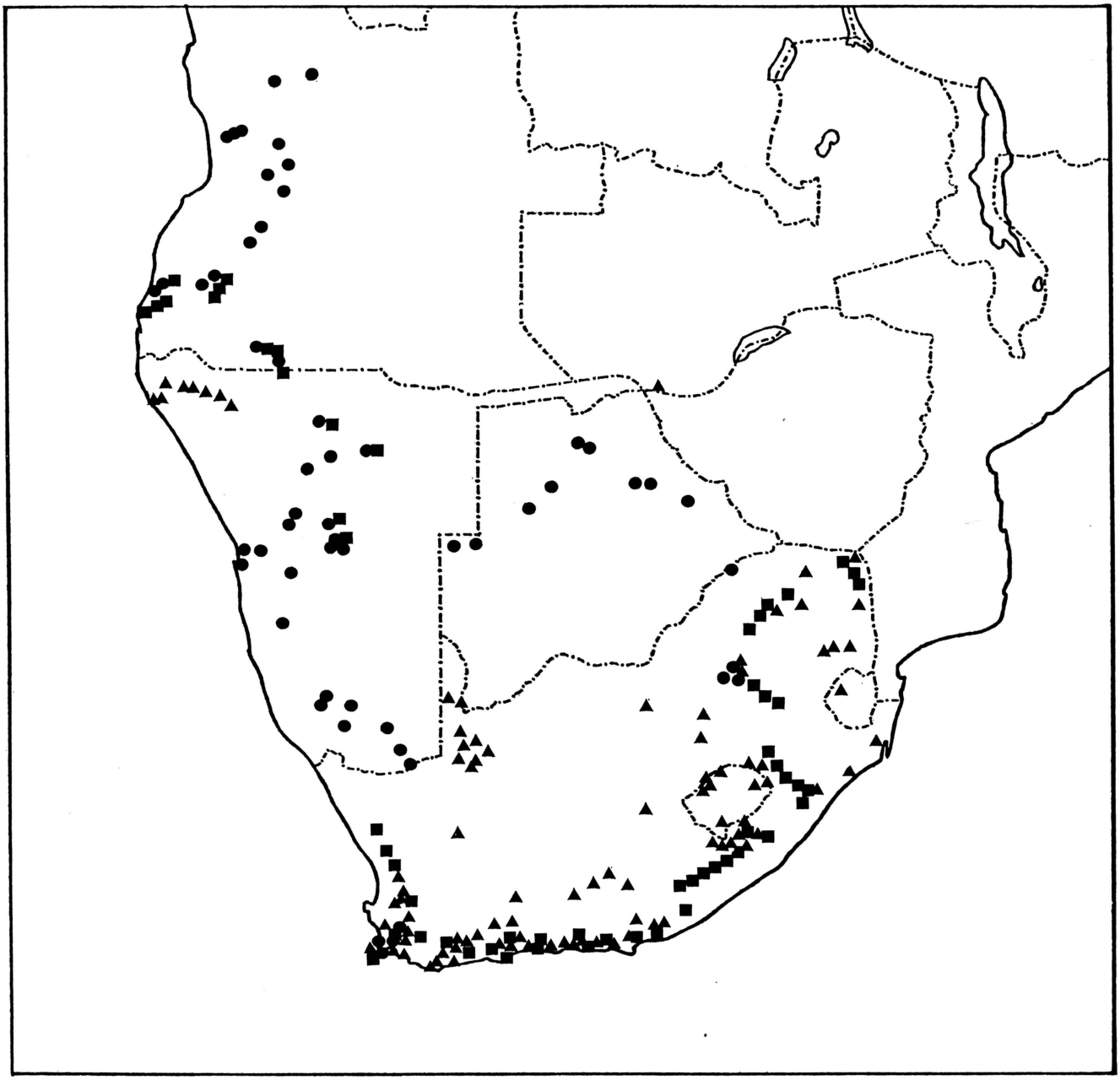


Figure 10. Localities in Southern Africa visited during the course of three entomological expeditions and where waterside situations or other "*Stenus* habitats" were or were probably investigated in order to collect Coleoptera. Triangles = Swedish Expedition (1950–1951). Squares = BMNH Expedition (Balfour-Browne—1954). Circles = BMNH Expedition (1971–1972).

tentatively suggested by Puthz (1971*a*), that *S. ruandae* (as the name with priority) will prove to be a highly variable and widespread species which includes *S. torrentum* Cameron, and possibly also *S. subascendens* Puthz.

The genitalia and sternites of the eighth and ninth abdominal segments of males referred to both *S. torrentum* (Congo, Southern Angola) and *S. ruandae* (Northern Angola, Guinea) which I have examined are all very similar. Variation in external characters is considerable and specimens from each of the geographical areas exhibit some peculiar features. Unless *several* species are involved, a single species varying on a geographical basis appears to be indicated. The character utilized by Puthz (1971*a*: 301) to separate *S. torrentum* from other members of the *ascendens*-group falls down in at least some cases: all paratypes of *S. guineanus* Cameron (a synonym of *S. ruandae* according to Puthz, 1971*a*) have a smooth, shining patch in the middle of the upper surface of the head while this patch is not always clearly marked in specimens from southern Angola.

Stenus convergens Benick

ANGOLA: 1 ♀, Humpata (St.N. 248), on Alto Plano Plateau, 5 800 ft, in clear sand stream and pools alongside, 7–8.VI. 1954 (Balfour-Browne) (BMNH);

SOUTH AFRICA: 1 ♂, Natal, Lions River district, between Lidgetton and Balgowan (St.N. 134), on marshy edges of river, 4 000 ft, 1.VI.1954 (Balfour-Browne) (BMNH).

Not previously known from Angola and the record for that country extends the known range of *S. convergens f. typ.* considerably to the west. Both specimens noted above compare well with the holotype of *S. oligocephalus* Bernhauer (BMNH) and are to be referred to the nominate form of *S. convergens*.

Stenus prospector Fauvel

ANGOLA: 1, Roçadas (A 2), at light near River Cunene, c. 3 600 ft, 21.II.1972 (BMNH);

BOTSWANA: 3, c. 2 ml. N. Gweta (B 19) (20°11′S, 25°15′E), c. 2 900 ft, in mud and humus beside semi-permanent pool, 22.IV.1972 (BMNH);

SOUTH WEST AFRICA: 2, 7 mi. NE. Grootfontein (St.N. 228), c. 4 700 ft, in dolomite, 29.V.1954 (Balfour-Browne) (BMNH); 5, Namutoni (St.N. 235), c. 4 900 ft, water-hole, very thick rushes and stream, 31.V.1954 (Balfour-Browne) (BMNH);

TANZANIA: 1, Mwanza, near Lake Victoria, sweet potato channels, 31.VII.1957 (Walton) (BMNH).

Recently recorded for South Africa by Puthz (1971*b*) but previously unrecorded from Botswana, South West Africa and Angola. Despite an extremely wide distribution in Africa there are no records of this species from the Congo basin or other areas of rainforest. The present records, like most others, are for grassland areas.

Stenus grandipennis Benick
= *S. melanostolus* Puthz, 1971*a*: 307, **n. syn.**

SOUTH AFRICA: 6, Cape Province, Knysna-Avontuur Rd. (St.N. 65), farm dam, 900 ft 17.III.1954 (Balfour-Browne) (BMNH); 2, C.P., Witte Elbosch, Groot River (St.N. 78), rapid, weedy and mossy stream with dead edges, 19.III.1954 (Balfour-Browne) (BMNH); 1, C.P., near Humansdorp (St.N. 81), small shallow pool in cut reeds, 20.III.1954 (Balfour-Browne) (BMNH); 1, C.P., Van Staadens Pass (St.N. 84), in small gravel at edge of running water stream, 21.III.1954 (Balfour-Browne) (BMNH); 2, Orange Free State, near Harrismith (St.N. 160), farm dam with much grass, c. 5 500 ft, 7.IV.1954 (Balfour-Browne) (BMNH).

These specimens and others of this species which I have studied are extremely variable in size and puncturation of the upper surface although the genitalia and secondary sexual features of the abdomen of males are extremely constant, and indistinguishable from those of *S. melanostolus* Puthz. The type locality of *S. melanostolus* has now been shown (see above under *S. sybaris* Puthz) to be in Transvaal. Additional records of *S. grandipennis* (Puthz, 1971*b*: 142; Scheerpeltz, 1974: 50 [specimens examined by me]; and those given above) for Cape Province, Orange Free State and Transvaal indicate that *S. melanostolus* falls within the geographical range of *S. grandipennis* as well as its range of morphological variation.

Stenus callens Puthz

SOUTH AFRICA: 1 ♀, Cape Province, Concordia, Knysna (St.N. 62), large pool with *Scirpus* (at edge only), c. 800 ft, 17.III.1954 (Balfour-Browne) (BMNH).

Known to date only from the original series from eastern Cape Province (Puthz, 1971*b*: 142).

(*Stenus cursorius rorellus* Fauvel)

See under *S. c. caffer* Puthz, *S. furcifer* Puthz and *S. irroreus* Fauvel below.

Stenus cursorius caffer Puthz

ANGOLA: 3, Bruco (A 11), c. 3 000 ft, banks of stream in gallery forest, 1.III.1972 (BMNH); 2, Tundavala (A 18), c. 6 600 ft, in wet moss by stream above waterfall, 4.III.1972 (BMNH);

BOTSWANA: 1, 20 ml. SE. Nata (B 22) (20°25′S, 26°23′E), c. 3 100 ft, swept from vegetation on banks of River Semowane, 24.IV.1972 (BMNH).

Although widely distributed in southern Africa this subspecies has not been noted from the very arid areas of the south and west of the region. It may be noted that in all three of the localities listed above the waterside was overlooked by trees and bushes, and other vegetation was present on the banks. Shade from plant cover, absent from most waterside situations in the most arid areas, may be a feature of its preferred habitat.

The specimens from Pretoria (South Africa) (Loc. No. 282), recorded by Scheerpeltz (1974: 50) as *S. cursorius rorellus* Fauvel (and which I have examined) should be referred to *S. c. caffer*.

Stenus furcifer Puthz

BOTSWANA: 1, Moremi Game Reserve (B 11) (19°23′S, 23°33′E), c. 2 700 ft, swept from vegetation near large pools with much grass and reeds, 19.IV.1972 (BMNH).

The specimen from the Kruger National Park (South Africa) (Loc. No. 289), recorded by Scheerpeltz (1974: 50) as *S. cursorius rorellus* Fauvel (and which I have examined) should be referred to *S. furcifer*.

These records extend the known range of this widespread species some five hundred miles to the south.

Stenus irroreus Fauvel

ANGOLA: 61, Roçadas (A 2), c. 3 600 ft, on banks of temporary pools near the River Cunene, 20.II.1972 (BMNH); 4, Parque das Cachoeiras (A 32), c. 20 mi. SW. Gabela, c. 1 200 ft, on sand banks by small pools below small waterfall, 18.III.1972 (BMNH); 1, Roçadas (A 42) (as A 2), at light beside small pool with open banks, 30.III.1972 (BMNH); 6, Humpata (St.N. 248), Alto Plano Plateau, 5 800 ft, in clear sand stream and pools alongside, 7–8.VI.1954 (Balfour-Browne) (BMNH).

These records confirm that *S. irroreus* is widespread in western Angola, from which country there are previous records for Moçâmedes, Naulila and unspecified localities (Puthz, 1967). The specimens from near Otju (South West Africa, Kaokoveld)

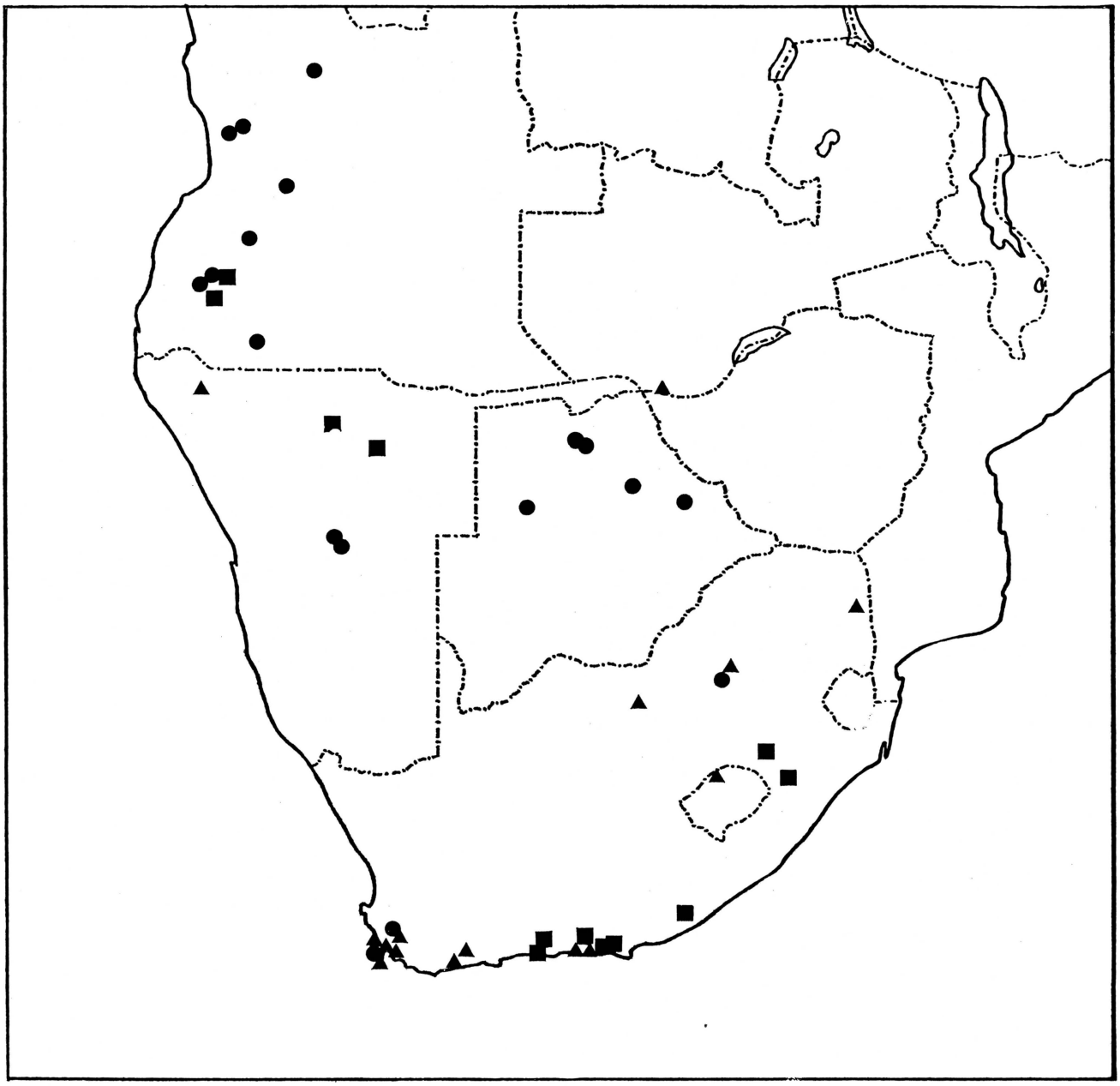


Figure 11. Localities in southern Africa where species of *Stenus* were collected during the course of three entomological expeditions. Triangles = Swedish Expedition (1950–1951). Squares = BMNH Expedition (Balfour Browne—1954). Circles = BMNH Expedition (1971–1972).

(Loc. No. 327), recorded by Scheerpeltz (1974: 50) as *S. cursorius rorellus* Fauvel (and which I have examined) are to be referred to *S. irroreus*. The only other records for the African mainland are for western Congo (near the coast) and Zambia (Mwengwa); the single Zambian record, although included by Puthz (1971*a*, fig. 210) in a map, is omitted from the list of countries given for *S. irroreus* in the same work. Records of *S. irroreus* for Madagascar and Aldabra are summarized by Puthz (1972).

III. COMPOSITION OF THE STENINE FAUNA OF SOUTHERN AFRICA

Representatives of each of the 21 species-groups recognised by Puthz (1971*a*) are known from Africa south of the equator. These groups, for most of which there is good evidence of monophyly, may be categorized in terms of their continental distribution and the part they play in the fauna of southern Africa.

Two groups (*aethiopicus*-group, *leleupi*-group) have no known representatives in southern Africa proper; both are montane; species of the former are restricted to mountains of Ethiopia and East Africa while one member of the latter is found as far south as Central Angola. Three other largely montane groups (*jovino*-group, *consobrinus*-group, members of subgenus *Parastenus*), although much better represented in mountainous areas to the north, are also known from southern Africa. Records of species belonging to these montane groups from southern Africa proper are confined to a few areas of southern Cape Province, Natal and Rhodesia, areas which are frequently centres of endemicity for montane, hygrophilous insects (see fig. 81, Brinck, 1955*b*).

A further eight species-groups, although containing montane species in some cases, are typical of tropical forest and include few species occurring beyond the limits of the principal African forest areas. However, all of them are represented in southern Africa, although two (*subopacus*-group, *ascendens*-group) reach southwards only to Rhodesia. The remaining six tropical elements (*attenuatus*-group, *bifrons-nairobiensis*-group, *mombassanus*-group, *bauerinae-pilus*-group, *kisantuanus*-group, *semisericeus*-group) are represented in South Africa. Three species-groups (*hessei*-group, *asper*-group, members of subgenus *Tesnus*) appear to be endemic to southern Africa. All but one of the species of these groups are known only from South Africa, the majority only from Cape Province. Relationships of these groups with other African Steninae appear to be distant and their sister-groups are most likely to be found in other continents (see Puthz, 1971*a*).

Finally, five groups which may be considered pan-African (*mendicus*-group, *cameratus*-group, *fulgidus*-group, *spinifer*-group, *argentifer*-group) are well represented and include species of fairly wide distribution in southern Africa.

Table 4 summarizes the known distribution of *Stenus* species in southern Africa and adjacent areas. Records for Angola and Zambia are included as both countries contain areas which are transitional to the more arid regions of south-western Africa and the true arid zone extends into the former. The table thus effectively provides full lists of the species and subspecies of Steninae known from each of the following countries: —Angola, Botswana, Rhodesia, South Africa, South West Africa and Zambia, along with an indication of the total range for those species and subspecies which occur outside of southern Africa. Records for Malawi are omitted as only one species (*Stenus obconicus malawianus* Puthz) is so far known from that country. Puthz (1971*a*: 43) notes that Mozambique, which is also omitted from table 4, is completely lacking in records of Steninae although a map in the same work (p. 215) includes a record of *S. nairobiensis* Fauvel for that country. Further collecting will undoubtedly demonstrate the presence of several species of *Stenus* in both Malawi and Mozambique.

The Stenine fauna of southern Africa proper is likely to be substantially richer than is indicated by table 4, which includes fifty-four species and subspecies known from the area. It is to be expected that most previously unknown forms which remain to be collected will belong to species-groups which are centered on the principal forest areas of Africa or species-groups which are endemic to southern Africa. An example of the former type (*Stenus levivestis*) has recently been described by Scheerpeltz (1974) from Cape Province. Few of the species recorded to date from Angola or Zambia but no further south (see table 4) are likely to be found in southern Africa proper. Several of them (e.g. *Stenus trepidillus* Cameron, *S. vilhenai* Puthz, *S. assimulatus* Puthz, etc.) will undoubtedly prove to be endemic to forest areas of Angola. Those which are known to be widespread in tropical Africa, whether of largely tropical species-groups (e.g. *S. torrentum* Cameron), montane species-groups (e.g. *S. chyuluensis* Cameron) or pan-African groups (e.g. *S. decemguttatus* Benick) are perhaps a little more likely to be found further south in due course. One such widespread species (*S. trepidus* Waterhouse) is recorded from southern Africa for the first time in the present paper.

The species of Steninae presently known from southern Africa proper exhibit a variety of distribution patterns. The ranges of the many endemic species or subspecies belonging to species-groups which are largely tropical in distribution or endemic to south-

ern Africa are very restricted. Most are found only within a narrow southern and south-eastern belt of South Africa, the usual centres of endemicity for moisture requiring insects; in a few cases endemics of this type are also found in Transvaal or Rhodesia. However, several members of pan-African species-groups depart from this usual pattern. Although some of them, especially those endemic to parts of southern Africa, are largely confined to the south and east, several are more widespread or known in southern Africa only from other areas. Several species belonging to pan-African groups have succeeded, to varying degrees, in invading the drier areas. These will be discussed in a little more detail in the following section.

IV. STENINAE IN THE DRIER AREAS OF SOUTHERN AFRICA

Most Staphylinidae are essentially hygrophilous; very few of them exhibit structural features well adapted to resist desiccation. Those species which are to be found in the arid regions of the tropics and sub-tropics are generally restricted to micro-habitats (such as dung, carrion, rotting fruit and other sappy vegetable matter, nests of termites, etc.) which ensure protection from the full rigours of the climate. The presence of surface or underground water in otherwise arid areas naturally provides many micro-habitats suitable for hygrophilous Staphylinidae and other insects. The smallest, most temporary and isolated of water-holes is able to support an insect fauna.

Although in the temperate regions of the world a few species of Steninae are to be found in relatively dry situations, the great majority, and probably more or less all African species, are ripicoles or inhabit moist humus and vegetable debris. In the case of Steninae the distinction between ripicolous and humicolous habits is not always clear-cut as some "ripicoles" occur in waterside situations only where moist humus or plant debris is to be found, and some "humicoles" are more or less restricted to humus which is in the vicinity of open water. In Africa, truly humicolous species of Steninae appear to be largely confined to the areas of forest or the less arid areas of grassland. Only in these regions is permanently moist humus or plant debris to be found. In drier areas, humus or permanently moist plant debris is virtually absent, even from the borders of aquatic habitats.

Figure 12 gives an indication of the relative numbers of species found in different parts of southern Africa and adjacent areas. Despite extremely uneven collecting the general pattern illustrated is likely, especially in the south and south-west, to be fairly representative. However, some collecting "holes", notably in central and south-east Angola and parts of Mozambique, are evident. Much useful data on the occurrence of Steninae in southern Africa and western Angola has been provided by three recent entomological expeditions. Localities visited by these expeditions and where Steninae were searched for in apparently suitable habitats are shown in figure 10 and those where Steninae were actually found in figure 11. It should be noted that many localities lacking habitats even remotely suitable for Steninae, especially in the Kalahari and Namib deserts, were investigated by members of these expeditions, but are not included in these maps.

Not surprisingly, the general picture is one of decreasing numbers of species of Steninae from the less to the more arid regions (fig. 12) and an almost complete lack of records from the most arid (fig. 13). The humid forest areas are occupied by a fairly large and varied Steninae fauna, while only a limited range of species, mostly ripicoles, is known from the semi-arid (*sensu* Meigs, see Koch, 1962) areas and the low altitude grassland or open woodland at their periphery.

The extent of the arid regions and their various subdivisions in southern Africa may vary considerably according to the criteria utilized in estimating aridity. The isohyets (10" and 20" annual rainfall) used in figure 13 illustrate only one of the factors involved, although a principal one. The divisions employed by Aubréville (1949) in classifying parts of southern Africa in terms of relative aridity appear to correspond fairly closely with patterns of distribution exhibited by Steninae. Aubréville's fourth and fifth categories (subdésertiques and désertiques) of dry, tropical climatic zones agree fairly well with the area from which there are no records of Steninae. The third category in the same classification (including the 'Kalahari extérieur', 'Orange', 'Limpopo' and 'Transvaal occidental' regions) is more or less equivalent to the area in which only one or two species of Steninae have so far been found in any one place. However, even a classification (as that of Aubréville, 1949) based largely on vegetational zones does not fully account for all local variations in conditions resulting from the pattern of drainage and the distribution of isolated water-holes. For example, the extensive run-off into the Okavango basin from areas to the north-west means that the basin and its vicinity is richer in species of hygrophilous insects than might be expected from its position in most classifications of climate.

Whatever the precise factors (e.g. availability of food, etc.) determining the distributions of species of Steninae in Africa, humidity of the micro-habitat is clearly of considerable importance. Many of the species whose ranges closely approach but do not include any part of the semi-arid areas of southern and south-western Africa are local endemics. Their present limited range is likely to have been deter-

mined in part by historical as well as existing ecological factors. Such species, particularly numerous in the southern parts of Cape Province, are largely humicolous although frequently associated with fast-running streams. Most species which are widespread in tropical Africa and approach but do not generally occur within the semi-arid areas are also humicoles. They would appear to be absent from semi-arid regions largely because of a lack of suitable habitats rather than for historical reasons. Among species of this type which occur in southern Africa and adjacent areas (all belonging to the subgenus *Hypostenus*) it may be possible to distinguish two categories. Species such as *Stenus bifrons* Waterhouse and *S. trepidus* Waterhouse are found in wet or riparial situations where reeds and other semi-aquatic plants occur. They may be largely plant-climbers and may require the presence of a layer of permanently moist plant debris. Other species which are more strictly confined to the vicinity of fast-running streams and

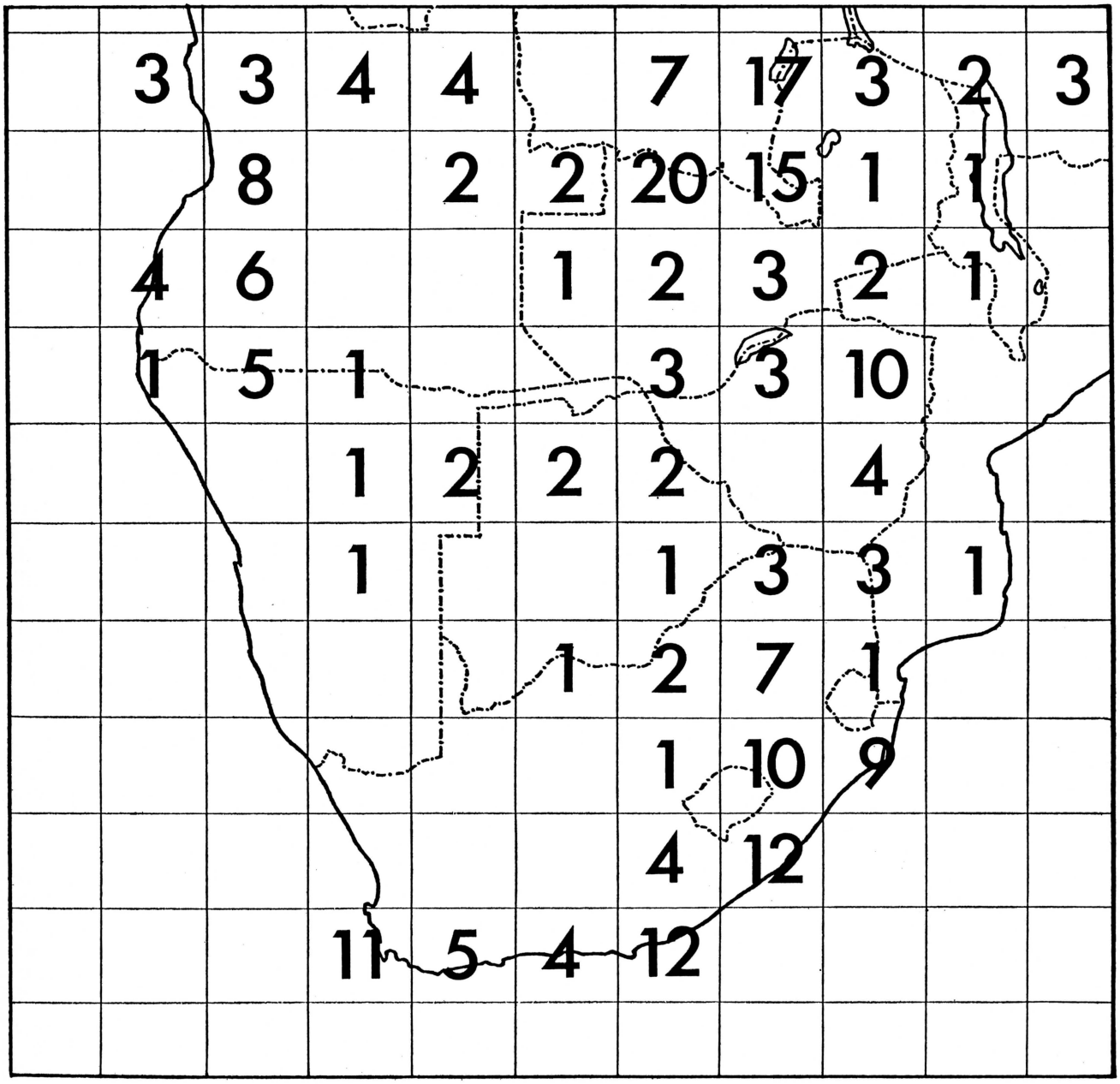


Figure 12. Summary of records of *Stenus* species in southern Africa and adjacent areas. The figures represent the number of species recorded in the area of each square. Records derived principally from the work of Puthz (1971*a*), but also from other sources, including later publications and previously unrecorded collections. The paucity of records for some areas of relative high rainfall (e.g. Central Angola) is probably due largely to lack of collecting.

rivers, usually in forest areas, may be less dependent on humus but require a high level of humidity throughout their habitat. Such species (e.g. *Stenus torrentum* Cameron) are to some extent ripicolous and may be seen running over stones and sand beside streams which have adequate cover from vegetation and where the air may be presumed to be humid.

It is unfortunate that any analysis of the species found in drier areas is hampered by taxonomic difficulties. Conclusions concerning the interrelationships of allopatric forms must be very provisional unless based on study material from very many localities. Unlike those species which are confined to forest or montane areas few assumptions can be made concerning the continuity of populations. In the absence of material from intermediate localities decisions concerning the status of samples from widely separated localities can only be tentative (for examples see discussion under *Stenus mendicus* above). In the case of all five species-groups represented in the drier areas, but especially the *cameratus*-group and *mendicus*-group, it is difficult to assess the relationships between populations from southern Africa and those from further north or between populations from within the southern area in some instances. However, it is to be hoped that investigation of the factors influencing the distribution of species in the drier areas will contribute to a knowledge of their historical zoogeography, and thus to their taxonomy.

All five of the pan-African species-groups of Steninae are represented in the drier areas of southern Africa. The same five groups, and no others, are also to be found represented in the semi-arid areas of Africa north of the equator (see Puthz, 1971*a*) where no species reaches the extremely arid areas (*sensu* Meigs) but one, *Stenus mendicus arens* Peyerimhoff, occurs within areas which are generally arid. In several cases the same species are to be found in the semi-arid areas bordering both the Sahara and the deserts of south-western Africa. Other instances of possible conspecificity can not be confirmed because of the taxonomic difficulties noted above.

Nine taxa regarded as specifically distinct are on record from the semi-arid regions of southern and south-western Africa; they are *Stenus mendicus* Erichson (various forms), *S. cameratus* Benick, *S. peringueyi* Benick, *S. obconicus damarensis* Puthz, *S. prospector* Fauvel, *S. grandipennis* Benick, *S. cursorius caffer* Puthz, *S. furcifer* Puthz and *S. irroreus* Fauvel. All of these are apparently more or less ripicolous in habit. Two of them, *S. cursorius caffer* and *S. furcifer*, are known to date only from the fringes of the semi-arid regions; both species may be in some measure plant-climbers and dependent on shade from plants providing a relatively humid micro-environment.

The known distribution of *Stenus furcifer*, although extending from Senegal to Transvaal, does not include most of the more humid areas (Puthz, 1971*a*, fig. 210). The great majority of records are for areas of grassland and open woodland and *S. furcifer* appears to be largely confined to the zone between the limits of rain-forest and those of the semi-arid areas (see Koch, 1962, Map 1). In the southern part of its range the only record which closely approaches or lies within the semi-arid areas is one for the Okavango basin which, as noted above, receives considerable run-off from areas of higher rainfall. There is little indication that this species is particularly associated with running water; banks of pools or rivers where semi-aquatic vegetation is to be found may be regarded as typical habitats.

Stenus cursorius caffer, like *S. cursorius rorellus* Fauvel, which replaces it in central and eastern Africa, although infrequently recorded from areas of rain-forest, is less restricted to grassland zones and appears to be more associated with running water than *S. furcifer*. *S. c. caffer* has been found in company with forest species typical of humid and shaded situations (see tables 2 & 3). In the Sá da Bandeira area of southern Angola, at both Bruco and Tundavala, *S. c. caffer* was taken in company with *S. humidulus* Cameron, and in the former locality also with *S. torrentum* Cameron. However, the distribution of *S. c. caffer* in southern Africa is extensive and includes relatively dry areas of Transvaal and Botswana.

The remaining seven species are probably more important components of the Stenine fauna of the semi-arid areas. One of them, however, is particularly poorly known. *S. obconicus damarensis* is known from a single male found at Oshikango, South West Africa and a single female from Botswana which is tentatively attributed to this subspecies. It should be noted that the symbol representing the type locality of this subspecies in the map provided by Puthz (1971*a*, fig. 176) is mis-placed by some two or three hundred miles, as Oshikango is situated at the border of Ovamboland with Angola (see fig. 13). The data available is scarcely sufficient for any discussion of range or ecological tolerances of this subspecies. However, *S. o. damarensis* is exceptional in being slow-moving and much larger than the other species known from the semi-arid areas. It may be in some measure a plant-climber.

S. prospector has a recorded distribution north of southern Africa not unlike that of *S. furcifer* (see above). It too may be associated with aquatic habitats where waterside vegetation is to be found. However, the greater number of records for the semi-arid zone of south-western Africa (fig. 13), if at all significant, may indicate a lesser dependence on the shade of semi-aquatic vegetation. Its occurrence at fairly isolated pools and water-holes in South West Africa and Botswana suggests that good dispersal

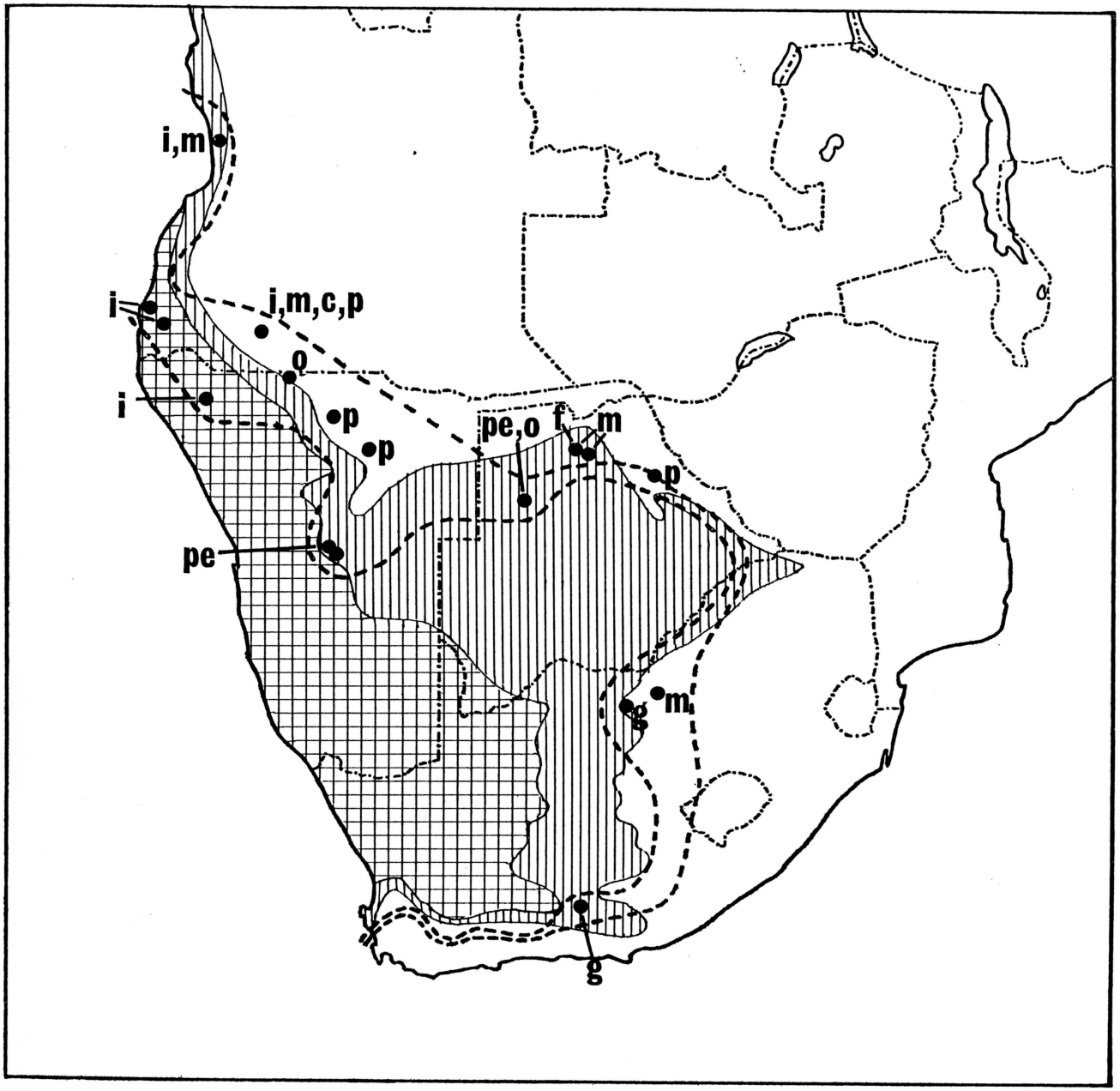


Figure 13. The restricted occurrence of *Stenus* species in southern Africa in relation to areas of low rainfall. Squared lines = area of less than 10" annual rainfall; vertical lines = area of between 10" and 20" annual rainfall. The area enclosed by the inner line of thick black dashes (much of South West Africa, Botswana and northern Cape Province) is that within which no *Stenus* species have been found to date. Further collecting, especially in parts of Botswana, may considerably diminish the extent of this area. The area enclosed by the outer line of thick dashes is that within which only a limited range of *Stenus* species have been found, namely *cameratus, grandipennis, irroreus, mendicus, obconicus, peringueyi* and *prospector*. All known captures of *Stenus* species within the area of less than 20" annual rainfall are recorded on the map. c = *cameratus* f. typ.; f = *furcifer*; g = *grandipennis*; i = *irroreus*; m = *mendicus* (various forms); o = *obconicus damarensis* or cf. *damarensis*; p = *prospector*; pe = *peringueyi* f.typ.

ability may also be a factor contributing to its presence in semi-arid areas where suitable habitats are widely separated.

S. grandipennis appears to frequently occupy habitats which are similar to those of *S. prospector*. It is unique among the species found in the semi-arid areas of Southern Africa, as it is, on present evidence, the only endemic southern African species to be found in such areas and the only species of *Stenus* so far found in the less humid parts of Cape Province. Available distributional and habitat data suggest that this species is eurytopic and it is likely to be the most generally distributed species of *Stenus* in South Africa.

Stenus irroreus, *S. cameratus*, the nominate subspecies of *S. peringueyi* and the forms of *S. mendicus* to be found in southern and south-western Africa are all to be regarded truly ripicolous and are typically to be found on the open banks of slow-running or still water. Although precise habitat requirements undoubtedly vary to some degree between these species, none of them appear to depend on the presence of waterside vegetation.

Unlike the races of *Stenus mendicus* found in the Saharan region, those known from Angola, Botswana and South Africa are not presently known from localities which lie far within the semi-arid zones of these countries. The only records definitely attributable to *S. mendicus senegalensis* in the semi-arid zones of the south are for the Okavango area. The differences between habitats where samples of morphologically distinct populations of *S. mendicus* were taken in the Okavango area, at Roçadas (River Cunene) and Cachoeiras in Angola have been noted above in discussion of the taxonomy of the *mendicus*-complex. Records suggest that *S. mendicus* is largely a river-bank species.

Stenus cameratus is similarly not known in the south from as far within the semi-arid areas as it is in the Saharan region. The only record for semi-arid areas in the south is that for Roçadas (River Cunene) where it was taken in great numbers. Apparently typical of river-banks, it does not appear to depend greatly on shade or cover. At Roçadas individuals were observed on the bare, black mud left by evaporating pools in the river bed, running in and out of cracks. Apart from a single record for Rhodesia *S. cameratus* is unknown from southern Africa proper, but further taxonomic study may establish a close genetic link with *S. nigerrimus* Cameron, which is known to date only from south-western Cape Province.

S. peringueyi is the only species of *Stenus* found in the central part of South West Africa. Individuals from the Windhoek area are undoubtedly conspecific with and very similar to those of the nominate subspecies found in the southern parts of Cape Province. Both aquatic habitats where *S. peringueyi* was found in the Windhoek area result from human activity in constructing "dams" and are more than two hundred miles from any other presently known localities for species of *Stenus*. Importation of the species, by human agency, from South Africa thus seems possible. However, if the Windhoek populations are relicts from a previous pluvial period when the species was more continuously distributed, then a connection with present populations to the north of the Kalahari (e.g. in northern Botswana) is likely. Unfortunately, any commentary on this species is particularly hampered by a poor understanding the relationships between the nominate subspecies of *S. peringueyi* and other allopatric forms of a similar type, including members of the *cameratus*-group which are currently regarded as specifically distinct. *S. irroreus* is the only species to have been found well within the truly arid areas (*sensu* Meigs) of south-western Africa, but is known (in Africa) from no further south than the northermost parts of South West Africa. Although a member of the subgenus *Hypostenus* it would appear to be very largely a species of open shores where shore-line vegetation and plant debris are absent. Specimens recorded in the present paper from Angola (see above and table 2), as well as those taken by the present writer in two Madagascan localities, were all found on open, more or less sandy banks of still water. At Cachoeiras and Roçadas (Angola) and near Amboasary (Madagascar) numerous individuals were observed to run fairly rapidly over open areas of sand or sandy mud in the vicinity of shallow, river-bed pools. The known African range of *S. irroreus* is curiously restricted. Its presence in the arid areas of southern Angola and northern South West Africa might lead one to expect a more extensive distribution in southern Africa. *S. irroreus* is known from Madagascar as well as Africa and is the only species of *Stenus* recorded from the Aldabran islands. As its presence in Aldabra is likely to be the result of fairly recent colonization a high dispersal ability is probable. *S. irroreus* is clearly widespread in Madagascar, where it is known from the eastern belt of rain-forest (e.g. at Perinet), as well as in less humid areas, and may be long-established there. Indeed, as the *argentifer*-group of species, to which *S. irroreus* belongs, is represented in Madagascar by endemic species, *S. irroreus* may be truly native to that island. If this is the case, its patchy distribution on the African mainland could be explained by relatively recent colonization from Madagascar. If it is a relatively recent arrival in Africa it is likely to have been transported there by human agency. In Congo, Angola and South West Africa *S. irroreus* has been found only fairly near the coast in situations (sand banks, etc.) which are appropriate for its transport to have taken place by removal of its habitat for ships' ballast. Many European beetle species have been shown to have been carried to North America in this way (Lindroth, 1957), al-

though Puthz (1971*a*: 31) suggests that problems of desiccation en route are likely to be more serious for hygrophilous insects transported in ballast through the tropics. More support for the view that *S. irroreus* is not a colonist in Africa may be provided by futher definition of the relationship between *S. irroreus* and the very similar *S. argentatus* Puthz, known only from Africa north of the equator. However, if any species of Stenus has successfully colonized tropical Africa from Madagascar (or *vice versa*), with the help of man, *S. irroreus* would appear to be the most likely candidate.

One of the most characteristic features of the Steninae known from the arid and semi-arid zones of southern Africa is their ripicolous habit. Most species inhabit the open banks of pools and rivers. Although members of several insect groups are known to be preyed upon by Steninae, it is likely that species of *Stenus* found in the drier areas feed largely or solely on Collembola. Members of this latter group frequently abound in the habitats occupied by *Stenus* while other insects suitable as prey are absent. All of the species of *Stenus* found in the drier areas are fully winged and, like other ripicoles, are likely to possess good flight ability. However, it is not clear to what extent flight is used for dispersal. In general, Steninae are rarely observed in flight and, unlike the majority of ripicolous Staphylinidae, they are rarely taken in traps for flying insects. Whether the almost complete absence of Steninae from light-trap catches is due primarily to infrequent flight, to principally diurnal patterns of activity or other behavioural characteristics has not been established. Certainly, there are few records of nocturnal activity. In the course of the BMNH 1971–1972 expedition to southern Africa light-traps were frequently operated at sites where *Stenus* were known to occur, sometimes within a few feet of or even within a small area where adults were taken in the daytime. During this expedition several hundred thousand Staphylinidae were taken at light-traps but this number included only two individuals of *Stenus*. Both of these (see records for *S. irroreus* and *S. prospector* above) were taken at Roçadas on the banks of pools where *Stenus* were found in numbers during the day. As the two individuals were found on a white sheet placed on the ground beneath a mercury-vapour lamp, it is by no means certain that they flew to the light. When banks of water were searched at night with a 'Tilley' lamp for Diptera, Carabidae, etc., *Stenus* were found to be active at two localities (Cachoeiras, Angola and Windhoek). In both instances they appeared to avoid the light, generally running directly away from it, and crawled into cracks or under surface debris. This behaviour may be associated with the shade-seeking tropic activity exhibited by some Steninae during the day. The absence of Steninae from the more isolated (but otherwise apparently suitable) habitats in generally arid areas lends support to the view that dispersal by flight is strictly limited throughout this subfamily. However, at least in comparison with most other southern African species of *Stenus*, those found in the semi-arid areas are bound to utilize flight for short-range dispersal relatively frequently. In most instances dispersal flights are unlikely to exceed a few miles but the presence of *S. irroreus* (Kaokoveld) and *S. prospector* (north-central Botswana) in fairly isolated aquatic habitats where introduction by human agency is unlikely sugests successful flights of at least twenty or thirty miles in these cases. It may not be purely coincidental that the two species taken at light-traps at Roçadas (*S. irroreus* and *S. prospector*) are apparently among the most successful in colonizing relatively isolated aquatic habitats. In comparison with other African Steninae the species known from the semi-arid areas possess certain characteristic morphological features. In some cases it is possible to suggest how these features might be associated with the exigencies of life in a dry area. Most of the species exhibit a compact build, fairly small size, relatively thick cuticle, fairly short antennae, moderately short femora and tibiae, uniform black colouration (except for parts of the appendages), small eye-facets, fully-developed wings and fairly well developed mechanisms for folding and manipulating the wings. In many cases they also exhibit fairly close puncturation and pubescence of the upper surface and in some cases (notably *S. irroreus* and *S. cursorius caffer*) the eyes occupy a more ventral position than is usual. Many of these features are likely to be associated with the need to resist desiccation while others are possibly connected with a ground-running habit, predation on Collembola, a relatively frequent need for flight or other behavioural characteristics shared by most Steninae of the semi-arid areas.

In comparison with many ripicolous Staphylinidae and other insects Steninae appear to exhibit a strictly limited distribution in south-western Africa. In each of the 57 localities listed in table 2 and in most other localities visited by the BMNH 1971–1972 expedition, even those where no surface water was observed, some ripicolous and aquatic Coleoptera were taken. In most cases ripicolous species of such genera as *Bledius*, *Carpelimus* and *Scopaeus* (Staphylinidae), *Tachys*, *Heterocerus* (see Charpentier, 1965) and *Limnichus* abounded. These Coleoptera and truly aquatic forms (Dytiscidae, etc.) are to be found in many parts of the semi-arid and arid zones, including very temporary habitats, where Steninae are absent. As transport by human agency is unlikely to be of significance and few of these insects exhibit morphological adaptations to resist desiccation, good dispersal ability and fossorial habits are likely to be major factors contributing to their success in colonizing temporary and isolated habitats. Unlike Steninae, many of these ripicolous Staphylinidae and

other Coleoptera, and even many Dytiscidae under certain conditions, burrow deeply in mud, sand or gravel where moisture is to be found. Flight by such species may be observed frequently during the day, especially when washed from their burrows or otherwise disturbed, but dispersal flights are likely to be largely nocturnal. Great numbers are often to be taken in light traps. Many species of ripicolous Staphylinidae, Carabidae, Heteroceridae, etc. are also tolerant of saline or alkaline conditions, a characteristic that does not appear to be shared by any African Steninae, with the possible exception of *S. irroreus*.

Amongst the other groups of moisture-requiring or aquatic insects which have been investigated in south-western Africa, only the Mecoptera (Tjeder, 1956) appear to exhibit distribution patterns which in any way resemble those of Steninae. The Odonata (Brinck, 1955*c*) are known from a much greater part of the semi-arid and arid zones; in this case some strong-flying and eurytopic species have extended their ranges into otherwise arid areas by colonization of isolated water-holes and reservoirs resulting from human activity. Similarly, the truly aquatic Coleoptera are fairly well represented in temporary and isolated habitats. Some species of Dystiscidae (Omer-Cooper, 1965) and Gyrinidae (Brinck, 1955*b*) are known from the arid zones, well beyond the limit of records for Steninae.

More or less permanent water is to be found in each of the localities in southern and south-western Africa where Steninae have been taken. In each case other water sources are rarely more than a few miles distant and no Steninae have been found in association with permanent but isolated bodies of water in otherwise arid areas. In Africa a '*Stenus*-index' might be useful as a measure of relative aridity, conversely to the 'Tenebrionid-index' which has been proposed (see Koch, 1962).

Negative evidence concerning the occurrence of Steninae in southern Africa is naturally of limited value as this group of insects has been relatively little collected. The list of species known from the more arid areas is likely to be extended and many more localities within these areas will undoubtedly prove to contain habitats where Steninae are found. In particular, captures of Steninae from several parts of Botswana which presently lack records are to be expected, as that country has been particularly neglected with regard to the collection of Staphylinidae. However, the fact that Steninae have been found in only a small number of the localities (see figs 9 and 10 and table 2) where they have been carefully searched for suggests that members of this subfamily may be absent from large areas of south-western Africa. No records are available for the whole of north-western Cape Province, southern and much of western South West Africa. The nearest westerly-running river to the Cape, where Steninae have been found, is the Cunene in southern Angola. The Orange, Fish, Kuiseb, Swakop, Okahandja and Kahn rivers in South West Africa and some of their tributaries were all carefully investigated during the course of the BMNH 1971–1972 expedition (see table 2) but no Steninae were found. With the exception of at least the upper parts of the Orange River, it is quite possible that these rivers, like the water-holes and other aquatic habitats in the same areas, are completely lacking in a Stenine fauna. Some rivers a little further to the south, such as the Olifants River in Cape Province, have not been carefully investigated and records of Steninae are more likely to result from further collecting. The seasonal nature of the rivers between the Orange and the Cunene and their location to the west of the principal watershed in South West Africa undoubtedly contribute to their lack of a Stenine fauna. In Africa, Steninae, like Gyrinidae (Brinck, 1955*b*) and some other insect groups, appear to be more frequently associated with running water than in the temperate zones. In generally arid areas, even those species of Steninae which favour the banks of still water are likely to depend on river systems for opportunity to distribute themselves widely. The westerly-running rivers of South West Africa and the north-western Cape Province are well isolated from other river systems and much of south-western Africa lacks permanent aquatic connections with the more humid areas of southern Africa. This isolation has probably been a major factor in preventing the invasion of the western parts of southern Africa by Steninae, and may explain the apparently total absence of Steninae from the many otherwise suitable habitats which do occur.

V. GENERAL CONCLUSIONS

The more arid areas of southern and 'south-western' Africa are poor in species of *Stenus*. Some nine species have been found within areas classed as semi-arid and one of these within the truly arid zone. Although the results of recent collecting expeditions reported in the present paper have provided much new data concerning the drier areas, records of Steninae from much of South West Africa, northern Cape Province, much of Botswana and parts of western Angola are still wanting. Much of this arid south-western area is probably without a Stenine fauna. The *Stenus* species found in the semi-arid areas are all ripicolous and, unlike the majority of 'ripicolous' Steninae in Africa, are able to tolerate, to varying degrees, waterside situations where humus or moist plant debris and the shade of waterside plants is lacking. They are, however, largely restricted to permanent aquatic habitats. Relatively poor powers of dispersal are likely to be responsible for their absence from relatively isolated but otherwise

possibly suitable habitats in which other aquatic and ripicolous insects abound.

The close association between many ripicolous Staphylinidae and large river-systems in the south-west and other relatively arid parts of Africa suggests that watersheds between such river-systems may be effective barriers to the spread of Steninae in drier areas. The poorly understood nature of barriers, extremely slight knowledge of ecology ,and consequently of historical zoogeography of Steninae in these areas contribute to continuing problems with their taxonomy. Partial barriers between possibly incipient geographical races have probably been broken down repeatedly during previous pluvial periods. Any isolation of population in the drier areas which has occurred since the last pluvial is likely to have produced disjunctures in the clinal variation of previously continuous populations but is unlikely to have resulted in much new morphological variation on a geographical basis.

VI. TAXONOMIC CONCLUSIONS

One species is resurrected from synonymy:—
Stenus humidulus Cameron **sp. rev.** (*not* a synonym of *S. kaguruensis* Bernhauer)

One new subspecies is described:—
Stenus jovino magnopunctatus **n. subsp.**

Two new synonymies are noted:—
Stenus sybaris Puthz, 1971*a*: 250
= *S. pseudobconicus* Scheerpeltz, 1974: 50, **n. syn.**
Stenus grandipennis L. Benick, 1933: 318
= *S. melanostolus* Puthz, 1971*a*: 307, **n. syn.**

Previously unrecorded geographical variation in *Stenus mendicus* Erichson is discussed at some length. A need for further taxonomic work in the *mendicus*-group and also in the *cameratus*-group is indicated.

VII. SUMMARY

New data concerning the occurrence of Steninae in 'south-western' Africa and adjacent regions are presented. Most of these data, largely concerning distribution and ecology, relate to Angola, Botswana, South Africa and South West Africa. The taxonomy of several species is reviewed; one species is resurrected from synonymy, one new subspecies is described and two specific synonymies are newly recognised. The male genitalia and other structures of several species are figured. New ecological and distributional data are utilized in a discussion of factors involved in the distribution of Steninae and other hygrophilus insects in 'south-western' Africa. Four maps are included to illustrate the distributional characteristics of Steninae in this area. A chart is also given, listing the species of Steninae now known from each of the following countries: Angola, Botswana, Rhodesia, South Africa, South West Africa and Zambia.

ZUAMMENFASSUNG

Neue Angaben über das Vorkommen der Steninae im „südwestlichen" Afrika und den angrenzenden Gebieten werden vorgelegt. Die meisten dieser Angaben, größtenteils die Verbreitung und Ökologie betreffend, beziehen sich auf Angola, Botswana, Südafrika und Südwestafrika. Die Taxonomie mehrerer Arten wird besprochen; ein Synonym ist wieder zur guten Art erhoben, eine neue Unterart ist beschrieben und zwei spezifische Synonyme sind neu erkannt. Die männlichen Geschlechtsorgane und andere Teile mehrerer Arten sind abgebildet. Neue ökologische und Verbreitungsangaben wurden in einer Besprechung der Faktoren, die eine Rolle in der Verbreitung der Steninae und anderer feuchtigkeitsliebenden Insekten im „südwestlichen" Afrika spielen, benutzt. Vier beigegebene Karten zeigen die Verbreitung der Steninae in diesem Gebiet. Eine Tabelle zeigt die bis jetzt bekannten Arten der Steninae von jedem der folgenden Länder: Angola, Botswana, Rhodesien, Südafrika, Südwestafrika und Zambia.
(Summary translated by W. Giess)

VIII. ACKNOWLEDGEMENTS

My thanks are due to Professor P. Brinck, Mrs. I. Rudebeck and Dr. E. Luna de Carvalho for the loan of specimens and also to Professor Brinck for making possible a visit to Lund University where I was able to study material relevant to the present paper. I am most grateful to Mr. J. Balfour-Browne for providing data concerning specimens collected by himself in southern Africa and to Dr. V. Puthz for comparing specimens of some critical species with specimens in his own collection. Finally I must thank my colleagues and companions during the BMNH Expedition to Southern Africa 1971–72 — B. H. Cogan, M. C. Day, D. Hollis and R. I. Vane-Wright — for help in collecting specimens and patiently accommodating frequent sampling of riparial Coleoptera in an already full programme of work.

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Table 1. Dimensions of fore-parts in specimens of the *mendicus*-complex from various localities.

	Sex	Maximum breadth of head	Maximum breadth of pronotum	Maximum length of pronotum	Maximum breadth of elytra	Maximum length of elytra	Assignation in accordance with the classification of Puthz (1971a)
Mt. Zuquála (Ethiopia)	♀	78.5	60	70	95	96	ssp. *azeganus* Fvl.
Naivasha (Kenya)	♂	74.5	61	67.5	89	91	ssp. *naivashensis* Puthz
Lèopoldville — Coquilhatville	♂	81.5	63	71	93	92	ssp. *senegalensis* Bnh.
Chianga (Angola)	♀	78	64	68	91	94	,,
,, ,,	♂	77	60	65	89	90	,,
Moremi (Botswana)	♀	72	61	62	88	88	,,
,, ,,	♂	73	57	60	81	81	,,
nr. Bamako (Mali)	♀	74	61	67	89	84	,,
Badoumbè (Mali)	♀	66.5	56	63	80	80	,,
Chari Basin (C. Afr. Republic)	♀	72	58	63	85	82.5	,,
Roçadas (Angola)	♀	75	59	66	87	83	cf. *senegalensis* Bnh.
,, ,,	♀	73.5	61.5	67.5	92	81	,,
,, ,,	♀	68	57	60	80	81	,,
,, ,,	♂	74	60	62	91	89	,,
,, ,,	♂	71	58.5	62	86.5	88	,,
,, ,,	♂	70	56	62	85	86	,,
Cachoeiras (Angola)	♀	72	58	65	89	90	cf. *protector* Fvl.
,, ,,	♀	70	59	63	91	90	,,
,, ,,	♀	67	55	60	86	82	,,
,, ,,	♂	71	57	59	86	86	,,
,, ,,	♂	69	57	62	85	84	,,
,, ,,	♂	69	55	61	85	85	,,
"Arabia"	♀	68.5	55	61.5	83	80	ssp. *arens* Peyer.
Perinet (Madagascar)	♀	69	56	58	85	81	ssp. *protector* Fvl.
Dunbrody (S.Africa, Cape Prov.)	♂	63	50	57	76	75	ssp. *separatus* Benick
Barberspan (S.Africa, Tvl.)	♀	69	58.5	61	88	84	ssp. *pretoriensis* Puthz

Table 2. Waterside and other habitats where Steninae were searched for during BMNH expedition to Southern Africa (1971–1972). Collecting stations are referred to by a code number: S = South Africa; W = South West Africa; A = Angola; B = Botswana.

Collecting station	Location	General nature of habitat	Composition of banks	Plant or other cover	Collecting methods etc.	Species of *Stenus* found
S 1	Tvl., Johannesburg	artificial lake	mud	grass	searching	–
S 2	Tvl., Hartebeest-poort	large reservoir	mud	aquatic plant debris	searching & debris samples	–
S 3	Tvl., nr. Johannes-burg	large reed-bed	mud	tall reeds and debris	reed litter samples	*trepidus*
S 5	C.P., Kloof Nek	almost dry stream in gulley	mud/gravel	mixed vegetatoin, some plant debris	litter samples	–
S 6	C.P., Silvermine N.R.	stream in gulley	mud/gravelly sand	reeds, bushes, trees etc.	wet moss & litter samples, etc.	*linearis*
S 7	C.P., nr. Muizen-burg	small lagoon among dunes, ½ mi. from sea	muddy sand	a little grass, etc.	splashing banks	–
S 9	C.P., Assegaaibosch	large stream	mud/gravel	grass, trees, etc.	rush & grass tussocks	–
S 11	C.P., Du Toits Kloof	small hillside stream	mud	thick grass, bushes, etc.	plant debris sample	*jovino magnopunc-tatus*
W 1	Onseepkans	Orange River	muddy sand	mostly open, bushes, etc. in places	large flood & river-bank debris samples	–
W 2	nr. Karasburg	shallow pools on plateau	muddy sand with stones	completely open (in semi-desert)	searching	–
W 3	Noachabeb	small pool used by cattle, nr. dry river-bed	muddy sand	mostly open, a little short grass	searching	–
W 7	Fish River Canyon	Fish River small stream	sand gravel	open river banks open banks of small pools in stream bed	searching searching & large sample washed from gravel	– –
W 9	nr. Seeheim	Fish River	very muddy sand	open, without cover	small sample of river bank debris	–
W 11	nr. Aus	small artificial "dam"	mud with stones	open, without cover	searching	–
W 12	nr. Aus	waterhole and stream feeding it in gulley	sand/gravel/shingle	open, without cover	searching & washing	–
W 18	Sossusvlei	shallow pools	salty mud	open, but over-looked by a few trees	sample of sparse plant debris	–

Collecting station	Location	General nature of habitat	Composition of banks	Plant or other cover	Collecting methods etc.	Species of *Stenus* found
W 22	Kuiseb Canyon	shallow pools in almost dry river-bed	sand	open, without cover	searching	–
W 24	Walvis Bay	artificial lake among dunes at sewage works	mud/sand	mostly open	large sample of aquatic plant debris	–
W 25	Swakopmund	small artificial pool in dry river bed	mud/sand	part open/part reeds	large sample of aquatic plant debris	–
W 28	Goanikontes	very small artificial farm reservoir	very muddy sand	a few reeds, etc.	splashing, treading, etc.	–
W 29	nr. Usakos	dry bed of River Kahn	sand	mostly open, some trees	sample of moist leaf litter in crevices under trees	–
W 30	nr. Usakos	small hillside stream	rock/gravel/mud	mostly open, some reeds & grass	searching	–
W 32	Windhoek	large artificial reservoir	mud	mostly open, some plant debris	searching at night	*peringueyi*
		dry stream bed	rock	wet leaf litter in pockets	large litter sample	–
W 33	nr. Windhoek	large farm "dam"	mud/some stones	open, a little fine shore debris	searching	*peringueyi*
W 34	nr. Windhoek	small farm "dam" on hillside	mud/some stones	open	searching	–
W 35	nr. Okahandja	Swakop River	muddy sand	open/grassy	searching	–
W 36	Otjikoko	large farm "dam"	muddy sand	open, a little debris	sample of debris	–
		medium farm "dam"	muddy sand	open, a little debris	sample of debris	–
		outlet stream in gulley	muddy sand	reeds, moss, mixed vegetation	samples of moss & reed litter, etc.	–
W 37	Otjitambi	large farm "dam"	mud/stones	open, a little fine shore debris	sample of debris, etc.	–
W 43	Onguma (Etosha Pan)	shallow pools in grassland	mud	dense grass & reeds	searching only	–
A 2	Roçadas	semi-permanent pools in bed of River Cunene	mud/muddy sand	open/some aquatic vegetation/overlooking trees	searching; splashing; samples of plant debris & mud	*mendicus* cf. *senegalensis cameratus; prospector; irroreus*
A 6	Tundavala	stream on hillside	sand/rock	mixed vegetation, bushes, etc.	splashing, etc.	–
A 11	Bruco	stream in riverine forest at foot of escarpment	rock/mud/gravel/sand	various: open sandbars, some reeds, moss, etc.; much damp leaf litter	large samples of moss, leaf litter, reed litter, etc.	*humidulus; torrentum; cursorius caffer;*

A 14	nr. Moçâmedes	drainage ditch	muddy sand	grass, etc.	sample of wet leaves, etc. washed up at water's edge	–
A 16	nr. Moçâmedes	small pools	sand	reeds in places	searching sand banks only	–
A 18	Tundavala	stream on hillside with waterfall	rock/muddy sand	overlooked by trees and other vegetation	sample of wet moss from rocks above waterfall	*humidulus* *cursorius* *caffer*
A 20	nr. Cacula	damp, reedy hollow in *Brachystegia* woodland	yellow mud	dense reeds	sample of reed litter	*jovino* f. typ.
A 21	nr. Nova Lisboa	small stream	black mud	reeds, dense grass & other vegetation	searching	–
A 23	nr. Alto Hama	small stream in gulley	sand/rock/gravel	bare banks but overlooked by trees, etc.	searching & splashing	–
A 24	nr. Santa Comba	stream through pasture land	mud	grass, etc.	brief searching	–
A 26	nr. Salazar	moist forest litter small stream in forest	sandy mud/rock/ gravel	varied situations varied, mostly in coffee forest	large samples searching, damp litter and moss from cascade	– –
A 27	Duque de Bragança Falls	river at waterfall	rock/sand bars	varied, overlooked by trees in places	searching, samples of wet moss, etc.	*machadoi*
A 30	nr. Gabela	moist forest litter stream in dense coffee forest	mud/sand/rock	overlooked by dense vegetation	large samples searching & sample of wet litter	– *humidulus* *amaniensis*
A 31	nr. Gabela	stream in open coffee forest	mud/rock	bushes, grass, etc.	sample of wet litter	–
A 32	Gabela/Novo Redondo	river and small pools below waterfall	sand	open sand-bars, without cover	wet moss from waterfall searching sand-bars	– *mendicus* cf. *protector; kisantuanus; irroreus*
A 35	nr. Moco	stream on hillside	muddy sand	grassy banks with occasional sand-bars	splashing, etc.	–
A 36	as A 21	moist litter in *Brachystegia* woodland moist cut vegetation on reservoir banks			sample of litter large sample	– *jovino* f. typ.
A 37	nr. Negola	stream in *Brachystegia* woodland	muddy sand	mixed vegetation	splashing, etc.	–

Collecting station	Location	General nature of habitat	Composition of banks	Plant or other cover	Collecting methods etc.	Species of *Stenus* found
A 40	Tundavala	stream on hillside with waterfalls, etc.	rock/muddy sand	overlooked by trees & other vegetation	sample of wet moss from waterfall	*humidulus*
					moist heap of cut grass	*jovino* f. typ.
A 42	as A 2	by pools in bed of River Cunene			MV light-trap only	*prospector*
A 43	nr. Santa Clara	temporary pools	muddy sand	open, grassy	searching	—
W 49	nr. Grootfontein	pool at spring	mud	reeds, etc.	searching	—
W 52	nr. Okahandja	River Swakop in flood	sand	open, some grass, etc.	large flood debris sample	—
B 1	Gobabis/Ghanzi	ephemeral roadside pools	sand	open, bare	rapid searching	—
B 2	Gobabis/Ghanzi	large, shallow pools	chalky mud/stones	open, bare	searching	—
B 7	Ghanzi/Maung	small water-holes	mud/muddy sand	open/some water-side vegetation	searching	*peringueyi obconicus* cf. *damarensis*
B 9	nr. Lake Ngami	small river	sand	open, bare	searching	—
B 11	Okavangu	shallow pools	mud	grass & reeds	searching	*mendicus senegalensis; furcifer*
B 13	nr. Okavangu	small water-hole	muddy sand	open/some water-side vegetation	searching	*mendicus senegalensis*
B 19	nr. Makarikari pans	shallow pool	friable muddy sand	open but with mats of dead algae etc.	large sample of dead algae, etc.	*prospector*
B 20	Makarikari pans	large salt pans	salt-encrusted mud	open, bare	searching	—
B 22	Makarikari/ Francistown	small pool in stream bed	muddy sand/stones	overhanging trees and other vegetation	searching & splashing	*cursorius caffer*
S 17	Groblersbrug	River Limpopo	sand & gravel bars	overhanging trees and other vegetation	searching & splashing	—

Table 3. The common occurrence of species of Stenus at certain localities in Southern Africa. A solid circle indicates that species have been taken together in large numbers and/or fairly frequently. An open circle indicates that species have been taken at the same locality but have not been proved to occupy precisely the same habitat.

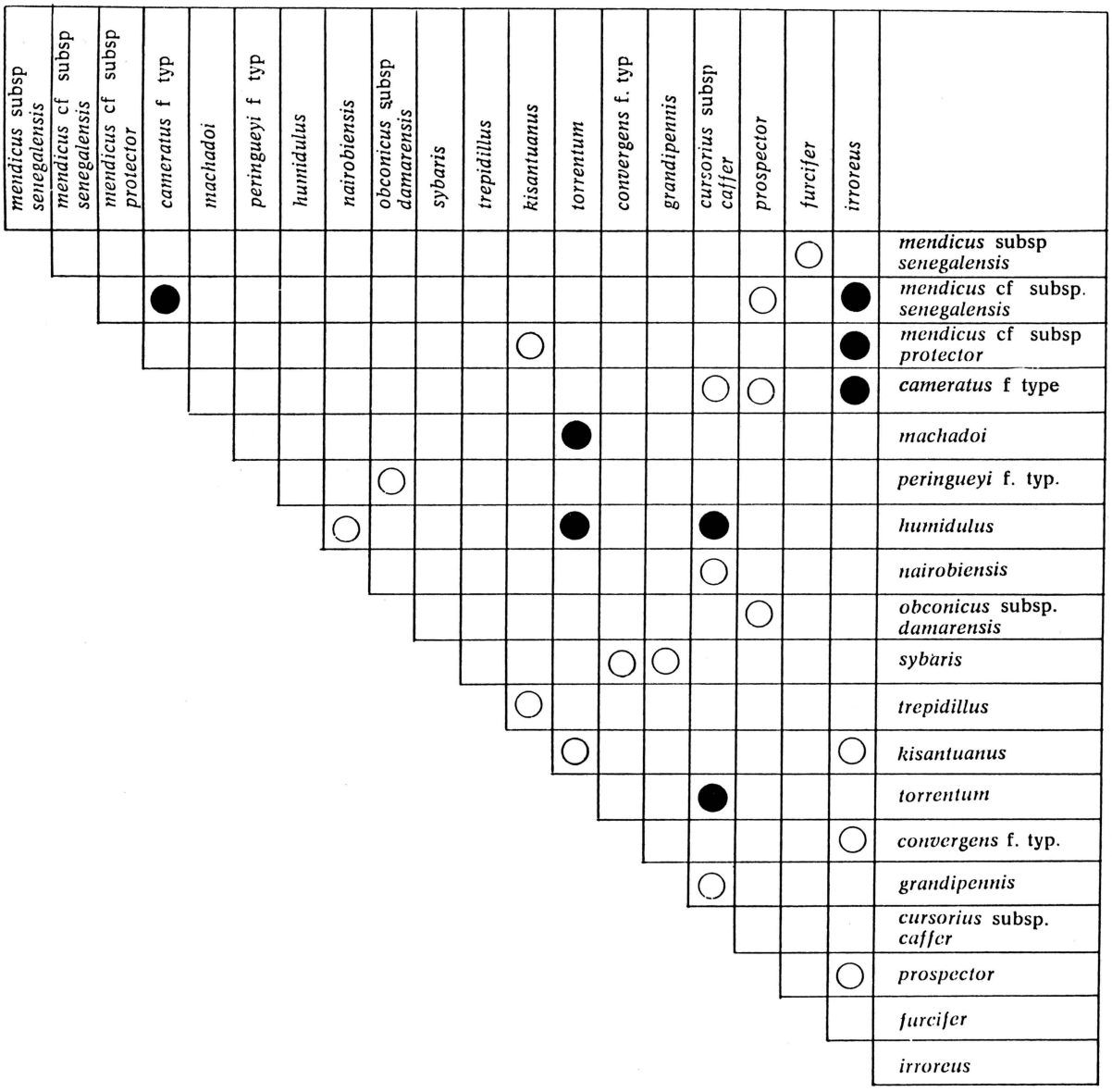

Table 4. List of the Steninae of Southern Africa and their geographical distribution.

Stenus species	South Africa	South West Africa	Botswana	Angola	Rhodesia	Zambia	Beyond the limits of Southern Africa
1. *Stenus mendicus senegalensis* Bernh. . .	–	–	●	●	–	●	Tropical Africa
2. *S. mendicus* cf. *senegalensis* Bernh. . .	–	–	–	●	–	–	?
3. *S. mendicus pretoriensis* Puthz	●	–	–	–	–	–	–
4. *S. mendicus separatus* Benick	●	–	–	–	–	–	–
5. *S. mendicus* cf. *protector* Fvl.	–	–	–	●	–	–	?
6. *S. jovino* Eich. f. typ.	–	–	–	●	●	–	Africa (montane)
7. *S. jovino magnopunctatus* subsp. nov. . .	●	–	–	–	–	–	–
8. *S. cameratus* Benick f. typ.	–	–	–	●	●	●	Africa (not rain-for.)
9. *S. machadoi* Cam.	–	–	–	●	–	–	Congo (Kinshasa)
10. *S. peringueyi Benick* f. typ.	●	●	●	–	●	–	–
11. *S. nigerrimus* Cam.	●	–	–	–	–	–	–
12. *S. kaguruensis Bernh.*	?	–	–	–	–	●	Tanzania; ?Congo, etc.
13. *S. humidulus* Cam. sp. rev.	–	–	–	●	–	–	?E. Africa
14. *S. dekeyseri* Cam.	–	–	–	–	–	●	Tropical Africa
15. *S. oneili* Puthz	●	–	–	–	–	–	–
16. *S. hessei* Benick	●	–	–	–	–	–	–
17. *S. cryptophagus* Benick	●	–	–	–	–	–	–
18. *S. linearis* Puthz	●	–	–	–	–	–	–
19. *S. linearis exsectior Puthz*	●	–	–	–	–	–	–
20. *S. transvaalensis* Puthz	●	–	–	–	–	–	–
21. *S. depsarius* Benick	●	–	–	–	–	–	–
22. *S. capensis* Puthz	●	–	–	–	–	–	–
23. *S. eques* Puthz	●	–	–	–	–	–	–
24. *S. asper* Benick	●	–	–	–	●	–	–
25. *S. deplanatus* Benick	●	–	–	–	–	–	–
26. *S. deplanatus acutior* Puthz	●	–	–	–	–	–	–
27. *S. depressiusculus* Benick	●	–	–	–	–	–	–
28. *S. parastenoides* Puthz	●	–	–	–	–	–	–
29. *S. fallaciter* Puthz	●	–	–	–	–	–	–
30. *S. amaniensis* Eich.	–	–	–	●	●	–	Tropical Africa
31. *S. continentalis* Bernh.	–	–	–	●	–	–	Tropical Africa
32. *S. diana* Bernh.	–	–	–	–	●	–	E. Africa
33. *S. subopacus* Fvl. f. typ.	●	–	–	–	–	–	E. Africa
34. *S. reticulatus parcipennis* Bernh.	●	–	–	–	–	–	–
35. *S. chyuluensis* Cam.	–	–	–	●	–	–	Tropical Africa
36. *S. levivestis* Scheerp.	●	–	–	–	–	–	–
37. *S. assimulatus* Puthz	–	–	–	●	–	–	–
38. *S. bifrons* Waterh.	●	–	–	–	–	●	Africa
39. *S. marshalli* Puthz	●	–	–	–	–	–	–
40. *S. nairobiensis* Fvl.	●	–	–	●	●	–	C. & E. Africa
41. *S. obconicus damarensis* Puthz	?	●	?	–	–	–	–
42. *S. obconicus malawianus* Puthz	?	–	–	–	–	●	Malawi
43. *S. decemguttatus* Benick	–	–	–	–	–	●	Tropical Africa
44. *S. sybaris* Puthz	●	–	–	–	–	–	–
45. *S. vilhenai* Cam.	–	–	–	●	–	–	–
46. *S. andreae* Benick	●	–	–	–	–	–	–
47. *S. consobrinus* Benick	●	–	–	–	–	–	Africa (montane)

48. *S. trepidillus* Puthz	–	–	–	●	–	–	–
49. *S. trepidus* Waterh.	●	–	–	–	–	●	Africa
50. *S. uluguruensis* Bernh.	●	–	–	–	–	–	E. Africa
51. *S. pilus* Schub.	●	–	–	–	●	–	Africa (montane)
52. *S. favoides pilosus* Puthz	–	–	–	–	●	–	–
53. *S. natalensis* Bernh.	●	–	–	–	–	–	–
54. *S. luandaensis* Puthz	–	–	–	●	–	–	–
55. *S. capicola* Benick	●	–	–	–	–	–	–
56. *S. ravus* Puthz	–	–	–	●	–	–	Tropical Africa
57. *S. kisantuanus* Bernh.	●	–	–	●	–	–	Africa
58. *S. semisericeus mashonaensis* Puthz	–	–	–	–	●	–	–
59. *S. torrentum* Cam.	–	–	–	●	–	●	Tropical Africa
60. *S. ruandae* Bernh.	–	–	–	●	●	●	Tropical Africa
61. *S. angolanus* Puthz	–	–	–	●	–	–	–
62. *S. convergens* Benick f. typ.	●	–	–	●	●	–	Africa, mostly East
63. *S. prospector* Fvl.	●	●	●	●	–	●	Africa (not rain-for.)
64. *S. grandipennis* Benick	●	–	–	–	–	–	–
65. *S. callens* Puthz	●	–	–	–	–	–	–
66. *S. cursorius caffer* Puthz	●	–	●	●	●	●	–
67. *S. furcifer* Puthz	●	–	●	●	●	●	Africa
68. *S. irroreus* Fvl.	–	●	–	●	–	●	Africa; Madagascar
69. *S. primus* Puthz	●	–	–	–	–	–	–
Total	42	4	6	25	14	14	

Table 4. List of the Steninae of Southern Africa and their geographical distribution.

Stenus species	South Africa	South West Africa	Botswana	Angola	Rhodesia	Zambia	Beyond the limits of Southern Africa
1. *Stenus mendicus senegalensis* Bernh.	–	–	●	●	–	●	Tropical Africa
2. *S. mendicus* cf. *senegalensis* Bernh.	–	–	–	●	–	–	?
3. *S. mendicus pretoriensis* Puthz	●	–	–	–	–	–	–
4. *S. mendicus separatus* Benick	●	–	–	–	–	–	–
5. *S. mendicus* cf. *protector* Fvl.	–	–	–	●	–	–	?
6. *S. jovino* Eich. f. typ.	–	–	–	●	●	–	Africa (montane)
7. *S. jovino magnopunctatus* subsp. nov.	●	–	–	–	–	–	–
8. *S. cameratus* Benick f. typ.	–	–	–	●	●	●	Africa (not rain-for.)
9. *S. machadoi* Cam.	–	–	–	●	–	–	Congo (Kinshasa)
10. *S. peringueyi Benick* f. typ.	●	●	●	–	●	–	–
11. *S. nigerrimus* Cam.	●	–	–	–	–	–	–
12. *S. kaguruensis Bernh.*	?	–	–	–	–	●	Tanzania; ?Congo, etc.
13. *S. humidulus* Cam. sp. rev.	–	–	–	●	–	–	?E. Africa
14. *S. dekeyseri* Cam.	–	–	–	–	–	●	Tropical Africa
15. *S. oneili* Puthz	●	–	–	–	–	–	–
16. *S. hessei* Benick	●	–	–	–	–	–	–
17. *S. cryptophagus* Benick	●	–	–	–	–	–	–
18. *S. linearis* Puthz	●	–	–	–	–	–	–
19. *S. linearis exsectior Puthz*	●	–	–	–	–	–	–
20. *S. transvaalensis* Puthz	●	–	–	–	–	–	–
21. *S. depsarius* Benick	●	–	–	–	–	–	–
22. *S. capensis* Puthz	●	–	–	–	–	–	–
23. *S. eques* Puthz	●	–	–	–	–	–	–
24. *S. asper* Benick	●	–	–	–	●	–	–
25. *S. deplanatus* Benick	●	–	–	–	–	–	–
26. *S. deplanatus acutior* Puthz	●	–	–	–	–	–	–
27. *S. depressiusculus* Benick	●	–	–	–	–	–	–
28. *S. parastenoides* Puthz	●	–	–	–	–	–	–
29. *S. fallaciter* Puthz	●	–	–	–	–	–	–
30. *S. amaniensis* Eich.	–	–	–	●	●	–	Tropical Africa
31. *S. continentalis* Bernh.	–	–	–	●	–	–	Tropical Africa
32. *S. diana* Bernh.	–	–	–	–	●	–	E. Africa
33. *S. subopacus* Fvl. f. typ.	●	–	–	–	–	–	E. Africa
34. *S. reticulatus parcipennis* Bernh.	●	–	–	–	–	–	–
35. *S. chyuluensis* Cam.	–	–	–	●	–	–	Tropical Africa
36. *S. levivestis* Scheerp.	●	–	–	–	–	–	–
37. *S. assimulatus* Puthz	–	–	–	●	–	–	–
38. *S. bifrons* Waterh.	●	–	–	–	–	●	Africa
39. *S. marshalli* Puthz	●	–	–	–	–	–	–
40. *S. nairobiensis* Fvl.	●	–	–	●	●	–	C. & E. Africa
41. *S. obconicus damarensis* Puthz	?	●	?	–	–	–	–
42. *S. obconicus malawianus* Puthz	?	–	–	–	–	●	Malawi
43. *S. decemguttatus* Benick	–	–	–	–	–	●	Tropical Africa
44. *S. sybaris* Puthz	●	–	–	–	–	–	–
45. *S. vilhenai* Cam.	–	–	–	●	–	–	–
46. *S. andreae* Benick	●	–	–	–	–	–	–
47. *S. consobrinus* Benick	●	–	–	–	–	–	Africa (montane)