

**Studies on spiroboloid millipeds. VIII. The generic name
Centrobolus revived, with some remarks on
several poorly-known species¹**

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With 17 figures in the text

Introduction

Nearly 50 species of the diplopod order Spirobolida have been recorded from the Union of South Africa, most of them either originally or subsequently referred to the single genus *Chersastus*. Inasmuch as three recent papers have dealt to some extent with this group, it has become fairly well-known in terms of general composition and taxonomic characteristics. A close examination will show, however, that the genus remains afflicted with the same misfortunes as the great majority of other diplopods, and that doubtless many years will pass before the status of its many species will be correctly perceived and established. A number of names proposed in the last century have remained in doubt down to the present time and still lurk in the literature as threats to nomenclatorial stability; there currently exists a tendency to base specific concepts upon details of coloration and other external variables almost to the neglect of the male genitalic apparatus; no one has yet, apparently, considered the possibility that perhaps a majority of the known taxa may be reduced to the status of geographic races of several polytypic species.

Obviously a definitive work on this genus can be produced only by a resident South African specialist having the opportunity to collect extensively over the entire range of the group. Yet there seems to be ample justification for preliminary studies of more modest scope, especially with respect to the clarification of the more enigmatic names published by earlier workers. The recent receipt of fresh material from several sources, and the valuable opportunity to examine types of several old species, provided an incentive for the following brief studies which, although obviously fragmentary in nature, will at least establish the characters of some forms and, I hope, generate some interest in the prosecution of taxonomically critical work on their congeners.

I have to acknowledge here with considerable gratitude the highly appre-

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ciated cooperation of several of my colleagues: Dr. E. S. Ross (California Academy of Sciences) for the loan of well-preserved fresh material, Frl. Dr. Gisela Rack (Zoologisches Museum, Hamburg) for the opportunity to restudy types of E. Voges; the late Dr. W. Crome (Zoologisches Museum des Humboldt Universitat) for access to the great collection at Berlin; and especially Dr. Gunnar Hallin (Naturhistoriska Riksmuseet, Stockholm) for making available types of the South African species described by C. O. von Porat.

Family **Pachybolidae**

Subfamily *Trigoniulinae*

Trigoniulidae Attems, 1909, in Sjostedt, *Ergeb. Schwed. Exp. Kilimandjaro*, vol. 3, no. 19, p. 25. — Brolemann, 1913, *Bull. soc. ent. France*, no. 19, p. 477. — Attems, 1926, *Handb. Zool.*, vol. 4, p. 196.

Trigoniulinae (as subfamily of Pachybolidae): Hoffman, 1963, *Rev. Suisse Zool.*, vol. 69, p. 760.

Since the appearance of my 1963 notes on pachybolids, in which I suggested devaluating Attems' family to the status of subfamily, I have found no reason to revise this opinion. Although it is true that the characters stipulated by Brolemann (1913, 1914) to distinguish the two as coordinate families still hold good, but only in a general way and the difference between such "pachybolid" forms as *Pachybolus* and *Trachelomegalus* on one hand and *Brachyspirobolus* and *Kompsobolus* on the other appears greater to me than that between *Pachybolus*, *Trigoniulus*, and *Centrobolus*. The originally-stated distinctions lie chiefly in the form of the coxa of the phallopod. The Trigoniulidae was considered to contain forms in which the coxa and telopodite are attached by a flexible joint, the coxa with two glands or chambers near its proximad end; the Pachybolidae made up however of species in which the coxa and telopodite are fused into a single, right-angled structure, the coxal division of which having only a single basal chamber. The South African genus *Centrobolus* neatly bestrides these two categories, having the basic two-segmented phallopod the coxa of which, however, contains only a single chamber. As I remarked earlier, this entirely subjective evaluation of relationships must eventually be tested by a careful revision of the entire group.

Remarks on the status of two poorly-known species

1. *Spirobolus arcuosus* Porat

Von Porat's paper of 1893 contains the description, under the name of *Spirobolus arcuosus*, of a male spiroboloid from Damara, Southwest Africa. In the absence of gonopod drawings or adequate descriptions of these appendages, the identity of this species has remained in doubt down to the present time. Jeekel (1956: 93) noted the numerous differences between *arcuosus* and the other South African spiroboloids but concluded that ". . . we do not have the slightest hint as to its generic position."

Since the type was a mature male, which was found in the Stockholm collection and kindly forwarded to me by Dr. Hallin, I looked forward with

great interest to the prospect of finally solving the mystery. Ironically, however, of all the Porat material that I studied, this particular specimen was the only one in which the gonopods had been exposed for study, and in this case they were removed and missing.

So it seems that the name *arcuosus* is destined to persist for an indefinite time in a state of limbo. Possibly someone will be so fortunate as to obtain topotypes (if the species did, in fact, originate in Damara) or perhaps it may be eventually proven that von Porat returned the gonopods accidentally to another bottle of specimens after his examination of them. A careful search through the Stockholm collection can someday test this possibility.

In any event, it can be safely asserted that although *arcuosus* is not congeneric with the species of *Centrobolus*, it is obviously confamilial, as there is a close agreement in general external structure. As noted by von Porat, there are 54 segments, no scobinae, and no tarsal pads. That author did not, however, remark the occurrence of prominent coxal lobes on the anterior legs, which are represented in Figure 1 of this paper. Perhaps the addition of this character to what is known of the species may facilitate identification of the name *arcuosus* with some Asiatic species possibly introduced into Southwest Africa (or, more probably, erroneously tagged with that locality data). The general facies of the male type suggest a position rather close to *Spirostrophus*, or possibly *Arostrophus*, and although the gonopods may completely refute this point of view, I strongly suspect that *arcuosus* is a member of an East Indian trioniulid genus.

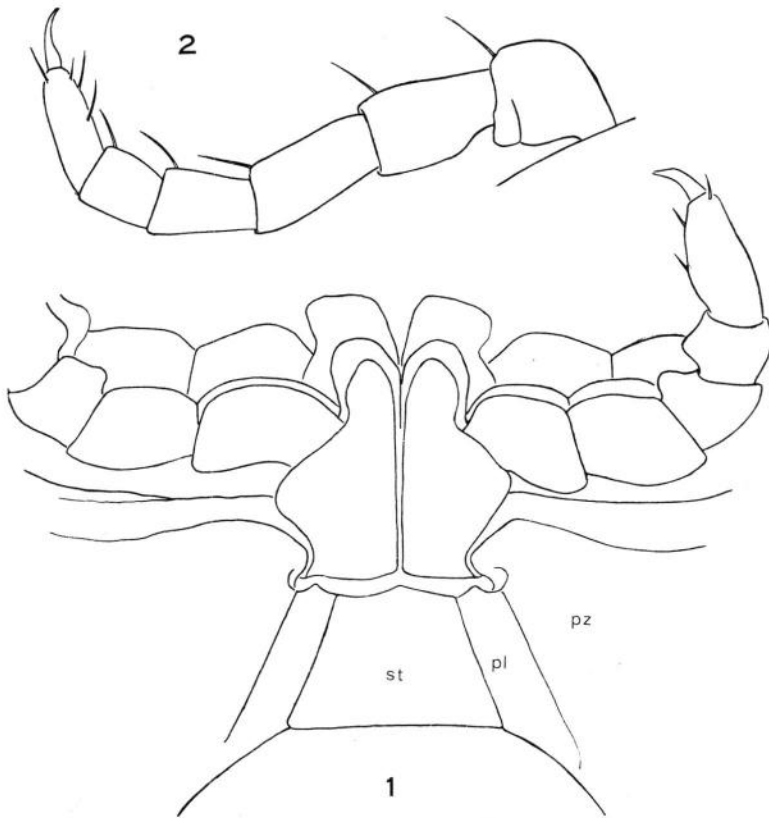
Von Porat's account of the gonopods runs as follows: "lamina ventralis aequae longa ac laminae anteriores, quarum pars superior anguste producta quam laminae posteriores brevior est; hae supra ovato-incrassatae in latera exteriori spiraliter canaliculatae; (flagellum?)" which I translate generally to mean

"Sternum medially produced to about the level of coxal endite lobes, of which the distal part is narrowly produced although shorter than the posterior parts [telopodites], the latter ovally thickened above, with the lateral side sinuously grooved; posterior gonopods not examined."

2. *Spirobolus elegans* Brandt

This species was described on the basis of material said to be from the Cape of Good Hope (Brandt, 1841). The name went through a period of obscurity until 1872 when C. O. von Porat revived it for a series of spiroboloids taken by Wahlberg in South Africa. Attems (1928) only listed the name among a category of dubious species, and cited Porat's 1872 paper as authority instead of Brandt's original description, seeming to imply that von Porat was responsible for what little was then known of the name. Subsequently, Jeekel (1956) cited the name *elegans* with the joint authority "Brandt-Porat" to indicate that the species under discussion was that form identified by the latter author as *elegans*, and not necessarily conspecific with Brandt's original. Jeekel further remarked that this "*elegans*" in the sense of von Porat might be found to be the same as *Chersastus anulatus* Attems, a supposition which can now be confirmed, see page 153.

The status of the name *elegans*, *sensu* Brandt, has therefore never really been settled, so it was with considerable interest that I discovered, in August



Figs. 1, 2. *Spirobolus arcuosus* Porat. 1, anterior legs (3rd—5th pairs) to show prominent coxal apophyses; 3rd leg of left side broken off beyond prefemur. 2, leg from midbody segment to show proportions of podomeres and setation, and a partial subdivision of coxa near its distal end. Drawings from holotype.

of 1966, an incomplete male specimen labeled "*Spirobolus elegans* Brandt" in the Berlin Zoological Museum. Although the types of this species were stated to be in the museum at Saint Petersburg, it seems clear that in this case (as well as others), Brandt must have split the series and shared the types between the two museums with which he was associated. Although the Berlin specimen is not designated unequivocally as a "type" it carries an old pin label "P. b. Sp. Lichten." which I judge to mean "Promontorium bonae spei, Lichtenstein".

There are at present only 31 segments, the dried specimen broken and the posterior fourth of the body either discarded or lost as it could not be found in the bottom of the drawer. The coloration has undoubtedly altered greatly as a result of drying; presently the body segments are blackish gray, with head, antennae, and legs reddish-brown. The collum is still bright red, however, and each body segment has a large oval middorsal blood-red spot on the metazonite and a smaller, rounded spot on the mesozonite, the two spots in

contact and giving the impression of a red middorsal band with serrated edges. The male genitalia were dissected out and found to be similar to those of the Indian species currently going by the name *Xenobolus carnifex* (Fabr.). Allowing for changes in pigmentation through drying, the animal agrees fairly well with Brandt's description, and the locality label would seem to confirm that the specimen is one of the original types. My colleague C. A. W. Jeekel has advised me (oral communication) that it was not uncommon in the early part of the commerce between Europe and southeast Asia, when practically all shipments went by way of Capetown, for natural history specimens originating actually in India or beyond to be labeled as coming from South Africa. Almost certainly something of this sort happened in the case of the material of *elegans*.

Spirobolus elegans Brandt, 1841, is herewith tentatively regarded as a junior subjective synonym of *Iulus carnifex* Fabricius, 1791. It must be recalled however, that the taxonomy of the genus *Xenobolus* is still unsettled (Hoffman, 1962) and it remains to be determined if *X. acuticonus* Attems, 1936, is a valid species or only a phenotypic color variant of *carnifex*. It may be shown that *elegans* is applicable to this presumptive additional species instead of *carnifex* in the strict sense. In any event, the specific name *elegans* is removed from consideration as an African spiroboloid.

Genus *Centrobolus* Cook

Centrobolus Cook, 1897, Brandtia, no. 13, p. 74. Proposed with one species. Type: *Spirobolus luctuosus* Peters, 1855, by monotypy and original designation.
Chersastus (nec Attems, 1926) Attems, 1928, Ann. S. Afr. Mus., vol. 26, p. 300. — Jeekel 1956, Beaufortia, vol. 5, p. 85. — Schubart, 1966, South African Animal Life, vol. 12, p. 34. — Lawrence, 1967, Ann. Natal Mus., vol. 18, p. 608.

Diagnosis: A South African endemic genus of Pachybolidae with reduced segmentation (38—46 body segments in the known forms); a general tendency toward attenuation of the anterior end of the body; prominent tarsal pads developed in the male sex; anterior coxae of males without distinct lobes. Scobinae may be present or absent.

Gonopods basically trigoniulid in outlines; sternum of coleopods roughly Y-shaped, its dorsal edge strongly curved downward to permit passage of the enteron, the ventral edge usually strongly produced medially into an acute process (which however may occasionally be much shorter and distally truncate); coxal endite lobes prominent, usually as long as the telopodite apices, distally acute. Coxae somewhat inturned along their medial edge which may be virtually straight (Figure 5) or reflexed (Figure 13), the dorsal part of the edge continuous as a sclerotized membrane attaching to the inner surface of the trachial apodeme. Telopodite elements smaller than usual for the order, partly or entirely concealed behind coxal endite lobes, their apices either subglobose thickened and bearing a laterally-directed acute process (Figure 9) or modified into an elongate, vertically oriented lobe of the medial edge (Figure 13) in which case the acute spinous process is wanting. Distal lobe of telopodite often minutely spinulose. Coxa abruptly cut off on the caudolateral side of coleopods, thus lacking medially directed projection and posterior extension of sternum broadly in contact with base of telopodite.

Phallopods relatively large and robust, the coxae oriented parallel to the

medial body axis and fused posteriorly to an arcuate sternal remnant; sternal apodemes dislocated from existing ends of the sternum and loosely pivoted against dorsal side of coxae midway between two prominent apodemes for muscle attachment (Figure 12). Coxae elongate, nearly or quite as long as telopodite, with a single digitiform process on the dorsomedial side adjacent to the globose enlargement of the spermal groove; latter runs along the dorsal side of coxa onto base of telopodite, whence it curves around to the medial side and terminates at about the midlength of the telopodite, never, however, on a special branch or process as occurs in Asiatic genera of trigoniulids. Coxa and telopodite articulated by a prominent, flexible joint and readily separated although no internal musculature is evident in the coxa; a distinct subconical projection of the latter extends into the base of the telopodite on the lateral side. Telopodite highly variable in form, both as regards its distal lobes and processes and the detailed outline of the membranous inner surface. In many forms there occurs a prominent cavity on the lateral side, in some, an erect digitiform process possibly homologous with the so-called "tarsal" remnant of *Metiche*.

Taxonomic notes: It has previously been remarked that the generic name *Chersastus* was first validly published in 1926, in vol. 4 of the "Handbuch der Zoologie" and that its type species by monotypy is *Trigonoilulus braueri* Attems, 1903, from the Seychelles (Hoffman & Keeton, 1960, p. 11). In 1928, *Chersastus* was again proposed as a new generic name to include 11 species, seven of them described as new, although no type was designated. Even though it seems quite obvious from the structure of the original species, as well as their distribution, that a considerable diversity was embraced by the concept of *Chersastus*, the homogeneity of the genus and the correctness of the inclusion of South African species has never been seriously questioned down to the present time.

As a matter of fact, however, I think there are two good reasons to replace *Chersastus* as the generic name for the large group of spiroboloids endemic in South Africa. The first is that, in my opinion, *C. braueri* is not congeneric with the mainland species. It lacks ventral tarsal pads in the male sex, the number of body segments is much higher (54 as opposed to a range of 38—46), and the anterior gonopods, especially their telopodites, have a somewhat different form. These departures from the relatively uniform structure of the 42 nominal South African "*Chersastus*" species would certainly seem to warrant a generic separation, with the restriction of *Chersastus* to the single species *braueri* in the Seychelles Islands. Another generic name must then be sought for the African mainland taxa.

Jeekel (1956) has already pointed out the availability of the name *Centrobolus*, but did not formally resurrect it owing to an uncertainty of how many genera might occur in southeastern Africa. I think it is now possible to state with some confidence that the type of *Centrobolus*, *luctuosus* Peters, is doubtless congeneric with the species included by Lawrence (1967) in the most recent review of *Chersastus*.

C. luctuosus was described from a male specimen taken at Inhambane, Mozambique, which is less than 100 km east of the easternmost locality (Masiene) recorded for species "*Chersastus*", and Lawrence himself suggests (1967: 611) that the coastal range of "*Chersastus*" extends as far as Inhambane

or even to Beira. There is no convincing geographical argument that *luctuosus* could represent a different genus.

More importantly, the type specimen of *luctuosus* is still preserved in good condition in the Zoological Museum at Berlin, and I was able to examine it in 1966 through the kind cooperation of the late Dr. W. Crome. In all external characters, the specimen agrees completely with the species heretofore referred to *Chersastus*, although, unfortunately, the gonopods have been removed (perhaps by Cook in 1894) and are no longer with the specimen. A search for a possible microscope preparation was made in the Berlin collection, and subsequently among Cook's slides now at the U. S. National Museum, regrettably without success. Since the structure of the gonopods is the ultimate generic criterion among most spiroboloids, the loss of the appendages from the type of *luctuosus* might be cited as a justification for the continued suppression of *Centrobolus*. But in my view, the brief description of the gonopods published by Cook in 1897 is applicable to no other African group of pachybolids than the genus so far known as *Chersastus*:

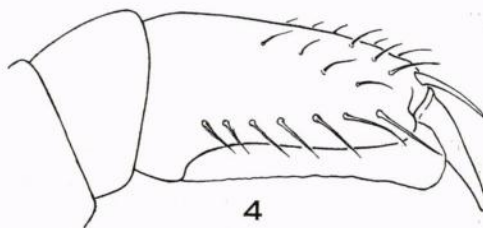
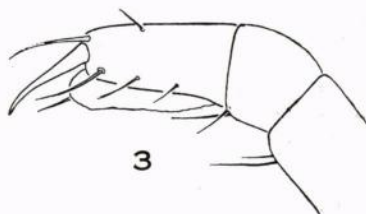
"Copulatory legs as a whole longer than broad, the anterior lamellae [= coxites] close together, much exceeded by the produced apices of the posterior lamellae [= telopodites], which are armed on their posterior face with a distinct spine."

Short as the preceding statement may be, I feel that it is nonetheless entirely descriptive of the great majority of the South African forms, particularly because of the reference to a "spine" on the posterior side of the coleopod telopodites. Until the type gonopods of *C. luctuosus* can be located, or topotypes of the species obtained, allocation of the name must remain on circumstantial grounds, but I think that the evidence is now overwhelmingly in favor of the course here formally proposed.

In passing, it may be remarked that inclusion of the East Indian species *badius*, *orinomus*, and *brachyurus* in the same genus with *Chersastus braueri* seems a little improbable, even though there is a well-known relationship between the faunas of South Africa and Indonesia in several milliped groups.

Species criteria in *Centrobolus*: Heretofore, partly because of the precedent set by von Porat, Koch, Pocock, and Brandt, the discrimination of species within this genus has been based to a very large extent upon external characters such as size, coloration, occurrence of scobinae, tergal sculpture, and distribution of tarsal pads in the male sex. Even though recent investigators (Jeekel, Schubart, Lawrence) have given good figures of the male genitalia, these appendages have not been accorded the taxonomic pre-eminence prevailing among most diplopod groups.

The color patterns are often dramatically developed in various combinations of blood-red and jet-black, and it is certainly to be appreciated that they would provide appealing basis for the recognition of species, although qualification was implied by Jeekel (1956: 90) in his admonition that coloration is known to be highly variable in many species of Diplopoda and may be also in *Centrobolus*. Lawrence (1967) based his species concepts to a large extent upon color pattern although not to the almost exclusive extent of Schubart in 1966. At the same time, a perusal of Lawrence's valuable paper shows that in many of his well-described taxa, there is both sexual dimorphism and geographic variation in pattern details. Obviously the real taxonomic signifi-



Figs. 3, 4. Distal podomeres of typical legs from midbody segments to show appearance of tarsal pads and setation. 3, *Centrobolus pococki* (Porat). 4, *Centrobolus saussurii* (Porat). Both drawings from lectotypes.

cance of color pattern variation can only be determined by the studies of someone able to make field as well as laboratory observations, but I am strongly inclined to the point of view that if no practical distinctions can be found in structural characters, the systematic value of pigmentational differences would be negligible.

Scobinae occur sporadically throughout the genus, and were used in species diagnosis by Attems in 1928. Jeekel suggested (1956: 98) that these pits seemed to vary considerably within a single species and were thus of limited value; Schubart (1966) mentioned scobinae in his descriptions but never in keys. Lawrence however restored them to a position of diagnostic importance, and it appears to me that in those species normally having large and prominent scobinae, some value may well be attached. In forms having small or rudimentary scobinae, it would seem that they might be more liable to sporadic or capricious suppression.

Lawrence has made good use of the distribution and degree of development of subtarsal pads in males which should be taken into account in all species descriptions for a future evaluation.

An additional variable afforded by these structures of the males in the occurrence of subtarsal macrosetae adjacent to the dorsal edge of the pads. Schubart has illustrated the appearance of the tarsus of the 3rd pair of legs in the species *C. promontorius*, *C. lawrencei*, *C. silvanus*, and *C. titanophilus*; Lawrence's recent paper shows the tarsus of various anterior legs of *C. decoratus*, *C. richardi*, and *C. anulatus*, and I provide herewith drawings of the tarsus of midbody (optimally developed) legs of *C. pococki* and *C. saussurii*. Possibly the number and disposition of the setae may afford some kind of correlations useful in confirming species groupings made on the basis of other characters.

Centrobolus digrammus (Pocock), new combination

- Spirobolus digrammus* Pocock, 1893, Ann. & Mag. Nat. Hist., ser. 6, vol. 11, p. 138, fig. 9. Syntypes (Brit. Mus.) from Hout's Bay, Cape Peninsula, H. A. Spencer leg. (Reg. No. 92.4.20.34): I examined this series in 1960 and designated a male as the lectotype.
- Spirobolus sabulosoides* Porat, 1893, Bih. Svenska Akad. vol. 18, no. 7, p. 33. Three syntypes (Naturh. Riksm. Stockholm) as follows: female with anterior end missing, labeled Cape Town, Taffelberget, 2/5/72, DeVlyder; male and female with the same data except that date is given as 2/5/73, perhaps an error; I herewith designate the male in this vial as the lectotype.
- Chersastus fasciatus* Attems, 1928, Ann. South African Mus., vol. 26, p. 301, figs. 216—220. Syntypes (S. Afr. Mus.) from a number of places in western Cape Province, no actual type designation was published by Attems nor do I here select any specimen as lectotype without having seen the material.
- Chersastus digrammus*: Schubart, 1966, South African Animal Life, vol. 12, p. 57, figs. 54—61 (with complete synonymy and biological data).

There now seems to be general agreement on the synonymy of this common species, as the examination of Pocock's and Porat's types confirmed the previously-made assumptions that the three names cited above are all based upon the same taxon.

Material examined: Cape Province: Hout's Bay, Cape Peninsula, types of *S. digrammus* Pocock; Cape Town, Table Mountain, types of *S. sabulosoides* Porat; Cape Point, 250 m., 1 ♀, April 26, 1958, E. S. Ross & R. E. Leech leg. [California Academy of Science].

Most of the previously known localities for *digrammus* are in the vicinity of Cape Town. Attems recorded material from several places in the Karroo, as well as from Durban, Grahamstown, and East London. Lawrence (1967: 636) expressed doubt about the Karroo localities as well as the record for Durban. I would personally challenge also the stations Grahamstown and East London had not Lawrence himself cited fresh material from the Alexandria forest near the first-mentioned place. Even so, such an apparently disjunct distribution seems curious, as there seem to be no intervening localities at all, and I think the matter is not yet closed. Is it possible that accidental introduction may account for the Grahamstown material?

Centrobolus pococki (Porat), new combination

Figs. 3, 5, 6

- Spirobolus Pococki* Porat, 1893, Bih. Konigl. Sv. Vet.-Akad. Handl., vol. 18, No 7, p. 32. 13 syntypes (Zool. Mus. Stockholm), labeled "Cape Colony, DeVlyder" (not *Kapstaden* as published by von Porat). A male has been isolated from this material and labeled as lectotype of the species.
- Spirobolus pococki*: Attems, 1928, Ann. S. Afr. Mus., vol. 26, p. 309 (as species *incertae sedis*).
- Spirobolus pococki*: Jeekel, 1956, Beaufortia, vol. 5, p. 94—96 (as possible senior synonym of *Chersastus atrophus* Attems).
- Chersastus pococki*: Schubart, 1966, South African Animal Life, vol. 12, p. 45.
- ?*Chersastus atrophus* Attems, 1928, Ann. S. Afr. Mus., vol. 26, p. 306, figs. 228—230. Syntypes (S. Afr. Mus.) from Hout Bay, Cape Town, and Wellington, Cape Province; the specimen upon which Attems based at least his illustrations is doubtless in the Naturhistorisches Museum, Wien. No lectotype designation is made in the absence of actual material.

Porat's description of the species is adequate as regards external characteristics with only a few exceptions, and of course must be referred to for information on coloration since the type specimens have now become largely

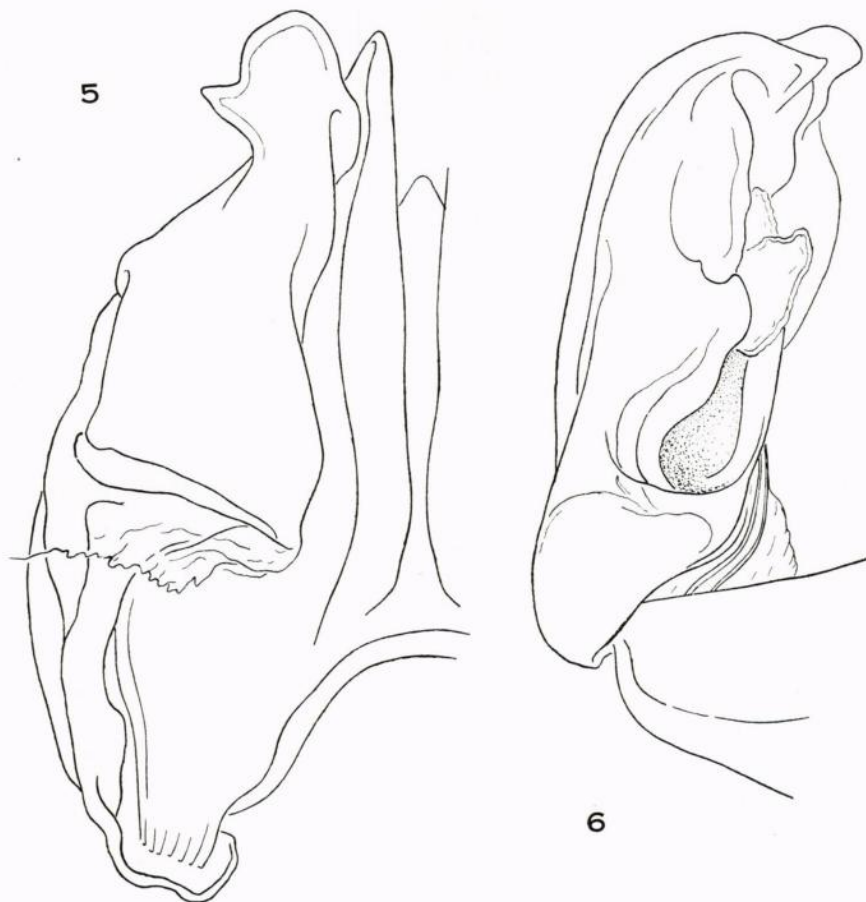


Fig. 5, 6. Gonopods of *Centrobolus pococki* (Porat). 5, Coleopods, right side, aboral aspect. 6, Right phallopod, lateral aspect, only distalmost end of coxal division shown.

bleached. On the basis of the published accounts, and apparent sympatry, Jeekel was quite justified in suspecting that the two names *pococki* and *atrophus* were based upon the same species of milliped, and his tentative suggestion was taken up with little reservation by Schubart in his important paper of 1966. His optimistic comment regarding the relationship of the two names ("Die Untersuchung des ♂ des *C. pococki* wird die Frage endgültig entscheiden.") unfortunately cannot be vindicated, as the examination of the types of *pococki* reveals discrepancies of some magnitude and I now think that the status of *atrophus* must remain unsettled until typical material of that name can be restudied!

A comparison of the gonopod drawings for *atrophus* published by Attems with the present illustrations (Figures 5, 6) made from the lectotype of *pococki* shows a general similarity in outline. It must be recognized that Attems' figures are obviously little better than rough sketches. The views of the

coleopod made from the oral and aboral aspects scarcely appear to represent the same species, for instance, and it might in fact be shown that Attems' type series was indeed heterogeneous. In any event, he shows the distal lobe of the telopodite to be ornamented with numerous small denticles, of which no trace appears in the specimens of *pococki*.

Additionally, the description of *atrophus* states "The tarsal pads wanting on the last 5—8 pairs of legs. Anterior legs with apophyses on the coxae." In the specimens of *pococki*, tarsal pads can be distinguished on all of the posterior legs, although those of the last six pairs are appreciably smaller and might be overlooked with low power magnification. The allusion to coxal apophyses is more difficult to reconcile, as the *pococki* types have no trace of any coxal modification, nor, to the best of my knowledge, do any other species of *Centrobolus*. Is it possible that Graf Attems was referring actually to the modified prefemora of the first pair of legs?

Here the matter rests pending an examination of the *atrophus* types. The recent discovery of *C. promontorius* (Schubart) on Cape Peninsula is sufficient evidence that more than one small species of the genus exists in that area sympatrically with *C. pococki* and *C. digrammus*.

The tarsal pads of *pococki* (Figure 3) are robust and prominent, and extend distad to about the midlength of the tarsal claws. Each pad is subtended on the oral and aboral side by usually three macrosetae, of which the distalmost is conspicuously longer than the other two, and reaches out nearly as far as does the tarsal claw.

Centrobolus strigosus (von Porat), new combination

Fig. 7

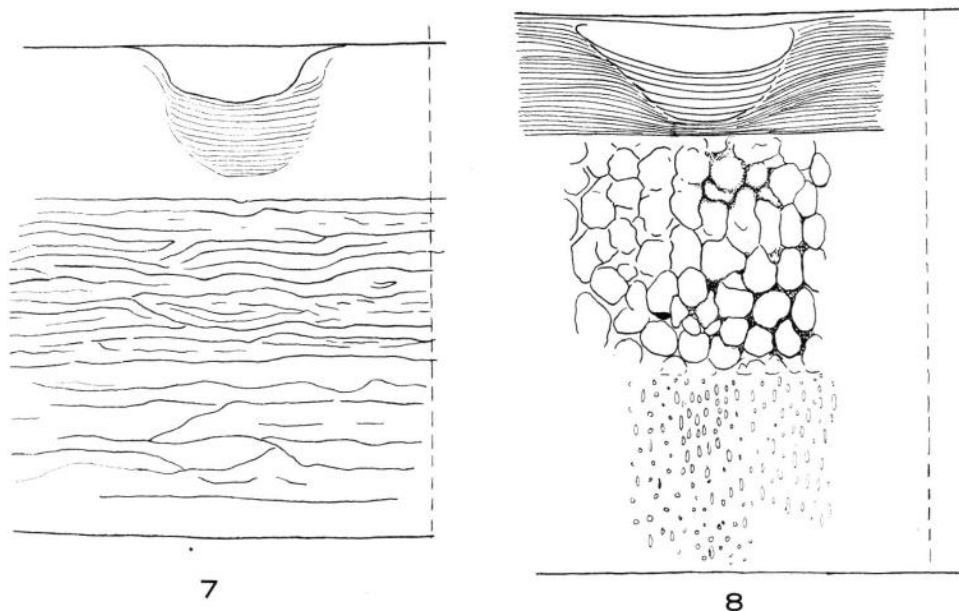
Spirobolus strigosus von Porat, 1872, Ofvers. Vetensk. Akad. Forh., vol. 28, No 5, p. 17.
Female holotype (Zool. Mus. Stockholm) from "Caffraria, 1840—45, J. A. Wahlberg".
Chersastus strigosus: Schubart, 1966, South African Animal Life, vol. 12, p. 65.

The single female type of this species is at present in very poor condition; most of the segments disarticulated and the legs missing; the coloration is entirely lost. Nonetheless, Porat's description gives an idea about the original color pattern, and it is possible to derive a good concept of the tergal sculpture from the type even in its present state.

Scobinae are present and quite prominent, separated from each other at the middorsal line by a space about equal to the width of a single scobina. As represented in Figure 7, the prozonite is essentially smooth, with its width largely transgressed by the striate area behind the scobinae. The mesozonite is finely and profusely wrinkled transversely, and the metazonite likewise sculptured although more coarsely.

In the keys recently published by Lawrence (1967: 637, 639), *strigosus* is placed in the same couplet with *C. striolatus* (Attems), from which it differs trenchantly not only in coloration but further in having the dorsal striations transversely oriented instead of concentrically arranged in curved series.

It seems only probable that eventually males referable to *strigosus* will be found in South Africa, facilitating a satisfactory placement of the species with reference to other members of the genus.



Figs. 7, 8. Middorsal tergal sculpture of two species of *Centrobolus*. 7, *C. stigosus* (Porat). 8, *C. coriaceus* (Porat). Drawings made to same scale, in each case from the female types, from a midbody segment. Middorsal line indicated by the vertical dashed line.

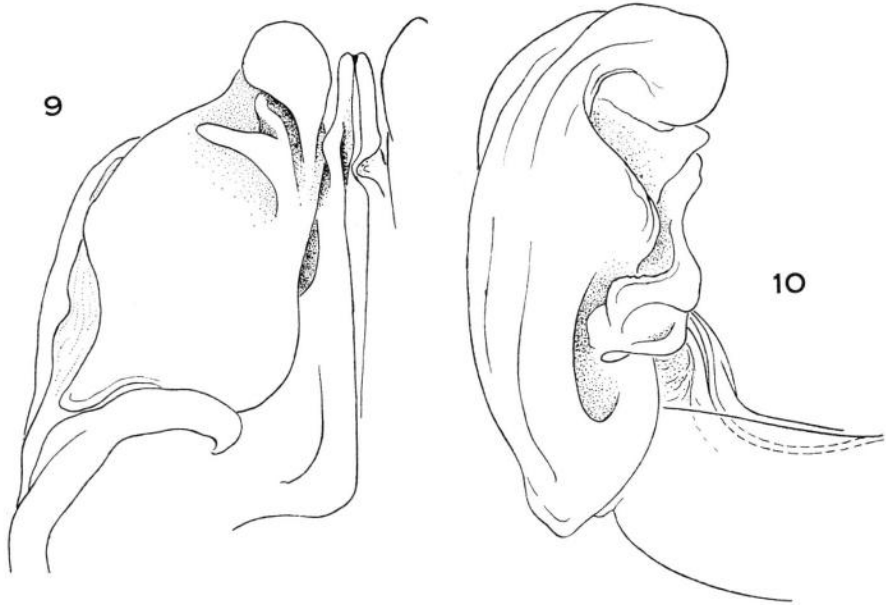
Centrobolus anulatus (Attems), new combination

Figs. 9, 11

- Chersastus anulatus* Attems, 1934, Ann. Natal Mus., vol. 7, p. 478. — Jeekel, 1956, Beaufortia, vol. 5 (no. 51), pp. 95, 96. — Schubart, 1966, South African Animal Life, vol. 12, p. 39. — Lawrence, 1967, Ann. Natal Mus., vol. 18, p. 633, fig. 45. Syntypes of *C. anulatus* dispersed, a female regarded by Lawrence as one of the original types is in the Natal Museum; at least one male was also involved and must be in the Naturhistorischen Museum, Wien. The type locality is Ifafa, south of Scottborough on the coast of Natal.
- Chersastus rubrofasciatus* Schubart, 1966, South African Animal Life, vol. 12, p. 41, figs. 30—33. — Lawrence, 1967, Ann. Natal Mus., vol. 18, p. 633 (regarded as junior synonym of *anulatus*). Male holotype and topoparatypes of both sexes (Zool. Mus. Lund), from "The Bluff" at Durban, Natal.
- Spirobolus elegans* (nec Brandt, 1841) Porat, 1872, Ofv. Konigl. Vetensk.-Akad. Förh., no. 5, p. 19. — Jeekel, 1956, Beaufortia, vol. 5, p. 85. — Schubart, 1966, South African Animal Life, vol. 12, p. 40. Specimens labeled only "Caffraria" but doubtless taken in the vicinity of Durban.

Taxonomic notes: Attems' original description of this species is very brief and inadequate. Lawrence has published new descriptive information from virtually topotypic specimens, but unfortunately did not illustrate the gonopod structure. Attems stated that these appendages are "like those of *vastus*" which could mean almost anything depending on how stringently one interpreted the meaning of "like"!

The Porat material of "*elegans*" contains several specimens in which the original color is still evident, and confirms Jeekel's suspicion of its identity



Figs. 9, 10. Gonopods of two species of *Centrobolus*. 9, Right side of coleopods of *C. anulatus* (Attems), lateral aspect, basal structure omitted. 10, Right phallopod, distal half, of *C. richardi* (Lawrence), lateral aspect.

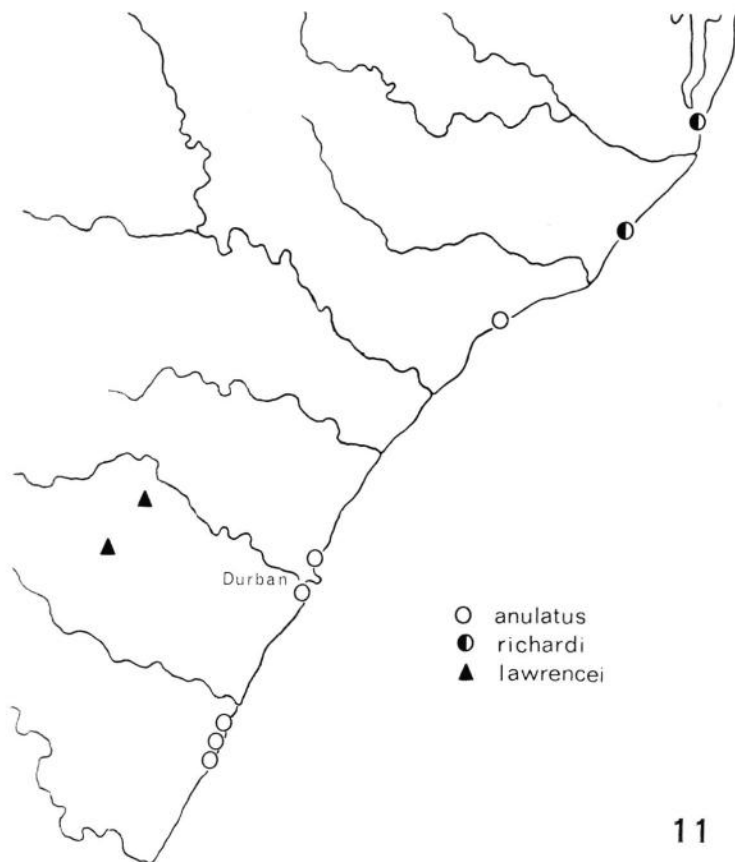
with *anulatus*. These specimens run out readily to *anulatus* in both of Lawrence's recent keys. Removal of the name *elegans* from the South African fauna (see page 144) of course established Attems' name as the correct one for the species.

The gonopods of the Porat specimens agree exactly in the minutest detail with Schubart's good drawings of *rubrofasciatus*, and there is no doubt that Lawrence's suggestion that the latter name is a junior synonym of *anulatus* is correct. Moreover, some recently preserved specimens from Natal correspond in both structure and coloration to Lawrence's account of this species, so it would appear that *anulatus* is a valid and distinctive form localized in the coastal strip of Natal around Durban, see figure 11.

However, to say that the gonopods are like those of *C. vastus* is misleading, the similarity being no more than generic in extent. The original gonopod drawings published by Attems (1934) for *vastus* are themselves very vague; Lawrence has since provided (1967: figs. 39—42) satisfactory illustrations for the species. A comparison with figure 9 of this paper will reveal a considerable difference between *vastus* and *anulatus*.

Material examined: "Caffraria", probably vicinity of Durban, Natal, 1 ♂, 5 ♀♀, Naturh. Riksm. Stockholm, J. Wahlberg, leg., 1840—45; determined by von Porat as *Spirobolus elegans* Brandt. Natal: without exact locality, 1 ♂, 2 ♀♀, S. Kiem, leg., 1964 (Hoffman Coll.).

Lawrence (1967: 633) records *anulatus* from Ifafa lagoon, Kelson Station, Scottburgh, Durban, Umhlanga Rocks (Natal) and Mtunzini (Zululand). These places are represented on the distribution map, Figure 11.



11

Fig. 11. Coastal region of Natal between Port Shepstone (bottom edge) and Lake Saint Lucia (top edge) showing known localities for the three related species *C. anulatus*, *C. lawrencei*, and *C. richardi*.

Centrobolus richardi (Lawrence), new combination

Fig. 10

Chersastus richardi Lawrence, 1967, Ann. Natal Mus., vol. 18, p. 621, figs. 17—20. Types (Natal Mus.) from Richards Bay, Zululand, South Africa.

At first glance this striking species appears similar to *C. anulatus*, but differs colorwise in that the head, antennae, and legs are bright red instead of black as in Attems' species. The two taxa share the reduction of tarsal pads in the male (absent from the last 16—18 pairs of legs in *anulatus*, and the 20—22 pairs in *richardi*), and have a generally similar gonopod structure.

With respect to the finer details of gonopod form, however, a much closer relationship can be noticed with *C. lawrencei* Schubart. Lawrence did not illustrate the phallopod of *richardi*, and I herewith provide a drawing to remedy the deficiency. The comparison of this figure with those given by

Schubart (1966: figs. 48, 49) shows virtual concordance in nearly all details (it must be observed that Schubart's Figure 48 is made from a slightly different aspect than Figure 10 of this paper, as well as being made from a preparation illuminated by reflected light, and I think may be slightly inaccurate in some of its fine points). The coleopods of these two entities are likewise similar, differing chiefly that in *richardi* the apical lobe of the telopodite is shorter and broader, with the posterior subapical spur visible from the front.

C. lawrencei differs from both *anulatus* and *richardi* in coloration and in having tarsal pads on all except the last pair, in the male sex. It is thus a little difficult to estimate the degree of affinity among these three forms, but certainly they must belong to a consanguineous group within the genus. There is no apparent reason to doubt the primacy of gonopod structure in *Centrobolus*, and I therefore tend to regard the characters of color pattern, scobinae, tarsal pads, and the like, as purely secondary in their relative importance.

From a geographic standpoint, the three taxa mentioned appear to be allopatric. *C. anulatus* seems confined to the coastal strip from Ifafa to Mtunzini; *C. richardi* likewise coastal north of the Tugela River; and *C. lawrencei* somewhat more inland, at Pietermaritzburg and Richmond. It certainly seems evident that the possibility of a subspecific relationship should not be discounted.

Lawrence (1967: 631) expressed the view that *lawrencei* might be most closely related to *inscriptus* Attems and *rubricollis* Schubart, especially to the latter. However, the phallopod has not yet been figured for *rubricollis* and the drawing given by Attems for *inscriptus* is certainly a vague one, so we cannot really make a good comparison of these two forms with *lawrencei*.

Several of the immature specimens of *lawrencei* from the collection cited below show a concentration of diffuse black pigment on the anterior half of the collum, presaging a condition that persists in the adults of other species.

Material examined: Zululand: St. Lucia, 50 m., 1 ♂, 2 ♀♀, 4 immatures, April 9, 1958, E. S. Ross & R. E. Leech, leg. [California Acad. Sci.].

C. richardi has already been recorded from this locality in the original description of the species.

Centrobolus immaculatus (Lawrence), new combination

Fig. 12

Chersastus immaculatus Lawrence, 1967, Ann. Natal Mus., vol. 18, p. 613, figs. 2—4. Types (Natal Mus.) from Garuso, Mozambique.

This striking species enjoys the distinction of being the reddest known member of the entire genus; only the legs depart from the dominant color in being brownish basally, yellowish-orange distally.

The posterior gonopods were not illustrated by Lawrence. I herewith give a drawing of a phallopod in lateral aspect for comparison with those of other species. The species appears to be a very distinctive one on the basis of genitalic structure as well as coloration, and I cannot match it closely with any of the better-described forms.

Material examined: Zambia: Chirinda Forest, 18 miles south of Chipinga,

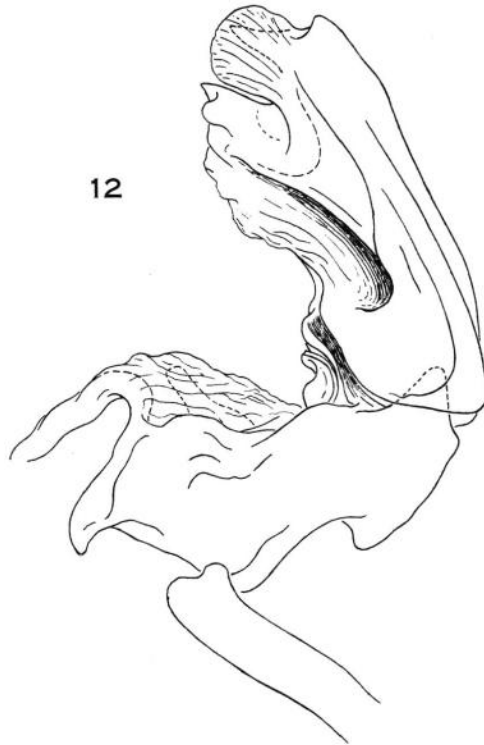


Fig. 12. *Centrobolus immaculatus* (Lawrence). Right phallopod, lateral aspect, with sternum shown intact, and base of apodeme.

1110 m., numerous males and females, March 18, 1958, E. S. Ross & R. E. Leech, leg. [California Acad. Sci.].

The species has already been recorded from this locality by Lawrence, in the original description.

Centrobolus coriaceus (Porat), new combination

Fig. 8

Spirobolus coriaceus Porat, 1872, Ofvers. Vetensk. Akad. Forh. vol. 29, no. 5, p. 19; Attems, 1928, Ann. S. Afr. Mus., vol. 26, p. 308; Jeekel, 1956, Beaufortia, vol. 5, p. 95.
Chersastus coriaceus: Schubart, 1966, S. Afr. Animal Life, vol. 12, p. 62.

Originally described on the basis of two females, this species has remained in doubt up to the present time, and Lawrence (1967) expressed the opinion that *coriaceus* (and some other Porat names) might best be stricken from the list of valid names.

My personal reaction is that although *coriaceus* is known only from females, the combination of segment number, coloration, and segment texture makes a pretty diagnostic effect, and it should be easily possible to recognize this species when it is again collected. Jeekel pointed out the similarity of the color pattern to that of *C. vulpinus* Attems; Lawrence later observed that

numerous small differences would seem to preclude actual conspecificity of the two.

The coloration is certainly unusual: the meso- and metazonites are said to be reddish, the prozonites testaceous-brown with a grayish-black median dorsal spot; legs and antennae blackish. Both specimens have a segment count of 42, lower than usual for the genus, but the dorsal sculpture really characterizes the species and justifies its name. As shown in the illustration, the prozonites are profusely and minutely transversely striolated, the metazonites covered with numerous elongate, close-set punctures, and the mesozonites very coarsely wrinkled. Scobinae are prominent and broad, nearly as wide as the middorsal space between them. Although there appears to be some sexual dimorphism in *Centrobolus* as regards tergal sculpture, it does not seem likely that males of *coriaceus* would depart much from such a prominent condition as that just accounted in the female sex.

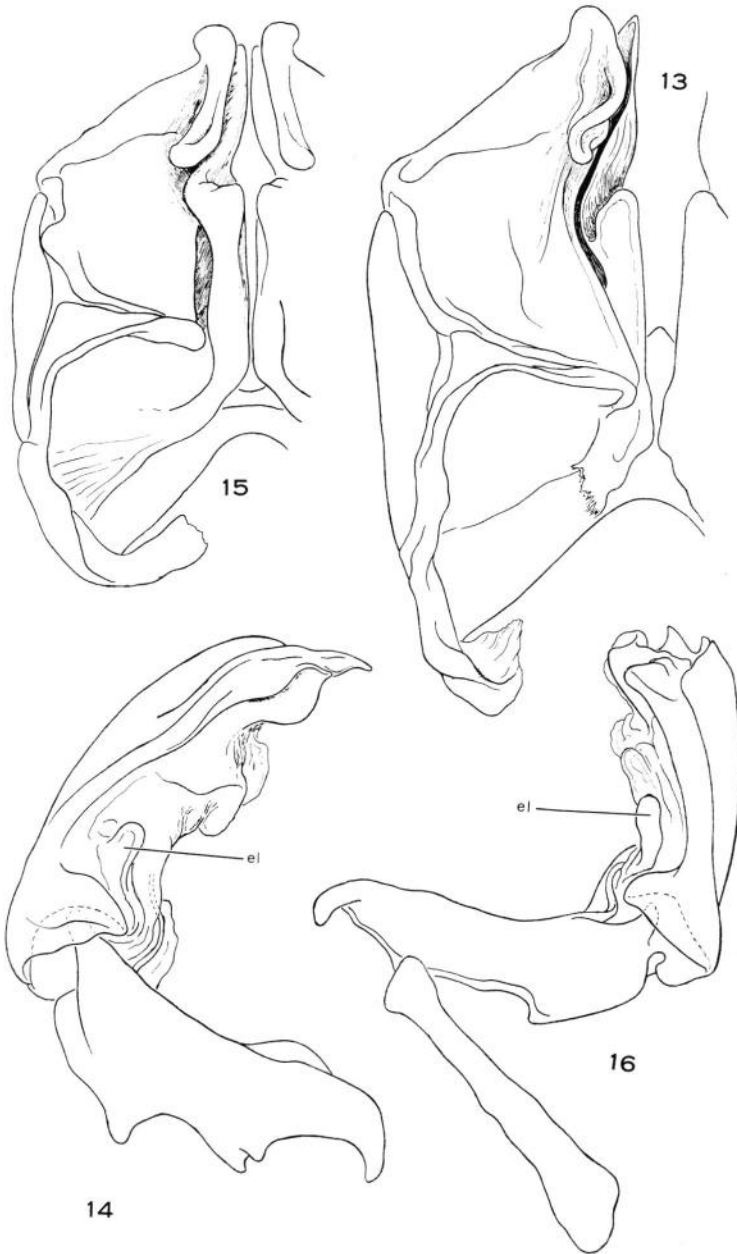
The *Centrobolus litoralis* Group

One of the results of my examination of pertinent type material and a consideration of recent literature has been the recognition of a small group of species characterized in particular by the telopodite of the coleopods. Here, instead of the usual laterally-directed acute subterminal spine on the posterior side, we find a single elongate vertical lobe (or minimally two short precursors) of singular appearance. Jeekel's species *C. erythroproctus* was the first member of the genus, having this type of gonopod, to be figured in the literature, and its author quite aptly remarked that "... the complete lack of a tibial process is characteristic and serves to distinguish *erythroproctus* from any other of the 9 forms mentioned [in which the gonopods were known]."

We now know some additional species having much the same gonopod configuration: *S. tessellatus* and *S. saussurii* of Porat, *C. sagatinus*, *C. titanophilus*, and *C. elizabethae* Schubart, *C. lugubris* Lawrence, and inferentially, *S. litoralis* Koch. All of these nominal forms occur in the central coastal region of South Africa, between 24° and 26° east longitude, and it seems appropriate to formalize their obvious relationship by the establishment of a "Litoralis Group".

The first critical work done on this ensemble was that of Pocock (1893) who combined Porat's name *tessellatus* with Koch's earlier *litoralis*, without comment. Attems in 1928 listed both as species "*incertae sedis*". Jeekel tended to support Pocock's action, his discussion of these forms included also his own *erythroproctus* which he separated from the other two because of differences in coloration. In the description of *C. lugubris*, Lawrence noted a similarity of his new form to *litoralis* and *erythroproctus* (among others) and separated *lugubris* primarily on the basis of its coloration. Schubart's good description of *C. elizabethae* did not compare it with any other form although it was keyed out in the vicinity of *C. formosus* because of color characters.

It now appears to me that several of the foregoing taxa, established only upon very minor differences in pigmentation, are probably best considered as conspecific, and I herewith propose to relegate the names *elizabethae* and *erythroproctus* to the synonymy of *litoralis*, as justified in the discussion of that form which follows. Certain others, including *lugubris* and *saussurii*,



Figs. 13—16. Gonopods of two species of the *Centrobolus litoralis* Group. 13, *C. saussurii* (Porat), right side of coleopods, aboral aspect, from lectotype. 14, phallopod of same specimen, lateral aspect. 15, *C. litoralis* (L. Koch), right side of coleopods, aboral aspect, specimen from Port Elizabeth. 16, phallopod of same specimen, lateral aspect. Abbreviation: *el*, presumed endite lobe of prefemur.

differ sufficiently in gonopod structure to warrant full specific status in the light of present knowledge.

Centrobolus litoralis (L. Koch), new combination

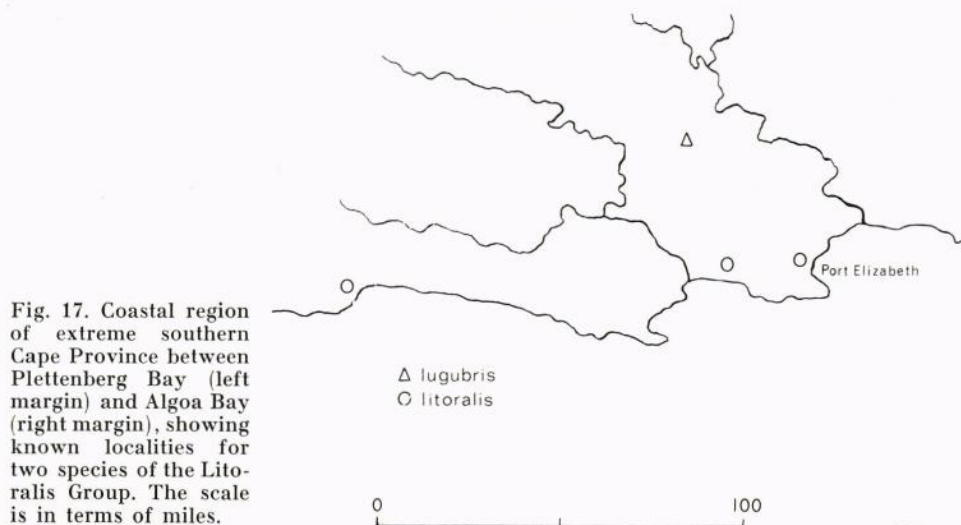
Fig. 15—17

- Spirobolus litoralis* L. Koch, 1865, Verh. zool.-bot. Gesellsch. Wien, vol. 15, p. 884. — Attems, 1928, Ann. S. Afr. Mus., vol. 26, p. 308. Two syntypes, an immature male and an adult female (Zool. Mus. Hamburg), from "Algoa Bay", I examined these specimens in 1960 but did not designate either as lectotype.
- Spirobolus tessellatus* Porat, 1872, Ofvers. Vetensk. Akad. Forh., vol. 29, no. 5, p. 21. — Attems, 1928, Ann. S. Afr. Mus., vol. 26, p. 309. Four syntypes (Naturh. Riksmus. Stockholm) as follows: one adult male and two adult females labeled "Caffraria 1840—45, J. A. Wahlberg"; one adult female labeled "Cap. Bon. Spei 1854, Victorin". I have selected the male from "Caffraria" as the lectotype. The female from the Cape of Good Hope is a specimen of *Centrobolus digrammus* (Pocock).
- Chersastus erythroproctus* Jeekel, 1956, Beaufortia, vol. 5, p. 89, figs. 17—19. New Synonymy! Male holotype (Zool. Mus. Amsterdam) from Plettenberg Bay, Cape Province.
- Chersastus litoralis*: Schubart, 1966, S. Afr. Animal Life, vol. 12, p. 69. — Lawrence, 1967, Ann. Natal Mus., vol. 18, p. 626.
- Chersastus elizabethae* Schubart, 1966, S. Afr. Animal Life, vol. 12, p. 65, figs. 69—74. New Synonymy! Male holotype (Zool. Mus. Lund) from Van Stadens Pass, 25 miles west of Port Elisabeth, Cape Province.

Taxonomic notes: The status of the name *litoralis* has been shrouded with doubt and uncertainty for over a century, but it seems possible now to advance a fairly confident resolution of the matter. Indeed, essentially the same proposal was suggested in 1956 by C. A. W. Jeekel on the basis of a deductive analysis of the fragmentary literature information.

It has been established that Wahlberg collected material in the vicinity of Port Elizabeth, which can probably also be regarded as roughly equivalent to the "Algoa Bay" locality of *litoralis*. Although the collector of the *litoralis* specimens is unknown it seems reasonable that zoological material captured anywhere around Algoa Bay during the first half of the last century would likely come from the vicinity of the major settlement of the region. The close similarities in the color patterns as described by the authors of *litoralis* and *tessellatus* have already been noted and regarded as indications of synonymy by Pocock, Jeekel, Schubart, and Lawrence. Finally, the male *tessellatus* lectotype shows a gonopod structure virtually identical with that of *elizabethae* (known from only a few miles west of Port Elizabeth). So it seems established beyond much doubt that Pocock's combination of the two names was in fact a correct one, and that Porat's material of *tessellatus* came from the vicinity of Port Elizabeth.

Granting the foregoing assumptions to be basically correct, we can further notice that the gonopods of the nominal species *litoralis*, *elizabethae*, and *erythroproctus* are extremely similar, allowing for differences in the method of illustration and for the fact that parts of the phallopods are membranous and variable. As already mentioned, these and many other forms of *Centrobolus* have been distinguished solely upon quite minor and subjective color differences noted in single preserved specimens by different people. Doubtless the important of such putative differences has been vastly overemphasized.



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Local variability of coloration thus becomes a matter of some taxonomic importance, and material loaned by the California Academy of Sciences is of great interest in indicating the dimensions of this particular parameter. A series of males and females from Humewood, Port Elizabeth, which may be regarded as topotypic of both *tesselatus* and *litoralis*, reveals that within a single sample the head may be clear red or marked with a dark interocular band, the collum may have two paramedian light spots or a single transverse blotch, and the paraprocts may be either uniformly red or uniformly nearly black with reddish edges.

Just 25 miles west of Port Elizabeth occurs a form, previously known only from a single specimen, named *C. elizabethae* by Schubart in 1966. This animal was described as having a reddish-yellow head with weakly indicated dark interocular marking and grayish-brown paraprocts margined with reddish. Lastly, from Plettenberg Bay, about 120 miles west of Port Elizabeth, came a single male described by Jeekel as *C. erythroproctus*. This entity agreed closely with the coloration of *litoralis* except for having the upper half of the head blackish and the paraprocts black margined with red. The gonopod drawings and anatomical descriptions published for *erythroproctus* and *elizabethae* are so entirely similar that it is puzzling Schubart did not notice or remark it.

A small series (Calif. Acad. Sci.) of recently preserved topotypes of *elizabethae* also shows considerable variation in pattern, quite irrespective of sex. In some the head is entirely reddish, in others there is a poorly defined interocular marking. Several specimens have uniformly reddish paraprocts, in one the distal margins are dark; two have the paraprocts distinctly diffuse grayish without marginal coloration. It seems likely to me that the normal phenotypic variation within the two samples nearly approximates the differences invoked to justify the various names mentioned previously, and that

small variations in both the shading and distribution of pigment have no real taxonomic significance when other features show no appreciable differences.

Material examined: "Caffraria", (here restricted to Port Elizabeth) Wahlberg leg. 1840—45, ♂ lectotype and 2 ♀ lectoparatypes [Zool. Mus. Stockholm]. Algoa Bay, collector and date unknown, ♀ and imm. ♂ syntypes of *S. litoralis* Koch [Zool. Mus. Hamburg]. Humewood, Port Elizabeth, E. S. Ross & R. E. Leech, leg. April 20, 1958, 4 ♂, 4 ♀ [Calif. Acad. Sci.]. Van Stadens Pass, 100 m, Ross & Leech leg. April 20, 1958, 3 ♂, 4 ♀, topotypes of *C. elizabethae* [Calif. Acad. Sci.].

Centrobolus saussurii (von Porat), new combination

Figs. 13, 14

Spirobolus Saussurii von Porat, 1872, Ofv. Konigl. Vets.-Akad. Forhandl., N:o 5, p. 20.

Twelve syntypes (Natur. Riksmus. Stockholm) labeled "Caffraria", 1840—45, J. A. Wahlberg. A male has been designated as lectotype.

Spirobolus falcatus Voges, 1878, Zeitschr. wissenschaft. zool., vol. 31, p. 182, figs. 37, 37 a.

Male holotype and male paratype (Zool. Mus. Hamburg), labeled "Zanzibar, Afrika", obviously in error. New Synonymy!

Spirobolus saussurei [sic]: Attems, 1928, Ann. S. Afr. Mus., vol. 26, p. 309.

Chersastus saussurei [sic]: Schubart, 1966, South African Animal Life, vol. 12, p. 50.

This well-marked species has been traditionally referred to *Chersastus* chiefly on the basis of external features and its geographic provenance. Examination of the gonopods provides ample confirmation of this placement, and shows that *saussurii* is in fact closely related to *litoralis* although we remain on ignorance of its actual range.

Voges' species *falcatus*, although well described and illustrated, has languished in total neglect ever since 1878, probably because it could not be easily reconciled with other spiroboloids known so far from coastal East Africa. With the dissection of a male of *saussurii*, it became immediately obvious that the name *falcatus* must be based upon a very similar species, and subsequent examination of the *falcatus* types showed in fact a complete identity at the species level. The locality "Zanzibar" is explainable only as an obvious mistake or transposition of labels.

Von Porat's original description of *saussurii* is entirely accurate and from an examination of the now completely bleached type material I can add nothing of interest aside the observation that tarsal pads are present on all legs of the males except the first two pairs. These pads are large and prominent, in nearly all cases extending to about the midlength of the tarsal claw, and are accompanied by a series of six or seven tarsal setae along both the anterior and posterior side. There are no scobinae. According to von Porat, the segments are annulated, the prosomites yellowish-brown and the exposed areas greyish-green, but whether this is the color pattern in life remains unknown.

In Lawrence's key (1967: 639) based upon structural features, *saussurii* runs out readily to *elizabethae* [= *litoralis*, see p. 160]. In Jeekel's key (1956: 98) it will come out with *erythroproctus* [also = *litoralis*]. The gonopods (Figures 13, 14) confirm this apparent relationship, which was first indicated by the full complement of tarsal pads and lack of scobinae.

Almost certainly *C. saussurii* will be rediscovered with future collecting

north and eastward of Port Elizabeth, from which region no members of the Litoralis Group have yet been verified.

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