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NEW TAXA OF *ONYMACRIS* ALLARD, AND
 RELATIONSHIPS WITHIN THE GENUS
 (COLEOPTERA: TENEBRIONIDAE)

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ABSTRACT

PENRITH, M.-L., 1984. New taxa of *Onymacris* Allard, and relationships within the genus (Coleoptera: Tenebrionidae). *Annals of the Transvaal Museum* 33 (31): 511-533.

The present paper is a supplement to an earlier revision of the genus *Onymacris* Allard (Coleoptera: Tenebrionidae) by the author in 1975. A new species, *Onymacris brainei* spec. nov., and a new subspecies, *O. unguicularis schulzeae* subsp. nov., are described. Recently collected material of *O. candidipennis* (Breme) and *O. paiva* (Haag), representing range extensions, is discussed. A key to all species and subspecies is given, the distribution of all species is mapped to illustrate several range extensions, and the phylogenetic relationships of the species are analysed.

INTRODUCTION

At the time of my revision of the genus *Onymacris* Allard (Penrith, 1975) I was unable to analyse relationships within the group owing to a lack of knowledge of the Adesmiini as a whole. None of the related southern African genera had been recently revised, and thus could not be studied on a comparative basis. A subsequent revision of the western southern African Adesmiini (Penrith, 1979) remedied this problem. During the last year I have had at my disposal very extensive material of tropical and Palaeartic Adesmiini, and this has enabled me to study the relationships within the tribe as a whole.

Owing to the discovery of new taxa within *Onymacris*, and in particular the unexpected discovery of a new species in the northern Namib, the study on *Onymacris* was given priority. As a dominant genus in the Namib desert, *Onymacris* excites much interest in a number of fields, including physiology and behaviour, and it is hoped that the present study will contribute to studies of this nature.

Details of the interrelationships of Adesmiini in general will be published at a later stage. The position of *Onymacris* in the tribe is briefly discussed here. In 1975 I suggested that *Onymacris* might not be strictly monophyletic, as its shared characters are all adaptive to the psammophilous mode of life. In my analysis of the whole tribe (Penrith, 1979), the genera *Onymacris*, *Physadesmia* Penrith, and *Eustolopus* Gebien emerge as a monophyletic assemblage on the basis of shared characters which, while probably adaptive, are not directly connected with psammophily and are unlikely to show parallelism. The characters used to establish these three genera in turn as monophyletic assemblages are possibly less convincing, but each does appear to be excluded from the direct ancestry of the others. For this reason *Onymacris* is believed to be, and henceforth is treated as, a monophyletic assemblage.

The *Onymacris-Physadesmia-Eustolopus* lineage is considered to have diverged rather early from the ancestral Adesmiini stock, before the present-day tropical lineages were established, but it is likely that the radiation of *Onymacris* took place at a much later date, as the south-western African sand deserts developed. My assumption in 1975 (Penrith, 1975) that *Onymacris* was closely related to *Physosterna* Solier and *Stenocara* Solier appears only to be true in the case of the species then included in *Physosterna* which now constitute the genus *Physadesmia* (Penrith, 1979). *Physosterna* as limited by Penrith (1979) and *Stenocara* belong to different lineages of Adesmiini; but the group is a closely knit assemblage, and similar environmental conditions are therefore likely to produce similar responses in different lineages. Thus species of *Stenocara*, *Physosterna*, and *Onymacris* may be superficially very similar indeed.

In *Onymacris*, as in *Physadesmia* and *Eustolopus*, the labrum is flat and the anterior margin of the eye is indented by the genal canthus; the part of the eye above the genal canthus is broadly ovate, while the part below is reduced and much narrower than the part above. All the species of *Onymacris* are characterised by having the first metatarsal segment shorter than the following two together, the tarsal claws at least as long as the unguis segment, and often expanded, and the tibial calcaria surpassing in length at least the first, and sometimes more tarsal segments.

KEY TO THE SPECIES AND SUBSPECIES OF *ONYMACRIS*

Note: in the key and in the taxonomic descriptions the terms pseudopleura and pseudopleural crest are used in the sense that Dr C. Koch used them in his numerous publications on the southern African Tenebrionidae, and which usage I have followed for the sake of conformity (see Penrith, 1977). They are equivalent to the more commonly used terms epipleura and epipleural ridge.

- 1 (27) Integument of elytra black, with or without waxy secretions.
- 2 (7) Pronotum with two large ovate impressions as well as a transverse prebasal impression;—elytral intercostae with reticulate sculpture.
- 3 (4) Appendages reddish; antennae stout, third segment less than twice length of second segment; claws slender; hindbody with normal sexual dimorphism, female a little broader than male but similar in shape *Onymacris hottentota* (Péringuey)
- 4 (3) Appendages black; antennae slender, third segment more than twice length of second; claws broad, foliaceous; hindbody of female ovate, that of male much broader, almost circular and laterally flattened *Onymacris plana* (Péringuey)
- 5 (6) Pronotum with confluent punctation, giving a vermiculate appearance
 *Onymacris plana plana* (Péringuey)

- 6 (5) Pronotum with round punctures, generally scattered, sometimes partly confluent *Onymacris plana debilis* Koch
- 7 (10) Disc of elytra smooth, without any sign of longitudinal sculpture or costae, only the apical declivity with three raised costae; protibiae and profemora of male with setose brushes; tarsal segments very short and stout *Onymacris unguicularis* (Haag)
- 8 (9) Pronotum about one and one third times as wide as long; epistome variable in shape and sculpture; Swakopmund southwards *Onymacris unguicularis unguicularis* (Haag)
- 9 (8) Pronotum almost twice as wide as long; epistome rather short, broad, and deeply indented anteriorly, smooth, often without any trace of granular sculpture; northern Namib coast, from Unjab River northwards *Onymacris unguicularis schulzeae* subsp. nov.
- 10 (7) Disc of elytra with costae or longitudinal raised sculptural elements.
- 11 (26) In caudal view, reflected part of elytra forming a sharp angle with disc, and separated from it by a strong costa or carina; anterior angles of pronotum broad, strongly produced forwards.
- 12 (21) Pronotum dull, with large rounded punctures at least laterally; elytral disc with two or three distinct costae, intercostae with granular to rugose sculpture, but without a distinct secondary costa developed, although sometimes with a median row of well-spaced granules; mesotibiae subcylindrical.
- 13 (16) Three elytral costae on disc, with strong, backwardly directed denticular granules; tarsal claws very slender *Onymacris paiva* (Haag)
- 14 (15) First elytral costa uniting with second before or at top of apical declivity; apical declivity between united costae usually with short transverse anastomosing costae *Onymacris paiva paiva* (Haag)
- 15 (14) First elytral costa either not uniting with second, which terminates freely before junction of first and third costae, or uniting with second on apical declivity; apical declivity between united costae without transverse costae *Onymacris paiva conjuncta* (Haag)
- 16 (13) Two discal elytral costae, low and with at most small granules; tarsal claws expanded.
- 17 (18) Intercostal elytral sculpture granular but not rugose; mesosternum with tubercular callosity anteriorly; tarsal claws moderately expanded *Onymacris lobicollis* (Fairmaire)
- 18 (17) Intercostal elytral sculpture rugose, especially on apical third; mesosternum without tubercular callosity anteriorly; tarsal claws strongly expanded *Onymacris rugatipennis* (Haag)
- 19 (20) Elytra with white waxy secretion forming a pattern in fresh specimens; hollows of elytral sculpture shallow, flattened at bottom, with dense microgranulation *Onymacris rugatipennis albotessellata* Schulze
- 20 (19) Elytra without white waxy secretion; hollows of elytral sculpture deeper, smooth or with a few microgranules *Onymacris rugatipennis rugatipennis* (Haag)
- 21 (12) Pronotum shiny, with at most fine punctures laterally; elytral disc with three or six distinct costae: where only three are well developed, intercostae usually with at least a faint median longitudinal element of sculpture; mesotibiae strongly bilaterally compressed.
- 22 (23) Metatibiae extremely broad, scarcely or not narrower than femur *Onymacris multistriata* (Haag)
- 23 (22) Metatibiae strongly compressed and slightly widened, but distinctly narrower than femur *Onymacris boschimana* (Péringuey)
- 24 (25) Pronotal disc with lateral edge granular; protarsal claws slightly expanded; legs very long, femora always as long as or much longer than elytral length *Onymacris boschimana subelongata* Gebien
- 25 (24) Pronotal disc with lateral edge punctate, not dull or granular; all tarsal claws slender; legs not exceptionally long, femora a little shorter or longer than elytral length *Onymacris boschimana boschimana* (Péringuey)

- 26 (11) In caudal view, reflected part of elytra almost continuous with disc, separated from it by a fine obsolescent carina; anterior pronotal angles narrow, scarcely produced; elytral disc with six fine costae *Onymacris laeviceps* Gebien
- 27 (1) Integument of elytra at least partly white, with various patterns, or pure white.
- 28 (41) Lateral margin of pronotum complete, finely carinate; elytra smooth, without distinct tubercles.
- 29 (38) Pseudopleural crest complete, sharply carinate over all or most of its length, at most somewhat flattened at middle.
- 30 (31) Elytra pure white, evenly rounded, without trace of lateral costa; claws expanded, foliaceous *Onymacris candidipennis* (Brême)
- 31 (30) Elytra variably coloured, never pure white; usually with a sharp lateral costa indicated; claws slender or slightly expanded *Onymacris langi* (Guérin)
- 32 (33) Elytra pure yellow, apical declivity and reflected parts of elytra sometimes white, occasionally with darker stripes, but these not as described in any of the succeeding couplets; lateral costa developed or not *Onymacris langi cornelii* Penrith
- 33 (32) Elytra variably patterned, but never pure yellow; lateral elytral costa sharp.
- 34 (35) Ground colour of elytra white or yellow; usually a dark line below lateral carina on deflected part of elytra; disc of elytra with two faintly indicated raised costae on either side of suture, corresponding with discal stripes if present; localities north of the Kunene River *Onymacris langi langi* (Guérin)
- 35 (34) Ground colour of elytra white or yellow, no dark line on lateral, deflected part of elytra; if costae indicated on disc of elytra, ground colour of elytra yellow; localities south of the Kunene River.
- 36 (37) Ground colour of disc of elytra yellow, with fine reddish brown longitudinal stripes; costae sometimes indicated *Onymacris langi visseri* Koch
- 37 (36) Ground colour of disc of elytra whitish, with a pattern consisting of yellow sutural and lateral stripes, with two very narrow, usually brownish, discal stripes, sometimes uniting apically; sometimes with a fine stripe between the two discal stripes, or only the lateral and sutural stripes developed *Onymacris langi meridionalis* Penrith
- 38 (29) Pseudopleural crest evanescent, sharply carinate only at humerus and cauda, at most indicated between these points by a faint impressed line.
- 39 (40) Suture, base, and pseudopleural area of elytra white, the rest variably patterned in yellow, frequently with yellow to greenish and black stripes *Onymacris marginipennis* (Brême)
- 40 (39) Elytra white, with three broad, apically tapering pale yellow to tan stripes, the broadest resting over the suture, the other two on the lateral margins of elytra; base of elytra narrowly tan *Onymacris brainei* spec. nov.
- 41 (28) Lateral margin of pronotum indistinct, at most indicated by a faint, impressed line; elytra white, with low, flattened tubercles *Onymacris bicolor* (Haag)

SYSTEMATICS

DESCRIPTIONS

Onymacris brainei spec. nov., Fig. 10 a-c.

Head and thorax, underparts, and appendages black; elytra white, with three broad pale yellow to light tan stripes. Epistome deeply emarginate anteriorly, with scattered round punctures, denser posteriorly, and finer on anterior margin. Frons with scattered punctures laterally. Supra-orbital ridges fine, subparallel, sharply raised only posteriorly, low and evanescent from front margin of eye forwards. Anterior margins of mentum not or scarcely

deflected. Antennae stout, short, third segment a little less than twice as long as second.

Pronotum about one third of elytral length, about one and a half times as wide as long, convex, with a faint transverse prebasal impression on either side. Anterior angles narrowly rounded. Anterior margin carinate laterally. Lateral margins weakly rounded to subparallel, finely carinate. Sculpture of fine scattered punctures on disc and slightly larger, scattered punctures laterally.

Prosternal apophysis deflected, almost meeting mesosternum, apex moderately broadly to broadly rounded, concave. Mesosternum without a raised callosity anteriorly.

Elytra white with a broad pale yellow to tan stripe on middle of disc, covering suture, tapering posteriorly and ending at top of apical declivity; on either side over rudimentary lateral costa a similarly coloured stripe of variable width, also tapering posteriorly and ending before apical declivity; anterior margin (base) of elytra the same colour as stripes. Elytra ovate, sides subparallel or weakly rounded in males, strongly rounded in females. Disc of elytra separated from subvertical sides by a fine evanescent carina. Apical declivity oblique; apex of elytra obtuse to rounded. Suture not impressed. Pseudopleural crest carinate for a brief distance anteriorly and posteriorly, absent over most of its length or indicated only by a faint impressed line. Elytral sculpture smooth to the naked eye; microscopically with a very faint sculpture of scattered punctures set in a faint reticulate background, and slightly raised longitudinal lines.

Legs slender, comparatively short (as in other 'white' species), longer in males; femora, tibiae and tarsi subcylindrical. Tarsi moderately stout, segments short; protarsal segments 1-4 about as long as wide; first metatarsal segment scarcely longer than second. Claws unequal, slender, outer claw slightly longer and wider; tibial spurs broadly spiniform.

Aedeagus straight, simple, heavily sclerotised and dark as in other 'white' species.

MATERIAL. Holotype ♂: 10.5 mm elytral length (Transvaal Museum), Kunene R. east of dunes at 17.12 S., 12.10 E., 13-15.02.1984, on dune hummocks, day, E-Y:2066, leg. M.-L. Penrith, R. Müller. Allotype ♀: 12.7 mm elytral length (Transvaal Museum), data as holotype. Paratypes: 14 ♂, 6 ♀, 9.5-13.5 mm elytral length (Transvaal Museum, 1 ♂, 1 ♀, in State Museum, Windhoek); data as holotype; 3 ♂, 2 ♀, elytral length 10.0-13.5 mm (State Museum, Windhoek), locality as holotype, 24.02.1983, coll. S. Braine, SM H 54976.

REMARKS. The new species differs from the remaining 'white' species of *Onymacris* as follows: from *O. langi* and *O. candidipennis* in lacking a carinate pseudopleural crest and in the deep, pointed clypeal emargination, as well as in the colour pattern and small size; from *O. bicolor* in the colour, the smooth texture of the elytra, and the fully developed pronotal lateral margin; and from *O. marginipennis* in the colour pattern, in the more reduced supra-orbital ridge, more slender legs, and sparser head sculpture.

Onymacris brainei is sympatric at the type-locality with *O. langi cornelii* and *O. bicolor*, and was collected together with these species under the same plants. *O. candidipennis* is present in the same area but mainly on the lower slopes of the dunes towards the Kunene River. The closest relative of *O. brainei*, with which it shares the apically strongly emarginate epistome, is *O. marginipennis*.

The two species are allopatric, but owing to the great difference in colour pattern and the lack of any intermediate specimens I can find no reason to consider *O. brainei* a subspecies of *O. marginipennis*.

All the specimens were collected on dune hummocks with rather dense green vegetation, including the 'narra', *Acanthosicyos horrida*, and flowering succulents.

I have great pleasure in naming this beautiful species after Mr Steven Braine of the Directorate of Nature Conservation, South West Africa/Namibia, who collected and drew my attention to the first specimens, and without whose kind help I could not have collected the rest.

The Status of the Northern Namib Population of Onymacris unguicularis (Haag)

In my revision of the genus *Onymacris* (Penrith, 1975) I did not recognize infraspecific taxa of *Onymacris unguicularis*, and suggested that the observed geographic variation in size and sculpture might be clinal. This is unlikely at least in the case of the northern Namib population (Fig. 6), which is geographically isolated from the southern and central Namib populations by a duneless stretch of nearly 300 km. Populations of *Lepidochora* Gebien and the subgenera *Tarsosis* Gebien and *Cardiosis* Deyrolle of *Zophosis* Latreille from the northern Namib dunes are specifically distinct from their southern congeners (Koch, 1952; Penrith, 1981; Endrödy-Younga, personal communication). I therefore re-examined the material, and also examined additional material of *Onymacris unguicularis* from the whole distribution range. A large amount of fresh material from localities between Bogenfels, south of the type-locality of Gebien's (1938) subspecies *polita*, and Swakopmund and Walvis Bay, had become available. On the basis of this material it was confirmed that the size and sculptural differences noted by Gebien (1938) and Koch (1951) are not significant. The proportion of specimens with stronger granular sculpture on the epistome and generally more impressions on the head increases northwards, but strongly sculptured specimens may be found at the southernmost locality, Bogenfels, and completely smooth-headed ones from Walvis Bay and Swakopmund in the north. The northern Namib specimens, however, always have smooth head sculpture.

Size is normally variable in *Adesmiini*, especially in the drier areas, and this is also the case in *Onymacris unguicularis*. The long series collected at Bogenfels by Koch in 1948 consists, with one or two exceptions, of very small specimens, but much larger ones have been collected there subsequently, as well as very small ones from localities further north. Size may be very dependent on conditions during larval development. Almost all the northern specimens are relatively small, but exceptions were found.

What the re-examination did show was variation in the shape of the epistome. Specimens from the whole southern part of the range (Bogenfels to Sandwich Harbour and Rooibank) have the epistome short and broad, as do the northern specimens, but specimens from Swakopmund and the coastal dunes at Walvis Bay have the epistome produced and narrowed. A few specimens from these localities have a relatively short epistome. Among the large number of specimens from Gobabeb, all the older material had short epistomes, only a few showing a slight tendency to elongation, but in a long series

collected in 1973, specimens with elongate epistomes predominated. It does not seem, therefore, that this variation could be satisfactorily reflected in the nomenclature.

While I cannot on the present evidence separate the northern population more than subspecifically from the southern populations, there may be some justification for giving it subspecific status. Gene flow does not occur between the two populations, but they could be very similar genetically. The northern specimens have consistently a short, broad and smooth epistome, which can also be found in specimens from southern parts of the range, but in the northern specimens the anterior margin of the epistome is generally more deeply indented. Furthermore, in the northern specimens the pronotum is more strongly transverse (the difference is actually more striking to the naked eye than measurements would suggest, cf. Table 1), less arcuate at the middle, and the elytra may be differently shaped (Figure 10 d-f), being less elongate, broader, and more abruptly tapered posteriorly. In addition, the prosternal apophysis in lateral view in all the southern specimens has the apex projecting tooth-like from the subvertical posterior margin, while in most of the northern specimens it does not project. The difference in shape between the northern subspecies and specimens from the southern parts of the distribution range is shown in Fig. 10 d-f.

Table 1
Pronotal measurements in *Onymacris unguicularis*
(PL = pronotal length; PW = pronotal width; d = standard deviation).

Subspecies	PL (mm)	PW (mm)	PW/PL		
			Range	Mean	d
<i>unguicularis</i>	3,8-5,0	5,7-7,7	1,4-1,7	1,5	0,07
<i>schulzeae</i>	2,9-3,9	5,2-6,6	1,5-2,0	1,7	0,12

Schulze (1962, 1964) noted a difference in early stage larvae between *Onymacris unguicularis* from Walvis Bay and Swakopmund and those from the north coast, the larvae of the latter having the ninth abdominal tergite shorter and broader.

In my opinion none of the abovementioned differences are strong or consistent enough to justify separation at species level, but diagnoses of two subspecies are given below.

Onymacris unguicularis unguicularis (Haag) (Fig. 10 d, e)

Elytral length 8,3-16,2 mm. Epistome variable, short and broad to elongate, smooth to strongly granular. Pronotum less transverse, at most slightly more than one and a half times as wide as long, usually about one and one third times as wide as long, middle of anterior margin strongly arcuate. Elytra elongate, distinctly dimorphic, broader in females, generally broadest some-

where behind middle. Prosternal apophysis in profile with apex prominent, projecting tooth-like from subvertical posterior margin.

MATERIAL EXAMINED: 8 ex., 15 mi. N. Luderitz; 28 ex., Swakopmund; 3 ex., Roobank; 1 ex., betw. Luderitz & Spencer Bay, E-Y:274; 13 ex., Anigab dunes, E-Y:298; 121 ex., Bogenfels, and east; 19 ex., Hottentot Bay; 5 ex., Elisabethbucht; 2 ex., Pomona; 10 ex., Grillental, E-Y:1795; 9 ex., Grasplatz; 5 ex., Charlottental; 32 ex., Walvis Bay and N.E.; 15 ex., Gobabeb; 59 ex., Gobabeb, E-Y:448; 1 ex., Chameis; 1 ex., Sandwich Bay; 2 ex., Conception Bay; 19 ex., Spencer Bay, E-Y:282; 4 ex., Spencer Bay, Noordhoek, E-Y:280; 1 ex., betw. Spencer Bay & Saddle Hill, E-Y:282; 22 ex., Blouberg, E-Y:287.

***Onymacris unguicularis schulzeae* subsp. nov., Fig. 10 f.**

Onymacris ex. aff. unguicularis: Schulze 1964: 3.

Elytral length 8.0–15.4 mm. Epistome short, broad, anterior margin deeply emarginate; smooth or (rarely) wrinkled, usually without distinct granular sculpture; sometimes with fine sparse punctures. Pronotum one and a half times to twice as broad as long, anterior margin less strongly arcuate in the middle. Elytra ovate, scarcely dimorphic, generally broadest in front of middle. Prosternal apophysis in profile usually inermous, rarely with apex prominent.

MATERIAL. Holotype ♂: 9.7 mm elytral length (Transvaal Museum), Kaokoveld, dunes 8 mi. E. Torra Bay, isolated barchan dunes. Allotype ♀: 10.9 mm elytral length (Transvaal Museum), data as holotype. Paratypes: 223 ex., 8.0–12.3 mm elytral length (Transvaal Museum): 67 ex., data as holotype, some with additional label 'Nov. 1967, W.J. Hamilton'; 1, Kaokoveld, coastal area btwn Unjab–Hoanib Rivers; 10 ex., Kaokov. coast btwn Koichab–Unjab Rivers, in high dunes; 30 ex., Kaokoveld dunes, 8 mi. E. Torra Bay, xi.1961, C. Koch; 4 ex., Lacrau, 8 mi. N. Foz do Cunene, Angola, 6.iv.1971, H.D. Brown; 96 ex., S.W.Afr., Namib, Unjab Riv. coast, 22.xi.1961, Koch, Dr L. Schulze, insectary no. 282; 12 ex., Unjab Riv., 5 mi. from mouth, x.1965, W.D. Haacke; 3 ex., Foz do Cunene, 8 mi. N., 5 mi. from coast. 57 ex., 10.0–15.4 mm elytral length (State Museum, Windhoek): (12), Torrabaai, 9/10/61; (1) Kunene R.M., S.W.A., SE1711Bc, 27 Sept. 1969, coll. C.G. Coetzee, SM H1472; (1), Foz do Cunene, Angola, SE1711Bc, 25–27 Sept. 1969, coll. C.G. Coetzee, SM H1474; (7), Unjab R.M., SE2013Aa, Kaokoland, 14 Aug. 1973, coll. M.-L. Penrith, J.B.U. Tebje, SM H13454; (4), Torrabaai, SE2013Aa, 19 May 1978, S. Louw, M.-L. Penrith, SM H36508; (4), 45 km S. Kunene R.M., SE1711Db, 18–22 Oct. 1978, S. Louw, M.-L. Penrith, SM H37128; (4), Hunkab R. at 19.49 S., 13.04 E., Skeleton Coast Park, 4–5 Apr. 1979, S. Louw, R. Wharton, SM H38971; (4), Skeleton Coast Park, 17.20 S., 11.48 E., 28 Jan. 1982, J. Irish, SM H50854; (1), Kunene R., 4 km from mouth, Skeleton Coast Park, 17.16 S., 11.47 E., 28 Jan. 1982, J. Irish, SM H50860; (1), 1 km E. Bosluisbaai, Skeleton Coast Park, 17.23 S., 11.46 E., 30 Jan.–2 Feb. 1982, J. Irish, SM H50868; (2), Bosluisbaai, Skeleton Coast Park, 17.23 S., 11.45 E., 30–31 Jan. 1982, J. Irish, SM H50870; (4), 3 km E. Bosluisbaai, Skeleton Coast Park, 17.23 S., 11.47 E., 1–3 Feb. 1982, J. Irish, SM H50883; (2), Skeleton Coast Park, 18.39 S., 12.19 E., 5 Feb. 1982, J. Irish, SM H50886; (1), Hoanib R. at SE1912Bd, Skeleton Coast Park, 1–2 May 1982, S. Braine, SM H54158; (5), Samanab R. at 20.02 S., 13.18 E., Skeleton Coast Park, 2–5 Aug. 1982, M.-L. Penrith, S. Braine, SM H54206; (4), Kharu–Gaiseb R., 11 km S. at 19.58 S., 13.14 E., Skeleton Coast Park, 5 Aug. 1982, M.-L. Penrith, S. Braine, SM H54246; 37 ex., 9.7–12.5 mm elytral length (National Collection of Insects, Pretoria): (36), 10 km SE Torra Bay, Kaokoveld coast, S.W. Afr., 20.iii.1972, H.D. Brown, E. Koster, D. Wessels; (1), Unjab R. Mouth, SE2013Ab, 15–x–1979, E. Holm, C.H. Scholtz.

REMARKS. I have pleasure in naming the new subspecies in honour of Dr Lieselotte Prozesky-Schulze, who has done much valuable work on the larvae of many Tenebrionidae, including *Onymacris unguicularis*.

SCULPTURAL VARIATION IN *ONYMACRIS* *PAIVA*

Several subspecies of *Onymacris paiva* have been described, of which Penrith (1975) recognized two, the nominate subspecies from the northern Namaqualand/Richtersveld coast north of the Buffels River, and *O. paiva conjuncta* from south of the Buffels River. Intensive collecting further south on the Namaqualand coast has yielded series that show further variability in *Onymacris paiva conjuncta*, especially south of the Groen River. These specimens differ from 'typical' *O. paiva conjuncta* in having the first dorsal costa of the elytra either free, not uniting with the others, or uniting with the second, but either very close to the union of the second with the third, or at least well below the start of the apical declivity. The observed range of variation is shown in Fig. 1.

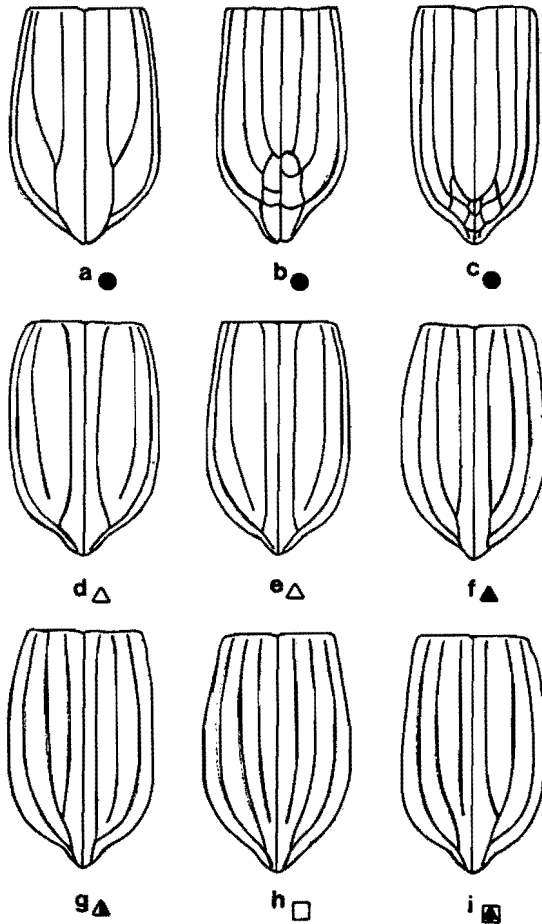


FIG. 1. *Onymacris paiva*. The symbol used in Fig. 2 is indicated with each variation. **a-c.** *O. paiva paiva*. a. Oograbies. b. Holgat. c. Port Nolloth. **d-i.** *O. paiva conjuncta*. d. Buffels River valley (northern part of range). e. Strandfontein farm. f, h, i. Variations found south of the Groen River. g. Variation found from Quaggafontein southwards. All elytra figured are male.

Series collected during the period 1977–1979 south of the Groen River showed a majority of specimens with either of these variations, and a rather high number in which the elytra were asymmetrically costate, i.e. with one elytron showing one variation and the other showing another (Fig. 1 g, i; Fig. 2). A small number of specimens (Dembergsdraai 1, Groenriviermond 3, Kotzesrus 3), showed asymmetrical intermediacy between 'typical' *O. paiva conjuncta* and one or other of the southern variations, i.e. on one elytron the second costa terminated without joining another costa. Such specimens occurred more commonly in the range of typical *O. paiva conjuncta*: Strandfontein farm 15, Gemsbokvlakte farm 5, Outspan farm 1, de Klipheuwel 1, Quaggafontein 3. Two of the specimens from Groenriviermond, and two collected at the southernmost point of the range, Kommandokraal, by the author in 1982, had 'typical' *O. paiva conjuncta* costae. Owing to this variability, the southern form is not given subspecific status. Throughout the subspecies *conjuncta*, the second elytral costa alters in length from south to north, being on average much shorter in the northern (Kleinsee, Buffels River, and Zwartduine) specimens. The form which Koch (1951) described as var. *disjuncta*, in which the first and third costae do not quite unite posteriorly, occurs variably at the northern localities.

The southern population described above represents a considerable southward extension of the known distribution range of the species. The distribution is shown in Fig. 2.

MATERIAL. *Onymacris paiva paiva*: 30 ex., Oograbies, 29.13 S., 17.08 E.; 5 ex., Holgat, 28.56 S., 16.47 E.; 2 ex., Daberas waterhole, 28.19 S., 16.47 E.; 23 ex., Manganese Mine, 28.40 S., 16.58 E.; 6 ex., 3 mi. E. Port Nolloth; 14 ex., Port Nolloth, 29.17 S., 16.51 E.; 3 ex., 4 mi. NE Port Nolloth; 13 ex., Grootmist coast; 15 ex., 18 mi. N. Kleinsee. *Onymacris paiva conjuncta*: 15 ex., Buffels R. nr Grootmist (Grootmist at 29.38 S., 17.05 E.) (type series of var. *disjuncta*); 60 ex., Buffels R. valley, 29.35–36 S., 17.14–17 E.; 1 ex., Buffels R. valley, 29.33 S., 17.27 E.; 13 ex., Kleinsee, 29.40 S., 17.05 E.; 3 ex., Schulpfontein, 30.04 S., 17.13 E.; 12 ex., Zwartduine, 30.00 S., 17.15 E.; 41 ex., Quaggafontein, 30.13 S., 17.33 E.; 16 ex., Hondeklip Bay, 30.20 S., 17.18 E.; 6 ex., Outspan farm, 30.28 S., 17.23 E.; 32 ex., Gemsbok Vlakke farm, 30.30 S., 17.25 E.; 134 ex., Strandfontein farm, 30.33 S., 17.22 E.; 1 ex., de Klipheuwel, 30.40 S., 17.35 E.; 12 ex., Dembergsdraai farm, 30.47 S., 17.43 E.; 6 ex., Groenriviermond, 30.50 S., 17.36 E.; 1 ex., Island Point, 30.52 S., 17.39 E.; 76 ex., Kotzesrus farm, 30.57 S., 17.50 E.; 1 ex., Titiesbaai, 3 km NW, 31.10 S., 17.46 E.; 7 ex., Katdoringvlei, 31.07 S., 17.52 E.; 13 ex., Rooidam farm, 31.04 S., 17.48 E.; 4 ex., Soutpan dunes, 31.15 S., 17.52 E.; 1 ex., Kommandokraal, 1979, 31.30 S., 18.12 E.; 2 ex., Kommandokraal, 1982, 31.30 S., 18.12 E.; 10 ex., Graskom, 30.18 S., 17.23 E., 1982.

REVISED DISTRIBUTION OF *ONYMACRIS* SPECIES

Since my previous revision (Penrith, 1975), further collecting has extended the ranges of several species of *Onymacris*. Revised distribution maps are given in Figs 2–7. These include southward extensions of the ranges of *O. candidipennis*, *O. marginipennis*, *O. rugatipennis*, *O. laeviceps*, *O. hottentota*, and *O. paiva*, and a westward extension of *O. multistriata*.

NOTE ON THE STATUS OF *ONYMACRIS CANDIDIPENNIS*

During a collecting trip to the site at the Kunene River east of the dune sea where *Onymacris brainei* was collected, a mixed population of *Onymacris langi cornelii* and *O. candidipennis* was sampled. *Onymacris candidipennis* is here recorded for the first time south of the Kunene River; at the site investigated, this

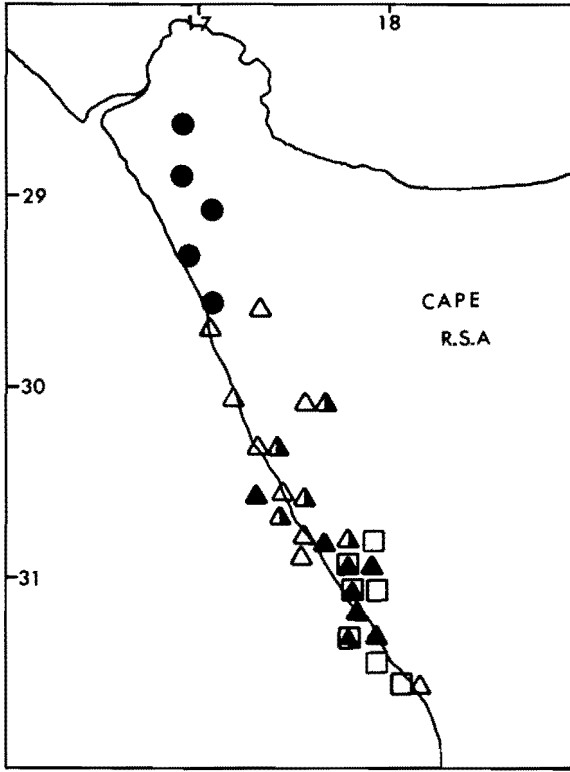


Fig. 2. Distribution of *Onymacris paiva*. The symbols used are as indicated in Fig. 1.

species is apparently largely confined to the lower dune slopes, towards the river. The sand in this region has partly covered the hills on the south bank, and falls more or less precipitously to the river over a distance of about 2 km. *O. langi cornelii* is common throughout the site area. On the lower slopes towards the river, in the zone in which *O. candidipennis* and *O. langi* occur together, specimens were collected which cannot be assigned to either *O. candidipennis* or *O. langi*. These specimens range in colour from white to yellowish, and features such as the lateral elytral costa of *O. langi* (which is often lost in western coastal specimens of *O. langi* but is consistently developed in the inland specimens, and the expanded tarsal claws of *O. candidipennis*, are variably developed, individuals possessing different combinations of the characters of the two species. At the same time 'typical' *O. candidipennis* and *O. langi* were taken. Since the problem of intermediate specimens only became apparent when the material was mounted and examined in Pretoria, no attempt was made at the site to assess the relative proportions of 'typical' and intermediate specimens, but the latter are certainly very numerous.

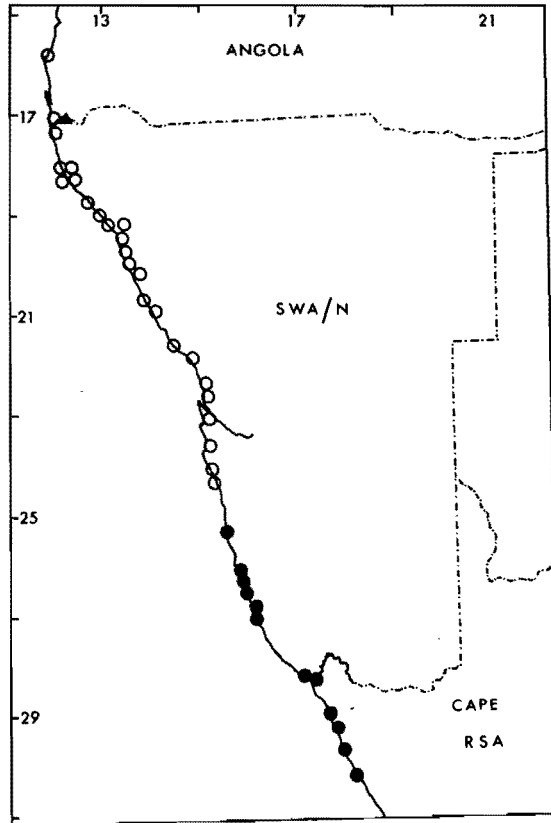


Fig. 3. Distribution of *Onymacris marginipennis* (open circles), *O. brainei* (closed triangle), *O. hottentota* (closed circles).

The situation allows two explanations. The two taxa are in contact over a limited area, possibly as a result of recent sand movements. The first explanation is that the specimens are interspecific hybrids, as discussed by Penrith (1975) in connection with populations of *Onymacris candidipennis* and *O. marginipennis* in limited contact in the region of the Kunene River mouth. The second explanation, which I prefer in view of the rather high occurrence of intermediate specimens, is that *O. candidipennis* is actually genetically compatible with and therefore only subspecifically distinct from *O. langi*, so that re-establishment of a contact zone immediately resulted in extensive cross-mating. Until experimental evidence decides the question either way, the specific status of *O. candidipennis* is retained.

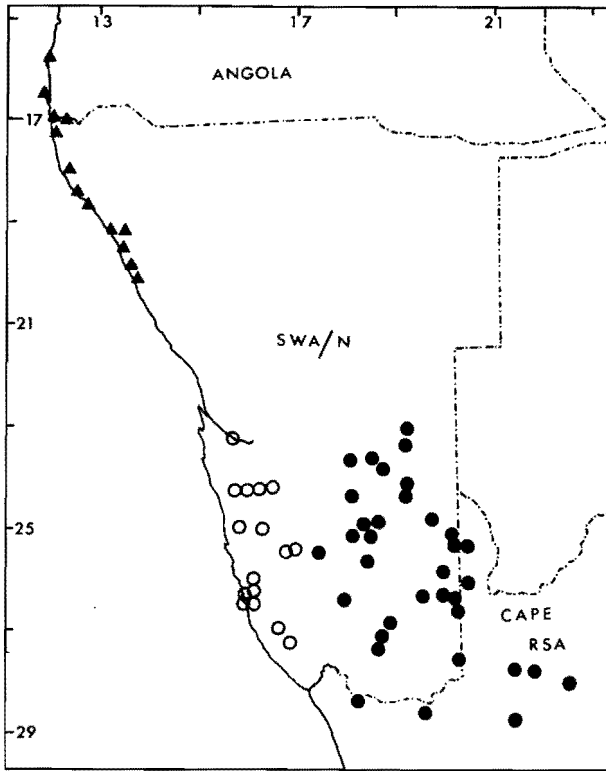


FIG. 4. Distribution of *Onymacris bicolor* (closed triangles), *O. laeviceps* (open circles), *O. multistriata* (closed circles).

RELATIONSHIPS IN THE GENUS *ONYMACRIS*

The cladogram presented for the 14 species (Fig. 9) is based on 23 characters, including the two shared apomorphies of the genus (Fig. 8). Originally more than 30 characters were considered, but several had to be rejected, some owing to suspected parallelism and others because the direction of development could not be ascertained. Characters suspected of parallelism were usually adaptations associated with deep-sand habitats, in particular vegetationless dunes. These rejected characters include expansion of the tarsal claws and length of the tarsal setation. While similar adaptations to a similar or identical habitat are not necessarily considered to demonstrate very close relationship, on the other hand two representatives of a monophyletic group which differ rather strongly in adaptive or non-adaptive characters but occupy similar or identical habitats are considered to be unlikely to be very closely related. The investigation has thus been approached from the point of view of a cladistic analysis and also of a comparison of species from similar habitats. The polarity of characters for the cladistic analysis was determined by out-

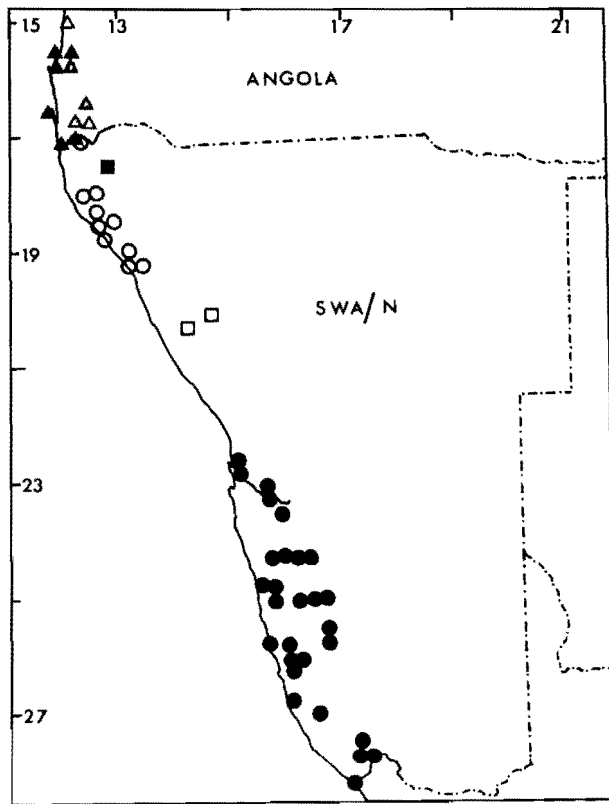


FIG. 5. Distribution of *Onymacris langi langi* (open triangles), *O. langi cornelii* (open circles), *O. langi visseri* (closed square), *O. langi meridionalis* (open squares), *O. candidipennis* (closed triangles), *O. plana* (closed circles). No distinction is made between the subspecies of *O. plana*.

group comparison with the related genera *Physadesmia* and *Eustolopus*, as well as with more plesiomorphic although evidently not directly ancestral groups such as *Renatiella* Koch and *Adesmia* Fischer. Characters for which the polarity could not be determined were rejected, for example characteristics of the pro-sternal apophysis and the development or lack of a callosity on the mesosternum. These characters vary without pattern throughout the tribe.

The characters used, their apomorphic states, and the suggested relationships of the species are shown in Figs 8 and 9. In Fig. 9 the numbers of shared apomorphies are shown in squares, while unique apomorphies are enclosed in circles. A solid circle on a branch indicates the existence of an early stage of a transformation towards an apomorphic character state.

On the present analysis, two major lineages within *Onymacris* emerged (Figs 8, 9). The first consists of the species *Onymacris lobicollis*, *O. rugatipennis*, *O. paiva*, *O. boschimana*, *O. multistriata*, and *O. laeviceps*, and the second of *Onymacris hottentota*, *O. plana*, *O. unguicularis*, and the five 'white' species, *O. langi*, *O. candidipennis*, *O. marginipennis*, *O. brainei*, and *O. bicolor*. In each lineage there is a

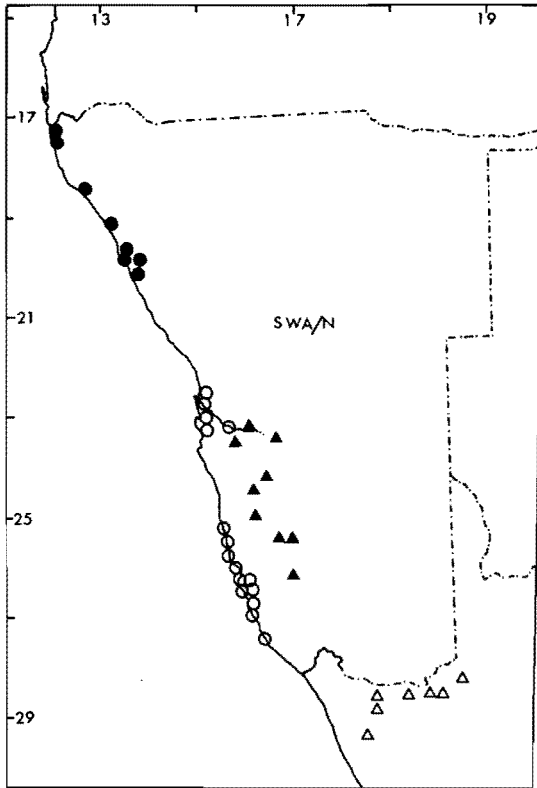


FIG. 6. Distribution of *Onymacris unguicularis unguicularis* (open circles), *O. unguicularis schulzeae* (closed circles), *O. boschimana boschimana* (open triangles), *O. boschimana subelongata* (closed triangles).

progression towards adaptation to an ultrapsammophilous habitat, *Onymacris laeviceps* in the first lineage and *O. unguicularis* and *O. bicolor* in the second being the species that habitually or invariably live on vegetationless dunes. The species *O. unguicularis* and *O. laeviceps* show a strong morphological similarity in the adults, and I assumed a close relationship between them (Penrith, 1975), as did Schulze (1962, 1964) as a result of her studies of the larvae. However, this analysis of relationships based on adult characters suggests that the two species belong to different lineages, and that the resemblance between the adults, and presumably the larvae, is the result of convergence due to adaptation to a new and identical habitat, i.e. barren dunes. This will be discussed in greater detail below.

In the first lineage, all the species have the metatarsi bilaterally compressed. *Onymacris lobicollis* and *O. rugatipennis* have lost the third, or outer, discal clytral

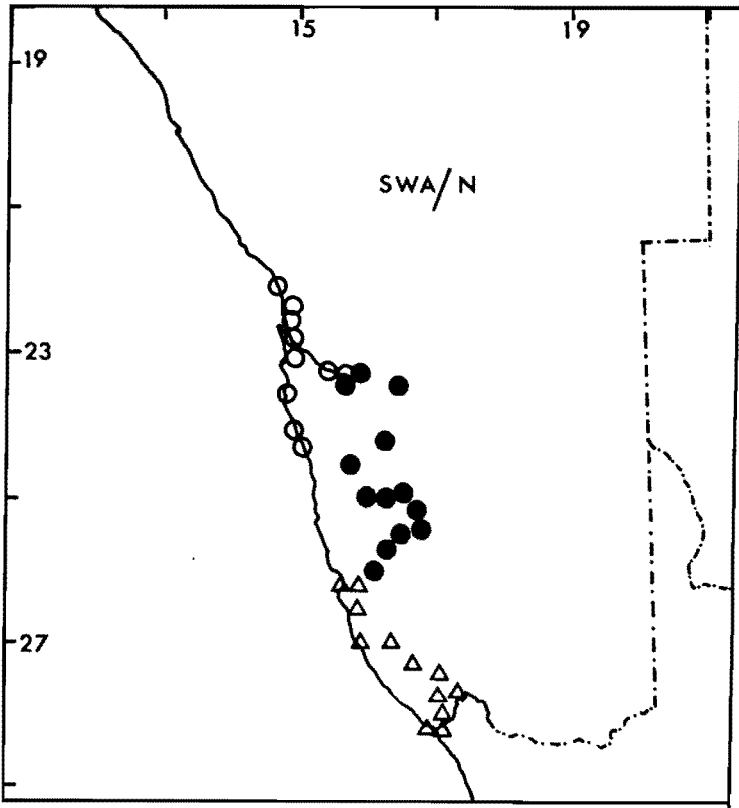


FIG. 7. Distribution of *Onymacris lobicolis* (open triangles), *O. rugatipennis rugatipennis* (open circles), *O. rugatipennis albofessellata* (closed circles).

costa; they are clearly sister species and are very similar in appearance. The remaining species of the lineage share an apomorphy in having the eye strongly sexually dimorphic, being very much larger and with the lower part better developed in males. This phenomenon also occurs in some species of *Stenocara*; a weak degree of ocular sexual dimorphism occurs variably in many Adesmiini. The strong ocular dimorphism shown by *O. paiva*, *O. boschimana*, *O. multistriata*, and *O. laeviceps* is considered likely to be a unique apomorphic development within *Onymacris*, and its absence or weak development in the other species to be plesiomorphic rather than by reduction. *O. boschimana*, *O. multistriata*, and *O. laeviceps* are united by what is considered the apomorphic development of a secondary costa between each pair of primary elytral costae. This is not always distinct in *O. boschimana boschimana*; it is presaged in *O. paiva* by the variable development of a row of rather widely spaced intercostal granules. It remains uncertain whether this character direction has been correctly determined, since the Adesmiini show a wide variety of sculptural variation, but

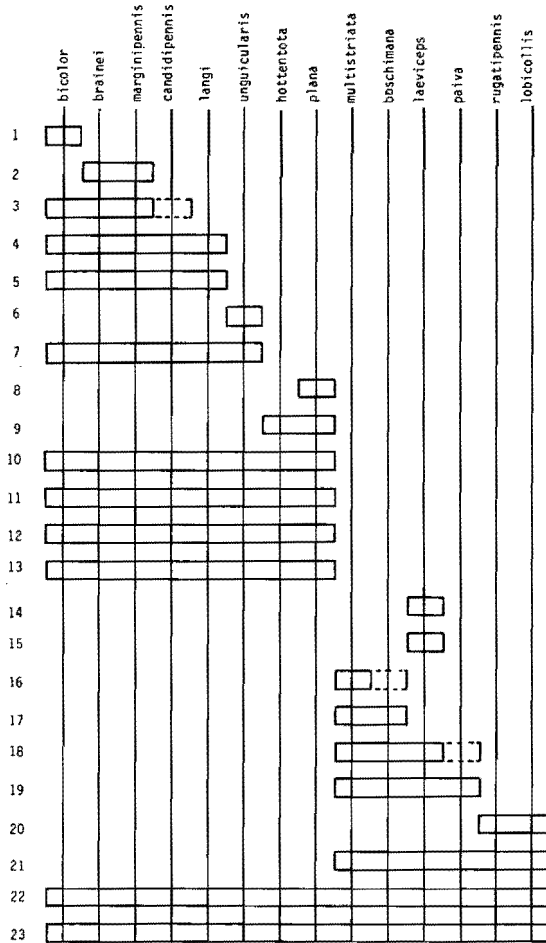


FIG. 8. Tabular representation of the shared apomorphies on which Figure 9 is based. The apomorphic states of the 23 characters used are as follows: **1.** Pronotal lateral margin lost. **2.** Epistome anteriorly with deep v-shaped median emargination. **3.** Pseudopleural crest strongly reduced/lost. **4.** Elytra 'white'. **5.** Aedeagus heavily sclerotised. **6.** Profemur and protibia with setose brushes in male. **7.** Elytral sculpture lost. **8.** Male broader than female ('plana'-shaped). **9.** Pronotum with two round impressions. **10.** Mesosternum broader. **11.** First metatarsal segment scarcely longer than next. **12.** Elytra without distinct microgranulation. **13.** Clypeus forming angle with gena at sulcus. **14.** Anterior pronotal lobes not produced. **15.** Protibia with long bristles on inner edge in both sexes. **16.** Metatibia broad, strongly compressed. **17.** Mesotibia strongly compressed. **18.** Elytral costae doubled. **19.** Eyes strongly sexually dimorphic. **20.** Elytral costae reduced to two. **21.** Metatarsi compressed. **22.** First metatarsal segment shorter than following two together. **23.** Tarsal claws and spurs long.

three primary elytral costae (excluding the lateral costa) seems likely to have been the plesiomorphic state, as it is recurrent in most of the lineages. In the tribes Adesmiini and Zophosini the number of costae on the elytra seems to

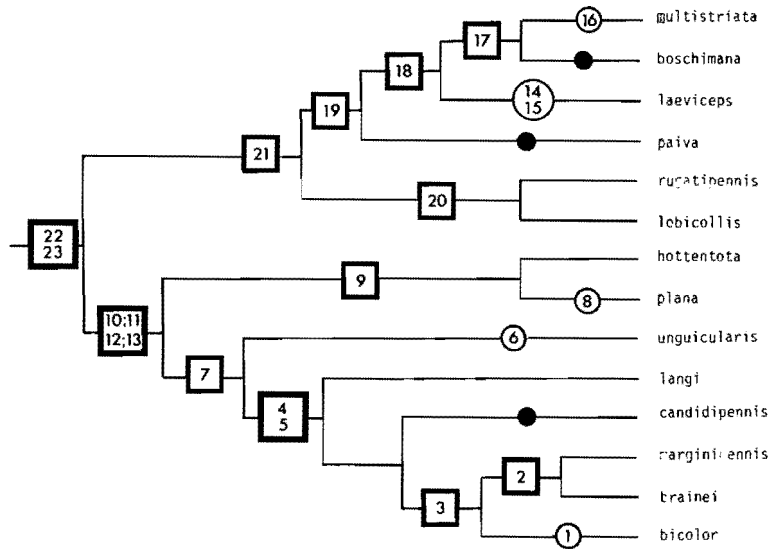


FIG. 9. Cladogram of hypothetical relationships within the genus *Onymacris*. Figures enclosed in squares indicate by numbers the shared apomorphies on a branch; figures enclosed in circles indicate by number unique apomorphies. Solid circles indicate a transitional state of a character which is expressed in the apomorphic state in related species.

bear no direct relation to their derivation from the ten primary rows primitive to tenebrionid clytra (Watt, 1974), in the sense that a higher number of costae should be plesiomorphic; no recognizable traces of the punctate primary rows are found in any of their representatives (nor in any of the subfamily to which they belong, Watt 1974). A further apomorphic state in their lineage shared by *O. boschimana*, *O. multistriata*, and *O. laeviceps* is the fine and smoothed pronotal sculpture; this has not been included in the figures, as it is highly repetitive in the Adesmiini and even in *Onymacris*, but in a single lineage it can be adduced as additional evidence. *O. multistriata* and *O. boschimana* share strongly compressed and broad meso- and metatibiae. The condition is much more pronounced in *O. multistriata* than in *O. boschimana*. The metatibia is compressed to a varying degree in many species of *Onymacris*, particularly in the related *O. paiva*, but it is clearly broader in *O. boschimana* and particularly *O. multistriata*, and only in these two species is the mesotibia modified. A similar tibial modification occurs in two Palearctic groups of Adesmiini, the subgenera *Oteroscelis* Solier and *Oteroscelopsis* Koch of *Adesmia*, which are obviously not closely related to *Onymacris*.

Onymacris laeviceps is the most psammophilous species of the lineage, occurring regularly on vegetationless dunes although it is not restricted to them, occurring also on vegetated dunes. In its bullet-shaped body, with a relatively long and voluminous pronotum, it resembles *O. unguicularis*, a species of the

other lineage that is confined to vegetationless dunes. The two are frequently taken together. A comparison of the two species shows that there are important differences, including characters associated with psammophily. In *O. unguicularis* the tarsal and antennal segments are short and compact, while in *O. laeviceps*, with the exception of the protarsi, they are long and slender. The claws of *O. unguicularis* are strongly expanded and foliaceous, while in *O. laeviceps* they are relatively slender. The clypeus is consistently elongate in *O. laeviceps*, and the elongation has taken place in front of the clypeal sulcus, whereas in *O. unguicularis* it is elongate only in a certain part of the distribution range, and elongation has taken place from the clypeal sulcus. The supra-orbital ridge is low and curved in *O. laeviceps*, sharp and straight in *O. unguicularis*. In *O. laeviceps* the inner edge of the protibia of both sexes bears a fringe of long, but not dense setae, while in *O. unguicularis* the female has a row of moderate, sparse setae (as in most species), while the male has a dense setose brush, the undersurface of the femur of males also being furnished with a dense setose brush. In *O. laeviceps* the body shape shows the normal sexual dimorphism of Adesmiini, the females being obviously broader than the males, while in *O. unguicularis* this dimorphism is reduced, and there is much overlap (see Penrith, 1975: table 1). The eyes of *O. unguicularis* are rather small and of the same size and shape in both sexes, while in *O. laeviceps* the eyes are very large, and in males very much larger than in females. In *O. laeviceps* the anterior pronotal angles are strongly reduced. The elytral sculpture of *O. unguicularis* is very strongly reduced, and where traces remain on the apical declivity there is no sign of secondary costae having existed. When these differences are considered in conjunction with the apomorphies shared on one hand by *O. laeviceps* with the species of the first lineage, and on the other hand by *O. unguicularis* with the representatives of the second lineage (which is discussed below), there seems to be little doubt that *O. laeviceps* and *O. unguicularis* are superficially convergent representatives of different lineages.

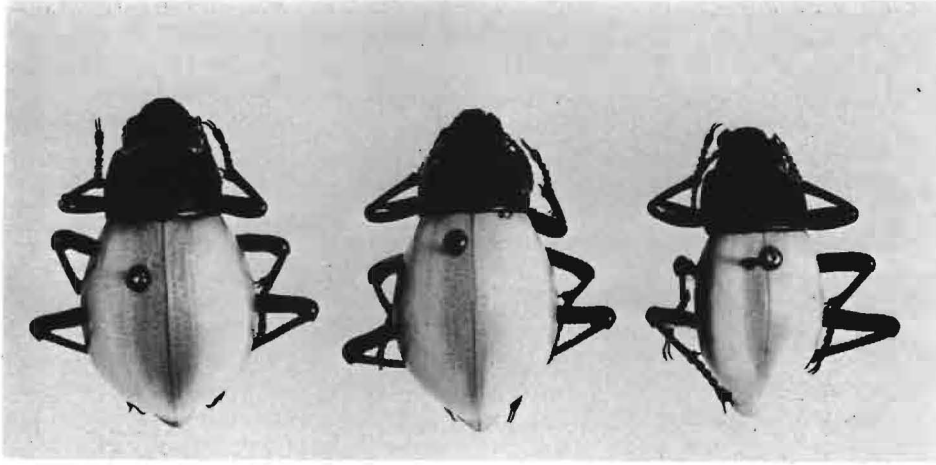
The second lineage, consisting of *O. hottentota*, *O. plana*, *O. unguicularis*, and the five 'white' species, is characterised by the relatively broad separation of the mesocoxae, the strong angle formed at the clypeal sulcus between the gena and the side of the epistome, and the short tarsal segments, the first metatarsal segment being scarcely or not longer than the second. An additional character, which has been used in the cladogram although its validity is possibly arguable, is the lack of the microgranular elytral sculpture that is usually characteristic of species that normally show a waxy bloom in life, such as is found in at least some populations of all the representatives of the first lineage. Dr E. McClain and her co-workers (1983) have shown that the development of a waxy bloom in species of *Onymacris* and other Tenebrionidae can be a response to low humidity, as has Hadley (1979) for the unrelated American species *Cryptoglossa verrucosa* (Le Conte) (Tribe Cryptoglossini), which also has microgranules from which the waxy bloom is secreted. *O. plana* can be induced to produce a waxy bloom by desiccation, although in normal conditions it rarely shows a bloom observable to the naked eye. Specimens of *O. hottentota* with a waxy bloom are not unknown. On the other hand, *O. multistriata* only rarely produces a waxy bloom under natural conditions; specimens of *O. lobicollis* from the course of the Orange River and the nominate subspecies of *O. rugatipennis*, which occurs along the Kuiseb River, do not develop a waxy bloom under natural conditions. In *O. boschimana* the bloom is confined to a band

around the elytra; and in *O. laeviceps* and *O. paiva* there is frequently no bloom. Nevertheless, the reduction or loss of microgranular sculpture, whether or not the bloom is affected thereby, is considered a useful supporting apomorphy for this lineage.

In the second lineage, *Onymacris hottentota* and *O. plana* form a well-defined species pair, sharing a particular, almost identical shape of pronotum that excludes them from the ancestry of any of the other species. Their facies is similar, but *O. hottentota* is a species of the coastal dune hummocks, while *O. plana* is a highly specialized dune dweller, although it is normally associated with vegetation (Koch, 1962; Holm and Scholtz, 1980). *O. plana* exhibits a peculiar form of sexual dimorphism in which the male is flattened and broader than the female. The claws are broad and foliaceous. The placing of *O. plana* in a different lineage from *O. rugatipennis* might appear to contradict the results of Lockey (1982a, b), working on cuticular hydrocarbons, which indicated a closer relationship between *O. plana* and *O. rugatipennis* than between either of them and *O. marginipennis*. However, he did point out that *O. plana* and *O. rugatipennis* were not very similar to one another, and the relative similarity that he found may indicate that both the black species are closer to the plesiomorphic state in the composition of their cuticular hydrocarbons than the 'white' *O. marginipennis*. The expansion of this line of study to include as many species as possible would be very valuable.

Onymacris unguicularis has been discussed in detail above, in conjunction with *O. laeviceps*. It shares with the 'white' species the virtual loss of the elytral sculpture in addition to all the other characteristics shared by all the members of the second lineage.

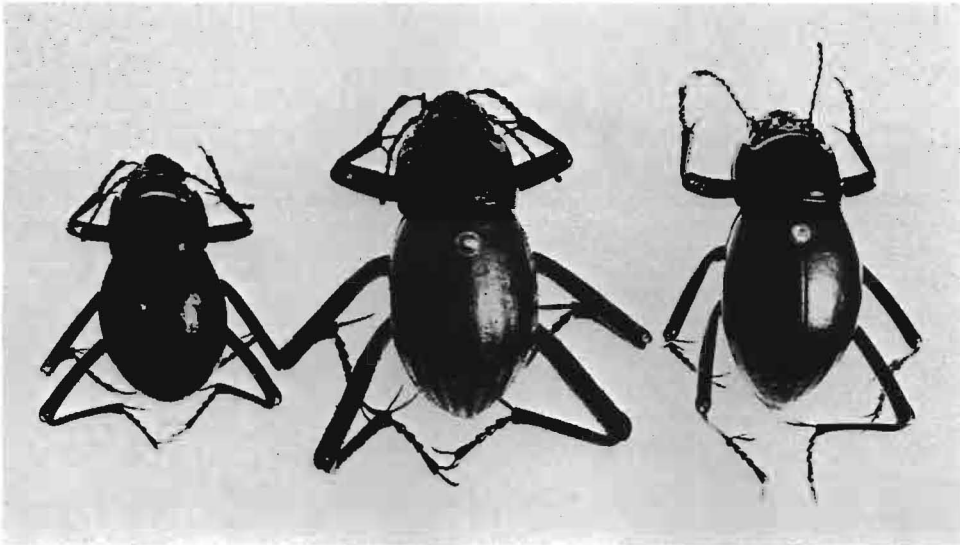
The 'white' species are united by the loss of pigmentation in the elytra and the dark sclerotin of the aedeagus. The loss of elytral pigmentation is considered a unique apomorphy in *Onymacris*, although it does occur in another lineage of the Adesmiini and in the subgenus *Calosis* Deyrolle of the Zophosini. The five 'white' species of *Onymacris* are extremely closely related, and hybridisation between two of them has been noted (see Penrith, 1975). The most plesiomorphic is considered to be the widespread and extensively subspeciated *O. langi*, in which the pseudopleural crest is complete. This is usually also the case in *O. candidipennis* (which, as mentioned above, may not be specifically distinct from *O. langi*), but occasional specimens show flattening and reduction of the pseudopleural crest at the middle. For this reason *O. candidipennis* is placed between *O. langi* and the species group with the pseudopleural crest evanescent, consisting of *O. marginipennis*, *O. brainei*, and *O. bicolor* in the cladogram. In the last three species the pseudopleural crest is strongly reduced, being indicated at most by a fine impressed line except at the humerus and caudally. In *O. marginipennis* and *O. brainei* the anterior margin of the clypeus has a deep v-shaped emargination; in the other 'white' species it is normally subtruncate, or (occasionally in *O. langi*) broadly emarginate. *O. bicolor* has lost the lateral pronotal margin. In *O. marginipennis*, *O. brainei*, and *O. bicolor* the supra-orbital ridge is variably reduced. An alternative to the diagram presented would be to unite *O. langi* and *O. candidipennis* in one group on the assumption that the ability to reach an unusually large size demonstrated by these species is a shared apomorphy. If, as I suspect owing to the Kunene River populations, *O. langi* and *O. candidipennis* are only subspecifically distinct from one another, this would certainly be the correct version of the cladogram.



a

b

c



d

e

f

FIG. 10. **a-c.** *Onymacris brainei* sp. n. a. Male. b, c. Females. **d-f.** *Onymacris unguicularis*. d. *O. unguicularis unguicularis*, Bogenfels (southernmost locality). e. *O. unguicularis unguicularis*, Swakopmund (central part of range, northernmost limit of nominate subspecies). f. *O. unguicularis schulzeae* subspec. nov., Torra Bay E.

The genus *Onymacris* is unusual among the southern African Adesmiini in showing a strong preference for sandy habitats. All the species are psamophilous. The more plesiomorphic species all occur on sandy hummocks or vegetated dunes, at least *O. boschimana subelongata* and *O. langi* occurring on sandy plains as well. In each lineage, highly derived species have evolved that occur either usually or invariably on vegetationless dunes. It is likely that all the lineages started to develop in coastal or riverine hummocks (a frequent or invariable habitat of *O. lobicollis*, *O. paiva*, *O. hottentota*, *O. marginipennis*, and *O. langi*), with subsequent radiation as aridity caused greater accumulations of sand.

None of the extant species would qualify as an ancestor of *Onymacris*, as might be expected. Such an ancestor would have been a black, long-legged adesmiine with the first metatarsal segment shorter than the following two together, although distinctly longer than the second; the elytra would have had three costae on the disc as well as a strongly developed lateral costa. The claws would have been slender but long, and the tibial calcaria elongate. It seems possible from the present-day distribution of the more plesiomorphic species (*Onymacris lobicollis*, *O. boschimana*, *O. paiva*, *O. hottentota*) that the ancestral stock may have developed in the western regions of the Orange River and northern Namaqualand, from where its descendants spread northwards with the northward-spreading sand. The species *O. paiva* and *O. hottentota* would have spread southwards from this area.

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