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## THE SPECIES OF *COMICUS* BRUNNER V. WATTENWYL (ORTHOPTERA: SCHIZODACTYLIDAE) WITH A DISCUSSION OF THEIR ORIGIN

by

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(With 59 figures)

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### ABSTRACT

**Irish, John. 1986.** The species of *Comicus* Brunner v. Wattenwyl (Orthoptera: Schizodactylidae) with a discussion of their origin. *Navors. nas. Mus. Bloemfontein* 5(10): 253-276. The seven known species of *Comicus*, five of which are new, are described and their distributions mapped. The Schizodactylidae is considered to be a monophyletic unit, with *Comicus* being an apomorphic derivative of *Schizodactylus*. A cladogram for *Comicus* species is provided, and their evolution is discussed in relation to the evolution of the psammophilous western southern African faunal component. (*Comicus*, Schizodactylidae, Namib).

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## INTRODUCTION

The gryllacridoid family Schizodactylidae Karny, 1937 includes two genera. *Schizodactylus* Brullé, 1935, with six described species, ranges from Turkey to Burma, and *Comicus*, with seven species of which five are newly described here, is found in western southern Africa. Brunner v. Wattenwyl (1888) described the type-species of *Comicus*, *C. capensis*, and Ramme (1931) added *C. arenarius*. Two other *Comicus* spp are listed in the literature. *C. inexpectatus* Werner 1901, from Turkey, was transferred to a monospecific genus *Dactylocomicus* by Karny (1931) but Uvarov (1952) has shown it to be based on an immature *Schizodactylus*. *C. namibensis* Lawrence 1959 is a *nomen nudum*.

The following institutional abbreviations are used:

- AM — Albany Museum, Grahamstown, South Africa; Dr F. Gess.
- BMNH — British Museum (Natural History), London; Mrs J. Marshall.
- NCI — National Collection of Insects, Pretoria; Mr R. Oberprieler.
- NM — National Museum, Bloemfontein; Dr S. Louw.
- SAM — South African Museum, Cape Town; Dr V. Whitehead.
- SM — State Museum, Windhoek, South West Africa.
- TM — Transvaal Museum, Pretoria; Dr M-L. Penrith & Mr R. Toms.
- ZMB — Zoologisches Museum, Humboldt Universität, Berlin; Dr K. Günther.

## SYSTEMATICS

Because of the uniformity of *Comicus* spp. with regard to most characters, a detailed description is given only for the genus, followed by a discussion of characters which show interspecific variation. Only these latter are mentioned in specific descriptions.

**Genus *Comicus* Brunner v. Wattenwyl**

*Comicus* Brunner v. Wattenwyl, 1888: 386.

Type-species: *C. capensis* Brunner v. Wattenwyl (by original monotypy)

**Description**

(Orthoptera : Ensifera : Gryllacridoidea : Schizodactylidae)

Total body length up to 25 mm, usually less; length of metafemur up to 16 mm. Colour usually pale yellowish ranging to dark brown in some specimens. Eyes black, kidney-shaped. Ocelli absent.

Antennae very long, up to five times body length when intact. Torulus well developed. Scapus large, bulbous, elongate. Pedicellus short, as wide as scapus. First flagellar annulus about half wider than those following on it. Flagellum often with faint annulations of brownish pigment alternating with narrow unpigmented rings.

Frontal ridge visible as a short groove flanked by two low ridges, situated dorso-medially of the torulae. Vertex with two shallow longitudinal depressions between the dorsal margins of the eyes, usually filled with faintly rugose sculpture, into which the antennal bases fit when the antennae are folded back. Occipital suture a strongly sclerotised ridge, dorsally interrupted opposite the inner margins of the eyes. Sclerotisation of anterior tentorial pits visible through integument. Two very distinct sub-ocular pigment spots are often present. Epistomal suture medially interrupted.

Distal clypeus capable of being retracted under its proximal part, pulling the labrum upwards while feeding. A transverse ridge just under the epistomal suture, and a median furrow on the clypeus, mark the places where the clypeus folds during retraction. Labrum subcordate, apically incised, usually with a few sparse setae centrally on the disc and a sparse marginal setal fringe. Mandibles large; inner edges and apices heavily sclerotised, with several teeth.

Maxilla: Palp with five segments, the tip of the apical segment subclavate. Inner side of lacinia with a brush of short stout setae, terminating in the sclerotised inner lacinial uncus. Outer lacinial uncus long, sclerotised, with a bifurcated or notched tip (simple in one species). Galeae subclavate, overlying laciniae, with a sparse outer fringe of long stout setae. Labium: Palp with four segments, the apical one short and subclavate.

Paraglossae large, thick, with sparse outer fringes of stout longish setae, corresponding to those on the galeae. Glossae small.

Thoracic sterna with mesosternal interspace open, metasternal interspace closed. Pronotum as long as meso- and metanota together, with anterior and posterior margins raised and lightly sclerotised, and often with a fringe of very short, stiff setae. Lateral lobes of pronotum rounded to truncate. Meso- and metanota simple, transverse. Apterous.

Legs: Pro- and mesotibiae and metafemur inflated to a greater or lesser degree. Femorae unspined. Pro- and mesotibiae (Figures 1-22) each with four apical spurs, of which some are often more developed than others. These spurs apically sclerotised. Metatibia apically with

three pairs of dactyliform spurs (Figures 23 & 24) which are apically sclerotised and carry a marginal setal fringe each; the apex of the proximal inner spur hooked. Pro- and mesotibiae with or without small subapical spines. Metatibia with or without one or two rows of dorsal spines along its length, of which the distal spines are usually longer than the proximal ones. Tarsi (Figures 23 - 25) with four tarsomeres and a well-developed pretarsus. First (proximal) tarsomere longest; simple on pro- and mesotarsi, but with a pair of setal-fringed lateral appendages halfway along its length on metatarsus. Second and third tarsomeres short, each with a pair of clavate, setated lateral appendages. Fourth tarsomere slender, simple. Pretarsus in the form of a pair (Figures 23 & 24) or a single (Figure 25) slender setated filament, shorter on the pro- and mesotarsi, but elongate and often asymmetrical on the metatarsus; each tipped by a minute claw.

Abdomino-femoral stridulatory mechanism present, consisting of an inner ridge on the metafemur, and oblique rows of tubercles on the lateral hind margins of the anterior abdominal tergites; best developed on the second and third abdominal segments (Mason 1961). Both sexes with one pair of setated cerci (Figures 34-42), those of the male in some species with a knob on the inner side. Subgenital plate (Figures 43-56) apically sclerotised and with a species- and sex-specific shape in fully mature individuals. Paraprocts visible as two sclerotised hooks, medial to the cercal bases. No externally visible primary genitalia in either sex.

#### Characters of *Comicus* species

**Tibial spination.** The number of spines on the tibiae show little intraspecific variation. Where this is present, it shows up as asymmetry of spination in limited numbers of individuals. Broken spines leave small scars. Most individuals can be readily identified by referring to tibial spination alone.

**Cerci.** The male cerci in some species carry knobs of which the size and position is intraspecifically stable. Immature males lack these knobs, and in one species there is some age-related variation in the general appearance of the cerci.

**Subgenital plates.** The eighth abdominal sternum in the female, and the ninth in the male, has a shape characteristic for each sex of each species in fully mature individuals. Young nymphs have simple, posteriorly straight subgenital plates, which acquire their characteristic shape step by step towards maturity. Thus, different developmental stages of different species may have similarly shaped subgenital plates. In the absence of both wings and external genitalia, one is left with but the subjective character of size to judge an individual's maturity, robbing the subgenital plate of much of its potential usefulness. Also, in dry material dessiccation distorts the shape of the subgenital plate. Figures 43-56 were done from the largest available wet preserved specimens, but should not be regarded as the only shapes possible even for apparent adults of a particular species.

**Other.** Both the tip of the outer lacinial uncus and the pretarsal morphology were found to be aberrant in the same one species, but uniform in all the others. The normally invaginated male phallic complex, which has proved very useful for separating species in the related family Rhabdophoridae Kirby, 1883, may yield more distinguishing characters in future. The presence of invaginated male genitalia in *Comicus* was verified by dissection, but could not be utilised because evagination of the phallic complex is best done in live material, of which none was available for this study. All other characters were found to be either constant or to show overlapping degrees of variation.

Key to the species of *Comicus*

(Note: Do not confuse tibial spurs with tibial spines)

1. Metatibia with three to eight dorsal spines (Figures 27-33) ..... 2  
— Metatibia completely spineless (Figure 26); Angolan Namib *C. cabonegrus* spec. nov.
2. Metatibia with three to five spines, arranged in a single row (Figures 27, 29, 30, 32, 33) 4  
— Metatibia with four to eight spines arranged in two rows of which the inner row usually consists of four spines, and the outer row of usually three and sometimes only one spine (Figures 28 & 31) ..... 3
3. Protibia with two to three spines (Figures 9 & 10); mesotibia with one spine only; Kalahari sand system ..... *C. calaharicus* spec. nov.  
— Pro- and mesotibiae completely spineless (Figures 5 & 6); main Namib dune sea ....  
..... *C. calcaris* spec. nov.
4. Protibia with two to four, mesotibia with one to two spines ..... 5  
— Pro- and mesotibiae completely spineless (Figures 3, 4, 15, 16); coastal Namib desert  
..... *C. arenarius* Ramme
5. Mesotibia with one spine (Figures 17-20); protibia with two to three spines (Figures 7, 8, 11, 12) ..... 6  
— Mesotibia with two spines (Figures 21 & 22); protibia with four spines .....  
..... *C. cavillorus* spec. nov.
6. Protibia with two to three, usually three, spines (Figures 11 & 12); mesotibial spine more proximal, tip not reaching to level of base of nearest tibial spur (Figures 19 & 20); sandier habitats ..... *C. capensis* Brunner v. Wattenwyl  
— Protibia with two spines (Figures 7 & 8); mesotibial spine more distal, tip reaching to level of base of nearest tibial spur (Figures 17 & 18); less sandier to rocky habitats.  
..... *C. campestris* spec. nov.

*Comicus capensis* Brunner v. Wattenwyl*Comicus capensis* Brunner v. Wattenwyl, 1888 : 387; Karny 1929 : 147 (p.p.); Ramme 1931 : 165 (p.p.).

Length of metafemur up to 11 mm (females) and 9,5 mm (males). Protibia with three subapical spines (Figures 11 & 12). Mesotibia with one subapical spine, the tip of which does not reach to the level of the base of nearest tibial spur (Figures 19 & 20). Metatibia with a single row of four dorsal spines (Figure 32). Pretarsus double. Female cercus long, simple. Male cercus long, with a subapical inner knob (Figure 40). Subgenital plates as in Figures 43 & 54.

**Material examined**

Holotype, female metafemoral length 8,5 mm, labelled: *Pr. b. sp.* Meyer, Type, 3892, *Comicus Capensis* Br. (ZMB). Brunner v. Wattenwyl (1888) mentions a further type or types, deposited in "*Mus. Genav.*" These could not be traced through the Natural History Museum in Genève. SOUTH AFRICA, CAPE PROVINCE : 3 females, 8 males, 5 juv., Mata Mata (2520 Cc) S. Kalahari, IX. 1957, C. Koch (TM); 4 females, 1 male, Twee Rivieren (2620 Bc), Kalahari Gemsbok Park, 15 & 17.II.1961, L. Vári (TM); 1 female, 1 male, 3 juv., Auob-Nossob Junct. (2620 Bc), Apr. 1933, G. van Son (TM); 1 female, 2 males, 1 juv., Jakkalsputs, Namaqualand (2816 Db), 15.9.85, N.M.

Bfn. Ent. Dept. (NM); 1 female, Aughrabies falls (2820 Cb), Kenhardt C.P., 11/12/71, E. Holm (NCI); 1 female, Spektakelberg (2917 Da), 13-15 Sept 1982, M-L. Penrith, H 60249 (SM); 1 male, Pofadder, 100 km W (2918 Bc), 25 August 1977, Groundtraps, 62 days, E-Y 1331E (TM); 1 juv., Swartkops fm. (3021 Aa), unbaited trap, vegetated dune, 1-7 May 1985, E-Y 2205 (TM); 2 females, Olifantsvlei fm. (3021 Ba), Vegetated dunes, 4 May 1985, coll. M.-L. Penrith, E-Y 2215 (TM). SOUTH WEST AFRICA: 1 female, S.W. Protect., Otjituo (1918 Da), R.W. Tucker, Jan 1920 (SAM); 1 female, 40 km NW Tsumkwe, SE 1920 Ad, 12 - 14 June 1984, E. Griffin, Preservative pitfall trap, H 61946 (SM); 1 female, 1 male, 1 juv., S.W.A. Kungveld, 14 m. W of Tsumkwe, 1920 Da, Mangetti forest, 15.IX.61, Haacke (TM); 1 male, 1 juv., Ganab (2315 Ba), 16.iii.1983, C.D. Eardley (NCI); 1 male, Gobabeb, 70 m S.E. of Walvis Bay (2315 Ca) (TM); 1 male, 1 juv., S.W. Africa, Rehoboth (2317 Ac), 1450 m, 21. xii.1933, K. Jordan (BMNH); 1 female, Kub (2417 Ab), 19 Nov 1971, H 5146 (SM); 1 female, Guinasibberg (215 Ba), 22 June 1982, J. Irish, H 62443 (SM); 1 female, Near Awasisib (2515 Bc), 2 Sept. 1966, A. Bartsch, H 10077 (SM); 1 male, 1 juv., Kanaän 104 (2516 Cc), 6 Oct 1972, CGC, M-LP, HCS, H 61938 (SM); 1 female, 1 male, Welverdiend 328 (2519 Dd), 13-15 Oct. 1972, CG Coetzee, J Balt, H 10196 (SM); 1 female, 1 juv., No. 2392, Desert belt at Tschaukaib (2615 Da), Gunner Friedlander, May 3rd 1915 (AM); 1 female, No. 4056, Aus (2616 Cb) (AM); 1 female, 1 male, Donkermodder 60 (2618 Dc), 8 July 1982, J. Irish, At lighttrap on dunes, H 61943 (SM); 2 females, 2 males, Gt. Fish R., Aiais, S.W.A. (2717 Cd), Mus Staff, Nov. 1936 (SAM); 2 males, S.W. Africa (3), Noachabeb, 27 mls. NNE Grunau (2718 Ad), 10-12.1.1972 (BMNH); 1 female, Noachabeb 97 (2718 Ad), 7-12 Jan 1972, H 5827 (SM); 1 female, Gt Karas Mtns, S W A (ca. 2718 Bc), Mus Staff, Nov 1936 (SAM); 1 female, Obib dunes E. (2816 Ba), 16-20/9/73, CGC,MLP,JT, At night, H61939 (SM).

### Distribution (Figure 57)

Southern and northeastern South West Africa and northwestern Cape Province. Always associated with sand, but does not normally venture onto dunes, preferring consolidated sand such as at dune bases and in riverbeds. In the west it ranges up to the edge of the main Namib dune sea, and is also found around isolated mountains in the dunes, e.g. Guinasib. In the east it similarly ranges up to the edge of the Kalahari dunes, penetrating these along riverbeds such as the Auob.

### Remarks

May be confused with *C. campestris* and *C. calaharicus* specs. nov., see there. The specimens listed by Karny (1910), the Kaross specimen from Karny (1929), and Ramme's (1931) males all belong to *C. campestris* spec. nov. Karny's (1929) specimen from Jackals Water could not be traced.

### *Comicus arenarius* Ramme

*Comicus arenarius* Ramme, 1931 : 166.

Length of metafemur up to 13,5 mm (females) and 11,5 mm (males). Protibia lacking larger subapical spines, but with an irregular series of minute spinelets up the inner side (Figures 3 & 4). Mesotibia with a single row of four long apically upcurved dorsal spines (Figure 27). Pretarsus double (Figure 23). Cerci in both sexes short, simple (Figure 35). Subgenital plates as in Figures 49 & 50.

### Material examined

Holotype, male, metafemoral length 11,5 mm, labelled: Type, SW-Afrika, Namibwüste, 45 km S. Conceptionsbay, 12 km landeinwärts (2414 Bc) VI u VII 1927, leg. Joh. H. Gaerdes. (ZMB).

Allotype, female, metafemoral length 13,5 mm, labelled: Allo-Typus II, S.W. Afrika, Conceptionsbay (2314 Dc), Namibwüste, (Küstensone), III. 1926. Joh. H. Gaerdes I. (ZMB)

Paratype, nymph, labelled: Paratypus, rest as holotype. (ZMB)

Ten other paratypes stated by Ramme (1931) to be in ZMB could not be traced (K.K. Günther, pers. comm.). SOUTH AFRICA, CAPE PROVINCE : 1 female, 1 male, Alexander Bay Desert (ca. 2816 Da), -viii.1954, C. Koch (BMNH) (Referred to *C. arenarius* with some doubt, see below). SOUTH WEST AFRICA : 1 female, 40 km S of Kunene mouth (1711 Db), 25 Oct 1978, H 62242 (SM); 10 female, 8 males, 3 juv., 44 km S Kunene Riv. (1712 Cb), 17.2.1984, groundtraps 54 days, leg. Penrith, Müller, E-Y 2078 (TM); 1 female, Cape Fria Radio Station (1812

Aa), 24 Jan - 4 Feb 1982, Preservative traps, J. Irish, H 44932 (SM); 4 females, 3 juv., 30 miles SW Orumpembe (1812 Ad), 14 - 15 Nov 1965, W. Steyn, H 10076 (SM); 1 female, Mõwebaai (1912 Bc), 13-I-1980, Univ. v. Pretoria (TM); 1 female, South West Africa, "Hoas" Farm, Kamandjab (not traced, ? = Hoaswater, 1912 Bd), J. Labuschagne (AM); 1 female, 1 juv., Huab River, 5 km from mouth (2013 Cd), 22 Jan - 7 Feb 1982, Preservative traps, J. Irish, H 44933 (SM); 1 male, 1 juv., Walvis Bay (2214 Dc), Dūnen, Jan. 1937, F. Gaerdes, H 24553 (SM); 1 female, Walvis Bay (2214 Dc), VII. 1954, Vernay-Tvl. Mus. Expedition (TM); 1 juv., SE 2414 Dd3, Jan 1977, Namib-Expedition, Holm, Kirsten & Scholtz (TM); 1 female, Sylvia Hil (2514 Bb), 15 - 16 Sept 1971, H 5456 (SM); 2 females, 1 male, Elizabeth Bay (2615 Cc), 19.X.1977, White dunes at night (SAM).

### Distribution (Figure 57)

The whole of the coastal Namib between the Orange and Kunene Rivers. Always on coastal dunes, except in the far northern Namib where it also occurs on inland dunes.

### Remarks

Intraspecific variation: In two samples (total, 28 specimens) from the interior northern Namib there are three specimens with five dorsal spines on each metatibia, and a fourth specimen which has four spines on the one and five on the other metatibia. Other specimens from the same samples are typical *C. arenarius*, though a few have the minute protibial spinelets indistinct. I consider the above variation a population trend not yet worthy of subspecific status.

The two specimens from Alexander Bay are in fairly bad condition, but it is possible to see that the male has small subapical cercal knobs, similar to those found in *C. calcaris* spec. nov. In all other aspects they are typical *C. arenarius*. In the absence of more material from the Lüderitz/Oranjemund area, as well as from the Namaqualand coast, it is not possible to decide whether this is a subspecies of *C. arenarius* or a separate species. May be confused with *C. calcaris* spec. nov., see there.

### *Comicus cavillorus* spec. nov.

Length of metafemur up to 10 mm (females) and 11 mm (males). Protibia with three to four, usually four, subapical spines (Figures 13 & 14). Mesotibia with two subapical spines (Figures 21 & 22). Metatibia with a single row of four short dorsal spines (Figure 33). Pretarsus double. Female cercus short, simple. Male cercus short, with a distal inner knob (Figure 41). Subgenital plates as in Figures 55 & 56.

### Material examined

Holotype, female, metafemoral length 10 mm, labelled:

Oranjekrag, H.F. Verwoerd Dam (3025 Cb), 9 - 17.1.1969, Snyman & Strydom. (TM)

Allotype, male, metafemoral length 11 mm, labelled: P.K. le Roux Dam, van der Kloof, C.P. (3024 Ba), 19 - 25.X.1970, Snyman & Jones. (TM)

Paratypes: SOUTH AFRICA, CAPE PROVINCE: 1 female, Vredendal, 20 km N (3118 Da), 19 August 1983, Groundtraps, 76 days, Endrödy/Penrith, E-Y 1948E (TM); 1 female, Gouph, Lainsburg Dist (3321 Ab), S A Museum, Mus Staff, Sept 1942 (SAM); 1 male, Zwartskraal fm. (3322 Ba) 5 September 1979, Groundtraps, 44 days, E-Y 1638aG (TM); 1 juv., male, no label (SAM).

### Distribution (Figure 58)

Karoo. Normally on hard ground, not dunes.

### Remarks

The tibial setation, especially the presence of two subapical spines on the mesotibia, distinguishes this from all other *Comicus* spp., including *C. campestris* spec. nov., which resembles it in general appearance. The name, meaning "joker", is in keeping with the generic name.

### *Comicus campestris* spec. nov.

*Comicus capensis* Brunner v. Wattenwyl, 1888; Karny 1910: 39, 1929: 147; Ramme 1931: 165. [Misidentification].

Length of metafemur up to 11 mm (males and females). Protibia with two subapical spines (Figures 7 & 8). Mesotibia with one subapical spine, the tip of which usually reaches to the level of the base of the nearest tibial spur (Figures 17 & 18). Metatibia with a single row of three or four dorsal spines (Figures 29 & 30). Pretarsus double (Figure 24). Female cercus simple. Male cercus with a knob halfway along its length, the cercus itself being straight in younger animals (Figure 38), but bent at right angles in mature individuals (Figure 42). Subgenital plates as in figures 45 & 46.

### Material examined

Holotype, male, metafemoral length 11 mm, labelled: SM H 63801, 6 km N Arandis, Damaraland (2214 Bd), 12 Feb. - 11 March 1985, J. Irish; H. Rust, SM Type number T 269. (SM)  
 Allotype, female, metafemoral length 10 mm, labelled: SM H 63802, Upper Ostrich Gorge, Swakopmund district (2214 Bd), 11 March - 9 April 1985, J. Irish, H. Rust. (SM)  
 Paratypes : SOUTH WEST AFRICA : 1 male, D.S.W. - Afrika, Okahandya, IX.X.03, Windh., L. Schultze S. (ZMB) (This specimen det. Karny, publ. 1910, *C. capensis*. The other specimen from Karny (1910), also in ZMB, is today indet. due to damage); 1 male, Kaross S.W.A. (1914 Bc), Mus. Exped. Feb. 1925 (SAM) (This specimen det. Karny, publ. 1929, *C. capensis*); 2 males, S.W. Afrika, Namib, Al. Werter, 5.V.1925 (ZMB) (These specimens det. Ramme, publ. 1931, *C. capensis* Allotypus I & II (actually plesioallotypes)); 2 females, S.W.Afr., Kaokoveld, Kunene Riv., 44 km S (1712 Cb), 17-2-1984, E-Y 2078, groundtraps, 54 days, leg. Penrith, Müller (TM); 1 juv., 8 km NE Omatjenguma (1712 Cd), 22 - 25 Nv 1970, H 1109 (SM); 1 male, Okumutati (1814 Cd), Kaokoland, 18 February 1985, J. Irish & H. Rust, Lighttrap, H 61947 (SM); 1 female, Khowarib Schlucht, SE 1913 Bd, 15-1-1980, Univ. v. Pretoria (TM); 1 female, 50 myl vanaf Uis, N/W Brandberg (ca. 2114 Ab), P.S. Swart, W. Jankowitz, J.C. Cloete, 5:1:66, H 10065 (SM); 1 female, 2 males, ± 24 vanaf Uis, Oos van die Brandberg (ca. 2114 Bb), P.S. Swart, 5:1:1966, H 10066 (SM); 1 juv., male, Farm Ameib, Erongo, SE 2115Da (sic! = 2115 Dc), 10-X-1979, E. Holm, CH Scholtz (TM); 1 female, S.W. Africa : Sukses (2116 Bb), 17-22.XI.1933, K. Jordan (BMNH); 1 male, Okahandja (2116 Dd) S.W. Afrika, 5.12.1926 (durch Hautinge) (ZMB); 1 female, 7.9.41, Licht, OKA, H 811 (SM); 1 male, Okahandja Townlands, SE 2117 Cc, 4-19 Apr 1976, Red sand (1), H 32399 (SM); 1 juv., male, Tinkas Dam (2215 Cd), 18 November 1974, Groundtraps, 65 days, E-Y 480B (TM); 3 females, Bethel 89 (2215 Db), Karibib, 15 - 16 Apr. 1972, J. Balt, H 7582 (SM); 1 male, Windhoek (2217 Ca), 29 Jan 1985, H. Rust, Inside house, H 61945 (SM); 1 female, 22 km from Gobabeb to Mirabib (2315 Ad), November 1974, Groundtraps, 6 days, E-Y 557G (TM); 1 male, Arechadamabberg (2315 Ba), 22 January 1975, Groundtraps, 38 days, E-Y 6591 (TM); 1 male, Us Pass Road at (2315 Bb), 15 November 1974, groundtraps, 70 days, E-Y 473B (TM); 2 females, 2 males, Gobabeb, 70 m S.E. of Walvis Bay (2315 Ca) (TM); 1 female, 1 male, Gobabeb, Kuiseb Riv., Centr. Namib, X.1957, C. Koch (TM); 1 female, Gobabeb, S.W.A., Game Reserve No. 3, 11.V.1959, L. Vári (TM); 2 juv., Kaukausib Riverbed at (2615 Cd), Diamond Area 1, 10 - 22 Aug 1983, J. Irish/E. Griffin, Preservative traps, H 62442 (SM); 2 females, Kochasdrif, Fish River (2717 Dc), 12-X-1974, SM-staff, H62440 (SM); 3 males, S.W. Africa (3), Noachabeb, 27 Mls. NNE Grunau (2718 Ad), 10-12.1.1972, At light (BMNH). ANGOLA : 1 female, 30 km NE Iona, Angola (1612 Cb), 3 oct 1969, M-LP, B.K., J. Batista, H 10081 (SM); 1 unsexed, Manaculama, SE 1612 Dc, Angola, 4 Oct. 1969, H 812 (SM). Specimens referable to *C. campestris* with reasonable but not absolute certainty (due to damage), were also examined from the following additional localities: Gai-as (2014 Cc); Okonjeje (2015 Cd); Brandberg (ca. 2114 Ba). These were not designated as types.

### Distribution (Figure 58)

Southern and northwestern South West Africa, ranging into southwestern Angola. Prefers hard ground, not sand.



### Remarks

The specimens listed by Karny (1910), and the Kaross specimen from Karny (1929), as well as the specimens on which Ramme (1931) described the male of *C. capensis* were examined and found to belong to *C. campestris*. Most individuals of *C. capensis* and *C. campestris* can be separated on the basis of the number of protibial spines: two in *C. campestris*, usually three in *C. capensis*. In *C. capensis* specimens with aberrant protibial spination, the position of the mesotibial spine is diagnostic. The name refers to the fact that this is one of the *Comicus* species which prefer hard, flat ground.

### *Comicus calaharicus* spec. nov.

Length of metafemur up to 11,5 mm (females) and 11 mm (males). Protibia with two to three, usually three, subapical spines (Figures 9 & 10). Mesotibia with one subapical spine. Metatibia with two rows of dorsal spines: the inner row of four moderately long spines, and the outer row of one to four, usually three, short spines (Figure 31). Pretarsus double. Female cercus simple. Male cercus with a subapical knob (Figure 39). Subgenital plates as in Figures 51 & 52.

### Material examined

Holotype, female, metafemoral length 11,5 mm, labelled: SM H 10074, Leonardville, Gobabis (2318 Db), 12 Oct. 1963, P.J. Buys, SM type number T 267. (SM)

Allotype, male, metafemoral length 11 mm, labelled as holotype. (SM)

Paratypes: SOUTH AFRICA, CAPE PROVINCE: 4 females, 1 male, Mata Mata (2520 Cc), S. Kalahari, IX. 1957, C. Koch (TM); 1 male, Stille Woning, Vorstershoop, NW Cape, RSA, SE 2523 Cc, 28 Feb - 1 Mar 1980, S. Louw, M.-L. Penrith, H 41161 (SM); 1 male, S. Afr., C.P., Vostershoop (2523 Cc), 29 II 80, Whitehead (SAM); 2 females, Twee Rivieren (2620 Bc), 9.II.1959, Kalahari Gemsbok National Park, H. Brown (TM); 4 females, Twee Rivieren, V. 1956, Kalahari Gemsbok Park Expedition (TM); 1 male, Van Zylsrus (2622 Cc), Gordonia Distr., 14.II.1961, L. Vári (TM); 1 female, Niekerk's Hope (2922 Bd), Hay Distr., Cape Prov., X.1955, C. Koch, in the night on red windblown sand (BMNH). SOUTH AFRICA, TRANSVAAL: 1 female, Rochdale 700 (2229 Dc), Soutpansberg Distr., 20-24.I.1972, Potgieter & Jones (TM). SOUTH WEST AFRICA: 4 females, 12 males, 1 juv., labelled as holotype (SM); 2 females, Duineveld, SWA, Elephants Riv., Kalah. (2418 Db), 21-24.II.1957, Transv. Mus. Exped. (TM); 1 male, Gochas, Gibeon, SE 2418 Dd, 31 May 1972, MJ + M-LP, H 8624 (SM); 1 female, Aranos (2419 Aa), R. vGaudecker, Jan. 1971 (TM); 1 female, 2 juv., Hohedun 277 (2719 Bc), Karasburg District, 9 July 1982, J. Irish, At night on dune, H 61941 (SM); 2 males, Ortmansbaum 120, Warmbad, SE 2818 Bd, 18-21 Oct 1971, H4636 (SM). BOTSWANA: 1 male, 40 miles S.W. of Ghanzi (2121 Cc), 29/10-9/11/61, W. Haacke, O. Prozeski (TM); 1 female, Botswana, Ghanziland, Dekar, 2121 Db, 26.X.61, W. Haacke (TM); 1 female, N. Bechuanaland, Ghanzi, Mongalatsila (2121 Dc), 192-. J. Maurice (BMNH); 2 females, 1 male, 11 miles W Orapa, 25 E 21 S Ac (2125 Ac), Mopane Shrub, Area 3, 30/XII/1972, J.F. Barker (NCI); 3 juv., // 115, Botswana Central Dist., Gaborone — Francistown Rd., 153 km NNE Gaborone (2326 Bc), 23 ii 1984, Otte Toms + Cade (TM).

A damaged specimen probably belonging to *C. calaharicus* was also examined from the following additional locality: 50 km NW Hotazel (2622 Dd). This was not designated a type.

### Distribution (Figure 58)

Southern Kalahari sand system. In the southwestern Kalahari it is only found on dunes, but towards the north and east any sandy substrate seems to suffice.

### Remarks

*C. calaharicus* may be distinguished from *C. capensis* by having two rows of metatibial spines instead of one only. Since the outer row may be reduced to a single, hard to discern spine, care is needed in separating the two species. The smallest spines are more easily seen in lateral than dorsal aspect. The name refers to the Kalahari desert, where the species occurs.

*Comicus calcaris* spec. nov.

Length of metafemur up to 16 mm (females) and 15 mm (males). Protibia (Figures 5 & 6) and mesotibia both lacking subapical spines. Metatibia with two rows of dorsal spines: the inner row of four, occasionally three, long spines, and the outer row of one to four, usually three to four, moderately long spines (Figure 28). Pretarsus double. Female cercus short, simple (Figure 36). Male cercus short, subapically notched (Figure 37). Subgenital plates as in Figures 43 & 44.

**Material examined**

Holotype, male, metafemoral length 11 mm, labelled: SM H 10192, Kanaän 104, Lüderitz District (2516 Cc), 6 Oct. 1972, CGC, M-LP, HCS, SM type number T 266. (SM)

Allotype, female, metafemoral length 11,5 mm labelled as holotype. (SM)

Paratypes : SOUTH WEST AFRICA : 2 females, Gobabeb, Walvisbaai (2315 Ca), Dec 1962, W Steyn, Uitgegrawe in duine, H 10071 (SM); 2 females, 5 males, Gobabeb, 23.3 S 15.0 E, 408 m (TM); 1 male, S.W.Africa, near Gobabeb, dunes, 23-24.1.1972, David Hollis (BMNH); 1 male, Flodden Moor, near Gobabeb (2315 Ca), Jan. 1984, M. Villet (TM); 2 females, 1 male, Tsondab, SE 2315 Cd1, 11-VII-1975, Dept. of Entomology, University of Pretoria, dune, night (TM); 1 male, Tsondap, SE 2315 Dc1, Dept. of Entomology, University of Pretoria, night, dune (TM); 1 female, 90 km SSE Ururas, SE 2414 Bb, 14-X-1979, E Holm, CH Scholtz (UP); 4 females, 1 male, Dunes W Sossusvlei, SE 2415 Cc, Lüderitz, 13-14 Sept 1971, H 5457 (SM); 1 male, SE2515Ac4, Jan 1977, Namib-Expedition, Holm, Kirsten & Scholtz (TM); 1 juv., W. Guiniasiberg, 2515Ad2, 6.7.76, Dept. of Entomology, University of Pretoria (TM); 1 female, SE 2515Cc2, Jan 1977, Namib-Expedition, Holm, Kirsten & Scholtz (TM); 1 male, SE 2515Cd2, Jan 1977, Namib-Expedition, Holm, Kirsten & Scholtz (TM); 1 female, 2 males, labelled as holotype (SM); 1 female, 6038, Luberitzlucht (*sic!* = Lüderitzbucht, 2615 Ca), Fr. Eberlanz, March 26th 1929 (AM); 1 male, Agaatstrand, Lüderitz, SWA, SE 2615Ca2, VII.1978, E. Holm (TM); 1 juv., Haalenberg (2615 Da), X. 1950, G. van Son (TM); 1 female, 3 males, Tsaus dunes at 2716 Aa, Diamond Area 1, 13 August 1983, J. Irish, At night on dunes, H 61940 (SM); 2 females, 2 males, Obib dunes, E. at 2816 Ba, Lüderitz, 16-20 Sept. 1973, CGC, M-LP, JT, At night, H 28284 (SM); 2 females, NO van Oranjemund, SE 2816Cb2, VII-1982, E. Holm (TM); 1 male, X 41 (TM).

A damaged specimen probably referable to *C. calcaris* was also examined from the following additional locality : Ururas (2314 Ba). This was not designated a type.

**Distribution (Figure 58)**

Main (southern) Namib dune sea, ranging south to the Orange River. Found on dunes only, and usually on inland rather than coastal dunes.

**Remarks**

*C. calcaris* is very similar to *C. arenarius*, but may always be distinguished by its possessing two rows of metatibial spines instead of one only. The name refers to the well developed tibial spurs.

*Comicus cabonegrus* spec. nov.

Length of metafemur up to 10 mm (females) and 11 mm (males). Protibia (Figures 1 & 2) and mesotibia both lacking subapical spines. Metatibia (Figure 26) lacking dorsal spines. Pretarsus single (Figure 25). Cerci in both sexes short, simple (Figure 34). Subgenital plates as in Figures 47 & 48. Tip of outer lacinial uncus simple (notched or bifurcate in all other species).

**Material examined**

Holotype, female, metafemoral length 10 mm, labelled: SM H 10080, Cabo Negro, Angola (1511 Db), 17/18 Sept 1969, C.G. Coetzee, SM type number T 268. (SM)

Allotype, male, metafemoral length 11 mm, labelled as holotype, (SM)

**Distribution (Figure 57)**

Known only from the type locality on the coast of southwestern Angola. Presumably an inhabitant of coastal dunes.

**Remarks**

The complete absence of tibial spination distinguishes this from all other *Comicus* spp. The name refers to the type locality.

## DISCUSSION

The phylogenetic position of the Schizodactylidae within the Gryllacridoidea Zeuner, 1935 (which latter may not be a natural group) is not clear. Hubbell (1978) discussed the various systems that have been proposed for the Gryllacridoidea. From this the consensus seems to be that the Schizodactylidae are most closely related to the Rhabdophoridae, and that both are very early offshoots of the phylogenetic lineage which includes all other Gryllacridoidea, both Gryllacridoidea and Tettigonioidea, or all Ensifera, depending on which system one accepts.

The position within the Schizodactylidae itself is much clearer, and I believe them, at least, to be a natural (= monophyletic) group. Ramme (1931) stated that, though the disjunct distribution of the family arouses the suspicion that their similarity may be due to convergence, they share a number of unique synapomorphies which prove otherwise. Among these may be mentioned the possession of tarsal appendages, the degeneration of the ovipositor, and the anterior and middle tibiae which are more strongly developed than their respective femora.

A cladogram for *Comicus* species and *Schizodactylus* as a genus is given in Figure 59. This must be regarded as tentative only, because of the very few characters available for analysis, as well as the absence of comparative data for many *Schizodactylus* species. The only character for which absolute certainty exists is that the winged state in *Schizodactylus* is relatively more plesiomorphic than the secondary aptery of *Comicus*. The total aptery in *Comicus* is anticipated by the brachyptery of *S. inexpectatus*, and the fact that all other *Schizodactylus* species, though they have fully developed wings, normally carry these with the apices rolled up. The experiments of Khattar (1972) shows them to be capable of limited flight under stress, but they probably seldom fly voluntarily under natural conditions and then fly very poorly. It is easy to see how this situation could have led to eventual aptery in *Comicus*.

If one assumes that, along with the winged state, *Schizodactylus* also retained the relatively more plesiomorphic state for most other characters, the possession of many tibial spines, especially on the pro- and mesotibiae, must be considered plesiomorphic for *Schizodactylus*, and their progressive loss in *Comicus* species as apomorphic. The status of the other available characters are deduced mainly from their relation to the tibial spination sequence in *Comicus*.

The following characters were utilised, with the relatively more plesiomorphic state mentioned first in each case:

1. Winged; apterous.
2. Number of protibial spines: more than four; four or less; absent.
3. Number of mesotibial spines: more than two; two or one; absent.
4. Habitat: Hard ground; hard sand; soft sand (dunes).
5. Male cercal knobs. On generic level: absent; present. For *Comicus* spp.: present; absent.
6. Position of male cercal knobs: medial; distal; apical; terminal; absent.
7. Number of spines per row, metatibia: more than five; five or less; absent.
8. Number of spinal rows, metatibia: two or more; one; none.
9. Pretarsus: double; single.
10. Inner lacinial tooth : double; single.

The distribution of these character states among the species concerned is given in Table 1, and the resultant cladogram in Figure 59.

The probable phylogenetic history of *Comicus* may then be summarised as follows: turning first to *Schizodactylus*, we find that four of the six known species are confined to the northeast of the Indian subcontinent (Bengal, Sikkim, Assam, Burma). They are *S. monstrosus* (Drury), *S. burmanus* Uvarov, *S. minor* Ander and *S. tuberculatus* Ander. *S. hesperus* [Bey-Bienko] occurs in northeastern Afghanistan, and *S. inexpectatus* (Werner) in central southern Turkey. Until *Schizodactylus* is revised, the only clue to the internal phylogeny of the genus lies in the brachyptery of *S. inexpectatus*, which is considered apomorphic. Since the majority of species occur in the Indian subcontinent, and the apomorphic *S. inexpectatus* at the opposite end of the generic distribution range, one may assume that the genus originated in India, whence it spread westwards. This spread from a subtropical to desert and semi-desert areas, was probably made possible by the same (largely unknown) pre-adaptations which allowed *Comicus* to disperse into increasingly drier habitats, as will be seen below.

Accepting the monophyly of *Schizodactylus* and *Comicus*, their common origin must be traced back to the last contact between the Indian subcontinent and the southern half of Africa. According to Smith, Hurley & Briden (1981) India was still attached to Africa in the late Jurassic (140 Ma), had begun to move away but remained attached *via* Madagascar by the early Cretaceous (120 Ma), and was completely separated by the mid Cretaceous (100 Ma). This traces the existence of the Schizodactylidae back to at least the late Jurassic. Since the earliest known fossil Orthoptera *s.s.* date from the late Triassic (*ca.* 190 Ma) (Riek 1970) the existence of the Schizodactylidae before 140 Ma corresponds to the inferred early divergence of the schizodactylid/rhaphidophorid lineage from other Orthoptera or other Ensifera, mentioned above.

The schizodactylid population left on the African continent after the separation of India lost their wings and most of their tibial spines with time, and evolved into *Comicus*. The ancestral *Comicus* was probably similar to the present *C. cavillorus* and *C. campestris*, both of which have similar male cerci, and it probably inhabited fairly hard substrates, as do these two species. All other *Comicus* spp. are psammophilous descendants of this line. Pre-adaptation, of which tarsi suited to fossorial activity may have been part, probably prompted psammophilous adaptation and speciation at whatever time in the past suitable

**Table 1:** Distribution of character states. Numbers of characters as in text. Apomorphic states indicated by (\*), intermediate states by (+) and plesiomorphic states unmarked.

Characters	<i>Comicus</i> spp.							<i>Schizodactylus</i>
	<i>cabonegrus</i>	<i>arenarius</i>	<i>calcaris</i>	<i>calaharicus</i>	<i>capensis</i>	<i>campestris</i>	<i>cavillorus</i>	spp.
10	single*	double	double	double	double	double	double	double?
9	single*	double	double	double	double	double	double	double
8	nil*	one+	two	two	one+	one+	one+	two (?more)
7	nil*	4 - 5+	1 - 4+	1 - 4+	four+	3 - 4+	four+	five or more
6	absent*	absent*	terminal*	apical+	apical+	medial	distal	absent
5	absent*	absent*	present+	present+	present+	present+	present+	absent
4	dunes*	dunes*	dunes*	dunes*	hard sand+	hard ground	hard ground	hard sand ?+
3	nil*	nil*	nil*	one+	one+	one+	two+	three or more
2	nil*	nil*	nil*	2 - 3+	three+	two+	3 - 4+	four or more
1	apterous*	apterous*	apterous*	apterous*	apterous*	apterous*	apterous*	winged/ brachypterous+

habitats became available in response to increased aridification of western southern Africa. The first psammophilous *Comicus* probably occupied consolidated sand, as does *C. capensis* today. *C. capensis* and *C. calaharicus* are closely related, sharing especially the three protibial spines and the apical position of the male cercal knobs. Where *C. capensis* and *C. calaharicus* occur together, as in the southwestern Kalahari, they are ecologically separated, with *C. calaharicus* occurring on the dunes, and *C. capensis* in riverbeds, interdune valleys and on dune bases. (Where they occur singly, *C. calaharicus* also occurs on consolidated sand, e.g. northwestern Transvaal, and *C. capensis* ranges onto dunes, e.g. Bushmanland, Cape Province.) From this I deduce that *C. calaharicus* evolved from *C. capensis*-like ancestors in response to increased aridification and hence psammification of the Kalahari.

*C. calaharicus* and the Namib *C. calcaris* share the possession of two metatibial spinal rows. If this is considered to be synapomorphic, it means that *C. calcaris* evolved from *C. calaharicus*, and, since both species live mainly on dunes, that there had been some direct past connection between the Namib and Kalahari dunes. I doubt this on the present evidence, as the two characters may not be homologous. The metatibial spines of *C. calaharicus* are short and straight, as in *C. capensis* and the other more plesiomorphic *Comicus* spp., while those of *C. calcaris* are long and curved, as in *C. arenarius*. Looking at the totality of characters, the species pairs *C. capensis/C. calaharicus* and *C. calcaris/C. arenarius* are more similar to each other than *C. calaharicus* is to *C. calcaris*. The significance of the double row of metatibial spines is not clear, but since both species which possess it live on inland dunes, it may be related to the habitat and as such may have evolved more than once. The fact that the only known inland populations of the normally coastal *C. arenarius* (northern Namib) are undergoing multiplication of the metatibial spines seems to confirm this.

The three Namib species *C. calcaris*, *C. arenarius* and *C. cabonegrus* share the absence of both pro- and mesotibial spines. *C. calcaris* possesses male cercal knobs, which the other two lack. The ancestor of the Namib *Comicus* spp., should then have possessed male cercal knobs, but lacked pro- and mesotibial spines. These conditions are fulfilled by the Alexander Bay specimens of "*C. arenarius*". I expect further collecting to show this taxon to be widespread along the Namaqualand coast, and to be a distinct species. The Orange River probably acted as a barrier to gene flow, allowing speciation in those populations of *Comicus* north of the river. There are two possible reasons why two instead of one species evolved from the unnamed taxon at this point. Since *C. arenarius* is a coastal, and *C. calcaris* an inland species, either the origins of the coastal and inland dunes were separated temporally or spatially, or the different selective pressures arising from life in mobile unvegetated coastal dunes as opposed to more stabilised vegetated inland dunes prompted the development of two species, analogous to the situation at present in inland northern Namib *C. arenarius* populations. The present data does not allow a decision between these two alternatives.

*C. arenarius*, being a coastal species, dispersed northwards on moving barchan dunes (*sensu* Endrödy-Younga 1982). The coastal dunes of the main Namib dune sea are from the viewpoint of habitat pressures on a species, no more than confluent barchan dunes, though this is not necessarily their origin. They would present no obstacle to the northward dispersal of a species arriving at the southern border of the dune sea on a barchan. In the case of *C. arenarius*, dispersal into the inland dunes was prevented by *C. calcaris* already filling the available niche. The dispersal of *C. arenarius* across the presently duneless area between

Swakopmund and Torrabaai (excepting the Huab River dune patch) must similarly have taken place on moving barchan dunes. *C. calcaris* did not disperse northwards beyond the Kuiseb River, because it was adapted to life on inland dunes, not on moving barchans, and therefore does not occur in the northern Namib. A similar situation exists in the Lepismatidae of the Thysanura (Irish, unpublished), where only those species of the main Namib dune sea which are able to survive in the coastal dunes, or on inland slipfaces (a barchan is simply a moving slipface) occur also in the northern Namib, while the dune base, interdune valley and hummock-dwelling species of the main Namib dune sea are absent from the northern Namib.

While accepting that the rate of movement of barchans depends on many factors, notably wind speed and barchan size, an estimate of the time of last barchan movement between the main dune sea and the northern Namib may be made. Endrödy-Younga (1982) quotes measurements of between 24,2 and 60,6 m/p. a., with average 43 m p. a., for barchan movement in the far southern Namib. At these rates, it would have taken barchan dunes between 4 800 and 12 000 years, with average 6 700, to cross the 290 km between Swakopmund and Torrabaai. The Huab River dunes, 225 km north of Swakopmund, may represent either the still moving last barchan train to be detached from the main dune sea, or a relict patch of the last barchan train which is today maintained by sand accumulating in the riverbed, which acts as a sand-trap. If one accepts the former possibility, the estimates above change to between 3 700 and 9 300 years, with average 5 200. *C. arenarius* occurs on the Huab River Mouth dunes.

The northern Namib dunes consist of an uninterrupted coastal dune stretch between Torrabaai and the Hoarusib River, where the dunes start to break up into barchan trains. North of the Khumib River there are only barchan trains, but many of them and all actively moving, up to the Engo River and Dunedin Star. North of here is again a consolidated dune field. This dune field, and some of the barchan trains south of it, stretch up to 50 km inland. The *C. arenarius* populations which invaded the available niche in these inland dunes (occupied by *C. calcaris* further south) are evolving away from the typical coastal *C. arenarius*, which occurs up to the Kunene River Mouth. *C. cabonegrus*, also a species of coastal dunes and the most apomorphic member of the genus, probably shares an ancestor with *C. arenarius*, and the Kunene River may have provided the barrier to gene flow which initiated this.

The above has some bearing on the evolutionary history of the psammophilous western southern African faunal component. While it is accepted that different taxa will respond differently to the same environmental pressures, and that the evolution of one group may not necessarily be deduced from that of other groups in the same area, experience has taught that the ultrapsammophilous taxa of the Namib desert do share the same gross evolutionary and distributional trends. This is perhaps to be expected in a case where a whole community and a portion of their habitat is isolated from the parent community and transported away, as occurs during dispersal on barchan dunes.

The inferred evolution of *Comicus* therefore confirms

- a) the derivation of the psammophilous Namib desert fauna: primarily from the Namaqualand region and secondarily from the rest of the South West Arid; and
- b) the south to north evolutionary trend in ultrapsammophilous Namib taxa, caused by barchan dispersal and the dominant southerly wind trend.

Both the above were stated in or can be deduced from the results of a number of taxonomic revisions of Namib taxa, the most recent of which was Penrith (1984).

The present study further introduces the concept that

- c) the reason for the absence of some common taxa of the main Namib dune sea from the northern Namib dunes may be habitat related, in that these taxa are adapted to life on vegetated inland dunes and unable to survive nor disperse on moving barchans, a fact which should be foreshadowed by their not occurring on the slipfaces of the main Namib dune sea dunes.
- d) Lastly, the barchan movement between the main Namib dune sea and the northern Namib is estimated to have ceased (averages) 5 000 - 6 000 years b.p.

### AFRIKAANS SUMMARY

Die genus *Comicus* Brunner v. Wattenwyl 1888 (Orthoptera: Schizodactylidae) word hersien. Benewens die twee bekende spesies word 'n verdere vyf nuwe spesies beskryf. Die taksonomiese kenmerke vir gebruik by die uitkenning van spesies word bespreek, en die nuttigste blyk die aantal tibiale stekels en die bou van die manlike cerci te wees.

'n Sleutel tot die spesies word voorsien. Die genus is inheems aan die droër dele van suidelike Afrika. Die evolusionêre geskiedenis van die groep word vervolgens bespreek. Hieruit blyk dit dat die bestaan van die Schizodactylidae terug dateer tot minstens die vroeë Kryt, ongeveer 120 miljoen jaar gelede. As gevolg van kontinentale drywing is die oer-Schizodactylidae toe geskei in twee bevolkings. Die een, op die toekomstige Indiese subkontinent, het mettertyd ontwikkel tot die huidige Oriëntaal-Palearktiese genus *Schizodactylus*. Die ander bevolking, in die toekomstige suidelike Afrika, was die voorgangers van *Comicus*. Die mees plesiomorfe tans lewende *Comicus* spesies bewoon harde substrate, terwyl progressief meer apomorfe spesies progressief sanderiger habitate bewoon. Die mees apomorfe *Comicus* spesies bewoon die kusduine van die Namibwoestyn. Die filogenie van *Comicus* bevestig dit wat reeds vir ander ultrapsammofiele Namib-taksa bekend is, nl. dat hulle primêr uit die psammofiele fauna van Namakwaland stam, en dat hulle evolusionêre tendens van suid na noord is, met die mees apomorfe spesies in die verre noord-Namib en suidwes-Angola. Daar word voorgestel dat dié rede vir die afwesigheid van sommige algemene suid-Namib taksa uit die noord-Namib mag wees as gevolg van hulle onvermoë om op bewegende barkaan-duine te oorleef, en dat lg. afgelei kan word uit hulle afwesigheid uit die suid-Namib kusduine. Dit volg dat die noord-Namib primêr deur middel van bewegende barkaan-duine met die suid-Namib kusduin-fauna gekoloniseer is, en daar word bereken dat grootskaalse barkaan-beweging in hierdie gebied ongeveer 5 000 tot 6 000 jaar gelede gestaak het.



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