REVISION OF THE WEEVIL GENUS *LEPTOSTETHUS* WATERHOUSE, 1853 (COLEOPTERA: CURCULIONIDAE: ENTIMINAE)

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I. INTRODUCTION

Leptostethus is a fairly large genus of elongate broad-nosed weevils which occurs in western southern Africa, predominantly in the Karoo, Bushmanland, Namaqualand, Namib and southern Kalahari regions (fig. 1). The genus, with two included species, was described by G. R. Waterhouse in 1853. Further species were described by Péringuey, 1892 (3) and 1908 (1); by Marshall, 1920 (1), 1926 (1), 1938 (1) (all seven in other genera), 1949 (2), 1959a (2) and 1959(b) (1) and by Voss, 1974 (3). To these are now added a further nineteen species and three subspecies. With one of Voss's species placed in synonymy, the genus now comprises thirty-five species and three subspecies. Several species are known from single specimens or short series. It seems likely, therefore, that although the number of described species is here more than doubled, many more await discovery.

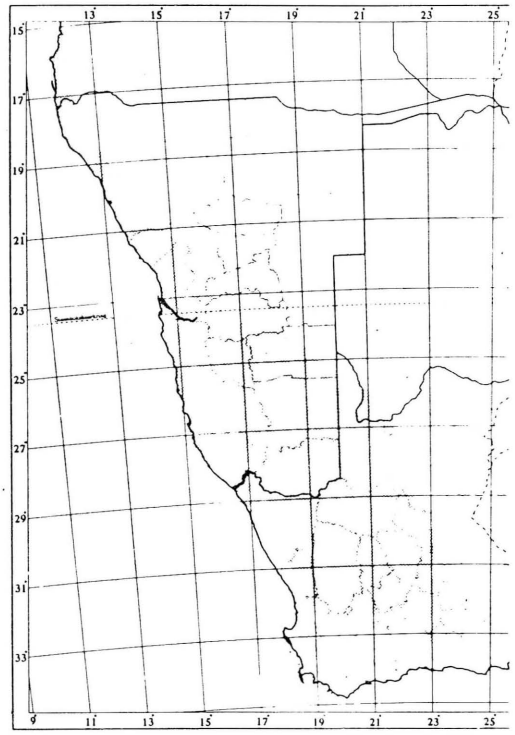


Figure 1. Map showing range of *Leptostethus* (shaded area).

Few biological observations have been made on *Leptostethus* and the larvae are unknown (though they are presumably root-feeders). Holm & Scholtz (1980) give details of behaviour, incidence and food plants for three species at Gobabeb (*L. waltoni, L. speciosus* and *L. marginatus).* Accounts of the incidence and egg-laying habits of the blue weevil (*L. speciosus)* are provided by Seely (pers. comm.) and Praetorius (1982: 10) (see below, p. 50).

My interest in *Leptostethus* began in 1966 when the late Dr Charles Koch asked me to describe the famous blue weevil of the Namib. Among the material he sent me were several other, less spectacular, species which proved very difficult to separate. Even the genitalia were, at first, unhelpful. I then began to examine the male internal sac, using the procedure described by previous authors. Although small rigid structures were found in some species, the sacs were otherwise entirely membranous. That they had a complex structure was obvious but this could not be demonstrated while they remained flaccid. Eventually I devised a method for inflating the sacs (see Appendix, p. 77). This revealed a quite unexpected wealth of complex and beautiful shapes which have enabled me both to separate the species and to group them in a satisfactory manner.

The taxonomic study which follows suggests that *Leptostethus* originated in the southern Karoo and spread north-westwards through Namaqualand to the Namib. It has also made two separate invasions into the Kalahari. The ranges of the Karoo-Namaqualand species are small and strictly allopatric (fig. 143) but those of the Namib species are mostly larger and often partly or entirely sympatric. The components of some species complexes are separated by altitude.

DEPOSITORIES

BMNH	British Museum (Natural History), London.
IRSN	Institut Royal des Sciences Naturelles, Brussels.
MGF	Museum G. Frey, Tutzing, Munich.
MNHN	Muséum national d'Histoire naturelle, Paris.
NCI	National Collection of Insects, Pretoria.
SAM	South African Museum, Cape Town.
SM	State Museum, Windhoek
TM	Transvaal Museum, Pretoria
ZM	Zoological Museum, Lund.
ZMHU	Zoologische Museum der Humboldt Universität, Berlin.
ZS	Zoologische Staatssammlung, Munich.

Specimens received from the Namib Desert Research Station have been returned to the Transvaal Museum, where the bulk of its collection now is. Similarly, the collection of the University of Pretoria has been transferred to the Transvaal Museum and material received from the University is cited as 'TM' here.

II. SYSTEMATICS

GENUS *LEPTOSTETHUS* WATERHOUSE

Leptostethus Waterhouse, 1853: 175; Lacordaire 1863: 259; Marshall 1948: 137; 1949: 180; Voss 1974: 424.

Type species: *Leptostethus marginatus* Waterhouse, 1853 (by original designation).

Diagnosis

Apterous entimine Curculionidae measuring 4-28 mm in length. Form elongate, length/breadth ratio 2.2-3.2.

Head and rostrum more or less deflexed ventrad; frons broad, flat or weakly convex; eyes lateral, round or ovate, more or less acuminate below, weakly to moderately convex; rostrum stout, shorter than width of head, very variously shaped and sculptured; scrobes

lateral, deep, well defined, usually strongly decurrent but not extending to underside of rostrum; pterygia weakly developed or absent; nasal plate undefined or very indistinct; rostro-frontal sulcus present or absent; mandibles squamose, outer aspect with 2-6 large setae and 0-7 smaller ones, upper cusp much larger than lower one, deciduous processes slender, blade-like, without lateral teeth, of normal size in some species but relatively very small in others; mentum with 2 large and 0-many smaller setae.

Antennae relatively small, 0.7-1.2 times as long as pronotum; scape clavate, not reaching eye, exposed part from about as long as funicle to only two-thirds as long; funicle segment 1 about twice as long as broad and usually twice as long as 2 (range 1.6-3.0), segment 2 quadrate or slightly elongate, as long as or longer than 3, segments 3-7 quadrate or weakly transverse, subequal; club stout, as long as preceding $2\frac{1}{2}$-5 funicle segments, apparently 4-segmented, sutures transverse, segment 1 slightly shorter than 2 plus 3.

Prothorax from as broad as long to 1.4 times broader than long, often inflated or with strongly rounded sides (rarely sides almost straight), width, when inflated, often equalling or exceeding maximum width of elytra; base straight or weakly bisinuate; sides produced anteriorly to form weak to very strong post-ocular lobes, hind angles sometimes similarly produced posteriad; lower margins of post-ocular lobes continuous with broad median ventral emargination which permits deflexion of head by up to 90° to the horizontal, when vibrissae may cover lower part of eye (pl. 3g).

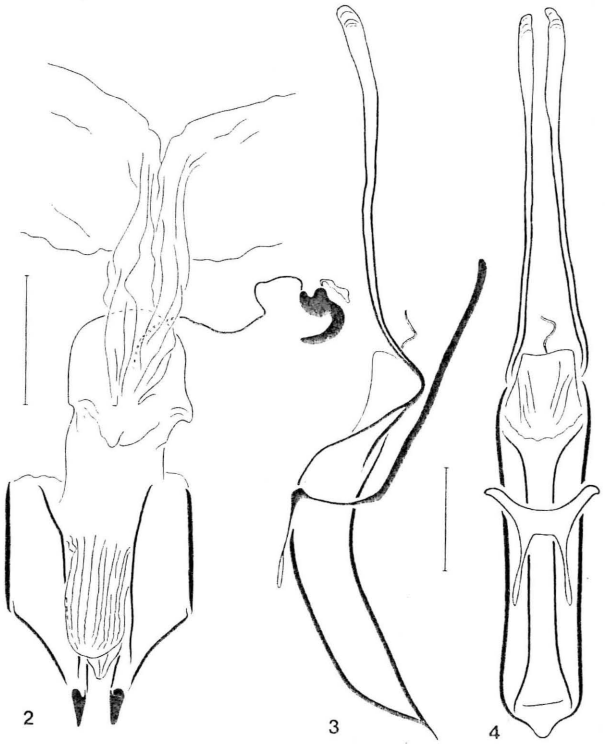
Elytra elongate-ovate, more or less keeled at base (at least towards sides), without any humeral swelling (except in *L. transversalis*); apex mucronate or not; costal margin almost straight to distinctly sinuous, with or without notch to receive enlarged anterior end of metepisternum; striae marked by impressed lines and puncture-rows, stria 10 usually complete but sometimes broadly interrupted in middle; scutellum always present and distinct but not always raised above level of rest of mesonotum.

Prosternum with variable intercoxal processes which may separate fore coxae widely, narrowly or (rarely) not at all; mesosternum with intercoxal process usually about as long as broad (fig. 5) but sometimes distinctly transverse; mesepimeron reduced, so that mesepisternum is usually in contact with elytron for about one half of former's exposed length; metasternum not strongly transverse, shortest distance between middle coxal cavity and posterior margin equal to 0.8-2.0 times longitudinal diameter of a middle coxa; metepisternum very variable in shape but suture with metasternum always complete; metepimeron exposed (figs 7, 9, 11) or not.

Venter variably convex (rarely inflated); intercoxal process of ventrite 1 usually narrower (rarely wider) than an adjacent coxa, sides straight, converging apicad, apex obtusely wedge-shaped; ventrite 2 from 0.6-0.8 times as long as 1 (measured in midline), 3 and 4 subequal, about half as long as 2 and 5, apex of 5 broadly ogival in female, more or less truncate in male (not otherwise modified in either sex); suture between ventrites 1 and 2 sinuous or angulate (rarely almost straight).

Legs subequal, fore legs not larger than hind; femora weakly to moderately swollen but never inflated and without any teeth or other projections; tibiae mucronate, mucro on hind tibiae often reduced or obsolete and concealed by setae, inner (ventral) edge of each tibia with variable row of teeth, those on hind tibia often very small or granuliform (sometimes absent), corbels of hind tibiae very variable, usually more or less imperfectly enclosed; tarsi variable, densely setose beneath, at least at sides of segments 1 and 2 with adhesive pads on segment 3; claws simple, free, divergent, often squamose or setose at base.

Aedeagus with median lobe about as long as pronotum (sometimes only half as long), curved, subcylindrical, 3.5-5.4 times as long as broad, apex shortly acuminate, phallotreme pre-apical; apodemes about as long as median lobe (rarely nearly twice as long); internal sac membranous, often with complex paired and median lobes, apex sometimes with rigid folds forming a distinctive shape (the signum) in each species; transfer apparatus very small, usually including a thorn-like structure suspended in opening of gonopore; tegminal ring complete, with well developed dorsal processes (figs 3 & 4), manubrium 0.5-0.8 times as long as median lobe; spiculum gastrale about as long as median lobe.



Figures 2-4. Genitalia of *Leptostethus marginatus*. 2. Female, 3-4. Male (aedeagus and tegmen in lateral and dorsal view). Scale-lines = 1 mm.

Ovipositor (fig. 2) rather strongly sclerotized and pigmented, very stout, from slightly longer than broad to about twice as long; valves subparallel-sided, coxites very strongly tapering, apices strongly mucronate, styli absent; bursa copulatrix small, S-shaped, without any special structures; spermatheca relatively very small, duct-lobe and gland-lobe juxtaposed, duct about 3 times as long as spermatheca, gland roughly cylindrical;

sternite 8 in form of oblong plate, apex rounded and finely setose, with median emargination, apodeme 0.4-1.1 times as long as plate.

Remarks

Contrary to the statement by Marshall (1949: 180) *L. marginatus* was designated as type species of *Leptostethus* by Waterhouse when he erected the genus; Marshall's designation of the same species is therefore unnecessary and Voss's attribution (1974:425) of the designation to Marshall is incorrect.

Although the species of *Leptostethus* are all apterous (the wings are represented by a delicate ribbon of membrane, unsupported by any veins), their elongate form, free elytra, distinct scutellum and the persistence of the metepisternum as a visible and separate sclerite all indicate that aptery is a recently acquired condition. The presence of adhesive tarsal pads, rapidly lost in ground-living weevils, indicates that *Leptostethus* species spend much of their time on plants. The deciduous mandibular processes show a dramatic reduction in relative size in the nominate subgenus and especially in the Namib species. If, as is generally assumed, these processes help the newly-emerged adult to dig its way out of the earth, their reduction in dune-dwelling species is to be expected.

The cuticle is usually black, brown or blackish red but some species have bright red legs and a few (notably *L. speciosus)* have a red rostrum. A number of *Leptostethus s. str.* are more or less extensively covered with brilliant metallic blue or green scales; in others the scales at the sides of the elytra are bright yellow or orange (but not metallic). This matt colour seems to be caused by a cuticular exudate similar to the 'pollinosity' described by Jekel (1860), remarked upon by Marshall 1916: 15) and reported in *Catasarcus* (Entiminae) by Thompson (1968). In *Leptostethus,* however, it is seldom detectable as solid granules but is more like a stain. Marshall (1938: 181) refers to a 'suffusion of orange' on the sides of the elytra in *L. viridicollis.* Only soft scales are affected. The bleaching of the cuticle noted in *Catasarcus* by Thompson (1968: 364) has been observed in a few specimens of *L. speciosus* and *L. marginatus.* I am convinced that this is a *post mortem* effect caused by intense insolation and sand-blasting. This view is supported by Holm & Scholtz's observation (1980: 24) that 'dead but intact specimens [of *L. speciosus*] littered the dunes at the end of July' at Gobabeb.

As with many entimines, the size ranges within the individual species are often wide. More remarkable in this case, however, is the range of size among the species which extends from 4-28 mm. Expressed more graphically, the smallest specimen is shorter than the pronotum of the largest! This, together with the wealth of curious, even bizarre, features they display makes this one of the most fascinating of weevil genera.

While I unreservedly follow Marshall (1949: 180) in maintaining the integrity of *Leptostethus*, I am able to distinguish within it two subgenera and, in one of these, a series of species groups. These groups are based on characters of the internal sac of the aedeagus. Happily, they correlate both with certain external characters and with the ranges of the species (figs 48, 137-147).

Notes on the key

The key is largely a natural one, *i.e.* the dichotomies reflect the taxonomic grouping of the species. This should enable additional species to be recognized as such and inserted at the appropriate point without having to recast large sections of the key. Although most species exhibit sexual dimorphism, I have usually managed to bring both sexes out together by using non-sexual characters. The male internal sac, which is not readily demonstrable, is used only where there is no alternative. Supplementary characters are given in parenthesis. Ranges are included as they are often diagnostic.

Body length was measured from the front of the eyes to the apex of the elytra, excluding any mucrones and making due allowance for any displacement of the prothorax. Rostral length was measured from the front margins of the eyes to the cleft between the apical lobes, using an eye-piece scale with cross-lines; the cross-lines at right angles to the scale was laid across the eyes and the scale moved into position between them. The antennal and tarsal segments were measured from the basal constriction between the segment proper and its condyle. Elytral length presents a special problem in that accuracy can only be guaranteed if the specimen is tipped forward so that the base and apex of the elytra lie in the same focal plane. In this case, however, since the elytra are rather elongate, I took the measurement parallel to the horizontal axis of the specimen. It is also difficult to measure the proportions of the intercoxal process of the mesosternum since its base is undefined and its sides taper. The method used here is shown in fig. 5. The setae on the mentum can only be clearly seen when they are inclined towards the observer and thus catch the light. This positioning is often difficult to arrange, especially if the head is strongly deflexed. The greatest care must be taken to distinguish between the setae on the mentum and those arising from the maxillae (at the sides) and from elsewhere on the labium (in front) (pl. 1a-c). I have used the term 'flocculent' to describe soft-looking scales which, when crowded together and partly raised, somewhat resemble the tufts of a carpet. Because of variation in shape, the width of the median lobe of the aedeagus was measured at the middle of its length and is therefore a minimum, rather than a maximum, figure. For notes on the correct interpretation of the figures of the internal sac, see Appendix, p. 79.

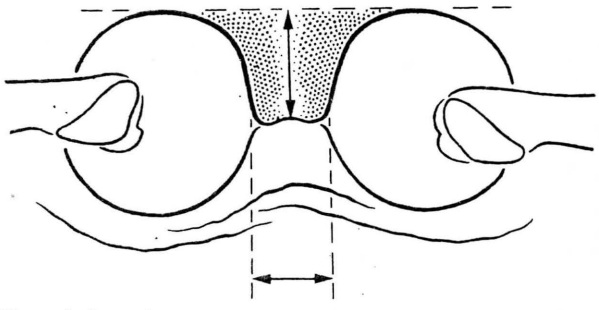


Figure 5. Part of sternum of *Leptostethus marginatus* showing how proportions of intercoxal process of mesosternum (shaded) are measured.

Material examined
(9 specimens)

Type material: Holotype ♂, Namib Desert, Gobabeb, 20 m S, June 1969, E. Holm (TM).

Paratypes: 2 ♂, Gobabeb, 23°03'S, 15°0'E, 408 m (TM, BMNH); 1♂, ditto, plus trap no. 1255 and 'probable locality' (BMNH); 1♀, Gobabeb, 70 m SE of Walvis Bay, June, 'sandy dunes'; 1♂, Namib Park, SE corner, 23°34'S, 15°45'E, 10 April 1975, S. Endrödy-Younga, E-Y: 845, 'ground traps 62 day'; 1♂, Rehoboth District, Hebron Farm, 2 May 1969, H.D. Brown; 1♀, Tsondabvlei 30 April 1969, H.D. Brown (all TM); 1♀, Guinasibberg, SE 2515 Ba3, 5 July 1976 (collector unknown) (TM).

Distribution: Recorded in the northern part of the southern Namib (fig. 146).

Remarks

This species is fairly readily distinguished from the other two members of the subgroup by its more strongly tapering rostrum, elongate rostral declivity and pale stripe on elytral interstria 5. The present specimens show considerable variation in the shape of both the prothorax and the elytra (especially in the females). The pronotum is finely granulate in larger specimens but smooth in some of the smaller ones. The hind angles of the prothorax are prominent in some specimens but not in others. In view of this variation and considering the extensive area from which these specimens come, it seems likely that some subdivision of the species will prove necessary when more material becomes available.

The name refers to the striped effect produced by the dense pale scales on suture and interstria 5 of each elytron.

A specimen from 'Buellsport' (= Büllspoort), taken with the types of *L. fallax*, appears to belong to a further member of the *uniformis* subgroup. It is one of the specimens which Voss (1974: 429) doubtfully identified as *L. simplex* (Péringuey).

LEPTOSTETHUS WALTONI SUBGROUP

These are medium-sized species (7-15 mm), distinguished from all others by having a dense fringe of setae along the inner edge of the fore tibia and the hind tibia flattened or weakly sulcate on its dorsal spect, towards the apex. The subgroup comprises two species complexes, one consisting of three fairly distinct species, the other of an uncertain number, of which two are here described.

LEPTOSTETHUS WALTONI COMPLEX

Of the three components of this complex, one is isolated from the others and has a very restricted range; the other two have extensive ranges which are contiguous. Although these two species are normally easily distinguished, some specimens from the area of contact show intermediate characteristics.

Leptostethus (L.) waltoni Waterhouse
(Figs 100-105, 144; pl. 1b; pl. 7b)

Leptostethus waltoni Waterhouse, 1853: 177; Lacordaire 1863: 260; Gemminger & Harold 1871: 2318; Schenkling & Marshall 1931: 47; Marshall 1949: 180, 182; Holm & Scholtz 1980: 10, 16, 18, 20, 24, 30, 31, 36, fig. 6-101.

Redescription

Male. Length 7.3-13.5 mm. Head and body black, femora wine-red (apices usually blackish), rest of legs and antennae blackish red or black, rostrum sometimes red; scales either all large, soft, loose and strongly imbricate (flocculent) and suffused with yellow stain, or those on legs, head, pronotum and disc of elytra smaller, hard, round, appressed, bluish grey, with pearly lustre; setae on body inconspicuous.

Head with frons flat or weakly convex, smooth, with irregularly scattered punctures of two sizes, surface becoming rugose posteriorly and strongly granulo-rugose on vertex; scales scattered irregularly or occupying depressions, sometimes forming patterns of anastomosing lines (never covering surface completely); eyes every broadly ovate-acuminate, moderately convex, surrounded by deep scale-filled groove.

Rostrum 1.14-1.26 times longer than broad, sides straight, weakly tapering apicad, genae narrowly exposed in dorsal view; upper surface flat, more or less level with frons and separated from latter by sharp furrow (often incomplete in midline), sometimes with broad median sulcus, lined with concentric arcuate rugae, and pair of weak adlateral grooves, weakly diverging apicad, running from base to level of antennal insertions, but usually without either; apical declivity evenly rounded in side view, very steep, central part raised and defined by pair of short, smoothly rounded, ill defined, longitudinal carinae which evanesce at top of declivity; surface smooth, evenly punctured throughout, entirely covered with small, mostly tessellate pearly scales; genae, mandibles and scrobes with similar but larger, mostly contiguous scales, upper surface with similar but less dense scales; mandibular scars very small, their longest diameter equal to about one third of length of genal socket (base of mandible).

Antennae with scape evenly curved, gradually and strongly clavate; funicle segment 1 strongly and evenly widening from base to near apex, 2.0-2.4 times longer than broad, segment 2 half as long as 1 and 1.4 times longer than broad, segments 3-7 quadrate or weakly transverse; club fusiform, 2.2 times longer than broad and as long as four preceding funicle segments; scape and funicle covered with small, mostly imbricate, often elongate scales; setae small and pale, those on scape mostly recumbent and inconspicuous.

Prothorax weakly inflated, slightly narrower than elytra (but appearing wider), 1.36-1.50 times broader than long, broadest about middle, sides strongly and fairly evenly rounded, apex distinctly narrower than base; apex straight, base bisinuate; post-ocular lobes well developed, not, or weakly constricted at base; disc of pronotum almost flat, with faint traces of impressed median line; entire upper surface and sides (except narrow

anterior border) uniformly covered with flattened, irregularly shaped, shiny granules, interspaces usually packed with pale scales, producing speckled effect (pl. 7b); setae small, pale (hyaline), recumbent and inconspicuous; fore coxae separated by prosternal processes.

Elytra 1.58-1.73 times longer than broad, broadest about one third of length from base, sides very weakly and evenly rounded in basal half, becoming increasingly strongly so towards ogival apex; dorsal profile similar to side; interstria 1 raised near apex and terminating in a very small, blunt mucro; costal margin weakly sinuous, including shallow excision to receive enlarged anterior end of metepisternum; striae weakly and narrowly impressed, strial punctures deep, seldom distorting interstriae but gaps between successive punctures narrow, septiform; interstriae weakly convex, 5 often broader than 4 and 6, covered with scales which almost obscure strial punctures; interstrial setae small, hyaline and recumbent, difficult to see against scales but granules from which they arise clearly visible as scattered black points; strial setae much smaller but clearly visible in linear gap between scales of adjacent interstriae; scutellum broadly rounded posteriorly, covered with imbricate pearly scales.

Legs with femora moderately swollen; fore tibiae slender, incurved in apical third, mucro small, concealed in dense fringe of soft hyaline setae which extends along apical half of ventral (inner) aspect; middle and hind tibiae slightly shorter than fore, straight, mucrones concealed in apical tuft of soft setae; corbel of hind tibia surrounded by soft hyaline setae, bevel distinct but poorly defined, covered with pale, shiny, flattened, elongate recumbent squamiform setae; fore and middle tibiae with about 6 small, widely spaced, peglike teeth on inner aspect, hind tibiae without or with very small teeth but with long, suberect, soft setae all round (except on flattened dorsal aspect); tarsi subequal, fore slightly larger than others, segments 1 and 2 subtriangular, slightly broader than long, claw segment 1.5-1.7 times as long as segment 3, segment 1 larger than 2 and with longer, denser fringing setae, longest sometimes equal to width of segment; claws stout, strongly curved, with setae and scales at base.

Sternum with mesosternal process narrow, tapering, middle coxae separated by 0.3-0.4 times diameter of one of them; metepisternum narrow, covered with imbricate scales (about two rows); venter with small bare spot on hind margin of ventrite 1 and broad, very shallow sulcus near apex of ventrite 5; vestiture as on elytral interstriae except scales smaller and less strongly imbricate on ventrite 5.

Median lobe of aedeagus 3.7-4.1 times longer than broad, strongly curved in basal half, sides almost straight, very weakly and evenly tapering apicad and weakly widening around phallotreme, apex ogival, tip thin, straight, underside of apex with transverse rugae in basal half; apodemes 1.2-1.3 times as long as median lobe (mature examples); internal sac (figs 100-101) very complex, dorso-apical chamber with lateral lobes tapering and median anterior lobe deeply bifid, posterolateral lobes of terminal chamber produced posteriad to level of apex, proximal chamber strongly dilated ventrally and signum 6-lobed (figs 102-103).

Female. Length 8.0-15.0 mm. Differs from male as follows: head with frons sometimes higher than rostrum; latter usually transversely convex, variably sculptured, with narrow but distinct median carina and 2-4 less distinct admedian carinae but surface sometimes almost smooth throughout; prothorax not at all inflated, broadest in middle (small specimens) or behind middle (large specimens), distinctly narrower than elytra, pronotal granules each with distinct, setiferous puncture; elytra slightly broader, on average, 1.4-1.7 times longer than broad; ventrite 5 with apex narrowly rounded, disc flat but not sulcate.

Material examined
(436 specimens)

Type material: Holotype ♀, with BMNH 'Type H.T.' disc, 'Type.' (printed on white paper), '5206' (written on blue paper), white disc with '[B.M. 18]75.36', 'Leptostethus Waltoni, Wat. S.W. Africa' and 'examined by Lacordaire' (both in G.R. Waterhouse's hand) (BMNH).

Other material: 315 TM, 80 SM, 16 BMNH, 9 ZS, 8 SAM, 5 National Museum of Natural History, Washington, 2 NCI. Localities (from S to N): Lüderitz; Rechenberge, dunes S of, 30 m NE Lüderitz; (no locality), SE 2615 Ab4, 26°00'S, 15°30'E; Koichab, SE 2615 Bb4, Bc1, Cb2; Koichab Pan, SE 2615 Ba3, Bc; Spencer Bay, SE 2515 Cd; Awasib, 9 km W at 25°26'S, 15°24'E; Awasib sand dunes; Uri-Hauchab, 25°18'S, 15°11'E, *idem*, SE 2515 Ac2; Guinasib Mt, SE 2515 Ad, Bc1; St Francis Bay, SE 2514 Bb1, Bb2; Sesriem 137, SE 2415 Dc; Witberg, SE 2415 Cc; Sossus Vlei, SE 2415, Cb3, Cd1, Da3, Da4; Ururas, 90 km SSE, SE 2414 Bb; *idem*, 50 km SSE, SE 2315 Db; Rooibank, dunes S, SE 2314 Bc; Sandwich Harbour, SE 2314 Ad; Natab, 15 m E; Tsondab Plains, SE 2315 Cc1, Cc2, Cc3, Dc, Dd2; *idem*, 23°59'S, 15°26'E, singled on dunes; Kuiseb River, SE 2314 Bd; Kuiseb Delta, SE 2314 Ba; Spitskoppe, SE 2214 Db; Mt Swartbaken; Homeb, SE 2315 Ca, Ca/c; *idem*, 10 m ESE Gobabeb; Namib Desert Park, 2 km S of Homeb, 450 m, open sparsely vegetated dunes; Gobabeb, 23°03'S, 15°00'E, 408 m, sandy dunes, gravel plains; *idem*, 70 m SE of Walvis Bay, sandy dunes; *idem*, SE 2315 Ca3; *idem*, 10 m S, 11-20 m SE; *idem*, Game Res. No. 3.

Doubtful records: 1 ex., Torra Bay, 45 m E, November 1967, Coetzee; 1 ex., Angola, Espinheira, 10 m S, March 1968, Holm (both in TM and labelled by the same hand). These localities are well outside the established range of the species. A series of 29 specimens from Klinghartsberge (TM) appear to have been wrongly labelled; this locality lies within the range of *L. argentatus* and a long series of identically labelled specimens are recorded under that species.

Distribution: Recorded widely in the southern Namib from Rössing Mts in the north to Lüderitz in the south and up to 150 km from the coast in the Tsondab Plains (fig. 144).

Biology: This species has been been collected in every month from January to October inclusive. At Gobabeb, the adult feeds on annual plants (mainly grasses) and all three

local perennials, viz. *Trianthema hereroensis* Schinz, *Stipagrostis sabulicola* (Pitger) de Winter and *Acanthosicyos horrida* Welwitsch (Holm & Scholtz, 1980: 24).

Remarks

I have accepted Waterhouse's specimen as the unique holotype in the absence of any evidence to the contrary and because two characters mentioned in the description apply to it which occur in only a small minority of specimens, viz '[the] anterior portion of the rostrum is of a pitchy brown colour' and '[ventrite 5] is destitute of scales'. Most of the scales are, in fact, present but darkened by grease, thus contrasting sharply with the clean pale scales on the other segments. The BMNH register records only a single specimen as having been received from Waterhouse in 1875. Waterhouse does not say how he obtained the specimen and gives no precise locality for it.

This species exhibits both local and clinal variation. The granulation of the head and pronotum is much stronger in the southern half of its range (south of 25°S) than in the northern half, where, in some of the northernmost localities (Kuiseb Delta and Rössing Mts), the head is quite smooth and the pronotal granules are so weak that the surrounding scales encroach on them (as in *L. argentatus),* thus destroying the speckled effect which is normally characteristic of this species (pl. 7b). Throughout most of its range, the scales on the legs, pronotum and elytra are uniformly flocculent and tinted pale yellow but in specimens from the Tsondab Plains those on the femora, disc of pronotum and along the elytral suture are small, hard, appressed and bluish grey in colour. They contrast sharply with the flocculent scales on the rest of the elytra, which tend to be of a deeper yellow, especially towards the sides. On the femora, these smaller, separate, often translucent scales allow the red colour of the cuticle to show through, even in fresh specimens. Considerable variation also occurs in the dorso-apical chamber of the internal sac (figs 101, 105) but this does not seem to be correlated with the variation in external characters.

Leptostethus (L.) argentatus sp. n.
(Figs 30, 109-111, 144; pl. 1g; pl. 2e; pl. 7c)

Description

Male. Length 7.3-13.5 mm. Head and body black, apex (or more) of rostrum usually red, femora red (apices usually blackish), tibiae red or black, antennae and tarsi usually black; scales pale silvery grey, on dorsum shiny and with weak pearly lustre, on sides matt and more strongly imbricate, forming distinct white stripe, this marked off from greyer dorsal scales by narrow zone of smaller, subcontiguous scales which, by exposing underlying cuticle between them, create a dark stripe adjacent to the bright lateral stripe; scales at sides sometimes with faint yellow stain.

Head as in *L. waltoni* except vertex seldom strongly granulose and scales denser, often covering surface almost completely.

Rostrum as in *L. waltoni* but upper surface less often smooth and distinctly sulcate, more often flat on disc and strongly rugose or irregularly multicarinate; apical region abruptly declivous and weakly transverse (strongly transverse in *L. waltoni*), central area more clearly defined and broadly sulcate; mandibular scars smaller, their diameter about one quarter length of genal socket.

Antennae as in *L. waltoni* except club and funicle segments, on average, less elongate (funicle segment 2 often quadrate).

Prothorax 1.27-1.38 times broader than long, not, or very weakly, inflated, slightly narrower than elytra, usually broadest behind middle; upper surface and sides uniformly covered with tightly packed granules covered with scales and largely obscured by them, though position of each is indicated by tiny black spot where very small seta is inserted; otherwise as in *L. waltoni.*

Elytra elongate, 1.64-1.87 times longer than broad; apex bluntly mucronate (fig. 30); scales on interstriae 1-5 round, appressed, more or less imbricate, on 6 and 7 smaller or darker (or translucent), on 8-10 larger, softer and more strongly imbricate; strial setae very small but often squamiform and clearly visible against black spot which marks centre of puncture; otherwise as in *L. waltoni.*

Legs and sternum as in *L. waltoni* except claw segment of tarsi relatively longer, 1.7-1.8 times longer than segment 3 and setae on venter much larger and stiffer.

Aedeagus as in *L. waltoni* except internal sac with postero-dorsal lobes of dorso-apical chamber rounded, not tapering, and basal chamber less dilated ventrally (figs 109-110); signum (fig. 111) with four lobes, not six.

Female. Length 7.3-13.6 mm. Closely similar to male except upper surface of rostrum never smooth, prothorax slightly broader, 1.39-1.46 times broader than long and elytra not more than 1.8 times longer than broad.

Material examined
(458 specimens)

Type material: Holotype ♂, 'SO van Klinghartsberge', SE 2715 Db2, July 1982, E. Holm (TM).

Paratypes: 93 ♂, 107 ♀, with same data as holotype (180 TM, 20 BMNH); 14 ♂, 10 ♀, NO van Oranjemund, SE 2816 Cb2, July 1982, E. Holm; 1 ♀, Oranjemund, SE 2816, Cb2, July 1982, E. Holm; 1 ♂, same locality, SE 2816 Cb, March 1978, Izak Brewer; 5 ♂, 4 ♀, ditto, 28°33'S, 16°31'E, 27 July 1981, S. Endrödy-Younga, E-Y: 1802, 1803, 'day, on dunes'; 1 ♀, ditto, 28°35'S, 16°26'E, 28 July 1981, E-Y: 1807; 'night, hummocks'; 2 ♂, ditto, 5 November 1949, C. Koch (all TM); 5 ♂, ditto, 28°33'S, 16°37'E, 27-28 July 1981, M-L. Penrith, H 43546 (SM); 2 ♂, Orange River, 6 km from mouth, N bank, SE 2816 Cb2, 19 November 1980, J. Irish; 6 ♂, 1 ♀, Klinghard Mt, 27°18'S, 15°42'E, 29 July 1981, S. Endrödy-Younga, E-Y: 1808, 'day, sandy valley'; 2 ♂, 11 ♀, Klinghartsberge, 8 m SE, 22 November 1962, H. D. Brown & W. Fürst; 1 ♀, same locality, 10 km SO, SE

the structure of the internal sac of the aedeagus. It also supports the *prima fascie* unlikely associations of *L. namib* with the *simus* group and *L. viridicollis* with the *speciosus* group. It is also noteworthy that the first dichotomy within the nominate subgenus separates groups from the northern and southern Namib. While the nominate subgenus shows a series of derived character states in relation to subgenus *Enicoderus*, the phylogeny of its constituent species groups is quite unclear.

V. SUMMARY

The genus *Leptostethus* comprises two distinct subgenera. One of these, *Enicoderus*, with at least a dozen allopatric species, occurs mainly in the Karoo and Namaqualand while the other, *Leptostethus s. str.*, with about 30 (often sympatric) species, occurs mainly in the Namib. The nominate subgenus is better desert-adapted than *Enicoderus* and has several derived structural features including streamlining of the body, reduction in size of the deciduous mandibular processes and narrowing of the metepisternum.

The genus as a whole is remarkable for (1) strong sexual dimorphism which mostly affects the rostrum and pronotum but may also affect the antennae (*L. anatirostris* Marshall), the venter and the corbel of the hind tibia (both in *L. viridicollis* Marshall) and (2) variation in the structure of the corbel. The reduction in size of the deciduous mandibular processes is interpreted as a response to pupation in loose sand instead of soil, rendering digging by the newly emerged adult unnecessary. Contrarily, enlargement of the hind corbel in some species is interpreted as an adaptation to digging in sand before oviposition, a view supported by field observations (see above, p. 50). Judging by the shape of the rostrum and mandibles, it seems that some species may have adopted specialized feeding habits: members of the *dives* group have sharp, extrorse flanges on their mandibles (pl. 1c) while those of the *simus* subgroup have the rostrum laterally compressed, with virtually asetose genae. In the *waltoni* group, and especially in the *uniformis* subgroup, the rostrum is dorsally swollen and this swelling bears strongly against the food plant during feeding, becoming distinctly worn down as a result (pl. 2b).

The shape of the internal sac of the aedeagus provides a reliable guide for the separation of species and, in the nominate subgenus at least, a means of arranging them in groups. External characters, even gross and striking ones, are less reliable indicators of affinity and may be positively misleading. The functional significance of the varied and complex shapes of the internal sac is a subject for speculation. They may serve as a reproductive isolating mechanism (*cf. L. varius* sp. n., p. 44) but, if so, the inappropriateness of the pairing can only become apparent at a late stage in coitus.

The affinities of *Leptostethus* within the Entiminae are entirely obscure.

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