Zootaxa 3509: 35–54 (2012)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

urn:lsid:zoobank.org:pub:D0480008-24AD-47DF-93CC-4D5FDFE9042C

New leafhopper genera and species (Hemiptera: Cicadellidae) which feed on Velloziaceae from Southern Africa, with a discussion of their trophobiosis

MICHAEL STILLER
Biosystematics Division, ARC-Plant Protection Research Institute, Private Bag X134, Queenswood 0121, South Africa; E-mail: StillerM@arc.agric.za

Abstract

Four new species in two new genera of leafhoppers (Hemiptera, Auchenorrhyncha, Cicadellidae, Deltocephalinae) are described. All are associated with *Xerophyta* species (Velloziaceae, Pandanales), and are usually tended by ants. Observations and discussions of the ant associations are provided. The new leafhopper genera and species are: *Xerophytavorus furcillatus* gen.n & sp.n., from Malawi, and the following from South Africa, *Xerophytavorus rastrullus* gen.n & sp.n. (Opsiini), *Xerophytacolus claviverpus* gen.n & sp.n. and *Xerophytacolus tubuverpus* gen.n & sp.n. (Opsiini).

Key words: Afrotropical, phytophagous, ants, *Xerophyta* spp, Cicadellidae, Auchenorrhyncha

Introduction

This paper describes and illustrates two new leafhopper genera with four new species from Southern Africa, all associated with *Xerophyta* (Velloziaceae, Pandanales). The new taxa are are allocated to the Deltocephalinae, which now comprises more than 6200 species (Zahniser & Dietrich 2010). This is a rare occurrence in Opsiini of a trophobiotic relationship with ants on a monocotyledon [Trophobiosis – the relationship in which ants (Formicidae) receive honeydew from members of the Auchenorrhyncha and provide these insects with protection in return (Torre-Bueno 1989)]. Trophobiosis has been reported on *Terminalia* spp. (Combretaceae) by Knight (1973) between the ant, *Camponotus* and the leafhopper, *Hishimonus viraktamathi* Knight. More well known examples are in Macrostelini (*Dalbullus* DeLong) on *Zea* (Moya-Raygoza & Nault 2000; Moya-Raygoza & Larsen 2008) and Balcluthini (*Balclutha* Kirkaldy) on *Calamagrostis* (Steiner *et al*. 2004). One of the new genera, *Xerophytavorus*, was often observed in groups with ants in attendance on *Xerophyta*. This plant genus is distributed throughout Central and Southern Africa, Madagascar and Arabia (Stevens 2001). *Xerophyta retinervis* Baker has mainly been examined in South Africa for the presence of ants and by sweeping for leafhoppers. Some populations in South Africa and elsewhere (*e.g*. *Xerophyta* sp., in Swaziland, Figs 22, 23, and Zimbabwe, Fig. 24) were devoid of leafhoppers, possibly as a result of regular fires or competition from aphids (personal observation). Some plants have hairy leaves (Fig. 25) from which the other new genus, *Xerophytacolus* was also collected, but more rarely with ants. Most observations were undertaken in a nature reserve within an urban environment (Fig. 27). No leafhopper species have yet been found on the low-growing *Xerophyta viscosa* Baker. None of the 190 examined adult leafhopper specimens showed signs of parasitism by Strepsiptera, Dryinidae or Diptera. Four nymphs of *Xc. claviverpus* carried pupal cases of dryinids on their abdomens.

Ant associations with leafhoppers

Regular anecdotal personal observations concerned mainly colonies of adults and nymphs of *Xerophytavorus* species attended by ants (Figs 15–21). Aphid colonies were common and always tended by ants, whereas leafhopper colonies were never found on the same plant with aphids, and rarely with more than one leafhopper

Accepted by C. Dietrich: 26 Sept. 2012; published: 8 Oct. 2012

colony per plant. Adults of *Xerophytacolus* (Figs 8–14) could be observed while feeding, but have rarely been observed with ants. As the nymphs (Figs 5, 9 and 14) of both genera are so similar in color and shape, it is possible that both occur together in a single group, although this was not observed. Occasionally adults or nymphs were seen on the dark trunk of *Xerophyta* and at the base of leaf clusters.

The larger ant species such as *Camponotus eugeniae* Forel (Formicidae) have been observed in attendance of *Xv. rastrullus*, and appeared to be more successful in herding the leafhoppers and keeping them in a group, often on exposed leaves (Figs 19–21). They were probably more adept at preventing the leafhoppers from jumping or walking away especially when disturbed and possibly keeping predators away, as was also reported by Moya-Raygoza & Nault (2000), Larsen *et al.* (2001) and Rico-Gray & Oliveira (2007). These ants also appeared to protect the leafhoppers more vigorously than smaller sized ants. The large ants would vibrate their bodies and face towards the threat with opened mandibles. Even late in the season one or two leafhoppers were closely guarded by *C. eugeniae*. Large and small-sized species of ants were occasionally observed together at a colony of leafhoppers, where the latter appeared to steal secreted droplets.

The smaller ants, such as *Lepisiota incisa* (Forel) attending leafhoppers were more difficult to find and observe. They were near the base of the leaf or leaves, or where leaves were close together (Figs 15, 16). Smaller ants appeared less successful at keeping the leafhoppers together and required more individuals to succeed. One group of leafhoppers tended by small ants was observed over three weeks but it eventually disappeared. Adjacent leafhopper colonies that were tended by larger ants persisted longer. In both cases colonies disappeared as the plant became moribund, and as nymphs matured. The smaller ants possibly derived greater reward from the relatively larger volume of liquid expelled by the leafhoppers and were more successful at finding the droplets. Leafhoppers were not induced to expel fluid, unlike the habit reported by Steiner *et al.* (2004), and as is the case in Membracidae and Tettigometridae (Quartau 1990, Delabie 2001, Rico-Gray & Oliveira 2007). Medium sized ants (Figs 17, 18) were as successful as the larger ants, and showed less aggression when disturbed, although leafhoppers were seen to reflex their hind legs in a defensive stance, which with larger or smaller tending ants resulted in leafhoppers dispersing.

The leafhoppers in Malawi were easily found by looking for knotted or touching leaves of *X. splendens*. In this situation the ants constructed encasements of chewed plant material around the leafhopper. *Crematogaster* sp. (Formicidae) ants were associated with *Xv. furcillatus* in Malawi, which nests in trees and all *Crematogaster* species actively tend homopterans. Moya-Raygoza & Larson (2008) reported on encasements produced by ants on gamagrass (*Tripsacum dactyloides*) in Mexico which protected leafhoppers against parasitoids. Encasements in South Africa on *Xerophyta* have hitherto only been found around aphid colonies and appeared to have been constructed by *Crematogaster* ants. The plants in Malawi where these leafhoppers were collected were tall, and therefore probably protected from grass fire. By contrast, a patchy distribution of leafhoppers on *Xerophyta* species in South Africa and their apparent absence in Swaziland could be the result of fire. Occasionally taller plants (e.g. Fig. 26) were examined and produced fewer leafhoppers. In this region the plants were much shorter and probably susceptible to fire as was noticed in a population at Ezemvelo Nature Reserve. A similar situation on gamagrass was reported by Moya-Raygoza (1995) in Mexico. So far no accumulation of sooty mould has been observed on *Xerophyta*, unlike that reported by Nault *et al.* (1983) on *Tripsacum* and *Zea* species.

Xerophytavorus rastrullus was tended by *Myrmicaria natalensis* (F.Smith) and *Camponotus eugeniae* (Figs 19–21), collected from Klapperkop, Pretoria. *Anoplolepis custodiens* (F.Smith) tended this leafhopper at Bronberg, Swawelpoort (Figs 17, 18), which is more than 10 km due east of Klapperkop.

Xerophytacolus tubuverpus has a wide distribution, but myrmecophily by *Lepisiota incisa* (Figs 15, 16, tending *Xerophytavorus* sp.) was only observed once at Faerie Glen, Pretoria. This ant has become very abundant in cities in South Africa, especially in well-vegetated suburbs. It is very abundant in the Kruger National Park rest camps but absent from the surrounding savannas, and seems to be indigenous to Africa but might not be indigenous to South Africa.

Common cases of ant attendance in South Africa are found in *Macropsis* Lewis (Macropsinae) and in *Batracomorphus* Lewis (Iassinae). Linnavuori (1978) and Quartau (1990) reported that only *M. myrmecophila* was associated with ants. In South Africa a rare observation was made of a heavy infestation of *Macropsis* sp. near *M. octopunctata* China, on a small *Acacia* (Fabaceae) tree growing under the tree canopy associated with ants of the species *Pheidole megacephala* Fabricius (collected from Elandskrans Resort, Waterval Boven, Mpumalanga Province). This ant occurs in various habitats ranging from savanna to woodland and even in gardens and orchards.

It is a tramp species but is indigenous to Africa where it has a wide distribution in mesic habitats with trees, and nests in soil or in dead wood on the ground or in trees. It often tends homopterans, *e.g. Hilda patruelis* Stål, Tettigometridae (Compton & Robertson 1988). On the other hand, one species of *Batracomorphus* has been observed more often in attendance by ants in South Africa, mostly on *Combretum* sp. (Combretaceae). Quartau (1981) mentioned the rare event of ant-leafhopper associations in *B. punctatissimus* (Melichar). However Knight (1983) in the revision of the Eastern and Australian members of *Batracomorphus* did not mention an association with ants. Thus far none of the reports of ant-leafhopper interactions recorded by Dietrich and McKamey (1990) from North and West Africa have been observed in South Africa.

Material and methods

Specimens were collected with a sweep net, DVac vacuum collection machine and directly from plants. Dissections were made from abdomens cleared in cold KOH. Drawings were made with a drawing tube on a dissecting and transmission microscope. Images were captured in the field with various digital cameras, and in the laboratory with an Olympus SZH microscope and dedicated digital camera. Terminology follows Blocker & Triplehorn (1985) with additional terms for leg chaetotaxy following Rakitov (1998). Type material is deposited in the South African National Collection of Insects Pretoria (SANC), with additional paratypes in the Natural History Museum, London (BMNH) and Illinois Natural History Survey, Champaign, Illinois, USA (INHS).

Xerophytavorus gen.n.

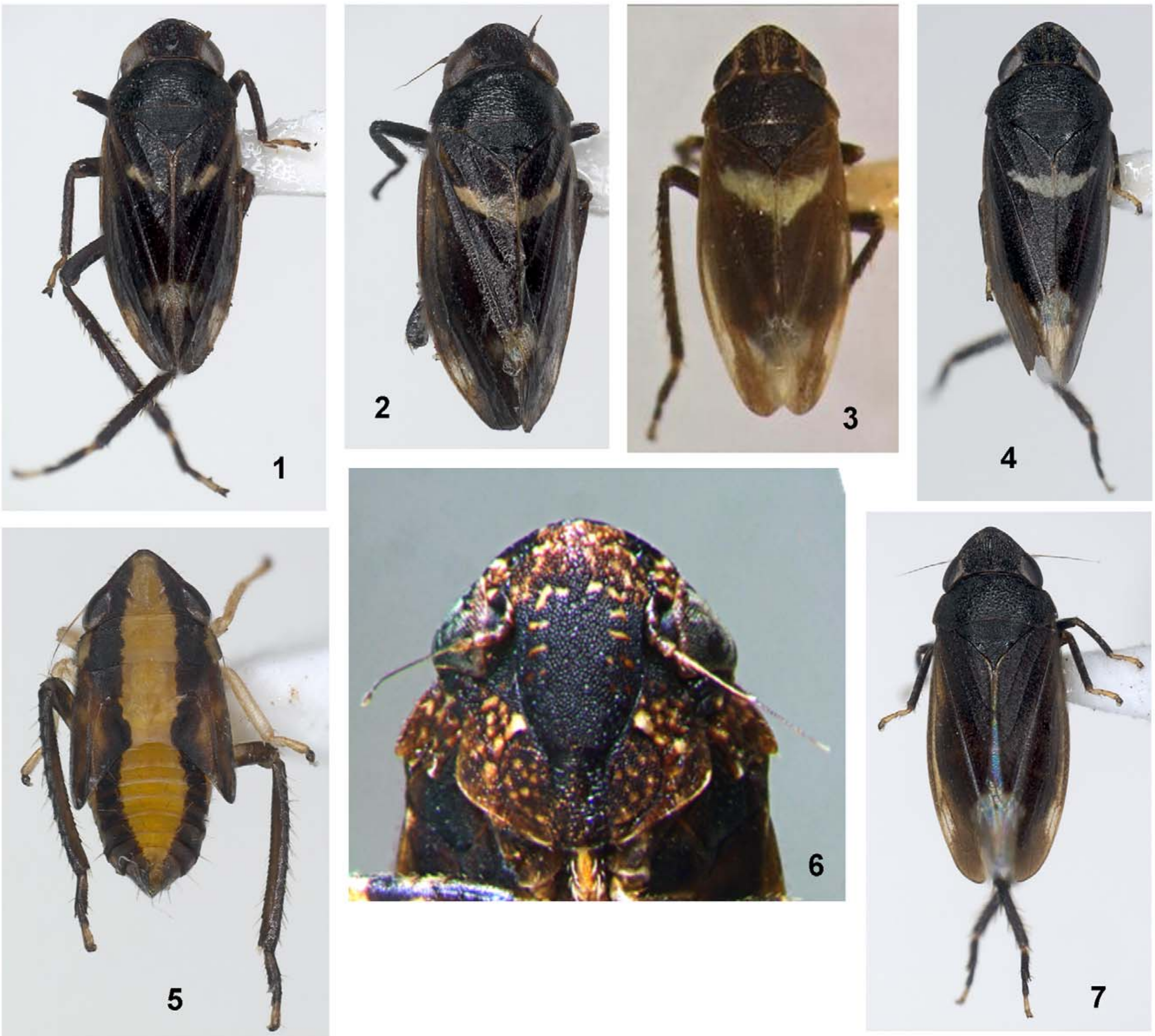
Type species: *Xerophytavorus rastrullus* sp.n.
(Figs 3–7, 52–76)

Gender masculine

Diagnosis. Fuscous dorsally, sometimes with whitish or yellowish transverse marking in claval region of tegmina (Figs 1–4, absent as in Fig. 7). Vertex and pronotum rugose. Transition between vertex and face with dorsal carina (Figs 28, 30). Aedeagal shaft biramous (Figs 38, 54), connective closely articulated with aedeagus, arms widely separated, stem short, about half as long as arms. Paired pygofer process with modified apex arising medioventrally from pygofer (Figs 40, 60). Pygofer lobe medially with dense cluster of setae (Figs 35, 40, 59, 60). Subgenital plate without macrosetae (Fig. 37).

Etymology. Compound word in Latin, *Xerophyta*, generic name for the host plant, *voro*, to eat, consume, as this leafhopper feeds on this plant.

Male and female. **External morphology**. Vertex, pronotum and scutellum fuscous; dorsum punctate, pubescent (short setae arising in punctures); vertex longitudinally rugose. Pronotum rugose. Tegmina with veins and cells dark brown or brown, translucent transverse bar in claval cells, translucent area at first apical cell and in distal part of costal cell (Figs 1–4). Margin between face and vertex sharp, forming short, dorsal carina (Figs 28–30). Ocellus on face, close to dorsal margin, in front of eye, above antenna. Clypeus shagreened (Fig. 6), wide, few setae laterally. Clypellus parallel-sided, longer than wide, transclypeal suture weakly developed (Fig. 29). Genae surrounding lora distally (Fig. 29). Pronotum distinctly wider than head (Figs 1–7, 28), lateral margins carinate (Fig. 30), nearly as long as eye. Tegmina opaque with veins obscure, indicated by fine pubescence (Figs 31, 52, 64), vein R three-branched, crossvein r-m1 connected to R basad of fork, three anteapical cells present, inner anteapical cell open; vein M apparently unbranched, only 3 apical cells present, inner apical cell extended to distal margin, claval veins indistinct; appendix present, but poorly distinguished from adjacent inner apical cell. Hind wing with three apical cells (anterior branch of R absent), jugal lobe well developed (Fig. 65). Legs and venter brown, setae on hind leg pale. Pro- and meso-tarsomeres 1–3 pale, metatarsomere 3 pale or light brown. Protibia setal formula 3+1. Metafemur dorsoapical macrosetae 2+2 (Fig. 33). Profemur with anteromedial, intercalary, and anteroventral rows poorly differentiated, irregular, short across most of length of femur, longer distally, with 1–3 longer setae near apex, AM1 well differentiated. (Fig. 32). Metatibia with posteroventral row consisting of narrow, acute setae, with 2–3 distal setae slightly longer and thicker than more basal setae; anteroventral, anterodorsal and posterodorsal setae robust, wide across base, acute apically; dorsal rows interspersed with small, fine setae. Metatibial setae in PV row about half as long as width of metatibia medially; AV, PD and AD setae about as long as width of metatibia medially. Tarsomere 1 about twice as long as tarsomere 2 or 3, plantar surface with two rows of 7 macrosetae, apex with spur with seta laterally and 4 spurs with platellae medially. Tarsomere 2 with 2 platellae medially.



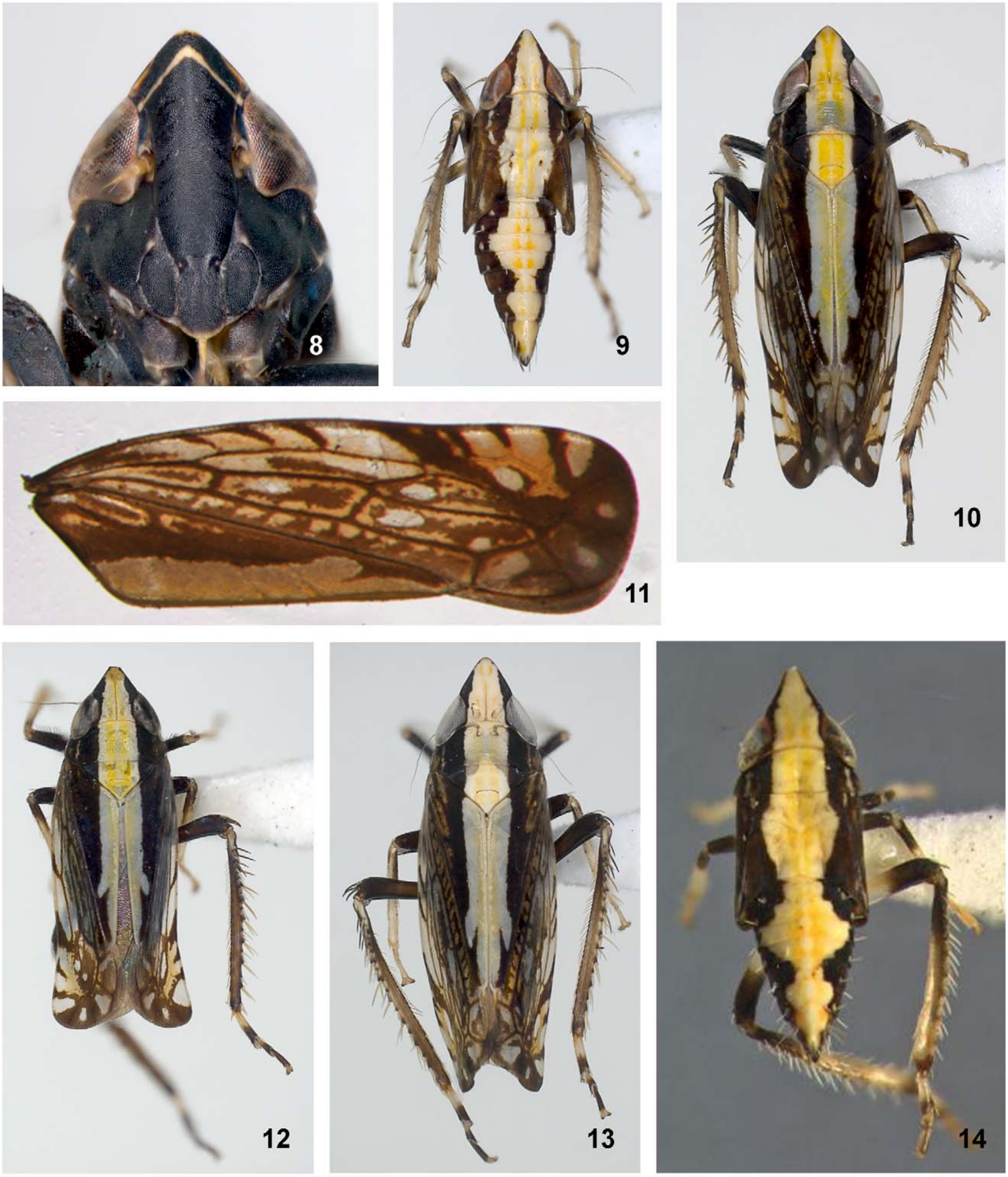
FIGURES 1–7. *Xerophytavorus* gen.n.. **1**, **2**, *Xerophytavorus furcillatus* gen.n. & sp.n., Specimen from Malawi; **1**, male; **2**, female; **3–7**, *Xerophytavorus rastrullus* gen.n. & sp.n.; **3**, female, Pretoria, collected 1970; **4**, female, Dome Kloof, Magaliesberg; **5**, nymph, Koppie Alleen; **6**, male, face; **7**, female, Swawelpoort.

Male. **Internal morphology**. Abdominal apodemes with anterior apodeme in dorsal view with rounded, membranous lobes, as long as wide (Figs 55–57). Tentorium recessed into head, base sclerotized, wide, attached near base of antenna, extending dorsally, apex tapered, membranous, branched, dorsal branch reaching vertex, right-angled ventral branch reaching face anteriad of ocellus.

Male. **Genitalia**. Pygofer, dorsally with anal tube inserted half-way or further into pygofer, anal tube triangular (Figs 35, 58). Pygofer lobe ventromedially with posteriorly directed process, apex modified (Figs 36, 40, 59, 60); pygofer lobe with cluster of macrosetae at ventromedial subapical margin, arising from variably shaped base (Figs 40, 60). Subgenital plate narrow, lateral margin concave or straight, medial margin straight, with sparse ventral setae irregularly arranged, macrosetae absent (Figs 37, 61). Paired aedeagal shaft C- or U-shaped in dorsal view

(Figs 38, 54), arms of shaft serrate medially, articulation with connective membranous. Connective Y-shaped, arms bowed laterad, stem short (Figs 38, 54). Style with preapical lobe well developed, acute, bearing several conspicuous setae (Figs 34, 63).

Female. **Genitalia**. Sternite 7 with deep median notch, margins variable (Figs 41, 67). Valvula 3 with numerous macrosetae on distal and ventral margin (Figs 42, 66). Valvula 2 elongate, apical half slightly wider than basal half (Figs 48, 72), finely serrate (Figs 49–51, 74–76). Valvula 1 lanceolate (Figs 44, 68), covered with fine semicircular or rectangular scale-like microsculpture (Figs 43, 45–47, 69–71).



FIGURES 8–14. *Xerophytacolus* gen.n. **8–11**, *Xerophytacolus claviverpus* gen.n. & sp.n.; **8**, male, face; **9**, nymph; **10**, male, The Downs, Orrie Baragwanath Pass, South Africa; **11**, forewing. **12–14**, *Xerophytacolus tubuverpus* gen.n. & sp.n., Faerie Glen, Pretoria; **12**, male; **13**, female; **14**, nymph.

Relationships. This new genus is placed in Opsiini based on the paired aedeagal shafts, each bearing a separate gonopore. Other Afrotropical Opsiini, which also have the biramous aedeagus, have the vertex rounded to the face with a smooth or at most with a shagreened texture. The new genus apparently belongs to the group of genera that includes *Aladzoa* Linnavuori, *Hishimonus* Ishihara, *Naevus* Knight, *Nesophrosyne* Kirkaldy, *Opsius* Fieber and *Orosius* Distant, in which the biramous shaft originates basally. *Eremophlepsius* Zachvatkin (Palaearctic Region), also a member of this group, has a similarly up-turned facial margin (J. Zahniser, personal communication).

***Xerophytavorus furcillatus* sp.n.**
(Figs 1–2, 28–51)

Diagnosis. Pygofer process with apex bifurcate (Fig. 40). Pygofer lobe medially with elongate area of densely set short macrosetae (Figs 36, 40). Aedeagus with shaft biramous, depressed, medial, distal margins serrate (Fig. 38).

Etymology. Latin, *furcilla*, a little fork, for the forked shape of the pygofer process.

Male, **female and nymph**. **External morphology**. Adult with pale spots and markings only on anterior part of clypeus, face (as in Fig. 6, no markings on gena and lora), lateral margin of pronotum and vertex. Tegmina with narrow translucent or whitish marking in claval cells (Figs 1, 2). Tegmina with two translucent regions or sometimes continuous band in costal and anteapical cells as well as in first apical and inner anteapical cells (Figs 1, 2). Nymph dark brown, without median, yellow longitudinal line; legs with distal tarsomeres pale (legs as in *Xv. rastrullus*, Fig 5).

Abdominal apodemes. Similar to that of *Xv. rastrullus* (Figs 55–57).

Male. **Measurements**. (n=9) Length: apex of vertex to apex of tegmina 2.10–2.24 mm; apex of vertex to apex of abdomen 1.81–2.06 mm; vertex 0.33–0.35 mm; next to eye 0.20–0.25 mm; pronotum 0.42–0.46 mm; scutellum 0.43–0.46 mm. Width: head 0.91–0.95 mm; pronotum 0.99–1.02 mm; scutellum 0.61–0.67 mm. Ocellus: diameter 2.50–3.80 µm; ocellocular distance 7.40–8.70 µm.

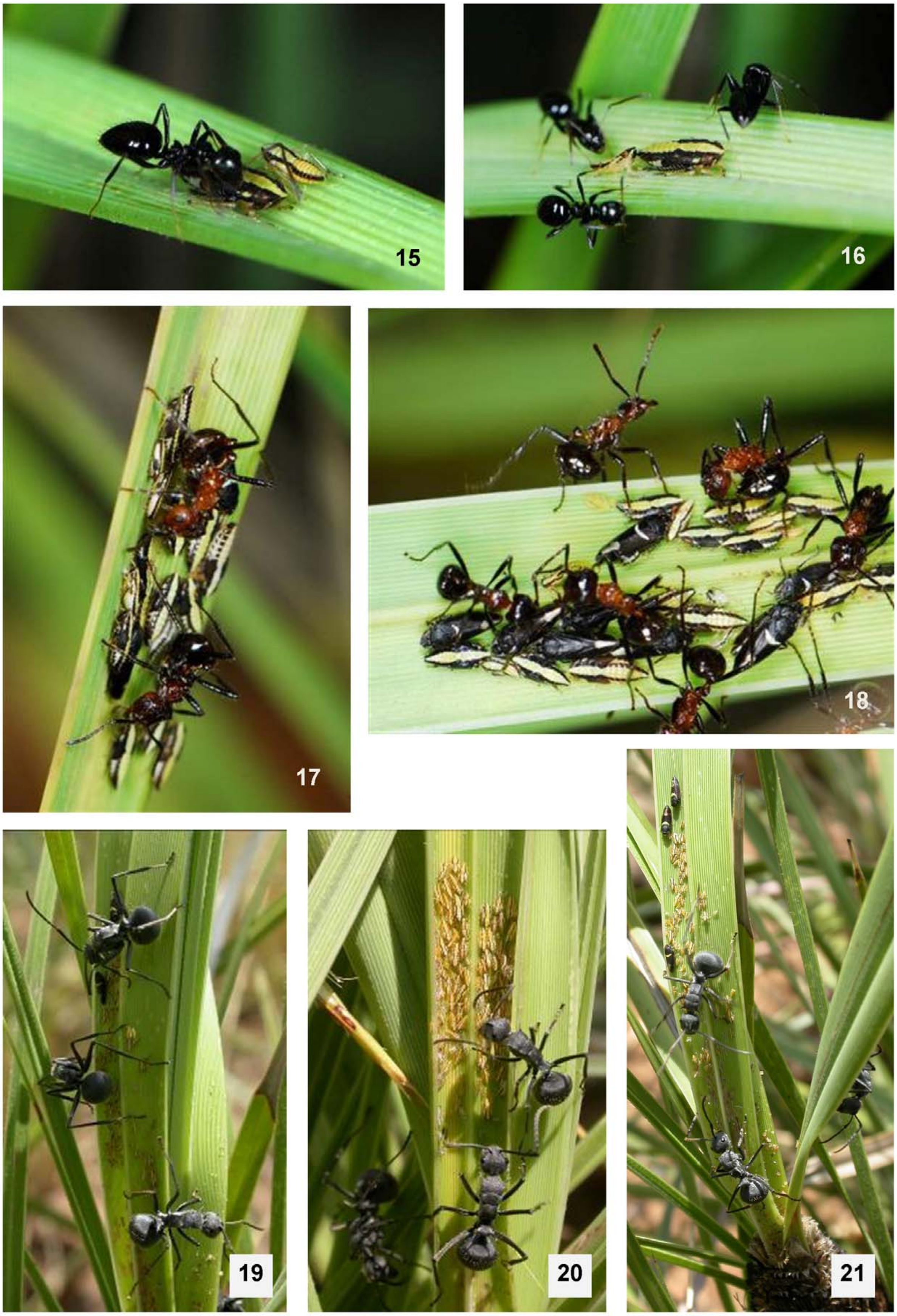
Male. **Genitalia**. Pygofer lobe with ventromedial process, apex asymmetrically biramous (Figs 36, 40); lobe subapically with medial elongate band of macrosetae (Figs 36, 40); anterior apodeme large (Figs 35, 36). Aedeagal shafts widely separated, inner margins denticulate (Figs 38, 39). Plate narrowly triangular, without macrosetae, but short, fine setae, mainly at apex (Fig. 37), lateral subapical margin rugose. Style with elongate, acuminate apophysis, tooth medioventrally; preapical angle deep, rounded; preapical lobe acute; lateral anterior lobe large, wide, right-angled, medial anterior lobe short, triangular (Fig. 34).

Female. **Measurements**. (n=9) Length: apex of vertex to apex of tegmina 2.15–2.26 mm; apex of vertex to apex of abdomen 2.11–2.26 mm; vertex 0.32–0.34 mm; next to eye 0.21–0.24 mm; pronotum 0.43–0.46 mm; scutellum 0.45–0.50 mm. Width: head 0.94–0.97 mm; pronotum 1.01–1.07 mm; scutellum 0.65–0.72 mm. Ocellus: diameter 2.95–5.14 µm; ocellocular distance 7.53–9.74 µm.

Female. **Genitalia**. Sternite 7 with deep median V-shaped notch, margins variable, prone to damage (Fig. 41). Valvula 3 (Fig. 42), numerous marginal setae from apex to base, apex narrowly rounded. Valvula 2 (Fig. 48) lanceolate; apex slightly wider than base, finely serrate (Figs 49, dorsal serration basally, Figs 50, 51, serration at apex). Valvula 1 (Fig. 44) lanceolate; microsculpturing imbricate, as in Fig. 46, near base and Fig. 47 at apex; shape of apex variable, Fig. 43, narrowed apex, Fig. 45, triangular apex.

Material examined. Holotype male. **Malawi**. Chambe Hut, Mulanje Mountain 15°58′S, 35°38′E, 1750 m, 22.xii.2002, M. Stiller, hand collected on *Xerophyta splendens* (SANC). Paratypes. 8♂, 9♀, 12 nymphs, *Ibid.* holotype (BMNH, SANC).

Remarks. This species (Figs 1, 2) and *Xv. rastrullus* (Figs 3, 4, 7) are similar in colour and shape. The pale markings in the claval region of both species are variable, with the pubescence in *Xv. furcillatus* appearing slightly longer than in *Xv. rastrullus*. Internal male genitalia provide the best means of separation of species. The distinguishing features are the shape of the pygofer process and the shape of the base of the cluster of macrosetae on the inner apex of the pygofer lobe. In *Xv. furcillatus* the pygofer process has the apex with two points, and the cluster is elongate. In *Xv. rastrullus* the pygofer process has multiple prongs at the apex, giving it the appearance of a comb, and the cluster is round. Difference in the aedeagus are also present, but more subtle. The shaft in *Xv. rastrullus* is wider with larger teeth and in *Xv. furcillatus* the shaft is tubular with smaller teeth. Nymphs are clearly distinguishable with *Xv. furcillatus* brown, and *Xv. rastrullus* with a pale marking across the length of the body (Fig. 5).



FIGURES 15–21. Ants tending leafhopper colonies on *Xerophyta* sp. **15**, **16**, Small sized ants (*Lepisiota incisa)* tending leafhoppers, Faerie Glen (images courtesy P. Webb); **17**, **18**, Moderate sized ant species (*Myrmicaria natalensis*) tending *Xerophytavorus rastrullus*, Irene (images courtesy P. Webb); **19–21**, Large sized ant (*Camponotus eugeniae*) tending *Xerophytavorus rastrullus*, Magaliesberg, (images courtesy D. Shcherbakov).

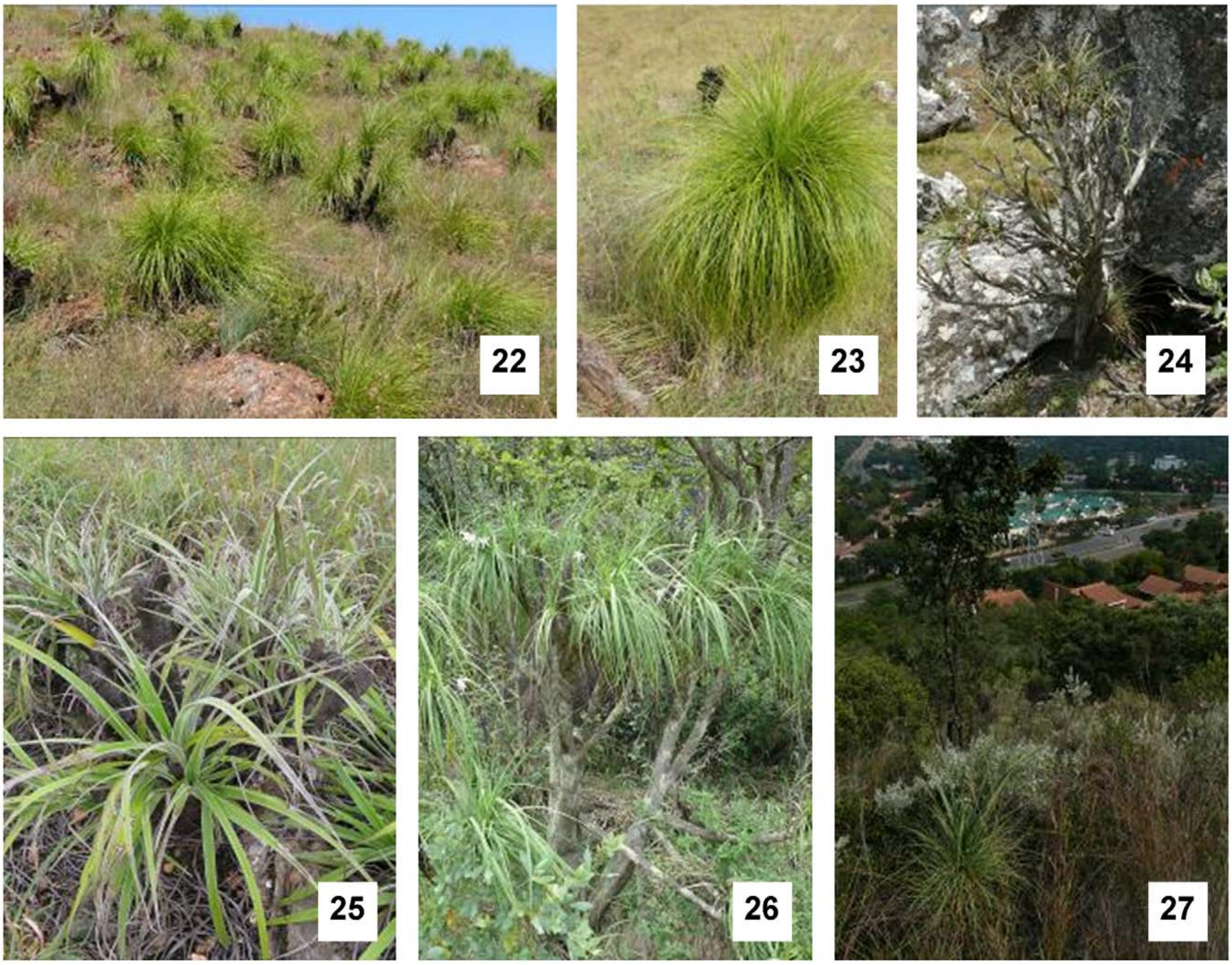
***Xerophytavorus rastrullus* sp.n.**
(Figs 3–7, 52–76)

Diagnosis. Pygofer process apex with comb-like structure (Fig. 60). Pygofer lobe medially with oval cluster of macrosetae (Figs 59, 60). Aedeagus with shaft depressed, medial and distal margins serrate (Figs 54, 62).

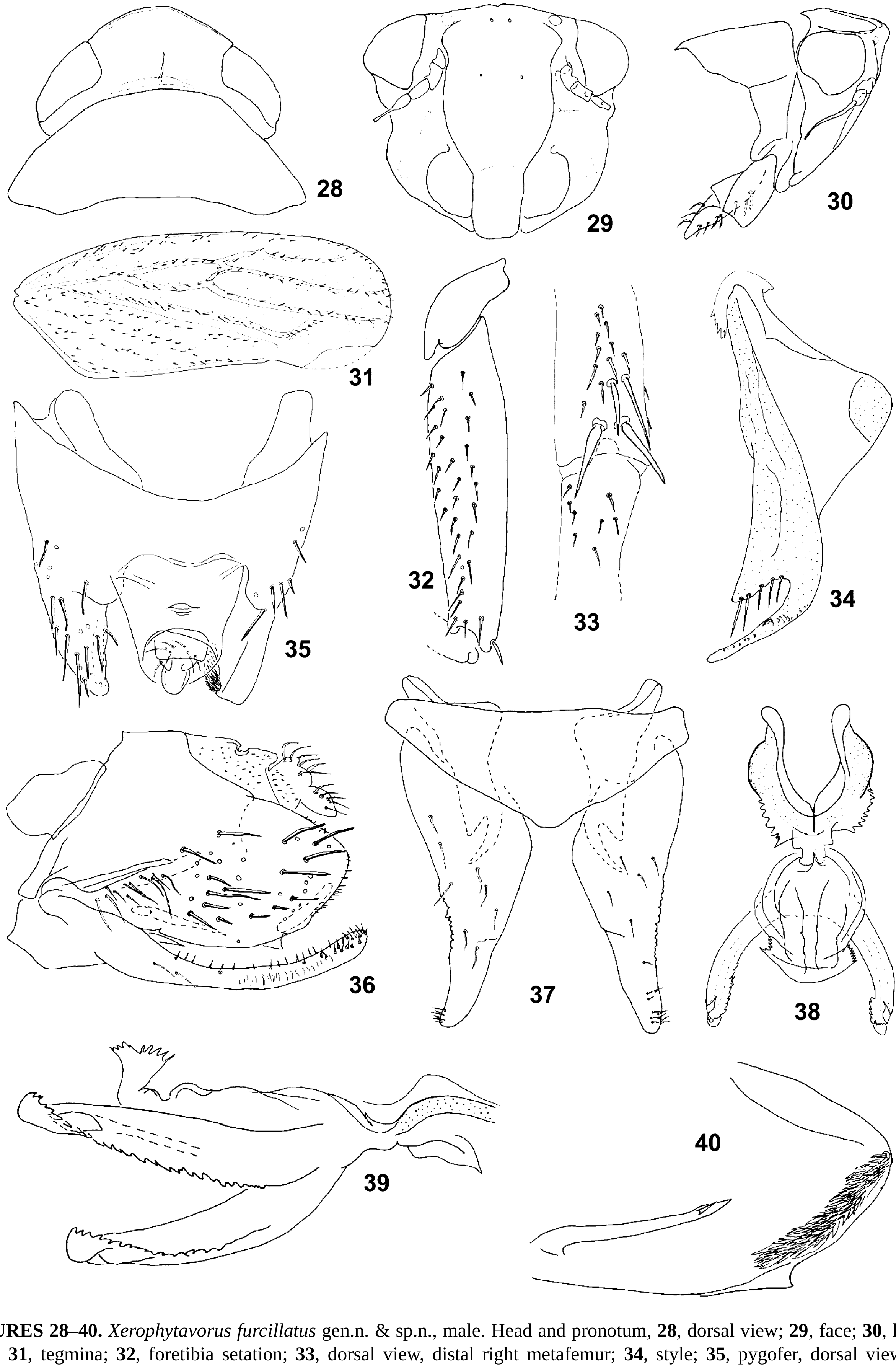
Etymology. Latin, *rastrullus*, diminutive for rake or comb, for the appearance of the row of teeth on the pygofer process.

Male, **female and nymph**. **External morphology**. Pale spots and markings on face, lateral margin of pronotum and vertex (Figs 3, 4, 6, 7). Tegmina with triangular translucent, whitish or yellow marking in claval cells on some specimens only. Marking was present (as in Figs 3, 4) or absent (as in Fig. 7) in about equal proportions in males and females (142 examined pinned and specimens in a capsule). Tegmina in male in Fig. 52, claval veins poorly developed, microsetae on most veins; apically with weakly developed or without cross-veins; appendix narrow. Female tegmina (Fig. 64) with two anteapical cells and two apical cells. Hind wing as in Fig. 65. Nymph with yellow longitudinal stripe, flanks brown; fore- and mid-legs pale, hind legs pale with distal apex of femur and tibia dark (Fig. 5).

Abdominal apodemes. Abdominal apodemes (Figs 55–57) with posterior apodeme wide, with narrow medial lobes (Fig 55, anterior view, Fig 57, dorsal view); anterior apodeme with elongate apical arms and membranous rounded, medial lobes (Fig 55, anterior view, Fig. 56, dorsal view).



FIGURES 22–27. Images of *Xerophyta* species, host plants of *Xerophytavorus* gen.n. and *Xerophytacolus* gen.n. species. **22**, **23**, *Xerophyta* sp. in grassland at Malolotja Nature Reserve, Swaziland; **24**, approx. 1 m tall plant in Chimanimani Nature Reserve, Zimbabwe; **25**, hairy-leaved *Xerophyta* sp. in The Downs, Orrie Baragwanath Pass, South Africa; **26**, up to 2 m tall plant near Lydenburg, South Africa; **27**, habitat at Faerie Glen Nature Reserve, Pretoria, where most trophobiosis observations were made.



FIGURES 28–40. *Xerophytavorus furcillatus* gen.n. & sp.n., male. Head and pronotum, **28**, dorsal view; **29**, face; **30**, lateral view; **31**, tegmina; **32**, foretibia setation; **33**, dorsal view, distal right metafemur; **34**, style; **35**, pygofer, dorsal view; **36**, pygofer, lateral view; **37**, plate and valve, ventral view; **38**, aedeagus and connective, dorsal view; **39**, aedeagus and connective, lateroventral view; **40**, process and apical macrosetae cluster on pygofer, medial view.

Male. **Measurements**. (n=43) Length: apex of vertex to apex of tegmina 1.97–2.16 mm; apex of vertex to apex of abdomen 1.72–1.98 mm; vertex 0.34–0.39 mm; next to eye 0.19–0.21 mm; pronotum 0.37–0.43 mm; scutellum 0.37–0.45 mm. Width: head 0.83–0.90 mm; pronotum 0.90–1.00 mm; scutellum 0.55–0.63 mm. Ocellus: diameter 3.60–4.50 µm; ocellocular distance 7.06–8.47 µm.

Male. **Genitalia**. Pygofer lobe medioventrally with process with comb-like apex (Figs 59, 60), lobe with apex with cluster of macrosetae, arising from ovoid base (Figs 59, 60); dorsal view as in Fig. 58, anterior apodeme short (Figs 58, 59). Aedeagal shafts sub-parallel, inner margins membranous, denticulate (Fig. 54), laterally as in Fig. 62. Plate triangular as in Fig. 61, lateral subapical margin rugose. Style with elongate, acuminate apophysis, ridge medioventrally; preapical angle deep, rounded; preapical lobe acute; lateral anterior lobe large, wide, right-angled; medial anterior lobe short, triangular (Fig. 63).

Female. **Measurements**. (n=30) Length: apex of vertex to apex of tegmina 2.02–2.18 mm; apex of vertex to apex of abdomen 1.83–2.06 mm; vertex 0.34–0.38 mm; next to eye 0.19–0.22 mm; pronotum 0.39–0.43 mm; scutellum 0.39–0.46 mm. Width: head 0.86–0.92 mm; pronotum 0.93–1.00 mm; scutellum 0.58–0.65 mm. Ocellus: diameter 3.82–4.35 µm; ocellocular distance 6.97–8.66 µm.

Female. **Genitalia**. Sternite 7 with deep median V-shaped notch, margins depicting damage (Fig. 67). Valvula 3 (Fig. 66) with uniseriate setae marginally, apex rounded. Valvula 2 (Fig. 72) lanceolate, apical half serrate, slightly narrowed medially; serration regular, fine as in Figs 74, 75 at apex, Fig. 76, medially), medial sclerotized section as in Fig. 73. Valvula 1 (Fig. 68) lanceolate; dorsal and ventral microsculpture imbricate, as in Figs 69, 71 at apex, and Fig. 70 medially.

Material examined. Holotype male. **South Africa**, Gauteng. Pretoria, 25°45′S, 28°12′E, 1450 m, 21.i.1970, B. Buys (SANC). Paratypes. 51♂, 44♀, 17 nymphs. **Gauteng**. 14♂, 8♀, *ibid.* holotype, 21.i.1970; 3♂, 2♀, *ibid.* holotype, 13.xi.1976; 5♂, 7♀, *ibid.* holotype, 13.xi.1977; 5♂, 2♀, 7 nymphs, Faerie Glen Koppies, Pretoria, 25°46′S, 28°17′E, 4.iii.1994; 1♂, 1♀, 2 nymphs, Rietfontein suburb, Pretoria, 25°41′S, 28°14′E, 1300 m, 26.xii.2001; 5♂, 3♀, Swawelpoort, Bronberg, SE Pretoria, 25°48′S, 28°22′E, 1550 m, 17.xi.2004; 2♂, 6♀, 1 nymph, Klapperkop, Pretoria, 25°46′S, 28°12′E, 1469 m, 3.iii.2006; 9♂, 7♀, 7 nymphs, Smuts Koppie, Irene suburb, Pretoria, 25°53′32.6″S, 28°14′14.5″E, 1494 m, 4.iv.2012, hand collected. **KwaZulu-Natal**. 1♂, Orange River catchment, 28°53′S, 29°01′E, 2880 m, 16.iv.2006, sweeping grass and forbs in wetland; **North-West Province**. 6♂, 7♀, Dome Kloof, Magaliesberg, near Mooinooi, 25°50′S, 27°32′E, 13.iii.2005. All collected by M. Stiller. All collected from *Xerophyta retinervis*, except where stated otherwise (BMNH, INHS, SANC).

Remarks. Differentiation between species provided under remarks on *Xv. furcillatus* above. The single, high altitude record from the Drakensberg of KwaZulu-Natal Province is not considered an error, but rather the result of migration on air currents.

Xerophytacolus gen.n.

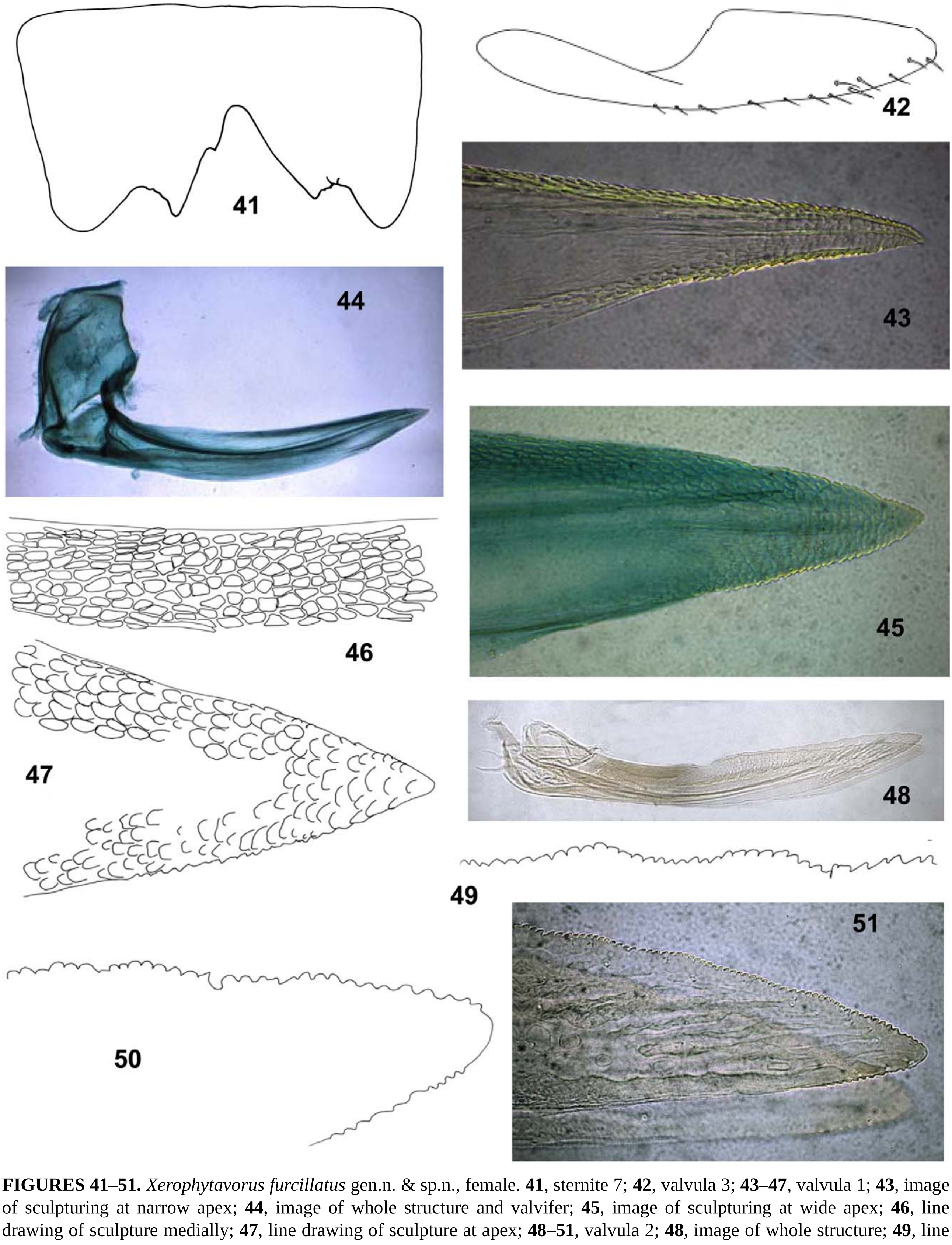
Type species: *Xerophytacolus tubuverpus* sp.n.
(Figs 12–14, 98–122)

Gender masculine

Diagnosis. Coloration distinct, with median yellowish longitudinal stripe flanked laterally by solid fuscous marking extending into tegmina with translucent and yellow cells (Figs 10–13). Face fuscous with single, narrow yellow submarginal line (Figs 8, 99, 100). Head acutely produced, longer than width between eyes. Male pygofer lobe at apex with median process (Figs 83, 84, 105, 107, 108). Plate generally rectangular, with lateral and medial margins convergent; macrosetae present, apex truncate (Figs 81, 106).

Etymology. Compound word in Latin, *Xerophyta*, name of the associated plant; suffix -*cola*, inhabitant.

Male, **female and nymph**. **Colour**. Base color fuscous. Dorsum with yellowish median longitudinal stripe, extending into tegmina to claval suture (Figs 9, 10, 12–14). Face with single, pale yellow transverse submarginal line (Figs 8, 99, 100). Venter fuscous, with some pale yellow spots or markings. Abdomen with yellowish caudal margin on male sternite 8 and female sternites 4–6. Tegmina with cells fuscous or translucent, costal cells with recurved markings; apical cells brown, light brown and some translucent areas; veins dark brown (Fig. 11). Legs with femur black, tibia pale. Nymph dorsally with longitudinal yellowish median bar, somewhat narrowed at wing base and medially on abdomen; laterally fuscous (Figs 9, 14); abdominal tergites with three pairs of spines; legs pale with femur and tibia with narrow brown bands.



FIGURES 41–51. *Xerophytavorus furcillatus* gen.n. & sp.n., female. **41**, sternite 7; **42**, valvula 3; **43–47**, valvula 1; **43**, image of sculpturing at narrow apex; **44**, image of whole structure and valvifer; **45**, image of sculpturing at wide apex; **46**, line drawing of sculpture medially; **47**, line drawing of sculpture at apex; **48–51**, valvula 2; **48**, image of whole structure; **49**, line drawing of serration medially; **50**, line drawing of serration at apex; **51**, image of serration at apex.

Male, **female and nymph**. **External morphology**. Body elongate, vertex acutely angled to face (Fig. 100). Body glabrous. Vertex in dorsal view acutely produced (Fig. 98), face shagreened, dorsally with disc smooth. Pronotum lateral margin carinate. Ocellus marginal, close to eye. Hair-like seta on gena close to lateral frontal suture, close to antennal socket (Fig. 99). Suture between clypeus and clypellus absent or at most weakly developed. Gena very broad, not incised below eye, extended onto dorsum of head and visible behind eye, below lorum not extended beyond clypellus. Tegmina with four apical cells, each of similar size, two anteapical cells (crossvein m-cu2 absent), four recurved veins between costa and outer anteapical cell, some recurved veins arising from outer anteapical cell not attainting costa, with recurved dark markings in basal costal cell not representing veins; claval veins reduced (Figs 11, 101), with two (Fig. 77) or three (Fig. 101) closed anteapical cells. Hind wing venation complete, with four apical cells, jugal lobe well developed (Fig. 102). Profemur setae of anteroventral row with basal setae short, intercalary setae stout, 2–4 times longer than basal setae, AM_1 variable, about as long as or slightly longer than intercalary setae. Metafemur dorsoapical setal formula 2+2+1; PD_2 setum pale, about ⅓ shorter than AD_1 and PD_1, AD_3 pale, as long as AD_1 and PD_1; metatibial setae on row PV with 3 sections of setae, based on length and thickness: basal third short (? as long as greatest width of tibia), medial third longer (⅓ as long as greatest width of tibia) and distal third with 5–7 slightly longer and thicker setae (⅔ as long as greatest width of tibia); all setae on rows AV and PD and AD as long as or much longer than greatest width of tibia; PD and AD interspersed with short, robust setae. Tarsomere 1 more than twice as long as tarsomere 2 or 3, plantar surface with two rows of up to 7 macrosetae, apex with spur with seta laterally and 4 spurs with platellae medially. Tarsomere 2 with 2 platellae medially. Protibia setal formula 1+4, metatibia 4+4.

Male. **Internal morphology**. Abdominal apodemes, with anterior apodeme, in dorsal view with membranous lobe elongate, about twice long as wide. Tentorium branched symmetrically, Y-shaped, all branches of similar thickness (Fig. 98)

Male. **Genitalia**. Pygofer lobe shallowly bilobate, membranous, apex with process, arising marginally or from inner margin (Figs 83, 84, 107, 108). Anal tube with phragma attached to dorsal apodeme of aedeagus. Pygofer with narrow anterior apodeme (Figs 78, 83, 105, 107). Plate rectangular or somewhat converging, apex truncate (Figs 81, 106), uniseriate macrosetae, marginal at base, medial at apex of row; apex membranous; valve broad. Connective Y-shaped (Figs 87, 111), articulating with aedeagus (Figs 86, 87, 109–111). Style with apophysis acute (Fig. 82) or blunt (Fig. 112), preapical lobe acute, medial anterior lobe short, blunt, lateral anterior lobe short. Aedeagal shaft biramous, symmetrical (Figs 85, 86, 109, 110).

Female. **Genitalia**. Sternite 7 with posterior margin concave or W-shaped (Figs 88, 113). Valvula 3 with up to 10 marginal macrosetae (Figs 89, 114). Valvula 2 apical half serrate, medially slightly narrowed (Figs 97, 122), fine denticulation on irregular, crescent-shaped ridges (Figs 94–96, 119–121). Valvula 1 lanceolate (Figs 90, 116) with fine circular microsculpture apically (Figs 91, 93, 115, 117) and rectangular basally (Figs 92, 118).

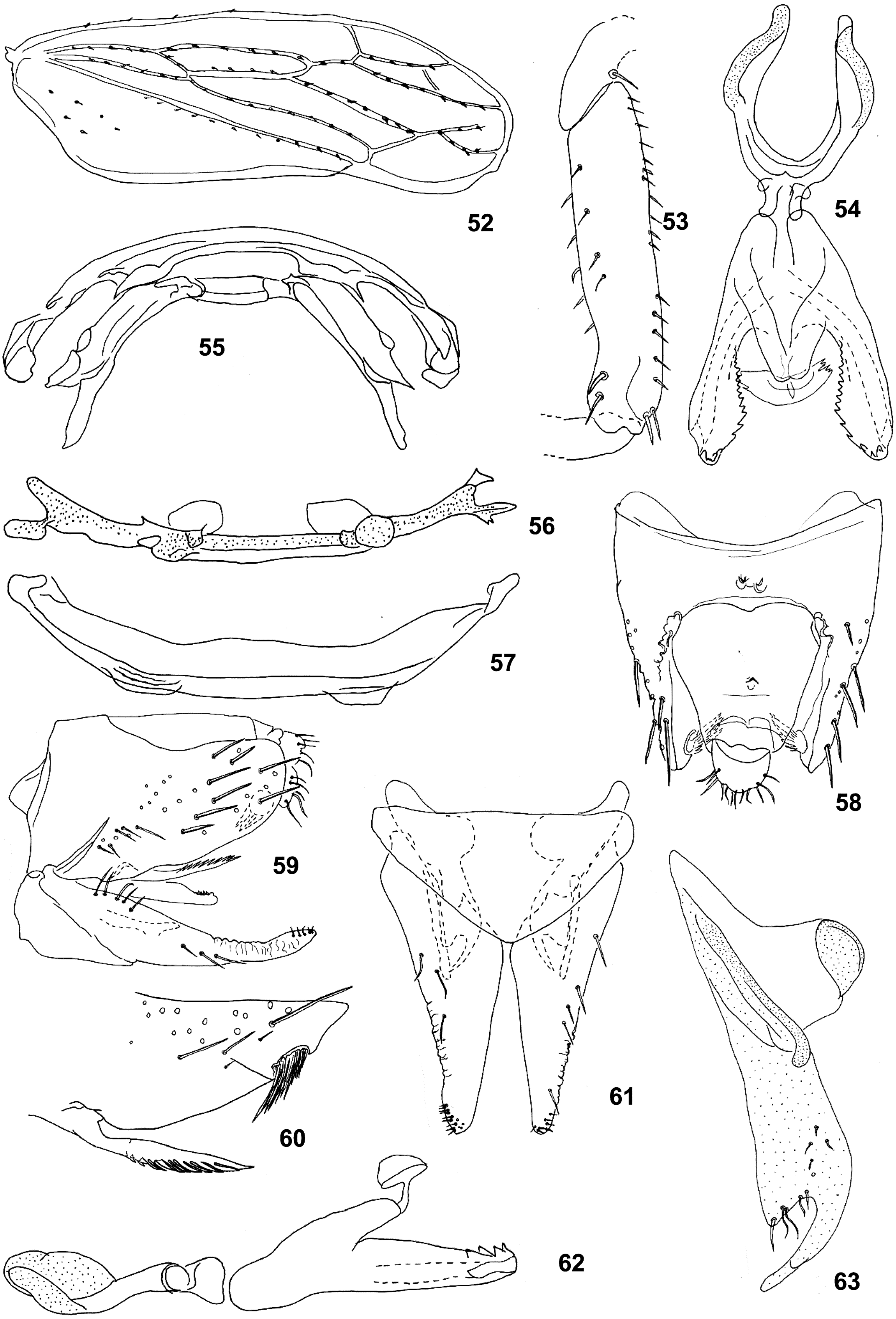
Relationships. *Xerophytacolus* is assigned to Opsiini, based on the biramous aedeagal shaft, connective articulated with the aedeagus and the pygofer lobe process. These three features are present in *Circulifer* Zachvatkin and *Opsius* Fieber, the latter both with a pygofer process, and in *Hishimonus* Ishihara and *Libengaia* Linnavuori but without the pygofer process. Unusual in *Xerophytacolus* is the sharp margin between the face and vertex, which in most other members of Opsiini is distinctly rounded, but present in *Eremophlepsius* Zachvatkin from the Palaearctic Region.

Xerophytacolus claviverpus **sp.n.**
(Figs 8–11, 77–97)

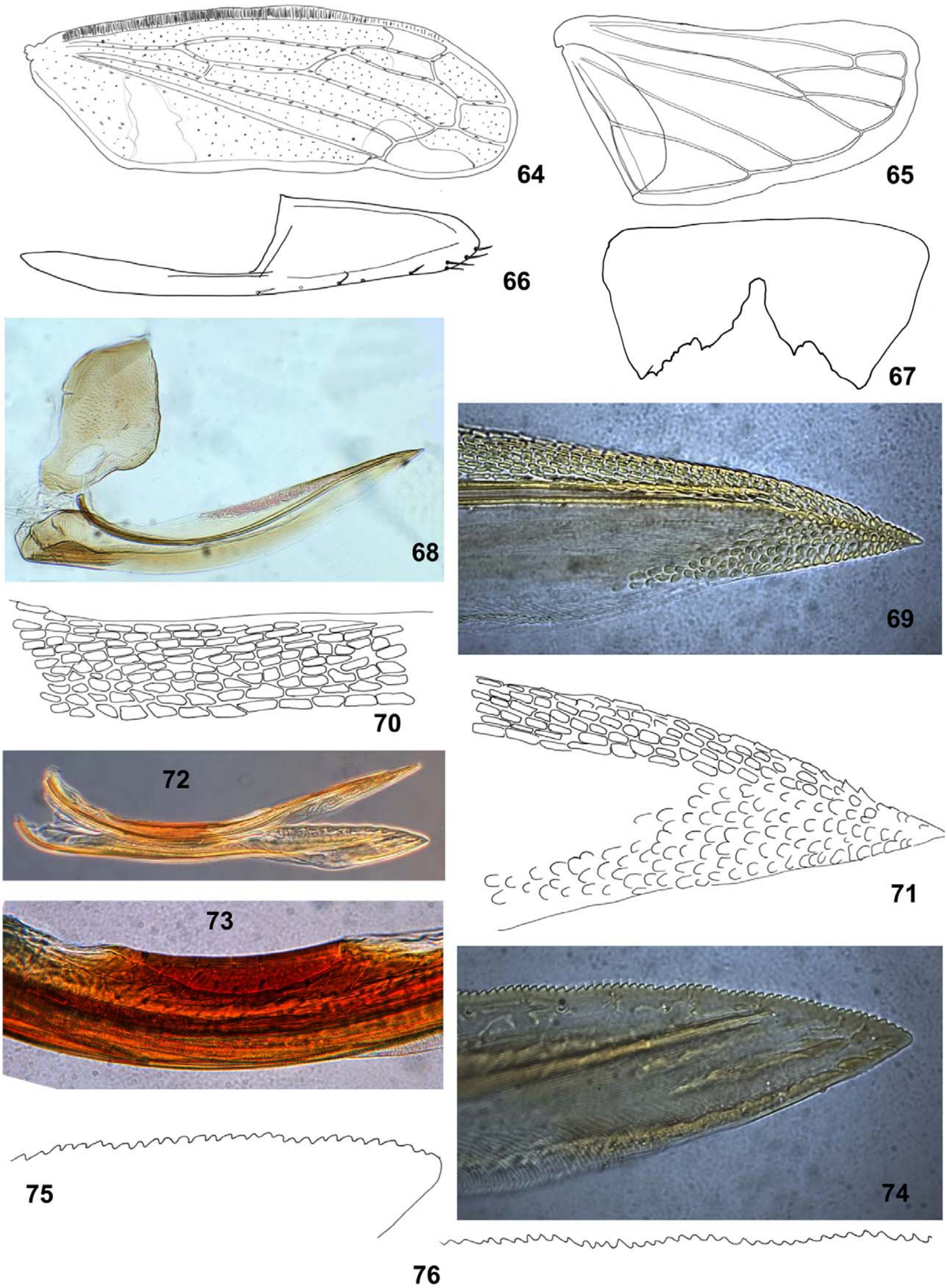
Diagnosis. Aedeagal shaft biramous with subbasal spine; shaft and spine about right-angled to basal part of shaft (Figs 85, 86). Pygofer lobe with median process curved dorsoposteriad (Figs 83, 84). Plate at apex dorsolaterally with finely striated concave region (Figs 81, 83). Sternite 7 of female with W-shaped posterior margin (Fig. 88).

Etymology. Latin, *clavus* nail, spike, *verpus*, penis, for the ventral subbasal spines on the aedeagal paired shaft.

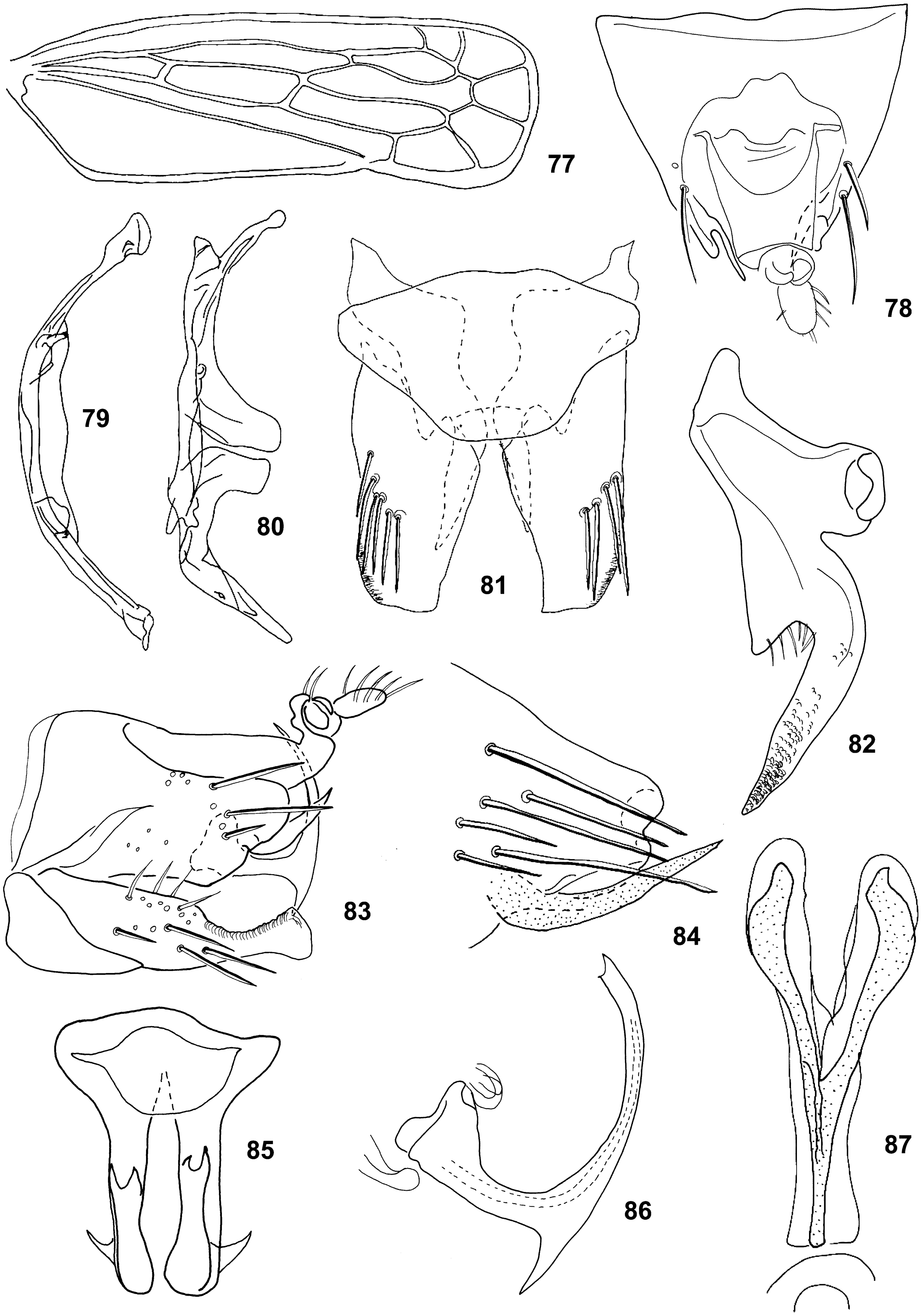
Male. **Measurements**. (n=13) Length: apex of vertex to apex of tegmina 2.39–2.51 mm; apex of vertex to apex of abdomen 1.91–2.18 mm; vertex 0.47–0.51 mm; next to eye 0.31–0.34 mm; pronotum 0.39–0.42 mm; scutellum 0.43–0.50 mm. Width: head 0.86–0.90 mm; pronotum 0.80–0.85 mm; scutellum 0.56–0.62 mm. Ocellus: diameter 2.65–3.07 µm; ocellocular distance 1.24–1.46 µm.



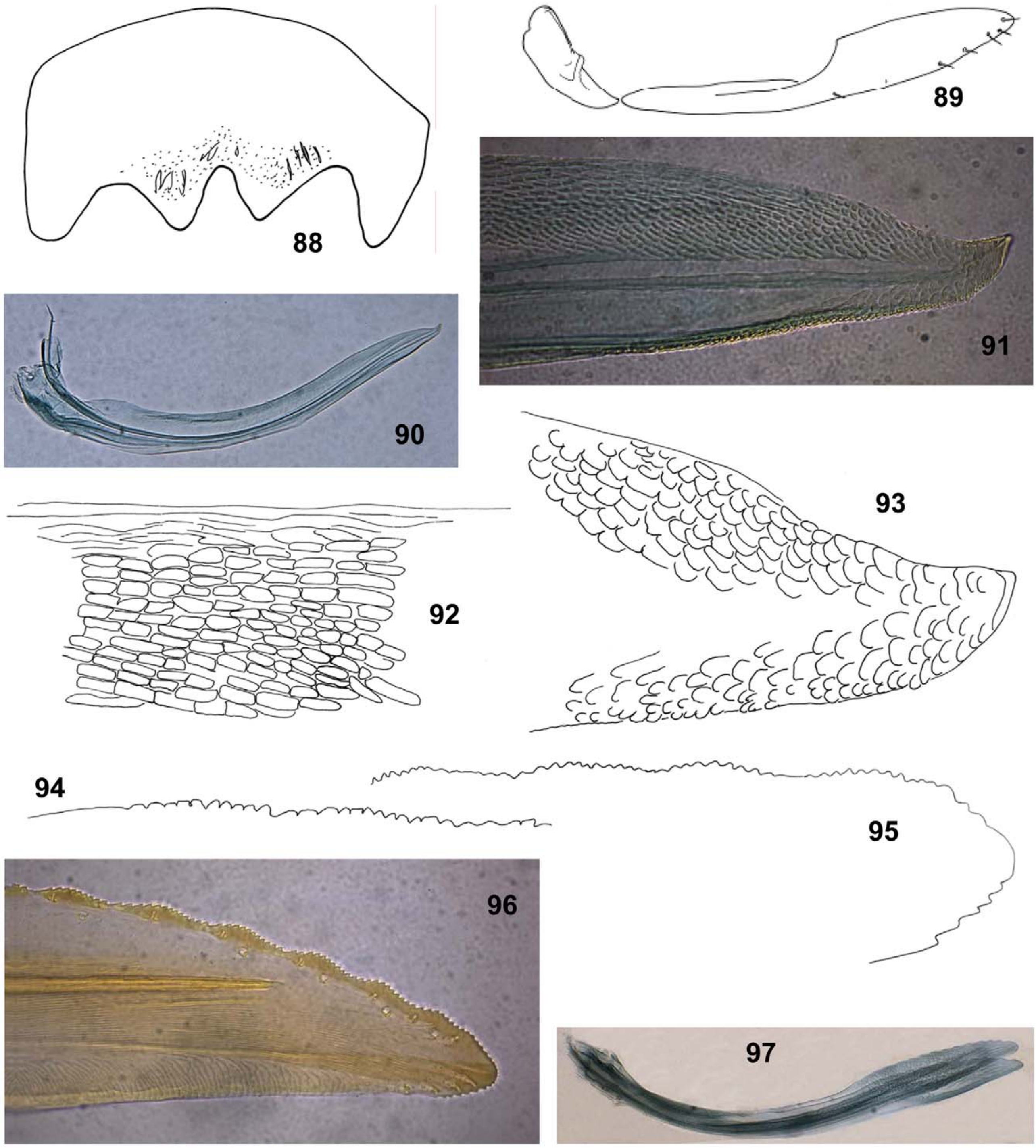
FIGURES 52–63. *Xerophytavorus rastrullus* gen.n. & sp.n., male. **52**, tegmina; **53**, foretibia setation; **54**, aedeagus and connective, dorsal view; **55**, anterior and posterior abdominal apodemes, anterior view; **56**, posterior abdominal apodeme, dorsal view; **57**, anterior abdominal apodeme, dorsal view; **58**, pygofer, dorsally; **59**, pygofer, lateral view; **60**, process and apical macrosetae cluster on pygofer, ventral view; **61**, plate and valve, ventral view; **62**, aedeagus, lateral view; **63**, style.



FIGURES 64–76. *Xerophytavorus rastrullus* gen.n. & sp.n., female. **64**, tegmina; **65**, hind wing; **66**, valvula 3; **67**, sternite 7; **68–71**, valvula 1; **68**, image of whole structure and valvifer; **69**, image of sculpturing at apex; **70**, line drawing of sculpture medially; **71**, line drawing of sculpture at apex; **72–76**, valvula 2; **72**, image of whole structure, apex distorted; **73**, image of sclerotized medial section; **74**, image of serration at apex; **75**, line drawing of serration at apex; **76**, line drawing of serration medially.

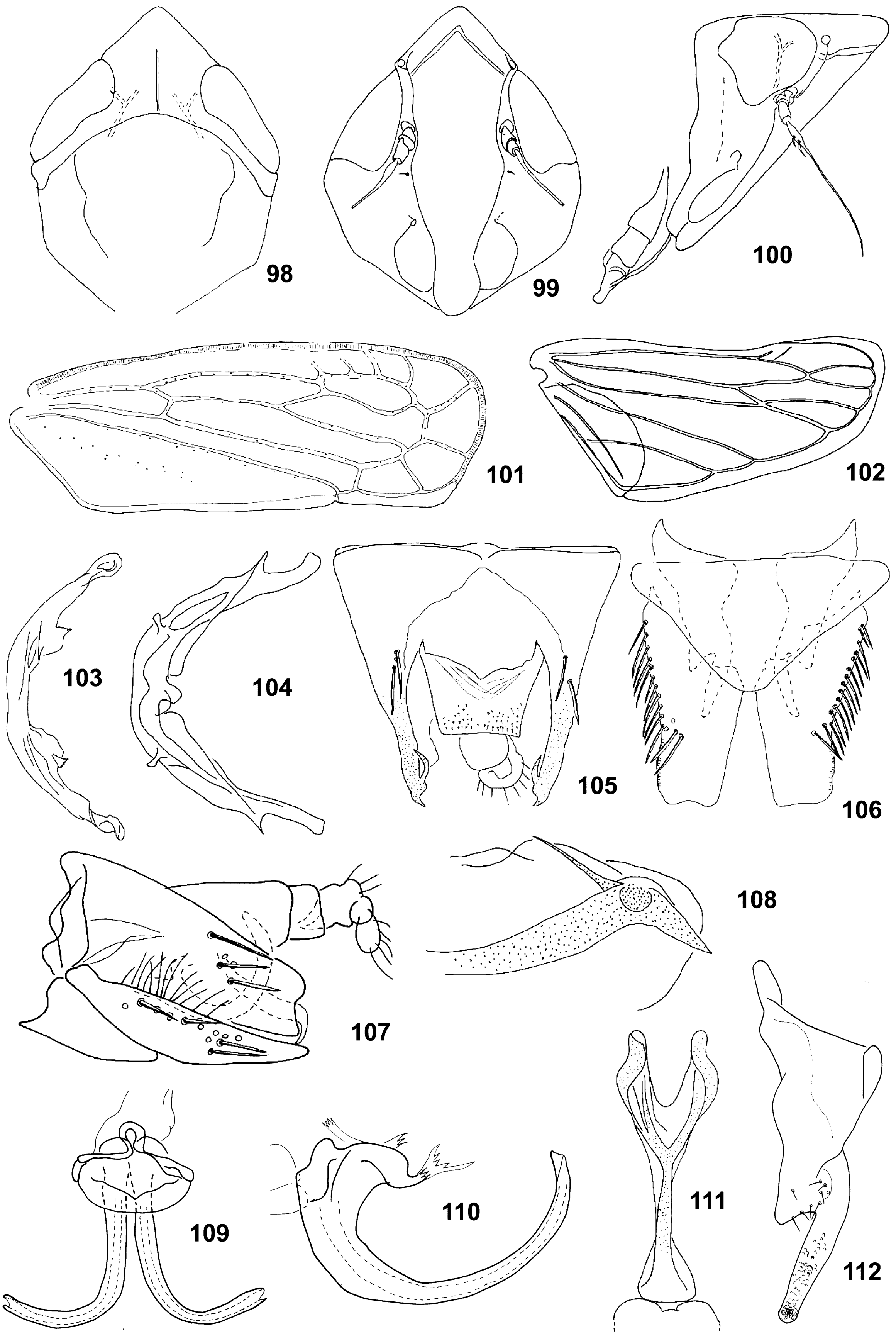


FIGURES 77–87. *Xerophytacolus claviverpus* gen.n. & sp.n., male. **77**, tegmina; **78**, pygofer, dorsal view; **79**, anterior abdominal apodeme, dorsal view; **80**, posterior abdominal apodeme, dorsal view; **81**, plate and valve, ventral view; **82**, style; **83**, pygofer, lateral view; **84**, process at pygofer lobe apex, lateral view; **85**, aedeagus, dorsal view; **86**, aedeagus, lateral view; **87**, connective.

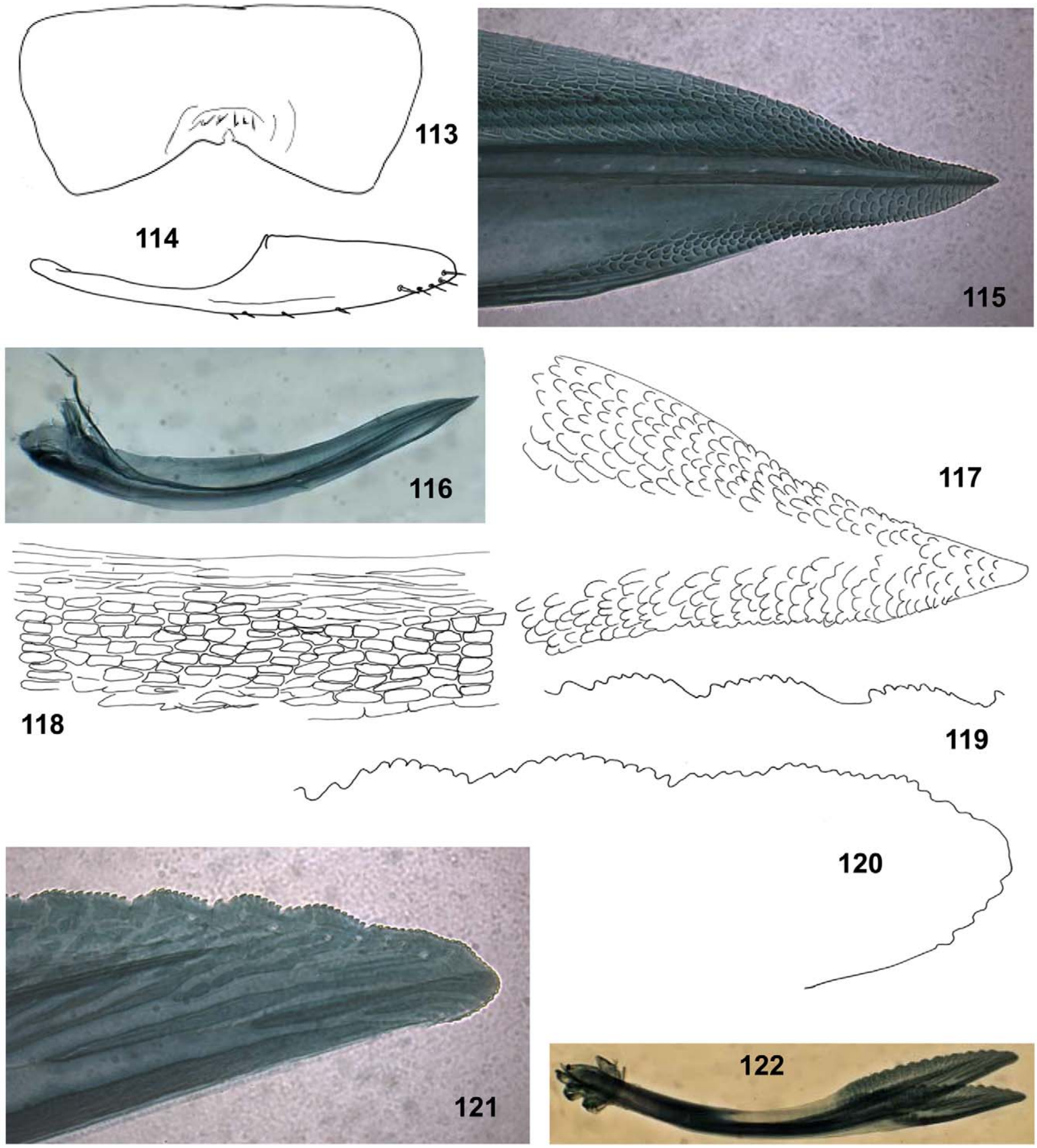


FIGURES 88–97. *Xerophytacolus claviverpus* gen.n. & sp.n., female. **88**, sternite 7; **89**, valvula, 3; **90–93**, valvula 1; **90**, whole structure; **91**, image of sculpture at apex; **92**, line drawing of sculpture medially; **93**, line drawing of sculpture at apex; **94–97**, valvula 2; **94**, whole structure; **95**, image of serration at apex; **96**, line drawing of serration at apex; **97**, line drawing of serration medially.

Male. **Genitalia**. Pygofer lobe with median process, arising marginally, process straight, directed dorsoposteriad (Figs 83, 84). Paired aedeagal shafts tubular, parallel throughout, apical ⅔ right angled to base, apex bifurcate, gonopore at base of bifurcation; subbasally with ventral, acute spine (Figs 85, 86). Connective with stem and arms of similar length, stem narrow, arms swollen (Fig. 87). Style with apophysis acute (Fig. 82). Plate in ventral view (Fig. 81) with apex truncated, angulate; 7–8 macrosetae; in lateral view with apical half emarginate with finely striated transverse ridges (Fig. 83). Pygofer dorsally with anal tube incised half-way (Fig. 78). Posterior abdominal apodeme, viewed dorsally, with expanded median lobes (Fig. 80), anterior abdominal apodeme narrow (Fig. 79), in anterior view similar to that of *Xc. tubuverpus* (Figs 103, 104).



FIGURES 98–112. *Xerophytacolus tubuverpus* gen.n. & sp.n., male. **98**, head, dorsal view; **99**, face; **100**, head, lateral view; **101**, tegmina; **102**, hind wing; **103**, anterior abdominal apodeme, anterior view; **104**, posterior abdominal apodeme, anterior view; **105**, pygofer, dorsal view; **106**, plate and valve, ventral view; **107**, pygofer, lateral view; **108**, apical pygofer process, medial view; **109**, aedeagus, dorsal view; **110**, aedeagus, lateral view; **111**, connective; **112**, style.



FIGURES 113–122. *Xerophytacolus tubuverpus* gen.n. & sp.n., female. **113**, sternite 7; **114**, valvula, 3; **115–118**, valvula 1; **115**, image of sculpture at apex; **116**, image of whole structure; **117**, line drawing of sculpture at apex; **118**, line drawing of sculpture medially; **119–122**, valvula 2; **119**, line drawing of serration medially; **120**, line drawing of serration at apex; **121**, image of serration at apex; **122**, image of whole structure.

Female. **Measurements**. (n=10) Length: apex of vertex to apex of tegmina 2.59–2.80 mm; apex of vertex to apex of abdomen 2.27–2.63 mm; vertex 0.54–0.58 mm; next to eye 0.33–0.36 mm; pronotum 0.42–0.44 mm; scutellum 0.44–0.50 mm. Width: head 0.91–0.95 mm; pronotum 0.87–0.91 mm; scutellum 0.57–0.63 mm. Ocellus: diameter 2.64–3.11 µm; ocellocular distance 1.40 µm.

Female. **Genitalia**. Sternite 7 with W-shaped posterior margin (Fig. 88). Valvula 3 with about 10 marginal setae (Fig. 89). Valvula 2 parallel-sided, slightly narrower than serrate apex (Fig. 97); serration regular, fine (Figs 95, 96 serration at apex, 94, serration basally). Valvula 1 (Fig. 90) lanceolate; microsculpture imbricate dorsally and ventrally (Figs 91, 93 at apex, Fig. 92 medially).

Material examined. Holotype male. South Africa, Gauteng. Ezemvelo Nature Reserve, 25°39′S, 28°57′E, 1336 m, 14.xii.2005, M. Stiller, on *Xerophyta retinervis* (SANC). Paratypes. 11♂, 11♀, 11 nymphs. **Gauteng**. 5♂, 3♀, 10 nymphs, *ibid.* holotype; 1♀, Ezemvelo Nature Reserve, 25°42′S, 28°55′E, 1402 m, 14.xii.2005; **Mpumalanga**. 3♀, Loskopdam near Middelburg, 25°30′S, 29°15′E, 1032 m, 30.iv.1993; all collected by M. Stiller; 1♂, Two Rivers Platinum Mine, Dwarsrivier Farm portion 372KT, 24°55′S, 30°05′E, 1255 m, 23.iii.2008, P. Hawkes, J. Fisher, sweeping grass, forbs and shrubs; 2♂, 1♀, east of Middelburg, 25°46′10.12″S, 29°32′44.12″E, 1526 m, 8.iv.2011, DVac; 1♀, 1 nymph, Sterkfontein farm portion 52JT, Everest Mine near Lydenburg, 25°9′19.2″S, 30°6′50.6″E, 1280 m, 9.ii.2012, M. Stiller, sweeping tall *X. retinervis* on rock outcrop; **Limpopo**: 2♂, 3♀, The Downs, Orrie Baragwanath Pass, 24°11′38.08″S, 30°14′53.03″E, 1414 m, 25.iv.2009, collected on *Xerophyta* sp. on dolomite outcrop. All collected from *Xerophyta retinervis*, unless stated otherwise (BMNH, INHS, SANC).

Remarks. This species and *Xc. tubuverpus* are almost identical in shape and colouration, but have distinct male and female genitalia. The shape of the vertex in dorsal view in *Xc. claviverpus* is more obtuse and shorter (vertex length, male 0.47–0.35 mm, female 0.53–0.61 mm) and that of *Xc. tubuverpus* is more acute, and longer (vertex length, male 0.52–0.60 mm, female 0.60–0.71 mm). The dorsal apophysis of the style in *Xc. claviverpus* is acute, and in *Xc. tubuverpus* it is blunt. The aedeagus differs distinctly between these two species. In *Xc. claviverpus* the paired shafts are parallel, has a subbasal spine and the apex is incised. In *Xc. tubuverpus* the paired shafts are divergent, tubular and without any spine. The sternite 7 of the female in *Xc. claviverpus* has the posterior margin W-shaped, and in *Xc. tubuverpus* it is widely emarginate.

Xerophytacolus tubuverpus sp.n.

(Figs 12–14, 98–122)

Diagnosis. Aedeagal shaft tubular, uniformly curved dorsolaterally (Figs 109, 110). Pygofer lobe with apex of median process curved ventrad (Figs 107, 108). Plate apex truncate; laterally weakly striate; basally lateral and medial margins convergent, subparallel (Fig. 106). Sternite 7 of female with wide, shallow rounded notch, about as wide as sternite (Fig. 113).

Etymology. Latin, *tubus* pipe, *verpus* penis, for the tubular shape of the paired aedeagal shafts.

Male. **Measurements**. (n=10) Length: apex of vertex to apex of tegmina 2.40–2.53 mm; apex of vertex to apex of abdomen 2.00–2.12 mm; vertex 0.52–0.60 mm; next to eye 0.33–0.35 mm; pronotum 0.38–0.41 mm; scutellum 0.40–0.48 mm. Width: head 0.85–0.90 mm; pronotum 0.82–0.89 mm; scutellum 0.55–0.62 mm. Ocellus: diameter 2.64–3.13 µm; ocellocular distance 1.24–1.73 µm.

Male. **Genitalia**. Pygofer lobe with median process, attached subbasally on inner margin, apex curved ventrad (Figs 107, 108) with narrow, variable process directed dorsoanteriad (Fig. 108). Anal tube incised half way into pygofer (Fig. 105). Aedeagal shafts tubular, parallel at base, curved dorsad and divergent apicad (Figs 109, 110), gonopore apical, oblique. Connective weakly sclerotized (Fig. 111). Style apophysis apex blunt, small subapical ventral spine (Fig. 112). Plate apex truncate, right-angled, weakly sclerotized (Fig. 106), 12–17 macrosetae. Anterior and posterior abdominal apodemes in posterior view as in Figs 103 and 104, in dorsal view similar to the apodemes of *Xc. claviverpus* (Figs 79, 80).

Female. **Measurements**. (n=6) Length: apex of vertex to apex of tegmina 2.56–2.83 mm; apex of vertex to apex of abdomen 2.31–2.68 mm; vertex 0.60–0.71 mm; next to eye 0.34–0.37 mm; pronotum 0.41–0.44 mm; scutellum 0.42–0.50 mm. Width: head 0.91–0.96 mm; pronotum 0.87–0.93 mm; scutellum 0.54–0.65 mm. Ocellus: diameter 2.87–4.13 µm; ocellocular distance 1.23–1.80 µm.

Female. **Genitalia**. Sternite 7 with wide, rounded notch (Fig. 113). Valvula 3 with about 7 setae in apical half (Fig. 114), additional fine setae basally. Valvula 2 (Fig. 122) serrate dorsally on apical third, serration very fine, on rounded protrusions (Figs 120, 121, serration at apex, Fig. 119, serration medially). Valvula 1 lanceolate (Fig. 116), imbricate microsculpture (Figs 115, 117, at apex, Fig. 118, more rectangular medially).

Material examined. Holotype male. South Africa, Gauteng. Faerie Glen Nature Reserve, Pretoria, 25°46′S, 28°17′E, 1450 m, 18.iii.1998, M. Stiller, on *Xerophyta retinervis* (SANC). Paratypes. 11♂, 7♀, 14 nymphs. **Gauteng**. 3♂, 1♀, 1 nymph, Pienaarspoort, 25°44′S, 28°27′E, 1400 m, 23.iii.1993, sweeping grass; 1♀, 4 nymphs, Faerie Glen Nature Reserve, Pretoria, 25°46′S, 28°17′E, 1450 m, 12.iii.1998; 4♂, 2♀, 7 nymphs, *ibid.*, holotype; 2♂, Rietfontein suburb, Pretoria, 25°41′S, 28°14′E, 1300 m, 26.xii.2001; 1♀, Zonderwater, south of Cullinan, 25°42′S, 28°31′E, 1488 m, 14.xii.2005; 1♂, 1♀, Ezemvelo Nature Reserve, at small dam, 25°43′S, 28°58′E, 1320 m, 4.iv.2006. **Limpopo**. 1♀, Kransberg summit, NE of Thabazimbi, 24°28′S, 27°37′E, 2000 m, 23.iv.2005. **Mpumalanga**. 1♀, Balmoral vicinity, 25°52′S, 28°55′E, 1460 m, 17.ii.2005, sweeping grass with some *Xerophyta retinervis* present; 1♂, Loskopdam Nature Reserve, 25°31′2.8″S, 29°15′2.3″E, 1174 m, 8.iv.2012. All collected by M. Stiller, on *Xerophyta retinervis*, except where stated otherwise (BMNH, INHS, SANC).

Remarks. This species and *Xc. claviverpus* are similar in color and shape, with distinguishing features present in male and female genitalia, and which are discussed in the remarks under the description of *Xc. claviverpus*.

Acknowledgments

I am grateful to Nokuthula Mbanyana (Iziko South African Museum) for ant identifications and ant distributions. Numerous colleagues, referees, Mick Webb and Jamie Zahniser are thanked for their constructive criticism and reviews. Dmitri Shcherbakov, Peter Hawkes and Peter Webb are thanked for photographing ants and leafhoppers and for their permission to publish these images.

References

Blocker, H.D. & Triplehorn, B.W. (1985) External Morphology of Leafhoppers. *In* The Leafhoppers and Planthoppers, L.R. Nault and J. G. Rodriguez, eds. John Wiley & Sons. pp. 41–60.

Compton, S.G. & Robertson, H (1988) Complex Interactions Between Mutualisms: Ants Tending Homopterans Protect Fig Seeds and Pollinators. *Ecology*, 69(4), 1302–1305.

Delabie, J.H.C. (2001) Trophobiosis between Formicidae and Hemiptera (Sternorrhyncha and Auchenorrhyncha): an Overview. *Neotropical Entomology*, 30(4), 501–516.

Dietrich, C.H. & McKamey, S.H. (1990) Three new Idiocerine leafhoppers (Homoptera: Cicadellidae) from Guyana with notes on ant-mutualism and subsociality. *Proceedings of the Entomological Society of Washington*, 92(2), 214–223.

Knight, W.J. (1973) A new species of *Hishimonus* Ishihara (Homoptera, Cicadellidae) attacking *Terminalia* spp in India, with comment on the relationship of the genus to *Cestius* Distant. *Annales Entomologica Fennica*, 39(4), 153–156.

Knight, W.J. (1983) The leafhopper genus *Batracomorphus* (Cicadellidae, Iassinae) in the eastern Oriental and Australian Regions. *Bulletin of the British Museum (Natural History) Entomology*, 47, 27–210.

Larsen, K.J., Staehle, L.M. & Dotseth, E.J. (2001) Tending ants (Hymenoptera: Formicidae) regulate *Dalbulus quinquenotatus* (Homoptera: Cicadellidae) population dynamics. *Environmental Entomology*, 30(4), 757–762.

Linnavuori, R. (1978) Studies on the family Cicadellidae (Homoptera, Auchenorrhyncha). 1. A revision of the Macropsinae of the Ethiopian Region. *Acta Entomologica Fennica*, 33, 1–17.

Moya-Raygoza, G. (1995) Fire effects on insects associated with the gamagrass *Tripsacum dactyloides* in Mexico. *Annals of the Entomological Society of America*, 88(4), 434–440.

Moya-Raygoza, G. & Nault, L.R. (2000) Obligatory mutualism between *Dalbulus quinquenotatus* (Homoptera: Cicadellidae) and attendant ants. *Annals of the Entomological Society of America*, 93(4), 929–940.

Moya-Raygoza, G. & Larsen, K.J. (2008) Positive effects of shade and shelter construction by ants on leafhopper–ant mutualism. *Environmental Entomology*, 37(6), 1471–1476.

Nault, L.R., DeLong, D.M., Triplehorn, B.W., Styer, W.E. & Doebley, J.F. (1983) More on the association of *Dalbulus* (Homoptera: Cicadellidae) with Mexican *Tripsacum* (Poaceae), including the description of two new species of leafhoppers. *Annals of the Entomological Society of America*, 76, 305–309.

Quartau, J.A. (1981) Ecological notes on *Batracomorphus* Lewis (Insecta, Homoptera, Cicadellidae) in Africa. *Boletim da Sociedade Portuguesa de Entomologia*, 14, 1–8.

Quartau, J.A. (1990) On some Homoptera Auchenorrhyncha associated with ants in Angola. *Arquivos do Museu Bocage*, 1(36), 499–503.

Rakitov, R. (1998) On differentiation of cicadellid leg chaetotaxy. *Russian Entomological Journal*, 6, 7–27.

Rico-Gray, V. & Oliveira, P.S. (2007) The Ecology and Evolution of Ant-Plant Interactions. University of Chicago Press, Chicago, U.S.A. 331pp.

Steiner, F.M., Schlick-Steiner, B.C., Holzinger, W., Komposch, C., Pazoutova, S., Sanetra, M. & Christian, E. (2004) A novel relationship between ants and a leafhopper (Hymenoptera: Formicidae; Hemiptera: Cicadellidae). *European Journal of Entomology*, 101, 689–692.

Stevens, P. F. (2001 onwards) Angiosperm Phylogeny Website. Version 9, June 2008 http://www.mobot.org/ MOBOT/research/ APweb/ (accessed 22 February 2012).

Torre-Bueno, J.R. de la (1989) The Torre-Bueno Glossary of Entomology. American Museum of Natural History, New York, USA. 840pp.

Zahniser, J.N. & Dietrich, C.H. (2010) Phylogeny of the leafhopper subfamily Deltocephalinae (Hemiptera: Cicadellidae) based on molecular and morphological data with a revised family group classification. *Systematic Entomology*, 35, 489–511.