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A new Ugandan species of *Pterotiltus* (Orthoptera, Acrididae, Oxyinae) with epiphyllic oviposition

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Abstract

Pterotiltus hollisi n. sp. is described from the forests of Southern and Western Uganda, and compared with the type of the genus, *P. impennis*. The new species is the most easterly known representative of the genus. It feeds on broad-leaved monocotyledonous plants, especially of the families *Marantaceae* and *Commelinaceae*. The eggs are laid in groups of 4 to 6 in packets of foam, sandwiched between leaf surfaces of these foodplants. The female ovipositor valves have a form extremely like those found in unrelated epiphyllous egg-layers in the Neotropics, such as *Tela* (Acrididae, Proctolabinae) and the details of oviposition are similar to those of *Euprepacris* (Romaleidae, Bactrophorinae). On the basis of the ovipositor, it is postulated that the related genera *Badistica* and *Digentia* probably also have epiphyllic oviposition habits.

Key words

Orthoptera, Acrididae, Oxyinae, taxonomy, oligophagy, epiphyllic oviposition, Uganda, tropical forest

Introduction

The genus *Pterotiltus* Karsch, 1893, contains to date 11 described species, all from the wet forests of West and Central Africa. It is in need of revision, several species being known only from female types or poorly preserved material. The genus is currently excluded from the 2 recognized tribes of the subfamily, together with several other wet-forest oxyine genera of similar habitus, including the African *Badistica*, *Caryanda*, *Cylindrotiltus*, *Digentia*, *Genditia* and *Gerista*, and several Asian genera.

Hollis (1975), in his revision of the Oxyinae, redefined the genus and wrote the following discussion: "Species of this genus are forest-living and seem to represent the culmination of adaptation to forest life in the *Oxyinae*. The wings are completely reduced, many of the species have adopted aposematic coloration, the hind tibiae are cylindrical and have lost all trace of flattening or expansion, and the ovipositor valves have become smooth and obviously adapted to specialised oviposition sites". He also figured (his fig. 69, p. 127) the epiphallus of a specimen from Uganda, but did not determine, name or further describe this taxon.

In this article I describe a new species of the genus from Western and Southern Uganda, which appears to be the taxon figured by Hollis, and describe its epiphyllous oviposition on broad-leaved monocotyledonous food-plants. I also compare its genitalic structures with those of the type of the genus, *P. impennis* (Karsch 1891), which have not been previously illustrated.

Materials and methods

Specimens were observed and caught in the 1960s and during the past decade in various forests of Western and Southern Uganda at altitudes between 1100 and 1400 m. Recent specimens were caught under the terms of permit no. EC 575 from the Uganda National Council on Science and Technology to the author and exported for study under an associated materials transfer agreement. I also had available for comparison topotypic examples of both sexes of *P. impennis*, the Cameroonian type of the genus.

Taxonomic methods were standard, including the preparation of the internal male and female genitalia by dissection, maceration in KOH solution, staining with acid fuchsin and microscopic examination. Measurements were made with a digital stage accurate to 0.02 mm under appropriate magnification.

Food-plants were determined by association, field observation of feeding behavior, and feeding trials with caged insects and identified plants.

Abbreviations of depositories

BMNH	British Museum of Natural History, London.
MNHU	Naturhistorisches Museum der Humboldt-Universität, Berlin.
MUZM	Makerere University Zoology Museum, Kampala.

Taxonomy

Pterotiltus Karsch, 1893: 108.
= *Pyrgostolus* Karsch 1891 (name preoccupied).

Type species.— *Pterotiltus impennis* (Karsch, 1891) from Cameroon (MNHU).

Subsequent literature.— Ramme 1929: 313. Johnston 1956: 258. Jago 1964: 190-204 (distribution only). Dirsh 1965: 579. Johnston 1968: 173. Dirsh 1970: 119. Hollis 1975: 226.

Diagnosis.— (from Hollis 1975). "Head conical; fastigium, from above, pentagonal, about as wide as long, median longitudinal carinula weakly present or absent; frontal ridge sulcate, evanescing below median ocellus: lateral facial keels complete. Eyes bulbous. Antenna longer than combined lengths of head and pronotum. Prosternal process simple, conical with acute apex. Dorsum of prono-

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tum cylindrical, deeply crossed by 3 transverse sulci, median carina very weak, lateral carinae absent; mesosternal interspace as wide as (long) or longer than wide. Tegmina and hind wings extremely reduced, represented by small folds of integument on meso- and metathorax. Lower genicular lobe of hind femur spined; hind tibia not expanded apically and with rounded margins; external apical spine of hind tibia present. In male postero-dorsal margin of 10th abdominal tergite with a furcula or an unpaired structure resulting from fusion of 2 lobes of furcula; epiphallus with divided bridge, without ancorae and with 1 or 2 pairs of lophi. Female ovipositor valves long, slender, smooth".

This diagnosis covers the new species too. Ancorae are present (see below) but very weak.

***Pterotiltus hollisi* n. sp.**

Holotype.— ♂: UGANDA: Buganda: Mpigi Distr.: Mpanga Forest, 13.03.98 (Rowell CHF), specimen no. 98034 (BMNH).

Paratypes.— All UGANDA: **Buganda**: Same data as holotype, but ♀, specimen no. 98032 (BMNH). *Mpigi Distr.*: Mpanga Forest, 15 Oct 1965 (Rowell CHF), specimen nos 2003123, 2003124 (MUZM). Same data, but 4 Jul 1992, specimen no. 92008 (RC). Same data, but 5 Jul 1992 (Rowell CHF), 92013 (RC). Same data, but 13 Mar 1998 (Rowell CHF), specimen no. 98033 (RC). *Wakiso Distr.*: Kisubi: Zika Forest. 13 Mar 2002 (Rowell CHF), specimen no. 2002002 (MUZM). *Mukono Distr.*: Mabira Forest, 5 km E of Najjembe, 8 March 1998 (Rowell CHF) specimen no. 98006 (RC). **Tooro**: *Kabarole Distr.*: Kibale Forest: Kanyawara, 15.4.1965 (Rowell CHF), specimen no. 2003125 (MUZM). Same data, but 12 Jul 1992 (Rowell CHF), specimen nos 2003126, 2003127, 2003128 (MUZM). Same data, but 16 Mar 2003 (Rowell CHF), specimen no. 2003019 (MUZM). Same data, but 18 Mar 2003 (Rowell CHF), specimen no. 2003041 (MUZM). Same data, but 18 Mar 2003 (Rowell CHF), specimen no. 2003056 (MUZM). Same data, but 18 Mar 2003 (Rowell CHF), specimen no. 2003057 (MUZM). Same data, but 21 Mar 2003 (Rowell CHF), specimen nos 2003068, 2003069 (MUZM). Same data, but 29 Mar 2003 (Rowell CHF), specimen no. 2003073 (RC). Same data, but 29 Mar 2003 (Rowell CHF), specimen no. 2003074 (RC). Same data, but 30 Mar 2003 (Rowell CHF), specimen no. 2003076 (MUZM). Same data, but 1 Apr 2003 (Rowell CHF), specimen no. 2003079 (RC). *Kabarole Distr.*: Kibale Forest: Sebitoli, 18 Mar 2003 (Rowell CHF), specimen no. 2003055 (MUZM).

Etymology.— Named for the British entomologist David Hollis, who first recorded the existence of this taxon.

Diagnosis.—Habitus as in Fig. 1. Rather small for the genus, L_{male} = 14.43 to 17.74, mean 16.05 mm; L_{female} = 17.99-22.16, mean 19.86 mm. Antennal flagellum of 22 segments. Integument smooth and shiny; frons, genae, pronotum, terga of meso- and metathorax and of first abdominal segment coarsely pitted. Mesosternal interspace longer than broad. Hind knee with a terminal apical spine and spined lower lobes (Fig. 2D).

Dimensions: see Table 1. Hind tibia with 6 to 7 (median 7) external and 7 to 9 (median 8) internal spines. Sexual dimorphism moderate: P_{male}/P_{female} = 0.85. In comparison with females, males have relatively longer antennae, smaller fastigia, and narrower interocular spaces.

Male: (Figs 2A, C). Furcula small and simple, with broadly triangular points, not fused in the midline nor produced into median process as in *P. impennis* (Fig. 2B). Cerci straight, simple, narrowing

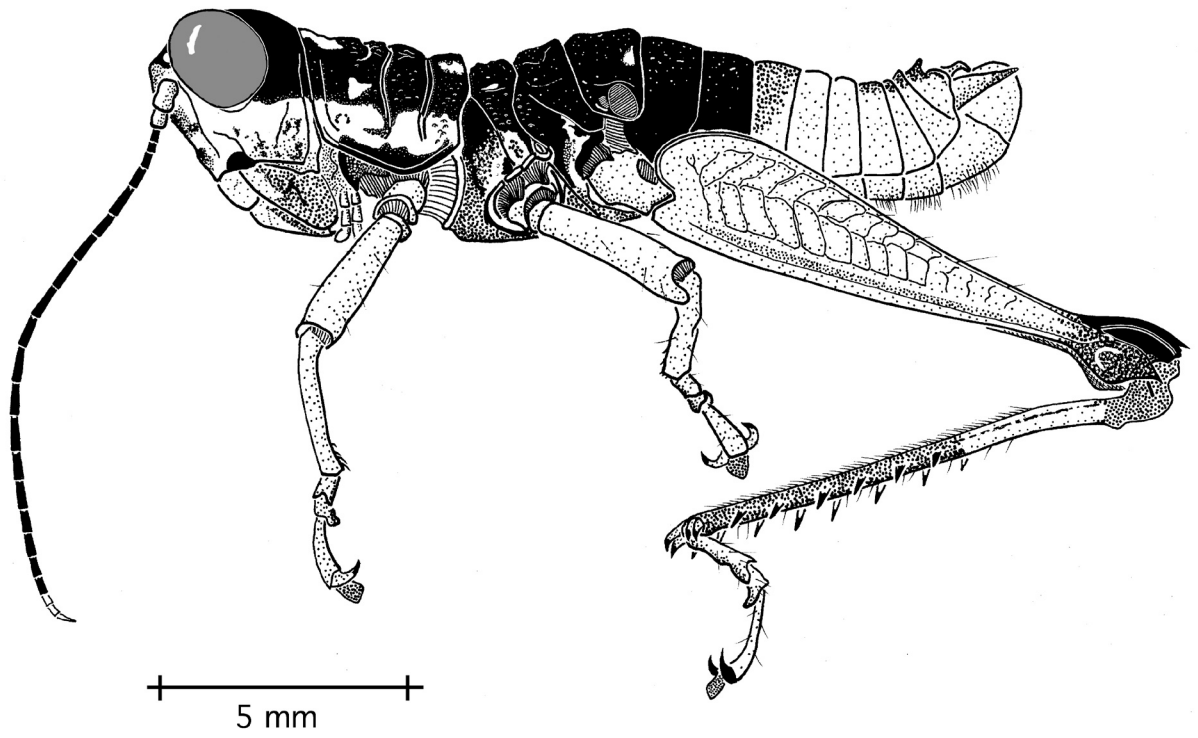


Fig. 1. *Pterotiltus hollisi* n. sp. Male. Habitus.

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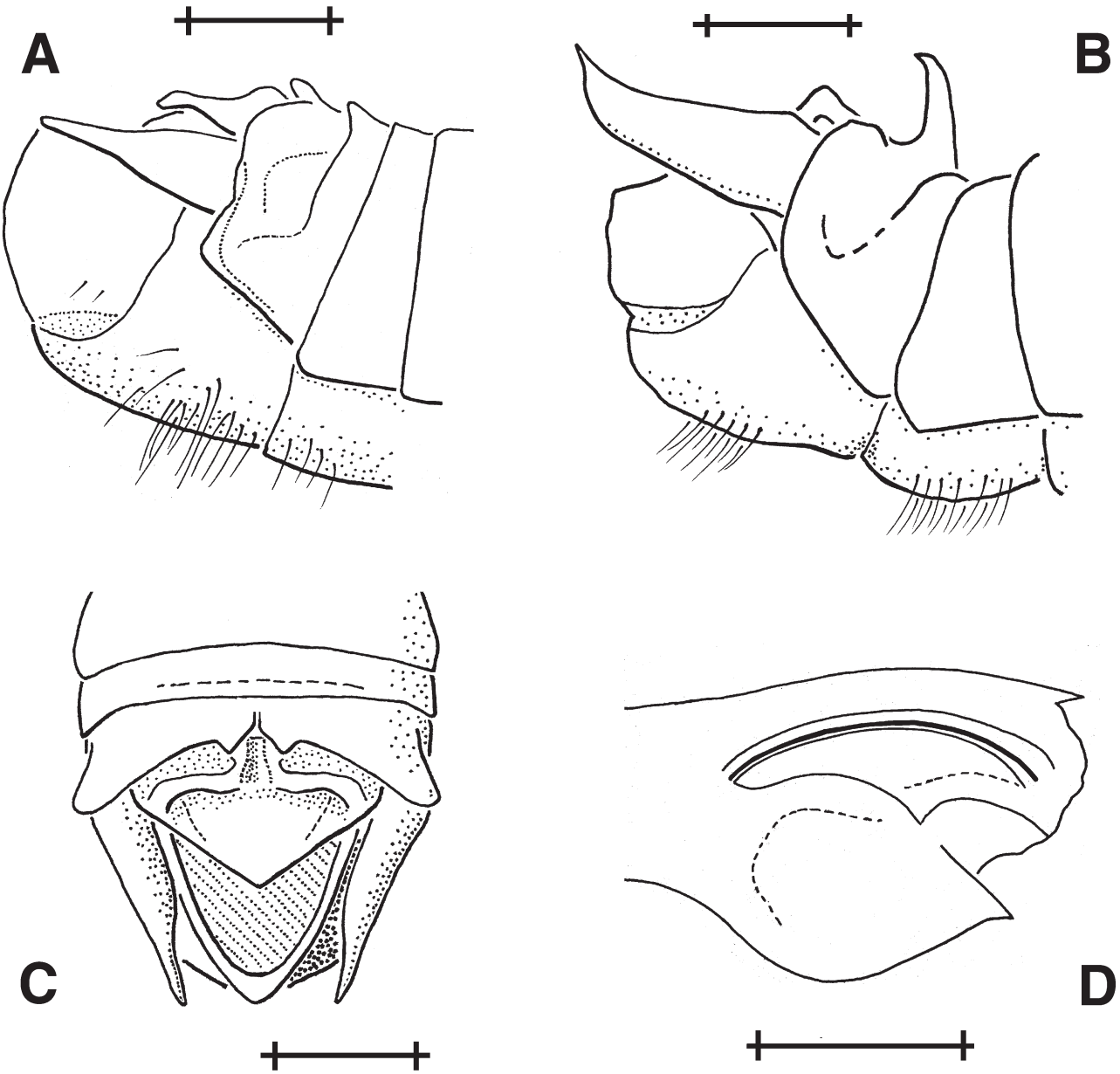


Fig. 2. A. *P. hollisi*, male external genitalia, lateral. B. *P. impennis*, male external genitalia, lateral. C. *P. hollisi*, male external genitalia, dorsal. D. *P. hollisi*, male hind knee, lateral. Scale bars, 1 mm.

before tip, pointed. Subgenital plate bluntly rounded at apex, upper margin drawn into a more acute point. Pallium thick and extensive, completely covering aedeagus.

Phallic complex: (Fig. 3). Epiphallus wide, bridge-shaped, divided, with a large outer pair and smaller inner pair of lophi, and weakly developed ancorae; oval sclerites present, large (Figs 3E, F). Ventrolateral sclerites (Fig. 3A) present, strap shaped, running ventrally and forward to join under the phallus, the ventral ends being invaginated inside the membrane and ending in a membranous apodeme running anteriorly below the ejaculatory sac. Apodemes of cingulum (Fig. 3G) short and broad, anterior ends widely separated; rami extending ventrally from almost the full length of the cingular apodemes, bulging convexly towards the rear, and meeting ventrally under the endophallus (Fig. 3C). Ectophallic membrane posterior to zygoma of cingulum produced into a sac which partially covers the aedeagus. Arch of cingulum integrated with ectophallic membrane and the fused dorsal aedeagal valves (Figs 3C, G), to form a large elaborate cover for the ventral aedeagal sclerites, the paired tips arching dorsally and forwards, shaped rather like 2 rabbit's ears fused in the midline near their tips. Endophallus (Fig. 3D, H, I) small, apodemes laterally compressed; extending only minimally over the dorsolateral spermatophore sac; flexure very tenuous, vertical; ventral aedeagal valves short and spatulate, laterally compressed, barely protruding from the complex of the dorsal aedeagal valves. Ejaculatory sac large and bipartite, with a proximal cylindrical portion receiving the ductus and a spherical ventral sac. Gonopore processes (Figs 3D, I) short, straight, oblong.

The phallic complex of *P. impennis*, the type of the genus, differs considerably from the above in detail (Fig. 4). The ventrolateral sclerites are much larger; as usual in this subfamily they fuse in the ventral midline, forming a sclerotized band around the phallus, but do not give rise to an internal anterior median apodeme as in *P. hollisi*. The structure formed by the fused dorsal aedeagal valves is

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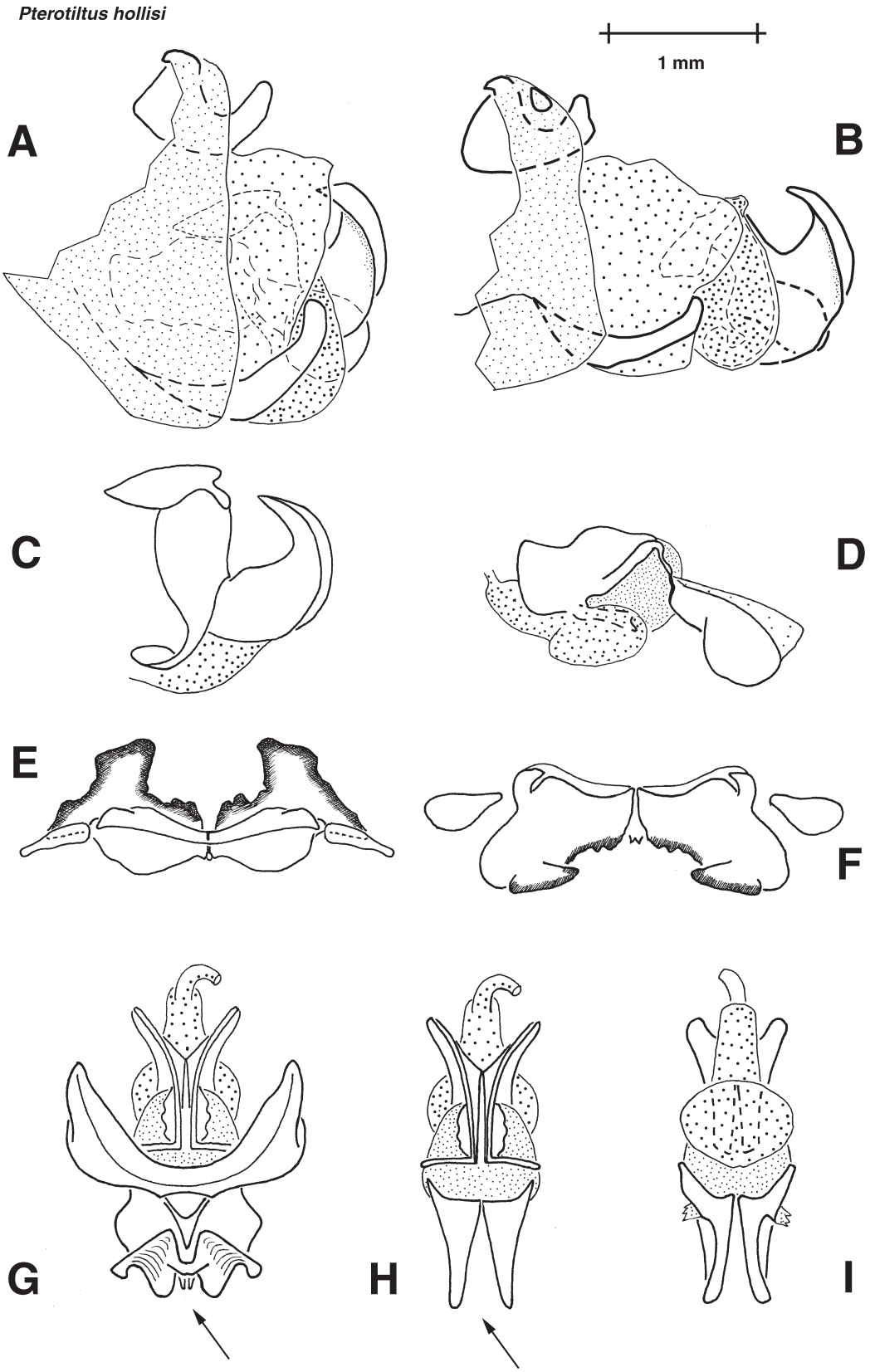


Fig. 3. P. hollisi, phallic structures. A. Entire phallic complex, retracted, lateral. B. As A, extended. C. Cingulum, arch and dorsal aedeagal valves. D. Endophallus, lateral. E. Epiphallus, axial. F. Epiphallus, dorsal. G. Phallic complex with epiphallic layer removed, dorsal. H. Endophallus, dorsal. I. Endophallus, ventral. Arrows in G and H indicate tips of the ventral aedeagal valves.

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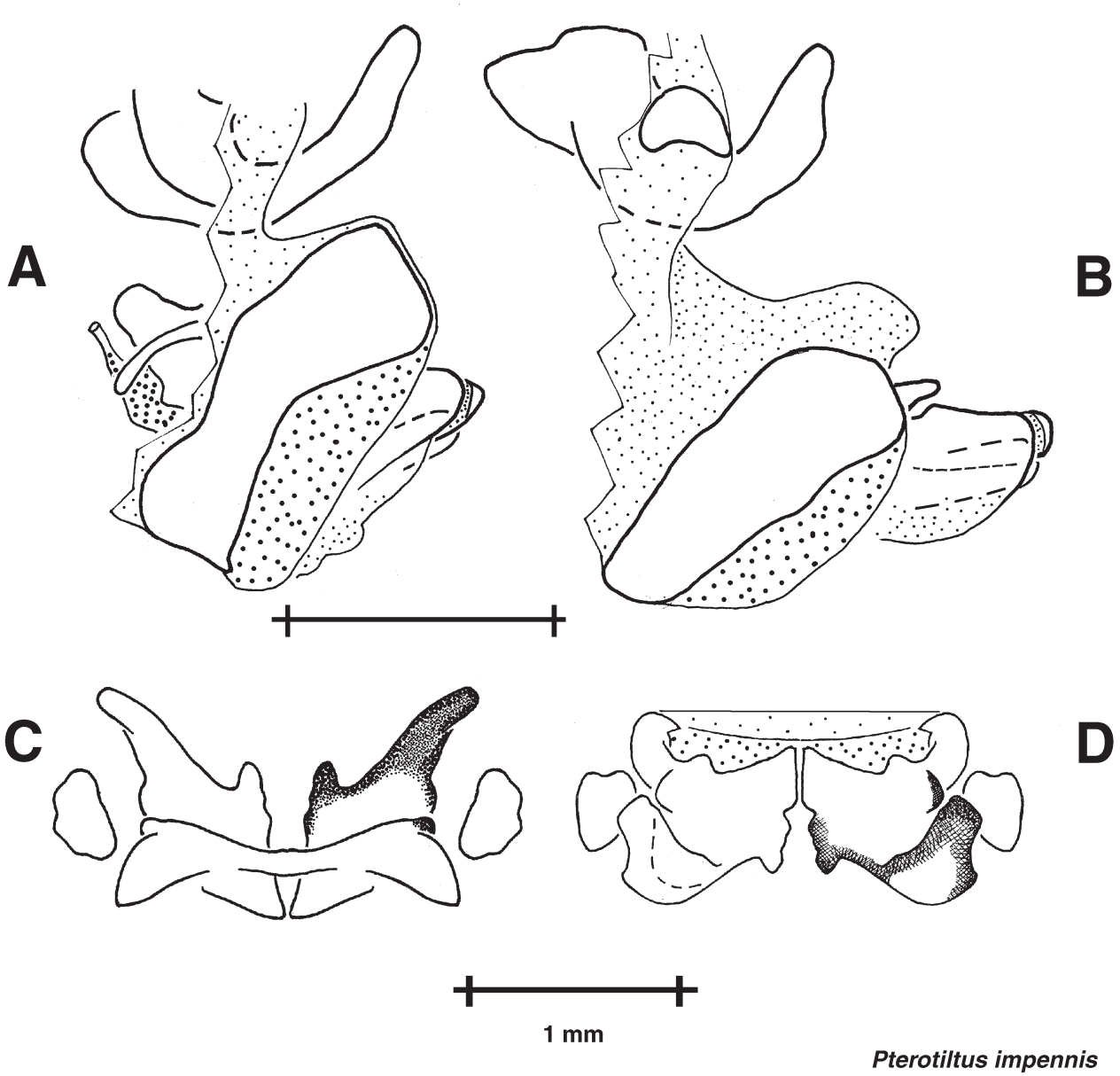


Fig. 4. *P. impennis*, phallic structures. A. Entire phallic complex, retracted, lateral. B. As A, extended. C. Epiphallus, axial. D. Epiphallus, dorsal.

smaller and simpler than in *P. hollisi*. The ancorae of the epiphallus, rudimentary in *P. hollisi*, are better developed in *P. impennis*. The apodemes of the cingulum are longer, narrower and more parallel in *P. impennis* than in *P. hollisi*.

Female: (Fig. 5). Dorsal ovipositor valves flattened and spatulate, diverging towards the tips, slightly deeper than wide, rounded in profile at tip, devoid of teeth; ventral valves long, slender, smooth and rod-like, approximately circular in cross-section (Figs 5A, B). (The ovipositor of *P. impennis* is not significantly different). Posterior margin of subgenital plate (Fig. 5F) smoothly triangular, with a straight, pointed egg guide, laterally compressed at the tip and rather oblong in profile, and 1 pair of large sclerotized columellae. Bursa copulatrix (Fig. 5D, E) large, the walls ornamented with short projections, somewhat asymmetrical distally, but not as pronouncedly so as in *P. impennis* (Fig. 6A). Spermathecal duct fairly short; spermatheca simple with a hooked terminal ampulla (Fig. 5C), lacking the small lateral diverticulum seen in *P. impennis* (Fig. 6C, D).

Coloration (in life).— Antennae black, tipped greenish white. Eyes black. Vertex, fastigium, upper genae, black. Frons white, densely speckled grey-green. Palps and proximal parts of mandibles pale green. Lower genae white tinged with gold, increasingly speckled with green towards their central margins. The white band of the genae is continued backwards across the pronotal lobes and epimera and episterna of the meso- and metathorax. Dorsal half of thorax and the first 3 abdominal segments black, ventral half green. Rest of abdomen olive green, including genitalia. Paired spots on dorsa of pronotum, metathorax and 1st abdominal segment, gold or yellow. Middle and forelegs green, tarsal joints blue-green, underside and aroleum reddish. Hind femur leaf green, upper part of knee black, ventral lobes blue; hind tibia blue, with a leaf green post genicular band. Hind tarsi pinkish white, aroleum pink. In the female the white areas of the pronotum are often tinged with yellow or pink, the abdomen can be tinged with olive brown, and the blue areas

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of the legs are greyer in color.

In dried material the blue color tends to be lost and replaced by green, and in badly discolored specimens the green itself is replaced by yellow. The eyes turn brown when dried.

Distribution.—Relatively common in wet forests of the northwestern shore of Lake Victoria, south and west of the Nile (*i.e.* in the kingdoms of Buganda, Tooro, Ankole and Bunyoro). It occurs also in the Bwindi (Inpenetrable) Forest of Kigezi District in southwest Uganda, but less commonly than elsewhere. It is not known whether it extends into the Ituri region of the Congo or into the Kigoma area of Tanzania. It has not been recorded east of the Nile in Uganda, nor from the Kakamega forest of western Kenya, which is the most easterly outpost of many Ugandan forest grasshopper species.

Natural history.—*P. hollisi* is found in light gaps and along paths in secondary vegetation in wet forest, and is strongly associated with broad-leafed monocots, especially with *Marantochloa leucantha* (Marantaceae). It eats this plant both in the wild and in captivity. It is also found on and eats a variety of Commelinaceous plants, especially the large forest-floor herbs *Pollia congesta* and *Palisota schweinfurthi*, but will also accept *Commelina bengalensis* and other smaller species. It is sometimes found on *Afromomum angustifolium* (Zingiberaceae), but eats this only sparingly in captivity. It appears to be narrowly oligophagous, refusing in captivity various species of Poaceae, Rosaceae, Asteraceae, Euphorbiaceae and ferns, all of which are eaten by sympatric acridid species.

The highly modified structure of the ovipositor (which is almost identical to that of the neotropical genus *Tela* (Acrididae, Proctolabinae) strongly suggests epiphyllic oviposition. This hypothesis was confirmed by observations on a female which laid eggs in captivity in the enclosed cavity of a folded *Marantochloa* leaf (Fig. 7). The young leaves of this plant are folded flat along their main axis. The 4 eggs were arranged parallel to each other in a flat mass of proteinaceous foam, placed like the filling of a sandwich between the 2 leaf surfaces. The upper edge of the foam packet projected slightly above the distal edge of the leaf, and cemented the leaf in its unexpanded state.

Mature adult females on dissection contain 4 to 6 large mature eggs, but never more, indicating that clutches of this size are the normal practice. The same oviposition strategy as used with *Marantachloa* could be applied to the sheathing leaf bases of *Pollia*.

The form of the egg mass, its placement between leaves, and the number of eggs in the egg mass and the ovaries are virtually identical to that described by Descamps (1978) for the completely unrelated Neotropical *Euprepacris charpentieri* (Romaleidae, Bactrophorinae).

Discussion

Biogeography and distribution.— The genus *Pterotiltus* is centered on the central african forest block, from Cameroon to the Congo basin. It has 2 outlying species in West Africa (Togo, Fernando Po). The new species described here extends the range of the genus eastwards of the Congo Basin, into the forests of East Africa. This pattern of distribution is seen in a number of forest grasshopper genera, including, *e.g.*, *Auloserpusia*, *Serpusia*, *Gemeneta*, *Apoboleus*, *Kassongia*, *Pachynotacris* and *Afromastax*.

Food-plant specialization and epiphyllous oviposition.—In the Neotropics, a considerable proportion, perhaps a majority, of wet-forest acridoids are narrowly oligophagous (*e.g.*, Rowell 1978, Amédégnato 1997). Among these specialists there are taxa in at least 5 subfamilies (Bactrophorinae, Proctolabinae, Ommatolampinae, Copiocerinae and Leptysminae) that use epiphyllous or endophytous oviposition techniques, which have the obvious advantage of ensuring that the newly emerged larvae find their food plant. The degree of food-plant specialization in african forest grasshoppers is less well known, but the existing observations suggest that the same may apply there too.

The morphological parallels between the neotropical Leptysminae and the old world Oxyinae have often been remarked upon. From molecular systematic evidence it seems that the two are not closely related phylogenetically (see *e.g.*, Rowell and Flook 1998) and the morphological convergence is probably due to ecological convergence. In both subfamilies some genera specialize on swamp grasses and others on broad-leaved monocots. Many of these latter plants also grow in swampy habitats, but others are characteristic of wet forest, both as understory plants and as epiphytes. It seems likely that in both grasshopper subfamilies the original adaptation was to plants of swampy habitat, and that extension into the forest was a consequence of successful exploitation of families of swamp plants, which also occur in wet forest (*e.g.*, Araceae, Marantaceae). Under these circumstances the morphological convergence (*e.g.*, in coloration, body form, ovipositor structure and egg-laying modus, and the adaptation of the hind legs for swimming) is not surprising.

In view of the observations on *Pterotiltus*, it is of interest to compare its ovipositor with those of other african forest oxyines. The genera *Digentia*, and some species of *Badistica* (Oxyinae), have ovipositors of the same type as *Pterotiltus*; Couturier *et al*. (1984) record *Badistica ornata* as being associated with *Marantachloa*, and that it has been seen eating this plant. It may be speculated that these genera too are epiphyllous in their egg laying, and probably also specialised on broad-leafed monocots. (My observation relates only to *B. bellula*, the type of the genus. Dirsh (1965) says of *Badistica* that the valves have serrated margins. This is not true of *B. bellula*, but presumably applies to other species. Hollis 1975, following Jago 1966, divides the genus into 2 species groups: perhaps one has the ovipositor valves more toothed than the other.) The genus *Caryanda* (=*Austeniella*, =*Dibastica*) on the other hand, though similar in general habitus to the above genera, has rather narrow ovipositor valves of more conventional shape, with numerous small teeth, and Hollis (1975) describes a similar ovipositor in *Cylindrotiltus* and *Gerista*. This ovipositor structure suggests rather an endophytous or possibly terrestrial mode of laying.

The bright colors characteristic of this genus (and exemplified in *P. hollisi*) were attributed by Hollis (1975) to aposematism. This seems *a priori* unlikely; most flightless acridids in wet forest, apart from geophilous species, are brightly colored and highly visual, and use their coloration for purposes of intraspecific recognition and communication. No distasteful properties could be discerned experimentally (using birds and lizards as predators) in the brilliantly colored proctolabine genera *Drymophilacris* and *Ampelophilus* (Rowell, unpubl. obs), which eat Solanaceae and Asteraceae, plant families highly suitable for sequestration of distasteful or toxic compounds. *P. hollisi* is eaten in the wild by spiders and mantises, but experiments with vertebrate predators have not been carried out.

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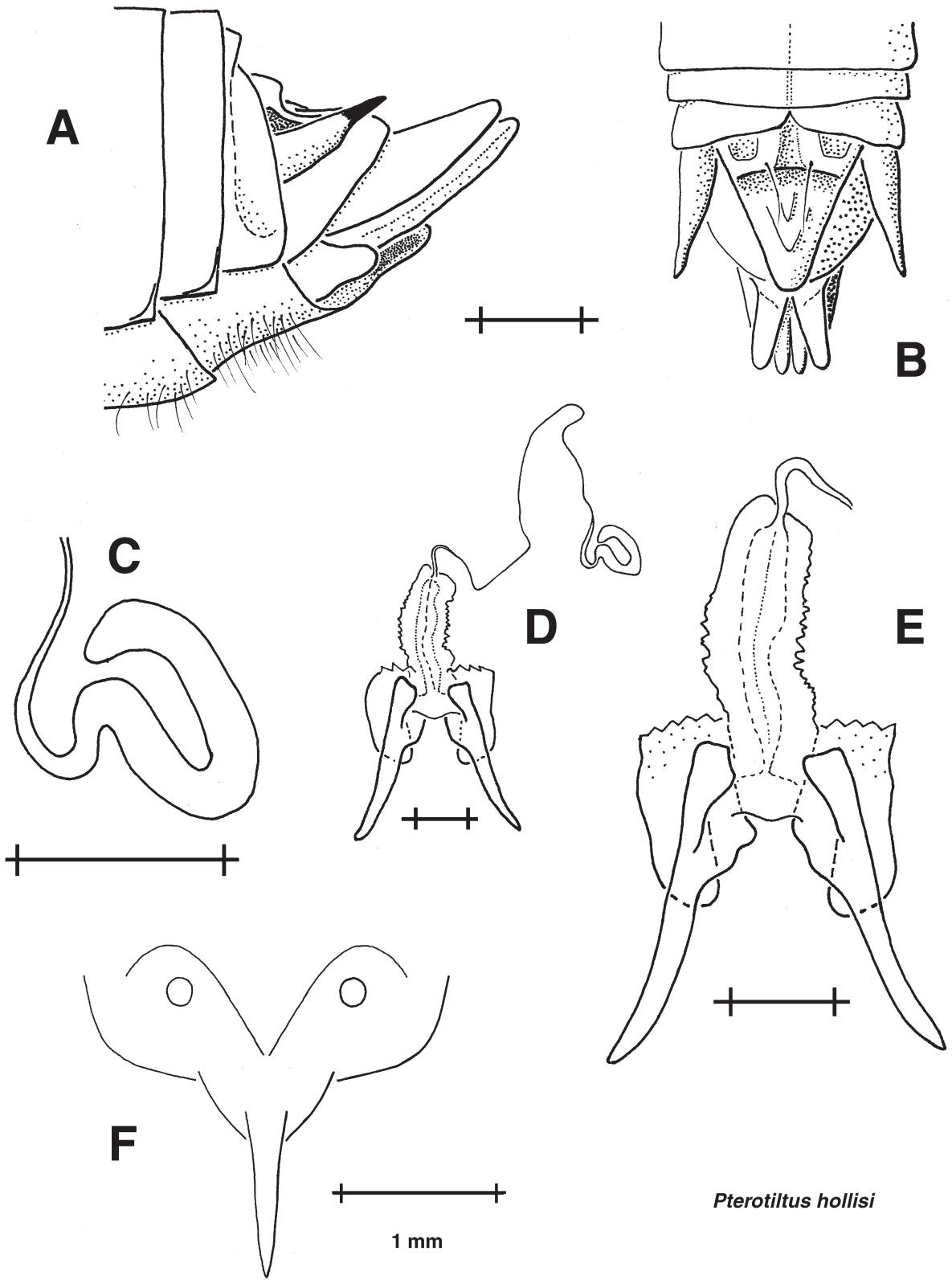


Fig. 5. *P. hollisi*, female reproductive structures. A. External genitalia, lateral. B. External genitalia, dorsal. C. Spermatheca. D. Spermatheca, spermathecal duct, bursa copulatrix. E. Bursa copulatrix. F. Subgenital plate, internal surface. Scale bars, 1 mm.

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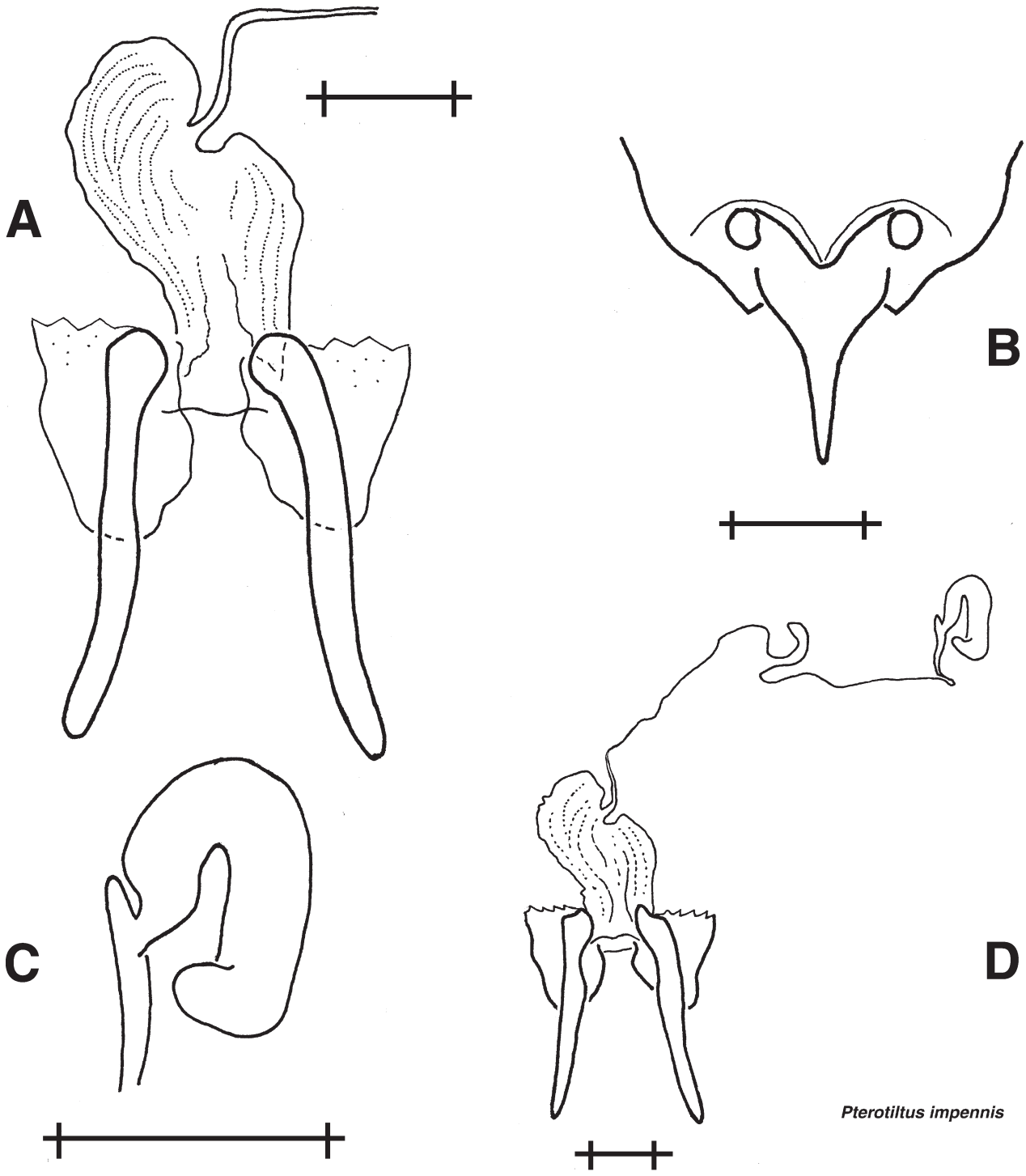


Fig. 6. *P. impennis*, female reproductive structures. A. Bursa copulatrix. B. Subgenital plate, internal surface. C. Spermatheca. D. Spermatheca, duct and bursa. Scale bars, 1 mm.

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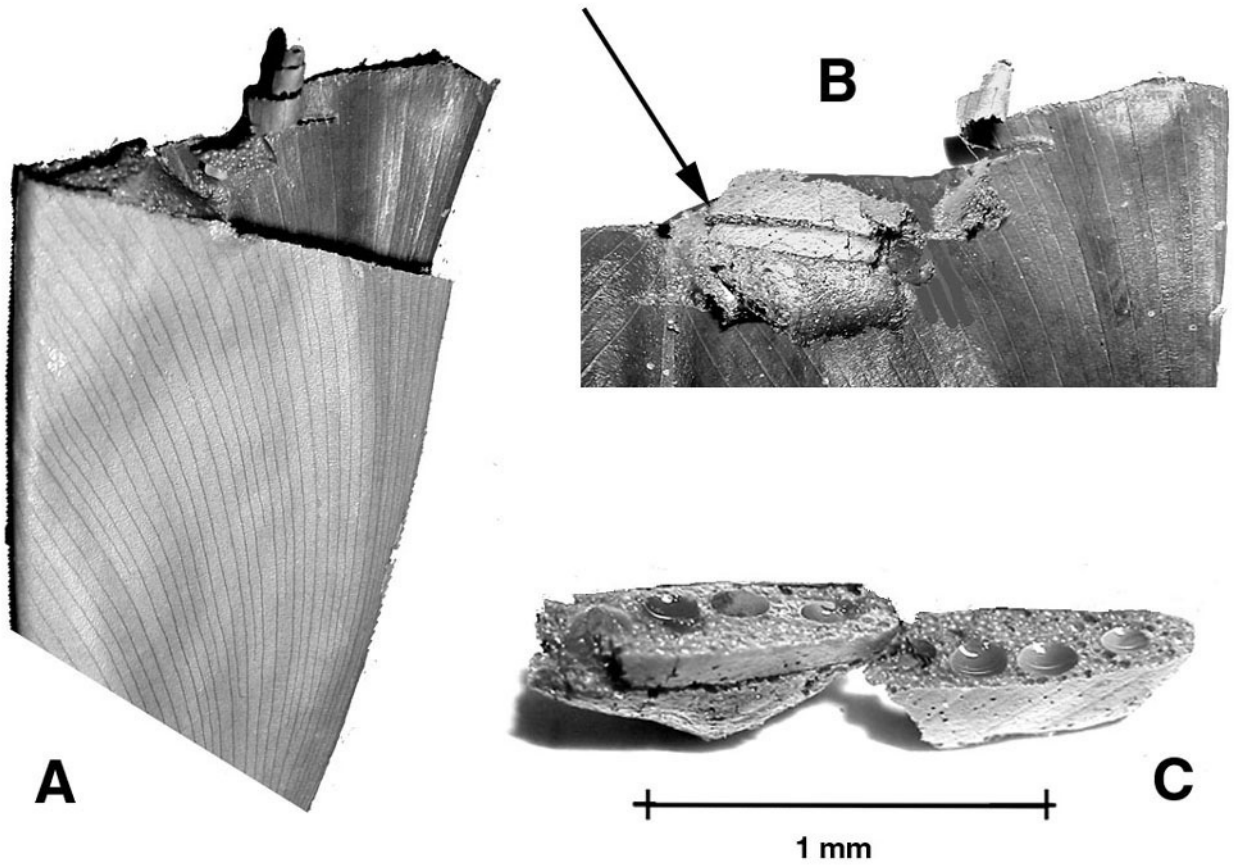


Fig. 7. *P. hollisi*, egg mass. A. portion of young leaf of *Marantochloa leucantha* (Marantaceae), folded as in the unopened state. The tip of the egg mass sandwiched within is visible. B. The egg mass exposed by opening up the leaf and tearing one surface away from the foam of the egg mass. The egg mass shows two parallel lines; the lower is the mark of the detached leaf, the upper (arrow) the scalpel cut which exposes the eggs in C. C. The egg mass detached from the leaf and the top cut off, exposing 4 eggs which are embedded vertically in the foam. Scale bar refers only to C.

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Table 1. *Pterotiltus hollisi*: Dimensions (mm). The structures measured are defined as follows: P, length of pronotum in midline. L, maximum distance between tip of fastigium and hindermost point of abdomen. Ant, antennal flagellum (excluding scape and pedicel). IOS, inter-ocular space. E-E, distance between the outer surfaces of the two eyes. Fast B, breadth of fastigium, measured in dorsal view, between the inner edges of the 2 lateral ocelli. Fast L, length of fastigium, measured in dorsal view, anterior to the most anterior portion of the compound eyes. F, maximum length of the hind femur. FD, maximum width of hind femur, measured at right angles to the axis defined by F. Ta1, 2, & 3, lengths of tarsal joints of the hind foot. The foot formula is the relative lengths of the 3 hind tarsal joints, expressed as percentages of the total length of the foot. External and Internal spines refers to the number of spines on the hind tibia. For illustration of these structures in another taxon and a fuller discussion of their measurement, see Rowell 2003.

Pterotiltus hollisi n. sp.

Males: measurements																External	Internal
No.	Locality	P	L	Ant	IOS	E-E	Fast B	Fast L	F	FD	Ta1	Ta2	Ta3	Ta1+2+3		spines	spines
98034	Mpanga	3.36	17.74	11.66	0.45	3.86	0.82	0.35	11.32	2.36	1.37	0.46	1.90	3.73		7	8
92008	Mpanga	2.78	15.95	10.99	0.34	3.61	0.88	0.32	10.56	2.32	1.14	0.47	1.72	3.33		7	8
98006	Mabira	2.73	15.99	8.58	0.38	3.56	0.80	0.27	10.02	2.22	1.15	0.50	1.76	3.41		7	8
2002002	Zika	3.34	16.70	10.92	0.36	3.80	0.85	0.35	11.27	2.40	1.37	0.52	1.87	3.76		7	9
2003019	Kanyawara	2.89	17.57	broken	0.31	3.61	0.89	0.31	10.87	2.32	1.24	0.50	1.85	3.59		7	8
2003057	Kanyawara	2.87	15.28	9.31	0.34	3.38	0.79	0.30	9.68	2.17	1.12	0.50	1.74	3.36		7	8
2003069	Kanyawara	2.73	14.43	10.00	0.31	3.44	0.75	0.28	9.82	2.30	1.18	0.48	1.71	3.37		7	8
2003079	Kanyawara	2.65	15.85	10.06	0.35	3.40	0.81	0.29	10.24	2.27	1.19	0.57	1.87	3.63		7	8
2003074	Kanyawara	2.77	14.92	10.94	0.39	3.51	0.79	0.38	10.52	2.24	1.32	0.47	1.81	3.60		7	8
	Minimum	2.65	14.43	8.58	0.31	3.38	0.75	0.27	9.68	2.17	1.12	0.46	1.71	3.33		7	8
	Maximum	3.36	17.74	11.66	0.45	3.86	0.89	0.38	11.32	2.40	1.37	0.57	1.90	3.76		7	9
	Average	2.90	16.05	10.31	0.36	3.57	0.82	0.32	10.48	2.29	1.23	0.50	1.80	3.53	Median:	7	8
	N	9	9	8	9	9	9	9	9	9	9	9	9	9		9	9

Males: ratios										Foot formula:	35%	14%	51%			
No.	Locality	L/P	Ant/P	IOS/P	E-E/P	Fast B/P	Fast L/P	F/P	FD/P	Ta1/P	Ta2/P	Ta3/P	Ta1-3/P	F/FD	Ta1-3/F	Fast L/B
98034	Mpanga	5.28	3.47	0.13	1.15	0.24	0.10	3.37	0.70	0.41	0.14	0.57	1.11	4.80	0.33	0.43
92008	Mpanga	5.74	3.95	0.12	1.30	0.32	0.12	3.80	0.83	0.41	0.17	0.62	1.20	4.55	0.32	0.36
98006	Mabira	5.86	3.14	0.14	1.30	0.29	0.10	3.67	0.81	0.42	0.18	0.64	1.25	4.51	0.34	0.34
2002002	Zika	5.00	3.27	0.11	1.14	0.25	0.10	3.37	0.72	0.41	0.16	0.56	1.13	4.70	0.33	0.41
2003019	Kanyawara	6.08		0.11	1.25	0.31	0.11	3.76	0.80	0.43	0.17	0.64	1.24	4.69	0.33	0.35
2003057	Kanyawara	5.32	3.24	0.12	1.18	0.28	0.10	3.37	0.76	0.39	0.17	0.61	1.17	4.46	0.35	0.38
2003069	Kanyawara	5.29	3.66	0.11	1.26	0.27	0.10	3.60	0.84	0.43	0.18	0.63	1.23	4.27	0.34	0.37
2003079	Kanyawara	5.98	3.80	0.13	1.28	0.31	0.11	3.86	0.86	0.45	0.22	0.71	1.37	4.51	0.35	0.36
2003074	Kanyawara	5.39	3.95	0.14	1.27	0.29	0.14	3.80	0.81	0.48	0.17	0.65	1.30	4.70	0.34	0.48
	Minimum	5.00	3.14	0.11	1.14	0.24	0.10	3.37	0.70	0.39	0.14	0.56	1.11	4.27	0.32	0.34
	Maximum	6.08	3.95	0.14	1.30	0.32	0.14	3.86	0.86	0.48	0.22	0.71	1.37	4.80	0.35	0.48
	Average	5.55	3.56	0.12	1.24	0.28	0.11	3.62	0.79	0.43	0.17	0.62	1.22	4.58	0.34	0.39
	N	9	8	9	9	9	9	9	9	9	9	9	9	9	9	9

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Table 1. cont.

Females: measurements																External	Internal
No.	Locality	P	L	Ant	IOS	E-E	Fast B	Fast L	F	FD	Ta1	Ta2	Ta3	Ta1+2+3		spines	spines
98032	Mpanga	3.75	20.77	9.00	0.71	4.39	1.11	0.44	13.55	2.90	1.48	0.60	2.34	4.42		7	8
98033	Mpanga	3.36	22.16	9.29	0.63	4.18	1.03	0.49	12.53	2.65	1.46	0.54	2.21	4.21		7	8
92013	Mpanga	3.67	19.32	11.08	0.68	4.22	1.05	0.43	13.13	2.81	1.46	0.65	2.08	4.19		7	9
2003073	Kanyawara	3.24	17.99	8.44	0.50	3.70	1.07	0.41	11.24	2.45	1.30	0.56	1.95	3.81		6	7
2003076	Kanyawara	3.35	20.82	8.71	0.58	4.18	1.09	0.43	12.26	2.72	1.28	0.53	2.19	4.00		6	8
2003068	Kanyawara	3.45	19.28	9.56	0.56	4.12	1.02	0.37	12.48	2.84	1.42	0.60	2.32	4.34		7	8
2003055	Sebitoli	3.19	18.65	9.09	0.53	4.02	1.04	0.42	11.97	2.68	1.39	0.60	2.25	4.24		7	8
	Minimum	3.19	17.99	8.44	0.50	3.70	1.02	0.37	11.24	2.45	1.28	0.53	1.95	3.81		6	7
	Maximum	3.75	22.16	11.08	0.71	4.39	1.11	0.49	13.55	2.90	1.48	0.65	2.34	4.42		7	9
	Average	3.43	19.86	9.31	0.60	4.12	1.06	0.43	12.45	2.72	1.40	0.58	2.19	4.17	Median:	7	8
	N	7	7	7	7	7	7	7	7	7	7	7	7	7		7	7
Females: ratios									Foot		34%	14%	53%				
No.	Locality	L/P	Ant/P	IOS/P	E-E/P	Fast B/P	Fast L/P	F/P	FD/P	Ta1/P	Ta2/P	Ta3/P	Ta1-3/P	F/FD	Ta1-3/F	Fast L/B	
98032	Mpanga	5.54	2.40	0.19	1.17	0.30	0.12	3.61	0.77	0.39	0.16	0.62	1.18	4.67	0.33	0.40	
98033	Mpanga	6.60	2.76	0.19	1.24	0.31	0.15	3.73	0.79	0.43	0.16	0.66	1.25	4.73	0.34	0.48	
92013	Mpanga	5.26	3.02	0.19	1.15	0.29	0.12	3.58	0.77	0.40	0.18	0.57	1.14	4.67	0.32	0.41	
2003073	Kanyawara	5.55	2.61	0.15	1.14	0.33	0.13	3.47	0.76	0.40	0.17	0.60	1.18	4.59	0.34	0.38	
2003076	Kanyawara	6.22	2.60	0.17	1.25	0.33	0.13	3.66	0.81	0.38	0.16	0.65	1.19	4.51	0.33	0.39	
2003068	Kanyawara	5.59	2.77	0.16	1.19	0.30	0.11	3.62	0.82	0.41	0.17	0.67	1.26	4.39	0.35	0.36	
2003055	Sebitoli	5.85	2.85	0.17	1.26	0.33	0.13	3.75	0.84	0.44	0.19	0.71	1.33	4.47	0.35	0.40	
	Minimum	5.26	2.40	0.15	1.14	0.29	0.11	3.47	0.76	0.38	0.16	0.57	1.14	4.39	0.32	0.36	
	Maximum	6.60	3.02	0.19	1.26	0.33	0.15	3.75	0.84	0.44	0.19	0.71	1.33	4.73	0.35	0.48	
	Average	5.80	2.72	0.17	1.20	0.31	0.12	3.63	0.79	0.41	0.17	0.64	1.22	4.58	0.34	0.40	
	N	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	
Sexual dimorphism:															External	Internal	
		P	L	Ant	IOS	E-E	Fast B	Fast L	F	FD	Ta1	Ta2	Ta3	Ta1+2+3	spines	spines	
		0.85	0.81	1.11	0.60	0.87	0.77	0.74	0.84	0.84	0.88	0.85	0.82	0.85	1	1	
		L/P	Ant/P	IOS/P	E-E/P	Fast B/P	Fast L/P	F/P	FD/P	Ta1/P	Ta2/P	Ta3/P	Ta1-3/P	F/FD	Ta1-3/F	Fast L/B	
		0.96	1.31	0.71	1.03	0.92	0.88	1.00	1.00	1.04	1.01	0.98	1.00	1.00	1.01	0.96	
			*	*		*	*										

* significant deviation from unity. Male has longer antennae, narrower IOS, and smaller fastigium

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