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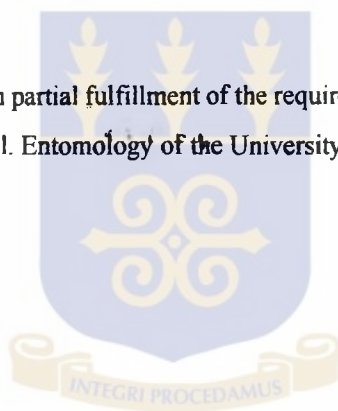


**A revision of the Afrotropical members of the subgenus *Uresipedium* Sasa
et Kikuchi, 1995, of the genus *Polypedium* Kieffer, 1912, with the
description of eleven new species (Diptera: Chironomidae)**

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B. Sc. (Hons) Zoology

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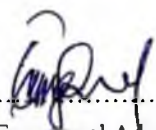
Collaborating Departments: Zoology (Faculty of Science) & Crop Science (Faculty of Agriculture)

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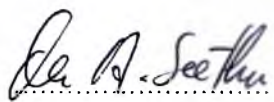


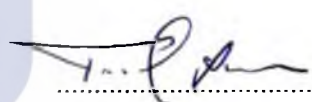
DECLARATION

This is to certify that this thesis has not been submitted for a degree to any university. It is entirely my own work under the supervision of Professor Ole A. Sæther and Associate Professor Trond Andersen both of the Department of Zoology, University of Bergen, Norway.


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DEDICATION

To my loving and caring family.



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ABSTRACT

A revision of the Afrotropical members of the subgenus *Uresipedium* Sasa et Kikuchi, 1995 showed that most of the earlier species were misidentified. Ten new Afrotropical species are identified and described: *P. (U.) spinibojum* sp. n., *P. (U.) plautum* sp. n., *P. (U.) lehmanni* sp. n., *P. (U.) praegnans* sp. n., *P. (U.) harrisoni* sp. n., *P. (U.) freemani* sp. n., *P. (U.) dosse nudum* sp. n., *P. (U.) acutulum* sp. n., *P. (U.) kakumense* sp. n., and *P. (U.) gladysae* sp. n. Two species, *P. (P.) ephippium* Freeman and *P. (P.) anderseni* sp. n. which belong to the nominal subgenus *Polypedilum* are also described or redescribed because they were misidentified by Freeman (1958) due to the similar colour pattern with *P. (U.) freemani* sp. n. Two Afrotropical species, *P. (U.) annulatum* Freeman and *P. (U.) kibatiense* Goetghebuer, and one European *P. (U.) convictum* Walker are redescribed. Only males and a few associated immatures are described. Females and immatures are still in want for description.

Generic diagnosis and systematics of the genus *Polypedilum* Kieffer are given. A key to the male imagines, pupae and larvae (adapted from Sæther & Sundal, 1977) of the subgenera species groups and types of *Polypedilum* is given. A key is also raised for the male imagines of the Afrotropical members of the subgenus *Uresipedium*.

The ecology and distribution of the Afrotropical species of *Uresipedium* show that in general, the Ghanaian species are smaller with lower chaetotaxy than those from Eastern and Southern Africa. This might be an adaptation to the different climatic conditions. The Ghanaian species are known from a warm and humid rain-forest, whereas the species from Eastern and Southern Africa occupy a montane or much cooler habitats.

The systematics is based on all available material of *Uresipedilum* from all the six zoogeographical regions. The subgenus can be divided into three distinct groups when a parsimony analysis is done using PAUP version 3.1.1 and McClade on a Macintosh IIsi. The *annulatum* group consists of five Afrotropical and two Nearctic species as their sister group. The *convictum* group consists of three Japanese species, two Nearctic species, and the Palaearctic and Oriental species. The *oresitrophum* group consists of three Afrotropical species, three species from New Zealand, and one from Australia. There are other groups or species which belong to uncertain placement. The three distinct groups confirmed the initial splitting of Pangaea into Laurasia and Gondwanaland before the subsequent splitting of Laurasia and Gondwanaland.

Chapter 1

INTRODUCTION

1.1 Introduction to Chironomids

1.1.1 Geographical range and physiological diversity

Chironomids (Diptera: Chironomidae) are non biting midges belonging to the suborder Nematocera. They are among the most widely distributed free-living holometabolous insects, and also the most abundant in fresh or brackish water (Oliver, 1971; Pinder, 1986; Armitage *et al.*, 1995). In addition there are many terrestrial and semi-terrestrial species, primarily in the subfamily Orthocladiinae. There are also some marine species (Pinder, 1989).

Chironomid larvae can be found in habitats with low levels of dissolved oxygen; and are the only insects present in profundal benthic sediments. Immature stages of some chironomid species are able to exploit extremes of temperature, pH, salinity, depth, current velocity and productivity (Armitage *et al.*, 1995). Oliver and Corbet (1966) found a diverse community at Ellesmere Island, at Lake Hazen 81° 49' N. At the other extreme, the Antarctic mainland is home to three species with *Parochlus steinenii* (Grecke) and *Belgica antarctica* Jacobs reaching 62° S and 68° S respectively (Usher & Edwards, 1984; Edwards & Usher, 1985).

Chironomids have physiological mechanisms that make them cold tolerant. They are known to live in the glaciated areas of the highest mountains, including elevations of up to 5,600 m in the Himalaya (Kohshima, 1984; Sæther & Willassen, 1987) and are active at temperatures of -16° C. The larvae of *Sergentia* can survive at over 1,000 m depth in the abyssal of the world's deepest body of freshwater, Lake Baikal (Linevich, 1963).

Chironomids can exploit varying and unpredictable habitats in many parts of the world where rainwater gathers temporarily in depressions in rock surfaces. They may either be drought resisting and able to survive at least some degree of desiccation or they may persist in permanently wet or moist habitats (Armitage *et al.*, 1995). A spectacular example is the larva of

Polypedilum vanderplanki Hinton which is reported in Africa to survive for several years almost totally desiccated, but quickly rehydrates after the next rainfall. In desiccated condition, the larva is able to withstand remarkable extremes of temperature, from -270°C to 102°C. It can survive 10 cycles of dehydration and rehydration (Hinton, 1951, 1960a, b). The larvae of *P. pilosella* could survive for 4 years in dry soil, while *P. vanderplanki* survived for 17 years in sealed glass tube containing silica gel (Adams, 1983).

1.1.2 Brief biology and ecology

Chironomids are most familiar as adults that swarm beside productive standing waters, and they are ubiquitous inhabitants of organically enriched places (Armitage *et al.*, 1995). There are species that thrive in almost every conceivable freshwater environment (Oliver, 1971; Edward, 1986; Pinder, 1986). The immature stages can be found in ice-cold glacial trickles, hot springs, phytotelmata, conventional flowing waters (trickles, torrents, streams, rivers), standing waters (puddles, pools, lakes), rain pools and even thin film of water on high-altitude glaciers (Kohshima, 1984, Sæther & Willassen, 1987). Some chironomid species tolerate high osmotic levels in brackish and shoreline saline pools, and several genera include intertidal and marine species. The semi-aquatic species live in moist soil or vegetation. The truly terrestrial chironomid species are found predominantly in humic soils with decaying vegetation, and in exceptional cases, in green house vegetation (Cranston, 1987). A most unusual biotope adopted by any terrestrial chironomid is fresh cow dung, the sole habitat of immature *Camptocladius stercorarius* DeGeer, 1776.

Adult chironomids are short-lived, lasting from a few days to several weeks (Oliver, 1971; Pinder, 1986). Many species form conspicuous aerial mating swarms, although there are some species that mate on the ground or on water surface. The swarming period is commonly controlled by light intensity, with twilight swarming being common, but the response to light may be modified by temperature (Oliver, 1971). Males are attracted to females that enter the swarm by the sound produced by the female's wings. Syrjämäki (1968) observed that in the case of *Smittia extrema* Holmgren, 1869, in Spitzbergen, males remain motionless on the ground until stimulated to swarm by the sound of a nearby female. Swarming could also be

induced by humming the appropriate note. After mating the female may fly away from the swarming site to deposit her eggs onto water or soil suited to the development of the larvae. The emerging larvae feed on micro-organisms, algae and detritus till pupation. They then leave the water or soil as adults which may feed on honey, honeydew, nectar, pollen and fresh fly dropping on water (Armitage *et al.*, 1995; Sasa & Kikuchi, 1995).

1.1.3 The role played by chironomids in the environment

Chironomids are known to be tolerant to low oxygen, heavy metals, low pH or high conductivity, thus they serve as indices of environmental deterioration since different species are found in specific chemical or physical environments. Some species are excellent biological indicators of the degree of water pollution, and different species are found in water of varying physical qualities even when the chemical quality is nearly the same - for example, in rivers or lakes, where a stream is slow or rapid, or where the bottom sediment is mud, sand, or stone. Chironomids are therefore useful in classifying freshwater and in monitoring organic pollution or eutrophication. The science of limnology and/ or ecology use chironomid communities as indicators of the trophic states of freshwaters (Brundin, 1949, 1956; Sæther, 1979, 1980b).

Chironomid larvae consume organic substances in the bottom of water bodies or in the soil, to increase their body weights; they ultimately emerge from the water or soil as adult midges, or are eaten by carnivorous insects or fishes. They play an important role in the disposal of nutrients from the environment, thus preventing rivers, lakes, and rice paddies from eutrophication or fouling (Sasa & Kikuchi, 1995). Chironomids therefore have a potential role as biological filters of waste water.

The theory of plate tectonic (continental drift) only became generally accepted by biologists after the work of Brundin (1966) on transantarctic relationships of chironomids. Fossils of chironomids show that the family constitutes a very old group with most present genera represented already between the Jurassic and the Cretaceous periods (Brundin, 1976).

1.1.4 Food value

The approximate mean percentage composition of chironomid larvae are as follows: moisture content, 86; protein, 48; lipid, 14; carbohydrate, 23; chitin, 4; ash, 9 and utilised energy is 4.1 kcal g⁻¹ (Yurkowski & Tabachek, 1979). Protein is a principal source of amino acid for insects, fish and other vertebrates. In a comparison of several diets for fish, it was found that chironomid larval biomass showed the highest total amino acid content of 47.51 mg/100 mg dry weight (De la Noüe & Choubert, 1985). The relative high protein content, the high digestibility (73.6%: De la Noüe & Choubert, 1985) and the apparent function in small quantities as a growth promoter in fish diets (Yashouv, 1956; Yashouv & Ben Shachar, 1967) make chironomid larvae a rich food for many organisms.

The high production and ubiquitous occurrence of chironomid population both in aquatic and aerial stages are low in the food chain because they contribute largely to the food of other groups of animals ranging from small to the large predators. It serves as food for *Hydra* (Grzybkowska, 1988) through to bats (Griffiths & Gates, 1985) and humans, especially those living around some large African lakes. It is popular among Ugandans around Lake Victoria and other Ugandan lakes (Armitage *et al.*, 1995).

Chironomids are major food of both juvenile and adult fish. In the Volta Lake, Ghana, chironomids form a major component of the diet of mormyrids (Armitage *et al.*, 1995). Olatunde and Moneke (1985) also found that all the four species of mormyrids studied in Zaria, Nigeria used chironomid larvae as their main food source. Chironomids are also used as fish food by aquarists in live or dried form and occasionally as baits by anglers. The rising pupa and nearly emerged adult form frequent models for fly-fishers' lures. Clearly chironomids are vital in the trophic pathway of aquatic environments since they transmit nutrients along the food chain in nature.

1.1.5 Medical importance

Chironomid swarms often limit human activity outdoors because the adults can be inhaled or fly into the mouth, eyes, or ears, and may even cause asphyxia in cattle (Grodhaus, 1963). The swarms are hazardous to passengers and crews on trains, buses, cargo vessels and boats in

Venice, Italy (Ali *et al.*, 1992). The attraction of adult midges to light causes great discomfort in residential areas.

Allergic diseases include the symptoms of dermal irritation and/ or respiratory allergy and this is caused by abnormal stimulation of the immune system (Armitage *et al.*, 1995). Earlier on Carpenter (1920), reported of the arrival of clouds of chironomids which produced an outbreak of nasal catarrh amongst the white inhabitants in Entebbe, Uganda. In Sudan, allergic symptoms ranging from urticaria, dermatitis, allergic rhinitis to fatal attacks of asthma are linked with the seasonal mass emergence of Nilotic midges, including *Cladotanytarsus lewisi* Freeman, 1950 (Kay *et al.*, 1978; Cranston *et al.*, 1981; Armitage *et al.*, 1995). At least one third of asthma attacks in Japan are caused by inhalation of dust containing chironomid midges (Sasa & Kikuchi, 1995). Asthma related mortalities arise by problems associated with respiratory failure and anaphylaxis.

1.1.6 Species richness and conclusion

Estimates of global species richness of Chironomidae ranges from 8,000 to about 20,000 species (Armitage *et al.*, 1995). Considering the fact that only the western Palaearctic (with about 1,000 or more species) has been investigated with anything approaching thoroughness, an estimate towards the higher end of this range is certainly justifiable. There are discrepancies in these global estimates because of our relative ignorance of species richness and the levels of endemism (Armitage *et al.*, 1995). Considering the species richness of chironomids, and the discovery of high numbers of previously undescribed species encountered, much work needs to be done to describe these new species and also redescribe the previously known species. When this is done a more realistic global estimate can then be made.

1.2 Taxonomic background

It is estimated that there are as many as 15,000 species of chironomids world-wide (Armitage *et al.*, 1995) of which about 6,000 are described (Sæther pers. comm.). However, the basis for such estimates ought to be examined critically because most of the chironomid

taxonomists have been Europeans, and more recently, North American and Japanese scientists. Research work carried out by Petr (1970) and Amakye (1980) have also shown that chironomids are important components of the freshwater fauna in the Afrotropical Region.

Amakye and Samman (1981) reported that in the West African subregion, up to 50% of the benthic invertebrate fauna belong to the Chironomidae. Most of the major studies in this subregion have however been limited to standing waters like lakes, reservoirs and large rivers. Petr (1969) studied the fauna in the Volta Lake, Ghana. Whyte (1975) carried out studies on Lake Bosomtwi in Ghana, McLachlan (1965, 1969) on the Kariba Lake in Zimbabwe, and Dejoux (1968) and Hopson (1967) on Lake Chad. Many Afrotropical chironomid genera and species of small rivers and streams, especially in forest areas, probably remain undescribed. Thus knowledge about the chironomid fauna of the Afrotropical region remains scanty, and further work needs to be done. Even in the relatively well-documented areas, undescribed species are still being discovered sporadically (Armitage *et al.*, 1995).

From the Afrotropical region, 526 species representing 114 genera have been recorded (Lehmann, 1979, 1981; Freeman & Cranston, 1980; Willassen & Cranston, 1986; Cranston, 1989; Cranston & Judd, 1989; Harrison, 1991, 1992; Andersen & Sæther, 1993a, b, 1994, 1996; Sæther & Andersen, 1993, 1995, 1996a, b; Amakye, 1995; Ferrington & Sæther, 1995; Sæther, 1996; Sæther & Wang, 1996; Sæther & Sundal, 1997). In the material collected by the Museum of Zoology, University of Bergen, from Tanzania, there is an additional 2 or 3 presumed new genera and about 20 new species (Sæther pers. comm.). Most Afrotropical Chironomidae are known as imagines only. This is because most attempts made to rear the immature till pupation are unsuccessful. The immature stages as well as the females of the bulk of the chironomids from the Afrotropical region are still in want of description, only a few species have been described (Sæther, 1977; Epler, 1988).

By the end of 1993, a checklist based on published records from Ghana indicated that, there were 87 species in 31 genera belonging to 3 subfamilies in the country (Amakye, 1993). Tanypodinae is represented by 12 species (14%), Orthocladiinae by 6 species (7%) and Chironominae by 69 species (79%). The only two species originally described from Ghana before 1992, were *Dicrotendipes crispus* Freeman, 1957 and *Tanytarsus zariae* Freeman, 1958.

Four Afrotropical species, *Collartomyia hirsuta* Goetghebuer, 1936, *Henrardia quadrispinosa* Goetghebuer, 1936, *Microtendipes lentiginosus* Freeman, 1955 b, and *Dicrotendipes multispinosa* Freeman, 1957, have been redescribed for both sexes and all stages by Amakye and Sæther (1992, 1993). Kyerematen (1996) described seven new Afrotropical species of *Rheotanytarsus* Kieffer, 1921 including five from Ghana while Adam (1996) described four new species of *Nilothauma* Kieffer, 1921, with three from Ghana in their unpublished theses. Amakye (1995) described a new species *Collartomyiadiscaudata* from Agumatsa. Kristoffersen (1996) in her unpublished thesis described the new species *Stenochironomus aliquantus* from the White Volta in Ghana and *S. notater* from the Ankasa area, and also redescribed *S. spatuliger*, Kieffer, 1922 and *S. polychaetus*, Kieffer, 1922 partly based on material from Ghana. Sæther and Andersen (1996a) described *Doithrix longipes*, *D. amegabei*, *Georthocladus longicalcaneum*, and *G. amakyei*, all from the Ankasa area in Ghana. Sæther and Andersen (1996b) described the new genus *Friederia* with the single included species *F. villosa*, also from the Ankasa area. Sæther and Sundal (1997) described a new subgenus of *Polypedilum*, *Cerobregma*, including two new species from Ghana, *P. (C.) bulbocaudatum* and *P. (C.) subulatum*, and redefined *P. (C.) ramiferum* Kieffer partly based on material from Ghana. Numerous additional, and probably new Afrotropical species from Ghana are yet to be described from collections made by the Norwegian Universities Committee for Development, Research and Education (NUFU) team. Material belonging to the genera *Stenochironomus* Kieffer, *Polypedilum* Kieffer (in addition to *Tripodura* Townes), *Rheotanytarsus* Thienemann et Bause, *Tanytarsus* v. d. Wulp, and *Thienemanniella* presently are being revised by Sæther *et al.* Most of the species described above were collected by the NUFU team.

Chironomidae is currently divided into eleven subfamilies, namely: Diamesinae Kieffer, 1923; Orthoclaadiinae Edwards, 1929; Podonominae Thienemann, 1937; Chironominae Macquart, 1938; Telmatogetoninae Brundin, 1966; Tanypodinae Thienemann et Zavrel, 1966; Aphroteniinae Brundin, 1966; Prodiamesinae Sæther, 1976; Buchonomyiinae Brundin et Sæther, 1978; Chilenomyiinae Brundin, 1983 and Usambaromyiinae Andersen et Sæther, 1994.

The Chironominae appear to be the most abundant and the most species rich of the subfamilies in Africa south of the Sahara. It has been found that species of the subfamily are especially typical of warm water environments (Freeman, 1957) and also seem to prefer standing or slow flowing water (Freeman & Cranston, 1980). They are found in all zoogeographical regions except the Antarctica (Cranston *et al.*, 1989). The subfamily is quite homogenous being recognised in the adult stage by the absence of vein MCu; the anterior tibia being subequal or shorter than the anterior tarsomere 1 (leg ratio, LR_1 , subequal to or greater than 1); the anterior tibia terminating (on the inner side) in a "scale" which may be low and rounded, or oval and more pronounced, and in either case may carry a bristle-like spur. The middle and posterior tibiae normally bear two apical combs which are composed of basally fused spinules, the tibial spurs are associated with these combs, but one or both spurs may be reduced or absent, and the combs may be fused or separate. In the males, the gonostylus is virtually fused to the gonocoxite with little or no flexion permitted. However, in a few genera (*Stictochiromus* Kieffer, 1919, *Phaenopsectra* Kieffer, 1921 and *Sergentia* Kieffer, 1922) the gonostylus is flexible but the angle of flexion rarely allows folding inwards.

The three tribes recognised within the subfamily Chironominae are the long-recognised Chironomini, Tanytarsini and the Pseudochironomini, a more recent designation by Sæther (1977). Members of Chironomini are distinguished by the wing membrane bearing no macrotrichia, or if present, then the squama has a marginal fringe of long setae, and the cross-vein R-M is oblique to vein R_{4+5} . The tribe was divided by Kieffer (1921c) into two groups depending on whether the posterior tibia has one or two spurs in association with the combs. This method of dividing the bulk of the species was also adopted by Edwards (1929) and Goetghebuer (1937). For most species this is satisfactory, but not phylogenetically correct. Kieffer's original method of dividing the tribe was followed by Freeman (1957), but some of the definitions were modified because of the presence of intermediate species between the genera, and also the presence of single spurred species in the genera which are normally two spurred.

The genus *Polypedilum* belongs in the tribe Chironomini. It is a genus of eurytopic species, occurring in all standing and flowing waters, except those at high latitude and altitude. The

larvae of most species occur in sediments, with a few species mining wood or grazing epilithic surfaces. The genus is world-wide, occurring in all zoogeographical areas except Antarctica. The Holarctic fauna includes at least 100 species. In the Afrotropical region, it is one of the dominant genus with 39 of 415 species recorded (Freeman & Cranston 1980).

Polypedilum is the only genus with only one spur on the posterior tibia, and it is quite heterogeneous, with a particular variation in the male hypopygium. It is among the genera with 13 flagellomeres in male and 5 in females, without strongly reduced medially widely separated anteprenotal lobes and with the scutum scarcely overreaching the anteprenotum. The male *Polypedilum* is principally distinguished by the anterior tapering of tergite VIII to a narrow waist where it is connected to segment VII. In its widest sense it is one of the better defined genera of the family. In doubtful cases, examination of the pulvilli (deeply bifid) and the eighth segment of the male abdomen affords a ready means of identifying the genus (Freeman, 1958). The absence of the discrete group of short setae on the inner subapex of the gonostylus appears to be a valuable discriminating character (Cranston *et al.*, 1989).

In reviewing the Nearctic Chironomini, Townes (1945) divided the *Polypedilum* into three subgenera, *Polypedilum sensu strictus* Kieffer, 1913, *Pentapedilum* Kieffer 1913 and *Tripodura* Townes, 1945. Within the subgenus *Polypedilum*, he recognised two species groups, the *fallax* group and the *convictum* group, based on the adult characters: body size, antennal ratio (AR), foreleg ratio (LR₁) and ending point of vein R₄₊₅. The genus until recently consisted of four subgenera: *Polypedilum s. str.*, *Pentapedilum*, *Tripodura* and *Uresipedilum* Sasa et Kikuchi, 1995. Sæther (1977) placed the *Polypedilum* group of genera in his wider *Phaenopsectra* group as the sister group to the remaining genera of the tribe Chironomini except the more basally placed *Microtendipes* group. Recently Sæther and Sundal (1997) erected a new subgenus, *Cerobregma*, and regarded *Asheum* Sublette et Sublette as an additional subgenus of *Polypedilum*. The subgenus *Uresipedilum* was erected by Sasa and Kikuchi (1995) for the *Polypedilum convictum* group *sensu* Niitsuma (1992b). However, the name was first used without a description and *Uresipedilum* Sasa et Okazawa (1991), thus was *nomen nudum*. The *convictum* species group of the genus *Polypedilum* Kieffer, 1912, was first erected by Lenz (1941) for those species characterised by the pupae having 4-6 small branches in their thoracic

respiratory organ, the larvae having the second medium mentum teeth smaller than the first and third, and the two larval eye spots fused on each side of the head. The adult subgenera are different from other groups by the following: the basal portion of dorsal appendage much longer than wide; with a posterior lobe bearing one to several long setae; apical process arising from inner margin of the base and directed inwards; wing vein R_{2+3} almost in contact with R_1 .

Most of the characters used by Townes (1945) for grouping and separating species are of no use, except for the shape of the superior volsella, since they may vary between individuals (Niitsuma, 1992b). The analysis of the shape is usually considered more taxonomically important than size, although size may influence shape if allometry exists. Species are frequently characterised by colouration or colour patterns. Colour patterns are more useful than colouration which is not only relative and subjective, but cannot be frequently discernable from preserved specimens, although it may be quantitative by wavelength or by reference to an international colour standard (Wiley, 1981). Also a change in the direction of the light may reverse the colours, especially when the pruinosity is heavy, as found on the thorax of most specimens. It would be very difficult to differentiate species from the above characters and by the measurement of AR, LR_1 , and wing length (WL) only, as was done by previous workers. Also most of the earlier specimens were poorly mounted, resulting in some characters becoming concealed, coupled with inaccurate drawings (Freeman, 1955b), and unstated number of specimens used. With the development of new terminology for the general morphology of chironomids by Sæther (1980a) and the use of new standards for description, it has become necessary to review and redescribe the previously known Afrotropical species of *Uresipedilum*.

In this thesis, several new species were found in Ghana during the collection done in connection with the Norwegian Universities' (NUFU) project in collaboration with the Zoology Department, University of Ghana and the Institute of Aquatic Biology (IAB) in Ghana between 1992-1995. Other new species were recognised in material collected by University of Bergen research team in the West Usambara mountains in North East Tanzania. Some new species were also recognised from borrowed material from Natal Province in South Africa, Zoologisches Staatssammlung, Munich in Germany and The Natural History Museum (British Museum). All these new species were described, and the previously known Afrotropical species redescribed.

Chapter 2

MATERIALS AND METHODS

2.1 MATERIALS

The materials studied consist primarily of all *Polypedilum* (*Uresipedilum*) collected in Ghana during the NUFU programme, 1993 and 1994. Others were collected in Malaise traps during an expedition by the Museum of Zoology, University of Bergen to North East Tanzania in 1990. Two specimens were borrowed from Natal Province, South Africa. Several specimens were also borrowed from The Natural History Museum (British Museum), London, Zoologisches Staatssammlung, Germany. Out of these were five paratypes, one each of *P. (U.) annulatum*, *P. (U.) freemani* and three *P. (P.) ephippium*. There were also one holotype each of *P. (U.) kibatiense*, and *P. (U.) stilatum*. These were redescribed and used to compare and confirm the other groups examined

The holotypes of the new species are deposited at the Museum of Zoology, University of Bergen (ZMBN). Paratypes when available, will be deposited at the Department of Zoology, University of Ghana, Legon, Ghana; Zoologisches Staatssammlung, Munich, Germany and the Museum of Zoology, University of Bergen, Norway.

2.2 FIELD METHODS

Different methods were employed during the collection of the chironomids. The adults were collected with light traps, Malaise traps and sweep nets. Dip nets, hand nets and drift nets were used to collect larvae and exuviae from streams and rivers.

2.2.1 Terrestrial

Light traps

Light traps collect insects that are attracted to light after dusk. They consist of a metal funnel over a collecting jar containing 70% ethanol placed about 1 m away from a white calico sheet supported by sticks to form a screen. A 250 W mercury vapour bulb powered by a generator was suspended over a funnel. The traps were usually operated from 18⁰⁰ - 21⁰⁰ hours (or when darkness fell or until a reasonable amount of insects were collected). The insects attracted to the light either fell directly through the funnel into the collecting jar/ receptacle or were collected on the screen using test tubes, pooters and collecting bottles containing 70% ethanol (Plate 1).

Malaise traps

Malaise traps collect flying insects that encounter them. The traps used during the NUFU project were of the "Woodhouse" type. They are made of a black nylon net and the strings of the trap were tied to twigs, trees or pegs. The Malaise trap when put up looks like a tent (Plate 2). A number of these traps were set up along the banks of streams, rivers, waterfalls and wet or humid areas in the forest. The insects were killed when they entered through the opened sides and flew along the sloping edges upwards into an opening leading to a collecting plastic bottle that contained 70% ethanol. The bottles were emptied every 3 to 5 days or were left for a week, after which the traps were completely removed. The catches were sorted out later in the laboratory.

Sweep nets

Sweep nets were made of fine mesh (250 μ m) of nylon net fitted onto a metal ring, that is attached to a wooden or metal handle, Fig. 1A. The net used was about 60 cm in diameter, and 90 cm deep, with a handle of about 1 m long. Chironomids were either caught swarming or by sweeping over vegetation around or away from water bodies. After sweeping the net was twisted in a way such that the net folded over to trap the insects below. Insects caught were

carefully transferred into collecting bottles containing 70% ethanol by inserting the bottle into the net.

2.2.2 Aquatic Habitats

Dip nets

They consist of a fine plankton net cloth with a mesh size of 250 μm . The net was fitted to a metal ring of about 20 cm in diameter forming a depth of about 15 cm, and attached with a metal handle of about 40 cm (Fig. 1 B). The nets were used to collect exuviae (especially where scum was formed) floating on the water surface, mostly along fringes of vegetation. Larvae and pupae were sampled on the surface of shallow lakes, streams, rivers and ponds. The contents were put into trays containing some water. After the sediments had settled, live chironomid larvae and pupae were collected with pipettes and transferred into collecting bottles two - thirds full of water from the sampled locality. Dead larvae, pupae and exuviae were put into different collecting bottles containing 70% ethanol.

Hand nets

Hand nets made of fine mesh (250 μm) of nitex material fitted onto a metal ring that is attached to a wooden handle of about 1m long. The net used was about 60 cm in diameter and 80 cm deep (Fig. 1 C). Hand nets were used to collect larvae and pupae which were submerged amongst debris in the streams, rivers, lakes or splash zones of waterfalls. The contents of the nets were emptied into trays containing some of the water sampled. After the sediments had settled the live immature were collected with pipettes into collecting bottles about two-thirds full of water from the locality sampled.

Drift nets

The drift net also known as Brundin net used consists of a plankton net cloth with a mesh size of 250 μm fitted to a metal ring onto which strings were attached. The nets were approximately 30 cm in diameter and 75 cm deep (Fig. 1 D). The drift nets were used only



Plate 1. Light trap with a 250 W mercury vapour and tungsten bulb powered by a generator (Photo Jostein Kjærandsen).



Plate 2. A Malaise trap along the bank of Agumatsa stream (Photo Jostein Kjærandsen).

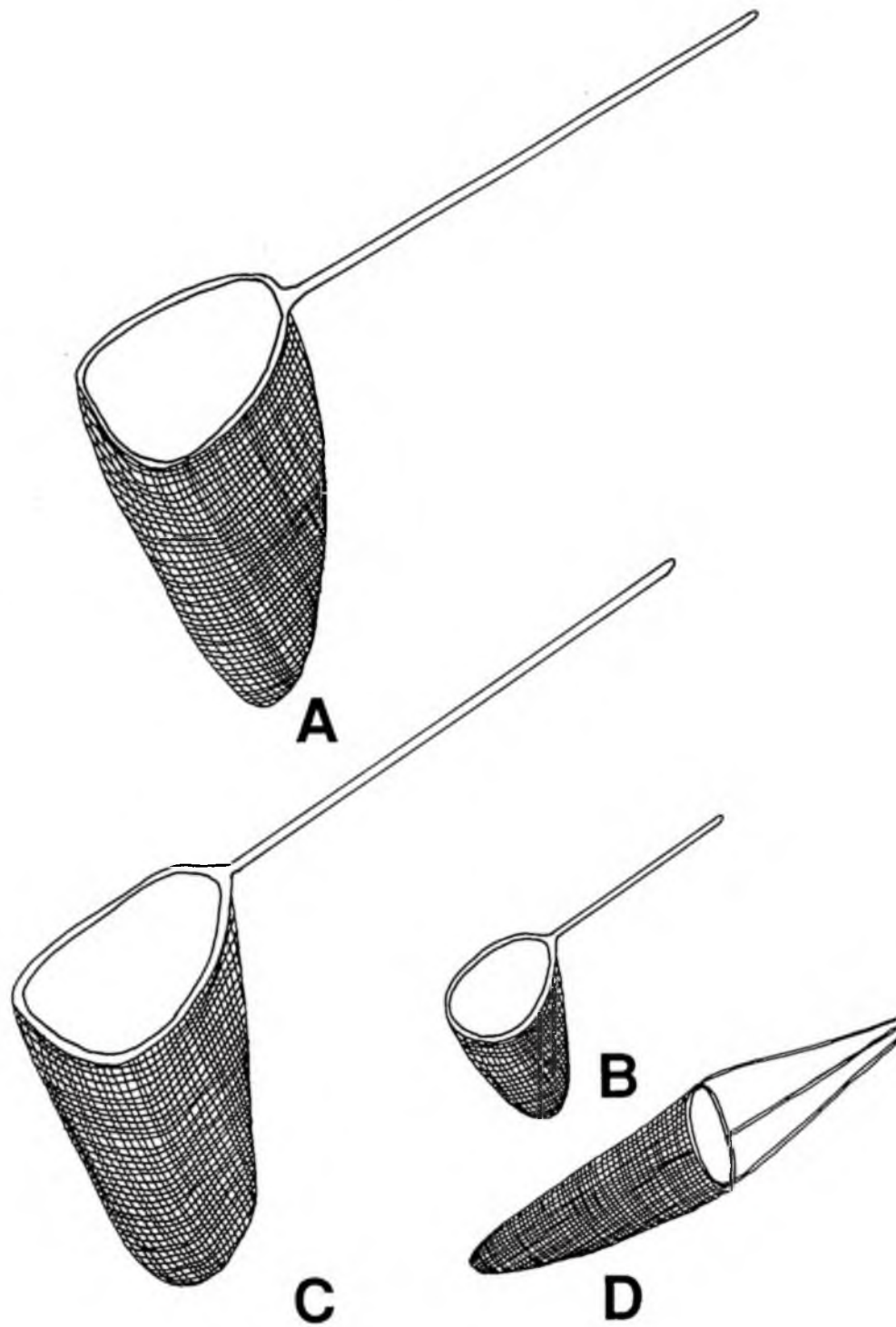


Fig. 1. Sampling nets. - A. Sweep net. - B. Dip net. - C. Hand net. - D. Drift net.

diameter Petri dish one-half filled with water from the various habitats from which the larvae was collected. The cover of the Petri dishes had three tabs equally spaced inside, and along the rim, this ensured free exchange of air under laboratory conditions with temperatures between 24° C to 25° C. The set-up was checked daily for emergence, dead larvae or pupae.

The death rate of the larvae was initially high, probably due to the drastic change in conditions from the natural habitats, or from the attack by fungus. However, a few larvae managed to pupate while a few survived to reach the adult stage. Most of the larvae stayed alive for weeks without pupating and the few that died within a couple of days. The few that reached the adult stage were immobilised in a freezer within a few minutes. They were then put into screw cap vials together with the exuviae and larval skins, filled with 70% ethanol for preservation. The dead larvae and pupae were also put separately into screw cap vials filled with 70% ethanol. All the vials measuring 45 mm high and 12 mm in diameter were labelled appropriately and brought to the Museum of Zoology, University of Bergen, Norway.

2.3.2 Slide preparation of adults

Slides of adults were prepared using the methods outlined by Schlee (1966) and Sæther (1969).

- From the 70% ethanol (preservation solution), the wings (including the squama), one antenna and the legs on the left side were carefully detached using fine forceps. These were put into absolute ethanol (100% ethyl alcohol) for at least 15 minutes to dehydrate.
- The rest of the body was warmed in 8% KOH-solution (the time varied from 3–45 minutes) to remove musculature. Thereafter it was neutralised in glacial acetic acid for 15 minutes. Then it was placed in absolute ethanol for at least 10 minutes to dehydrate.
- The body was later put in a mixture of absolute ethyl alcohol and cedar wood oil for 10 minutes to clear the specimen at this stage any trapped air bubble was gently removed.
- The body was dissected using a stereo-microscope: the other antenna was removed using fine dissecting needles; using fine forceps; the head was removed using a hooked fine needle; the abdomen was carefully pulled off the thorax using fine forceps.
- The various parts were cleared in cedar wood oil for about 10 minutes.
- Using fine forceps, the various parts were mounted in Canada balsam in position, as shown in Fig. 2.
- * The anterior side of the head faced up, placed together with the antennae.

- * The side of the thorax faced up with legs still attached.
- * The abdomen was centred (male, dorsal side up; female, ventral side up).
- * The wings were carefully placed to clearly show the squama.
- * The left legs were also carefully placed.
- * Allowed to harden while the parts are in the desired positions

A second layer of Canada balsam was dropped on the first before carefully covering with the cover slips.

— The slides were left in the oven at 40°C (or between 35°C - 50°C) for about two weeks to dry.

2.3.3 Slide preparation of larvae and pupae

Slides made for larvae and pupae followed the same technique as for the adults. The head of the larva was usually removed from the body before heating in 8% KOH - solution, to ensure good results.

2.3.4 Slide preparation of larval skins and pupal exuviae

These were not heated in 8% KOH-solution but placed directly in glacial acetic acid. The rest of the method followed the procedure for the adults. In mounting the exuviae, the ventral side faced up.

If the adult specimen was associated with larval and/ or pupal exuviae through individual rearing, these were mounted on the same slides as shown in Fig. 2.

2.3.5 Identification

After mounting, the chironomids were identified to the genus level with the aid of a phase contrast microscope (Leica Dialux 20), using keys in Pinder and Reiss (1983, 1986) and Cranston *et al.* (1989).

2.3.6 Calibration of measuring scale

Measurements were taken using a Leica Dialux 20 phase contrast camera lucida microscope. The eye piece of the camera had 100 units which is divided into 10 units each of 10 sub-units. The eye piece was calibrated using a calibration slide (graticule) measuring 2 mm in diameter. It was divided into 20 intervals, therefore every interval was 0.1 mm. The calibration slide was placed on the stage of the microscope and the units matched with that of the eyepiece

by putting the zero points to a close fit. The best fit scales were read off and the units counted for that of the eyepiece to that of the calibration slide. This was done for the various magnifications of the objectives of the microscope. By simple proportion the units of the eyepiece were determined.

The following values were obtained during the calibration:

4X.....4.5 units = 0.1 mm

10X.....11 units = 0.1 mm

25X.....45 units = 0.16 mm

40X.....72 units = 0.16 mm

For example : 40 X

72 units of the eyepiece matched with 0.16 mm on the calibration scale

Thus if 72 units = 0.16 mm

then 1 unit = 0.16 mm/ 72 units (X 1000)

= 2.22 μ m

The calibration of the various magnifications of the objectives of the microscope were calculated using similar proportion (Table 1).

Table 1. The calibration (in μ m) of the various objectives of the Leica Dialux 20 microscope.

Objectives (magnifications)					
Microscope	4 X	10 X	25 X	40 X	100X
Calibration	22.22	9.090	3.555	2.222	

2.3.7 Drawing techniques

Using drawing tubes mounted unto microscopes, large drawings were made first in pencil on A3 sheets. The drawings were reduced to 85-50% using a photocopying machine and pasted onto A3 sized sheets. The drawings were then inked on tracing paper using Rotring pens numbers 0.25, 0.35 and 0.50. Using the photocopier again, the drawings were reduced to A4 size.

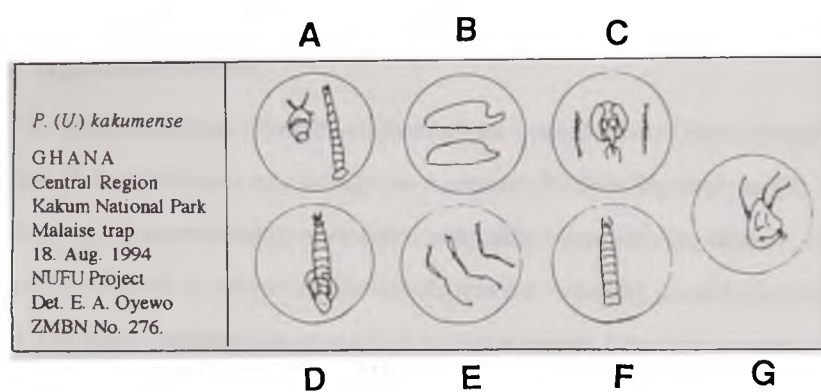


Fig. 2. Microscope slide preparation of reared adult male. - A. Larval skin. - B. Wings. C. Head and antennae. - D. Pupal exuviae. - E. Legs of one side. - F. Abdomen and hypopygium. - G. Thorax with one side of legs attached.

Chapter 3

LOCALITIES

The various localities in Ghana where the specimens were collected during the NUFU project are as shown in Fig. 3. Plate 7 shows a locality in Tanzania where other specimens were collected by the Museum of Zoology, University of Bergen research team.

3.1 GHANA

3.1.1 Agumatsa stream

The Agumatsa stream (Plate 2), originates from Togo. It enters Ghana through three high cascades of waterfall and it runs through the Agumatsa Wildlife Sanctuary at Wli, Volta Region. The Sanctuary is surrounded by steep-sided rocky hills where soils are shallow. The hills are covered by savannah woodland and the bottom riverine valleys by dense Moist Semi-deciduous forest. The upper reaches of the river which is approximately 5 m wide are quite fast flowing, and the bottom substratum is composed of stones and gravel.

The forest belongs to the Dry Semi-deciduous fire zone subtype, where most of the tallest trees are between 30–45 m, forming a more or less continuous canopy. In the Volta Region mean annual rainfall often exceeds 1,500 mm, especially near the higher hills (Hall & Swaine, 1981). One specimen of *P. (P.) anderseni* sp. n. was caught in light traps set along the stream.

3.1.2 Ankasa Game Production Reserve (5° 15' N and 2° 36' W)

This Game Production Reserve is located in the south west corner of the country in the Western Region, close to the Ghana-Côte d'Ivoire border (Fig. 3). It covers an area of 348.7 km². In this part of Ghana lies the Wet Evergreen Forest; it is floristically very rich with high diversity of species (Hall & Swaine, 1981). The tree canopy rarely exceeds 40 m, and many life

forms encountered in this forest are absent or rare elsewhere in the country. The average annual rainfall exceeds 1,750 mm, and it can even be higher than 2,000 mm in some places within the forest (Hall & Swaine, 1981). Due to the high rainfall, the soils are severely leached with pH values between 3.8-4.3 and the soils are forest oxysols (Hall & Swaine 1981). Many streams and small rivers run through this reserve, either fast flowing on stony substratum or slow flowing on muddy, sandy, stony and gravel substratum (Plate 3). One specimen of *P. (U.) acutulum*, sp. n. two specimens of *P. (U.) gladyssae*, sp. n. *P. (P.) anderseni* sp. n. and three specimens of *P. (U.) dossenudum* sp. n. were caught in Malaise traps set in the moist/ wet areas and along the banks of the streams and rivers of the forest.

3.1.3 Boti waterfalls (6° 12' N and 0° 14' W)

The waterfalls (Plate 5) is located in the Eastern Region (Fig. 3). Boti waterfalls lies in a forest reserve which was declared in 1969. It occupies an area of 1.3 km² and lies within the Moist Semi-deciduous south-east subtype of forest. It has an annual rainfall range of 1,200-1,800 mm and the soil pH is between 5-6. Trees in the forest are dominated by evergreen species which can be as high as 60 m. The upper canopy is discontinuous and the under storey trees are sometimes gregarious (Hall & Swaine, 1981).

The waterfalls cascade down into a ravine from where the river continues down the valley. Below the waterfalls, the river forms a small, shallow pool with sandy bottom. However, there are rocks and stones closer to the waterfalls. The river flows rather rapidly downstream and the bottom substratum consists of sand, gravels, larger stones and rocks. Malaise traps were set up along the edges of the river below the waterfalls. One specimen of *P. (U.) dossenudum* sp. n. was caught in dip net sweeps around the waterfalls.

3.1.4 Kakum National Park (5° 26' N and 1° 19' W)

The National Park was set up in 1991 from an initial forest reserve established in 1931. The Kakum National Park is located and lies North-west of Cape Coast, Central Region (Fig. 3). It occupies an area of 212.4 km² in a Moist Evergreen forest, the annual rainfall ranges between 1,200-1,800 mm (Hall & Swaine, 1981). The soils in the park are forest oxysol-ochrosol intergrades which are poor in nutrients as compared to the wet evergreen forest. It has a great floristic diversity, but the number of characteristic species are fewer. The tallest trees have an average height of 43 m, however deciduous trees form only a small portion of the canopy (less than 20%).

There are several hills with many small streams and rivers draining into a relatively bigger river called Kakum, the source of water supply for Cape Coast Municipality. These small streams and rivers are mostly slow-flowing with coarse sand and gravel substratum, however, there are a few rocks (Plate 4). Malaise traps set up in the forest caught two specimens of *P. (U.) kakumense* sp. n.

3.1.5 Legon Botanical Gardens (5° 33' N and 0° 15' W)

The University of Ghana, Legon, is located near Accra, in the Greater Accra Region, which lies within the coastal savannah plains otherwise referred to as the Accra plains (Fig. 3). It is located within the dry equatorial zone, having an average annual rainfall of about 890 mm (Frempong, 1995). Situated at the lowest lying periphery of the Legon botanical garden is the Vaughan Pond (Plate 6). It is a dug-out pond created originally to receive sewage effluent of the University of Ghana, but the sewage system broke down some 19 years ago. The pond has no rivers or streams draining into it. Although it is entirely rain fed most of the drainage system of the University ends up in it (Armah pers. comm.).

One specimen of *P. (U.) dossenudum* sp. n. and one of *P. (U.) harrisoni* sp. n. were caught in the Vaughan Pond.

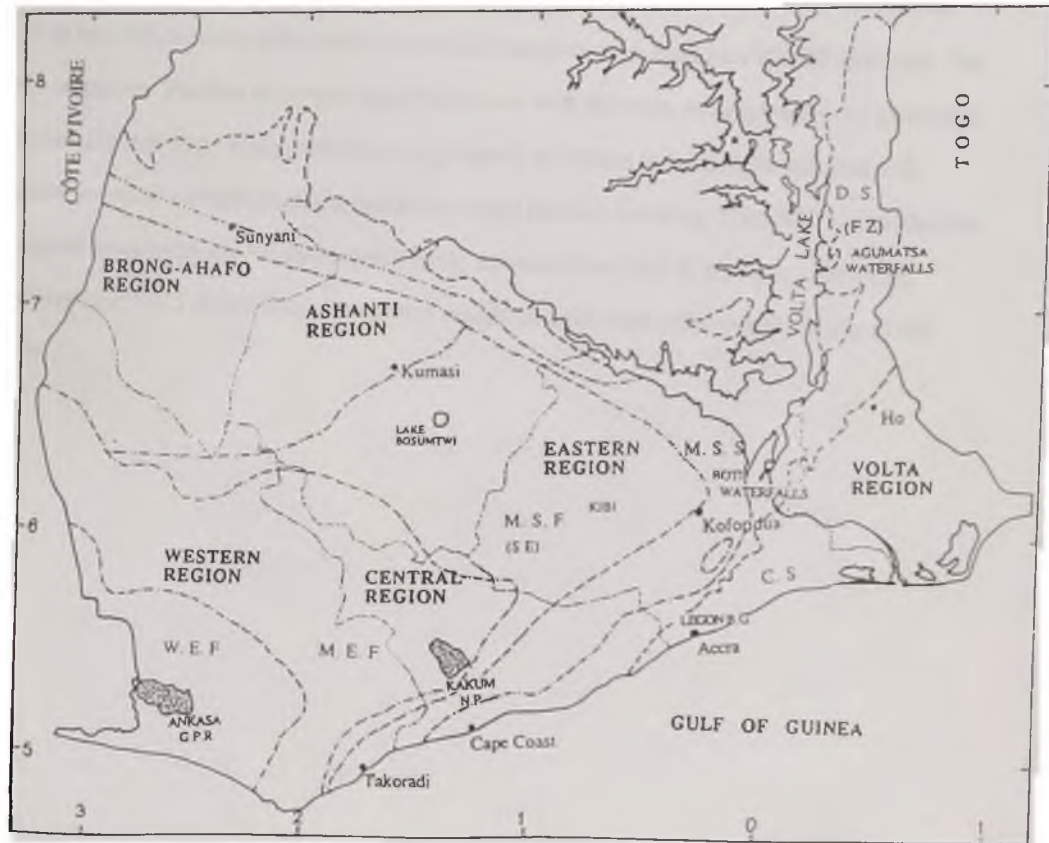


Fig. 3 Map of Southern Ghana showing the localities where *P. (Uresipeditum)* and *P. (Polpedulim)* species were collected (Redrawn from Hall & Swaine, 1981).

3.1.6 Subri stream at Kibi(0° 31' W 6° 11' N)

Located in the Eastern Region of Ghana is this moderately fast flowing stream with pebbles, gravels and some sand as the bottom substratum. The stream passes through Kibi (Fig. 3), and it was at this site that chironomids were collected using light traps within the Upland Evergreen forest, which occurs in the isolated hill ranges (500-750 m elevations) within the Moist-Semi deciduous forest type (Hall & Swaine, 1981). The hills are steep-sided with more or less flat summits which leads to reduced temperatures, high rainfall and mistiness. The forest is uneven. Patches of closed canopy alternate with thickets, swamps and even grassland. The soils are rich clays which have been aggregated by humus to form light-textured soil. Bauxite occurs at various depths, a condition which favours leaching. The soils are too shallow to support large trees and the tallest trees rarely exceed 45 m (Hall & Swaine, 1981). One specimen of *P. (U.) dossenudum* sp. n. was caught in light traps set along the banks of the stream.



Plate 3. Fast-flowing river in the Ankasa Game Production Reserve in the Western Region of Ghana (Photo Jostein Kjærandsen).



Plate 4. Slow-flowing river in Kakum National Park in the Central Region of Ghana (Photo Jostein Kjærandsen).



Plate 5. Boti Waterfalls in Boti, in the Eastern Region of Ghana (Photo Geir E. E. Sølvi).



Plate 6. The Vaughan Pond in Legon Botanical Garden, University of Ghana, Legon in the Greater Accra Region of Ghana (Photo Jostein Kjærandsen).



Plate 7. Kaputu Stream in the Mazumbai Forest Reserve in the West Usambara Mountains, north-eastern Tanzania (Photo Geir E. E. Sølvi).

3.2 TANZANIA

3.2.1 Mazumbai Forest Reserve

According to Andersen & Johanson (1992), the forest reserve is located on the Kwagoroto Hill in the West Usambara Mountains, Tanga Region, Tanzania. The West Usambara Mountains belong to the eastern arc, a chain of mountains stretching along the east coast of Tanzania. These mountains have many steep slopes as a result of uplifting and faulting of the main East African plateau. A stable and most favourable coastal climate of warm, wet sea air and easterly winds has given rise to a moist climate in these mountains. The eastern arc mountains are covered with forest of different types, depending on the altitude and rainfall which has a mean of 1,138 mm in Mazumbai Forest Reserve. The Reserve has two main vegetation types of intermediate forest and montane rain forest which are supposed to be very old. The forest is nearly undisturbed and it is among the most interesting endemic centers of Africa. The trees in the intermediate forest can reach a height of 50 m, while trees in the forest at higher altitudes gradually becomes shorter.

Several small streams drain the moist, forest-covered Kwagoroto Hill. The Kaputu stream originates at about 1,860 m altitude and runs parallel to the eastern side of Mazumbai Forest Reserve down to a marshy area at about 1,400 m. There are four relatively large waterfalls located along the stream, at location number 10 (fig. 4) where the water current is moderate, 14 specimens of *P. (U.) spinibojum* sp. n. were caught in a Malaise trap at an altitude of 1,420 m (Plate 7). Two specimens of *P. (U.) plautum* were caught in light traps and sweep nets. Also caught in the forest was one specimen of *P. (U.) gladysae*. The width and depth of the stream is 0.5-2.0 m and 10-20 cm respectively with fine sand, mud, larger stones substrate and some litter. The measured pH was 5.9 and temperatures varied between 14.6° C and 17.6° C.

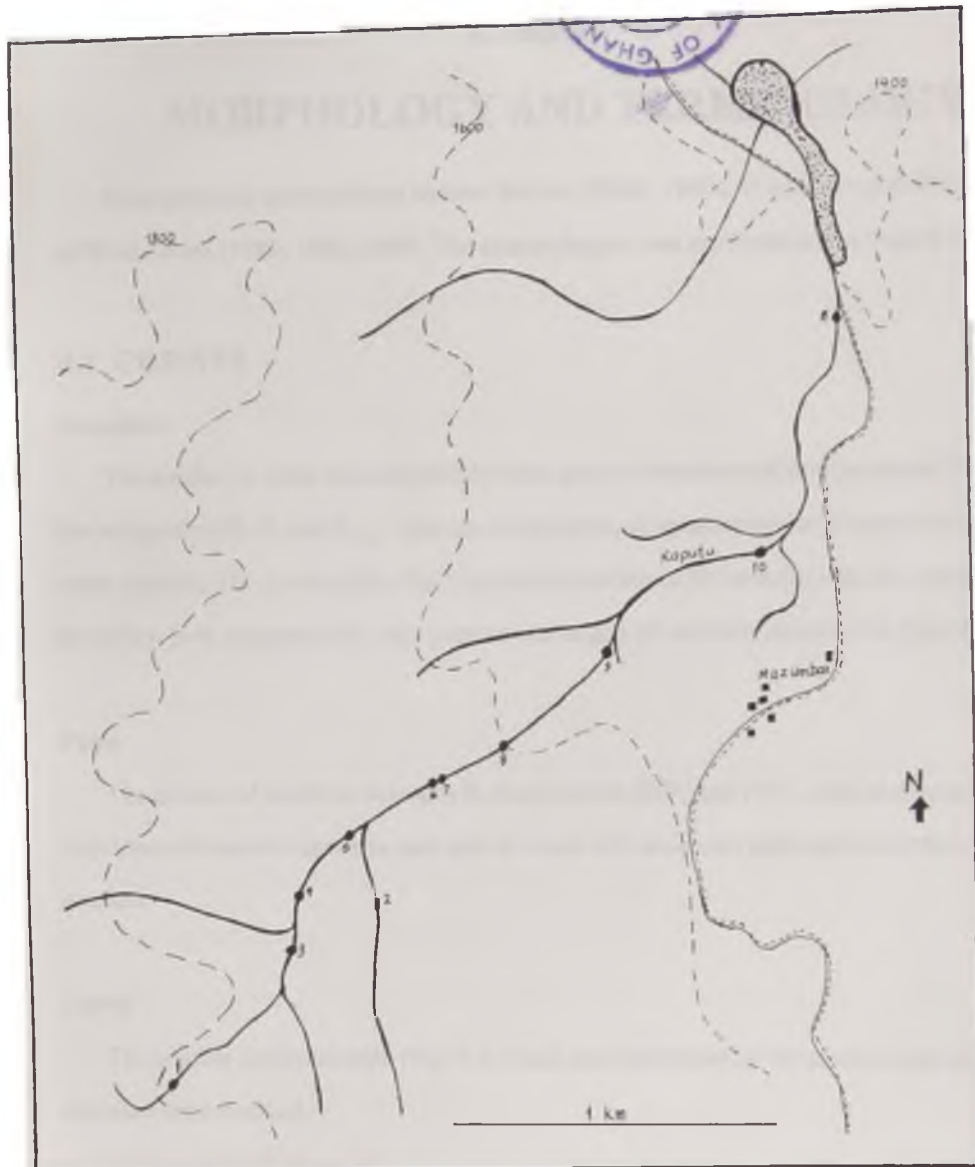


Fig. 4a. Map of the Kwagoroto Hill, West Usambara, N E Tanzania, showing the location of sampling sites along Kaputu Stream (Redrawn from Anderson & Johanson, 1992).

Chapter 4

MORPHOLOGY AND TERMINOLOGY

Morphological nomenclature follows Sæther (1980a, 1990a, b) with some of them illustrated in Wiederholm (1983, 1986, 1989). The terminologies used are illustrated in Figs 4-6.

4.1 COUNTS

Imagines

The number of setae were counted on some parts or structures of the specimens. These were the wing veins (R, R₁ and R₄₊₅), squama, brachiolum, clypeus, temporals (inner verticals, IV; outer verticals, OV; postorbitals, Po), thorax (dorsocentrals, Dc; acrostichals, Ac; prealars, Pa; scutellars, Scts; anteprenotals, Aps), abdominal tergite IX and laterosternite IX (Figs 4-5).

Pupa

The number of hooklets on tergite II, conjunctives III/IV and IV/V, setae and taeniae on the individual abdominal segments, anal spur or comb with accessory teeth and anal lobe fringe were counted.

Larva

The number of mental teeth (Fig. 6 A), anal setae and claws on the posterior parapods of the abdomen were counted.

4.2 MEASUREMENTS AND RATIOS

Measurements and ratios were given as ranges followed by a mean, if more than three specimens were measured. Figures in parenthesis indicate the number of specimens measured,

unless otherwise stated. The measurements and ratios used are described below and shown in Figs (4-6).

4.2.1 MEASUREMENTS

Imagines

- Total length (TL): length of abdomen plus length of thorax. Abdomen is measured from the concave anteriomedian margin of segment 1 to the apex of gonocoxite, while the thorax is measured from the posterior margin of the postnotum to the anterior apex of the scutum in lateral view.
- Wing length (WL): Distance from arculus to apex of wing.
- Cubitus (Cu) length: Distance from arculus to the outer margin of cubital fork (FCu).
- Media (M) length: Distance from arculus to the outer margin of the crossvein.
- Tentorium length: The total longitudinal length.
- Sieve pore width (W sp): Width of tentorium at the sieve pore, i.e. the widest width of the tentorium.
- Posterior tentorial pit width (W ptp): Width of the apparent hole in the tentorium near the dorsal, slender end.
- Stipes length: The total longitudinal length.
- Palp segment length: Total lengths.
- Leg segment lengths: The length of the legs was measured not as total lengths, the basal and apical elongation were not included. On the tibia, it was taken to where the spur or comb begins, according to Schlee (1966). The lengths of the spurs and combs were also measured.
- Width of tibia (fore, middle, hind): Total maximum width at the apices.

Males imagines

- Anal point length: Measured from the base to the apex.
- Width at base of anal point: Width at the widest point at base.

- Width at apex of anal point: Width at the tip.
- Length of phallapodeme and transverse sternapodeme.
- Length of gonocoxite (LGc): Measured from the apex where it overlaps the gonostylus to where it comes into contact with the other gonocoxite.
- Length of gonostylus (LGs): Measured from the apex to the point where it overlaps the gonocoxite.
- Length of superior volsellae (LSVo): Total length a , and the length of extension b .
- Length of inferior volsellae (LIVo): Total length.
- Length of flagellomere 1-12 and thirteenth flagellomere.

Pupa

- Total length: Length of abdomen plus length of thorax.
- Frontal setae length: Total length.

Larva

- Total length: Total length of head capsule plus total length of abdomen.
- Head capsule: Distance across the widest points.
- Width of basal antennal segment: Maximum width.
- Length of basal antennal segment: Total length.
- Length of second segment: Total length.
- Premandible length: Total length.
- Mandible length: Total length.
- Width of mentum: Width at widest point.
- Length of supraanal setae: Total length.
- Length of anal seta: Total length.
- Postmentum length: Measured from the apex of median teeth to posteriomedian occipital margin.

- Width of ventromental plate: Width at widest point.
- Height of ventromental plate: Total height.
- Distance between ventromental plates: Distance between apicomedian ends.
- Length of procercus: Total length.
- Width of procercus: Maximum width.
- Height of procercus: Maximum height.
- Length of tubuli: Total length.

4.2.2 RATIOS

- Venarum ratio (VR): Length of Cu/ length of M.
- Antennal ratio (AR): Length of the thirteenth flagellomere/ combined length of flagellomere 1-12 and pedicel.
- Leg ratio (LR): The ratio of ta_1 / ti ta = tarsus
- "Beinverhältnisse" (BV): The ratio of $fe + ti + ta_1$ / ta_2 - ta_5 . ti = tibia
- "Schenkel-Schiene-Verhältnis" (SV): The ratio $fe + ti$ / ta_1 . fe = femur
- Bristle ratio (BR): The longest seta/ width of ta_1 (measured 1/3 away from the distal part of ta_1).
- WL/ P_{fe}: Ratio of wing length to profemur.
- TL/ WL: Total length to wing length.
- HR: Length of gonocoxite/ length of gonostylus.
- HV: Length of male/ length of gonostylus X 10.

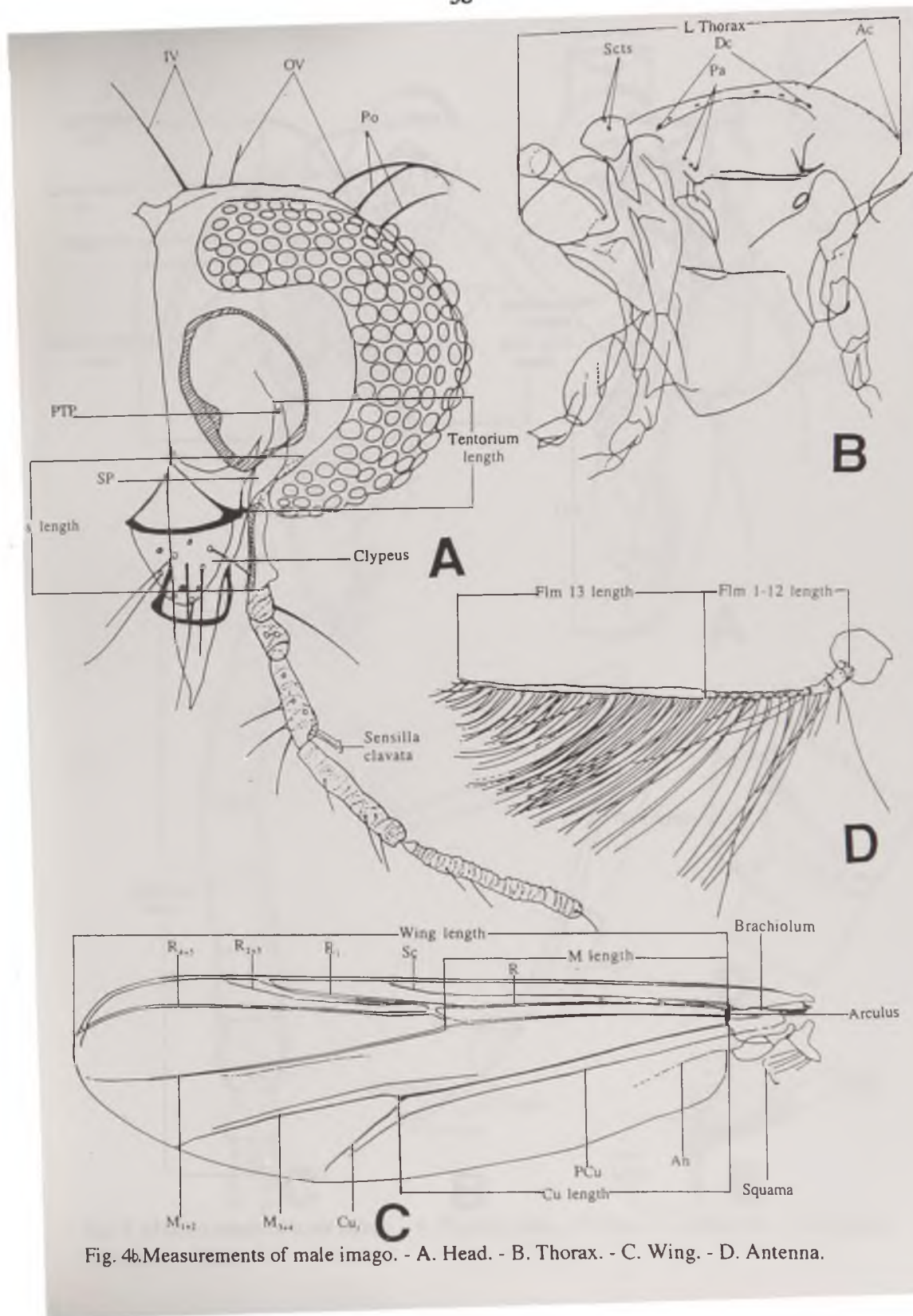


Fig. 4b. Measurements of male imago. - A. Head. - B. Thorax. - C. Wing. - D. Antenna.

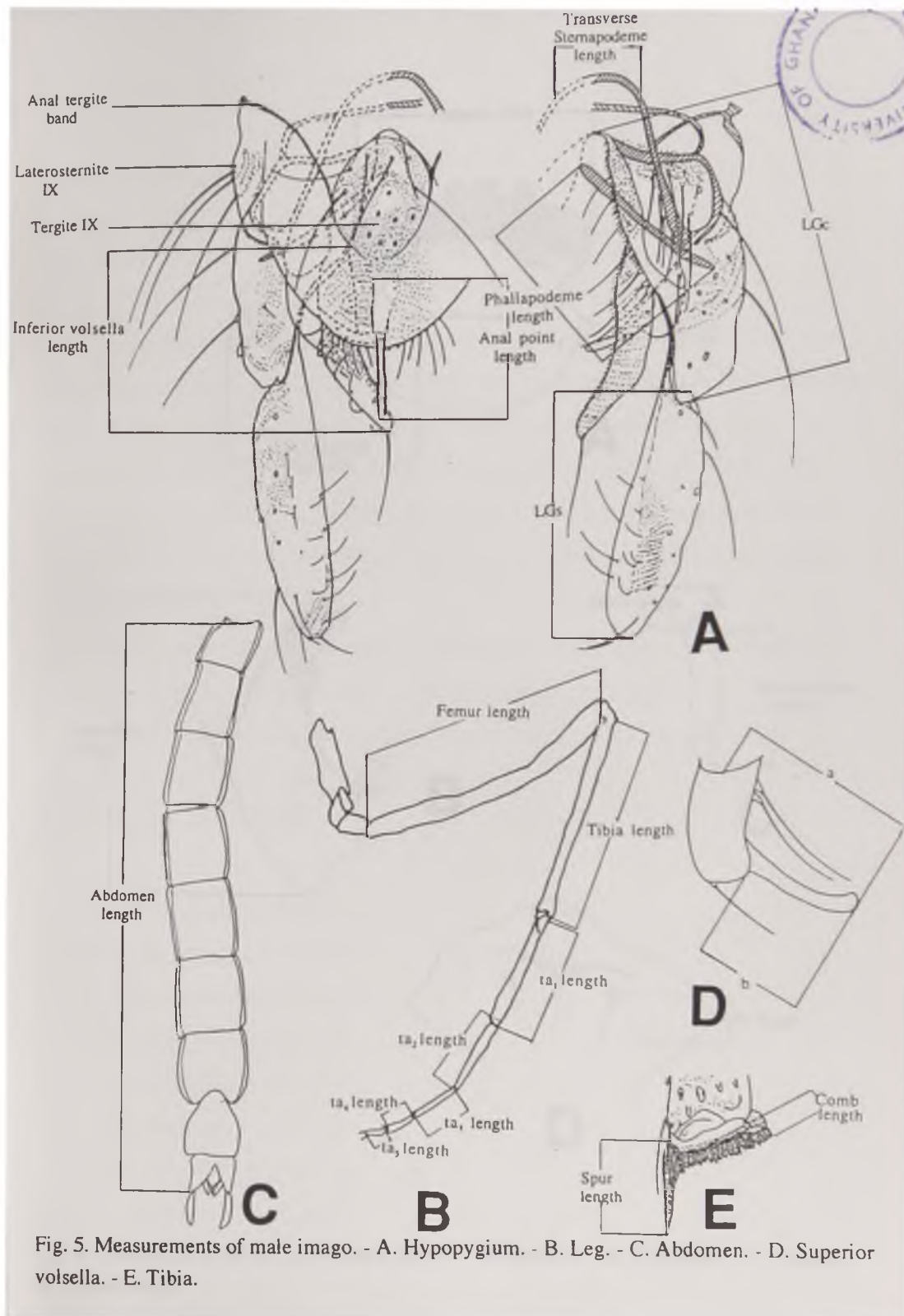


Fig. 5. Measurements of male imago. - A. Hypopygium. - B. Leg. - C. Abdomen. - D. Superior volsella. - E. Tibia.

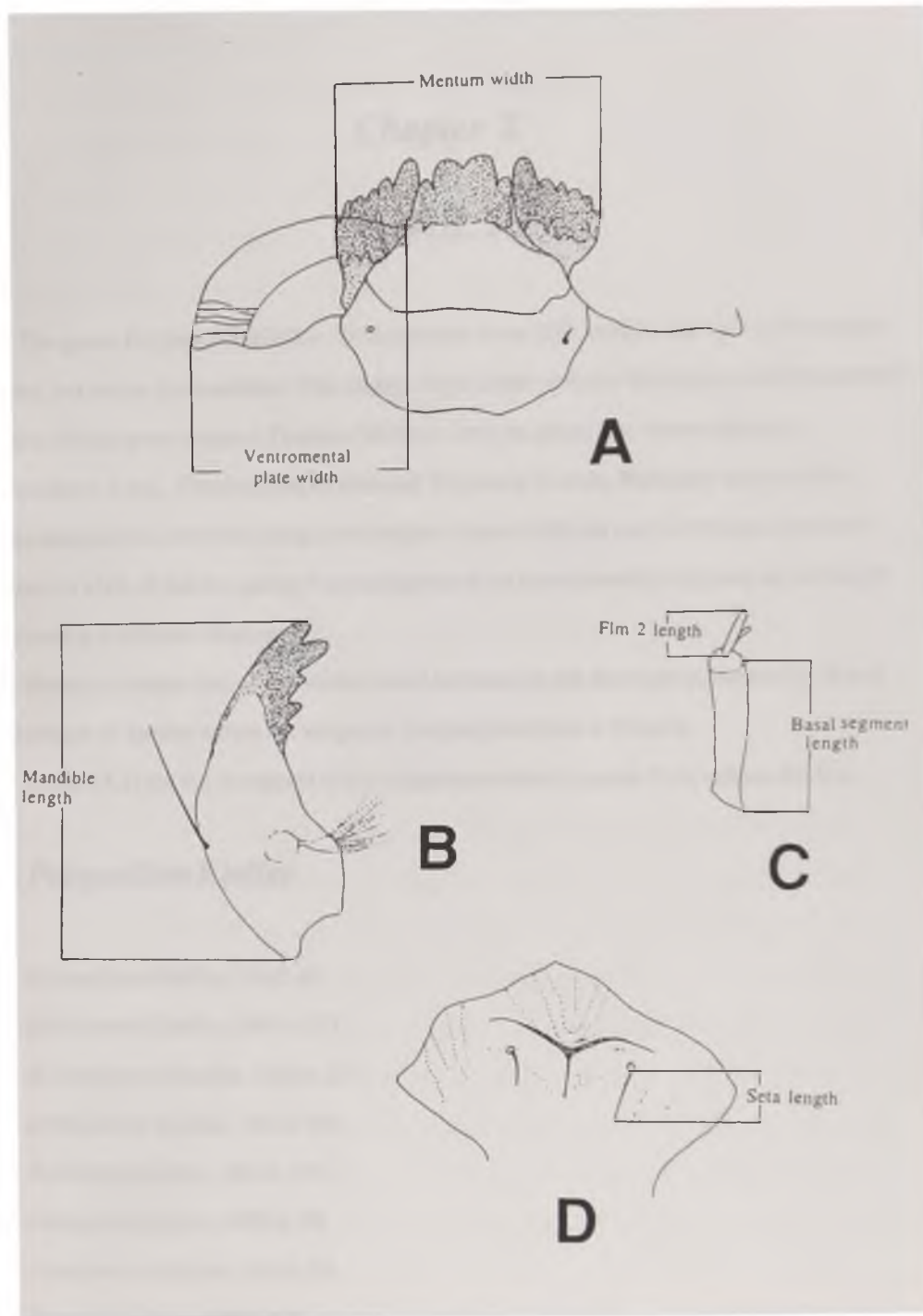


Fig. 6. Measurements of larva (A-C) and pupa D. - A. Mentum. - B. Mandible. - C. Antenna. D. Cephalic area.

Chapter 5

RESULTS

The genus *Polypedilum* Kieffer, 1912 includes about 230 species, and about 50 more are known, but not as yet described. This makes *Polypedilum* probably the largest of all chironomid genera (Sæther pers. comm.). Townes (1945) divided the genus into three subgenera:

Polypedilum s. str., *Pentapedilum* Kieffer and *Tripodura* Townes. Presently there are five subgenera; the two additions being *Uresipedilum* Sasa et Kikuchi and *Cerobregma* Sæther et Sundal. In view of this the genus *Polypedilum* needs to be reviewed or updated, as well as the relationship within the subgenera.

However a major part of the results would be based on the description, redescription and the revision of species within the subgenus *Uresipedilum* Sasa et Kikuchi.

Below (5.1) are the synonyms of the subgenera under the genus *Polypedilum* Kieffer.

5.1 *Polypedilum* Kieffer

Polypedilum Kieffer, 1912: 41.

Kribiocharis Kieffer, 1921a: 271.

Kribionympha Kieffer, 1921a: 271.

Kribiophilus Kieffer, 1921b: 98.

Kribiotima Kieffer, 1921a: 274.

Pentapelma Kieffer, 1921b: 98.

Pentapedilum Kieffer, 1913: 25.

Propedilum Lenz, 1937: 271.

Tripedilum Kieffer, 1921a: 271

Tripodura Townes, 1945: 36.

Uresipedilum Sasa et Okazawa, 1991: 54, *nomen nudum*.

Asheum Sublette et Sublette, 1983: 34.

Uresipedilum Sasa et Kikuchi, 1995: 119.

Cerobregma Sæther et Sundal, 1997 (in press)

Rosenia Kieffer, 1921a: 275, *nec Rosenia* Waagen et Wentzel, 1886.

Chironomini Genus C Pinder et Reiss, 1986: 362.

Type species: *Polypedilum pelostolum* Kieffer, 1912 (= *Chironomus nubifer* Skuse, 1889), by subsequent designation of Ashe (1981: 58).

5.2 Diagnostic characters of *Polypedilum* Kieffer

Male imago: Among genera with 13 flagellomeres and narrowly separated anteprenotal lobes the genus is distinguished by the deeply bifid pulvilli; the triangular, proximally narrowed eighth abdominal segment; and by having the setae along inner margin of style moderately to extremely long and evenly spaced.

Pupa: The pupae are very heterogeneous and it is not possible to find unifying characters for all species. The subgenus *Cerobregma* Sæther et Sundal is characterised by having the cephalic tubercles fused to form a dark, slender sclerotized chitinized cone; and a large anal comb with apical teeth and the surface covered with numerous toothlets. In other subgenera the cephalic tubercles mostly are reduced to low humps, but they may be well developed in a few species especially in the subgenus *Tripodura*. In *Asheum* cephalic tubercles, pedes spurii A and B all are absent. Most species are characterised by having thoracic horn with few branches, basal ring not constricted and with only one tracheal mark; tergites II-VI with anterior band of spinules or spines; segments V-VIII usually with 3, 3, 4, 4 taeniate LS setae respectively; and anal spur or comb present except in *P. (P.) braseniae* (Leathers). The anal lobe has dorsal setae in *Tripodura* and in some *Polypedilum* s. str.

Larva: Also the larvae are very heterogeneous and it is not possible to find unifying characters for all species. Among larvae with 5 segmented antenna; small opposite placed Lauterborn

organs (except *P. nubifer* with alternate Lauterborn organs, but typical *Polypedilum* mentum); tripartite, distally serrated pecten epipharyngis (except *P. braseniae* with unserrated teeth); the larvae are recognisable by having a straight anterior margin of the frontoclypeal apotome, which is nearly always anterolaterally broadened to form lobes on which the S3 are inserted. The typical *Polypedilum* mentum have one pair of high central median teeth, one lower pair of outer median teeth, and tall first lateral tooth. The mentum, however, may be modified in different ways with the differences between the teeth minimal or, in *P. braseniae*, central median teeth very small or absent and outer median teeth higher and wider. The four median teeth are set off from the rest of the mentum and in contact with the anteriorly produced median ends of the ventromental plates in *Uresipedilum*, but not in the other subgenera. Most *Uresipedilum* also have well developed posterior lobes on the ventromental plates, while most *Tripodura* have very short antennal segment 3 and often also short segments 4 and 5.

5.3 Diagnosis of *Polypedilum* Kieffer

(The diagnosis for the most part are in accordance with Sæther 1977; Pinder & Reiss, 1983, 1986; and Cranston *et al.* 1989).

IMAGO

Small to medium species. Colouration pale to dark. Wings sometimes patterned or infusate. Sometimes with variable darkening on legs.

Head. Eyes bare, with strong dorsomedial parallel sided extension. Cephalic tubercles mostly absent, or small. Palp 5 segmented, with sensilla subapically on third segment, sometimes in shallow pit. Antenna with 13 flagellomeres. Antennal ratio (AR) 0.4-3.5. Female with 6 flagellomeres.

Thorax. Anteprenotal lobes somewhat narrowed dorsally and medially narrowly separated, with or usually without setae. Scutum reaching or slightly overreaching anteprenotum, tubercle usually absent. Acrostichals long, uniserial; dorsocentral long, uni- to multiserial; prealars uni- to biserial; scutellars uni- to multiserial.

Wing. Membrane without setae, or with variably extensive macrotrichia (*Pentapedilum*), with moderate to coarse punctuation. Anal lobe weak to undeveloped. Costa not extended, ending close to wing apex; R_{2+3} often evanescent, or at most ending about 1/3 distance between apices of R_1 and R_{4+5} ; FCu opposite or, mostly distal to RM. R, R_1 and R_{4+5} setose. Squama with relatively few long setae.

Legs. Fore tibia scale either triangular, with spinose apex not evenly tapering from base, or oval, usually bearing subapical small spur. Mid and hind tibiae with broad, unspurred anterior comb separated from posterior (narrower, taller) comb with elongate spur. Sensilla chaetica at most, few on subapex of mid tarsomere 1, always absent on hind leg, pseudospurs absent. Pulvilli characteristically bifurcate.

Abdomen. Variably but often densely setose with elongated setae. Tergite VIII diagnostically tapered basally, triangular.

Hypopygium. Anal tergite bands moderately to strongly developed, sometimes fused basal to median anal tergite setae; with diffuse to well delimited oval area of long median anal tergite setae, separated from few weaker apical anal tergite setae lateral to anal point. Tergite IX apically rounded, tapered or with lateral projections (most *Tripodura*). Anal point variable, often narrow, parallel-sided, sometimes dilate, occasionally with a basal plate between anal point and medial group of setae, not T-shaped in cross section. Superior volsella variable, often with setose and microtrichiose base and curved, apically hooked; digitiform extension, bare or with microtrichia in basal 1/2; digitiform part usually with lateral midbasal to subapical strong seta(e); sometimes digitiform extension may be absent, with only microtrichiose and setose pad-like base; base may be reduced to 2-3 stout setae on slight expansion (particularly in *Pentapedilum*). Median volsella absent. Inferior volsella parallel-sided to apically clubbed, usually microtrichiose ventrally and dorsally, usually with apical, long, strong seta directed posteriorly, sometimes arising from very prominent tubercle. Gonostylus variable in shape and length relative to gonocoxite, often narrowed at junction with gonocoxite; setal row of inner surface submarginal, long to extremely long, evenly spaced, not clumped (i. e. without any row of differentiated inner subapical setae). Sometimes setae split to setose with few to many lateral

branches (*Cerobregma*). Transverse sternapodeme inverted and slightly U-shaped (almost straight), without oral projections.

Female genitalia. Gonocoxapodeme VIII with main branch on dorsomesal lobe of gonapophysis VIII and more or less distinct connection mesally, anterior of vagina. Gonapophysis VIII divided into large dorsal lobe and smaller brush-like ventrolateral lobe. Apodeme lobe weak. T XI normal. Gonocoxite with 1-10 setae. Segment X with 3-10 setae to each side. Postgenital plate triangular, usually pointed at apex, occasionally rounded. Cerci normal. Seminal capsules spherical to oval, relatively small. Spermathecal ducts straight, nearly straight (typical of *Tripodura*), or with about a 90° bend.

PUPA

Small to large size. Exuviae pale to medium brown, seldom segments VI-VIII darker than rest of abdomen (*fallax* (Johannsen), *pedestre* (Meigen)).

Cephalothorax. Cephalic tubercles well developed to low humps, well developed in only a few species. Frontal setae almost always present. Frontal warts only exceptionally present, in *simulans* Townes they are extremely long.

Thorax. Thoracic horn with about 16 branches, exceptionally with about 50 fine branches (*tetracrenatum* Hirvenoja); basal ring oval to long elliptical with 1 tracheal branch. Prealar tubercle mostly absent.

Abdomen. Tergite I bare; II-VI with anterior band of spines or spinules (II, small and reduced in *flavus* and *aviceps*; absent in *convictum* and *plautum*); median part of II-VI with variably shaped field of shagreen; posterior, transverse band almost always present (II absent in *convictum*, *flavus* and *aviceps*); VII-VIII with 2 round or longitudinal patches of shagreen, seldom absent in VIII; IX bare. Conjunctives III/IV and IV/V mostly with continuous band or rows of spinules; sometimes interrupted medially, absent in III/IV or additionally present on V/VI. All conjunctives bare in *arundinetum* Goetghebuer. Pedes spurii A and pedes spurii B almost always present. Anal spur or comb present, except in *brasseniae* (Leathers); spur almost always bear accessory teeth. Comb may be unusually large, yellow, with longitudinally

arranged teeth (subgenus *Tripodura*), or compound or laterally protruding, brown with anally directed teeth (subgenus *Pentapedilum*).

Abdominal setation: Segment 1 without setae; II-IV with 1-3 L setae; V-VI with 3 LS setae VII-VIII with 4 LS setae (except *braseniae* with 2 L and 2 LS setae on VII). Tergites and sternites with 1 pair of O setae.

Anal lobe with about 15-105 setae in single row; dorsal setae mostly absent, 1 present in all investigated Holarctic species of subgenus *Tripodura*, in *P. cultellatum* Goetghebuer and in few species from outside the Holarctic region.

LARVA

Long. Reddish orange to deep red in colour. Two pairs of separate eyes.

Frontoclypeal apotome anteriorly broadened into lateral lobes on which S 3 is inserted. Anterior margin straight, not concave or convex. Labral sclerite 1 absent; sclerite 2 present.

Antenna. Five segmented; segment 3-5 always shorter than segment 1; segment 3 minute in some *Tripodura* species. Blade usually shorter than or as long as segments 2-5. Lauterborn organs variable in size (alternate Lauterborn organs in *P. nubifer*).

Labrum. S I usually broad, leaf-like and plumose on both sides; S II almost always plumose on both sides, seldom simple (*P. nubeculosum* (Meigen)); S III, S IV and labral lamella normal. Seta premandibularis usually simple, seldom divided distally (*P. pedestre* (Meigen)). Pecten epipharyngis always consisting of 3 separate platelets, which are almost always serrated distally, only exceptionally unserrated (*P. braseniae* (Leathers)). Premandible normally with 3 teeth, 1 found in *P. braseniae*.

Mandible. Dorsal tooth prominent and dark when present; apical tooth followed by 2, occasionally 3, inner teeth. Seta subdentalis always simple and slender, distally straight or weakly curved.

Mentum. All teeth dark; normal type with 4 median and 6 pairs of lateral teeth; either with a tall central pair, short outer median followed by a tall first lateral and progressively decreasing remainder, or all mental teeth decreasing uniformly laterally; in aberrant types only 5 pairs of

lateral teeth are present (including *P. braseniae* and *P. ontario* Walley). Ventromental plates never contiguous medially, very variable, but widely separated, at most about 1.2x as wide as mentum; striae usually continuous, fine or coarse. Setae submenti simple.

Body. Lateral and ventral tubules absent.

5.4 Systematics within the subgenera of *Polypedilum* Kieffer

The genus *Polypedilum*, including *Asheum* Sublette and Sublette, in the adult stage forms a clearly distinct and easily recognisable group of species. Adults can be recognised by the deeply bifid pulvilli combined with the triangular shaped eighth abdominal segment. The immatures form less easily distinguishable groups. The genus has been divided into six subgenera: *Polypedilum s. str.* with two species groups, the *nubeculosum* and the *nubifer* group; *Pentapedilum* Kieffer; *Tripodura* Townes; *Uresipedilum* Sasa et Kikuchi; and the recently erected *Cerobregma* Sæther et Sundal. The genus *Asheum* according to Sæther and Sundal (1997) does not deserve generic status, while *Collartomyia* Goetghebuer only with some reservation deserve generic status. Most species fall into one of these subgenera in all stages without any difficulty. However, a number of species will key to one subgenus in the adult stage and a different one in the pupal or larval stages. There also are some quite aberrant species which do not fit well into any of the recognised subgenera. *P. (Polypedilum) braseniae* Leathers, for instance, is a typical member of the *nubeculosum* group as a male imago, while the pupa and larva are different from all other species of the genus. *P. (Pentapedilum) kijabensis* Freeman has hairy wings as in other members of the subgenus, but tergite IX has projections to each side of the anal point as in most *Tripodura*. *P. (Tripodura) acifer* Townes differs from all other known members of the subgenus by having superior volsella with an apical extension as in the *nubeculosum* group. The type species of the genus *P. (Polypedilum) nubifer* Skuse is a typical member of the *nubifer* group as male imago, while the pupa appears to be a *Tripodura* and the alternating Lauterborn organs of the larva set it apart from all other known larvae of the genus. The recently erected subgenus *Uresipedilum* apparently is well defined in the adult and larval stages. Some pupae, however, have a dorsal seta on the anal lobe like in *Tripodura* and *P.*

nubifer. Clearly most of the subgenera are in need of redefinition and delimitation. However, the differences between the different types are much greater than between several other full genera of the Chironomini.

A new key had to be prepared to identify the status of *Uresipedium* within the subgenera.

5.4.1 Key to subgenera, species groups and types of *Polypedium* Kieffer

[Adapted from Sæther and Sundal (1997)]

Male imagines

1. Wing membrane with numerous setae. Superior volsella with only slightly developed basal microtrichiose part *P. subgen. Pentapedilum* Kieffer
- Wing membrane without setae. Superior volsella usually with well developed microtrichiose and setose basal part 2
2. Superior volsella broad, pad-like, covered entirely by microtrichiae, with 1 to several long posterior setae and without bare distal or inner process. Tergite IX often with projections lateral to each side of anal point..... *P. subgen. Tripodura* Townes *pro parte*
- Superior volsella widest at base and with bare, horn-like posterior or inner process. Tergite IX posteriorly rounded, without projections except in *P. (Tripodura) acifer* 3
3. Tergite IX with projections lateral to each side of anal point
..... *P. (Tripodura) acifer* Townes, 1945: 46
- Tergite IX posteriorly rounded, without projections 4
4. Basal portion of superior volsellae much longer than wide, with posterior lobe bearing 1 to several setae, apical process arising from inner margin of base and directed inwards..... 5
- Basal portion of superior volsella low and broad, often with long inner setae, gradually continuous to bare, horn-like apical process..... 6
5. Gonocoxite balloon-shaped with deep incisure between gonocoxite and gonostylus; gonostylus short, blunted, with strikingly long inner setae; wing vein R_{2+3} distinct from R_1
..... *P. subgen. Asheum* Sublette et Sublette

- Gonocoxite normal, no deep incisure between gonocoxite and gonostylus; gonostylus normal, inner setae usually short, never very long; wing vein R_{2+3} almost in contact with R_1
.....*P. subgen. Uresipedilum* Sasa et Kikuchi
- 6. Anal tergal band strongly developed, fused basal and usually apical to median anal tergite setae; gonocoxite with bulb-like apicolateral extension; gonostylus with basolateral swelling; with deep incisure between gonocoxite and gonostylus
.....*P. subgen. Cerobregma* Sæther et Sundal
- Anal tergal band moderately developed to absent, never fused basal apical to median anal tergite setae; gonocoxite without bulb-like apicolateral extension; gonostylus without basolateral swelling; no deep incisure between gonocoxite and gonostylus
.....*P. subgen. Polypedilum* Kieffer ..7
- 7. Apical portion of superior volsella without long lateral seta.*P. nubifer* group
- Apical portion of superior volsella with long lateral seta*P. nubeculosum* group

Pupae

1. Cephalic tubercles fused or nearly fused to form a dark slender, strongly chitinized cone. Anal comb with numerous scale-like toothlets. Tergites II-VI with or without anterior band of shagreen*P. subgen. Cerobregma* Sæther et Sundal
- Cephalic tubercles, if present, not fused to form dark cone. Anal comb, when present, not as above. Tergites II-VI or II-VI with anterior band of shagreen often consisting of strong, dark spinules. 2
2. Well developed cephalic tubercles or frontal warts often present. When these not present cephalothorax without tubercle anterior to base of wing sheath, conjunctive III/IV with spinules, anal combs without small basal spines but with apical accessory spines, and anterior rows of large spinules on tergites III-IV about the same size or smaller than caudal hooklets on tergite II. Anal lobe with dorsal setae. 3
- Without well developed cephalic tubercles or frontal warts. Cephalothorax sometimes with tubercle anterior to base of wing sheath. Conjunctive III/IV with or without spinules. Anal

- comb with or without basal spines. Anterior rows of large spinules on tergites II-IV often distinctly larger than caudal hooklets on tergite II. Anal lobe without dorsal setae. 6
3. Anal lobe with dorsal taenia just inwards of fringe. Anal comb extended as short golden spur, with at least the apical tooth broad and blunt. *P. (Tripodura) acifer* Townes
- Anal lobe with dorsal taenia set towards inner edge of lobe. Anal comb usually in the form of several strong teeth or toothed spur with additional strong teeth..... 4
4. Conjunctives III/IV - V/VI with bands of spinules; median point bands present on tergites II and III *P. (Polypedilum) nubifer* (Skuse)
- If conjunctive V/VI with spinule band, tergites II and III without a median point patch 5
5. Spinules on conjunctives III/IV and IV/V as conspicuous as caudal hooklets of tergite II *P. subgen. Uresipedilum* Sasa et Kikuchi *proparte*
- Spinules less conspicuous *P. subgen. Tripodura* Townes *proparte*
6. Conjunctive IV/V with medially interrupted band of strong, dark, orally directed spines, situated in dark pits; conjunctive II/IV bare; pedes spurii A and B absent; male genital sac conspicuously long and slender..... *P. subgen. Asheum* Sublette et Sublette
- Conjunctive IV/V with less spinules or bare; conjunctive III/IV with or without spinules; pedes spurii A usually present, pedes spurii B present or absent; male genital sac not conspicuously long and slender..... 7
7. Conjunctive III/IV without spinules; or when with spinules cephalothorax either with distinct tubercle anterior to base of wing sheath and tergite II nearly completely covered with relatively large and prominent spinules; or when tubercle absent anterior row of spinules on tergite II nearly absent to multiserial but very weak, spinules at most only slightly larger than shagreen spinules; or when anterior spinules on tergite II stronger, anal spur a weakly curved spur with few and small points..... *P. subgen Uresipedilum* Sasa et Kikuchi *proparte*
- Conjunctive III/IV with or without spinules; when without anterior row of spinules on tergite II multiserial, large and prominent; when with and cephalothorax with tubercle anterior to base of wing sheath, tergite II with less extensive and generally smaller and weaker spinules; when

- with and cephalothorax without prealar tubercle anal spur or comb not a weakly curved spur
..... 8
8. Anterior transverse row of spinules on tergite II nearly always large and prominent. When
conjunctive III/IV without spinules shagreen pattern on tergites IV and V in 4 separate patches.
When conjunctive III/IV with spinules base of anal comb with many small spines in addition to
apical accessory spines and shagreen pattern on tergites sparse but without fenestrations.
Cephalothorax without tubercle anterior to base of wing sheath
.....*P. subgen. Pentapedilum* Kieffer
- Anterior transverse row of spinules on tergite II nearly absent to prominent. When conjunctive
III/IV without spinules shagreen pattern on tergites IV and V with medial longitudinal row
usually connecting anterior row with posterior spinules. When conjunctive III/IV with spinules
base of anal comb with or without small spines; when with shagreen pattern on tergites
extensive or when sparse with large fenestration. Cephalothorax occasionally without tubercle
anterior to base of wing sheath. Anal comb occasionally absent.....*Polypedilum s. str.*

Larvae

1. Head triangular, mouthparts unusually small. Striations on approximately triangular
ventromental plates not distinct. Teeth of mentum of about equal height. Premandible bi- trifid.
.....*P. subgen. Cerobregma* Sæther et Sundal
- Head and mouth parts of normal size and shape. Striations of ventromental plates distinct, or if
indistinct, plates very wide. Teeth of mentum of about equal height or first lateral teeth much
smaller than medial teeth and second lateral teeth. Premandible occasionally single..... 2
2. Median teeth of mentum set off from rest of mentum and in contact with anteriorly produced
median ends of ventromental plates. Ventromental plates with well developed posterior lobes,
or when posterior lobes barely indicated or absent antennal blade clearly longer than flagellum
and first lateral teeth of mentum much smaller than medial teeth and second lateral teeth, or
mola with spines*P. subgen. Uresipedilum* Sasa et Kikuchi

- Median ends of ventromental plates pointing posteriad or towards each other. Ventromental plates without posterior lobes. When antennal blade longer than flagellum and teeth of mentum of distinctly unequal height, third antennal segment short, $1/3$ or less length of second segment. Mola without spines.....3
- 3. First lateral teeth of mentum much smaller than medial teeth and second lateral teeth, or when only slightly smaller ventromental plates contiguous, partially overlapping medially. Third antennal segment short, $1/3$ or less length of second segment
.....*P. subgen. Tripodura* Townes
[Also the larva of *P. (Pentapedilum) K1* in Cranston (1996) will key here]
- Mental teeth of about equal height or first lateral teeth much smaller than medial teeth and second lateral teeth, ventromental plates not contiguous. When mental teeth of unequal height, third antennal segment $1/2$ or more length of second segment 4
- 4. Ventromental plates occasionally very broad with width about 5 times the distance between plates, with indistinct striations visible only in medial part and mental teeth of subequal height. When ventromental plates less than 4 times the distance between ventromental plates, Lauterborn organs small, indistinct or absent, and first lateral teeth of mentum much smaller than medial and second lateral teeth
.....*P. subgen. Pentapedilum* Kieffer and *P. subgen Asheum* Sublette et Sublette
- Ventromental plate width no more than 4 times the distance between ventromental plates, with distinct striations. When first lateral teeth of mentum much smaller than medial and second lateral teeth, Lauterborn organs distinct reaching midpart of third antennal segment or beyond
.....*Polypedilum s. str.*

5.5 Phylogeny

Sæther and Sundal (1997) did a preliminary analysis of the relationships within the genus *Polypedilum* and its closest relatives. As the coding of the data in large part was based on the literature, their results can only be regarded as tentative. In addition to their own findings the coding was based on among others Freeman (1958), Maschwitz (1975), Sasa (1979, 1983, 1989a, 1989b, 1990), Pinder and Reiss (1983, 1986), Rossaro (1985), Sasa and Hasegawa (1988), Cranston *et al.* (1989), Langton (1991), Niitsuma (1991; 1992 a, b), Sasa and Okazawa (1991), Cranston (1994, 1996), Bidawid and Fittkau (1995), Sasa and Kikuchi (1995), and Bidawid (1996).

Furthermore, numerous species are yet to be described or redescribed, and for most species the immature stages are unknown. There also are a number of potential trends likely to be found in the female genitalia (Sæther, 1977). The gonocoxapodeme may be straight and ending on the apex of the dorsomesal lobe, or it may be more curved and with a weaker connection anterior to the vagina. The dorsomesal lobe may be long and parallel-sided as in some *Tripodura*, it may be rounded as in some *Polypedilum s. str.* or it may be large and bluntly triangular as in *Cerobregma*. The ventrolateral lobe may be well developed and brush-like as in most members of the genus or it may be reduced to vestigial as in *Cerobregma*. Gonocoxite IX may be bare as in most *Cerobregma* or carry up to about 10 setae. Segment X may have few to numerous setae on each side. The spermathecal duct may be straight as in *P. nubeculosum* or with a 90° bend as in *Cerobregma* and in some *Pentapedilum*. However, as very few female imagines are described and associated, it is not known whether these trends are of specific or subgeneric value. Although they apparently confirm that a subgeneric division is warranted these trends were not included in their preliminary parsimony analysis.

The strict consensus tree and the majority rule tree for the full data matrix with all trends unordered and unweighted, and with *Pseudochironomus* as outgroup are shown in Fig. 7 A. When some trends were ordered and some more reliable and significant trends weighted the results were as in Fig. 7 B. The *ontario* group, *kamoterti* and *okigrandis* combined constitute their new subgenus *Cerobregma*.

Sæther and Sundal (1997) regarded the result shown in Fig. 7 B as the most realistic one. From the trees shown here as well as from their other results it is clear that the subgenus *Uresipedium* either forms the sister group of the other subgenera of *Polypedium* (*Asheum* included) combined or it forms the sister group of an emended or redefined subgenus *Tripodura* alone.

5.6 *Polypedium* subgenus *Uresipedium* Sasa et Kikuchi

Polypedium subgenus *Uresipedium* Sasa et Kikuchi, 1995: 119.

Polypedium subgenus *Uresipedium* Sasa et Okazawa, 1991: 54, *nomen nudum*.

Type species: *Chironomus convictum* Walker, 1856:161 [= *Polypedium convictum*] by present designation.

[Sasa & Kikuchi (1995) did not designate a type species, but mention that their new subgenus is identical to the *cultellatum* or the *convictum* group. Accordingly *P. cultellatum* Goetghebuer or *P. convictum* (Walker) should be designated as the type species. *P. convictum* with well developed posterior lobes as larva is the more typical member of the subgenus, although the Nearctic specimens may belong to a species different from the European specimens [*P. flavus* (Johannsen)] according to Epler (1995: 7.95)].

5.6.1 Diagnostic characters

The adult males can be separated from the other subgenera by having the basal portion of the superior volsella much longer than wider, and in most cases almost covered by microtrichia; bearing one to several long setae on the posterior margin and a bare horn-like inner blade attached to near its posterior corner; apicomedial projection of superior volsella arising from the inner margin of the base and directed inwards; anal tergal band weakly developed of H type or

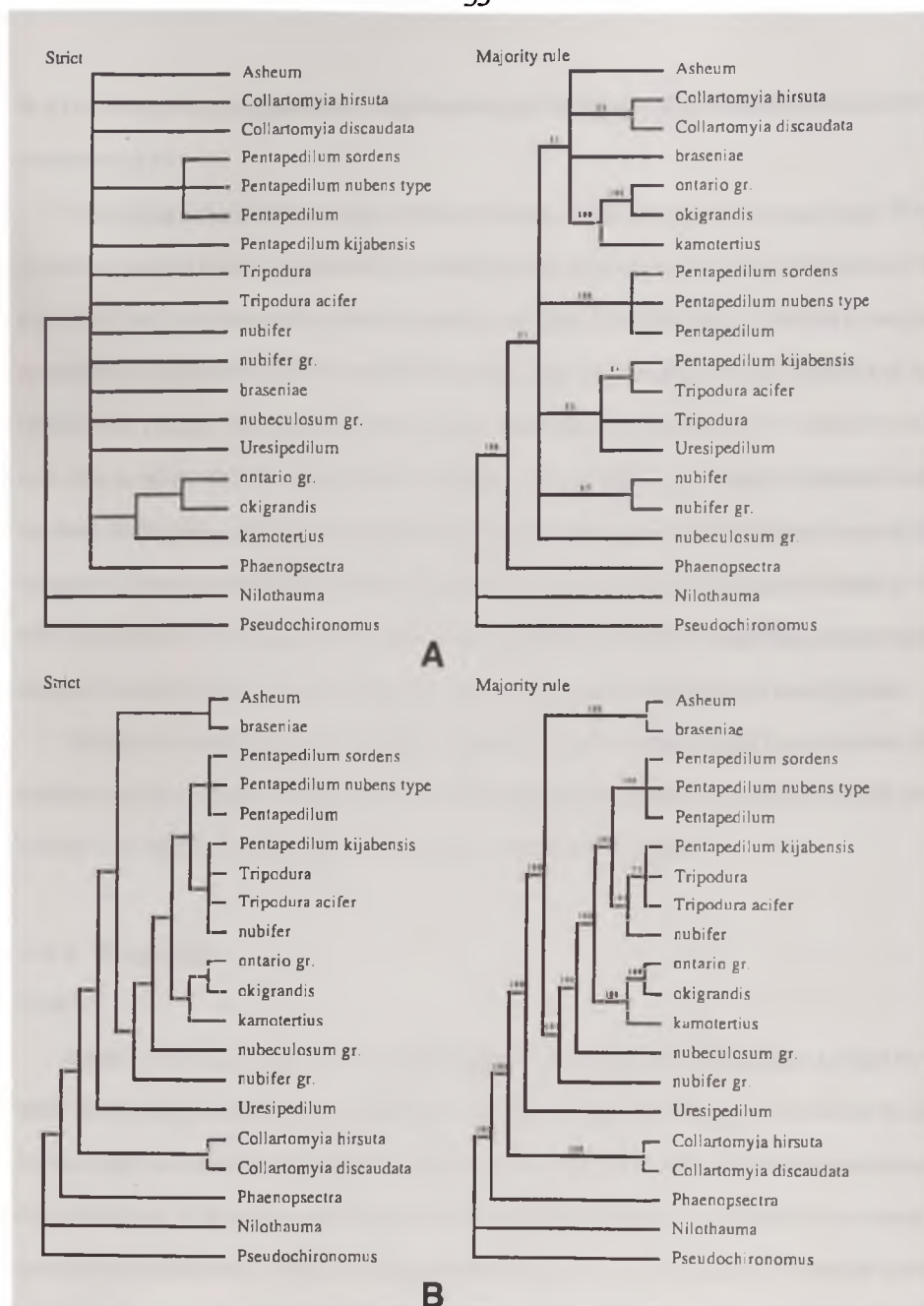


Fig. 7. Parsimony analysis of the relationships within *Polypedium* Kieffer and its closest relatives. - A. Strict consensus and majority rule trees of full data matrix with trends unordered and unweighted. - B. Strict consensus and majority rule trees of species with some trends ordered and weighted.

in a few cases absent median anal tergite setae; and wing vein R_{2+3} evanescent and almost in contact with R_1 .

The pupae fall into two groups, with or without dorsal taeniae on the anal lobe. When dorsal taeniae set towards inner edge of anal lobe are present conjunctive V/VI either is without a spinule band or, when such a band is present, tergites II and III lack a median point patch; the spinules on conjunctives III/IV and IV/V are as conspicuous as the caudal hooklets of tergite II. In the other group, without dorsal setae on the anal lobe, conjunctive III/IV either is without spinules; or when spinules are present the cephalothorax either has a distinct tubercle anterior to the base of the wing sheath and tergite II nearly completely covered with prominent spinules; or when the tubercle is absent the anterior row of spinules on tergite II is nearly absent or weak with spinules at most slightly larger than the shagreen spinules; or when the anterior spinules on tergite II are stronger the anal spur is a weakly curved spur with few and small points.

The larvae are distinguished by having the four median teeth set off from the rest of the mentum and in contact with the anteriorly produced median ends of the ventromental plates, and usually well developed posterior lobes on the ventromental plates.

5.6.2 Diagnosis

IMAGO

Small to medium sized species, wing length 1.0-3.3 mm. Abdomen pale yellow to various dark brown stripes on segments; dark brown apices or banded. Thorax pale yellow to dark brown with various colouration patterns on vittae, preepisternum, postnotum, anteprepronotum, and scutellum; dark brown spots on postnotum, anteprepronotum, preepisternum or almost completely dark brown or black. Wings clear. Legs pale yellow, yellow, yellowish brown; some with dark brown femora or tarsi apices.

Antenna. Antennal ratio usually higher than 1. Males with 13, females with 5 flagellomeres.

Head. Eyes bare, frontal tubercle absent. Third palpal segment bearing 2-5 short blunt-tipped sensilla clavata subapically. Tentorium without microtrichia. Temporals consisting of inner verticals, outer verticals and postorbitals.

Thorax. Antepronotum reduced, widely separated, without setae. Scutal tubercle absent. Acrostichals numerous, long, and biserial; dorsocentrals long, few to many, in single row; prealars few. Scutellum with few to many setae, uni- to multiserial. Supraalars absent; preepisternum and anepisternum bare.

Wing. Membrane without setae. R_1 and R_{2+3} almost parallel; R_{2+3} evanescent; R with few to many setae; R_1 with few to many setae; R_{4+5} with many or occasionally few setae; RM and M mostly bare, or occasionally with a few setae. Squama with few to several setae. Brachium with 1 seta.

Legs. Fore tibial scale rounded or triangular, without apical or preapical spine. Mid and hind tibiae with broad, unspurred anterior comb separated from posterior (narrower) comb with elongate spur, occasionally combs fused. Sensilla chaetica probably always absent. Pulvilli present and well developed.

Abdomen. Densely setose with long setae.

Hypopygium. Anal tergal bands moderately developed, fused basal to median anal tergite setae; slightly delimited area of long median anal tergal setae; weaker apical anal tergite setae present lateral to anal point. Anal point variable, but often narrow, tapered apically to nearly parallel-sided apex. Superior volsella with well developed base, with or without microtrichia; with 2-4 inner setae, but setae absent in a few cases; and 1-4 apical setae; with digitiform, medially directed extension. Inferior volsella mostly parallel-sided or laterally broadened subapically, microtrichiose with apical, long seta directed posteriorly arising from tubercle. Gonocoxite commonly narrowed midway with outer margin gradually tapering to rounded apex. Gonostylus with outer margin gradually tapering and broadest in middle, apex usually with short seta on tubercle; inner margin more or less straight with few setae.

Female genitalia. Not described.

PUPA

Small to medium sized pupae. Exuviae pale brown to brown or black with margins of wing sheath golden brown, mesal paratergital margins of segments VI-VII and caudal spur brown.

Cephalothorax. Frontal setae, if present slender and long, on short conical tubercle. Cephalic tubercles barely indicated or forming low humps. Frontal apotome smooth or very slightly wrinkled laterally. Prealar tubercle absent, weakly developed or occasionally distinct.

Abdomen. Tergite I without spinules and shagreen; II-VI and occasionally VII with relatively large anterior rows of spinules; II (III)-VI with relatively strong extensive median and posterior band of shagreen (*convictum*, *flavus* and *aviceps* without shagreen on tergite II). Tergite VII and VIII with weak and small patches of shagreen, spinules if present small and usually arranged in rows; IX bare. Tergite II with coarse or occasionally small caudal hooklets. Conjunctives III/IV, IV/V and occasionally V/VI may bear uniserial to irregular biserial similar spines. Pedes spurii A may be present on segment IV and occasionally on V and VI or absent. Pedes spurii B well developed on segment II or on both I and II. Sternites usually bare, occasionally sternite I or II with weak shagreen or spinules. Segment VIII with posterolateral (anal) comb or spur bearing 1 large spine and usually 0-3 or several lateral teeth, occasionally composed of few spines.

Abdomen. Segment II-IV with 1-3 hair-like L setae; V and VI with 3, VII and VIII with 4 L setae, all normally taeniate.

Anal lobe well developed, usually with complete fringe of medium to long taeniae confined to posterior half, dorsal taenia absent or when present set towards inner edge of lobe.

LARVA

Small to medium size. Head capsule yellowish brown with postoccipital margin of mentum and mandible brownish black.

Antenna. Five segmented. Basal antennal segment with ring organ near base. Antennal segment 3 shorter than 4; Lauterborn organ usually just reaching apex of antennal segment 3,

occasionally shorter or longer. Blade arising from apex of basal segment usually shorter, occasionally longer than flagellum.

Labrum. S I moderately expanded laterally towards apex, apex filamentously branched; S II narrow, more or less distinctly branched on both sides. Labral lamella well developed. Pecten epipharyngis usually distinctly divided into 3 platelets, each with well developed teeth.

Mandible. Dorsal tooth dark brown, similar in colour to apical tooth and 3 inner teeth. Seta subdentalis well developed. Seta interna usually consisting of 4 main branches with numerous branches. Pecten mandibularis with numerous secondary filaments. Mola occasionally with spines.

Mentum. Four median teeth of mentum set off from rest of mentum and in contact with anteriorly produced median ends of ventromental plates, 6 pairs of lateral teeth. Inner median tooth taller than outer median tooth, first lateral tooth high followed by remaining progressively shorter lateral teeth, or median mental teeth all approximately of same size and lateral teeth decreasing uniformly laterally. Ventromental plates with well developed posterior lobes or when posterior lobes barely indicated or absent antennal blade longer than flagellum and outer median teeth of mentum much smaller than median teeth and first lateral teeth, or mola with spines.

Body. Anal lobe more or less be well developed. Claws of posterior parapods all simple. Procercus short, bearing medium to long anal setae. Anal tubules well developed.

5.6.3 Description

The generic description is based on the examination of all available material of *P. Uresipedilum*, as well as previously described species.

Male imago

Total length 1.9-5.0 mm. Wing length 1.0-3.3 mm.

Head. AR 0.6-2.2. Third palpal segment with 2-3 short blunt-tipped sensilla clavata. Temporal setae 5-17. Tentorium 67-182 μ m long, stipes 60-204 μ m long. Clypeus with 9-22 setae.

Thorax. Dorsocentrals 6-22, acrostichals 10-28, prealars 3-11. Scutellum with 3-29 setae.

Wing. VR 1.10-1.33. R 4-32, R₁ 0-64, R₄₊₅ 1-58 setae. Squama with 3-20 setae.

Legs. LR₁ 1.2-2.60, LR₂ 0.44-0.69, LR₃ 0.65-0.83.

Pupa

Medium sized pupa, 3.0-5.7 mm long.

Cephalothorax. Frontal setae 56-90 µm long, or absent.

Abdomen. Fringe of anal lobe with 18-85 taeniae.

Larva

Large size. Total length of about 4.7-7.0 mm.

5.7 SYSTEMATICS

5.7.1 Previously described species

The subgenus *Uresipeditum* of the genus *Polypeditum* occurs in all the six zoogeographical regions. Up to now twenty-one species have been described from all zoogeographical regions, Table 2.

5.7.2 Relationships within the subgenus

For *P. (U.) aviceps*, *P. (U.) convictum*, *P. (U.) flavus*, *P. (U.) cultellatum*, *P. (U.) oresitrophum*, *P. (U.) paraviceps*, *P. (U.) dossenudum* and *P. (U.) surugense* all developmental stages are known. Male imagines and pupae are known from *P. (U.) lehmanni*, *P. (U.) plautum*, *P. (U.) microzoster* and *P. (U.) tesfayi*. The remaining species are known only as imagines. This, of course, makes both a parsimony analysis and a manual analysis tentative and difficult.

The parsimony analysis used PAUP (phylogenetic analysis using parsimony) version 3.1.1 and McClade on a Macintosh Iisi (computer programmes used to calculate cladogram using the same data matrix. Most searches were heuristic due to the high number of question marks and

polymorphies, but when species with unknown immatures were eliminated branch and bound could be used.

For the parsimony analysis the following trends were used:

IMAGINES

- T 1. WL less than 2.0 mm (0), WL more than 2.0 mm (1).
- T 2. Abdomen uniformly pale, pale yellow to yellow, greenish, brown or blackish (0), abdomen with segment apices dark (1), abdomen distinctly banded (2), segment VI or VII-IX dark (3).
- T 3. Thorax pale yellow or yellow (0), thorax with 3 dark spots (1), thorax with various dark patches (2), thorax almost totally dark (3).
- T 4. Legs unicoloured (0), with darker markings at coxae, femora or tarsi apices (1).
- T 5. AR more than 1 (0), less than 1 (1).
- T 6. Scutellum with 3-6 setae (0), with 7-11 setae (1), with 12 or more (2).
- T 7. Wing vein R_{2+3} relatively well separated from R_1 (0), almost in contact with R_1 (1).
- T 8. R_{4+5} with more than 29 setae (0), with 9-29 (1).
- T 9. Setae present on M (0), absent (1).
- T 10. Squama with more than 7 setae (0), with 2-7 (1).
- T 11. Fore tibial scale with subapical spur (0), without (1).
- T 12. LR_1 lower than 2 (0), higher than 2 (1).
- T 13. Superior volsella with low base and apicomedial projection (0), with large base and apicomedian projection (1), with large base and no projection (2).
- T 14. Projection of superior volsella at least as long as 1/2 total length of volsella (or absent) (0), between 1/2 and 1/3 the length (1), between 1/3 and 1/4 (2).
- T 15. Base of superior volsella without basal inner swelling and small hook-shaped projection (0); with, as in figs 22 B & C (1).
- T 16. Superior volsella with distinct usually broad base and well set off projection (0); base slender, projection not well set off, as in fig. 34 B (1).

- T 17. Base of superior volsella with apex nearly straight (0), rounded (1), with pronounced heel (2).
- T 18. Superior volsella with microtrichiae (0), without (1).
- T 19. Base of superior volsella either covered with microtrichiae or completely bare (0), microtrichiae present both basally and apically, but with microtrichiae-free areas (1); microtrichiae present at base only (2), microtrichiae at apex only (3).
- T 20. Base of superior volsella with 4 inner setae (0), with 3 (1), with 2 or less (2), without (3).
- T 21. Base of superior volsella with 1 apical setae (0), with 2 or more (1).
- T 22. Inferior volsella parallel-sided (0), laterally broadened subapically (1).
- T 23. Median setae on tergite IX less than 10 (0), more than 9 (1).
- T 24. Anal tergite bands absent (0); weak, not fused basal to median anal tergite setae (1); fused basal to setae (2).
- T 25. Anal point parallel-sided or tapering (0), slightly spatulate at apex (1).
- T 26. Anal point not conspicuously broadened (0), conspicuously broadened (1).
- T 27. Setae along apical inner margin of gonostylus short, not different from more basal setae (0); setae longer and differentiated (1), setae extremely long and well differentiated (2).

PUPAE

- T 28. Cephalic tubercles normal to strongly developed (0), reduced to low humps (1), absent (2).
- T 29. Frontal setae long (0), short (1), absent (2).
- T 30. Prealar tubercle absent (0), present (1).
- T 31. Tergites II-VI without anterior, transverse band of spines or spinules (0); tergites II-VI and sometimes VII with anterior transverse band or row of spines or strong spinules (1), tergite II with small spinules reduced to anterior and posterior band, tergites III-VI with relatively large anterior band of spinules and tergite VII-VIII with very small spinules usually arranged in rows (2).

- T 32. Tergites II without shagreen, tergites III-VI with extensive band of shagreen (0); tergites II-VI with extensive median and posterior band of shagreen consisting of moderately developed spinules, and sometimes VII-VIII with weakly developed shagreen at the anterior corners (1).
- T 33. Conjunctive III/IV with spinules (0), without (1).
- T 34. Pedes spurii A present (0), absent (1).
- T 35. Anal spur single with or without accessory teeth (or absent) (0), anal comb present (1).
- T 36. Anal spur or comb with few teeth (0); comb compound, with numerous teeth or spinules (1).
- T 37. Anal lobe fringe with more than 20 taeniae (0), with less (1).
- T 38. Anal lobe fringe with less than 25 taeniae (0), with 25-45 taeniae (1), with more than 45 taeniae (2).

LARVA

- T 39. Antennal segment 3 relatively long, longer than or only slightly shorter than 4 (0); shorter, distinctly shorter than 4, or when not, segment 4 also reduced (1).
- T 40. Lauterborn organs reaching midpart of antennal segment 3 or beyond (0); Lauterborn organs small, indistinct or absent (1).
- T 41. Blade shorter than flagellum (0), longer (1).
- T 42. Mentum with all mental teeth decreasing in size approximately uniformly laterally, or all approximately of the same size or mentum with median tooth slightly taller than first lateral tooth which are slightly shorter than second lateral tooth followed by the remainder of short lateral teeth (0); mentum with tall median tooth taller than first lateral tooth which is shorter than second lateral followed by progressively shorter lateral teeth (1).
- T.43. Ventromental plates with well developed posterior lobes (0), posterior lobes not well developed or barely indicated (1).

- T 44. Distance between ventromental plates at most about as long as width of 4 median teeth (0), distance between ventromental plates at least about as long as width of 6 median teeth (1).
- T 45. Median teeth or first lateral teeth of mentum in contact with anteriorly produced apicomedian ends of ventromental plates (0), median ends of ventromental plates pointing posterior or towards each other (1).

A data matrix is given in Table 3. The genus *Phaenopsectra* is used as outgroup and the subgenus *Tripodura* as well as other *Polypedilum* (i. e. excluding *Uresipedilum* and *Tripodura*) also included. Using the full data matrix with trends unordered yields more than 4000 trees each with 254 steps and a strict consensus tree (Fig. 8 A) showing a basal polytomy with only three consistent groupings within the subgenus: *acutulum* to *pedatum*, *albicorpum* plus *cultellatum* and species related to *convictum*. The majority tree shows that in 94 per cent of the trees *Uresipedilum* is monophyletic. The consistency index (CI) is 0.620, the retention index (RI) 0.557, and the rescaled consistency index (RC) 0.336.

Because of the many question marks in the data matrix it is better to perform parsimony analyses excluding species with unknown immatures or at least unknown pupae. The strict consensus and majority rule trees of the 21 trees arrived at when excluding species known only as imagines, using *Phaenopsectra* as outgroup is shown in Fig 8 B. The trees have 170 steps, a consistency index (CI) of 0.741, retention index (RI) of 0.532, and a rescaled consistency index (RC) of 0.394.

However, most of the trends used for the imagines are unlikely to be of significance for anything else than separating closely related species as they concern colouration, size or setal counts. Such trends are much exposed to parallelism and convergence and should accordingly receive less weight. They often are excluded from parsimony searches, but to do that is to defeat the rationale of parsimony. A few of the trends among the imagines, primarily those concerning the superior volsella, and several of the trends among the immatures, however, are highly significant and unique within the genus or even among chironomids. Such trends

obviously should receive higher weight. Accordingly trends 7, 13, 15, 26, 39, 40, 43, and 45 are given a weight of 8; trends 16, 28, 29, 33, and 41 a weight of 5; and trends 2, 17, 18, 20, 21, 30, 31, 34, 35, 36, and 37 a weight of 3. It also is customary to order trends with more than two steps when there is some evidence for doing so. However, for the trends used here there is no clear evidence of directed morphoclines. When all species are included there are 64 trees with a CI of 0.646, a RI of 0.594, and a RC of 0.384. Reweighting these trees according to the rescaled consistency index (RC) gives essentially the same result, but with full resolution within the *convictum* group and moving *P. (U.) microzoster* outside the group (Fig. 9 A). There are 10 trees, the CI is 0.743, the RI 0.698, and the RC 0.518. Eliminating species with unknown immatures results in 6 trees with a CI of 0.748, a RI of 0.616, and a RC of 0.460 (Fig. 9 B).

When all species are included the subgenus can be divided into three major groups plus several smaller groups or single species of uncertain placement: one group which can be called the *annulatum* group, containing five Afrotropical species with two Nearctic species as their sister group; one group which can be named the *convictum* group consisting of *convictum*, three Japanese species, one Japanese and Nearctic, and one Nearctic species; and a third group, the *oresitrophum* group, consisting of three Afrotropical species, three species from New Zealand, and one species from Australia (Fig. 9 A). When species with unknown immatures are eliminated these groups are maintained.

It would have been advantageous to study the phylogeny inside the subgenus *Uresipedilum* also by Hennigian methods, i. e. by a scheme of argumentation. However, in view of the decisive importance of the immatures and the lack of information on most of these, such an attempt would be as tentative and preliminary as the present argumentation.

Table 2. List of previously described species of *Polypedilum* subgen. *Uresipedilum* Sasa et Kikuchi

Palaeartic species:

aviceps Townes, 1945: 61; Japan, Nearctic.
convictum (Walker, 1856: 161); Oriental.
cultellatum Goetghebuer, 1931: 212; Palaeartic incl. Algeria.
hirosimaense Kawai et Sasa, 1985; Japan.
kibatiense Goetghebuer 1936: 487; Israel, Afrotropical.
paraviceps Niitsuma, 1992b: 703; Japan.
pedatum Townes, 1945: 55; Japan, Nearctic.
surugense Niitsuma, 1992b: 700; Japan.
tamasemusi Sasa, 1983: 15; Japan.

Nearctic species:

aviceps Townes 1945: 61; widespread Canada, USA, Japan.
cinctum Townes 1945: 59; Oregon, California, Nevada, Virginia.
flavus (Johannsen, 1905: 225); Nearctic, (= *convictum* auct. nec Walker).
pedatum Townes, 1945: 55; widespread Canada, USA, Japan.
suliceps Townes, 1945: 58; widespread USA.

Australasia and Oceania species:

albicorpus Tokunaga, 1964: 593; Micronesia.
canum Freeman, 1959: 434; New Zealand.
cumberi Freeman, 1959: 434; New Zealand.
oresitrophum (Skuse, 1889:247); Australia.
harrisi Freeman, 1959: 433; New Zealand.

Oriental region:

convictum (Walker), 1856: 161); China, Palaeartic.

Neotropical species:

microzoster Sublette et Sasa, 1994:43; Guatemala.
pseudoconvictum Bidawid-Kafka, 1996: 194; Peru.

Afrotropical species:

annulatum Freeman, 1954: 22; South Africa.
convictum sensu Lehmann nec Walker (= *plautum* sp. n.); South Africa, Zaire (now Democratic Republic of Congo).
ephippium Freeman, 1958: 292; *pro parte* (= *freemani* sp. n.); Sudan.
kibatiense Goetghebuer 1936: 487; Democratic Republic of Congo, Senegal, Sudan, Uganda, Zimbabwe, South Africa, Israel.
tesfayi Harrison 1996: 80; Ethiopia.

The species *Polypedilum* (*Polypedilum*) *sabbuhi* Bidawid-Kafka, 1996:200, possibly could belong in the subgenus *Uresipedilum*. However, unlike other *Uresipedilum* it has a long spur on the tibial scale of the front leg.

Table 3. Character matrix used for the parsimony analysis (T 1-45) of the relationships within the subgenus *Uresipedilum* Sasa et Kikuchi.

Trends	1	2	3	4	5	6	7	8	9	10	11	12
<i>acutulum</i>	0	0	1	0	1	0	1	1	0	0	1	1
<i>albicorpum</i>	0	0	0	0	0	1	1	?	?	0	1	1
<i>annulatum</i>	0&1	2	3	0	0	2	1	0	0	0&1	1	0
<i>aviceps</i>	0&1	0	2	1	0	2	1	0&1	0	0	1	1
<i>canum</i>	1	1	2	1	0	?	1	?	1	?	1	0
<i>cinctum</i>	1	3	2	0	0	2	1	0	1	0	1	0
<i>convictum</i>	0&1	0	0	1	0	2	1	?	1	0	1	0
<i>cultellatum</i>	0&1	0	2	0	0	2	1	0	1	0	1	0&1
<i>cumberi</i>	1	0	3	0	1	?	1	?	1	?	1	0
<i>dossenuidum</i>	0	1	3	0	0	1	1	1	1	0&1	1	1
<i>flavus</i>	0&1	0	0	1	0	2	1	0	1	0&1	1	0
<i>fremani</i>	0	3	2	1	0	0	1	1	1	1	1	?
<i>gladyssae</i>	0	0	1	0	0	0	1	1	1	1	1	0
<i>harrisi</i>	1	3	2	1	0	?	1	?	1	?	1	?
<i>harrisoni</i>	0	2	3	0	0	0&1	1	1	1	0&1	1	0
<i>hiroshimaense</i>	0	0	2	1	0	2	1	?	1	0&1	1	0
<i>kakumense</i>	0	0	1	0	0	1	1	1	1	0	1	0
<i>kibatiense</i>	0	0	2	0	0	1	1	1	1	1	1	?
<i>lehmanni</i>	1	0	0	0	0	?	1	0	0	0	1	0
<i>microzoster</i>	0	2	0&1	1	0	2	1	1	1	0	1	0
<i>oresitrophum</i>	0	1	3	1	1	?	1	?	1	0	1	0
<i>paraviceps</i>	0&1	0	2	1	0	2	1	?	1	0	1	0
<i>pedatum</i>	0&1	0	3	0	0&1	2	1	0&1	1	0	1	0
<i>plautum</i>	1	0	1	0	0	2	1	0	1	0	1	0
<i>praegnans</i>	0	2	3	0	0	0	1	1	1	1	1	?
<i>pseudoconvictum</i>	0	0	3	0	0	0	1	?	?	?	1	1
<i>spinibojum</i>	1	0	3	0	0	1&2	1	0	0	0	1	0
<i>suliceps</i>	0&1	3	3	0	0	2	1	0&1	1	0	1	0
<i>surugense</i>	0	0	2	1	0	2	1	?	1	0	1	0
<i>tamasemusi</i>	0	0	3	0	0	1&2	1	?	1	0&1	1	0
<i>tesfayi</i>	1	0	1	0	0	2	1	0	0	0	1	0
<i>Tripodura</i>	0&1	0	0	1	0&1	0&1&2	0	?	1	0&1	0	0&1
<i>Polypedilum</i>	0&1	0	2&3	1	0&1	0&1&2	0	0&1	1	0&1	0	0&1
<i>Phaenopsectra</i>	1	0	3	0	0	2	0	0&1	0	0	0&1	0

[illegible]

Trends	25	26	27	28	29	30	31	32	33	34	35	36
<i>acutulum</i>	0	0	1	?	?	?	?	?	?	?	?	?
<i>albicorpum</i>	0	0	0	?	?	?	?	?	?	?	?	?
<i>annulatum</i>	0	0	0	?	?	?	?	?	?	?	?	?
<i>aviceps</i>	0	1	0&1	?	?	?	2	0	1	0	0	0
<i>canum</i>	0	0	1	?	?	?	?	?	?	?	?	?
<i>cinctum</i>	0	0	0	?	?	?	?	?	?	?	?	?
<i>convictum</i>	1	0	1	?	1	?	0	0	1	0	0	0
<i>cultellatum</i>	0	0	0&1	1	1	1	1	1	0	0	0	0
<i>cumberi</i>	0	0	1	?	?	?	?	?	?	?	?	?
<i>dossenuum</i>	0	0	1	1	1	0	1	1	1	0	0	0
<i>flavus</i>	0	0	1	?	1	?	2	0	1	0	0	0
<i>freemani</i>	0	0	0	?	?	?	?	?	?	?	?	?
<i>gladysae</i>	0	0	0	?	?	?	?	?	?	?	?	?
<i>harrisi</i>	0	0	1	?	?	?	?	?	?	?	?	?
<i>harrisoni</i>	0	0	1	?	?	?	?	?	?	?	?	?
<i>hiroshimaense</i>	0	0	0	?	?	?	?	?	?	?	?	?
<i>kakumense</i>	0	0	0	?	?	?	?	?	?	?	?	?
<i>kibatiense</i>	0	0	1	?	?	?	?	?	?	?	?	?
<i>lehmanni</i>	0	0	1	?	2	0	1	1	1	1	0	0
<i>microzoster</i>	0	0	1	?	?	?	?	?	?	?	?	?
<i>oresitrophum</i>	1	0	0	?	?	1	1	1	1	1	1	1
<i>paraviceps</i>	0	1	1	2	?	0	1	1	0&1	1	0	0
<i>pedatum</i>	0	0	1	?	?	?	?	?	?	?	?	?
<i>plautum</i>	0	0	0	1	?	0	1	0	1	1	0	0
<i>praegnans</i>	0	0	0	?	?	?	?	?	?	?	?	?
<i>pseudoconvictum</i>	1	0	1	?	?	?	?	?	?	?	?	?
<i>spinibojum</i>	0	0	0	?	?	?	?	?	?	?	?	?
<i>suliceps</i>	0	0	0	?	?	?	?	?	?	?	?	?
<i>surugense</i>	0	1	0	2	?	0	1	1	0&1	1	1	1
<i>tamasemusi</i>	0	0	0	?	?	?	?	?	?	?	?	?
<i>tesfayi</i>	0	0	0	1	2	?	1	1	1	0	0	0
<i>Tripodura</i>	0	1	0&1	0&1	0&1	?	1	1	0	0	1	0
<i>Polypedilum</i>	0	1	1	0&1	0&1	0	1	0&1	0&1	0&1	0&1	0&1
<i>Phaenopsectra</i>	0	0	0	0	1	0	1	1	0	0	1	0

Trends	37	38	39	40	41	42	43	44	45
<i>acutulum</i>	?	?	?	?	?	?	?	?	?
<i>albicorpum</i>	?	?	?	?	?	?	?	?	?
<i>annulatum</i>	?	?	?	?	?	?	?	?	?
<i>aviceps</i>	0&1	0	1	0	0	1	0	1	1
<i>canum</i>	?	?	?	?	?	?	?	?	?
<i>clinctum</i>	?	?	?	?	?	?	?	?	?
<i>convictum</i>	?	0&1	1	?	0	0	0	1	1
<i>cultellatum</i>	0	1	1	?	1	1	0	1	1
<i>cumberi</i>	?	?	?	?	?	?	?	?	?
<i>dossenuidum</i>	0	1	?	?	?	1	1	0	0
<i>flavus</i>	?	0&1	1	0	1	1	0	1	1
<i>freemani</i>	?	?	?	?	?	?	?	?	?
<i>gladysae</i>	?	?	?	?	?	?	?	?	?
<i>harrisi</i>	?	?	?	?	?	?	?	?	?
<i>harrisoni</i>	?	?	?	?	?	?	?	?	?
<i>hiroshimaense</i>	?	?	?	?	?	?	?	?	?
<i>kakumense</i>	?	?	?	?	?	?	?	?	?
<i>kibatiense</i>	?	?	?	?	?	?	?	?	?
<i>lehmanni</i>	?	?	?	?	?	?	?	?	?
<i>microzoster</i>	?	?	?	?	?	?	?	?	?
<i>oresitrophum</i>	0&1	0	1	?	1	1	1	1	0
<i>paraviceps</i>	0	2	1	0	0	1	0	1	0
<i>pedatum</i>	?	?	?	?	?	?	?	?	?
<i>plautum</i>	?	?	?	?	?	?	?	?	?
<i>praegnans</i>	?	?	?	?	?	?	?	?	?
<i>pseudoconvictum</i>	?	?	?	?	?	?	?	?	?
<i>spinibojum</i>	?	?	?	?	?	?	?	?	?
<i>suliceps</i>	?	?	?	?	?	?	?	?	?
<i>surugense</i>	0	1&2	1	0	0	1	0	1	1
<i>tamaseusi</i>	?	?	?	?	?	?	?	?	?
<i>tesfayi</i>	?	?	?	?	?	?	?	?	?
<i>Tripodura</i>	1	0	1	1	1	1	1	0	1
<i>Polypedilum</i>	1	0	0	0&1	0	0&1	1	0&1	1
<i>Phaenopsectra</i>	0	1&2	0	0	1	0	1	0	0

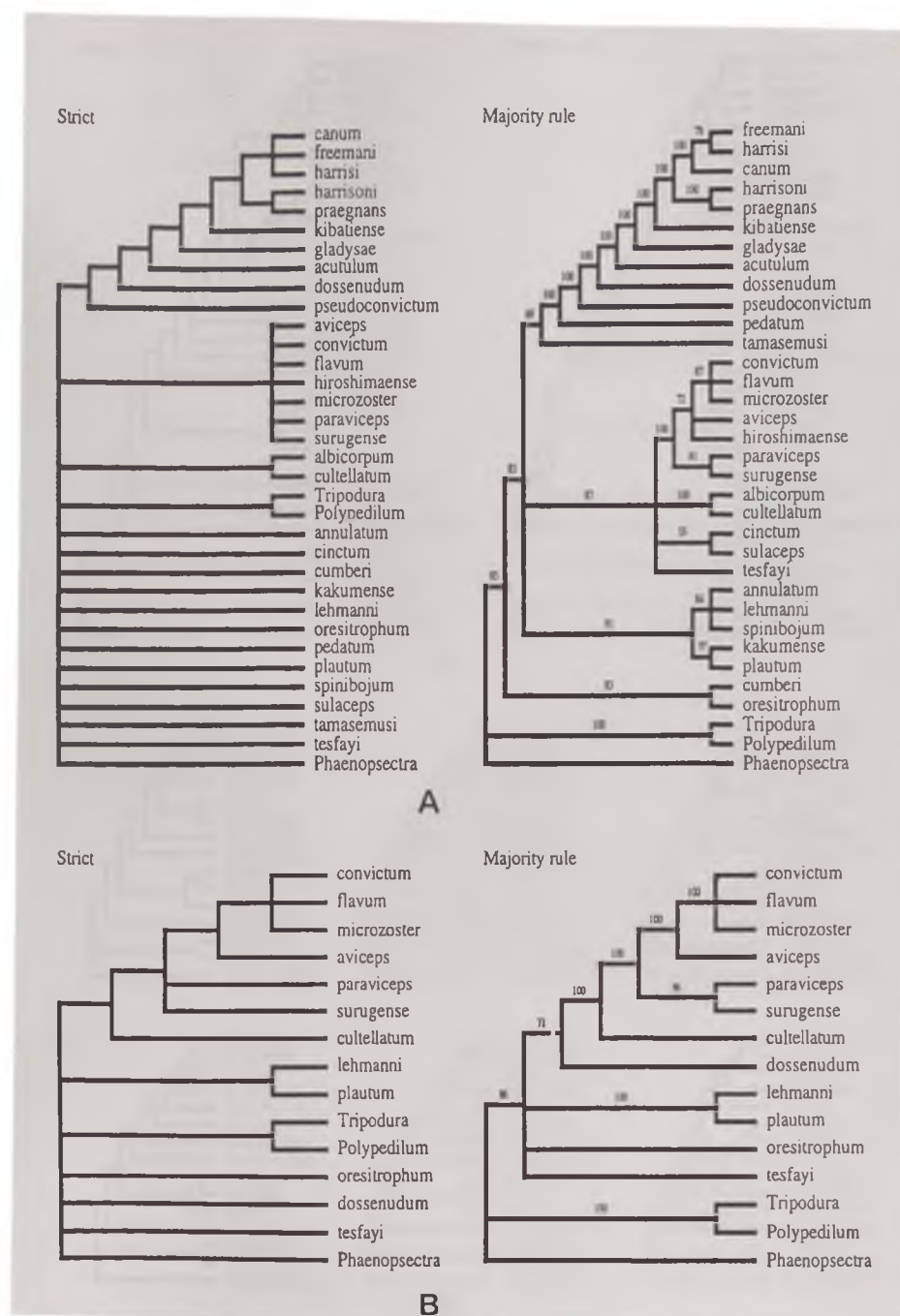


Fig. 8. Parsimony analysis of the relationships within *Polypedilum* subgenus *Uresipedilum* Sasa et Kikuchi. - A. Strict consensus and majority rule trees of full data matrix with trends unordered and unweighted. - B. Strict consensus and majority rule trees of species with immatures, or at least pupae known.

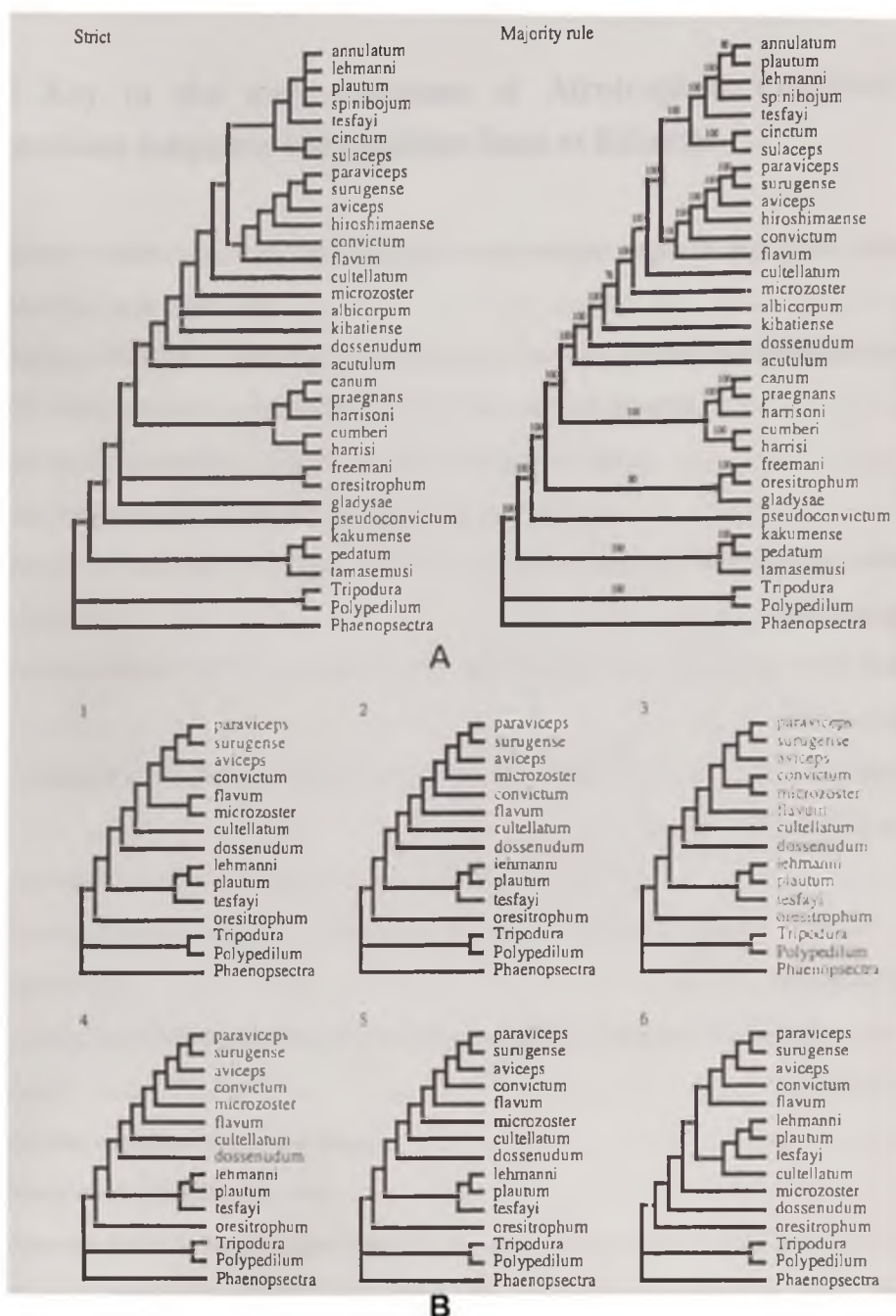


Fig. 9. Parsimony analysis of the relationships within *Polypedilum* subgenus *Uresipedilum* Sasa et Kikuchi. - A. Strict consensus and majority rule trees of full data matrix with trends unordered and unweighted. - B. The trees obtained when species without known immatures are excluded and some trends weighted.

5.7.3 Key to the male imagines of Afrotropical members of *Polypedilum* subgenus *Uresipedilum* Sasa et Kikuchi

1. Superior volsella without microtrichiae, apex nearly straight; tergite IX with 12-26 median setae; R_{4+5} with 21-50 setae.....2
 - Superior volsella with at least some microtrichiae, heel often pronounced; tergite IX with 4-20 median setae; R_{4+5} either with 1-29 or with more than 50 setae.....6
2. Base of superior volsella narrow, apicomedial projection straight 3
 - Base of superior volsella broad, apicomedial projection curved.....4
3. Superior volsella with relatively short apicomedial projection and apical setae; R_{4+5} with 21-25 setae*P. (U.) kakumense* sp. n.
 - Superior volsella with very long apicomedial projection and apical setae, R_{4+5} with 38 setae *P. (U.) lehmanni* sp. n.
4. Abdomen distinctly banded; thorax almost completely dark, anteprenotum without spine....
 -*P. (U.) annulatum* Freeman.
 - Abdomen not banded; anteprenotum with or without a spine.....5
5. Anteprenotum usually with a spine, thorax dark; M and RM with 1-5 and 1-2 setae respectively.....*P. (U.) spinibojum* sp. n.
 - Anteprenotum without spine; thorax with dark vittae and a dark spot; M and RM without setae.....*P. (U.) plautum* sp. n.
6. Superior volsella without inner setae.....7
 - Superior volsella with inner setae 9
7. Abdomen distinctly banded; thorax almost completely dark; superior volsella with 3-4 apical setae and short apicomedial projection; tergite IX with 4-12 median setae; R with 15-18 setae, R_1 with 7-12 setae, R_{4+5} with 9-12 setae; scutellum with 4-7 setae.....8
 - Abdomen and thorax pale yellow; superior volsella with 1 apical setae; relatively long apicomedial projection arises subterminally and points inwards; tergite IX with 20 median setae; R with 32 setae, R_1 with 23 setae, R_{4+5} with 52 setae; scutellum with 26 setae.....

-*P. (U.) tesfayi* Harrison
8. Base of superior volsella swollen and broad; tergite IX with 12 median setae.....
*P. (U.) praegnans* sp. n.
- Base of superior volsella narrow; tergite IX with 4-6 median setae...*P. (U.) harrisoni* sp. n.
9. Abdominal segments VI-IX mostly dark; superior volsella with 2-4, usually 3 inner setae
 and long apicomedial projection*P. (U.) freemani* sp. n.
- Abdomen either with all segments yellow to pale yellow with or without dark apices or
 distinctly banded; thorax either completely dark or pale, but with vittae not dark or scutellum
 dark 10
10. Abdomen pale yellow or at most with segment apices dark; thorax almost completely dark
 or with various dark patches; long to moderately long apicomedial projection 11
- Abdomen yellow without dark apices; thorax with 3 dark spots; short apicomedial projection
 12
11. Superior volsella with strong projecting, bulbous heel; inner setae of superior volsella
 placed on apicomedial projection; thorax dark at anteprenotum, postnotum and scutellum;
 tergite IX with 5-13 median setae; R_{4+5} with 23-29 setae; median setae
*P. (U.) kibatiense* Goetghebuer
- Superior volsella with nearly flat to slightly projecting bulbous heel; apicomedial projection
 appear as separated or attached subterminally to the base; thorax dark at postnotum and
 anteprenotum or almost completely dark; tergite IX with 8-18 median setae; R_{4+5} with 14-23
 setae.....*P. (U.) dossenudum* sp. n.
12. Apical setae relatively short; AR about 0.74; LR_1 about 2.60; M with about 2 setae
*P. (U.) acutulum* sp. n.
- Apical setae relatively long; AR 1.21-1.28; LR_1 1.84-1.87.....*P. (U.) gladysae* sp. n.

5.8 DESCRIPTION OF SPECIES

The species described below are the known Afrotropical species belonging to the subgenus *Uresipedilum*. In addition the Palaearctic species *P. (U.) convictum*, here designated as type species of the subgenus, is described for comparison. *P. (Polypedilum) ephippium* and *P. (Polypedilum) anderseni* sp. n. are also described since they together with *P. (U.) freemani* sp. n. are part of the same type series of *P. (P.) ephippium*.

5.8.1 *convictum* group

The group consists mostly of moderately large species with wing lengths less than 2.0 mm; legs with some markings; anal tergite bands fused basal to setae; anal point often conspicuously broadened; superior volsella usually with microtrichiae at apex only; cephalic tubercles of pupae sometimes reduced to low humps, but mostly absent; and larval ventromental lobes with well developed posterior lobes. The superior volsellae are of the shapes shown in Fig. 10. The following authors have also given illustration of these: Townes (1945: 184, fig. 62); Lehmann (1971: 545, fig. 37); Pinder (1978: 137, fig. 66 F); Rossaro (1985: 22, fig. 11); Niitsuma (1992b: 698, fig. 7), and Sasa & Kikuchi (1995: 244, fig A) for *P. (U.) convictum*; Townes (1945: 184, fig. 64); Maschwitz (1975: 301, fig. 53), and Niitsuma (1992b: 698, fig. 9) for *P. (U.) aviceps*; Niitsuma (1992b: 700, fig. 11) for *P. (U.) surugense*; Niitsuma (1992b: 704, fig. 18) for *P. (U.) paraviceps*; Maschwitz (1975: 299, fig. 48) for *P. (U.) flavus*; Kawai & Sasa (1985: 19 fig. 4) and Sasa & Kikuchi (1995: 244, plate 32 fig. D) for *P. (U.) hirosimaense*.

From the drawings and descriptions of the larvae there appears to be three species described as *P. (U.) convictum* known from Europe (Pinder & Reiss, 1983), Russia (Chemovskii, 1949; Pankratova, 1983) and USA (Maschwitz, 1975). However, two adults could be associated, of which one (from USA) is believed to be *P. (U.) flavus* (Johannsen) according to Epler (1995). The species described by Lehmann (1981) as *P. (P.) convictum* is likely to be *P. (U.) plautum* sp. n. described on p. 90. The European *P. convictum* is redescribed below for comparison.

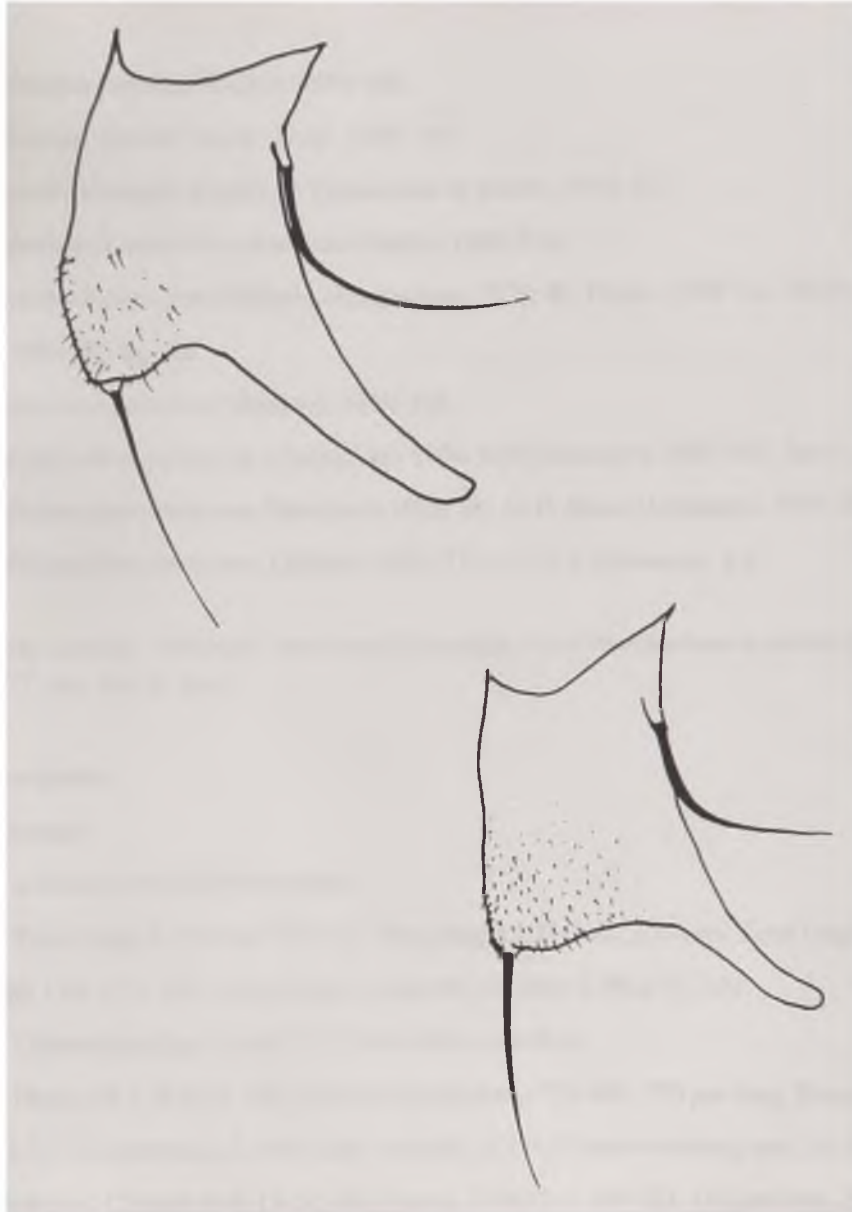


Fig. 10. *P. (U.) convictum* (Walker). Superior volsellae.

***Polypedilum (Uresipedilum) convictum* (Walker)**

(Fig. 10, 12 J, 13 F)

Chironomus convictus Walker, 1856: 161.*Chironomus blandus* van der Wulp, 1858: 164.*Polypedilum nympa* Kieffer, in Thienemann & Kieffer, 1916: 523.*Polypedilum nympa* var. *ploenensis* Kieffer, 1922: 359.*Polypedilum convictum* (Walker), Goetghebuer, 1928: 92; Pinder, 1978: fig. 168 B; Rossaro, 1985: 22, fig. 10.? *Chironomus testaceum* Macquart, 1826: 142.*nec Polypedilum convictum*, Chernovskii, 1949: 153; Pankratova 1983: 247, figs 1-4.*nec Polypedilum convictum*, Maschwitz 1975: 181 [= *P. flavus* (Johannsen, 1905: 225)].*nec Polypedilum convictum*, Lehmann 1981: 71 [= *P. (U.) plautum* sp. n.].*Material examined.* - GERMANY: South Bonn, Siebengebirge Nature Protection Reserve, Mucher Wiesenbach, 6 ♂♂, May 1990, S. Stern.**Description****Maleimago**

(n= 6, except when otherwise stated).

Total length 3.75-3.94, 3.83 mm. Wing length 2.21-2.42, 2.29 mm. Total length/ wing length 1.63-1.71, 1.67. Wing length/ length of profemur 2.38-2.75, 2.55.

Colouration (figs 11 J & 12 F). Pale yellow to yellow.

Head. AR 1.78-1.93, 1.83. Ultimate flagellomere 733-843, 795 μm long. Temporal setae 8-14, 11 (5) including 3-5, 4 (5) inner verticals, 3-5, 4 (5) outer verticals, and 2-6, 4 (5) postorbitals. Clypeus with 15-21, 18 (5) setae. Tentorium 109-133, 124 μm long, 22-33, 29 μm wide at sieve pore and 3-9, 6 (3) μm wide at posterior tentorial pit. Stipes 153-185, 166 μm long. Palp segment lengths (in μm): 20-49, 37; 36-56, 48; 107-171, 145; 98-153, 127; 139-246, 192 (5). Fifth palpal segment/ third palpal segment 1.88-1.46, 1.34 (5).

Thorax. Acrostichals 16-22, 19; dorsocentrals 15-18, 17, prealars 4-5, 5. Scutellum with 9-11, 10 setae.

Wing. VR 1.19-1.23. Brachiolum with 1 seta; R with 23-29, 26; R₁ with 17-21, 19; R₄₊₅ 35-48, 42, Squama with 9-14, 11 setae.

Legs. Spur on front tibia 29-32, 31 μm long. Spurs on middle 44-56, 50 tibia μm long, on hind tibia 49-63, 56 μm long. Comb on middle tibia 20-30, 24 μm long, long and short comb on hind tibia 20-31, 25 μm and 18-27, 22 μm long respectively. Width at apex of front tibia 49-62, 56 μm ; of middle tibia 49-62, 57 μm ; of hind tibia 60-80, 69 μm . Lengths and proportions of legs as in Table 4.

Table 4. Lengths (in μm) and proportions of legs of *Polypedilum (Uresipedilum) convictum* (Walker)

	fe	ti	ta ₁	ta ₂
p ₁	819-965, 910	673-748, 705	968-1082, 952 (4)	742-783, 760 (4)
p ₂	933-1070, 1010	854-943, 887	463-506, 482	258-303, 279
p ₃	1029-1150, 1068	961-1068, 1015	687-748, 715	356-388, 377
	ta ₃	ta ₄	ta ₅	LR
p ₁	463-552, 517 (4)	345-424, 392 (4)	153-164, 158 (4)	1.42-1.47, 1.44 (4)
p ₂	195-224, 209	110-123, 121	59-68, 65	0.54-0.56, 0.54
p ₃	310-342, 327	178-192, 183	75-93, 82	0.68-0.73, 0.70
	BV	SV	BR	
p ₁	1.44-1.51, 1.48 (4)	1.57-1.62, 1.60 (4)	2.1-2.3, 2.2 (4)	
p ₂	3.35-3.63, 3.53	3.85-4.00, 3.93	3.5-5.5, 4.4	
p ₃	2.77-2.99, 2.91	2.82-3.96, 2.94	4.8-6.2, 5.4	

Hypopygium. Tergite IX with 11-19, 16 median setae and 14-20, 17 posterior setae to both sides of anal point. Laterosternite IX with 3-5, 4 setae. Anal point 54-87, 70 μm long, 7-18, 11 μm wide at base, gradually tapering to nearly parallel-sided towards apex which is 6-9, 7 μm wide. Transverse sternapodeme 89-127, 109 μm long; phallapodeme 36-56, 46 μm long. Gonocoxite 178-211, 192 μm long. Total length of superior volsella including apicomedial projection 67-78, 73 μm and 33-43, 39 μm long apicomedial projection; base with 1 inner setae and 1 apical seta; microtrichiae present (fig. 10). Inferior volsella 129-144, 134 μm long;

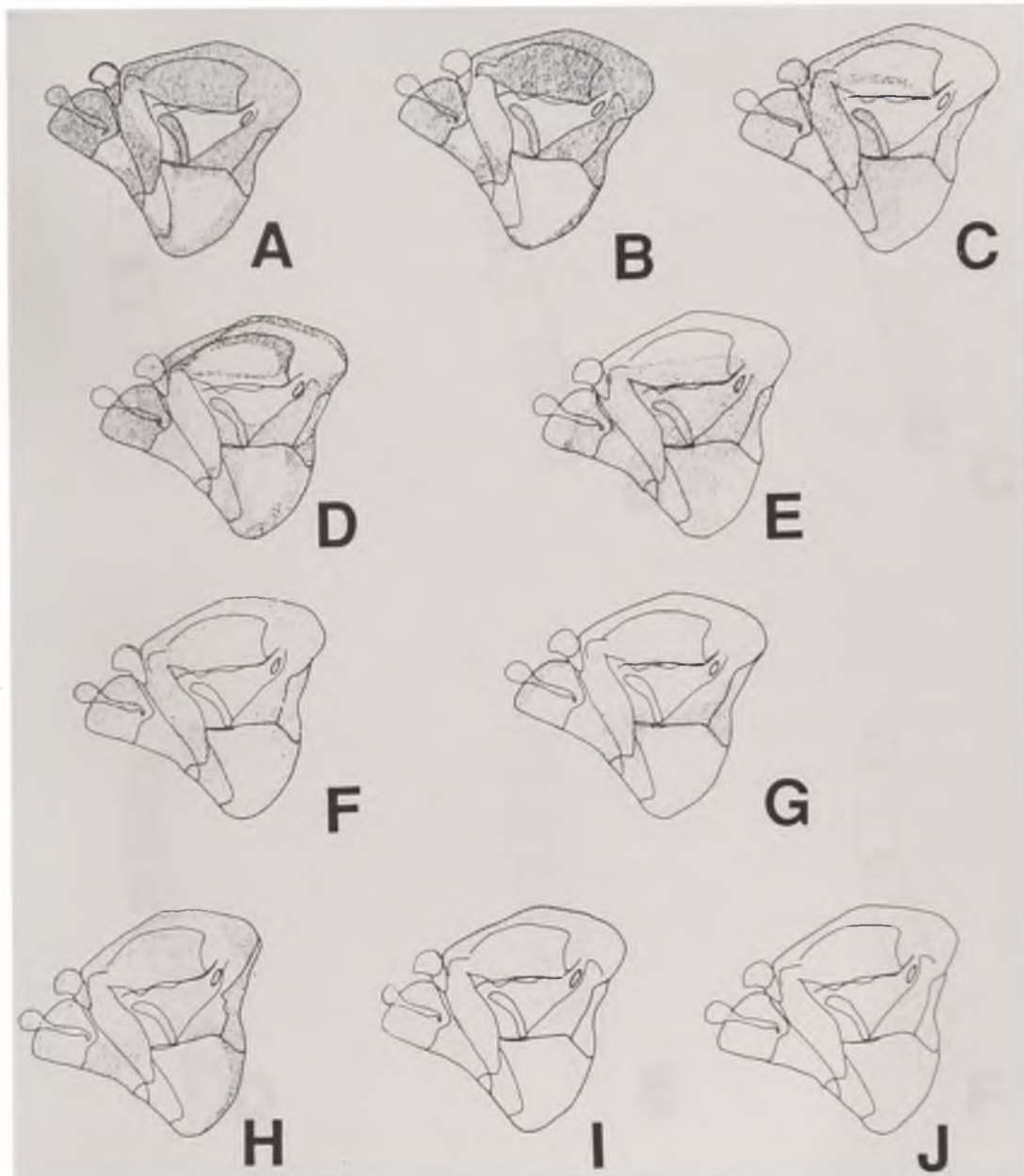


Fig. 11. *Polypedilum* subgenus *Uresipedilum* Sasa et Kikuchi. Colouration patterns of thorax.

A. *P. (U.) annulatum* Freeman, *P. (U.) praegnans* sp. n., *P. (U.) dossenudum* sp. n., *P. (s. str.) ephippium* Freeman. - B. *P. (U.) dossenudum* sp. n. - C. *P. (U.) freemani* sp. n. D. *P. (U.) harrisoni* sp. n., *P. (U.) praegnans* sp. n. E. *P. (U.) spinibojum*.sp. n. - F. *P. (P.) anderseni* sp. n. - G. *P. convictum* (Walker), *P.(U.) acutulum* sp. n., *P. (U.) gladysae* sp. n. H. *P. (U.) kibatiense* Goetghebuer - I. *P. (U.) plautum* sp. n. - J. *P.(U.) lehmanni* sp. n., *P. (U.) kakumense* sp. n.

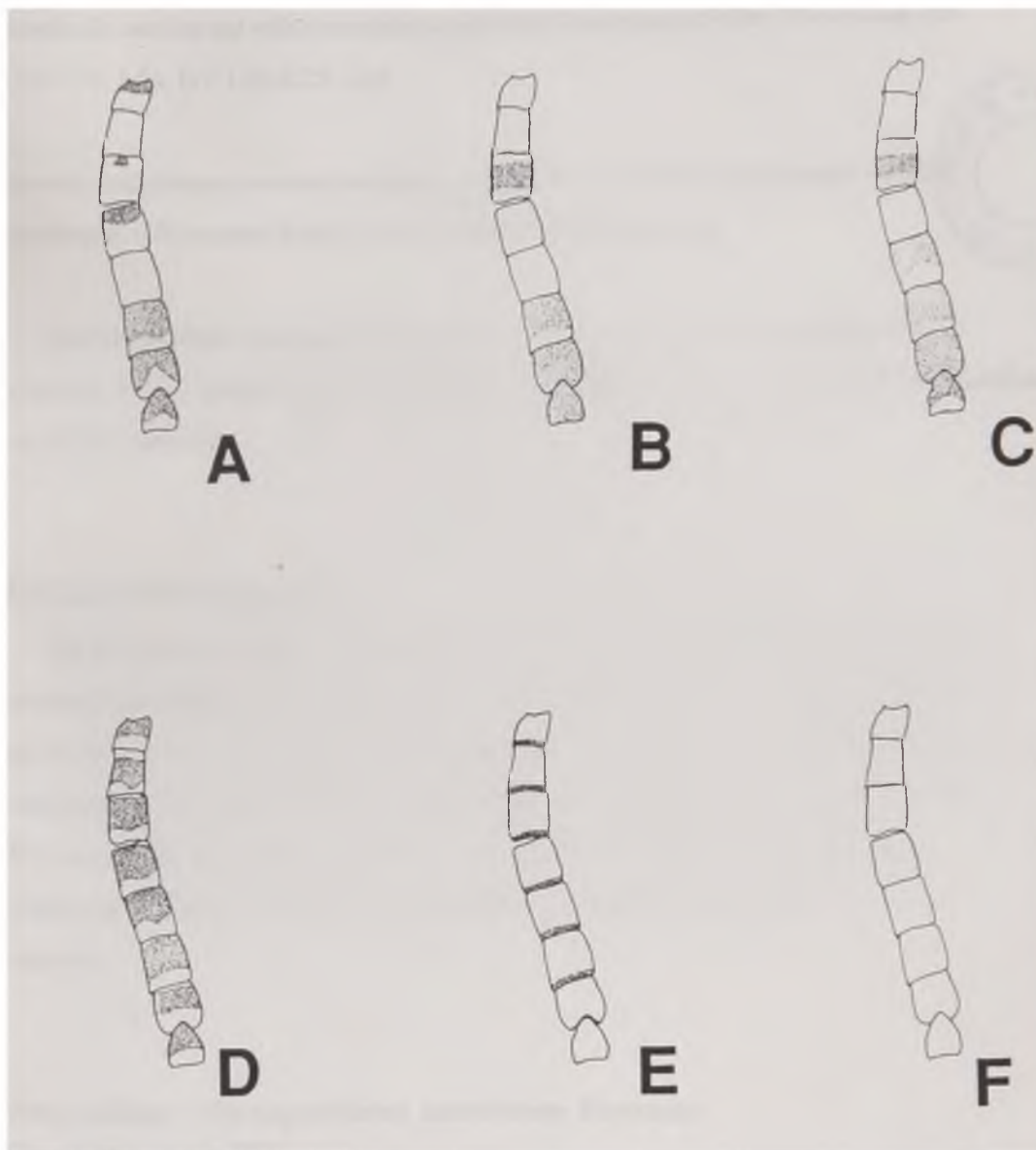


Fig. 12. *Polypedilum* subgenus *Uresipedilum* Sasa et Kikuchi. Colouration patterns of abdomen. - A. *P. (P.) anderseni* sp. n. - B. *P. (s. str.) ephippium* Freeman. - C. *P. (U.) freemani* sp. n. - D. *P. (U.) annulatum* Freeman, *P. (U.) harrisoni* sp. n., *P. (U.) praegnans* sp. n. - E. *P. (U.) dossenudum* sp. n. - F. *P. (U.) convictum*, *P. (U.) spinibojum* sp. n., *P. (U.) plautum* sp. n., *P. (U.) lehmanni* sp. n., *P. (U.) acutulum* sp. n., *P. (U.) gladysae* sp. n., *P. (U.) kakumense* sp. n.

subapically swollen and with a prominent apical seta. Gonostylus 169-189, 179 μ m long. HR 1.00-1.19, 1.06. HV 1.88-2.25, 2.08.

Remarks. - All the species examined appear to have only 1 inner seta on the superior volsella.

Distribution. - Widespread in the Palearctic region and Oriental China.

The other species belonging to the group are: *P. (U.) aviceps*, *P. (U.) paraviceps*, *P. (U.) surugense*, *P. (U.) flavus*, *P. (U.) hiroshimaense* and probably *P. (U.) microzoster*, *P. (U.) cultellatum* and *P. (U.) albicorpum*.

5.8.2 *annulatum* group

The group consists mostly of relatively large species with wing lengths more than 2.0 mm; unmarked legs; abdomen sometimes banded; superior volsella almost always bare, at most with microtrichiae at apex only; cephalic tubercles of known pupae reduced to low humps and frontal setae lacking. The superior volsellae are of the shapes shown in Figs 14 B, 16 B & C, 19 B & E-G, and 20 B; Townes (1945: 184, fig. 61); Maschwitz (1975: 301, fig. 52) for *P. (U.) cinctum*; and Townes (1945: 184, fig. 60) and Maschwitz (1975: 303, fig. 55) for *P. (U.) sulaceps*.

***Polypedilum (Uresipedilum) annulatum* Freeman**

(Figs 13-14, 11 A & 12 D)

Polypedilum (Polypedilum) annulatum Freeman, 1954: 22; 1958: 295, *pro parte*

nec Polypedilum (Polypedilum) annulatum Freeman, 1958: 295, *pro parte* [= *P. (U.) praegnans* sp. n. and *P. (U.) harrisoni* sp. n.]

nec Polypedilum (Polypedilum) annulatum Harrison, 1996: 78 [= *P. (U.) harrisoni* sp. n.]

Material examined. - SOUTH AFRICA: Cape Province, Kirstenbosch, paratype ♂, 25. XI. 1952, K. M. F. Scott. (BMNH, B. M. 1953-79); Wellington, 1 ♂, 29. XI. 1955, (BMNH, B. M. 195); Natal, Mooi R., Kamberg Game Reserve, 1 ♂, 14-30. IX. 1953, A. D. Harrison, (BMNH, B. M. 1954-280).

Diagnostic characters. - Differs from other banded abdomen members of the subgenus in having no setae on the superior volsella, and very high setal counts on the wing veins.

Description

Male imago

(n= 3, except when otherwise stated).

Total length 3.74-3.78 (2) mm. Wing length 1.96-2.11 mm. Total length/ wing length 1.66-2.03 (2). Wing length/ length of profemur 2.28-2.62.

Colouration (Figs 11 A & 12 D). Thorax almost completely brown and abdomen brown with dark brown bands. Femur, tibia and tarsi pale yellow.

Head (Fig. 13 A). AR 1.22-1.64. Ultimate flagellomere 544-702 μm long. Temporal setae 11-17 including 4-7 inner verticals, 4-5 outer verticals, and 5-8 (2) postorbitals. Clypeus with 12-20 setae. Tentorium 167-180 (2) μm long, 33-42 (2) μm wide at sieve pore and 7-11 (2) μm wide at posterior tentorial pit. Stipes 95-162 μm long. Palp segment lengths (in μm): 36-47; 42-47; 144-180; 139-159; 215-231 (2). Fifth palpal segment/ third palpal segment 1.42-1.50.

Third palpal segment with 2 sensilla clavata.

Thorax (Fig. 13 B). Acrostichals 24-28 (2); dorsocentrals 17-22, prealars 5-7. Scutellum with 18 setae.

Wing (Fig. 13 C). VR 1.66-1.24. Brachiolium with 1 seta; R with 20-26; R₁ with 18-22; R₄₊₅ 31-47; M with 2-5 (2), Squama with 7-11 setae.

Legs (figs 13 D-F). Spur on front tibia 31-38 μm long. Spurs on middle 54-68 tibia μm long, on hind tibia 60-84 μm long. Comb on middle tibia 13-27 μm long, long and short comb on hind tibia 28-29 μm and 20-27 μm long respectively. Width at apex of front tibia 44-58 μm ; of middle tibia 54-62 μm ; of hind tibia 60-71 μm . Lengths and proportions of legs as in Table 5.

Table 5. Lengths (in μm) and proportions of legs of *Polypedilum (Uresipedilum) annulatum* Freeman

	fe	ti	ta ₁	ta ₂	ta ₃	
p ₁	826-1011	591-662	986-1024 (2)	680-751 (2)	513-520 (2)	
p ₂	961-1050 (1)	787-844	499-488	253-288	206-239	
p ₃	951-1129	904-1053	374-712	356-420	299-356	
	ta ₄	ta ₅	LR	BV	SV	BR
p ₁	381-402 (2)	1125-146 (2)	0.65-1.67	1.36-1.45	1.41-1.50	2.8 (1)
p ₂	117-151	53-61	0.56-0.62	3.37-3.61 (2)	3.72-3.92 (2)	-
p ₃	171-221	64-85	0.65-0.77	2.72-2.81	2.65-3.12	5.2 (1)

Hypopygium (Figs 14 A-C). Tergite IX with 19-26 median setae and 16-20 posterior setae to both sides of anal point. Laterosternite IX with 2-6 setae. Anal point 56-83 μm long, 29-33 μm wide at base, gradually tapering to nearly parallel-sided towards apex which is 4-7 μm wide. Transverse sternapodeme 42-60 μm long; phallapodeme 89-100 μm long. Gonocoxite 199-218 μm long. Total length of superior volsella including apicomedial projection 77-78 μm and 30-31 μm long apicomedial projection; base with 2 inner setae and 1 apical seta; microtrichiae absent. Inferior volsella 133-142 μm long; parallel sided and with a prominent apical seta. Gonostylus 206-220 μm long. HR 0.97-0.99; HV 1.75-1.79.

Remarks. - The shape of the superior volsella is similar to *P. (U.) spinibojum* and *P. (U.) plautum*, but can be distinguished from banded abdomen colouration and pattern.

Distribution. - Known from waterbodies in South Africa.

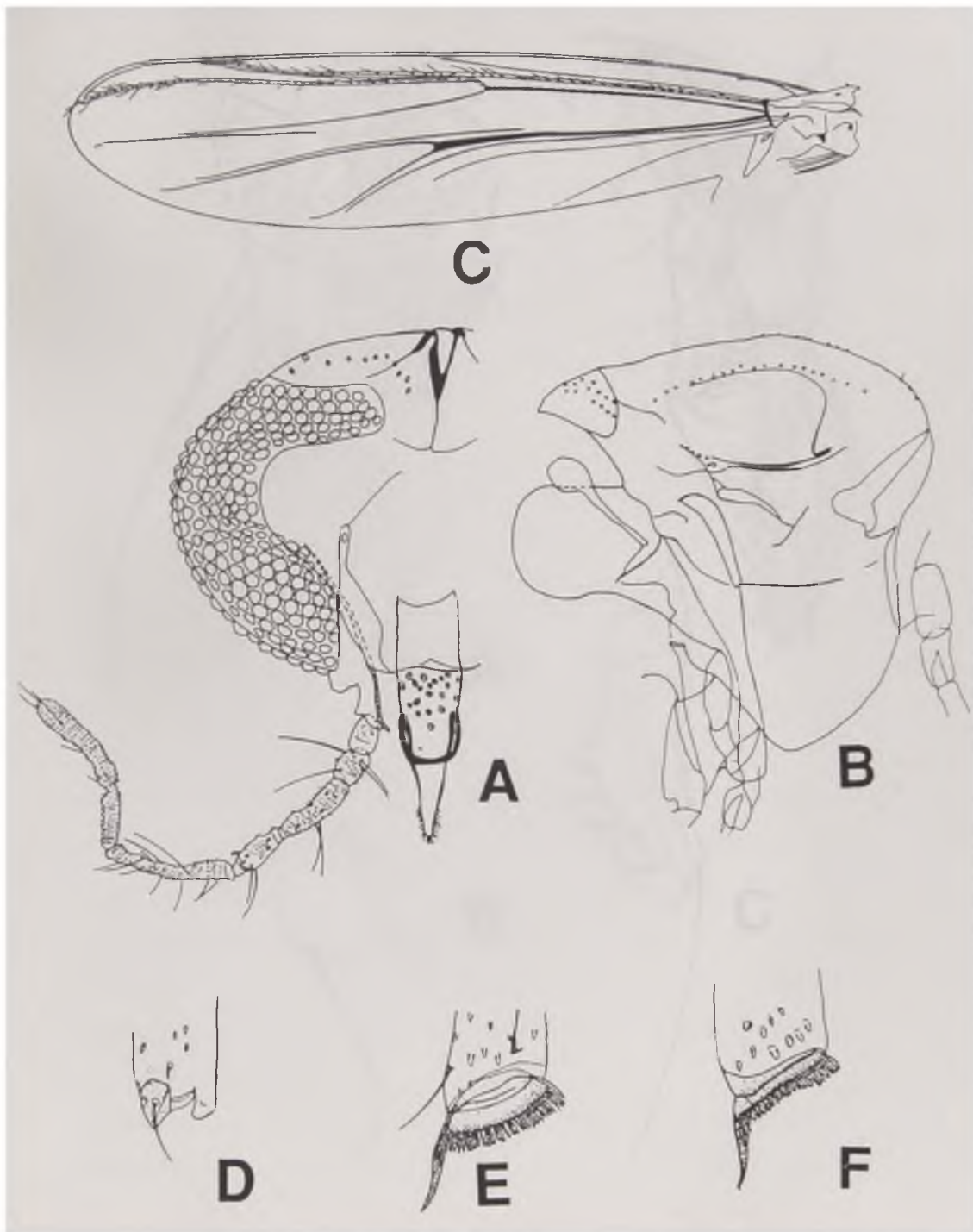


Fig. 13. *P. (U.) annulatum* Freeman. - A. Head. - B. Thorax. - C. Wing. - D. Fore tibia. E. Mid tibia. - F. Hind tibia.

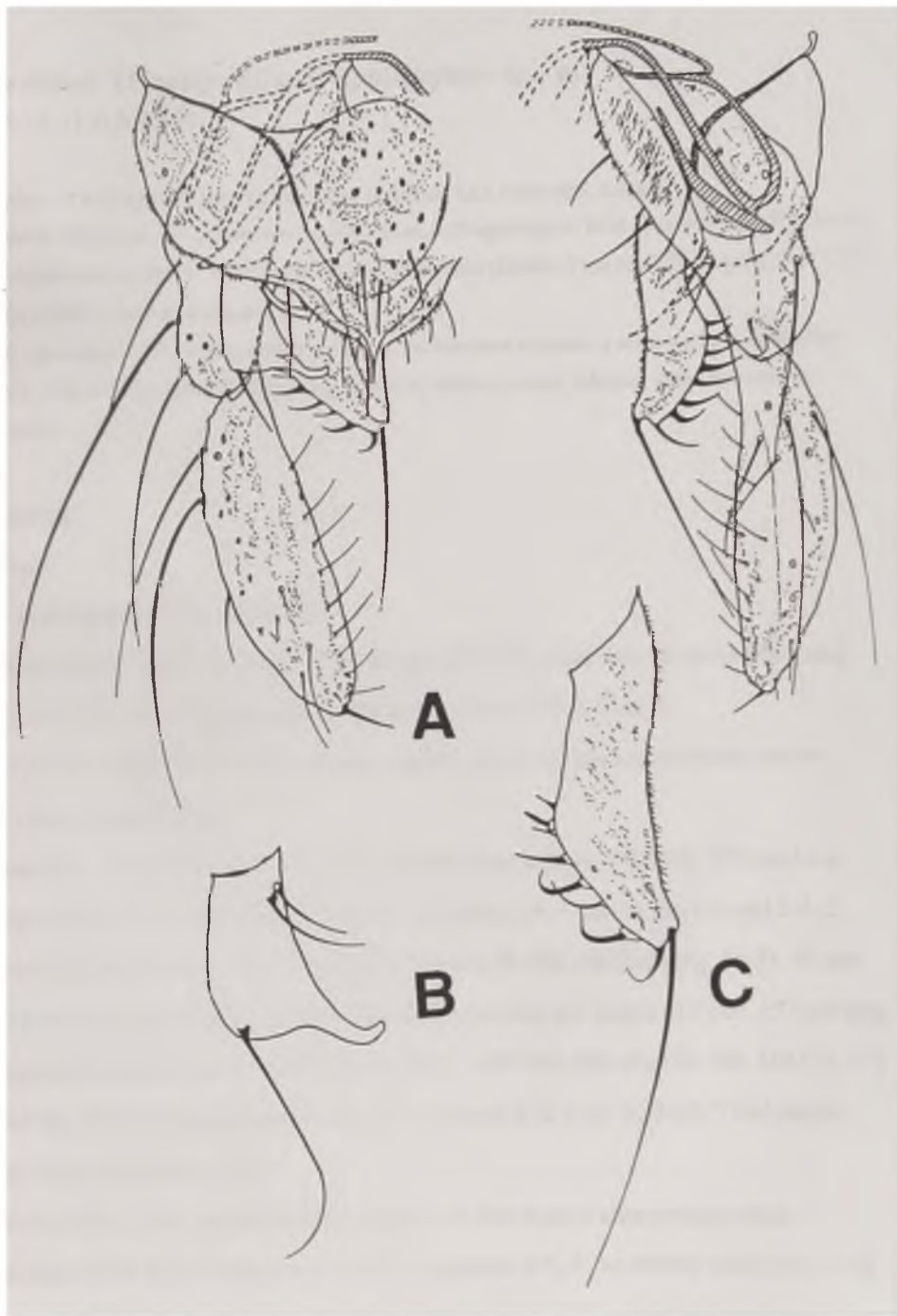


Fig 14. *P. (U.) annulatum* Freeman. - A. Hypopygium. - B. Superior volsella. - C. Inferior volsella.

Polypedilum (Uresipedilum) spinibojum* sp. n.*(Figs 15-16, 11 E & 12 F)**

Type locality. - TANZANIA: Tanga Region, West Usambara Mts. Mazumbai, Kaputu.

Type material. - Holotype ♂, here designated, TANZANIA: Tanga Region, West Usambara Mts., Mazumbai, Kaputu, Malaise trap st. 10. XI. 1990. ZMB Tanzania expedition (ZMBN, Type No. 271). Paratypes: 12 ♂♂, as holotype (ZMBN) same data as holotype.

Diagnostic characters. - Differs from other members of the subgenus in having a spine on the anteprepronotum.

Etymology. - From Latin, *spina*, meaning spine, and *boja*, meaning collar, referring to the spine on the anteprepronotum.

Description**Male imago**

(n= 10, except when otherwise stated).

Total length 3.31-4.07, 3.70 mm. Wing length 2.13-2.42, 2.26 mm. Total length/ wing length 1.52-1.73, 1.63. Wing length/ length of profemur 2.07-2.32, 2.21.

Colouration (Figs 11 E & 12 F). Thorax yellow to dark brown and abdomen yellow.

Femur, tibia and tarsi yellow.

Head (Fig. 15 A). AR 1.61-1.91, 1.71. Ultimate flagellomere 700-899, 792 μ m long. Temporal setae 7-13, 11 including 3-6, 4 inner verticals, 2-6, 4 outer verticals, and 1-4, 2 postorbitals. Clypeus with 15-21, 19 setae. Tentorium 91-182, 159 μ m long, 33-51, 42 μ m wide at sieve pore and 6-13, 9 μ m wide at posterior tentorial pit. Stipes 111-204, 157 μ m long. Palp segment lengths (in μ m): 33-53, 42; 44-60, 52; 167-200, 182 (8); 153-183, 164 (7); 171-286, 244 (6). Fifth palpal segment/ third palpal segment 0.92-1.60, 1.35 (6). Third palpal segment with 2 sensilla clavata.

Thorax (Fig. 15 B). Anteprepronotum with more or less distinct anteprepronotal spine. Acrostichals 18-26, 23; dorsocentrals 13-20, 17; prealars 4-6, 6. Scutellum with 9-14, 11 (9) setae.

Wing (Fig. 15 C). VR 1.19-1.27, 1.21. Brachiolium with 1 seta; R with 24-30, 27; R₁ with 20-27, 23; R₄₊₅ 40-50, 26; M 1-5, 4 (6) and RM with 1-2 (2) setae. Squama with 8-10, 10 setae.

Legs (Figs 15 D-F). Spur on front tibia 22-36, 31 μm long. Spurs on middle tibia 42-64, 57 μm long, on hind tibia 53-73, 61 μm long. Comb on middle tibia 14-27, 20 μm long, long and short comb on hind tibia 12-42, 21 μm and 12-31, 20 μm long respectively. Width at apex of front tibia 51-78, 60 μm ; of middle tibia 49-64, 58 μm ; of hind tibia 62-73, 67 μm . Lengths and proportions of legs as in Table 6.

Table 6. Lengths (in μm) and proportions of legs of *Polypedilum (Uresipedilum) spinibojum* sp. n.

	fe	ti	ta ₁	ta ₂
p ₁	997-1161, 1052	673-801, 748	1178 (1)	844 (1)
p ₂	9.51- 1285, 1117	712-1050, 950	523- 570, 544 (5)	302-331, 310 (5)
p ₃	1060-1299, 1174	954-1161, 1075	790-797 (2)	409-434 (2)
	ta ₃	ta ₄	ta ₅	LR
p ₁	614 (1)	477 (1)	182 (1)	1.57 (1)
p ₂	214-233, 225 (5)	135-210, 156 (5)	53-75, 67 (5)	0.44-0.59, 0.53 (5)
p ₃	352-367 (2)	189-217 (2)	84-89 (2)	0.70-0.74 (2)
	BV	SV	BR	
p ₁	1.42 (1)	1.55 (1)	3.4 (1)	
p ₂	3.28-3.73, 3.54 (5)	3.77-4.10, 3.92 (5)	3.3-3.9, 3.6 (5)	
p ₃	2.68-2.90 (2)	2.79-2.96 (2)	3.3-4.6 (2)	

Hypopygium (Figs 16 A-D). Tergite IX with 16-23, 19 median setae and 12-18, 16 posterior setae to both sides of anal point. Laterosternite IX with 1-5, 3 setae. Anal point 73-129, 113 μm long, 44-124, 98 μm wide at base, gradually tapering to nearly parallel-sided towards apex which is 4-7, 6 μm wide. Transverse sternapodeme 21-56, 35 μm long; phallapodeme 88-144, 111 μm long. Gonocoxite 178-220, 197 μm long. Total length of superior volsella including apicomedial projection 60-89, 77 μm and 24-44, 35 (9) μm long

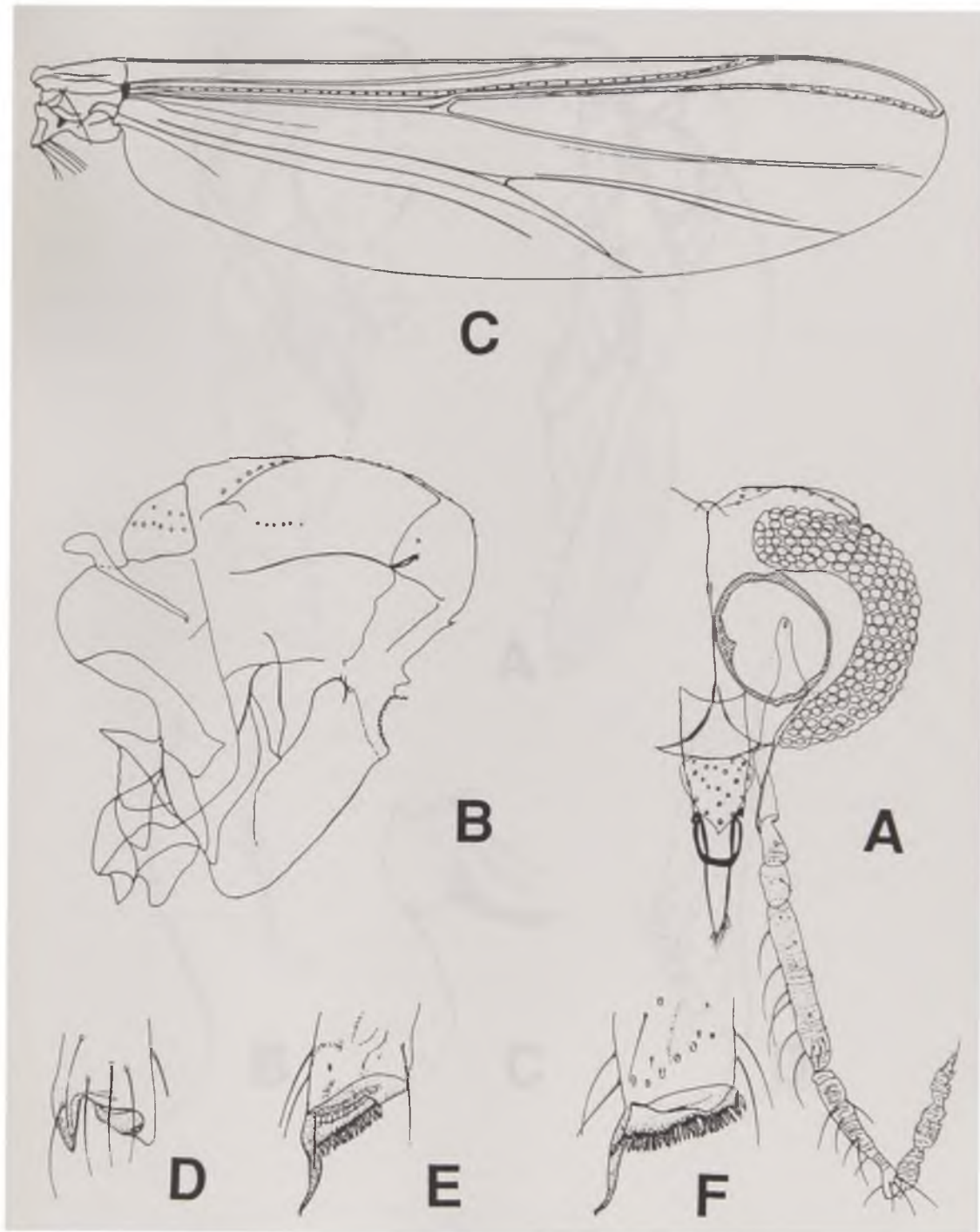


Fig. 15. *P. (U.) spinibojum* sp. n. - A. Head. - B. Thorax. - C. Wing. - D. Fore tibia. E. Mid tibia. - F. Hind tibia.

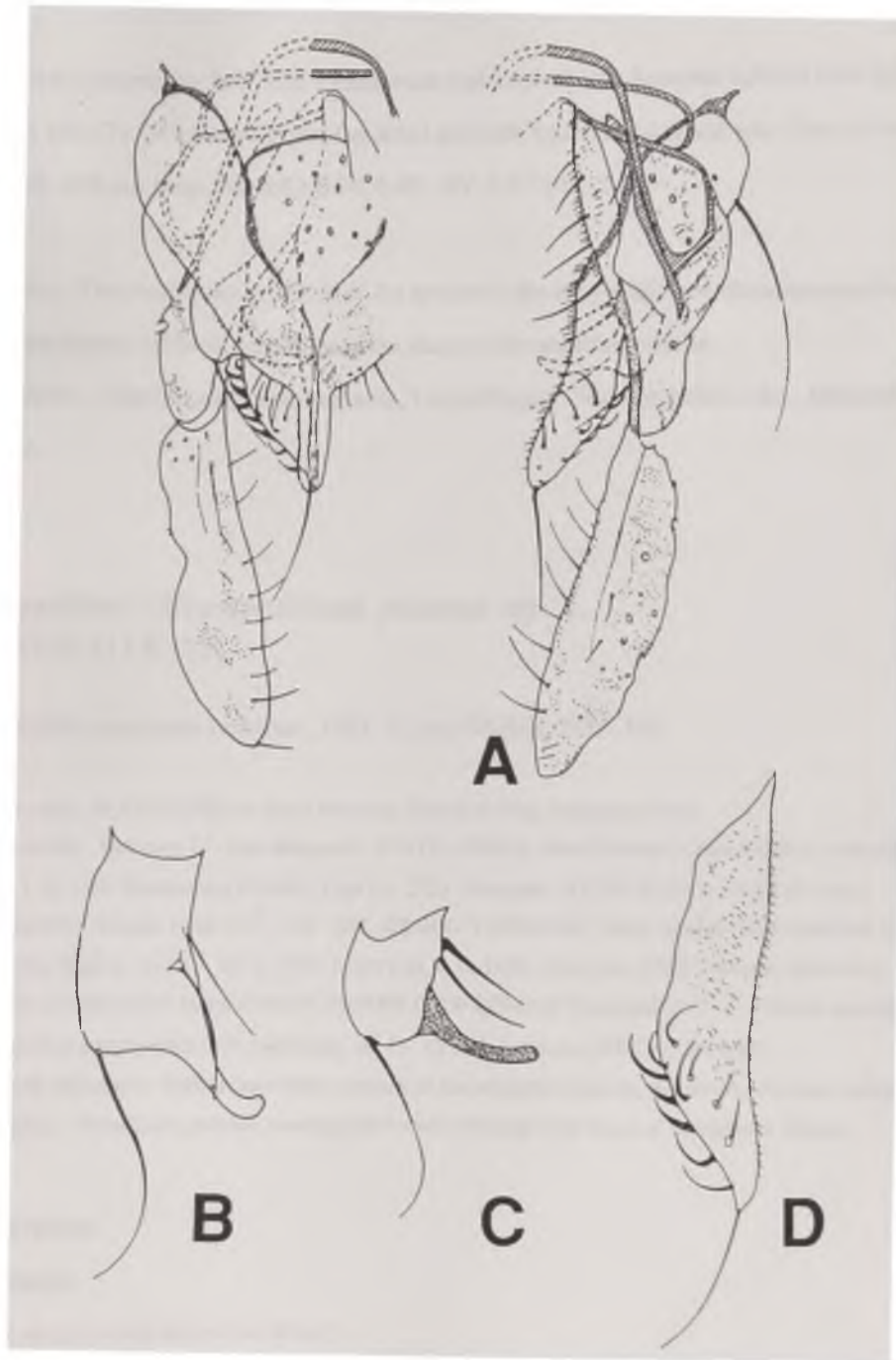


Fig. 16. *P. (U.) spinibojum* sp. n. - A. Hypopygium. - B. Superior volsella. - C. Superior volsella variation. - D. Inferior volsella.

apicomedial projection; base with 2 **inner** setae and 1 apical seta. Superior volsella bare. Inferior volsella 100-171, 144 μm long; parallel sided and with a prominent apical seta. Gonostylus 188-240, 222 μm long. HR 0.82-0.94, 0.89; HV 1.57-1.89, 1.70.

Remarks. - The most striking feature of the species is the unique spine on the antepnotum.

There are slight individual variations in the shape of the superior volsella.

Distribution. - Known only from Tanzania, Tanga Region, West Usambara Mts., Mazumbai, Kaputu.

***Polypedilum (Uresipedilum) plautum* sp. n.**
(Figs 17-19, 11 I & 12 F)

Polypedilum convictum Lehmann, 1981: 71, *nec* Walker, 1856: 161

Type locality. - SOUTH AFRICA: Natal Province, Cathedral Peak, Indumeni Forest.

Type material. - Holotype ♂, here designated, SOUTH AFRICA: Natal Province, Cathedral Peak, Indumeni Forest, 1. X. 1991 Stuckenberg (ZMBN, Type No. 272). Paratypes: SOUTH AFRICA: Natal Province, Cathedral Peak, Doreen Falls, 1 ♂, 2. X. 1991, (ZMBN); TANZANIA: Tanga Region, West Usambara Mts., Mazumbai, Kaputu, 2 ♂♂, 28. II. 1990, Light trap, 4. II. 1990, Sweep net. ZMB Tanzania Expedition (ZMBN); ZAIRE (NOW DEMOCRATIC REPUBLIC OF CONGO): Kisangani, 2 ♂♂ with one associated pupal exuviae misidentified as *P. convictum*, 28. IV. 1975, J. Lehmann (ZSM No. EI 1980).

Diagnostic characters. - Differs from other members of the subgenus in having postnotum and vittae brown.

Etymology. - From Latin *plautum*, meaning flat-footed, referring to the shape of the superior volsella.

Description

Male imago

(n= 6, except when otherwise stated).

Total length 3.31-3.72, 3.46 (5) mm. Wing length 1.82-2.29, 2.17 (5) mm. Total length/ wing length 1.49-1.81, 1.61 (5). Wing length/ length of profemur 1.96-2.50, 2.20 (5).

Colouration (Figs 11 I & 12 F). Thorax with postnotum and vittae brown, abdomen pale yellow. Femur, tibia and tarsi yellow.

Head (Fig. 17 A). AR 1.23-1.90, 1.51 (5). Ultimate flagellomere 268-733, 536 μm long. Temporal setae 6-15, 10 (5) including 2-4, 3 inner verticals, 2-5, 3 outer verticals, and 2-3 (5) postorbitals. Clypeus with 13-21, 17 setae. Tentorium 140-155, 146 (4) μm long, 27-48, 39 (4) μm wide at sieve pore and 6-12, 9 (4) μm wide at posterior tentorial pit. Stipes 78-144, 124 (4) μm long. Palp segment lengths (in μm): 34-44, 39; 36-47, 42; 128-213, 166; 120-186, 145 (5); 214-270, 193 (5). Fifth palpal segment/ third palpal segment 1.27-1.68 (3). Third palpal segment with 3 sensilla clavata.

Thorax (Fig. 17 B). Acrostichals, 11-27, 19 (5); dorsocentrals 16-25, 19; prealars 4-6, 5. Scutellum with 9-17 (5) setae.

Wing (Fig. 17 C). VR 1.20-1.28, 1.25. Brachiolum with 1-5, 2 setae; R with 23-26, 24 (5); R_1 with 18-26, 22 (5); R_{4+5} 38-46, 43 (5); M bare. Squama with 9-14, 12 (5) setae.

Legs (Figs 17 D-F). Spur on front tibia 26-32, 30 (5) μm long. Spurs on middle tibia 44-58, 52 (5) μm long, on hind tibia 53-64, 60 (5) μm long. Comb on middle tibia 12-24, 22 (5) μm long, long and short comb on hind tibia 24-36, 29 (5) μm and 11-32, 26 (5) μm long respectively. Width at apex of front tibia 44-53, 49 (5) μm ; of middle tibia 49-60, 56 (5) μm ; of hind tibia 56-70, 62 (5) μm . Lengths and proportions of legs as in Table 7.

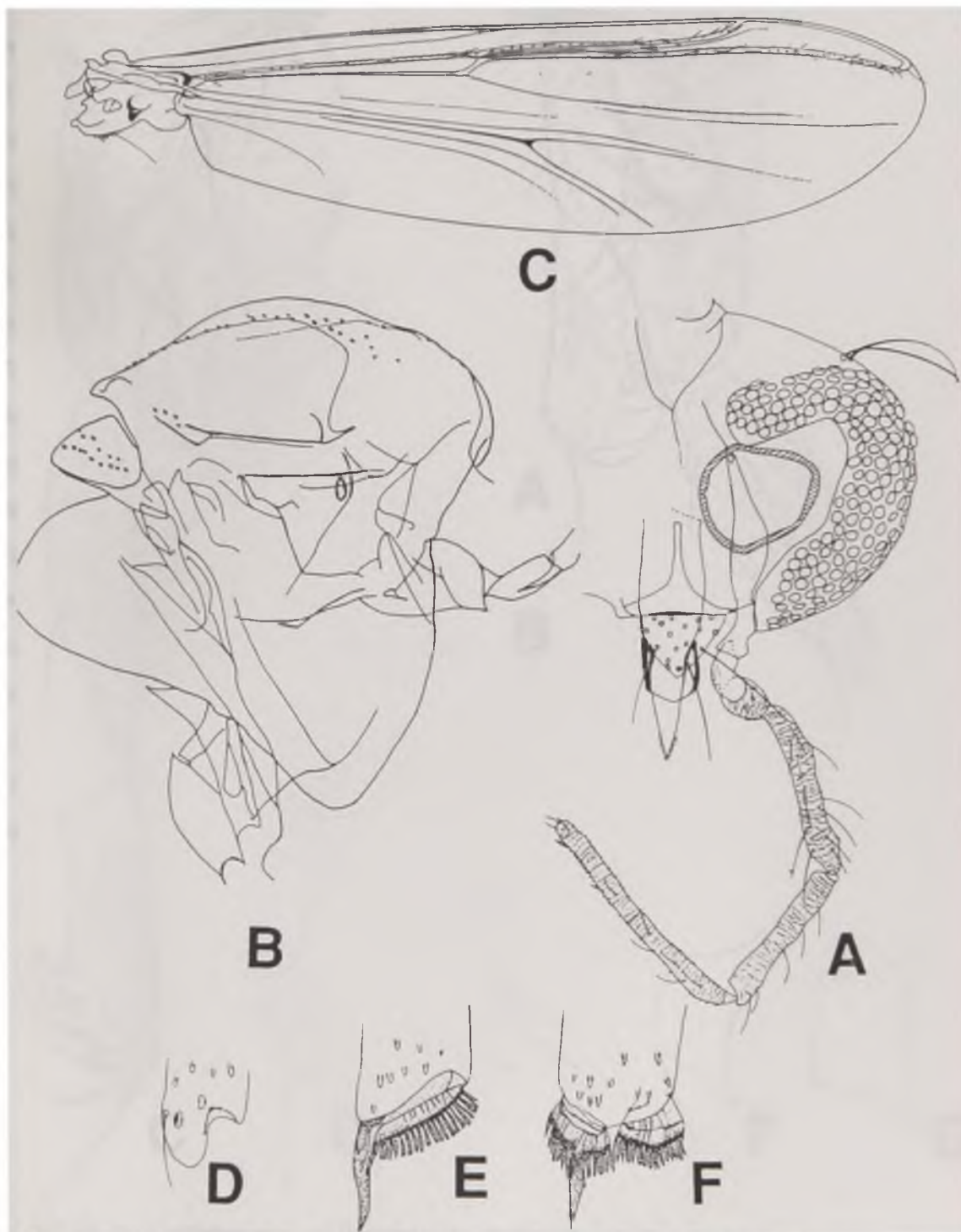


Fig. 17. *P. (U.) plautum* sp. n. A. Head. - B. Thorax. - C. Wing. - D. Fore tibia. E. Hind tibia. F. Hind tibia.

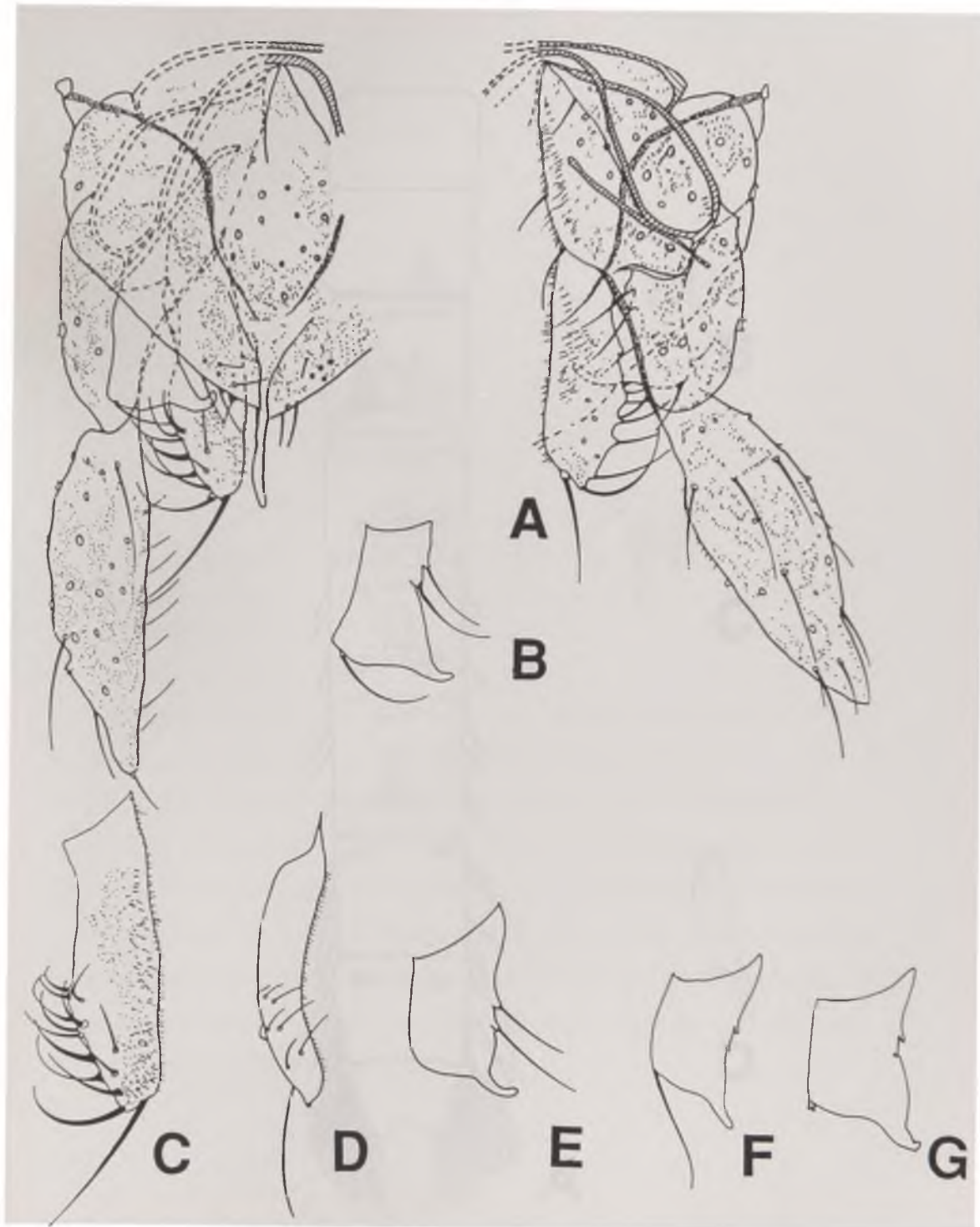


Fig. 18. *P.(U.) plautum* sp. n. - A. Hypopygium. - B. Superior volsella. - C. Inferior volsella of holotype. - D. Inferior volsella variation. - E-G. Superior volsella variation.

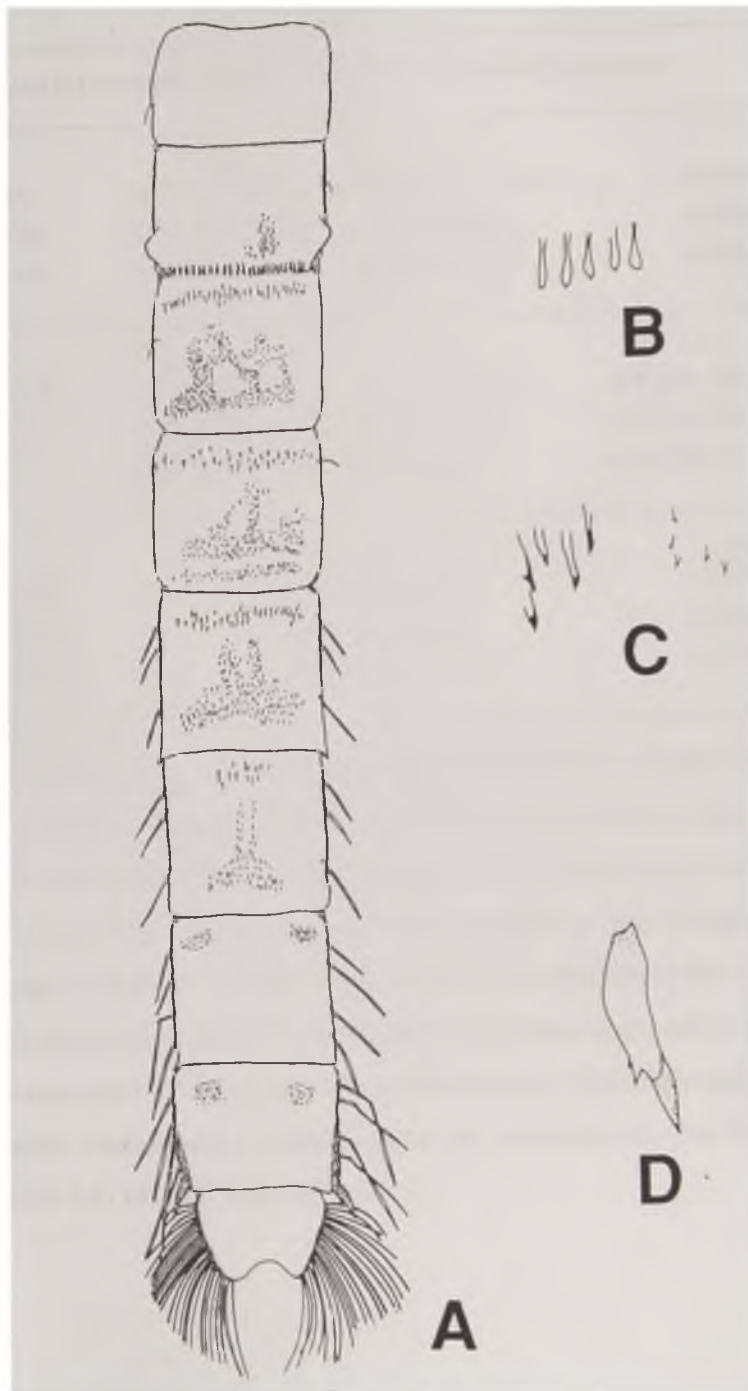


Fig. 19. *P. (U.) plautum* sp. n., pupa. - A. Abdomen. - B. Tergite II hooklets. - C. Tergite II spinules and shagreen. - D. Anal spur.

Table 7. Lengths (in μm) and proportions of legs of *Polypedilum* (*Uresipedilum*) *plautum* sp. n.

	fe	ti	ta ₁	ta ₂
p ₁	850-1144, 985 (5)	619-816, 692 (5)	1022-1208, 1103 (5)	758-904, 819 (5)
p ₂	936-1184, 1038 (5)	776-1040, 879 (5)	452-544, 502 (4)	249-304, 273 (4)
p ₃	958-1240, 1084 (5)	908-1152, 1017 (5)	662-800, 740 (5)	363-464, 399 (5)
	ta ₃	ta ₄	ta ₅	LR
p ₁	513-608, 559 (5)	406-520, 473 (5)	146-208, 175 (5)	1.48-1.70, 1.60 (5)
p ₂	171-212, 187 (4)	107-136, 121 (4)	46-57, 52 (4)	0.58-0.64, 0.60 (4)
p ₃	288-376, 326 (5)	164-240, 199 (5)	64-88, 77 (5)	0.68-0.78, 0.73 (5)
	BV	SV	BR	
p ₁	1.35-1.42, 139 (5)	1.47-1.62, 1.53 (5)	1.8-3.4, 2.4 (5)	
p ₂	3.52-3.75, 3.67 (4)	3.33-3.79, 3.62 (4)	2.2-4.6 (3)	
p ₃	2.72-2.93, 2.84 (5)	2.67-3.05, 2.84 (5)	3.1-5.1 (3)	

Hypopygium (Figs 18 A-G). Tergite IX with 10-15, 13 (5) median setae and 10-22, 17 (4) posterior setae to both sides of anal point. Laterosternite IX with 2-4, 3 (4) setae. Anal point 54-93 (3) μm long, 33 (3) μm wide at base, gradually tapering to nearly parallel-sided towards apex which is 4-7 (3) μm wide. Transverse sternapodeme 22-40, 32 μm long; phallapodeme 82-110, 97 μm long. Gonocoxite 149-189, 167 (5) μm long. Total length of superior volsella including apicomedial projection 56-89, 71 μm and 10-34, 21 μm long apicomedial projection; base with 2 inner setae and 0-1, 1 apical seta; without microtrichiae. Inferior volsella 109-140, 127 μm long; parallel sided and with a prominent apical seta. Gonostylus 122-216, 184 μm long. HR 0.81-1.24, 0.81 (4); HV 1.56-2.00, 1.78 (5).

Pupa

(n= 1).

Total length about 4.5 mm. Exuviae cephalothorax, margins of segments and caudolateral spur brown.

Cephalothorax. Cephalic tubercles barely indicated or absent. Frontal setae broken. Prealar tubercle apparently absent.

Abdomen (Figs 19 A-D). Tergites I & II bare; tergites III-VI each with strong anterior row of spinules, absent on. Tergites II-VI each with extensive strong median and posterior band of shagreen; tergites VII and VIII each with two anteriomedian spots of shagreen; tergite IX bare. Tergite II with small and weak anterior spinules, rest of sternites apparently bare. Conjunctions absent. Sternite II with a single row of 27 caudal hooklets. Pedes spurii A absent. Pedes spurii B well developed on I and II. Anal spur with strong apical tooth, 1 strong lateral tooth, and 0-1 minute lateral tooth.

Abdominal setation: Segment I-III each with 1 seta, IV with 3 setae and none taeniate; V and VI each with 3 taeniae; VII and VIII each with 4 taeniae. Fringe of anal lobe with 25, no dorsal seta.

Remarks. - This species is similar to *P. (U.) spinibojum* and *P. (U.) annulatum*, but differs in the colouration pattern of thorax and abdomen. *P. (U.) plautum* has no setae on M.

Distribution. - The species is known from South Africa, Democratic Republic of Congo and Tanzania.

Polypedilum (Uresipedilum) lehmanni sp. n.

(Figs 20-21, 11 J & 12 F)

P. (P.) kibatiense Lehmann 1979: 57 *pro parte*

nec P. (P.) kibatiense Goetghebuer 1936a: 487

Type locality. - ZAIRE (NOW DEMOCRATIC REPUBLIC OF CONGO): Kalengo.

Type material. - Paratype ♂, reared from larva, here designated, DEMOCRATIC REPUBLIC OF CONGO: Kalengo, 2.-XI.-72, (No. E1/ 1980).

Diagnostic characters. - Differs from other members of the subgenus in having a longer, straight apicomedial projection and a slender parallel-sided inferior volsella.

Etymology. - Named after Dr. Jens Lehmann, who first described this species as *P. (U.) kibatiense*.

Description

Male imago

(n= 1).

Total length not measurable (Abdomen and thorax incomplete). Wing length 2.07 mm.

Wing length/ length of profemur 2.00.

Colouration (Figs 11 J & 12 F). Thorax pale yellow; abdomen yellow. Femur, tibia and tarsi yellow.

Head. AR 1.56. Ultimate flagellomere 728 μm long. Temporal setae 7 including 2 inner verticals, 3 outer verticals, and 2 postorbitals. Clypeus with 18 setae. Tentorium 18 μm long, 9 μm wide at sieve pore and 6 μm wide at posterior tentorial pit. Stipes 189 μm long. Palp segment lengths (in μm): 36; 44; 167; 147; 248. Fifth palpal segment/ third palpal segment 1.49.

Thorax. Acrostichals 20; dorsocentrals 15; prealars 6 setae. Scutellum not measurable (part of thorax torn).

Wing. VR 1.28. Brachiolium with 1 seta; R with 24 ; R₁ with 18; R₄₊₅ 46; M with 3.

Squama with 10 setae.

Legs. Spur on front tibia 27 μm long. Spurs on middle tibia 58 μm long, on hind tibia 59 μm long. Comb on middle tibia 27 μm long, long and short comb on hind tibia 27 and 24 μm long respectively. Width at apex of front tibia 56 μm ; of middle tibia 58 μm ; of hind tibia 73 μm . Lengths and proportions of legs as in Table 8.

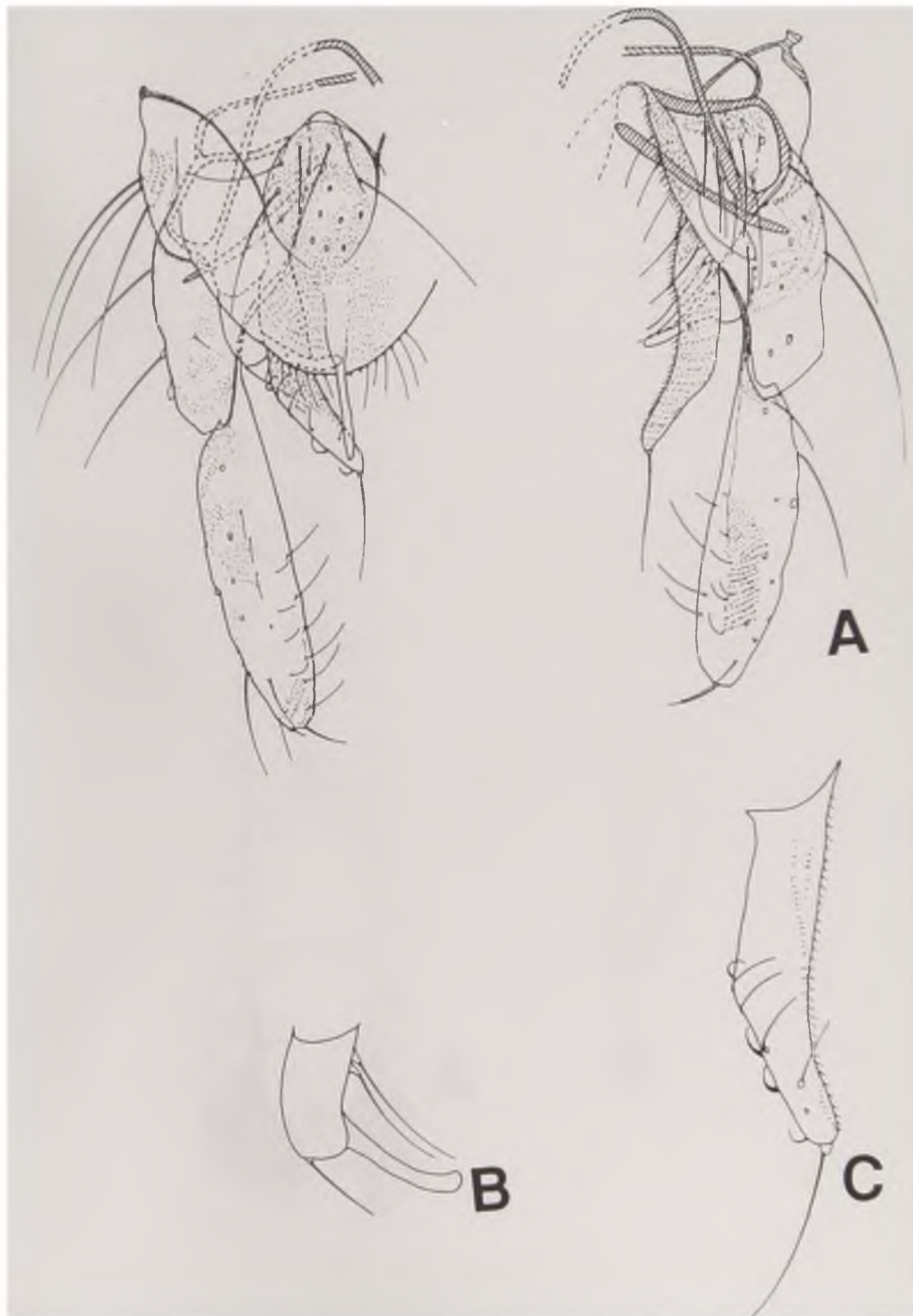


Fig 20. *P. (U.) lehmanni* sp. n. - A. Hypopygium. - B. Superior volsella. - C. Inferior volsella.

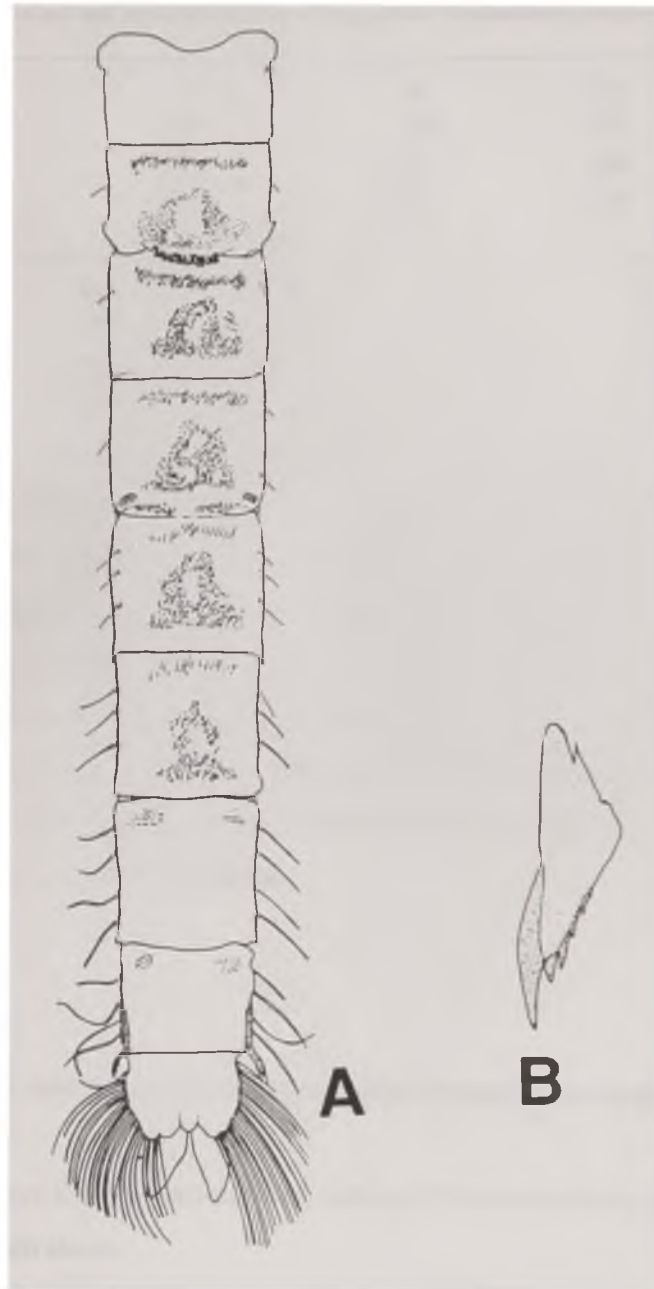


Fig. 21. *P. (U.) lehmanni* sp. n., pupa. - A. Abdomen. - B. Anal spur.

Table 8. Lengths (in μm) and proportions of legs of *Polypedilum (Uresipedilum) lehmanni* sp. n.

	fe	ti	ta ₁	ta ₂	ta ₃
P ₁	972	673	1050	787	577
P ₂	1047	876	491	285	189
P ₃	1107	1007	730	392	338

	ta ₄	ta ₅	LR	BV	SV	BR
P ₁	459	167	1.56	1.35	1.57	2.5
P ₂	128	64	0.56	3.63	3.91	0.2
P ₃	199	89	0.72	3.79	2.90	0.2

Hypopygium (Figs 20 A-C). Tergite IX with 17 median setae and 20 posterior setae to both sides of anal point. Laterosternite IX with 3 setae. Anal point 31 μm long, 9 μm wide at base, gradually tapering to nearly parallel-sided towards apex which is 7 μm wide. Transverse sternapodeme 33 μm long; phallapodeme 119 μm long. Gonocoxite 186 μm long. Total length of superior volsella including apicomedial projection 78 μm and 58 μm long apicomedial projection; base with 2 inner setae and 1 apical seta; without microtrichiae. Inferior volsella 138 μm long; parallel sided, slender and with a prominent apical seta. Gonostylus 189 μm long. HR 0.99; HV - (abdomen broken, incomplete).

Pupa

(n= 1)

Total length about 5.2 mm. Exuviae cephalothorax, margins of segments and caudolateral spur brown.

Cephalothorax. Cephalic tubercles barely indicated. Frontal setae barely indicated. Prealar tubercle apparently absent.

Abdomen (Figs 21 A-B). Tergite I bare; tergites II-VI each with strong anterior row of spinules and strong median and posterior band of shagreen, extensive on II-V; tergites VII and VIII each with two anteriomedian spots of shagreen; tergite IX bare. Sternites bare. Tergite II

with 26 caudal hooklets. Conjunctive IV/V with 33 irregular biserial spines which appear to be divided into two parts. Pedes spurii A well developed on segment IV. Pedes spurii B well developed on I and II. Anal spur with strong apical tooth, 1 strong lateral tooth, and 3-5 minute lateral teeth.

Abdominal setation: Segment I without setae; II-III with 1 seta, IV with 3 setae and none taeniate; V and VI each with 3 taeniae; VII and VIII each with 4 taeniae. Fringe of anal lobe with 25 and 29 taeniae on each side, no dorsal seta.

Remarks. - This species is similar to *P. (U.) spinibojum* and *P. (U.) plautum* but separable from these species by having a longer apicomedial projection and a different thorax colouration.

Distribution. - Known only from Democratic Republic of Congo.

***Polypedilum (Uresipedilum) tesfayi* Harrison**

Polypedilum (Polypedilum) tesfayi Harrison, 1996: 80, figs 136-139.

This species from Addis Ababa, Ethiopia, has been extensively described by Harrison (1996). The species belongs to *Polypedilum (Uresipedilum)* as shown by the shape of the superior volsella. The superior volsella is similar to *Polypedilum (Uresipedilum) dossenuudum* sp. n., described on p.119.

P. (U.) cinctum and *P. (U.) suliceps* are considered as sister species belonging to this group.

5.8.3 *oresitrophum* group

The group consists mostly of moderately large species with wing lengths less than 2.0 mm; often low antennal ratios; superior volsella with very long projection, almost always without inner setae, base covered with microtrichiae or with microtrichiae at base only; pupa with prealar tubercle; antennal blade of known larvae longer than flagellum; and larval ventromental lobes with reduced posterior lobes. The superior volsellae are of the shapes shown in Figs 22 B & C; 23 B & D, and 25 B; Freeman (1959: 431, fig. 5 g) for *P. (U.) canum*; Freeman (1959: 431, fig. 5 d) for *P. (U.) harrisi*; and Freeman (1959: 431, fig. 5 f) for *P. (U.) cumberi*.

***Polypedilum (Uresipedilum) praegnans* sp. n.**

(Figs 22, 11 A & 12 D)

Polypedilum (Polypedilum) annulatum Freeman 1958: 295 *pro parte*

nec Polypedilum (Polypedilum) annulatum Freeman 1954: 22.

Type locality. - SENEGAL: Dakar

Type material. - Holotype 1 ♂, here designated, SENEGAL: Dakar II-III. 1960, M. Emerit (BMNH). Paratype: ZAIRE (NOW DEMOCRATIC REPUBLIC OF CONGO); Lumbubashi, Elisabethville 1 ♂, 15. XII. 1938, H. J. Bredo (BMNH, 12.204).

Diagnostic characters. - Differs from other members of the subgenus in the bulging shape of the superior volsella with very short apicomedial projection.

Etymology. - From Latin, *praegnans*, with child, referring to the bulging shape of the superior volsella resembling a pregnant woman.

Description

Male imago

(n= 2, except when otherwise stated).

Total length 3.15 (1) mm. Wing length 1.45-1.58 mm. Total length/ wing length 2.17 (1).

Wing length/ length of profemur nil, profemur lost.

Colouration (Figs 11 A & 12 D). Thorax almost completely brown and abdomen brown with dark brown bands. Femur, tibia and tarsi pale yellow.

Head. AR 1.66 (1). Ultimate flagellomere 613 (1) μm long. Temporal setae 10 (1) including 3 inner verticals, 4 outer verticals, and 3 postorbitals. Clypeus with 16 (1) setae. Tentorium 133 (1) μm long, 22 (1) μm wide at sieve pore and 4 (1) μm wide at posterior tentorial pit. Stipes 89 (1) μm long. Palp segment lengths (in μm): 24 (1); 36 (1); 91 (1); 78 (1). Fifth palpal segment lost. Third palpal segment with 3 sensilla clavata.

Thorax. Acrostichals 12; dorsocentrals 11; prealars 4. Scutellum with 4-5 setae.

Wing. VR 1.19-1.27. Brachiolium with 1 seta; R with 17-18; R_1 with 10-12; R_{4+5} 10 (1); M bare. Squama with 5-7 setae.

Legs. Spur on front tibia 47 (1) μm long. Spurs on middle tibia 52 (1) μm long, on hind tibia 53-56 μm long. Comb on middle tibia 22 (1) μm long, long and short comb on hind tibia 13-18 μm and 18-20 μm long respectively. Width at apex of front tibia 44 (1) μm ; of middle tibia 58 (1) μm ; of hind tibia 44-53 μm . Lengths and proportions of legs as in Table 9.

Table 9. Lengths (in μm) and proportions of legs of *Polypedilum (Uresipedilum) praegnans* sp. n.

	fe	ti	ta ₁	ta ₂	ta ₃	ta ₄
P ₁		473 (1)	-	-	-	-
P ₂	148 (1)	623 (1)	399 (1)	196 (1)	146 (1)	93 (1)
P ₃	758-811	659-712	548 (1)	271 (1)	214 (1)	139 (1)

	ta ₅	LR	BV	SV	BR
P ₁	-	-	-	-	-
P ₂	39 (1)	0.64 (1)	3.74 (1)	3.44 (1)	3.8 (1)
P ₃	46 (1)	0.83 (1)	3.02 (1)	2.68 (1)	3.3 (1)

Hypopygium (Figs 22 A-D). Tergite IX with 12 (1) median setae and 16 (1) posterior setae to both sides of anal point. Laterosternite IX with 5 setae. Anal point 64 μm long, 27-40 μm wide at base, gradually tapering to nearly parallel-sided towards apex which is 4 μm wide.

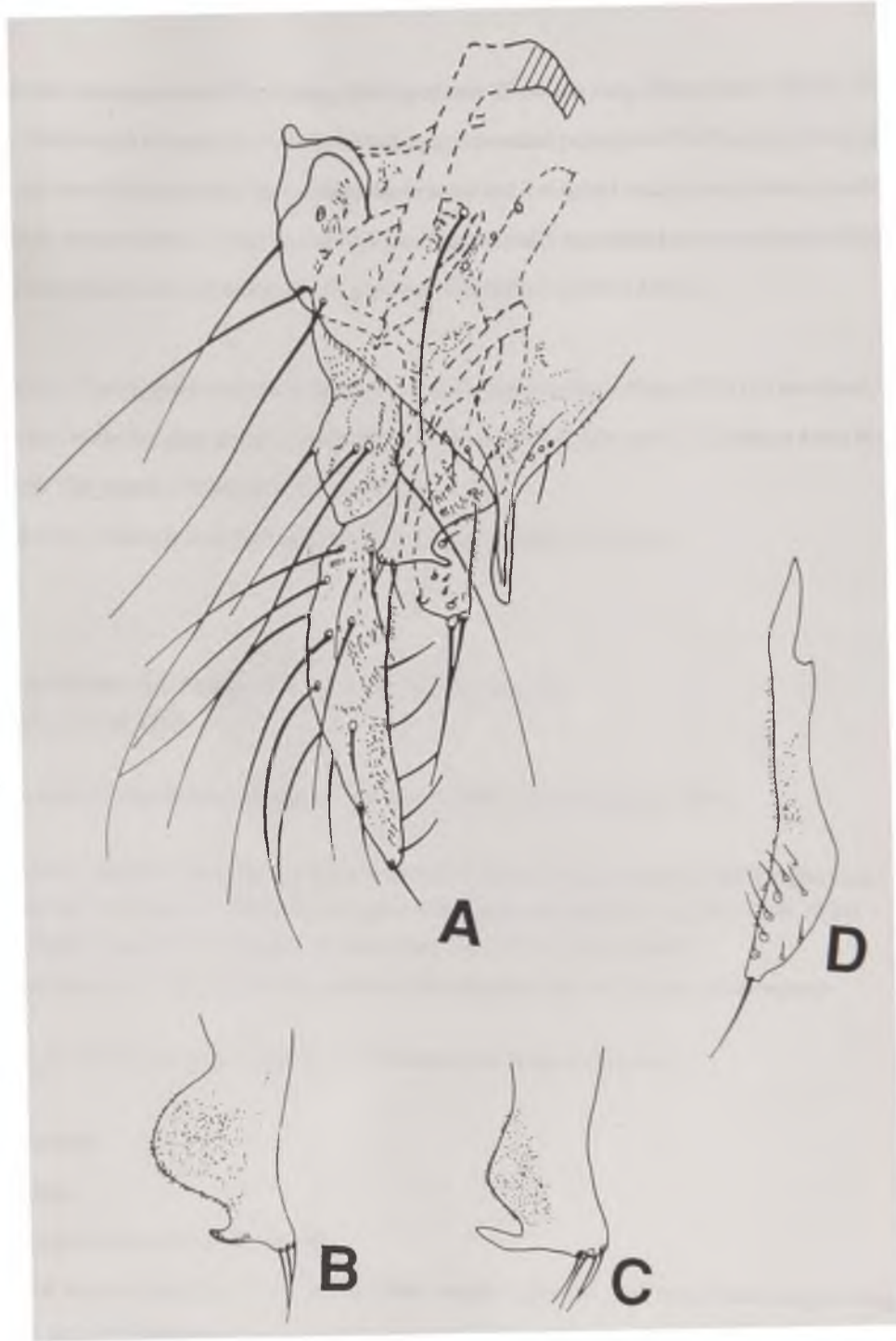


Fig. 22. *P. (U.) praegnans* sp. n. - A. Hypopygium. - B. Superior volsella. - C. Superior volsella variation. - D. Inferior volsella.

Transverse sternapodeme 27 μm long; phallapodeme 75-80 μm long. Gonocoxite 142 (1) μm long. Total length of superior volsella including apicomedial projection 75-95 μm and 9-22 μm long apicomedial projection; base with no inner setae and 3-4 apical seta; microtrichiae present on dorsal surface Inferior volsella 113-124 μm long; laterally broadened subapically and with a prominent apical seta. Gonostylus 173 μm long. HR 0.82 (1); HV 1.85 (1).

Remarks. - The superior volsella of this species has a heel similar to that of *P. (U.) harrisoni*, but differs in the bulging shape of the superior volsella. It is similar to *P. (U.) canum* from New Zealand. The superior volsella lacks inner setae.

Distribution. - Known from Senegal and Democratic Republic of Congo.

***Polypedilum (Uresipedilum) harrisoni* sp. n.**

(Figs 23, 11 D & 12D)

Polypedilum (Polypedilum) annulatum Harrison, 1996: 78 *nec* Freeman, 1954.

Type locality. - GHANA: Greater Accra Region, University of Ghana, Legon, Botanical garden Vaughan pond.

Type material. - Holotype σ^7 , here designated, Legon, Botanical garden Vaughan pond, 3-6. II. 1993, NUFU project (ZMBN Type No 273). Paratypes: SUDAN, Yiroi, 7 $\sigma^7 \sigma^7$, XII. 1954, (BMNH).

Diagnostic characters. - Differs from other members of the subgenus in the heel-like shape of the superior volsella.

Etymology. - The species is named after Dr. A. D. Harrison, Fish Hoek, South Africa.

Description

Male imago

(n= 7, except when otherwise stated).

Total length 2.54-3.32, 3.10 (5) mm. Wing length 1.27-1.52, 1.41 mm. Total length/ wing length 1.85-2.23, 2.09 (5). Wing length/ length of profemur 2.04-2.32, 2.15 (6).

Colouration (Figs 11 D & 12 D). Thorax almost completely brown and abdomen brown with dark brown bands. Femur, tibia and tarsi pale yellow.

Head. AR 1.72-1.82 (3). Ultimate flagellomere 528-635 (3) μm long. Temporal setae 5-9, 7 including 2-3, 2 inner verticals, 3-4, 3 outer verticals, and 1-2, 2 (5) postorbitals. Clypeus with 10-22, 16 setae. Tentorium 91-95, 94 (6) μm long, 18-26, 23 (6) μm wide at sieve pore and 3-7, 5 μm wide at posterior tentorial pit. Stipes 111-144, 124 μm long. Palp segment lengths (in μm): 22-33, 28; 32-44, 38; 71-95, 85; 98-111, 102; 138-167, 149 (5). Fifth palpal segment/ third palpal segment 1.47-1.97, 1.76 (5). Third palpal segment with 2 sensilla clavata.

Thorax. Acrostichals 14-16, 14; dorsocentrals 7-10, 9; prealars 3-5, 4. Scutellum with 4-7, 5 setae.

Wing. VR 1.15-1.25, 1.20. Brachiolium with 1 seta; R with 15-17, 15 (6); R_1 with 7-10, 9 (6); R_{4+5} 9-15, 12 (6); M bare. Squama with 5-9, 6 setae.

Legs. Spur on front tibia 29-44, 36 (6) μm long. Spurs on middle tibia 44-56, 49 (5) μm long, on hind tibia 44-64, 59 μm long. Comb on middle tibia 13-20, 16 (6) μm long, long and short comb on hind tibia 14-24, 19 μm and 9-17 μm long respectively. Width at apex of front tibia 38-42, 44 (6) μm ; of middle tibia 38-56, 46 (6) μm ; of hind tibia 40-56, 50 μm . Lengths and proportions of legs as in Table 10.

Table 10. Lengths (in μm) and proportions of legs of *Polypedilum (Uresipedilum) harrisoni* sp. n.

	fe	ti	ta ₁	ta ₂	ta ₃
P ₁	605-756, 692 (6)	370-477, 430 (6)	730 (1)	452 (1)	320 (1)
P ₂	623-716, 671 (5)	513-609, 578 (6)	292-347 (2)	155-180 (2)	122-132 (2)
P ₃	641-813, 749	406-694, 653	402-559, 485 (3)	214-256, 240 (3)	178-217, 201 (3)

	ta ₄	ta ₅	LR	BV	SV	BR
P ₁	249 (1)	107 (1)	1.86 (1)	1.53 (1)	1.37 (1)	3.8 (1)
P ₂	71-75 (2)	36-43 (2)	0.57-0.59 (2)	3.75-3.82 (2)	3.63-3.89 (2)	3.4-3.6 (2)
P ₃	103-121, 114 (3)	41-57, 51 (3)	0.73-1.01 (3)	2.91-3.11 (3)	2.56-2.92 (3)	4.0-6.1 (2)

Hypopygium (Figs 23 A-E). Tergite IX with 4-6, 5 median setae and 10-14, 13 posterior setae to both sides of anal point. Laterosternite IX with 1-4, 2 (6) setae. Anal point 53-69, 61 μm long, 24-47, 40 μm wide at base, gradually tapering to nearly parallel-sided towards apex

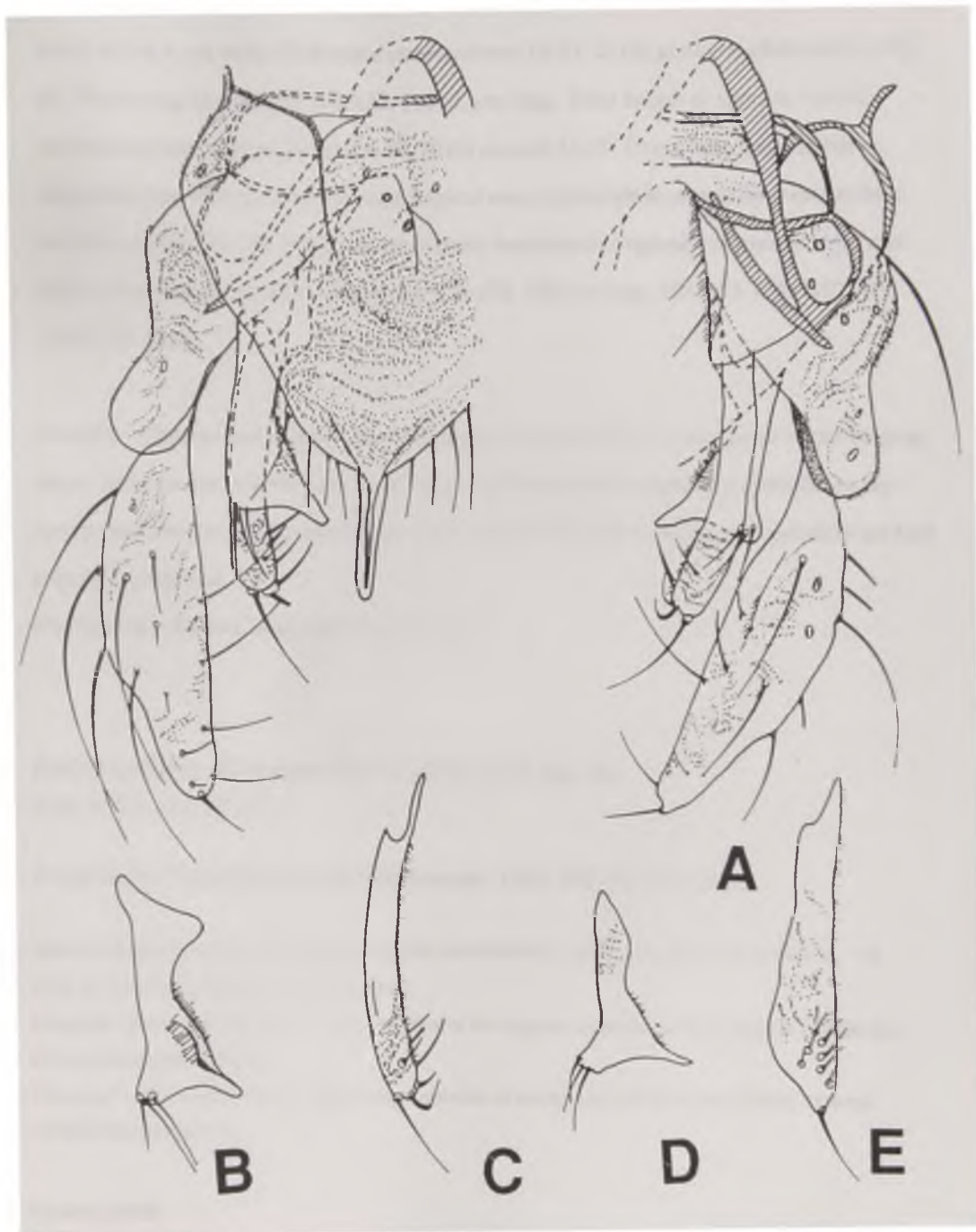


Fig. 23. *P. (U.) harrisoni* sp. n. - A. Hypopygium. - B. Superior volsella. - C. Inferior volsella. - D & E. Variation of volsellae.

which is 2-4, 4 μm wide. Transverse sternapodeme 16-27, 23 (6) μm long; phallapodeme 60-82, 70 μm long. Gonocoxite 122-153, 142 (2) μm long. Total length of superior volsella including apicomedial projection 64-78, 70 (6) μm and 11-20, 15 μm long apicomedial projection; base with no inner setae and 3 apical seta; microtrichiae present on dorsal surface. Inferior volsella 100-129, 118 μm long; laterally broadened subapically or parallel sided and with a prominent apical seta. Gonostylus 124-175, 158 μm long. HR 0.75-1.00, 0.92; HV 1.91-2.18, 2.03.

Remarks. - The superior volsella has a heel similar to that of *P. (U.) praegnans* but no bulging shape. The superior volsella bears no inner setae. The species is regarded as identical to the species described as *P. (P.) annulatum* by Harrison (1996), but in the present specimen the heel is more pronounced.

Distribution. - Known from Ghana and Sudan.

***Polypedilum (Uresipedilum) freemani* sp. n.**

(Figs 24-25, 11 C & 12 C)

Polypedilum (Polypedilum) ephippium Freeman, 1958: 292-294, *pro parte*.

Material examined. - Holotype ♂, here designated, misidentified *P. ephippium*. SUDAN: Mvolo, VI.-VII. 1954, E. T. M. Reid (BMNH, B. M. 1954-603).

Diagnostic characters. - Differs from other members of the subgenus in the shape of the superior volsella and abdominal colouration pattern.

Etymology. - Named after Paul Freeman, keeper emeritus of entomology at The Natural History Museum (British Museum), London.

Description

Male imago

(n= 1).

Total length not measurable (abdomen broken and incomplete). Wing length 1.4 mm. Wing length/ length of profemur 1.98.

Colouration (Figs 11 C & 12 C). Thorax almost completely dark brown and abdomen with segments I, II and IV pale, segments III and V partly dark brown. Legs yellowish brown or bright yellow, except for about one third of foreleg femur, ta_5 of mid and hindleg which are brown.

Head (Fig. 24 A). AR 1.91. Ultimate flagellomere 639 μ m long. Temporal setae 7 including 2 inner verticals, 4 outer verticals, and 1 postorbitals. Clypeus with 16 setae. Tentorium 109 μ m long, 18 μ m wide at sieve pore and 2 μ m wide at posterior tentorial pit. Stipes 118 μ m long. Palp segment lengths (in μ m): 23; 36; 83; 98; 160. Fifth palpal segment/ third palpal segment 1.92. Third palpal segment with 2 sensilla clavata.

Thorax (Fig. 24 B). Acrostichals 10; dorsocentrals 7; prealars 3. Scutellum with 4 setae.

Wing (Fig. 24 C). VR 1.14. Brachiolum with 1 seta; R with 12; R_1 with 7; R_{4+5} ; M bare. Squama with 4 setae.

Legs (Figs 24 D-F). Spur on front tibia 37 μ m long. Spurs on middle tibia 39 μ m long, on hind tibia 47 μ m long. Comb on middle tibia 12 μ m long, long and short comb on hind tibia 16 μ m and 14 μ m long respectively. Width at apex of front tibia 42 μ m; of middle tibia 40 μ m; of hind tibia 46 μ m. Lengths and proportions of legs as in Table 11.

Table 11. Lengths (in μ m) and proportions of legs of *Polypedilum (Uresipedilum) freemani* sp. n.

	fe	ti	ta1	ta2	ta3
P ₁	723	441	-	-	-
P ₂	708	609	363	182	128
P ₃	751	680	513	256	214

	ta4	ta5	LR	BV	SV	BR
P ₁	-	-	-	-	-	
P ₂	93	45	0.60	3.44	3.63	
P ₃	123	57	0.75	3.00	2.79	

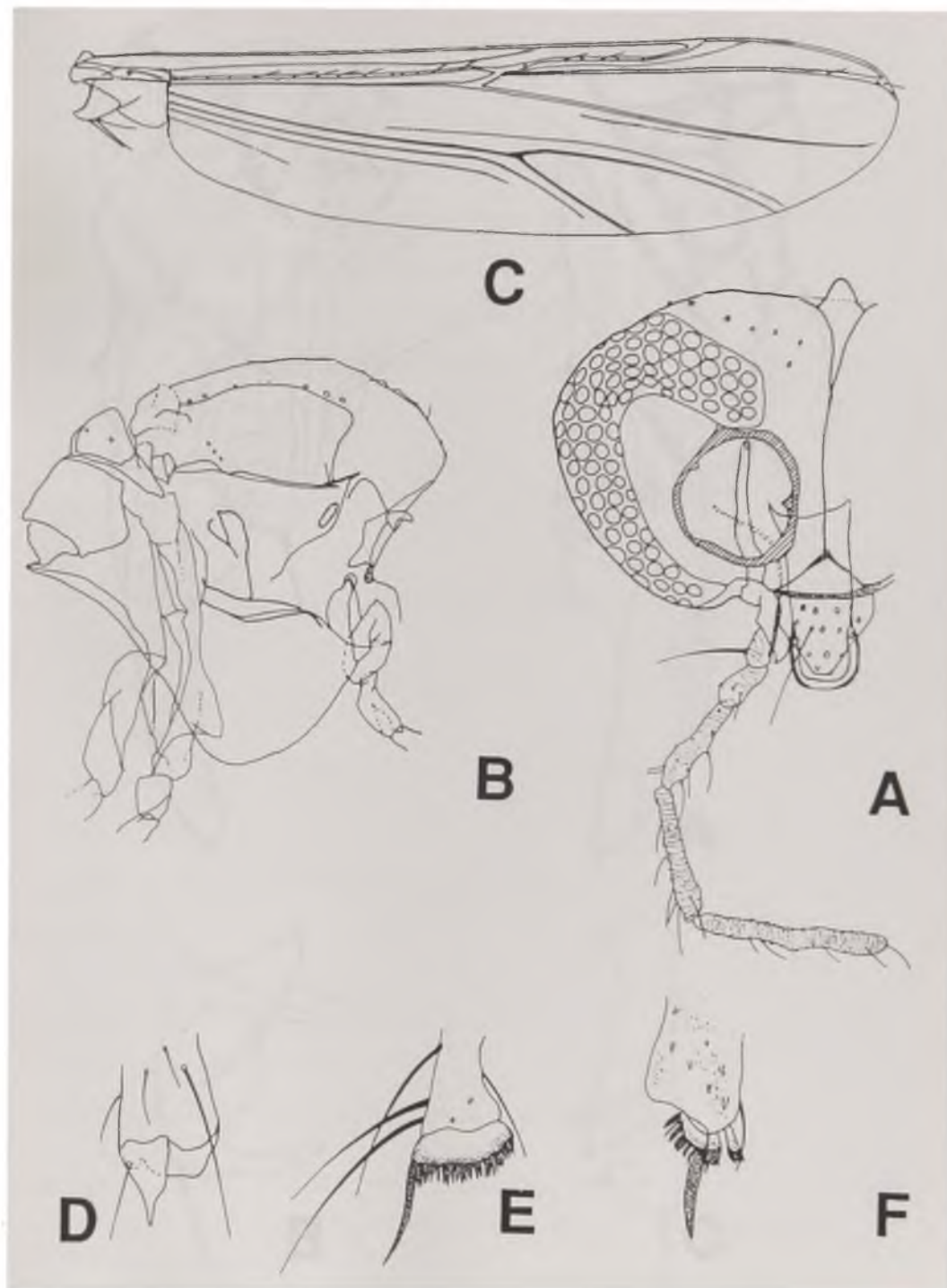


Fig. 24. *P. (U.) freemani* sp. n. - A. Head. - B. Thorax. - C. Wing. - D. Fore tibia. - E. Mid tibia. - F. Hind tibia.

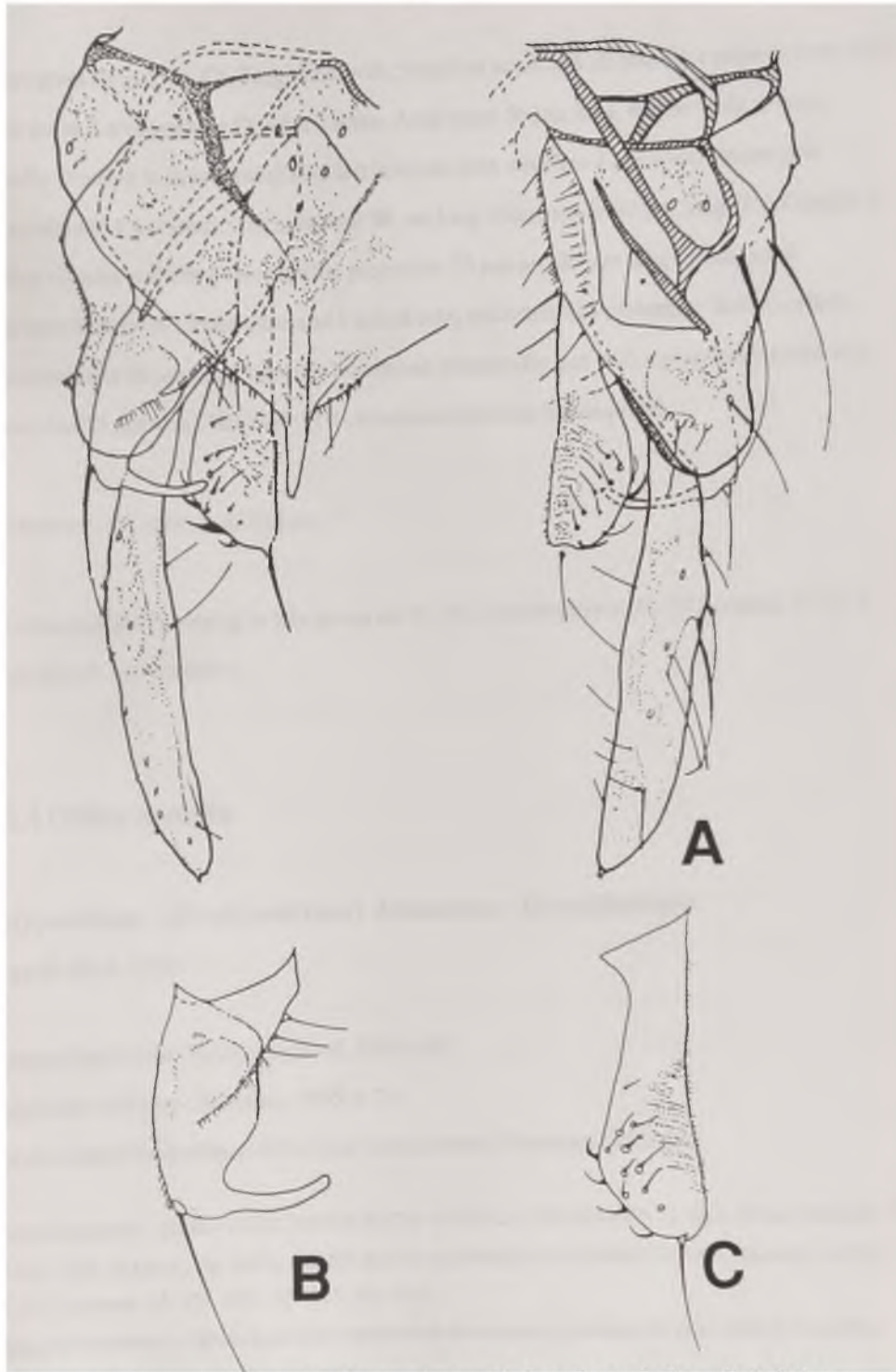


Fig. 25. *P. (U.) freemani* sp. n. - A. Hypopygium. - B. Superior volsella. - C. Inferior volsella.

Hypopygium (Figs 25 A-C). Tergite IX with 5 median setae and 10 posterior setae to both sides of anal point. Laterosternite IX with 2 setae. Anal point 56 μm long, 62 μm wide at base, gradually tapering to nearly parallel-sided towards apex which is 4 μm wide. Transverse sternapodeme 11 μm long; phallapodeme 56 μm long. Gonocoxite 60 μm long. Total length of superior volsella including apicomedial projection 53 μm and 33 μm long apicomedial projection; base with 3 inner setae and 1 apical seta; microtrichiae present on dorsal surface. Inferior volsella 88 μm long; laterally broadened subapically and with a prominent apical seta. Gonostylus 75 μm long. HR 0.80; HV - (abdomen broken/ incomplete).

Distribution. - Known from Sudan.

The other species belonging to this group are *P. (U.) oresitrophum*, *P. (U.) canum*, *P. (U.) harrisi* and *P. (U.) cumberi*.

5.8.4 Other species

***Polypedilum (Uresipedilum) kibatiense* Goetghebuer**

(Figs 26-28 & 11 H)

Polypedilum kibatiense Goetghebuer, 1936: 487.

Polypedilum stilatum Freeman, 1955 a: 29.

Polypedilum (Polypedilum) kibatiense Goetghebuer; Freeman, 1958: 294.

Material examined. - ZAIRE (NOW DEMOCRATIC REPUBLIC OF CONGO): N. Kivu, Kibati, holotype ♂ XI-XII. 1933, (KMMA, No. 3082). DEMOCRATIC REPUBLIC OF CONGO: N. Kivu, Rutshuru, holotype ♂ of *P. stilatum*, 25. XII. 1933, (KMMA, No. 132).

Diagnostic characters. - Differs from other members of the subgenus by having the inner setae of the superior volsella placed on the apicomedial projection.

Etymology. - Named after Kibati, and the Latin suffix *-ense*, denoting place, locality.

Description**Male imago**

(n= 2, except when stated otherwise).

Total length not measurable (abdomen incomplete). Wing length 1.50-1.90 mm. Wing length/ length of profemur 2.28-2.31.

Colouration (Fig. 11 H). Thorax dark brown around anteprenotum, postnotum and scutellum; abdomen lost. Femur, tibia and tarsi pale.

Head (Figs 26 A). AR 1.41 (1). Ultimate flagellomere 620 (1) μm long. Temporal setae 7-8 including 2-4 inner verticals, 3 outer verticals, and 1-2 postorbitals. Clypeus with 9-11 setae. Tentorium 118-127 μm long, 24-33 μm wide at sieve pore and 2 (1) μm wide at posterior tentorial pit. Stipes 133-135 μm long. Palp segment lengths (in μm): 29-33; 31-36; 128; 80; 151. Fifth palpal segment/ third palpal segment 1.18 (1). Third palpal segment with 3 sensilla clavata.

Thorax (Fig. 26 B). Acrostichals 16-18; dorsocentrals 13-15; prealars 4-5. Scutellum with 8 setae.

Wing (Fig. 26 C). VR 1.24-1.27. Brachiolum with 1 seta; R with 16-21; R_1 with 8-9; R_{4+5} 23-29; M bare. Squama with 2-7 setae.

Legs (Figs 26 F-D). Spurs on front tibia 33-40 μm long. Spur on middle tibia 62 (1) μm long on hind tibia 64-68 μm long. Comb on middle tibia 20 (1) μm long, long and short comb on hind tibia 20-27 μm and 18-24 μm long respectively. Width at apex of front tibia 33-46 μm ; of middle tibia 44 (1) μm ; of hind tibia 31-52 μm . Lengths and proportions of legs as in Table 12.

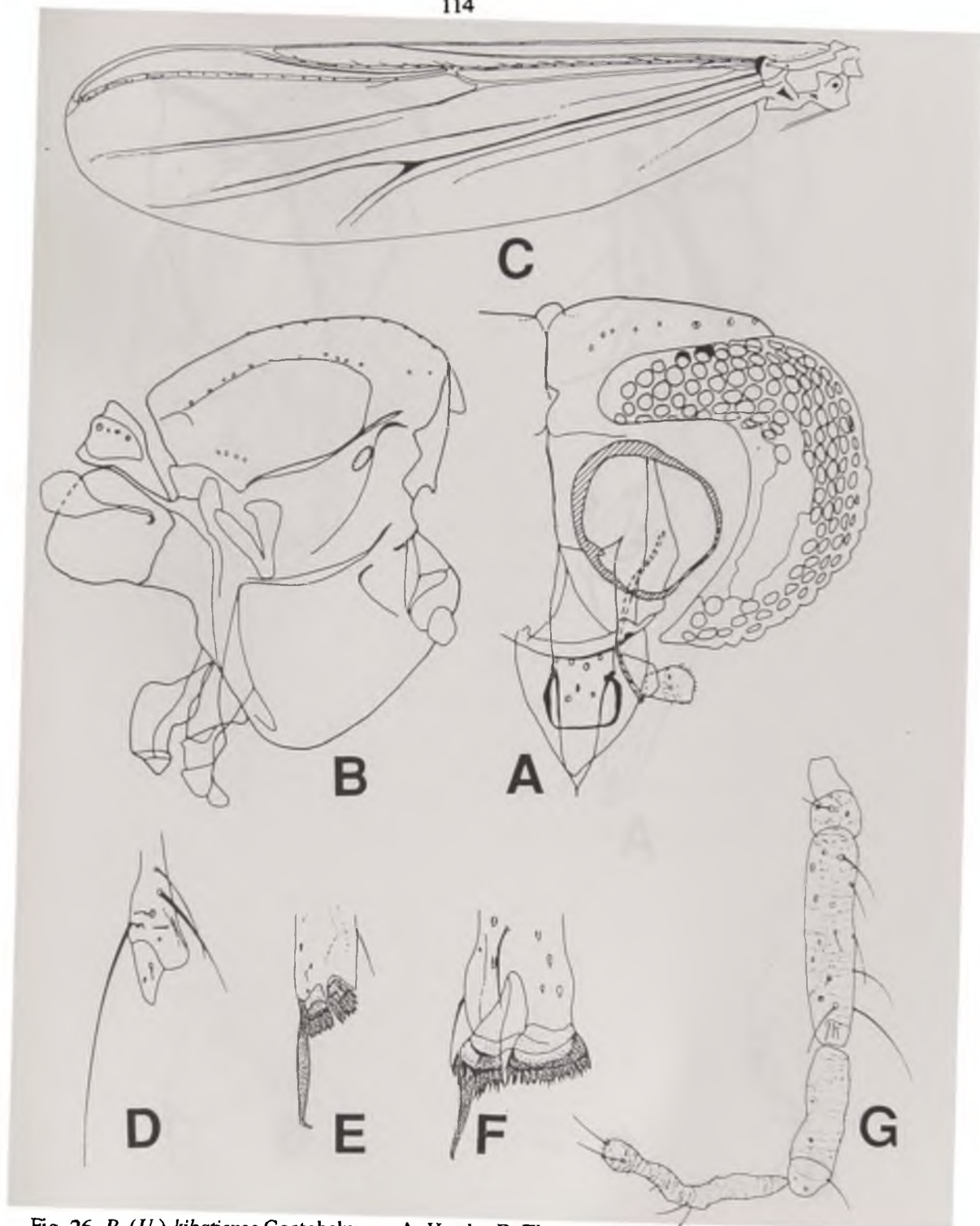


Fig. 26. *P. (U.) kibatiense* Goetghebuer. - A. Head. - B. Thorax. - C. Wing. - D. Fore tibia. - E. Mid tibia. - F. Hind tibia. - G. Palp.

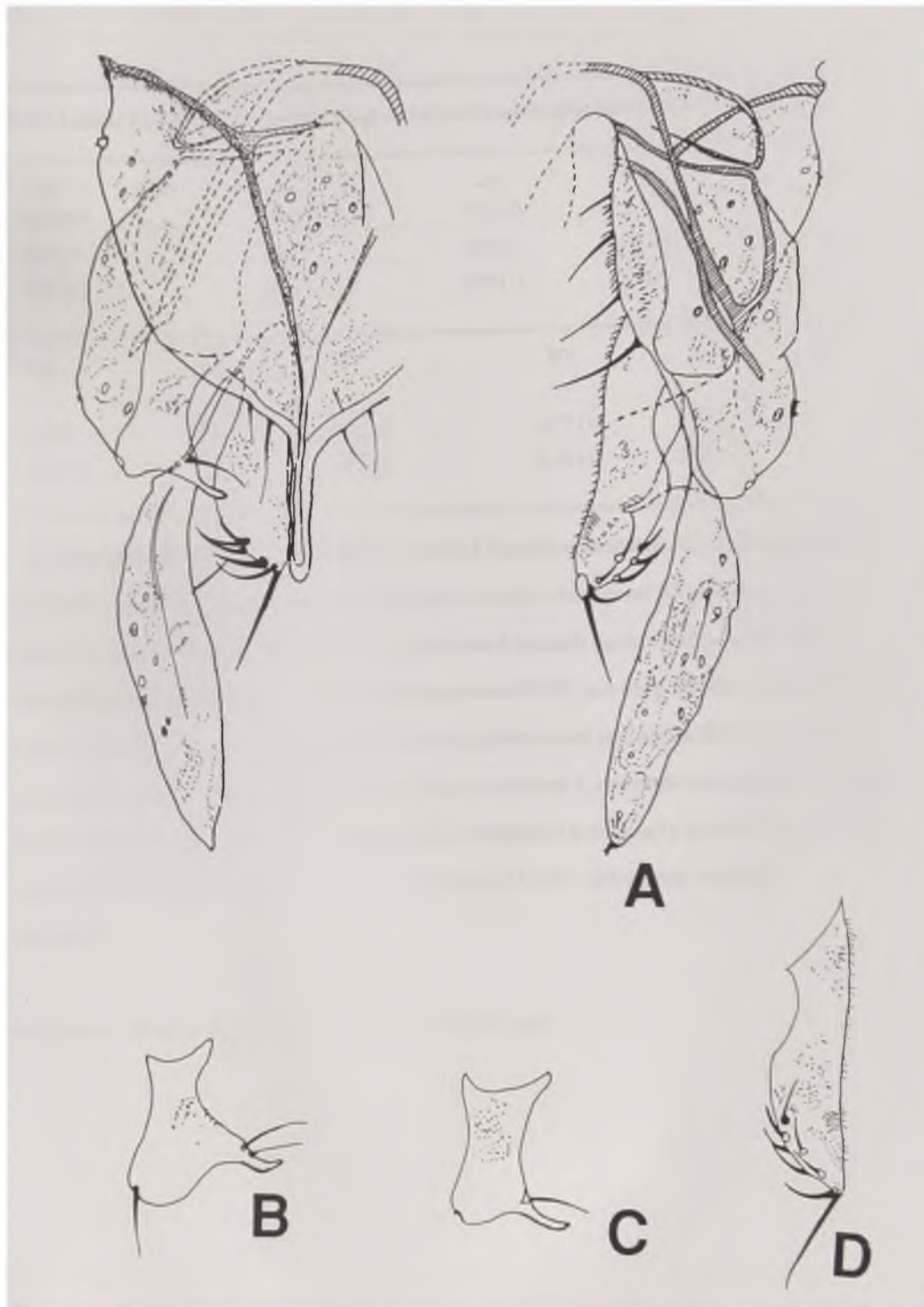


Fig. 27. *P. (U.) kibatiense* Goetghebuer. - A. Hypopygium. - B & C. Superior volsellae. D. Inferior volsella.

Table 12. Lengths (in μm) and proportions of legs of *Polypedilum* (*Uresipedilum*) *kibatiense* Goetghebuer

	fe	ti	ta1	ta2	ta3
p ₁	662-833	401-534	972 (1)	-	-
p ₂	854 (1)	65 (1)	424 (1)	196 (1)	112 (1)
p ₃	662-911	513-765	584 (1)	302 (1)	217 (1)

	ta4	ta5	LR	BV	SV	BR
p ₁			-	-	-	-
p ₂	66 (1)	32 (1)	0.64 (1)	4.77 (1)	3.57 (1)	-
p ₃	110 (1)	71 (1)	0.76 (1)	3.22 (1)	2.87 (1)	-

Hypopygium (Figs 27 A-D). Tergite IX with 5-13 median setae and 10 (1) posterior setae to both sides of anal point. Laterosternite IX with 3-4 setae. Anal point 67 μm long, 58 μm wide at base, gradually tapering to nearly parallel-sided towards apex which is 4 μm wide. Transverse stemapodeme 29-31 μm long; phallapodeme 80-87 μm long. Gonocoxite 124-152 μm long. Total length of superior volsella including apicomedial projection 58-71 μm and 27 μm long apicomedial projection; base with 1-2 inner setae and 1; microtrichiae present on dorsal surface. Inferior volsella 97-107 μm long; laterally broadened subapically and with a prominent apical seta. Gonostylus 133-149 μm long. HR 0.93-1.02; HV - (abdomen broken or incomplete).

Distribution. - Known from Democratic Republic of Congo.

***Polypedilum (Uresipedilum) dosse nudum* sp. n.**

(Figs 28-30, 11 A & B, 12 E)

Type locality. - GHANA: Eastern Region, Boti Falls.

Type material. - Holotype ♂, reared from larva, here designated, GHANA: Eastern Region, Boti Falls, 14. X. 1994, NUFU project (ZMBN Type No. 274). Paratypes: UGANDA: L. Victoria, 1 ♂, 1950-52, W. W. Macdonald (BMNH, B. M. 1953-560); ZAIRE (NOW DEMOCRATIC REPUBLIC OF CONGO): Lualaba, 1 ♂, 25. I. 1939, H. J. Bredo (BMNH, Belg. I. G. 12.290); GHANA: Eastern Region, Subri River, 1 ♂, 4. II. 1993, Light trap, NUFU project (ZMBN, No. 66); Greater Accra Region, Legon Botanical garden, Vaughan pond, 1 ♂, 2. XI. 1994, NUFU project (ZMBN, No. 161); Western Region, Ankasa Game Production Reserve, 3 ♂♂, 6-12. XII. 1993, Malaise trap Nos. 1&12, NUFU project (ZMBN, Nos. 84, 86, 983); CONGO: Brazzaville, 5 ♂♂, 3. V. 1957, Hamon, (BMNH, A. E. F).

Diagnostic characters. - Differs from other members of the subgenus in having the apicomedial projection with upcurved tip and appearing as separated or attached subterminally to the base. It is the only species having the apices of the segments dark.

Etymology. -From Latin, *dosse nus*, clown, jester, and, *udo*, sock, shoe, referring to the shape of the superior volsella.

Description**Male imago**

(n= 10, except when otherwise stated).

Total length 2.41-3.52, 2.72 (9) mm. Wing length 1.28-1.69, 1.43 mm. Total length/ wing length 1.77-2.26, 1.93. Wing length/ length of profemur 1.14-2.04, 1.84 (9).

Colouration (Fig. 11 A & B, 12 E). Thorax yellowish brown at postnotum and antepronotum or almost completely brown. Abdomen with pale yellow segments, dark apices. Femur, tibia and tarsi yellow.

Head (Fig. 28 A). AR 1.40-1.80, 1.60 (9). Ultimate flagellomere 547-710, 603 (9) μ m long. Temporal setae 7-15 (9) including 3-5, 4 inner verticals, 2-7, 4 outer verticals, and 1-4, 2 postorbitals. Clypeus with 13-21, 18 setae. Tentorium 98-167, 129 μ m long, 26-34, 29 μ m wide at sieve pore and 2-9, 6 μ m wide at posterior tentorial pit. Stipes 120-168, 147 μ m long. Palp segment lengths (in μ m): 22-47, 31; 29-53, 40; 42-120, 85; 87-123, 100; 95-200, 157.

Fifth palpal segment/ third palpal segment 1.44-2.26, 1.93 (7). Third palpal segment with 2 sensilla clavata.

Thorax (Fig. 28 B). Acrostichals 14-20, 17; dorsocentrals 12-18, 14; prealars 4-6, 5.

Scutellum with 7-10, 8 setae.

Wing (Fig. 28 C). VR 1.11-1.24, 1.17. Brachiolium with 1 seta; R with 15-24, 18; R₁ with 10-15, 12; R₄₊₅ 14-23, 17; M bare. Squama with 6-11, 9 setae.

Legs (Figs 28 D - F). Spur on front tibia 20-44, 27 (6) μm long. Spurs on middle tibia 55-109, 74 (9) μm long, on hind tibia 47-80, 60 μm long. Comb on middle tibia 11-22, 18 (9) μm long, long and short comb on hind tibia 22-31, 27 μm and 13-29, 22 μm long respectively.

Width at apex of front tibia 42-53, 46 (9) μm ; of middle tibia 42-48, 45 (9) μm ; of hind tibia 40-60, 50 (9) μm . Lengths and proportions of legs as in Table 13.

Table 13. Lengths (in μm) and proportions of legs of *Polypedilum (Uresipedilum) dossenudum* sp. n.

	fe	ti	ta ₁	ta ₂
P ₁	649-840, 753 (9)	331-506, 418 (9)	776-947, 886 (6)	534-735, 624 (6)
P ₂	694-894, 775 (9)	520-687, 606 (9)	285-381, 328 (9)	192-231, 204 (9)
P ₃	708-947, 812	530-822, 692	402-587, 486	139-320, 267
	ta ₃	ta ₄	ta ₅	LR
P ₁	384-443, 409 (6)	274-320, 304 (6)	103-142, 122 (6)	2.10-2.34, 2.23 (6)
P ₂	128-167, 142 (9)	71-117, 88 (9)	32-46, 37 (9)	0.50-0.58, 0.54 (9)
P ₃	199-295, 239	117-196, 148	43-75, 59	0.66-0.76, 0.71
	BV	SV	BR	
P ₁	1.29-1.45, 1.40 (6)	1.25-1.34, 1.29 (6)	1.0-2.9, 2.3 (6)	
P ₂	3.26-3.91, 3.56 (9)	3.94-4.67, 4.26 (9)	2.2-11.8, 5.3 (7)	
P ₃	2.58-3.26, 2.80	3.01-3.21, 3.10	2.9-7.6, 5.0 (8)	

Hypopygium (Figs 29 A-H). Tergite IX with 8-18, 12 (8) median setae and 10-18, 15 (8) posterior setae to both sides of anal point. Laterosternite IX with 2-5, 3 setae. Anal point 53-90, 73 (8) μm long, 34-69, 51(8) μm wide at base, gradually tapering to nearly parallel-sided towards apex which is 2-7 (9) μm wide. Transverse sternapodeme 16-44, 25 (9) μm long;

phallapodeme 56-104, 80 μm long. Gonocoxite 122-169 μm long. Total length of superior volsella including apicomedial projection 58-78, 66 μm and 24-36, 32 μm long apicomedial projection; base with 2-3 inner setae and 1 apical seta; microtrichiae present on dorsal surface. Inferior volsella 102-122, 112 (9) μm long, parallel sided and with a prominent apical seta. Gonostylus 142-189, 149 (9) μm long. HR 0.86-1.12, 0.95 (9); HV 1.63-2.16, 1.86 (9).

Pupa

(n= 1).

Total length about 3.8 mm. Exuviae with brown cephalothorax with margins of wing sheath golden brown, and mesal paratergital margins of segments VI-VIII and caudolateral spur brown.

Cephalothorax. Cephalic tubercles barely indicated. Frontal setae 56 μm long (Fig. 30 B). Prealar tubercle apparently absent.

Abdomen (Figs 30 A-C). Tergite I bare; tergites II-VI each with strong anterior band of spinules and strong median and posterior shagreen; tergites VII and VIII each with two anteriomedian spots of shagreen; tergite IX bare. Sternites bare. Tergite II with 46 caudal hooklets. Conjunctive III/IV with 46 uniserial, mostly anteriorly directed, hook-like spines; conjunctive IV/V with 63 uni-biserial similar spines. Pedes spurii A well developed on segment IV. Pedes spurii B well developed on I and II. Anal spur with strong apical tooth, 1 strong lateral tooth, and 1-3 minute lateral teeth.

Abdominal setation: Segment I without setae; II-IV with 3 setae, none taeniate; V and VI each with 3 taeniae; VII and VIII each with 4 taeniae. Fringe of anal lobe with 29 taeniae, no dorsal seta.

Larva

(n= 1).

Total length about 4.7 mm. Head capsule 0.99 mm long. Postmentum 188 μm long. Head capsule yellowish brown with postoccipital margin, teeth of mentum and mandible brownish black.

Head. Basal antennal segments 62 μm long, second segment 21 μm long, remaining segments lost. Basal antennal segment 15 μm wide, ring organ 9 μm from base, mark of seta 45 μm from base. Pecten epipharyngis consisting of 3 platelets, each with 3 subequal teeth. Premandible 81 μm long. Mandible (Fig. 30 E) 126 μm long with apical tooth, 3 inner teeth, and dorsal tooth; seta subdentalis well developed; seta interna with about 10 branches. Mentum (Fig. 30 D) 95 μm wide, with 8 pairs of mental teeth. Four median teeth, 2 inner median teeth each 11.5 μm wide and 2 outer median teeth (otherwise referred to as first lateral teeth), much lower and smaller than inner median and first pair of lateral teeth (second pair of lateral teeth); 6 pairs of lateral teeth, with a much lower second and minute sixth. Ventromental plate 83 μm wide, 41 μm high, distance between plate 49 μm ; with 26 striae; median apices of plates upturned joining outer margins of median teeth.

Abdomen. Procercus 7 μm high, 7 μm wide; with about 10 anal setae, 539 μm long. Supraanal seta 387 μm long, 0.72 times as long as anal setae. Posterior parapods each with 14 claws. Anal tubules about 143 μm long.

Remarks. - There are individual variation in the shape of the superior volsella within the species.

Ecology and distribution. - The species is known from smaller rivers and ponds in southern Ghana. It is also known from Uganda, Democratic Republic of Congo and Congo.

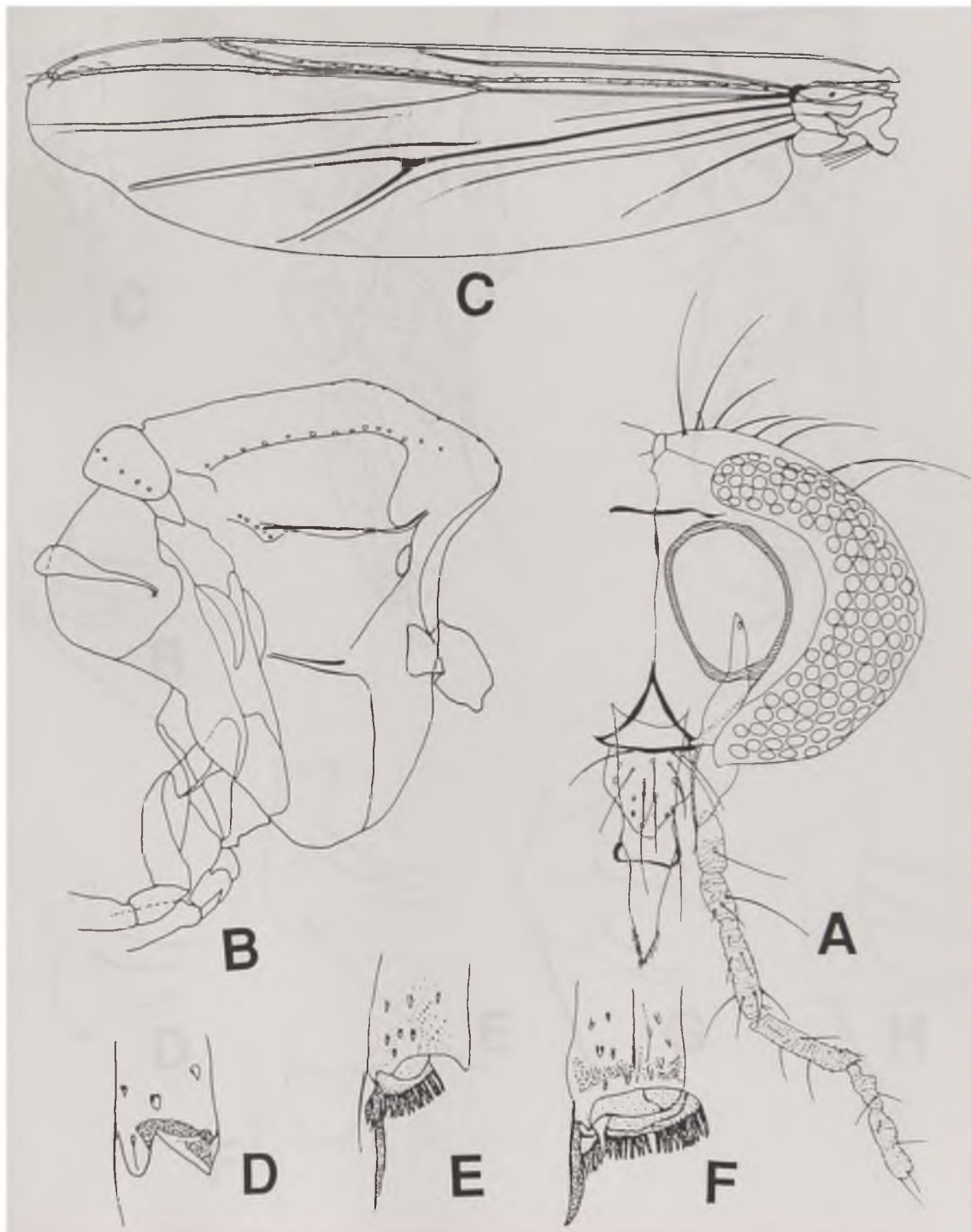


Fig. 28. *P. (U.) dossenudum* sp. n. - A. Head. - B. Thorax. - C. Wing. - D. Fore tibia. E. Mid tibia. - F. Hind tibia.

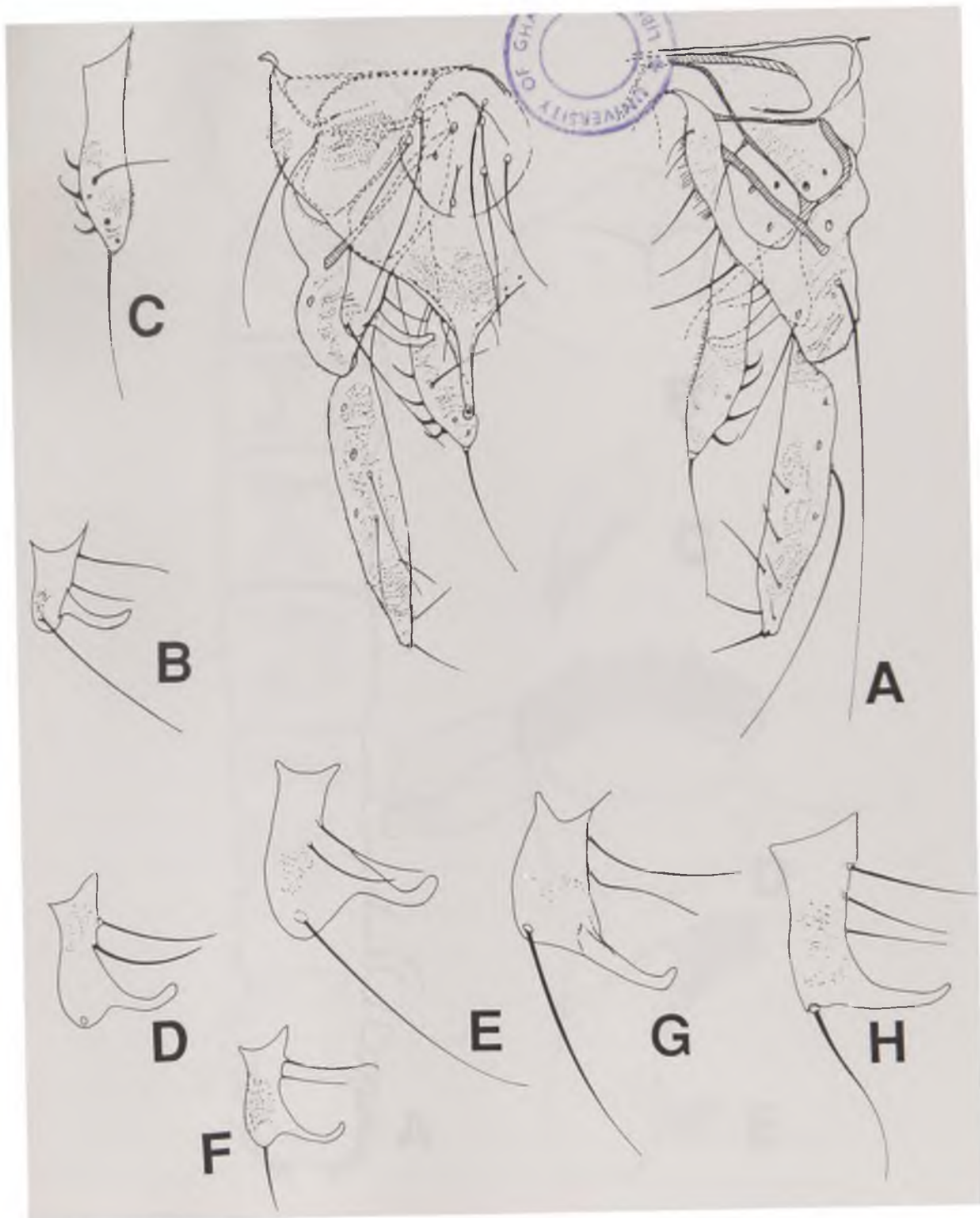


Fig. 29, *P. (U.) dossevadum* sp. n. - A. Hypopygium. - B. Superior volsella. - C Inferior volsella. - D-H. Superior volsellae variation.

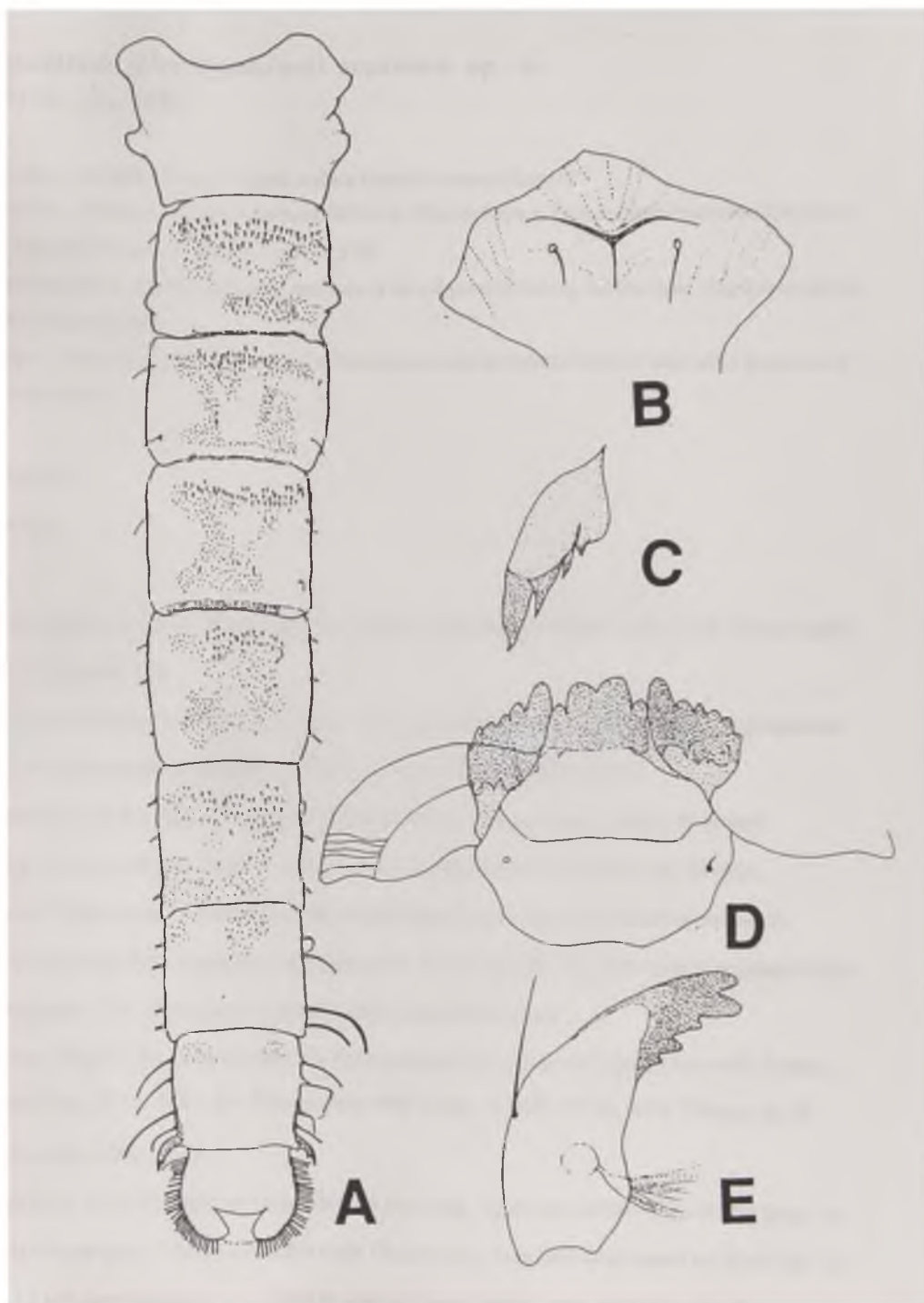


Fig. 30. *P(U.) dossenudum* sp. n. - A-C. Pupa. - A. Abdomen. - B. Cephalic area. - C. Anal spur. - D-E. Larva. - D. Mentum.

***Polypedilum (Uresipedilum) acutulum* sp. n.**

(Figs 31-32, 11G, 12 F)

Type locality. - GHANA: Western Region, Ankasa Game Production Reserve.*Type material.* - Holotype ♂, here designated, GHANA: Western Region, Ankasa Game Production Reserve, 6-12. XII. 1993, NUFU project (ZMBN Type No. 275).*Diagnostic characters.* - Differs from other members of the subgenus in having AR less than 1; median projection of superior volsella pointed.*Etymology.* - From Latin *acutulum*, referring to the tiny structure and pointed nature of the medial projection of the superior volsella.**Description****Male imago**

(n= 1).

Total length 1.92 mm. Wing length 1.13 mm. Total length/ wing length 1.70. Wing length/ length of profemur 2.33.

Colouration (Figs 11G & 12 F). Thorax with 3 brown spots on postnotum, anteprepronotum and part of preepisternum; abdomen yellow. Femur, tibia and tarsi yellow.

Head (Fig. 31 A). AR 0.74. Ultimate flagellomere 273 μ m long. Temporal setae 6 including 2 inner verticals, 2 outer verticals, and 2 postorbitals. Clypeus with 10 setae. Tentorium 73 μ m long, 10 μ m wide at sieve pore and 4 μ m wide at posterior tentorial pit. Stipes 69 μ m long. Palp segment lengths (in μ m): 16; 27; 42; 60; 73. Fifth palpal segment/ third palpal segment 1.74. Third palpal segment with 3 sensilla clavata.

Thorax (Fig. 31 B). Acrostichals 16; dorsocentrals 10; prealars 3. Scutellum with 3 setae.

Wing (Fig. 31 C). VR 1.24. Brachiolium with 1 seta; R with 17; R₁ with 7; R₄₊₅ 18; M with 2. Squama with 9 setae.

Legs (Fig. 31 D-F). Spur on front tibia 24 μ m long. Spurs on middle tibia 44 μ m long, on hind tibia 44 μ m long. Comb on middle tibia 13 μ m long, long and short comb on hind tibia 16 μ m and 11 μ m long respectively. Width at apex of front tibia 31 μ m; of middle tibia 31 μ m; of hind tibia 24 μ m. Lengths and proportions of legs as in Table 14.

Table 14. Lengths (in μm) and proportions of legs of *Polypedilum (Uresipedilum) acutulum* sp. n.

	fe	ti	ta ₁	ta ₂	ta ₃
p ₁	495	245	644	395	263
p ₂	516	381	239	103	64
p ₃	570	495	331	173	141

	ta ₄	ta ₅	LR	BV	SV	BR
p ₁	171	75	2.60	1.54	1.15	5.0
p ₂	36	30	0.63	4.87	3.76	5.4
p ₃	68	36	0.72	3.26	3.11	5.4

Hypopygium (Figs 32 A-C). Tergite IX with 5 median setae and 8 posterior setae to both sides of anal point. Laterosternite IX with 2 setae. Anal point 44 μm long, 33 μm wide at base, gradually tapering to nearly parallel-sided towards apex which is 2 μm wide. Transverse sternapodeme 20 μm long; phallapodeme 63 μm long. Gonocoxite 89 μm long. Total length of superior volsella including apicomedial projection 30 μm and 13 μm long apicomedial projection; base with 2 inner setae and 1 apical seta; microtrichiae present on dorsal surface. Inferior volsella 87 μm long; parallel sided and with a prominent apical seta. Gonostylus 104 μm long. HR 0.85; HV 1.86.

Remarks. - This species is similar to *P. (U.) gladyssae* but differ in the pointed end of the medial projection and the bulbous heel of the superior volsella.

Distribution. - Known only from rivers in the Ankasa Game Production Reserve, Ghana.

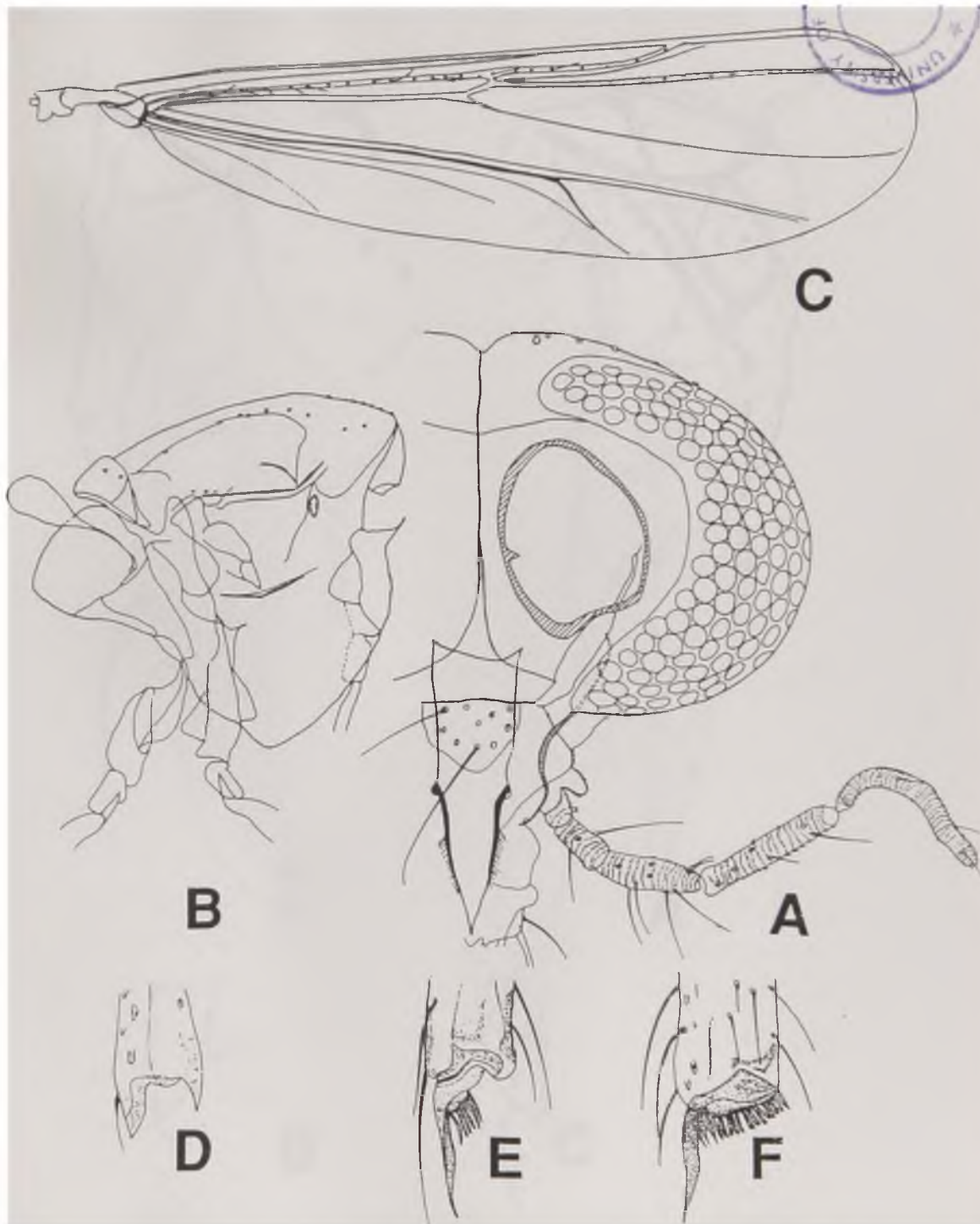


Fig. 31. *P (U.) acutulum* sp. n. - A. Head. - B. Thorax. - C. Wing. - D. Fore tibia. - E. Mid tibia. - F. Hind tibia.

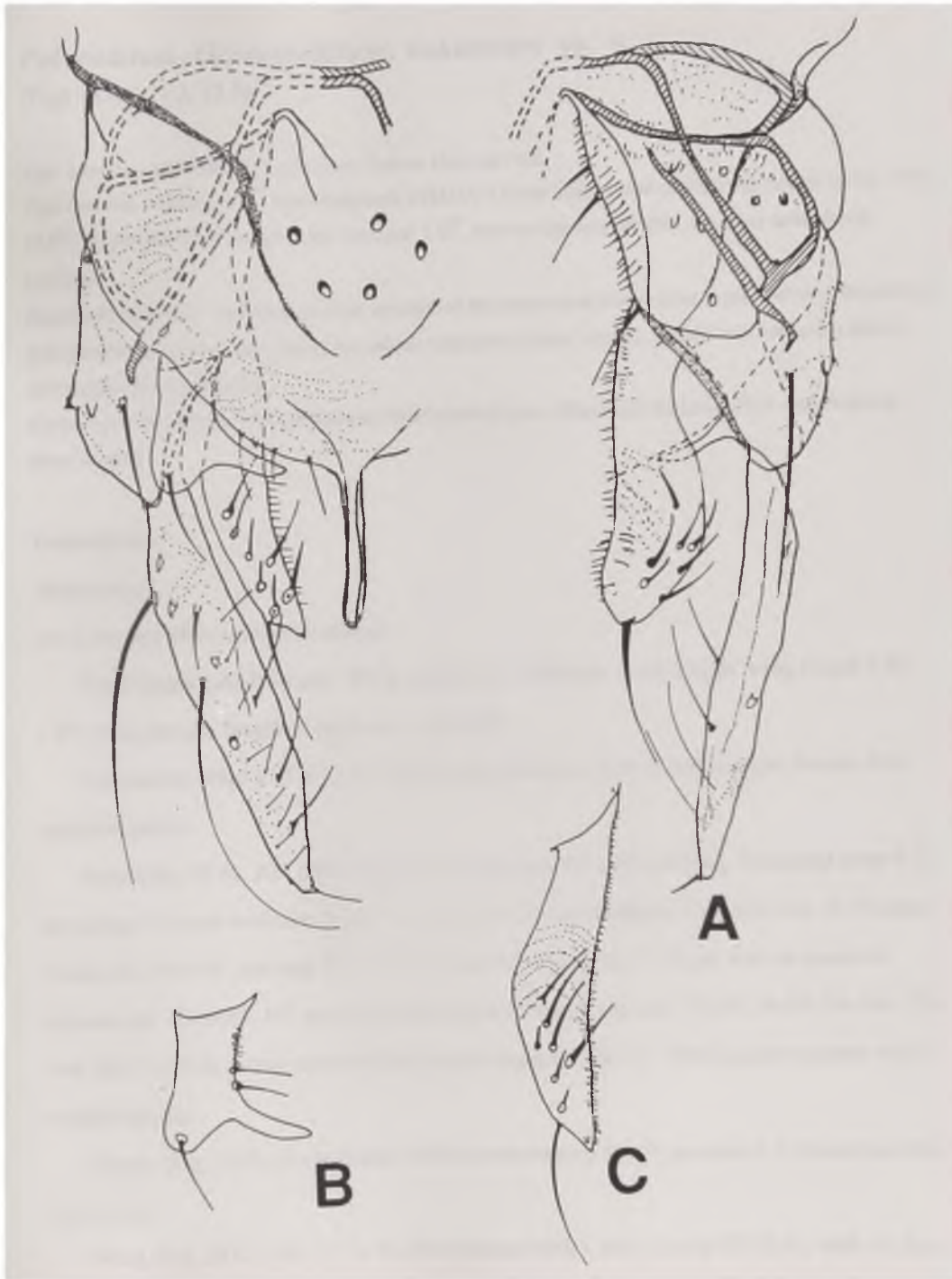


Fig. 32. *P. (U.) acutulum* sp. n. - A. Hypopygium. - B. Superior volsella. - C. Inferior volsella.

***Polypedilum (Uresipedilum) kakumense* sp. n.**

(Figs 33-34, 11 J, 12 F)

Type locality. - GHANA: Central Region, Kakum National Park.

Type material. - Holotype ♂, here designated, GHANA: Central Region, Kakum National Park, 8-18. XI. 1994, NUFU project (ZMBN Type No. 276). Paratype: 1 ♂, same as holotype (BMNH, No. 631) same data as holotype.

Diagnostic characters. - Differs from other members of the subgenus in having clear to pale yellow colouration of both the abdomen and thorax. Among the species with bare superior volsella, it is the only one with a slender and straight medial projection.

Etyymology. - Named after Kakum National Park Central Region, Ghana, and the Latin suffix *-ense* denoting place, locality.

Description**Male imago**

(n= 2, except when otherwise stated).

Total length 2.62-2.96 mm. Wing length 1.33-1.60 mm. Total length/ wing length 1.84-1.97. Wing length/ length of profemur 1.82-2.03.

Colouration (Figs 11 J & 12 F). Thorax and abdomen clear or pale yellow. Femur, tibia and tarsi yellow.

Head (Fig. 33 A). AR 1.66. Ultimate flagellomere 591-650 μm long. Temporal setae 9-12 including 2-3 inner verticals, 4 outer verticals, and 2-6 postorbitals. Clypeus with 16-20 setae. Tentorium 144-145 μm long, 27-31 μm wide at sieve pore and 7-13 μm wide at posterior tentorial pit. Stipes 82-147 μm long. Palp segment lengths (in μm): 27-29; 33-38; 38-144; 131-144; 202 (1). Fifth palpal segment/ third palpal segment 1.40 (1). Third palpal segment with 2 sensilla clavata.

Thorax (Fig. 33 B). Acrostichals 18-20; dorsocentrals 11-17; prealars 3-5. Scutellum with 8-11 setae.

Wing (Fig. 33 C). VR 1.17-1.20. Brachiolum with 1 seta; R with 17-23; R_1 with 14; R_{4+5} ; M bare. Squama with 9-10 setae.

Legs (Figs 11 D-F). Spur on front tibia 20-22 μm long. Spurs on middle tibia 53-56 μm long, on hind tibia 51-62 μm long. Comb on middle tibia 18-22 μm long, long and short comb on hind tibia 22-27 μm and 18-20 μm long respectively. Width at apex of front tibia 40-51 μm ; of middle tibia 42-51 μm ; of hind tibia 49-53 μm . Lengths and proportions of legs as in Table 15.

Table 15. Lengths (in μm) and proportions of legs of *Polypedilum* (*Uresipedilum*) *kakumense* sp. n.

	fe	ti	ta ₁	ta ₂	ta ₃
p ₁	744-801	484-568	815-940	623-719	424-477
p ₂	701-794	605-723	217-244	164-182	164-182
p ₃	659-879	662-776	509-605	278-352	249-288

	ta ₄	ta ₅	LR	BV	SV	BR
p ₁	342-388	132-153	1.66-1.68	1.33-1.34	1.46-1.51	2.5-3.2
p ₂	96-103	36-50	0.54-0.56	3.17-3.46	3.82-3.87	3.7 (1)
p ₃	142-189	61-71	0.77-0.78	2.51	2.59-2.74	1.3-5.9

Hypopygium (Figs 34 A-C). Tergite IX with 12-17 median setae and 16-18 posterior setae to both sides of anal point. Laterosternite IX with 3 setae. Anal point 67-89 μm long, 78-100 μm wide at base, gradually tapering to nearly parallel-sided towards apex which is 4 μm wide. Transverse sternapodeme 20-22 μm long; phallapodeme 78-82 μm long. Gonocoxite 151-158 μm long. Total length of superior volsella including apicomedial projection 78 μm and 24-27 μm long apicomedial projection; base with 2 inner setae and 1 apical seta; without microtrichiae. Inferior volsella 89-135 μm long; parallel sided and with a prominent apical seta. Gonostylus 158-167 μm long. HR 0.91-1.00; HV 1.68-1.79.

Distribution. - The species is known from the rivers in Kakum National Park, Ghana.

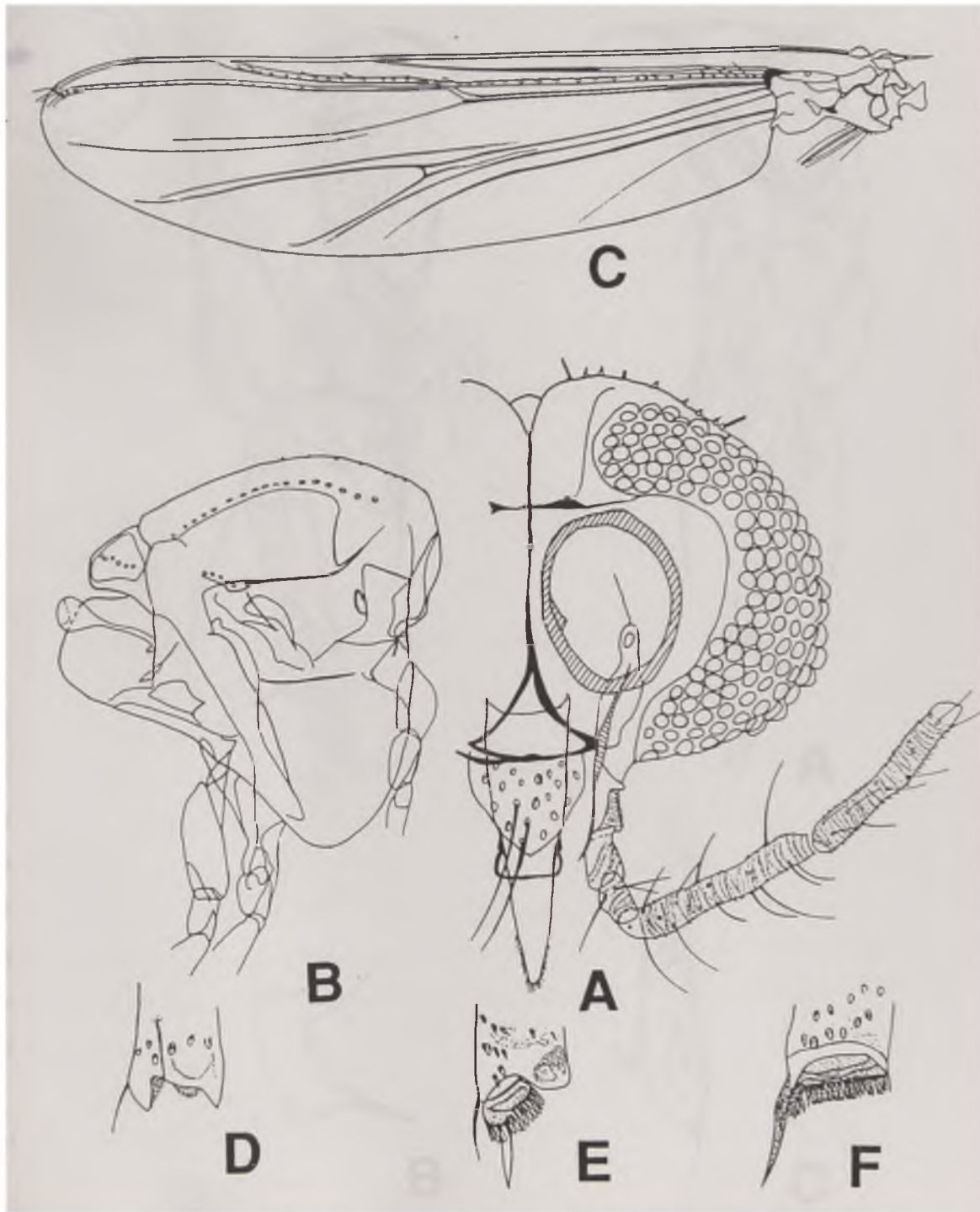


Fig. 33. *P. (U.) kakumense* sp. n. - A. Head. - B. Thorax. - C. Wing. - D. Fore tibia. E. Mid tibia. - F. Hind tibia.

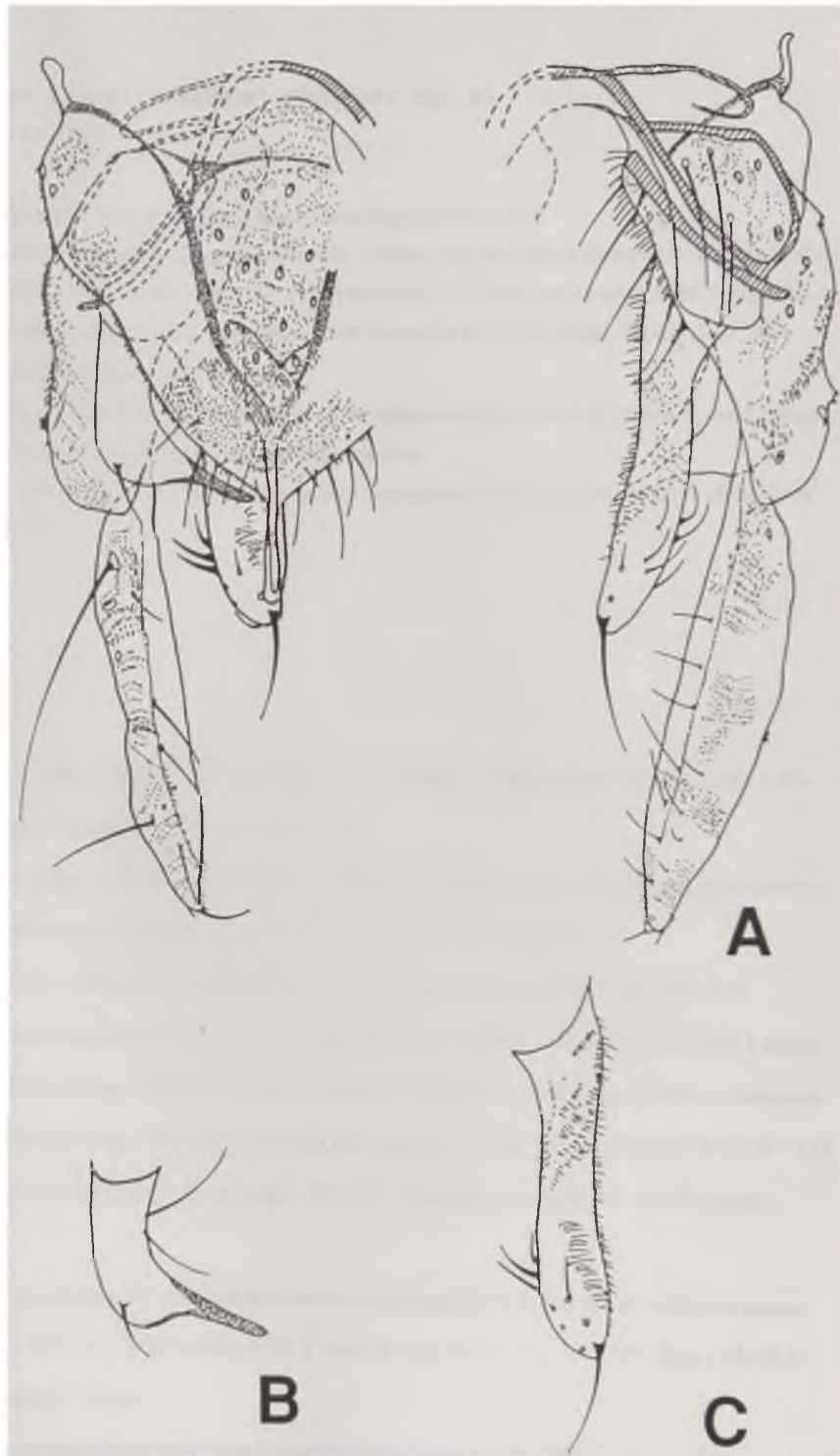


Fig. 34. *P. (U.) kakumense* sp. n. A. Hypopygium. - B. Superior volsella. - C. Inferior volsella.

***Polypedilum (Uresipedilum) gladysae* sp. n.**

(Figs 35, 11 G & 12 F)

Type locality. - GHANA: Western Region, Ankasa Game Production Reserve.

Type material. - Holotype ♂, here designated, GHANA: Western Region, Ankasa Game Production Reserve, 6-12. XII. 1993, NUFU project (ZMBN Type No. 277). Paratypes: 1 ♂, same as holotype (BMNH, No. 103), data same as holotype. TANZANIA: Tanga Region, West Usambara Mts., Mazumbai, Kaputu, 1 ♂, Nov. 1990. ZMB Tanzania expedition (ZMBN, No. III).

Diagnostic characters. - Differs from other members of the subgenus in having a slightly bulging inner margin of the superior volsella and a relatively short apicomedial projection.

Etymology. - Named after Gladys Ramirez who was very instrumental in the preparation of most of the slides examined in this thesis.

Description

Male imago

(n= 3).

Total length 2.02-2.09 mm. Wing length 1.00-1.59 mm. Total length/ wing length 1.80-2.09. Wing length/ length of profemur 2.03-2.34.

Colouration (Figs 11 G & 12 F). Thorax with 3 brown spots on postnotum, antepnotum and part of preepisternum; abdomen yellow. Femur, tibia and tarsi yellow.

Head. AR 1.21-1.28. Ultimate flagellomere 377-528 μ m long. Temporal setae 6-8 including 2-3 inner verticals, 2-3 outer verticals, and 2 postorbitals. Clypeus with 10-11 setae. Tentorium 71-92 μ m long, 16-20 μ m wide at sieve pore and 2-6 μ m wide at posterior tentorial pit. Stipes 60-124 μ m long. Palp segment lengths (in μ m): 20-32; 24-50; 62-64; 75-77; 97-113. Fifth palpal segment/ third palpal segment 1.55-1.76. Third palpal segment with 3 sensilla clavata.

Thorax. Acrostichals, 12-14; dorsocentrals 6-14; prealars 3-4. Scutellum with 3-4 setae.

Wing. VR 1.25-1.33. Brachiolum with 1 seta; R with 15-17; R₁ with 8-9; R₄₊₅ 15-28 M bare. Squama with 4-7 setae.

Legs. Spur on front tibia 24-34 μ m long. Spurs on middle tibia 47 μ m long, on hind tibia 47-66 μ m long. Comb on middle tibia 11-18 μ m long, long and short comb on hind tibia 14-20

μm and 13-26 μm long respectively. Width at apex of front tibia 31-42 μm ; of middle tibia 22-44 μm ; of hind tibia 24-50 μm . Lengths and proportions of legs as in Table 16.

Table 16. Lengths (in μm) and proportions of legs of *Polypedilum (Uresipedium) gladysae* sp. n.

	fe	ti	ta ₁	ta ₂	ta ₃
p ₁	434-784	271-424	498-605	345-423	221-287
p ₂	516-720	277-576	246-256	110-114	68-77
p ₃	530-800	395-668	324-349	149-183	143

	ta ₄	ta ₅	LR	BV	SV	BR
p ₁	146-196	78-82	1.84-1.87	1.48-1.52	1.41	3.4-4.2
p ₂	39-43	23-36	0.60-0.65	4.26-4.99	3.66-3.68	4.7-6.1
p ₃	78-82	41-46	0.71-0.82	3.01-3.08	2.89-2.93	7.9-10.3

Hypopygium (Figs 35 A-C). Tergite IX with 5-8 median setae and 10-16 posterior setae to both sides of anal point. Laterosternite IX with 2-3 setae. Anal point 56-60 μm long, 46-53 μm wide at base, gradually tapering to nearly parallel-sided towards apex which is 2-3 μm wide.

Transverse sternapodeme 20-50 μm long; phallapodeme 48-94 μm long. Gonocoxite 89-120 μm long. Total length of superior volsella including apicomedial projection 44-51 μm and 11-21 μm long apicomedial projection; base with 2 inner setae and 1 apical seta; microtrichiae present on dorsal. Inferior volsella 71-98 μm long; parallel sided or laterally broadened subapically and with a prominent apical seta. Gonostylus 89-120 μm long. HR 0.96-1.10 ; HV 1.93-2.31.

Remarks. - This species is similar to *P. (U.) acutulum*, but can be distinguished by the shape of the superior volsella. *P. (U.) gladysae* has a slightly bulging inner margin of the superior volsella, *P. (U.) acutulum* has a pointed apicomedial projection, also the latter has AR less than 1.

Distribution. - Known from Ghana, and Tanzania.

The following non-Afrotropical species also are not placeable in any group: *P. (U.) albicorpus*, *P. (U.) cultellatus*; *P. (U.) pedatum* and *P. (U.) tamasemusi*.

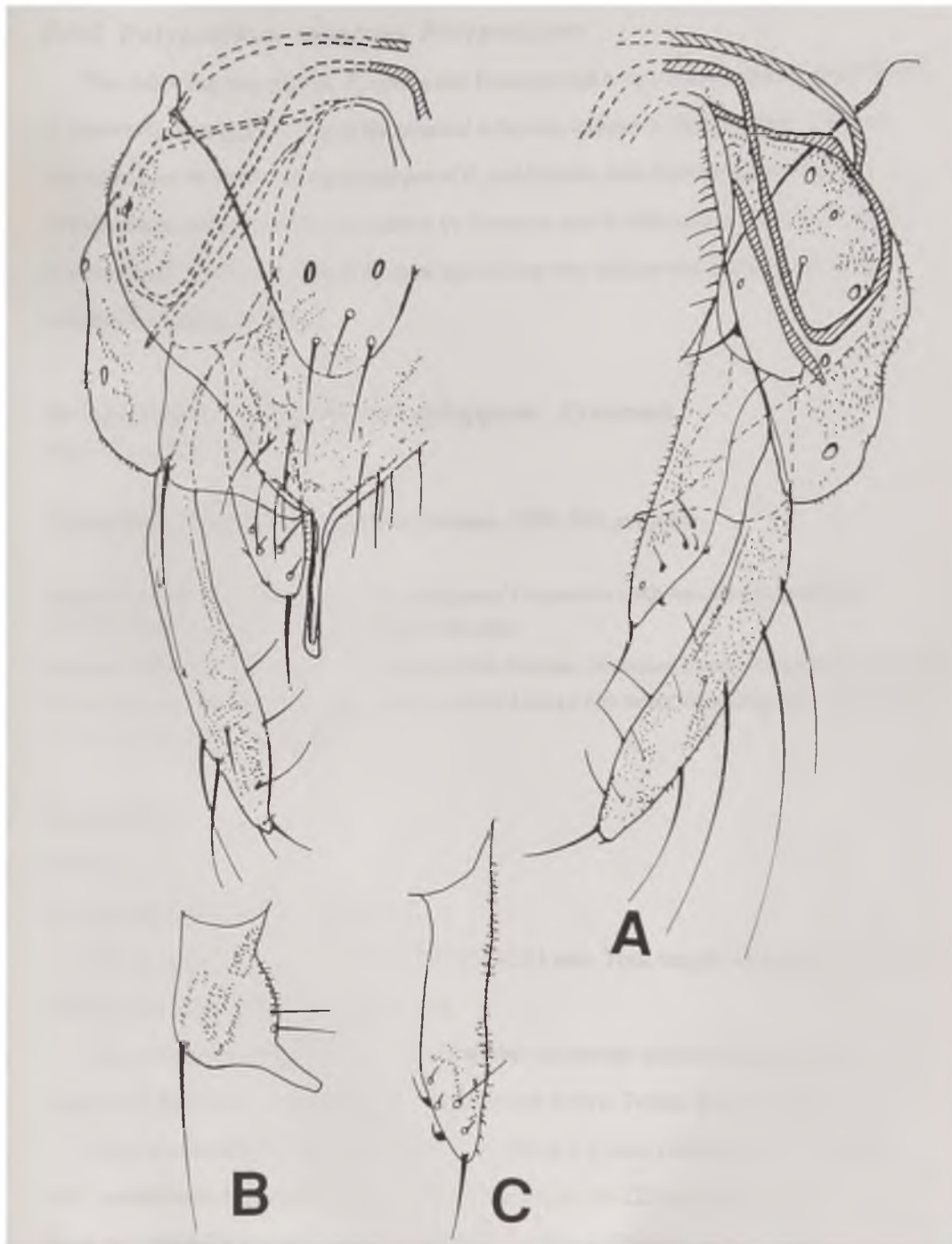


Fig. 35. *P. (U.) gladysae* sp. n. - A. Hypopygium. - B. Superior volsella. - C. Inferior volsella.

5.8.5 *Polypedilum* subgenus *Polypedilum*

The following two species, *P. ephippium* Freeman and a very similar species from Ghana, *P. anderseni* apparently belong to the nominal subgenus and not to *Uresipedilum*. They are described here as another of the paratypes of *P. ephippium*, does belong to the subgenus *Uresipedilum*, appear to be the one drawn by Freeman, and is redescribed above as *P. (U.) freemani* sp. n. The colour pattern of these species are very similar and probably led to the misidentification by Freeman.

Polypedilum (Polypedilum) ephippium Freeman

(Figs 37, 11 A & 12 B)

Polypedilum (Polypedilum) ephippium Freeman, 1958: 292, *pro parte*.

Material examined. - S. ZIMBABWE: Harare, paratypes of *Polypedilum ephippium*, all data as holotype, 3 ♂♂, IV. 1956, E. T. M. Reid (BMNH, B. M. 1956-288).

Diagnostic characters. - The species can be separated from the other Afrotropical species of the nominal subgenus by lacking spots on the wings and frontal tubercles, and by having a dark thorax and an abdomen with segments I-V yellow with median half of III dark.

Description

Male imago

(n= 3, except when otherwise stated).

Total length 3.56 (1) mm. Wing length 1.78-1.91 mm. Total length/ wing length 1.88 (1). Wing length/ length of profemur 2.06-2.10.

Colouration (Figs 11A & 12 B). Thorax almost completely dark brown and abdomen with segments I, II, IV and V pale, segment III partly dark brown. Femur, tibia and tarsi yellow.

Head. Antennae lost. Temporal setae 7-8 including 2-3 inner verticals, 4 outer verticals, and 1 postorbitals. Clypeus with 11-15 setae. Tentorium 122-125 μ m long, 23-26 μ m wide at sieve pore and 4-7 μ m wide at posterior tentorial pit. Stipes 109-155 μ m long. Palp segment lengths (in μ m): 27-40; 40 (1); 133-140 (2); 122-131 (2); 282 (1). Fifth palpal segment/ third

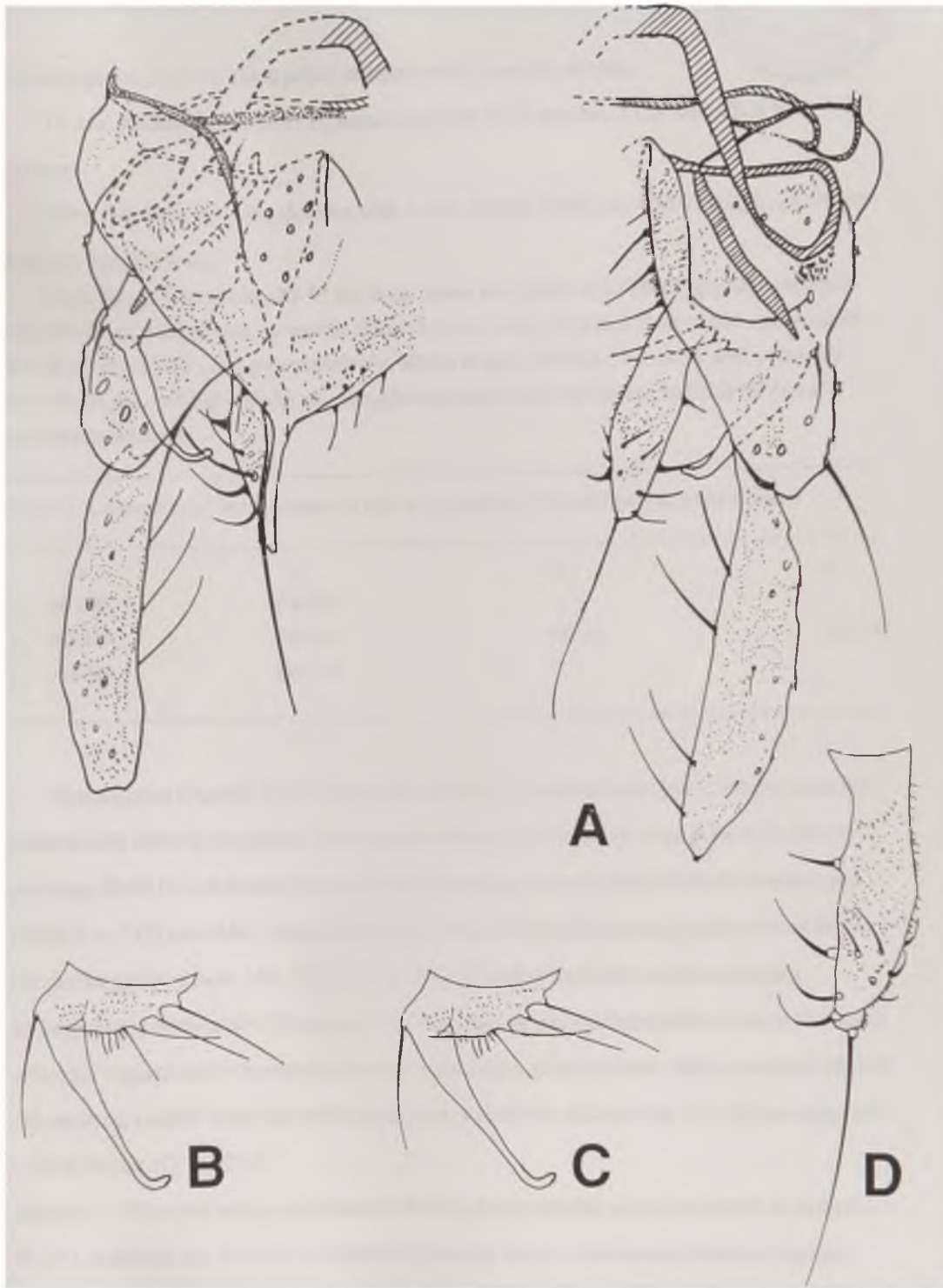


Fig. 36. *P (P.) ephippium*.
volsella.

- A. Hypopygium. - B & C. Superior volsella. - D. Inferior

palpal segment 2.12 (1). Third palpal segment with 2 sensilla clavata.

Thorax. Acrostichals 14-16 (2); dorsocentrals 6-8 (2); prealars 3 (2). Scutellum with 4-6 (2) setae.

Wing. VR 1.18-1.19. Brachiolium with 1 seta; R with 14-20; R₁ with 11-12; R₄₊₅; M bare.

Squama with 3-5 setae.

Legs. Spur on front tibia 40-53 μm long. Spurs on middle tibia 49-62 μm long, on hind tibia 58-73 μm long. Comb on middle tibia 20-22 μm long, long and short comb on hind tibia 20-22 μm and 18-20 μm long respectively. Width at apex of front tibia 44-51 μm ; of middle tibia 49-53 μm ; of hind tibia 56 μm . Lengths and proportions of legs as in Table 17 (most tarsomeres missing).

Table 17. Lengths (in μm) and proportions of legs of *Polypedilum* (*Polypedilum*) *ephippium* Freeman

	fe	ti	ta ₁	SV
P ₁	860-933	548-687	-	-
P ₂	869-929	737-801	459 (1)	3.62 (1)
P ₃	940-997	869-918	-	

Hypopygium (Figs 36 A-D). Tergite IX with 6-7 (2) median setae and 12-16 (2) posterior setae to both sides of anal point. Laterosternite IX with 2-3 (2) setae. Anal point 111-118 (2) μm long, 58-69 (2) μm wide at base, gradually tapering to nearly parallel-sided towards apex which is 4-7 (2) μm wide. Transverse sternapodeme 27-36 (2) μm long; phallapodeme 84-89 (2) μm long. Gonocoxite 162-171 μm long. Total length of superior volsella including apicomедial projection 87-122 μm and 75-77 μm long apicomедial projection; base with 4 inner setae and 1 apical seta; microtrichiae present on dorsal surface and base. Inferior volsella 98-118 (2) μm long; parallel sided and with a prominent apical seta. Gonostylus 173-193 μm long. HR 0.89-0.94 (2); HV 1.88 (1).

Remarks. - This species has a peculiar attachment of apicomедial projection which is similar to *P. (P.) anderseni*, but it can be distinguished from the latter in abdomen colouration pattern, also the inner setae are four.

Distribution. - The species is known from Harare, S. Zimbabwe.

***Polypedilum (Polypedilum) anderseni* sp. n.**

(Figs 37, 11 F & 12 A)

Type locality. - GHANA: Western Region, Ankasa Game Production Reserve.

Type material. - Holotype ♂, here designated, GHANA: Western Region, Ankasa Game Production Reserve, 7-11. XII. 1993, NUFU project (ZMBN Type No. 278). Paratypes: 1 ♂, as holotype (ZMBN, No. 104); GHANA: Volta Region, Wli, Agumatsa waterfalls, 1 ♂, 17-20. XI. 1993, NUFU project (ZMBN, No. 162).

Diagnostic characters. - The species can be separated from the Afrotropical species of the nominal subgenus by lacking spots on the wings and frontal tubercles, and by having dark thorax and an abdomen with segments I-V yellow with anterior third of segment I and IV and a small anterior spot on segment III dark. The apicolateral seta of the superior volsella is placed at the apex of the base and not on the projection.

Eymology. - Named after Associate Professor Trond Andersen, one of my supervisors, in appreciation of his immense technical assistance in the use of the computer, drawing, inking, and for making my stay here in Bergen memorable.

Description**Male imago**

(n= 3, except when otherwise stated).

Total length 2.40-2.62 mm. Wing length 1.14-1.19 mm. Total length/ wing length 2.08-2.27. Wing length/ length of profemur 1.88-2.00.

Colouration (Figs 11 F & 12 A). Thorax almost completely dark brown except for part of the preepisternum. Abdomen with segment I partly dark brown, II pale, III and IV with dark brown anterior triangular spots. About two thirds of foreleg femur brown, rest of femur, tibia, tarsi, midleg and hindleg yellowish brown or bright yellow.

Head. AR 1.59-1.73. Ultimate flagellomere 484-543 μm long. Temporal setae 7-9 including 2-3 inner verticals, 2-4 outer verticals, and 2-3 postorbitals. Clypeus with 11-13 setae. Tentorium 67-78 μm long, 14-22 μm wide at sieve pore and 3-6 μm wide at posterior tentorial pit. Stipes 89-104 μm long. Palp segment lengths (in μm): 24-27; 22-28; 49-83; 83-89; 118-131. Fifth palpal segment/ third palpal segment 1.57-2.41. Third palpal segment with 3 sensilla clavata.

Thorax. Acrostichals 18-20; dorsocentrals 7; prealars 3. Scutellum with 5-6 setae.

Wing. VR 1.14-1.21. Brachiolum with 1 seta; R with 4-6; R₁ with 0; R₄₊₅ 1-4; M bare.

Squama with 4-5 setae.

Legs. Spur on front tibia 30-47 μm long. Spurs on middle tibia 23-34 μm long; on hind tibia 44-47 μm long. Comb on middle tibia 7-11 μm long, long and short comb on hind tibia 16-27 μm 10-11 μm long respectively. Width at apex of front tibia 22-36 μm ; of middle tibia 33-38 μm ; of hind tibia 38-42 μm . Lengths and proportions of legs as in Table 18.

Table 18. Lengths (in μm) and proportions of legs of *Polypedilum (Polypedilum) anderseni* sp. n.

	fe	ti	ta ₁	ta ₂	ta ₃
p ₁	587-637	320-345	673-724	424-477 (2)	320-342 (2)
p ₂	598-634	431-491	267-285	114-135	85-100
p ₃	655-708	534-580	402-417	217-231	178-203

	ta ₄	ta ₅	LR	BV	SV	BR
p ₁	253-267 (2)	103 (1)	2.10 (2)	1.44 (1)	1.34-1.35 (2)	2.9-4.1 (2)
p ₂	52-61	25-32	0.58-0.62	4.22-4.70	3.81-3.99	2.4-3.8
p ₃	101-117	39-45	0.69-0.78	2.84-3.00	2.87-3.20	6.6-6.7

Hypopygium (Figs 37 A-D). Tergite IX with 6-8 median setae and 10-12 posterior setae to both sides of anal point. Laterosternite IX with 2-3 setae. Anal point 78-84 μm long, 49-58 μm wide at base, gradually tapering to nearly parallel-sided towards apex which is 2-4 μm wide. Transverse sternapodeme 18-20 μm long; phallapodeme 53-59 μm long. Gonocoxite 113-122 μm long. Total length of superior volsella including apicomedial projection 52-58 μm and 22-42 μm long apicomedial projection; base with 2-3 inner setae and 1 apical seta; microtrichiae present on dorsal surface and base. Inferior volsella 84-89 μm long; parallel-sided and with a prominent apical seta. Gonostylus 129-133 μm long. HR 0.88-0.92; HV 1.84-2.05.

Remarks. - This species is similar to *P. (P.) ephippium* Freeman, but can be distinguished by the colouration pattern of the thorax and abdomen. *P. (P.) anderseni* has no setae on R₁; and R₄₊₅ and R have less than 5 and 7 setae respectively.

Distribution. - The species has been found in rivers in the Ankasa Game Production Reserve and at the Agumatsa waterfalls, Ghana.

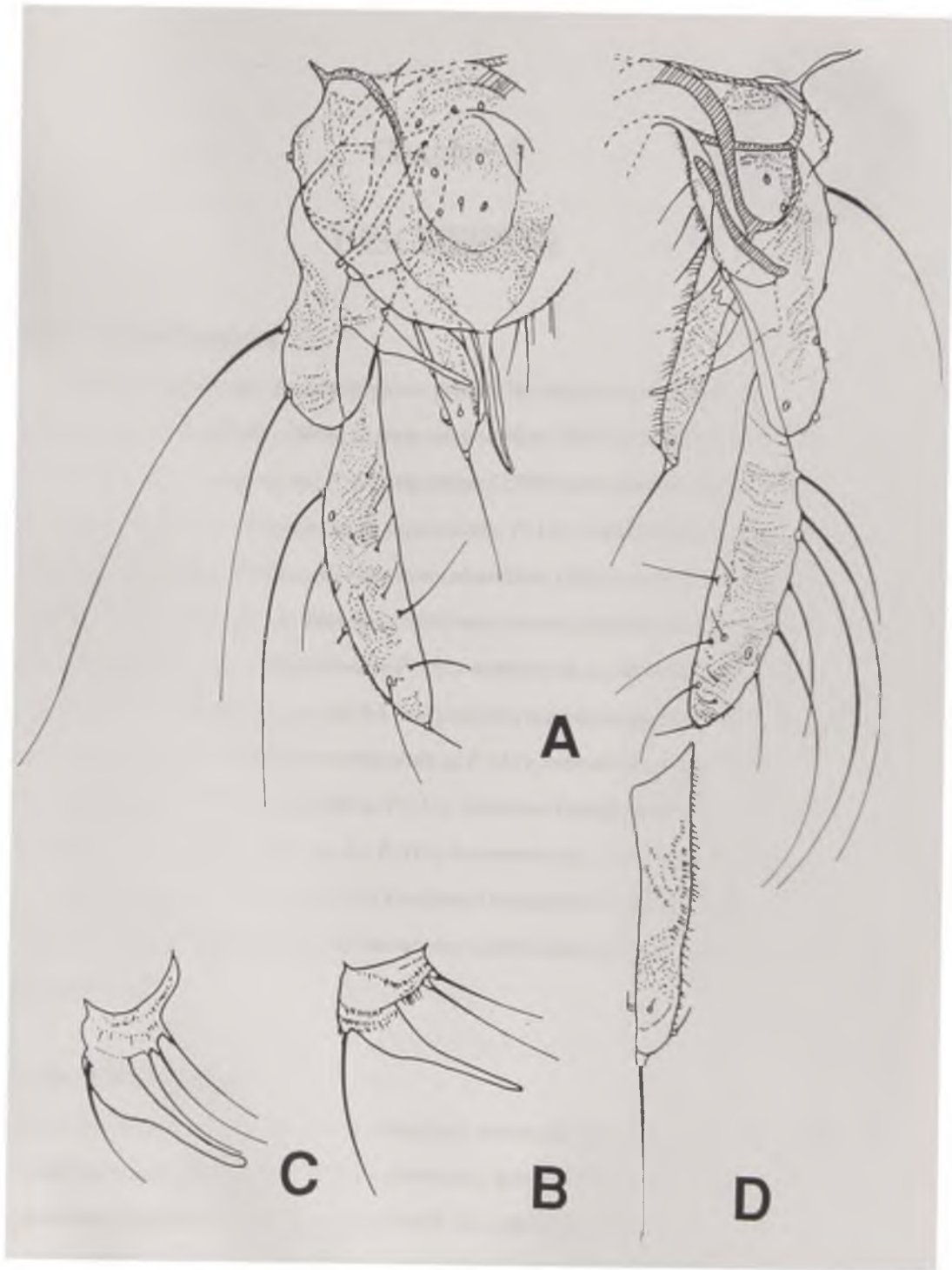


Fig. 37. *P. (P.) anderseni* sp. n. - A. Hypopygium. - B. Superior volsella. - C. Superior volsella variation. - D. Inferior volsella.

Chapter 6

DISCUSSION

6.1 Revision of species

Most of the previously described species prior to the terminology and general morphology by Sæther (1980a, 1990a, b) were misidentified. What Lehmann (1979, 1981) referred to as *P. (P.) convictum* and *P. (P.) kibatiense* (1979) were redescribed as *P. (U.) plautum* sp. n. and *P. (U.) lehmanni* sp. n. respectively. *P. (U.) convictum*, only known from the Palaearctic and Oriental regions was however redescribed. Only two available specimens described as *P. (P.) annulatum* by Freeman (1958) were correct, however seven specimens and one by Harrison (1996) were redescribed as *P. (U.) harrisoni* sp. n.; also one by the former was actually *P. (U.) praegnans* sp. n. Of the four available specimens described as *P. (U.) ephippium* Freeman (1958), one was redescribed as *P. (U.) freemani* sp. n. Most of the specimens described by Freeman (1958) as *P. (U.) kibatiense* Goetghebuer 1936, were redescribed as *P. (U.) dossenudum* sp. n., *P. (U.) kakumense* sp. n. or *P. (U.) gladysae* sp. n.

The most striking feature of *P. (U.) kibatiense* Goetghebuer is that the inner setae are placed on the apicomedial projection. All the species misidentified as *P. (U.) kibatiense* had no such feature.

6.2 Species described

Out of the fourteen Afrotropical species described, eleven are new. Two of these species, (*P. anderseni* sp. n. and paratypes *P. ephippium* Freeman), however, belong to the subgenus *Polypedilum*. The new *Uresipedilum* species are *P. (U.) spinibojum*, *P. (U.) plautum*, *P. (U.) lehmanni*, *P. (U.) praegnans*, *P. (U.) harrisoni*, *P. (U.) freemani*, *P. (U.) dossenudum*, *P. (U.)*

acutulum, *P. (U.) kakumense*, and *P. (U.) gladysae*. In addition paratypes of *P. (U.) annulatum* Freeman and *P. (U.) kibatiense* Goetghebuer are redescribed.

In describing and identifying the species a number of characters were taken into consideration. The shape and the presence or absence of microtrichia on the superior volsella; colouration and colouration pattern of the abdomen and thorax; setae on wing vein R_{4+5} and scutellum; and microtrichia on tergite IX.

6.3 Adaptation of Chironomids to their environment

Generally the species found in Ghana were smaller with lower chaetotaxy than the species from Eastern and Southern Africa. Even with individuals within the same species, those found in Ghana are smaller. This might be an adaptation to the warm, humid and high rainfall pattern in the rainforest of Ghana where most of the species were collected. Species from the Eastern and Southern Africa are mostly found in montane localities with cooler climate (Sæther & Andersen 1996 a). The species which were endemic to Ankasa and Agumatsa in Ghana had the shortest wing length and some setation, especially on tergite IX, than those from Zaire (now Democratic Republic of Congo), Tanzania and South Africa. A smaller size means less surface area and consequently less water loss from the warm climate with no need of hairs for insulation. The species from Eastern and Southern Africa are from areas of higher elevations and cooler climate thus much hair is very necessary for insulation. *P. (U.) acutulum* only found in Ankasa has a very low AR and a very small superior volsella. *P. (U.) spinibojum*, from Tanzania, *P. (U.) annulatum* from South Africa and *P. (U.) plautum* from South Africa, Tanzania and Democratic Republic of Congo, have very high chaetotaxy, large wing length, and a similar very large bare superior volsella.

6.4 Zoogeographical relationships and distribution

The subgenus *Uresipedilum* appears to be cosmopolitan with species found in all the zoogeographical regions. A parsimony analysis of all the species within the subgenus gave three major groups plus several smaller groups or single species of uncertain placement. The

zoogeographical distribution is shown in Fig. 38, where the Cosmopolitan group to the left represents the sister group of *Uresipedilum*. The *annulatum* group consists of the Afrotropical *P. (U.) annulatum*, *P. (U.) spinibojum*, *P. (U.) plautum*, *P. (U.) lehmanni*, and *P. (U.) tesfayi*, with the Nearctic species of *P. (U.) cinctum*, and *P. (U.) sulaceps* as sister group; the *convictum* group of the Nearctic *P. (U.) aviceps* (also occurring in Japan) and *P. (U.) flavus*; the Japanese *P. (U.) paraviceps*, *P. (U.) surugense* and *P. (U.) hirosimaense*; and the Palaearctic and Oriental *P. (U.) convictum*; while the *oresitrophum* group consists of the Afrotropical species *P. (U.) praegnans*, *P. (U.) harrisoni*, and *P. (U.) freemani*, and the Australasian and Oceanian species *P. (U.) canum*, *P. (U.) harrisi*, *P. (U.) oresitrophum* and *P. (U.) cumberi*. The zoogeographical distribution of the three groups is shown in Fig. 39 and Table 19.

The *annulatum* group consists of species that are confined or endemic to Eastern and Southern Africa. This must be an old lineage, and these species were present in Africa when it was part of the Pangaea but probably never lived in other parts of the super-continent. The two sister species in North America might have been a result of pre-drift dispersal by a continental route before Pangaea first divided into two large continents, Laurasia and Gondwanaland (Banarescu, 1995).

The *convictum* group consists of Palaearctic and Nearctic species and appear to be a Laurasian lineage. However, most of the Palaearctic species are limited to Japan and the lineages may be much younger. A possible dispersal route for the Eastern Asian and North American lineages may be through the northern Bering Strait during the Quaternary Ice Age where there was a broad landbridge. Since the Palaearctic *P. (U.) convictum*, and the Japanese *P. (U.) paraviceps*, *P. (U.) hirosimaense* and *P. (U.) surugense* on one hand, and the Nearctic species *P. (U.) flavus*, *P. (U.) aviceps*, on the other are very closely related, it is likely that the last group dispersed relatively recently during the Quaternary Ice Age to North America. The Palaearctic *P. (U.) cultellatum*, *P. (U.) microzoster* from Guatemala and *P. (U.) albicorpum* from Micronesia all often fall in the *convictum* group and almost certainly should be regarded as members of the group. Normally, the eastern North America lineages are much better

represented on the Gulf slope of Central Mexico, which has never been sharply isolated from that of the USA (Banarescu, 1995). This then explains the presence of one Neotropical species of *convictum* group from Guatemala.

The *oresitrophum* group consists of species that are Afrotropical, Australasian and Oceanian. The lineages are confined to areas that belonged to the eastern part of Gondwanaland. The probable Gondwanaland split was the initial and older separation of Africa from India (lower to middle Cretaceous) before South America (upper Cretaceous). But, while the African/ South American connection ceased definitively during the late Cretaceous, Africa re-established contact with Asia (actually with western Asia, but indirectly also with India) during the Miocene (Banarescu, 1995). The closer affinities between Africa and southern Asian members are still evident by the unitary continent. Some faunal exchange between Africa and western Asia/ India took place even later in Miocene or Pliocene times.

The species of uncertain placement are *P. (U.) cultellatum*, *P. (U.) microzoster*, *P. (U.) albicorpum*, *P. (U.) kibatiense*, *P. (U.) dosse nudum*, *P. (U.) acutulum*, *P. (U.) gladysae*, *P. (U.) pseudoconvictum*, *P. (U.) kakumense*, *P. (U.) pedatum*, and *P. (U.) tamasemusi*. *P. (U.) cultellatum* is widespread in Europe, in Asia it is found in Lebanon, Korea and Japan, in Africa it is found only in Algeria. *P. (U.) microzoster* is described from Guatemala; *P. (U.) albicorpum* from Micronesia; *P. (U.) kibatiense* is Afrotropical, but also known from Israel. *P. (U.) dosse nudum*, *P. (U.) acutulum*, *P. (U.) gladysae* and *P. (U.) kakumense* are the new Afrotropical species described; *P. (U.) dosse nudum* is found in Ghana, Uganda, Democratic Republic of Congo and Congo; *P. (U.) acutulum* and *P. (U.) kakumense*, are found in Ghana only while *P. (U.) gladysae* is found in Ghana and Tanzania. *P. (U.) pseudoconvictum* is known from Peru; while *P. (U.) pedatum* is found in Japan, USA and widespread in Canada.

Ten new Afrotropical species of *Uresipedilum* are described in this thesis and twenty-one species have been previously described world-wide. This brings together thirty-one known species of *Uresipedilum* so far. Out of this number thirteen are Afrotropical and three are previously described species.

Table 19. The countries, zoogeographical regions and groups where the various species are found.

SPECIES	COUNTRY	ZOOGEOGRAPHICAL GROUP		
		REGION		
<i>P. (U.) annulatum</i>	South Africa	Afrotropical	annulatum group	
<i>P. (U.) spinibojum</i>	Tanzania			
<i>P. (U.) plautum</i>	South Africa, Tanzania			
<i>P. (U.) lehmanni</i>	Democratic Republic of Congo			
<i>P. (U.) tesfayi</i>	Ethiopia			
<i>P. (U.) cinctum</i>	California, Nevada, Virginia	Nearctic		
<i>P. (U.) sulaceps</i>	widespread USA			
<i>P. (U.) aviceps</i>	Japan, widespread Canada, USA	Nearctic & Palaeartic		
<i>P. (U.) paraviceps</i>	Japan			
<i>P. (U.) hiroshimaense</i>	Japan	Palaeartic	convictum group	
<i>P. (U.) surugense</i>	Japan			
<i>P. (U.) convictum</i>	Oriental China, widespread	Nearctic		
<i>P. (U.) flavus</i>	USA			
<i>P. (U.) freemani</i>	Sudan	Afrotropical	oresitrophum group	
<i>P. (U.) praegnans</i>	Senegal, Democratic Republic of Congo			
<i>P. (U.) harrisoni</i>	Ghana, Sudan	Australasia		
<i>P. (U.) oresitrophum</i>	Australia			
<i>P. (U.) harrisi</i>	New Zealand	Oceania		
<i>P. (U.) cumberi</i>	New Zealand			
<i>P. (U.) canum</i>	New Zealand			

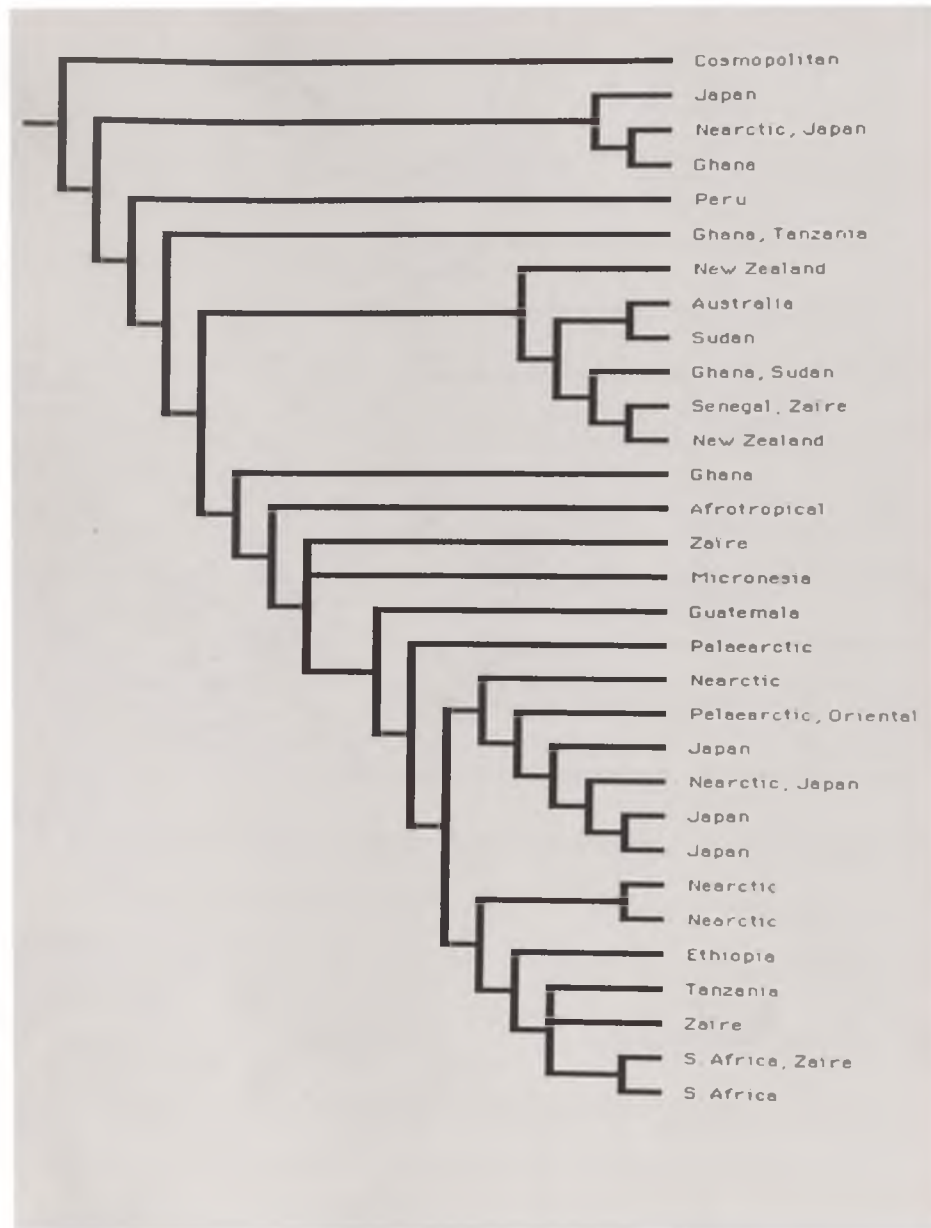


Fig. 38. The zoogeographical distribution of the subgenus *Uresipedilum*.

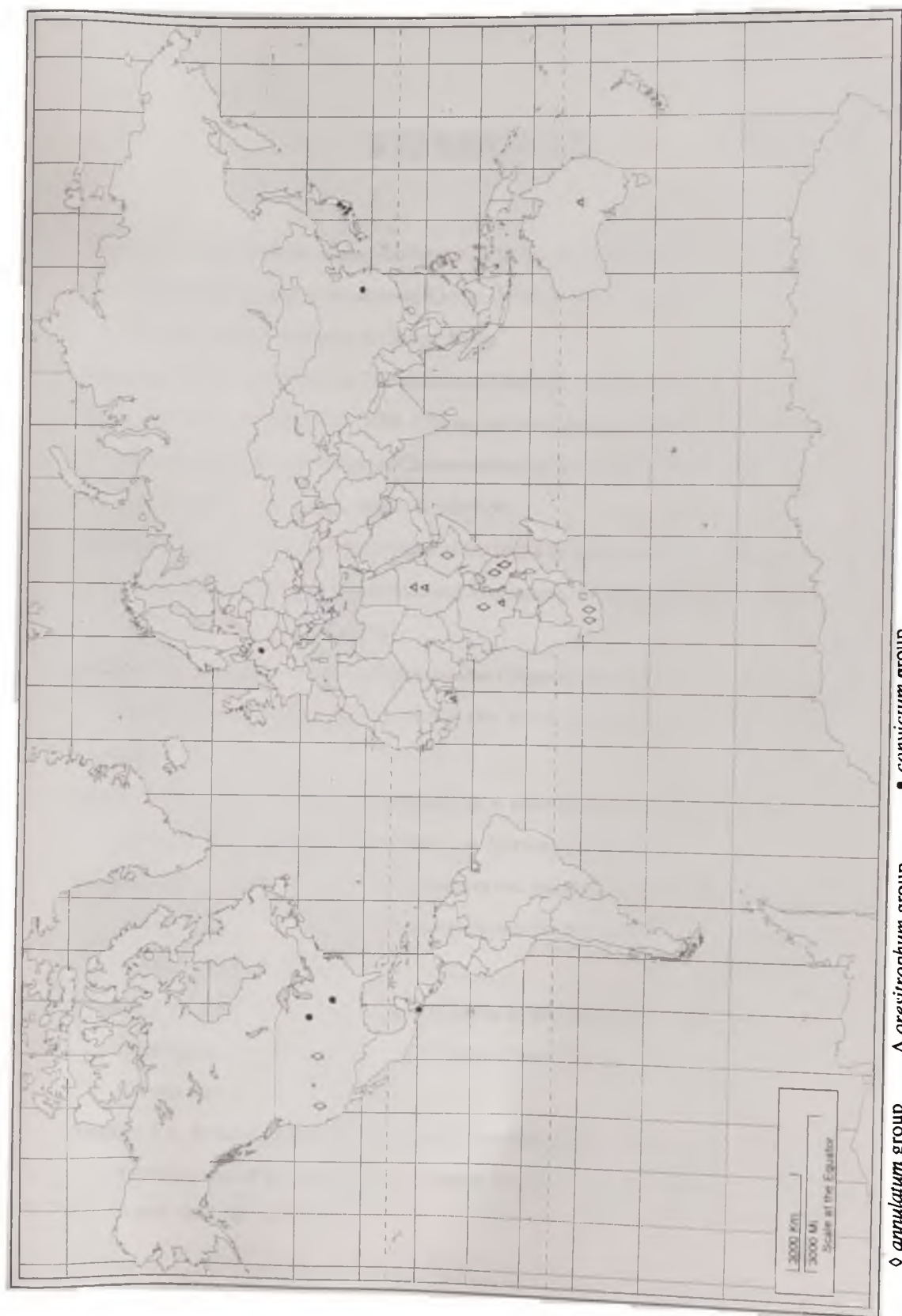


Fig. 39. Zoogeographical distribution of the *annulatum*, *oresitrophum* and *convictum* groups.

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