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Mealybugs of the genera *Eumyrmococcus* Silvestri and *Xenococcus* Silvestri associated with the ant genus *Acropyga* Roger and a review of the subfamily Rhizoecinae (Hemiptera, Coccoidea, Pseudococcidae)

D.J. WILLIAMS
*Department of Entomology, The Natural History Museum, Cromwell Road, London
SW7 5BD.*

CONTENTS

SYNOPSIS.   The hypogeic mealybug genera *Eumyrmococcus* Silvestri and *Xenococcus* Silvestri, their distribution throughout southern Asia and Australasia, and their association with the ant genus *Acropyga* Roger are discussed. *Eumyrmococcus* is also discussed from Europe and South Africa. Descriptions or redescriptions of 17 species of *Eumyrmococcus* are presented and illustrated, including *E. corinthiacus* Williams, *E. falciculosus* sp. n., *E. kolombangarae* sp. n., *E. kruiensis* sp. n., *E. kusiacus* sp. n., *E. lamondicus* sp. n., *E. lanuginosus* sp. n., *E. maninjauensis* sp. n., *E. neoguineensis* sp. n., *E. nipponensis* Terayama, *E. queenslandicus* sp. n., *E. recalvus* sp. n., *E. sarawakensis* sp. n., *E. scorpioides* (De Lotto), *E. smithii* Silvestri, *E. sulawesicus* sp. n. and *E. taylori* sp. n. The genus *Xenococcus* includes two species, *X. acropygae* sp. n. and *X. annandalei* Silvestri. It is now known that *X. annandalei* is a local species from a small area in India. The female pupal instar, already known in *Xenococcus*, is also discussed in *Eumyrmococcus*. Full page illustrations for each species and keys to species of *Eumyrmococcus* and *Xenococcus* are provided.

The position of *Eumyrmococcus* and *Xenococcus* within the subfamily Rhizoecinae is discussed and a review of all the genera included in the subfamily is provided. A new genus and species, *Leptorhizoecus deharvengi*, is described from Sumatra and the generic name *Radicoccus* Hambleton is synonymised with *Rhizoecus*.

INTRODUCTION

In a list of family-group names of the Coccoidea, Williams (1969a) erected the tribe Rhizoecini, within the mealybug family Pseudococcidae, for *Rhizoecus* Künckel d'Herculais and a few related genera, all inhabiting soil, leaf litter, rotting logs or feeding on roots. Some of these genera are now known to be identical with others and some other genera have been added since. After a comprehensive study of the labium of the Coccoidea, Koteja (1974a, 1974b) accepted the group as the subfamily Rhizoecinae, mainly on the basis that the labium is very narrow. This group also lacks cerarii and the antennae are usually strongly geniculate, with never more than 6 antennal segments, the terminal segment always tapering and pointed. The subfamily status has been accepted by most workers. The other subfamilies Trabutininae, Pseudococcinae and Sphaerococcinae, discussed by Koteja, have also been accepted by many students of the Coccoidea although the status of each subfamily is still ill-defined.

The purpose of this work is to revise the genera *Eumyrmococcus* and *Xenococcus*. A few species of *Eumyrmococcus* had been studied already for the author's current work on the mealybugs of southern Asia. Some interesting collections, however, sent by Dr R.W. Taylor, CSIRO, Canberra, from Australasia, associated with the ant genus *Acropyga,* have revealed some remarkable species. Any attempt to publish on southern Asian species without a knowledge of all the others would be undesirable. It is for this reason that a study is presented here of all the known species of *Eumyrmococcus*, now totalling 17.

It is clear that most of the records of the related genus *Xenococcus* have been based on a misconception. The type species *X. annandalei* Silvestri, appears to be a local species, at present living only on Barkuda I., Orissa Province, India. Another species, previously identified as *X. annandalei* from India, most of southern Asia and Australasia, is different, and is here described as new.

Eumyrmococcus and *Xenococcus* were also included in the subfamily Rhizoecinae by Tang (1992) who erected the tribe Xenococcini for them. According to Tang, this tribe differs from the Rhizoecini, the only other tribe, in lacking ostioles. The distinction may hold for Chinese and neighbouring species but not in the subfamily as a whole as known worldwide. It is difficult to separate *Eumyrmococcus* and *Xenococcus*, for instance, without reference to *Neochavesia*

Williams & Granara de Willink, a South American genus. This study of *Eumyrmococcus* and *Xenococcus* is followed, therefore, by a discussion of all genera of the subfamily Rhizoecinae. Included genera accepted here are *Rhizoecus, Capitisetella* Hambleton, *Pseudorhizoecus* Green, *Geococcus* Green, *Leptorhizoecus* gen. nov., *Pygmaeococcus* McKenzie, *Neochavesia, Eumyrmococcus* and *Xenococcus*. A key to these genera is also included.

Few specimens of *Eumyrmococcus* have been available for this study. Collecting these mealybugs is not easy and acknowledgement is always due to the collectors who have searched for them in ants' nests or have taken the trouble to extract them from soil samples. Species records represent isolated collections over a wide area. All the species are minute and their preparation on to microscope slides is often tedious. Distinguishing adults from immatures preserved in vials is almost impossible and it is often disappointing to find only one or two adult females in any sample. Even more disappointing is the complete absence of adults.

The present study of *Eumyrmococcus* and *Xenococcus* must be recognized as a preliminary identification guide and not a phylogenetic study. Some possible species-groups can be distinguished and these are discussed in the introduction to the section on 'Species and Genera' (p. 7). It is hoped that the present study of these mealybugs and their ant relationships will form the basis for a future cladistic study. Such a study could also be extended to the other rhizoecine genera discussed here, at least to some of the monotypic genera which need further investigation.

MATERIAL AND METHODS

The slide-mounting techniques and the methods of illustration described by Williams & Watson (1988) and Williams & Granara de Willink (1992) are followed. The terminology in these works is adopted here except for the terms bitubular and tritubular pores. In the present work they are referred to as bitubular cerores and tritubular cerores, terms that were widely used by Hambleton (1976) and adopted from MacGillivray (1921).

Measurements of the body length and width are in millimetres but all other measurements, even if larger than the body length, are given in microns.

ABBREVIATIONS OF INSTITUTIONS

The following acronyms are used throughout for the depositories of specimens.

ANIC   Australian National Insect Collection, Canberra, Australia.

BMNH   The Natural History Museum, London, UK.

IEAUN   Istituto di Entomologia Agraria dell'Università di Napoli, Portici, Italy.

MNHN   Muséum National d'Histoire Naturelle, Paris, France.

NIAES   National Institute of Agro-Environmental Science, Tsukuba-shi, Japan.

QM   Queensland Museum, South Brisbane, Queensland, Australia.

SANC   National Collection of Insects, Pretoria, South Africa.

USNM   National Museum of Natural History [Scale insect Collection], Beltsville, Maryland, USA.

HABIT AND ECONOMIC IMPORTANCE

It has been been postulated by Koteja (1984, 1985) and well summarised by Gullan & Kosztarab (1997) that the ancestors of present-day Coccoidea lived on the leaf-litter layer, feeding on dead and decaying matter, or even on associated fungi and bacteria. Some soil-inhabiting coccoids are, apparently, secondarily inhabitants but Koteja suggests that *Margarodes* Guilding (Margarodidae) and *Rhizoecus* (Pseudococcidae) might have spent all of their phylogeny in soil or litter. The underground habit of *Rhizoecus* could not have been acquired secondarily from an aerial habit on stems, twigs and leaves (Koteja, 1985).

Endosymbionts of scale insects are diverse and may have been acquired via the alimentary canal during the original leaf-litter habit. Mealybugs may have even changed their feeding behaviour by living a symbiotic relationship with ants (Tremblay, 1989) but the endosymbionts of most mealybugs, although different, are nevertheless related (Buchner, 1969). The symbionts of *Puto* Signoret and *Macrocerococcus* Leonardi are different from others in the Pseudococcidae and those of *Rastrococcus* Ferris are so distinct that *Rastrococcus* should be separated from the Pseudococcidae (Buchner, 1957, 1969). Tremblay (1977) recognizes two main symbiotic adaptations among the pseudococcids, the *Pseudococcus* Westwood type and the *Puto* type. No symbionts of *Rhizoecus* and its close relatives have been studied but Silvestri (1924) showed that *Xenococcus* has a pseudococcid type of endosymbiosis. Buchner (1957, 1969) apparently studied symbionts of *Eumyrmococcus* (without mentioning the species) and commented that these are a pseudococcid type, near those of *Phenacoccus* Cockerell.

Rhizoecinae live underground, mostly feeding on rootlets. Many species have only been collected from Berlese funnel apparatus but many are known from leaf litter and rotting logs. The only aerial habit reported is that of *Rhizoecus mexicanus* (Hambleton) on leaves of *Zygocactus truncatus*; otherwise this mealybug normally feeds on cactus roots (Hambleton, 1979).

Species of many genera of Rhizoecinae are associated with ants of the genus *Acropyga* Roger which attend the mealybugs and feed on their excreted honeydew. The association may be an old one because some of these ant species are known to be obligate coccidophiles and many of the mealybug species are probably obligate myrmecophiles, although some mealybug species reported with ants are capable of living without them. *Rhizoecus coffeae* Laing is a pest of coffee in Brazil where it lives on the roots in association with *Acropyga (Rhizomyrma) paramibensis* Borgmeier (Bünzli, 1935). The mealybug is well protected from excessive change in dryness and wetness caused by the weather because the nests are well drained and the mealybugs are capable of moving to suitable feeding sites. According to Bünzli, the situation is different from that of the ant-free mealybugs. Flanders (1957) reported that

the myrmecophilous mealybug *Eumyrmococcus (= Neochavesia)* sp. only feeds on roots exposed by the ant *A. (Rhizomyrma) fuhrmanni* Forel and that the number of mealybugs feeding at any one time is regulated by the ant.

Ants associated with *Eumyrmococcus* and *Xenococcus* are also species of *Acropyga* and these mealybugs have been collected within the ants' nests, in ant tunnels, or from the mandibles of flying queens. A few *Eumyrmococcus* species described here as new, have been collected without ant data or simply labelled 'with ants' but it is reasonable to suggest that all these mealybugs may be associated with *Acropyga* (see list of *Acropyga*-Rhizoecinae associations p. 30).

When carrying mealybugs in the mandibles, ants grip species of *Rhizoecus* and *Geococcus* at a point near the metathorax (Bünzli, 1935). Ants apparently grasp individuals of *Eumyrmococcus* at the dilated cephalothorax (Roepke 1930; Prins 1982; Buschinger *et al.*, 1987).

Ants of the genus *Acropyga* are discussed here in the four subgenera listed by Bolton (1995a). Some of the unidentified species of Australasian *Acropyga* may be undescribed if not discussed by Taylor and Brown (1985) or Taylor (1992). Of the 56 species of *Acropyga*, about half occur in the Neotropical Region and the remainder are distributed mainly in the Indo-Australasian Region, with a few described from the Palaearctic, Afrotropical and Oriental Regions (Bolton, 1995b). This ant distribution appears to be correlated with the number of mealybug species found in these regions. A few non-rhizoecine mealybugs may be associated with *Acropyga* in South America (Bünzli, 1935), and it seems unlikely that species of *Acropyga* in other regions will not exploit mealybug trophobionts in other subfamilies.

Bünzli (1935) has listed *R. coffeae, R. caladii* Green, *R. moruliferus* Green (= *R. falcifer* Künckel d'Herculais), *Geococcus coffeae* Green, *Pseudorhizoecus proximus* Green and *Capitisetella migrans* (Green) as attacking coffee roots in Brazil. All the indigenous host plants of these mealybugs are grasses, and Bünzli has shown that the mealybugs have migrated to the new host plant *Coffea liberica*.

Other rhizoecine mealybugs associated with *Acropyga* in South America, attacking economic plants, are *Neochavesia caldasiae* (Balachowsky) on roots of coffee in Colombia, *N. eversi* (Beardsley) on roots of banana in Panama, and *N. trinidadensis* (Beardsley) on roots of cacao in Trinidad.

In India, Dr C.A. Viraktamath, University of Agricultural Sciences, Bangalore, has sent specimens of *X. acropygae* sp. n., that were feeding on the rootlets of grape, causing a severe reduction in yield. The mealybug also attacked many weed species in the vicinity of the vines.

LIFE CYCLES

In the family Pseudococcidae, there are usually four instars in the female and five in the male. Normally the female is regarded as neotenic and all instars feed. In the male, feeding is restricted to the first two instars followed by the non-feeding prepupa, pupa and adult. Koteja (1985) suggests that loss of wings in the female occurred only once and was an adaptation to the original leaf-litter or hypogeic habitat. Normally adult males are much smaller than the adult female. Koteja (1985) hypothesizes that in the original leaf litter, small males were able to crawl among soil particles to reach the females. This small size could be realized only by a cessation of feeding, i.e. at the end of the second instar. In order for the males and females to emerge simultaneously, the last male instars became resting and non-feeding instars known as the prepupa and pupa.

The life cycles of *Rhizoecus* and near relatives are virtually unknown. Bünzli (1935) discusses four female instars in *R. coffeae* and three male instars but he may have overlooked the pupal instars. Schmutterer (1952) discusses four female instars in *R. albidus* Goux in Germany and mentions nymphs and adults in the male without further details.

The adult males in some of the *Rhizoecus* group are wingless and morphologically degenerate but in other species they are winged (Schmutterer, 1952; Beardsley, 1962). Surprisingly, winged males in slide collections of *Rhizoecus* are not uncommon (D.R. Miller, personal communication).

The first record of a female pupal instar was described by Williams (1988) for the genus *Xenococcus*. This instar replaces the normal third or feeding instar and probably acts as a resting stage for the female to develop in the presence of attending ants. A similar type of pupa has now been found and is discussed here in at least five species of *Eumyrmococcus*.

Unfortunately, no first-instar nymphs of *Eumyrmococcus* are known from any of the material at hand except for a single specimen still within the egg membrane. This first-instar nymph is densely covered in short setae and shows unusual developmemt of many characters as in the first instar of *Xenococcus* (Fig. 24). Second-instar nymphs are available in 11 species of *Eumyrmococcus* but these remain unsexed. Normally second-instar mealybugs show strong dimorphism, with the second-instar male usually possessing more tubular ducts and pores to form a waxy covering for the prepupa and pupa. These characters are usually absent or fewer in the second-instar female. In *Eumyrmococcus*, the female pupal instar and the male prepupal and pupal instars are without any coverings and any sexual differences in the second instar are not apparent.

Female pupae show a well developed labium and this is evidenced by at least four species of female pupae with the developing adult female still inside (Fig. 1B). It is thus easy to separate female pupae from male prepupae and pupae which lack the well developed labium (Figs 21, 25). Male prepupae are available with the developing pupae still inside and pupae are at hand with the developing adult male inside just before the final moult (Fig. 1A). All female pupae, and male prepupae and pupae, lack dermal structures such as pores and setae. Unlike most male pupae in the Pseudococcidae, which usually possess longer limbs and antennae than those of the prepupae, these characters in the pupa of *Xenococcus* are shorter, presumably in preparation for the adult male which possesses minute tubercle-like antennae and short legs.

Studies of the adult male of *Rhizoecus* are remarkably few. Beardsley (1962) described the adult male of *R. falcifer* in detail and showed that the head bears only two pairs of eyes and lacks the normal lateral ocelli. Furthermore, the head is not separated from the thorax by a constricted neck. The penial sheath, according to Beardsley, is related to that of *Phenacoccus* Cockerell. Similar features are present in the male of *R. albidus* as shown by Schmutterer (1952).

The adult male of *Neochavesia eversi* (Beardsley) is morphologically degenerate, without wings, eyes or thoracic sclerotization, and the penial sheath and aedeagus resemble those of *Puto* (Beardsley, 1970). Adult males of three species of *Eumyrmococcus* are available, one of which is not described here because no adult females were collected. The males are disparate. All are without eyes, wings and thoracic sclerotization and possibly resemble males of *Neochavesia*. The genital capsule in the Australian species studied, possesses a long dorsal style and a long pointed aedeagus. It is not clear why there should be such development when the tip of the female abdomen is normally curled dorsally, presenting easy access. Adult males of *E. sarawakensis* sp. n. are elongate, curled ventrally, with most of the genital capsule internal. Both the male and female in any one species of *Eumyrmococcus* are about the same size.

Peculiar development in the adult male of *Xenococcus* is described on p. 24. The legs are placed at the anterior end of the body and the claws have the strangest development known in any scale insect, with apparent digitules larger and stouter than the actual claw.

PARASITISM

Of about 160 species described in the subfamily Rhizoecinae, only a single record of a parasitoid has been published. Schmutterer (1952) reported a very effective chalcid parasitising *R. albidus* Goux in Germany. The parasitoid was recorded later as *Anomalicornis tenuicornia* Mercet (Hymenoptera: Encyrtidae) by Ferrière (1956), a fairly common Old World species.

The Encyrtidae have successively parasitised the other three mealybug subfamilies Trabutininae, Pseudococcinae and Sphaerococcinae recognized by Koteja (1974a, 1974b) as evidenced by the host parasitoid index of encyrtid parasitoids of mealybugs in Noyes and Hayat (1994). The views of Koteja (1984, 1985) that *Rhizoecus*, which we may substitute as the Rhizoecinae, could have spent the whole of their phylogeny underground, may be a reason for the lack of parasitism. Many of the mealybugs in the other three subfamilies live underground or are concealed and are known to be parasitised. The hypogeic habit is, therefore, not a barrier. Many Rhizoecinae have a symbiotic relationship with ants which could successfully exclude parasitoids but conversely many Rhizoecinae are not associated with ants. Parasitoids may not recognize rhizoecine mealybugs as suitable hosts. J.W. Beardsley (personal communication) has commented that the Rhizoecinae may have branched off from the main mealybug lineage before the evolution of the Encyrtidae and may not be recognized as normal encyrtid hosts. It is possible, however, that parasitoids have simply not been collected from the Rhizoecinae.

MORPHOLOGY OF *EUMYRMOCOCCUS* AND *XENOCOCCUS* (ADULT FEMALES)

BODY. All descriptions of the adult female in life indicate that the cephalothorax is strongly dilated, or shows some sign of dilation, with a narrow tapering abdomen which curls dorsally. When prepared on microscope slides, the anal lobes are poorly developed and are recognizable by infolding on both the dorsum and venter with the apex of each lobe bearing three long setae, collectively referred to here as anal lobe setae. In *E. neoguineensis* sp. n., each lobe has 8 anal lobe setae and in *E. lanuginosus* sp. n., the anal lobe setae are not differentiated from other setae on the anal lobes. Usually there are 3 anal lobe setae that are long and stout at the bases with wide setal collars. They are similar to those in many other genera of the Rhizoecinae. In *Eumyrmococcus* and *Xenococcus*, there are usually one ventral and two dorsal setae on each anal lobe but occasionally two are placed ventrally and one dorsally.

ANAL RING. The anal opening projects slightly between the anal lobes and the anal ring is normally

simple with a crescentic sclerotized band without cells. Three pairs of anal ring setae appear to be usual but occasionally there are 4–7 pairs. The anal ring setae are normally detached from the anal ring, lying just anterior to it except in *E. corinthiacus* Williams, which possesses 4 pairs, apparently attached to the outer edge of the ring. In all species the anterior pair of setae are short and slender, the second pair either the same length as the anterior pair or longer, and the posterior pair often long and stout, sometimes as long as the anal lobe setae.

ANTENNAE. The antennae are 2–4-segmented and differ in shape and position. In *E. lanuginosus*, they are 2-segmented, short and tubercle-like. In most species of *Eumyrmococcus* the antennae are 2-segmented, with a short basal segment and a long tapering second segment. They are placed fairly wide apart on either the ventral or dorsal margin of the head. In *E. sarawakensis* sp. n. and *E. sulawesicus* sp. n., the antennae are situated well on the dorsum of the swollen cephalothorax. The 4-segmented antennae of *E. neoguineensis* are unusual in possessing spine-like setae on the leading edge. *Xenococcus* has 4-segmented antennae that are long, sometimes as long as the body, with strong articulation between the first and second segments. The second segment is provided with small points at the proximal end which fit into grooves at the distal end of the first segment. This articulation allows the antennae to fold against the dorsum of the body. A pair of peg-like setae are present at the tip of each fourth segment.

LEGS. The legs are always well developed with few setae. The setae are stout and flagellate but sometimes a few on the outer edge of the femur in *Eumyrmococcus* are blunt and sensory. In *Xenococcus*, the leg setae may be unusually long on the distal end of the femur, almost as long as the femur. In most species the tibia is swollen distally before narrowing towards the tarsus. The tarsus is usually swollen near the base then tapers gradually, sometimes for nearly half its length. In one species of *Xenococcus*, the tibia and proximal end of the tarsus are straight. The claw in *E. scorpioides* (De Lotto) is broad but in all other species it is long, pointed and slender with a pair of short setose digitules. These digitules are difficult to discern in some species except for the bases. A campaniform sensillum is present at the base of all tarsi.

EYES. These are completely absent in all species of *Eumyrmococcus* and *Xenococcus*.

LABIUM. In most species the labium is narrow with 3 segments, often longer than the clypeolabral shield. The setae on the anterior surface of the apical segment are often widely spaced and the subapical setae are sometimes reduced to 3 pairs. A few species possess 2 pairs of setae on the clypeolabral shield.

CEPHALIC PLATE. This sclerotized area on the frons in many species of *Rhizoecus* is not apparent in any species of *Eumyrmococcus* or *Xenococcus*.

CIRCULI. The type species of *Eumyrmococcus*, *E. smithii* Silvestri, is the only species studied without a circulus. In other species the circuli number 1–3, situated within the borders of the segments. When only a single circulus is present it is situated either on abdominal segment II or III. When 2 are present they lie on abdominal segments II and III, and a third in *Eumyrmococcus* is sometimes present on the metathorax. In *Xenococcus*, when a third is present, it lies on abdominal segment IV. Each circulus is round and may be small (the smallest studied only 8.75 µm in diameter) or unusually large (up to 85.0 µm in diameter). The outer edge of each circulus may be flat or raised slightly from the surrounding derm. In one species the circulus is almost conical but the centre in all circuli is cupped, sometimes deeply in *Eumyrmococcus*, or shallowly in *Xenococcus*, so that the circulus resembles a crater. A similar type of circulus is present in *Neochavesia*, and Beardsley (1970) has cautiously termed these 'circulus-like projections'. The form of the circulus in all these genera is different from that of other genera in the Rhizoecinae which possess circuli that are usually truncate-conical with the centre part flat and often reticulate or faveolate.

A function of the circulus as an adhesive organ has been demonstrated for *Pseudococcus adonidum* (L.) (=*P. longispinus* (Targioni Tozzetti)) and *Planococcus citri* (Risso) by Pesson (1939) and in other species by Lloyd and Martini (1957). Ferris & Murdock (1936), from histological sections, discussed the circulus in *Pseudococcus maritimus* (Ehrhorn) as a secretory organ. Pesson (1939), in a detailed study, found that the circulus of *Pseudococcus* is an exsertile organ, lacking secretory pores between the organ and the cuticle and that the epithelium is only a part of the hypoderm. The epithelium is responsible for the formation of the peripheral chitin, which protects it, and of a mucin which hardens after secretion. In the circulus, the substance secreted appears to be a chitin which remains soft longer with the gluey properties of a mucin and hence gives the circulus adhesive properties. It is easy to see the exsertile action of the circulus, according to Pesson, by placing the mealybug on a microscope slide so that it has difficulty in taking hold with its claws. The mealybug can then hold on to the surface by the circulus.

It is not clear if the circulus of *Eumyrmococcus* and *Xenococcus* has the same function as those studied above. Silvestri (1924) studied histological sections of the circulus of *X. annandalei* and concluded that there are numerous elongate-pyriform cells directly under the shallow central cup. Silvestri thought that the

circulus secretes some kind of liquid which may be attractive to the ants attending the mealybugs. Any exsertile properties of the circulus in *Eumyrmococcus* and *Xenococcus*, or even in any Rhizoecinae, remain unproved. The term circulus is retained for the species under discussion.

OSTIOLES. These structures are always absent in *Eumyrmococcus, Xenococcus* and *Neochavesia* but are usually well defined in some other genera of the Rhizoecinae.

SETAE. One of the striking characters of *Eumyrmococcus* and *Xenococcus* is the abundance of short setae on the dorsum of the abdomen. They extend to the venter of the abdomen in *Eumyrmococcus* and may be present on the head and thorax of both surfaces. In *Xenococcus*, they extend to the head and thorax of the dorsum and to the ventral lateral margins of the head and thorax. They lie in well defined bands across the segments leaving clear areas on the intersegmental lines. Normally these setae are flagellate, often slightly curved, but in *E. falciculosus* sp. n., they are mostly sickle-shaped, and in *Xenococcus*, there are patches of sickle-shaped setae among the flagellate setae on the dorsum of the thorax.

Stout and longer flagellate setae are usually present on the mid-venter of the thorax. In *Xenococcus*, these extend to the entire venter of the abdomen also. Sensory setae are sometimes present in *Eumyrmococcus*. These are slightly swollen at the apices and may be the only setae present on the head and thorax in some species. In other species, they are either long or short and sometimes mingle with the short, flagellate setae. The sensory setae may also be lanceolate or extremely minute and can be detected with certainty only by oil-immersion studies. Some short setae in *E. neoguineensis* are set in dermal pockets, forming clusters on the venter of the thorax.

MICROTRICHIA. Elongate microtrichia, resembling setae, are so abundant in some species that they almost completely cover the insect so that the setae are obscured. The setae in these species are only recognizable by the presence of setal collars. At present, species with dense microtrichia are only known from the more equatorial areas, Sumatra, Sarawak and Sulawesi.

PORES AND DUCTS. Some genera of Rhizoecinae contain species possessing trilocular pores, multilocular disc pores and tubular ducts. Normally, trilocular pores secrete fine wax to protect the surface from contamination by the insect's own honeydew. Excreted honeydew balls are often coated with this wax. Multilocular disc pores secrete wax to help in the production of ovisacs or to protect eggs. They are sometimes present in second-instar males to secrete wax in the formation of the cocoon (Cox and Pearce, 1983).

Tubular ducts in the Rhizoecinae are usually small, often narrower than the trilocular pores. Normally, tubular ducts in the adult female secrete wax to form the ovisac, or in the second-instar male, to help form a cocoon.

Pores and ducts are completely absent in *Eumyrmococcus* and *Xenococcus*. Honeydew excreted is probably taken entirely by the ants without need for the mealybugs to secrete wax as an anti-contaminent. Apparently the species are ovoviviparous and first-instar nymphs would be protected and transported by ants along with any other instars. Second instars lack pores and ducts and succeeding male prepupae and pupae are not enclosed in cocoons. The dense covering of short setae on the abdomen of all species and the complete covering of microtrichia in some species may help to protect the mealybugs from any possible contamination of honeydew and from excessive humidity in the nests and tunnels formed by the ants.

In *Neochavesia*, trilocular pores are found in the type species only but these pores are unlike any other trilocular pores in possessing a minute filament at the centre. Normal trilocular pores and tubular ducts are present in *Leptorhizoecus* gen. nov. (Fig. 28).

GENERA AND SPECIES

Eumyrmococcus and *Xenococcus* are closely related and it could be argued that *Xenococcus* is a subordinate clade within *Eumyrmococcus*. Both genera occupy similar geographical areas in southern Asia and Australasia (Figs 29, 30) and the species in both genera are mostly associated with specific ants of the same genus (p. 30). *Xenococcus* possesses unusual 4-segmented antennae, almost as long as the body, with remarkable articulationn between the first and second segments. In *Eumyrmococcus*, the antennae are much shorter and lack this special articulation. Furthermore, all species of *Eumyrmococcus* have a dense covering of short setae on both the dorsum and venter of the abdomen. In *Xenococcus*, short setae are restricted to the dorsum of the abdomen only and any ventral abdominal setae on the abdomen are long and stout. Although both genera have many shared characters, the genera are regarded here as distinct, in the interests of nomenclatural stability, pending future cladistic studies. A key to separate both genera is included in the general key on p. 30.

Some species of *Eumyrmococcus* share a large type of circulus, others a small type, and two species lack any type. Although it may be possible to recognise species-groups based on the type of circulus, the circulus is not a stable character in some other genera of Rhizoecinae when any single species may possess 0–2 (Williams, 1996).

Species-groups could be recognised on other characters. The *E. smithii*-group contains species with abundant short flagellate setae covering the dorsum and venter and lacking any sensory setae. In addition to the type species, *E. smithii*, this group also contains *E. kolombangarae* and *E. kusiacus*. Another group, found near the equator, comprises *E. kruiensis, E. lanuginosus, E. maninjauensis, E. sarawakensis* and *E. sulawesicus*. All are densely covered in elongate microtrichia. In possessing similar 4-segmented antennae, *E. corinthiacus* in Europe, is probably related to *E. scorpioides* from South Africa even though the claws in *E. scorpioides* are stout and different from the long slender claws in any other species. The Australian species, *E. lamondicus, E. queenslandicus, E. recalvus* and *E. taylori* appear to be related to the Japanese species, *E. nipponensis*. All possess similar 2-segmented antennae, with the second segment elongate and tapering, and with elongate posterior setae on the anal ring.

Most of the abundant abdominal setae in *E. falciculosus* are sickle-shaped, unlike the setae in any other species, although similar setae are present in small numbers in both species of *Xenococcus*. A final species, *E. neoguineensis*, has an unusual combination of characters. The 4-segmented antennae are the longest of any species and, although the articulation between the first and second segments is normal, these antennae possibly come nearest in structure to those of *Xenococcus*. Furthermore, the anal lobes in *E. neoguineensis* contain numerous setae and the body shape is unusual, without such a marked dilated cephalothorax. This species may form a distinct group.

The two adult males described here in *Eumyrmococcus* are so disparate that if discovered without accompanying adult females, it would be difficult to place them in the same genus. The difference between these adult males is as great as the difference between either and the adult male of *Xenococcus acropygae*. Similar differences in male morphology are expected among the different species-groups of *Eumyrmococcus* discussed here.

Eumyrmococcus Silvestri

Eumyrmococcus Silvestri, 1926: 271.

Type species *Eumyrmococcus smithii* Silvestri, by original designation.

DESCRIPTION

Adult female. Body pyriform, broadly pyriform, or elongate-pyriform, with cephalothorax usually strongly dilated, often constricted between second and third abdominal segments, then abdomen tapering to narrow abdominal segment VIII. In life, tip of abdomen curled dorsally. Posterior end rounded, anal lobes not developed but recognizable by inner edges slightly

grooved, each lobe usually terminating in long, stout flagellate setae forming a group of 3, sometimes nearly as long as body, sometimes stout and short or in groups of numerous slender flagellate setae. Antennae each with 2–4 segments, placed fairly wide apart on venter of head margin or displaced to dorsum of head when prepared on microscope slides; terminal segment usually tapering, sometimes tubercle-like or long and slender. Legs well developed, tibia and tarsus subequal in length, tarsus swollen from joint with tibia then tapering to narrow distal end, all segments with fairly stout flagellate setae, set well apart; occasionally with sensory setae on outer edges of femur and tibia. Claw normally long and slender, pointed, except in one species with claw relatively stout at base; each with a pair of short, slender setose digitules but these difficult to recognise in some species. Labium longer than wide, often with 3 pairs of subapical setae, widely spaced. Clypeolabral shield with 1 or 2 pairs of setae. Anal ring dorsal, sclerotized, usually crescentic except in one species when circular; simple, without cells; with normally 3 pairs of setae; first 2 pairs usually detached, lying just anterior to ring, second pair sometimes longer than anterior pair, posterior pair sometimes stout and as long as anal lobe setae; sometimes ring with 4–7 pairs of setae, variously placed. Circuli present or absent; when present numbering 1–3, all round, small to unusually large and conspicuous, always deeply cupped.

Body setae short and abundant, at least on abdomen, sometimes present on entire body, usually flagellate but sometimes most abdominal setae replaced by sickle-shaped setae.

Setae on head and thorax often longer and stouter. Sensory setae, either lanceolate or with slightly swollen blunt tip, sometimes distributed over entire body with the flagellate setae, or situated at anterior end of body only: occasionally minute bulbous setae present. Microtrichia sometimes present, covering entire body, these often nearly as long as setae giving the insect a woolly appearance and often masking the short body setae. Ostioles absent. Tubular ducts, multilocular disc pores and trilocular pores absent.

First instar. Well clothed in short setae as evidenced by single specimen still within egg membrane.

Second instar. Similar to adult female but with fewer setae and usually shorter antennae and legs.

Female pupa. Recognizable by elongate labium, antennae showing segmentation, legs well developed.

Male prepupa and pupa. Similar to female pupa but with shorter limbs and antennae. Labium not developed.

Adult male. Wingless and morphologically degenerate, of diverse appearance. Genital capsule well developed, either exposed or mostly enclosed within abdomen; when exposed, with conspicuous anal opening and dorsal style, penial sheath rounded apically,

ventral slit rounded near base then widening apically, basal ridge of penial sheath well defined ventrally, aedeagus long and pointed. Posterior edge of abdominal segment VIII forming possible anal ring as in female, with 3 pairs of setae. Legs well developed, slender. Body setae numerous. Antennae 2-segmented. Eyes absent. When genital capsule mostly enclosed within abdomen then ventral slit almost square, anal opening oval at posterior end of abdomen at base of sclerotized extension, possibly representing a short style. Legs squat. Antennae short, 2-segmented. Body almost naked except for a few minute setae.

COMMENTS.   The description of the adult male is based on two species and another still within the pupal instar. The wide disparity in shape and form may indicate a much wider range of variation.

Key to Species of *Eumyrmococcus* (Adult Females)

SPECIES DESCRIPTIONS

Eumyrmococcus corinthiacus Williams

(Fig. 2)

Eumyrmococcus corinthiacus Williams, 1993: 218.
   Holotype adult♀, Greece, Corinth (BMNH) [exam-
   ined].

DISTRIBUTION

Greece: Corinth, Perachora, near Lautraki, carried by
swarming ant *Acropyga* sp., 7.x.1985 *(A. Buschinger)*;
without locality, carried by queens of *Acropyga* sp.
during mating flight, x. 1992 *(W.H.O. Dorow)*.

COMMENTS.   This species was described recently by
Williams (1993). Important characters are the 4-seg-
mented antennae and thick setae in groups of 3 on the
anal lobes, 2 in each group distinctly longer and
stouter than the other. The dorsal and ventral setae are
abundant, all flagellate, becoming less numerous on
the thorax and head. As in other species, the circulus is
concave and cup-shaped when viewed laterally.

The original material, the first known from Europe,
was sent for identification by Professor A. Buschinger,
Institut für Zoologie Technische Hochschule,
Darmstadt, Germany. When discussing the habit,
Buschinger *et al.*, (1987) recorded the ant as *Plagiolepis*
sp. and this name was used by Williams (1993). Pro-
fessor Buschinger (personal communication) has since
indicated that the ant is actually a species of *Acropyga*.
The most likely species is *A.(Rhizomyrma) paleartica*
Mennozzi, the only species known in Greece.

The accompanying figure first appeared in the Ento-
mologist's Gazette and is reproduced here from the
original illustration with slight modification.

Eumyrmococcus falciculosus sp. n.

(Fig. 3)

DESCRIPTION

Adult female on microscope slide membranous, elon-
gate, largest specimen 1.15 mm long, 0.50 mm wide,
widest at about mesothorax; head and thorax rounded,
constricted slightly between abdominal segments II and
III, abdomen tapering and narrowing between abdomi-
nal segments VII and VIII, posterior end of body
rounded, abdominal segment VIII 200 µm wide at base.

Positions of each anal lobe with 2 stout dorsal setae, each
about 188µm long, and 1 ventral seta about 125µm long,
forming a group of 3. Antennae situated on ventral head
margin, each 65–77 µm long, with 2 segments; basal
segment wide, second segment tapering. Legs well
developed, slender; hind trochanter + femur 115–
118 µm long, hind tibia + tarsus about 100µm long, claw
slender, about 20 µm long. Ratio of lengths of hind tibia
+ tarsus to hind trochanter + femur 0.84–0.86. Ratio of
lengths of hind tibia to tarsus 0.73–0.81. Tibiae swollen
then tapering, tarsi widening near base then narrowly
tapering. Leg setae pointed. Labium about 117–125 µm
long, as long as clypeolabral shield, 77–80 µm wide;
ratio of length to width 1.51–1.56. Circulus present,
distorted in available specimens but at least 50µm wide,
situated near middle of abdominal segment III. Anal ring
about 75 µm wide, with 6 slender setae, the anterior pair
each about 32.5 µm long, the second and posterior pairs
longer but not complete in available material.

Dorsal surface with unusual sickle-shaped setae,
fairly crowded, present as far forward as abdominal
segment III, those posteriorly on abdominal segment
VIII each about 20 µm long, others on abdomen
mostly 12.5 µm long. A few flagellate setae each
12.5 µm long, present among the sickle-shaped setae.
Setae on head, thorax and abdominal segments I and
II, curved but fairly stiff and pointed, mostly about
15 µm long, moderately numerous. Thicker sensory
setae, each bluntly tipped and with large setal collars,
few, distributed mainly around margins.

Ventral surface with a similar distribution of sickle-
shaped setae, pointed setae and thick sensory setae, to
those on dorsum. A few long, stout sensory setae
present in medial area of thorax.

MATERIAL

HOLOTYPE.   Adult ♀, **Indonesia: Sumatra**, Krui,
Kubu Prau, among primary forest litter, 800 m,
29.v.1991 *(L. Deharveng & A. Bedos)* (MNHN).

PARATYPE.   **Indonesia: Sumatra**, same data as
holotype. 1 adult ♀ (BMNH).

Non-type material, **Indonesia**: Sumatra, Jambi Prov-
ince, Rantau Pandan, in soil in *Hevea* plantation,
9.vi.1991 *(L. Deharveng & A. Bedos)*.

COMMENTS.   This is a curious species with peculiar
sickle-shaped setae on the abdomen and short 2-seg-
mented antennae. It has no close relatives thus far
discussed here. The antennae are similar to those of *E.
lanuginosus* sp. n., also described from Sumatra, but
E. lanuginosus is extensively clothed in long
microtrichia whereas in *E. falciculosus* any microtrichia
are short and barely perceptible.

The specimen recorded from Rantau Pandan is
extremely poor but is recognisable as this species by
the sickle-shaped setae.

The epithet '*falciculosus*' is based on the Latin word

'*falcicula*' meaning small sickle, and the Latin suffix '*-osus*' meaning 'abundance of', referring to the numerous setae of this shape.

Eumyrmococcus kolombangarae sp. n.

(Fig. 4)

DESCRIPTION

Adult female on microscope slide broadly oval, about 0.90 mm long, 0.60 mm wide, widest at mesothorax, tapering to a constriction between abdominal segments VII and VIII, base of abdominal segment VIII 180 μm wide. Posterior end of body rounded; positions of each anal lobe with 2 ventral setae and 1 dorsal seta forming a group of 3, each seta about 80 μm long. Antennae lying on ventral head margin, each about 110 μm long, with two segments, the second tapering. Legs well developed; hind trochanter + femur about 168 μm long, hind tibia + tarsus 142 μm long, claw slender, unusually long, about 45 μm long. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0.84. Ratio of lengths of hind tibia to tarsus 1.84. Tarsi each swollen near base then tapering to narrow distal end. All leg setae stout and flagellate. Labium distorted in available specimen but at least 100 μm long and fairly wide, about as long as clypeolabral shield. Circuli numbering 2, each about 15 μm wide, situated near posterior edges of abdominal segments II and III but within borders of segments. Anal ring about 75 μm wide, with 6 setae, each about 65 μm long.

Dorsal surface with crowded flagellate setae occupying most of surface except for well marked intersegmental areas; setae on abdominal segment VIII mostly 15 μm long, anteriorly about 12.5 μm long; a few setae on any segment with larger setal collars.

Ventral surface with crowded setae as on dorsum except in medial area of thorax where they are longer and not numerous. Long stout setae, each about 35 μm long, present in pairs near mid-line of abdominal segments II–VII.

MATERIAL

HOLOTYPE. Adult ♀, **Solomon Islands**: New Georgia Group, Kolombangara, E. Kusi, 600 m, associated with *Acropyga lauta* in log, 30.viii.1965 *(Isiah)* (ANIC).

PARATYPES. **Solomon Islands**: same data as holotype, 1 2nd instar (ANIC), 1 ♀ pupa (ANIC), 1 ♀ pupa (BMNH).

COMMENTS

This species is related to the type species *E. smithii* in the arrangement of the densely crowded flagellate setae, at least on the dorsum, but differs in possessing

two small circuli. *E. smithii* lacks circuli completely. Furthermore, in *E. kolombangarae*, the anal lobe setae are at most only 80 μm long and the posterior anal ring setae are about 65 μm long, whereas in *E. smithii*, these setae are noticeably much longer, at least 500 μm long.

E. kolombangarae is very close to *E. kusiacus*, herein described, differing mainly in lacking long stout setae in rows at the posterior edges of the dorsal and ventral abdominal segments. In *E. kolombangarae*, long stout setae are present in pairs only near the midline of the venter of abdomen.

The description of this species has also been based on an almost perfect adult female still within the pupal instar. A single second instar is also available. This is similar to the adult female, differing mainly in having shorter limbs, a single circulus present on abdominal segment III, and in the body setae which are not so dense.

The epithet is based on the Latin genitive of the place name meaning 'of' or 'from'.

Eumyrmococcus kruiensis sp. n.

(Fig. 6)

DESCRIPTION

Adult female on microscope slide, elongate, membranous 0.81mm long, 0.38 mm wide, widest at mesothorax, abdomen gradually tapering, slightly constricted between abdominal segments VII and VIII, base of abdominal segment VIII 120 μm wide, posterior end of body fairly straight. Positions of each anal lobe with 2 stout dorsal setae and 1 ventral seta, each about 70 μm long, forming a group of three. Antennae placed on ventral head margin, each 82.5 μm long, with 2 segments, the second segment 60 μm long, tapering. Legs well developed; hind trochanter + femur about 117.5 μm long, hind tibia + tarsus 95 μm long, claw slender, about 27.5 μm long, 5 μm wide at base. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0.80. Ratio of lengths of hind tibia to tarsus 1.11. Tibiae swollen then tapering to narrow distal ends. All legs with stout flagellate setae. Labium about 92.5μm long, same length as clypeolabral shield, 65 μm wide; ratio of length to width 1.42. Circulus large, about 45 μm wide, situated near posterior end of abdominal segment III but within borders of segment. Anal ring about 70 μm wide, with 6 setae; anterior and middle pairs slender, each 25–37 μm long, posterior pair stout, each about 75 μm long, similar to anal lobe setae.

Dorsal surface densely covered in hair-like microtrichia and slender flagellate setae except for intersegmental areas. Most setae on abdominal segment VIII about 15 μm long, those on anterior abdominal segments 10.0–12.5μm long, most on head and thorax 5.0–12.5 μm long.

Ventral surface with similar microtrichia and setae to those on dorsum; on abdominal segment VIII, some setae as long as 40 μm, most other setae on abdomen about 25 μm long, marginal areas of head and thorax with short slender setae each about 12.5 μm long. Long, stout flagellate setae, each 25–30 μm long, with large setal collars, present on head and submarginal and medial areas of thorax.

MATERIAL

HOLOTYPE. Adult ♀, **Indonesia, Sumatra**, Krui, Pahmungan, in soil of dammar plantation, 23.v.1991 *(L. Deharveng & A. Bedos)* (MNHN).

PARATYPES. **Indonesia, Sumatra**, same data as holotype, 3 2nd instars (MNHN), 2 2nd instars (BMNH).

COMMENTS. This is a distinctive species within the group extensively clothed in hair-like microtrichia. The stout setae in groups of three on the anal lobes and the posterior pair on the anal ring are much shorter than those in *E. maninjauensis, E. sarawakensis* and *E. sulawesicus. E. kruiensis* also differs from these three species in lacking any sensory setae with swollen tips.

There are also available five second instars. These are similar to the adult female in the dense covering of microtrichia but the limbs are shorter and the body setae are fewer.

The epithet is based on the place name 'Krui' and the Latin suffix *'-ensis'* denoting origin.

Eumyrmococcus kusiacus sp. n.

(Fig. 6)

DESCRIPTION

Adult female on microscope slide broadly oval, 1.12 mm long, 0.65 mm wide, widest at mesothorax, abdomen tapering, abdominal segment VIII 220 μm wide at base. Positions of each anal lobe with 2 stout dorsal setae and 1 ventral seta forming a group of 3, each about 100 μm long. Antennae placed near ventral head margin, each 112–120 μm long, with 2 segments, the second tapering, both segments with long stout setae. Legs well developed, slender; hind trochanter + femur about 200 μm long, hind tibia + tarsus 158–162 μm long, claw slender, about 58 μm long. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0.79–0.81. Ratio of lengths of hind tibia to tarsus 1.02–1.16. Tarsi each swollen near base then tapering to narrow distal end. All legs with stout flagellate setae. Labium 150–162 μm long, about same length as clypeolabral shield, 75–80 μm wide; ratio of length to width 1.50–1.62. Circuli numbering 2 situated near posterior edges of abdominal segments II and III but within borders of segments, diameter on abdominal segment II about 10 μm, on abdominal

segment III about 17.5 μm, each deeply cupped. Anal ring about 100 μm wide with 6 setae; anterior and second pairs each 75 μm long, posterior pair each about 87 μm long, the anterior pair with setal collars touching.

Dorsal surface with crowded flagellate setae; on abdominal segment VIII mostly about 40 μm long, anteriorly on abdomen and remainder of body mostly about 15 μm long except towards posterior edges of abdominal segments, mostly about 25 μm long. Setae on abdomen in fairly narrow bands leaving extensive intersegmental bare areas. Setae on head and thorax much more crowded than on abdomen. Long stout setae, each 80–90 μm long, present in rows at posterior edges of abdominal segments II–VII.

Ventral surface with similar setae to those on dorsum, sparse on venter of thorax. Long stout setae as on dorsum, present at posterior edges of abdominal segments I–VII.

MATERIAL

HOLOTYPE. Adult ♀, **Solomon Islands**: New Georgia Group, Kolombangara, Kusi, 1220 m, associated with *Acropyga lauta*, in log, 29.viii.1965 *(Isiah)* (ANIC).

PARATYPE. **Solomon Islands**: same data as holotype, 1 adult ♀ (BMNH).

COMMENTS. *E.kusiacus* is related to *E. smithii* but differs in possessing two small circuli, and short stout setae on the anal lobes. These setae are scarcely longer than the width of the anal ring. In *E. smithii*, the circuli are absent and the setae on the anal lobes are conspicuously longer than the width of the anal ring. *E. kusiacus* is very close to *E. kolombangarae*, differing mainly in possessing long stout setae on the dorsum and venter at the posterior edges of the abdominal segments. In *E. kolombangarae*, there are long stout setae in the medial areas of the ventral abdominal segments only.

The name is based on 'Kusi', the place of origin, and the Latin suffix *'-acus'* meaning 'belonging to'.

Eurmyrmococcus lamondicus sp. n.

(Fig. 7)

DESCRIPTION

Adult female on microscope slide elongate, slender, largest specimen 1.28 mm long, 0.53 mm wide (holotype 1.40 mm long, 0.40 mm wide), widest at about mesothorax, head and thorax rounded, narrowing at abdominal segment III then narrowly tapering to small constriction between abdominal segments VII and VIII, base of abdominal segment VIII about 100 μm wide. Positions of each anal lobe with 2 stout dorsal setae and 1 ventral seta, each about 325 μm long, forming a group of 3. Antennae placed on dorsal head margin, each 330–340 μm long, with 2 segments, the

second 260–280 µm long, tapering. Legs well developed, slender; hind trochanter + femur 193–218 µm long, hind tibia + tarsus 112–122 µm long, claw slender, about 27.50 µm long, 6.25 µm wide at base. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0.91–1.00. Ratio of lengths of hind tibia to tarsus 1.38–1.43. Tibiae swollen then tapering abruptly to narrow distal ends. All legs with stout pointed setae. Labium 127.5–137.5 µm long, slightly longer than clypeolabral shield, 80–105 µm wide; ratio of length to width 1.21–1.66. Circuli numbering 2, situated near middle of abdominal segments II and III, cup-shaped, about as deep as wide; on abdominal segment II about 12.5 µm wide, on abdominal segment III about 11.0 µm wide. Anal ring about 45 µm wide, with 6 setae; anterior pair slender, each about 72 µm long, second and posterior pairs stouter, each about 187 µm long, resembling anal lobe setae.

Dorsal surface with short crowded setae in bands across segments as far forward as prothorax; setae at posterior end of abdominal segment VIII each about 30 µm long, most on abdominal segment VII about 12.5 µm long, anteriorly mostly 7.5–10.0 µm long; a few on most segments with larger setal collars; on prothorax and mesothorax setae occupying medial areas except for marginal band, absent from head and in noticeable intersegmental areas. Stout flagellate setae, 32.5–37.5 µm long, present in medial area of head, interspersed with a few smaller setae. Short lanceolate sensory setae, each about 10 µm long, not numerous, mingled with the slender setae posteriorly to abdominal segment VI. Slender sensory setae, each about 10 µm long, and bluntly tipped, represented by a few on abdominal segment II only, these in addition to lanceolate setae.

Ventral surface with similar slender setae to those on dorsum, those on venter of thorax in deep marginal bands. Lanceolate sensory setae as on dorsum, few, present on most segments. Slender sensory setae occurring on abdominal segment II only. Stout flagellate setae present on head and medial area of thorax.

MATERIAL

HOLOTYPE. Adult ♀, **Australia**: Queensland, Mt Lamond, 12°44'S 143°18'E, associated with *Acropyga* sp., in rotting wood, 9–15.vi.1971 *(R.W. Taylor & G.J. Feehan)* (ANIC).

PARATYPES. **Australia**: Queensland, same data as holotype, 3 adult♀♀ (ANIC), 2 adult♀♀ (BMNH), 4 2nd instars (ANIC), 3 2nd instars (BMNH).

COMMENTS. The distribution of the dorsal and ventral slender setae and the shape of the antennae, place this species near *E. nipponensis. E. lamondicus*, however, comes closest to *E. queenslandicus* sp. n. in possessing minute lanceolate sensory setae, whereas those of *E. nipponensis* are blunt and swollen apically.

E. lamondicus differs from *E. queenslandicus* in possessing also some slender blunt sensory setae on abdominal segment II and having two small circuli. In *E. queenslandicus* the blunt sensory setae are absent and there is only a single but large circulus. The slender setae on the venter of the thorax in *E. lamondicus* are also in much deeper marginal bands than in *E. queenslandicus*.

The epithet '*lamondicus*' is based on the place name Mt Lamond and the Latin suffix '*-icus*' meaning 'belonging to'.

Eumyrmococcus lanuginosus sp. n.

(Fig. 8)

DESCRIPTION
Adult female on microscope slide elongate-oval, membranous, largest specimen 1.00 mm long, 0.50 mm wide, widest at mesothorax then gently tapering to abdominal segment VII, with a constriction between abdominal segments VII and VIII, posterior end of body rounded. Positions of each anal lobe with numerous long stout setae, mostly about 75 µm long. Antennae placed on ventral margin of head, short, each 35.0–37.5 µm long, with 2 segments, second segment tapering, almost conical. Legs well developed, robust, hind trochanter + femur 145–150 µm long, hind tibia + tarsus 97.5–110.0 µm long, claw slender, 10.0–12.5 µm long, 7.5 µm wide at base. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0.67–0.73. Ratio of lengths of hind tibia to tarsus 1.00–1.09. Tibiae each swollen near base then tapering to narrow distal end. All legs with stout flagellate setae. Labium 95–100 µm long, 50.0–62.5 µm wide, ratio of length to width 1.6–1.9. Circuli numbering 2 or 3, when 3 then situated near middle of mesothorax and abdominal segments II and III. When only 2 then absent from mesothorax; each circulus about 12.5 µm in diameter except on abdominal segment III when about 10 µm in diameter, truncate-conical but deeply cupped from apex. Anal ring 70–74 µm wide, with 6 setae; anterior pair slender, each about 30 µm long, second pair each about 50 µm long, posterior pair stouter, each about 80 µm long; anal ring setae difficult to discern because of surrounding setae.

Dorsal surface extensively covered in fine hair-like microtrichia and short fine setae except for bare intersegmental areas. Short setae on abdominal segment VIII mostly about 15 µm long, those anteriorly mostly about 7.5 µm long except for a few about 12.5 µm long with slightly larger setal collars. Long stout setae present towards posterior edges of abdominal segments IV–VIII, those on abdominal segment VIII numerous, 55–75 µm long; anteriorly mostly 55 µm long, distributed across the segments except on abdominal segment IV where they are sparse.

Ventral surface with similar microtrichia and setae to those on dorsum, covering most of surface; the short setae fine in medial area of thorax. Long flagellate setae, much more numerous than on dorsum, present towards posterior edges of abdominal segments and in medial areas of head and thorax. A few stout sensory setae, each with swollen tip, present laterally on thorax.

MATERIAL

HOLOTYPE.   Adult ♀, **Indonesia: Sumatra**, Si Antar [2°40′N 98°43′E], with ants (Smithsonian Expedition), 1937 *(W.M. Mann)* (USNM). The holotype is the middle specimen of five, all mounted in a row on the same slide and is clearly marked.

PARATYPES.   **Indonesia: Sumatra**, same data as holotype, 3 adult ♀♀, clearly marked in row with holotype, 1 2nd instar to right of other specimens (USNM).

COMMENTS.   *E. lanuginosus* belongs to the group of species extensively covered in minute hair-like microtrichia. It differs from all the other species in possessing only short, almost conical antennae, and numerous stout setae on the positions of each anal lobe, not differentiated into groups of three.

The specimens were first studied by Harold Morrison who noted on the envelope that the species had been discussed by Roepke (1930). Although Roepke's illustration of the mealybug is rather simple, it does show the small tubercle-like antennae. The ant species was provisionally identified as *Cladomyrma* sp. but the equally simple illustration of the ant with the mealybug held in the mandibles, may be a species of *Acropyga*.

The epithet *'lanuginosus'* is a Latin adjective meaning downy or woolly, referring to the dense covering of microtrichia.

Eumyrmococcus maninjauensis sp. n.

(Fig. 9)

DESCRIPTION
Adult female on microscope slide, membranous, pyriform, about 0.83 mm long, 0.48 mm wide, widest at mesothorax, narrowing abruptly at about abdominal segment II, then gently tapering to rounded posterior end; abdominal segment VIII 150 μm wide at base. Positions of each anal lobe with 2 stout dorsal setae and 1 ventral seta, each about 275 μm long, forming a group of 3. Antennae situated on ventral head margin, each 95 μm long, with 2 segments, the second segment about 62.5 μm long, tapering, 1 antenna partly divided on 1 side only. Legs well developed, slender, hind trochanter + femur about 107.5 μm long, hind tibia + tarsus about 105 μm long, claw, slender, about 25 μm long, 5.0 μm wide at base. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0.97. Ratio of lengths of hind tibia to tarsus 1.0. Tibiae each narrow

at base, widening, then tapering abruptly to narrow distal end. All legs with outer setae sensory, each with slightly swollen tip, inner setae flagellate. Labium fairly wide, difficult to measure in available specimen, about same length as clypeolabral shield. Circulus large, about 32.5 μm wide, placed near middle of abdominal segment III. Anal ring about 75 μm wide, with 6 setae; anterior pair slender, each 67.5 μm long, second pair similar, each about 70 μm long, posterior pair stout and long, about 220 μm long, resembling anal lobe setae.

Dorsal surface densely covered in hair-like microtrichia and short, fine setae, except for intersegmental areas. Setae on abdominal segment VIII flagellate, mostly about 20 μm long; similar setae 10–20 μm long, present towards posterior edges of abdominal segments IV–VII; anteriorly, setae much more slender, 6.25–12.00 long, sometimes difficult to discern amongst the dense microtrichia.

Ventral surface with similar microtrichia and setae to those on dorsum. Obanal and cisanal setae present, each about 50 μm long; stout flagellate setae present on abdominal segment VIII, as long as 67 μm but most at posterior edge of abdominal segments about 50 μm long, mixed with others about 20 μm long. Minute slender setae distributed around margins of thorax. Medial area of thorax with stout flagellate setae; medial area of head and lateral area of thorax with a few stout sensory setae, each 15–20 μm long, with slightly expanded tips and with wide thick setal collars.

MATERIAL

HOLOTYPE.   Adult ♀, **Indonesia: Sumatra**, Barat Province, Kotomalintang, nr Lake Maninjau, in soil, extracted by Berlese funnel apparatus, 19.xii.1994 *(L. Deharveng & A. Bedos)* (MNHN).

COMMENTS.   Among the group of species with a dense covering of hair-like microtrichia, *E. maninjauensis* seems to be related to *E. sarawakensis* and *E. sulawesicus* in possessing long stout setae in groups of three on the positions of each anal lobe, and a pair of similar posterior setae on the anal ring. The antennae of *E. sarawakensis* and *E. sulawesicus*, however, are placed well on the dorsum of the cephalothorax, whereas in *E. maninjauensis* they are placed on the ventral head margin. Furthermore, any stout sensory setae with swollen tips in *E. maninjauensis* are distributed on the venter only, whereas in the other two species they occur on the dorsum also.

The epithet is based on the place name 'Lake Maninjau' and the Latin suffix *'-ensis'* denoting locality.

Eumyrmococcus neoguineensis sp. n.

(Fig. 10)

DESCRIPTION

Adult female on microscope slide membranous except for abdominal segment VIII lightly sclerotized; elongate-oval, largest specimen 1.15 mm long, 0.57 mm wide, widest at about abdominal segments II and III; head and thorax rounded, anterior margin of head sometimes straight, constricted slightly at mesothorax, then widening to anterior abdominal segments, remainder of abdomen tapering, base of abdominal segment VIII about 230 µm wide, apparent anal lobes set well apart, apex of abdomen protruding. Position of each anal lobe with 3 or 4 dorsal setae and usually 5 ventral setae forming a group of 8 or 9; inner ventral setae slender, each about 150 µm long, others increasing in length distally, outer ventral and dorsal setae stout, 550–600 µm long. Antennae situated on dorsal head margin, each 420–440 µm long, with 4 segments, second segment longest with a row of short conical setae on anterior edge, increasing in length distally; setae on third and fourth segments long, longest on third segment, about 325 µm long. Legs well developed; hind trochanter + femur 188–232 µm long, hind tibia + tarsus 180–220 µm long, claw slender, about 34 µm long, 7.5 µm wide. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0.93–0.95. Ratio of lengths of hind tibia to tarsus 1.20–1.29. First legs with noticeably larger coxae than in other legs and longer trochanter + femur, 232–245 µm long, and longer tibia + tarsus, 260–272 µm long. Tibiae of all legs swollen near bases and narrowly tapering distally. All legs with long slender setae, except for some stout setae on posterior surface of femur of each first leg. Labium 162–175 µm long, 87–100 µm wide, longer than clypeolabral shield; ratio of length to width 1.62–1.86. Circulus present near anterior end of abdominal segment II but placed well within borders of segment, 20–25 µm in diameter, deeply cupped, about as deep as wide or slightly deeper. Anal ring about 90 µm wide, with 14 slender setae, each about 110 µm long.

Dorsal surface densely covered in slender flagellate setae except around antennal bases and intersegmental areas; some setae at posterior end of abdominal segment VIII each about 87 µm long, those at anterior end of segment about 25 µm long. Anteriorly on abdomen, as far forward as abdominal segment V, mostly 17–25 µm long; in medial area of abdominal segment VI, medial and anterior areas of abdominal segment V, and all anterior segments of abdomen, thorax and head, extensively covered in minute setae 10.0–12.5 µm long. Posterior edges of abdominal segments each with a row of stout setae, each about 100 µm long, a few at lateral edges of abdominal segments each about 125 µm long.

Ventral surface with a similar distribution of setae to that on dorsum but mainly bare on medial areas of head and thorax except for a few short setae. A bunch of invaginated setae present lateral to each first and second coxa, these lightly sclerotized when prepared on slides.

MATERIAL

HOLOTYPE. Adult♀, **Papua New Guinea**, East Sepik Province, Yawasora [Yauwasoru], near Wewak, associated with *Acropyga (Atopodon) ambigua* Emery, in rotting log, 4–6.vii.1972 *(R.W. Taylor)* (ANIC).

PARATYPES. **Papua New Guinea**, same data as holotype, 3 adult♀♀ (ANIC), 2 adult♀♀ (BMNH); same data but in mountain log, 1 adult ♀ (BMNH); Morobe Province, 16 km NW Lae, 'Timber Track', in rotting wood, with *A. (Atopodon) ambigua*, 12.vi.1976 *(R.W. Taylor)*, 1 adult ♀ (ANIC).

COMMENTS. This species shares with *E. corinthiacus* and *E. scorpioides* the character of 4-segmented antennae but the antennae of *E. neoguineensis* are much longer, with long setae on the third and fourth segments, and conical setae on the anterior edge of the second segment. Furthermore, the long stout setae on each anal lobe number eight or nine, whereas those in the other two species are in groups of three. The affinities of *E. neoguineensis* are obscure but *Xenococcus annandalei* also possesses large groups of long stout setae on the anal lobes and the antennae are also 4-segmented with long setae on the third and fourth segments. In *Xenococcus*, however, the antennae are much longer, about as long as the body, and there is well developed articulation between the first and second segments. The bunches of invaginated setae in *E. neoguineensis* have not been seen in any other species. Despite the unusual characters, the true affinities of this spectacular species appear to be with the genus *Eumyrmococcus* to which it is here assigned.

The epithet is a Latinized word for New Guinea with the Latin suffix '-*ensis*' meaning 'belonging or pertaining to'.

Eumyrmococcus nipponensis Terayama

(Fig. 11)

Eumyrmococcus nipponensis Terayama, 1986: 509; 1988: 645; Ben-Dov, 1994: 152. HOLOTYPE ♀, Japan, Noboritachi, Mikura-jima Is, Tokyo, on rootlets of plants in nests of *Acropyga [Atopodon] nipponensis* Terayama, 30.viii.1980 *(K. Masuko)* (NIAES).

DESCRIPTION

Adult female on microscope slide pyriform, largest specimen 1.40 mm long, 0.60 mm wide, widest at mesothorax, abdomen tapering, constricted slightly between abdominal segments VII and VIII, base of abdominal segment VIII about 180 µm wide. Position of each anal lobe with 2 long, stout ventral setae and 1 dorsal seta, forming a group of 3, each seta about

450 μm long. Antennae situated on ventral head margin, each 2-segmented, 260–270 μm long, second segment tapering, 210–215 μm long. Legs well developed, slender; hind trochanter + femur 180–200 μm long, hind tibia + tarsus 182–195 μm long, claw slender, about 30 μm long. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0.95–1.01. Ratio of lengths of hind tibia to tarsus 1.05–1.21. Tibiae swollen near middle then narrowly tapering. All legs with outer setae stout, sensory, swollen apically; inner setae flagellate. Labium 138–150μm long, 75.0–77.5μm wide, slightly longer than clypeolabral shield; ratio of length to width 1.84–1.93. Circulus present, round to slightly elliptical, 20–30 μm wide, deeply cupped, about as deep as wide, situated near middle of abdominal segment III. Anal ring 68–75 μm wide, with 6 setae; anterior pair slender, each about 27 μm long, second pair stouter, each about 62 μm long, posterior pair stout and long, each about 450μm long, resembling anal lobe setae.

Dorsal surface extensively covered with short slender flagellate setae, sparse near head margin and absent in wide intersegmental areas; at posterior end of body each seta about 15 μm long, anteriorly on abdominal segment VIII mostly 12.5 μm long, elsewhere mostly about 7.5 μm long. Short stout sensory setae, each with noticeable swollen tip, fairly numerous across segments and mixed with the short flagellate setae; at posterior end of body, each about 11 μm long but most anteriorly each about 7.5 μm long. Head with longer stout sensory setae 12.5–25.0 μm long. Most setae with setal collars probably slightly raised from surrounding derm so that setae appear to be surrounded by halos.

Ventral surface with similar short setae as on dorsum but not so dense; absent from medial area of thorax. Long sensory setae, each about 35 μm long, present at posterior edge of abdominal segment VII; similar setae, each about 25 μm long, present on head. Other sensory setae shorter, those around margins, each 7.5μm long as on dorsum, others 12–28μm long, distributed across segments. Long, stout flagellate setae present in medial area of thorax. Three very slender sensory setae sometimes present on each side of circulus. Obanal setae stout and long, about as long as anal lobe setae. Many flagellate setae at posterior end of body with thick setal collars.

MATERIAL

Japan: Yakushima Is, Amboh, on rootlets of plants in nests of *Acropyga (Atopodon) nipponensis* Terayama, 17.x.1984 *(M. Terayama)*; Tokunoshima Is, Tampatsuyama, same data but 8.viii.1984 (all labelled paratypes).

COMMENTS.   *E. nipponensis* differs from *E. smithii*, the only other species known from Japan, in possessing a circulus and sensory setae with expanded tips. In *E. smithii*, the circulus is absent and all setae are

flagellate. *E. nipponensis* seems to have affinities with two Australian species, *E. lamondicus* and *E. recalvus*, in possessing similar 2-segmented antennae, each with the second segment long and tapering; also with minute flagellate setae on the dorsum distributed at least as far forward as the prothorax. Most of the sensory setae in the two Australian species, however, are lanceolate, whereas those in *E. nipponensis* are blunt and widely expanded distally.

The ant attending this mealybug was described originally by Terayama (1985), from material collected at the same time.

The accompanying illustration has been prepared from paratypes kindly made available by Dr M. Terayama.

Eumyrmococcus queenslandicus sp. n.

(Fig. 12)

DESCRIPTION

Adult female on microscope slide elongate, largest specimen 1.30 long, 0.65 mm wide, widest at mesothorax, head and thorax rounded, abdomen tapering to rounded posterior end, constricted between abdominal segments VII and VIII, segment VIII about 150 μm wide at base; positions of each anal lobe with 2 dorsal setae and 1 ventral seta, each about 300 μm long, forming a group of 3. Antennae situated on dorsal head margin, each 270–300 μm long, with 2 segments, the second tapering, 220–240 μm long. Legs well developed, slender; hind trochanter + femur 190–192 μm long, hind tibia + tarsus 110–117 μm long, claw slender, about 27.5μm long, 5.0μm wide at base. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0.97–1.02. Ratio of lengths of hind tibia to tarsus 1.37–1.41. Tibiae swollen then tapering towards narrow distal ends. All legs with stout pointed setae. Labium 130–138 μm long, slightly longer than clypeolabral shield, 75–100 μm wide; ratio of length to width 1.38–1.70. Circulus present near middle of abdominal segment II, large and conspicuous, 52–60 μm in diameter, deeply cupped with almost parallel sides but wider than deep. Anal ring 52.5–60.0 μm wide, with 6 setae; anterior pair slender, each about 100 μm long, second pair thicker, each about 220 μm long, posterior pair each about 250μm long, almost as thick and as long as anal lobe setae.

Dorsal surface with crowded slender flagellate setae as far forward as thorax, those on prothorax represented by a medial band, absent laterally on mesothorax leaving bare areas on head and laterally on prothorax, mesothorax and intersegmentally. Setae towards posterior end of abdominal segment VIII each about 37.5 μm long, anteriorly on next few segments mostly 10–20 μm long, on thorax and anterior abdominal segments mostly 10 μm long; some setae on any segment with larger setal collars than others. A

few sensory lanceolate setae, each about 10 μm long, present on thorax and abdominal segments I–V. Setae on head sparse, mostly stout and flagellate, 35–42 μm long.

Ventral surface with similar setae to those on dorsum. Short slender setae present around margins only of thorax and first abdominal segment, few. Long stout setae, 35–42 μm long, not numerous, present on head and medial area of thorax. Sensory lanceolate setae, same as on dorsum, few, distributed on abdominal segments II–V.

MATERIAL

HOLOTYPE. Adult ♀, **Australia**: Queensland, Kirrama Range, NE slope of Mt Pershouse, 700 m, associated with *Acropyga* sp., 5.v.1969 *(E. Kennedy & R.W. Taylor)* (ANIC).

PARATYPES. **Australia**: Queensland, same data as holotype, 7 adult ♀♀ (ANIC), 5 adult ♀♀ (BMNH), 1 adult♀ (USNM), 1 2nd instar (ANIC), 1 2nd instar (BMNH); 4.5 km W of Cape Tribulation, 760 m, taken in the mandibles of *Acropyga* sp. in flight, 20–23.iv.1983 *G.B. Monteith & D.K. Yeates)*, 1 adult ♀ (QM).

COMMENTS. Among the species already described, *E. queenslandicus* comes nearest to *E. nipponensis* in possessing similar antennae, each with a long second segment, and with the thorax and abdomen densely covered in slender setae. In *E. nipponensis*, the sensory setae are blunt and expanded apically, whereas in *E. queenslandicus* they are lanceolate. *E. queenslandicus* comes closest to *E. lamondicus* sp. n. Both species have short lanceolate sensory setae but in *E. queenslandicus* there is a large single circulus only, present on abdominal segment III. In *E. lamondicus* there are two small circuli present on each of abdominal segments II and III. Furthermore, *E. lamondicus* possesses some short, blunt sensory setae on abdominal segment II in addition to lanceolate sensory setae. These blunt setae are absent from *E. queenslandicus*.

Two second instars are also available. These have a similar appearance to the adult females but the short flagellate setae are present only as far forward as abdominal segment IV.

The epithet is based on the locality 'Queensland' and the Latin suffix '-icus' meaning 'belonging to'.

Eumyrmococcus recalvus sp. n.

(Fig. 13)

DESCRIPTION

Adult female on microscope slide, narrow, elongate, 1.40 mm long, 0.65 mm wide, widest at about metathorax; head and thorax rounded, constricted slightly between abdominal segments III and IV, then tapering to posterior end of body, sharply narrowing

between abdominal segments VII and VIII; abdominal segment VIII 162 μm wide at base before tapering abruptly, projecting beyond positions of anal lobes. Each anal lobe with a group of 3 long stout setae, 2 on dorsum and 1 on venter, each seta at least 240 μm long but difficult to measure in available specimen. Antennae each about 270 μm long, with 2 segments, the second segment curved, 205 μm long. Legs well developed, slender; hind trochanter + femur about 170 μm long, hind tibia + tarsus about 140 μm long, claw slender, about 28 μm long. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0.82. Ratio of lengths of hind tibia to tarsus 1.8. Inner leg setae flagellate, outer setae sensory, with slightly swollen tips. Tibiae swollen towards distal ends then narrowing, tarsi expanding then tapering to narrow distal ends, no thicker than bases of claws. Labium about 112 μm long, 82.5 μm wide, about same length as clypeolabral shield; ratio of length to width 1.35; all labial setae flagellate. Circuli numbering 2, each about 10 μm wide, situated near middle of each of abdominal segments II and III, deeply cupped. Anal ring about 48 μm wide with 6 setae; 2 anterior pairs slender, curled in available specimen but about twice length of diameter of anal ring, posterior pair thicker, almost as long as apical setae.

Dorsal surface with crowded slender setae as far forward as abdominal segment II; those on abdominal segment VIII each about 25 μm long, on abdominal segments V–VII mostly 17.5 μm long, anteriorly about 12.5 μm long; some on any segment with larger setal collars. Setae on head, thorax and abdominal segment I, all sensory with only minutely swollen tips, not numerous; many on head and medially on thorax each up to 37.5 μm long; others on thorax and abdominal segment I 12.5 μm long, mingled with minute and slightly swollen setae each about 3.7 μm long.

Ventral surface with similar setae to those on dorsum as far forward as abdominal segment II; anteriorly not numerous; metathorax and abdominal segment I with short sensory setae as on dorsum, on margins of head and thorax mostly long and sensory, up to 37.5 μm long; others on medial areas of thorax, long and flagellate.

MATERIAL

HOLOTYPE. Adult ♀, **Australia**, Queensland, Byfield, 22°51′S, 150°39′E, associated with *Acropyga* sp., 26.x.1976 *(R.W. Taylor, T.A. Weir)* (ANIC).

PARATYPES. **Australia**, same data as holotype, 4 2nd instars (ANIC), 2 2nd instars (BMNH).

COMMENTS. This species is very close to *E. taylori* sp. n., differing mainly in the shape of the setae anterior to abdominal segment II. In *E. reclavus*, these setae on the dorsum and around the ventral margins are all sensory and slightly expanded apically, the only

flagellate setae are those situated medially on the venter of the thorax. In *E. taylori*, all setae in these positions are flagellate.

Material at hand also contains six second instars. These resemble the adult female but the minute flagellate setae are not so crowded and the appendages are slightly smaller.

The epithet *'recalvus'* is the Latin adjective meaning 'bald in front', referring to the paucity of setae at the anterior end of the body.

Eumyrmococcus sarawakensis sp. n.

(Figs. 14, 15)

DESCRIPTION

Adult female on microscope slide extremely slender, largest specimen 1.35 mm long, 0.52 mm wide, widest at about prothorax, then gently tapering, abdominal segment VIII about 115 μm wide at base. Position of each anal lobe with 1 stout dorsal seta and 2 ventral setae forming a group of 3, each 430–488 μm long. Antennae placed well on dorsum of cephalothorax, each 260–267 μm long, with 2 segments, second tapering, 210–215 μm long. Legs well developed, slender; hind trochanter + femur 162.5–182.0μm long, hind tibia + tarsus 160–185 μm long, claw slender, about 22.5 μm long, 6.25 μm wide at base. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0.97–1.01. Ratio of lengths of hind tibia to tarsus 1.00–1.05. Outer setae on legs sensory, with swollen tips, inner setae flagellate. Labium about 137 μm long, longer than clypeolabral shield, 70.0–82.5 μm wide, ratio of length to width 1.66–1.96. Circulus large, round to slightly elliptical, 75–85 μm wide, situated in middle of abdominal segment III, cupped or bowl-shaped, not so deep as wide. Anal ring 65–70μm wide, with 6 setae; anterior pair each about 32.5 μm long, second pair each about 62.5 μm long, posterior pair about 390 μm long, similar to anal lobe setae.

Dorsal surface with minute setae and hair-like microtrichia covering entire surface except for intersegmental areas. Setae on abdominal segment VIII each about 10.0–12.5μm long, others anteriorly mostly about 5 μm long, difficult to discern among microtrichia. Stout sensory setae with swollen tips, present on head, each 17.5– 22.5 μm long, not numerous. A few sensory setae, each about 12.5 μm long, present on thorax and abdominal segment I.

Ventral surface with similar setae and microtrichia to those on dorsum. Stout sensory setae present on head and thorax, not numerous; short sensory setae, 10–15 μm long, few, distributed across abdominal segments II–VI.

Second instar
Similar in shape to adult female. Legs and antennae shorter. Hair-like microtrichia present on abdomen

only. Short sensory setae extending to abdominal segment VII. Circulus large as in adult female.

Adult Male (Fig. 15).
Body of adult male degenerate, elongate, slender, largest specimen 1.35 mm long, 0.50 mm wide, widest at mesothorax, head and thorax rounded, then gently tapering to rounded posterior end, base of abdominal segment VIII about 150 mm wide. Area between antennae on venter tessellated. Antennae short, almost conical, 2-segmented, 37.5–45.0 mm long, situated near ventral head margin. Legs squat, coxae wide; trochanter + femur fused, unsegmented, stout, about 67.5 mm long; tibia + tarsus slender, 50–57 mm long, sometimes with indistinct segmentation; claw distorted, stout and almost triangular, about 12.5 mm long. Genital capsule retracted inside abdomen, ventral slit almost square. Aedeagus about 100 mm long, stout, almost trumpet-shaped at apex. Anus oval, situated at posterior end of abdomen at base of sclerotized extension to abdominal segment VIII, this extension about 1.5 mm wide and long, hook-shaped in profile, equivalent to long style in male of *E. taylori*.

Dorsal and ventral surfaces practically naked except for some minute setae, each with setal length considerably smaller than width of collar, except on dorsum of thorax where setae slightly longer.

COMMENTS.   There is available also a single male pupa with an adult male inside. Also available are some female pupae, one of which shows the developing adult female inside.

MATERIAL

HOLOTYPE.   Adult ♀, **Malaysia, Sarawak**, 1°38′N 113°35′E, associated with *Acropyga* sp., 25.ii.1963 *(A. Emerson)* (ANIC).

PARATYPES. ♀, **Malaysia, Sarawak**, same data as holotype, 1 adult ♀, 7 adult ♂♂ (ANIC), 2 adult ♀♀, 7 adult ♂♂ (BMNH), 2 2nd instars (ANIC), 2 2nd instars (BMNH), 5 pupae ♀♀ (ANIC), 3 pupae ♀♀ (BMNH), 3 pupae ♂♂ (ANIC), 2 pupae ♂♂ (BMNH).

COMMENTS.   This singular species has an unusual shape, evenly tapering posteriorly from the prothorax. It belongs to a group collected within the tropics and is extensively clothed in hair-like microtrichia and minute setae. *E. sarawakensis* comes closest to *E. sulawesicus* from which it differs mainly in possessing shorter and fewer stout sensory setae on the cephalothorax, mostly 17.5–22.5 μm long. In *E. sulawesicus*, these setae are noticeably longer, 45–50μm long and more numerous.

Most of the differences are small but both species are known from widely isolated localities and at present this separation is justified.

The epithet is based on the name of the locality and the Latin suffix *'-ensis'* indicating origin.

Eumyrmococcus scorpioides (De Lotto)

(Fig. 16)

Xenococcus scorpioides De Lotto, 1977: 33. HOLOTYPE♀, SouthAfrica, Cape Province, Jacobs Bay (SANC) [examined].
Eumyrmococcus scorpioides (De Lotto), Williams, 1993: 217; Ben-Dov, 1994: 152.

DESCRIPTION

Appearance in life not recorded. Adult female on microscope slide elongate, body membranous except for moderately sclerotized abdominal segment VIII, largest specimen 1.55 mm long, 0.77 mm wide, widest at mesothorax, head and thorax rounded, with a constriction between abdominal segments III and IV, narrowing abruptly, remainder of abdomen tapering with a further constriction between abdominal segments VII and VIII; segment VIII about 170μm wide at base, posterior end rounded. Positions of each anal lobe with 2 stout ventral setae and 1 dorsal seta, each about 800μm long, forming a group of 3.Antennae slender, 4-segmented, each 175–190 μm long. Legs well developed; hind trochanter + femur 170–180μm long, hind tibia + tarsus 150–162 μm long, claw about 27.5 μm long, stout, 12.5 μm wide at base. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0.87–0.92. Ratio of lengths of hind tibia to tarsus 1.41–1.61. Outer setae on legs sensory, slightly swollen at tips; inner setae flagellate. Labium 147–150 μm long, about as long as clypeolabral shield, 50–65 μm wide; ratio of length to width 2.26–3.00. Circuli numbering 2, situated anteriorly on abdominal segments II and III but within borders of segments; circulus on abdominal segment II about 25 μm in diameter, on segment III about 15 μm in diameter, both cup-shaped. Anal ring 57–60 μm wide, with 6 slender setae; posterior pair each about 87 μm long, anterior 2 pairs shorter but curled in available specimens.

Dorsal surface with crowded flagellate setae on abdomen, those at posterior end of abdominal segment VIII each about 75μm long, on abdominal segment VII mostly about 37μm long, anteriorly about 25μm long. Head and thoracic setae mostly sensory, with slightly swollen tips, 12.5–25.0 μm long but some flagellate setae present mingled with the sensory setae.

Ventral surface with similar setae to those on dorsum, crowded and flagellate as far forward as abdominal segment III but a few sensory setae also present on abdominal segment III. Anteriorly, setae mostly sensory with swollen tips except in medial area of thorax where they are mostly flagellate but a few sensory setae also present.

MATERIAL

South Africa: Cape Province, Jacobs Bay, in nests of *Acropyga (Malacomyrma) arnoldi* Sanschi, 7.viii.1969 *(A.J. Prins)*.

COMMENTS. In possessing 4-segmented antennae and in the general distribution of body setae, this species is related to *E. corinthiacus*. Most dorsal and ventral setae on the head and thorax of *E. scorpioides*, however, are sensory with slightly swollen tips, whereas in *E. corinthiacus* they are all flagellate. Moreover, the long setae on the anal lobes of *E. scorpioides* are each over 800 μm long and those of *E. corinthiacus* are thicker but at most only about 200–230 μm long. *E. scorpioides* differs from all other known species of *Eumyrmococcus* in possessing stout claws, those in other species being much more slender.

The accompanying illustration is based on the holotype and two paratypes kindly made available for this work by Ian Millar, Plant Protection Research Institute, Pretoria, South Africa.

Eumyrmococcus smithii Silvestri

(Fig. 17)

Eumyrmococcus smithii Silvestri, 1926: 273; Williams, 1970: 138; 1978: 63; Ben-Dov. 1994: 152. LECTOTYPE♀, **China**: Macao, [on roots of plants, attended by the ant *Acropyga (Rhizomyrma) sautori* Forel], designated by Williams, 1978: 63 (IEAUN) [examined].

COMMENTS. This species was described and illustrated in detail by Williams (1970) from material collected in various localities in China and Japan. Dr M. Terayama has kindly made available some fresh material collected in Okinawa and a new illustration is presented here based on this material.

The most important characters are the 2-segmented antennae, the absence of a circulus, long stout setae in groups of three on each apparent anal lobe, each seta about 500 μm long in the species illustrated but up to 700 μm long in other specimens. The anal ring possesses 6 setae, the 2 anterior pairs short and slender and the posterior pair stout, about as long as the anal setae. All the body setae are short, slender and flagellate, occupying all the dorsal surface except for intersegmental areas. A striking character, not seen in any other species, is a long wide extension on each hind coxal process.

In lacking any sensory setae with blunt or swollen tips, *E. smithii* is related to *E. kolombangarae* and *E. kusiacus*, described here from the Solomon Islands. It differs from both of these species in lacking a circulus.

MATERIAL

China: Macao, in nest of *Acropyga (Rhizomyrma) sauteri*. **Taiwan**: Taichu, on sugarcane, 24.ii.1933 *(M. Yanagihara)*. **Japan**: Ryukyu Is, Okinawa Is, in nest of *A. (Rhizomyrma) sauteri*, 15.viii.1984 *(M. Terayama)*; without locality, ex coll. R. Takahashi.

The species was also recorded from Shanghai by

Silvestri (1926, 1927) and from Taiwan by Takahashi (1934).

Eumyrmococcus sulawesicus sp. n.

(Fig. 18)

DESCRIPTION

Adult female on microscope slide narrowly elongate, membranous, largest specimen 1.50 mm long, 0.60 wide, widest at mesothorax; head and thorax rounded then constricting slightly between abdominal segments VII and VIII, abdominal segment VIII 162 μm wide at base. Position of each anal lobe with 2 stout dorsal setae and 1 ventral seta, forming a group of 3, each 510–525 μm long. Antennae placed well on to dorsum, each 275–295 μm long, with 2 segments, second tapering, 215–232 μm long. Legs well developed, slender; hind trochanter + femur 200–205 μm long, hind tibia + tarsus 182.5–205.0 μm long, claw slender, about 27.5 μm long, 7.5 μm wide at base. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0.90–1.02. Ratio of lengths of hind tibia to tarsus 0.87–0.95. Leg setae short and sensory on outer edges, each with swollen tip, flagellate on inner edges. Labium about 142.5 μm long, longer than clypeolabral shield, 95 μm wide, ratio of length to width 1.5. Circulus large, round to slightly elliptical. Anal ring 72–78 μm wide with 6 setae; anterior pair slender, each about 45 μm long, second pair each about 75 μm long, posterior pair stout, each about 475 μm long, resembling anal lobe setae with which they are sometimes intertwined.

Dorsal surface entirely covered with minute slender setae and fine microtrichia. Setae on abdominal segment VIII mostly about 15 μm long, anteriorly about 6–10 μm long, many of longer setae with larger setal collars, density less towards head and thorax. Long sensory setae, each with swollen tip, 45–50 μm long, present on head and thorax. Microtrichia dense, hair-like, short and stouter on abdominal segment VIII, very slender anteriorly. Setae and microtrichia absent from intersegmental areas.

Ventral surface with similar setae and microtrichia to those on dorsum, covering entire surface except for intersegmental areas. Long, stout sensory setae, as on dorsum, present on head and thorax, fairly numerous, becoming shorter, 17.5–25.0 μm long, towards anterior abdominal segments except for one or two, each about 32 μm long near circulus. Sensory setae towards abdominal segment V mostly about 15 μm long, sometimes blunt, without swollen tips. Setae stout and flagellate on medial area of thorax.

MATERIAL

HOLOTYPE. Adult ♀, **Indonesia, Sulawesi**, Sulawesi Utara, Toraut forest, Dumoga-Bone National Park, with *Acropyga (Atopodon)* sp., 15.iii.1985 *(R.H.L. Disney)* (BMNH).

PARATYPES. **Indonesia, Sulawesi**, same data as holotype, 3 adult ♀♀ (BMNH), 6 2nd instars (BMNH).

COMMENTS. This species, covered in hair-like microtrichia, is noticeably elongate with the antennae placed well on the dorsum of the cephalothorax. It is closely related to *E. sarawakensis* in most characters but the stout sensory setae on the head and thorax are longer, up to 50 μm long, and more numerous. In *E. sulawesicus* these setae are at most about 22.5 μm long.

A few second instars are also available. They differ from the adult female in having much fewer minute setae and microtrichia, but the stout sensory setae are more numerous, extending posteriorly as far as abdominal segment VII.

The epithet is based on the country of origin, Sulawesi, and the Latin suffix '-icus' meaning 'pertaining to'.

Eumyrmococcus taylori sp. n.

(Figs 19–22)

DESCRIPTION

Appearance in life not recorded. Adult female (Fig. 19) on microscope slide elongate, narrow, membranous except for posterior end of body moderately sclerotized; longest specimen 1.30 mm long, 0.50 mm wide, widest at mesothorax; constricting between abdominal segments IV and V, widening at abdominal segment VI, then narrowly tapering between abdominal segments VII and VIII, base of abdominal segment VIII 117–125 μm wide; posterior end of body rounded, projecting beyond actual anal lobes, these each with 2 ventral setae and 1 long stout seta forming a group of 3, each seta about 315 μm long. Antennae each situated on dorsal margin when flattened on slide, 310–390 μm long, with 2 segments, second segment long, about 290–330 μm long, curved and tapering. Legs well developed, slender, hind trochanter + femur 170–210 μm long, hind tibia + tarsus 150–190 μm long, claw slender, about 27 μm long. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0.88–0.90. Ratio of lengths of hind tibia to tarsus 1.14–1.25. Tibia swollen towards distal end then tapering. Tarsus swollen then tapering to narrow distal end, about as wide as base of claw. Leg setae all flagellate. Labium about as long as clypeolabral shield, 117–120 μm long, 77.5–82.5 μm wide; ratio of length to width 1.41–1.51. Circuli numbering 1 or 2, situated within borders of abdominal segments II and III; if only 1 circulus then present on abdominal segment III; circulus on abdominal segment II about 8.75 μm wide, on abdominal segment III about 11.25 μm wide, each circulus deeply cup-shaped. Anal ring 53–57 μm wide, with 6 setae; anterior pair each about 67 μm long, second pair each about 112 μm long, posterior pair thicker, each about 275 μm long, resembling the apical setae.

Dorsal surface with crowded flagellate setae as far forward as abdominal segment II, mostly about 17.5–25.0 µm long on abdominal segment VIII, those on anterior segments each about 15 µm long, very slender. Minute swollen setae present, each about 3.75 µm long, sparse, mingled with the flagellate setae on abdominal segments II–IV. Setae anterior to abdominal segment II mostly thick and flagellate, 25–50 µm long, not numerous. A few minute swollen setae present on head, each about 3.5 µm long, slightly narrower than those on abdomen.

Ventral surface with similar setae to those on dorsum, crowded as far forward as abdominal segment II, with a few minute swollen setae on abdominal segments II–VI. Anteriorly a few thicker flagellate setae present as on dorsum, and a few minute swollen setae also present on head and around anterior spiracles.

Second instar (Fig. 20)

Body pyriform, 1.05–1.10 mm long, 0.45–0.58 mm wide, widest at about mesothorax, tapering abruptly to abdominal segment IV then gradually to posterior end of body; base of abdominal segment VIII 75–92 µm wide; posterior end of body projecting beyond actual anal lobes, each lobe with 1 dorsal and 2 stout ventral setae each 375–470 µm long. Antennae each 290–350 µm long, with 2 segments; first 40–50 µm long, second curved, with setae of various lengths, longest at distal end about 100 µm long. Legs well developed; hind trochanter + femur 155–195 µm long, hind tibia + tarsus 157.5–185.0 µm long, claw slender, about 22.5 µm long. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0.94–1.04. Ratio of lengths of hind tibia to tarsus 1.03–1.25. First pair of legs longer, trochanter + femur 170–200 µm long, tibia + tarsus 185–207 µm long. Labium broad, 105–115 µm long, longer than clypeolabral shield. Circulus present within borders of abdominal segment III, 7.50–11.25 µm in diameter, deeply cupped. Anal ring 35–40 µm wide, with 6 setae; 2 anterior pairs slender, each about 75 µm long, posterior pair stout but not so stout as anal lobe setae, each about 350 µm long.

Dorsal surface with long stout setae 95–120 µm long at posterior edges of abdominal segments III–VII; other abdominal setae, each about 25 µm long, present on abdominal segment VIII, and others, each about 20 µm long, at anterior edges of abdominal segments IV–VII; slenderer setae on these segments mostly about 15 µm long. Other setae on head, thorax and abdominal segments I–III, each 20–55 µm long, not numerous. Minute clavate setae present on abdominal segments II–IV, and others, about same size but with smaller collars, present on head and lateral area of metathorax.

Ventral surface with similar setae to those on dorsum. Abdominal segments V and VI each with a few elongate sensory setae; abdominal segments III and IV each with a few shorter sensory setae. Minute clavate setae present anterior to each spiracle and posterior to each second spiracle.

COMMENTS. Material from Baroalba Spring possesses legs and antennae slightly longer than that from Sawcut Gorge but the proportions of the segments are about the same. At present, specimens from both areas are treated here as conspecific.

Female pupa (Figs 1B, 21A)

Body membranous, elongate-pyriform, 0.90–0.99 mm long, 0.38–0.43 mm wide, widest at mesothorax, abdomen gently tapering, posterior end projecting only slightly, segmentation distinct on abdomen. Antennae situated on dorsal margin, 2-segmented, curved, 262–270 µm long, apex rounded. Legs tapering to pointed developing claws, 325–390 µm long, with faint segmentation. Labium distinct, 100–120 µm long, longer than clypeolabral shield. Anal ring dorsal, at apex of abdomen. Spiracles present.

COMMENTS. Specimens are available showing the adult female inside, almost ready to emerge (Fig. 1B).

Adult Male (Fig. 22)

Body of adult male elongate-pyriform, 104 µm long, 40 µm wide, widest at mesothorax, head and thorax rounded, tapering abruptly to anterior end of abdominal segment IV, remainder of abdomen narrow, tapering gradually, base of abdominal segment VII 90 µm wide. Apparent anal lobes each with 1 stout dorsal seta and 2 ventral setae, each 200–250 µm long, forming a group of 3. Antennae 2-segmented, 310–400 µm long; second segment curved, 270–350 µm long, longest setae about 90 µm long. Legs well developed, slender; hind trochanter + femur 155–175 µm long; hind tibia + tarsus 147.5– 175.0 µm long; claw slender, 25 µm long, 5 µm wide at base. Ratio of lengths of hind tibia + femur to trochanter + femur 0.94–1.01. Ratio of lengths of hind tibia to tarsus 1.03–1.33. First legs longer; trochanter + femur 180–210 µm long, tibia + tarsus 180–200 µm long. Mouthparts represented by tentorium, remains of clypeolabral shield with a few setae, and a small vestigial labium. Genital capsule almost triangular, 65 µm wide, length about the same, venter of penial sheath rounded apically, ventral slit rounded near base then widening slightly apically; basal ridge of penial sheath well defined ventrally; aedeagus long and pointed, 250–262 µm long. Dorsal aspect with an apparent anal ring and anal ring setae at posterior edge of abdominal segment VIII; 2 anterior pairs of setae each about 45 µm long, posterior pair thicker, each about 58 µm long, situated near curved ends of anal ring and lateral to large, almost triangular anus, about 30 µm wide. Dorsal part of capsule extending from anus as a slender elongate style, about 125 µm long, shorter than aedeagus, slightly expanded

apically then pointed, tip bearing a few spicule-like extensions; base of style with 2 pairs of short setae.

Dorsal surface of body with short, flagellate setae, each about 12.5–15.0 μm long, on abdominal segment VIII. Anteriorly on all segments including head, with transverse rows of long, slender flagellate setae 62–70 μm long, these sometimes absent; posterior abdominal segments also with a few short flagellate setae. Minute sensory setae, each with slightly swollen tip and scarcely longer than a setal collar, present in moderate numbers across segments anterior to abdominal segment VIII.

Ventral surface with similar distribution of setae to those on dorsum, the long flagellate setae sometimes absent. Minute sensory setae present as on dorsum but fewer on thorax.

Male prepupa (Fig. 21B)

Body elongate-pyriform, about 0.90 mm long, 0.40 mm wide at mesothorax; abdomen with distinct segmentation, tapering to rounded apex. Antennae situated on dorsal margin, 2-segmented, tapering, apex rounded, 220–240 μm long. Legs 305–330 μm long, segmented, developing claws pointed. Anal ring present at apex of abdomen. Mouthparts represented by remains of clypeolabral shield and small lobes of labium. Spiracles distinct.

COMMENTS. Specimens are available showing the developing pupa inside.

Male pupa (Fig. 21C)

Body narrowly pyriform, 1.00–1.27 mm long, 0.40–0.43 mm wide, widest at mesothorax, narrowing to abdominal segment V then tapering to developing genital capsule, posterior end elongate, pointed; segments distinct on abdomen. Antennae tapering to pointed distal end, 285–300 μm long, situated on dorsal head margin. Legs tapering to pointed claws, 320–360 μm long. Mouthparts represented by indistinct clypeolabral shield. Spiracles present. Anal ring situated dorsally towards anterior end of abdominal segment VIII.

COMMENTS. Some specimens available show the adult male complete, almost ready to emerge (Fig. 1A).

MATERIAL

HOLOTYPE. Adult ♀, **Australia**: Northern Territory, Sawcut Gorge, 12°55′S, 132°56′E, associated with *Acropyga* sp., 19.xi.1972 *(R.W. Taylor)* (ANIC).

PARATYPES. **Australia**: same data as holotype, 1 adult ♀, 2 adult ♂♂ (ANIC), 1 2nd instar, 2 ♂♂ pupae, 1 ♀ pupa (ANIC), 1 adult ♀, 3 adult ♂♂, 1 ♂ pupa (BMNH): same data but 13.vi.1973, 1 adult ♂, 4 2nd instars, 2 prepupae ♂♂, 1 pupa ♂, 2 pupae ♀♀ (ANIC); 2 2nd instars, 1 prepupa ♂ (BMNH). Baroalba Spring,

12°47′S, 132°51′E, with *Acropyga* sp., 17.xi.1972 *(R.W. Taylor)*, 1 adult ♂, 7 2nd instars, 7 pupae ♀♀ (ANIC), 1 2nd instar, 3 pupae ♀♀ (BMNH); same data but 17.xi.1971, 1 adult ♂ (ANIC).

COMMENTS. In possessing a general distribution of short crowded setae in the adult female, only as far forward as abdominal segment II, this species closely resembles *E. recalvus* sp. n. In *E. taylori*, however, all the dorsal setae on the head, thorax and first abdominal segment are flagellate except for a few minute swollen sensory setae. In *E. recalvus*, all the dorsal setae at the anterior end of the body are sensory and bluntly tipped or slightly swollen. Furthermore, the outer setae on the legs of *E. taylori* are flagellate, whereas those of *E. recalvus* are sensory.

There are available some second instars from all localities. These differ from the adult female in lacking the wide bands of dense setae across the segments and instead there are long slender setae, similar to those of the adult male.

Adult males appear to be of two forms, with or without long flagellate body setae. Most of the adult males from Sawcut Gorge possess the long setae except in one specimen. One of the adult males from Baroalba Spring also lacks these long setae as does the specimen still enclosed within the pupal instar. All specimens are here regarded as representing the same species. Such wide differences occur also in adult females of *Molluscococcus fibrillae* Hall, redescribed by Miller and Williams (1995). This species normally possesses extremely long setae, 812–928 μm long over most of the dorsum, but there are also specimens with short setae only, 44–61 μm long.

The only adult females available for study from Baroalba Spring are still within the pupal instar and they appear to be identical with adult females from Sawcut Gorge. If there is evidence in future that the two forms of adult male discussed here, represent two distinct species, then the matter can easily be corrected.

The species is named after the collector, R.W. Taylor, CSIRO, Canberra, Australia, who sent many of the mealybugs discussed in this work.

Xenococcus Silvestri

Xenococcus Silvestri, 1924: 312; Williams, 1978: 63.

TYPE SPECIES. *Xenococcus annandalei* Silvestri, by original designation and monotypy.

DESCRIPTION

Body of adult female broadly oval, membranous, abdomen tapering abruptly to narrow sclerotized apical segment. Anal lobes not developed, recognizable by inner ventral grooves, position of each lobe with a group of 3 long, stout setae, 2 ventral and 1 dorsal.

Anal ring protruding between anal lobes, represented by crescentic dorsal band without cells, with 8 anal ring setae, the 2 anterior pairs of setae slender, the third pair thicker and longer, detached from ring, the fourth pair ventral in position, about as long as anal lobe setae. Antennae 4-segmented, placed on dorsal margin, tapering, about as long as body with strong articulation between first and second segments. Legs well developed, long and slender; claw elongate, slender. Labium elongate, longer than wide, setae on upper surface well spaced. Circuli present, round and shallowly cupped. Dorsal body setae minute and abundant, extending to lateral ventral margins on thorax. Ventral setae mostly long and stouter. Sickle-shaped setae usually present on thorax. Eyes absent. Ostioles absent. Pores and ducts absent.

COMMENTS. In life, the abdomen of *Xenococcus* curls slightly to the dorsum as in *Eumyrmococcus*. The genus differs from *Eumyrmococcus* in possessing very long antennae with well developed articulation between the first and second segments. Although the abdomen tapers, it narrows abruptly to a narrow abdominal segment VIII and the body is widest at about the metathorax. In *Eumyrmococcus*, the whole cephalothorax is dilated and the abdomen tapers gradually. Furthermore, only the dorsal abdominal setae in *Xenococcus* are short and crowded, those on the venter of the abdomen, although numerous, are long and stouter, similar to the medial ventral setae on the head and thorax. The ventral abdominal setae in *Eumyrmococcus* are always short and crowded, similar to the dorsal abdominal setae.

At present, two species are recognized, always associated with the ant genus *Acropyga*. The female possesses a pupal instar and the adult male of one of the species is described on p. 24.

Key to Species of *Xenococcus* (Adult Females)

1   Legs with tibia shorter than tarsus. Antennae each about 860–1090 µm long .... *acropygae* (p. 23)

–   Legs with tibia about twice as long as tarsus. Antennae about 1480–1550 µm long .... *annandalei* (p. 25)

Xenococcus acropygae sp. n.

(Figs 23–26)

Xenococcus annandalei Silvestri, Williams, 1985: 390; Williams and Watson, 1988: 221 (mis-identifications).

DESCRIPTION
Adult female (Fig. 23) on microscope slide pyriform, narrowing at abdominal segment VII; 1.27–1.65 mm long, 0.74–1.08 mm wide, widest at about metathorax;

body membranous except for sclerotized abdominal segment VIII, posterior end of body projecting beyond anal lobes; base of abdominal segment VIII 180–220 µm wide; anal lobes each with 1 dorsal and 2 ventral setae, all stout, forming a group of 3, each 875–920 µm long. Antennae conspicuous, each 860–1090 µm long, with 4 segments; segment 1 170–230 µm long (type series 90–120), segment 2 280–300 µm long (type series 330–360), segment 3 90–130 µm long (type series 90–120), segment 4 200–300 µm long (type series 240–300); segment 1 170–230 µm wide, segments progressively narrowerer to segment 4 60–100 µm wide, segment 4 tapering. All antennal segments with long stout setae, segment 2 with about 30 setae on ventral surface; longest setae on segment 4 400 µm long, setal bases 3–5 µm wide with correspondingly wide setal collars. Segments 1 and 2 strongly articulated with grooves at distal end of segment 1 and minute projections at proximal end of segment 2. Tip of segment 4 with a pair of peg-like setae each 10.0–12.5 µm long. Legs well developed; hind trochanter + femur 270–380 µm long (type series 290–340), hind tibia + tarsus 280–415 µm long (type series 310–360), claw slender about 35–45 µm long. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 1.01–1.13. Ratio of lengths of hind tibia to tarsus 0.66–0.95; tarsus always longer than tibia. Hind tarsus swollen then narrowing distally. All legs with long stout setae, the longest at distal end of femur, 250–300 µm long. Labium 165–220 µm long, longer than clypeolabral shield, setae well separated. Circuli normally numbering 2 within borders of abdominal segments II and III, each 27.5–47.0 µm in diameter, with rim projecting from surrounding derm, inner part cup-shaped, shallow. Occasionally a small third circulus present on abdominal segment IV. Anal ring 77.5–85.0 µm wide with 8 setae; 2 anterior pairs slender, each about 130 µm long, 2 posterior pairs stout, each about as long as anal lobe setae, 1 pair on dorsum and the posteriormost pair usually placed on venter.

Dorsal surface densely covered with slender setae except in intersegmental areas and on head, mostly curved, each about 15 µm long towards anterior edges of segments, and about 20 µm long towards posterior edges of segments; a few longer setae, each about 25 µm long with larger collars, present across all segments; abdominal segment VIII with fewer but longer setae. Sickle-shaped setae usually present on thorax and anterior abdominal segments but sometimes absent entirely, each with slender tip. Setae near each antennal base slender, stouter on head margin.

Ventral surface with stout setae on abdomen and medial areas of head and thorax, 40–165 µm long except for some on margins of abdominal segment VIII, each about 300 µm long. Short slender setae as on dorsum, present around margins of anterior ab-

dominal segments and thorax. A few sickle-shaped setae usually present near margin of thorax.

COMMENTS.   This species differs from *X, annandalei* mainly in the lengths and ratios of the tibiae and tarsi. In *X. acropygae*, the tarsus is longer than the tibia but in *X. annandalei*, the tibia is about twice as long as the tarsus. Furthermore, the setal bases on the antennae of *A. acropygae* are mostly narrower than those of *X. annandalei*. Moreover, the antennae and legs of *A. acropygae* are shorter than those of *A. annandalei*.

First instar (sex not determined) (Fig. 24)

COMMENTS.   This instar was described by Williams (1978) from specimens collected in India, Mysore, on coconut roots under the name *X. annandalei*. Specimens from southern Asia and Australasia agree with these first instars but show wider variation. The body varies from 0.70–1.05 mm long and 0.27–0.58 mm wide. Antennae 4-segmented, 740–880 µm long, with long stout setae, the longest on segment 4 about 250 µm long. Hind trochanter + femur 175–250 µm long, hind tibia + tarsus 215–270 µm long. Ratio of lengths of hind tibia + tarsus to trochanter + femur 1.08–1.27. Ratio of lengths of hind tibia to tarsus 0.58–0.74, tarsus always noticeably longer than tibia. All segments with long stout setae, longest at distal end of femur about 160 µm long. Anal ring with 4 pairs of setae; 2 anterior pairs slender, each about 60–110 µm long, third pair stouter, 295–360 µm long, fourth pair stoutest, 535–750 µm long, resembling the anal lobe setae. Anal lobe setae, stout, usually curled when prepared on slides, 675–700 µm long, forming a group of 3 on each anal lobe, 1 on venter and 2 on dorsum. Body setae short and curved on head and thorax, each 12–15 µm long, accompanied by a few sickle-shaped setae on dorsum. Other body setae 40–88 µm long except on margins where they are 100–120 µm long.

A new illustration has been prepared for this work based on specimens collected at the type locality, Sulawesi.

Third-instar female (pupa) (Fig. 25A)

Body broadly oval, 0.84–0.90 mm long, 0.55–0.67 mm wide, membranous, with only faint signs of segmentation at posterior end of abdomen. Antennae dorsal, 660–760 µm long, tapering. Legs tapering, 425–530 µm long, segmentation faint. Labium distinct, 135–145 µm long, longer than clypeolabral shield. Spiracles distinct.

COMMENTS.   The female pupal instar is always recognizable by the well developed labium and the long dorsal antennae. Some specimens available have the developing adult female still within the pupal instar.

Adult male (Fig. 26)

Body normally curved ventrally and distorted when prepared on microscope slides. When flattened, broadly oval, about 1.0 mm long, 0.70 mm wide, sides sub-parallel, widest at about abdominal segments II and V. Head and abdominal segment I sclerotized dorsally except at anterior end surrounding antennae; ventrally, sclerotized laterally on thorax. Antennae situated on dorsal membranous area, each 1-segmented, tubercle-like, with 6 stout setae, each 30–35 µm long. Legs placed well anterior on body, of an unusual shape, squat and robust. Coxae large. Trochanter + femur stout, about 70 µm long, fused except for faint line apparent in some specimens, trochanter with the usual 2 pairs of sensory pores. Tibia + tarsus much narrower, tapering, about 75 µm long. Claw about 20 µm long, unusual, with well developed wide base, actual claw pointed and slender with apparently a pair of stout blunt digitules. Genital capsule about 290 µm long, 110 µm wide, mostly internal, the external venter of penial sheath about 170 µm long; ventral slit indistinct, at distal end of sheath; tip of sheath with a few minute setae. Aedeagus strongly sclerotized, elongate. Base of genital capsule dorsally with a pair of lobes, each with a group of 3 stout setae, 30–37 µm long, and usually 4 short setae, the lobes situated on each side of a minute projecting plate; anus, when viewed laterally, opening under the plate; entire area normally lying between the genital capsule and dorsal surface of abdomen when flattened on slide.

Body setae of 2 types. A band of setae present across anterior edges of venter of abdominal segments II and III, each seta minute and shorter than diameter of heavily sclerotized collar. A minute type of seta with membranous collar, present across dorsal and ventral segments; setae in a row near ventral edge of abdominal segment IV either with membranous or sclerotized collars.

Third-instar male (prepupa) (Fig. 25B)

Body almost rotund, 0.78–0.86 mm long, 0.66–0.70 mm wide. Segmentation discernible on dorsum and venter of abdomen. Antennae dorsal, tapering to blunt apex, 185–260 µm long. Legs 180–240 µm long, tapering, with faint segmentation. Remains of clypeolabral shield and labium present. Spiracles well developed.

COMMENTS.   The prepupal instar is recognizable by the dorsal developing antennae, only about one-third the length of those of the female pupa. There are faint signs of the labium and clypeolabral shield.

Fourth-instar male (pupa) (Fig. 25C)

Body broadly oval, 0.86–0.98 mm long, 0.65–0.75 mm wide, with signs of segmentation on abdomen. Anten-

nae reduced to small triangular flaps on venter of head, 25–30 µm long, 50–65 µm wide. Legs 155–200 µm long, stout and tapering to sclerotized points or developing claws, segmentation not discernible. Small area of clypeolabral shield present only. Spiracles distinct.

COMMENTS. In the male pupa the legs are usually shorter than those of the prepupa but the lengths sometimes overlap. The most distinctive pupal character is the shape of the antennae which are short, triangular and present on the anterior edge of the head to contain the short developing antennae which in the adult male lie dorsally.

MATERIAL

HOLOTYPE. Adult ♀, **Indonesia, Sulawesi**, Sulawesi Utara, Dumoga-Bone National Park, Toraut forest, with *Acropyga (Acropyga) acutiventris* Roger, 19.iii. 1985 *(R.H. Disney)* (BMNH).

PARATYPES. **Indonesia, Sulawesi**, same data as holotype but *(R.H. Disney* or *R.H. Disney & J.H. Martin)*, 3 adult ♀♀ (BMNH), 10 adult ♂♂ (BMNH), 1 adult♂ (ANIC), 1 adult♂ (MNHN), 1 adult♂ (USNM), 18 1st instars, 24 pupae ♀♀, 4 prepupae ♂♂, 3 pupae ♂♂ (BMNH).

Non-type material (all ♀♀). **Indonesia**, Krakatau, Anak Krakatau, Rakata (in mandibles of *A. acutiventris*). **India**, Mysore, on roots of *Cocos nucifera*, 21.vi.1937 *(T.V. Subramanian)* (first instar); Karnataka, Bangalore, on roots of *Vitis vinifera*, 18.i.1996 *(A. Virakramath & B.K. Rajagopal)*. **Singapore**; Botanical Gardens, in soil under wood, with *A. acutiventris*, 21.v.1968. **Philippine Islands**, Palawan (spirit material). **Malaysia, Sabah**, Tawau, Quoin Hill, with *A. acutiventris*, 10.vi.1968. **Papua New Guinea**, Morobe Province, 16 km N.W. Lae, in soil under wood, with *A. acutiventris*, 12.vi.1972 *(R.W. Taylor)*; Wau, McAdam Park, in rotting log, with *A. acutiventris*, 14.vi.1972 *(R.W. Taylor)*; Bulolo (spirit material, with *A. acutiventris* and *A. (Atopodon) ambigua*): East Sepik Province, Angoram, from rotting log, 2.vi.1972 *(R.W. Taylor)*; Yawasora, nr Wewak, from rotting log, 4–6.vii.1972 *(R.W. Taylor)*; Hayfield, nr Maprik, in soil under wood (all with *A. acutiventris)*: West Sepik Province, Pes, nr Aitape, in soil under wood with *A. acutiventris*, 8–9.vii.1972: Northern Province, Kokoda, associated with dying *Theobroma cacao*, ix.1990 *(G. Lockwood)*; nr Kokoda, in soil under wood, with *A. acutiventris*, 1.vi.1972 *(R.W. Taylor)*. **Solomon Islands**, San Cristobal, Guadalcanal, Nggela (spirit material), with *A. acutiventris* and *A. (Rhizomyrma) lauta* Mann. **Australia, Queensland**, Iron Range, 12°42′S 143°18′E, 9–15.vi.1971 *(R.W. Taylor & J. Feehan)*; Waugh, from rotten log, 11.vi.1962 *(R.W. Taylor)*; Cape York Peninsular, Bemaga, from mandibles, xii.1983 *(J. Sedlack)*; Finch Hatton Gorge, 21°05′S

148°38′E, 11.xi.1976 *(R.W. Taylor & T.A. Weir)*; Josephine Falls (spirit material): **Northern Territory**, Baroalba Spring, 12°47′S 132°51′E, in soil under wood, 16, 17, 20.xi.1972, 13.vi.1973 (all with *A. acutiventris)*.

COMMENTS. Specimens recorded under the name *X. annandalei* from Hong Kong, Vietnam and Penang by Williams (1978) are probably this species and await verification.

Xenococcus annandalei Silvestri

(Fig. 27)

Xenococcus annandalei Silvestri, 1924: 312; 1926: 275; 1927: 253. LECTOTYPE ♀, INDIA: Barkuda I. [Chilka (Chilika) Lake, Madras District (now Orissa Province), on roots of *Ficus obtusa*, with ants*Acropyga acutiventris* Roger] (IEAUN, Portici) designated by Williams 1978: 66 [examined].

COMMENTS. Williams (1978) described the adult female in detail and the illustration is reproduced here with slight modification. Some further notes are now added to distinguish the species from *X. acropygae*.

The antennae are 1480–1550 µm long, longer than in any specimen of *X. acropygae* so far studied. In *X. acropygae*, the range is 860–1090 µm long. Furthermore, although the distribution of the antennal setae are about the same in the two species, there are many more shorter and more slender setae in *X. annandalei*. The bases of the setae in the antennae of *X. annandalei* vary in width from 2.5 µm to 7.5 µm with a corresponding difference in size of the setal collars, whereas in *X. acropygae* there is less variation, with the width of the setal bases 3–5 µm. The legs of *X. annandalei* differ from those of *X. acropygae*. In *X. annandalei*, they are longer, with the hind trochanter + femur 440–480 µm long and the hind tibia + tarsus 530–560 µm long. The ratio of lengths of hind tibia + tarsus to those of the hind trochanter + femur is 1.16–1.18 and the most striking difference is the ratio of the hind tibia to tarsus, with the tibia always about twice as long as the tarsus. Besides, the tibiae and tarsi are fairly uniform in width for most of their lengths, although the tarsi narrow and taper distally. In *X. acropygae*, the tarsus is always longer than the tibia and the tibia is swollen before narrowing abruptly to a long slender distal end.

The short flat setae on the dorsum discussed by Williams (1978) are, in fact, sickle-shaped in profile, similar to those of *X. acropygae*.

The third instar discussed by Williams (1978) is now known to be the second instar (Williams, 1988). It is also evident that the first instar discussed by Williams (1978) from Mysore, on coconut roots, is the first instar of *X. acropygae*.

MATERIAL

At present the species is only known from India, Orissa Province, Barkuda I., on roots of *Ficus obtusa* and *F. religiosa*.

REVIEW OF GENERA IN THE RHIZOECINAE

In addition to *Eumyrmococcus* and *Xenococcus*, already discussed, the following genera have been included in the subfamily at one time or another and their current status is discussed.

Tang (1992) erected the subtribes Rhizoecina, Prorhizoecina and Pseudorhizoecina for some of the genera, but this action seems unnecessary. These names, nevertheless, remain available.

The opportunity is taken to describe a new genus from southern Asia because it resembles *Eumyrmococcus* superficially but is clearly more related to *Rhizoecus*.

Brevicoccus Hambleton

Brevicoccus Hambleton, 1946a: 10; Williams & Granara de Willink, 1992: 68. Type species: *Brevicoccus clavisetosus* Hambleton, by original designation and monotypy.

DIAGNOSIS. Body broadly oval, anal lobes poorly developed, each without any development of long setae. Antennae placed close together, strongly geniculate, 4-segmented, last segment triangular. Legs well developed; claws long and narrow, Anal ring fairly simple, with a few cells and 8–16 short knobbed setae. Ostioles present. Eyes absent. Cephalic plate present. Body setae short, clavate. Trilocular pores present. Multilocular disc pores present on venter. Minute oval disc pores present.

COMMENTS. The characters of the anal ring and antennae are distinct and the genus is recognized by most workers as belonging to the Rhizoecinae. This is a monotypic genus, known only from Brazil, and the single species is reported to live on roots of Gramineae and Cyperaceae in ant tunnels.

Capitisetella Hambleton

Capitisetella Hambleton, 1977: 40; Williams & Granara de Willink, 1992: 71. Type species: *Pseudorhizoecus migrans* Green, by original designation and monotypy.

DIAGNOSIS. Body almost pyriform, abdomen constricted slightly near posterior end. Anal lobes not developed, without differentiated anal lobe setae. Antennae placed fairly wide apart, 3-segmented, the third segment tapering, antennal setae clavate. Legs stout, with capitate setae, claws elongate. Anal ring heavily sclerotized, with a few elongate cells and 6 setae. Ostioles absent. Cephalic plate absent. Eyes absent. Body setae all capitate. Trilocular pores present. Multilocular pores absent. Large granular discoidal pores present at posterior end of body.

COMMENTS. The combination of a constriction at the posterior end of the body, reduction of antennal segments to three, the capitate body setae and the absence of ostioles, link this South American genus with *Eumyrmococcus*. In *Capitisetella*, there are a few elongate cells on the anal ring and these are absent in *Eumyrmococcus*. Furthermore, *Capitisetella* lacks the abundant setae on the abdomen, present in *Eumyrmococcus* or even in *Neochavesia*, also possibly related to *Capitisetella*. The single species lives in association with *Acropyga (Rhizomyrma) paramaribensis* (Bünzli, 1935). At present, the genus is accepted in the Rhizoecinae.

Geococcus Green

Geococcus Green, 1902: 262; Williams, 1969b: 508. Type species: *Geococcus radicum* Green, by original designation.

DIAGNOSIS. Body elongate to oval, anal lobes well developed, sclerotized, each terminating in a stout, spine-like seta. Antennae geniculate, 6-segmented. Legs well developed, inner edges of tibia and tarsus with stout setae, claws long and slender. Anal ring with large cells and 6 setae. Ostioles present. Circuli present, raised. Cephalic plate present. Multilocular disc pores present. Trilocular pores present. Large trilocular pores present, usually much larger than the normal trilocular pores. Body setae fairly abundant, short and flagellate.

COMMENTS. The genus is widely accepted in the Rhizoecinae. At present six species are assigned to the genus from South-East Asia, southern Asia and the Indo-Australian Region but there are many species awaiting to be described. The genus is well known for the spread of *G. coffeae* throughout much of the tropics. Although this species was described from Surinam, where it is associated with *Acropyga (Rhizomyrma) paramaribensis* on coffee roots and other plants, it is undoubtedly native to southern Asia.

The peculiar large trilocular pores, always present, may be modified tritubular cerores. It is often difficult to study the anal ring because it is concealed between the sclerotized anal lobes.

Leptorhizoecus gen. nov.

TYPE SPECIES. *Leptorhizoecus deharvengi* sp. n.

DESCRIPTION

Body membranous, elongate, with dilated cephalothorax, abdomen narrow, subparallel, narrowing abruptly to abdominal segment VIII; posterior end of body sclerotized, rounded. Anal lobes not developed; setae on positions of anal lobes not differentiated from other setae on abdominal segment VIII. Anal ring ventral, crescentic, with a single row of minute elongate cells and 6 spine-like setae. Antennae placed close together on venter of head margin, 6-segmented. Legs well developed; with thick pointed setae on inner edge of tibia and tarsus. Claw elongate and slender. Labium narrow, longer than wide. Ostioles and circulus present. Body setae flagellate, mostly short and fairly numerous. Trilocular pores present on dorsum and venter. Quadrilocular pores present next to circulus. Tubular ducts absent.

COMMENTS. This genus is typically rhizoecine but the body shape resembles species of *Eumyrmococcus* in exhibiting a dilated cephalothorax. It differs from *Eumyrmococcus* in possessing 6-segmented antennae, placed close together, and in having ostioles and trilocular pores. The ventral anal ring is unlike any so far described in the Rhizoecinae.

Leptorhizoecus is probably intermediate between the *Rhizoecus* and *Eumyrmococcus* groups and the shape suggests it is possibly attended by ants.

The name *Leptorhizoecus* is based on the Greek word 'Leptos', meaning fine and delicate, combined with the extant genus name *Rhizoecus*.

Leptorhizoecus deharvengi sp. n.

Fig. 28.

DESCRIPTION

Appearance in life not recorded. Adult female on microscope slide elongate, cephalothorax dilated, abdomen subparallel, widening slightly to abdominal segment VII, narrowing abruptly to rounded posterior end, body membranous except for rounded posterior half of apical segment of abdomen; 0.80–0.92 mm long, 0.27–0.36 mm wide; anal lobes not developed, anal lobe setae not differentiated from others on apical segment. Antennae placed close together on ventral head margin, each 115–135 μm long, with 6 segments; falcate setae well developed on segments 5 and 6. Legs well developed; hind trochanter + femur about 92.5 μm long, hind tibia + tarsus 97.5–100.0 μm long, claw slender, elongate and slightly curved, about 27.5 μm long. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 1.05–1.08. Ratio of lengths of hind tibia to tarsus 0.97–1.00. Leg setae flagellate, placed well apart, inner edges of tibia and tarsus with thicker

setae. Labium 77.5–82.0 μm long, about 37.5 μm wide, ratio of length to width 2.06–2.18; longer than clypeolabral shield. Clypeolabral shield with 2 pairs of setae. Circulus slightly oval, about 17.5 μm wide, situated within borders of abdominal segment II; structure difficult to determine in available material. Ostioles present, posterior pair fairly well developed but without associated setae; anterior pair represented by indistinct slits. Anal ring ventral in position, oval to triangular, 25–30 μm wide, with a single row of minute elongate cells in posterior arc, accompanied by 6 stout, elongate-conical setae, each 17.5 μm long (cells and setae actually anterior if ring transferred to dorsum). Eyes present.

Dorsal surface with long setae, each about 60 μm long, on sclerotized apical segment of abdomen; shorter setae, each about 25 μm long, situated at anterior end of apical segment. Anteriorly on abdomen, setae all about 25 μm long, in moderate numbers in well defined bands across middle of segments leaving bare intersegmental areas. Shorter setae, each 12.5–18.0 μm long, present on head and thorax. All setae flagellate. Trilocular pores present, not numerous, evenly distributed among the setae.

Ventral surface with similar distribution of setae to those on dorsum. Multilocular disc pores represented by a few quadrilocular pores, near circulus, each about 5 μm in diameter. Trilocular pores scattered, not so numerous as on dorsum.

MATERIAL

HOLOTYPE. Adult ♀, **Indonesia, Sumatra**, Rantau Pandan, in soil of *Hevea* sp., 9.vi.1991 *(L. Deharveng & A. Bedos)* (MNHN).

PARATYPE. **Indonesia, Sumatra**, same data as holotype. 1 adult ♀ (BMNH).

COMMENTS. The species is named after Louis Deharveng, Université Paul Sabatier, Toulouse, one of the collectors. Dr Deharveng has sent interesting samples from southern Asia collected from Berlese funnel apparatus.

Neochavesia Williams & Granara de Willink

Chavesia Balachowsky, 1957: 158; Beardsley, 1970: . [Preoccupied by *Chavesia* Dollfus, 1889, Isopoda].
Neochavesia Williams & Granara de Willink, 1992: 232 [replacement name]. Type species *Chavesia caldasiae* Balachowsky, by original designation.

DIAGNOSIS. Body in life with tip of abdomen curled to dorsum, scorpion-like. Slide-mounted specimens with cephalothorax dilated, abdomen narrowing to a pair of protuberant, rounded anal lobes bearing many long flagellate setae. Anal ring situated at base of anal lobes, simple, with 6 or a few setae around anterior

sclerotized half, without cells. Antennae each with 4 or 5 segments. Legs well developed, tarsi tapering, claws long and slender. Ostioles absent. Circuli conical, each with centre cupped. Labium with 3 pairs of subapical setae. Eyes absent. Body setae short and abundant on cephalothorax, longer and in bands across abdominal segments. Trilocular pores present in type species only, each with a minute internal filament arising from centre of pore. Multilocular disc pores and tubular ducts absent.

COMMENTS. In the strong development of the cephalothorax, the simple anal ring without cells, the absence of ostioles, and the presence of cupped circuli, this South American genus comes closest to *Eumyrmococcus* and *Xenococcus*. Many species originally and provisionally identified as *Eumyrmococcus* in South America, associated with ants of the genus *Acropyga*, refer to *Neochavesia*. The genus is here accepted as belonging to the Rhizoecinae.

Prorhizoecus Miller & McKenzie

Prorhizoecus Miller & McKenzie, 1971: 583. Type species *Prorhizoecus atopoporus* Miller & McKenzie, by original designation and monotypy.

DIAGNOSIS. Body oval, anal lobes not developed; positions of each anal lobe with a single normal apical seta. Antennae each with 4 or 5 segments. Legs well developed, slender, hind coxae with translucent pores. Anal ring heavily sclerotized with thick rim, cells, and 6 setae. Cerarii present on anal lobes, each cerarius with 2 conical setae and a group of trilocular pores. Ostioles present. Eyes present. Body setae short and abundant. Trilocular pores present. Multilocular disc pores present, each with 12 loculi. Tubular ducts present, each with narrow oral rim and heavily sclerotized bulbous duct.

COMMENTS. Although the antennae resemble those of *Rhizoecus*, the other characters, cerarii, translucent pores on the hind coxae, an anal ring with a broad rim, and peculier oral rim ducts, exclude this genus from the Rhizoecinae. The single species is known only from Mexico and feeds on grass roots. The genus may be related to *Cryptoripersia* Cockerell or *Syrmococcus* Ferris.

Pseudorhizoecus Green

Pseudorhizoecus Green, 1933: 55; Hambleton, 1977: 38; Williams & Granara de Willink, 1992: 463. Type species *Pseudorhizoecus proximus* Green, by original designation.

DIAGNOSIS. Body rotund; anal lobes not developed, without differentiated anal lobe setae. Antennae placed close together, each with 5 segments, tapering. Legs well developed, tarsi tapering, claws long and slender.

Anal ring terminal, wider than long, irregularly outlined, with 2–5 short setae, a few small cells, and numerous protuberances. Ostioles, eyes and cephalic plate absent. Body setae abundant, short and flagellate. Trilocular pores present.

COMMENTS. This unusual genus is probably related to *Capitisetella* but the anal ring possesses numerous protuberances and all the body setae are flagellate. The only included species has a fairly wide distribution in Central and South America and is associated with *Acropyga (Rhizomyrma) rutgersi* and *A. paramaribensis*.

The adult male is morphologically degenerate, without wings, resembling the adult female in body shape and possessing similar 5-segmented antennae. Beardsley (1970) remarked that the genitalia appeared to be similar to the genitalia of *Capitistella* and *Neochavesia*.

Pygmaeococcus McKenzie

Pygmaeococcus McKenzie, 1960: 741. Type species *Pygmaeococcus morrisoni* McKenzie, by original designation and monotypy.

DIAGNOSIS. Body of adult female minute, elongate, anal lobes not developed, position of each lobe with 1 long ventral and 2 long dorsal setae, forming a group of 3. Antennae each with 5 segments. Legs well developed, with stout, spinose setae present on inner edges of tibiae and tarsi; claw long and slender, digitules clavate, equalling or surpassing claw in length. Cephalic plate present. Anal ring terminal, with elongate-oval cells and 6 long setae. Ostioles present. Circulus present. Eyes present. Body setae short and sparse. Trilocular pores present. Tubular ducts present, each heavily sclerotized and slightly dome-shaped at inner end with, apparently, a septum. Bitubular and tritubular cerores absent.

COMMENTS. The only distinguishing characters separating this monotypic genus from *Rhizoecus* is the unusual type of duct. The genus, known from California, is accepted by most workers on scale insects but further related species may help to clarify its position.

Rhizoecus Künckel d'Herculais

Rhizoecus Künckel d'Herculais. 1878: 163. Type species *Rhizoecus falcifer* Künckel d'Herculais, by monotypy.

Ripersiella Tinsley, in Cockerell 1899:278. Type species *Ripersia rumicis* Maskell, by subsequent designation of Cockerell, 1901: 165. Synonymised by Hambleton, 1974: 147.

Pararhizoecus Goux, 1941: 197, as a subgenus of *Rhizoecus*. Type species *Rhizoecus (Pararhizoecus) petiti* Goux, by original designation and monotypy.

Synonymised with *Ripersiella* by Morrison & Morrison, 1966: 147, and with *Rhizoecus* by Ben-Dov, 1994: 286.

Morrisonella Hambleton, 1946a: 16. Type species *Morrisonella poensis* Hambleton, by original designation. Homonym of *Morrisonella* Bartsch, 1920. Synonymised by Ferris, 1953: 426.

Radicoccus Hambleton, 1946a: 47. Williams & Granara de Willink, 1992: 492. Type species *Rhizoecus globosus* James, by original designation. **Syn. nov.**

Coccidella Hambleton, 1946b: 177. Replacement name for *Morrisonella* Hambleton. Synonymised by Ferris, 1953: 426.

Neorhizoecus Hambleton, 1946a: 40. Type species *Rhizoecus coffeae* Laing, by original designation. Synonymised by Lindinger, 1957: 550.

DIAGNOSIS.   Body normally small, elongate to rotund, anal lobes usually not developed, their positions each usually with 3 long anal lobe setae, or more rarely, with numerous setae. Antennae usually placed close together, short, strongly geniculate, each with 5 or 6 segments, these often wider than long, terminal segment tapering, almost triangular; with sensory falcate setae well developed on terminal and penultimate segments, these in addition to normal flagellate setae. Labium elongate, longer than wide. Anal ring with 6 setae, these usually flagellate or occasionally clavate; with fairly large elongate to triangular cells that can easily be counted to distinguish between species. Legs normally well developed; tarsus tapering to a long slender claw with short setose or dilated digitules, sometimes about as long as claw; without translucent pores but occasionally with large vacuolate pores; setae on inner edges of tibia and tarsus often elongate spine-like. Eyes present or absent. Circulus present or absent, when present usually truncate conical, distal surface often reticulate or faveolate, usually situated on abdominal segment III within borders of segment; sometimes as many as 6 circuli present distributed singly among other abdominal segments and occasionally present on metathorax. Ostioles present, placed well on dorsum, sometimes reduced to posterior pair only and occasionally barely perceptible. Frons often with sclerotized cephalic plate.

Body setae usually short and flagellate, often abundant, rarely very sparse. Bilocular or trilocular cerores present, never both types present together, rarely absent altogether. Trilocular pores present, often abundant, sometimes few. Tubular ducts present or absent, when present usually minute with parallel or subparallel sides. Multilocular disc pores present or absent. Medioventral pore groups sometimes present on abdomen. Mushroom bodies occasionally present on dorsum and venter.

COMMENTS.   The above description should be ad-equate to separate the genus from all others discussed here. The tritubular and bitubular cerores are unique to the genus and some attempts have been made to distinguish between *Rhizoecus* with tritubular cerores and *Ripersiella* with bitubular cerores but there are many variations of the cerores. Sometimes the tubes of the bitubular cerores are so appressed as to appear unitubular and often their true structure can only be determined by the use of oil immersion. Besides, *R. andensis* (Hambleton) and *R. colombiensis* Hambleton, both South American species, and *R. cobelopus* Williams from Australia, are without either type but appear to be congeneric in other characters.

Emphasis on the presence or absence of eyes, the length and type of the claw digitules, and the shape of the bitubular and tritubular cerores to distinguish among genera has been challenged by Takagi & Kawai (1971) who commented on the variability of these characters.

The position of *Radicoccus* needs special mention. Hambleton (1946a) erected this genus for five species, each with a fairly stout body, the legs and antennae, although well developed, are minute for the size of body, and body setae are sparse. The species show widely diverse characters but these fall within the present concepts of *Rhizoecus*. These five species and another transferred since, are discussed as follows:

Rhizoecus globosus James. This African species, was illustrated by De Lotto (1957) and, considering the poor material on which the illustration was based, the illustration is fairly comprehensive. Some further notes are now added although a study of fresh material is needed. The species possesses 3 circuli and large tritubular cerores of two distinct sizes, each with short stout ducts giving the whole ceroris a flat appearance. Anterior and posterior ostioles are present although they are small and almost imperceptible.

Rhizoecus incrassatus James. This African species is similar to *R. globosus*, differing in possessing only 2 circuli and tritubular cerores of one size. Anterior and posterior ostioles are present. The species was illustrated by De Lotto (1957).

Rhizoecus kelloggi Ehrhorn & Cockerell. This North American species has sparse body setae, lacks bitubular or tritubular cerores but possesses distinctive tubular ducts, each with the orifice elliptical; nevertheless, the sides of each duct are parallel. Ostioles are present although they are represented by mere slits (D.R. Miller, personal communication). There are no good reasons to exclude this species from *Rhizoecus*.

Radicoccus hawaiiensis Hambleton. It was shown by Beardsley (1966) that this species possesses all the characters of *Rhizoecus* to which it was transferred.

Rhizoecus poltavae Laing. For some reason this species, described from Ukraine, has always been regarded as distinct in lacking bitubular or tritubular cerores but bitubular cerores are plainly discernible in the original material, a character noted by Matile-

Ferrero (1976) who included the species in *Ripersiella*. The species is here retained in *Rhizoecus*.

Rhizoecus cocois Williams. Although this species, described from India, was transferred to *Radicoccus* by Tang (1992) because of the globular body and paucity of body setae, the action was unnecessary. The species is related to *R. globosus* and *R. incrassatus* and should be retained in *Rhizoecus*.

All the species, therefore, that have been assigned to *Radicoccus* can be comfortably included in *Rhizoecus* and the name *Radicoccus*, as listed by Ben-Dov (1994), is here synonymised with *Rhizoecus*.

Key to Genera of the Subfamily Rhizoecinae (Adult Females)

1 Anal ring with protuberances; anal ring setae short, much shorter than diameter of anal ring, numbering 2–5, unevenly distributed .... ***Pseudorhizoecus*** (p. 28)

– Anal ring without protuberances, anal ring setae conspicuous, usually at least as long as diameter of anal ring or almost as long, numbering 6–16, distributed evenly on ring or detached from ring and lying in an arc anterior to ring (sometimes anal ring masked by heavily sclerotized anal lobes) 2

2 Anal ring distinctly ventral in position, with a single row of elongate cells and thick spine-like anal ring setae around posterior edge (actually anterior edge if transferred to dorsum) .... ***Leptorhizoecus*** (p. 27)

– Anal ring always dorsal in position, anal ring setae not spine-like, at least the 2 anterior pairs slender. Cells present or absent 3

3 Anal ring with large elongate to triangular cells, anal ring setae arising from surface of anal ring. Body rotund, elongate-oval or weakly pyriform, never with cephalothorax strongly dilated. Circulus, if present, never cupped in centre. Ostioles present or absent. Tubular ducts present or absent. 4

– Anal ring simple, without elongate cells, anal ring setae detached from ring or at edge of ring, usually lying in an arc anterior to ring, sometimes difficult to distinguish from dorsal setae of abdominal segment VIII. Cephalothorax dilated, abdomen narrow, tapering (in *E. neoguineensis*, the cephalothorax is dilated but the abdomen widens before tapering). Circulus, if present, cupped in centre, even if only shallowly. Ostioles always absent. Tubular ducts always absent 8

4 All body setae knobbed. Antennae each with 3 or 4 segments 5

– All body setae flagellate. Antennae each with 5 or 6 segments 6

5 Antennae each with 4 segments. Multilocular disc pores present. Anal ring with 8–16 short capitate setae .... ***Brevicoccus*** (p. 26)

– Antennae each with 3 segments. Multilocular disc pores absent. Anal ring with 6 pointed setae ....

.... ***Capitisetella*** (p. 26)

6 Anal lobes well developed, protruding well beyond posterior end of body, each lobe terminating in a stout spine-like seta .... ***Geococcus*** (p. 26)

– Anal lobes barely perceptible or not developed. Any setae on anal lobes or on normal positions of anal lobes, flagellate, not spine-like 7

7 Body with conspicuous dome-shaped tubular ducts, each heavily sclerotized. Bitubular and tritubular cerores always absent .... ***Pygmaeococcus*** (p. 28)

– Body without conspicuous dome-shaped tubular ducts; if tubular ducts are present they are minute with parallel or subparallel sides. Bitubular or tritubular cerores often present. Body setae usually abundant, rarely sparse .... ***Rhizoecus*** (p. 28)

8 Anal lobes protruding, rounded, each with numerous flagellate setae. Antennae each with 4 or 5 segments. Anal opening situated at base of anal lobes. Trilocular pores present or absent. Circuli present .... ***Neochavesia*** (p. 27)

– Anal lobes not protruding, posterior end of body rounded, each lobe often with long setae, sometimes almost as long as body. Circuli present or absent. Antennae each with 1–4 segments. Trilocular pores always absent 9

9 Antennae short, each with 2–4 segments; any articulation between first and second segments poorly developed. Claws normally long and slender except in one species with stout claws. Minute setae abundant, always present on dorsum and venter of abdomen, most on abdomen sometimes replaced with short sickle-shaped setae. Clavate sensory setae present or absent on body ***Eumyrmococcus*** (p. 8)

– Antennae conspicuously long, always with 4 segments, almost as long as body, the first and second segments with well developed articulation, the proximal end of second segment with small points which fit into grooves at distal end of first segment. Claws long and slender. Minute setae abundant on dorsum of abdomen only, absent from venter of abdomen; ventral setae on abdomen mostly long and stout. If sickle-shaped setae are present they form small groups on thorax only. Clavate sensory setae always absent .... ***Xenococcus*** (p. 22)

LIST OF RHIZOECINAE ASSOCIATED WITH *ACROPYGA* WITH DISCUSSION OF SPECIFICITY OF THE MEALYBUG-ANT ASSOCIATIONS

Eumyrmococcus corinthiacus, Greece, with *Acropyga (Rhizomyrma) paleartica*, with queen in flight.
Eumyrmococcus falciculosus, Sumatra with ? ant, primary forest litter, *Hevea* soil.
Eumyrmococcus kolombangarae, Solomon Islands,

with*Acropyga (Rhizomyrma) lauta* in log, queen in flight.

Eumyrmococcus kruiensis, Sumatra, with ? ant, in soil.

Eumyrmococcus kusiacus, Solomon Islands, with *Acropyga (Rhizomyrma) lauta* in log, queen in flight.

Eumyrmococcus lamondicus, Australia, with*Acropyga* sp. in rotting wood.

Eumyrmococcus lanuginosus, Sumatra, with 'ants'.

Eumyrmococcus maninjauensis, Sumatra, with ? ants, in soil.

Eumyrmococcus neoguineensis, Papua New Guinea, with*Acropyga (Atopodon) ambigua*, in rotting log.

Eumyrmococcus nipponensis, Japan, with *Acropyga (Atopodon) nipponensis*, on rootlets of plants or in rotten wood.

Eumyrmococcus recalvus, Australia, with *Acropyga* sp.

Eumyrmococcus sarawakensis, Sarawak, with *Acropyga* sp.

Eumyrmococcus scorpioides, South Africa, with *Acropyga (Malacomyrma) arnoldi*, in nests and mandibles.

Eumyrmococcus smithii, S.E. Asia, with *Acropyga (Rhizomyrma) sauteri*, in nests.

Eumyrmococcus sulawesicus, Sulawesi, with*Acropyga* sp., rain forest.

Eumyrmococcus taylori, Australia, *Acropyga* sp., in nests.

Eumyrmococcus sp., Papua New Guinea, with *Acropyga (Rhizomyrma) oceanica*, in log.

Eumyrmococcus sp., Papua New Guinea, with *Acropyga* sp., in rainforest.

Xenococcus acropygae, Southern Asia, Australasia, with *Acropyga (Acropyga) acutiventris, A. (Atopodon) ambigua, A. (Rhizomyrma) lauta*, in nests and mandibles of flying queens.

Xenococcus annandalei, India, with *Acropyga (Acropyga) acutiventris*, in nests and with flying queens.

Neochavesia caldasiae, Colombia, Trinidad, with *Acropyga (Rhizomyrma) robae*.

Neochavesia eversi, Colombia, Panama, with*Acropyga (Rhizomyrma) kathryna*.

Neochavesia trinidadensis, Colombia, Trinidad, with *Acropyga* sp.

Neochavesia weberi, Guyana, with *Acropyga (Rhizomyrma) paludis*.

Capitisetella migrans, Colombia, Guyana, Surinam, Trinidad, with *Acropyga (Rhizomyrma) rutgersi*.

Pseudorhizoecus proximus, Colombia, Costa Rica, Ecuador, Guatemala, Surinam, with *Acropyga (Rhizomyrma) rutgersi, A. (Rhizomyrma) paramibensis*.

Rhizoecus coffeae, Brazil, Costa Rica, Surinam, with *Acropyga (Rhizomyrma) paramibensis*.

Rhizoecus caladii, Brazil, Colombia, Guyana, Surinam, with *Acropyga (Rhizomyrma) paramibensis*.

Rhizoecus moruliferus (= R. flalcifer), Surinam, Trinidad, with *Acropyga (Rhizomyrma) paramibensis*.

Geococcus coffeae, South America, with *Acropyga (Rhizomyrma) paramibensis*.

Where possible the ant species are listed in the four subgenera of *Acropyga* presented by Bolton (1995a). Other Rhizoecinae associated with *Acropyga* species in South America have been recorded mentioning mealybug genera only. It is not certain if voucher specimens were kept and at present the species cannot be identified.

There is no doubt that *Xenococcus acropygae* and *X. annandalei* are always attented by *Acropyga (Acropyga) acutiventris* and the mealybug may be found eventually wherever the ant is located. The symbiotic association suggests that neither ant nor mealybug can live without the other. Taylor (1992) discusses the distribution of the ant in more detail with special reference toAustralia. Records of*A. (Atopodon) ambigua* in Papua New Guinea and of*A. (Rhizomyrma) lauta* in the Solomon Islands, associated with *X. acropygae*, cannot be taken too seriously because they are listed from spirit material only. The type locality of *A. acutiventris* is Sri Lanka but so far no species of *Xenococcus* have been reported from there despite extensive collecting of mealybugs by E.E. Green at the beginning of this century.

A much better picture of ant-mealybug specificity would have emerged if some of the ants had been identified and recorded. Present records indicate that each species of *Eumyrmococcus* may be attended by a different ant species. The type species of *Eumyrmococcus, E. smithii*, has an apparent wider distribution than any other in the genus and it is always attended by *A. (Rhizomyrma) sauteri. E. kolombangarae* and *E. kusiacus*, two closely-related species, are attended by *A. (Rhizomyrma) lauta* in the Solomon Islands but the mealybugs are known from only a few specimens. *E. neoguineensis* is attended by *A. (Atopodon) ambigua* in Papua New Guinea and an interesting species of *Eumyrmococcus*, known from immatures only, is associated with *A. (Rhizomyrma) oceanica*. these mealybugs in the Solomon Islands and Papua New Guinea live close to colonies of*A. acutiventris* attending *X. acropygae*.

In Europe, *E. corinthiacus* is apparently associated with*A. (Rhizomyrma) paleartica* and*E. scorpioides* in SouthAfrica is attended by *A. (Malacomyrma) arnoldi*.

Central and South American mealybug species in other genera are always associated with *Rhizomyrma*, the only subgenus in the area, and normally each mealybug species appears to be specific to a particular ant species.

The wide gap in records of *Eumyrmococcus* be-

tween Europe and South Africa in the west and southern Asia and Australasia in the east may be due to lack of collecting. Another possibility could be that species of *Eumyrmococcus* have been collected there but, at present, are lying in ant vials waiting to be sorted or are present in soil sample material extracted by students of Acari or Collembola.

There must be instances when ant species overlap and it seems difficult to believe that any species of *Acropyga* would reject a strange species of *Eumyrmococcus* if it were offered. *Geococcus coffeae* is readily attended by *A. (Rhizomyrma) paramaribensis* in Brazil although the mealybug originated in southern Asia.

These listed associations probably represent only a fraction of similar *Acropyga*-mealybug associations throughout southern Asia and Australasia. The associations may be widespread and just await further study.

The mealybug–ant system offers itself as an excellent future candidate for detailed coevolutionary studies based on independent cladistic analyses of the partner groups.

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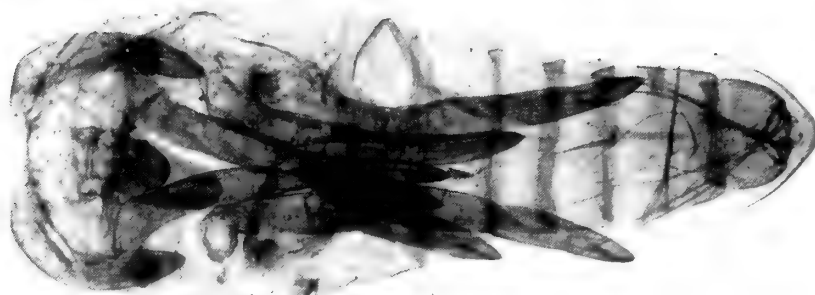
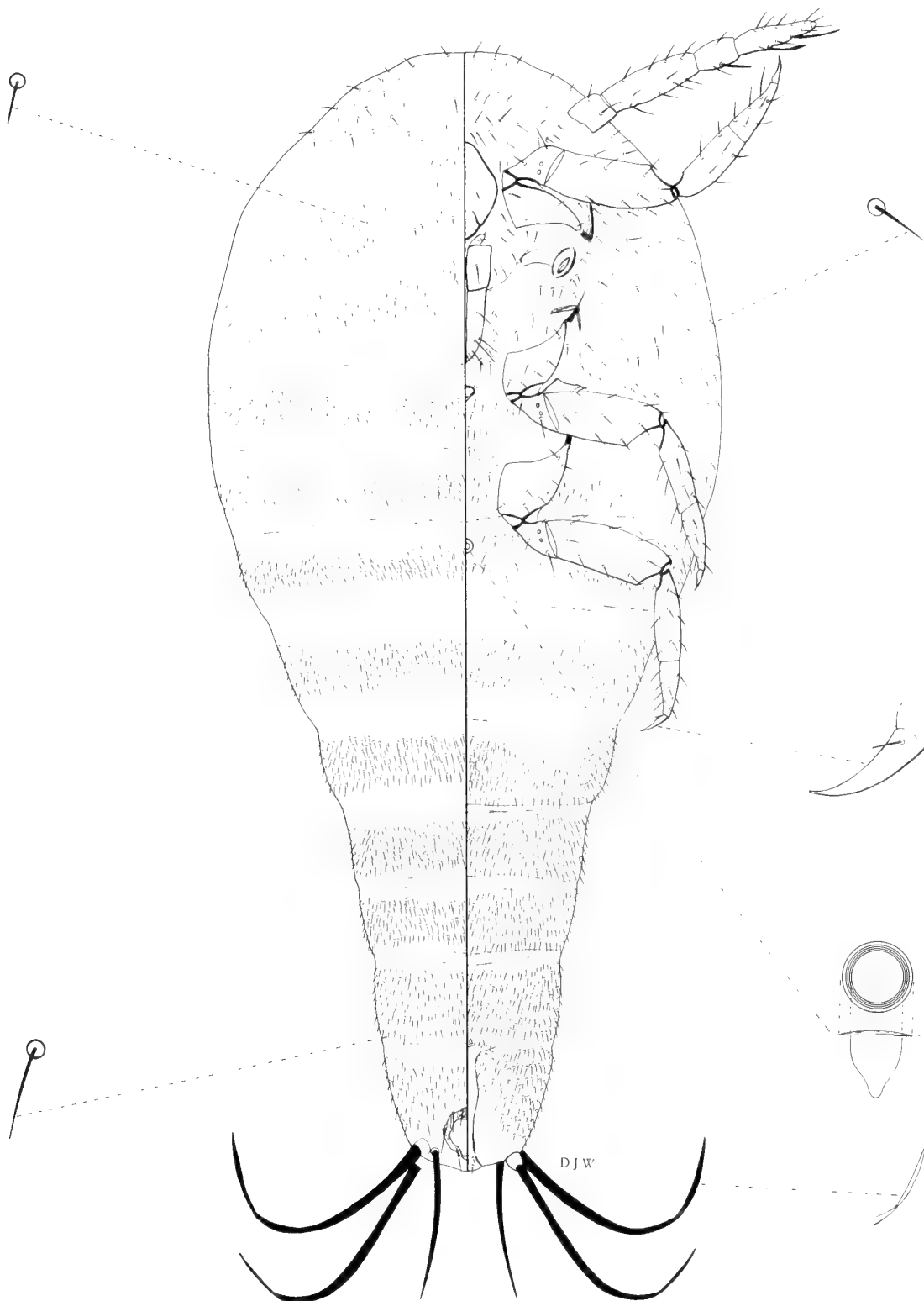Fig. 1   *Eumyrmococcus taylori* sp. n. A. Male pupa enclosing adult male. B. Female pupa enclosing adult female.

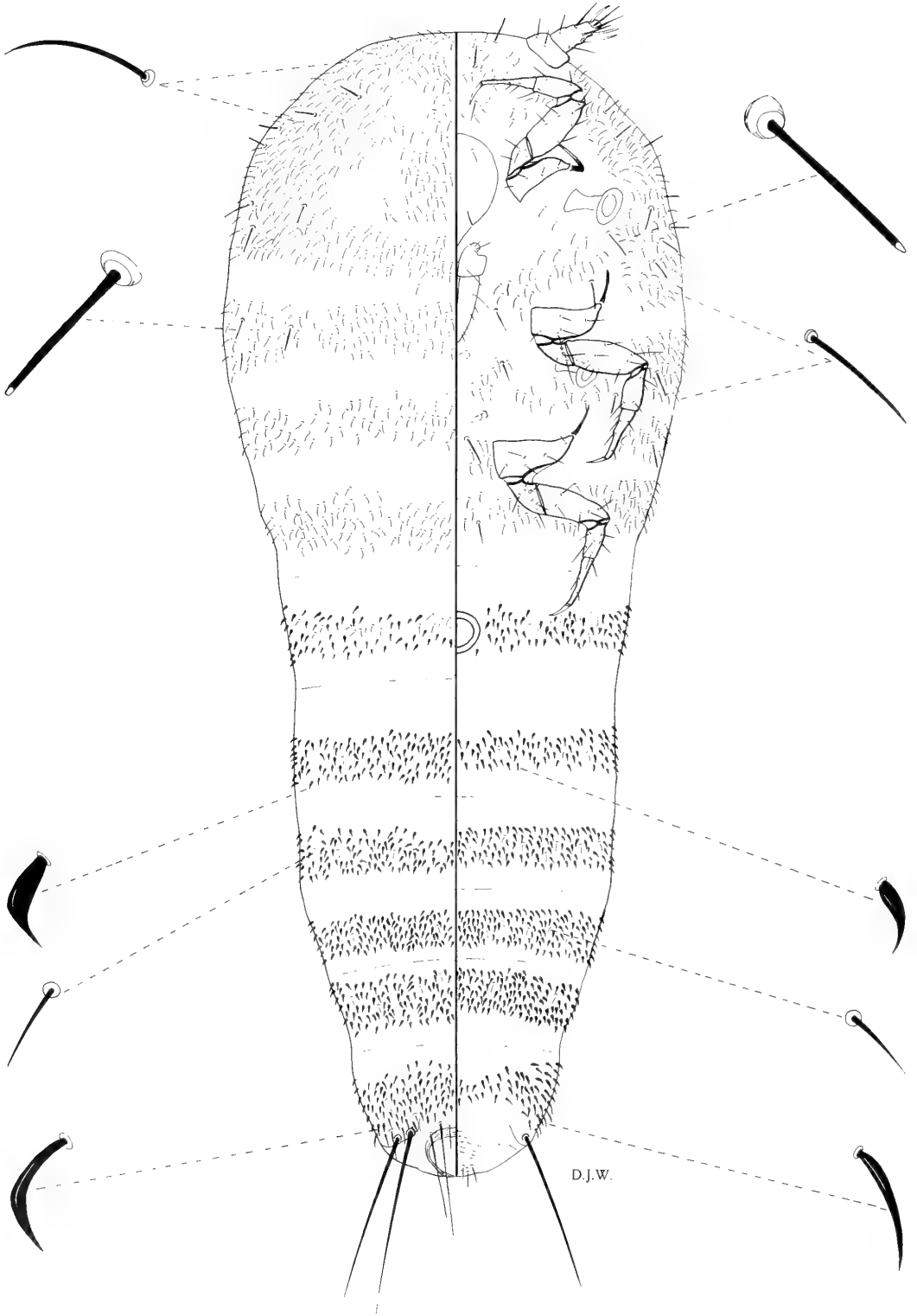**Fig. 2** *Eumyrmococcus corinthiacus* Williams. Adult female.

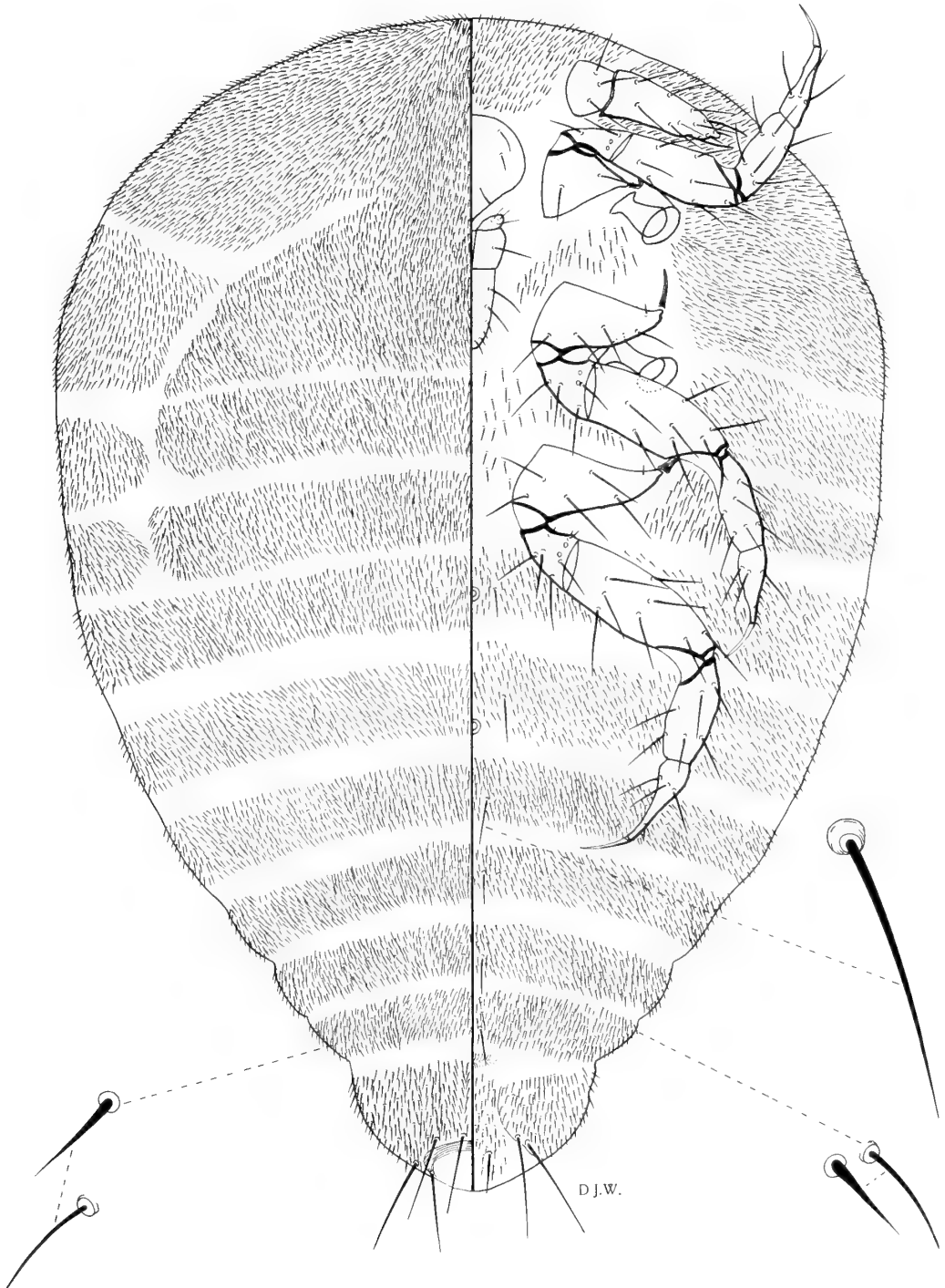**Fig. 3** *Eumyrmococcus falciculosus* sp. n. Adult female.

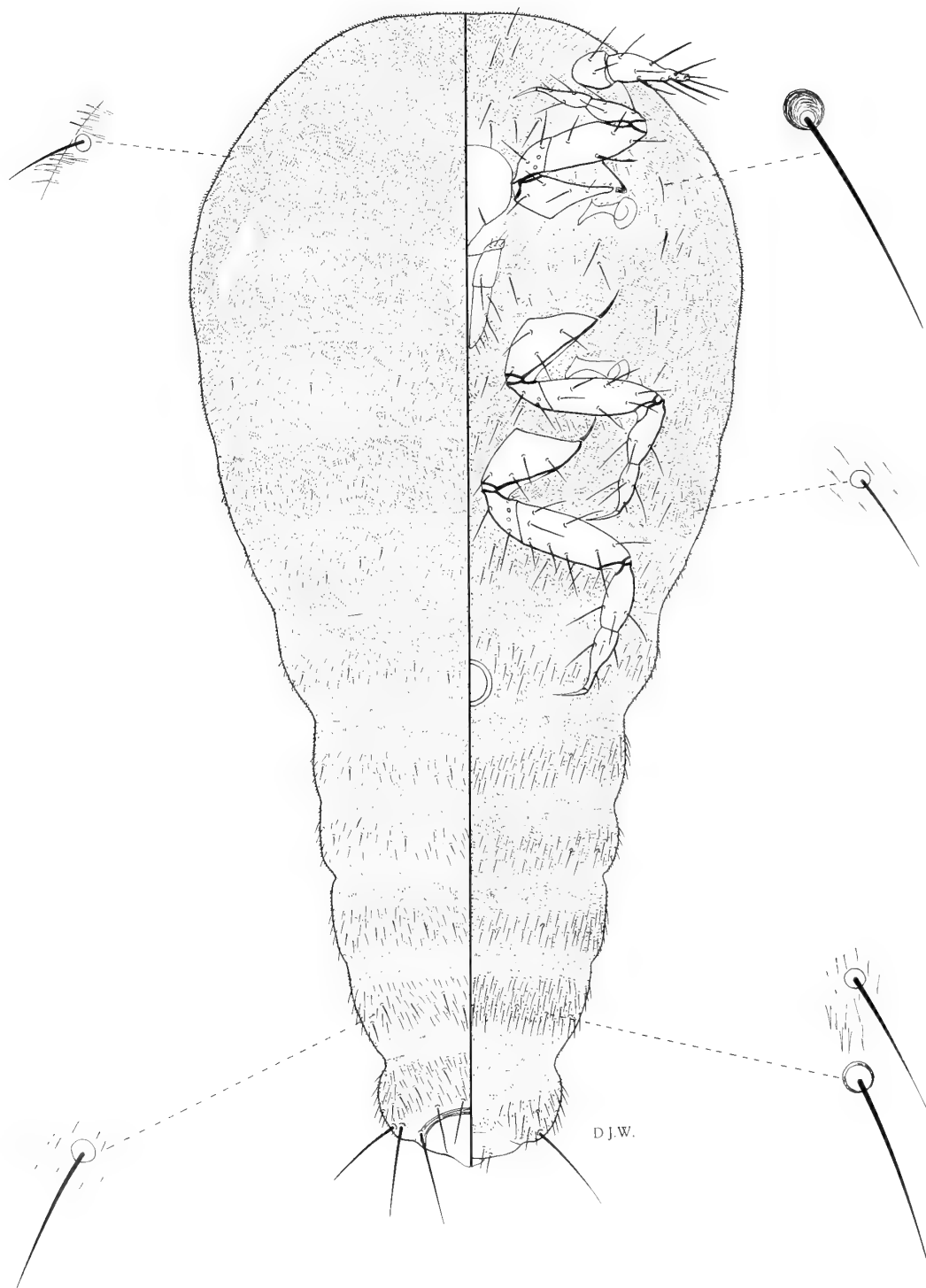**Fig. 4**   *Eumyrmococcus kolombangarae* sp. n. Adult female.

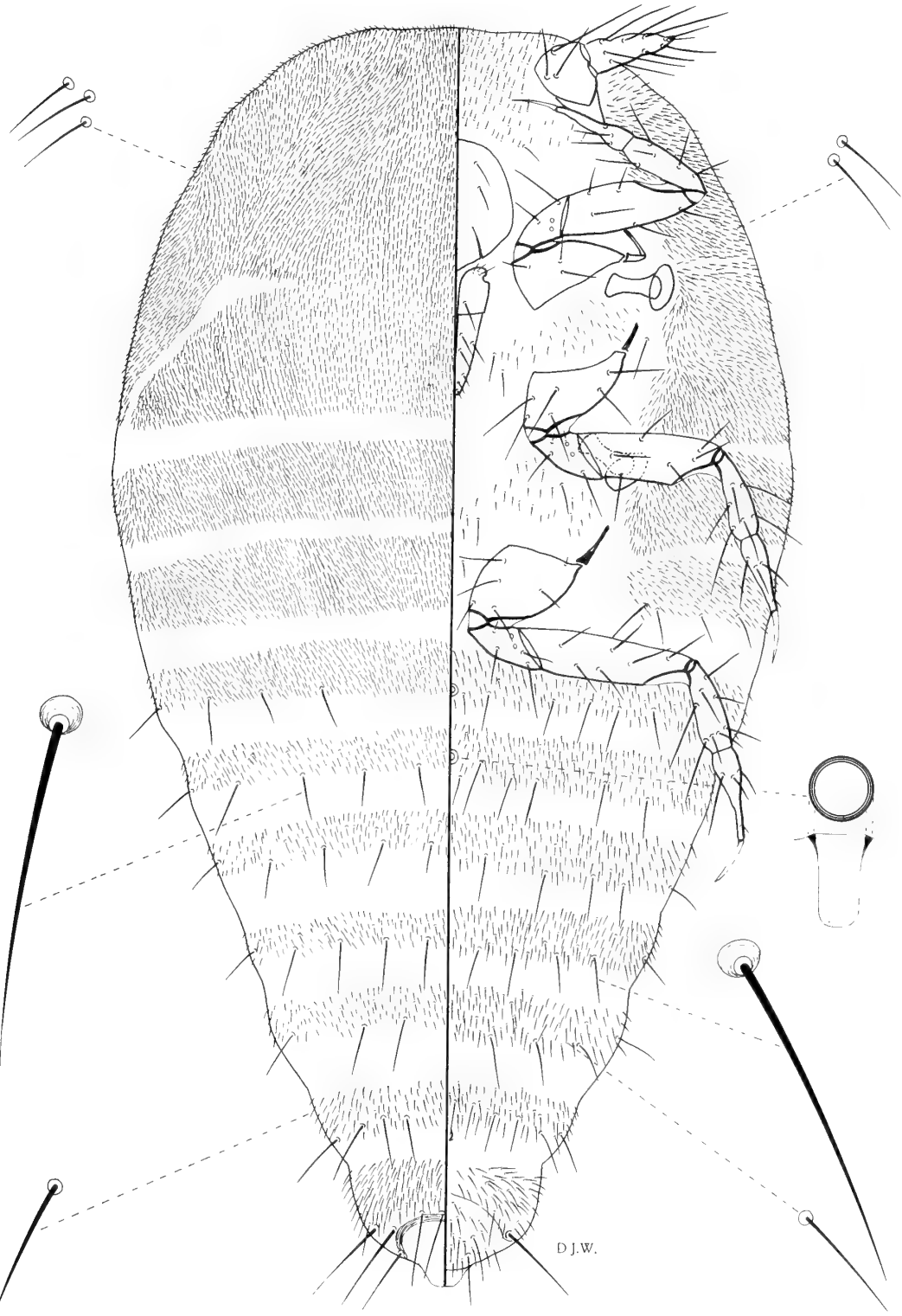**Fig. 5** *Eumyrmococcus kruiensis* sp. n. Adult female.

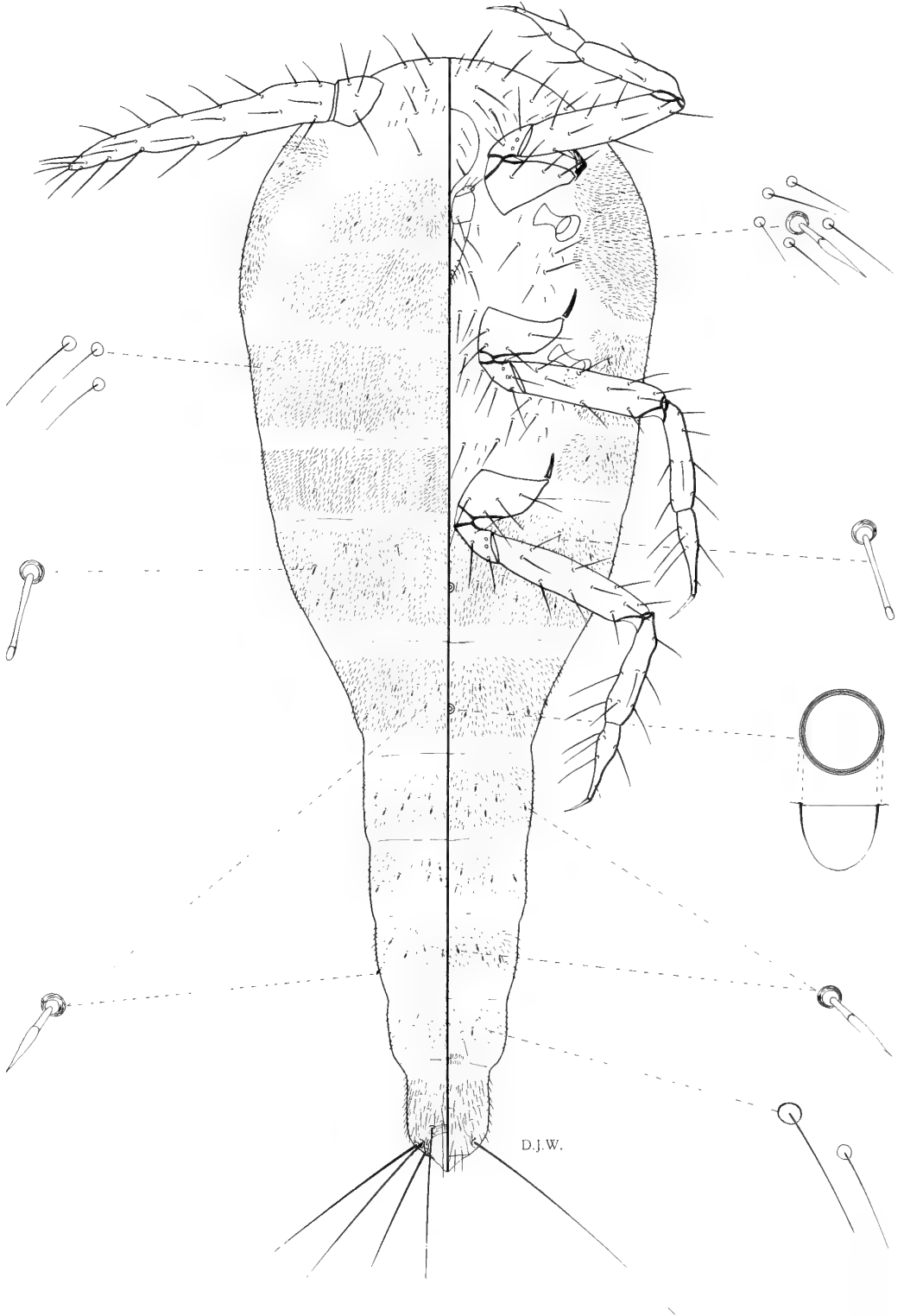**Fig. 6** *Eumyrmococcus kusiacus* sp. n. Adult female.
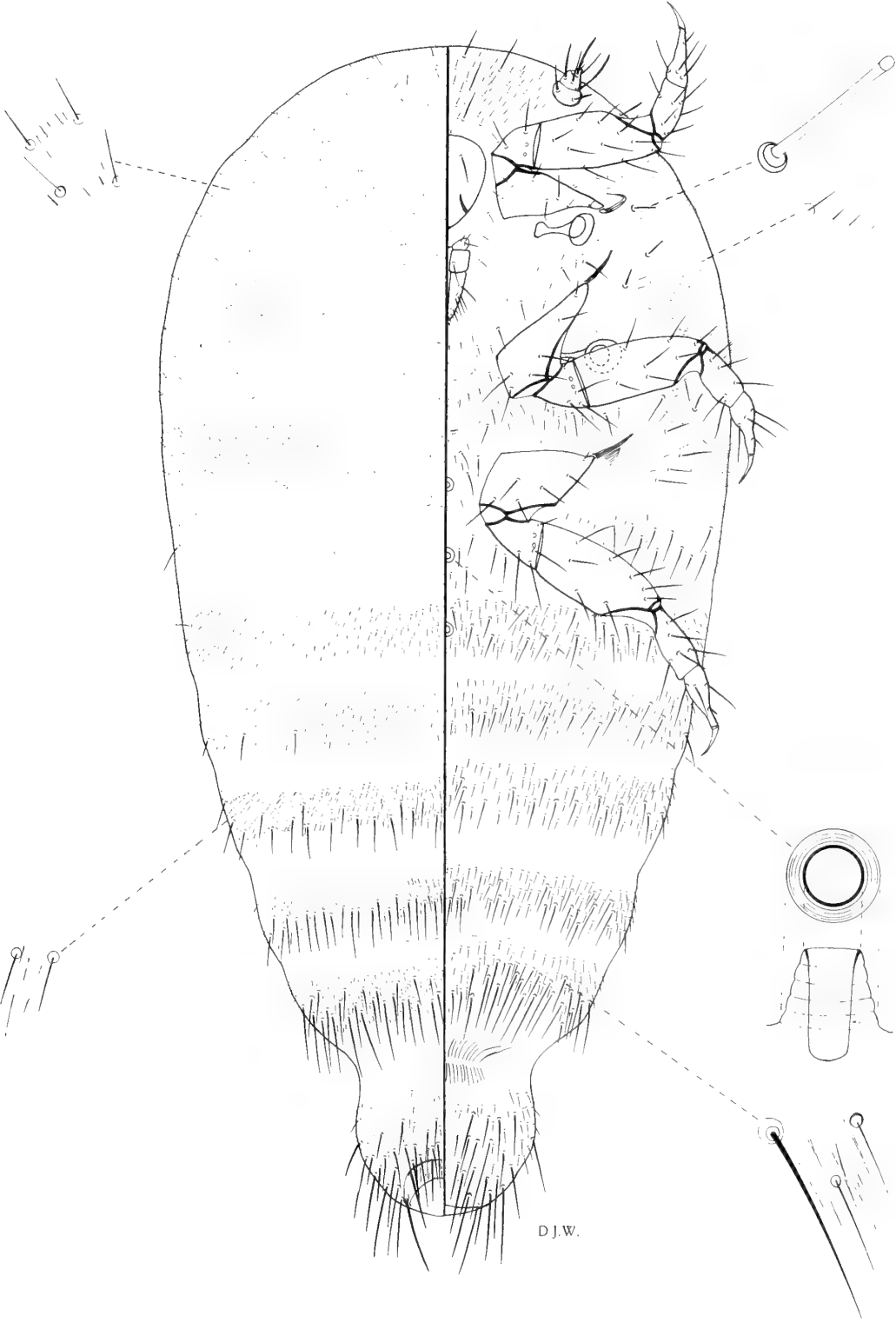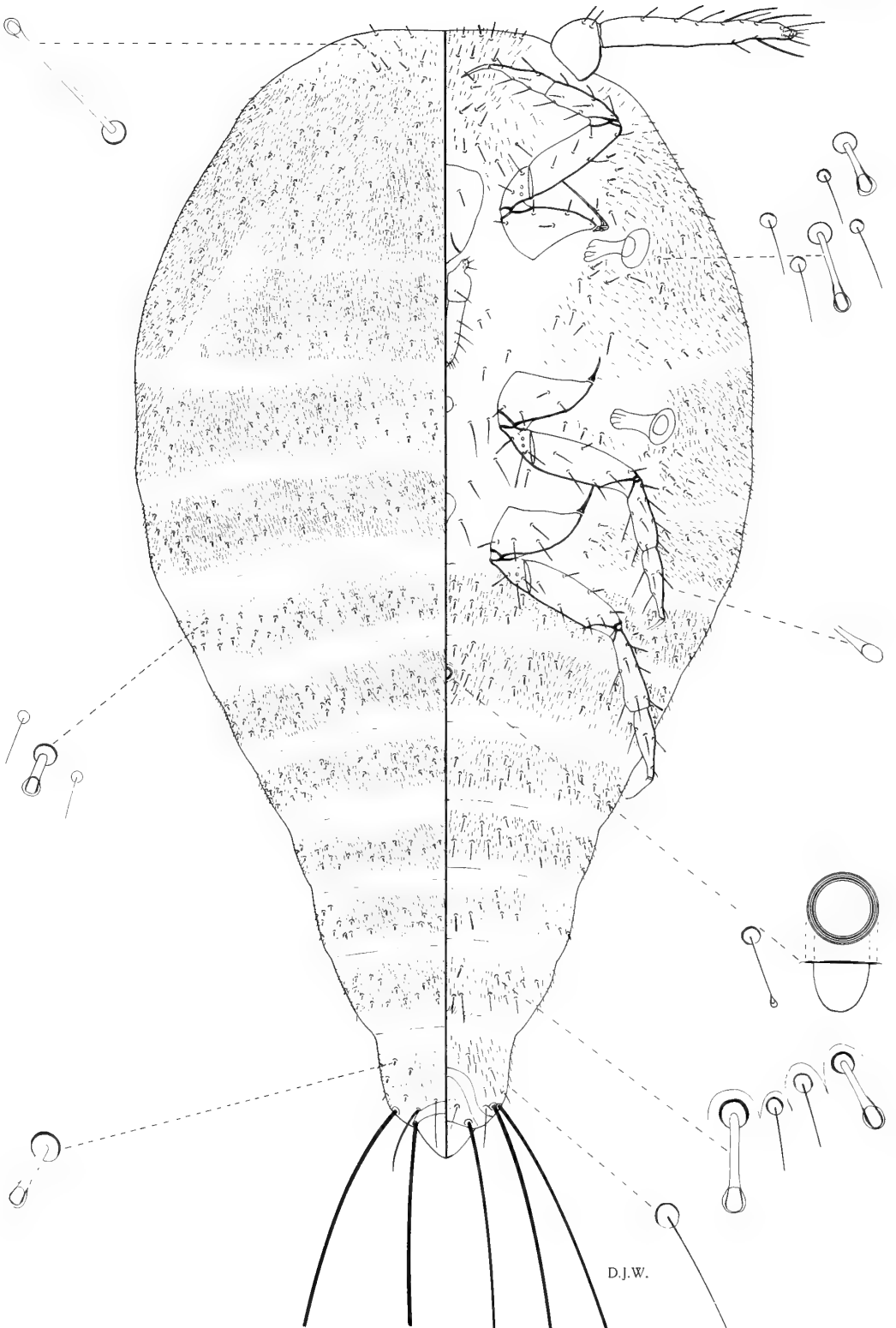
Fig. 7 *Eumyrmococcus lamondicus* sp. n. Adult female.

Fig. 8 *Eumyrmococcus lanuginosus* sp. n. Adult female.

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Fig. 9   *Eumyrmococcus maninjauensis* sp. n. Adult female.
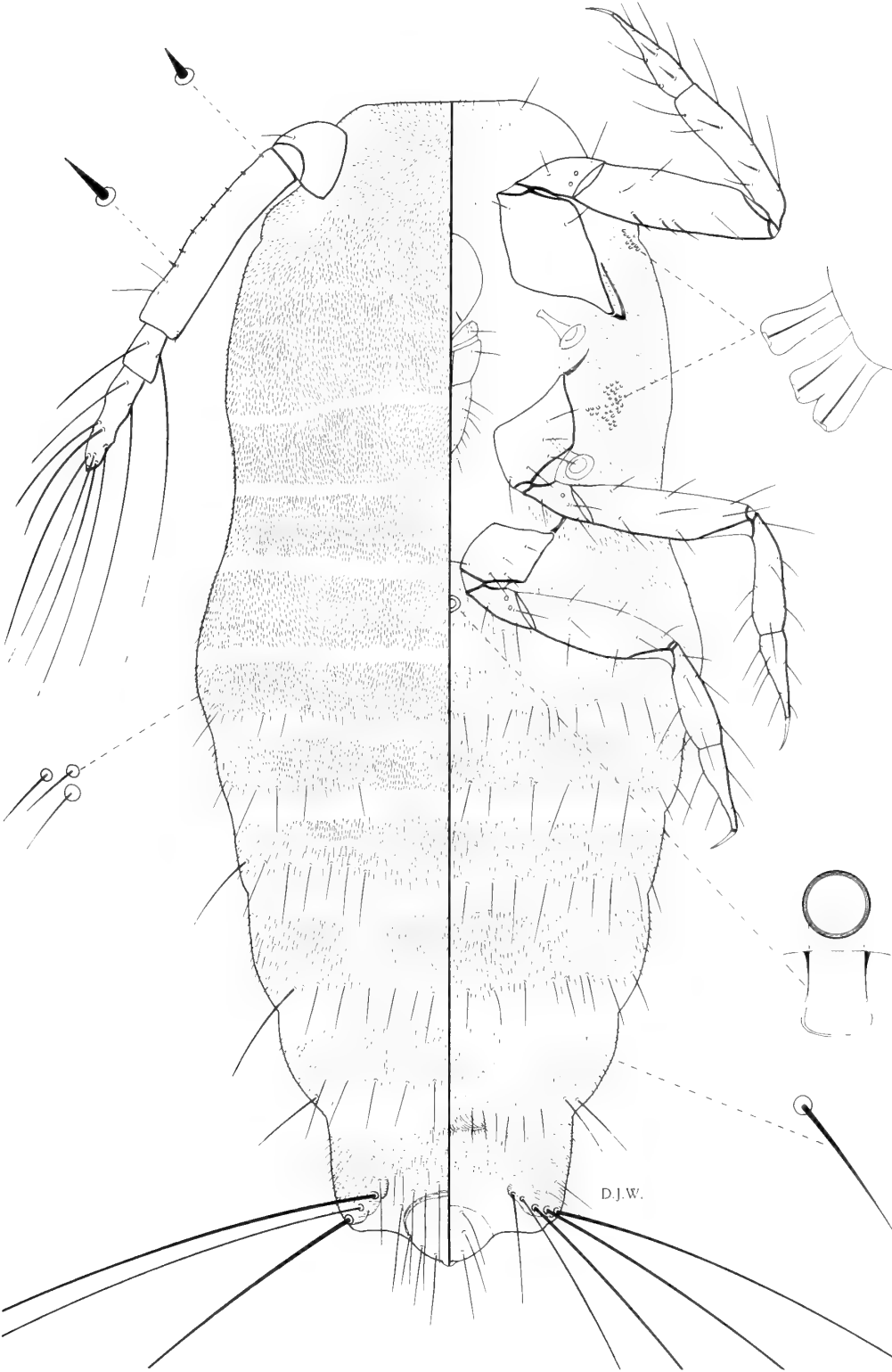
Fig. 10 *Eumyrmococcus neoguineensis* sp. n. Adult female.

Fig. 11 *Eumyrmococcus nipponensis* Terayama. Adult female.
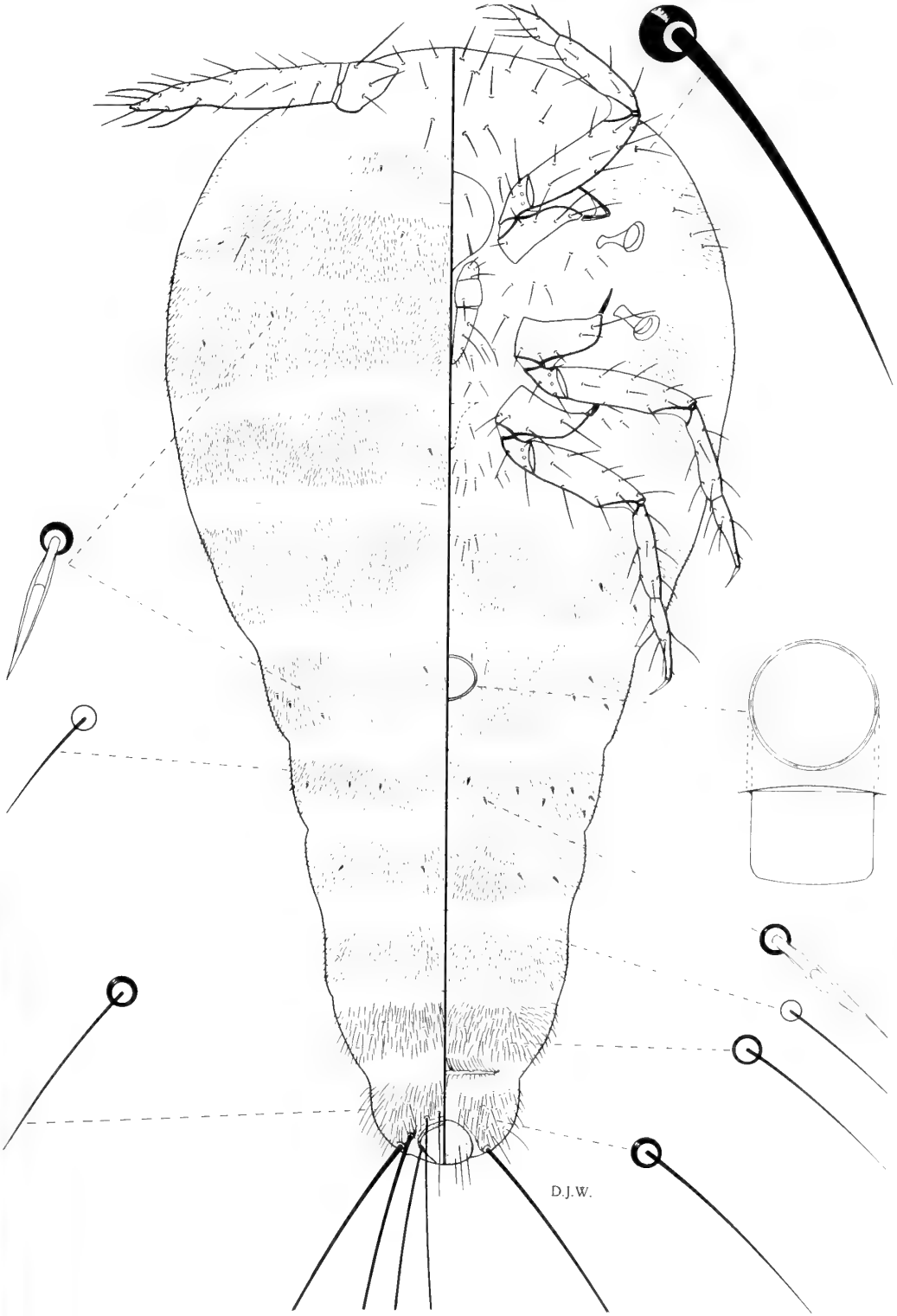
Fig. 12   *Eumyrmococcus queenslandicus* sp. n. Adult female.
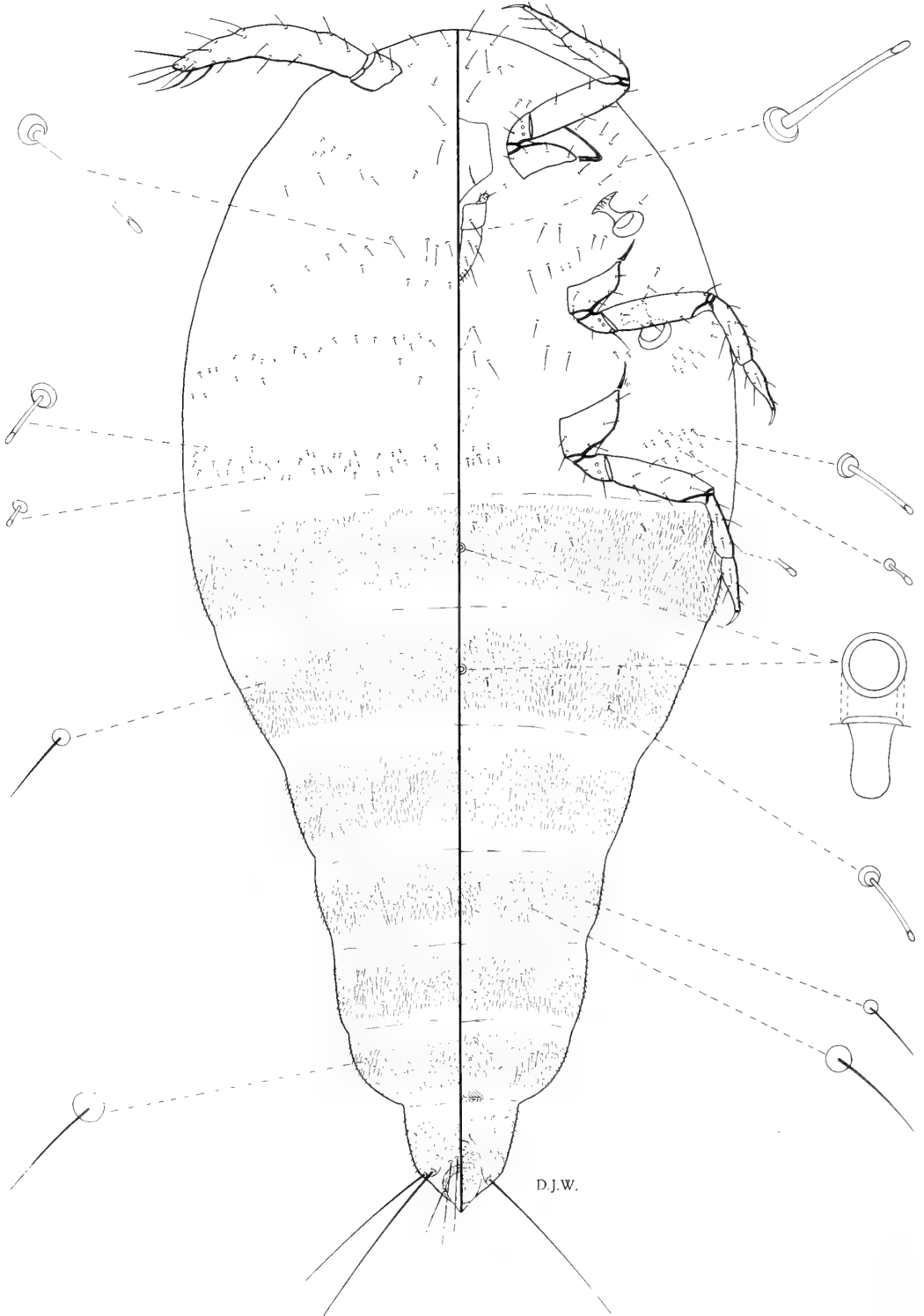
Fig. 13   *Eumyrmococcus recalvus* sp. n. Adult female.
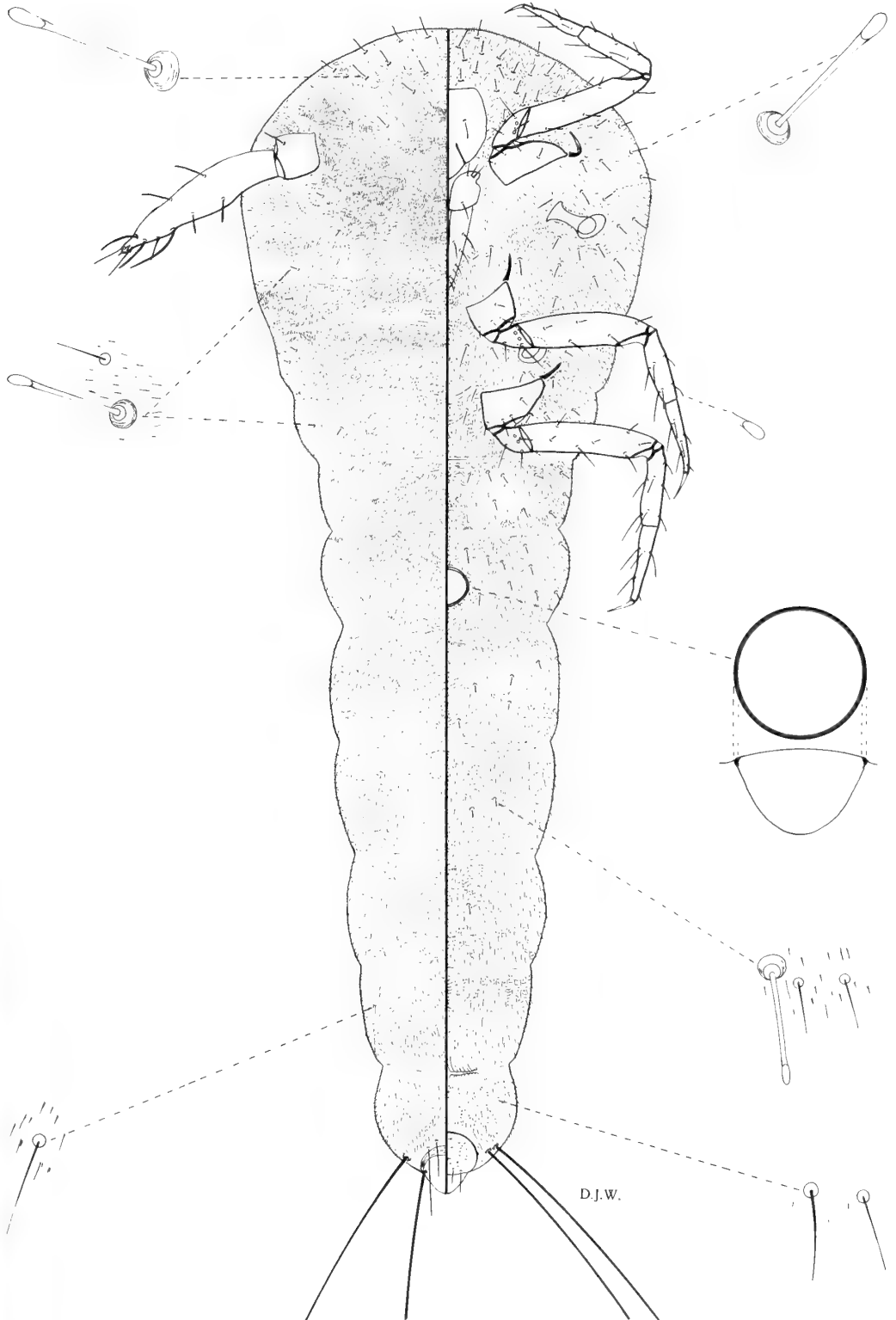
Fig. 14   *Eumyrmococcus sarawakensis* sp. n. Adult female.

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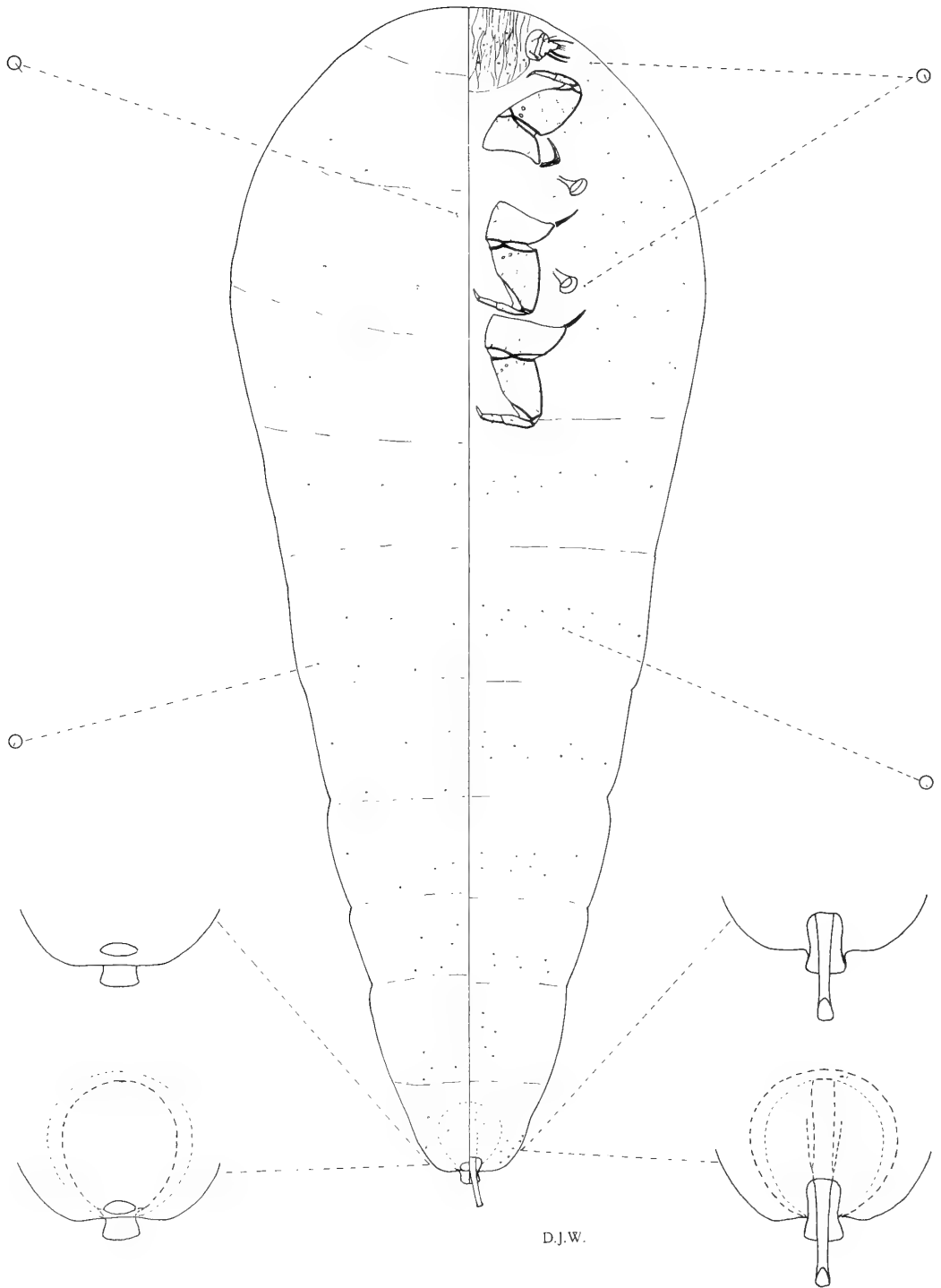
Fig. 15 *Eumyrmococcus sarawakensis* sp. n. Adult male.
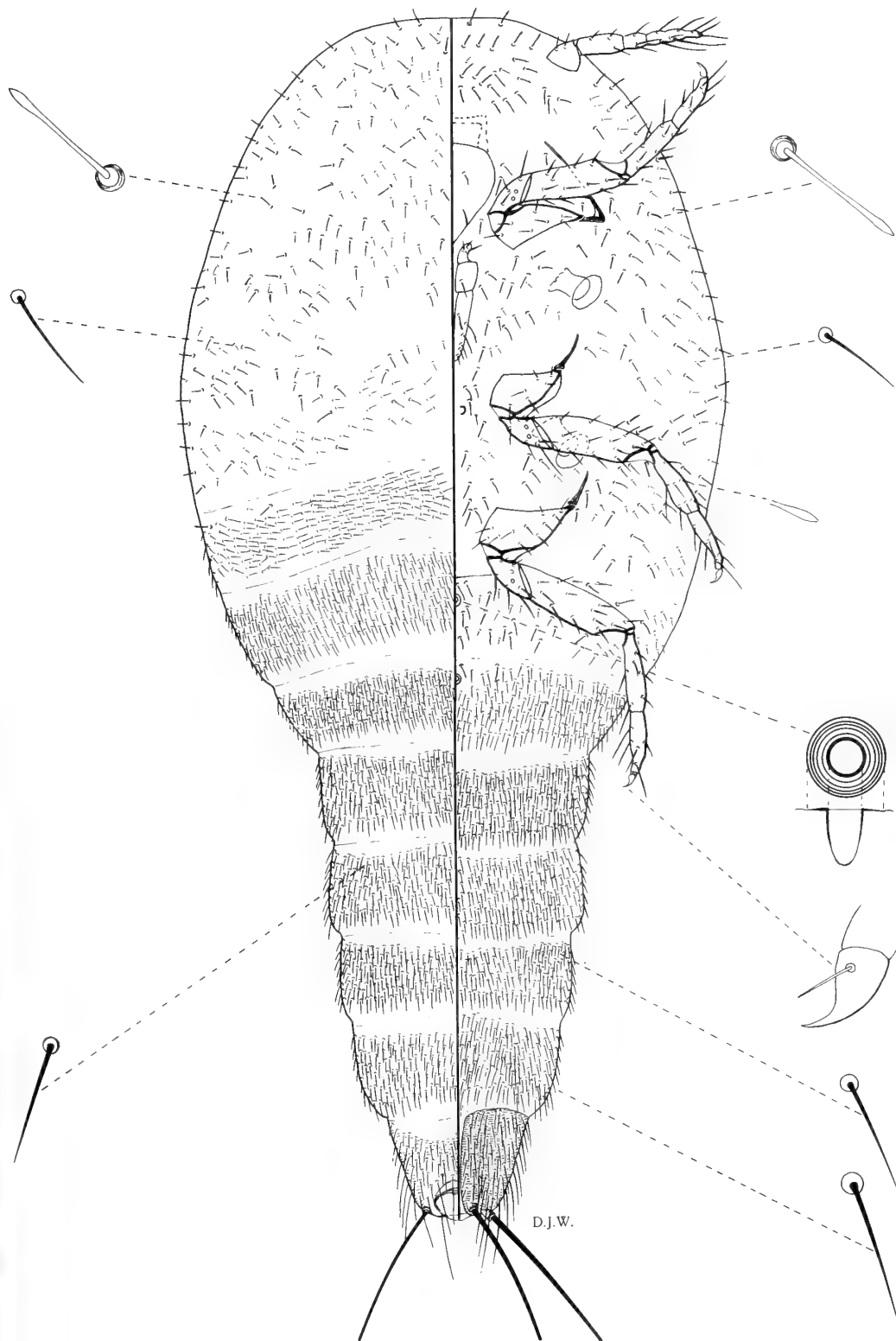
Fig. 16 *Eumyrmococcus scorpioides* (De Lotto). Adult female.
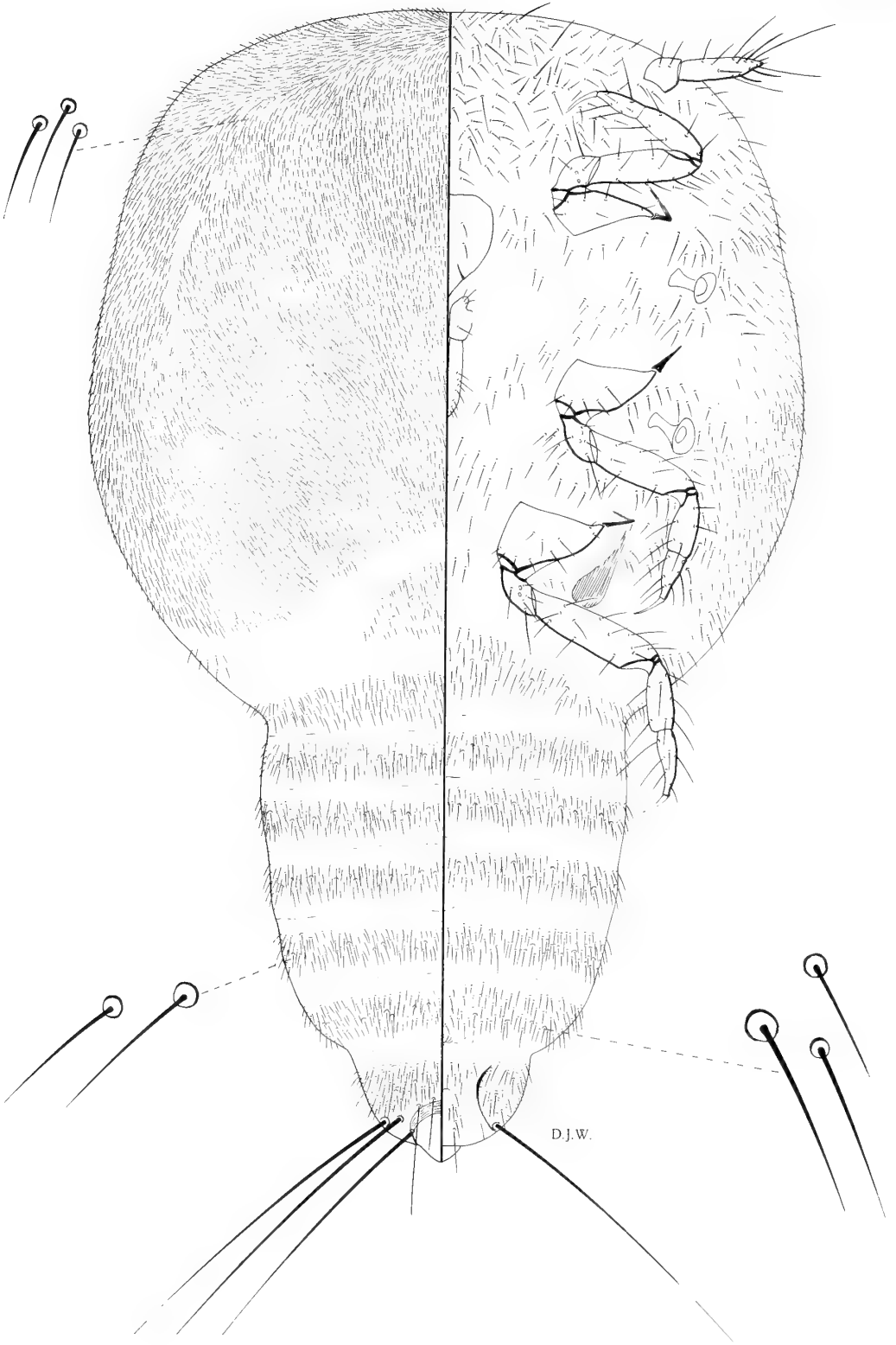
Fig. 17 *Eumyrmococcus smithii* Silvestri. Adult female.

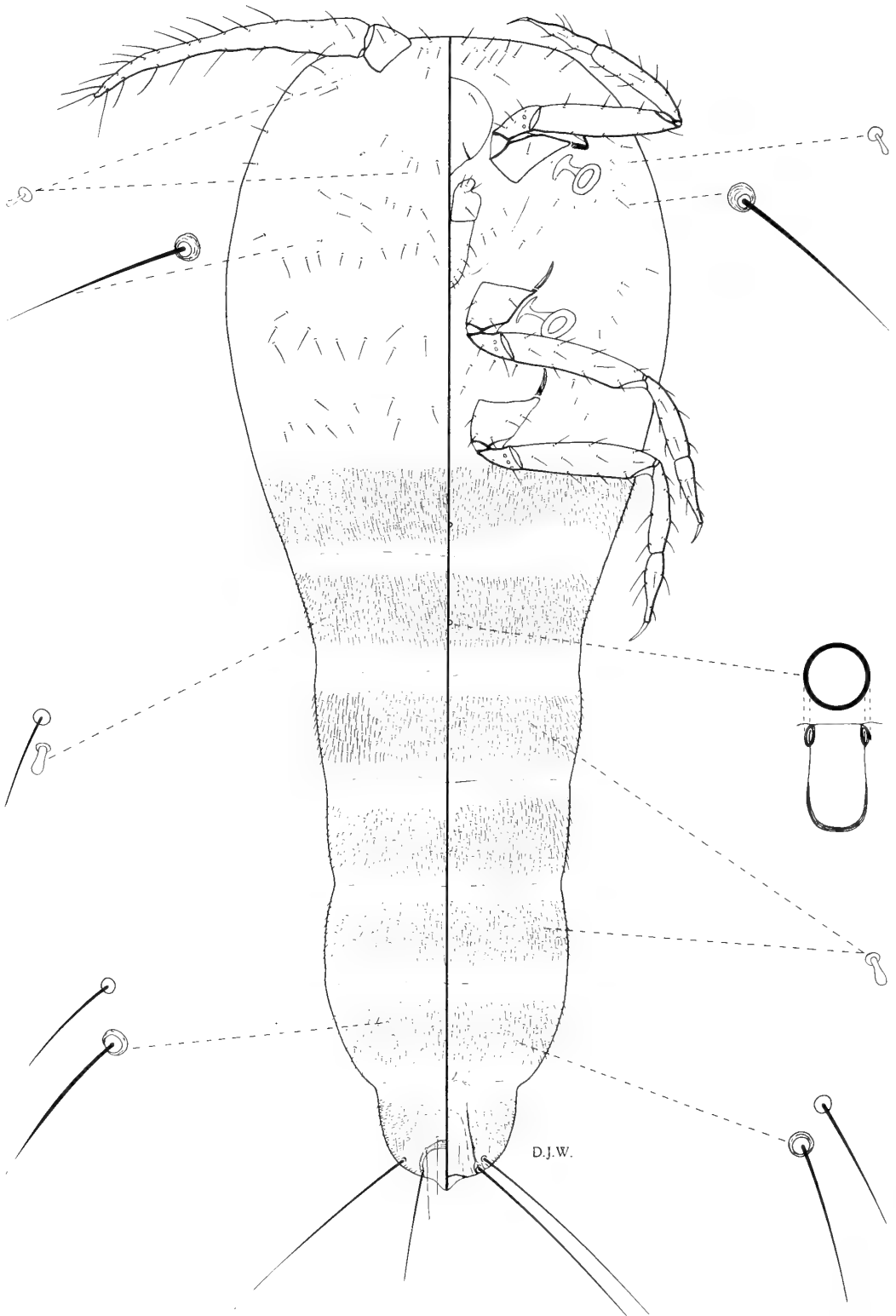**Fig. 18** *Eumyrmococcus sulawesicus* sp. n. Adult female.
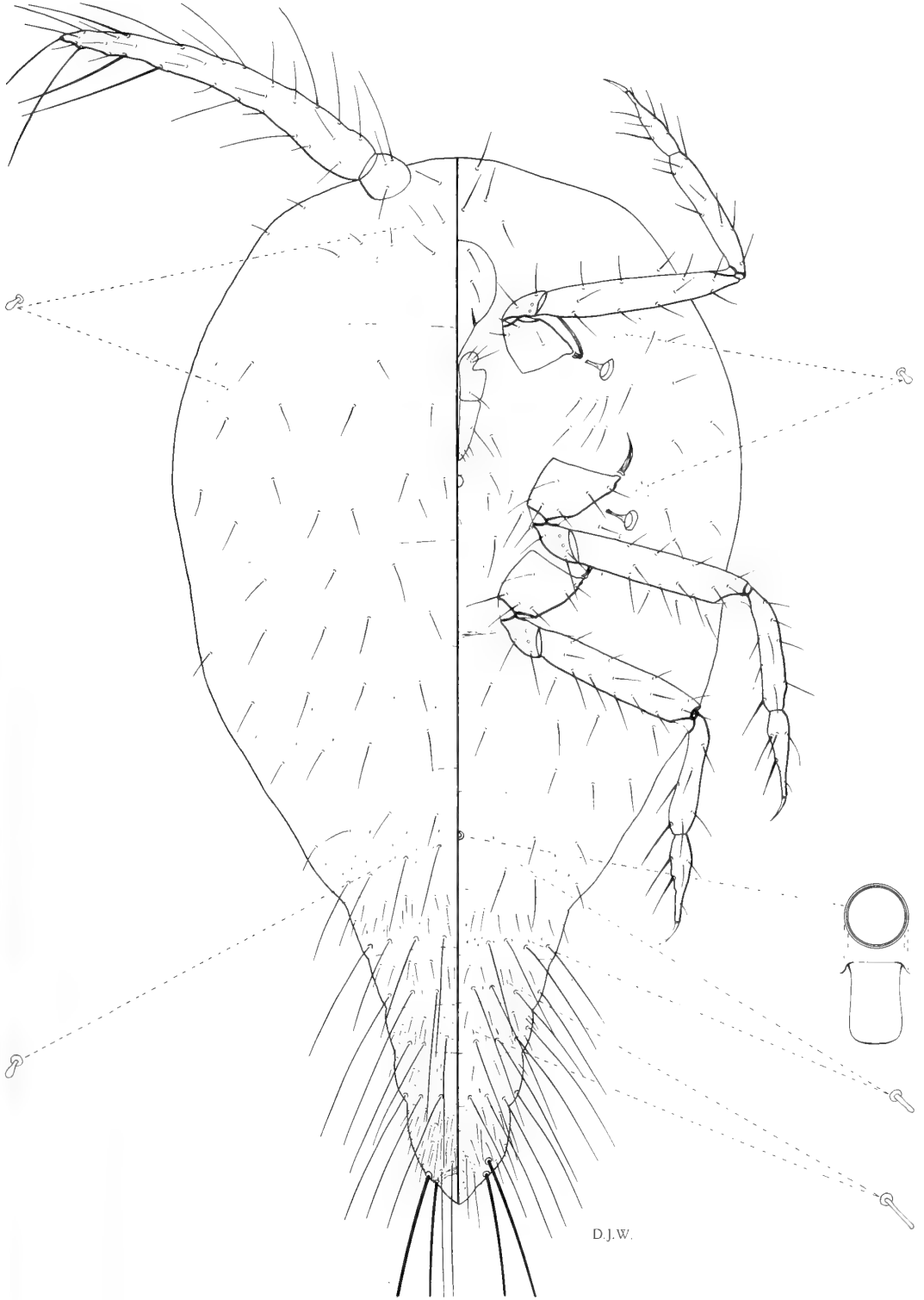
Fig. 19 *Eumyrmococcus taylori* sp. n. Adult female.

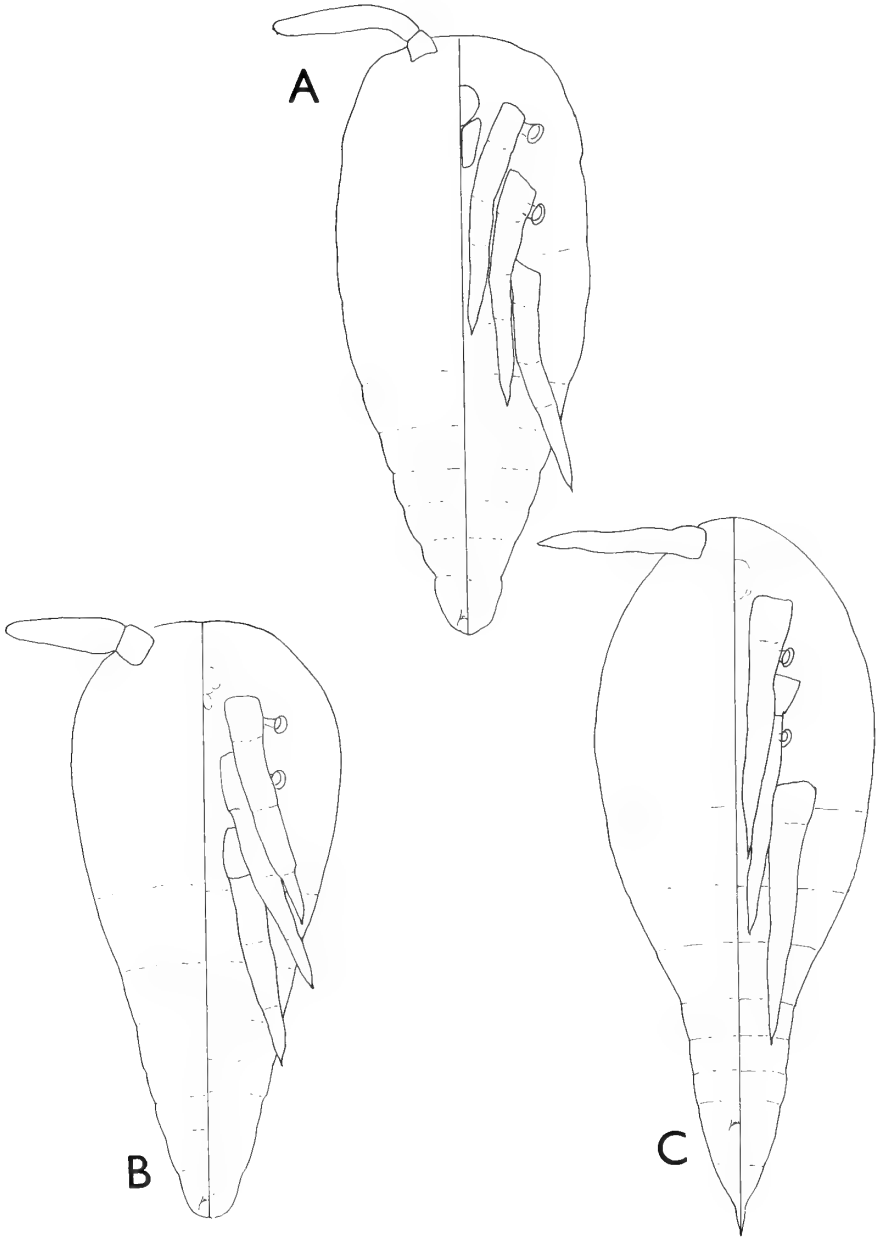**Fig. 20**   *Eumyrmococcus taylori* sp. n. Second instar.

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Fig. 21   *Eumyrmococcus taylori* sp. n. A. Female pupa. B. Male prepupa. C. Male pupa.
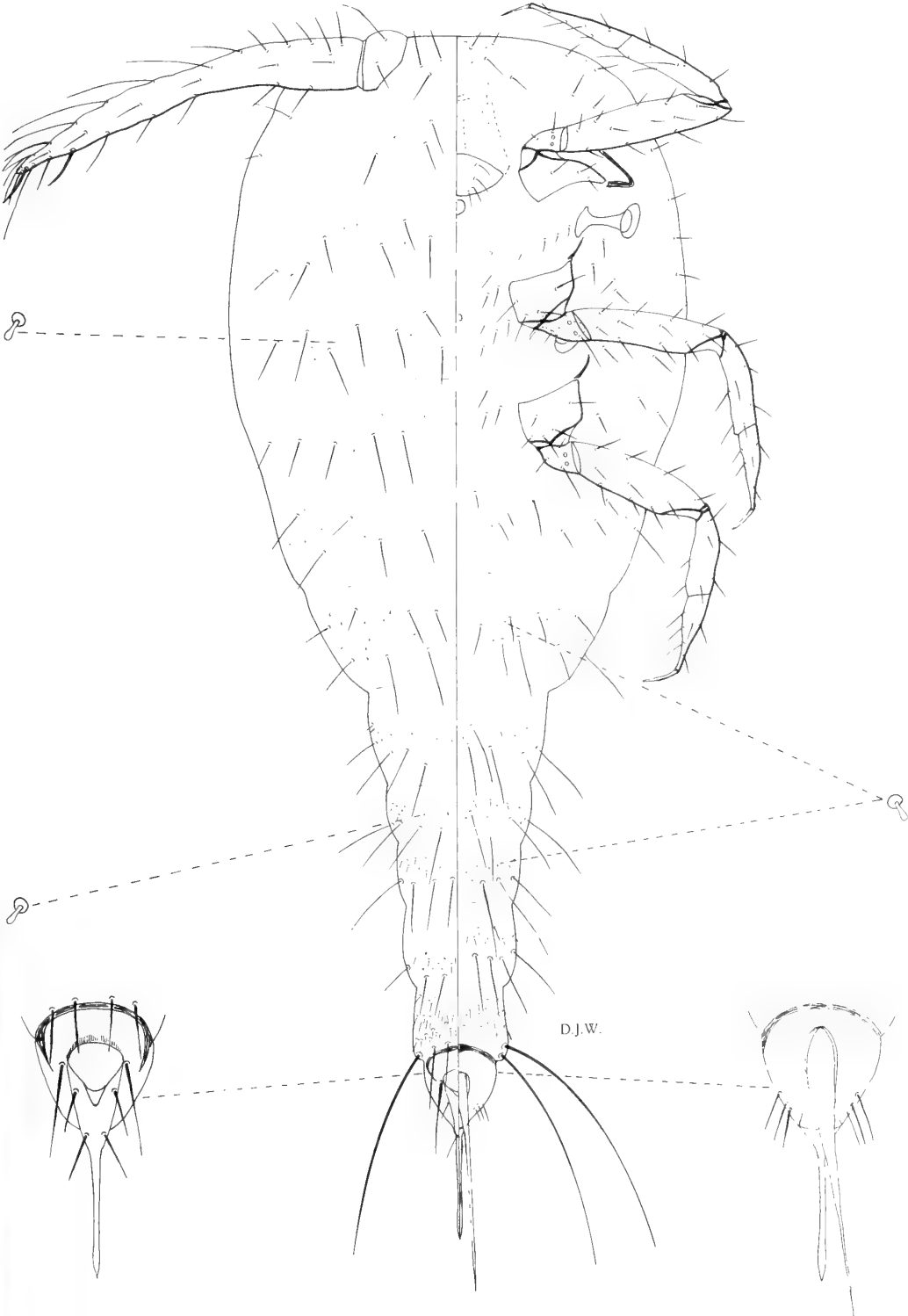
Fig. 22   *Eumyrmococcus taylori* sp. n. Adult male.

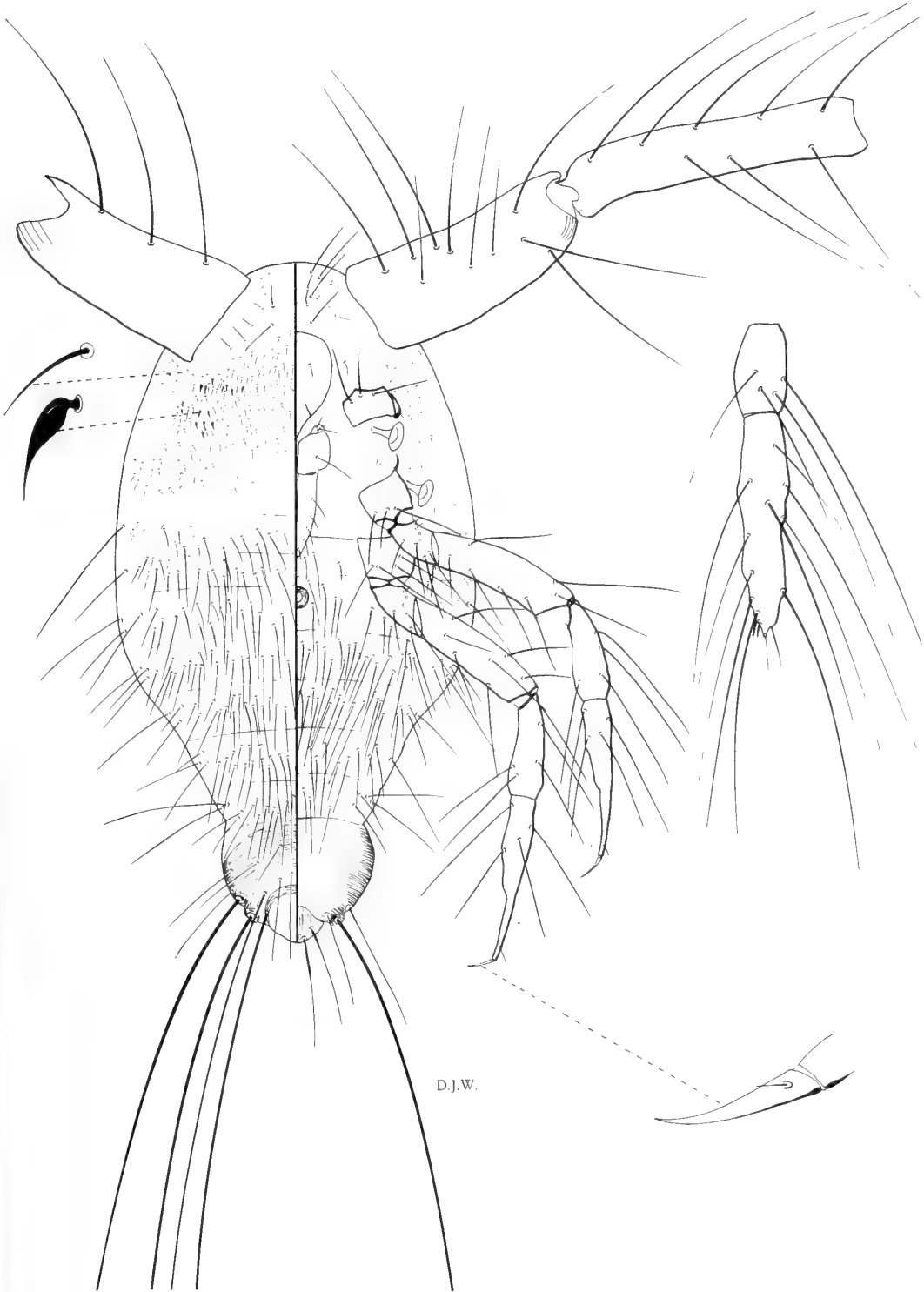**Fig. 23** *Xenococcus acropygae* sp. n. Adult female.

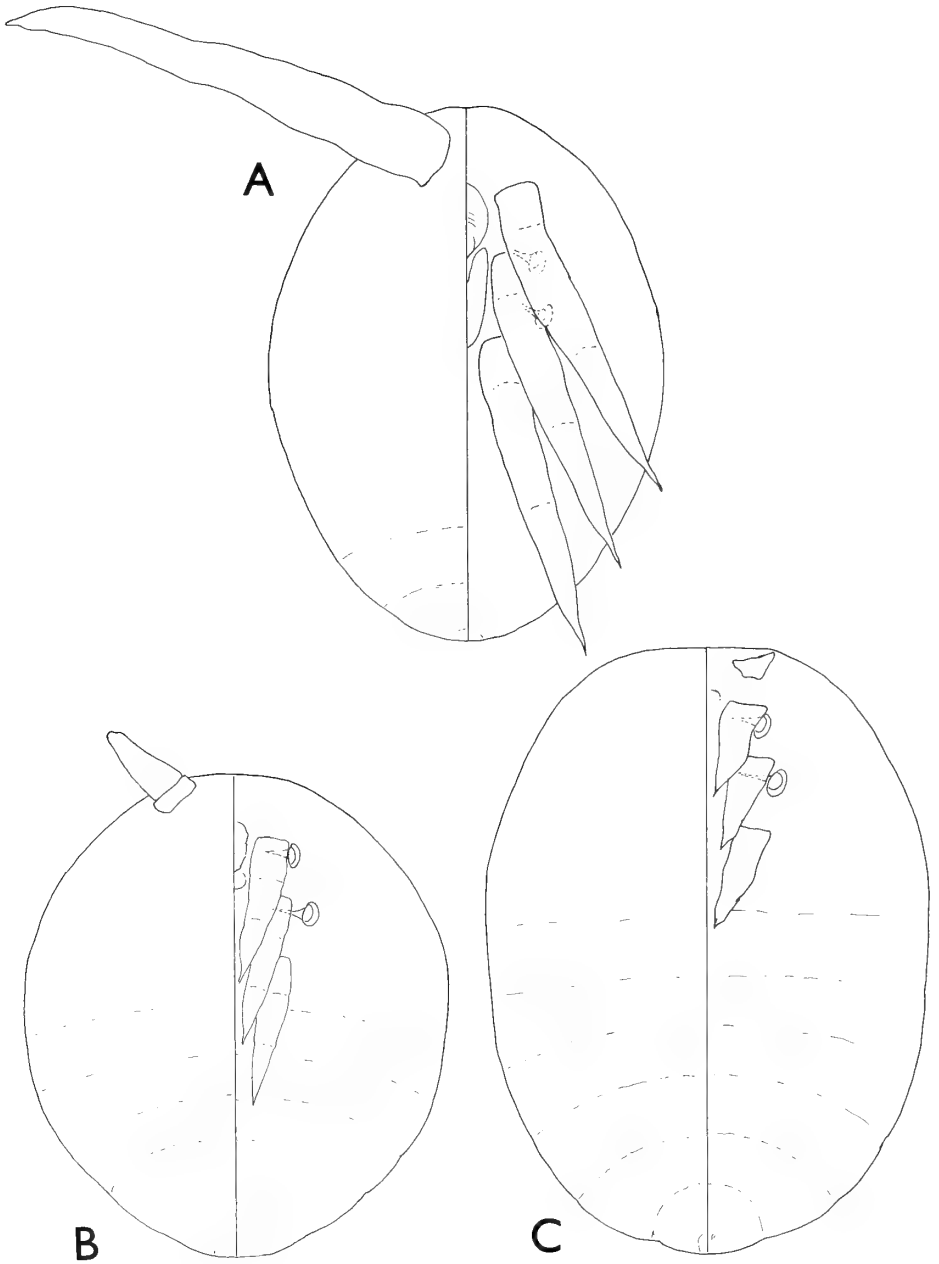**Fig. 24** *Xenococcus acropygae* sp. n. First instar.

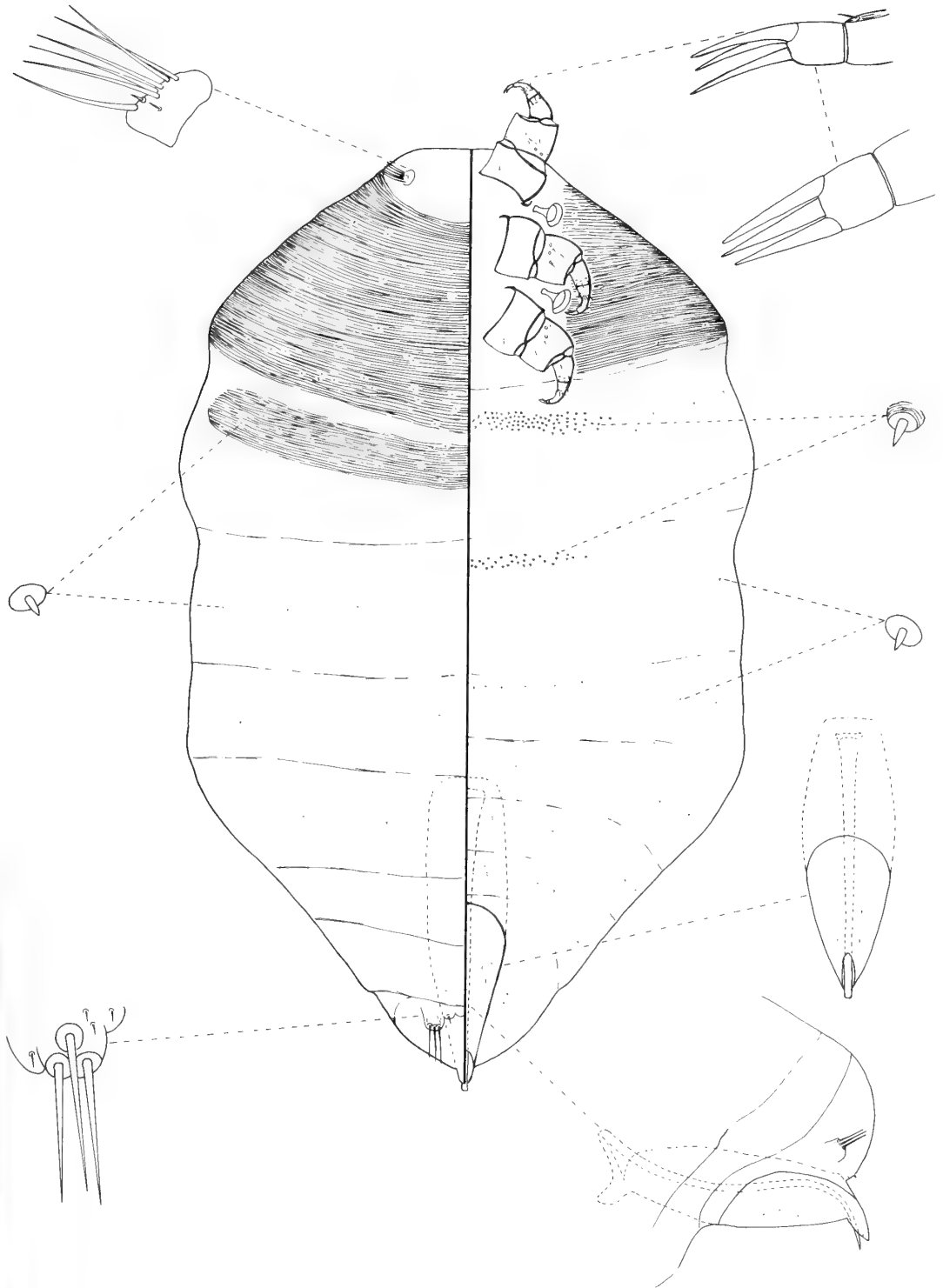**Fig. 25** *Xenococcus acropygae* sp. n. A. Female pupa. B. Male prepupa. C. Male pupa.

Fig. 26   *Xenococcus acropygae* sp. n. Adult male.

Fig. 27 *Xenococcus annandalei* Silvestri. Adult female.
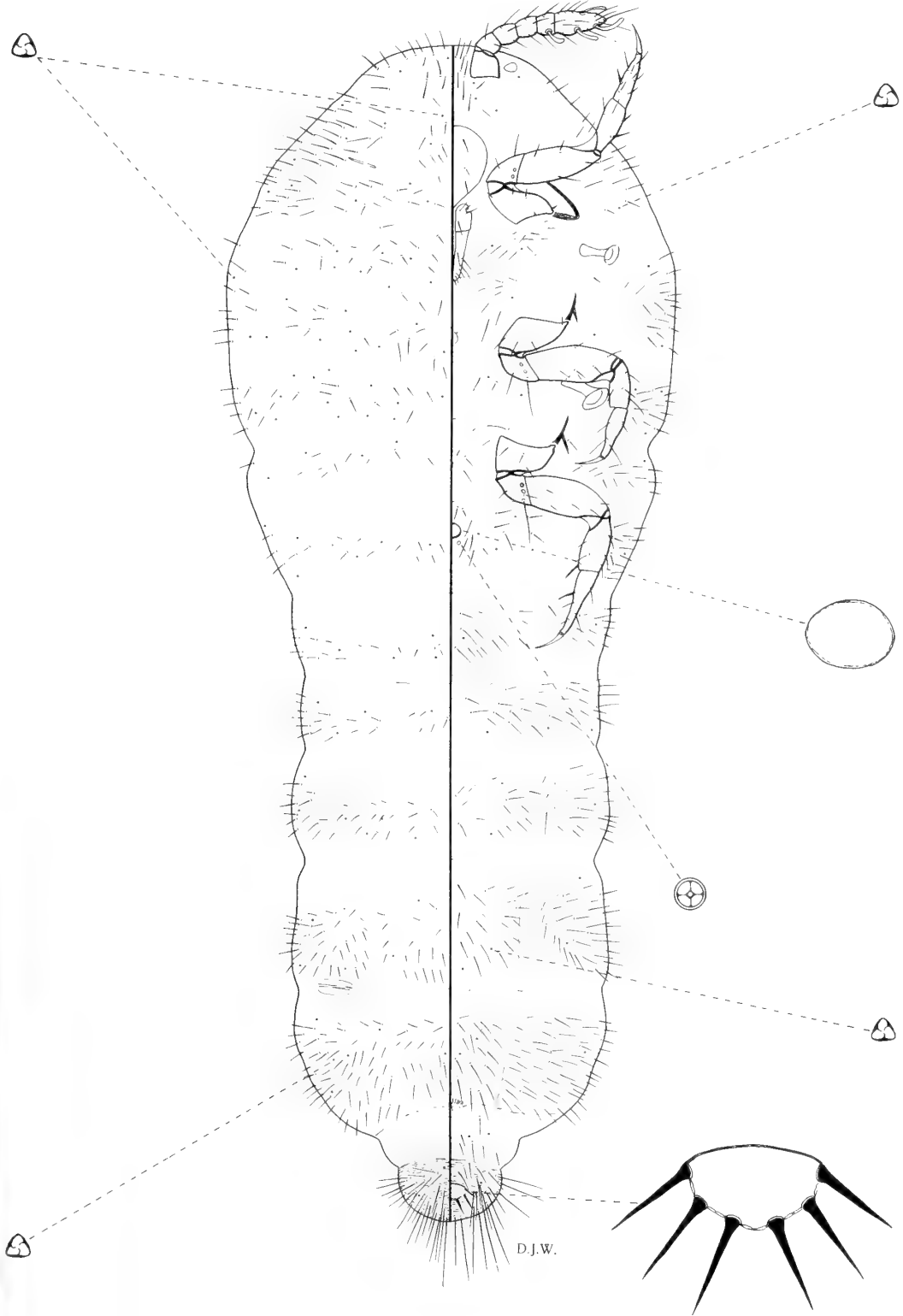
Fig. 28 *Leptorhizoecus deharvengi* sp. n. Adult female.

1 *E. corinthiacus*
2 *E. falciculosus*
3 *E. kolombangarae*
4 *E. kruiensis*
5 *E. kusiacus*
6 *E. lamondicus*
7 *E. lanuginosus*
8 *E. maninjauensis*
9 *E. neoguineensis*
10 *E. nipponensis*
11 *E. queenslandicus*
12 *E. recalvus*
13 *E. sarawakensis*
14 *E. scorpioides*
15 *E. smithii*
16 *E. sulawesicus*
17 *E. taylori*
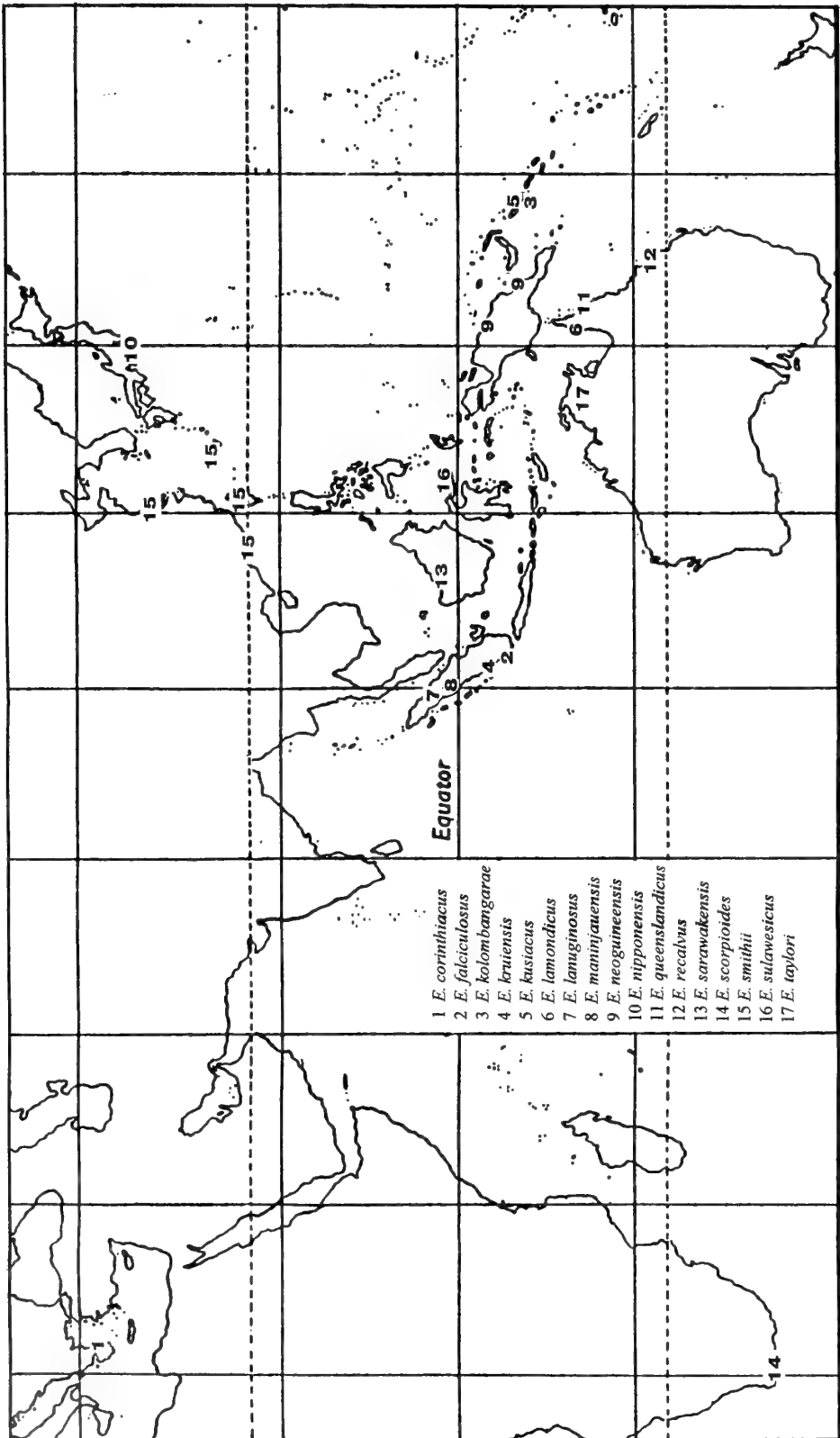
Fig. 29   Distribution map of species of *Eumyrmococcus*.
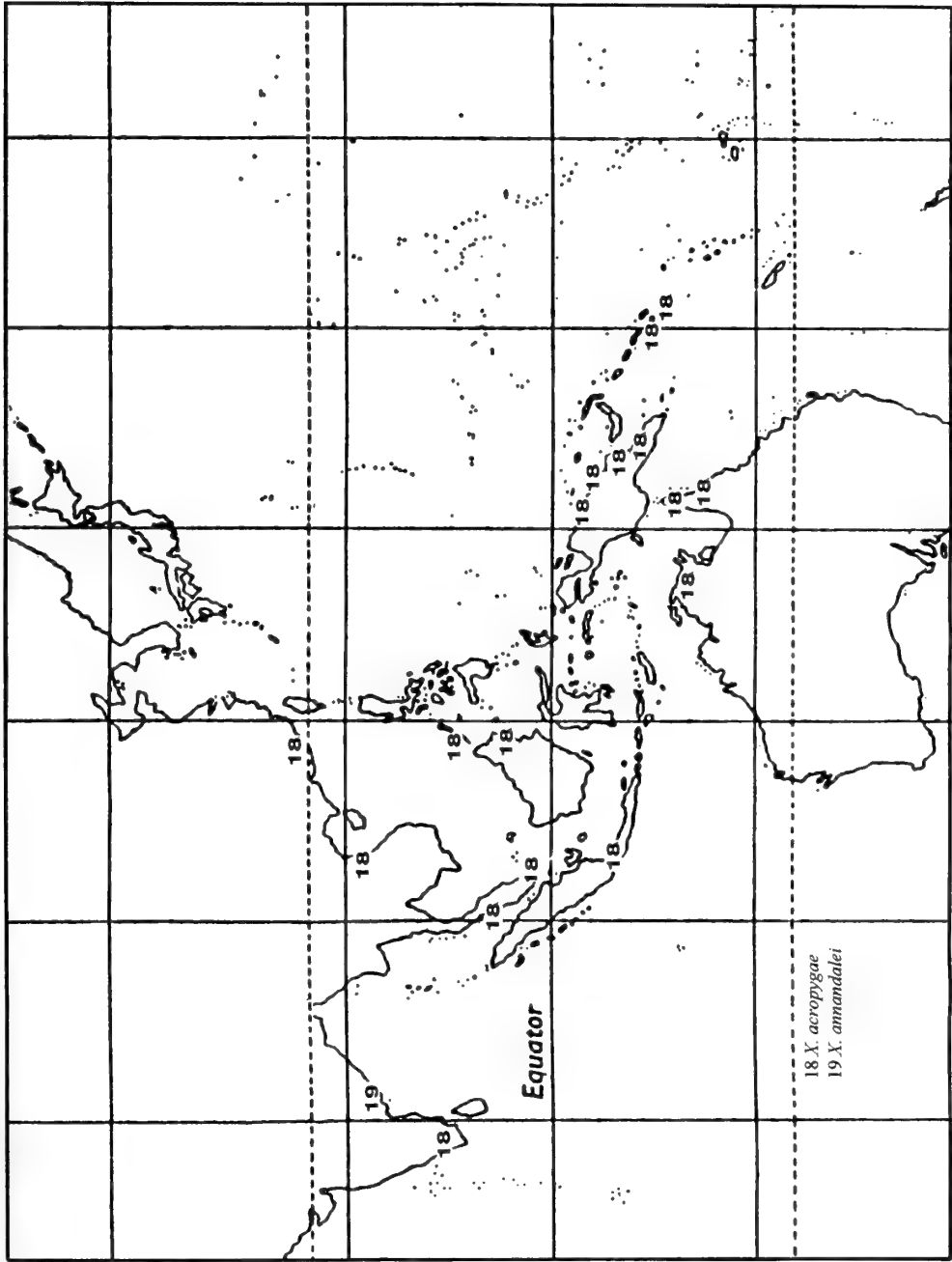
Fig. 30 Distribution map of species of *Xenococcus*.

18 X. acropygae
19 X. annandalei

INDEX

Synonyms and misidentifications are in *italics*; main citations in **bold**

Monophyly of the dacetonine tribe-group and its component tribes (Hymenoptera: Formicidae)

BARRY BOLTON

Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK (e-mail: bb@nhm.ac.uk)

CONTENTS

SYNOPSIS. Within the large subfamily Myrmicinae three independent tribes of ants, Basicerotini, Dacetonini and Phalacromyrmecini, are each recognised as monophyletic and are shown together to constitute a monophyletic tribe-group, here termed the dacetonine-group. Synapomorphies uniting the tribe-group and autapomorphies isolating each tribe are identified and discussed; comments on potential synapomorphies among the three tribes are given.

INTRODUCTION

For many years it has been obvious that the classification of the ant subfamily Myrmicinae at tribe rank is inadequate, with genera or groups of genera being associated on flimsy evidence or merely on superficial similarity. The most recent synoptic classifications (Hölldobler & Wilson, 1990; Bolton, 1994) only serve to stress the rather decrepit nature of the structure. Detailed analysis of the subfamily to produce an accurate higher classification at this rank is in its infancy. Past work on myrmicine larvae (G. C. Wheeler & J. Wheeler, 1976) and sting structure (Kugler, 1979) has

done little to clarify the overall position, although the latter does indicate a number of potentially interesting groupings. An investigation of myrmicine comparative morphology which is currently taking place is unearthing many characters of value in establishing a natural tribe-rank classification. The aim of this paper is to establish, through morphological characters, the monophyly of three tribes within the Myrmicinae, namely Basicerotini, Dacetonini and Phalacromyrmecini, and to show that the three together form a monophyletic group.

Most members of all three tribes nest and forage in leaf litter, topsoil or rotten wood where they form small, usually monogynous, colonies. Only few for-

age openly on the surface of the ground and few are arboreal or occur very deep in the soil. All known species are predatory, mainly catching entomobryomorph Collembola but with numerous species also preying on a wide range of other small arthropods such as sminthurid Collembola, Diplura, Symphyla, Chilopoda, Pseudoscorpiones, Acarina, Araneae, Isopoda, Amphipoda, and many orders of small Insecta and their larvae (Wilson, 1953, 1956; Carlin, 1982; Masuko, 1985; Wilson & Brown, 1985; Dejean, 1987a, 1987b and included references). Species and individuals are common in Berlese or Winkler bag samples of leaf litter or rotten wood throughout the tropics. They may be numerous or locally abundant (e.g. Belshaw & Bolton, 1994; Fisher, in press).

Dacetonini is a large tribe with a world wide distribution. At the last count it included 395 described species (Bolton, 1995a) but many more species have been diagnosed since and their taxonomy is currently being studied by the author. The vast majority of dacetonine species are tropical or subtropical but the tribe is also well represented in zones with a mediterranean climate. Some species occur endemically as far north as Switzerland and Georgia in the West Palaearctic (Kutter, 1977; Arakelian & Dlussky, 1991), and Japan in the East Palaearctic (Morisita, Kubota, *et al.*, 1992). In North America one species ranges as far north as the USA – Canada border (Brown, 1953a). In the southern hemisphere dacetonine species occur as far south as New Zealand (Brown, 1953b), the southernmost parts of South Africa (Bolton, 1983), and central Argentina (Brown, 1962).

Basicerotini mostly shows a Gondwanic distribution, with many species occurring in the Neotropical and Australasian regions (Brown & Kempf, 1960). In the New World basicerotines have been recorded as far north as Florida in the USA (Deyrup, Johnson, *et al.*, 1989) and as far south as Argentina (Kempf, 1972). The tribe is also well represented in Indonesia, Malaysia, the Philippines and the Pacific islands (Taylor, 1990) but is absent from the Holarctic, Afrotropical, Malagasy and Oriental regions. Currently there are 64 described species (Bolton, 1995a), but more await description in various collections.

Phalacromyrmecini is a widely distributed but small and apparently relict tribe that contains only 3 described species (Bolton, 1984), each comprising a monotypic genus. Two of these have only been collected once. They have been found in Brazil, Madagascar and Malaysia.

The three tribes together thus have 462 described species, representing over 10% of the subfamily Myrmicinae, itself easily the largest subfamily in the family Formicidae. The Myrmicinae, which contains 4377 species, represents over half the total described for the entire family. The monophyly of Myrmicinae is probably certain and is documented elsewhere (Baroni Urbani, Bolton & Ward, 1992). Bolton (1994) gives a modern definition of the subfamily and keys to its genera, and all its species are catalogued in Bolton (1995b).

TAXONOMIC HISTORY

Dacetonini is the oldest suprageneric name in the group, initiated by Forel (1892) to include the genera (in the order that he gave them) *Strumigenys, Orectognathus, Epitritus, Hypopomyrmex* [a fossil taxon], *Daceton, Acanthognathus, Rhopalothrix, Ceratobasis* [now a synonym of *Basiceros*] and *Cataulacus*. By modern reckoning this is a fairly disparate group and Forel gave no definitive diagnosis. The next year Forel (1893) listed these same genera, as Myrmicinae tribe Dacetonii, in a synoptic classification. Emery (1895) also produced a synopsis in which he rendered the tribe name as Dacetii. He did not mention the fossil *Hypopomyrmex* and rightly excluded *Cataulacus* from the tribe. The first formal diagnosis of Dacetonini was produced in key form by Emery (1896) with the above inclusions and exclusions. The tribe remained stable with these seven genera for a number of years (W. M. Wheeler, 1910).

In later synopses and classifications other genera, described in the intervening years and referred to Dacetonini, were added, for instance *Stegomyrmex, Microdaceton, Pentastruma* by the time of Emery (1914), who spelled the tribe name as Dacetini; *Glamyromyrmex* and *Epopostruma* by the time of Forel (1917); *Blepharidatta* by the time of Emery (1922); *Codiomyrmex* by the time of W. M. Wheeler (1922), who also correctly excluded *Stegomyrmex* and *Blepharidatta*.

Over the twenty years that followed this a number of authors added further genera to the tribe, until by 1945 the number of genera stood at about 21. Shortly afterwards Brown (1948) began a series of revisionary studies on the generic composition of the tribe, adding a number of new genera. Subsequent papers (Brown, 1949a, 1949b, 1949c, 1950a, 1950b, 1952, 1953a, 1954) refined his concept of the tribe and its component genera. Several more new genera were described, some were synonymised, a number of incorrectly placed taxa were excluded, and the ranks of several genus-group taxa were adjusted. The tribe was subdivided into five subtribes (Brown, 1952) and a proposed evolutionary sequence within the tribe was produced (Brown & Wilson, 1959). A very old name, the fossil *Hypopomyrmex* that had been one of the original members of the tribe (and sole member of subtribe Hypopomyrmiciti), was finally reassesed (Brown & Carpenter, 1979) and decisively excluded.

In one paper of his revisionary series Brown (1949c) recognised that a number of closely related genera

formed a uniform group that could be excluded from Dacetonini. These genera (*Acanthidris, Basiceros, Creightonidris, Heptastruma, Octostruma, Rhopalothrix* and *Talaridris* in the 1949 paper) were grouped together as the tribe Basicerotini. The species of all these were later fully revised on a world basis by Brown & Kempf (1960).

At about the same time Kempf (1960) described an oddly dacetonine-like genus (*Phalacromyrmex*) which together with two other small genera was diagnosed as a discrete genus group by Bolton (1984). A tribe rank name, Phalacromyrmecini, was applied to this group by Dlussky & Fedoseeva (1988), citing the Bolton (1984) definition. [Earlier uses of the name Phalacromyrmecini by G. C. Wheeler & J. Wheeler (1976, 1985) are unavailable as they do not satisfy Article 13 (a) of the International Code of Zoological Nomenclature, third edition, 1985.]

Thus by the early 1990s the classification and generic content of the three tribes had reached the state outlined below, full references for which can be obtained from Bolton (1995b). The synopsis given here indicates all names in the genus group that are currently included in the three tribes. The names listed in parentheses are current junior synonyms. Figures in square brackets after the tribe names indicate the number of species examined for characters visible without dissection; a list of species dissected is appended below.

Tribe **Dacetonini** [569]

Subtribe Dacetoniti [5]
  Genera: *Acanthognathus, Daceton (=Dacetum)*.
Subtribe Epopostrumiti [15]
  Genera: *Colobostruma (=Alistruma, =Clarkistruma), Epopostruma (=Hexadaceton), Mesostruma, Microdaceton*.
Subtribe Orectognathiti [14]
  Genus: *Orectognathus (=Arnoldidris)*.
Subtribe Strumigenyiti [535]
  Genera: *Asketogenys, Chelystruma, Cladarogenys, Codiomyrmex, Codioxenus, Dorisidris, Dysedrognathus, Epitritus, Glamyromyrmex (=Borgmeierita), Gymnomyrmex, Kyidris (=Polyhomoa), Neostruma, Pentastruma, Quadristruma, Serrastruma, Smithistruma (=Cephaloxys, =Miccostruma, =Platystruma, =Weberistruma, =Wessonistruma), Strumigenys (=Eneria, =Labidogenys, =Proscopomyrmex, =Pyramica), Tingimyrmex, Trichoscapa*.

Tribe **Basicerotini** [49]

  Genera: *Basiceros (=Ceratobasis, =Aspididris), Creightonidris, Eurhopalothrix, Octostruma, Protalaridris, Rhopalothrix (=Acanthidris, =Heptastruma), Talaridris*.

Tribe **Phalacromyrmecini** [3]

  Genera: *Ishakidris, Phalacromyrmex, Pilotrochus*.

Until 1994 characters defining the tribes tended to be of an inclusive nature. They were organised in such a way that all taxa showing a particular combination of characters were included in the tribe, those not showing such a combination were excluded. Usually none of these characters could be obviously pointed out as apomorphic. Along these lines the most recent inclusive definitions of the tribes were Brown (1953a) for Dacetonini, Brown & Kempf (1960) for Basicerotini and Bolton (1984) for Phalacromyrmecini.

Baroni Urbani & de Andrade (1994) identified the first synapomorphy exhibited by, and thus unifying, all three tribes: opposing, as distinct from overlapping, mandibles. They also demonstrated that some characters regarded in the past as potential synapomorphies (head shape, specialised hairs) had no real value. Failing to find apomorphies for the individual tribes within the bounds of their synapomorphy, they terminated the independent existence of Basicerotini and Phalacromyrmecini, treating them as junior synonyms of Dacetonini. Although the Baroni Urbani & de Andrade (1994) position was summarily reversed in Bolton's (1995b) catalogue, their approach provided a useful starting point for a detailed investigation. Based on the result of their work, the hypothesis postulated was that only a single real tribe is represented. Characters were then sought and analysed to validate or disprove the results of that assumption. The results obtained indicate that the hypothesis is incorrect and that three tribes should be recognised. The diagnosis and discussion of the relevant characters follows this section.

The present investigation is based upon the worker caste, although most if not all of the characters mentioned are also applicable to known queens. Males are excluded from the survey for the simple reason that they remain utterly unknown in phalacromyrmecines and in several genera of the other tribes. Even in the larger genera males are only very scantily represented. This means that selection of universal characters cannot even be implied, let alone be guaranteed. For the sake of this paper each currently recognised genus in the classification outlined above is assumed to be a valid taxon at genus rank, although work in progress indicates that many should not have such status.

MONOPHYLY OF THE DACETONINE TRIBE-GROUP

The tribes Basicerotini plus Dacetonini plus Phalacromyrmecini share five worker/queen synapo-

morphies and therefore together form a monophyletic group within the subfamily Myrmicinae. The synapomorphies are listed and discussed below, each under its own heading. Character polarity here and in subsequent sections is determined by comparison with those groups currently recognised as the most morphologically generalised Myrmicinae (Myrmicini, Tetramoriini, Formicoxenini). Characters and states across the entire subfamily have been taken into consideration to account for cases of convergence.

Synapomorphies of the dacetonine tribe-group

Masticatory margins of mandibles oppose but do not overlap at full closure
Throughout the three tribes the masticatory (inner) margins of the mandibles fail to overlap or cross over when the mandibles are fully closed. In taxa with serially dentate mandibles the main dental rows interlock tightly at full closure (Figs. 5, 10, 15, 23) rather than the dental row on one mandible passing over the other (Figs. 1, 2, 4), although a few teeth at the extreme apices may cross over (Figs. 11, 22). In taxa with elongate or linear mandibles the inner margins oppose each other, or touch for part of their length at full closure, but do not overlap (Figs. 13, 14, 24). In such forms where a long preapical spiniform tooth occurs, or where an apical fork of spiniform teeth is developed, the teeth themselves may interlock or cross, but the margins from which they arise do not do so (Figs. 13, 14, 33).

This is the character first recorded by Baroni Urbani & de Andrade (1994) and is apomorphic through the groups under consideration. With one exception other Myrmicinae, including all the tribes regarded as morphologically most generalised on other grounds (Myrmicini, Tetramoriini, Pheidolini, Formicoxenini), have the mandibles plesiomorphically overlapping at full closure (Figs. 1, 2, 4). The exception is the peculiar monotypic genus *Tatuidris* (Fig. 6), the sole extant member of tribe Agroecomyrmecini, which also has opposing mandibles. That this is a non-homologous parallelism with the dacetonine-group is easily demonstrated.

Tatuidris has the following apomorphies; the corresponding plesiomorphies exhibited throughout the dacetonine-group are given in square brackets.

1. Tergite and sternite of first gastral segment (abdominal segment 4) are fused. [First gastral tergite and sternite unfused.]
2. First gastral sternite reduced, very much shorter than tergite, so that first gastral segment is directed ventrally with respect to the postpetiole. [First gastral sternite full-sized; first gastral segment not directed ventrally.]

3. Mandible with a thick brush of stout setae on inner surface. [Mandible without setal brush.]
4. Eyes at extreme posterior apex of scrobe. [Eyes not at posterior apex of scrobe.]
5. Antennal sockets extremely widely separated. [Antennal sockets relatively close together.]
6. Alitrunk very short and compact, in profile higher than long. [Alitrunk elongate; in profile usually longer than high.]
7. Apicotibial brush of thick dense setae present on foretibia opposite strigil. [Apicotibial brush absent.]

Conversely *Tatuidris*, beside lacking other dacetonine-group apomorphies, has the following characters exhibiting plesiomorphic states; their corresponding apomorphic expressions in the dacetonine-group (and mostly elsewhere in the Myrmicinae) are in square brackets.

1. Postpetiole very large, very broadly articulated to gaster. [Postpetiole small and narrowly articulated to gaster.]
2. Sternite of postpetiole large, in profile almost as extensive as tergite. [Sternite of postpetiole reduced, much smaller than tergite.]
3. Petiole sessile. [Petiole pedunculate.]
4. Tibial spurs pectinate, strongly developed on middle and hind legs. [Tibial spurs not pectinate, vestigial to absent on middle and hind legs.]

Anterior head capsule is narrowed from side to side
In the three dacetonine-group tribes the head in full-face view, anterior to the antennal sockets, is relatively narrow. A line drawn parallel to the long axis of the head, touching the outermost point of the torulus, will pass outside or very close to the point where the outer margin of the fully closed mandible intersects the anterior clypeal margin (Figs. 5, 7, 10, 13, 14, 15, 22, 23, 24, 33). In all other Myrmicinae (except for the few with radically migrated toruli discussed below) a line so constructed will pass considerably mesad of the point where the outer margin of the fully closed mandible intersects the anterior clypeal margin (Fig. 1).

The anterior narrowing of the head can be expressed as a ratio, the Mandibular-Torular Index (MTI), which with the head in full-face view may be defined as: distance between points where outer margins of fully closed mandibles intersect anterior clypeal margin *divided by* distance between outermost points of lower margins of toruli. Thus when MTI =1.0 the two measurements are equal. MTI range of 0.5–1.3 is shown by the dacetonine-group of tribes, and also by *Tatuidris* (Fig. 6), *Cataulacus* (Fig. 4) and some Cephalotini. Other tribes of Myrmicinae together have MTI range 1.5–>3.0. The reason why these three non-dacetonine taxa have a similar MTI range to the dacetonine-group

is that whilst their heads have remained plesiomorphically broad anteriorly, their toruli have secondarily migrated outwards on the cephalic dorsum, bringing them into line with the clypeal intersection points of the mandibles. Thus two completely different evolutionary routes, static toruli combined with narrowed anterior head (the dacetonine-group), *versus* static broad anterior head combined with outwardly migrated toruli (*Tatuidris, Cataulacus,* some Cephalotini), will give the same overall MTI result. For an illustration of this character spanning the entire subfamily compare the full-face view photographs of the various myrmicine genera in Bolton (1994).

As a direct result of the narrowing of the anterior head the dacetonine-group shows a number of other derived characters that are unavoidable corollaries of this modification.

1. Width of labrum at base, and consequently also of clypeo-labral hinge, is reduced (see below).
2. Width of buccal cavity, and consequently also of labio-maxillary complex, is reduced (compare Fig. 3 with Figs. 12, 26, 28).
3. Anterolateral surface of head tends to be vertical, or nearly so, and is very close to or more or less directly below the antennal socket (e.g. Figs. 11, 18, 19, 32).

Preocular carina is present
With the head in profile or dorsolateral view there is a ridge, carina or lamella that originates at the posterolateral termination of the clypeus, extends posteriorly below the antennal socket and usually continues for some distance towards the level of the eye (Figs. 11, 18, 19, 30, 32). In many taxa this preocular carina is also visible in full-face view, at least anteriorly (Figs. 13, 23, 25, 31), but usually cannot be seen in this view in those species or genera where the frontal lobes and frontal carinae are strongly expanded laterally (Fig. 7).

Morphologically the carina represents the exaggerated outer margin of the antennal fossa and is another corollary of the narrowing of the head (particularly of number 3, immediately above). At its weakest the carina is a ridge that emphasises the dorsalmost line of the more or less vertical side of the head capsule. At its strongest it is a broad, laterally projecting lamella. The structure is perhaps better termed the subtorular carina or subantennal carina as this area is always where it is strongest developed, but earlier literature has used preocular carina so much that the name will probably be retained.

Specialised range-finder/trigger hairs are developed on the mouthparts
In the dacetonine-group hunting always seems to involve an open-mandible approach to the prey, followed

by a rapid strike with the mandibles (see references above, particularly Masuko, 1985). The strike may be followed by static pressure of the mandibles, merely to retain a grip on the prey until the sting can be brought into use ('strike-hold-sting' technique), or dissipation of the kinetic energy of the strike itself may be sufficient to shock the prey into immobility, even if only temporary, until the sting can be brought into play, particularly if the prey is lifted clear of the ground immediately after the strike ('strike-lift-sting' technique). Whatever the technique, the explosive closing of the mandibles is initiated by activation of a trigger which consists of one or more specialised hairs on the mouthparts. Contact with prey by these hairs commences a sequence of events that causes the mandibles to snap shut (Masuko, 1985; Gronenberg, 1996). In the vast majority of dacetonine-group taxa these hairs arise from the anterior margin of the labrum or the apices of the labral lobes (Figs. 16, 25–31 (broken off short in 26), 27, 33), more rarely from the mandible itself; such trigger hairs are not found elsewhere in the Myrmicinae.

Specialisation of the labrum
Except for the dacetonine-group of tribes the structure of the labrum is very uniform and generalised in the Myrmicinae (Gotwald, 1969 and present investigation), and this same structure is prevelent throughout the Formicidae. Outside the dacetonine-group the labrum is a simple sclerite (Fig. 3) that is broader than long and broadly hinged to the clypeus. Its posterior margin, which is attached to the clypeus, is more or less straight. Its anterior (free) margin is indented or cleft medially so that in general the labrum appears broadly B-shaped, or D-shaped with a median indentation in the anterior free margin. The clypeo-labral hinge is mobile so that at rest the labrum folds back and down with respect to the clypeus. In this position it tightly overlaps and protects the delicate apical portions of the labio-maxillary complex. In the Myrmicinae this is the plesiomorphic shape and position. It is encountered in all the morphologically more generalised tribes (e.g. Myrmicini, Tetramoriini, Pheidolini, Pheidologetonini, Formicoxenini, Solenopsidini), as well as in those that are rather more specialised morphologically (e.g. Attini, Cataulacini, Cephalotini, Crematogastrini, Stenammini, Agroecomyrmecini).

Tribes in the dacetonine-group show a number of modifications away from the generalised structure illustrated in Fig. 3, but all are based on labral narrowing and elongation, and loss of the basic broadly B- or D-shaped outline.

In taxa with mandibles that use static pressure, regardless of whether the mandibles are long or short, the labrum becomes longer and narrower, sometimes longer than broad. The sclerite usually terminates in

one or two exaggerated anterior lobes or linguiform prominences that bear the trigger hairs (Figs. 12, 16, 25, 28, 29, 31). In these forms the labrum can usually still flex down very slightly, but it is not capable of tight closure against the labio-maxillary complex (Figs. 12, 28). Conversely, in some taxa the labrum is hypertrophied and elongate-linguiform; instead of concealing only the apex of the labio-maxillary complex it covers the entire buccal cavity (Fig. 32). Taxa with long kinetic mandibles tend to have the labrum very narrow basally, and more distally to develop a pair of laterally projecting processes or arms; the sclerite therefore tends to be roughly T-shaped and its apex functions to prop open the mandibles prior to striking (Figs. 26, 27, 30). One long-mandibulate genus (*Acanthognathus*) has eliminated the labrum from this function and here it is represented only by a very slender, inverted Y-shaped sclerite.

Some characters considered but not used at tribe-group rank

Presence of 2-segmented antennal club
An antennal club of two segments is universal in the tribes Basicerotini, Dacetonini and Phalacromyrmecini, though only very poorly expressed in *Daceton*. This may be the result of a single evolutionary event in the dacetonine-group, but a two-segmented club is also developed in a wide range of non-dacetonine myrmicine taxa. For example, a strongly defined two-segmented club is universal in Melissotarsini (*Melissotarsus, Rhopalomastix*), present in all the core genera of Pheidologetonini (*Afroxyidris, Carebara, Oligomyrmex, Paedalgus, Pheidologeton*), present in some but by no means all Stenammini (*Adelomyrmex, Baracidris, Lachnomyrmex, Mayriella, Tetheamyrma*), occurs in a few Solenopsidini (*Carebarella, Solenopsis*) and is present in the single extant genus of Agroecomyrmecini (*Tatuidris*). It is weakly developed in some Blepharidattini (*Blepharidatta, Wasmannia*), and in some but not all species of *Cardiocondyla* (Formicoxenini) and *Crematogaster* (Crematogastrini).

Antennomere count
Although very useful as a character in keys, antennomere count was ignored in this survey because in some myrmicines there is variation within genera (e.g. 10, 11 or 12 in *Tetramorium* (Tetramoriini); 4, 5 or 6 in *Smithistruma* (Dacetonini)). Also, within the tribes of the dacetonine-group there is a wide range of counts that makes analysis very difficult. For example in Dacetonini counts of 4, 5, 6 and 11 have been recorded; in Basicerotini 7, 8, 9 and 12, and in Phalacromyrmecini 8, 9 and 11. I am convinced that these counts indicate independent morphoclinal reductions within each tribe, with no significance at tribe rank.

Absence of tibial spurs
Throughout the tribes of the dacetonine-group spurs are absent from the middle and hind tibiae. This condition is apomorphic among the Myrmicinae but unfortunately is so extremely widespread through the subfamily that it has very little analytical value in the current survey.

MONOPHYLY OF TRIBE BASICEROTINI

Basicerotini Brown

Basicerotini Brown, 1949c: 86. Type-genus: *Basiceros* Schulz, 1906: 156. [Basicerotini relegated as junior synonym of Dacetonini by Baroni Urbani & de Andrade, 1994: 10; revived from synonymy by Bolton, 1995b: 9.]

Apomorphies of tribe Basicerotini

Each worker apomorphy is briefly described, in some cases with added comments where unrelated taxa show similar but non-homologous modifications. The plesiomorphic state of each character is given in square brackets; in some cases alternative apomorphic conditions are also noted for comparative purposes.

LABRUM
Distal of the hinge with the clypeus the labrum has a deeply incised transverse groove or trench across its entire dorsal width. The distal margin of this groove is defined by a sharp edge, ridge or crest (Fig. 16; also visible between the closed mandibles in Figs. 13, 14). [Labrum without sharply defined transverse groove distal of hinge.]

In the basicerotines this groove, or at least its sharp distal margin, is usually located far enough anteriorly on the labrum as to be visible in ordinarily mounted specimens which have the mandibles ajar and the labrum slightly depressed.

TORULUS
The dorsal lobe of the torulus is hypertrophied and strongly curved downwards (Figs. 18, 19); its outer surface is nearly vertical so that it conceals part to most of the condylar bulb of the scape and the antennal socket itself. [Torulus a simple annulus or with a small lobe present dorsally that is horizontal and does not conceal the condylar bulb of the scape and the antennal socket.]

SCAPE NECK ARTICULATION
Because of the size and shape of the torulus the space in which the basal neck of the scape (the short narrow section between condylar bulb and scape shaft proper)

can move is narrow and directed fore and aft (Figs. 18, 19). [Space in which basal neck of scape can move is not restricted to a narrow fore and aft motion.]

BASE OF SCAPE
Scape shaft near base is bent downwards through a right-angle or near right-angle; the articulatory condyle at the extreme base projects forward from this through another right-angle that is not in the same plane as the first bend but rather is rotated through about 90 degrees (Figs. 8, 9). [Scape shaft in a straight line with basal condyle; or if scape angled downward near base then angle of basal condyle remains in the same plane as the shaft and is not rotated through 90 degrees.]

ANTENNAL FOSSA
Antennal fossa separated from scrobe by at least a cuticular rim or crest; the depressed fossal area surrounded on all sides by raised or prominent cuticle (Figs. 18, 19). [Antennal fossa and scrobe confluent (when the latter is developed).]

SCROBE
Scrobe always present and located below the eye (Figs. 18, 19), the latter usually situated on the extreme dorsolateral rim of the scrobe, more rarely towards underside of upper scrobe rim (very rarely eye absent). [Scrobe absent, or present but extending above the eye (eye sometimes absent).]

Some other myrmicine taxa have a scrobe that extends below the eye, namely *Cataulacus*, some Cephalotini, and the Dacetonini related to *Epopostruma* (Epopostrumiti in the synoptic classification above). *Cataulacus* and the few cephalotines with this condition can be dismissed as obvious convergence. Not only is the basic structure of the scrobe dissimilar but also the detailed structure of the head is very different. They lack, of course, the apomorphies of the dacetonine-group of tribes and exhibit their own series of apomorphies. The Epopostrumiti, on the other hand, belong in the dacetonine-group. Apart from possessing the apomorphies of Dacetonini and lacking those of Basicerotini, the scrobes in Epopostrumiti lack sharply defined posterior margins, usually lack ventrolateral margins and, except in a very few species, fail to extend forward to the mandibular articulation (Fig. 32); all of these are developed in Basicerotini. Finally, a morphocline of species in the genera *Colobostruma – Mesostruma – Epopostruma* is present that exhibits a gradual increase in development and definition of the scrobe; no basicerotine could be inserted into the series, nor added to either end.

OCCIPITAL FORAMEN
The occipital foramen is set in a deep depression on the occipital surface of the head; cuticular margination is continuous around the depressed area (Fig. 17). [Occipital foramen not set in a continuously marginate deep depression.]

A very few Dacetonini have a transverse ventral rim of cuticle below the occipital foramen. This structure is very different from the basicerotine organisation.

HELCIUM
Helcium arises from the base of a broad, deeply concave depression or excavation in the anterior surface of the postpetiole (Fig. 20). [Helcium not set in a concave depression.]

GASTER
First gastral tergite and sternite each distinctly transversely marginate basally, immediately behind the postpetiole (Fig. 21). [First gastral tergite and sternite not marginate basally.]

Members of the strumigenyite group of Dacetonini genera have a specialised transverse crest on the first gastral tergite, the limbus, which is an apomorphy of that group. The limbus is located prebasally and is inclined towards the base proper, where it overhangs the presclerites of the segment. It is not a homologue of the basal margination developed in Basicerotini. No Dacetonini have a basally marginate first gastral sternite.

SCULPTURE
First gastral tergite and sternite with characteristic sculpture of dense, sharply incised, separated punctures (e.g. Fig. 21). [First gastral tergite and sternite unsculptured, or with different sculpture.]

This character may seem rather imprecise, but the form of sculpture is striking and not obviously repeated elsewhere. A very few individual basicerotine species have secondarily reduced or effaced the sculpture. Elsewhere in the dacetonine-group, and in the Myrmicinae as a whole, are many species with sculptured gasters. Even when the sculpture in these is of a basically punctate form it tends to be reticulate-punctate or sparse, or on one sclerite but not the other. It is not the dense deeply-incised punctation exhibited by the Basicerotini on both sclerites.

MONOPHYLY OF TRIBE DACETONINI

Dacetonini Forel

Dacetonini Forel, 1892: 344. Type-genus: *Daceton* Perty, 1833: 136.

Apomorphies of tribe Dacetonini

The two worker apomorphies are briefly described and comments added. The plesiomorphic state of each character is given in square brackets.

MANDIBLE
Mandible with a medially projecting cuticular process present on the inner margin close to the base

(basimandibular process); the process not merely a modified tooth (Figs. 25, 26, 27, 31, 33). [Mandible without a basimandibular process.]

In some dacetonine taxa the basimandibular process is visible in ventral view in ordinarily mounted specimens, but in most the mandibles need to be opened quite widely or the labrum depressed. The process is variably shaped in different dacetonine taxa, taking the form of a lobe, a short or long spur, or a lamella (basal lamella). In all dacetonines except *Acanthognathus* the basimandibular process inserts between the clypeus (above) and the labrum (below) when the mandibles are closed and is part of the jaw locking mechanism. In *Acanthognathus* the process is hypertrophied but passes ventral to the labrum as the latter is vestial in this genus and no longer serves in the jaw locking mechanism.

A few basicerotine species in the genera *Eurhopalothrix* and *Octostruma* have the basal tooth of the mandible flattened or lengthened. This is not homologous with the dacetonine basimandibular process, which is derived from the mandible itself and not from a tooth. Basicerotine species with a modified basal tooth are exceptional and certainly best regarded as independent acquisitions. The usual condition is to have the basal tooth quite normal; presence/absence of a flattened basal tooth cannot be used diagnostically either at genus or species-group rank.

LABRUM
Dorsal surface of labrum with an impression or pair of impressions located medially on the labral shield, distal of the basal hinge but proximal of the labral lobes (Figs. 27, 30). [Labrum without mid-dorsal impression.]

The labral impression receives the basimandibular processes of the mandibles when they are fully closed. The character is not repeated anywhere else in the Myrmicinae. It is secondarily lost in *Acanthognathus* because, as pointed out above, the labrum is secondarily extremely reduced in this genus.

MONOPHYLY OF TRIBE
PHALACROMYRMECINI

Phalacromyrmecini Dlussky & Fedoseeva

Phalacromyrmecini Dlussky & Fedoseeva, 1988: 80 [based on diagnosis in Bolton, 1984: 381]. Type-genus: *Phalacromyrmex* Kempf, 1960: 89. [Phalacromyrmecini relegated as junior synonym of Dacetonini by Baroni Urbani & de Andrade, 1994: 10; revived from synonymy by Bolton, 1995b: 9.]

Apomorphies of tribe Phalacromyrmecini

Each worker apomorphy is briefly described and comments added. The plesiomorphic state of each character is given in square brackets.

MANDIBLE
Dentition of alternating large and small teeth from base to apex; largest tooth usually the basal. [Dentition not of alternating large and small teeth; largest tooth usually the apical.]

A few isolated species or small species-groups in the dacetonine genus *Glamyromyrmex* have the basal tooth the largest on the masticatory margin, but these lack alternating dentition.

MESOPLEURON
Katepisternum with an impression or groove extending obliquely downward from posterior margin of mesopleural hair-filled gland towards metapleuron; impressed area usually bounded by ridges or carinae. [Katepisternal oblique groove absent.]

SCAPE
Scape slender basally, clavate apically; entire scape roughly Indian-club shaped. [Scape subcylindrical.]

POTENTIAL SYNAPOMORPHIES
BETWEEN PAIRS OF COMPONENT
TRIBES

The object of this paper has been to establish the monophyly of the tribes and the tribe-group, rather than to produce a formal phylogeny. However, a number synapomorphies potentially linking pairs of tribes within the group have been noticed and these are mentioned below. The plesiomorphic state expressed by the isolated tribe in each set is given in square brackets.

Potential synapomorphies of Dacetonini + Phalacromyrmecini

POSTPETIOLE-GASTER ARTICULATION
Diameter of presclerites of abdominal segment 4 (=first gastral segment) small and constricted so that the postpetiole-gaster articulation is relatively narrow. [Basicerotini: diameter of these presclerites broad so that the postpetiole-gaster articulation is relatively wide.]

PRESCLERITE OF FOURTH ABDOMINAL SEGMENT
Pretergite of abdominal segment 4 (=first gastral segment) subtended by a short narrow neck-like constriction. [Basicerotini: pretergite subsessile to sessile.]

BASIMANDIBULAR GLAND

Basimandibular gland present. [Basicerotini: basimandibular gland absent.]

This gland is variously developed in many genera of these two tribes (*Ishakidris*, *Microdaceton*, *Strumigenys*, *Glamyromyrmex*); it is universally absent from basicerotines. Its absence from some dacetonines (*Orectognathus*, *Acanthognathus*) may be secondary.

MESOPLEURAL GLAND

Anterolateral angle of mesopleuron bears a hair-filled glandular structure set in an emargination of the rim of the sclerite. [Basicerotini: mesopleural gland absent.]

This supposed gland varies from absent to massively hypertrophied in Dacetonini and Phalacromyrmecini. It is universally absent in Basicerotini.

Potential synapomorphies of Basicerotini + Phalacromyrmecini

BASE OF MANDIBLE

Base of mandible with a long stiff ventrally directed seta on ventral margin. [Dacetonini: such a seta absent.]

This specialised seta is present in all Basicerotini. In Phalacromyrmecini it is obvious in *Ishakidris*. Not recorded in the single specimen of *Phalacromyrmex* currently available, but this is in poor condition and badly mounted.

PROPODEAL SPIRACLE

Propodeal spiracle low on side of sclerite, abutting the margin of the small metapleural gland bulla. [Dacetonini: propodeal spiracle high on side, widely separated from metapleural gland.]

In the dacetonine genus *Acanthognathus* the spiracle abuts the metapleural gland bulla but here the spiracle is high on the side and the bulla is secondarily extended upwards.

Potential synapomorphies of Dacetonini + Basicerotini

None detected.

APPENDIX: Species dissected

The parts of all dissected specimens, whether partially or completely disarticulated, have been remounted on green-flagged card points and are deposited in The Natural History Museum, London. [List does not include the many taxa mounted with mandibles open and mouthparts displayed, but not otherwise dissected; these have been mounted on blue-flagged card points in the Natural History Museum, London, collection.]

Basicerotini

Basiceros: discigera, manni, militaris, singularis.

Eurhopalothrix: australis, biroi, bolaui, dubia, floridana, gravis, heliscata, insidiatrix, jennya, omnivaga, procera, punctata, speciosa, spectabilis, szentivanyi.

Octostruma: balzani, betschi, iheringi, inca, rugifera, stenognatha.

Protalaridris: armata.

Rhopalothrix: ciliata, isthmica, plus 1 unidentified species.

Dacetonini

Acanthognathus: brevicornis, ocellatus, rudis.

Codiomyrmex: thaxteri.

Colobostruma: alinodis, cerornata, plus 1 unidentified species.

Daceton: armigerum.

Epitritus: argiolus, hexamerus, laticeps, roomi.

Epopostruma: frosti.

Glamyromyrmex: beebei, excisa, flagellatus, semicomptus, sistrurus, tukultus, plus 2 unidentified species.

Gymnomyrmex: villiersi.

Kyidris: mutica, plus 1 unidentified species.

Mesostruma: browni, turneri.

Microdaceton: exornatum, tibialis, plus 1 unidentified species.

Neostruma: brevicornis, crassicornis, myllorhapha, zeteki.

Orectognathus: antennatus, clarki, mjobergi, szentivanyi, versicolor.

Pentastruma: sauteri.

Quadristruma: emmae.

Serrastruma: lujae, ludovici, serrula.

Smithistruma: alberti, angulata, dohertyi, fridericimuelleri, microthrix, ornata, transversa, truncatidens, plus 6 unidentified species.

Strumigenys: biolleyi, chyzeri, denticulata, doriae, elongata, gundlachi, godmani, koningsbergeri, louisianae, micretes, nidifex, pallestes, perplexa, precava, prospiciens, rogeri, rukha, saliens, signeae, subedentata, tigris, trieces, trudifera, plus 12 unidentified species.

Trichoscapa: membranifera.

Phalacromyrmecini

Phalacromyrmex: fugax.
*Ishakidris: ascitaspis.*

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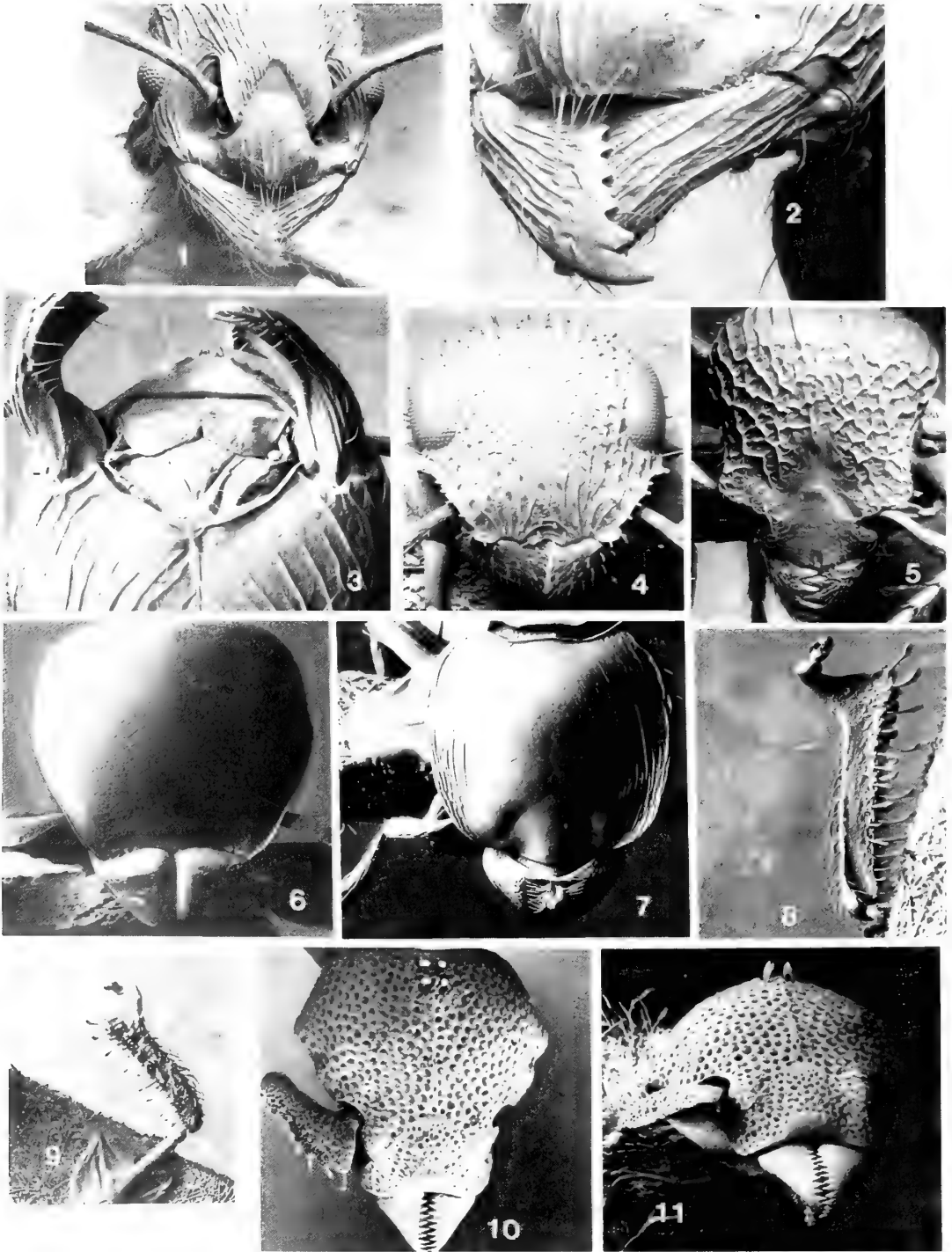
Figs. 1–11. Worker ants: **1–3**, Head of *Myrmica rubra*; 1, tilted slightly back from full-face view; 2, oblique close-up of fully closed mandibles; 3, ventral view to show buccal cavity; **4**, head of *Cataulacus lujae*, tilted back from full-face view; **5–7**, heads in full-face view of 5, *Pilotrochus besmerus*; 6, *Tatuidris tatusia*; 7, *Ishakidris ascitaspis*; **8–9**, scape of *Basiceros singularis*, condyle uppermost; 8, ventral view; 9, dorsal view; **10–11**, head of *Eurhopalothrix platisquama*; 10, full-face view; 11, oblique frontal view.
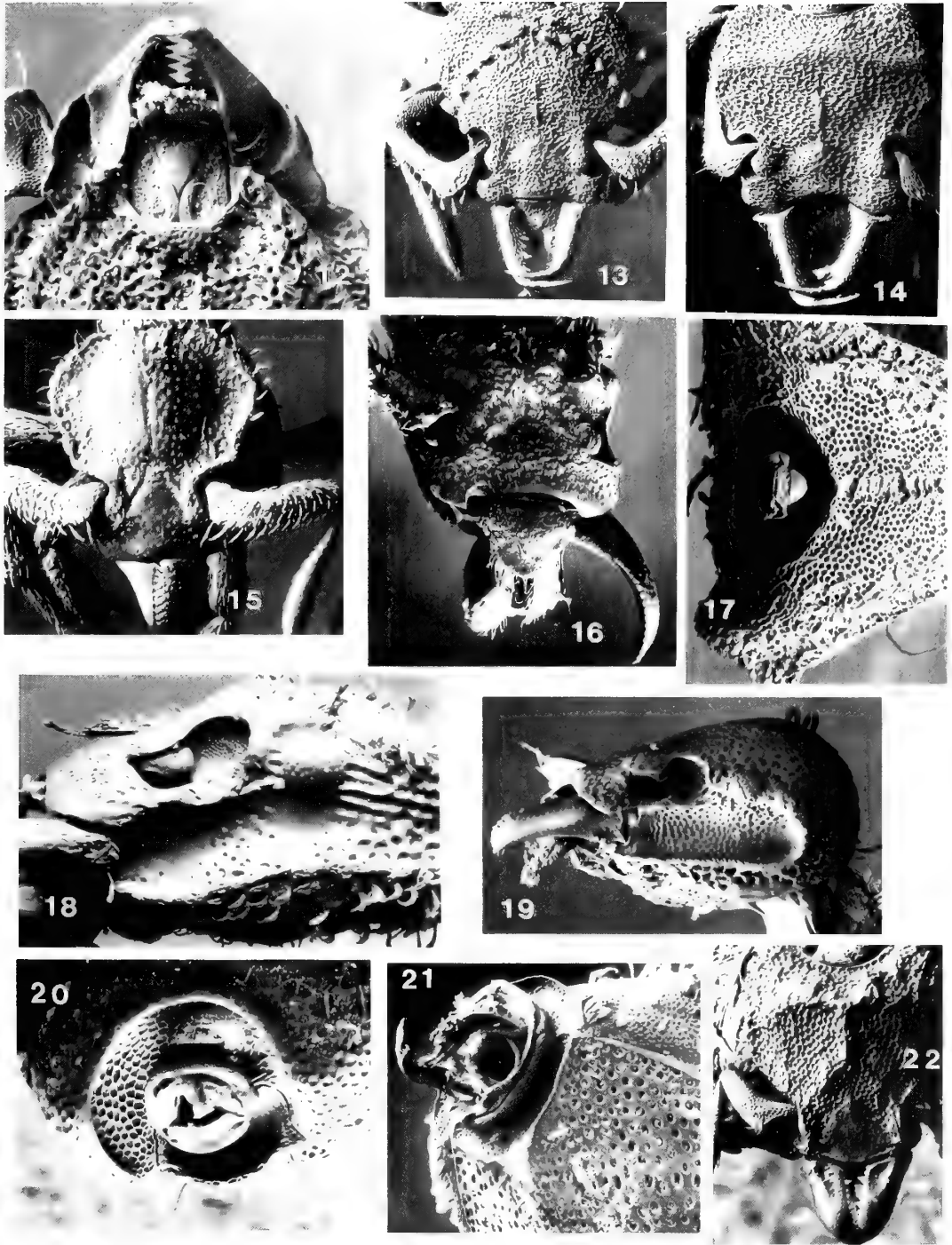
Figs. 12–22. Worker ants: **12**, ventral head to show buccal cavity of *Eurhopalothrix platisquama*; **13–15**, heads in full-face view of 13, *Rhopalothrix ciliata*; 14, *Protalaridris armata*; 15, *Basiceros discigera*; **16**, oblique frontal view of head of *Basiceros singularis*, mouthparts extended and right mandible removed; **17**, occipital foramen of *Eurhopalothrix heliscata*; **18–19**, lateral view of head with antenna removed, of 18, *Basiceros singularis*; 19, *Eurhopalothrix platisquama*; **20**, frontal view of helcium of *Eurhopalothrix procera*; **21**, base of gaster in oblique ventral view of *Basiceros singularis*; **22**, head in full-face view of *Dysedrognathus* sp. n.
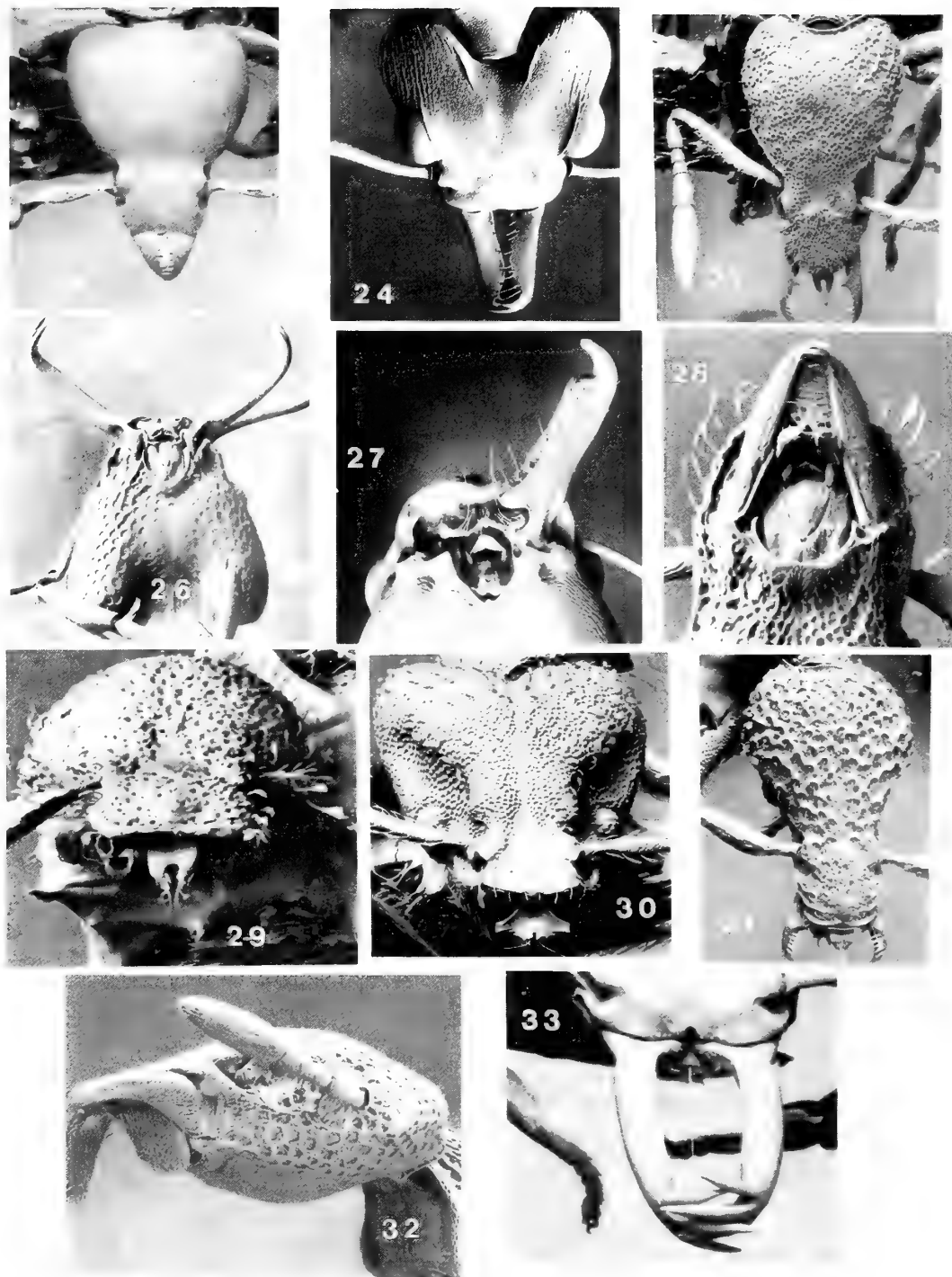
Figs. 23–33.   Worker ants. **23–25**, head in full-face view of 23, *Smithistruma* sp. n.; 24, *Daceton armigerum*; 25, *Smithistruma reliquia*, mandibles open; **26–28**, ventral view of head to show buccal cavity of 26, *Microdaceton* sp. n., mandibles open; 27, *Daceton armigerum*, right mandible and labio-maxillary complex removed; 28, *Smithistruma truncatidens*; **29–30**, oblique frontal view of head to show labrum, mandibles removed, of 29, *Smithistruma truncatidens*; 30, *Strumigenys* sp. n.; **31**, head in full-face view of *Smithistruma kerasma*, mandibles open; **32**, head in ventrolateral view of *Colobostruma* sp.; **33**, mandibles in oblique frontal view of *Microdaceton tibialis*.

An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini)

PAUL H. WILLIAMS

Department of Entomology, The Natural History Museum, Cromwell Road, South Kensington, London SW7 5BD

CONTENTS

SYNOPSIS. Bumble bees are among the minority of groups of organisms for which there is some evidence that most species have already been described. Nonetheless, a synoptic revision of the group has been delayed, in part by the difficulties imposed by an unusually high ratio of names to species (averaging more than 11). To explore some of the factors contributing to this phenomenon, historical and geographical trends in the naming of bumble bees are summarised. This shows that most taxa were named by European authors, beginning with the most widespread European species, moving later to not only the more narrowly distributed species and to species from other parts of the world, but also to taxa at progressively lower nomenclatural ranks, particularly within the more widespread European species. Nearly half of all of these names have been published since the last world-wide checklist in 1922. In attempting to bring this up to date, the present checklist adopts broad interpretations of species and recognises a total of 239 recent species (including the social parasites but excluding fossil taxa), with 24 new synonyms and 29 provisional synonyms. The list also includes notes on alternative interpretations of taxonomic status and on nomenclatural problems, drawing attention to those cases where further research is most urgently needed. In particular, suggestions are presented for an application to the International Commision on Zoological Nomenclature to use its Plenary Power in order to conserve current usage of the commonly used names *atratus, balteatus, distinguendus, flavifrons, humilis, hyperboreus, mesomelas, mixtus, norvegicus, polaris, pyrenaeus, soroeensis* and *variabilis*.

INTRODUCTION

Bumble bees have long been popular with collectors. Just as with butterflies, part of the attraction may be explained by their bright colours, large body size, activity during daylight hours, and abundance in the north-temperate regions where most collectors have lived. As a result, large samples of bumble bee specimens have now been assembled, even from remote parts of the world.

A problem for biologists trying to identify bumble bee species, all the more apparent because of the large amount of material available, is that while bumble bees can be described as morphologically relatively 'monotonous' (Michener, 1990), they are often extraordinarily variable in the colour patterns of their pubescence. The situation is made worse by a strong tendency for species to converge locally on different colour patterns (Plowright & Owen, 1980).

Faced with this variation, generations of taxonomists since the starting point of Linnaean nomenclature in 1758 have described differing individuals under a plethora of more than 2800 formal names (Williams, unpublished catalogue, including names for species, subspecies and synonyms, as well as infrasubspecific names, misspellings and other unavailable names). Most of these names are for taxa below the rank of species, and just 239 taxa are interpreted here as separate species. Arguably, the nomenclatural burden of more than 11 names per species (median 5, maximum 186) has slowed progress towards a complete revision of the group. Hence there is a need for an overview which, although bound to require revision, will provide an improved framework for more detailed regional studies. It is also important to understand any regional or taxon-directed bias in patterns of taxonomic description when seeking to interpret patterns in diversity, ecology and biogeography. The present checklist begins to address these needs.

Past lists of species

There have been few attempts to present complete revisions, catalogues or checklists of all bumble bee species from which to see summaries of past views. Latreille (1809) included 13 species in his genus *Bombus*. Most of the early lists included just those species seen by their authors, usually from particular collections, and often from just one region. For example, Smith (1854) catalogued 87 bumble bee species (79 *Bombus* + 8 *Apathus* [= *Psithyrus*]) in the collection of the British Museum. The only truly synoptic catalogue of bumble bees was published by Dalla Torre (1896), with 255 (non-fossil) species (228 *Bombus* + 27 *Psithyrus*). It included many varietal names, synonyms and early references. The reason

why Dalla Torre's species count exceeds the total now recognised as described before 1899 (159 species, Fig. 1) is of course that many of his species are now treated as synonyms or subspecies. Later, Skorikov (1922a) listed 237 species (plus 70 '*Bombi incertae sedis*'), but with few synonyms and without including *Psithyrus*. Nonetheless, Skorikov's list did arrange most of the known species within his genera and subgenera, which form the basis of the current subgeneric system (Richards, 1968).

Taken together, the few past lists of bumble bees show that the number of taxa accepted as species at a particular date grew rapidly during the nineteenth century, but has since remained relatively stable, with a slight decline to the conservative estimate of 239 species in the present list. Undoubtedly part of the explanation for this decline lies in the relatively conservative species concept accepted at present (see below). This reflects a gradual shift in emphasis among criteria for recognising species from the use of colour characters to the use of morphological characters, particularly to using characters of the male genitalia (see the introductory comments by Radoszkowski, 1884). A similar pattern of growth and decline has been found for past numbers of milkweed butterfly species (Ackery & Vane-Wright, 1984). However, there might now be another period of rapid growth if molecular characters and phylogenetic species concepts (discussed below) were to be applied (cf. discussion of the number of bird species by Martin, 1996; Patterson, 1996; Zink, 1996, 1997; Snow, 1997).

History of discovery of species

The dates of first formal description for the currently recognised bumble bee species show that the highest rates of species discovery were in the latter half of the nineteenth century through to the First World War (Fig. 1, median date 1877). These species are recognised retrospectively from the present list, rather than as the numbers accepted within each time period. The larger dips in overall rate of discovery may be associated with factors such as war and its aftermath (e.g. Napoleonic and Second World Wars), presumably through constraints on resources and on freedom of travel.

Some authors described many more bumble bee species than others: 45% of presently accepted species were described by just 10% of the authors who described these species (Smith 32 species, Skorikov 19, Cresson 17, Morawitz 15, Radoszkowski 13, and Friese 12). Similarly, Gaston, Scoble & Crook (1995) found a skewed pattern of activity among authors describing geometrid moths. But of the six authors who described the most bumble bee species, only Ezra Cresson (Snr) actually worked in the New World, whereas the other five were based in Europe (including European Russia).
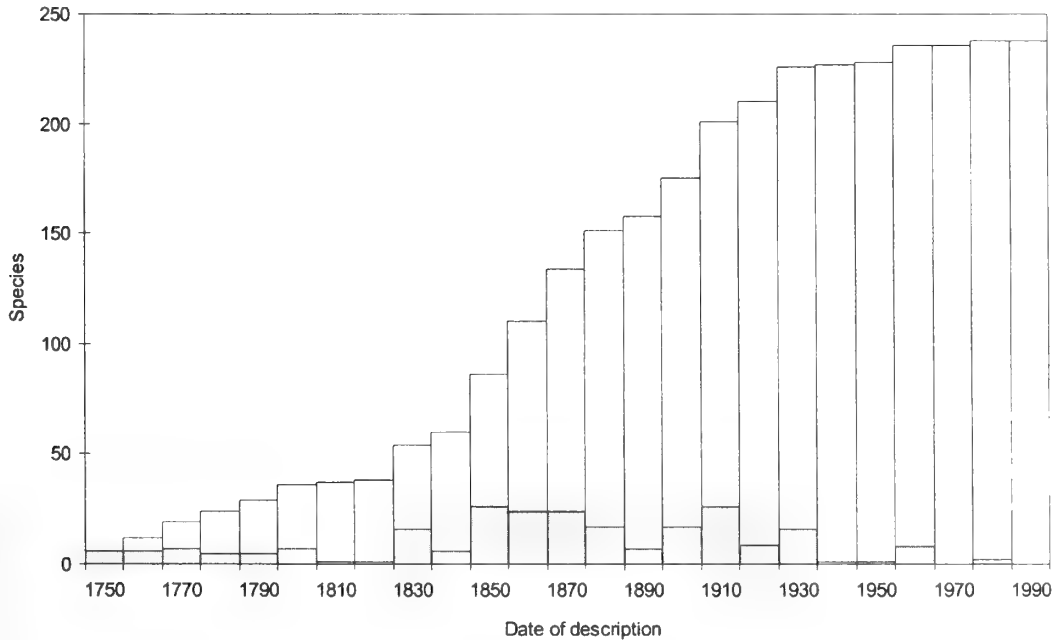
Fig. 1   Rate (lower grey) and cumulative number (upper white) of first formal descriptions of presently recognised bumble bee species (dates from the oldest available names in the sense of ICZN, 1985).

Rates of discovery of bumble bee species vary to some extent among biogeographic regions (Fig. 2). Again, this was also found for geometrid moths by Gaston, Scoble & Crook (1995). For bumble bees, the recent proportional discovery rates have been lowest in the New World and highest in the Oriental Region. The Neotropical Region appears to have a small known bumble bee fauna for its large area. There is no obvious evidence that descriptive effort has been lacking, although detailed revisionary work is needed and species with small range sizes may remain to be discovered. In contrast, the Oriental Region's high recent proportional rate of species discovery, despite its smaller area than the other regions, is possibly explained in part because it has been studied intensively for a shorter period.

The world-wide rate of discovery of genuinely unknown bumble bee species appears now to be slowing down (Fig. 1). Undiscovered species are very likely to remain, although there is no evidence that large numbers of species are awaiting description in collections (although some known subspecific taxa might yet be recognised as species if changes were to occur in species concepts or in the availability of character evidence, see Martin, 1996; Patterson, 1996; Zink, 1996). The sigmoidal pattern of species discovery in Fig. 1 is also shown by a few other relatively well known groups such as birds, although for most large groups (including Hymenoptera as a whole) the rates of description continue to be high or are even increasing (Hammond in Groombridge, 1992; Tennessen, 1997).

History of publication of names

The present checklist is intended only to address the question of taxa at the rank of species (see below). For this purpose it is not necessary to consider concepts of taxa at the rank of subspecies and below and subspecific names may be treated in analyses as further synonyms of species (Gaston & Mound, 1993). This is not to say that subspecific taxa ought not to be recognised if they were considered useful in the context of other studies. In addition, some authors have applied classical names to taxa at even lower nomenclatural ranks, for example in referring to 'varieties' or 'forms' within subspecies. These are now interpreted as infrasubspecific names and are 'unavailable' for use in the sense of the *International Code of Zoological Nomenclature* (ICZN, 1985). They have had to be included in a manuscript catalogue (unpublished) in order to avoid confusion by explicitly resolving questions of nomenclatural status and availability. Infrasubspecific names are included in this analysis as a category separate from specific or subspecific names because of their particular significance for understanding historical patterns in the description of diversity at the lowest nomenclatural ranks.

Bumble bees have the highest known levels of synonymy (83%, or 92% if infrasubspecific names were to be included) in comparison with the range of insect taxa reviewed by Gaston & Mound (1993). Their results showed synonymy levels ranging from 7% for Siphonaptera to 80% for Papilionidae and
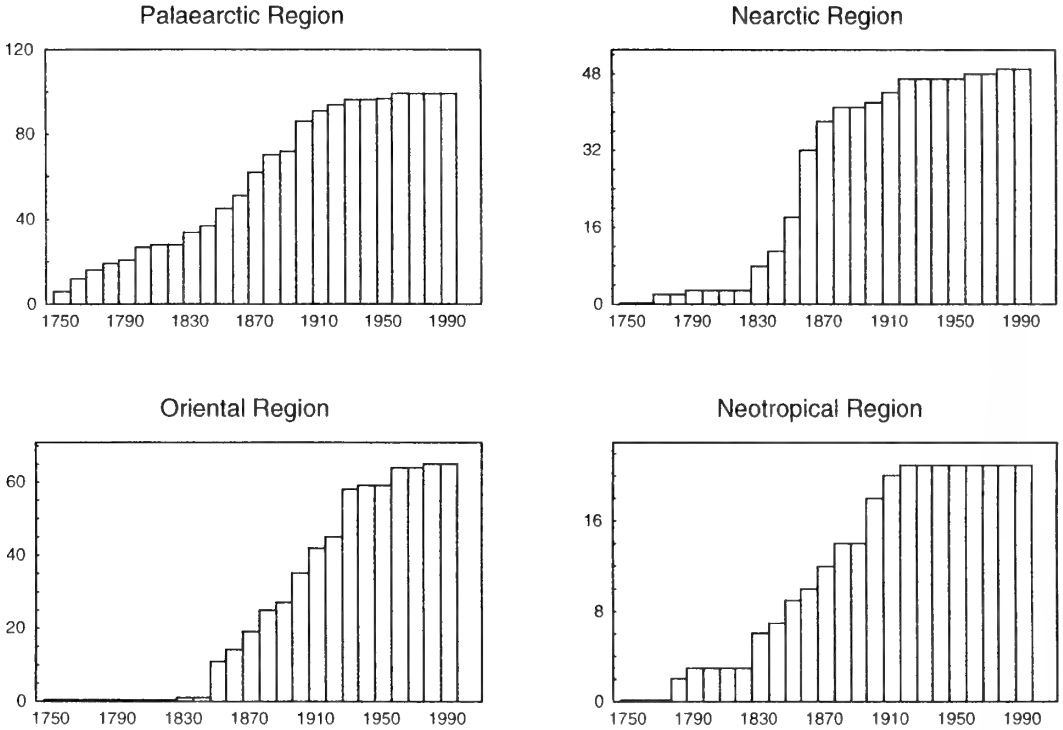
Fig. 2 Cumulative number of first formal descriptions of presently recognised bumble bee species with centres of area of occupancy (so species lists do not overlap) in each of the four principal biogeographic regions occupied by bumble bees (dates from the oldest available names in the sense of ICZN, 1985; regions defined in Williams, 1996*b*: fig. 1; Oriental includes northern and southern Oriental Regions; Nearctic includes northern, central and southern Nearctic Regions; Neotropical includes northern, central and southern Neotropical Regions; the Arctic Region is excluded; species that are exclusively peri-Tibetan Oriental but which nevertheless have range centres in Palaearctic central Tibet by simple range averaging are included as Oriental species).

Pieridae combined. It must be born in mind that the insect taxa that they surveyed are all more speciose than the bumble bees by a factor of at least four, and extreme values for larger groups are less likely. None-theless, Gaston & Mound (1993) also noted that the two families of most brightly coloured butterflies have the highest levels of synonymy and that these families have many more subspecific names than the smaller and duller-coloured hesperiid butterflies. R. I. Vane-Wright (pers. com.) suggests that synonymy rates may be particularly high among the large, colourful butter-flies of the Danainae and *Parnassius*.

In contrast to the discovery of currently recognised species, the greatest activity in publishing names for all supposed bumble bee taxa at the rank of species and below was concentrated slightly later than for pres-ently recognised species, in the first half of the twentieth century (Fig. 3, median date 1922). This difference may be explained in part by the logical inevitability that synonyms and names for taxa below the rank of species can only be published subsequently to valid

species names (i.e. the oldest available names, exclud-ing junior homonyms, in the sense of ICZN, 1985). If these names were in effect to represent the redescription of known species at random, then the earlier described species might be expected to have accumulated more names. Studies of other taxa have also shown that both the date of first description and the number of syno-nyms per species may be affected by variation in the size of a species' geographic range (as well as by other factors such as body size). Large range size is likely to affect the date of first description because it contrib-utes to a greater 'apparency' of the species to collectors (Gaston, Blackburn & Loder, 1995), particularly as broad correlations between range size and abundance suggest that widespread species also tend to have higher local densities (Brown, 1984; Gaston, 1994; for bumble bees, see Hanski, 1982; Williams, 1988). Apart from enhancing the chances of random redescription, large range size is also likely to affect the number of synonyms because there is a greater likelihood that specimens collected in one area will be regarded as
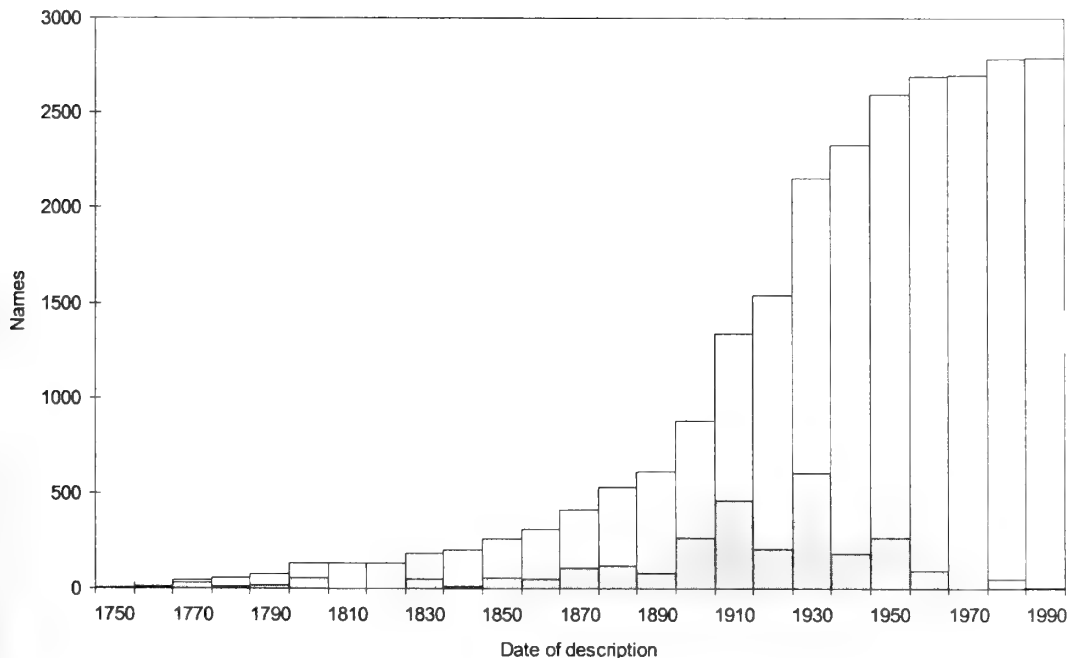
Fig. 3 Rate (lower grey) and cumulative number (upper white) of all descriptions with classical names for bumble bee species, subspecies and infrasubspecies since the starting point of zoological nomenclature in 1758 (from a manuscript catalogue, unpublished).

distinct from specimens collected from another distant area, because character variation is apt on average to be greater (Gaston, Blackburn & Loder, 1995).

For the bumble bee catalogue data, the number of synonyms (including subspecies, but excluding infrasubspecies) is correlated with both the date of first description and the range size of a species independently of one another, although slightly more of the variation is explained by variation in range size (partial r, Table 1). Many of the species with large range sizes, early dates of first formal description and many synonyms are found in western Europe (i.e. triangles at the left and upper part of Fig. 4). Most of these species occur in either the lowland areas of Europe where early naturalists were most active, such as Britain, or else are nearly circumpolar in their distribution.

Curiously, all of the infrasubspecific names (34% of all names as interpreted at present) belong to the bumble bee species of the Old World (Fig. 5). Species of the Old World also have more synonyms and subspecies per species than do the species of the New World (numbers of names log-transformed and excluding 6 Holarctic species, $t_{232} = 3.81$ with separate variance estimates, $p < 0.001$).

One possible explanation for the greater numbers of names per species for bumble bees of the Old World is that they might have broader distributions than the species of the New World (see above). This could arise because the Old World has a slightly larger total area of suitable habitat (bumble bees occupy 131 of the 611,000 km² grid cells in the Old World and 117 in the New), which is apparently subdivided into fewer well differentiated biogeographic assemblages of bumble bee species (e.g. Williams, 1996b: fig. 1). However, this explanation is not strongly supported by the bumble bee data, which show the difference in range sizes between the two hemispheres to be not significant, (range sizes log-transformed and excluding 6 Holarctic species, $t_{232} = -1.24$ with separate variance estimates, $p = 0.22$). Consequently, while an effect of differences in habitat area will deserve future consideration, other effects are likely to be more important.

A second possibility is that whereas bumble bee taxa of uncertain rank may have tended to be regarded more often as subspecies in the Old World, in the New World they may have tended to be regarded as species (see the discussion below of criteria to recognise species). While this factor could have contributed to the observed patterns, it is unlikely to explain why (at a lower rank) so many infrasubspecific names were described exclusively for taxa from the Old World.

A third possibility is that the diversity of languages used for taxonomic publications in the Old World may

Table 1   Results of multiple regression of numbers of synonyms/subspecific names (infrasubspecific names are excluded; from a manuscript catalogue, unpublished) on date of first formal description for presently accepted species and range size (number of occupied 611,000 km² grid cells world-wide). Partial r values indicate the correlations with the synonyms variable after adjusting for the other predictor variable in each case.

$\log_{10}(\text{synonyms}+1) = 6.316(\pm0.969) - 0.003(\pm0.0005).\text{date} + 0.401(\pm0.057).\log_{10}(\text{range})$			
	multiple $r = 0.72$	$F_{(2,236)} = 129.76$	$p < 0.0001$
	partial r	t_{236}	p
date	−0.390	−6.51	< 0.0001
$\log_{10}(\text{range})$	0.418	7.08	< 0.0001
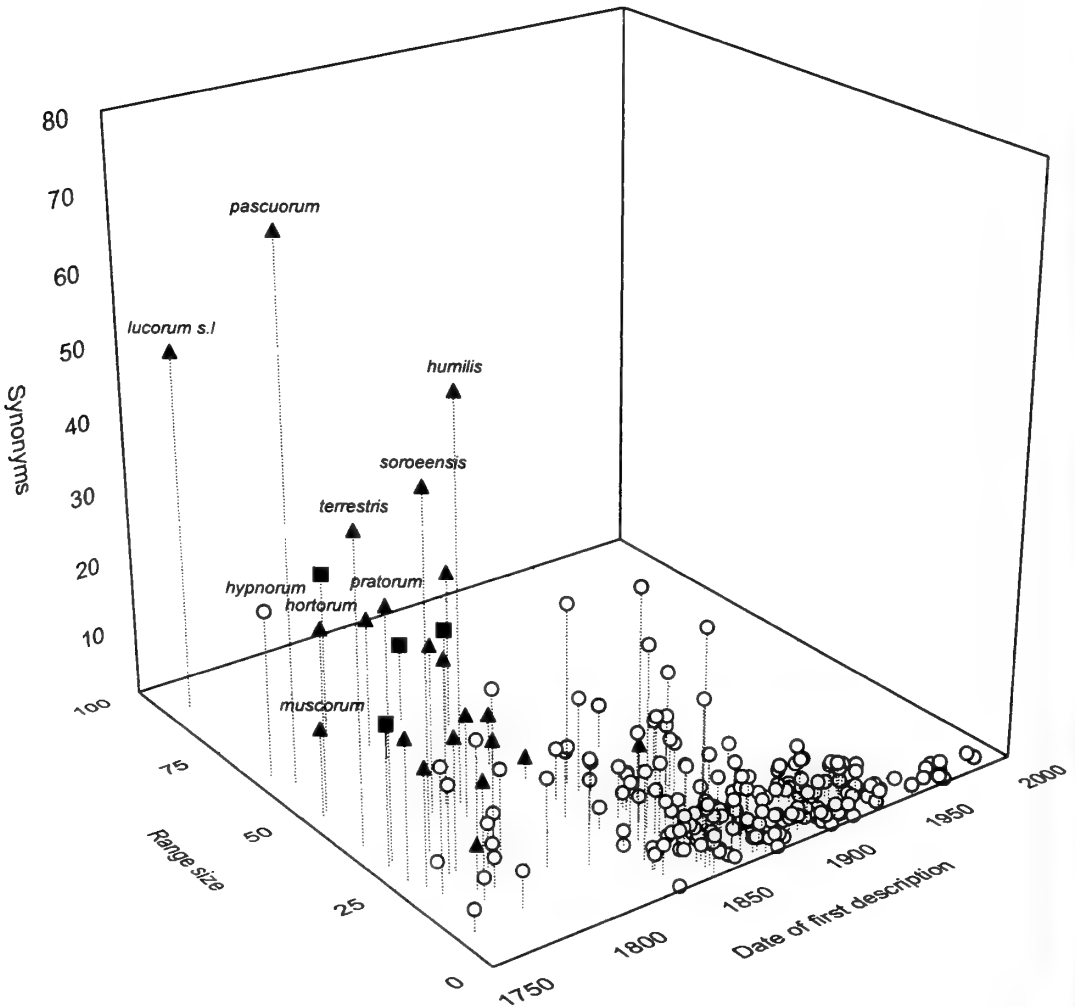
Fig. 4   Scatterplot of 239 presently accepted bumble bee species by range size (number of occupied 611,000 km² grid cells world-wide), date of first formal description and numbers of synonyms/subspecific names (infrasubspecific names are excluded; from a manuscript catalogue, unpublished). The British fauna is distinguished as filled triangles, the nearly circumpolar fauna (*B. hyperboreus, B. balteatus, B. polaris* and *B. lapponicus*) as squares, and some British and widespread European species are labelled individually.
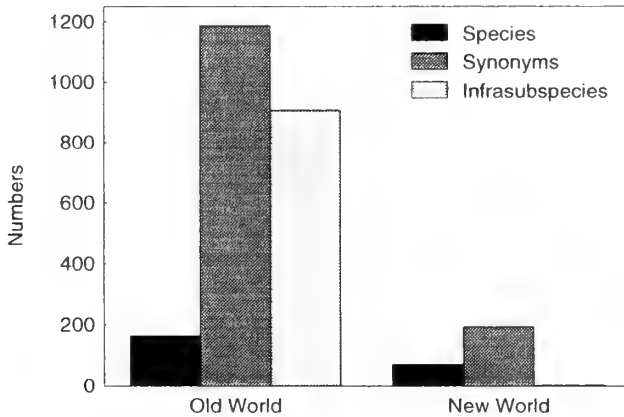
Fig. 5 Number of presently recognised bumble bee species, synonyms/subspecific names and infrasubspecific names for the Old World and the New World (from a manuscript catalogue, unpublished).

have impeded communication and lead to more frequent re-description of taxa than in the New World, where English was much more dominant (C. O'Toole, pers. com.). Again, while this factor is likely to have contributed to the observed patterns of synonyms, it does not explain why (at a lower rank) so many infrasubspecific names were described exclusively for taxa from the Old World.

Another possible interpretation, which might explain more of the differences in description dates between Figs. 1–3 as well as the differences in the distribution of bumble bee subspecies, synonyms and infrasubspecific names between hemispheres (Fig. 5), is that during the twentieth century, effort for describing the variety of these insects may have become, in effect, re-directed towards finer distinctions and lower nomenclatural ranks within known species. This is perhaps likely as undescribed species became inevitably more difficult to find close to home for the most active taxonomists, who were based in Europe. Three lines of evidence are consistent with this explanation. First, slightly more of the variation in richness of infrasubspecific names among species is accounted for by variation in the date of first description of the species (partial r, Table 2), rather than by variation in total range size. This is in contrast to the pattern for synonyms alone (cf. Table 1), although species that are sufficiently widespread in lowland Europe to include Britain within their distributions still tend to have high numbers of both synonyms and infrasubspecific names (Fig. 6, e.g. *B. pascuorum, B. lucorum*). A second intriguing observation is that compared to the number of authors who have published presently accepted species names, only one third the number of authors (20) have published infrasubspecific names, even though there are nearly four times as many infrasubspecific names. Indeed, just three of these authors (Bruno Pittioni, Edgar Krüger and Alexander

Skorikov) are responsible for 70% of the infrasubspecific names (all of the species with many infrasubspecific names had been described before these three authors became active in publishing infrasubspecific names between 1910 and 1960, see Fig. 7). Many similar examples are known from work on butterflies (R. I. Vane-Wright, pers. com.), with authors choosing a particular favoured species and describing large numbers of infrasubspecific names (e.g. Bright & Leeds, 1938). The third point is that the three most prolific authors all worked in Europe, and there is a correlation among all 239 bumble bee species between the number of infrasubpecific names and the breadth of the species' distributions just within Europe (measured as the number of occupied 611,000 km² grid cells between Britain and the Urals, but excluding Atlantic islands, North Africa, Turkey and the Caucasus; Spearman $r = 0.67, t_{237} = 13.99, p < 0.001$). Thus, a high proportion of the many infrasubspecific names were published by very few European authors, for previously described species that are also particularly widespread in Europe.

High numbers of synonyms and infrasubspecific names for *B. terrestris* and *B. lucorum* (subgenus *Bombus*) and for *B. humilis* and *B. pascuorum* (subgenus *Thoracobombus*) in Fig. 6 raise the possibility that large numbers of names are associated with particular groups of species, perhaps with particular subgenera. Number of names per species is plotted against range size per species for subgenera in Fig. 8. These properties are correlated (log-transformed data, correlation $r = 0.58, F_{1,36} = 18.16, p < 0.001$), but it is the subgenera with high scores that are more informative. The subgenus *Kallobombus* includes many names, but only a single, very variable species *B. soroeensis*, which is broadly distributed in Europe (see below and Reinig, 1939: fig. 10). The subgenera *Alpinobombus* and *Laesobombus* also have broadly distributed

Table 2 Results of multiple regression of numbers of infrasubspecific names (from a manuscript catalogue, unpublished) on date of first formal description for presently accepted species and range size (number of occupied 611,000 km² grid cells world-wide). Species without infrasubspecific names were excluded from the analysis. Partial r values indicate the correlations with the infrasubspecific names variable after adjusting for the other predictor variable in each case.

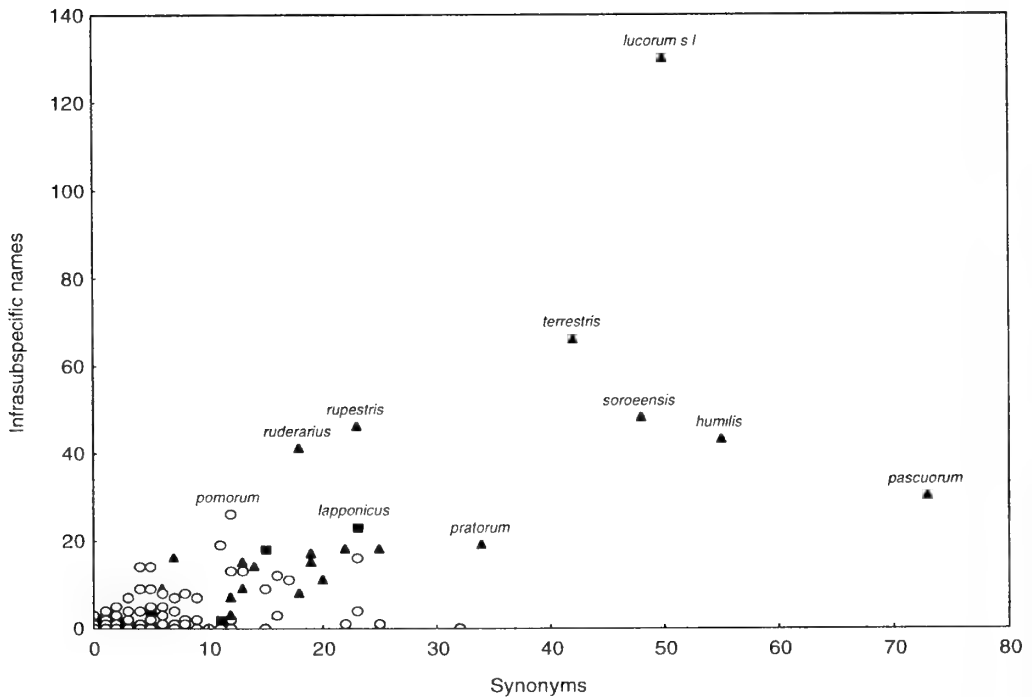| $\log_e(\text{infrasubspecifics}+1) = 14.169(\pm3.638) - 0.007(\pm0.002).\text{date} + 0.742(\pm0.212).\log_{10}(\text{range})$			
	multiple $r = 0.66$	$F_{(2,94)} = 36.57$	$p < 0.0001$
	partial r	t_{94}	p
date	-0.364	-3.79	< 0.001
$\log_{10}(\text{range})$	0.340	3.50	< 0.001

Fig. 6 Scatterplot of 239 presently accepted bumble bee species by numbers of infrasubspecific names and numbers of synonyms/subspecific names (from a manuscript catalogue, unpublished). The British fauna is distinguished as filled triangles, the nearly circumpolar fauna (*B. hyperboreus*, *B. balteatus*, *B. polaris* and *B. lapponicus*) as squares, and some widespread European species are labelled individually.

species but relatively few names, perhaps because they are absent or not abundant in those parts of Europe where the authors publishing most bumble bee names have worked, despite several of the species being very variable in colour pattern (e.g. *B. balteatus*). In contrast, the high ratio of names per species for the subgenus *Bombus* shows the keen interest by some European authors such as Krüger (1951, 1954, 1956, 1958) in describing the finer points of variation, not so

much within the North American species, but particularly within the widespread European species, *B. terrestris* and *B. lucorum*.

Summary of historical and regional trends in describing bumble bees

Based on the evidence of asymptotic tendencies in species-discovery curves, a higher proportion of all
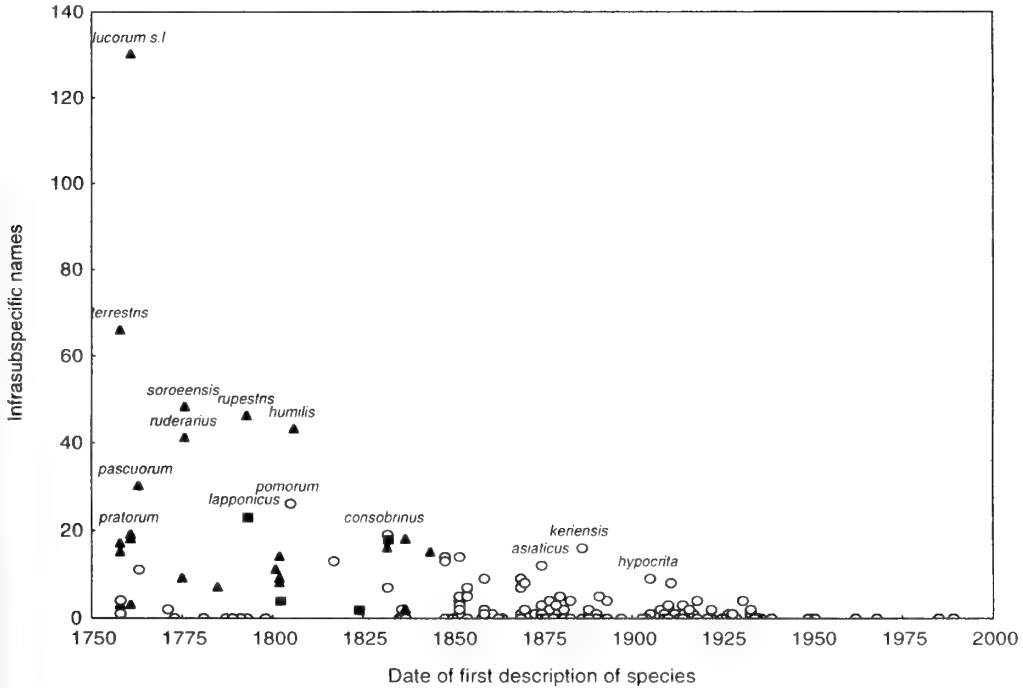
Fig. 7   Scatterplot of 239 presently accepted bumble bee species by numbers of infrasubspecific names (from a manuscript catalogue, unpublished) and date of first formal description of species. The British fauna is distinguished as filled triangles, the nearly circumpolar fauna (*B. hyperboreus*, *B. balteatus*, *B. polaris* and *B. lapponicus*) as squares, and some species with more infrasubspecific names are labelled individually.

species appear to be known for bumble bees than for many other groups of organisms. Most of these bumble bee species have been described by authors working in Europe (including European Russia). The species with the largest geographic range sizes, and particularly the European species with the largest ranges, have tended to be described first. The same species have also attracted the highest numbers of synonyms and subspecific names. As a group, bumble bees have an unusually high ratio of synonyms and subspecific names per species, which is otherwise known for some of the groups of larger and more colourful butterflies.

A few European authors were disproportionately prolific between 1910 and 1960 in describing finer variation at infrasubspecific rank, which now accounts for one third of all bumble bee names. Again, this more detailed effort has been largely concentrated on the earlier-described species that are more widespread within Europe (in contrast, New World bumble bees have been ignored at this level), presumably because large samples were more readily accessible to the most active authors. Determining whether this re-direction of activity towards lower nomenclatural ranks was a logical progression in the recognition of useful taxa, a fashion in taxonomic concepts, or in some cases merely a less disruptive channelling of the enthusiasm of

some authors to publish more names (the '*mihi* itch'), is beyond the scope of this preliminary review.

All of these patterns in the descriptions of bumble bees must, as yet, be interpreted with caution. Much work still remains to be done on the rates of description of taxa at different nomenclatural ranks (species, subspecies, infrasubspecies), on rates of recognition of synonymy and of changes in rank, and particularly on how this activity is partitioned among different time periods, different geographic regions, different taxonomic subgroups and different authors.

Fundamental to almost all analyses are taxonomic revisions and checklists of bumble bee species. A revised checklist is now overdue, because nearly half (49%) of all names for bumble bees have been published since the last synoptic checklist (Skorikov, 1922*a*).

Development of a revised checklist

To begin to bring a checklist up to date, a draft was made in 1980 and first circulated for comment in 1985 (Williams, 1985*a*). This project was developed during a more detailed study of the west Himalayan fauna (Williams, 1991) and as part of continuing work on the large fauna of China in collaboration with Wang S.-f.
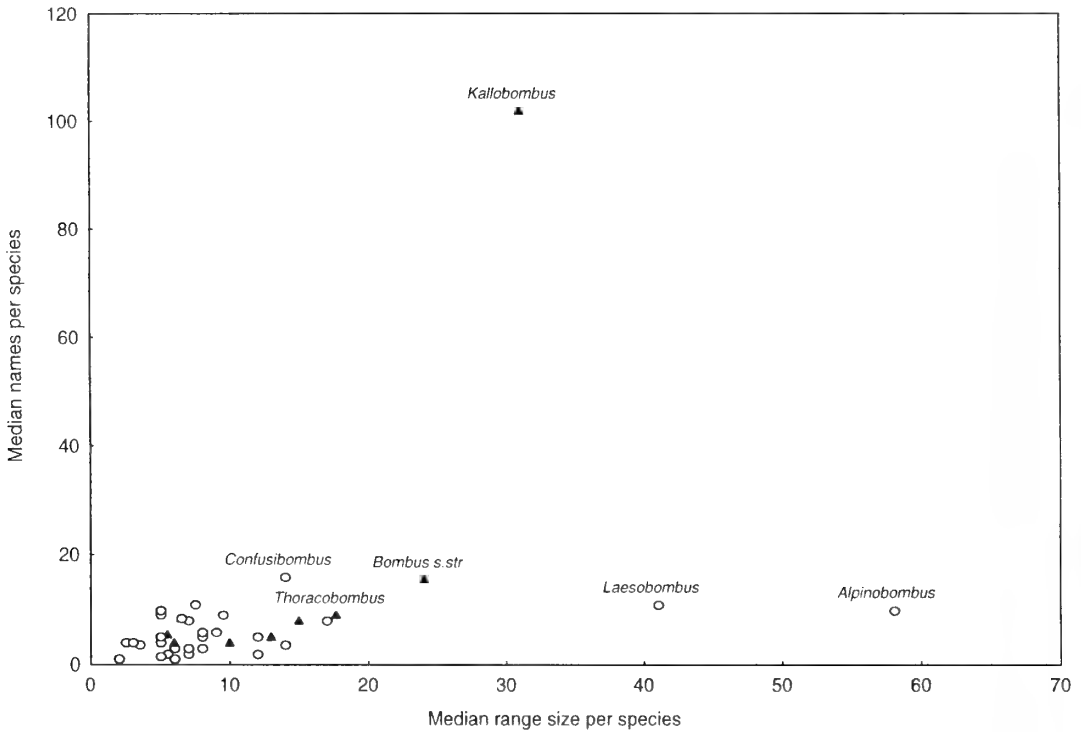
Fig. 8   Scatterplot of 38 bumble bee subgenera by median numbers of all names per species (including synonyms, subspecific and infrasubspecific names; from a manuscript catalogue, unpublished) and median range size per species (number of occupied 611,000 km² grid cells world-wide). The subgenera represented in the British fauna are distinguished as filled triangles and some subgenera are labelled individually.

and Yao J. (unpub.). Some of the broader revisions that have had the greatest influence on this include works by Vogt (1909, 1911), Franklin (1913), Stephen (1957), Milliron (1970b, 1971, 1973a, b), Løken (1973, 1984), Pekkarinen (1979), Reinig (1981), Wang (1982, 1987, 1988), Rasmont (1983, 1988), Thorp et al. (1983), Labougle (1990), and especially the publications by Skorikov (1910–1938) and Tkalců (1959–1989). Inevitably, the present checklist cannot be expected to solve all biological and nomenclatural problems, but it is hoped that by identifying some of the major problems it will stimulate further research.

Acknowledgements

TAXONOMY

Bumble bees are a monophyletic group (Williams, 1985b, 1995), constituting the tribe Bombini. They may be distinguished from other bees (family Apidae) by the following diagnosis (from Williams, 1991, which includes descriptions of the characters and discussion of homologies):

Bombini have the labrum at least twice as broad as long. The

labrum lacks a longitudinal median ridge, although for the females it has a strong transverse basal depression. The clypeus has a transverse subapical depression and the apico-lateral corners are curved back towards the occiput. A malar area (= malar space) separates the compound eye from the base of the mandible, often by a distance greater than the breadth of the mandible at its base. The hind wings lack a jugal lobe (= anal lobe). The volsella (= lacinia) of the male genitalia is greatly enlarged and is produced apically beyond the gonostylus (= squama).

Bumble bees are large (body length 7–27 mm) robust insects. Their bodies have a dense covering of variously coloured long plumose hairs, although these are few or absent on some parts of the ventral surface of the gaster, on parts of the propodeum, on parts of of the anterior face of gastral tergum I, and on parts of the head. The sclerites are usually black, or lighter brown on the distal parts of the limbs, but are never marked with bright yellow, red or metallic (= interference) colours. The wings may be transparent (= hyaline) to strongly darkened (= infuscated), but rarely show strongly metallic reflections.

Female bumble bees have 12 antennal 'segments' (= scape, pedicel and 10 flagellomeres) and six visible gastral terga and sterna (abbreviated to TI–VI, SI–VI). Males have 13 antennal 'segments' (= scape, pedicel and 11 flagellomeres) and seven visible gastral terga and sterna (abbreviated to TI–VII, SI–VII).

Where possible, a divisive, 'top-down' approach to the description of bumble bee diversity has been followed, in the sense of concentrating initially on higher-rank relationships and then distinguishing progressively the species groups, species and then variation within species (as opposed to beginning with described infraspecific taxa and searching 'upwards' for close relatives). At the rank of species, this accepts those putative species or species complexes that are supported by consistent evidence for separate status, and which can be reliably identified throughout their range for the purpose of mapping distributions. This kind of broad over-view at least has the potential to apply consistent criteria across all taxa, even though it is appreciated that not all taxa at the rank of species are necessarily of the same kind (Ackery & Vane-Wright, 1984; de Queiroz & Donoghue, 1988). Specialists will need to modify this list as further information becomes available for particular species groups.

Phylogeny, supra-specific taxa and ordering of species

From available cladistic evidence (Williams, 1991, 1995), use of *Psithyrus* as a genus for the social parasites separate from the remainder of the social bumble bees in *Bombus* can no longer be justified, so a single genus *Bombus* is used for all of the species of bumble bees (see the comments under the subgenus *Psithyrus*).

A system of subgenera has become widely used by specialists who wish to label assemblages of the more closely similar species. This system is summarised with subgeneric diagnoses and keys by Richards (1968). For a review of supraspecific classifications of bumble bees, see Ito (1985).

The subgeneric system would be more useful if the names were applied only to strictly monophyletic groups. Unfortunately, Richards's (1968) concepts of the bumble bee subgenera do not always agree well with recent estimates of phylogeny, because some of these assemblages now appear to be paraphyletic (e.g. *Mendacibombus*) or even polyphyletic (e.g. *Sibiricobombus* in the sense of Richards, 1968, includes *Obertobombus*, whereas he placed *B. (Sibiricobombus) flaviventris* in *Subterraneobombus*) (Williams, 1991).

Furthermore, the system of subgenera would probably be more useful if it were simplified (e.g. Menke & Carpenter, 1984; and reply by Williams, 1985c). For example, in the New World, both the monophyletic *fraternus*-group of subgenera and the subgenus *Fervidobombus* are endemic, and these are the only two groups represented south of the Panama isthmus. But whereas *Fervidobombus* has been treated nearly consistently as a single, relatively large subgenus (20 species in this list), the *fraternus*-group (18 species in this list) has regularly been split into as many as nine subgenera.

However, no attempt is made in this checklist to revise radically the subgeneric system, because stability will only be served when a revision can be supported by a comprehensive cladistic analysis. This should include not only a broad sample of species, but also a broad range of morphological and molecular characters. Minor modifications from the subgeneric system described by Richards (1968) are detailed in the list after the subgeneric names.

Full synonymy of supraspecific names is included in this checklist, along with details of type species, because these have been revised since Richards (1968). The given generic combination for subgeneric names is shown. Where a genus-group name was published at the rank of genus and subsequently treated at subgeneric rank, the first such action is listed separately. The two-letter abbreviations for subgeneric names are based on those used by Ito (1985).

Species are listed in an order (Table 3) that represents their phylogenetic relationships (after the sequencing convention of Nelson, 1972) as these are currently understood from cladistic studies of the adult morphology of both sexes (Williams, 1995, and many references therein). Within subgenera, this information is still of a very preliminary nature (e.g. Williams, 1991). Many other estimates of relationship exist and would result in different sequences of species names. An alphabetic index is provided as an aid to finding names in this list.

Table 3   List of names for subgenera of the genus
Bombus, with numbers of species recognised in this
checklist. The subgeneric classification is based on
Richards (1968), modified to accommodate recent
publications (see text; no attempt is made to revise the
subgeneric system, because stability will only be served
when a revision can be supported by a comprehensive
cladistic analysis). Subgenera are listed in an order that
represents their phylogenetic relationships (after the
sequencing convention of Nelson, 1972) as these are
currently understood from cladistic studies of the adult
morphology of both sexes (Williams, 1995).

	Subgenus	Number of species
1	*Mendacibombus*	12
2	*Bombias*	2
3	*Confusibombus*	1
4	*Mucidobombus*	1
5	*Eversmannibombus*	1
6	*Psithyrus*	29
7	*Laesobombus*	1
8	*Orientalibombus*	3
9	*Exilobombus*	1
10	*Thoracobombus*	19
11	*Tricornibombus*	3
12	*Fervidobombus*	20
13	*Senexibombus*	4
14	*Diversobombus*	4
15	*Megabombus*	14
16	*Rhodobombus*	3
17	*Kallobombus*	1
18	*Alpinobombus*	5
19	*Subterraneobombus*	9
20	*Alpigenobombus*	6
21	*Pyrobombus*	43
22	*Festivobombus*	1
23	*Rufipedibombus*	2
24	*Pressibombus*	1
25	*Bombus s.str.*	10
26	*Cullumanobombus*	4
27	*Obertobombus*	2
28	*Melanobombus*	14
29	*Sibiricobombus*	5
30	*Fraternobombus*	1
31	*Crotchiibombus*	1
32	*Robustobombus*	5
33	*Separatobombus*	2
34	*Funebribombus*	2
35	*Brachycephalibombus*	2
36	*Rubicundobombus*	1
37	*Coccineobombus*	2
38	*Dasybombus*	2

Criteria to discriminate species

It is not possible or appropriate to discuss species
concepts in detail in this paper (though the selected
references provide some introduction; for recent re-
views, see Claridge *et al.,* 1997; Mallet, 1997).
However, in order to interpret the checklist, where
possible it would be useful to make the species-dis-
criminating criteria explicit. It is equally important to
convey the present belief that there is no simple solu-

tion to the problem, and that no single known approach
can resolve all of the cases in a uniform and entirely
satisfactory manner.

Species concepts (ideas or general notions of the
class of objects) and species diagnoses (operational
determinations of individual objects) are contentious
and probably unresolvable issues. Therefore there is
arguably no single 'true' list of species, only more or
less valid interpretations from different viewpoints.

Unresolveable conflicts may arise from opposing
views of the nature of species. Species have been
regarded either as typological classes, with member-
ship to be defined by some shared essence (reviewed
by Templeton, 1981), or as individuals, to be discov-
ered (Ghiselin, 1975). There are also conflicting
opinions concerning criteria (characteristics or stand-
ards by which an object may be judged) for recognising
species, based in part on differing emphasis on pattern
or process (de Queiroz & Donoghue, 1988).

Species may be considered not to differ from taxa at
other ranks (e.g. genera, subspecies) in any qualitative
way. There may be quantitative differences in the
numbers of character differences that distinguish them
in comparison with taxa of lower rank. For example,
according to Mallet (1995:294), Darwin (1859) held
this view. The problem with quantitative criteria
(whether applied to genetic or phenotypic characters)
is there is no reason to believe that any choice of
threshold in the degree of difference used to recognise
taxa at the rank of species is anything other than
essentially arbitrary and thus idiosyncratic to particu-
lar authors.

In another view, species may be considered to differ
qualitatively from taxa at other ranks. It is widely
accepted, though often implicitly, that taxa at the rank
of species should be recognised so as to mark the
boundary between, on the one hand, reticulate rela-
tions (for sexually reproducing organisms), and on the
other, more consistently divergent genealogical rela-
tions. One problem is that this distinction may require
predictions as to whether or not currently distinct
groups of individuals are likely to show reticulate
relationships again in the future.

Interbreeding and the associated genetic recombi-
nation is an important part of Dobzhansky's (1937)
'modern synthesis' of Mendelian genetics with Dar-
win's natural selection theory for evolution.
Emphasising interbreeding as a criterion for recognis-
ing species characterised what Mayr (1940, 1963)
called the 'biological' species concept. These ideas
have been modified in the recognition concept of
species (Paterson, 1985). One problem with inter-
breeding or mate recognition as criteria for recognising
species is that direct and reliable evidence is rarely
available and the results of tests under artificial condi-
tions cannot necessarily be generalised (Splitter, 1982).
Another is that the capacity for interbreeding is an

ancestral condition (i.e. not an homology) and so cannot provide support for recognising taxa in the phylogenetic sense (Rosen, 1979).

In practice, all that is usually available to discriminate species as 'different' is evidence from character differences and their patterns of concordance among individuals. The phylogenetic species concept (Cracraft, 1989) is popular because it also embodies the notion that species mark the boundary between different patterns of relationship among individuals and yet it does not rely on inference of interbreeding. The problem is that discovery of phylogenetic species as minimum cladistically-diagnosable (discrete) groups of individuals requires that these groups uniquely share homologies (synapomorphies), which may not always be the case (Ackery & Vane-Wright, 1984; Frost & Kluge, 1994).

Mallet (1995) has argued for minimising the number of assumptions built into species concepts. He suggests that two nominal taxa should be considered conspecific until it can be demonstrated that data for multiple characters distinguish consistent subgroups of individuals with few or no intermediates (the character-cluster concept of species). Although he was arguing against the use of the widely-held biological species concept, he recognised that his prescription differs little from recent common practice. The problem with the cluster concept is how to decide on a threshold for permissable numbers of intermediate individuals between taxa for them still to be considered separate species.

Ultimately, species may be seen as useful conventions to aid in the communication of information gathered about the individuals that are their parts. It may be argued that the most important initial goal is to describe the nature of the variation in each particular case and to avoid presenting only theory-laden (and constrained) interpretations. In this way, basic information on variation will remain available for re-interpretation as theory changes.

For the sake of illustration, four principal classes of problems in geographical variation may be distinguished within the spectrum of kinds of relationships, with the following examples:

Broad co-occurrence of differing individuals

Skorikov (1931) and Reinig (1935) recognised that throughout much of the range of *B. keriensis*, both yellow-banded and cream- or white-banded individuals with indistinguishable morphology co-occur (Fig. 9). From available evidence, it is possible that *B. niveatus / vorticosus* may show a similar pattern of yellow/white variation, as may *B. impetuosus/potanini*, although with differing degrees of geographical variation in colour-form frequency (see the comments on these species). Consequently, taxa in these pairs are

also treated as conspecific for the present (it is possible that in some cases such colour differences may be controlled by alleles at a single locus, see Owen & Plowright, 1980, on *B. melanopygus*; and Williams, 1991, on *B. asiaticus*; or by small numbers of loci, see Plowright & Owen, 1980, on *B. rufocinctus*). In contrast, although the yellow-banded *B. shaposhnikovi* and the white-banded *B. handlirschianus* also show a broadly-overlapping pattern of distribution, the one white-banded male that I have seen is distinct from the yellow-banded males in the morphology of its genitalia (Williams, 1991).

Broad clinal variation

Many species show broad trends in variation across continents, most obviously in colour pattern (e.g. *B. cingulatus*, Fig. 10; and the *trifasciatus*-group, Fig. 13, which may be combined with locally convergent colour variation, e.g. within the *haemorrhoidalis*-group, *breviceps*-group and *rotundiceps*-group, see Sakagami & Yoshikawa, 1961; Tkalcü, 1968b, 1989). In North America, several pairs of nominal taxa were described originally from individual type-specimens with differing colour patterns from eastern and western regions respectively (e.g. *B. auricomus/nevadensis, B. fervidus / californicus, B. pensylvanicus / sonorus, B. terricola / occidentalis*). These taxon pairs have long caused difficulties, for example with Franklin (1913:239) commenting on a list including these taxa and others that are now considered conspecific that 'it must be entirely a matter of personal opinion whether they should be given full species rank or be considered as only subspecies' (although, intriguingly, *B. auricomus/nevadensis* were not included in Franklin's list). In at least some of these cases, many individuals with what appears to be a continuum of intermediate colour patterns are now known from broad intervening areas, so that threshold criteria for distinguishing these taxa appear to be essentially arbitrary (e.g. making decisions based on whether a particular tergum has the pubescence entirely yellow, rather than having a few black hairs present). In consequence, taxa in these taxon pairs are treated here as conspecific and maps are compiled for the more clearly recognisable, more inclusive taxa (but see the comments on *B. auricomus / nevadensis*).

Narrow hybrid zones

In some cases, otherwise discrete colour forms with closely similar morphology meet in narrow zones (of the order of a few km in breadth), where there may be evidence of intermediate or genetically recombinant individuals. In Europe this is best known for *B. ruderatus / argillaceus* (Fig. 11; Scholl, Obrecht & Zimmermann, 1992), and in Asia it has been suggested
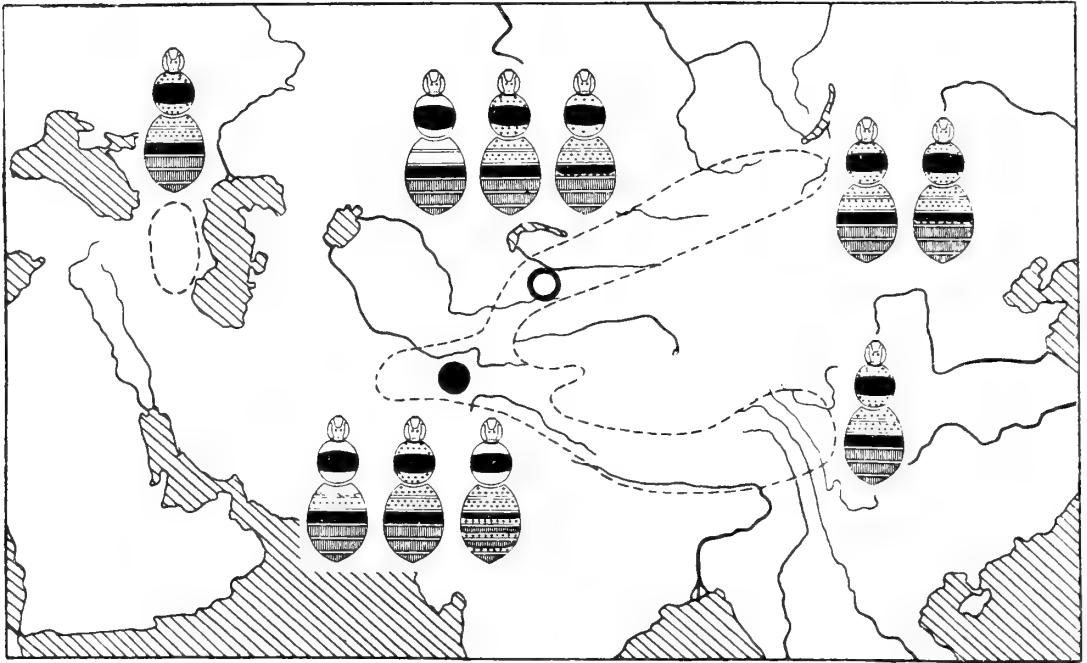
Fig. 9 Approximate distribution range (area within the dotted line) and principal colour variation for *B. keriensis* from Reinig (1939: fig. 23). Many more records are available now, but the pattern remains similar, with broad overlap of yellow- and white-banded individuals in Mongolia, Tien Shan, Pamir and western Himalaya. Yellow and cream pubescence is shown on the bees by crosses; red pubescence by vertical hatching.
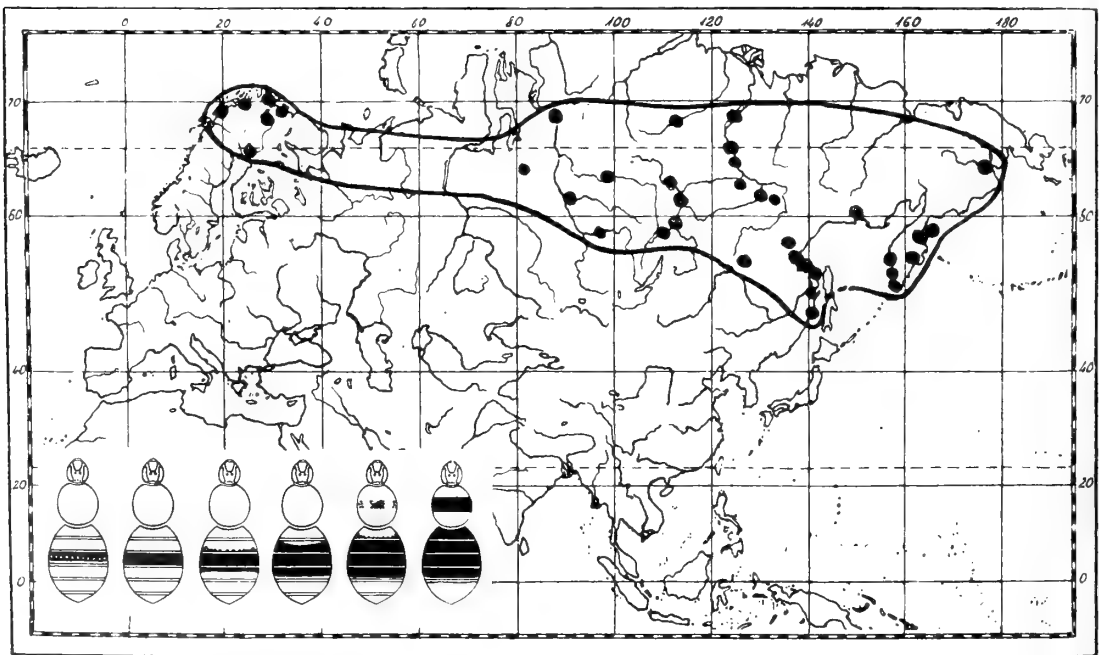

Fig. 10 Distribution records (spots), approximate range (area within the line) and principal colour variation for *B. cingulatus* in the northern Palaearctic Region from Reinig (1939: fig. 7). The lightest individuals occur in the east (Kamchatka) and the darkest individuals (with the black thoracic band) occur in the west, with intermediate individuals in intervening areas.
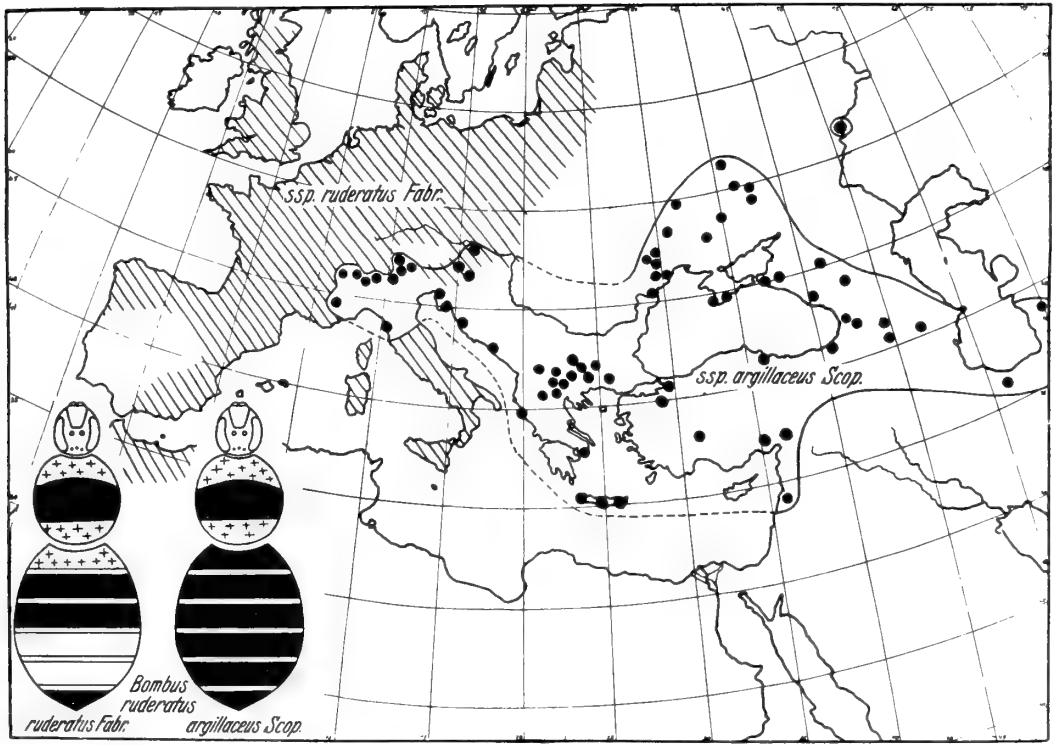
Fig. 11 Distribution records (spots), approximate range (area within the cross-hatching, left, and line, right) and principal colour variation between queens of *B. ruderatus* and *B. argillaceus* in Europe from Reinig (1939: fig. 7). These taxa were regarded as subspecies by Reinig, but have recently been treated as separate species. Although there is evidence of a hybrid zone between some areas of parapatry, the hybrid individuals are very rare (Scholl, Obrecht & Zimmermann, 1992). Yellow pubescence is shown on the bees by crosses.
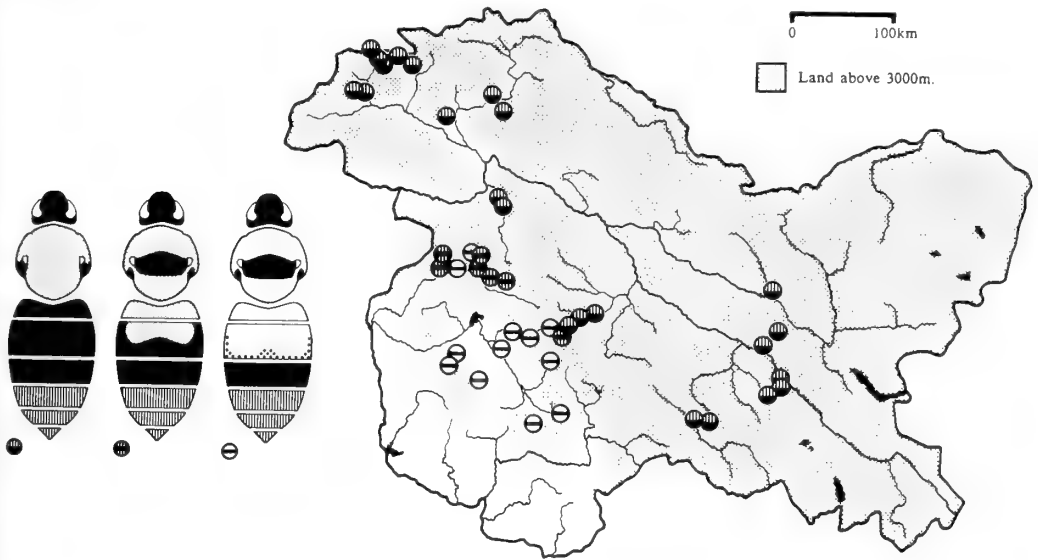
Fig. 12 Distribution records (spots) and principal colour variation for *B. asiaticus* in Kashmir from Williams (1991: map 48). There is evidence of a hybrid zone between some areas of parapatry, such as some high passes along the divide of the Great Himalaya Range, where there are abundant hybrid individuals. The spot symbols show the locally most abundant colour pattern. Yellow pubescence is shown on the bees by fine stippling; red pubescence by vertical hatching.
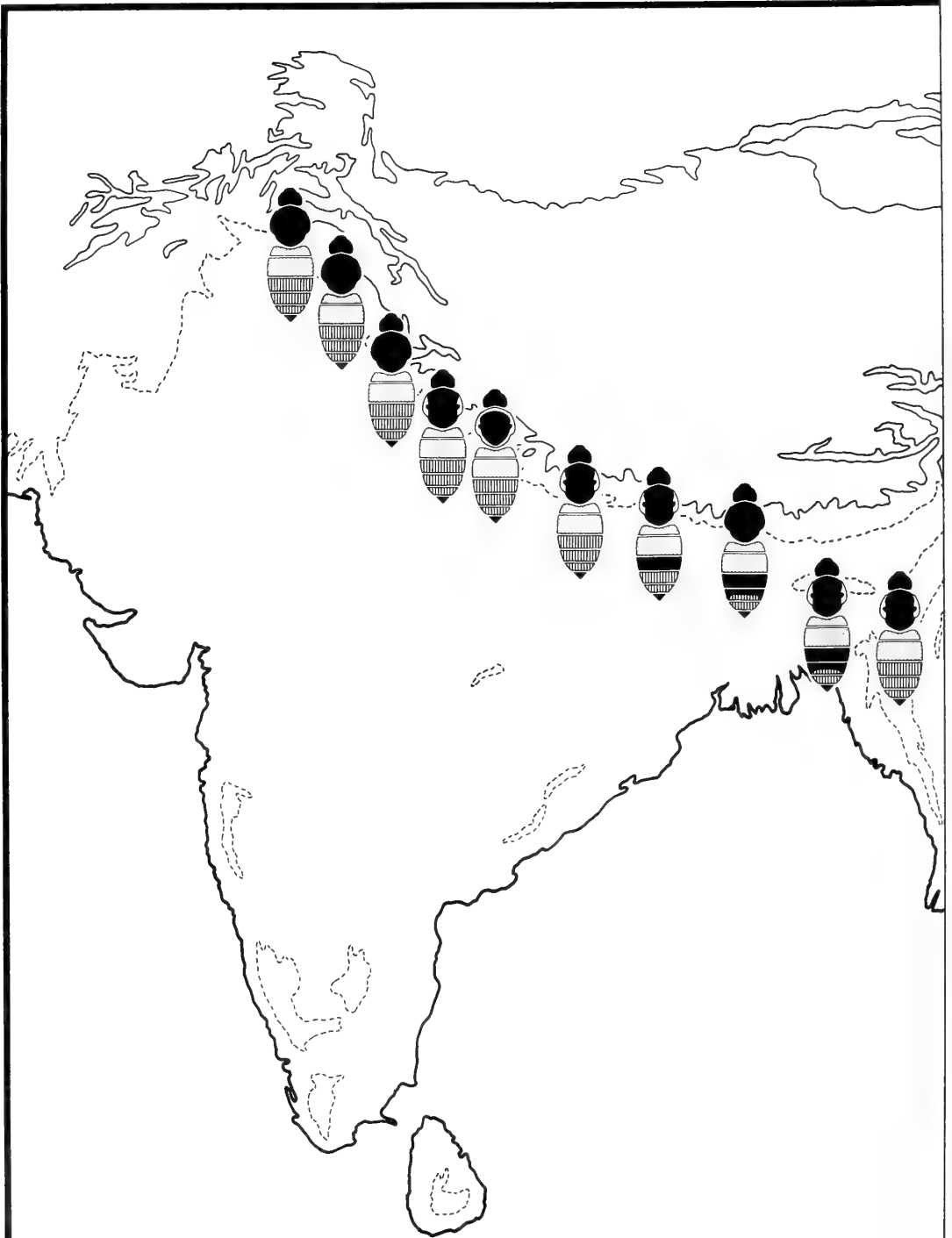
Fig. 13 Distribution records and principal colour variation within the *trifasciatus*-group in Asia (updated from Williams, 1991: fig. 11). The individuals may all be considered parts of a single species, *B. trifasciatus*, depending on which species-defining criterion is accepted. The dashed line shows the 1000 m contour above sea level and the solid line shows the 4000 m contour. Yellow pubescence is shown on the bees by fine stippling, orange pubescence by coarse stippling, red pubescence by vertical hatching.
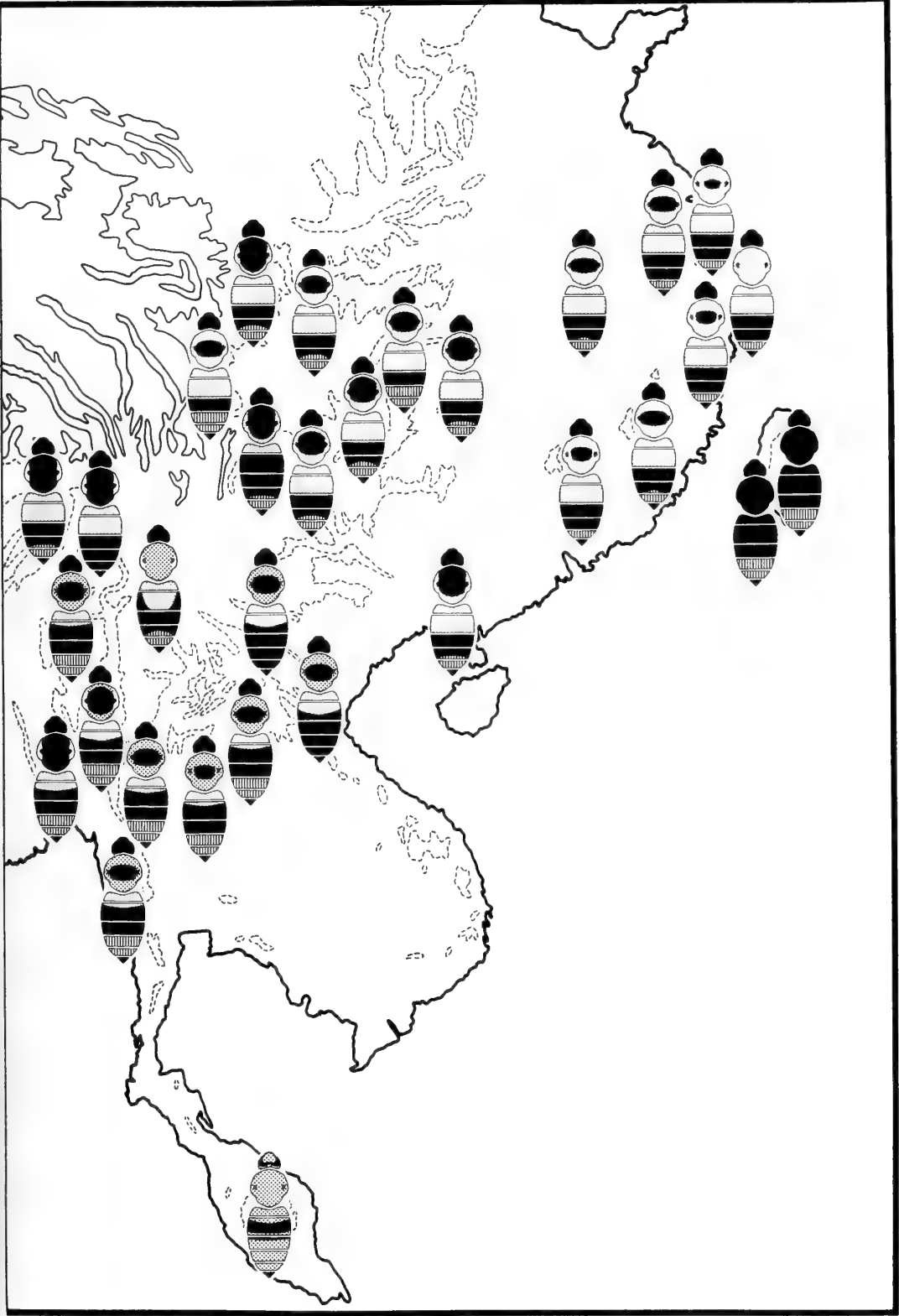
for *B. asiaticus / longiceps* (Fig. 12; Williams, 1991). Other possible examples include *B. lapponicus / monticola* in Europe and *B. pyrosoma / friseanus / miniatus* in China. In the case of *B. asiaticus / longiceps*, I have treated them as conspecific, because intermediate individuals greatly outnumber 'typical' individuals at some localities. For the other cases, I have followed earlier treatments of these taxa as separate species, because intermediate individuals are rare or not well known (although this may be a consequence of poor sampling in some inaccessible areas).

Disjunct peripheral populations

Some peripheral populations on offshore islands or habitat islands (e.g. mountains) show some divergence in colour pattern with little morphological divergence. European examples include *B. terrestris / canariensis* and *B. hortorum / reinigiellus*. Asian examples include *B. schrencki / honshuensis*, *B. trifasciatus / maxwelli* (Fig. 13, Peninsular Malaysia), *B. trifasciatus / wilemani* (Fig. 13, Taiwan), *B. breviceps / angustus*, *B. parthenius / sonani*, *B. flavescens / rufoflavus* and *B. flavescens / baguionensis*. For the application of the biological species concept, in these cases there is no 'natural' meeting of individuals between the taxon pairs and so no admissible evidence on interbreeding (Splitter, 1982). For the application of Mallet's (1995) cluster concept, quantitative analysis of patterns of variation is urgently needed. Where this information is absent, I agree with his prescription of treating taxa in these taxon pairs as provisionally conspecific. *Bombus honshuensis* and *B. schrencki* are mapped separately here because, from published accounts and a small sample of material examined, their colour differences appear to coincide with stronger and more consistent morphological distinctions.

It is hoped that further information may help to clarify these cases. In the interests of pluralism, I aim to report not only a preferred interpretation in the comments on each species, but also at least the more widely-held alternative interpretations.

Sub-specific taxa

For this checklist the interest is primarily in problems of recognition and nomenclature for taxa at the rank of species. Subspecific names refer to parts of species, and so for present purposes these can be treated as synonyms of specific names (e.g. Schwarz *et al.*, 1996). This is not to say that subspecific taxa should not be recognised if they are considered useful, and of course other biologists may add subspecies to this list (cf. Rasmont *et al.*, 1995).

NOMENCLATURE

Nomenclature should be seen as the servant of biology: its purpose is to provide labels that enable biologists to communicate information about organisms with minimal confusion concerning the organisms to which they refer. Accounts of the history of nomenclature for many groups of organisms (e.g. on British bumble bees: Alford, 1975; Prŷs-Jones & Corbet, 1987:82) show that this is not a trivial matter and that rules are necessary.

Treatment of names follows the *International Code of Zoological Nomenclature* (*International Commission on Zoological Nomenclature* [ICZN], 1985). The Principle of Priority is generally adhered to, although regard is given to the stated purpose of priority (ICZN, 1985: Article 23b): namely that it should be used to promote stability and is not intended to be used to upset a long-accepted name in its accustomed meaning (Article 79c) through the introduction of an unused name that is its senior synonym. Similar action is also suggested where cases of homonymy affect current usage, although this action cannot be taken when it is felt desirable to maintain availability of a senior homonym. My suggestions for applications to ICZN for conservation of names in current use are indicated by stars (✪).

Typographical conventions

Bombus b-us	valid name in the species group,
c-us	available name in the species group, including synonyms of a valid species name,
?d-us	available name in the species group, a provisional synonym of a valid species name,
[*e-us*]	unavailable name, informally associated with a valid species name,
f-us examined	type material for species-group name *f-us* examined (in whole or in part),
●	comments on status of species,
○	comments on application of names,
✪	suggestion for application to ICZN.
?Bombus g-us	valid name in the species group, for a taxon that is recognised provisionally as a separate species from *B. b-us*.

A question mark (?) before a valid name shows that, while it refers to a taxon that is considered likely to be a separate species, it may be conspecific with the preceding taxon in the list (i.e. while *Bombus g-us* may be conspecific with *Bombus b-us*, *Bombus d-us* is much more likely to be conspecific with *Bombus b-us*).

Names in the more detailed references are followed by names of authors, date of first publication (within the meaning of ICZN, 1985), and page reference. Wherever possible, the true first date of publication is given in preference to any purported date of publication when these differ. If a name were published originally in a different generic combination, then the original genus is shown in brackets. If the name had been published originally with a different termination, or with capital initial letters, diacritic marks etc., then the original form is shown without the mandatory changes (with the exception that small capital letters are reduced to lower case).

Selection of synonyms

This checklist is based on a much longer catalogue of over 2800 names. As a checklist, it is not required to include the full list of synonyms, so synonyms are selected for this list primarily where they help to clarify the identity and scope of the species (including the subspecies included by some authors), particularly with reference to those names in most common use in the literature of the last 25 years. Misidentifications are not included with the lists of synonyms and are discussed only when necessary to clarify the application of problematic names.

Applications to ICZN

Flexibility in interpretation of the status of taxa is possible where the evidence to distinguish among interpretations is absent, inconclusive, or may permit different interpretations under different species concepts. Otherwise flexibility in the application of names depends on whether systematists are eager to apply to the International Commission on Zoological Nomenclature to use its Plenary Power in order to conserve a preferred usage of names (e.g. Løken *et al.*, 1994; ICZN, 1996).

I propose that this could be achieved in a single application to include all names for which action is currently known to be required (*atratus, balteatus, distinguendus, flavifrons, humilis, hyperboreus, mesomelas, mixtus, norvegicus, polaris, pyrenaeus, soroeensis* and *variabilis*). Comments on this proposal would be welcomed.
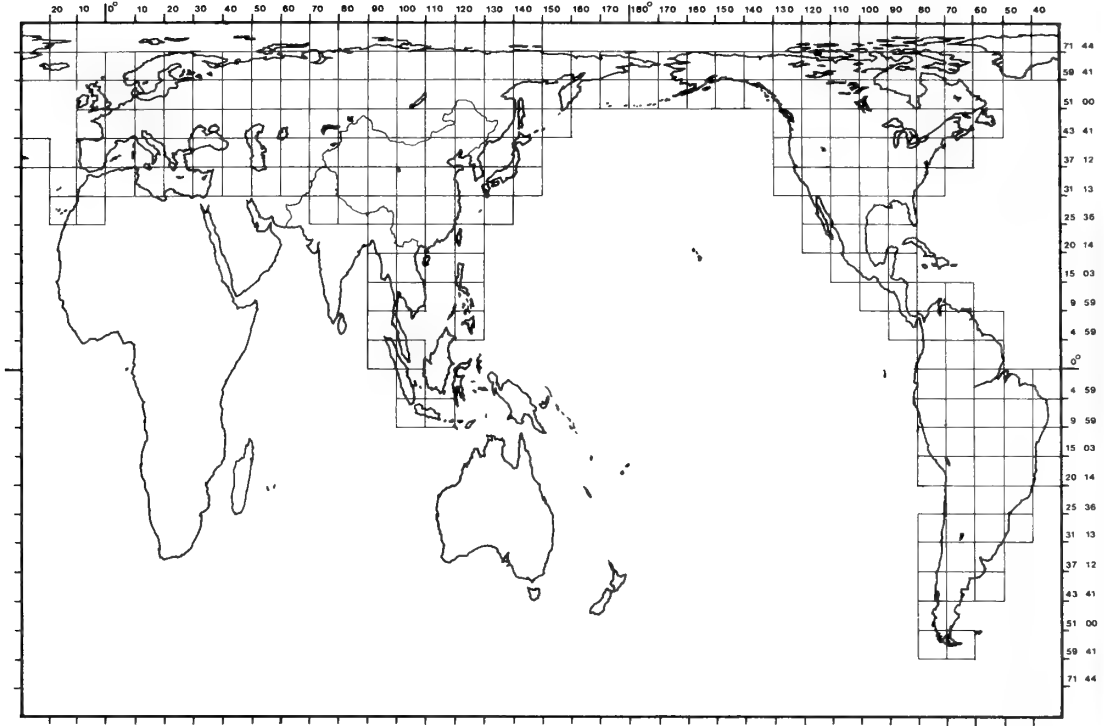
DISTRIBUTION MAPS

This checklist was compiled in conjunction with distribution data in support of biogeographic studies.

Maps of world-wide distribution at a coarse grain size were designed for use in comparisons of regional bumble bee faunas (e.g. Williams, 1989, 1991, 1993, 1995, 1996*a, b*; Williams & Seddon, 1993; Williams & Humphries, 1996).

Aside from any difficulties in identifying species or localities, comparisons among faunas are complicated by two principal factors: first, by differences in sampling effort (as illustrated by 'species-accumulation curves', e.g. Colwell & Coddington, 1994); and second, by differences in the extent of sampling areas ('species-area effects', e.g. Connor & McCoy, 1979). Fortunately for the first problem, the attractiveness of bumble bees to collectors has ensured that they have been relatively intensively sampled, so that most faunas are relatively well known. But in order to reduce this problem further, rather than extrapolate local richness and lose information on individual species, the expected distributions of some species are interpolated on the basis of knowledge of their habitat associations (see the legend to Fig. 14). To reduce the second problem of species-area effects, equal-area grid cells were established using a cylindrical, equal-area projection of the world, marked at intervals of 10° of longitude and calculated intervals of latitude (Fig. 14). However, this does not ensure equal land areas among grid cells, or equal areas of habitat suitable for bumble bees.

Because the intention is to study biogeographic patterns, maps are required to show all historical records, including data from areas where species may now be extinct. On the other hand, data exclude fossil taxa (reviewed by Zeuner & Manning, 1976) and documented introductions (e.g. Oliff, 1895; Frison, 1925*b*; Gurr, 1957; Prŷs-Jones *et al.*, 1981; Arretz & Macfarlane, 1982; Cardale, 1993).

The maps for every species are not included with this checklist because many data are still being collected, although for each subgenus a preliminary map of species richness is included as a general guide (or for monotypic subgenera, a map of records for the single species is included). The numerical values for the grey-scale classes differ between maps and are not shown. This is because I have adopted an alternative approach of using equal frequency classes, which have the advantage that each grey-scale class remains consistent in its relative richness among all maps (e.g. dark grey always shows the richest one fifth of occupied cells excluding the maximum etc.). The sources of the distribution data have not been included because this will be included in a later atlas.

Key to map symbols:

Maps for single species
- ● specimens examined,
- ◉ precise literature records (e.g. 'Dungeness TR01, UK'),
- ○ vague locality data (e.g. 'Florida'),
- ○ interpolations of expected distribution (following common practice for range-filling maps; the rules adopted here are to fill cells between occupied cells when filled cells are known to have had a high proportion of suitable habitat within recorded history; these records amount to < 10% of all gridcell records at this scale, Williams, 1993).

Maps for multiple species

maximum species counts are shown in black, otherwise counts are divided into five grey-scale classes of approximately equal size by numbers of grid cells.

Fig. 14   Map of the world (excluding Antarctica) using a cylindrical equal-area projection that is orthomorphic (minimum shape distortion) at 46° North and South (where bumble bee records are particularly plentiful). Intervals of 10° longitude (top of map) are used to calculate intervals of latitude (right of map) that provide equal-area grid cells of c. 611,000 km². The portion of the grid shown covers the known, native distribution of bumble bees. Map symbols are shown above for (a) plotting individual species, for which different spots distinguish different data categories (Map 3); or (b) for plotting coincidence maps for multiple species, using a grey scale for variation in species richness (Map 1).

LIST OF SPECIES
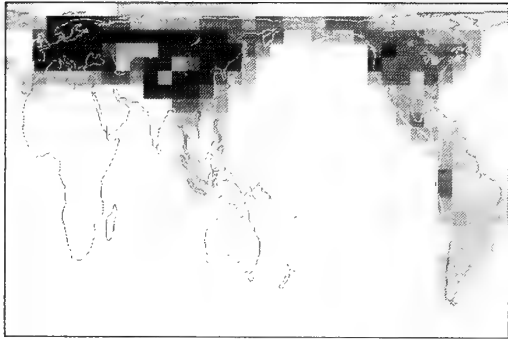
(plot of total species richness with grey scale, for explanation see Fig. 14)

Genus *BOMBUS* Latreille in the broad sense

[*Bremus* [Jurine], 1801:164, type-species *Apis terrestris* Linnaeus (= *Bombus terrestris* (Linnaeus)) by subsequent designation of Morice & Durrant, 1915:429, suppressed by ICZN, 1939]

Bombus Latreille, 1802*a*:437, type-species *Apis terrestris* Linnaeus (cited as *Apis terrestris* F.) (= *Bombus terrestris* (Linnaeus)) by monotypy

Bombus Latreille, 1802*b*:385, type-species *Apis terrestris* Linnaeus (= *Bombus terrestris* (Linnaeus)) by monotypy, redescribed

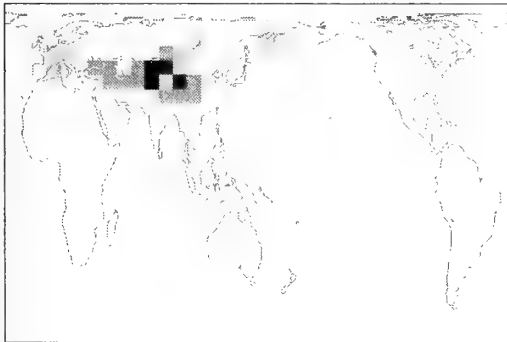[*Bremus* Panzer, 1805:pl. 19–21, type-species *Apis agrorum* Fabricius (= *Bombus pascuorum* (Scopoli)) by subsequent designation of Sandhouse, 1943:532, suppressed by ICZN, 1954]

[*Bombellus* IIE, 1931:248, incorrect subsequent spelling]

Subgenus *MENDACIBOMBUS* Skorikov

Mendacibombus Skorikov, 1914*a*:125, type-species *Bombus mendax* Gerstaecker by subsequent designation of Sandhouse, 1943:572

Bombus (Mendacibombus) Krüger, 1917:62

COMMENT. The species of *Mendacibombus* appear to be paraphyletic with respect to the rest of the

bumble bees and in consequence are not a 'natural' group (Williams, 1991, 1995).

Bombus (Md.) avinoviellus (Skorikov)

avinoviellus (Skorikov, 1914*a*:126 [*Mendacibombus*]) examined

callophenax Cockerell, 1917:122, examined

Bombus (Md.) mendax Gerstaecker

mendax Gerstaecker, 1869:323, examined

latofasciatus Vogt, 1909:50, not of Vogt, 1909:42 (= *B. lucorum* (Linnaeus))

pyrenes (Tkalcü, 1975:173 [*Mendacibombus*]) replacement name for *latofasciatus* Vogt, 1909:50

Bombus (Md.) makarjini Skorikov

makarjini Skorikov, 1910*a*:329, examined

Bombus (Md.) superbus (Tkalcü)

superbus (Tkalcü, 1968*a*:22 [*Mendacibombus*]) examined

Bombus (Md.) himalayanus (Skorikov)

?*varius* (Skorikov, 1914*a*:125 [*Mendacibombus*]) examined, not of Lepeletier, 1832:381 (= *B. campestris* (Panzer))

himalayanus (Skorikov, 1914*a*:127 [*Mendacibombus*]) examined

Bombus (Md.) marussinus Skorikov

marussinus Skorikov, 1910*a*:330, examined

afghanus Reinig, 1940:230, examined

Bombus (Md.) turkestanicus Skorikov

turkestanicus Skorikov, 1910*a*:329, examined

Bombus (Md.) defector Skorikov

defector Skorikov, 1910*a*:330

?*altaicus* Skorikov, 1910*a*:329, not of Eversmann, 1846:436 (= *B. melanurus* Lepeletier)

?*margreiteri* Vogt, in Skorikov, 1910*a*:330, examined

● TAXONOMIC STATUS. Skorikov's (1910*a*) descriptions of varieties of *B. mendax* are all of females. Many of these nominal taxa have subsequently been treated as separate species (e.g. Skorikov, 1931; Rasmont, 1988).

However, I have examined type material or other material identified by Skorikov for all of these taxa and find some of them to be morphologically closely similar. The females of *defector, altaicus* and *margreiteri* differ from one another principally in

colour, and the only males I have seen associated with them (collections in London, Petersburg, Beijing) have very similar genitalia (which are distinct from *B. mendax*).

Until more evidence to the contrary is available from critical studies of patterns of variation, I shall continue to treat *B. defector, B. altaicus* and *B. margreiteri* as parts of a single variable species, *B. defector* (Williams, 1985a, 1991).

O   NOMENCLATURE.   Williams (1991) regarded *B. defector, B. altaicus* and *B. margreiteri* as likely to be conspecific and following the Principle of First Reviser (ICZN, 1985: Article 24) chose *B. defector* as the name for the species.

Bombus (Md.) handlirschianus Vogt
Handlirschianus Vogt, 1909:49

### Bombus (Md.) shaposhnikovi Skorikov
shaposhnikovi Skorikov, 1910a:329

Bombus (Md.) waltoni Cockerell
chinensis Skorikov, 1910a:330, examined, not of Morawitz, 1890:352 (= *B. chinensis* (Morawitz))
waltoni Cockerell, 1910b:239, examined

Bombus (Md.) convexus Wang
lugubris Morawitz, 1880:339, examined, not of Kriechbaumer, 1870:159 (= *B. maxillosus* Klug)
convexus Wang, 1979:190, examined
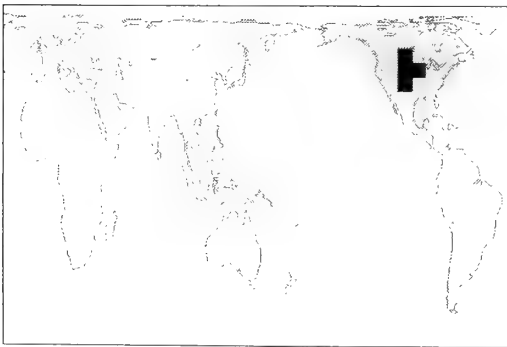
Subgenus *BOMBIAS* Robertson
Bombias Robertson, 1903:176, type-species *Bombias auricomus* Robertson (?= *Bombus nevadensis* Cresson) by original designation
Bombus (Bombias) Franklin, 1913:138
Nevadensibombus Skorikov, 1922a:149, type-species *Bombus nevadensis* Cresson by subsequent designation of Frison, 1927:64
Bremus (Boopobombus) Frison, 1927:59 (proposed as a

section name but stated by Frison to include those forms considered by Franklin, 1913, to belong to the subgenus *Bombias* Robertson), type-species *Bombias auricomus* Robertson (= *Bombus auricomus* (Robertson)) by subsequent designation of Williams, 1995:339.

Bombus (Bi.) nevadensis Cresson
nevadensis Cresson, 1874:102

COMMENT.   A single queen of *B. nevadensis* has been reported from Hidalgo, Mexico, by Milliron (1971) and Hurd (1979), although the species is not listed for Mexico by Labougle (1990).

?Bombus (Bi.) auricomus (Robertson)
auricomus (Robertson, 1903:176 [*Bombias*])

●   TAXONOMIC STATUS.   *B. nevadensis* and *B. auricomus* have been regarded both as conspecific (e.g. LaBerge & Webb, 1962; Milliron, 1971; Thorp *et al.*, 1983; Laverty & Harder, 1988) and as separate species (e.g. Franklin, 1913; Rasmont, 1988; Scholl, Thorp, Owen & Obrecht, 1992; Poole, 1996).

B. nevadensis from western North America was not mentioned in the original description of *B. auricomus* (lectotype worker from Illinois by designation of Milliron, 1971:78), although the latter was described using characters of morphology and of colour pattern. The two taxa have generally been distinguished on the basis of the extent of the black pubescence on the dorsum of the female thorax and laterally on the male gastral terga (e.g. Franklin, 1913).

The only study to investigate variation in characters used to distinguish the two taxa at a fine spatial scale in their area of overlap was by LaBerge & Webb (1962). They reported (p. 26) that 'Throughout the broad middle half of Nebraska *nevadensis* seems to be rather rare and most specimens, although referable to subspecies *auricomus* show some indication of intergrading with the typical subspecies [*nevadensis*] in the west. . . . Many specimens from Nebraska in the range of the typical subspecies [*nevadensis*] show some tendency toward the darker coloration of subspecies *auricomus*.' They concluded that these variable bees are all parts of the same species.

Recently, Scholl *et al.* (1992) distinguished two groups of individuals on the basis of differing mobility morphs of five enzymes. The individuals in one enzyme group were all extensively dark-banded, and Scholl *et al.* associated these with the name *B. auricomus*. However, individuals in the other enzyme group, which Scholl *et al.* associated with the name *B. nevadensis*, apparently included not only the contrasting, extensively pale individuals (*B. nevadensis*), but also a few of the extensively dark-banded individuals (*B. auricomus*) similar to those in the first group (8/49

individuals had gastral tergum I almost completely black; 3/49 individuals had the scutellum predominantly black). Thus the enzyme evidence does identify two groups of individuals, but (1) these do not appear to correspond precisely to the two traditional colour groups; (2) some of the key areas likely to support intermediate or recombinant individuals still need to be sampled for enzyme variation (e.g. in the Dakotas, L. Day *in litt.*); and (3) inheritance of enzyme and colour states needs to be better understood, including the unusual enzyme morphs of the heterozygous bees (detected in 20/141 queens). They concluded that these bees represent two species.

A. Scholl (*in litt.*) reports a further intriguing morphometric study. A random subsample of 20 queens from the enzyme study was scored for 15 characters and analysed by linear discriminant analysis. This method seeks a combination of characters that best discriminates any two *a priori* sets, in this case using three measurements of parts of the radial cell, eye and antenna. However, although this approach may be useful for discriminating previously recognised taxa, it does not provide evidence that they are necessarily separate species (it could also be used to discriminate morphological subsets within a single, variable population, e.g. among breeds of domestic dogs).

From an examination of 41 females, so far I have found only one subtle morphological character to distinguish eastern, banded bees (*B. auricomus*), on the one hand, from western unbanded (*B. nevadensis*) and banded (e.g. Vancouver Island) bees, on the other. This concerns the anterior part of a band of large punctures along the inner eye margin, dorsally opposite the ocelli, just before these punctures meet a more anterior, very dense patch of small punctures. The western bees have areas between the large punctures conspicuously shining, with few fine punctures and lacking microsculpture. In contrast, the eastern bees have these areas appearing rather dull, often with more of the fine punctures, and more particularly with a very fine, wrinkled or reticulate microsculpture. A similar difference may be present in the males, posteriolaterally to the ocelli, though the sample sizes available to me are too small for much confidence.

I regard the conflicting evidence available at present as not entirely conclusive as to whether these bees are parts of the same population or two separate species. As far as is known, both the variations of the colour pattern and of the enzyme mobilities are inherited and genetically determined, but details of patterns of inheritance and of the spatial aspects of any association between these characters are unknown. In view of the multiple enzymes differences found and of the apparent association between the enzyme groups and the morphological character states, I shall follow the treatment of these taxa as two separate species until more evidence is available.
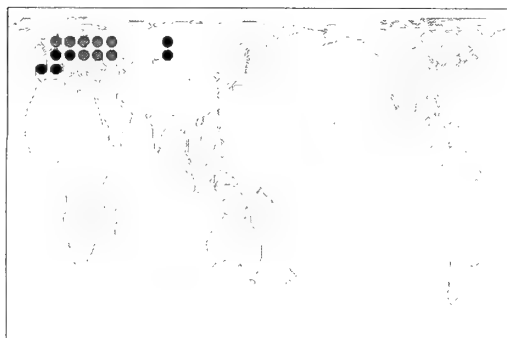
(plot of records for a single species, for explanation and key see Fig. 14)

Subgenus *CONFUSIBOMBUS* Ball

Bombus (Confusibombus) Ball, 1914:78, type-species *Bombus confusus* Schenck by monotypy

Bombus (Sulcobombus) Krüger, 1917:65, type-species *Bombus confusus* Schenck by subsequent designation of Sandhouse, 1943:602

Confusobombus Skorikov, 1922a:156, type-species *Bombus confusus* Schenck by subsequent designation of Richards, 1968:214

Bombus (Cf.) confusus Schenck

confusus Schenck, 1859:135

paradoxus Dalla Torre, 1882:18

festivus Hoffer, 1882:80, not of Smith, 1861:152 (= *B. festivus* Smith)

● TAXONOMIC STATUS. *B. confusus* and *B. paradoxus* differ in the colour pattern of the pubescence (e.g. Reinig, 1939: fig. 19). Rasmont (1988) reports that in north western Europe, the yellow-banded and white-tailed *B. paradoxus* occurs only as rare individuals within the population of predominantly unbanded and red-tailed *B. confusus*. In contrast, all of the individuals that I have seen from the disjunct population in Central Asia have the yellow-banded and white-tailed *B. paradoxus* colour pattern.
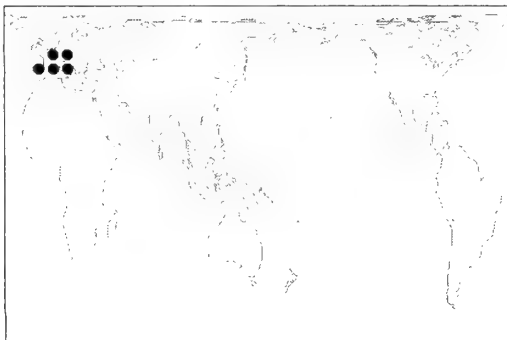
Subgenus *MUCIDOBOMBUS* Krüger

Mucidobombus Krüger, 1920:350, type-species *Bombus mucidus* Gerstaecker by monotypy

Bombus (Mucidobombus) Pittioni, 1937:97

Bombus (Mc.) mucidus Gerstaecker

mucidus Gerstaecker, 1869:324
atratus Friese, 1911:572, examined

Subgenus EVERSMANNIBOMBUS Skorikov

Agribombus (Eversmannibombus) Skorikov, 1938a:145,
  type-species Mucidobombus eversmanniellus (=
  Bombus persicus Radoszkowski) by monotypy
Bombus (Eversmannibombus) Richards, 1968:214

Bombus (Ev.) persicus Radoszkowski

calidus Eversmann, 1852:133, examined, not of Erichson
  in Middendorff, 1851:65 (= B. hypnorum (Linnaeus))
persicus Radoszkowski, 1881:v, examined
Persicus Radoszkowski, 1883:214, redescribed
eversmanni Friese, 1911:572, not of Skorikov, 1910c:581
  (= B. modestus Eversmann), replacement name for
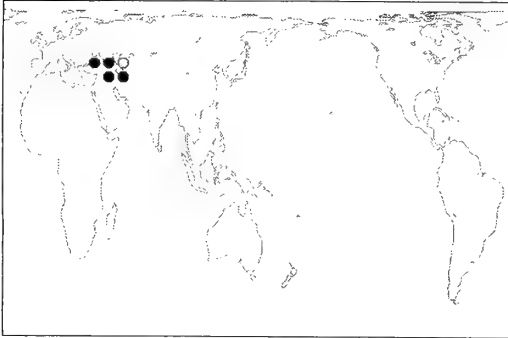 calidus Eversmann, 1852:133
eversmanniellus (Skorikov, 1922a:149 [Mucidobombus])
  replacement name for eversmanni Friese, 1911:572

Subgenus PSITHYRUS Lepeletier

Psithyrus Lepeletier, 1832:373, type-species Apis rupestris
  Fabricius (= Bombus rupestris (Fabricius)) by subse-
  quent designation of Sandhouse, 1943:572
Apathus Newman, 1835:404, replacement name for
  Psithyrus Lepeletier, incorrectly stated to be a junior
  homonym of Psithyros Hübner, [1819]:132 (=
  Macroglossum Scopoli, 1777:414)

?Psithyrus (Laboriopsithyrus) Frison, 1927:69, type-spe-
  cies Bombus laboriosus Fabricius (= Emphoropsis
  laboriosus (Fabricius) in the sense of Frison (=Bombus
  citrinus (Smith), a misidentification, see Milliron,
  1960:99, requiring designation by ICZN) by original
  fixation ✪
Psithyrus (Ashtonipsithyrus) Frison, 1927:69, type-spe-
  cies Apathus ashtoni Cresson (= Bombus ashtoni
  (Cresson)) by original designation
Psithyrus (Fernaldaepsithyrus) Frison, 1927:70, type-spe-
  cies Psithyrus fernaldae Franklin (= Bombus fernaldae
  (Franklin)) by original designation
Psithyrus (Eopsithyrus) Popov, 1931:134, type-species
  Apathus tibetanus Morawitz (= Bombus tibetanus
  (Morawitz)) by original designation
Psithyrus (Metapsithyrus) Popov, 1931:135, type-species
  Apis campestris Panzer (= Bombus campestris (Pan-
  zer)) by original designation
Psithyrus (Allopsithyrus) Popov, 1931:136, type-species
  Apis barbutella Kirby (= Bombus barbutellus (Kirby))
  by original designation
Psithyrus (Ceratopsithyrus) Pittioni, 1949:270, type-spe-
  cies Psithyrus klapperichi Pittioni (= Bombus cornutus
  (Frison)) by original designation
Psithyrus (Citrinopsithyrus) Thorp in Thorp et al., 1983:50,
  type-species Apathus citrinus Smith (=Bombus citrinus
  (Smith)) by original designation
Bombus (Psithyrus) Williams, 1991:44
[Psithyrus (Fernaldepsithyrus) Amiet, 1996:86, incorrect
  subsequent spelling]

● TAXONOMIC STATUS. It has long been consid-
ered useful to regard Psithyrus as a separate genus in
recognition of the distinctive behaviour of the species,
as social parasites in colonies of the remaining
Bombini, and in recognition of their distinctive mor-
phology. However, most recent studies have shown (if
phenograms are interpreted along with cladograms as
phylogenetic estimates) that, although Psithyrus is
itself very likely to be monophyletic, the remaining
bumble bees are not (Plowright & Stephen, 1973;
Obrecht & Scholl, 1981; Ito, 1985; Williams, 1985b,
1991, 1995; Pamilo et al., 1987).

I have previously attempted to retain the use of the
names Psithyrus and Bombus for monophyletic genera
by recognising a third genus, Mendacibombus
(Williams, 1985b). However, further study of all of the
species of Mendacibombus (Williams, 1991, 1995)
showed that it is likely to be paraphyletic with respect
to all other bumble bees, with the consequence that as
many as another nine genera (mostly for single spe-
cies) might be required to maintain monophyly
alongside a genus Psithyrus. In the face of this evi-
dence, a pragmatic solution was recommended,
recognising a single genus Bombus for all bumble
bees, to include Psithyrus as a subgenus. This is a
return to an emphasis of the more widely shared
characters and the more distant affinities for the ge-
neric concept, encouraged by the opinion of Michener
(1990) that bumble bees are 'morphologically mo-

notonous' in comparison with variation among species within closely related groups such as Euglossini (orchid bees) and Meliponini (stingless bees). One advantage of a single genus for all bumble bees is that it recognises a group for which evidence of monophyly is particularly strong, so that nomenclature is most likely to remain stable in the future. Use of a single genus *Bombus* for all bumble bees (Williams, 1991) has now been accepted by most recent authors (e.g. Rasmont & Adamski, 1995; Rasmont *et al.*, 1995; Schwarz *et al.*, 1996).

The subgenera within the former genus *Psithyrus* have often been considered less distinct from one another than have the other subgenera of *Bombus* (Pittioni, 1939a; Ito, 1985; Williams, 1985b; Michener, 1990) and therefore may be treated as synonyms of *Psithyrus* (Milliron, 1961; Williams, 1991, 1995). In an alternative treatment, Rasmont *et al.* (1995) include the former subgenera of the former genus *Psithyrus* as separate subgenera within the genus *Bombus*.

O NOMENCLATURE. The names of six species of the subgenus *Psithyrus* from Kashmir were explicitly stated to be new combinations with the genus *Bombus* by Williams (1991). Rasmont *et al.* (1995) have since listed the other European species in this combination. No formal statements of new combination are made here for the remaining species of the subgenus *Psithyrus* because a principle of implied combinations (Poole, 1996) is followed after the change in status of *Psithyrus* from genus to a subgenus of *Bombus*.

✪ APPLICATION TO ICZN. Because the type species of *Laboriopsithyrus* was misidentified (discussed by Milliron, 1960:99), ICZN is required to designate as type species whichever species will best serve nomenclatural stability (ICZN, 1985: Art. 70b). It is suggested that, in the interests of stability (ICZN, 1985: Article 23b), an application be made to ICZN to use its Plenary Power to select the species actually involved (*Bombus laboriosus* in the sense of Frison, = *Bombus citrinus* (Smith)), which was wrongly named in the type fixation (ICZN, 1985: Art. 70b(i)).

COMMENT. The highest richness of species of the subgenus *Psithyrus* occurs in the Old World (there are no species known from south of Panama), although the earliest-diverging species appear to be North American (unpublished). This is the opposite pattern to that shown by species of the largest subgenus, *Pyrobombus* (see the comments on the subgenus *Pyrobombus*).

All species of the subgenus *Psithyrus* are believed to be obligate social parasites in colonies of other *Bombus* species (reviewed by Alford, 1975; Fisher, 1987). There is variation in the degree of host specificity. See also the comments on *B. inexspectatus* and *B. hyperboreus*.

Bombus (Ps.) insularis (Smith)

interruptus Greene, 1858:11, not of Lepeletier, 1832:381 (= *B. rupestris* (Fabricius))
insularis (Smith, 1861:155 [*Apathus*]) examined
consultus (Franklin, 1913:459 [*Psithyrus*])
?*bicolor* (Franklin, 1913:460 [*Psithyrus*]) not of Höppner, 1897:33 (=*B. soroeensis* (Fabricius)) (provisional synonym)
crawfordi (Franklin, 1913:464 [*Psithyrus*])

● TAXONOMIC STATUS. According to D. Yanega (*in litt.*), who has examined the type material, *B. bicolor* Franklin is conspecific with *B. interruptus*.

Bombus (Ps.) citrinus (Smith)

citrinus (Smith, 1854:385 [*Apathus*]) examined
contiguus (Cresson, 1863:112 [*Apathus*])

Bombus (Ps.) variabilis (Cresson)✪

intrudens (Smith, 1861:154 [*Apathus*]) examined
variabilis (Cresson, 1872:284 [*Apathus*]) **new synonym**
?*guatemalensis* (Cockerell, 1912:21 [*Psithyrus*]) (provisional synonym)
?*sololensis* (Franklin, 1915:173 [*Psithyrus*]) (provisional synonym)
?*mysticus* (Frison, 1925a:138 [*Psithyrus*]) (provisional synonym)

● TAXONOMIC STATUS. Specimens in the NHM collection from Mexico and Guatemala labelled '*intrudens*' and '*sololensis*' appear to me to be closely similar to *B. variabilis*. Frison (1925a) believed that *B. sololensis* is a colour form of *B. guatemalensis*. Nevertheless, he proceeded to distinguish *B. mysticus* as a separate species on the basis of colour pattern alone. I am unaware of any reason (other than minor differences in colour pattern) why *B. variabilis*, *B. intrudens*, *B. sololensis*, or *B. guatemalensis* and *B. mysticus* (judging from the published descriptions at least), should not be considered conspecific.

O NOMENCLATURE. A female in the NHM collection has three labels '*Apathus* / *intrudens* / Smith.', '58.135 MEX. / (Oajaca.)', 'Holo- / type' and I am unaware of any problems with this designation. If this is correct and the type is conspecific with *B. variabilis*, then *B. intrudens* is the oldest available name for this species. D. Yanega (*in litt.*) agrees with this interpretation.

✪ APPLICATION TO ICZN. Although *B. intrudens* is the oldest available name for the present interpretation of this species, the name *B. variabilis* has been in common use for the species since 1947 (e.g. Stevens, 1948; Chandler, 1950; LaBerge & Webb, 1962; Mitchell, 1962; Medler & Carney, 1963; Hobbs, 1966; Plowright & Stephen, 1973; Hurd, 1979; Husband *et al.*, 1980; Michener, 1990; Poole, 1996). I know of no publications using the name *B. intrudens* since 1947. It

is suggested that, in the interests of stability (ICZN, 1985: Article 23b), an application be made to ICZN to use its Plenary Power to suppress the unused senior synonym (ICZN, 1985: Article 79) (see the comments on *B. muscorum*). However, the consequence of this action would be that *B. intrudens* would no longer be available for a species or for a subspecies of *B. variabilis* (Cresson).

Bombus (Ps.) suckleyi Greene
Suckleyi Greene, 1860:169

Bombus (Ps.) vestalis (Geoffroy)
vestalis (Geoffroy in Fourcroy, 1785[see Hagen 1862:246]:450 [*Apis*])

Bombus (Ps.) perezi (Schulthess-Rechberg)
perezi (Schulthess-Rechberg, 1886:275 [*Psithyrus*])

Bombus (Ps.) ashtoni (Cresson)
Ashtoni (Cresson, 1864:42 [*Apathus*])

Bombus (Ps.) bohemicus Seidl
nemorum (Fabricius, 1775:380 [*Apis*]) examined, not of Scopoli, 1763:307 (= *B. subterraneus* (Linnaeus)), not of Fabricius, 1775:382 (= *B. distinguendus* Morawitz)
bohemicus Seidl, 1837:73
?chinganicus (Reinig, 1936:8 [*Psithyrus*]) (provisional synonym)
hedini (Bischoff, 1936:26 [*Psithyrus*]) not of Bischoff, 1936:15 (= *B. hedini* Bischoff)

● TAXONOMIC STATUS. I am unaware of any reason (other than the small body size of the holotype female and three paratype females of *B. chinganicus*) why *B. bohemicus* and *B. chinganicus* should not be considered conspecific. Consistent with this, body sizes do appear to vary considerably within British species of the subgenus *Psithyrus,* including *B. bohemicus.*

Bombus (Ps.) coreanus (Yasumatsu)
coreanus (Yasumatsu, 1934:399 [*Psithyrus*])

Bombus (Ps.) barbutellus (Kirby)
Barbutella (Kirby, 1802:343 [*Apis*]) examined
?richardsi (Popov, 1931:150,190 [*Psithyrus*]) not of Frison, 1930:6 (= *B. rufipes* Lepeletier)
?licenti (Maa, 1948:34 [*Psithyrus*]) examined

○ NOMENCLATURE. Løken (1984) interpreted *B. saltuum* (Panzer, 1801) as conspecific with *B. barbutellus*. Consequently, *B. saltuum* would appear to be the oldest available name for this species. However, Løken made no further comment on this and used the name *Psithyrus barbutellus* (= *B. barbutellus*), possibly because she remained unsure of the identity of *B. saltuum*. In contrast, Warncke (1986) interpreted

B. saltuum as conspecific with *B. subterraneus*. See the comments on *B. subterraneus*.

?Bombus (Ps.) maxillosus Klug
maxillosus Klug in Germar, 1817:269
lugubris (Kriechbaumer, 1870:159 [*Psithyrus*])
unicolor (Kriechbaumer, 1870:159 [*Psithyrus*])
mixta (Kriechbaumer, 1870:160 [*Psithyrus*])
šusterai (May, 1944:267 [*Psithyrus*]) not infrasubspecific after Tkalcü, 1977:224

● TAXONOMIC STATUS. As Rasmont (1988) notes, *B. maxillosus* is closely similar to *B. barbutellus* in morphology and habitat, so that specimens cannot always be distinguished reliably. Consequently these nominal taxa might be considered conspecific. More evidence is awaited.

Bombus (Ps.) cornutus (Frison)
cornutus (Frison, 1933:338 [*Psithyrus*])
pyramideus (Maa, 1948:19 [*Psithyrus*]) examined
acutisquameus (Maa, 1948:21 [*Psithyrus*]) examined
klapperichi (Pittioni, 1949:273 [*Psithyrus*]) examined, not of Pittioni, 1949:266 (= *B. picipes* Richards)
?canus (Tkalcü, 1989:42 [*Psithyrus*])

Bombus (Ps.) expolitus Tkalcü
expolitus (Tkalcü, 1989:44 [*Psithyrus*]) examined

Bombus (Ps.) turneri (Richards)
turneri (Richards, 1929a:141 [*Psithyrus*]) examined
?monozonus (Friese, 1931:304 [*Psithyrus*]) not of Friese, 1909:674 (= *B. lucorum* (Linnaeus))
?decoomani (Maa, 1948:26 [*Psithyrus*]) examined
?martensi (Tkalcü, 1974b:314 [*Psithyrus*]) (provisional synonym)

● TAXONOMIC STATUS. Several of these nominal taxa have been treated as separate species. However, aside from differences in colour pattern, they are closely similar in morphology. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

Bombus (Ps.) tibetanus (Morawitz)
tibetanus (Morawitz, 1886:202 [*Apathus*])
?latefasciatus (Friese, 1931:304 [*Psithyrus*])

Bombus (Ps.) chinensis (Morawitz)
chinensis (Morawitz, 1890[April 30]:352 [*Apathus*])
morawitzi (Friese, 1905:516 [*Psithyrus*]) not of Radoszkowski, 1876:101 (= *B. morawitzi* Radoszkowski)
hönei (Bischoff, 1936:26 [*Psithyrus*]) not of Bischoff, 1936:10 (= *B. friseanus* Skorikov)

Bombus (Ps.) novus (Frison)
  novus (Frison, 1933:340 [*Psithyrus*])
  ?*nepalensis* (Tkalcü, 1974b:318 [*Psithyrus*]) examined

Bombus (Ps.) branickii (Radoszkowski)
  Branickii (Radoszkowski, 1893:241 [*Psithyrus*]) examined
  chloronotus (Morawitz, 1894:6 [*Apathus*])
  elisabethae (Reinig, 1940:231 [*Psithyrus*]) examined
  [*branichi* (Kim & Ito, 1987:32 [*Psithyrus*]) incorrect subsequent spelling]

Bombus (Ps.) rupestris (Fabricius)
  rupeftris (Fabricius, 1793:320 [*Apis*])
  Pyrenæus (Lepeletier, 1832:375 [*Psithyrus*])
  Interruptus (Lepeletier, 1832:381 [*Psithyrus*])
  armeniacus (Reinig, 1970:77 [*Psithyrus*]) not of Radoszkowski, 1877b:202 (= *B. armeniacus* Radoszkowski)

Bombus (Ps.) ferganicus (Radoszkowski)
  ferganicus (Radoszkowski, 1893:241 [*Psithyrus*]) examined
  ochraceus (Morawitz, 1894:5 [*Apathus*])
  indicus (Richards, 1929a:139) examined

Bombus (Ps.) morawitzianus (Popov)
  morawitzianus (Popov, 1931:148,183 [*Psithyrus*]) examined
  redikorzevi (Popov, 1931:160,181 [*Psithyrus*])

○ NOMENCLATURE.   Grütte (1937) regarded *B. morawitzianus* and *B. redikorzevi* as conspecific and, following the Principle of First Reviser (ICZN, 1985: Article 24), chose *B. morawitzianus* as the name for the species.

Bombus (Ps.) campestris (Panzer)
  campeftris (Panzer, 1801(74):11 [*Apis*])
  Varius (Lepeletier, 1832:381 [*Psithyrus*])
  flavus (Pérez, 1884:265 [*Psithyrus*])
  flavo-thoracicus (Hoffer, 1889:49 [*Psithyrus*])
  ?*šusterai* (Tkalcü, 1959:251 [*Psithyrus*]) examined, not of May, 1944:267 (= *B. maxillosus* Klug) (provisional synonym)
  ?*susteraianus* (Tkalcü, 1977:224 [*Psithyrus*]) replacement name for *susterai* Tkalcü, 1959:251 (provisional synonym)

● TAXONOMIC STATUS.   I am unaware of any reason (other than minor differences) why *B. campestris* and *B. susteraianus* should not be considered conspecific.

Bombus (Ps.) bellardii (Gribodo)
  Bellardii (Gribodo, 1892:108 [*Psithyrus*]) examined
  pieli (Maa, 1948:29 [*Psithyrus*]) examined, **new synonym**
  tajushanensis (Pittioni, 1949:277 [*Psithyrus*]) examined, not of Pittioni, 1949:244 (= *B. kulingensis* Cockerell), **new synonym**

● TAXONOMIC STATUS.   *B. bellardii*, *B. pieli* and *B. tajushanensis* are closely similar in morphology and I am unaware of any reason why these nominal taxa should not be considered conspecific.

○ NOMENCLATURE.   For this species, the oldest available name is *B. bellardii*, which becomes the valid name. The only subsequent publications using the name *B. pieli* of which I am aware are by Maa (1948), Sakagami (1972), Tkalcü (1987) and Williams (1991), so this change of valid name is not a serious disruption of common usage.

Bombus (Ps.) norvegicus (Sparre-Schneider)✪
  norvegicus (Sparre-Schneider, 1918:40 [*Psithyrus*]) not of Friese, 1911:571 (= *B. monticola* Smith)
  transbaicalicus (Popov, 1927:269 [*Psithyrus*])

○ NOMENCLATURE.   With *Psithyrus* regarded as being a subgenus of the genus *Bombus* (Williams, 1991, 1995), *P. norvegicus* Sparre-Schneider (1918) becomes a junior secondary homonym in *Bombus* of *B. lapponicus* var. *norvegicus* Friese (1911) (deemed subspecific, see ICZN, 1985: Article 45g(ii)), and therefore the name *P. norvegicus* Sparre-Schneider is invalid (ICZN, 1985: Article 57c). For this species, the oldest available name of which I am aware is *P. norvegicus* var. *transbaicalicus* Popov, 1927 (deemed to be subspecific, see ICZN, 1985: Article 45g(ii)), so *B. transbaicalicus* would become the valid name.

✪ APPLICATION TO ICZN.   Although *B. transbaicalicus* is the oldest available name for this species, the name *B. norvegicus* has been in common use for the species since 1947 (e.g. Faester & Hammer, 1970; Delmas, 1976; Ito & Tadauchi, 1981; Pekkarinen *et al.*, 1981; Reinig, 1981; Løken & Framstad, 1983; Rasmont, 1983; Løken, 1984; Ito, 1985; Pekkarinen & Teräs, 1993; Rasmont *et al.*, 1995). It is suggested that, in the interests of stability, an application be made to ICZN to use its Plenary Power to suppress the senior homonym (ICZN, 1985: Article 79) (see the comments on *B. muscorum*). However, the consequence of this action would be that *norvegicus* Friese would no longer be available for a subspecies of *B. monticola*.

Bombus (Ps.) fernaldae (Franklin)
  fernaldæ (Franklin, 1911:164 [*Psithyrus*]) examined

Bombus (Ps.) flavidus Eversmann

flavidus Eversmann, 1852:131
lissonurus (Thomson, 1872:49 [Apathus])

● TAXONOMIC STATUS. Rasmont (1988) reports
that the Pyrenean population of *B. flavidus* is
morphometrically distinct from the disjunct Scan-
dinavian population (comparable distinctions are not
known within its close relatives *B. norvegicus* and *B.
sylvestris*, which share these areas of distribtuion).
Nevertheless he continues to treat them as conspecific
and I shall follow this, at least until further evidence in
support of two separate species is available.

Bombus (Ps.) skorikovi (Popov)

skorikovi (Popov, 1927:267 [Psithyrus]) examined
?gansuensis (Popov, 1931:202 [Psithyrus])
?kuani (Tkalcü, 1961b:362 [Psithyrus])

Bombus (Ps.) quadricolor (Lepeletier)

Quadricolor (Lepeletier, 1832:376 [Psithyrus])
globosus (Eversmann, 1852:126 [Psithyrus])
meridionalis (Richards, 1928b:351 [Psithyrus]) not of
   Dalla Torre, 1879:13 (= B. hortorum (Linnaeus))

Bombus (Ps.) sylvestris (Lepeletier)

Sylvestris (Lepeletier, 1832:377 [Psithyrus])
Brasiliensis (Smith, 1854:385 [Apathus]) examined, not of
   Lepeletier, 1836:470 (= B. brasiliensis Lepeletier)
citrinus   (Schmiedeknecht,   1883[see   Baker,
   1996c:297]:23[407] [Psithyrus]) not of Smith, 1854:385
   (= B. citrinus (Smith))
[silvestris (Dalla Torre, 1896:571 [Psithyrus]) incorrect
   subsequent spelling]
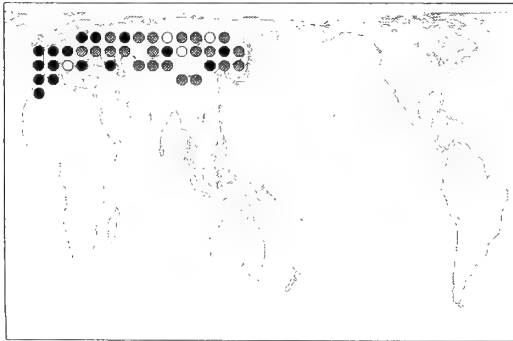
Subgenus LAESOBOMBUS Krüger

Bombus (Laesobombus) Krüger, 1920:350, type-species
   Bombus laesus Morawitz by monotypy
Agrobombus (Laesobombus) Skorikov, 1922b:20, type-
   species Bombus laesus Morawitz by monotypy
Agribombus (Laesibombus) Skorikov, 1938a:145, unjusti-
   fied emendation

Bombus (Ls.) laesus Morawitz

laesus Morawitz in Fedtschenko, 1875:3
Mocsáryi Kriechbaumer, 1877:253
?maculidorsis (Skorikov, 1922b:23 [Agrobombus]) not
   infrasubspecific after Panfilov, 1956:1328
?tianschanicus Panfilov, 1956:1327 (provisional synonym)
ferrugifer Reinig, 1971:158

● TAXONOMIC STATUS. Panfilov (1956) regarded
B. laesus, *B. mocsaryi*, *B. maculidorsis* and *B. tian-
schanicus* as separate species, differing particularly in:
(1) the colour of the pubescence on the thoracic dor-
sum; (2) the number of large punctures on the clypeus;
(3) the strength of the median keel on gastral sternum
VI; and (4) the length of the hair of the dorsum.
However, from the material I have examined (collec-
tions in London, Beijing), these character states do not
appear to be either discreet or strongly associated.
Until more evidence to the contrary is available from
critical studies of patterns of variation, I shall treat
them as parts of a single variable species.
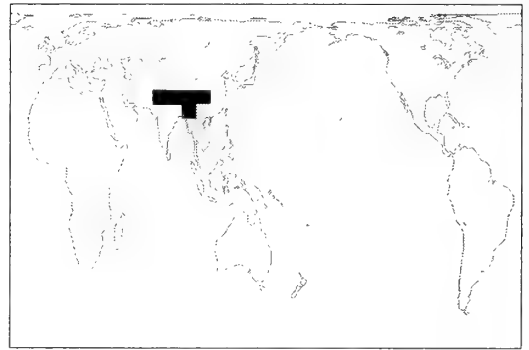
Subgenus ORIENTALIBOMBUS Richards

Bombus (Orientalibombus) Richards, 1929c:378, type-
   species *Bombus orientalis* Smith (= *Bombus
   haemorrhoidalis* Smith) by original designation
Bombus (Orientalobombus) Kruseman, 1952:102, unjus-
   tified emendation

Bombus (Or.) funerarius Smith

funerarius Smith, 1852b:47, examined
priscus (Frison, 1935:349 [Bremus])
birmanus (Tkalcü, 1989:47 [Orientalibombus]) examined

Bombus (Or.) braccatus Friese

braccatus Friese, 1905:512, examined
metcalfi (Frison, 1935:357 [Bremus]) examined

Bombus (Or.) haemorrhoidalis Smith

hæmorrhoidalis Smith, 1852a:43
orientalis Smith, 1854:402, examined
assamensis Bingham, 1897:550, examined

montivolans Richards, 1929*c*:382, examined
semialbopleuralis (Tkalcü, 1974*b*:322 [*Orientalibombus*])
cinnameus (Tkalcü, 1989:47 [*Orientalibombus*]) examined

● TAXONOMIC STATUS. Several of these nominal taxa have been treated as separate species, most recently in the case of *B. montivolans* [Burma to southern China] (e.g. Tkalcü, 1968*b*, 1989). However, aside from differences in colour pattern, they are all closely similar in morphology with a range of variation (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.
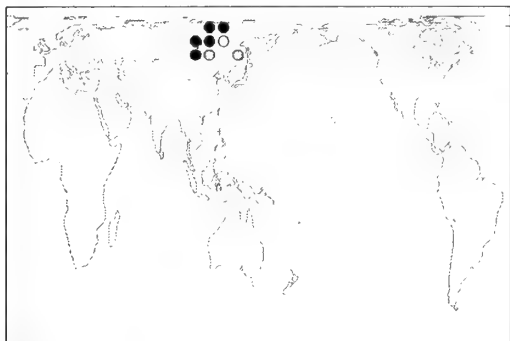
Subgenus *EXILOBOMBUS* Skorikov

Mucidobombus (Exilobombus) Skorikov, 1922*a*:150, type-species *Mucidobombus exil* Skorikov (cited as *exiln.*) (= *Bombus exil* (Skorikov)) by monotypy
Megabombus (Exilnobombus) Milliron, 1973*a*:81, unjustified emendation

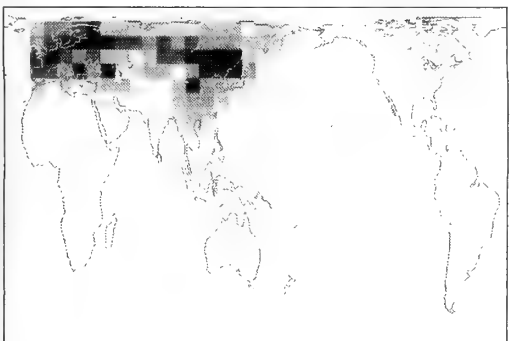### Bombus (Ex.) exil (Skorikov)

exiln. nov. (Skorikov, 1922*a*:150 [*Mucidobombus*]) [not a replacement name]
[*exul* (Skorikov, 1931:216 [*Mucidobombus*]) incorrect subsequent spelling]
exil (Milliron, 1961:56 [*Megabombus*]) justified emendation
[*exilis* Richards, 1968:254, incorrect subsequent spelling]
exul (Tkalcü, 1974*a*:42 [*Megabombus*]) unjustified emendation

Subgenus *THORACOBOMBUS* Dalla Torre

Bombus (Thoracobombus) Dalla Torre, 1880:40, type-

species *Apis sylvarum* Linnaeus (= *Bombus sylvarum* (Linnaeus)) by subsequent designation of Sandhouse, 1943:604
Bombus (Chromobombus) Dalla Torre, 1880:40, type-species *Apis muscorum* Linnaeus (= *Bombus muscorum* (Linnaeus)) by subsequent designation of Sandhouse, 1943:538
Bombus (Agrobombus) Vogt, 1911:52, type-species *Apis agrorum* Fabricius (= *Bombus pascuorum* (Scopoli)) by subsequent designation of Sandhouse, 1943:523
[*Agrabombus* Skorikov, 1914*a*:119, incorrect subsequent spelling]
Bombus (Ruderariobombus) Krüger, 1920:350, type-species *Apis ruderaria* Müller (= *Bombus ruderarius* (Müller)) by subsequent designation of Yarrow, 1971:27
Agrobombus (Adventoribombus) Skorikov, 1922*a*:150, type-species *Agrabombus adventor* Skorikov (= *Bombus filchnerae* Vogt) by subsequent designation of Sandhouse, 1943:522, **new synonym**
[*Agrobombus (Adventoriobombus)* Skorikov, 1931:218, incorrect subsequent spelling]
Agribombus Skorikov, 1938*a*:145, unjustified emendation
[*Bombus (Thoraocbombus)* Esmaili & Rastegar, 1974:52, incorrect subsequent spelling]
[*Bombus (Thoracibombus)* Schwarz *et al.*, 1996:197, incorrect subsequent spelling]

● TAXONOMIC STATUS. Richards (1968) treated *Thoracobombus* and *Adventoribombus* as separate subgenera, although he questioned whether they should be kept separate. I have followed Tkalcü (1974*a*) in treating *B. adventor* (= *B. filchnerae*) as part of a single subgenus *Thoracobombus*.

Bombus (Th.) filchnerae Vogt

Filchnerae Vogt, 1908:100, examined
adventor (Skorikov, 1914*a*:119 [*Agrabombus*])
lii Tkalcü, 1961*b*:355

Bombus (Th.) muscorum (Linnaeus)

Mufcorum (Linnaeus, 1758:579 [*Apis*]) examined
pallidus Evans, 1901:47, not of Cresson, 1863:92 (= *B. pensylvanicus* (DeGeer))
[*fulvofasciatus* Friese, 1905:520, infrasubspecific]
laevis Vogt, 1909:63
?*nigripes* Pérez, 1909:158, not of Haliday in Curtis *et al.*, 1837:321 (= *B. dahlbomii* Guérin-Méneville)
?*pereziellus* (Skorikov, 1922*a*:150 [*Agrobombus*]) replacement name for *nigripes* Pérez, 1909:158
?*bannitus* (Skorikov in Popov, 1930:98 [*Agrobombus*])
?*liepetterseni* Løken, 1973:152
celticus Yarrow, 1978:15, replacement name for *pallidus* Evans, 1901:47

● TAXONOMIC STATUS. *B. bannitus* (= *B. smithianus* of authors, a misidentification (=*B. pascuorum*)) has been regarded as a separate species by some authors (e.g. Richards, 1935; Tkalcü, 1987; Rasmont & Adamski, 1995) on the basis of its semi-melanic colour pattern and more coarsely sculptured surface of

gastral terga IV–V. However, Løken (1973: fig. 81) found no difference between these taxa in a morphometric study (other authors reporting no clear morphological differences include Richards, 1935; Alford, 1975; Pekkarinen, 1979; Rasmont, 1982; Baker, 1996*a*). Furthermore, I have collected many specimens with a range of intermediate colour patterns on the Isle of Skye in western Scotland. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

B. pereziellus has also been regarded as a separate species by Rasmont & Adamski (1995), because of its dark colour pattern (even darker than *B. bannitus*, *B. pereziellus* has the thoracic dorsum black rather than red-brown, and has more black hairs on gastral tergum II, whereas these black hairs tend to be more frequent on tergum I for *B. bannitus*) and because it is endemic to the island of Corsica. Morphologically it was considered by Rasmont (1982) to show no perceptible differences from *B. muscorum* or *B. bannitus*. Furthermore, a male with a colour pattern apparently intermediate between *B. muscorum* and *B. pereziellus* is mentioned by Delmas (1976:271). Depending on the species concept embraced, some differences might be expected for a peripheral population such as this even if it were conspecific and I shall treat them as parts of a single variable species. Further evidence is awaited.

O   NOMENCLATURE.   Richards (1935, 1968), Yarrow (1968) and Løken (1973) recognised that none of the admissable syntypes in the Linnean collection agreed with the traditional interpretation of *B. muscorum*, which is very rare in the parts of Sweden where Linnaeus collected (Richards, 1935; Løken, 1973; Day, 1979), but took no action. When Day (1979) came to fix the application of the name, he had no reason to believe that Linnaeus had not described his *A. muscorum* from the syntype specimen that was subsequently described as lectotype (= *B. humilis* Illiger).

To reaffirm the traditional usage of *B. muscorum*, a case was made to ICZN by Løken *et al.* (1994). This sought an Opinion from ICZN (ICZN, 1996) that set aside by use of its Plenary Power (ICZN, 1985: Articles 78b, 79) the lectotype designation for *A. muscorum* by Day from application of the Code (ICZN, 1985) and then designated a neotype (ICZN, 1996: 64) to conserve the traditional usage of the name for even the narrowest concept of the taxon (ICZN, 1985: Article 75).

Bombus (Th.) anachoreta (Skorikov)
    anachoreta (Skorikov, 1914*a*:121 [*Agrobombus*])

Bombus (Th.) opulentus Smith
    opulentus Smith, 1861:153, examined

Bombus (Th.) zonatus Smith
    zonatus Smith, 1854:389

Bombus (Th.) humilis Illiger❍
    fulveſcens (Schrank, 1802:367 [*Apis*])
    ?*humilis* Illiger, 1806:171
    ?*tristis* Seidl, 1837:69
    ?*variabilis* Schmiedeknecht, 1878:424, not of Cresson,
        1872:284 (= *B. variabilis* (Cresson))
    ?*subbaicalensis* Vogt, 1911:42,54

O   NOMENCLATURE.   When Day (1979) came to fix the application of *A. muscorum* Linnaeus (see the comments on *B. muscorum*), he had no reason to believe that Linnaeus had not described this taxon from the syntype specimen that was subsequently described as lectotype (= *B. humilis* Illiger). This action brought *B. humilis* Illiger into subjective junior synonymy with *B. muscorum* (Linnaeus).

To reaffirm the traditional usage of *B. muscorum* and *B. humilis*, a case was made to ICZN by Løken *et al.* (1994). This sought an Opinion from ICZN (ICZN, 1996) that set aside by use of its Plenary Power (ICZN, 1985: Articles 78b, 79) the lectotype designation for *A. muscorum* by Day from application of the Code (ICZN, 1985) and then designated a neotype (ICZN, 1996: 64) to conserve the traditional usage of *B. muscorum* and *B. humilis* (ICZN, 1985: Article 75).

However, Warncke (1986) recognised *B. fulvescens* (Schrank) as questionably conspecific with *B. humilis*. I have seen no type specimens, but the description is consistent with this interpretation. *B. fulvescens* is therefore likely to be the oldest available name for this species.

✪   APPLICATION TO ICZN.   Although *B. fulvescens* may be the oldest available name for the present interpretation of this species, the name *B. humilis* has been in common use for the species since 1947 (e.g. case and references in Løken *et al.*, 1994). In contrast, I know of no publications using the name *B. fulvescens* (Schrank) since 1947. Warncke (1986:98) followed the listing of this name with 'Art. 23b', which is a reference to purpose of the Principle of Priority (ICZN, 1985). I agree that, in the interests of stability, an application be made to ICZN to use its Plenary Power to suppress the unused senior synonym (ICZN, 1985: Article 79) (see the comments on *B. muscorum*).

Bombus (Th.) deuteronymus Schulz
    senilis Smith, 1879:131, examined, not of Fabricius,
        1775:382 (= *B. pascuorum* (Scopoli))
    deuteronymus Schulz, 1906:267, replacement name for

senilis Smith, 1879:131
velox (Skorikov, 1914a:120 [Agrobombus])
[superequester (Skorikov, 1914c:405 [Agrobombus])
   infrasubspecific]
superequester (Skorikov, 1925:116 [Agrobombus])
bureschi Pittioni, 1939b:1, examined

Bombus (Th.) schrencki Morawitz

Schrencki Morawitz, 1881:123
Schrencki Morawitz, 1881:250, redescribed
konakovi Panfilov, 1956:1330

?Bombus (Th.) honshuensis (Tkalců)

honshuensis (Tkalců, 1968a:47 [Megabombus])

● TAXONOMIC STATUS. B. honshuensis and B. schrencki have allopatric distributions in northern Japan (Sakagami & Ishikawa, 1969; Ito & Munakata, 1979: fig. 6; Ito, 1993), with B. honshuensis being possibly a disjunct peripheral population of B. schrencki. The two taxa are closely similar, and yet despite some variation in morphology, apparently consistent differences have been described (Tkalců, 1968a; Sakagami & Ishikawa, 1972). Nonetheless, some differences might be expected even if they were conspecific, depending on the species concept accepted (see the comments on B. ruderatus), so further evidence is awaited.

Bombus (Th.) impetuosus Smith

impetuosus Smith, 1871:249, examined
Potanini Morawitz, 1890:350, new synonym
yuennanensis Bischoff, 1936:14, examined
combai Tkalců, 1961b:357, new synonym

● TAXONOMIC STATUS. The white-banded B. potanini is morphologically closely similar to the yellow-banded B. impetuosus. Some individuals from Sichuan are intermediate in colour pattern in that they have the pale bands of the thorax and gastral tergum I white, and the pale band of tergum II yellow. There is considerable variation in the male gonostylus, but this variation appears to overlap between the the colour forms and I shall treat them as parts of a single variable species. S.-f. Wang and J. Yao (in litt.) also believe that the two taxa may be conspecific. Further evidence is awaited.

Bombus (Th.) remotus (Tkalců)

remotus (Tkalců, 1968a:45 [Megabombus]) examined

Bombus (Th.) pseudobaicalensis Vogt

Pseudobaicalensis Vogt, 1911:43,53
gilvus (Skorikov, 1925:117 [Agrobombus])

Bombus (Th.) hedini Bischoff

unicolor Friese, 1905:514, examined, not of Kriechbaumer, 1870:159 (= B. maxillosus Klug)
hedini Bischoff, 1936:15

Bombus (Th.) ruderarius (Müller)

ruderaria (Müller, 1776:165 [Apis])
Derhamella (Kirby, 1802:363 [Apis]) examined
montanus Lepeletier, 1836:463
simulatilis Radoszkowski, 1888:317, examined

Bombus (Th.) inexspectatus Tkalců

lutescens Krüger, 1939:105, not of Pérez, 1890:154 (= B. flavidus Eversmann)
inexspectatus (Tkalců, 1963:187 [Agrobombus])
[inexpectatus (Reinig, 1981:161 [Megabombus]) incorrect subsequent spelling]

COMMENT.   On the grounds of its peculiar morphology, B. inexspectatus has been suggested to be an obligate social parasite in colonies of other Bombus species, with B. ruderarius being the most likely host (Yarrow, 1970). As yet, there is no direct evidence for this behaviour (Rasmont, 1988). See the comments on the subgenus Psithyrus and on B. hyperboreus.

Bombus (Th.) sylvarum (Linnaeus)

fylvarum (Linnaeus, 1761:425 [Apis]) examined
Daghestanicus Radoszkowski, 1877a:vii
Dagestanicus Radoszkowski, 1877b:211, redescribed

Bombus (Th.) veteranus (Fabricius)

veterana (Fabricius, 1793:324 [Apis])
arenicola Thomson, 1872:31

Bombus (Th.) mlokosievitzii Radoszkowski

Mlokosievitzii Radoszkowski, 1877a:viii
Mlokassewiczi Radoszkowski, 1877b:212, redescribed
pérezi Vogt, 1911:55, not of Schulthess-Rechberg, 1886:275 (= B. perezi (Schulthess-Rechberg))
vogtiellus (Tkalců, 1977:224 [Megabombus]) replacement name for perezi Vogt, 1911:55
[mlokossowiczi (Reinig, 1981:161 [Megabombus]) incorrect subsequent spelling]

○ NOMENCLATURE.   There are particularly many incorrect subsequent spellings of B. mlokosievitzii.

Bombus (Th.) pascuorum (Scopoli)

Pafcuorum (Scopoli, 1763:306 [Apis])
fenilis (Fabricius, 1775:382 [Apis])
agrorum (Fabricius, 1787:301 [Apis]) not of Schrank, 1781:397 (= B. mesomelas Gerstaecker)
thoracicus Spinola, 1806:30

arcticus Dahlbom, 1832:50, not of Quenzel in Acerbi, 1802:253 (= *B. hyperboreus* Schönherr)
cognatus Stephens, 1846:17, examined
smithianus White, 1851:158

● TAXONOMIC STATUS. Warncke (1986) listed *B. cognatus* as a synonym of *B. muscorum*, possibly following Stephens (1846), who wrote of *B. cognatus*: 'Closely allied to Bo. Muscorum, of which the examples I possess may be immature specimens'. Pagliano (1995) listed *B. cognatus* as a species separate from both *B. muscorum* and *B. pascuorum*, but without any explanation.

Saunders (1896:366–367) wrote 'I have re-examined the type of *cognatus*, Steph., . . . F. Smith placed it in the British Museum collection. . . .' Saunders considered this specimen to be conspecific with *B. agrorum* (Fabricius), continuing: 'It is certainly not the species known on the Continent as *cognatus*'.

A female in the NHM collection bears the following labels: (1) a red-edged printed 'Type'; (2) *'cognatus.'* in handwriting identical to that of F. Smith; (3) '= agrorum / I.H.H.Y.' in handwriting identical to that of I. Yarrow; (4) 'B.M. Type / HYM. / 17B.1163'. I have examined this specimen and am unaware of any reason why it should not be considered the type of *B. cognatus* and (ignoring minor differences in colour pattern) conspecific with *B. pascuorum*.

○ NOMENCLATURE. Løken (1973) listed *B. cognatus* Stephens, 1846, as a *nomen nudum*, citing Sherborn (1925). However, the reference by Sherborn is to an earlier paper by Stephens (1829), so this does not affect the use of the name *B. cognatus* Stephens, 1846.
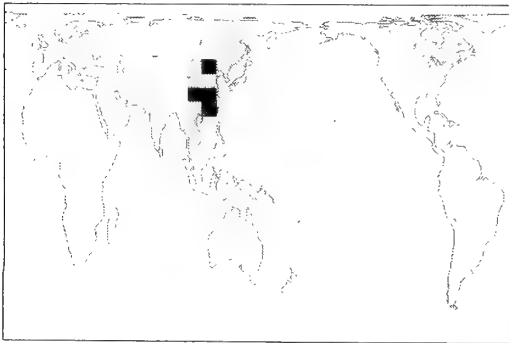
Subgenus ***TRICORNIBOMBUS*** Skorikov
Agrobombus (Tricornibombus) Skorikov, 1922a:151, type-species *Bombus tricornis* Radoszkowski by monotypy
Bombus (Tricornibombus) Tkalcü, 1960:70

Bombus (Tr.) tricornis Radoszkowski
tricornis Radoszkowski, 1888:319, examined

Bombus (Tr.) atripes Smith
atripes Smith, 1852a:44, examined

Bombus (Tr.) imitator Pittioni
imitator Pittioni, 1949:251, examined
flavescens Pittioni, 1949:254, not of Smith, 1852a:45 (=*B. flavescens* Smith)

Subgenus ***FERVIDOBOMBUS*** Skorikov
Fervidobombus Skorikov, 1922a:153, type-species *Apis fervida* Fabricius (= *Bombus fervidus* (Fabricius)) by subsequent designation of Frison, 1927:69
Bombus (Fervidobombus) Franklin, 1954:47
Bombus (Digressobombus) Laverty et al., 1984:1051, type-species *Megabombus digressus* Milliron (= *Bombus digressus* (Milliron)) by original designation

● TAXONOMIC STATUS. The subgenus *Digressobombus* was described subsequent to Richards (1968). I have treated *Digressobombus* as part of a single subgenus *Fervidobombus* (Williams, 1995), as has Labougle (1990). While this study found no evidence for monophyly of the combined group, I believe that this is more likely (unpublished data) than monophyly of the subgenus *Fervidobombus* excluding *Digressobombus*.

COMMENT. This is the only early-diverging and large subgenus of bumble bees to occur in the New World other than the subgenus *Psithyrus*. Although it makes up only a small part of the fauna of America north of Mexico, it makes up most of the low- to mid-altitude bumblebee fauna of Central and South America. It also includes the only species of bumble bees genuinely occurring in tropical lowland wet forest (e.g. Moure & Sakagami, 1962; Milliron, 1973a; Cameron & Whitfield, 1996). The species with more temperate distributions appear to occupy similar habitats and show similar flower-depth preferences to species of subgenera such as *Thoracobombus* and *Megabombus* in the Old World.

Bombus (Fv.) fervidus (Fabricius)
feruida (Fabricius, 1798:274 [*Apis*])
?*Californicus* Smith, 1854:400, examined
Dumoucheli Radoszkowski, 1884:78
sonomæ Howard, 1902:pl. II

● TAXONOMIC STATUS. *B. fervidus* and *B.*

californicus have been regarded both as conspecific (e.g. Milliron, 1973*a*; Labougle, 1990) and as separate species (e.g. Franklin, 1913; Stephen, 1957; Thorp *et al.*, 1983; Poole, 1996). Both Franklin (1913:239) and Stephen (1957) also considered the possibility that they are conspecific as quite reasonable.

Many specimens from the north west of North America show a reduction in the extent of the yellow bands on the scutellum and gastral terga I–III and appear to be intermediate or recombinant individuals. Indeed, Stephen's (1957:32) figure 2 shows several patterns that could represent a continuum in variation between the two forms. Thorp *et al.* (1983) found no intermediate females in California, although some of the males of *B. californicus* were said to approach the pattern of *B. fervidus*.

In view of the existence of apparent intermediates between these nominal taxa in at least part of their range, they are treated here as likely to be conspecific. More evidence is awaited.

O NOMENCLATURE. *Apis feruida* is the original spelling in Fabricius (1798). The orthography of this publication employs 'u' in place of 'v' widely, a common practice of the period. This convention has since changed and subsequent authors have consistently used 'v' for *B. fervidus*.

In fact, whatever the interpretation of the Code, pragmatically it matters little which spelling of *fervidus* is used unless either of the spellings were to be published as the name of another taxon in *Bombus*. See the comments on the spelling of *B. pensylvanicus*.

Bombus (Fv.) pensylvanicus (DeGeer)

penfylvanica (DeGeer, 1773:575 [*Apis*])
americanorum Fabricius, 1804:346
?*sonòrus* Say, 1837:413
pallidus Cresson, 1863:92
Pensylvanicus Cresson, 1863:94
flavodorsalis Franklin, 1913:409
pennsylvanicus Hurd, 1979:2204, unjustified emendation

● TAXONOMIC STATUS. *B. pensylvanicus* and *B. sonorus* have been regarded both as conspecific (e.g. Milliron, 1973*a*; Labougle *et al.*, 1985; Labougle, 1990; Poole, 1996) and as separate species (e.g. Franklin, 1913 [but see p. 239]; Stephen, 1957; Thorp *et al.*, 1983; S. Cameron *in litt.*).

From the few males from the United States (not Mexico) that I have examined in detail, there appear to be subtle differences in the male genitalia (e.g. in the shape of the penis valve head). However, Labougle (1990) reports that the two 'forms are geographically intermixed in México, and chromatically intermediate specimens occur, mainly in northeastern México and southwestern Texas'. He went on to say that 'In fact, it is sometimes difficult to place a Mexican specimen in either subspecies because there are specimens with the

coloration of the scutellum and the punctation of the clypeus intermediate between the two taxa. Average differences of certain proportions are found . . . but do not differentiate all specimens'. G. Chavarría (pers. com.) also believes that intermediate specimens occur in Mexico and that they are conspecific. Taking an extreme viewpoint, it is even possible to see the 'typical' *B. sonorus* colour pattern as intermediate between *B. pensylvanicus* (in the strict sense) and the extreme pale form that has the thoracic dorsum and gastral tergum I entirely yellow (*flavodorsalis*, see Thorp *et al.*, 1983: fig. 137b).

In view of the existence of apparent intermediates between these nominal taxa in at least part of their range, they are treated here as likely to be conspecific. More evidence is awaited.

O NOMENCLATURE. *Apis penfylvanica* is the original spelling in DeGeer (1773). The orthography of this publication employs 'ʃ' in place of 's' widely, a common practice of the period. This convention has since changed and subsequent authors (e.g. Cresson, 1863) have consistently used 's' for *B. pensylvanicus*.

Technically, according to the Code (ICZN, 1985: Article 32b), *pensylvanicus* with just two 'n's is the correct original spelling, to be preserved unaltered unless it is demonstrably incorrect under Article 32c. Article 32c(ii) states that clear evidence of an inadvertent error is only admissable if it lies within the original publication, *without recourse to any external source of information* (DeGeer, 1773, spelled Penʃylvanie and *penfylvanica* consistently in this way). Any intentional change to that spelling in a subsequent publication is an unjustified emendation under Article 33b(iii).

In fact, whatever the interpretation of the Code, pragmatically it matters little which spelling of *pensylvanicus* is used unless either of the spellings were to be published as the name for another taxon in *Bombus*. No doubt many will prefer to use *B. pennsylvanicus*, although the name does appear as *B. pensylvanicus* in the recent checklist by Poole (1996) (and by analogy, the similar spelling of *Vespula pensylvanica* (Saussure) has been accepted, e.g. by Akre *et al.*, 1980; Edwards, 1980).

COMMENT. This species was deliberately introduced into the Philippines, but is not known to have persisted (Frison, 1925*b*).

Bombus (Fv.) excellens Smith

excellens Smith, 1879:133, examined

Bombus (Fv.) dahlbomii Guérin-Méneville

Dahlbomii Guérin-Méneville, [1835, see Cowan, 1971:29]:pl.75
nigripes Haliday in Curtis *et al.*, 1836:321

O NOMENCLATURE.   Cowan (1971), considering Guérin-Méneville's insect volume, states that 'it is quite certain that valid publication [of the *Insectes* text] under the International Code of Nomenclature did not take place until August or September 1844.' However, he lists plate 75, on which *B. dahlbomii* appears as figure 3 together with a legend containing the name, as having been published in livraison 39 in June 1835. This meets the criteria for valid publication (ICZN, 1985: Article 8). Therefore *B. dahlbomii* is the oldest available name for this species.

Bombus (Fv.) morio (Swederus)

morio (Swederus, 1787:283 [*Apis*]) examined
velutinus Illiger, 1806:175
violaceus Lepeletier, 1836:473
carbonarius Handlirsch, 1888:241, not of Menge, 1856:27 [fossil]
Kohli Cockerell, 1906:75, replacement name for *carbonarius* Handlirsch, 1888:241

Bombus (Fv.) diligens Smith

diligens Smith, 1861:154, examined
dolichocephalus Handlirsch, 1888:244

Bombus (Fv.) opifex Smith

opifex Smith, 1879:133, examined

Bombus (Fv.) rubriventris Lepeletier

rubriventris Lepeletier, 1836:472, examined

● TAXONOMIC STATUS. *B. rubriventris* is known from a single female specimen from 'St. Domingue' (?= São Domingos, Goiás) (Milliron, 1973*a*). This specimen has dark brown wings and the pubescence is black, except that most of the hairs of the thorax are grey-tipped, and the hairs of gastral terga II–IV are bright 'coppery' red.

This colour pattern resembles the Andean *B. excellens*, although the pubescence of *B. rubriventris* is much shorter and more even; the oculo-malar area is nearly square rather than nearly twice as long as the basal breadth of mandible; and tergum VI is raised subapically. Franklin (1913) had not seen *B. rubriventris* but suggested that it was probably a 'freak specimen' of *B. carolinus* (a misidentification, = *B. excellens*). Milliron (1973*a*) had examined *B. rubriventris* and considered the morphological characters to be very much like those of *B. bellicosus*. However, *B. rubriventris* can be distinguished by the much finer punctures in the centre of the clypeus and by an absence of a median ridge on tergum VI. I consider *B. rubriventris* to be more similar in these characters to *B. opifex*, although it can be distin-

guished from that species by a pair of characteristically slightly recessed bands of fine punctures extending anteriorly from the ocello-ocular areas and by a shallow median groove in the subapically raised area of tergum VI.

The colour pattern is very distinctive among non-Andean bumble bees in South America and does not appear to be the result of abnormal colour development. The specimen has had the gaster glued back into place, although the characters of both the head and gaster appear to be distinctive, so there is no reason to believe that the specimen is a composite and not genuine.

COMMENT.   Milliron (1973*a*) researched the history of this specimen and believed that it may have been collected as early as 1800. He concluded that it was probably a highland species from southeastern Brazil and that it may now be extinct. If so, and accepting that it is very difficult to establish the absence of a species, this would be one of the few known cases of complete extinction of an insect species.

Bombus (Fv.) bellicosus Smith

thoracicus Sichel, 1862:121, not of Spinola, 1806:30 (=*B. pascuorum* (Scopoli))
bellicosus Smith, 1879:131, examined
Emiliae Dalla Torre, 1890:139, replacement name for *thoracicus* Sichel, 1862:121

Bombus (Fv.) pullatus Franklin

pullatus Franklin, 1913:122

Bombus (Fv.) transversalis (Olivier)

tranfverfalis (Olivier, 1789:65 [*Apis*])
Cajennenfis (Fabricius, 1798:273 [*Apis*])
incarum Franklin, 1913:131

Bombus (Fv.) atratus Franklin❂

azurea (Christ, 1791:129 [*Apis*])
?*atratus* Franklin, 1913:118, not of Friese, 1911:572 (=*B. mucidus* Gerstaecker) (provisional synonym)
?*niger* Franklin, 1913:120, examined (provisional synonym)
?*nigriventris* Friese, 1913:87 (provisional synonym)

● TAXONOMIC STATUS. At least four species of the subgenus *Fervidobombus* from Central and South America have many individuals for which the pubescence is almost entirely black. The genitalia of the males are quite distinctive, but association of the conspecific females with these males has caused problems.

In the original description of *B. niger*, Franklin stated that '*atratus* is possibly the male of *niger*' (p.

121), whereas in the original description of *B. atratus* he stated both that '*Niger* may represent the females of this species' (p. 118) and that 'This may be the true male of *kohli*' (p. 119). *B. niger* was described from a syntype series of four queens and four workers, of which one queen in the Smithsonian collection carries, amongst others, a red label 'LECTOTYPE / *Bombus* / *niger* Franklin / H.E.Milliron '59' and a label 'Boquete / Chiriqui'. This Central American locality was mentioned by Franklin, but is outside the known distribution of the species (Milliron, 1973a) to which the specimen belongs. In my opinion, this lectotype of *B. niger* is not conspecific with *B. pullatus* (contrary to the suggestion by Labougle, 1990, see also Milliron, 1962) but rather is conspecific with *B. atratus* Franklin.

Another possibility is that this variable species is the *Apis azurea* of Christ (1791). I know of no type specimens and the type locality was said to be in Africa ('Ist in Afrika am Vorgebürg der guten Hofnung zu Haus'). The description and figure of the colour pattern do not agree with any African bees that I have been able to trace, but do resemble closely the yellow-banded individuals of the South American *B. niger*, the Central American *B. medius* Cresson, and the South American *B. transversalis* (Olivier) (although for the last named species the yellow bands on the thorax are usually broader). Among the specimens to hand, the wings do appear slightly more 'Schwarzblaue' for *B. niger*, as described for *A. azurea*, although these grounds seem slim justification from which to establish the application of a name.

O NOMENCLATURE. *B. azureus* is possibly the oldest available name for this species.

Milliron (1962), without mention of the name *B. azureus*, first regarded *B. atratus* and *B. niger* as conspecific and, following the Principle of First Reviser (ICZN, 1985: Article 24), chose *B. atratus* as the valid name for the species.

Unfortunately, *B. atratus* Franklin, 1913, is a junior primary homonym of *B. mucidus* var. *atratus* Friese, 1911 (deemed to be subspecific, see ICZN, 1985: Article 45g(ii)), therefore the name *B. atratus* Franklin is invalid (ICZN, 1985: Article 57b).

✪ APPLICATION TO ICZN. The name *B. azureus* has not been used since the original publication. The name *B. atratus* has been used for this species since 1947 (e.g. Moure & Sakagami, 1962; Sakagami & Zucchi, 1965; Sakagami *et al.*, 1967; Milliron, 1971, 1973a; Sakagami, 1976; Ito, 1985; Labougle, 1990; Varela, 1992; Silveira & Cure, 1993). It is suggested that, in the interests of stability (ICZN, 1985: Article 23b), an application be made to ICZN to use its Plenary Power to suppress both the unused senior synonym (ICZN, 1985: Article 79) and the senior homonym. This would achieve both an unambiguous, valid name for this species (see the comments on *B. muscorum*) and also

help to protect the validity of the names *B. medius* and *B. transversalis* from future change. However, the consequence of this action would be that *atratus* Friese would no longer be available for a subspecies of *B. mucidus*.

Bombus (Fv.) digressus (Milliron)
digressus (Milliron, 1962:730 [*Megabombus*]) examined

Bombus (Fv.) brasiliensis Lepeletier
brasiliensis Lepeletier, 1836:470, examined

Bombus (Fv.) steindachneri Handlirsch
Steindachneri Handlirsch, 1888:239

● TAXONOMIC STATUS. *B. medius* and *B. steindachneri* have been regarded both as separate species (Milliron, 1973a; Labougle, 1990) and as conspecific (G. Chavarría, pers. com.).

Labougle (1990) reports that 'Although the chromatic differences between *B. medius* and *B. steindachneri* are conspicuous, the male genitalia are extremely similar'. Labougle listed four character differences from the male genitalia and I can confirm two of these: (1) that the head of the penis valve of *B. steindachneri* has fewer fine teeth or serrations; and (2) that the interior process of the volsella (misinterpreted as the preapical tooth of the 'gonostylus'; for discussion of homologies see Williams, 1991) of *B. steindacheri* is narrower. However, I have examined only a few males and these characters might be expected to vary among other individuals. Labougle (1990) continued: 'The lack of chromatic and morphological intermediates supports the idea of two different species'.

Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as two separate species.

Bombus (Fv.) medius Cresson
medius Cresson, 1863:97

Bombus (Fv.) weisi Friese
laboriosus Smith, 1861:153, examined, not of Fabricius, 1804:352 (= *Emphoropsis laboriosus* (Fabricius))
weisi Friese, 1903:253, examined
nigrodorsalis Franklin, 1907:90

O NOMENCLATURE. The lectotype female of *B. weisi* by designation of Milliron (1960:98) was recognised as conspecific with *B. nigrodorsalis* by Labougle (1990) (I have examined the lectotype of *B. weisi* at the MNHU, Berlin, and agree with Labougle). He then

used *B. weisi* (the oldest available name) as the valid name for this species. However, a case could be made in favour of the use of either name.

For Labougle's (1990) use of this previously unused senior synonym to be considered by ICZN as a *prima facie* case of upsetting the use of a long-accepted name in its accustomed meaning (ICZN, 1985: Article 23b), the name *B. weisi* should not have been used in this sense in the preceding fifty years; and at least five authors should have used the junior name, *B. nigrodorsalis*, in at least ten publications during the same period (ICZN, 1985: Article 79c). As far as I am aware, no other admissable publications have used *B. weisi* (Williams, 1995, disclaimed any nomenclatural action in a list of names for material examined), although publications using the junior name *B. nigrodorsalis* Franklin for this species since 1947 are more common, including Milliron (1961, 1962, 1971, 1973a), Laverty *et al.* (1984), Labougle *et al.* (1985), Williams (1985b) and Asperen de Boer (1992b). Other such references may exist, therefore this may be seen as a borderline case, requiring an application to be made to ICZN to use its Plenary Power if suppression of the unused senior synonym, *B. weisi*, is required (see the comments on *B. muscorum*).

On the other hand, a change of valid name from *B. nigrodorsalis* to *B. weisi* does not appear to be a serious disruption of common usage, so there is no obvious need for action to retain *B. nigrodorsalis* and I have continued to use *B. weisi*.

Bombus (Fv.) trinominatus Dalla Torre

>*modestus* Smith, 1861:153, examined, not of Eversmann, 1852:134 (= *B. modestus* Eversmann)
>*trinominatus* Dalla Torre, 1890:139, replacement name for *modestus* Smith, 1861:153
>*xelajuensis* Asperen de Boer, 1992b:162, examined (provisional synonym)

● TAXONOMIC STATUS. The description of *B. xelajuensis* shows that this nominal taxon, known from a single location, diverges only slightly in colour pattern and morphology from the otherwise restricted and uncommon mountain species *B. trinominatus*. Therefore it seems most likely to be conspecific with *B. trinominatus*, with a slightly different colour pattern. However, the information available at present is not conclusive, and it remains possible that it represents a separate species, and further evidence is awaited.

Bombus (Fv.) mexicanus Cresson

>*mexicanus* Cresson, 1878:187

Bombus (Fv.) brevivillus Franklin

>*brevivillus* Franklin, 1913:119
>?*abditus* (Tkalců, 1966:271 [*Megabombus*])

● TAXONOMIC STATUS. The single known female of *B. abditus* was described as originating from 'Rep. de Guinée Beyla' (equatorial Africa). However, it is indistinguishable from *B. brevivillus* according to Sakagami (1976:427) and probably represents an introduced or mislabelled individual (Michener, 1979).
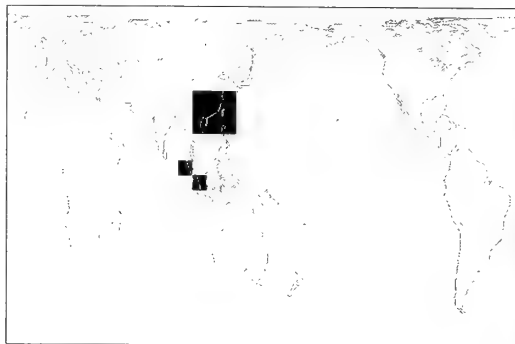
Subgenus *SENEXIBOMBUS* Frison

>*Bremus (Senexibombus)* Frison, 1930:3, type-species *Bombus senex* Vollenhoven by original designation
>[*Bombus (Senecibombus)* Kruseman, 1952:101 incorrect subsequent spelling]
>*Bombus (Senexibombus)* Richards, 1968:217

Bombus (Sx.) kulingensis Cockerell

>*kulingensis* Cockerell, 1917:266
>*tajushanensis* Pittioni, 1949:244

Bombus (Sx.) bicoloratus Smith

>*bicoloratus* Smith, 1879:132, examined

Bombus (Sx.) senex Vollenhoven

>*Senex* Vollenhoven, 1873:229

Bombus (Sx.) irisanensis Cockerell

>*irisanensis* Cockerell, 1910a:416, examined

Subgenus *DIVERSOBOMBUS* Skorikov

Bombus (Diversobombus) Skorikov, 1914c:406, type-species *Bombus diversus* Smith by subsequent designation of Sandhouse, 1943:546

Diversibombus Skorikov, 1938b:2, unjustified emendation

Bombus (Dv.) trifasciatus Smith

trifasciatus Smith, 1852a:43, examined
montivagus Smith, 1878:168, examined
montivagus Smith, 1879:131, redescribed
?*wilemani* Cockerell, 1911:100, examined
albopleuralis Friese, 1916:108, examined
?*maxwelli* Pendlebury, 1923:67, examined
mimeticus Richards, 1931b:529, examined
malaisei (Skorikov, 1938b:2 [*Diversibombus*]) not of Bischoff, 1930:4 (= *B. sporadicus* Nylander)
atropygus (Tkalcü, 1989:58 [*Megabombus*]) examined

● TAXONOMIC STATUS. Several of these nominal taxa have been treated as separate species, for example as *B. albopleuralis* (= *B. mimeticus*) [Himalaya], *B. montivagus* [northern Burma to southern China], *B. maxwelli* [Peninsular Malaysia] and *B. wilemani* [Taiwan] (Tkalcü, 1968b, 1989). However, aside from differences in colour pattern (Fig. 13), they are closely similar in morphology and show a range of variation (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall continue to treat them as parts of a single variable species.

Bombus (Dv.) longipes Friese

longipes Friese, 1905:511
hummeli Bischoff, 1936:18, examined

Bombus (Dv.) diversus Smith

diversus Smith, 1869:207, examined
tersatus Smith, 1869:207, examined

○ NOMENCLATURE. Tkalcü (1965) first explicitly regarded *B. diversus* and *B. tersatus* as conspecific and, following the Principle of First Reviser (ICZN, 1985: Article 24), chose *B. diversus* as the valid name for the species.

Bombus (Dv.) ussurensis Radoszkowski

Ussurensis Radoszkowski, 1877b:196
[*ussuriensis* Morawitz, 1881:254, incorrect subsequent spelling]

Subgenus *MEGABOMBUS* Dalla Torre

Bombus (Megabombus) Dalla Torre, 1880:40, type-species *Bombus ligusticus* Spinola (= *Bombus argillaceus* (Scopoli)) by monotypy

Bombus (Megalobombus) Schulz, 1906:267, unjustified emendation

Bombus (Hortobombus) Vogt, 1911:56, type-species *Apis hortorum* Linnaeus (= *Bombus hortorum* (Linnaeus)) by subsequent designation of Sandhouse, 1943:559

Bombus (Odontobombus) Krüger, 1917:61,65 (proposed as a section name but stated by Milliron, 1961:53, to be equivalent to his concept of the subgenus *Megabombus* Dalla Torre), type-species *Apis argillacea* Scopoli (= *Bombus argillaceus* (Scopoli)) by subsequent designation of Williams, 1995:339

[*Nortobombus* Skorikov, 1922b:map 3, incorrect subsequent spelling]

Hortibombus Skorikov, 1938a:146, unjustified emendation

Bombus (Mg.) supremus Morawitz

supremus Morawitz, 1886:196
linguarius Morawitz, 1890:351

Bombus (Mg.) gerstaeckeri Morawitz

Gerstäckeri Morawitz, 1881:242
Gerstaeckeri Hoffer, 1883:55, mandatory correction (ICZN, 1985: Article 32d)

Bombus (Mg.) consobrinus Dahlbom

consobrinus Dahlbom, 1832:49

Bombus (Mg.) tichenkoi (Skorikov)

[*tichenkoi* (Skorikov, 1922a:156 [*Hortobombus*]) published without description]
tichenkoi (Skorikov, 1925:115 [*Hortobombus*])

?*yezoensis* Matsumura, 1932:pl. 1
?*przewalskiellus* (Skorikov, 1933*a*:59 [*Hortobombus*])
kurilensis Sakagami, 1954:92

● TAXONOMIC STATUS. *B. tichenkoi* and *B. yezoensis* have apparently been regarded both as conspecific and as separate species.

Sakagami (1954) described *kurilensis* as a (semi-melanic) subspecies of what he called '*B. tersatus*' (a misidentification, = *B. diversus*). Following Tkalců (1962), Sakagami subsequently identified his '*B. tersatus*' as *B. yezoensis* (Ito & Sakagami, 1980). In this later paper he went on to recognise *kurilensis* as conspecific with *B. tichenkoi*, but then, despite having regarded *kurilensis* as a subspecies of what he now believed to be *B. yezoensis* in the earlier paper, listed *B. tichenkoi* as a species separate from *B. yezoensis*. The apparent contradiction was not explained, although morphological comparisons between these taxa, *B. argillaceus* and *B. sushkini* were tabulated (which show primarily that *B. argillaceus* is very different). He even noted the allopatric distributions of *B. tichenkoi* and *B. yezoensis* between the northern and southern Kurile Islands and the 'resemblance of *tichenkoi* and dark individuals of *yezoensis*, especially in workers.'

Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat *B. tichenkoi* and *B. yezoensis* as parts of a single variable species.

Bombus (Mg.) sushkini (Skorikov)

[*saltuarius* (Skorikov, 1922*a*:156 [*Hortobombus*]) published without description]
sushkini (Skorikov, 1931:235 [*Hortobombus*]) examined
saltuarius (Skorikov, 1931:235 [*Hortobombus*])

● TAXONOMIC STATUS. *B. sushkini* and *B. saltuarius* have been regarded both as conspecific (Bischoff, 1936) and as separate species (Skorikov, 1931; Tkalců, 1974*a*). I have as yet seen no evidence that more than one species is involved. More evidence is awaited.

○ NOMENCLATURE. Skorikov (1931) provided the first valid publication of the names *B. sushkini* and *B. saltuarius* as two separate species. Subsequently, Bischoff (1936) regarded the two as conspecific and, following the Principle of First Reviser (ICZN, 1985: Article 24), chose *B. sushkini* as the valid name for the species.

Bombus (Mg.) portchinsky Radoszkowski

Portchinskij Radoszkowski, 1883:208
Portchinsky Radoszkowski, 1883:208[210], 209[211], 210[212]

○ NOMENCLATURE. Radoszkowski (1883) published two different spellings of *B. portchinsky*,

repeating this second form several times (page numbers 207 and 208 are repeated twice for different pages, so the two spellings do not occur on the same page). Precedence of the correct original spelling should be determined using the Principle of the First Reviser (ICZN, 1985: Article 24), but to date I have not found an author who has correctly cited both names and then chosen one in precedence to the other (there are many incorrect subsequent spellings, e.g. Dalla Torre, 1896). Since the second form of the name has been used more recently (e.g. Baker, 1996*b*), I suggest that it should be given precedence. This form is a simple noun in apposition and so retains the same ending whatever the gender of the generic name with which it is combined (ICZN, 1985: Article 31b(ii)).

Bombus (Mg.) hortorum (Linnaeus)

hortorum (Linnaeus, 1761:424 [*Apis*]) examined
meridionalis Dalla Torre, 1879:13
hispanicus Pittioni, 1939*c*:244, not of Friese, 1911:571 (= *B. monticola* Smith)
asturiensis (Tkalců, 1975:181 [*Megabombus*]) replacement name for *hispanicus* Pittioni, 1939*c*:244
?*reinigiellus* (Rasmont, 1983:43 [*Megabombus*])

● TAXONOMIC STATUS. The Spanish *B. asturiensis* has been considered a separate species from *B. hortorum* by Rasmont (1983, 1988), although they have been treated as conspecific by Pittioni (1939*c*), Tkalců (1975), Ornosa (1986*a*, 1986*b*, 1991), Castro (1988, 1993) and, more recently, by Rasmont *et al.* (1995). The two taxa are closely similar.

The Spanish *B. reinigiellus* has also been considered both as conspecific with *B. hortorum* (Castro, 1987) and as a separate species (e.g. Rasmont, 1983; Castro, 1988; Ornosa, 1991). The two taxa are allopatric (Rasmont, 1983), with *B. reinigiellus* being narrowly restricted to the Sierra Nevada of Spain, possibly as a disjunct peripheral population. *B. reinigiellus* is closely similar to *B. hortorum*, although subtle differences in characters of colour and morphology have been described (e.g. Rasmont, 1983; Castro, 1988; Ornosa, 1991). From the material I have examined, the morphological differences appear to be analogous to the variation between mainland and island populations of *B. terrestris* (see the comments on *B. terrestris*).

Depending upon the species concept embraced, such subtle differences as those between *B. reinigiellus* and *B. hortorum* might be expected even within a single population and I shall treat all three taxa as conspecific for the present. More evidence is awaited.

COMMENT. *B. hortorum* has been introduced into New Zealand (e.g. Gurr, 1957; Macfarlane & Gurr, 1995) (see the comments on *B. ruderatus, B. subterraneus* and *B. terrestris*). It occurs in Iceland, where it has also probably been introduced (Prŷs-Jones *et al.*, 1981) (see the comments on *B. lucorum*).

Bombus (Mg.) argillaceus (Scopoli)
  Argillacea (Scopoli, 1763:305 [*Apis*])
  ligusticus Spinola, 1806:29

?Bombus (Mg.) ruderatus (Fabricius)
  ruderata (Fabricius, 1775:380 [*Apis*]) examined
  Perniger (Harris, 1776:131 [*Apis*])
  villarricaensis Asperen de Boer, 1992a:133

● TAXONOMIC STATUS. *B. argillaceus* and *B. ruderatus* are similar in most characters and differ principally in the colour patterns of the queens (e.g. Reinig, 1939; Fig. 11). Scholl, Obrecht & Zimmermann (1992) found that hybrid queens between *B. argillaceus* and *B. ruderatus* do occur in parts of southeastern France, but are very rare. Whether or not the taxa on either side of this hybrid zone are considered to be separate species therefore depends on which species concept is preferred. Because Scholl, Obrecht & Zimmermann (1992) estimated that only slight gene flow is occurring, I shall continue to treat them as separate species.

COMMENT. This species has been introduced into New Zealand (e.g. Gurr, 1957; Macfarlane & Gurr, 1995) (see the comments on *B. hortorum, B. subterraneus* and *B. terrestris*) and Chile (Arretz & Macfarlane, 1982; Asperen de Boer, 1993b). *B. ruderatus* also occurs on the Azores (which have never had a continental connection), where it may be presumed to be an introduction (Yarrow, 1967).

Bombus (Mg.) czerskii Skorikov
  czerskii Skorikov, 1910b:413, examined

Bombus (Mg.) koreanus (Skorikov)
  koreanus (Skorikov, 1933a:59 [*Hortobombus*])
  pekingensis Bischoff, 1936:21, examined
  ?notocastaneus Tkalcŭ, 1961a:52 (provisional synonym)

● TAXONOMIC STATUS. *B. notocastaneus* was described from a single male from Hubei. From the description, it appears most likely to be conspecific with *B. koreanus*.

Bombus (Mg.) melanopoda Cockerell
  melanopoda Cockerell, 1910a:416, examined

● TAXONOMIC STATUS. *B. melanopoda* is known from a single female specimen (labelled 'Sumatra', reverse '92.182.') in the NHM collection in London.

According to the accessions catalogue, the number on the label of this specimen refers to 8 Hymenoptera presented in November 1892 by H. O. Forbes. The area of origin is given as Borneo, although this has been crossed out and Sumatra added. Forbes' (1885) account of his travels of 1878–1883 in Indonesia shows that he did not visit Borneo, although he did visit the mountains of southern Sumatra. There is no direct account of the collection of this specimen, although he recorded bees from at least three possible localities at higher altitudes: first, in late 1880 he climbed Gunung Tenggamus, where he recorded (p. 159) 'a few bees' at 7200 ft (2160 m); second, in 1881 he visited Gunung Dempa, where he recorded (p. 208) 'a fine grey-haired humble-bee (*Bombus senex*)' (identification by Forbes) between 7000–7700 ft (2100–2310 m); and later in the same year, near the summit of Gunung Kaba (1983 m), he recorded again (p. 228) 'A large humble-bee (*Bombus senex*)'.

B. melanopoda appears to be a morphologically distinct species. It can be distinguished from the only other long-tongued bumblebee species known from Sumatra, *B. senex*, by the longer oculo-malar area of *B. melanopoda*, which is more than 1.5 times longer than the basal breadth of the mandible. Otherwise, the most closely related long-tongued bumble bee in any neighbouring area is *B. trifasciatus* from the Cameron Highlands of Peninsular Malaysia. However, like most queens of the subgenus *Megabombus*, the holotype of *B. melanopoda* is easily distinguished by its narrow longitudinal median groove subapically on gastral tergum VI (for *B. trifasciatus* this area is uniformly convex). The colour pattern of the *B. melanopoda* female is predominantly black, but the hairs of terga IV–V are very slightly paler, so there is some similarity to the darkest queens of *B. koreanus*, which have this pubescence brownish cream. However, unlike the few queens of *B. koreanus* available to me, the type of *B. melanopoda* has the unpunctured areas around the ocelli extending to less than half the ocello-ocular distance; the dorsal furrow of the gena (between the vertex and the post-ocular area) is strongly marked anteriorly; and the dorsal face of the labral tubercles (the face adjacent to the clypeus) is more sharply separated from the anterior ventral face and more densely marked by moderate-sized punctures.

Since no further individuals have been found, the possibility that the holotype of *B. melanopoda* is a mislabelled melanic specimen of another species of the subgenus *Megabombus* ought to be explored, perhaps initially through a morphometric analysis.

COMMENT. Like most other Sumatran bumble bees (with the notable exception of the extensively greyish-white queens of *B. senex,* see Sianturi *et al.*, 1995), the holotype of *B. melanopoda* is almost entirely black. It is likely that females of this species would be particularly easily mistaken for black individuals of *B. senex* (although males of *B. melanopoda* might be paler, as for *B. koreanus*).

Bombus (Mg.) securus (Frison)
> *securus* (Frison, 1935:346 [*Bremus*]) examined
> *yuennanicus* Bischoff, 1936:23, examined

Bombus (Mg.) religiosus (Frison)
> *religiosus* (Frison, 1935:344 [*Bremus*]) examined
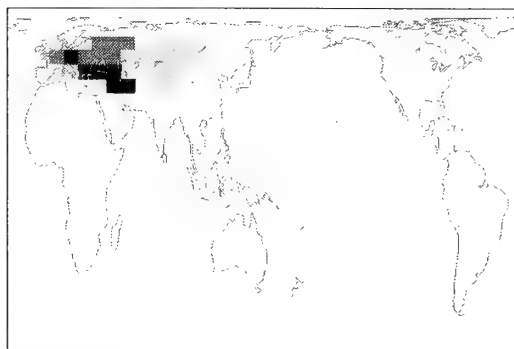
Subgenus ***RHODOBOMBUS*** Dalla Torre
> *Bombus (Rhodobombus)* Dalla Torre, 1880:40, type-species *Bremus pomorum* Panzer (= *Bombus pomorum* (Panzer)) by subsequent designation of Sandhouse, 1943:596
> *Bombus (Pomobombus)* Krüger, 1917:65, type-species *Bremus pomorum* Panzer (= *Bombus pomorum* (Panzer)) by subsequent designation of Sandhouse, 1943:589
> *Pomibombus* Skorikov, 1938a:145, unjustified emendation

Bombus (Rh.) armeniacus Radoszkowski
> *armeniacus* Radoszkowski, 1877b:202

Bombus (Rh.) mesomelas Gerstaecker⊙
> *Agrorum* (Schrank, 1781:397 [*Apis*])
> *arvenfis* (Gmelin in Linnaeus, 1790:2786 [*Apis*]) unjustified replacement name for *agrorum* Schrank, 1781:397
> *mesomelas* Gerstaecker, 1869:321

○ NOMENCLATURE. Warncke (1986) listed *B. agrorum* (Schrank) as questionably conspecific with *B. distinguendus*, but without any explanation. Although I know of no extant type specimens, Schrank's (1781) description of his *B. agrorum* of 'Habitat ruri' from Austria appears to me to be almost certainly of the same species as *B. mesomelas*, because the head is described as black and the pale hairs of the thorax and of gastral tergum I are described as grey, with the remainder of the gaster rusty or tawny-yellow (the head and the pale pubescence of the thorax and gaster are more uniformly dull yellowish for *B. distinguendus*). See the comments on *B. distinguendus*.

⊙ APPLICATION TO ICZN. Although *B. agrorum* is the oldest available name for the present interpretation of this species, the name *B. mesomelas* has been in common use for the species since 1947 (e.g. Tkalců, 1969, 1975; Delmas, 1976; Reinig, 1974, 1981; Özbek, 1983; Rasmont, 1983; Ornosa, 1986a, b; Rasmont et al., 1987, 1995). I know of no publications using the name *B. agrorum* (Schrank) since 1947, although the name *B. agrorum* (Fabricius) was in widespread use for another species (= *B. pascuorum*) until Richards (1968). It is suggested that, in the interests of stability (ICZN, 1985: Article 23b), an application be made to ICZN to use its Plenary Power to suppress the unused senior synonym, *B. agrorum*, and its unjustified replacement name, *B. arvensis* (ICZN, 1985: Article 79) (see the comments on *B. muscorum*).

Bombus (Rh.) pomorum (Panzer)
> *pomorum* (Panzer, 1805(86):18 [*Bremus*])
> *Lefebvrei* Lepeletier, 1836:461
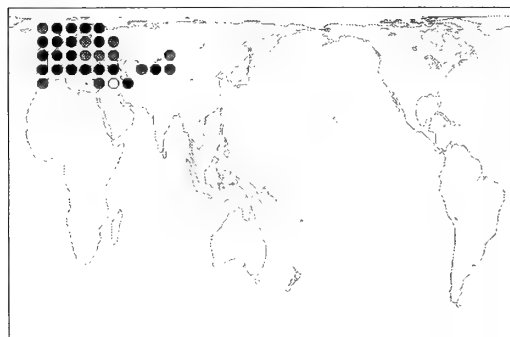
Subgenus ***KALLOBOMBUS*** Dalla Torre
> *Bombus (Kallobombus)* Dalla Torre, 1880:40, type-species *Apis soroeensis* Fabricius (= *Bombus soroeensis* (Fabricius)) by subsequent designation of Sandhouse, 1943:561
> *Bombus (Callobombus)* Dalla Torre, 1896:503, unjustified emendation
> *Bombus (Soroeensibombus)* Vogt, 1911:63, type-species *Apis soroeensis* Fabricius (= *Bombus soroeensis* (Fabricius)) by monotypy
> [*Bombus (Soroensibombus)* Ball, 1914:78, incorrect subsequent spelling]
> [*Sorocoënsibombus* Skorikov, 1922a: map 15, incorrect subsequent spelling]

Bombus (Kl.) soroeensis (Fabricius)⊙
> *Cardui* (Müller, 1776:165 [*Apis*])
> *foroeenfis* (Fabricius, [1777, see Baker, 1996a:9]:246 [*Apis*])
> *Proteus* Gerstaecker, 1869:325
> *perplexus* Radoszkowski, 1884:82, not of Cresson, 1863:91 (= *B. perplexus* Cresson)
> *Radoszkowskyi* Dalla Torre, 1890:139, replacement name for *perplexus* Radoszkowski, 1884:82
> *miniatocaudatus* Vogt, 1909:56

○ NOMENCLATURE. Baker (1996a) has established

that the name *B. cardui* has narrow priority over *B. soroeensis* by publication date.

⊙ APPLICATION TO ICZN.   Although *B. cardui* is the oldest available name for the present interpretation of this species, the name *B. soroeensis* has been in common use for the species since 1947 (e.g. Tkalcù, 1969, 1975; Løken, 1973; Alford, 1975; Delmas, 1976; Pekkarinen, 1979; Reinig, 1981; Özbek, 1983; Rasmont, 1983; Ito, 1985; Ornosa, 1986*a*; Rasmont *et al.*, 1995). The only publications using the name *B. cardui* since 1947 are those of Baker (1996*a, b*). Using this name contrary to the purpose of priority is not accepted as usage in the sense of the Code (ICZN, 1985: Article 23b), and so cannot justify the continued use of the name *B. cardui* in place of *B. soroeensis*. It is suggested that, in the interests of stability, an application be made to ICZN to use its Plenary Power to suppress the unused senior synonym (ICZN, 1985: Article 79) (see the comments on *B. muscorum*).

Subgenus ***ALPINOBOMBUS*** Skorikov

> *Alpinobombus* Skorikov, 1914*a*:123, type-species *Apis alpina* Linnaeus (= *Bombus alpinus* (Linnaeus)) by subsequent designation of Frison, 1927:66
> *Bombus (Alpinobombus)* Krüger, 1917:62
> *Alpinibombus* Skorikov, 1937:53, unjustified emendation

COMMENT.   Species of the subgenus *Alpinobombus* make up the most northerly distributed of all bee faunas (e.g. K.W. Richards, 1973). Indeed, three of the five species have a nearly circumpolar distribution, as a major component of an Arctic bumble bee fauna (Williams, 1996*b*). This relative homogeneity of the Arctic fauna among northern continents resembles the pattern in the Arctic flora, which shows little regional differentiation in comparison with more southern floras (Hooker, 1861; Walker, 1995).

Bombus (Al.) hyperboreus Schönherr⊙

> *Arctica* (Quenzel in Acerbi, 1802:253 [*Apis*])
> *hyperboreus* Schönherr, 1809:57, unjustified replacement name for *arcticus* Quenzel, 1802:253
> *clydensis* Yarrow, 1955:151, examined

● TAXONOMIC STATUS.   The identity of *B. arcticus* (Quenzel) has been uncertain. Warncke (1986) listed *B. arcticus* (Quenzel) as conspecific with *B. lapponicus* without any explanation. Presumably this was because *B. lapponicus* is extensively pale on the dorsum, although the pale pubescence is differentiated into yellow and red areas and much of it is much paler than Quenzel's description. I agree with Løken (1973) that, from the original description and the illustration (no type specimen is known to exist), *B. arcticus* (Quenzel) is most likely to be conspecific with *B. hyperboreus*, which has the pale pubescence uniformly brownish yellow.

○ NOMENCLATURE.   The name *B. arcticus* has rarely been used for this species in preference to *B. hyperboreus*, and perhaps only as a misidentification of *B. arcticus* Kirby (see e.g. Franklin, 1913; Richards, 1931*a*). Løken (1973) considered *B. arcticus* (Quenzel) to be a *nomen oblitum*, so she continued to use the name *B. hyperboreus*. However, *nomina oblita* are not supported for a publication of this date by the present Code (ICZN, 1985: Article 79c(iii)), although it does allow that *B. arcticus* (Quenzel) could be suppressed by use of the Plenary Power. See the comments on *B. polaris* Curtis.

⊙ APPLICATION TO ICZN.   Although *B. arcticus* is the oldest available name for the present interpretation of this species, the name *B. hyperboreus* has been in common use for the species since 1947 (e.g. Løken, 1973; Milliron, 1973*a*; K.W. Richards, 1973; Svensson & Lundberg, 1977; Hurd, 1979; Pekkarinen, 1979; Pekkarinen *et al.*, 1981; Reinig, 1981; Rasmont, 1983; Pekkarinen & Teräs, 1993). It is suggested that, in the interests of stability (ICZN, 1985: Article 23b), an application be made to ICZN to use its Plenary Power to suppress the unused senior synonym (ICZN, 1985: Article 79), in order to confirm usage of *B. hyperboreus* as the valid name (see the comments on *B. muscorum*).

COMMENT.   *B. hyperboreus* has been suggested to be a social parasite in colonies of *B. polaris*, at least facultatively in some parts of its range (Milliron & Oliver, 1966; Løken, 1973; K.W. Richards, 1973). See the comments on *Psithyrus* and *B. inexspectatus*.

Bombus (Al.) balteatus Dahlbom⊙

> *balteatus* Dahlbom, 1832:36
> *nivalis* Dahlbom, 1832:40
> *tricolor* Dahlbom, 1832:41
> ?*Kirbiellus* Curtis in Ross, 1835:lxii
> *kirbyellus* Dalla Torre, 1896:527, unjustified emendation
> *tristis* Sparre-Schneider in Friese, 1902:495, not of Seidl, 1837:69 (= *B. humilis* Illiger)

● TAXONOMIC STATUS.   *B. balteatus* and *B. kirbiellus* have been considered conspecific by most authors (e.g. Thomson, 1872; Richards, 1931*a*; Skorikov, 1937;

Pittioni, 1942; Løken, 1973; Hurd, 1979; Thorp *et al.*, 1983), although Milliron (1973*a*) considered them to be separate species that co-occur in some areas, particularly in Alaska.

Milliron (1973*a*) described several characters by which to discriminate *B. balteatus* and *B. kirbiellus*, placing particular emphasis on the shape of male gastral sternum VIII and the female malar area.

From the small samples I have examined, I have been unable to find convincing evidence of discrete differences in these characters. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

O NOMENCLATURE.   Richards (1931*a*) believed *B. balteatus, B. nivalis* and *B. tricolor* to be conspecific and selected the name *B. balteatus* to have precedence because it was published on an earlier page (page priority is not a mandatory part of the Code, only a recommendation, see ICZN, 1985: Recommendation 24A). However, Thomson (1872:35) had already chosen the name *B. nivalis* in precedence to *B. balteatus* and, following the Principle of the First Reviser (ICZN, 1985: Article 24), Thomson's action should now stand. Consequently, the valid name for this species is *B. nivalis*, although the Code (ICZN, 1985) allows that this name could be suppressed by use of the Plenary Power.

✪ APPLICATION TO ICZN.   Although *B. nivalis* is the valid name for this species, the name *B. balteatus* has been in common use for the species since 1947 (e.g. Løken, 1973; Milliron, 1973*a*; Plowright & Stephen, 1973; Hurd, 1979; Pekkarinen, 1979; Reinig, 1981; Rasmont, 1983; Thorp *et al.*, 1983; Laverty & Harder, 1988; Pekkarinen & Teräs, 1993). It is suggested that, in the interests of stability, an application be made to ICZN to use its Plenary Power to suppress the unused name (ICZN, 1985: Article 79) (see the comments on *B. muscorum*). However, the consequence of this action would be that *nivalis* Dahlbom would no longer be available for a subspecies of *B. balteatus*.

Bombus (Al.) neoboreus Sladen

> *strenuus* Cresson, 1863:102, not of Harris, 1776:131 (= *B. lapidarius* (Linnaeus))
> *neoboreus* Sladen, 1919:28

O NOMENCLATURE.   *B. strenuus* Cresson (1863) is a junior secondary homonym in *Bombus* of *Apis strenuus* Harris (1776), and therefore the name *B. strenuus* Cresson is invalid (ICZN, 1985: Article 57c). For this species, the oldest available name is *B. neoboreus*, which becomes the valid name. The only publications using the name *B. strenuus* Cresson since 1947 of which I am aware are by Hurd (1979), Milliron (1973*a*) and Poole (1996), so this change of valid name is not a serious disruption of common usage.

Bombus (Al.) polaris Curtis✪

> *Arcticus* Kirby in Parry, 1824:ccxvi, examined, not of Quenzel in Acerbi, 1802:253 (= *B. hyperboreus* Schönherr)
> *Polaris* Curtis in Ross, 1835:lxiii, examined
> *diabolicus* Friese, 1911:571
> *alpiniformis* Richards, 1931*a*:13

O NOMENCLATURE.   Løken (1973) used the name *B. arcticus* Kirby for this species because she considered *B. arcticus* (Quenzel) to be a *nomen oblitum*. However, this is not supported by the present Code for a publication of this date (ICZN, 1985: Article 79c(iii)), although it does allow *B. arcticus* (Quenzel) to be suppressed by use of the Plenary Power. See the comments on *B. hyperboreus*.

✪ APPLICATION TO ICZN.   It is suggested above that, in the interests of stability (ICZN, 1985: Article 23b), an application be made to ICZN to use its Plenary Power to suppress *B. arcticus* (Quenzel), the unused senior synonym (ICZN, 1985: Article 79) of *B. hyperboreus*. This would free *B. arcticus* Kirby from junior primary homonymy with *B. arcticus* (Quenzel) (ICZN, 1985: Article 57b), so that it would become the valid name for this species (see the comments on *B. hyperboreus*). However, although the name *B. arcticus* Kirby has been in use for this species (e.g. Løken, 1973; Sakagami, 1976; Svensson & Lundberg, 1977; Reinig, 1981), the more frequently used name has been *B. polaris* (e.g. Milliron & Oliver, 1966; Milliron, 1973*a*; K.W. Richards, 1973; Hurd, 1979; Pekkarinen, 1979; Pekkarinen *et al.*, 1981; Rasmont, 1983; Pekkarinen & Teräs, 1993). In the interests of stability, the application to ICZN might be extended to suppress *B. arcticus* Kirby, in order to conserve the current usage of *B. polaris* as the valid name.

Bombus (Al.) alpinus (Linnaeus)

> *alpina* (Linnaeus, 1758:579 [*Apis*]) examined

Subgenus *SUBTERRANEOBOMBUS* Vogt

> *Bombus (Subterraneobombus)* Vogt, 1911:62, type-species *Apis subterranea* Linnaeus (=*Bombus subterraneus* (Linnaeus)) by subsequent designation of Frison, 1927:68

Subterraneibombus Skorikov, 1938*a*:145, unjustified
emendation

Bombus (St.) melanurus Lepeletier
melanurus Lepeletier, 1836:469, examined
?*difficillimus* Skorikov, 1912:609, examined
subdistinctus Richards, 1928*a*:333, examined

● TAXONOMIC STATUS. Several of these nominal
taxa have been treated as separate species and at least
B. difficillimus may indeed prove to be a separate
species. However, aside from differences in colour
pattern, they are closely similar in morphology with a
range of variation (Williams, 1991). Until more evi-
dence to the contrary is available from critical studies
of patterns of variation, I shall treat them as parts of a
single variable species.

Bombus (St.) fragrans (Pallas)
fragrans (Pallas, 1771:474 [*Apis*])
?*mongol* Skorikov, 1912:607, examined
?*charharensis* Yasumatsu, 1940:94 (provisional synonym)

● TAXONOMIC STATUS. This taxon is interpreted
here in the broadest sense, to include a complex of
poorly-known taxa (Williams, 1991). More evidence
is awaited.

Bombus (St.) amurensis Radoszkowski
Amurensis Radoszkowski, 1862:590, examined

● TAXONOMIC STATUS. I have seen no males of
this species and its precise relationships remain un-
clear.

Bombus (St.) fedtschenkoi Morawitz
Fedtschenkoi Morawitz in Fedtschenko, 1875:5

Bombus (St.) personatus Smith
personatus Smith, 1879:132, examined
Roborowskyi Morawitz, 1886:197, examined

Bombus (St.) subterraneus (Linnaeus)
fubterranea (Linnaeus, 1758:579 [*Apis*]) examined
Nemorum (Scopoli, 1763:307 [*Apis*])
?*faltuum* (Panzer, 1801(75):21 [*Apis*])

○ NOMENCLATURE. Løken (1984) interpreted *B.
saltuum* as being conspecific with *B. barbutellus* (see
the comments on *B. barbutellus*). Warncke (1986)
interpreted *B. saltuum* as having been described from
a male (presumably because the antennae were de-
scribed as rather long) conspecific with *B.
subterraneus*. No type specimen is known. The de-

scription of the anterior part of the gaster of *B. saltuum*
as ashen and the middle part as nearly bald is perhaps
slightly closer to *B. subterraneus,* because although
both species may have gastral tergum I with pale hair
and terga I–III sparsely haired, this hair is much shorter
on *B. subterraneus* and the posterior fringing hairs of
the terga often appear greyish-white.

If *B. saltuum* were not accepted as most likely to be
conspecific with *B. subterraneus,* then further action
would be required. If both interpretations were con-
sidered to remain supportable, then it might be
considered appropriate (ICZN, 1985: Article 75b) to
designate a specimen of *B. subterraneus* as neotype
of *Apis saltuum* in order to conserve the current usage
of *B. barbutellus.* Alternatively, if *B. saltuum* were
considered more likely to be conspecific with *B.
barbutellus,* then *B. saltuum* would become the oldest
available name for that species, even though the name
has not been used in the last 50 years. In the interests
of stability (ICZN, 1985: Article 23b), an application
could then be made to ICZN to use its Plenary Power
to suppress the unused senior synonym (ICZN, 1985:
Article 79).

COMMENT. This species has been introduced into
New Zealand (e.g. Gurr, 1957; Macfarlane & Gurr,
1995).

Bombus (St.) distinguendus Morawitz❂
nemorum (Fabricius, 1775:382 [*Apis*]) not of Scopoli,
1763:307 (= *B. subterraneus* (Linnaeus)), not of
Fabricius, 1775:380 (?= *B. bohemicus* Seidl)
elegans Seidl, 1837:67
*distinguendus* Morawitz, 1869:32

○ NOMENCLATURE. The name *B. elegans* has been
applied to several taxa by different authors. Tkalců
(1969:901–903) reasoned that Seidl had originally
described *B. elegans* from an individual of the species
that has more recently been known by the name *B.
distinguendus,* although Seidl's original type is lost.
According to Tkalců, a specimen of *B. mesomelas* may
then have been substituted as the type, but now this
cannot be found either. Any remaining confusion could
be resolved by the designation of an appropriate
neotype. See the comments on *B. mesomelas.*

❂ APPLICATION TO ICZN. Although *B. elegans* may
be the oldest available name for the present interpreta-
tion of this species, the name *B. distinguendus* has
been in common use for the species since 1947 (e.g.
Tkalců, 1969, 1974*a*; Løken, 1973; Alford, 1975;
Delmas, 1976; Sakagami, 1976; Pekkarinen, 1979;
Reinig, 1981; Pekkarinen *et al.,* 1981; Rasmont, 1983;
Pekkarinen & Teräs, 1993; Rasmont *et al.,* 1995). I
know of no publications using the name *B. elegans* for
this taxon (only for *B. mesomelas* Gerstaecker as a
misidentification) since 1947. It is suggested that, in

the interests of stability (ICZN, 1985: Article 23b), and to prevent confusion with *B. mesomelas*, an application be made to ICZN to use its Plenary Power to suppress the unused senior synonym (ICZN, 1985: Article 79) (see the comments on *B. muscorum*).

Bombus (St.) appositus Cresson
  appositus Cresson, 1878:183

Bombus (St.) borealis Kirby
  borealis Kirby, 1837:272
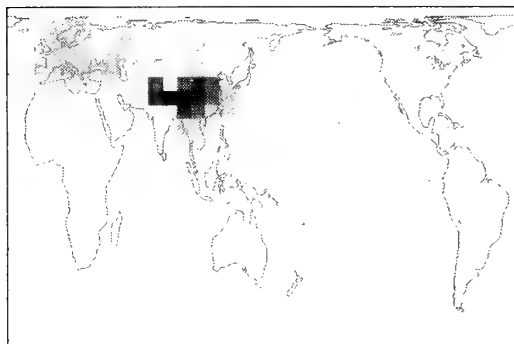
Subgenus ALPIGENOBOMBUS Skorikov
  Alpigenobombus Skorikov, 1914a:128, type-species *Alpigenobombus pulcherrimus* Skorikov (= *Bombus kashmirensis* Friese) by subsequent designation of Williams, 1991:65
  Bombus (Mastrucatobombus) Krüger, 1917:66, type-species *Bombus mastrucatus* Gerstaecker (= *Bombus wurflenii* Radoszkowski) by monotypy
  Bombus (Alpigenobombus) Frison, 1927:64
  [*Nobilibombus* Skorikov, 1933a:62, published without fixation of type-species]
  [*Bombus (Nobilibombus)* Bischoff, 1936:12, type-species *Nobilibombus morawitziides* Skorikov (= *Bombus nobilis* Friese) by monotypy, published as a junior synonym]
  Alpigenibombus Skorikov, 1938b:1, unjustified emendation
  [*Pyrobombus (Nobilibombus)* Milliron, 1961:54, type-species *Bombus nobilis* Friese (cited as *Bombus nobilis* Skorikov) by original designation, published as a junior synonym]
  Bombus (Nobilibombus) Richards, 1968:222, type-species *Bombus nobilis* Friese by original designation (see Williams, 1991)
  [*Alpegenobombus* Wang, 1979:188, incorrect subsequent spelling]

● TAXONOMIC STATUS. Richards (1968) treated *Alpigenobombus* and *Nobilibombus* as separate subgenera. Following Bischoff (1936), I have treated them as a single subgenus *Alpigenobombus* (Williams, 1991), for which the evidence for monophyly is strong (Williams, 1995).

Bombus (Ag.) kashmirensis Friese
  kashmirensis Friese, 1909[September, Tkalcü, 1974b]:673 examined
  stramineus Friese, 1909[September, Tkalcü, 1974b]:673
  tetrachromus Cockerell, 1909[November, Tkalcü, 1974b]:397, examined
  pulcherrimus (Skorikov, 1914a:128 [*Alpigenobombus*])

● TAXONOMIC STATUS. Several of these nominal taxa have been treated as separate species. However, aside from differences in colour pattern, they are closely similar in morphology with a range of variation (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

○ NOMENCLATURE. Tkalcü (1974b) first regarded *B. kashmirensis* and *B. stramineus* as conspecific and, following the Principle of First Reviser (ICZN, 1985: Article 24), chose *B. kashmirensis* as the name for the species.

Bombus (Ag.) wurflenii Radoszkowski
  Wurflenii Radoszkowski, 1859:482, examined
  [*Wurfleini* Radoszkowski, 1877b:191, incorrect subsequent spelling]
  mastrucatus Gerstaecker, 1869:326, examined
  alpigenus Morawitz, 1874:132

Bombus (Ag.) nobilis Friese
  ?*validus* Friese, 1905:510, examined (provisional synonym)
  nobilis Friese, 1905:513
  ?*sikkimi* Friese, 1918:82, examined (provisional synonym)
  [*morawitziides* Skorikov, 1922a:159, published without description]
  [*morawitziides* Skorikov, 1931:203, published without description]
  ?*morawitziides* (Skorikov, 1933a:62 [*Nobilibombus*]) examined (provisional synonym)
  ?*xizangensis* Wang, 1979:188, examined (provisional synonym)
  chayaensis Wang, 1979:189, examined, **new synonym**

● TAXONOMIC STATUS. Several of these nominal taxa have been treated as separate species.

Friese (1905) described *B. validus* initially (p. 510) as having a quadrate malar area and untoothed mandibles, but went on (p. 517) to place it within the *mastrucatus* (= *B. wurflenii*) group, which he characterised as having a short malar area and toothed mandibles. Tkalcü (1987) designated as lectotype of *B. validus* a female with a quadrate malar area and multi-toothed mandibles. He also synonymised *B. morawitziides* with *B. validus*.

The type specimens of *B. nobilis* have also been in some doubt (Richards, 1968). In the same publication

as the description of *B. validus*, Friese (1905) described the female of *B. nobilis* as having a 'quadratisch' malar area and 4–5 teeth on the mandible (even though he placed it [p. 519] in a group with *B. lapidarius*). The original description lists several females (particularly from Sichuan), but the only putative type female that I have been able to examine (although it carries no Friese 'type' label) is in the Berlin museum collection and is a specimen of *B. friseanus* labelled 'Kashgar' (this locality is outside the known distribution range of either *B. nobilis* or *B. friseanus*). The specimen does not match the original description of the mandibles of *B. nobilis* and so cannot be considered a valid syntype. Nonetheless, the identity of *B. nobilis* is clear from the original description, so the designation of a neotype is not justified (ICZN, 1985: Article 75b).

B. chayaensis appears to me to be very closely similar to the yellow banded *B. nobilis* (in the strict sense) and I am unaware of any reason to treat them as separate species.

B. nobilis is interpreted here in the broadest sense, to include a complex of morphologically closely similar taxa (Williams, 1991). At least some of the taxa included may prove to be separate species from *B. nobilis*. The most obvious variation is in the colour of the pale thoracic bands, which may be yellow (*B. nobilis*), yellow-white (*B. sikkimi*), gey-white (*B. morawitziides*), or almost completely replaced by black (*B. validus*). However, aside from these differences in colour pattern, they are similar in morphology with a range of variation. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

O NOMENCLATURE. Following the Principle of First Reviser (ICZN, 1985: Article 24), and as the first author to regard these taxa as conspecific, I select the name *B. nobilis* as the valid name in preference to *B. validus* from the available names for this species from Friese (1905).

Bombus (Ag.) genalis Friese
genalis Friese, 1918:84, examined

● TAXONOMIC STATUS.   I have seen no males of this species and its precise relationships remain unclear.

Bombus (Ag.) grahami (Frison)
grahami (Frison, 1933:334 [*Bremus*])

Bombus (Ag.) breviceps Smith
nasutus Smith, 1852a:44, examined
breviceps Smith, 1852a:44, examined
dentatus Handlirsch, 1888:227
simulus Gribodo, 1892:114, examined

orichalceus Friese, 1916:107
*rufocognitus* Cockerell, 1922:4, examined
pretiosus Bischoff, 1936:11, examined, not of Friese, 1911:571 (= *B. polaris* Curtis)
?angustus Chiu, 1948:59 (provisional synonym)
bischoffiellus (Tkalcü, 1977:224 [*Alpigenobombus*]) replacement name for *pretiosus* Bischoff, 1936:11

● TAXONOMIC STATUS.   Several of these nominal taxa have been treated as separate species. At least *B. dentatus* [Himalaya] and *B. angustus* [Taiwan] may prove to be separate species (e.g. Tkalcü, 1968b, 1989). However, aside from differences in colour pattern, they are similar in morphology with a range of variation (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

O NOMENCLATURE.   Tkalcü (1968b) first regarded *B. nasutus* and *B. breviceps* as likely to be conspecific and, following the Principle of First Reviser (ICZN, 1985: Article 24), chose *B. breviceps* as the name for the species.
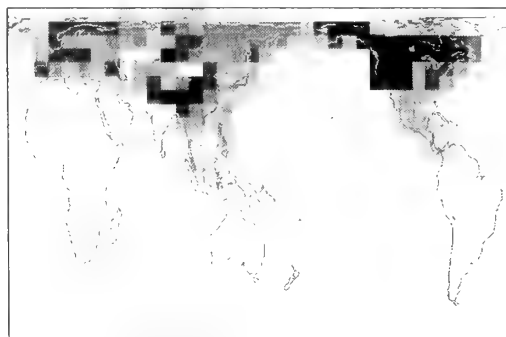
Subgenus *PYROBOMBUS* Dalla Torre
Bombus (Pyrobombus) Dalla Torre, 1880:40, type-species *Apis hypnorum* Linnaeus (= *Bombus hypnorum* (Linnaeus)) by monotypy
Bombus (Poecilobombus) Dalla Torre, 1882:23, type-species *Bombus sitkensis* Nylander by subsequent designation of Sandhouse, 1943:589
[*Bombus (Pyrrhobombus)* Dalla Torre, 1882:28, incorrect subsequent spelling]
Bombus (Pyrrhobombus) Dalla Torre, 1896:503, unjustified emendation
Bombus (Pratobombus) Vogt, 1911:49, type-species *Apis pratorum* Linnaeus (= *Bombus pratorum* (Linnaeus)) by subsequent designation of Frison, 1927:67
[*Bombus (Pratibombus)* Ball, 1914:78, incorrect subsequent spelling]
Bombus (Anodontobombus) Krüger, 1917:61,65 (proposed as a section name but stated by Milliron, 1961:53, to be synonymous with his concept of the subgenus *Pyrobombus* Dalla Torre), type-species *Apis hypnorum* Linnaeus (= *Bombus hypnorum* (Linnaeus)) by subsequent designation of Williams, 1991:69

Bombus (Uncobombus) Vogt in Krüger, 1917:65 (proposed as a group name but stated by Milliron, 1961:53, to correspond to his concept of *Pyrobombus* Dalla Torre), type-species *Apis hypnorum* Linnaeus (=*Bombus hypnorum* (Linnaeus)) by subsequent designation of Williams, 1991:69

Bombus (Lapponicobombus) Quilis-Pérez, 1927:19, type-species *Apis lapponica* Fabricius (=*Bombus lapponicus* (Fabricius)) by subsequent designation of Milliron, 1961:58

[*Bombus (Hypnorubombus)* Quilis-Pérez, 1927:19, incorrect original spelling]

[*Bombus (Laponicobombus)* Quilis-Pérez, 1927:63, incorrect original spelling]

Bombus (Hypnorobombus) Quilis-Pérez, 1927:97, type-species *Apis hypnorum* Linnaeus (=*Bombus hypnorum* (Linnaeus)) by monotypy

Pratibombus Skorikov, 1938b:1, unjustified emendation

COMMENT. This is the largest subgenus of *Bombus*. The highest richness of *Pyrobombus* species occurs in the New World (there are no species known from south of Panama), although the earliest-diverging species within the subgenus appear to be in the Old World (Williams, 1991). This is the opposite pattern to that shown by the next-largest subgenus (of social parasites), *Psithyrus* (see the comments on the subgenus *Psithyrus*).

Bombus (Pr.) abnormis (Tkalcü)

abnormis (Tkalcü, 1968a:33 [*Pyrobombus*]) examined

Bombus (Pr.) hypnorum (Linnaeus)

Hypnorum (Linnaeus, 1758:579 [*Apis*]) examined

leucopygus Illiger, 1806:172

calidus Erichson in Middendorff, 1851:65

fletcheri Richards, 1934:90, examined

insularis Sakagami & Ishikawa, 1969:180, not of Smith, 1861:155 (= *B. insularis* (Smith))

koropokkrus Sakagami & Ishikawa, 1972:610, replacement name for *insularis* Sakagami & Ishikawa, 1969:180

● TAXONOMIC STATUS. *B. hypnorum* is a broadly distributed species with a fairly easily recognised brown-black-white colour pattern (e.g. Reinig, 1939; Williams, 1991). Recently, Starr (1992) has described what appears to be a divergent, brownish-black orange-tailed colour form from a disjunct peripheral population on the island of Taiwan.

Bombus (Pr.) perplexus Cresson

perplexus Cresson, 1863:91

Bombus (Pr.) haematurus Kriechbaumer

haematurus Kriechbaumer, 1870:157

Bombus (Pr.) subtypicus (Skorikov)

leucopygus Morawitz in Fedtschenko, 1875:3, not of Illiger,

1806:172 (= *B. hypnorum* (Linnaeus))

[*leucopygos* (Skorikov, 1914b:294 [*Pratobombus*]) incorrect subsequent spelling]

subtypicus (Skorikov, 1914b:294 [*Pratobombus*]) examined

leucurus Bischoff & Hedicke, 1931:391, replacement name for *leucopygus* Morawitz in Fedtschenko, 1875:3

kohistanensis (Tkalcü, 1989:49 [*Pyrobombus*]) examined

Bombus (Pr.) mirus (Tkalcü)

mirus (Tkalcü, 1968a:37 [*Pyrobombus*]) examined

?tibetanus Friese, 1913:86, examined, not of Morawitz, 1886:202 (= *B. tibetanus* (Morawitz))

Bombus (Pr.) lemniscatus Skorikov

lemniscatus Skorikov, 1912:607, examined

flavopilosus Friese, 1918:84, examined

peralpinus Richards, 1930:646, examined

Bombus (Pr.) lepidus Skorikov

lepidus Skorikov, 1912:606, examined

genitalis Friese, 1913:85, examined

tetrachromus Friese, 1918:85, examined, not of Cockerell, 1909:397 (= *B. kashmirensis* Friese)

?yuennanicola Bischoff, 1936:7, examined

Bombus (Pr.) infirmus (Tkalcü)

leucurus Bischoff, 1936:8, examined, not of Bischoff & Hedicke, 1931:391 (= *B. subtypicus* (Skorikov))

infirmus (Tkalcü, 1968a:24 [*Pyrobombus*]) replacement name for *leucurus* Bischoff, 1936:8

Bombus (Pr.) parthenius Richards

parthenius Richards, 1934[14April, Williams & Cameron, 1993]:89, examined

?sonani (Frison, 1934[30 April, Williams & Cameron, 1993]:175 [*Bremus*]) examined

?infrequens (Tkalcü, 1989:56 [*Pyrobombus*]) examined (provisional synonym)

● TAXONOMIC STATUS. Several of these nominal taxa have been treated as separate species. At least *B. sonani* [Taiwan] and *B. infrequens* [northern Burma to southern China] may prove to be separate species. However, aside from differences in colour pattern, they are closely similar in morphology (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

Bombus (Pr.) luteipes Richards

luteipes Richards, 1934:89, examined

?avanus (Skorikov, 1938b:2 [*Pratibombus*]) (provisional synonym)

signifer (Tkalcü, 1989:52 [*Pyrobombus*]), examined

● TAXONOMIC STATUS. The identity of *B. avanus*

is in doubt because the type cannot be found. The description of the colour pattern resembles *B. parthenius* and *B. luteipes,* and the description of the longer than usual squama (= gonostylus) and the half-crooked apex of the sagitta (= penis valve) appear to be closely similar to *B. luteipes,* so these taxa are very likely to be conspecific. More evidence is awaited.

Bombus (Pr.) flavescens Smith

flavescens Smith, 1852a:45, examined
mearnsi Ashmead, 1905:959
baguionensis Cockerell, 1920:631, **new synonym**
tahanensis Pendlebury, 1923:65, examined
?*rufoflavus* Pendlebury, 1923:66, examined (provisional synonym)

● TAXONOMIC STATUS. Several of these nominal taxa have been treated as separate species. *B. rufoflavus* [Peninsular Malaysia] and *B. baguionensis* [Philippines] are particularly distinct in colour pattern. They may prove to be separate species, but from the material available from a few sites, they appear to me to be closely similar in morphology to *B. flavescens* (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

Bombus (Pr.) rotundiceps Friese

rotundiceps Friese, 1916:108, examined
montivolanoides Sakagami & Yoshikawa, 1961:431
shillongensis (Tkalcü, 1974b:334 [Pyrobombus]) examined

Bombus (Pr.) beaticola (Tkalcü)

beaticola (Tkalcü, 1968a:28 [*Pyrobombus*]) examined

Bombus (Pr.) picipes Richards

flavus Friese, 1905:517, examined, not of Pérez, 1884:265 (= *B. campestris* (Panzer))
picipes Richards, 1934:90, examined
klapperichi Pittioni, 1949:266, examined
?*nikiforuki* Tkalcü, 1961b:354 (provisional synonym)

● TAXONOMIC STATUS. *B. nikiforuki* was described from a single worker from Qinghai. From the description, it appears to be closely similar to *B. picipes* and is likely to be conspecific.

○ NOMENCLATURE. With *Psithyrus* regarded as being a subgenus of the genus *Bombus* (Williams, 1991, 1995), *B. pratorum* subsp. *flavus* Friese (1905) becomes a junior secondary homonym in *Bombus* of *Psithyrus campestris* var. *flavus* Pérez (1884) (deemed to be subspecific, see ICZN, 1985: Article 45g(ii)), and therefore the name *B. flavus* Friese is invalid (ICZN, 1985: Article 57c). For this species, the oldest available name of which I am aware is *B. parthenius*

var. *picipes* Richards, 1934 (deemed to be subspecific, see ICZN, 1985: Article 45g(ii)), which becomes the valid name, *B. picipes*. The only publications using the name *B. flavus* Friese since 1947 of which I am aware are by Sakagami (1972), Ito (1993) and Yao & Luo (1997), so this change of valid name is not a serious disruption of common usage.

Bombus (Pr.) ardens Smith

ardens Smith, 1879:133, examined
andreae Friese, 1910:405, examined

Bombus (Pr.) modestus Eversmann

modestus Eversmann, 1852:134
Baïkalensis Radoszkowski, 1877b:203
nymphae Skorikov, 1910b:409
eversmanni Skorikov, 1910c:581, not infrasubspecific after Skorikov, 1922a:149

Bombus (Pr.) cingulatus Wahlberg

cingulatus Wahlberg, 1854:208

COMMENT. The distribution of *B. cingulatus* according to Reinig (1939) is shown in Fig. 10.

?*Bombus (Pr.) oceanicus* Friese

oceanicus Friese, 1909:675, examined
oceanicus Friese & Wagner, 1910:52, redescribed

● TAXONOMIC STATUS. *B. oceanicus* is known only from the Kurile Islands. A particularly close relationship with the otherwise broadly distributed *B. cingulatus* (absent from the Kuriles, but present in Kamchatka, Reinig, 1939; Ito & Sakagami, 1980; Fig. 10) has been suggested by Ito & Sakagami (1980) and it is possible that they are conspecific. More evidence is awaited.

Bombus (Pr.) brodmannicus Vogt

Brodmannicus Vogt, 1909:49, examined

Bombus (Pr.) pratorum (Linnaeus)

pratorum (Linnaeus, 1761:424 [*Apis*]) examined

COMMENT. This species was deliberately introduced into Sydney, Australia, although it is not known to have persisted (Oliff, 1895). Until the twentieth century, *B. pratorum* was not known from Ireland, where it is now well established (see references in Alford, 1975, 1980) (see comments on *B. monticola*).

Bombus (Pr.) jonellus (Kirby)

Jonella (Kirby, 1802:338 [*Apis*]) examined
alboanalis Franklin, 1913:385

● TAXONOMIC STATUS. *B. alboanalis* has been regarded both as a separate species (Franklin, 1913; Frison, 1927) and as conspecific with either *B. frigidus* (Burks, 1951; Hurd, 1979; Poole, 1996) or *B. jonellus* (Williams, 1991 [as *B. jonellus* from western Canada]; Scholl *et al.*, 1995).

Recently, Scholl *et al.* (1995) concluded from studies of enzyme mobility morphs that whereas *B. alboanalis* and *B. frigidus* have separate gene pools, in contrast, *B. alboanalis* and *B. jonellus* show a low level of genetic differentiation. They also noted the lack of colour gradation between sympatric *B. alboanalis* and *B. frigidus*.

From the limited amount of material I have examined, I believe that *B. alboanalis* and *B. jonellus* are morphologically closely similar. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

Bombus (Pr.) pyrenaeus Pérez❂

  pyrenaeus Pérez, [1880, see Baker, 1996*d*:300]:127, not of Lepeletier, 1832:375 (= *B. rupestris* (Fabricius))
  tenuifasciatus Vogt, 1909:49
  [*pyreneus* Pagliano, 1995:23, incorrect subsequent spelling]

○ NOMENCLATURE. With *Psithyrus* regarded as being a subgenus of the genus *Bombus* (Williams, 1991, 1995), *B. pyrenaeus* Pérez (1880) becomes a junior secondary homonym in *Bombus* of *Psithyrus pyrenaeus* Lepeletier (1832), and therefore the name *B. pyrenaeus* Pérez is invalid (ICZN, 1985: Article 57c). The next available name, *tenuifasciatus*, was used by Vogt (1909) for individuals with particular colour patterns from both *B. pyrenaeus* Pérez and *B. sichelii*. The choice of which of these two homonyms should have precedence depends on the Principle of the First Reviser (ICZN, 1985: Article 24). As far as I have been able to discover, Tkalcü (1973:266) is the first author to have recognised this problem. He recognised precedence for *B. pyrenaeus* ssp. *tenuifasciatus* Vogt. Consequently, the oldest available name for this species, and therefore the valid name, is *B. tenuifasciatus*.

❂ APPLICATION TO ICZN. Although *B. tenuifasciatus* is the oldest available name for this species, the name *B. pyrenaeus* has been in common use for the species since 1947 (e.g. Krusemen, 1958; Tkalcü, 1969, 1973, 1975; Reinig, 1972, 1981; Delmas, 1976; Rasmont, 1983; Ornosa, 1986; Williams, 1991; Rasmont *et al.*, 1995). It is suggested that, in the interests of stability, an application be made to ICZN to use its Plenary Power to suppress the senior homonym (ICZN, 1985: Article 79) (see the comments on *B. muscorum*). However, the consequence of this action

would be that *pyrenaeus* (Lepeletier) would no longer be available for a subspecies of *B. rupestris*.

Bombus (Pr.) biroi Vogt

  biroï Vogt, 1911:51, examined
  nursei Friese, 1918:84, examined
  ?agnatus Skorikov, 1933*b*:248, examined, not of Skorikov, 1912:97 (= *B. monticola* Smith)
  ?kotzschi Reinig, 1940:227, examined

● TAXONOMIC STATUS. Several of these nominal taxa have been treated as separate species. However, aside from differences in colour pattern, they are closely similar in morphology with a range of variation (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

Bombus (Pr.) frigidus Smith

  frigidus Smith, 1854:399, examined

Bombus (Pr.) sandersoni Franklin

  sandersoni Franklin, 1913:353

Bombus (Pr.) flavifrons Cresson❂

  pleuralis Nylander, 1848:231, examined
  flavifrons Cresson, 1863:105, **new synonym**

● TAXONOMIC STATUS. *B. pleuralis* and *B. flavifrons* were regarded as separate species by Franklin (1913), and Poole (1996) also lists them as separate species, without explanation. In my opinion, the lectotype of *B. pleuralis* designated by Milliron (1960:95) is an individual of the dark form of *B. flavifrons* (see descriptions of variation by e.g. Stephen, 1957; Thorp *et al.*, 1983). See also the comments on *B. mixtus*.

○ NOMENCLATURE. *B. pleuralis* is the oldest available name for this species.

❂ APPLICATION TO ICZN. Although *B. pleuralis* is the oldest available name for the present interpretation of this species, the name *B. flavifrons* has been in common use for the species since 1947 (e.g. Stephen, 1957; Thorp, 1969, 1970; Plowright & Stephen, 1973; Macior, 1975; Sakagami, 1976; Hurd, 1979; Plowright & Owen, 1980; Thorp *et al.*, 1983; Laverty & Harder, 1988). I know of no publications using the name *B. pleuralis* since 1947, apart from the list by Poole (1996). It is suggested that, in the interests of stability (ICZN, 1985: Article 23b), an application be made to ICZN to use its Plenary Power to suppress the unused senior synonym (ICZN, 1985: Article 79) (see the

comments on *B. muscorum*). However, the consequence of this action would be that *pleuralis* would no longer be available for a species or for a subspecies of *B. flavifrons*.

Bombus (Pr.) centralis Cresson
   centralis Cresson, 1864:41

Bombus (Pr.) vandykei (Frison)
   vandykei (Frison, 1927:375 [*Bremus*])
   cascadensis (Milliron, 1970a:382 [*Pyrobombus*])

Bombus (Pr.) caliginosus (Frison)
   caliginosus (Frison, 1927:376 [*Bremus*])

Bombus (Pr.) vagans Smith
   vagans Smith, 1854:399, examined

Bombus (Pr.) mixtus Cresson❖
   Praticola Kirby, 1837:274
   mixtus Cresson, 1878:186, not of Kriechbaumer, 1870:160
      (= *B. maxillosus* Klug), **new synonym**

● TAXONOMIC STATUS. The identity of *B. praticola* has remained uncertain (e.g. Cresson, 1863; Franklin, 1913). Recently, Poole (1996) has listed *B. praticola, B. mixtus* and *B. flavifrons* as separate species without explanation.

Although I know of no type material, Kirby provided a description of *B. praticola* from northern Canada (latitude 65° North) with a colour pattern (including anterior half of abdomen yellow, posterior ferruginous) that for individuals from this area is most likely to be conspecific either with *B. mixtus* (some individuals have few black hairs on gastral terga II–III), or with *B. flavifrons* (which has terga V–VI black, although this is not always apparent from the dorsal view). In his original description of *B. flavifrons*, Cresson (1863) conceded that this might be the same species as Kirby's *B. praticola*, and he went on to write (p. 106) that he had not yet identified *B. praticola*. Franklin (1913:371) wrote that he had 'been unable to decide whether the original description of *B. praticolus* [sic] referred to this species [*B. flavifrons*] or to the colour variant of *pleuralis* [intermediate colour patterns between *B. flavifrons* and *B. pleuralis*].' Milliron (1971:42) subsequently listed *Pyrobombus praticola flavifrons* (Cr.) as a member of his 'Praticola Group'.

However, here I follow R. Miller (*in litt.*), who believes that the original material was more likely to have been of the species that has come to be known as *B. mixtus*. See the comments on *B. flavifrons*.

○ NOMENCLATURE. *B. praticola* is probably the oldest available name for this species. Any remaining confusion could be resolved by the designation of an appropriate neotype (e.g. see the comments on *B. subterraneus*).

❖ APPLICATION TO ICZN. Although *B. praticola* is probably the oldest available name for this species, the name *B. mixtus* has been in common use for the species since 1947 (e.g. Stephen, 1957; Thorp, 1970; Plowright & Stephen, 1973; K. W. Richards, 1973; Macior, 1975; Sakagami, 1976; Hurd, 1979; Plowright & Owen, 1980; Thorp *et al.*, 1983; Laverty & Harder, 1988; Macfarlane *et al.*, 1994). It is suggested that, in the interests of stability, an application be made to ICZN to use its Plenary Power to suppress the senior synonym and homonym (ICZN, 1985: Article 79) (see the comments on *B. muscorum*). However, the consequence of this action would be that *mixtus* (Kriechbaumer) would no longer be available for a subspecies of *B. maxillosus*.

Bombus (Pr.) sitkensis Nylander
   Sitkensis Nylander, 1848:235

Bombus (Pr.) melanopygus Nylander
   melanopyge Nylander, 1848:236
   Edwardsii Cresson, 1878:184
   melampygus Handlirsch, 1888:231, unjustified emendation
   [*melanopygus* Viereck, 1904:99, incorrect subsequent spelling]
   melanopygus Franklin, 1913:334, justified emendation

● TAXONOMIC STATUS. *B. melanopygus* and *B. edwardsii* were shown by Owen & Plowright (1980) to differ principally by a single allele controlling the colour of the pubescence on gastral terga II–III. There can be little doubt that they are conspecific.

Bombus (Pr.) lapponicus (Fabricius)
   lapponica (Fabricius, 1793:318 [*Apis*])
   ?*sylvicola* Kirby, 1837:272
   zhaosu Wang, 1985:162, examined, **new synonym**

● TAXONOMIC STATUS. *B. sylvicola* is morphologically closely similar to *B. lapponicus,* and it has been suggested repeatedly that they may be conspecific (e.g. Sladen, 1919; Skorikov, 1922a, 1937; Pittioni, 1942, 1943; Thorp, 1962; Thorp *et al.*, 1983).

B. zhaosu was described from material from Xinjiang, China, and is closely similar to *B. lapponicus*.

These three nominal taxa have been treated as separate species. However, aside from differences in colour pattern, they are closely similar in morphology. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

?*Bombus (Pr.) monticola* Smith

> *montanus* Smith, 1844:549, not of Lepeletier, 1836:463 (=
> B. ruderarius (Müller))
> *monticola* Smith, 1849:lx, replacement name for *montanus*
> Smith, 1844:549
> *lugubris* Sparre-Schneider, 1909:155, not of Kriechbaumer,
> 1870:159 (= *B. maxillosus* (Klug))
> *scandinavicus* Friese, 1912:684, replacement name for
> *lugubris* Sparre-Schneider, 1909:255

● TAXONOMIC STATUS. *B. scandinavicus* (= *B. monticola*) and *B. lapponicus* are names that were applied initially to two colour forms in Scandinavia.

Løken (1973) reported that these two taxa overlap narrowly in distribution and intergrade. However, they have been found to differ consistently (for samples analysed) in the composition of cephalic secretions (Bergström & Svensson, 1973; Svensson & Bergström, 1977). Svensson (1973, 1979) also described subtle differences in morphological characters, although other morphological studies by Løken (1973) and Pekkarinen (1979) found no distinct differences. Pekkarinen (1982, *in litt.*) now believes that they are separate species.

It remains possible that there is a hybrid zone where the colour forms intergrade, with some gene flow. In this case, depending on the species concept embraced, these taxa might be considered conspecific (see the comments on *B. ruderatus*). Until further evidence is available, I shall continue to treat them as separate species.

COMMENT.   Until the twentieth century *B. monticola* was not known from Ireland, where it is now established (see references in Alford, 1975, 1980) (see comments on *B. pratorum*).

Bombus (Pr.) bimaculatus Cresson

> *bimaculatus* Cresson, 1863:92

Bombus (Pr.) impatiens Cresson

> *impatiens* Cresson, 1863:90

Bombus (Pr.) vosnesenskii Radoszkowski

> *Vosnesenskii* Radoszkowski, 1862:589

Bombus (Pr.) bifarius Cresson

> *bifarius* Cresson, 1878:185
> *andamanus* Gribodo, 1882:268, examined
> *fernaldi* Franklin, 1911:157, not a replacement name

● TAXONOMIC STATUS. *B. andamanus* was described as originating from 'Andaman' (= Andaman Islands, Indian Ocean), but appears to be a mislabelled queen of *B. bifarius* from western North America (Tkalcü, 1966). I have examined this specimen and agree with this identification (i.e. contrary to Richards, 1929*b*, it is not a species of the subgenus *Bombus* s. str.).

Bombus (Pr.) huntii Greene

> *Huntii* Greene, 1860:172

Bombus (Pr.) ternarius Say

> *ternàrius* Say, 1837:414
> *ornatus* Smith, 1854:398, examined

Bombus (Pr.) ephippiatus Say

> *ephippiàtus* Say, 1837:414
> *formosus* Smith, 1854:403, examined
> *lateralis* Smith, 1879:134, examined
> ?*wilmattæ* Cockerell, 1912:21, examined
> ?*alboniger* Franklin, 1915:409, examined
> *folsomi* (Frison, 1923:322 [*Bremus*]) examined

● TAXONOMIC STATUS. *B. wilmattae*, *B. alboniger* and *B. ephippiatus* have been regarded both as conspecific and as separate species. Recently, *B. wilmattae* and *B. ephippiatus* were regarded as separate species by Labougle *et al.* (1985) and Labougle (1990), who described diagnostic characters of colour pattern and morphology. However, D. Yanega (*in litt.*) and G. Chavarría (pers. com.) believe that all of these nominal taxa are part of the widespread and variable *B. ephippiatus*. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

B. folsomi was described as originating from 'Kina Bala / N. Borneo' (= Gunung Kinabalu, Sabah), but appears to be a mislabelled queen of *B. ephippiatus,* probably from Costa Rica or Panama (Starr, 1989). I have examined this specimen and agree with this identification.
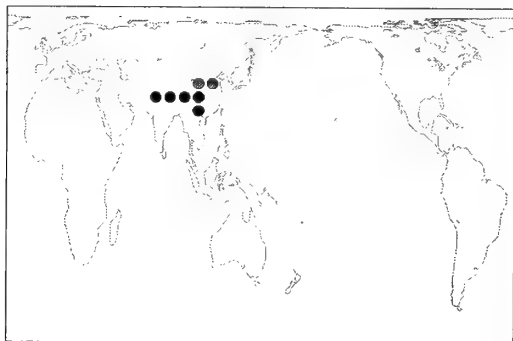
Subgenus FESTIVOBOMBUS Tkalcü

> [*Atrocinctob.*[*ombus*] Skorikov, 1933*b*:244, published without description]
> *Pyrobombus (Festivobombus)* Tkalcü, 1972:26, type-species *Bombus festivus* Smith by original designation
> *Bombus (Festivobombus)* Williams, 1985*b*:240

● TAXONOMIC STATUS. Richards (1968) treated *B. atrocinctus* (= *B. festivus*) as a species of the

subgenus *Pyrobombus,* even though this required numerous exceptions in the diagnosis. I have followed Tkalcü(1972, 1974*b*) in treating *Festivobombus* and *Pyrobombus* as separate subgenera (Williams, 1991), because together they do not form a monophyletic group (Williams, 1995).

Bombus (Fs.) festivus Smith
festivus Smith, 1861:152, examined
atrocinctus Smith in Horne, 1870:193, examined
*terminalis* Smith in Horne, 1870:193, examined
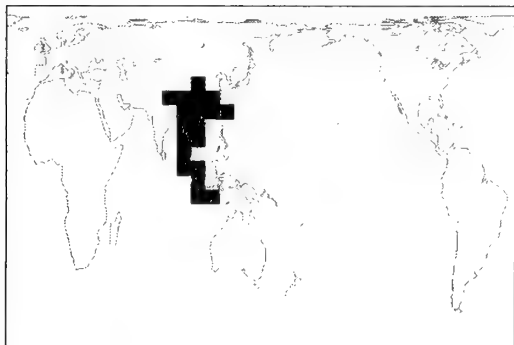
Subgenus RUFIPEDIBOMBUS Skorikov
Rufipedibombus Skorikov, 1922*a*:156, type-species *Bombus rufipes* Lepeletier by monotypy
Bombus (Rufipedibombus) Richards, 1930:638
Bombus (Rufipedobombus) Kruseman, 1952:102, unjustified emendation

Bombus (Rf.) rufipes Lepeletier
rufipes Lepeletier, 1836:473
richardsi (Frison, 1930:6 [*Bremus*])

Bombus (Rf.) eximius Smith
eximius Smith, 1852*b*:47, examined
latissimus Friese, 1910:405
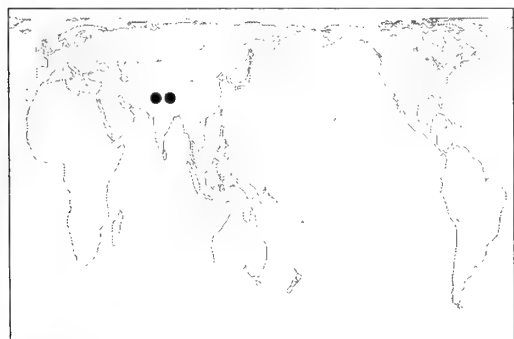
Subgenus PRESSIBOMBUS Frison
Bremus (Pressibombus) Frison, 1935:342, type-species

Bremus pressus Frison (= *Bombus pressus* (Frison)) by original designation
Bombus (Pressobombus) Kruseman, 1952:102, unjustified emendation
Bombus (Pressibombus) Richards, 1968:217

Bombus (Pe.) pressus (Frison)
pressus (Frison, 1935:342 [*Bremus*])

Subgenus BOMBUS in the strict sense
Bombus (Leucobombus) Dalla Torre, 1880:40, type-species *Apis terrestris* Linnaeus (= *Bombus terrestris* (Linnaeus)) by subsequent designation of Sandhouse, 1943:564
Bombus (Terrestribombus) Vogt, 1911:55, type-species *Apis terrestris* Linnaeus (= *Bombus terrestris* (Linnaeus)) by subsequent designation of Frison, 1927:67

Bombus (Bo.) sporadicus Nylander
sporadicus Nylander, 1848:233
malaisei Bischoff, 1930:4

Bombus (Bo.) tunicatus Smith
tunicatus Smith, 1852*a*:43, examined
vallestris Smith, 1878:8
gilgitensis Cockerell, 1905:223, examined

Bombus (Bo.) franklini (Frison)
franklini (Frison, 1921:147 [*Bremus*])

● TAXONOMIC STATUS. This species has been treated as conspecific with *B. occidentalis* (= *B. terricola*) by Milliron (1971), but has since been shown to be very distinct in morphology by Plowright & Stephen (1980) and Williams (1991), and in enzyme mobilities by Scholl, Thorp & Obrecht (1992).

COMMENT. *B. franklini* has one of the narrowest distributions of any bumble bee species world-wide. All recent specimens have been collected within a 60 mile (38 km) radius of Grants Pass, Oregon (Thorp, 1970; Thorp *et al.,* 1983).

Bombus (Bo.) affinis Cresson
affinis Cresson, 1863:103

Bombus (Bo.) ignitus Smith
ignitus Smith, 1869:207, examined
terminalis Smith, 1873:206, examined, not of Smith in
     Horne, 1870:193 (= *B. festivus* Smith)
japonicus Dalla Torre, 1890:139, replacement name for
     terminalis Smith, 1873:206

Bombus (Bo.) terrestris (Linnaeus)
terreſtris (Linnaeus, 1758:578 [*Apis*])
Audax (Harris, 1776:130 [*Apis*]) not of Harris, 1776:137
     (= *Anthophora* sp.)
canariensis Pérez, 1895:191
maderensis Erlandsson, 1979:191

● TAXONOMIC STATUS. *B. terrestris, B. maderensis*
and *B. canariensis* have been regarded both as
conspecific and as separate species.

Erlandsson (1979) argued that the dark individuals
from the Canary Islands, previously placed within *B. terrestris* by for example Krüger (1954, 1956), are a
separate species, *B. canariensis*. Erlandsson also ar-
gued that individuals from the island of Madeira,
previously placed within *B. terrestris* by Bischoff
(1937), are a separate species, *B. maderensis*. In both
cases the morphological characters used to support
these distinctions are not strongly divergent from the
broad variation within *B. terrestris* in the broad sense.
Rasmont (1984) regarded these three taxa as separate
species, but Pekkarinen & Kaarnama (1994) treated
them as conspecific.

Recent work by Estoup *et al.* (1996) has found that
although European mainland populations do not vary
significantly among themselves in mitochondrial
genes, *all* island populations studied (from six Medi-
terranean islands in addition to *B. canariensis*) show
significant differences from the mainland populations.

Consequently, viewing these three nominal taxa as
separate species may be one interpretation, but this
appears to depend on adopting a species concept that
admits little colour, morphological or genetic varia-
tion within a species and regards current geographical
isolation as highly indicative. I prefer to regard these
taxa as conspecific until further evidence is available.

○ NOMENCLATURE. Day (1979) described how
none of the admissable syntypes of *A. terrestris*
Linnaeus is in agreement with the current usage of the
name.

To reaffirm the traditional usage of this particularly
widely used name, a case was made to ICZN by Løken
et al. (1994). This sought an Opinion from ICZN
(ICZN, 1996) that set aside, by use of its Plenary
Power (ICZN, 1985: Articles 78b, 79), the lectotype
designation for *A. terrestris* by Day from application

of the Code (ICZN, 1985), and then designated a
neotype (ICZN, 1996: 64) to conserve the traditional
usage of the name for even the narrowest concept of
the taxon (ICZN, 1985: Article 75).

COMMENT. This species has been introduced into
New Zealand (e.g. Gurr, 1957; Macfarlane & Gurr,
1995) (see the comments on *B. hortorum, B. ruderatus,*
and *B. subterraneus*), Tasmania (Cardale, 1993), and
Japan (I. Washitani, *in litt.*). It was also apparently
introduced into mainland Australia (New South Wales)
without persisting (W. Froggatt in Franklin, 1913).

Bombus (Bo.) hypocrita Pérez
hypocrita Pérez, 1905:30

Bombus (Bo.) patagiatus Nylander
patagiatus Nylander, 1848:234
vasilievi Skorikov, 1913:172

Bombus (Bo.) lucorum (Linnaeus)
lucorum (Linnaeus, 1761:425 [*Apis*]), examined
?*cryptarum* (Fabricius, 1775:379 [*Apis*])
?*modestus* Cresson, 1863:99, not of Eversmann, 1852:134
     (= *B. modestus* Eversmann)
?*moderatus* Cresson, 1863:109, replacement name for
     modestus Cresson, 1863:99
monozonus Friese, 1909:674
?*magnus* Vogt, 1911:56
?*jacobsoni* Skorikov, 1912:610, examined
?*burjaeticus* Krüger, 1954:277
?*florilegus* Panfilov, 1956:1334
?*reinigi* Tkalcü, 1974b:322, examined

● TAXONOMIC STATUS. These bees have received
particularly close attention by authors describing the
minutiae of colour variation, using at least 186 classi-
cal names (see the introduction). At least some of these
nominal taxa have been regarded as separate species
by some authors (e.g. Rasmont, 1983, 1984, 1988;
Scholl & Obrecht, 1983; Scholl *et al.*, 1990; Scholl,
Thorp & Obrecht, 1992; Rasmont *et al.*, 1995; Amiet,
1996; Özbek, 1997; Pamilo *et al.*, 1997). In contrast,
B. cryptarum and the North American *B. moderatus*
have recently been treated as conspecific with *B. lucorum* by Poole (1996).

There are conflicting patterns of variation among
some characters of these taxa, which are not fully
understood (Pekkarinen, 1979; Pamilo *et al.*, 1984;
Amiet, 1996; Pamilo *et al.*, 1997). As far as I can tell
from the evidence available at present, separation of
the taxa for mapping is still not reliable, at least in
some areas of their distribution, and particularly in
Central and Eastern Asia, where there appears to be a
broad range of variation with some intergradation of
character combinations (Williams, 1991). Therefore,

because complete mapping of separate taxa is not yet possible for me, *B. lucorum* is interpreted here in the broadest sense, to include a complex of similar taxa. However, these taxa require more critical work to clarify population patterns of variation and inheritance, even in relatively well known areas such as Britain.

O   NOMENCLATURE.   When Day (1979) came to fix the application of *A. terrestris* Linnaeus (see the comments on *B. terrestris*), he had no reason to believe that Linnaeus had not described this taxon from the syntype specimen that was subsequently described as the lectotype (= *A. cryptarum* Fabricius, see Rasmont, 1988:52, ?= *B. lucorum* (Linnaeus)). This action brought *B. lucorum* (Linnaeus) into subjective junior synonymy with *B. terrestris* (Linnaeus).

To reaffirm the traditional usage of *B. terrestris* and *B. lucorum*, a case was made to ICZN by Løken *et al.* (1994). This sought an Opinion from ICZN (ICZN, 1996) that set aside, by use of its Plenary Power (ICZN, 1985: Articles 78b, 79), the lectotype designation for *A. terrestris* by Day from application of the Code (ICZN, 1985), and then designated a neotype (ICZN, 1996: 64) to conserve the traditional usage of *B. terrestris* and *B. lucorum* (ICZN, 1985: Article 75).

COMMENT.   This species occurs in Iceland, where it has probably been introduced (Prŷs-Jones *et al.*, 1981) (see the comments on *B. hortorum*).

Bombus (Bo.) terricola Kirby
  Terricola Kirby, 1837:273
  ?occidentalis Greene, 1858:12

●   TAXONOMIC STATUS.   *B. terricola* and *B. occidentalis* have been regarded both as conspecific (e.g. Milliron, 1971; Poole, 1996) and as separate species (e.g. Franklin, 1913 [but see p. 239]; Stephen, 1957; Thorp *et al.*, 1983; Scholl *et al.*, 1990).

Many specimens from the north west of North America show a reduction in the extent of the yellow bands on gastral terga II and III, with an expansion of the pale pubescence on tergum IV, and so appear to be intermediate or recombinant individuals. Indeed, Stephen's (1957:74) figure 4 shows several patterns that could represent a continuum of variation between the two forms. Furthermore, Thorp *et al.* (1983: fig. 140a) illustrate individuals of '*B. occidentalis*' from California that look very similar to eastern *B. terricola*. In view of this, Stephen's conclusion that there is no intergradation may result from adopting colour criteria (identifying *B. terricola* in the strict sense either by completely black pubescence of female terga V–VI [p. 15] and male tergum IV [p. 19], or by completely yellow pubescence of tergum II [pp. 19, 71], two character states that do not always occur together, even

in the east) that could be considered as essentially arbitrary points on a continuum (see the comments on *B. fervidus*).

In view of the existence of apparent intermediates between these nominal taxa in at least part of their range, they are treated here as likely to be conspecific. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.
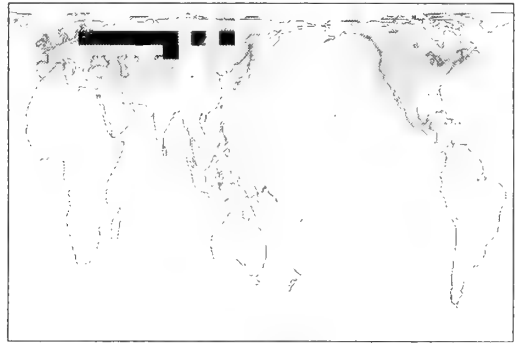
Subgenus **CULLUMANOBOMBUS** Vogt
  Bombus (Cullumanobombus) Vogt, 1911:57, type-species
    Apis cullumana Kirby (= *Bombus cullumanus* (Kirby))
    by subsequent designation of Frison, 1927:66
  Bremus (Rufocinctobombus) Frison, 1927:78, type-species *Bombus rufocinctus* Cresson by monotypy
  Cullumanibombus Skorikov, 1938a:145, unjustified emendation

Bombus (Cu.) rufocinctus Cresson
  rufo-cinctus Cresson, 1863:106

Bombus (Cu.) cullumanus (Kirby)
  Cullumana (Kirby, 1802:359 [*Apis*]) examined
  serrisquama Morawitz, 1888:224
  Silantjewi Morawitz, 1892:132
  apollineus Skorikov, 1910b:412

●   TAXONOMIC STATUS.   Several of these nominal taxa have been treated as separate species. However, aside from differences in colour pattern, they are closely similar in morphology (Panfilov, 1951). Rasmont (1988) has drawn attention to the co-occurrence of the white-banded *B. apollineus* with the yellow-banded *B. serrisquama* in northern Iran, apparently without intermediate individuals. But by analogy, it is possible that this colour difference could be the effect of a single allele for pigment (cf. *B. melanopygus*, see also the comments on *B. keriensis*). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

Bombus (Cu.) unicus Morawitz

unicus Morawitz, 1883:235
controversus Skarikov, 1910*b*: 411

● TAXONOMIC STATUS. *B. unicus* is similar to *B. cullumanus* and could possibly be conspecific. However, the male genitalia appear to be more distinct (Panfilov, 1951) from those of the other taxa traditionally considered subspecies of *B. cullumanus*.

Bombus (Cu.) semenoviellus Skorikov

semenoviellus Skorikov, 1910*b*:410
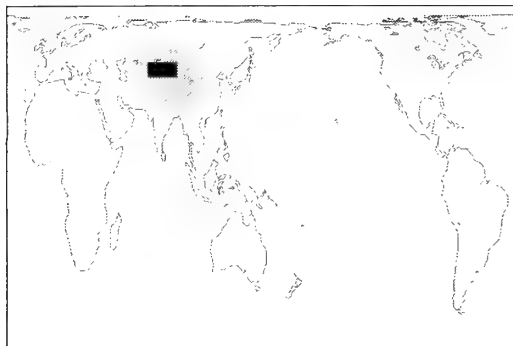
Subgenus *OBERTOBOMBUS* Reinig

Bombus (Obertobombus) Reinig, 1930:107, type-species
   Bombus oberti Morawitz by monotypy
[*Obertibombus* Skorikov, 1931:239, incorrect subsequent
   spelling]
Bombus (Obertibombus) Reinig, 1934:167, unjustified
   emendation

● TAXONOMIC STATUS. Richards (1968) treated *Obertobombus* as a synonym of the subgenus *Sibiricobombus*. I have recognised *Obertobombus* and *Sibiricobombus* as separate subgenera, because together they do not form a monophyletic group (Williams, 1995).

Bombus (Ob.) morawitzi Radoszkowski

Morawitzi Radoszkowski, 1876:101, examined
hydrophthalmus Morawitz, 1883:240, examined

Bombus (Ob.) oberti Morawitz

Oberti Morawitz, 1883:238, examined
Semenovi Morawitz, 1886:198, examined
xionglaris Wang, 1982:432, examined, **new synonym**
duanjiaoris Wang, 1982:444, examined
zhadaensis Wang, 1982:444, examined, **new synonym**

● TAXONOMIC STATUS. *B. xionglaris* and *B. zhadaensis* are closely similar to *B. oberti* in morphology and in colour pattern. These bees occur at high altitudes and are not common in collections (Williams, 1991). However, I know of no reason why these nominal taxa should not be considered conspecific.
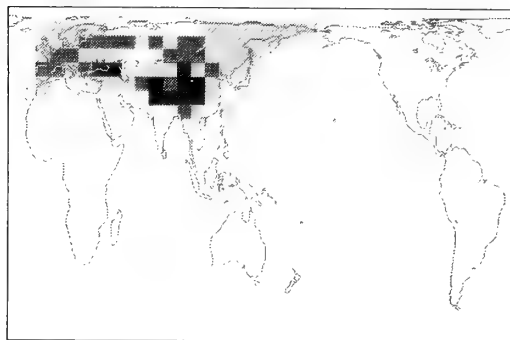
Subgenus *MELANOBOMBUS* Dalla Torre

Bombus (Melanobombus) Dalla Torre, 1880:40, type-spe-
   cies *Apis lapidaria* Linnaeus (= *Bombus lapidarius*
   (Linnaeus)) by subsequent designation of Sandhouse,
   1943:569
Bombus (Lapidariobombus) Vogt, 1911:58, type-species
   Apis lapidaria Linnaeus (= *Bombus lapidarius*
   (Linnaeus)) by subsequent designation of Sandhouse,
   1943:562
Kozlovibombus Skorikov, 1922*a*:152, type-species *Bombus
   kozlovi* Skorikov, 1910*b* (=*Bombus keriensis* Morawitz)
   in the sense of Skorikov, 1922*a* (based on males =
   Bombus pyrosoma Morawitz, a misidentification, see
   Reinig, 1934:169, requiring designation by ICZN), by
   subsequent fixation of Sandhouse, 1943:561
Bombus (Kozlowibombus) Bischoff, 1936:10, unjustified
   emendation
Lapidariibombus Skorikov, 1938*a*:145, unjustified emen-
   dation
?*Bombus (Tanguticobombus)* Pittioni, 1939*d*:201, type-
   species *Bombus tanguticus* Morawitz by original
   designation (provisional synonym)
[*Bombus (Lapedariobombus)* Esmaili & Rastegar, 1974:52,
   incorrect subsequent spelling]

Bombus (Ml.) tanguticus Morawitz

tanguticus Morawitz, 1886:200

● TAXONOMIC STATUS. Queens of *B. tanguticus* are morphologicaly very distinctive (discussed in Williams, 1991), so much so that Pittioni (1939*d*) considered the species warranted a subgenus of its own. The male remains apparently unknown (the species occurs at high altitudes in Tibet [= Xizang] and is very rare in collections), so that its precise relationships are difficult to resolve at present and a separate subgenus seems premature.

Bombus (Ml.) simillimus Smith

simillimis Smith, 1852*b*:48, examined
[*similis* Smith, 1854:403, incorrect subsequent spelling]
[*simillimus* Dalla Torre, 1896:548, incorrect subsequent
   spelling]
grossiventris Friese, 1931:303, examined

oculatus (Frison, 1933:335 [*Bremus*]) examined
tonsus (Skorikov, 1933b:248 [*Sibiricobombus*]) examined
simillimus Williams, 1991:99, justified emendation

Bombus (Ml.) richardsiellus (Tkalcü)

richardsiellus (Tkalcü, 1968a:42 [*Pyrobombus*]) examined

Bombus (Ml.) pyrosoma Morawitz

pyrosoma Morawitz, 1890:349, examined
pyrrhosoma Dalla Torre, 1896:544, unjustified emendation
wutaishanensis (Tkalcü, 1968a:39 [*Pyrobombus*]) examined

● TAXONOMIC STATUS.   *B. pyrosoma* has been considered conspecific with *B. friseanus* (Bischoff, 1936) and has been considered conspecific with *B. formosellus, B. friseanus* and *B. flavothoracicus* (= *B. miniatus*) (Williams, 1991). From a preliminary analysis of colour variation, S.-f. Wang and J. Yao report (*in litt.*) that these taxa appear to remain discrete and are likely to be separate species. More evidence is awaited.

?Bombus (Ml.) formosellus (Frison)

formosellus (Frison, 1934:163 [*Bremus*]) examined

● TAXONOMIC STATUS.   *B. formosellus* has been considered conspecific with *B. pyrosoma, B. friseanus* and *B. flavothoracicus* (= *B. miniatus*) (Williams, 1991), as a disjunct peripheral population on Taiwan. From a preliminary analysis of colour variation, S.-f. Wang and J. Yao report (*in litt.*) that these taxa appear to remain discrete and are likely to be separate species. More evidence is awaited.

?Bombus (Ml.) friseanus Skorikov

friseanus Skorikov, 1933a:62, examined
hönei Bischoff, 1936:10, examined

● TAXONOMIC STATUS.   *B. friseanus* has been considered conspecific with *B. pyrosoma* (Bischoff, 1936; Tkalcü, 1961b; Sakagami, 1972) and has been considered conspecific with *B. pyrosoma, B. formosellus* and *B. flavothoracicus* (= *B. miniatus*) (Williams, 1991). From a preliminary analysis of colour variation, S.-f. Wang and J. Yao report (*in litt.*) that these taxa appear to remain discrete and are likely to be separate species. More evidence is awaited.

?Bombus (Ml.) miniatus Bingham

flavothoracicus Bingham, 1897:552, examined, not of Hoffer, 1889:49 (= *B. campestris* (Panzer))
miniatus Bingham, 1897:553, examined
eurythorax Wang, 1982:435, examined, **new synonym**

stenothorax Wang, 1982:439, examined, **new synonym**

● TAXONOMIC STATUS.   *B. miniatus* has been considered conspecific with *B. pyrosoma, B. formosellus* and *B. friseanus* (Williams, 1991).

Evidence of intermediates between *B. miniatus* and *B. friseanus* is not strong, but not least because so little material is available from where these taxa occur in close proximity in the eastern Himalaya. The few workers and males from this area that I have seen are difficult to assign to either taxon with any confidence, although the queens are closer to the colour pattern of *B. miniatus* (Williams, 1991). More evidence is awaited.

B. eurythorax and *B. stenothorax* are closely similar in morphology and colour pattern to *B. miniatus*. I know of no reason why these nominal taxa should not be considered conspecific.

○ NOMENCLATURE.   With *Psithyrus* regarded as being a subgenus of the genus *Bombus, B. flavothoracicus* Bingham (1897) becomes a junior secondary homonym in *Bombus* of *Psithyrus campestris* var. *flavothoracicus* Hoffer (1889) (deemed to be subspecific, see ICZN, 1985: Article 45g(ii)), and therefore the name *B. flavothoracicus* Bingham is invalid (ICZN, 1985: Article 57c).

For this species, the oldest available name is *B. miniatus*, which becomes the valid name. The only subsequent publications of which I am aware that use the name *B. flavothoracicus* for this taxon as a species are by Tkalcü (1974b), Wang (1982) and Macior (1990), so this change of valid name is not a serious disruption of common usage.

Bombus (Ml.) rufofasciatus Smith

rufo-fasciatus Smith, 1852b:48, examined
Prshewalskyi Morawitz, 1880:342
rufocinctus Morawitz, 1880:343, examined, not of Cresson, 1863:106 (= *B. rufocinctus* Cresson)
chinensis Dalla Torre, 1890[June 25]:139, replacement name for *rufocinctus* Morawitz, 1880:343; not of Morawitz, 1890[April 30]:352 (= *B. chinensis* (Morawitz))
waterstoni Richards, 1934:88, examined

Bombus (Ml.) ladakhensis Richards

ladakhensis Richards, 1928a:336, examined, not infrasubspecific after Tkalcü, 1974b:335
phariensis Richards, 1930:642, examined, not infrasubspecific after Tkalcü, 1974b:336
variopictus Skorikov, 1933b:248, examined
reticulatus Bischoff, 1936:7, examined

Bombus (Ml.) semenovianus (Skorikov)

semenovianus (Skorikov, 1914a:127 [*Lapidariobombus*]) examined

Bombus (Ml.) incertus Morawitz
  incertus Morawitz, 1881:229

Bombus (Ml.) lapidarius (Linnaeus)
  Lapidaria (Linnaeus, 1758:579 [*Apis*]) examined
  Strenuus (Harris, 1776:131 [*Apis*])
  eriophorus Klug, 1807:265, examined
  caucasicus Radoszkowski, 1859:482, examined

Bombus (Ml.) keriensis Morawitz
  keriensis Morawitz, 1886:199, examined
  separandus Vogt, 1909:61, examined
  kohli Vogt, 1909:61, examined, not of Cockerell, 1906:75
    (= *B. morio* (Swederus))
  kozlovi Skorikov, 1910b:413, replacement name for *kohli*
    Vogt, 1909:61
  tenellus Friese, 1913:86
  [*alagesianus* (Skorikov, 1922a:152 [*Lapidariobombus*])
    published without description]
  alagesianus Reinig, 1930:89
  richardsi Reinig, 1935:341, not of Frison, 1930:6 (= *B.
    rufipes* Lepeletier)
  tibetensis Wang, 1982:439, replacement name for *richardsi*
    Reinig, 1935:341
  trilineatus Wang, 1982:441, examined, **new synonym**

● TAXONOMIC STATUS. Several of these nominal taxa have been treated as separate species (e.g. Skorikov, 1931), although *B. keriensis* has also long been considered a broadly-distributed and variable species, including both yellow-banded and white-banded individuals throughout much of its range (Reinig, 1935, 1939; Williams, 1991; Fig. 9).

  B. trilineatus is morphologically closely similar to *B. keriensis*. I know of no reason why these nominal taxa should not be considered conspecific.

Bombus (Ml.) sichelii Radoszkowski
  Sichelii Radoszkowski, 1859:481, examined
  [*Sicheli* Radoszkowski, 1877b:213, incorrect subsequent
    spelling]
  tenuifasciatus Vogt, 1909:49, not of Vogt, 1909:49 (= *B.
    pyrenaeus* Pérez) after Tkalcü, 1973:266
  chinganicus Reinig, 1936:6, not of Reinig, 1936:8 (?= *B.
    bohemicus* Seidl)
  erzurumensis (Özbek, 1990:209 [*Pyrobombus*]) examined,
    new synonym

● TAXONOMIC STATUS. Until recently, the white-banded form of *B. sichelii* has been known from west of the Caspian Sea only from the Caucasus (Reinig, 1935). Now that *B. erzurumensis* (morphologically closely similar to *B. sicheli-**

i and with white bands) has been described from Turkey, it could be interpreted as another white-banded, western colour form. By analogy (cf. comments on *B. melanopygus*), the difference in colour could be the

effect of a single allele for pigment.

  Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.
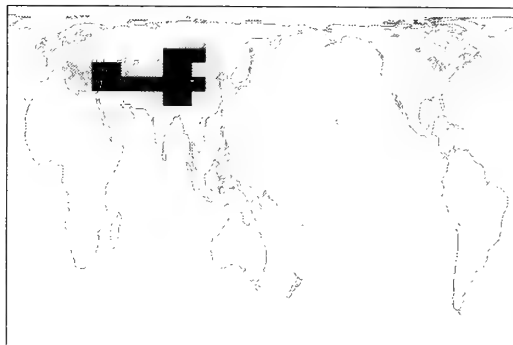
Subgenus *SIBIRICOBOMBUS* Vogt
  Bombus (*Sibiricobombus*) Vogt, 1911:60, type-species *Apis
    sibirica* Fabricius (= *Bombus sibiricus* (Fabricius)) by
    subsequent designation of Sandhouse, 1943:599
  Sibiricibombus Skorikov, 1938a:145, unjustified emenda-
    tion
  [*Bombus* (*Sibericobombus*) Kruseman, 1952:101, incor-
    rect subsequent spelling]

Bombus (Sb.) sibiricus (Fabricius)
  fibirica (Fabricius, 1781:478 [*Apis*]) examined
  flaviventris Friese, 1905:514, examined, **new synonym**
  ochrobasis Richards, 1930:655, examined, **new synonym**

● TAXONOMIC STATUS. *B. sibiricus* and *B. flavi-ventris* have been regarded as separate species. Females of *B. flaviventris* are morphologically closely similar to those of *B. sibiricus*, but differ in having the orange pubescence dorsally between the wing bases and on gastral terga IV–VI replaced with black. S.-f. Wang and J. Yao have kindly shown me the male of *B. flaviventris*, which is closely similar in its genitalia to *B. sibiricus*.

  B. ochrobasis appears to differ from *B. flaviventris* only in the lighter hue of the yellow pubescence of *B. ochrobasis*.

  At present I know of no good biological reason why these three nominal taxa should not be regarded as conspecific. More evidence is awaited.

COMMENT. *B. flaviventris* has long been placed in the subgenus *Subterraneobombus* (e.g. Skorikov, 1922a; Richards, 1930, 1968), although the characters of the females (Williams, 1991) and the males (Wang & Yao, unpublished) agree with the species of the subgenus *Sibiricobombus*.

Bombus (Sb.) obtusus Richards
  obtusus Richards, 1951:196, examined

Bombus (Sb.) asiaticus Morawitz
  asiatica Morawitz in Fedtschenko, 1875:4, examined
  longiceps Smith, 1878:8
  Regeli Morawitz, 1880:337, examined
  regelii Dalla Torre, 1896:544, unjustified emendation
  [*miniatocaudatus* Vogt, 1909:50, infrasubspecific]
  miniatocaudatus Vogt, 1911:61, examined, not of Vogt,
    1909:56 (= *B. soroeensis* (Fabricius))
  heicens Wang, 1982:430, examined, **new synonym**
  huangcens Wang, 1982:430, examined, **new synonym**
  flavicollis Wang, 1985:163, examined, **new synonym**
  baichengensis Wang, 1985:164, examined, **new synonym**

● TAXONOMIC STATUS. Several of these nominal taxa have been treated as separate species.

B. heicens, B. huangcens, B. flavicollis and *B. baichengensis* are morphologically closely similar to *B. asiaticus* and differ only in details of the colour pattern. In the case of the yellow unbanded colour form and the grey banded colour form in Kashmir (Fig. 12), there is evidence of interbreeding, with many recombinant individuals in some localities (Williams, 1991).

Aside from differences in colour pattern, these taxa are similar in morphology with a range of variation (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

Bombus (Sb.) niveatus Kriechbaumer
  niveatus Kriechbaumer, 1870:158
  ?*vorticosus* Gerstaecker, 1872:290, examined (provisional
    synonym)

● TAXONOMIC STATUS. *B. niveatus* and *B. vorticosus* have been regarded both as conspecific (Schmiedeknecht, 1883; Handlirsch, 1888; Dalla Torre, 1896; Schulz, 1906) and, more recently, as separate species (e.g. Skorikov, 1922a; Pittioni, 1938; Tkalců, 1969; Reinig, 1981; Rasmont, 1983).

As far as I am aware, the white-banded *B. niveatus* occurs only within the broader distributional bounds of the yellow-banded *B. vorticosus* (within its 'extent of occurrence' in the sense of Gaston, 1994). Although they differ in the colour of the pale pubescence (Pittioni, 1939a), they are closely similar in morphology (Williams, 1991; Baker, 1996b). Pittioni (1938) and Baker (1996b) report that they occur at different altitudes, without intermediate colour forms. However, the significance of this is unclear, because Baker (1996b) notes that the white-banded *B. niveatus* co-occurs with other bumble bees (*B apollineus* (= *B. cullumanus*), *B. simulatilis* (= *B. ruderarius*)) that also show strong convergences in these areas towards the white-banded colour pattern, while elsewhere they are more broadly distributed in yellow-banded colour forms. By analogy with other species (cf. comments

on *B. melanopygus, B. keriensis*), the difference in colour could be the effect of a single pair of alleles for pigment. It is suspicious that both colour forms show identical variation in the extent of pale fringes to the pubescence on the posterior of tergum II.

Until more evidence for differences between these nominal taxa other than colour is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

Bombus (Sb.) sulfureus Friese
  sulfureus Friese, 1905:521, examined
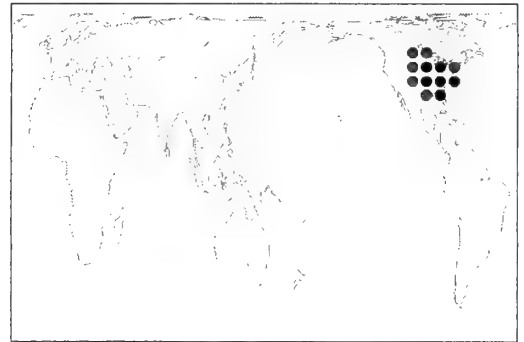
Subgenus **FRATERNOBOMBUS** Skorikov
  Alpigenobombus (Fraternobombus) Skorikov, 1922a:156,
    type-species *Apathus fraternus* Smith (= *Bombus
    fraternus* (Smith)) by subsequent designation of Frison,
    1927:63
  Bombus (Fraternobombus) Franklin, 1954:44

Bombus (Fr.) fraternus (Smith)
  fraternus (Smith, 1854:385 [*Apathus*]) examined
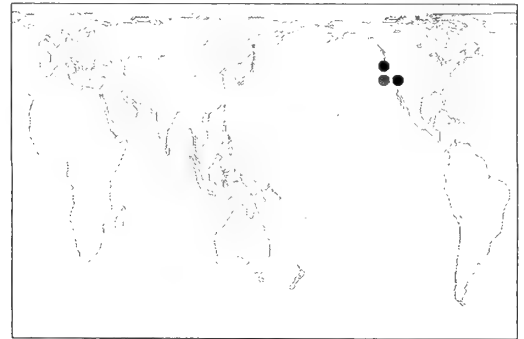
Subgenus **CROTCHIIBOMBUS** Franklin
  Bombus (Crotchiibombus) Franklin, 1954:51, type-spe-
    cies *Bombus crotchii* Cresson by original designation

Bombus (Cr.) crotchii Cresson

Crotchii Cresson, 1878:184
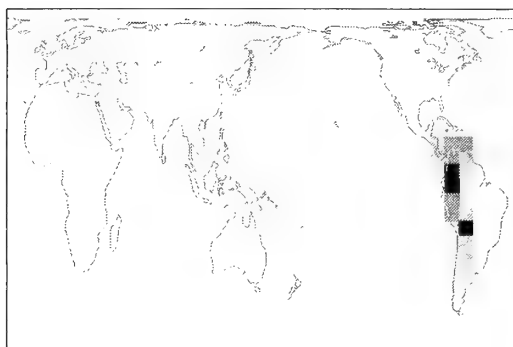
Subgenus ***ROBUSTOBOMBUS*** Skorikov

Volucellobombus Skorikov, 1922a:149, type-species
  Bombus volucelloides Gribodo (?= *B. melaleucus*
  Handlirsch) by monotypy
Alpigenobombus (Robustobombus) Skorikov, 1922a:157,
  type-species *Bombus robustus* Smith by subsequent
  designation of Sandhouse, 1943:597
Bombus (Robustobombus) Richards, 1968:217

COMMENT.   Variation within and among the species
of this subgenus is particularly poorly understood and
a critical review is urgently needed.

Bombus (Rb.) melaleucus Handlirsch

melaleucus Handlirsch, 1888:228, examined
?*volucelloides* Gribodo, 1892:119 (provisional synonym)
?*vogti* Friese, 1903:254 (provisional synonym)
?*nigrothoracicus* Friese, 1904:188, examined (provisional
  synonym)
melanoleucus Schulz, 1906:267, unjustified emendation

● TAXONOMIC STATUS.   Several of these nominal
taxa have been treated as separate species.

B. *volucelloides* is closely similar to B. *melaleucus*,
but has been considered to be a separate species (e.g.
Milliron, 1973b). B. *vogti* is also closely similar to B.
volucelloides, and these two taxa have been consid-
ered both as conspecific (e.g. Franklin, 1913; Labougle,
1990) and as separate species (e.g. Milliron, 1973b).
G. Chavarría (pers. com.) also believes that B.
melaleucus, B. *volucelloides* and B. *vogti* are all
conspecific.

In addition, it seems to me that B. *nigrothoracicus* is
more likely to be conspecific with B. *vogti* than with B.
ecuadorius (see the comments on B. *ecuadorius*).

Thus B. *melaleucus* is interpreted here in a very
broad sense, to include much variation that is not yet
well understood. Until more evidence to the contrary
is available from critical studies of patterns of varia-
tion, I shall treat them as parts of a single variable
species.

○ NOMENCLATURE.   For this species, the oldest
available name of which I am aware is B. *melaleucus*,
which becomes the valid name. The name B.
volucelloides has been in most common use, although
for just part of this species. However, it seems prema-
ture to conserve B. *volucelloides* by suppressing B.
melaleucus until the taxa are better understood, be-
cause the name B. *melaleucus* might yet be required
for a separate species or subspecies.

Bombus (Rb.) ecuadorius Meunier

Ecuadorius Meunier, 1890:66
?*butteli* Friese, 1903:254, examined (provisional syno-
  nym)

● TAXONOMIC STATUS.   B. *butteli* is closely simi-
lar to B. *ecuadorius*. They have been considered to
be separate species (e.g. Franklin, 1913; Milliron,
1973b), although Franklin conceded that B. *butteli*
(which has grey hairs intermixed on the thoracic
dorsum) might be 'only a variety or subspecies' of
B. *ecuadorius* (which has the thoracic dorsum en-
tirely black).

B. *ecuadorius* females are very rare in collections.
For example, Milliron (1973b) had seen only five
putative specimens (as opposed to 42 specimens of
B. *butteli*). Of these five specimens, four were fe-
males, and just one was a male, which is the same
specimen as the holotype of B. *nigrothoracicus* (see
the comments on B. *melaleucus*). This male is la-
belled 'Bolivia / ?Peru', whereas the rest of
Milliron's B. *ecuadorius* are from Ecuador, with the
exception of one queen from 'Peru' (it carries no
further locality data). This putative male of B.
ecuadorius differs from the females in having yellow
hairs intermixed on the front and rear of the thorax.
This was not mentioned in the original description of
this male (under the name B. *nigrothoracicus*) by
Friese (1904), which Franklin (1913) used subse-
quently as the sole basis for associating the male
with B. *ecuadorius*.

Currently I favour another possible interpretation.
This views the male holotype of B. *nigrothoracicus*
instead as a semi-melanic male of B. *melaleucus*
(the males of B. *volucelloides* [= B. *melaleucus*] that
I have seen have the thoracic dorsum extensively
yellow). This might explain the difference in colour
pattern and distribution of this male from other B.
ecuadorius. However, a consequence of this inter-
pretation would be that the only remaining known
difference between B. *ecuadorius* and B. *butteli*
would be in colour pattern, because the main mor-
phological justification for regarding them as
separate species (the broader apical process of the
gonostylus of the putative male B. *ecuadorius*, now
B. *melaleucus* in the broad sense) would have been
removed. Further evidence is awaited.

Bombus (Rb.) robustus Smith
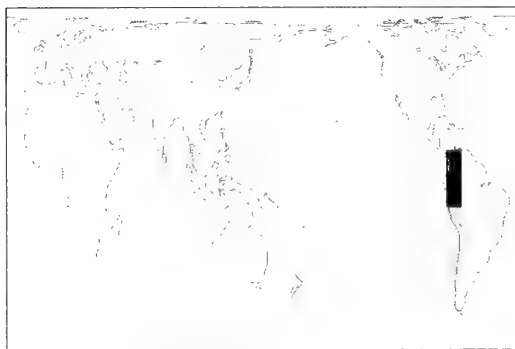 robustus Smith, 1854:400, examined

? Bombus (Rb.) hortulanus Friese
  hortulanus Friese, 1904:188, examined
  [hortulans Frison, 1925a:155, incorrect subsequent spell-
    ing]

● TAXONOMIC STATUS. *B. robustus* and *B. hortu-
lanus* have been considered both as conspecific (e.g.
Franklin, 1913; Frison, 1925a; G. Chavarría, pers.
com.) and as separate species (e.g. Milliron, 1973b;
Asperen de Boer, pers.com.).

B. robustus and *B. hortulanus* are morphologically
similar. Among the specimens I have seen, individu-
als that have the sides of gastral terga I–II yellow (*B.
robustus*) also have pubescence extending to the mid-
dle or almost to the middle of tergum I, and the males
have the space between the inner basal process of the
gonostylus and the inner apical process narrower
than the apical process. Conversely, individuals with
the sides of terga I–II black (*B. hortulanus*) have at
least the medial third of tergum I hairless, and the
space between the inner processes of the male gono-
stylus is wider than the breadth of the apical process.

Until more evidence to the contrary is available
from critical studies of patterns of variation, I shall
treat them as separate species.

Bombus (Rb.) tucumanus Vachal
  tucumanus Vachal, 1904:10
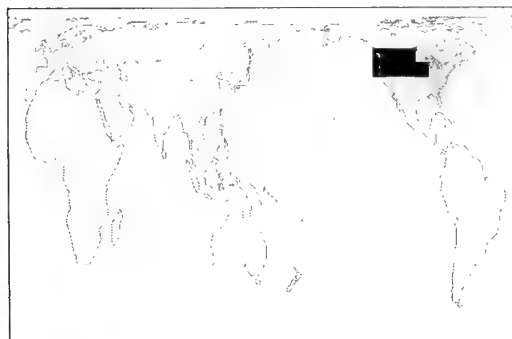
Subgenus **SEPARATOBOMBUS** Frison
  Bremus (Separatobombus) Frison, 1927:64, type-species
    Bombus separatus Cresson (= Bombus griseocollis
    (DeGeer)) by original designation
  Bombus (Separatobombus) Franklin, 1954:44

Bombus (Sp.) morrisoni Cresson
  Morrisoni Cresson, 1878:183

Bombus (Sp.) griseocollis (DeGeer)
  grifeo-collis (DeGeer, 1773:576 [Apis])
  separatus Cresson, 1863:165

Subgenus **FUNEBRIBOMBUS** Skorikov
  Alpigenobombus (Funebribombus) Skorikov, 1922a:157,
    type-species Bombus funebris Smith by monotypy
  Bombus (Funebribombus) Richards, 1968:214

Bombus (Fn.) funebris Smith
  funebris Smith, 1854:400, examined

Bombus (Fn.) rohweri (Frison)
  rohweri (Frison, 1925a:144 [Bremus])

● TAXONOMIC STATUS. *B. funebris* and *B. rohweri*
have been regarded both as conspecific (Milliron,
1962) and as separate species (Frison, 1925a; Asperen
de Boer, 1993a; G. Chavarría, pers. com.). They have
been distinguished with reference to subtle morpho-
logical characters as well as to the consistently and
strongly differing colour patterns. Both Asperen de
Boer (1993a) and G. Chavarría (pers. com.) found that
they co-occur at some localities without intermediate
colour patterns. Further evidence is awaited.

Subgenus **BRACHYCEPHALIBOMBUS** Williams
  Bombus (Brachycephalibombus) Williams, 1985b:247,
    type-species Bombus brachycephalus Handlirsch by
    original designation

● TAXONOMIC STATUS.   *B. brachycephalus* was not explicitly placed in any subgenus by Richards (1968). I described a separate subgenus *Brachycephalibombus* for *B. brachycephalus* and *B. haueri* (Williams, 1985*b*), in order to maintain monophyletic groups (Williams, 1995).

Bombus (Br.) brachycephalus Handlirsch
brachycephalus Handlirsch, 1888:244
neotropicus (Frison, 1928:151 [*Bremus*])
krusemani Asperen de Boer, 1990:1, examined, **new synonym**

● TAXONOMIC STATUS.   The description of *B. krusemani* shows that this nominal taxon, known from a single location, diverges slightly in colour pattern from the otherwise widespread, common and variable Central American species, *B. brachycephalus*. The information available at present for *B. krusemani* is consistent with the known range of variation within *B. brachycephalus* (e.g. Labougle, 1990). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

Bombus (Br.) haueri Handlirsch
Haueri Handlirsch, 1888:234

COMMENT.   Franklin (1913) and Labougle (1990) believed that this species is closely related to *B. crotchii* (although Labougle had not examined any males). Surprisingly, Milliron (1973*b*) placed *B. haueri* in his 'Dentatus-group', without explanation (*B. dentatus* is a junior synonym of the Indo-Chinese *B. breviceps* of the subgenus *Alpigenobombus*). Possibly Milliron, at least, may have been influenced by Skorikov (1922*a*), who placed *B. haueri* in the subgenus *Alpigenobombus* (as *Alpigenobombus (Alpigenobombus) haueri*, which he also listed next to *Ag. (Ag.) crotchii*). However, both sexes of species of the subgenus *Alpigenobombus,* as it has been accepted recently (Richards, 1968; Williams, 1991), are easily distinguished from any New World bumble bees because they have more teeth on the mandibles.

I have examined the morphology of both sexes and, on the basis of cladistic analysis, have grouped *B. haueri* with *B. brachycephalus* (Williams, 1985*b*, 1995) and with *B. rubicundus* (Williams, 1995). Further evidence is awaited.
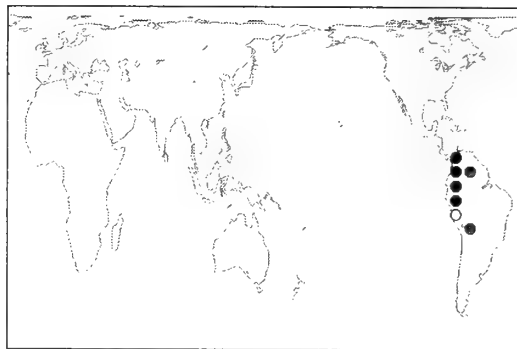
Subgenus *RUBICUNDOBOMBUS* Skorikov
Fervidobombus (Rubicundobombus) Skorikov, 1922*a*:154, type-species *Bombus rubicundus* Smith by subsequent designation of Sandhouse, 1943:597
Bombus (Rubicundobombus) Richards, 1968:217

Bombus (Rc.) rubicundus Smith
[*Napensis* Spinola in Osculati, 1850:201, published without description]
rubicundus Smith, 1854:400, examined
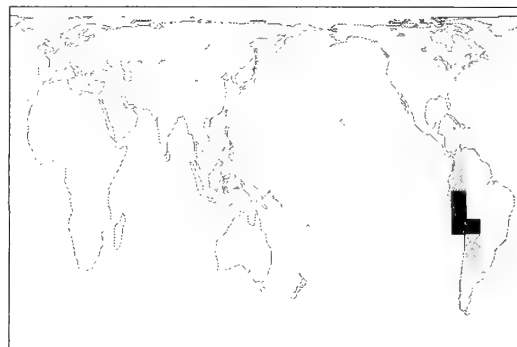
Subgenus *COCCINEOBOMBUS* Skorikov
Alpigenobombus (Coccineobombus) Skorikov, 1922*a*:157, type-species *Bombus coccineus* Friese by subsequent designation of Sandhouse, 1943:539
Bombus (Coccineobombus) Richards, 1968:214

Bombus (Cc.) coccineus Friese
coccineus Friese, 1903:254, examined

Bombus (Cc.) baeri Vachal
Baeri Vachal, 1904:10
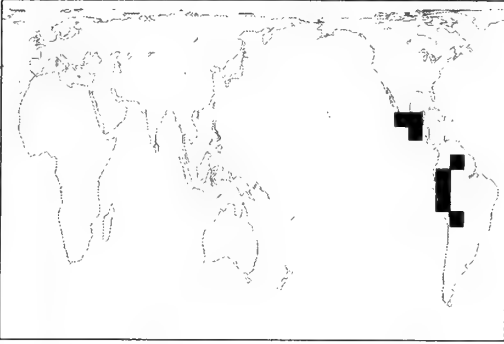
Subgenus *DASYBOMBUS* Labougle & Ayala

Bombus (Dasybombus) Labougle & Ayala, 1985:49, type-species *Bombus macgregori* Labougle & Ayala by original designation

● TAXONOMIC STATUS.   *B. handlirschi* was not explicitly placed in any subgenus by Richards (1968), and *B. macgregori* had yet to be described. I have grouped *B. handlirschi* with *B. macgregori* in the subgenus *Dasybombus* (Williams, 1995).

Bombus (Ds.) macgregori Labougle & Ayala

macgregori Labougle & Ayala, 1985:50, examined

menchuae Asperen de Boer, 1995:47, examined, **new synonym**

● TAXONOMIC STATUS.   *B. menchuae* was described from a single location and, on the basis of the worker and male I have examined, appears to diverge from *B. macgregori* only in colour pattern. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

Bombus (Ds.) handlirschi Friese

handlirschi Friese, 1903:255, examined

COMMENT.   Franklin (1913) believed that this species is closely related to *B. rubicundus*. Milliron (1973b) knew 'of no closely related species in the Western Hemisphere'. I have examined the morphology of both sexes and, on the basis of cladistic analysis, have grouped *B. handlirschi* with *B. macgregori* as sister species (Williams, 1995).

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