

Ant genera of the tribe Dacetonini (Hymenoptera: Formicidae)

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The genera of the myrmicine ant tribe Dacetonini are revised and redefined. A phylogenetic analysis, new classification and key to genera are presented. Diagnoses of the genera and groups of genera are given and known aspects of their biology, taxonomy and distribution are summarized. The functional morphology of the mandible is investigated; two modes of action are differentiated and their significance is discussed. Nine genera are recognized: *Acanthognathus*, *Colobostruma*, *Daceton*, *Epopostruma*, *Mesostruma* (**gen. rev.**), *Microdaceton*, *Orectognathus*, *Pyramica* (**gen. rev.**) and *Strumigenys*. Seventeen names in the genus-group are newly synonymized with *Pyramica*: *Asketogenys*, *Chelystruma*, *Cladarogenys*, *Codiomyrmex*, *Codioxenus*, *Dorisidris*, *Dysedrognathus*, *Epitritus*, *Glamyromyrmex*, *Gymnomyrmex*, *Kyidris*, *Neostruma*, *Pentastruma*, *Serrastruma*, *Smithistruma*, *Tingimyrmex* and *Trichoscapa*.

KEYWORDS: Formicidae, Myrmicinae, Dacetonini, genera, mandible morphology, phylogeny, classification, key.

Introduction

A recent paper (Bolton, 1998) established the monophyly of a group of three myrmicine ant tribes (Basicerotini + Dacetonini + Phalacromyrmecini), together termed the dacetonine tribe group, and discussed the monophyly of each of the tribes within the group. The current contribution continues that study by investigating the generic composition of the largest of those tribes, the Dacetonini.

A synopsis of the taxonomic history of Dacetonini and its component genera was outlined in Bolton (1998). In summary, the generic classification of the tribe up to now is the product of a series of revisionary papers by Brown (1948, 1949a, b, c, 1950a, b, 1952a, 1953a, 1954a) which overlaid, refined and added to the concepts of earlier authors; other contributions were also made by Brown and Wilson (1959) and Brown and Carpenter (1979). By the end of this period the classification of the tribe was as follows.

Tribe Dacetonini

Subtribe Dacetoniti

Genera: *Acanthognathus*, *Daceton* (= *Dacetum*).

Subtribe Epopostrumiti

Genera: *Colobostruma* (= *Alistruma*, = *Clarkistruma*), *Epopostruma* (= *Hexadaceton*), *Mesostruma*, *Microdaceton*.

Subtribe Orectognathiti

Genus: *Orectognathus* (= *Arnoldidris*).

Subtribe Strumigenyiti

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*.

This classification, basically that given in Bolton (1994), was challenged the same year by Baroni Urbani and de Andrade (1994) who proposed many new synonyms. The main impact of that paper was the relegation of all the genus-group names of *Strumigenyiti* into junior synonymy under *Strumigenys*. The analysis that follows takes the classification listed above as its starting point, rather than the reduced number of terminal taxa of Baroni Urbani and de Andrade (1994), and adopts an opening hypothesis that every genus-group name listed be regarded as invalid until proved otherwise by the establishment of apomorphic characters.

The investigation is based upon the worker caste and includes all the 395 previously described dacetonine species listed in the census and catalogue (Bolton, 1995a, b), plus more than 250 undescribed species that are currently being compiled into a species-rank taxonomic survey of the entire tribe. Most if not all of the characters discussed in the text that follows are also applicable to known queens. Males are excluded from the survey for the simple reason that they remain unknown in some nominal genus-group taxa and unknown or only very scantily represented in most species groups within the larger genera. This means that selection of universal characters in this sex cannot even be implied, let alone be guaranteed. For similar reasons larvae are not utilized here. Baroni Urbani and de Andrade (1994) comment that larvae of over 40 dacetonine species have been described by G. C. Wheeler and J. Wheeler (1955, 1960, 1969, 1973, 1976, 1986, 1991), but this is only a small fraction of the more than 700 species now known and does not provide any concrete conclusions. Karyology of the tribe is in its infancy, with less than a dozen species investigated (Crozier, 1968; Imai *et al.*, 1977, 1984, 1985); comparative molecular data pertaining to dacetonines remains non-existent.

Most members of *Dacetonini* nest and forage in leaf litter, topsoil or rotten wood where they form small, usually monogynous, colonies. Only few forage 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 *smynthurid Collembola*, *Diplura*, *Symphyla*, *Chilopoda*, *Pseudoscorpiones*, *Acarina*, *Araneae*, *Isopoda*, *Amphipoda*, and many orders of small *Insecta* and their larvae (Wilson, 1954; Carlin, 1982; Masuko, 1985; Brown, 1971; Dejean, 1987a, b and included references). Species and individuals are common in Berlese or Winkler bag samples of leaf litter or rotten wood throughout the tropics, where they may be numerous or locally abundant (e.g. Belshaw and Bolton, 1994).

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 and Dlussky, 1991), and Japan in the East Palaearctic (Morisita *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).

Mandibles and the Dacetonini

The rather strange mandibles of dacetonines form one of the most striking general features of the tribe as a whole. In morphology and mode of action they do not conform to the general pattern seen elsewhere in the Myrmicinae, and their mode of action is only known to be duplicated by the related basicerotine ants. Structurally the mandibles are modified for a carnivorous lifeway and most of their specializations reflect techniques of prey seizure. Throughout the tribe the base of the mandible lacks the trulleum and canthellus (which may be an apomorphic loss or a plesiomorphic absence) but possesses a unique basimandibular process (figures 5, 14, 18, 54–56, 94, 101, 107, 113) that serves in the jaw-locking mechanism and is an apomorphy of Dacetonini.

Within the tribe, seizure of prey has a uniform initiation phase but thereafter follows one of two patterns. Before or during the approach to a prey animal the mandibles are opened and locked in that position. In most genera this is achieved by the basimandibular processes catching on the lateral margins of the labrum but in *Acanthognathus* the apices of the basimandibular processes themselves engage. This braces the mandibles open against the closing force of the adductor muscles. When the prey animal contacts the specialized trigger hairs on the dacetonine's mouthparts the basimandibular processes disengage, the full force of the already tensed adductor muscles is released and the mandibles close explosively in an extremely rapid strike (Brown and Wilson, 1959; Masuko, 1985; Dietz and Brandao, 1993; Gronenberg, 1996; Gronenberg *et al.*, 1998). In all short-mandibulate forms, and in some long-mandibulate taxa also, the strike is followed by static pressure of the mandibles. This is merely to retain a strong grip on the prey until the sting can be brought into use to kill or paralyse it. However, in most long-mandibulate dacetonines dissipation of the kinetic energy of the strike itself is intended to kill the prey, through shock or massive structural damage, or at least to shock it into immobility. The sting is not invariably used and often the prey is lifted clear of the substrate. The hunting strategies associated with these two techniques, outlined in more detail under *Pyramica* and *Strumigenys*, respectively, are associated with different mouthpart morphologies.

Static pressure mandibles

In full-face view static pressure mandibles are generally triangular to elongate-triangular (figures 22–43, 100, 106) but sometimes the mandible is narrowed so that it is sublinear or linear, pliar-like or forceps-like in appearance (figures 44–51). In a few the elongation may be extreme, up to a Mandibular Index of 85 (figure 59). The extreme ventral base of the mandible is broad (figures 89–91, 101). Dentition is usually serial, with numerous teeth and denticles on the masticatory margin, though some are almost edentate and others possess specialized dentition. Teeth are

usually much more numerous than in the following group and isolated enlarged apical teeth are rare. The maximum gape of the mandibles is $60\text{--}90^\circ$ and the labrum lacks specialized lateral projections (figures 52–56, 101, 107). The basimandibular processes are usually large and conspicuous when the mandibles are open (figures 42, 53–55), but are reduced in some groups (figure 56). When the mandibles close the basimandibular processes slide between the clypeus (above) and the labrum (below) and form a lock that prevents twisting or dislocation of the mandibles by struggling prey. The main mandibular function is to obtain and maintain a firm grip on prey. The initial strike is to establish that grip, the subsequent static pressure to retain it. Static pressure mandibles, regardless of shape and length, are universal in *Colobostruma* (figures 100–103), *Mesostruma* (figures 106–108) and *Pyramica* (figures 22–59) (Wesson and Wesson, 1939; Wilson, 1954; Masuko, 1985; Dejean, 1985a, b, 1988). In the first two of these the mandibles are always triangular, but in *Pyramica* variation in mandible morphology is extreme (see discussion under *Pyramica*). However, even *Pyramica* species with the longest mandibles (Brown, 1959b, 1960) retain a static pressure mode of action.

In the vast majority of taxa with this mode of mandibular action the principal dental row that is used to ensure a firm grip tends to be basal and consists of 4–7 teeth distal of the basimandibular process (figures 22–34). The teeth in this region are usually the largest and in some may be conical or very coarse (figures 39–42). However, some species have teeth or denticles of approximately equal size all along the masticatory margin (figures 35–37) and in some there are particular groups of teeth that have become specialized, to improve the mandibular grip at a particular point. In most of the foregoing species the masticatory margins of the two mandibles tend to oppose through most or all of their length at full closure. Taxa with more elongate or forceps-like mandibles tend to shift the principal gripping part of the mandible towards the apex and in many of these only the extreme apical portions oppose at full closure (figures 44–51).

It seems that narrowly opened mandibles followed by a convulsive snap at prey and subsequent static pressure of the mandibles is plesiomorphic within the dacetonine tribe group as a whole. Described predation in Basicerotini follows this pattern (Wilson, 1956; Wilson and Brown, 1985; Wilson and Hölldobler, 1986) and manipulation of the mandibles of both short-mandibulate and long-mandibulate basicerontines does not permit the enormous gape obtained by similar manipulation of dacetonines with a kinetic mode of mandibular action.

Kinetic mandibles

Kinetic mandibles in full-face views are always narrow, sublinear to linear and usually, though not always, long; at full closure they only engage at their extreme apices (figures 4, 10, 18, 71–82, 95). The extreme ventral base of the mandible tends to be narrow (figures 5, 12, 13, 18, 81, 82, 94). They have a small number of distally located teeth, some of which may be relatively large, and enlarged apical teeth are universal (figures 4, 7, 10–12, 18, 19, 71–86, 94–97, 113). The maximum gape of the mandibles is at least 170° . The labrum has specialized lateral projections that serve to prop the mandibles open at this extreme gape (figures 12, 13, 18, 81, 93, 94, 113), or the basimandibular processes alone may serve this function (figure 5). The main mandibular function is to kill or cripple prey by dissipation of the kinetic energy of the initial strike. Kinetic mandibles, regardless of shape and length, are universal in *Acanthognathus* (figures 4, 5, 7) (Dietz and Brandao, 1993; Gronenberg

et al., 1998), *Daceton* (figures 10–13) (Gronenberg, 1996), *Orectognathus* (figures 18, 19) (Brown, 1953b; Carlin, 1982), *Microdaceton* (figures 94–97), *Epopostruma* (figures 111, 113) and *Strumigenys* (figures 71–86, 90, 91) (Brown and Wilson, 1959; Masuko, 1985; Dejean, 1987b; Gronenberg, 1996).

The question arises: why are kinetic mandibles usually linear, long, slender and have only sparse dentition of relatively large apical teeth, whilst static pressure mandibles can exhibit enormous morphological variation? It is suspected that once a kinetic system has been initiated there would be intense selection pressure to maximize its efficiency and that relatively simple considerations would dictate the direction of evolution.

- (1) If a kinetic mandibular system is to work most efficiently (by instantly disabling or killing prey with a single snap) then longer mandibles are an advantage because of the greater kinetic energy at the apex when accelerated shut. Therefore there would be selection pressure to increase the length.
- (2) But the kinetic energy of the closing mandibles depends only upon work done by the adductor muscles in accelerating the mandibles shut; length of the mandibles is irrelevant. This implies that the upper limit to the length of the mandible depends only upon the maximum length and weight that the ant can physically manipulate, and the weight can be reduced by reducing its width. Hence the mandibles become slender.
- (3) However, in long mandibles the bite force at the apex will be only a fraction of the muscle force expended in closing the mandibles, and moreover the bite force will diminish as the mandible length increases. This may serve to impose an upper limit to mandible length so that it falls short of the maximum that the ant can physically manipulate.
- (4) Whatever the length of the mandibles the dissipation of the kinetic energy accumulated by accelerating them shut must be achieved most efficiently. There is therefore considerable selective advantage in having few but relatively exaggerated acute teeth close to the mandibular apex, which would both maximize the kinetic energy accumulated by closure and dissipate that energy through a small number of sharp points. This would maximize the shocking/killing ability of the strike.
- (5) As the strike efficiency increases so does its ability to utterly disable or kill outright. Thus the need invariably to follow the mandibular strike with a sting to subdue the victim would diminish.

Following this reasoning one would expect kinetic mandibles always to be relatively longer and more slender than static pressure mandibles, but there are exceptions. Some taxa with a kinetic mode of action have relatively short or apparently secondarily shortened mandibles (e.g. figures 78–80). Conversely, some taxa that utilize static pressure have evolved slender forceps-like mandibles with an apical grip (e.g. figures 46, 47, 49–51). This variation is probably because a few taxa, within either of the mandibular modes of action, have later and separately evolved specialized hunting techniques that are restricted to particular methods in particular habitats. For instance, extracting prey from narrow crevices, attacking prey in very confined spaces, or subduing prey animals that have specialized defences. Summing the standard MI (Mandibular Index) for all Afrotropical and Neotropical *strumigenyiform* species indicates that about 75% of *Pyramica* have an MI range of 5–30, whilst about 75% of *Strumigenys* have an MI range of 30–70. In *Pyramica* only

about 15% have $MI > 35$, whilst only 1.5% of *Strumigenys* species have $MI < 30$ (the remaining 23.5% of *Strumigenys* species have $MI > 70$). Thus the great majority of taxa with the kinetic mode of mandibular action do indeed have mandibles that are longer and more slender than those utilizing the static pressure technique.

Direction of evolution

The final problem that requires comment involves the direction of mandibular evolution within the Dacetoniini. Which of the kinetic or the static pressure modes of mandibular action, with their differing morphologies, was ancestral in the tribe?

Brown and Wilson (1959) presented an evolutionary scenario in which they postulated that those forms now regarded as having kinetic mandibles were ancestral and that forms with static pressure mandibles were derived from them. They supported this contention with behavioural considerations, regarding the hunting technique of kinetic forms as primitive because such taxa have a relatively short approach period toward prey, have an extremely violent trap-like action of the mandibles, and sometimes dispense with a sting-thrust following the mandible strike. In contrast, the static pressure forms were considered derived because they relied more on a very slow and stealthy approach to prey, had less shocking power but a more tenacious grip in the mandibular strike, and always followed the strike with a stinging thrust.

Philip Ward (University of California) has recently added support to the Brown–Wilson hypothesis. He pointed out that from the evidence of the phylogenetic analysis presented below it is most parsimonious to regard kinetic mandibles as plesiomorphic in the tribe as this requires only one origination (at base of Dacetoniini) followed by two reversals to static pressure mandibles (*Pyramica* and (*Colobostruma* + *Mesostruma*), see figure 3). Conversely, to regard static pressure mandibles as plesiomorphic would require four to six independent evolutions of the kinetic form. Despite all this the validity of the hypothesis remains dubious. It appears to be contradicted by evidence from the comparative morphology of the mouthparts, which implies that the static pressure system should be regarded as plesiomorphic. It is also possible that the Brown–Wilson interpretation of which hunting technique is primitive and which derived may be the wrong way round as Basicerotini have the supposedly derived pattern (Wilson, 1956; Wilson and Brown, 1985; Wilson and Hölldobler, 1986).

In static pressure taxa the labrum lacks lateral projections, the labral lobes are large and the maximum gape of the mandibles is small ($60\text{--}90^\circ$). All of these approximate the plesiomorphic conditions of the Myrmicinae as a whole and correspond to the conditions seen in the phylogenetically closely related tribes Basicerotini and Phalacromyrmecini. In kinetic taxa the labrum is usually T-shaped, with lateral projections (not in *Acanthognathus*, see below), the labral lobes are reduced or vestigial and the maximum gape of the mandibles is very large (170° or more). Such states are most definitely apomorphic conditions in terms of the Myrmicinae as a whole, and would also appear to be so in terms of the dacetonine tribe group.

Within the single very strongly supported clade *Strumigenys* + *Pyramica*, to develop a *Strumigenys*-like kinetic form of mandible from a *Pyramica*-like static pressure form the necessary morphological changes would include at least the following:

- (1) vastly increase the maximum gape of the mandibles;
- (2) develop lateral processes on the labrum so that the mandibles can be propped open at the increased gape;

- (3) reduce the labral lobes;
- (4) emphasize the mandibular strike capability over its gripping function;
- (5) lengthen and narrow the mandible;
- (6) lengthen the trigger hairs;
- (7) decrease the number of preapical teeth and enlarge a small number of apical teeth on the mandible.

A morphocline may operate in both directions, so reversal of these states would produce a static pressure form of mandible from a kinetic one. But all seven features noted above represent changes from more ancestral to more derived states. To run the morphocline in the reverse direction requires the re-acquisition of a whole suite of generalized states, and requires a reversion to conditions that closely approximate those seen in the related tribes *Basicerotini* and *Phalacromyrmecini*, from morphologically more derived states. This is not impossible, but it seems unlikely.

The unique mandibles of *Acanthognathus* (figures 4, 5, 7) also need to be considered. In this genus the labrum is vestigial (figure 6) and plays no part in the mandibular locking mechanism. At full gape the mandibles are held open solely by the abutting apices of the very long basimandibular processes. To derive this from the morphology of a static pressure mandible is quite easy, requiring only a narrowing of the labrum and increase in length of the basimandibular processes (e.g. figure 53). Derivation from the usual kinetic form, which has a broad T-shaped labrum (e.g. figures 13, 93), is more difficult. In fact the mouthparts of *Acanthognathus* (see discussion of genus) are so different from those of all the other kinetic taxa that it is difficult to envisage it having a common origin with them. The question then arises: if two origins of kinetic mandibles are possible within the tribe, then why not more?

Some other features reinforce this doubt. For instance the kinetic-mandibulate genera show two different developments of the mandibular apex. In *Daceton*, *Epopostruma* and *Strumigenys* the apex has a fork of two teeth that overlap at full closure; in *Acanthognathus*, *Orectognathus* and *Microdaceton* there are three teeth that interlock at full closure. This also may imply two originations of kinetic mandibles. Again, if two are possible then why not more?

In summary, the problem of direction of evolution with regard to the mandibles and their modes of action remains equivocal. If the strict parsimony hypothesis is accepted it implies that the history of the tribe began, probably in the early Tertiary, with a kinetic-mandible ancestor that radiated to produce other kinetic-mandible derivatives. Some, maybe all, of these have persisted to the present (*Daceton*, *Acanthognathus*, *Orectognathus*, *Microdaceton*, *Epopostruma*, *Strumigenys*), all except the last now with a very limited, or perhaps always limited, distribution. The last two named give rise to sister groups with static pressure mandibles (*Pyramica* and (*Mesostruma* + *Colobostruma*), respectively). *Pyramica* became so successful that like its progenitor *Strumigenys* it now has over 300 species and a world-wide distribution, being feebly represented only in Australia. The (*Mesostruma* + *Colobostruma*) pair, like their antecedent *Epopostruma*, remain mostly confined to Australia. The remainder either did not produce static pressure-mandible groups (if they did not then why not, as the adaptation is apparently extremely successful?), or they did so but the descendants later went extinct (in competition with *Pyramica*?).

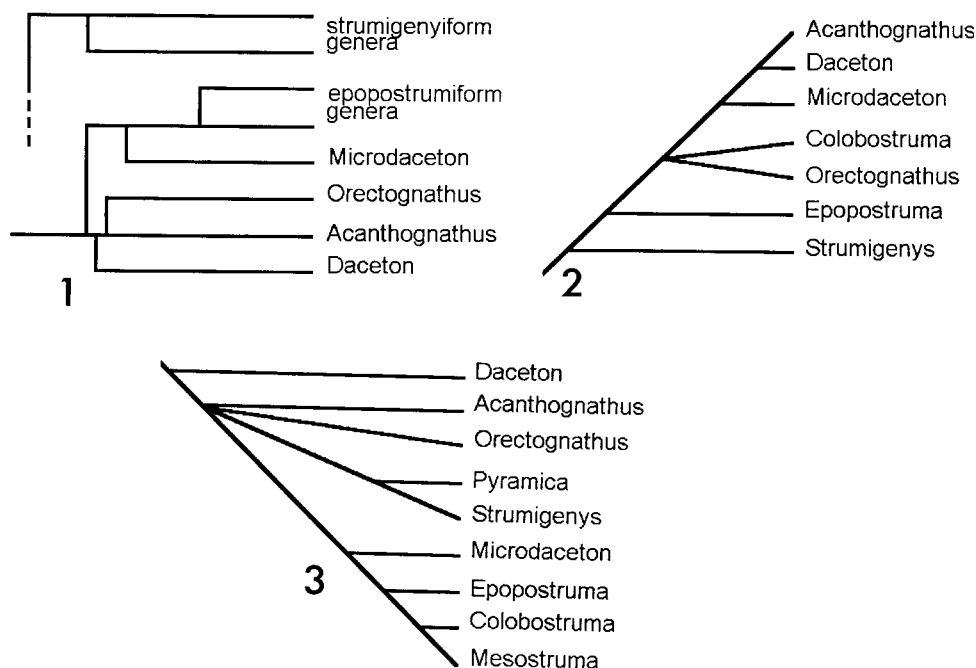
Alternatively, the early Tertiary common ancestor had static pressure mandibles

that functioned very like those of the Basicerotini. This quickly radiated into a number of genera only three of which now survive (*Pyramica*, *Colobostruma*, *Mesostruma*). However, several genera, both extant and now extinct, independently gave rise to forms with kinetic mandibles. Most of these had limited distributions but one (*Strumigenys*) was extremely successful. The static pressure mandible antecedents of genera such as *Acanthognathus* and *Daceton* later went extinct in competition with the enormously successful *Pyramica*. In Australia, hardly penetrated by *Pyramica*, the local group of static pressure forms (*Mesostruma* + *Colobostruma*) independently gave rise to their own kinetic derivative (*Epopostruma*).

Phylogeny of Dacetonini genera

Two earlier phylogenies have been presented for the genera of Dacetonini. The first of these was by Brown and Wilson (1959) and was largely intuitive; its main features are reproduced in figure 1. A cladistic analysis carried out by Baroni Urbani and de Andrade (1994) also included members of the tribes Basicerotini and Phalacromyrmecini. The section of their phylogeny covering the dacetonine genera is redrawn in figure 2.

In the current survey the nine monophyletic genera recognized were coded for the worker characters tabulated and described below. The matrix was analysed by Dr Philip S. Ward (University of California, Davis), using Hennig86. In the matrix four polymorphic characters were treated as ('?') and three characters (6, 16, 26) were treated as unordered. *Myrmica* was used as outgroup, with all states coded '0'



FIGS 1–3. Phylogeny of dacetonine genera. (1). Intuitive phylogeny of Brown and Wilson (1959), redrawn to show main features only. (2) Cladogram of Baroni Urbani and de Andrade (1994), redrawn to show only dacetonine genera (note that in this system *Pyramica* is included in *Strumigenys* and *Mesostruma* is included in *Colobostruma*). (3) Cladogram as result of current analysis.

except for characters 6, 7 and 10 which are not represented in Myrmicini and hence were coded as unknown. Use of the 'ie' command of Hennig86, which finds all the most parsimonious trees, resulted in four trees of length 59, consistency index 0.66, and retention index 0.70. The strict consensus tree derived from these is shown in figure 3.

The analysis provided support for the monophyly of five clades, in addition to the tribe itself: (*Pyramica* + *Strumigenys*); (*Mesostruma* + *Colobostruma*); {*Epopostruma* + (*Mesostruma* + *Colobostruma*)}; [*Microdaceton* + {*Epopostruma* + (*Mesostruma* + *Colobostruma*)}]; and all genera except *Daceton*.

The relevant characters and their effects on the classification are described or discussed in the section dealing with the genera. The failure of resolution of *Acanthognathus* and *Orectognathus*, where considerable ambiguity remains, is disappointing. It seems obvious that characters derived from worker morphology alone are insufficient to resolve this part of the phylogeny satisfactorily. Molecular data (currently non-existent), or perhaps even characters of the larvae (currently insufficient) or males (inadequately known), when they become available, may contribute to solving the problem.

List of characters

- (1) Maxillary palp with five segments (0); with three segments (1); with one or no segments (2).
- (2) Labial palp with three segments (0); with two segments (1); with one segment (2).
- (3) Labrum not T-shaped (0); labrum T-shaped (1).
- (4) Labrum capable of full reflexion over buccal cavity, able to close tightly over labio-maxillary complex (0); labrum not capable of full reflexion over buccal cavity, not able to close tightly over labio-maxillary complex (1).
- (5) Labral shield not hypertrophied, not concealing entire buccal cavity (0); labral shield enormous, hypertrophied, when reflexed concealing entire buccal cavity (1).
- (6) Trigger hairs labral and paired, lateral (0); trigger hair labral and single, median (1); trigger hairs on mandible, not labrum (2).
- (7) Mandibles engaging through most of their length (0); mandibles engaging only apically (1).
- (8) Mandibles with apical two to three teeth overlapping (0); mandibles with apical two to three teeth interlocking (1).
- (9) Basimandibular process absent (0); basimandibular process present (1).
- (10) Basimandibular process an evenly rounded thick lobe (0); basimandibular process a spur, dentiform or lamellate (1).
- (11) Antenna with 11 segments (0); antenna with four to six segments (1).
- (12) Two-segmented antennal club indistinct (0); two-segmented antennal club developed (1).
- (13) Scape when laid back in normal resting position passing above the eye (0); scape when laid back in normal resting position passing below the eye (1).
- (14) Scape not downcurved at extreme base (0); scape downcurved at extreme base (1).
- (15) Scape apical section not angled anteriorly (0); scape apical section angled anteriorly (1) (full-face view with scape extended in both instances).

Character matrix

Taxon

Myrmica
Acanthognathus
Colobostruma
Daceton
Epopostruma
Mesostruma
Microdaceton
Orectognathus
Pyramica
Strumigenys

Character number

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	
0	0	0	0	0	?	?	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
2	2	0	1	0	2	1	1	1	1	1	0	1	0	0	1	0	0	0	0	1	1	0	1	1	2	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	?	0	0	0	0	1	1	0	1	1	1	1	0	1	0	1	0	1	0	1
0	0	1	1	0	0	1	0	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	0	2	0	0	0	1	1	0	1	1	1	1	0	1	0	1	0	1	0	1
0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0	2	0	0	0	1	1	0	1	1	1	1	0	1	0	1	0	1	0	1
1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	0	0	1	1	0	1	1	0	1	1	1	1	0	1	1	0	1	0	1	0
0	0	1	1	0	0	1	1	1	1	1	0	0	1	?	0	0	0	0	0	1	0	0	?	1	0	0	0	0	0	0	0	0	0	0
2	2	0	1	0	0	?	0	1	1	1	1	0	1	0	1	1	0	1	1	1	0	1	0	1	0	1	1	1	0	0	1	0	1	0
2	2	1	1	0	0	1	0	1	1	1	1	1	0	1	0	1	1	0	1	1	1	0	1	0	1	0	1	1	1	0	0	1	0	1

- (16) Scrobe absent (0); scrobe present that extends above eye (1); scrobe present that extends below eye (2).
- (17) Eye in profile view not ventrolateral (0); eye in profile view ventrolateral (1).
- (18) With mandible at full closure and in profile no gap present between base of mandible and margin of head capsule (0); with mandible at full closure and in profile a gap present between base of mandible and margin of head capsule (1).
- (19) Basimandibular gland absent (0); basimandibular gland present (1).
- (20) Apicofemoral and apicotibial glands absent (0); apicofemoral and apicotibial glands present (1) (bullae usually visible).
- (21) Metapleural gland orifice visible (0); metapleural gland orifice not visible (1).
- (22) Metapleural gland bulla widely separated from annulus of propodeal spiracle (0); metapleural gland bulla abutting or very close to annulus of propodeal spiracle (1).
- (23) Hair-lined gland of mesopleural anterior margin absent (0); hair-lined gland of mesopleural anterior margin present (1).
- (24) Promesonotum without cuticular processes (0); promesonotum with cuticular processes on pronotum, mesonotum or both (1).
- (25) Propodeal spiracle in profile view at about midlength of sclerite (0); propodeal spiracle in profile view close to or at declivity (1).
- (26) Metapleural gland bulla low and widely separated from propodeal spiracle (0); metapleural gland bulla low and abutting propodeal spiracle (1); metapleural gland bulla high and abutting propodeal spiracle (2).
- (27) Bizarre pilosity not developed (0); bizarre pilosity developed (1).
- (28) Petiole and postpetiole without lateral (tergal) or ventral (sternal) lobes or outgrowths of any form (0); petiole and postpetiole with lateral (tergal) or ventral (sternal) lobes or outgrowths of some form (1).
- (29) Petiole and postpetiole without discretely arranged lateral (tergal) or ventral (sternal) lobes of spongiform tissue (0); petiole and postpetiole with discretely arranged lateral (tergal) or ventral (sternal) lobes of spongiform tissue (1).
- (30) Tergite of petiole and postpetiole without lateral cuticular processes (0); tergite of either petiole or postpetiole with lateral cuticular processes (1).
- (31) Postpetiolar spiracle lateral (0); postpetiolar spiracle ventral (1).
- (32) Limbus (defined below) absent from first gastral tergite (0); limbus present on first gastral tergite (1).
- (33) Suture between first gastral tergite and sternite rounded laterobasally (0); suture between first gastral tergite and sternite angulate laterobasally (1).
- (34) Base of first gastral sternite not truncated (0); base of first gastral sternite truncated (1).

A single new morphological term is introduced, the **limbus**. This is a raised cuticular crest or ridge that traverses the width of the first gastral tergite close to its base. It arises some distance behind the true base of the tergite and is inclined anteriorly so that it overlaps and conceals the true base and the presclerites of the segment (figures 64, 92; see also figures 65–70, 87–91).

The genera of Dacetonini

The nine genera recognized as a result of this analysis are individually diagnosed and discussed below. Paragraphs defining monophyletic groups of genera have been inserted where such groups have been definitely identified. In the diagnoses of the genera an unequivocal autapomorphy is indicated by [A] immediately following the character; for groups of genera a synapomorphy is indicated by [S]. Plesiomorphic characters with value in identification are included in the generic diagnoses. For a discussion of the monophyly of Dacetonini and related tribes see Bolton (1998).

Acanthognathus Mayr

(Figures 4–9)

Acanthognathus Mayr, 1887: 578. Type-species: *Acanthognathus ocellatus* Mayr, 1887: 579, by monotypy.

Diagnosis of genus (workers)

Mandibles linear and elongate (figures 4, 5), their bases extremely closely approximated (figure 6) [A] and with kinetic mode of action, each with an apical fork of three spiniform teeth that interlock at full closure. Preapical dentition sometimes present but often absent.

Mandibles at full gape open to 170° or more.

Basal process of mandible a long curved spur that is minutely bifurcated apically [A]; when mandibles fully closed the basal processes cross over and are ventral to the labrum and the apex of the labio-maxillary complex (figures 5, 7) [A]; when fully open the mandibles are braced in that position by opposition of the basal processes alone [A].

Trigger hairs arise from the mandibles (one from each) [A]; trigger hairs lie flat against margin when mandible closed, becoming erect as mandible opens [A].

Palp formula 0,1 [A].

Labrum extremely reduced to vestigial, represented by a narrow Y-shaped sclerite (figure 6) [A]; labrum not taking part in mandibular locking mechanism [A].

Buccal cavity narrow, parallel-sided anteriorly; labio-maxillary complex narrow.

Clypeus long and narrow in full-face view, its median portion very narrow posteriorly, narrower than either of the frontal lobes where it passes between them (figure 4).

Eye not located ventrolaterally on side of head.

Antenna with 11 segments, the two apical segments forming a well-developed club (figure 4).

Scape, when laid back in its normal resting position, passes above the relatively large eye; apical portion of extended scape curved anteriorly when seen in full-face view; scape not abruptly downcurved near base.

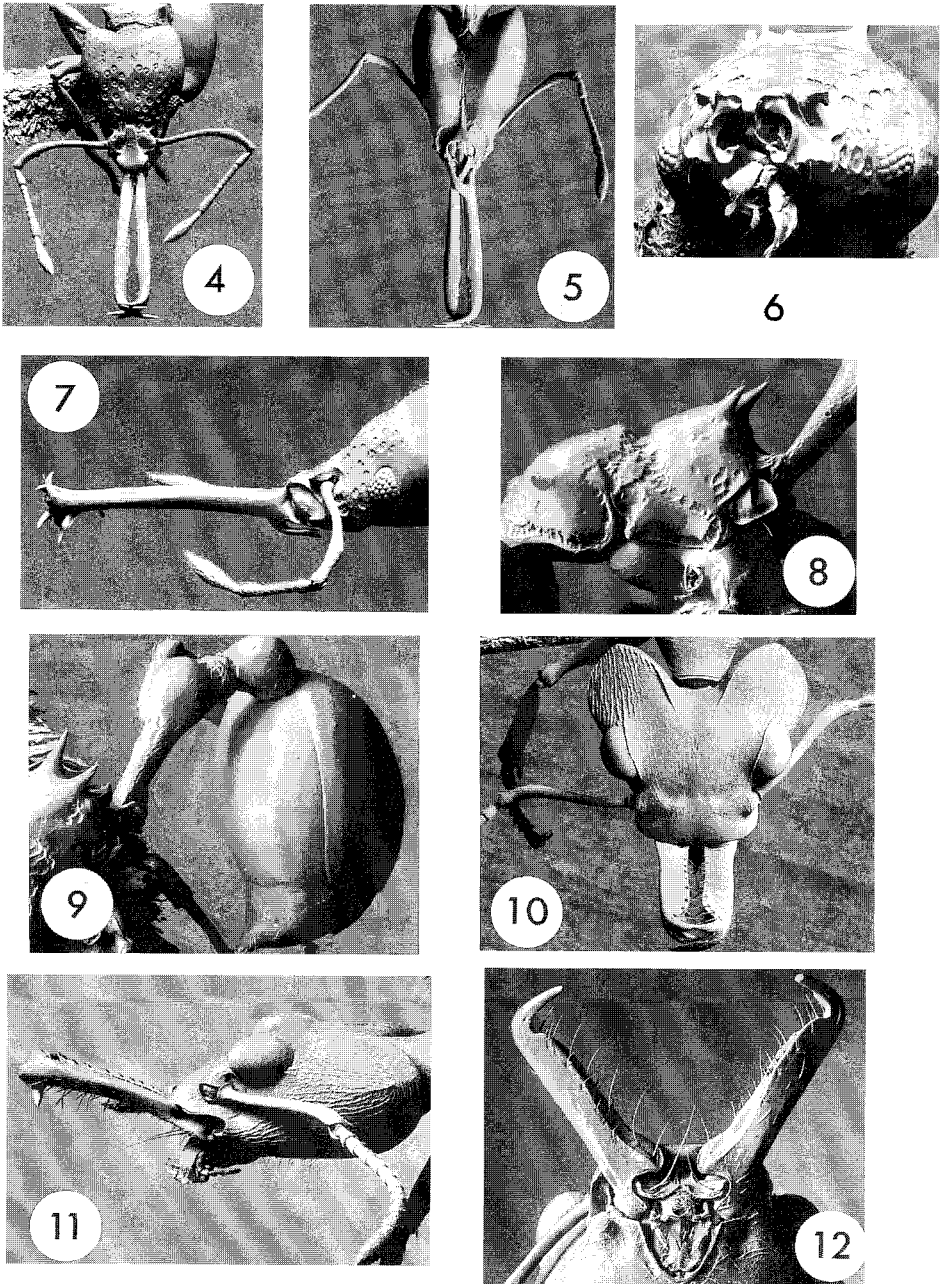
Scrobes absent.

Pronotal humeri each with a cuticular tumulus or low bluntly triangular tooth-like process.

Propodeal spiracle high on side of sclerite and close to margin of declivity when seen in profile (figure 8).

Metapleural gland bulla hypertrophied, extending obliquely upward and its dorsal-most point about level with the dorsal-most point of the annulus of the propodeal spiracle [A].

Waist segments without spongiform tissue and without lateral laminar cuticular



FIGS 4–12 Dacetonine workers. (4–9) *Acanthognathus brevicornis*. (4) Full-face view of head. (5) Ventral view of head. (6) Anterior view of head, mandibles removed and labio-maxillary complex depressed. (7) Profile of mandible and anterior head. (8) Profile of alitrunk. (9) Oblique view of waist segments and gaster. (10–12) *Daceton armigerum*. (10) Full-face view of head. (11) Profile of head. (12) Ventral view of anterior head, mandibles ajar.

processes (figure 9); petiole node unarmed; postpetiole not dorsoventrally flattened; postpetiolar spiracle lateral.

Limbus absent from first gastral tergite (figure 9); suture between first gastral tergite and sternite evenly rounded laterobasally; basigastral costulae absent.

In the evolution of its mouthparts *Acanthognathus* has followed a unique route, radically different from all the other dacetonine genera (Dietz and Brandao, 1993; Gronenberg *et al.*, 1998). In all other dacetonines the basimandibular processes pass below the clypeus and above the labrum when the mandibles close, and at full closure the apices of the processes lock into a depression on the dorsal surface of the labrum, near its base. In this fully closed position the basal processes, sandwiched between clypeus and labrum, effectively lock the mandibles and prevent them twisting or rolling. In *Acanthognathus* the basimandibular processes are represented by long spurs that abut apically when the mandibles are fully open. They serve to brace the mandibles in the fully open position, against the potential closing force of the adductor muscles, prior to striking at prey. When the mandibles are closed the basal mandibular processes pass ventral to the extremely reduced labrum and extend posteriorly below the apical portions of the labio-maxillary complex (figures 5, 7).

The extremely reduced labrum takes no part in the mandibular locking mechanism and its reduction may be a consequence of this loss of function. It is represented only by a slender sclerite, roughly Y-shaped, and apparently serves only to separate and brace the extreme inner bases of the mandibles when they close, and to allow a slight rotation of the mandibles as they open. As a consequence of the extreme labral reduction the mandibular articulations are more closely approximated here than in any other dacetonine genus (figure 6) and the buccal cavity is short but narrow.

Perhaps also because of labral reduction the trigger hairs are not located there, as they are in all other dacetonine genera. Instead they arise on the mandibles in *Acanthognathus* and are erectile, lying flat against the inner margin of the mandible when it is closed and becoming erect as the mandible opens (Dietz and Brandao, 1993; Gronenberg *et al.*, 1998), a unique mechanism found only here among the entire Myrmicinae.

Palp formula (PF) for the genus was given as 5,3 by Brown (1954a) and this count has been repeated in subsequent papers (e.g. Brown and Kempf, 1969; Baroni Urbani and de Andrade, 1994). In actuality all sexes and castes of this genus appear to have PF 0,1 (dissections of workers of *A. ocellatus*, *A. rudis*, *A. brevicornis*, and *in situ* observation of queens of these three, worker of *A. teledectus* and male of *A. brevicornis*).

The metapleural gland is strangely hypertrophied in *Acanthognathus*, its externally visible bulla being relatively much larger here than in any other dacetonine genus. The bulla is not apparent in scanning electron microscope photographs (figure 8) but its structure is obvious under light microscopy. This is because light can penetrate the thin cuticle of the bulla but an electron beam is fully reflected from its surface. In profile the dorsal-most point of the gland bulla is at least level with the top of the annulus of the propodeal spiracle, and the spiracle itself is located high on the side of the propodeum.

Acanthognathus is a small, compact and easily defined genus. Its species were first keyed by M. R. Smith (1944) and a revision of the genus with an expanded key was provided by Brown and Kempf (1969). The genus is distributed only in the

Neotropical region and contains six extant species and one fossil form from the Dominican Amber (Baroni Urbani and de Andrade, 1994). The known species are as catalogued in Bolton (1995b) and aspects of biology and behaviour of the species are described by Brown and Kempf (1969) and Dietz and Brandao (1993). An outline of the distribution of the species can be obtained from Kempf (1972) and Brandao (1991).

Hunting behaviour in *A. rudis* has been summarized by Gronenberg *et al.* (1998). The hunting ant moves slowly towards a prey animal with its mandibles open to about 160° (maximum gape is over 200°) until antennal contact is made, confirming prey identity. The ant then orientates its body in line with the prey, draws back its antennae, fully opens the mandibles and continues its slow approach until contact is made with the mandibular trigger hairs. This initiates an extremely rapid strike which the authors estimate takes less than 2.5 ms, and may be as quick as 1 ms.

***Daceton* Perty**

(Figures 10–17)

Daceton Perty, 1833: 136. Type-species: *Formica armigera* Latreille, 1802: 244, by monotypy *Dacetum* Agassiz, 1848: 332, unjustified emendation of *Daceton* [Synonymy by Brown, 1973b: 179]

Diagnosis of genus (workers)

Mandibles linear and elongate (figures 10–12), with kinetic mode of action, each with an apical fork of two teeth that overlap at full closure; lower tooth the largest; preapical dentition absent. Base of mandible highly polished dorsally and with a longitudinal deep cleft that extends distally from the vicinity of the mandalus (figure 14) [A].

Mandibles at full gape open to 170° or more.

Basal process of mandible a broadly rounded shallow lobe (figure 14); at full mandibular closure process is dorsal to labrum and fits into a mediadorsal impression on labrum (figures 12, 13).

Palp formula 5,3.

Labrum roughly T-shaped (figure 13), short and not capable of reflexing to conceal the labio-maxillary complex, which is permanently exposed. Each lateral labral arm locks into a deep emargination near the inner mandibular base at closure (figure 12).

A single long trigger hair arises from each transverse arm of the T-shaped labrum (figures 12, 13).

Side of head with a broad gap between base of mandible and margin of head capsule when mandibles fully closed (figure 11).

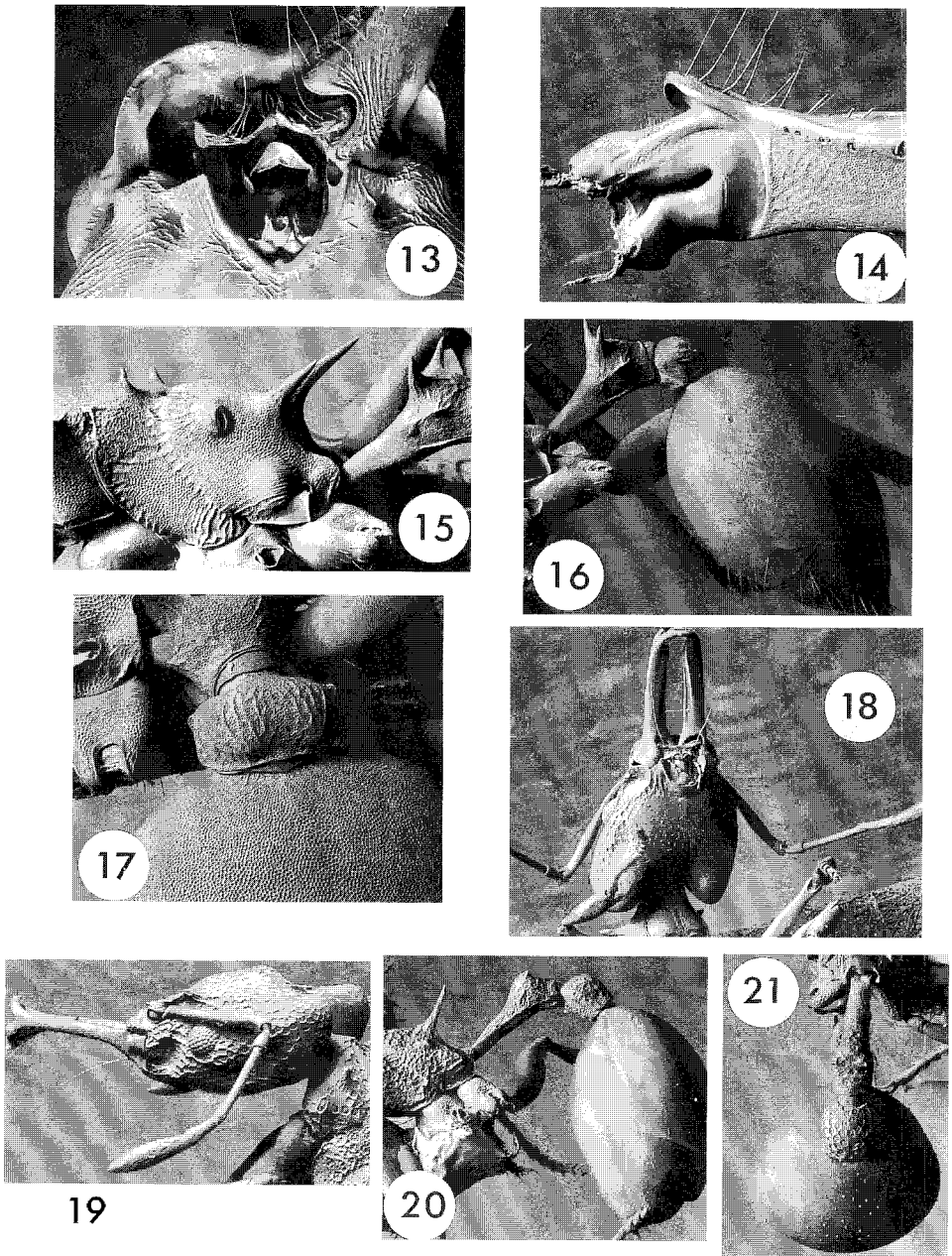
Frontal lobes absent (figures 10, 11) [A]; antennal socket surrounded only by an enlarged torulus, the dorsal part of the torulus hypertrophied above the condylar bulb [A].

Eye large, set upon on a broad low cuticular prominence (figure 11) [A], not sessile, not located ventrolaterally on side of head.

Occipital foramen located very high on occiput [A].

Antenna with 11 segments, without a distinctly differentiated club (figure 11).

Scape, when laid back in its normal resting position, passes below the eye (figures 10–12) [A]; apical portion of extended scape curved anteriorly when seen in full-face view; scape not abruptly downcurved near base.



FIGS 13-21. Dacetonine workers. (13-17) *Daceton armigerum*. (13) Buccal cavity, labio-maxillary complex and right mandible removed. (14) Dorsal view of base of right mandible, basimandibular process uppermost. (15) Profile of alitrunk. (16) Profile of waist segments and gaster. (17) Dorsal view of postpetiole and base of gaster. (18-21) *Orectognathus* species. (18) Oblique ventral head of *O. versicolor*. (19-21) *O. clarki*. (19) Profile of head. (20) Profile of waist segments and gaster. (21) Dorsal view of waist segments and gaster.

Scrobe absent.

Pronotal humeri spinose; mesonotum with a pair of sharp tubercles.

Propodeal spiracle high on side and far forward, at about the midlength of the sclerite (figure 15). Orifice of propodeal spiracle vertically oval [A], not round.

Metapleural gland bulla with its apex widely separated from propodeal spiracle (figure 15); orifice of metapleural gland posterior, visible.

Waist segments without spongiform tissue and without lateral laminar cuticular processes; petiole node bidentate; postpetiole not dorsoventrally flattened; post-petiole spiracle lateral (figure 16).

Limbus absent from first gastral tergite (figure 17); suture between first gastral tergite and sternite evenly rounded laterobasally; basigastral costulae absent.

A monotypic and easily defined genus confined to rain-forest areas in the Neotropics (Wilson, 1962; Kempf, 1972). The sole species (*D. armigerum*) is an arboreal forager and has a polymorphic worker caste. Worker polymorphism is rare in dacetonines. Apart from *Daceton* itself it has been developed only in one species of *Orectognathus* (see there) and a single small species group of *Strumigenys* in New Guinea, the *loriae*-group. Aspects of the ecology and behaviour of *Daceton armigerum* have been investigated by Wilson (1962) and the mode of action of its mandibles has been described in great detail by Gronenberg (1996). Physical castes of the *Daceton* worker have been investigated by Moffett and Tobin (1992).

In the old classification (Brown, 1952b, 1954a; Brown and Wilson, 1959) *Daceton* and *Acanthognathus* were linked, through characters of high antennomere count (11) and high palp formula (5,3), in a subtribe Dacetiti. Both these characters are plesiomorphic and therefore of limited phylogenetic value, though interesting in a diagnostic sense. Unfortunately one of them, PF 5,3, is now known to be incorrect for *Acanthognathus* where its true value is 0,1. This, combined with the results of the phylogenetic analysis, indicates that 'subtribe Dacetiti' has no foundation in reality. Interestingly, in earlier references *Daceton* was always regarded as the 'basal' genus of the tribe but Wilson (1962) suggested that *Acanthognathus* may occupy that position on behavioural grounds. The morphological analysis presented here reinstates the original view, indicating that *Daceton* is the sister group of the remainder of the tribe.

As in the epopostrumiform genera the scape of *Daceton*, when laid back in its normal resting position, passes below the eye rather than above it. This is certainly autapomorphic in each case as it has been achieved by very different adaptations. In *Daceton* the eye is elevated on a cuticular prominence and the scape is straight; in the epopostrumiforms the eye is sessile and the scape strongly downcurved basally (compare figure 11 with figures 102, 108, 111).

Orectognathus F. Smith

(Figures 18–21)

Orectognathus Smith, F. 1853: 227. Type-species: *Orectognathus antennatus* Smith, F. 1853: 228, by monotypy

Arnoldidris Brown, 1950b: 143. Type-species: *Orectognathus chyzeri* Emery, 1897: 571, by original designation. [Synonymy by Brown, 1973b: 178 (provisional); Taylor, 1977: 581 (confirmed)]

Diagnosis of genus (workers)

Mandibles linear and elongate (figures 18, 19), with kinetic mode of action, each with an apical fork of three spiniform teeth that interlock at full closure.

Mandibles at full gape open to 170° or more.

Basal process of mandible a curved spur; at full mandibular closure process is dorsal to labrum and fits into a mediodorsal impression on labrum (figure 18).

Palp formula 5,3.

Labrum roughly T-shaped, short and not capable of reflexing to conceal the labio-maxillary complex, which is permanently exposed. Each lateral labral arm locks into a deep emargination near the inner mandibular base (figure 18).

A single long trigger hair arises from each transverse arm of the T-shaped labrum.

Eye not located ventrolaterally on side of head (figure 19). Antenna with five segments [A], of which the second funicular segment (= third antennal) is an elongate bar-like fusion segment (figures 18, 19) [A]; with a weakly differentiated apical club of two segments.

Scape, when laid back in its normal resting position, passes above the eye (figure 19); apical portion of extended scape not to distinctly curved anteriorly when seen in full-face view; scape slightly downcurved near base.

Scrobe absent to weakly present.

Pronotal humeri and mesonotum armed or unarmed, the former more usual.

Propodeal spiracle well in front of margin of declivity, at approximately the midheight of the sclerite (figure 20).

Metapleural gland bulla small, with its apex widely separated from the propodeal spiracle.

Waist segments without spongiform tissue and without lateral laminar cuticular processes (figures 20, 21); petiole node unarmed to bidentate; postpetiolar spiracle lateral.

Limbus absent from first gastral tergite; suture between first gastral tergite and sternite rounded laterobasally; basigastral costulae absent (figures 20, 21).

Orectognathus was placed in its own subtribe, *Orectognathiti*, in the earlier classification (Brown, 1954a; Brown and Wilson, 1959) because of its elongate bar-like second funicular segment and consistently five-segmented antennae. The first character remains as a striking autapomorphy of the genus although a few species with five-segmented antennae are now also known in *Pyramica* and *Colobostruma*. However, in both these genera the majority of species have six antennomeres and some have four; in *Orectognathus* all have five. Thus in *Orectognathus* the acquisition of five-merous antennae can be interpreted as a single evolutionary event whereas the species with five antennomeres in *Pyramica* and *Colobostruma* are certainly stages in independently derived morphoclinal reductions of antennomere number (and in which the second funicular segment reduces in size rather than enlarges). Their antennal segment count cannot be considered homologous with that of *Orectognathus*.

The species-rank taxonomy of *Orectognathus* has been extensively investigated, with major contributions by Brown (1953b, 1958), Taylor and Lowery (1972) and Taylor (1977, 1978, 1980). What little is known of the general biology is summarized by Brown (1953b), who also observed that *O. clarki* had a maximum mandibular gape of over 180°. Of the 29 described species (Taylor, 1980) one, *O. versicolor*, has evolved worker polymorphism. Division of labour in this species has been studied

by Carlin (1982) and contrasted with the worker polyethism described by Wilson (1962) in the polymorphic *Daceton armigerum*. Hölldobler (1982) has shown that *O. versicolor* is also a trail-layer, a rare feature among the dacetonines.

The strumigenyiform genera (figures 22–93)

The two genera included here, *Strumigenys* and *Pyramica*, together form an emphatically monophyletic and extremely speciose group whose distribution is world wide. They form Brown's (1954a) old subtribe Strumigenyiti and are united by the following characters within the Dacetonini.

Palp formula 0,1 or 1,1 [S].

Labrum not capable of reflexion over buccal cavity, not closing tightly over labio-maxillary complex (figures 42, 52–59, 81, 82).

Basal process of mandible a lamella (the basal lamella, figures 42, 53–56) [S].

Antenna with four, five or six segments, the two apical segments forming a distinct club (e.g. figures 35, 38, 41, 51, 58, 72, 77, 79).

Scape, when laid back in its normal resting position, passes above the eye (figures 60–63, 65–70, 83–86, 90, 91); basal part of scape downcurved.

Scrobe usually distinctly present, extending above the eye (figures 60–63, 65–70, 83–86, 90–91).

Eye located ventrolaterally on side of head, at or close to the ventrolateral margin (figures 60–63, 65–70, 83–86, 90–91) [S].

Series of paired exocrine glands present on scapes, femora, tibiae and mesopleuron (discussed below) [S].

Metapleural gland with apex of bulla widely separated from the annulus of the propodeal spiracle (figures 64, 87).

Propodeal spiracle located high on side of sclerite and very close to or at the margin of the declivity (figures 65–70, 87–91).

Waist segments with spongiform tissue present that is arranged in discrete lobes on both tergites and sternites (figures 64–70, 87–91) [S] (discussed below).

Postpetiolar spiracle lateral (frequently concealed by spongiform tissue).

Limbus present on first gastral tergite (figures 64, 92; see also figures 65–70, 87–91) [S].

Suture separating first gastral tergite and sternite evenly rounded laterobasally.

First gastral sternite truncated basally [S].

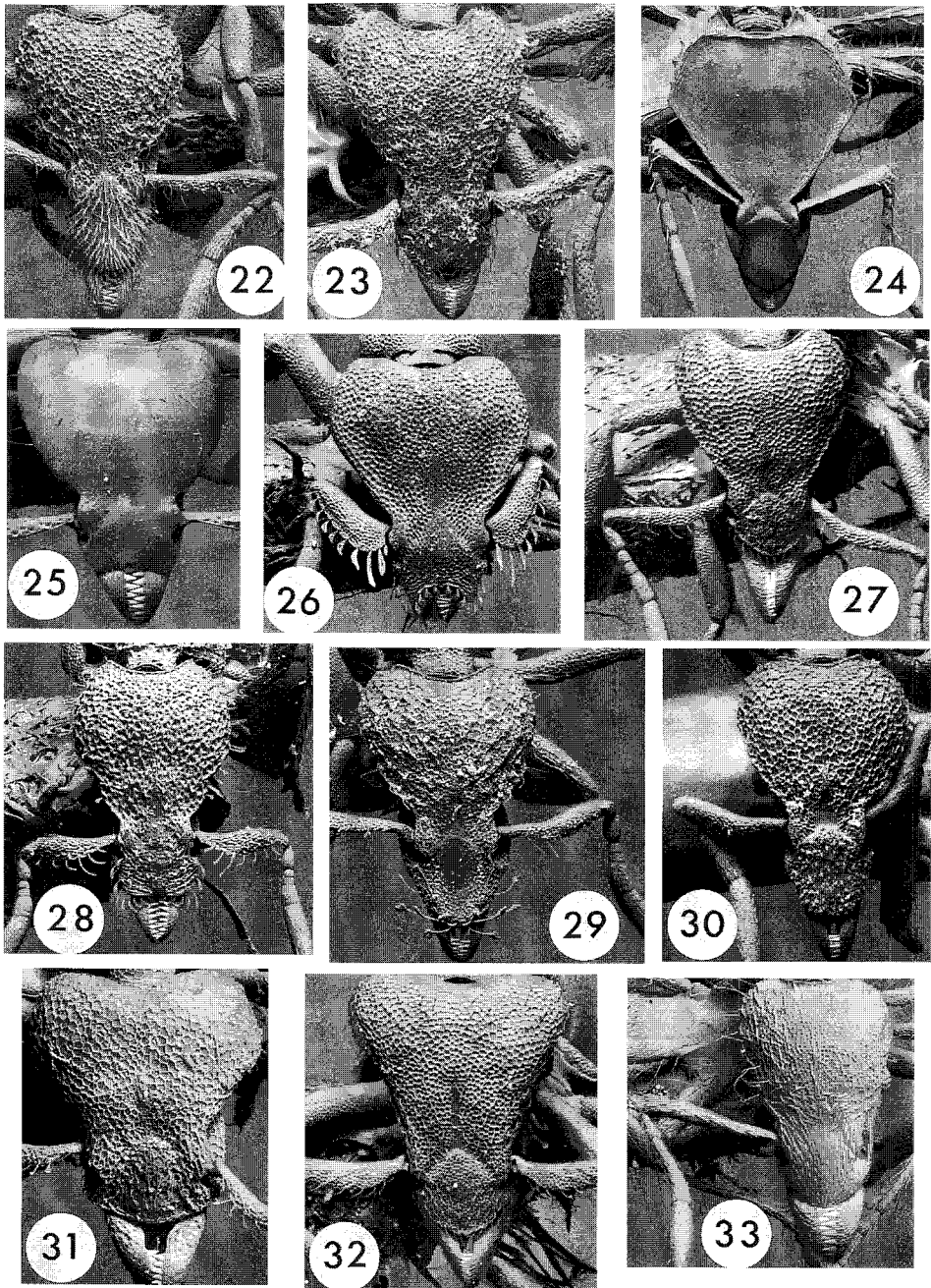
Bizarre pilosity of some form usually developed [S] (discussed below).

The extremely reduced palp formula is apomorphic in this group, having certainly been achieved independently of the similar count seen in *Acanthognathus*.

Presence of a mandibular basal lamella is universal; only in some species of the Afrotropical *Pyramica lujae*-group has its function changed. In most species of this group the basal lamella, instead of forming part of the locking mechanism of the mandible, has become denticulate on its inner free margin and been pressed into service as part of the masticatory margin (Bolton, 1983).

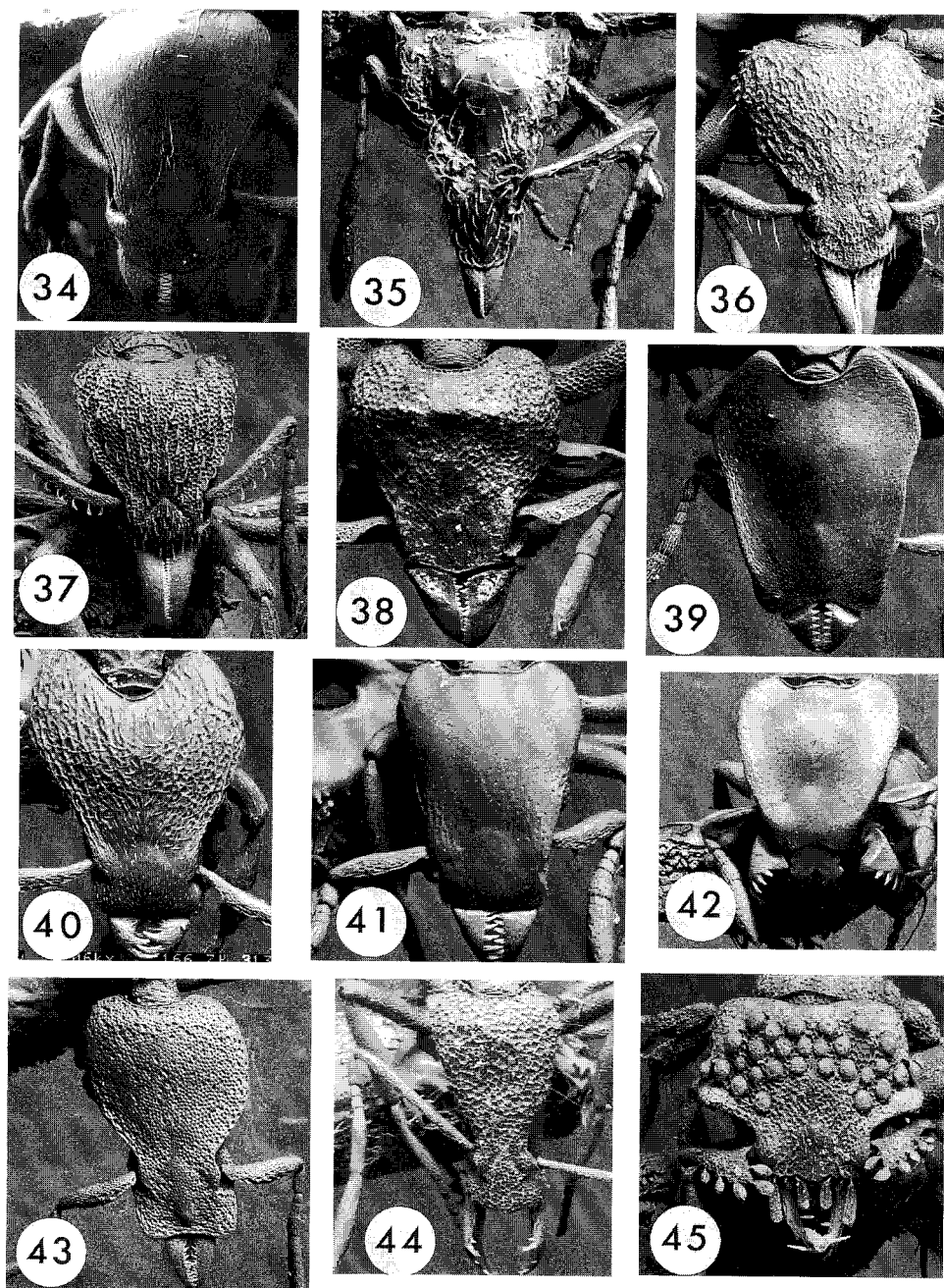
Exocrine glands

Exocrine glands are extensively developed in a number of fixed locations throughout this group. Many species groups in both genera exhibit distinctive bullae for all the glands but in some species groups, or in isolated species within groups, one or more of the glands may be hypertrophied, or conversely may be reduced or

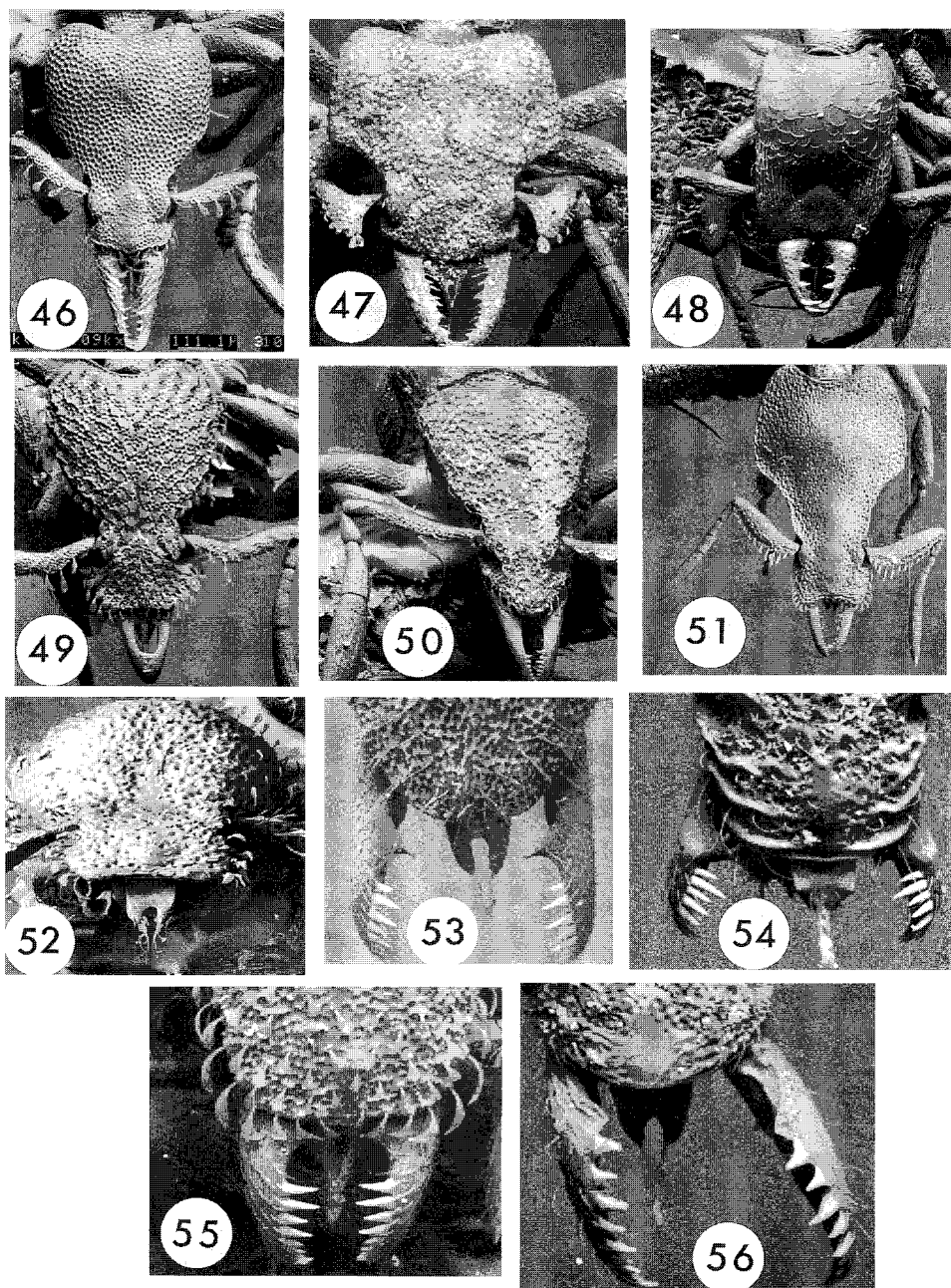


FIGS 22–33. Dacetonine workers; *Pyramica* species. Full-face view of head. (22) *pilinasis*. (23) *margaritae*. (24) n. sp. (25) n. sp. (26) *tigrilla*. (27) *alberti*. (28) *hensekta*. (29) *ornata*. (30) *filitalpa*. (31) n. sp. (32) *media*. (33) n. sp. (New species to be described in forthcoming publication.)

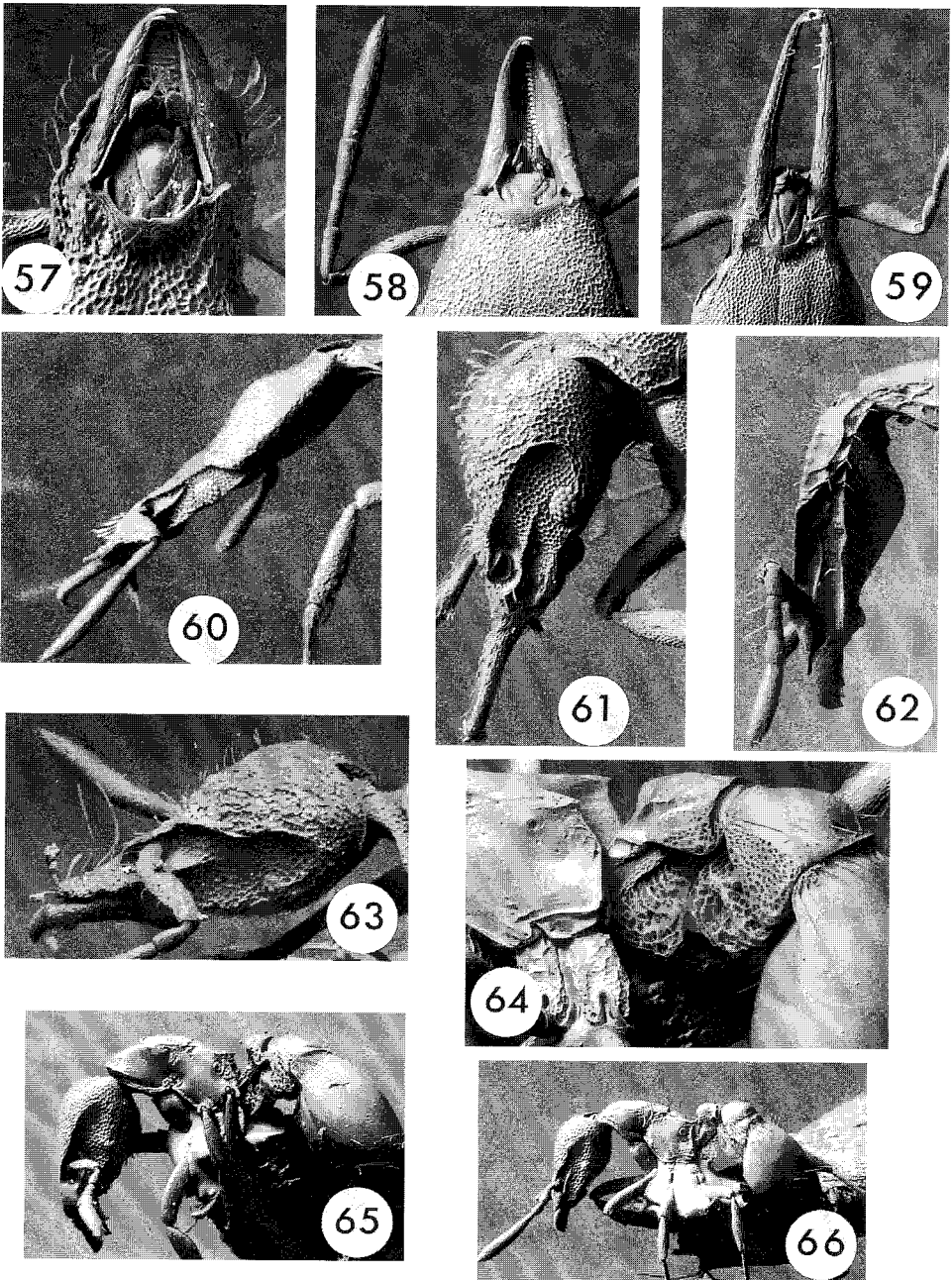
apparently absent, at least not discernable by external examination. The observed variation in size and presence or apparent absence of one or more of the glands can only be derived from a basic pattern where all the glands are present.



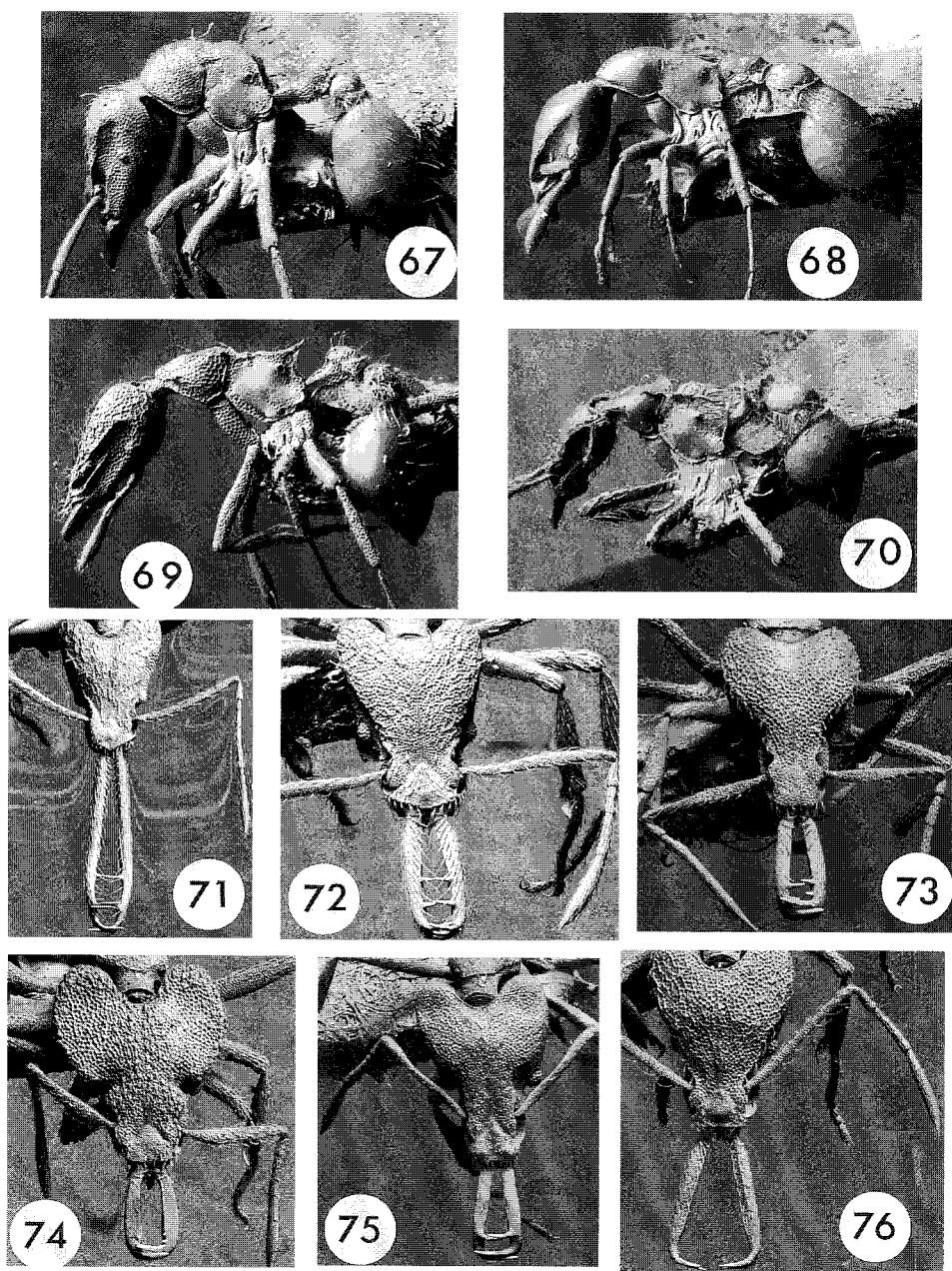
FIGS 34-45. Dacetonine workers; *Pyramica* species. Full-face view of head. (34) n. sp. (35) *mirabilis*. (36) n. sp. (37) *maynei*. (38) n. sp. (39) n. sp. (40) n. sp. (41) n. sp. (42) *tetragnathus*. (43) *canina*. (44) *acubecca*. (45) *roomi*. (New species to be described in forthcoming publication.)



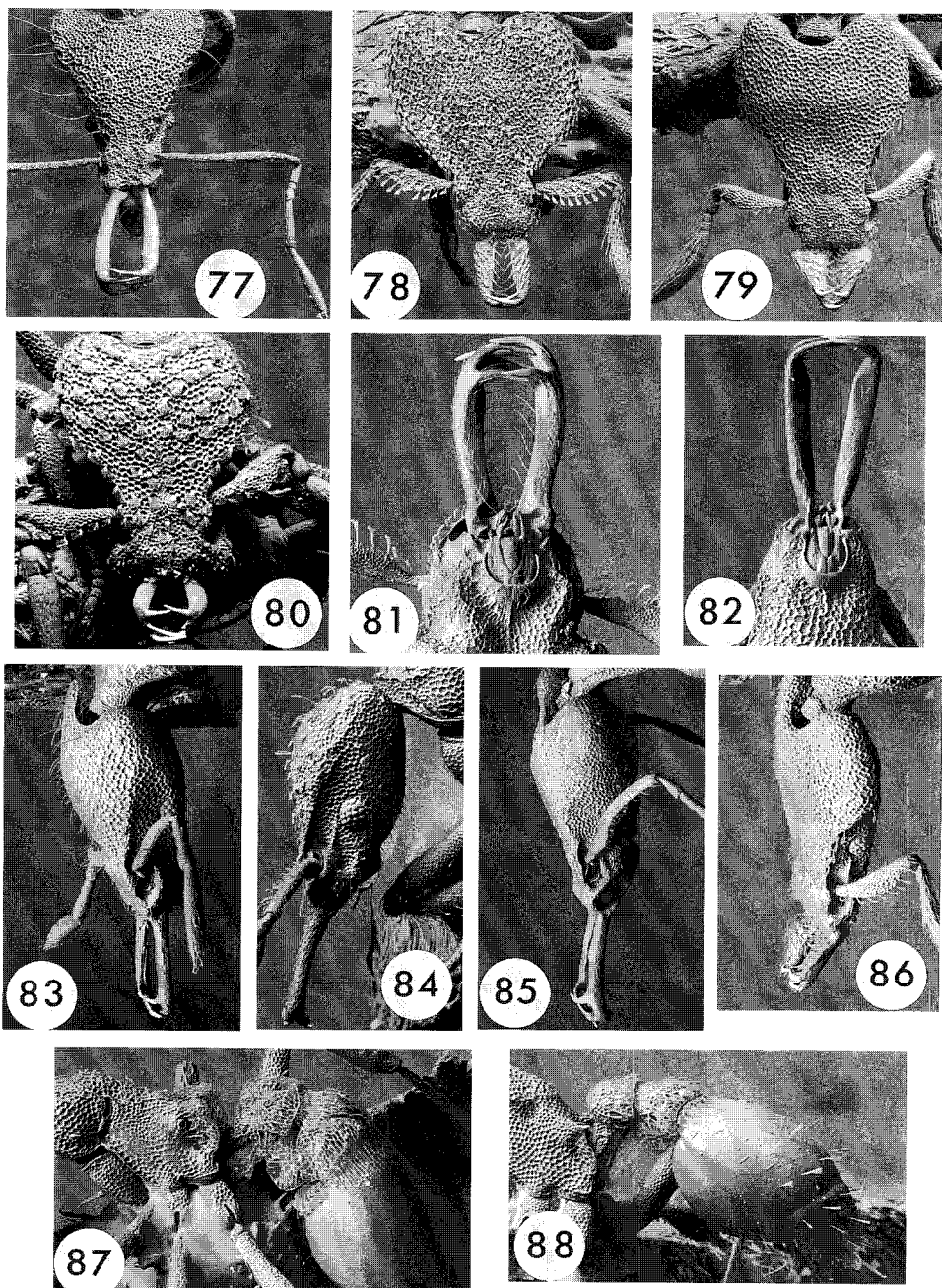
FIGS 46-56. Dacetonine workers; *Pyramica* species. (46-51) Full-face view of head. (46) *mustelina*. (47) n. sp. (48) *nitens*. (49) *pergandei*. (50) *tanyrastax*. (51) n. sp. (52-56) Anterior clypeus, labrum and mandibles. (52) *truncatidens*, mandibles removed. (53) *reliquia*. (54) *kerasma*. (55) *creightoni*. (56) *kichijo*. (New species to be described in forthcoming publication.)



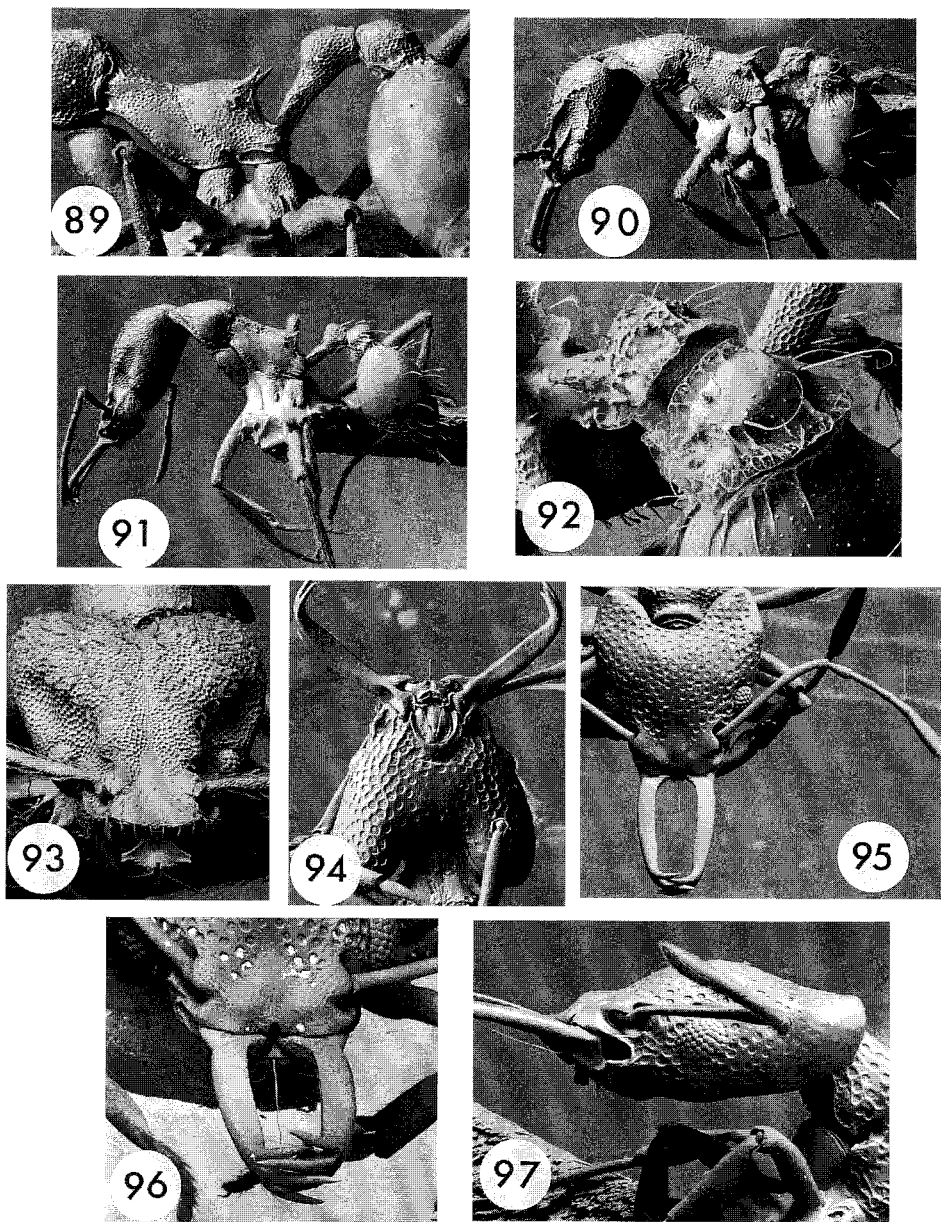
FIGS 57-66. Dacetonine workers; *Pyramica* species. (57-59) Ventral view of mouthparts. (57) *truncatidens*. (58) *lujae*. (59) *myllorhapha*. (60-63) Profiles of head. (60) n. sp. (61) *subedentata*. (62) n. sp. (63) *ornata*. (64) Waist segments of n. sp. (65-66) Body profiles. (65) *dagon*. (66) n. sp. (New species to be described in forthcoming publication.)



FIGS 67-76. Dacetone workers. (67-70) *Pyramica* species, body profiles. (67) n. sp. (68) n. sp. (69) *hyphata*. (70) *mirabilis*. (71-76) *Strumigenys* species, full-face view of head. (71) n. sp. (72) *saliens*. (73) *rogeri*. (74) *cacaoensis*. (75) *tigris*. (76) *ludia*. (New species to be described in forthcoming publication.)



FIGS 77–88. Dacetonine workers; *Strumigenys* species. (77–80) Full-face view of head. (77) *doriae*. (78) *chapmani*. (79) n. sp. (80) *emmae*. (81–82) Ventral view of mouthparts. (81) n. sp. (82) *elongata*. (83–86) Profile of head. (83) *godeffroyi*. (84) n. sp. (85) *tigris*. (86) n. sp. (87–88) Waist segment profiles. (87) n. sp. (88) n. sp. (New species to be described in forthcoming publication.)



FIGS 89–97. Dacetonine workers. (89–93) *Strumigenys* species. (89–91) Body profiles. (89) *tigris*. (90) *micretes*. (91) n. sp. (92) Oblique dorsal view of waist segments in n. sp. (93) Anterior view of head of n. sp. to show labrum, mandibles removed. (94–97) *Microdaceton* species. (94) Ventral head of n. sp., trigger hair broken. (95–97) *M. tibialis*. (95) Full-face view of head. (96) Oblique frontal view. (97) Profile of head. (New species to be described in forthcoming publication.)

- (1) Basimandibular gland. Bulla when visible present as a pale patch or streak ventrally or lateroventrally close to the base of the mandible. [This gland also occurs in *Microdaceton* where it may be homologous, it is therefore not scored as a strumigenyiform synapomorphy above.]
- (2) Ventral gland of scape. Bulla when visible appears as a circular, oval or more elongate patch of pale tissue on the ventral surface of the scape, close to its apex but proximal of the articulation with the first funicular segment. It is usually more obvious in taxa where the scape is dorsoventrally flattened.
- (3) Femoral dorsal gland. Bulla usually appears as a blister-like patch that is paler than the adjacent cuticle. It is usually located dorsally on the femur in the apical third of its length but may sometimes be shifted proximally. When obvious it is very variable in size. The gland is apparently absent, or at least has no externally visible bulla, in some whole species groups and a number of individual species. Sometimes a bulla is visibly present on only one or two pairs of legs rather than all three and rarely a bulla can be seen in queens but not workers of the same species.
- (4) Tibial dorsal gland. Bulla usually appears as a small blister-like patch that is paler than the adjacent cuticle. It is located dorsally on the tibia in the apical third of its length. Variation is as for the femoral dorsal gland. In some taxa a femoral bulla is present but not a tibial, but in general if the former is distinct then so is the latter.
- (5) Mesopleural gland. Shape and size variable but usually a roughly circular excavation in the anterior margin of the mesopleuron at its junction with the posterolateral pronotal margin, posterior to the insertion of the first coxa. The excavation is frequently lined with small setae that are directed towards the central point of the cavity.

Spongiform tissue

Spongiform lobes on the waist segments, at their fullest development, are as listed below. There is considerable variation in shape and size of the various lobes, sometimes in individual species within a species group and sometimes throughout entire species groups. Rarely one, several or all the spongiform lobes may be secondarily reduced, vestigial or lost, or they may become secondarily sclerotized. The fundamental point is that all the observed variation can only be derived from a basic pattern where all the lobes are present (figures 64, 87).

Elsewhere in the Myrmicinae spongiform tissue is developed in the genera *Tettheomyrma* and *Dacotinops* (both of tribe Stenammini) but in these the spongiform tissue is diffuse and not organized into discrete lobes along the following pattern.

- (1) Sternite of petiole with a longitudinal strip or curtain extending most or all of its length; often this curtain extended in places by deeper lobes or frills; sometimes the curtain reduced to a narrow crest and sometimes absent (figures 89, 91).
- (2) Tergite of petiole with a lateral lobe on each side of the node, linked by a transverse collar across the posterior margin of the node. Lateral lobe very variable in shape and size, usually obvious but sometimes appearing as no more than an expansion of the posterior transverse collar on each side; rarely vestigial or absent. Posterior transverse collar may be reduced or absent in some.

- (3) Sternite of postpetiole with a ventrally directed lobe on each side, frequently these linked by a transverse isthmus of spongiform tissue across the width of the sternite ventrally. Base of sternite lobe, where it joins the sternite proper, is often overlapped by the lateral postpetiolar lobe. Ventral lobe variable in shape and size but only extremely rarely secondarily absent.
- (4) Tergite of postpetiole with a lateral spongiform lobe of variable size (rarely absent) and the disc usually also with a narrow anterior and a broader posterior transverse collar. The latter may extend posteriorly and abut the margin of the limbus on the first gastral tergite.

As well as these spongiform lobes the base of the first gastral sternite very often bears a pad or strip of spongiform tissue. When present this may margin or mask the truncated ventral base of the gaster. Dejean (1985a) suggests that the spongiform tissue may produce a prey-attracting, or maybe prey-calming, allomone; the possibility that this may be a function of some of the exocrine glands, particularly the ventral gland of the scape, remains to be investigated.

Bizarre pilosity

The genera *Pyramica* and *Strumigenys* exhibit a very wide variety of general body pilosity and frequently some or all of it is represented by bizarrely shaped hairs. Along with such ground-pilosity, and usually located at specific points on the head and body, there are often also paired specialized bizarre setae with a specific orientation. These setae are not duplicated anywhere else in the tribe. They vary greatly in shape and size, being flagellate, remiform, spatulate or clavate, but are generally distinctly different from any other setae that arise near them. They all probably serve a sensory function and provide the ant with data about its spatial orientation, perhaps especially when hunting or moving in confined spaces. As with other characters discussed here, these specialized hairs are very variably developed through the hundreds of species of the two genera, and may be partially or entirely unrepresented in some taxa. However, the observed variation only makes sense if one assumes a common ancestor in which the specialized setae were present. Such a distribution would be as follows.

- (1) Dorsolateral margin of head. A freely laterally projecting specialized hair at about the level of the apex of the scrobe. Several taxa have other laterally projecting hairs anterior or posterior to this, on the upper scrobe margin or the lateral margin of the occipital lobe; these may be regarded as secondary developments as may loss of the specialized hair.
- (2) Cephalic dorsum. One or more pairs of erect specialized hairs, close to highest point of vertex or close to occipital margin.
- (3) Pronotal humeri. A specialized hair at each humeral angle that freely projects dorsolaterally or laterally. Dorsum of pronotum sometimes has a long erect pair at each posterolateral corner, at the junction with the mesonotum.
- (4) Mesonotum. An anteriorly situated pair of erect specialized hairs, generally close to the dorsolateral margin. Posteriorly there may be one or two further marginal pairs.

This group of two genera contains by far the largest number of species in the tribe. It is overwhelmingly the dominant group in the world except for Australia where *Orectognathus* and the epopostrumiform genera are strongly represented. In

- (1) Basimandibular gland. Bulla when visible present as a pale patch or streak ventrally or lateroventrally close to the base of the mandible. [This gland also occurs in *Microdaceton* where it may be homologous, it is therefore not scored as a strumigenyiform synapomorphy above.]
- (2) Ventral gland of scape. Bulla when visible appears as a circular, oval or more elongate patch of pale tissue on the ventral surface of the scape, close to its apex but proximal of the articulation with the first funicular segment. It is usually more obvious in taxa where the scape is dorsoventrally flattened.
- (3) Femoral dorsal gland. Bulla usually appears as a blister-like patch that is paler than the adjacent cuticle. It is usually located dorsally on the femur in the apical third of its length but may sometimes be shifted proximally. When obvious it is very variable in size. The gland is apparently absent, or at least has no externally visible bulla, in some whole species groups and a number of individual species. Sometimes a bulla is visibly present on only one or two pairs of legs rather than all three and rarely a bulla can be seen in queens but not workers of the same species.
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- W. M. Wheeler, 1915: 488, by monotypy. [Synonymy with *Strumigenys* by Baroni Urbani and de Andrade, 1994: 14] **Syn. n.**
- Codiomyrmex* W. M. Wheeler, 1916: 326. Type-species: *Codiomyrmex thaxteri* W. M. Wheeler, 1916: 327, by monotypy. [Synonymy with *Glamyromyrmex* by Brown, 1973b: 179 (provisional). Synonymy with *Strumigenys* by Baroni Urbani and de Andrade, 1994: 14] **Syn. n.**
- Tingimyrme* Mann, 1926: 104 [as subgenus of *Strumigenys*]. Type-species: *Strumigenys (Tingimyrme) mirabilis* Mann, 1926: 105, by monotypy. [Raised to genus by Brown, 1948: 11. [Synonymy with *Strumigenys* by Baroni Urbani and de Andrade, 1994: 15] **Syn. n.**
- Codioxenus* Santschi, 1931: 278 [as subgenus of *Epitritus*]. Type-species: *Epitritus (Codioxenus) simulans* Santschi, 1931: 278, by monotypy. [Raised to genus by Brown, 1948: 123. Synonymy with *Strumigenys* by Baroni Urbani and de Andrade, 1994: 14] **Syn. n.**
- Smithistruma* Brown, 1948: 104. Type-species: *Cephaloxys capitata* Smith, F. 1865: 77 [not *Strumigenys pulchella* Emery, 1895a: 327; incorrect subsequent designation by Brown, 1948: 104]. [Replacement name for *Cephaloxys* Smith, F. 1865: 76. [Synonymy with *Strumigenys* by Baroni Urbani and de Andrade, 1994: 14] **Syn. n.**
- Weberistruma* Brown, 1948: 106 [as subgenus of *Smithistruma*]. Type-species: *Strumigenys (Cephaloxys) leptothrix* Wheeler, W. M. 1929: 55, by original designation. [Raised to genus by Brown, 1949b: 7. Synonymy with *Smithistruma* by Brown, 1973a: 35]
- Wessonistruma* Brown, 1948: 106 [as subgenus of *Smithistruma*]. Type-species: *Strumigenys pergandei* Emery, 1895a: 326, by original designation. [Synonymy with *Smithistruma* by Brown, 1973a: 35]
- Serrastruma* Brown, 1948: 107 [as subgenus of *Smithistruma*]. Type-species: *Strumigenys simoni* Emery, 1895b: 42, by original designation. [Raised to genus by Brown, 1949b: 6. Synonymy with *Strumigenys* by Baroni Urbani and de Andrade, 1994: 14] **Syn. n.**
- Neostruma* Brown, 1948: 111. Type-species: *Strumigenys crassicornis* Mayr, 1887: 577, by original designation. [Synonymy with *Strumigenys* by Baroni Urbani and de Andrade, 1994: 12] **Syn. n.**
- Dorisidris* Brown, 1948: 116. Type-species: *Strumigenys (Codiomyrmex) nitens* Santschi, 1932: 413, by original designation. [Synonymy with *Strumigenys* by Baroni Urbani and de Andrade, 1994: 14] **Syn. n.**
- Miccostruma* Brown, 1948: 123. Type-species: *Epitritus mandibularis* Szabó, 1909: 27, by original designation. [Synonymy with *Smithistruma* by Bolton, 1983: 274]
- Kyidris* Brown, 1949b: 3. Type-species: *Kyidris mutica* Brown, 1949b: 3, by original designation. [Synonymy with *Strumigenys* by Baroni Urbani and de Andrade, 1994: 15] **Syn. n.**
- Polyhomoa* Azuma, 1950: 36. Type-species: *Polyhomoa itoi* Azuma, 1950: 36 (junior synonym of *Kyidris mutica* Brown, 1949b: 3), by monotypy. [Synonymy with *Kyidris* by Creighton, 1950: 93; Brown and Yasumatsu, 1951: 93]
- Chelystruma* Brown, 1950a: 33 [as subgenus of *Glamyromyrmex*]. Type-species: *Glamyromyrmex (Chelystruma) lilloana* Brown, 1950a: 34, by monotypy. [Raised to genus by Kempf, 1959: 338. Provisional synonymy with *Glamyromyrmex* by Brown, 1973b: 179. Synonymy with *Strumigenys* by Baroni Urbani and de Andrade, 1994: 14] **Syn. n.**
- Borgmeierita* Brown, 1953a: 23. Type-species: *Codiomyrmex excisus* Weber, 1934: 51, by original designation. [Synonymy with *Glamyromyrmex* by Brown, 1973a: 35]
- Platystroma* Brown, 1953a: 112 [as subgenus of *Smithistruma*]. Type-species: *Strumigenys (Cephaloxys) depressiceps* Weber, 1934: 47, by original designation. [Synonymy with *Smithistruma* by Brown, 1973a: 35]
- Gymnomyrmex* Borgmeier, 1954: 279. Type-species: *Gymnomyrmex splendens* Borgmeier, 1954: 279, by original designation. [Synonymy with *Strumigenys* by Baroni Urbani and de Andrade, 1994: 14] **Syn. n.**
- Dysedrognathus* Taylor, 1968: 132. Type-species: *Dysedrognathus extemenuus* Taylor, 1968: 133, by original designation. [Synonymy with *Strumigenys* by Baroni Urbani and de Andrade, 1994: 13] **Syn. n.**
- Asketogenys* Brown, 1972: 23. Type-species: *Asketogenys acubecca* Brown, 1972: 23, by original designation. [Synonymy with *Strumigenys* by Baroni Urbani and de Andrade, 1994: 15] **Syn. n.**
- Cladarogenys* Brown, 1976: 33. Type-species: *Cladarogenys lasia* Brown, 1976: 34, by original designation. [Synonymy with *Strumigenys* by Baroni Urbani and de Andrade, 1994: 14] **Syn. n.**

Diagnosis of genus (workers)

With characters of the strumigenyiform genus group listed above, and the following.

Mandibles with very variable morphology: see discussion below.

Mandibles at full gape open to only 60–90°; with static pressure mode of action.

Mandibles in ventral view broad at extreme base, their articulations located at about the midlength of the labio-maxillary complex (figures 57–59) [A].

Labral lobes hypertrophied [A], forming exaggerated distal processes (figures 42, 52–59). Labral lobes variously shaped but always well developed and prominent, arising from across entire width of labrum. Labral shield not T-shaped; labrum capable of slight depression but not capable of reflexion over the labio-maxillary complex.

Buccal cavity relatively short and wide, lateral margins of cavity (anterior hypostoma) not converging anteriorly (figures 57–59).

Roger's old name *Pyramica*, out of all the genus-group names applied to the strumigenyiform dacetonines, appears as the earliest available name that covers all taxa except for *Strumigenys* and its current junior synonyms. *Pyramica* is therefore revived from junior synonymy under *Strumigenys*, reinstated as a genus, and made the senior synonym of all the names in the genus-group that are catalogued above.

The vast majority of these genus-group names were created by the description of autapomorphic characters of single species or very small groups of species. Most of the names were introduced when dacetonines were considered rare and only a few species had been discovered. In consequence their individual peculiarities assumed major proportions because the taxonomic distance between these rarities appeared so great. Baroni Urbani and de Andrade (1994) mention most earlier characters that were used to split supposed genera from the mass: antennomere count, the striking specializations in mandible form, the presence or absence of an apical fork, and the head shape. All of these, alone or in combination, produced many new names in the genus-group but introduced the precedent, which quickly became an orthodoxy, that any such differences merited another new genus. This concentration on differences in limited aspects of cephalic morphology tended to deflect attention from overall similarities and perhaps to some extent stifled the search for other useful characters.

There are about 64 species groups recognized within *Pyramica* in the forthcoming revision and many possess obvious autapomorphies. Some of these groups correspond with some of the pre-existing generic names, but many do not. If all the groups exhibiting autapomorphies were to be given generic names, I estimate that a minimum of 30 more, over and above those listed in the synonymy, would be needed, and there would almost certainly be a paraphyletic residue. So is this mass best treated as a single large genus or as many small genera? The problem boils down to a question of value to systematics and usefulness for identification and taxonomic purposes. Is it more useful to have one large, diverse but definable genus or a plethora of smaller genera, some of which have apomorphies but all of which are intrinsically more difficult to define, key and understand? It seems to me that a huge proliferation of monotypic or small genera here serves no useful taxonomic purpose and indeed may even obscure the broader similarities. I conclude that it is therefore best to treat all these forms as a single genus, *Pyramica*, with the above definition.

Prey capture in this genus is usually a much more stealthy affair than in *Strumigenys*. The usual sequence is that when a hunting *Pyramica* worker detects prey all movement stops, the antennae are folded into the scrobes and the head is lowered. The prey is then approached extremely slowly or the ant stays still and waits for the prey to approach of its own accord. When the prey is in striking distance, or sometimes when it actually touches the ant, the mandibles open to their maximum gape of about 60–90° and there may be brief antennation. When the trigger hairs are touched the mandibles snap shut. The strike is usually directed at one of the prey's appendages but in the case of small prey the body may be struck. The sting is then invariably brought into play (Wesson, 1936; Wesson and Wesson, 1939; Wilson, 1954; Masuko, 1985; and personal observation). Dejean (1985b, 1988) has documented a more rapid approach to the prey, and a less organized attack, in ants that are starving or are following up an initial strike that missed its target. This hunting technique is the same as that of the Basicerotini (Wilson, 1956; Wilson and Brown, 1985; Wilson and Hölldobler, 1986). It is most probably the ancestral hunting behaviour for the entire dacetone tribe group, from which the more specialized technique of the genera with kinetic mandibles has been evolved.

Taxonomic studies in the genus are mostly small, scattered and fragmentary, mainly because *Pyramica* was previously subdivided into so many insignificant genera. Principal publications with identification keys, or with direct comparison of related species that allows identification, include: Brown (1952a) and Bolton (1983) [former *Serrastruma* species]; Brown (1953a, 1964), Bolton (1983), Ward (1988), Terayama *et al.*, (1996), Ogata and Ononyama (1998) [former *Smithistruma* species]; Brown (1959a) [former *Neostruma* species]; Brown (1960) [former *Strumigenys gundlachi*-group species]; Brown and Boisvert (1979) [former *Pentastruma* species]; Wilson and Brown (1956) [former *Kyidris* species]; Kempf (1960) and Perrault (1986) [former *Gymnomyrmex* species]; Bolton (1972, 1983) [former *Epitritus* species]; Kempf (1960) and Bolton (1983) [former *Glamyromyrmex* species]. A taxonomic revision of the world fauna of *Pyramica* has been concluded by the current author and approaches publication.

Main trends in mandible evolution within Pyramica

One problem with *Pyramica* is that the mandibles of its more than 300 species are very morphologically diverse when compared with other genera in the tribe. Rapid evolutionary radiation to exploit all the possibilities of the predatory technique within the genus has produced an enormous range of modifications some, but not all, of which can be arranged into morphoclinal sequences. From the morphological survey the basic mandible form in the genus, which is also that encountered in most species groups, is described first. Major derivations are then outlined but no attempt has been made to cover all the myriad minor variations observed, some of which are intermediate in form. Earlier generic names applicable to each described form are indicated in square brackets; note that some of the earlier names occur in more than one category.

1. Mandible triangular, slender to moderately broad and of short to moderate length (MI ca 8–20) (figures 22–28, 57), with a basal lamella of varying shape and size and a serially dentate masticatory margin that usually has a total of 12 teeth and denticles, though in some the number may be somewhat increased; masticatory margins engage throughout their length. The principal dental row consists of the basal five or seven teeth, which are the largest on the margin, and there is no

diastema (or only a tiny diastema) between basal lamella and basal tooth. Such forms are numerous in every zoogeographical region. Characters associated with mandibles of this general form include: labrum always bitriangular or biconical, anterior clypeal margin usually overhangs mandible at least to level of basal tooth, and outer margin of mandible lacks an inflected prebasal angle (e.g. the Afrotropical *emarginata*-, *oxysma*- and *weberi*-groups, the Malesian *capitata*-group, the Nearctic *clypeata*-group, the Neotropical *alberti*-, *schulzi*- and *splendens*-groups, the widespread *baudueri*- and *rostrata*-groups, and the tramp *membranifera*-group). [Most *Smithistruma*, some *Pentastruma*, all *Gymnomyrmex* and *Trichoscapa*.]

2. As above but with a long edentate diastema present between basal lamella and basal tooth (figures 29–32, 53, 55). The conical labral lobes are usually visible through the gap that results from the opening of the diastema (e.g. the Nearctic *pulchella*-group, the Malesian *gyges*-group, the widespread *mutica*-group; development of this form of mandible has been independent in each group). [*Kyidris*, several groups of *Smithistruma*.]

3. Mandibles more massively developed and the dental row containing 12–18 teeth and denticles (figures 33, 34); associated characters as in 1 (e.g. the widespread *leptothrix*-group). [Part of *Smithistruma*; *Codiomyrmex*.]

4. Mandibles elongate-triangular and strong, equipped with serial denticles (figures 35–37, 58) without a differentiated principal basal tooth-row; associated characters as in 1 but basal lamella may be reduced (e.g. *lujae*-group in Africa, part of *capitata*-group in Malesia and the Neotropical *mirabilis*). [*Serrastruma*, some *Smithistruma*, *Tingimyrme*.]

5. Mandibles broad, triangular and elongate, powerfully constructed, only fully engaging in the apical half or less but with the entire masticatory margin dentate (figure 38) and the total dental count increased to 22–24; associated characters as in 1 but basal lamella very small (e.g. the Malesian *extemena*-group). [*Dysedrognathus*.]

6. Mandibles shortened, powerfully triangular to bear-trap-like and often strongly downcurved (figures 39–42). Principal basal dental row consists of a few enlarged teeth and the total dental count may be as low as 5 (range 5–11). In these groups the labrum is usually bluntly bilobate (figure 42) rather than biconical and the outer margin of the mandible frequently acquires an inflected prebasal angle (e.g. the Afrotropical *tagon*-, *tetragnatha*- and *thuvida*-groups, the Neotropical *appretiata*-, *beebei*-, *excisa*- and *substricta*-groups, the Malesian and Australasian *semicompta*-group, and the Malagasy *olsoni*-group). In some groups the head becomes short and broad, losing the classical dacetonine pyriform shape. It should be stressed that each group given as an example appears to represent a convergent but unique evolutionary event. [Most *Glomyromyrme*; *Codioxenus*, *Chelystruma*.]

7. Mandibles lose the basic triangular shape by narrowing from side to side so that they become sublinear to linear and only engage at their apices at full closure (figures 43–51). They may become elongate and have reduced dentition or have dentition confined to the apical quarter. There is usually a large space between the mandibles through which the labral lobes can be seen. Labral lobes usually remain bitriangular or biconical but in at least one species (*nitens*) they are broad and bilobate, derived from a category 6 form. The basal lamella is frequently reduced and shifted distally on the mandible.

It is very obvious that pliar-like to forceps-like mandibles of this narrowed or narrowed-elongate form have evolved independently several times. It should be

stressed that even in species and groups where the mandibles are very long they can only be opened to less than 90° at full gape (e.g. *gundlachi*-group, Brown, 1959a, 1960) and are not kinetic in mode of action. Relatively few species are involved but their mandibular specializations have attracted a disproportionate number of names in the genus-group. Previously described long-mandibulate forms (there are many new ones) are as follows; their original combinations are noted as are their relationships, if known or suspected.

- P. acubecca* [*Asketogenys*] (figure 44), one species, Malaysia: this species appears to be a long-mandibulate derivative of the *P. leptothrix*-group (category 3, above).
- P. argiola*-group [part of *Epitritus*] (figure 45), seven species, Palaearctic and Afrotropical: relationship(s) not apparent, group probably paraphyletic.
- P. canina* [*Pentastruma*] (figure 43), China and Japan: a long-mandibulate member of the otherwise short-mandibulate Oriental and East Palaearctic *P. sauteri*-group (category 1, above).
- P. gundlachi*-group [*Strumigenys gundlachi*- and *S. connectens*-groups, plus *Neostruma*] (figures 46, 59), 16 species, Neotropical: the *P. schulzi*-group, also Neotropical, may be the sister group (category 1, above).
- P. lasia* [*Cladarogenys*], one species, Gabon: forms a monophyletic unit with the *P. lujae*-group (category 4, above).
- P. murphyi*-group [part of *Epitritus*] (figure 47), two species, Oriental and Malesian: sister group of similarly distributed *P. extemena*-group (formerly *Dysedrognathus*, category 5, above).
- P. nitens* [*Dorisidris*] (figure 48), one species, Cuba: a second species, also a Cuban endemic and with which *nitens* forms a monophyletic group, is short-mandibulate and in category 6, above.
- P. pergandei*-group [*Smithistruma*] (figure 49), two species, USA and extreme southern Canada: possibly sister group of, or perhaps derived from, *P. rostrata*-group (category 1, above).
- P. tanymastax* [*Smithistruma*] (figure 50), one species: Venezuela, Brazil, Paraguay: relations unknown.
- P. terroni* [*Smithistruma*] (figure 51), one species, Cameroun: forms a monophyletic unit with the short-mandibulate *P. emarginata*-group (category 1, above).

New combinations in Pyramica

The following names are all new combinations in *Pyramica*. They are listed under their previous combinations as catalogued in Bolton (1995b) or as they have appeared in publications subsequent to the catalogue (Terayama *et al.*, 1995; Terayama *et al.*, 1996; Lattke and Goitia, 1997; Deyrup, 1998; Deyrup and Cover, 1998; Ogata and Onoyama, 1998). From *Asketogenys*: *acubecca*. From *Chelystruma*: *lilloana*. From *Cladarogenys*: *lasia*. From *Codiomyrmex*: *thaxteri*. From *Codioxenus*: *simulans*. From *Dorisidris*: *nitens*. From *Dysedrognathus*: *extemenus*. From *Epitritus*: *argiolus*, *formosus*, *hexamerus*, *hirashimai*, *laticeps*, *minimus*, *murphyi*, *roomi*, *tiglath*. From *Glamyromyrmex*: *africanus*, *appretiatius*, *aztecus*, *beebei*, *convexiceps*, *crypturus*, *dagon*, *excisus*, *flagellatus*, *loveridgei*, *ravidurus*, *reticeps*, *sahurus*, *semicomptus*, *sistrurus*, *substrictus*, *tetragnathus*, *thuidus*, *trymalus*, *tukultus*, *wheeleri*. From *Gynomyrmex*: *abditus*, *comis*, *dentinasis*, *minusculeus*, *rugithorax*, *splendens*, *villiersi*. From *Kyidris*: *media*, *mutica*, *takasago*, *yaleogyna*. From *Neostruma*: *brevicornis*, *crassicornis*, *metopia*, *mustelina*, *myllorhapha*, *zeteki*. From *Pentastruma*:

canina, *sauteri*. From ***Serrastruma***: *bequaerti*, *concolor*, *dotaja*, *geoterra*, *inquilina*, *ludovici*, *lujae*, *maynei*, *miccata*, *serrula*, *simoni*, *sulumana*. From ***Smithistruma***: *abdita*, *alberti*, *anarta*, *angulata*, *arahana*, *archboldi*, *arizonica*, *assamensis*, *baudueri*, *behasya*, *bimarginata*, *bunki*, *californica*, *capitata*, *carolinensis*, *castanea*, *cavinasis*, *chiricahua*, *chyatha*, *cinninnata*, *circothrix*, *cloydi*, *clypeata*, *conspersa*, *creightoni*, *datissa*, *dendexa*, *depressiceps*, *dietrichi*, *dohertyi*, *dubia*, *electrina*, *elegantula*, *emarginata*, *emiliae*, *enkara*, *epinotalis*, *fenkara*, *filirrhina*, *filitalpa*, *formosimonticola*, *fridericimuel-leri*, *fulda*, *gatuda*, *hensekta*, *hiroshimensis*, *hyphata*, *impidora*, *incerta*, *inezae*, *inopina*, *inuitata*, *jacobsoni*, *japonica*, *karawajewi*, *kempfi*, *kerasma*, *kichijo*, *kyidriiformis*, *laev- inasis*, *lamellignatha*, *leptothrix*, *malaplastax*, *mandibularis*, *margaritae*, *marginata*, *masu- koi*, *mazu*, *mekaha*, *memorialis*, *microthrix*, *minkara*, *missouriensis*, *morisitai*, *mumfordi*, *nepalensis*, *nigrescens*, *ninda*, *nykara*, *ohioensis*, *orchibia*, *ornata*, *oxysma*, *pedunculata*, *pergandei*, *pilinasis*, *placora*, *probatrrix*, *pulchella*, *reflexa*, *reliquia*, *rohweri*, *rostrata*, *rostrataeformis*, *rudinodis*, *rusta*, *schulzi*, *sharra*, *schleorum*, *stu- diosi*, *sublucida*, *synkara*, *tacta*, *taipingensis*, *talpa*, *tanyastax*, *tenuipilis*, *tenuissima*, *terrioni*, *tigrilla*, *tolomyia*, *transversa*, *truncatidens*, *vodensa*, *weberi*, *wrayi*. From ***Strumigenys***: *connectens*, *denticulata*, *eggersi*, *gemella*, *jamaicensis*, *laevipleura*, *nubila*, *subdentata*, *trieces*, *xenognatha* (previously members of the *Strumigenys* *gundlachi*-group and *S. connectens*-group; *gundlachi* itself is a revived combination in *Pyramica*). From ***Tingimyrme***: *mirabilis*. From ***Trichoscapa***: *membranifera*.

***Strumigenys* F. Smith**

(Figures 71–93)

- Strumigenys* Smith, F. 1860: 72. Type-species: *Strumigenys mandibularis* Smith, F. 1860: 72, by monotypy.
- Labidogenys* Roger, 1862: 249. Type-species: *Labidogenys lyroessa* Roger, 1862: 251, by monotypy. [Synonymy by Roger, 1863: 40; Dalla Torre, 1893: 145; Bingham, 1903: 147. Revived from synonymy by Brown, 1948: 102. Resynonymized by Brown and Wilson, 1959: 281; Brown, 1960: 38; Bolton, 1983: 358]
- Proscopomyrmex* Patrizi, 1946: 294. Type-species: *Proscopomyrmex londianensis* Patrizi, 1946: 295, by monotypy. [Synonymy by Brown, 1949b: 15]
- Eneria* Donisthorpe, 1948: 598. Type-species: *Eneria excisa* Donisthorpe, 1948: 598 (junior synonym of *Strumigenys lorae* Emery, 1897: 576), by original designation. [Synonymy by Brown, 1949b: 15]
- Quadristuma* Brown, 1949a: 47. Type-species: *Epitritus emmae* Emery, 1890: 70, by original designation. [Synonymy by Baroni Urbani and de Andrade, 1994: 12]

Diagnosis of genus (workers)

With characters of the strumigenyiform genus group listed above, and the following.

Mandibles sublinear to linear (figures 71–86, 90, 91), with kinetic mode of action, straight or curved and terminating in an apical fork of two (rarely three) spiniform teeth, of which the apicodorsal is the longest; apical fork teeth overlap at full closure. Between or below the spiniform apical teeth may be one or two intercalary small teeth or denticles.

Preapical dentition of mandible of zero to two teeth or denticles (figures 71–77).

Mandibles at full gape open to 170° or more.

Mandibles in ventral view narrow at extreme base, apparently arising from the apex of the labio-maxillary complex (figures 81, 82).

Mandible in profile with lateral surface concave at extreme base.

Labrum with distal lobes reduced to papillae or vestigial, not arising from across

entire width of labrum (figure 93) [A]. Shield of labrum proximal of lobes extended laterally, the sclerite roughly T-shaped (figure 93); anterior margins of T-shape thickened dorsoventrally.

Buccal cavity relatively long and narrow [A]; lateral margins of cavity (anterior hypostoma) converging anteriorly towards labrum (figures 81, 82) [A] so that labio-maxillary complex narrows apically.

The species composition of *Strumigenys* mostly remains as recorded in Bolton (1995b). Changes include the removal of two Neotropical groups (*gundlachi*-group and *connectens*-group) to *Pyramica*, as listed above, and the inclusion in *Strumigenys* of the two species formerly placed in *Quadristruma* (*emmae* **comb. n.**, and *eurycera* **comb. n.**).

Within the genus about 45 species groups can be recognized. Most of these have a fairly limited distribution but some are very widespread and others contain well-known tramp-species. The 45 species groups can be roughly aggregated into three major assemblages of taxa, with a few species of uncertain affinity.

The first aggregation includes all the New World species, which may have originated from a single ancestor. In these the mandibular insertions tend to be very closely approximated basally when seen with the mandibles fully closed, either in ventral (figure 82) or full-face view. In consequence the lateral arms of the labrum are relatively short, because at full mandibular gape the basimandibular processes, which engage the lateral labral arms to prop the mandibles open, remain quite close together. Disregarding tramp-species and other introductions the preapical dentition of New World species is characteristically of two quite widely separated teeth, or a tooth plus a denticle (figures 71, 72), although some taxa are known that are reduced from this pattern or even preapically edentate (figure 76). However, when the basic pattern is present the proximal tooth or denticle is always smaller than the distal. Labral lobes in New World forms tend to be papilliform rather than vestigial.

Old World species in general have longer lateral labral arms (figure 81) and basally more widely separated mandibular insertions. In some Malesian groups the labral arms are so long that they project laterally beyond the outer margins of the mandibles when the latter are fully closed. The labral lobes of Old World species tend to be very small or vestigial, much more reduced than in the New World taxa. Species groups of Afrotropical origin mainly exhibit a preapical dentition of two teeth, though reductions from this are known. Characteristically the two preapical teeth are sited quite close together in about the apical third of the mandible, and the proximal tooth is distinctly larger than the distal (figures 73, 74); the reverse of the predominant dentition of the New World forms. Species groups that predominate in the Oriental, Malesian and Australasian regions mostly show only a single preapical tooth (figures 75, 79) though a couple of small and very specialized species groups with two are known. The relationship of these latter species to the Afrotropical taxa remains to be investigated.

All species of this genus have mandibles with a kinetic mode of action (see discussion of mandibles), the mechanism of which was first mentioned by Brown and Wilson (1959) and described in detail by Gronenberg (1996). When prey is detected by a hunting ant the mandibles open to about 180° and are locked in that position. The ant may then adopt a stealthy or swift approach to the prey and there may or may not be antennation. Contact with the long labral trigger hairs initiates an extremely fast convulsive snap of the mandibles that impales the prey, the strike

being directed at any part of the body. The prey is then usually lifted clear of the ground and the sting may subsequently be brought into use, but this is not obligate behaviour (Wilson, 1950, 1954; Masuko, 1985; Dejean, 1987b; and personal observation).

The taxonomy of *Strumigenys* species is at present mostly confined to the literature of original descriptions, for which see the catalogue of Bolton (1995b). Relatively recent synthesizing studies with keys to regional faunas are sparse. They include Brown (1962), Kempf (1976) and Latke and Goitia (1997) for the Neotropical region, and Brown (1954b) and Bolton (1983) for the Afrotropical species. Keyed species of smaller areas include Morisita *et al.* (1992) for Japan; Dlussky (1993) for Samoa, Tonga and the Fiji Islands; Lin and Wu (1996) for Taiwan. A taxonomic study of the world fauna is currently approaching completion.

The clade *Microdaceton* plus epopostrumiform genera (figures 94–113)

In the older classification (Brown, 1954a; Brown and Wilson, 1959) the Afrotropical *Microdaceton* was included with the mainly Australasian genera *Colobostruma*, *Mesostruma* and *Epopostruma* in a subtribe Epopostrumiti. Taylor (1977) speculated that *Microdaceton* may in fact be more closely related to *Orectognathus*, but the mandible and scape characters he cited are also applicable to *Acanthognathus* and therefore much more likely to be convergencies than homologies.

The present morphological analysis confirms the isolation of *Microdaceton* from both *Orectognathus* and *Acanthognathus* and implies that the early classification was accurate because *Microdaceton* appears as the sister group of the epopostrumiform genus group (*Colobostruma* + *Mesostruma* + *Epopostruma*). Supporting this grouping are the following characters.

- (1) Propodeal spiracle shifted posteriorly and downwards on the side so that it is very close to or abutting the apex of the short metapleural gland bulla (figures 99, 104, 109, 112) [S].
- (2) Postpetiolar spiracle located ventrally [S].
- (3) Suture between first gastral tergite and sternite angulate laterobasally [S].
- (4) Lateral, non-spongiform, cuticular outgrowths developed on the petiole or postpetiole (figures 98, 104, 105, 109, 110) [S].

***Microdaceton* Santschi**

(Figures 94–99)

Microdaceton Santschi, 1913: 478. Type-species: *Microdaceton exornatum* Santschi, 1913: 478, by monotypy. [*Microdaceton* also described as new by Santschi, 1914: 33]

Diagnosis of genus (workers)

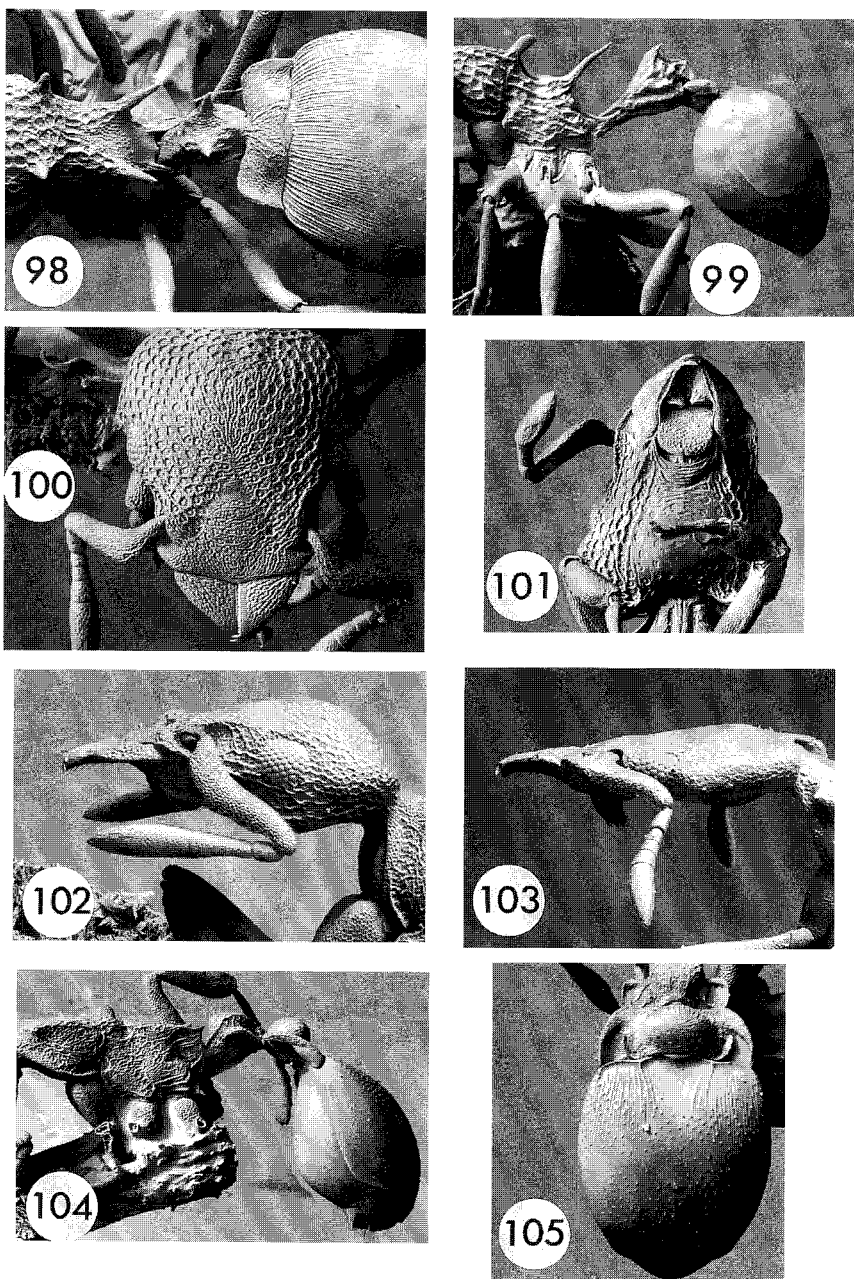
Mandibles linear and elongate (figures 94–96), with kinetic mode of action, each with an apical fork of three spiniform teeth that interlock at full closure. Preapical dentition absent.

Mandibles at full gape open to 170° or more.

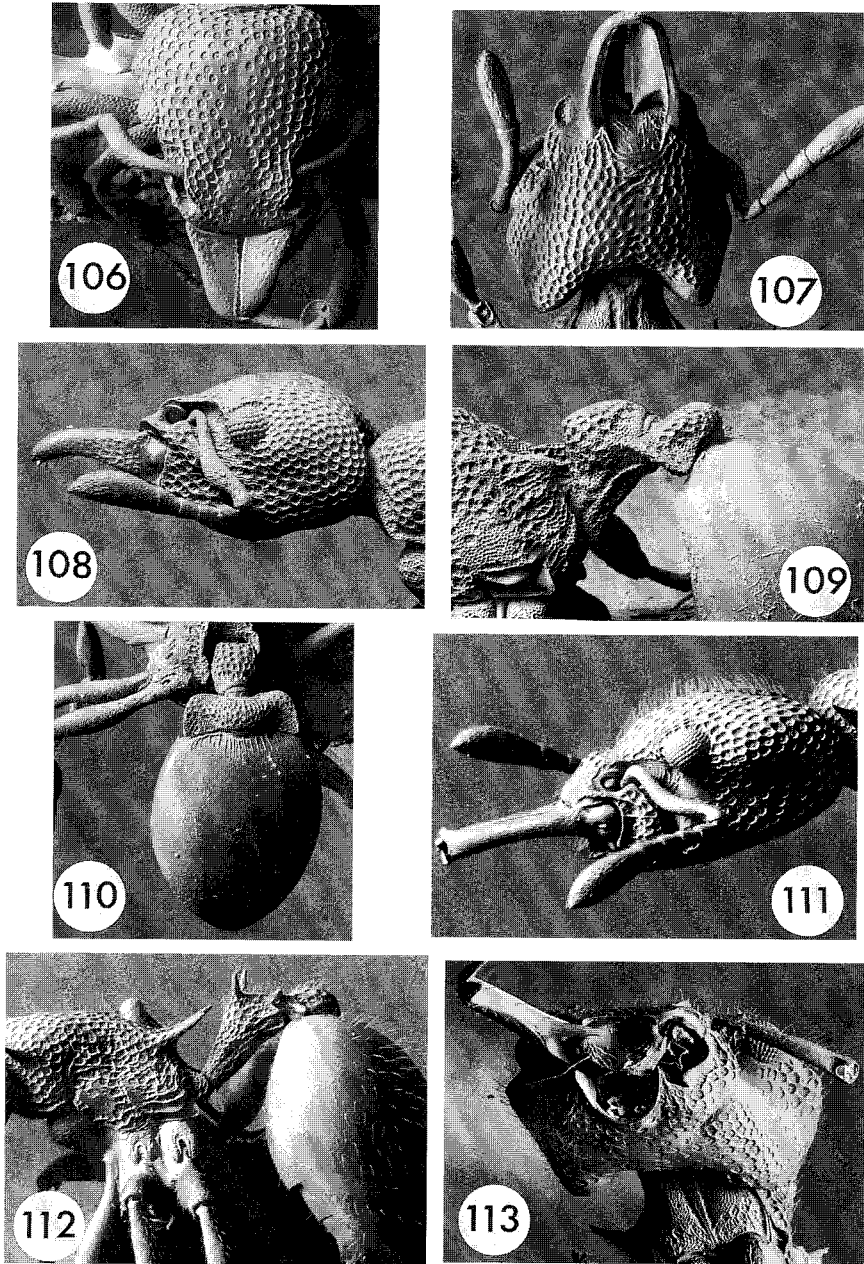
Basal process of mandible a curved spur (figure 94); at full mandibular closure process is dorsal to labrum and fits into a mediodorsal impression on labrum.

Basimandibular gland bulla conspicuous on ventral or ventrolateral surface.

Palp formula 3,2 [A].



FIGS 98–105. Dacetonine workers. (98–99) *Microdaceton* species. (98) Dorsal view of waist segments of *exornatum*. (99) Body profile of n. sp. (100–105) *Colobostruma* species. (100–103) Unidentified species. (100) Full-face view of head. (101) Ventral view of head. (102) Profile of head. (103) Profile of head. (104–105) *C. alinodis*. (104) Body profile. (105) Dorsal view of waist segments and gaster.



FIGS 106–113. Dacetonine workers. (106–110) *Mesostruma* species. (106) Full-face view of head of *eccentrica*. (107–110) *M. turneri*. (107) Ventral view of head. (108) Profile of head. (109) Body profile. (110) Dorsal view of waist segments and gaster. (111–113) *Epopostruma frosti*. (111) Profile of head. (112) Body profile. (113) Anteroventral view of head, labio-maxillary complex and left mandible removed.

Labrum roughly T-shaped, short and not capable of reflexing to conceal the labio-maxillary complex, which is permanently exposed (figure 94). Each lateral labral arm locks into a deep emargination near the inner mandibular base.

Trigger hair single, arising from midpoint of anterior margin of the labrum (figures 94–97, broken off short in figure 94) [A].

Eye not located ventrolaterally on side of head (figure 97).

Side of head with an extensive gap between base of mandible and margin of head capsule when mandibles fully closed (figure 97) [A].

Antenna with six segments, with a weakly differentiated apical club of two segments (figure 95).

Scape, when laid back in its normal resting position, passes above the eye (figure 97); apical portion of extended scape curved anteriorly when seen in full-face view; scape not abruptly downcurved near base.

Scrobe absent.

Pronotal cervix anteriorly with an abruptly raised thick transverse rim or collar that is preceded by a broad deep transverse groove [A].

Pronotal humeri unarmed; mesonotum with a pair of tubercles or teeth (figures 98–99).

Propodeal spiracle very close to margin of declivity, at approximately the midheight of the sclerite (figure 99).

Metapleural gland bulla with its apex very close to the propodeal spiracle (figure 99).

Waist segments without spongiform tissue (figures 98, 99); petiole node bidentate; postpetiole markedly dorsoventrally flattened and expanded laterally [A]; postpetiolar spiracles ventral, on undersides of the lateral expansions.

Limbus absent from first gastral tergite (figures 98, 99); basigastral costulae present or absent.

Suture between first gastral tergite and sternite angulate laterobasally.

The single median trigger hair on the labrum appears in fact to be composed of a pair of hairs that are tightly fused together. Generally the structure appears single even using electron microscopy (figures 95–97), but in small specimens of *M. tibialis* maceration in sodium hydroxide sometimes results in the separation of the two components.

Species of this small genus are restricted to, but widespread in, the Afrotropical region. Their taxonomy was investigated by Bolton (1983). Four species have been discovered to date (revision in manuscript) and the genus has been found in Ivory Coast, Ghana, Cameroun, Gabon, Zaire, Uganda, Kenya, Zambia, Zimbabwe and South Africa. Nothing is known of their biology except that they are a sparse component of the leaf litter fauna in forested regions (e.g. Belshaw and Bolton, 1994).

The epopostrumiform genera (figures 100–113)

The three genera included here, *Colobstruma*, *Epopostruma* and *Mesostruma*, form a monophyletic group. Distribution is mainly Australian, with isolated species extending the range into New Guinea and the Solomon Islands. They form the core of Brown's (1954a) old subtribe Epopostrumiti and are united by the following characters within the Dacetonini.

Palp formula 5,3.

Labrum large or very large (figures 101, 107, 113), forming a massive shield in

Colobostruma and *Mesostruma* that can reflex tightly over the labio-maxillary complex and completely cover the buccal cavity (figures 101, 107); somewhat smaller in *Epopostruma* where it covers approximately the apical half of the labio-maxillary complex (see below) [S].

Basimandibular gland bulla absent.

Antenna with four, five or six segments.

Scape, when laid back in its normal resting position, passes below the eye or across the ventral margin of the eye (figures 102, 103, 108, 111) [S]; basal part of scape strongly downcurved.

Scrobe usually present, extending below the eye (see below) [S], the latter not located ventrolaterally on side of head.

Femora and tibiae lack gland bullae on their dorsal surfaces close to the apices.

Pronotal humeri usually armed.

Metapleural gland with apex of bulla close to or abutting the annulus of the propodeal spiracle (figures 104, 109, 112).

Propodeal spiracle at about the midheight of the sclerite, separated from margin of declivity.

Tergite of petiole or postpetiole with lateral cuticular laminar outgrowths, but these outgrowths not spongiform (figures 104, 105, 109, 110, 112).

Postpetiolar spiracles ventral.

Limbus absent from first gastral tergite (figures 105, 109, 112).

Suture separating first gastral tergite and sternite angulate laterobasally.

Bizarre pilosity never developed.

The labral morphology seen in *Epopostruma* (figure 113) is certainly a secondarily acquired state from the hypertrophied labrum that forms such a strong synapomorphy for *Colobostruma* + *Mesostruma* (figures 101, 107). The condition seen in *Epopostruma* can easily be derived from that of the other two genera of the group, and is correlated with other shared characters.

In most species a scrobe is apparent, but in some species of *Colobostruma* it may be feeble or even absent. There is a morphoclineal development of the scrobe through this genus but it is not obvious which way the morphocline runs. At one end are species with very flattened heads and no trace of scrobe (figure 103); at the other are deep-headed species with moderate (figure 102) to conspicuous scrobes.

***Colobostruma* Wheeler**

(Figures 100–105)

Colobostruma W. M. Wheeler, 1927: 32 [as subgenus of *Epopostruma*]. Type-species: *Epopostruma (Colobostruma) laeae*, W. M. Wheeler, 1927: 32, by monotypy. [Raised to genus by Brown, 1948: 118]

Alistruma Brown, 1948: 117. Type-species: *Epopostruma foliaceae*, Emery, 1897: 573, by original designation. [Synonymy by Brown, 1959b: 1; Brown and Wilson, 1959: 281]

Clarkistruma Brown, 1948: 124. Type-species: *Epopostruma alinodis* Forel, 1913: 179, by original designation. [Synonymy by Brown, 1959b: 1; Brown and Wilson, 1959: 281]

Diagnosis of genus (workers)

With characters of the epopostrumiform genus-group listed above, and the following.

Mandibles short triangular (figures 100, 101), serially dentate; preapical and apical teeth enlarged, apical the largest.

Mandibles at full gape open to only 60–90°; with static pressure mode of action.

Mandible with an inflected prebasal-external angle (figure 101) [A]; in profile mandible abruptly downcurved basally (figures 102, 103) [A].

Basal process of mandible small and truncated, located below the plane of the masticatory margin (figure 101) [A]; at full mandibular closure basal process dorsal to labrum, not fitting into a depression in labral dorsum [A].

Labrum hypertrophied, forming a massive shield that can reflex tightly over the entire labio-maxillary complex and completely cover the buccal cavity (figure 101); its apical margin evenly convex to very broadly bilobate.

Trigger hairs on anterior margin of labrum and very reduced, or absent.

Side of head without a vertical preocular groove (figures 102, 103).

Scrobe usually present below eye but absent or incipient in some species, especially those with abnormally flattened head.

Tergite of petiole with lateral lobes at the node (figures 104, 105) [A].

Tergite of postpetiole with lateral laminae or lobes (figure 105).

The hypertrophied shield-like labrum is present in both *Colobostruma* and *Mesostruma*, and is a synapomorphy of these two genera.

This small genus contains nine described species (Bolton, 1995b). Most are Australian but one is known from Papua New Guinea; currently undescribed species are known from both these states and also from the Solomon Islands. Taxonomy of the genus consists only of the literature of original descriptions; no synthesizing study has yet been undertaken.

***Mesostruma* Brown gen. rev.**

(Figures 106–110)

Mesostruma Brown, 1948: 118. Type-species: *Strumigenys (Epopostruma) turneri* Forel, 1895: 424, by original designation. [Synonymy with *Colobostruma* by Baroni Urbani and de Andrade, 1994: 15] **Gen. rev.**

Diagnosis of genus (workers)

With characters of the epopostrumiform genus group listed above, and the following.

Mandibles elongate triangular (figures 106, 107), with a larger apical and smaller preapical tooth; proximal of this the margin is edentate and lamellate [A]. Mandible without an inflected basal-external angle and not downcurved basally (figures 107, 108).

Mandibles at full gape open to only 60–90°; with static pressure mode of action.

Basal process of mandible large, truncated apically, located in the same plane as the masticatory margin (figure 107).

Labrum hypertrophied, forming a massive shield that can reflex tightly over the entire labio-maxillary complex and completely cover the buccal cavity (figure 107); its apical margin evenly convex, not bilobate.

Trigger hairs present on dorsum of labrum.

Side of head with a vertical preocular groove (figure 108), this groove not extending on to the ventral surface.

Tergite of petiole without lateral lobes at the node. Tergite of postpetiole with or without lateral laminae or lobes (figures 109, 110).

A small genus, endemic in Australia where there are six known species and a number of undescribed forms. Taxonomic revisions of genus have been produced by Brown (1952b) and Taylor (1973).

***Epopostruma* Forel**

(Figures 111–113)

Epopostruma Forel, 1895: 422 [as subgenus of *Strumigenys*]. Type-species: *Strumigenys* (*Epopostruma*) *quadrispinosa* Forel, 1895: 422, by subsequent designation of W. M. Wheeler, 1911: 163. [Raised to genus by Emery, 1897: 573]

Hexadaceton Brown, 1948: 120. Type-species: *Hexadaceton frosti* Brown, 1948: 120, by original designation. [Synonymy by Brown, 1973b: 181 (provisional); Taylor and Brown, 1985: 63 (confirmed)]

Diagnosis of genus (workers)

With characters of the epopostrumiform genus-group listed above, and the following.

Mandibles linear (figure 111), with kinetic mode of action, edentate except for two enlarged teeth apically that overlap at full closure; in ventral view without an inflected basal-external angle.

Mandibles at full gape open to 170° or more.

Basal process of mandible a curved truncated bar (figure 113). Labrum covers approximately the apical half of the labio-maxillary complex, its anterior margin not evenly convex; side of labrum with a small rectangular process (figure 113).

Labrum mediodorsally with a very broadly and deeply concave depression in its proximal half (figure 113) [A].

Trigger hairs two in number, long and stout, arising from labrum and widely separated.

Side of head with a deep vertical preocular groove (figure 111), this groove extending on to the ventral surface [A].

Scrobe strongly present, extending below eye (figures 111, 113).

Only three species have been described in this genus (Taylor and Brown, 1985), all from Australia. There is no synthesizing taxonomic study.

Key to Dacetonini genera (workers)

Ideally one or two specimens of each series should be mounted with the mandibles open, so that mouthpart characters can be examined easily. However, in most taxa mouthpart characters can be seen in ventral view in normally (card-point) mounted specimens. Labral characters can usually be seen adequately in ventral view, or in dorsal view if the mandibles are ajar.

- 1 Limbus absent from first gastral tergite (figures 9, 16, 17, 20, 21, 98, 99, 104, 105, 109, 110, 112). With the head in profile the eye not situated at the ventrolateral margin (figures 7, 11, 19, 97, 102, 103, 108, 111). Spongiform tissue absent from postpetiole but if a narrow waxy border present (extremely rare) it is not arranged in discrete lateral and ventral lobes in profile view 2
- Limbus present on first gastral tergite (figures 64–70, 87–92). With the head in profile the eye situated at the ventrolateral margin (figures 60–63, 65–70, 83–86, 90–91) or rarely eye absent. Spongiform tissue usually present on postpetiole (only extremely rarely absent); when present it is arranged into discrete lateral and ventral lobes in profile view 8

- 2 With head in profile the scape, when laid back in its normal resting position, passes above the eye (figures 19, 97). Mandible always linear, with three apical teeth in a more or less vertical or oblique series that interlock at full closure (figures 4, 5, 7, 18, 19, 95, 96) 3
- With head in profile the scape, when laid back in its normal resting position, passes below the eye or across the ventral margin of the eye (figures 11, 102, 103, 108, 111). Mandible triangular (figures 100, 106) or linear (figures 10, 111), if linear then with two apical teeth in a more or less vertical or oblique series that overlap at full closure (figures 11, 113) 5
- 3 Basal process of mandible passes below the labrum at full mandibular closure (figures 5, 7). Labrum vestigial, a minute Y-shaped sclerite between the mandibular insertions (figure 6). Trigger hairs arise from mandible. Maxillary palps absent. Apex of metapleural gland bulla level with dorsalmost point of propodeal spiracle. Antenna with 11 segments. Transverse sulcus present on mesopleuron. (Neotropical) *Acanthognathus*
- Basal process of mandible passes above the labrum at full mandibular closure (figures 18, 94). Labrum large, a conspicuous transverse sclerite between the mandibular insertions (figures 18, 94). Trigger hairs arise from labrum (figures 18, 96). Maxillary palps with three to five segments. Apex of metapleural gland bulla far below level of dorsalmost point of propodeal spiracle. Antenna with five or six segments. Transverse sulcus absent from mesopleuron 4
- 4 Second funicular (=third antennal) segment extremely elongate (figures 18, 19), at least approaching the combined length of the apical plus preapical segments. Antenna with five segments in total. Basimandibular gland absent. Palp formula 5,3. Labral trigger hairs paired, lateral (figure 18). Anterolateral margin of head with a minute gap or no gap between head capsule and base of mandible when the latter fully closed (figure 19). Pronotal cervix dorsally without a thickly rounded anterior collar. (New Guinea, Australia, New Caledonia, New Zealand) *Orectognathus*
- Second funicular (=third antennal) segment short (figure 95), only a fraction of the combined length of the apical plus preapical segments. Antenna with six segments in total. Basimandibular gland present. Palp formula 3,2. Labral trigger hair single, median (figures 95, 96). Anterolateral margin of head with a large U-shaped gap between head capsule and base of mandible when the latter fully closed (figure 97). Pronotal cervix dorsally with a thick rounded anterior collar. (Afrotropical) *Microdaceton*
- 5 Frontal lobes absent; antennal socket surrounded only by an extension of the torulus (figures 10, 11). Antenna with 11 segments. Base of scape shaft continuing line of main length of shaft, straight or nearly straight to the level of the small flange or rim that immediately follows the neck of the articulatory condyle (figure 11), not abruptly downcurved. Propodeal spiracle in profile close to dorsal margin of sclerite (figure 15), widely separated from metapleural gland bulla. Suture between first gastral tergite and sternite rounded laterobasally. (Neotropical) *Daceton*
- Frontal lobes present (figures 100, 106); torulus visible ventral to the lobe (figures 108, 111). Antenna with four to six segments. Base of scape shaft not continuing line of main length of shaft, instead scape abruptly downcurved before reaching the small flange or rim that immediately follows the neck of the articulatory condyle (figures 102, 108, 111). Propodeal spiracle in profile low on side of sclerite, abutting metapleural gland bulla (figures 104, 109, 112). Suture between first gastral tergite and sternite angled laterobasally 6
- 6 Labrum very large, shield-like, at full reflexion capable of covering the entire buccal cavity and completely concealing the labio-maxillary complex (figures 101, 107). Mandible triangular to elongate-triangular (figures 100–106) 7
- Labrum not a large shield, at full reflexion not capable of covering the entire buccal cavity, leaving much of the labio-maxillary complex exposed (figure 113). Mandible linear (figures 111, 113). (Australia) *Epopostruma*

- 7 Mandible edentate from basal process to preapical tooth (figures 106, 107). In ventral view outer margin of mandible without an inflected basal angle (figure 107); in profile mandible not sharply angled downward near base (figure 108). Basal process of mandible large, in same plane as the masticatory margin (figure 107). Petiole node without lateral laminar outgrowths (figures 109, 110). (Australia) *Mesostruma*
- Mandible denticulate from basal process to preapical tooth (figure 100). In ventral view outer margin of mandible with an inflected basal angle (figure 101); in profile mandible sharply angled downward near base (figures 102, 103). Basal process of mandible small, depressed below plane of masticatory margin (figure 101). Petiole node with lateral laminar outgrowths (figures 104, 105). (Solomon Is, New Guinea, Australia) *Colobostruma*
- 8 Labrum with reduced distal lobes and specialized proximal shield. Labral lobes small, papilliform or vestigial, not arising from across entire width of labrum (figures 81, 82, 93). Shield of labrum proximal of lobes with laterally extended margins (figures 81, 93) that are thick in anterior view; whole sclerite usually roughly T-shaped. Buccal cavity relatively long and narrow, lateral margins of cavity converging anteriorly and the mandibles in ventral view apparently arising from the apex of the labio-maxillary complex (figures 81, 82). Maximum gape of mandibles 170° or more. (World wide) *Strumigenys*
- Labrum with exaggerated elongate distal lobes and unspecialized proximal shield. Labral lobes variously shaped but always well developed and prominent, arising from across entire width of labrum (figures 42, 52–56). Shield of labrum proximal of lobes without laterally extended margins (figures 42, 52–59); whole sclerite never T-shaped. Buccal cavity relatively short and wide, lateral margins of cavity not converging anteriorly and the mandibles in ventral view not arising from the apex of the labio-maxillary complex (figures 57–59). Maximum gape of mandibles 90° or less. (World wide) *Pyramica*

Classification of Dacetonini genera

Tribe Dacetonini (= Dacetiti, = Epopostrumiti, = Orectognathiti, = Strumigeniti)

Genus *Daceton* (= *Dacetum*)

Genus *Acanthognathus*

Genus *Orectognathus* (= *Arnoldidris*)

strumigenyiform genus group

Genus *Pyramica* (= *Asketogenys*, = *Chelystruma*, = *Cladarogenys*, = *Codio-myrmex*, = *Codioxenus*, = *Dorisidris*, = *Dysedrognathus*, = *Epitritus*, = *Glamyromyrmex* (= *Borgmeierita*), = *Gymnomyrmex*, = *Kyidris* (= *Polyhomoa*), = *Neostruma*, = *Pentastruma*, = *Serrastruma*, = *Smithistruma* (= *Cephaloxys*, = *Miccostruma*, = *Platysturma* = *Weberistruma*, = *Wessonistruma*), = *Tingimyrmex*, = *Trichoscapa*

Genus *Strumigenys* (= *Eneria*, = *Labidogenys*, = *Proscopomyrmex*, = *Quadristuma*)

clade of *Microdaceton* + epopostrumiform genus group

Genus *Microdaceton*

epopostrumiform genus group

Genus *Colobostruma* (= *Alistruma*, = *Clarkistruma*)

Genus *Mesostruma*

Genus *Epopostruma* (= *Hexadaceton*).

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