Cesare Baroni Urbani* & Maria L. de Andrade*

THE ANT TRIBE DACETINI: LIMITS AND CONSTITUENT GENERA, WITH DESCRIPTIONS OF NEW SPECIES

(HYMENOPTERA, FORMICIDAE)

> *"As new species are discovered... the characters separating... genera are gradually losing their distinctiveness, and it seems likely that we may eventually see most of these genera merged again in one large genus".*
>
> W. L. Brown (1973a: 3)

1. INTRODUCTION

Baroni Urbani & de Andrade (1994) synonymized under the tribal name Dacetini the two tribal names Phalacromyrmecini and Basicerotini and merged a number of genera within the tribe.

This result was promptly contrasted by Bolton (1995: 47) who wrote: "I consider this action too extreme by far as it is based on a grossly inadequate character set", and added "In consequence their [i.e. Baroni Urbani & de Andrade's] results are very insecure, and their proposed synonyms are all **revived from synonymy** [boldface by Bolton] here". As a matter of fact Baroni Urbani & de Andrade (1994) reached their conclusions after examining each and every character used by Bolton and others to separate the genera in question. As a consequence of this, Bolton's statement of character inadequacy applies much better to his generic resurrections than to the synonymies proposed by Baroni Urbani & de Andrade (l. c.).

All these generic names re-appeared hence as valid names in Bolton (1995) and most of them also in a number of subsequent papers, including Bolton (1998) and in other papers published afterwards by uncritical entomologists.

* Institut für Natur-, Landschafts- und Umweltschutz, Biogeographie, Universität Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland.

None of these 1995-1998 generic revivals, however, is listed where one would expect to find them, i.e. under the "taxonomic history" of generic names in BOLTON (2003).

The reason for this omission is that only one year after his unexplained revival of our synonyms, BOLTON (1999), with a dramatic inversion of course, synonymized again all genera already synonymized by BARONI URBANI & DE ANDRADE (1994) under *Strumigenys* under two genera, i.e. *Strumigenys* (including only *Quadristruma* as proposed by ourselves in 1994) and the revived genus *Pyramica*, a former synonym of *Strumigenys* now including all other genera that we previously synonymized under *Strumigenys*.

Pyramica, described by ROGER (1862), was considered as a synonym of *Strumigenys* only one year after its description by the same ROGER (1863b) and never received generic status again until BOLTON (1999). This last, entirely new and radically different classificatory scheme is adopted by BOLTON (2000, 2003) and by all his uncritical followers that rejected our synonymies only one year before.

BOLTON's (1999-2003) classificatory system is supported by an impressive display of morphological erudition enforcing generic boundaries, phylogenies, and conclusions by introducing a remarkable set of new characters. Unfortunately, many of these characters are used for the first time with the sole support of unclear descriptions, and are seldom backed by good illustrations, definitions and unequivocal statements about their presence or absence among critical taxa.

One of the greatest difficulties that we faced was interpreting a number of Bolton's characters. Often slightly different rewordings of the same sentence are used in different papers to define presumably different synapomorphies. For instance:

BOLTON (1998: 72) states that the "labrum with an impression... on the labral shield, distal of the basal hinge but proximal to the labral lobes" is synapomorphic for all his "dacetonines". But, one year later, BOLTON (1999: 1681) defines the "labrum mediodorsally with a very broadly and deeply concave depression in its proximal half" as autapomorphic for the genus *Epopostruma*. We are unable to understand why these two very similar definitions should be considered as two independently derived characters related to two different clades and not as two slightly different rewordings of the same

character description. We already raised this point in a web document (BARONI URBANI & DE ANDRADE, 2006b) and BOLTON (2006b) replied by adding that his 1998 definition is repeated in BOLTON (2003:54). This is perfectly true, of course, but it does not justify at all the double role attributed to the same character in two different positions within the same clade.

In other instances, two characters used by Bolton in the same context but for different purposes simply contradict each other:

BOLTON (1998: 73) writes that the "propodeal spiracle low on side of sclerite, abutting the margin of the small metapleural gland bulla" is unique to the Basicerotini and Phalacromyrmecini, while the "Dacetonini (sic!)... [have the] propodeal spiracle... widely separated from metapleural gland". But BOLTON (1999: 1649, character 22 and table 1), contradicting his own former statement, attributes the "metapleural gland bulla abutting or very close to annulus of propodeal spiracle" to 5 out of 9 genera of Dacetini considered...

Other characters, like the katepisternal groove, given as synapomorphic for the tribe Phalacromyrmecini, proved to be present in only one species and absent even in the type genus of the tribe, *Phalacromyrmex* (see later the discussion of our character # 36), i.e. they appear to have been imagined only to support a particular classification. BOLTON (2006a) admits *obtorto collo* the failure of this character but insists that it should be re-defined and considered just the same....

These three examples, among many more possible ones, should be sufficient to show the need for the present study and to justify our previous appreciation of Bolton's work. Other examples will be dealt with under the individual character analysis in this paper.

Another very important difference lies on the fact that in BOLTON (1999-2000), absence or presence of a given trait in a taxon are often declared *a priori* as due to secondary loss or to homoplastic gain. These statements, however plausible they may be, are equivalent to the assertion that the evolutionary path of the group is already known and invalidate the meaning of any phylogenetic deduction based on them.

We made an effort to ban potential proclamations of faith from our analysis.

This was already anticipated by BARONI URBANI & DE ANDRADE (2006b) but BOLTON (2006b) insists on the correctness of his approach and this forces us to further explain two additional aspects: 1. In this paper, to infer phylogeny and classification, we shall code a trait as present or absent or polymorphic in a given genus according to its observed record in that genus; BOLTON (1999), on the contrary, codes it in the way that he thinks better reflecting his idea of the phylogeny. This has nothing to do with the plausibility of Bolton's ideas; it is simply a matter of method. 2. Assuming that a clade can be defined by a trait presumably lost in some of its members is unacceptable since this would potentially allow creation of unlimited clades (and taxa) for any set of species with and without the trait in question. To do so, one needs only to suppose the secondary loss of a critical apomorphy among the species without it.

Our working hypothesis is that the differences in method between Bolton and us are worth consideration and should yield significantly different results.

In spite of its pertinence to the subject, we shall pay less attention to a recent contribution by DIETZ (2004). The reasons for this are twofold: 1) Dietz's analysis is largely inspired by and, in its motivations, differs insignificantly from the ones of BOLTON (1998-2000), and 2) Dietz's data differ considerably from those of Bolton and also from Dietz's own character descriptions. We tentatively explain this anomaly by a number of typing mistakes in Dietz's published data matrix, mistakes presumably absent from or unlike those of the matrix that Dietz used for calculations. Our hypothesis is supported by the fact that searching for the shortest tree(s) for DIETZ's (2004) published data by means of PAUP 4.0b (see later, the methods chapter) yields results radically different from those of DIETZ (2004).

These discrepancies between character descriptions and character coding render difficult any attempt to evaluate Dietz's arguments and conclusions and, for this reason, in this paper we will discuss only the most controversial of them.

In this paper, on the contrary, we shall discuss all the characters used by Bolton on the base of the factual evidence available to us.

2. MATERIAL AND METHODS

We were able to study material deposited in the institutions listed below.

ANIC.   Australian National Insect Collection, C.S.I.R.O., Canberra, Australia.

BMNH.   The Natural History Museum, London, UK.

FMNH.   Field Museum of Natural History, Division of Insects, Chicago, U.S.A.

GOPC.   The amber collection George O. Poinar, Jr. maintained at the Oregon State University, Corvallis, Oregon.

MCZC.   Museum of Comparative Zoology, Harvard University, Cambridge, Mass.

MHNG.   Muséum d'Histoire Naturelle, Genève, Switzerland.

MIZA.   Museo del Instituto de Zoología Agrícola "Francisco Fernández Yépes", Maracay, Venezuela.

MSNG.   Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy.

MZSP.   Museu de Zoologia, Universidade de São Paulo, Brazil.

NHMB.   Naturhistorisches Museum, Basel, Switzerland.

PUCE.   Museo de Zoología QCAZ, Escuela de Biología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

In addition, we were able to study two Baltic amber specimens (a worker and a gyne) from the collection of Mr Jörg Wunderlich, Straubenhardt (Baden-Württemberg, Germany) that we identified as *Agroecomyrmex duisburgi* (Mayr) or a species very close to it. In spite of its relevance for the present study, the genus *Agroecomyrmex* was not explicitly included in our analysis. Examination of the two specimens from the collection Wunderlich did not allow assessment of some characters needing proper mounting or dissection and did not permit morphological inferences much better than those already possible from the figures of WHEELER (1915a).

To assess optimal rank of and phylogenetic relationships between taxa, we performed a cladistic analysis including all genera considered as valid by BOLTON (1998-2000) and as many as possible of the characters used by BOLTON (1999) and elsewhere.

2.1. OUTGROUP COMPARISON

BARONI URBANI & DE ANDRADE (1994), for their cladistic analysis, choose as outgroup the Attini and two genera with presumably superficial similarities with the Dacetini, i.e. *Stegomyrmex* Emery and *Calyptomyrmex* Emery. BOLTON (1999) used only *Myrmica* Latreille as outgroup. Bolton's choice was not explained but it can be probably justified since it includes an apparently unspecialized myrmicine. We are still convinced that our earlier choice has better chances to include a near relative of the Dacetini than the one of Bolton, but *pro bono pacis*, for this study we consider most of our former outgroups plus *Myrmica* as Bolton did. On the other hand, the Attini were not considered any more in the present analysis. The reasons for this are that, for a better comparison with our ingroup taxa, all Attini genera should have been individually considered for the analysis and this would have raised the total number of taxa under study to a figure preventing any form of exact search for the shortest tree(s).

In addition to our 1994 outgroups, we included in the analysis also a representative of the genus *Tatuidris* Brown & Kempf, a purportedly distantly related genus belonging to a different subfamily according to BOLTON (2003) but possessing a mandibular kinetic similar to the one apomorphic for the Dacetini according to BARONI URBANI & DE ANDRADE (1994: 10) and BOLTON (1998: 68-70). We regard this state of affairs as an excellent reason to include *Tatuidris* in our analysis. To avoid that our search might force *Tatuidris* to appear too close to the dacetine genera (e. g. by choosing *Myrmica* as sole outgroup and *Tatuidris* + the dacetines as ingroup) or unnaturally too far from them (e. g. by artificially transferring *Tatuidris* among the outgroups), we included in our study two genera clearly belonging to two separate but related subfamilies, i.e. *Pseudomyrmex* Lund and *Myrmecia* Fabricius. In our parsimony analyses we considered *Pseudomyrmex* and *Myrmecia* as the sole outgroups. *Pseudomyrmex* is meant to represent the subfamily Pseudomyrmicinae, i.e. the sister-subfamily of all other ants considered in this paper and *Myrmecia* is the sole genus constituting the subfamily Myrmeciinae, also close to the Myrmicinae (BARONI URBANI *et al.* 1992; BARONI URBANI 2005).

Study of the possible phylogenetic relations of *Tatuidris* by means of *Pseudomyrmex* and *Myrmecia* as outgroups will not ben-

efit from consideration of their respective autapomorphies. On the contrary, we considered for our analysis the three synapomorphies of the Myrmicinae as given by BOLTON (2003: 52). These should exclude *Tatuidris* from the Myrmicinae. But we thought it fair considering also two potential Myrmicinae synapomorphic characters described by BARONI URBANI *et al.* (1992) and shared by all classic Myrmicinae genera, including *Tatuidris*.

To assess presence or absence of some internal structures among the taxa under consideration we dissected the following species:

Basiceros disciger (Mayr).

Calyptomyrmex sp.

Colobostruma sisypha Shattuck.

Eurhopalothrix bruchi (Santschi), *platisquama* Taylor, *procera* (Emery).

Mesostruma turneri (Forel).

Myrmecia pyriformis F. Smith.

Myrmica scabrinodis Nylander.

Octostruma sp., *O. stenognatha* Brown & Kempf.

Orectognathus sp.

Protalaridris sp.

Pseudomyrmex sp. 1 & sp. 2.

Pyramica alberti (Forel), *argiola* (Emery), *decipula* (Bolton), *denticulata* (Mayr), *eggersi* (Emery), *jacobsoni* (Menozzi), *kichijo* (Terayama, Lin & Wu), *membranifera* (Emery), *minima* (Bolton), *myllorhapha* (Brown), *nannosobek* Bolton, *nepalensis* (de Andrade), *semicompta* (Brown), *subedentata* (Mayr), *tenuissima* (Brown), *urrhobia* Bolton, *zeteki* (Brown).

Rhopalothrix ciliata Mayr.

Stegomyrmex vizottoi Diniz.

Strumigenys chapmani Brown, *doriae* Emery, *ekasura* Bolton, *elongata* Roger, *emmae* (Emery), *exilirhina* Bolton, *godmani* Forel, *grandidieri* Forel, *harpyia* Bolton, *koningsbergeri* Forel, *lanuginosa* Wheeler, *lyroessa* (Roger), *micretes* Brown, *paranetes* Brown, *rogeri* Emery, *saliens* Mayr.

Tatuidris tatusia Brown & Kempf.

If, on one hand, this list may be shorter than what we wished, on the other the number of structures apparently escaped to the attention of former students and discovered by us in the species listed above is surprising. Moreover, the monograph by BOLTON (2000) alone revealed a precious, nearly exhaustive source of reliable information contrasting with the information contained in BOLTON's (1998 & 1999) previous character descriptions and generic boundaries.

For our phylogenetic analysis the evolution of all characters was considered as unordered. BOLTON (1999) states that only three of the characters considered by him were treated as unordered without specifying how the remaining characters were considered. By analysing Bolton's data and considering all characters as unordered, we obtain the same results as Bolton (l. c.). We explain this coincidence by supposing that Bolton coded most of his characters as ordered but, as a matter of fact, since most of his characters are binary, there is no difference between ordered and unordered binary characters. Differences arise only when computing with multi-state characters.

In the following we give a list of all the characters that we retained as potentially phylogenetically significant and of their coding. Differences with BOLTON (1999), if any, will be explained and justified in each character description. We felt compelled to exclude from computation some characters resulting from the literature. A list of these excluded characters and the justification for their exclusion will be given after the list of the characters used.

A parsimony analysis of all genera treated as valid in the most recent literature was performed by PAUP 4.0b10 (SWOFFORD 2002). Search for the shortest tree(s) was done by means of the mathematically exact algorithm "Branch-and-Bound".

Some graphic display and character tracing was obtained by MacClade 4.05 (MADDISON & MADDISON 2002).

To enable a simple judgement on valid or invalid genera, whenever possible, we tried to include in our data at least one known and undoubted autapomorphy for each genus. Genera that, at the end of our analysis, resulted destitute of any kind of apomorphies (i.e. genera without valid apomorphies already known from the literature and without apomorphies representing secondary gains or losses of other characters appearing as a result of our character optimization) will be considered as synonyms of their closest related genus.

While discussing the results of the phylogenetic analyses and in order to give a possible evaluation term of the characters on which our classification is based, all critical apomorphies implying a nomenclatorial decision are reported with their individual Consistency Index and Retention Index as computed by PAUP 4.0b10 and MacClade 4.05 on the Strict Consensus Tree of Figs. 33 and 34. Determining the number and quality of the synapomorphies at critical branches was performed by means of MacClade.

Measurements and indices used in the text for species descriptions are the following:

HL   = Head Length: the maximum measurable distance between the medial margin of the vertexal angles and the antero-medial margin of the clypeus with the head in full frontal view.

HW = Head Width: maximum measurable head width with the head in full frontal view.

ML   = Mandible Length: maximum length of the mandible between the antero-medial margin of the clypeus (concave margin excluded when present) and the mandibular apex.

EL   = Eye Length: maximum length of the eye.

SL   = Scape Length: length of scape shaft, excluding the basal condyle.

WL = Weber's Length: diagonal length of mesosoma from the anterior pronotal border (excluding neck) to the distal edge of the propodeal lobe.

TL   = Total Length: combined head length in full-face view (closed mandibles included), Weber's length of mesosoma, petiole and postpetiole lengths (in profile) and length of gaster (in profile).

CI   = Cephalic Index: $(HW/HL) \times 100$

MI   = Mandibular Index: $(ML/HL) \times 100$

SI   = Scape Index: $(SL/HL) \times 100$

MTI = Mandibular-Torular Index: (Distance between the intersections of the external margins of the closed mandibles with the anterior clypeal border/Distance between the outermost points of lower margins of toruli) $\times 100$. BOLTON (1998) proposes an operational "Mandibular-Torular

Index (MTI)" to quantitatively express the old qualitative dacetine character "pear-shaped head". However, according to the anthropological and biometric practice as already codified in myrmecology by RAIGNER & VAN BOVEN (1955) and current use in ant literature including other Bolton's printed papers, Bolton's MTI is a ratio (and also Bolton calls it so) and not an index. An index should be the ratio between two measures where the presumably smallest one, multiplied by 100, is divided by the larger one. The ant literature already offers several examples of such indices, like the Cephalic Index (CI), the Scape Index (SI), Petiolar Index (PI), etc. Bolton's quotient, hence, should be called "Mandibular-Torular Ratio" or, to maintain the name index and the acronym MTI as we did in the present paper for uniformity with the other indices, Bolton's MTI should be multiplied by 100. Furthermore, percent expressions like CI = 125, SI = 56, for example, offer small diction and mnemonic facilities as compared with rough ratios like CI = 1.25 and SI = 0.56.

Defenders of the deregulation may object that, in this same paper, we also use the name index for ratios like the Consistency Index and the Retention Index for characters and for phylogenetic trees. These terms, however, are already established in the cladistic literature and the linguistic consistencies or homoplasies of cladism are far beyond the scope of the present work.

3. CHARACTER CHOICE AND TAXONOMIC RANK

There are no general rules but only intuitive guesses drawn on taxonomic experience on which characters could be "good" or "bad" in defining genera or tribes.

Though the temptation was strong, we will not discard any of Bolton's generic characters as BOLTON (1987: 285) did for the genus *Diplorhoptrum* by means of vague statements like "I am unable to regard... [this morphology of the male volsellae] as being significant above the species-group level", even if we believe that this same statement would better fit any of Bolton's Dacetini genus-level characters rather than *Diplorhoptrum*. As a matter of fact, *Diplorhoptrum*

appears as the perfectly sound and well-defined sister-genus genus of *Solenopsis* as shown by BARONI URBANI (1995), a citation omitted by BOLTON (2003) in his synopsis of ant classification. Irreducible sceptics, in addition, may have a glance to the *Diplorhoptrum* male volsellae by means of a SEM: they will discover a previously unknown, new structure in ant morphology. We consider this, still unpublished, ultrastructural particularity as a redundant, impressive argument in favour of *Diplorhoptrum*'s generic validity.

The current situation of the Dacetini classification forces us to acknowledge the obvious: 'good' supraspecific taxa like genera and tribes, in ants as in other organisms, must be characterized by at least one unequivocal synapomorphy holding for all the species involved. Homoplasy occurs among distantly related taxa. When the same trait appears occasionally in closely related clades, this is more likely to be due to common ancestry and, until proof of the contrary, this trait cannot be used to separate monophyletic genera or tribes. Stated otherwise, all members of a taxon (species, genus, tribe, or subfamily), and not just the majority of them, should share at least one, clear synapomorphy characterizing that taxon. This is not the case of the Dacetini genera as they are currently defined. In this respect, the present study should be considered as a considerable but still far from optimal improvement of the existing classification.

The numerical and morphological diversity of the Dacetini is still much inferior e.g. to the one known for the ant genus *Camponotus* (see e. g. EMERY 1925). On the other hand, some of the repeatedly blamed *Camponotus* subgenera are better defined and biogeographically more meaningful than some currently accepted Dacetini genera.

In our research we entirely concur with BOLTON (1999:1640) in adopting "an opening hypothesis that every genus-group name listed be regarded as invalid until proved otherwise by the establishment of apomorphic characters". But, contrarily to BOLTON (l. c.), decisions about individual character apomorphy in this study will be taken only by means of standard algorithms like PAUP 4.0b10 (SWOFFORD, 2002) and MacClade 4.05 (MADDISON & MADDISON, 2002) applied to observed character distributions and not on personal opinions.

We are aware that a species-level cladistic analysis of the ca. 900 known Dacetini species might suggest additional branches supported

by weak synapomorphic characters convergent with other clades or secondarily disappearing in other, closely derived branches. Such a species-level analysis is too difficult for a so high number of species although one might expect that it will weaken or strengthen currently accepted synapomorphies. In our genus-level approach, the classificatory value of true or presumed generic apomorphies was evaluated in terms of Consistency and Retention Indices within the same genus-level analysis as already stated in the Methods chapter.

We made an effort to use as many as possible of the characters employed in the papers by BOLTON (1998 & 1999) (see the discussion about the individual characters' inclusion or exclusion). This approach poses nonetheless a dilemma about the phylogenetic value of many of the characters that we used. A practical example should be sufficient to exemplify our doubts.

BOLTON (1998) used for the first time characters like presence or absence of a katepisternal groove and deeply (as opposed to superficially) impressed labium and other similar traits to define genera and tribes for members of his "dacetonine tribe group". One may be tempted to discard these characters as phylogenetically irrelevant.

But Bolton's work should not be detracted so simply. BOLTON (l.c.) tried to strengthen his work by identifying more than one often apparently insignificant characters overlapping in distribution.

Discovery of such overlapping character sets might influence our phylogenetic reconstructions and even apparently insignificant characters, by reciprocally supporting each other, might result in plausible supraspecific synapomorphies. Since sharing of the same trait among closely related branches is better explained by common descent rather than by homoplasy, these apparently insignificant traits can be considered as synapomorphic and, hence, can be used to construct phylogenies, only if A) they are uniform within all the taxa to be classified and B) they affect all and only the taxa in question.

Unfortunately, one of the major results of our study will be that neither condition A nor B is ever met for most characters supposed to be relevant for the dacetine phylogeny. Stated otherwise, all current attempts of phylogenetic reconstructions for the Dacetini (BARONI URBANI & DE ANDRADE, 1994; BOLTON, 1998; present study) are weakened at the root by being drawn on characters of doubtful phylogenetic significance. There is no mention of better characters

in the ant literature and we were unable to discover superior ones. All these studies, however, find their justification in proposing a classificatory model as sound and as credible as possible.

For instance, the most impressive known synapomorphy for the tribe Phalacromyrmecini so far is the presence of a katepisternal groove. Rank attribution to a character (and hence to the taxon possessing it) is always a subjective evaluation. For the Phalacromyrmecini our study will show that the katepisternal groove is not synapomorphic since it is present in only one species of one genus among the three genera supposed to constitute the tribe (see later, the discussion of our character # 36). Nonetheless, assuming that a scientist will discover a species of a genus whatever with a katepisternal groove, or with a deeply (as opposed to superficially) impressed labium, should this hypothetical scientist place this species in a different genus and tribe? And, assuming that our hypothetical myrmecologist would really do so, how many other myrmecologists will follow him/her accepting the new genus and tribe? Our guess is none. Or, at least, we so hope.

Our optimistic guess is likely to be contradicted anyway by numerous students of behaviour, ecology, histology, etc. These students will even not try to understand the possible phylogenetic meaning of a katepisternal groove. Of course: they are not taxonomists. They will nonetheless use the newly proposed nomenclature in order to show that they are knowledgeable *even* with the latest novelties of taxonomy.

We cannot change this situation but we regret that mentally lazy taxonomists may also follow the same course of action. During the tormented history of the Dacetini classification, this already happened when 18 Dacetini genera like *Smithistruma*, *Epitritus*, *Kyidris*, *Glamyromyrmex*, *Dorisidris*, etc., considered as synonyms by BARONI URBANI & DE ANDRADE (1994), were erroneously revived by BOLTON (1995) as everybody admits today.

4. RESULTS

4.1. LIST OF CHARACTERS AND OF THEIR RECORDED STATES

Before discussing the morphological characters used to construct the phylogeny and classification of the Dacetini, a physiological trait,

the mode of action of the mandibles, should be briefly considered. Although without using it directly in his analysis, BOLTON (1999) makes an extensive description and treatment of it emphasizing its phylogenetic relevance.

The two modes of mandibular action observed among the Dacetini are seemingly mutually exclusive and were improperly named as "static pressure" as opposed to "kinetic" mandibles. Naturally, every kind of movement, including those necessary to exercise a pressure whatever, is kinetic and never static by definition.

The "static pressure" and "kinetic" mandibles, however, have been observed in a too small number of species to be seriously considered as a taxonomic character, but, in our character analysis, we shall discuss the distribution of their presumed most important morphological correlate which is assumed to be taxonomically and phylogenetically relevant according to BOLTON (1999). This is the maximum angle between the open mandibles. This biometric character resulted too variable to be considered among the phylogenetically significant ones listed below but it will be nonetheless discussed in detail for its presumed discriminatory value between the "genera" *Pyramica* and *Strumigenys* (see later the definition of the genus *Strumigenys* in Chapter 4.5).

Nonetheless it must be added that, from a purely cladistic point of view, the whole discussion has little interest since the mandibular kinetic alone − as its morphological correlate(s) alone - are inadequate to the separation of the two "genera" since one of the two will inevitably result paraphyletic to the other.

The following is an annotated list of the morphological characters tentatively retained to infer a phylogenetically drawn classification of the Dacetini. In the great majority of cases, all characters referred to the worker caste in the literature and in the following list may be assumed to repeat the (unknown) gyne condition as well.

1. Worker. Maxillary palps six-jointed (0), five-jointed (1), four-jointed (2), three-jointed (3), two-jointed (4), one-jointed (5), absent (6). This is character # 8 of BARONI URBANI & DE ANDRADE (1994) and character # 1 of BOLTON (1999), transformed respectively from five and three to seven steps to better consider genera not considered by BARONI URBANI & DE ANDRADE (l. c.) and by BOLTON (l. c.). DIETZ (2004, character # 7) also increases the number of

steps of this character as we did, but from three to six steps only.
The reason for this is that no outgroups with six jointed maxillary
palps are considered in his work. Our coding for *Octostruma* differs
from the count of BOLTON (2003) as a result of the dissection of a
specimen of *O. stenognatha* (1-jointed instead of 2-jointed maxillary
palps) as already reported in our 1994 paper (p. 19). *Ishakidris* was
coded as 2-jointed according to BOLTON (1984) and DIETZ (2004).
BOLTON's (2003: 283) record of 3-jointed maxillary palps for this
genus is probably due to a typing or printing mistake. Dietz's table
2 contains a number of erroneous codings for this character (e. g.
for *Acanthognathus, Strumigenys, Basiceros,* a. o.).

2. Worker. Labial palps, four-jointed (0), three-jointed (1),
two-jointed (2), one-jointed (3). This is character # 9 of BARONI
URBANI & DE ANDRADE (1994), char. # 2 of BOLTON (1999) and
char. # 8 of DIETZ (2004) (where labial palps are called "palpos
mandibulares"). The range of this character is amplified here to
include outgroups with four-jointed palps. BOLTON (1999 & 2003)
and DIETZ (2004) differ each other in coding this character. In a
few doubtful cases that we were unable to examine we recorded the
counts of both authors.

3. Worker. Labrum, not T-shaped (0), or T-shaped (1). This
is character 3 of BOLTON (1999) but coded polymorphic (instead
of never T-shaped) for *Pyramica* because of presence of T-shaped
labium in some species like *Pyramica subedentata* (Mayr) (Fig. 1).
We coded nonetheless the "T-shaped" structure as regularly present
in *Strumigenys* as Bolton did, although the morphology within the
genus is far from being unequivocal and constant (Fig. 2).

4. Worker. Labrum capable of full reflexion over the buccal
cavity (0), or not (1). This is char. # 4 of BOLTON (1999).

5. Worker. Labral shield not hyperthrophied, not conceal-
ing the entire buccal cavity (0), or enormous, hypertrophied, when
reflexed concealing entirely the buccal cavity (1). This is char. # 5
of BOLTON (1999). We hesitated to add this character to the matrix
since it is logically negatively correlated with character # 4. As a
further proof of this, within Bolton's "dacetonine tribe-group" it
is distributed among the genera considered in a perfectly comple-
mentary way with character # 4, with the sole exception of *Epo-
postruma*. By considering character # 5, there is hence the risk of
overweighting the former char. # 4. Our conclusion is confirmed by
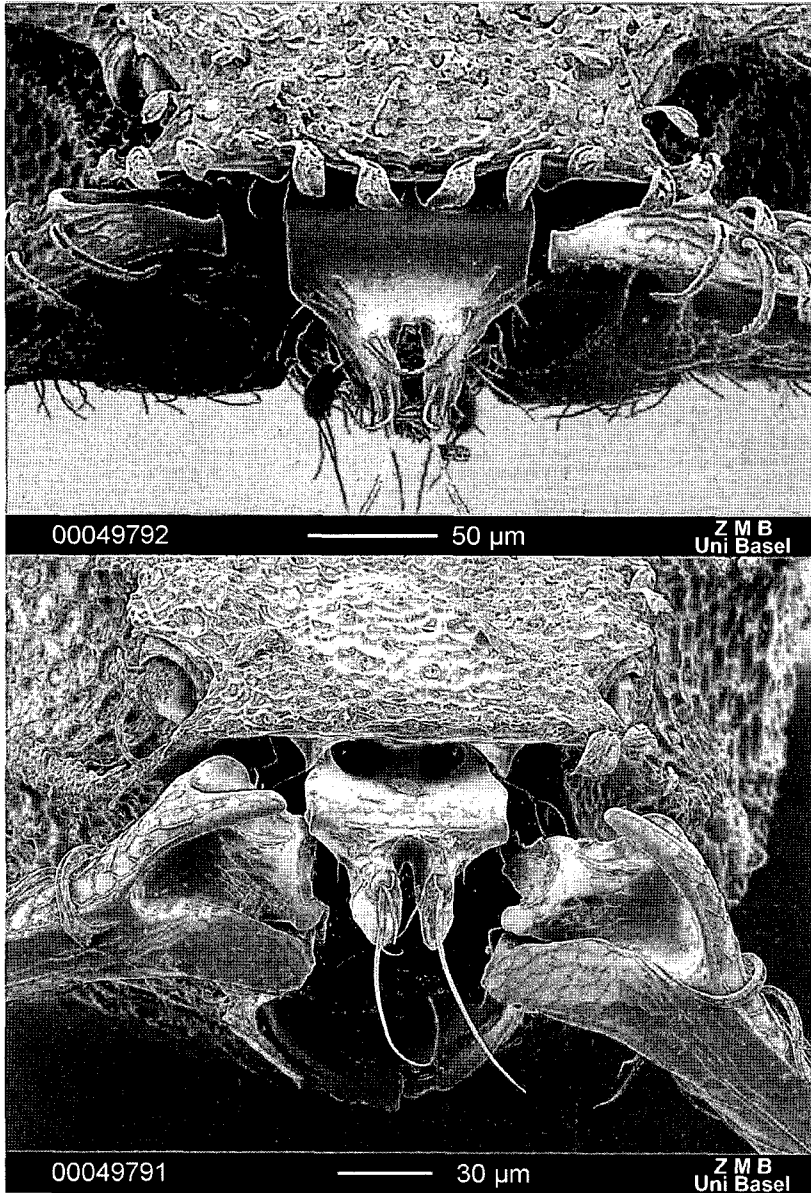
Fig. 1 - "T-shaped labrum" of *Pyramica subedentata* (Mayr), (top) and *Strumigenys exilirhina* Bolton (bottom). The "T-shaped" construction should be synapomorphic for *Strumigenys* and absent in *Pyramica* according to BOLTON (1999, 2000)
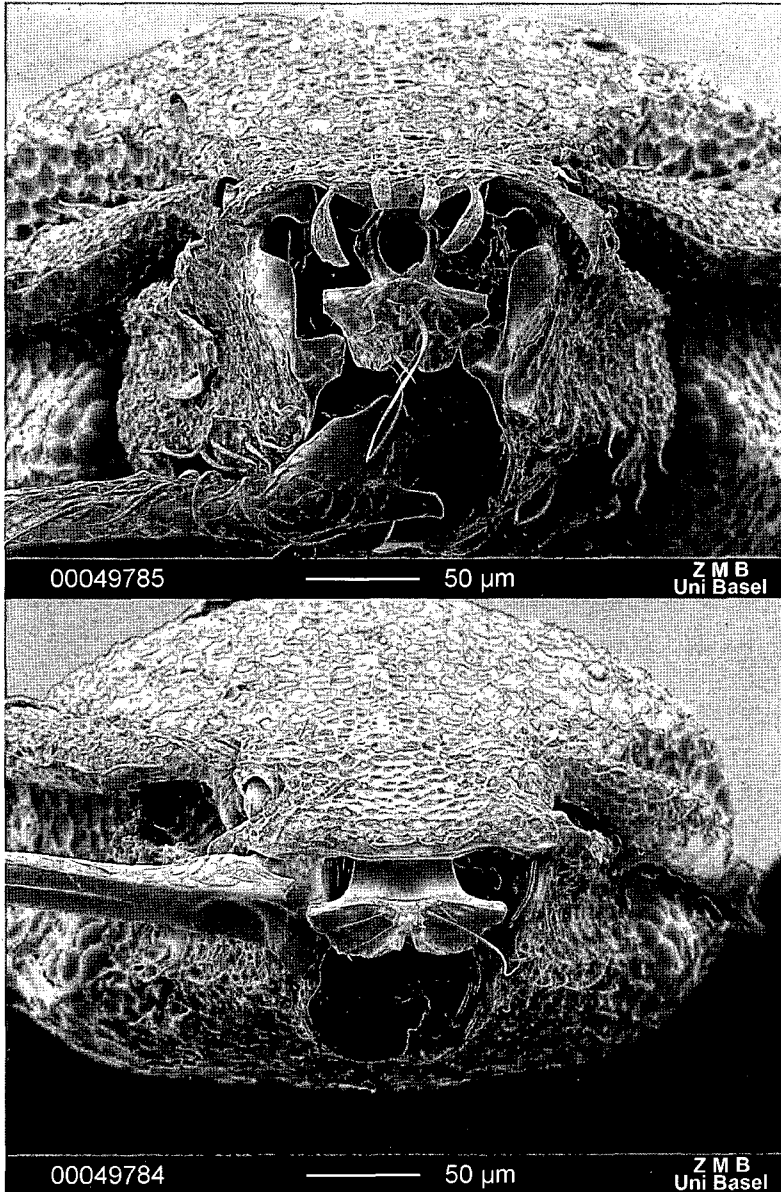
Fig. 2 - Labia of *Strumigenys rogeri* Emery (top) and *S. harpyia* Bolton (bottom) showing intrageneric variation beyond the presumed synapomorphic "T" shape.

examination of BOLTON's (l. c.) character matrix where 0's and 1's are antithetically distributed between characters 4 and 5. One might expect *a priori* that a hypertrophied labrum (char. # 5) should be unable of complete reflexion (char. # 4).

6. Worker. Labrum without (0), or with a deeply incised, transverse groove defined by a sharp ridge (1). Presence of this ridge is given by BOLTON (1998: 70) as synapomorphic for the tribe Basicerotini. The ridge, however, is faint in some Basicerotini species, like *Octostruma stenognatha* Brown & Kempf (Fig. 3) and present in a distantly related genus like *Stegomyrmex*, and in some species of the non-basicerotine ingroups *Pyramica* and *Strumigenys* (Fig. 4), and *Colobostruma* (Fig. 5, bottom).
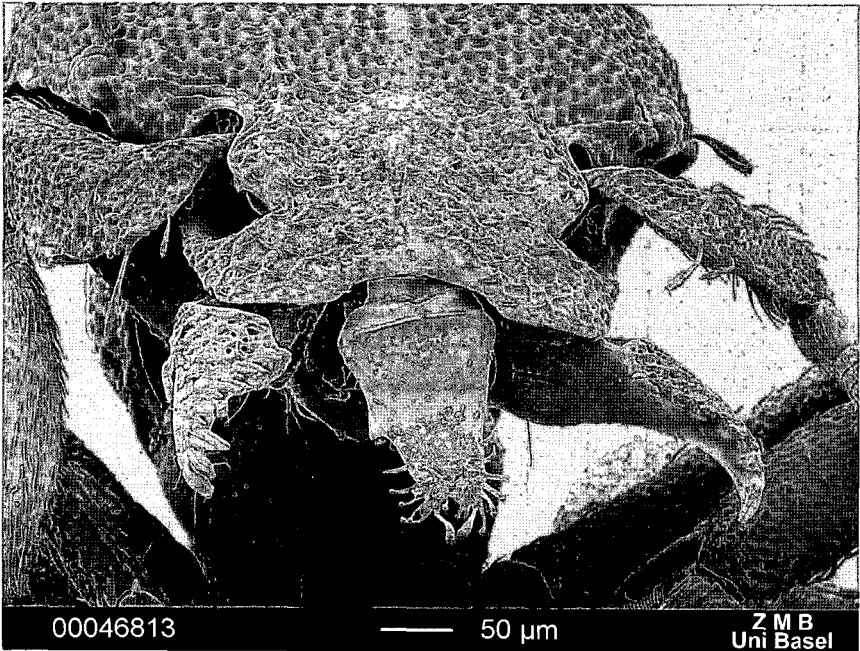

Fig. 3 - Labrum of *Octostruma stenognatha* Brown & Kempf with superficial (not deeply incised) transversal ridge perfectly comparable to the one of some *Strumigenys* and *Pyramica* of Fig. 4.

7. Worker. Labrum without mid-dorsal impression (0), or with a dorsal impression or pair of impressions (1). This character
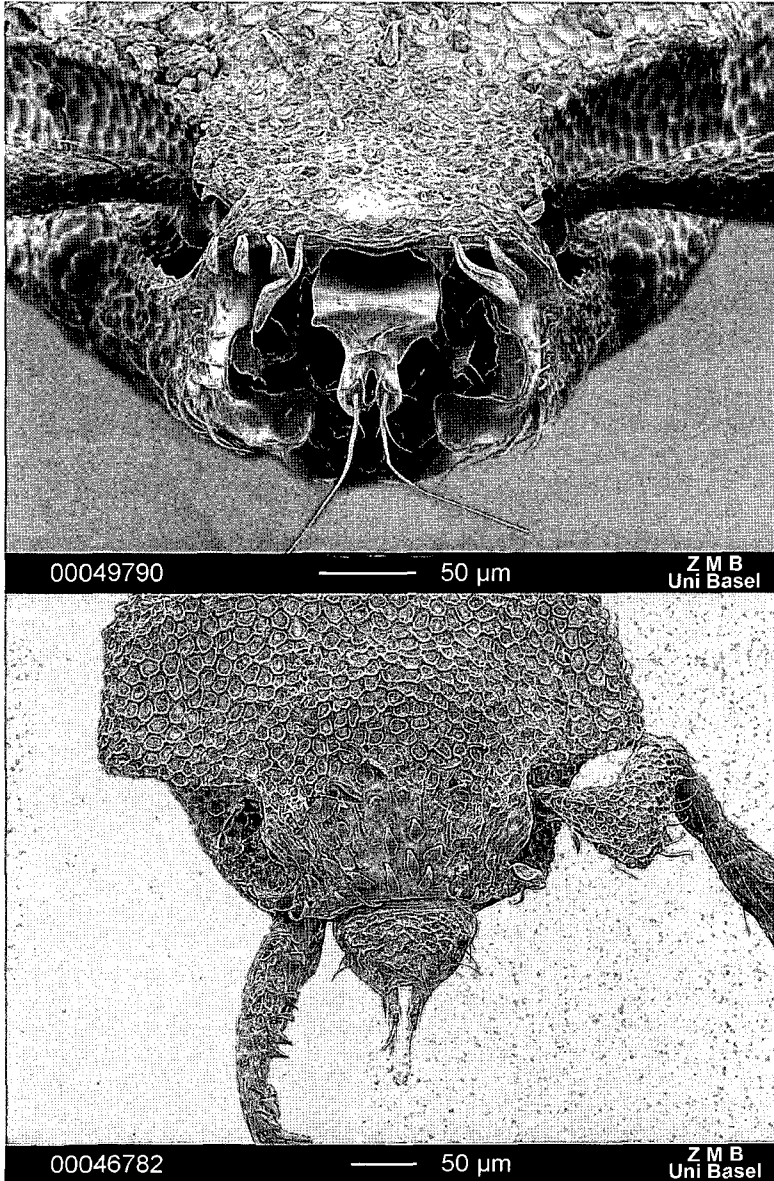
Fig. 4 - Labrum with deeply incised transversal groove, a basicerotine synapomor-
         phy, according to BOLTON (1998) present also among non-basicerotine spe-
         cies, like *Strumigenys elongata* Roger (top) and *Pyramica nannosobek* Bolton
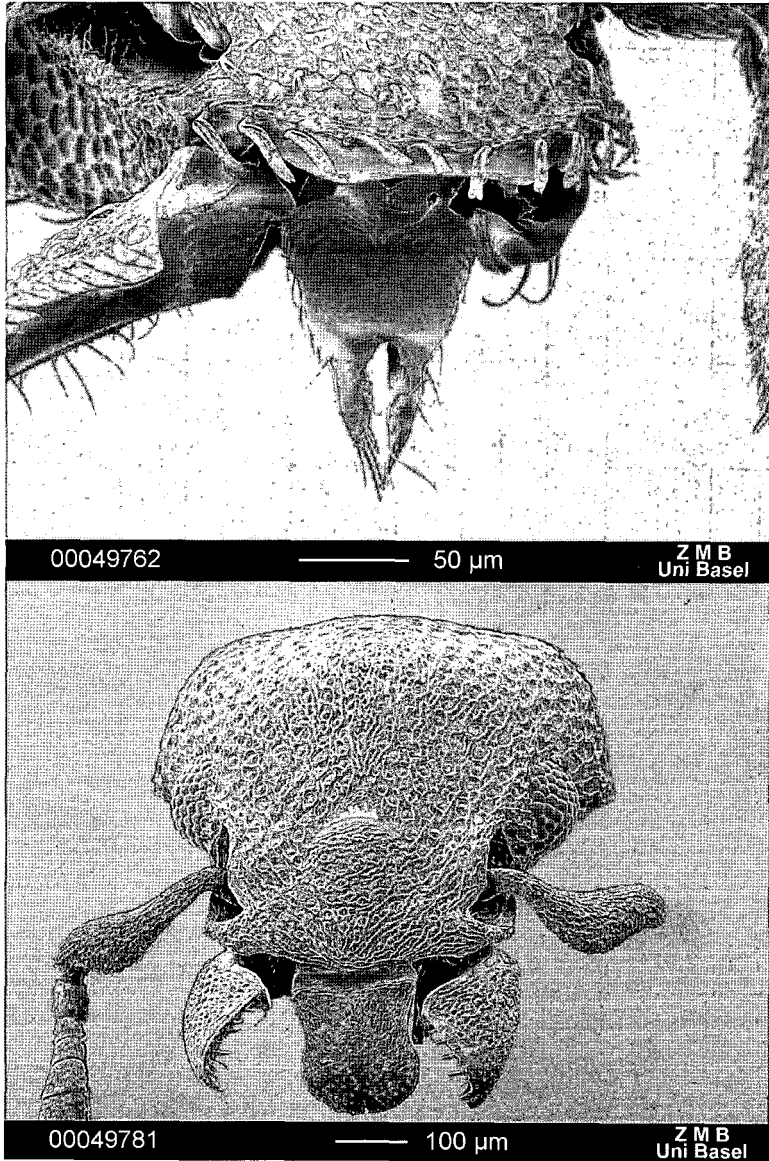   (bottom).

Fig. 5 - Labrum without dorsal impression in some dacetine species. *Pyramica alberti* (Forel) (top) and *Colobostruma sisypha* Shattuck (bottom). Presence of the impression is considered as a dacetine synapomorphy by BOLTON (1998). Notice also the absence of "trigger hairs" (a presumed synapomorphy of all dacetine genera) from the labium of *C. sisypha*.

is given by BOLTON (1998: 72) as uniquely derived for the Dacetini and secondarily lost in *Acanthognathus*. There are no traces of the impression also in the dacetine *Colobostruma* species examined for the present study, and in some *Pyramica* species (Fig. 5, top). We are unable to assess the state of this character in the holotype unique of *Pilotrochus*.

8. Worker. Trigger hairs absent (0), or present (1). The term "trigger hairs", introduced by BROWN & WILSON (1959) appears to be another "ant term" unknown in entomology textbooks. The hairs described by BROWN & WILSON (l. c.) are obviously hair-shaped mechanoreceptors and we doubt that the peg-like structures of probable chemoreceptor function visible e. g in most Basicerotini and also drawn e. g. by KEMPF (1960) for *Phalacromyrmex* could be considered as homologous of the former. Presence of "trigger hairs" on the mouthparts should be a synapomorphy of the "dacetonine tribe-group" according to BOLTON (1998: 69). Since the myrmeco-logical term "trigger hairs" implies simply response to a stimulus exerted on the ant mandibles without specifying its nature, we try to follow BOLTON (1998) and code uniformly presence of probable chemoreceptor and mechanoreceptor structures on the mouthparts. This same character is used also by DIETZ (2004, character # 6) where it is also coded as universally present among all and only the dacetine genera (s. l.). In our matrix *Pyramica* was coded polymor-phic for this character because of the absence or strong reduction of these hairs in some species (Fig. 6). This anomaly is partially admit-ted also by BOLTON (2000: 178). Some *Colobostruma* species also exhibit no "trigger hairs" (Fig. 5, bottom). Among our outgroups, the clypeal hairs of some *Myrmecia* species (OGATA, 1991) are mor-phologically indistinguishable from the "trigger hairs" of some dacetines. We coded nonetheless *Myrmecia* as "0" for this charac-ter in the (vague) hypothesis that differences in behaviour between *Myrmecia* and dacetines may account also for differences in homol-ogy. Moreover, presence of trigger hairs is obviously homologous in function among all ants provided with such hairs but we doubt of its morphological homology when the hairs are located on different sclerites as it is the case for several Dacetini. We thought it neces-sary formulating this precision but, to reduce confrontation with Mr Bolton on purely academic ground, we coded nonetheless the simple presence or absence of "trigger hairs" as a unique dacetine tribal

group character as Bolton and Dietz did. At least patent absence of "trigger hairs" of any kind, of course, was recorded as absence.
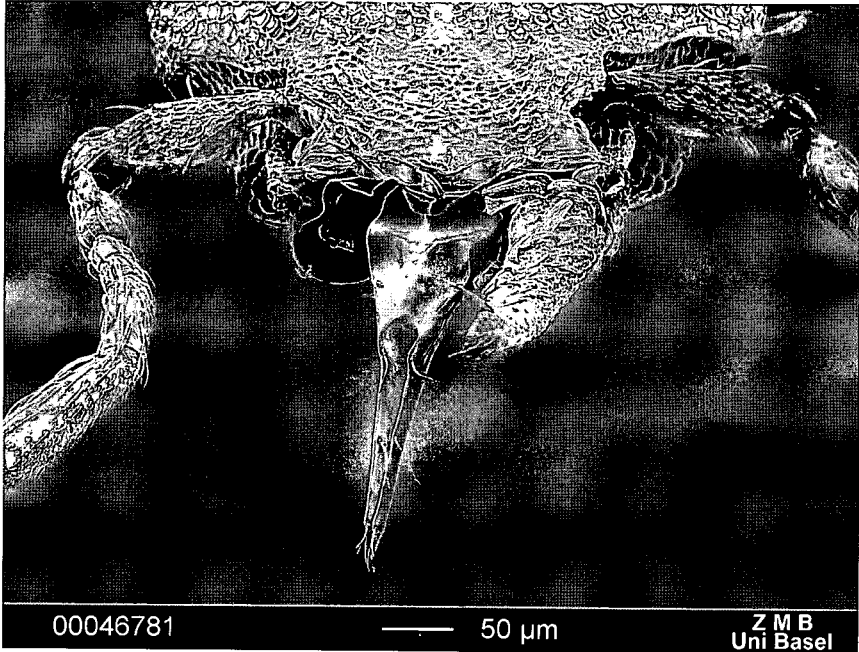

Fig. 6 - *Pyramica myllorhapha* (Brown) without morphologically differentiated "trigger hairs" on the mouthparts. Presence of "trigger hairs" is considered as a synapomorphy of his "dacetonine tribe group" by BOLTON (1998 & 1999).

9.   Worker. Mandibles at rest crossing (0) or crossing in their distal part of the masticatory border and opposing in the basal one (1), or opposing on their whole border (2). State 2 is the synapomorphy of the Dacetini (s. l.) according to BARONI URBANI & DE ANDRADE (1994) (character # 6) and of the "dacetonine tribe-group" of BOLTON (1998: 67) and DIETZ (2004, character # 1). Acceptance of the meaning of this character might propose re-inclusion of the Sicilian Miocene *Hypopomyrmex bombiccii* EMERY, 1891, among the Dacetini (see e. g. Emery's Table 1, Fig. 11). This latter hypothesis was not tested in the following due to the poor preservation conditions of the sole known *Hypopomyrmex* specimen. BARONI URBANI & DE ANDRADE (1994), misinterpreting a figure by KEMPF (1960), con-

sidered as entirely opposing also the mandibles of *Phalacromyrmex*. This is erroneous as shown by a more careful scrutiny of Kempf's figure and by the examination of the holotype and paratype of *Ph. fugax*. BOLTON (1998) and DIETZ (2004) repeated nonetheless the same error. The *Pilotrochus* holotype appears to exhibit a condition very similar to the one of *Phalacromyrmex*. For this reason, we thought it better to code both genera as state "1", intermediate between the crossing and opposing conditions. Moreover, in spite of the presumable hierarchic importance of this character, it is not clear which one should be the formicid plesiomorphic condition. The mandibles are able of both, crossing and opposing in the unspecialized ant genus *Prionomyrmex* and among wasps, the sister family of ants.

10. Worker. Mandibles engaging through most of their length (0), or only apically (1). This is char. # 7 of BARONI URBANI & DE ANDRADE (1994) and character # 7 of BOLTON (1999). Polymorphism in *Strumigenys* added here in consideration of *Strumigenys guttulata* Forel as described by BOLTON (2000: 976, explicit description, and Fig. 530, illustration) and *S. horvathi* Emery (present study). DIETZ (2004) does not consider this structure for his phylogenetic analysis. The reason for it – we believe – lies in the fact that this character is polymorphic among some genera like *Octostruma* (see e. g. DIETZ's l. c. Figs. 27 A and C). In our matrix, *Octostruma* and other genera where we observed polymorphism are consequently coded as polymorphic for this character. *Rhopalothrix* should be coded as polymorphic for this character after transfer to it of *Eurhopalothrix bruchi* (Santschi) as suggested by DIETZ (2004: 200). Our examination of the 5 specimens representing the type series of *bruchi* does not support Dietz's conclusion. The mandibular morphology represents well an average *Eurhopalothrix* and both mandibles at rest engage through most of their length. The distribution of this character is perfectly equivalent to Dietz's character # 9 (forma das mandíbulas: triangulares ou especializadas) since the shape of the mandibles is just another expression of their capacity to engage each other. Our coding differs nonetheless from the one of DIETZ (l. c.) for *Colobostruma* and *Mesostruma* whose mandibles engage through most of their length and where we see no traces of specialization.

11. Worker. Mandibles normally toothed (0), or with alternating small and large teeth (1). This, according to BOLTON (1998: 72) and DIETZ (2004, character # 10) is a synapomorphic trait of the genera of the tribe Phalacromyrmecini. Alternating small and large teeth, however, are present also in *Pyramica bunki* (Brown) (BOLTON, 2000, Fig. 113), *Pyramica kichijo* (Terayama, Lyn & Wu), *Octostruma betschi* Perrault (PERRAULT, 1988: Fig. 2), and *Octostruma balzani* (Emery) from Ecuador (Fig. 7) equally exhibit teeth alternating in size. Since the tribe Phalacromyrmecini comprises only three monotypic genera, this presumed tribal character is present in three phalacromyrmecines and at least in four, closely related, but non-phalacromyrmecine species. BARONI URBANI & DE ANDRADE (2006a) already called the attention on these species not fitting Bolton's classification but BOLTON (2006a) states that the cases above are not comparable to the phalacromyrmecine morphology because of minute differences and because the *Pyramica* species have a basal lamella (see also our discussion of the lamella under character # 13). One cannot consider the mandibular dentition and the lamella as two independently derived characters (as Bolton and ourselves did to construct our phylogenies) and use one of the two characters as an attribute of the other as did BOLTON (2006a). BOLTON (2006a) blames our use of the dentition without considering presence or absence of the lamella but our way is the sole correct way of considering both structures as independently derived characters and hence of using both characters in phylogenetic studies. As far as the morphological differences in dentition are concerned, we must admit that probably there are no two ant teeth looking exactly the same, but to see a phylogenetic meaning in details of the magnitude of those used by Bolton, to use Bolton's words, one needs to be cleverer than "other mere mortals".

12. Worker. 2-3 apical mandibular teeth overlapping (0), or interlocking (1). This is char. # 8 of BOLTON (1999). In addition to the distribution of this character as given by Bolton (l. c.), the apical teeth interlock also in a number of *Strumigenys* (among other possible examples, *S. percrypta* Bolton (BOLTON, 2000, Fig. 375) and S. *rogeri* Emery (BOLTON, 2000, Fig. 368)) and *Pyramica*, like *P. vartana* Bolton (BOLTON, 2000, Fig. 135) species (see also our Fig. 8 for additional examples encountered during the present study).
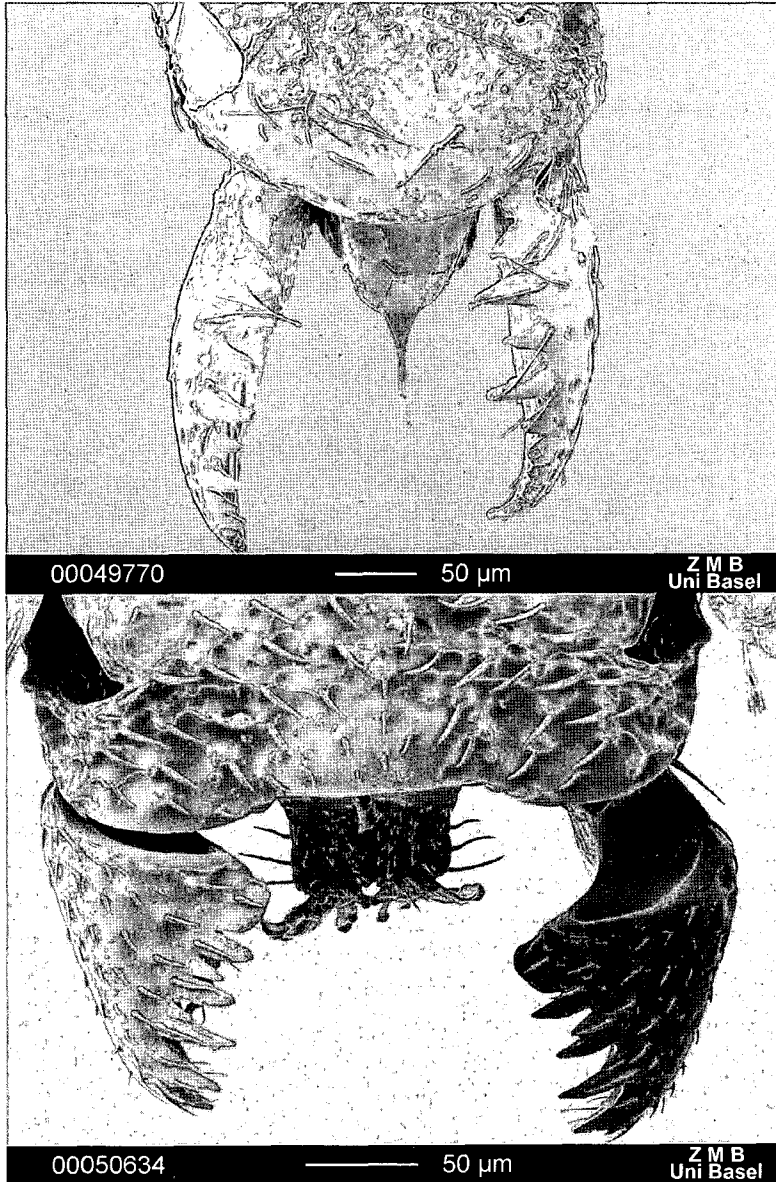
Fig. 7 - *Pyramica kichijo* Terayama, Lin & Wu (Dacetini) (top) and *Octostruma balzani* (Emery) from Yasuní, Ecuador (Basicerotini) (bottom). Mandibles with alternating large and small teeth. Mandibular teeth alternating in size is considered as a phalacromyrmecine synapomorphy by BOLTON (1998).
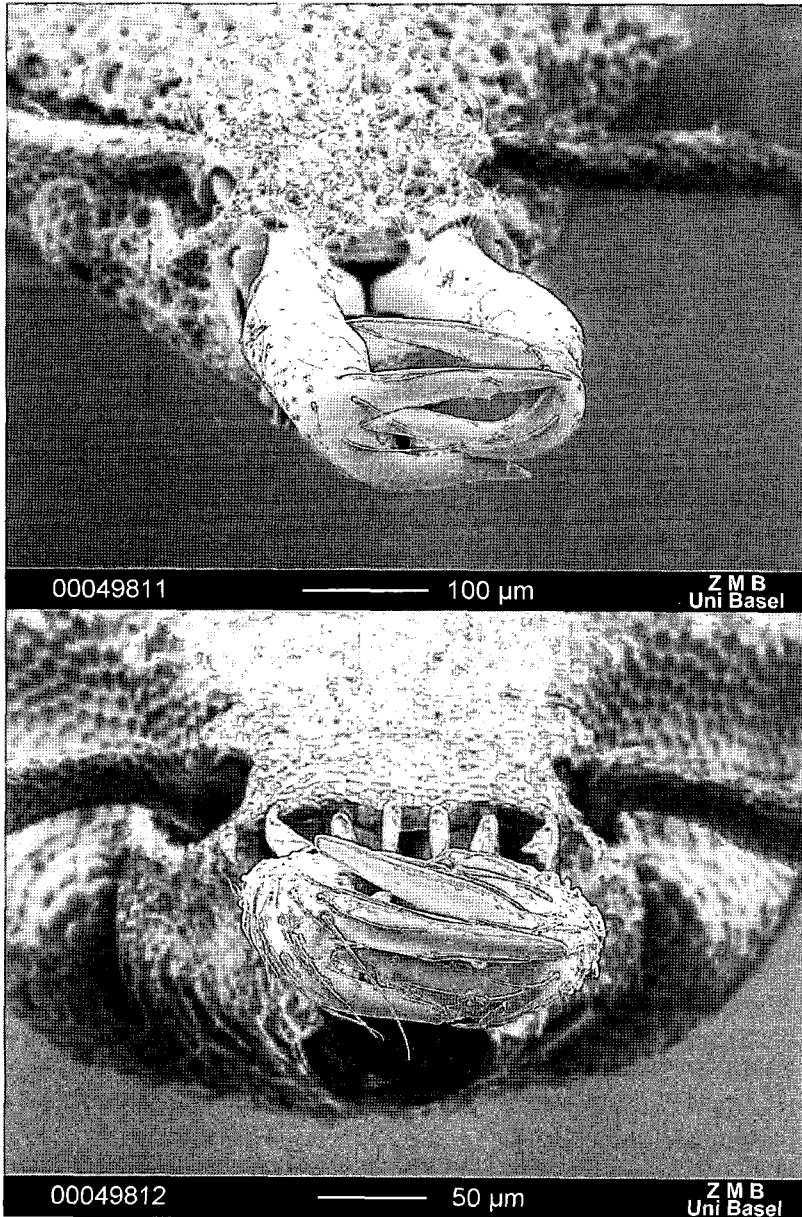
Fig. 8 - *Strumigenys doriae* Emery (top) and *S. rogeri* Emery (bottom). Mandibles with apical teeth interlocking (not interlocking according to the table of BOLTON, 1999).

13. Worker. Basimandibular process absent (0), or present but not bifurcated (1), or present, long and apically bifurcated (2). This character results from merging chars. # 9 of BOLTON (1999) (= char. # 13 of DIETZ, 2004, i.e. presence or absence of the basimandibular process) and char. # 10 of BOLTON (1999) (i.e. basimandibular process round and thick vs. a spur, dentiform, or lamellate). We decided to merge Bolton's two characters in one because A) the variation in shape that we observed is difficult to reduce to Bolton's two binary categories (Fig. 9), and, B) Bolton's coding of his character # 10 as autapomorphic for *Daceton* renders it cladistically uninformative. Our coding might still need to be further modified in the future since an apparent basimandibular process is present also among most Basicerotini, *Stegomyrmex*, *Tatuidris* and *Calyptomyrmex*. This reality is admitted only in part by BOLTON (1998: 72) who states "Basicerotine species with a modified basal tooth are exceptional and certainly best regarded as independent acquisitions". We follow hence BOLTON (l. c.) and code the basimandibular process as absent among the Basicerotini in our matrix. Additionally, at least in some dacetine species currently classified in *Pyramica*, like *P. argiola* (Emery) and *P. nannosobek* Bolton (Fig. 10) the process is so reduced to be barely distinguishable or invisible. Note that *P. argiola* is one of the species dissected by BOLTON (1998) to define his Dacetonin but no mention to the absence of basimandinbular tooth is made in this paper. Analogously BOLTON (2000:12) defines the Dacetini as unequivocally characterized by the presence of the lamella. Only in a different context, i.e. in the species-level discussion he admits (page 286) that in the *argiola*-group the lamella is "small, dentiform to low triangular and inconspicuous" (description which we regard as exaggerated if compared with the morphology visible in Fig. 10), in the *murphyi*-group is "reduced to a very narrow stripe not visible in full face view", and in the *mnemosyne*-group is "minute to vestigial, at most a mere ridge on the margin". BOLTON (2006b) regards his former (insufficiently) reductive statements as a clear argument in favour of the validity of the basal lamella as a tribal character. We would consider it as a proof of the contrary but followed nonetheless BOLTON (1999, 2003) in coding the process as uniformly present in *Pyramica* and considering these previously neglected cases as secondary losses of the process as suggested by the presence of its remnants, though we are not always sure to

be able to see such remnants. BOLTON (2006a) states that absence of the lamella in the closely related "Phalacromyrmecini" is "presumably plesiomorphic". We don't see the difference with the very similar condition of *Pyramica argiola, nannosobek*, etc. cited above, unless one already has in mind his own favourite phylogeny instead of trying to construct the most probable one. But even BOLTON (l. c.) apparently notices the contradiction and tries to avoid it by calling the previous exceptions to his general rule "a few documented cases of obvious secondary reduction or modification of function". We never saw these documents. In favour of our point of view we must notice also that BOLTON (1988:71), while reviving his Dacetini s. str. (under the name Dacetonini), emphasizes the importance of the basimandibular process without mention of "cases of obvious secondary reduction". On the internal margin of the mandibles of *Phalacromyrmex fugax* there is a small, denticulate swelling. We find it difficult to consider this structure as a typical example of absence of the lamella in *Phalacromyrmex* and the morphology e.g. of *Pyramica argiola* (Fig. 10) as a documented demonstration of secondarily 'lost presence' of it. The bifurcated condition of the lamella is a classic, undoubted autapomorphy for *Acanthognathus*.

14. Worker. Basimandibular seta absent (0), or present (1). This is a potential synapomorphy for Basicerotini and Phalacromyrmecini in BOLTON (1998: 73) and is coded as such by DIETZ (2004, character # 4). Actually a basimandibular seta is present also in *Stegomyrmex* and in some *Strumigenys* and *Pyramica* species (Figs. 11, 12 & 13), though in the latter two genera the position of the seta is slightly more distal than in *Stegomyrmex* and Basicerotini.

15. Worker. Number of antennal joints: 11-12 (0), or less than 11 (1). This is char. # 4 of BARONI URBANI & DE ANDRADE (1994), character # 11 of BOLTON (1999) and char. # 20 of DIETZ (2004), coded in binary form as already done by BOLTON (1999) and DIETZ (2004). There is increasing consensus on the poor phylogenetic value of the dacetine antennal count variation. Already BOLTON (1983) concluded "the reduction in antennomere count has little or no value at genus level...". Experimental attempts of cladistic analyses in which the actual antennal counts were given for each genus and considered as unordered, ordered, "Dollo", or irreversible, regularly yielded very implausible phylogenetic reconstructions. We agree with BOLTON (l.c.) that polarization of two states at the extremes of
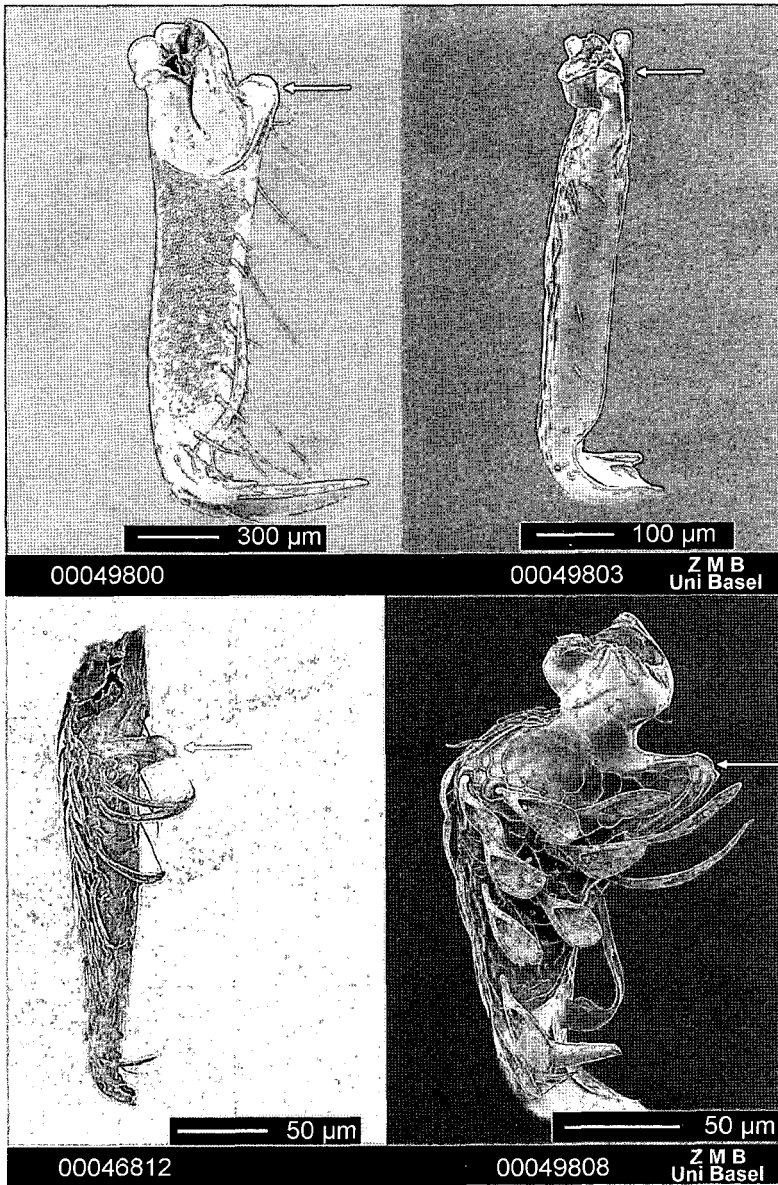
Fig. 9 - Variability of the basimandibular process among some dacetine ants. *Daceton armigeron* (Perty) (top left), *Strumigenys micretes* Brown (top right), *Pyramica zeteki* (Brown) (bottom left), *Strumigenys lyroessa* (Roger) (bottom right).
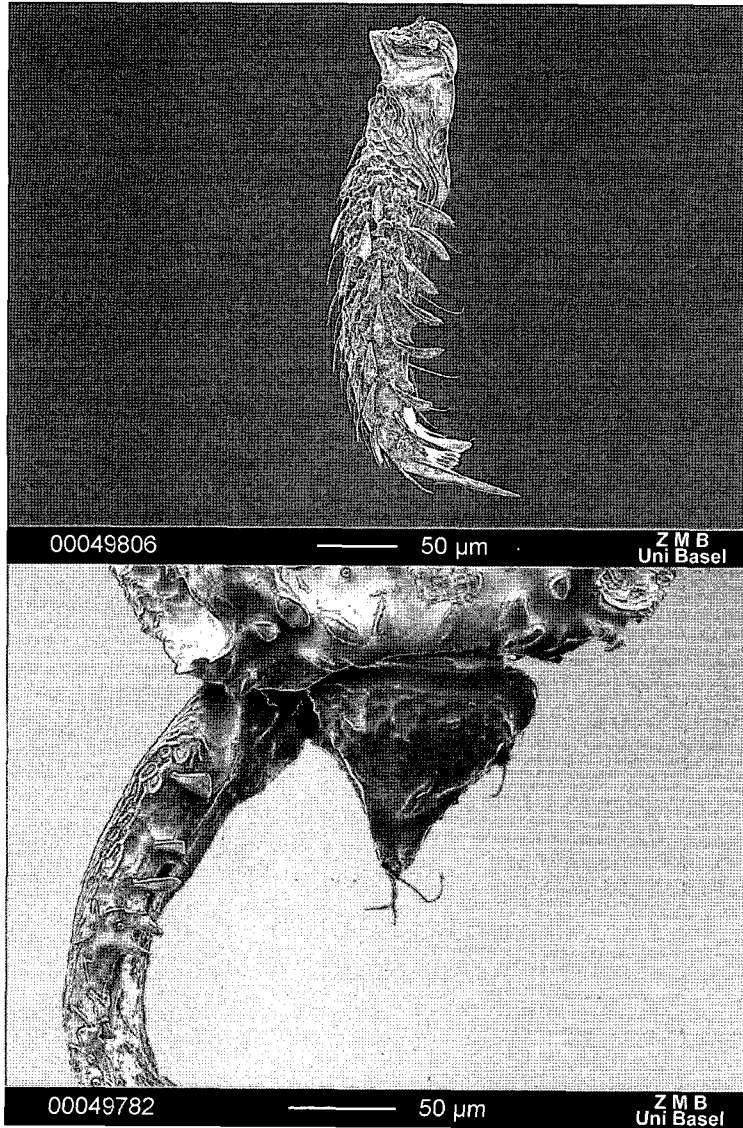
Fig. 10 - *Pyramica argiola* (Emery) (top) and *P. nannosobek* Bolton (bottom) with basimandibular process barely distinguishable or absent. *P. argiola* has no visible process but it shows two internal longitudinal ridges, which could be both interpreted as a remnant of the basimandibular process. Presence of the process or of its or remnants should be synapomorphic for the tribe Dacetini according to BOLTON (1999, 2003).
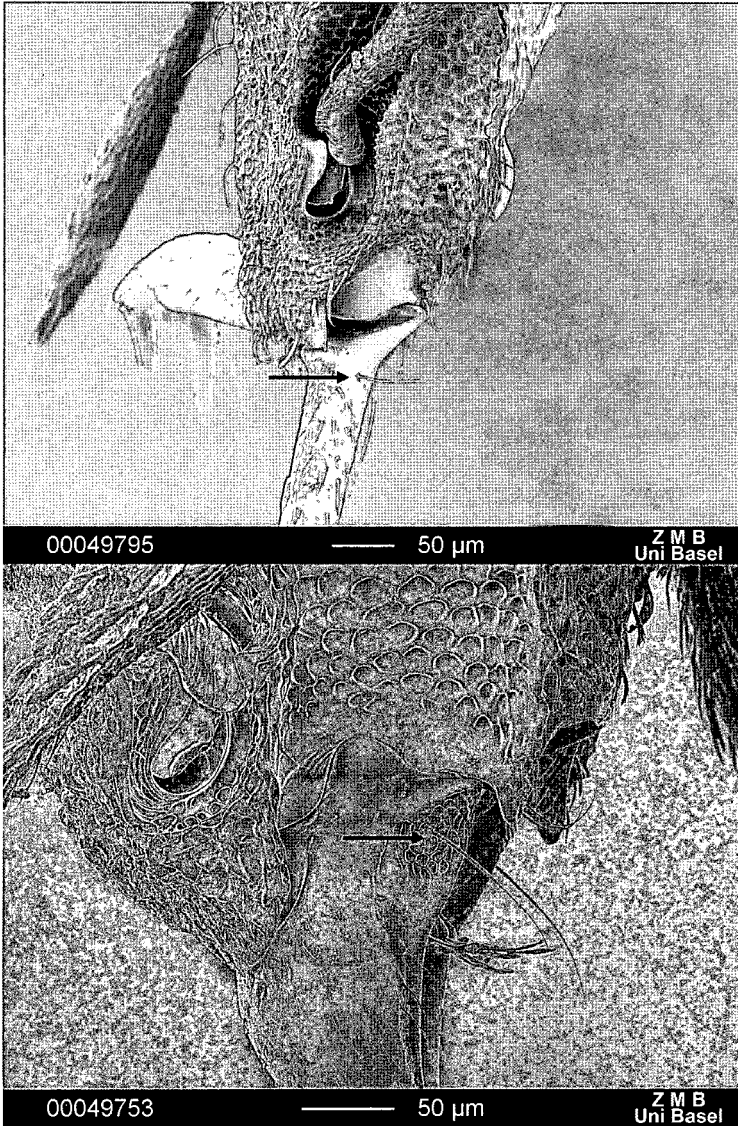
Fig. 11 - *Strumigenys paranetes* Brown (top) (Dacetini) and *Octostruma* nr. *batesi* (Emery) (Basicerotini) (bottom) showing the basimandibular seta (pointed by the arrow). Presence of the seta should be synapomorphic for the tribe Basicerotini according to BOLTON (1998).
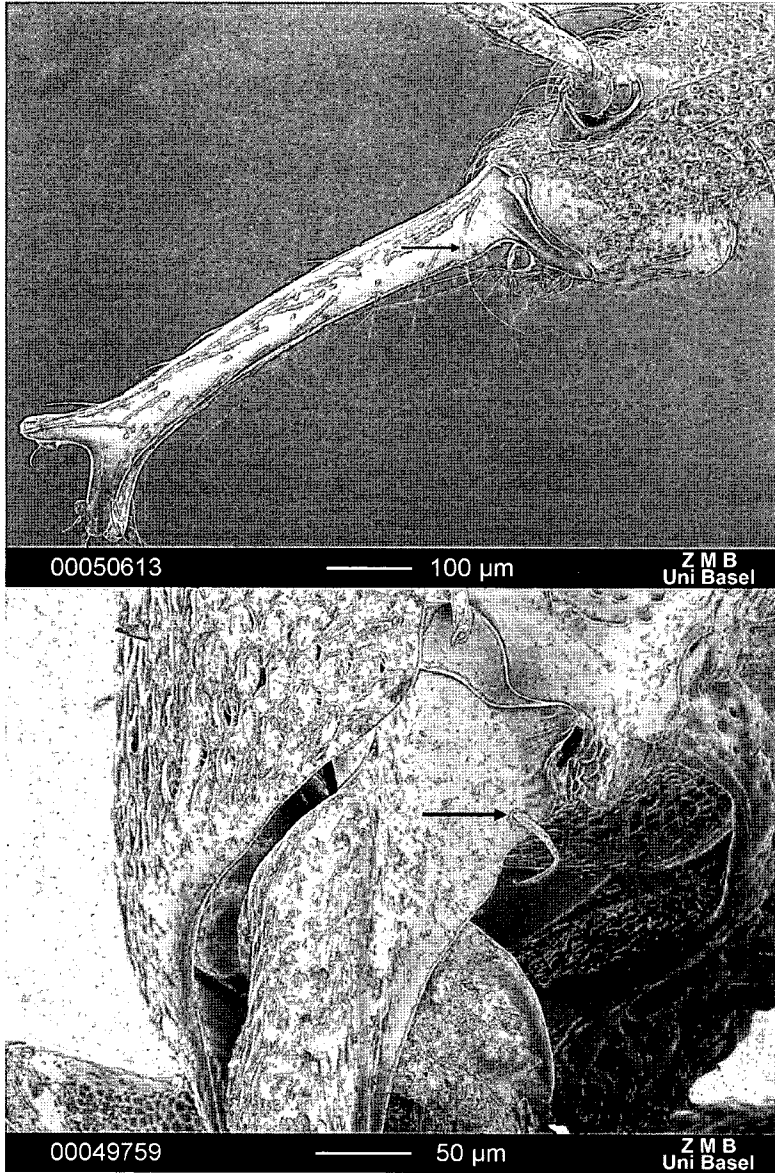
Fig. 12 - *Strumigenys gloriosa* Bolton. (Dacetini) (top) and *Eurhopalothrix platisquama* Taylor (Basicerotini) (bottom) showing the basimandibular seta (pointed by the arrow). Presence of the seta should be synapomorphic for the tribe Basicerotini according to BOLTON (1998).

Fig. 13 - *Pyramica denticulata* (Mayr) (Dacetini) (top) and *Stegomyrmex vizot-toi* Diniz (Stegomyrmecini) (bottom) showing the basimandibular seta (pointed by the arrow). Presence of the seta should be synapomorphic for the tribe Basicerotini according to BOLTON (1998).
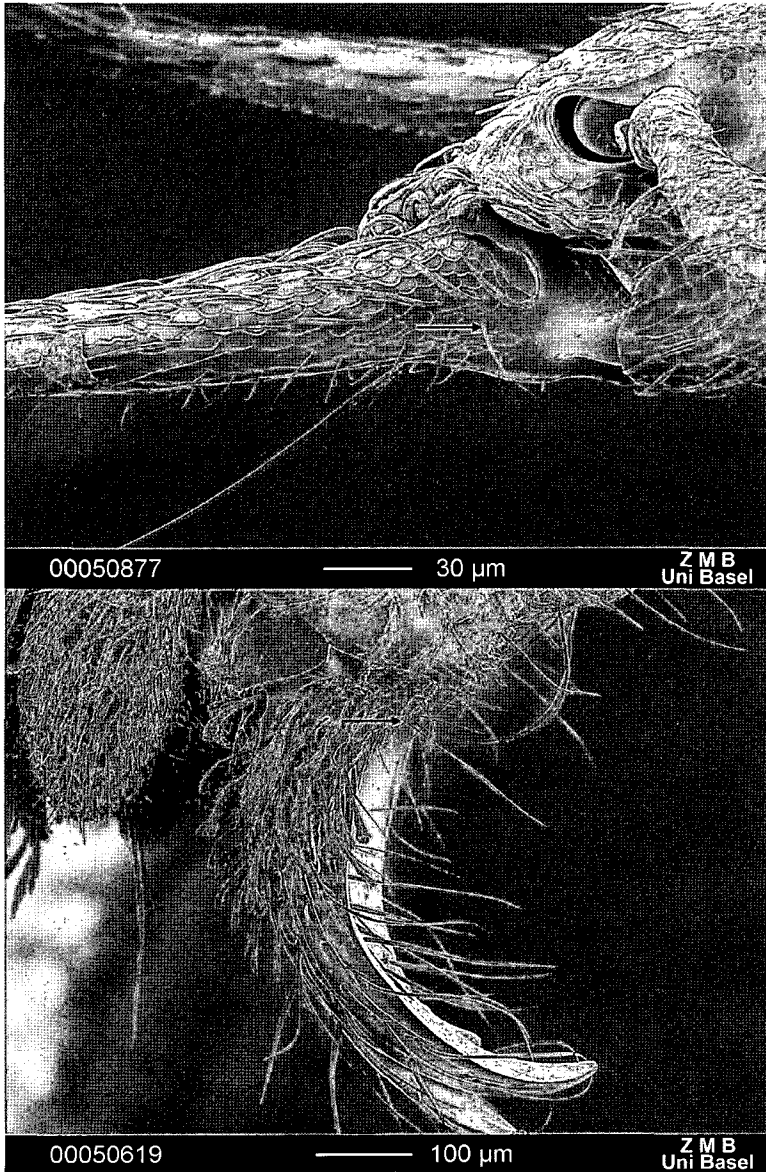
the sole known gap (10 antennomeres) among the ants considered in the present study appears the most reasonable way of considering this character.

16.   Worker. Two-segmented antennal club absent or indistinct (0), or well developed (1). This is char. # 12 of BOLTON (1999) and a simplification of BARONI URBANI & DE ANDRADE's (1994) character # 5.

17.   Worker. Scape straight at base (0), or gently downcurved at base (1). This is char. # 14 of BOLTON (1999).

18.   Worker. Base of scape straight or at least complanar with basal condyle (0), or scape bent at right angle near the base (1). The curved or angular scape is a synapomorphy of the Basicerotini according to BOLTON (1998: 71). Separating this character from the previous one might need some dialectic exercise. We kept the two separate because of the presumed important phylogenetic meaning of the latter if the independent evolution of the two traits will be confirmed. Examples of non-basicerotine species exhibiting the basicerotine condition are *Pyramica decipula* (Bolton), *Pyramica nannosobek* Bolton (Figs. 14 & 15) and *Colobostruma froggatti* (Forel) (partially visible in Fig. 38). If we understand properly DIETZ (2004) this character should be equivalent or very similar to his character # 22 but we are unable to verify his recording for different taxa. In spite of differences in definition and coding, we did not consider DIETZ (l. c.) as referring to another, different character since we already fear that consideration of our characters 17, 18 and 19 could overweight the shape of the scape within our data.

19. Worker. Scape not clavate (0), or clavate (1). Presence of a clavate scape is given by BOLTON (1998: 72) and DIETZ (2004, chars. # 21 and # 23) as synapomorphic for the tribe Phalacromyrmecini. We are unable to see differences between the descriptions of DIETZ's char. # 21 "Clava da antena: ausente (0); presente (1). A clava é um alargamento do escapo...estrutura distinta e característica...da tribo Phalacromyrmecini" and char. # 23 "Escapo clavado: não clavado (0); clavado (1)". Differences, however, are impressive within their respective coding by DIETZ (l. c.). According to our observations, a clavate scape, in addition than in the Phalacromyrmecini, is present also in *Stegomyrmex*, *Tatuidris*, in *Pyramica warditera* Bolton (BOLTON, 2000, Fig. 165) and *P. reticeps* (Kempf) (BOLTON, 2000,

Fig. 14 - Inadequacy of the scape shape as a tribal character for the Basicerotini.
Example 1. Morphological similarity between *Pyramica decipula* (Mayr)
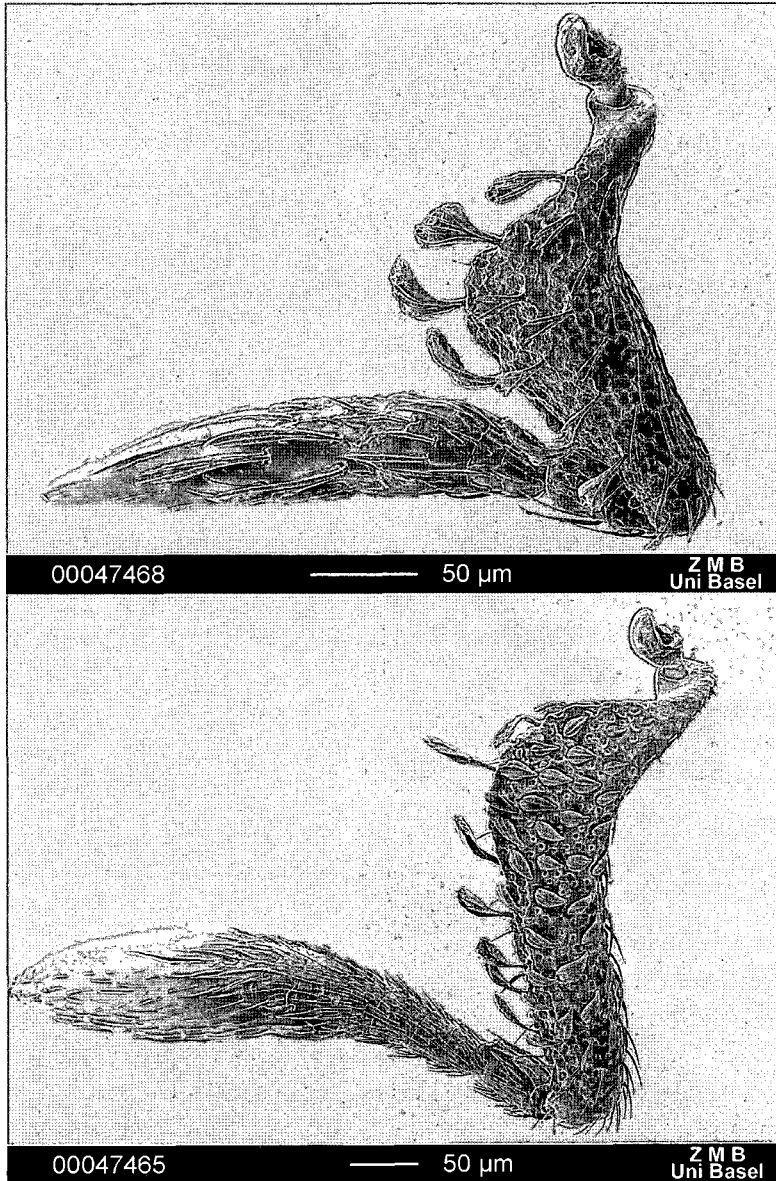(Dacetini) (top) and *Rhopalothrix ciliata* Mayr (Basicerotini) (bottom).
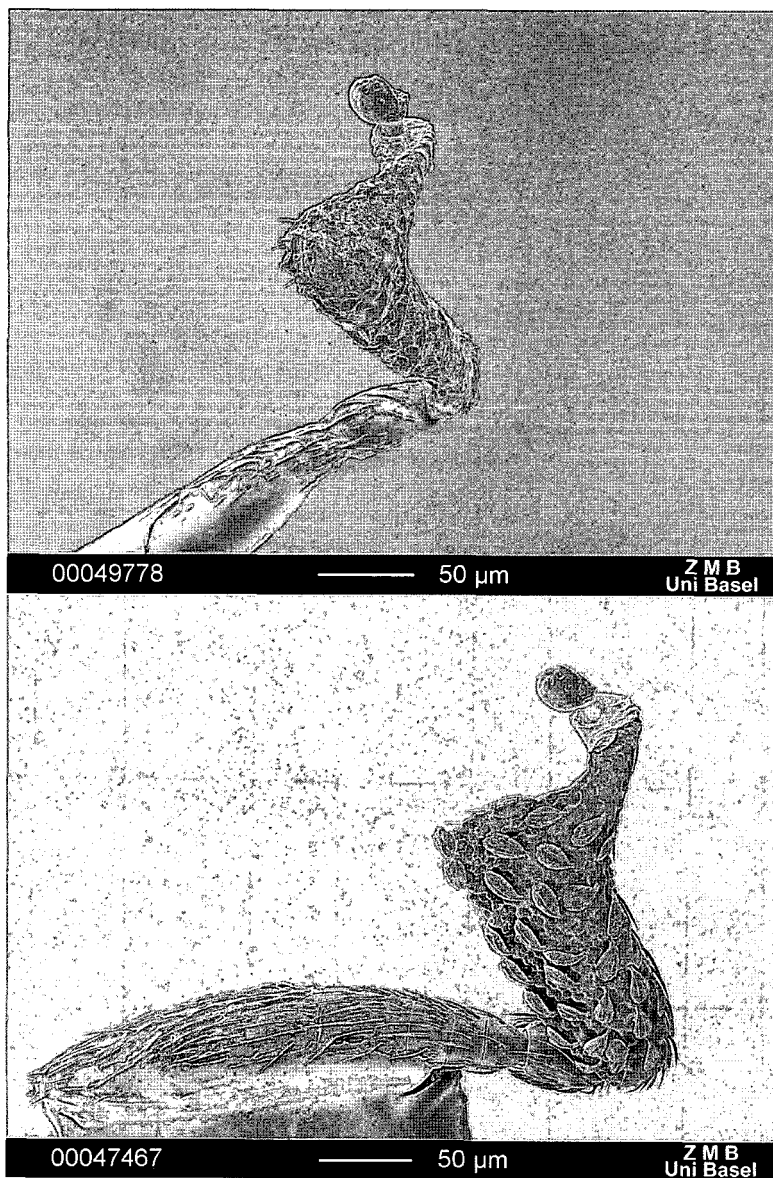
Fig. 15 - Inadequacy of the scape shape as a tribal character for the Basicero-
          tini. Example 2. Morphological similarity between *Pyramica nannosobek*
          Bolton (Dacetini) (top) and *Eurhopalothrix bruchi* (Santschi) (Basicerotini)
          (bottom).

Fig. 162). We are unable to explain DIETZ's explicit reference to the Phalacromyrmecini for his character # 21 (p. 32) and his recording of this character in his table 2. In this table the clavate scape is given as unknown in *Phalacromyrmex* and present in a number of non-phalacromyrmecine genera like the Attini, *Platythyrea*, *Stegomyrmex*, *Blepharidatta*, *Microdaceton*, *Daceton*, *Orectognathus*, *Colobostruma*, *Mesostruma*, *Epopostruma*, *Pyramica*, *Strumigenys*, *Basiceros*, *Eurhopalothrix*, *Octostruma*, *Protalaridris*, *Rhopalothrix*, *Talaridris*. See also our worries about redundancy of the scape characters expressed under our description of character 18.

20.   Worker. Torulus simple or with a small lobe at most (0), or with hypertrophied dorsal lobe and strongly curved downwards (1). This is given by BOLTON (1998: 70) and by DIETZ (2004, char. # 15) as a synapomorphy of the Basicerotini. A hypertrophied torulus, however, is present also in *Tatuidris*, *Mesostruma eccentrica* Taylor, *M. bella* Shattuck, *Colobostruma alinodis* (Forel), and in some *Strumigenys* and *Pyramica* species (Figs. 16 & 17).

21.   Worker. Second funicular joint normal (0), or hypertrophic (1). This is a clear autapomorphy for *Orectognathus*.

22.   Worker. Antennal fossa and scrobe (when present) confluent (0), or separated from each other by at least a cuticular rim or crest (1). This is another basicerotine synapomorphy according to BOLTON (1998: 71) and DIETZ (2004, char. # 16). The crest is indistinct in some *Eurhopalothrix* species like *E. bruchi* (Santschi) (Fig. 16, top) and *E. heliscata* Wilson & Brown (Fig. 18, top). On the contrary, a distinct crest is visible in some *Pyramica* and *Strumigenys* species (Fig. 18, bottom). A number of Dacetini species have been already illustrated by Bolton with photographs showing the presumed basicerotine structure in these non-basicerotine genera (see e. g. BOLTON, 2000: Figs. 352, 483, 516 for *Strumigenys*; BOLTON, 1999: Fig. 60 and BOLTON, 2000: Figs. 236, 241 for *Pyramica*; and BOLTON 2000: Fig. 46 for *Colobostruma sisypha* Shattuck).

23.   Worker. Antennal scrobe absent (0), present and above the eyes (1), present and below the eyes (2), or with the eyes at its posterior border (3). This is character # 2 of BARONI URBANI & DE ANDRADE (1994) where it was coded as two-states only, character # 16 of BOLTON (1999) and character # 18 of DIETZ (2004) with addition of state 3 (present study). Character state 3 was added here in
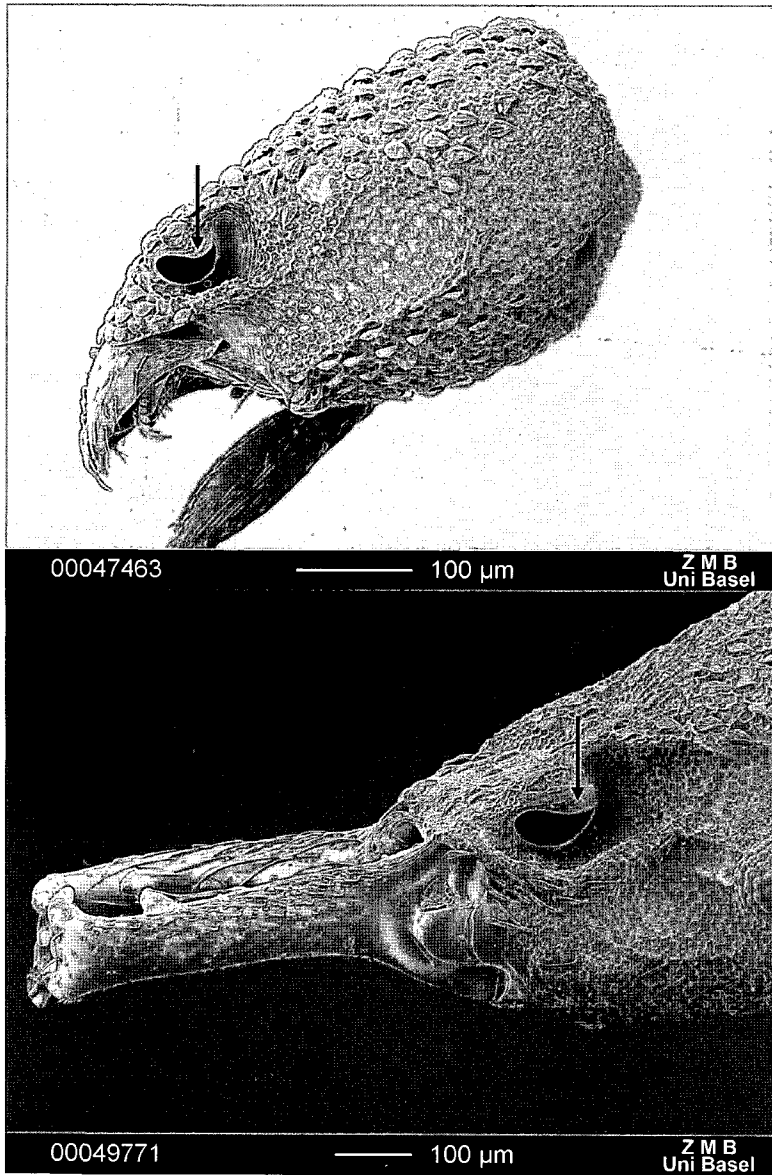
Fig. 16 - Inadequacy of the torulus shape as a tribal character for the Basicero-
tini. Example 1. Morphological similarity between *Eurhopalothrix bruchi*
(Santschi) (Basicerotini) (top) and *Strumigenys godmani* Forel (Dacetini)
(bottom).
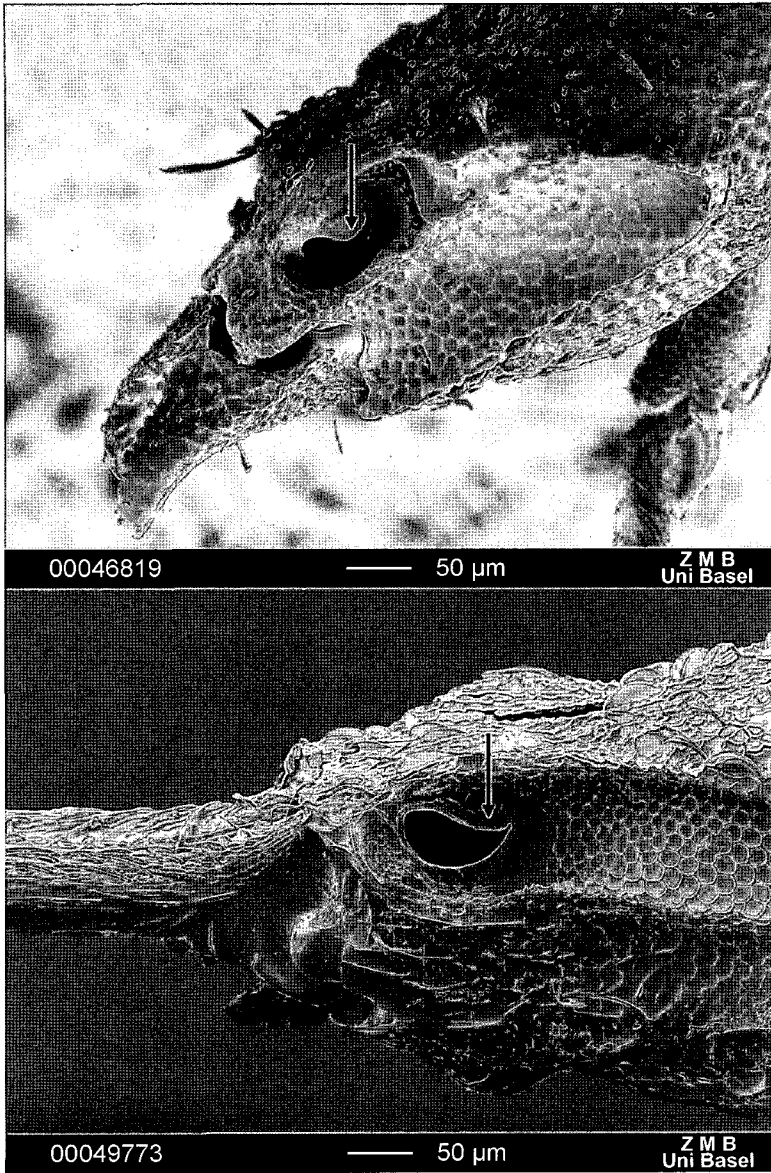
Fig. 17 - Inadequacy of the torulus shape as a tribal character for the Basicero-
tini. Example 2. Morphological similarity between *Octostruma betschi*
Perrault (Basicerotini) (top) and *Strumigenys micretes* Brown (Dacetini)
(bottom).
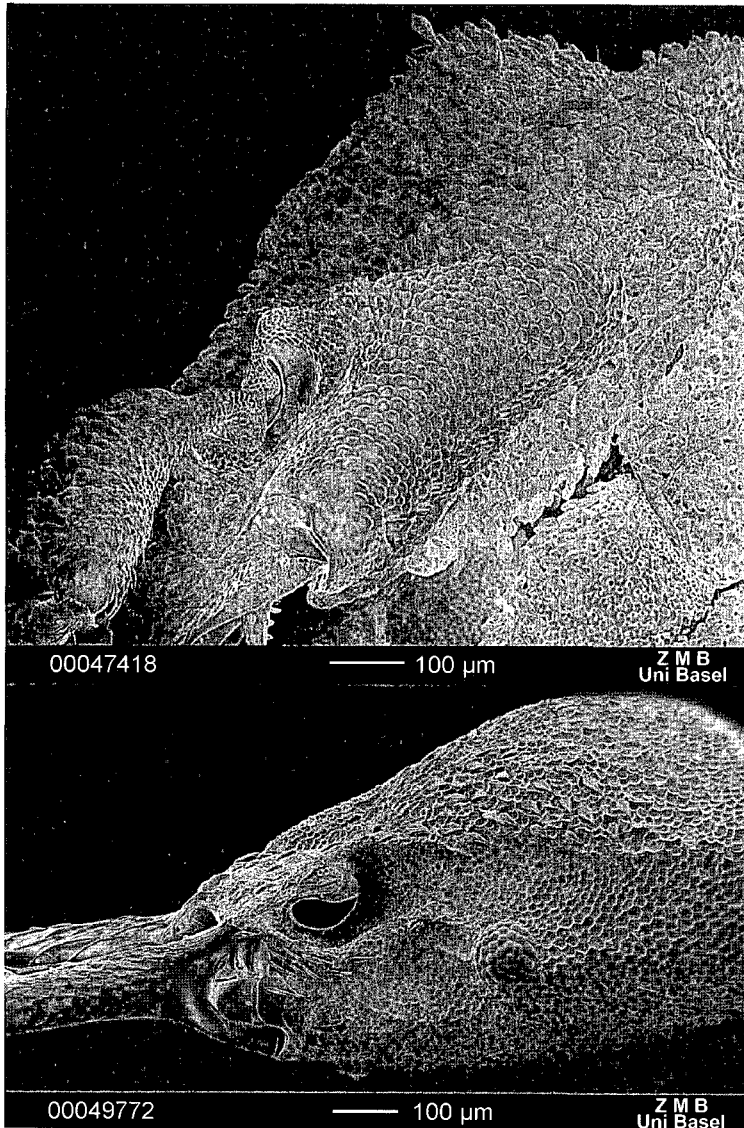
Fig. 18 - Variability of the antennal fossa as a tribal character for the Basicero-
tini. The basicerotine *Eurhopalothrix heliscata* Wilson & Brown with fossa
weakly separated from the scrobe (top) (the fossa should be separated
by a crest in all basicerotines) and *Strumigenys godmani* Forel (Dacetini)
with crest separating the fossa from the scrobe (bottom) (fossa and scrobe
should be confluent, without separating crest among Dacetini).

order to properly code *Tatuidris* not considered by BOLTON (l. c.) and DIETZ (2004). State "2" appears only in the character description and not in the relative table 2 of DIETZ (2004). Polymorphism in *Colobostruma* added to the table because of the (possibly secondary) reduction or absence of the scrobe in some *Colobostruma* species with flat head, as noted by Shattuck in BOLTON (2000:31).

24.   Worker. Eyes absent (0), dorsolateral (1), lateral (2), or ventral (3). This is character # 3 of BARONI URBANI & DE ANDRADE (1994), unchanged, and character # 17 of BOLTON (1999) with the addition of state 0 in order to account for some blind *Rhopalothrix* species (BROWN & KEMPF, 1960: 231) and for the first record of a blind "*Pyramica*" (see later the discussion under *Strumigenys inopinata* (de Andrade)). Considering *Rhopalothrix inopinata* de Andrade in *Pyramica* – as suggested by DIETZ (2004) and provisionally accepted for the present study – or leaving it in *Rhopalothrix* as it was originally described, does not affect either the number or the topology of the possible shortest trees. Only the tree length is one-step shorter when *inopinata* is left in *Rhopalothrix*.

25.   Worker. Occipital foramen not in a depression (0), or in a deep depression surrounded by a continuous cuticular margination (1). This should be another basicerotine synapomorphy according to BOLTON (1998: 71) and DIETZ (2004, char. # 19). There is no completely marginate depression at least in *Octostruma balzani* Emery and *Rhopalothrix ciliata* Mayr. On the contrary, some *Strumigenys* and *Pyramica* species have the occipital foramen in a much more marginate depression than the one of the previous basicerotine examples (see Figs. 19 & 20). In *Pyramica minkara* (Bolton), not photographed for the present study, the phenomenon is even more evident.

26.   Worker. Head of normal shape (0), or pyriform (1). This is the dacetine "typical" character of the classic literature (e. g. EMERY, 1924), equivalent to char. # 1 of BARONI URBANI & DE ANDRADE (1994). It is also equivalent to the "anterior head capsule is narrowed from side to side" of BOLTON (1998: 68) where it is given as synapomorphy of the "dacetonine tribe-group". BOLTON (1998), carefully reflected in DIETZ (2004), defines much better this character and suggests a "Mandibular-Torular Index (MTI)" to quantitatively express it. As we already explained in the Methods chapter (q. v.), as it was originally formulated, this is a Ratio and not an
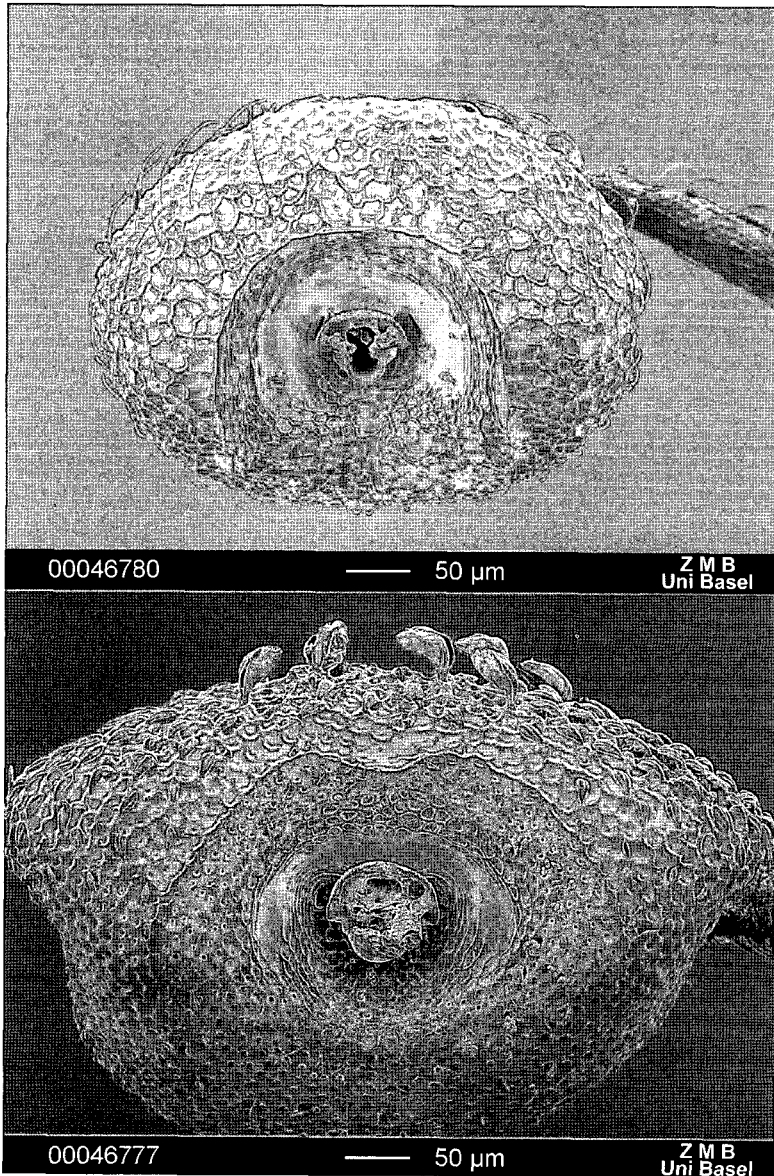
Fig. 19 - Inadequacy of the occipital foramen as a tribal character for the Basicero-
tini. *Pyramica tenuissima* (Brown) (top) and *Rhopalothrix ciliata* Mayr
(bottom). Note the margination of the foramen absent or weak in *Rho-
palothrix* and the deep margination in *Pyramica*.
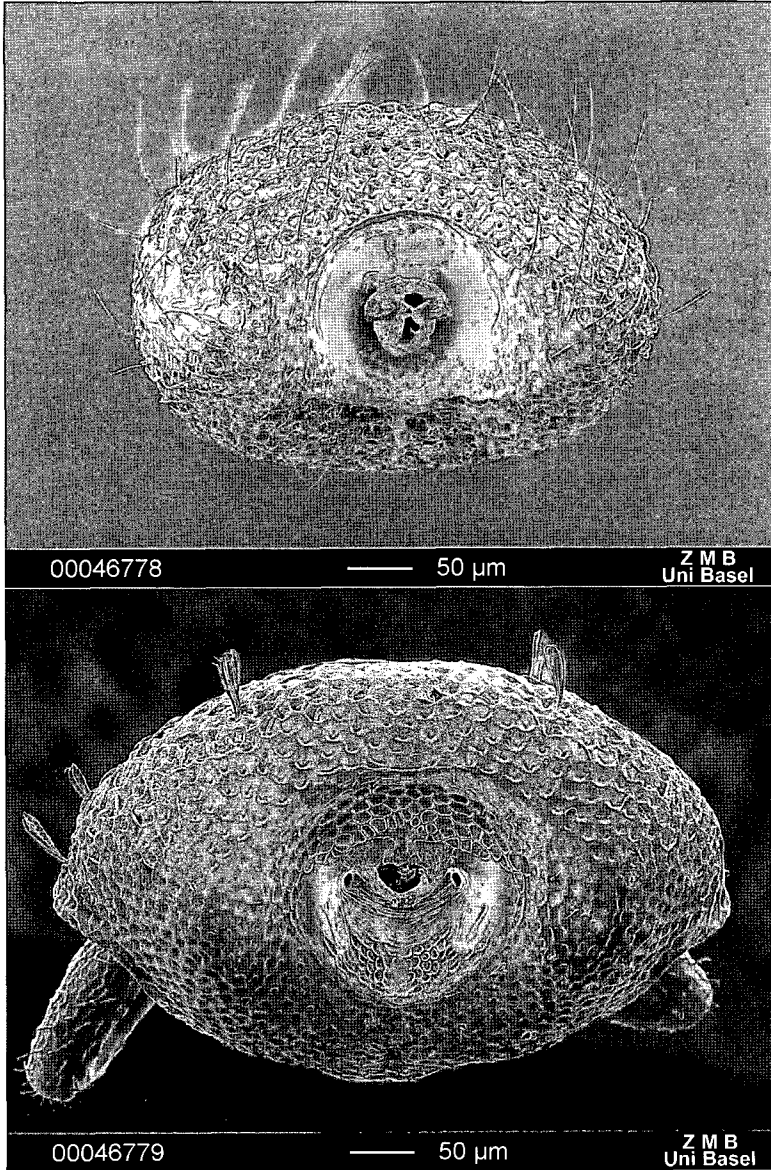
Fig. 20 - Inadequacy of the occipital foramen as a tribal character for the Basicero-
tini. *Strumigenys ekasura* Bolton (top) and *Octostruma balzani* (Emery)
(bottom). Note the margination of the foramen absent or weak in *Octo-
struma* and the deep margination in *Strumigenys*.

Index. Bolton's quotient, hence, should be called "Mandibular-Tor-
ular Ratio". In our case, the Dacetini should have a ratio 0.5-1.3,
and most remaining Myrmicinae a ratio between 1.5-3.0. Maintain-
ing the MTI as an index means its reformulation as MTI = (dis-
tance between the points where the outer margin of the fully closed
mandibles intersect the anterior clypeal margin) X 100 / (maximum
distance between the lower margins of the toruli). In our matrix,
hence, MTI > 150 (0), and MTI < 130 (1). In *Tatuidris* MTI ≈ 90.

27.   Worker. Occipital foramen posterior (0), or dorsal (1). The
dorsal position is a classical, excellent autapomorphy for *Daceton*.

28.   Worker. Pronotal cervix without (0) thick, transverse rim,
or with a thick, transverse rim (1). This should be a synapomorphic
trait for *Microdaceton* according to BOLTON (1999).

29.   Worker. Promesonotal suture mobile (0), or fused (1). The
dorsal position is character # 10 of BARONI URBANI et al. (1992).

30.   Worker. Cuticular processes of promesonotum absent (0),
or present (1). This is character # 24 of BOLTON (1999) but coded
differently from BOLTON (l. c.) in a number of genera for the fol-
lowing reasons: *Epopostruma*, polymorphic (instead of present only)
because of absence of process in *E. curiosa* Shattuck (BOLTON, 2000,
Fig. 88); *Mesostruma*, polymorphic (instead of present only) because
of absence of the process in *M. browni* Taylor (BOLTON, 2000, Fig.
57). *Strumigenys*, polymorphic (instead of absent only) because of
presence of the process in *S. loriae* Emery (BOLTON, 2000, Fig.
485).

31.   Worker. Mid and hind tibial spurs present (0), or vestigial
to absent (1). Absence of tibial spurs is regarded as potentially syn-
apomorphic for the "dacetonine-group" by BOLTON (1998: 70). As
Bolton correctly writes, the commonness of the apomorphic condi-
tion among Myrmicinae renders it difficult attributing phylogenetic
value to this character. Tibial spurs are missing in *Stegomyrmex* and
in *Calyptomyrmex*, but present in *Tatuidris*.

32.   Worker. Mesosternal hair beds invisible in profile (0), vis-
ible in profile (1), or hypertrophic in profile (2). BROWN (1978) first
described this structure in *Pilotrochus* adding: "this organ appears to
be the external part of an exocrine gland or glands". BARONI URBANI
& DE ANDRADE (1994: 61 & Fig. 36) recorded a similar structure in
Strumigenys assamensis and called it "mesopleural presumed glandu-

lar area". BOLTON (1998) seized this belief under the name "meso-pleural gland" and later (BOLTON, 1999) called it "hair-lined gland of mesopleural anterior margin". DIETZ (2004) also calls it "glândula da mesopleura" referring to BOLTON (1998). As a matter of fact there is no visible gland in this body region. There are broad hair beds probably made out of sensilla trichoidea on the mesosternum. When these hairs are particularly developed and/or abundant, they became visible also on the profile (Fig. 21) and have been misinterpreted as a glandular opening. This trait is given as a potential synapomor-phy of Dacetonini + Phalacromyrmecini by BOLTON (1998: 73) and is practically equivalent to character # 23 in BOLTON (1999) where it appears as synapomorphic for *Pyramica* and *Strumigenys* only (sic!). DIETZ (2004, char. # 25) also uses this character and refers to BOLTON (1998) but presents it as exclusive of the Phalacromyr-mecini. The hairs, however, are well visible in profile also in some *Colobostruma*, *Mesostruma*, *Epopostruma*, *Orectognathus*, *Basiceros*, *Eurhopalothrix*, *Rhopalothrix*, and in *Octostruma balzani* (Emery).

33. Worker. Metapleural gland orifice absent, round or not covered by a longitudinal integumental ridge never opening dorsally to posterodorsally (0), or with a longitudinal slit or narrow crescent opening dorsally to posterodorsally (1). This is given as myrmicine synapomorphy by BOLTON (2003: 52) and should exclude *Tatuidris* from the subfamily Myrmicinae.

34. Worker. Metapleural gland opening visible, i. e. not covered by the slit of character # 33 (0), or invisible (1). This is character # 21 of BOLTON (1999).

35. Worker. Metapleural gland bulla [widely, according to Bolton] separated from annulus of propodeal spiracle more than the diameter of the spiracle [Dietz] (0), or [very close to the annulus of the propodeal spiracle (Bolton)], at most equal to the diameter of the spiracle and often touching the border of the bulla [Dietz] (1). This is character # 22 of BOLTON (1999) and character # 26 of DIETZ (2004). Coding of this character, however, differs diametri-cally between Bolton and Dietz. There are obvious difficulties in standardizing some of Bolton's words like "widely" or "very". For this reason, we followed DIETZ's (2004) definition and we further precise it by stating that we consider as spiracle only the true tra-cheal opening without the surrounding bulging area. Having said
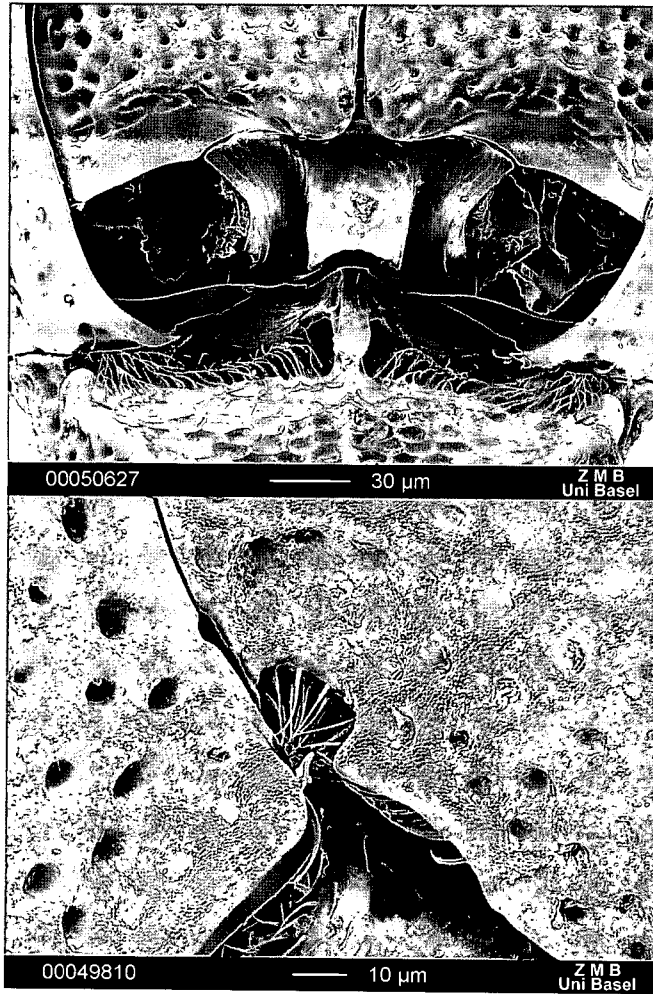
Fig. 21 - *Octostruma balzani* (Emery) (Basicerotini). Sensilla trichoidea grouped to form mesosternal hair beds (top) in ventral view. The hair beds under normal conditions and in ventral view are concealed by the procoxae; they turn out to be visible here after dissection. When the sensilla are particularly long or abundant they become visible also on the profile (bottom). This structure, widespread among several genera included in this study, was interpreted as an exocrine gland in the previous literature, and was given as synapomorphic for the tribes Dacetini + Phalacromyrmecini by BOLTON (1998) and as synapomorphic for the genera *Strumigenys* and *Pyramica* alone by BOLTON (1999). According to DIETZ (2004), the "gland" is autapomorphic for the Phalacromyrmecini.

that, our coding of this character is drawn from our own study of
the ants and differs from both, slightly from the one of Bolton in
the polymorphism of *Colobostruma* only, and radically from the one
of Dietz. We can easily and entirely defend our coding on the base
of the species that we studied.

36.   Worker. Katepisternal oblique groove absent (0), or present
(1). Presence of the groove should be a synapomorphy of the tribe
Phalacromyrmecini according to BOLTON (1998: 72). Examination of
the holotype of *Phalacromyrmex fugax* Kempf shows that there is
no trace of groove in the type genus of the tribe, *Phalacromyrmex*
(Fig. 22). Our "discovery" is confirmed by the original description
by KEMPF (1960a) and by the redescription by BOLTON (1984). Both
authors, for *Phalacromyrmex*, speak only of oblique costulation, a
trait used also by BOLTON (1984: 378) to differentiate *Phalacromyr-
mex* (where the groove is absent) from *Ishakidris* (groove present).
A few pages later, BOLTON (1984: 381) adds that the "mesopleu-
ral organ... in *Pilotrochus*... is... apparently not subtended by the
open groove seen in *Ishakidris*". The katepisternal groove, hence, is
coded as autapomorphic for *Ishakidris* in this paper. Its synapomor-
phic value for the Phalacromyrmecini pretended by BOLTON (1998)
was already discredited in an earlier paper by BOLTON (1984). But
BOLTON (2006a) defends again the tribal status of Phalacromyrmecini
on the generic presence of "some katepisternal system that appears
to channel the products of the mesopleural gland posteroventrally".
Unfortunately the gland in question has been not yet discovered and
the hair-like structures suggesting its existence are sensilla trichoidea
widespread among the Dacetini (see our discussion under character
32). The holotype of *Pilotrochus besmerus* Brown equally shows no
traces of the katepisternal groove or, if such a "katepisternal system"
is present, there are three equivalent systems pointing respectively
frontward, upwards and backwards. This situation is perfectly visi-
ble also in BROWN's (1978) Fig. 2 cited by BOLTON (2006a) to defend
his recording the presence of the groove. No katepisternal system of
any kind is visible in *Phalacromyrmex* (Fig. 22).

37.   Worker. Lower mesopleura without (0), or with marked
longitudinal costulation (1). This seems to be the most impres-
sive autapomorphy for the genus *Phalacromyrmex* within the broad
sample of genera considered here.

Fig. 22 - *Phalacromyrmex fugax* Kempf, holotype worker, type species of the genus
Phalacromyrmex which is, in turn, the type genus of the "tribe Phalacro-
myrmecini". Mesosoma in profile without traces of katepisternal oblique
groove; presence of the groove appears to be the most salient character
of the "tribe Phalacromyrmecini" according to BOLTON (1988). Distance
between two scale bars 0.1 mm.

38. Worker. Propodeal spiracle in profile at about midlength
of sclerite (0), or close to or at declivity (1). This is character # 25
of BOLTON (1999).

39. Worker. Petiole dorsoventrally unfused (0), or fused (1).
This is character # 16 of BARONI URBANI *et al.* (1992).

40. Worker. Petiole in posterior view with tergum and ster-
num differently shaped (0), or with tergum and sternum equally
convex, forming a circle (1). This is given as myrmicine syna-
pomorphy by BOLTON (2003: 52) and should exclude *Tatuidris*
from the subfamily Myrmicinae. We coded the character as pres-
ent in all Myrmecinae and absent in *Tatuidris*. Tergum and ster-
num are actually round also in *Myrmecia* and *Pseudomyrmex*.
These structures, however, differ from the one of *Tatuidris* and
from the Myrmicinae for being unfused instead of fused. Dis-
regarding the fused or unfused state, as BOLTON (2003) did,
this character results parsimony uninformative in our context.

41. Worker. Lateral outgrowths of pedicel absent (0), or present (1). This is character # 28 of BOLTON (1999) coded differently from BOLTON (l. c.) in some genera for the following reasons: *Mesostruma* (polymorphic instead of present only) because of absence in *M. eccentrica* Taylor (BOLTON, 2000, Fig. 56 and present study) *Epopostruma* (polymorphic instead of present only) because of absence of outgrowths in *E. quadrispinosa* (Forel) (BOLTON, 2000, Fig. 76 and present study). BOLTON's (l. c.) matrix records the regular presence of outgrowths for *Pyramica* and *Strumigenys*. This corresponds approximately to the truth only if one considers all outgrowths together, i. e. integumental spines and spongiform appendages. We accepted this interpretation in our matrix but excluded Bolton's next character (character # 29, petiole and postpetiole with or without spongiform tissue) as redundant. In addition, this character should be coded differently from BOLTON (l. c.) in both, *Pyramica* and *Strumigenys*. In *Pyramica* presence of the spongiform appendages is polymorphic (instead of present only) because of absence of spongiform appendages at least in *Pyramica denticulata* (Mayr) (Fig. 23, top) and in *P. eggersi* (Emery) (BOLTON, 2000: 184). Analogously, for *Strumigenys*, BOLTON (2000: 903) states that the whole species group *szalayi* Emery has "spongiform appendages of waist very reduced or absent". *S. tigris* Brown also has no traces of spongiform appendages (Fig. 23, bottom). Bolton's character # 29 (spongiform appendages) alone, after the above corrections concerning *Pyramica* and *Strumigenys*, results cladistically uninformative. Additionally, spongiform appendages are present also in *Colobostruma cerornata* Brown (BROWN, 1959: 2 [description] and Fig. 2; BOLTON, 2000: 39 [description] and Fig. 45); nonetheless *Colobostruma* is coded as without spongiform appendages in BOLTON (1999: 1648) and in the present paper. BOLTON's (1999) character # 29 is also equivalent to character # 27 of DIETZ (2004). BOLTON's (1999) description of his character # 28 as "lateral or ventral outgrows of any form" would practically change only the coding for a number of basicerotine genera as polymorphic instead of absent only, and further blunt the separation between Dacetini and Basicerotini, a universally undesired feature, we suppose.

42. Worker. Postpetiolar tergum and sternum overlapping at junction (0), or meeting end to end (1), This is given as myrmicine synapomorphy by BOLTON (2003: 52) and should exclude *Tatuidris* from the subfamily Myrmicinae.
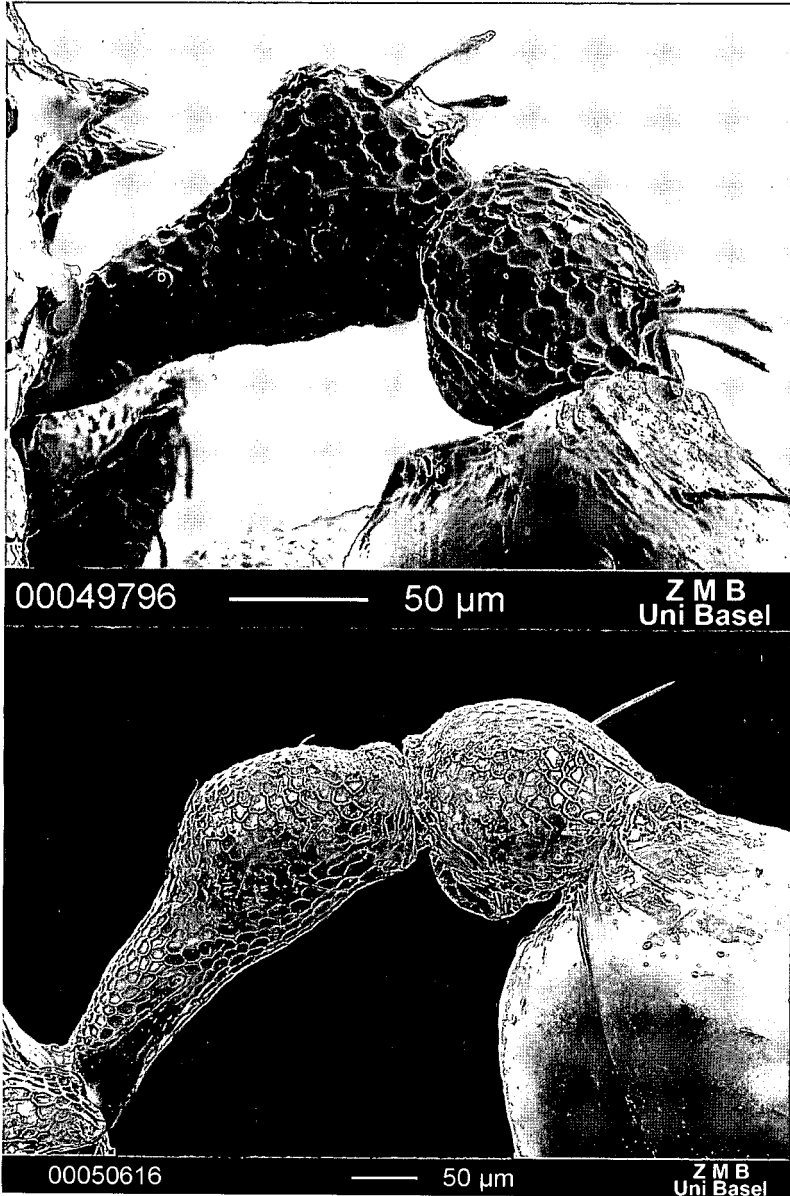
Fig. 23 - Absence of spongiform appendages in *Pyramica denticulata* (Mayr) (top) and *Strumigenys tigris* Brown (bottom). Presence of spongiform appendages is given as synapomorphic for these two genera in BOLTON (1999).

43. Worker. Articulation between gaster and postpetiole narrow (0), or broad (1). A narrow articulation is given as potentially synapomorphic for the Dacetini + Phalacromyrmecini by BOLTON (1998: 72). The narrow condition, however, is widespread in a number of Myrmicinae including most outgroups considered in the present paper. This character, for the ingroup species, is coded polymorphic according to the variation observed while examining the material available for the present study (e. g. *Strumigenys horwathi* Emery and *Pyramica crassicornis* (Mayr) with broad articulation and *Basiceros disciger* (Mayr) with narrow articulation (Fig. 24)). Inclusion or exclusion of this character from calculations or its coding with or without polymorphism affect the length but not the number and the topology of the shortest trees. This is also character # 28 of DIETZ (2004).

44. Worker. Postpetiolar presclerites not set in a concavity or depression (0), or arising from the base of a broad, deeply concave depression (1). This is a synapomorphy for the Basicerotini according to BOLTON (1998: 71) and DIETZ (2004, char. # 24). The postpetiolar presclerites of some *Pyramica* species like *P. denticulata* (Mayr) (Fig. 25) or *P. eggersi* (Emery) (Fig. 26) arise from a deep depression of size and shape perfectly comparable to the one of some Basicerotini.

45. Worker. Pretergite of first gastral segment neck-like (0), or subsessile to sessile (1). State 0 of this character is given as potentially synapomorphic for the Dacetini and Phalacromyrmecini by BOLTON (1998: 72). We added it to our data matrix notwithstanding some perplexities about its meaning (e.g. the neck-like condition seems to be plesiomorphic among myrmicines and, neck-like − a morphological trait − is not perfectly antonymic of sessile) and presence in some taxa. Within the sample of genera considered in the present paper, the sessile condition was coded as synapomorphic for the Basicerotini in spite of numerous cases in which species belonging to the two tribes appear to be indistinguishable (see e.g. Fig. 27, among other possible examples). An anonymous referee insisted that the sessile condition applies also to *Tatuidris*, a condition that we were unable to verify by dissection of the specimens available for the present study. Inclusion or exclusion of this character for parsimony analyses of our data does not affect the number and topology of the shortest tree(s).
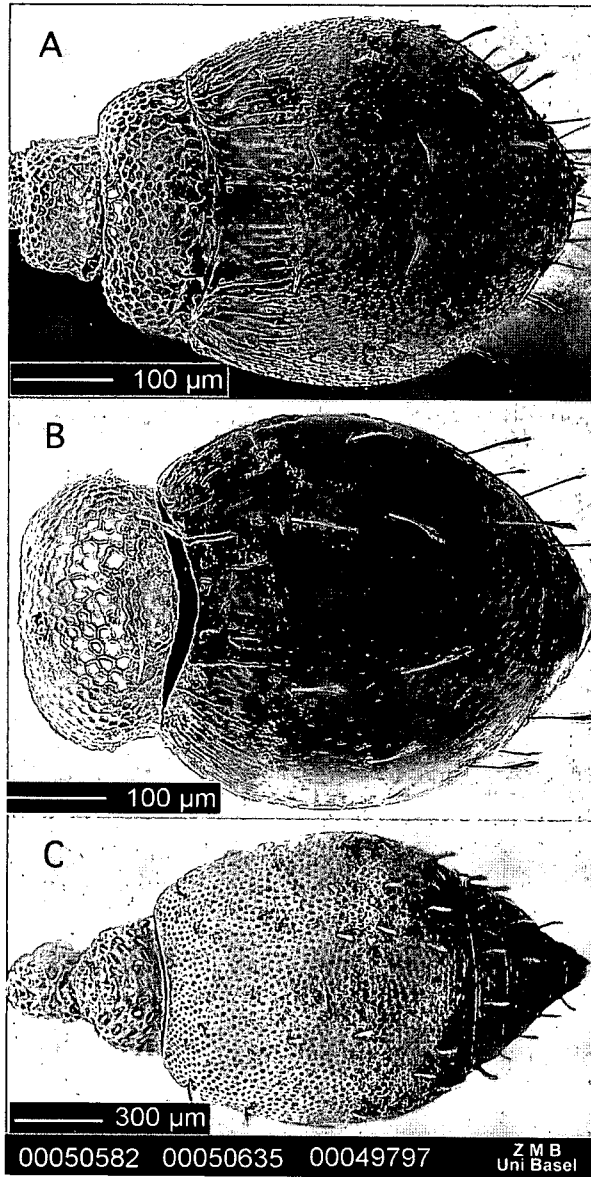
Fig. 24 - Comparably broad articulations between postpetiole and gaster in the dacetines *Strumigenys horwathi* Emery (A), *Pyramica crassicornis* (Mayr) (B) and in the basicerotine *Basiceros disciger* (Mayr) (C). A broad articulation is supposed to be synapomorphic for the basicerotines.
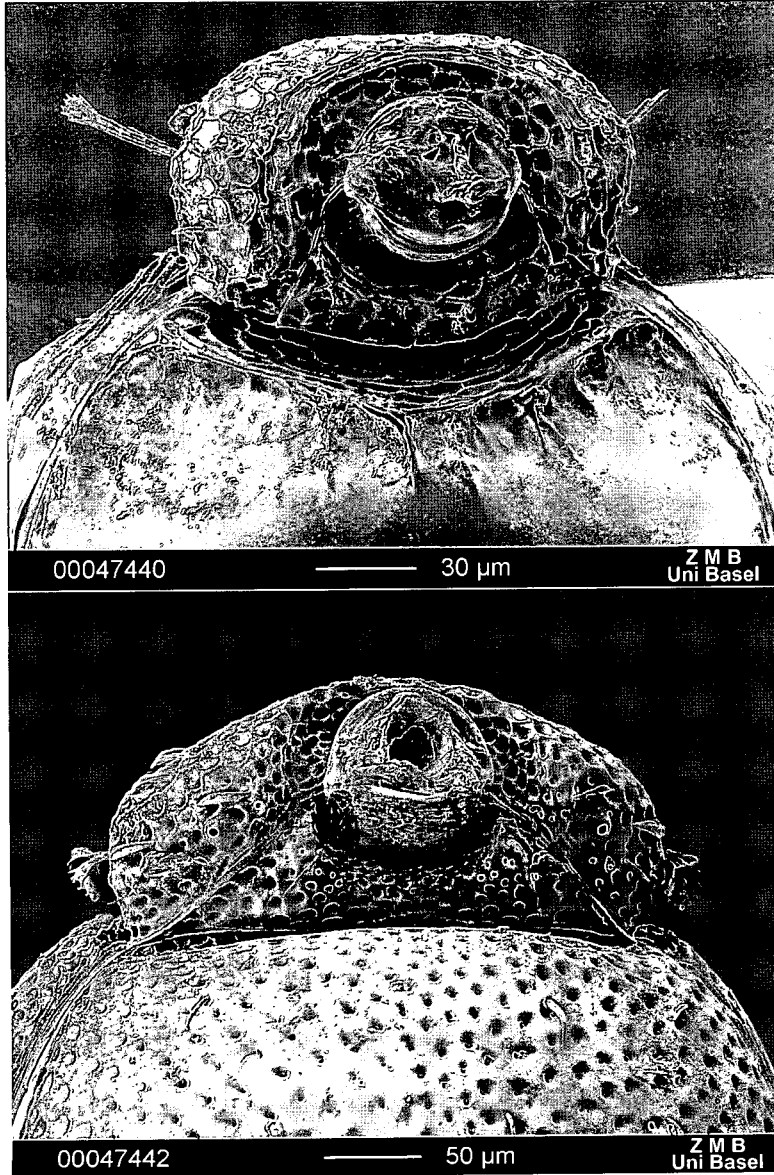
Fig. 25 - Similarity of structure of the postpetiolar presclerites among Dacetini and
        Basicerotini: *Pyramica denticulata* (Mayr) (Dacetini, top) and *Rhopalothrix
        ciliata* Mayr (Basicerotini, bottom).
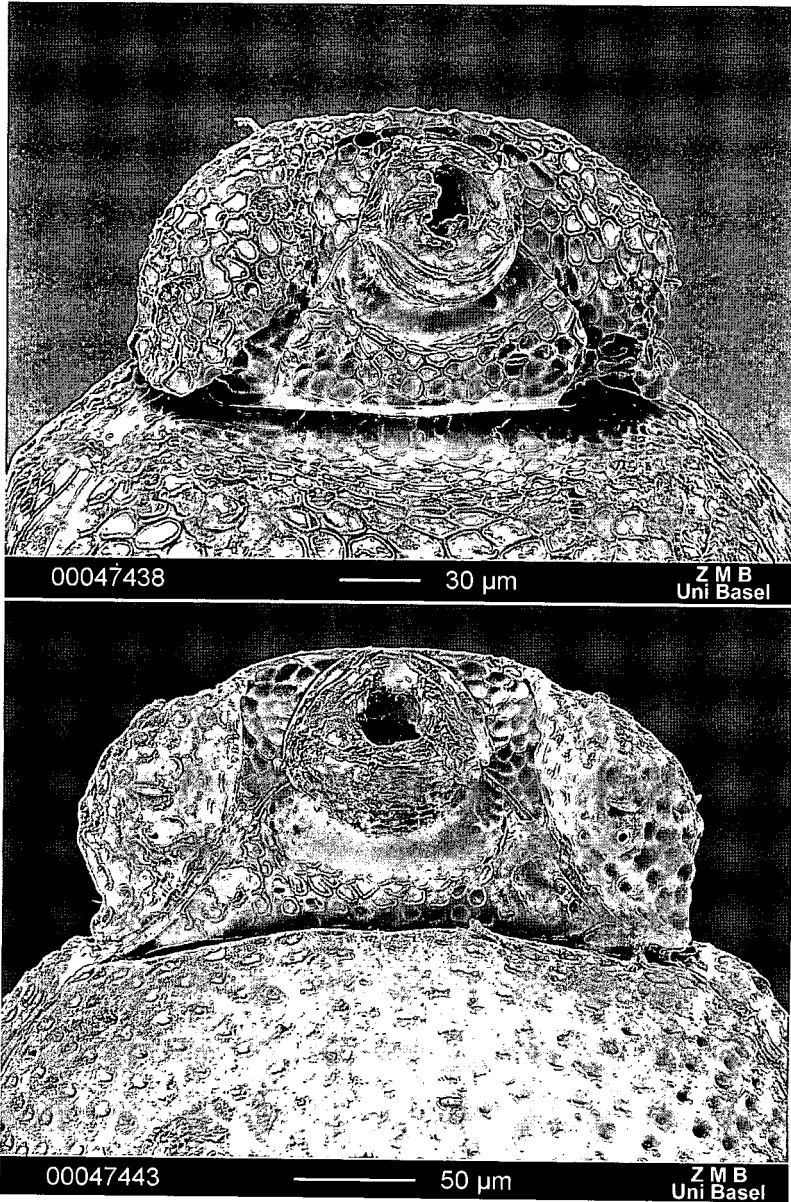
Fig. 26 - Similarity of structure of the postpetiolar presclerites among Dacetini and Basicerotini: *Pyramica eggersi* (Emery) (Dacetini, top) and *Octostruma balzani* (Emery) (Basicerotini, bottom).

46. Worker. "Limbus" (i. e. anterior transverse cuticular ridge of the first gastral tergum) absent (0), or present (1). This is character # 32 of BOLTON (1999). In Bolton's matrix the character is synapomorphic for *Pyramica* and *Strumigenys*. On the other hand BOLTON (1998: 71) states that the first gastral tergite and sternite of the Basicerotini are synapomorphically marginate basally, immediately behind the postpetiole and adds that "the limbus... is an apomorphy... of the strumigenyite group of Dacetini...and... it is not a homologue of the basal margination developed in Basicerotini". Not only we are sceptic about this *a priori* declaration of homoplasy, but we are also unable to see differences between the tergal morphology of some basicerotines and the one of some dacetines (Fig. 27). With the best of our will we are unable to see BOLTON's (1998) differentiation between the presence of this structure "basally" (= Basicerotini only), or "prebasally" (= Dacetini only and not homologous of the former). Our Fig. 27 should be a good support for our interpretation among many other possible ones. In addition, a cuticular ridge is present also on the first gastral tergum of *Colobostruma cerornata* Brown and *Phalacromyrmex fugax* Kempf (present study). DIETZ (2004, character # 30) apparently also disagrees with BOLTON (1998) and considers this character as a synapomorphy of the basicerotines + phalacromyrmicines in his character description but, in his table 2, he codes nonetheless the ridge as present in the basicerotine genera only. In our matrix we coded simply the presence or absence of the sole cuticular ridge that we were able to see.

47. Worker. Suture between first gastral tergite and sternite anteriorly rounded (0), or angulated (1). This is character # 33 of BOLTON (1999).

48. Worker. Base of the first gastral sternum in profile rounded (0), or truncated (1). This is character # 34 of BOLTON (1989) where the truncated condition results as synapomorphic for *Strumigenys* and *Pyramica*. The truncated condition, however, is present also in all Basicerotini, *Colobostruma cerornata* Brown, *Ishakidris* and *Stegomyrmex*. There are, on the other hand, species of both *Pyramica* (e. g. *P. mutica* (Brown)) and *Strumigenys* (e. g. *S. nigra* Brown, *S. tigris* Brown (BOLTON, 2000: Fig. 514)) without truncation.

49. Worker. First gastral tergum and sternum smooth or at least not sharply punctuated (0), or with dense and deep punctures (1). A
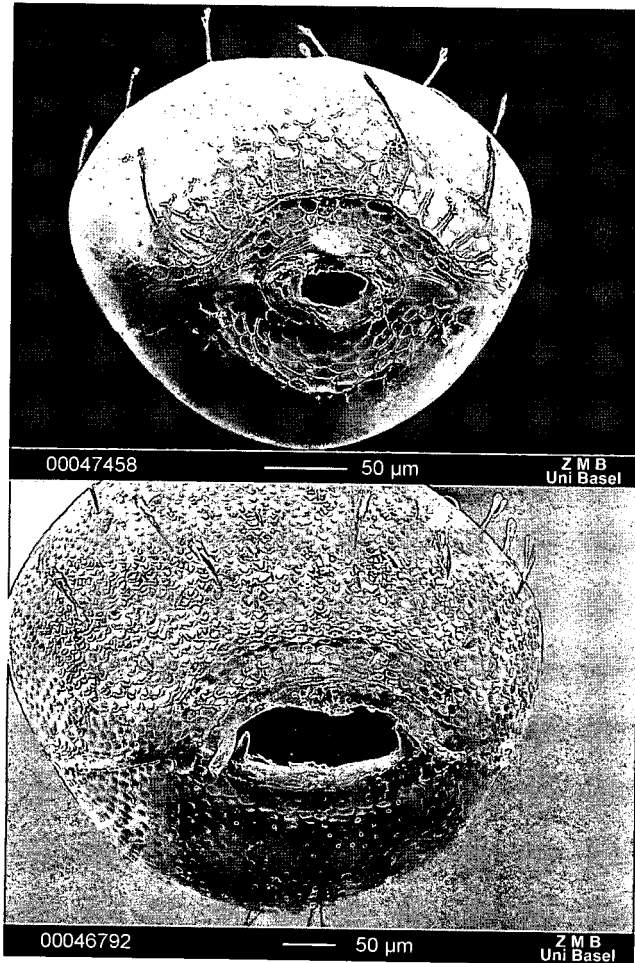
Fig. 27 - Similarity in morphology of the "limbus", (an anterior cuticular ridge on the first gastral tergum) in the dacetine *Pyramica denticulata* (Mayr) (top) and the basicerotine *Octostruma stenognatha* Brown & Kempf (bottom). This structure is interpreted as synapomorphic for the Basicerotini and, independently derived from this, synapomorphic also for *Strumigenys* + *Pyramica* in BOLTON (1998). The difference between the two synapomorphies is supposed to lie on the fact that no Dacetini have the margination extending to the sternum. In this figure the dacetine *Pyramica* exhibits a much stronger sternal margination than the basicerotine *Octostruma*. Another putative difference between Dacetini and Basicerotini (char.# 45) is a neck-like anterior articulation of the gaster believed to be present among Basicerotini only. Note the practically identical morphology of the two species illustrated here.

punctuated first gastral segment is given as synapomorphic for the Basicerotini by BOLTON (1999: 71). In the same paper BOLTON (l. c.) admits that in some species this sculpture may be "secondarily reduced or effaced". As stated at the beginning of this paper, we coded what we observed without *a priori* decisions on its phylogenetic meaning. There are no traces of punctures in *Basiceros* (=*Octostruma*) *onorei* Baroni Urbani & de Andrade (Fig. 28, top), in some *Eurhopalothrix* species already illustrated by TAYLOR (1990) and in *Octostruma balzani* (Emery) from Ecuador (Fig. 28, bottom). DIETZ (2004) also retains this character as basicerotine synapomorphy (his character # 29), but admittedly following BOLTON (l. c.) and without checking the species available to him. In addition, there are a few *Pyramica* species with gastral sculpture perfectly comparable to the one of some basicerotines (Fig. 29).

50. Worker. Bizarre pilosity absent or poorly developed (0), or present and well developed (1). This is character # 27 of BOLTON (1999) but coded differently for *Colobostruma* (polymorphic instead of absent only) because of the presence of bizarre hairs in *C. cerornata* Brown (BOLTON, 2000, Fig. 45). We are not sure about what "bizarre" should or should not include but we followed BOLTON (1999) in coding this character as present in *Strumigenys* and *Pyramica*. As a consequence of this we coded it present also for *Pilotrochus* and *Tatuidris* since the hairs of these genera are virtually identical to those e.g. of *Pyramica medusa* Bolton (BOLTON, 2000, Fig. 296) and *Strumigenys caniophanes* Bolton (BOLTON, 2000, Fig. 490). On the other hand, at least *Pyramica mitis* Brown is completely destitute of standing hairs of any kind (BOLTON, 2000: 442). *Pyramica*, as a consequence of this, was coded as polymorphic. We suppose that this character should be equivalent to DIETZ's (2004) character # 31 "Pêlos especiais no escapo, pigídio e esternito do 1° segmento do gáster".

51. Male. Mandibles normally developed (0), or reduced (1). This is character # 34 of DIETZ (2004) differently coded, i.e. developed instead of unknown for *Stegomyrmex* (DINIZ, 1990: 279), and *Orectognathus* (EMERY, 1924: 318 and personal observations), polymorphic instead of reduced only in *Pyramica* (mandibles well developed at least in *P. rostrata* (Emery) and *P. baudueri* (Emery)), polymorphic instead of reduced only in *Eurhopalothrix* because of a
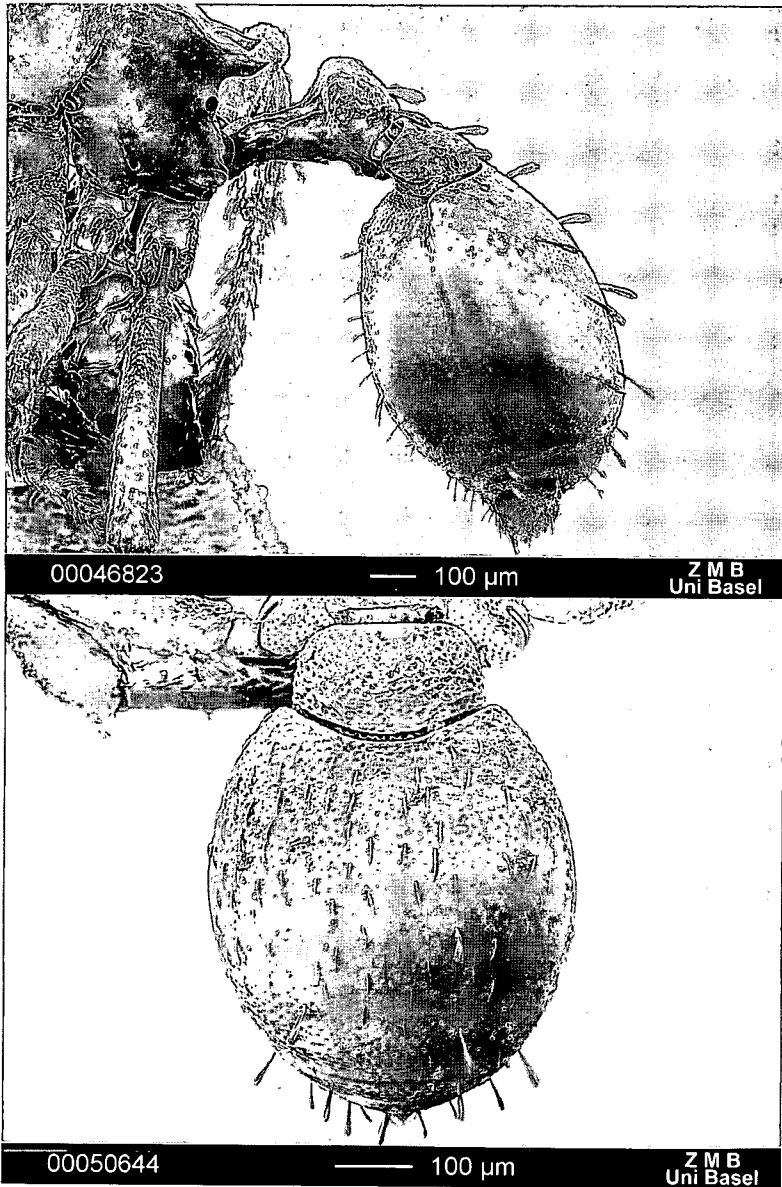
Fig. 28 - Lack of sculpture on the first gastral tergum and sternum in *Basiceros* (=*Octostruma*) *onorei* n. sp. (top) and in *B. balzani* (Emery) from Ecuador (bottom).

sentence of MANN (1922: 41) attributing "mandibles well developed" to the male of *Eurhopalothrix gravis* (Mann).
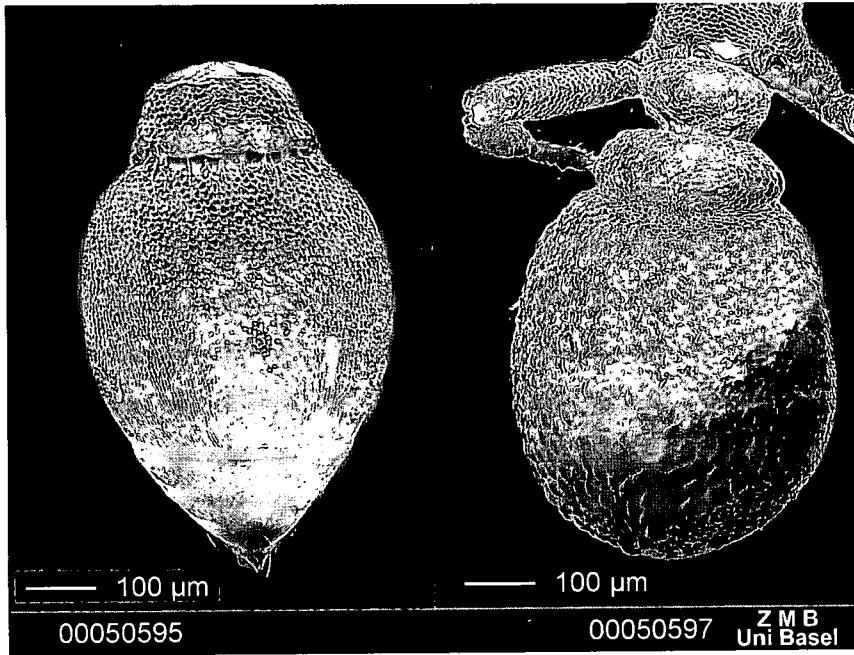
Fig. 29 - Comparable sculpture of the first gastric tergite in the dacetine *Pyramica margaritae* (Forel) (left) and in the basicerotine *Eurhopalothrix bruchi* (Santschi) (right). A sculptured gaster is supposed to be synapomorphic for the Basicerotini and absent among Dacetini.

52.   Gyne and male. Anterior wing with (0) or without (1) cell RS. This is character # 37 of DIETZ (2004). Due to the exiguity of the material available to us, except for a few outgroups not considered by DIETZ (2004), this character is coded entirely *fide* DIETZ (2004). This character is cladistically informative only because of the differences between outgroup and ingroup taxa. Within the dacetinomorph genera, this character remains invariant or unknown and, as such, it is without interest for our purpose.

53.   Gyne and male. First anal vein of the anterior wing present (0), or absent (1). This is character # 38 of DIETZ (2004). Due to the exiguity of the material available to us, except for a few outgroups

Table 1 - Distribution of the retained characters and character states among the taxa considered in the present study. Character numbering and state coding as explained in the text.

	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
Myrmecia	0	0	0	0	0	0	0	0	0	0&1	0&1	0	0	0	0	0	0	0	0	0	0	?	0	1	0	0	0
Pseudomyrmex	0&1&2	0&1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	1	0	0	0
Myrmica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0&1	0	0	0	0	0	0	2	0	0	0
Stegomyrmex	4	2	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	2	0	0	0
Calyptomyrmex	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	2	1	0	0
Tatuidris	5	2	0	0	0	0	0	0	2	0	?	?	0	0	0	1	1	0	0	1	0	0	3	2	0	1	0
Acanthognathus	6	3	0	1	0	0	0	1	2	1	0	1	2	0	1	1	0	0	0	1	0	0	0	2	0	1	0
Colobostruma	1	1	0	0	1	0&1	0&1	0&1	2	0	0	0	1	0	1	1	1	0&1	0	0&1	0	0&1	0&2	1	0	1	0
Mesostruma	1	1	0	0	1	0	1	1	2	0	0	0	1	0	1	1	1	0	0	0&1	0	0	2	1	0	1	0
Epopostruma	1	1	0	0	0	0	1	1	2	1	0	0	1	0	1	1	1	0	0	0	0	0	2	1	0	1	0
Microdaceton	3	2	1	0	0	0	1	1	2	1	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	1	1
Daceton	1	1	1	1	0	0	1	1	2	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1
Orectognathus	1	1	1	1	0	0	1	1	2	1	0	1	1	0	1	0	1	0	0	0	1	0	0&1	2	0	1	1
Pyramica	5&6	3	0&1	1	0	0&1	0&1	0&1	2	0&1	0&1	0&1	1	0&1	1	1	1	0&1	0&1	0&1	0	0&1	1	0&3	0&1	1	0
Strumigenys	5&6	3	1	1	0	0&1	1	0&1	2	0&1	0	0&1	1	0&1	1	1	1	0	0	0&1	0	0&1	1	3	0&1	1	0
Phalacromyrmex	3	2	0	1	0	0	0	1	1	0	1	0	0	1	0	1	1	0	1	1	0	0	1	3	1	1	0
Ishakidris	4	2	0	1	?	0	0	1	2	0	1	0	0	1	1	1	?	0	1	0	0	0	1	3	1	1	0
Pilotrochus	3	2	0	1	0	0	?	1	1	0	1	0	0	1	1	1	1	0	1	1	0	0	1	3	?	1	0
Basiceros	4&5	2&3	0	1	0	1	0	1	2	0	0	0	0	1	1	1	1	1	0	1	0	1	2	2	1	1	0
Eurhopalothrix	5	2&3	0	1	0	1	0	1	2	0	0	0	0	1	0	1	1	1	0	1	0	0&1	2	2	1	1	0
Octostruma	4&5	2&3	0	1	0	1	0	1	2	0&1	0&1	0	1	1	1	1	1	1	1	1	0	1	2	2	0&1	1	0
Protalaridris	5	2	0	1	0	1	0	1	2	1	0	0	0	1	1	1	1	1	0	1	0	1	2	2	1	1	0
Talaridris	5	3	0	1	0	1	0	1	2	1	0	0	0	1	1	1	1	1	0	1	0	1	2	2	1	1	0
Rhopalothrix	5	2	0	1	0	1	0	1	2	1	0	0&1	0	1	1	1	1	1	0	1	0	1	2	0&2	0&1	1	0

Table 1 - (Continued) Distribution of the retained characters and character states among the taxa considered in the present study. Character numbering and state coding as explained in the text.

	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
Myrmecia	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Pseudomyrmex	0	0	0&1	0	0	0	0	0	0	0	0	0	1	0	0	0&1	0	0	0	0	0	0	0	0	0	0	0
Myrmica	0	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Stegomyrmex	0	1	0	1	0	1	1	0	0	0	0	1	1	0	1	0	0	0	1	0	1	0&1	1	0	0&1	0	?
Calyptomyrmex	0	1	0	1	0	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	?	?	?
Tatuidris	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0
Acanthognathus	0	1	1	1	0	0	1	1	0	0	1	1	0	1	1	0	0	0	0	1	0	0	0	1	1	0&1	0
Colobostruma	0	1	1	1	0&1	1	1	0&1	0	0	1	1	1	0	1	0	0	0	0&1	1	0&1	0	0&1	?	?	?	0
Mesostruma	0	1	0&1	1	0&1	1	1	1	0	0	1	1	1	0&1	1	0	0	0	0	1	0	0	0	1	1	0	0
Epopostruma	0	1	0&1	1	0&1	1	1	1	0	0	1	1	1	0&1	1	0	0	0	0	1	0	0	0	?	?	?	?
Microdaceton	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	0	0	0	0	1	0	0	0	1	1	0	?
Daceton	0	1	1	1	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0
Orectognathus	0	1	0&1	1	0&1	1	1	0	0	0	1	1	1	0&1	1	0&1	0&1	0	0	0	0&1	0&1	0&1	0&1	1	1	0
Pyramica	0	1	0	1	1	1	1	0	0	0	1	1	1	0&1	1	0&1	0	0	1	0	0&1	0&1	1	1	1	1	0
Strumigenys	0	1	0&1	1	1	1	1	0	0	0	1	1	1	0&1	1	0&1	0	0	1	1	0&1	0	1	1	?	1	?
Phalacromyrmex	0	1	1	1	1	1	?	1	1	1	1	1	1	0	1	0	1	0	1	0	1	0	1	?	?	?	?
Ishakidris	0	1	0	1	1	1	1	0	0	0	1	1	1	0	1	0	?	0	1	?	1	0	1	?	?	?	?
Pilotrochus	0	1	0	1	2	1	1	0	0	0	1	1	1	0	1	0	1	1	1	0	0	0	1	0	1	0	0
Basiceros	0	1	0	1	0&1	1	1	0	0	0	1	1	1	0	1	0&1	1	1	1	0	1	1	1	0	1	0&1	1
Eurhopalothrix	0	1	0	1	0&1	1	1	0&1	0	0	1	1	1	0	1	1	1	1	1	0	1	0&1	1	0&1	1	0&1	1
Octostruma	0	1	0	1	0&1	1	1	0&1	0	0	1	1	1	0	1	1	1	1	1	0	1	0&1	1	0	1	0	?
Protalaridris	0	1	0	1	0	1	1	1	0	0	1	1	1	0	1	1	1	1	1	0	1	1	1	?	?	?	?
Talaridris	0	1	0	1	?	1	1	0	0	0	1	1	1	0	1	1	1	1	1	0	1	1	1	?	1	?	?
Rhopalothrix	0	1	0	1	0&1	1	1	0&1	0	0	1	1	1	0	1	1	1	1	1	0	1	1	1	?	1	1	0

not considered by DIETZ (2004), this character is coded essentially *fide* DIETZ (2004: table 2); Dietz's table, however, records the anal vein as present in *Eurhopalothrix*, but Dietz's generic diagnosis (p. 66) states that in *Eurhopalothrix* the anal veins can be "ausentes, incompletas, ou na forma de veias espectrais". For this reason we coded the anal vein as polymorphic in *Eurhopalothrix*. In addition, DIETZ (l. c.) codes the anal vein as absent in *Acanthognathus* but we considered it as polymorphic because of a drawing by BROWN & KEMPF (1969. Fig. 7) depicting a male of *A. rudis* with anal vein.

54. Gyne and male. Pterostigma present (0), or absent (1). Absence of pterostigma is an autapomorphy of the genus *Eurhopalothrix* according to DIETZ's (2004) character # 36.

The distribution of these character states among the taxa included in the present study is given in Table 1.

4.2. CHARACTERS USED IN OTHER PHYLOGENETIC STUDIES AND EXCLUDED FROM THE PRESENT ONE

As already stated in the paragraph devoted to the outgroup selection we did not consider the 7 autapomorphies and the 4 plesiomorphies attributed by BOLTON (1998: 68) to *Tatuidris*. These are parsimony non-informative by definition (see e. g. HENNIG, 1950, WILEY, 1980, and MADDISON & MADDISON, 2002, among many other possible sources). Autapomorphies and plesiomorphies may be very useful in appreciating how distinctive a taxon can be but contribute nothing to its placement within a phylogeny. Stated otherwise, considering all the characters listed by BOLTON (1998) and even adding many more similar new ones would not affect our phylogenetic reconstruction.

Other characters appearing in the literature and excluded from the present study are listed in the following.

Presence of a preocular carina (synapomorphy of the "dacetonine tribe-group" in BOLTON (1998:69)). Equal to character # 14 of DIETZ (2004). We are unable to see traces of the carina in a number of dacetines like, e.g. *Epopostruma natalae* Shattuck, *Microdaceton tibialis* Weber, *Daceton armigerum* (Latreille), *Acanthognathus ocellatus* (Mayr). The carina, on the other hand, is present in a number of non-dacetine myrmicines like several Attini.

BOLTON's (1999) character # 6. Number and position of trigger hairs. In Bolton's matrix this character is unique (i. e.) autapomorphic for *Microdaceton* and *Acanthognathus* with a different character state for each of these genera. Unfortunately, coding all the other genera considered by Bolton as uniformly with paired trigger hairs is far from being satisfactory. In some instances (e. g. in *Pyramica myllorhapha* (Brown)) the labral hairs are so small that we strongly hesitate to differentiate them from normal hairs and to call them trigger hairs. In addition, the remaining genera considered in the present paper but excluded by BOLTON (1999) show a wide array of different morphologies, which, wrestling with character definitions, could lead only to a longer set of doubtful generic autapomorphies at most. The simple presence of "trigger hairs" on the mouthparts is given as synapomorphic for the "dacetonine-group" by BOLTON (1998) and retained as such also by us (our char. # 8).

BOLTON's (1999) character # 13 and DIETZ (2004) character # 17. Scape in "normal resting position" above or below the eye. This character is either equivalent to Bolton's char. # 16 states 1-2 ("scrobe above... below eye") or impossible to assess on preserved material in which the antennae have been mounted.

BOLTON's (1999) character # 15 (scape apical section angled or not angled). Either we misunderstand Bolton's description of it or we should code this character in a way rather different from BOLTON (1. c.). It can be excluded without losses for Bolton's phylogeny since in Bolton's original resulting tree (BOLTON, 1999, Fig. 3) this character has CI = 0.33 and does not contribute at all to Bolton's phylogeny (RI = 0.0).

BOLTON's (1999) character # 17. "Eyes... not ventrolateral" vs. "eyes... ventrolateral" is excluded in favour of BARONI URBANI & DE ANDRADE's (1994) information richer char. # 3, eyes absent, dorso-lateral, lateral, or ventral.

BOLTON's (1999) character # 18. Gap between mandibles and head capsule in profile. This character, in Bolton's matrix, is shared by *Daceton* and *Microdaceton* only, although the two genera appear as distantly related in Bolton's phylogeny. We excluded it simply because we are unable either to understand its description or we'd code it in a different way. Bolton's original coding, anyway, does not support his phylogenetic reconstructioin. As a consequence of

this, later on in the same paper (BOLTON, 1999:1678), this character state is given as autapomorphic for *Microdaceton*.

BOLTON's (1999) character # 19. Presence or absence of the basimandibular gland. In BOLTON (1998:73) this character is given as synapomorphic for the tribes Dacetini and Phalacromyrmecini. In BOLTON's (1999) matrix, this character is recorded for *Pyramica*, *Strumigenys* and *Microdaceton* only. We excluded it simply because either we are unable to understand its description or we'd code it in a way different from both BOLTON (1998) and BOLTON (1999) (e. g. polymorphic for *Strumigenys*, *Pyramica* and *Rhopalothrix*). As a further proof of our claim, we remember that this same character in DIETZ (2004) (char. # 5, table 2) is coded differently from BOLTON (1999) for the following genera: *Microdaceton*, *Pyramica*, and *Strumigenys*.

BOLTON's (1999) character # 20. Presence of apicofemoral and apicotibial glands (or, more generically, "series of paired exocrine glands"). This trait is given as synapomorphic for *Strumigenys* and *Pyramica*. But, a few pages later, BOLTON (l.c.: 1665) adds "the [apicofemoral] gland is apparently absent or at least has no externally visible bulla, in some whole groups and a number of individual species". And, for the apicotibial gland "variation is as for the femoral dorsal gland". The observed polymorphism of these glands in both, *Pyramica* and *Strumigenys*, renders their use for the cladistic analysis parsimony uninformative.

BOLTON's (1999) character # 26 "Metapleuralal gland bulla low and widely separated from propodeal spiracle...", versus "abutting propodeal spiracle". This is a repetition of BOLTON's (1999) character # 22 "Metapleural gland bulla widely separated from annulus of propodeal spiracle...". It differs from it for being coded in three steps instead of two. The newly added third step (metapleural gland bulla high and close to spiracle) appears only once as redundant autapomorphy for *Acanthognathus*. Otherwise chars. 22 and 26 have exactly the same score and appear synapomorphic for five dacetine genera. A very similarly defined character ("Propodeal spiracle low ... abutting the... metapleural gland bulla") was already used by BOLTON (1998: 73) as synapomorphy for the tribes Basicerotini and Phalacromyrmecini contradicting in this way BOLTON's (1999) definition. We regard this multiple use and different coding of similarly defined characters as an additional reason for exclusion from our data matrix.

BOLTON's (1999: 1649) character # 29. Presence of spongiform appendages of petiole and postpetiole. This was originally formulated as a plausible synapomorphy for *Strumigenys* and *Pyramica* (but see also discussion under our character 41). Presence or absence of spongiform appendages on the pedicel was already included in BOLTON's character # 28 (1999: 1649) under the more generic definition of "lobes or outgrowths of any form" and, under this definition, is also considered in our analysis as character # 41.

BOLTON's (1999) character # 30. "Tergite of petiole and postpetiole without lateral cuticular processes". Excluded since we are unable to understand the difference with Bolton's char. # 28 "Petiole and postpetiole without lateral (tergal) or ventral (sternal) lobes or outgrowths of any form...".

BOLTON's (1999) character # 31. Postpetiolar spiracle lateral or ventral. We are sceptic about this character due to the difficulty in observing it. The spiracle is practically in the same position among most of the species that we examined. When the petiole is laterally expanded or bears a lateral lamella, the spiracle appears to be more ventral than when the expansions or the lamellae are absent. Coding this character as Bolton did and considering it with the others in our search for the shortest tree(s) does not affect the number and topology of the shortest trees but increases the tree length.

BOLTON (1999: 1681). Labrum "mediodorsally with a very broadly and deeply concave depression in its proximal half". This should be an *Epopostruma* synapomorphy. In contrast with this assumption, the morphology of *Mesostruma turneri* (Forel) is perfectly comparable e.g. to the one of *Epopostruma alata* Shattuck (Fig. 30).

BOLTON's (1998: 70) synapomorphy for the Basicerotini "scape neck articulation" is another formulation of and correlated with his previous character "torulus" described at the same page and already included in our data matrix.

DIETZ's (2004) character # 3, "Forma do labro". The labrum should be longer than broad in all dacetine genera and broader than long in other ants. This rule of thumb applies well to a majority of species but there are numerous exceptions like broad labia in *Daceton* (present study), *Rhopalothrix* (BROWN & KEMPF, 1960, Figs. 57 & 58), *Basiceros* (nr. *singulare*, present study), *Pyramica* (e. g. BOLTON, 2000, Fig. 215 and *P. nannosobek*, our Fig. 4, bottom), and *Strumi-*
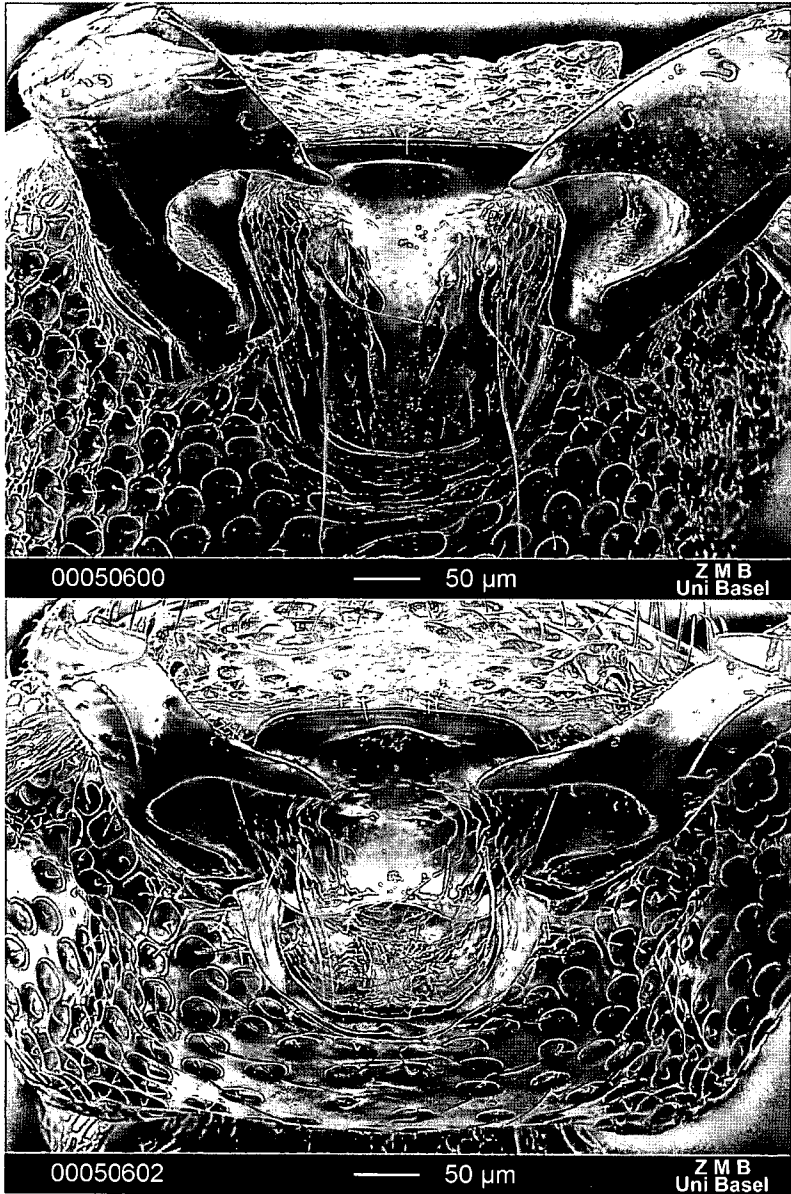
Fig. 30 - Comparable morphology of the labral concavity (a presumed *Epopostruma* synapomorphy) in *Mesostruma turneri* (Forel) (top) and *Epopostruma alata* Shattuck (bottom).

genys (Bolton, 1999, Fig. 93, and *S. harpyia*, present study). Since there are little doubts about the monophyly of the dacetine genera, a monophyly already supported by a number of synapomorphies, we thought it better to exclude this redundant but questionable character.

Dietz's (2004) character # 9 "Forma das mandíbulas". Elongated or specialized (i.e. non triangular) mandibles are coded as present in a number of dacetine genera not corresponding to any tribal grouping proposed so far. In addition we'd code as triangular at least the mandibles of *Colobostruma* and of some *Mesostruma* species (see e. g. the figures in Bolton, 2000). Accepting Dietz's revived combination of *Eurhopalothrix bruchi* in *Rhopalothrix* also the latter genus should have been coded as polymorphic (instead of specialized only). The specialization of the mandibles, moreover, is perfectly correlated with their capacity of engaging apically only or not. As such this character would overweight our character # 10 (q. v.).

Dietz's (2004) character # 11, "Forma das mandíbulas laminares". Presence or absence of an apical fork is coded in a very subjective way (for instance absence of apical fork in *Daceton*, unknown presence in *Colobostruma*, *Pyramica* and *Microdaceton*) that we are unable of understanding. Since Dietz states that the dacetine apical forks "probably evolved separately" we consider this statement alone as a reason good enough to exclude this character.

Dietz's (2004) character # 12, "Número de dentes das forquillas apicais". The two-state coding of this character (three vs. four teeth) by Dietz is difficult to maintain and is contradictory even within Dietz's text and matrix. In Dietz's table 2, for instance, only *Rhopalothrix* and *Protalaridris* share the four-toothed state, but, according to Brown (1980, with whom we concur), *Protalaridris* possess only one apical spine and according to the same Dietz (2004: 187), *Protalaridris* should have a five-toothed fork... Even solving somehow the problem of a correct coding for *Protalaridris*, there are other relevant and pertinent morphologies not accounted for and difficult to classify in this character definition. Examples of such morphologies are the two-toothed fork of *Daceton* (coded "?" by Dietz, l. c.), the two-toothed and three-toothed fork of *Strumigenys* (coded as three-toothed only by Dietz, l. c.), a. o.

Dietz's (2004) character # 32. "Espinhos nos tarsos anteriores". Presence of some undefined type of tarsal spines should be a syn-

apomorphy for the Phalacromyrmecini and Basicerotini, though the
author admits that similar but not homologous spines are present
also in *Daceton* (and other genera, our study). Fig. 31 shows simi-
larity of structures in *Strumigenys* and *Octostruma*. This and other
similar cases encountered during the present study prevent consid-
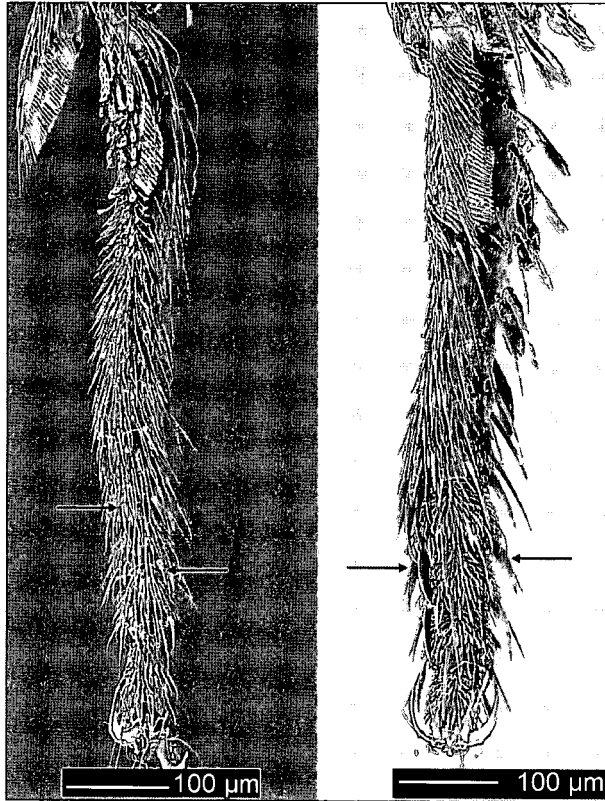eration of this character as phylogenetically sound.

Fig. 31 - Tarsal spines in the dacetine *Strumigenys grandidieri* Forel (left) and in the
basicerotine *Octostruma balzani* (Emery), a synapomorphy for Basicerotini
+ Phalacromyrmecini according to Dietz (2004).

DIETZ's (2004) character # 33. "Hábito de forrageamento". We
concur with the description of this character that we consider as
plausible in spite of obvious miscoding in Dietz's matrix (e. g. *Pyra-*

mica and *Strumigenys* epigaeic or arboreal only) but we consider our behavioural knowledge of these ants as by far too scanty to allow phylogenetic inferences.

DIETZ's (2004) character # 35. "Asa – conexão de cu-a próximo a 1M (0); distante de 1M basalmente (1); distante de 1M distalmente (2)". State 0 is recorded only among outgroups and state 2 should be autapomorphic for *Eurhopalothrix*. We are unable to see differences in this trait between the wings of the specimens of *E. procera* (Emery) and *Octostruma balzani* (Emery) available to us.

DIETZ's (2004) character # 40. "Presença de asas". This is an autapomorphy of Dietz's outgroup genus *Blepharidatta* (not considered in the present study) and, as such, totally irrelevant in this context.

DIETZ's (2004) character # 41. "Segunda linha de dentes". This is an autapomorphy of the genus *Eurhopalothrix* and, as such, redundant of our character 54 in this context. This trait, moreover,
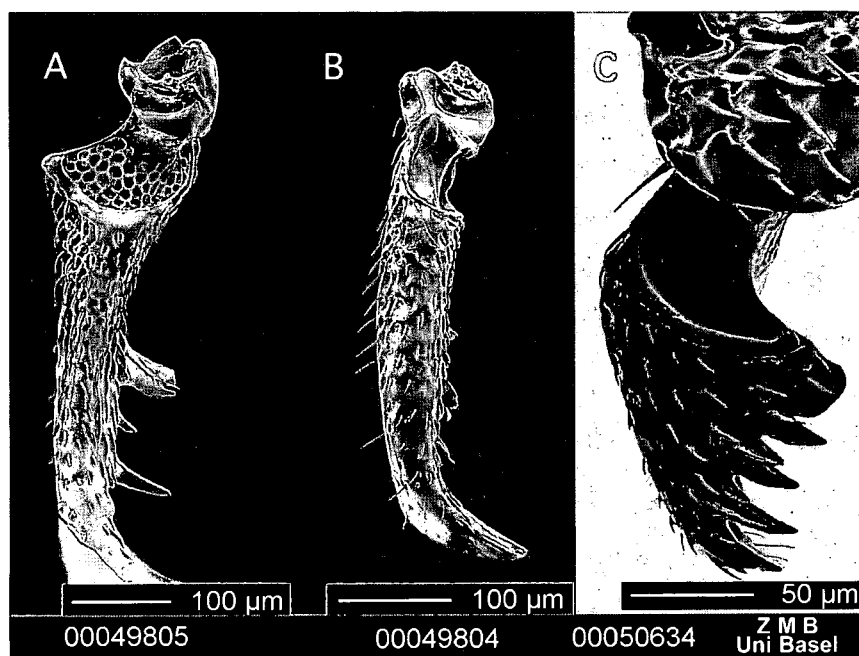

Fig. 32 - Basimandibular depression in *Protalaridris* near *armata* Brown (A), *Rhopalothrix ciliata* Mayr (B) and *Octostruma balzani* (Emery) (C).

is not synaptomorphic for *Eurhopalothrix* since it is absent at least in an undescribed "*Eurhopalothrix*" species available for this study and to be described in chapter 6 (Species-level additions) as *Basiceros papuanum* (Fig. 46).

Basimandibular depression absent (0), or present and distally marginate (1). This character (Fig. 32), shared by *Rhopalothrix*, *Protalaridris* and *Talaridris* is mentioned by DIETZ (2004) in the generic descriptions of the first two genera only but is not used in his phylogenetic analysis. We observed it in *Talaridris* as well and a similar structure is visible also in some *Octostruma*. Some *Pyramica* species also have some kind of basimandibular depression.

Larval hairs bifid or not. This is character # 10 of BARONI URBANI & DE ANDRADE (1994). This is a classic synapomorphy for all "dacetiform" genera resulting from the literature but verified in a too small number of taxa to be attributed unmistakable phylogenetic value.

4.3. RESULTS OF THE CLADISTIC ANALYSIS

Our parsimony analysis yields 414 equally shortest trees of length 208 (considering polymorphism as multiple speciation events), Consistency Index (CI) 0.746, Retention Index (RI) 0.785, and Rescaled Consistency Index (RC) 0.592. The strict consensus tree is given in Fig. 33.

Fig. 34 depicts the same consensus tree as the one of Fig. 33 but expressed as phylogram, i.e. with the branch lengths proportional to the number of synapomorphies supporting each branch. In it the synapomorphic characters for each branch are also added to the different branches with the same character numbering as in the previous text. The tree has the same number of branches as the input genera in our data and horizontal square brackets on top of the drawing indicate genera merged as a result of our analysis with their oldest available synonym. Synonymies of genera are inferred on the base of missing or too weak synapomorphies as shown on the tree and discussed in detail under the genus group systematics (chapter 4.5). Weakness and strength of the individual synapomorphies will be judged in terms of Consistency Index and Retention Index on the Consensus Tree of Figs. 33 and 34.
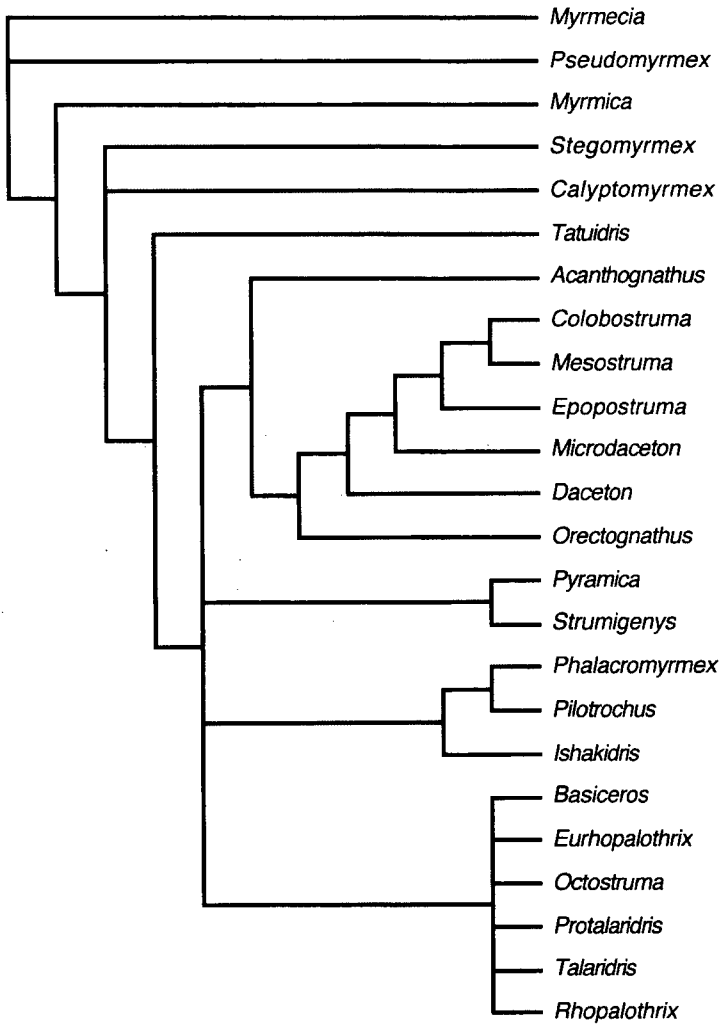
Fig. 33 - Strict consensus tree of the 414 equally most parsimonious trees drawn
          from the characters and taxa discussed in the text. Length of the indi-
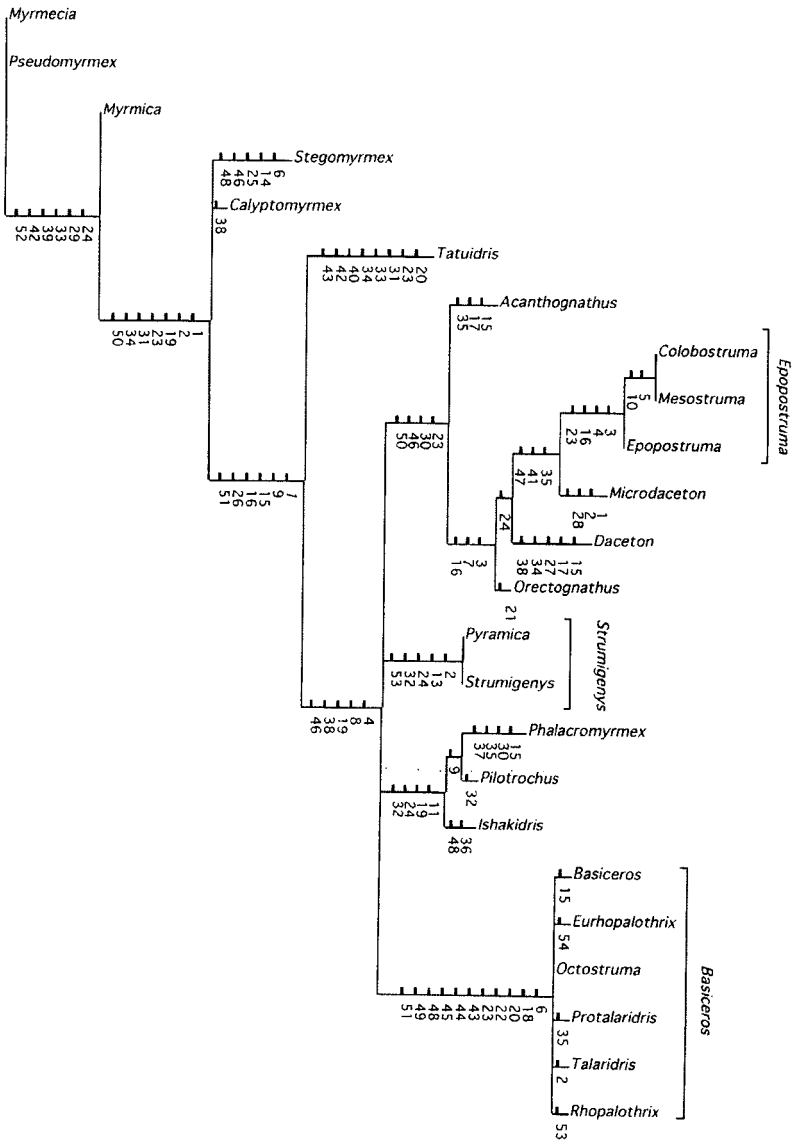   vidual trees 208.

Fig. 34 - Same strict consensus tree as the one of Fig 33 expressed as phylogram, i. e. with the branch lengths proportional to the number of derived characters changing on them. Character numbering as in text. The number of taxa is the same as in the inputted data. The square brackets embracing groups of taxa show synonymies to be proposed in this paper because of missing or too weak synapomorphies for one or more contained genera.

We refrain from attributing great phylogenetic value to this tree. The main reasons for our evaluation are its construction, drawn on a great number of phylogenetically insignificant characters and our incapacity to find better ones. The scarcity and weakness of the known characters on which our phylogeny is based can be better appreciated on the tree of Fig. 35, a 50% majority consensus tree drawn from 100 bootstrap replicates.

The phylogeny of Figs. 33-35, however, is an excellent discriminant criterion to decide what can be actually said or not on dacetine classification.

We insist that a good number of the characters from which our phylogenetic reconstruction is drawn are of doubtful generic or tribal value and are highly variable within the taxa considered. The phylogenetic value of a character may be a rather subjective topic but at least its variability will be described and taken into account in the classificatory scheme proposed below.

Another phylogenetic issue worth discussing here is the plesiomorphic condition of the dacetine mandible morphology. In our former Dacetini study (BARONI URBANI & DE ANDRADE 1994: 11) we contrasted a widespread belief for which elongate mandibles should be the plesiomorphic dacetine state and short mandibles the apomorphic one (BROWN & WILSON, 1959). Our conclusion was based on parsimony evidence drawn from analysis of morphological data and on the effortless consideration that any conceivable Dacetini sister-group should also have short mandibles.

BOLTON (1999: 1644) equated the two terms "long mandibulate" and "short mandibulate" already established in the literature with his "kinetic" and "static pressure mandibles". Our lack of enthusiasm for the use of these terms has been already justified at the beginning of chapter 4.1. But BOLTON (l.c.) adds: "Philip Ward (University of California) has recently added support to the Brown-Wilson hypothesis". This statement is explained by the tracing by Ward of the most parsimonious evolution of the mandibular length on Bolton's own cladogram (BOLTON, 1999: fig. 3). Irrespectively from the quality of the cladogram in question, this result is a straightforward consequence of the nature of the studied sample and wondering about the size of the ancestral mandibles, in this context, would be absurd. In fact, in a 9-taxa tree where all 8 most basal branches
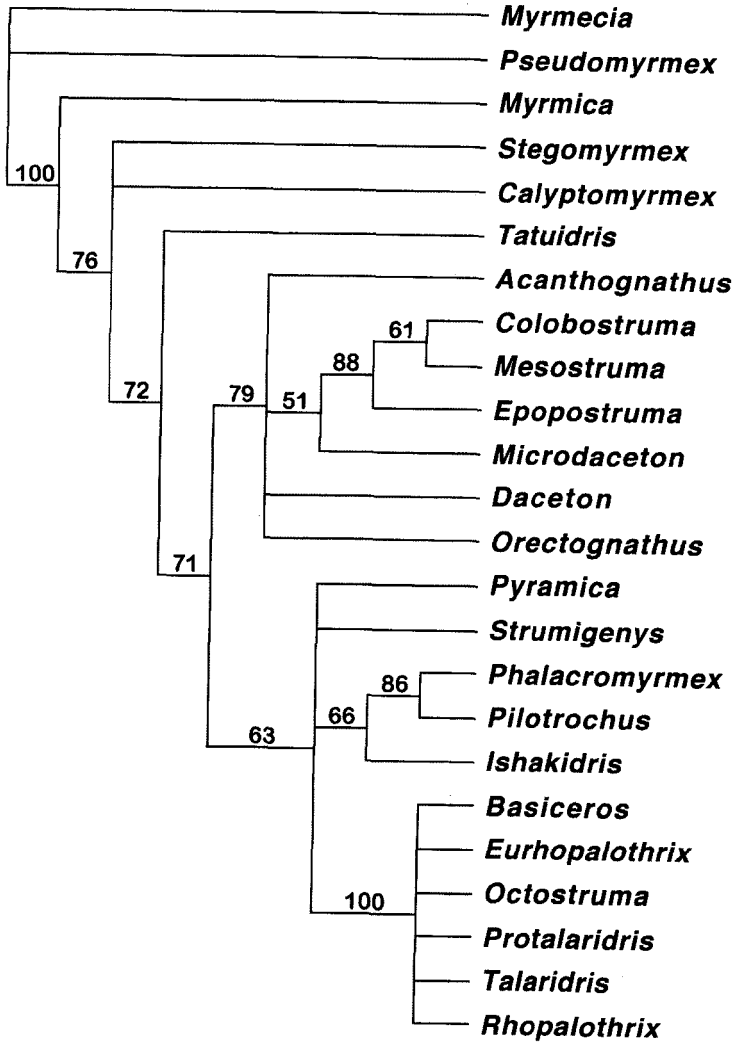
Fig. 35 - 50% Majority Rule consensus tree resulting from 100 bootstrap replicate analyses of the data of Table 1. The figures on the branches give their relative frequencies among the replicates in percent.

represent long mandibulate taxa (as is Bolton's cladogram), there is
no arithmetical possibility for the hypothetical common ancestor to
be short mandibulate. This conclusion is trivial and the sole hypo-
thetical ancestor worth speculation is not this one but an earlier one
connecting the observed long mandibulate clade to the short man-
dibulate sister clade. Dr. Ward's conclusions, in this case, are either
easily predictable and hence unimportant, or erroneous by trying to
extrapolate a deduction outside the observed variation range.

Performing again the same analysis on a broader sample of long
and short mandibulate taxa like the one considered in the present
study, confirms our former hypothesis and the common sense induc-
tion that long mandibulate Dacetini should have originated from a
short mandibulate ancestor (Fig. 36).

The information contained in the tree of Figs. 33-36 forces to
take nomenclatorial action on a number of problems, which, in hier-
archically decreasing taxonomic rank, are the following:

4.4. FAMILY-GROUP SYSTEMATICS

Tribe **Agroecomyrmecini** Carpenter

Agroecomyrmicini [sic] CARPENTER, 1930: 34. Type genus †*Agroecomyrmex* by
    inference. Tribe of Myrmicinae.
Agroecomyrmecini Carpenter, BROWN & KEMPF, 1968: 184. First correct spelling.
Agroecomyrmecinae Carpenter, BOLTON, 2003: 51. Subfamily of Formicidae.

BOLTON (1998) lists a set of 7 autapomorphies and 4 plesiomor-
phies for *Tatuidris* aimed to prove the exclusion of this genus from
his "dacetonine tribe-group". Autapomorphies, however, are cladis-
tically uninformative and plesiomorphies cannot be used to infer
phylogenetic relationships (see e. g. HENNIG, 1950; WILEY, 1980;
and MADDISON & MADDISON, 2002). Later on, BOLTON (2003: 51)
places *Tatuidris*, together with two poorly known fossil genera,
Agroecomyrmex and *Eulithomyrmex*, in a new separate subfamily,
the Agroecomyrmecinae. All the characters supposed to characterize
and separate the Agroecomyrmecinae from the Myrmicinae as given
by Bolton appear sporadically also among other Myrmicinae genera,
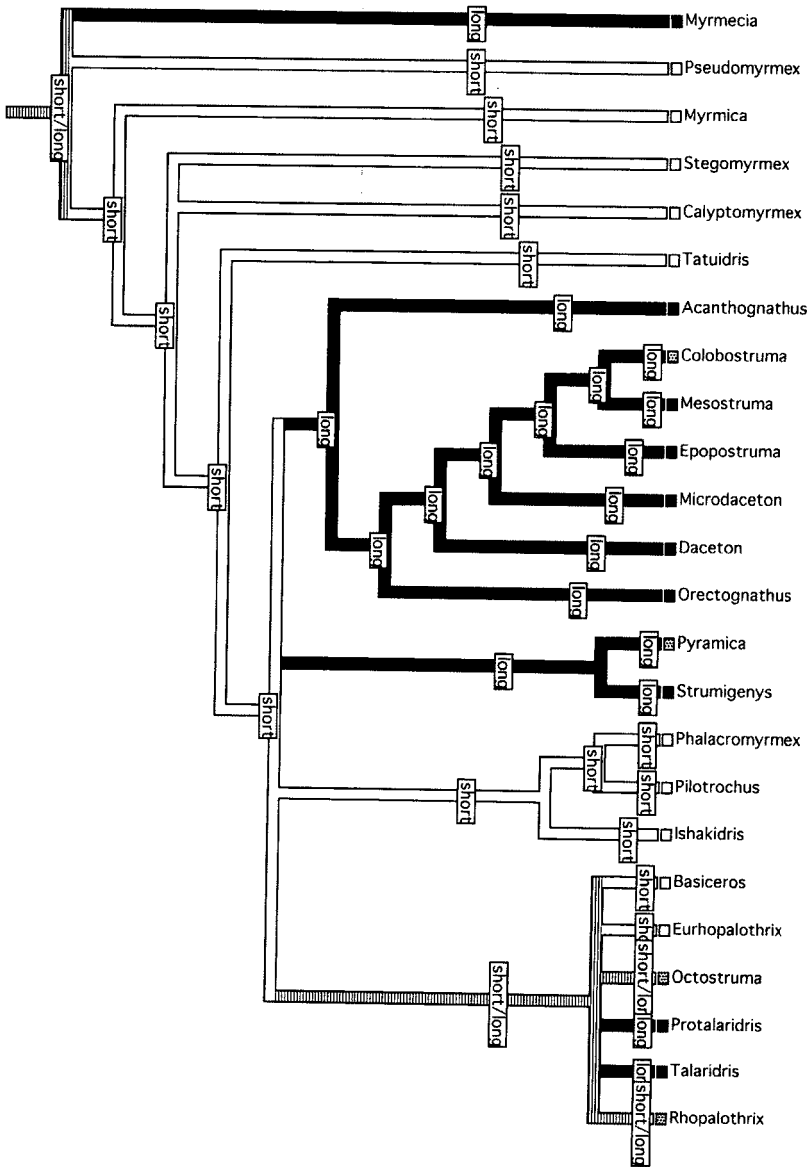though in a convergent way according to BOLTON (l. c.).

Fig. 36 - Same tree as in Figs. 33 & 34 on which the most parsimonious recon-
struction of the evolution of the size of the mandibles is traced. Graphic
display by accelerated transformation. Contrarily to a common belief sup-
ported by BOLTON (1999), long mandibulate Dacetini appear to originate
from a short mandibulate ancestor.

The following character states shared by *Tatuidris* with the other myrmicine genera considered for the present study result as plausibly synapomorphic for the whole subfamily Myrmicinae:

1. Promesonotal suture fused (from an unfused ancestor). CI 1.00, RI 1.00. All known myrmicines have a fused promesonotal suture.

2. Petiole dorsoventrally fused (from an unfused ancestor). CI 1.00, RI 1.00. All known myrmicines have a dorsoventrally fused petiole.

3. Loss or fusion of the second radial cell (from an ancestor with recognizable second radial cell). CI 1.00, RI 1.00. Among the ingroup taxa considered in the present study, only *Stegomyrmex* is polymorphic for this trait.

4. Eyes position: lateral (vs. dorsolateral). CI 0.67, RI 0.80. The ancestral position dorsolateral reappears homoplastically among some dacetine taxa.

Since all potentially valid characters tending to exclude *Tatuidris* (and, by inference, *Agroecomyrmex* and *Eulithomyrmex*) from the Myrmicinae were included in our data matrix and failed to fulfil their supposed role, we feel compelled to re-propose the following rank revival within the Myrmicinae:

Subfam. Myrmicinae: Tribus Agroecomyrmicini CARPENTER, 1930: 34. Type genus: *Agroecomyrmex*. **Tribal status revived**.

=Subfamily Agroecomyrmecinae Carpenter, BOLTON, 2003: 51 (downgraded to tribal rank in the present paper).

And the consequent subfamilial transfers

†*Agroecomyrmex* WHEELER, 1910: 265 et auctorum omnium recentiorum. Genus ad Myrmicinae. Nec *Agroecomyrmex*, genus ad Agroecomyrmicinae, BOLTON, 2003: 51. **Subfamilial transfer**.

†*Eulithomyrmex* CARPENTER, 1935: 91 et auctorum omnium recentiorum. Genus ad Myrmicinae. Nec *Eulithomyrmex*, genus ad Agroecomyrmicinae, BOLTON, 2003: 52. **Subfamilial transfer**.

Tatuidris BROWN & KEMPF, 1968: 186 et auctorum omnium recentiorum. Genus ad Myrmicinae. Nec *Tatuidris*, genus ad Agroecomyrmicinae, BOLTON, 2003: 52. **Subfamilial transfer**.

Notice that our conservative appreciation of *Tatuidris* within the Myrmicinae holds in spite of equivalent consideration of all the cladistically informative characters that, according to BOLTON (2003), should prove its exclusion.

In our phylogenetic reconstruction, there are six synapomorphies bringing *Tatuidris* within the Myrmicinae in the same cluster as all the Dacetini and excluding as less related other undoubted Myrmicinae genera like *Myrmica*, *Stegomyrmex*, and *Calyptomyrmex*. These synapomorphies are the following:

1. Mandibles at rest opposing at least in part (instead of crossing). CI 1.00, RI 1.00. This is one of the strongest dacetine synapomorphies.

2. MTI < 130 (as opposed to MTI > 150). CI 1.00, RI 1.00. This is another strong dacetine synapomorphy.

3. Reduction of the maxillary palps from 2-jointed to 1-jointed. CI 0.85, RI 0.80. The one-jointed condition should be the original dacetine morphology, though a number of dacetine genera and individual species underwent secondarily inverted evolutionary trends.

4. Reduction of the male mandibles. CI 0.75, RI 0.80. This appears to be a general dacetine trait with a few known exceptions in *Pyramica* and *Eurhopalothrix*.

5. Presence of a two-segmented antennal club. CI 0.33, RI 0.71. This appears to be a universal dacetine trait with the sole exceptions of the small genera *Microdaceton*, *Daceton*, and *Orectognathus*.

6. Reduction of the number of antennal joints from 11-12 to 9 or less. CI 0.20, RI 0.50. *Acanthognathus*, *Daceton*, *Phalacromyrmex* and *Basiceros* should represent evolutionary inversions according to our phylogenetic reconstruction, but we already wrote about the doubtful phylogenetic meaning of this character while describing it.

Our result contrasts, however, with the results of a "preliminary analysis" based on sequence data from seven nuclear genes by WARD *et al.* (2005), from a phylogenetic tree inferred from Bayesian posterior probabilities drawn from portions of five nuclear genes and one mitochondrial gene by MOREAU *et al.* (2006a), and from an analogous tree drawn from seven nuclear gene fragments by BRADY

et al. (2006a). According to these results, *Tatuidris* should belong to a clade opposed to most other known ants.

We believe that two important aspects of these results should be remembered.

The first is that assuming that molecular-drawn phylogenies are always correct or at least better than morphology based ones – as several myrmecologists seem to believe – is equivalent to the belief that all computer-drawn results must be true. BRADY *et al.* (2006b: Table 7) unfortunately omit fossil-based minimum ages for the Dacetini from their data but (2006a:1) point out correctly to "apparent conflicts between fossil, morphological, and molecular data". Actually, the main source of conflict among this triplet of factors is the molecular data. We consider as alarming the fact that genetic similarity measures contradict both, obvious morphological similarity suppositions and morphology-based parsimony measures.

Second, molecular data are radically different from morphological data by the difficulty of arguing in favour or against their results. Morphological results may appear more or less plausible according to the characters on which they are drawn, but the sole chance to discuss the validity of results obtained from molecular data is to compare them with results obtained from morphological data (the so-called congruence criterion). It is obvious that in this case there is total lack of congruence between the available molecular and morphological information. Both aspects need to be further improved.

We assume, moreover, that the differences within the most recent molecular ant phylogenetic reconstructions by BRADY (2003), OHNISHI *et al.* (2003), ASTRUC *et al.* (2004), SAUX *et al.* (2004), WARD *et al.* (2005), MOREAU *et al.* (2006a), and BRADY *et al.* (2006a), should be sufficient to impose some prudence before blindly preferring molecular to morphological results.

However interesting the *Tatuidris* molecular outcome may be, we consider it as Dr. Ward, co-author of two of the previously cited molecular analyses (WARD *et al.*, 2005; BRADY *et al.*, 2006a), considered it in a recent web document (WARD, 2005), where he writes that *Tatuidris* "are rather specialized ants, and it seems plausible to me [i. e. P. S. Ward] that their divergent evolution includes extreme modification of the myrmicine groundplan". In the analysis by MOREAU *et al.* (2006a) and BRADY *et al.* (2006a), *Tatuidris* appears

as the sister genus of *Paraponera*, a phylogenetic position difficult to digest when considering our present morphological understanding of these two genera.

This presumed strict phylogenetic relationships between *Tatuidris* and *Paraponera*, however, is based on Bayesian posterior probabilities, while maximum likelihood bootstrap (MOREAU *et al.*, 2006a) and maximum parsimony bootstrap analyses (MOREAU *et al.*, 2006a; BRADY *et al.*, 2006b) failed to support the presumed sister pair (*Tatuidris*, *Paraponera*) and any of the nodes intermediate between this pair and the basal node of Formicidae (MOREAU *et al.*, 2006b).

We wish that these results, at this stage, will be considered as a stimulating molecular challenge to our organismic knowledge of ants.

Within our data set, assignment of *Tatuidris* to a unique clade with the other dacetines is supported by 72% of the bootstrap replicates and its classification among Myrmicinae by 100% bootstrap replicates (Fig. 35), confirming in this way WARD's (2005) morphologically based intuitive hypothesis.

Our data, nonetheless, might be insufficient to take a durable decision about the monophyly or diphyly of the opposable mandibles among the Myrmicinae. Our cladogram of Fig. 33 strongly suggests a unique origin of the mandible opposability. But we are aware that to obtain a firmer certainty (supported e. g. by high bootstrap frequencies) one might need to consider all myrmicine genera and many more additional characters. Once the sister-group relationship between the dacetines and the agroecomyrmicines will be confirmed, considering them as two separate tribes or only one tribe becomes irrelevant and just a matter of taste ad a phylogenetically irrelevant issue. The poor characterization of the tribe Dacetini (q. v.) after exclusion of the Agraocomyrmecini may be considered as an argument in favour of merging the two tribes together. We maintain the two tribes separate in this paper, at least provisionally, in order to promote nomenclatorial stability.

Assuming that the characters observed in the extant *Tatuidris* can be attributed by inference to the two fossil genera *Agroecomyrmex* and *Eulithomyrmex*, the tribe Agroecomyrmecini is characterized by the two following uniquely derived characters:

Petiolar tergum and sternum in posterior view differently shaped (CI 1.00, RI 0.00).

Eyes at the posterior border of the antennal scrobe (CI 0.71, RI 0.83).

BOLTON (1998, 2003) lists other potentially autapomorphic characters not considered for the present analysis since they are parsimony uninformative but which may prove useful in further diagnosing these ants as a separate tribe.

Tribe **Dacetini** Forel

Dacetonini FOREL, 1892: 344. Type genus *Daceton* Perty, by inference. Tribe of Myrmicinae.

<Dacetonini Forel, BOLTON, 1998: 71.

Dacetonii FOREL, 1893a: 164.

Dacetii Forel, EMERY, 1895c: 770.

Dacetini Forel, EMERY, 1914: 34 & 39.

Dacetiti Brown, 1952: 10. Type genus: *Daceton* Perty, by original designation. BARONI URBANI & DE ANDRADE, 1994: 9. Junior synonym of Dacetini.

Dacetini Forel, BARONI URBANI & DE ANDRADE, 1994: 9.

<Dacetini Forel, BOLTON, 2000: 12.

Basicerotini BROWN, 1949c. Type genus *Basiceros* Schulz by inference. **Synonymy reinstated**.

Basicerotini BROWN, BARONI URBANI & DE ANDRADE, 1994: 10. Junior synonym of Dacetini.

Basicerotini Brown, BOLTON, 1998: 70. Tribe of Myrmicinae.

Arestognathiti BROWN, 1952: 10. Misspelling for Orectognathiti.

Orectognathiti BROWN, 1952: 10. Type genus: *Orectognathus* Smith, by original designation. BARONI URBANI & DE ANDRADE, 1994: 9. Junior synonym of Dacetini.

Epopostrumiti BROWN, 1952: 10. Type genus: *Epopostruma* Forel, by original designation. BARONI URBANI & DE ANDRADE, 1994: 9. Junior synonym of Dacetini.

Strumigeniti BROWN, 1952: 10. Type genus: *Strumigenys* Forel, by original designation. BARONI URBANI & DE ANDRADE, 1994: 9. Junior synonym of Dacetini.

Phalacromyrmecini WHEELER & WHEELER, 1976: 60. Unavailable name.

Phalacromyrmecini DLUSSKY & FEDOSEEVA, 1988: 80. First available name (reference to a description). Type genus *Phalacromyrmex* Kempf by inference. **Synonymy reinstated**.

Phalacromyrmecini, BARONI URBANI & DE ANDRADE, 1994: 10. Junior synonym of Dacetini.

Phalacromyrmecini, BOLTON, 1994: 106. Tribe of Myrmicinae.

Basicerotini is a junior synonym of Dacetini.

The possibility to separate from the remaining Dacetini a small set of peculiar genera corresponding to the Basicerotini was already considered and discarded by EMERY (1924: 313) who wrote:

"Un premier groupe comprend les genres à fosses antennaires placées au-dessus des yeux: *Acanthognathus*, *Microdaceton*, *Orectognathus*, *Strumigenys*, *Pentastruma*, *Epitritus* (*Acanthognathus* a la scrobe réduite à peu près de rien).

Un deuxième groupe comprend les genres *Basiceros*, *Rhopalothrix* et *Epopostruma*, qui ont la scrobe placée au dessus de l'oeil. ...

Le genre *Daceton*, bien qu'il ait l'arête frontale prolongée un peu au dessous de l'oeil, me semble se rattacher au premier groupe".

When BROWN (1949c) separated along the same line as EMERY (1924) his new tribe Basicerotini, he did not use the relative position of the antennal scrobe to define it but referred only to some differences in hair morphology. BARONI URBANI & DE ANDRADE (1994) proposed the synonymy of Basicerotini with Dacetini after showing the inconsistency of this character.

BOLTON (1998) apparently agreed with this since he abandoned all references to the hair morphology but revived the tribe Basicerotini on the base of 10 newly defined synapomorphies. One of them is the position of the antennal scrobe already described and discarded by EMERY (1924). All BOLTON's (1998) characters are either considered for the present analysis or excluded from the analysis after justification of their exclusion.

Here we propose again that the name Basicerotini should be considered as a junior synonym of Dacetini for a cladistic reason, a practical reason, and several general taxonomic reasons.

The cladistic reason is that maintaining the Basicerotini as a tribe separate from the Dacetini would render the first paraphyletic to the second or, at least to the Dacetini as they are understood by Bolton (see Fig. 32).

The practical reason is well exemplified by the case of *Rhopalothrix inopinata* de Andrade, a species originally described as a basicerotine and now transferred to the dacetine *Strumigenys* in spite of the fact that its sole clearly visible synapomorphic character is a basicerotine character (see later under the treatment of *Strumigenys*).

The general taxonomic reasons are that the homogeneity of the morphological boundaries of this hypothetical tribe result much less precise than what is commonly accepted for valid ant tribes. The following analysis of all eleven potentially synapomorphic traits of the Basicerotini should further justify our appreciation.

- Base of scape bent at right angle. CI 1.00, RI 1.00. Universal among the Basicerotini, a similar scape is known also for a few Dacetini species of the genera *Colobostruma* and *Pyramica*.
- Antennal fossa separate from the antennal scrobe. CI 1.00, RI 1.00. The separation is indistinct in the basicerotines *Eurhopalothrix bruchi* and *E. heliscata*. On the contrary the antennal fossa and scrobe are clearly separate in some *Strumigenys*, *Pyramica*, and *Colobostruma*.
- Pretergite of the first gastral segment sessile. CI 1.00, RI 1.00. Formally this character state, considered as plesiomorphic by BOLTON (1998), is the sole unequivocal synapomorphy of the Basicerotini. This prominent position in our character analysis is derived essentially from our coding of it. BOLTON (1998: 72) considered the complementary state of this same trait (i. e. pretergite neck-like) as synapomorphic for his Dacetini + Phalacromyrmecini.
- First gastral segment densely punctuated. CI 1.00, RI 1.00. There are a few *Eurhopalothrix* and *Octostruma* species with the first gastral segment smooth. On the other hand some *Stegomyrmex* and *Pyramica* species have a definitely punctuated first gastral segment.
- Hypertrophied torulus. CI 0.83, RI 0.83. A hypertrophied torulus can be found also in some scattered species of *Pyramica*, *Strumigenys*, *Mesostruma*, *Colobostruma* and *Tatuidris*.
- Labrum with transversal groove. CI 0.80, RI 0.83. This trait, universal within the Basicerotini, is found also in some *Pyramica*, *Strumigenys* and *Colobostruma* species among Dacetini s. str., and in *Stegomyrmex*.
- Male mandibles not reduced in size. CI 0.75, RI 0.80. Most (not all) known dacetine and agroecomyrmecine males underwent a reduction of the mandibles that should have secondarily re-grown among most (not all) known basicerotine males. The paucity of known males of these ants parallels the plausibility of this hypothesis.
- Postpetiolar presclerites arising from a deep concavity. CI 0.67, RI 0.86. As we already wrote in the characters' description, this same morphology is known also for some *Pyramica* species.
- Base of first gastral sternum truncate. CI 0.67, RI 0.71. Originally defined by BOLTON (1999) as synapomorphic for *Strumige-*

nys and *Pyramica*, in addition than among all basicerotines, this character state is present also in *Ishakidris, Stegomyrmex*, and in some but not all *Colobostruma, Pyramica*, and *Strumigenys* species.

- Antennal scrobe below the eyes. CI 0.60, RI 0.83. This trait, constant among basicerotines, is shared with the dacetines *Colobostruma, Mesostruma*, and *Epopostruma*.
- Articulation between gaster and postpetiole broad. CI 0.33, RI 0.66. The complementary state of this character (i. e. articulation narrow) was originally proposed by BOLTON (1998:72) as potentially synapomorphic for the Dacetini + Phalacromyrmecini. On the contrary, within the Basicerotini the articulation can be narrow in some *Basiceros* and outside them it is broad in *Tatuidris* and in some *Pyramica* and *Strumigenys*.

One should not forget that the goodness of fit of some of the above traits on the resulting phylogeny and classification as shown by high CI values is a trivial product of our coding these traits as invariant among in- and/or out-group taxa as Bolton did. As a matter of fact, exceptions to these *a priori* homogeneity (= monophyly) hypotheses are regularly described and photographically documented in our initial characters' description (chapter 4.1).

Phalacromyrmecini is a junior synonym of Dacetini.

The first to recognize similarities between the three genera included in this tribe, i. e. *Phalacromyrmex, Ishakidris*, and *Pilotrochus*, was BOLTON (1984) who wrote that there is "no advantage to adding yet another formal [i.e. tribal] name to the confusion". In this paper these genera were correctly compared with the dacetine genus *Glamyromyrmex* (= *Pyramica*). The name Phalacromyrmecini was introduced without definition or description by WHEELER & WHEELER (1976) and repeated (among others) by DLUSSKY & FEDOSEEVA (1988) who rendered the name available by referring to BOLTON's (1984) description (International Code of Zoological Nomenclature 13 (a) (ii)).

BARONI URBANI & DE ANDRADE (1994) considered the Phalacromyrmecini as a junior synonym of Dacetini. Unexpectedly, this view was immediately contrasted by BOLTON (1995) without giving

reasons for it and later by BOLTON (1998) who defined the tribe by means of three synapomorphies. In the present paper we already showed that one of them (presence of a katepisternal groove) was artificially introduced by BOLTON (1998) only to support separation of the Phalacromyrmecini. In a former paper, in fact, BOLTON (1984) uses the presence of this same character in *Ishakidris* to differentiate it from the other two genera now attributed to the Phalacromyrmecini where the groove is absent.

Other potential "Phalacromyrmecini" synapomorphies evidenced by our analysis are the following:

- Mandibles with alternating small and large teeth. CI 1.00, RI 1.00. If there is no variation of this character within the tribe (one should remember perhaps that this tribe comprises only three species classified in three different monotypic genera), mandibles with teeth alternating in size are known also in an equivalent number of *Pyramica* and *Octostruma* species (see our character description). The high CI and RI values of this character, hence, are due to our following Bolton's interpretation of it totally ignoring ascertained outgroup variability (see p. 24 for our discussion of char. # 11).

- Mesosternal hair beds visible. CI 0.91, RI 0.67. We reaffirm that the consistency of this character state within this pretended three-species tribe is due to the exiguity of species included in the tribe. The same character state is widespread among Dacetini and Basicerotini sensu BOLTON (1998) and was used also as a synapomorphy for *Strumigenys* and *Pyramica* by BOLTON (1999).

- Eyes ventral. CI 0.67, RI 0.80. Another trait shared with *Strumigenys* and *Pyramica* as well.

- Clavate scape. CI 0.50, RI 0.60. A clavate scape is known also in *Stegomyrmex*, *Calyptomyrmex*, *Tatuidris*, and some *Pyramica* species.

Each of these characters has a variability outside this three-species tribe far beyond what is normally accepted for other ant tribes.

BOLTON's (2006) additional argument in favour of retaining the Phalacromyrmecini, i.e. absence of the basimandibular process is untenable. In fact the presence of the process is supposed to be

apomorphic for the Dacetini and as BOLTON (l. c.) states, its absence among Phalacromyrmecini is "presumably plesiomorphic".

Limits and definition of the Dacetini

After merging the Basicerotini and the Phalacromyrmecini in it, the tribe Dacetini may be characterized by the following five potential synapomorphies, only the first of which, in our opinion, can be considered phylogenetically relevant.

-   Presence of "trigger hairs". CI 1.00, RI 1.00. We wrote earlier in this paper that the dacetine "trigger hairs", as used by BOLTON (1998) and in the present study may be homologous in function but they are obviously not homologous in morphology when they arise from different sclerites. Nonetheless, in spite of being widespread among Dacetini, at least a few *Colobostruma* and *Pyramica* species are deprived of such hairs. Given their rarity, these cases could be interpreted as secondary losses.

-   Labrum not capable of full reflexion. CI 0.50, RI 0.87. This character matches perfectly its scope as dacetine synapomorphy, except for its absence in *Colobostruma*, *Mesostruma* and *Epopostruma*.

-   Scape subcylindrical. CI 0.50, RI 0.60. We already discussed the phylogenetic meaning of this character for its alternative state (scape clavate) as potential synapomorphy for the Phalacromyrmecini.

-   Presence of limbus. CI 0.50, RI 0.80. Evidentiation of this character seems to be an artefact of character optimization. The limbus, in fact, is absent among several Dacetini genera although it is present only in *Stegomyrmex* outside this clade.

-   Propodeal spiracle close to propodeal declivity. CI 0.33, RI 0.60. The spiracle is at about midlength of the sclerite in *Daceton* and, among the outgroups, it is again close to the declivity in *Calyptomyrmex*.

The above synapomorphic weaknesses of the Dacetini repropose the opportunity of separating them from the Agroecomyrmecini. If, on one hand, there is no doubt that only one Dacetini tribe including the Agroecomyrmecini would automatically result much better defined and stable, we see no urgent practical reasons to take this decision immediately.

4.5. GENUS-GROUP SYSTEMATICS

In the following taxa discussion we shall report only the most recent or the most significant references and synonyms. A more exhaustive list of the older ones can be found in BARONI URBANI & DE ANDRADE (1994), BOLTON (1995) and BOLTON (2000).

All our classificatory inferences are drawn from our Fig. 33, which, we repeat, we consider essentially as an operational picture of our factual Dacetini knowledge.

The following ingroup genera, listed in alphabetical order, appear as actually or potentially taxonomically sound by possessing one or more plausible synapomorphy each:

Acanthognathus Mayr

Acanthognathus MAYR, 1887: 567. Type species *Acanthognathus ocellatus* Mayr by monotypy.

Synapomorphies resulting from our analysis:

Worker (and gyne) metapleural gland very close to propodeal spiracle. CI 0.62, RI 0.40. This trait appears also in *Epopostruma, Microdaceton, Protalaridris,* a. o. as coded also by BOLTON (1999, Table 1) for his Dacetonini.

Worker (and gyne) scape straight at base. CI 0.50, RI 0.33. The straight condition of *Acanthognathus* is shared with *Daceton.*

Worker (and gyne) antennae 11-jointed. CI 0.20, RI 0.50 for the 11-12 jointed state.

This list, however, does not evidentiate the main synapomorphy for the species of the genus, i.e. our char. #13, state 2, the basimandibular process long and apically bifurcated. The reason for this omission is a purely logical pitfall: since state #2 appears only in *Acanthognathus* and state #1 is present in all the other genera of the clade, it is impossible to ascertain whether the ancestor of the whole clade presented state #1 or #2 and hence if #2 is exclusive of *Acanthognathus* or common to *Acanthognathus* and the hypothetical ancestor of the whole clade.

The extant *Acanthognathus* species were revised and keyed by BROWN & KEMPF (1969). Afterwards BARONI URBANI & DE ANDRADE (1994) described one fossil species from Dominican amber.

Basiceros Schulz

Ceratobasis SMITH, 1860: 78. Type species *Meranoplus singularis* Smith by monotypy. Nec *Ceratobasis* Lacordaire, 1848 (Coleoptera).

Basiceros SCHULZ, 1906: 156 (replacement name for *Ceratobasis*).

Aspididris WEBER, 1950: 3. Type species *Aspididris militaris* Weber by monotypy. Synonymy by BROWN, 1974: 132.

Creightonidris BROWN, 1949c: 89. Type species *Creightonidris scambognatha* Brown by original designation. Synonymy by DIETZ, 2004: 48.

Rhopalothrix MAYR, 1870: 415. Type species *Rhopalothrix ciliata* Mayr designated by WHEELER, 1911b: 172. **New synonymy**.

Heptastruma WEBER, 1934: 54. Type species *Heptastruma wheeleri* Weber by original designation. Synonymy with *Rhopalothrix* by BROWN & KEMPF, 1960: 230. **New synonymy**.

Acanthidris WEBER, 1941: 188. Type species *Acanthidris isthmicus* Weber by original designation. Synonymy with *Rhopalothrix* by BROWN & KEMPF, 1960: 230. **New synonymy**.

Rhopalothrix subg. *Octostruma* FOREL, 1912b: 196. Type species *Rhopalothrix simoni* designated by WHEELER, 1913: 82. **New synonymy**.

Octostruma Forel, BROWN, 1948: 102.

Talaridris WEBER, 1941: 184. Type species *Talaridris mandibularis* Weber by original designation. **New synonymy**.

Eurhopalothrix BROWN & KEMPF, 1960: 202. Unavailable name without designation of type species.

Eurhopalothrix BROWN & KEMPF, 1961: 44. Type species *Rhopalothrix bolaui* Mayr by original designation. **New synonymy**.

Protalaridris BROWN, 1980: 36. Type species *Protalaridris armata* Brown by original designation. **New synonymy**.

The genus *Basiceros* may be identified and characterized by the set of synapomorphies that we already listed and discussed for the tribe Basicerotini. If tribal rank for them appears exaggerated to say the least, recognizing to these synapomorphies generic rank seems to be more plausible and satisfactory.

No explicit synapomorphy characterizes *Basiceros*. The good score of the pretergite of the first gastral segment sessile (as opposed to pedunculate) is due essentially to our coding of it. See our Fig. 27 as an example in which this character can not be detected.

Other useful but also not universally distributed characters are:

- Antennal fossa separate from the antennal scrobe. Exceptions *Basiceros* (= *Eurhopalothrix* = *Rhopalothrix*) *bruchi* and *heliscatum*. This trait is present also in other Dacetini outside the clade (species of *Strumigenys* and *Epopostruma*).

- First gastral segment densely punctuated. Exceptions *Basiceros* (= *Octostruma*) *balzani* and *onorei*. This trait is present also in some *Strumigenys*.

We are aware that even after downgrading the tribe Basicerotini to genus level, the ensuing genus *Basiceros* results more ill-defined than most other ant genera, but we regard the present proposal as the one coupling the minimum nomenclatorial change with the maximum practical utility.

All the new genus-level synonymies above flow directly either from the total lack of synapomorphies or from the implausibility of the known ones as they result in our Fig. 34. These "genera", however, are present in a number of practical keys where they are separate on the basis of the number of antennal joints. By being a meristic character, transitional forms in antennomere counts cannot be expected and this makes such counts excellent practical characters. Their poor phylogenetic value was already stressed explicitly or implicitly by BOLTON (1999), DIETZ (2004) and ourselves (present paper) by coding their 8-steps variability in a reduced binary form only.

Further evidence for the generic synonymies proposed above results from the following critical summary of all known but insufficient synapomorphies on which these generic names were based:

Rhopalothrix: loss of the anal vein. CI 0.75, RI 0.50. Besides the reduced number of known wing venations in the whole tribe, the anal vein is missing also in some *Eurhopalothrix*, *Strumigenys*, and *Acanthognathus*.

Octostruma: no synapomorphies for this genus result from our data.

Talaridris: reduction of the number of labial palps from two to one CI 0.70, RI 0.67. One-jointed labial palps are known, among others, also in *Strumigenys*, *Acanthoghathus*, *Basiceros*, *Eurhopalothrix* and *Octostruma*. The apomorphic condition attributed to *Talaridris* is a consequence of the fact that one-jointed palps are a secondary reduction from 2 jointed, the state assigned to the ancestor of the whole clade.

Eurhopalothrix: loss of the pterostigma. CI 1.00, RI 0.00. This is a potentially excellent character discovered by DIETZ (2004). Note that DIETZ (l. c.) was able to study the males of 7 *Eurhopalothrix*

out of a total of 39 known species and that he examined gynes of 29 species, although it is not specified if these were all winged or not. DIETZ (2004: 34) adds also presence of a second row of mandibular teeth [among gynes] as apomorphic for *Eurhopalothrix* but the gyne of *Basiceros papuanus* n. sp. (a species with 7 antennal joints - as *Eurhopalothrix* should be - to be described later in the present paper) has no trace of the second row of teeth. Assuming that *Eurhopalothrix* could be separate from the other genera discussed here on the basis of the lack of pterostigma, *Basiceros* would result paraphyletic to it.

Protalaridris: metapleural gland bulla close to the annulus. CI 0.62, RI 0.40. This same character state re-appears in some *Eurhopalothrix*, *Octostruma* and in a number of other, less related Dacetini.

The generic synonymies above imply the following new combinations:

Note: The name *Basiceros* is composed of the two Greek words "βάσις" (=basis, foot), feminine, and "κέρας" (=horn), neuter. It is hence a neuter noun and established species names like *singularis* or *militaris* must be changed to *singulare* and *militare*.

Basiceros acutipilis (Kempf). **New combination** for *Rhopalothrix acutipilis* KEMPF, 1962: 28.

Basiceros allopeciosum (Brown & Kempf). **New combination** for *Eurhopalothrix allopeciosa* BROWN & KEMPF, 1960: 206.

Basiceros apharogonium (Snelling). **New combination** for *Eurhopalothrix apharogonia* SNELLING, 1968: 1.

Basiceros armatum (Brown). **New combination** for *Protalaridris armata* BROWN, 1980: 37.

Basiceros australe (Brown & Kempf). **New combination** for *Eurhopalothrix australis* BROWN & KEMPF, 1960: 218.

Basiceros balzani (Emery). **New combination** for *Rhopalothrix balzani* EMERY, 1894: 217 and *Octostruma balzani* (Emery), BROWN, 1949c: 92.

Basiceros batesi (Emery). **New combination** for *Rhopalothrix batesi* EMERY, 1894: 218 and *Octostruma batesi* (Emery), BROWN, 1949c: 92.

Basiceros betschi (Perrrault). **New combination** for *Octostruma betschi* PERRAULT, 1988: 303.

Basiceros biroi (Szabó). **New combination** for *Rhopalothrix biroi* SZABÓ, 1910: 365 and *Eurhopalothrix biroi* (Szabó), BROWN & KEMPF, 1960: 222.

Basiceros bolaui (Mayr). **New combination** for *Rhopalothrix bolaui* MAYR, 1870: 415 and *Eurhopalothrix bolaui* (Mayr), BROWN & KEMPF, 1960: 210.

Basiceros brevicorne (Emery). **New combination** for *Rhopalothrix brevicornis* EMERY, 1897: 572 and *Eurhopalothrix brevicornis* (Emery), BROWN & KEMPF, 1960: 215.

Basiceros browni (Taylor). **New combination** for *Eurhopalothrix browni* TAYLOR, 1990: 404.

Basiceros bruchi (Santschi). **New combination** for *Rhopalothrix bruchi* SANTSCHI, 1922: 256 and *Eurhopalothrix bruchi* (Santschi), BROWN & KEMPF, 1960: 214.

Basiceros caledonicum (Brown & Kempf). **New combination** for *Eurhopalothrix caledonica* BROWN & KEMPF, 1960: 220.

Basiceros chapmani (Taylor). **New combination** for *Eurhopalothrix chapmani* TAYLOR, 1990: 406.

Basiceros ciliatum (Mayr). **New combination** for *Rhopalothrix ciliata* MAYR, 1870: 415.

Basiceros cinnameum (Taylor). **New combination** for *Eurhopalothrix cinnamea* TAYLOR, 1970: 50.

Basiceros clypeatum (Brown & Kempf). **New combination** for *Eurhopalothrix clypeata* BROWN & KEMPF, 1960: 205.

Basiceros coronatum (Taylor). **New combination** for *Eurhopalothrix coronata* TAYLOR, 1990: 407.

Basiceros depressum (Ketterl *et al.*). **New combination** for *Eurhopalothrix depressa* KETTERL *et al.*, 2004: 45.

Basiceros diadema (Brown & Kempf). **New combination** for *Rhopalothrix diadema* BROWN & KEMPF, 1960: 239.

Basiceros dubium (Taylor). **New combination** for *Eurhopalothrix dubia* TAYLOR, 1990: 409.

Basiceros emeryi (Forel). **New combination** for *Rhopalothrix emeryi* FOREL, 1912a: 58 and *Eurhopalothrix emeryi* (Forel), BROWN & KEMPF, 1960: 230.

Basiceros floridanum (Brown & Kempf). **New combination** for *Eurhopalothrix floridana* BROWN & KEMPF, 1960: 207.

Basiceros grave (Mann). **New combination** for *Rhopalothrix gravis* MANN, 1922: 40 and *Eurhopalothrix gravis* (Mann), BROWN & KEMPF, 1960: 211.

Basiceros greensladei (Taylor). **New combination** for *Eurhopalothrix greensladei* TAYLOR, 1968a: 342.

Basiceros heliscatum (Wilson & Brown). **New combination** for *Eurhopalothrix heliscata* WILSON & BROWN, 1985: 410.

Basiceros hoplites (Taylor). **New combination** for *Eurhopalothrix hoplites* TAYLOR, 1980b: 231.

Basiceros iheringi (Emery). **New combination** for *Rhopalothrix Iheringi* EMERY, 1888: 361 and *Octostruma iheringi* (Emery), BROWN, 1949c: 92.

Basiceros impressum (Palacio). **New combination** for *Octostruma impressa* PALACIO, 1997: 411.

Basiceros inca (Brown & Kempf). **New combination** for *Octostruma inca* BROWN & KEMPF, 1960: 185.

Basiceros insidiator (Taylor). **New combination** for *Eurhopalothrix insidiatrix* TAYLOR, 1980b: 238.

Basiceros isabellae (Mann). **New combination** for *Rhopalothrix isabellae* MANN, 1919: 357 and *Eurhopalothrix isabellae* (Mann), BROWN & KEMPF, 1960: 225.

Basiceros isthmicum (Weber). **New combination** for *Acanthidris isthmicus* WEBER, 1941: 188.

Basiceros jennya (Taylor). **New combination** for *Eurhopalothrix jennya* TAYLOR, 1990: 413.

Basiceros kusnezovi (Brown & Kempf). **New combination** for *Rhopalothrix kusnezovi* BROWN & KEMPF, 1960: 238.

Basiceros lenkoi (Kempf). **New combination** for *Eurhopalothrix lenkoi* KEMPF, 1967: 358.

Basiceros omnivagum (Taylor). **New combination** for *Eurhopalothrix omnivaga* TAYLOR, 1990: 413.

Basiceros orbis (Taylor). **New combination** for *Rhopalothrix orbis* TAYLOR, 1968a: 336.

Basiceros mandibulare (Weber). **New combination** for *Talaridris mandibularis* WEBER, 1941: 185.

Basiceros petiolatum (Mayr). **New combination** for *Rhopalothrix petiolata* MAYR, 1887: 580 and *Octostruma petiolata* (Mayr), BROWN, 1949c: 92.

Basiceros philippinum (Brown & Kempf). **New combination** for *Eurhopalothrix philippina* BROWN & KEMPF, 1960: 224.

Basiceros piluliferum (Brown & Kempf). **New combination** for *Eurhopalothrix pilulifera* BROWN & KEMPF, 1960: 208.

Basiceros platisquama (Taylor). **New combination** for *Eurhopalothrix platisquama* TAYLOR, 1990: 417.

Basiceros plaumanni (Brown & Kempf). **New combination** for *Rhopalothrix plaumanni* BROWN & KEMPF, 1960: 235.

Basiceros procerum (Emery). **New combination** for *Rhopalothrix procera* EMERY, 1897: 572 and *Eurhopalothrix procera* (Emery), BROWN & KEMPF, 1960: 225.

Basiceros punctatum (Szabó). **New combination** for *Rhopalothrix punctata* SZABÓ, 1910: 366 and *Eurhopalothrix punctata* (Szabó), BROWN & KEMPF, 1960: 221.

Basiceros rothschildi (Taylor). **New combination** for *Eurhopalothrix rothschildi* TAYLOR, 1990: 418.

Basiceros rugiferum (Mayr). **New combination** for *Rhopalothrix rugifer* MAYR, 1887: 579 and *Octostruma rugifera* (Mayr), BROWN, 1949c: 92.

Basiceros rugiferoide (Brown & Kempf). **New combination** for *Octostruma rugiferoides* BROWN & KEMPF, 1960: 200.

Basiceros seguense (Taylor). **New combination** for *Eurhopalothrix seguensis* TAYLOR, 1990: 421.

Basiceros simoni (Emery). **New combination** for *Rhopalothrix simoni* EMERY, 1890: 67 and *Octostruma simoni* (Emery), BROWN, 1949c: 92. Junior synonym of *Octostruma iheringi* Emery, BROWN & KEMPF, 1960: 187. *Octostruma simoni* (Emery), DIETZ, 2004: 127.

Basiceros speciosum (Brown & Kempf). **New combination** for *Eurhopalothrix speciosa* BROWN & KEMPF, 1960: 203.

Basiceros spectabile (Kempf). **New combination** for *Eurhopalothrix spectabilis* KEMPF, 1962: 27.

Basiceros stannardi (Brown & Kempf). **New combination** for *Rhopalothrix stannardi* BROWN & KEMPF, 1960: 236.

Basiceros stenognathum (Brown & Kempf). **New combination** for *Octostruma stenognatha* BROWN & KEMPF, 1960: 196.

Basiceros stenoscapum (Palacio). **New combination** for *Octostruma stenoscapa* PALACIO, 1997: 414.

Basiceros szentivanyi (Taylor). **New combination** for *Eurhopalothrix szentivanyi* TAYLOR, 1968a: 346.

Basiceros weberi (Brown & Kempf). **New combination** for *Rhopalothrix weberi* BROWN & KEMPF, 1960: 234.

Basiceros wheeleri (Mann). **New combination** for *Rhopalothrix wheeleri* MANN, 1922: 43. *Octostruma wheeleri* (Mann), BROWN, 1949c: 92.

The known species of *Basiceros* have been recently keyed and redescribed by DIETZ (2004) under the name of their new generic synonyms proposed above.

Daceton Perty

Daceton PERTY, 1833: 136. Type species *Formica armigera* Latreille, by monotypy.

Autapomorphies for this monotypic genus included in our data matrix are the following:

Worker (and gyne) *foramen occipitale* dorsal, CI 1.00, RI 0.00.

Worker (and gyne) scape straight at base. CI 0.50, RI 0.33. The straight condition of *Daceton* is shared with *Acanthognathus*.

Worker (and gyne) orifice of the metapleural gland visible. CI 0.33, RI 0.50. The visible condition of *Daceton* appears to be unique among the Dacetini. The low CI and RI values are due to variation among the outgroups.

Worker (and gyne) propodeal spiracle median (instead of posterior). CI 0.33, RI 0.60. The median location of *Daceton* appears to be unique among the Dacetini. The low CI and RI values are due to variation among the outgroups.

Worker (and gyne) antennae 11-jointed. CI 0.20, RI 0.50 for the 11-12 jointed state.

The above apomorphy list is largely sufficient to regard *Daceton* as a separate genus.

The genus contains only one known species, *D. armigerum* (Latreille).

Epopostruma Forel

Strumigenys subg. *Epopostruma* FOREL, 1895: 422. Type species *Strumigenys (Epopostruma) quadrispinosa* Forel, designated by WHEELER, 1911b: 163.

Epopostruma Forel, EMERY, 1897: 573. Raised to genus.

Hexadaceton BROWN, 1948: 120. Type species *Hexadaceton frosti* Brown, by original designation. Synonymy by BROWN, 1973b.

Colobostruma WHEELER, 1927: 32 (subgenus ad *Epopostruma*). Type species *Epopostruma leae* Wheeler by monotypy. **New synonymy**.

Colobostruma BROWN, 1948: 118. Raised to genus.

Alistruma BROWN, 1948: 117. Type species *Epopostruma foliacea* Emery, by original designation. Synonymy with *Colobostruma* by BROWN, 1959. **New synonymy**.

Clarkistruma BROWN, 1948: 124. Type species *Epopostruma alinodis* Forel, by original designation. Synonymy with *Colobostruma* by BROWN, 1959. **New synonymy**.

Mesostruma BROWN, 1948: 18. Type species *Strumigenys turneri* Forel, by original designation. Synonymy with *Colobostruma* by BARONI URBANI & DE ANDRADE, 1994: 15; revived from synonymy BOLTON, 1999: 1680. **New synonymy**.

Our search was unable to point out at synapomorphies for this genus in its narrow sense, as it was understood in the most recent papers. Neither synapomorphies described in the literature nor emerged in this study as a result of character optimization result from our search. BOLTON (1999: 1681) gives the following two

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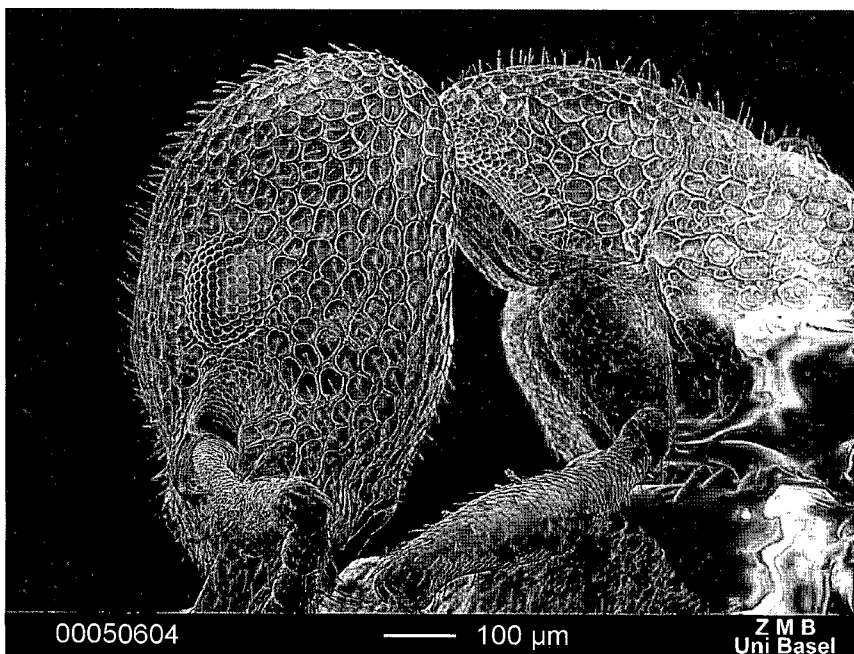   Uni Basel

Fig. 37 - *Epopostruma quadrispinosa* (Forel), worker without preocular groove. Presence of the groove is given as synapomorphic for *Epopostruma* in BOLTON (1999).

generic synapomorphies: presence of the labral concavity and of a vertical preocular groove. We previously pointed out that the labral concavity was given by BOLTON (1999:1681) as synapomorphic for *Epopostruma* and by BOLTON (1998:72) for all the Dacetini (see the introduction). Moreover, the labral concavity of some *Epopostruma* is very similar to the one of *Mesostruma* (Fig. 30). On the other hand, the *Epopostruma*'s vertical preocular groove is well visible only in some *Epopostruma* species illustrated by Shattuck's photographs (in BOLTON, 2000) but much less or not at all in others (see also our Fig. 37).

Without clear synapomorphies distinguishing it, *Epopostruma* is destined to remain in the literature as the oldest available generic name of a small clade with *Colobostruma* and *Mesostruma* as junior synonyms as already suggested by BARONI URBANI & DE ANDRADE (1994).

According to BOLTON (1999: 1680) *Mesostruma* (with 8 Australian species) should differ from *Colobostruma* (with 16 Australian species) for only one synapomorphy: "Mandibles elongate triangular, with a larger apical and smaller preapical tooth; proximal of this the margin is edentate and lamellate". Elongate triangular mandibles are present also in *Colobostruma cerornata* Brown (BOLTON, 2000, page 39 [description] and Fig. 38 [figure]) and in *C. froggatti* (Forel) (Fig. 38). The dentition of the mandibles is identical at least in *Colobostruma sisypha* Shattuck (SHATTUCK in BOLTON (2000, Fig. 39)) and *Mesostruma eccentrica* Taylor (SHATTUCK in BOLTON (2000, Fig. 52)). (BOLTON (1999: 1679) lists five synapomorphies for *Colobostruma* as a genus different from *Mesostruma*. These, of course, loose their meaning after demonstrating the paraphyly of the second versus the first. Both generic names together (i.e. *Colobostruma* and *Mesostruma*) are characterized by an excellent synapomorphy (hypertrophied labium) but are in their turn paraphyletic to the oldest available name for the whole clade: *Epopostruma* for which there are no known convincing synapomorphies.

The following four synapomorphies resulting from our data for the broader *Epopostruma* (i.e. including also *Colobostruma* and *Mesostruma*) are all the product of character optimization; three of them are character-states found also in an ancestor and hence representing an evolutionary reversal:
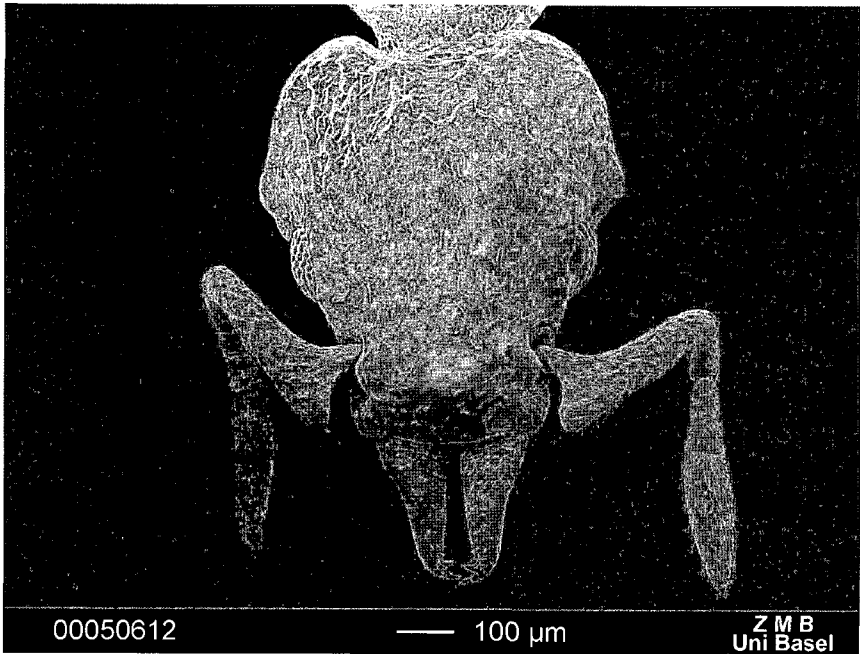
Fig. 38 - *Colobostruma froggatti* (Forel) showing elongate mandibles, a supposed apomorphy for the genus *Mesostruma* according to BOLTON (1999).

Worker (and gyne) antennal scrobe below the eyes. CI 0.71, RI 0.83. This trait, according to our phylogenetic reconstruction, should have been secondarily lost in some *Epopostruma* species actually included in *Colobostruma* and re-appears homoplastically among all basicerotine genera. We consider this pretended secondary loss as plausibly due to head flattening in some species and as a result the most significant synapomorphy for the genus.

Worker (and gyne) labrum capable of full reflexion. CI 0.50, RI 0.87. All remainder dacetine genera have a labium incapable of full reflexion. The low CI and RI values are due to variability among the outgroups. The validity of this character is further weakened by the fact that the capability of full reflexion is widespread among ants and its presumed apomorphic value, in this case, would require a tertiary re-gain of this property.

Worker (and gyne) labrum not T-shaped. CI 0.50, RI 0.33.

This is a widespread dacetine character absent among three immediate *Epopostruma* outgroup genera.

Worker (and gyne) 2-segmented antennal club. CI 0.33, RI 0.71. All remainder dacetine genera have a 2-segmented antennal club. The low-CI and RI values are due to variability among the outgroups.

The species previously included in *Epopostruma*, *Colobostruma*, and *Mesostruma* are keyed and described under these three generic names by SHATTUCK (in BOLTON, 2000).

Our synonymies imply the following new or reaffirmed generic transfers:

Epopostruma alinodis FOREL, 1913. *Clarkistruma alinodis* (Forel), BROWN, 1948: 124. *Colobostruma alinodis* (Forel) BROWN & WILSON, 1959: 281. **Combination in Epopostruma reinstated**.

Epopostruma australis (Brown). **New combination** for *Colobostruma australis* BROWN, 1959: 4.

Epopostruma bella (Shattuck). **New combination** for *Mesostruma bella* SHATTUCK in BOLTON, 2000: 48.

Epopostruma biconcava (Shattuck). **New combination** for *Colobostruma biconcava* SHATTUCK in BOLTON, 2000: 35.

Epopostruma biconvexa (Shattuck). **New combination** for *Colobostruma biconvexa* SHATTUCK in BOLTON, 2000: 35.

Epopostruma bicornis (Shattuck). **New combination** for *Colobostruma bicorna* (sic) SHATTUCK in BOLTON, 2000: 45. Note: the Latin word *cornu* is a neuter noun and cannot be declined in the feminine form. The feminine adjective for two-horned is *bicornis* (Horatius, Vergilius).

Epopostruma browni (Taylor). **New combination** for *Mesostruma browni* TAYLOR, 1962: 1.

Epopostruma cerornata (Brown). **New combination** for *Colobostruma cerornata* BROWN, 1959: 1.

Epopostruma eccentrica (Taylor). **New combination** for *Mesostruma eccentrica* TAYLOR, 1973: 31.

Epopostruma elliotti (Clark). **New combination** for *Epitritus elliotti* CLARK, 1928: 42, and *Clarkistruma elliotti* (Clark), BROWN, 1948: 124, and *Colobostruma elliotti* (Clark), TAYLOR & BROWN, 1985: 60.

Epopostruma foliacea Emery, 1897. *Alistruma foliacea* (Emery), BROWN, 1948: 117. *Colobostruma foliacea* (Emery) BOLTON, 1995: 146. **Combination in Epopostruma reinstated**.

Epopostruma froggatti Forel, 1913. *Alistruma froggatti* (Forel), BROWN, 1948: 117. *Colobostruma froggatti* (Forel) TAYLOR & BROWN, 1985: 60. **Combination in Epopostruma reinstated**.

Epopostruma inornata (Shattuck). **New combination** for *Mesostruma inornata* SHATTUCK in BOLTON, 2000: 51.

Epopostruma lacuna (Shattuck). **New combination** for *Colobostruma lacuna* SHATTUCK in BOLTON, 2000: 36.

Epopostruma laevigata (Brown). **New combination** for *Mesostruma laevigata* BROWN, 1952: 12

Epopostruma leae Wheeler. *Colobostruma leae* (Wheeler), BROWN, 1948: 118. **Combination in *Epopostruma* reinstated**.

Epopostruma loweryi (Taylor). **New combination** for *Mesostruma loweryi* TAYLOR, 1973: 35.

Epopostruma mellea (Shattuck). **New combination** for *Colobostruma mellea* SHATTUCK in BOLTON, 2000: 37.

Epopostruma nancyae (Brown). **New combination** for *Colobostruma nancyae* BROWN, 1965b: 22.

Epopostruma papulata (Brown). **New combination** for *Colobostruma papulata* BROWN, 1965a: 21.

Epopostruma sisypha (Shattuck). **New combination** for *Colobostruma sisypha* SHATTUCK in BOLTON, 2000: 37.

Epopostruma turneri (Forel). *Strumigenys* (*Epopostruma*) *turneri* FOREL, 1895: 424. *Epopostruma turneri* (Forel), EMERY, 1924: 330. *Mesostruma turneri* (Forel), BROWN, 1948: 119. **Combination in *Epopostruma* reinstated**.

Epopostruma unicornis (Shattuck). **New combination** for *Colobostruma unicorna* (sic) SHATTUCK in BOLTON, 2000: 46. Note: the Latin word *cornu* is a neuter noun and cannot be declined in the feminine form. The feminine adjective for single horned is *unicornis* (Plinius, Tertullianus).

Ishakidris Bolton

Ishakidris BOLTON, 1984: 374. Type species *Ishakidris ascitaspis* Bolton, by original designation.

The two genus-level apomorphies resulting for this genus are:

Worker (and gyne?) with visible katepisternal groove (CI 1.00, RI 0.00).

Worker (and gyne?) with first gastral sternum truncated at base (CI 0.67, RI 0.71). This latter character, already considered as synapomorphic for *Basiceros*, is widespread in *Strumigenys* and irregularly present also among other outgroups.

The pretended generic apomorphies above are likely to be a by-product of the clustering together of the three "Phalacromyrmecini" genera, a clustering that we already showed as being based on weak characters (see the discussion under the synonymy of the tribe Phalacromyrmecini). We suspect that all the former Phalacromyrmecini genera might be better understood as atypical *Strumigenys* species.

Microdaceton Santschi

Microdaceton SANTSCHI, 1913b: 478. Type species *Microdaceton exornatum* Santschi, by monotypy.

The following characters result apomorphic for this genus:

Worker (and gyne) pronotal cervix with thick transverse rim. CI 1.00, RI 0.00.

Worker (and gyne) maxillary palps three-jointed. CI 0,85, RI 0.80. Among the Dacetini the three-jointed condition is known only in *Phalacromyrmex* and *Pilotrochus*.

Worker (and gyne) labial palps two-jointed. CI 0.70, RI 0.67. Among the Dacetini the two-jointed condition is known in *Phalacromyrmex*, *Pilotrochus*, *Ishakidris* and some *Basiceros* species.

Other plausible generic synapomorphies not included in our data matrix are listed by BOLTON (1999: 1675).

The four *Microdaceton* species known so far are keyed and described by BOLTON (2000)

Orectognathus Smith

Orectognathus SMITH, 1853: 227. Type species *Orectognathus antennatus* Smith, by monotypy.

Only one, convincing, synapomorphy is known for this genus: the hypertrophy of the second funicular joint of workers and gynes (CI 1.00, RI 0.00).

The known species of this genus have been keyed and described by TAYLOR (1980a).

Phalacromyrmex Kempf

Phalacromyrmex KEMPF, 1960a: 89. Type species *Phalacromyrmex fugax* Kempf, by original designation.

Only one unequivocal synapomorphy for this genus results from our data, the presence of mesopleural costulation. CI 1.00, RI 0.00.

We doubt, however the generic rank of this character. Other apomorphic characters resulting from our analysis are:

Worker (and gyne?) presence of a cuticular process of the mesonotum. CI 0.86, RI 0.75. Cuticular projections of the mesonotum are known also in *Epopostruma* and *Strumigenys*.

Worker (and gyne?) metapleaural gland bulla close to the annulus. CI 0.62, RI 0.40. The same character state is encountered in a number of non-related Dacetini genera like *Protalaridris*, *Microdaceton*, *Epopostruma*, a. o.

Worker (and gyne?) antennae 11-jointed. CI 0.20, RI 0.50. A character state shared with several outgroups and with *Daceton* and *Acanthognathus*.

The pretended generic apomorphies above are likely to be a by-product of the clustering together of the three "Phalacromyrmecini" genera, a clustering that we already showed as being based on weak characters (see the discussion under the synonymy of the tribe Phalacromyrmecini). We suspect that all the former Phalacromyrmecini genera might be better understood as atypical *Strumigenys* species.

Pilotrochus Brown

Pilotrochus Brown, 1978: 218. Type species *Pilotrochus besmerus* Brown, by original designation.

The sole known apomorphy for this genus is the hypertrophic development of the mesosternal hair beds, visible on the profile, CI 1.00, RI 0.00. Mesosternal hair beds are widespread in ants. Whether the hypertrophic development visible in *Pilotrochus* should be considered as a genus-level apomorphy or not may be debated. This doubt, together with the clustering of the three "Phalacromyrmecini" genera that we already showed as being based on doubtful characters (see the discussion under the synonymy of the tribe Phalacromyrmecini) weakens considerably the credibility of *Pilotrochus* as a valid monotypic genus. We suspect that all the former Phalacromyrmecini genera might be better understood as atypical *Strumigenys* species.

Strumigenys Smith

Strumigenys SMITH, 1860: 72. Type species *Strumigenys mandibularis* Smith, by monotypy.

Labidogenys ROGER, 1862: 249. Type species *Labidogenys lyroessa* Roger by monotypy. *Labidogenys* Roger as a synonym of *Strumigenys*, ROGER, 1863b: 40.

Pyramica ROGER, 1862: 251. Type species *Pyramica gundlachi* Roger by monotypy. *Pyramica* Roger as a synonym of *Strumigenys*, ROGER, 1863b: 40. *Pyramica* Roger, revived from synonymy, BOLTON, 1999: 1667. **Synonymy with *Strumigenys* reinstated**.

Cephaloxys SMITH, 1865: 76. Type species *Cephaloxys capitata* Smith by monotypy. Junior homonym of *Cephaloxys* Signoret, 1847 (Hemiptera). Replacement name *Smithistruma* BROWN, 1948: 104.

Epitritus EMERY 1869a: 136. Type species *Epitritus argiolus* Emery by monotypy. *Epitritus* Emery as a synonym of *Strumigenys*, BARONI URBANI & DE ANDRADE, 1994: 32. *Epitritus* Emery revived from synonymy, BOLTON, 1995: 188. *Epitritus* Emery as a synonym of *Pyramica*, BOLTON, 1999: 1667. **Synonymy with *Strumigenys* reinstated**.

Trichoscapa EMERY, 1869b: 24 (subgenus ad *Strumigenys*). Type species *Strumigenys membranifera* Emery by monotypy. *Trichoscapa* Emery as a synonym of *Strumigenys*, DALLA TORRE (1893: 145). *Trichoscapa* Emery as a synonym of *Cephaloxys*, WHEELER (1922: 668). *Trichoscapa* Emery as a good genus, BROWN, 1948: 112. *Trichoscapa* as a synonym of *Strumigenys*, BARONI URBANI & DE ANDRADE, 1994: 32. *Trichoscapa* Emery revived from synonymy, BOLTON, 1995: 421. *Trichoscapa* Emery as a synonym of *Pyramica*, BOLTON, 1999: 1667. **Synonymy with *Strumigenys* reinstated**.

Pentastruma FOREL, 1912a: 50. Type species *Pentastruma sauteri* Forel by monotypy. *Pentastruma* Forel as a synonym of *Strumigenys*, BARONI URBANI & DE ANDRADE, 1994: 32. *Pentastruma* Forel revived from synonymy, BOLTON, 1995: 316. *Pentastruma* Forel as a synonym of *Pyramica*, BOLTON, 1999: 1667. **Synonymy with *Strumigenys* reinstated**.

Glamyromyrmex WHEELER, 1915b: 487. Type species *Glamyromyrmex beebei* Wheeler by monotypy. *Glamyromyrmex* Wheeler as a synonym of *Strumigenys*, BARONI URBANI & DE ANDRADE, 1994: 32. *Glamyromyrmex* Wheeler revived from synonymy, BOLTON, 1995: 207. *Glamyromyrmex* Wheeler as a synonym of *Pyramica*, BOLTON, 1999: 1667. **Synonymy with *Strumigenys* reinstated**.

Codiomyrmex WHEELER, 1916: 326. Type species *Codiomyrmex thaxteri* Wheeler by monotypy. *Codiomyrmex* Wheeler as a synonym of *Strumigenys*, BARONI URBANI & DE ANDRADE, 1994: 32. *Codiomyrmex* Wheeler revived from synonymy, BOLTON, 1995: 146. *Codiomyrmex* Wheeler as a synonym of *Pyramica*, BOLTON, 1999: 1668. **Synonymy with *Strumigenys* reinstated**.

Tingimyrmex MANN, 1926: 104 (subgenus ad *Strumigenys*). Type species *Strumigenys mirabilis* Mann by monotypy. *Tingimyrmex* Mann as a good genus, BROWN, 1948: 111. *Tingimyrmex* Mann as a synonym of *Strumigenys*, BARONI URBANI & DE ANDRADE, 1994: 32. *Tingimyrmex* Mann revived from synonymy, BOLTON, 1995: 420. *Tingimyrmex* Mann as a synonym of *Pyramica*, BOLTON, 1999: 1668. **Synonymy with *Strumigenys* reinstated**.

Codioxenus SANTSCHI, 1931: 278 (subgenus ad *Epitritus*). Type species *Epitritus simulans* Santschi by monotypy. *Codioxenus* Santschi as a good genus, BROWN, 1948: 123. *Codioxenus* Santschi as a synonym of *Strumigenys*, BARONI URBANI &

DE ANDRADE, 1994: 32. *Codioxenus* Santschi revived from synonymy, BOLTON, 1995: 146. *Codioxenus* Santschi as a synonym of *Pyramica*, BOLTON, 1999: 1668. **Synonymy with *Strumigenys* reinstated**.

Proscopomyrmex PATRIZI, 1946: 294. Type species *Proscopomyrmex londianensis* Patrizi by monotypy. *Proscopomyrmex* Patrizi as a synonym of *Strumigenys*, BROWN, 1949b: 15.

Eneria DONISTHORPE, 1948: 598. Type species *Eneria excisa* Donisthorpe by original designation. *Eneria* Donisthorpe as a synonym of *Strumigenys*, BROWN, 1949b: 15.

Smithistruma BROWN, 1948: 104. Type species *Cephaloxys capitata* Smith. Nomen novum pro *Cephaloxys* Smith 1865 nec *Cephaloxys* Signoret 1847. *Smithistruma* Brown as a synonym of *Strumigenys*, BARONI URBANI & DE ANDRADE, 1994: 32. *Smithistruma* Brown revived from synonymy, BOLTON, 1995: 383. *Smithistruma* Brown as a synonym of *Pyramica*, BOLTON, 1999: 1668. **Synonymy with *Strumigenys* reinstated**.

Weberistruma BROWN, 1948: 106 (subgenus ad *Smithistruma*). Type species *Strumigenys leptothrix* Wheeler by original designation. Raised to genus by BROWN, 1949b. *Weberistruma* Brown as a synonym of *Smithistruma*, BROWN, 1973a: 35. *Weberistruma* as a synonym of *Pyramica*, BOLTON, 1999: 1668. Undoubted synonym of a synonym of *Strumigenys* supported in this paper. **New synonymy**.

Wessonistruma BROWN, 1948: 106 (subgenus ad *Smithistruma*). Type species *Strumigenys pergandei* Emery by original designation. *Wessonistruma* Brown as a synonym of *Smithistruma*, BROWN, 1973a: 35. *Wessonistruma* as a synonym of *Pyramica*, BOLTON, 1999: 1668. Undoubted synonym of a synonym of *Strumigenys* supported in this paper. **New synonymy**

Serrastruma BROWN, 1948: 107 (subgenus ad *Smithistruma*). Type species *Strumigenys simoni* Emery by original designation. *Serrastruma* Brown as a good genus, BROWN, 1949b: 6. *Serrastruma* Brown as a synonym of *Strumigenys*, BARONI URBANI & DE ANDRADE, 1994: 32. *Serrastruma* Brown revived from synonymy, BOLTON, 1995: 382. *Serrastruma* Brown as a synonym of *Pyramica*, BOLTON, 1999: 1668. **Synonymy with *Strumigenys* reinstated**.

Neostruma BROWN, 1948: 111. Type species *Strumigenys crassicornis* Mayr by original designation. *Neostruma* Brown as a synonym of *Strumigenys*, BARONI URBANI & DE ANDRADE, 1994: 32. *Neostruma* Brown revived from synonymy, BOLTON, 1995: 292. *Neostruma* Brown as a synonym of *Pyramica*, BOLTON, 1999: 1668. **Synonymy with *Strumigenys* reinstated**.

Dorisidris BROWN, 1948: 116. Type species *Strumigenys nitens* Santschi by original designation. *Dorisidris* Brown as a synonym of *Strumigenys*, BARONI URBANI & DE ANDRADE, 1994: 32. *Dorisidris* Brown revived from synonymy, BOLTON, 1995: 177. *Dorisidris* Brown as a synonym of *Pyramica*, BOLTON, 1999: 1668. **Synonymy with *Strumigenys* reinstated**.

Miccostruma BROWN, 1948: 116. Type species *Epitritus mandibularis* Szabó by original designation. *Miccostruma* Brown as a synonym of *Smithistruma*, BOLTON, 1983: 274. *Miccostruma* Brown as a synonym of *Pyramica*, BOLTON, 1999: 1668. Undoubted synonym of a synonym of *Strumigenys* supported in this paper. **New synonymy**.

Quadristruma BROWN, 1949a: 47. Type species *Epitritus emmae* Emery by original designation. *Quadriustruma* Brown as a synonym of *Strumigenys*, BARONI URBANI

& DE ANDRADE, 1994: 32. *Quadristruma* Brown revived from synonymy, BOLTON, 1995: 377. *Quadristruma* Brown synonymy with *Strumigenys* reinstated, BOLTON, 1999: 1672.

Kyidris BROWN, 1949b: 3. Type species *Kyidris mutica* Brown by original designation. *Kyidris* Brown as a synonym of *Strumigenys*, BARONI URBANI & DE ANDRADE, 1994: 32. *Kyidris* Brown revived from synonymy, BOLTON, 1995: 219. *Kyidris* Brown as a synonym of *Pyramica*, BOLTON, 1999: 1668. **Synonymy with** ***Strumigenys*** **reinstated**.

Polyhomoa AZUMA, 1950: 36. Type species *Polyhomoa itoi* Azuma by monotypy. *Polyhomoa* Azuma as a synonym of *Kyidris*, CREIGHTON, 1950: 93. *Polyhomoa* Azuma as a synonym of *Pyramica*, BOLTON, 1999: 1668. Undoubted synonym of a synonym of *Strumigenys* supported in this paper. **New synonymy**.

Chelystruma BROWN, 1950a: 33 (subgenus ad *Glamyromyrmex*). Type species *Glamyromyrmex lilloana* Brown by monotypy. *Chelystruma* Brown as a good genus, KEMPF, 1959: 338. *Chelystruma* as a synonym of *Strumigenys*, BARONI URBANI & DE ANDRADE, 1994: 32. *Chelystruma* Brown revived from synonymy, BOLTON, 1995: 145. *Chelystruma* Brown as a synonym of *Pyramica*, BOLTON, 1999: 1668. **Synonymy with** ***Strumigenys*** **reinstated**.

Borgmeierita BROWN, 1953: 23. Type species *Codiomyrmex excisus* Weber by original designation. *Borgmeierita* Brown as a synonym of *Glamyromyrmex*, BROWN, 1973a: 35. *Borgmeierita* Brown as a synonym of *Pyramica*, BOLTON, 1999: 1668. Undoubted synonym of a synonym of *Strumigenys* supported in this paper. **New synonymy**.

Platystruma BROWN, 1953: 112 (subgenus ad *Smithistruma*). Type species *Strumigenys depressiceps* Weber by original designation. *Platystruma* Brown as a synonym of *Smithistruma*, BROWN, 1973a: 35. *Platystruma* Brown as a synonym of *Pyramica*, BOLTON, 1999: 1668. Undoubted synonym of a synonym of *Strumigenys* supported in this paper. **New synonymy**.

Gymnomyrmex BORGMEIER, 1954: 279. Type species *Gymnomyrmex splendens* Borgmeier by original designation. *Gymnomyrmex* Borgmeier as a synonym of *Strumigenys*, BARONI URBANI & DE ANDRADE, 1994: 32. *Gymnomyrmex* Borgmeier revived from synonymy, BOLTON, 1995: 211. *Gymnomyrmex* Borgmeier as a synonym of *Pyramica*, BOLTON, 1999: 1668. **Synonymy with** ***Strumigenys*** **reinstated**.

Dysedrognathus TAYLOR, 1968b: 132. Type species *Dysedrognathus extemenus* Taylor by original designation. *Dysedrognathus* Taylor as a synonym of *Strumigenys*, BARONI URBANI & DE ANDRADE, 1994: 32. *Dysedrognathus* Taylor revived from synonymy, BOLTON, 1995: 183. *Dysedrognathus* Taylor as a synonym of *Pyramica*, BOLTON, 1999: 1668. **Synonymy with** ***Strumigenys*** **reinstated**.

Asketogenys BROWN, 1972: 23. Type species *Asketogenys acubecca* Brown, by original designation. *Asketogenys* Brown as a synonym of *Strumigenys*, BARONI URBANI & DE ANDRADE, 1994: 32. *Asketogenys* Brown revived from synonymy, BOLTON, 1995: 75. *Asketogenys* Brown as a synonym of *Pyramica*, BOLTON, 1999: 1668. **Synonymy with** ***Strumigenys*** **reinstated**.

Cladarogenys BROWN, 1976: 33. Type species *Cladarogenys lasia* Brown, by original designation. *Cladarogenys* Brown as a synonym of *Strumigenys*, BARONI URBANI & DE ANDRADE, 1994: 32. *Cladarogenys* Brown revived from synonymy, BOLTON, 1995: 145. *Cladarogenys* Brown as a synonym of *Pyramica*, BOLTON, 1999: 1668. **Synonymy with** ***Strumigenys*** **reinstated**.

In our study this genus results characterized by the following synapomorphies:

Worker (and gyne) reduction of the labial palps from 2 to 1. CI 0.70, RI 0.67. This trait is shared also with *Acanthognathus* and with some *Basiceros* species previously included in *Talaridris*.

Worker (and gyne) presence of a basimandibular process. CI 0.67, RI 0.86. The synapomorphic state of this character (sometimes of doubtful detection, see Fig. 10) is an artefact of character optimization due to the fact that the basimandibular process is absent in *Phalacromyrmex*, *Pilotrochus*, *Ishakidris*, *Basiceros*, and the hypothetical ancestor of *Acanthognathus* (process present in highly transformed form) and the remaining Dacetini genera (process present). Because of its widespread presence in a number of Dacetini genera, presence of the basimandibular process is a poor discriminant trait to identify *Strumigenys*.

Worker (and gyne) mesosternal hair beds visible in profile. CI 0.91, RI 0.67. In spite of its perfect match within *Strumigenys*, this character is irregularly distributed among several dacetine genera including the three monotypic genera *Phalacromyrmex*, *Pilotrochus* and *Ishakidris*. Moreover, we regard the character itself as insecure: mesosternal hair beds are widespread and coding their visibility in profile as phylogenetically significant needs some imagination and abstraction capacity.

Worker (and gyne) eyes ventral. CI 0.67, RI 0.80. This trait is shared with all and only the former Phalacromyrmecini, but was coded as polymorphic in "*Pyramica*" as a result of our transfer to *Strumigenys* of the blind species *inopinata* (see below, the list of new combinations in *Strumigenys*) originally described in "*Rhopalothrix*". The position of the eyes, otherwise, is likely to represent the main synypomorphy of the genus.

Gyne (and male?) secondary loss of the anal vein. CI 0.75, RI 0.50. This trait appears to be constant among *Strumigenys* but it reappears in some *Acanthognathus* and *Basiceros* species.

Strumigenys (including *Pyramica*) results weakly defined from our analysis, unable to focus on one single clear-cut synapomorphy. On the other hand, by appearing as branch in a tetratomy, its sister-group with which it could eventually be merged is also not clearly identified. For these reasons and for nomenclatorial conser-

vationism we prefer to provisionally maintain *Strumigenys* as a valid genus defined by a combination of characters, a procedure seldom accepted in phylogenetic studies.

Finally, no apomorphies separating *Pyramica* from *Strumigenys* appeared as a result of our character optimization and we were unable to include a single one in our data.

The reason for this exclusion is that no one of the characters listed by BOLTON (1999, 2000) to separate the two genera appear to hold even after a superficial scrutiny.

The following four characters should separate the two genera according to BOLTON (1999, 2000):

1) "Mandibles in ventral view broad at extreme base, their articulations located at about the midlength of the labio-maxillary complex". In BOLTON (1999) this is given as apomorphic for *Pyramica* as opposed to "Mandibles in ventral view narrow at extreme base, apparently arising from the apex of the labio-maxillary complex" in *Strumigenys*. This character is not used to separate the two genera in the key by BOLTON (2000: 15). We are greatly embarrassed in tracing a boundary between the two categories defined by BOLTON (l. c.) and find it difficult understanding the character definition even on the basis of some of Bolton's examples (see e. g. BOLTON 1999: Figs. 59 & 81). Our Figs. 39 - 41 exemplify cases of comparable mandibular morphology for both *Pyramica* and *Strumigenys*.

2) "Mandibles at full gap open to only 60-90°" in *Pyramica*, vs. "Mandibles at full gape open to 170° or more" in *Strumigenys*. Documenting this character may be difficult for the risks to tear the adductor muscles, an action that would result in too great opening angles and for the tendency to contract the muscle bundles yielding smaller opening angles in drying specimens. Fig. 42 records two examples drawn from a wider array of species contradicting BOLTON's (1999 & 2000) use of this character and observed on relaxed material. Another case was already documented in a web publication by de ANDRADE & BARONI URBANI (2005)

3) "Labral lobes hypertrophied" (synapomorphic) versus "arising from across entire width of labium" (plesiomorphic) in *Pyramica*; or "labrum with distal lobes reduced... or vestigial" (ple-
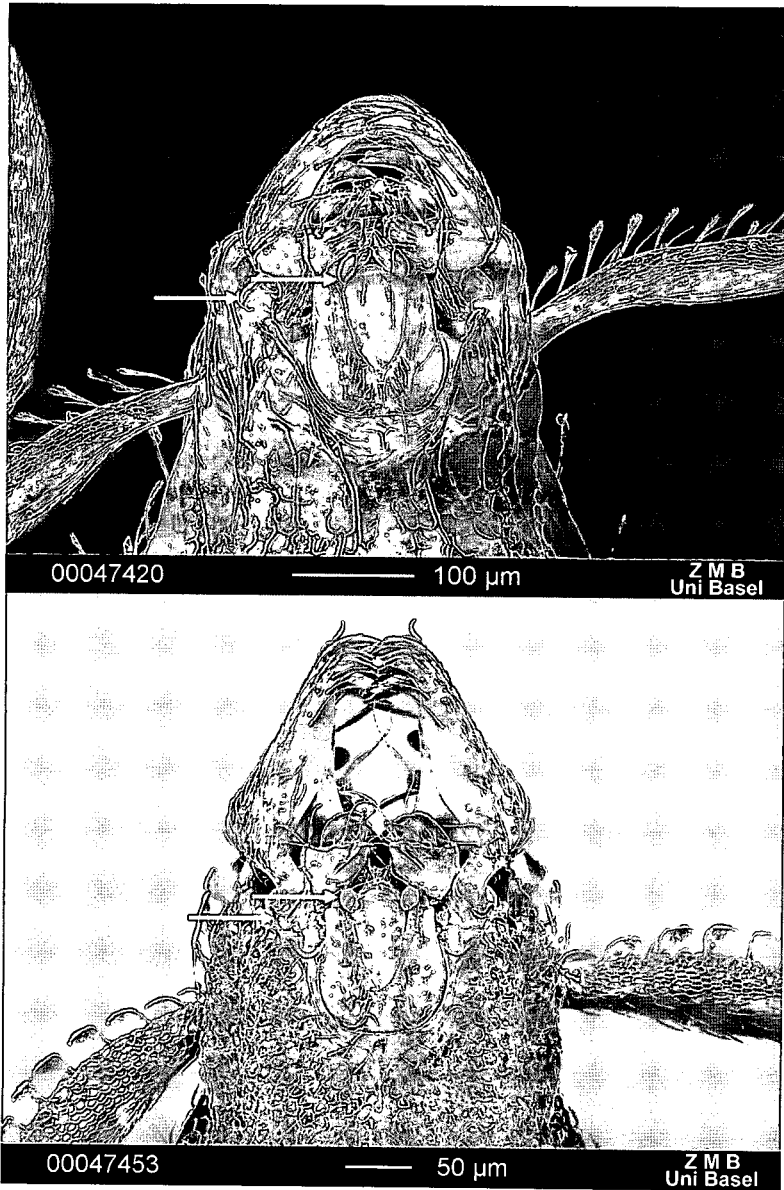
Fig. 39 - Comparable width and position of the base of the mandibles in *Pyramica semicompta* (Brown) (top) and *Strumigenys lyroessa* (Roger) (bottom). The arrows show the position of the mandibular articulations and of the labial palpi as indicator of the distal border of the labio-maxillary complex.
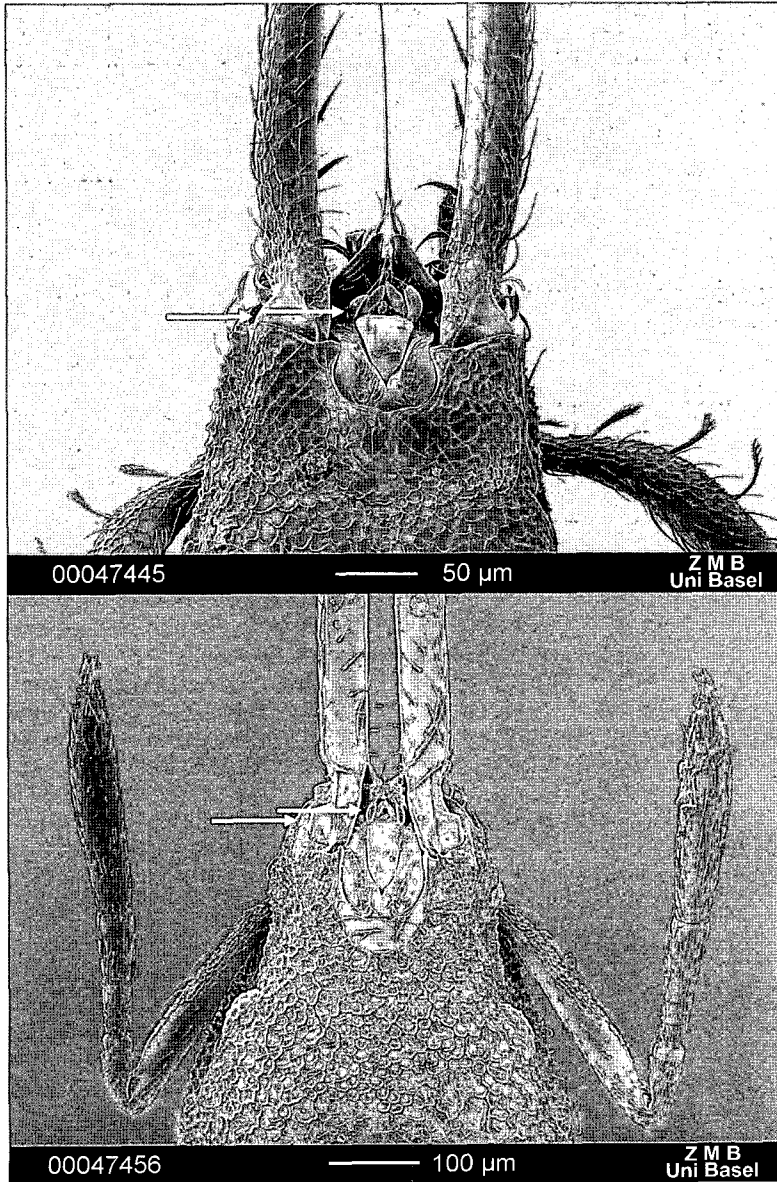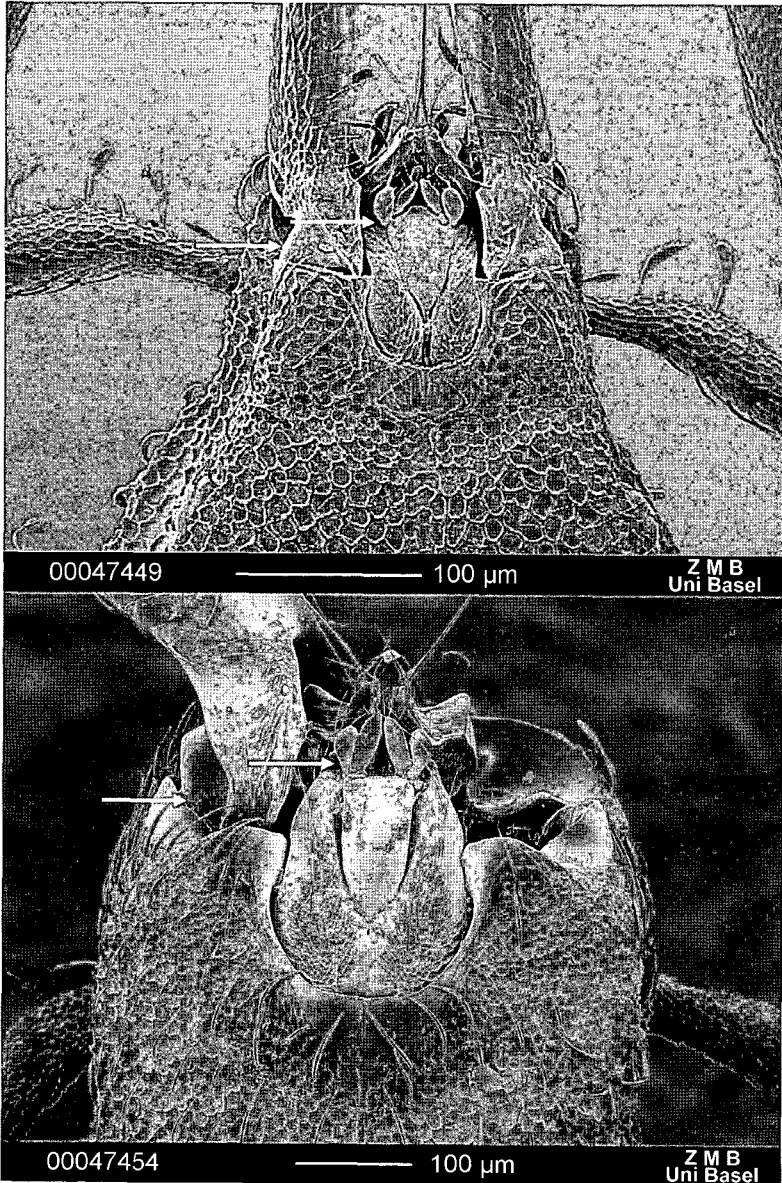
Fig. 40 - Comparable width and position of the base of the mandibles in *Pyramica denticulata* (Mayr) (top) and *Strumigenys lanuginosa* Wheeler (bottom). The arrows show the position of the mandibular articulations and of the labial palpi as indicator of the distal border of the labio-maxillary complex.

Fig. 41 - Comparable position of the base of the mandibles in *Pyramica eggersi* (Emery) (top) and *Strumigenys godmani* Forel (bottom). The arrows show the position of the mandibular articulations and of the labial palpi as indicator of the distal border of the labio-maxillary complex.
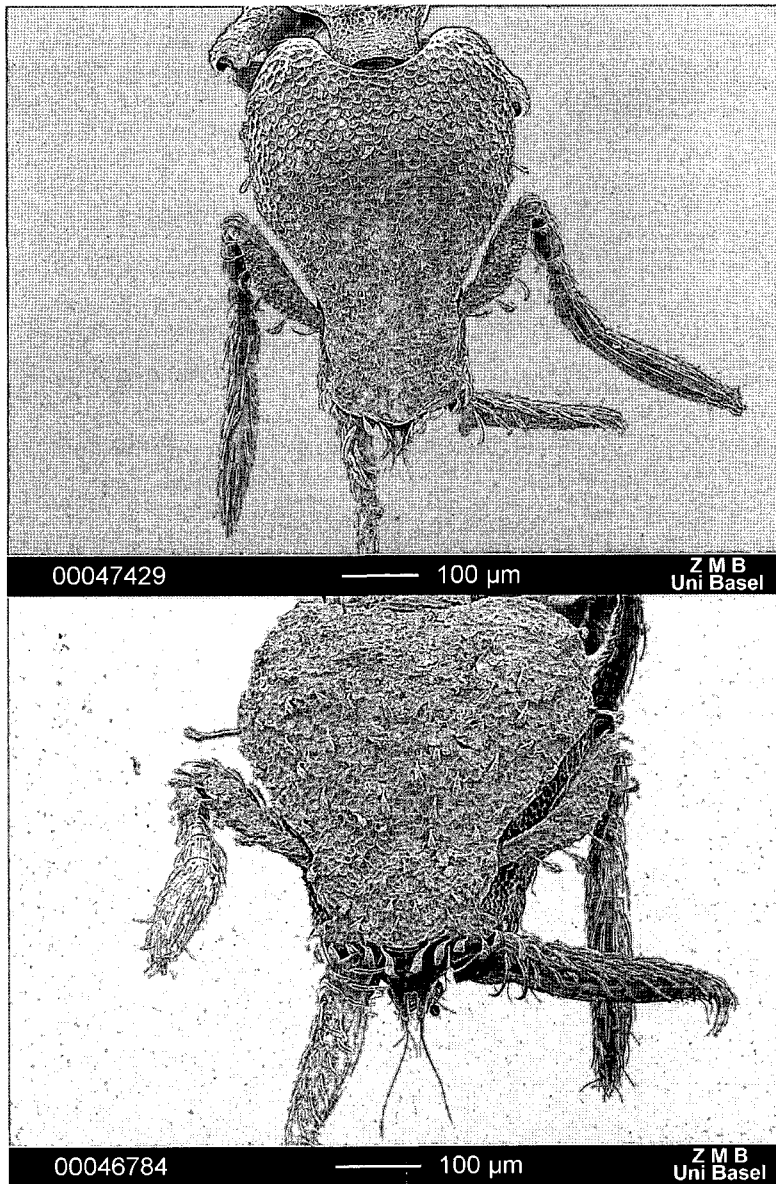
Fig. 42 - *Pyramica zeteki* (Brown) (top) and *Pyramica subedentata* (Mayr) (bottom) opening the left mandible at 90° (= 180° for both mandibles). *Pyramica* species were supposed to never open their mandibles wider than 90°.

siomorphic) "not arising from across entire width of labium" (synapomorphic) in *Strumigenys*. Figures 43 - 44 should be sufficient to exemplify the indefensibility of this partition. Another case contradicting Bolton's classification was already published in a web document by DE ANDRADE & BARONI URBANI (2005).

4)   [?Opening of the] "buccal cavity relatively short and wide, lateral margins of cavity... not converging anteriorly" (plesiomorphic) in *Pyramica*, as opposed to "relatively long and narrow, lateral margins of cavity... converging anteriorly", synapomorphic for *Strumigenys*. Figures 45 - 46 show four cases of contradictory distribution of this character among two *Strumigenys* and two "*Pyramica*" species.

In addition and as a general consideration, any attempt to regard *Strumigenys* and *Pyramica* as valid genera separated by the mandibular kinetic or by any of its morphological correlates would inevitably render one of the two fictitious genera invalid for being paraphyletic to the other as it was already shown under chapter 4.1.

The erroneous separation of *Pyramica* from *Strumigenys* yields to the following, unfortunately necessary list of reaffirmed or new combinations and replacement names for new homonyms in *Strumigenys*. Only the most important references are reported in our list. Additional ones can be found in BOLTON (2000). Needless to say, the tormented nomenclatorial fate of the species listed below (some of them were attributed to three different genera in less than 20 years) can be regarded as an additional proof of the opportunity of merging all *Strumigenys* satellite genera in one. The following is a list of species affected by nomenclatorial changes as compared with the nomenclature adopted by BOLTON (2000) and not a *Strumigenys* species list. The species list can be easily extracted from the monograph of BOLTON (2000).

Strumigenys abdita WESSON & WESSON, 1939: 106. *Smithistruma abdita* (Wesson & Wesson), SMITH, 1951: 827. *Pyramica abdita*, BOLTON, 1999. 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys abditivata (Bolton). **New combination** for *Pyramica abditivata* BOLTON, 2000: 231.

Strumigenys acheron (Bolton). **New combination** for *Pyramica acheron* BOLTON, 2000: 416.

Strumigenys acubecca (Brown). **New combination** for *Asketogenys acubecca* BROWN, 1972: 23 and *Pyramica acubecca*, BOLTON, 1999: 1672.
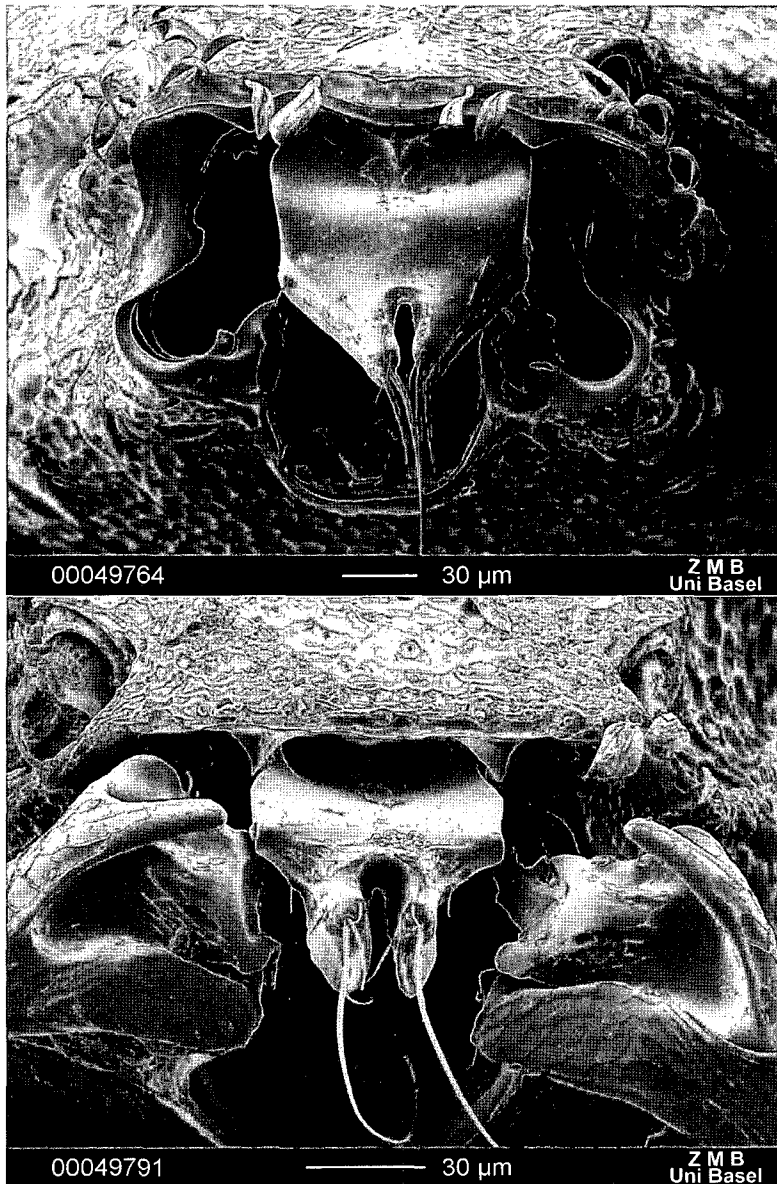
Fig. 43 - Uniformity of shape of the labium among putative *Pyramica* and *Strumigenys* species. *Pyramica xenognatha* (Kempf) (top) and *Strumigenys exilirhina* Bolton (bottom).
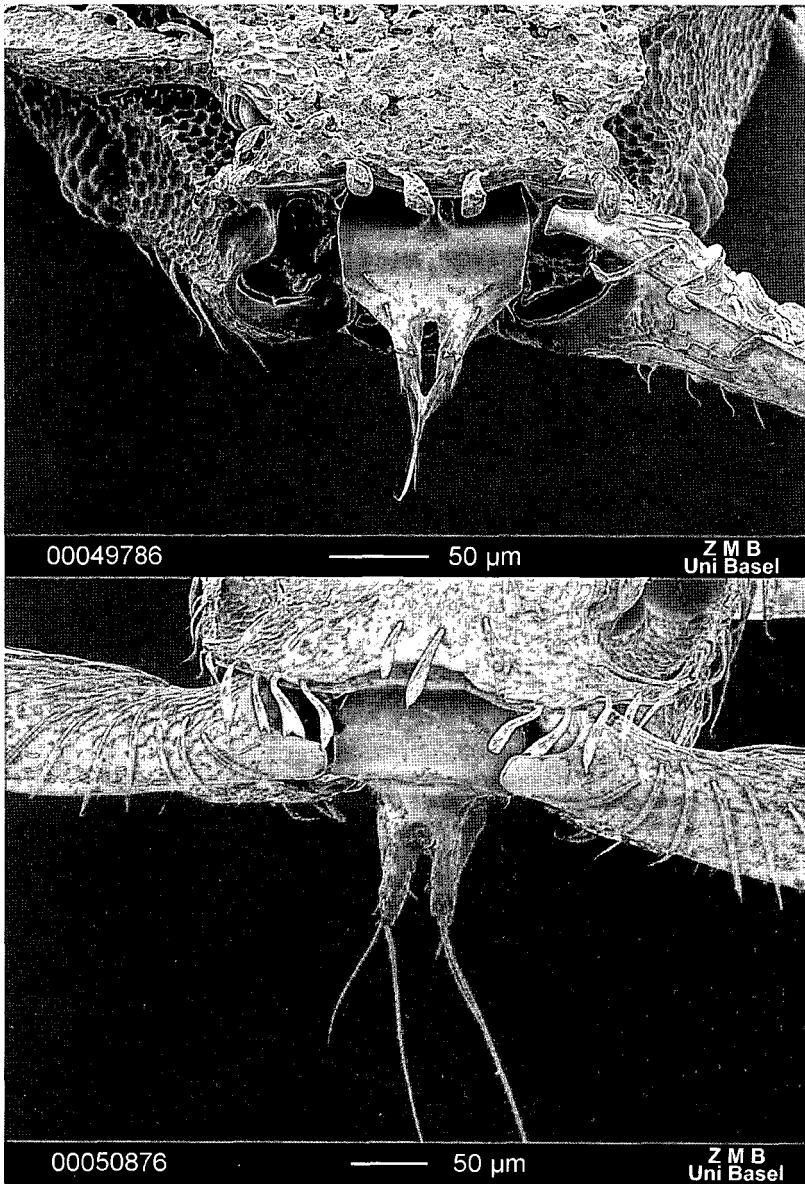
Fig. 44 - Uniformity of shape of the labium among putative *Pyramica* and *Strumi-genys* species. *Pyramica subedentata* (Mayr) (top) and *Strumigenys micretes* Brown (bottom).
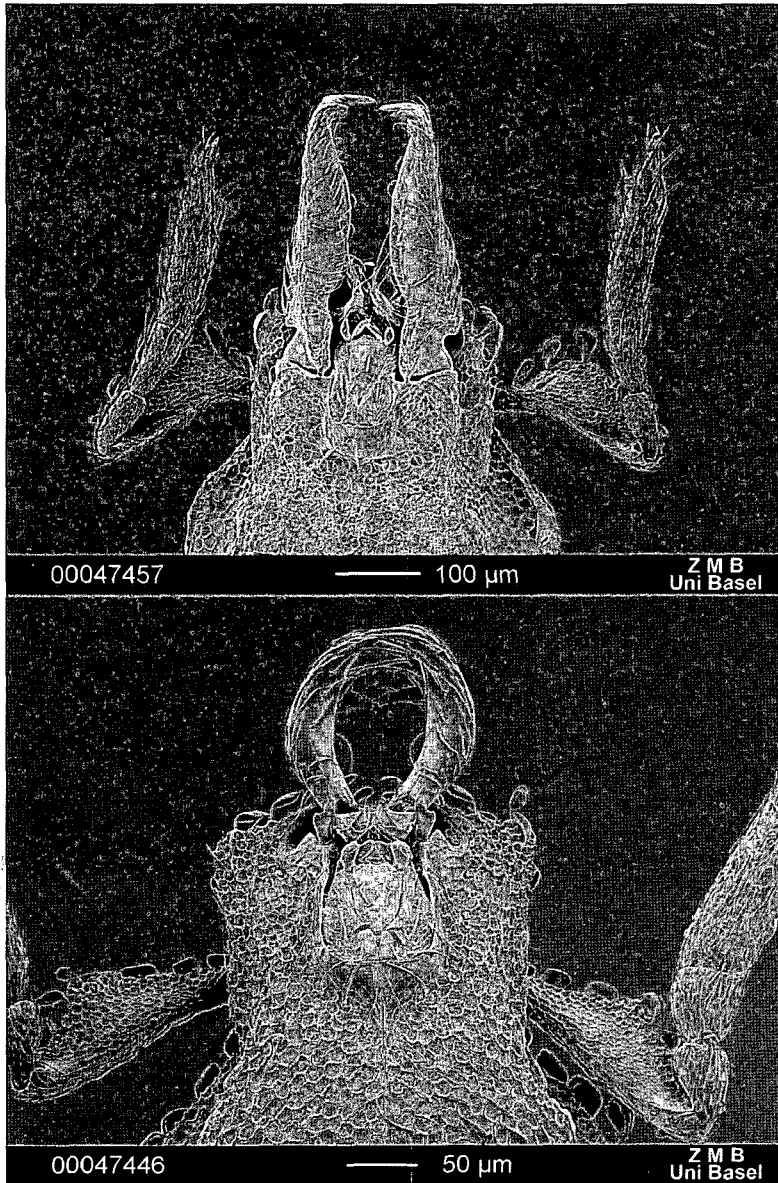
Fig. 45 - *Pyramica decipula* Bolton (top) with narrow opening and subparallel mar-
gins of the buccal cavity and *Strumigenys emmae* (Emery) (bottom) with
broad opening and convergent margins of the buccal cavity. The opposite
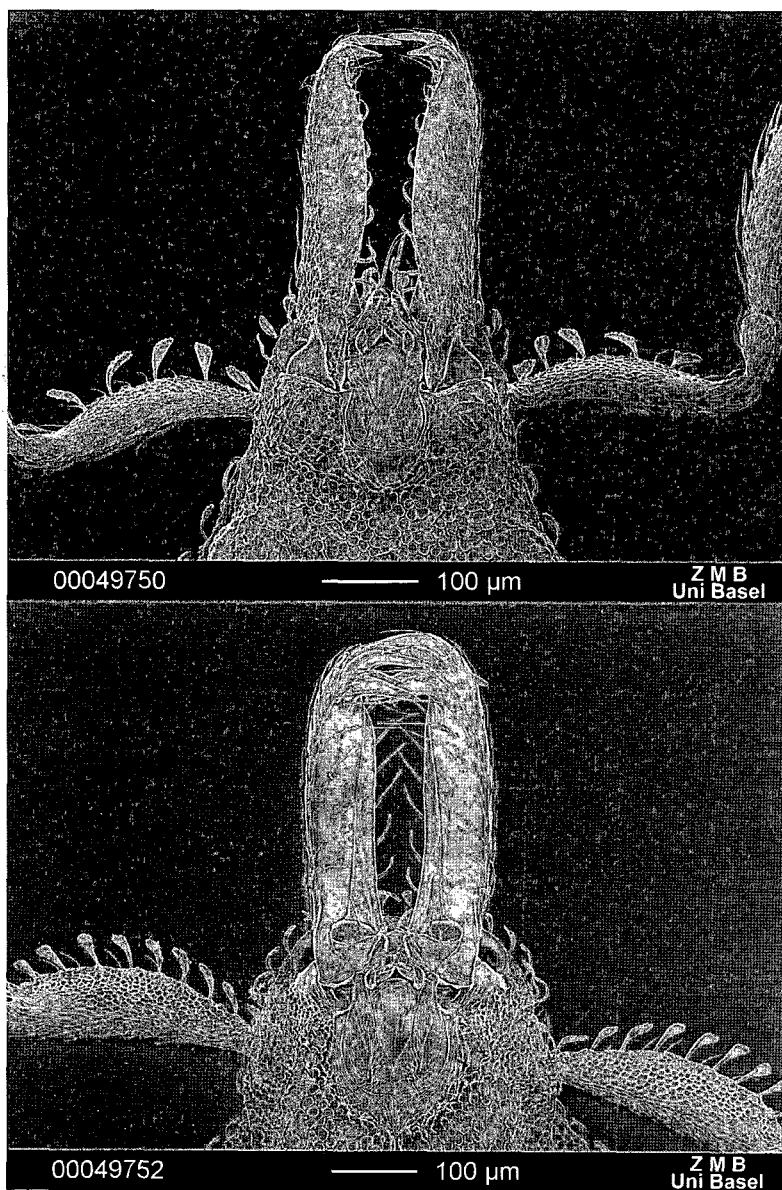state of this character should characterize the two genera.

Fig. 46 - *Pyramica subedentata* (Mayr) (top) with narrow opening and subparallel
margins of the buccal cavity and *Strumigenys chapmani* Brown (bottom)
with broad opening and convergent margins of the buccal cavity. The
opposite state of this character should characterize the two genera.

Strumigenys aello (Bolton). **New combination** for *Pyramica aello* BOLTON, 2000: 416.

Strumigenys aethegenys (Bolton). **New combination** for *Pyramica aethegenys* BOLTON, 2000: 179.

Strumigenys africana (Bolton). **New combination** for *Glamyromyrmex africanus* BOLTON, 1983: 322 and *Pyramica africana*, BOLTON, 1999: 1672.

Strumigenys agnosta (Bolton). **New combination** for *Pyramica agnosta* BOLTON, 2000: 293.

Strumigenys agostii (Bolton). **New combination** for *Pyramica agostii* BOLTON, 2000: 412.

Strumigenys ailaoshana (Xu & Zhou). **New combination** for *Pyramica ailaoshana* XU & ZHOU, 2004: 440.

Strumigenys alberti FOREL, 1893b. 380. *Smithistruma alberti* (Forel) BROWN 1953: 93. *Pyramica alberti*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated.**

Strumigenys alecto (Bolton). **New combination** for *Pyramica alecto* BOLTON, 2000: 429.

Strumigenys ambatrix (Bolton). **New combination** for *Pyramica ambatrix* BOLTON, 2000: 355.

Strumigenys anarta (Bolton). **New combination** for *Smithistruma anarta* BOLTON, 1983: 314 and *Pyramica anarta*, BOLTON, 1999: 1673.

Strumigenys anderseni (Bolton). **New combination** for *Pyramica anderseni* BOLTON, 2000: 474.

Strumigenys angulata SMITH, 1931: 697. *Smithistruma angulata* (Smith) BROWN, 1953: 54. *Pyramica angulata*, BOLTON, 1999. 1673. **Combination in *Strumigenys* reinstated.**

Strumigenys anorbicula (Bolton). **New combination** for *Pyramica anorbicula* BOLTON, 2000: 287.

Strumigenys appalachicolensis (Deyrup & Lubertazzi). **New combination** for *Pyramica appalachicolensis* DEYRUP & LUBERTAZZI, 2001: 15.

Strumigenys appretiata (Borgmeier). **New combination** for *Glamyromyrmex appretiatus* BORGMEIER, 1954: 282 and *Pyramica appretiata*, BOLTON, 1999: 1672.

Strumigenys arahana (Bolton). **New combination** for *Smithistruma arahana* BOLTON, 1983: 300 and *Pyramica arahana*, BOLTON, 1999: 1673.

Strumigenys archboldi (Deyrup & Cover). **New combination** for *Smithistruma archboldi* DEYRUP & COVER, 1998: 217 and *Pyramica archboldi*, BOLTON, 1999: 1673.

Strumigenys arges (Bolton). **New combination** for *Pyramica arges* BOLTON, 2000: 462.

Strumigenys argiola (Emery). *Epitritus argiolus* EMERY, 1869a: 136. *Strumigenys argiola* (Emery), BARONI URBANI, 1998: 163. *Pyramica argiola*, BOLTON, 1999: 1672. **Combination in *Strumigenys* reinstated.**

Strumigenys arizonica (Ward). **New combination** for *Smithistruma arizonica* WARD, 1988: 121 and *Pyramica arizonica*, BOLTON, 1999: 1673.

Strumigenys asaphes (Bolton). **New combination** for *Pyramica asaphes* BOLTON, 2000: 171.

Strumigenys assamensis de Andrade in BARONI URBANI & DE ANDRADE, 1994: 61. *Smithistruma assamensis* (de Andrade), BOLTON, 1995: 384. *Pyramica assamensis*, BOLTON, 1999. 1673. **Combination in *Strumigenys* reinstated.**

Strumigenys atopogenys (Bolton). **New combination** for *Pyramica atopogenys* BOLTON, 2000: 417.

Strumigenys atropos (Bolton). **New combination** for *Pyramica atropos* BOLTON, 2000: 457.

Strumigenys auctidens (Bolton). **New combination** for *Pyramica auctidens* BOLTON, 2000: 179.

Strumigenys augustandrewi (Longino). **New combination** for *Pyramica augustandrewi* LONGINO, 2006: 140.

Strumigenys azteca (Kempf). **New combination** for *Glamyromyrmex aztecus* KEMPF, 1960b: 444 and *Pyramica azteca*, BOLTON, 1999: 1672.

Strumigenys baudueri (Emery). *Epitritus baudueri* EMERY, 1875: 474. *Strumigenys baudueri* (Emery), MAYR, 1887: 571 et auctorum omnium recentiorum usque ad 1948. *Smithistruma baudueri* (Emery), BROWN, 1948: 105. *Pyramica baudueri*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys beebei (Wheeler). **New combination** for *Glamyromyrmex beebei* WHEELER, 1915b: 488 and *Pyramica beebei*, BOLTON, 1999: 1672.

Strumigenys behasyla (Bolton). **New combination** for *Smithistruma behasyla* BOLTON, 1983: 286 and *Pyramica behasyla*, BOLTON, 1999: 1673.

Strumigenys belial (Bolton). **New combination** for *Pyramica belial* BOLTON, 2000: 331.

Strumigenys bellatrix (Bolton). **New combination** for *Pyramica bellatrix* BOLTON, 2000: 336.

Strumigenys benten (Terayama, Lin & Wu). **New combination** for *Smithistruma benten* TERAYAMA, LIN & WU, 1996: 329.

Strumigenys bequaerti SANTSCHI, 1923: 286. *Serrastruma bequaerti* (Santschi) CONSANI, 1951: 171. *Pyramica bequaerti*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys bimarginata WESSON & WESSON, 1939: 95. *Smithistruma bimarginata* (Wesson & Wesson) SMITH, 1951: 827. *Pyramica bimarginata*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys boltoni (Deyrup). **New combination** for *Pyramica boltoni* DEYRUP, 2006: 1.

Strumigenys brevicornis MANN, 1922: 38. *Neostruma brevicornis* (Mann), BROWN, 1948: 111. *Pyramica brevicornis*, BOLTON, 1999: 1672. **Combination in *Strumigenys* reinstated**.

Strumigenys brontes (Bolton). **New combination** for *Pyramica brontes* BOLTON, 2000: 463.

Strumigenys browni (Bolton). **New combination** for *Pyramica browni* BOLTON, 2000: 168.

Strumigenys bubisnoda (Bolton). **New combination** for *Pyramica bubisnoda* BOLTON, 2000: 393.

Strumigenys bunki (Brown). **New combination** for *Smithistruma bunki* BROWN, 1950b: 41 and *Pyramica bunki*, BOLTON, 1999: 1673.

Strumigenys californica (Brown). **New combination** for *Smithistruma californica* BROWN, 1950b: 40 and *Pyramica californica*, BOLTON, 1999: 1673.

Strumigenys canina (Brown & Boisvert). **New combination** for *Pentastruma canina* BROWN & BOISVERT, 1979: 203 and *Pyramica canina*, BOLTON, 1999: 1673.

Strumigenys capitata (Smith). *Cephaloxys capitata* SMITH, 1865: 77. *Strumigenys capitata* (Smith), MAYR, 1866: 517. *Smithistruma capitata* (Smith), BROWN, 1948:

105. *Pyramica capitata*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys carinognatha (Bolton). **New combination** for *Pyramica carinognatha* BOLTON, 2000: 418.

Strumigenys carnassa (Bolton). **New combination** for *Pyramica carnassa* BOLTON, 2000: 475.

Strumigenys carolinensis (Brown). **New combination** for *Smithistruma carolinensis* BROWN, 1964: 185 and *Pyramica carolinensis*, BOLTON, 1999: 1673.

Strumigenys cascanteae (Longino). **New combination** for *Pyramica cascanteae* LONGINO, 2006: 138.

Strumigenys cassicuspis (Bolton). **New combination** for *Pyramica cassicuspis* BOLTON, 2000: 216.

Strumigenys castanea (Brown). **New combination** for *Smithistruma castanea* BROWN, 1953: 107 and *Pyramica castanea*, BOLTON, 1999: 1673.

Strumigenys cavinasis (Brown). **New combination** for *Smithistruma cavinasis* BROWN, 1950b: 42 and *Pyramica cavinasis*, BOLTON, 1999: 1673.

Strumigenys charybdys (Bolton). **New combination** for *Pyramica charybdys* BOLTON, 2000: 396.

Strumigenys chiricahua (Ward). **New combination** for *Smithistruma chiricahua* WARD, 1988: 119 and *Pyramica chiricahua*, BOLTON, 1999: 1673.

Strumigenys chyatha (Bolton). **New combination** for *Smithistruma chyatha* BOLTON, 1983: 288 and *Pyramica chyatha* BOLTON, 1999: 1673.

Strumigenys cincinnata (Kempf). **New combination** for *Smithistruma cincinnata* KEMPF, 1975: 419 and *Pyramica cincinnata*, BOLTON, 1999: 1673.

Strumigenys circothrix (Ogata & Onoyama). **New combination** for *Smithistruma circothrix* OGATA & ONOYAMA, 1998: 280 and *Pyramica circothrix*. BOLTON, 1999: 1673.

Strumigenys clotho (Bolton). **New combination** for *Pyramica clotho* BOLTON, 2000: 413.

Strumigenys cloydi (Pfitzer). **New combination** for *Smithistruma cloydi* PFITZER, 1951: 198 and *Pyramica cloydi*, BOLTON, 1999: 1673.

Strumigenys clypeata ROGER, 1863a: 213 [*clipeata!*]. *Smithistruma clypeata* (Roger) SMITH, 1951: 827. *Pyramica clypeata*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys comis (Kempf). **New combination** for *Gymnomyrmex comis* KEMPF, 1959: 342 and *Pyramica comis*, BOLTON, 1999: 1672.

Strumigenys concolor SANTSCHI, 1914b: 375. *Serrastruma concolor* (Santschi), WEBER, 1925: 6. *Pyramica concolor*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys connectens KEMPF, 1958: 59. *Pyramica connectens*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys conspersa EMERY, 1906: 169. *Smithistruma conspersa* (Emery), BROWN, 1953: 100. *Pyramica conspersa*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys convexiceps SANTSCHI, 1931: 277. *Pyramica convexiceps*, BOLTON, 1999: 1672. **Combination in *Strumigenys* reinstated**.

Strumigenys crassicornis MAYR, 1887: 569. *Neostruma crassicornis* (Mayr) BROWN, 1948: 111. *Pyramica crassicornis*, BOLTON, 1999: 1672. **Combination in *Strumigenys* reinstated**.

Strumigenys creightoni SMITH, 1931: 705. *Smithistruma creightoni* (Smith), SMITH, 1951: 827. *Pyramica creightoni*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys crementa (Bolton). **New combination** for *Pyramica crementa* BOLTON, 2000: 182.

Strumigenys cryptura (Bolton). **New combination** for *Glamyromyrmex crypturus* BOLTON, 1983: 327 and *Pyramica cryptura*, BOLTON, 1999: 1672.

Strumigenys dagon (Bolton). **New combination** for *Glamyromyrmex dagon* BOLTON, 1983: 325 and *Pyramica dagon* Bolton, 1999: 1672.

Strumigenys dapsilis (Bolton). **New combination** for *Pyramica dapsilis* BOLTON, 2000: 217.

Strumigenys daspleta (Bolton). **New combination** for *Pyramica daspleta* BOLTON, 2000: 445.

Strumigenys datissa (Bolton). **New combination** for *Smithistruma datissa* BOLTON, 1983: 289 and *Pyramica datissa*, BOLTON, 1999: 1673.

Strumigenys dayui (Xu). **New combination** for *Epitritus dayui* XU, 2000: 297.

Strumigenys decipula (Bolton). **New combination** for *Pyramica decipula* BOLTON, 2000: 183.

Strumigenys deinognatha (Bolton). **New combination** for *Pyramica deinognatha* BOLTON, 2000: 419.

Strumigenys deinomastax (Bolton). **New combination** for *Pyramica deinomastax* BOLTON, 2000: 160.

Strumigenys denticulata MAYR, 1887: 570. *Pyramica denticulata*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys dentinasis (Kempf). **New combination** for *Gymnomyrmex dentinasis* KEMPF, 1960b: 450 and *Pyramica dentinasis*, BOLTON 1999: 1672.

Strumigenys dentiscapa (Bolton). **New combination** for *Pyramica dentiscapa* BOLTON, 2000: 396.

Strumigenys depilosa (Bolton). **New combination** for *Pyramica depilosa* BOLTON, 2000: 312.

Strumigenys depressiceps WEBER, 1934: 47. *Smithistruma depressiceps* (Weber), BROWN, 1953: 112. *Pyramica depressiceps*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys deyrupi (Bolton). **New combination** for *Pyramica deyrupi* BOLTON, 2000: 119.

Strumigenys dictynna (Bolton). **New combination** for *Pyramica dictynna* BOLTON, 2000: 294.

Strumigenys dietrichi SMITH, 1931: 696. *Smithistruma dietrichi* (Smith), SMITH, 1951: 827. *Pyramica dietrichi*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys disjuncta (Bolton). **New combination** for *Pyramica disjuncta* BOLTON, 2000: 414.

Strumigenys dispalata (Bolton). **New combination** for *Pyramica dispalata* BOLTON, 2000: 213.

Strumigenys dohertyi EMERY, 1897: 576. *Smithistruma dohertyi* (Emery), BROWN, 1948: 105. *Pyramica dohertyi*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys dontopagis (Bolton). **New combination** for *Pyramica dontopagis* BOLTON, 2000: 172.

Strumigenys doryceps (Bolton). **New combination** for *Pyramica doryceps* BOLTON, 2000: 211.

Strumigenys dotaja (Bolton). **New combination** for *Serrastruma dotaja* BOLTON, 1983: 339 and *Pyramica dotaja*, BOLTON, 1999: 1673.

Strumigenys dyschima (Bolton). **New combination** for *Pyramica dyschima* BOLTON, 2000: 451.

Strumigenys eggersi EMERY, 1890: 69. *Pyramica eggersi*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys electrina de Andrade in BARONI URBANI & DE ANDRADE, 1994: 38. *Smithistruma electrina* (de Andrade), BOLTON, 1995: 384. *Pyramica electrina*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys elegantula (Terayama & Kubota). **New combination** for *Smithistruma elegantula* TERAYAMA & KUBOTA, 1989: 788 and *Pyramica elegantula*, BOLTON, 1999: 1673.

Strumigenys emarginata MAYR, 1901: 26. *Smithistruma emarginata* (Mayr), BROWN, 1948: 105. *Pyramica emarginata*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys emeswangi (Bolton). **New combination** for *Pyramica emeswangi* BOLTON, 2000: 458.

Strumigenys emiliae FOREL, 1907: 11. *Smithistruma emiliae* (Forel), BROWN, 1953: 104. *Pyramica emiliae*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated.**

Strumigenys enkara (Bolton). **New combination** for *Smithistruma enkara* BOLTON, 1983: 301 and *Pyramica enkara*, BOLTON, 1999: 1673.

Strumigenys enopla (Bolton). **New combination** for *Pyramica enopla* BOLTON, 2000: 185.

Strumigenys epinotalis WEBER, 1934: 46 [*Strumigenys studiosi epinotalis*]. *Smithistruma epinotalis* (Weber), BROWN, 1953: 101. *Pyramica epinotalis*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys epipola (Bolton). **New combination** for *Pyramica epipola* BOLTON, 2000: 399.

Strumigenys erikae (Longino). **New combination** for *Pyramica erikae* LONGINO, 2006: 141.

Strumigenys erynnes (Bolton). **New combination** for *Pyramica erynnes* BOLTON, 2000: 351.

Strumigenys euryale (Bolton). **New combination** for *Pyramica euryale* BOLTON, 2000: 432.

Strumigenys excisa (Weber). **New combination** for *Codiomyrmex excisus* WEBER, 1934: 51 and *Pyramica excisa*, BOLTON, 1999: 1672.

Strumigenys exiguaevitae Baroni Urbani. **New name** for *Pyramica hoplites* BOLTON, 2000: 347, transferred to *Strumigenys* in the present paper. Nec *Strumigenys hoplites* BROWN, 1973c: 266. Derivatio nominis: from the Latin *exigua* = short + *vita* = life, referred to the short life of the specific name *hoplites* in combination with the generic name *Pyramica*.

Strumigenys extemena (Taylor). **New combination** for *Dysedrognathus extemenus* TAYLOR, 1968b: 133 and *Pyramica extemena*, BOLTON, 1999: 1672.

Strumigenys exunca (Bolton). **New combination** for *Pyramica exunca* BOLTON, 2000: 302.

Strumigenys fautrix (Bolton). **New combination** for *Pyramica fautrix* BOLTON, 2000: 355.

Strumigenys fenkara (Bolton). **New combination** for *Smithistruma fenkara* BOLTON, 1983: 302 and *Pyramica fenkara*, BOLTON, 1999: 1673.

Strumigenys filirrhina (Brown). **New combination** for *Smithistruma filirrhina* BROWN, 1950b: 37 and *Pyramica filirrhina*, BOLTON, 1999: 1673.

Strumigenys filitalpa (Brown). **New combination** for *Smithistruma filitalpa* BROWN, 1950b: 39 and *Pyramica filitalpa*, BOLTON, 1999: 1673.

Strumigenys fisheri (Bolton). *Pyramica fisheri* BOLTON, 2000: 330. **New combination**.

Strumigenys flagellata (Taylor). **New combination** for *Codiomyrmex flagellatus* TAYLOR, 1962: 7 and *Pyramica flagellata*, BOLTON, 1999: 1672.

Strumigenys formosa (Terayama, Lin & Wu). **New combination** for *Epitritus formosus* TERAYAMA, LIN & WU, 1995: 85 and *Pyramica formosa*, BOLTON, 1999: 1672.

Strumigenys formosimonticola (Terayama, Lin & Wu). **New combination** for *Smithistruma formosimonticola* TERAYAMA, LIN & WU, 1996: 331 and *Pyramica formosimonticola*, BOLTON, 1999: 1673.

Strumigenys fridericimuelleri FOREL, 1886: 213. *Smithistruma fridericimuelleri* (Forel), BROWN, 1953: 98. *Pyramica fridericimuelleri*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys fulda (Bolton). **New combination** for *Smithistruma fulda* BOLTON, 1983: 282 and *Pyramica fulda*, BOLTON, 1999: 1673.

Strumigenys furtiva (Bolton). **New combination** for *Pyramica furtiva* BOLTON, 2000: 156.

Strumigenys gatuda (Bolton). **New combination** for *Smithistruma gatuda* BOLTON, 1983: 292 and *Pyramica gatuda*, BOLTON, 1999: 1673.

Strumigenys gemella KEMPF, 1975: 416. *Pyramica gemella*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys geoterra (Bolton). **New combination** for *Serrastruma geoterra* BOLTON, 1983: 341 and *Pyramica geoterra*, BOLTON 1999: 1673.

Strumigenys glenognatha (Bolton). **New combination** for *Pyramica glenognatha* BOLTON, 2000: 160.

Strumigenys grytava (Bolton). **New combination** for *Pyramica grytava* BOLTON, 2000: 220.

Strumigenys gundlachi (Roger). *Pyramica Gundlachi* ROGER, 1862: 253. *Strumigenys Gundlachi* (Roger), ROGER 1863b: 40 et auctorum omnium recentiorum usque ad 1999. *Pyramica gundlachi*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys gyges (Bolton). **New combination** for *Pyramica gyges* BOLTON, 2000: 424.

Strumigenys hadrodens (Bolton). **New combination** for *Pyramica hadrodens* BOLTON, 2000: 161.

Strumigenys halosis (Bolton). **New combination** for *Pyramica halosis* BOLTON, 2000: 162.

Strumigenys hathor (Bolton). **New combination** for *Pyramica hathor* BOLTON, 2000: 346.

Strumigenys hemisobek (Bolton). **New combination** for *Pyramica hemisobek* BOLTON, 2000: 452.

Strumigenys hensekta (Bolton). **New combination** for *Smithistruma hensekta* BOLTON, 1983: 293 and *Pyramica hensekta*, BOLTON, 1999: 1673.

Strumigenys hexamera (Brown). *Epitritus hexamerus* BROWN, 1958: 70. *Strumigenys hexamera* (Brown) BARONI URBANI & DE ANDRADE, 1994: 13. *Pyramica hexamera*, BOLTON 1999: 1672. **Combination in *Strumigenys* reinstated**.

Strumigenys hirashimai (Ogata). **New combination** for *Epitritus hirashimai* OGATA, 1990: 197 and *Pyramica hirashimai*, BOLTON, 1999: 1672.

Strumigenys hiroshimensis (Ogata & Onoyama)). **New combination** for *Smithistruma hiroshimensis* OGATA & ONOYAMA, 1998: 281 and *Pyramica hiroshimensis*, BOLTON, 1999: 1673.

Strumigenys hyalina (Bolton). **New combination** for *Pyramica hyalina* BOLTON, 2000: 128.

Strumigenys hyphata (Brown). **New combination** for *Smithistruma hyphata* BROWN,1953: 110 and *Pyramica hyphata*, BOLTON, 1999: 1673.

Strumigenys impidora (Bolton). **New combination** for *Smithistruma impidora* BOLTON, 1983: 294 and *Pyramica impidora*, BOLTON, 1999: 1673.

Strumigenys incerta (Brown). **New combination** for *Smithistruma incerta* BROWN, 1949b: 10 and *Pyramica incerta*, BOLTON, 1999: 1673.

Strumigenys inopina (Deyrup & Cover). **New combination** for *Smithistruma inopina* DEYRUP & COVER, 1998: 215 and *Pyramica inopina*, BOLTON, 1999: 1673.

Strumigenys inopinata (de Andrade). **New combination** for *Rhopalothrix inopinata* de Andrade in BARONI URBANI & DE ANDRADE, 1994: 54. DIETZ (2004) repeatedly suggests the transfer of this species to *Pyramica* without proposing the new combination. His reasons are a set of characteristic (not synapomorphic) *Strumigenys* characters visible in our 1994 figures. The unique, damaged *inopinata* holotype exhibits one presumed, important "basicerotine" synapomorphy according to BOLTON (1998), a deep transverse labial ridge, and some circumstantial ones, like bizarre pilosity on the scape, scape shape, extreme reduction of the eyes, etc. We already showed in the present paper (see our discussion of character # 6) that the transverse labial ridge may be absent in some "basicerotine" species and present in other *Strumigenys* species. After some hesitation we propose the transfer of *inopinata* to *Strumigenys* for possession of one *Strumigenys* + "Phalacromyrmecini" weak synapomorphy: the presence of the mesepisternal hair beds. These beds, otherwise, are visible also in a few "*Octostruma*" species. *S. inopinata*, moreover, possesses spongiform appendages on the peduncle and gaster, another trait that we don't consider as synapomorphic but only typical of *Strumigenys*. Nonetheless it must be noted that retention of *inopinata* in *Rhopalothrix* (= *Basiceros*), as it was originally described, would strengthen *Strumigenys*' generic boundaries (see our generic definition above).

Strumigenys inquilina (Bolton). **New combination** for *Serrastruma inquilina* BOLTON, 1983: 342 and *Pyramica inquilina*, BOLTON, 1999: 1673.

Strumigenys insula (Bolton). **New combination** for *Pyramica insula* BOLTON, 2000: 400.

Strumigenys inusitata (Lattke). **New combination** for *Trichoscapa inusitata* LATTKE, 1992: 142 and *Smithistruma inusitata* (Lattke), BOLTON, 1995: 384 and *Pyramica inusitata*, BOLTON, 1999: 1673.

Strumigenys jacobsoni MENOZZI, 1939: 180. *Smithistruma jacobsoni* (Menozzi), BROWN, 1948: 105. *Pyramica jacobsoni*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated.**

Strumigenys jamaicensis BROWN, 1959: 6. *Pyramica jamaicensis*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated.**

Strumigenys japonica ITO, 1914: 40. *Smithistruma japonica* (Ito), BROWN, 1948: 105. *Pyramica japonica*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated.**

Strumigenys karawajewi BROWN, 1948: 44. *Smithistruma karawajewi* (Brown), BROWN, 1948: 105. *Pyramica karawajewi*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated.**

Strumigenys kempfi (Taylor & Brown). **New combination** for *Smithistruma kempfi* TAYLOR & BROWN, 1978: 35 and *Pyramica kempfi*, BOLTON, 1999: 1673.

Strumigenys kerasma (Bolton). **New combination** for *Smithistruma kerasma* BOLTON, 1983: 303 and *Pyramica kerasma*, BOLTON, 1999: 1673.

Strumigenys khakaura (Bolton). **New combination** for *Pyramica khakaura* BOLTON, 2000: 348.

Strumigenys kichijo (Terayama, Lin & Wu). **New combination** for *Smithistruma kichijo* TERAYAMA, LIN & WU, 1996: 335 and *Pyramica kichijo*, BOLTON, 1999: 1673.

Strumigenys kompisomala (Bolton). **New combination** for *Pyramica kompisomala* BOLTON, 2000: 234.

Strumigenys kyidriformis (Brown). **New combination** for *Smithistruma kyidriformis* BROWN, 1964: 188 and *Pyramica kyidriformis*, BOLTON, 1999: 1673.

Strumigenys lachesis (Bolton). **New combination** for *Pyramica lachesis* BOLTON, 2000: 389.

Strumigenys laevinasis SMITH, 1931: 701. *Smithistruma laevinasis* (Smith), SMITH, 1951: 827. *Pyramica laevinasis*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated.**

Strumigenys laevipleura KEMPF, 1958: 64. *Pyramica laevipleura*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated.**

Strumigenys lalassa (Bolton). **New combination** for *Pyramica lalassa* BOLTON, 2000: 189.

Strumigenys lasia (Brown). **New combination** for *Cladarogenys lasia* BROWN, 1976: 34 and *Pyramica lasia*, BOLTON 1999: 1672.

Strumigenys laticeps (Brown). **New combination** for *Epitritus laticeps* BROWN, 1962: 77 and *Pyramica laticeps*, BOLTON, 1999: 1672.

Strumigenys leptothrix WHEELER, 1929: 55. *Smithistruma leptothrix* (Wheeler), BROWN, 1948: 107. *Weberistruma leptothrix* (Wheeler), BROWN, 1949: 8. *Pyramica leptothrix*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated.**

Strumigenys lilloana (Brown). **New combination** for *Glamyromyrmex lilloana* BROWN, 1950a: 34 and *Pyramica lilloana*, BOLTON, 1999: 1672.

Strumigenys longinoi (Bolton). **New combination** for *Pyramica longinoi* BOLTON, 2000: 173.

Strumigenys loveridgei (Brown). **New combination** for *Codiomyrmex loveridgei* BROWN, 1953: 21 and *Pyramica loveridgei*, BOLTON, 1999: 1672.

Strumigenys lucifuga (Bolton). **New combination** for *Pyramica lucifuga* BOLTON, 2000: 314.

Strumigenys ludovici FOREL, 1904: 369. *Serrastruma ludovici* (Forel), WEBER 1952: 6. *Pyramica ludovici*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys lujae Forel in WASMANN, 1902: 294. *Serrastruma lujae* (Forel), WEBER, 1952: 6. *Pyramica lujae*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys lygatrix (Bolton). **New combination** for *Pyramica lygatrix* BOLTON, 2000: 204.

Strumigenys malaplax (Bolton). **New combination** for *Smithistruma malaplax* BOLTON, 1983: 304 and *Pyramica malaplax*, BOLTON, 1999: 1673.

Strumigenys marchosias (Bolton). **New combination** for *Pyramica marchosias* BOLTON, 2000: 290.

Strumigenys margaritae FOREL, 1893b: 378. *Smithistruma margaritae* (Forel), SMITH, 1951: 827. *Pyramica margaritae*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys marginata (Santschi). **New combination** for *Epitritus marginatus* SANTSCHI, 1914a: 114 and *Miccostruma marginata* (Santschi), BROWN, 1948: 123 and *Smithistruma marginata* (Santschi), BOLTON, 1983: 312 and *Pyramica marginata*, BOLTON, 1999: 1673.

Strumigenys masukoi (Ogata & Onoyama). **New combination** for *Smithistruma masukoi* OGATA & ONOYAMA, 1998: 283 and *Pyramica masukoi*, BOLTON, 1999: 1673.

Strumigenys maxillaris Baroni Urbani. **New name** for *Epitritus mandibularis* SZABÓ, 1909: 27, transferred to *Strumigenys* in the present paper. Nec *Strumigenys mandibularis* SMITH, 1860: 72. Derivatio nominis: from the Latin *maxillaris*, practically a synonym of the preoccupied name *mandibularis*. *Miccostruma mandibularis* (Szabó), BROWN, 1948b: 123. *Smithistruma mandibularis* (Szabó), BOLTON, 1983: 283. *Pyramica mandibularis*, BOLTON, 1999: 1673.

Strumigenys maynei FOREL, 1916: 427. *Serrastruma maynei* (Forel), BROWN, 1952: 77. *Pyramica maynei*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys mazu (Terayama, Lin & Wu). **New combination** for *Smithistruma mazu* TERAYAMA, LIN & WU, 1996: 337 and *Pyramica mazu*, BOLTON, 1999: 1673.

Strumigenys media (Wilson & Brown). **New combination** for *Kyidris media* WILSON & BROWN, 1956: 445 and *Pyramica media*, BOLTON, 1999: 1672.

Strumigenys medusa (Bolton). **New combination** for *Pyramica medusa* BOLTON, 2000: 436.

Strumigenys megaera (Bolton). **New combination** for *Pyramica megaera* BOLTON, 2000: 437.

Strumigenys mekaha (Bolton). **New combination** for *Smithistruma mekaha* BOLTON, 1983: 305 and *Pyramica mekaha*, BOLTON, 1999: 1673.

Strumigenys membranifera EMERY, 1869b: 24. *Trichoscapa membranifera* (Emery), BROWN, 1948: 113. *Pyramica membranifera*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys memorialis (Deyrup). **New combination** for *Smithistruma memorialis* DEYRUP, 1998: 81 and *Pyramica memorialis*, BOLTON, 1999: 1673.

Strumigenys metazytes (Bolton). **New combination** for *Pyramica metazytes* BOLTON, 2000: 121.

Strumigenys metopia (Brown). **New combination** for *Neostruma metopia* BROWN, 1959: 11 and *Pyramica metopia*, BOLTON, 1999: 1672.

Strumigenys metrix (Bolton). **New combination** for *Pyramica metrix* BOLTON, 2000: 222.

Strumigenys miccata (Bolton). **New combination** for *Serrastruma miccata* BOLTON, 1983: 348 and *Pyramica miccata*, BOLTON, 1999: 1673.

Strumigenys microthrix (Kempf). **New combination** for *Smithistruma microthrix* KEMPF, 1975: 422 and *Pyramica microthrix*, BOLTON, 1999: 1673.

Strumigenys minima (Bolton). **New combination** for *Epitritus minimus* BOLTON, 1972: 205 and *Pyramica minima*, BOLTON, 1999: 1672.

Strumigenys minkara (Bolton). **New combination** for *Smithistruma minkara* BOLTON, 1983: 306 and *Pyramica minkara*, BOLTON, 1999: 1673.

Strumigenys minuscula (Kempf). **New combination** for *Gymnomyrmex minusculus* KEMPF, 1962: 24 and *Pyramica minuscula*, BOLTON, 1999: 1672.

Strumigenys mira (Bolton). **New combination** for *Pyramica mira* BOLTON, 2000: 324.

Strumigenys mirabilis MANN, 1926: 105. *Tingimyrmex mirabilis* (Mann), BROWN, 1948: 111. *Pyramica mirabilis*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys missouriensis SMITH, 1931: 701. *Smithistruma missouriensis* (Smith), SMITH 1951: 828. *Pyramica missouriensis*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys mitis (Brown). **New combination** for *Pyramica mitis* Brown in BOLTON, 2000: 442.

Strumigenys mnemosyne (Bolton). **New combination** for *Pyramica mnemosyne* BOLTON, 2000: 446.

Strumigenys moloch (Bolton). **New combination** for *Pyramica moloch* BOLTON, 2000: 235.

Strumigenys morisitai (Ogata & Onoyama). **New combination** for *Smithistruma morisitai* OGATA & ONOYAMA, 1998: 284 and *Pyramica morisitai*, BOLTON, 1999: 1673.

Strumigenys mormo (Bolton). **New combination** for *Pyramica mormo* BOLTON, 2000: 290.

Strumigenys mumfordi WHEELER, 1932: 160. *Smithistruma mumfordi* (Wheeler), BROWN, 1953: 124. *Pyramica mumfordi*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys murphyi (Taylor). **New combination** for *Epitritus murphyi* TAYLOR, 1968b: 130 and *Pyramica murphyi*, BOLTON, 1999: 1672.

Strumigenys mutica (Brown). **New combination** for *Kyidris mutica* BROWN, 1949: 3 and *Pyramica mutica*, BOLTON, 1999: 1672.

Strumigenys myllorhapha (Brown). **New combination** for *Neostruma myllorhapha* BROWN, 1959: 12 and *Pyramica myllorhapha*, BOLTON, 1999: 1672.

Strumigenys nannosobek (Bolton). **New combination** for *Pyramica nannosobek* BOLTON, 2000: 453.

Strumigenys necopina (Bolton). **New combination** for *Pyramica necopina* BOLTON, 2000: 223.

Strumigenys nepalensis de Andrade in BARONI URBANI & DE ANDRADE, 1994: 57. *Smithistruma nepalensis* (de Andrade) BOLTON, 1995: 385. *Pyramica nepalensis*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys nigrescens WHEELER, 1911a: 28 [*Strumigenys alberti* var. *nigresens*]. *Smithistruma nigrescens* (Wheeler), BROWN, 1953: 96. *Pyramica nigrescens*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys ninda (Bolton). **New combination** for *Smithistruma ninda* BOLTON, 1983: 284 and *Pyramica ninda*, BOLTON, 1999: 1673.

Strumigenys nimravida (Bolton). **New combination** for *Pyramica nimravida* BOLTON, 2000: 332.

Strumigenys nitens SANTSCHI, 1932: 413. *Codiomyrmex nitens* (Santschi), WEBER, 1934: 52. *Dorisidris nitens* (Santschi), BROWN, 1948: 116. *Pyramica nitens*, BOLTON, 1999: 1672. **Combination in *Strumigenys* reinstated**.

Strumigenys noara (Bolton). **New combination** for *Pyramica noara* BOLTON, 2000: 304.

Strumigenys nongba (Xu & Zhou). **New combination** for *Pyramica nongba* XU & ZHOU, 2004: 440.

Strumigenys nubila LATTKE & GOITÍA, 1997: 387. *Pyramica nubila*, BOLTON: 1999. 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys nykara (Bolton). **New combination** for *Smithistruma nykara* BOLTON, 1983: 307 and *Pyramica nykara*, BOLTON, 1999: 1673.

Strumigenys oconitrilloae (Longino). **New combination** for *Pyramica oconitrilloae* LONGINO, 2006: 139.

Strumigenys ocypete (Bolton). **New combination** for *Pyramica ocypete* BOLTON, 2000: 420.

Strumigenys ogyga (Bolton). **New combination** for *Pyramica ogyga* BOLTON, 2000: 324.

Strumigenys ohioensis KENNEDY & SCHRAMM, 1933: 98. *Smithistruma ohioensis* (Kennedy & Schramm) SMITH, 1951: 828. *Pyramica ohioensis*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys olsoni (Bolton). **New combination** for *Pyramica olsoni* BOLTON, 2000: 353.

Strumigenys orchibia (Brown). **New combination** for *Smithistruma orchibia* BROWN, 1953: 105 and *Pyramica orchibia*, BOLTON, 1999: 1673.

Strumigenys ornata MAYR, 1887: 571. *Smithistruma ornata* (Mayr), SMITH, 1951: 828. *Pyramica ornata*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys oxysma (Bolton). **New combination** for *Smithistruma oxysma* BOLTON, 1983: 315 and *Pyramica oxysma*, BOLTON, 1999: 1673.

Strumigenys paniaguae (Longino). **New combination** for *Pyramica paniaguae* LONGINO, 2006: 137.

Strumigenys paradoxa (Bolton). **New combination** for *Pyramica paradoxa* BOLTON, 2000: 210.

Strumigenys parsauga (Bolton). **New combination** for *Pyramica parsauga* BOLTON, 2000: 157.

Strumigenys pasisops (Bolton). **New combination** for *Pyramica pasisops* BOLTON, 2000: 192.

Strumigenys pedunculata (Brown). **New combination** for *Smithistruma pedunculata* BROWN, 1953: 118 and *Pyramica pedunculata*, BOLTON, 1999: 1673.

Strumigenys peetersi (Bolton). **New combination** for *Pyramica peetersi* BOLTON, 2000: 474.

Strumigenys pergandei EMERY, 1895a: 326. *Smithistruma pergandei* (Emery), BROWN, 1948: 106. *Pyramica pergandei*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys perissognatha (Bolton). **New combination** for *Pyramica perissognatha* BOLTON, 2000: 238.

Strumigenys phasma (Bolton). **New combination** for *Pyramica phasma* BOLTON, 2000: 403.

Strumigenys pholidota (Bolton). **New combination** for *Pyramica pholidota* BOLTON, 2000: 225.

Strumigenys pilinasis FOREL, 1901: 339. *Smithistruma pilinasis* (Forel), SMITH, 1951: 828. *Pyramica pilinasis*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys piliversa (Bolton). **New combination** for *Pyramica piliversa* BOLTON, 2000: 339.

Strumigenys placora (Bolton). **New combination** for *Smithistruma placora* BOLTON, 1983: 308 and *Pyramica placora*, BOLTON, 1999: 1673.

Strumigenys podarge (Bolton). **New combination** for *Pyramica podarge* BOLTON, 2000: 421.

Strumigenys prex (Bolton). **New combination** for *Pyramica prex* BOLTON, 2000: 174.

Strumigenys probatrix (Brown). **New combination** for *Smithistruma probatrix* BROWN, 1964: 186 and *Pyramica probatrix*, BOLTON, 1999: 1673.

Strumigenys pulchella EMERY, 1895a: 327. *Smithistruma pulchella* (Emery), SMITH, 1951: 828. *Pyramica pulchella*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys pydrax (Bolton). **New combination** for *Pyramica pydrax* BOLTON, 2000: 466.

Strumigenys raptans (Bolton). **New combination** for *Pyramica raptans* BOLTON, 2000: 162.

Strumigenys ravidura (Bolton). **New combination** for *Glamyromyrmex ravidurus* BOLTON, 1983: 331 and *Pyramica ravidura*, BOLTON, 1999: 1672.

Strumigenys reflexa WESSON & WESSON, 1939: 102. *Smithistruma reflexa* (Wesson & Wesson), SMITH, 1951: 828. *Pyramica reflexa*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys reliquia (Ward). **New combination** for *Smithistruma reliquia* WARD, 1988: 117 and *Pyramica reliquia*, BOLTON, 1999: 1673.

Strumigenys reticeps (Kempf). **New combination** for *Codiomyrmex reticeps* KEMPF, 1969: 286 and *Pyramica reticeps*, BOLTON, 1999: 1672.

Strumigenys rhea (Bolton). **New combination** for *Pyramica rhea* BOLTON, 2000: 403.

Strumigenys robertsoni (Bolton). **New combination** for *Pyramica robertsoni* BOLTON, 2000: 305.

Strumigenys rogata (Bolton). **New combination** for *Pyramica rogata* BOLTON, 2000: 175.

Strumigenys rohweri SMITH, 1935: 214. *Smithistruma rohweri* (Smith), SMITH, 1951: 838. *Pyramica rohweri*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys roomi (Bolton). **New combination** for *Epitritus roomi* BOLTON, 1972: 206 and *Pyramica roomi*, BOLTON, 1999: 1672.

Strumigenys rostrata EMERY, 1895a: 329. *Smithistruma rostrata* (Emery), SMITH, 1951: 828. *Pyramica rostrata*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys rostrataeformis (Brown). **New combination** for *Smithistruma rostrataeformis* BROWN, 1949: 12 and *Pyramica rostrataeformis*, BOLTON, 1999: 1673.

Strumigenys rudinodis STÄRCKE, 1941: ii [*Strumigenys inezae* var. *rudinodis*]. *Weberistruma rudinodis* (Stärcke), BROWN, 1953: 26. *Smithistruma rudinodis* (Stärcke), BOLTON, 1995: 385. *Pyramica rudinodis*, BOLTON: 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys rugithorax (Kempf). **New combination** for *Gymnomyrmex rugithorax* KEMPF, 1959: 339 and *Pyramica rugithorax*, BOLTON, 1999: 1672.

Strumigenys runa (Bolton). **New combination** for *Pyramica runa* BOLTON, 2000: 447.

Strumigenys rusta (Bolton). **New combination** for *Smithistruma rusta* BOLTON, 1983: 3138 and *Pyramica rusta*, BOLTON, 1999: 1673.

Strumigenys sahura (Bolton). **New combination** for *Glamyromyrmex sahurus* BOLTON, 1983: 326 and *Pyramica sahura*, BOLTON, 1999: 1672.

Strumigenys sardonica (Bolton). **New combination** for *Pyramica sardonica* BOLTON, 2000: 326.

Strumigenys sauteri (Forel). **New combination** for *Pentastruma sauteri* FOREL, 1912a: 51 and *Pyramica sauteri*, BOLTON, 1999: 1673.

Strumigenys schleeorum Baroni Urbani in BARONI URBANI & DE ANDRADE, 1994: 35. *Smithistruma schleeorum* (Baroni Urbani), BOLTON, 1995: 385. *Pyramica schleeorum*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys schulzi EMERY, 1894: 213. *Smithistruma schulzi* (Emery), BROWN, 1953: 108. *Pyramica schulzi*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys scolapax (Bolton). **New combination** for *Pyramica scolapax* BOLTON, 2000: 439.

Strumigenys scylla (Bolton). **New combination** for *Pyramica scylla* BOLTON, 2000: 439.

Strumigenys semicompta (Brown). **New combination** for *Codiomyrmex semicomptus* BROWN, 1959: 9 and *Pyramica semicompta*, BOLTON, 1999: 1672.

Strumigenys serket (Bolton). **New combination** for *Pyramica serket* BOLTON, 2000: 349.

Strumigenys serradens (Bolton). **New combination** for *Pyramica serradens* BOLTON, 2000: 404.

Strumigenys serraformis (Bolton). **New combination** for *Pyramica serraformis* BOLTON, 2000: 405.

Strumigenys serrula SANTSCHI, 1910: 390 [*Strumigenys lujae* var. *serrula*]. *Serrastruma serrula* (Santschi), WEBER, 1952: 5. *Pyramica serrula*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys seti (Bolton). **New combination** for *Pyramica seti* BOLTON, 2000: 349.

Strumigenys sharra (Bolton). **New combination** for *Smithistruma sharra* BOLTON, 1983: 295 and *Pyramica sharra*, BOLTON, 1999: 1673.

Strumigenys shattucki (Bolton). **New combination** for *Pyramica shattucki* BOLTON, 2000: 475.

Strumigenys siagodens (Bolton). **New combination** for *Pyramica siagodens* BOLTON, 2000: 163.

Strumigenys simoni EMERY, 1895a: 42. *Smithistruma simoni* (Emery), BROWN, 1948: 107. *Serrastruma simoni* (Emery), BROWN: 1952: 82. *Pyramica simoni* (Emery), BOLTON: 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys simulans (Santschi). **New combination** for *Epitritus simulans* SANTSCHI, 1931: 278 and *Codioxenus simulans* (Santschi), BROWN, 1948: 123 and *Pyramica simulans*, BOLTON, 1999: 1672.

Strumigenys sinensis (Wang). **New combination** for *Pyramica sinensis* Wang in BOLTON, 2000: 390.

Strumigenys sistrura (Bolton). **New combination** for *Glamyromyrmex sistrurus* BOLTON, 1983: 329 and *Pyramica sistrura*, BOLTON 1999: 1672.

Strumigenys splendens (Borgmeier). **New combination** for *Gymnomyrmex splendens* BORGMEIER, 1954: 279 and *Pyramica splendens*, BOLTON, 1999: 1672.

Strumigenys stauroma (Bolton). **New combination** for *Pyramica stauroma* BOLTON, 2000: 226.

Strumigenys stenotes (Bolton). **New combination** for *Pyramica stenotes* BOLTON, 2000: 192.

Strumigenys subedentata MAYR, 1887: 570. *Pyramica subedentata*, BOLTON: 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys sublucida (Brown). **New combination** for *Smithistruma sublucida* BROWN, 1953: 99 and *Pyramica sublucida*, BOLTON, 1999: 1673.

Strumigenys subsessa (Bolton). **New combination** for *Pyramica subsessa* BOLTON, 2000: 306.

Strumigenys substricta (Kempf). **New combination** for *Glamyromyrmex substrictus* KEMPF, 1964: 68 and *Pyramica substricta*, BOLTON, 1999: 1672.

Strumigenys sulumana (Bolton). **New combination** for *Serrastruma sulumana* BOLTON, 1983: 352 and *Pyramica sulumana*, BOLTON, 1999: 1673.

Strumigenys stheno (Bolton). **New combination** for *Pyramica stheno* BOLTON, 2000: 440.

Strumigenys symmetrix (Bolton). **New combination** for *Pyramica symmetrix* BOLTON, 2000: 356.

Strumigenys synkara (Bolton). **New combination** for *Smithistruma synkara* BOLTON, 1983: 309 and *Pyramica synkara*, BOLTON, 1999: 1673.

Strumigenys tacta (Bolton). **New combination** for *Smithistruma tacta* BOLTON, 1983: 317 and *Pyramica tacta*, BOLTON, 1999: 1673.

Strumigenys takasago (Terayama, Lin & Wu). **New combination** for *Kyidris takasago* TERAYAMA, LIN & WU, 1995: 87 and *Pyramica takasago*, BOLTON, 1999: 1672.

Strumigenys talpa WEBER, 1934: 63. *Smithistruma talpa* (Weber), SMITH 1951: 828. *Pyramica talpa*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys tanymastax (Brown). **New combination** for *Smithistruma tanymastax* BROWN, 1964: 183 and *Pyramica tanymastax*, BOLTON, 1999: 1673.

Strumigenys taphra (Bolton). **New combination** for *Pyramica taphra* BOLTON, 2000: 448.

Strumigenys tarbosyne (Bolton). **New combination** for *Pyramica tarbosyne* Bolton, 2000: 422.

Strumigenys tathula (Bolton). **New combination** for *Pyramica tathula* BOLTON, 2000: 352.

Strumigenys tenuipilis EMERY, 1915: 264 [*Strumigenys baudueri* var. *tenuipilis*]. *Smithistruma tenuipilis* (Emery), BROWN, 1953: 132. *Pyramica tenuipilis*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys tenuissima (Brown). **New combination** for *Smithistruma tenuissima* BROWN, 1953: 133 and *Pyramica tenuissima*, BOLTON, 1999: 1673.

Strumigenys teratrix (Bolton). **New combination** for *Pyramica teratrix* BOLTON, 2000: 163.

Strumigenys terayamai (Bolton). **New combination** for *Pyramica terayamai* BOLTON, 2000: 468.

Strumigenys terroni (Bolton). **New combination** for *Smithistruma terroni* BOLTON, 1983: 299 and *Pyramica terroni*, BOLTON, 1999: 1673.

Strumigenys tethepa (Bolton). **New combination** for *Pyramica tethepa* BOLTON, 2000: 328.

Strumigenys tethys (Bolton). **New combination** for *Pyramica tethys* BOLTON, 2000: 406.

Strumigenys tetragnatha (Taylor). **New combination** for *Codiomyrmex tetragnathus* TAYLOR, 1966: 225 and *Pyramica tetragnatha*, BOLTON, 1999: 1672.

Strumigenys thaxteri (Wheeler). **New combination** for *Codiomyrmex thaxteri* WHEELER, 1916: 327 and *Pyramica thaxteri*, BOLTON, 1999: 1672.

Strumigenys theia (Bolton). **New combination** for *Pyramica theia* BOLTON, 2000: 407.

Strumigenys themis (Bolton). **New combination** for *Pyramica themis* BOLTON, 2000: 407.

Strumigenys thuvida (Bolton). **New combination** for *Glamyromyrmex thuvidus* BOLTON, 1983: 332 and *Pyramica thuvida*, BOLTON, 1999: 1672.

Strumigenys tiglath (Bolton). **New combination** for *Epitritus tiglath* BOLTON, 1983: 357 and *Pyramica tiglath*, BOLTON, 1999: 1672.

Strumigenys tigrilla (Brown). **New combination** for *Miccostruma tigrilla* BROWN, 1973a: 32 and *Smithistruma tigrilla* (Brown), BOLTON, 1983: 284 and *Pyramica tigrilla*, BOLTON, 1999: 1673.

Strumigenys tisiphone (Bolton). **New combination** for *Pyramica tisiphone* BOLTON, 2000: 390.

Strumigenys tlaloc (Bolton). **New combination** for *Pyramica tlaloc* BOLTON, 2000: 244.

Strumigenys tolomyla (Bolton). **New combination** for *Smithistruma tolomyla* BOLTON, 1983: 310 and *Pyramica tolomyla*, BOLTON, 1999: 1673.

Strumigenys transversa SANTSCHI, 1913: 258. *Smithistruma transversa* (Santschi), BROWN, 1948: 105. *Pyramica transversa*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys trauma (Bolton). **New combination** for *Pyramica trauma* BOLTON, 2000: 408.

Strumigenys trieces BROWN, 1960: 50. *Pyramica trieces*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys truncatidens (Brown). **New combination** for *Smithistruma truncatidens* BROWN, 1950b: 43 and *Pyramica truncatidens*, BOLTON, 1999: 1673.

Strumigenys trymala (Bolton). **New combination** for *Glamyromyrmex trymalus* BOLTON, 1983: 333 and *Pyramica trymala*, BOLTON, 1999: 1672.

Strumigenys tukulta (Bolton). **New combination** for *Glamyromyrmex tukultus* BOLTON, 1983: 334 and *Pyramica tukulta*, BOLTON, 1999: 1672.

Strumigenys turpis (Bolton). **New combination** for *Pyramica turpis* BOLTON, 2000: 176.

Strumigenys umboceps (Bolton). **New combination** for *Pyramica umboceps* BOLTON, 2000: 227.

Strumigenys urrhobia (Bolton). **New combination** for *Pyramica urrhobia* BOLTON, 2000: 228.

Strumigenys vartana (Bolton). **New combination** for *Pyramica vartana* BOLTON, 2000: 195.

Strumigenys vescops (Bolton). **New combination** for *Pyramica vescops* BOLTON, 2000: 409.

Strumigenys victrix (Bolton). **New combination** for *Pyramica victrix* BOLTON, 2000: 356.

Strumigenys villiersi (Perrault). **New combination** for *Gymnomyrmex villiersi* PERRAULT, 1986: 1 and *Pyramica villiersi*, BOLTON, 1999: 1672.

Strumigenys vodensa (Bolton). **New combination** for *Smithistruma vodensa* BOLTON, 1983: 317 and *Pyramica vodensa*, BOLTON: 1999: 1673.

Strumigenys warditeras (Bolton). **New combination** for *Pyramica warditeras* BOLTON, 2000: 246.

Strumigenys weberi (Brown). **New combination** for *Smithistruma weberi* BROWN, 1959: 7 and *Pyramica weberi*, BOLTON, 1999: 1673.

Strumigenys wheeleriana Baroni Urbani. **New name** for *Glamyromyrmex wheeleri* SMITH, 1944: 266, transferred to *Strumigenys* in the present paper. *Pyramica wheeleri*, BOLTON, 1999: 1672. Nec *Epitritus wheeleri* DONISTHORPE, 1916: 121, junior synonym of *Strumigenys emmae* (Emery). Nec *Strumigenys wheeleri* MANN, 1921: 466, secondary homonym of *Epitritus wheeleri* DONISTHORPE, 1916: 121.

Strumigenys wilsoniana Baroni Urbani. **New name** for *Pyramica wilsoni* Wang in BOLTON, 2000: 469. Nec *Strumigenys wilsoni* BROWN, 1969: 28.

Strumigenys wrayi (Brown). **New combination** for *Smithistruma wrayi* BROWN, 1950b: 38 and *Pyramica wrayi*, BOLTON, 1999: 1673.

Strumigenys xenochelyna (Bolton). **New combination** for *Pyramica xenochelyna* BOLTON, 2000: 165.

Strumigenys xenognatha KEMPF, 1958: 64. *Pyramica xenognatha*, BOLTON, 1999: 1673. **Combination in *Strumigenys* reinstated**.

Strumigenys xenomastax (Bolton). **New combination** for *Pyramica xenomastax* BOLTON, 2000: 471.

Strumigenys yaleogyna (Wilson & Brown). **New combination** for *Kyidris yaleogyna* WILSON & BROWN, 1956: 443 and *Pyramica yaleogyna*, BOLTON, 1999: 1672.

Strumigenys yangi (Xu & Zhou). **New combination** for *Pyramica yangi* XU & ZHOU, 2004: 445.

Strumigenys zeteki (Brown). **New combination** for *Neostruma zeteki* BROWN, 1959: 10 and *Pyramica zeteki*, BOLTON, 1999: 1672.

5. KEY TO THE EXTANT GENERA OF AGROECOMYRMECINI AND DACETINI

The key to the Dacetini genera by BOLTON (2000), in spite of the facilitation due to the exclusion of *Basiceros* and some small genera, contains a number of invalid statements if one broadens the number of taxa examined. For instance, presence or absence of the limbus as used in the first couplet to separate his "strumigenyte genera" from the other dacetines does not hold if *Phalacromyrmex* and *Basiceros* are also considered. Several elements of BOLTON's (2000) key cannot be used in our context. On the other hand, uncertainties are implicitly recognized also by Bolton while qualifying characters as "extremely rare" or "extremely rarely absent". Several other characters were already shown during the present study to hold for a majority of species only.

The following key should be of broader validity due to the more rigorous and operational generic definitions adopted for the present study. Although imprecise, the key still contains also some probabilistic statements similar to those employed by Bolton since they may facilitate identification in a number of cases.

1. Eyes present and posterior to the antennal scrobe. Petiolar tergum and sternum differently shaped. No specialized large mechanoreceptors on the mouthparts. Neotropical .... *Tatuidris*

- Eyes generally present and never posterior to the antennal scrobe, or, very rarely (*Strumigenys inopinata*) absent. Petiolar tergum and sternum equally convex. Mouthparts nearly always with some large, specialized mechanoreceptors (exceptions a few *Strumigenys* and *Epopostruma* species).. 2

2. Pretergite of first gastral segment subsessile to sessile. Base of scape bent at right angle near the base. First gastral segment nearly always sculptured. Neotropical, Indomalayan, Australian .... *Basiceros*

- Pretergite of first gastral segment neck like. Base of scape straight or at least complanar with the basal condyle, rarely bent at right angle. First gastral segment almost never sculptured (exceptions, a few *Strumigenys* species) 3

3. Mandibles with alternating small and large teeth. Scape clavate. Basimandibular process absent....................4

-   Mandibular dentition different, or, if alternating large and small teeth present, the scape is never clavate. Basimandibular process nearly always present 6

4. Katepisternal oblique groove deeply impressed. Vertexal angles pointed backwards, mesosoma dorsally marginate. Malaysia ....*Ishakidris*

-   None of the characters above... 5

5. Mesosternal hair beds hypertrophied. Long and flexuous pilosity on the whole body. Head sculpture deeply reticulate. Antennae eight jointed. Madagascar. ....*Pilotrochus*

-   Mesopleurae obliquely costulate. Pilosity rare and short. Frontal lobes strongly developed. Antennae eleven jointed. Brazil ....*Phalacromyrmex*

6. Eyes ventral or, very rarely, absent. Labial palps one jointed. Basal process of the mandibles never hypertrophied. World tropics and temperate areas ....*Strumigenys*

-   Eyes always present, dorsal or lateral. Labial palps generally two or three jointed, if one jointed, the basal process of the mandibles is hypertrophied 7

7. Basimandibular process hypertrophic and bifurcated at the apex, situated below the labrum with closed mandibles. Maxillary palps absent. Neotropical ....*Acanthognathus*

-   Basimandibular process normally developed, situated above the labrum with closed mandibles. Maxillary palps present 8

8. Second funicular joint hypertrophic, longer than the last segment. Indomalayan and Australian .... *Orectognathus*

-   Second funicular joint normally developed, shorter than the last segment.......................................9

9. Antennae eleven jointed. Eyes dorsal. Occipital foramen dorsal. Neotropical. ....*Daceton*

- Antennae four to eight jointed. Eyes dorsolateral. Occipital
  foramen posterior 10

10. Large pre-genal cavity visible in profile behind the base of
    the mandibles. Palp formula 3,2. Labrum not capable of full
    reflexion over the buccal cavity. Antennal scrobes absent.
    Ethiopian . . . . *Microdaceton*

- Gap between mandibles and head capsule reduced in pro-
  file. Palp formula 5,3. Labrum capable of full reflexion
  over the buccal cavity. Antennal scrobes below the eyes.
  Australian . . . . *Epopostruma*

6. SPECIES-LEVEL ADDITIONS

Basiceros floridanum (Brown and Kempf)

Cuba: Sancti Spiritus Province: way between Topes de Col-
lantes and Trinidad, 19.XII.2000, 1 worker, M. L. de Andrade &
C. Baroni Urbani, Winkler extraction from litter (MSNG). Ciego
de Avila Province: way between Ciego de Avila and Majagua,
17.XII.2000, 1 worker, C. Baroni Urbani & M. L. de Andrade,
Winkler extraction from litter (MSNG).

This species was previously known only from Florida, from
where there is an extensive list of locality records, and from Mexico
(DEYRUP *et al.*, 1997). BROWN & KEMPF (1960) suggest that the
species may have been introduced to Florida from Latin America.
DEYRUP *et al.* (1997) substantially agree with this supposition but
note that the lack of West Indian records should be considered as a
counter-argument for the hypothesis. The two Cuban records above
fill this gap.

Basiceros o n o r e i Baroni Urbani & de Andrade n. sp.

Type material: holotype worker (unique) from Ecuador labelled:
Baños de Água Santa, Prov. Tungurahua, 01°24'S 78°25'W, 1860 m, sendero Bella
Vista, leaf-litter, 26.VIII.2004, C. Baroni Urbani & M. L. de Andrade (PUCE).

Derivatio nominis. This species is named after Prof Dr Giovanni
Onore who facilitated in multiple ways our Dacetini field work in Ecuador.

Diagnosis. A *Basiceros* species belonging to the *petiolatum*-group as defined by BROWN & KEMPF (1960) (in *Octostruma*) and differing from all species of this group, *inca*, *jheringi*, *stenoscapum*, *petiolatum* and *wheeleri* (BROWN & KEMPF, 1960; PALACIO, 1997), by the following combination of characters: occipital margin with a row of four clavate hairs, each upper scrobe margin with one clavate hair, pronotum and mesonotum with a pair of clavate hairs each, gaster with 4 rows of erect, clavate hairs (2,2,2,4), sides of the basal face of the propodeum strongly marginate, and propodeum, pleurae and gaster largely smooth, sub-opaque to shining.

Worker description (Fig. 47). Head dorsum weakly convex in full dorsal view. Postero-lateral sides of the head with the two anterior thirds diverging posteriorly into a round angle and the posterior third gently converging into a weakly concave vertexal margin. Frontal lobes weakly expanded and convex. Antennal fossae ventrally with a marked carina visible in full-face view, straight, covering the lower margin of the scrobes and ending below the eye. Eyes small, with 4 ommatidia in the longest row, placed on the upper margin of the antennal scrobes. With head in profile the scrobe very distinct, with the upper margin behind the eye broad, lamellaceous, semitransparent and the lower one strongly carinate. Anterior clypeal border medially with a broad concavity. Scapes slightly compressed dorsoventrally, with strong subbasal bend. Antennae with eight joints. Apical funicular joint slightly longer than the rest of the funiculus. Mandibles triangular, with a series of 5 teeth and two irregular denticles before the subround apex.

Mesosoma anteriorly convex and posteriorly sloping in profile. Dorsum of the mesosoma medially with a broad, superficial, longitudinal sulcus spacing from the pronotum to the mesonotum. Propodeal suture superficially impressed. Posterior half of the basal face of the propodeum gently concave. Sides of the basal face of the propodeum strongly marginate. Propodeal teeth large, lamellaceous, transparent, apically pointed and with broad base. Upper bases of propodeal teeth strongly marginate, connected each other and forming a clear carina dividing the basal and declivous faces. Lower base of propodeal teeth ending on the middle of the declivous face. Posterior half of the declivous propodeal face weakly marginate. Propodeal spiracle large and below the lower base of the propodeal tooth.

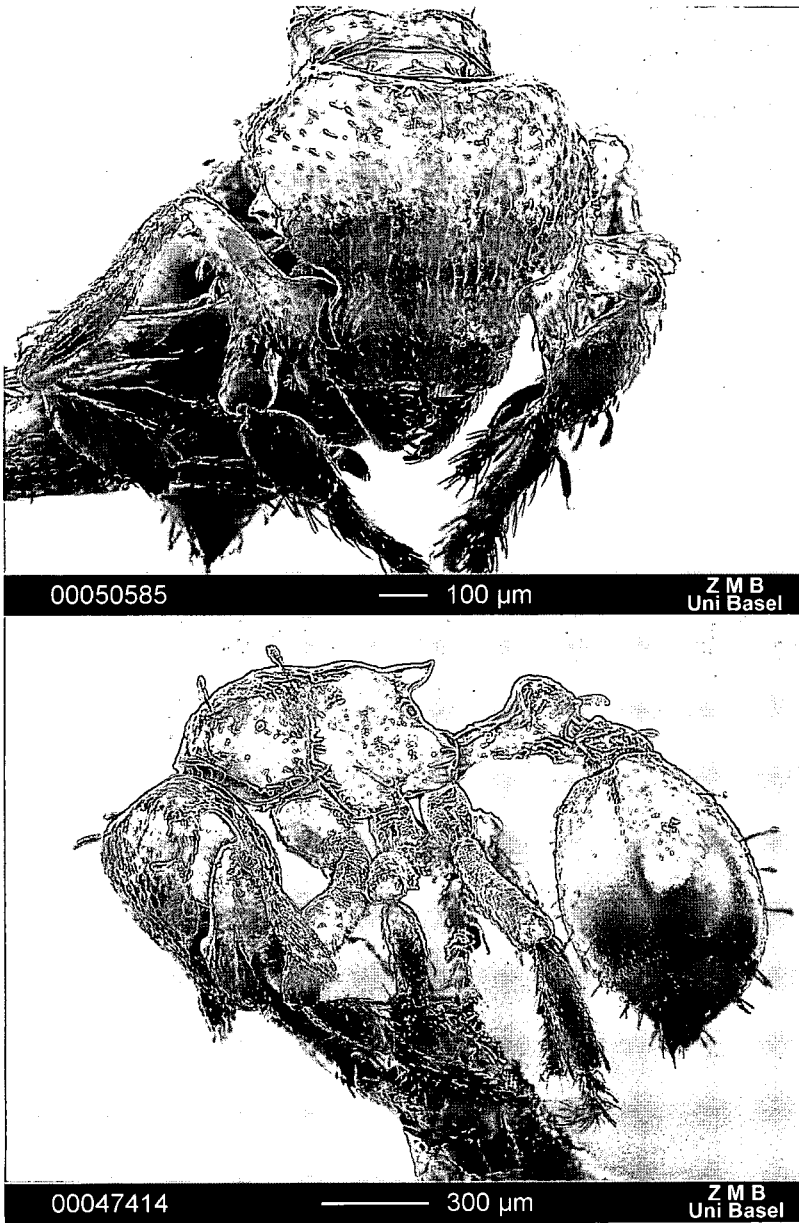00050585 — 100 µm — ZMB Uni Basel

00047414 — 300 µm — ZMB Uni Basel

Fig. 47 - *Basiceros onorei* n. sp. from Ecuador. Worker, head in dorsal view (top) and entire profile (bottom).

Petiole with a long neck and with the node high anteriorly and sloping posteriorly. Ventral surface of the petiolar neck anteriorly with a small lamellaceous tooth pointed forwards. Postpetiole almost flat in side view; in dorsal view the anterior and posterior borders well marked by a thicker and anteriorly semitransparent carina.

Gaster oval. Base of the first gastral tergite clearly marginate. Base of the first gastral sternite superficially marginate.

Sculpture. Head reticulate-punctuate and with thin, irregular longitudinal rugosities. Pronotum and mesonotum irregularly reticulate and very superficially punctuate, the reticulation less marked on the posterior half of the mesonotum. Propodeum and pleurae smooth and shining, in addition the pleurae with a few minute punctures. Gaster smooth and shining, in addition the posterior border of the first gastral tergite, the anterior and posterior borders of the first gastral sternite and all remaining tergites and sternites with well impressed, large punctures.

Pilosity. Body with appressed, short, thin, decumbent hairs, very rare on the dorsum of the propodeum and pleurae. Posterior margin of the head dorsum with a row of four clavate erect hairs. Upper antennal scrobes with one clavate erect hair each. Pronotum, mesonotum and posterior half of the petiole and postpetiole with a pair of clavate, erect hairs each. First gastral tergite with four rows of clavate erect hairs, the first up to the third rows with two clavate hairs and the fourth row with four hairs close to the posterior border. Remaining gastral tergites with four clavate hairs, thinner than on the first tergite. First gastral sternite medially with erect, truncate or weakly clavate hairs; posterior half of the first gastral sternite and remaining gastral sternites with clavate hairs much thinner than on the tergites. Apex of the tibiae with a few clavate hairs.

Colour. Dark brown with slightly lighter antennae and legs.

Measurements (in mm) and indices: TL 2.84; HL 0.67; HW 0.74; SL 0.45; ML 0.22; EL 0.06; WL 0.76; CI 110.4.

Discussion. *B. onorei* differs from the 5 known species of the *petiolatum*-group of "*Octostruma*" as defined by BROWN & KEMPF (1960) by the combination of characters listed in the diagnosis. *B. onorei* shares with *iheringi* the head dorsum with irregular rugosities but differs from *iheringi* mainly by the presence of standing hairs on the mesosoma and gaster. *B. onorei* shares with *petiolatum* the

mesosoma and gaster superficially smooth but differs from it mainly by having 6 standing hairs instead of 16 on the head dorsum and by the head weakly instead of broadly convex.

Basiceros p a p u a n u m   de Andrade n. sp.

T y p e   m a t e r i a l :   holotype worker (left antenna and left hind tibia and tarsus missing) from Papua New Guinea labelled: Papua NG: Morobe, Wau, 1150 m, 17.V.1992, G. Cuccodoro, # 2C (MHNG). Paratype: 1 dealate gyne (right funiculus missing), same data and collection as the holotype.

D e r i v a t i o   n o m i n i s .   "Papuanus" is a neologism indicating the provenance of this species from Papua New Guinea.

D i a g n o s i s .   A *Basiceros* species belonging to the *"brevi-cornis*-group" of *"Eurhopalothrix"* as defined by BROWN & KEMPF (1960) and TAYLOR (1968a), resembling *B. brevicorne* but differing from it by the following combination of characters: erect specialized hairs on the head dorsum 10 (8+2) instead of 16 (8+4+4), first gastral tergite without standing hairs instead of with 3 pairs, and larger size (TL 2.1 mm instead of 1.7-1.8 mm).

Worker description (Fig. 48). Head dorsum gently convex in full dorsal view. Postero-lateral sides of the head with the two anterior thirds diverging posteriorly to a subround angle and the posterior third gently converging into a weakly concave vertexal margin. Frontal lobes weakly expanded and convex. Antennal fossae ventrally with a marked carina visible in full-face view, straight, covering the lower margin of the scrobes and ending below the eye. Eyes small, with 2 ommatidia in the longest row, placed on the upper margin of the antennal scrobes. With head in profile the scrobes are very distinct, with the upper margin behind the eye with a thin margin, and the lower one thicker and lamellaceous. Anterior clypeal border medially with a broad concavity. Scapes slightly compressed dorso-ventrally, with subbasal strong bend. Antennae with seven segments. Apical funicular joint slightly longer than the rest of the funiculus. Mandibles triangular, with a series of 12 teeth, teeth 3-5-7-9 much longer than the remaining ones.

Mesosoma in profile with pronotum and mesonotum forming a convex arch and basal face of the propodeum strongly sloping posteriorly. Propodeal suture very superficially impressed. Area between
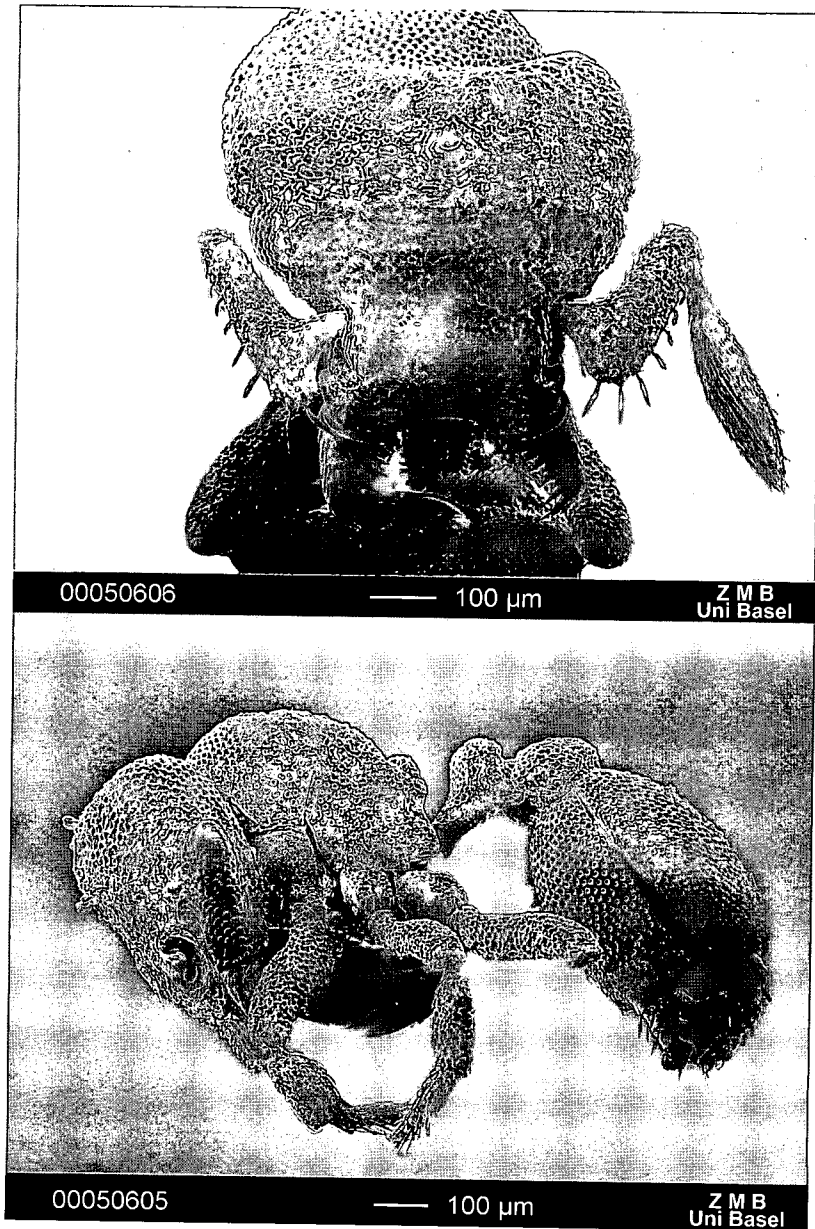
Fig. 48 - *Basiceros papuanum* n. sp. from Papua New Guinea. Head of the gyne in dorsal view (top) and entire profile of the worker (bottom).

basal and declivous faces of the propodeum with a small triangular sub-lamellaceous tooth prolonging to the declivous face as a thin lamella.

Petiole with a long neck and with high, convex node. Petiolar node slightly more than 1/2 broader than long. Ventral surface of the petiolar neck with a small lamellaceous tooth pointed forwards anteriorly. Postpetiole convex in side view and about 1/2 broader than long and broadly connected to the gaster.

Gaster oval. Base of the first gastral tergite clearly marginate. Base of the first gastral sternite superficially marginate.

Sculpture. Head, mesosoma, petiole, postpetiole and gaster densely foveolate, the foveae slightly sparser on the first gastral sternite. Legs strongly punctuate.

Pilosity. Body with appressed, short, decumbent hairs, very rare on the anterior face of pronotal dorsum, on the lower pro- and mesopleurae, and on the propodeum, thicker on the remaining part of the pronotum and mesonotum, thinner and slightly longer on the posterior part of the first gastral tergite, longer and decumbent on the posterior half of the first gastral sternite. Frons with two rows of specialized hairs, the anterior row composed by 8 clavate hairs forming an arch connecting the eyes and the posterior row composed by 2 hairs on the middle of the vertex. Remaining gastral tergites and sternites with few, subdecumbent, spatulate hairs. In addition the second, third and fourth gastral sternites with subdecumbent, long and slightly spatulate hairs. Distal outer face of the tibiae and upper outer face of tarsi with one or two thick spatulate hairs each.

Colour. Ferruginous-brown.

Measurements (in mm) and indices: Worker (holotype): TL 2.10; HL 0.48; HW 0.53; SL 0.29; ML 0.13; EL 0.04; WL 0.49; CI 110.4; SI 54.7; MI 27.1.

Gyne description. Similar to the worker but differing in the following details. Eyes large. Ocelli present. Scape and mandibles as in Fig. 48. Mesosoma robust and flat in profile. Parapsidal furrows weakly impressed. Sides of the scutellum converging posteriorly to form a rounded posterior border. Basal face of the propodeum very short and in the same plane as the declivous one. Propodeal tooth and lamellae less developed.

Pilosity. Similar to the worker but the anterior half of the mesonotum with two pairs of short, thin, erect hairs on the centre and each side of the mesonotum with a similar hair as the dorsal ones. Pre-scutellum and scutellum with a clavate hair on each side, thicker on the scutellum.

Gyne (paratype): TL 2.51; HL 0.55; HW 0.62; SL 0.33; ML 0.20; EL 0.13; WL 0.72; CI 112.7; SI 53.2; MI 36.4.

D i s c u s s i o n .   The *brevicorne* group is known from the literature to be composed by six species, *australe*, *biroi*, *brevicorne*, *caledonicum*, *philippinum* and *punctatum* (BROWN & KEMPF, 1960; TAYLOR, 1968a). Among these six species, the new species described here as *papuanum*, resembles *brevicorne* in general shape. *B. papuanum* is the sole species of the group having the specialized hairs on the head dorsum distributed in two rows of 8 and 2 hairs each instead of 8:4:4 or 2 or without hairs. TAYLOR (1967) mentions a dealate gyne from N. E. New Guinea (Kunai Creek, Bulolo River Valley) resembling *punctatum* and *brevicorne* or an undescribed species. Later, TAYLOR (1970) suggests that the gyne from Kunai Creek seems unlikely to be *punctatum*. This gyne from Kunai Creek differs from *brevicorne* mainly by the head with 12 hairs divided in two rows of 8:4 instead of 8:4:4, by the first gastral tergite without specialized hairs and by the larger size. It differs from gyne of *papuanum* by the larger values of HL and WL and by the specialized hairs on the head dorsum 8:4 instead of 8:2. Considering the cephalic chaetotaxy the Kunai Creek specimen could be attributed either to a new species very close to *papuanum*, or to true *papuanum*, if one considers that the type material of *papuanum* might have lost both lateral hairs of the second row of hairs on the middle of the vertex.

Basiceros sp. nr. *ciliatum* (Mayr)

Ecuador, Pichincha, S. José de Guaramal, 1,900 m, August 3, 2004, 1 dealate gyne, G. Osella (PUCE).

This specimen should be referred to *B. ciliatum* Mayr, the gyne of which is still unknown. Since this unique gyne is not accompanied by workers, our attribution remains tentative.

Strumigenys v e d d h a de Andrade n. sp.

T y p e m a t e r i a l : holotype worker (unique) from Sri Lanka labelled: Ceylan North central, Alut Oya, 3.II.[19]70, Mussard, Besuchet & Löbl (MHNG).

D e r i v a t i o n o m i n i s : from the Veddhas, the name of one of the Sri Lanka's indigenous inhabitants. It is used as a noun in apposition.

D i a g n o s i s . A *Strumigenys* belonging to the *lyroessa*-group and to the *prosopis*-complex as defined by BOLTON (2000) and differing from the six species of this complex by the CI = 73.3 instead of ≥ 77, by the cephalic dorsum without standing hairs and by the much more superficial sculpture on the head and mesosoma, and, in particular, from the species *loricata* Bolton, *panopla* Bolton, *prosopis* Bolton and *strenosa* Bolton by the petiole with a pair of standing hairs, and from *anchiplex* Boltonn and *propinqua* Bolton by the smaller values of SI < 57 instead of ≥ 60, by the lack of pronotal humeral hairs and by the first gastral tergite with basal and apical pairs of erect hairs only.

Worker description (Fig. 49). Head strongly converging anteriorly, with round vertexal corners and moderately flattened dorsoventrally. Frontal lobes weakly expanded and convex. Antennal fossae ventrally with a developed carina visible in full-face view, straight, covering the lower margin of the scrobes and ending in front of the eyes. Eyes small, with 5 ommatidia in the longest row, placed over the ventral margin of the antennal scrobes, and not visible in dorsal view. Scrobe distinct in profile, with marked upper and lower margins only. Lateral clypeal margin gently converging anteriorly to a straight margin. Scapes less than half of the head length, slightly thicker on the posterior half and surpassing the eyes posteriorly. Antennae with six segments. Apical funicular joint longer than the rest of the funiculus. Mandibles short, broad proximally and tapered distally; their outer margin convex basally. Apical fork of the mandible with two spiniform teeth, the apicodorsal one larger; space between the two apical spiniform teeth bearing one intercalary denticle. Preapical dentition consisting of 1 spiniform tooth.

Mesosoma in profile slightly flat and gently sloping posteriorly. Propodeal teeth subtended by a broad lamella.

Petiole with a long neck and round node. Ventral surface of the petiole with a broad spongiform lamina. Petiolar node with posterior sides and posterior margin surrounded by spongiform processes. Postpetiole gently convex in profile. Anterior, lateral and posterior
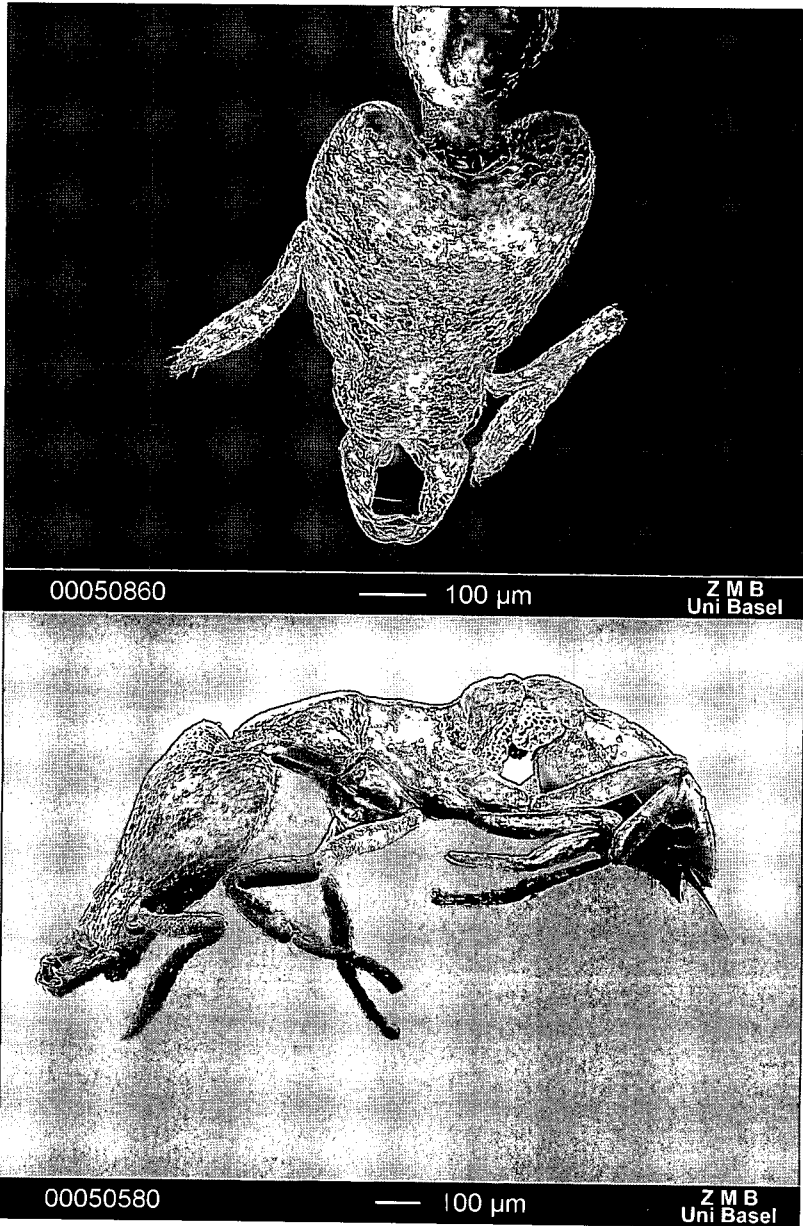
Fig. 49 - *Strumigenys veddha* n. sp. from Sri Lanka. Worker, head in dorsal view (top) and entire profile (bottom).

faces of the postpetiole surrounded by spongiform processes broader posteriorly. Ventral surface of the postpetiole with large and dense spongiform process.

Gaster oval and with a few, short costulae. Base of the first gastral tergite and sternite with spongiform pad larger on the tergite.

Sculpture. Head and anterior half of propleurae finely reticulate-punctuate and superficially shining. Mesosomal dorsum and petiolar node largely smooth and shining, with very sparse, faint, minute reticulation-punctuation. Posterior half of the propleurae and remaining pleurae smooth. Postpetiole and gaster smooth and shining.

Pilosity. Head dorsum with appressed, thin, short hairs only. Upper scrobes margin and leading edge of scape with similar but thicker and slightly longer hairs than on the head dorsum. Apicoscrobal hair missing. Mesosoma, petiole, postpetiole and gaster with hairs similar to those on the head dorsum but much sparser. Mesosoma and postpetiole without erect hairs. Petiole with a pair of stiff standing hairs. First gastral tergite with two pairs of erect stiff hairs, one pair near the base, the other near the apex.

Colour. Light yellowish.

Measurements (in mm) and Indices: TL 2.12; HL 0.58; HW 0.425; SL 0.24; ML 0.17; EL 0.06; WL 0.56; CI 73.3; SI 56.5; MI 29.3.

Discussion. Among the 6 species of the *prosopis*-complex *S. veddha* resembles especially *loricata*. *Veddha* and *loricata* share the cephalic dorsum finely reticulate-punctuate and the promesonotum with sculpture similar to the one on the head but less impressed. But *veddha* differs from *loricata* mainly by the longer head (CI = 73.3 instead of $\geq$ 82) and by the first gastral tergite with two pairs of stiff hairs, one near to the base and another near to the apex (*loricata* has no standing hairs on the first tergite). Among the six species of the *prosopis*-complex only *veddha* and *panopla* have the first gastral tergite with one pair of stiff hairs near the base and another pair near the apex.

Strumigenys onorei Baroni Urbani & de Andrade n. sp.

Type material: holotype worker from Ecuador labelled: Baños de Água Santa, Prov. Tungurahua, 01°24'S 78°25'W, 1860 m, sendero Bella Vista, leaf-litter, 26.VIII.2004, Juan Manuel Vieira Correa (PUCE). Paratype: 1 worker, same data and collection as the holotype.

Derivatio nominis. This species is named after Prof Dr Giovanni Onore as a sign of gratitude for his multiple helps during our fieldwork in Ecuador.

Diagnosis. A *Strumigenys* belonging to the *gundlachi*-group and *gundlachi*-complex as defined by BOLTON (2000), resembling *enopla* (Bolton), but differing from it by the smaller SI values ($\leq$ 79.5 instead of $\geq$ 84), by the shorter propodeal spines, by the postpetiole with the ventral spongiform process larger and by the standing hairs on head and gaster shorter.

Worker description (Fig. 50). Head strongly converging anteriorly and with round vertexal corners. Frontal lobes slightly expanded and convex. Antennal fossae ventrally with a marked carina visible in full-face view, straight, covering the lower margin of the scrobes and ending close to the upper border of the eye. Eyes with 3-4 ommatidia in the longest row, placed over the ventral margin of the antennal scrobes, and partially visible in dorsal view. With the head in profile the scrobe distinct, with the upper margin more marked than the lower one. Lateral clypeal margins gently converging anteriorly into a straight margin. Scapes slightly compressed dorsoventrally, with weak sub-basal bend, about 2/3 of the head length and surpassing the eyes posteriorly. Antennae with six segments. Apical funicular joint slightly longer than the rest of the funiculus. Mandibles elongate. Apical fork of the mandibles with two teeth and with two intercalary denticles. Preapical dentition consisting of a row with 4-6 minute denticles.

Mesosoma in profile gently sloping posteriorly. Propodeal teeth small and triangular; declivous propodeal face with a narrow lamella.

Petiole with a long pedicel and with the node high and convex. Ventral surface of the petiole without spongiform lamina. Petiolar node with marked posterior margin and without spongiform process. Postpetiole gently convex in profile. Postpetiole with marked anterior face; lateral and posterior faces surrounded by narrow spongiform processes slightly broader on the posterior face. Ventral surface of the postpetiole with spongiform process shorter than the height of the node in profile.

Gaster oval and with few, short costulae. Base of the first gastral tergite with narrow, spongiform pad.

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00050624   ⸻ 100 µm   Z M B
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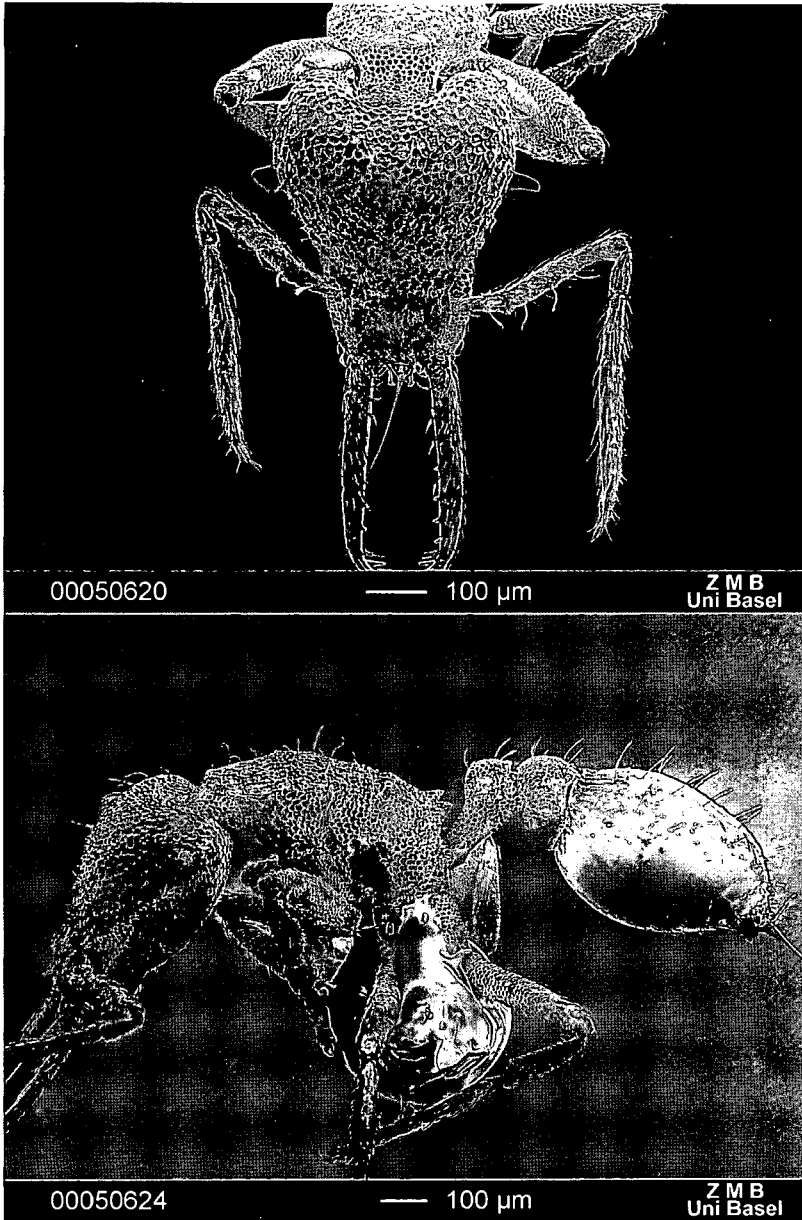
Fig. 50 - *Strumigenys onorei* n. sp. from Ecuador. Worker, head in dorsal view
(top) and entire profile (bottom).

Sculpture. Head, mesosoma, petiole and postpetiole reticulate-punctuate. Lower mesopleurae and gaster smooth.

Pilosity. Head and mesosoma with subdecumbent or decumbent, weakly remiform hairs, rarer on the pronotum and mesonotum, missing on the propodeum. Apicoscrobal hair long and flagellate. Cephalic dorsum with two pairs of standing hairs, one close to the vertexal margin and the other close to the highest point of the vertex. Pronotal humeral hair long and flagellate. Mesonotal dorsum with 1 pair of erect, flagellate hairs. The holotype shows on the left side of the mesonotum one erect stiff hair before the flagellate one. This hair is missing in the unique paratype worker. Petiole, post-petiole and first gastral tergite with erect, sparse, weakly remiform hairs slightly longer on the gaster. Posterior half of the first gastral sternites and remaining sternites with appressed and erect pointed hairs.

C o l o u r .   Dark brown-black.

Measurements (in mm) and indices: TL 2.10-230; HL 0.49-0.54; HW 0.39-0.43; SL 0.31-0.34; ML 0.37-0.39; EL 0.06; WL 0.52-0.58; CI 79.6; SI 79.1-79.5; MI 72.2-75.5.

D i s c u s s i o n .   The 15 species of the *gundlachi*-complex can be divided in 4 clusters of closely related species. *S. onorei* can be placed in the *gundlachi* s. str. cluster comprising the following 5 species: *denticulata* Mayr, *eggersi* Emery, *enopla* (Bolton), *gundlachi* (Roger) and *jamaicensis* Brown. Among these five species, *onorei* resembles *enopla*, and both species share the SI $\geq$ 79-100. Of the other species of the *gundlachi* complex, only some specimens of *jamaicensis* and *denticulata* may have SI 80-81, but *jamaicensis* differs from *onorei* and *enopla* by the strongly developed preapical dentition (inconspicuous in *onorei* and *enopla*) and by the larger spongiform process of postpetiole, while *denticulata* differs from both, *onorei* and *enopla* by the pair of erect hairs on the mesonotum shorter and stiff instead of long and flagellate and by the spongiform process of postpetiole much more reduced or absent. *S. onorei* differs from all the 5 species mentioned above by having the smallest propodeal teeth and probably also by the mesonotum with 2 pairs of erect hairs instead of one (see the description). By using the identification key by BOLTON (2000) for the Neotropical species of *Pyramica*, *S. onorei* will fall in the couplet 26 where it can be differentiated from

jamaicensis by using all characters of the first couplet and exclud-
ing only " head slightly shorter and broader, CI 77-85", and from
enopla by the following characters: SI < 80, standing hairs on the
head about as long as the eye length, spongiform process of the
postpetiole at least 1/3 as height to the exposed cuticle of side of
postpetiole disc.

Strumigenys longimala de Andrade n. sp.

Type material: holotype worker from Ecuador labelled: Yasuní
Scientific Station, Prov. Orellana, 00° 40' 760" S, 76° 23' 032" W, 230 m, leaf-
litter, 28.VIII.2004, M. L. de Andrade & C. Baroni Urbani (PUCE). Paratypes:
2 worker and 1 dealate gyne same data and collection as the holotype (PUCE, 1
paratype worker MHNG).

Derivatio nominis: from the Latin *longus* (= long) and *mala* (=
mandible), referred to the length of the mandibles, among the longest of the genus.

Diagnosis. A *Strumigenys* belonging to the *trudifera*-group
as defined by BOLTON (2000), but differing from the sole species of
the group (i. e. *trudifera* Kempf & Brown), in the worker and gyne
by the smaller values of SI ≤ 104.5 instead of 108.0, by the propo-
deal spines shorter, and by the flagellate hairs on the gaster sparser;
in the worker only by the smaller values of MI (≤103) instead of
≥110; and in the gyne only by MI 91.6 instead of 102.8.

Worker description (Fig. 51). Head strongly converging anteri-
orly and with round vertexal angles. Frontal lobes slightly expanded
and convex. Anterior half of the dorsal margin of the antennal
scrobes broad and ending in a subround denticle over the eyes.
Antennal fossae ventrally with a broad carina visible in full-face
view, straight and medially denticulate, covering the lower margin
of the scrobes and ending close to the upper border of the eye. Eyes
with 3 ommatidia in the longest row, placed over the ventral margin
of the antennal scrobes, and partially visible in dorsal view. With
the head in profile the scrobes are distinct, almost reaching the ver-
texal angles, with ventral margin and posterior half of the dorsal
margin superficially marked. Lateral clypeal margins gently convex
and anteriorly concave in the middle. Postbuccal groove impressed.
Scapes subcylindric, slightly more than 2/3 of the head length and
surpassing the eyes posteriorly. Antennae with six segments. Apical
funicular joint as long as the rest of the funiculus. Mandibles very

long, about as long as the head length. Apical fork of the mandibles with two teeth and without intercalary denticles. Preapical dentition consisting of one long, spiniform tooth only.

Mesosoma in profile convex anteriorly and slightly raised posteriorly before the propodeal spines. Propodeal spines long but shorter than the the basal face of the propodeum; declivous propodeal face with a thin lamella.

Petiole with a long pedicel and with convex node. Ventral surface of the petiole with a thin lamina. Petiolar node with marked posterior margin and with a small spongiform process on the posterior lateral third. Postpetiole convex in profile, with marked anterior and posterior faces; lateral faces surrounded by broad spongiform process. Ventral surface of the postpetiole with very broad spongiform process.

Gaster oval and with costulae on its anterior third. Base of the first gastral tergite and sternite with spongiform pad broader on the sternite.

Sculpture. Head, mesosoma, petiole and postpetiole reticulate-punctuate. Gaster and area between meso- and metapleurae smooth.

Pilosity. Head and mesosoma with subdecumbent or decumbent, narrow spatulate hairs, rarer on the mesosoma. Apicoscrobal hair long and flagellate. Cephalic dorsum with two pairs of standing hairs. Leading edge of the scape with 2 long hairs that curve toward the base of the scape. Pronotal humeral hair long and flagellate. Mesonotum with 1 pair of erect, flagellate hairs. Petiole, postpetiole, first and second gastral tergites with flagellate hairs. Posterior half of the first gastral sternite and remaining sternites with sparse, erect pointed hairs.

C o l o u r .   Dark brown.

Measurements (in mm) and indices: TL 2.78-2.94; HL 0.64-0.66; HW 0.44-0.46; SL 0.46-0.48; ML 0.65-0.68; EL 0.05-0.06; WL 0.62-0.64; CI 68.7-69.7; SI 104.3-104.5; MI 101.5-103.0.

Gyne description. Similar to the worker but differing in the following details. Eyes large. Ocelli present. Mesosoma robust and weakly convex in profile. Parapsidal furrows impressed. Sides of the scutellum with a thin lamella converging posteriorly to form an obtuse angle. Basal face of the propodeum declivous posteriorly.
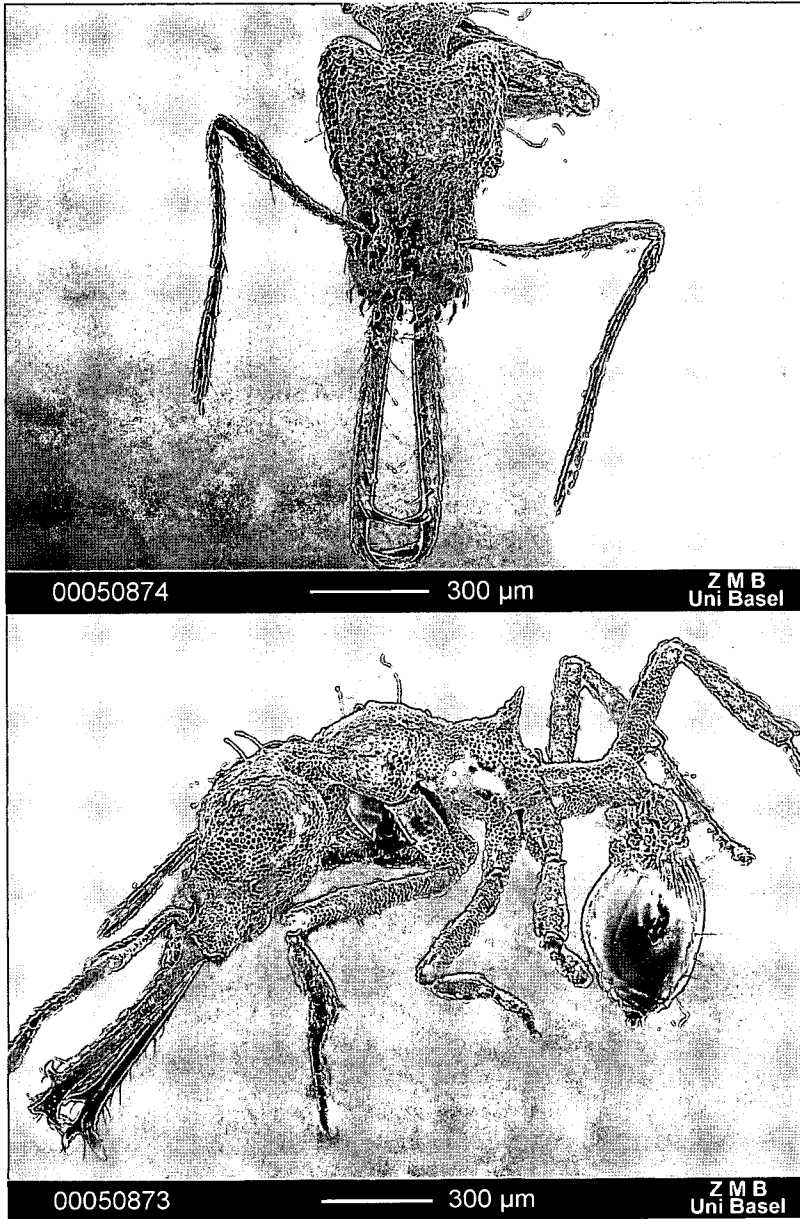
Fig. 51 - *Strumigenys longimala* n. sp. from the Yasuní Scientific Station (Ecuador). Worker, head in dorsal view (top) and entire profile (bottom).

Propodeal spines large and continuing to the declivous face as a lamella.

Ventral surface of the petiole with a broader lamina.

Sculpture. Head and mesosoma with irregular rugosities, more regular and denser on the mesosoma.

Pilosity. Similar to the worker but the mesonotum with 3 pairs of flagellate hairs. Pre-scutellum and scutellum with a flagellate hair on each side.

Measurements (in mm) and indices: TL 3.26; HL 0.72; HW 0.52; SL 0.50; ML 0.66; EL 0.10; WL 0.76; CI 72.2; SI 96.1; MI 92.9.

D i s c u s s i o n .   *S. longimala* is obviously the sister species of *trudifera* (Brazil, Colombia and Venezuela) with which it shares all most remarkable traits. Both species constitute the *trudifera*-group characterized by the very long mandibles and by the scape with 2 hairs curved towards the base. *S. longimala* and *trudifera* can be easily separated from all other species of the genus by the values of SI, MI (see diagnosis) and by the number of flagellate hairs on the first gastral tergite. The worker and gyne of *longimala* have 16 and 22 flagellate hairs respectively on the first gastral tergite while those of *trudifera* have 20 and 26.

Strumigenys a d u n c o m a l a   de Andrade n. sp.

T y p e   m a t e r i a l :   holotype worker (unique) from India labelled: Upper Shillong, 1900 m, 13.V.1976, Meghalaya, W. Wittmer & C. Baroni Urbani (NHMB).

D e r i v a t i o   n o m i n i s :   from the Latin *aduncus* (= curved), and *mala* (= mandible), referred to the very curved shape of the mandibles.

D i a g n o s i s .   A *Strumigenys* belonging to the *caniophanes*-group and to the *caniophanes*-complex as defined by BOLTON (2000), resembling *lacunosa* Lin & Wu, but differing from it by the dorso-lateral margin of the head with 2 instead of 3 hairs projecting later-ally, by its smaller size (TL = 2.52 mm instead of 3.1 mm) and by the lower MI (43.7 instead of 50).

Worker description (Fig. 52). Head converging anteriorly, with round vertexal corners. Frontal lobes weakly expanded and convex. Antennal fossae ventrally with a narrow carina visible in full-face view, straight, not covering the lower margin of the scrobes and

ending much before the eyes. Eyes small, with 3-4 ommatidia in the longest row, placed over the ventral margin of the antennal scrobes, and visible in dorsal view. With head in profile the scrobe distinct, with weakly marked upper and lower margins. Lateral clypeal margins gently converging anteriorly into a straight margin. Scapes subcylindrical, about 1/2 of the head length and surpassing the eyes posteriorly. Antennae with six joints. Apical funicular joint moderately constricted basally and longer than the rest of the funiculus. Mandibles curved. Apical fork of the mandible with two spiniform teeth, the apicodorsal larger; space between the apical teeth bearing one intercalary denticle. Preapical dentition consisting of one tooth.

Mesosoma in profile weakly convex anteriorly and sloping posteriorly. Propodeal teeth pointed; declivous propodeal face marginate only. Mesepisternal hair beds large but smaller than the maximum width of the fore coxa.

Petiole with a long neck and round node. Ventral surface of the petiole with a broad spongiform lamina. Petiolar node with posterior sides and posterior margin surrounded by spongiform process. Postpetiole gently convex in side view. Anterior, lateral and posterior faces of the postpetiole surrounded by spongiform processes broader posteriorly. Ventral surface of the postpetiole with large and dense spongiform process.

Gaster oval and with thin, short costulae. Base of the first gastral tergite and sternite with spongiform pad larger on the tergite.

Sculpture. Head, dorsum of the mesosoma, propleurae and petiole densely reticulate-punctuate. Postpetiole with very sparse, superficial punctures. Meso- and metapleurae and gaster smooth.

Pilosity. Head, mesosoma, petiole and postpetiole with appressed, thin, hairs. Dorsolateral margin of the head in full-face view with 2 freely laterally projecting flagellate hairs, one in apicoscrobal position and one just posterior to the eye. Cephalic dorsum with a transverse row of 4 erect fine hairs along the occipital margin, and with 2 pairs of similar hairs anterior to this, the anterior pair shorter and on the frons and the posterior pair on the middle of the occipital lobes. Pronotal humeral hairs flagellate and long. Dorsum of the pronotum with two pairs of erect fine hairs. Dorsum of the mesonotum with 4 pairs of erect flagellate hairs, the anterior and posterior pairs shorter. Dorsum of the propodeum with rare subdecumbent
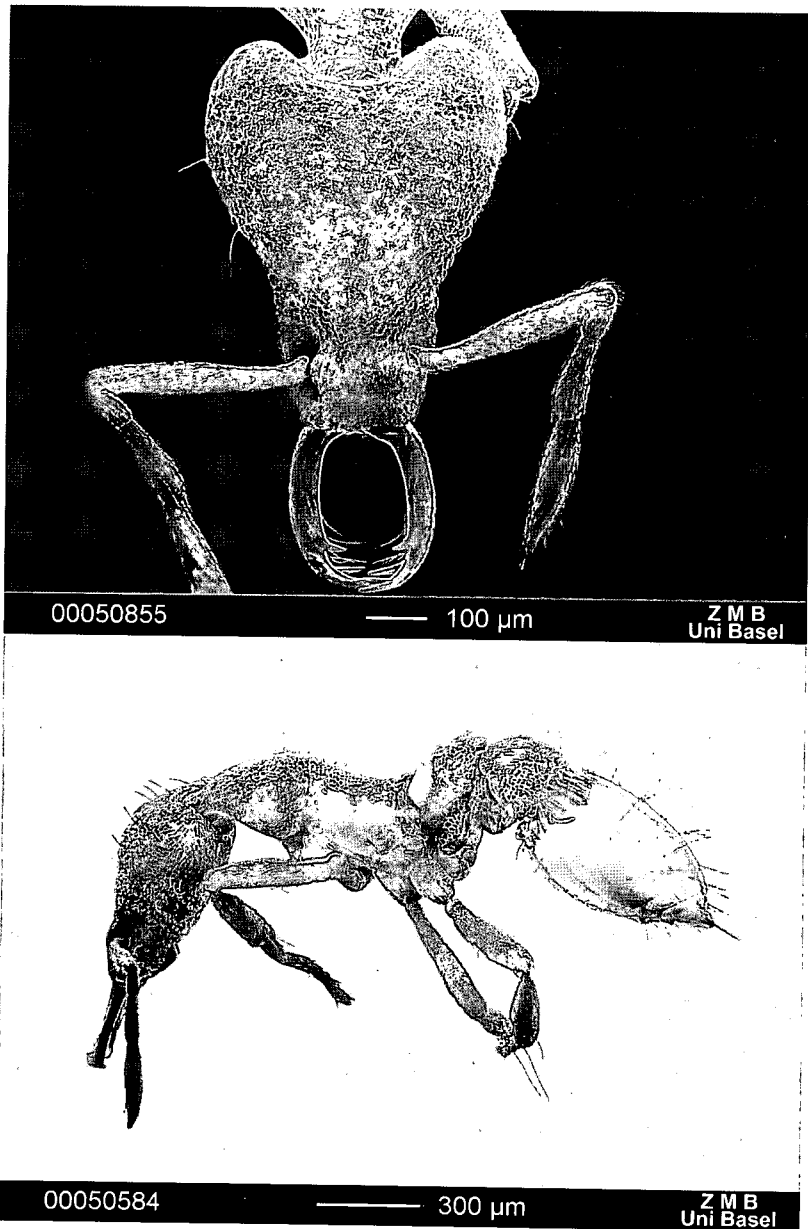
Fig. 52 - *Strumigenys aduncomala* n. sp. from Meghalaya (India). Worker, head in dorsal view (top) and entire profile (bottom).

fine hairs. Petiolar node with three pairs of fine hairs, the posterior pair longer and flagellate. Postpetiole and gaster with long flagellate hairs. Femora and tibiae with a few erect or suberect hairs. Mid- and hind basitarsi with 2 long fine erect hairs.

C o l o u r .   Light brownish.

Measurements (in mm) and indices: TL 2.52; HL 0.64; HW 0.46; SL 0.34; ML 0.28; EL 0.04; WL 0.69; CI 71.9; SI 73.9; MI 43.7.

D i s c u s s i o n .   Among the 12 species of the *caniophanes*-complex, *aduncomala* resembles more *lacunosa*. *S. aduncomala and lacunosa* share the apical funicular segment moderately constricted basally, the dorsum of the pronotum with at least 2 pairs of erect hairs and the dorsum of the mesonotum with about 4 pairs of erect hairs. At first glance *S. aduncomala* superficially resembles *exilirhina* Bolton in general body shape, for having the dorsolateral margin of the head in full-face view with 2 projecting hairs, and for the basal constriction of the apical funicular antennomere. But *exilirhina* belongs to the *mayri*-group whose component species are characterized mainly by the anterior clypeal margin with a U-shaped or V-shaped median notch and by the apical antennomere strongly constricted basally. *S. aduncomala* has the anterior clypeal margin straight and the apical antennomere moderately constricted basally.

Strumigenys c a n i o p h a n o i d e s   de Andrade n. sp.

T y p e   m a t e r i a l :   holotype worker (unique) from Bhutan labelled: Phuntsholing, 2/400 m, 16.IV.1972, Nat. Hist. Museum Basel-Bhutan Expedition (NHMB).

D e r i v a t i o   n o m i n i s :   from the existing *Strumigenys* species name *caniophanes* and the Greek εἶδος (= look), referred to the similarity between *caniophanes* and the new species.

D i a g n o s i s .   A *Strumigenys* belonging to the *caniophanes*-group and to the *caniophanes*-complex as defined by BOLTON (2000), resembling *caniophanes* Bolton and *paraposta* Bolton, but differing from *caniophanes* by the mandibles with a preapical denticle (without denticle on *caniophanes*), by the rugae on the side of mesosoma irregular and sparser, and from *paraposta* by its larger size (TL 3.38-3.42 mm instead of 2.9-3.0 mm) and by the dorsolateral margin of the head with more than 5 hairs projecting laterally, and from both, *caniophanes* and *paraposta*, by the SI 80.0-81.7 instead of 68-78.

Worker description (Fig. 53). Head with sides converging anteriorly and with round occipital corners. Frontal lobes weakly expanded and convex. Antennal fossae ventrally with a marked carina visible in full-face view, straight, covering the lower margin of the scrobes and ending in front of the eyes. Eyes small, with 5 ommatidia in the longest row, placed over the ventral margin of the antennal scrobes, and visible in dorsal view. With head in profile the scrobe distinct, with weakly marked upper and lower margins. Clypeal dorsum concave medially. Lateral clypeal margin gently converging anteriorly into a straight margin. Scapes subcylindrical, about 3/5 of the head length and surpassing the eyes posteriorly. Antennae with six joints. Apical funicular joint slightly shorter than the rest of the funiculus. Mandibles elongate, basally and apically weakly convex and medially straight. Apical fork of the mandibles with two spiniform teeth and one intercalary denticle. Preapical dentition consisting of one tooth near the apex.

Mesosoma in profile weakly convex anteriorly and sloping posteriorly. Propodeal teeth pointed; declivous propodeal face marginate only.

Petiole with a long neck and with low and long node. Ventral surface of the petiole with a broad spongiform lamina. Petiolar node with posterior margin surrounded by spongiform process that in profile covers the posterior third of the node's sides. Postpetiole gently convex in side view. Anterior, lateral and posterior faces of the postpetiole surrounded by spongiform processes broader posteriorly. Ventral surface of the postpetiole with large and dense spongiform process.

Gaster oval and with thin, short costulae. Base of the first gastral tergite and sternite with spongiform pad larger on the tergite.

Sculpture. Head coarsely and densely reticulate-punctuate. Mesosoma reticulate-punctuate and with irregular longitudinal rugosities; the rugosities slightly more regular on the pleurae and missing on the lower mesopleurae. Petiole and postpetiole densely reticulate-punctuate. Gaster smooth. Outer face of fore coxae with transversal rugosities.

Pilosity. Head, mesosoma, petiole and postpetiole with appressed, thin hairs. Dorsolateral margin of the head in full-face view with more than 5 freely laterally projecting hairs. Cephalic dorsum at

00050579 ——— 100 µm Z M B Uni Basel

00047411 —————— 500 µm Z M B Uni Basel
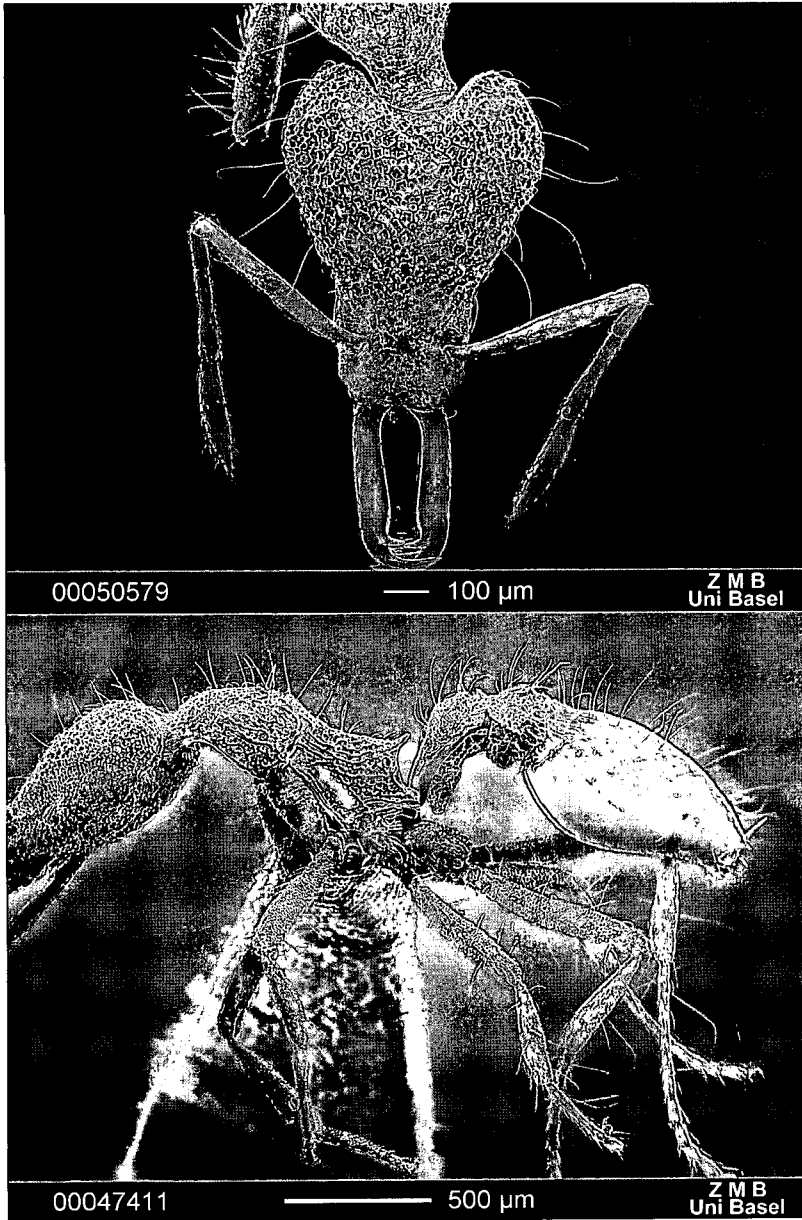
Fig. 53 - *Strumigenys caniophanoides* n. sp. from Bhutan. Worker, head in dorsal view (top) and profile (bottom).

level of the eyes with fine standing hairs of different lengths. Prono-
tal humeral hairs long and flagellate. Dorsum of the mesosoma, pet-
iole, postpetiole and gaster with erect, fine hairs of different lengths,
longer on the gaster. Femora, tibiae and tarsi with numerous erect,
fine hairs of different lengths, two of which on the tibiae and two
of which on the tarsi much longer than the others.

C o l o u r .   reddish brown.

Measurements (in mm) and indices: TL 3.42; HL 0.82; HW 0.60; SL 0.49;
ML 0.40; EL 0.08; WL 0.90; CI 73.2; SI 81.7; MI 48.8.

Additional material: Nepal: Prov. Kosi, Distr. Sankhuwasawa,
Vallée d'Arun, vic. Num, 1100 m, 21.IV.1984, 1 worker, I. Löbl &
A. Smetana (MHNG).

Measurements (in mm) and indices of the Nepalese worker: TL 3.38; HL 0.82;
HW 0.60; SL 0.48; ML 0.40; EL 0.08; WL 0.88; CI 73.2; SI 80.0; MI 48.8.

D i s c u s s i o n .   Among the 12 species of the *caniophanes*-
complex *S. caniophanoides* is particularly similar to *caniophanes* and
paraposta. *S. caniophanoides* shares with *caniophanes* the large size
and the dorsolateral sides of the head in full dorsal view with more
than 5 projecting hairs. *S. caniophanoides* shares with *paraposta* the
pleurae with irregular rugae, the lower mesopleurae largely smooth
and the presence of preapical dentition on the mandibles.

Strumigenys *h i n d u*   de Andrade n. sp.

T y p e   m a t e r i a l :   holotype worker (unique) from Nepal labelled: Pokhara,
820 m, 15-18.VI.1976, Nepal, W. Wittmer, C. Baroni Urbani (NHMB).

D e r i v a t i o   n o m i n i s :   the Hindu religion, one of the two major
religions of Nepal is used here as a noun in apposition.

D i a g n o s i s .   A *Strumigenys* belonging to the *godeffroyi*-
group and to the *godeffroyi*-complex as defined by BOLTON (2000),
resembling *uberyx* Bolton and *buddhista* de Andrade (q. v.), but
differing from these two species by its larger size (TL = 2.5 mm
instead of 1.8-1.9 mm) and by the SI = 102.6 (instead of ≤ 91).

Worker description (Fig. 54). Head sides converging anteri-
orly, with round vertexal corners. Frontal lobes weakly expanded
and convex. Antennal fossae ventrally with a marked carina vis-

ible in full-face view, straight, covering the lower margin of the
scrobes and ending close to the eyes. Eyes small, with 2 ommatidia
in the longest row, placed over the ventral margin of the antennal
scrobes, and slightly visible in dorsal view. With the head in pro-
file the scrobe distinct, with superficially marked upper and lower
margins. Clypeal dorsum gently concave medially. Lateral clypeal
margin gently converging anteriorly into a straight margin. Scapes
subcylindrical, about 2/3 of the head length and surpassing the eyes
posteriorly. Antennae with six joints. Apical funicular joint much
longer than the rest of the funiculus. Mandibles curved. Apical fork
of the mandibles with two spiniform teeth and with two intercalary
denticles. Preapical dentition consisting of one spiniform tooth near
the apex.

Mesosoma in profile weakly convex anteriorly and sloping pos-
teriorly into the gently convex basal face of the propodeum. Pro-
podeal teeth pointed and ventrally connected to a medially convex
lamella.

Petiole with a long neck and with the node high, dorsally almost
flat and anteriorly tumuliform. Ventral surface of the petiole with a
broad spongiform lamina. Petiolar node with posterior margin and
whole sides surrounded by spongiform process. Postpetiole gently
convex in side view. Anterior, lateral and posterior margins of the
postpetiole surrounded by spongiform processes. Ventral surface of
the postpetiole with large and dense spongiform process.

Gaster oval and with thin, short costulae. Base of the first gas-
tral tergite and sternite with spongiform pad larger on the tergite.

Sculpture. Head reticulate and minutely punctuate. Pronotum,
pleurae and declivous face of the propodeum smooth. Mesonotum,
basal face of the propodeum and petiole punctuate, the punctures
fainter and sparser on the petiole. Postpetiole and gaster smooth.

Pilosity. Head, mesosoma, petiole and postpetiole with appressed,
thin hairs. Dorsolateral margin of the head in full-face view with the
apicoscrobal flagellate hair only. Cephalic dorsum with three rows of
erect hairs, the first row with 4 hairs close to the occipital margin,
the second row with 4 standing hairs and the third row with 2 hairs
on the frons. Upper scrobal margin with narrow spoon-shaped hairs
curved anteriorly. Clypeal border with hairs similar to those of the
upper scrobe. Scapes with hairs also similar to those on the upper
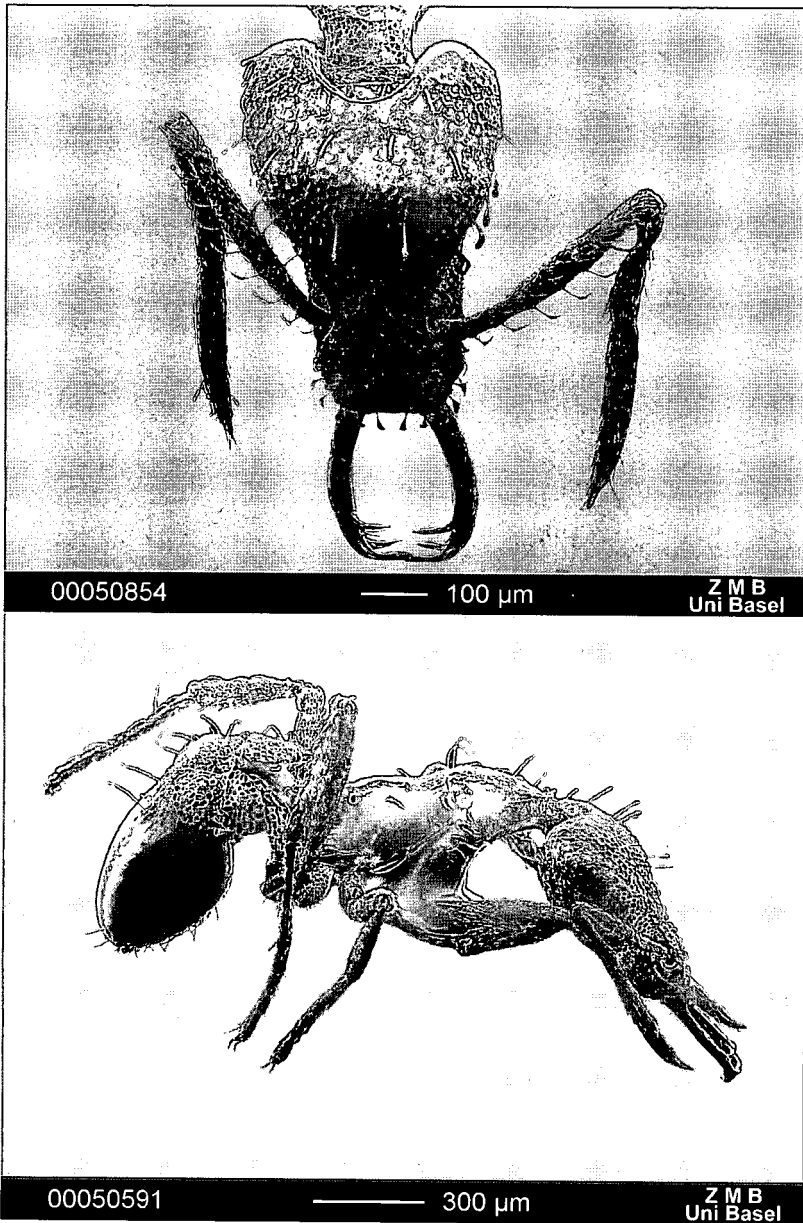
Fig. 54 - *Strumigenys hindu* n. sp. from Nepal. Worker, head in dorsal view (top) and entire profile (bottom).

scrobes and curved posteriorly. Pronotal humeral hairs long and flagellate. Dorsum of the pronotum with a pair of erect long hairs. Mesonotum with a pair of erect flagellate hairs. Petiole, postpetiole and gaster with few erect flagellate hairs. Dorsal face of hind femora with an erect fine hair on the basal third. Outer face of mid and hind tibiae with an erect, long flagellate hair. Hind basitarsi with 1-2 pairs of erect, long flagellate hairs.

C o l o u r .   light brown.

Measurements (in mm) and indices: TL 2.50; HL 0.62; HW 0.38; SL 0.39; ML 0.26; EL 0.03; WL 0.66; CI 61.3; SI 102.6; MI 41.9.

D i s c u s s i o n .   *S. hindu, uberyx* and *buddhista* are very similar each other but the characters listed in their respective species diagnosis separate them clearly.

Strumigenys *b u d d h i s t a*   de Andrade n. sp.

T y p e   m a t e r i a l :   holotype worker (unique) from Nepal labelled: Pokhara, 820 m, 15-18.VI.1976, Nepal, W. Wittmer, C. Baroni Urbani (NHMB).

D e r i v a t i o   n o m i n i s :   name derived from the Buddhism, the second major religion in Nepal.

D i a g n o s i s .   A *Strumigenys* belonging to the *godeffroyi*-group and to the *godeffroyi*-complex as defined by BOLTON (2000), resembling *uberyx* and *hindu*, but differing from *uberyx* by the mandibles longer and with less convex sides and by the anterior face of the petiolar node more protruding anteriorly, and from *hindu* by its smaller size (TL 1.96 mm instead of 2.50 mm), by the smaller SI (90.9 instead of SI = 102.6), and from both, *uberyx* and *hindu*, by the standing hairs on the head dorsum, less numerous.

Worker description (Fig. 55). Head sides converging anteriorly, with round vertexal corners. Frontal lobes weakly expanded and convex. Antennal fossae ventrally with a marked carina visible in full-face view, straight, covering the lower margin of the scrobes and ending close to the eyes. Eyes small, with 2 ommatidia in the longest row, placed over the ventral margin of the antennal scrobes, and slightly visible in dorsal view. With the head in profile the scrobe distinct, with superficially marked upper and lower margins. Clypeal dorsum weakly concave medially. Lateral clypeal margin

gently converging anteriorly into a straight margin. Scapes subcylindrical, about 3/5 of the head length and surpassing the eyes posteriorly. Antennae with six segments. Apical funicular joint longer than the rest of the funiculus. Mandibles diverging anteriorly and curved on the two anterior thirds. Apical fork of the mandibles with two spiniform teeth and with one intercalary denticle. Preapical dentition consisting of one spiniform tooth near the apex.

Mesosoma in profile with weakly convex mesonotum and with a longitudinal carina starting from the mesonotum and ending on the anterior half of the basal face of the propodeum; the carina thicker and shaped as a small triangular protuberance on the propodeum. Posterior half of the propodeum declivous. Propodeal teeth pointed and ventrally connected to a lamella.

Petiole with a long neck and with the node high, weakly convex dorsally and broadly tumuliform anteriorly. Ventral surface of the petiole with a broad spongiform lamina. Petiolar node with posterior margin and posterior sides surrounded by spongiform process. Postpetiole gently convex in profile. Anterior, lateral and posterior margin of the postpetiole surrounded by spongiform processes. Ventral surface of the postpetiole with large and dense spongiform process.

Gaster oval and with few, thin, very short costulae. Base of the first gastral tergite and sternite with a spongiform pad larger on the tergite.

Sculpture. Head minutely reticulate-punctuate. Pronotum, pleurae and declivous face of the propodeum smooth; in addition the pronotum with a few sparse punctures. Mesonotum, basal face of the propodeum and petiole punctuate. Postpetiole and gaster smooth.

Pilosity. Head, mesosoma, petiole and postpetiole with appressed hairs, denser on the petiole. Dorsolateral margin of the head in full-face view with only the apicoscrobal flagellate hairs. Cephalic dorsum with three rows of erect hairs, the first row with 4 hairs close to the occipital margin, the second row with 2 standing hairs and the third row with 2 standing hairs on the frons. Upper scrobal margin with narrowly spoon-shaped hairs curved anteriorly. Clypeal border with similar hairs as the upper scrobe. Scapes with similar hairs as the upper scrobes and curved posteriorly. Pronotal humeral hairs long and flagellate. Dorsum of the pronotum with a pair of erect, long flagellate hairs. Mesonotum
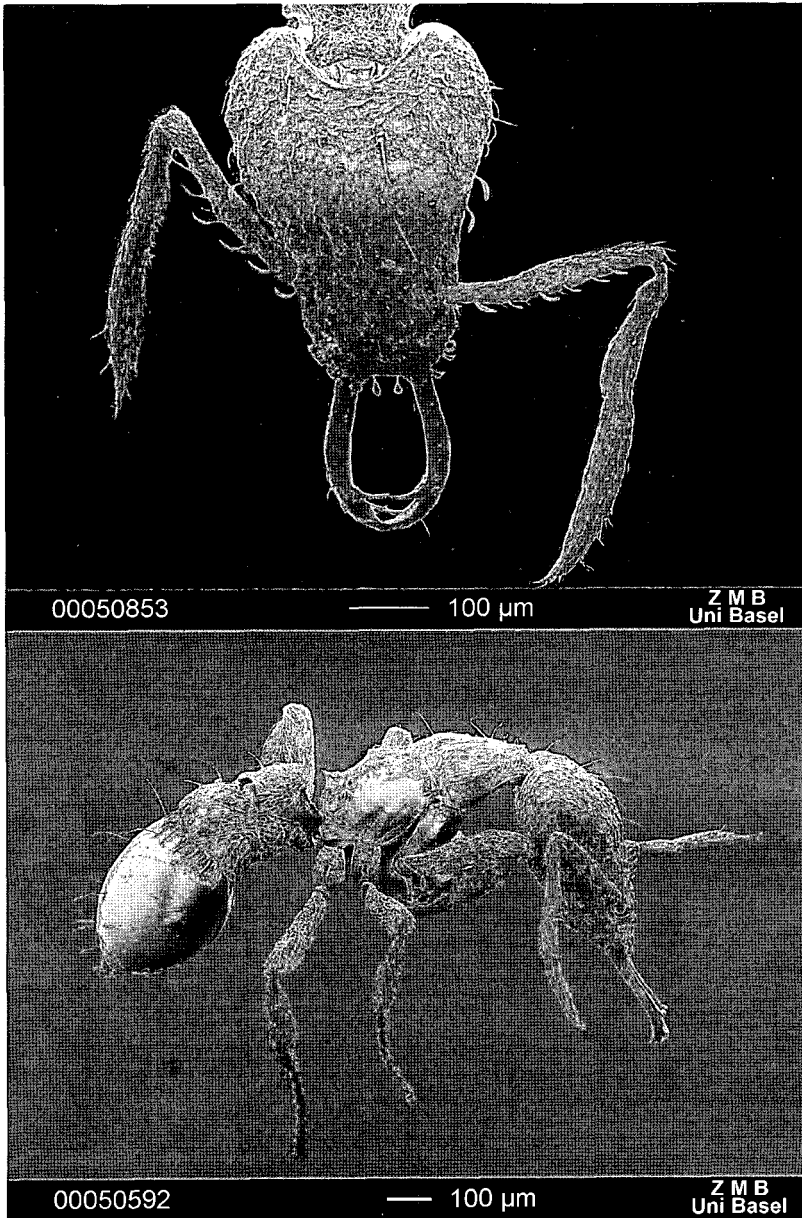
Fig. 55 - *Strumigenys buddhista* n. sp. from Nepal. Worker, head in dorsal view (top) and entire profile (bottom).

with a pair of erect, flagellate hairs. Petiole, postpetiole and gaster with few erect flagellate hairs. Outer face of mid and hind tibiae with an erect, long, flagellate hair. Hind basitarsi with 1 pair of erect, long, flagellate hairs.

C o l o u r .   light brown.

Measurements (in mm) and indices: TL 1.96; HL 0.50; HW 0.33; SL 0.30; ML 0.23; EL 0.02; WL 0.51; CI 66.0; SI 90.9; MI 46.0.

D i s c u s s i o n .   *Strumigenys buddhista* is very similar to *uberyx* and *hindu*. These three species have similar body sculpture but the number of standing hairs on the head dorsum helps to separate them. The three rows of standing hairs on the head dorsum are placed as follows: 1 row close to the vertexal margin, 1 row at the same line as the dorsolateral flagellate hairs and 1 row at the level of the eyes. In *buddhista* the rows have 4,2,2 hairs, in *uberyx* the rows have 4,4,4 hairs and in *hindu* the rows have 4,4,2 hairs. Besides the differences in the number of standing hairs on the head dorsum, *buddhista* differs from *uberyx* and *hindu* by the higher value of MI (46 instead of MI 41-42 as in *uberyx* and *hindu*). In addition, *buddhista* and *uberyx* share the small size and *buddhista* and *hindu* share the anterior face of the petiole protruding anteriorly and tumuliform.

Strumigenys   n a g e l i   Baroni Urbani & de Andrade n. sp.

T y p e   m a t e r i a l :   holotype worker from Ecuador labelled: Esmeralda, Rioverde, Via San Lorenzo, Km 67, leaf-litter, 22.VIII.2004, C. Baroni Urbani & M. L. de Andrade (PUCE). Paratypes: 4 workers, same data as the holotype (PUCE, MSNG).

D e r i v a t i o   n o m i n i s :   this species is named after Prof Dr Peter Nagel.

Diagnosis. A *Strumigenys* belonging to the *elongata*-group as defined by BOLTON (2000), resembling *spathula* Lattke & Goitía but differing from it by the apicoscrobal hairs short and spatulate instead of long and flagellate, by the humeral hairs long and thicker in their distal half, instead of long and filiform and by the spatulate standing hairs on the gaster, longer and thinner.

Worker description (Fig. 56). Head sides converging anteriorly, with round vertexal corners. Frontal lobes weakly expanded and convex. Antennal fossae ventrally with a narrow carina visible in

full-face view, straight, not covering the lower margin of the scrobes and ending close to the eyes. Eyes small, with 4 ommatidia in the longest row, placed over the ventral margin of the antennal scrobes, and visible in dorsal view. With head in profile the scrobe distinct, with marked upper margin only. Clypeus triangular. Lateral clypeal margin gently converging anteriorly to a straight or gently concave margin. Scapes subcylindrical, about 2/3 of the head length and largely surpassing the eyes posteriorly. Antennae with six joints. Apical funicular joint much longer than the rest of the funiculus. Mandibles elongate. Apical fork of the mandible with two spiniform teeth and without intercalary denticles.

Mesosoma in profile weakly convex anteriorly and sloping posteriorly to the convex basal face of the propodeum. Propodeal teeth pointed. Declivous face of the propodeum with a very faint margin.

Petiole with a long neck, the node high and convex dorsally. Ventral surface of the petiole with a narrow lamina on the anterior third. Petiolar node with posterior margin surrounded by spongiform process. Postpetiole convex in profile. Anterior and posterior margins of the postpetiole surrounded by spongiform processes, the process narrow on the anterior margin. Ventral surface of the postpetiole with dense spongiform process.

Gaster oval and with thin, short costulae. Base of the first gastral tergite and sternite with spongiform pad irregular on the sternite.

Sculpture. Head, mesosoma, petiole and postpetiole reticulate-punctuate, this sculpture less marked on the postpetiole. Centre of the lower mesopleurae smooth. Gaster smooth.

Pilosity. Head, mesosoma, petiole and postpetiole with subdecumbent or decumbent, spatulate hairs, very sparse on the mesosoma and rare on the pedicel. Apicoscrobal hair spatulate. Cephalic dorsum with one pair of standing spatulate hairs close to the occipital margin. Humeral hairs long, increasing in width from mid-length to near the apex and apically gently pointed or truncate. Mesonotal dorsum with 1 pair of erect hairs similar to the humeral ones but shorter. Petiole, postpetiole and gaster with erect, long, spatulate hairs very sparse on the pedicel.
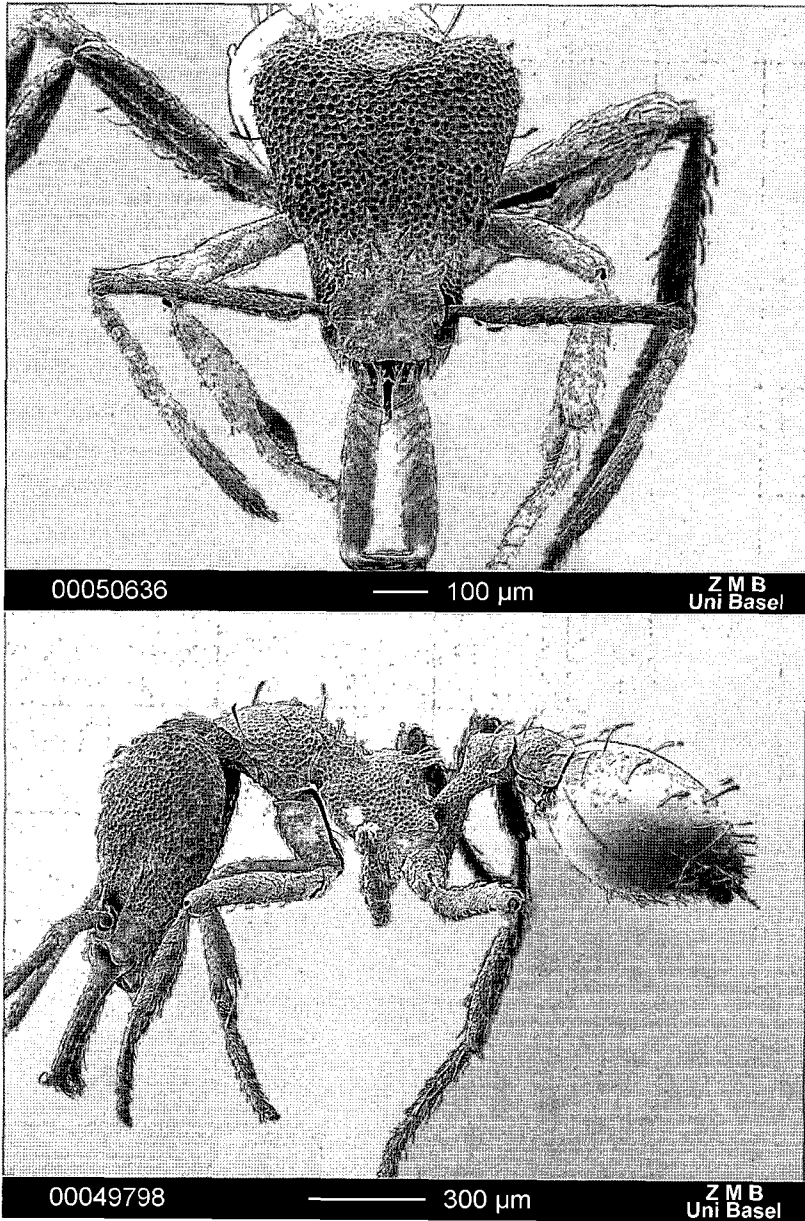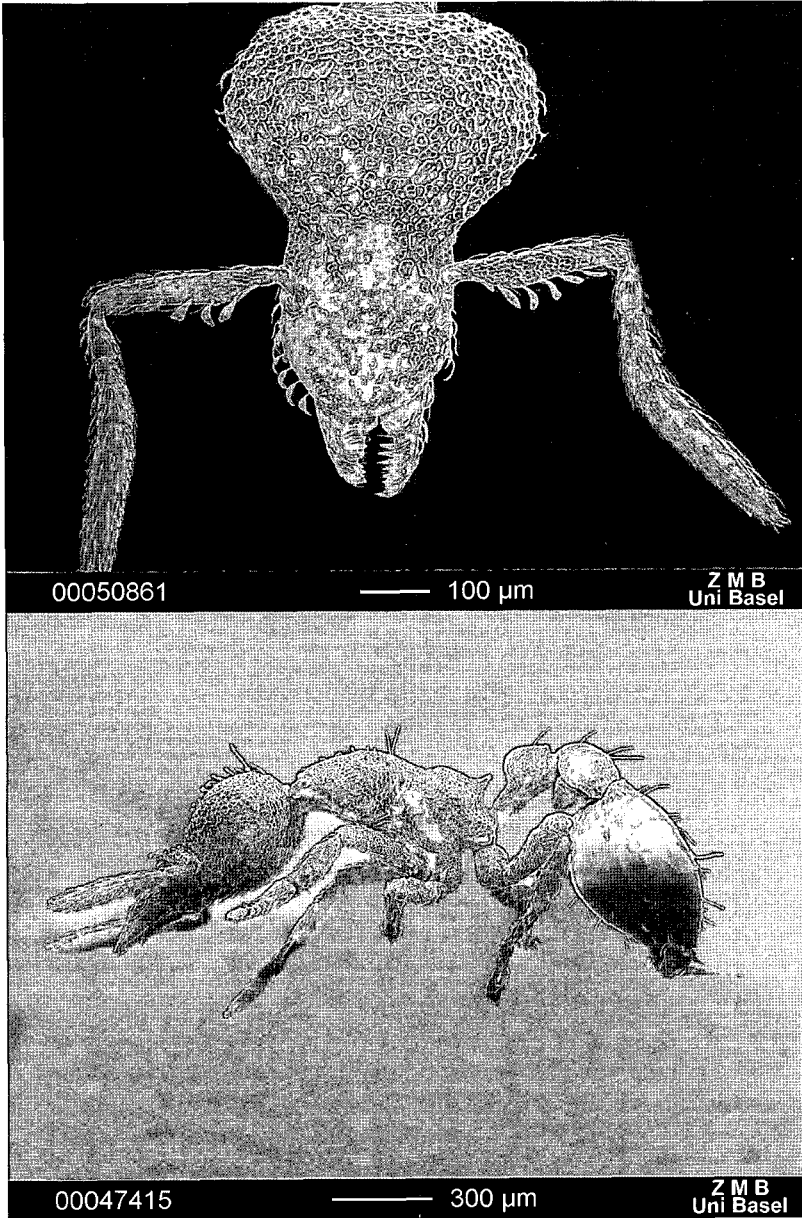
Fig. 56 - *Strumigenys nageli* n. sp. from Ecuador. Worker, head in dorsal view (top) and entire profile (bottom).

Colour. brown with slightly darker gaster.

Measurements (in mm) and indices: TL 2.44-2.58; HL 0.63-0.66; HW 0.49-0.50; SL 0.45; ML 0.38-0.40; EL 0.05-0.06; WL 0.60-0.65; CI 75.7-77.7; SI 90.0-91.8; MI 60.3-60.6.

Discussion. *S. nageli* is very similar to *spathula* from Venezuela, Trinidad and Central America but the characters listed in the diagnosis permit easy separation of the two species.

Strumigenys aequinoctialis de Andrade n. sp.

Type material: holotype and paratype workers from Ecuador (Pichincha) labelled: km 38 road Calacalí - La Independencia, 21.VIII.2004, 2000 m, leaf litter, C. Baroni Urbani & M. L. de Andrade (MSNG).

Derivatio nominis: from the Latin *aequinoctialis* (=equinoctial), the closest concept to the Equator in Roman times.

Diagnosis. A *Strumigenys* belonging to the *schulzi*-group as defined by BOLTON (2000), resembling *umboceps* (Bolton), but differing from it by its standing hairs much longer, by its propodeal spines longer, by its vertex with 4 longer, erect hairs, by its larger size and darker colour.

Worker description (Fig. 57). Head strongly converging anteriorly and with round vertexal corners. Head in profile with posterior half strongly tumuliform. Frontal lobes slightly expanded and convex. Antennal fossae ventrally with a carina visible in full-face view, straight, covering the lower margin of the scrobes and ending before the upper border of the eye. Eyes with 4-5 ommatidia in the longest row, placed over the ventral margin of the antennal scrobes. With the head in profile the scrobe is superficial, with the upper and lower margins weakly marked. Anterior clypeal margin broadly convex. Scapes slightly compressed dorsoventrally, with sub-basal bend, about half of the head length and surpassing the eyes posteriorly. Antennae with six segments. Apical funicular joint longer than the rest of the funiculus. Mandibles short, triangular. Basal tooth broad, subtriangular and followed by 11 teeth or denticles. Tooth 1 (basal), 2 and 3 the longest, subequal in size, tooth 4 smaller than 1-3, tooth 5 slightly shorter than teeth 1-3, teeth 6-10 diminishing in size apically, apical tooh small but pointed.

Mesosoma in profile convex anteriorly and gently sloping poste-
riorly. Propodeal teeth pointed and subtended by a carina.

Petiole with node high and convex and with long peduncle. No
spongiform processes on the petiole, except a very thin whitish carina
on its posterior border. Postpetiole broadly convex, with developed
spongiform processes ventrally. Anterior and posterior postpetiolar
borders with a narrow spongiform crest, the crest broader posteriorly.

Gaster oval and with few, short costulae. Base of the first gas-
tral tergite with narrow limbus. Base of the first gastral sternite with
narrow spongiform pad.

Sculpture. Head, mesosoma and petiole reticulate-punctuate.
Mesopleurae largely smooth. Postpetiole and gaster smooth and
shining, except a few reticulations on the posterior half of the post-
petiolar dorsum.

Pilosity. Head, mesosoma and petiole with suberect or subdecum-
bent, spatulate hairs, slightly shorter on the clypeus, sparser on the
mesosoma and rare on the petiole. Apicoscrobal hair absent. Cephalic
dorsum with 4 long, erect hairs, slightly thicker on the apical half.
Leading edge of the scapes with spatulate hairs curved basally and api-
cally. Lateral clypeal margins with spatulate hairs curved anteriorly.
Pronotal humeral hair present, long and weakly flagellate. Sides of the
mesonotum with 1 erect, long, truncated, hair. Petiole, postpetiole,
and gaster with erect-suberect, truncated hairs, rare on the petiole.

C o l o u r . Holotype dark brown; paratype reddish brown
with darker gaster.

Measurements (in mm) and indices: TL 2.30-2.60; HL 0.62-0.72; HW 0.45-
0.52; SL 0.31-0.36; ML 0.11-0.15; EL 0.06-0.09; WL 0.63-0.74; CI 72.2-72.6; SI
68.8-69.2; MI 17.7-20.8.

D i s c u s s i o n . S. aequinoctialis and its closest relative, umbo-
ceps (Bolton) occupy an isolate position within the genus for their
high-domed cephalic capsule. S. aequinoctialis is easily distinguished
from umboceps for the four long hairs behind the highest point of
the vertex as already described in the diagnosis. The two aequinoc-
tialis specimens differ from the holotype unique of umboceps in the
MCZC also for the presence of standing hairs on the mesosoma.
Since there are differences in the number of hairs also between the
aequinoctialis holotype and paratype, one cannot exclude that the
umboceps unique had lost all its standing hairs during manipulation.

Fig. 57 - *Strumigenys aequinoctialis* n. sp. from Ecuador. Worker, head in dorsal view (top) and entire profile (bottom).

†*Strumigenys p i l o s u l a* de Andrade n. sp.

T y p e   m a t e r i a l :   holotype, winged gyne (unique) in Dominican amber (GOPC) No. H 10-190.

D e r i v a t i o   n o m i n i s :   *pilosulus* is the diminutive of the Latin adjective *pilosus* (= hairy) and is referred to the smaller number of macrochaetae that differentiate this species from its closest relative, *S. schleeorum* Baroni Urbani.

D i a g n o s i s .   A *Strumigenys* species resembling the fossil *schleeorum* but differing from it by having 4 standing hairs close to the vertexal margin instead of 2, by a pair of standing hairs close to the ocelli (no such hairs in *schleeorum*), and by the leading edge of scape without freely projecting hairs instead of with freely project- ing hairs.

Gyne description (Figs. 58, 59, 60). Head strongly converging anteriorly and with round vertexal corners. Frontal lobes slightly expanded and convex. Antennal fossae ventrally with a marked carina visible in full-face view, straight, covering the lower margin of the scrobes and ending close to the upper border of the com- pound eyes. Compound eyes large, very protruding, occupying large part of the posterior half of the antennal scrobe, and largely visible in dorsal view. Ocelli developed. With the head in profile the scrobes are superficial, with the upper margin indistinct and the lower one marked anteriorly only. Lateral clypeal margin con- verging anteriorly into an anterior convex margin weakly tumu- liform medially. Scapes weakly dorsoventrally compressed, with sub-round bend, slightly less than 1/2 of the head length and slightly surpassing the eyes posteriorly. Antennae with six joints. Apical funicular joint slightly longer than the rest of the funiculus. Mandibles about 1/2 of the head length, touching each other only at the apex when opposed, with slightly convex external borders. Internal border of the mandibles with a broad basal lamella fol- lowed by a row of minute, poorly differentiated denticles and by a single spiniform tooth. Labral lobes large and partially visible between the mandibles.

Mesosoma robust and gently convex in profile. Parapsidal fur- rows weakly impressed. Scutellum with the sides converging pos- teriorly and with the posterior border rounded. Basal face of the propodeum long and declivous posteriorly; its sides marginate and its dorsum gently concave. Area between basal and declivous faces
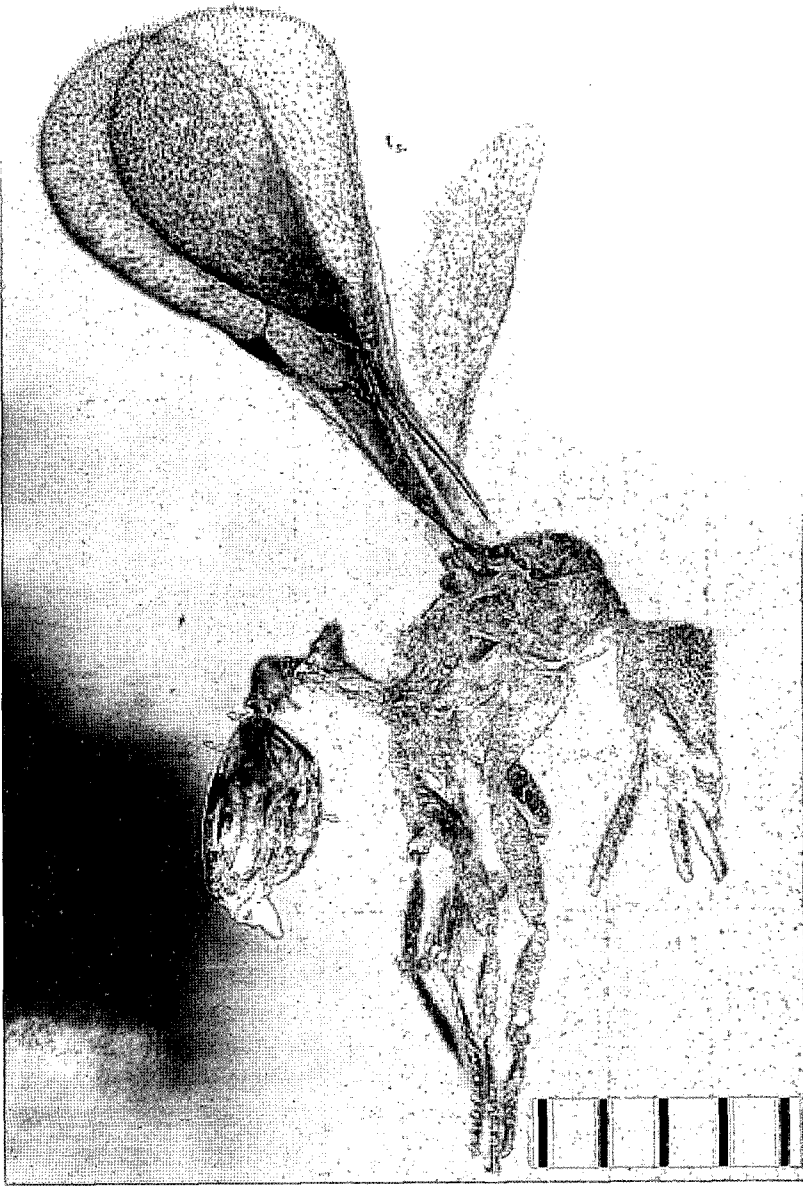
Fig. 58 - *Strumigenys pilosula* n. sp. from Dominican amber. Gyne, profile. Distance between two scale bars 0.1 mm.
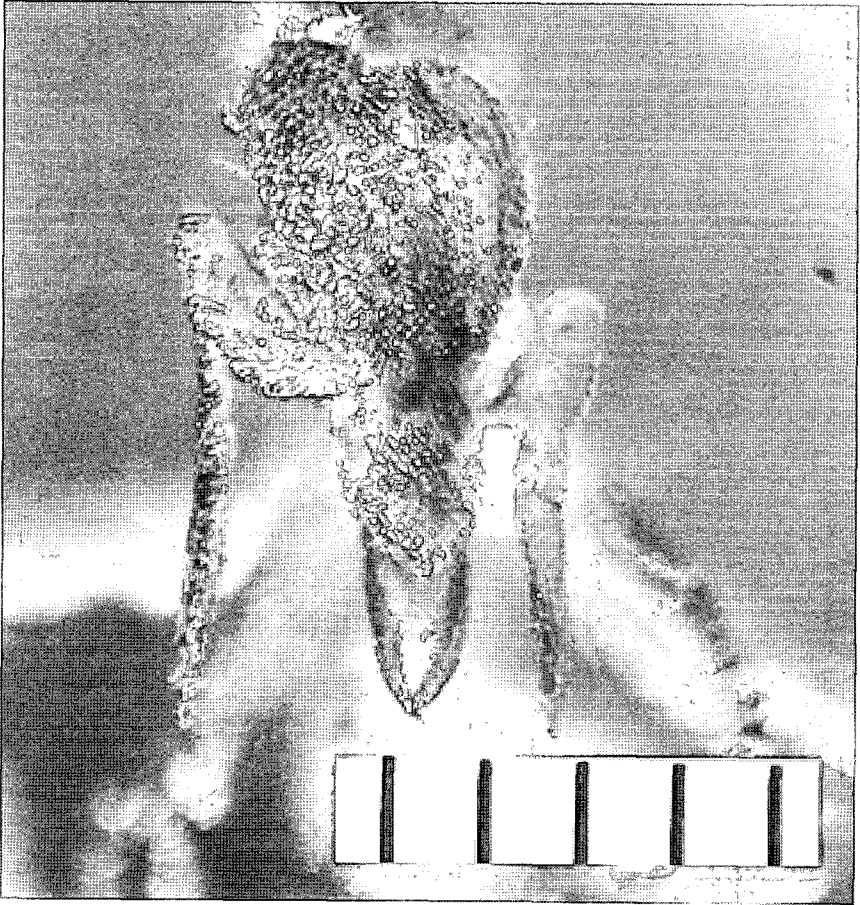
Fig. 59 - *Strumigenys pilosula* n. sp. from Dominican amber. Gyne, head in dorsal view. Distance between two scale bars 0.1 mm.
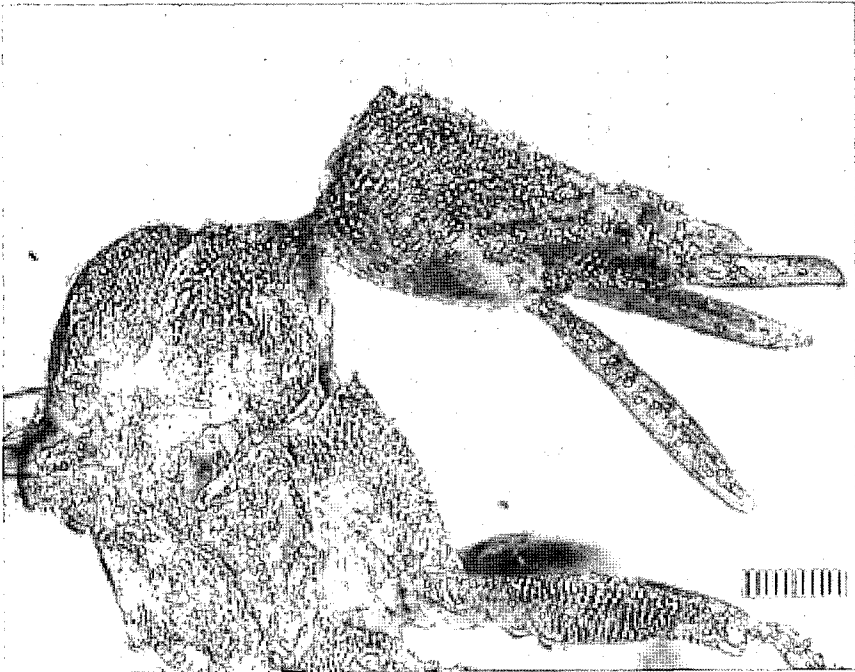
Fig. 60 - *Strumigenys pilosula* n. sp. from Dominican amber. Gyne, head and mesosoma in profile showing the pilosity. Distance between two scale bars 0.1 mm.

of the propodeum with a lamellaceous, pointed, transparent tooth that prolongs to the declivous face as a broad lamella.

Petiole with a long neck and with the node high and convex. Ventral surface of the petiole without spongiform lamina. Petiolar node with marked posterior margin and without spongiform process. Postpetiole convex in profile and without spongiform processes.

Gaster oval. Base of the first gastral tergite with developed anterior transverse cuticular ridge.

Sculpture. Head, mesosoma, petiole and postpetiole minutely reticulate, the reticulation more superficial on the postpetiolar dorsum. Mesopleurae, lower metapleurae and gaster smooth.

Pilosity. Dorsum of the head and scapes with sparse, weakly remiform hairs, subdecumbent on the head and appressed on the scapes. Leading edge of the scapes without free hairs. Border of the clypeus with few, free, weakly remiform hairs pointed medially. Apicoscrobal hair slightly pointed. Cephalic dorsum with 4 standing hairs close to the vertexal margin and a pair of hairs close to the ocelli. Pronotal humeral hairs long. Sides of the mesonotum with 2 pairs of hairs, the anterior pair much longer and thicker than the posterior one. Dorsum of the mesonotum with 2 pairs of erect hairs, one pair close to the anterior border and the second close to the parapsidal furrows. Petiole with a pair of pointed hairs dorso-laterally. Postpetiole with 2 pairs of pointed hairs, the anterior pair dorso-lateral and longer, the posterior pair dorsal and close to the posterior border. Ventral surface of the postpetiole with a thick hair. Gaster with few erect pointed hairs.

C o l o u r .   light brown.

Measurements (in mm) and indices: TL 2.30; HL 0.58; HW 0.30; SL 0.27; ML 0.14; EL 0.14; WL 0.67; CI 51.7; SI 90.0; MI 24.1.

M a t e r i a l   e x a m i n e d .   The unique *pilosula* example is embedded in a small, cut and polished, yellowish amber sample 0.5 x 0.5 x 1.5 cm containing only this specimen. The amber sample bears the No. H 10-190 in the GOPC. The preservation conditions are good, although the right side of the ant is slightly flattened.

D i s c u s s i o n .   *S. pilosula* resembles another previously known Dominican fossil, *S. schleeorum* (compare the figures of the present study with Figs. 22 & 23 by BARONI URBANI & DE ANDRADE, 1994). Both species share a peculiar mandibular shape, with rela-

tively short, curved and pointed mandibles without differentiated apical teeth touching each other only at the apex when closed. This structure is unknown among extant *Strumigenys* and appears to characterize a now extinct Dominican amber clade.

†*Strumigenys p o i n a r i* Baroni Urbani & de Andrade n. sp.

T y p e   m a t e r i a l : holotype worker in Dominican amber (GOPC No. H 10-220). Paratypes: 4 workers in the same amber piece and collection as the holotype.

D e r i v a t i o   n o m i n i s : this species is named after Dr. George O. Poinar, Jr. who permitted us to study this and many more interesting amber samples.

D i a g n o s i s . A *Strumigenys* belonging to the *rostrata*-group as defined by BOLTON (2000), resembling *carolinensis* (Brown), but differing from it by the presence of 4 suberect hairs on the vertexal margin, by the pronotal humeral hair gently spatulate instead of long and flagellate, and by the hind basitarsi without flagellate hairs.

Worker description (Figs. 61 & 62). Head strongly converging anteriorly and with round vertexal corners. Frontal lobes slightly expanded and convex. Antennal fossae ventrally with a carina visible in full-face view, straight, covering the lower margin of the scrobes and ending before the upper border of the eye. Eyes with about 5 ommatidia in the longest row, placed over the ventral margin of the antennal scrobes. With the head in profile the scrobes are distinct, with the upper and lower margins superficially marked. Lateral clypeal margins gently converging anteriorly into a convex margin. Scapes slightly compressed dorsoventrally, with sub-basal bend gently convex, slightly less than 1/2 of the head length and surpassing the eyes posteriorly. Antennae with six segments. Apical funicular joint longer than the rest of the funiculus. Mandibles short. Internal border of the mandibles with broad and triangular basal lamella followed by 12 teeth or denticles. Tooth 1 (basal) and 2 small, subequal in size, tooth 3 the longest, tooth 4 half size than 3, tooth 5 slightly shorter than 3, teeth 6 and 7 similar to 1 and 2 and followed by 4 denticles and by a small apical tooth.

Mesosoma in profile gently sloping posteriorly. A short longitudinal ruga runs on the dorsum of the pronotum and mesonotum. Propodeal teeth large, triangular and subtended by a broad lamella.
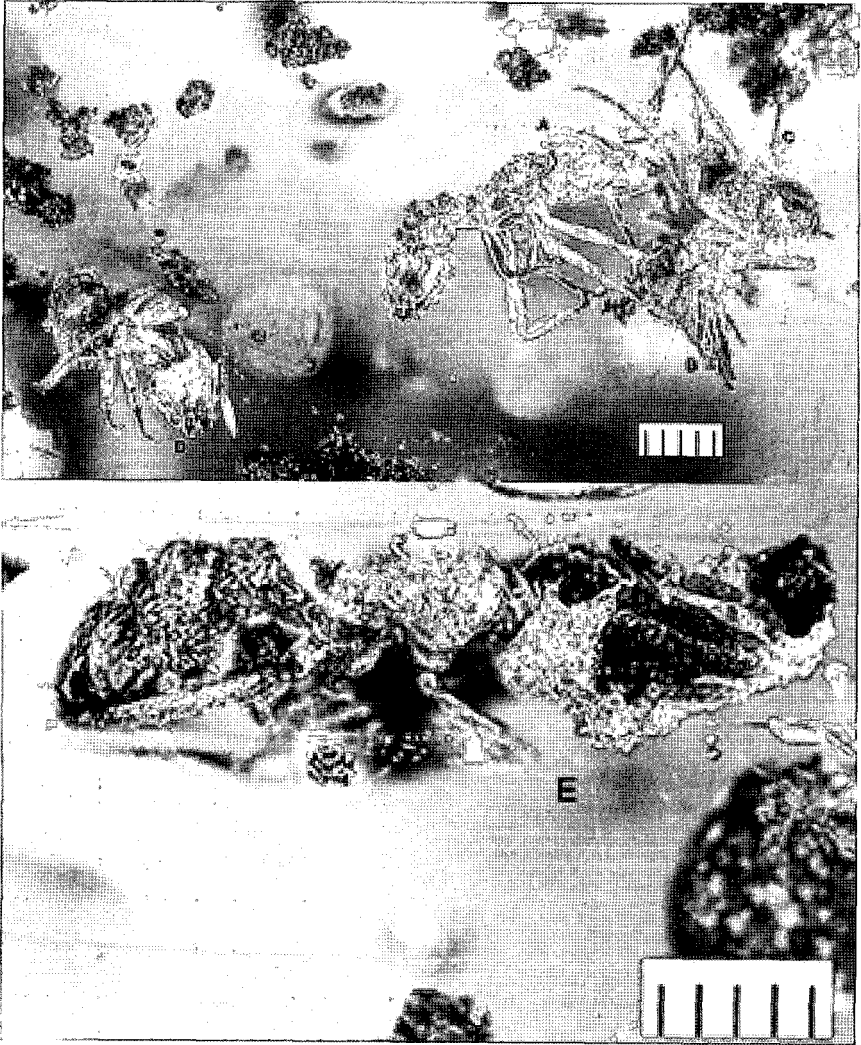
Fig. 61 - *Strumigenys poinari* n. sp., Dominican amber fragment including the holotype (A) and paratypes B-D (top) and paratype E at another location in the same amber fragment (bottom). Distance between two scale bars 0.1 mm.
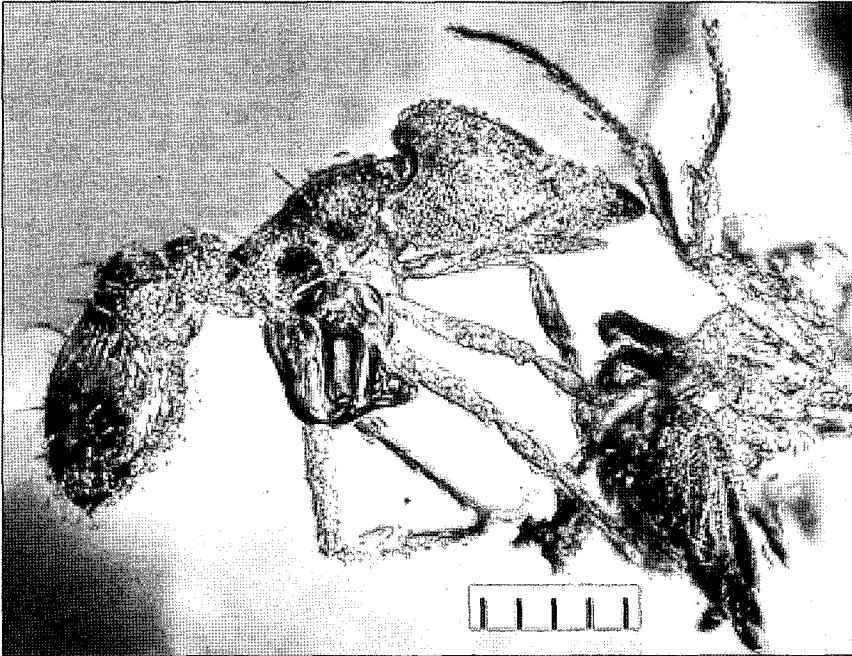
Fig. 62 - *Strumigenys poinari* n. sp. from Dominican amber. Holotype worker in
profile. Distance between two scale bars 0.1 mm.

Petiole with node high and convex and with developed spongiform
processes. Ventral surface of the petiole with spongiform lamina. Post-
petiole convex in profile and with developed spongiform processes.

Gaster oval and with few, short costulae. Base of the first gas-
tral tergite with broad limbus. Base of the first gastral sternite with
spongiform pad.

Sculpture. Head, mesosoma and petiole reticulate-punctuate, the
reticulation-punctuation larger on the head. In addition the mesono-
tum with sparse, very thin, longitudinal rugosities, much sparser
on the mesonotum and propodeum. Mesopleurae and metapleurae
largely smooth and shining. Dorsum of the postpetiole minutely
punctuate and superficially shining. Gaster smooth and shining.

Pilosity. Head and mesosoma with subdecumbent or decumbent,
spatulate hairs, rarer on the mesosoma. Apicoscrobal hair absent.

Cephalic dorsum with 4 suberect, spatulate hairs close to the vertexal margin. Leading edge of the scapes with spatulate hairs curved basally and apically. Lateral clypeal margins with spatulate hairs curved anteriorly. Pronotal humeral hair short and slightly spatulate. Sides of the mesonotum with 1 erect, curved, thick, flagellate hair. Petiole, postpetiole and first gastral tergite with sparse, curved, thick flagellate hairs. First gastral sternites with suberect spatulate hairs.

C o l o u r .   dark brown.

Measurements (in mm) and indices: TL 2.15-2.20; HL 0.58-0.59; HW 0.39-0.40; SL 0.27-0.28; ML 0.13; EL 0.05; WL 0.54-0.56; CI 66.1-69.0; SI 67.5-71.8; MI 22.0-22.4.

M a t e r i a l   e x a m i n e d .   Holotype and 4 paratype workers, all embedded in the same yellow amber sample 1.6 x 2.1 x 0.7 cm containing 5 workers of *Strumigenys*, a *Diplorhoptrum* worker (gaster and large part of postpetiole and right legs missing), an unidentified small insect and many debris. GOPC H 10-220. The preservation conditions of the *Strumigenys* specimens are good.

D i s c u s s i o n .   *S. poinari* resembles *S. carolinensis* in general habitus and mandibular dentition but the two species can be easily separate on the basis of the pilosity (see the diagnosis). *S. carolinensis* is known only from North and South Carolina and from Florida. Clearly Nearctic relationships are an uncommon trait among Dominican amber ants. There are no obvious relationships between *S. poinari* and two other *Strumigenys* previously described from Dominican amber (*S. pilosula* de Andrade, present paper, and *S. schleeorum* Baroni Urbani & de Andrade, (BARONI URBANI & ANDRADE, 1994)). On the contrary *S. poinari* and the third known Dominican fossil *Strumigenys*, *S. electrina* de Andrade might belong to a unique small clade. The two species, however, differ from each other in a number of details like presence of apicoscrobal hairs (*electrina* only), larger size of *poinari*, etc.

in Ecuador. This fresh material represents the primary source for the dissections used in this paper.

MZSP, Prof Dr C. R. F. Brandão, who, in spite of his commitments as Director of the Museu de Zoologia in San Paulo, was able to organize the sending of the specimens under his care after six months confrontation with new Brazilian Federal laws imposing unparalleled bureaucratic formalities.

If, on one hand, we can only repeat our gratitude to all those who spent their time in order to permit us to study specimens under their care, on the other we consider the bureaucratic and practical difficulties encountered somewhere as perilous for the free access to scientific information and we wish that the authorities responsible of them may undertake as soon as possible the necessary steps to improve the situation faced by us.

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9. ABSTRACT

The authors perform a critical analysis of potentially related genera currently included or excluded from the tribe Dacetini and of the characters used to justify inclusions or exclusions in these and other, related family—group taxa.

A major methodological difference between the present study and the analysis of BOLTON (1999) will explain the diversity of results. For the present study a trait is

recorded as present, absent, or polymorphic in a given taxon according to its observed presence or absence. BOLTON (1999) analysis does not consider known presences or absences when he thinks that these are due to homoplasy. This favours subjective judgment and, in this way, it might allow construction and defence of countless hypothetical clades including species without the synapomorphies characteristic of the clade since these relevant characters may be supposed to have been secondarily lost.

Among the results of the morphological analysis, the so called "mesopleural gland" supposed to be characteristic of the Dacetini is described as constituted by differently developed brushes of hair beds (sensilla trichoidea) widespread among several ant genera and unrelated to visible glandular structures.

A cladistically constructed phylogeny of the genera examined is supported by few undoubted synapomorphies and is considered mainly as a decisional criterion to build a classification based on unequivocal characters only, a condition entirely missing in the current classification.

The following changes result as a consequence of this analysis and of the principle that at least one unequivocal apomorphy must characterize a taxon:

The subfamily Agroecomyrmecinae is a junior synonym of Myrmicinae. Its downgraded status as a separate tribe, Agroecomyrmecini, sister tribe of Dacetini within the Myrmicinae, is maintained provisionally to preserve nomenclatorial continuity. As a matter of fact the Dacetini alone appear much more ill defined than a broader tribe including Agroecomyrmecini+Dacetini.

The tribal names Basicerotini and Phalacromyrmecini are considered as synonyms of Dacetini.

A number of genera already considered as synonyms of *Strumigenys* by BARONI URBANI & DE ANDRADE (1994), emended by BOLTON (1995), and considered again as synonyms of a single emended name by BOLTON (1999) are re-established as *Strumigenys*' synonyms. These are: *Pyramica, Epitritus, Trichoscapa, Cephaloxys, Pentastruma, Glamyromyrmex, Codiomyrmex, Tingimyrmex, Codioxenus, Smithistruma, Weberistruma, Wessonistruma, Serrastruma, Neostruma, Dorisidris, Miccostruma, Kyidris, Polyhomoa, Chelystruma, Borgmeierita, Platystruma, Gymnomyrmex, Dysedrognathus, Asketogenys, Cladarogenys*. The following genera are new synonyms of *Epopostruma: Colobostruma, Alistruma, Clarkistruma, Mesostruma*. The following genera are new synonyms of *Basiceros: Rhopalothrix, Heptastruma, Acanthidris, Octostruma, Talaridris, Eurhopalothrix, Protalaridris*.

The following species are described as new: *Basiceros onorei* from Ecuador, *B. papuanum* from Papua New Guinea, *Strumigenys veddha* from Sri Lanka, *S. aduncomala* from India, *S. caniophanoides* from Bhutan, *S. hindu* from Nepal, *S. buddhista* from Nepal, *S. nageli* from Ecuador, *S. onorei* from Ecuador, *S. longimala* from Ecuador, *S. aequinoctialis* from Ecuador, *S. pilosula* from Dominican amber (Miocene), *S. poinari* from Dominican amber (Miocene).

10. RIASSUNTO

La tribù dei Dacetini: limiti e generi che la compongono, con descrizioni di specie nuove (Hymenoptera, Formicidae).

Si analizzano criticamente alcuni generi attualmente inclusi od esclusi dalla tribù dei Dacetini ed i caratteri impiegati per giustificare le rispettive inclusioni od esclusioni in questo ed altri prossimi taxa di livello sopragenerico.

Una cospicua differenza metodologica tra questo studio e quello di BOLTON (1999) spiega largamente la diversità dei risultati. In questo studio ciascun carattere è stato considerato presente, assente o polimorfico in un taxon a seconda delle presenze ed assenze realmente osservate. BOLTON (1999), al contrario, non tiene cura delle presenze ed assenze da lui ritenute a priori risultato di convergenza o di perdita secondaria. Questo modo di vedere favorisce la valutazione soggettiva e, di conseguenza, permette la creazione e la difesa d'innumerevoli taxa comprendenti specie in cui le apomorfie del taxon in questione sono assenti perché quest'ultime potrebbero essere state perdute secondariamente.

Tra i risultati delle osservazioni morfologiche è da notare che la cosiddetta "ghiandola mesopleurale", correntemente considerata caratteristica di molti Dacetini, viene descritta come costituita da gruppi di sensilli tricoidei presenti in molte formiche disparate e dissociati da strutture ghiandolari visibili.

Un'analisi di parsimonia dei dati morfologici permette la costruzione di un cladogramma dei generi studiati, cladogramma giustificato da poche sinapomorfie indiscutibili e proposto essenzialmente come criterio decisionale per costruire una classificazione del gruppo non equivoca, una caratteristica del tutto assente nella classificazione corrente.

Le seguenti modifiche classificatorie e nomenclatoriali conseguono direttamente dall'analisi del cladogramma e dall'applicazione del principio per cui un taxon deve essere caratterizzato da almeno un'apomorfia inequivocabile.

La sottofamiglia Agroecomyrmecinae è un sinonimo juniore di Myrmicinae. Il suo stato subordinato di tribù gemella dei Dacetini all'interno dei Myrmicinae viene mantenuto provvisoriamente per conservare una certa continuità nomenclatoriale. I Dacetini da soli, infatti, appaiono molto più superficialmente caratterizzati di una tribù più ampia comprendente gli attuali Dacetini + Agroecomyrmecini.

Le tribù Basicerotini e Phalacromyrmecini vengono considerate sinonimi dei Dacetini. Numerosi generi già considerati sinonimi di *Strumigenys* da BARONI URBANI & DE ANDRADE (1994) e resuscitati da BOLTON (1995) e poi considerati sinonimi di un altro genere resuscitato da BOLTON (1999) sono riproposti come sinonimi di *Strumigenys*. Questi sono: *Pyramica*, *Epitritus*, *Trichoscapa*, *Cephaloxys*, *Pentastruma*, *Glamyromyrmex*, *Codiomyrmex*, *Tingimyrmex*, *Codioxenus*, *Smithistruma*, *Weberistruma*, *Wessonistruma*, *Serrastruma*, *Neostruma*, *Dorisidris*, *Miccostruma*, *Kyidris*, *Polyhomoa*, *Chelystruma*, *Borgmeierita*, *Platystruma*, *Gymnomyrmex*, *Dysedrognathus*, *Asketogenys*, *Cladarogenys*. I generi seguenti sono nuovi sinonimi di *Epopostruma*: *Colobostruma*, *Alistruma*, *Clarkistruma*, *Mesostruma*. I generi seguenti sono nuovi sinonimi di *Basiceros*: *Rhopalothrix*, *Heptastruma*, *Acanthidris*, *Octostruma*, *Talaridris*, *Eurhopalothrix*, *Protalaridris*.

Le specie seguenti, studiate per la presente revisione, vengono descritte come nuove: *Basiceros onorei* dell'Ecuador, *B. papuanum* di Papua Nuova Guinea, *Strumigenys veddha* dello Sri Lanka, *S. aduncomala* dell'India, *S. caniophanoides* del Bhutan, *S. hindu* del Nepal, *S. buddhista* del Nepal, *S. nageli* dell'Ecuador, *S. onorei* dell'Ecuador, *S. longimala* dell'Ecuador, *S. aequinoctialis* dell'Ecuador, *S. pilosula* dell'ambra dominicana (Miocene), *S. poinari* dell'ambra dominicana (Miocene).

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