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First Description of Fossil Dacetini Ants with a Critical Analysis of the Current Classification of the Tribe

(Amber Collection Stuttgart: Hymenoptera, Formicidae. VI: Dacetini)

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With 33 Figures and 2 Tables

Summary

This paper contains the description of three new species from Dominican amber representing the first known fossil Dacetini. The current systematics of the tribe is in a very unstable status and a plausible assignment of the fossils needed a considerable amount of revisionary work on the whole tribe. The changes introduced here include 2 tribal, 4 subtribal, and 19 generic new synonyms. The classification proposed in this paper is nonetheless provisional and unsatisfactory since some genera are still characterized by weak apomorphies and two of them result paraphyletic. A cladistic analysis of the most probable generic relationships within the tribe is also presented.

The Dominican amber Dacetini are described in two extant genera as follows:

Strumigenys schleorum n. sp. This is not particularly related to any other known species. Its mandibular morphology reflects what appears to be the beginning of an important evolutionary trend arisen convergently in several dacetine clades. Recent species with comparable mandibular organizations are also known but they regularly differ from the fossil in important structural details.

Strumigenys electrina n. sp. This species appears to be very closely related to a Recent Nearctic species (*S. ohioensis*).

Acanthognathus poinari n. sp. In our cladistic analyses the genus *Acanthognathus* appears as one of the most specialized dacetine genera and the amber species *poinari* as one of its more specialized species. To match the high number of evolutionary events that presence of such a specialized species in amber suggests, together with the minimum age determination of Dominican amber, one must assume very irregular evolutionary rates for different clades of the tribe.

Zusammenfassung

Es werden drei neue Arten von Ameisen aus Dominikanischem Bernstein beschrieben, die ersten bekannt gewordenen fossilen Vertreter der Dacetini. Die Systematik dieses Tribus ist gegenwärtig sehr unsicher, und deshalb erforderte eine einsichtige Zuordnung der Fossilien

eine gründliche Revision des ganzen Tribus. Es ergaben sich Änderungen in Form neuer Synonymien, und zwar zwei auf Tribus-Ebene, vier auf Subtribus-Ebene und neunzehn auf Gattungs-Ebene. Trotzdem ist die hier vorgeschlagene Systematik noch nicht zufriedenstellend und deshalb vorläufig, weil einige Gattungen noch auf schwachen Apomorphien beruhen und zwei von ihnen paraphyletisch sind. Eine cladistische Analyse der wahrscheinlichsten Gattungsbeziehungen innerhalb des Tribus wird zudem gegeben.

Die Dominikanischen Bernstein-Dacetini werden im Rahmen zweier bis heute ausdauernden Gattungen beschrieben:

Strumigenys schleorum n. sp. – Diese Art steht nicht in näherer Beziehung zu irgendeiner anderen bekannten Art. Die Morphologie ihrer Mandibeln spiegelt den wahrscheinlichen Beginn einer bedeutenden Entwicklungsrichtung wider, die konvergent in verschiedenen Zweigen der Dacetini eingeschlagen wurde. Rezenten Arten mit vergleichbarem Bau der Mandibeln sind auch bekannt, jedoch unterscheiden sie sich regelmäßig von den fossilen in wesentlichen Einzelheiten ihrer Struktur.

Strumigenys electrina n. sp. – Diese Art dürfte mit einer rezenten nearktischen Art, *S. ohioensis*, nahe verwandt sein.

Acanthognathus poinari n. sp. – In unserer cladistischen Analyse erscheint *Acanthognathus* als eine der am höchsten spezialisierten Gattungen der Dacetini, und die Bernstein-Art *poinari* wiederum als eine besonders hoch spezialisierte Art. Setzt man die erhebliche Zahl von Entwicklungsschüben, die das Vorkommen einer so hoch spezialisierten Art im Bernstein nahelegt, in Beziehung zu der geringsten Altersschätzung von Dominikanischem Bernstein, muß man sehr unregelmäßige Entwicklungsgeschwindigkeiten für verschiedene Zweige des Tribus annehmen.

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1. Introduction and historical perspective

Members of the ant tribe Dacetini are Myrmicinae sharing to different degrees many unusual traits such as highly modified mandibles, bizarre pilosity, specialized feeding habits, reductions in the number of antennal joints, spongiform and/or lamelliform body appendages of unknown nature and function, etc., which can be unequivocally interpreted as secondary adaptations.

The monotypic genus *Hypopomyrmex* EMERY, 1891, from Sicilian amber (Middle Miocene) has long been thought to be the sole known fossil member of the tribe and to represent a clade somehow intermediate between Recent members of the tribe and less specialized Myrmicinae (EMERY, 1920). This idea had been already accepted with some scepticism by FOREL (1892: 344) one year after Emery described the genus and BROWN & CARPENTER (1979), after a re-study of the single badly preserved winged gyne on which the genus is based, advanced serious doubts on this interpretation and on the phylogenetic position of *Hypopomyrmex*, which they suggest to be related to *Pheidologeton* (tribe Pheidologetini).

More recently WILSON (1985) mentions the presence of the dacetine genera *Smithistruma* and *Octostruma* (the latter is currently assigned to the tribe Basicerotini, but the synonymy of the two tribes will be proved later in this paper) in Dominican amber examined by him without explicitly describing them.

The present discovery of three different new species, undoubtedly of Dacetini in Dominican amber, estimated to be 15 to 45 million years old (POINAR, 1992), is hence of potentially great interest since it may allow the first concrete insights into some evolutionary pathways leading to one or more traits of the "dacetine morphological syndrome".

Unfortunately, the current classification of the Dacetini is far from being unequivocal at both generic and suprageneric levels, and a minimum reasonable placement of the amber fossils to be described in this paper as well as a tentative interpretation of their significance requires considerable revisionary work. It may seem easy to argue that some of the characters we employed in our analysis are likely to have a weak synapomorphic value. Actually all these characters are currently used to define dacetine genera in the literature and our main accomplishment will be showing true or potential weaknesses in the extant system. Our ambitions in writing this paper were modest: our main target was a rigorous application of logical rules to pre-existing information on characters and taxa.

Some unsound classification criteria applied to the genera of Dacetini will be corrected in this paper. In addition we will attempt a phylogenetic analysis in order to trace the most probable relationships within the tribe. We are far from regarding our results as definitive but we like to think that they should constitute the proper way to indicate strong and weak points in dacetine understanding and classification and, as such, a useful starting point for further revisionary studies.

2. The current classification of Dacetini, Basicerotini, and other related genera

We shall show later, in the definition of the tribe Dacetini in chapter 3, that all true dacetines are characterized by at least one strong synapomorphy, namely the incapacity to cross the mandibles at rest. All and only the Myrmicinae genera listed in the present chapter share this character. In the following we give a non-critical list of them, together with their tribal and sub-tribal attributions as found in the literature. Probable synonyms involving one or more of these taxa are sometimes cursorily mentioned in the literature but they have not yet been formally proposed.

Tribus Dacetini FOREL (Dacetonini)

Subtribus Dacetiti BROWN 1952

Acanthognathus MAYR 1877

Daceton PERTY 1833

Subtribus *Orectognathiti* BROWN 1952
Orectognathus SMITH 1853

Subtribus *Epopostrumiti* BROWN 1952
Colobostruma WHEELER 1927
Epopostruma FOREL 1895
Mesostruma BROWN 1948
Microdaceton SANTSCHI 1913

Subtribus *Strumigeniti* BROWN 1952
Asketogenys BROWN 1972
Chelystruma BROWN 1950 a
Cladarogenys BROWN 1976
Codiomyrmex WHEELER 1916
Codioxenus SANTSCHI 1931
Dorisidris BROWN 1948
Dysedrognathus TAYLOR 1968 a
Epitritus EMERY 1869 b
Glamyromyrmex WHEELER 1915
Gymnomyrmex BORGMEIER 1954
Kyidris BROWN 1949 a
Neostruma BROWN 1948
Pentastruma FOREL 1912 a
Quadrstruma BROWN 1949 b
Serrastruma BROWN 1948
Smithistruma BROWN 1948
Strumigenys SMITH 1860
Tingimyrmex MANN 1926
Trichoscapa EMERY 1869 a.

Tribus *Basicerotini* BROWN 1949

Basiceros SCHULZ 1906
Eurhopalothrix BROWN & KEMPF 1960
Octostruma FOREL 1912 b
Protalaridris BROWN 1980
Rhopalothrix MAYR 1870

Tribus *Phalacromyrmecini* WHEELER & WHEELER 1976

Ishakidris BOLTON 1984
Phalacromyrmex KEMPF 1960
Pilotrochus BROWN 1977

Most genera included in the previous list had been originally described as *Dacetini* or (those listed here as *Phalacromyrmecini*) have been regarded as related to the *Dacetini* by BOLTON (1983, 1984). Some of them had been separated or subsequently described in the cognate tribe *Basicerotini* during the last 40 years (see discussion in Chapter 3). The status of the tribe *Phalacromyrmecini* is more puzzling. We find mentions of this tribe by WHEELER & WHEELER (1976: 60 and 1985: 258), by DLUSSKY & FEDOSEEVA (1988: 80), and by HÖLLDOBLER & WILSON (1990: 16). Both DLUSSKY & FEDOSEEVA (l. c.) and HÖLLDOBLER & WILSON (l. c.) list the genera *Ishakidris*, *Phalacromyrmex*, and *Pilotrochus* as constituting the tribe. We have been unable to locate the description of this tribe both in the pertinent literature available to us and in the Zoological Record from 1960 (date of the first description of *Phala-*

cromyrmex) until today. References to such a tribe are also missing from papers where one would expect to find it, like KEMPF (1972), or BOLTON (1984). The latter author, however, offers a detailed analysis of potential apomorphies and homoplasies pertinent to the three genera and to other dacetine genera. To the best of our knowledge, hence, this tribe was never formally described and, as a consequence of this, we attribute to it the authorship WHEELER & WHEELER (1976), i. e. the oldest mention of this name we have been able to trace in the literature.

3. Limits and definition of the tribe Dacetini

The tribe Dacetini FOREL, 1892 has been last characterised on a world-wide scale by EMERY (1922). Subsequent research focused essentially on description of new genera and species and on removal of taxa from the tribe as defined by EMERY without adding new tribal characters or seriously challenging EMERY's last definition. A remarkable exception is represented by the monograph of BOLTON (1983) where a very exhaustive comparative analysis is carried out at tribal, sub-tribal, and generic levels, but the analysis is limited to the Afrotropical species only. As a result of this, most of the diagnostic characters employed by BOLTON (l. c.) are admittedly valid for the African fauna, but they can not be used with full confidence on a world-wide scale.

EMERY's (1922) diagnosis lists over a dozen potential tribal characters, but a quick examination of all of them shows immediately that only one has some chance of being considered uniquely derived within the tribe: the cordate head. In the same year, WHEELER (1922) actually used this character in his key of the world genera of ants, excluding in this way from the Dacetini the genus *Blepharidatta*, which was included in the tribe by EMERY (l. c.). Following the dichotomy of the myrmicines with cordate heads one finds all true Dacetini divided from the new tribe *Stegomyrmecini*, including only the genus *Stegomyrmex*. The diagnostic characters of the new tribe are (1) normally falcate mandibles as compared to specialized among Dacetini, an obvious plesiomorphy, and (2) fore wings with two closed cubital and one closed radial cell (as opposed to one closed cubital and one open radial cell in Dacetini). We concur with the exclusion of *Stegomyrmex* from Dacetini and we would add that the head of *Stegomyrmex* exhibits deep antennal scrobes like several Dacetini but can not be considered as truly cordate in shape (see also MACHADO DINIZ, 1990).

EMERY (1922: 313) divided the Dacetini into two informal groups according to the position of the antennal scrobe, over the eyes in one or under the eyes in the other. The value of this character, apparently excellent, is greatly reduced by the fact that in the dacetine genus *Acanthognathus* the scrobes are extremely reduced but oriented over the eyes and in *Daceton*, the type genus of the tribe, they are practically absent but the frontal carinae are directed under the eyes. For this reason EMERY ranged *Daceton* within the first group but with doubts.

In the following years, other genera not belonging to the Dacetini had been assigned to this tribe and BROWN (1949 c) correctly excluded two of them (*Peronomyrmex* VIEHMEYER and *Weberidris* DONISTHORPE), but he went a step further excluding from the Dacetini six known genera and a newly described one to be included in the new tribe *Basicerotini*. The description of the new tribe contains only one diagnostic character expressed in a generic statement that the "hairs [of *Basicerotini* are] not closely resembling those of the Dacetini in basic details".

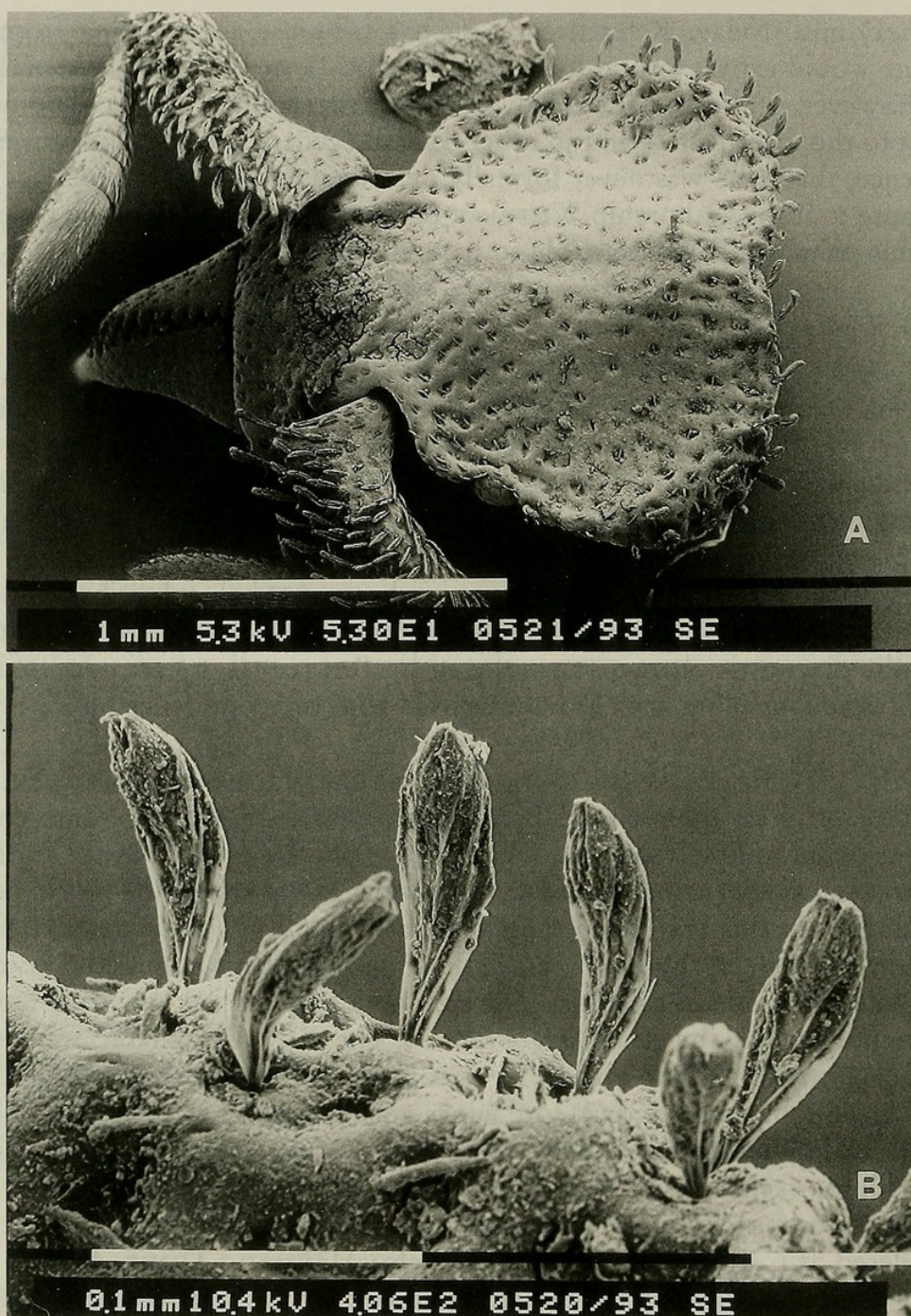


Fig. 1. *Basiceros discigerum* (MAYR). — A. Head in dorsal view. — B. Detail showing hair morphology.

A similar course of action was taken by BROWN & KEMPF (1960) who, defining the Basicerotini, state that "a somewhat similar array of bizarre seta types is found in the tribe Dacetini, but detailed comparison between superficially similar hairs from dacetine and basicerotine species reveals basic differences in microstructure". The authors, on the other hand, admit that "a few [Basicerotini] species are nearly completely hairless" (as are some Dacetini). As a matter of fact, a Ceylonese "basicerotine" new species described later in this paper as *Rhopalothrix inopinata* is equally virtually destitute of body hairs of any kind. Only the appendages bear short, non-specialized hairs similar to those known for the majority of ants. One might, of

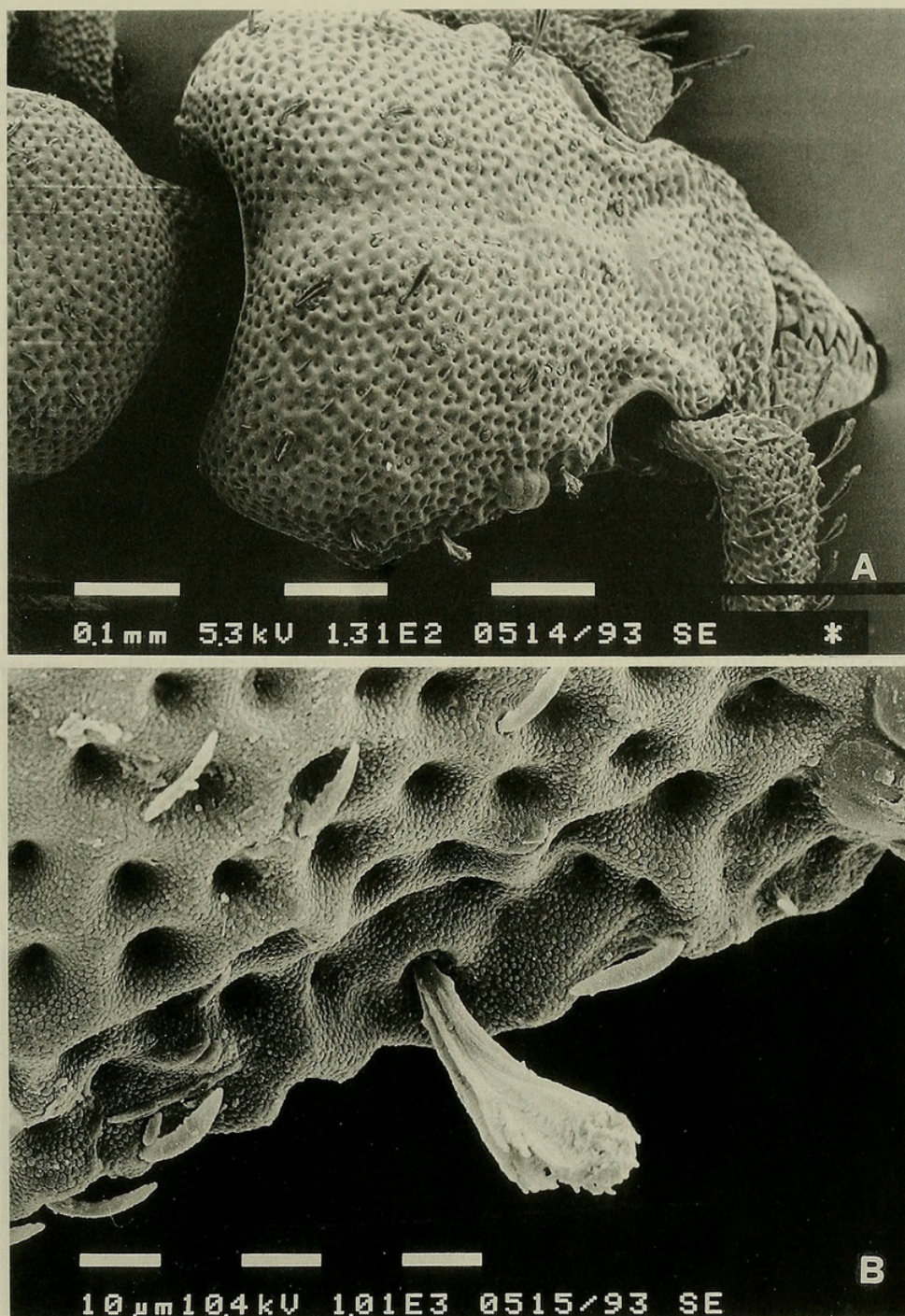


Fig. 2. *Octostruma stenognatha* BROWN & KEMPF. — A. Head in dorsal view. — B. Detail showing hair morphology.

course, explain these cases by secondary loss. Recently HÖLLDOBLER & WILSON (1986) published very instructive SEM micrographs of hairs of four "basicerotine" and one *Stegomyrmex* species. It is obvious that these hairs — due to their submicroscopic size — can not be the same as those referred to by BROWN (1949) and BROWN & KEMPF (1960) who only had access to light microscopy. As a matter of fact HÖLLDOBLER & WILSON (1986) never stated that these hairs correspond to those already mentioned in the taxonomic literature, though some readers may get this impression, as neither claimed that the hairs described by them represent a previously unknown synapomorphy for the Basicerotini. According to HÖLLDOBLER & WILSON (l. c.)

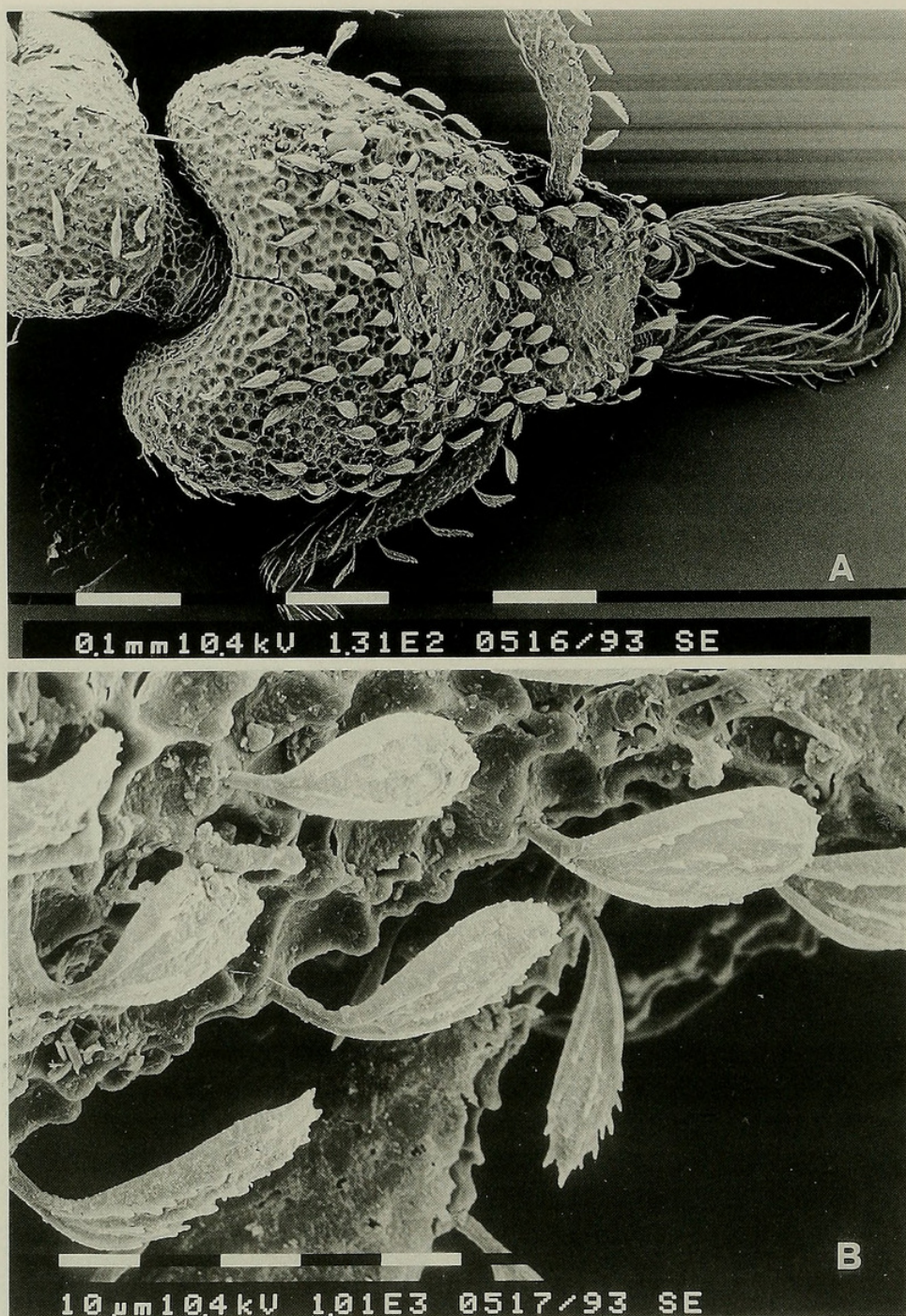


Fig. 3. *Strumigenys louisianae* ROGER. — A. Head in dorsal view. — B. Detail showing hair morphology.

Octostruma batesi, in addition to "normal" clavate hairs, appears to possess previously undescribed appressed soil-holding hairs. In the same paper other hairs with the same function but with completely different morphologies are described for other basicerotine species and for *Stegomyrmex* as well. In another paper (WHEELER & HÖLLDOBLER, 1985), the soil-binding hairs of the basicerotine *Eurhopalothrix* are said to be "identical" to hairs observed to serve the same function in two species of *Zacryptocerus* (tribe Cephalotini). It may prove difficult, therefore, to maintain a tribal partition on pilosity characters alone since these characters are very likely to serve homologous functions by means of only partly homologous structures. In

addition, presence of the same type of hairs in a probably closely related but extraneous genus (*Stegomyrmex*), also makes use of this character as basicerotine apomorphy questionable.

Finally, even forcing somehow the soil-binding or other hairs to be a synapomorphy of Basicerotini, there is a risk that the remaining Dacetini may be left as a paraphyletic group. Figures 1–3 show the pilosity of the head and hair details of two "basicerotine" genera (*Basiceros* and *Octostruma*) and of a "dacetine s. str." (*Strumigenys*). It should be evident that no significant differences can be observed among them. Both *Basiceros* and *Octostruma* species (Figures 1, 2), show brush hairs perfectly comparable to those of *Strumigenys* (Fig. 3). The two "basicerotines" photographed here, in addition, show very small (soil-holding?) hairs not observed in the latter genus. Since this type of hair is equally missing in the "basicerotine" *Basiceros manni* (HÖLLDOBLER & WILSON, 1986), it is obvious that presence of such hairs can not be regarded as a tribal character. In the literature there is mention of one potential synapomorphy for the "Dacetini s. str.": the presence of bifid larval hairs, as described by WHEELER & WHEELER (1954, 1960, 1969, 1973, 1976) and as noted by BROWN & KEMPF (1960). An incomplete but relatively important set of Dacetini s. str. is known in their larval morphology (40 species in 10 nominal genera, out of less than 400 described species in 27 genera presently recognised), and information about lack of bifid hairs among Basicerotini relies on examination of five species in three genera (out of some 60 species in 5 genera). In addition to the insecure sample adequacy, however, one should consider the legitimacy of considering this larval hair morphology as a synapomorphy: the flexuous and denticulate hairs of *Basiceros* and *Rhopalothrix* have been described from *Strumigenys* as well, and the deeply bifid hairs supposed to be characteristic of Dacetini s. str. occur in a wide variety of genera like *Eusphinctus*, *Aphaenogaster*, *Rhytidoponera*, *Carebara*, *Mayriella*, *Oligomyrmex*, *Paedalgus*, *Pheidologeton*, *Apsychomyrmex*, *Chelaner*, *Cataulacus*, *Tetramorium*, *Phyracaces*, and *Pristomyrmex* (WHEELER & WHEELER, 1976).

Under the present state of knowledge, considering the Dacetini as a single monophyletic tribe in a sense similar to the one employed by EMERY (1922) and WHEELER (1922) – after removal of some extraneous genera like *Stegomyrmex*, *Peronomyrmex* and *Weberidris* – and merging the Basicerotini in the same taxon seems to be the most reasonable course of action and this will be the one followed in the rest of this paper. Hence we propose the following tribal nomenclature (older partial synonyms resulting from catalogues omitted):

Tribus Dacetini FOREL 1892

Dacetonini FOREL 1892. Type genus *Daceton* PERTY, by inference.

Dacetonii, FOREL 1893

Dacetii, EMERY 1895

Dacetini, EMERY 1914

Dacetiti BROWN 1952. Type genus *Daceton* PERTY, by original designation. *Synonymia nova*.

Orectognathiti BROWN 1952. Type genus *Orectognathus* SMITH, by original designation. *Synonymia nova*. (= *Arestognathiti*, *ibidem*, misspelling.)

Epopostrumiti BROWN 1952. Type genus *Epopostruma* FOREL, by original designation. *Synonymia nova*.

Strumigeniti BROWN 1952. Type genus *Strumigenys* SMITH, by original designation. *Synonymia nova*.

Basicerotini BROWN 1949 c. Type genus *Basiceros* SCHULZ, by inference. *Synonymia nova*.

Phalacromyrmecini [no author name given], WHEELER & WHEELER 1976. Type genus *Phalacromyrmex* KEMPF, by inference. *Synonymia nova*.

We regard as synonyms the four subtribal names proposed by BROWN (1952) essentially for their low explanatory value and for the difficulty to include in them, alone or with the addition of new subtribes, all dacetine genera. One of these names, the Orectognathiti, contains only one genus (*Orectognathus*). In the present paper we shall show that this is the most probable fate of another subtribe, the Strumigeniti, destined to include *Strumigenys* only. The Epopostrumiti contain three genera recognised by us in this paper but they are likely to be a polyphyletic group (see later, the results of the cladistic analysis). In the nominal subtribe, the Dacetiti, we recognise two valid genera, as BROWN did, and we agree on its probable monophyly but we see no advantage in maintaining three subtribal names for four genera together with over a dozen genera in the same tribe without subtribal assignment.

At tribal level we have already documented the synonymy of the Basicerotini with the Dacetini in the first part of this chapter.

The sole known potential dacetine synapomorphy, at the present status of knowledge, remains the shape of the head, pyriform. More recently, however, a discrete number of new genera showing close morphological similarity with the Dacetini but without pyriform head have been described from tropical countries. The first to recognize a more than superficial relationship between some of these genera and the Dacetini was BOLTON (1983 and 1984). In his second paper BOLTON (1984: 31) saw "no advantage to adding yet another formal [i. e. tribal] name to the confusion" and we concur entirely with this opinion. One of these genera of the "*Phalacromyrmex* group" (*Pilotrochus*), in addition, shows a head approaching the pyriform shape and thus rendering difficult both solutions, i. e. its exclusion from the Dacetini on the basis of the shape of the head and its inclusion in a newly defined tribe in which the shape of the head results highly variable. Actually, a few species of "typical" Dacetini equally lack a pyriform head (see e. g. *Smithistruma dagon* BOLTON, 1983).

We think there is at least one character uniquely derived among all the Myrmicinae and grouping all these related genera together. This is the loss of the capacity to cross the mandibles at rest. Only one more myrmicine genus (*Tatuidris* BROWN & KEMPF, 1967) appears to be unable to cross the mandibles at rest and we do not include it among the Dacetini since the mandibles of this genus appear destitute of any kind of pointed or spiniform teeth as is the case for all remainder genera included in the Dacetini in this paper. This fact, coupled with substantial differences in habitus, suggest a different function and origin of the mandibular posture in *Tatuidris*. We define, hence, as true dacetini, all myrmicine ants opposing (not crossing) a pair of sharp, toothed or pointed mandibular blades. In the following, all ants sharing this character will be considered as Dacetini and will be compared together in an attempt to cast some light on this difficult complex of taxa. BROWN & WILSON (1957) described the Malayan-Oceanian genus *Dacetinops* as very similar in habitus to the true Dacetini but they regarded these similarities as due to convergence. BARRY BOLTON (personal communication) informed us that species of this genus can cross their mandibles to variable extents confirming in this way the convergence hypothesis already formulated by BROWN & WILSON (1957). Attempting a precise description and interpretation of some amber fossils available for the present study forced us to this

broader analysis, the results of which, later, will force us to many more changes. These changes will be explained and justified step by step in the following text.

4. Some generic synonymies partly resulting from already available information

Many current dacetine genera are based on remarkable characters representing odd apomorphies of single species, the recognition of which would inevitably make paraphyletic the closest related clade. To this objective difficulty it must be added the large number of new species described in recent years which often exhibit transitional forms between extremes of characters formerly reputed to be of generic rank. At least a good proportion of the synonymies proposed here for the first time, therefore, have been already suspected or informally suggested in some papers by BROWN (1973 a), BROWN & BOISVERT (1978), BOLTON (1983), and LATTKE (1992). It is clear that to continue applying the currently dominant classification rules to all known dacetine species would imply a further proliferation of additional monotypic taxa around one or few indefinable genera containing the great majority of the species. Good candidates to further generic separation if such criteria are consistently applied are, just to make some examples, *Smithistruma terroni* (BOLTON, 1983) and the amber species to be described in this paper as *Strumigenys schleorum*. It is significant that the last described dacetine species (*Trichoscapa inusitata* LATTKE, 1992), in spite of several characters much more unusual than others already used to separate monotypic genera, was described in an already existing genus, but not in the closest available one (*Smithistruma*), rather under *Trichoscapa* since this genus, considered monotypic until that date, bears an elder name. We shall show, later, that even this solution is likely to imply untenable generic definitions and that the older name *Strumigenys*, at the present state of knowledge, represents the most reasonable generic name to be applied to all these and many other species.

To explain the objective difficulties in dacetine classification, one should remember that the "classical" dacetine genera were essentially based on the number of antennal joints. W. L. BROWN (1948–1979), in an important set of papers only incompletely cited here, criticized with right the indiscriminate use of this character which is, nonetheless, still widely employed. As a matter of fact, the antennal segmentation may represent a very easy, practical and clear-cut character to split a number of dacetine genera, though cases of infrageneric and infraspecific variability are known. BROWN (l. c.) proposed several taxonomic changes and based most of his generic revisions on the mandibular shape. In retrospect, the many new species described since the beginning of his revisionary work seem to show that the shape of the mandibles is even more variable and less suitable than the antennal segmentation in tracing generic boundaries. Contrary to some statements repeated in the literature, we are convinced that the plesiomorphic condition of the dacetine mandibles is triangular in shape and armed with two series of denticles opposing each other on the masticatory borders (among other reasons, this is the condition found in any conceivable sister group of the Dacetini). From this character state, the tendency to evolve longer and more slender mandibles, along with a reduction in number and/or size of the medial and basal teeth up to their complete loss, often accompanied by hypertrophy of one, or a fork of two or more distal teeth, occurred several times independently in different clades. Within the current dacetine classification this parallel, repeated morphocline can be observed within *Smithistruma*, *Rhopalothrix*, and the

related genera *Serrastruma* and *Cladarogenys*. In this paper we shall add other examples. As a result of all this, the Dacetini appear to contain a reduced number of genera with most species concentrated in the genus *Strumigenys* only. We can not exclude that the discovery of new characters may permit the definition of additional genera within the tribe. In this case some of these genera will be properly named using one or more of the available names that we regard as synonyms here. We have no difficulties in admitting that we searched for such new characters but in vain. At the present state of knowledge, the classificatory position we assume in this paper is still very tolerant and very conservative in comparison with the standard accepted today for the remaining ants. The classification we adopt in this paper is very close to the one already informally suggested by BROWN (1973 a: 35). The sole novelties not foreseen in BROWN's paper and introduced here for the first time are the synonymies *Basicerotini* = *Dacetini* and *Trichoscapa* = *Strumigenys*. In spite of our best efforts we have been unable to find a single valid reason to rescue these two names.

Strumigenys SMITH, 1860, J. ent. 1: 71. Type species *Strumigenys mandibularis* SMITH.

Neostruma BROWN, 1948, Trans. Amer. ent. Soc. 74: 111. Type species *Strumigenys crassicornis* MAYR. New Synonymy. This genus is based on small differences in mandibular dentition as compared with *Strumigenys*. Considering the variability in dacetine mandibular morphology known today, the generic validity of *Neostruma* on the basis of this sole character appears fragile, to say the least. If, on one hand, the monophyly of the six Neotropical species included in this genus needs confirmation but appears plausible, a hypothetical retention of *Neostruma* as generically separate from *Strumigenys* would made the latter paraphyletic.

Quadristruma BROWN, 1949, Trans. Amer. ent. Soc. 75: 47. Type species: *Epitritus emmae* EMERY. New Synonymy. The distinction between *Quadristruma* and *Strumigenys* relies exclusively on the number of antennal joints (4 and 6 respectively). This same difference in antennal counts has been already universally recognised as not worthy of generic separation for several phylogenetically close species of *Epitritus* and *Smithistruma*. The synonymy between *Quadristruma* and *Strumigenys*, though not formally proposed, has been already suggested by BOLTON (1983: 400).

Epitritus EMERY, 1869, Bull. Soc. ent. Ital. 1: 136. Type species *Epitritus argiolus* EMERY. New Synonymy. The synonymy of *Epitritus* with *Strumigenys* contrasts one of the most established ideas in recent dacetine classification: the division of genera on the basis of the presence/absence of an apical mandibular fork. Theoretically, a true fork should be present only in *Strumigenys*, *Neostruma*, and *Quadristruma*. All remaining "Dacetiti" should not possess this structure. Curiously enough, nobody ever defined what a true apical fork should be. The major source of information on the subject remains BROWN (1949 b) who, while separating *Quadristruma* from *Epitritus*, attributes to the former a "true apical fork of two spiniform teeth as in *Strumigenys*". The figure in BROWN's paper compares the mandibular morphology of *Quadristruma emmae* with the one of *Epitritus argiolus* (the type species of the genus *Epitritus*) in a convincing way. Nine years later, BROWN (1958 a) described the Japanese *E. hexamerus*, a species coupling an undoubted general habitus of *Epitritus* with a mandibular dentition fitting BROWN's former definition of *Quadristruma* (Fig. 4). BROWN, however, noticed the importance of this discovery and added that similar morphologies are present by convergence in *Heptastruma* (= *Rhopalothrix*) and in *Strumigenys chapmani* (BROWN, 1954). Figures 4 and 31, in fact, show the near identity of structure for *E. hexamerus* and *Rhopalothrix inopinata*. We concur entirely with BROWN (1958 a) in interpreting the presence of this structure in isolated species of different "genera" as due to pure convergence but, in addition, we regard this conclusion as the main reason for not considering the presence/absence of the fork as a valid generic character. No other known characters can be claimed to separate the species currently included in *Strumigenys* from those of *Epitritus*.

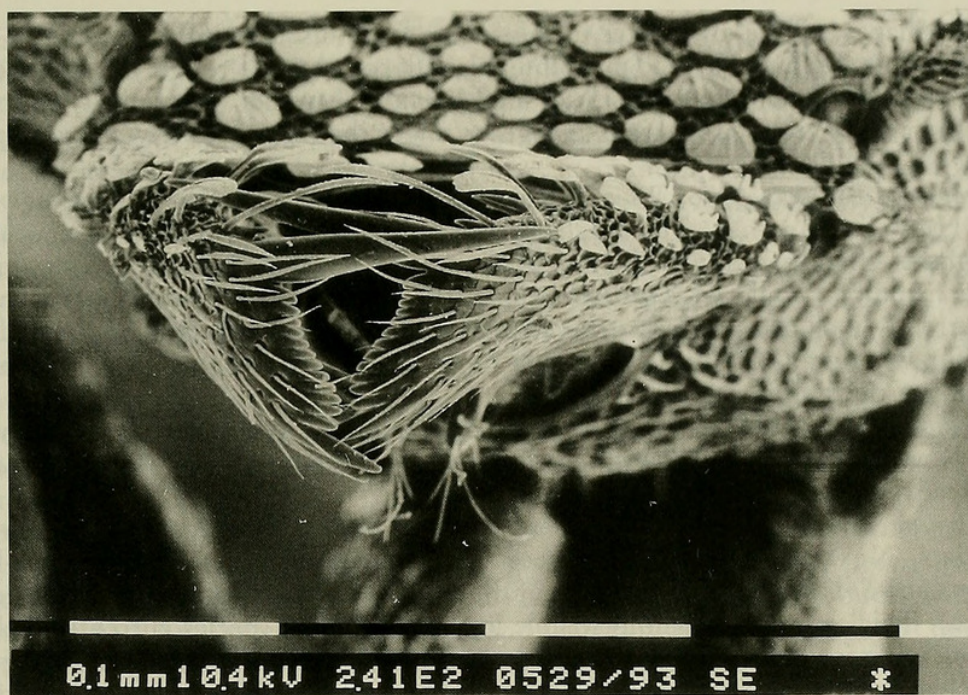


Fig. 4. *Strumigenys hexamera* (BROWN), new combination. Anterior view of the closed mandibles showing the presence of a dorsal and a ventral pointed tooth forming together an apical fork.

Dysedrognathus TAYLOR, 1968 a, J. Aust. ent. Soc. 7: 132. Type species *Dysedrognathus extemenus* TAYLOR. New Synonymy. This genus contains only one species from Singapore described as "close to *Epitritus*. . . and falling within the scope of its diagnosis in all details except the mandibular structure". *D. extemenus*, in fact, possesses triangular mandibles with a row of denticles on their masticatory borders. We have already said that, contrary to other literature statements, we consider this to be the plesiomorphic condition for the dacetines. Even supposing that our interpretation is wrong (i. e. the elongated mandibles with "fork" being the plesiomorphic condition and the triangular mandibles of *Dysedrognathus* being apomorphic), separating *Dysedrognathus* as a valid genus on the basis of this "apomorphy" would leave *Strumigenys* without apomorphic characters.

Trichoscapa EMERY, 1869, Ann. Accad. Aspir. Nat. 2: 24. Type species *Strumigenys membranifera* EMERY. New Synonymy. BROWN (1973 a) already foresaw that most dacetine genera should be merged under the oldest available name, i. e. *Trichoscapa*. This point of view had been already accepted and practiced by LATTKE (1992). BROWN's prediction, however, concerned only the "short mandibulate" dacetines, as opposed to the "long mandibulate" ones. The idea of maintaining this separation based on mandibular length is appealing when studying limited samples of species and most authors attempted to quantify it by computing a Mandibular Index (MI) in which the absolute length of the mandibles is normalized to absolute head length. Unfortunately, MI shows a great variability: among African species it ranges continuously between 7 and 69 (26–50 in the "long mandibulate" *Strumigenys*) without showing clear-cut generic patterns (BOLTON, 1983) and it may well reach values over 120 among Neotropical *Strumigenys* (see e. g. BROWN, 1958 b). In the previous pages we already synonymized a "short mandibulate genus" (*Dysedrognathus*) with a "long mandibulate" one (*Strumigenys*) on purely phylogenetic arguments. To the phylogenetic incongruency and to the practical difficulty in defining a boundary between long and short mandibles, one should add that the subjective appreciation of long or short mandibles depends not only on true mandibular length but on mandibular width as well, as already noted by BOLTON (1983: 353). Normalizing the mandibular length to their width instead than to head length, however, besides implying practical difficulties in taking standard measurements, would further contribute to clustering together traditional genera formerly considered separate and already synonymized in this paper, like *Epitritus* and *Strumigenys*. Further examples of the continuous range of

mandibular shapes will be given later in this paper while discussing the synonymy of other genera. The value attributed here to mandibular length corresponds roughly to the one already established in the older dacetine classification of EMERY-WHEELER where most "short mandibulate" genera were grouped within *Strumigenys* under the subgenus *Cephaloxys* (a preoccupied name).

Cladarogenys BROWN, 1976, Pilot Register Zool.: 33. Type species *Cladarogenys lasia* BROWN. New Synonymy. The single species described in this genus is another good example of the difficulty of the distinction between long and short mandibulate dacetines. Although its mandibles could be regarded as long, the general affinity with short mandibulate species currently included in "*Serrastruma*" is also evident. BOLTON (1983: 353) had already suggested its synonymy with the latter "genus" in spite of the mandibular difference but without formally proposing it.

Serrastruma BROWN, 1948, Trans. Amer. ent. Soc. 74: 107. Type species *Strumigenys simoni* EMERY. New Synonymy. This genus is linked to *Strumigenys* by means of *Cladarogenys* (q. v.), already synonymized with the former.

Smithistruma BROWN, 1948, Trans. Amer. ent. Soc. 74: 104. Type species *Strumigenys pulchella* EMERY. New Synonymy. Most recent literature emphasizes the difference between *Serrastruma* and *Smithistruma* on the basis of the absence of a basal lamella in the mandibles of *Serrastruma*. This character is wholly visible in the 11 African species currently included in *Serrastruma* but it is much less so in some *Smithistruma* where the lamella is indistinguishable from the basal tooth (e. g. *Smithistruma rostrata*). The gap in mandibular dentition postulated between the two genera and claiming >20 denticles in *Serrastruma* and ≤17 denticles for *Smithistruma* is fully trespassed by the inclusion of "*Cladarogenys*" in "*Serrastruma*" as already suggested by BOLTON (1983: 353), as "*Cladarogenys*" *lasia* possesses a basal lamella and a row of some 14–15 minute denticles. BROWN and BOISVERT (1978: 201) had already suggested that *Smithistruma* should be treated as a synonym of *Trichoscapa*.

Glamyromyrmex WHEELER, 1915, Bull. Mus. comp. Zool. 59: 487. Type species *Glamyromyrmex beebei* WHEELER. New Synonymy. The generic validity of this taxon had been doubted previously by BROWN (1973 a: 35), and BOLTON (1983: 321) suggested that it should be considered a synonym of "*Smithistruma*" (q. v.). We agree entirely and perform here the easy task of doing what had already been suggested.

Dorisidris BROWN, 1948, Trans. Amer. ent. Soc. 74: 116. Type species *Strumigenys nitens* SANTSCHI. New Synonymy. This genus, originally described as intermediate between *Glamyromyrmex* and *Strumigenys*, is, as such, an additional proof of some of the new synonymies we are proposing in this paper.

Chelystruma BROWN, 1950, Trans. Amer. ent. Soc. 76: 33. Type species *Glamyromyrmex lilloana* BROWN. New Synonymy. As for *Glamyromyrmex*, the generic validity of *Chelystruma* had already been doubted by BROWN (1973 a: 35) and its synonymy with *Glamyromyrmex* was already suggested but not formally proposed by BOLTON (1983: 321).

Codiomyrmex WHEELER, 1916, Bull. Mus. comp. Zool. 60: 326. Type species *Codiomyrmex thaxteri* WHEELER. New Synonymy. The validity of this genus, comprising only two Neotropical species, was also questioned by BROWN (1973 a: 35). BOLTON (1983: 321) suggested its synonymy with *Glamyromyrmex*. Its pretended apomorphies are (1) swollen mandibles, present also in *Glamyromyrmex tetragnathus*, and (2) a short head. Actually, the head of the type species (*Codiomyrmex thaxteri*) is much longer than, e. g., those of *Glamyromyrmex sistrurus* or *G. africanus* (see BOLTON 1983, figs. 24 and 27).

Codioxenus SANTSCHI, 1931, Rev. Ent. 1: 278. Type species *Epitritus simulans* SANTSCHI. New Synonymy. The single Cuban species included in this genus differs from a "traditional *Glamyromyrmex*" only in having 4 instead than 6 antennal joints. The inadequacy of this character in separating dacetine genera has already been shown by BROWN and BOISVERT (1978), BOLTON (1983), and in this paper.

Gymnomyrmex BORGMEIER, 1954, Rev. Bras. Biol. 14: 279. Type species *Gymnomyrmex splendens* BORGMEIER. New Synonymy. The six species comprising this genus are all Brazilian and are characterized by an elongate head and a hairless head and trunk, a combination of characters also recognizable in other Dacetini, like *Pentastruma canina* (BROWN and BOISVERT 1978). BROWN (1973 a: 35) suggested that *Gymnomyrmex* should be a synonym of *Trichoscapa* (= *Strumigenys*) and we can only concur with his opinion.

Kyidris BROWN, 1949, Mushi 20: 3. Type species *Kyidris mutica* BROWN. New Synonymy. This genus, rather than by one clear apomorphy, is separated by means of a combination of characters, namely the mandibular morphology, not dissimilar from the one known from *Gymnomyrmex* or *Pentastruma*, absence of propodeal spines, known in several *Strumigenys* species, and an impressed propodeal groove, a condition commonly found in "*Serrastruma*". Considering the paramount variability demonstrated in *Strumigenys* in this paper it seems difficult to maintain *Kyidris* as a separate genus on a logical base.

Pentastruma FOREL, 1912, Ent. Mitt. 1: 50. Type species *Pentastruma sauteri* FOREL. New Synonymy. Previously BROWN (1973: 75) and BROWN & BOISVERT (1978: 201) suggested that this genus should be considered as a synonym of *Trichoscapa*. We can only agree.

Tingimyrme MANN, 1926, Psyche 33: 104. Type species *Tingimyrme mirabilis* MANN. New Synonymy. The single Bolivian species described in this genus could be reasonably considered different enough from other known Dacetini to deserve generic separation. The sole difficulty in this course of action is that the remaining *Strumigenys*, in this way, would constitute a paraphyletic group.

Asketogenys BROWN, 1972, Psyche 79: 23. Type species *Asketogenys acubecca* BROWN. New Synonymy. Considerations similar to those already applied to *Tingimyrme* can be easily extended to *Asketogenys*. This monotypic genus was based on the two following characters, mandibles with a multidentate apical fork and a laterally marginate trunk. At this point of our discussion we don't need to insist further on the poor generic value of the mandibular morphology. The marginate trunk is present in a few other otherwise "normal" African *Strumigenys* which have been formerly grouped under "*Glamyromyrme*" and in some Neotropical "*Gymnomyrmex*". *Asketogenys* was described from S. Asia (Malaya) from where no species with marginate trunk are known: a second Asian *Strumigenys* showing this character but with entirely different mandibular morphology will be described in the appendix of this paper as *Strumigenys assamensis*.

Colobostruma WHEELER, 1927, Quart. Rev. Biol. 2: 32. Type species *Epopostruma leae* WHEELER.

Mesostruma BROWN, 1948, Trans. Amer. ent. Soc. 74: 118. Type species *Strumigenys turneri* FOREL. New Synonymy. *Colobostruma*, originally based on the peculiar morphology of a single gyne never more collected since the original description, proved afterwards to exhibit striking apomorphies in the worker caste which bears remarkable wing-like expansions on the sides of the petiole and postpetiole. *Mesostruma* was separate from *Colobostruma* to include species exhibiting the plesiomorphic condition, i. e. wing-like expansions absent either from the petiole only, or from both, petiole and postpetiole.

We would only add that we are ready to accept the point of view of non-cladist taxonomists refusing our paraphyly arguments and, hence, maintaining this last and a few other generic names as valid. Our main target, however, remains understanding the relationships and possible evolutionary patterns of the Dacetini. And this goal is not going to benefit in the slightest way from the separation of three or four genera containing only one or a few species each.

The generic synonymies proposed here are destined to imply over 170 binomial new combinations or emendations, essentially for the species transferred to *Strumigenys* from the genera sunk into its synonymy. At least some of these generic transfers will imply new homonyms as well. We refrain from introducing these changes here for the following reasons:

1. We are convinced that such species-level changes would find much better place within a complete revision of all the species involved and such a revision is far beyond the scope of the present paper.

2. Our incapacity to split *Strumigenys* into two or more sound genera should not be regarded as the final word on this genus. We still hope that a student more gifted

than we are may be able to find credible generic synapomorphies for groups of species to which already available generic names will be applied.

3. The status of our newly interpreted *Strumigenys* as well as that of other dacetine genera treated here is far from being fully understood and freed from criticisms and doubts about their meaning, limits, and validity. Some characters currently used, like the palpal formula, need confirmation from a broader sample of species dissected. Other genera resulting from the literature and still separate by us in this paper appear without apomorphies (e. g. *Epopostruma*), or are based on weak apomorphies (e. g. *Eurhopalothrix*, *Protalaridris*).

In an attempt to advance at least a step our knowledge on dacetine classification and probable evolutionary trends we performed the cladistic analysis of the genera actually recognizable within the Dacetini and we shall present the results in the following sections.

5. Methods of analysis

A strict cladistic approach has been adopted in this paper in identifying genera and their probable relationships. We stress that, independent of personal beliefs in taxonomic schools, the present status of dacetine classification contains so high a number of contradictory evaluations of the same (set of) character(s) that this course of action appears as the sole approach allowing at least a certain amount of clarity.

The following computer programs have been used for this paper: the search for the most parsimonious tree(s) was performed by PAUP 3.1.1 (SWOFFORD, 1993); evolutionary tracing of significant characters and their graphic display have been obtained by MacClade 3.01 (MADDISON & MADDISON, 1992).

The search for the shortest tree(s) was always performed by the mathematically exact branch-and-bound algorithm (HENDY & PENNY, 1982).

In tracing the most probable character evolution, we regularly reconstructed the character states for the internal nodes of our cladograms by means of the ACC-TRAN (= accelerated transformation) optimization model which maximizes evolutionary reversals over parallelisms.

For the outgroup comparison, given the very insecure status of the suprageneric classification of all the Myrmicinae, we did not dare a serious guess on the most probable sister group of the Dacetini. EMERY (1920) proposed the otherwise specialized tribe Attini to represent the closest relatives of the Dacetini. This idea remains a plausible guess and the only hypothesis on their relationships available to date.

An exact identification and definition of the sister group of the tribe is far beyond the scope of the present paper since it would imply a complete generic and tribal revision of the whole subfamily Myrmicinae. EMERY's hypothesis that the Attini are the sister group of the Dacetini (characterized by the pyriform head), offers the advantage that at least one remaining apomorphy still characterises the Attini: the great reduction or loss of pterostigma.

Because of these insecurities, we included in the analysis the following outgroups in addition to the Attini:

Stegomyrmex (Stegomyrmecini): this genus has been long considered a dacetine; it shares with several dacetine genera some superficial morphology and with the "Basi-cerotini" the soil-binding pilosity.

Calyptomyrmex (Meranoplini): this is another highly specialized myrmicine genus and its consideration among the outgroups has been used as a working hypothesis.

Superficial similarities between *Calyptomyrmex* and the Dacetini may be imputable to homoplasy, but, a posteriori, this genus appears to be closer to the Dacetini than *Stegomyrmex*, another outgroup which had long been included among Dacetini.

6. Characters used in searching for generic relationships

The great majority of the genera dealt with in this paper differ from each other in the combination of a restricted number of characters. Presence or absence of the same character, in addition, has been often evaluated in a different way in different genera.

The whole classification of the Dacetini is based exclusively on worker characters which — as a general rule — match quite well the gyne morphology. Dacetine males are too poorly known to allow delimitation of generic boundaries in a credible way.

The sole potentially significant larval character already mentioned in section 3, namely the presence or absence of bifid larval hairs, has been also included in the data matrix.

Most of these characters appear much more visible and of greater magnitude than other characters used in ant generic classification. Their exceptional appearance is compensated by a broad range of variation in which each character appears to fluctuate in a way completely independent from the others. In fact, if it might appear reasonable to order the genera considered here along a morphocline expressing e. g. their progressive reduction of the number of antennal joints, this ordering sharply contrasts with the variation of mandibular morphology and other characters. On the other hand, ordering these ants according to the progressive mandibular specialization, for instance, contrasts with the most probable evolution of the palpal formula, with the position of the antennal scrobes, etc.

The characters we used for the cladistic analysis represent the best we have been able to extract from the present knowledge about Dacetini. In spite of a number of weak points we regard them as quite rational but a great deal of feebleness remains because of their reduced number. This reduced number of characters (10 characters for 15 ingroup taxa) is nonetheless slightly misleading due to the high proportion of multistate characters. The ratio number of character states / number of taxa is 2.2.

No efforts have been made to list generic autapomorphies at this level of the analysis; these will be listed and described later when necessary.

Only the features described in the following and reported here with their respective coding are recognized as having potential synapomorphic value at generic level:

1. Head pyriform (1) or of different shape (0). This is the dacetine synapomorphy resulting from the classic literature, absent only among the outgroups, in some *Strumigenys* (see e. g. *S. inusitata*) and among most genera considered as of doubtful affinities in the recent literature.

2. Antennal scrobes present (1) or absent (0).

3. Eyes absent (0), dorsolateral (1), lateral (2), or ventral (3).

4. Number of antennal joints 12 (0), 11 (1), 10 (this state is not [yet?] recorded among the clade(s) considered in this paper) (2), 9 (3), 8 (4), 7 (5), 6 (6), 5 (7), or 4 (8). This is the main character on which most traditional classification of the Dacetini was based. We agree on the weak evolutionary value of this character as demonstrated recently by its intraspecific variability in some *Strumigenys* species and we shall add further examples of this variability in this paper. Species of "*Epitritus*" (=

Strumigenys) are now known to exhibit either 4 or 6 antennal joints independent of their presumable phyletic relationships. But most variability in counts of antennal joints is concentrated among species previously included in "*Smithistruma*". BROWN (1973 a) was the first to report the presence of individual specimens of *Strumigenys baudueri* (normally with 6-jointed antennae) with complete fusion of the antennomeres III, IV and V, resulting in 4-jointed antennae. Similar specimens of the same species have been collected by one of us (CBU) at Sirolo (Ancona, Central Italy) in a nest where individuals with 6 and with 4 antennal joints coexisted. Until recently, the 4-jointed antennae of isolate individuals of *S. baudueri* have been regarded as a rare specific monstrosity and three African species with 4-jointed antennae had been separate in the genus *Miccostruma* on the basis of this sole character. BOLTON (1983), adding four new Ethiopian species with 4-jointed antennae, showed that this fusion of antennal joints is relatively common among African species and not worthy of generic separation. In the appendix of this paper we will describe *Strumigenys nepalensis* from Nepal, a species with probable African affinities independent of antennal segmentation (it belongs to a species group of "normally" antennate *Strumigenys*) but equally exhibiting 4-jointed antennae. In the same appendix we will describe also *Rhopalothrix inopinata* n. sp. from Sri Lanka. Species of *Rhopalothrix* are known to have 7-segmented antennae but our new species shows fusion of segments V + VI and appears as 6-segmented.

We are nonetheless convinced that transition, e. g., between the 12 antennal joints of *Basiceros* and the 6–4 (maximum generic and absolute formicid minimum known) of *Strumigenys*, still implies a considerable amount of evolutionary change worth taking into account. This view, in spite of current criticisms on the use of antennal segmentation in dacetine classification, persists in established opinions about dacetine phylogeny (on which we do not agree). Just to make an example, one of the few undoubted facts unanimously resulting from the literature is that "primitive" dacetines are those exhibiting the highest antennal counts since these counts coincide with or are closer to the 12-segmented myrmicine and formicid ground plan. This hypothesis appears plausible, but it is contradicted when other characters are considered at the same time, which we will do later in this paper.

5. Funiculus without abnormally developed joints (0), with the last two joints much longer than the others (1), with only the last joint much longer than the others (2), or with the second joint enormously developed (3). We have been reluctant to include this character in the data matrix due to its possible correlation with character 4. It is intuitive, in fact, that abnormal development of one funicular joint may be due to fusion of two "normal" joints. If this simple hypothesis was true, one should be able to see some kind of correlation between the presence of abnormal funicular joints and total number of funicular joints. However, if such a correlation exists it is not very evident since elongation of the last or of the last two antennal joints is found mostly in multimerous antennate genera like *Octostruma*, *Protalaridris*, *Rhopalothrix*, *Acanthognathus*, and *Phalacromyrmex*. In addition, at least in a few instances, this character appears to represent a strong and credible generic autapomorphy (e. g. state 3 in *Orectognathus*), and it is for this reason that we include it.

6. Mandibles crossing (0) or opposing (1) each other at rest. State 1 of this character represents the sole known potential synapomorphy for all the taxa dealt with in this paper.

7. Mandibles opposing a large portion of the masticatory margin (0), or opposing only an apex (1). The apex may or may not be differentiated in a fork. This character description is the best coding we have been able to formulate in order to retain in the data matrix the widespread idea of the division between "long and short mandibulate" Dacetini. We already criticised the use of this character in splitting genera within *Strumigenys*, but, in a working hypothesis similar to the one adopted for the antennal segmentation, we will test the usefulness of this character within other clades of the Dacetini.

8. Number of maxillary palp joints 5 (0), 4 (1) (this state was not observed among the ants included in the analysis), 3 (2), 2 (3), or 1 (4).

9. Number of labial palp joints 3 (0), 2 (1), or 1 (2). This character and the previous one must be used with great caution due to the small number of specimens dissected. For instance, all of what is known on the basicerotine palpal formula is drawn from the paper by BROWN & KEMPF (1960) which give palpal counts for four species in three genera. One of these genera (*Octostruma*), on the basis of its sole dissected species (*O. inca*) is reported to have the palpal formula 2,2. In the course of the present study we dissected two workers of *O. stenognatha* and we found the palpal formula to be 1,1. *Octostruma*, hence, has been coded as polymorphic for this character in our data matrix. For the purpose of the cladistic analysis we must admit that in a number of cases we have been forced to accept the current practice of extrapolating to a whole genus palpal counts drawn from some of its members only.

10. Larval hairs at least in part bifid (1), or not (0). Presence of bifid larval hairs is a potential synapomorphy of the former tribe Dacetini s. str. Absence among "Basicerotini" may need to be confirmed by examination of more material. Actual presence/absence of bifid hairs among the genera considered here is coded according to WHEELER & WHEELER (1954-1983).

Tab. 1. Matrix with the presence/absence of the characters described in text and of their states among the recognized genera of Dacetini and the outgroups.

Taxa	Characters									
	1	2	3	4	5	6	7	8	9	10
<i>Acanthognathus</i>	1	0	2	1	1	1	1	0	0	1
<i>Basiceros</i>	1	1	2	0	0	1	0	3	2	0
<i>Colobostruma</i>	1	0	1	6	2	1	0	0	0	1
<i>Daceton</i>	1	0	1	1	0	1	1	0	0	1
<i>Epopostruma</i>	1	1	1	6	2	1	1	0	0	1
<i>Eurhopalothrix</i>	1	1	2	5	0	1	0	4	2	0
<i>Ishakidris</i>	0	1	2	3	1	1	0	3	1	?
<i>Microdaceton</i>	1	0	1	6	0	1	1	2	1	?
<i>Octostruma</i>	1	1	2	4	2	1	0	3+4	1+2	?
<i>Orectognathus</i>	1	0	2	7	3	1	1	0	0	1
<i>Phalacromyrmex</i>	0	1	3	1	1	1	0	2	1	?
<i>Pilotrochus</i>	1	1	3	4	1	1	0	?	?	?
<i>Protalaridris</i>	1	1	2	3	1	1	1	?	?	?
<i>Rhopalothrix</i>	1	1	0+1	5+6	2	1	1	?	?	0
<i>Strumigenys</i>	0+1	1	3	6+8	1+2	1	0+1	1	2	1
<i>Stegomyrmex</i>	0	1	3	0	0	0	0	?	?	?
<i>Calyptomyrmex</i>	0	1	2	0	0+2	0	0	3	1	1
Attini	0	0+1	2	1	0	0	0	0+1+2	1+2	0

The distribution of these character states among the taxa considered for the analysis is given in Table 1.

7. Assumptions about character evolution and character weight

For the cladistic analysis only presumably "important" potential synapomorphies affecting clades commonly reputed as being of generic rank have been considered. For this reason we preferred to code our characters as ordered. This way of coding does not affect binary characters but, for multistate characters, it implies, e. g., that transition between 12 and 6 antennal joints will be computed as 6 evolutionary steps corresponding to the loss of the 12th, 11th, . . . 7th joints respectively. Evolutionary inversions in which a clade with a low number of joints may re-acquire an originally lost higher number are permitted but each secondarily acquired joint is equally computed as an additional evolutionary step.

Although this model of step by step evolution appears to be plausible for the characters we employed, it has, on the other hand, the drawback of overweighing multi-state characters as compared with binary ones. To avoid this disadvantage which could greatly affect the results in the case e. g. of the number of antennal joints, we adopted a method of weighting as objective as possible. Each character was given equal weight (100) regardless of its number of states. In this way gain (or loss) of the antennal scrobes is weighted 100 as the reduction of the number of antennal joints from 12 to 4 or the reduction of maxillary palpomeres from 5 to 1. This kind of *a priori* weighting based on the individual character variability implies that loss (or

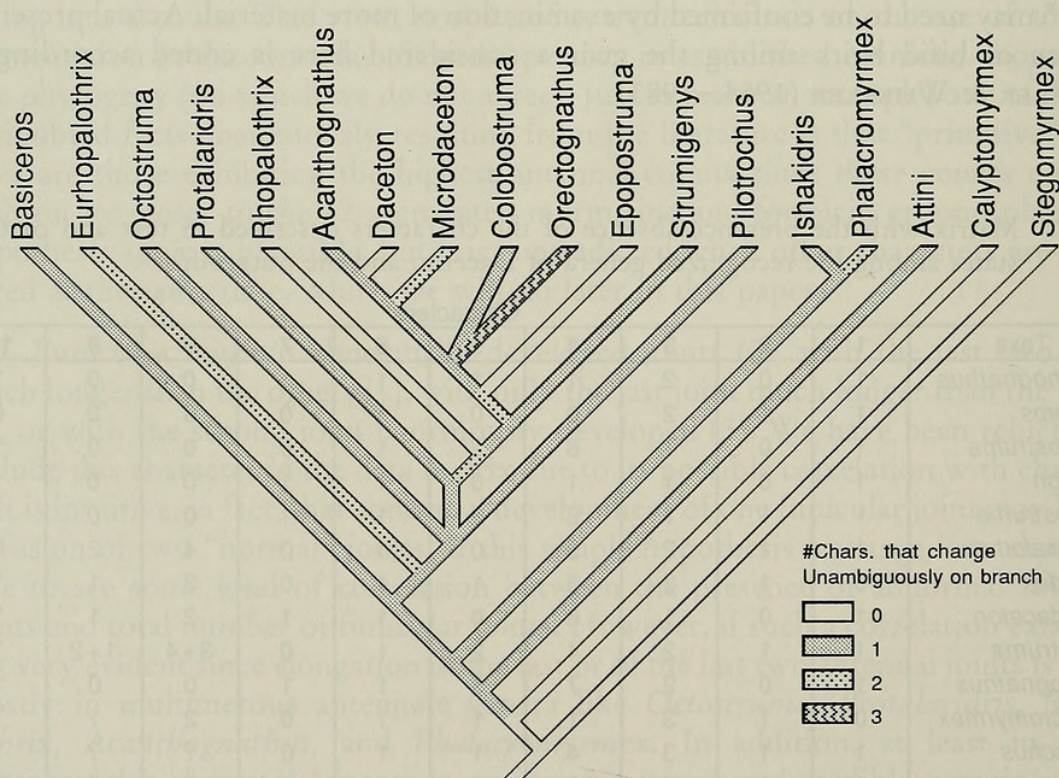


Fig. 5. Cladogram illustrating the probable phylogeny of the Dacetini as resolved in this paper. The three taxa to the right (*Attini*, *Stegomyrmex* and *Calyptomyrmex*) are out-groups. Partially polytomous strict consensus tree derived from 9 equally most parsimonious trees. The different patterns on the branches indicate the number of apomorphies recognizable for each branch.

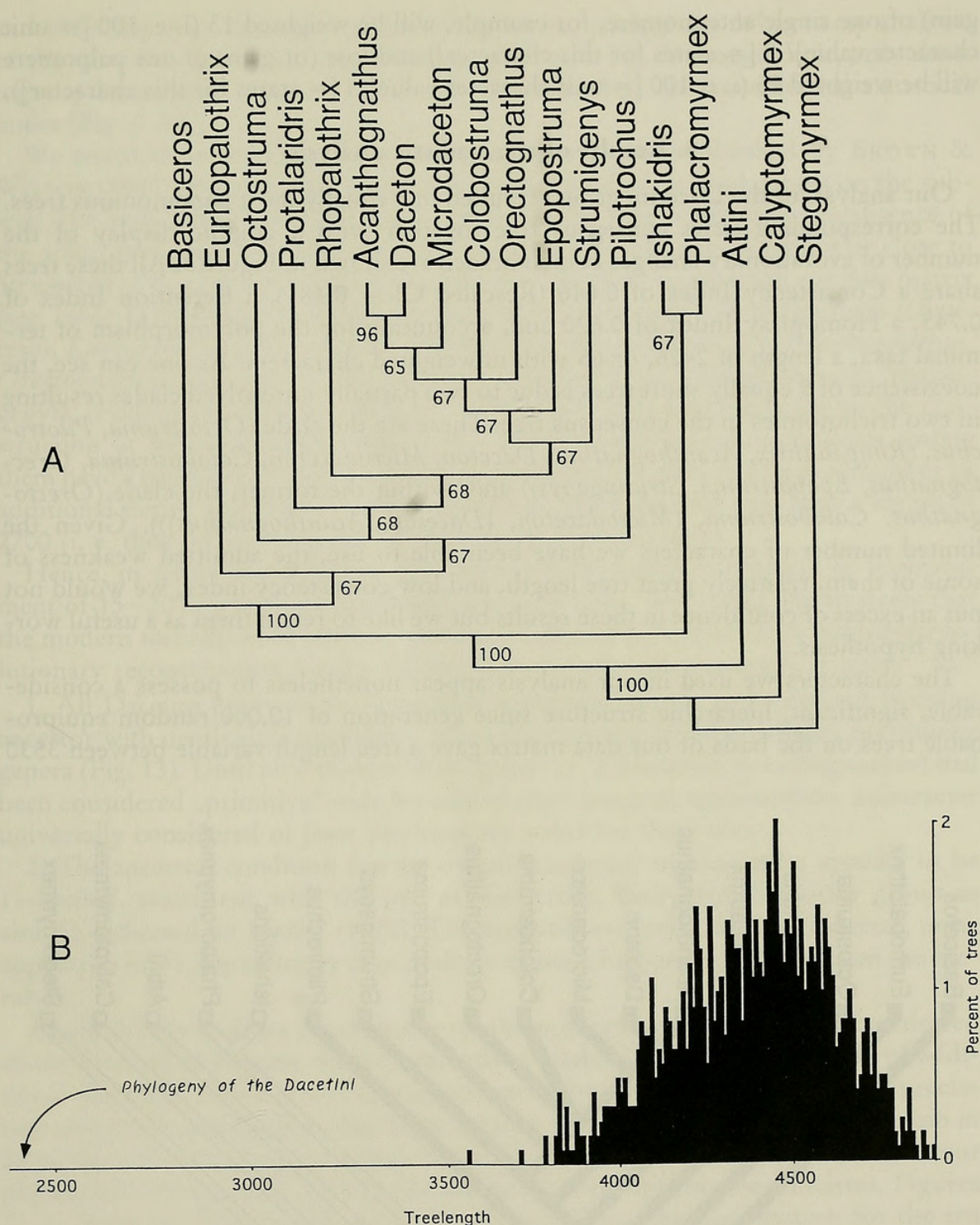


Fig. 6. Some indications on the reliability of the tentative dacetine phylogeny drawn from the data of Table 1. — A. Same cladogram as in Fig. 5 obtained here as 50% majority rule tree from 1,000 bootstrap replicates. For the bootstrap analysis the characters have been sampled according to their weight. The figures on the internal branches indicate the percent of presence among all replicates. — B. Relative frequency distribution of the length of 10,000 randomly equiprobably generated trees drawn from the data matrix of Table 1. The tree proposed in Fig. 5 as dacetine phylogeny is much shorter than any random tree in a highly significant way.

gain) of one single antennomere, for example, will be weighted 13 (i. e. $100 [= \text{unit character value}] / 8 [= \text{states for this character}]$) and loss (or gain) of one palpomere will be weighted 25 (i. e. $100 [= \text{unit character value}] / 4 [= \text{states for this character}]$).

8. Results of the cladistic analysis

Our analysis of the Dacetini genera resulted in 9 equally most parsimonious trees. The corresponding strict consensus tree together with a graphic display of the number of evolutionary changes at each branch are shown in Figure 5. All these trees share a Consistency Index of 0.646 (Rescaled CI = 0.481), a Retention Index of 0.745, a Homoplasy Index of 0.620 and, accounting for the polymorphism of terminal taxa, a length of 2426, or 65 with unweighted characters. As one can see, the coexistence of 9 equally short trees is due to two partially unresolved clades resulting in two trichotomies in the consensus tree. These are the clade (*Octostruma*, *Pilotrochus*, (*Rhopalothrix*, *Acanthognathus*, *Daceton*, *Microdaceton*, *Colobostruma*, *Orectognathus*, *Epopostruma*, *Strumigenys*)) and, within the former, the clade (*Orectognathus*, *Colobostruma*, (*Microdaceton*, (*Daceton*, *Acanthognathus*))). Given the limited number of characters we have been able to use, the admitted weakness of some of them, relatively great tree length, and low consistency index, we would not put an excess of confidence in these results but we like to retain them as a useful working hypothesis.

The characters we used in our analysis appear nonetheless to possess a considerable, significant, hierarchic structure since generation of 10,000 random equiprobable trees on the basis of our data matrix gave a tree length variable between 3530

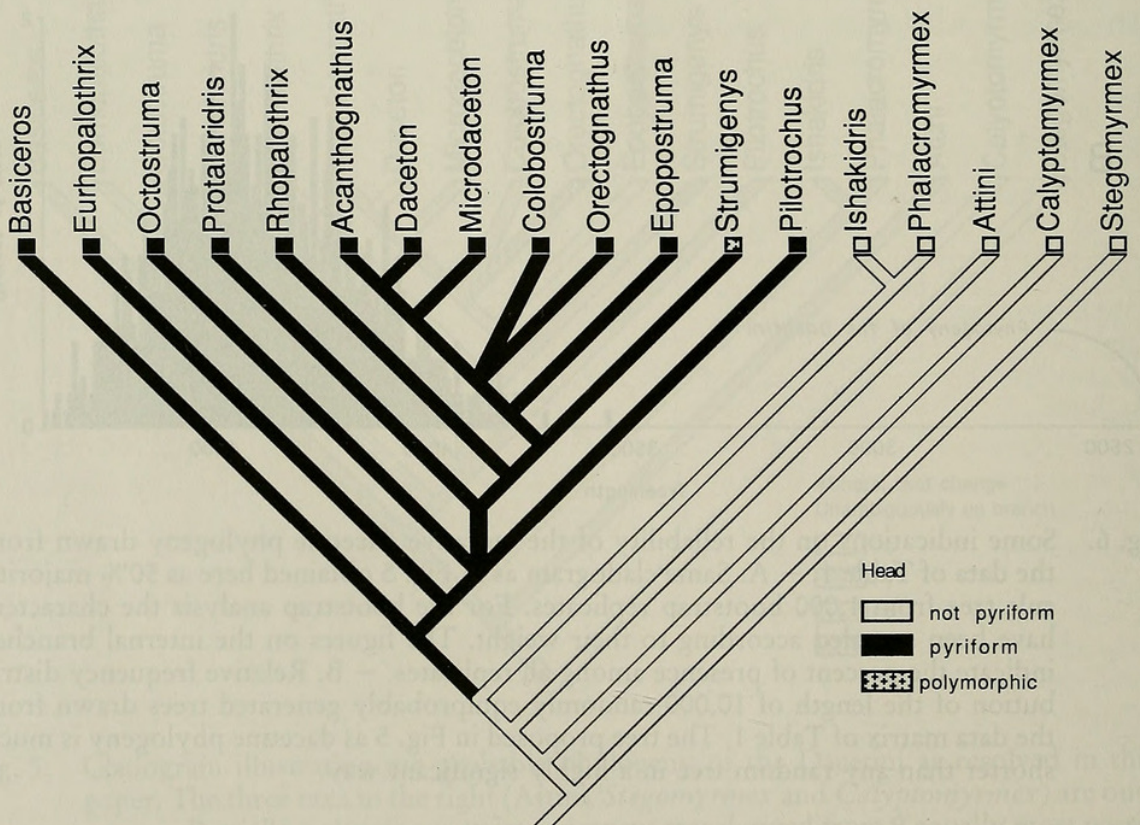


Fig. 7. Most parsimonious reconstruction of the evolution of the shape of the dacetine head according to the hypothetical phylogeny of Fig. 5.

and 4880 (Fig. 6 B) as compared with 2426 for our cladogram. A bootstrap analysis of the same data produced the same cladogram as in Fig. 5, though, in it, only three ingroup branchings appear in frequencies greater than the conventional statistical limits (Fig. 6 A).

We tested the reliability of the phylogeny previously established by BROWN & WILSON (1959) by using the characters already found in classical papers on the subject. The sole „traditional“ character omitted by us here is the presence/absence of the apical fork which, since it has only been used to split genera within or close to *Strumigenys*, does not affect the general picture. We have re-analysed our data matrix (see Table 1) by inputting a partially unresolved constraint tree of the form ((*Basicros*, *Eurhopalothrix*, *Octostruma*, *Protalaridris*, *Rhopalothrix*), ((((*Acanthognathus*, *Orectognathus*), *Daceton*), (*Microdaceton*, (*Epopostruma*, *Colobostruma*))), *Strumigenys*), (*Pilotrochus*, *Phalacromyrmex*, *Ishakidris*)). This constraint allows the construction of 945 compatible cladograms. The 20 most parsimonious ones among them have a length of 79 with unweighted characters (i. e. they need a minimum of 14 additional steps), and, with weighted characters, the 5 shortest ones have a length of 2700 (i. e. they are ca. 15% longer than those proposed here).

Hence, in terms of parsimony, our tentative phylogeny represents an improvement of 15–20% when compared with previous ones. We would like to stress that the modern techniques of cladistic analysis employed here offer more plausible evolutionary reconstruction for the following two important characters at least:

1. All Dacetini genera with specialized mandibles appear to be derived from an ancestor with denticulate mandibles, as are the majority of the remainder myrmicine genera (Fig. 13). Until now most of these genera (e. g. *Daceton*, *Acanthognathus*) had been considered „primitive“ only because of their antennal segmentation, a character universally considered of poor phylogenetic value for these ants.

2. The ancestral condition for the dacetine antennal segmentation appears to be 11-jointed, consistent with the one of the Attini, their probable sister group as already indicated by EMERY (1920). The probable evolution of this character, now, appears to be 11 steps shorter than in the previous phylogeny resulting from the literature.

As we already said, we consider our results as the maximum which can be inferred about dacetine phylogeny on the presently available information. The use of additional characters undiscovered or misunderstood by us may lead to a better appreciation of generic relationships. For these reasons we think it is important to explain in detail the evolutionary assumptions needed for each character we considered in our phylogenetic hypothesis. This should aid future confirmations or criticisms. Figures 7–16 show the most parsimonious reconstructed evolutionary pattern for the ten characters included in the analysis according to the ACCTRAN (= accelerated transformation) model.

From these figures it should be possible to speculate that the origin of the Dacetini has to be placed in an ant hunting mobile prey and killing or immobilizing it by means of the mandibles. The mandibles, therefore, developed increasingly a pincers' function and appearance. This accounts for the diversity of bizarre mandibular morphologies of all known dacetine species and for the necessity of their movement on one plane. Once this immobilizing capacity and the "pincers mandibles" had been acquired, increase in mandibular power and mandibular motility was an obvious, rewarding adaptation selected very early in dacetine evolutionary history.

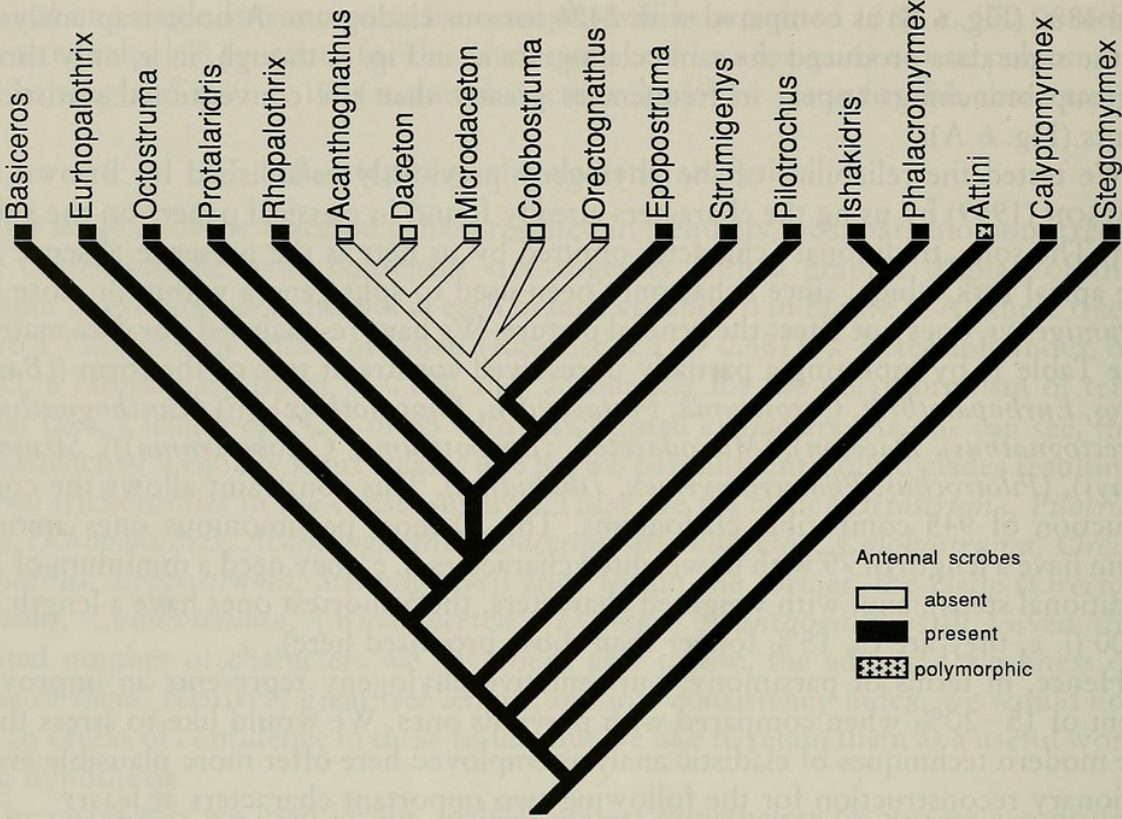


Fig. 8. Most parsimonious reconstruction of the evolution of the dacetine antennal scrobes according to the hypothetical phylogeny of Fig. 5.

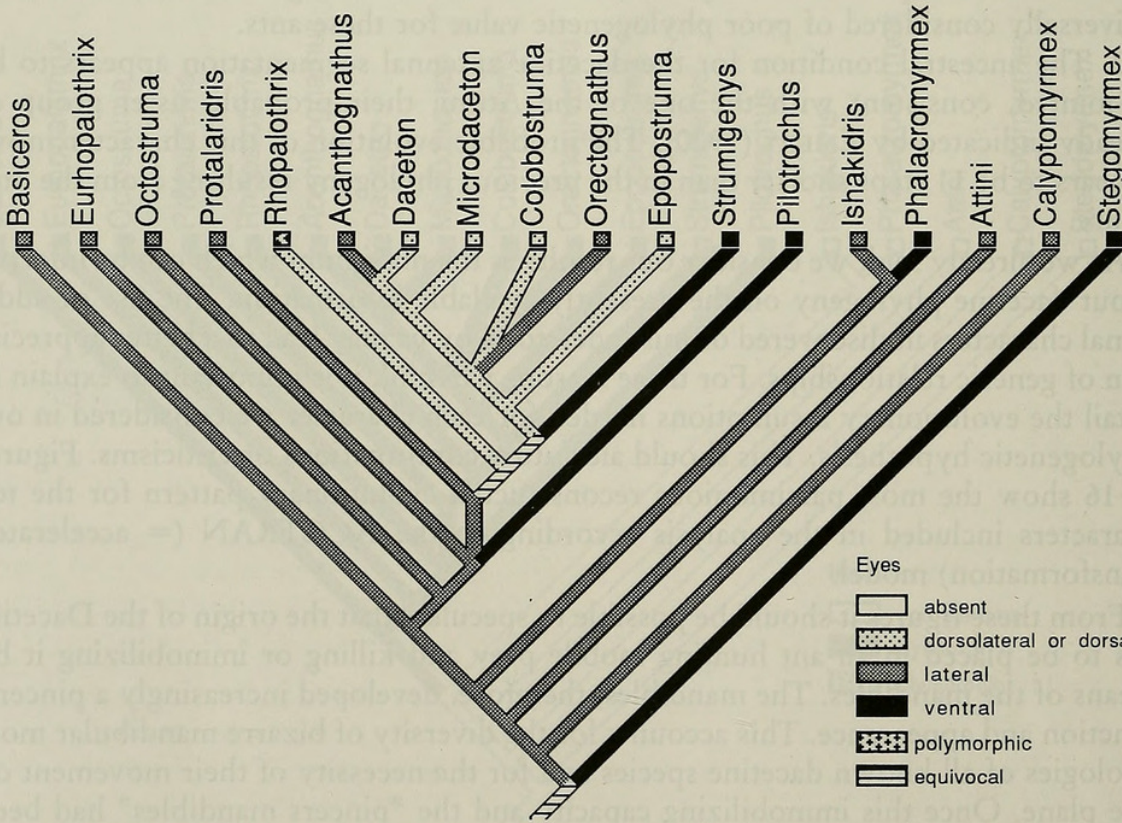


Fig. 9. Most parsimonious reconstruction of the dorsoventral migration of the dacetine eyes according to the hypothetical phylogeny of Fig. 5.

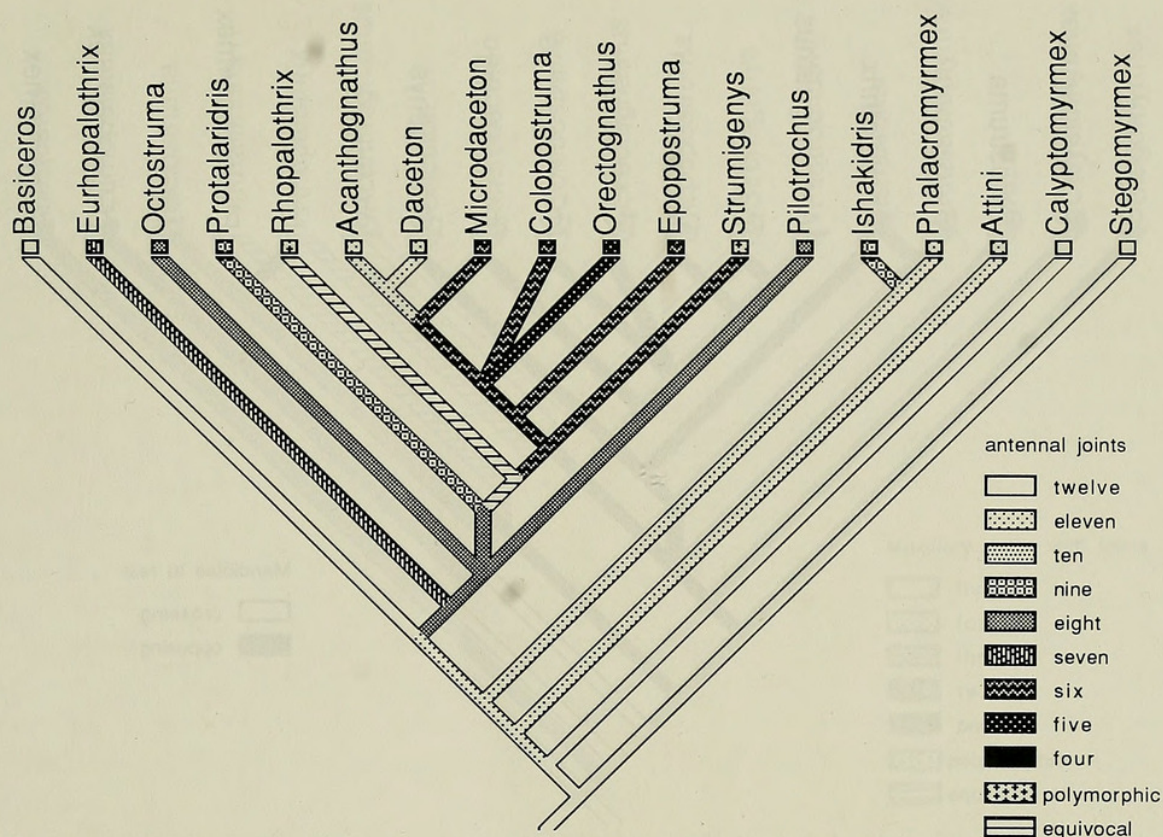


Fig. 10. Most parsimonious reconstruction of the evolution of the dacetine antennal segmentation according to the hypothetical phylogeny of Fig. 5.

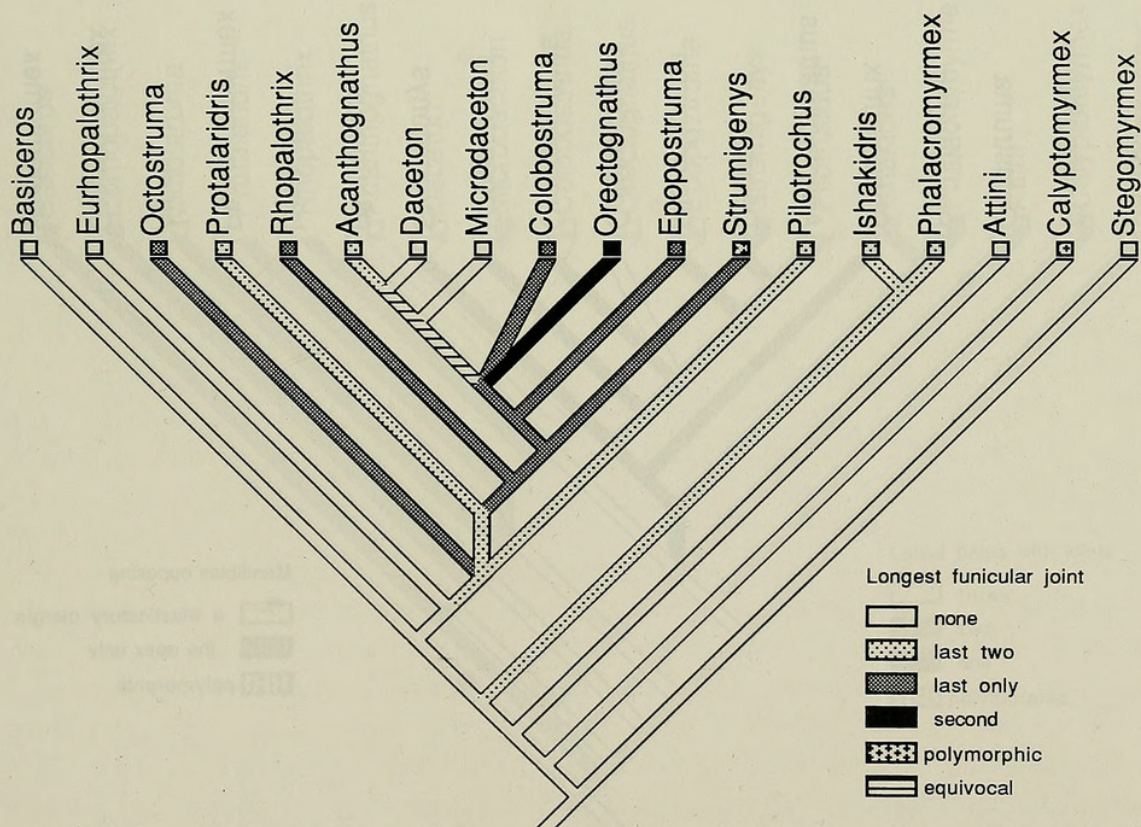


Fig. 11. Most parsimonious reconstruction of the evolution of the dacetine antennal joints according to the hypothetical phylogeny of Fig. 5.

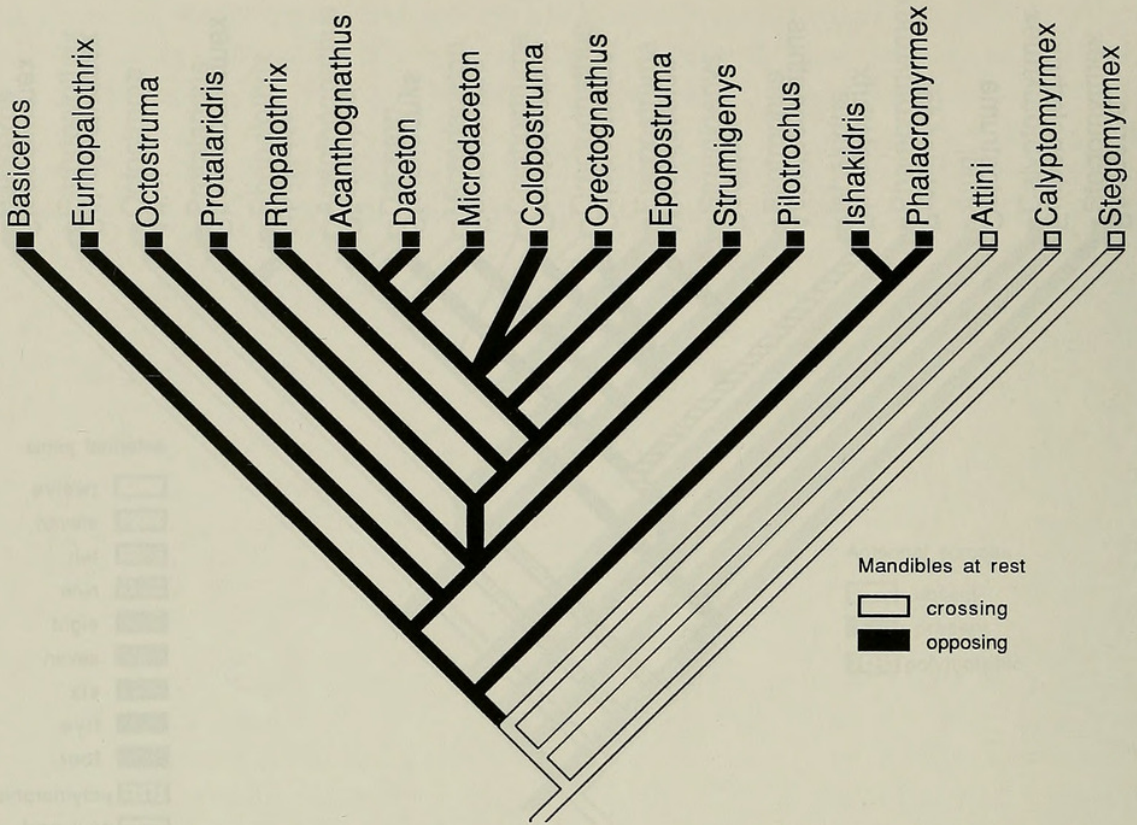


Fig. 12. Most parsimonious reconstruction of the evolution of the mandibular opposability (the sole known dacetine apomorphy) according to the hypothetical phylogeny of Fig. 5.

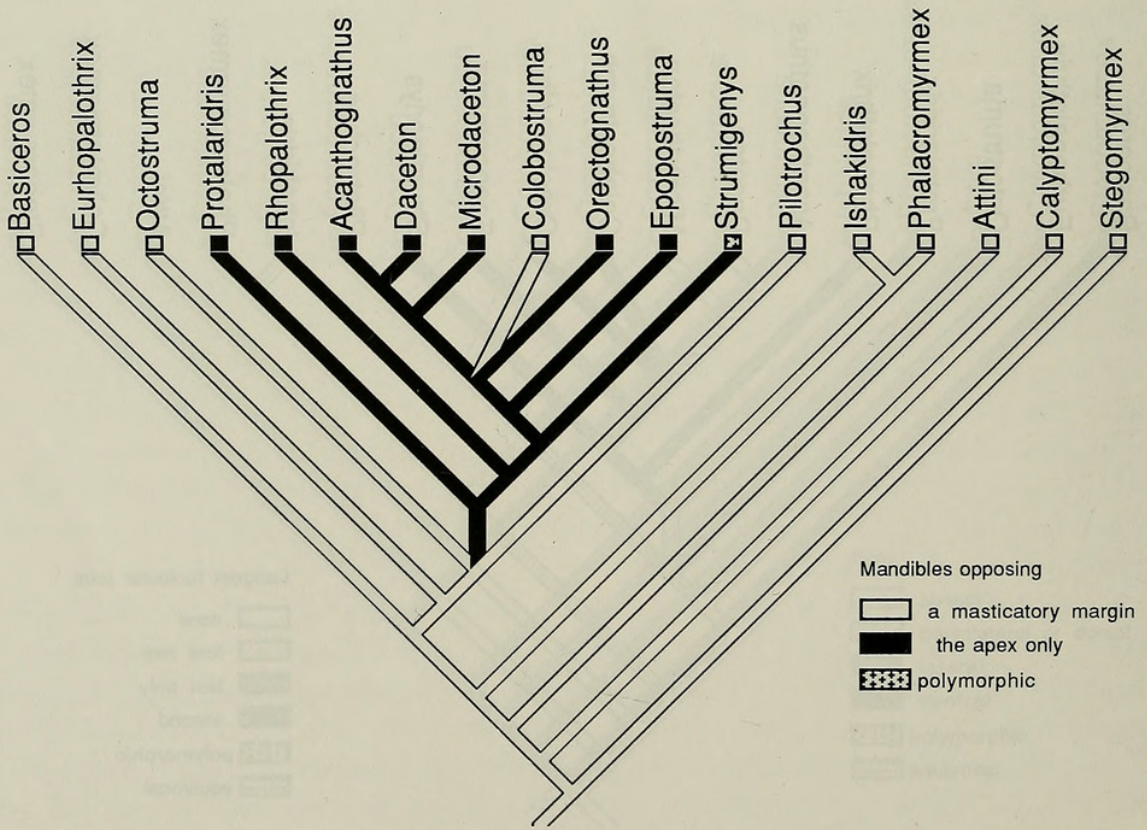


Fig. 13. Most parsimonious reconstruction of the evolution of the dacetine mandibular morphology according to the hypothetical phylogeny of Fig. 5.

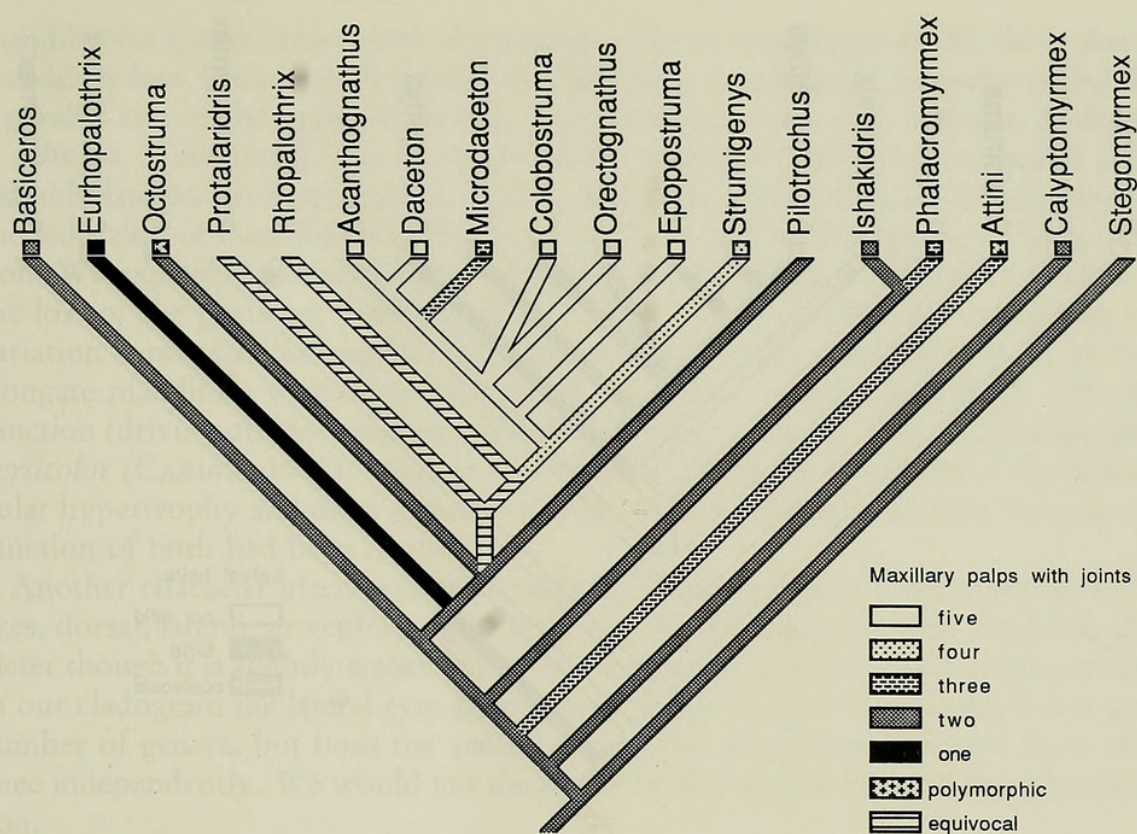


Fig. 14. Most parsimonious reconstruction of the evolution of the dacetine segmentation of maxillary palps according to the hypothetical phylogeny of Fig. 5.

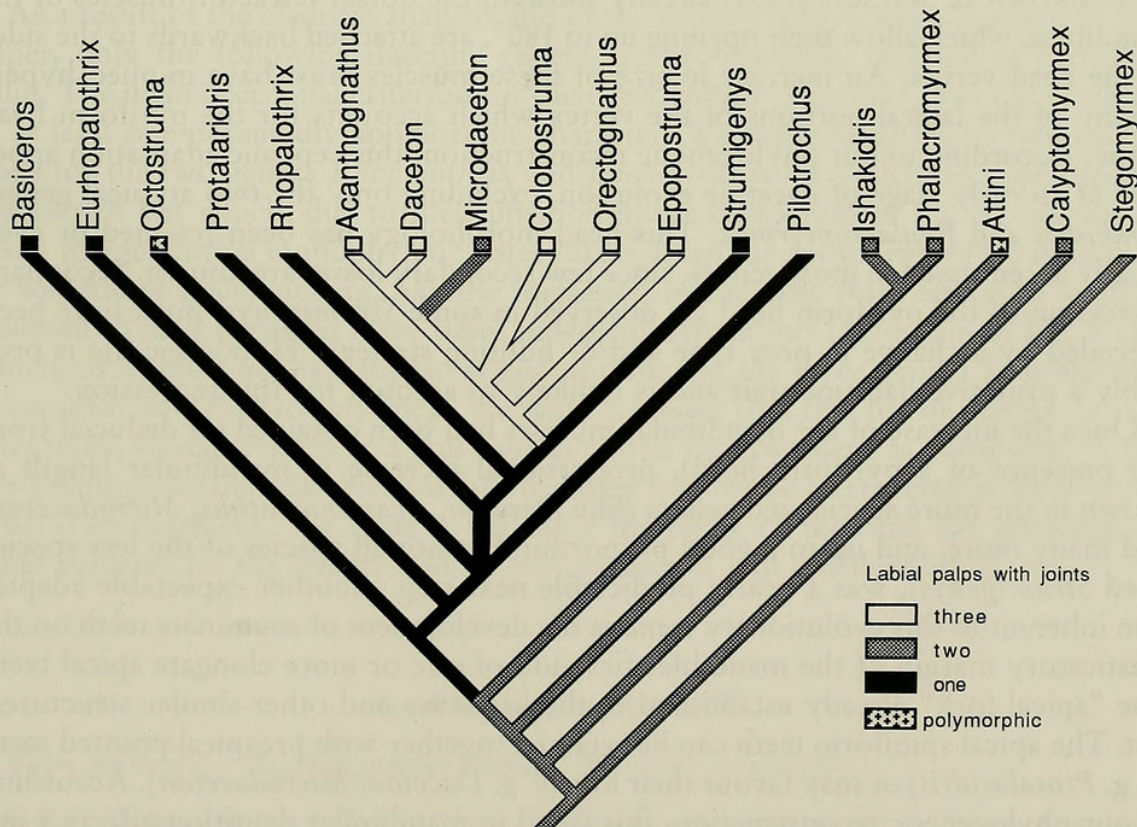


Fig. 15. Most parsimonious reconstruction of the evolution of the dacetine segmentation of labial palps according to the hypothetical phylogeny of Fig. 5.

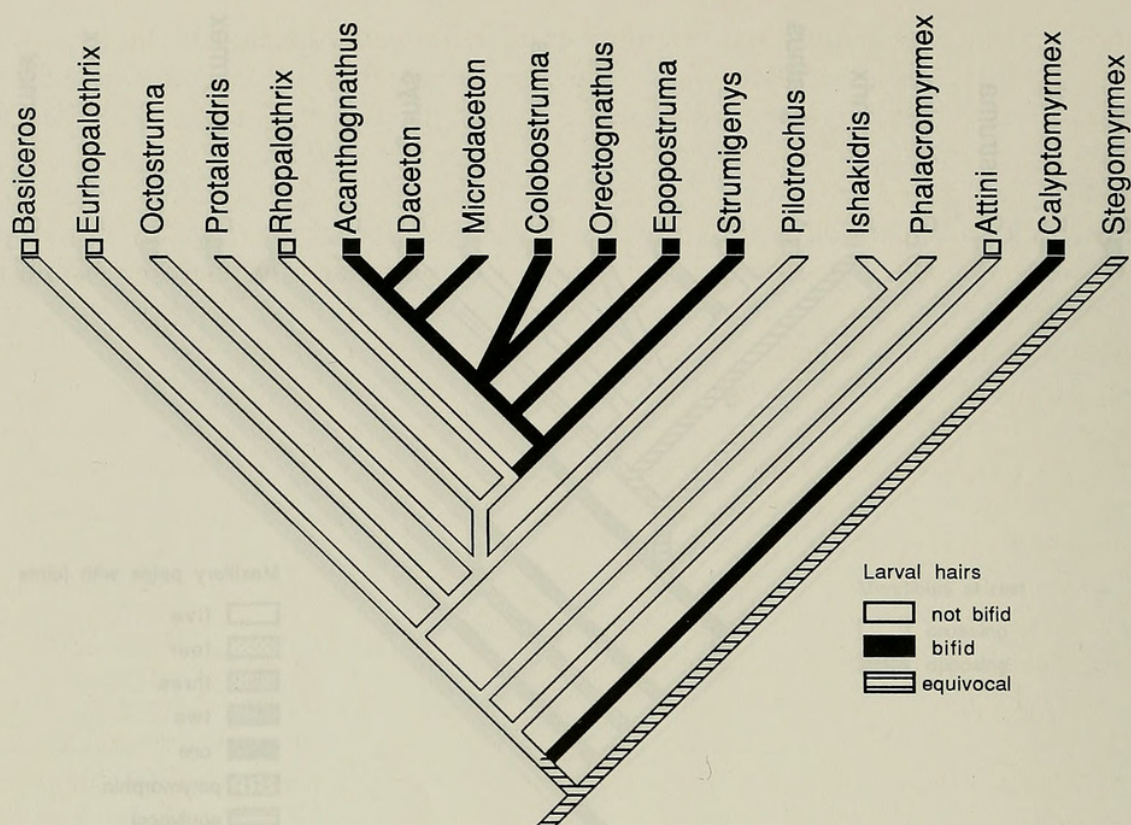


Fig. 16. Most parsimonious reconstruction of the evolution of dacetine larval bifid hairs according to the hypothetical phylogeny of Fig. 5.

As BROWN & WILSON (1959) already showed, the dorsal retractor muscles of the mandibles, which allow their opening up to 180° , are attached backwards to the sides of the head vertex. An increase in size of these muscles must have implied hypertrophy of the lateral portions of the vertex which accounts for the pyriform head shape. According to our phylogenetic reconstruction, this cephalic adaptation appeared at an early stage of dacetine evolution, excluding only the two atypical genera *Ishakidris* and *Phalacromyrmex*. This head morphology has been retained or even greatly accentuated in most genera, since few secondary losses are known. Secondary regression of the pyriform head (as observed in some *Strumigenys*) must have been preceded by a change in prey type and/or hunting strategy. Hypogaecic life is probably a primitive dacetine trait and is unlikely to account for this regression.

Once the increase of the mandibular muscles had been obtained (as deduced from the presence of a pyriform head), proportional increase in mandibular length as shown in the more specialized genera (like *Daceton*, *Acanthognathus*, *Microdaceton*, and many more, and up to a good proportion but not all species of the less specialized *Strumigenys*), was a nearly predictable next step. Another expectable adaptation inherent to this evolutionary trend is the development of acuminate teeth on the masticatory margin of the mandibles first and of one or more elongate apical teeth (the "apical fork" already established in the literature and other similar structures) last. The apical spiniform teeth can be retained together with preapical pointed teeth (e. g. *Protalaridris*) or may favour their loss (e. g. *Daceton*, *Microdaceton*). According to our phylogenetic reconstruction, this trend in mandibular dentition affects 8 out of the 17 possibly valid dacetine genera (see Fig. 13) and by far the great majority of species. Another unpredicted result of our phylogeny is that the presence of short

mandibles in *Colobostruma* and in a number of *Strumigenys* species should be due to secondary loss. Only a small number of these short-mandibulate *Strumigenys* exhibit a parallel loss of the pyriform head as one could expect (e. g. *S. vodensa*, *S. dagon*, *S. sahurus*, *S. inusitata*). The retention of the pyriform head by a number of short mandibulate dacetines renders difficult to extend the explanation we already gave for the reduction of mandibular musculature to the reduction of mandibular specialization. We explained the secondary reduction of mandibular musculature (visible in the loss of the pyriform head shape) by a shift in prey quality. But explaining the variation in mandibular length in the same way may be an oversimplification. In fact, elongate mandibles without pointed teeth are known to play an entirely different function (driving out potential nest invaders) at least in the Australian *Orectognathus versicolor* (CARLIN, 1981). One can not exclude, therefore, retention of the mandibular hypertrophy and of its partial correlate, pyriform head, even after the primary function of both had been lost.

Another character often used in identifying dacetine genera is the position of the eyes, dorsal, lateral, or ventral on the head capsule. This appears to be a reliable character though it is slightly weakened by the occurrence of a few species without eyes. In our cladogram the lateral eyes are the plesiomorphic condition retained in a great number of genera, but both the ventral and dorsal migrations appeared more than once independently. We would not dare a functional explanation for this phenomenon.

9. The generic classification of the Dacetini

As a result of the cladistic analysis and of the synonymies newly proposed in this paper, only the following dacetine genera are provisionally retained as probably valid. The main decisional criterion for their recognition, however, was the presence of at least one potentially apomorphic character. We made nonetheless two exceptions for the two genera *Rhopalothrix* and *Epopostruma* for which no apomorphies are known but which, due to their position in the cladogram of Fig. 5, can not be easily merged into a monophyletic sister taxon. Even the apomorphies we used may be sometimes unconvincing, like the migration of the eyes from lateral to ventral, assumed to have occurred three times independently in our cladogram in Fig. 9 and which, as a result of that, appear as apomorphic for the three genera *Strumigenys*, *Pilotrochus* and *Phalacromyrmex*. We want to stress that this list of genera, in our intentions, should represent a still candid partial improvement as compared to the pre-existing dacetine classification but it can by no way be interpreted as a definitive generic arrangement. We hope it will have the effect of focusing the attention of other students on the quality and on the number of still unsolved problems.

Acanthognathus MAYR 1877

Type species: *Acanthognathus ocellatus* MAYR by monotypy.

In our cladogram the following two characters appear as apomorphic for *Acanthognathus*: the eyes lateral on the head capsule and the two-jointed antennal club. To these one must add at least the basal mandibular process, unique among related taxa.

Basiceros SCHULZ 1906

Type species: *Meranoplus singularis* SMITH by monotypy.

Synonyms: *Ceratobasis* SMITH 1860. Nec *Ceratobasis* LACORDAIRE 1848.
Aspididris WEBER 1950. Synonymy by BROWN, 1974.

This genus, in our data matrix, appears to be characterized by the 12-jointed antennae.

Colobostruma WHEELER 1927

Type species: *Epopostruma leae* WHEELER by monotypy.

Synonyms: *Alistruma* BROWN 1948. Synonymy by BROWN, 1959 b.

Clarkistruma BROWN 1948. Synonymy by BROWN, 1959 b.

Mesostruma BROWN 1948. Synonymy proposed in this paper.

The apomorphic character of this genus resulting from our analysis is short mandibles opposing each other over the whole masticatory margin. The peculiar morphology of the head of the single known gyne and on which WHEELER originally based his description of *Colobostruma* as a new subgenus of *Epopostruma* can be also retained as generic apomorphy if it can be confirmed for other species.

Daceton PERTY 1833

Type species: *Formica armigera* LATREILLE by monotypy.

Synonym: *Dacetum* AGASSIZ 1846 (Emendation).

The dorsal position of the eyes in the sole representative of this genus does not appear as apomorphic in our cladogram since we did not separate this condition from the dorsolateral condition of *Acanthognathus*. A very strong generic apomorphy, unique among all ants and not included in our data matrix, is the occipital foramen situated in the superior part of the occiput, allowing the mouthparts to move over the body's transversal plane.

Epopostruma FOREL 1895

Possible paraphyletic genus

Type species: *Strumigenys quadrispinosa* FOREL, designated by WHEELER, 1911.

Synonym: *Hexadaceton* BROWN 1948. Synonymy by BROWN, 1973 b.

No unequivocal apomorphies result from our data matrix nor are any known from the literature and we are unable to propose credible candidate characters. We maintain *Epopostruma* generic status in this paper for its position between *Strumigenys* and *Orectognathus* as it appears in our cladogram. We suspect, however, that this result may be changed by the discovery of new characters or by a different interpretation of those we used. The actual position of *Epopostruma* in the present cladogram is probably due to our inclusion of the mandibular morphology as a potential apomorphic character in the data matrix. The probable placement of this genus is likely to be the one in which *Colobostruma* (q. v.) will be merged with *Epopostruma* in a single genus with polymorphic mandibles as is already the case for *Strumigenys* and *Rhopalothrix*. This latter solution, if adopted, would correspond to WHEELER's original idea when first describing *Colobostruma* as a subgenus of *Epopostruma*.

Eurhopalothrix BROWN & KEMPF 1960

Type species: *Rhopalothrix bolani* MAYR designated by BROWN & KEMPF, 1961.

The 7-jointed antennae and loss of one maxillary palp (from two to one) appear to represent the apomorphies of this genus, which appears closer to *Basiceros* than to *Rhopalothrix* in our phylogenetic reconstruction. The reason for this is again our retention of the mandibular morphology as potential apomorphy.

Ishakidris BOLTON 1984

Type species: *Ishakidris ascitaspis* BOLTON by original designation.

The reduction of antennal joints from eleven to nine appears apomorphic for this genus in our phylogeny. In addition to this character, at least the following two, deduced from the description of BOLTON (1984), can be safely considered apomorphic: the ventrolateral margins of the head carinate and the base of first gastral sternite carinate.

Microdaceton SANTSCHI 1913

Type species: *Microdaceton exornatum* SANTSCHI by monotypy.

The two generic apomorphies for this genus resulting from our data are the maxillary palps three-jointed and the labial palps two-jointed.

Octostruma FOREL 1912 b

Type species: *Rhopalothrix simoni* EMERY designated by WHEELER, 1913.

This genus appears to be characterized by the hypertrophy of the last funicular joint.

Orectognathus SMITH 1853

Type species: *Orectognathus antennatus* SMITH by monotypy.

Synonym: *Arnoldidris* BROWN 1950 b. Synonymy by BROWN, 1973 b.

The following characters appear as generic apomorphies in our cladogram: eyes lateral on the cephalic capsule, antennae 5-jointed, and hypertrophy of the second funicular joint.

Phalacromyrmex KEMPF 1960

Type species: *Phalacromyrmex fugax* KEMPF by original designation.

The two apomorphies resulting from our data are ventral eyes and three-jointed maxillary palps.

Pilotrochus BROWN 1977

Type species: *Pilotrochus besmerus* BROWN by original designation.

The position of the eyes (ventral) appears apomorphic for this genus in our phylogenetic reconstruction.

Protalaridris BROWN 1980

Type species: *Protalaridris armata* BROWN by original designation.

The increase from 8 to 9 antennal joints results as the sole apomorphy for this genus in our data matrix.

Rhopalothrix MAYR 1870

Possible paraphyletic genus

Type species: *Rhopalothrix ciliata* MAYR designated by WHEELER, 1911.

Synonyms: *Heptastruma* WEBER 1934. Synonymy by BROWN & KEMPF, 1960.

Acanthidris WEBER 1941. Synonymy by BROWN & KEMPF, 1960.

Talaridris WEBER 1941. Synonymy by SNELLING, 1981.

No apomorphies for this genus result in our data matrix and we have been unable to find additional potentially credible ones. In case of better demonstrated paraphyly, however, *Rhopalothrix* remains the oldest available name and other, junior genera should be sunk into synonymy with it. Given the many insecurities still affecting the classification of these ants we prefer to provisionally leave the situation as it is.

Strumigenys SMITH 1860

Type species: *Strumigenys mandibularis* SMITH by monotypy.

Synonyms: *Labidogenys* ROGER 1862. Synonymy by BROWN, 1959 a.

Pyramica ROGER 1862. Synonymy by BROWN, 1959 a.

Proscopomyrmex PATRIZI 1946. Synonymy by BROWN, 1949 a.

Eneria DONISTHORPE 1948. Synonymy by BROWN, 1949 a.

Asketogenys BROWN 1972. Synonymy proposed in this paper.

Chelystruma BROWN 1950 a. Synonymy proposed in this paper.

Cladarogenys BROWN 1976. Synonymy proposed in this paper.

Codiomyrmex WHEELER 1916. Synonymy proposed in this paper.

Codioxenus SANTSCHI 1931. Synonymy proposed in this paper.

Dorisidris BROWN 1948. Synonymy proposed in this paper.

Dysedrognathus TAYLOR 1968 a. Synonymy proposed in this paper.

Epitritus EMERY 1869 b. Synonymy proposed in this paper.

Glamyromyrmex WHEELER 1915. Synonymy proposed in this paper.

Borgmeierita BROWN 1953. Synonymy with *Glamyromyrmex* by BROWN, 1973 a.

Gymnomyrmex BORGMEIER 1954. Synonymy proposed in this paper.

Kyidris BROWN 1949 a. Synonymy proposed in this paper.

Polyhomoa AZUMA 1950. Synonymy with *Kyidris* by BROWN & YASUMATSU, 1951.

Neostruma BROWN 1948. Synonymy proposed in this paper.

Pentastroma FOREL 1912 a. Synonymy proposed in this paper.

Quadrastroma BROWN 1949 b. Synonymy proposed in this paper.

Serrastroma BROWN 1948. Synonymy proposed in this paper.

Smithistruma BROWN 1948 (nomen novum for *Cephaloxys*). Synonymy proposed in this paper.

Cephaloxys SMITH 1865. Nec *Cephaloxys* SIGNORET 1847. Synonymy with *Smithistruma* by BROWN, 1948.

Wessonistruma BROWN 1948. Synonymy with *Smithistruma* by BROWN, 1973 a.

Weberistruma BROWN 1948. Synonymy with *Smithistruma* by BROWN, 1973 a.

Platystroma BROWN 1953. Synonymy with *Smithistruma* by BROWN, 1973 a.

Miccostruma BROWN 1948. Synonymy with *Smithistruma* by BOLTON, 1983.

Tingimyrme MANN 1926. Synonymy proposed in this paper.

Trichoscapa EMERY 1869 a. Synonymy proposed in this paper.

The sole apomorphy known for this genus is the position of the eyes, ventral.

10. Fossil Material

Four samples of Dominican amber including Dacetini were available for the present study. They are as follows:

Do-3854 from the Staatliches Museum für Naturkunde, Stuttgart. It contained 4 complete workers which have been separately cut, polished, and numbered respectively as Do-3854-1 (a specimen with the head covered by a silverish gaseous layer and the body surrounded by numerous minute amber fissures not affecting the morphological examination), Do-3854-2 (Fig. 17) (a specimen with head and trunk covered by a gaseous layer; the specimen, in addition, appears greatly darkened, a circumstance rendering it particularly suitable for morphological inspection), Do-3854-3 (a poorly visible specimen due to proximity with some impurities and to the presence of veins or cracks in amber filled with brown material), Do-3854-4 (Fig. 18) (a specimen affected by one thoracic dorsal analogous brown amber vein but suitable for profile and head in full-face view observation). One additional amber fragment (Do-3854-5) has been isolated since it contains a worker without head, but otherwise complete of the same dacetine species which could not be cut away from a worker of *Oxydris* sp. Nine additional *Oxydris* workers were included in the same amber fragment, together with one winged myrmicine female which we tentatively attribute to *Rogeria*, due to difficulties in observing the clypeal morphology. Other than ants, this amber sample contained also several pieces of insect excrement, many soil and sand particles, three fragments of roaches, a pseudoscorpion, a mite, two collembola, many fungal hyphae, and seeds.

Do-3853 from the Staatliches Museum für Naturkunde, Stuttgart. This piece includes only one dacetine worker, well preserved and deep in the amber, together with one *Oxydris*, and several centipedes. This specimen appears to belong to the



Fig. 17. Specimen Do-3854-2 (black specimen), habitus, lateral view.

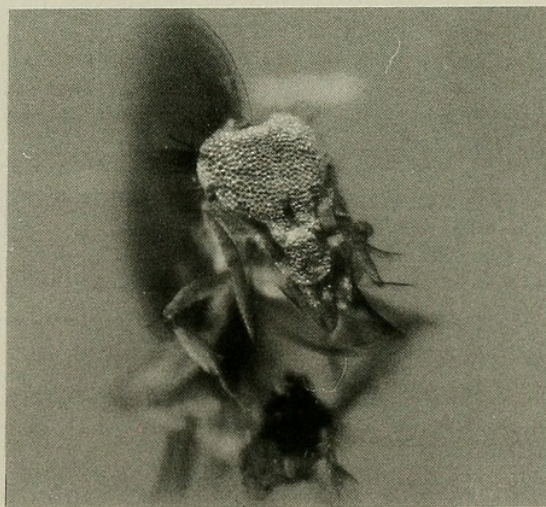


Fig. 18. Specimen Do-3854-4, frontal view of the head.

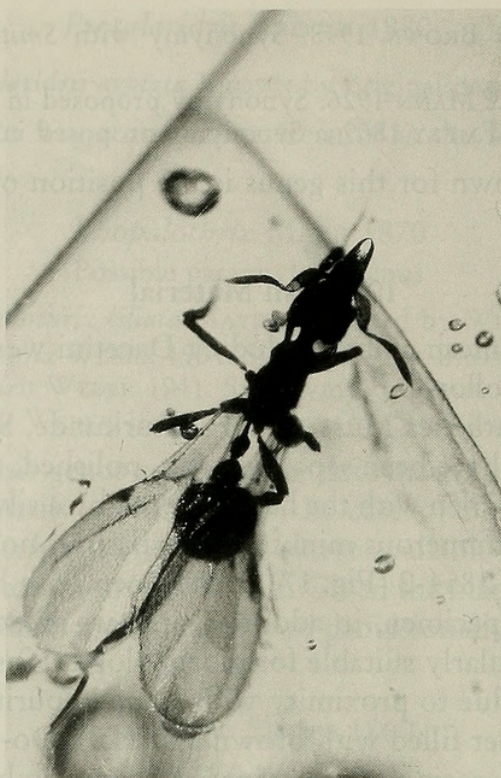


Fig. 19. Specimen Do-4909, dorsal view.

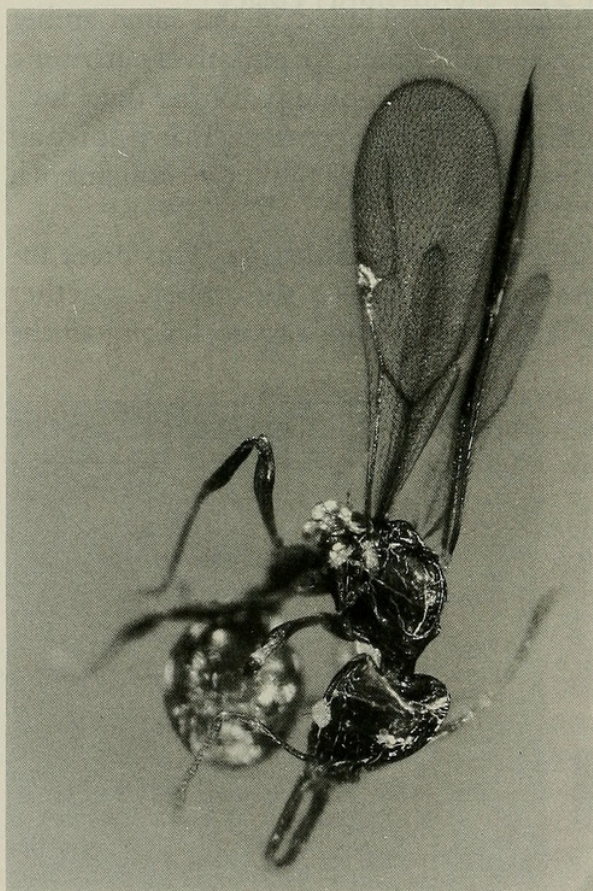


Fig. 20. Specimen H-10-135, habitus, oblique fronto-dorsal view.

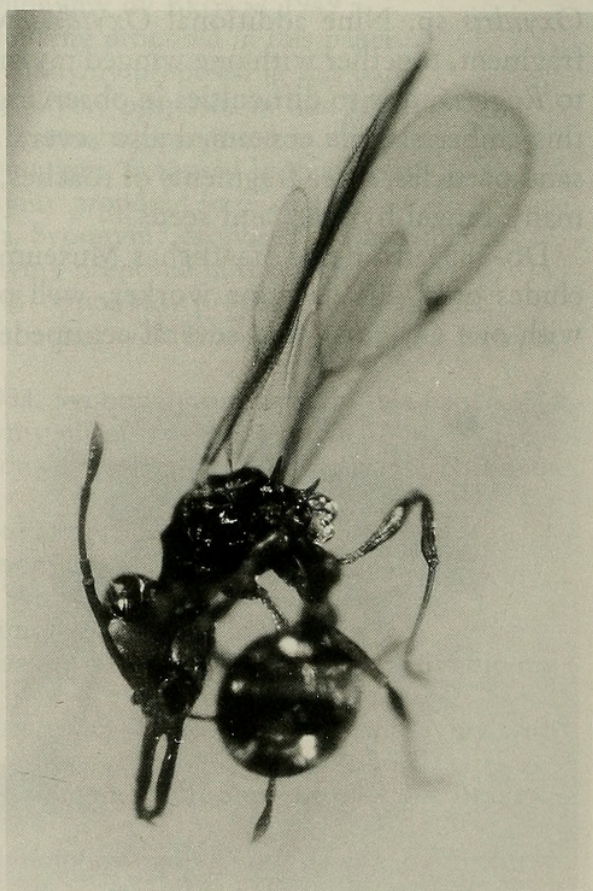


Fig. 21. Specimen H-10-135, habitus, oblique postero-dorsal view.

same species as the one included in the sample Do-3854. According to Dr. SCHLEE (personal communication), both samples originate from the same amber piece which had been cut into several pieces for commercial reasons. The single dacetine contained in this sample has not been cut and re-polished to avoid damaging other valuable material. For this reason this worker has not been properly measured and examined in a way comparable to the other material discussed in this paper and it is equally excluded from the type material. The dacetine specimen is nonetheless very well preserved and its attribution to the same species as the one described from the sample Do-3854 remains a reasonable certainty.

Do-4909-1 from the Staatliches Museum für Naturkunde, Stuttgart (Fig. 19). It includes one complete winged dacetine female. Other parts of the same amber fragment contained a termite wing, a chalcidid wasp and a small liquid drop with an air bubble.

H-10-135 from the collection of Dr. GEORGE O. POINAR, Jr. (Figs. 20, 21). A clear amber sample containing one winged Dacetini gyne, six specimens of Diptera, a leaf piece and other vegetable fragments, and relatively few soil particles.

11. Description of the fossil taxa

The description of new species follows established monographs of the group like BROWN & KEMPF (1960 and 1969), TAYLOR (1968 b) or BOLTON (1983). Exhaustive descriptions of the measurements employed and of the indices calculated on them can be found in these papers. Accordingly, the following abbreviations have been used: HL (= head length), HW (= head width), SL (= scape length), ML (= mandibular length), AL (= alitrunk length), PW (= pronotum maximum width), CI (= cephalic index), SI (= scape index), MI (= mandibular index), SMI (= scapo-mandibular index):

Strumigenys schleeorum BARONI URBANI n. sp.

Fig. 22, 23

Holotype: Winged gyne (unique) in Dominican amber, preserved in the amber collection of the State Museum of Natural History, Stuttgart (Department of Phylogenetic Research), No. Do-4909-1.

Derivatio nominis: The species is named for DIETER and HEIDE-BERNA SCHLEE for their long effort in creating and curating the amber collection where this and many other valuable specimens are preserved.

Diagnosis. — A *Strumigenys* species with extremely reduced mandibular dentition and mandibles touching each other only at an undifferentiated apex when closed.

Winged gyne (Fig. 22). Measurements (in mm) and indices: total length (mandibles included) 1.92; HL 0.48; HW 0.32; SL 0.24; eye maximum length 0.12; ML 0.12; AL 0.56; PW 0.24; petiole length 0.12; petiole maximum width 0.09; postpetiole maximum width 0.16; gaster maximum width 0.40. CI 66.6; SI 75; MI 25; SMI 200.

Description. — Head (Fig. 23) with anteriorly strongly converging sides, rounded posteriorly and occipital border moderately concave. Eyes very protruding, their maximum diameter as long as the masticatory border of the mandibles; their exact position in relation to the antennal scrobe could not be precisely located in the single available specimen. Preocular laminae convex and slightly crenulate externally, running backwards from the postero-lateral sides of the clypeus without reaching the

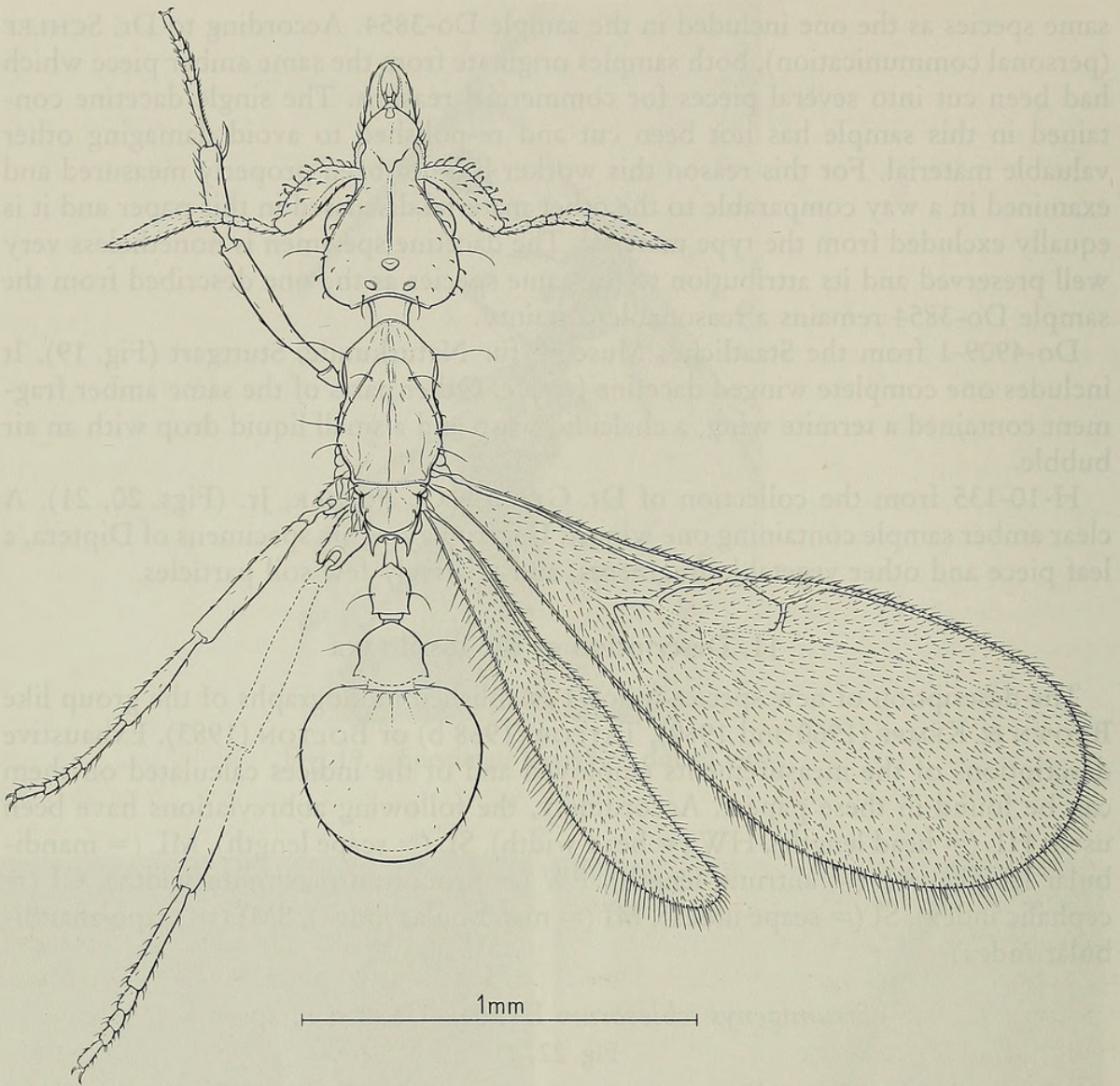


Fig. 22. *Strumigenys schleorum* n. sp. Winged gyne, holotype. General habitus in dorsal view. Dotted lines indicate body parts visible but impossible to focus adequately in the fossil. Drawing by ARMIN CORAY.

eyes. Clypeus slightly longer than broad, with convex sides, and acute posterior margin. A marked medial line between the posterior margin of the clypeus and the median ocellus. Antennae with 6 antennomeres. Scapes $\frac{1}{2}$ of the head length, not reaching the occipital border posteriorly when folded backwards, short, broad, flattened, bent very close to the base, its external border slightly convex and crenulated, and the internal border nearly straight. Last funicular joint nearly as long as the sum the preceding ones. Mandibles $\frac{1}{3}$ of head length, touching each other only at the apex when opposed, with slightly convex external sides; internal border with a basal lamella followed by a set of 8–9 minute denticles decreasing apically in size and only superficially differentiated; mandibular apex continuing the row of denticles without fork or other differentiate structures, constituted only by a single spiniform tooth. Labrum with a pair of anteriorly projecting lobes easily visible between the mandibles.

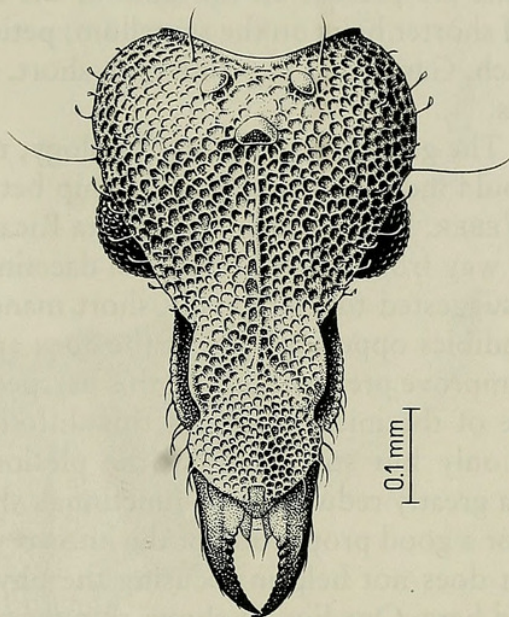


Fig. 23. *Strumigenys schleeorum* n. sp. Winged gyne, holotype (specimen Do-4909-1). Full frontal view of the head and mandibles. Drawing by ARMIN CORAY.

Trunk: pronotum with poorly marked humeral angles. Mesonotum adjecting medially and cranially over the pronotum, slightly convex on the sides, and straight posteriorly. Scutellum rounded posteriorly. Propodeal spines straight, directed backwards, slightly shorter than the petiole width. A faint median line visible on the mesonotum and scutellum.

Petiole bell shaped in dorsal view, $\frac{1}{3}$ longer than broad. Postpetiole $\frac{1}{3}$ broader than the petiole, with rounded anterior face. Spongiform appendages absent.

Gaster round in dorsal view, truncated anteriorly.

Wings: fore wings with marked pterostigma. R+Sc complete. 2r ending in a trace of Rs+M. Mf1 equally marked. Only traces of other veins. Hind wings with clearly visible costal vein only.

Sculpture: clypeus deeply and finely reticulate, the same structure broader and more accentuated on the cephalic dorsum; trunk and abdominal peduncle with effaced reticulation superimposed by irregular, light striation; gaster, mandibles and appendages superficially punctuated. Median area of the anterior portion of the gaster with three effaced costulae.

Colour: dark brown, opaque with slightly lighter antennae and legs.

Pilosity: dorsum of the head with sparse, short, subdecumbent spatulate hairs slightly longer towards the sides; longer, pointed subdecumbent hairs on the antero-lateral sides of preocular laminae, the edges of clypeus and, more scattered, on the mandibles; vertex with a pair of standing setae directed upwards three times longer than the spatulate hairs on the rest of the cephalic dorsum; a pair of standing setae, longer than the maximum diameter of the eyes on the postocular sides; scapes equally covered by spatulate hairs slightly longer than those on the head on the

superior and anterior border, comparable in length to the smallest cephalic ones on the posterior border; sides of pronotum and mesonotum with short, appressed spatulate hairs; pronotal humeri with a pair of long, filiform hairs; two pairs of similar but slightly shorter hairs are present on the sides of the mesonotum; another two pairs of similar but still shorter hairs on the scutellum; petiole and postpetiole with a pair of filiform hairs each. Gaster and legs with rare, short, acuminate hairs similar to those on the mandibles.

Relationships. — The general cephalic morphology, the small clavate hairs and the size of the eyes would indicate a close relationship between *Strumigenys schleeorum* and *S. studiosi* WEBER, known only from Costa Rica. *S. schleeorum*, however, differs in a remarkable way from any other known dacetinae by its mandibular morphology. We already suggested that originally short mandibulate dacetines started developing longer mandibles opposing only at the apex and then differentiated the apical morphology to improve prey capture. In this perspective *S. schleeorum* is very likely to represent one of the initial stages of this differentiation, with mandibles opposing at the apex only but still retaining the plesiomorphic, serially dentate masticatory margin in a greatly reduced, non-functional, shape. If, on one hand, this explanation accounts for a good proportion of the known variation in dacetinae mandibular morphology, it does not help in focusing the phylogenetic position of the amber species described here. Our Fig. 13 shows that the most parsimonious reconstruction of the evolution of dacetinae mandibular morphology assumes this change to have occurred at the root of *Protalaridris* but that within *Strumigenys* a certain number of evolutionary inversions must have occurred. Among contemporary species, at least *Strumigenys terroni* from Cameroon shows a visibly different but functionally equivalent morphological organization. Until a cladistic analysis of the whole genus is performed it is useless to speculate when and how many times this phenomenon may have happened and which are the most directly concerned taxa.

Strumigenys electrina DE ANDRADE n. sp.

Fig. 24, 25

Holotype: Worker in Dominican amber, preserved in the amber collection of the State Museum of Natural History, Stuttgart (Department of Phylogenetic Research), No. Do-3854-1.

Paratypes: 4 workers included in the same piece of amber and separate for the present study as Nos. Do-3854-2 to Do-3854-5, the latter without head.

Additional material: We refer to this species also the amber specimen Do-3853 examined in the Stuttgart collection but not available for the present study.

Derivatio nominis: From the Latin *electrinus* (= made of amber).

Diagnosis. — A short mandibulate *Strumigenys* close to *ohioensis* and differing from it in several small characters, such as the teeth being subequal in size and the sculpture coarsely reticulate-punctuate on the legs and missing on the postpetiolar node.

Worker (Fig. 24). Measurements (in mm) and indices: total length (mandibles included) holotype 1.88, paratypes 1.84 – 1.88; HL holotype 0.44, paratypes 0.40 – 0.44; HW holotype 0.32, paratypes 0.32 – 0.36; SL holotype and paratypes 0.20; ML holotype and paratypes 0.12; AL holotype and paratypes 0.48; PW holotype and paratypes 0.16; petiole length holotype and paratypes 0.20; petiole maximum width holotype and paratypes 0.08; postpetiole maximum width holotype and paratypes 0.12; gaster maximum width holotype and paratypes

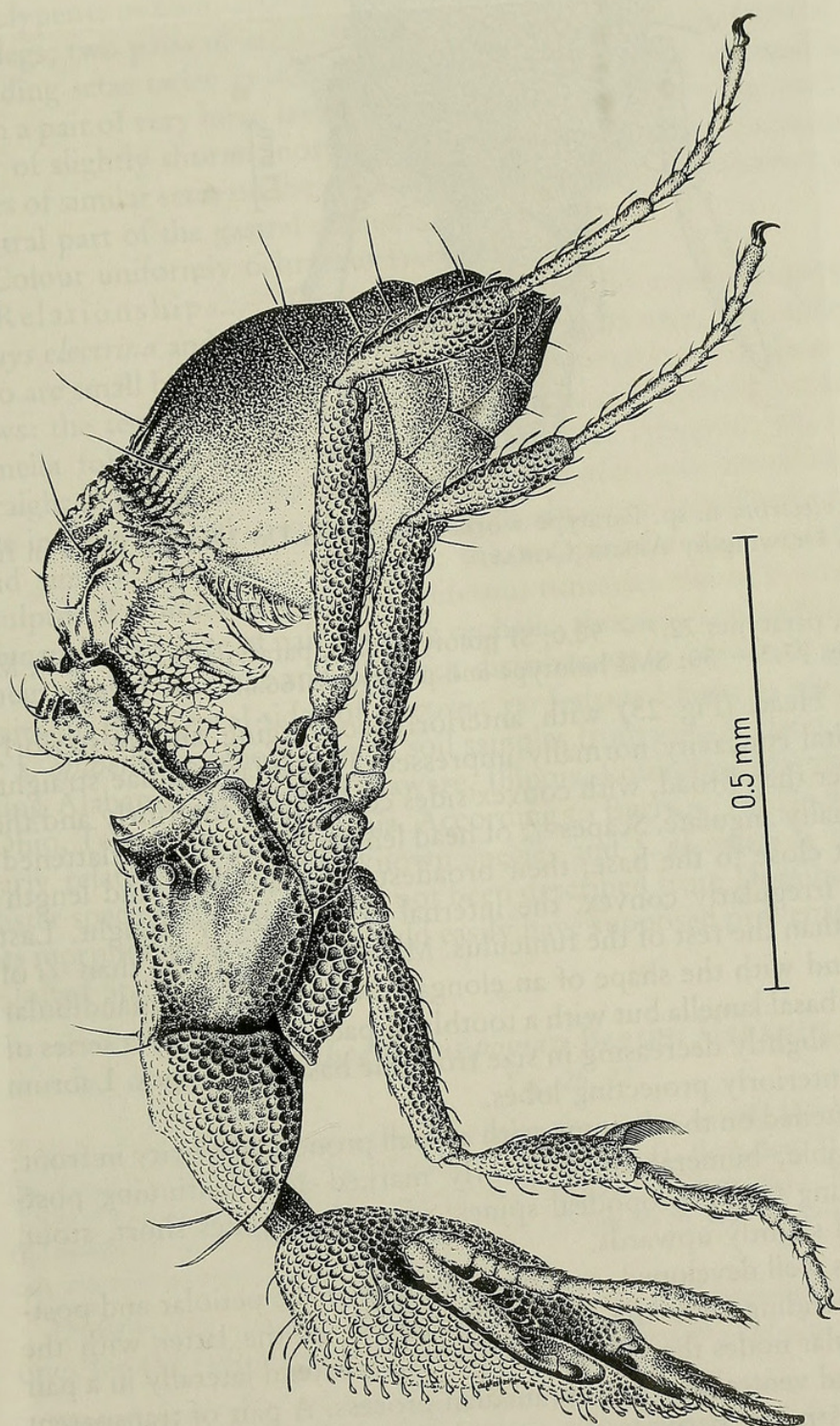


Fig. 24. *Strumigenys electrina* n. sp. Worker, general habitus in lateral view. Reconstruction based on multiple specimens. General shape and most details drawn from the specimen Do-3854-1 (the holotype); Head essentially based on the specimen Do-3854-1, tibia Do-3854-4; Forelegs : coxa, trochanter, femur and tarsus from Do-3854-1, tibia Do-3854-4; Mid leg : coxa, trochanter, femur, tarsomeres 3-5 from Do-3854-4; Hind leg : coxa, trochanter, femur, tarsomeres 1-2 from Do-3854-2 (and, to a lesser extent, Do-3854-1, tibia and tarsomeres 1-2 from Do-3854-1); Pilosity particularly from Do-3854-2 but also from Do-3854-1 & -4. Reconstruction and drawing by ARMIN CORAY.

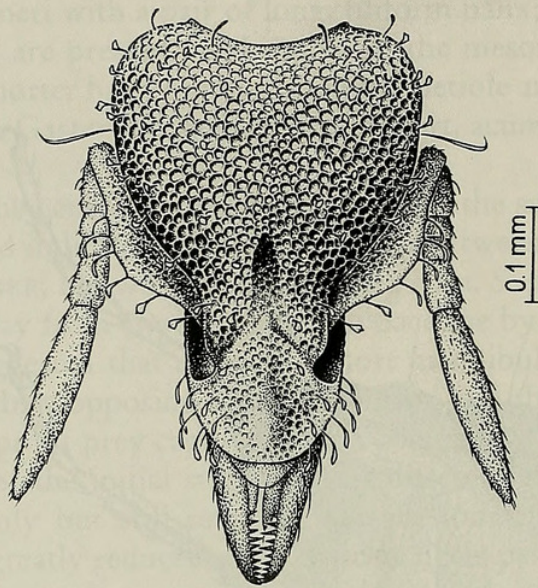


Fig. 25. *Strumigenys electrina* n. sp. Paratype worker (specimen Do-3854-4). Head in full frontal view. Drawing by ARMIN CORAY.

0.28. CI holotype 72.7, paratypes 72.7 – 90.0; SI holotype 62.5, paratypes 55.5 – 62.5; MI holotype 27.3, paratypes 27.3 – 30; SMI holotype and paratypes 166.6.

Description. — Head (Fig. 25) with anteriorly converging and posteriorly rounded sides; occipital concavity normally impressed. Preocular laminae straight. Clypeus slightly longer than broad, with convex sides converging anteriorly and the posterior margin medially angulate. Scapes $\frac{1}{2}$ of head length, short, broad, flattened, but only slightly bent close to the base; their broadest point about at mid length; their external border irregularly convex, the internal border nearly straight. Last funicular joint longer than the rest of the funiculus. Mandibles short, less than $\frac{1}{4}$ of head length, narrow and with the shape of an elongated triangle; inner mandibular border without visible basal lamella but with a toothless space followed by a series of 11 acute denticles only slightly decreasing in size from the base to the apex. Labrum with a visible pair of anteriorly projecting lobes.

Trunk essentially flattened on the dorsum, with a small pronotal declivity in front; propodeal suture invisible; humeral angles poorly marked and continuing posteriorly in an edge leading to the propodeal spines; propodeal spines short, stout, directed backwards and slightly upwards.

Spongiform processes well developed, covering the sides of the petiolar and post-petiolar nodes, and extending over the whole articulation of the latter with the gaster; on both peduncular nodes the spongiform processes extend laterally in a pair of short lateral wings and ventrally in a long, median process. A pair of transparent infraspinal lamellae run straight between the propodeal spines and the ventral posterior border of the trunk.

Gaster oval and not anteriorly truncated in dorsal view.

Sculpture: cephalic dorsum, trunk and legs covered with coarse reticulation, more superficial on the anterior half of the head, trochanters, femora, and tibiae and nearly effaced on the clypeus and on the scapes; mandibles and funiculi punctuate only;

very evident smooth areas on the mesopleurae and on the postpetiolar node; anterior portion of the first gastral tergite strongly costulate.

Pilosity: dorsum of the head with sparse, suberect spatulate hairs slightly longer on the sides of the clypeus; a row of similar, longer, hairs on the anterior border of the clypeus; minute, appressed, simple hairs on the mandibles and the funiculi and the legs; two pairs of erect, slightly spatulate setae on the vertical area and a pair of standing setae twice as long protrude from behind the antennal scrobes; pronotum with a pair of very long, feebly spatulate setae close to its anterior border and another pair of slightly shorter, normally acuminate setae on the promesonotal suture; 1–2 pairs of similar setae on the abdominal segments; pairs of shorter, similar setae on the ventral part of the gastral segments.

Colour uniformly ochraceous feebly shining.

Relationships. — We already mentioned the close similarity between *Strumigenys electrina* and *S. ohioensis* KENNEDY & SCHRAMM. The differences between the two are small but numerous; at least the most important of them can be listed as follows: the teeth of *electrina*, subequal in size and without basal lamella vs. a basal lamella followed by irregular medial teeth in *ohioensis*; the infraspinal lamellae straight in profile in *electrina* and concave in *ohioensis*; the pronotum simply reticulate in *electrina* and irregularly rugose in *ohioensis*; legs deeply reticulate in *electrina* and simply punctate in *ohioensis*; the postpetiolar node smooth in *electrina* and sculptured in *ohioensis*; clypeal piliferous tubercles absent in *electrina* and present in *ohioensis*; presence of pairs of long cephalic, thoracic, and gastral hairs in *electrina* vs. their smaller number and different distribution in *ohioensis*; presence of spatulate hairs on the clypeal sides of *electrina* vs. J-shaped hairs in *ohioensis*.

S. ohioensis is reported from soil samples from several states of the U. S. A. including Alabama, Arkansas, Delaware, Illinois, Louisiana, Maryland, North Carolina, Ohio, Tennessee, and Virginia. According to BROWN (1953) *ohioensis* is not particularly related to any other known species and *S. electrina* is likely to represent its sister species. If *electrina* had not been described from Dominican amber, then from its morphology alone, one could easily have supposed provenance from the southern United States.

Acanthognathus poinari BARONI URBANI n. sp.

Fig. 26, 27

Holotype: Winged gyne (unique) from the amber sample H-10-135 in the collection of Dr. GEORGE O. POINAR, Jr., University of California, Berkeley, U. S. A.

Derivatio nominis: This species is dedicated to GEORGE O. POINAR, Jr., the owner of the holotype who, with his enthusiasm for all aspects of amber study, has been able to revive our interest in amber ants.

Diagnosis. — An *Acanthognathus* species distinguishable from all other known ones for the transverse rugulation on the posterior cephalic angles.

Winged gyne (Fig. 26). Measurements (in mm) and indices: total length (mandibles included) 3.0; HL 0.68; HW 0.48; SL 0.48; eyes maximum length 0.16; ML 0.48; AL 0.64; PW 0.32; petiole length 0.36; petiole maximum width 0.12; postpetiole length 0.20; postpetiole maximum width 0.16; gaster width 0.56. CI 70.6; SI 100; MI 70.6; SMI 100.

Description. — Head (Fig. 27) elongate, with nearly straight sides gradually converging anteriorly, feebly emarginate occipital border and angulate posterior corners. Compound eyes oval, slightly protruding and situated in the middle of the head

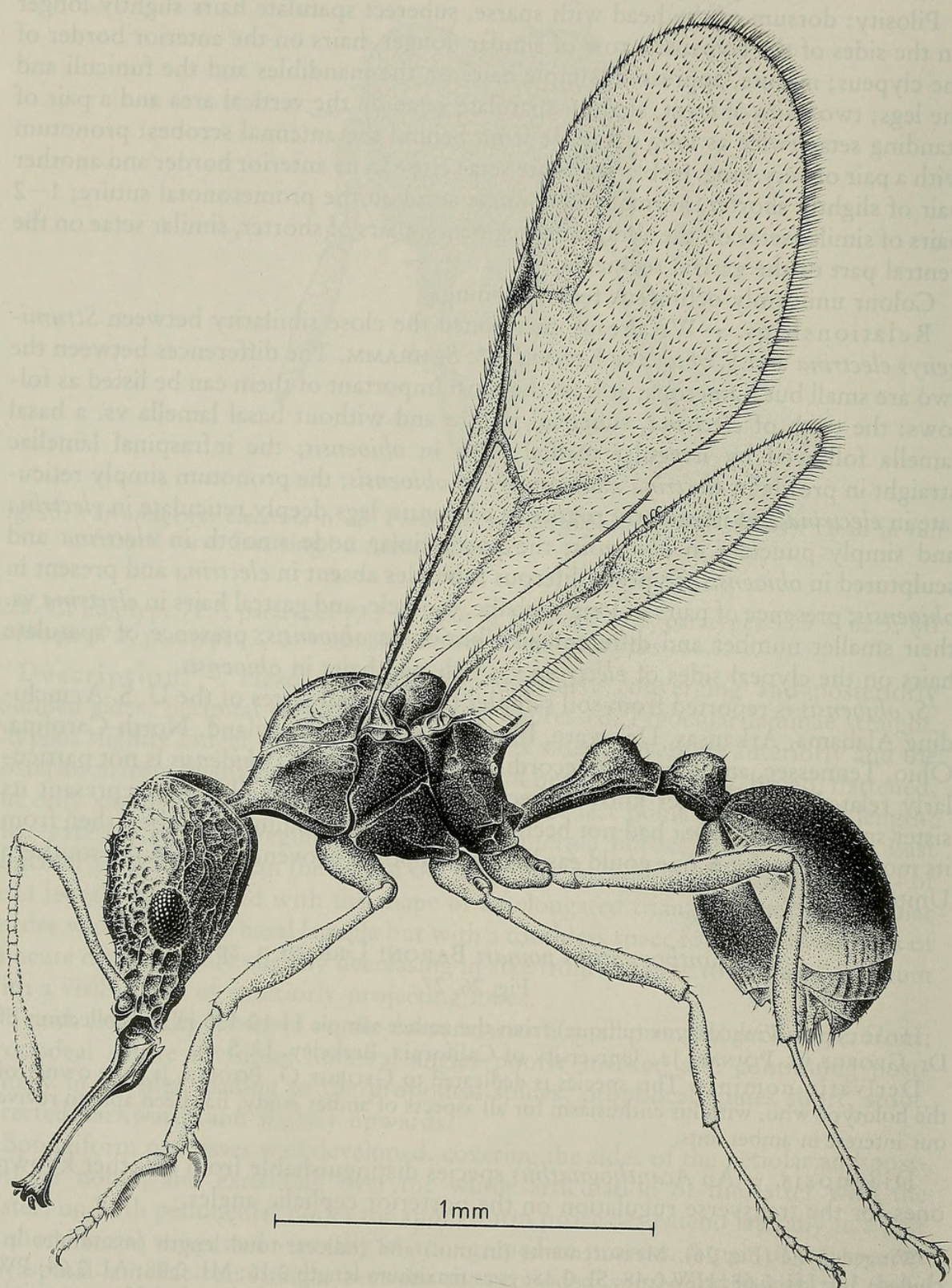


Fig. 26. *Acanthognathus poinari* n. sp. Winged gyne, holotype (specimen H-10-135). General habitus in lateral view. Drawing by ARMIN CORAY.

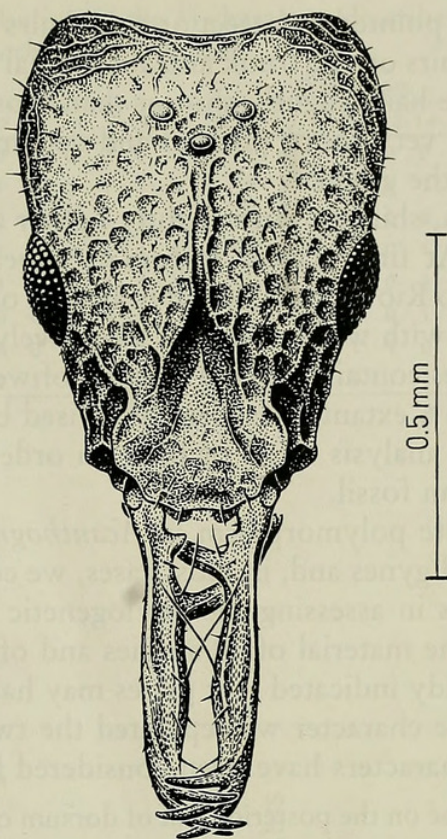


Fig. 27. *Acanthognathus poinari* n. sp. Winged gyne, holotype (specimen H-10-135). Full frontal view of the head with mandibles. Drawing by ARMIN CORAY.

sides. Anterior border of clypeus irregularly rounded and only feebly protruding. Scapes and mandibles shorter than head length. Antennae with clearly two-jointed club.

Trunk short and globose, with a flat dorsal plane constituted by part of the meso- and metanotum; the latter descending abruptly posteriorly in profile. Propodeal spines pointed, relatively short, directed upwards. Propodeal declivity only slightly concave.

Petiole three times longer than broad, with a long anterior peduncle and rounded node in profile. Postpetiole slightly longer than broad with comparably rounded node.

Gaster round in dorsal view.

Wings: fore wings with marked pterostigma and $R+Sc$, traces of $M+CuA$ and $2r$. Other veins partially or completely indistinguishable. Hind wings only with a long portion of $M+CuA$ clearly visible.

Sculpture: dense, deep polygonal fossae diminishing in density and deep from the genae towards the vertex; the vertex proper with transverse striae continuing longitudinally over the posterior half of the sides of the head and on its ventral face. Trunk very slightly longitudinally striate and with effaced fossae. Petiole and postpetiole covered by feeble, longitudinal striae, partly effaced on the petiolar node and completely so on the postpetiolar one. Posterior borders of the first and second gastral segments with longitudinal costulations. Rest of the body smooth or slightly punctate only.

Pilosity: sparse, short, pointed, suberect or erect hairs on the dorsum of the head. Similar, slightly longer hairs on the trunk and abdominal peduncle. Scape, mandibles and legs with rare, sparse hairs slightly shorter than those on the head, pointed and semi-decumbent. Dense, very short, pointed and decumbent hairs on the funicular joints, much sparser on the gaster.

Colour reddish-brown, shining, with slightly lighter antennae and legs.

Relationships. — At first glance, *A. poinari* appears most closely related to *A. brevicornis* (Panama to Rio Grande do Sul in Brazil) or *teledectus* (Costa Rica and Colombia), two species with which it shares a relatively smooth integument. Since the genus *Acanthognathus* contains a small number of well-defined species (7, including *A. poinari*, with the 6 extant ones already revised by BROWN & KEMPF, 1969) we attempted a cladistic analysis of all of them in order to trace the phylogenetic position of the Dominican fossil.

Given the reduced caste polymorphism in *Acanthognathus*, most characters are invariant for workers and gynes and, in most cases, we could use the same character definition for both castes in assessing the phylogenetic position of *A. poinari*. We have been able to examine material of all species and of all castes described in this genus, and, when our study indicated that gynes may have a variation pattern different from workers in one character we separated the two castes in describing that feature. The following characters have been considered for the analysis:

1. Worker and gyne. Fossae on the posterior half of dorsum of the head small or absent (0), or large (1).
 2. Worker and gyne. Occipital border smooth (0), with fossae (1), striate (2) or reticulate-punctate (3).
 3. Worker and gyne. Cephalic hairs clavate or at least slightly clavate (0), or simply pointed (1).
 4. Worker. SL \leq 67 (0), or \geq 68 (1).
 5. Gyne. SL \leq 67 (0), or \geq 70 (1).
 6. Worker. SI \leq 100 (0), or \geq 106 (1).
 7. Gyne. SI \leq 100 (0), or \geq 109 (1).
 8. Worker. SMI \leq 81 (0), or \geq 100 (1).
 9. Gyne. SMI \leq 100 (0), or \geq 104 (1).
 10. Worker and gyne. MI \leq 98 (0), or \geq 120 (1).
 11. Worker and gyne. Preapical inner mandibular border without teeth (0), or with teeth or denticles (1).
 12. Worker and gyne. With 2 (0), or 3 (1) apical teeth on each mandible.
 13. Worker and gyne. Clypeus shorter than the last funicular joint (0), or longer (1).
 14. Worker and gyne. Thorax with prevailing effaced sculpture (0) or normally sculptured (1).
 15. Worker. Humeral angles with small denticles only (0), or with short, true spines (1).
 16. Worker. Propodeal spines shorter than their distance at the apex (0), or longer (1).
 17. Worker. Propodeal declivity straight (0), or concave (1).
 18. Worker and gyne. Petiolar peduncle less than 2 times as long as its node (0) or about 3 times as long as its node (1).
 19. Worker and gyne. Petiolar dorsum smooth (0), punctate (1), or lightly striate (2).
 20. Worker and gyne. Petiolar node rounded in profile (0), or triangular (1).
- In addition, the following generic apomorphies have been added to the data matrix for the sole purpose of separating *Acanthognathus* from its sister taxon while constructing a phylogram:
21. Worker and gyne. Eyes lateral (0), or dorsal (1).
 22. Worker and gyne. Antennal club present (1), or absent (0).
 23. Worker and gyne. Mandibles with (1), or without (0) basal process.
 24. Worker and gyne. Occipital foramen posterior (0), or dorsal (1).

Tab. 2. Matrix with the distribution of the 24 characters described in text among the known species of *Acanthognathus* and *Daceton*.

Species	Characters																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
<i>Acanthognathus brevicornis</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0
<i>Acanthognathus lentus</i>	1	1	0	1	?	1	?	1	?	0	0	1	0	1	1	0	0	0	0	0	0	1	1	0
† <i>Acanthognathus poinari</i>	0	2	1	?	0	?	0	?	0	0	0	1	0	0	?	?	?	0	2	0	0	1	1	0
<i>Acanthognathus ocellatus</i>	0	1	0	1	1	1	1	1	1	0	0	1	0	1	0	1	0	0	0	0	0	1	1	0
<i>Acanthognathus rudis</i>	0	1	0	1	1	1	1	1	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0
<i>Acanthognathus stipulosus</i>	1	0	0	0	?	1	?	1	?	0	0	1	0	1	1	0	1	1	0	1	0	1	1	0
<i>Acanthognathus teledectus</i>	0	0	0	1	?	1	?	0	?	1	1	1	1	0	1	0	1	0	0	0	0	1	1	0
<i>Daceton armigerum</i>	0	3	1	1	1	0	0	1	1	0	1	0	1	1	1	0	0	0	1	1	1	0	0	1

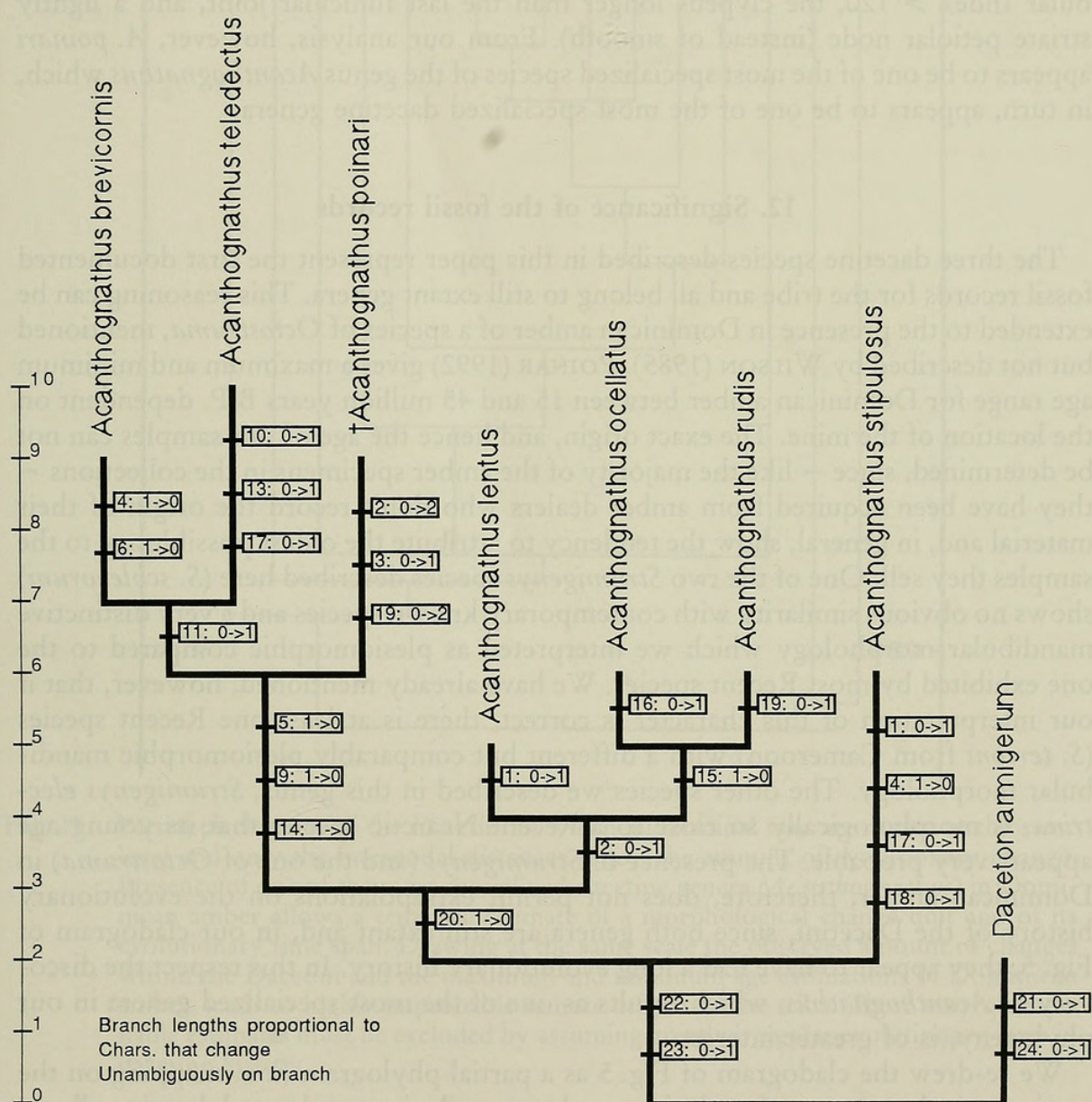


Fig. 28. Unique most parsimonious phylogram showing the probable relationships of the known species of *Acanthognathus* together with their sister taxon, *Daceton armigerum*. The scale on the left shows the number of evolutionary steps accounting for each branch. The frames include the character changes corresponding to each branch with their respective identification number as given in the text and the apomorphic state change.

For the outgroup comparison, in accordance with traditional views on dacetine classification and with the results of our cladistic analysis which both indicate the monotypic genus *Daceton* as the sister genus of *Acanthognathus*, we choose *Daceton armigerum*. All characters have been considered unordered and of equal weight.

The distribution of these characters and of their states among the taxa included in the analysis is given in Table 2.

Only one most parsimonious tree of length 35 with a Consistency Index of 0.772 (0.704 excluding autapomorphies) and Retention Index 0.579 was found.

This result is given graphically in Fig. 28 in form of phylogram. From the graphic it appears that *Acanthognathus poinari* is the sister species of a clade containing *A. brevicornis* and *teledectus*. It differs from both these species in having a Mandibular Index > 120 , the clypeus longer than the last funicular joint, and a lightly striate petiolar node (instead of smooth). From our analysis, however, *A. poinari* appears to be one of the most specialized species of the genus *Acanthognathus* which, in turn, appears to be one of the most specialized dacetine genera.

12. Significance of the fossil records

The three dacetine species described in this paper represent the first documented fossil records for the tribe and all belong to still extant genera. This reasoning can be extended to the presence in Dominican amber of a species of *Octostruma*, mentioned but not described by WILSON (1985). POINAR (1992) gives a maximum and minimum age range for Dominican amber between 15 and 45 million years B.P. dependent on the location of the mine. The exact origin, and hence the age of our samples can not be determined, since – like the majority of the amber specimens in the collections – they have been acquired from amber dealers who don't record the origin of their material and, in general, show the tendency to attribute the oldest possible age to the samples they sell. One of the two *Strumigenys* species described here (*S. schleorum*) shows no obvious similarity with contemporary known species and a very distinctive mandibular morphology which we interpreted as plesiomorphic compared to the one exhibited by most Recent species. We have already mentioned, however, that if our interpretation of this character is correct, there is at least one Recent species (*S. terroini* from Cameroon) with a different but comparably plesiomorphic mandibular morphology. The other species we described in this genus, *Strumigenys electrina*, is morphologically so close to a Recent Nearctic species that its young age appears very probable. The presence of *Strumigenys* (and the one of *Octostruma*) in Dominican amber, therefore, does not permit extrapolations on the evolutionary history of the Dacetini, since both genera are still extant and, in our cladogram of Fig. 5, they appear to have had a long evolutionary history. In this respect the discovery of *Acanthognathus*, which results as one of the most specialized genera in our phylogeny, is of greater interest.

We re-drew the cladogram of Fig. 5 as a partial phylogram (i. e. mapping on the vertical axis the amount of evolutionary change at the internodes and drawing all terminal taxa at the same level). Assuming equal evolutionary speed for all the Dacetini, together with the minimum and maximum estimated ages for the fossil *Acanthognathus*, should allow us to attempt a guess on the origin of the Dacetini and on its evolutionary speed. The results of our undertaking are reported graphically in Fig. 29. From the figure one can see that extrapolating the minimum and maximum

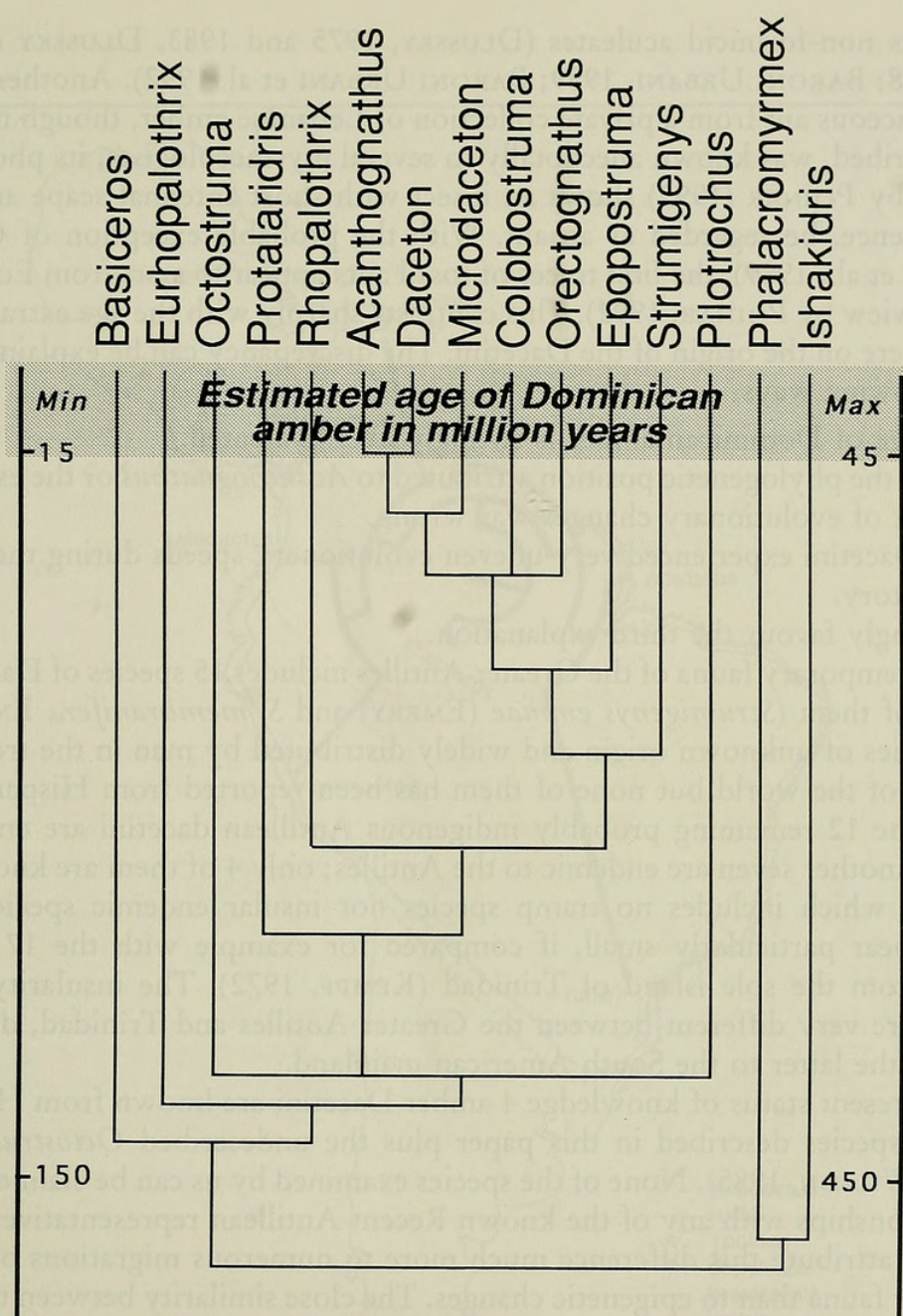


Fig. 29. Partial phylogram of the Dacetini in which all terminal taxa are drawn at the same level and only the internodal distances reflect the amount of evolutionary change. Presence of one of the most specialized dacetine genera (*Acanthognathus*) in Dominican amber allows a tentative estimate of a morphological change unit and of its evolutionary time span. Drawing at the same scale the observed amount of changes within the Dacetini and the maximum and minimum age estimations of Dominican amber, leads to highly improbable remote origins of the tribe. These very questionable estimates must be excluded by assuming greatly irregular evolutionary rates in dacetine history.

age determinations for our *Acanthognathus* (i. e. those of Dominican amber) would give, respectively, a minimum and maximum age determination for the first Dacetini of ca. 200 or 600 million years B. P. Actually only one probably true ant is known from Lower-Cretaceous (ca. 100 million years B. P.) (BRANDÃO et al., 1989), while other presumed Cretaceous Formicidae mentioned in the literature are currently

regarded as non-formicid aculeates (DLUSSKY, 1975 and 1983, DLUSSKY & FEDOSEEVA, 1988; BARONI URBANI, 1989; BARONI URBANI et al. 1992). Another putative early Cretaceous ant from a private collection of Lebanese amber, though never formally described, was known anecdotally to several myrmecologists; its photograph, published by POINAR (1992) shows an insect with short antennal scape and which can not, hence, be regarded as an ant. With the probable exception of *Cariridris* (BRANDÃO et al., 1989), the first traces of fossil ants appear to start from Eocene (see e. g. the review by POINAR, 1992). This contrasts sharply with the age extrapolations we made here on the origin of the Dacetini. The discrepancy can be explained in one of the following ways:

1. The age of Dominican amber is strongly over-evaluated.
2. Either the phylogenetic position attributed to *Acanthognathus* or the estimate of the amount of evolutionary changes was wrong.
3. The Dacetini experienced very uneven evolutionary speeds during their evolutionary history.

We strongly favour the third explanation.

The contemporary fauna of the Greater Antilles includes 15 species of Dacetini. At least two of them (*Strumigenys emmae* (EMERY) and *S. membranifera* EMERY) are tramp species of unknown origin and widely distributed by man in the tropics and subtropics of the world but none of them has been reported from Hispaniola yet. Three of the 12 remaining probably indigenous Antillean dacetini are endemic to Cuba and another seven are endemic to the Antilles; only 4 of them are known from Hispaniola which includes no tramp species nor insular endemic species. These figures appear particularly small, if compared for example with the 17 Dacetini reported from the sole island of Trinidad (KEMPE, 1972). The insularity factors, however, are very different between the Greater Antilles and Trinidad, due to the vicinity of the latter to the South American mainland.

At the present status of knowledge 4 amber Dacetini are known from Hispaniola (the three species described in this paper plus the undescribed *Octostruma* mentioned by WILSON, 1985). None of the species examined by us can be claimed to have close relationships with any of the known Recent Antillean representatives. We are inclined to attribute this difference much more to numerous migrations of the original amber fauna than to epigenetic changes. The close similarity between the amber *Strumigenys electrina* and the Nearctic *S. ohioensis* already discussed in the description of the former is a good example of this. Moreover, the same number of species (four) is known as fossil and as Recent from Hispaniola: it is very probable that the fossil sample is much more incomplete than the Recent one and this implies that the amber fauna must have been much richer than the present one. Reduction in the number of species can be easily explained by insularity and this explanation agrees with the presumed existence of an Early Miocene Caribbean land mass connected with Florida (KHUDDOLEY & MEYERHOFF, 1971). The land connection with Florida accounts very well for the similarity between *Strumigenys electrina* and *S. ohioensis* (actually including Florida in its distribution area). We have already said that we are unable to guess precise relationships between *S. schleorum* and any other known species. *Acanthognathus poinari* shows much clearer Neotropical affinities (Fig. 30) but these may be easily explained by the Lesser Antilles functioning as "stepping stones" connecting the Miocene amber fauna to the mainland and thus making the assumption of additional land bridges or of longer migratory routes redundant.

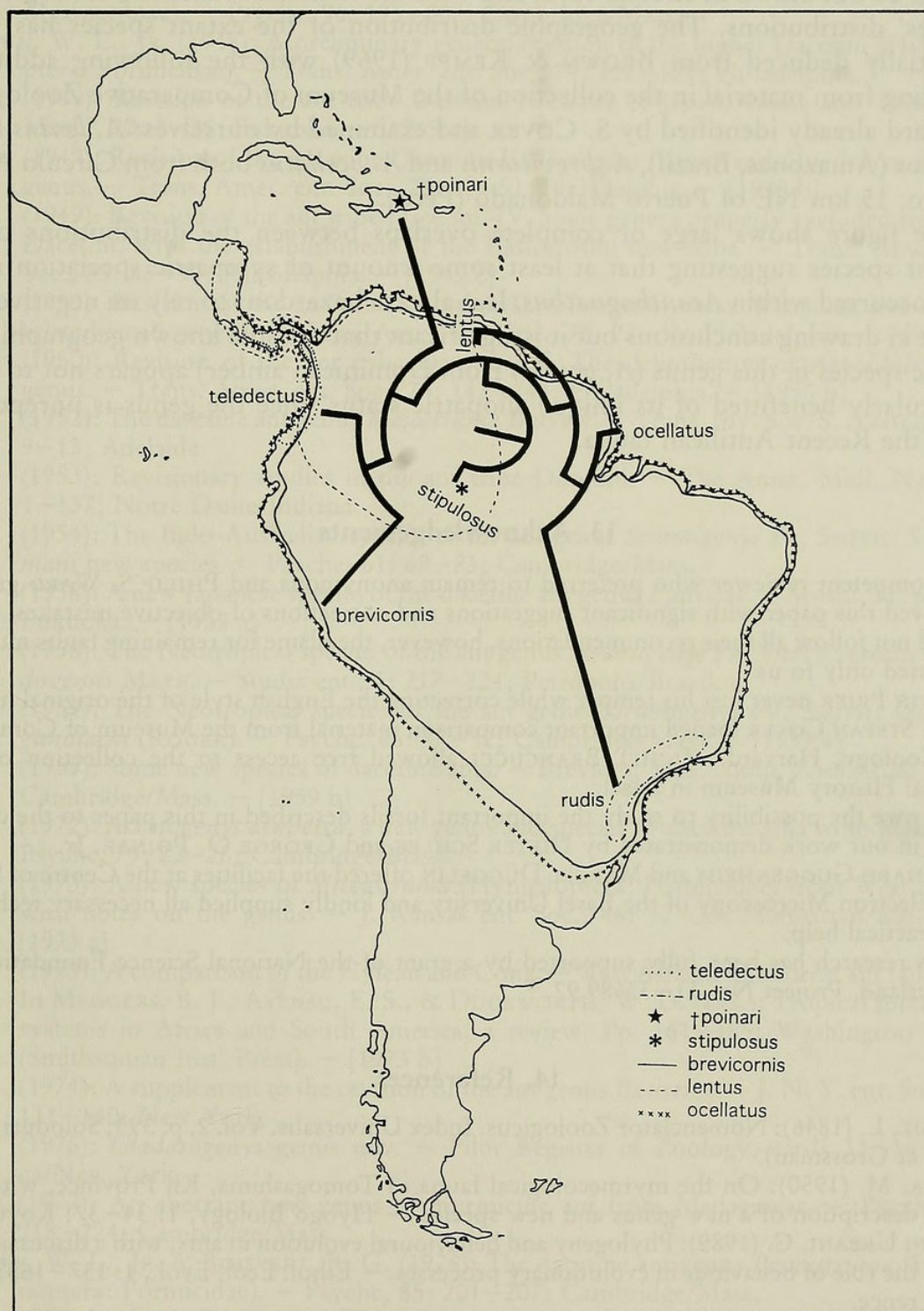


Fig. 30. Circular cladogram expressing the most parsimonious relationships among the species of the genus *Acanthognathus* superimposed on a map of the Neotropical Realm where the distribution of each species is indicated by the corresponding terminal branch. Both the actual species distributions and their probable phylogenetic relationships suggest the occurrence of parapatric or sympatric speciation as opposed to probable extinction of the sole known allopatric species, the Dominican fossil *A. poinari*. Further explanations in the text.

Fig. 30 is the same most parsimonious phylogeny of the *Acanthognathus* species as in Fig. 28 but drawn in circular form and with the terminal branches pointing to the species' distributions. The geographic distribution of the extant species has been essentially deduced from BROWN & KEMPF (1969) with the following additions resulting from material in the collection of the Museum of Comparative Zoology at Harvard already identified by S. COVER and examined by ourselves: *A. lentus* from Manaos (Amazonas, Brazil), *A. brevicornis* and *A. ocellatus* both from Círculo Amazónico, 15 km NE of Puerto Maldonado (Peru).

The figure shows large or complete overlaps between the distributions of all Recent species suggesting that at least some amount of sympatric speciation must have occurred within *Acanthognathus*. It is always hazardous to rely on negative evidence in drawing conclusions but it is significant that the sole known geographically isolate species in this genus (*A. poinari* from Dominican amber) appears not to have particularly benefitted of its unique allopatric status since the genus is unreported from the Recent Antillean fauna.

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Appendix 1

Descriptions of new Recent taxa
significant for the generic analysis presented in this paper

Rhopalothrix inopinata DE ANDRADE n. sp.

Fig. 31, 32

Holotype: worker (unique with postpetiole and gaster detached but glued on the same triangular support), Central Ceylon, Kandy, 600 m, Mussard Besuchet Löbl leg., deposited in the Musée d' Histoire Naturelle, Geneva.

Derivatio nominis: From the Latin *inopinatus* (= unexpected).

Diagnosis. – A small *Rhopalothrix* species characterised by the following combination of characters: body virtually hairless except on the appendages, six antennal joints, mandibles with an apical fork composed of one apical tooth and a row of seven denticles distally increasing in size.

Measurements (in mm) and indices: TL 1.86; HL 0.48; HW 0.48; ML 0.20; SL 0.20; AL 0.50; petiole maximum length 0.24; petiolar node maximum width 0.16; postpetiole maximum length 0.16; postpetiole maximum width, 0.28. CI 100; MI 35.7; SI 41.7.

Description. – Head as broad as long, with feebly excised posterior border and sides projecting posteriorly to the antennal scrobes. Clypeus triangular, reaching the genae laterally and with nearly straight anterior border. Median sulcus evident. Eyes absent. Mandibles with straight external borders; masticatory border armed with four distal, medium-size denticles followed by an apical acuminate tooth and a set of denticles forming an apical fork as described in the diagnosis. Labrum broad posteriorly, anteriorly bilobed and projecting as to fill the intramandibular gap. Scapes as long as the mandibles, strongly bent at the base. Funiculi 5-segmented, resulting so from the fusion of antennal joints V + VI, as indicated by a set of equally long hairs in a row, like those present on the distal border of each joint and still recognizable at

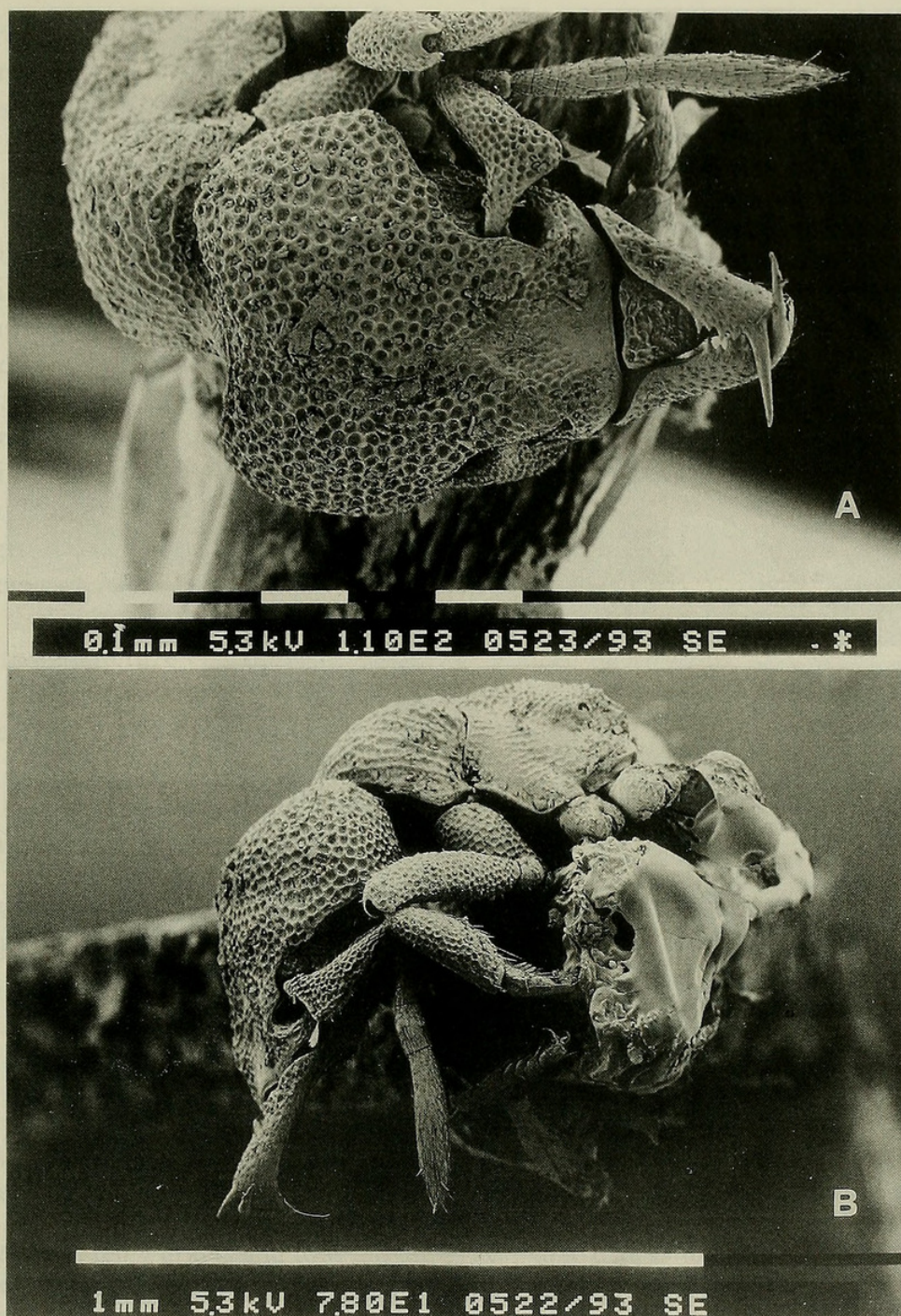


Fig. 31. *Rhopalothrix inopinata* n. sp. from Sri Lanka. Holotype worker. — A. Head in dorsal view. — B. Side view.

mid-length of actual joint V. Last funicular joint longer than the sum of the remaining ones.

Trunk slightly longer than the cephalic capsule. Pronotum and propodeum convex in side view; promesonotal suture highly visible, mesonotal dorsum lower than the propodeal dorsum and propodeal suture barely visible on the sides. Propodeum with superior face slightly marginate on each side by a carina followed by a denticle; its descending face concave and equally marginate on each side by a low lamelliform carina.

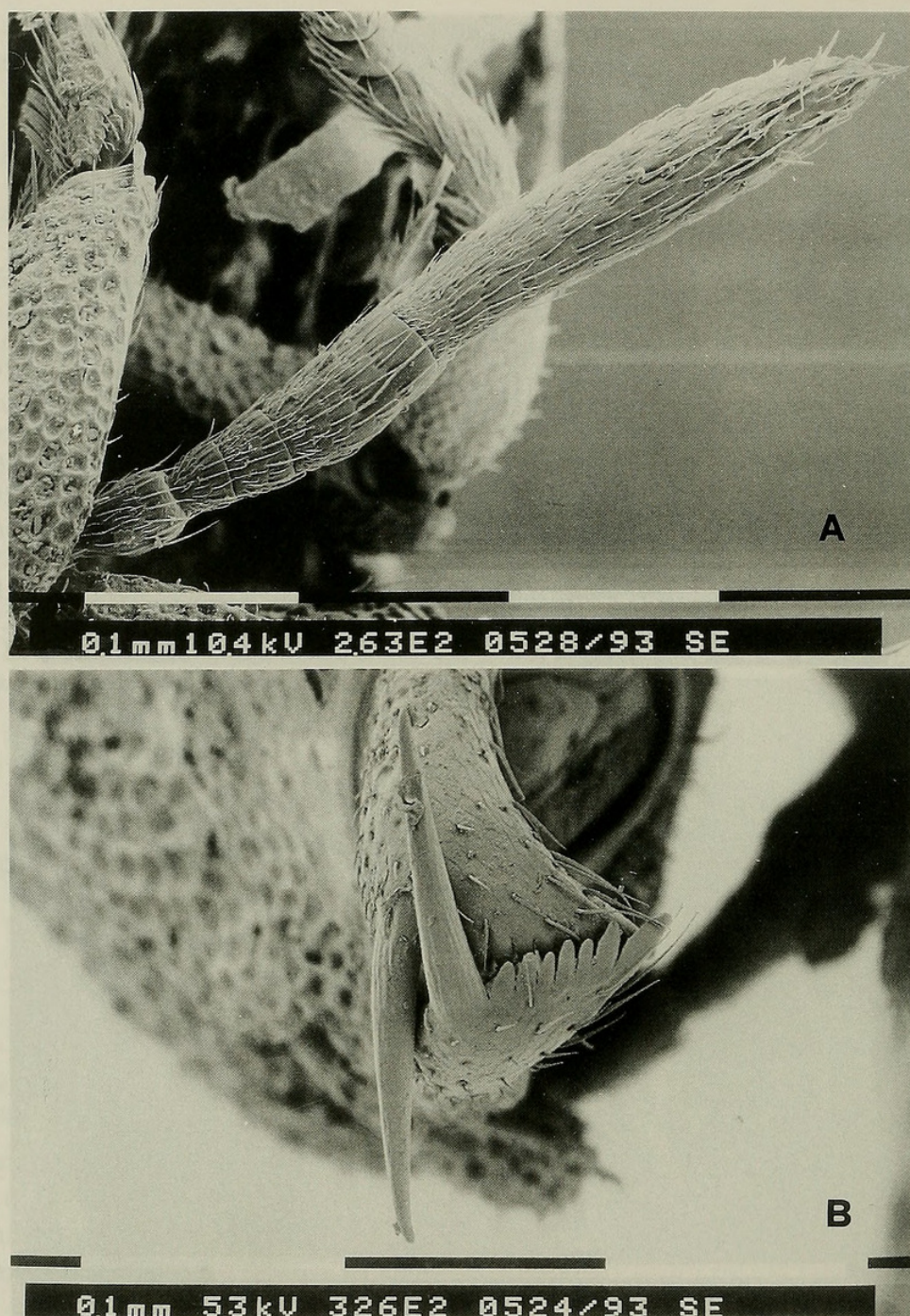


Fig. 32. *Rhopalothrix inopinata* n. sp. from Sri Lanka. Holotype worker. — A. Detail of the 5-jointed funiculus. — B. Apical fork in frontal view (notice the similarity in structure with *Strumigenys hexamera* in Fig. 4).

Peduncle of the petiole short and dorsolaterally marginate by a carina; petiolar node as broad as the length of the postpetiole. Postpetiole posteriorly as broad as the anterior face of the gaster and articulated to it over its whole width. Spongiform processes on posteriolateral sides of the petiole, posterior dorsum of postpetiole and anterior face of the gaster poorly developed. Ventrolateral sides of the postpetiole with well developed spongiform processes.

Gaster oval in dorsal view and with protruding sting.

Sculpture: dorsum of the head covered with deep foveae, less deep on the posterior half of the clypeus and completely missing on its central and anterior parts. A similar

structure, more superficial and organized in longitudinal ridges on the dorsum of the trunk and on the sides of the pronotum; mesopleurae and propodeal sides only very lightly sculptured. Scapes and legs with foveae smaller and thicker than those on dorsum; basal portion of the mandibles with the foveae irregular and spaced; distal part of the mandibles and funiculus simply punctate. Petiole and gaster shining and slightly punctate. Anterior third of the first gastral tergite costulate.

Colour: light brown.

Pilosity: dorsum of the head and trunk with extremely rare and minute (< 0.01 mm long), at least partly clavate hairs arising from the centre of a few foveae. Mandibles, dorsal surface of scapes, funiculus, tibiae and tarsi with pointed decumbent hairs ca. 0.02 mm long. One single plumate hair over the anterior edge of the angular part of the scape. Similar, longer and appressed hairs on the last two funicular joints, on the internal border of the tibiae and around the apical fork of the mandibles.

Relationships. — We already mentioned this species in the previous discussion on the genera of Dacetini for some unusual and significant characters, like the 6-jointed antennae (Fig. 32 A), the lack of eyes, the body nearly hairless, and the apical fork of the mandibles. Comparison between Fig. 32 B and Fig. 4 should show how similar this structure can be in *Strumigenys* and *Rhopalothrix*.

Most previously known *Rhopalothrix* species are Neotropical except two species described from the Old World (*R. diadema* BROWN & KEMPE, endemic to New Guinea and *R. orbis* TAYLOR from Queensland). *R. inopinata* differs from all these species for the combination of characters just mentioned and for many more details. If a similarity with another species has to be established, for the triangular labrum and the angular scape we would suggest its geographically "closest" species: *R. diadema*. *R. inopinata*, nonetheless, can not be confounded with any other known species and represents a new extension of some 6,000 km of the previously known distribution of the genus.

Strumigenys nepalensis DE ANDRADE n. sp.

Fig. 33, 34

Holotype: worker, 6 km NW of Narainghat, 250 m, Nepal. Natural History Museum Basel Nepal Expedition, 1976, in the collection of the Natural History Museum, Basel, Switzerland.

Paratypes: ten workers and four dealate gynes, same data as the holotype; three workers from 5 km E of Manhari, 350 m, Nepal. Natural History Museum Basel Nepal Expedition, 1976; one worker from Darugiri, 450 m, Garo Hills, (Meghalaya, India), Natural History Museum Basel Meghalaya Expedition, 1976. Most paratypes in the Natural History Museum, Basel; some paratypes deposited in the Natural History Museum, London.

Derivatio nominis: *nepalensis* is a Latin neologism indicating the provenance from Nepal.

Diagnosis. — A *Strumigenys* tentatively assigned to the *transversa* species group from which it differs for the four-jointed antennae and presence of 5 pairs of long dorsal hairs on the trunk.

Worker. Measurements (in mm) and indices: TL, holotype 1.49, paratypes 1.44–1.49; HL holotype 0.39, paratypes 0.39–0.40; HW holotype 0.29, paratypes 0.29–0.30; eye maximum diameter holotype and paratypes 0.03; SL holotype 0.18, paratypes 0.17–0.19; ML holotype 0.09, paratypes 0.08–0.09; AL holotype 0.41, paratypes 0.39–0.42; PW holotype 0.19, paratypes 0.19–0.20; petiolar node maximum length holotype 0.10, paratypes 0.09–0.10; maximum width of the petiole holotype and paratypes 0.10; postpetiolar node maximum

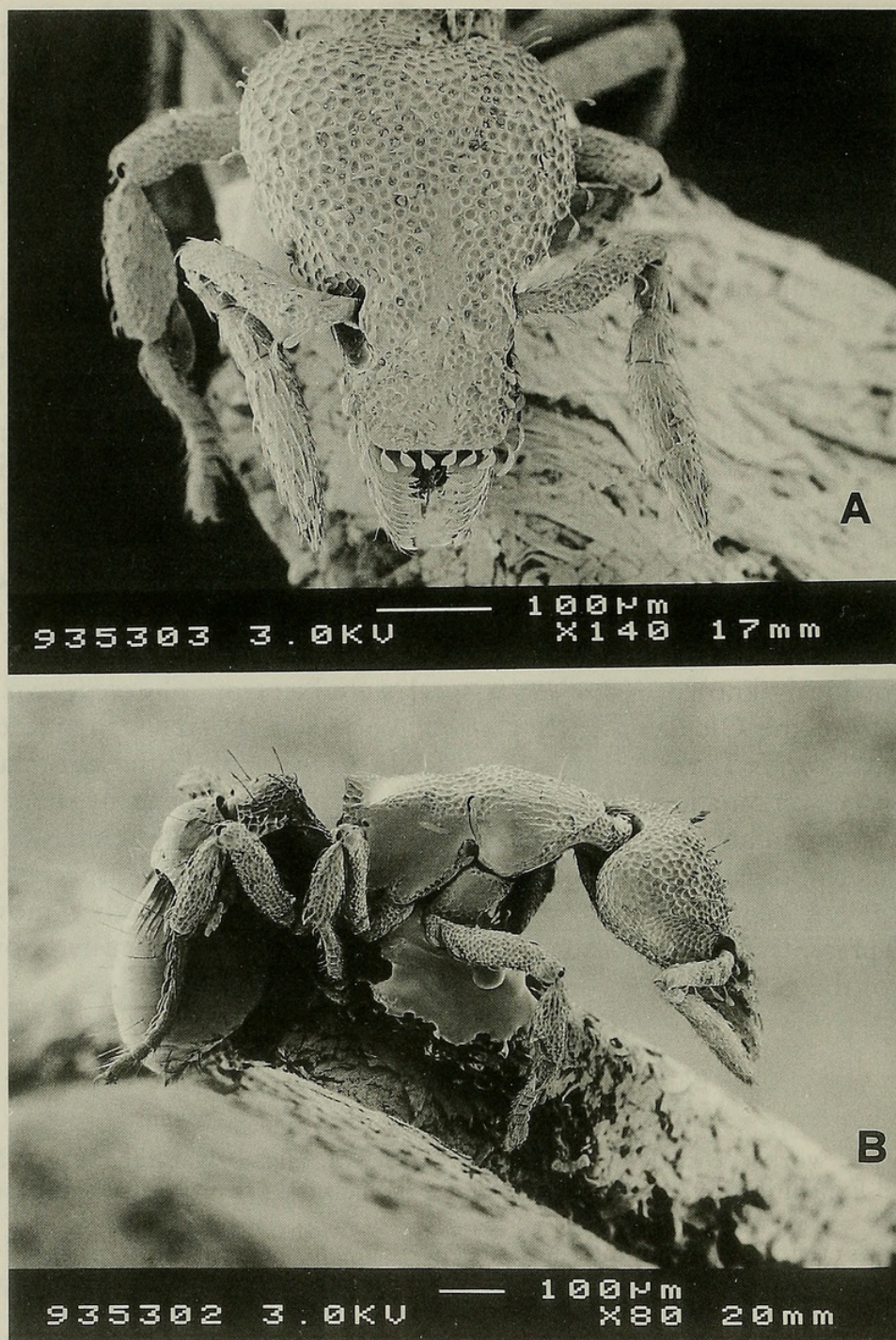


Fig. 33. *Strumigenys nepalensis* n. sp. from Nepal and NE India. Paratype worker. — A. Head in dorsal view. — B. Side view.

length holotype 0.13, paratypes 0.12–0.13; maximum width of the postpetiole holotype 0.17, paratypes 0.17–0.18; gaster maximum width holotype 0.27, paratypes 0.25–0.28. CI holotype 74, paratypes 74–77; SI holotype 62, paratypes 57–62; MI holotype 23, paratypes 20–23; SMI holotype 200, paratypes 200–237.

Description. — Head strongly converging anteriorly and with rounded occipital corners. Dorsal border of the antennal scrobes laminar. Eyes small, ventral to the antennal scrobes. Preocular lamina narrow and straight. Clypeus as broad as long. Anterior clypeal margin transverse, its median portion with a small promi-



Fig. 34. *Strumigenys nepalensis* n. sp. from Nepal and NE India. Paratype gyne. — A. Head in dorsal view. — B. Side view.

nence. Scapes slightly less than $\frac{1}{2}$ of the head length, moderately broadened, flat and sharply bent at the base. Antennae with four antennomeres, the last joint longer than the rest of the funiculus. Labrum elongate, broad and rounded, longer than half of the masticatory margin. Mandibles short, less than $\frac{1}{4}$ of the head length, slightly narrow and triangular; base of the masticatory border with a short diastema (partly covered by the clypeus when the mandibles are closed) and a stout and blunt tooth. True masticatory margin with a row of 5 teeth of which the third is the longest one, followed by two smaller teeth and a denticulate space before the pointed apex.

Trunk: dorsum with a faint median longitudinal carina bifurcating posteriorly on the anterior part of the propodeum. Promesonotal suture visible in dorsal view. Mesonotum in side view slightly convex. Lateral sides of mesonotum and propodeal dorsum marginate. Propodeum in profile angled at about 100° . Propodeal teeth triangular, acute and with broad infradental lamella.

Spongiform processes well developed on the pedicel, more projecting ventrally than laterally; the lateral projections connected each other by a thin dorsal lamina on the posterior articulation of the nodes. Ventral side of the petiole with a broad spongiform lamina narrower under the node. Petiolar lateral spongiform processes widening caudally. Posterolateral processes of the postpetiole reaching the gaster caudally.

Petiolar node slightly truncate anteriorly, ca. $\frac{1}{3}$ shorter than the postpetiole. Postpetiole more than half wider than the petiole.

Gaster oval with protruding sting.

Sculpture: clypeus, cephalic dorsum, dorsum of the alitrunk and petiole reticulopunctate. Scapes and legs simply punctate. Mandibles and dorsum of the postpetiole finely punctate and shining. Pleurae smooth and shining except some punctures on the anterior portion of the propleurae and on the dorsal border of the pleurae. Propodeal declivity smooth. Base of the first gastral tergite costulated, the remaining portion of the gaster smooth and shining.

Colour: generally brownish, slightly lighter on the trunk and appendages.

Pilosity: cephalic dorsum with short, subdecumbent, clavate hairs directed anteriorly. The same type of hairs but shorter on most of the clypeus. Rare, suberect, slightly clavate hairs twice as long than the preceding ones on posterior part of the vertex. Lateral sides of the head, external border of the scape, lateral and anterior sides of the clypeus with decumbent spatulate hairs, slightly longer than those on the dorsum of the head. Mandibles and funiculi with short, appressed, pointed hairs. Dorsum of alitrunk with 5 pairs of long, erect setae; two similar pairs on the petiole, and another two on the postpetiole; similar setae irregularly sparse over the gaster. Rare, appressed clavate hairs on the dorsum of the alitrunk and petiole. Legs covered with ticker, appressed, pointed hairs.

Gyne (Fig. 34). Measurements (in mm) and indices: TL 1.71–1.74; HL 0.42; HW 0.32; eye maximum diameter 0.06; SL 0.18–0.19; ML 0.09; AL 0.47; PW 0.23–0.24; petiolar node maximum length 0.07–0.10; petiolar node maximum width 0.12; postpetiolar node maximum length 0.13–0.15; postpetiolar node maximum width 0.18–0.20; gaster maximum width 0.35–0.39. CI 76; SI 56–59; MI 21; SMI 200–211.

Except for the usual differences due to caste determination, very similar to the worker from which it differs essentially in the following characters:

Trunk: with the propodeal suture impressed. Posterior portion of mesonotal disc and scutellum flat.

Petiole truncate anteriorly and slightly concave, its node almost two times broader than long.

Pilosity: dorsum of alitrunk with 7–8 pairs of long, erect setae similar to those of the worker.

Relationships. — We assigned this species to the *transversa* species group of BOLTON (1983) which included, until now, only *S. transversa* SANTSCHI from S. Africa. The two species share the broadly lobed basal lamella on the mandibles and the large infradental lamella on the propodeum. They are otherwise very dissimilar

and we suppose that this superficial affinity could be explained by the scanty information available on Asian *Strumigenys* as compared with the African ones. We mentioned this species in the generic discussion for its 4-jointed antennae: this character alone will easily separate *nepalensis* from *transversa* and from any other known potentially related Asian species.

Strumigenys assamensis DE ANDRADE n. sp

Fig. 35, 36

Holotype: worker, Cherrapunjee, 1200 m (Meghalaya, India). Natural History Museum Basel Nepal Expedition, 1976. Deposited in the collection of the Natural History Museum, Basel, Switzerland.

Paratypes: 10 workers, same data as the holotype, deposited in the Natural History Museum, Basel, Switzerland, and in the Natural History Museum, London.

Derivatio nominis: *assamensis* is a Latin neologism to indicate the provenance of this species from the Indian state of Meghalaya, formerly considered part of Assam.

Diagnosis. — A *Strumigenys* species superficially close to the *tetragnatha* group (BOLTON 1983), but differing from both species included in it for the mandibles with 13 teeth and denticles (see description), the clypeus with a median dorsal carina, the anterior clypeal border convex, and a virtually hairless body.

Worker. Measurements (in mm) and indices: TL holotype 2.78, paratypes 2.75–2.77; HL holotype 0.65, paratypes 0.64–0.65; HW holotype 0.51, paratypes 0.50–0.51; SL holotype 0.30, paratypes 0.29–0.30; ML holotype and paratypes 0.12; AL holotype 0.76, paratypes 0.72–0.75; PW holotype 0.27, paratypes 0.26–0.27; petiolar node maximum length holotype 0.26, paratypes 0.25–0.26; petiolar node maximum width holotype 0.14, paratypes 0.14–0.15; postpetiole maximum length holotype 0.17, paratypes 0.16–0.18; postpetiole maximum width, holotype 0.20, paratypes 0.19–0.22; gaster maximum width, holotype 0.47, paratypes 0.45–0.47. CI, holotype 78.5, paratypes 78–79.7; SI holotype 59, paratypes 57–59; MI holotype 18.5, paratypes 18.5–18.7; SMI holotype 250, paratypes 241–250.

Description. — Head with the dorsum posteriomedially raised into a broad tumulus. Occipital lobes small and flattened. Eyes small and ventral to the scrobes. Clypeus in dorsal view with a median carina, its latero-posterior sides connected with a narrow preocular lamina. Sides of the clypeus convex and converging anteriorly. Anterior clypeal margin convex. Preocular lamina narrow. Scape slightly less than half the head length, narrow and with marginate external border. Antennae six-jointed. Labrum bilobed, triangular and hidden by the mandibles at rest. Mandibles with a triangular basal tooth followed by three acuminate, long teeth and four denticles alternating in size; five smaller denticles on the apical part.

Trunk: anterior border of the pronotum slightly marginate, its sides strongly marginate and rounded. Pronotum flat and with a feebly median longitudinal carina. Promesonotal suture well visible laterally and terminally impressed towards the dorsum. Sides of mesonotum and propodeum dorsally marginate but without transversal crest or carina. Mesopleural presumed glandular area well developed and bearing a brush of long setae (Fig. 36 B). Propodeal suture feebly impressed only on the lower pleural area. Propodeal teeth short and stout with a broad infradental lamella originating from their apex.

Spongiform process on the ventral side of the petiole well developed longitudinally and as high as the petiolar node. Sides of the petiole with a broad lamella directed ventrally. Posterior border of the petiole with a thin transversal lamella. Ventral spongiform process of the postpetiole broad and rounded. Postpetiole with a

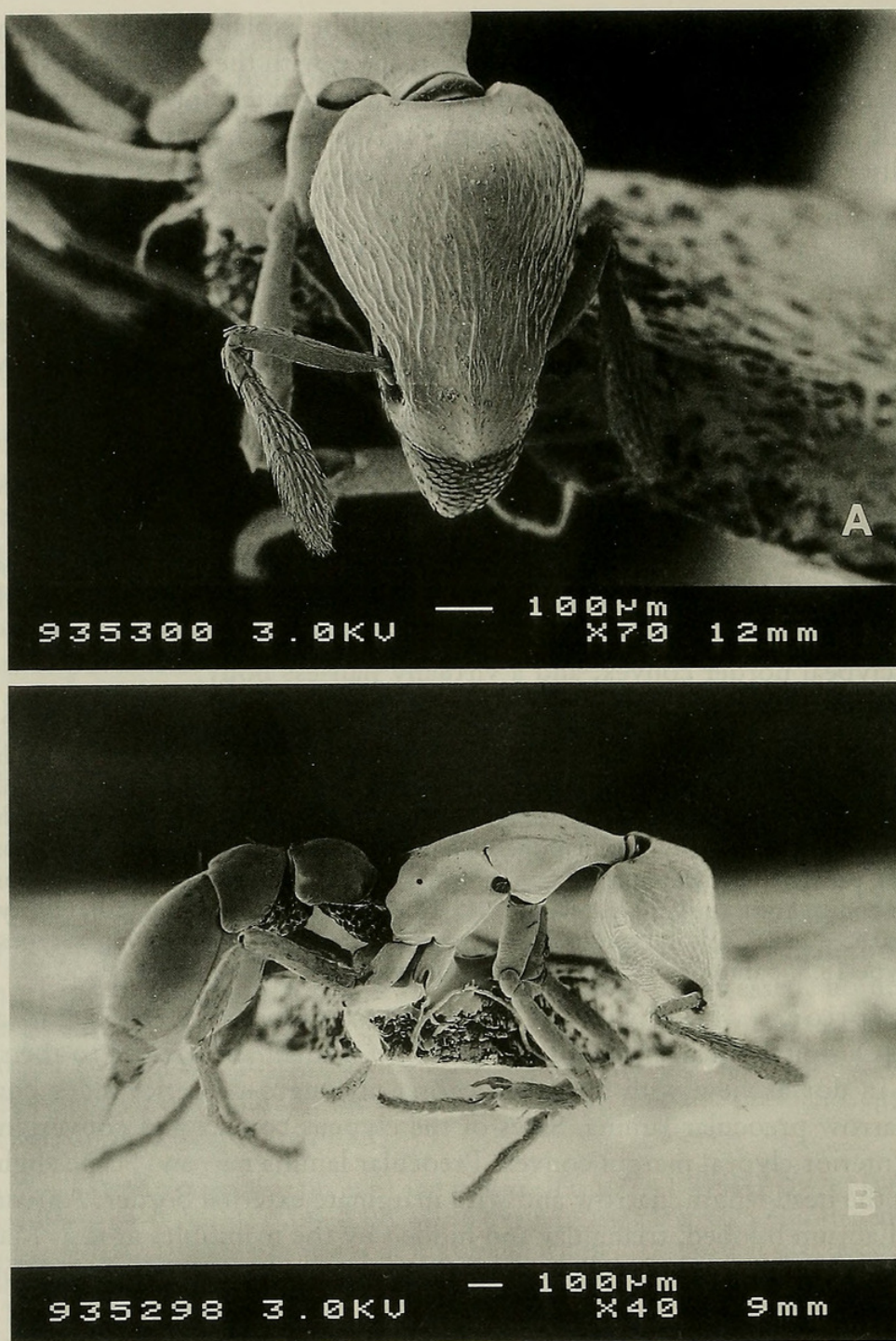


Fig. 35. *Strumigenys assamensis* n. sp. from Assam. Paratype worker. — A. Head in dorsal view. — B. Side view.

well developed lamella embracing its lateral and posterior sides. Petiolar node rounded, $\frac{2}{3}$ longer than the postpetiole. Postpetiole $\frac{1}{4}$ broader than the petiolar node, slightly convex and hexagonal in dorsal view.

Gaster oval, slightly broader than the postpetiole. Sting protruding. Anterior border of the gaster with a broad, transverse lamella in part covered by the postpetiolar lamella.

Sculpture: head irregularly striate and punctate on the lateral and anterior parts and on the posterior border of the clypeus. Cephalic tumulus only slightly reticulo-

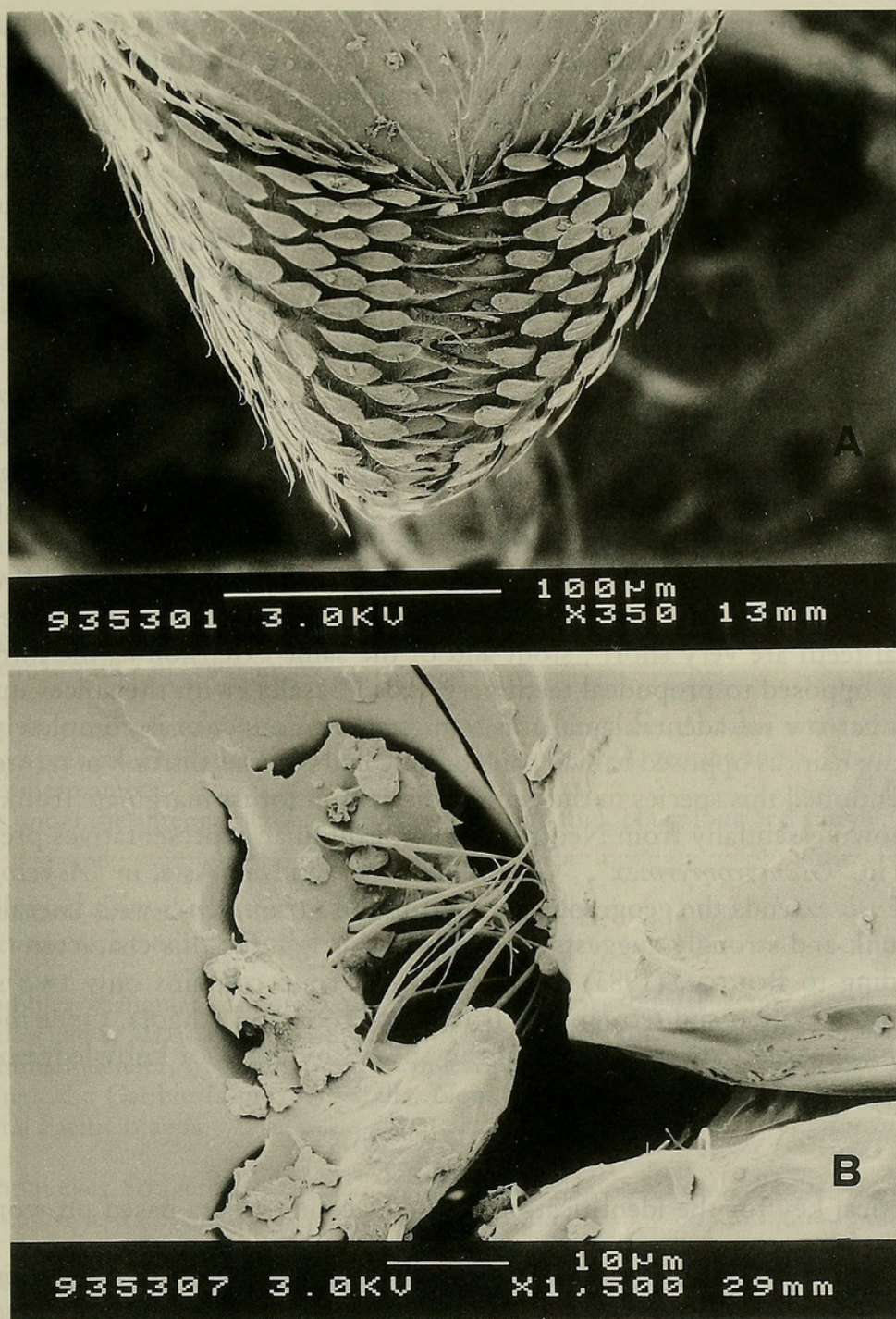


Fig. 36. *Strumigenys assamensis* n. sp. from Assam. Paratype worker. – A. Mandibles in dorsal view showing the dentition and spatulate hairs. – B. Detail of the mesopleural presumed glandular area with the long setae.

punctate. Clypeus, antennae, mandibles and legs punctate. Alitrunk and abdomen shining and feebly punctate.

Pilosity: dorsum of the head, clypeus, antennae and legs with sparse appressed short hairs, longer over the antennae, the sides of the mandibles, and legs, and denser over the funiculi and mandibular sides. Dorsum of the mandibles covered by thick, spatulate hairs (Fig. 36 A). Thorax and abdomen with rare, appressed hairs as long as those on the dorsum of the head. Dorsum of the postpetiole with a pair of subdecumbent hairs as long as those on the antennae. Erect, thick, truncate, slightly longer

hairs over the dorsum of the gaster arranged as follows: a row of four on the anterior border of the first segment and on the posterior border of the third segment, two on the posterior border of the second segment, and four on the fourth gastral segment.

Colour: body reddish-brown, shining, lighter on the clypeus, the antennae and the legs. A dark brown rim marks the posterior border of the clypeus, the antennal scrobes, the ventral border of the mesopleura, the dorsal margin of the alitrunk and propodeal declivity, and the dorsal border of the pedicel. Postpetiole with a thick dark, lateral expansion appearing as a spine embedded in the lamelliform process. A similar but much less evident spiniform colour pattern on the posterior border of the petiole and on the anterior border of the postpetiole.

Relationships. — *S. assamensis* resembles the African *S. tetragnatha* (TAYLOR). As was to be expected from their geographic distance, the differences between these two species are numerous and some major ones can be listed as follows: mandibles with 13 teeth in *assamensis* as opposed to 8 teeth in *tetragnatha*; clypeus anteriorly convex and dorsally carinate in *assamensis* as opposed to anteriorly indented and without carina in *tetragnatha*; in *assamensis* the occipital lobes less broad and rounded as opposed to *tetragnatha* with broad and rounded occipital lobes; in *assamensis* the propodeal teeth are very short, stout and of the same extension as the infradental lamella as opposed to propodeal teeth very broad basally, with the apices upcurved and with narrow infradental lamella in *tetragnatha*; *assamensis* is completely destitute of long hairs as opposed to two pairs of long hairs on the alitrunk in *tetragnatha*.

We mentioned this species in the generic discussion for its marginate trunk, a character known essentially from Neotropical and Ethiopian representatives previously included in "*Glomyrmex*", "*Gymnomyrmex*", and, in Asia, in "*Asketogenys*". *S. assamensis* extends the geographical repertoire of *Strumigenys* with laterally marginate trunk and strongly suggests a homoplastic origin for this character.

According to BOLTON (1983) the *tetragnatha*-group contains only two species: *africana* from Gabon and *tetragnatha* from Cameroon and Angola. Once more, we explain the apparent African affinity of this species by the poor knowledge of Asian *Strumigenys*.

Appendix 2

A practical key for the identification of the Dacetini genera based on workers

1. Antennae 12-jointed. Neotropical *Basiceros*
- Antennae with 11 or fewer joints 2
2. Antennae with 11 joints 3
- Antennae with 9 or fewer joints 5
3. Head with antennal scrobes. Eyes ventral, below the scrobe. Head with parallel sides. Masticatory border of the mandibles with an alternation of longer and shorter small teeth. Neotropical *Phalacromyrmex*
- Head without antennal scrobes. Eyes lateral or dorsal 4
4. Eyes large and dorsal. Occipital foramen dorsal. Workers polymorphic. Antennal club not differentiated. Neotropical *Daceton*
- Eyes lateral. Occipital foramen posterior. Workers monomorphic. A ventral spiniform process at the base of the mandibles. Antennal club two-jointed. Neotropical and fossil in Dominican amber *Acanthognathus*

5. Head without antennal scrobes 6
- Antennal scrobes present 8

6. Antennae 5-jointed. Second funicular joint much longer than the others. Australia and New Guinea *Orectognathus*
- Antennae 6-jointed. Second funicular joint not enlarged 7

7. Occipital lobes dentate. Mandibles long, opposing an apical fork of three spiniform teeth. Central and South Africa *Microdaceton*
- Occipital lobes rounded. Mandibles short, opposing a broad masticatory margin. Australia. *Colobostruma*

8. Antennae 9-jointed 9
- Antennae with 8 or fewer joints 10

9. Head pyriform. Mandibles elongate, with three long, spiniform distal teeth intervalled by minute denticles. Ecuador and Colombia. *Protalaridris*
- Head rounded on the sides. Mandibles short, triangular, with short, spiniform teeth over the whole masticatory border, longer on the basal half. Malaysia. *Ishakidris*

10. Antennae 8-jointed 11
- Antennae with 7 or fewer joints 12

11. Eyes over the antennal scrobes. Scape angulate at the base. At least a few clavate hairs always present. From the West Indies and Mexico to N. Argentina and S. Brazil. Fossil in Dominican amber. *Octostruma*
- Eyes under the antennal scrobes. Scape straight and thin. Hairs long and simple. Madagascar *Pilotrochus*

12. Antennae 7-jointed 13
- Antennae with 6 or fewer joints 14

13. Mandibles triangular, opposing the whole masticatory border when closed. From the Antilles and S. Mexico to Argentina; New Guinea, Australia. *Rhopalothrix* (in part)
- Mandibles slender, opposing only the apical part at closure. From Florida to Argentina through the Caribic Islands, Australia, New Caledonia, New Guinea, Philippines, and several Pacific islands *Eurhopalothrix*

14. Without eyes. Sri Lanka. *Rhopalothrix* (in part)
- Eyes present 15

15. Eyes ventral to the antennal scrobes. Tropics and temperate areas of the world. Fossil in Dominican amber *Strumigenys*
- Eyes dorsal to the antennal scrobes. Australia *Epopostruma*

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