Taxonomic and phylogenetic problems in Old World eucerine bees, with special reference to the genus *Tarsalia* Morawitz, 1895 (Hymenoptera: Apoidea: Anthophoridae)

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A tribe Ancylini was established by Michener (1944: 273) for the two genera *Ancyla* and *Tarsalia*, but the two are not closely allied and *Tarsalia* appears rather to be an aberrant member of the Eucerini. The previously-described species-group taxa of *Ancyla* are listed, and *Ancyloscelis heterodoxa* Cockerell, 1937, is synonymized with *Ancyla oraniensis* Lepeletier, 1841. The previously described species-group taxa of *Tarsalia*, including *cellularis* (Cameron, 1898), transferred from *Tetralonia*, and *mimetes* (Cockerell, 1933), transferred from *Tetraloniella*, both new combinations in *Tarsalia*, are reviewed. *Tarsalia strobilanthae*, sp. nov., is described from India. *Glazunovia*, gen. nov., is proposed for *Melissina* of Popov, 1962, a misidentified taxon. The position of the anomalous eucerine *Tetralonia brevipennis* Cameron, 1898, is discussed.

KEYWORDS: Ancylini, *Ancyla*, *Melissina*, *Glazunovia* gen. nov., *Tarsalia strobilanthae* sp. nov., asymmetrical structures in Eucerini, taxonomy, biodiversity.

Introduction: a tribe Ancylini?

Michener (1944: 273) established a tribe *Ancylini* for the two genera *Ancyla* Lepeletier, 1841 (= *Plistotrichia* Morawitz, 1874) and *Tarsalia* Morawitz, 1895. The characters given by Michener for the tribe, which need not be recapitulated here, seem to have been based, so far as the female was concerned, exclusively on *Ancyla* ('The scopa, at least in *Ancyla*, is large and consists of plumose hairs'); and, so far as the male was concerned, on some possibly misidentified specimen or specimens: the statement 'The males lack pygidial plates and have the posterior legs more or less enlarged' applies *in toto* neither to *Ancyla* (in which a pygidial plate is present: *cf.* Warncke, 1979: 188) nor to *Tarsalia* (where the posterior legs, unlike those of *Ancyla*, are neither enlarged nor otherwise modified). Certainly, in his key to the tribes of the Anthophorinae (p. 270), *Tarsalia* runs not to the Ancylini but to the Eucerini. (*Ancyla* itself, in the same key, perhaps runs better to couplet 8 (Emphorini/ Hemisiini), agreeing well with neither alternative, rather than to the Ancylini in couplet 21).

In a subsequent study of the classification and relationships of the more primitive non-parasitic anthophorine bees, Michener and Moure noted (1957: 399) that 'The small and rare Eurasian genera *Ancyla* [and] *Tarsalia*' were related to the group

under consideration [the exclusively New World Exomalopsini and their immediate relatives] but had been excluded because the authors had 'no new data to present concerning them and because their relationships to the genera discussed ... [were] ... not close'. The Ancylini thereafter remained virtually in a limbo until 1993.

In that year Roig-Alsina and Michener published a study of the phylogeny and classification of the long-tongued bees. They noted (1993: 158) that the Ancylini appeared in their Cladograms 1a and 1b as the sister group to the Eucerini and in the consensus trees for their Analyses A, C and D in various polytomies all including the Eucerini. They formed the impression that the Ancylini represented a basal branch of the eucerine clade, but, since the evidence was not clear, maintained the Ancylini as a tribe. However, only *Tarsalia* (represented by *T. ancyliformis* Popov) had been studied, and it is quite clear that the authors had no conception of the extent of the differences between that genus and *Ancyla*.

In the same year and virtually as an appendix to Roig-Alsina and Michener's paper, Silveira published a study of the phylogenetic relationships of the Exomalopsini and Ancylini (Silveira, 1993). The *Tarsalia* material studied was apparently the same as that available to Roig-Alsina and Michener, namely *T. ancyliformis*; of *Ancyla* there were available 'one female and two males, identified by J. Bequaert as *A. oraniensis* Lepeletier, and a male *Ancyla* sp.'. It is evident that the author can have had little or no cognizance of the extent of inter-specific variation in the two genera and had failed to note, for example, such a remarkable apomorphy as the presence of a functional metasomal scopa in *Tarsalia* (coded '0' in table 2, p. 139), certainly weak in *ancyliformis* but very well developed in such species as *mimetes* (Cockerell, 1933). Silveira came to the conclusion that, 'considering the uncertain sister-group relationship between *Ancyla* and *Tarsalia* and the uncertain close relationship between them and Exomalopsini, it ... [seemed] ... advisable to keep the former as separate genera, constituting a tribe separate from the Exomalopsini' (Silveira, 1993: 172).

After more than 50 years, neither the validity of a tribe Ancylini, comprising the two genera *Ancyla* and *Tarsalia*, nor its relationships with the Exomalopsini on the one hand or the Eucerini on the other, can be said to have been unequivocally demonstrated.

Phylogenetic analysis: relationships between *Ancyla*, *Tarsalia* and Old World Eucerini

Comparison of unequal entities

There are always likely to be problems in comparing monogeneric or oligogeneric tribes with polygeneric tribes, or monospecific or oligospecific genera with polyspecific genera: smaller units, whatever their rank, inevitably show greater numbers of differences *inter se* than will appear when they are compared severally or jointly with larger (genus-rich or species-rich) units where the overall range of variation may be very great. It is not, therefore, practical to compare *Ancyla* and *Tarsalia* with the highly variable and species-rich Exomalopsini as such or with the equally variable and species-rich Eucerini as such, as even a cursory inspection of Michener and Moure's table 1 (1957: 400) will make clear. [Variation in the Eucerini is even more marked than the table, which was biased in favour of New World forms, indicates.] For this reason, and since among Old World anthophorid bees the nearest relatives of *Ancyla* and *Tarsalia* may clearly, from Roig-Alsina and Michener's paper

(1993), be expected to be found among the Eucerini, they are compared here with representatives of the two largest and most widely distributed genera of that tribe, *Eucera* and *Tetraloniella.*

Ancyla and Tarsalia

The species of *Ancyla* were treated by Warncke (1979). Eight species were recognized, including one described as new (*orientalica*). Warncke omitted one taxon, *heterodoxa* (Cockerell, 1937), described as '*Ancylosceles* (?)' [*Ancyloscelis*]. The holotype of *heterodoxa*, B.M. Type Hym. 17 b 754), labelled 'Algerie/$^{49}_{65}$' [i.e., one of 248 Hymenoptera in a mixed lot from Algeria, purchased of [Ch.] Parzudaki: Zoological Accessions, Annulosa, 2, 1840–1849], and '*Ancylosceles/heterodoxa*/Ckll Type', has been examined. It is a female of *A. oraniensis* Lepeletier, 1841, which is the earliest name for the species: syn. nov. The key given by Warncke is adequate for the recognition of the species.

The species of *Tarsalia*, regarded by him as a subgenus of *Ancyla*, were treated by Warncke in the same paper, which was not accompanied by figures. Three species, all previously described, were recognized. Warncke was unaware that two species described in other genera were in fact *Tarsalia*, and also was not cognizant of the description of *T. deccana* by Baker (1972).

In the matrices that follow (Appendices 2 and 3), seven species of *Tarsalia* are compared with a representative species of *Ancyla* [the common *A. holtzi* Friese, 1902, of which syntypes as well as other specimens were available], with the type species of *Eucera*, *E. longicornis* (L., 1758), with a typical, less specialized eucerine, *Tetraloniella dentata* ([Klug *in litt.*] Germar, 1839), and with the enigmatic Indian species *Tetralonia brevipennis* Cameron, 1898 (*vide* Annex A). The *Tetraloniella* selected is not the type species of that genus (*graja* Eversmann, 1852, on which *vide* Baker, 1996: 542) but a common western palaearctic relative of *graja* auctt.

How many characters?

The number of morphological characters that might be used in such a comparison, is, as with any group of advanced organisms, potentially unlimited. The use of a very large set of characters may have certain advantages: it may nullify or at least greatly reduce the impact of the presence of extreme, unique modifications in individual taxa; it may minimize the effect of any false codings; and it may provide some assurance that further expansion of the character set will not significantly alter resolution. It may at the same time have the sensible disadvantage that a higher proportion of the characters employed, and this will apply particularly to internal or normally concealed characters, will not be observable in unique type specimens or in instances where material of both sexes is not available. However, a smaller set of characters may yield results that are sufficiently reliable for classificatory purposes within existing systems, provided that it embraces a wide selection of characters: clearly, sets of characters drawn exclusively or largely exclusively from restricted areas, such as the mouthparts, the male genitalia and associated structures, or the pollen-collecting apparatus, are, owing to discordant evolution in those areas, likely to yield appreciably different results. The question arises, how many characters is enough? Two facts are self-evident: a smaller set should be adequate for a small group of conspicuously diverse entities, whatever the category; a larger set might be desirable for some species-rich and relatively homogenous group such as *Andrena*, with some hundreds of very similar species. This suggests that the number of

characters to be studied in any particular group should in some way be related to *n*, the number of taxa in that group (rather than be determined by the time available or by the boredom threshold of the investigator). A universally valid relationship may prove elusive. Clearly this cannot be factorial *n*, since already, where *n* was as little as 7, the examination of 5040 characters would be entailed. Practical experiment suggests that $10.\sqrt{n}$ (for groups of 5, 25 and 125 taxa this would give character sets of 22, 50 and 112) should be a satisfactory norm and avoid overkill: limited resources should not be wasted. Comparison with a few recently published papers taken at random indicates some measure of agreement:

	n	characters	$10.\sqrt{n}$
Roig-Alsina and Michener, 1993 (adults, table 2) [Hymenoptera]	83	131	91
Garrison 1994 [Odonata]	22	41	47
de Jong 1994b [Diptera]	76	85	87
Miller, 1996 [Lepidoptera]	26	86	51
Yeates and Irwin, 1996 [Diptera]	24	77	49
McKamey and Deitz, 1996 [Hemiptera]	25	47	50

What characters?

While the Ancylini have been labelled as primitive anthophorids, in certain characters they certainly are not, and it seems paradoxical that any bee possessing such extraordinary and obviously derived characters as those appearing in the concealed sterna and genitalia of male *Tarsalia*, or as the presence in the female of a functional metasomal scopa [better known as a synapomorphy of the Megachilidae] in addition to massively developed tibial and basitarsal scopae, could be regarded as a primitive element of any suprageneric taxon to which it might be assigned. Extraordinarily complex sternal structures do of course occur in other bees regarded as primitive or relict forms, e.g., in the Colletidae (cf. Michener, 1965: 81, fig. 201–209, *Trichocolletes*) and in the Melittidae (cf. Baker, 1993: 24–31, *passim*, fig. 3–4, *Haplomelitta*, 14–21, *Samba*), and many other strange modifications, affecting variously many parts of the body and commonly confined to a single sex, do occur, apparently at random, throughout the Apoidea. However, while the possession of highly derived characters or suites of characters does not necessarily subvert primitive placement of a taxon within a clade, it may be suggested that such characters are best not used in classification at higher levels, preference being given instead to using, as already noted in connection with discordant evolution in different body regions, as wide a selection of characters as possible. It is of course accepted that in some body regions suitable characters, and preferably characters common to both sexes, may be difficult to find or be more subtle and less readily defined than might be wished. The search should however be made.

Because characters that may be drawn from the concealed sterna and genitalia are so numerous and so readily observable, there is an obvious possibility that they may outnumber other characters employed in a data matrix prepared for the development of a cladogram [cf. Miller, 1996, where 39 of 59 adult characters are drawn

from the terminalia (δ) or genitalia ($\female$)] and have a disproportionate influence on the outcome; on the other hand, to use them only selectively or to give them a low weighting is to ignore or diminish a part of the evidence. [The reference here is to phyletic weighting and not to diagnostic weighting, where emphasis may be very differently placed.] The problem is in essence similar to that of the conflicting cladograms that may be derived from imaginal and earlier stadia, or, among bees, from the inclusion or exclusion of cleptoparasitic forms.

Characters employed

For various reasons, but especially because of the limited material of *Tarsalia* available, it was not possible to observe closely the foregoing discussion and recommendations. The eleven species here concerned were compared in 63 selected characters (25 drawn from the males, nine from the females, 29 common; 27 drawn from the head, 16 from the mesosoma, 18 from the metasoma, two general), of which 41 were treated as binary, 22 as multistate (appendix 1). Some potentially useful characters were necessarily excluded from consideration: two of the seven *Tarsalia* are known only from the unique type specimens, rendering the examination of certain characters inadvisable, and three were available only in a single sex. [Similar problems were encountered by Masch (1993) in dealing with a group of Ethiopian *Erichsonius* (Coleoptera), six of the 11 species being represented only by the holotypes, three others only by males, four by females. Cladograms developed for the males and females independently were, unsurprisingly, not congruent.] Other characters were excluded owing to problems in defining mutually exclusive states, or stating them in clearly reproducible fashion: for example, the breadth of the anterior face of the mesepisternum when this is not delimited by an omaulus or, as in *Ancyla*, by a relatively abrupt change in sculpture or vestiture.

Non-morphological characters (e.g. geographical distribution, which would probably serve only to emphasize grouping of the Indian *Tarsalia*, pollen sources, which would be worth considering in view of the diversity of scopal structures but which are not known for all species, and flight periods, again inadequately known) have not been used, although geographical distribution has been included with morphological characters in some recent studies (e.g. Graybeal, 1997: 304).

Taxa were not excluded because they could not be coded for any particular character or group of characters: Wiens and Reeder (1995: 556–557) concluded that the inclusion of 'incomplete taxa' (taxa with missing data) might have a minor depressing effect on phylogenetic accuracy but was unlikely to be positively misleading, and that the exclusion of characters because of incompleteness alone might lead to unnecessarily discarding useful phylogenetic information. In any event, it is only in very well known groups, where ample material is available, that all taxa can be compared in all selected characters.

Character states were polarized with reference to a hypothetical, primitive, short-tongued bee. '0' assumed a primitive condition, '1', '2' and '3' derived conditions (not necessarily in terms of increasing complexity in a single direction, although where applicable this approach was obviously preferred, since the derived conditions may be fundamentally dissimilar), '—' inapplicability. Of course, the polarity of some states is uncertain, and some states labelled as primitive may in fact represent secondary specialization or reversal. Since the Ancylini, sensu Michener, are, *ex hypothesi*, at or near the root of the Anthophorinae, characters in which they differ

from the Eucerini were generally, but not always, interpreted as showing in the Ancylini the more primitive expression.

In Matrix 1 (Appendix 2), the matrix derived directly from Appendix 1, male and female characters were coded '?' where material was not available. Rarely, some published datum could be used. Common characters also were coded '?' where the state could not satisfactorily be determined in the available material: the unique specimen of *Tarsalia cellularis* and both specimens of *T. strobilanthae*, for example, are in poor condition, and the type of *Tetralonia brevipennis* is both in poor condition and lacking the mouthparts.

To minimize the effects of the number of unresolved states appearing in the original matrix, a second matrix, Matrix 2 (Appendix 3), substitutes, for certain states coded '?' in Matrix 1, states that may reasonably be inferred as common to all *Tarsalia* species. In this matrix, also, *Eucera longicornis*, where vein 1r–m is normally absent, has been coded for characters 34, 36 and 37 on the basis of specimens where this vein is, exceptionally, present.

Phylogenetic analyses

Matrices 1 (Appendix 2) and 2 (Appendix 3) were analysed independently.

Matrix 1 was analysed using the computer programme Hennig86 (Farris, 1988). All characters were treated as unordered. Cladograms were built using the algorithm ie* [branch-and-bound algorithm, guaranteeing minimum-length cladograms]. There were 17 cladograms of length 122 [$ci = 0.72$; $ri = 0.57$]. The application of successive approximations character weighting produced one cladogram identical with cladogram 0 of the original 17. This cladogram is reproduced at Appendix 4A.

11 characters had retention indices of zero. These were characters 1, 13, 32, 33, 36, 37, 38, 45, 47, 56, 57. Of these, characters 13, 36, 37, 45, 47, and 56 had been regarded as strong (not, or less, dependent on judgment). In further work, the others (1, 32, 33, 38, 57), more subjective or less readily quantifiable, might well be dropped.

Matrix 2 was analysed using the computer programmes PAUP, Version 3.1 (Swofford, 1993), and, for the graphic display and printing of cladograms, MacClade, Version 3.0 (Maddison and Maddison, 1992).

An initial bootstrap analysis (Felsenstein, 1985) with branch-and-bound search, using the procedure available in PAUP, was carried out [Starting seed = 1; number of bootstrap replicates = 100; initial upper bound = unknown; addition sequence = furthest; zero-length branches not collapsed; topological constraints not enforced]. This gave the 50% majority-rule consensus tree reproduced at Appendix 5. The tree shows a basal trichotomy separating *holtzi* (*Ancyla*) and *brevipennis* ('*Tetralonia*') independently from all other taxa and a polytomy grouping all species of *Tarsalia*. It may be noted at this point that the characterization of *brevipennis*, known from a single female, depended heavily on Cameron's description and figures of the mouthparts, now lost. Confirmation or otherwise of Cameron's data and knowledge of the male of *brevipennis* could reduce the node to a dichotomy.

Subsequent exhaustive search for the shortest tree(s) [Settings: zero-length branches not collapsed; topological constraints not enforced] gave results: number of trees evaluated = 34 459 425; length of shortest tree found = 122; length of longest tree found = 166; number of trees retained = 17. The cladograms 1–17 were all essentially similar, *holzi* separating at the basal node, *brevipennis* at the second, and the two recognized eucerines, *longicornis* (*Eucera*) and *dentata* (*Tetraloniella*) appearing on one branch. The previous polytomy grouping the *Tarsalia* species was

in all instances completely resolved, variation being confined to their relative positions on a *Tarsalia* branch. Cladogram 4, which grouped the Indian species of *Tarsalia* on one sub-branch, has been selected for reproduction (Appendix 6) [Tree length 122; $ci = 0\cdot721$; $ri = 0\cdot575$; $rc = 0\cdot415$].

The results of the Hennig86 analysis, based on the original data matrix, and of the PAUP 3.1 analysis, based on the same matrix but with inferred states for certain characters in *Tarsalia* added, were essentially the same. Since few taxa were involved, and since resolution was already complete, there was little point in proceeding to further analysis. The contingency had of course been considered, but it had been decided that such steps as the introduction of differential weighting or the re-examination of characters would neither of them have proved a satisfactory alternative to the acquisition, certainly problematic, of better material. As to differential weighting, this was considered undesirable as being likely to accentuate the predominance of correlated characters such as those occurring in the male genitalia and associated sternal structures. As to the re-examination of characters, it was considered that this also was undesirable. Where re-examination might be prompted by the appearance of apparently identical states, potentially indicative of convergence, in different clades, and while as a result of re-examination it might well be found possible to distinguish between these states (either by redefining the character or by multiplying the number of states), and so further differentiate between their possessors, it was considered that such action would tend to circularity of argument. Searching for characters to strengthen preconceived relationships is as indefensible as ignoring characters that may weaken them. Many of the characters initially listed and subsequently employed or dropped had already, of course, been more or less extensively revised in the course of examination of material and compilation of the data matrices.

Cladograms and systematic categories

The immediate suggestions of the consensus cladograms are:-

(a) That the recognition of a tribe Ancylini comprising the genera *Ancyla* and *Tarsalia* is not warranted.
(b) That *Ancyla* is so strongly differentiated from the eucerine clade (see, especially, Appendix 6) as to merit recognition at an equivalent taxonomic level.
(c) That *Tarsalia* represents a branch of the eucerine clade.
(d) That the species *Tetralonia brevipennis* is best treated as an aberrant eucerine pending the availability of further material.

The immediate suggestions of cladograms can, however, rarely be translated automatically into taxonomic terms. Cladograms may not legitimately be accepted as incontrovertible representations of relationships, still less as determining the appropriate systematic categories of the branches or clades they identify. Any cladogram showing purported relationships in any group comprising more than a very few taxa is likely, if strictly interpreted, to demand far more systematic categories than are available in conventional classificatory systems. It is to be viewed, rather, either as confirming views derived from traditional or conventional approaches, even if these reduce to the informed opinion of a specialist on the group in question, or as pointing to weaknesses or errors in received classifications. It may also be observed that cladograms are two-dimensional while evolution takes place in space and time. Three-dimensional models that would better explain convergence and geographical

distribution are much to be desired. However, the generation of pictorial representations such as that presented by Milne and Milne (1939) (for case-construction by trichopterous larvae) clearly requires judgment and vision transcending the merely mechanistic production of the now almost obligatory cladogram. (The citation is not, of course, to be construed as comment on the validity or otherwise of the Milnes' interpretation.)

Some authors maintain that the Linnean system of taxonomy is fundamentally flawed because it has no evolutionary basis, and that it should be replaced by a system in which taxon names, at all levels, are determined by phylogenetic relationships. While this might appear to be desirable, and may even be practicable in the instance of some small and well-studied groups, it founders in the instance of such large and imperfectly known groups as the Apoidea (c. 25 000–30 000 species) where fully comprehensive studies at genus-group level (c. 2050 names) are unlikely to be achieved in the immediately foreseeable future. From purely practical considerations, the relative stability of the Linnean system is in any event to be preferred to a phylogenetic system where groupings, and consequently names, could alter materially and frequently with the discovery of previously unknown forms or with the use of different sets of characters or the differential weighting of characters.

Polytomies in cladograms

Although no polytomies remain in the trees illustrated at Appendices 4A and 6, it may be observed that there is no logical reason why branching should necessarily be assumed always to be dichotomous. If peripheral or other populations become isolated through climatic or other physical change, there is no reason why the species should not continue unchanged (or, more accurately, imperceptibly changing, since no species can be entirely static) in the major area of its distribution, while in the detached populations, where infraspecific variation may initially be less and where gene-flow will be reduced, more rapid change leading to recognizable subspeciation and eventually full speciation may be expected. In the event of widespread physical changes, such as past transgression of the Sunda and Sahul shelves, or recent large-scale deforestation, the splintering of populations could give rise nearly simultaneously, in geological time in the former instance, in real time in the latter, to numbers of isolates, in other words to polytomous branching. Where cladograms yield unresolved polytomies, the taxa involved need clearly to be investigated not so much on additional morphological or other intrinsic characters but in relation to distributional, climatic and other physical factors. While it is already late, it should not be impossible to select some large area undergoing rapid fragmentation as a result of human interference for thorough, long-term sampling of selected taxa (particularly species with limited capacity for dispersal) that might, ultimately, if sufficiently refined techniques were employed, provide some measure of proof for multiple branching.

Conclusions: the systematic positions of Ancyla and Tarsalia

Ancyla is accepted as representing a monobasic Old World tribe Ancylini (Michener, 1944), distinct on the one hand from the Eucerini (as represented by Old World forms: present paper) and on the other from the exclusively New World Exomalopsini (Silveira, 1993). [*Ancyla*, as noted above, was not included in Roig-Alsina and Michener's study (1993).]

Additional characters, not used in the computer analysis, that support the

isolation of *Ancyla* include, for example, the more compact habitus, the broad and clearly defined anterior face of the mesepisternum, the generally coarser surface sculpture, and, in the males, the absence of a well-developed, apically setigerous, parapenial process (figures 20, 24) and the presence (in some species) of marked modifications of the mandibles, of the legs and of the exposed sterna. [The species examined, apart from *holtzi*, used in the analyses, were all those listed under *Ancyla* (*infra*) except *stolli* and *nitida*.]

Tarsalia is accepted as representing a basal branch of a eucerine clade (Roig-Alsina and Michener, 1993: 158), arising before the divergence of *Tetraloniella* and *Eucera* (cf. Appendix 6: the characters indicated may be identified from Appendix 1). It is not sufficiently differentiated to merit recognition at tribal level and is therefore referred to the Eucerini.

These views are further developed in the cladogram at Appendix 4B, which is Appendix 4A with some branches rotated to reflect the geographical relationships of the *Tarsalia* species: geographically, the species fall into two groups, one Eremian (xeric or desert areas of the Palaearctic/Mediterranean and Ethiopian/African regions/subregions), the other Oriental/Peninsular. *Tarsalia* appears here as a sister-group of *Tetraloniella + Eucera*, but (1) the characters used in Appendix 1 did not of course reflect the full range of variation within the latter two genera and the selection of additional species with characters not appearing in *Tarsalia* would conceivably have altered materially the branching sequence, and (2) the further study of other Old World Eucerini (see below) may well modify the present placement.

Was the computer exercise worthwhile? Yes, in the sense that it confirmed prior suspicions that *Ancyla* and *Tarsalia* were not as closely related as previously supposed, and that the latter genus was better regarded as a primitive member of the Eucerini rather than as the second component of a tribe Ancylini. No, in the sense that it consumed an inordinate amount of recording effort and computing resources. The point is, has a laborious cladistic approach revealed anything more about the relationships of the two genera that any competent systematist might have arrived at through normal processes of thought and observation? As Scoble (1996: 254) has remarked, 'often high levels of taxonomic resolution can be achieved with a good collection, a microscope and carefully planned fieldwork … substantially greater resolution is by no means certain in analyses with large morphological datasets or with molecular data'. The difference is essentially between reliance on the cladistic analysis of a published data matrix and reliance on informed opinion. Increasingly the mechanical approach will come to be relied on, and in any large group of organisms, or wherever a large number of characters may be employed, the sheer volume of data may necessitate such an approach. However, the results of cladistic analyses need to be viewed with caution, if not scepticism. One need only point to two very recent papers (Lee, 1997, deBraga and Rieppel, 1997), both dealing with substantially the same body of taxa, both utilizing substantial numbers of characters, that drew totally incongruous conclusions. If either had appeared on its own, it would presumably have been accepted by most readers as presenting an acceptable classification.

On asymmetric structures in Tarsalia

Professor K. W. Cooper has pointed out (*in litt.*, 7 April 1987) that asymmetries of the terminalia are common and species-specific in syrphid flies (Diptera, Syrphidae) and some Coleoptera; mirror-imagery of asymmetric terminalia occurs

within some groups of Carabidae (Coleoptera), where it is left-handed as opposed to the right-handed state common to most carabids. For the Hymenoptera, Mr C. O'Toole has drawn attention (verbal communication) to asymmetry of the penis-valves in *Timulla* (Mutillidae), but here the asymmetry is not very pronounced.

Differences in the concealed sterna and genitalia in male *Tarsalia* are not merely highly species-specific but so extensive as to suggest that, in the event of a breakdown of behavioural or chemical barriers, successful interspecific copulation would be difficult to achieve. However, while pronounced species-specific differences may be important in maintaining reproductive isolation where a number of related species occur together, they would appear superfluous or irrelevant in circumstances where, as with *Tarsalia*, related forms are not merely not sympatric but widely separated spatially. In this context, the addition of marked asymmetry would seem an unnecessary complication.

However, both Professor Cooper and Mr O'Toole have suggested independently that the asymmetry in *Tarsalia* may be associated with some unusual position in copulation. Professor Cooper notes that if Rozen's suggestion (1958: 58) is correct (that the subgenital sterna serve as an aid in the extrusion of the terminalia), it may be that the striking asymmetry of S7 and the lesser asymmetry of S8 result not only in extrusion but in a turning of the terminalia towards the right side. [Rotation (by 180°) of the male terminalia (strophandry) is characteristic of certain Tenthredinoidea (chiefly Tenthredinidae), but here it is not accompanied by asymmetry.] Could the asymmetry of the penis valves then be an asset? Unfortunately, no detailed observations on mating behaviour in *Tarsalia* appear to have been recorded, and there are at present no grounds for supposing it to assume some form other than that usual among bees. Unfortunately also, fresh material that would permit examination of the soft tissues (including the origins and insertions of the sternal muscles) and experimentation to establish whether flexure or rotation could be induced, and so possibly be helpful in judging, in the absence of exact field observations, what might occur, is not available.

In female *Tarsalia*, there appears to be no asymmetry corresponding with that of the male. In *Timulla* also there appears to be no complementary asymmetry in the sclerotized parts of the female genitalia (O'Toole, 1975, and additional references there given) and the asymmetry in the male penis-valves has not been explained. It cannot be seen as a necessary supplement to other modifications apparently designed to ensure secure linkage during copulation, which, while pairing takes place on the ground (female *Timulla* are flightless), continues in flight.

Further studies: classification of the Old World Eucerini

Ancyla and *Tarsalia* were compared above with single representatives of the two Old World genera *Eucera* and *Tetraloniella* and with the Indian eucerine described as *Tetralonia brevipennis*. It would now obviously be desirable to extend that comparison to representatives of other Old World eucerine genera, notably *Cubitalia*, *Eucara*, *Glazunovia* (*nom. nov.* for *Melissina sensu* Popov, 1952, type species *Tetralonia nigriceps* Morawitz, 1895: *vide* Annex B), *Melissina*, *Notolonia*, *Synhalonia*, *Thygatina* and *Tetralonia*. These are all clearly not primitive but highly specialized forms, and all neither, except *Synhalonia*, species-rich, nor, except *Synhalonia* and *Tetralonia*, very widely distributed. Such a study is beyond the scope of the present paper. As to *Eucera* itself, in recent years a number of small segregates of dubious

value, based on few characters apparently selected arbitrarily, have been raised to genus-group rank at the expense of the very large conventional genus [Tkalcŭ, 1978: *Hetereucera, Pareucera, Stilbeucera*; Tkalcŭ, 1984: *Atopeucera, Pteneucera*; Pesenko and Sitdikov, 1988: *Opacula*]. [The full description of *Stilbeucera* was: 'Weibchen: Metafemora ventral ohne scharfe Längskante (im gedachten Querschnitt also gleichmäßig gerundet). Männchen: Sagitten des Kopulationsapparats basal mit breiter sackartiger Öffnung'.] Some of these taxa have very obviously been described in the absence of knowledge that the characters on which they were based are to be found also in other combinations in species occurring in faunal areas other than those treated. Work of this kind, which leaves by far the greater number of species of a genus unplaced and unplaceable, does entomology a great disservice. A revision at genus-group level of the Old World eucerines, based on multi-character analysis of a fully representative sample of species, is much needed, but this also is beyond the scope of the present paper, which is essentially a study of the taxonomy of *Tarsalia*.

Taxonomy of *Ancyla*

Ancyla Lepeletier, 1841

Ancyla Lepeletier, 1841: 294; type species *Ancyla oraniensis* Lepeletier, 1841 (monobasic).

Plistotrichia Morawitz, 1874: 134; type species *Nomia flavilabris* Lucas, Morawitz, 1874 (monobasic). Morawitz's material, from Derbent, of what he misidentified as *flavilabris* Lucas, 1849, was apparently *asiatica* Friese. Synonymized with *Ancyla* by Pérez (1895: clxxiii).

Ancyla oraniensis Lepeletier, 1841

Ancyla oraniensis Lepeletier, 1841: 294; ♀♂; Oran.

Nomia flavilabris Lucas, 1849: 186, pl. 7 fig. 4; '♀' [♂]; [Algeria:] dans les bois du lac Tonga, aux environs du cercle de Lacalle.

Ancylosceles (?) *heterodoxa* Cockerell, 1937: 282; ♀; Algerie.
  Holotype ♀ (B.M. Type Hym. 17 b 754), BMNH, examined. Syn. nov.

Ancyla brevis Dours, 1873

Ancyla brevis Dours, 1873: 292; ♀; Alg[érie]. Described from ten syntypes; no lectotype subsequently designated. Type material probably lost with Dours' collection, but see below.
  A short series identified as *brevis* in MNHNP (♂, Tanger [printed, on greenish blue paper]; ♀, green disc/Mascara [ink]/1839 [ink: Pérez's catalogue no.]/Museum Paris Coll. J. Pérez 1911 [standard Museum printed label]; ♀, Alg 8 64 [ink, on grey paper]/Museum Paris Algérie Coll. O. Sichel 1867 [standard Museum printed label]) differs from Dours' description in that the wings are not 'fumatissimis ... très-enfumées'. However, given the close association between Dours and Sichel (Dours, 1870: 5–7, *passim*), it is not impossible that the ex-Sichel ♀ may be a syntype of Dours' species.
  In the Tanger male, the legs are not modified (basitarsus III not arcuate); S5 is almost simple, shallowly emarginate in median third, its impunctate margin narrowly interrupted medially where the discal punctation becomes denser and extends to the margin; a distinct mandibular 'beard' is not developed, merely a thin fringe of moderately long pale hairs being present; the clypeus and two spots on the supraclypeal area are yellow. In the females the scopa is pale on the tibiae basally and beyond that black ('Jambes et premier article des tarses postérieurs hérissés de poils rudes, longs, trés-noirs, si ce n'est sur le tibia ou ils sont un peu mêlés de roux').

Ancyla punica Friese, 1922: 65; ♀♂; Tunis merid. Described from four syntypes; no lectotype subsequently designated. Syntypes MNHUB.
  Placed here following Warncke (1979: 188), who noted 'Stimmt völlig mit *A. brevis* Drs. überein—syn. nov. !' but gave no indication of having examined type material of *brevis*. Friese described the scopa in *punica* as 'braun'.
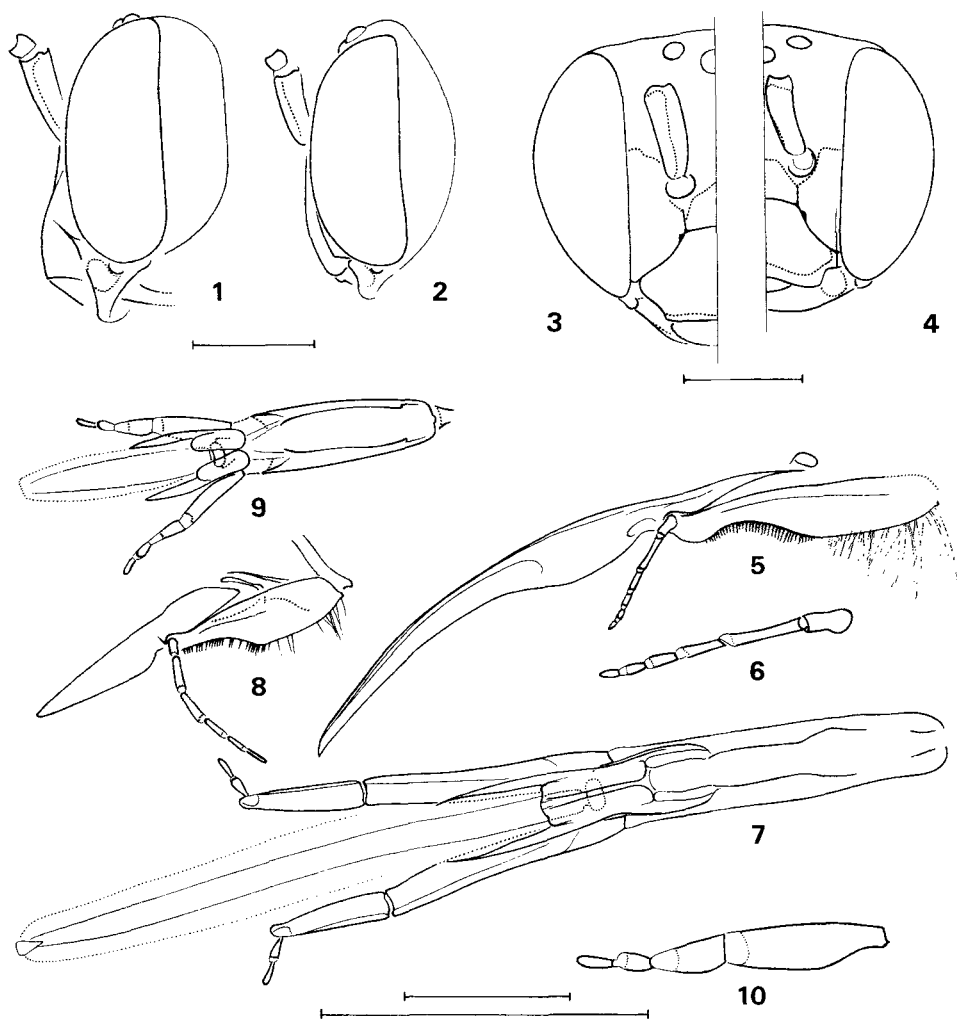
Ancyla holtzi Friese, 1902

    Ancyla holtzi Friese, 1902: 105; ♀♂; Süd-Morea bei Kalavryta.

    Described from 12♂ and 2♀ syntypes; no lectotype subsequently designated. Syntypes MNHUB, DBB, and probably elsewhere.

    Ancyla holtzi anatolica Warncke, 1979: 191; ♀♂; Holotype ♀, [Turkey:] Ankara, 5 viii 1972 (*Warncke*), OLL (Warncke Collection). Status uncertain owing to the curious distribution: Warncke recorded nominotypical *holtzi* from the Peloponnese, Bulgaria, Cyprus and Iraq.

Figures 2, 4, 8–10, 13, 14, 16, 21–24, 28–30.

FIGS 1–10. (1–4) Head in ♂♂, lateral and frontal aspects, of (1, 3) *Tarsalia ancyliformis mediterranea* Pitt., 1950 [Cyprus: Cherkes (*G. A. Mavromoustakis*)]; (2, 4) *Ancyla holtzi* Fr., 1902 [Turkey: Ankara, Dikmen (*Guichard and Harvey*)]. (5–10) Mouthparts in ♀♀ of (5–7) *Tarsalia ancyliformis mediterranea* Pitt., 1950 [Cyprus: Asomatos, 26 vii 1951 (*G. A. Mavromoustakis*)] (5) maxilla and appendages; (6) maxillary palpus, further enlarged; (7) prementum and appendages); (8–10) *Ancyla holtzi* Fr., 1902 [Cyprus: Limassol, 1vi 1934 (*G. A. Mavromoustakis*)] (8) maxilla and appendages; (9) prementum and appendages; (10) labial palpus, further enlarged). Scale lines represent 1 mm (lowest line for figure 6 and 10 only).
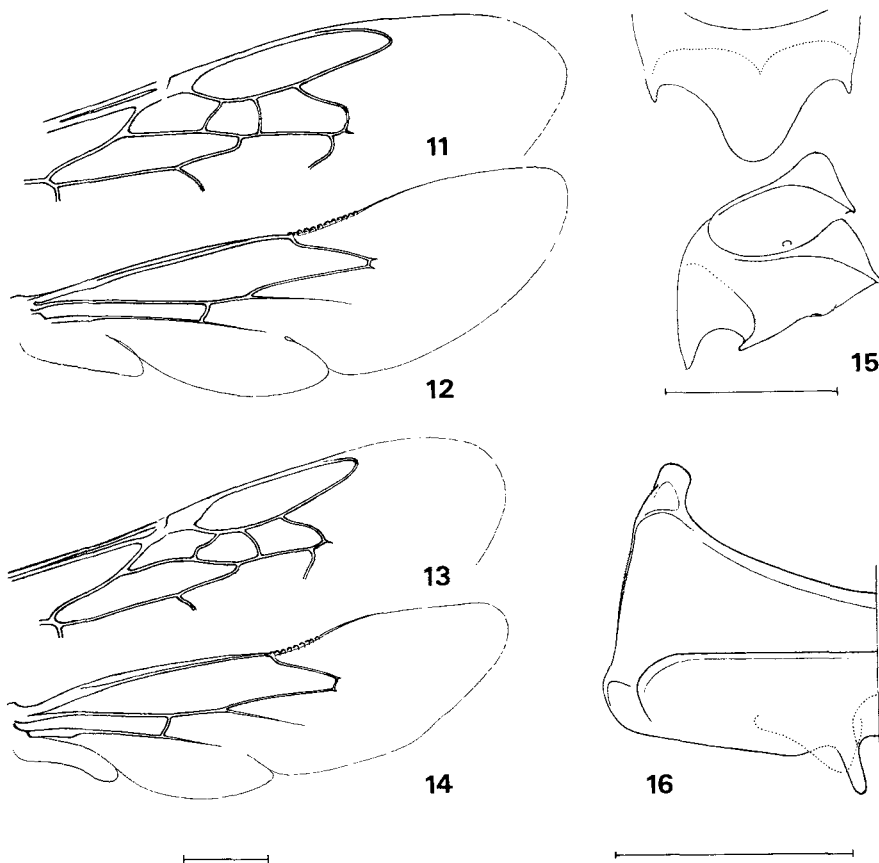
Figs 11–16. (11–14) Characteristic part of forewing, and hindwing, in (11, 12) *Tarsalia ancyliformis mediterranea* Pitt., 1950 [Sardinia: Torralba, 19 viii 1957 (*E. Priesner*)]; (13, 14) *Ancyla holtzi* Fr., 1902 [Turkey: Ilgaz (*Guichard and Harvey*)]. (15) Tergum 7 in *Tarsalia strobilanthae* sp. nov. [paratype] in dorsolateral aspect with (above) apex of sclerite in dorsal aspect. (16) Sternum 5 in *Ancyla holtzi* Fr., 1902 [Turkey. Preparation 21/0000]. Scale lines represent 1 mm.

Ancyla nitida Friese, 1902

    Ancyla nitida Friese, 1902: 105; ♂; Armenien. Lectotype ♂, Kasikoporan, Russ. Armenien [Turkey: Kars, Kazkoparan, 40° 02′ N 43° 26′ E], designated by Warncke (1979: 188), MNHUB.

    Ancyla nitida var. *nigricornis* Friese, 1902: 106; ♂; Griechenland.
        Holotype ♂ MNHUB.

Ancyla cretensis Friese, 1902

    Ancyla cretensis Friese, 1902: 106; ♀; Kreta (Griechenland). Holotype ♀ MNHUB.
    Ancyla cretensis kilikia Warncke, 1979: 189; ♀♂; Türkei: Tarsus.
        Holotype ♀, 1886 (*Korb*), OLL (Warncke Collection). Insufficiently distinguished by Warncke from *cretensis*, known to him only from the holotype: syn. nov.

Ancyla asiatica Friese, 1922

    Ancyla asiatica Friese, 1922: 66; ♀; von Beirut (Syrien) ... und von Kleinasien. Described from two syntypes. LECTOTYPE, by present designation, the ♀ from 'Kleinasien', which agrees better with Friese's description. MNHUB.

    [*Plistotrichia flavilabris*, Lucas, Morawitz, 1874: 135, ♂, ?♀; misidentification.]
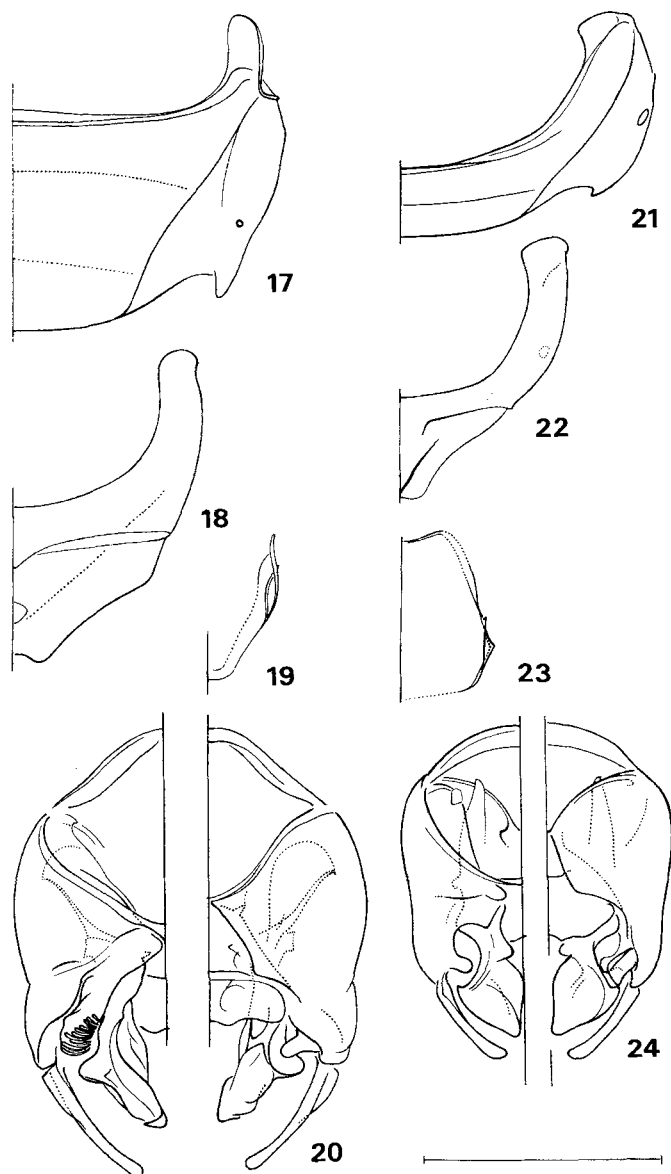
FIGS 17–24.   (17–19), (21–23) Terga 6, 7 and 8 in ♂♂ of (17–19) *Tarsalia ancyliformis mediterranea* Pitt., 1950 [Cyprus: Cherkes, 23 vii 1951 (*G. A. Mavromoustakis*). Preparation 22/2180]; (21–23) *Ancyla holtzi* Fr., 1902 [Turkey. Preparation 21/0000]. (20, 24) ♂ genitalia (right half, in ventral, left, and dorsal, right, aspects) of (20) *Tarsalia ancyliformis mediterranea* Pitt., 1950 [Sardinia: Torralba, 19 viii 1957 (*E. Priesner*). Preparation 2181.]; (24) *Ancyla holtzi* Fr., 1902 [Turkey. Preparation 21/0000]. Scale line represents 1 mm.

[The species may be found in collections under a manuscript name *melanopogon*.]

Material examined. Adana, 21 vi [year ?], 1♂; Adana, '7.8' [7 viii ?], 1♀; Adana, viii, 4♂ 3♀ (all MNHNP, Coll. J. Vachal 1911).
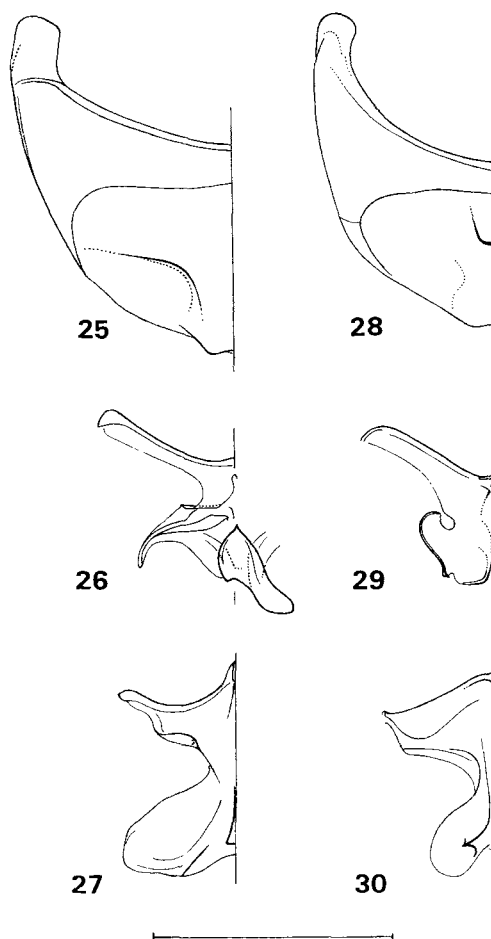
FIGS 25–30.   Sterna 6, 7 and 8 of ♂♂ of (25–27) *Tarsalia ancyliformis mediterranea* Pitt., 1950 [Sardinia: Torralba, 19 viii 1957 (*E. Priesner*). Preparation 2181.]; (28–30) *Ancyla holtzi* Fr., 1902 [Turkey. Preparation 21/0000]. Scale line represents 1 mm.

Ancyla stolli Friese, 1922
   Ancyla stolli Friese, 1922: 66; ♂; Beirut in Syrien. Holotype ♂ MNHUB.

Ancyla orientalica Warncke, 1979
   Ancyla orientalica Warncke, 1979: 185, 187 (in keys), 190; ♀♂; Banias/Syrien. Holotype ♂, Banias, Syrien, 13 vii 1953 (*Schmidt*), OLL (Warncke Collection).
   [*Ancyla lyrata* Baker MS holotype ♂ Adana, viii [year?] [MNHNP, Coll. J. Vachal, 1911]. Warncke saw material in MNHNP [Adana, viii; 3♂♂] labelled by the present author as *lyrata* and published the species as *orientalica*. The MS name is listed here since material may be found standing under that name in collections.]

Taxonomy of *Tarsalia*

Tarsalia Morawitz, 1895

Tarsalia Morawitz, 1895: 9; type species *Tarsalia hirtipes* Morawitz, 1895 (monobasic).

Tarsalia hirtipes Morawitz, 1895
   Tarsalia hirtipes Morawitz, 1895: 9; ♀♂; bei Surabad.

Tarsalia hirtipes cypriaca Mavromoustakis, 1952: 840; ♀♂; Cyprus: Charkes [for Cherkes].
[*T. h. cypriaca* may be found in collections variously determined by Mavromoustakis as
'*Anthophora cypriaca* Fr.' or '*Tetralonia cypriaca* mihi' or '*Tarsalia cypriaca* Mavr.': the
name was originally a manuscript name proposed by Friese.]

The species, although described in a paper entitled 'Beitrag zur Bienenfauna Turkmeniens',
was collected by Glazunov in Iran (Surabad = Zūrābād, 35° 43′ N 61° 05′ E) [For a note on
Glazunov's travels *vide* Semenov-Tian-Shansky, 1914.] For no very apparent reason, Warncke
(1979: 194) identified Surabad with 'Salehabad', ignoring the fact that there are numerous
places of that name (Şālehābād) in Iran, none of them, according to the USBGN Gazetteeer
(Official, 1956: 462), with coordinates similar to those of Zūrābād.

Tarsalia cellularis (Cameron, 1898)
    Anthophora cellularis Cameron, 1898: 80; ♂; [India:] Poona. Holotype ♂, labelled
        '*Anthophora Cellularis* Cam. type Poona', B.M. Type Hym. 17 b 622, BMNH. Comb. nov.
    '*Anthophora* or *Amegilla*' *cellularis* Cameron, Brooks, 1988: 450.

    Figures 31–33, 37.

Descriptive notes.   Ocelli of normal proportions; POL : OOL = 1 : 0·58; lateral ocelli
separated from vertex by slightly more than their own diameter; third antennal
segment longer than broad, as 1 : 0·82; lengths of third and fourth antennal segments
as 1 : 1·12. Femur III slightly inflated. T7 without gradular teeth. S6 acute, narrowly
rounded at apex, rostrate, with fine median carina. S7, S8: figures 31, 32. Genitalia
(figure 33) with spatha present, well-developed; external margins of gonocoxites
divergent apicad; gonostyli slender, elongate, slightly shorter than distance from
point of insertion to basal extremity of gonocoxite. Hair of mesoscutum short, erect,
strongly plumose (vestiture in holotype extensively abraded); fasciae of marginal
areas of terga of appressed plumose hairs, diverging from margin mesad, all entire.
Facial markings: figure 37.

Tarsalia mimetes (Cockerell, 1933)
    Tetraloniella mimetes Cockerell, 1933: 135; ♀; Sudan: Nuri [? Nūrī, Northern
        Province, 18° 33′ N 31° 54′ E]. Holotype ♀, Nuri, 25·5.[19]10 (*H. H. King*), B.M.
        Type Hym. 17 b 871, BMNH. Comb. nov.
    Tetraloniella mimetes Ckll, Cockerell, 1937: 284.

    Figure 41.

Descriptive notes. Ocelli enlarged; POL : OOL = 1 : 1; lateral ocelli separated from
vertex by less than their own diameter; third antennal segment elongate, slender,
length : breadth as 1 : 0·46; lengths of third and fourth antennal segments as 1 : 0·46.
Hair of mesoscutum short, subsquamiform, subdecumbent; tergal fasciae filling
marginal areas, entire on T3–T5, interrupted in median half on T2, reduced to
lateral patches confluent with those of disc on T1; a metasomal scopa well developed
on S2–5, lax, of long, apically spirate, hairs. Facial markings: figure 41.

    Additional record. Egypt: Qena [Qinā], 8 vi 1916 (*Adair*), ♀.

Tarsalia ancyliformis Popov, 1935
    Tarsalia ancyliformis Popov, 1935: 400, figure 16–18; ♀♂; Kuljab, Tadzhikistan.
        Type depository not indicated.
    Tarsalia ancyliformis mediterranea Pittioni, 1950: 74; ♂♀; [Cyprus:] Paphos-
        Yeroskipos. Syntypes ZMUH.
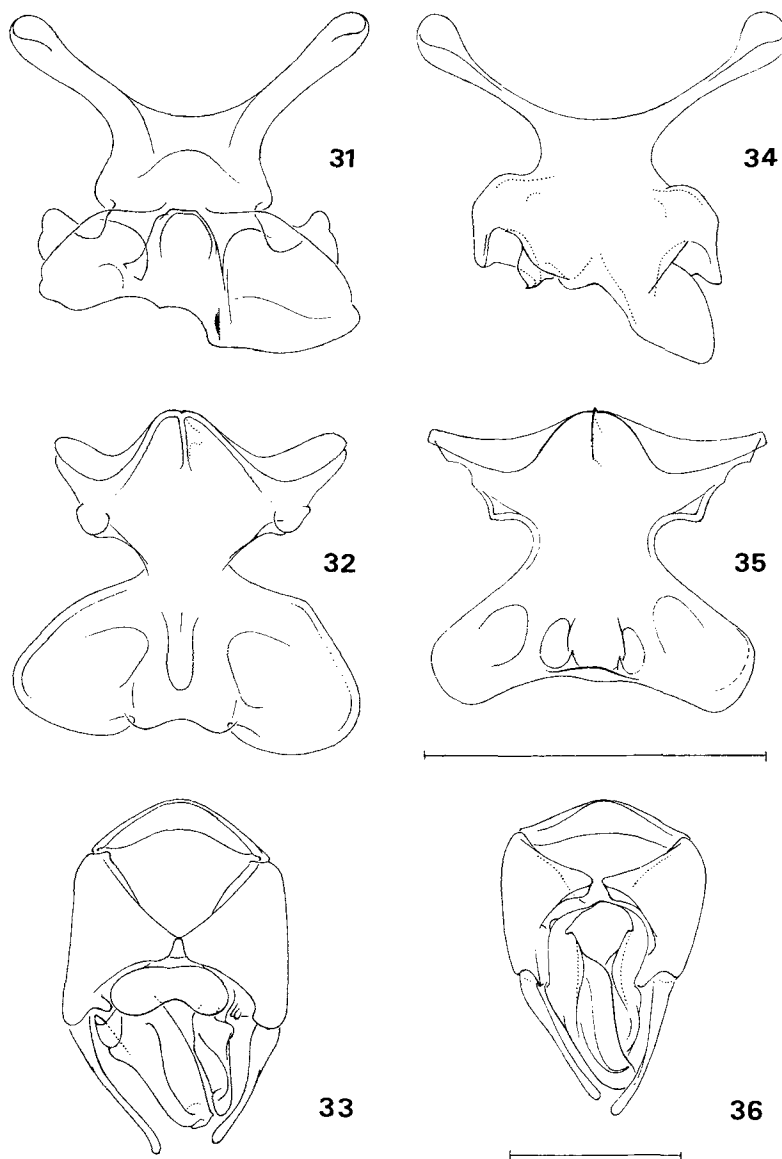
FIGS 31–36. Sterna 7 and 8 in ventral aspect and genitalia in dorsal aspect in ♂♂ of (31–33) *Tarsalia cellularis* (Cam., 1898) [holotype]; (34–36) *T. strobilanthae* sp. nov. [34, 35 paratype, 36 holotype]. Scale lines represents 1 mm (lower line for figure 33, 36).

[*T. a. mediterranea* may be found in collections determined by Mavromoustakis as '*Tetralonia pyriformis* Fr.'.]
Tarsalia ancyliformis Popov, Baker, 1972: figure 1–3.

Figures 1–3, 5–7, 11, 12, 17–20, 25–27.

Tarsalia deccana Baker, 1972
Tarsalia deccana Baker, 1972: 246, figure 4–6; ♂; South India: Pondicherry State, Karikal. Holotype ♂ DBB.

D. B. Baker
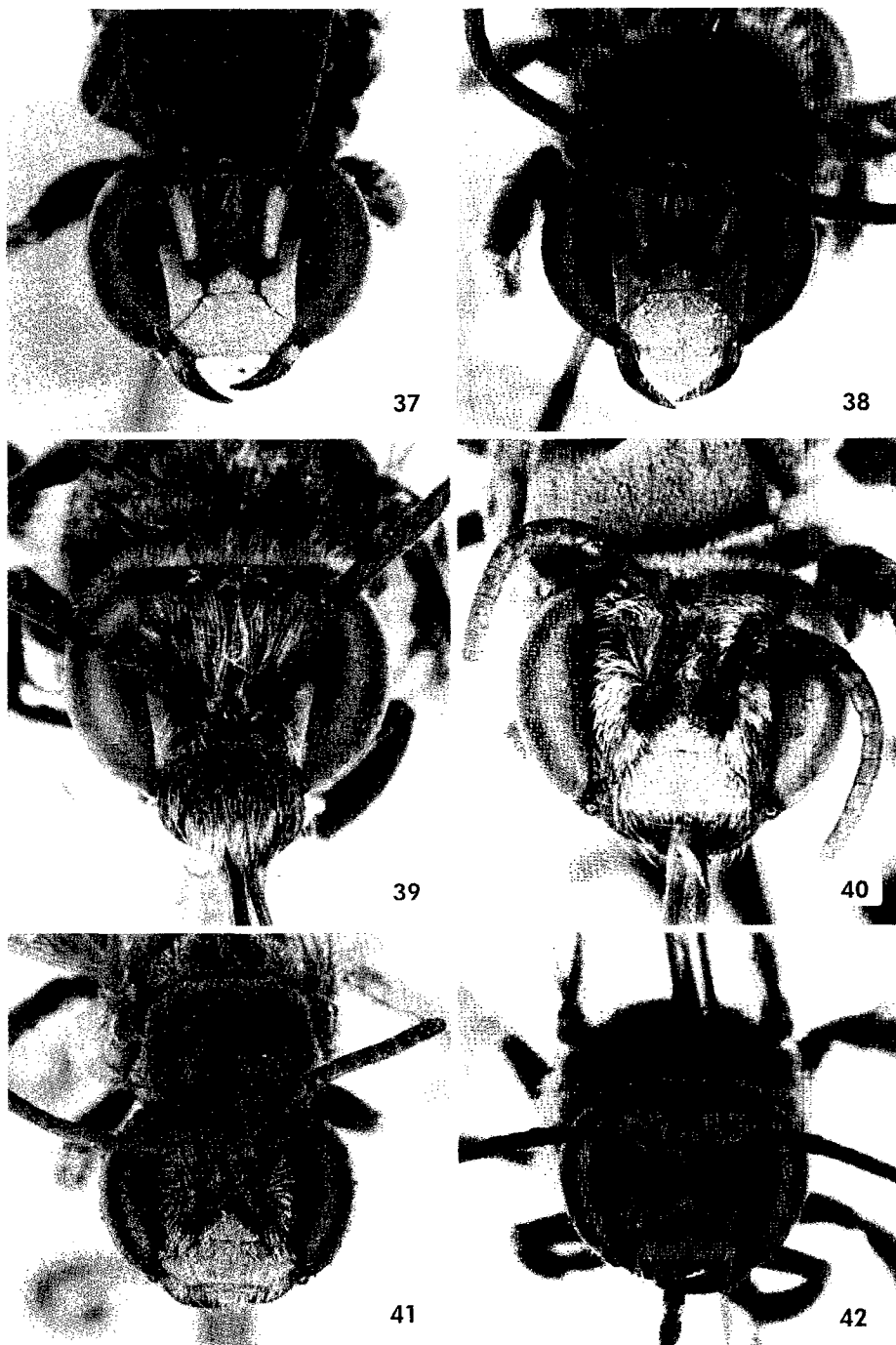
FIGS 37–42.   Faces of ♂♂ of (37) *Tarsalia cellularis* (Cam., 1898), [holotype] [Neg. 152·08]; (38) *T. deccana* Baker, 1972 [holotype] [Neg. 152·11]; (39) *T. strobilanthae* sp. nov. [paratype] [Neg. 152·01]. Faces of ♀♀ of (40) *T. persica* (Wncke, 1979) [Iran: Malāvi] [Neg. 152·14]; (41) *T. mimetes* (Ckll, 1933) [Egypt: Qena] [Neg. 152·17]; (42) *T. sp.* [W. India: W. Ghats, Lonavla: *vide* text under *deccana*] [Neg. 152·05]. All figures to same scale.

Figure 38.

Additional record: A small ♀ *Tarsalia* taken by Father Wain in western India [W. Ghats, Lonavla, 650m, 2 iii (two ex.) and 4 iii 1970 (one ex.), all at *Blumea*, UMNHO/DBB] may, on account of its size (5·5 mm) be referred here rather than to the larger species *strobilanthae*, where also the facial markings (figure 39) would be anomalous (more extensive in ♀ than in ♂). The white tergal fasciae are broad, filling the marginal areas, entire on T3–5, interrupted in median third on T2, reduced to short lateral vittae on T1. While a well-developed metasomal scopa is not present (cf. *mimetes*), sterna 2–5 are clothed with simple (at 37·5 ×) hairs that become much longer, and then apically crinkled, towards the apex of each sternum, and these hairs, especially, do carry pollen (presumably, in the specimens examined, that of *Blumea*).

Blumea is a member of the Asteraceae, on which family, from Popov's records for *hirtipes* and *ancyliformis* (1967: 269) and from other observations, *Tarsalia* would appear to be virtually monolectic. Unfortunately the flower-visiting habits of the other Indian *Tarsalia* are unrecorded, apart from male *strobilanthae*.

Tarsalia persica (Warncke, 1979)
  Ancyla persica Warncke, 1979: 185, 186 (in keys), 192; ♀♂; [Iran:] Haft Tapeh [Tappeh], 300 km N di Abadan (Khuzestan). Holotype ♀, Haft Tapeh, 300 km N di Abadan/Khuzestan, 30.6–1.7.1965 (*Giordani Soika* and *Mavromoustakis*), OLL (Warncke Collection). Comb. nov.
  [The species may be found in collections (Karaj *et al.*) under the earlier manuscript name *pulchra* Baker.]

Figure 40.

Additional record: Iran: Khuūzestān, Melavy [probably Malāvī, on Ahvāz road c. 60 km SW of Khorramābād], 8 vi 1966 (*S. Tirgari*).

Tarsalia strobilanthae sp. nov.

Figures 15, 34–36, 39

Etymology
  From *Strobilanthes*, at which the type material was collected by Father Wain. *Strobilanthes* (Acanthaceae) is a large genus of herbs and small shrubs, mostly from warm parts of Asia, some cultivated either for the blossom or the foliage (Bailey, 1949: 918).

Diagnosis
  T. strobilanthae is immediately distinguished, in the male, from other species by the unusual facial markings, broad paraocular vittae but no other parts of the face being yellow (figure 39).

Description

Male (female not known). Length c. 8·5 mm, forewing 6·6 mm.

Head.   Ocelli of normal proportions; POL:OOL = 1:0·74; lateral ocelli separated from vertex by slightly less than their own diameter. Third antennal segment longer than broad, as 1:0·72; lengths of third and fourth antennal segments as 1:0·74.

Mesosoma.   Basal area of propodeum not defined. Legs without special characters. Basitarsus II elongate, slightly curved, the tibial calcar reaching to about its mid-point. Femur III little thicker than femur II.

Metasoma.   T1 dorsally with weak carina separating anterior and dorsal surfaces. T2–6 with progressively weaker postgradular sulci; marginal areas broad but only weakly differentiated, widening mesad. T7 (figure 15) with rounded, deflexed apex and well-developed gradular teeth. S1–5 without special characters. S6 acute, apically narrowly rounded, rostrate, the marginal area concave on either side to form a strong, median, weakly sulcate ridge; dorsally with small pre-apical tubercle. S7 (figure 34) strongly asymmetric, the large apico-lateral lobe of the right side represented on the left by a much smaller and differently formed process; S8 (figure 35) weakly asymmetric [N.B. Both S7 and S8 drawn in ventral aspect.] Genitalia (figure 36) asymmetric: gonocoxites with outer margins convergent apicad, apically with well-developed inner lobes; gonostyli slender, elongate, slightly longer than distance from point of insertion to basal extremity of gonocoxite; *spatha absent*; penis valves inflated basally and, in lateral aspect, rising slightly above dorsum of gonocoxites, that of right side much reduced.

Integument.   Punctation of supra-antennal area fine and reticulate beneath the ocelli, becoming coarser, spaced and oblique towards the antennal sockets; of supraclypeal area coarser, shallow and irregular; of clypeus shallow, irregular, subreticulate; the area of the yellow paraocular markings nearly impunctate, glossy. Punctation of mesoscutum simple, moderately strong, dense, subreticulate, the interspaces glossy; of terga similar but less dense, finer on marginal areas, the extreme margins narrowly impunctate on basal terga but becoming successively more widely so. Sterna 2–4 more coarsely but less densely punctate with broadly impunctate marginal areas.

Vestiture.   (Partially abraded in both examples.) The body generally thinly clothed with grey pubescence, short and erect on terga 2–5, sparse on sterna 2–5 except laterally where there are longer hairs. Terga 1–5 with narrow fasciae of appressed plumose hairs confined to the base of the marginal areas and consequently diverging from the margin mesad, on T1 reduced to lateral vittae, on T2 obsolecent medially. Hair of inner face of basitarsi III fuscous.

Colour.   Black, the paraocular areas with yellow vittae (figure 39) [in the paratype, the labrum with a small, indistinct apical macula]; apices of mandibles and tegulae castaneous.

Type material

HOLOTYPE ♂ labelled 'S. India [print]/Kankan [Konkan]/Matheran/730m./19 i 1965//[on reverse] 711/at *Strobilanthes* [all MS]/F. L. Wain [print]. SFS. PARATYPE ♂ India: Konkan, Matheran, 21 i 1965/on *Strobilanthes* sp. [*F. L. Wain*]. UMNHO.

Comment

T. strobilanthae is the third *Tarsalia* to become known from India. The three or four Indian species, in contrast to the non-Indian species, which all inhabit more or

less strongly xeric biotopes, are inhabitants of areas variously categorized in maps of natural vegetation as monsoon forest or monsoon tropophilous woodland/open jungle. On the unusual nature of the type locality, Matheran, where the rainfall is very heavy, see Longstaff 1912: 389–390.

Separation of the species

Of the species listed above, only two, *hirtipes*, readily distinguished by its relatively large size (both sexes exceeding 10 mm), and *ancyliformis*, are represented in the available material by adequate material of both sexes. In the males of these two species the dorsal surface of T7 is sharply marginate laterad, forming a distinct, apically concavo-truncate pygidial area. For *ancyliformis*, good descriptions and figures of both sexes are given by Popov (1935) and the concealed sterna and genitalia are also figured in the present paper (figures 20, 25–27).

Of the other species, three, *cellularis*, *deccana* and *strobilanthae*, are represented only by males, two, *mimetes* and *persica* (and a possible third: see text, under *deccana*), only by females. The three Indian males are readily separable by their facial markings (figures 37–39), confirmed by examination of the concealed sterna and the genitalia (*cellularis*, figures 31–33; *deccana*, Baker, 1972, figures 4–6; *strobilanthae*, figures 34–36). In *strobilanthae* T7 bears gradular teeth (figure 15). The females of the Iranian *persica* and the NE African *mimetes* are separable by their facial markings (figures 40, 41); *persica* is additionally immediately distinguished by the dense, short, appressed, squamiform, hair of the mesoscutum, *mimetes* by the exceptionally well-developed metasomal scopa.

Annex A On the systematic position of *Tetralonia brevipennis* Cameron, 1898

Tetraloniella brevipennis (Cameron, 1898) **comb. nov.**

 Tetralonia brevipennis Cameron, 1898: 78, pl. 4 fig. 6; ♀; [India: Uttar Pradesh,] Allahabad. Holotype ♀, labelled '*Wroughtonia brevipennis* Cam. type. Allahabad' [Cameron's hand], UMNHO (not registered).

 [*Tetralonia ruficornis* (F.), Dover (1925: 225): false synonymy based on misidentified material of a *Tetraloniella* species in BM(NH).]

Cameron apparently intended originally to describe *brevipennis* under a new generic name *Wroughtonia*: 'As Mr Rothney's ♀ [*brevipennis*] differs in many respects from Mr. Wroughton's male [*Tetralonia punctata* Cameron, 1898: 79, Poona (*Wroughton*), = *Tetraloniella aliena* Cockerell, 1911, **syn. nov.**] and from the described genera, I give a generic description of it here', and labelled his type accordingly. However, *brevipennis* was published under the generic name *Tetralonia* and Cameron subsequently (1899: 56) used the name *Wroughtonia* for another insect (*Wroughtonia cornuta* Cameron, Braconidae, Helconini).

Cameron's figure (6) portrays well the curious habitus of the species (the wings, frayed and incomplete in the type, are restored in the drawing), although the volume of the scopa, suggesting *Tarsalia*, is a little exaggerated. The mouthparts of the type, removed by Cameron for description and illustration, are lost. They were described by Cameron as follows: 'Tongue [glossa] not elongate, if anything shorter than the palpi; the apex ending in a button [flabellum]; paraglossæ a little longer than the tongue; densely pilose; the two basal [labial] palpal joints greatly enlarged and thickened; the basal slightly longer than the second; the apical two joints of nearly equal length. The stipes [maxilla] longer and broader than the galea by about one-

fourth; the top on the inner side rounded inwardly and fringed with long, stout, stiff hairs; the first and third joints of the [maxillary] palpi are nearly equal in length; the fourth is slightly shorter; the second is the longest'.

From examination of the type, which is in poor condition, and from Cameron's description and figures of the mouthparts, it is clear that *brevipennis* is a eucerine nearly related to *Tetraloniella*, but differing in the short mouthparts (which it shares with *Ancyla*, although the paraglossæ are relatively long), reduced maxillary palpi and short wings. Superficially and in many details it resembles, among the numerous unpublished small SW Asian *Tetraloniella*, a species known from Saudi Arabia and Qatar, but in that species the mouthparts are normal for the genus and the head bears yellow integumentary markings. Cameron obviously had reason to question the generic placement of *brevipennis*, a question that cannot be resolved pending discovery of the male. Provisionally, the species is treated as an anomalous *Tetraloniella*.

The following notes on the type may be added to the original description: head transverse; inner orbits slightly convergent anteriorly; clypeus short, in frontal aspect projecting little below anterior extremity of eyes; labrum short; mandibles blunt; forewing (wings in type ragged and apices of both forewings lost) with marginal cell apparently slightly longer than distance from its apex to wingtip, broader than submarginals and rather broadly rounded at apex; hindwing with second abscissa of M + Cu approximately equal to M; tibia III internally with area of keirotrichia vestigial and the hair clothing otherwise nearly uniform, the hairs appearing similar to but longer and more slender than those of the external surface of the tibial scopa; scopa moderately dense, the hairs stiff, not branched but at 60 × appearing roughened (leg LIII at some time broken off and crudely re-attached); marginal areas of terga punctate; pygidial area rather broadly rounded apically, its lateral margins concave, flaring basad.

Annex B On *Melissina* and *Glazunovia* (Anthophoridae: Eucerini)

Melissina and *Glazunovia*, **gen. nov.**, are two little-known monotypic genera of eucerine bees, the former known only from Pakistan, the latter more widely distributed in Central Asia, Anatolia and Iran. While they differ in a number of characters (table 1: the list is not exhaustive), they share the following:-

Clypeus little protuberant in lateral aspect, not or scarcely produced beyond lower orbits in frontal aspect; malar area rudimentary.

Male antennae elongate, but scape short and inflated and A3 less than 1/5 length of succeeding segments.

Radial cell exceptionally broad (figures 47, 48).

Legs simple (frequently modified in *Eucera* and other eucerines).

Opposed faces of male femur and tibia II without specialized pubescence (modified in *Synhalonia*).

Female basitibial plate present.

Male pygidial plate present.

Male S7 with deep apical emargination (figure 52, *Melissina*; Popov, 1962, figure 4, *Glazunovia*).

Male S8 of typical eucerine form (figure 53, *Melissina*; Popov, 1962, figure 5, *Glazunovia*).

Table 1.   Differences between *Melissina* and *Glazunovia*.

Melissina	*Glazunovia*
Head	
head ($\male$) strongly transverse, length:width ratio 1:1·7	head ($\male$) less transverse, length:width ratio 1:1·5
gena narrow, <0·5 width eye	gena wide, >0·5 width eye
clypeal margin laterally gently curved to rear	clypeal margin laterally abruptly curved to rear
ocelli enlarged, touching ($\female$) or nearly touching ($\male$) occipital ridge	ocelli not enlarged, separated from occipital ridge by about their diameter
$\female$ antenna slender, A3–A12 all longer than wide	$\female$ antenna thick, A3 longer than wide, A5–A11 all transverse
maxillary palpi 4-segmented	maxillary palpi 5-segmented
Mesosoma	
basal area of propodeum ($\female$) defined, weakly coriaceous, glabrous	basal area of propodeum ($\female$) ill-defined, glossy, glabrous
stigma shorter than prestigma but more than half its length, abruptly contracted beyond origin of r (figure 47)	stigma much shorter than prestigma, about half its length, the base of the marginal cell rounded (figure 48)
length:width marginal cell 1:0·34	length:width marginal cell 1:0·28
marginal cell broader in relation to submarginal cells, twice as broad as length of 1r-m	marginal cell narrower
2r-m and 2m-cu interstitial on M	2m-cu received by M before 2r-m
hindwing m-cu very oblique, forming an angle of about 45° with 1st abscissa of M + Cu, more than half as long as 2nd abscissa	hindwing m-cu nearly perpendicular to 1st abscissa of M + Cu, less than half as long as 2nd abscissa
Metasoma	
T1 with transition between anterior and dorsal surfaces convex, not sharply defined	T1 with transition between anterior and dorsal surfaces abrupt, carinate
T7 with lateral flanges overlapping base of pygidial plate (figure 51)	T7 not thus modified
S6 with median sulcus and sublateral carinae	S6 not sulcate; sublateral carinae obsolete
S7: figure 52	S7: Popov, 1962: figure 4
gonostylus elongate, slender, geniculate, apically inflected (figures 54, 55)	gonostylus short, broad, not geniculate (Popov, 1962: figures 6, 7)
apical margin of spatha with lateral emarginations (figure 54)	apical margin of spatha with median incision (Popov, 1962: figure 6)
penis valves with slightly retrorse, more acute lateral lobes and strong, subtriangular, inner dorsal lobe (figure 54)	penis valves with broader lateral lobes and weak inner dorsal lobe (Popov, 1962, figure 6)
Integument	
dull, finely, densely punctate	relatively coarsely, the mesoscutum in $\female$ irregularly, punctate
$\male$ clypeus, labrum and base of mandibles yellow; $\female$ with apex of clypeus broadly, labrum, and base of mandibles obscurely, yellow	face in both sexes black

Table 1.   (*continued*).

Melissina	*Glazunovia*
Vestiture	
♀ clypeus with long, moderately dense, semi-decumbent hair	♀ clypeus with short, sparse, fine, erect, inconspicuous hair
mesoscutum in both sexes uniformly pubescent	mesonotum anteriorly in both sexes with conspicuous ruff of long, erect, plumose hairs, posteriorly in ♀ glabrous, in ♂ thinly pubescent
tegulae (♂) densely pubescent throughout, (♀) partially bare (abraded?)	tegulae largely bare
♀ scopal hairs finely plumose	♀ scopal hairs coarsely plumose
♀ keirotrichia restricted to a narrow zone in apical half of tibia III	♀ keirotrichia absent, posterior face of tibia III uniformly clothed with long, simple (at 25 ×) hairs
T1 ♀ except marginal area with dense, long, erect hair (figure 45)	T1 ♀ with anterior face thinly clothed with short, erect hair, the dorsal surface with sparse, longer hairs
T2 ♀ with broad fascia filling whole of disc apart from marginal area (figure 45)	T2 ♀ with narrow postgradular fascia
T3 ♀ with broad fascia filling whole of disc apart from marginal area	T3 ♀ with postgradular and marginal fasciae, the disc otherwise bare

Melissina Cockerell, 1911
(Figures 43–47, 51–55)

Melissina Cockerell, 1911: 670; type species *Melissina viator* Cockerell, 1911 (monobasic and implicit in original designation).

Included species. Melissina viator Ckll, 1911: 670; ♀♂; Karachi, N.W. India.

The ♀ in NHML labelled by Cockerell as 'type', B.M. Type Hym. 17 b 868, labelled 'E. Comber/Karachi [print] Aug 09 [MS]', 'Bombay Presidency./pres. by E. Comber./1910–255.' [B.M. printed label], and '*Melissina/viator* Ckll/Type' [MS], is now designated as Lectotype. The size of the type series is not known, but Cockerell evidently saw two or more females: 'The following description of the mouthparts is taken from a female of the type species'. The female on which his description and measurements of the mouthparts were based was possibly retained by him.

Diagnostic notes. The enlarged ocelli, 4-segmented maxillary palpi, short stigma and broad radial cell are distinctive. There is a curious error in Cockerell's description: 'It [*Melissina*] differs at once from *Cubitalia*, Friese, which resembles it in the five-jointed maxillary palpi', a correct description being given, however, a few lines below. Characters shared with *Glazunovia* are indicated above, differences in table 1. The species has not previously been figured.

Glazunovia gen. nov.
(Figures 48–50; Popov, 1962, figures 1–7)

Glazunovia
  [*Melissina* Ckll, Popov, 1962; misidentification.] Popov was presumably misled in referring *nigriceps* to *Melissina* by the exceptionally broad marginal cell shared with that genus, and by Cockerell's inadequate description.
  [*Melissina* Ckll, Pesenko and Sitdikov, 1988, *p.p.*; misidentification]
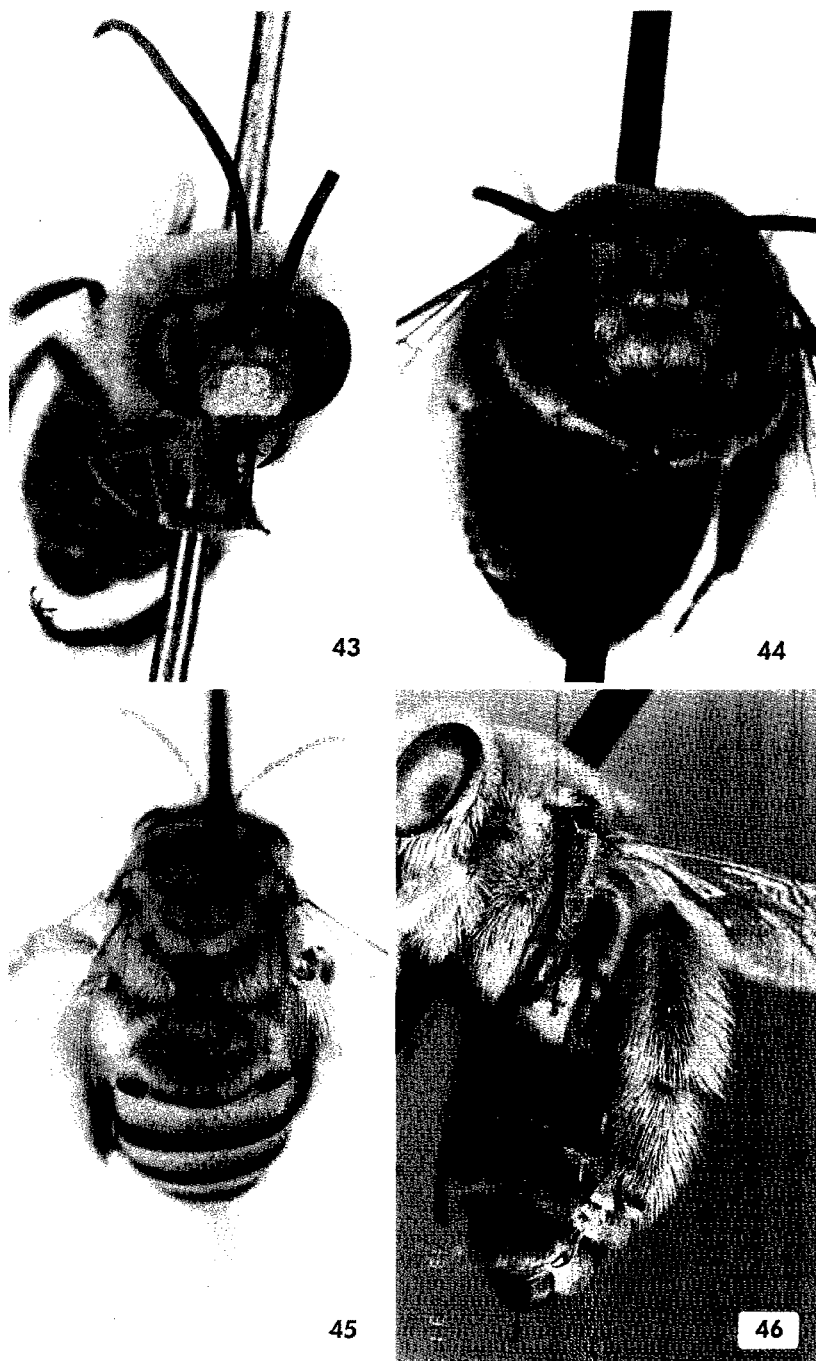
FIGS 43–46.   *Melissina viator* Ckll, 1911. 43, head of ♂ [paratype, Pakistan: Karachi, vi 1909 (*E. Comber*), BMNH] [Neg. 133·20]. (44–46) ♀ [Pakistan: Karachi]: (44) head [Neg. 133·21]; (45) habitus, dorsal [Neg. 133·22]; habitus, lateral, to show scopa [Neg. 135·20].

47   **48**

49   **50**

FIGS 47–50.   (47) *Melissina viator* Ckll, 1911, ♀ [Pakistan: Karachi], forewing [Neg. 134·01].
48–50. *Glazunovia nigriceps* (Mor., 1895): (48) forewing [♀, Turkey: Çankırı, Ilgaz
(village), 22 vii 1962 (*Guichard and Harvey*)] [Neg. 134·09]; (49) habitus [♀, Tajikistan:
Dushanbe, 10 vii 1943 (*V. V. Popov*)] [Neg. 134·13]; (50) head [♀, Turkey: same
specimen as figure 48] [Neg. 134·15].
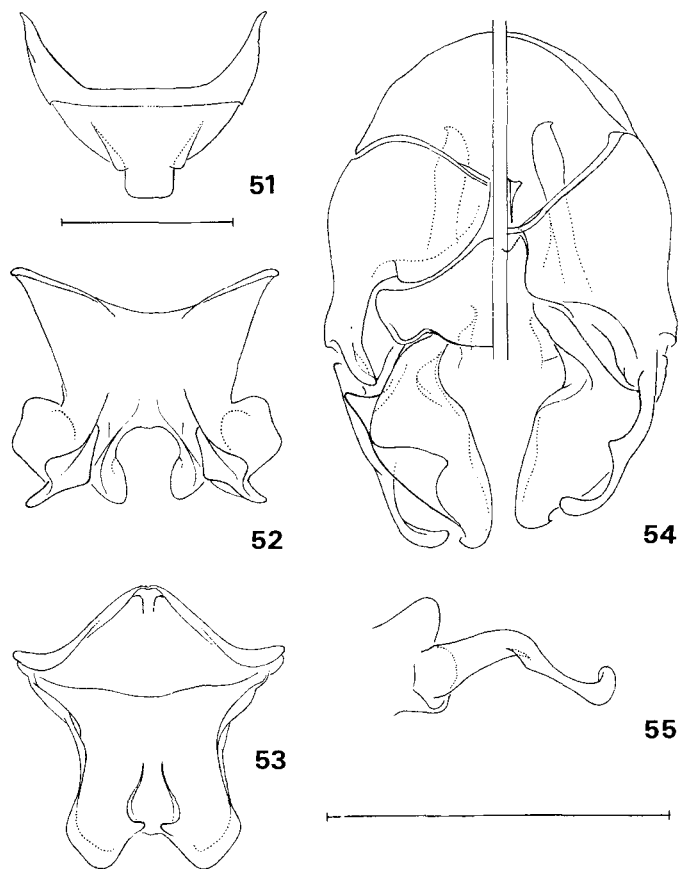
FIGS 51–55. *Melissina viator* Ckll, 1911, ♂ [paralectotype, Pakistan: Karachi, vi 1909 (*E. Comber*), BMNH]: (51) tergum 7; (52) sternum 7, ventral aspect; (53) sternum 8, ventral aspect; (54) genitalia, dorsal and ventral aspects; (55) gonostylus, lateral aspect. Scale lines represent 1 mm.

Etymology
    Glazunov, Dmitry Konstantinovich (1869–1913), who collected the type material of *nigriceps*.

Type species.   Tetralonia nigriceps Morawitz, 1895.

Included species.
Glazunovia nigriceps (Morawitz, 1895)
    Tetralonia nigriceps Mor., 1895: 12; ♀♂; [Turkmenistan:] Surabad.
    Melissina nigriceps (Mor.) Popov, 1962: 294.

Diagnostic notes. The short stigma, broad radial cell, and the peculiar thoracic ruff are distinctive. The type species was well described by Morawitz.

Additional records. Popov listed localities in Turkmenistan, Tajikistan and Uzbekistan. Material collected by Popov at Stalinabad [Dushanbe] (Botanical

Gardens), 10 vii 1943, at *Centaurea calcitrapa* L., has been examined. The range of the species extends to Anatolia and Iran: **Turkey**: Çankırı, Ilgaz (village), 900m, 22 vii 1962 (*Guichard and Harvey*), B.M. 1962–299 [Guichard and Harvey (1967: 236) noted: 'Roosting Hymenoptera on standing corn at evening']; **Iran:** Damavand, vii 1964, at Compositae (*Tirgari* ?); Pasargadae, 24 vi 1971 (*Cottrill and Tremewan*).

Abbreviations

Collections
BMNH	Natural History Museum, London [formerly British Museum (Natural History)]
DBB	D. B. Baker, Ewell.
MNHNP	Musée National d'Histoire Naturelle, Paris.
MNHUB	Museum für Naturkunde der Humboldt-Universität zu Berlin.
OLL	Oberösterreichisches Landesmuseum, Linz.
SFS	The late Professor S. F. Sakagami, private collection (permanent location not known).
UMNHO	University Museum of Natural History, Oxford.
ZMUH	Zoologiska Muset, Universitets Helsinki.

Morphology
A1, A2 etc	Antennal segments
LP; LP1, LP2 etc	Labial palpus; segments
MP; MP1, MP2 etc	Maxillary palpus; segments
LI, II, III: RI, II, III	Left/right anterior, intermediate, posterior legs
T1, T2 etc	Metasomal terga
S1, S2 etc	Metasomal sterna

Acknowledgements

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Appendix 1   Characters and character-states

Head

(01) ♂ head shape in lateral aspect: 0 oblong; 1 lenticular.

(02) ♂ vertex between compound eye and lateral ocellus: 0 flat or weakly concave; 1 concave.

(03) ♂ inner orbits: 0 parallel or subparallel; 1 markedly convergent anteriorly; 2 markedly divergent anteriorly.

(04) c clypeus shape in lateral aspect: 0 not or little protuberant; 1 moderately protuberant; 2 strongly protuberant.

(05) c clypeus length in frontal aspect: 0 not produced beyond lower orbits; 1 moderately produced; 2 strongly produced.

(06) c clypeus apical margin: 0 evenly convex or nearly so; 1 laterally curved more strongly to rear; 2 laterally bent abruptly to rear.

(07) c malar space: 0 rudimentary; 1 developed.

(08) c basal tubercle of labrum: 0 present; 1 absent.

(09) ♀ mandibular apex: 0 narrowly rounded; 1 broadly truncate.

(10) ♂ antenna length: 0 normal; 1 elongate.

(11) ♂ A1 (scape): 0 slender, elongate; 1 inflated, short.

(12) ♂ A1 maculation: 0 absent; 1 present.

(13) ♂ A3 (1st flagellar segment) proportions: 0 longer than apical width; 1 quadrate; 2 transverse.

(14) ♂ A3/A4 relative lengths: 0 A3 distinctly longer than A4; 1 A3 and A4 equal or subequal; 2 A3 distinctly shorter than A4; 3 A3 shorter than 0·33 length A4.

(15) ♂ A4–8 shape: 0 simple, cylindrical; 1 tuberculate.

(16) c mouthparts: 0 short; 1 elongate.

(17) c galea: 0 broad near base, then attenuate; 1 tapering evenly to apex.

(18) c maxillary palpus segments (number): 0 6; 1 5; 2 4.

(19) c palpi relative lengths: 0 MP and LP of about equal length; 1 MP
          much shorter than LP.

(20) c LP shape: 0 segments of similar form; 1 LP1, LP2 long, expanded;
          LP3, LP4 minute.

(21) c LP length: 0 equal to or longer than prementum; 1 shorter than
          prementum.

(22) c LP1 length: 0 little shorter than prementum, longer than succeeding
          segments combined; 1 much shorter than prementum, about equal
          to succeeding segments combined.

(23) c LP3 insertion: 0 LP3 and LP4 collinear with LP1 and LP2; 1 LP3 and
          LP4 divergent, LP3 inserted laterally near apex of LP2.

(24) c paraglossa length: 0 not attaining apex of LP1; 1 extending to about
          mid-point of LP2; 2 exceeding LP.

(25) c glossa length: 0 not longer than prementum; 1 longer than prementum.

(26) ♂ maculation: 0 absent; 1 clypeus; 2 clypeus and paraocular area;
          3 paraocular area only.

(27) ♀ maculation: 0 absent; 1 clypeus ($\pm$ supraclypeal area).

Mesosoma

(28) c metanotum: 0 unmodified: 1 with weak transverse ridge; 2 with
          median tubercle or strong hair-tuft.

(29) c propodeum: 0 with defined subhorizontal area; 1 without.

(30) c basal area of propodeum: 0 impunctate and glabrous; 1 punctate and
          setose.

(31) c stigma width: 0 broader than distance from inner margin of prestigma
          to wing margin; 1 equal; 2 narrower. This is not an entirely
          satisfactory character since contraction in dried material may bring
          the costa and prestigma abnormally close.

(32) c stigma length: 0 equal to prestigma; 1 shorter. The stigma apically,
          whether or not there is an intermediate angulation, normally merges
          imperceptibly with R_1. The length of the stigma is therefore
          measured to the angle between the posterior margin of the stigma
          and r.

(33) c apex of R: 0 slightly divergent from wing margin; 1 more widely
          divergent.

(34) c r length: 0 distinctly shorter than length of SM2 on Rs; 1 equal or
          subequal to SM2; 2 distinctly longer than SM2.

(35) c 1r-m: 0 present; 1 lost. State 1 is characteristic of *Eucera*, but the
          venation in *Eucera* is unstable, and specimens may be found in
          which 1r-m is present, in one or both wings, giving three
          submarginal cells, and, conversely, specimens may be found in
          which the 1st abscissa of Rs [after the separation of Rs and M] is
          absent, resulting in the presence of a single submarginal cell.

(36) c convergence of 1st abscissa Rs and 1r-m: 0 weak or moderate;
          1 strong.

(37) c   SM2 length: 0 markedly shorter than SM1 or SM3 (measured on
          Rs + M/M); 1 SM1-3 subequal.
(38) c   hw jugal lobe: 0 reaching to or beyond mid-length or vannal lobe; 1
          not reaching mid-length.
(39) ♂   tarsus III: 0 normal; 1 modified. Basitarsus III is not greatly modified
          in *ancyliformis*, but, in other *Ancyla* strongly so in both form and
          vestiture.
(40) ♀   tibial scopa: 0 dense; 1 open. An open scopa with branched hairs is
          usually a specialized condition associated with the collection of large
          (>100 μ) pollen grains, e.g., those of Malvaceae.
(41) ♀   scopal hairs: 0 stiff, simple; 1 lax, plumose.
(42) ♀   zone of keirotrichia on tibia III: 0 wide, apically exceeding half width
          internal surface of tibia; 1 reduced, narrow or obsolete.
(43) ♀   basitarsal scopa: 0 of normal proportions; 1 copious, exceeding apex
          of segment.

Metasoma
(44) c   T1: 0 with distinct carina separating anterior and dorsal surfaces; 1
          carina weak or absent.
(45) ♂   T5: 0 gradular teeth absent; 1 gradular teeth present.
(46) ♂   T6: 0 gradular teeth absent; 1 gradular teeth present.
(47) ♂   T7 gradular teeth: 0 absent; 1 present.
(48) ♂   T7 pygidial plate: 0 a raised pygidial plate present; 1 a pygidial area
          defined by lateral carinae present, the apex of the tergite emarginate;
          2 a pygidial plate or area absent, apex of tergite produced, rounded.
(49) ♀   S2 gradulus: 0 normal; 1 birecurved. A birecurved gradulus is a
          synapomorphy for the Eucerini.
(50) ♂   S5: 0 unmodified; 1 with median lobe; 2 with paired median processes.
(51) ♂   S6: 0 with median basal tubercle; 1 with median carina; 2 with paired
          apico-lateral carinae.
(52) ♂   S7 lateral processes: 0 small, symmetric, strongly sclerotized, auricular;
          1 moderate, symmetric, laminar; 2 large, more or less asymmetric,
          weakly sclerotized, of variably complex form. Asymmetric apical
          sterna and genitalia appear to be a synapomorphy for *Tarsalia*, but
          it has not been possible to examine them in all species.
(53) ♂   S7 apical processes: 0 small, symmetric, not laminar; 1 larger,
          symmetric, laminar; 2 of unequal size, that of L side large,
          hypertrophied, laminar.
(54) ♂   S8 shape: 0 not constricted at mid-length, apically without spreading
          lateral lobes, symmetric; 1 strongly constricted at mid-length, with
          spreading lateral lobes not attaining width of sclerite across
          apodemes, symmetric; 2 strongly constricted at mid-length, with
          spreading lateral lobes exceeding width across apodemes, more or
          less asymmetric.
(55) ♀   metasomal scopa: 0 absent; 1 present; 2 present, strongly developed. A
          metasomal scopa is a synapomorphy for the non-parasitic
          Megachilidae, where a tibial scopa is not developed. In *Tarsalia* it is
          probably an adaptation to pollen collection from, especially,
          Asteraceae. However, *Tarsalia* retains the long mouthparts
          associated with nectar-gathering from tubular flowers.

(56) ♀ fasciae of T2–3: 0 confined to marginal areas; 1 marginal but encroaching on disc; 2 covering all or most of postgradular surfaces but not marginal areas; 3 narrow, confined to immediate postgradular areas.

(57) ♂ gonocoxite shape: 0 external margins subparallel or divergent apicad; 1 weakly convergent apicad; 2 strongly convergent apicad.

(58) ♂ gonostyli shape: 0 straight or simply curved; 1 sinuous; 2 geniculate. A geniculate gonostylus occurs randomly in the Eucerini.

(59) ♂ penis valves symmetry: 0 symmetric; 1 of L side hypertrophied.

(60) ♂ penis valves proportions: 0 normal, not inflated at base; 1 basally inflated.

(61) ♂ spatha: 0 absent; 1 present. A spatha is normally present in Anthophoridae.

Size
(62) c length: 0 < 10mm; 1 > 10 mm.

Integument
(63) c ground colour: 0 black; 1 metasoma pale castaneous; 2 integument generally pale castaneous.

Appendix 2 Matrix 1, Observed states

									1										2	
1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1
holtzi	1	0	0	0	0	0	0	0	0	0	0	1	1	2	1	0	1	0	0	0	1
hirtipe	0	0	2	1	1	1	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0
cellula	0	0	1	1	1	0	0	1	?	0	0	1	0	2	0	1	?	?	?	?	?
mimetes	?	?	?	1	1	1	0	1	0	0	0	?	?	?	0	1	?	?	?	?	?
ancylif	1	0	0	1	1	1	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0
deccana	0	0	1	1	1	0	0	1	?	0	0	1	1	1	0	1	0	0	1	1	0
persica	?	?	?	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0
strobil	1	0	1	1	1	1	0	1	?	0	0	0	0	0	0	1	?	?	?	?	?
dentata	0	1	0	2	1	0	0	1	1	1	1	0	2	3	0	1	1	1	1	1	0
longic	0	1	0	2	2	2	1	1	1	1	1	0	0	3	0	1	1	0	1	1	0
brevipe	?	?	?	0	1	1	0	1	?	?	?	?	?	?	?	0	?	2	1	1	0

								3									4		
2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
holtzi	1	0	1	0	2	0	2	0	0	0	0	0	1	0	1	1	1	1	0	1	1
hirtipe	0	1	0	1	2	0	0	1	1	1	0	0	0	0	0	1	1	0	0	1	1
cellula	?	?	?	?	2	?	0	0	1	1	1	0	2	0	1	0	1	0	?	?	?
mimetes	?	?	?	?	?	1	0	1	1	1	0	0	2	0	1	0	1	?	0	1	1
ancylif	0	1	0	1	2	1	0	1	1	2	1	1	1	0	1	0	1	0	0	1	1
deccana	0	1	0	1	2	?	0	1	1	1	1	0	1	0	1	0	0	0	?	?	1

persica	0	1	0	1	2	1	0	0	1	1	1	1	1	0	1	0	0	?	1	0	1
strobil	?	?	?	?	3	?	1	1	1	1	0	0	2	0	1	0	?	0	?	?	?
dentata	0	1	2	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1
longic	0	1	2	1	1	0	0	0	1	1	1	0	–	1	–	–	1	0	0	0	0
brevipe	1	1	1	1	?	0	0	0	0	1	1	1	1	0	0	0	0	?	0	0	1

							5										6			
3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3

holtzi	1	1	0	1	0	0	0	2	0	1	1	1	0	0	1	0	0	0	1	0	0
hirtipe	1	0	1	1	?	1	1	0	1	?	?	?	1	0	?	?	?	?	?	1	0
cellula	?	1	0	0	0	2	?	0	1	2	2	2	?	?	0	0	1	0	1	0	0
mimetes	1	1	?	?	?	?	?	?	?	?	?	?	2	0	?	?	?	?	?	0	1
ancylif	1	0	0	1	0	1	1	0	1	2	2	2	1	1	0	0	?	0	1	1	0
deccana	1	1	0	0	0	2	?	1	1	2	2	2	1	1	0	0	1	0	1	0	0
persica	1	0	?	?	?	1	1	?	?	?	?	?	1	1	?	?	?	?	?	0	2
strobil	?	0	0	1	1	2	?	0	1	2	2	2	?	?	2	0	1	1	0	0	0
dentata	0	0	1	1	1	0	1	0	2	0	0	0	0	2	0	1	0	0	1	1	0
longic	0	0	0	1	0	0	1	0	2	0	0	0	0	0	1	2	0	0	1	1	0
brevipe	0	1	?	?	?	?	1	?	?	?	?	?	0	2	?	?	?	?	?	0	0

Appendix 3   Matrix 2, Matrix 1 with inferred states added

									1									2	
1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1

holtzi	1	0	0	0	0	0	0	0	0	0	0	1	1	2	1	0	1	0	0	0	1
hirtipe	0	0	2	1	1	1	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0
cellula	0	0	1	1	1	0	0	1	0	0	0	1	0	2	0	1	0	0	1	1	0
mimetes	?	0	?	1	1	1	0	1	0	0	0	?	?	?	0	1	0	0	1	1	0
ancylif	1	0	0	1	1	1	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0
deccana	0	0	1	1	1	0	0	1	0	0	0	1	1	1	0	1	0	0	1	1	0
persica	?	0	?	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0
strobil	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0
dentata	0	1	0	2	1	0	0	1	1	1	1	0	2	3	0	1	1	1	1	1	0
longic	0	1	0	2	2	2	1	1	1	1	1	0	0	3	0	1	1	0	1	1	0
brevipe	?	?	?	0	1	1	0	1	?	1	?	?	?	?	?	0	?	2	1	1	0

							3									4		
2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2

holtzi	1	0	1	0	2	0	2	0	0	0	0	0	1	0	1	1	1	1	0	1	1
hirtipe	0	1	0	1	2	0	0	1	1	1	0	0	0	0	0	1	1	0	0	1	1
cellula	0	1	0	1	2	?	0	0	1	1	1	0	2	0	1	0	1	0	?	?	1
mimetes	0	1	0	1	?	1	0	1	1	1	0	0	2	0	1	0	1	0	0	1	1
ancylif	0	1	0	1	2	1	0	1	1	2	1	1	1	0	1	0	1	0	0	1	1
deccana	0	1	0	1	2	?	0	1	1	1	1	0	1	0	1	0	0	0	?	?	1
persica	0	1	0	1	2	1	0	0	1	1	1	1	1	0	1	0	0	0	1	0	1

D. B. Baker

strobil	0	1	0	1	3	?	1	1	1	1	0	0	2	0	1	0	?	0	?	?	1
dentata	0	1	2	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1
longic	0	1	2	1	1	0	0	0	1	1	1	0	2	1	1	0	1	0	0	0	0
brevipe	1	1	1	1	?	0	0	0	0	1	1	1	1	0	0	0	0	?	0	0	1

						5										6					
3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3

| holtzi	1	1	0	1	0	0	0	2	0	1	1	1	0	0	1	0	0	0	1	0	0
hirtipe	1	0	1	1	?	1	1	0	1	?	2	2	1	0	?	0	1	?	?	1	0
cellula	1	1	0	0	0	2	1	0	1	2	2	2	?	?	0	0	1	0	1	0	0
mimetes	1	1	?	?	?	?	1	?	1	2	2	2	2	0	?	0	1	?	?	0	1
ancylif	1	0	0	1	0	1	1	0	1	2	2	2	1	1	0	0	1	0	1	1	0
deccana	1	1	0	0	0	2	1	1	1	2	2	2	1	1	0	0	1	0	1	0	0
persica	1	0	?	?	?	1	1	?	1	2	2	2	1	1	?	0	1	?	?	0	2
strobil	1	0	0	1	1	2	1	0	1	2	2	2	?	?	2	0	1	1	0	0	0
dentata	0	0	1	1	1	0	1	0	2	0	0	0	0	2	0	1	0	0	1	1	0
longic	0	0	0	1	0	0	1	0	2	0	0	0	0	0	1	2	0	0	1	1	0
brevipe	0	1	?	?	?	?	1	?	?	?	?	?	0	2	?	?	?	?	?	0	0

Appendix 4 Cladograms derived from Appendix 2

(A) Original cladogram 0
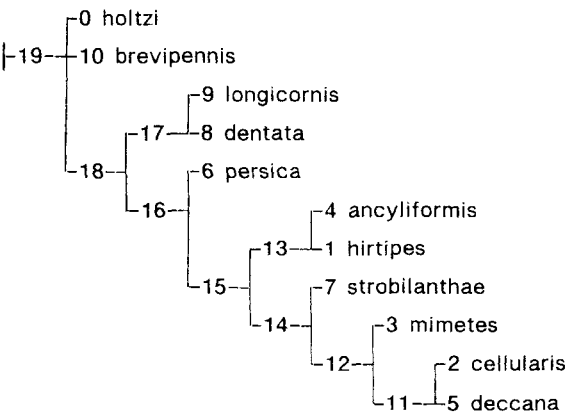
(B) Cladogram (A) with branches 7 and 12 rotated to express geographical relationships in *Tarsalia* and with suggested generic and tribal classification superimposed.
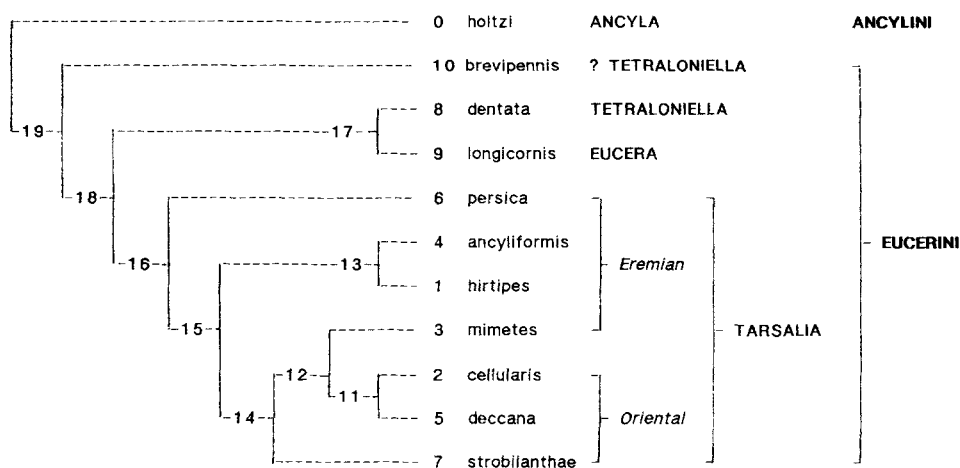
Appendix 5 **Bootstrap 50% majority-rule consensus tree derived from Appendix 3**
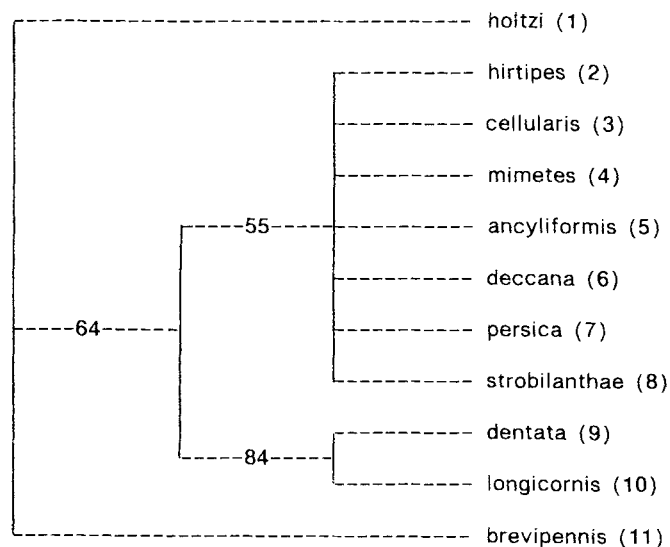
Appendix 6 Cladogram derived from Appendix 3

Cladogram 4. (Treelength 122; ci 0·721; ri 0·575; rc 0·415.) For identification of characters see Appendix 1. Reversals are indicated by x; synapomorphies (for basal clades) by solid squares. Nodes (A) (Eucerini), (B) (*Eucera + Tetraloniella*) and (C) (*Tarsalia*) are each supported by four synapomorphies. Intervals on abscissa and ordinate are not meaningful.