

20. Family-Level Phylogeny and the Proto-Bee

Phylogeny, presumably, was at least in the back of the minds of the proponents of some of the classifications (and their modifications) summarized in Section 18. Recent studies, directed toward understanding the relationships of major groups like families, subfamilies, and tribes, provide a more overt and detailed look at bee phylogeny than was available in the past. These studies (Roig-Alsina and Michener, 1993; Alexander and Michener, 1995, and Danforth et al., 2006), however, leave various aspects of bee phylogeny still in doubt. Aspects of the phylogeny among major groups of bees, mostly families, will be considered here; phylogeny within families will be considered when possible in the systematic treatment later in this book. The emphasis here is on which is the basal branch of bee phylogeny, i.e., what is the sister group to all the rest of the bees? Of course this involves consideration of what was the protobee, i.e., the most recent common ancestor of all the bees (see Michener, 2000; Radchenko and Pesenko, 1994a,b)?

There are two principal hypotheses in answer to this question. The traditional view is that the Colletidae is the sister to other bees, principally because all female and

most male colletids have the glossa bilobed or truncate, resembling in shape that of most other Hymenoptera, e.g., the Crabronidae, the sister group to the bees (Sec. 14). The alternative view is that the truncate or emarginate glossa of female colletids is a derived feature that functions to paint the characteristic colletid cell lining onto the brood cells. Thus the ancestral bee had a pointed glossa, and the Melittidae + L-T bees is the sister group to a clade that includes all other S-T bees (Fig. 20-1d). Although I prefer the second alternative, both are elaborated below.

The phylogenetic studies of Roig-Alsina and Michener (1993) and Alexander and Michener (1995) were based primarily on adult characters of 124 species of bees, one or more representatives of nearly every tribe, including representatives of virtually all genera whose familial affinities were in doubt. The methods were parsimony analyses of various kinds, as explained in the papers cited above; the S-T and L-T bees were analyzed separately. Each analysis resulted in several to many equally parsimonious trees, a common result when many of the characters used are convergent. Outgroups for the study of L-

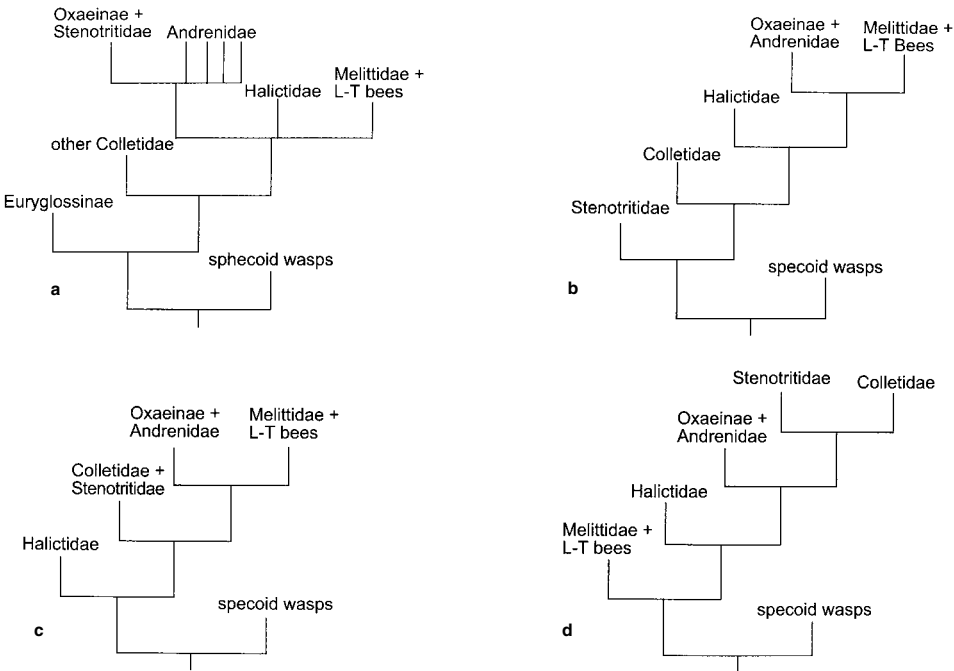


Figure 20-1. Representative alternative cladograms showing relations among families of S-T bees, with certain subfamilies of doubtful position also shown. The Euryglossinae are within the Colletidae except in cladogram a. The Sphecoid wasps (Spheciformes) are shown here in a simplified way; as indicated in Sections 14 and 15, they are a paraphyletic group from which the bees arose. **a**, Tree for families, modified from figure 5 of Alexander and Michener (1995), which was a strict consensus tree based on 109 characters

weighted equally for 57 bee taxa and 8 spheciform taxa, derived from minimum-length trees found by Goloboff's NONA; **b**, Same, but from figure 6 of Alexander and Michener (1995), using Goloboff's implied weights of characters; **c**, Same, from figure 10 of Alexander and Michener (1995), based on 114 characters of equal weight in an island of 226 trees; **d**, Same, from figure 12 of Alexander and Michener (1995), based on 114 characters of equal weight in an island of 336 trees.

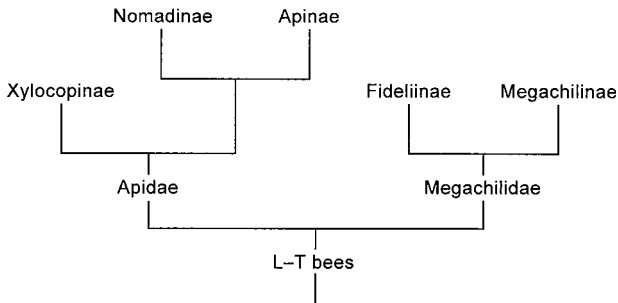


Figure 20-2. Cladogram showing relations among families and subfamilies of L-T bees, modified from figure 2b of Roig-Alsina and Michener (1993).

T bees were six melittid genera; for S-T bees, eight sphecoid wasps. The trees showed relationships among exemplars, i.e., the 124 species studied, but for practical purposes the relationships were considered to be among genera. For the most part these results were summarized to show relationships among subfamilies or families, since those taxa were in general supported by the phylogenetic analyses.

Figure 20-1 illustrates some of the results for S-T bees. The L-T bees were consistently found to have been derived from among the S-T melittid bees, verifying the conclusions of Michener and Greenberg (1980). Our 1995 study included only six melittids, however, and the relations of L-T bees to the different melittids are inconsistent; a new study with a larger sample of melittids should be made to determine, if possible, more about the origin of L-T bees from among the melittids. A problem with the Melittidae as the term is used in this book is that it is almost certainly paraphyletic. For this reason Alexander and Michener (1995) and Danforth et al. (2006) recognized three families, the Dasypodidae, the Meganomiidae, and the Melittidae s. str. For this book, I have retained Melittidae in its usual sense because a phylogenetic analysis using more genera and more characters is needed. A phylogeny of the whole family Melittidae s. l. was given by Michener (1981a), but it did not clearly show what groups should have the family level. I think it is best to retain the Melittidae s. l. as a known paraphyletic family until it is clear how it should be divided; for example, are there three (or some other number) of groups to be regarded as families? The best supported hypothesis is that of Danforth et al. (2006); see below and Section 68.

Roig-Alsina and Michener (1993) determined that the L-T bees should be divided into only two families, Megachilidae and Apidae, as shown in Figure 20-2, but it would be easy to justify division of the Megachilidae into Fideliidae and Megachilidae s. str., particularly if the Pararhophitini and Fideliini are clearly sister groups. Our analyses indicated uncertainty on this point.

Returning now to the S-T bees, there are major differences among the cladograms of Alexander and Michener, as indicated in the sample shown in Figure 20-1. Note that the first or basal branch of bee phylogeny is depicted, in different trees, as being every S-T family except the Andrenidae! In the account below, factors supporting each of the principal hypotheses about the basal group of bees are considered.

The proto-bee was colletid-like: As noted above, phylogenetic trees for bees have ordinarily been envisioned as having the Colletidae at the base. The traditional reason for this view is the truncate or emarginate glossa of members of this family (Figs. 10-4c, 19-4a, 20-3a), which is shaped like that of the sphecoid wasps and other Hymenoptera, the assumption being that the pointed glossa of other bees is a derived character. Michener (1944), after listing 36 characters that he regarded as ancestral for bees, and thus characteristic of the hypothetical proto-bee, found that bees of the tribe Paracolletini possessed all of them. With some exceptions these characters were possible or probable plesiomorphies, shared with sphecoid wasps. Alternatively, as noted above, the suggestion has recently been made (Michener, 1981a: 17) that the Melittidae rather than the Colletidae might be near the root of the phylogenetic tree of bees. This possibility will be explored below, after further consideration of colletid characters.

The colletids are united by diverse plesiomorphies mostly shared with various other families of S-T bees. For example, except for the tribes Diphaglossini and Disoglottini and the genus *Hesperocolletes* in the Colletinae, colletids have a well-formed episternal groove extending

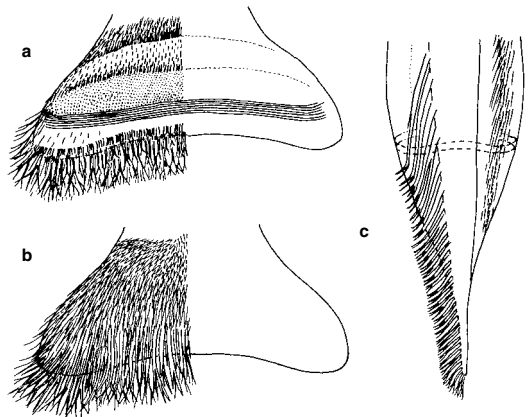


Figure 20-3. Diagrams of glossae of *Palaeorhiza parallela* (Cockerell). **a, b**, Anterior and posterior views of female; **c**, Posterior view of male, showing seriate hairs and, by broken lines, the course of one of the annuli (rows of hairs) on the anterior surface of the glossa. (The terminologies for these two glossal types are shown in Figure 19-4a, e.) From Michener and Brooks, 1984.

well below the scrobal groove (Fig. 20-5b). Moreover, the volsellae are free, with distinct digitus and cuspis (Fig. 10-15a). These are among the ancestral characters listed in 1944, as noted above. Another such character is that colletids (only five genera examined) are the only bees known to have seven pairs of ostia in the metasomal part of the dorsal vessel of males, six in females (Wille, 1958). Other bees have reduced numbers of ostia.

A supposed plesiomorphy of some colletids, the lack of scopal hairs for carrying pollen, has been considered evidence of a near-root position for the Colletidae. Jander (1976) suggested that internal (crop) pollen-carrying by Hylaeinae (a colletid subfamily) is ancestral relative to external (scopal) transport by other bees. He observed that in *Hylaeus* pollen-grooming movements that get pollen to the mouth only take pollen from the head and forelegs. Pollen on other parts of the body is groomed off and lost. I have verified these observations with another species of *Hylaeus*. Jander considered evolution from less to more efficient gathering, so that pollen landing on all parts of the body can be utilized, to be more probable than the reverse. The possession of plesiomorphic pollen transport by the colletid subfamilies Hylaeinae and Euryglossinae, but of apomorphic scopal transport in other bees, would support the near-root position for Colletidae.

As Jander noted, however, the slender, nearly hairless *Hylaeus* body is similar to that of *Ceratina* (see Pl. 1) and other small Xylocopinae that also nest in stems. In these xylocopines the scopa, although present, is reduced, and they presumably carry much of their pollen in the crop. Since these bees were apparently derived from hairy, fully scopate ancestors, I believe that the slender body, hairlessness, lack of scopa, and resultant loss of the ability to use pollen landing on the thorax and metasoma may be derived features of Hylaeinae associated with nesting in narrow burrows. I believe that the Hylaeinae, like the Ceratinini, arose from hairy bees that had a scopa. If this is true, Jander's observations do not indicate a near-root position for the Hylaeinae or the Colletidae, but rather a derived scopal loss.

Female and most male colletids have certain glossal features that are not found in other bees but that also occur in sphecoid wasps. Thus the glossal shape, the broad disannulate surface of the glossa, and the lack of differentiated seriate hairs (Fig. 20-3b) are as in sphecoid wasps and many other Hymenoptera, and the classical view is that these characters are plesiomorphic for bees, suggesting that Colletidae is the sister group to all other bees. Certain other glossal characters, the glossal lobes and brush and the preapical fringe (Fig. 19-4a) (the latter absent in some Euryglossinae), are found only in the Colletidae and are presumably apomorphic for this family. Along with the form of S7 of the male, these colletid synapomorphies indicate that Colletidae is a monophyletic group.

Extrinsic information that has been used to strengthen the classical hypothesis (Colletidae as the sister group to all other bees) is biogeographical: A major colletid clade, the Paracolletini, is greatly developed in Australia and temperate parts of South America, with the perhaps related Scraptrini in Southern Africa. Such a disjunct southern distribution is at least suggestive of antiquity.

The Euryglossinae is endemic to Australia and the Hylaeinae is most diverse there.

The protobee was melittid-like: Perkins (1912) and McGinley (1980), as explained by Michener (1981b, 1992c), Michener and Brooks (1984), Radchenko and Pesenko (1994a, b), and Alexander and Michener (1995), cast doubt on the classical hypothesis that an obtuse glossa is ancestral among bees, and suggested that the acute glossa of certain male Australian and New Guinea colletids (*Hemirhiza*, *Meroglossa*, and *Palaeorhiza*) may be ancestral, with the obtuse or bilobed glossa being a "special development" in the words of Perkins. According to this idea, here called the Perkins-McGinley hypothesis, the most ancestral bees or the wasps from which they evolved must have had a short, acute glossa like that of most S-T bees. It is not outlandish to believe that a crabronid-like wasp could have had such a glossa, for the crabronid genus *Pseudoscolia* today has exactly that, a remarkably beelike glossa (Michener, 2005), although its other structures are those of a crabronid wasp.

According to this hypothesis, the male glossa has no known special function different from that of females, but female colletids evolved a broad, obtuse glossa which serves to paint their distinctive cellophane-like lining material onto the cell and sometimes the burrow walls. Males initially would have retained an acute glossa, and in three genera they still do (Fig. 20-3c), but perhaps because the acute glossa had no special advantages for males and required maintenance of separate genetic machinery, it disappeared in most male colletids. The truncate or bilobed glossa and associated characters of all female and most male colletids would then be synapomorphies among bees, and reversions toward the ancestral sphecoid glossal shape.

But it is not legitimate to assume reversion in glossal

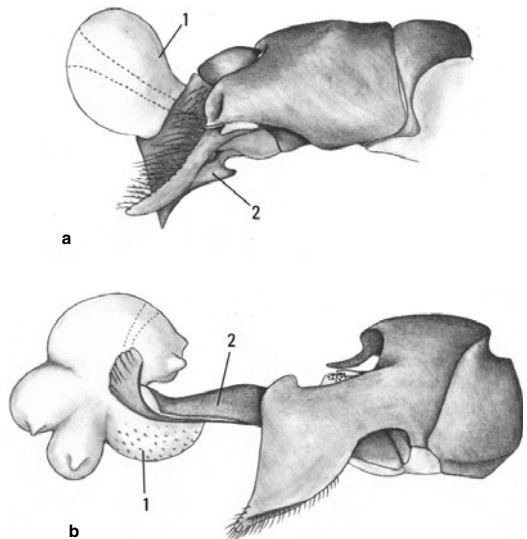


Figure 20-4. Lateral views of male genital capsule with endophallus everted. **a**, *Ptilothrix bombiformis* (Cresson); **b**, *Perdita albipennis* Cresson. (1, endophallus, 2, penis valve.)

From Roig-Alsina, 1993.

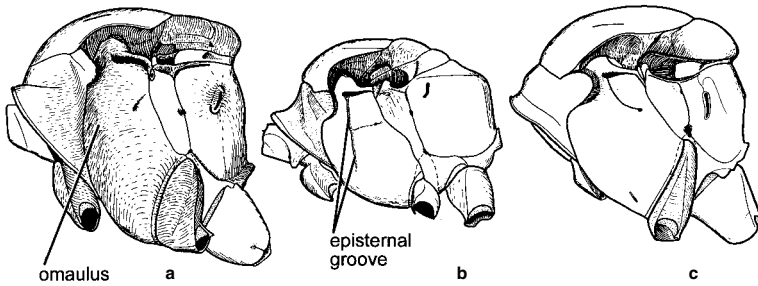


Figure 20-5. Lateral views of thoraces. **a**, *Anthidium atripes* Cresson; **b**, *Halictus farinosus* Smith; **c**, *Bombus* sp. (The upper internal extension of the middle coxa, when present, is indicated by broken lines.) From Michener, 1944.

shape to the sphecoid glossal form from an acute antecedent unless one also accepts the reversion in the associated features. I emphasize the gross difference in nearly every attribute between male and female glossae (Fig. 20-3) in *Hemirhiza*, *Meroglossa*, and *Palaeorhiza*. The male structures can easily be compared and the parts homologized in detail with those of most bees with a short, acute glossa like that of *Andrena*, whereas the female glossa is like that of other colletids (see Michener and Brooks, 1984). Other Hylaeinae in which males have somewhat intermediate glossae (*Amphylaeus* and *Hylaeus* subgenus *Hylaeorhiza*; Michener, 1992c and Fig. 46-1) do not help in locating the root of the phylogenetic tree, since they could have retained a glossa of an intermediate type irrespective of whether the evolutionary direction was from acute to obtuse or the reverse.

A character that was not used in the phylogenetic analyses but nonetheless seems to be of interest at the family level is the eversible endophallus of the male genitalia (Fig. 20-4). Unlike sphecoid wasps and other Hymenoptera, most bees have such a structure (Roig-Alsina, 1993). On the basis of 122 species of bees studied, it is absent in Colletidae and in the Oxaeinae and Andreninae, but is present in all other bees, including the Stenotritidae, Alocandreninae, and Panurginae. If its absence is plesiomorphic and derived from the wasps, its distribution supports the basal position of Colletidae, but as with the glossal characters, the endophallus might have arisen in the proto-bee and been lost in Colletidae and some Andrenidae.

Another character worth special attention that was used in the analyses by Alexander and Michener (1995) is the middle coxa. In sphecoid wasps and melittid and L-T bees the coxa is fully exposed (Fig. 20-5a,c). In other bees, i.e., S-T bees except melittids, the coxa is hemicryptic, meaning that it is elongate with its upper end hidden under the pleura (Fig. 20-5b) (Michener, 1981b). No doubt the latter is a derived condition, a synapomorphy for S-T bees except melittids, and therefore a strong support for the phylogeny shown in Figure 20-1d, in which the melittid/L-T clade is the sister group to all the rest.

The form of S7 of the male is relevant to this discussion. In various families of bees, unlike sphecoid wasps, it has apical processes or lobes, often elaborate in shape and vestiture. It attains a sort of culmination of such features in most Colletidae, in which the disc is greatly reduced, and the one to three pairs of apical processes are often complex and large (Fig. 13-2). This not only is a synapomorphy for Colletidae but suggests the origin of Colleti-

dae from among the other families of S-T bees that have less extreme modification of S7. Sphecoid wasps have nothing of this sort.

Further discussion: Returning now to family-level cladograms, Figures 20-1a and 1b suggest the classical hypothesis of glossal evolution, the glossal characters being polarized on the basis of a sphecoid wasp outgroup. They show the Colletidae at or near the base of the tree. Figure 20-1d, however, supports the Perkins-McGinley hypothesis of glossal evolution. For purposes of coding glossal characters, sexual dimorphism was considered an intermediate state between an ancestral state with a pointed glossa (and associated characters described above) in both sexes and a derived state in which both sexes have a broadly truncate or bilobed glossa. In Figure 20-1c Halictidae is the basal branch, sister to all other bees, an idea for which I see little support.

Extrinsic support for the antiquity of the clade S-T bees except Melittidae comes from the widely disjunct distribution of certain components. They are the *Hesperapis-Eremaphanta* clade of Dasypodainae, found in the western USA, southern Africa, and Central Asia (Michener, 1981a); the Fideliinae, found in Chile, South Africa, Morocco, and Central and southwestern Asia; and the Meliponini, found in tropical regions of the world. The Meliponini show little vagility; for example, among Recent meliponine taxa none or almost none reached the Antilles without human aid in spite of their abundance and diversity on the Caribbean continental margins. Their widely disjunct distribution, therefore, must indicate a long history.

The fossil record also suggests that the S-T families Colletidae, Andrenidae, and Halictidae may have arisen later than the melittid and L-T families; see Section 23 and Michener, 1979a; Zeuner and Manning, 1976; Michener and Grimaldi, 1988a, b; and Michener and Poinar, 1996. If this is true, it supports the topology of Figure 20-1d. The main points are these (they may well be significant, although negative paleontological data [absence of fossils] are always questionable): The oldest known fossil bee is an L-T bee (Meliponini), from the Cretaceous. Late Eocene fossils from the Baltic Amber, totaling about 36 species of bees, include diverse L-T taxa, various probable Melittidae, one halictid, and no andrenids, no colletids. Later, Oligomiocene bees from the Dominican amber include not only L-T bees, but also colletid, andrenid (panurgine), and numerous halictid taxa. For more details, see Section 23.

Analysis of glossal characters coded in the light of the

Perkins-McGinley hypothesis resulted in various cladograms (Alexander and Michener, 1995), of which Figure 20-1d summarizes one that showed the melittid/L-T clade as the sister group to all other bees, and colletids as a more recent clade. In no case, however, did *Meroglossa*, the only colletid in the cladistic study with a pointed glossa in the male, appear in a basal position within or outside of the Colletidae. It always appeared within the Hylaeinae, which was not a basal group of Colletidae in any of the analyses. (This position of the Hylaeinae is consistent with biogeographical information; see Sec. 23.) Thus the pointed glossa was shown as an apomorphy appearing within the Colletidae, convergent with the pointed glossa of noncolletid bees, and contrary to the Perkins-McGinley hypothesis. I believe one still must say that we do not know whether the colletid glossal shape is a plesiomorphy derived from sphecoid wasps or a synapomorphy of female and most male colletids, although to me the latter seems more likely.

I find it probable, as did Radchenko and Pesenko (1994a, b), that the proto-bee was not similar to the Hylaeinae, the colletid subfamily containing three genera with a pointed glossa in males. Assuming that the pointed glossa is ancestral for bees, it evolved into a colletid glossa once in females; males retained a pointed glossa that was converted to a female-type glossa on several occasions but is retained in three hylaeine genera (Michener, 1992c). The alternative, that the pointed glossa is derived, would require that it appear independently in some male hylaeinae and in an ancestor to Andrenidae, etc. It is a complex structure, as indicated above, far more so than is shown by shape alone, and unlikely to have evolved twice, but it clearly did evolve independently in *Pseudoscolia*.

Given, then, that the proto-bee was not *Hylaeus*-like, I agree with Radchenko and Pesenko (1994a, b) that it was a hairy bee that carried pollen externally, probably in a scopa. To judge by the behavior of andrenids, halictids, melittids, and many colletids, it stored doughlike rather than liquid provisions as larval food, made nests consisting of branching burrows in the soil (see Sec. 7), each leading to a horizontal cell (vertical cells often contain liquid provisions), tamped the cell walls with the pygidial plate, metamorphosed in cocoons made by mature larvae, and perhaps did not line its cells with secreted material (since cocoon-spinning forms sometimes do not secrete cell linings). These features could be correct whether its glossa was colletid-like or acute, i.e., whether it was colletid-like or melittid-like.

A reasonable speculation is that the proto-bee carried pollen among the hairs on its general surface, as *Pararhophites* seems to do, although it does have a small hind tibial scopa. Some bees evolved a sternal scopa and became megachilids. They may not have had ancestors with leg scopae. Others evolved a scopa on the hind leg, the scopa largely tibial in the Melittidae, Apidae, Stenotritidae, and Panurginae; in other taxa the scopae were not only tibial, but also femoral and trochanteral. In this last

group, some bees added to their pollen-carrying capacity with scopal hairs on the metasomal sterna and on the sides of the terga, as in *Dieunomia*, *Systropha*, and *Homalictus*. Others added hairs and even a corbicula on the side of the propodeum, as in *Andrena*. Perhaps the scopa was reduced in Xeromelissinae and lost in Hylaeinae and Euryglossinae. Consideration of individual characters and how they might be interpreted in the study of the evolutionary history of bees is useful and informative. However, the best way to construct reliable phylogenetic patterns is through analyses involving simultaneous use of many characters. Figure 20-1 illustrates results of such analyses using morphological characters. Phylogenetic trees are hypotheses, not factual, and new studies often result in changes. No doubt the most reliable such tree for family groups of bees is that of Danforth et al. (2006), upon which Figure 20-6 is based. The data used were morphological (109 characters following Roig-Alsina and Michener, 1993, and Alexander and Michener, 1995) and molecular, using data from five genes (4,229 nucleotide sites). Analyses of both the DNA data and DNA + morphology, using both parsimony and Bayesian methods, gave well-supported similar trees (Fig. 20-6) that support the paraphyly of the Melittidae s. l., the basal position of this group relative to other bees, and the clade consisting of the other S-T families.

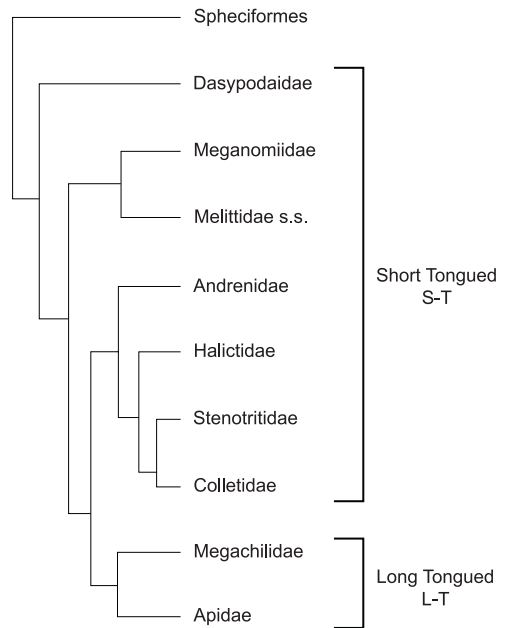


Figure 20-6. Relationships among families of bees. Data used were from 58 genera of bees (1 to 6 species each) and, for outgroups, 16 genera of spheciform wasps. Parsimony and Bayesian analyses of data from 109 morphological characters and five genes (4,299 nucleotide sites) gave similar topological results.