On the origin of the bees (Hymenoptera: Apidae, Sphecidae)

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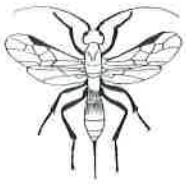

The bees are best to be regarded as a specialized subgroup of the superfamily Sphecoidea, and a cladistic analysis results in accepting the "Sphecidae" as being paraphyletic in terms of the bees. The Sphecoidea is distinguished by three strong synapomorphic traits, and it is demonstrated that the bees share at least two apomorphic characters with the "higher" sphecids, leaving the Sphecinae + the Ampulicinae as the least specialized members of the complex. The Sphecoidea is suggested to include the following families, of which the two first constitute the "Sphecidae" of earlier authors, viz. 1) Sphecidae (Sphecinae + Ampulicinae), 2) Larridae (remaining sphecid subfamilies), and 3) Apidae.
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The hypothesis that the Sphecidae include members that are to be regarded as the closest relatives of the bees was originally advanced by Robertson (1904), who suggested that "pygidialate" (i.e. pygidial plate present) and "apygidialate" (i.e. pygidial plate absent) bees might have evolved from pygidialate and apygidialate sphecoid wasps, respectively. Handlirsch (1908) suggested the Sphecidae being paraphyletic in terms of the bees, and Malyshev (1968) discussed this problem at great length, mainly argumenting from biological evidence. Michener (1944) discussed the origin of the bees rather thoroughly and concluded that "A classification of the Hymenoptera should place the bees as a division of the superfamily Sphecoidea; to rank them as a superfamily separate from the Sphecoidea obscures the close relationship between these wasps and the bees, unless some category higher than superfamily is employed to unite the two groups". See also Bradley (1958). Also Michener (1944) stated that the bees does not seem to have originated from any existing group of wasps, i.e. that a sister group relationship possibly exists between the Sphecidae s.l. and the Apidae s.l. Michener's view is adopted by many recent authors (c.f. Hennig 1981 and Königsmann 1978) but no attempts have been published to describe the exact kind of phylogenetic relations between these two groups.

Discussion

Notes on the fossil record (Fig. 1)

It is generally accepted that the bees evolved in close affinity with the flowering plants, i.e. the Angiospermae. The origin of these plants probably can be dated back to the Cretaceous or late Jurassic times, i.e. about 150 million years ago, but entomophilous "flowers" probably appeared much later, about 100 million years ago, in Upper Cretaceous (Dahlgren 1979). The earliest fossils that without any doubt can be identified as members of the Sphecidae s.l. are known from strata in Lower Cretaceous (Rasnitsyn 1980). These species apparently display a combination of character-states not present in any Recent sphecid taxon. *Archisphex* Evans, 1969, *Cretosphex* Rasnitsyn, 1975 and *Angarosphex* Rasnitsyn, 1975 might be referred to the Pemphredoninae, which are to be considered among the least specialized (advanced) subfamilies within the Sphecidae. However, Rasnitsyn (1980) suggested the last two mentioned genera to be members of the Ampulicinae, but the morphol-

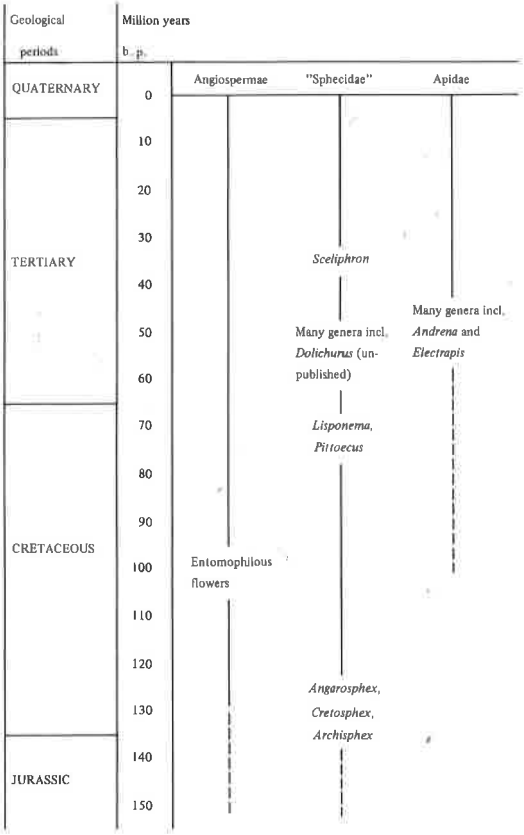

Fig. 1. The approximate occurrences of the Angiospermae and the Sphecoidea are presented to illustrate the presumed initial appearence of the taxa in question. Representatives of some of the earliest known fossil bees and wasps are mentioned.

ogy of the propodeal synsclerite and the fore wing venation as shown (Rasnitsyn 1980; 117, figs. 171 and 172) clearly demonstrate that they cannot be regarded ampulicines. If my interpretation of *Cretosphex* and *Angarosphex* is correct, there is no published evidence of the existence of the Sphecinae or the Ampulicinae prior to Oligicene times, i.e. about 35 million years ago. The Zoological Museum, Copenhagen, possesses a Baltic amber specimen of *Dolichurus* (Ampulicinae) and two specimens of *Crossocerus* (Crabroninae). These specimens are of early Eocene age, i.e. about 55 million years old. A series of strongly specialized pemphredonines, i.e. *Lisponema* Evans, 1969, and *Pittoecus* Evans, 1973, are known from strata from Upper Cretaceous. Since the Pemphredoninae represents a slightly more advanced stage in sphecid evolution as represented by the Sphecinae-Ampulicinae-line and since the crabronines must be considered representatives of highly differentiated members of the Larrinae, (Fig. 2) it is therefore assumed that the earliest members of the Sphecidae must have existed at least in late Jurassic times. If the Sphecidae existed about 50 million years prior to the first appearance of the bees and the entomophilous angiosperm flowers, the ancestry of the bees may be elucidated in applying a comparative study including species of the Sphecidae representing a higher evolutionary stage as exemplified by members of the Sphecinae-Ampulicinae line.

One can, of course, wonder why the earliest found sphecid wasp fossils are not sphecines or ampulicines rather than pemphredoninines. Most Recent species of the two first mentioned taxa (i.e. all the less advanced types) are ground nesting and hunt on the ground, while the Pemphredonini are arboricolous or twig-nesting, mainly hunting for aphids and other small Homoptera on leaves of bushes and trees. Therefore, it seems logical to assume that the chance of getting trapped in a drop of resin is much greater when displaying arboricolous nesting and hunting habits. The earliest known fossil bee can be dated back to Eocene times, i.e. about 50 million years ago. The Tertiary bees were all very close to Recent species (Baker & Hurd 1968), and many are members of the Apinae, i.e. social species, c.f. *Electrapis* Cockerell, 1909 (Larsson 1978). A few species of less advanced bees e.g. of the genus *Andrena* are also known from Eocene amber.

The sphecid-apid complex (Fig. 2)

Malyshev (1968) pointed out some striking biological similaritis between *Hylaeus* (Apidae, Colletinae) and especially *Psenulus* (Sphecidae, Pemphredoninae):

1) the lining of the larval cell with a "pellicula", i.e. a hardened secrete of the female salivary and mandibular glands;

2) the sting in certain pemphredonines is not used in paralyzing the prey;

3) that the pemphredonine prey is composed of "sweet-tasting" aphids or other homopterans;

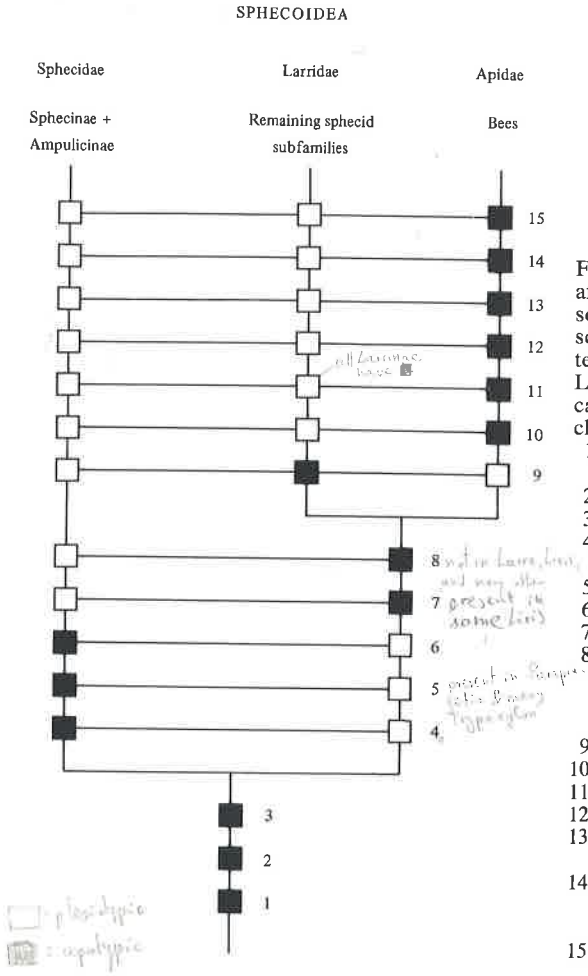

Fig. 2. Cladogram presenting the phylogenetic affinities of the bees and the sphecid wasps. Filled squares represent apomorphic characters, open squares represent homologous plesiomorphic character states.

List of apomorphic traits (derived characters) to indicate the branching sequencies in Fig. 2. Plesiomorphic character states in parentheses.

1. Humeral tubercle widely separated from tegula (almost in contact with tegula).
2. Metapostnotum strongly extended (not extended).
3. Metepimeron greatly expanded (not expanded).
4. Propodeal synsclerite strongly elongate (not elongate).
5. Propodeal sternite present (absent).
6. Pygidial plate absent (present).
7. Subbasal claw tooth absent (present).
8. Propodeal synsclerite much shortened, with a median furrow terminating in a shallow depression (not shortened, without a median furrow terminating in a shallow depression).
9. Larval spinneret paired (not paired).
10. Pilosity plumose (simply attenuate).
11. Mid-tibia with a single spur (with two spurs).
12. Larval maxilla without galea (galea present).
13. Seventh gastral tergum entirely desclerotized medially (not entirely desclerotized medially).
14. Only a single sperm cell is developed from the spermatocyte (White, 1954) (four sperm cells develop from each spermatocyte).
15. Vegetarians (carnivors).

4) the pemphredonines actually collect the provision rather than hunt for it.

It is, however, very difficult to classify these similarities in accordance with cladistic terminology, especially because detailed observations on relevant sphecids are wanting. At present I am unable to decide at what taxonomic level these similarities can possibly be regarded synapomorphies.

Rayment (1955) published a new genus, *Astaurus* (= *Clitemnestra* Spinola, 1851) which he believed formed "the actual bridge linking the wasps and the bees ...". He also pointed out the "astonishing resemblance to certain hylaeid males ... and to the genus *Phaenacolletes* and *Tachytes* (Sphecidae, Larrinae) ...". *Clitemnestra* is a member of the gorytinine sphecids (Nyssoninae), being regarded the least specialized member of the subfamily (Bohart & Menke 1976: 489). *Hylaeus* and *Phaenacolletes* are included in the Colletinae s.l., considered the least specialized (sub-) family of the bees (Michener 1944: 229). The Paracolletini, of which *Phaenacolletes* is a member, is treated as the "most primitive group of the bees" (Michener 1944).

The basal dichotomies in the evolution of the "higher" sphecids, i.e. excl. the sphecines and the ampulicines, have not been analyzed in detail, but Lomholdt (in press) suggests close phylogenetic relations to exist between the Astatinae, Nyssoninae, Philanthinae, and the Larrinae, of which the least specialized members

are very similar, usually provided with yellow markings on frons, thorax, and gaster, and therefore reminding of the primitive bees. Also several *Pseunulus* are provided with yellow markings. *Clitemnestra,* as *Psenulus,* and other gorytinines, prey on small homopterans—sweet-tasting insects, usually collected in great numbers to provision a single cell.

I here re-advocate the idea that the Apidae s.l. is to be treated a subordinate group of the Sphecoidea, possibly more closely related to the relatively more advanced sphecids as the Pemphredoninae, and the argumentation below supports this view. Three synapomorphic characters link the bees with the sphecid wasps:

1) the expanded metapostnotum (= the propodeal triangle or "area cordiformis") (Brothers 1976);

2) a wide separation between the posterior margin of the enlarged humeral tubercle (= pronotal lobe) and the tegula, whereby mesoscutum attains contact with mesopleuron anterodorsally;

3) the metepimeron is greatly expanded anteroventrally so that the pleural sulcus issues from a pit just above the mesocoxa and passes posterodorsally to the endophragmal pit (Brothers 1976).

These characters do not occur anywhere else in the Hymenoptera. See also Königsmann 1978. Börner (1919) almost exclusively applied symplesiomorphic character-states in uniting (widely separated) taxa within the Aculeata, refusing to accept character 1 (Fig. 2) as a synapomorphy for the sphecoid wasps and the bees. His argumentation for phylogenetic relations was largely based on the presence or absence of the hind tibial calcar (strigilis). According to this arrangement the aculeates were divided into 1) the "Haplocnemata" (hind tibial calcar absent), including the ants, the scolioid wasps, and the bees, and 2) the "Diplocnemata" (hind tibial calcar present), comprising the sphecoid wasps, the pompilids, and the vespids. In some members of the least specialized bees, however, a calcar is actually present. Loss of the calcar probably occurred convergently along several evolutionary lines. Lanham (1960) summarized the literature on this particular item stressing the possible phylogenetic significance of the presence/absence of this structure.

Within the Sphecidae (i.e. the digger wasps) the Sphecinae and the Ampulicinae must be regarded as the least advanced subfamilies (Evans 1964). They most probably constitute a monophyletic unit, but not incontestable synapomorphies was ever detected linking these taxa. It might be argued that the long petiolus (extended gastral sternum I) might be considered a synapomorphic trait, but a very similar condition is observed in the Pemphredoninae. Also, the strongly elongate propodeal synsclerite (i.e. metapostnotum + propodeum) links the Sphecinae with the Ampulicinae. A similar modification is present in many Larrainae, but is believed to be convergently developed there. The claws of the sphecines and the ampulicines have a subbasal tooth, not found in any other sphecid or apid genera except *Kohliella* and the subgenus *Motes* in *Liris* (Larrinae) in which it is believed to be developed secondarily. Bohart & Menke (1976) and Brothers (1975) considered this tooth a component of the set of ground-plan characters of the Sphecoidea (s.l.). Consequently, the absence of this tooth must be considered a derived state, linking all sphecid subfamilies except the Sphecinae and the Ampulicinae, with the bees. Another important character separating the Sphecinae + Ampulicinae from most other Sphecoidea (s.l.) is the propodeal sternite (Menke 1966) (= metapectus of Oeser 1971) in these two subfamilies. This sclerite is a Y-shaped sclerotized reinforcement of the extended intersegmental membrane, probably convergently developed in *Parapiagetia* and *Trypoxylon* (Larrinae), secondarily possessing a petiolate gaster (entire gastral segment I elongate and narrowed). A pygidial plate was probably present in the common ancestor of the sphecid wasps and the bees. Such a structure is, however, absent in the Sphecinae and the Ampulicinae (as well as in numerous other, especially arboricolous sphecid and apid genera). The absence of this structure in the two first mentioned subfamilies may be interpreted as a synapomorphic trait. Richards & Davis (1977) brought attention to the fact that only two thoracic ganglia are present in the bees and the Crabroninae (included in the Larrinae sensu Evans 1964). In other Apocrita the meso- and metathoracic ganglia are separated. Fusion of the ganglia may be considered a synapomorphic trait, but further investigations are necessary to elucidate the distribution of this character among the Sphecidae s.l.

In summary, the Sphecinae and the Ampuli-

cinae differ from the remaining Sphecoidea in possessing the synapomorphic characters, nos. 4, 5, and 6 (Fig. 2). In addition, these two groups are characterized (primarily) by hunting only a single prey specimen for each larva. Most other sphecid wasps provide several prey specimens for each larva. This condition should probably be regarded as an apomorphism linking the "higher" sphecids with the bees. The following combination of characters, viz. a short propodeal synsclerite and the loss of the subbasal tooth on the claws (characters no. 7 and 8 in Fig. 2) link the remaining sphecid subfamilies with the bees. Michener (1944) listed 36 characters to distinguish the more specialized bees from the less specialized ones. From this list the following can be extracted as representing synapomorphies for the entire groups (characters nos. 10–15 in Fig. 2), and when supplied with other information available, the bees are very distinctive in numerous aspects, mainly associated with the collecting and transport of pollen and nectar. The extensive series of autapomorphic traits defining the bees as a monophyletic entirety does not contribute to the understanding of the origin of this taxon, i.e. in elucidating its ancęstry and divergence from the sphecoid wasps.

In this paper only two or three—I must admit—not very convincing synapomorphies were found to link the bees with a subgroup within the Sphecoidea, but some biological and palaeontological aspects are briefly discussed in favour of the hypothesis that the bees derived from a subgroup within the sphecid wasps. Only a single derived character is recognized to unite the "higher" sphecids, i.e. the paired opening of the larval spinneret. In all other Hymenoptera the openings of the salivary ducts are fused to form a transverse, slit-like structure, sometimes bordered by strongly raised margins.

Conclusion

From the argumenting-diagram (Fig. 2) it appears that the bees are best to be regarded a subordinate group of the Sphecoidea, more closely related to the "higher" sphecids than to any other group. It is therefore proposed to regard the Sphecoidea as composed of the following three families:

1) the Sphecidae comprising the Sphecinae and the Ampulicinae;

2) the Larridae comprising all remaining "sphecid" subfamilies;

3) the Apidae.

This arrangement is a result of a cladistic analysis grouping taxa sharing synapomorphic characters.

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