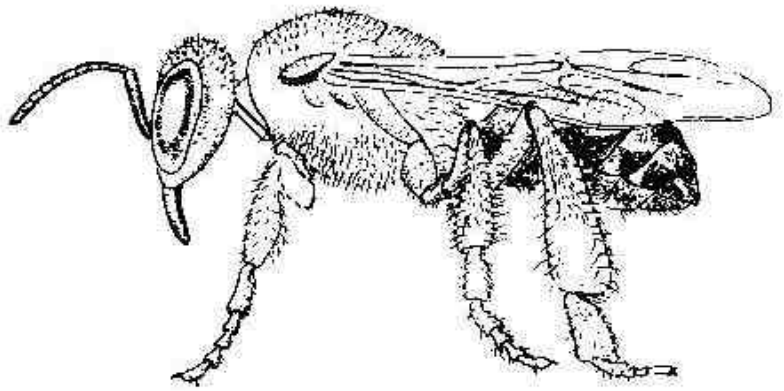
IN THE BEEGINNING: the genesis of the order Hymenoptera

Recently, fossils of what are thought to be the nests of solitary bees were found in 200-million-year-old petrified wood in Arizona. These are "trace" fossils meaning that only circumstantial evidence, like footprints, rather than fossilized parts of the organism itself were discovered-- so there is some doubt as to whether the galleries bored in the wood were made by bees or by some other insect. Much less questionable is the fossilized bee which was discovered in the late 1980's preserved in a lump of 80-million-year-old amber from what is now New Jersey.(1) That means that the poor creature became mired in the (then) sticky tree sap at a time when the dinosaurs were galumphing about the future sites of Hackensack and Passaic. The dinosaurs played their parts and then faded from center stage to become modern birds (or petroleum deposits). Today, few people would have trouble distinguishing an archaeopteryx from a flamingo (or a brontosaurus from a can of Valvoline)-- but even to the trained eye the 80-million-year-old bee is remarkably similar to existing species of bees. Bees were already a well established part of the ecosystem during the hey-day of the dinosaur and had, by this time, developed the biological structures and behaviors necessary to successfully maintain the ecological niche which they still occupy. Although the aforementioned specimen represents the oldest known fossil bee, its highly specialized form indicates that, by the end of the Cretaceous period of the Mesozoic era, bees were already seasoned travellers on the road of evolution (and had already developed sociality) and it is estimated that the first protobee appeared about 125 million years ago-- a time when flowering plants were assuming a more prevalent role in the global ecosystem(2).



Trigona prisca, A stingless meliponine bee-- a fossil of which was peserved in Cretaceous amber 74-96 million years ago. (sketch by author after Grimaldi).

Raison d' eater.

The flowering plants, or angiosperms, arose from another, older, division of seed-producing plants, the cone-bearers, or gymnosperms.(3) In both cases the male and female sex cells are separated into distinct organs. For fertilization to occur, pollen, which carries the male germ plasm, must first be conducted to the female organs of the plant- - this, of course, is pollination. The gymnosperms produce air-borne pollen, as, most likely, did the first flowering plants. The success of air-borne pollen in pollination is dependent on

the whims of wind and on the amount of pollen that a plant produces. So plants that tended to produce large quantities of pollen had a greater chance for competitive success. All this pollen represented a source of high energy lipids and proteins-- food-- to the insect world. Competition for food sources represents a major selective pressure and serves to mold the life history of an organism. Insects that were better able to exploit this resource, because of behavior or physiology (form and function) appropriate to the task, had a better chance for survival and thus more of their offspring survived.(4)

These insects, in their rummaging about for food, became the agents of pollination, as the pollen adhering to their bodies was transferred to the female organs of the plant. Thus, not only were the plants benefitted by increased pollination but the insects were helping to pave the way for an ensured supply of their food source. Eventually, both plants and insects became more and more specialized as a result of this relation. Many of the insects evolved behavior and physiology completely dependent upon the cycles of flowering plants. Similarly, certain plants developed flower structures in which pollination was possible only with the intervention of an insect intermediary.

Even the structure of pollen, itself, changed. Air-borne pollen, like that of the gymnosperms and some angiosperms, is generally smooth, small and light. Pollen that is transferred by insects or other animals usually has spines, ridges or an adhesive surface which aids in attaching to the animal vector.(5) Expanding this adaptive arsenal even further, some plants even developed certain organs, nectaries, that secreted a sugary liquid, nectar, at the base of the flower. This proved to be an adaptive advantage for the plant since the nectar, as a food source, was a further attraction to many insect species whose, now, increased rummaging promoted the success of pollination and seed-set even further. The lifestyles of flowering plants and of pollinating insects became forever intertwined.

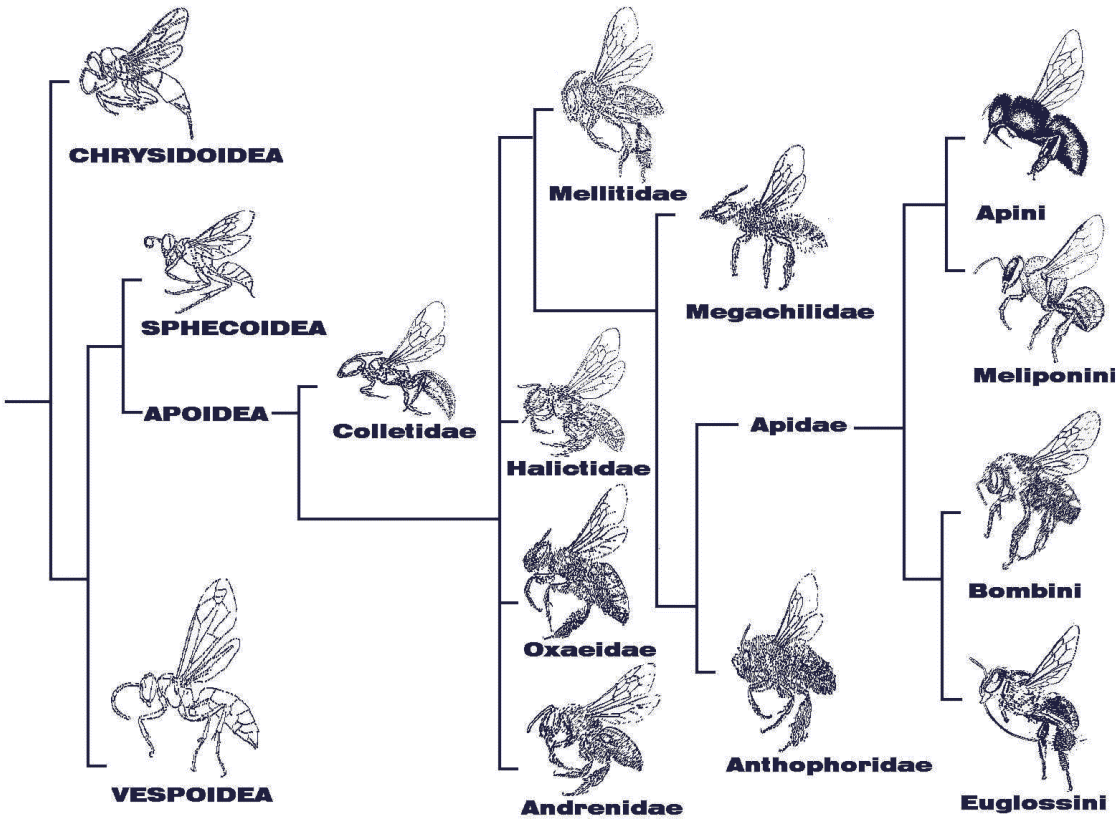
The mutualistic relationship between plants and insects may have begun as long ago as 200 million years-- when the first flowering plants were benefitted by the visitations of foraging beetles. About this same time (during the Triassic period) the order Hymenoptera, to which bees belong, arose from either an off-shoot of the Mecoptera(6) (represented today by the scorpionflies and allies(7)) or the Neuroptera(8) (fishflies, snakewings and lacewings(9)). The earliest Hymenoptera were probably completely herbivorous-- and thus in direct competition with a vast array of other plant-eating organisms-- strong evolutionary incentive to maintain any favorable random mutations that inevitably occurred and which eventually led to specialized life- styles assisting in survival. Some hymenopteran species developed a larval stage which burrowed into the plant tissue and eventually developed special adaptations which regulate the growth of plant tissues at the place where the larvae feeds, stimulating gall formation-- the galls offering both a food source and a protective defense against predators.

Adult females of some of these species developed the trait of using their ovipositor to cut slits in foliage or twigs-- into which eggs were laid (hence their appellation as "sawflies"(10)). The adaptation of the ovipositor, refined as an aid to deposit the eggs within plant tissue, provided the necessary tool for yet another life-style: parasitism. Certain sawflies probably developed the ability to penetrate, during oviposition, galls of other species(11)). The larvae of these "cuckoo insects" would then suck the body juices of the gall's original inhabitant and then feed on the gall tissues. From this adaptation further development was possible in which eggs could be laid on, or injected into, the body of a non-gall-forming insect host. Such parasitic behavior is, today, exhibited by many of the wasps. Some 125 million years ago the flowering plants were enjoying a period of

expansion due to the cooling climate of the era, against which their protected seeds gave them some defense(12). It was at this point that some sphecoid wasp species turned away from its predaceous existence to find nurture in the pollen and nectar produced by the flowering plants-- giving rise to the bees. Bees, as a group (the superfamily Apoidae), are distinguished from wasps in that they have plumose body-hairs, that is, branched or feathery hairs (rather than smooth hairs as for the wasps)(13) and in that bees derive all their food from floral sources while wasps are frequently carnivorous (scavenging on dead animals or attacking other insects-- including bees(14)).

This series of shifts in life-style, from external foliage feeding to gall-forming to parasitism to pollen and nectar foraging, also provided the basic anatomical tools to allow the development of another adaptation that is almost uniquely Hymenopteran: eusociality. The "fortuitous" acquisition of certain behaviors, which are, in fact, adaptive in themselves, seems to have neatly predisposed the order for the development of eusocial existence. In an impressive example of evolutionary convergence, eusociality has arisen independently in the Hymenoptera at least eleven times and only once-- in termites-- among other insects. The preconditions that favored the development of such eusocial behavior include: parental care of offspring, including feeding and nest defense, mutualism, parental manipulation and indirect kin selection.

To offer some idea of the diversity and venerableness represented by the order Hymenoptera in general (of which over 100 thousand species have been described) and of the bees in particular: bees are today represented by over 20,000 modern species (15)-- as many different species of bees as there are individual honeybees in an average wild colony.



A "family tree" for the Aculeata (hymenoptera with stings) showing the most likely relationship between super families (in CAPITAL LETTERS) and, for the super family APOIDEA, the deduced lines of descent of some of the more common families of bees (and tribes within the family Apidae). (All sketches except Apini, Meliponinin and Euglossini byy S. Rigby of Agriculture Cana; Apini by W. Park of USDA and Meliponi and Euglossoni by author).

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