

# AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024

Number 2903, pp. 1–21, figs. 1–39, 1 table

December 30, 1987

## Nesting Biology, Immature Stages, and Phylogenetic Placement of the Palaearctic Bee *Pararhophites* (Hymenoptera: Apoidea)

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### ABSTRACT

The following subjects are described for the bee *Pararhophites orobinus* (Morawitz) from Pakistan: nest architecture, egg deposition, development, larval behavior, cocoon construction, floral relationships, and nest provisions. The authors present a cladistic analysis of the phylogenetic relationships of *Pararhophites* with other taxa of long-tongued bees using characters of nesting biology and of larval and adult anatomy. The authors agree

that *Pararhophites* probably belongs to the megachilid lineage rather than to the anthophorid/apid line where it has been assigned in the past. McGinley does not make a formal transfer of the genus now because of the unsettled relationships of the families of long-tongued bees; Rozen places *Pararhophites* in the subfamily Pararhophitinae and places it in the Megachilidae [NEW SUBFAMILY, NEW PLACEMENT].

### INTRODUCTION

The Palaearctic bee genera *Pararhophites*, *Tarsalia*, and *Ancyla* are the only Old World representatives thought to be closely related to such New World primitive anthophorids as the Exomalopsini, Tetrapediini, and Melitomini (Michener and Moure, 1957). Because knowledge of the immature stages and nesting biology of numerous New World anthophorids has grown considerably in recent

years, comparable data on the Old World bees would enable a fuller analysis of their interrelationships with the better known New World ones. On a recent trip to Pakistan we were successful in finding nests of *Pararhophites orobinus* (Morawitz) and report here on the nesting behavior and ecology and on the larvae and eggs of this species.

The information we uncovered was so dif-

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Figs. 1, 2. 1. Killi Sarda, Baluchistan, Pakistan. Adults of *Pararhophites orobinus* commonly visited *Peganum harmala*, the dominant plant in this picture. Nesting aggregations occurred in several areas

ferent from that for other anthophorid bees and so unexpected that it forced us to undertake a broad comparison of *Pararhophites* not only with the primitive anthophorids, but also with other long-tongued bees. This comparison involved adult and larval anatomy, and nesting biology. The present paper gives our conclusions about the relationship of *Pararhophites* with these bees.

Although Michener (1944) referred *Pararhophites* to the Exomalopsini, Popov (1949) assigned it to its own tribe in the Anthophorinae, a practice that Michener and Moure (1957) later adopted. Warncke (1977) placed the genus in the Melittidae, but Michener (1981) pointed out that adult characters were inconsistent with such a placement.

Both authors of this paper contributed fully to all aspects of the research and are in agreement with respect to the conclusions. Rozen initially drafted the section on biology; McGinley provided the description of the larva and drafted the phylogenetic analysis.

#### ACKNOWLEDGMENTS

We acknowledge the field assistance and companionship of Mr. Sarfraz Lodhi, Scientific Assistant, Department of Entomology, American Museum of Natural History and Mr. Ian Stupakoff, City College, City University of New York. We extend our gratitude to the following individuals and their institutions in Pakistan for assisting us in numerous ways in fulfilling the goals of the field trip: Dr. Rafiq Ahmad, National Co-ordinator, Honeybee Research Programme, Pakistan Agricultural Research Council, Islamabad, Pakistan; Dr. Manzoor Ahmed, Department of Zoology, University of Karachi, Pakistan; Dr. Abdul Hameed Bajoi, Entomologist, Agricultural Research Institute, Quetta. The field trip was made possible through the support of the Smithsonian Institution's Foreign Currency Program and we wish to thank Gretchen Ellsworth, Director, Office of Fellowships and Grants (Smithsonian Institution), and her staff for assisting us

in seeking and obtaining the support. Elaine R. S. Hodges (Smithsonian Institution) prepared figures 21–36.

We thank the following persons for critically reviewing and improving the completed manuscript: George C. Eickwort, Cornell University; Terry L. Griswold and Frank D. Parker, U.S.D.A. Bee Biology and Systematics Laboratory; and Robert W. Brooks and Charles D. Michener, University of Kansas.

The pollen plant of *Pararhophites orobinus* was kindly identified by Dan H. Nicolson, Department of Botany, Smithsonian Institution.

#### BIOLOGY OF *PARARHOPHITES OROBINUS*

We made the following observations primarily at Killi Sarda (figs. 1, 2), a small village 12 km south of Quetta, Baluchistan, Pakistan, between May 10 and 14, and again on May 22, 1984.

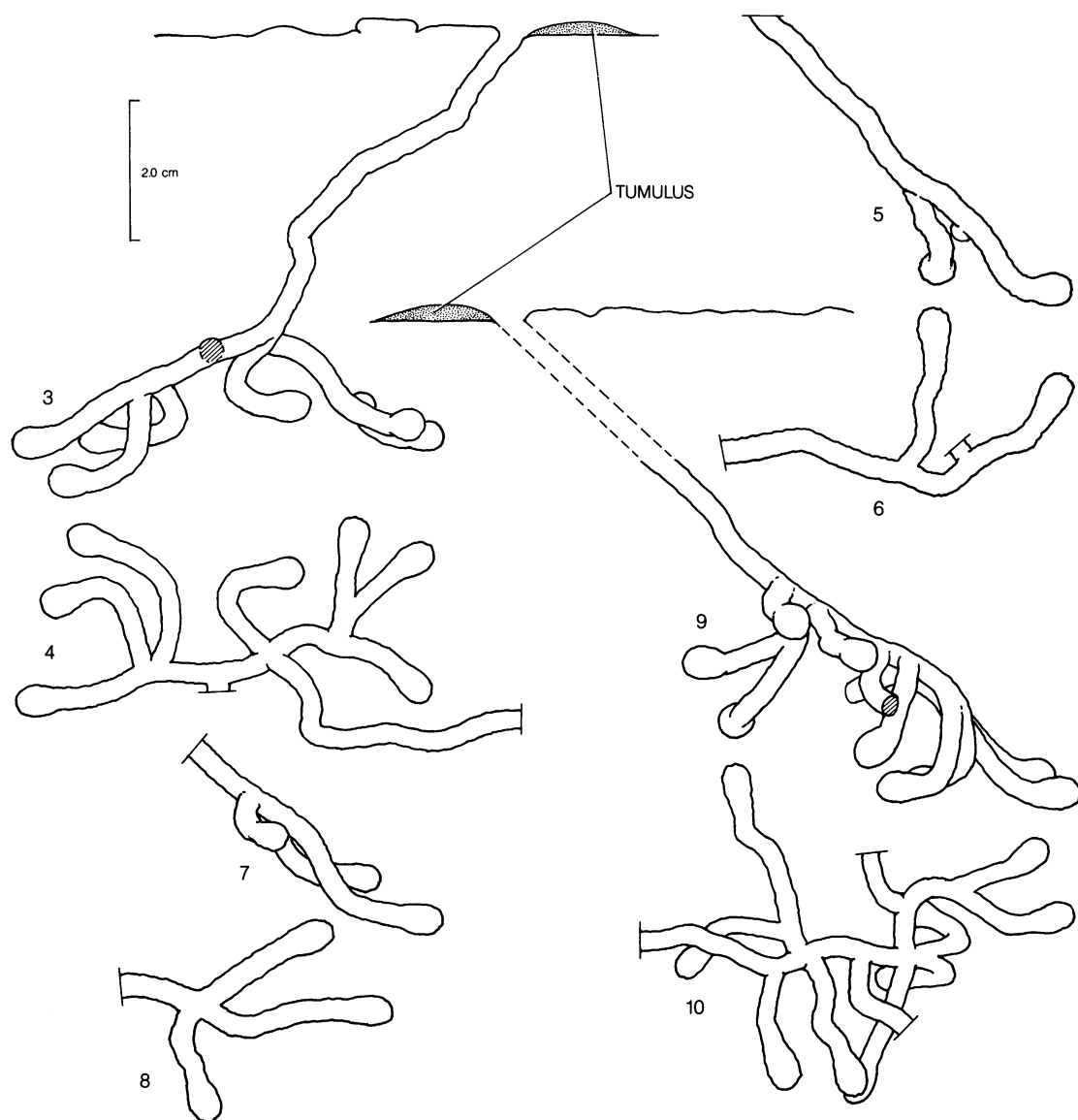
**DESCRIPTION OF AREA:** Quetta valley is a moderately high desert region (elevation 1900 m) with an approximate mean annual temperature of 7°C, and an approximate mean annual rainfall of 150 mm. Precipitation occurs primarily in the winter months, and desert flowering follows in the spring. The vegetation away from agriculture and other human disturbances is low, sparse, and herbaceous (figs. 1, 2).

The pollen plant, *Peganum harmala* L. (Zygophyllaceae), was the most common angiosperm blooming throughout the Quetta valley during our stay. Popov (1949) also recorded *P. harmala* to be the pollen plant for *Pararhophites* at other localities. The plant, locally called "*kisan kur*" in Brohi (local language) meaning "lying farmer," ranges from Lebanon to Mongolia. It dominated the nesting area at Killi Sarda, where almost no other plant species were present. The ground cover was less than 50 percent, and the pollen plants cast little shade because of their fine leaves (fig. 2).

The nesting site, trodden intermittently by

←

in fore- and middle ground. 2. A nesting aggregation was found in left foreground. *Peganum harmala* is abundant in fore- and middle ground.



Figs. 3–10. Nests of *Pararhophites orobinus*. 3. Entire nest, side view. 4. Same nest, top view. 5. Lower part of small nest, side view. 6. Same nest, top view. 7. Lower part of small nest, side view. 8. Same nest top view. 9. Entire nest, side view. 10. Same nest, top view. Scale refers to all figures.

people, goats, and sheep, was in a nearly horizontal field approximately 100 m wide and more than twice that long (fig. 1). The high, dried mud walls of the living compounds of the local people bordered the field on the sides near the site.

*Pararhophites orobinus* was the most abundant bee at Killi Sarda during the study.

**DESCRIPTION OF NESTING SITES:** Although widely scattered over most of the vast field, nests of *Pararhophites orobinus* seemed to be clustered in irregular groups, several containing 10 to 15 obvious nests as identified by their tumuli or by entering females. The largest cluster, within a rectangular area of 3.0 by 4.8 m, contained 28 irregularly distributed

nests identified by entering females and many other nests identified by tumuli alone. Seven nests contained two females each and one, three females. Multiple nest occupancy was probably more common than these limited observations would indicate, although nests containing numerous females were unlikely because all nests excavated were shallow.

Nest entrances were generally unshaded, and the ground surface was either crusted or consisted of a top layer of loose, fine, very dry earth as much as several centimeters thick, depending upon the extent of churning by passing livestock. Below, the soil was fine-grained, compact, and dry, requiring knives to penetrate to the cell level (4.5 to 7 cm). The earth seemed to become less consolidated below the cell level. The soil on the surface as well as below contained no stones and few roots.

**DESCRIPTION OF NESTS:** Cells ranged in depth from 4.5 to 7 cm with most occurring between 5 and 6 cm, so that nests were shallow, with moderately short laterals ending in single cells. Nests had a dense, compact aspect as in figures 3–10.

Females constructed almost all nest entrances at the edge of surface crust where the ground had been broken by passing livestock or persons. The main tunnels entered obliquely beneath the crust, and most entrances were at the edge of the tumuli.

Tumuli (figs. 3, 9) consisted of low mounds of fine powdery material approximately 1.5 to 2 cm long, 2.5 cm wide, and 0.5 cm at the highest point. Entrances were open (not plugged with soil) and the tunnels, 3.0 mm in diameter, descended in an irregular, meandering fashion, at about a 45° angle. The main tunnel of larger nests branched, with several branches in turn giving rise to laterals of the same diameter, each of which led to a cell. Laterals tended to descend only slightly, less so than the main branches, and often curved or angled horizontally. They were filled with powdery soil after cell closure. The main tunnel, branches, and laterals had rough, uncoated walls which readily absorbed moisture when tested with water droplets. Part of the main tunnel and branches may have been filled at various places with powdery soil, although this was hard to judge because our excavations may have clogged tunnels with

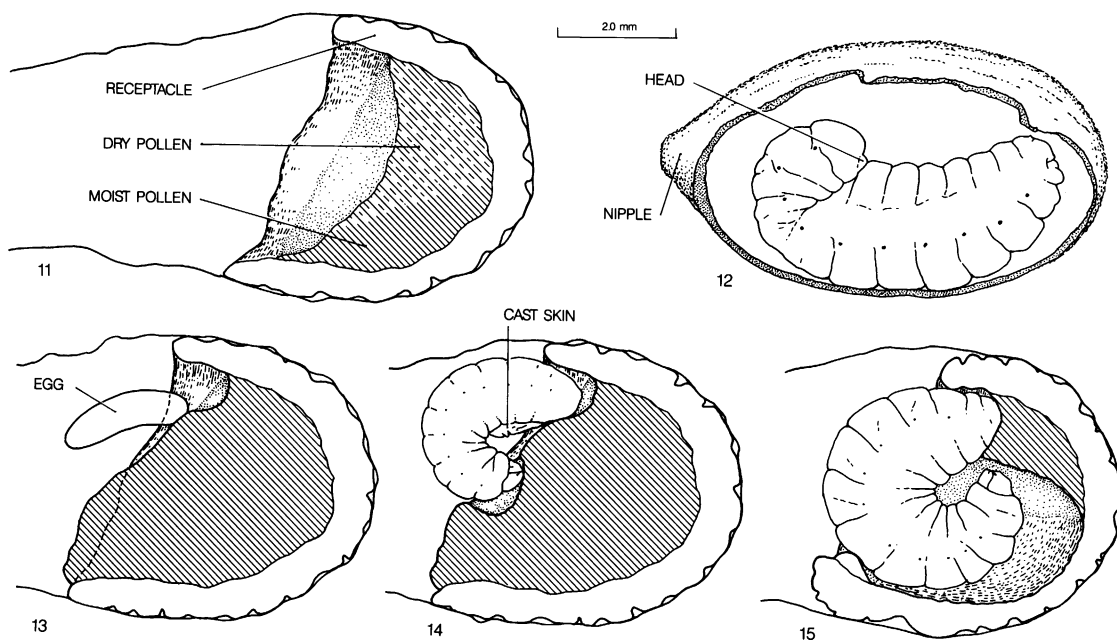
loose surface soil. In general the nest pattern was similar to that of the *Fideliinae* (Rozen, 1970, 1973b, 1977b).

Cells (figs. 11, 16) were essentially horizontal, although the front end may have been slightly higher than the rear in some cases. They were elongate ovals, with the rear end rounded, but their exact shape was uncertain because of their small size and the rough nature of the cell walls. We could not ascertain, for example, if they were symmetrical or if the floor of the cell was flatter than the ceiling. Their maximum diameter was 4.0 to 5.0 mm (5 measurements) and length 7.0 to 7.5 mm (5 measurements), although the latter measurement is somewhat arbitrary because cell closures were never in place to define the front boundary of the cell. Cells, like those of the *Fideliinae* (*ibid.*), were merely chambers carved from the substrate; their walls were as rough as those of the burrows, not plastered or built-in, without a secreted lining of any sort, and they absorbed water droplets nearly instantaneously.

In most cases, cell closures seemed to be merely the powdery soil of the lateral that we normally blew away as a result of our using aspirators to remove loose soil from the excavation. In one case, however, we noted a moist area at the closure end of a newly completed cell, suggesting that a female may apply a moist stopper of soil and then fill the laterals, and that no trace of the "special closure" persists after the moisture dries.

Nests normally contained numerous cells. Three nests carefully excavated contained 8, 9, and 11 cells each (figs. 3, 4, 9, 10). Other nests in early stages of construction had only two or three cells (figs. 5–8).

**PROVISIONING:** Stored provisions were of an unusual nature and form (figs. 11, 13) in that they were fashioned from: (1) an outer part forming a cuplike receptacle of sand, about 0.6 mm thick, that fitted into the rounded rear of the cell, and (2) the inner content of the receptacle consisting of yellow pollen moistened by a sticky liquid, presumably nectar. The sand of the receptacle was fine, of the same grain size as the substrate and glued together by a liquid. The receptacle had a porous texture, a tarlike consistency, and a brown "wet sand" color, distinctly darker than the dry, pale tan of the surround-



Figs. 11–15. 11. Cell with partial food mass. 12. Cocoon cut away to show mature postdefecating larva. 13. Food mass and egg. 14. Food mass and young feeding larva. 15. Food mass and older larva. All figures in side view and in same scale.

ing substrate. When exposed receptacles dried, they became harder (but remained darker than the substrate), suggesting that the liquid was nectar. Provisioning females presumably constructed the receptacle from earth either from the anterior end of the cell or from the burrow. Their offspring later incorporated the earth into the cocoon as described below.

One open cell contained a receptacle not yet filled with pollen, indicating that females first construct the receptacles and then provision them with food. Another open cell had the cup incompletely filled with wet and dry pollen (fig. 11).

In fully filled receptacles, the front surface of the receptacle and moist pollen was somewhat irregular and sloped downward at an angle, as in figure 13.

**DEVELOPMENT:** In all observed cases, the posterior end of the egg was attached or perhaps partly inserted into the upper middle part of the front surface of the provisions so that newly deposited eggs angled down slightly, as in figure 13. Eggs were widest in their posterior halves and tapered anteriorly to the rounded front ends. In general, they were thick

by comparison with eggs of most bees and were slightly curved. They measured 2.0 to 2.3 mm long (6 measurements) and 0.6 to 0.7 mm in maximum diameter (6 measurements). The chorion was thin, smooth, and semitransparent. In two preserved eggs, the embryo was clearly oriented with its ventral side up so that its dorsum was next to the ventral surface of the egg. Hence, larvae must reorient before hatching by rotating 180° on their long axes, as has been reported for some other bees (Torchio, 1984).

After hatching, the larva remained in the same position that it occupied as an egg, that is, attached by its posterior end to the upper front surface of the provisions. However, it (fig. 14) now curved downward, so that its head reached the provisions, and consumed the pollen-nectar mixture directly beneath its head. As it fed, the cavity that developed in the mixture grew deeper and larger, but the receptacle remained intact until most of the mixture had been consumed. The larva did not crawl, and at the start of the last stadium it was still attached to the provisions as before. At least until the fourth instar, its cast

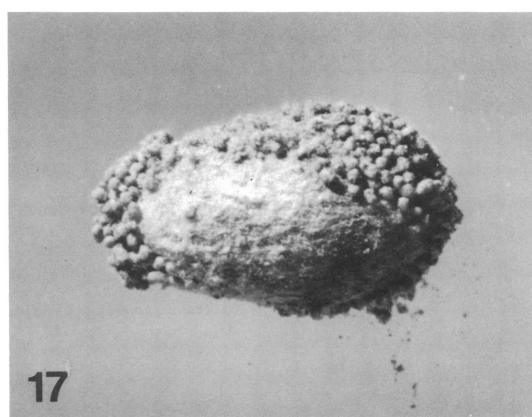
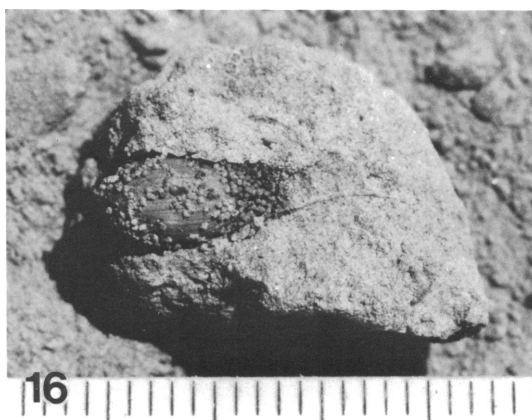
skins accumulated beneath the rear of its body, often, if not invariably, with the collapsed head capsules appressed to its venter, one in front of the previous one in an orderly sequence (fig. 14). During feeding, the growing larva curved its body more and more to reach the receding food surface, which came closer to the surface to which the larva's posterior end was attached (figs. 14, 15).

Toward the end of feeding on the pollen-nectar mixture, the larva also began consuming the receptacle starting at the lower rear (fig. 15), and eventually completely ingested the entire receptacle as well as its contents.

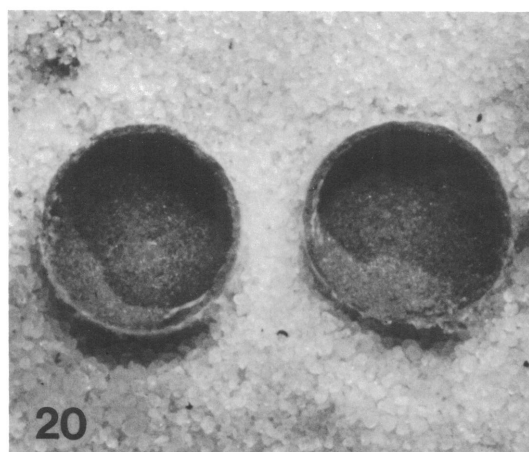
Larvae commenced defecation before they had depleted the food, apparently at the onset of the last instar. Evidence suggested that the fecal material first consisted of vacuolated pollen grains, but that as the larva fed on the receptacle, the material included sand. On one preserved food mass with the receptacle still intact, pellets, twice as long as wide and composed entirely of pollen grains, clung to one side of the larva's attachment to the food. Larvae partly reared in artificial containers discharged dry, elongate yellow pellets, some containing fine-grain inorganic material from the receptacle as well as pollen. Toward the end of defecation, fecal pellets consisted almost entirely of sand material and were short and ovoid, as evidenced by the pellets clinging to excavated cocoons (figs. 16, 17).

Before completely consuming the provisions, larvae were capable of spinning very fine silk from the elongate, narrow salivary lips although they did not start cocoon construction until after feeding.

The finished cocoons (figs. 12, 16–18) were elongate ovoids, nipped at one end and evenly rounded at the other. The nipped end faced the cell closure and the postdefecating larva within normally had its head at the same end (fig. 12). Only one out of 13 cocoons opened in the laboratory in October 1984 contained a larva that had its posterior end at the nipped part of the cocoon. As this larva, unlike the other 12, did not have its head partly buried in its venter, we probably had excavated it before it completed spinning and had thereby upset its normal development. Pellets of sand-laden feces clung to the outer surfaces of the cocoons, particularly at the nipple and at the rear end, so that the



Figs. 16–18. 16. Cell containing cocoon and fecal pellets, side view, with front end to the right. 17. Cocoon with some fecal pellets attached, front end to the left. 18. Cocoon with most fecal pellets removed, with elongate fecal ribbons showing through silk covering, front end to the left.



Figs. 19, 20. 19. Cocoon in early stages of construction, cut in half, inner view, showing ribbons of dried fecal matter adhering to white silk. Polar ends are in the middle of each half. 20. Cocoon, final stage of construction, cut in half, inner view, showing fecal material covering entire surface.

cocoons in most places did not contact the cell wall. These feces were ovoid, little longer than broad, with a maximum length of approximately 0.3 to 0.4 mm.

Freshly completed cocoons were grayish-tan, with a covering of whitish silk through which could be seen a darker, hard layer bearing lines that ran from one end to the other (fig. 18). Cocoons ranged from 6.2 to 7.2 mm (mean 6.9 mm) long (12 measurements) and 3.5 to 4.3 mm (mean 3.9 mm) in maximum diameter (12 measurements). The inner hard layer consisted of fine sand (and no pollen)

cemented together, and was approximately 0.2 mm thick but was somewhat thicker at both the rear and the nipped ends. The sand material seemed to contain some fibrous silk, as seen when the casing was broken. The casing was extremely hard and brittle, unyielding to pressure except that when squeezed too hard it suddenly collapsed like a pressed hen's egg. The fibrous silk added negligible strength under these circumstances. The inner surface of the cocoon consisted only of the cemented sand grains held together by a glistening, semitransparent material, the color of wet sand. At least in a few cocoons, (probably in all), the larva had applied to the middle of the inner cocoon surface a patch of pale tan, opaque, amorphous material lacking both sand and pollen grains, undoubtedly the final part of the meconium.

A few cocoons from the previous year were tan on the outside with no indication of fibrous silk, the outer surface appearing granular and with the fecal lines extending from one end to the other. The white silk material had apparently broken down chemically.

The spinning of numerous cocoons revealed the construction process. After partial defecation, larvae started spinning soft fine white webbing that isolated them from the cell walls and feces. This webbing, at first semitransparent and open, eventually looked like soft white tissue paper enveloping the entire larva, at which time the cocoon nipple was in evidence. The larva was still filled with fecal material which, because of the sand contents, showed through the integument as dark gray rather than yellow as before. Then the larva started extruding the sand-laden feces as dark, elongate, flexible, flat ribbons, 0.3 mm wide and the thickness of a single layer of sand (fig. 19). Ribbons generally ran from one end of the cocoon to the other and quickly hardened. Larvae pressed them to the silken fabric but the ribbon material did not penetrate it appreciably in that some ribbons were accidentally pulled away from the fabric while the cocoons were being cut open. Larvae applied ribbons side by side, ribbon overlapping ribbon (fig. 19), to all surfaces of the cocoon until they completely coated the inner surface. In the early stages of fecal deposition, the nipped end of the cocoon was left uncoated, but with the application of layer after

layer this opening eventually became completely coated (fig. 20).

The source of the "glue" that held together the sand grains and cemented them into a rigid casing was presumably either a by-product of digestion or a secretion of the larva. Apparently the larva voids the pollen-laden feces before the sandy material because the pollen of the provisions is consumed before the receptacle.

After finishing the cocoon, the larva positioned itself on its back and bent the anterior end of its body so that the lower part of the head was completely buried in the larva's anterior venter (fig. 12), a pose not known for any other bee larva. The larva then became inactive. This pose was characteristic of quiescent, postdefecating larvae recovered from cocoons. It was observed in at least 14 cases, and was also assumed by all eight larvae (observed in October 1984) that matured without properly formed cocoons in plastic rearing dishes. Only two quiescent larvae had their heads fully exposed; at least one of these was oriented backward in the cocoon, which suggested that we had disrupted its normal behavior.

Last-stage larvae collected before they finished feeding survived remarkably well in plastic containers. Their hardiness, like that of the Megachilidae, is unusual because most bee larvae are fragile. Whether or not they had finished feeding, they defecated and spun cocoons of silk that were white at first but turned pale tan over the following months. However, these cocoons were misshapen and different in texture from those completed in the ground.

**ADULT ACTIVITY:** Males and females flew around the pollen plant, *Peganum harmala*, during much of the day. On one clear morning they were uncommon on the plants at 10:15 a.m. but by 10:30 were numerous. Both sexes were still flying in midafternoon. Females were collected while foraging around 3:00 p.m. on a cloudy day at another locality.

We observed no matings, probably because the bees' small size and light integumental color made them difficult to see against the pale ground surface and because the strong breezes in the Quetta valley created dancing plant shadows on the ground. However, matings almost certainly are brief or we would

have detected them. Males commonly patrolled in strong but erratic flights around the flowers. They occasionally landed on flowers, presumably for nectar, and they just as frequently landed on the ground for several seconds before departing swiftly to continue patrolling. Females rarely rested on the ground; when they did males did not approach. Males did not patrol the clusters of nest entrances, suggesting that mating probably occurs at the pollen plants.

Females foraged from flowers in various stages of bloom. They entered flowers in which the petals had not yet unfolded by landing on the flower and pushing their way through the overlapping petals on the side of the blossom. They also visited the fully opened flowers and even flowers that had dropped some petals. The period of visitation to a blossom ranged from 3 to 15 seconds (10 measurements) although another visit to a closed blossom lasted 53 seconds.

*Pararhophites* diapauses as an inactive postdefecating larva in its cocoon and almost certainly has only one generation a year. More than one generation a year would probably be impossible because of the extreme dry conditions of the area and because the precipitation period occurs only in the winter. Small larvae recovered from nests on May 10 increased appreciably in size during a few days, suggesting that development was rapid, perhaps a necessity considering the shallowness of the nest, the direct sunlight on the ground, and the lack of any sort of cell lining to conserve the moisture in the provisions. Most of these larvae were spinning cocoons in plastic containers by May 22, whether or not they had entirely consumed the food and receptacle.

When we last visited the site on May 22, we saw some females and almost no males on the food plants, which were much further advanced, having fewer blooms and numerous forming fruits. Nesting activity was greatly reduced, and numerous larvae were spinning or had completed cocoons. We encountered mostly final instars, indicating that the nesting season was ending.

**PARASITISM:** No cuckoo bees flew over the extensive nesting area of *Pararhophites orobinus* nor did we recover their immatures from cells. A small bombyliid was commonly

seen ovipositing at the site. We discovered its larvae in the cells, and extracted two mature larvae from cocoons of *Pararhophites*.

COMPARISONS WITH OTHER SPECIES OF *PARARHOPHITES*: Popov (1949) believed that all three species of *Pararhophites* would be found only in sandy habitats and recorded the Egyptian *P. quadratus* Friese nesting in sand and visiting flowers of *Zygophyllum*. He also thought that all species would nest gregariously, as we found to be the case with *P. orobinus*.

#### DESCRIPTION OF THE MATURE LARVA

Figures 21–29

DIAGNOSIS: The broad clypeus and distinctive labral sclerite of the mature larva of *Pararhophites orobinus* permit it to be separated from larvae of all other bees except those of the Megachilidae (Fideliinae, Lithurginae, and Megachilinae) and Ctenoplectridae. Unlike larval megachilids, larvae of *Pararhophites* have body setae that are greatly reduced, so that under normal stereoscopic examination, setae are not visible. Megachilid larvae are usually conspicuously hairy with long setae and seta-length spicules. The mandible (figs. 23–25) of *Pararhophites* is distinctive, similar only to that of the South American *Neofidelia* (Rozen, 1973b).

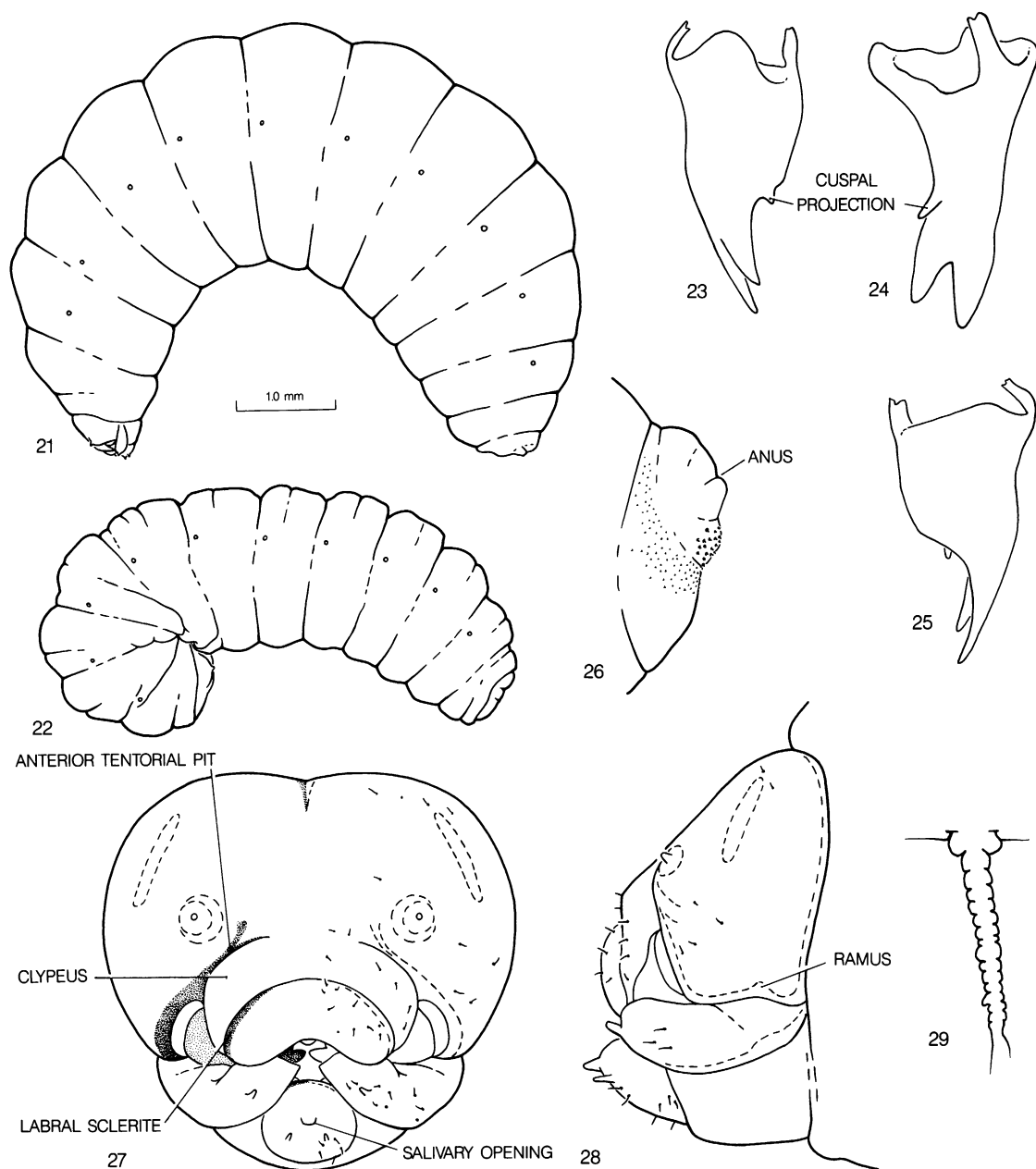
Live postdefecating larvae (figs. 12, 22) can be distinguished from those of all other bees because most of the head is buried in the venter of the thorax.

HEAD (figs. 27, 28): Integument with scattered setae on head capsule, clypeus, labrum, and labiomaxillary region; setae elongate but not as conspicuous, as long, or as abundant as those of most megachilids; labral, epipharyngeal, hypopharyngeal, and maxillary spiculation absent. Pigmentation of head capsule light; internal ridges somewhat darker; apical third of mandible heavily pigmented. Head capsule, in frontal view (fig. 27), wider than long. Tentorium complete, thin; anterior tentorial pit moderately high on face, well removed from mandibular pre-coila; posterior tentorial pit normal in position, i.e., at junction of posterior thickening of head capsule and hypostomal ridge; posterior thickening of head capsule complete, moderately developed; median portion of

posterior thickening of head capsule curving forward as seen in dorsal view (this state is characteristic of many megachilid larvae); posterior boundary of head capsule normal, i.e., defined by single ridge; median longitudinal thickening of head capsule developed only dorsally, extending about one-third of way to level of anterior tentorial pits; hypostomal ridge well developed, divided posteriorly with inconspicuous dorsal ramus directed toward posterior thickening of head capsule (fig. 28; similar to that of many megachilids); hypostomal ridge moderately elongate, nearly forming a right angle with posterior thickening of head capsule; pleurostomal ridge well developed; epistomal ridge well developed laterad of anterior tentorial pits but mesiad of those pits, incomplete, fading medially; another internal sclerotic ridge extending dorsally from pit and mesiad of the antennae; epistomal depression arching dorsally to level of lower margin of antennal discs. Parietal bands indistinct but present.

Antennal prominence weakly developed, inconspicuous; antennal disc small; antennal papilla small but distinctly developed, slightly longer than basal diameter, bearing 2–3 sensilla. Vertex, in lateral view, broadly, evenly rounded, not produced forward; frontal swellings and tubercles above antennae absent; genal tubercle absent; clypeus wide, with well-developed labral sclerite; fronto-clypeal area, in lateral view, normal, not strongly produced beyond labrum; labrum, in lateral view, not strongly projecting beyond clypeus; labral sclerite well developed; labral tubercles absent; labral apex, in frontal view, broadly and deeply emarginate; sensilla-bearing swellings on labral apex absent; epipharynx normal, not produced into a distinct lobe.

Mandible (figs. 23–25) moderately elongate, moderately robust in dorsal and adoral views, and nonattenuate in adoral view; dorsal mandibular spiculation absent; outer surface of mandible without seta-bearing tubercle; mandibular apex strongly bifid; ventral apical tooth larger than dorsal tooth; mandibular cusp weakly defined but with conspicuous, sharp cuspal projection, otherwise, cuspal area smooth, lacking teeth or spicules; dorsal apical edge without teeth or single large



Figs. 21–29. Mature larva. 21. Last-stage defecating larva. 22. Postdefecating larva. 23–25. Right mandible, dorsal, inner, ventral views. 26. Apex of abdomen, lateral view. 27. Head, frontal view. 28. Head, lateral view. 29. Spiracle, side view.

tooth near cusp; ventral apical edge not visible in dorsal view, in line with dorsal apical edge; mandibular apical concavity well developed, somewhat scooplike; spines on apical concavity absent; teeth on ventral apical edge of mandible absent.

Labiomaxillary region produced but not as strongly so as in many cocoon-spinning larvae; labium and maxilla distinct apically, not obviously fused; labium exceeding maxilla in length; maxilla normal in size, not conspicuously enlarged. Maxilla with inner margin

strongly and narrowly produced mesially; cardo and stipes strongly sclerotized; articulating arm of stipital sclerite (see Rozen and Michener, in prep.) well defined, pigmented; maxillary palpus present, elongate, slender, length slightly more than twice basal palpal diameter; as seen in lateral view, palpus positioned ventrally on maxillary apex; galea absent. Labium divided into prementum and postmentum; premental sclerite narrow but distinct near articulating arms of stipital sclerite; labial palpus elongate, approximately three times as long as basal diameter, subequal in length to maxillary palpus.

Salivary lips well developed, moderately elongate and narrow, tapering apically (figs. 27, 28); salivary opening narrowly transverse; salivary plate absent. Hypopharynx normal in size, not conspicuously enlarged, strongly bilobed with lobes projecting strongly dorsally; hypopharynx exceeded in length by labiomaxillary region; hypopharyngeal groove distinct between articulating arms of stipital sclerites.

BODY (figs. 21, 22): Integument without sclerites, mostly nonspiculate but with patches of minute spicules on dorsolateral areas of cephalic annulets; small, short, inconspicuous but distinct setae scattered over much of body surface with some arranged in transverse row on each caudal annulet; setae abundant only immediately below anus. Body moderately elongate; predefecating form somewhat robust (fig. 21); postdefecating form slender (fig. 22); intersegmental lines moderately incised; intrasegmental lines distinct; dorsal tubercles absent or possibly evident as slightly elevated caudal annulets without depressions along midline of body; median dorsal abdominal tubercles absent; lateral abdominal tubercles virtually absent; ventrolateral tubercles absent; venter of abdominal segment IX rounded, not protuberant; abdominal segment X (fig. 26) short, rounded as seen in lateral view, centrally attached to segment IX; venter of abdominal segment X not produced, without conspicuous, darkened spiculation; dorsal surface of segment X without transverse ridge and without dorsal median projection; anus positioned dorsally on segment X.

Spiracles conspicuously small, not on elevations and not surrounded by sclerites; atria

somewhat flattened but globose, produced above body surface; atrial wall perhaps faintly ridged, but without spicules, denticles, or spines; atrial rim present; peritreme moderately wide; primary tracheal opening circular, with short collar; collar apparently smooth; spiracular subatrium elongate, length greater than four times that of atrium, consisting of approximately 12 to 15 annulations. Male with ventral median, transverse cuticular scar immediately in front of intersegmental line between segments IX and X; imaginal disc visible on some specimens; female sexual characters (cuticular scars and imaginal discs) not visible.

MATERIAL STUDIED: Approximately 35 live and preserved predefecating and postdefecating larvae, Killi Sarda, 12 km south of Quetta, Baluchistan, Pakistan, various dates, May 1984 (J. G. Rozen, R. J. McGinley).

#### PHYLOGENETIC RELATIONSHIPS OF *PARARHOPHITES*

A study of the phylogenetic relationships of *Pararhophites* to other long-tongued bees was based on a cladistic analysis of the biological, larval, and adult characters listed below. Most characters were polarized into plesiomorphic (0) and apomorphic (1) states based on outgroup considerations. In addition to *Pararhophites*, the study taxa included: *Ctenoplectra*, the apparent sister-group of all long-tongued bees (Michener and Greenberg, 1980); Exomalopsini, a presumed relatively primitive group of anthophorids (Michener and Moure, 1957); and the three megachilid subfamilies, Lithurginae, Fidelinae, and Megachilinae. While most genera of the included study groups were examined for character coding, our coverage of megachiline taxa was limited. The character matrix analyzed is presented in table 1.

#### NESTING BIOLOGY CHARACTERS

1. Specialized glandular cell lining: (0) present; (1) absent or lining made from foreign materials, e.g., leaves, pebbles, resin, etc. Most bees including ctenoplectrids (Rozen, 1978), the apparent sister-group to long-tongued bees, line their cells with a waxy or varnishlike substance that they

TABLE 1  
Character Matrix Used for Analyzing Relationship of *Pararhophites* to Other Long-Tongued Bees

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
<i>Ctenoplectra</i>	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Pararhophites</i>	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	0	0	0	1
Fideliinae	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	0	1	0	1	1	2	0	0	1
Lithurginae	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	2	1	0	0	0
Megachilinae	1	0	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	2	1	0	0	0
Exomalopsini	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	1	1	0

produce themselves. The absence of a lining is here considered to be an apomorphic loss.

2. Cocoon: (0) without incorporated sand layers; (1) with sand layers derived from ingested sand. Among all Apoidea, the ingestion of sand by the mature larva and incorporation of this material into the cocoon is known only in fideliines (Rozen, 1977b) and *Pararhophites*. It, therefore, seems to be a remarkable synapomorphy. However, in *Pararhophites* the origin of the sand is the larval food receptacle manufactured by the ovipositing female. In the fideliines there is no food receptacle, and instead the feeding larva is believed to gather sand from the cell wall. In spite of the different sources of the sand we hypothesized that the sand layer in the cocoon in the two groups is a behavioral homolog because in both taxa (1) the sand is ingested, (2) it is deposited as part of the excreta after most of the normal feces have been discharged, (3) it is incorporated within the outer silken cocoon layer, and (4) it is deposited in elongate strips tending to run from one pole to the other. These are unique features for the Apoidea.
3. Cocoon: (0) rounded at both ends; (1) with "nipple" at one or both ends (figs. 12, 18). A nipple-shaped projection on the anterior end of the cocoon is characteristic of many Megachilinae (Stephen et al., 1969; Rust, 1986), all of the Fideliinae (Rozen, 1977b), but absent in the Lithurginae (Frank D. Parker and Terry L. Griswold, personal commun.). This character is found elsewhere in the Apoidea only in *Pararhophites*.

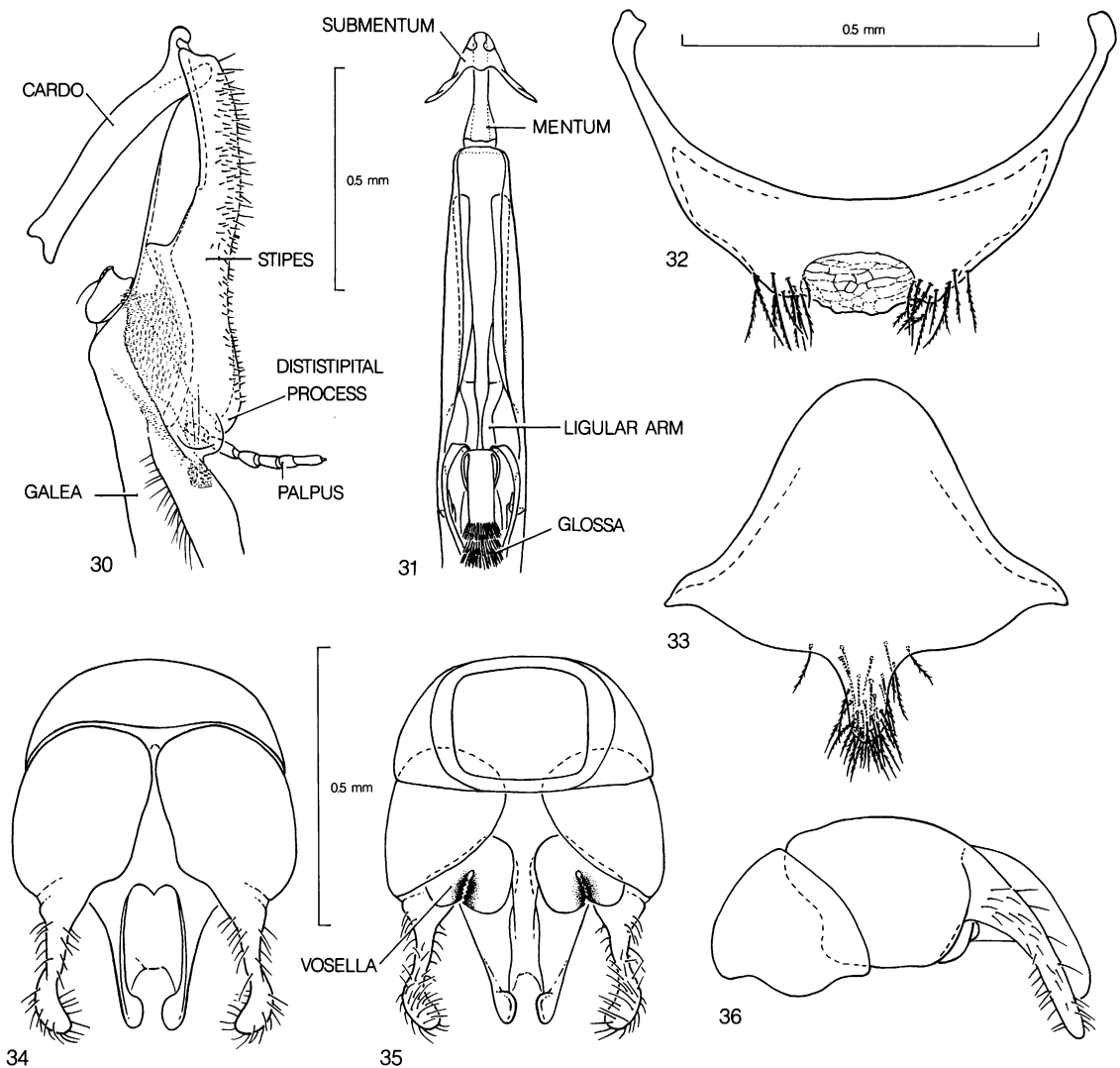
#### LARVAL CHARACTERS

4. Sharp-pointed dorsal projection on mandibular cusp: (0) absent; (1) present (figs. 23–25). These projections are so similar in position and shape in the fideliines, lithurgines, and *Pararhophites* that we consider them homologous. Somewhat different and nonhomologous cuspal projections are found in species of *Melitturga* (Rozen, 1965b), *Caupolicana* (McGinley, 1981), and Augochlorini (Eickwort and Eickwort, 1972) but are most likely independently derived and nonhomologous to similar projections found in fideliines, lithurgines, and *Pararhophites*.
5. Teeth on dorsal and ventral apical mandibular edges: (0) present; (1) absent. Denticulate mandibular edges are characteristic of all short-tongued bee families (Colletidae, Andrenidae, Oxaeidae, Halictidae, and Melittidae). This condition is found scattered throughout most other bee families and is here considered plesiomorphic; however, this polarity should be considered tenuous at present.
6. Epistomal ridge or depression: (0) not reaching level of antennal discs; (1) extending to or beyond level of antennal discs (fig. 27). The low position of the epistomal ridge in relation to the antennal discs is found in andrenids (Micheener, 1953; Rozen, 1966b, 1973a), stenotritids (McGinley, 1981), halictids (McGinley, 1981), oxaeids (Rozen, 1965a), and melittids (Rozen and McGinley, 1974a). The highly arched ridge, presumably of multiple origin, is found in virtually all known colletid lar-

- vae (except *Paracolletini*, McGinley, 1981), megachilids (Michener, 1953; Rozen, 1970, 1973b, 1973c, 1977b), *Ctenoplectra* (Rozen, 1978), *Pararhophites*, most apids (Michener, 1953), and such scattered anthophorid groups as *Ammobatini* (Rozen and McGinley, 1974b), *Ceratina* (McGinley, 1981) and many allodapines (Michener, 1975, 1976). As for the previous character, this polarity should be considered tenuous.
7. Clypeus: (0) moderately elongate and broad, width at most approximately 2.5 its length; (1) short and extremely broad, width approximately 4 times its length (fig. 27). The extremely broad clypeus is highly characteristic of all known megachilid (including fideline) larvae. It is found elsewhere only in the larvae of *Pararhophites* and certain colletids (*Euryglossinae*, *Xeromelissinae*).
  8. Labral sclerite: (0) absent; (1) present (fig. 27). The sclerotized and often pigmented labral sclerite extends across the base of the labrum of *Ctenoplectridae* (Rozen, 1978), megachilines (Michener, 1953), lithurgines (Rozen, 1973c), fidelines (Rozen, 1970, 1973b) (reduced in *Parafidelina*), as well as *Pararhophites*. This sclerite is absent in noncocoon spinning larvae and is absent or reduced in cocoon-spinning *Colletidae* (*Diphaglossinae*) (McGinley, 1981), *Halictidae* (*Dufourea*) (new information), and *Melittidae* (*Meganomiinae*, *Melittinae*) (Rozen and McGinley, 1974a; Rozen, 1977a). It is also absent (or reduced), presumably as a secondary loss, in the cocoon-spinning *Anthophorinae* (Rozen, 1957, 1965c), *Nomadinae* (Rozen, 1966a; Rozen et al., 1978), and *Apidae* (Michener, 1953) except for *Bombus* (new information).
  9. Labral apex: (0) rounded to shallowly emarginate; (1) deeply and broadly emarginate (fig. 27). The conspicuously broad labral apical emargination is characteristic of megachilids (including fidelines) and *Pararhophites*. This condition is possibly correlated with a short and broad clypeus (character 7).
  10. Salivary opening: (0) broad to moderately broad; (1) conspicuously narrow (fig. 27). Among bee larvae that spin cocoons, the salivary lips are normally very broad. This is also true for those sphecoid wasps with transverse salivary lips [*Ampulicidae*, *Sphecidae*; the salivarium in other sphecoids is entirely different, represented by laterally projecting paired spouts (Evans, 1958)]. Conspicuously narrow projecting salivary lips are characteristic of fideline, lithurgine, and *Pararhophites* larvae but not of megachilines.

#### ADULT CHARACTERS

11. Mandibular apex: (0) bifid; (1) multidentate. Multidentate mandibles are found only in megachilines and lithurgines among the taxa being compared here.
12. Dististipital process: (0) absent; (1) weakly to strongly developed. Winston (1979) reported that "all megachilids except *Dioxys* have a dististipital process perpendicular to the distal end of the stipes, extending anteriorly." This may be represented in *Pararhophites* by a very short distal bulge (fig. 30), similar to that found in *Lithurge* (Winston, 1979, fig. 7a).
13. Stipital comb: (0) present; (1) absent or only weakly developed. The presence of a stipital comb is an apparent synapomorphy of the *Ctenoplectridae* and long-tongued bees (Michener and Greenberg, 1980). It presumably is secondarily lost in *Pararhophites*, fidelines, lithurgines, and most megachilines.
14. Galeal blade: (0) without rib; (1) with rib. The presence of a galeal rib is a synapomorphy of long-tongued bees, i.e., megachilids, anthophorids, and apids (Michener and Greenberg, 1980).
15. Labial palpal segments 1 and 2: (0) not sheathlike, usually short; (1) sheathlike, elongate. Sheathlike palpal segments are an apparent synapomorphy of long-tongued bees (Michener and Greenberg, 1980).
16. Glossal rod: (0) absent; (1) present. Glossal rods are found only in long-tongued bees (Michener and Greenberg, 1980) including *Pararhophites*.



Figs. 30–36. 30. Basal part of right adult maxilla, inner aspect. 31. Base of adult labium, dorsal view. 32, 33. Male sterna, VII and VIII, respectively. 34–36. Male genital capsule, dorsal, ventral, and lateral views. Scales refer to 30–31, 32–33, and 34–36, respectively.

17. Ligular arm: (0) fused with prementum; (1) distinct from prementum, with no region of continuous sclerotization between them. Ligular arms are lateral extensions of the premental wall in virtually all short-tongued bees and other Hymenoptera. Winston (1979) hypothesized that a distinct ligular arm represents a synapomorphy for all long-tongued bees plus *Ctenoplectra* and *Melitta*, and that the fused condition in long-tongued

groups represents a secondary condition, i.e., a synapomorphy for anthophorids, apids, and fidelines. However, he emphasized that this polarity may be reversed upon further study. Examination of a mouthpart preparation of *Ctenoplectra* in the Smithsonian collection shows that the ligular arm in this species is free posteriorly but is entirely fused at its point of connection with the premental wall. Michener and Greenberg (1980,

- fig. 3) also indicate that the ligular arm is fused in *Ctenoplectra fuscipes*. Because ctenoplectrids have been hypothesized to be the sister-group of all long-tongued bees (Michener and Greenberg, 1980), a distinct ligular arm is herein treated as an apomorphy found in *Pararhophites*, (fig. 31) lithurgines, and megachilines.
18. Labrum: (0) broad, length at most subequal to width; (1) elongate, longer than broad. An elongate labrum is found only in the Megachilidae among the taxa being treated here (although it is found in certain Nomadinae).
  19. Upper portion of preepisternal groove: (0) present; (1) absent. Among bees in this study, the complete loss of the preepisternal groove is found in *Pararhophites*, lithurgines, and megachilines.
  20. Oblique brush of midtibia: (0) distinct; (1) weak or absent. The loss of this brush is an apparent synapomorphy for long-tongued bees (Michener and Greenberg, 1980).
  21. Basitibial plate of hind leg: (0) present; (1) absent or only weakly developed. Basitibial plates, characteristic of most ground nesting bees, are apparently lost in many different lineages. Among bees in this analysis, they are absent or weakly developed in *Pararhophites*, fidelines, and megachilines.
  22. Scopa on: (0) hind legs; (1) hind legs and metasoma; (2) metasoma. While the abdominal scopa would appear to be an obvious synapomorphy for megachilids, coding *Pararhophites* for this character proved difficult. *Pararhophites* females, laden with copious pollen, carry it on the hind legs and also on the other legs, venter of head, venter of mesosoma, as well as on the apical, seta-bearing parts of the metasomal sterna. Pollen is also scattered on the mesosomal pleural areas and lateral parts of the metasomal terga. Hence, a restricted, well-defined scopal area cannot be identified and the position of the scopa cannot be related to scopal distribution of other bees. As a result, this character was not ordered or polarized in this analysis.
  23. Volsellae: (0) well developed, digitus and cuspis distinct; (1) reduced, digitus and cuspis fused. Among bees<sup>3</sup> in this study, the volsellae are generalized and well developed only in *Pararhophites* and fidelines.
  24. Number of ovarioles in ovary: (0) three; (1) four. Rozen (1986) reports that for those specimens of solitary, noncleptoparasitic bees examined to date, three ovarioles per ovary are characteristic of all bee families except Anthophoridae and Apidae, where four or more ovarioles per ovary occur. While this synapomorphy for anthophorids and apids should be considered provisional, it is interesting that *Pararhophites* has only three ovarioles.
  25. Median part of metasomal tergum VI of female: (0) variously sculptured but nonpapillate, with or without setae; (1) regularly papillate, devoid of setae. In either state, the area may or may not be elevated as a pygidial plate. The papillate area in the Fidelinae occupies most of the dorsomedian part of the tergum and is probably homologous to the pygidial process of other bees. The area in *Pararhophites* is restricted to the median part of the marginal area and because it is not elevated into a distinct plate, it is less clearly homologous to the pygidial plate. Nonetheless, the similarity of the sculpturing between *Pararhophites* and the fidelines is apparently a unique feature for the Apoidea and is treated here as a synapomorphy.
- Characters were analyzed with the PAUP program (Phylogenetic Analysis Using Parsimony) written by David L. Swofford. The small size of the character matrix made it possible to use the branch and bound algorithm which can be extremely time consuming if used for analysis of large and complex data sets; this method is guaranteed to find all most parsimonious trees (Swofford, 1985, unpubl. ms). Because all characters except character 22 were polarized prior to the PAUP analysis, the networks were rooted at a hy-

<sup>3</sup> Terry L. Griswold (personal commun.) states that *Noteriades* (Megachilini) also possesses well-developed volsellae, but, as we have no specimens available, we are unable to assess the significance of this fact.

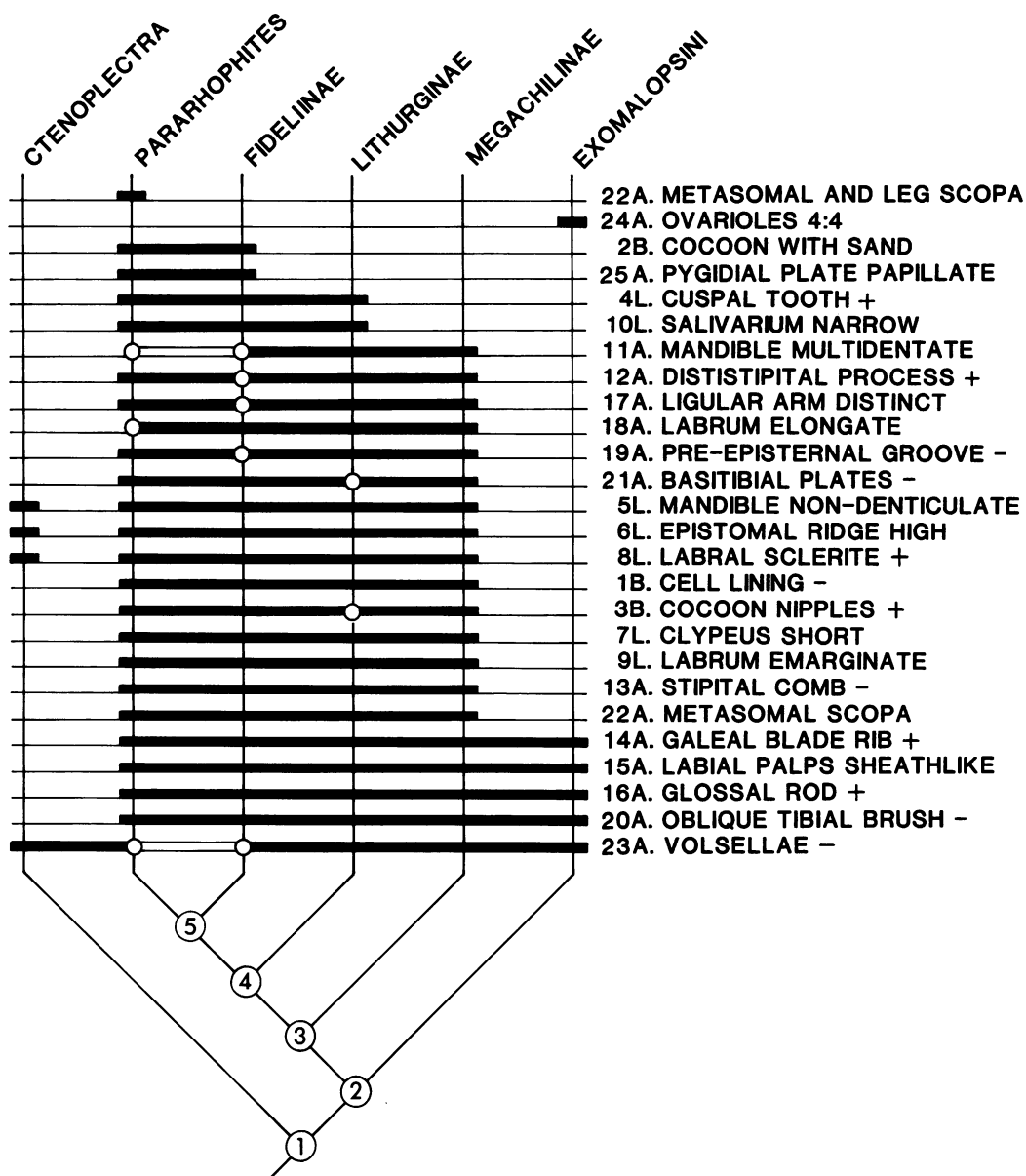


Fig. 37. Cladogram of long-tongued bee taxa and *Ctenoplectra* based on biological (B), larval (L), and adult (A) characters (length = 37; consistency index = 0.70). Black bars indicate the presence of apomorphic character states; circles indicate character state reversals; white bars indicate shared character state reversals; minus sign = feature absent or reduced, + sign = features present or developed.

pothetical ancestor, coded as having all plesiomorphic states.

Two most parsimonious trees were found, both with a length of 37 steps and a consistency index of 0.70. The trees differ only in the placement of megachilines and lithur-

gines relative to the *Pararhophites*-fideline component at node 5 (fig. 37). Both trees are corroborated by the biological characters at node 5 (cocoon with incorporated sand, character 2) and at node 3 (lack of specialized cell linings, character 1). Analyzing the larval

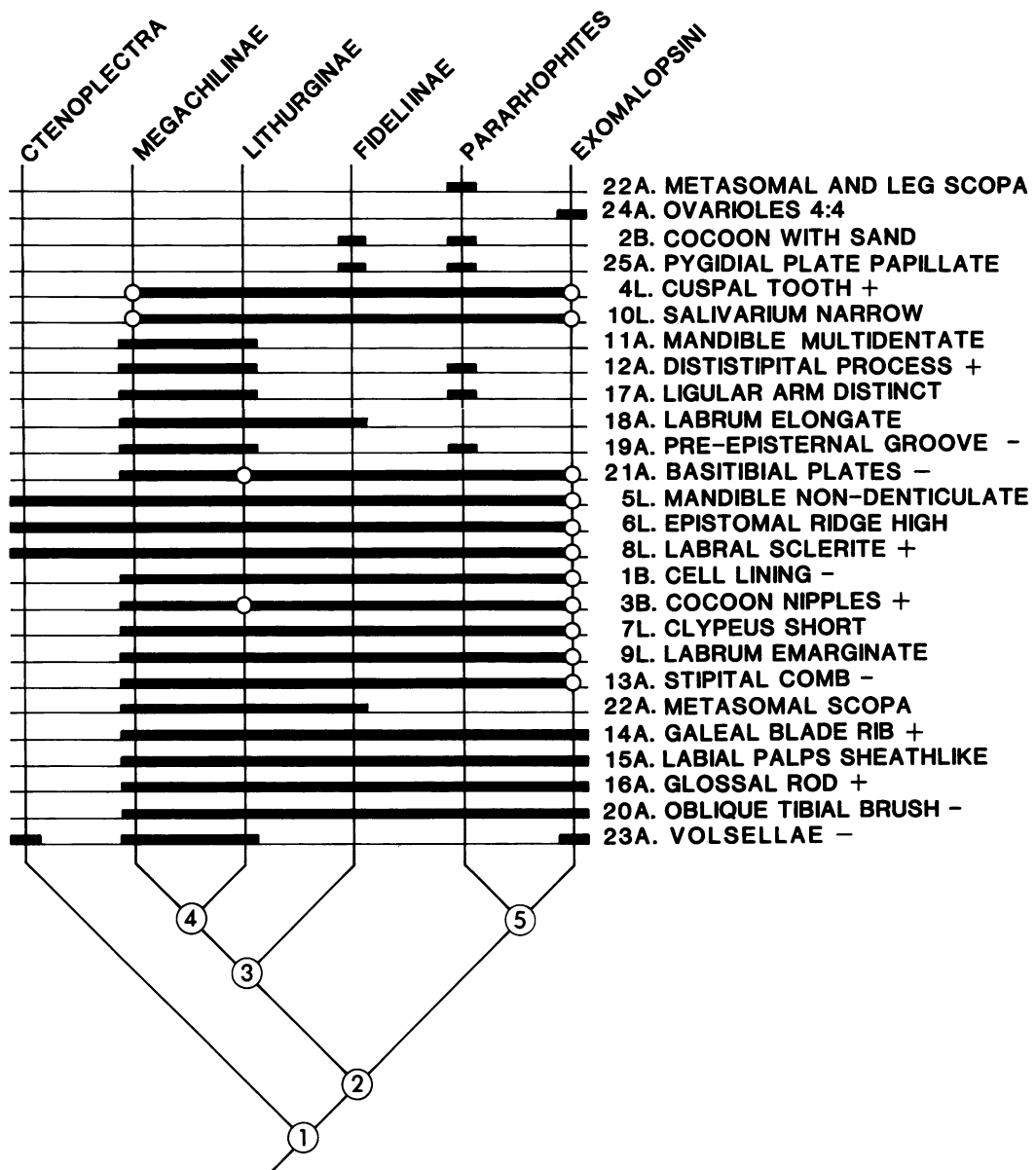


Fig. 38. Cladogram with specified topology, incorporating megachilid intrarelationshihs hypothesized by Michener (1983) and aligning *Pararhophites* with Exomalopsini (Anthophoridae) (length = 48; consistency index = 0.54); for explanation, see text.

characters separately produced only one most parsimonious tree which corroborated the topology of the tree presented in figure 37. In this tree, node 4 [(*Pararhophites*, *Fideliinae*) (*Lithurginae*)] is supported by the very unusual cuspal mandibular projections of the larvae as well as the conspicuously narrow,

larval salivary lips. In the other most parsimonious tree (not figured), the sister-group relationship of the Megachilinae to the *Pararhophites*-*Fideliinae* component is supported by character 21 (reduction or loss of basitibial plates).

Because the focus of this investigation is



not suggest a relationship of *Pararhophites* with the Melittidae, as proposed by Warncke (1977). The authors agree that the biological, larval, and adult characters analyzed above indicate that, although the exact relationships of *Pararhophites* remain uncertain, the affinities of this genus are most likely with the megachilid lineage rather than with the anthophorids and apids. However, each author reaches a separate conclusion as how to classify the genus:

1. McGinley believes that formal transfer of this genus to the Megachilidae or proposing new family status for this taxon seems premature given the intensive amount of work currently underway on the higher classification of apoids. It should remain provisionally classified as an enigmatic tribe in the Anthophorinae. Of major significance is that the Anthophoridae as presently recognized cannot be substantiated on the basis of known synapomorphies. Fundamental questions such as this should be addressed before major modifications in the higher classification of bees are proposed. Hopefully, the characters presented in this paper will be addressed in future studies.
2. Rozen points out that the information presented here demonstrates that retention of *Pararhophites* in the Anthophoridae is palpably incorrect because the family would be polyphyletic. He proposes, therefore, to place the genus as a subfamily (Pararhophitinae) (NEW SUBFAMILY, NEW PLACEMENT) coordinate with the Fideliinae, Lithurginae, and Megachilinae in the Megachilidae. He recognizes that such a placement may indeed be temporary for reasons expressed by McGinley. He argues, however, that a firm understanding of the phylogenetic relationships of the higher apoid taxa may or may not be approaching soon, that the new placement is correct in terms of monophyly and consistent with the present higher classification of bees, and that inserting *Pararhophites* into the megachilids will bring this enigmatic genus to the attention of other bee workers.

Each author sees the validity in the other's position and leaves the final decision to the reader.

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