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Phylogenetic Relationships of *Euherbstia* with Other Short-tongued Bees (Hymenoptera: Apoidea)

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ABSTRACT

The nesting biology of the Chilean *Euherbstia excellens* Friese (Andrenidae: Andreninae) is presented, including nest site preference, nest architecture, provisioning, egg deposition, larval feeding habits, larval defecation, seasonal activity, and daily adult activity. Its egg and mature larva are described. The latter is compared with larvae of *Andrena*, the Panurginae, the Oxaeidae, and the Stenotritidae. The phylogenetic relationships of these taxa are considered on the basis of biological

information and of anatomy of the mature larvae. Data on nesting biology do not appear helpful at this time in revealing the interrelationships of these taxa. Cladistic analysis of 24 larval characteristics suggests that the *Euherbstia* and the Oxaeidae are sister groups which in turn are a sister group of the Panurginae and *Andrena*, and that the Stenotritidae is a sister group of the rest, i.e., (Stenotritidae + ((Panurginae + *Andrena*) + (*Euherbstia* + Oxaeidae))).

INTRODUCTION

This paper explores the evolutionary relationships of the monotypic Chilean genus *Euherbstia* (Andrenidae: Andreninae) with *Andrena*, Panurginae, Oxaeidae, and Stenotritidae. The primary source of data comes from the discovery of nests of *Euherbstia excellens* (Friese) on the southern border of the Atacama Desert in Chile. As a result infor-

mation about the nesting biology of this taxon is now available, and the mature larva can be compared with the immatures of other primitive bees. The first part of the paper presents the information on nesting and describes the mature larva; the second part analyses the new data (particularly with reference to the larva) in an attempt to show

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how *Euherbstia* and the Andreninae are related to other bees thought now, or in the recent past, to be tied to the Andreninae.

The Andrenidae is one of the largest families of short-tongued bees. It is currently divided into two subfamilies, the Andreninae and Panurginae. Information about the biology and immatures of the Andreninae, which contains only six genera (Michener, 1986), has been extremely limited. The nesting biology of a number of species of *Andrena* has been published (see Batra, 1990, and Miliczky, 1988, for references), but other andrenine genera have not been so treated except for a paper by Rozen (1992) which presented incomplete information for *Ancylandrena larreae* Timberlake and a brief mention of the nests of *Euherbstia excellens*. Of the six andrenine genera, larvae of only *Andrena* have been described taxonomically (see McGinley, 1989, for references).

Of all the possible relatives, the Panurginae have been, and continue to be, the group most closely tied to the andrenines. The biology and immature stages of the Panurginae, which contains conservatively 35 described genera as well as a number of undescribed ones, have been extensively studied in recent years. See Rozen (1989) for references concerning life history information, and McGinley (1989), concerning immatures.

The Oxaeidae, a small, homogeneous family identified by many autapomorphies, had in the past been linked to the Andrenidae. Michener (1944) considered it one of the three distinct subfamilies of the Andrenidae because the Old World panurgine genus *Melitturga* shared many similarities with it and therefore seemed to be a phylogenetic intermediate between the Panurginae and the Oxaeinae. Rozen (1964) found the mature larva of *Protoxaea gloriosa* Fox to be markedly different from that of any known panurgine (that of *Melitturga* then unknown) or of *Andrena*. Subsequently he (Rozen, 1965) demonstrated that the larva of *Melitturga clavicornis* (Latreille) shared no significant features with the larva of *Protoxaea* and was able to explain most of the adult similarities as evolutionary convergences associated with mating behavior.

The only feature that could not be so explained was the presence of two pairs of sub-

antennal sutures shared by the oxaeines and typical andrenids, a character upon which Michener (1944) had relied heavily when he included the oxaeines in Andrenidae. Rozen (1965) placed less importance on this feature because double sutures forming a triangle beneath each antenna had also been reported for the Australian colletid genus *Stenotritus* (now placed in the Stenotritidae, McGinley, 1980) and because males of a few *Heterosarus* and *Pterosarus* (formerly placed in the single panurgine genus *Pseudopanurgus*) possessed only a single pair of subantennal sutures. (We now also know that the males of the rophitine genus *Penapis* has four subantennal sutures.) I concluded that the oxaeids should be accorded family status, a judgment that was accepted by most (Hurd, 1979) but not all specialists (Graf, 1966).

Rozen (1964, 1965) was unable, however, to demonstrate the relationship of the Oxaeidae with other bee groups but suggested that a tie with the stenotritines should be evaluated. This linkage was not supported when Houston (1975) discovered and described nests and larvae of *Stenotritus pubescens* (Smith). Synapomorphies between larval *Stenotritus* and oxaeids could not be demonstrated, and the shared features of adults appeared to be convergent, relating to premating behavior (as was the case with *Melitturga*).

Hurd and Linsley (1976) extensively reviewed the literature on many aspects of the biology of the Oxaeidae. Roberts (1973) gave a relatively complete account of the nest of *Oxaea flavescens* Klug, and his information agrees closely with my unpublished observations on *Protoxaea gloriosa* and *Mesoxaea nigerrima* (Fries). Larvae of these three oxaeid taxa are also remarkably similar (Rozen, 1964; Roberts, 1973; unpublished information).

McGinley (1980) recognized Stenotritidae as a family separate from Colletidae, but was unable to establish its affinities with other groups of bees. Hence this family and the Oxaeidae consisted of small assemblages of genera removed from obvious ties with other short-tongued bees. Houston (1975, 1984) and Houston and Thorp (1984) have written a number of papers exploring the biology of Stenotritidae and describing their larvae, and

stenotritid larvae have been made available to me for this study.

The present availability of data on the biology and mature larva of *Euherbstia* combined with similar information about the Panurginae, Oxaeidae, and Stenotritidae invites reconsideration of the possible relatedness of these taxa at this time.

ACKNOWLEDGMENTS

I would like to thank Elizabeth Chiappa, Luisa Ruz, and Haroldo Toro for showing me the site (which was then inactive) in 1989. I extend my sincere appreciation to Luis E. Peña Guzman and Alfredo Ugarte Peña for their assistance and companionship during field investigations in 1991. Richard H. Kruzensky kindly analyzed the soil from the nesting area.

Some of the specimens of *Andrena* examined in this study are on loan from the Essig Museum of Entomology, University of California, Berkeley; the Snow Museum, University of Kansas, Lawrence; and the USDA Bee Laboratory, Utah State University, Logan. I would like to thank Ronald J. McGinley for allowing me to examine the larvae of Stenotritidae which he plans to describe taxonomically by arrangement with Terry F. Houston. The late Radclyffe B. Roberts kindly deposited voucher specimens of larvae of *Oxaea flavescens* in the American Museum of Natural History, making direct comparisons with that species possible.

Thanks are due Wallace E. LaBerge and Charles D. Michener, both of whom reviewed this manuscript.

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NESTING BIOLOGY

DESCRIPTION OF SITE: The nesting site was discovered by Elizabeth Chiappa accompanied by Haroldo Toro and Luisa Ruz in October 1987 in an unpaved roadway approximately 6 km south of Vicuña, Elqui Province, Chile, elevation 600 m. Although the site was completely inactive in October 1989 (no doubt because of the very dry winter), it was fully active when visited on October 16, 1991,

at the start of the present investigation. I studied it intensively for three days and continued thereafter to make casual observations while pursuing other investigations through October 20. I revisited the site on November 15 and 16.

The site was on an arid mountainside at the southern end of the Atacama Desert. This region has been called the Coquimban Desert by Peña (1966) and O'Brien (1971). O'Brien characterized the Coquimban Desert as having "a rich xerophytic flora, with many cacti and shrubby legumes." Prof. Dr. Rodolfo Gajardo, University of Chile, refers to its vegetation type as desertic shrubby (Peña, personal commun.) and believes that the area contains remnants of the old flora that existed in the Atacama Desert. Gajardo suggests that *Euherbstia* and the related *Orphana* may also be relicts. Ground cover in the vicinity of the site (fig. 1) was dominated by low herbaceous plants and scattered shrubs. Precipitation, which obviously strongly influences the ecology of the area, occurs during the winter, and flowering coincides with spring warming. Hot dry summers follow, with no new flowering on the mountainside. Consequently, adult activity of bees is limited to the spring.

The pollen-nectar plant of *Euherbstia excellens* at the site was not found even though three persons collected in the area for the five days of study. This fact suggests that the food source was remote from the nesting site.

Approximately 20 nests were discovered, all restricted to a completely unvegetated, recently graded, unpaved road (figs. 1, 2), at the base of a *cuesta*, far from any source of permanent or semipermanent water (5 km from the Elqui River). Nests were in the identical place where Chiappa had found them abundant in 1987; they were scattered in an area about 6 m long and 1.5 m wide on the side of the road, where the surface sloped 20° from horizontal. The nesting surface was completely unshaded and rarely traversed by motor vehicles. The substrate contained numerous irregular cracks created by the shrinking of soil as it dried. These cracks were obscured in many places by a thin (approximately 1 cm) layer of fine loose powdery soil.

Subsurface soil was moist and had a clay texture. Particle size on analysis was found



Fig. 1. Nesting site of *Euherbstia excellens* in unpaved road (arrow), 6 km south of Vicuña, Elqui Province, Chile.

to be 30% sand, 26% silt, and 44% clay. The soil was difficult to dig because of its hard, compact nature and tendency to fracture into large chunks. Other areas in the roadway seemed equally suitable for nesting by *Euherbstia* so that it is unclear why the nests were restricted to this limited area.

The cracks in the soil, resulting from its clay composition, appeared to be important not only for *Euherbstia* but also for a number of other bee taxa. *Tapinotaspis* sp., a long-tongued undescribed panurgine genus, and *Leioproctus erithrogaster* Toro and Rojas and its cleptoparasite, *Kelita toroi* Ehrenfeld and Rozen (New Information) commonly nested in the roadway and used these cracks as entrances to the subsurface.

In addition, other bees were encountered in the area but were not detected nesting in the roadway. *Chilimalopsis parvula* Toro was abundant during the October study, and four females of the andrenine *Orphana*² were col-

lected between 6:06 and 7:40 p.m. on November 15 and 16 on the flowers of *Adesmia*. Nests of neither of these bees were found, but two nests of *Parasarus atacamensis* Ruz were observed nearby but not in the same road and in different soil conditions.

DESCRIPTION OF NESTS: We examined three nests with care and encountered numerous others from the current year as well as from previous years while reaching these three and while searching at random for immatures.

Nests were constructed and occupied by single females, and all nest entrances were in cracks (fig. 3). Tumuli, always of loose soil, were apparently invariably present but were often inconspicuous because much of the excavated soil accumulated in cracks rather than on the surface. Hence entrances were best

cies are currently recognized (Rozen, 1971), the females collected here bridge the coloration differences of the two species and raise the question as to whether the species are distinct. Now that we suspect the vespertine habits of *Orphana*, series of males (and more females) can perhaps be collected to answer this question.

² This genus, considered rare, may be vespertine as suggested by the hours of collection. Although two spe-

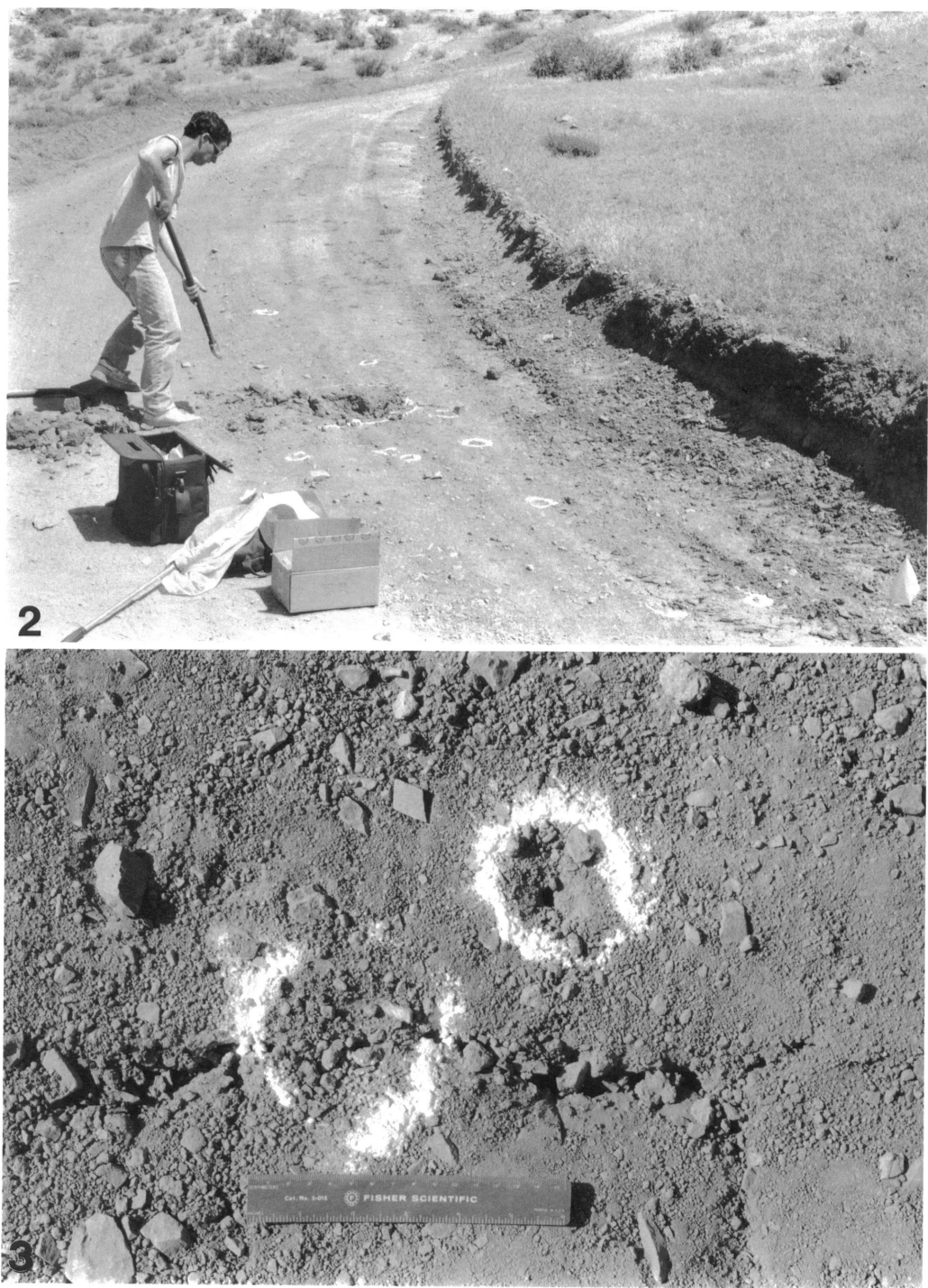


Fig. 2. Nesting site of *Euherbstia excellens*. White circles of plaster-of-Paris powder mark nest entrances.
Fig. 3. Close-up of two nest entrances.

identified by observing returning females as they descended into cracks. One conspicuous tumulus was about 7 to 8 cm in diameter and less than 1 cm high. Excavated material tended to accumulate on the downhill sides of entrances.

Within the cracks, entrances were open, and main tunnels descended following a meandering path first through the crack itself and then into the substrate. Main tunnels were generally open; apparent occasional short plugs may have been created either by the female or by our own excavation accidentally allowing soil to fall into the tunnel. Circular in cross section and 6.0 to 7.0 mm in diameter, tunnels were unlined, and their walls were rather rough and completely absorbent to water droplets when tested. Microscopic examination of the walls showed distinct imprints of the females' pygidial plates, indicating that females tamped the walls repeatedly during excavation.

Apparently females excavated main tunnels to their lowest level before starting cell construction. Cells, connected by short side tunnels to the main tunnel, were then excavated, provisioned, and closed one by one in a generally ascending order. Hence, lower cells tended to contain the oldest immatures, and cells at the upper levels were most recently constructed and provisioned. However, groups of cells in a nest at approximately the same depth not infrequently were found to have a slightly older immature above a younger one. This might be explained if some side tunnels sloped more than others or if a female, after filling a side tunnel, constructed the next one at a slightly greater depth because the main tunnel had not been completely filled to the level of the last constructed cell.

Side tunnels leading to cells were short, as evidenced by cells being closely grouped around main tunnels. Distances between cells in a group measured 2, 2, 2.5, 2.5, 3, 3, and 5 cm for a sample of seven pairs of cells from a number of nests. Side tunnels were the same diameter (approximately 6.5 mm) as main tunnels except they narrowed at the cell entrance to about 5.0 mm. Their walls bore pygidial impressions like those of main tunnels. Side tunnels were filled after cell closure

and usually became indistinguishable from the substrate.

Cells were arranged singly (i.e., not in linear series) at a depth of 13 to 49 cm. They were elongate ovals, 16.0 mm long ($N = 7$) and 8.0–9.2 mm in maximum diameter (median 9.0 mm; $N = 9$). Rounded at the rear, they appeared somewhat asymmetrical in that the ceiling was perhaps slightly more vaulted than the floor. Cell orientation varied greatly, with the long axis tilting from 35 to 85° (median 50°; $N = 19$) from horizontal, the front end always higher than the rear.

Cell walls (as distinct from linings) were not distinguishable in texture, hardness, or color from the substrate. Cell linings were shiny, and covered the entire surface of the cell except for the closure. When the substrate was allowed to dry, the cell lining appeared semitransparent and waxlike in that it could be scraped with sharp forceps leaving a shiny trough and a ribbon of scraping. Furthermore, the lining could not be peeled from fragments of moist cell wall as the wall was broken. However, this material was not waxlike in that, when a piece of cell wall was heated on a hot plate to 700°F, the lining did not melt but rather it charred (as does paper at the same temperature). When a piece of dried cell wall with attached lining was submerged in water, the wall fell apart and separated from the lining. However, a thin layer of very fine soil continued to adhere to the lining, suggesting that the lining material (presumably a secretion) had slightly impregnated the cell wall and had bound together fine soil particles as it was applied by the female. The lining was completely waterproof when tested with a droplet of water. The inner cell surface was quite smooth and shiny although some small pebbles jutted into the lumen of a few cells. All such protrusions were covered by the lining. Some cells also exhibited faint impressions presumably made by the female's pygidial plate.

In addition to the lining, fresh cells bore a liquid over most of the inner surface except near the closure. This liquid imparted a high gloss that was more reflective than that of the cell lining alone. In some cells it beaded into small flattened bubbles as if an oil were involved in addition to a water-soluble liquid.

When cells dried after excavation, the liquid disappeared. The source and significance of this liquid are unknown. However, the thin veil of mold (described below) on the inner surface of cell closures and cell walls adjacent to closures (surfaces without the liquid) might suggest that the liquid is a mold inhibitor.

Cell closures were distinct spirals on the inner surfaces which varied from being slightly concave to having the center coils considerably more recessed than the outer ones so that surfaces were more strongly concave. The fill of the side tunnel fused with the closure in most cases, so that the presence of a concave outer surface is uncertain. One closure may have had a distinct outer surface in which case the closure was 3.0 mm thick in the middle. In any event, closures were unlike the elongate, loosely filled ones of *Ancylandrena larreae* (Rozen, 1992) and the double or multipartitioned closures of Stenotritidae and Oxaeidae.³ The coils of the spiral closure were

³ Houston (1984, 1987) and Houston and Thorp (1984) recognized and carefully described cell closures of the Stenotritidae as consisting of one or more outwardly concave septa of soil ("false cell bases") in the lateral in front of a plug of soil closing the cell mouth. The inner surface of the plug bore a concave spiral pattern (characteristic of many groups of bees); its outer surface was identical to the concave septa in front of it. Between the outer surface and the septum in front of it, the lateral was filled with loose soil and gravel, as were spaces between septa if there was more than one septum. Because such closures had not been observed before, Houston (1987) believed them to be restricted to the Stenotritidae. I now believe that the elongate cell closure of *Ancylandrena* (Rozen, 1992) may be a homologous behavioral feature. Furthermore, on examining the cell closures of *Protoxaea gloriosa* Fox deposited in the American Museum of Natural History, I found that they too routinely possessed concave septa—in one case as many as 11 septa in addition to the outer surface of the plug! This matter becomes even more complex because in the same unpaved road where *Euherbstia excellens* nests, a new panurgine genus with an extremely long tongue nested and its cell closures consisted of three to four septa (including the outer surface of the plug). Hence what seemed at first to be a behavioral autapomorphy of the Stenotritidae is actually also found in the Panurginae and Oxaeidae (but presumably not in *Euherbstia*). Further investigations into other groups of bees should be pursued in order to understand the evolutionary implications of this feature.

In the case of Stenotritidae, *Ancylandrena*, and the

distinct, rough, and uncoated. They varied considerably in width from cell to cell so that some cells had as few as three coils, and others as many as five, although most had four to five coils. Diameter of the inner surface of cell closures ranged from 5.2 to 6.5 mm (median 6.0 mm; N = 11). These figures are greater than the diameter of the cell entrance because most closures extend into the cell beyond the narrowest part of the cell entrance.

All except very fresh cells exhibited a mass of white, interwoven, fine mold hyphae covering the inner cell closure and extending several millimeters onto the cell wall and into the cell lumen. This mass partly obscured the spiral structure of the closure but was not sufficiently dense to hide the pattern completely.

PROVISIONING AND DEVELOPMENT: Larval provisions of *Euherbstia excellens* were mealy moist, grayish orange masses formed into flattened spheres. The spheres had a height (minimum diameter) of 5.3 to 6.0 mm (median 5.5 mm; N = 9) and a horizontal diameter (maximum diameter) of 7.0 to 7.6 mm (median 7.2 mm; N = 10). One pollen mass was slightly elongate with a height of 5.7 mm, greater horizontal diameter of 7.2 mm, and the other horizontal diameter of 6.7 mm. The flattened spheres were dull on the surface and lacked a coating of either nectar or waterproof material. Because the masses were sweet to taste, nectar is thought to be the liquid that held the pollen together. The flattened spheres were positioned toward the rear of the cell with the plane of the maximum diameter approximately parallel to the long axis of the cell.

Eggs and larvae rested on top of the pollen mass (i.e., the surface opposite to that which

new panurgine, brood cells are horizontal or nearly so, but the *Protoxaea* cells are vertical. Cell walls of Stenotritidae, *Ancylandrena*, and *Protoxaea* are thick and harder than the substrate and in all of these three genera the cell wall extends forward surrounding the lateral where the concave septa are found but no farther. Because of the hard walls surrounding the septa, I think of the septa and the spiral plug together as the components of the cell closure. The cell wall of the new panurgine is thin so that whether it extends forward to surround the septa is uncertain.

was in contact with the cell floor). One egg, 3.1 mm long and 0.7 mm in maximum diameter, was attached to the pollen mass only by its posterior end while its more blunt anterior end, raised from the food mass, pointed toward the cell closure. It was white, and its chorion was nonreticulate and shiny.

Young larvae fed on the pollen-nectar mass immediately beneath their heads, and, as they grew, more and more of the front of the sphere disappeared. Their position in relation to the food mass did not change, so that, even when one third or one fifth of the food mass remained, the large larva rested on the remaining food (which appeared as a crescent seen in lateral view) even though the abdominal apex touched the rear cell floor. Larvae did not reorient to rest on their dorsa on the cell floor, as do many panurgines. With most (but certainly not all) Panurginae, larvae that have eaten approximately half the food move onto their dorsal tubercles, cradle the food masses on their venters, and bring their heads upward toward the food to complete ingestion.

Larval feeding of *Euherbstia excellens* progressed rapidly. Nesting activity (nest construction, foraging, egg-laying, and larval growth) was at the maximum during the initial investigation in mid-October, and by November 16 all larvae encountered at the site had completed feeding, had defecated, and had taken on all aspects of postdefecating forms including darkening and hardening of the integument and pigmentation of the spiracular tubercles.

Fecal material was deposited as a single curved thin mass appressed to the rear and one "side" of the cell. The curvature of the mass conformed to the curvature of the cell. Because of the uniformity of this placement in many cells, it seems likely that the "side" of the cell was actually the ceiling, as is usually the case with panurgines. Feces-laden cells were not observed in situ so that further study is required.

Larvae of *Euherbstia* do not spin cocoons, and as described below do not have the anatomical structures typical of cocoon-spinning larvae. Postdefecating larvae had a rigid integument, so that when punctured or severed in two, their bodies retained their shape.

Emerging adults exited from the cells through the cell closure. Vacated cells were filled with soil, and the fecal material remained at the rear of the cell as did the larval integument which could easily be recognized by the sclerotized and distinctive spiracular tubercles.

SEASONAL AND DIURNAL ACTIVITIES: All immatures encountered at the last visit to the site (November 15 and 16, 1992) were postdefecating larvae so that there is no doubt that this species has at most a single generation per year. Furthermore, a significant part of the population may take two (or more) years to mature because during the October study we found many postdefecating larvae obviously remaining from the previous year and no pupae (which meant that none of these larvae were destined to develop further during the current year). Lack of total population emergence in any one season might have an adaptive advantage for bees living in the vicinity of Vicuña because of the uncertainty of winter precipitation from one year to the next. Flowering of food plants apparently is not a dependable annual event, as indicated by the absence of *Euherbstia* nesting in October 1989.

Postdefecating larvae that developed in 1991 remained slightly active even two months after reaching that stage. They continuously (even when not touched by forceps) rotate the abdominal apex very slowly by slightly flexing the middle segments of the abdomen. With one specimen, the complete rotation took 20 seconds. In the brood cell such activity apparently results in a slow shifting of the larval position or even rotation of the entire larva. The advantage (if any) of such activity is unknown. After this observation was noted on 15 larvae from the current season, I examined three postdefecating larvae remaining from the previous season and found them completely inactive. Surviving larvae from the current season had become inactive by July, nine months after defecating, but I did not observe when they had reached that stage. In any event muscular activity ceases before the following season of emergence. This prolonged period of slow abdominal flexing by postdefecating, hibernating larvae is uncommon in the Apoidea; most

bee larvae when diapausing become inactive within a matter of days upon becoming postdefecating forms. Indeed, the term "postdefecating larva" was originally coined to describe overwintering, completely inactive larvae after they had voided their fecal material and assumed (at least in the cases of noncocoon-spinning larvae) integumental changes that apparently help insure against water loss.

Adults of *Euherbstia excellens* were active during the warm part of the day. Provisioning for a few females started before 10:00 a.m. and still continued into late afternoon, but peak activity seemed to be around midday. Many males were observed a few meters from the nesting area searching the ground for crevices, presumably their nighttime location, around 3:00 p.m. Females almost certainly spend the night in their nests. A few females seen searching the ground late in the day for convenient cracks in which to spend the night were probably individuals that had either completed their nests or had not yet started nesting.

PARASITISM: No cuckoo bees were associated with any nests of *Euherbstia excellens*. Cells were heavily infested by meloids. Bombiliids, while common in the area, did not appear to attack *Euherbstia* nests in that no larvae were recovered from any of the cells.

DESCRIPTION OF MATURE LARVA

Figures 4–14

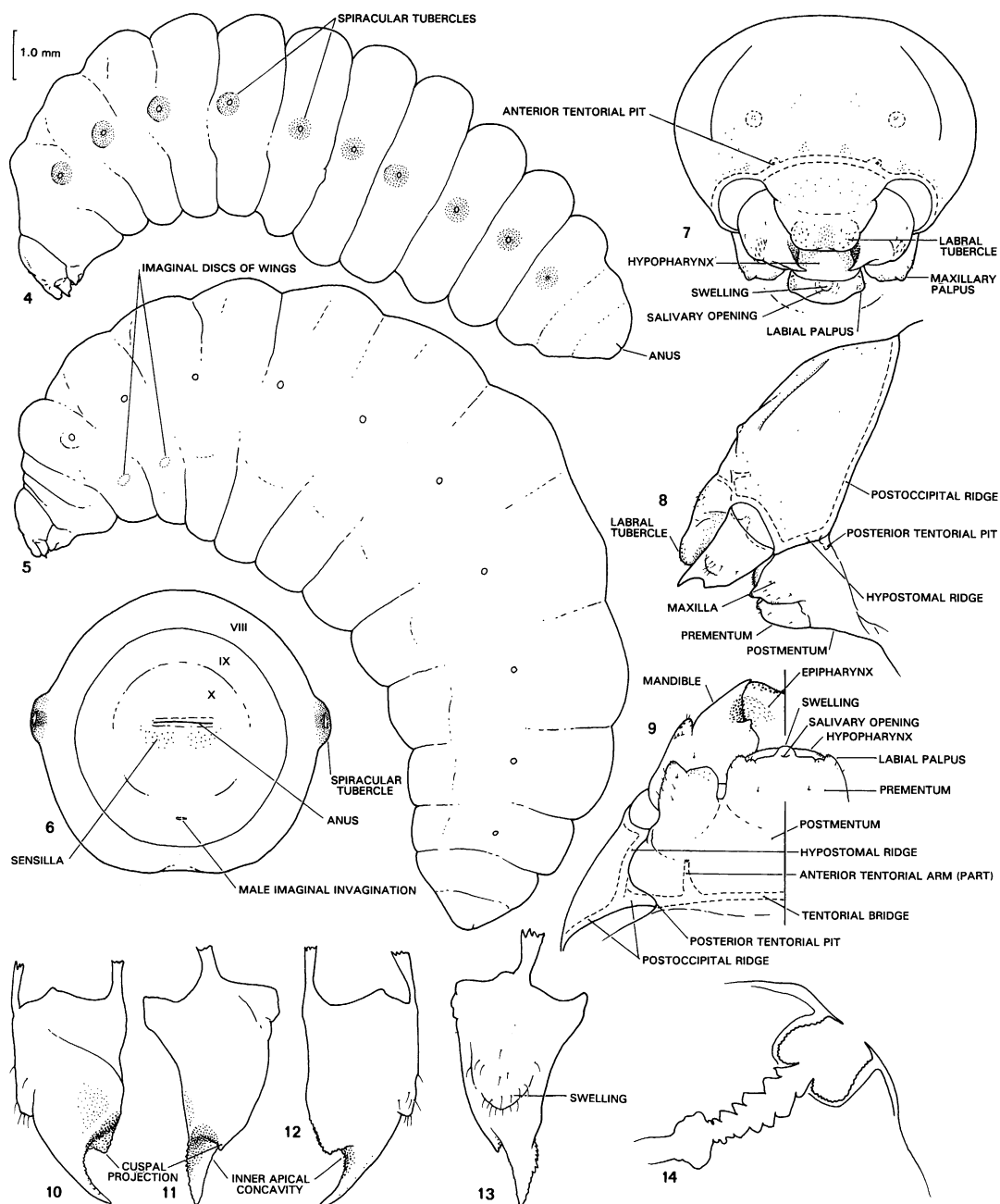
DIAGNOSIS: The mature larva of *Euherbstia* can be distinguished from available larvae of *Andrena* by the features listed here. Characteristics of *Andrena* are given in parentheses with figure numbers referring to Rozen (1973). Vertex not produced and without swelling on each side above antenna (fig. 8) (produced on each side and in many cases with distinct swelling above antenna, Rozen, 1973: figs. 5, 6); antenna on vague swelling (fig. 8) (on pronounced swelling, Rozen, 1973: fig. 6); epistomal ridge between anterior tentorial pits well developed (fig. 7) (absent, Rozen, 1973: fig. 5); mandible robust at base, slender and tapering apically (figs. 11, 13) (tapering throughout its length to slender apex, Rozen, 1973: fig. 9); mandibular cusp pro-

duced into acute, toothlike projection (figs. 10–13) (not strongly produced, obtuse, Rozen, 1973: figs. 8, 10, except in *Andrena*⁴ sp. from Chiapas, Mexico⁵); swelling on outer surface of mandible pronounced (figs. 10, 12, 13) (small, inconspicuous, Rozen, 1973: fig. 8, except in *Andrena* spp. from Chiapas, Mexico, and Lusignan, France); labiomaxillary region greatly recessed (fig. 8) (only moderately recessed, Rozen, 1973: fig. 6); cardo and stipes not sclerotized, vaguely pigmented (more sclerotized); spiracular tubercles present (figs. 4, 6) (absent, Rozen, 1973: figs. 3, 4, 7); body without dorsolateral tubercles (figs. 4, 5) (with more or less transverse tubercles on anterior segments; on abdominal segments these tubercles distinctly transverse and appearing as elevated caudal annulets in lateral view, Rozen, 1973: fig. 3).

The Panurginae as larvae are a diverse group. Although many of their larvae have been described (McGinley, 1989), others are still unknown. The mature larva of *Euherbstia excellens* can probably be separated from most if not all Panurginae by the following (panurgine features in parentheses) but this listing is not necessarily complete: Labral tubercles apical, rounded (figs. 7, 8) (arising from labral disc, usually acutely pointed); mandibular cusp produced into acute, toothlike, denticulate projection (figs. 10–13) (not pro-

⁴ These species include the following: (*Callandrena*) *accepta* Viereck, (*Thysandrena*) *bisalicis* Viereck, (*Scrapteropsis*) *morrisonella* Viereck, (*S.*) *imitatrix* Cresson, (*Tylandrena*) *hallii* Dunning, (*T.*) *perplexa* Smith, (*Leucandrena*) *erythronii* Robertson, (*L.*) *placida* Smith, (*Euandrena*) *caerulea* Smith, (*Melandrena*) *flexa* Malloch, (*Larandrena*) *miserabilis* Cresson, and two unidentified species of *Andrena*, one from Lusignan, France, and the other from San Cristobal de las Casas, Chiapas, Mexico. In addition, the published descriptions and/or illustrations of larvae of other *Andrena* species listed in McGinley (1989) seem to agree.

⁵ The mandible of this species is similar to that of *Euherbstia excellens* both because of its produced, dentate cusp and because the outer swelling is large and closer to the mandibular apex than base. In other respects the larva agrees with the characteristics of *Andrena* presented here, and the cuspal teeth are substantially larger than those of *Euherbstia*. Unfortunately, no adults are associated with these specimens.



Figs. 4–14. Mature larva of *Euherbstia excellens*. 4. Postdefecating larva, lateral view. 5. Predefecating larva, lateral view. 6. Abdominal segments VIII–X, posterior view (drawn to larger scale than figs. 4, 5). 7, 8. Head, frontal and lateral views. 9. Right half of head, ventral view (drawn to larger scale than figs. 7, 8). 10–13. Right mandible, dorsal, adoral, ventral, and outer views, respectively. 14. Spiracle, side view. Scale refers to figures 4 and 5.

duced, obtuse, or, if so produced as in *Melitturga* [Rozen, 1965: figs. 9, 10, 13], projection not denticulate); spiracular tubercles present (absent); body without dorsolateral tubercles (most segments with conical dorsolateral tubercles).

The following description follows closely the format adopted in Rozen and Michener (1988). Comparisons with oxaeids were made after examination of larvae of *Protoxaea gloriosa*, *Oxaea flavescens*, and *Mesoxaea nigerima*, all in the collection of the American Museum of Natural History. Larvae of the following stenotritids, kindly loaned by R. J. McGinley, were also examined comparatively: *Ctenocolletes nicholsoni* Cockerell, *C. ordensis* Michener, and *Stenotritus greavesi* (Rayment).

LENGTH: Postdefecating larva 12–13 mm.

HEAD (figs. 7, 8): Integument of head capsule without long setae but with scattered sensilla some of which are bristlelike when seen under high magnification; head integument of postdefecating larva moderately pigmented except following more darkly pigmented: clypeus, labrum, mandibles, mandibular coria, and apices of labiomaxillary parts; that of predefecating larva faintly pigmented except for more darkly pigmented mandibles (but not mandibular coria), their apices very darkly pigmented.

Head size of postdefecating larva (figs. 4, 5) small by comparison with rest of body. Vertex (fig. 8) not greatly produced on each side above antenna so that in profile top of head sloping in contrast to that of *Andrena accepta* Viereck (Rozen, 1973: fig. 6); front-to-back length of head capsule short compared to height as is characteristic of andrenids, not elongate as in oxaeids (Rozen, 1964: fig. 3). Tentorium of predefecating larva moderately developed (i.e., not robust) but complete including dorsal arms; anterior tentorial pits moderately low on face; posterior tentorial pits below junction of postoccipital ridge (i.e., posterior thickening of head capsule⁶) and hypostomal ridges, connected to postoccipital thickening by mesoventral extension of thickening, this condition sim-

ilar to that found in oxaeids (Rozen, 1964: fig. 3) except area around pits more strongly recessed and pits larger; postoccipital ridge, hypostomal ridge, pleurostomal ridge, and epistomal ridge (including section mesad of anterior tentorial pits) well developed; epistomal ridge nearly straight between anterior tentorial pits, not arching upward; median longitudinal thickening of head capsule only faintly developed near postoccipital ridge, absent below. Parietal bands distinct. Antennal prominences only vaguely developed; each antenna a small, low convexity with approximately four sensilla; antennal disc small. Labrum (figs. 7, 8) bearing two rounded tubercles (swellings) apically, similar to those of *Andrena accepta* (Rozen, 1973: figs. 5, 6) and much more rounded than the acutely pointed labral tubercles of oxaeids (Rozen, 1964: figs. 2, 3); labral apex nearly straight or shallowly emarginate, not cleft or deeply, narrowly emarginate as in Oxaeidae; median part of labrum bearing very fine setiform spicules; sides of labrum as well as epipharyngeal surface with pronounced, nonsetiform spicules; epipharynx vaguely produced medially and without large median preoral lobe as found in Oxaeidae.

Mandibular base robust; mandibular apex (figs. 10–13) slender, curved, simple (i.e., ending in single point), its inner surface directed adoroventrally (contrasting with slender but straight bladelike mandibular apex of oxaeids, the inner surface of which is directed ventrally while the upper serrated edge is directed adorally); upper apical edge distinctly serrate; lower apical margin smooth or with a few irregularities; cusp strongly developed into acute, toothlike projection; cuspal surface and inner apical concavity strongly, evenly denticulate; dorsal surface bearing spicules; outer surface with pronounced swelling bearing numerous bristles. Labiomaxillary region (fig. 8) greatly recessed, extensively fused basally. Maxilla distinct apically, its apex produced mesially and with some spicules; galea not evident; palpus moderately large, about as long as basal di-

⁶ Although this ridge, arching dorsally over the foramen magnum, has usually been called the posterior

thickening of the head capsule, it is the postoccipital ridge, identified as such by the posterior tentorial pits at its lower extremities.

ameter, rounded apically; cardo and stipes perhaps visible as faintly pigmented areas but not as sclerites.

Labium (figs. 8, 9) inconspicuously divided into prementum and postmentum, distinct apically; labial palpus rounded apically, similar in appearance to, but somewhat smaller than, maxillary palpus. Salivary opening appearing as a curved slit but in actuality opening essentially a small transverse slit beneath small median swelling below hypopharyngeal groove, so that folds of integument around this swelling give appearance of curved slit (in *Andrena accepta*, salivary opening similar except labium slightly more projecting on each side of opening so that curvature of folds seems more pronounced; in *Protoxaea gloriosa*, opening also similar except swelling not bordered above by hypopharyngeal groove which is absent medially in all Oxaeidae and integumental folds around swelling pronounced only below). Hypopharynx a single lobe (not bilobed) with surface spiculate laterally and adorally, similar to that of *Andrena accepta*; hypopharyngeal groove deep, clearly separating hypopharynx from base of labium.

BODY: Integument of postdefecating larva rigid, thick, pigmented, of predefecating larva normally soft, thin, unpigmented; integument without setae but with scattered sensilla particularly noticeable below anus and at summits of body segments; some areas minutely spiculate; postdefecating larva with low, rounded spiracular tubercles that are sclerotized and pigmented; predefecating larvae with these tubercles apparently sclerotized but unpigmented; atrial walls of both predefecating and postdefecating larvae darkly pigmented. Body (figs. 4, 5) without dorsolateral tubercles; mesothorax and metathorax dorsally divided into cephalic and caudal annulets; abdominal segments at most indistinctly so divided; body without tubercles except for those supporting spiracles (figs. 4–6); intersegmental lines deeply incised on postdefecating larva except between abdominal segments VIII and IX, and IX and X (fig. 4); venter of abdominal segment IX not produced; segment X attached to IX centrally; segment X without dorsal ridges or plates; venter of abdominal segment X projecting

posteriorly somewhat farther than dorsum. Anus a transverse slit positioned apically (rather than dorsally or ventrally), with faint but distinct lips. Spiracles moderate in size, on distinct sclerites forming top of spiracular tubercles; those of abdominal segment VIII slightly smaller than others; peritreme flat; atrium not projecting beyond spiracular sclerite; atrial wall without denticles or teeth but finely ringed; primary tracheal opening with collar, circular (i.e., not slitlike as in Oxaeidae, Rozen, 1964: figs. 5, 6); subatrium consisting of approximately eight chambers. Male postdefecating larva ventrally bearing short, transverse, median cuticular invagination toward rear of abdominal segment IX; female postdefecating larva ventrally with pairs of paramedian cuticular scars on abdominal segments VII, VIII, IX, each pair closer together than proceeding one.

MATERIAL STUDIED: 28 mature larvae, 6 km south of Vicuña, Elqui Province, Chile, October 17, 18, and November 16, 1991 (J. G. Rozen, A. Ugarté).

PHYLOGENETIC RELATIONSHIPS BASED ON BIOLOGIES AND MATURE LARVAE

BIOLOGIES: Data presented here are not revealing in sorting out the affinities of *Euherbstia* with other short-tongued bees because most aspects of nesting biology appear to be plesiomorphic or not significantly different from the nesting biologies of the other taxa. These aspects include nest configuration, cell orientation and shape, spiral cell closure, appearance of cell linings, shape and position of provisions, and lack of cocoons. *Euherbstia*, the other andrenines, and the Stenotritidae differ from the Oxaeidae in that the latter has vertical cells (also true for some *Andrena*) and provisions that are semiliquid and unshaped. These features presumably are autapomorphies of the oxaeids, and do not illuminate the affinities of that family to the other taxa.

MATURE LARVAE: Because of the uncertain relationships of the involved taxa to one another, a phylogenetic analysis was attempted to determine the interrelationships of *Eu-*

TABLE 1

Explanation of Characters of Mature Larvae of *Euherbstia*, *Andrena*, Panurginae (*Protandrena*), Oxaeidae, and Stenotritidae Used in Phylogenetic Analysis

(Plesiomorphy = 0; apomorphy = 1, 2)

0. Vertex in lateral profile evenly curved (fig. 8) (0); strongly angulate (Rozen, 1970: fig. 14) or even bulbous above each antenna (1). The plesiomorphic condition is found widely among bee families; the apomorphic condition is restricted to *Andrena* and the primitive Panurginae. A reversal of the apomorphic condition occurs in the higher panurgines, but the plesiomorphic condition exists in *Protandrena* and such other primitive members of the subfamily as *Lipanthus*, *Pseudopanurgus*, *Pterosarus*, *Metapsaenythia*, *Rhopitulus*, *Psaenythia*, and *Anthemurgus*.
1. Front-to-back head length normally short (fig. 8) (0); elongate (Rozen, 1964: fig. 4) (1). Among short-tongued bees, the apomorphic condition is found only in the Oxaeidae.
2. Posterior tentorial pit at junction of postoccipital ridge and hypostomal ridge as seen in lateral view (Rozen, 1970: fig. 14) (0); below junction of postoccipital ridge and hypostomal ridge (Rozen, 1964: fig. 3) (in *Euherbstia*, this condition is best seen in ventrolateral view rather than lateral view, fig. 8) (1). Among short-tongued bees, the apomorphic condition is found only in Oxaeidae and *Euherbstia* and would seem to be a strong synapomorphy. However, there may be a correlation between 1) the position of the pits relative to the hypopharyngeal ridge and 2) the fusion of the elements of the labiomaxillary region (character 13) and reduction of the maxillary sclerites (character 15).^a It is unknown whether there is a functional relationship between these features, but the weight to be placed on the position of the pits as a synapomorphy is reduced.
3. Epistomal ridge between anterior tentorial pits complete (fig. 7) or nearly so (0); absent between pits (Rozen, 1973: fig. 5) (1). Multiple losses of the midsection of the epistomal ridge seem more likely than the midsection evolving de novo time and again. Hence the presence of the midsection was considered plesiomorphic.
4. Antennal prominence weak (fig. 8) (0); strong (Rozen, 1973: fig. 6) (1). Because strongly de-

TABLE 1—(Continued)

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- veloped antennal prominences are uncommon in bee larvae, their presence was considered apomorphic.
5. Labral tubercles low, rounded, positioned apicolaterally on labrum (0); acutely pointed, arising abruptly from labral disc (Rozen, 1970: fig. 10) (1). Larvae of many different groups of bees (e.g., Melittidae, Colletidae, Halictidae, Anthophoridae) characteristically have rounded apicolateral labral swelling bearing sensilla, so that this condition is thought to be plesiomorphic. Distinct, sharp-pointed tubercles on the labral disc presumably arose independently in the Panurginae, Oxaeidae, *Euryglossa* (Colletidae), and Nomadinae.
 6. Labral apex entire or weakly broadly emarginate medially (fig. 7) (0); deeply cleft medially (Rozen, 1964: fig. 2) (1). The latter is a unique apomorphy of the Oxaeidae.
 7. Labrum nonspiculate medially on dorsal surface (Rozen, 1970: 13) (0); bearing fine spicules medially (Rozen, 1973: fig. 5) (1). Fine spiculation on the dorsal surface of the labrum is an uncommon phenomenon among bees and hence was judged apomorphic.
 8. Epipharynx without basal swelling (0); with distinct basal swelling (Rozen, 1964: fig. 4) (1). The latter is a unique apomorphy of the Oxaeidae.
 9. Outer surface of mandible with conspicuous tubercle which in some cases extends across dorsal surface of mandible forming a distinct line distally (figs. 10, 12, 13) (0); without a tubercle or with very small one (Rozen, 1973: figs. 8, 10) (1). The polarity of these character states is problematical. At one time, the large tubercle on the outer surface of the mandible appeared to be an autapomorphy of the Halictidae (Michener, 1953; McGinley, 1987). However, the presence of this feature in *Euherbstia*, the Oxaeidae (though somewhat reduced), and in *Ctenocolletes* but not *Stenotritus* in the Stenotritidae (hence coded "?" in table 2), as well as in most but not all halictids suggests that it is a primitive feature that has been lost in numerous different lines.
 10. Mandibular apex normal so that inner apical surface adoral (figs. 10–12) (0); bladellike, rotated so that dorsal apical edge adoral (Rozen, 1964: figs. 10–12) (1). The latter state is found only in the Oxaeidae.
 11. Mandible with subapical tooth (Rozen, 1970: figs. 11, 12) (0); without subapical tooth (figs. 10–12) (1). The polarity of this character is uncertain. The inner apical angle of the sem-
-

^a A similar correlation appears to exist in the Nomadinae among the long-tongued bees (Rozen, 1966).

TABLE 1—(Continued)

- itruncated mandibular apex (Rozen, 1964: figs. 10, 12) of the Oxaeidae is tentatively interpreted as representing a subapical tooth. The differently shaped mandibular apex in the Stenotritidae makes interpretation of its character state uncertain (coded “?” in table 2).
12. Mandibular cusp without strong projection (Rozen, 1973: figs. 8–10) (0); with strong projection (figs. 10–13) (1). The latter condition in *Euherbstia* may or may not be homologous with a similar condition in *Ctenocolletes* and perhaps *Stenotritus*. It is probably not homologous with the cuspal projection of *Melitturga* (Rozen, 1965: figs. 8–13).
 13. Labiomaxillary region produced (0); recessed (Rozen, 1973: fig. 6) (1); greatly recessed (fig. 8; Rozen, 1964: fig. 3) (2). None of the taxa under consideration spins a cocoon, and therefore their larvae have more or less recessed labiomaxillary regions. As discussed under character 2, the apomorphic states of this character may be linked with the apomorphic states of characters 2 and 15. The plesiomorphic condition is characteristic of cocoon-spinning larvae.
 14. Maxilla spiculate at least apically (Rozen, 1973: fig. 5) (0); completely nonspiculate (Rozen 1964: figs. 2–4) (1). Although the polarity of this feature is uncertain, it seems more likely that spiculation is lost rather than regained. The latter is an autapomorphy of the Oxaeidae.
 15. Cardo and stipes well sclerotized (0); evident though weak (1); faint so as to be virtually nonexistent (fig. 8) (2). Strongly developed maxillary sclerites are a primitive wasplike feature; the near loss of any suggestion of them in *Euherbstia* and the Oxaeidae is derived. However, because such evolutionary losses might well happen independently, they should not be considered a strong synapomorphy.
 16. Labium divided into a well-defined prementum and postmentum (0); weakly divided into prementum and postmentum (figs. 8, 9) (1); not divided (Rozen, 1964: fig. 3) (2). The plesiomorphic condition is characteristic of cocoon-spinning bee larvae.
 17. Salivary opening not associated with a curved groove descending from hypopharyngeal groove (0); opening at lower extremity of curved fold or groove extending either from hypopharyngeal groove or, in Oxaeidae which has no such groove, from hypopharyngeal/labial surface above (1). The apomorphic condition exhibits considerable variability (as indicated in the description of the larva of *Eu-*

TABLE 1—(Continued)

- herbstia*), and its anatomical structure and functional basis are not understood at this time. Its significance as a synapomorphy is questionable.
18. Hypopharyngeal groove deep (fig. 7) (0); absent (Rozen, 1964: fig. 2) (1). This groove is present in most groups of bees, suggesting that it is plesiomorphic; rarely is it absent. Among the groups being considered, it is an autapomorphy of the Oxaeidae.
 19. Spiracles not on tubercles (Rozen, 1973: fig. 3) (0); on tubercles that on postdefecating larvae become pigmented and sclerotized (figs. 3–6) (1). Because sclerotized spiracular tubercles on larvae of other short-tongued bees are unknown, their presence is considered apomorphic.
 20. Dorsolateral body tubercles either low and transverse or absent (figs. 4, 5) (0); present on most segments as distinct transverse tubercles, which arise from caudal annulets (Rozen, 1973: fig. 1) (1); present on most segments as conical tubercles (caudal-cephalic annulations not clearly defined on abdominal segments) (Rozen, 1970: fig. 9) (2). In many groups of bees, caudal body annulets are elevated dorsally and in some cases these elevations appear as low transverse tubercles. Hence this condition appears to be plesiomorphic. Among the taxa under consideration distinct, well-defined transverse tubercles are found in only *Andrena* (although this condition has arisen presumably de novo in such groups as the Halictinae and Nominae). Conical tubercles are far less common and among short-tongued bees occur (presumably as separate evolutionary events) only in the Panurginae and Rophitinae. This character is treated as additive, the assumption being that pronounced transverse tubercles are a precursor to conical tubercles.
 21. Spiracular atrium moderately or strongly produced above body wall (Rozen, 1973: fig. 7; 1964: figs. 5, 6) (0); not produced above body wall (figs. 6, 14) (1). The latter appears to be an autapomorphy of *Euherbstia*.
 22. Atrial wall smooth (Rozen, 1973: fig. 7) (0); ridged (fig. 14) (1); spinose (Rozen, 1964: figs. 5, 6) (2). Because both smooth and ornamented atrial walls are found in many bee groups, the polarity of these states is uncertain, and that character was coded nonadditive.
 23. Primary tracheal opening circular (fig. 14) (0); slitlike (Rozen, 1964: figs. 5, 6) (1). The latter condition is unique to the Oxaeidae.

TABLE 2

Data Matrix for Analysis of Relationships of *Euherbstia*, *Andrena*, Panurginae (*Protandrena*), Oxaeidae, and Stenotritidae on Basis of Larval Characteristics

(Character codings given in table 1)

Taxon	Character states				
	01234	56789	11111	11111	2222
Ancestor	00000	00000	0?000	00000	00?0
<i>Euherbstia</i>	00100	00100	01120	21101	0110
<i>Andrena</i>	10011	00101	01010	11100	1000
<i>Protandrena</i>	10011	10001	00010	12100	2000
Oxaeidae	01100	11010	10021	22111	0021
Stenotritidae	00000	0000?	0?110	12000	0000

herbstia excellens, *Andrena*, the panurgines, oxaeids, and stenotritids based on mature larvae. Footnote 4 lists the species of *Andrena* whose larvae were available. The Panurginae are a large diverse group so that the larva of one exemplar, *Protandrena verbesinae* (Timberlake),⁷ was examined because of its large size and because the genus is relatively primitive within the Panurginae (Ruz, 1986) and, therefore, its connections to nonpanurgine taxa might be more obvious than those of highly specialized panurgines. In the Oxaeidae, larvae of *Protoxaea gloriosa*, *Oxaea flavescens*, and *Mesoxaea nigerrima* were used, as well as were larvae of the stenotritids *Ctenocolletes nicholsoni*, *C. ordensis*, and *Stenotritus greavesi*.

Table 1 discusses the larval features used in the analysis, and table 2 is the character matrix. The analysis, using James S. Farris' Hennig86 Version 1.5 program (Farris, 1988), was executed with the *ie* command. Autapomorphies (1, 6, 8, 10, 14, 18, and 21) were coded inactive, and character 22 was coded nonadditive. The result was a single, most parsimonious cladogram (fig. 15), length 28, ci 78, ri 62.

This tree (fig. 15) suggests that, on the basis of larval features, *Euherbstia* and the Oxaei-

dae are sister groups and that they in turn are a sister group of *Andrena* and the Panurginae (as represented by *Protandrena*). The monophyly of the *Andrena*-Panurginae-*Euherbstia*-Oxaeidae clade is supported by a single synapomorphy (17), the presence of a curved groove in which is found the salivary opening (a character first identified and used by McGinley, 1981). As stated in table 1, this character state exhibits considerable variability, and its anatomical structure and functional basis are not understood at this time. These facts suggest that it may not be reliable. Therefore, the analysis was performed again, with this feature coded inactive. Three most parsimonious cladograms resulted (length 27, ci 77, ri 60):

1. (Ancestor + (*Euherbstia* + Oxaeidae) + (Stenotritidae + (*Andrena* + *Protandrena*))).
2. (Ancestor + (*Andrena* + *Protandrena*) + (Stenotritidae + (*Euherbstia* + Oxaeidae))).
3. (Ancestor + Stenotritidae + ((*Andrena* + *Protandrena*) + (*Euherbstia* + Oxaeidae))).

With the exclusion of character 17, the relationship of the Stenotritidae to the other taxa became ambiguous, but the sister-group linkage between *Andrena* and the Panurginae and between *Euherbstia* and the Oxaeidae persisted. Nonetheless, the synapomorphies (2, 13², 15², and 19; 0, 3, 4, 9, and 20¹) uniting each of these two groups are not particularly strong as explained in table 1. Furthermore, the appearance de novo of the apomorphic states of characters 7 and 11 in *Andrena* and *Euherbstia* raises the possibility that they might actually be synapomorphies.

In last analysis, I am not convinced of the phylogenetic relationships suggested by the study of larval characters. At the same time, the hypothesized linkages may be accurate, and they do offer the following avenues of study: (1) Adult characters should be reinvestigated to test the results of the present study. (2) Larvae of other andrenine taxa (*Megandrena*, *Ancylandrena*, *Alocandrena*, and *Orphana*) need to be found and examined to see what bearing they have on the proposed relationships. (3) Although biological characteristics of *Euherbstia* and other

⁷ The larva (and pupa) of this species was misidentified in Rozen (1970) and later in McGinley (1981) as *Psae-nythia bicolor* Timberlake. However, the species attribution to *Protandrena bicolor* (Timberlake) (as *Psae-nythia bicolor* Timberlake) in Rozen (1967) regarding nesting activity and nest architecture was correct.

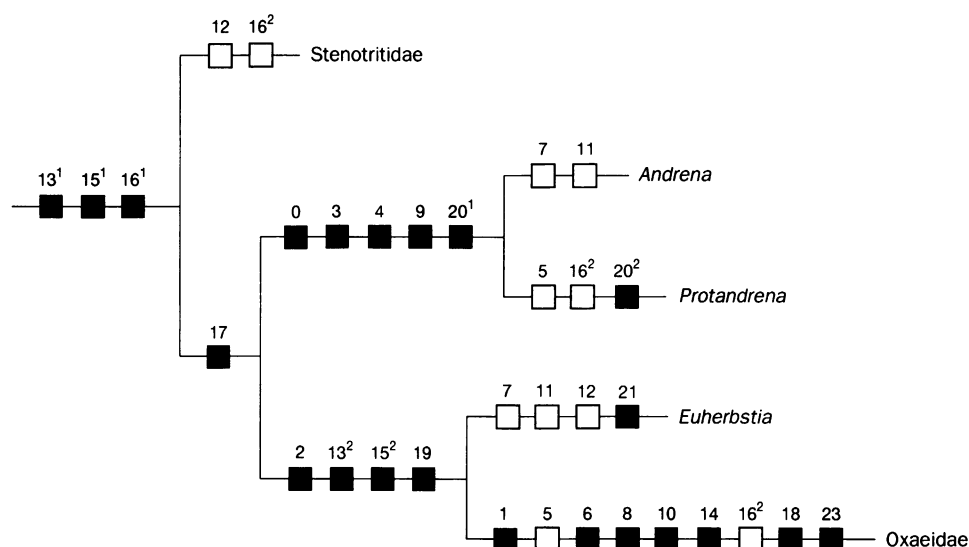


Fig. 15. The single most parsimonious cladogram of *Euherbstia*, *Andrena*, *Protandrena*, the Oxaeidae, Stenotritidae, and a hypothetical ancestor, based on characters of mature larvae. Solid squares are unique character states; open squares are parallel states. Character 11 assumes that the loss of the mandibular subapical tooth is apomorphic, and the undivided labium (character 16) is depicted to have evolved three times from a weakly divided one. All autapomorphies were coded inactive, and character 22 was excluded because its polarity was uncertain. For further explanation, see text.

taxa have not been helpful in defining affinities within this group, new life history features should be identified and additional taxa of Andreninae should be investigated biologically in search of useful comparative data:

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