

The Relictual Bee Genus *Manuelia* and Its Relation to Other Xylocopinae (Hymenoptera: Apoidea)

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Abstract.—The bee genus *Manuelia* Vachal (subfamily Xylocopinae) is redescribed, and its three species, all found in Chile and Argentina, are also characterized. Although *Manuelia* looks superficially like *Ceratina*, it is intermediate in its character combination between the tribes Xylocopini and Ceratinini, and has a few synapomorphies of its own. Its nests are more similar to those of *Xylocopa* than to those of *Ceratina*. It appears to be a relict genus, nearer than any other to the ancestral group from which Xylocopini and Ceratinini diverged. The three species of *Manuelia* are redescribed and emphasis is placed on striking morphological characters that make them as different from one another as subgenera in other Xylocopinae.

Ceratina herbsti Friese is shown to be a new synonym of *Manuelia gayatina*. Because of nomenclatural confusion the type species of *Manuelia* and of the halictid generic name *Corynogaster* Sichel are designated.

A genus of small xylocopine bees, *Manuelia*, consisting of three species found in Chile and Argentina, is so similar superficially to the widespread genus *Ceratina* that it has attracted relatively little attention. Our study, however, shows that it is a relict type, almost as close to *Xylocopa* as to *Ceratina*.

This study was first made by two of us (HVD and JSM) over 20 years ago, then independently repeated with additional material by SFS and CDM; the two manuscripts were amalgamated by CDM since the coverage and conclusions were too similar to justify independent publication. Each manuscript was stronger than the other in some features, and each recorded some significant characters not noted in the other. The illustrations except for the maps were made by SFS.

Nomenclatural Problems

The taxonomic history of the three species is confused and involves the generic name *Manuelia* as well as the names *Corynura* and *Corynogaster* in the Halictidae. Spinola (1851) described the three species of *Manuelia* as species of *Halictus* that possessed certain distinctive characters not shared by other Halictinae. The bees were *Halictus gayi* (p. 208, no. 10, female, male), *H. posticus* (p. 208, no. 11, female, male) and *H. gayatinus* (p. 209, no. 12, female). In the same volume he described the

male of a genuine halictid bee, *Corynura gayi* (p. 301, no. 1), but placed it in the Thynnidae. His associated female was a wasp, but the male was described first and the name *Corynura* has been used for the bee; the problem was discussed by Alfken (1926). Following Spinola, Smith (1854:424–425) listed all three species of *Manuelia* as *Halictus*. Sichel (1867:146) described as new “*Halictus (Augochlora) Smith chrysurus*”; it is apparently a synonym of *H. gayi*. Correctly recognizing the male of *Corynura gayi* as a bee, he also erected a new genus, *Rhopalictus*, to include “*Corynogaster gayi* Spinola” (p. 301, no. 1) and others. Spinola did not mention *Corynogaster* and we must assume that Sichel meant Spinola’s *Corynura gayi* of the same page and number. This was also the interpretation of Herbst (1917) and is supported by the fact that Sichel recognized the difference between the *Halictus gayi* and the *Corynura gayi* of Spinola. Eickwort (1969), in listing *Corynogaster*, noted “*lapsus for Corynura?*” *Rhopalictus* is a synonym of *Corynura* although its type species is *C. flavofasciata* Spinola, not *C. gayi*.

Until 1896 the use of the specific name *gayi* for two unrelated bees, one a xylocopine incorrectly placed in *Halictus*, the other a true halictid, had not resulted in confusion of the two. However, while correctly listing *Halictus posticus* and *H. gayatinus* under *Halictus*, Dalla Torre (1896) placed *H. gayi* in *Corynura* and gave the reference as *Halictus (Corynura) gayi* Spinola, “p. 208 n. 10 & p. 301 n. 1.” Placement of the *Corynura gayi* and the *Halictus gayi* of Spinola as the same species by Dalla Torre, without the recognition that they were different species (indeed they are different families), began a long line of confused nomenclature. Dalla Torre further listed *Rhopalictus gayi* Sichel (“p. 146, n. 1”) as a synonym (the reference should have been to no. 3). As shown above, *Rhopalictus* is concerned only with *Corynura*, not with *Manuelia*.

Alfken (1904:141), recognizing that they are long-tongued bees not related to *Halictus*, placed *Halictus gayi*, *H. posticus*, and *H. gayatinus* in *Ceratina*. Friese (1910) concurred by redescribing *H. gayatinus* as *Ceratina herbsti*. Vachal (1905) erected a new genus, *Manuelia*, in honor of M. Manuel-J. Rivera, for the three species. Vachal did not mention Alfken’s transfer, but arrived at the same general conclusion, namely, that these species are near *Ceratina*. Cockerell (1905) listed *Halictus posticus* and *H. gayatinus* with the comment that Alfken placed them in *Ceratina* and Vachal erected a new genus for them. He incorrectly placed *H. gayi* as a synonym of *Rhopalictus gayi*, i.e., *Corynura gayi* Spinola (p. 301, no. 1), but Cockerell objected to Dalla Torre’s association of *Corynura* with this species. On the other hand, Friese (1916:554) listed *Halictus gayi* (Spinola p. 208), but his description indicates that he had *Corynura gayi* (Spinola p. 301) and he could not distinguish his specimens from *Halictus rubellus* Haliday, a species of *Corynura*.

Sandhouse (1943), apparently following Dalla Torre (1896), designated *Halictus (Corynura) gayi* Spinola as the type species of each of the following generic names: *Corynura*, *Corynogaster*, and *Manuelia*. She listed the last two as synonyms of the first. The combination “*Halictus (Corynura) gayi* Spinola,” however, involves two different species (and families) of bees described by Spinola on different pages. To avoid further confusion, we regard *Halictus (Corynura) gayi* Spinola used by Dalla Torre (1896) and Sandhouse (1943) as a meaningless combination. It is not possible to say whether Sandhouse designated *Halictus gayi* Spinola or *Corynura gayi* Spinola as the type species of the three generic names concerned. Therefore she did not designate valid type species for these genera. The type of *Corynura* was designated

by Alfken before Sandhouse's work, but for the other genera we designate type species here, using Sandhouse's format:

Corynura Spinola (= *Corynogaster* Sichel)

Historia fisica y politica de Chile . . . por Claudio Gay, Zool., vol. 6, p. 296, 1851. Two species.

Type species.—*Corynura gayi* Spinola, 1851, *Ibid.*, p. 301. (By designation of Alfken, 1926, Deutsche Entom. Zeitschr., 1926: 146.)

(*Corynogaster* Sichel) = *Corynura* Spinola

Novara-Expedition. Zoologischer Theil, vol. 2, Hymenoptera, Fossoria et Mellifera. Suppl. p. 146, 1867. Two species.

Type species.—*Corynura gayi* Spinola, 1851, Historia fisica y politica de Chile . . . por Claudio Gay, Zool., vol. 6, p. 301. (Present designation.)

Manuelia Vachal

Bull. Soc. Ent. France, p. 25, 1905. Three species.

Type species.—*Halictus gayi* Spinola, 1851, Historia fisica y politica de Chile . . . por Claudio Gay, Zool., vol. 6, p. 208. (Present designation.)

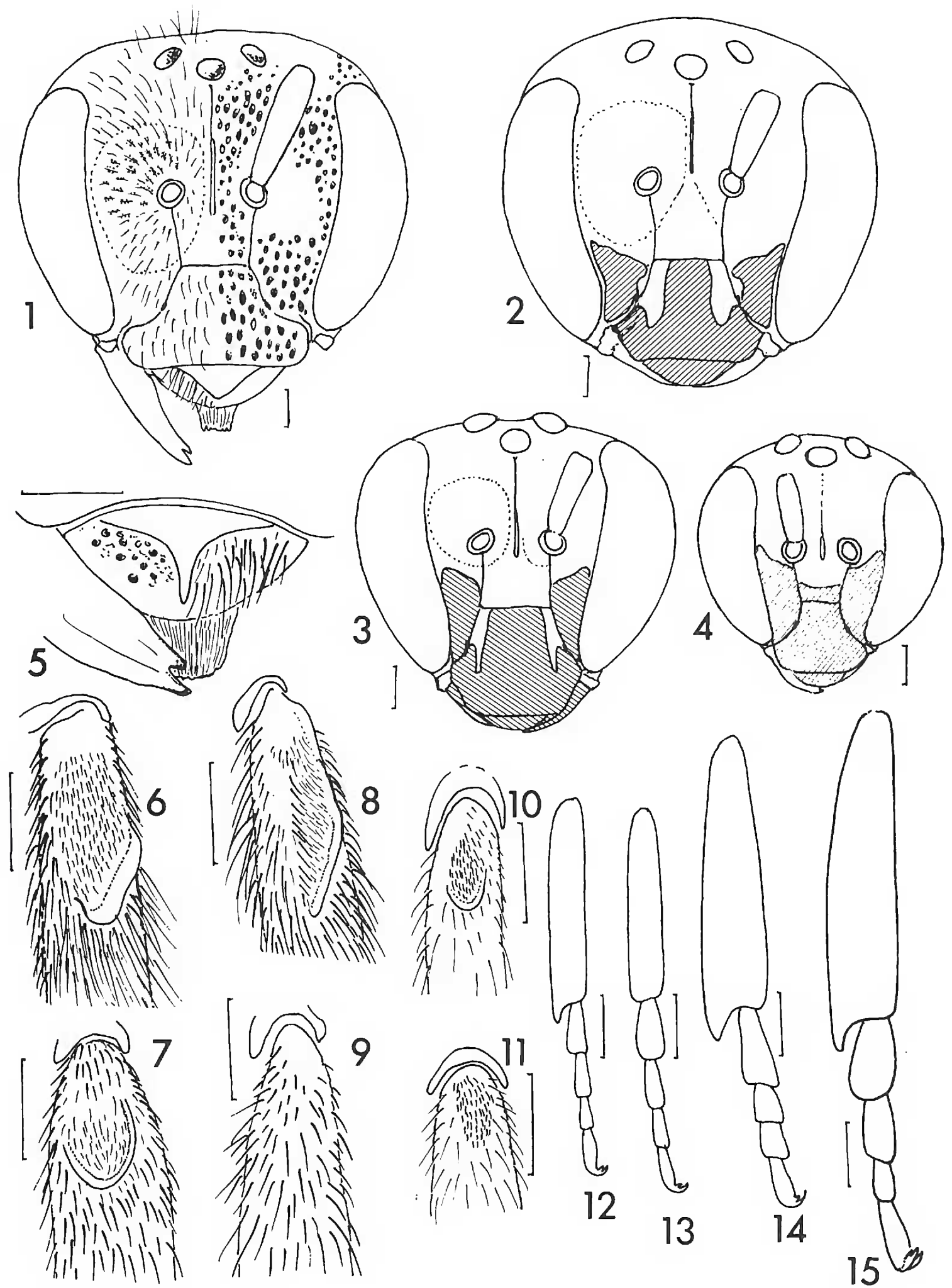
Sandhouse also lists *Halictus gayatinus* Spinola as the type species of "*Presbia* Spinola." In his discussion of the possible generic relationships of *H. gayatinus*, Spinola states (p. 209) that this species does *not* belong to "*Presbia* Illig." Like Sandhouse, we have been unable to discover Illiger's publication of *Presbia* and we regard this name as a nomen nudum. Therefore *H. gayatinus* is not the type species of a genus *Presbia* Spinola, as indicated by Sandhouse.

Genus *Manuelia* Vachal

Description.—Many specific characters are indicated in this description in order to show the variability within the genus. Characters not relating to all three species are marked with the abbreviated names of the species that possess them, as follows: ga = *M. gayi*, po = *M. postica*, and gt = *M. gayatina*. Other characters are indicated in Table 1 and in the illustrations. Some important features are italicized. Terga and sterna are abbreviated T and S and numbered as metasomal structures. Features resembling Ceratinini are annotated "(C)"; those resembling Xylocopini, "(X)," and special features of *Manuelia*, "(M)." An asterisk indicates that variation exists so that the statement of similarity, while generally true, breaks down in certain cases.

Female.—Body slender, 4.9–8.5 mm long (C). Color dull metallic blue (ga, similar to *Pithitis unimaculata*) or black with apical segments reddish (po) or not (gt); legs, tegula, mandible tending to be brownish, tergal margins not depigmented. *No pale maculations* (X*). Wings grayish hyaline, veins and stigma dark brown to black. Pilosity sparse, not hiding surface except fringe of lateral lobe of pronotum and (ga) area on each side of pygidial plate; predominantly whitish to pale yellow, ferruginous on T6 (ga, po).

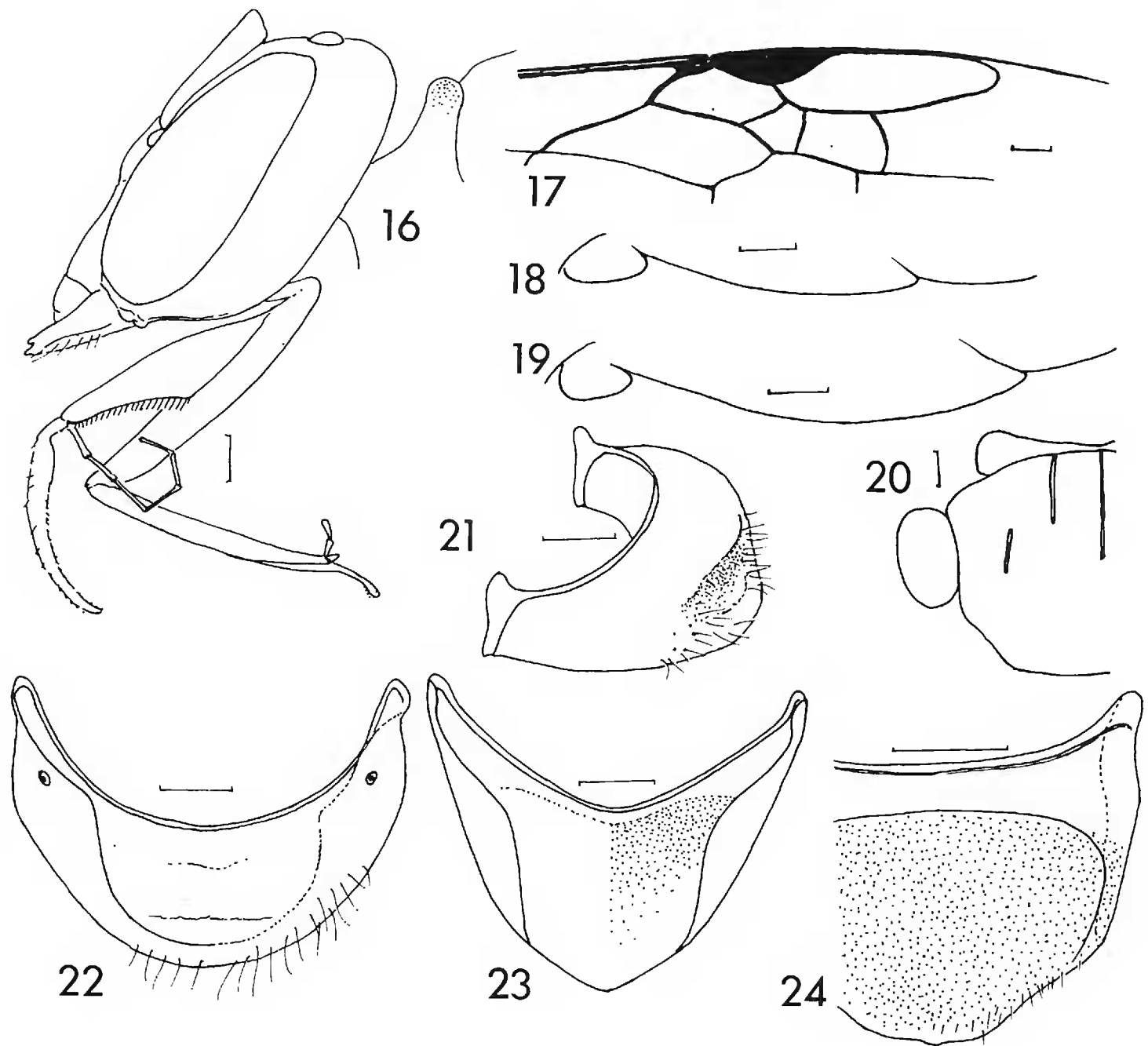
Head (Figs. 1–4, 16) slightly wider than long, more elongate than in most *Ceratina* and *Xylocopa* but less so than in *Braunsapis*. Outer and inner orbits convergent below, more so than in most *Ceratina* and *Xylocopa*. Antennae slightly above middle of eyes. Vertex seen frontally gently convex. Preoccipital and paraocular carinae absent. *Circumalveolar depression wide*, from antennal base down nearly to level of lower margin of supraclypeal area, up an equal distance, and laterally nearly to inner orbit in its median one third. Antennocellar triangle much larger than ocellar triangle. Supraclypeal area above with narrow frontal carina, extending upward as



Figures 1-15. 1. Face of *Manuelia gayi*, female. 2-4. Faces of males, *M. gayi*, *postica*, and *gayatina*; shaded areas are yellow. 5. Labrum of female, *M. postica*. 6-11. Bases of left hind tibia, even numbers, females, odd numbers, males; 6, 7. *M. gayi*; 8, 9. *M. postica*; 10, 11. *M. gayatina*. 12-15. Hind tarsi; 12, 13. *M. gayatina*, female, male; 14, 15. *M. gayi*, female, male. In these and all other illustrations, the scale line = 0.25 mm.

linear, shallow frontal sulcus nearly attaining anterior ocellus. *Clypeus flat*, its upper half contrasting with gently convex, raised supraclypeal area. Lower margin of clypeus straight, extending beyond lower end of eye; lower lateral part only obliquely and briefly bent backward at side of labrum; lateroclypeal carina represented by weak ridge. *Lateral clypeal margin mildly concave, giving shape of clypeus neither typically inverted T form as in Ceratina nor hourglass form as in allodapines (X*)*. Tentorial pit at upper third of clypeus (X). Upper margin of clypeus nearly straight (ga, gt) or gently convex (po); summit of clypeus about as wide as paraocular area at same level. Mandibular axis slightly behind ocular axis. Malar area linear, much shorter than scape width. Gena (Fig. 16) narrower than eye, moderately convex, seen laterally not declivous immediately behind summit of eye. Labrum (Figs. 1, 5) in repose at right angle to clypeal surface, about twice as broad as long, semicircular, apex with wide tuft of long, dense simple orange-brown hairs (M but resembling X). Labrum *basally with triangular, slightly elevated, hairless smooth "disc" as in some Xylocopa (X*)*. Mandible tapering from base, not abruptly narrowed as in *Ceratina* (X). Mandible *apically bidentate* (Figs. 1, 5, 16), fringed beneath with long, white or yellowish simple hairs. Maxillary palpus 6-segmented, *reaching nearly to apex of galea* (X), segments approximately equal in length, progressively more slender apically (Fig. 16). Galea six or more times as long as broad (C). Stipes with comb of moderate strength (C). Mentum over five times as long as wide (C). Flabellum with posterior surface smooth, setal row in middle to near apex of flabellum (C). Proboscis with sclerotic roof (C). *Antenna relatively long*, much longer than in *Ceratina*, surpassing middle of mesoscutum (M). *Scape relatively short* (Figs. 1–4), attaining lower margin of anterior ocellus (about as in *Ceratina*), about 4 times as long as wide (C). *Flagellum* (Figs. 25–30) 2.5 (ga), 2.7 (gt) or 3.0 (po) times as long as scape (M). First flagellomere as long as or shorter than pedicel (C).

Mesosoma generally smooth and polished, partly coriaceous (especially in ga), punctures rather sparse and coarse. Pronotum not carinate. Prosternal apophyseal arms with apices separate (C) (fused in *Xylocopa*). Mesoscutum anteriorly not carinate, *notaulus strong, parapsidal sulcus shorter than in Ceratina, Braunsapis, and Xylocopa*, less than half length of tegula which is fairly large, only slightly shorter than half scutal length (Fig. 20). Metasternum projecting considerably behind lower condyle of hind coxa (X). *Wings apically pubescent, not papillate* (C). *Stigma broad* (Fig. 17), shorter than costal margin of marginal cell (only slightly so in po) (C). Marginal cell broad with apex rounded, apart from wing margin (C). Submarginal cell 2 distinctly and 3 slightly (or much in gt) shorter than 1 (C). Recurrent veins 1 and 2 respectively near to transverse cubitals 2 and 3. Basal vein slightly apical to cu-v. *Jugal lobe* (Figs. 18, 19) *less than one fifth as long as vannal lobe* (M). Hamuli 7–10; hamular sinus as deep as wide (C). Fore coxa with apical hairy spine short (C*) (long in gt). Strigilis as in *Ceratina* and *Braunsapis* (C). Arolia large; claws bifid. Fore and mid tibial spines acute, hind tibia without spine (C). Fore and midtibial spurs normal (as in *Ceratina* and *Braunsapis*) (C). Tibial scopa of sparsely plumose (often trifid) hairs (C), moderately developed (ga, po. Fig. 31) or sparser (gt, Fig. 32). Hind tibial spurs microserrate, apically gently (gt, Fig. 32) or rather strongly bent (ga, po. Fig. 31). *Basitibial plate distinct* (Figs. 6, 8, 10), simple (C), with short white hairs basally. *Hind basitarsus produced* as bluntly pointed process beyond base of second tarsal segment (X) (Figs. 12, 14). Coxae, trochanters, and femora with white plumose or

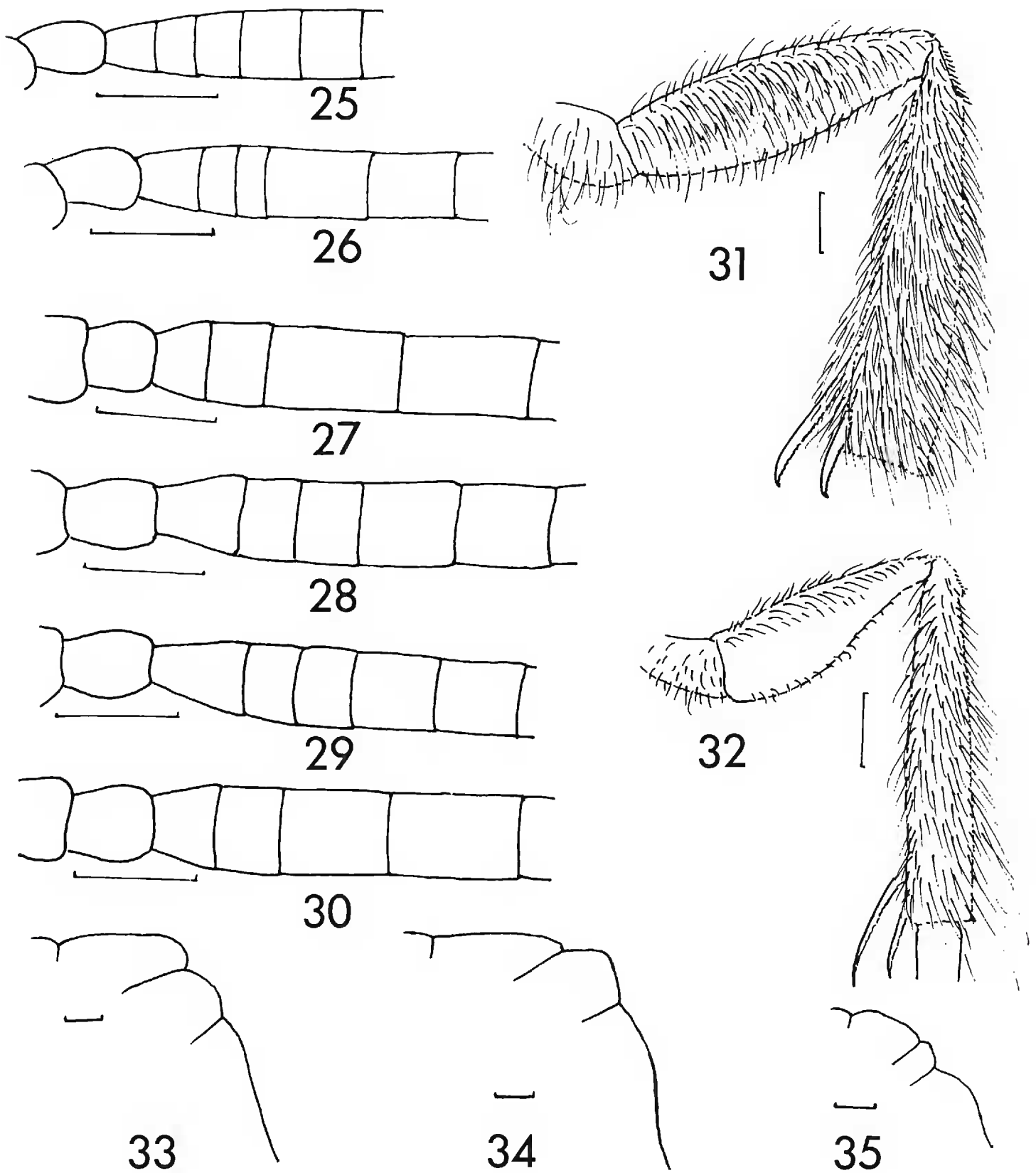


Figures 16–24. 16. Lateral view of head and mouthparts, *Manuelia gayi* female. 17. Part of forewing of same. 18, 19. Posterior basal margins of hind wings, *M. gayi* and *postica*. 20. Pronotum and scutum, *M. gayi* female. 21, 22. T7, male, *M. gayi*, dorsolateral and ventral views. 23, 24. S6, male, inner view, *M. gayi* and *M. gayatina*.

simple hairs; fore and mid tibiae and tarsi with abundant, white to yellowish, mostly simple hairs; apex of second trochanter and base of second femur each with a mesal patch of dense, short, erect, white, simple hairs.

Metasoma widest at middle. Metasomal terga transversely microlineolate and dully polished, punctures rather sparse, coarser on apical terga. T1 basally oblique, basal part not sharply declivous or differentiated. Graduli 2–5 laterally not much extending posteriorly beyond spiracles; apical terga not flattened as in allodapines. Sterna without recognizable glandular areas (X); ventral hairs sparse, not forming scopa. T6 not slanting down apically, *with narrow, spine-like, apically upraised, dorsally flattened pygidial plate* (X) *surrounded with dense plumose hairs* (pygidial fimbria) (X) (Fig. 57) which become longer and sparser laterad.

Male (differences from female only).—Face with yellow markings (Figs. 2–4). Inner orbits below more convergent in po and gt (Figs. 3, 4). Head (and other parts,



Figures 25–35. 25–26. Pedicel and base of flagellum, *Manuelia gayatina*, female and male. 27, 28. Same, *M. postica*. 29, 30. Same, *M. gayi*. 31, 32. Outer side of hind leg of female, *M. postica* and *gayi*. 33–35. Profiles of posterior part of thorax and propodeum of females, *M. gayi*, *postica*, and *gayatina*.

too) generally less coriaceous and more polished than in female. Labrum uniformly gently convex and punctate. Mandible bidentate (ga) or simple (po, gt). Scape not attaining anterior ocellus.

Legs slender, without special modifications, hind tibia and basitarsus with white plumose hairs, in ga densely hairy, suggesting female scopa. Basitibial plate with edge strong but less developed than in female (ga, Fig. 7) or absent (po, Fig. 9, gt Fig.

11), the plate represented by gentle swelling. Hind tibia with two apical spurs (C). Hind basitarsus apically produced as in female in ga and po, not in gt (Figs. 13, 15).

Metasomal T7 directed downward, apical margin broadly rounded, slightly raised along margin so that disc is depressed (Figs. 21, 22); apparent apex of T7 formed by a short, wide, thin, shelf-like, subapical extension with true apex recessed beneath. *S6 apically rounded, without subapical modification as in Ceratina* (X); gradulus reduced, shown merely by different coloration in ga (Fig. 23) or present in gt and po (Fig. 24). *S7 short, transverse*, with elongate lateral arms and no apical process or lobes (Figs. 43, 47, 56) (M). *S8 with sclerotized vessel-like main body, robust lateral apodeme and hollow, apical, sparsely hairy process* (Figs. 41, 42, 48, 49, 54, 55) (M). Gonocoxite robust with wide, dorsal emargination, ventroapically not produced. Volsella absent but "cuspis" (? sense of Marikovskaya, 1975) distinct, small, with fine hairs in ga and po (Figs. 44, 50) but not in gt (Fig. 39). *Gonostylus unornamented, semisclerotized, not fused with gonocoxite* (C*). Penis valve stout, not rod-like, sclerotized, basal bridge strongly sclerotized. Spatha absent (though ventral side of penis weakly sclerotized in po, Fig. 44) or present in gt (Figs. 39, 40).

The "cuspis" is similar to that of Euglossini and may be homologous to some of the anthophorine structures so labelled by Marikovskaya (1975). In addition to those structures, which may not be homologous among themselves, there are other structures in the same vicinity such as the ventroapical plate of the gonocoxite in Allodapini (Michener, 1975) and even the squama between the gonocoxite and gonostylus of Bombini. Further investigation of these structures is needed in order to reliably determine the homologies.

Biology.—Claude-Joseph (1926) described the nesting biology of *M. gayatina* and *M. gayi*. Unfortunately he provided no data by which one might judge the reliability of his statements. For example one does not know how many nests he examined. However, he obviously examined several and perhaps many for each species. As with the morphological characters, the biological ones differ considerably between the two species that have been studied.

The nests are branching burrows in dead stems or rotting wood, sometimes utilizing abandoned beetle burrows (Jaffuel and Pirion, 1926). *M. gayatina* nests in dry stems or twigs; in spring females may clean and reuse old nests or construct new burrows in dead stems of brambles (*Rubus?*). A female does not enter at a broken end of a stem as do females of *Ceratina* and Allodapini. Instead, she cuts into the side of a stem, then makes one branch burrow going down, the other up. Occasionally one bee uses the lower branch, another the upper, with common use of the entrance, but usually there is only one bee per nest entrance. In about a month the first generation emerges and is composed of both sexes. Claude-Joseph (1929) noted that both sexes return to the old galleries for the night. The females of this generation may select, in addition to bramble, dry twigs of wicker, willow, peach, or southern hazel. Toward the end of fall, the second generation metamorphoses, but is said to be composed only of females. The septa between cells are gradually destroyed and the adults move about together in the burrow until spring.

M. gayi makes branching burrows in rotten logs of poplar and weeping willow, starting in November. Each branch is said to be made by one female; obviously there is a common entrance burrow used by several females. Claude-Joseph indicates that up to eight or ten may use one entrance. The burrows enter across the grain of the wood but then turn parallel to the grain. Gazulla and Ruiz (1928) record this species

also nesting in dry stems of zarzamora (*Rubus ulmifolius*); this is as in *M. gayatina*. Apparently there is only one generation per year, for Claude-Joseph indicates that the young grow through December and transform to adults near the end of summer and that both sexes hibernate in their cells until spring. Both sexes may return to their burrows to spend the night (Claude-Joseph, 1929).

The cells of both species are in series in the burrows, separated by partitions made of particles of wood cemented together, evidently as in *Xylocopa* or *Ceratina*. Both upper and lower surfaces of the partitions are illustrated as concave. At least in *M. gayi* the cells are barrel-shaped, narrowed at each end as in *Xylocopa*, rather than cylindrical as usual in *Ceratina*.

The females of *M. gayatina* bring pollen from diverse kinds of flowers to form the elongate firm pollen loaf with a depression in the upper part (or lower part in the upper branch burrow in a vertical stem). The egg is laid in this depression. The food masses are rather similar in shape to those of *Ceratina*, but the egg is evidently on the upper (i.e., toward the nest entrance) rather than the lower part of food. In *M. gayi*, however, the food mass is described and illustrated as a ball occupying the lower end of the cell, with the egg laid on top of it. This is as in many other bees but is unique for the Xylocopinae. The observation needs to be verified.

M. gayatina overwinters as groups of adult females (only), crowded together in the burrows in which cell partitions have been destroyed. This is as in *Ceratina* and *Xylocopa*; such groups have been called prereproductive assemblages by Michener (1985 and in press). In *M. gayi*, however, each adult bee overwinters in its cell with the cell partitions left intact. Overwintering in cells is otherwise unknown in the Xylocopinae and may be an ancestral feature of *M. gayi*, for such behavior is well known in various other bees.

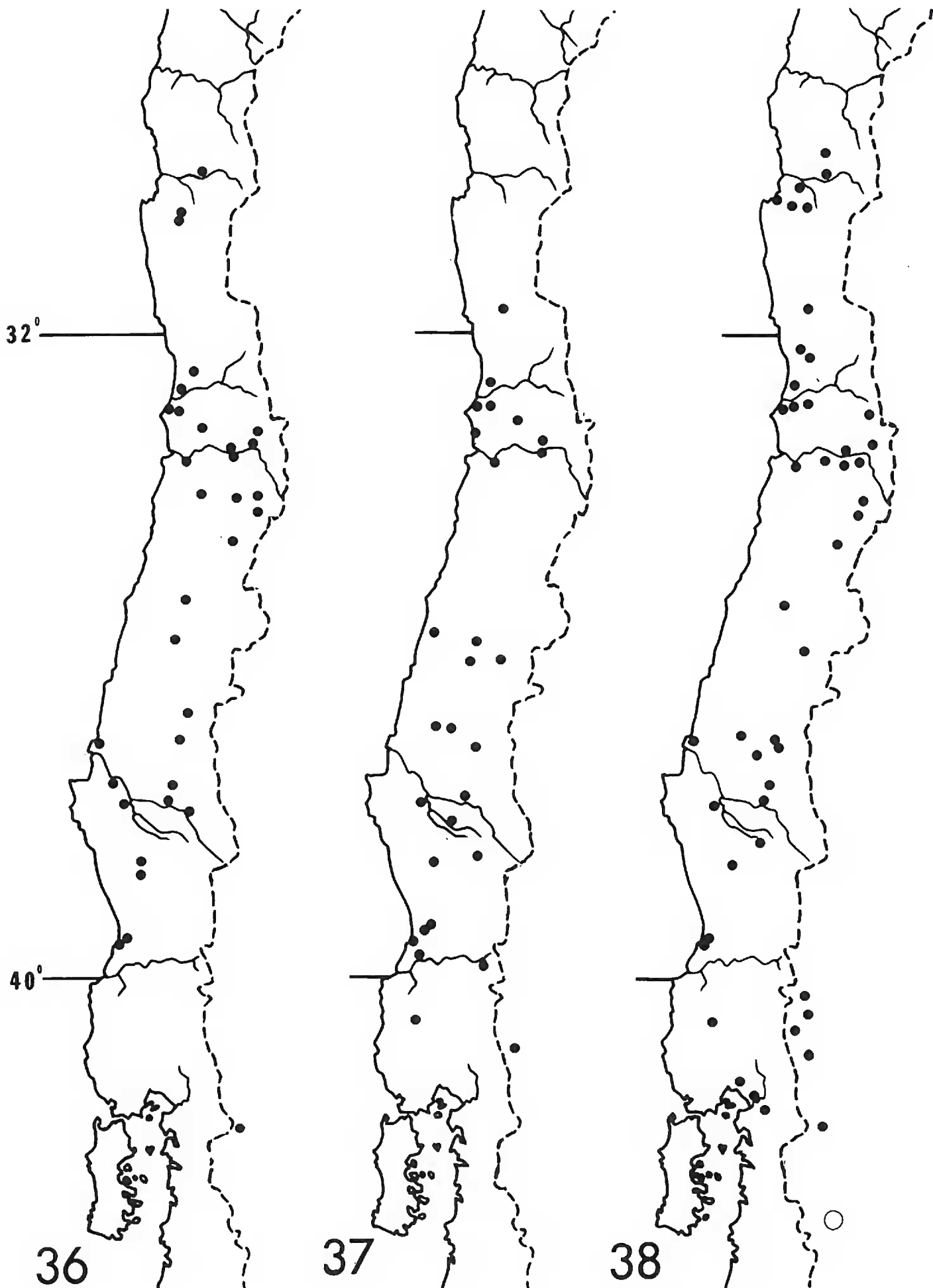
In both species, after hibernation, old burrows are reused while other females excavate new nests. Claude-Joseph believed that in *M. gayatina*, with only females surviving the winter, the first brood is produced parthenogenetically. It is much more likely that the overwintering females mate in the preceding summer or autumn. In view of the longevity now known for other Xylocopinae (Michener, 1985 and in press), it is probable that females of *M. gayatina* live much longer than Claude-Joseph supposed.

Collecting records indicate long seasons of flight. Specimens of all three species have been taken every month from August to March. The rather numerous floral records indicate broad polylecty. There are records of all species from various introduced as well as native flowers. Families reported include the following: Compositae, Cruciferae, Euphorbiaceae, Hydrophyllaceae, Labiatae, Malvaceae, Rosaceae, Scrophulariaceae, Verbenaceae.

Geographical Distribution.—The three species are broadly sympatric in central Chile and the lake district of Argentina. Thus *Manuelia* is characteristic of the Araucanian faunal region (Ringuelet, 1961) which is faunistically so different from the rest of the neotropics that it might be considered a separate faunal realm if it were larger. Among bees such genera as *Diphaglossa*, *Cadeguala*, *Corynura*, and *Neofidelia* are restricted to it. Such large genera as *Alloscirtetica* (Eucerinae) and *Chilicola* (Xeromelissinae) are most abundant in the Araucanian region although extending into other temperate or xeric parts of the neotropics. The Araucanian is also the region inhabited by most of the archaic South American types that show faunal or floral connections with Australia, e.g., Paracolletini among bees and among trees, *Nothofagus* and *Araucaria*. The region also has some faunal

resemblances to Africa, exemplified among bees by the Fideliidae which are found only in Africa and central Chile.

All three species range from rather xeric Coquimbo Province south to moist cool temperate Osorno or Llanquihue Provinces (Figs. 36–38), and from sea level to over



Figures 36–38. Locality records for *Manuelia gayatina*, *postica*, and *gayi*, based on specimens seen by us or by Haroldo Toro of Valparaiso. On the map for *M. gayi* the circle represents unknown localities in Chubut Province, Argentina.

1000 m altitude. While they may attain higher altitudes in the north than in the south, the meager altitude data probably do not show this, for *M. gayi* has been taken at 1400–1600 m altitude at its southernmost known locality in Llanquihue Province. Both *M. gayi* and *postica* have been taken at 1700–2200 m in Santiago Province. Unfortunately most collectors have not recorded altitudes.

There are two locality records that indicate that *Manuelia* also ranges across Argentina. Specimens of all three species in the Snow Entomological Museum are labelled Fundo Malcho, Parral, Córdoba, Argentina. They were taken on various dates in 1956. In the same collection are specimens of *M. gayi* and *gayatina* labelled San Isidro, Buenos Aires Province, Argentina (M. Senkute), also collected on different dates. Could these labels be wrong? Elizabeth Chiappa T. of the Universidad Católica de Valparaíso writes that there is a Parral, Fundo Malcho, in Chile (Valparaíso area), a finding that suggests bad labelling. Alternatively, might they represent introductions, which could easily occur with nests in wood? There are no old reports of *Manuelia* from eastern or central Argentina, so far as we are aware, e.g., in the works of Holmberg (1903), Friese (1908), and Jörgensen (1912a, b). Recent collections by bee collectors (A. Roig A., R. B. Roberts, and J. F. Neff) at San Isidro and elsewhere in eastern and central Argentina do not include *Manuelia*. We have therefore chosen to regard the records for eastern and central Argentina as probable errors or possible introductions that did not persist, and have omitted these localities from our maps. Future collectors, however, should watch for *Manuelia* in these areas.

The Species of *Manuelia*

The three species of *Manuelia* seem about as different from one another as subgenera in other xylocopine bees. Indeed two of us at one time prepared a manuscript providing a subgeneric name for each species. Such multiplication of genus-group names seems unnecessary, but the distinctiveness of the species should be remembered. Table 1 summarizes the more striking characters including those of the male terminalia which are illustrated, but not included in the specific descriptions.

The characters of the three species are further summarized in the key below. We have not worked out a meaningful cladistic pattern for them because polarity of the specific variables is difficult to determine. For example, for bees in general, a horizontal metanotum and propodeal base like those of most wasps is plesiomorphic relative to the apomorphic slanting or vertical orientations of these surfaces or parts of them, as in *M. postica*. These apomorphies are part of the development of a relatively spherical thorax associated with the rapid flight of many bees. But slender bodies are characteristic of various small bees that nest in narrow burrows in wood or twigs, and such a body form results in reversion to a horizontal metanotum and propodeal base. Examples are *Chelostoma*, *Heriades*, and *Hoplitis* in the Megachilidae; *Hylaeus* and its relatives (especially *Heterapoides*) in the Colletidae; and Ceratinini and Allodapini in the Anthophoridae. Hence the horizontal base of the propodeum of *M. gayatina*, the smallest and most slender species of *Manuelia*, could be primitive features retained from primitive bees or derived features adaptive to life in narrow burrows. Similar problems exist in the interpretation of several other variables.

Table 1. Major characters of *Manuelia* species. Asterisks (*) mark variables common to males and females.

Variable	<i>gayi</i>	<i>postica</i>	<i>gayatina</i>
	Female		
*Coloration	dark metallic blue	black with reddish apical segments	black
Lateral margin of labral disc	straight	----- strongly concave -----	
*Lateral angle of pronotum	protuberant above	not above level of middle of collar	protuberant above
*Rear thoracic declivity	beginning at rear edge of scutellum; propodeum straight in profile	beginning in middle of metanotum; propodeum nearly straight in profile	beginning before middle of metanotum but interrupted by horizontal propodeal base
Basitibial plate	marginal carina high, erect apically	marginal carina high, oblique apically	marginal carina strong but low
Male			
Mandibular apex	bidentate	----- simple -----	
Vertex	posterior ocelli in front of summit	----- posterior ocelli on summit -----	
Flagellomere 3	----- much longer than broad, like 4 -----		much broader than long, like 2
Apex of hind basitarsus	----- produced -----		not produced
Basitibial plate	present	absent, hairs sparse	absent, hairs dense
Sternum 6	gradulus evanescent	----- gradulus complete -----	
Sternum 7	apical margin truncate	apical margin gently rounded	apical margin gently pointed medially
Sternum 8	--- basally rounded; apical process basally wide, --- tapering apicad, with sparse hairs		basally truncate; apical process slender, densely haired
Gonobase	wide	narrow	wide
Gonocoxite	----- long, ventrally with preapical process -----	“cuspis” but without	short, ventrally without “cuspis” but with small preapical process
Gonostylus	with sparse but moderately long hairs; base simple	with sparse but moderately long hairs; base bifurcated	with sparse and minute hairs; base simple
Penis valves	robust	----- rather slender -----	
Penis	not sclerotized	----- partly semichitinous -----	
Spatha	----- absent -----		present

KEY TO THE SPECIES OF *Manuelia*

1. Entirely black with sparse white pubescence; body length about 5 mm; profile of propodeum curved, with anterior portion horizontal and posterior portion subvertical; metanotum horizontal; anterior coxa with a long median apical spine; true apex of T7 of male without hairs; gonostyli long, equal in length to gonocoxite. *gayatina*
 —Blue or black, at least in female with some caudal integument or hairs orange-brown; body length about 8 mm; profile of propodeum slightly curved or straight, steeply sloping; metanotum subvertical; anterior coxa with small median apical spine; true apex of T7 of male with hairs; gonostyli short, about half length of gonocoxite. 2
2. Black with at least two caudal terga and sterna orange-brown; profile of propodeum slightly curved; curvature of metanotum forming summit of posterior thoracic declivity; labrum of female with basal triangle confluent with subapical margin by a narrow median area; mandible of male without teeth; male without basitibial plate. *postica*
 —Metallic blue, last exposed tergum of female with orange-brown hairs; profile of propodeum straight; posterior margin of scutellum at summit of posterior thoracic declivity, the metanotum declivous; labrum of female with basal triangle elevated apically and separated from subapical margin by a complete transverse punctured area; mandible of male bidentate; male with small basitibial plate. *gayi*

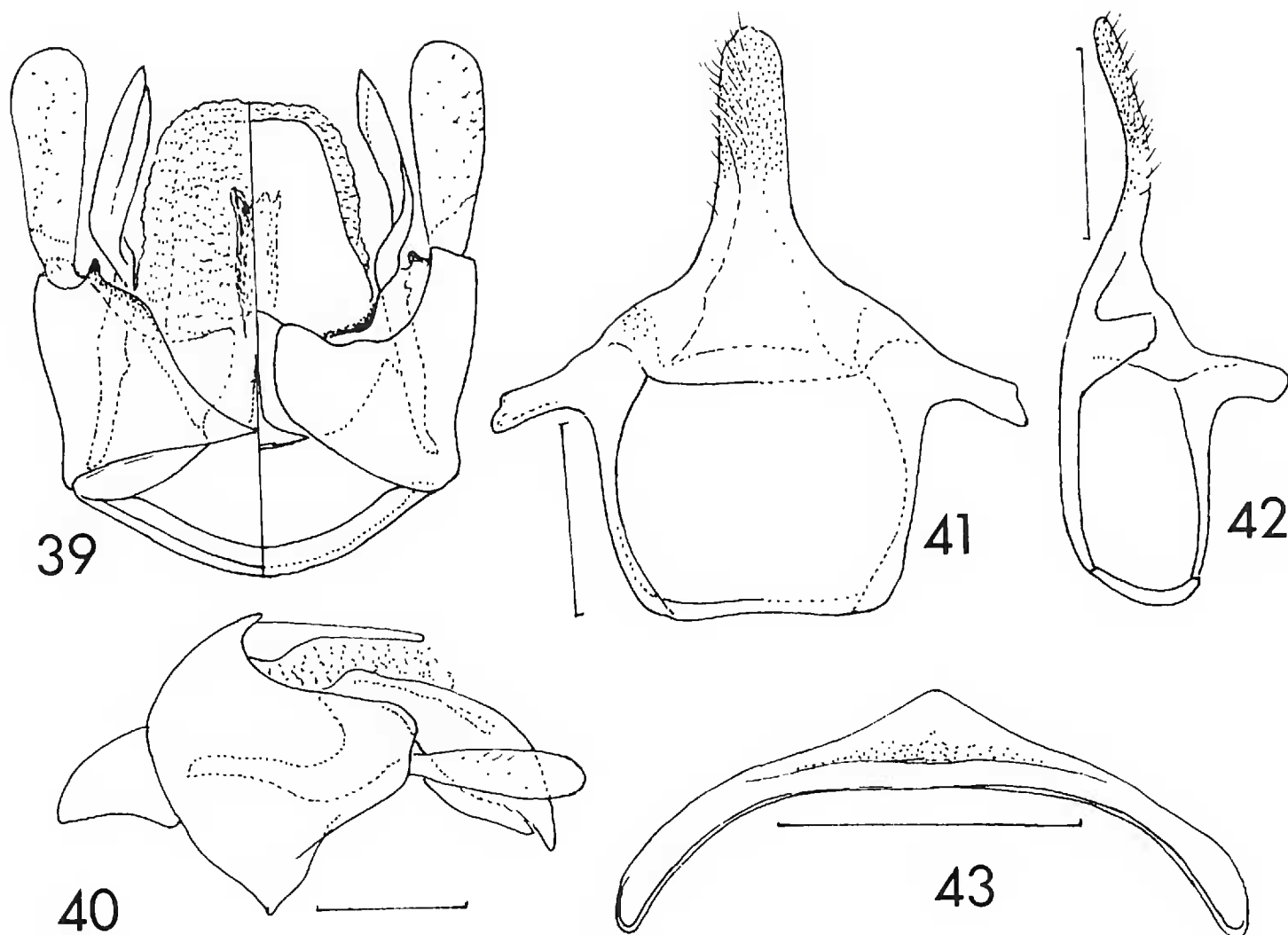
Manuelia gayatina (SPINOLA)

(Figs. 4, 10–13, 24–26, 32, 35, 36, 39–43)

Halictus gayatinus Spinola, 1851:209; Cockerell, 1905:355.*Ceratina gayatina*: Alfken, 1904:141.*Manuelia gayatina*: Vachal, 1905:26; Claude-Joseph, 1926:216; Jaffuel and Pirion, 1926:370; Moldenke and Neff, 1974:9, 29.*Ceratina herbsti* Friese, 1910:703 (new synonym).

A female “typus” of *Ceratina herbsti* Friese in the American Museum of Natural History appears to be a cotype; it is from Concepción, the type locality, collected by Herbst in 1903. Although the synonymy of *herbsti* seems not to have been published, it was recognized long ago for there is a note by Cockerell indicating the synonymy on a specimen in the California Academy of Sciences.

Female.—Average and range of forewing lengths (5 specimens): 4.79 mm; 4.50–5.15 mm. *Head*. Integument shiny dark brown to black; antenna, labrum, mandible black. Circumalveolar depression rather shallow. Subapical margin and basal triangle of labrum shiny and impunctate, confluent by a narrow median area and separated laterad by a transverse punctured area bearing long, yellowish, simple hairs; lateral margin of basal triangle concave. Hypostomal carina low. *Thorax*. Pronotum with lateral angle protuberant above. Thoracic capsule elongate; posterior declivity beginning at scutellar-metanotal suture, scutal-scutellar tangent not touching metanotum; metanotum and anterior dorsal portion of propodeum sloping in same plane, posterior portion of propodeum with steeper slope and clearly not in the same plane as the anterior portion. Integument shiny dark brown to black; anterior dorsal portion of propodeum impunctate and roughened, lateral and posterior portions punctured and with appressed, short, white, plumose hairs; lateral



Figures 39–43. *Manuelia gayatina*, male. 39, 40. Genitalia, ventral, dorsal, and lateral. 41, 42. S8, dorsal, ventral, and lateral. 43. S7.

portions of pronotum and metepisternum with similar vestiture; remainder of thorax punctured throughout, dorsum with erect, white, simple hairs, longer laterally; mesepisternum with sparser, longer, simple to plumose hairs. Tegula brown; number of hamuli (5 specimens): 7. Legs dark brown, paler distally; hairs yellowish distally; scopa sparse. Basitibial plate broad, width about one-half distance from base of tibia to apex of plate, apical edge evenly rounded, strong but low; hind tibial spurs only gently curved apically. *Metasoma*. Elongate ovoid; shiny dark brown to black; T1 and 2 sparsely punctured, remaining terga more densely punctured, with short, ascending to erect, white, simple hairs. T6 with black spine (pygidial plate) flanked by dense, yellowish white, plumose hairs which become longer and sparser laterad. S1–5 with ascending, white, simple or plumose hairs which are longest subapically on each sternum; S6 with appressed to ascending, yellowish, simple to plumose hairs which are dense at apex.

Male.—Forewing length (two specimens): 4.0 mm, 4.4 mm. *Head*. Coloration as in female but the following pale yellow: labrum, paraocular area up to base of antenna, entire clypeus and lower half of supraclypeal area. Mandible simple. Posterior ocelli on summit of vertex. Third flagellomere much broader than long.

Thorax. As in female. Basitibial plate not perceptible. Hind basitarsus not produced at apex. *Metasoma*. Dark brown to black, shiny above, paler and duller beneath; sparsely punctured, especially anteriorly; dorsum and venter with short ascending to erect, white, simple hairs which become longer and frequently plumose laterad. T7 with true apex without hairs. Terminalia as illustrated.

This is the least common of the three species in most collections but the large number of specimens in the collection of Prof. Haroldo Toro in Valparaiso indicates that it is abundant. Probably its small size results in less frequent capture as compared to the larger species. The distribution is shown in Figure 36; the northernmost locality is Vicuña, Coquimbo Prov., the southernmost in Chile is Valdivia, Valdivia Prov. The only locality in western Argentina is El Bolsón, Rio Negro Prov. Altitudes range from sea level to 1100 m at Cabrería, Cordillera Nahuelbuta, Malleco Prov.

Manuelia postica (SPINOLA)

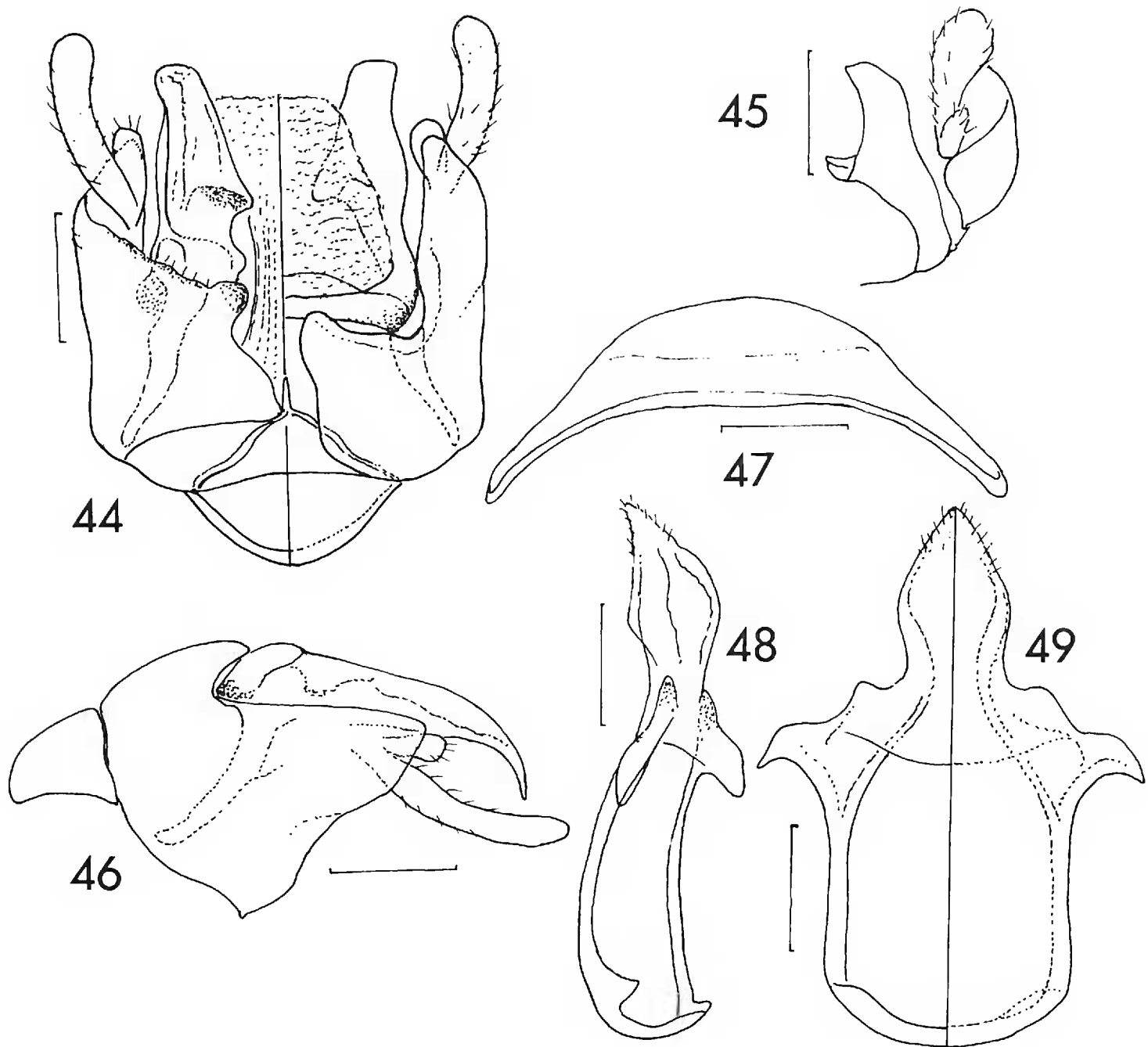
(Figs. 3, 5, 8, 9, 18, 19, 27, 34, 37, 44–49)

Halictus posticus Spinola, 1851:208; Cockerell, 1905:355.

Ceratina postica: Alfken, 1904:141.

Manuelia postica: Vachal, 1905:26; Jaffuel and Pirion, 1926:370; Gazulla and Ruiz, 1928:301.

Female.—Average and range of forewing lengths (64 specimens): 6.92 mm, 6.10–7.60 mm. *Head*. Integument shiny black; antenna, labrum, and mandible black. Circumalveolar depression rather shallow. Subapical margin and basal triangle of labrum shiny and impunctate, confluent by a narrow median area and separated laterally by a transverse punctured area bearing long, yellowish, simple hairs; lateral margin of basal triangle concave. *Thorax*. Pronotum with lateral angle not elevated above level of middle of pronotal collar. Thoracic capsule ovoid; propodeum slightly convex and steeply sloping; metanotum at summit of posterior thoracic declivity, touched by a scuto-scutellar tangent. Integument colored like head; punctures close around margin of scutum, on scutellum and on metanotum, less dense on mesepisternum, sparse on dorsum, absent in triangle at summit of propodeum; surface shiny except propodeum which is finely roughened; surface with short, erect, white, plumose hairs on dorsum, hairs longer laterally and longest ventrally; propodeum and pronotum laterally with additional sparse, long, erect, white, plumose hairs. Tegula black; average and range of hamuli (64 specimens): 8.2, 7–10. Tarsi dark brown, remainder of legs shiny black with yellowish white hairs; scopa moderately developed. Basitibial plate elongate, width about one-third of distance from base of tibia to apex of plate; apex acute, marginal carina high and oblique apically; hind tibial spurs strongly curved at apices. *Metasoma*. Elongate ovoid; T1–3 shiny black, punctured throughout, and with sparse, short, erect, white, simple hairs; coloration of subsequent exposed terga shows variation apparently uncorrelated with geography in the 69 specimens before us: 24 have basal three-quarters of T4 with color and vestiture like preceding terga while the apical quarter and subsequent exposed terga are translucent orange-brown; 43 have this color restricted to fifth and sixth terga; and in the remaining two bees, T5 and 6 are dark and only faintly orange-brown. Hairs on these terga colored like their corresponding terga and longer and denser caudad. T6 with black spine (pygidial



Figures 44–49. *Manuelia postica*, male. 44. Genitalia, ventral, and dorsal. 45. Inner view of gonostylus and adjacent structures (sketch). 46. Genitalia, lateral view. 47. S7, 48, 49. S8, lateral, dorsal, and ventral.

plate) flanked by abundant, ascending, orange brown, simple or plumose hairs which become longer and sparser laterally. Sterna with vestiture like corresponding terga; S6 with apical portion clothed with dense plumose hairs.

Male.—Average and range of forewing lengths (17 specimens): 6.85 mm, 5.85–7.05 mm. *Head*. Coloration as in female but the following areas pale yellow: base of mandible, labrum, paraocular area up to half-way between summit of clypeus and lower margin of antennal socket, and a variable area of clypeus. Sometimes dark color of upper head extends down along lateral portions of epistomal suture to below anterior tentorial pits and mesad from this suture to almost one-third of clypeal width; others show reduction of the dark extensions and expansion of yellow above clypeus. Mandible simple, dark brown apically. Posterior ocelli on summit of vertex. Third flagellomere longer than broad. *Thorax*. Largely as in female. Mesepisternum below scrobal suture with circular patch of appressed, short, white, plumose hairs;

average number and range of hamuli (17 specimens): 7.9, 7–9. Basitibial plate not perceptible. Hind basitarsus with apex produced. *Metasoma*. Shaped as in female; T1–3 and S1–3 shiny black with short, ascending, white, simple hairs; coloration of subsequent exposed terga and sterna varies in 18 males before us: 1 has T4–7 and S4–6 translucent orange-brown; 6 have the basal portions of T4 and S4 black, the apical margins and subsequent segments orange-brown; 8 have T5–7 and S5, 6 orange-brown; 1 has the apical portions of T5 and S5 and subsequent terga and sterna so colored; and two have the apical segments dark with orange-brown colors only faintly expressed. Hairs white on black areas, orange on orange brown areas. T7 with true apex bearing short, orange-brown, plumose hairs. Terminalia as illustrated. The distribution of this species is shown in Figure 37. In Chile the northernmost locality is Cuesta Cavilolén, Illapel, Coquimbo Prov., and the southernmost is Osorno, Osorno Prov. An Argentine record, Isla Victoria, Neuquén Prov., is slightly farther south than any Chilean locality known to us. Altitudes of collections range from near sea level to 125 m in Cautin Prov., 1500 m in Linares Prov. and 1700–2200 m in Santiago Prov.

Manuelia gayi (SPINOLA)

(Figs. 1, 2, 6, 7, 14–18, 20–23, 29–31, 33, 38, 50–57)

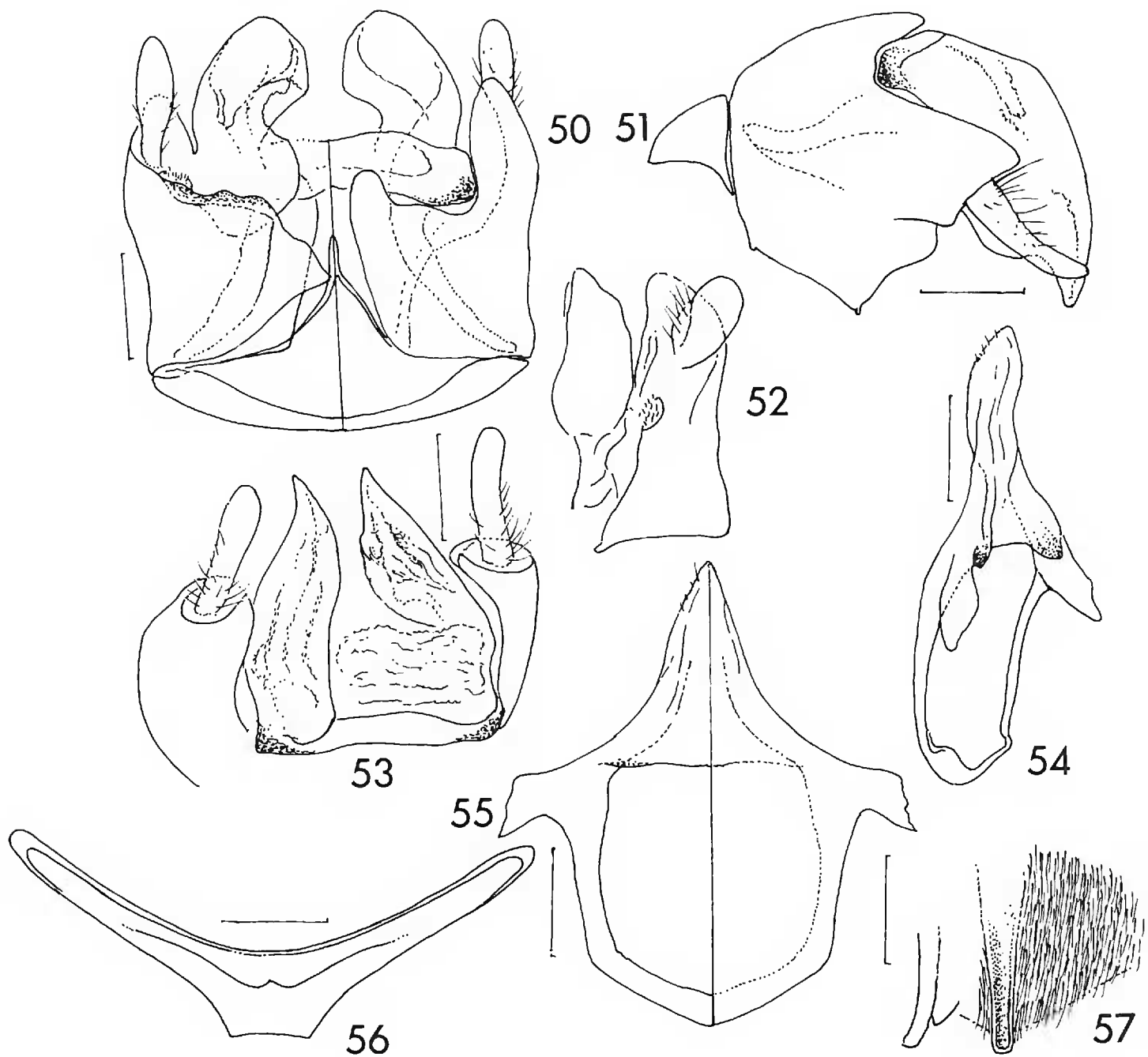
Halictus gayi Spinola, 1851:208.

Corynura gayi: Dalla Torre, 1896:93 (part).

Ceratina gayi: Alfken, 1904:141.

Manuelia gayi: Vachal, 1905:26; Jaffuel and Pirion, 1926:370; Claude-Joseph, 1926:220, 1929:417; Gazulla and Ruiz, 1928:301; Moldenke and Neff, 1974:29; Michener and Brooks, 1984:56, 59.

Female: Average and range of forewing lengths (66 specimens): 6.17 mm, 5.50–6.55 mm. *Head*. Integument shiny metallic blue; scape colored like head, flagellum ruddy brown beneath, brown above; labrum and mandibles black. Circumalveolar depression relatively deep. Subapical margin and elevated basal triangle of labrum shiny and impunctate; lateral margin of basal triangle of labrum straight. Median part of hypostomal carina expanded, almost lamella-like, sloping inward over proboscoidal fossa. *Thorax*. Pronotum with lateral angle protuberant above. Thoracic capsule roughly spherical; metanotum and propodeum steeply sloping. Integument colored as head; punctures close around margins of scutum, on scutellum and on metanotum, becoming less dense on mesepisternum, sparse on dorsum of scutum and absent in triangle at summit of propodeum; surface shiny except for propodeum which is finely roughened; pubescence short, erect, white, plumose on dorsum, hairs longer laterally and longest ventrally; propodeum with long, erect, white, plumose hairs which become short and appressed laterally. Tegula brown with bluish reflections; average and range of hamuli (66 specimens): 8.6, 7–10. Tarsi dark brown, remainder of legs brown with bluish reflections; scopa moderately developed. Basitibial plate broad, its width about half distance from base of tibia to apex of plate, apical edge bluntly pointed, marginal carina high, erect apically; hind tibial spurs strongly curved at apices. *Metasoma*. Ovoid; T1–4 colored like head and thorax and bearing on their dorsa short, erect, white, simple hairs which become longer laterally; base of T5 with coloration and vestiture like preceding terga, but apical margin translucent and orange-brown; T6 dark brown with the black spine (pygidial plate) flanked by orange-brown, mossy plumose hairs



Figures 50–57. *Manuelia gayi*. 50, 51. Male genitalia, ventral, dorsal, and lateral. 52. Sketch of dorsal apical view of male gonocoxite, gonostylus, and penis valve. 53. Sketch of dorsal apical view of male genitalia. 54. S8, male, lateral view. 55. Same, dorsal and ventral views. 56. S7, male. 57. Apex of T6, female, dorsal view with lateral view at left.

which grade laterally into longer, white, plumose hairs. S1–5 with less bluish reflections than terga, each clothed subapically with ascending, white, simple hairs; S6 like preceding in color, but with abundant, medio-apical, orange-brown, mossy plumose hairs.

Male.—Average and range of forewing lengths (6 specimens): 5.76 mm, 5.40–6.55 mm. *Head*. Coloration as in female but labrum, most of clypeus, and lower paraocular areas up to level of summit of clypeus light yellow; dark color of head extends down along the epistomal suture to anterior tentorial pit. Mandible bidentate. Posterior ocelli in front of summit of vertex. Flagellomere 3 longer than broad. *Thorax*. Largely as in female. Average and range of hamuli (7 specimens): 8.4, 7–10. Third leg with distinct basitibial plate in position and form similar to that of

female. *Metasoma*. Slightly more elongate than in female; T1–6 with color and vestiture as in T1–4 of female; T7 with median impunctate area and lateral long, white, simple hairs; true apex of T7 bearing short, white, plumose hairs. S1–6 as in female. Terminalia as illustrated.

The distribution of this common species is shown in Figure 38. In Chile the northernmost locality is Vicuña, Coquimbo Prov.; the southernmost is Colegual, Llanquihue Prov. In Argentina the southernmost located collection site is El Bolsón, Rio Negro Prov., but specimens are labelled El Hoyo and El Turbio, Chubut Prov. (New York, Lawrence); the probable vicinity is indicated by a circle in Figure 38. Altitudes of most collections are not given on the labels but range from near sea level to 1400–1600 m (Llanquihue Prov.), 1100 m (Talca Prov.) and 1700–2200 m (Santiago Prov.); in the lake district of Argentina, altitudes are indicated as 650 to 850 m.

Relationships of *Manuelia* to Other Xylocopinae

The anthophorid subfamily Xylocopinae as delimited by Michener (1944, p. 269), Hurd and Moure (1963) and others includes both the large, robust bees of the tribe Xylocopini and the smaller and usually slender forms of the tribes Ceratinini and Allodapini. The last, recently segregated from Ceratinini (Michener, in press), has many derived characters and is not particularly relevant to *Manuelia*. The resemblances of *Manuelia* to Xylocopini (*Xylocopa*, *Lestis*, *Proxylocopa*) and to Ceratinini (*Ceratina*, *Pithitis*, *Megaceratina*) have been indicated in the generic description above, using for brevity the letters X (Xylocopini), C (Ceratinini), and M (for special features of *Manuelia*). In that description 22 characters are marked C; 12, X; and 6, M. Thus *Manuelia* is most similar to Ceratinini, but also has numerous features like Xylocopini in spite of its ceratinine appearance. A cladistic approach to relationships among tribes of Xylocopinae is presented by Sakagami and Michener (in press).

In some other features, not listed because they are variable and therefore not generic characters of *Manuelia*, this genus is nonetheless intermediate between Xylocopini and most Ceratinini. For example, the declivity of the posterior part of the thorax extends downward vertically from the posterior edge of the scutellum in some Xylocopini while in most Ceratinini and in *Manuelia gayatina* (Fig. 35) the base of the propodeum is more or less horizontal. The situation for the other species of *Manuelia* is shown in Figures 33 and 34.

The nest characteristics of *Manuelia* are similar to those of Xylocopini. The branching burrows and barrel-shaped cells are unlike those of any other small Xylocopinae, but resemble those of Xylocopini.

Since most bees, and more specifically most Anthophoridae, nest in the ground, the Xylocopinae probably arose from ground-nesting forms. Malyshev (1913:55–56) and Hurd (1958:368) attached much importance to the ground-nesting habits and certain anatomical conditions (basitibial and pygidial plates) of *Proxylocopa* that also occur in ground-nesting anthophorines but not in other Xylocopinae. Because *Proxylocopa* is a member of the tribe Xylocopini, Malyshev regarded that tribe as more closely related to the ground-nesting ancestor than is the Ceratinini. This view is supported by the clustered cells and constructed cell walls of *Proxylocopa*, described and illustrated by Gutbier (1915), and by the brood-cell linings secreted by

Dufour's gland also found in *Proxycopa* but not known in other Xylocopinae (Kronenberg and Hefetz, 1984).

The nesting habits of *Proxycopa* were assumed by Malyshev and Hurd to be primary, although there are examples in both tribes of flexible behavior which could have led to a return to the ground as a nesting site. In the large carpenter bees, Hurd (1978) cites reports of nests in bricks and other soft substrates, Lucas (1868) noted a nest in a copper tube, and Hardouin (1943) found that an individual of a species presumably unaccustomed to bamboo accepted a bamboo tube offered experimentally. Of the small carpenter bees, allodapines are reported by Brauns (1926) to nest in the ground in the absence of suitable plants or in vacant beetle galleries in wood. While constructed cell walls and linings derived from Dufour's gland are usual in soil-nesting anthophorids, and might seem unlikely to reappear in *Proxycopa* if it reverted to the soil, the partitions between cells in *Xylocopa* are in reality constructed cell walls that do not extend to the sides of the cell in a wood substrate. Reversion to soil could result in extension of partition-construction to produce cell walls. Less likely, probably, would be reversion to production of the hydrocarbon-rich hydrophobic cell lining. Thus while the nests of *Proxycopa* offer a basis for considering the genus as similar to the ancestral Xylocopinae, there is the possibility that nesting in the ground is an adaptation to desertic environments lacking plants for nesting. Independently, Hurd (in personal communication to Daly) entertained the same explanation. Furthermore, Maa (1954) considered the species of *Proxycopa* to be closely related on the basis of morphology; such similarity does not suggest the antiquity to be expected of ancestors of the other Xylocopinae. *Proxycopa* is noteworthy for its close resemblance to other genera of the tribe Xylocopini.

Although *Manuelia* shares its nesting pattern with the Xylocopini, *Ceratina* and *Pithitis* are quite different in their nesting activities and social organization (Michener, in press), giving little indication of ground-nesting ancestry.

In the majority of anatomical features the Ceratinini rather than the Xylocopini show the most plesiomorphic features, as judged by Michener's (1944:228–229) list: short first flagellar segment, horizontal metanotum, propodeum with horizontal basal area, large pterostigma, long notaulus, relatively long second abscissa of vein M + Cu in the rear wing, long jugal lobe, and hairy wings. The Xylocopini show more specialized conditions of the same variables. Some ceratinine characters of the wings and thorax may relate to the general body size and shape, associated with nesting in small burrows. Nevertheless, other characters, presumably not related to size and slenderness, also indicate the more primitive anatomy of the small carpenter bees. For example, male Ceratinini have two hind tibial spurs and, in *Manuelia* and *Ceratina* (*Euceratina*), have gonostyli, while the large carpenter bees have only one tibial spur and no gonostyli. The basitibial plate is near the base of the tibia in females of ground-nesting bees; Ceratinini have the plate usually in this position when it is present, while only *Proxycopa*, among the Xylocopini, has it in this location. Wille (1958) found the dorsal circulatory vessel to be straight in the Ceratinini, a condition considered by him to be primitive among the bees. *Xylocopa* possesses a specialized condition with the thoracic portion arching between the longitudinal muscles and the petiolar portion coiled.

In view of the primitive features occurring in members of both tribes (Ceratinini

and Xylocopini), we cannot agree that the Xylocopini is closer to the stem of the subfamily than Ceratinini. Moreover, we do not think that *Proxycopa* is particularly close to the ancestral Xylocopini; undoubted specialized features of *Proxycopa* include the reduced notauli. The ancestor for all modern members of the subfamily Xylocopinae should combine the nesting pattern of the Xylocopini with the primitive anatomical features of both Ceratinini and the Xylocopini.

It seems reasonable to suppose, as did Malyshev, that the ancestor nested in relatively thick pieces of dead plant tissue (soft or rotten wood). The ancestor of the large carpenter bees continued nesting in the thicker pieces of wood. Once the outer layer has been broken, this medium places little restriction on the dimensions or pattern of the nest. There was probably a trend of increasing body size and more powerful jaws, together with the changes in the thorax and wings which impart the specialized facies to the modern tribe Xylocopini. The nesting habits, however, remained largely unaltered. The smaller forms of the ancestral stock could nest in small beetle burrows and slender stems and consequently there was the trend to smaller body size and slender form which led to the modern Ceratinini.

We believe that *Manuelia* is a surviving remnant of the early small carpenter bees. Moreover, it is the most primitive of the subfamily Xylocopinae and nearer than any other form to the phyletic dichotomy which separated the tribes Ceratinini and Xylocopini. The restriction of the species to Central Chile and Argentina, the fact that the genus is made up of three species fully as different as subgenera elsewhere among bees, together with the anatomical and biological relations enumerated above, support the conclusion that *Manuelia* is a relict genus. In view of its presumed antiquity, *Manuelia* exhibits an interesting use of introduced plants both for provisions and as nesting substrates. This is not surprising, however, since most Xylocopinae are polylectic feeders and seem to select nesting sites according to their physical characteristics without regard to the kind of plant concerned.

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