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South American Panurgine Bees (Andrenidae: Panurginae), Part II. Adults, Immature Stages, and Biology of *Neffapis longilingua*, a New Genus and Species with an Elongate Glossa

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ABSTRACT

A new genus and species of panurgine bee, ***Neffapis longilingua*** Ruz, is described from the southern end of the Atacama desert of Chile. Associated with the plant *Malesherbia humilis* Poeppig from which it gathers pollen, this bee is remarkable because of its elongate glossa and labial palpi, presumably adaptations for reaching the nectaries of the host flower. Its biology is described, including the following: nesting site characteristics, nest architecture, provisioning, egg deposition, larval feeding habits, larval defecation, phenology, mating, and parasitism. The egg, mature larva, and pupa are also described. The phylogenetic relationships of this bee to other panurgine groups is briefly discussed, but no certain affinities can be established at this time in spite of the abundant information concerning the anatomy of adults and immatures stages.

RESUMEN

Un nuevo género y especie de abeja panurginae, *Neffapis longilingua* Ruz, se describe para el extremo Sur del Desierto de Atacama de Chile. Asociada con la planta *Malesherbia humilis* Poeppig, de la cual obtiene el polen, esta abeja se destaca por su larga glosa y palpo labial, lo que presumiblemente corresponde a adaptaciones para alcanzar los nectarios de la flor huésped. La descripción de su biología incluye los siguientes aspectos: características del área de nidificación, arquitectura del nido, aprovisionamiento, postura del huevo, hábitos alimenticios de la larva, fenología, cópula y parasitismo. Además se describe: huevo, larva madura y pupa. Las relaciones filogenéticas de esta abeja con otros grupos de panurginae son brevemente discutidas, aunque afinidades entre ellos aun no ha sido posible establecer con certeza, a pesar de la abundante información concerniente a la anatomía de adultos y de estados inmaduros.

INTRODUCTION

This paper is the second in a series devoted to describing and naming new taxa of South American Panurginae, giving information about their nesting biology, and recording the anatomy of their immature stages. The bee treated here is uncommon even in its known range; it is remarkable because of its extremely long glossa and labial palpi, presumably an adaptation for extracting nectar from its host plant.

The first author (JGR) was primarily responsible for the descriptions of the immature stages and the treatment of the biological information, and the second author (LR) for the generic and species descriptions of the adults.

Samples of nest components and immature stages are preserved in the collections of the American Museum of Natural History. Deposition of adult specimens is treated after the species description.

ACKNOWLEDGMENTS

JGR acknowledges the kind assistance of Luis E. Peña Guzmán and Alfredo Ugarte Peña, who accompanied him to the nesting site and helped to collect the type series. The host plant identification was provided by C. Marticorena and M. Quezada, Departamento Botánica, Universidad de Concepción, Chile. Soil texture was analyzed by Richard H. Kruzansky. Illustrations of adult structures were inked by Carmen Tobar, Universidad Católica de Valparaíso (UCV), Valparaíso, Chile.

We thank Bryan N. Danforth and Harold Toro who carefully reviewed the manuscript and contributed valuable comments for its improvement.

ADULTS

Descriptions of adults follow the format used for *Parasarus* Ruz (Ruz and Rozen, 1993). Morphological terms, such as duplication, keirotrichia, fragmentum, and flabellum, and delimitation of certain structures such as paraglossa and labrum are based mainly on Michener (1944, 1981), Michener and Brooks (1984), Winston (1979), Ruz (1991), Ruz and Rozen (1993). Terminology for the sting apparatus and for the male genitalia is based on Snodgrass (1956) and Rozen (1951), respectively. Abbreviation for tergum is T, for sternum S. Ratios are expressed in units in which 25 units equal 1 mm.

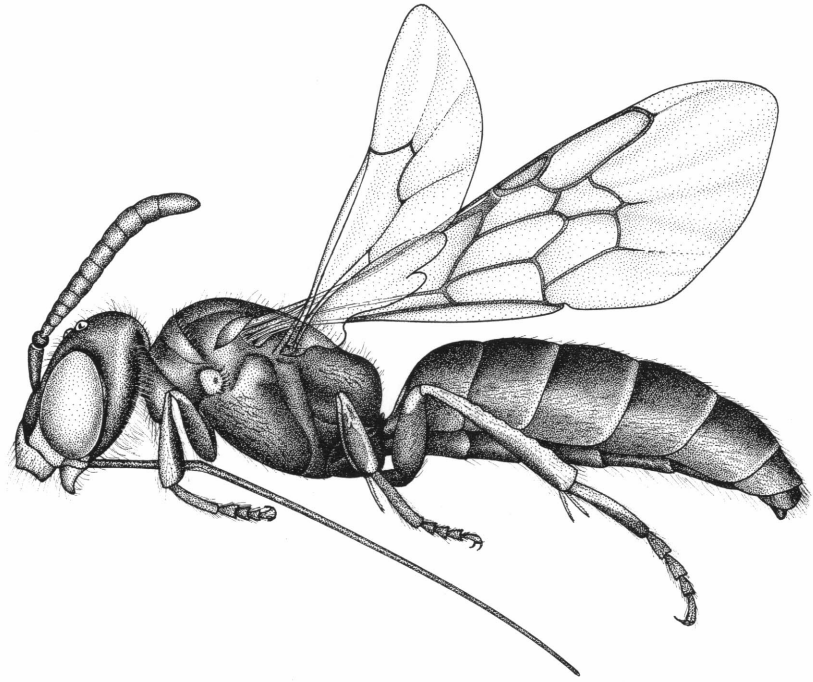


Fig. 1. *Neffapis longilingua*, n. sp., male, lateral view.

Neffapis Ruz, new genus
Figures 1–20

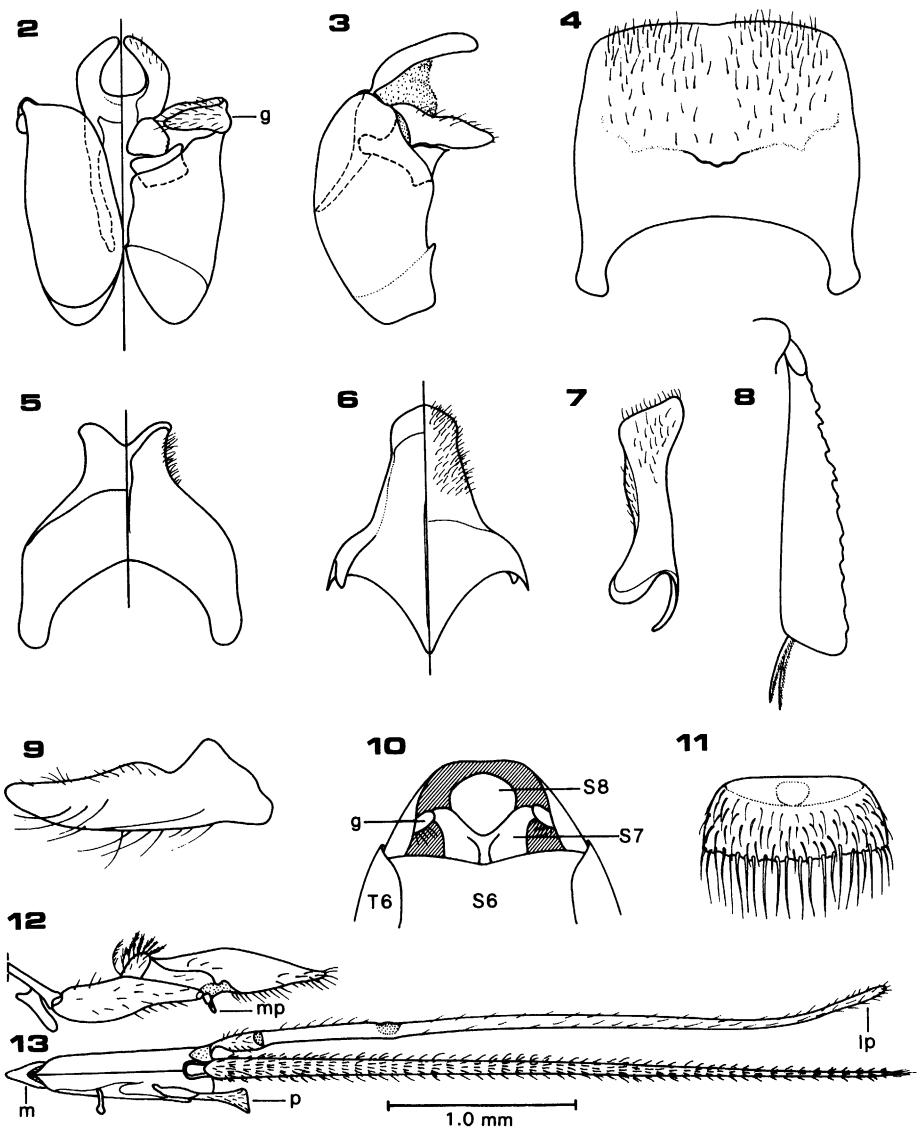
TYPE SPECIES: *Neffapis longilingua*, n. sp.

DIAGNOSIS: *Neffapis* can be easily distinguished from all other known panurgines by its long glossa and labial palpi, which, in resting position, almost reach the tip of the metasoma. The labial palpus is 3-segmented, with segment 3 being the longest, and the maxillary palpus has only two small segments. The male gonostyli are strongly sclerotized and oriented almost at right angles to the gonocoxites.

Except for the mouthparts, *Neffapis* superficially resembles the South American *Rhophitulus* mainly because of the very fine, dense punctation on the scutum and hypoepimeral area and the extremely short hairs on the mesosomal dorsum. It clearly differs from *Rhophitulus*, however, in having the following characteristics: shorter head, lower position of the antennal sockets, almost flat labrum, longer scutal hairs intermixed with short ones, fovea of metasomal tergum 2 (T2) almost invisible, and absence of gonobase. Other features of *Neffapis* such as the male genital capsule and the ventral tip of the metasoma show some similarity to *Panurginus*; however, these similarities may not reflect true relationships (see Discussion of Phylogenetic Relationships, below). Male *Panurginus* can be recognized by the distally bilobed metasomal sternum 6 (S6) (in addition to wing venation); in *Neffapis* the exposed bilobed structure is S7 (fig. 10).

Characters presented in italics below will probably be of greatest use for identification purposes.

DESCRIPTION: Body length small (about 6 mm), black, with yellow markings on face and mesosoma (including legs); markings more distinct in males than in females. Pubescence in general short and yellowish white; on dorsal mesosoma, pubescence very short, appressed to integument, rather dense, and with sparse longer hairs intermixed; propodeal triangle with pubescent patches laterally; setae minute on most parts of metasomal segments in male, in female short but clearly visible and denser on distal parts of segments, especially terminal ones; sterna of males with



Figs. 2–13. *Neffapis longilingua*, n. sp., male. **2.** Genital capsule, dorsal and ventral views. **3.** Genital capsule, lateral view. **4.** S6, ventral view. **5.** S7, dorsal and ventral views. **6.** S8, dorsal and ventral views. **7.** S8, lateral view. **8.** Hind tibia. **9.** Mandible (left). **10.** Metasoma tip, ventral view. **11.** Labrum. **12.** Maxilla. **13.** Labium. g, gonostylus; lp, labial palpus; m, mentum; mp, maxillary palpus; p, paraglossa. Scale refers to figures 12 and 13. Figures 2–7, 10 show distal part up; 2, 3, 5–8 with dorsal view at left and ventral view at right.

setae sparser than on terga, almost absent medially. Integument of propodeal triangle areolate, with striae; integument of metasoma slightly areolate and shiny, especially on sterna. Punctation of body integument, in general, fine, rather dense on metasomal terga, deeper in female than in male; sparser on sterna of both sexes.

Head broader than metasoma, although only slightly so in female. *Mandible with basal projection (fig. 9).* Other mouthparts (figs. 12, 13): Prementum basally with no frag-

mentum. *Glossa much longer than prementum, with no distal specialization or flabellum. Paraglossa widened distally (fig. 13, p). Labial palpus 3-segmented; segment 3 distinctly longer than 2 and much longer than 1. Maxillary palpus 2-segmented (fig. 12, mp).* Galeal comb absent. *Labrum with basal part smooth, impunctate, delimited by slight ridge; distal part rather flat, not reflexed (figs. 11, 20).* Anterior tentorial pit at intersection of epistomal suture and outer subantennal suture. Antennal socket below middle of face and close to epistomal suture, especially in male (figs. 14, 15). *Facial fovea shallow, poorly delimited.* Middle ocellus just above orbital tangent (frontal view). Vertex convex. Pronotum, on dorsal margin, with rounded ridge laterally. Pre-episternal groove distinct, extending below scrobe. Wings (fig. 1): Forewing with distance from base of pterostigma to point where vein r branches from it longer than prestigma; side of pterostigma basal to vein r slightly diverging from costa; side within marginal cell somewhat curved. Marginal cell slightly longer than distance from its apex to wing tip. *Two submarginal cells.* First submarginal cell about as long as second. Second cell M (= 2nd discoidal cell) shorter than first one. First recurrent vein not interstitial with first transverse cubital vein. Forewing with cu-v longer than second abscissa M+Cu. Hind wing with cu-v about ⅕ or ⅙ as long as second abscissa M+Cu. Basitarsus 1 longer and narrower in male than in female. Femur 2 of female basally with comb on ventral border, not well defined. Middle tibial spur of female clearly shorter than basitarsus 2, with minute and fine teeth. Basitarsus 2 about as long as 1 and longer than 3. Tibia 3 of female slightly more than twice as long as basitarsus 3, with keirotrichia on most of inner surface; male with dorsal margin of tibia 3 slightly and irregularly serrate (fig. 8), with keirotrichia as in female. Scopal hairs on tibia 3 of female simple, rather sparse, somewhat longer than hairs at apex of metasoma and bent toward their apices. Hind tibial spurs with teeth minute and subequal in length, outer one somewhat curved toward apex; both spurs slightly longer in female than in male. Basitibial plate of male well delimited, with margins as ridges. Tarsus 3 unmodified. Claws bifurcate, rather deeply cleft; rami subequal in male, inner ramus shorter than outer in female. *T2 with lateral fovea extremely weak, visible only as shinier area than surrounding integument. Pygidial plate rather broad in female (fig. 17), absent in male.* T7 of female (hemitergite) with anterior part of upper margin narrowly produced forward (fig. 18). T8 of male trapezoidal-. *S6 of male distally with slight median emargination (fig. 4). S6 of female with basal margin straight; inner surface of this sternum with sclerotized area forming short longitudinal ridge (fig. 16) on each side;* this surface also with strong inner-curved ridge on lateral margin; duplication membranous; distal margin slightly projecting in middle; exposed distal area of S6 (ventral view) basally with minute sparse hairs; those hairs on premarginal area oblique, somewhat longer and denser than basal ones, and forming patch on each side of midline. *S7 of male with two distal, medium-sized lobes exposed (figs. 5, 10). S8 of male with* distal projection rounded at apex; *basal area pointed with slight longitudinal ridge on dorsal surface (figs. 6, 7).* Genital capsule with well-developed gonocoxal apodeme; gonocoxites elongate, fused proximally only; *gonostylus strongly sclerotized, oriented at nearly right angle to gonocoxite (figs. 2, 3),* and fused to gonocoxite through small membranous area. Volsella apparently free mesally, with denticles. Penis valves simple, rounded and curved at apices, fused to each other by preapical bridge. Sting elongate (not surpassing stylus); first valvula well sclerotized; valve present (fig. 19).

The only presently known species of this genus is found in northern Chile.

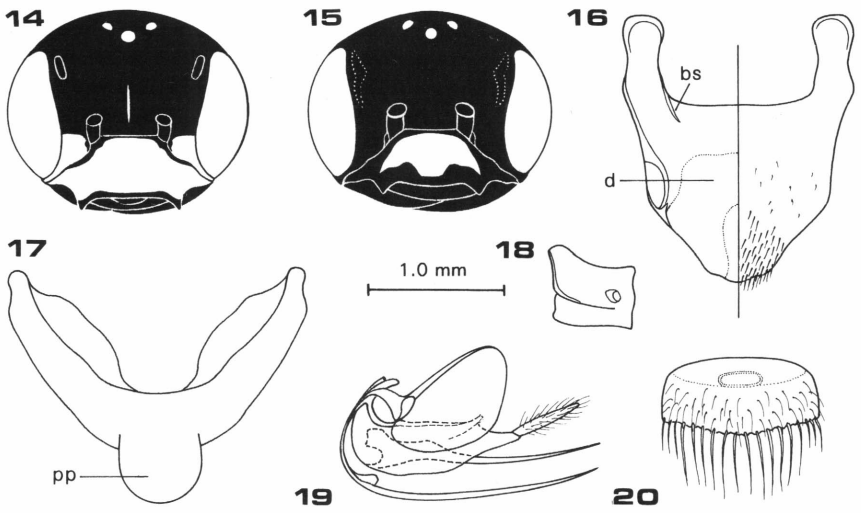
ETYMOLOGY: The genus name is in honor of Dr. John L. Neff, of the Central Melittological Institute, in recognition of his important contributions to bee research and collections.

Neffapis longilingua Ruz, new species

Figures 1–20

DIAGNOSIS: The generic diagnosis gives the characters by which this species can be distinguished from all other known Panurginae.

DESCRIPTION: *Male*. Length about 6.0 mm; head width 1.6 mm; mesosoma width 1.3 mm; forewing length about 4.0 mm.



Figs. 14–20. *Neffapis longilingua*, n. sp. **14.** Male, head, frontal view. Figs. 15–20, female. **15.** Head, frontal view. **16.** S6, dorsal and ventral views. **17.** T6, dorsal view. **18.** T8 (= hemitergite). **19.** Sting. **20.** Labrum.

Abbreviations: bs, basal sclerotization; d, duplication; pp, pygidial plate. Scale refers to figures 14 and 15.

COLORATION: Black, except flagellum brown dorsally and testaceous ventrally and following parts yellow: Basal half of mandible; most of labrum (except distal part in middle); clypeus; ventral fourth of paraocular area; pronotal lobe; base of tegula; on foreleg, apex of femur, dorsal surface of tibia extending partially along anterior surface, and dorsal suface of basitarsus; on midleg, apex of femur, dorsal surface of tibia at both ends and along posterior margin, basal half of anterior surface of basitarsus; on hind leg, apex of femur, anterior (outer) and posterior (inner) surfaces at both ends of tibia and along its dorsal (posterior) margin, and along dorsal surface of basitarsus (other tarsomeres brown). Wings slightly smoky, veins and stigma brown, although latter testaceous in middle. PUBESCENCE: In general short, yellowish white, mostly tiny, simple, and appressed to integument; face, most of mesosoma, apical metasomal terga, and each sternum distally with sparse, somewhat longer, intermixed branched hairs (except hairs of sterna apparently simple); propodeal triangle laterally with patch of hairs minutely branched; first three sterna almost bare medially; hairs scarce and extremely short on basitibial plate. PUNCTATION: Head and mesosoma areolate, with fine, rather dense, deep punctures; punctures more minute on mesoscutum, sparse on mesopleura below scrobe and on metapleura. Propodeum more strongly areolate; propodeal triangle with fine longitudinal striae basally. Metasoma with integument mostly smooth and shiny, except dull on premarginal area of first three terga; punctures fine on metasomal terga; sparser, somewhat coarser and shallow on sterna, especially toward distal part of apical ones; integument scarcely punctate on basal sterna, shiny, smooth and somewhat swollen on exposed area of S7. STRUCTURE: Head broader than long (40:30) (fig. 14). Mandible with strong basal projection. Labrum twice as broad as long (12:6), rather flattened, with basal area (above ridge) shorter than distal one (fig. 11). Mouthparts (figs. 12, 13): Prementum about as long as galea, which is very short relative to elongate glossa and labial palpus. Maxillary palpus with segment 1 twice as long as segment 2 (1:0.5). Glossa more than 4 times as long as prementum (95:22). Paraglossa almost one-fourth as long as prementum (6:22). Labial palpus with segment 1 almost one-third as long as segment 2; segment 3 almost 3 times as long as 1 and 2 together (7:18:69), somewhat spatulate distally; articulation area

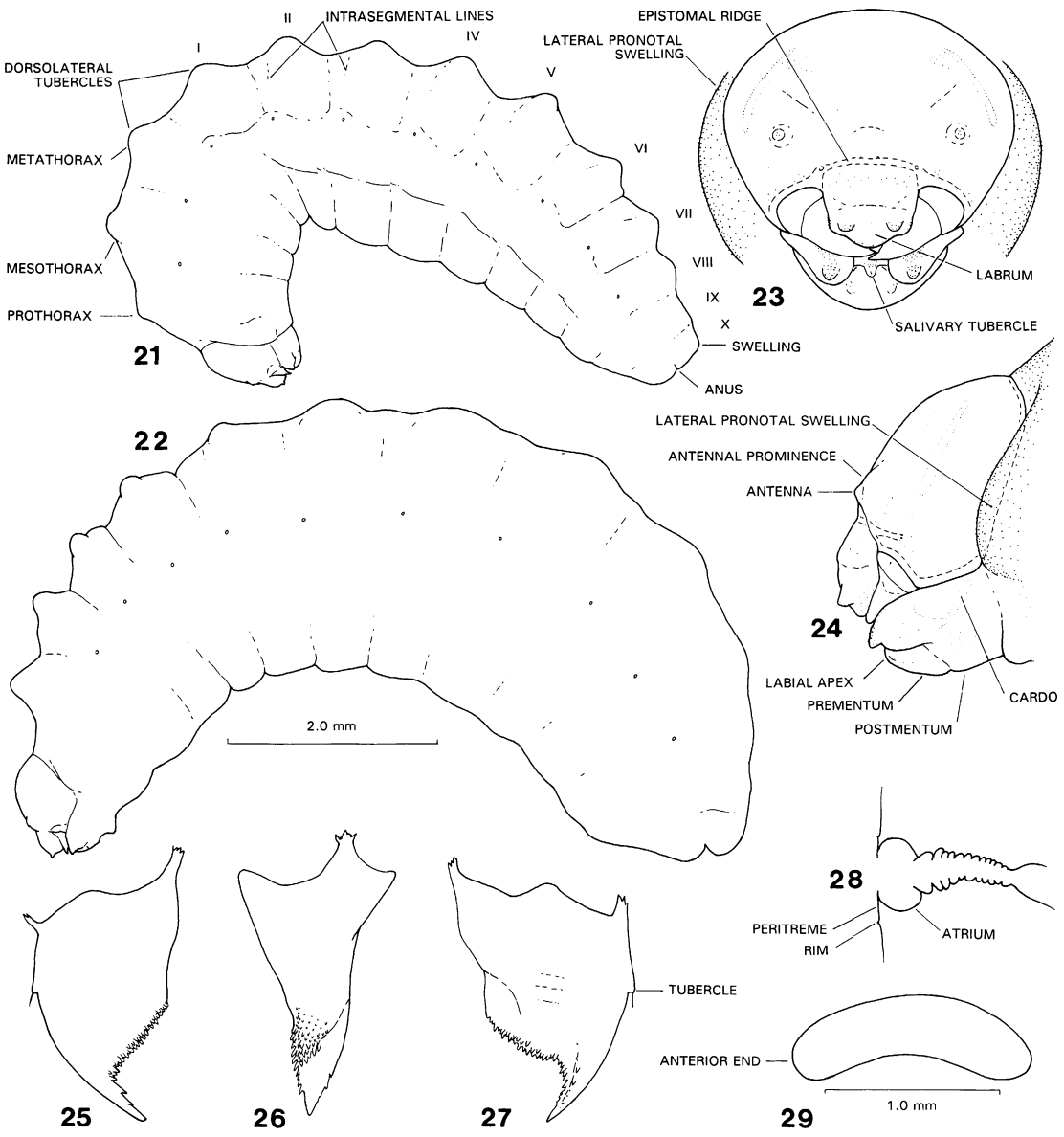
between segments 2 and 3 widely membranous on one side. Clypeus convex in central area, little less than three times broader than long (25:9). Facial fovea about 4 times as long as broad and about twice as long as inner subantennal suture (4:1:2). Supraclypeal area scarcely produced between antennal sockets. Frontal line carinate at approximate level of antennal sockets. Distance from inner orbit to antennal socket a little less than distance between sockets (5:7). Eye length to head length 22:30; inner margin of eyes diverging above. Maximum width of gena in lateral view narrower than eye. Venter of mesosoma with deep longitudinal groove along midline, receiving reposed glossa. Forewing: Ratio of length of pterostigma measured from base to point where vein r branches from it, to maximum width of pterostigma, to width of prestigma 6:3:2 (fig. 1). Marginal cell slightly longer than distance from its apex to wing tip (21:18). Submarginal cell 1 slightly longer than submarginal cell 2 along posterior margins (12:11). Basal part of propodeal triangle longer than metanotum (6:4). Basitibial plate narrowing slightly toward apex. Middle tibial spur about half as long as basitarsus, finely serrate. Hind tibia with spurs subequal in length and almost straight. Lateral fovea of T2 weakly depressed, small, narrow, difficult to see. S6 with distal margin slightly emarginate in midline and broadly recurved laterally (fig. 4). S7 distally with V-shaped emargination, with thumb-shaped lobe on each side and longitudinal groove in midline (figs. 5, 10). S8 with distal projection gradually and slightly narrowed but rounded and somewhat expanded at apex; S8 proximally tapered and with slight longitudinal ridge on midline of ventral side (figs. 6, 7, 10). Genital capsule as illustrated (figs. 2, 3)-.

Female. Length about 6.0 mm; head width 1.7 mm; mesosoma width 1.6 mm; forewing length 4.0 mm. As described for male except: COLORATION: Black, with following parts yellow: median part of clypeus with mushroom-shaped spot, basal part of tibia 1 and 2. Metasomal terga black to brown, somewhat reddish in some specimens; sterna brown. PUBESCENCE: Somewhat longer than that of male on lateral and distal areas of apical metasomal segments. Hairs of tibial scopa rather sparse, apparently simple. PUNCTATION: Integument of metasoma mostly shiny, clearly dull only on T2; integument of apical metasomal segments with punctures somewhat coarser than those of male. STRUCTURE: Head width to length 43:30 (fig. 15). Mandible with basal projection smaller than in male. Labrum width to length 14.5:7, with smooth basal part a little longer than in male (fig. 20). Clypeus width to length 26:10. Facial fovea four times longer than broad and six times longer than inner subantennal suture (12:3:2), of irregular shape, and broader on dorsal half. Frontal line at level of antennal sockets a very short, slight ridge. Distance from inner orbit to antennal socket versus distance between sockets 6:8. Marginal cell longer than distance from its apex to wing tip 24:22. Basitibial plate kidney-shaped. Middle tibial spur more than half as long as basitarsus. Hind tibia with spurs slightly curved. Lateral fovea of T2 larger than that of male, more distinct as black spot when terga are reddish. T6 with pygidial plate wide, rounded at apex (fig. 17). T7 as in figure 18. S5 with distal margin slightly and widely procurved, almost straight. S6 as in figure 16. Sting as illustrated (fig. 19).

Holotype male and allotype: 6 km S. Vicuña, Elqui Province, Chile, October 16, 1991 (J. G. Rozen and L. Peña) in the collection of the American Museum of Natural History.

Paratypes: 5 males and 15 females, same locality and collectors as holotype and allotype, October 16–21, 1991; 2 males and 3 females, same except for November 16, 1991; 1 female, same as preceding except on *Malesherbia humulis*; 1 female, same except for October 21, 1991, no flower data (J. G. Rozen, L. Peña, and A. Ugarte); 3 males, same except October 23–25, 1992 (Rozen, Sharkov, Snyder); 5 females, same except October 24, 1983 (J. Neff); 1 female, Las Breas, Coquimbo Province [now Limari Province], January 5, 1962 (R. Wagenknecht). Paratypes will be deposited in the following collections: American Museum of Natural History; Snow Entomological Museum, University of Kansas, Lawrence, Kansas; Central Melittological Institute, Austin, Texas; and Universidad Católica de Valparaíso, Valparaíso, Chile.

ETYMOLOGY: The specific name, from Latin, refers to the long glossa.



Figs. 21–29. *Neffapis longilingua*, n. sp. **21.** Postdefecating larva, lateral view. **22.** Predefecating, mature larva, lateral view. **23.** Mature larva, head, frontal view. **24.** Same, lateral view. **25–27.** Mature larva, right mandible, dorsal, inner, and ventral views. **28.** Spiracle. **29.** Egg, side view. Scales refer to figures 21 and 22 and to figure 29, respectively.

DISTRIBUTION: This species has been found only in Elqui Province, Chile.

Comments: *Neffapis longilingua* is the only known species of this genus and the only panurgine bee with a glossa and labial palpi that are strikingly long. Species of *Perdita* belonging to the subgenus *Glossoperdita* possess elongate glossae, but the labial palpi are much shorter and consist of the normal four segments. Some Calliopsini (Ruz, 1986, 1991), such as *Calliopsis (Nomadopsis) zonalis* Cresson, and some Melitturgini (Ruz, 1986), such as *Mermiglossa rufa* Friese, exhibit somewhat elongate glossae which, however, are

not as long as those of *Neffapis*. Furthermore, the labial palpus among all other Panurginae is always 4-segmented, with segment 3 shorter than 1; in *Neffapis* the palpus has only 3 segments and segment 3 is the longest

IMMATURE STAGES

EGG

Figure 29

Eggs of this species, like those of all known Panurginae, are unremarkable. They are moderately elongate, curved, whitish, and possess a completely smooth, shiny chorion. The posterior end is slightly more pointed than the anterior end. Two measured 1.4 and 1.7 mm long, and one was 0.4 mm in maximum diameter. One preserved egg in which the first instar was already well formed, showed the embryo oriented so that its dorsum faced the venter of the chorion. No doubt the embyro of *Neffapis* rotates 180° shortly before hatching, a feature that appears normal for most bees (see Torchio et al., 1988; Torchio, 1989; and references therein).

MATURE LARVA

Figures 21–28

The following diagnosis and description are comparative with recent treatments of mature panurgine larvae (see McGinley, 1989, for references; see also Ruz and Rozen, 1993, for the larval description of *Parasarus atacamensis* Ruz; Rozen, 1988, for that of *Camptopoeum bakeri* Rozen; and Neff and Rozen, in press., for that of *Anthemurgus passiflorae* Robertson).

DIAGNOSIS: The mature larva of *Neffapis longilingua* can be separated from the known larvae of the Anthemurgini sensu lato[3] (*Protandrena, Anthemurgus, Pseudopanurgus, Pterosarus, Heterosarus, Parasarus, Cephalurgus, Metapsaenythia, Psaenythia, Rhophitulus,* and *Anthrenoides*) and *Melitturga* because its thoracic dorsolateral tubercles are unmodified, that is, they do not form lateral pockets between the prothorax and mesothorax and between the mesothorax and metathorax (see Neff and Rozen, in press, for a discussion of this character in the Anthemurgini). It can also be distinguished from the larvae of *Arhysosage, Spinoliella,* and *Callonychium* which also possess highly modified dorsolateral thoracic tubercles. The thoracic dorsolateral tubercles of the remaining panurgine genera whose larvae are known (*Meliturgula, Camptopoeum, Panurgus, Panurginus, Calliopsis* sensu lato, and *Perdita*) agree with those of *Neffapis* in that they are not elongate and modified to form pockets. Among this group, the presence of the median section of the epistomal ridge is characteristic of only *Neffapis* and *Panurginus*, and these two genera also share very low abdominal dorsolateral tubercles. However, absence of pronounced antennal prominences and the more pronounced labium of *Neffapis* immediately set it apart form *Panurginus*.

Characters italicized below summarize the salient features of this genus.

DESCRIPTION: Head (figs. 23, 24). Integument of head capsule with scattered nonsetiform sensilla; head integument of postdefecating larva faintly pigmented except following distinctly pigmented: antennae, labral tubercles, and maxillary and labial palpi; mandibular apices even more darkly pigmented; integument of predefecating larvae less pigmented than that of postdefecating form.

Head size moderately small in relation to rest of body of postdefecating larva; head capsule wider than maximum length from vertex to lower clypeal margin. Tentorium including dorsal arms well developed; anterior pits in normal position on face; posterior tentorial pit normal in position; postoccipital ridge moderate in thickness, not curving forward medially as seen in dorsal view; posterior margin of head capsule normal in position; median longitudinal thickening of head capsule absent; hypostomal ridge well developed, without ramus; pleurostomal ridge well developed; *epistomal ridge* well developed between anterior mandibular articulations and anterior tentorial pits, and, as in *Panurginus, moderately well developed between pits;* epistomal depression moderately pronounced. Parietal bands distinct. *Antennal prominences weakly developed;* antennal disc and papilla moderate in size; papilla with three sensilla. Vertex in lateral view (fig. 24) evenly rounded, without projections or ele-

[3] As defined by Ruz (1986).

vations; frontoclypeal area normal in length and configuration. *Labrum* normal in size and shape for Panurginae except *apically produced medially as seen in frontal view,* without sclerite; paired labral tubercles arising from labral disc, moderate in size; epipharyngeal integument spiculate laterally.

Mandible (figs. 25–27) moderately slender; dorsal surface nonspiculate; outer surface with small seta-bearing tubercle near base; apex tapering, slender, simple, without subapical tooth that is larger than other teeth along dorsal apical edge; both dorsal and ventral apical edges with teeth; cusp moderately produced, not produced ventrally as in *Panurgus*, without large cuspal tooth as in *Melitturga*, but with numerous moderate-sized teeth. Labiomaxillary region recessed, and, except for maxillary apices, fused; *maxillary apex (except for palpus) approximately in line with labial apex as seen in lateral view (fig. 24),* not greatly recessed as in the Anthemurgini and *Panurginus*. Cardo and stipes unpigmented, discernible as integumental thickenings; articulating arm of stipital sclerite not evident, presumably embedded in lateral parts of hypopharyngeal groove; palpus large, somewhat larger than labral tubercle, with dorsal surface curving downward; this surface and dorsal surface of maxilla with conspicuous spicules. Labium weakly divided into prementum and postmentum; premental sclerite not evident; labial palpus distinct, smaller than maxillary palpus, represented by sclerotized swelling. Salivary opening in deep, curved groove, surrounding salivary tubercle (fig. 23; i.e., median swelling, pronounced in some Andrenidae, delimited by curved groove anteriorly and laterally and hypopharynx posteriorly, Rozen, 1994: fig. 15, 23); this tubercle moderately produced and spiculate dorsally, presumably as continuation of hypopharyngeal spiculation. Hypopharynx spiculate; hypopharyngeal groove pronounced laterally because of projection of apex of labium on either side of salivary tubercle.

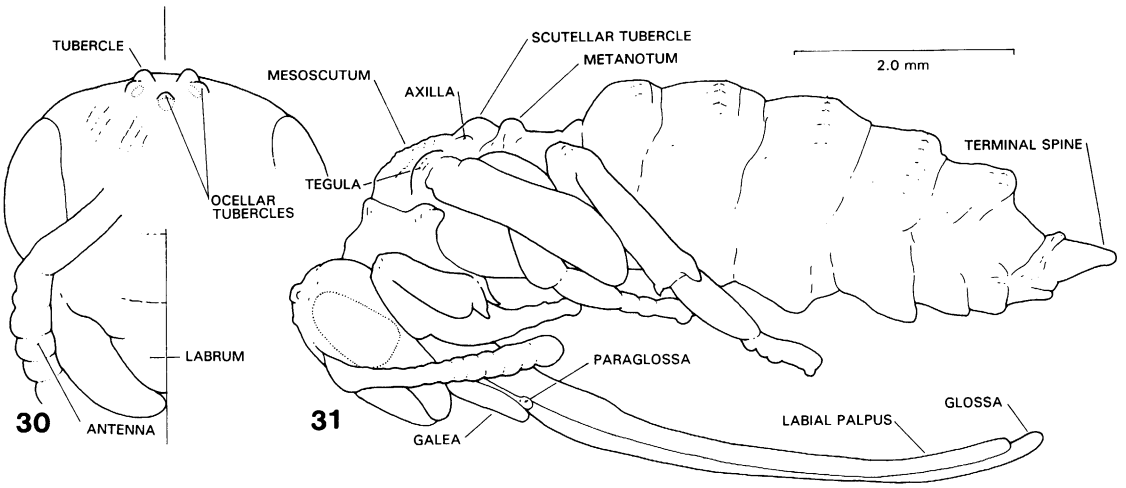
Body (figs. 21, 22). Integument with widely scattered minute nonsetiform sensilla, without setae, extensively spiculate except for apices of dorsolateral tubercles; spicules moderately large on anterior part of body, becoming much finer on posterior part of body, evenly spaced, discernible on predefecating larva but scarcely noticeable on postdefecating larva because of thickening and hardening of integument; lateral pronotal swellings beset with spicules similar to those on dorsal anterior part of body. Body form (figs. 21, 22) moderately robust; intersegmental lines moderately incised on postdefecating larva; intrasegmental lines faintly evident on midbody segments of postdefecating larva; lateral pronotal swellings small but evident; *paired dorsolateral body tubercles low; those of thorax approximately same size and shape as those of abdominal segments I and II;* those of abdominal segments III–VII not differing greatly from those of I and II on postdefecating larva (fig. 21) but on predefecating larva (fig. 22) much less defined than those of I and II; dorsal abdominal tubercles conical (i.e., not transverse); pleural region somewhat produced on postdefecating larva; abdominal segments VII with dorsolateral tubercles scarcely evident; IX and X without tubercles; abdominal segment X of postdefecating larva with vague transverse swelling dorsally midway to apex; segment X attached centrally to IX, not produced posteriorly or ventrally. Spiracles (figs. 21, 22, 28) very small, unpigmented; subequal in size; peritreme (fig. 28) present, large in diameter relative to diameter of atrium; atrium not projecting above body wall but with rim; atrial wall unornamented; primary tracheal opening with collar; subatrium of moderate length, consisting of approximately 10–12 chambers. Male sex characters consisting of median pair of contiguous ventral imaginal discs near posterior edge of abdominal segment IX; these discs associated with transverse linear cuticular invagination; female sex characters consisting of pair of ventral imaginal discs on abdominal segments VII, VIII, and IX; those of VII farthest apart; those of IX contiguous; faint cuticular scars associated with these discs on cleared postdefecating larva.

MATERIAL STUDIED: >50 predefecating and postdefecating larvae, 6 km south Vicuña, Elqui Province, Chile, October 19, November 15, 16, 1991 (J. G. Rozen).

PUPA

Figures 30, 31

DIAGNOSIS: This pupa can be easily distinguished from all other panurgine pupae be-



Figs. 30, 31. *Neffapis longilingua*, n. sp., pupa. **30.** Head, right side and part of left side, frontal view. **31.** Entire body, lateral view. Scale refers to figure 31.

cause of its extremely long glossa and labial palpi. In general it has fewer tubercles than do other panurgines. The combination of characters italicized below is unique to this genus.

The format follows that used in Yager and Rozen (1966).

DESCRIPTION: Length 6.2–7.5 mm; body without setae.

Head: Outer surface of scape not swollen; pedicel without tubercle. Mandible without tubercle. *Vertex with rounded tubercle immediately mesad of lateral ocellus;* ocellar tubercles evident; frons without tubercles although various parts of frons and vertex with varicosities; gena without tubercle.

Mesosoma: Lateral angles of pronotum not produced; posterior lobes of pronotum somewhat produced but not tuberculate; *mesoscutum without distinct tubercles although with varicosities;* mesoscutellum with pair of low rounded tubercles; axilla faintly produced; metanotum produced on each side; mesepisternum without tubercle. *Tegula without distinct tubercle but somewhat varicose.* Anterior part of forewing scarcely produced near base, without nodelike swelling. Fore and mid coxae each with long apical tubercle; hind coxa with shorter apical tubercle; fore and mid trochanters each with apical tubercle; hind trochanter apically produced ventrally; fore femur swollen at base; *base of hind tibia without low tubercle on outer surface.*

Metasoma: Terga I–VI (male) and II–V (female) each with transverse apical row of faint tubercles, some of which are sharp-pointed. *Terminal spine moderately short, apically rounded, nonsclerotized.*

MATERIAL STUDIED: 5 male and 7 female pupae, 6 km south Vicuña, Elqui Province, Chile, November 16, 1991 (J. G. Rozen).

BIOLOGY

DESCRIPTION OF SITE: Several aggregations of nests of this species were discovered along the sides of an unpaved road that sloped 5–10° 6 km south of Vicuña, Elqui Province, Chile. The region, at the southern end of the Atacama Desert, is subject to winter precipitation (scant in some years) and long dry summers. The vegetation consists of low-growing herbs, grasses, and widely spaced bushes and small trees. The nests were discovered during an investigation of the andrenine bee *Euherbstia excellens*; further details of the region as well as pictures of it are presented in Rozen (1993). A significant feature of the site, important to many species of bees nesting there, was the heavy clay texture of the soil, consisting of 30% sand, 26% silt, and 44% clay. When the soil dried, it became extremely hard and compact and at the same time shrank so that numerous irregular cracks transcended the substrate. These cracks, some more than 1 cm wide, were used as entrance

ways to the moist, softer soil below not only by *Neffapis* but also by *Euherbstia excellens*, *Leioproctus erithrogaster*, and other bees. On the surface, cracks were often partly covered by a thin layer of loose dry soil.

Nests of this bee were studied on October 19 and 20, 1991, and again on November 15 and 16, 1991. Aggregations of nests could be identified because males flew low over the ground at the aggregations where they mated with females. Two aggregations about 50 m apart were studied.

NEST ARCHITECTURE: Numerous females of *Neffapis longilingua* entered cracks at one point (suggesting a communal nest entrance; see Discussion of Biological Features, below). All excavated tunnels discovered opened on the wall of cracks, so that the crack itself represented the main descending element in the nest. Excavated tunnels appeared to be short; three still in the substrate measured 0.8–1.5 cm long. Segments of others preserved measured 0.7–1.2 cm (N = 6), but these may not have been complete. More or less horizontal, they penetrated the soil at right angles to the crack face but most, if not all, turned or twisted until ending at the cells. Those leading to closed cells were soil-filled in a fashion discussed below in connection with cell closure. Unfilled tunnels leading to open cells were circular, 2.5–2.7 mm (N = 4) in diameter and possessed an unlined, uneven wall with numerous impressions of the female's pygidial plate. The wall surface immediately absorbed a drop of water placed on it. The female apparently constructed a tunnel merely by digging through it with her mandibles and by tamping it with her pygidial plate, which left an impression in the moist soil.

All cells, generally 8–17 cm deep (with many at the 15 cm level) were oriented more or less with their closure end facing the crack surface. Cells were nearly horizontal or tipped to the rear no more than 15°. They were normal in shape in that they possessed a rounded rear end, and they were symmetrical around their long axis (i.e., the ceiling was not more vaulted than the cell floor). However, the plane of the cell opening appeared in many cases not to be at right angles to the long axis of the cell, perhaps as a result of the tunnel bending away from the cell opening. Cells were 6.0–7.0 mm long (N = 10), 3.3–3.8 mm in maximum diameter (N = 19). Cell entrances were 2.1–2.3 mm in diameter (N = 5) which is to say that the tunnel narrowed just before the cell opening. Cell walls were somewhat uneven due in part to small pebbles often protruding into the cell lumen. However, embossing of the female's pygidial plate could not be detected, and the surface was distinctly smoother than the walls of yet unfilled tunnels. A very thin cell wall may have been present but it was so closely bonded to the cell lining that it may have been the by-product of the lining that was applied to the cell cavity. This lining imparted a somewhat shiny aspect to the cell surface and accounted for the waterproof quality of the surface, tested with a water droplet.

The cell closure, a deep-concave spiral (3–4 coils) on the inside, was 2.2–2.8 mm in diameter and was constructed so that the inner surface was just inside the cell opening. Its outer surface was concave, not spiral, and embossed by the female's pygidial plate. The material of the closure was moderately compact and gave no indication of having been moistened by the female as she closed the cell. In addition to this concave outer surface, the tunnel invariably possessed a number of nearly identical concave surfaces created by the female as she filled the tunnel. Six tunnels leading to cells each bore a total of three to four such concave septa (including the one next to the closure). They were nearly identical except the spaces between the surfaces, all filled with loose soil, were variable in length, even within one tunnel. The presence of these septa has been noted for this genus and for a number of other unrelated genera in Rozen (1993: fn. 3).

PROVISIONING AND DEVELOPMENT: Females of *Neffapis longilingua* gathered pollen from *Malesherbia humilis* Poeppig (Malesherbiaceae) (also, observed by Neff, personal communication with LR), a low-growing white-flowered herb that was scattered over the slopes adjacent to the road. This plant is distributed in Chile from Atacama to Santiago, and from the coast to the pre-Andes region in the Coquimbo area (Ricardi, 1967). The bee, however, has been found in a more restricted area within the known range of the plant species.

The distinctive purple-colored pollen of *Malesherbia* was the only pollen found on all pollen-laden females. The white flowers (4.1–

5.7 mm long) have stamens and pistils exerted well beyond the petals and sepals. The proximal parts of the sepals and petals form a deep throat with nectaries at the bottom while the distal parts splay outward in a nearly flat plane. A female landing on a flower does not insert her head into the flower throat, perhaps because of the exerted reproductive parts, but rather remains with her body parallel to the radiating petals. Her long glossa and labial palpi are an important feature permitting her to reach the nectaries. The extreme anatomical modification of the mouthparts (and the deeply grooved venter of the mesosoma) make it likely that the bee is monolectic with respect to *Malesherbia*. Foraging females transport provisions as large moist pollen-nectar masses on the anterior surface of their hind tibiae and basitarsi; that is, provisions do not encircle the hind leg.

Many of the food masses in the cells were spherical, and all had a rather uneven surface. Three spherical masses were 2.2–2.5 mm in diameter. Some of the food masses, however, seemed to be slightly flattened, one being 1.4 × 1.6 mm and another 2.7 × 2.9 mm. Food masses varied considerably in size, an observation not clearly reflected in the figures given above. Provisions were uniformly mealy-moist and lacked the waterproof coating of the Calliopsini. It is unknown whether or not early provision loads in a cell are shaped before the formation of the completed food mass.

As is generally the case in the Panurginae, eggs were deposited on top of the provisions in the longitudinal midplane of the cell, the anterior end facing the closure. More curved than the surface of the food sphere, eggs were attached by their anterior and posterior ends.

Larvae remained stationary on top of the food after hatching. They consumed the provisions from the front (i.e., side closest to closure) of the food ball beneath their head. As they grew, the ball was reduced only from the front. This behavior was in sharp contrast to such panurgines as *Calliopsis* sensu lato, in which the larva, after completing part of the provisions, reorients in the cell so that it rests on its dorsum and consumes the remaining food cradled on its venter. No such reorientation took place in the case of *Neffapis* at any time during eating. However, some predefecating, fully fed larvae were observed resting on their dorsa with their head end at the cell rear. More observations are required to understand how this comes about.

Postdefecating larvae also rested on their venter while their head end was next to the cell closure. Feces were always applied to the rear and rear ceiling of the cell as an irregular yellowish mass with a rough surface. Outlines of elongate flattened fecal pellets were more or less visible on the surface of the mass.

PHENOLOGY: When the site was first studied on October 19 and 20, 1991, many eggs and feeding larvae were recovered, but only one larva was starting to defecate. This specimen, kept alive, pupated on October 28, 1991. No quiescent postdefecating larvae were found in the October study. When JGR returned on November 15, the age demographics had altered. At this time many pupae were found as well as eggs and feeding larvae. However, many quiescent postdefecating larvae (presumably overwintering forms) were also uncovered. These observations suggest a variable voltinism, with part of the spring brood entering diapause as quiescent postdefecating larvae (univoltine) after they finish eating and the other part of the brood pupating soon after finishing feeding and producing another generation in the same year (bivoltine or perhaps multivoltine). Presumably overwintering occurs in the form of mature diapausing larvae, as is characteristic of the Panurginae.

PARASITISM: No cuckoo bees were observed exploring the nests of this species, and no immatures of cuckoo bees were discovered in cells. Some cells were parasitized by unidentified meloid larvae.

DISCUSSION OF BIOLOGICAL FEATURES

With bees that nest in cracks, the terms "main tunnels" and "laterals" (i.e., side tunnels leading to cells), nest components usually easily identified for most other ground nesting bees, become difficult to apply. There was no indication that females of *Neffapis longilingua* constructed descending main tunnels, for all females entering the ground descended through cracks which were sufficiently wide that the females did not have to excavate them to reach the cell depth. Whether to call their horizontal excavated tunnels laterals or main tunnels depends on whether

the natural crack should be interpreted as the counterpart (not to say behavioral homolog) of the descending main tunnel of other panurgines. Nesting in cracks has been reported for the apids *Exomalopsis nitens* Cockerell (Rozen and Snelling, 1986) and *E. chionura* Cockerell (Rozen and MacNeill, 1957). In the case of the former species but apparently not in the case of the latter, the horizontal tunnels appeared to be constructed by a single female. Because many other species of *Exomalopsis* do not nest in cracks and all are thought to be communal nesters (Rozen, 1984), the cracks used by *E. nitens* seem to take the place of descending main tunnels. We have been unable to identify close relatives of *Neffapis*, and therefore we cannot follow the reasoning applied to the case of *E. nitens*.

This confusion in terminology regarding nest architecture leads to a related problem in categorizing social behaviors. Assuming that each female of *Neffapis longilingua* excavates her own horizontal tunnel (which seems likely), should the species be considered communal because numerous nesting females enter the ground at a single point in a surface crack? Only if this species (or some related ones) were discovered nesting in soil that did not crack, could this question be addressed, as was the case of *Exomalopsis nitens*, above.

Such confusions in terminology, though interesting, may be superficial. More fundamental is what causes some bees to nest in aggregations or communally. Further studies of *Neffapis* at nesting sites with different edaphic conditions could lead to a better understanding of these social behaviors, at least for this species.

DISCUSSION OF PHYLOGENETIC RELATIONSHIPS

The relationships between *Neffapis* and other Panurginae are difficult to establish at this point. The general external appearance of the adults and many of their traits (such as the type of gonocoxite, volsella, penis valve, pre-episternal groove surpassing scrobe, and S6 of female) suggest that it is one of the Anthemurgini sensu lato. However, such features as short subantennal sutures and almost flat labrum (especially in males) are rarely found among the Anthemurgini. Instead, this combination of characters is present mainly among some species of the most derived Panurginae, i.e., the Calliopsini. The extremely elongate glossa and labial palpi, reduction in the number of segments in the maxillary palpus, 3-segmented labial palpus with segment 3 the longest, apically expanded paraglossa, and gonostylus angled at about 90° in relation to the long axis of the gonocoxite are presumably derived characters. The last three characters are apparently unique to *Neffapis*, since they have not been observed in any other Panurginae.

Such larval features as the relatively inconspicuous and little modified dorsolateral thoracic tubercles do not correspond to those of the Anthemurgini and for that matter to those of the highly derived calliopsine genera *Callonychium, Arhysosage,* and *Spinoliella*. One larval feature of *Neffapis*, the complete epistomal ridge, is shared uniquely with *Panurginus*, which has unmodified dorsolateral thoracic tubercles similar to those of *Neffapis*. However, neither adult nor pupal features seem to strongly support a possible relationship between these two genera. The relationships of *Neffapis* to the panurgines will be considered again and in more detail at the end of this series of papers. By that time more taxa will have been described and our knowledge of immatures of all panurgines will have been expanded.

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