

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

MAY 6, 1959

NUMBER 107

A REVISION OF THE DACETINE ANT GENUS *NEOSTRUMA*

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INTRODUCTION

The genus *Neostruma* Brown includes six known neotropical species forming a compact and distinctive group in subtribe *Strumigeniti* of tribe *Dacetini*. This genus evidently was derived within the New World tropics from the *gundlachi* group ("subgenus *Pyramica*") of the large tropicopolitan genus *Strumigenys* Fr. Smith.

The *S. gundlachi* group is also neotropical in distribution. It contains a graded series of species, linked to the more "typical" *Strumigenys* through the *S. connectens* group (Kempf, 1958, *Rev. Brasil. Ent.*, 8:59-68), that foreshadow *Neostruma* in head shape, development of serial denticulation of the mandibles, lengthening of labral lobes, reduction of pilosity and spongiform appendages, and other characters.

Neostruma is set off from these by its very long labral lobes with their short trigger hairs, and by the distinctive form and armament of the mandibles, featuring very short apical fork teeth and a series of denticles on each side of a submedian (pre-apical) tooth (Fig. 5). With the exception of *N. myllorhapha* new species (Fig. 4), a "countercurrent" specialist with secondarily elongate mandibles, the *Neostruma* species show a co-adaptive complex of characters converging toward those of *Smithistruma* Brown, but not reaching the same degree of completeness (see Brown and Wilson, in press). Among the characters involved in this complex are the following:

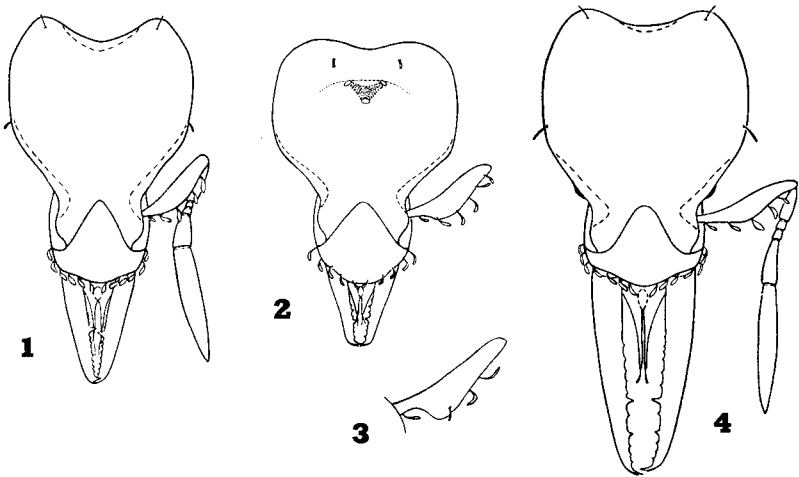
1. Shortening of mandibles.
2. Reduction of apical fork.

3. Development of serial mandibular denticulation.
 4. Transformation of basal tooth into a perpendicular "basal lamella."

5. Slight lengthening, depression and narrowing of head, with some lessening in prominence of occipital lobes and occipital excision.

6. Shortening and incrassation of antennal scapes.

7. Elongation of labral lobes.



Figs. 1-4. *Neostruma* spp., dorsal views of heads, mandibles and antennae. Fig. 1. *N. zeteki* n. sp., paratype worker. Fig. 2. *N. metopia* n. sp., holotype female, funiculus omitted. Fig 3. *N. crassicornis* (Mayr), left antennal scape of worker. Fig. 4. *N. myllorhapha* n. sp., holotype worker. All figures drawn to same scale.

8. Reduction in length of labral trigger hairs.

9. Inability to open mandibles widely (limit is much less than 180°).

10. Hunting behavior is of "strike-hold-sting" type (as based on observation of *N. mustelina*; see below).

11. Foraging less active and less frequent (*N. mustelina*) than in several *Strumigenys* species studied, but much as in *Smithistruma* spp.

The species form small colonies, chiefly in the leaf litter of rain forest or tropical evergreen forest, and nests occupy cavities in rotting twigs, pieces of bark or similar forest-floor vegetable debris so far as we know. Four of the species (*brevicornis*, *myl-lorhapha*, *metopia*, *zeteki*) occur in Central America, one (*mustelina*) is widespread in tropical Mexico, and one (*crassicornis*) is known only from southeastern Brazil. It seems strange that no records of the genus are available for northern or Amazonian South America, but then collecting in these regions has scarcely begun so far as the Dacetini are concerned. All of the records we now have are from mainland localities; the genus apparently is absent from the West Indies. In the areas where it occurs, the genus is usually not scarce, but exists in fair numbers along with species of *Strumigenys*, particularly of the *gundlachi* group, and many other cryptobiotically foraging ants. The food, judging from what we know of *Neostruma mustelina*, consists primarily of small entomobryomorph Collembola and possibly some other minute terrestrial arthropods as well. Hunting behavior is like that of *Smithistruma* rather than like the *Strumigenys* so far studied.

The material used in this study has come from various sources (see Acknowledgements at end of paper), but the principal places of deposition are the United States National Museum, Washington (USNM), and the Museum of Comparative Zoology at Harvard College, Cambridge, Massachusetts (MCZ).

The measurements and proportions used, and their abbreviations, are as in my other papers on dacetine ants; see especially Brown, 1953, *Amer. Midl. Nat.*, 50: 7-15, or Brown, 1953, *Jour. New York Ent. Soc.*, 61: 53, 101.

NEOSTRUMA BROWN

= *Neostruma* Brown, 1948, *Trans. Amer. Ent. Soc.*, 74:111. Type species:

Strumigenys crassicornis Mayr, 1887, by original designation (+ 3 spp.).
< *Strumigenys*, *auct.* (+ 3 spp.).

Worker. Small to minute, resembling members of the *Strumigenys gundlachi* group (from which *Neostruma* appears to have been derived; see Brown and Wilson, in press). Mandibles inserted rather far apart, linear, tapering to an apical fork of two very short teeth separated by 2-4 minute intercalary den-

ticles. Basal lamella present, separated from basal condyle by a deep notch, perpendicular to shaft, broad and flat, subtruncate or rounded at apex, normally hidden beneath clypeus when mandible is closed. Inner borders of mandibles armed with a row of small teeth or denticles on the apical half or two-thirds, arranged as follows: a *preapical* series of 3-8 denticles, immediately proximad of apical fork; a single larger submedian tooth; proximad of this, a short *medial* series of indistinct denticles, beyond which the shaft is unarmed to the basal lamella (Fig. 5). Labrum with a broad basal part and greatly elongate, parallel tapered lobes, extending half or more the exposed length of the closed mandibles. At their apices, the labral lobes each bear 2-3 short trigger hairs; one or two additional pairs of fine hairs on their upper surfaces before the tips. When the man-

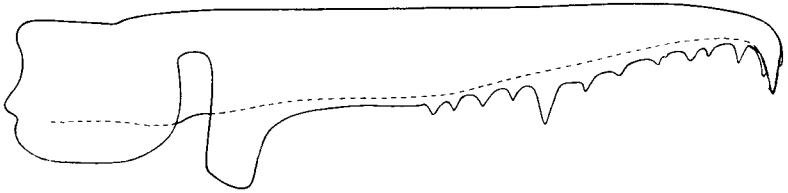


Fig. 5. *Neostruma zeteki* n. sp., greatly magnified dorsal view of left mandible as dissected out of the head.

dibles are closed, the labrum is tilted ventrad, but when they are open, it is raised to point straight forward between them. Apparently the same "springtrap" arrangement holds in this genus as in *Strumigenys*. Palpi segmented 1, 1, as in *Strumigenys*.

Head rather elongate, depressed, with moderately expanded occipital lobes, narrowed anterior portion, and moderately well-developed elliptical compound eyes set well forward of midlength, but only partly or not at all visible from above. There is a tendency, best seen in *brevicornis*, *zeteki* and especially *metopia*, for the head to be impressed or concave in front of the vertex. Antennae 6-segmented, as in *Strumigenys*, but scape shortened and incrassate, with curved (and sometimes lobulate) anterior margin.

Alitrunk compact; pronotum depressed and nearly plane above, bounded by a distinct anterior and less distinct lateral margins, meeting at blunt humeral angles. In profile, the dorsal outline is convex from pronotum to propodeum, with a depression (or flat area) in the region of the mesonotum. Promesonotal suture obsolete; metanotal groove weak to absent. Propodeal teeth laterally compressed, acute, their apices directed slightly dorsad, their infradental lamellae narrow and concave. Petiole pedunculate, its rounded node with a feebly developed posterodorsal collar of spongiform lamella; no ventral appendages. Postpetiole subreniform, much broader than petiole, with weak lateral and ventral spongiform appendages. Gaster with a narrow basal spongiform margin and a band of short basal costulae; rest of surface smooth and shining.

Head, alitrunk, legs, and both nodes finely and evenly reticulate-punctulate and opaque, except for a smooth, shining patch on the mesokatepisternum.

Mandibles with oblique pointed and linear-spatulate hairs directed mesad from dorsal surfaces, especially near insertions. Clypeal and anterior scape margins each with a series of bordering spatulate hairs; one erect truncate, clavate or remiform erect hair on the posterior edge of each occipital lobe, one on each lateral occipital border (Figs. 1 and 4), one on each humerus, and one on each side of the mesonotum (these hairs are often small and fragile, and are often missing in part); two on the petiolar node, four on the postpetiole, and 16-20 on the gastric dorsum. Ground pilosity moderately developed to obsolete except in *N. crassicornis*, consisting of sparse, fine, reclinate or subreclinate hairs on the head, legs and antennae, often invisible on head, shorter on clypeus.

Color varying from ferruginous yellow to dark brown. The gaster is often darker than the rest of the body.

Female like worker, but with larger eyes and fully developed flight apparatus, and otherwise differing from the workers as *Strumigenys* workers differ from their females. Forewing as in Wheeler's figure 11D in his book, "Ants," p. 25, except that in *Neostruma* the apical section of R (labeled "f" by Wheeler) is lacking.

Males known only for *N. mustelina*; these are basically like males of the smaller species of *Strumigenys*.

SPECIES EVOLUTION AND RELATIONSHIPS

The six species recognized here represent six morphologically distinguishable samples; of these, *crassicornis* is distinct in a number of good characters from the other five samples, and there is every reason to maintain it as a good species. Its range in southern Brazil and northern Argentina, so far as the present incomplete collections show, is separated by the bulk of the South American continent, or over 3,000 miles, from the nearest known locality of any of the other species. In Panama, we find two sympatric species, *zeteki* and *metopia*, which are very different from one another (Figs. 1 and 2). In *zeteki*, the head is long and exceedingly flattened, and the mandibles are fairly long, with many denticles, while *metopia* has a deep, short, broad head and very short mandibles. So far, our knowledge of the distribution of both of these species is limited to knowing that they both have been taken on Barro Colorado Island in the Canal Zone.

Two of the remaining three species (*brevicornis* and *mustelina*) are very similar to one another and to *zeteki*, and *mustelina* also approaches *metopia*. In fact, these four species can be arranged as the morphocline *zeteki* \longrightarrow *brevicornis* \longrightarrow *mustelina* \longrightarrow *metopia*. In their distribution, however, *zeteki* and *metopia* occur together in Panama, *brevicornis* is in Costa Rica and Honduras (and presumably also in between, in Nicaragua), and *mustelina* is widespread in tropical Mexico. Thus we see that the morphocline is partly also a geographical cline running from Panama to Mexico: *zeteki* \longrightarrow *brevicornis* \longrightarrow *mustelina*. This situation suggests that *zeteki*, *brevicornis* and *mustelina* could amount to one clinally varying species occupying much of Central America and tropical Mexico, and that the *zeteki* population may represent extreme character displacement in the presence of *metopia*, which is itself displaced toward the other extreme. An alternative possibility should not yet be excluded: *metopia* could belong with *brevicornis* and *mustelina*, and could represent a reversal of cline where *zeteki* is present and displaces it. Despite the interest of this possible character displacement situation (see Brown and Wilson, 1956, Syst. Zool., 5: 49-64), we unfortunately lack the material needed to confirm it at the present time. We have no samples from Guatemala

(between the ranges of *mustelina* and *brevicornis*) or from western Panama (between *brevicornis* and *zeteki* with *metopia*). A second difficulty is that the available material of *brevicornis*, and especially of *mustelina*, each representing a wide and varied range in Central America and Mexico respectively, shows no obvious infraspecific clinal trends corresponding to that seen among the several species. Instead, allowing for individual or local nest-series variation in size, color and other minor characters, the constancy of the "diagnostic" characters holds very well, allowing a complete separation of four morphological species. In view of all of the facts outlined, and the various interpretations possible, I am treating *mustelina*, *brevicornis*, *zeteki* and *metopia* provisionally as separate species without strong prejudice as to their eventual status.

The last species to be discussed is the remarkable *N. myllorhapha*, known only from the single type worker from Costa Rica. As Figure 4 shows, this species is quite distinct from all its congeners. It represents an apparent reversal of the trend in *Neostruma* toward shortening of the mandibles. That this is a true reversal is attested by the great elongation of the labral lobes. The *Neostruma* ancestor of *N. myllorhapha* obviously had the shortened mandibles, reduced trigger hairs, and elongate labral lobes characteristic of all the existing species of the genus. When the mandibles started to elongate in the line leading to *myllorhapha*, the trigger hairs did not elongate again, but instead the labral lobes bearing them were drawn out to an extreme length, in this way compensating for the unrecovered loss of length of the hairs needed to activate the snap-closure of such long mandibles.

NEOSTRUMA MUSTELINA (Weber)

Strumigenys mustelina Weber, 1934, Revista de Ent., 4:34, fig. 11, female.

Type locality: Jicoltepec, Veracruz. Syntypes in MCZ.

Worker (8 specimens measured from 3 nest series). TL 1.6-1.8, HL 0.41-0.46, ML 0.15-0.16, WL 0.43-0.46 mm.; CI 79-81, MI 35-39, ICD 48-52. Habitus intermediate between Figure 1 and Figure 2. The dimensions and proportions overlap those of *N. brevicornis*, but the tendency in *N. mustelina* to smaller size, relatively broader and deeper head, shorter mandibles, and

deeper promesonotum is evident on comparison of series. The space between the apical fork and the submedian tooth is shorter than in *brevicornis*, and bears only 4 preapical denticles, a number quite constant in 55 worker and female specimens examined, representing 13 separate nests. These preapical denticulae are longer and more acute than is usual in *brevicornis*, and the third one (counting from the apex toward the submedian tooth) is a little larger than its fellows. It is the constancy of the preapical denticular number in Mexican series which, above all other considerations, leads me to recognize *mustelina* as a species distinct from *brevicornis*. (Before the recent acquisition of several good Mexican series, I had considered *N. mustelina* to be synonymous with *N. brevicornis*, and had sent out specimens labeled accordingly. All such material labeled as "*N. brevicornis*" from Mexican localities should now be considered as belonging to *N. mustelina*.)

The color varies from light yellowish-ferruginous to dark brown. Other characters as in *brevicornis*.

Female (3 specimens measured from 3 different localities): TL 1.9-2.3, HL 0.48-0.52, ML 0.18-0.20, WL 0.51-0.55, forewing L 1.6-1.8 mm.; CI 83-84, MI 36-38, ICD 49-51.

Male (1 specimen reared from nest taken at Las Hamacas, Veracruz): TL 1.7, HL 0.38, HW across eyes 0.38, WL 0.52 mm.

Habitus much like that of other small strumigenite males; head rather large compared to rest of body. Mandibles simple, acute, too small to be opposable. Labrum broad, divided, not elongate. Strong longitudinal frontal groove in front of median ocellus. Antennae not clavate. Notauli present, moderately distinct. Angle of propodeum obtusely rounded; teeth reduced to low carinae, rounded above. Petiole low, node rounded; both petiolar and postpetiolar nodes smooth and shining, like entire gaster and lower posterior sides of alitrunk. Rest of body reticulate-punctulate, appendages finely punctulate, opaque. Erect hairs few and fine, positioned more or less like the clavate hairs of the female. Sparse fine reclinate ground hairs on both surfaces of head and on appendages. Color brown, head blackish, appendages tan.

Material examined. 13 nest series, half of them extensive, all from Mexico: TAMAULIPAS: Aldama (F. Bonet leg.). VERACRUZ:

Jicotepec, syntypes of *mustelina*, collector unknown. Pueblo Nuevo, near Tetzonapa, and Las Hamacas, about 17 km. north of Santiago Tuxtla (E. O. Wilson leg.; see notes below). Volcan San Martin, dark brown series, ca. 1100 m., forest debris (C. J. Goodnight leg.). GUERRERO: Oaxtepec (F. Bonet leg.). CHIAPAS: Ocosingo and Finca El Real, Ocosingo Valley, leaf mold in hillside (C. and M. Goodnight and L. J. Stannard leg.).

Several colonies of this ant were taken by Wilson during August, 1953, at Pueblo Nuevo and Las Hamacas, Veracruz, in tropical evergreen forest. The ants were found foraging in the leaf litter and nesting in small rotting bits of wood in the litter. One nest (No. 235) contained 24 workers, 1 queen, 4 worker pupae and 5 larvae. Another (No. 237) held 26 workers, 1 queen, 18 worker pupae, 13 larvae of various sizes, and a number of eggs. In one natural nest, an entomobryid was found with larvae feeding on it. Nests in captivity readily captured entomobryid Collembola, including one *Orchesella*-like species. The ants are sluggish hunters, and often show immobile "ambush" behavior, with mandibles held open at about 30°-40° (as in *Strumigenys gundlachi*). When the ant strikes a springtail, the springtail almost always jumps, often several times in rapid succession. The ant hangs on, bulldog-fashion, and immediately curls in a rapid attempt to sting. On one occasion, the collembolan prey jumped and left behind a leg in the jaws of the ant, which bore it back to the nest. Small symphylans, millipedes, campodeids, a mosquito, mites and other arthropods offered to the *Neostruma* were ignored or avoided. One small symphylan was caught, but later rejected. One nest was maintained in the laboratory for two years, during which time it produced two separate sets of males and winged females (sexes in about equal numbers). From this nest, placed under a bell jar in the sunlight, the males and winged females flew out, but remained inactive for days on the ceiling and upper walls of the jar, apparently without mating. They appeared to try to move toward the light. During the two years we kept this colony in a small plaster nest, it was given nothing to eat but entomobryid and isotomid collembolans, a diet which allowed it to maintain itself in a flourishing condition.

One Las Hamacas colony produced an anomalous individual, probably a gynandromorph, in which the right half of the head

and both mandibles are worker, while the left half of the head is fully male.

NEOSTRUMA BREVICORNIS (Mann)

Strumigenys brevicornis Mann, 1922, Proc. U. S. Nat. Mus. 61(13):38, worker, female. Type locality: La Ceiba, Honduras. Syntypes in USNM, MCZ.

Worker (10 specimens measured from 4 nest series). TL 1.8-2.2, HL 0.45-0.53, ML 0.17-0.22, WL 0.44-0.53 mm.; CI 75-80, MI 37-42, ICD 46-50. Habitus intermediate between Figure 1 and Figure 2. Although its dimensions and proportions overlap those of *N. mustelina*, *N. brevicornis* is generally larger and has a slightly narrower head and longer mandibles, and the head and promesonotum are usually a little more strongly depressed. The space between the apical fork and submedian tooth is relatively a little longer and usually bears 5 minute, subequal pre-apical denticulae, these appearing smaller than the preapical denticulae of *N. mustelina*. Very rarely, 6 denticulae are present, and one specimen was seen with 5 on one side and 4 on the other.

Medial denticulae 3-5 in number, small and irregular.

Color varying widely from yellowish-ferruginous to dark brown. The dark brown specimens (Tablazo) apparently come from a highland area in Costa Rica that has produced melanic variants of many wide-ranging dacetine species.

Female (2 specimens from 2 nests): TL 2.1-2.3, HL 0.48-0.52, ML 0.19-0.20, WL 0.58 mm.; CI 77-81, MI 38-40, ICD 50.

Color as in corresponding workers or a little darker.

Material studied: HONDURAS: La Ceiba (W. M. Mann leg.; syntypes). COSTA RICA: Bataan, Abaca Plantation, "in rhizome" (C. H. Batchelder leg.). "Costa Rica," without further locality, 2 separate series (F. Nevermann leg.). Turrucares (A. Bierig leg.) Tablazo, dark brown series (A. Bierig leg.). Peralta Sta. (P. P. Calvert).

NEOSTRUMA ZETEKI new species (Figs. 1 and 5)

Holotype worker. TL 2.0, HL 0.53, ML 0.20, WL 0.52 mm., CI 68, MI 38, ICD 38. Paratypes: TL 1.8-2.1, HL 0.50-0.56, ML 0.19-0.22, WL 0.47-0.53 mm., CI 67-70, MI 37-40, ICD 37-39.

This species is distinguished from *brevicornis* by its relatively narrow head and by the very strong depression of the head and alitrunk. The mandibles show 6 to 8 subapical denticles and a quite distinctly enlarged submedian tooth. The medial denticular series varies from 4-7 units. The coloration is light to medium ferruginous, gaster darker brown. The average size is also larger than that of *brevicornis*, but these two species are very similar in all other respects.

Dealate female. TL 2.5, HL 0.58, ML 0.22, WL 0.63, CI 71, MI 38, ICD 41. Male unknown.

Holotype (USNM): Barro Colorado Island, Panama Canal Zone (James Zetek). Paratypes (USNM, MCZ, etc.) Several small series, received mixed with other dacetine and basicerotine species, mainly collected by Mr. Zetek on Barro Colorado during 1941-1943. Known only from the type locality.

Several colonies are represented in the type material, and judging from these the species seems very constant and distinctive.

NEOSTRUMA METOPIA new species
(Fig. 2)

Holotype female, dealate. TL 2.2, HL 0.50, WL 0.56, CI 78, MI 32, ICD ca. 50.

Very close to *brevicornis*, and similar to the female of that species except in the much shorter mandibles and the form of the vertico-occipital region of the head. In *metopia*, the ocellar triangle is raised on a blunt ridge or prominence, the latter almost rectangular in lateral view. The ocelli are much closer together than in *brevicornis*; the distance between the anterior and each posterior ocellus being $2\text{-}2\frac{1}{2}$ ocellar diameters, while in *brevicornis*, this same distance equals $4\text{-}4\frac{1}{2}$ ocellar diameters. The vertex in front of the raised ocellar area falls away rather sharply and is here decidedly concave. In full face view the prominence appears as a curved, blunt and poorly defined transverse ridge centering at the ocellar triangle. The small space between the posterior ocelli is shining and partly smooth, and much of the region inside the triangle is blackened. A single small, suberect, spatulate occipital hair rises posterior to, and to each side of the ocellar triangle, but there are no other specialized erect or suberect hairs on the verticoccipt. The *brevi-*

cornis female usually has an additional pair of hairs placed even with or a bit anterior to the ocelli. This character is, however, subject to damage, and should not be trusted on the basis of one specimen.

The preapical denticles are 3 in number on both mandibles. Medial denticles 3-4, uneven. Submedian tooth slightly but distinctly larger than the largest of the denticles.

Color medium-light ferruginous. Color sculpture and other characters as in *brevicornis*.

Holotype (Weber Coll.). Barro Colorado Island, Panama Canal Zone (N. A. Weber leg., 1938, no. 871).

NEOSTRUMA CRASSICORNIS (Mayr)

(Fig. 3)

Strumigenys crassicornis Mayr, 1887, Verh. zool.-bot. Ges. Wien, 37:577, worker. Type locality: "St. Catharina." Types in Naturhistorisches Museum, Vienna.

Worker. TL 2.0-2.3, HL 0.52-0.57, ML 0.18-0.20, WL 0.47-0.53 mm., CI 70-75, MI 34-37, ICD 48-50. This species, which ranges in the Parana Basin and eastward, is distinguished from the four Central American species by its slightly larger size, by the peculiar, sublobately incrassate antennal scapes, by its more swollen, reniform postpetiole, by the extreme reduction of its spongiform appendages, and by the more broadly spatulate ground pilosity of the head.

The preapical mandibular series of denticles varies in number of units from 3-7, and the submedian tooth is relatively large and distinct (contrary to Emery's figure, otherwise a fairly good representation). Color light to medium ferruginous.

Female (one specimen measured). TL 2.7, HL 0.58, ML 0.22, WL 0.62 mm., CI 78, MI 38, ICD ca. 50.

Material examined. Southeastern BRAZIL: Parecy Novo, 2 series (Hansen leg., Rambo leg.). Nova Teutonia, S. Catarina (F. Plaumann leg.). ARGENTINA: Posadas, Misiones (F. Silvestri leg.).

NEOSTRUMA MYLLORHAPHA sp. nov.

(Fig. 4)

Holotype worker. TL 2.4, HL 0.58, ML 0.37, WL 0.62, scape L 0.23, funiculus L 0.52 mm.; CI 74, MI 64, ICD 45.

Like *brevicornis*, but differing in the strikingly elongate, coarsely denticulate mandibles and the correspondingly long labral lobes and antennal funiculi. Head gently and evenly convex above, without a distinct impressed area in the center. Ali-trunk rather evenly convex in lateral-view profile, mesonotal area slightly flattened, but not impressed. Sculpture and erect hairs as in *brevicornis*, the hairs rather fine, truncate.

Color light ferruginous, mandibles and appendages more yellowish, gaster brown.

Holotype and sole known specimen labeled simply, "Costa Rica" (F. Nevermann leg.), from the collection of Father Thomas Borgmeier of Jacarepaguá, Brazil.

ACKNOWLEDGEMENTS

Thanks are due to Father Thomas Borgmeier, Dr. M. R. Smith and Dr. Neal A. Weber for the opportunity to study material under their care. Dr. E. O. Wilson furnished valuable notes on the behavior and ecology of *N. mustelina* in its natural habitat, and furnished captive live nests of this species for laboratory study; he also criticized the manuscript before publication. The figures were mostly drawn by Mrs. Nancy Buffer.