

MESOAMERICAN *ONTHOPHAGUS* LATREILLE IN THE DICRANIUS AND MIRABILIS SPECIES GROUPS (COLEOPTERA: SCARABAEIDAE)

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Abstract

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The taxonomy and phylogeny of two related species groups of Mexican and Central American *Onthophagus* are considered. The dicranius group is composed of four species, including two new species, *O. asperodorsatus* and *O. petenensis*. The mirabilis group contains three species, one of these new, *O. solisi*. A fourth new species, *O. quetzalis*, shares characters with both species groups. All species in these groups are described and illustrated. A suggested phylogeny is presented. Our analysis indicates that these groups, including *O. quetzalis*, may be more closely related to Indo-Malaysian species than to other New World groups of *Onthophagus*.

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Résumé

On trouvera ici une étude de la taxonomie et de la phylogénie de deux groupes apparentés d'espèces du genre *Onthophagus* au Mexique et en Amérique centrale. Le groupe dicranius se compose de quatre espèces, dont deux nouvelles, *O. asperodorsatus* et *O. petenensis*. Le groupe mirabilis contient trois espèces, dont une nouvelle, *O. solisi*. Une quatrième espèce nouvelle, *O. quetzalis*, possède des caractéristiques des deux groupes. Toutes les espèces de ces groupes sont décrites et illustrées et une phylogénie est proposée. Notre analyse indique que ces groupes, y compris *O. quetzalis*, s'apparentent davantage à des espèces indo-malaises qu'aux autres groupes d'*Onthophagus* du Nouveau Monde.

[Traduit par la rédaction]

INTRODUCTION

The purpose of this paper is 2-fold: first to define and describe two groups of Mesoamerican *Onthophagus* and second to illustrate a few of the problems encountered when trying to analyse species relationships in a limited geographic area. These problems are particularly evident when the genus (*Onthophagus*) is large, relatively "modern," and world-wide in distribution.

In the late 1980's Cambefort (1991) estimated the number of described species in *Onthophagus* as follows: Nearctic, 38; Neotropical, 95; Palaearctic, 220; Oriental, 345; Afrotropical (= Ethiopian), 790; Australian, 280; for a total of 1768 species. Since this estimation was done, approximately 100 new species have been described and many others await description. In discussing the evolution of the Onthophagini, Cambefort (1991) considers the group to be good dispersers, and to be a very successful and relatively modern group, i.e. probably arising in the Oligocene or at least in the Cenozoic.

Partly because of the size of the genus *Onthophagus*, only regional studies have been attempted. Balthasar (1963, vol. 2) in his monograph of Palaearctic and Oriental *Onthophagus* recognized 18 subgenera of *Onthophagus*. Additional subgenera were added by Zunino (1979) and "artificial" and "natural" groups were discussed. However when the characters defining the proposed subgenera are applied to species from other geographic areas the subgeneric limits become confused. As Matthews (1972) stated "the difficulty lies

largely in the fact that no one person has been able to consider *Onthophagus* on a world-wide basis." When Boucomont (1932) treated the majority of the then known New World species he recognized 13 "groups" even though some subgeneric names were available. Matthews (1972) in his excellent revision of Australian *Onthophagus* followed the species group approach. We continue this practice because most recent workers have used this method, particularly in studies involving New World species.

In this paper we describe two new species in the dicranius species group, one new species in the mirabilis species group, and a fourth new species in or near the mirabilis group. The fourth species shares some character states with both groups, but also shares character states with several species from New Guinea. In the "group" keys the unusual fourth species is placed in the mirabilis group. Relationships within and between these groups are discussed in a concluding section.

All of the species treated here share several distinctive characters. Large (major) males all have a nearly vertical horn at the anterior median edge of the clypeus. The horn can be slender and apically bifurcate (Fig. 22), or truncate (Fig. 1), or rounded (Fig. 25); some species in the dicranius group have the horn laterally expanded apically with the broad apex feebly emarginate (Figs. 7 and 8), or truncate (not figured). Males of all species lack a carina on the vertex and also lack any indication of a posterior horn near the eye. Females have the anterior clypeal edge sharply bidentate and any transverse carinae or conical tubercles are located midway between or anterior to (but not behind) the eyes. Both sexes in both groups have the pronotum moderately to coarsely punctate, most punctures being separated by less than 1–1.5 diameters; elytral intervals are closely punctate. All species have the pygidium coarsely punctate, at least apically. Colour in both groups ranges from brown to black and all species lack any trace of blue or green iridescence on the elytra commonly seen in other Mesoamerican groups of *Onthophagus*. The femora of some species are light brown, darker or not near the ends.

METHODS

In considering the relationships in and between the mirabilis and dicranius groups, we used both external characters and those of the male genitalia. Zunino (1981) used the rods and plates of the male internal sac in his *Onthophagus* studies; we have illustrated these structures as well, although they do not seem to be particularly useful in establishing phylogenetic relationships. Zunino (1981) has termed the U-shaped plate in the internal sac the copulatory lamella. The remaining rods and spines have not been named and we defer from doing so because this task would best be accomplished after a detailed study of their functional morphology. Such a study is well beyond the scope of this paper.

It was not necessary to use KOH to soften the genitalia if the specimens being studied had been killed with ethyl acetate or in liquid preservative other than Formalin or some alcohols. We placed specimens in gently boiling water for several minutes, extracted the genitalia and then, without distorting the parameres or phallobase, withdrew the internal sac through the basal opening of the phallobase using a sharp pair of forceps. We originally cleared the internal sac and spread the rods that are basal to the large U-shaped apical plate. However, we found it extremely difficult to make comparisons using this technique, because the asymmetrical rods are twisted in various ways. Spreading the rods produced a great variety of different shapes depending on the angle of viewing. When this is done it is nearly impossible to relate the position of one rod to the next. To avoid these problems we drew the plate and spines in the position that they were found within the sac. The sac was oriented so that the posteriorly directed arms of the plate showed the maximum distance between the inner edges of the opposing arms. Using this technique we could compare both the shape of the plates and the relative positions of the rods. All of our figures of the internal sac were done in this way. Because the internal sacs of only some species have been examined and a

slight rotation of the rods gives a different impression, we have not used the characters of the internal sacs in our descriptions nor for reconstructing the phylogeny. A genus-wide study of the internal sac is needed to establish character state polarities for species group analyses.

We have used the "group" concept basing our groups on a number of shared characters which are mentioned in the systematic section. Zunino (1978) considered *Caccophilus* Jekel, a subgenus of *Caccobius* Thomson, to be the most likely sister genus of *Onthophagus*. We follow this concept. Many species of *Caccobius* are small (total length under 5 mm as measured by an ocular micrometer), moderately punctate, and lack most of the spectacular male sexual ornamentation frequently found in *Onthophagus*. Unfortunately many characters found in *Onthophagus*, particularly those pertaining to sexual dimorphism, are not found in *Caccobius* and we have had to use other groups of *Onthophagus* in addition to *Caccobius* to polarize the character states as listed in Table 1; thus we have in a fashion hypothesized a composite ancestor.

The possibility of convergence always must be considered and, for a worldwide genus, whether shared characters in two widely disjunct species represent shared ancestry or are due to convergence is one of our problems. The high frequency with which male sexual characters such as horns behind the eyes or a shelf-like projection of the pronotum over the head occurs in species on different continents seems best explained by shared ancestry because these characters are complex structures. Certainly in the cases presented herein where both male and female characters are shared in disjunct species we interpret these shared characters as strong evidence for common ancestry rather than convergence.

Abbreviations used for locations of specimens are as follows: INBIO = Instituto Nacional de Biodiversidad, San Jose, Costa Rica; HAHC = H. and A. Howden Collection, Ottawa, Canada.

In other cases the last name of the individual owning the collection is cited; for these see Acknowledgments.

TAXONOMY

THE DICRANIUS SPECIES GROUP

Species in this group share the following character states: pronotal punctures annulate, most punctures on elytral intervals setose (setae sometimes very minute), middle and hind femora distinctly bicoloured; males with pronotum rounded or with two conical protrusions (Figs. 1, 4, 8), females with pronotum evenly convex anteriorly, length less than 7 mm.

KEY TO THE DICRANIUS SPECIES GROUP

1. Setae on each elytral interval fine to obsolete, usually in two rows on second interval; pronotum of major males with two angular, laterally flattened protrusions (Figs. 4, 7, 13) 2
- Setae on each elytral interval stout, in three or more irregular rows on second interval; pronotum of major males unevenly rounded, lacking protrusions (Fig. 1); Panama *O. dorsipilulus* Howden and Gill
- 2(1) Elytron with strial punctures conspicuously impressed, punctures distinctly wider than stria; punctures on intervals with diameters distinctly less than those in striae 3
- Elytron with strial punctures very feebly impressed, punctures slightly wider than stria; punctures on intervals as large or larger than those in adjacent striae; Panama to Ecuador. *O. dicranius* Bates
- 3(1) Pronotum and elytron with most punctures on disc bearing conspicuous, semierect, yellowish setae (Fig. 11); pronotal punctures mostly separated by approximately 1 diameter or less; Veracruz, Mexico *O. asperodorsatus* **sp.nov.**
- Pronotum and elytron with only a few punctures on disc bearing minute setae (Fig. 12); pronotal punctures on disc mostly separated by more than 1 diameter; British Honduras; Chiapas, Mexico *O. petenensis* **sp.nov.**

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***Onthophagus dorsipilulus* Howden and Gill**
(Figs. 1–3)

Onthophagus dorsipilulus Howden and Gill, 1987: 216.

Males. Length 5.2–6.6 mm, greatest width 3.1–3.6 mm. Dorsum brown, closely punctate, punctures small, separated by approximately 1 diameter or less, punctures on pronotum and elytra each with very short semierect seta; length of seta approximately equal to diameter of puncture. Head (Fig. 1) with clypeal horn on anterior medial margin, horn slightly expanded toward apex, in male majors about twice as long (high) as wide, apex very shallowly emarginate. Surface of clypeus minutely punctate, vertex more coarsely punctate. Pronotum (Fig. 1) in anterior third with feebly defined triangular tumosity; apex of tumosity near median edge of anterior margin, posterior angles each defined by vague tubercle. Pronotal surface with numerous shallow, finely setose punctures; lateral pronotal margin evenly arcuate, posterior margin with marginal bead obsolete. Elytron with striae on disc slightly impressed; elytral intervals very feebly convex, each with numerous irregularly placed, shallow, setose punctures. Pygidium large, feebly convex, closely punctate, most punctures with fine, straight setae. Mesosternum medially densely punctate, metasternum sparsely, minutely punctate, surface shining; midline posteriorly feebly depressed. Genitalia as in Figure 3.

Females. Length 4.7–6.4 mm, greatest width 2.7–3.6 mm. Similar to males except in the following respects: clypeus (Fig. 2) lacking horn, margin medially sharply bidentate, slightly reflexed, teeth close, separated by narrow V-shaped notch; clypeus with punctures similar to vertex; pronotal disc uniformly convex, lacking protuberances.

Distribution. Known only from the Fortuna Dam area, Chiriqui Province, Panama.

Remarks. *Onthophagus dorsipilulus* is a rather atypical member of the dicranus complex. It is placed in the complex based on its bicoloured legs; closely punctate dorsum, most of the punctures with setae; clypeus in males with anterior median horn; vertex in both sexes lacking horns or distinct tubercles or carina (feebly developed, low, rounded swellings present between eyes); clypeus of females anteriorly sharply bidentate.

The body shape is more elongate, the pronotum in males lacks the two flattened anteriorly projecting swellings or horns characteristic of other species in the group, and the parameres of the male genitalia (Fig. 3) are very different (distinctive). However the sclerotized plates and rods of the male internal sac (not figured) are similar to the species in the dicranus complex.

***Onthophagus dicranus* Bates**
(Figs. 4–6, 35)

Onthophagus dicranus Bates, 1887: 72; Howden and Young, 1981: 112.

Males. Length 4.5–6.0 mm. Dorsum brown, densely punctate, most punctures each with small, inconspicuous seta; all dorsal punctures, including those on pygidium, shallow, usually feebly ocellate. Clypeus of male major (Fig. 4) with anterior median margin vertically reflexed, forming a transversely flattened, apically truncate or feebly emarginate horn, horn widened or not apically, approximately as high as wide; remainder of clypeal margin evenly arcuate and moderately reflexed; clypeal surface medially obsoletely punctate, shining and with small median tubercle posterior to horn; remainder of head densely punctate. In minor males clypeal horn reduced to rounded elevation with width not greatly reduced. Margin of gena continuing arcuate line of clypeal margin; vertex lacking any indication of carina. Pronotum (Fig. 4) in anterior third with a triangular longitudinal horn (plate) on each side close to midline, summit of projection obtusely angled or rounded at anterior third of pronotum, anterior face not slanted anteriorly; horns apically impunctate or

feebly punctate, remainder of pronotum closely punctate, evenly convex. Elytron with striae feebly impressed, strial punctures equal or smaller in size than numerous punctures on intervals. Metasternum closely punctate except near midline. Foretibia of major males elongate, with distinct tuft of setae at apex. Genitalia as in Figure 6, internal sac as in Figure 35.

Females. Length 4.5–5.3 mm, greatest width 2.7–3.4 mm. Clypeus (Fig. 5) anteriorly sharply bidentate, teeth acute, moderately reflexed; head lacking any indication of carinae; pronotum evenly convex, anterior seventh of midline impunctate, smooth and shining, remainder of pronotal surface closely punctate.

Distribution. From Chiriqui Province, Panama, to Santo Domingo de los Colorados area of Pichincha Province, Ecuador.

Remarks. South American *O. dicranius* may represent an extremely close sibling species of the Panamanian *O. dicranius*; however this problem is beyond the scope of the present paper. A superficially close species, *O. dicranoides* Balthasar, also occurs in Ecuador. This species, although resembling *O. dicranius*, lacks most of the group characters; the legs are not bicoloured, dorsal punctures are small, many specimens have a greenish tinge, and males have a small, sharp tubercle on each side at the posterior edge of the vertex. Females also have tubercles indicated on the vertex and have two small protrusions on the anterior fourth of the pronotum. All of these characters relate *O. dicranoides* to the *O. praecellens* Bates group of species rather than to the *dicranius* complex. *Onthophagus dorsopilulus* and the following species are, we believe, the closest relatives of *O. dicranius* (Fig. 44).

***Onthophagus asperodorsatus* sp.nov.**
(Figs. 7–11, 37)

Holotype. Male, length 5.7 mm, greatest width 3.5 mm. Dorsally head brownish black, pronotum and elytra black. Clypeus (Fig. 8) with short, moderately stout, T-shaped horn on median anterior edge, anterior edge broadly, shallowly U-shaped; clypeus with median ridge or carina extending posteriorly from base of horn, surface declivous on each side of ridge; clypeus narrow near base of horn, edge on each side curved abruptly outward to lobe midway between horn and gena; clypeal sides then flared outward, merged with expanded edge of gena, edge rounded anteriorly, obtusely angled posteriorly; clypeus, except for sides and top of ridge, shallowly, coarsely punctate. Vertex almost flat medially, coarsely punctate. Gena flared and elevated toward anterior lateral edge, surface coarsely punctate. Pronotum (Figs. 7 and 8) with two closely proximate, anteriorly directed triangular, laterally compressed projections, these fused along midline for more than half of total length, free portion of projections parallel, apices rounded, separated by less than 0.3 mm; pronotal surface near anterior angles shallowly concave, shallowly punctate; pronotal surface posterior to projections and concave area, shallowly annularly punctate, most punctures each with distinct yellowish seta; most punctures separated by approximately 1 diameter, surface between smooth, shining. Elytron with striae slightly impressed near inner anterior third, more distinctly so posteriorly and laterally; strial punctures large, striae crenulate; intervals with transverse shallow depressions, each with one to three irregular rows of setae, each seta inserted in minute puncture; surface of intervals shining; third to sixth intervals posteriorly above apical declivity distinctly elevated, fifth interval most strongly elevated. Pygidium coarsely punctate, each puncture with short, erect seta; surface between punctures shining. Metasternum with midline narrowly indented in posterior half, surface on each side coarsely punctate, some punctures each with recumbent seta; surface between shining. Foretibia slender, elongate, with apical tuft of setae; four teeth on outer margin evenly separated from each other. Femora bicoloured, bases and extreme apices dark, remainder tan; posterior or ventral surface of each femur with two to five scattered coarse punctures, otherwise surface

smooth, shining. Parameres of genitalia (Fig. 10) similar to those of *O. dicranus*, internal sac as in Figure 37.

Allotype. Female, length 5.2 mm, greatest width 3.0 mm. Clypeus (Fig. 9) bidentate anteriorly, each tooth reflexed, apically abruptly rounded; emargination between teeth V-shaped; clypeal margin on each side slightly, outwardly arcuate, junction with gena feebly notched; posterior carina low, almost straight, absent in lateral fourths; clypeal surface punctate, and feebly, transversely rugose. Vertex irregularly feebly convex, lacking tubercles or carina, surface coarsely punctate. Pronotum (Fig. 9) slightly more convex in anterior fourth posterior to head, median eighth in posterior half feebly concave; surface coarsely punctate, most punctures each with short yellowish seta; surface between punctures smooth, shining. Elytron, pygidium, and metasternum not differing obviously from those of male. Foretibia not elongate, apical tuft of setae lacking. Femora with larger dark basal markings, otherwise similar to male.

Type Material. Holotype, male, Mexico, Veracruz, 33 km NE Catemaco, 160 m, Los Tuxtlas Biol. Sta., 1.VII.1983, S. & J. Peck, ravine litter and fungi Ber. (HAHC). Allotype, female, same data as holotype (HAHC).

Paratypes. 38 males, 38 females. Mexico: 54 same data as holotype; 13 same locality and collectors as holotype, 1.VII-1.VIII.1983, FIT (= flight intercept trap) in ravine rainforest; 10 same locality as holotype, 8-15.VI.1984, 22-29.VI.1984, 13-20.VII.1984, all D. Lindeman; 1, Veracruz, Santecomapan, 27.VIII.1970, A. Newton, 5M.1-2. Paratypes are in INBIO, Gill, HAHC, Halffter, Zunino.

Remarks. In males length varies from 4.0 to 6.1 mm and greatest width from 2.6 to 3.4 mm. In females length varies from 4.4 to 5.7 mm and greatest width from 2.7 to 3.2 mm. Small males have the clypeal horn reduced to a small, upright, almost semicircular lobe and the pronotal horns or plates are reduced to small, almost conical tubercles. The conspicuous elytral setae and punctures and the crowded pronotal punctures will separate *O. asperodorsatus* from other species in the group. Large males have a very distinctive median clypeal ridge (Fig. 8) extending posteriorly from the base of the horn almost to the posterior edge of the clypeus. This ridge or carina is lacking in related species.

The Latin epithet "asperodorsatus" refers to the roughened dorsal appearance due to the heavy punctation.

Onthophagus petenensis sp.nov.

(Figs. 12-15, 36)

Holotype. Male, length 6.3 mm, greatest width 3.5 mm. Dorsally black, margins of head and anterior angles of pronotum dark brown, sides of pronotum with iridescent golden cast. Clypeus (Fig. 13) anteriorly with median horn transverse, expanded near apex, T-shaped; broad apex feebly emarginate medially, left side slightly larger than right; margin on each side at base of horn lobed, then briefly almost straight, then side expanded, forming lobe with side of gena; surface of clypeus on each side near base of horn feebly concave and impunctate, midline lacking distinct ridge or carina; clypeus posteriorly and vertex feebly convex and coarsely punctate. Gena with outer angle near eye broadly rounded, surface coarsely, closely punctate. Pronotum (Fig. 13) anteriorly with two laterally compressed, anteriorly projecting, triangular horns, distance between horns approximately 0.5 mm, area between horns U-shaped, impunctate; surface on each side near anterior angles shallowly concave; disc posterior to horns with large, shallow, annular punctures, many with very minute, whitish seta; most punctures separated by 1-2 diameters, surface between smooth, shining. Elytron (Fig. 12) with striae feebly impressed, striae punctures large, shallow, causing shallow depressions in adjacent sides of intervals, intervals on disc with widely scattered small to minute punctures, conspicuous setae lacking except near sides of elytra;

third to sixth intervals of each elytron tumid at top of declivity. Pygidium coarsely punctate, each puncture with short, nearly vertical, brownish seta; surface alutaceous basally, shining near apex. Metasternum with midline not modified anteriorly, midline posteriorly slightly concave, impunctate; surface on each side coarsely, closely punctate. Foretibia slender, elongate, with apical tuft of setae; larger teeth on outer margin evenly spaced. Middle and hind femora distinctly bicoloured, ventral surface impunctate. Genitalia (Fig. 15) with parameres similar in shape to those of *O. dicranius*, internal sac as in Figure 36.

Allotype. Female, length 5.4 mm, greatest width 3.2 mm. Head and pronotum with greenish-golden cast. Clypeus bidentate anteriorly, teeth rounded apically, U-shaped between; clypeal sides feebly, outwardly arcuate to rounded posterior angle of gena; posterior clypeal carina feebly developed, anteriorly arcuate. Surface of head evenly, coarsely punctate, vertex almost flat medially. Pronotum (Fig. 14) most strongly convex near anterior margin medially; pronotal disc, except for anterior median area with moderate-sized, annular punctures, most separated by approximately 1 diameter, many punctures with very minute, white seta. Elytron, pygidium, and metasternum as described for male. Foretibia not elongate, lacking apical tuft of setae. Middle and hind femora similar to male.

Type Material. Holotype, male, Mexico, Chiapas, Bonampak Rd., 100 km SE Palenque, 8–24.VII.1983, S. & J. Peck, 230 m, rainforest FIT (HAHC). Allotype, female, same data as holotype (HAHC).

Paratypes. 2 males, 1 female. Two same data as holotype; 1, Br. Honduras [Belize], Caves Branch, 1–14.VIII.1972, S. & J. Peck, Berlese 241. Paratypes are in Gill, HAHC.

Remarks. Paratypes vary from 5.0 to 6.3 mm in length and from 3.0 to 3.5 mm in greatest width. The Belize specimen, a male, is similar to the holotype except that the clypeal horn is missing (broken or abraded) and the clypeal sides are only slightly lobed. The internal sac figured is from the Belize specimen. Of the species in the dicranius group, *O. petenensis* is the least densely setose-punctate. The smooth, polished surface between the relatively widely spaced pronotal punctures and the lack of conspicuous setae on the elytral disc will distinguish *O. petenensis* from others in the group. It is most similar to *O. asperodorsatus* from Veracruz, Mexico.

The name is derived from the biotic province where the species occurs, referred to as the “Peten”.

THE MIRABILIS SPECIES GROUP

Major males either with median conical horn projecting anteriorly (horn in some species bifurcate apically) or with broad anterior, transverse convexity with tubercle at each side (Figs. 19 and 22). Females with pronotum evenly convex or variously flattened or longitudinally concave.

Both sexes with legs not conspicuously bicoloured; elytral striae impressed on disc, striae punctures small; punctures on disc of pronotum and elytra moderate in size, distinctly impressed, feebly annulate or not; setae, except extremely minute ones, lacking; length 5–12 mm, most species over 7 mm.

KEY TO THE MIRABILIS SPECIES GROUP

- 1. Apical (external) abdominal sternite narrowed medially (MALES) 2
- Apical abdominal sternite not narrowed medially (FEMALES) 5

MALES

- 2. Anterior pronotal margin lacking tubercle or abrupt elevation at midline; pronotum in male majors with anteriorly directed horn, horn in most cases bilobed or bifurcate at apex 3
- Anterior pronotal margin with tubercle or abrupt elevation at midline; pronotum in male majors with broad elevation in anterior half, each side of summit of elevation delimited by small conical tubercle (Fig. 22); Costa Rica, Guanacaste *O. solisi* sp.nov.

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3. Dorsally brown to dark brown; basal segment of hind tarsus with small sharp projection near middle of outer margin just basad of long seta(e); apex of pronotal horn in male majors bituberculate; size 7 mm or more. 4
 — Dorsally greyish black to black; basal segment of hind tarsus lacking distinct, sharp projection near middle of outer margin near long seta; apex of pronotal horn (Fig. 16) in male majors expanded, rounded on each side of feeble emargination; size less than 7 mm; Costa Rica, Panama *O. quetzalis* sp.nov.
4. Clypeal horn slender (Fig. 25), apex rounded or truncate, in some major specimens the apex very slightly emarginate; pronotal horn, except in minor specimens, with apex bituberculate, tubercles conical, not divergent; Mexico to Guatemala *O. neomirabilis* Howden
 — Clypeal horn moderately slender (Fig. 19), apex deeply emarginate or in minor males horn moderately wide, flattened and with broad apex shallowly emarginate; Costa Rica to Ecuador *O. mirabilis* Bates

FEMALES

5. Posterior clypeal carina distinct, sharply defined; vertex just posterior to clypeus with tubercles or transverse ridges; size 7 mm or more. 6
 — Posterior clypeal carina indistinct; vertex lacking tubercles or ridges (Fig. 17); size less than 7 mm; Costa Rica, Panama *O. quetzalis* sp.nov.
6. Pronotum rounded or flattened medially in anterior half 7
 — Pronotum with anterior, median, longitudinal concavity (Fig. 20); Costa Rica to Ecuador *O. mirabilis* Bates
7. Anterior pronotal margin not strongly raised medially (Fig. 26); Mexico to Guatemala *O. neomirabilis* Howden
 — Anterior pronotal margin strongly, arcuately raised (Fig. 23), anterior and posterior surfaces of elevation vertical; Costa Rica, Guanacaste. *O. solisi* sp.nov.

Onthophagus mirabilis Bates

(Figs. 19–21, 38)

Onthophagus mirabilis Bates, 1887: 74; Howden, 1973: 334; Howden and Young, 1981: 116.*Onthophagus orphnoides* Bates, 1887: 75; Howden and Young, 1981: 116.

Males. Length 7.1–12.0 mm. Dorsum brown to dark brown, glabrous; head, pronotum, elytral intervals, and pygidium with close to contiguous, moderate-sized punctures, surface between shining; elytral striae distinctly impressed. Clypeal margin (Fig. 19) of major males converging on each side to anterior median horn, horn vertical, thickened near apex and narrowly, deeply emarginate; clypeal surface almost flat, feebly punctate. Genae with sides nearly parallel. Frons and vertex feebly convex, not carinate or horned. Pronotum (Fig. 19) in large specimens with conspicuous conical, anteriorly projecting median horn, horn extended over head and apically strongly bifurcate. Foretibia elongate and with conspicuous tuft of setae at base of apical spur; two distal teeth closer together than other teeth. Minor form with both clypeal and pronotal horns present as small tubercles; often some slight indication on clypeal horn of an emargination; foretibia not elongate, similar to female. Genitalia as in Figure 21, internal sac as in Figure 38.

Females. Large specimens (Fig. 20) with clypeus anteriorly bidentate, teeth reflexed and separated by U-shaped emargination; clypeal surface otherwise flat and closely punctate; posterior clypeal carina represented by low ridge. Vertex on each side between eyes with sharp tubercle; surface punctate before tubercles, impunctate behind. Pronotum with acute conical tubercle or horn medially at anterior margin; pronotum medially longitudinally concave, highest at obtuse angle either side of concavity at anterior third; concavity largely impunctate, remainder of pronotum punctate. Small specimens with clypeal teeth, tubercles

on vertex, and pronotal horn all reduced; pronotal concavity very feebly indicated, entire surface densely punctate.

Distribution. Costa Rica to Ecuador.

Remarks. Series of *O. mirabilis* taken at Monteverde and Volcan Cacao, Costa Rica, and in Chiriqui Province, Panama, exhibit few differences that can be related to geography. In general small specimens have more pronounced punctures and a reduction in the size of horns and carinae. Some small males have the semicircular sclerotized plate in the internal sac reduced about one-seventh in width compared with the same structure in large males; however the general shape of the plate shows little variation.

The deeply bifurcate clypeal horn of male majors, the pronotal concavity in females, and the range will separate *O. mirabilis* from related species.

***Onthophagus neomirabilis* Howden**

(Figs. 25–30, 39, 40)

Onthophagus neomirabilis Howden, 1973: 334; Zunino, 1981: 75.

Males. Length 8.5–10.5 mm, greatest width 4.5–5.7 mm. Dorsum brown, closely punctate. Clypeus (Fig. 25) with long, slender, vertical horn at anterior margin, apex of horn rounded and flattened, slightly narrowed; disc of clypeus with a distinct concavity behind horn. Frons and vertex nearly flat, with shallow transverse depression between eyes; surface finely punctate. Pronotum (Fig. 25) in male majors with anterior median conical horn extending over head; apex of horn narrowly emarginate, slightly bifurcate; pronotal surface coarsely punctate. Elytron with distinct striae, striae with large, distinct punctures separated by 2 or 3 times their diameters; intervals broadly convex, moderately, irregularly punctate. Foretibia elongate (as is typical for males in the group) and with apical tuft of setae; two distal teeth closer together than other teeth. Middle and hind femora with outer surfaces smooth, only a few vague fine punctures present. Metasternum with scattered coarse punctures except along midline. Genitalia as in Figure 28, internal sac as in Figures 39 and 40 (two localities).

Females. Length 8.9–10.8 mm, greatest width 4.6–5.8 mm. Large specimens with clypeus anteriorly narrowly bidentate, sides of clypeus convergent; posteriorly clypeal suture represented medially by irregular low carina. Vertex (Fig. 27) anteriorly with two low rounded transverse lobes or tubercles, these almost fused or not with posterior clypeal carina; vertex between eyes almost flat, coarsely punctate. Pronotum (Fig. 26) with disc flattened in median third, flattened area extending from slightly raised, thickened anterior pronotal margin posteriorly to small rounded tubercle on midline at posterior fourth; pronotum, including flattened area, coarsely punctate. Small specimens with pronotum evenly convex, midline in anterior half frequently impunctate.

Distribution. Oaxaca, Mexico, to Zacapa, Guatemala.

Remarks. *Onthophagus neomirabilis* has been collected in wet forest areas at approximately 1200 m altitude in Oaxaca, Mexico, near Coban, Alta Verapaz, and near La Union, Zacapa, Guatemala. Zunino (1981) described the female of *O. neomirabilis* from the Alta Verapaz locality.

Guatemalan females (Fig. 30) differ slightly from females from Oaxaca (Fig. 26) in having the tubercles on the vertex more conical and more widely separated from the clypeal carina. No major males have been examined from Guatemala but a single male from La Union (Fig. 29), measuring 9.3 mm, has the clypeal horn transversely flattened and slightly expanded near the almost truncate apex. In addition the anterior face of the pronotal horn is almost flat and only slightly overhangs the vertex. These characters coupled with some differences in the internal sac (Fig. 40) may indicate a complex of sibling species, but from present evidence we consider that these differences represent a geographic cline.

Onthophagus neomirabilis male majors can be recognized by the rounded apex of the clypeal horn and by the narrowly emarginate, slightly bituberculate pronotal horn. Females can be identified by the rounded, transverse tubercles at the anterior edge of the vertex, with the tubercles usually contiguous with the posterior clypeal carina. Also *O. neomirabilis* is the only species in the group known to occur in Mexico and Guatemala.

***Onthophagus solisi* sp.nov.**

(Figs. 22–24, 41)

Holotype. Male, length 9.6 mm, greatest width 5.6 mm. Dorsum brown; vertex, pronotum, and elytral intervals closely punctate; pronotal punctures feebly ocelate, separated by 1 diameter or less, surface between smooth; most elytral punctures with very minute seta. Clypeus (Fig. 22) at anterior median edge with upright, slightly transversely flattened horn, horn apically deeply bifurcate, Y-shaped; each side of clypeus from rounded edge of gena to base of horn almost straight, not outwardly arcuate; clypeal surface slightly uneven, feebly convex medially and with scattered punctures. Vertex with very small tubercle on each side near anterior inner edge of each eye; surface anterior to and between tubercles punctate, almost impunctate posteriorly. Pronotum (Fig. 22) with anterior margin raised medially, forming obtuse angle; pronotum in anterior median half with large transverse tumosity delimited on each side by distinct conical tubercle, tubercles separated by approximately 1.5 mm; anterior face of tumosity almost vertical with midline slightly convex; pronotal surface near anterior lateral angles concave; marginal bead of posterior margin obsolete medially. Elytron with striae distinctly impressed; intervals on disc with two or more irregular rows of punctures, surface between shining. Pygidium closely, contiguously punctate, surface between punctures alutaceous. Metasternum with distinctly separated punctures except impunctate along midline, midline feebly convex in anterior third, feebly concave in posterior half. Foretibia elongate, with terminal tuft of setae; apical and subapical teeth distinctly closer to each other than second to third or third to fourth teeth. All femora with posterior or ventral surface shallowly but moderately uniformly punctate. Genitalia as in Figure 24, internal sac as in Figure 41.

Allotype. Female, length 9.5 mm, greatest width 5.5 mm. Clypeus with anterior margin sharply bidentate, teeth reflexed, margin between U-shaped; clypeal margin on each side slightly outwardly arcuate, not reflexed; clypeus flat to low posterior transverse carina; surface transversely rugose. Gena with margin abruptly, obtusely angled at widest point. Vertex (Fig. 23) with two sharp, slightly transverse tubercles, each tubercle in line with anterior edge of eye and mesad about one-third distance between eyes; vertex medially posterior to tubercles concave; surface anterior to tubercles transversely rugose, posterior to tubercles punctate. Pronotum (Fig. 23) with anterior margin abruptly, strongly, arcuately elevated at median sixth; anterior median third of pronotum flattened, flattened area narrowed and slightly concave posteriorly, with posterior end delimited by low, rounded tubercle; pronotal surface otherwise convex. Elytron similar to male except striae less strongly impressed. Mesosternum and femora with larger punctures than in male. Foretibia not elongate, lacking apical tuft of setae.

Type Material. Holotype, male, Costa Rica, Guanacaste Prov., Estac. Cacao, 1000–1400 m, SW side Volcan Cacao, VI.1990, II curso Parataxonomos, UTM 323300, 375700 (INBIO). Allotype, female, same data as holotype (INBIO).

Paratypes. 13 males, 1 female. Same data as holotype. Paratypes are in INBIO, Gill, HAHC.

Remarks. Male paratypes vary in length from 7.8 to 9.6 mm and in greatest width from 4.5 to 5.5 mm. Male minors have the clypeal horn only slightly higher than wide with the apex shallowly emarginate. The pronotal tumosity may be reduced to a low swelling with the

tubercle on each side obsolete. The single female paratype is similar in size and in other respects to the allotype.

The species can be identified by the characters mentioned in the key. The broad pronotal swelling or tumosity, evident in even small males, will separate *O. solisi* from related species. The arcuately raised edge at the midline of the anterior pronotal margin will usually identify the females of *O. solisi*.

For most species in the mirabilis group the locality data of the species are diagnostic but on Volcan Cacao *O. solisi* occurs sympatrically with *O. mirabilis*. Within the mirabilis group, these two species appear to be the least similar.

The species is named for Angel Solis B. who was responsible for the collection of the series and acted as a gracious host when the senior author visited INBIO (Instituto Nacional de Biodiversidad).

Onthophagus quetzalis sp.nov.

(Figs. 16–18, 42)

Holotype. Male, length 6.5 mm, greatest width 3.6 mm. Dorsally greyish black to black. Clypeus (Fig. 16) with slender, upright, 1.5-mm-long horn on anterior median edge, horn transversely flattened, gradually widened in apical half, apex rounded on each side, very feebly emarginate medially; sides of clypeus feebly, outwardly arcuate, slightly reflexed; surface with indistinctly defined transverse punctures; posterior clypeal suture absent. Vertex feebly convex, coarsely punctate, carina or tubercles lacking. Gena slightly produced at junction with clypeus, obtusely angulate posteriorly. Pronotal horn (Fig. 16) projecting anteriorly over head, horn in cross-section triangular, wide dorsal portion longitudinally concave, apex rounded on each side, feebly emarginate medially; anterior pronotal margin not modified, posterior margin lacking distinct bead; pronotal surface adjacent to anterior angles concave; pronotal surface including top of horn with numerous moderate-sized punctures, most punctures separated by 1–2 diameters; many punctures each with very minute whitish seta. Elytron with striae moderately impressed; striae punctures distinct, wider than stria; intervals with one to three irregular rows of small punctures. Pygidium with large, shallow, annular punctures, surface between alutaceous. Metasternum irregularly, minutely punctate near midline, moderately punctate laterally; midline broadly convex anteriorly, feebly, narrowly concave posteriorly. Foretibia slightly elongate, lacking apical tuft of setae, four large teeth on outer margin evenly spaced. Forefemur with posterior ventral surface sparsely punctate, femur uniformly brown. Middle and hind femora very finely, sparsely punctate on ventral surface; dark brown in basal and apical thirds, yellowish brown in median third, change in colour more gradual than in dicranus group. Basal segment of hind tarsus with one small, stout seta near middle on outer edge, adjacent obtuse angulate projection lacking. Genitalia as in Figure 18, internal sac as in Figure 42.

Allotype. Female, length 6.1 mm, greatest width 3.6 mm. Clypeus (Fig. 17) at anterior median edge bidentate, teeth reflexed and narrowly V-shaped between; sides of clypeus convergent anteriorly, feebly outwardly arcuate; clypeal surface transversely rugose-punctate; posterior carina feebly developed medially, obsolete in lateral thirds. Vertex almost flat medially, coarsely punctate. Gena with lateral angle sharp, obtuse; surface very coarsely punctate. Pronotum (Fig. 17) more strongly convex in median anterior fifth, surface of convexity anteriorly finely punctate, remainder of pronotal surface coarsely punctate, similar to male; midline posteriorly slightly depressed. Elytron, surface of pygidium, and metasternum as described for male. Foretibia shorter than in male, teeth on outer margin wider, less acute. Femora more distinctly punctate than in male; middle and hind femora not obviously bicoloured, slightly yellowish at median third near posterior edges. Hind tarsus similar to male.

Type Material. Holotype, male, Costa Rica, Puntarenas Prov., Monteverde, 1400 m, 20.VIII.1987, H. & A. Howden, FIT (HAHC). Allotype, female, same data as holotype except 15–17.VIII.1987 (HAHC).

Paratypes. 5 males, 11 females, 13 with same data as holotype except various dates between 12 and 24.VIII.1987; 1, Costa Rica, Guanacaste Prov., Estac. Cacao, 1000–1400 m SW side Volcan Cacao, VI.1990, UTM323300, 375700; 1, Costa Rica, Alajuela Prov., Zarcero A.R., 20.III.1989, A. Solis B., muerto en excrementos secos de *Urocyon*; 1, Panama, Chiriqui Prov., 1500 m, 15 km NW H [ato el] Volcan, Hartmann Finca, 25.V.1975, S. Peck, dung trap. Paratypes are in INBIO, Gill, HAHC.

Remarks. Size varies in males from 5.3 to 6.6 mm in length and from 3.2 to 3.6 mm in greatest width. In females length varies from 5.5 to 6.4 mm and width from 3.1 to 3.6 mm. The smallest male minor has the clypeal horn reduced to a small upright rounded projection and the pronotal horn obsolete, represented by a small anteriorly truncate swelling just posterior to the anterior margin. The male from Volcan Cacao has the pronotal horn slightly wider than those of similar size from Monteverde. Pronotal punctation varies somewhat in spacing, specimens with pronotal punctures more widely spaced having a shinier appearance. No obvious geographic variation was noted in the short series available.

Relationships of *O. quetzalis* to other species in the mirabilis group are problematic. The single pronotal horn, apically narrow clypeal horn, and impressed striae seem to relate *O. quetzalis* to the mirabilis group, but the frequently bicoloured legs, density of pronotal punctures, and moderately small size seem to place it near the dicranus group. We consider it to be more or less a bridging species between these two groups. The problem of relationships is discussed in the following section.

Male majors of *O. quetzalis* are easily distinguished from other Central American species by the slender, non-bifurcate clypeal and pronotal horns. The size, moderately impressed elytral striae, and the very fine punctures on the anterior median pronotal convexity should identify the females.

This species is named after the resplendent quetzal which shares the montane habitat from which most of the type series was collected.

RELATIONSHIPS

For the groups treated here, Table 1 lists the characters and states that we have been able to polarize with some degree of confidence. Characters 1, 2, 4, 5, 6, 8, 12, and 22 were uninformative and therefore not shown in Figure 44. As mentioned under Methods, we postulated an hypothetical ancestor based on character trends in *Onthophagus* and *Caccobius*. In addition we have included two Central American species that, it could be argued, are close relatives to some species in our groups. The two are *O. dicranoides* Balthasar and *O. nasicornis* Harold. The former species is superficially close to *O. dicranus* but has small horns near the posterior edges of the eyes and several other differences. The second species, *O. nasicornis*, shares some of the clypeal and pronotal character states with *O. dorsipilulus*, but lacks the pronounced dorsal punctures, and the pronotal configuration is different. We have also included two New Guinea species, *O. latenasutus* Arrow (Figs. 31 and 32) and *O. eliptaminus* Balthasar (Figs. 33 and 34), that share a number of character states with the mirabilis-dicranus groups. Table 2 illustrates the scoring of the characters that have been used in the reconstructed phylogeny (Figs. 44 and 45). We used the PAUP program (Phylogenetic Analysis Using Parsimony version 3.0 by D.L. Swofford, 1991) using the rooted outgroup method with character state optimization and accelerated transformation to produce two trees of unordered transformation states (one shown in Fig. 44) and then an ordered character tree (Fig. 45) using a consensus of 10 trees. Both trees group the obviously related species into our respective dicranus and mirabilis groups, except for *O. quetzalis*. The consensus tree (Fig. 45) relates *O. quetzalis* on an equal basis with the

TABLE 1. Characters used in the reconstruction of the phylogeny

Character	Plesiomorphic (0) Plesiomorphic (0)	Transition (1)	Apomorphic (1) Apomorphic (2)
1 Size	<5 mm		>5 mm
Head			
2 ♂ Clypeal margin	No horn		Horn
3 ♂ Clypeal margin	Horn simple		Horn bifurcate or expanded
4 ♀ Clypeal margin	Rounded	Emarginate	Bidentate
5 ♂ Clypeal carina	Present		Absent
6 ♂ Vertex	No carina or horns	Carina	(Carina) and horns
7 ♀ Vertex	Carina and/or tubercles		No carina
8 ♀ Vertex	Carina posterior in position		Anterior in position
Pronotum			
9 ♂ Convexity	Evenly convex	Uneven	Horned
10 ♀ Convexity	Evenly convex	Uneven	Horned
11 Surface	Finely punctate	Moderately punctate	Coarsely punctate
12 Surface	Punctate		Tuberculate
13 Surface	Simple punctures		Ocellate
14 Surface	Punctures scattered		Close, <1 diameter
15 Setae	Absent	Short	Long
16 Colour	Tan to black		Green-blue copper cast
Elytra			
17 Striae	Distinctly impressed		Vaguely impressed
18 Striae	Finely punctate		Coarsely punctate
19 Intervals	Smooth		Granular
20 Intervals	Finely punctate	Moderately punctate	Coarsely punctate
21 Intervals	Non-setose	Finely setose	Distinctly setose
22 Colour	Tan to black		Green or blue cast
23 Pygidium	Impunctate or finely punctate		Coarsely punctate-rugose
24 ♂ Foretibia	Lacking apical tuft of setae		With apical tuft of setae

mirabilis and dicranius groups, and the single tree (Fig. 44) places *quetzalis* as basal to the dicranius group.

These trees illustrate our uncertainty on the exact placement of *O. quetzalis*. They also support our contention that, at least in *Onthophagus*, a worthwhile phylogeny must include more than just the species from a single geographic area.

As a consequence of our considering the relationships of the dicranius and mirabilis groups we also examined worldwide group relationships within *Onthophagus*. This is a subject touched upon by Matthews (1972) in his revision of the Australian *Onthophagini*. In this work, Matthews suggests (p. 23) that the origin of the genus may be in Africa and that the Australian elements (groups) seem to represent "34 original invasions" of Australia. Matthews also mentioned that members of the genus are good over-water dispersers. It would appear, according to Matthews, that most of the Australian invasions were through the Indo-Malayan archipelago subsequent to the breakup of the Gondwana landmass.

The origin and development of the Mesoamerican *Onthophagus* fauna seems to have certain similarities with that of Australia. Although the exact number of species groups in the Americas has not been established, there are more than 20 distinct groups. A number of these groups are endemic to the southern United States or Mexico, or both, and a number of

TABLE 2. Scoring of character states listed in Table 1. The number "3" represents an unscored (not applicable) state

<i>Onthophagus</i> sp.	Characters																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1 Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2 <i>dorsipilulus</i>	1	1	0	1	1	0	1	3	1	0	2	0	1	2	1	0	2	0	0	2	1	0	2	1
3 <i>dicranius</i>	0	1	1	1	1	0	1	3	2	0	2	0	1	2	1	0	2	1	0	2	1	0	2	1
4 <i>asperodorsatus</i>	0	1	1	1	1	0	1	3	2	0	2	0	1	2	2	0	2	0	0	1	2	0	2	1
5 <i>petenensis</i>	1	1	1	1	1	0	1	3	2	0	2	0	1	1	1	1	2	1	0	0	1	0	2	1
6 <i>solisi</i>	1	1	1	1	1	0	0	1	1	1	2	0	1	1	0	0	0	0	0	0	1	0	2	1
7 <i>mirabilis</i>	1	1	1	1	1	0	0	1	2	2	1	0	1	0	0	0	0	0	0	2	1	0	2	1
8 <i>neomirabilis</i>	1	1	0	1	1	0	0	2	2	1	1	0	1	1	0	0	0	2	0	0	1	0	2	1
9 <i>quetzalis</i>	1	1	0	1	1	0	1	2	2	0	2	0	1	1	0	0	1	1	0	1	1	0	1	0
10 <i>eliptaminus</i>	1	1	0	1	1	0	1	3	2	0	1	0	0	2	1	0	1	0	1	0	1	0	0	0
11 <i>latenasutus</i>	1	1	0	1	1	0	1	3	1	0	1	0	0	2	1	0	1	1	1	0	2	0	0	0
12 <i>dicranoides</i>	1	1	1	1	1	1	0	0	2	0	1	0	0	1	0	1	1	2	0	1	0	1	0	1
13 <i>nasicornis</i>	1	1	0	1	1	0	1	3	1	0	0	3	3	3	0	0	1	0	0	0	0	0	0	1

others are endemic to Mesoamerica. Except for lower altitudes in the northwest corner of South America, the southern continent has only four or five distinguishable species groups and all, we believe, show relationships with the Central American fauna. From this we hypothesize that there were at least 20 separate species (ancestors of different species groups) that radiated into North America over the Beringian arc. Dispersal from Europe using an Atlantic route seems less likely for two reasons. The first is that the American species are morphologically more similar to the Oriental species than they are to the European ones. Second, if Cambefort (1991) is correct in assuming that *Onthophagus* is a "modern" genus, the Beringian connection has been available more often and seemingly more recently than any Atlantic connection. The depauperate South American *Onthophagus* fauna which seems to lack any close African affinities also supports a fairly modern Cenozoic radiation for the genus. Subsequent radiation occurred in the varied topography of southern North America and Central America with possible extinction in the north due to Pleistocene glaciations.

Our analysis seems to at least partly support this hypothesis. The two New Guinea species, *O. eliptaminus* Balthasar (Figs. 33 and 34) and *O. latenasutus* Arrow (Fig. 31), share most group characters and many of the other character states (1, 2, 4, 5, 6, 8, 12, and 22) with the species groups considered here. Although we have not seen enough Oriental material to establish either the number of species in, or range of, the eliptaminus–latenasutus complex, we believe this complex shares a close relationship with the American groups. Based on this, it is not appropriate to study the relationships of the New World *Onthophagini* without considering the remaining World fauna.

ACKNOWLEDGMENTS

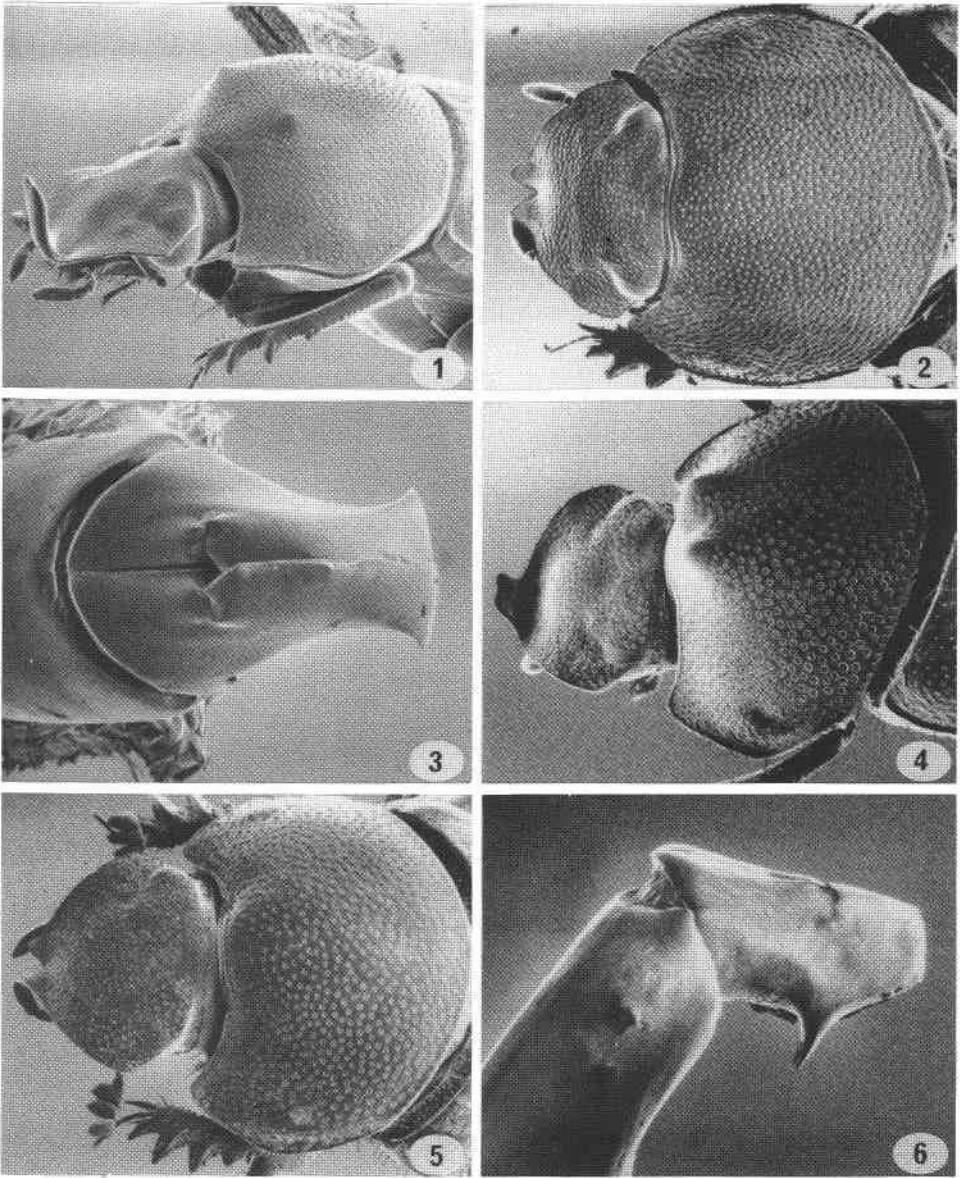
Gonzalo Halffter (Instituto de Ecología A.C., Xalapa, Mexico), Mario Zunino (Università di Torino, Italy), and Angel Solis (Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica) loaned specimens needed for this study. Fieldwork in Guatemala was facilitated by the Consejo Nacional de Areas Protegidas (CONAP) and by Jack Schuster, Dept. Biología, Universidad del Valle de Guatemala. In Panama we were assisted by the Dirección de Recursos Naturales Renovables (RENARE) and the Smithsonian Tropical Research Institution (STRI). John Heraty, Carleton University and Research Branch, Agriculture Canada, assisted us with the PAUP program and some of the graphics. Lewis Ling took the scanning electron micrographs and helped with the plates. Tessa MacKechnie typed various drafts of the manuscript. We thank all of the above for their contributions to

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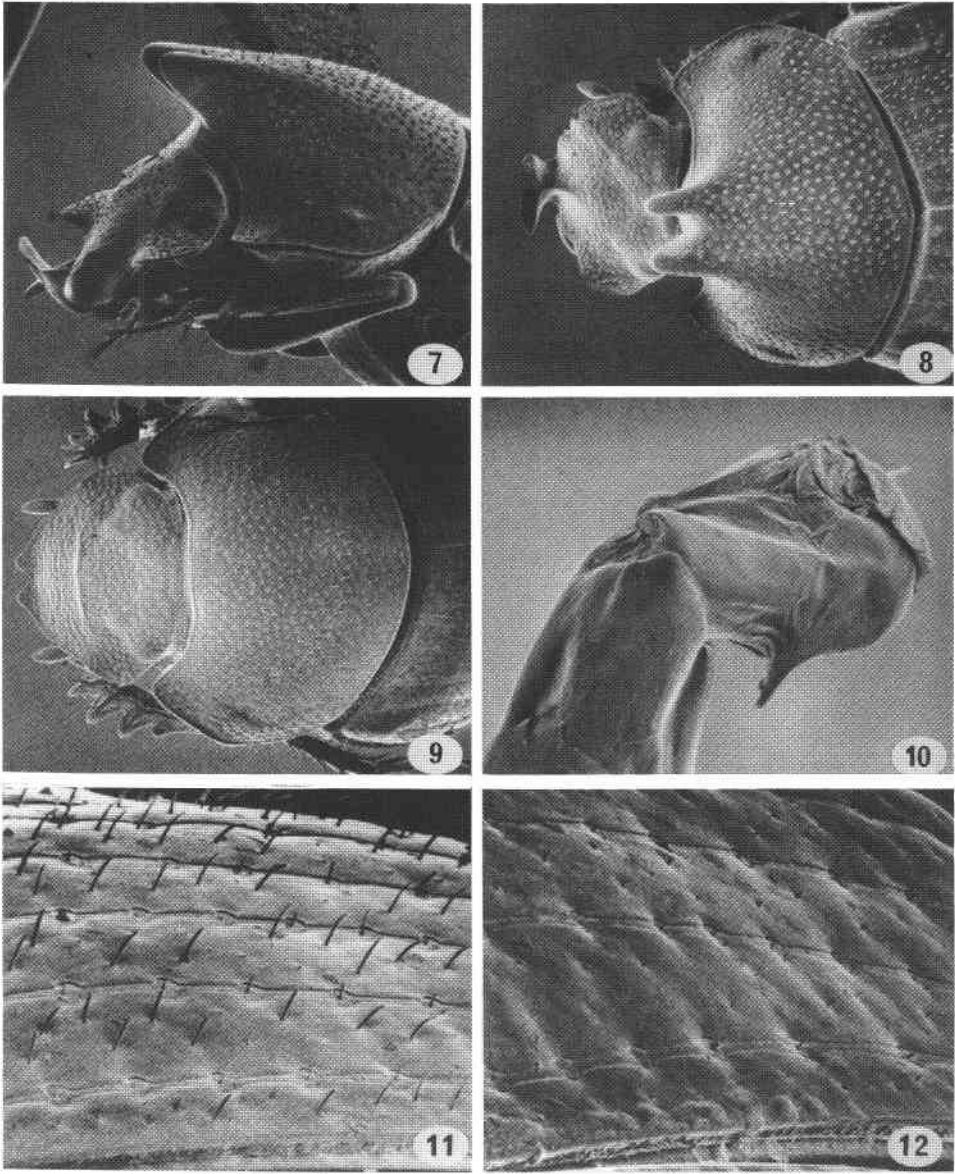
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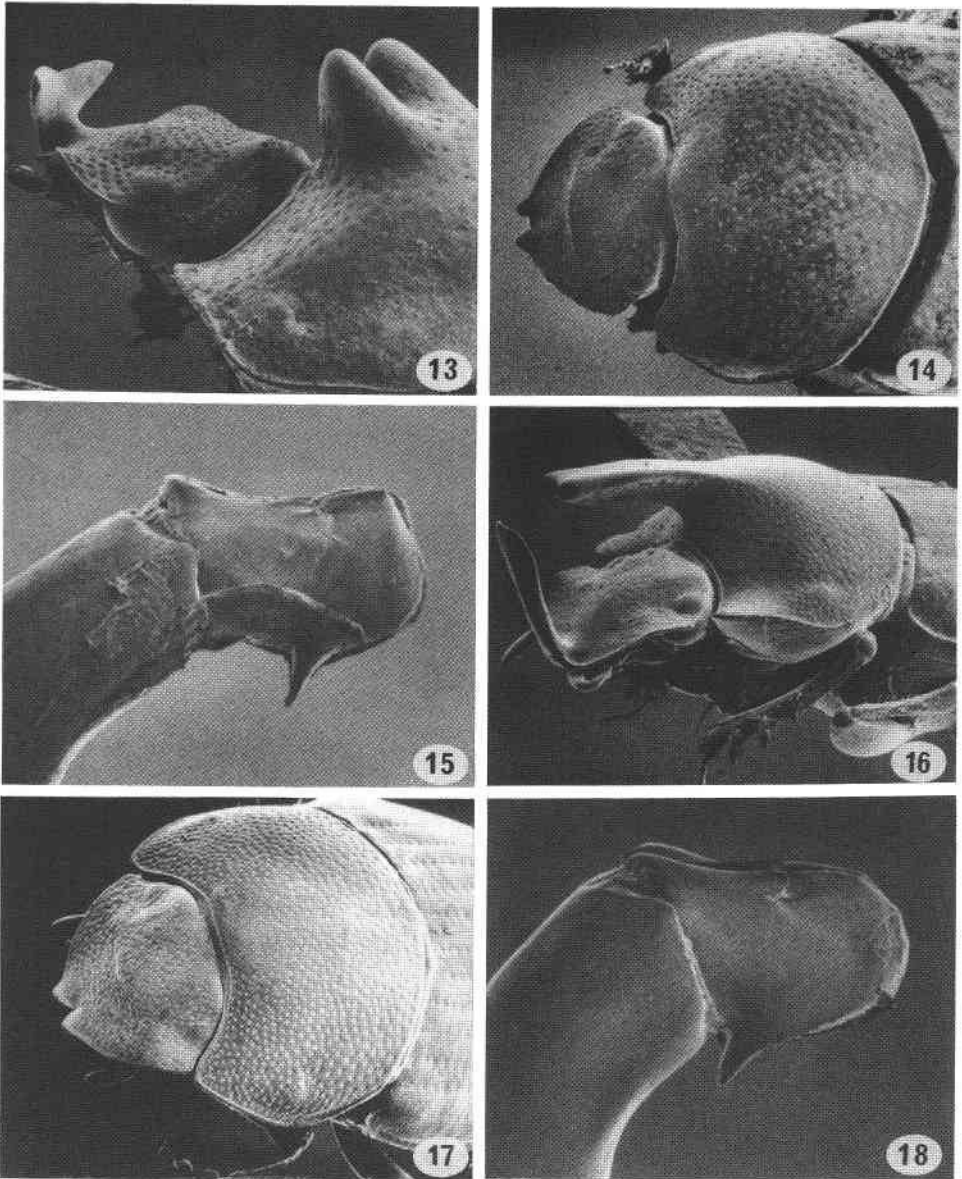
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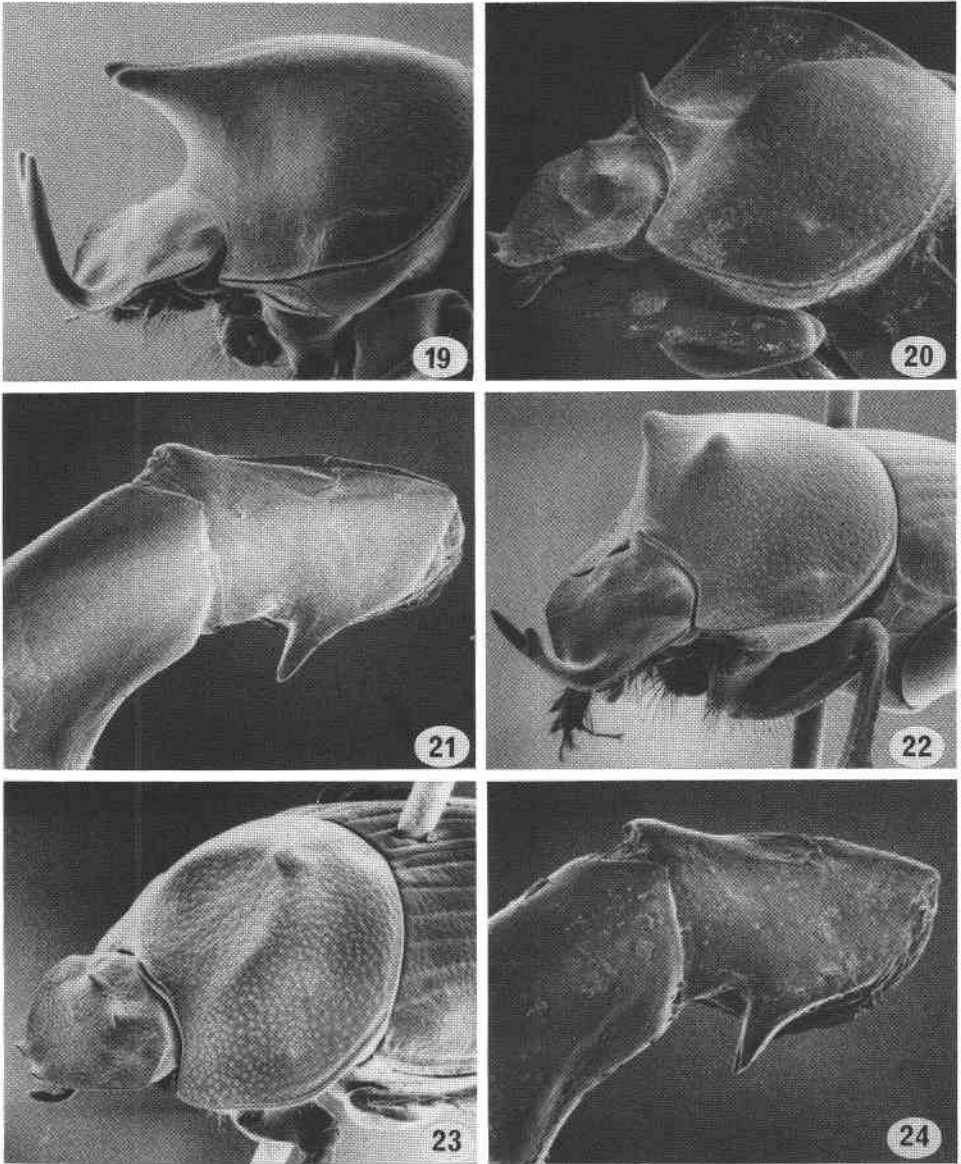
FIGS. 1-6. *Onthophagus* spp. 1-3, *O. dorsipilulus* Howden and Gill: 1, male head and pronotum; 2, female head and pronotum; 3, male genitalia. 4-6, *O. dicranius* Bates: 4, male head and pronotum; 5, female head and pronotum; 6, male genitalia.



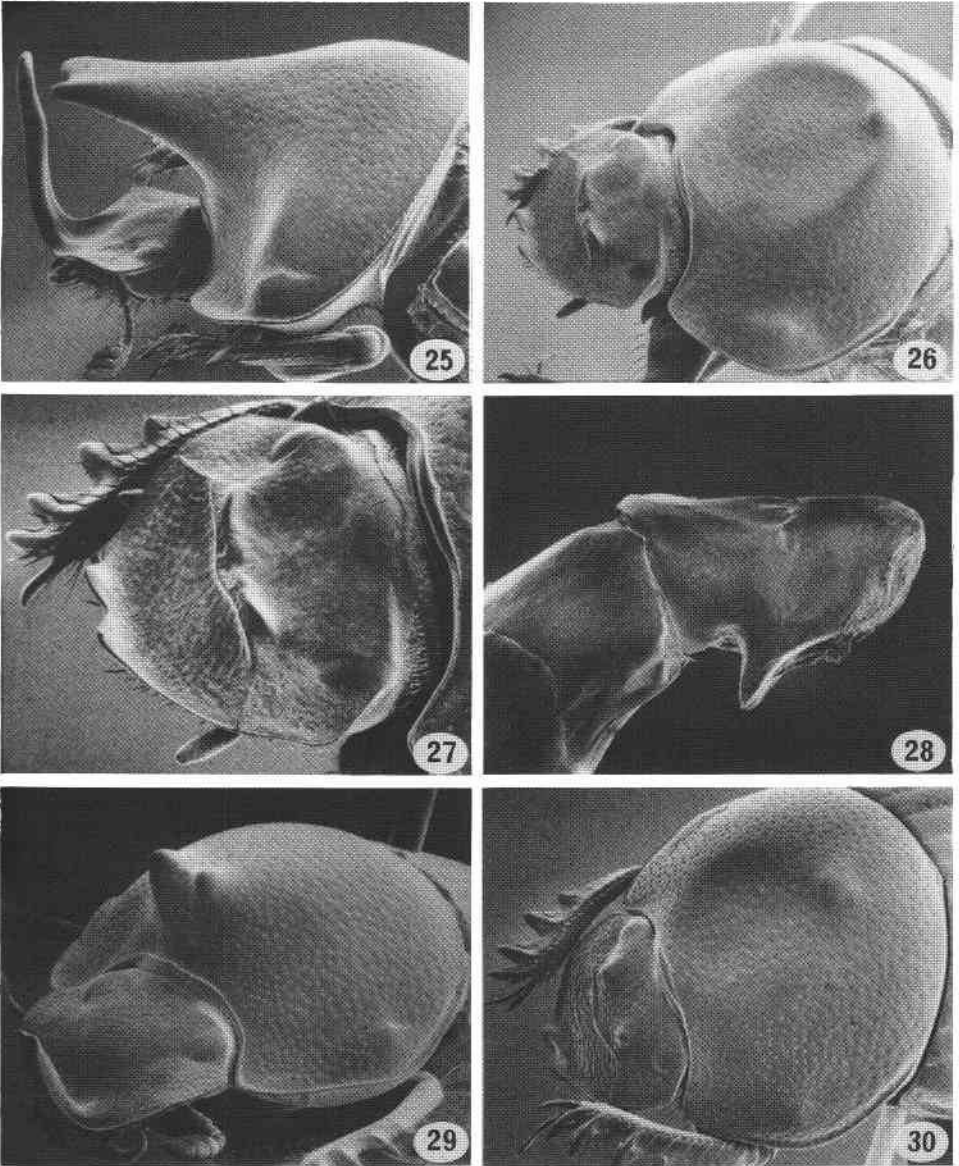
FIGS. 7-12. *Onthophagus* spp. 7-11, *O. asperodorsatus* sp.nov.: 7, male head and pronotum, lateral view; 8, male head and pronotum, dorsal view; 9, female head and pronotum; 10, male genitalia; 11, disc of elytron. 12, *O. petenensis* sp.nov., disc of elytron.



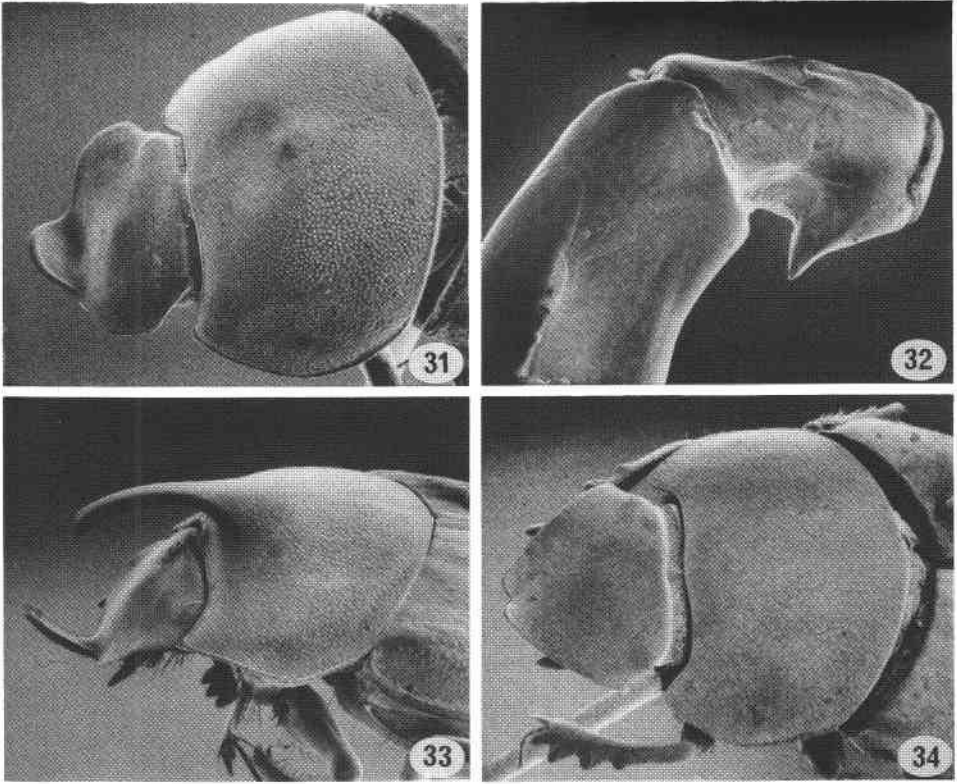
FIGS. 13–18. *Onthophagus* spp. 13–15, *O. petenensis* sp.nov.: 13, male head and pronotum; 14, female head and pronotum; 15, male genitalia. 16–18, *O. quetzalis* sp.nov.: 16, male head and pronotum; 17, female head and pronotum; 18, male genitalia.



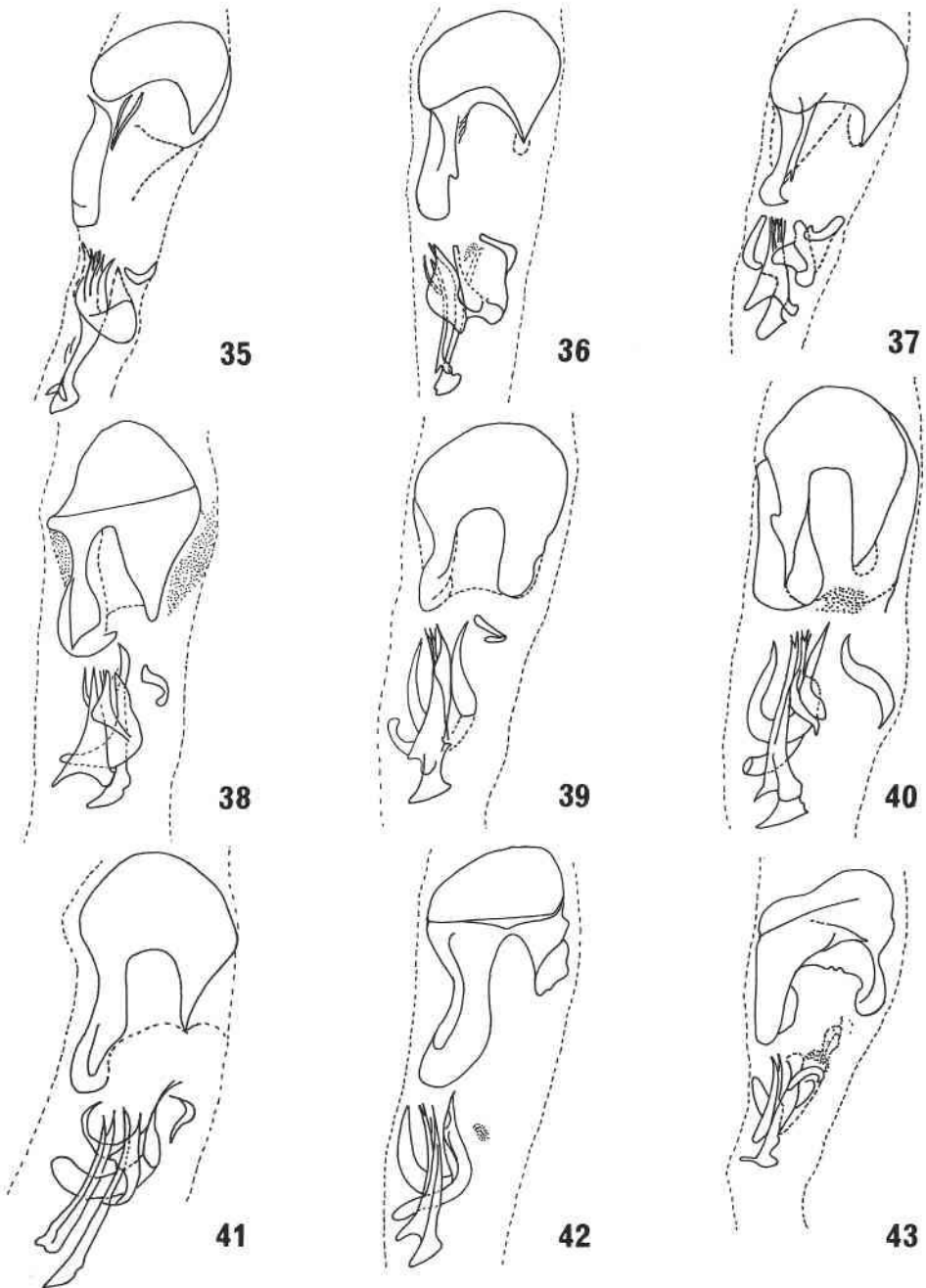
FIGS. 19–24. *Onthophagus* spp. 19–21, *O. mirabilis* Bates: 19, male head and pronotum; 20, female head and pronotum; 21, male genitalia. 22–24, *O. solisi* sp.nov.: 22, male head and pronotum; 23, female head and pronotum; 24, male genitalia.



FIGS. 25–30. *Onthophagus neomirabilis* Howden: 25, male head and pronotum, Oaxaca, Mexico; 26, female head and pronotum, Oaxaca, Mexico; 27, female head, Oaxaca, Mexico; 28, male genitalia, Oaxaca, Mexico; 29, male head and pronotum, La Union, Guatemala; 30, female head and pronotum, La Union, Guatemala.



FIGS. 31-34. *Onthophagus* spp. 31, 32, *O. latenasutus* Arrow: 31, male head and pronotum; 32, male genitalia. 33, 34, *O. eliptaminus* Balthasar: 33, male head and pronotum; 34, female head and pronotum.



FIGS. 35–43. *Onthophagus* spp., male internal sac: 35, *dicranus* Bates; 36, *petenensis* sp.nov.; 37, *asperodoratus* sp.nov.; 38, *mirabilis* Bates; 39, *neomirabilis* Howden, Oaxaca, Mexico; 40, *neomirabilis* Howden, La Union, Guatemala; 41, *solisi* sp.nov.; 42, *quetzalis* sp.nov.; 43, *eliptaminus* Balthasar.

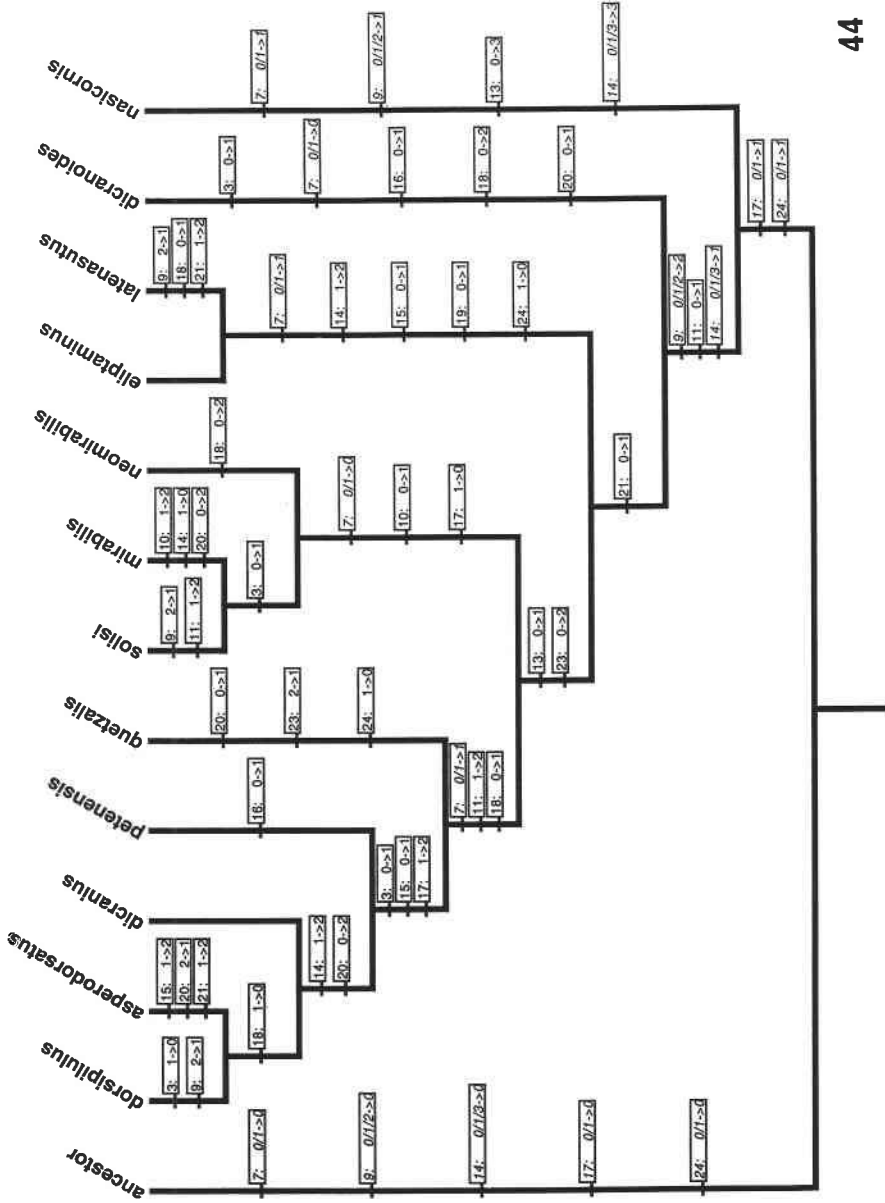


FIG. 44. One of two most parsimonious trees using unordered character states; transformations plotted using ACCTRAN optimization [PAUP program, Swofford (1991), version 3.0]. Tree length 58, CI=0.55, RI=0.59. Explanation of boxes: [9:] = character; [0/1/2] = transition series; \rightarrow 2 = character state as given in Table 2; 9:0/1/2 \rightarrow = character 9 that is polymorphic in outgroup; 0 \rightarrow 3 = character is not applicable (see scoring in Table 2).

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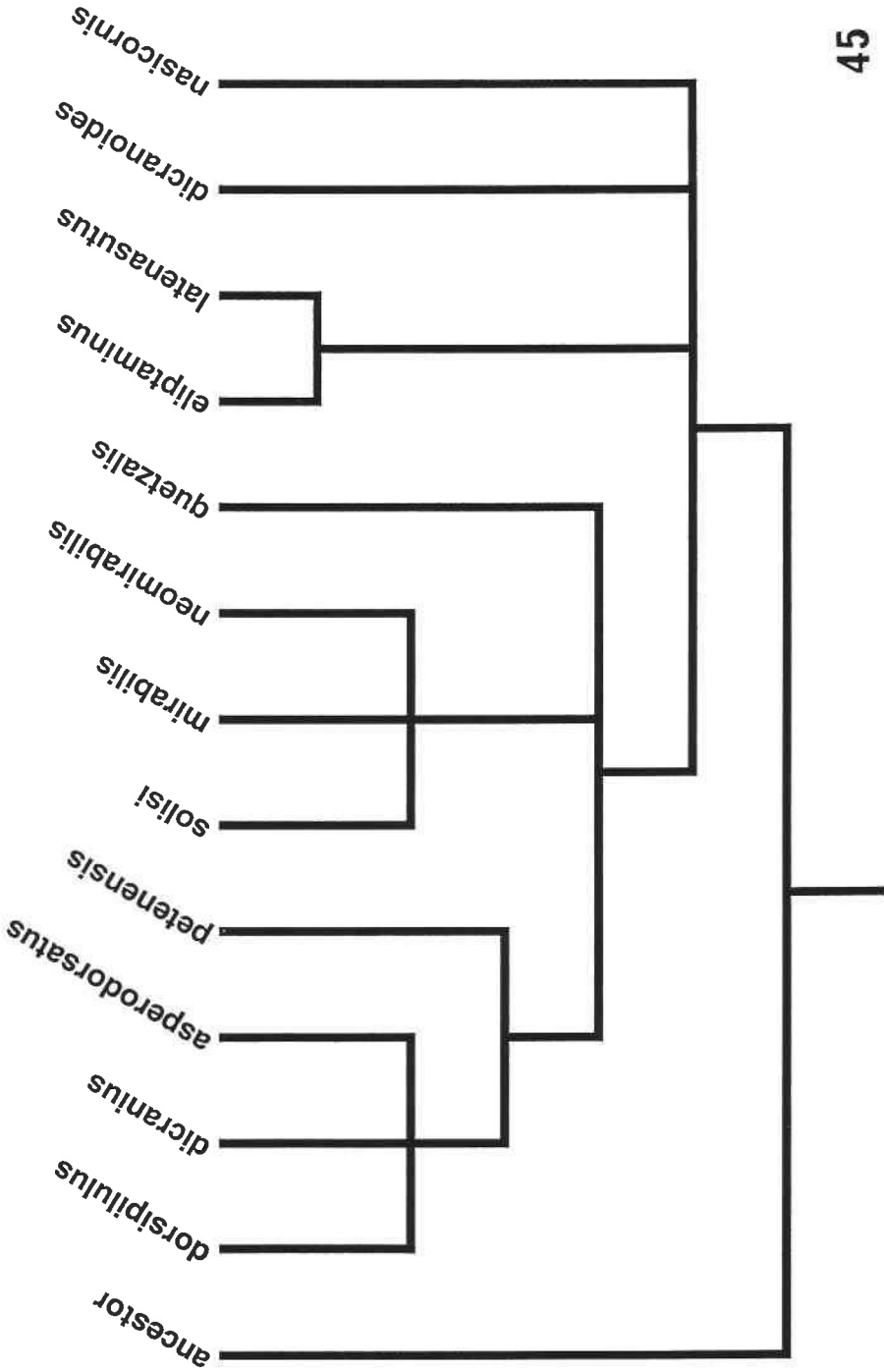


Fig. 45. Strict consensus solution for 10 trees produced using ordered character states. Tree length = 58, CI=0.50, RI=0.59.