SYNOPSIS OF THE NEOTROPICAL GENUS OZAENA OLIVIER: CLASSIFICATION AND RECONSTRUCTED EVOLUTIONARY HISTORY (COLEOPTERA: CARABIDAE: OZAENINI)

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Abstract


Descriptions and illustrations of structural features of adults, a key, and chorological data provide the basis for characterizing the genus Ozaena Olivier and classifying the 10 included species, two of which are new: O. maxi (type locality: Iracubo, CAYENNE), and O. manu (type locality: Manu National Park, Madre de Dios Province, PERU). With a geographical range that extends from ca. 30°S to 30°N in the New World, all species of Ozaena occur in cis-Andean South America, only two ranging farther north: O. dentipes Olivier, to Panama; and O. lemoulti Bänninger to southern Arizona, USA. A reconstructed phylogeny postulates the following: the genus Platycerzozaena Bänninger as the sister-group of Ozaena, together these genera comprising the Ozaena genus-group; within Ozaena, the O. dentipes group as sister-taxon of the O. lemoulti + convexa groups; within the O. dentipes group, O. maxi as sister-taxon of O. linearis Bänninger + dentipes; within the O. lemoulti group, the sequence O. ecuadorica Bän. (O. elavata Bänn. [O. lemoulti + martinezi Ogueta]); and within the O. convexa group, O. grossa Bän. as sister-taxon of O. convexa Bän. + manu.

Character evolution involves losses, gains, and shifts, in about equal numbers. Convergence is relatively rare, involving only three of 35 characters. The predominant mode of character evolution is simple, with few examples of sequential changes sustained through several speciation events. Basic modifications in evolution of the ground-plan of the Ozaena genus-group include reduction or loss (for example, tactile sense organs, antennal cleaner of the fore tibia, and adhesive vestiture of the male fore tarsi), and enhancement or gain (for example, scale-like sensilla basiconica on pronotum and elytra, concentration of sensilla basiconica in groups on the antennomeres, particularly antennomere 11). Within Ozaena, many modifications to the antennae and mouthparts indicate the importance of these organs to evolution of the group.

Based on phylogenetic relationships and the distribution pattern of the extant species, a reconstructed geographical history of Ozaena postulates the following: first, a vicariance event in South America separating the ancestral stock of Ozaena into a northern vicar that gave rise to the O. dentipes group, and a southern vicar that gave rise to the O. lemoulti and convexa groups; followed by cycles of range expansion and contraction that allowed for differentiation of successive stocks of species. The temporal range for these speciation events is estimated to extend over a period of about 12 million years, or from the latter part of the Miocene epoch to the Recent. The most recent speciation events are estimated to be of Pliocene age.

Based on lack of differentiation of South American and Middle American representatives of O. dentipes and O. lemoulti respectively, and extent of range in Middle America, these two species are postulated to be relatively recent invaders of the latter area, with O. dentipes being the more recent to arrive.


Résumé

Des descriptions et des dessins de caractères structuraux des adultes, une clé, et des données chorologiques forment une base pour caractériser le genre Ozaena Olivier et pour classifier les 10 espèces comprises, dont deux nouvelles: O. maxi (local type: Iracubo, CAYENNE), et O. manu (local type: Parc national Manu, Province de Madre de Dios, PÉROU). D’une étendue géographique à partir de ca. 30° sud à 30° nord au
Nouveau Monde, toutes les espèces de Ozaena se trouvent à l’Amérique de sud cis-Andine, avec deux seulement s’étendant plus au nord: O. dentipes Olivier jusqu’au Panama; et O. lemoulti Bänninger jusqu’au sud de l’Arizona, États-Unis d’Amérique.

Une phylogénie réclame: le genre Pterygozona Bänninger comme groupe consœur de Ozaena; en dedans du genre Ozaena, le groupe O. dentipes groupe comme taxon consorze des groupes O. lemoulti + convexa; en dedans du groupe O. dentipes, O. maxi comme taxon consorze de O. linearis Bänninger + dentipes; en dedans du groupe O. lemoulti, le séquence O. ecuatorica Bann. (O. elevata Bann. [O. lemoulti + martinezi Ogueta]); et en dedans du groupe O. convexa, O. grossa Bann. comme taxon consorze de O. convexa Bann. + manu. L’évolution de caractères entraîne des pertes, des gains et des changements, en parties à peu près égales. La convergence est relativement rare, n’entraînait que trois de 35 caractères. La modalité principale d’évolution de caractères est simple, avec peu d’exemples de changements de séquences soutenus à travers de plusieurs événements de formation d’espèces. Des modifications de base dans l’évolution du plan de fondation du groupe de genre d’Ozaena comprennent la réduction ou la perte (par exemple: les organes de perceptions tactiles, le nettoyeur d’antennes de l’avant-tibia, et le revêtement adhésif des avant-tarses des mâles), et l’augmentation ou le gain (par exemple: des sensilla basiconica ressemblant les écaillies au pronotum et aux élytres, la concentration de sensilla basiconica en groupes aux antenne), particulièrement à l’antennomère 11). En dedans d’Ozaena, plusieurs modifications aux antennes et aux parties buccales indiquent l’importance de ces organes à l’évolution du groupe.

Une histoire géographique reconstituée d’Ozaena, basée aux rapports phylogénétiques suppose: premièrement, un événement vicariant en Amérique du sud qui séparerait la souche ancestrale d’Ozaena dans un vicariant du nord qui a fait naître le groupe O. dentipes et un vicariant du sud qui a fait sortir les groupes d’O. lemoulti et convexa; suivi de cycles d’expansion et de contraction qui ont permis la différentiation de souches successives d’espèces. L’étendue temporelle de ces événements de formation d’espèces est présumée d’avoir pris une période de 12 million d’années approximativement, ou de la dernière partie de l’époque Miocène à l’époque Récente. Les événements les plus récents de formation d’espèces sont présumés de faire partie de l’âge de Pliocène.

D’une base de manque de différenciation des représentants d’O. dentipes et d’O. lemoulti de l’Amérique du sud et de l’Amérique centrale, respectivement, et l’étendue dans l’Amérique centrale, l’on prétend que ces deux espèces sont des envahisseurs récents de ce dernier territoire, avec O. dentipes étant l’espèce la plus récente d’arriver.

INTRODUCTION

Proposed by Olivier in 1812, the genus Ozaena was revised most recently by Ogueta (1965a), who provided a useful, well illustrated treatment of the species known to him. He did not offer a classification of the species, though the sequence in which he arranged them indicated an appreciation of their relationships. In the course of obtaining a general understanding of New World ozaenines, the senior author came across features of Ozaena that seemed useful in classification of the species, and also material of two undescribed species. This new information provides sufficient new insights to justify another review of the genus.

Accordingly, we offer here a revised description of the genus; a revised key to the species; an abbreviated taxonomic treatment of previously described species; descriptions of new species; range maps; a classification based partly on a more detailed assessment of antennal features first reported by Ogueta and partly on details of mandibular structure; and a consideration of the evolutionary implications of the taxonomic treatment.

MATERIAL AND METHODS

Material. This study is based on detailed examination of 125 specimens of Ozaena, including types, and on 20 specimens of other ozaenine taxa representing most of the other genera of the tribe Ozaenini.
In addition to the few specimens housed in the Strickland Entomological Museum, University of Alberta, Edmonton, Alberta (UASM), we studied material housed in the following institutions, arranged in alphabetical sequence according to coden, and with names of curators in parentheses.

**AMNH** Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York, USA 10024 (L.H. Herman).

**BMNH** Department of Entomology, British Museum (Natural History), Cromwell Road, London SW7 5BD, United Kingdom (M.J.D. Brendell).

**CASC** Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California, USA 94118 (D.H. Kavanaugh).

**CISC** California Insect Survey, Division of Entomology, University of California, Berkeley, California, USA 94720 (J. Chemsak).

**CNCI** Canadian National Collection of Insects, Biosystematics Research Centre, Agriculture Canada, K.W. Neatby Building, CEF, Ottawa, Ontario, Canada K1A 0C6 (Y. Bousquet).

**ETHZ** Entomologisches Institut, Eidgenössische Technische Hochschule-Zentrum, Universitätsstrasse 2 CH-8006, Zürich, Switzerland (W. Sauter).

**FSCA** Florida State Collection of Arthropods, Division of Plant Industry, 1911 34th Street S.W., P.O. Box 1269, Gainesville, Florida, USA 32602 (R.E. Woodruff).

**ICCM** Section of Insects and Spiders, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA 15213 (R. Davidson).

**JEWC** James E. Wappes Collection, RD 2, Box 16B, Chadds Ford, Pennsylvania, USA 19317.

**MCZC** Department of Entomology, Harvard University, Cambridge, Massachusetts, USA 02138 (S.R. Shaw).


**NHMW** Naturhistorisches Museum Wien, Zweite Zoologische Abteilung (Insekten), Bugring 7-Postfach 417, A-1014 Wien, Austria (H. Schönmann).

**SMCC** Scott McCleve Collection, 2210 13th Street, Douglas, Arizona, USA 85607.

**TAMU** Department of Entomology, Texas A & M University, College Station, Texas, USA 77843 (H.R. Burke).

**USNM** Department of Entomology, United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA 20560 (T.L. Erwin).

**ZSMC** Zoologische Sammlung des Bayerischen Staates, Münchhausenstrasse 21 D-8000, München 60, Bayern, Federal Republic of Germany (G. Scherer).

**Methods.** Taxonomic principles, criteria for ranking groups of specimens as species, and general working methods were the same as explained previously (Ball 1970, 1972, 1975; Ball and Negre 1972).

Usage of names of the species described by Bänninger was determined by examination of types, most of which are in his collection at ETHZ. See Erwin and Halpern (1978: 357–359) for general information about the collection, and below for details about the *Ozaena* types. We saw also one type specimen in the MCZC.

For many of the species descriptions based on more than one specimen, Bänninger labeled one specimen as “type” and the others as “co-types”, Erwin and Halpern (1978: 358) regarded all of such series as co-types, and for one species (*O. convexa* Bänn.), designated the “type” as lectotype. We follow this procedure.

Representative specimens were chosen by eye for measurements of the following: standardized body length (SBL), the sum of head length (base of mandible to posterior margin of eye), length of pronotum (along the mid-line), and length of elytra (plane of basal ridge to apex, along the suture); maximum width (measured across both elytra, at widest point); and proportions of labial palpomere 3 (maximum length/width at apex).

A Cambridge S-250 scanning electron microscope was used to examine and photograph gold-coated sclerites (Stork 1980: 174).

Distribution data are summarized for previously described taxa by symbols on maps, representing positions of localities for material that we have seen, and for published rec-
ords. The previously unpublished data on which these maps are based are summarized in an Appendix at the end of the paper. For previously described species, we provide the numbers of non-type specimens examined, and the institutions from which this material was borrowed. For new species and for types, we provide complete label data.

CLASSIFICATION

Genus *Ozaena* Olivier, 1812


*Ozena* Desmarest, 1825: 140 (unjustified emendation).

*Ozoena* Brullé, 1834: 240, 254 (unjustified emendation).


Notes about Synonymy. Castelnau (1835: 144) recognized that *Ictinus tenebrioides* and *Ozaena dentipes* were conspecific, and indicated the synonymy of the generic names of these two nominal species. Subsequently, however, the name *Ictinus* was used, incorrectly, by Brullé (1840: 48–49) for several ozaenine species that were transferred subsequently to *Pachyteles* Perty.

Derivation of Generic Name. From Greek, meaning to smell, presumably alluding to the ability of adults of this genus to produce a strong odor when disturbed.

Recognition. Adults of *Ozaena* are slender, with relatively short prothorax and parallel-sided elytra (Figs. 1 and 2). Though antennomeres 5–10 are moniliform, the antennae are long for ozaenines and extend posteriorly beyond the base of the elytra. The fore femur (Fig. 21) is slender, and has a dentiform projection antero-ventrally (Fig. 21). The antennal cleaner of the fore tibia (Fig. 22A, B) is reduced, with a small median expansion and without clip setae (Hlavac 1971). The dorsal surfaces of the pronotum and elytra bear scale-like sensilla (Fig. 16A).

In general form, adults of *Platyceorozaena* Banninger are similar to those of *Ozaena*, and both groups share the dorsal scale-like sensilla and reduced antennal cleaner of the fore tibia (Figs. 22A, B and 30A, B). However, differences are many, including the following: proportions and setation of the labrum (in *Ozaena*, transverse and with a row of apical setae [Fig. 18]; in *Platyceorozaena*, quadrate and without apical setae [Fig. 25]); antennae short in *Platyceorozaena* (Fig. 24), hardly extended posteriad the base of the pronotum; fore femur in *Ozaena* slender (Fig. 21), in *Platyceorozaena*, broadly swollen basally (Fig. 29), without the small dentiform projection that is characteristic of *Ozaena* adults.

Description. Size large for Ozaenini, SBL ca. 13–19 mm, maximum width ca. 4–6 mm. Habitus as in Figures 1 and 2, body elongate, slender.

Color. Piceous to black, except femora and tibiae of adults of some species rufous.

Vestiture. Dorsum generally sparsely setose; setae short, broad, thickened, each seta more-or-less cleft, ridged, and flattened (Fig. 16A, B). Venter setose, abdominal sterna densely so; setae normal, trichoid.

Microsculpture. Labrum with meshes isodiametric to slightly transverse, sculpticells small. Dorsal surface of head including clypeus with meshes isodiametric, sculpticells larger than those of labrum; ventral surface with meshes transverse. Pronotum with meshes isodiametric, slightly transverse, or laterally, slightly longitudinal, microlines broken,
incomplete; propleuron with meshes rectangular, obliquely oriented, sculpticells slightly convex or flat; prosternum with meshes transverse. Pterothorax: mesopleura with meshes transverse; metapleura with meshes isodiametric to transverse; meso- and metasterna with meshes transverse, on metasternum microlines obsolete. Elytra: intervals almost smooth, microlines few; interneurs with meshes isodiametric. Abdominal sterna with meshes transverse.

Chaetotaxy. Labrum with about 12 marginal setae; clypeus and vertex asetose. Temporal areas each side with several setae. Pronotum asetose. Elytra without parascutellar or discal setae, umbilical series with 25–30 setae. Antennae: antennomeres 1–4 sparsely setose, 5–10 sparsely setose marginally and apically, glabrous medially, 11 glabrous, except sense organs in shagreened areas. Scrobes of mandibles with numerous short setae. Maxillae: cardo and stipes each with 2 setae. Labium: submentum and mentum each with
3–5 setae; glossal sclerite with 2 setae; palpomeres glabrous. Legs (sequence—fore, mid, hind): coxae, 0-numerous-numerous; trochanters, numerous-numerous-few; femora, all, with small spines on antero-ventral surfaces; tibiae, all, with normal rows of setae; tarsi, all, setose dorsally and ventrally.

**Secondary sexual feature.** Males without adhesive vestiture on fore tarsomeres.

**Head.** Frontal impressions elongate, shallow, irregular. Supraantennal areas not reflexed but extended laterally each side as obtuse point. Temporal lobes each side prominent, extended to about posterior margin of eye. Eyes moderately convex, ovoid in outline, narrowed ventrally; posterior margin of each eye indented slightly by projection of postgena.

**Antennae.** Long, in retracted position apices extended posterior base of elytra. Antennomeres 1–4 cylindrical, 1 as broad near base as at apex, i.e. not constricted basally, 2 small, less than 0.5 length of 1, 3 and 4 longer than 2, 3 subequal to 1; antennomeres 5–10 moniliform, each constricted basally, lateral margins rounded; antennomere 11 longer, more-or-less strikingly widened (Figs. 3–9); shagreened area (i.e. densely pitted, with short sensory setae) confined to apical 0.33–0.50, apex sharp straight keel (Fig. 17C).

**Mouthparts.** Labrum: transverse, antero-lateral margins broadly rounded, anterior margin subtruncate (Fig. 18). Mandibles (Figs. 10–12) trigonal in dorsal aspect, lateral surfaces with well-developed scrobes, ventro-lateral margins extended laterally as broadly rounded flanges. Left mandible with terebral margin (tm) cutting edge, prominent; terebral tooth (tt) small; retinaculum extensive, anterior retinacular tooth (art) evident, directed medially, posterior tooth (prt) larger, directed posteriad; premolar tooth broad and blunt, set off from retinaculum by deep sinus (Figs. 10A, 11A, 12A); molar tooth hardly evident; ventral groove (vg) long, extended anteriad retinacular tooth, microtrichia (vm) dense, and moderately long (Figs. 10C, 11C, 12C). Right mandible similar to left, except anterior retinacular tooth more prominent (Figs. 10B, 11B, 12B). Maxillae: each with galeomere 2 distinctly longer than galeomere 1, lacinia with apical tooth short (Fig. 19), marginal setae extended as dense clump beyond apex, and palpomeres 2 and 3 short, palpomere 4 more-or-less broad. Labium (Fig. 20): mentum with sinus narrow, lateral lobes (ll) broadly rounded apically, medially sides about parallel to one another; tooth short, apex not notched; epilobes (el) narrow, not denticulate on inner margin, and short, not extended to apices of lateral lobes; glossal sclerite broad; paraglossae short, apices not extended beyond apex of glossal sclerite; palpomeres short and broad.

**Thorax.** Pronotum transverse to quadrato in shape, disc convex, sides various, but not crenate (Figs. 1 and 2); lateral grooves and postero-lateral impressions clearly developed. Prosternum with intercoxl process short, broad, without impressions. Mid coxal cavities separated from one another by projections of meso- and metasternum; metepisterna elongate, narrow.

**Elytra.** Narrow, humeri broadly rounded, denticulate or without lateral projections; sides parallel to one another. Flanges of Coanda average for ozaenines. Intervals broad, slightly elevated. Interneurs narrow, each with row of large punctures. Basal ridge very short, hardly evident.

**Legs.** Coxae and trochanters without special features; fore femora almost straight, parallel-sided, slightly expanded apically, with small setose denticle ventrally near base (Fig. 21, dpf). Antennal cleaner of fore tibia (Fig. 22A, B) as described under diagnostic features. Tarsomeres of all legs similar, thickened and compressed.

**Abdominal sterna.** Average for Carabidae.

**Male genitalia.** Median lobe compressed, apical portion in lateral aspect very short, broadly rounded, base open. Parameres: right paramere as long as median lobe, setose apically and along most of medial margin; left paramere much shorter, sparsely setose...
Figs. 3–5. Left antennomeres of *Ozaena* species: 3, *O. maxi*, new species (A, antennomeres 9–11, anterior aspect; B, antennomere 9, anterior aspect; C, same, ventral aspect; D, same, *sensilla basiconica*, ventral aspect); 4, *O. lineata* Bänninger (A, antennomeres 9–11, anterior aspect; B, antennomere 9, ventral aspect); 5, *O. dentipes* Olivier (A, antennomeres 9–11, anterior aspect; B, antennomere 9, anterior aspect; C, antennomere 9, *sensilla basiconica*, ventral aspect). *sb*, *sensilla basiconica*; *sbf*, field of *sensilla basiconica*. Scale bars = 200 μm for Figs. 3A–C, 4A–B, and 5A, B; 20 μm for Figs. 3D and 5C.
Figs. 6–9. Left antennomeres of *Ozaena* species: 6, *O. ecuadorica* Bänninger (A, antennomeres 9–11, anterior aspect; B, antennomere 9, ventral aspect; C, same, sensilla basiconica); 7, *O. elevata* Bänninger (left antennomeres 9–11, anterior aspect); 8, *O. martinezi* Ogueta (A, left antennomeres 9–11, anterior aspect; B, antennomere 9, ventral aspect); 9, *O. convexa* Bänninger (A, antennomeres 9–11, anterior aspect; B, antennomere 9, ventral aspect; C, same, sensilla basiconica). sb, sensilla basiconica; sbf, field of sensilla basiconica. Scale bars = 200 μm for Figs. 6A, B, 7, 8A, B, and 9A, B; 20 μm for Figs. 6C and 9C.
Figs. 10–12. Mandibles of *Ozaena* species: 10, *O. dentipes* Olivier (A and C, left mandibles, dorsal and ventral aspects, respectively; B and D, right mandible, dorsal and ventral aspects, respectively); 11, *O. lemoulti* Banninger (same); 12, *O. convexa* Banninger (same). *arr*, anterior retinacular ridge; *art*, anterior retinacular tooth; *i*, incisor; *mrt*, median retinacular tooth; *prt*, posterior retinacular tooth; *t*, terebra; *tm*, terebral margin; *ts*, terebral sinuation; *vg*, ventral groove; *vm*, ventral microtrichia. Scale bars = 200 μm.

Apically and along medial margin. Internal sac basally with slender rod, broadened apically; in everted position, with bilobed apical sclerite connected to more basal collar-like area with dense covering of microtrichia, these extended basally on left side.

Ovipositor. Stylomeres short, stout, apico-medially with numerous moderately long trichoid setae; preapical sensory furrow circular, with single short nematiform seta (*ns*) (Fig. 23A, B).
Geographical Distribution. The range of this genus extends from northern Argentina through Middle America, and northward to southern Arizona (Figs. 13-15).

Phylogenetic Relationships. This genus and Platycerozaena seem to be closely related, and together comprise the Ozaena genus-group.

Included Species. The genus Ozaena includes 10 species, arrayed in three species-groups. Details are provided below.

**KEY TO THE SPECIES OF OZAENA OLIVIER**

See Ogueta (1965a) for illustrations of the pronota of all of the species of Ozaena, except O. maxi and O. manu.

1 Pronotum (Fig. 1) with lateral margins very narrow, hardly wider toward anterior angles than medially... (O. dentipes group) ........................................... 2

1' Pronotum (Fig. 2) with lateral margins expanded, in form of explanation of varied width and elevation. Terminal palomeres clearly elongate. ........................................... 4

2. (1) Antennomeres 5–11 anteriorly and posteriorly with depression near base (Fig. 5A, B). 3

2' Antennomeres 5–11 without depressions on anterior and posterior surfaces. Pronotum slender, elongate (Fig. 1). Range: Brazil to Colombia (Fig. 13) ............................ O. maxi, new species, p. 789

3. (2) Size smaller, SBL 12–14 mm. Antennomeres 5–11 with depressions clearly marked. Labrum with anterior margin markedly convex. Femora red, black, or piceous. Range: Bolivia to Panama (Fig. 13) ............................ O. dentipes Olivier, p. 789

3' Size larger, SBL 16–18 mm. Antennomeres 5–11 with shallow depressions anteriorly and posteriorly. Labrum with anterior margin straight. Femora black or piceous, not red. Range: northern Argentina (Fig. 13) ............................ O. linearis Banninger, p. 789

4. (1') Antennomeres 5–10 each with group of more-or-less dense, fine punctures (sensilla basiconica) clearly evident on each side of mid-line, ventro-laterally (Figs. 6B, 8B)... (O. lemoulti group) ............................ 5

4' Antennomeres 5–10 without such clearly evident groups of punctures (present, but much smaller; cf. Fig. 9B)... (O. convexa group) ............................ 8

5. (4) Pronotum with lateral explanation elevated, narrowed toward middle, each delimited by more-or-less deep groove ............................ 6

5' Pronotum with lateral explanations flat, horizontal, about same width throughout, or only slightly narrowed medially, not delimited by sharply impressed grooves ............................ 7

6. (5) Pronotum transverse, slightly wider than long, anterior angles even with or slightly projected beyond central part of anterior margin; surface smooth, with scattered punctures. Antennomeres 5–10 ventro-laterally with group of punctures (sensilla basiconica) near middle (cf. Fig. 8B). Range: central cis-Andean South America, from Bolivia to Brazil (Fig. 14A) ............................ O. elevata Banninger, p. 792

6' Pronotum wider, anterior angles at same level as, or slightly behind, central part of anterior margin; surface transversely rugose, rugae radiated from mid-line, and densely punctate. Antennomeres 5–10 ventro-medially with group of sensilla basiconica toward apex (Fig. 6B). Known from southeastern Brazil and Ecuador, only ............................ O. ecuadorica Banninger, p. 792

7. (5') Antennomere 11 markedly widened (Fig. 8A), maximum width equal to length; distal band of sensilla basiconica about half width of article. Antennomeres and elytra very shiny. Pronotum with anterior margin sinuate, central portion slightly in advance of anterior angles; lateral margins markedly arcuate, but not sinuate anterior to posterior angles; posterior angles rectangular; disc markedly convex. Range: Bolivia to northern Brazil (Fig. 14A) ............................ O. martinezii Ogueta, p. 792

7' Antennomere 11 longer than wide (Fig. 7); distal band of sensilla basiconica normal, width much less than half surface area. Elytra with intervals densely punctate, surface not matt or rugose. Pronotum with anterior margin almost straight; disc slightly convex. Range: northern Argentina and Paraguay northward through Middle America to southern Arizona (Fig. 14A, B) ............................ O. lemoulti Banninger, p. 792
8. (4') Dorsal surfaces of mandibles with isolated punctures. Pronotum with lateral margins expanded, rounded, narrowed behind, with sides basally parallel; depressions deep at edges of elevated explanations. Elytron with intervals matt and rugose. Known only from northern Argentina and eastern Brazil (Fig. 15) .................... O. grossa Bänninger, p. 795

8' Mandibles with dorsal surfaces, except apices, longitudinally rugose, with scattered punctures between rugae (cf. Fig. 12A, B). Elytron with intervals glossy, densely punctate. Form more convex and narrow .................................................. 9

9. (8') Pronotum much wider than long, lateral margins quite flat. Range: northern Argentina to Venezuela (Fig. 15) .................... O. convexa Bänninger, p. 795

9' Pronotum slightly wider than long, lateral explanations slightly elevated; surface less rugose laterally. Known only from Amazonian Peru (Fig. 15) ....... O. manu, new species, p. 795

The Ozaena dentipes Species-group

**Type Material.** We have not seen type material of *Ozaena dentipes* Olivier, and do not know where it is located.

Type material of *Ozaena linearis* Bänninger, 1927 comprises three specimens. Two, in the Bänninger collection (ETHZ), are as follows. The LECTOTYPE (here designated) is a male, labeled: “République Argen. Chaco de Santiago Del Estero-Rio Salado”; “COLLECTION WAGNER” [orange paper]; “Ozaena linearis Bän, type”. The PARALECTOTYPE is a female, labeled same as the lectotype, except “Co-type”. A second PARALECTOTYPE, sex not determined, also from the Rio Salado, bears a “co-type” label, and is in the BMNH.

See below for data about type material of *Ozaena maxi*, new species.

**Recognition.** Adults of this species-group are recognized by means of the following combination of features: antennae (Figs. 3–5) with antennomeres 5–10 each with ventral basiconic sensilla in a single group, extended from near apex for at least half the length of the article (Figs. 3C, 4B, and 5B), pits of sensilla either opened widely (Fig. 3D), umbilicate in appearance, or narrower (Fig. 5C); antennomeres 5–10 each with or without basal depressions in anterior and posterior surface. Mandibles with dorsal surfaces sparsely punctate, almost smooth, with few short rugae (Fig. 10A, B); of average length and width (cf. Fig. 11A–D) or short, with terebrae broad and markedly curved (Fig. 10A–D); left mandible (Fig. 10A) with straight terebra and median retinacular tooth (mrt); right mandible with anterior portion of retinacular ridge not evident in dorsal aspect, concealed beneath terebral margin. Terminal palpomeres short, labial palpomere 3 length/width ca. 0.50. Pronotum (Fig. 1) with lateral grooves narrow, lateral margins narrow, not explanate.

**Included Species.** Three species are included in the *Ozaena dentipes* group: *O. maxi*, new species, described below; *O. linearis* Bänninger (Figs. 4A, B, and 13); and *O. dentipes* Olivier (Figs. 5A–C, 10A–D, and 13).

**Chorological Affinities.** The range of this group overlaps broadly those of the *O. lemoulti* and *O. convexa* species-groups (Fig. 13; cf. Figs. 14 and 15).

**Phylogenetic Relationships.** This group is postulated to be sister-group of the *O. lemoulti* + *O. convexa* groups. For details, see “Evolutionary Considerations” below.

**Material Examined.** In addition to the types, we have seen adults from the localities noted in the Appendix.

**Ozaena maxi, new species**  
(Figs. 1, 3A–D, and 13)


Derivation of the Specific Epithet. Latinized form of the given name of Max Bänninger, genitive case, in recognition of his contributions to knowledge of the Ozaenini.

Recognition. In addition to features noted in the key, adults of this species are distinguished from the other members of the O. dentipes group by relatively elongate mandibles.

Description. With character states of O. dentipes group and the following. Form slender (Fig. 1), similar to adults of Platycerozaena. SBL 13.5–14.3 mm, maximum width 3.8–4.4 mm.

Color. Body and legs piceous.

Microsculpture and Luster. Labrum opaque, with mesh pattern isodiametric to slightly transverse, sculpticells convex, surface thus beaded. Dorsal surface of head, pronotum, and elytra without microlines, shiny.

Macrosculpture and Punctation. Mandibles (dorsal surface and scrobes), dorsal surface of head and pronotum, moderately densely punctate, punctures separated from one another at least by their own diameters. Intervals of elytra each with single row of punctures; interneurs punctate. Supraantennal area of frons with few longitudinal rugulae, and few rugulae on dorsal surfaces of mandibles. Otherwise, surface smooth.

Head. Clypeus with anterior margin angularly but shallowly emarginate. Frontal impressions broad shallow basins. Eyes moderately prominent.

Mouthparts. Labrum moderately prominent, about rectangular. Mandibles of average length and form for Ozaena, but longer and more slender than in other members of the O. dentipes group.

Pronotum. As in Figure 1, subcordate with narrow lateral margins, rather slender, median length to maximum width—ca. 0.90. Anterior margin truncate, projected anteriad antero-lateral angles; antero-lateral and postero-lateral angles each ca. 90°; lateral margins narrowly beaded, bead each side widened posteriorly. Lateral grooves narrow, continuous posteriorly with broad, shallow postero-lateral impressions; median longitudinal impression shallow; anterior transverse impression indistinctly indicated. Disc moderately convex, lateral slopes broad and gradual.


Way of Life. Specimens have been collected in October, November, January, and July. Most localities are in tropical lowlands, but one specimen was taken at an altitude of 500 m.

Geographical Distribution (Fig. 13). This species is known from the northern half of cis-Andean South America, from the state of Mato Grosso, Brazil, eastward and northward to Cayenne.

Chorological Affinities. The range of O. maxi overlaps broadly that of O. dentipes.

Phylogenetic Relationships. This species is postulated to be sister of the species pair O. dentipes + linearis. See “Evolutionary Considerations” below, for details.
FIG. 13. South America and Lower Central America, illustrating geographical positions of collecting records for species of the *Ozaena dentipes* group.

The *Ozaena lemouli* Species-group

**Type Material.** Type material of *Ozaena lemouli* Bänniger, 1932, is in the Bänniger collection [ETHZ]. The HOLOTYPE is a male, labeled: “GUYANE FRANCSE St. Jean du Maroni Collection LeMoult”; “Ozaena lemouli Bänn”. The specimen is not labeled as type, but it fits the statements in the original description (Bänniger 1932: 185).
The HOLOTYPE of *Ozaena ecuadorica* Bänninger, 1949 is a female in the Bänninger collection, labeled: “Dr. Horn 3/6 [illegible word, possibly name of type locality] Ecuador” [written in pencil]; “Coll. Roeschke”; “[symbol for female]”; “Holo-type Ozaena ecuadorica Bänn 7.4.1941”.

Type material of *Ozaena elevata* Bänninger, 1956 is in the Bänninger collection, and in the Museum of Comparative Zoology, as follows. LECTOTYPE male (here designated), labeled: “Hansa XI Maller’; “Hansa Humboldt/ S. Cat. Brazil/ A. Maller”; [male genitalia, glued to point]; “MCZ Type 28729” [red paper]; “Ozaena elevata m. 1951 Type det. Bänninger” (MCZC). PARALECTOTYPES (MCZC), male and two specimens sex undetermined, labeled similarly to lectotype, except “cotype” on the determination label. PARALECTOTYPES (Bänninger collection, ETHZ), two males, labeled similarly to the lectotype, except “Cotype” on the determination labels. One specimen bears also the label “Ozaena lemoulti m. Bänninger det. V.1931”.

Type material of *Ozaena halfieri* Ogueta, 1965 was not seen. According to Ogueta (1965a: 87), the holotype is in his collection.

Type material of *Ozaena martinezi* Ogueta, 1965 was not seen. The HOLOTYPE was reported by Ogueta (1965a: 83) to have been deposited in his collection, and a PARATYPE in MNHP. Both specimens are from localities in Bolivia, plotted in Figure 14A.


**Recognition.** Adults of the *O. lemoulti* group are distinguished by the following combination of features. Antennae with ventral basiconic sensilla of antennomeres 5–10 in two groups (Figs. 6B and 8B) each side of mid-ventral line, either near middle of articles, or near apical margin; sensillar pits widely open (Fig. 6C); antennomeres 5–10 without depressions basally on anterior and posterior surfaces; antennomere 11 either not wider than antennomere 10 (Fig. 6A), or wider—slightly (Fig. 7), or markedly (Fig. 8A) so. Mandibles (Fig. 11A–D) with terebrae long and slender, dorsal surfaces moderately densely punctate and sub-rugose; left mandible (Fig. 11A) with preapical sinuation, retinaculum without median tooth; right mandible in dorsal aspect (Fig. 11B) with anterior part of retinacular ridge not evident, concealed beneath terebral margin. Palpomeres moderately long, labial palpomere 3 length/width ca. 0.6. Pronotum with lateral grooves relatively wide, lateral margins explanate, flat or more-or-less elevated.

**Included Species.** This group includes four species: *O. ecuadorica* Bänninger (Figs. 6A–C and 14A), *O. lemoulti* Bänninger (Figs. 11A–D, 14A–B, 16A–B, 17A–D, 18–21, 22A, B, and 23A, B), *O. elevata* Bänninger (Figs. 7 and 14A), and *O. martinezi* Ogueta (Figs. 8A, B, and 14A). The latter three species differ so slightly from one another that they may be conspecific—either geographical races or partially sympatric morphs.

**Geographical Distribution** (Fig. 14A, B). The range of this group extends through South America from northern Argentina and central Brazil northward through Middle America to southern Arizona, in southwestern United States. The middle part of the Amazon Basin seems not to be occupied by this group.

**Chorological Affinities.** See this topic for the *O. dentipes* group.

**Phylogenetic Relationships.** This taxon is postulated to be the sister-group of the *O. convexa* species-group. For details, see “Evolutionary Considerations,” below.

**Material Examined.** See the Appendix for a list of localities in which adults of *O. ecuadorica*, *O. lemoulti*, *O. elevata*, and *O. martinezi* have been collected.
FIG. 14. Geographical positions of collecting records for species of the *Ozaena lemoulti* group: A, South America and Lower Central America; B (next page), Middle and southern North America.

**The *Ozaena convexa* Species-group**

**Type Material.** The HOLOTYPE of *Ozaena grossa* Bänninger, 1927 is a female in the Bänninger collection (ETHZ), labeled: "Tacaagle/ Argentinien"; "Type *Ozaena grossa* Bglnn. 4.1926".

Type material of *Ozaena convexa* Bänninger in the Bänninger collection (ETHZ) is as follows: LECTOTYPE male, labeled: "Corumba MATO GROSSO"; "[point with male genitalia]"; "labrum biilb" [red ink]; "Type [male symbol] Ozaena convexa Bänn. 4.1926"; "LECTOTYPE [male symbol] Ozaena convexa by Erwin '74"; designated by

Data about type material of Ozaena manu, new species, are provided below.

**Recognition.** Adults of this species-group are distinguished by the following combination of features. Antennae with ventral sensilla of antennomeres 5–10 in two groups, one each side of mid-ventral line (Fig. 9B), pits small, basiconic sensilla short (Fig. 9C); antennomeres 5–10 without basal depressions in anterior and posterior surfaces; antennomere 11 (Fig. 9A) asymmetric, with apical margin subtruncate. Mandibles (Fig. 12A–D) with terebrae moderately long and slender, dorsal surfaces (Fig. 12A, B) moderately densely punctate-rugose to very rugose; left mandible (Fig. 12A) with terebral margin markedly simuate (ts) preapically, without median retinacular tooth; right mandible (Fig. 12B) with anterior part of retinacular ridge (arr) evident in dorsal aspect, projected beyond plane of terebral margin. Terminal palpomeres long, labial palpomere 3 length/width ca. 0.7. Pronotum (Fig. 2) with lateral margins explanate, flange-like (plf) flat or more-or-less elevated.

**Included Species.** This group includes three species: *O. grossa* Bänninger (Fig. 15); *O. manu*, new species (details below); and *O. convexa* Bänninger (Figs. 9, 12A–D, and 15). Erwin and Adis (1982: 360, fig. 19.3) provide an excellent illustration of the habitus of adults of *O. convexa*.

**Geographical Distribution** (Fig. 15). Confined to cis-Andean South America, the range of this group extends from northern Argentina northward to Venezuela. The main part of the Amazon Basin is not occupied by this group.

**Chorological Affinities.** See this topic for the *O. lemoulti* species-group.

**Material Examined.** See the Appendix for a list of localities in which adults of *O. grossa* and *O. convexa* have been collected.

**Ozaena manu, new species** (Figs. 2 and 15)


**Derivation of the Specific Epithet.** A noun in apposition, based on the name of the area in which the holotype was collected.

**Recognition.** In addition to the features noted in the key, the single known specimen of this species is the smallest member of the *O. convexa* group. Possibly relatively small body size is a specific character of *O. manu*.

**Description.** With character states of the *O. convexa* group and form slender, as in Figure 2. SBL 12.5 mm, maximum width 3.7 mm.

**Color.** Dark piceous, almost black, except frontal impressions of head, clypeus, labrum, and bases of mandibles rufo-piceous.

**Microsculpture and luster.** Labrum with mesh pattern predominantly isodiametric, sculpticcels slightly convex, surface opaque. Body surface with rather soft shine generally. Clypeus with surface nearly smooth, faint traces of microlines and meshes evident in spots. Frons and most of vertex with microlines indistinct, mesh pattern not evident; posterior part of vertex with mesh pattern isodiametric. Pronotum with mesh pattern obscure, evi-
dently transverse, but microlines evanescent. Elytra with mesh pattern isodiametric in interneurs, intervals smooth, except in apical fifth, mesh pattern obscure, isodiametric.

**Macrosculpture and punctuation.** Surface generally rugulose. Mandibles with dorsal surfaces in basal four-fifths moderately densely, obliquely and longitudinally, crenulate. Few punctures in crenulations; scrobes rather sparsely punctate and longitudinally crenulate. Clypeus and dorsal surface of head and pronotum generally finely but irregularly
punctate. Frons and vertex longitudinally crenulate laterally; pronotum transversely crenulate, lateral margins sparsely so. Elytra with intervals sparsely, irregularly punctate, transversely crenulate adjacent to interneurs, but tops of intervals relatively smooth. Interneurs moderately coarsely punctate throughout length.

**Head.** Clypeus with anterior margin broadly, slightly angularly emarginate. Frontal impressions each short, shallow, narrow basins. Eyes moderately prominent.

**Mouthparts.** Labrum with anterior margin broadly emarginate.

**Pronotum.** As in Figure 2, transverse, median length/maximum width 0.81. Anterior margin truncate, anterior angles produced slightly anteriad anterior margin. Posterior margin bisinuate, median area distinctly posteriad lateral areas. Antero-lateral angles acute, postero-lateral angles rounded and slightly obtuse. Lateral margins markedly sinuate posteriorly, sides markedly broadly reflexed anteriorly and posteriorly, very narrowly so medially (Fig. 2, plf). Lateral grooves moderately broad, continuous posteriorly with broad, rather linear postero-lateral impressions. Median longitudinal impression obscure; anterior transverse impression broad and shallow. Surface slightly convex, disc flattened medially, laterally gradually sloped, more markedly so posteriorly.


**Way of Life.** The holotype was collected at UV light, suggesting adults are nocturnal. The species probably resides in wet tropical forest.

**Geographical Distribution** (Fig. 15). Known only from the type locality, in Amazonian Peru.

**Chorological Affinities.** The locality for this species is isolated from the ranges of the other species of the *O. convexa* group.

**Phylogenetic Relationships.** This species seems to be the sister-species of *O. convexa*. For details, see "Evolutionary Considerations", below.

## EVOLUTIONARY CONSIDERATIONS

### Reconstructed Phylogeny

**Methods.** Out-group comparison was used for character-state polarization as explained by Ross (1974: 151–156), Wiley (1981: 139–146), Watrous and Wheeler (1981), and Maddison et al. (1984). Characters were not formally weighted because such was not required to make seemingly reasonable inferences about relationships. Lacking a formally reconstructed phylogeny of the Ozaenini, we used the observations of Ball and McCleve (1990) for postulating an out-group for the *Ozaena* genus-group.

**Taxa Studied.** In addition to the species of *Ozaena*, we examined in detail adults of the following: *Platycerozaena* (*P. panamensis* Bänninger, *P. brevicornis* [Bates], and *P. bordoni* Ogueta); *Pachytelea* (*P. [Tropopsis] marginicollis* [Solier], *P. [Goniotropis] parca* LeConte, *P. [G.] kuntzeni* Bänninger, *P. [sensu stricto] gyllenhalii* [Dejean], *P. mexicanus* Chaudoir, and *P. enischus* Ball and McCleve); *Physea* (*P. latipes* Schaum and *P. hirta* LeConte); *Mystropomus subcordatus* Chaudoir; and *Metrius contractus* Eschscholtz. We examined more cursorily material of most Old World genera of Ozaenini: *Anentmetus pluto* Andrewes; *Itamus castaneus* Castelnau; *Pseudozaena orientalis* (Chaudoir); *Afrozaena lutea* (Hope); *Dhanya bioculata* Andrewes; *Eustra maatanga* Andrewes; and *Microzaena angustior* Alluaud.

**Out-group.** The out-group for the *Ozaena* genus-group was *Pachytelea* (sensu lato) Perty, though we do not believe that the latter, as such, is sister-group to the former taxon. To us, *Pachytelea* represents a structurally less highly derived taxon than the *Ozaena* genus-group.
For *Ozaena*, *Platycerozaena* is the postulated sister-group. For most characters, the states in *Platycerozaena* are postulated as more derived than the states in *Ozaena*. Therefore, this sister-group relationship is of little value in reconstructing phylogenetic relationships of the species of the latter genus.

Together, *Ozaena* and *Platycerozaena* comprise the *Ozaena* genus-group (Ball and McCleve 1990), an assemblage distinguished from other groups of Ozaenini by a combination of apotypic states of characters 01–11 (see below for details, and Fig. 32).

**Characters**. Characters used in the phylogenetic analysis are those that were employed in visual recognition of the taxa treated, including features of integumentary sculpture, vestiture, chaetotaxy, antennae, mouthparts, pronotal form, and details of the female stylomers. We did not include features of the male genitalia because preliminary examination indicated little differentiation in these sclerites.

The 35 characters used are named below, numbered in the sequence of appearance in the reconstructed phylogeny (Fig. 33). Distribution of character states among the taxa is indicated in Figure 32.

**Character 01**, vestiture of dorsal surface. Two states: plesiotypic, setae of head, pronotum, and elytra trichoid, slender; apotypic, setae flattened, ribbed, each with broad, scalloped apex (Fig. 16A, B). The apotypic state, within the Ozaenini, is confined to the *Ozaena* genus-group.

**Character 02**, relative length of lateral lobes of mentum (Figs. 20 and 28). Two states: plesiotypic, shorter; apotypic, longer. See also characters 07 and 19.

**Character 03**, antennomere 11, form of apex and apical ridge. Three states: plesiotypic, tapered gradually, apex rounded; apotypic, stage 1, anterior and posterior surfaces sloped abruptly in apical third, to form a wedge-like apex of a distinct straight ridge (Fig. 17C); apotypic, stage 2, as for stage 1, but apical ridge sinuate (Fig. 24C).

**Character 04**, microsculpture of dorsal surface. Two states: plesiotypic, mesh pattern uniformly isodiametric; apotypic, mesh pattern clearly developed on labrum, only, otherwise integument nearly smooth, either without microlines, or these more-or-less isolated, not part of extensive networks.

**Character 05**, trichoid setae of antennomeres. Two states: plesiotypic, relatively numerous; apotypic, relatively few, number reduced.

**Character 06**, fixed trichoid setae. These include the more-or-less standard setae of carabid adults: clypeal, supraorbital, lateral pronotal, and elytral (parascutellar, and those of the discal intervals). Two states: plesiotypic, present; apotypic, absent.

**Character 07**, labium, mentum: epilobes. Two states: plesiotypic, broad medially, extended to apex of lateral lobe; apotypic, slender, terminated before apex of lateral lobe (Figs. 20 and 28, el).

**Character 08**, fore tibia, antennal cleaner. Two states: plesiotypic, tibia deeply channeled or grooved, with moderate medial expansion and long, sinuous clip setae; apotypic, groove shallow, median expansion slight (Figs. 22A, B, and 30A, B), and clip setae absent.

**Character 09**, male fore tarsus, ventral adhesive vestiture. Two states: plesiotypic, present; apotypic, absent. In adults of *Pachyteles*, both states are found. However, in most other ozaenine genera, and in *Metrius*, the out-group for the Ozaenini, male tarsomeres have such vestiture. Accordingly, that condition is probably plesiotypic for the Tribe.

**Character 10**, ovipositor, stylomers, size and setation. Two states: plesiotypic, relatively longer, with relatively short trichoid setae; apotypic, relatively shorter, with relatively long trichoid setae (Figs. 23A, B, and 31A, B). Within ozaenines generally, and within *Pachyteles* in particular, the stylomers exhibit appreciable variation in form and
size. However, they are relatively long and with few setae in the most primitive lineage of Ozaenini (Mystropomus), and in the out-group for the Ozaenini (Metrius).

**Character 11, ovipositor, stylomeres: size of nematiform setae.** Two states: plesiotypic, 2, relatively long, ca. half length of stylomere; apotypic, 1, short, not longer than trichoid setae of stylomere (Fig. 23A, B, ns). Most ozaenine females, including those of *Pachytele*, exhibit 2 relatively long nematiform setae on each stylomere. In the *Ozaena* genus-group, these setae are present, single and short (*Ozaena*) or absent (*Platyerozaena*; cf. character 23). We postulate step-wise reduction of the nematiform setae was as follows: shortening, loss of 1, then total loss. It is unclear whether the first stage in the sequence was shortening of both setae, or 1 seta was lost.

**Character 12, labrum, length.** Two states: plesiotypic, relatively short, sclerite distinctly transverse (Fig. 18); apotypic, relatively longer, quadrate (Fig. 25).

**Character 13, labrum, marginal setae.** Two states: plesiotypic, present (Fig. 18); apotypic, absent (Fig. 25).

**Character 14, labium, mentum, size of tooth.** Two states: plesiotypic, larger (Fig. 20); apotypic, smaller (Fig. 28). The tooth of *Ozaena* (Fig. 20), though regarded as plesiotypic in the *Ozaena* genus-group, is relatively small compared with tooth size of *Pachytele* and other ozaenine genera.

**Character 15, mandibles, size of terebra.** Two states: plesiotypic, relatively narrow (Figs. 11A, t, and 12A); apotypic, relatively broad (Figs. 10A, t, and 26A).

**Character 16, pronotum, lateral explanations.** The areas laterad the lateral grooves are referred to as explanations or lateral flanges (plf, Fig. 2). Five states: plesiotypic, moderately broad (Fig. 2); apotypic, narrow, reduced to thickened (beaded) margin (A –); apotypic, broad, flattened (B); apotypic, broad, slightly flattened (C); apotypic, markedly broadened, flat and rugose (C’). The complex postulated transformation series involves reduction of the lateral explanations, and their independent flattening and broadening.

**Character 17, antennomeres 5–10, ventral sensilla basiconica.** Six states: plesiotypic, each sensillum in small pit on ventral and ventro-lateral surfaces; apotypic, small, grouped in broad depressions each side of ventral keel (A; Fig. 24A); apotypic, pits large, but continuously distributed ventrally (B; Fig. 3B); apotypic, pits small, but in two groups, medially, each side of mid-ventral line (C; Fig. 9B); apotypic, pits large, in two groups medially, each side mid-ventral line (C’; Fig. 8B); and pits large, in two groups apically, each side of mid-ventral line (C”, Fig. 6B).

**Character 18, labium, palpomere 3, proportions.** Three states: plesiotypic, relatively long (width/length ca. 0.5); apotypic, stage 1, intermediate (width/length ca. 0.6); apotypic, stage 2, relatively short (width/length ca. 0.7).

**Character 19, labium, mentum: form of apices of lateral lobes.** Three states: plesiotypic, moderately broad, rounded; apotypic, acute (A; Fig. 28, ll); apotypic, very broadly rounded (B; Fig. 22, ll).

**Character 20, fore femur, form and armature.** Three states: plesiotypic, terete, more-or-less of same diameter throughout length; apotypic, with broad ventral protuberance ventrally (A; Fig. 29); apotypic, with narrow setose dentiform protuberance basally, antero-ventrally (B; Fig. 21).

**Character 21, mandibles: posterior retinacular tooth, size.** Three states: plesiotypic, of moderate size; apotypic, markedly reduced (A –; Fig. 26A, B, prt); apotypic, slightly enlarged (B; Fig. 11A, B).

**Character 22, antennomeres 5–10, length and proportions.** Three states: plesiotypic, quadrangular, slightly elongate; apotypic, shortened, flattened, and widened, antenna extended posteriorly only to base of pronotum (A –; Fig. 24A); apotypic, widened, lengthened, moniliform, antenna extended posteriorly of basal margin of pronotum (B; Figs. 1 and 2).
Character 23, ovipositor, stylomeres: number of nematiform setae. Three states: plesiotypic, two setae; apotypic stage 1 (−), single seta; apotypic stage 2 (−), setae absent. See also character 11, above.

Character 24, antennomere 11, distribution of sensilla basiconica (cf. Fig. 17D). Two states: plesiotypic, dorsally, ventrally, and apically (Fig. 24B); apotypic, in apical band (Fig. 17B).

Character 25, maxilla, lacinia: tooth form. Two states: plesiotypic, long and slender (Fig. 27); apotypic, short and broad, chisel-like (Fig. 19).

Character 26, left mandible, retinaculum. Two states: plesiotypic, without a median tooth (Figs. 11A and 12A); apotypic, with a median tooth (Fig. 10A, mrt).

Character 27, pronotum, proportions. Two states: plesiotypic, subcordate, transverse, lateral margins markedly rounded anteriorly (cf. Fig. 2); apotypic, more elongate, lateral margins subsinuate, sides nearly straight (Fig. 1).

Character 28, mandibles, proportions. Two states: plesiotypic, longer, straighter, and narrower (Figs. 11A–D and 12A–D); apotypic, shorter, broader, markedly curved (Fig. 10A–D).

Character 29, antennomeres 5–11, anterior and posterior surfaces basally. Three states: plesiotypic, without depressions; apotypic stage 1, depressions shallow; apotypic stage 2, depressions deeper (Fig. 5B, d).

Character 30, labrum, form of anterior margin. Three states: plesiotypic, straight, or slightly concave (Figs. 18 and 25); apotypic stage 1, slightly convex; apotypic stage 2, markedly convex.

Character 31, femora, color. Two states: plesiotypic, concolorous, piceous to black; apotypic, bicolored, black and bright rufous.

Character 32, antennomere 11, proportions. Three states: plesiotypic, slender, distinctly longer than wide (Fig. 6A); apotypic stage 1, slightly widened (Fig. 7); apotypic stage 2, markedly widened, length and width subequal (Fig. 9A).

Character 33, antennomere 11, form. Two states: plesiotypic, more-or-less symmetrical, with apex broadly rounded (Figs. 4A, 5A, 6A, 7, 8A, 17A, B, and 24A, B); apotypic, asymmetrical, with apex obliquely subtruncate (Fig. 9A).

Character 34, mandibles, occlusal surfaces. Two states: plesiotypic, left with tererebral margin straight (Fig. 11A), right with anterior part of retinacular ridge (Fig. 11B, arr) overhung by tererebral margin; apotypic, left mandible with tererebral margin subapically (Fig. 12A, ts), right with anterior part of retinacular ridge extended mesally of tererebral margin (Fig. 12B, arr).

Character 35, mandibles, sculpture of dorsal surface. Two states: plesiotypic, surface punctate, otherwise relatively smooth; apotypic, surface markedly longitudinally crenulate.

Monophyly. Figure 33 shows that monophyly for the Ozaena genus-group is established by synapotypy of characters 01–11. Eight of these features involve losses or reductions of structures postulated to have been present in the putative out-group.

At branching point A (Fig. 33), monophyly of Platycerozaena is established by the apotypic states of 13 characters, of which seven involve losses or reductions. Similarly, monophyly of Ozaena is established by apotypic states of eight characters, of which only two involve losses.

At branching point B, monophyly of the O. dentipes group is established by apotypy of three characters, of which two involve losses. Also, at branching point B, monophyly of the O. lemoulti and convexa groups is established by apotypy of one character only. This grouping is not accorded taxonomic recognition.
Figs. 16–23. Structural features of *Ozaena lemoulti* Blüning: 16, left elytron, dorsal aspect (A, setae; B, single sensillum basiconicum); 17, left antennomeres (A, 9–11, anterior aspect; B–D, antennomere 11—B, anterior aspect; C, apical aspect; D, sensilla basiconica, anterior aspect); 18, labrum, dorsal aspect; 19, left maxilla, lacinia, ventral aspect; 20, labium, mentum, ventral aspect; 21, left fore femur, anterior aspect; 22, left fore tibia (A, anterior aspect; B, inner aspect); 23, ovipositor, left stylomere (A, lateral aspect; B, apical aspect). ar, apical ridge of antenna; dfp, dentiform process of fore femur; el, epilobe of mentum; lf, lateral lobe of mentum; mex, median expansion of fore tibia; ns, nematiform seta of ovipositor; styomere 2; sb, sensilla basiconica; st, sensilla trichodea; tsb, setal band of fore tibia. Scale bars = 200 μm for Figs. 16A, 17A–C, and 18–23A; 20 μm for Figs. 16B, 17D, and 23B.
Figs. 24–31. Structural features of *Platycerusona* species. 24–30, features of *P. brevicornis* (Bates): 24, left antennomeres (A, antennomeres 7–11, anterior aspect; B, antennomere 11, anterior aspect; C, same, apical aspect); 25, labrum, dorsal aspect; 26, mandibles (A and C, left, dorsal and ventral aspects, respectively; B and D, dorsal and ventral aspects, respectively); 27, left maxilla, lacinia, galea, and palpus, ventral aspect; 28, labium, mentum, ventral aspect; 29, left fore femur, anterior aspect; 30, left fore tibia (A, anterior aspect; B, inner aspect). 31, ovipositor, left stylomere, of *P. panamensis* (Bates) (A, ventral aspect; B, apical aspect). ar, apical ridge of antenna; art, mandible, anterior retinacular tooth; el, epilobe of mentum; ll, lateral lobe of mentum; mex, fore tibia, median expansion; prt, mandible, posterior retinacular tooth; tm, mandible, terebral margin; tsb, fore tibia, setal band; tr, mandible, terebral tooth. Scale bars = 200 μm for Figs. 24A–31A; 20 μm for Fig. 31B.
At branching point E, monophyly of the *O. lemoulti* group is established by two apotypies, of which one involves a loss. Monophyly of the *O. convexa* group is also established by two apotypies.

**Temporal Aspects.** Figure 33 shows that, at branching point A, 21 apotypic character states (and/or stages) evolve; at B, four states; at C and E, 10 states; at F, two states; at G and I, three states; and at D, H, and J, five states. Inspection of Figure 33 shows that most of the evolutionary change occurred before evolution of the ancestor of the genus *Ozaena*.

**Losses and Gains.** Table 1 classifies character states as comprising "loss" (or reduction), "gain", or "shift". These are arbitrary classes, based on the authors' perceptions. For example, setae, as such, may be lost, but such a circumstance may be a crucial adaptation to gain entry to a new mode of life for a taxon. So, from the adaptational perspective, the loss becomes a gain. The term "shift" categorizes changes that seem to be neither gains nor losses but rather changes in position or organization of features: for example, arrangement of the basiconic sensilla of the antennae.

Table 1 shows that these three groups contain about an equal number of apotypic character states and stages. Thus, for *Ozaena*, loss has not been a dominant aspect of character evolution.

**Convergence.** Of 53 apotypic character states and stages, only three (15, 16<sup>r</sup>−, and 18<sup>r</sup>−) are postulated to have arisen more than once: each in only two lineages. These features involve changes in the following: mandibles (15), lateral margins of the pronotum (16), and labial palpomeres (18).

The significance of this convergence is not apparent. What is apparent, however, is the uncommonness of convergence. The conclusion that we draw is that the common pattern of character evolution in the *Ozaena* genus-group is one of divergence.

**Nature of Character Evolution.** Of 35 characters used in the phylogenetic analysis, 23 exhibit one apotypic state only, and four exhibit two apotypic states only. Such are regarded

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### Table 1. Apotypic character states of *Platycerozaena* Bänninger and species of *Ozaena*, classified as loss (or reduction), gain, or shift

<table>
<thead>
<tr>
<th>Loss or reduction</th>
<th>Gain</th>
<th>Shift</th>
</tr>
</thead>
<tbody>
<tr>
<td>04&lt;sup&gt;−&lt;/sup&gt;*</td>
<td>01</td>
<td>03</td>
</tr>
<tr>
<td>05&lt;sup&gt;−&lt;/sup&gt;</td>
<td>02</td>
<td>16&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>06&lt;sup&gt;−&lt;/sup&gt;</td>
<td>12</td>
<td>16&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>07&lt;sup&gt;−&lt;/sup&gt;</td>
<td>15</td>
<td>16&lt;sup&gt;c′&lt;/sup&gt;</td>
</tr>
<tr>
<td>08&lt;sup&gt;−&lt;/sup&gt;</td>
<td>20&lt;sup&gt;a&lt;/sup&gt;</td>
<td>17&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>09&lt;sup&gt;−&lt;/sup&gt;</td>
<td>20&lt;sup&gt;a&lt;/sup&gt;</td>
<td>17&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>10&lt;sup&gt;−&lt;/sup&gt;</td>
<td>21&lt;sup&gt;a&lt;/sup&gt;</td>
<td>17&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>11&lt;sup&gt;−&lt;/sup&gt;</td>
<td>22&lt;sup&gt;b&lt;/sup&gt;</td>
<td>17&lt;sup&gt;c′&lt;/sup&gt;</td>
</tr>
<tr>
<td>13&lt;sup&gt;−&lt;/sup&gt;</td>
<td>26</td>
<td>17&lt;sup&gt;c″&lt;/sup&gt;</td>
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<tr>
<td>14&lt;sup&gt;−&lt;/sup&gt;</td>
<td>29&lt;sup&gt;i&lt;/sup&gt;</td>
<td>19&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>16&lt;sup&gt;−&lt;/sup&gt;</td>
<td>29&lt;sup&gt;i&lt;/sup&gt;</td>
<td>19&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>18&lt;sup&gt;−&lt;/sup&gt;</td>
<td>30&lt;sup&gt;i&lt;/sup&gt;</td>
<td>25</td>
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<td>18&lt;sup&gt;−&lt;/sup&gt;</td>
<td>30&lt;sup&gt;i&lt;/sup&gt;</td>
<td>27</td>
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<tr>
<td>21&lt;sup&gt;−&lt;/sup&gt;</td>
<td>32&lt;sup&gt;i&lt;/sup&gt;</td>
<td>28</td>
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<tr>
<td>22&lt;sup&gt;−&lt;/sup&gt;</td>
<td>32&lt;sup&gt;i&lt;/sup&gt;</td>
<td>31</td>
</tr>
<tr>
<td>23&lt;sup&gt;−&lt;/sup&gt;</td>
<td>35</td>
<td>33</td>
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<tr>
<td>23&lt;sup&gt;−&lt;/sup&gt;</td>
<td>35</td>
<td>34</td>
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<tr>
<td>24&lt;sup&gt;−&lt;/sup&gt;</td>
<td>35</td>
<td>34</td>
</tr>
<tr>
<td><strong>Total:</strong></td>
<td>18</td>
<td>16</td>
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</table>

*Numbers designate apotypic character states (see text, and Fig. 32).
as relatively simple transformations, because they appeared once and were stabilized—
though each may be carried for an extended period in the lineage in which it arose.

More complex changes suggesting sustained selection for change are exhibited by
eight characters (03, 16, 17, 18, 23, 29, 30, and 32), for which at least one of the states
exhibits at least two stages. Only one of these, however (17'), exhibits more than two
stages. We conclude that the predominant mode of character evolution in the Ozaena
genus-group is one of simplicity.

Evolution within Functional Units. We recognize five functional units that give evidence
of change in development of the taxa of the Ozaena genus-group: sense organs; antennae;
mouthparts; legs; and ovipositor. In the following discussion, evolution of sense organs
is described separately, and is alluded to as parts of the organs on which each group is
located. Although we have been able to identify patterns of change, we are not able to
offer interpretations of such in functional terms, in part because of our own limitations,
but mainly because so little is known about ozaenines in general and Ozaena, in particular,
as living organisms.

Characters 05, 06, 11, 13, 17, 23, and 24 are the sense organ features. Loss is the
dominant feature in evolution of trichoid setae of the antennae (05), fixed body setae (06),
nematiform setae of the ovipositor (11 and 23), and labral setae (13). These are tactile
organs, and their loss seems indicative of selection for life in environments where the need
for sense of touch is somehow diminished. Collectively, these changes have occurred with
evolution of the ancestral stock of the Ozaena genus-group, or at branching point A (Fig. 33), i.e. early in the phylogeny of the ancestral stocks of each genus (Table 2). From
this, we surmise that reduction of the tactile sense was an important component of entering
and exploiting the adaptive zone that this group occupied, and that has channeled its sub-
sequent evolution.

Characters 17 and 24 are the sensilla basiconica of the antennae, and their grouping.
Evolutionary change includes concentration of these sensilla in clearly defined patches,
either at the apex of antennomere 11 (24), or ventro-laterally, on antennomeres 5–10 (17).
Character 17 includes as well enlargement of the pits that bear the sensilla. The apotypic
state of character 24 and state 17A evolved at branching point A, and characterize respec-
tively the ancestral stocks of Ozaena and Platycerozaena. Thus, these features were part
of the structural complex probably basic to entry into the adaptive zones of each of these
genera.
Change in character state 17C has been complex, and was continued through branching points B, E, and F. This suggests sustained mutation and selection, and seems indicative of the special importance of the antennae in continued adaptation of portions of the Ozaena stock.

Evolution of antennal structure involves the sense organs described above, and form (characters 22, 32, and 33) and proportions of the antennomeres. Apotypic states of character 22 evolved at branching point A, and are parts of the major adaptive complex of Platycerozaena and Ozaena, respectively. The apotypic states of characters 32 and 33 evolved later in Ozaena, at branching points F and E respectively, each being involved in the adaptive zones of monophyletic assemblages, with character 32 being modified through a second stage of enlargement, at branching point H.

The apotypic state of character 29 involves development of basal depressions in antennomers 5–10, and was sustained through two branching points (C and D), in the O. dentipes group.

In total, antennal modifications occur at nine of the 10 branching points illustrated in Figure 22, plus the ancestral stock of the Ozaena genus-group. From this observation, we conclude that antennal modifications have been an important ingredient in entering into and subsequently exploiting the adaptive zone of the Ozaena genus-group.

Excluding the sense organs, a total of 14 characters are involved in evolution of the mouthparts, as follows: labrum, two (12 and 30); mandibles, six (15, 21, 26, 28, 34, and 35); maxillae, one (25); and labium, five (02, 07, 14, 18, and 19). Collectively, these features exhibit change at six of the nine branching points (A–E, and I) in Figure 33, and are part of the adaptive complex of the Ozaena genus-group. Most of the changes occur at branching point A, indicating the importance of mouthparts in exploitation of the adaptive zones of Platycerozaena and Ozaena, respectively. However, changes in features at five additional branching points are evidence of substantial mutation and selection during continued speciation in Ozaena (Table 3).

Reduction and loss are components of evolution of mouthparts, involving five characters. In the ancestral stock of Platycerozaena + Ozaena, the mental epilobes (07) were reduced. In the Platycerozaena lineage, labral setae (13) were lost, the mandibular posterior retinacular tooth (21) was reduced, the mental tooth of the labium (14) was reduced, and labial palpomere 3 (19) was shortened.

Character gains or enhancements are exhibited in five characters. The enhancement exhibited by the ancestral stock of Platycerozaena + Ozaena is lengthening of the mental lobes of the labium (02). Other enhancements include the following: lengthening of the labrum (12 – Platycerozaena stock); terebral areas of the mandibles enlarged (15 – Platycerozaena stock, and independently, in the O. dentipes group); development on the mandibles of an enlarged posterior retinacular tooth (21 – ancestral stock of Ozaena); and development of a median retinacular tooth (26 – O. dentipes group).

Five features changed, but not in a way that is clearly classifiable as a gain or loss: labrum, form (character 30 – O. dentipes group); mandibular proportions (28 – O. dentipes group); details of the occlusal surfaces of the mandibles (34 – O. convexa group stock); mandibular sculpture (35 – O. convexa group); and form of the maxillary lacinia (25 – ancestral stock of Ozaena).

Evolutionary changes in the legs involved the following: grooming function (probably loss or reduction) of the fore tibia (08); adhesive function of the fore tarsomeres (09); and development of a projection at the base of the fore femur (20). Apotypic states of characters 08 and 09 arose in the ancestral stock of the Ozaena genus-group, and different apotypic states of character 20 arose independently in the ancestral stock of Platycerozaena and Ozaena.
Fig. 32. Phylogenetic designation and distribution of character states of *Platyceerozaena* Bänninger and of the species of *Ozaena* Olivier.
LEGEND

Plesiotypic

2-Stage Transformation Series, unidirectional

- Apotypic- gain/modification

- Apotypic- loss

3-Stage Transformation Series, unidirectional

Stage 1, apotypic, gain/modification

Stage 2, apotypic, gain/modification

Stage 1, apotypic loss

Stage 2, apotypic loss

2- or 3-Stage Transformation Series, bi or tri-directional

Stage 1, apotypic, gain/modification

Stage 2, apotypic, gain/modification

Stage 3, apotypic, gain/modification

Stage 1, apotypic, loss
Table 3. Relative times of modifications in structure of mouthparts of adult *Platycerozaena* Banninger and species of *Ozaena* Olivier, based on their reconstructed phylogeny (Fig. 33)

<table>
<thead>
<tr>
<th>Character state no.</th>
<th>Earlier Ancest. stock</th>
<th>Branching points</th>
<th>Later</th>
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<tbody>
<tr>
<td>35</td>
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<td>07</td>
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<td>Total:</td>
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<td>8</td>
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Evolution of the ovipositor involved changes in two characters. In the ancestral stock of the *Ozaena* genus-group, the stylomeres were reduced, but became markedly setose (10); and the nematiform setae (09) were reduced. Such modifications of the more primitive states of the ovipositor suggest that a change in mode of oviposition was an important component of entry into the adaptive zone of the *Ozaena* genus-group.

**Zoogeographical Aspects**

In the following discussion, we use these terms for the regions between the southern border of the United States and the northern border of the South American continent: Middle America, to include Mexico and Central America; Nuclear Middle America, to include Mexico plus the region including Guatemala, El Salvador, Honduras, and Nicaragua; Nuclear Central America, to include the area occupied by the Central American republics noted above; and Lower Central America, to include Costa Rica and Panama. Lower Central America consisted of a string of volcanic islands until they were joined by land emergence in late Tertiary time. Nuclear Middle America was emergent land throughout the Tertiary period.

**Distribution Pattern.** At the generic level, the pattern is one of concentration of taxa in northern South America and Lower Central America, where both genera occur sympatrically, and to which area *Platycerozaena* is confined. The range of *Ozaena* is far more extensive, however, extending from about 30°S to 30°N (Figs. 13 and 14B).

For *Ozaena*, Figures 13–15 show a simple subtraction pattern in species diversity from South America (with 10 species) to Lower Central America (with two species), and northward to southwestern United States, with a single species (Fig. 14B). The species in Middle America and southwestern United States are also in South America.
LEGEND

CHARACTER STATES: ● apotypic, loss, ○ apotypic, □ plesiotypic

3-STAGE TRANSFORMATION SERIES:

BRANCHING POINTS: A - J

Fig. 33. Reconstructed phylogeny of the species of Ozaena Olivier
Within cis-Andean South America, ranges of the three species-groups of *Ozaena* are comparable in extent, from ca. 30°S to ca. 10°N, and from between 40° and 50°W to between 70° and 80°W. Although the overall ranges of the three species-groups are comparable in extent, that of the *O. dentipes* group (Fig. 13) differs from the other two by extending into the lower (eastern) parts of the Amazon Basin, whereas the ranges of the *O. lemoulti* and *O. convexa* groups (Figs. 14A and 15) are circum-Amazonian. Data are insufficient to compare range extents at the species level.

There is some indication of vicariant distribution patterns of sister-species (cf. ranges of *O. dentipes-linearis*, *O. lemoulti-martinezi*, and *O. convexa-manu* clades [Figs. 13, 14A, and 15, respectively]).

Data are insufficient to describe the ranges in terms of forest types occupied by each. However, the distribution patterns suggest that members of the *O. lemoulti* and *O. convexa* groups occupy drier forests, whereas those of the *O. dentipes* group range from wet tropical lowland forest to the drier forests in northern Argentina.

**Geographical History.** The data presented here are too few to warrant more than perfunctory discussion. The shortage of locality data is enhanced by our uncertainty, expressed above, about weaknesses in our interpretation of the taxonomic data that we have. However, it is important to point out how the patterns identified relate to better documented patterns of other taxa.

The Ozaenini exhibit a Gondwanian distribution pattern (Ball and McCleve 1990) with all species of *Ozaena* in South America and all species of *Platyzerosena* in South America or Lower Central America (Ogueta 1965b). We infer that the genus-group is Neotropical in origin, and that probably it differentiated after South America became isolated from the rest of Gondwanaland, during early Cretaceous time (Howarth 1981). The occurrence of all extant species of *Ozaena* in South America suggests the genus originated there. Conceivably, a vicariance event could have led to differentiation of *Platyzerosena* and *Ozaena*, with the ancestral stock of the former isolated in Lower Central America in early Tertiary time (see Ball and Shpeley [1986: 339] for a brief summary of geological history of Middle America, based on a more extensive account of that subject by Savage [1982]). Subsequently, the ranges of the two genera became sympatric by dispersal in both directions.

Alternating periods of isolation and range extension have been postulated, as the refuge theory, to account for vicariant distribution patterns of Amazonian taxa (see, for example, papers in Prance 1982; Ball and Maddison 1987; and Cracraft and Prum 1988). Distribution patterns of the species of *Ozaena* seem interpretable in terms of the refuge theory, except that most of the species-level differentiation probably occurred before the Pleistocene epoch, the geological episode for which the most recent refugia have been postulated (see Whitehead [1976] for a general discussion of speciation rates in insects). Thus, application of the refuge theory to *Ozaena* requires both postulation of earlier periods of the same sort of cyclic perturbations that have been postulated (and partially documented) for the Pleistocene epoch in South America, and extending such beyond the confines of the Amazon Basin. Cracraft and Prum (1988: 616–617) postulate that at least some vicariance patterns pre-date Pleistocene time.

A more precise application of the refuge theory to the geographical history of *Ozaena* requires recognition of specific sites for the refugia in which the ancestral stocks of the extant sister-species differentiated from one another. Data permit only the outline of a dimly perceived sequence of events.

Center of origin of the species-groups of *Ozaena* is not easily postulated because of the extensive syntropy that they exhibit collectively. Numbers clues (Darlington 1957: 31) indicate northeastern South America as the source area for the *O. dentipes* group, and
similarly, the region south of the Amazon Basin could have been the source area for the other two species-groups of Ozaena.

The general coincidence of the distribution patterns of the *O. lemoulti* and *O. convexa* groups suggests a common history for these assemblages, probably with the Amazon Basin acting intermittently as a barrier, temporarily cutting off contacts between northern and southern stocks, which thus became vicars. Such isolation would permit differentiation, followed eventually by intermixing of the now specifically distinct isolates—assuming that, for example, *O. lemoulti* and *O. martinezi* (putative northern and southern vicars, respectively) are specifically different, and that these two species are specifically different from their putative sister-species, *O. elevata*. Differentiation of *O. dentipes* and *O. linearis* probably followed a similar set of circumstances, though the ranges of these two vicariads of the *O. dentipes* group have not yet come into contact.

Species differentiations took place probably during late Tertiary time (ca. 3–15 million years before present, i.e. Pliocene to late Miocene). More recently, perhaps beginning in the early part of the Quaternary epoch, *O. lemoulti* became widespread to the north; and still more recently, *O. dentipes* extended its range northward, reaching only Lower Central America. If these taxa had reached Middle America at earlier times, we believe that the resulting northern and southern vicars would have differentiated from one another. In the absence of such differentiation, we postulate relatively recent incursions into Middle America, the relative dates for *O. lemoulti* and *O. dentipes* being reflected in the distances that each lineage has penetrated into Middle America. More generally, these statements about temporal aspects were formulated through comparisons of our data on which the estimates were based with similar data for better documented groups (Savage 1981; Whitehead 1976: 187, specifically time of origin of the species-groups of the curculionid genus *Rhinochenus*; more specifically, accepting Whitehead's estimate of 3 million years as an average period between speciation events, and with five groups of such events in the reconstructed phylogeny [Fig. 33, dichotomies B, C + E, F, G + I, and D + H + J], evolution of the extant species of *Ozaena* is postulated to have extended over a period of not less than 15 million years).

**CONCLUDING STATEMENT**

This study has advanced knowledge of the genus *Ozaena* through reporting and characterizing new taxa, and by using characters not used previously. Also, we have shown that the postulated pattern of differentiation agrees generally with patterns reported for other taxa.

**ACKNOWLEDGMENTS**

We are grateful to curators noted under "Material" for loan of specimens. In addition, the senior author appreciates hospitality extended to him by these same curators and members of their respective staffs during his visits to their institutions.

S. McCleve, of Douglas, Arizona, provided the data (reported elsewhere) on the basis of which the limits of morphological variation of adults of *O. lemoulti* were determined, and he translated into English important parts of Ogueta's (1965a) revision of *Ozaena*.

We thank our colleagues G.D. Braybrook, in charge of our Department’s SEM facility, who prepared the SEM photographs, and J.S. Scott, who prepared the habitus photographs, the plates, and the final versions of the distribution maps. We thank also W.B. Barr for his efforts in organizing the locality data and preparing preliminary drafts of the maps.

We record our appreciation to Donald R. Whitehead and Gerald R. Noonan for their useful comments about a previous draft of the manuscript on which this paper is based. Although we did not accept all of the advice that they offered, we accepted much of it, and the final manuscript was improved accordingly.
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REFERENCES


(Date received: 20 November 1989; date accepted: 10 April 1990)

**APPENDIX**

*Ozaena linearis* Banninger

**Material Examined.** Thirteen adults, from the following localities in South America.


*Ozaena dentipes* Olivier

**Material Examined.** Ten adults, from the following localities.

**Middle America**


**South America**

**BOLIVIA.** Chapare Gebiet Oberer Rio Chipiriri 400 m; II.11.1953, W. Forster; IX.2.1957, Zischka (ZSM).

**BRAZIL.** Manacapuru, III.1926; S.M. Klages (ICCM).


**TRINIDAD.** St. George Co., ca. 3 km W Cumulo, Indian Walk Ride Forest Road, VII.27.1975; K.W. Knopf (FSCA).
Ozaena ecuadorica Bänninger

Material Examined. Ten adults, from the following localities in South America.

Ozaena elevata Bänninger

Material Examined. Thirty adults, from the following localities in South America.
- PARAGUAY. Alta Parana. Termissiones; F. Schade (MCZC).

Ozaena lemuerti Bänninger

Material Examined. Thirty-nine adults from the following localities.

North America

Middle America
- BELIZE. “Belize” (MNHP).
- PANAMA. Chiriqui. Costa Rica; M. Klages Coll. (ICCM).

South America
- ARGENTINA. Salta. Tablillas, IX.1933–II.1934; W.C. Harrington (CASC).
- BOLIVIA. Buena Vista, XI.XII.1948; L. Peña (CASC).
- COLOMBIA. Valle, Anchicaya Dam, 70 km E Buenaventura, II.17.1970; H. Hodden (UASM).
PARAGUAY. San Bernardino, XI.23, *Chrysophyllum lacunifidium*, in the crown, 10 m high, XI.23; K. Fieberg (USNM).

VENEZUELA. Maracay; P. Vogl. (ZSMC).

**Ozaena martinezi** Ogueta

**Material Examined.** Eight adults, from the following localities in South America.

BOLIVIA. Sara. X.1909, XI.1910; J. Steinbach (ICCM).


**Ozaena grossa** Bänninger

**Material Examined.** Two adults, from the following locality in South America.

ARGENTINA. *Distrito Federal*. Estacao Forestal, Cabeca do Veado, 100 m, X.23–27.1971; Munroe family (CNCI).

**Ozaena convexa** Bänninger

**Material Examined.** Six adults, from the following localities in South America.

BOLIVIA. Chaparé, 400 m, X.18.1954; Zischka (ZSMC). Santa Cruz de la Sierra, 450 m, XI.1909, XI.1910; J. Steinbach (ICCM, ZSMC).


VENEZUELA. Maracaj, X.30.1933; L.F. Martonell (MCZC).