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## A Revision of the Genus *Elmas* Blackwelder, 1952 (Coleoptera: Staphylinidae: Staphylininae: Xanthopygina), with a Preliminary Reconstructed Phylogeny of the Species<sup>1</sup>

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**ABSTRACT** The staphylinid genus *Elmas* Blackwelder 1952 (type species: *Selma modesta* Sharp 1876 from Chontales, Nicaragua) is revised for the first time. The two previously described species, *E. modesta* (Sharp) from Nicaragua and *E. strigella* (Bernhauer) from Brazil, are redescribed. Fifteen species are described as new: *Elmas brooksi* from Ecuador; *Elmas costaricensis* from Costa Rica; *Elmas ellassos* from Ecuador; *Elmas esmeraldas* from Ecuador; *Elmas falini* from Suriname; *Elmas gigas* from Peru; *Elmas guianas* from French Guiana; *Elmas hanleyi* from Costa Rica; *Elmas hibbsi* from Ecuador; *Elmas lambas* from Brazil; *Elmas lescheni* from Peru; *Elmas panamaensis* from Panama; *Elmas patillas* from Costa Rica; *Elmas spinosus* from Bolivia; and *Elmas windsori* from Panama. A key and illustrations of structural features and aedeagi are provided for identification of the known species. The phylogenetic relationships of the species of *Elmas* species are only weakly resolved by the available dataset. *Elmas* is strongly supported to be a monophyletic lineage, and *E. strigella* is the most basal species followed by *E. lambos* and *E. guianas* respectively. *E. spinosus* + *E. falini* + *E. gigas* are strongly supported to be a monophyletic group; *E. hibbsi* is weakly supported to be the sister group to these three species. The lineage (*E. windsori* + *E. costaricensis*) + (*E. panamaensis* + *E. patillas*) is weakly supported in all trees. The lineage *E. ellassos* + *E. hanleyi* + *E. esmeraldas* is also weakly supported, and the successive approximation analysis hypothesizes that *E. modesta* is also a member of this lineage.

**KEY WORDS:** Staphylinidae, Staphylininae, Xanthopygina, *Elmas*, revision, key, new species, phylogeny.

## INTRODUCTION

The staphylinid genus *Elmas* Blackwelder, 1952 was first described by Sharp (1876) as the genus *Selma* Sharp based on his newly described species *Selma modesta* Sharp from Nicaragua. Blackwelder (1952) recognized that the name *Selma* Sharp, 1876 was a junior homonym of *Selma* Adams, 1863, and proposed the replacement name of *Elmas* Blackwelder, 1952. Prior to this work only two described species were known, *Elmas modesta* (Sharp) from Nicaragua (Sharp 1876, 1884) and *Elmas strigella* (Bernhauer) from Brazil (Bernhauer 1915). In spite of the fact that these large black staphylinids have a striking appearance, specimens of *Elmas* are rare in collections, and there are no published data on their habits or habitat. The genus has not received comprehensive review since its description.

Over 12 years of active collecting in South and Central America by personnel of the Snow Entomological Collection at the University of Kansas have yielded a substantial collection of *Elmas*, primarily collected in flight inter-

cept traps, representing a number of undescribed species. The goal of this paper is to revise the genus, review the described species and describe the new species. To this end we have examined the type specimens of the described species, and borrowed additional specimens from a number of collections, including a substantial collection of specimens from the INBio collection in Costa Rica.

## ACKNOWLEDGMENTS

The authors thank the curators listed in the body of the paper for loan of specimens. Sara Taliaferro inked the drawings and prepared the plates; Darci Kampshroeder edited and prepared the habitus photographs. Alfred Newton, Jr., Vladimir Gusarov and Michael Engel read various drafts of the manuscript and made many helpful comments. This work was supported by National Science Foundation PEET grants DEB-9521755 and DEB-9978110 to James S. Ashe.

## MATERIALS AND METHODS

Standard methods for systematic study of the Staphylinidae were used. Dried specimens were first relaxed in warm soapy water; then apical abdominal segments containing the aedeagus were dissected from the abdomen. Because of the similarity of many species in external characteristics, the genitalia of all male specimens were extracted. Mouthparts of selected individuals also were dissected for study. The apical abdominal segments and mouthparts were cleared using 10% KOH, and the aedeagus removed from the inside of the abdomen for study. Body structure, mouthparts, and aedeagi were studied using an Olympus SMZ-10 dissecting microscope and an Olympus BSH compound microscope with differential interference contrast optics. Relative width of the galea is given as a ratio of least width (measured at narrowest transverse distance between the sutures):length (measured as the distance along the gula midline from a line connecting the posterior tentorial pits to the base of the gula). Relative size of punctures on the head, pronotum and elytra is

expressed in terms of the average number of punctures in a transverse linear distance of 0.2 mm measured in the middle of the upper right quadrant of the appropriate body part (frons of head, pronotum, or right elytron). Drawings were made with the aid of a drawing tube and camera lucida. Terms for structural features follow Blackwelder (1936) as modified and extended by Smetana and Davies (2000).

Specimens used in this revision were from the following collections:

- American Museum of Natural History, New York (Lee Herman) (AMNH)
- Field Museum of Natural History, Chicago (Alfred Newton, Jr.) (FMNH)
- Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (INBio)
- The Natural History Museum, London (Martin Brendell) (BMNH)
- Snow Entomological Collection, Natural History Museum, The University of Kansas, Lawrence (KSEM)

## TAXONOMIC TREATMENT

*Elmas* Blackwelder, 1952

*Selma* Sharp, 1876: 427, preoccupied, non *Selma* Adams 1863  
*Elmas* Blackwelder, 1952: 146, new name for *Selma* Sharp, 1876

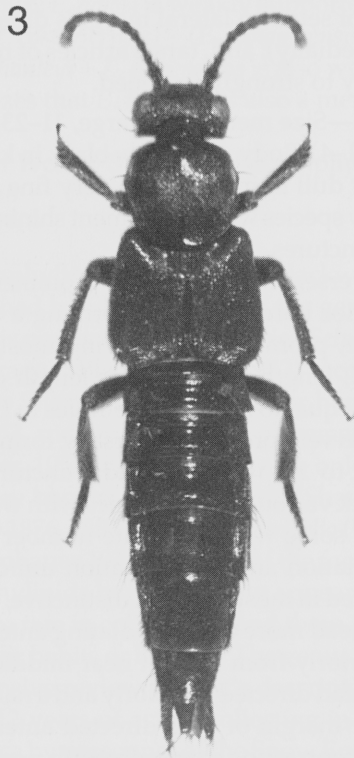
**Type Species.**—*Selma modesta* Sharp, 1876, fixed by Blackwelder (1952) by objective synonymy of *Elmas* Blackwelder with *Selma* Sharp, for which *S. modesta* Sharp had already been established as the type species by monotypy.

**Diagnosis.**—These large black staphylinids are among the most distinctive within the subtribe Xanthopygina. They are distinguished from all other members of the tribe by the combination of: large prominent eyes; prominent nuchal depression dorsally, forming a well-defined neck; distinctive head setation (setae on disc of head more or less radiating anteriorly, laterally, and posteriorly from a point near middle of frons, setae on base of head directed anteriorly and a narrow band of setae on inner margin of eyes directed anteriorly and anteromedially) (setation of *E. strigella* directed anteriorly and anteromedially); Antennal Articles 5–11 (4–11 in some) strongly flattened, and antenna appearing subserrate to strongly serrate on anterior margin; antenna black or dark brown with various of Articles 6–11 with paler markings (brown, pale brown, pale flavate, or white); mandibles strongly asymmetrical, right mandible with apex slender and acute, left mandible with apex flattened and more or less blade-like; apical article of maxillary and labial palpi uniformly broadened from base to obliquely truncate apex, apical width slightly to two or more times greater than basal width, and apical margins broad and filled with patch of membranous (presumably

sensory) tissue; distinctive arrangement of microsetae on elytra (directed posterolaterally in anterior half and more or less posteriorly in posterior half and a small to moderate sized patch of setae on lateral margins directed medially to posteromedially); and, tarsal articles of middle and hind legs slightly to strongly flattened.

**Description.**—Size medium to large, 11–23 mm in total length (Figs. 1–4). Body uniformly black in known species, body luster dull in most due to very fine and dense punctation, a few species with integument shining between more distant punctures.

Head transverse; posterior angles prominent, acutely rounded, posterior border of head forming a transverse ridge; eyes large, prominent, occupying most of lateral margins of head, length 3.0–4.5 times length of temples behind eyes (subequal to lengths of temples in *E. strigella*); nuchal depression very prominent dorsally, forming a well-defined neck 1/2 to 2/3 width of head; punctures on dorsal surface of neck various, a few species with widely scattered punctures, some with moderate number of denser punctures; punctation and microsetation uniformly and densely distributed in most; setation distinctive, most with setae on disc of head more or less radiating anteriorly, laterally and posteriorly from a point near middle of frons, setae on base of head directed anteriorly and a narrow band of setae on inner margin of eyes directed anteriorly and anteromedially (contrasting markedly with posterior and laterally directed setae on disc of frons); setation of some species (*E. strigella*) directed anteriorly and anteromedially.



Figs. 1-4. Representative species of *Elmas* species. 1, *Elmas hanleyi* n.sp., length = 14 mm. 2, *Elmas gigas* n.sp., length = 23 mm. 3, *Elmas guianas* n. sp., length = 14 mm. 4, *Elmas strigella* (Bernhauer), length = 19 mm.



Clypeus broadly and uniformly emarginate. Anteclypeus large, broadly U-shaped, moderately to strongly sclerotized; postclypeus deflexed into more vertical plane in most species, some species with reduced or absent setation and punctation on postclypeus, other species with postclypeus punctured similarly to disc of head, postclypeus with broad V-shaped depression medially between antennal bases in some, not depressed in others. Some species with a small, but distinct circular depression in middle of frons. Ventrally, head with postmandibular ridge; postmandibular ridge fully developed and subcarinate in some, interrupted or obsolete medially and replaced by patch of large irregular punctures in some, or present only near mandibular fossa in some (replaced by large irregular punctures in posterior 3/4 in *E. strigella*). Anterior margin of submentum arcuate or broadly rounded medially in most, prolonged into prominent medial spine in some. Gular sutures separated throughout; more broadly separated anteriorly in most, convergent to narrow or moderately wide separation before posterior third in most, divergent in posterior third in some. Gula with slight to distinct depression near posterior margin (outlined by subcarinate margin posteriorly in some). Antenna with Articles 5–11 (4–11 in some) distinctly and strongly flattened; articles 5–7 progressively longer anteriorly than posteriorly so that antenna appears subserrate to strongly serrate on anterior margin; Articles 5–10 slightly elongate, transverse or slightly transverse; antenna black or dark brown with various of Articles 6–11 with lighter markings (brown, light brown, pale flavate, or white), amount of light marking per article and number of articles with lighter color varies among individuals and species.

Labrum as in Figs. 59, 103.

Mandibles as in Figs. 5–8, 34–35, 42–44, 51–52, 60–61, 89–90, 104–105, 120–121; asymmetrical, right mandible with apex slender and acute (Figs. 7–8, 35, 44, 52, 61, 90, 105, 121); left mandible with apex flattened and more or less blade-like (strikingly so in some), and apex rounded or truncate (Figs. 5–6, 34, 42–43, 51, 60, 89, 104, 120); apex flattened in same plane as head in most, twisted toward vertical in a few (*E. strigella*); left mandible with well-defined groove in ventral surface; both mandibles reflexed ventrally in an angle of 25–30 degrees about 1/4–1/3 distance from base (visible in lateral view); both mandibles with a very small medial tooth on internal edge, or medial tooth obsolete or absent on right mandible.

Maxilla as in Figs. 62, 106. Maxillary palpi 4-articled; Article 4 triangular, uniformly broadened from base to obliquely truncate apex, apical width 2 or more times greater than basal width in many, less wide in others (only slightly broadened apically in *E. strigella*); apical margin broad and filled with circular, transverse or semi-lunulate patch of membranous (presumably sensory) tissue. Article

4 with numerous small setae more or less uniformly distributed.

Labium as in Figs. 63, 107. Ligula very short, membranous and emarginate medially. Labial palpi 3-articled. Article 3 triangular, uniformly broadened from base to obliquely truncate apex (only slightly broadened apically and article subcylindrical in *E. strigella*); apical margin broad and filled with circular, transverse or semi-lunulate patch of membranous (presumably sensory) tissue. Article 3 with numerous small setae more or less uniformly distributed.

Pronotum slightly transverse (greatest width:length ratio among known species = 1.12), subquadrate or slightly elongate (smallest width:length ratio among known species = 0.92). superior and inferior marginal lines of hypomeron separate throughout their lengths; superior line fully visible from above, prominent, subcarinate in some, extended around anterolateral margin of pronotum to make contact with inferior line at neck fossa, or, in some, fading just before contact with inferior line, no portion of dorsum of pronotum visible from below. Punctures numerous, close, more or less uniformly and densely distributed. Microsetae numerous, uniformly distributed, directed more or less posteriorly or posterolaterally.

Basisternum of prosternum without pair of prominent medial setae, anterior marginal depression various, not apparent to moderately developed; without medial carina. Sternocoxal ridge present, prominently subcarinate on anterior margin in some, intercoxal depression anterior to subcoxal ridge absent to weakly developed. Furca-sternum without prominent medial carina. Notum without translucent postcoxal process.

Elytra subequal in length to pronotum to slightly longer than pronotum (up to 1.2 times as long as pronotum), densely and uniformly punctate and microsetose. Microsetae directed posterolaterally in anterior half and more or less posteriorly in posterior half; small to moderate sized patch of setae on lateral margins directed medially to posteromedially, contrasting strongly with posterolaterally directed setae on disc. Hind wings fully developed in all known species.

Mesosternum with anterior margin reflexed into slight "lip"; without medial carina; mesosternal process broad, extended slightly between coxae, broadly rounded apically; metasternal process broad and rounded apically. Meso- and metasternal processes separated by a long, broad isthmus; mesocoxal cavities broadly separated.

Tarsal segmentation 5-5-5. Anterior tarsal Articles 1-4 of both sexes moderately to strongly transverse, covered ventrally by spatulate setae, ventral surface concave in some. Tarsal articles of middle and hind legs slightly to strongly flattened, Article 1 as long or longer than the next 3 articles combined. Empodial setae 2, small, setose, much shorter than the tarsal claws (less than 1/3 as long as tarsal claws in most).

Abdominal terga with transverse basal ridges present on Terga III–VIII, uniformly transverse or slightly curved posteriorly in medial areas, not sinuate or curved posteriorly in lateral areas; Terga III–V (Tergum VI slightly impressed in a few) with very deeply and sharply defined transverse impressions posterior to transverse marginal ridge.

Abdominal sterna with transverse basal ridges well developed on Sterna III–VIII, margin of transverse basal ridges uniformly arcuate, or slightly emarginate medially, lateral margins curved sharply posteriorly; Terga III–IV or III–V (VI slightly in some) with slight to moderate transverse depressions posterior to transverse basal ridge.

Male and female genitalia typical of Staphylininae (Blackwelder 1936: 48). Sternum IX of female divided into two lobes, each with large basal valvifer, smaller basal coxite and very small apical stylus. Aedeagus typical of Staphylininae, with large medial lobe and single (medially fused) paramere. Paramere with various combinations of apical peg setae, and short and inconspicuous apical setae.

**Secondary Sexual Characters.**—Females without obvious secondary sexual characters. Males with posterior margin of abdominal Sternum VII weakly to moderately strongly emarginate medially; Sternum VIII moderate to deeply emarginate medially; and Sternum X moderately to deeply emarginate medially.

**Habitat.**—Known from elevations of 20–700 m in wet tropical lowland forests (most specimens from  $\leq 200$  m), except in Bolivia where they have been collected in forests in the Yungas at 1000 and 1450 meters. No information about the habits of this rare genus is noted in the literature, and preferred microhabitat and habits are not known. We have seen one specimen collected “on dung”, but all other specimens with “habitat data” on their labels were collected in flight intercept traps or Malaise traps. The large number of specimens in the INBio collection lack habitat data, but the condition and date information of most specimens, and known INBio collecting protocols, suggest that they were probably collected in Malaise traps.

**Distribution.**—Known from Nicaragua to Bolivia.

**Relationships.**—Sharp (1876) noted the relative isolation of *Elmas* (under the name *Selma*) within the staphylinine staphylinids; he first placed *Elmas* in the staphylinine subtribe Xanthopygina where it has remained to the current time. Sharp proposed, with some hesitation, that *Elmas* may be related to the xanthopygine genera *Plociopterus* and *Nordus* (under the name *Brachydirus*), but he noted that it is very different from members of these latter two genera in appearance and structure of the palpi. He also considered the possibility that *Elmas* may be related to the oriental genus *Trichocosmetes*, but noted that the structure of the prothorax of *Elmas* was very different from that of *Trichocosmetes*. Smetana and Davies (2000)

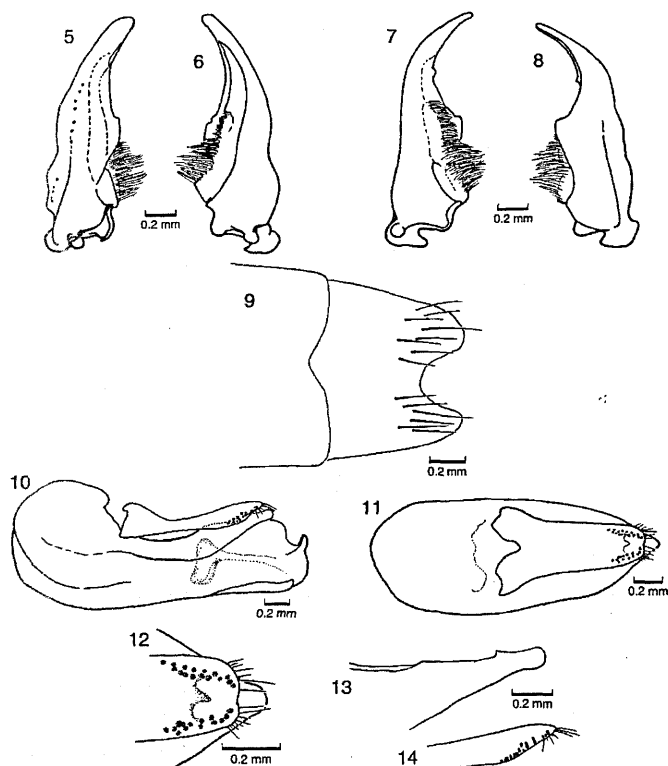
mention similarity between *Elmas* and *Plociopterus* in setation of the palpifer on the maxilla, but their paper was not intended to address the relationships of *Elmas* in a comprehensive way. At the time of this writing the relationships of *Elmas* remain obscure.

*Elmas brooksi* new species  
(Figs. 5–14)

**Diagnosis.**—Among those South American *Elmas* that do not have a distinct longitudinal groove on the external surface of the hind tibia, *E. brooksi* is most similar to *E. lescheni*; both have relatively large extent of pale flavate color on antenna, with Articles 9–11 fully or virtually completely pale; *E. brooksi* can be distinguished from *E. lescheni* only by its distinctive aedeagus (Figs. 10, 11, 12, 13).

**Description.**—Length 15–17 mm. Color black except for pale color on some antennal articles. Head with postclypeus slightly deflexed ventrally in relation to frons, virtually impunctate and subglabrous, strongly shining, except for a few small scattered punctures in antero-medial region; medial area between antennae without distinct shallow longitudinal V-shaped groove; eyes large, length about 4.5 times length of temples behind eyes; punctures moderate (about 6 punctures per 0.2 mm), uniformly distributed, punctures more or less round, very close, margins of punctures virtually contiguous, distance between punctures 0.1–0.2 times average width of punctures, punctate surfaces shining. Middle of frons depressed to form a shallow pit. Postmandibular carina present, complete and prominent anteriorly and on base of head, obsolete medially due to large irregular punctures. Mentum broadly, shallowly and uniformly arcuate around insertion of labium. Submentum subtruncate and slightly and broadly rounded medially, without large medial spinose process. Gula sutures convergent from broad apex to moderate medial area (least width: length ratio = 0.20). Maxillary palpus with apical segment dilated apically, apical width across oblique apex 2.0 times basal width; apex oblique, outer length about 1.3 times inner length. Labial palpus with apical segment moderately expanded apically, width across oblique apex 1.5 times width of base; apex oblique, outer length 1.2 times inner length. Mandibles (Figs. 5–8) with apex of left mandible flattened, obliquely truncate apically, twisted slightly dorsal to horizontal plane of head. Antenna black with light color (brown to pale flavate) limited to Articles 7–11, Article 7 fully or partially brown, Article 8 pale flavate or brown, Article 9 fully pale flavate or pale flavate with brown basal edge, Articles 10–11 completely pale flavate; Articles 5–10 of about equal greatest length and width.

Pronotum slightly wider than long, width:length ratio = 1.11; anterolateral angles obtusely rounded, lateral angles not subcariniform; superior lateral line extended



Figs. 5–14. *Elmas brooksi*. 5, left mandible, dorsal aspect. 6, left mandible, ventral aspect. 7, right mandible, dorsal aspect. 8, right mandible, ventral aspect. 9, male sterna VII–VIII. 10, aedeagus, lateral aspect. 11, aedeagus, dorsal aspect. 12, aedeagus, detail of apex of paramere and median lobe, dorsal aspect. 13, apex of median lobe, lateral aspect. 14, apex of paramere, lateral aspect.

to contact inferior lateral line, obsolete immediately before contact with inferior lateral line in some; punctures small (about 5–6 punctures per 0.2 mm), numerous, uniformly distributed, very close, edges of punctures virtually contiguous, distance between punctures 0.1–0.3 times average width of punctures, some slightly elongated in longitudinal or posterolateral direction, not coalesced into short, irregular longitudinal or posterolateral furrows; ridges between punctures shining; many specimens with longitudinal, very narrow, strongly shining, impunctate region in middle of disc or near posterior margin, extent of impunctate area varies from absent to slightly developed.

Elytra with punctures moderate sized (about 2–3 punctures per 0.2 mm), individual punctures not well defined, edges contiguous, elongated in longitudinal or posterolateral direction, irregularly coalesced into short, irregular furrows, punctate surface shining.

Anterior Tarsal Articles 1–4 uniformly covered with short, spatulate setae. Tarsal claws of middle and hind tarsi not modified, not very slender or sharply curved near middle. Hind tibia distinctly flattened, without distinct longitudinal groove on external surface, medial area of

external surface of tibia with distinct, longitudinal impunctate region, without scattered setae and punctures.

Abdominal Terga III–V with moderate transverse basal impressions; microsculpture on III–VIII obsolete to absent distal to basal transverse ridges, surface strongly shining.

Abdominal Sterna III–V with shallow transverse impressions; microsculpture on III–VIII obsolete or absent distal to basal transverse ridges, surface strongly shining.

**Secondary Sexual Characters.**—Male: distal margin of Tergum VII with shallow medial emargination; distal margin of Tergum VIII deeply emarginate (Fig. 9).

**Aedeagus.**—As in Figs. 10, 11; paramere broad and truncate apically, apex entire, with about 14–17 black sensory spinules on each side, arranged in a longitudinal band on each side of paramere (Figs. 11, 12, 14); apical lobe narrowed to acutely rounded apex, dorsal surface with 2 small semi-lunulate teeth, teeth close medially but not contiguous (Figs. 11, 13).

**Holotype.**—Male, with labels as follows: "ECUADOR: Sucumbios, Sacha Lodge, 270 m, 0°28'14" S, 76°27'35" W, 16–29-VIII-1994, P. Hibbs, malaise trap", bar code label "SM0023840, KUNHM-ENT", "HOLOTYPE, *Elmas brooksi* Ashe & Chatzimanolis, Design. Ashe & Chatzimanolis, 2001". Located in KSEM.

**Paratypes.**—9, with labels as follows: ECUADOR: Napo, Puerto Napo, 21 km E, Jatun Sacha Biological Station, 400 m, 13-VI-1994, F. Genier, flight intercept trap, SM45986 (1 KSEM). Sucumbios, Sacha Lodge, 270 m, 0°28'14" S, 76°27'35" W, 21–24-III-1999, R. Brooks, flight intercept trap, ECU1B99-047, SM153274, SM153267 (2 KSEM). Same locality, 10–21-X-1994, P. Hibbs, malaise trap, SM22072, SM22096 (2 KSEM). Same locality and collector, 25-VI-3-VIII-1994, malaise trap, SM23418 (1 KSEM). Tiputini Research Station, 220 m, 0°38'0"S, 76°9'0"W, 5–25-IX-2000, D. J. Inwaru, K. A. Jackson, BM2000:194 (3 BMNH).

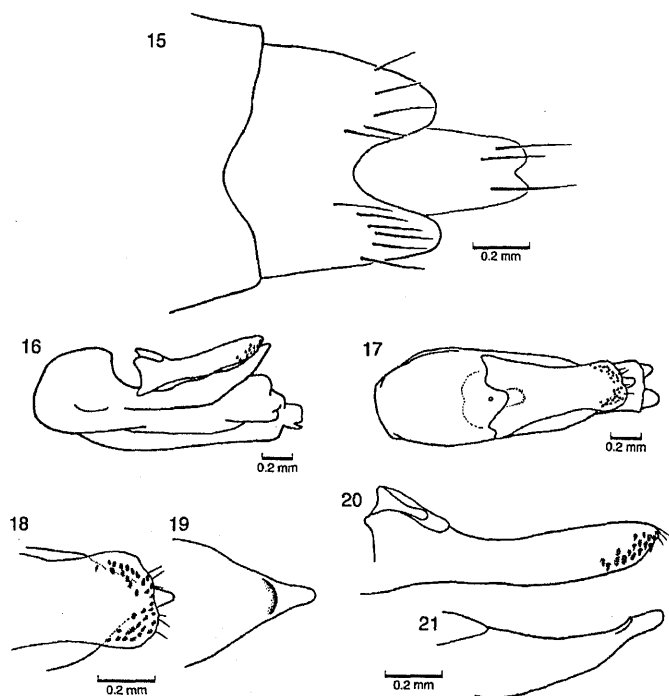
**Distribution.**—Currently known at elevations of 270–400 m in Napo and Sucumbios provinces, Ecuador (Fig. 129).

**Habitat and Habits.**—Not known. All specimens for which collecting data are available were collected using flight intercept or Malaise traps.

**Etymology.**—The specific epithet is in honor of Robert Brooks who collected a series of specimens of this species in Ecuador.

*Elmas costaricensis* new species  
(Figs. 15–21)

**Diagnosis.**—Among Central American species, *E. costaricensis* is similar to *E. windsori*, *E. panamaensis*, and *E. hanleyi* and distinguished from them by the relatively elongate pronotum (width:length ratio = 0.95, subquadrate or slightly transverse in *E. windsori*, *E. panamaensis* and *E. hanleyi*), and the distinctive aedeagus (Figs. 16, 17). This is



Figs. 15–21. *Elmas costaricensis*. 15, male sterna VII–VIII, X. 16, aedeagus, lateral aspect. 17, aedeagus, dorsal aspect. 18, aedeagus, detail of apex of paramere and median lobe, dorsal aspect. 19, aedeagus, detail of apex of median lobe, dorsal aspect. 20, apex of paramere, lateral aspect. 21, apex of median lobe, lateral aspect.

the only Central America *Elmas* known to occur on the Osa Peninsula and on the lowland Pacific side of Costa Rica as far northwest as Maritza Biological Station in Guanacaste Province.

**Description** — Length 14–16 mm. Color black except for pale color on some antennal articles. Head with postclypeus deflexed ventrally in relation to frons, punctured more sparsely than frons, especially laterally in most specimens; medial area between antennae without distinct shallow longitudinal V-shaped groove; eyes large, length about 4.0 times length of temples behind eyes; punctures small (about 5–6 punctures per 0.2 mm), uniformly distributed, punctures more or less round, very close, margins of punctures contiguous or virtually contiguous, separated by about 0.1–0.2 times average width of punctures, punctate surfaces shining. Middle of frons not depressed to form a shallow pit. Postmandibular carina present, prominent near maxillary insertion and weak on base of head, obsolete medially where replaced by irregular large punctures. Mentum broadly, shallowly and uniformly emarginate around insertion of labium. Submentum slightly and broadly emarginate, without large medial spinose process. Gula sutures convergent from broad apex to moderate medial area (least width: length ratio = 0.19). Maxillary palpus with apical segment dilated apically,

apical width across oblique apex about 2.0 times basal width; apex oblique, outer length about 1.3–1.4 times inner length. Labial palpus with apical segment expanded apically, width across oblique apex about 2.2 times width of base; apex oblique, outer length 1.3 times inner length. Mandibles with apex of left mandible flattened, obliquely truncate apically, and more or less in horizontal plane of head. Antenna black with pale color (pale flavate) limited to longitudinal band on posterior margins of various articles, most with pale color limited to Articles 8–11; Article 8 with trace of pale color at base up to 1/2 pale; Article 9 1/2–2/3 pale; Article 10 2/3–3/4 pale; Article 11 fully pale; Articles 5–10 subquadrate to very slightly longer than wide.

Pronotum slightly longer than wide, width:length ratio = 0.95; anterolateral angles obtusely rounded, lateral angles not subcariniform; superior lateral line extended to contact inferior lateral line; punctures small (about 5–6 punctures per 0.2 mm), numerous, uniformly distributed, close, edges of punctures virtually contiguous, separated by about 0.1–0.4 times average width of punctures, punctures round or slightly elongated anteriorly and medially, distinctly elongated in longitudinal or posterolateral direction laterally and posteriorly, not coalesced into short, irregular longitudinal or posterolateral furrows; ridges between punctures shining.

Elytra with punctures small (about 4 punctures per 0.2 mm), individual punctures poorly to moderately defined, edges contiguous, elongated in longitudinal or posterolateral direction, irregularly coalesced into short, irregular furrows, punctate surface shining.

Anterior Tarsal Articles 1–4 uniformly covered with short, spatulate setae. Tarsal claws of middle and hind tarsi not modified, not very slender or sharply curved near middle. Hind tibia flattened, with distinct, but narrow, longitudinal groove on external surface, medial area of groove narrowly impunctate longitudinally, without scattered setae and punctures.

Abdominal Terga III–V with moderate transverse basal impressions, Tergum VI with shallow transverse groove; microsculpture on III–V obsolete to absent distal to basal transverse ridges, surface shining; VI–VIII with moderate to obsolete reticulate microsculpture.

Abdominal Sterna III–V with moderate transverse impressions, Sternum VI with shallow transverse impression laterally; microsculpture on III–V obsolete or weakly reticulate to wavy distal to basal transverse ridges, surface shining; VI–VIII with reticulate to slightly wavy microsculpture.

**Secondary Sexual Characters.**—Male: distal margin of Tergum VII with broad and shallow emargination; distal margin of Tergum VIII deeply emarginate (Fig. 15).

**Aedeagus.**—As in Figs. 16, 17; paramere very broad and expanded apically, apex broadly arcuate and shallowly emarginate medially, with about 15–17 black sensory

spinules on each side, arranged in a broad band near apex and apico-laterally (Figs. 18, 20); apical lobe narrowed to acutely rounded apex, dorsal surface with single transverse broadly curved cariniform ridge (Figs. 19, 21).

**Holotype.**—Male, with labels as follows: "COSTA RICA: Puntarenas, Rincon, 7 km W., Osa Penn., Est. F.N. Aguas Buenas, 50 m, 21–25-VI-1997, S. & J. Peck, flight intercept trap, CR1P97-024", bar code label "SM0330818, KUNHM-ENT", "HOLOTYPE, *Elmas costaricensis* Ashe & Chatzimanolis, Design. Ashe & Chatzimanolis, 2001". Located in KSEM.

**Paratypes.**—102, with labels as follows: COSTA RICA: Guanacaste, Maritza Biol. Sta., 550 m, 10°58' N, 85°29' W, 22-V-1993, J. S. Ashe, A. K. Ashe, flight intercept trap, CR1AA93-036, SM45993 (1 KSEM). Puntarenas, Piedras Blancas, 24.0 km W R. F. Golfo Dulce, 200 m, 8°46' N, 83°24' W, I-II-1992, P. Hanson, SM45965 (1 KSEM). Puntarenas, Rincón, 3.0 km SW R.F. Golfo Dulce, 10 m, II-1992, P. Hanson, malaise trap, SM45979 (1 KSEM). Same locality and collector, I-1992, SM45958 (1 KSEM). Puntarenas, Corcovado National Park, Sirena Stn., lower Ollas Trail, 5 m, 8°24'48" N, 83°35'22" W, 24–28-VI-2000, Z. H. Falin, flight intercept trap, CR1ABF00-035, SM189729 SM189728 (2 KSEM). Puntarenas, Corcovado National Park, Sirena Stn., lower Río Claro Trail, 30 m, 8°27'59" N, 83°35'30" W, 28-VI-1-VII-2000, Z. H. Falin, flight intercept trap, CR1ABF00-060, SM189730 SM189731 (2 KSEM), Costa Rica, Prov. Puntarenas, Pennsula de Osa, Rancho Quemado, 200 m, 4–27-VII-1994, L. S. Marin, INBIO CR1001-890988, 891006, 890940, 891002 (4 INBio). Same locality, 1-XI-1-XII-1992, A. L. Marin #3197, INBIO CR1001-994821 (1 INBio). Same locality, 4–28-VI-1994, A. Marin #3013, INBIO CR1001-886776, 886716 (2 INBio). Same locality and collector, 1-27-I-1992, #1779, INBIO CR1001-731250 (1 INBio). Same Locality and collector, 12-III-3-IV-1994, #2796, INBIO CR1001-759629 (1 INBio). Same locality and collector, 6–28-IV-1994 #2851, INBIO CR1001-797267, 797296, 797287, 797294, 797268, 797295 (6 INBio). Same locality and collector, IX-1992, INBIO CR1001-960198 (1 INBio). Same locality and collector, 10–31-III-1992, INBIO CR1001-177679 (1 INBio). Same locality and collector, 1–21-XII-1992, INBIO CR1001-936946 (1 INBio). Same locality, 4–21-I-1994, A. H. Guitierrez #2570, INBIO CR1001-845738 (1 INBio). Same locality and collector, 19–27-IV-1993 #2302, INBIO CR1001-125173 (1 INBio). Same locality and collector, 7–27-I-1993 #1813, INBIO CR1001-676575 (1 INBio). Same locality and collector, 14–28-VII-1993, #2254, INBIO CR1001-155172, 155170, 155175, 155149, 155174, 155141 (6 INBio). Same locality and collector, 12–31-III-1993, INBIO CR1001-196464, 196488 (2 INBio). Same locality and collector, 12–24-V-1993, INBIO CR1001-188879, 188805 (2 INBio). Same locality, F. Quesada, VII-1991, INBIO CR1001-407439, 407435, 407427 (3 INBio). Same locality and collector, X-

1992, INBIO CR1001-964265 (1 INBio). Same locality and collector, VI-1992, INBIO CR1001-861880 (1 INBio). Same locality and collector, XII-1992, INBIO CR1001-462743 (1 INBio). Same locality and collector, VII-1992, INBIO CR1001-736392 (1 INBio). Same locality and collector, IX-1992, INBIO CR1001-8555104 (1 INBio). Same locality, F. Quesada & G. Varela, V-1992, INBIO CR1001-870230, 892265 (2 INBio). Same locality, M. Segura, INBIO CR1001-907312 (1 INBio). Costa Rica, Puntarenas, N. P. Corcovado, Est. Sirena, 0–100 m, II-1990, G. Fonseca, INBIO CR1001-122365, 122355, 122433, 122165, 122434 (5 INBio). Same locality and collector, III-1990, INBIO CR1001-170446 (1 INBio). Same locality and collector, IV-1990, INBIO CR1001-234956 (1 INBio). Same locality and collector, VI-1990, INBIO CR1001-520563 (1 INBio). Same locality and collector, VII-1991, INBIO CR1001-464028 (1 INBio). Same locality and collector, 17-VI-4-IX-1991, INBIO CR1001-685761 (1 INBio). Same locality and collector, XII-1989, INBIO CR1001-203843 (1 INBio). Puntarenas Prov., Est. Esquinas, Pennsula de Osa, 0 m, M. Segura coll. #2450, X-1993, INBIO CR1001-666122 (1 INBio). Same locality and collector, IV-1993, INBIO CR1001-161188 (1 INBio). Same locality, F. Quesada, I-1993, INBIO CR1001-296374 (1 INBio). Puntarenas Prov., Bosque Esquinas, Pennsula de Osa, 200 m, M. Segura coll., VI-1994, INBIO CR1001-898590, 898588 (2 INBio). Puntarenas, P. B. Carara, Est. Quebrada Bonita, 50 m, J. C. Saborio #3290, XI-1994, INBIO CR1001-054583, 054584, 054585, 054587 (4 INBio). Same locality and collector #2849, V-1994, INBIO CR1001-982682, 982676, 982678, 982672, 982675, 982684 (6 INBio). Same locality and collector #3288, X-1994, INBIO CR1001-045708, 045707 (2 INBio). Same locality and collector #2814, IV-1994, INBIO CR1001-754458, 754459 (2 INBio). Same locality and collector #2640, I-1994, INBIO CR1001-963570, 963622 (2 INBio). Same locality and collector #2641, II-1994, INBIO CR1001-916905 (1 INBio). Same locality and collector #2396, X-1994, INBIO CR1001-664207 (1 INBio). Same locality and collector, XII-1992, INBIO CR1001-9000485, 900415 (2 INBio). Same locality, M. Guzman, #2914, X-1994, INBIO CR1001-891923, 891915, 891918 (3 INBio). Same locality and collector #2572, I-1994, INBIO CR1001-941298 (1 INBio). Same locality and collector #2825, IV-1994, INBIO CR1001-782991 (1 INBio). Same locality and collector, XII-1992, INBIO CR1001-985690 (1 INBio). Same locality and collector, 6–27-XI-1992, INBIO CR1001-816277 (1 INBio). Same locality, R. Zuniga, I-1992, INBIO CR1001-293584 (1 INBio). Puntarenas, Est. Carara, Res. Biol. Carara, E. Zuniga, II-1990, INBIO CR1001-068861 (1 INBio). Puntarenas, Est. Aguias, Send. Zamia, 300 m, A. Azofrifa, #47914, 24–30-IV-1994, INBIO CR1001-562377 (1 INBio). Same locality and collector, #49918, 19-III-1998, INBIO CR1001-413890 (1 INBio). Same locality and collector, #7212, 9–28-III-1996, INBIO CR1001-381902 (1 INBio).

Guanacaste, Est Los Almendros, 300m, E. E. Lopez #4779, 3-20-XII-1994, INBIO CR1001-143343, 143342, 143344 (3 INBio). Same locality and collector, # 2990, 8-30-V-1994, INBIO CR1001-895853 (1 INBio). Guanacaste, Tierras Morenas, Tilarán, A. C. Arenál, 685 m, G. Rodriguez #3040, V-1994, INBIO CR1001-900287 (1 INBio)

**Distribution.**—Currently known at elevations of 0–685 m from the lowlands of the Pacific slope of Costa Rica from the Osa Peninsula northwest to Maritza Biological Station in Guanacaste Province (Fig. 128).

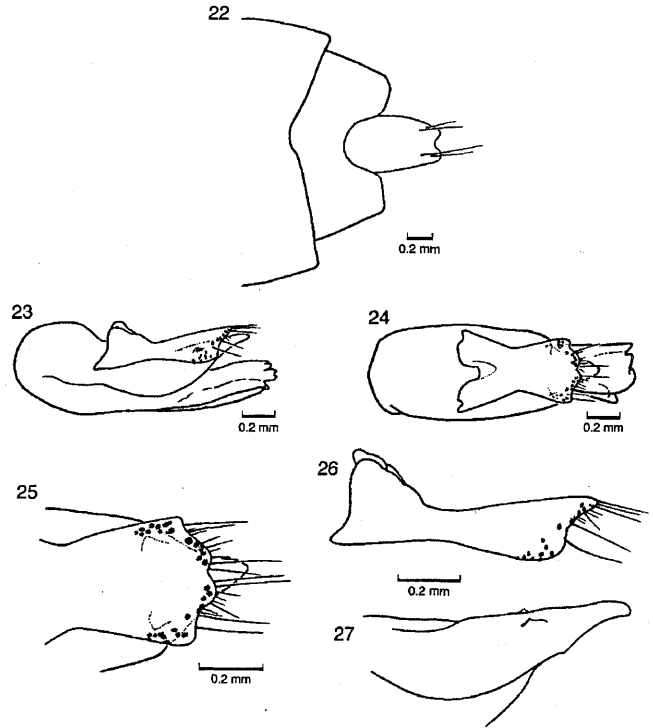
**Habitat and Habits.**—Not known. All specimens for which collecting data are available were collected in flight intercept or Malaise traps.

**Etymology.**—The specific epithet refers to Costa Rica from which all known specimens of this species have been collected.

*Elmas classos* new species  
(Figs. 22-27)

**Diagnosis.**—Among South America *Elmas* that do not have a groove on the external surface of the hind tibia, *E. classos* can be distinguished by: small size (the smallest known *Elmas*; known specimens 12–13 mm in total length); and the distinctive aedeagus (Figs. 23, 24).

**Description.**—Length 12–13 mm. Color black except for pale color on some antennal articles. Head with postclypeus slightly deflexed ventrally in relation to frons, punctured similar to frons; medial area between antennae without distinct shallow longitudinal V-shaped groove; eyes large, length about 4.7 times length of temples behind eyes; punctures small (about 4–5 punctures per 0.2 mm), uniformly distributed, punctures more or less round, very close, margins of punctures virtually contiguous, distance between punctures 0.1–0.3 times average width of punctures, punctate surfaces shining. Middle of frons slightly depressed to form a very shallow pit, pit and short region posterior to pit impunctate, shining. Postmandibular carina present, prominent anteriorly and less prominent on base of head, replaced medially by large irregular punctures. Mentum broadly, shallowly and uniformly arcuate around insertion of labium. Submentum subtruncate and slightly and broadly rounded medially, without large medial spinose process. Gula sutures weakly convergent from broad apex to broad medial area (least width: length ratio = 0.30). Maxillary palpus with apical segment dilated apically, apical width across oblique apex 2.0 times basal width; apex oblique, outer length about 1.2 times inner length. Labial palpus with apical segment very greatly expanded apically, width across oblique apex 2.0 times width of base; apex oblique, outer length 1.2 times inner length. Mandibles with apex of left mandible flattened, obliquely truncate apically, and slightly twisted dorsally



Figs. 22–27. *Elmas classos*. 22, male sternite VII–VIII, X, outline. 23, aedeagus, lateral aspect. 24, aedeagus, dorsal aspect. 25, aedeagus, detail of apex of paramere and median lobe, dorsal aspect. 26, apex of paramere, lateral aspect. 27, apex of median lobe, lateral aspect.

from horizontal plane of head. Antenna black with pale color (brown) limited Articles 8–11, Article 9 dark brown, Articles 9–11 uniformly brown; Articles 5–7 subquadrate, Articles 8–10 slightly transverse.

Pronotum subquadrate, width:length ratio = 1.02; anterolateral angles obtusely rounded, lateral angles not subcariniform; superior lateral line extended to contact inferior lateral line, weak immediately before contact with inferior lateral line; punctures small (about 6–7 punctures per 0.2 mm), numerous, uniformly distributed, very close, edges of punctures contiguous to virtually contiguous, distance between punctures 0.1–0.2 times width of punctures, many slightly elongated in longitudinal or posterolateral direction, not coalesced into short, irregular longitudinal or posterolateral furrows; ridges between punctures shining.

Elytra with punctures small (about 3–4 punctures per 0.2 mm), individual punctures moderately well defined, edges contiguous to separated by up to 0.5 times width of punctures, at most only slightly elongated in longitudinal or posterolateral direction, not coalesced into short, irregular furrows, punctate surface shining.

Anterior tarsal articles 1–4 uniformly covered with short, spatulate setae. Tarsal claws of middle and hind tarsi not modified, not very slender or sharply curved near

middle. Hind tibia very slightly flattened, without longitudinal groove on external surface, medial area of tibia punctured similar to remainder of tibia with scattered setae and punctures.

Abdominal Terga III–V with moderate transverse basal impressions, Tergum VI with very shallow transverse groove; microsculpture on III–VIII obsolete to absent distal to basal transverse ridges, surface shining.

Abdominal Sterna III–V with shallow transverse impressions; microsculpture on III–V obsolete or absent distal to basal transverse ridges, surface shining; Sterna VI–VIII with obsolete wavy microsculpture.

**Secondary Sexual Characters.**—Male: distal margin of Tergum VII with very broad and shallow emargination; distal margin of Tergum VIII deeply emarginate (Fig. 22).

**Aedeagus.**—As in Figs. 23, 24; paramere very broad and expanded apically, apex broadly arcuate and shallowly emarginate medially, with about 15–17 black sensory spinules on each side, arranged in a broad band near apex and apico-laterally (Figs. 25, 26); apical lobe narrowed to acutely rounded apex, dorsal surface with 2 widely separated medial teeth (Figs. 25, 27).

**Holotype.**—Male, with labels as follows: "ECUADOR: Napo, Onkone Gare Camp, 220 m, 0°39'10" S, 76°26'0" W, 5-7-X-1995, G. E. Ball, D. Shpeley, pitfall trap", bar code label "SM0140270, KUNHM-ENT", "HOLOTYPE, *Elmas elassos* Ashe & Chatzimanolis, Design. Ashe & Chatzimanolis, 2001". Located in KSEM.

**Paratypes.**—1, with labels as follows. ECUADOR: Napo Region, Tiputini Research Station, 220 m, 0°38'0" S, 76°9'0" W, 5-25-IX-2000, D. J. Inwaru, K. A. Jackson, BM2000:194 (BMNH).

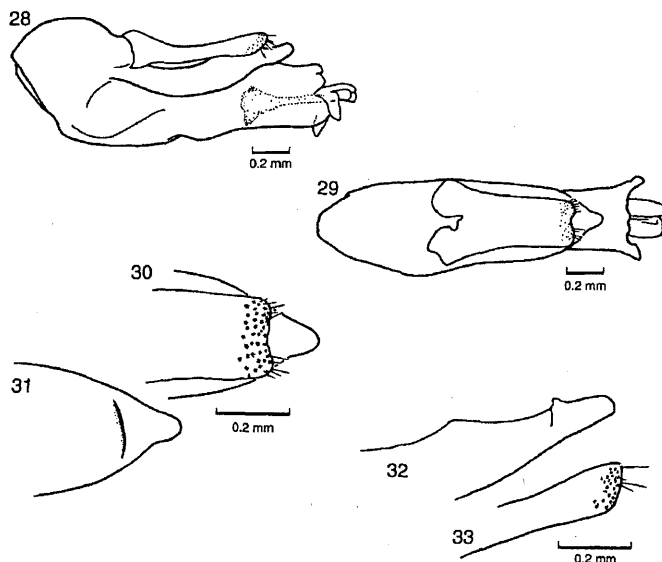
**Distribution.**—Currently known only from an elevation of 220 m in Napo Province, Ecuador (Fig. 129).

**Habitat and Habits.**—Not known. One of the two known specimens was collected in a pitfall trap; the label of the other does not include data about habitat or collecting method.

**Etymology.**—The specific epithet is derived from the Greek "ellassos", meaning "smaller", and refers to the relatively small size of this species.

*Elmas esmeraldas* new species  
(Figs. 28–33)

**Diagnosis.**—*Elmas esmeraldas* is similar to *E. hibbsi* except it is noticeably smaller (13–14 mm as compared to 15–18 mm), the postclypeus of *E. esmeraldas* is glabrous and shining except for scattered punctures in anteromedial region (compared to *E. hibbsi* in which it is similar to punctation on frons); the hind tibia of *E. esmeraldas* is slightly flattened, external surface not grooved longitudinally and



Figs. 28–33. *Elmas esmeraldas*. 28, aedeagus, lateral aspect. 29, aedeagus, dorsal aspect. 30, aedeagus, detail of apex of paramere and median lobe, dorsal aspect. 31, aedeagus, detail of apex of median lobe, dorsal aspect. 32, apex of paramere, lateral aspect. 33, apex of median lobe, lateral aspect.

uniformly punctured and setose, without glabrous longitudinal area; aedeagus similar to *E. hibbsi*, but *E. esmeraldas* has the apex of the paramere slightly and broadly emarginate, and the black sensory spinules are clustered closer to the apex (Figs. 29, 30); also the medial lobe of *E. esmeraldas* has a curved carina medially (Fig. 31) (as opposed to neither tooth nor carina in *E. hibbsi*).

**Description.**—Length 13–14mm. Color black except for pale color on some antennal articles. Head with postclypeus slightly deflexed ventrally in relation to frons, subglabrous, distinctly less punctured than frons except for scattered punctures in antero-medial region; medial area between antennae without distinct shallow longitudinal V-shaped groove; eyes large, length about 4.3 times length of temples behind eyes; punctures small (about 5–6 punctures per 0.2 mm), uniformly distributed, punctures more or less round, very close, margins of punctures contiguous, punctate surfaces shining. Middle of frons not depressed to form a shallow pit. Postmandibular carina present, complete and prominent to base of head or obsolete and replaced by large irregular punctures in medially beneath eye. Mentum broadly, shallowly and uniformly arcuate around insertion of labium. Submentum subtruncate and slightly and broadly rounded medially, without large medial spinose process. Gula sutures convergent from broad apex to moderately narrow medial area (least width: length ratio = 0.15). Maxillary palpus with apical segment dilated apically, apical width across oblique apex 1.5 times basal width; apex oblique, outer length



about 1.3 times inner length. Labial palpus with apical segment expanded apically, width across oblique apex 1.6 times width of base; apex oblique, outer length 1.2 times inner length. Mandibles with apex of left mandible flattened, narrowly obliquely truncate apically, and more or less in horizontal plane of head. Antenna black with pale color (light brown) limited to longitudinal band on posterior margins of various articles, most with pale color limited to Articles 9–11 (11 missing), and a trace of pale color on Article 8; Article 9 1/3 pale, Article 10, 1/3 pale, Article 11 missing in all available specimens; Articles 5–6 subquadrate, Articles 7–10 slightly transverse.

Pronotum subquadrate, width:length ratio = 1.02; anterolateral angles obtusely rounded, lateral angles not subcariniform; superior lateral line extended to contact inferior lateral line, obsolete immediately before contact with inferior lateral line in some; punctures small (about 5–6 punctures per 0.2 mm), numerous, uniformly distributed, very close, edges of punctures contiguous, anterior punctures more or less round, many posterior punctures elongated in longitudinal or posterolateral direction, not coalesced into short, irregular longitudinal or posterolateral furrows; ridges between punctures shining.

Elytra with punctures small (about 4 punctures per 0.2 mm), individual punctures moderately well defined, edges contiguous, elongated in longitudinal or posterolateral direction, weakly coalesced into short, irregular furrows posteriorly, punctate surface shining.

Anterior Tarsal Articles 1–4 uniformly covered with short, spatulate setae. Tarsal claws of middle and hind tarsi not modified, not very slender or sharply curved near middle. Hind tibia slightly flattened, without distinct longitudinal groove on external surface, medial area of external surface of tibia with scattered setae and punctures.

Abdominal Terga III–V with moderate transverse basal impressions; microsculpture on III–VII obsolete to absent distal to basal transverse ridges, surface shining; VIII with weak reticulate microsculpture.

Abdominal Sterna III–V with shallow transverse impressions; microsculpture on III–VII obsolete or absent distal to basal transverse ridges, surface shining; VIII with weak reticulate to wavy microsculpture.

**Secondary Sexual Characters.**—Male: distal margin of Tergum VII with broad medial emargination; distal margin of Tergum VIII deeply emarginate (similar to Fig. 71).

**Aedeagus.**—As in Figs. 28, 29; paramere broad and truncate apically, apex broadly and shallowly emarginate, with about 18–20 black sensory spinules on each side, arranged in a broad band near apex (Figs. 30, 33); apical lobe narrowed to acutely rounded apex, dorsal surface with slightly curved transverse carina (Figs. 31, 32).

**Holotype.**—“ECUADOR: Esmeraldas, Bilsa, 0°20'24" N, 79°42'36" W, 19-VII-1996, P. Hibbs, flight intercept trap, ECU1H96-024", bar code label “SM0075126, KUNHM-ENT”, “HOLOTYPE, *Elmas esmeraldas* Ashe & Chatzimanolis, Design. Ashe & Chatzimanolis, 2001”. Located in KSEM.

**Paratypes.**—2, with labels as follows: ECUADOR: Esmeraldas, Bilsa, 0°20'24" N, 79°42'36" W, 10-V-5-VI-1996, P. Hibbs, flight intercept trap, ECU1H96-016A, SM75071, SM75076 (2 KSEM)

**Distribution.**—Currently only known from Bilsa, Esmeraldas Province, Ecuador (Fig. 129)

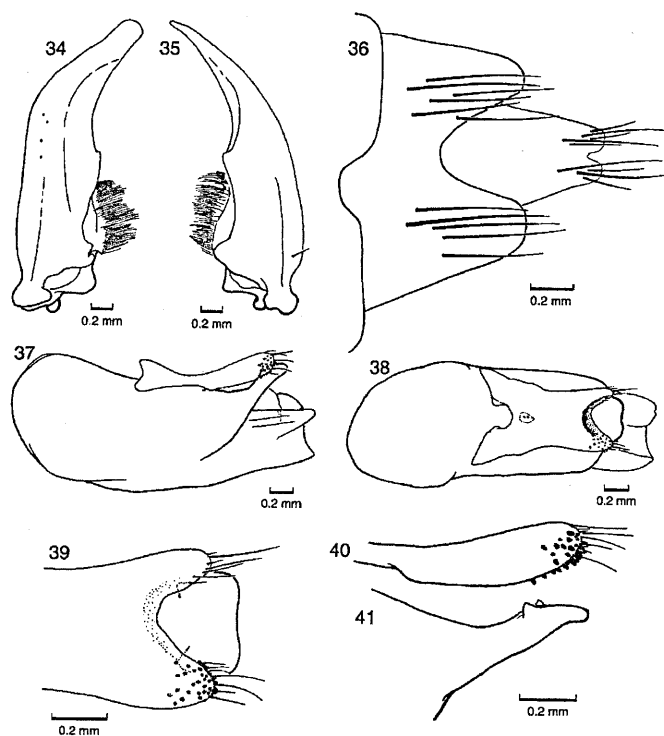
**Habitat and Habits.**—Not known. All specimens for which collecting data are available were collected in flight intercept traps.

**Etymology.**—The specific epithet refers to the Esmeraldas Province in Ecuador from which all known specimens of this species have been collected.

*Elmas falini* new species  
(Figs. 43–41)

**Diagnosis.**—*Elmas spinosus*, *E. falini*, and *E. gigas* are distinctive among all known *Elmas* because of the presence of a large medial spine on the submentum in these species. Among these three, *E. falini* and *E. gigas* are the largest known species of *Elmas*, with known specimens of 21–23mm in total length. *Elmas falini* is very similar to *E. gigas*, and difficult to distinguish from it based on external characteristics. *Elmas falini* differs from *E. gigas* in that: punctures on pronotum are slightly larger, many are distinctly elongated, and the punctures are coalesced into short irregular furrows; Tergum VI of available specimens has a slight transverse depression posterior to basal transverse ridge; and, distinctive aedeagus (Figs. 37, 38).

**Description** — Length 21–23 mm. Color black except for pale color on some antennal articles. Head with postclypeus deflexed ventrally in relation to frons, virtually impunctate except for a few small punctures and setae in anterolateral regions; medial area between antennae with distinct shallow longitudinal V-shaped groove; eyes large, length about 3.5 times length of temples behind eyes; punctures small (about 4–6 punctures per 0.2 mm), uniformly distributed, punctures more or less round, very close, margins of punctures virtually contiguous, distance between punctures 0.1–0.2 times average width of punctures, punctate surfaces shining. Middle of frons distinctly depressed to form a shallow pit. Postmandibular carina present, complete and prominent anteriorly and on base of head, prominent to interrupted medially by large irregular punctures. Mentum broadly, shallowly and uniformly arcuate around insertion of labium. Submentum with large medial spinose process. Gula sutures weakly



Figs. 34–41. *Elmas falini*. 34, left mandible, dorsal aspect. 35, right mandible, dorsal aspect. 36, male sterna VII–VIII, X. 37, aedeagus, lateral aspect. 38, aedeagus, dorsal aspect. 39, aedeagus, detail of apex of paramere and median lobe, dorsal aspect. 40, apex of paramere, lateral aspect. 41, apex of median lobe, lateral aspect.

convergent from broad apex to very broad medial area (least width: length ratio = 0.27). Maxillary palpus with apical segment strongly dilated apically, apical width across oblique apex 2.7 times basal width; apex strongly oblique, outer length about 1.5 times inner length. Labial palpus with apical segment very greatly expanded apically, width across oblique apex 2.5 times width of base; apex strongly oblique, outer length 1.6–1.7 times inner length. Mandibles (Figs. 34, 35) with apex of left mandible flattened, apically rounded, and in horizontal plane of head. Antenna black with pale color (light brown) limited to longitudinal band on posterior margins of Articles 8 (trace in of pale color on Article 7 in a few specimens)–11, 1/5–1/2 of Articles 8–10 with pale color, proportionally more pale color on progressively more apical articles, Article 11 with 2/3–4/5 pale color; Articles 5–7 very slightly longer than greatest width, Articles 8–10 of about equal greatest length and width.

Pronotum slightly wider than long, width:length ratio = 1.07; anterolateral angles obtusely rounded, lateral angles not subcariniform; superior lateral line extended to contact inferior lateral line, but fading and very weak immediately before contact with inferior lateral line; punctures very small (about 7–8 punctures per 0.2 mm), numerous, uniformly distributed, very close, edges of punc-

tures contiguous, many elongated in longitudinal or posterolateral direction, irregularly coalesced into short, irregular longitudinal or posterolateral furrows; ridges between punctures shining.

Elytra with punctures very small (about 6 punctures per 0.2 mm), individual punctures shallow and poorly defined, edges contiguous, elongated in longitudinal or posterolateral direction, many coalesced into short, irregular furrows with indistinct edges, punctate surface shining.

Anterior Tarsal Articles 1–4 uniformly covered with short, spatulate setae. Tarsal claws of middle and hind tarsi not modified, not very slender or sharply curved near middle. Hind tibia not greatly flattened, with distinct longitudinal groove on external surface, medial area of groove with scattered setae and punctures.

Abdominal Terga III–V with moderate transverse basal impressions, Tergum VI with very shallow transverse impression; microsculpture on III–V obsolete to absent distal to basal transverse ridges, surface shining; VI–VIII with dense, close reticulate microsculpture.

Abdominal Sterna III–V with shallow transverse impressions; microsculpture on III–V reticulate to weakly wavy distal to basal transverse ridges, surface shining; Sterna VI–VIII with dense, distinct reticulate microsculpture.

**Secondary Sexual Characters.**—Male: distal margin of Tergum VII with distinct medial emargination; distal margin of Tergum VIII broadly and deeply emarginate (Fig. 36).

**Aedeagus.**—As in Figs. 37, 38; paramere broad, deeply emarginate medially, with about 30–35 small black sensory spinules on each side (Figs. 39, 40); apical lobe broad and subtruncate apically, dorsal surface with 2 distinct large medial semi-lunulate teeth (Figs. 39, 41).

**Holotype.**—Male, With labels as follows: "SURINAME: Marowijne, Palumeu, 15 km NE, on Tapanahony River, trail to Poti Hill, 160 m, 3°27' N, 55°22' W, 6–7-VII-1999, Z. Falin, D. Konoe, flight intercept trap, SUR1F99-168, (1 KSEM) bar code label "SM0175091, KUNHM-ENT", "HOLOTYPE, *Elmas falini* Ashe & Chatzimanolis, Design. Ashe & Chatzimanolis, 2001". Located in KSEM.

**Paratypes.**—3, with labels as follows: SURINAME: Saramacca, West Suriname Road, 108 km WSW Zanderij Airport, 30 m, 5°13'37" N, 55°52'54" W, 8–10-VI-1999, Z. Falin, B. De Dijn, flight intercept trap, SUR1F99-054, SM175259 (1 KSEM). Marowijne, Palumeu, 160 m, 3°20'56" N, 55°26'18" W, 7–8-VII-1999, Z. Falin, flight intercept trap, SUR1F99-183, SM175075, SM175072 (2 KSEM)

**Distribution.**—Currently known at elevations of 30–160 m from north-central Suriname (Fig. 129).

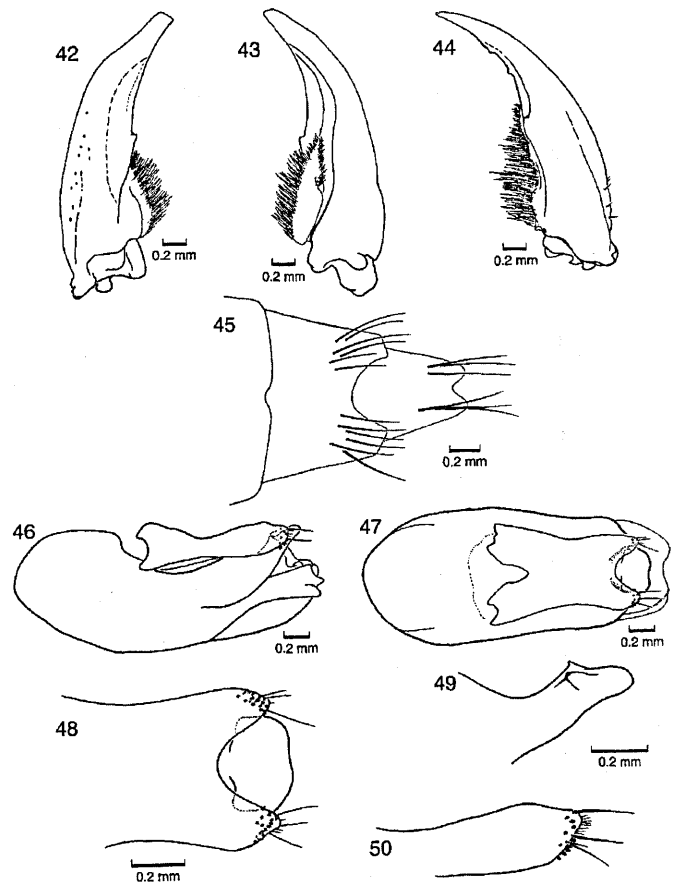
**Habitat and Habits.**—Not known. All specimens for which collecting data are available were collected in flight intercept traps.

**Etymology.**—The specific epithet is in honor of Zachary H. Falin who collected all known specimens of this species in Suriname.

*Elmas gigas* new species  
(Figs. 2, 42–50)

**Diagnosis.**—*Elmas spinosus*, *E. falini*, and *E. gigas* are distinctive among all known *Elmas* because of the presence of a large medial spine on the submentum in these species. Among these three, *E. falini* and *E. gigas* are the largest known species of *Elmas*, with known specimens of 21–23 mm in total length. *Elmas gigas* is very similar to *E. falini*, and difficult to distinguish from it based on external characteristics. *Elmas gigas* differs from *E. falini* in that: punctures on pronotum are smaller, most are not distinctly elongated, and the punctures are not clearly coalesced into short irregular furrows; Tergum VI of available specimens does not have any indication of a transverse depression posterior to basal transverse ridge; and, distinctive aedeagus (Figs. 46, 47).

**Description.**—Length 21–23 mm (Fig. 2). Color black except for pale color on some antennal articles. Head with postclypeus deflexed ventrally in relation to frons, virtually impunctate except for a few small punctures and setae in anterolateral regions; medial area between antennae with distinct shallow longitudinal V-shaped groove; eyes large, length about 3.2 times length of temples behind eyes; punctures small (about 4–6 punctures per 0.2 mm), uniformly distributed, punctures more or less round, very close, margins of punctures virtually contiguous, distance between punctures 0.1–0.2 times average width of punctures, punctate surfaces shining. Middle of frons distinctly depressed to form a shallow pit. Postmandibular carina present, complete to base of head, obsolete medially due to large irregular punctures. Mentum broadly, shallowly and uniformly arcuate around insertion of labium. Submentum with large medial spinose process. Gula sutures weakly convergent from broad apex to very broad medial area (least width: length ratio = 0.33). Maxillary palpus with apical segment strongly dilated apically, apical width across oblique apex 2.5 times basal width; apex strongly oblique, outer length about 1.7–1.8 times inner length. Labial palpus with apical segment very greatly expanded apically, width across oblique apex 3 times width of base; apex strongly oblique, outer length 1.7–1.9 times inner length. Mandibles (Figs. 42–44) with apex of left mandible flattened, apically rounded, and twisted slightly above horizontal plane of head. Antenna black with pale color (pale brown) limited to longitudinal band on posterior margins of Articles 8 (trace in of pale color on Article 7 in one specimen)–10, 1/4–2/3 of 8–10 with pale color in most (Article 8 black in 1 specimen), proportionally more pale color on progressively more apical Articles, Article 11



Figs. 42–50. *Elmas gigas*. 42, left mandible, dorsal aspect. 43, left mandible, ventral aspect. 44, right mandible, dorsal aspect. 45, male sternum VII–VIII, X. 46, aedeagus, lateral aspect. 47, aedeagus, dorsal aspect. 48, aedeagus, detail of apex of paramere and median lobe, dorsal aspect. 49, apex of median lobe, lateral aspect. 50, apex of paramere, lateral aspect.

with 2/3–4/5 pale color to fully pale; Articles 5–7 very slightly longer than greatest width, Articles 8–10 of about equal greatest length and width.

Pronotum slightly wider than long, width:length ratio = 1.05; anterolateral angles obtusely rounded, lateral angles not subcariniform; superior lateral line extended to contact inferior lateral line, but weak immediately before contact with inferior lateral line; punctures very small (about 7–8 punctures per 0.2 mm), numerous, uniformly distributed, very close, edges of punctures contiguous, punctures round or slightly elongated in longitudinal or posterolateral direction, not coalesced into short, irregular longitudinal or posterolateral furrows; surface shining within and between punctures.

Elytra with punctures very small (about 6 punctures per 0.1 mm), individual punctures shallow and poorly defined, edges contiguous, elongated in longitudinal or posterolateral direction, many coalesced into short, irregular furrows with indistinct edges, punctate surface shining.

Anterior Tarsal Articles 1–4 uniformly covered with short, spatulate setae. Tarsal claws of middle and hind tarsi not modified, not very slender or sharply curved near middle. Hind tibia not greatly flattened, with distinct longitudinal groove on external surface, medial area of groove with scattered setae and punctures (disto-medial third with very few setae, virtually glabrous).

Abdominal Terga III–V with moderate transverse basal impressions; microsculpture on III–V obsolete to absent distal to basal transverse ridges, surface shining; Terga VI–VIII with dense, close reticulate microsculpture.

Abdominal Sterna III–V with shallow transverse grooves (very shallow on Sternum V in some); microsculpture on III–V reticulate to weakly wavy distal to transverse impressions, surface shining; Sterna VI–VIII with dense, distinct reticulate microsculpture.

**Secondary Sexual Characters.**—Male: distal margin of Tergum VII with slight medial emargination; distal margin of Tergum VIII broadly and deeply emarginate (Figure 45).

**Aedeagus.**—As in Fig. 46, 47; paramere very broad, deeply and broadly emarginate medially, with about 15 small black sensory spinules on each side (Figs. 48, 50); apical lobe broad and subtruncate apically, dorsal surface with 2 large medial semi-lunulate teeth (Figs. 48, 49).

**Holotype.**—Male, with labels as follows: "PERU: Loreto, Teniente López, 240 m, 2°35' S, 76°6' W, 20–22-VII-1993, R. Leschen, flight intercept trap, PERU1L93-166, (1 KSEM) bar code label "SM0045988, KUNHM-ENT", "HOLOTYPE, *Elmas gigas* Ashe & Chatzimanolis, Design. Ashe & Chatzimanolis, 2001". Located in KSEM.

**Paratypes.**—4, with labels as follows: BRAZIL: Pará, Redenção vic., Fazenda Marajoara, 7°49.74' S 50°15.91' W, XI-1988, tropical evergreen seasonal lowland forest on sand/clay soil, at dung, P. Y. Scheffler (1 FMNH). PERU: Loreto, Teniente López, 240 m, 2°35' S, 76°6' W, 22–26-VII-1993, R. Leschen, flight intercept trap, PERU1L93-213, SM45987 (1 KSEM). Madre de Dios, Pantiacolla Lodge, Alto Madre de Dios River, 400m, 12°39'22" S, 71°13'55" W, 23–26-X-2000, R. Brooks, PERU1B00 099, flight intercept trap, SM0205044 (1 KSEM). Madre de Dios, Cocha Panchita, Reserved Zone, Manu National Park, 300 m, 12°13' S, 71°13'5" W, 21-X-2000, R. Brooks, PERU1B00 066, miscellaneous collecting, SM0205045 (1 KSEM).

**Distribution.**—Currently known from elevations of 240–400 m from Amazonian Peru and from the state of Para, Brazil (Fig. 129).

**Habitat and Habits.**—Not known. One specimen found "at dung"; all others for which collecting data are available were collected using flight intercept traps.

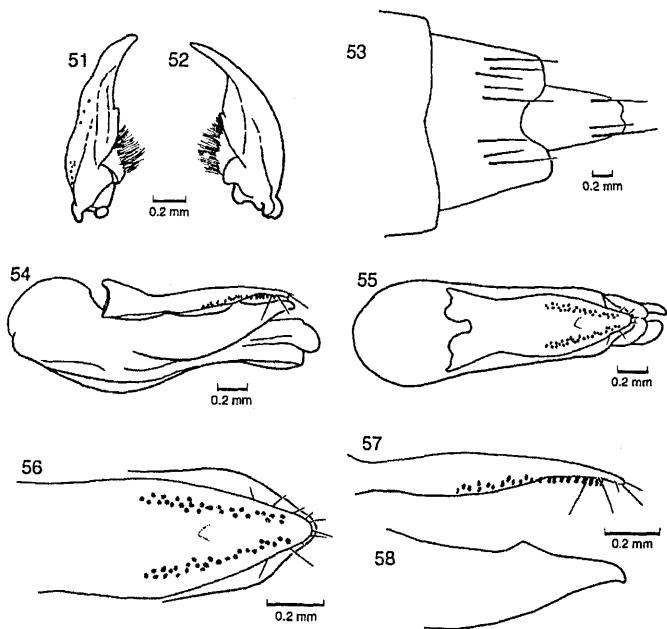
**Etymology.**—The specific epithet is derived from the Greek *gigas* meaning giant, and refers to the large size of this species.

**Discussion.**—*Elmas falini* and *E. gigas* appear to be very closely related. The external structures are similar and the aedeagi differ only in the number of black sensory spinules on the apex of the paramere (only about 15 on each side in *E. gigas* in contrast to 30–35 on each side in *E. falini*). However, this latter difference is consistent among all available specimens and supports the hypothesis that they represent different species.

*Elmas guianan* new species  
(Figs. 3, 51–58)

**Diagnosis.**—*Elmas guianan* is different from all other species except *E. lambas* in that most specimens of *E. guianan* have an impunctate, strongly shining, longitudinal line in the center of the pronotum. This impunctate area in *E. guianan* is much narrower than that in *E. lambas*; it may be complete, interrupted by punctate areas medially in some specimens, only present in basal third of pronotum in others, or completely absent in a few (4 of 39 available specimens); *E. guianan* also differs from *E. lambas* by presence of elongate punctures on head and pronotum that coalesce in furrows on base of head in *E. guianan* (compared to round punctures that do not coalesce into furrows in *E. lambas*); and, the very distinctive aedeagus (Figs. 54, 55).

**Description.**—Length 12–15mm (Fig. 3). Color black except for pale color on some antennal articles. Head with postclypeus slightly deflexed ventrally in relation to frons, punctured similar to frons except less punctured in extreme lateral region; medial area between antennae without distinct shallow longitudinal V-shaped groove; eyes large, length about 4.0 times length of temples behind eyes; punctures moderate sized (about 3–4 punctures per 0.2 mm), uniformly distributed, punctures more or less round anteriorly and distinctly elongated in longitudinal or posterolateral direction on lateral and posterior regions, distance between punctures various, contiguous anteriorly to separated by up to average width of punctures posteriorly, punctures on posterior and lateral regions irregularly weakly coalesced into short, irregular furrows, surfaces between punctures strongly shining. Middle of frons very slightly depressed to form a very shallow pit, punctation in pit various from impunctate and shining to punctured similar to frons. Postmandibular carina present, complete anteriorly and obsolete on base of head, obsolete or absent medially and replaced by large irregular punctures. Mentum broadly, shallowly and uniformly arcuate around insertion of labium. Submentum subtruncate, without large medial spinose process. Gula sutures convergent from broad apex to narrow medial area (least width: length ratio = 0.08). Maxillary palpus with apical segment slightly dilated apically, apical width across oblique apex 1.4 times basal width; apex slightly oblique, outer length about 1.1 times inner length. Labial palpus with apical segment ex-



Figs. 51–58. *Elmas guianas*. 51, left mandible, dorsal aspect. 52, right mandible, dorsal aspect. 53, male sterna VII–VIII, X. 54, aedeagus, lateral aspect. 55, aedeagus, dorsal aspect. 56, aedeagus, detail of apex of paramere and median lobe, dorsal aspect. 57, apex of paramere, lateral aspect. 58, apex of median lobe, lateral aspect.

panded apically, width across oblique apex 1.5 times width of base; apex slightly oblique, outer length 1.1–1.2 times inner length. Mandibles (Figs. 51, 52) with apex of left mandible flattened, obliquely truncate apically, and more or less in horizontal plane of head. Antenna black with pale color (pale brown to pale flavate) limited to Articles 7–11, a few with very narrow band of pale color in Articles 6 or 6–7; Article 7 uniformly brown to brown with up to pale flavate, Articles 8–9 pale brown to up to 3/4 pale flavate, Articles 10–11 fully pale flavate or pale flavate clouded with pale brown basally; Articles 5–10 of about equal greatest length and width.

Pronotum slightly wider than long, width:length ratio = 1.12; anterolateral angles obtusely rounded, lateral angles not subcariniform; superior lateral line extended to contact inferior lateral line, obsolete or weak immediately before contact with inferior lateral line in some; punctures moderate sized (about 4 punctures per 0.2 mm), numerous, uniformly distributed, close, edges of punctures contiguous to separated up to 0.7 times average width of punctures, distinctly elongated in longitudinal or posterolateral direction, irregularly coalesced into short, irregular longitudinal or posterolateral furrows, especially in posterior half, in some, not distinctly coalesced into furrows in others; ridges between punctures strongly shining. Most specimens with impunctate, strongly shining, longitudinal line in midline of pronotum, extent of impunctate line various from absent to present only faintly near posterior border, to complete from anterior to posterior border.

Elytra with punctures moderate sized (about 3–4 punctures per 0.2 mm), individual punctures moderately well defined, punctures mostly round and separated by 0.1–0.5 times average width of punctures in anterolateral third and elongated in longitudinal or posterolateral direction posteriorly and medially, distinctly to weakly coalesced into short, irregular furrows posteriorly and medially, surface strongly shining.

Anterior Tarsal Articles 1–4 uniformly covered with short, spatulate setae. Tarsal claws of middle and hind tarsi not modified, not very slender or sharply curved near middle. Hind tibia flattened, without distinct longitudinal groove on external surface, medial area of external surface of tibia broadly and distinctly impunctate longitudinally, without scattered setae and punctures, extent of impunctate area various from extensive to slight.

Abdominal Terga III–V with moderate transverse basal impressions; microsculpture on III–VIII absent distal to basal transverse ridges, surface strongly shining.

Abdominal Sterna III–V with very shallow transverse impressions; microsculpture on III–V absent distal to basal transverse ridges, surface shining; Sterna VI–VIII with microsculpture absent to obsolete and wavy, surface strongly shining.

**Secondary Sexual Characters.**—Male: distal margin of Tergum VII with very faint broad and shallow emargination; distal margin of Tergum VIII deeply emarginate (Fig. 53).

**Aedeagus.**—As in Figs. 54, 55; paramere narrowed in apical half to acutely rounded apex, apex entire, with about 27–30 black sensory spinules on each side, arranged in a long narrow band on each side of apical half (Figs. 56, 57); apical lobe narrowed to acutely rounded apex, dorsal surface with one large medial tooth (Figs. 56, 58).

**Holotype.**—“FRENCH GUIANA: Saul, 7 km N, 3 km NW Les Eaux Claires, Mt. La Fumee, 490 m, 3°39' N, 53°13' W, 1–8-VI-1997, J. Ashe, R. Brooks, flight intercept trap, FG1AB97-162”, bar code label “SM0133874, KUNHM-ENT”, “HOLOTYPE, *Elmas guianas* Ashe & Chatzimanolis, Design. Ashe & Chatzimanolis, 2001”. Located in KSEM.

**Paratypes** — 38, with labels as follows: FRENCH GUIANA: Roura, 8.4 km SSE, 200 m, 4°40' N, 52°13' W, 26-V-10-VI-1997, J. Ashe, R. Brooks, malaise trap, FG1AB97-183, SM96496 (1 KSEM). Same locality and collectors, 29-V-10-VI-1997, flight intercept trap, FG1AB97-182 SM330883 SM330884 (2 KSEM). Same locality and collectors, 25–29-V-1997, flight intercept trap, FG1AB97-088 SM133897 SM133897 SM131256 SM131260 (4 KSEM). Same locality and collectors, 22–23-V-1997, flight intercept trap, FG1AB97-011, SM94895 (1 KSEM). Roura, 39.4 km SSE, 270 m, 4°32' N, 52°8' W, 29-V-1997–10-VI-1997, J. Ashe, R. Brooks, flight intercept trap, FG1AB97-172, SM99370 SM99375 (2 KSEM). Roura, 27.4 km SSE, 280 m, 4°44' N, 52°13' W, 29-V-1997–10-VI-1997, J. Ashe, R. Brooks, flight intercept trap, FG1AB97-172, SM99370 SM99375 (2 KSEM).

52°13' W, 10-VI-1997, J. Ashe, R. Brooks, malaise trap, FG1AB97-178, SM133935 (1 KSEM). Same locality and collectors, 4°44' N, 52°13' W, 10-VI-1997, flight intercept trap, FG1AB97-177, SM133973 SM133972 SM133971 (3 KSEM). Cayenne, 33.5 km S and 8.4 km NW of Hwy N2 on Hwy D5, 30 m, 4°48' N, 52°28' W, 29-V-9-VI-1997, J. Ashe, R. Brooks, flight intercept trap, FG1AB97-171, SM100251 SM100252 SM100255 (3 KSEM). Matoury, 41.5 km SSW on Hwy N2, 50 m, 4°37' N, 52°22' W, 29-V-9-VI-1997, J. Ashe, R. Brooks, flight intercept trap, FG1AB97-170, SM100504 SM100502 SM100503 (3 KSEM). Same locality and collectors, 4°37' N, 52°22' W, 26-28-V-1997, flight intercept trap, FG1AB97-060, SM99448 (1 KSEM). Saul, 7 km N, Les Eaux Claires, 220 m, 3°39' N, 53°13' W, 30-V-4-VI-1997, J. Ashe, R. Brooks, flight intercept trap, FG1AB97-144, SM131294 (1 KSEM). Same locality and collectors, 30-V-4-VI-1997, flight intercept trap, FG1AB97-143B, SM99461 SM99458 SM99456 SM99463 (4 KSEM). Saul, 7 km N, 3 km NW Les Eaux Claires, Mt. La Fumee, 490 m, 3°39' N, 53°13' W, 1-8-VI-1997, J. Ashe, R. Brooks, flight intercept trap, FG1AB97-162, SM133872 SM133877 SM133880 (3 KSEM). Saul, 7 km N, 1 km NW Les Eaux Claires, along Rue de Belizon trail, 280 m, 3°39' N, 53°13' W, 4-8-VI-1997, J. Ashe, R. Brooks, flight intercept trap, FG1AB97-167, SM98923 SM98920 SM98922 SM98924 SM98924 SM98921 SM98931 (7 KSEM). SURINAME: Marowijne, Nassau Mountain, 500 m, 4°47'53" N, 54°31'16" W, 1-2-VI-1999, Z. Falin, B. De Dijn, flight intercept trap, SUR1F99-014, SM164633 (1 KSEM). Same locality and collectors, 2-4-VI-1999, flight intercept trap, SUR1F99-024, SM175388 (1 KSEM). Marowijne, Palumeu, 160 m, 3°20'56" N, 55°26'18" W, 5-9-VII-1999, Z. Falin, D. Konoe, flight intercept trap, SUR1F99-185, SM164571 (1 KSEM).

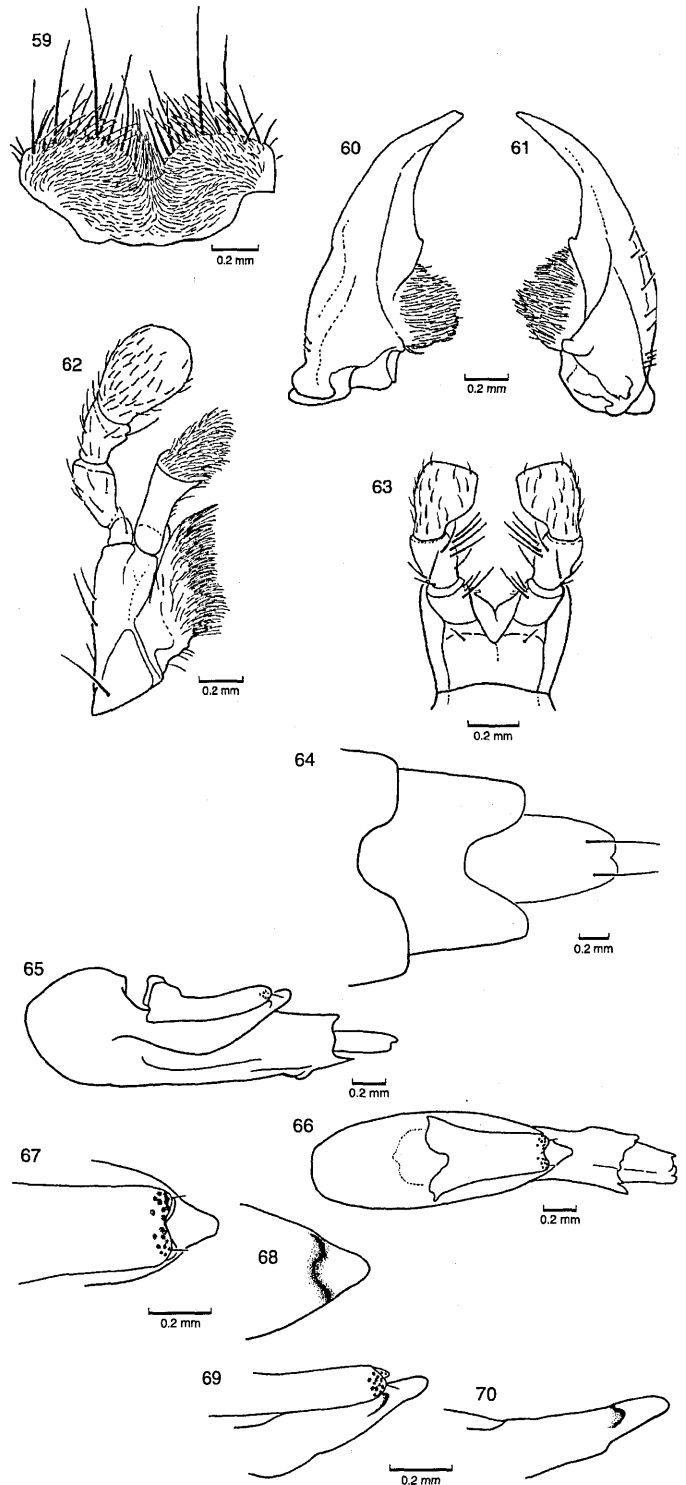
**Distribution.**—Currently known from elevations of 200–490 m from the northern and central lowlands of French Guiana and 160–500 m in north-central Suriname (Fig. 129).

**Habitat and Habits.**—Not known. All specimens for which collecting data are available were collected using flight intercept traps.

**Etymology.**—The specific epithet refers to the country of French Guiana from which a majority of the known specimens have been collected.

*Elmas hanleyi* new species  
(Figs. 1, 58–70)

**Diagnosis.**—Among Central American species, *Elmas windsori*, *E. panamaensis*, and *E. hanleyi* are similar and virtually impossible to distinguish on external characteristics, however, *E. hanleyi* is easily distinguished by the distinctive aedeagus (Figs. 65, 66). *Elmas hanleyi* has slightly more white on the apical antennal articles, and the hind



Figs. 59–70. *Elmas hanleyi*. 59, Labrum, dorsal aspect. 60, left mandible, dorsal aspect. 61, right mandible, dorsal aspect. 62, Maxilla, ventral aspect. 63, Labium, ventral aspect. 64, male sterna VII-VIII, X. 65, aedeagus, lateral aspect. 66, aedeagus, dorsal aspect. 67, aedeagus, detail of apex of paramere and median lobe, dorsal aspect. 68, apex of median lobe, dorsal aspect. 69, apex of paramere and median lobe, lateral aspect. 70, apex of median lobe, lateral aspect.

tibia is not clearly grooved in most, but because these characters vary among individuals, they are not reliable for distinguishing species. *Elmas hanleyi* is the only species of *Elmas* known to occur in the Atlantic lowlands of Costa Rica.

**Description.**—Length 13–15 mm (Fig. 1). Color black except for pale color on some antennal articles. Head with postclypeus deflexed ventrally in relation to frons, punctured more sparsely than frons, amount of punctation various from only slightly less than on frons to virtually absent; medial area between antennae without distinct shallow longitudinal V-shaped groove; eyes large, length about 4.0 times length of temples behind eyes; punctures small (about 5–6 punctures per 0.2 mm), uniformly distributed, punctures more or less round, very close, margins of punctures contiguous, punctate surfaces shining. Middle of frons not depressed to form a shallow pit, or very slightly depressed in a few. Postmandibular carina present, complete and prominent to base of head, or more or less obsolete medially. Mentum broadly, shallowly and uniformly arcuate around insertion of labium. Submentum subtruncate and slightly and broadly rounded medially, without large medial spinose process. Gula sutures convergent from broad apex to moderately narrow medial area (least width: length ratio = 0.15). Maxillary palpus (Fig. 62) with apical segment dilated apically, apical width across oblique apex about 2.0 times basal width; apex oblique, outer length about 1.3–1.4 times inner length. Labial palpus (Fig. 63) with apical segment expanded apically, width across oblique apex about 1.7 times width of base; apex oblique, outer length 1.3 times inner length. Mandibles (Figs. 60, 61) with apex of left mandible flattened, obliquely truncate apically, and more or less in horizontal plane of head. Antenna black with pale color (pale flavate) limited to longitudinal band on posterior margins of various articles, most with pale color limited to Articles 9–11, a few with Article 8 dark brown; Article 9 with trace of pale color at base up to 1/2 pale; Article 10 1/3–2/3 pale; Article 11 3/4 to fully pale; Articles 5–6 subquadrate, Articles 7–10 slightly transverse.

Pronotum slightly wider than long, width:length ratio = 1.08; anterolateral angles obtusely rounded, lateral angles not subcariniform; superior lateral line extended to contact inferior lateral line, obsolete immediately before contact with inferior lateral line in a few; punctures small (about 6–7 punctures per 0.2 mm), numerous, uniformly distributed, very close, edges of punctures contiguous or virtually contiguous, separated by about 0.1–0.3 times average width of punctures, punctures round anteriorly and medially or slightly elongated in longitudinal or posterolateral direction laterally and posteriorly, not coalesced into short, irregular longitudinal or posterolateral furrows; ridges between punctures shining.

Elytra with punctures small (about 4–5 punctures per 0.2 mm), individual punctures poorly to moderately defined, edges contiguous, elongated in longitudinal or posterolateral direction, faintly to moderately and irregularly coalesced into short, irregular furrows, punctate surface shining.

Anterior Tarsal Articles 1–4 uniformly covered with short, spatulate setae. Tarsal claws of middle and hind tarsi not modified, not very slender or sharply curved near middle. Hind tibia slightly flattened, without longitudinal groove on external surface or with very faint shallow groove, medial area of external surface of tibia variously punctate and setose, very narrowly impunctate longitudinally in some, punctate and setose similar to remainder of tibia in others.

Abdominal Terga III–V with moderate transverse basal impressions, Tergum VI with shallow transverse groove in some; microsculpture on III–V obsolete to absent distal to basal transverse ridges, surface shining; Terga VI–VIII with moderate to obsolete reticulate microsculpture.

Abdominal Sterna III–V with moderate transverse impressions, Sternum VI with shallow transverse impression in some; microsculpture on III–V obsolete or weakly reticulate to wavy distal to basal transverse ridges, surface shining; Sterna VI–VIII with reticulate to slightly wavy microsculpture.

**Secondary Sexual Characters.**—Male: distal margin of Tergum VII with moderate U-shaped emargination; distal margin of Tergum VIII deeply emarginate (Fig. 64).

**Aedeagus.**—As in Figs. 65, 66; paramere parallel-sided in apical half, apex truncate, apex broadly and shallowly emarginate, with about 10–12 moderately large black sensory spinules on each side, arranged in narrow apical band on apical lobes formed by emargination (Figs. 67, 69); apical lobe narrowed to acutely rounded apex, dorsal surface with one large cariniform ridge in shape of a broadly curved “U” that parallels the broadly emarginate shape of the apex of the paramere (Figs. 68, 70).

**Holotype.**—Male, with labels as follows: “COSTA RICA: Heredia, La Selva Biol. Res. Sta., 3 km. S. Puerto Viejo, 80m, 10°26' N, 84°1' W, 2–15-VI-1996, R. Hanley, flight intercept trap, CR1H96-016”, bar code label “SM0091596, KUNHM-ENT”, “HOLOTYPE, *Elmas hanleyi* Ashe & Chatzimanolis, Design. Ashe & Chatzimanolis, 2001”. Located in KSEM.

**Paratypes.**—110, with labels as follows: COSTA RICA: Heredia, La Selva, 3.2 km SE Puerto Viejo, 100 m, 10°26' N, 84°1' W, 6-III-1992, W. Bell, flight intercept trap, SM45974 SM45975 (2 KSEM). Same locality and collector, 17-III-1992, flight intercept trap, SM45953 SM45954 SM45956 SM45955 (4 KSEM). Same locality and collector, 17-II-1992, flight intercept trap, SM45961 SM45962 (2 KSEM). Same locality



and collector, 22-III-1992, flight intercept trap, SM45976 SM45949 (2 KSEM). Same locality and collector, 21-III-1992, flight intercept trap, SM45951 SM45950 SM45960 SM45959 (4 KSEM). Same locality and collector, 14-II-1992, flight intercept trap, SM45969 SM45963 SM45973 SM45964 SM45967 SM45968 (6 KSEM). Same locality and collector, 9-II-1992, flight intercept trap, SM45984 SM45983 SM45981 SM45982 (4 KSEM). Same locality and collector, 3-II-1992, flight intercept trap, SM45946 (1 KSEM). Same locality and collector, 30-I-1992, flight intercept trap, SM45948 (1 KSEM). Same locality and collector, 24-II-1992, flight intercept trap, SM45970 SM45972 (2 KSEM). Same locality and collector, 28-I-1992, flight intercept trap, SM45971 (1 KSEM). Same locality and collector, 28-II-1992, flight intercept trap, SM45952 (1 KSEM). Same locality and collector, 21-II-1992, flight intercept trap, SM45966 (1 KSEM). Same locality and collector, 19-II-1992, flight intercept trap, SM45957 (1 KSEM). Heredia, La Selva, W River Trail, 100 m, 10°26' N, 84°1' W, 3-III-1992, W. Bell, flight intercept trap, SM45943 SM45945 SM45944 (3 KSEM). Heredia, La Selva Biol. Res. Sta., 3 km. S. Puerto Viejo, 80m, 10°26' N, 84°1' W, 11-17-VI-1986, W. Hanson, G. Bohart, SM45977 (1 KSEM). Heredia, OTS, La Selva, 3.0 km S Puerto Viejo, 100 m, 10°26' N, 84°1' W, XI-1992, P. Hanson, malaise trap, SM45980 (1 KSEM). Heredia, La Selva Biol. Res. Sta., 3 km. S. Puerto Viejo, 80m, 10°26' N, 84° 1' W, 2-15-VI-1996, R. Hanley, flight intercept trap, CR1H96-016, SM91598 SM91608 SM91719 SM91600 SM91595 (5 KSEM). Same locality and collector, 4-10-VI-1996, flight intercept trap, CR1H96-010, SM88285 (1 KSEM). Limón, Valle La Estrella Hitoy Cerere, 50m, 21-22-V-1993, G. Carballo 2412, SM45992 (1 KSEM). Limón Prov., Sector Cerro Cocori, Finca de Elias Rojas, 100 m, E. Rojas coll., #2411, IX-1993, INBIO CR1001-522891 (1 INBio). Same locality and collector, 150m, 31-I-21-II-1992, INBIO CR1001-316967 (1 INBio). Same locality and collector, 150m, IV-1992, INBIO CR1001-879629 (1 INBio). Same locality and collector, 150m, VII-199, INBIO CR1001-586995, 596996, 596999, 59700 (4 INBio). Same locality and collector, 150m, 26-VII-2-VIII-1992, INBIO CR1001-736963 (1 INBio). Same locality and collector, 150m, 26-III-24-IV-1992, INBIO CR1001-770925, 770927 (2 INBio). Same locality and collector, 150m, I-1992, INBIO CR1001-333215, 333216, 333212 (3 INBio). Same locality and collector, 150m, VI-1991, INBIO CR1001-568359, 679921 (2 INBio). Same locality and collector, 150m, 28-V-17-VI-1992, INBIO CR1001-877489 (1 INBio). Same locality and collector, 150m, IV-1993, INBIO CR1001-346271 (1 INBio). Same locality and collector, 150m, VIII-1991, INBIO CR1001-581495, 581471, 581504 (3 INBio). Same locality and collector, 150m, I-1993, INBIO CR1001-404105, 404006 (2 INBio). Same locality and collector, 150m, V-1991, INBIO CR1001-675088, 651920, 562428, 562417, 562427, 562426 (6 INBio). Same locality and collector, 150m, XII-1992, INBIO

CR1001-961214, 961216, 550475, 961219, 961220, 961218 (6 INBio). Same locality and collector, 150m, XII-1991, INBIO CR1001-550475 (1 INBio). Same locality and collector, 150m, II-1993, INBIO CR1001-343513 (1 INBio). Same locality and collector, 150m, II-1992, INBIO CR1001-331287 (1 INBio). Limón Prov., Amubri, A. C. Amistad, 70 m, G. Gallardo coll., 8-30-III-1994, INBIO CR1001-791237, 791243, 791244 (3 INBio). Same locality and collector, 12-29-XI-1992, INBIO CR1001-900990 (1 INBio). Same locality and collector, 2-31-II-1996, INBIO CR1001-393678 (1 INBio). Same locality and collector, 1-19-II-1994, INBIO CR1001-707757 (1 INBio). Same locality and collector, 12-25-XI-1992, INBIO CR1001-901021 (1 INBio). Same locality and collector, 1-22-X-1994, INBIO CR1001-008880, 008876, 008873, 008816, 008818, 008824, 008875, 008879 (8 INBio). Limón Prov. 16 km W. Guapiles, 400 m, IV-1989, P. Hanson, INBIO CR1001-108472 (1 INBio). Limón Prov., P. N. Tortuguero, 0 m, VI-1990, M. Barreller coll., INBIO CR1001-569981, 569975 (2 INBio). Same locality, VI-1991, R. Delgado coll., INBIO CR1001-948945 (1 INBio). Same locality and collector, VII-1991, INBIO CR1001-364153 (1 INBio). Same locality and collector, X-1990, INBIO CR1001-285040 (1 INBio). Same locality, U. Chavarria coll., VII-1990, INBIO CR1001-244617 (1 INBio). Limón Prov., Est. Jalova, P. N. Tortuguero, 0 m, VII-1990, M. Barreller coll., INBIO CR1001-444737, 444736 (2 INBio). Limón Prov., Est. Hiloy Cerere, R. Cerere, Res. Bio. Hiloy Cerere, 100 m, 27-VI-22-VII-1992, K. Taylor coll., INBIO CR1001-538280 (1 INBio). Limón Prov., Est. Hiloy Cerere, R. Cerere, Res. Bio. Hiloy Cerere, 100-200 m, 14-II-20-V-1993, G. Carballo coll., INBIO CR1001-523013 (1 INBio). Limón Prov., Río Sardinias, R. N. F. S. Barra del Colorado, 10 m, 18-27-VII-1993, F. V. Araya coll., INBIO CR1001-954721, 954720 (2 INBio). Same locality and collector, 16-20-V-1994, INBIO CR1001-771177 (1 INBio). Same locality and collector, 1-14-II-1994, INBIO CR1001-877057, 877058 (2 INBio). Same locality and collector, 6-14-IV-1994, INBIO CR1001-848269, 848270 (2 INBio). Same locality and collector, 27-III-3-IV-1995, INBIO CR1001-191950 (1 INBio). Heredia Prov., Est. Magsasay, P. N. Braulio Carrillo, 200 m, E. Alcazar coll., VI-1990, INBIO CR1001-222558, 222615 (2 INBio).

**Distribution.**—Currently known from elevations of 10–400 m from the lowlands of the Atlantic slope of Costa Rica from the Limón Province in the south to La Selva Biological Station in Heredia in the northwest (Fig. 128).

**Habitat and Habits.**—Not known. All specimens for which collecting data are available were collected in flight intercept or Malaise traps.

**Etymology.**—The specific epithet is in honor of Rodney S. Hanley who collected a series of specimens of this species in Costa Rica.

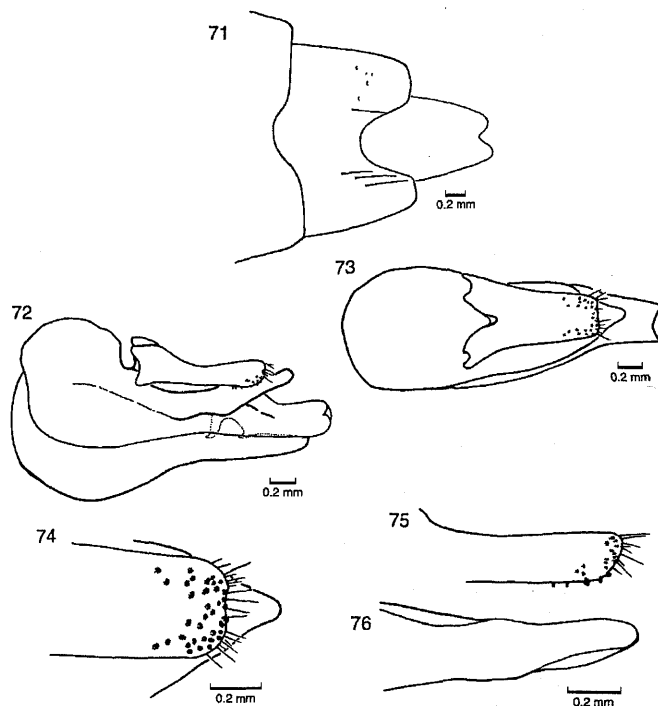
*Elmas hibbsi* new species

(Figs. 71-76)

**Diagnosis.**—Among South American *Elmas* that lack a medial spine on the submentum and that have a distinct longitudinal groove in the external surface of the hind tibia, *E. hibbsi* can be distinguished by the large size and extent of the groove in the hind tibia (occupying at least  $\frac{1}{2}$  of the width of the tibia at broadest point and at least  $\frac{1}{3}$  of the length of the tibia) and the distinctive aedeagus (Figs. 72, 73).

**Description.**—Length 15–18 mm. Color black except for pale color on some antennal articles. Head with postclypeus slightly deflexed ventrally in relation to frons, punctured similar to frons except less punctured in extreme antero-medial region; medial area between antennae without distinct shallow longitudinal V-shaped groove; eyes large, length about 4.3–4.5 times length of temples behind eyes; punctures small (about 6–7 punctures per 0.2 mm), uniformly distributed, punctures more or less round, very close, margins of punctures virtually contiguous, distance between punctures 0.1–0.2 times average width of punctures, punctate surfaces shining. Middle of frons not depressed to form a shallow pit. Postmandibular carina present, complete and prominent to base of head. Mentum broadly, shallowly and uniformly arcuate around insertion of labium. Submentum subtruncate and slightly and broadly rounded medially, without large medial spinose process. Gula sutures convergent from broad apex to moderate medial area (least width: length ratio = 0.17). Maxillary palpus with apical segment dilated apically, apical width across oblique apex 1.4–1.7 times basal width; apex oblique, outer length about 1.3–1.4 times inner length. Labial palpus with apical segment very greatly expanded apically, width across oblique apex 1.6–1.7 times width of base; apex oblique, outer length 1.5 times inner length. Mandibles with apex of left mandible flattened, obliquely rounded apically, and more or less in horizontal plane of head. Antenna black with pale color (brown to pale brown) limited to longitudinal band on posterior margins of various articles, most with pale color limited to Articles 9–11, a few with very narrow band of pale color in Articles 7 or 7–8; Article 9 black or with  $\frac{1}{5}$ – $\frac{1}{3}$  pale, Article 10, black or with  $\frac{1}{5}$ – $\frac{1}{3}$  black. Article 11 faintly pale at base or with  $\frac{1}{3}$ – $\frac{1}{2}$  pale; Articles 5–6 very slightly longer than greatest width, Articles 7–10 of about equal greatest length and width.

Pronotum subquadrate, width:length ratio = 1.03; anterolateral angles obtusely rounded, lateral angles not subcariniform; superior lateral line extended to contact inferior lateral line, obsolete immediately before contact with inferior lateral line in some; punctures moderate sized (about 8–9 punctures per 0.2 mm), numerous, uniformly



Figs. 71-76. *Elmas hibbsi*. 71, male sterna VII-VIII, X. 72, aedeagus, lateral aspect. 73, aedeagus, dorsal aspect. 74, aedeagus, detail of apex of paramere and median lobe, dorsal aspect. 75, apex of paramere, lateral aspect. 76, apex of median lobe, lateral aspect.

distributed, very close, edges of punctures contiguous, many elongated in longitudinal or posterolateral direction, not coalesced into short, irregular longitudinal or posterolateral furrows; ridges between punctures shining.

Elytra with punctures small (about 4–5 punctures per 0.2 mm), individual punctures moderately well defined, edges contiguous, elongated in longitudinal or posterolateral direction, not clearly coalesced into short, irregular furrows, punctate surface shining.

Anterior Tarsal Articles 1–4 uniformly covered with short, spatulate setae. Tarsal claws of middle and hind tarsi not modified, not very slender or sharply curved near middle. Hind tibia strongly flattened, with distinct longitudinal groove on external surface, medial area of groove broadly and distinctly impunctate, without scattered setae and punctures.

Abdominal Terga III–V with moderate transverse basal impressions, Tergum VI with very shallow transverse groove; microsculpture on III–V obsolete to absent distal to basal transverse ridges, surface shining; Terga VI–VIII with moderate reticulate microsculpture.

Abdominal Sterna III–V with shallow transverse impressions; microsculpture on III–V obsolete or weakly reticulate to wavy distal to basal transverse ridges, surface shining; Sterna VI–VIII with distinct reticulate microsculpture.

**Secondary Sexual Characters.**—Male: distal margin of Tergum VII with broad medial emargination; distal margin of Tergum VIII deeply emarginate (Fig. 71).

**Aedeagus.**—As in Figs. 72, 73; paramere broad and truncate apically, apex entire, with about 18–20 black sensory spinules on each side, arranged in a broad band near apex (Figs. 74, 75); apical lobe narrowed to acutely rounded apex, dorsal surface without medial teeth or semi-lunulate carinae (Figs. 74, 76).

**Holotype.**—Male, with labels as follows: "ECUADOR: Pichincha, Río Palenque Science Center, 200 m, 0°36'0" S, 79°21'0" W, 25-IV-6-VI-1996, P. Hibbs, flight intercept trap", bar code label "SM0092666, KUNHM-ENT", "HOLOTYPE, *Elmas hibbsi* Ashe & Chatzimanolis, Design. Ashe & Chatzimanolis, 2001". Located in KSEM.

**Paratypes.**—10, with labels as follows: ECUADOR: Pichincha, Tinalandia, Santo Domingo, 16 km E, 750 m, 0°16'53" S, 79°3'39" W, 26-27-III-1999, R. Brooks, D. Brzoska, flight intercept trap, ECU1B99-048, SM153411, SM153410 (2 KSEM). Pichincha, Río Palenque Science Center, 200 m, 0°36'0" S, 79°21'0" W, 25-IV-6-VI-1996, P. Hibbs, flight intercept trap, ECU1H96-002A, SM92673, SM92667, SM92669, SM92671, SM92668, SM92675, SM92674, SM92670 (8 KSEM).

**Distribution.**—Currently known from elevations of 200–750 in Pichincha Province, Ecuador (Fig. 129).

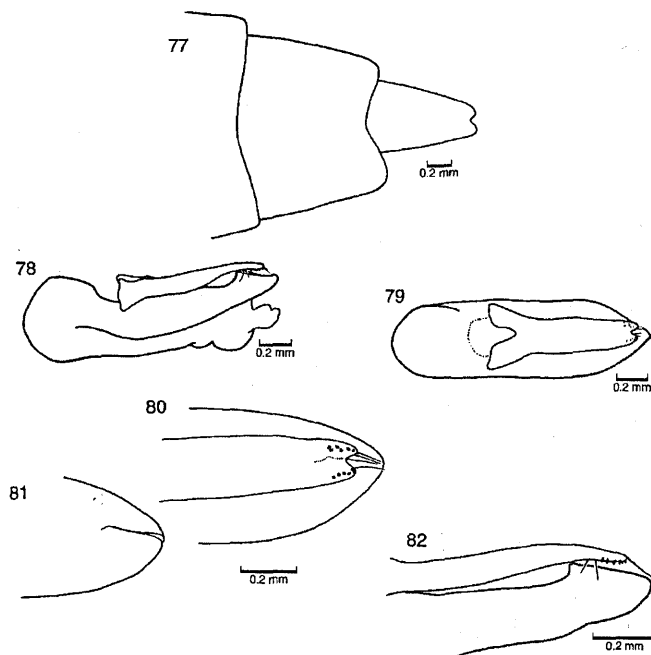
**Habitat and Habits.**—Not known. All specimens for which collecting data are available were collected using flight intercept traps.

**Etymology.**—The specific epithet is in honor of Peter Hibbs who collected most of the known specimens of this species in Ecuador.

*Elmas lambas* new species  
(Figs. 77–82)

**Diagnosis.**—Aedeagus (Figs. 78, 79) and secondary sexual characteristics (Fig. 77) of *E. lambas* are similar to those of *E. strigellus*, but *E. lambas* is smaller and punctation and microsculpture are completely different; also tarsal claws of *E. lambas* are not modified as in *E. strigellus*, and tip of left mandible is twisted slightly toward vertical but not as fully to vertical as in *E. strigellus*. *Elmas lambas* has the most widely separated punctures on head and pronotum of any described species, and elytral punctures not elongated or coalesced into irregular furrows. The pronotum of *E. lambas* has a strongly shining medial impunctate area extended from base to apex.

**Description.**—Length 14 mm. Color black except for pale color on some antennal articles. Head with postclypeus not noticeably deflexed ventrally in relation to frons, punctured similar to frons; medial area between



Figs. 77–82. *Elmas lambas*. 77, male sternite VII–VIII, X, outline. 78, aedeagus, lateral aspect. 79, aedeagus, dorsal aspect. 80, aedeagus, detail of apex of paramere and median lobe, dorsal aspect. 81, apex of median lobe, dorsal aspect. 82, apex of paramere and median lobe, lateral aspect.

antennae without distinct shallow longitudinal V-shaped groove; eyes large, length about 4.5 times length of temples behind eyes; punctures moderate sized (about 3–4 punctures per 0.2 mm), uniformly distributed, punctures more or less round, close but not contiguous, punctures separated by 0.1–0.3 times average width of punctures, punctures slightly more widely separated posteromedially, surfaces between punctures strongly shining. Middle of frons not depressed to form a shallow pit. Postmandibular carina present only near mandibular fossa, replaced medially and on base of head by large irregular punctures. Mentum broadly, shallowly and uniformly emarginate around insertion of labium. Submentum broadly emarginate, without large medial spinose process. Gula sutures convergent from broad apex to very narrow medial area (least width: length ratio = 0.09). Maxillary palpus with apical segment dilated apically, apical width across oblique apex about 2.2 times basal width; apex oblique, outer length about 1.2 times inner length. Labial palpus with apical segment expanded apically, width across oblique apex about 1.5 times width of base; apex oblique, outer length 1.3 times inner length. Mandibles with apex of left mandible flattened, broadly and obliquely truncate apically, and twisted dorsally above horizontal plane of head. Antenna black with pale color (pale flavate) limited to Articles 8–11, Article 8 pale flavate clouded with pale brown basally; Articles 9–11 fully pale; Articles 5–7 subquadrate, Articles 8–10 slightly transverse.

Pronotum slightly wider than long, width:length ratio = 1.05; anterolateral angles obtusely rounded, lateral angles not subcariniform; superior lateral line extended to contact inferior lateral line; punctures small (about 4–5 punctures per 0.2 mm), numerous, more or less uniformly distributed except for strongly shining impunctate medial area extended from base to apex, close but not contiguous, separated by about 0.1–1.0 times average width of punctures, punctures round or very slightly elongated in longitudinal or posterolateral direction, not coalesced into short, irregular longitudinal or posterolateral furrows; spaces between punctures strongly shining.

Elytra with punctures small (about 3–4 punctures per 0.2 mm), individual punctures moderately defined, edges close but not contiguous, not elongated in longitudinal or posterolateral direction, not coalesced into short, irregular furrows, punctate surface shining.

Anterior Tarsal Articles 1–4 uniformly covered with short, spatulate setae. Tarsal claws of middle and hind tarsi not modified, not very slender or sharply curved near middle. Hind tibia slightly flattened, with distinct longitudinal groove on external surface, medial area of groove impunctate longitudinally, without scattered setae and punctures.

Abdominal Terga III–V with moderate transverse basal impressions; microsculpture on III–V obsolete to absent distal to basal transverse ridges, surface shining.

Abdominal Sterna III–V with moderate transverse impressions; microsculpture on III–VIII obsolete to absent distal to basal transverse ridges, surface strongly shining.

**Secondary Sexual Characters.**—Male: distal margin of Tergum VII without emargination; distal margin of Tergum VIII slightly and broadly emarginate (Fig. 77).

**Aedeagus.**—As in Figs. 77, 79; paramere slender and parallel-sided, apex emarginate medially, with about 6–7 black sensory spinules arranged in a longitudinal band on each side (Figs. 80, 82); apical lobe broadly rounded with a single medial tooth dorsally, tooth extended to apex as a low, narrow ridge (Figs. 81, 82).

**Holotype.**—Male, with labels as follows: "BRAZIL: Pará, Redenção vic., Kayapo Territory, Pinkaiti Field Station on Riozinho River, 7°46.29' S 51°57.65' W, tropical evergreen seasonal lowland forest on clay soil, dung pitfall or flight intercept traps, P.Y. Scheffler, leg." "HOLOTYPE: *Elmas lambas* Ashe & Chatzamanolis, Design. Ashe & Chatzamanolis 2001". Located in FMNH.

**Paratypes.**—No other specimens known

**Distribution.**—Currently only known from the type locality in the state of Pará, Brazil (Fig. 129).

**Habitat and Habits.**—Not known. The only known specimen was either collected in a dung pitfall trap or a flight intercept trap (both present on label).

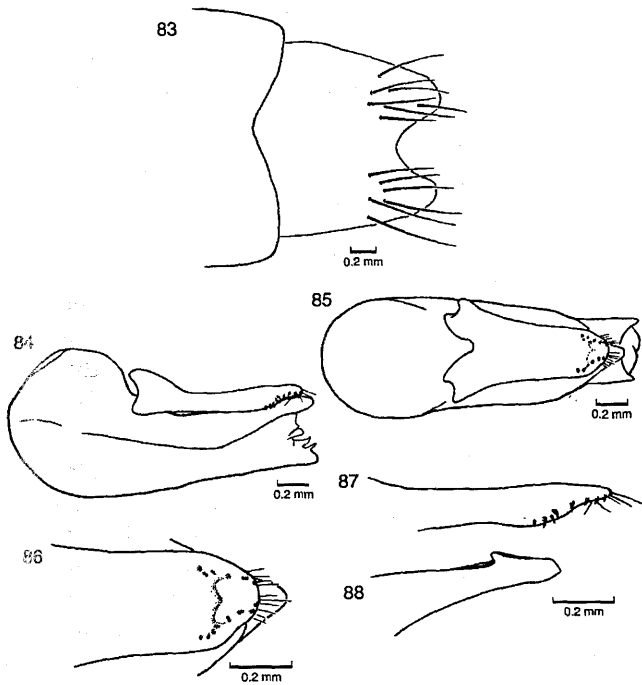
**Etymology.**—The specific epithet is derived from the Greek *lambo*, meaning to shine and refers to the shining integument between the relatively widely spaced punctures of this species.

*Elmas lescheni* new species  
(Figs. 83–88)

**Diagnosis.**—Among those South American *Elmas* that do not have a distinct longitudinal groove on the external surface of the hind tibia, *E. lescheni* is most similar to *E. brooksi*; both have relatively large extent of pale flavate color on antenna, with 9–11 fully or virtually completely pale; it can be distinguished from *E. brooksi* only by its distinctive aedeagus (Figs. 84, 85).

**Description.**—Length 14–15 mm. Color black except for pale flavate color on some antennal articles. Head with postclypeus very slightly deflexed ventrally in relation to frons, medial region punctured similarly to frons, with fewer punctures laterally especially near antennal insertions; medial area between antennae without distinct shallow longitudinal V-shaped groove; eyes large, length about 4.5 times length of temples behind eyes; punctures small (about 6–7 punctures per 0.2 mm), uniformly distributed, punctures more or less round, very close, margins of punctures contiguous, punctate surfaces shining. Middle of frons very faintly depressed to form a very indistinct and shallow depression. Postmandibular carina present, complete anteriorly and on base of head, interrupted medially by large irregular punctures. Mentum broadly, shallowly and uniformly arcuate around insertion of labium. Submentum subtruncate, without large medial spinose process. Gula sutures convergent from broad apex to moderately broad medial area (least width: length ratio = 0.22). Maxillary palpus with apical segment strongly dilated apically, apical width across oblique apex 2.3 times basal width; apex oblique, outer length about 1.3 times inner length. Labial palpus with apical segment very greatly expanded apically, width across oblique apex 1.7 times width of base; apex oblique, outer length 1.3 times inner length. Mandibles with apex of left mandible flattened, obliquely truncate apically, and rotated slightly dorsal to horizontal plane of head. Antenna black with pale color (very pale yellowish white) limited to Articles 8 (Article 7 dark brown in one specimen)–11, Article 8 uniformly pale except for brownish center, Articles 9–11 uniformly pale; Article 5 subquadrate, Articles 6–10 slightly transverse.

Pronotum subquadrate, width:length ratio = 1.01; anterolateral angles obtusely rounded, lateral angles not subcariniform; superior lateral line extended to contact inferior lateral line; punctures small (about 7–8 punctures per 0.2 mm), numerous, uniformly distributed, very close, edges of punctures contiguous, some slightly elongated in longitudinal or posterolateral direction, not coalesced



Figs. 83–88. *Elmas lescheni*. 83, male sterna VII–VIII. 84, aedeagus, lateral aspect. 85, aedeagus, dorsal aspect. 86, aedeagus, detail of apex of paramere and medial lobe, dorsal aspect. 87, apex of paramere, lateral aspect. 88, apex of median lobe, lateral aspect.

into short, irregular longitudinal or posterolateral furrows; ridges between punctures shining.

Elytra with punctures small (about 4 punctures per 0.2 mm), individual punctures moderately well defined, edges contiguous, elongated in longitudinal or posterolateral direction, not coalesced into short, irregular furrows, surface between punctures shining.

Anterior Tarsal Articles 1–4 uniformly covered with short, spatulate setae. Tarsal claws of middle and hind tarsi not modified, not very slender or sharply curved near middle. Hind tibia slightly flattened, without distinct longitudinal groove on external surface, medial area of tibia with longitudinal subglabrous area.

Abdominal Terga III–V with moderate transverse basal impressions, Tergum VI with very shallow transverse depression or not noticeably depressed; microsculpture on III–VIII obsolete to absent distal to basal transverse ridge, surface shining.

Abdominal Sterna III–V with very shallow transverse impressions; microsculpture on III–VIII obsolete to absent distal to basal transverse ridges, surface shining.

**Secondary Sexual Characters.**—Male: distal margin of Tergum VII with broad and shallow medial emargination; distal margin of Tergum VIII deeply emarginate (Fig. 83).

**Aedeagus.**—As in Figs. 84, 85; paramere broadly rounded apically, apex entire, with about 6–8 black sensory spinules on each side, arranged in longitudinal band on each

side of apex (Figs. 86, 87); apical lobe narrowed to acutely rounded apex, dorsal surface with 2 large medial semi-lunulate carinae, carinae contiguous medially (Figs. 86, 88).

**Holotype.**—Male, with labels as follows: “PERU: Loreto, Teniente López, 240 m, 2°35' S, 76°6' W, 18–20-VII-1993, R. Leschen, flight intercept trap, PERU1L93-136”, bar code label “SM0045990, KUNHM-ENT”, “HOLOTYPE, *Elmas lescheni* Ashe & Chatzimanolis, Design. Ashe & Chatzimanolis, 2001”. Located in KSEM.

**Paratypes.**—1, with labels as follows: PERU: Loreto, Campamento San Jacinto, 175–215 m, 2°18' S, 75°51' W, 5–7-VII-1993, R. Leschen, flight intercept trap, PERU1L93-043, SM45991 (1 KSEM)

**Distribution.**—Currently known from elevations of 175–240 m in northern Loreto Department in Amazonian Peru (Fig. 129).

**Habitat and Habits.**—Not known. All specimens for which collecting data are available were collected using flight intercept traps.

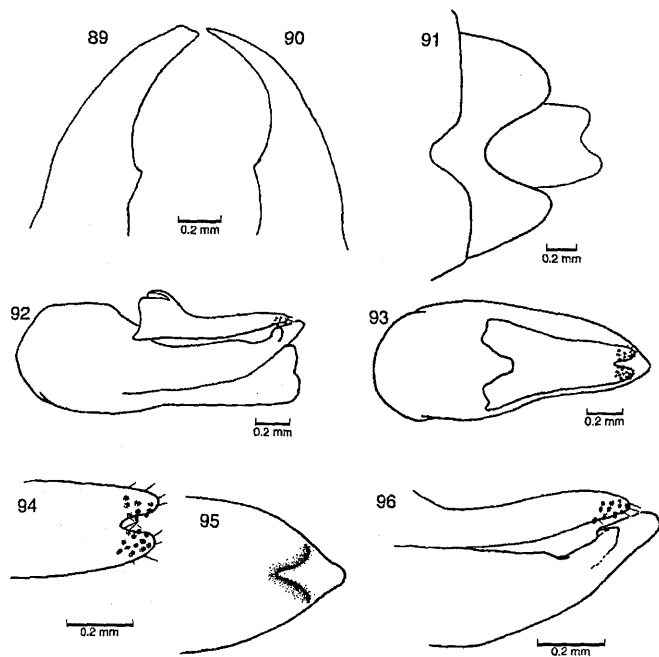
**Etymology.**—The specific epithet is in honor of Richard A. B. Leschen who collected all known specimens of this species in Peru.

*Elmas modesta* (Sharp), 1876  
(Figs. 89, 90)

*Selma modesta* Sharp, 1876: 427

**Diagnosis.**—*Elmas modesta* is similar to *E. hanleyi*, and cannot be distinguished from it based on external characteristics (see discussion below).

**Description.**—Length 13–15 mm. Color black except for pale flavate color on some antennal articles. Head with postclypeus deflexed ventrally in relation to frons, punctured more sparsely than frons, punctuation virtually absent; medial area between antennae without distinct shallow longitudinal V-shaped groove; eyes large, length about 4.0 times length of temples behind eyes; punctures small (about 5–6 punctures per 0.2 mm), uniformly distributed, punctures more or less round, very close, margins of punctures contiguous, punctate surfaces shining. Middle of frons slightly depressed to form a shallow pit or not depressed. Postmandibular carina present, complete and prominent to base of head, or more or less obsolete medially. Mentum broadly, shallowly and uniformly arcuate around insertion of labium. Submentum subtruncate and slightly and broadly rounded medially, without large medial spinose process. Gula sutures convergent from broad apex to moderate medial area (least width: length ratio = 0.15). Maxillary palpus with apical segment dilated apically, apical width across oblique apex about 2.0 times basal width; apex oblique, outer length about 1.3 times inner length. Labial palpus with apical segment expanded apically, width across oblique apex about 1.7 times width



Figs. 89–96. *Elmas modesta*. 89, left mandible, apex, dorsal aspect. 90, right mandible, dorsal aspect. Figs. 91–96. *Elmas panamaensis*. 91, male sterna VII–VIII, X. 92, aedeagus, lateral aspect. 93, aedeagus, dorsal aspect. 94, aedeagus, detail of apex of paramere, dorsal aspect. 95, apex of median lobe, dorsal aspect. 96, apex of paramere and median lobe, lateral aspect.

of base; apex oblique, outer length 1.3 times inner length. Mandibles (Figs. 89, 90) with apex of left mandible flattened, obliquely truncate apically, and more or less in horizontal plane of head. Antenna black with pale color (pale flavate) limited to Articles 8–11, Article 8 1/2 pale or fully dark brown; Article 9 1/2–3/4 pale; Article 10 3/4 to fully pale; Article 11 fully pale; Articles 5–6 subquadrate, Articles 7–10 slightly transverse.

Pronotum subquadrate, width:length ratio = 1.03–1.04; anterolateral angles obtusely rounded, lateral angles not subcariniform; superior lateral line extended to contact inferior lateral line; punctures small (about 6–7 punctures per 0.2 mm), numerous, uniformly distributed, very close, edges of punctures contiguous or virtually contiguous, separated by about 0.1–0.2 times average width of punctures, punctures round anteriorly and medially or slightly elongated in longitudinal or posterolateral direction laterally and posteriorly, not coalesced into short, irregular longitudinal or posterolateral furrows; ridges between punctures shining.

Elytra with punctures small (about 4–5 punctures per 0.2 mm), individual punctures poorly to moderately defined, edges contiguous, elongated in longitudinal or posterolateral direction, faintly to moderately and irregularly coalesced into short, irregular furrows, punctate surface shining.

Anterior Tarsal Articles 1–4 uniformly covered with short, spatulate setae. Tarsal claws of middle and hind tarsi not modified, not very slender or sharply curved near middle. Hind tibia slightly flattened, without longitudinal groove on external surface, medial area of external surface of tibia very narrowly impunctate longitudinally in available specimens.

Abdominal Terga III–V with moderate transverse basal impressions, Tergum VI with shallow transverse groove; microsculpture on III–V obsolete to absent distal to basal transverse ridges, surface shining; Terga VI–VIII with moderate to obsolete reticulate microsculpture.

Abdominal Sterna III–V with moderate transverse impressions, Sternum VI with very shallow transverse impression; microsculpture on III–V obsolete or weakly reticulate to wavy distal to basal transverse ridges, surface shining; Sterna VI–VIII with reticulate to slightly wavy microsculpture.

**Secondary Sexual Characteristics.**—None in female. Males not known.

**Aedeagus.**—Males not known.

**Holotype.**—Female, with Abdominal Segments IX–X dissected and glued on the bar next to the remainder of the body. Body glued onto a paper bar in a thick paper card between two glass plates, with labels as follows: on the paper card mount in D. Sharp's handwriting, "*Selma modesta*, Nicaragua, Type, D.S.", below, round red and white "Type" label, small round green label with handwritten "Chontales", and "B. C. A. Col. I. 2, *Selma modesta* Sharp". In the collection of the BMNH. Sharp (1876) specifically stated in the original description that he had only a single female specimen available; that specimen is therefore the holotype of the species.

**Other Specimens.**—A second female specimen, the one illustrated in the *Biologia Centrali Americana* (Sharp, 1884, Plate 8, Fig. 14), also is present in the collection of the Natural History Museum, London. It is glued onto a paper card and includes the following labels: on the paper card, in D. Sharp's handwriting, "*Selma modesta*" D. S., Chontales, Nicarag., Belt", on a label below, "Sp. Figured", below this a rectangular white label "Chontales, Nicaragua, T. Belt", below this "B. C. A. Col. I. 2, *Selma modesta* Sharp". It is not clear why Sharp failed to mention this specimen in his original description. Perhaps he received it from Thomas Belt later; collection dates are not given on the labels of either this or the type specimen. Without further information, we conclude that this specimen is not a member of the type series.

**Distribution.**—Known only from the type locality, Chontales, Nicaragua (Fig. 128).

**Habitat and Habits.**—Not known.

**Discussion.**—*Elmas modesta* is known from only two females collected at Chontales, Nicaragua by Thomas Belt. Because no males are included in the type series, and we have been unable to locate other specimens of *Elmas* that were subsequently collected from nearby areas in Nicaragua, it is not possible to confirm the specific status of other Central American species of *Elmas* in relation to *E. modesta*. *Elmas modesta* is most similar to *E. hanleyi*, and these two species cannot be distinguished on external characters. In addition to overall body form and size, these two species share: similar shape to the apex of the right mandible; similar shapes of apical articles of maxillary and labial palpi; amount and distribution of white on antennal articles (within range of variation of *E. hanleyi*); similar punctuation of head, pronotum, elytra and abdomen; lack of a longitudinal groove on external surface of hind tibia (with in range of variation of *E. hanleyi*); and hind tibia very narrowly impunctate medially (also within range of variation of *E. hanleyi*). Although the two available specimens of *E. modesta* have slightly more quadrate pronota (width:length ratio = 1.03–1.04) than those found in *E. hanleyi* (width:length ratio = 1.08), this difference is slight and not sufficient to distinguish between specimens of these two species. It is quite possible that *E. modesta* and *E. hanleyi* represent the same species. However, it is difficult and unreliable to distinguish among most Central American species of *Elmas* without examination of the male copulatory organ. Consequently, we recognize *E. modesta* as a separate species from *E. hanleyi* pending collection of additional specimens, including males, from (or near) the type locality of *E. modesta* that unambiguously can be assigned to the latter species.

*Elmas panamaensis* new species  
(Figs. 91–96)

**Diagnosis.**—Among Central American species, *E. windsori*, *E. panamaensis*, and *E. hanleyi* are similar and virtually impossible to distinguish based on external characteristics; *E. panamaensis* is easily distinguished by the distinctive aedeagus (Figs. 92, 93); *E. panamaensis* has less white on the apical antennal articles than does *E. hanleyi*, and has a narrow, impunctate groove on the external surface of the hind tibia (a feature shared with *E. windsori*, but not with *E. hanleyi*), but because these characters vary among individuals, they are difficult to use for distinguishing species. *Elmas panamaensis* is the only species of *Elmas* known to occur on Barro Colo-

rado Island in Panama; however, it has been collected in the adjacent areas of Pipeline Road and Gamboa with *E. windsori*.

**Description:** Length 14–16 mm. Color black except for pale color on some antennal articles. Head with postclypeus deflexed ventrally in relation to frons, punctured more sparsely than frons, especially laterally in most specimens; medial area between antennae without distinct shallow longitudinal V-shaped groove; eyes large, length about 4.2 times length of temples behind eyes; punctures small (about 4–5 punctures per 0.2 mm), uniformly distributed, punctures more or less round, very close, margins of punctures contiguous, punctate surfaces shining. Middle of frons not depressed to form a shallow pit, or very slightly depressed in a few. Postmandibular carina present, prominent anteriorly and on base of head in most, more or less obsolete medially. Mentum broadly, shallowly and uniformly arcuate around insertion of labium. Submentum subtruncate and slightly and broadly rounded medially, without large medial spinose process. Gula sutures convergent from broad apex to moderate medial area (least width:length ratio = 0.19). Maxillary palpus with apical segment dilated apically, apical width across oblique apex about 2.0 times basal width; apex oblique, outer length about 1.2–1.3 times inner length. Labial palpus with apical segment expanded apically, width across oblique apex about 2.2 times width of base; apex oblique, outer length 1.3 times inner length. Mandibles with apex of left mandible flattened, obliquely rounded apically, and more or less in horizontal plane of head. Antenna black with pale color (pale flavate) limited to longitudinal band on posterior margins of various articles, most with pale color limited to Articles 9–11, a few with very narrow band of pale color on Article 8; Article 9 without pale color up to 1/3 pale; Article 10 1/4–1/2 pale; Article 11 1/3–1/2 pale; Articles 5–6 subquadrate, Articles 7–10 slightly transverse.



Pronotum slightly wider than long, width:length ratio = 1.10; anterolateral angles obtusely rounded, lateral angles not subcariniform; superior lateral line extended to contact inferior lateral line, obsolete immediately before contact with inferior lateral line in some; punctures small (about 6–7 punctures per 0.2 mm), numerous, uniformly distributed, very close, edges of punctures contiguous or virtually contiguous, separated by about 0.1–0.2 times average width of punctures, punctures round or slightly elongated in longitudinal or posterolateral direction laterally and posteriorly, not coalesced into short, irregular longitudinal or posterolateral furrows; ridges between punctures shining.

Elytra with punctures small (about 4–5 punctures per 0.2 mm), individual punctures poorly to moderately defined, edges contiguous, elongated in longitudinal or posterolateral direction, irregularly coalesced into short, irregular furrows, punctate surface shining.

Anterior Tarsal Articles 1–4 uniformly covered with short, spatulate setae. Tarsal claws of middle and hind tarsi not modified, not very slender or sharply curved near middle. Hind tibia slightly flattened, with distinct, but narrow, longitudinal groove on external surface, medial area of groove narrowly impunctate longitudinally, without scattered setae and punctures.

Abdominal Terga III–V with moderate transverse basal impressions, Tergum VI with shallow transverse groove; microsculpture on III–V obsolete to absent distal to basal transverse ridges, surface shining; Terga VI–VIII with moderate to obsolete reticulate microsculpture.

Abdominal Sterna III–V with moderate transverse impressions, sternum VI with shallow transverse impression; microsculpture on III–V obsolete or weakly reticulate distal to basal transverse ridges, surface shining; Sterna VI–VIII with reticulate to slightly wavy microsculpture.

**Secondary Sexual Characters.**—Male: distal margin of Tergum VII with moderate U-shaped emargination; distal margin of Tergum VIII deeply emarginate (Fig. 91).

**Aedeagus.**—As in Figs. 92, 93; paramere rounded apically, apex deeply emarginate, with about 9–12 moderately large black sensory spinules on each side, arranged in a cluster on apical lobes formed by emargination (Figs. 94, 96); apical lobe narrowed to acutely rounded apex, dorsal surface with one large cariniform ridge in shaped of a curved “V” that parallels the emarginate shape of the apex of the paramere (Figs. 95, 96).

**Holotype.**—“PANAMA: Panama, Barro Colorado Island, 9°11' N, 79°51' W, 6–10-VII-2000, S. Chatzimanolis, PAN1C00 056, flight intercept trap”, bar code label “SM0205050, KUNHM-ENT”, “HOLOTYPE, *Elmas panamaensis* Ashe & Chatzimanolis, Design. Ashe & Chatzimanolis, 2001”. Located in KSEM.

**Paratypes.**—11, with labels as follows: PANAMA: Colón, Pipeline Rd, km 6.1, Parque Nac. Soberania, 40 m, 9°7' N, 79°45' W, 7–21-VI-1995, J. Ashe, R. Brooks, flight intercept trap, PAN1AB95-265, SM7076 (1 KSEM). Panama, Barro Colorado Island, 9°11' N, 79°51' W, 24-VIII-1994, D. Banks, flight intercept trap, SM45940 (1 KSEM). Same locality and collector, 16-VI-1994, flight intercept trap, SM45985 (1 KSEM). Same locality and collector, 7-VI-1994, flight intercept trap, SM45939 (1 KSEM). Same locality, 23-I-1967, M. G. Naumann, trap, SM45941 (1 KSEM). Same locality, 9°11' N, 79°51' W, 1–5-VII-2000, S. Chatzimanolis, PAN1C00 046, flight intercept trap, SM0205052 (1 KSEM). Same locality and collector, 6–10-VII-2000, PAN1C00 056, flight intercept trap, SM020501 (1 KSEM). Same locality and collector, 30-VI-2000, PAN1C00 034, flight intercept trap, SM0205049 (1 KSEM). Same locality and collector, 14–18-VII-2000, PAN1C00 013, flight intercept trap, SM0205048 (1 KSEM). Same locality and collector, 21–22-VII-2000, PAN1C00 082, flight intercept trap, SM0205047 (1 KSEM).

**Distribution.**—Currently known from the lowlands of Panama on Barro Colorado Island, and in the nearby areas of Pipeline Road and Gamboa (Fig. 128).

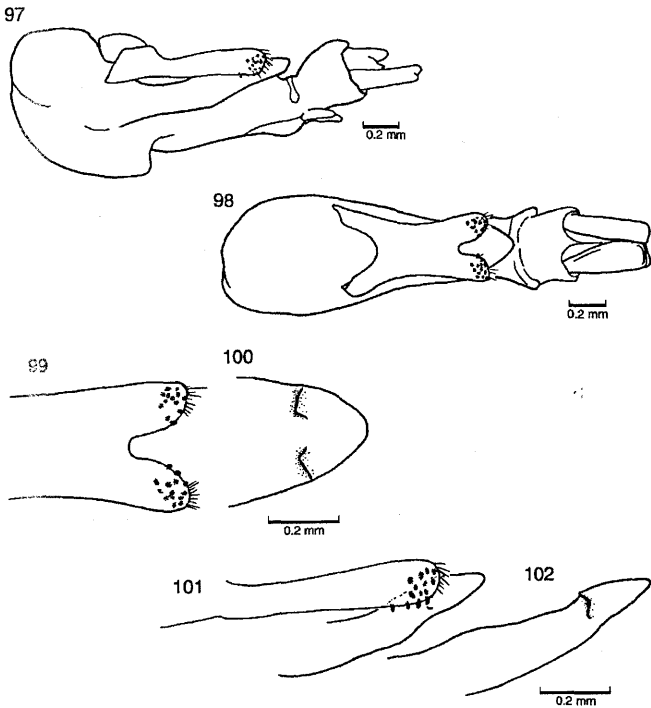
**Habitat and Habits.**—Not known. All specimens for which collecting data are available were collected using flight intercept traps.

**Etymology.**—The specific epithet refers to the country of Panama from which all known specimens of this species have been collected.

*Elmas patillas* new species  
(Figs. 97–102)

**Diagnosis.**—*Elmas patillas* is similar to *E. panamaensis* and very difficult to distinguish based on external characteristics. *Elmas patillas* is slightly larger (16–18mm as compared to 14–16 mm for *E. panamaensis*), and has more extensive light color on antenna. There are substantial differences in aedeagus (Figs. 97, 98): the paramere of *E. patillas* is broader apically and more deeply emarginate; and, the carinae on the dorsal surface of the median lobe are widely separated in *E. patillas* (contiguous and forming a “V”-shaped carina in *E. panamaensis*). *Elmas patillas* is the only *Elmas* species currently known to occur at Patilla Biological Station in Costa Rica.

**Description.**—Length 16–18 mm. Color black except for pale color on some antennal articles. Head with postclypeus slightly deflexed ventrally in relation to frons, impunctate except for a few scattered small punctures along anterior margin, strongly shining; medial area between antennae without distinct shallow longitudinal V-shaped groove; eyes large, length about 5.1 times length of temples behind eyes; punctures small (about 4–5 punc-



Figs. 97–102. *Elmas patillas*. 97, aedeagus, lateral aspect. 98, aedeagus, dorsal aspect. 99, aedeagus, detail of apex of paramere, dorsal aspect. 100, apex of median lobe, dorsal aspect. 101, apex of paramere and median lobe, lateral aspect. 102, apex of median lobe, lateral aspect.

tures per 0.2 mm), uniformly distributed, punctures more or less round, very close, margins of punctures contiguous or virtually so, punctate surfaces shining. Middle of frons slightly depressed to form a shallow pit. Postmandibular carina present, prominent anteriorly and weak on base of head in most, more or less obsolete medially and replaced by large irregular punctures. Mentum broadly, shallowly and uniformly arcuate around insertion of labium. Submentum subtruncate and slightly and broadly rounded medially, without large medial spinose process. Gula sutures only slightly convergent from broad apex to moderate medial area (least width: length ratio = 0.15). Maxillary palpus with apical segment dilated apically, apical width across oblique apex about 2.0 times basal width; apex oblique, outer length about 1.5 times inner length. Labial palpus with apical segment expanded apically, width across oblique apex about 1.8 times width of base; apex oblique, outer length 1.3 times inner length. Mandibles with apex of left mandible flattened, obliquely rounded apically, and more or less in horizontal plane of head. Antenna black with pale color (pale flavate) limited to Articles 8–11, a few with Article 7 dark brown; Article 8 dark brown with a trace of pale color on external apex up to 1/3 pale; Article 9–11 fully pale or 9 fully pale except for a trace of brown basally; Articles 5–7 slightly longer than wide, Articles 8–10 subquadrate.

Pronotum slightly wider than long, width:length ratio = 1.06; anterolateral angles obtusely rounded, lateral angles not subcariniform; superior lateral line extended to contact inferior lateral line, obsolete immediately before contact with inferior lateral line in some; punctures small (about 5–6 punctures per 0.2 mm), numerous, uniformly distributed, very close, edges of punctures contiguous or virtually contiguous, separated by about 0.1–0.2 times average width of punctures, punctures round on anterior third and slightly to moderately elongated in longitudinal or posterolateral direction laterally and posteriorly, not coalesced into short, irregular longitudinal or posterolateral furrows; ridges between punctures shining.

Elytra with punctures small (about 3–4 punctures per 0.2 mm), individual punctures poorly to moderately defined, edges contiguous, elongated in longitudinal or posterolateral direction, irregularly coalesced into short, irregular furrows, punctate surface shining.

Anterior Tarsal Articles 1–4 uniformly covered with short, spatulate setae. Tarsal claws of middle and hind tarsi not modified, not very slender or sharply curved near middle. Hind tibia slightly flattened, with distinct, but narrow, longitudinal groove on external surface, medial area of groove narrowly impunctate longitudinally, without scattered setae and punctures or, in a few, number of setae distinctly reduced in narrow groove compared to remainder of surface of tibia.

Abdominal Terga III–V with moderate transverse basal impressions, Tergum VI with shallow transverse groove; microsculpture on III–VI obsolete to absent distal to basal transverse ridges, surface shining; Terga VII–VIII with moderate to obsolete reticulate to wavy microsculpture.

Abdominal Sterna III–V with moderate transverse impressions; microsculpture on III–V obsolete or weakly reticulate or wavy distal to basal transverse ridges, surface shining; Sterna VI–VIII with reticulate to slightly wavy microsculpture.

**Secondary Sexual Characters.**—Male: distal margin of Tergum VII with moderate U-shaped emargination; distal margin of Tergum VIII deeply emarginate (similar to Fig. 91).

**Aedeagus.**—As in Figs. 97, 98; paramere slightly broadened apically, apex deeply emarginate, with about 13 moderately large black sensory spinules on each side, arranged in a cluster on apical lobes formed by emargination (Figs. 99, 101); apical lobe narrowed to rounded apex, dorsal surface with 2 large cariniform ridges on each side that parallel the lobes of the apex of the paramere (Figs. 100, 102).

**Holotype.**—“COSTA RICA: Guanacaste, Patilla Biological Station, 610 m, 10°59'22" N, 85°25'33" W, 13–15-VII-2000, J. Ashe, R. Brooks, Z. Falin, flight intercept trap,

CR1ABF00-135", bar code label "SM0189727, KUNHM-ENT", "HOLOTYPE, *Elmas patillas* Ashe & Chatzimanolis, Design. Ashe & Chatzimanolis, 2001". Located in KSEM.

**Paratypes.**—4, with labels as follows: COSTA RICA: Guanacaste, Patilla Biological Station, 610 m, 10°59'22" N, 85°25'33" W, 13–15-VII-2000, J. Ashe, R. Brooks, Z. Falin, flight intercept trap, CR1ABF00-135, SM189726 (1 KSEM). Guanacaste, Est. Patilla, 9 km S. Santa Cecilia, 700m, VII-1994, C. Moraga #3158, INBIO CR1001-001282, 001281 (2 INBio). Same locality, no specific date 1988, malaise trap, GNP Blod. Sur., INBIO CR1001-029050 (1 INBio).

**Distribution.**—Currently only known from Patilla Biological Station in Guanacaste Province, Costa Rica (Fig. 128).

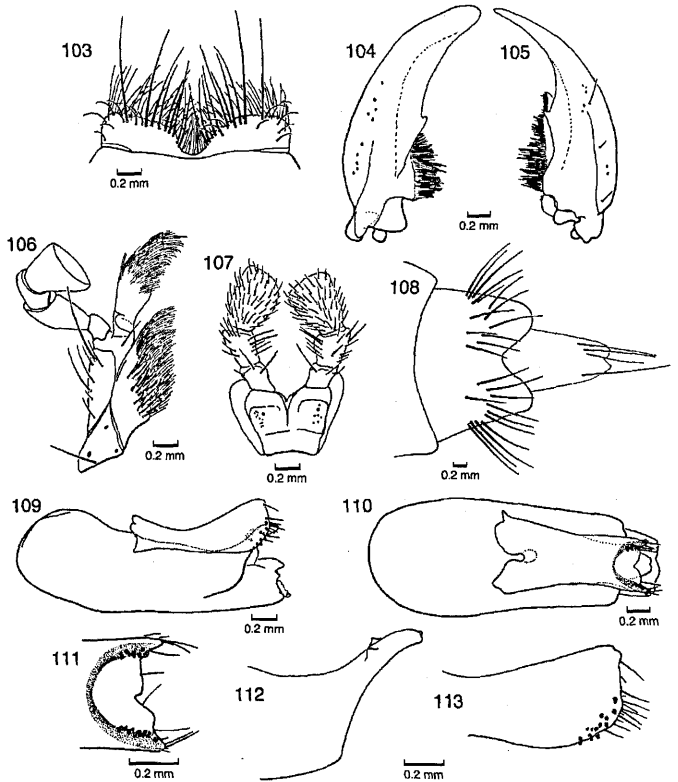
**Habitat and Habits.**—Not known. All specimens for which collecting data are available were collected using flight intercept or Malaise traps.

**Etymology.**—The specific epithet refers to Patilla Biological Station in Guanacaste Province, Costa Rica, the only known locality from which specimens of this species have been collected.

*Elmas spinosus* new species  
(Figs. 103–113)

**Diagnosis.**—*Elmas spinosus*, *E. falini*, and *E. gigas* are distinctive among all known *Elmas* because of the presence of a large medial spine on the submentum in these species. Among these three, *E. spinosus* can be recognized by: medial area of groove on external surface of hind tibia punctured and setose similarly to remainder of surface to tibia (longitudinally glabrous in *E. falini* and *E. gigas*); and, the distinctive aedeagus (Figs. 109, 110).

**Description.**—Length 18–20 mm. Color black throughout. Head with postclypeus deflexed ventrally in relation to frons, distinctly less punctured than remainder of head; medial area between antennae with shallow longitudinal V-shaped groove; eyes large, length about 3 times length of temples behind eyes; punctures moderate sized (about 4–4.5 punctures per 0.2 mm), uniformly distributed, punctures more or less round, very close, margins of punctures contiguous, punctate surfaces shining. Middle of frons very weakly depressed to form a faint, shallow pit. Postmandibular carina present, complete, prominent to subcarinate to base of head. Mentum broadly, shallowly and uniformly emarginate around insertion of labium. Submentum with large medial spinose process. Gula sutures convergent from broad apically to moderate medial area (least width: length ratio = 0.19). Maxillary palpus (Fig. 106) with apical segment strongly dilated apically, apical width across oblique apex 2.5 times basal width; apex strongly oblique, outer length about 1.5 times inner length. Labial palpus (Fig. 107) with apical segment very greatly expanded apically, width across oblique apex 2.5–



Figs. 103–113. *Elmas spinosus*. 103, labrum, dorsal aspect. 104, left mandible, dorsal aspect. 105, right mandible, dorsal aspect. 106, maxilla, ventral aspect. 107, labium, ventral aspect. 108, male sternum VII-VIII, X. 109, aedeagus, lateral aspect. 110, aedeagus, dorsal aspect. 111, aedeagus, detail of apex of paramere, dorsal aspect. 112, apex of median lobe, lateral aspect. 113, apex of paramere, lateral aspect.

2.7 times width of base; apex strongly oblique, outer length 2 times inner length. Mandibles (Figs. 104, 105) with apex of left mandible flattened, apically rounded, and in horizontal plane of head. Antenna black with pale color (pale brown) limited to longitudinal band on posterior margins of Articles 6 (1/5 to trace) and 7–11, 1/4–3/4 of Articles 7–11 with pale color, proportionally more pale color on progressively more apical articles; Articles 5–6 very slightly longer than greatest width, Articles 7–10 of about equal length and width.

Pronotum subquadrate, width:length ratio = 1.01; anterolateral angles obtusely rounded, lateral angles not subcariniform; superior lateral line fading or very weak immediately before contact with inferior lateral line; punctures very small (about 4–5 punctures per 0.2 mm), numerous, uniformly distributed, more or less round, very close, edges of punctures contiguous; punctate surface shining.

Elytra with punctures moderately large (about 2–3 punctures per 0.2 mm), individual punctures shallow and poorly defined, edges contiguous, some coalesced into short, faint, irregular furrows with indistinct edges, punctate surface shining.

Anterior Tarsal Articles 1–4 uniformly covered with spatulate setae. Tarsal claws of middle and hind tarsi not modified, not very slender or sharply curved near middle. Hind tibia flattened, with distinct longitudinal groove on external surface, medial area of groove without setae or punctures, glabrous and shining.

Abdominal Terga III–V with moderate transverse basal impressions; microsculpture on III–V obsolete to absent distal to basal transverse ridges, surface shining; Terga VI–VIII with fine, close reticulate microsculpture.

Abdominal Sterna III–V with moderate transverse impressions; microsculpture on III–V obsolete to absent distal to basal transverse ridges, surface shining; Sterna VI–VIII with fine, close reticulate to wavy, transverse microsculpture.

**Secondary Sexual Characters.**—Male: distal margin of Tergum VII with very broad and faint emargination; distal margin of Tergum VIII broadly and deeply emarginate (Fig. 108).

**Aedeagus.**—As in Figs. 109, 110; paramere very broad, truncate and emarginate medially, with about 11–13 black sensory spinules on each side (Figs. 111, 113); apical lobe narrowly rounded and weakly emarginate apically, dorsal surface with 2 distinct large medial teeth (Fig. 112).

**Holotype.**—Male, with labels as follows: "BOLIVIA: Cochabamba, Cochabamba, 117 km E, Yungas, Lagunitas, 1000 m, 17°6'22" S, 65°40'57" W, 6–8-II-1999, F. Genier, flight intercept trap, BOL1G99-037", bar code label "SM00174205, KUNHM-ENT", "HOLOTYPE, *Elmas spinosus* Ashe & Chatzimanolis, Design. Ashe & Chatzimanolis, 2001". Located in KSEM.

**Paratypes.**—2, with labels as follows: BOLIVIA: Cochabamba, Cochabamba, 109 km E, Yungas, (Cochabamba - Villa Tunari Rd.), 1480m, 17°8'50" S, 65°42'29" W, 1–6-II-1999, F. Genier, flight intercept trap, BOL1G99-027, SM173989, SM173994 (2 KSEM)

**Distribution.**—Currently known from elevations of 1000–1480 m from forest slopes in the Yungus of Cochabamba Province, Bolivia (Fig. 129).

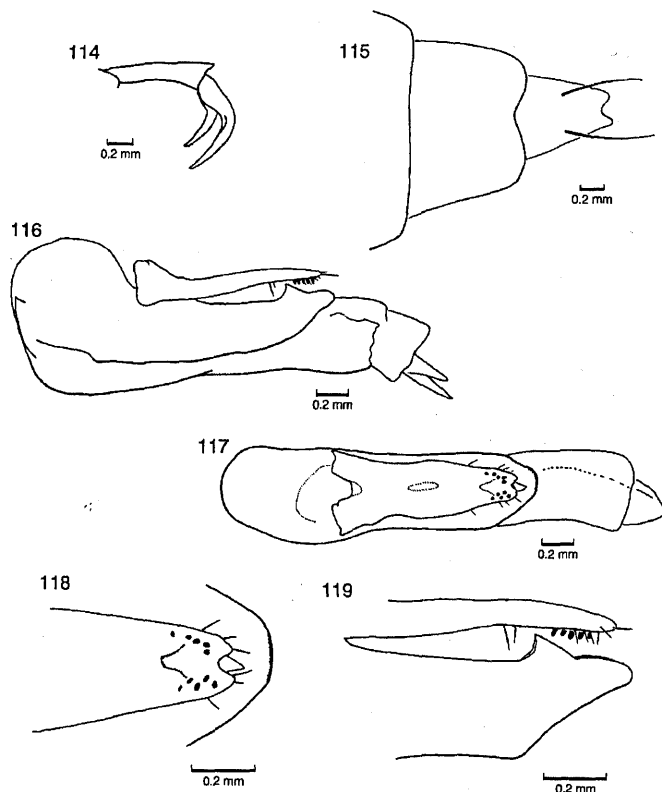
**Habitat and Habits.**—Not known. All specimens for which collecting data are available were collected using flight intercept traps.

**Etymology.**—The specific epithet is derived from the Latin *spina* meaning thorn and refers to the large spine on the submentum of this species.

*Elmas strigella* (Bernhauer), 1915  
(Figs. 4, 114–119)

*Selma strigella* Bernhauer, 1915:296.

**Diagnosis.**—*Elmas strigella* is one of the most distinctive and easily recognized species of *Elmas* and is unique



Figs. 114–119. *Elmas strigella*. 114, hind tarsus and tarsal claws. 115, male sternum VII–VIII, X, lateral aspect. 116, aedeagus, dorsal aspect. 117, aedeagus, detail of apex of paramere and median lobe, dorsal aspect. 118, aedeagus, detail of apex of paramere and median lobe, lateral aspect. 119, apex of paramere and median lobe, lateral aspect.

in a diversity of characteristics: the band of purplish iridescence on the lateral margins of the elytra; the flattened apex of the left mandible that is twisted into a vertical plane; relatively slight apical dilation of last segments of the maxillary and labial palpi; presence of the postmandibular carina only near the mandibular fossa; large, longitudinally or posterolaterally elongated punctures on the head and pronotum that are coalesced into short irregular grooves; the elongate pronotum with sharp, subcariniform anterolateral angles; the slender, medially strongly curved, tarsal claws on the middle and hind legs; and, the distinctive aedeagus (Figs. 116, 117).

**Description** — Length 17–20 mm (Fig. 4). Color black except for pale color on some antennal articles, many specimens with band of purplish iridescence on lateral margins of elytra. Head with postclypeus in same plane as frons, punctation similar to remainder of head; medial area between antennae flat, without longitudinal V-shaped groove; eyes relatively small, length subequal to length of temples behind eyes; punctures relatively large (about 3.0–3.5 punctures per 0.2mm), uniformly distributed, elongated in posterior or posterolateral direction, coalesced into short, irregular, more or less longitudinally or posterolaterally

directed grooves, ridges between grooves polished and shiny to faintly and irregularly reticulate. Middle of frons flat, without depressed area. Postmandibular carina present only near mandibular fossa, remainder of head beneath eyes rounded and densely irregularly punctate. Mentum broadly emarginate medially. Submentum truncate, without medial spinose process. Gula moderately narrow medially (least width: length ratio = 0.15). Maxillary palpus with apical segment only slightly dilated apically, apical width 1.1–1.2 times basal width, length about 2.5 times basal width. Labial palpus with apical segment subcylindrical, only slightly and very gradually dilated apically, apical width 1.2–1.3 times basal width, length 4.5 times basal width. Mandibles distinctive, left mandible flattened at apex and apex twisted into vertical plane. Antenna black with pale color (pale yellowish to whitish) limited to longitudinal band on posterior margins of Articles 7 (trace in most specimens), and 8–11, 1/3 to 1/2 of Articles 8–11 with pale color; all of Articles 5–10 longer than greatest width.

Pronotum distinctly longer than wide, width:length ratio = 0.92; anterolateral angles very prominent and acutely delimited, forming angle of about 90°, lateral angles subcariniform; superior lateral line extended to contact inferior lateral line; punctures relatively large (about 2.5–3.0 punctures per 0.2mm), elongated in more or less longitudinal direction, irregularly coalesced into short irregular longitudinal grooves, narrow ridges between grooves polished and shining.

Elytra with punctures large (about 2.5–3.0 punctures per 0.2mm), irregularly confluent, surface shining.

Anterior Tarsal Articles 1–4 uniformly covered with spatulate setae. Tarsal claws of middle and hind tarsi very slender and sharply curved near middle (Fig. 114). Hind tibia not flattened, without longitudinal groove on external surface, external surface uniformly setose.

Abdominal Terga III–V with moderate transverse basal impressions; surface moderately to densely reticulate within impressions and distal to transverse ridge on more posterior segments and moderately to obsoletely reticulate on distal half.

Abdominal Sterna III–IV with moderate transverse impressions, V with faint transverse impression; surface of sterna reticulate at base with wavy, transverse reticulation distally, distal 2/3–1/2 shining.

**Secondary Sexual Characters.**—Male: distal margin of Tergum VII without emargination; distal margin of Tergum VIII slightly and broadly emarginate (Fig. 115).

**Aedeagus.**—As in Figs. 116, 117; paramere emarginate medially, with about 5 large black sensory spinules on each side (Figs. 118, 119); apical lobe broadly rounded with a single large medial tooth dorsally (Figs. 118, 119).

**Holotype.**—Female, with labels as follows: "*Trichoderma strigellum* Fauv., Brasillien [sic]", "*Selma* sp.", *Selma strigella* Bernh. Typus, unic, Bang-Haas.", "Chicago NHM, Max Bernhauer Collection". Located in FMNH. Bernhauer (1915, p 297), in the original description of *E. strigella*, specifically stated that he had only a single specimen in type series; it is, by definition, the holotype (ICZN, 2000).

**Other Specimens Examined.**—BRAZIL: Pedropolis, H. Schultz, (det. M. Bernhauer) (1 FMNH). Corcovado, Rio de Janeiro, XI-1968, S. A. Fragoso (1 FMNH). Guanabara, Corcovado, XI-1971, N. Alvarenga (3 AMNH). Rio de Janeiro (?), Frye, 37520 (1 FMNH). Guanabara, Rio de Janeiro, XI-1969, N. Alvarenga (1 AMNH). Same locality and collector, II-1968, (1 AMNH). Same locality and collector, III-1968, (1 AMNH). Guanabara, Repressa do Rio Grande, III-1970, N. Alvarenga (1 AMNH). Itatiaya, Est. do Rio, 700 m, 20-I-1926, J. F. Zikan, (det. Bernhauer) (1 FMNH).

**Distribution.**—Currently known from the east-central lowlands of Brazil (Fig. 129).

**Habitat and Habits.**—Not known.

**Discussion.**—Curiously, Bernhauer (1915) did not mention the identification of "*Trichoderma strigellum* Fauv." which is written on the top label of the type specimen. *Trichoderma* Stephens, 1835 is a junior synonym of *Ontholestes* Ganglbauer, 1895 (Blackwelder 1952), and we cannot find any record that the species name *Trichoderma strigellum* Fauvel has been published.

#### *Elmas windsori* new species (Figs. 120–127)

**Diagnosis.**—Among Central American species, *E. windsori*, *E. panamaensis*, and *E. hanleyi* are very similar and virtually impossible to distinguish based on external characteristics; *E. windsori* is easily distinguished by the distinctive aedeagus (Figs. 122, 123); *E. windsori* has less white on the apical antennal articles than *E. hanleyi*, and has a narrow, impunctate groove on the external surface of the hind tibia (a feature shared with *E. panamaensis*, but not with *E. hanleyi*), but because these characters vary among individuals, they are difficult to use for distinguishing species. *Elmas windsori* co-occurs with *E. panamaensis* in the Pipeline Road and Gamboa areas of Panama, but the two species differ greatly in aedeagal structure (compare Figs. 123 and 93).

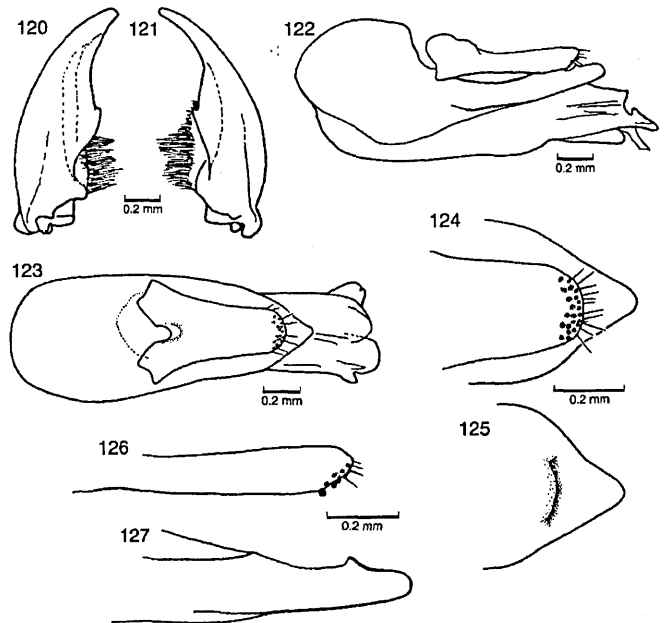
**Description.**—Length 15–16 mm. Color black except for pale color on some antennal articles. Head with postclypeus deflexed ventrally in relation to frons, punctured more sparsely than frons, especially medially in most specimens; medial area between antennae without distinct shallow longitudinal V-shaped groove; eyes large, length about 4.0 times length of temples behind eyes; punctures

small (about 4–5 punctures per 0.2 mm), uniformly distributed, punctures more or less round, very close, margins of punctures contiguous, punctate surfaces shining. Middle of frons not depressed to form a shallow pit, or very slightly depressed in a few. Postmandibular carina present, complete and prominent to base of head in most, or obsolete medially in a few. Mentum broadly, shallowly and uniformly arcuate around insertion of labium. Submentum subtruncate and slightly and broadly rounded medially, without large medial spinose process. Gula sutures convergent from broad apex to moderate medial area (least width: length ratio = 0.24). Maxillary palpus with apical segment dilated apically, apical width across oblique apex about 2.3 times basal width; apex oblique, outer length about 1.3–1.4 times inner length. Labial palpus with apical segment expanded apically, width across oblique apex about 2.0 times width of base; apex oblique, outer length 1.2 times inner length. Mandibles (Figs. 120, 121) with apex of left mandible flattened, rounded apically, and more or less in horizontal plane of head. Antenna black with pale color (pale flavate) limited to longitudinal band on posterior margins of various articles, most with pale color limited to Articles 8–11, a few with very narrow band of pale color on Article 7; Article 8 with trace of pale color at base up to 1/2 pale; Articles 9–10 1/3–1/2 pale; Article 11 1/2–4/5 light; Articles 5–6 subquadrate, Articles 7–10 slightly transverse.

Pronotum subquadrate, width:length ratio = 1.01; anterolateral angles obtusely rounded, lateral angles not subcariniform; superior lateral line extended to contact inferior lateral line, obsolete immediately before contact with inferior lateral line in some; punctures small (about 6–7 punctures per 0.2 mm), numerous, uniformly distributed, very close, edges of punctures contiguous or virtually contiguous, separated by about 0.1–0.2 times average width of punctures, punctures round or slightly elongated anteriorly and medially, distinctly elongated in longitudinal or posterolateral direction laterally and posteriorly, not or weakly coalesced into short, irregular longitudinal or posterolateral furrows; ridges between punctures shining.

Elytra with punctures small (about 4–5 punctures per 0.2 mm), individual punctures poorly to moderately defined, edges contiguous, elongated in longitudinal or posterolateral direction, irregularly coalesced into short, irregular furrows, punctate surface shining.

Anterior Tarsal Articles 1–4 uniformly covered with short, spatulate setae. Tarsal claws of middle and hind tarsi not modified, not very slender or sharply curved near middle. Hind tibia flattened, with distinct, but narrow, longitudinal groove on external surface, medial area of groove narrowly impunctate longitudinally in most, without scattered setae and punctures, punctate and setose similar to remainder of tibia in a few.



Figs. 120–127. *Elmas windsori*. 120, left mandible, dorsal aspect. 121, right mandible, dorsal aspect. 122, aedeagus, lateral aspect. 123, aedeagus, dorsal aspect. 124, aedeagus, detail of apex of paramere and median lobe, dorsal aspect. 125, apex of median lobe, dorsal aspect. 126, apex of paramere, lateral aspect. 127, apex of median lobe, lateral aspect.

Abdominal Terga III–V with moderate transverse basal impressions, Tergum VI with shallow transverse groove; microsculpture on III–V obsolete to absent distal to basal transverse ridges, surface shining; Terga VI–VIII with moderate to obsolete reticulate microsculpture.

Abdominal Sterna III–V with moderate transverse impressions, Sternum VI with shallow transverse impression; microsculpture on III–V obsolete or weakly reticulate to wavy distal to basal transverse ridges, surface shining; Sterna VI–VIII with reticulate to slightly wavy microsculpture.

**Secondary Sexual Characters.**—Male: distal margin of Tergum VII with broad and shallow emargination; distal margin of Tergum VIII deeply emarginate (similar to Fig. 91).

**Aedeagus.**—As in Figs. 122, 123; paramere parallel-sided, apex broadly rounded and entire medially, with about 10–14 black sensory spinules on each side, arranged in a narrow band around apex (Figs. 124, 126); apical lobe narrowed to acutely rounded apex, dorsal surface with single transverse broadly curved carina (Figs. 125, 127).

**Holotype**—“PANAMA: Coclé, El Copé, 7.2 km NE”, 730m, 8°37' N, 80°35' W, 20-V–7-VI-1995, J. Ashe, R. Brooks, flight intercept trap, PAN1AB95-140”, bar code label “SM0003436, KUNHM-ENT”, “HOLOTYPE, *Elmas windsori* Ashe & Chatzimanolis, Design. Ashe & Chatzimanolis, 2001”. Located in KSEM.

**Paratype.**—5, with labels as follows: PANAMA: Coclé, El Copé, 7.2 km NE, 730 m, 8°37' N, 80°35' W, 20-V-7-VI-1995, J. Ashe, R. Brooks, flight intercept trap, PAN1AB95-140, SM3449, SM3446, SM3448 (3 KSEM). Colón, Pipeline Rd, km 6.1, Parque Nac. Soberania, 40 m, 9°7' N, 79°45' W, 31-V-2-VI-1995, J. Ashe, R. Brooks, flight intercept trap, PAN1AB95-099, SM45994 (1 KSEM). Panama, Old Gamboa Rd, 9°4' N, 79°40' W, 1-VII-1993, D. Windsor, flight intercept trap, SM45942 (1 KSEM)

**Distribution.**—Currently known from elevations of 40–730 m in Panama from Pipeline Road and the Gamboa Area to El Copé in Coclé Province (Fig. 128).

**Habitat and Habits.**—Not known. All specimens for which collecting data are available were collected using flight intercept traps.

**Etymology.**—The specific epithet is in honor of Dr. Donald Windsor who collected a series of specimens of this species in Panama.

## DISTRIBUTION MAPS

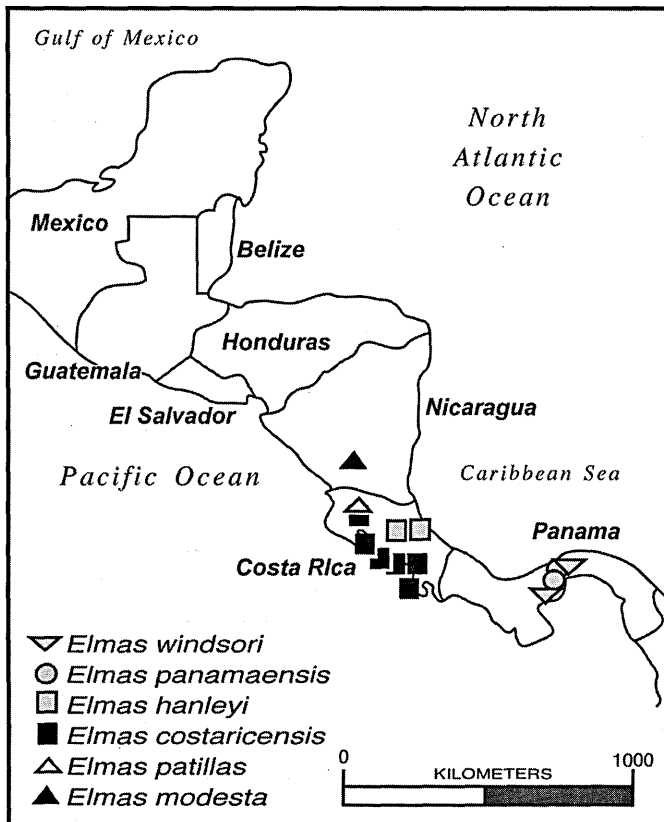


Fig. 128. Known distribution of Central American *Elmas* species.

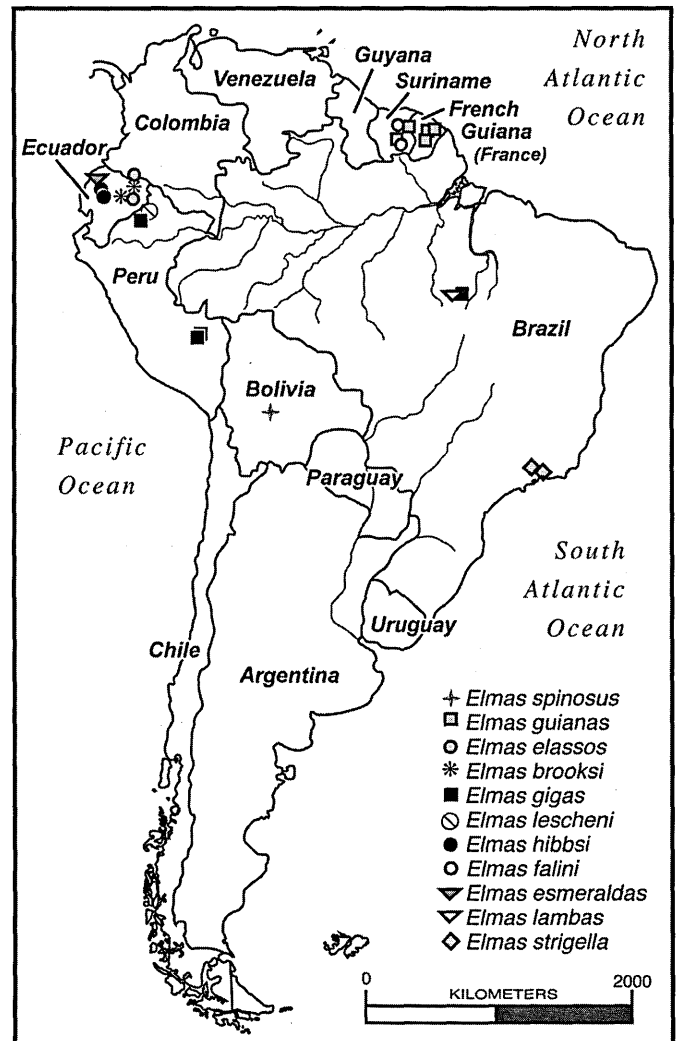


Fig. 128. Known distribution of Central American *Elmas* species.



KEY FOR IDENTIFICATION OF THE KNOWN SPECIES OF *ELMAS*

Many species of *Elmas* are similar and cannot be reliably identified on the basis of external features, although the male aedeagus is frequently quite distinctive. Many of these similar species have differences in details of punctuation, amount of pale color on the antenna (number of segments pale), or slight differences in the amount of setation/punctuation on the external surface of the hind tibia that can be distinguished when series of different species are compared carefully. However, these features are slight and difficult to describe with sufficient accuracy to reduce the likelihood of misinterpretation to an acceptable level. Also, such characters frequently vary among individuals so that they may overlap in a few specimens of each species. Such characters cannot be reliably used in a key. Therefore, this key has relies mainly, but not exclusively, on characters from the aedeagus. Consequently, only males can be reliably identified for many species; for these species, females can be identified only by association with males.

Because *Elmas modesta* (Sharp) is known only from two female specimens that cannot be unambiguously associated with any other species, *E. modesta* is not included in this key.

1. Pronotum distinctly longer than wide, width:length ratio 0.92; anterolateral angles of pronotum prominent and acutely delimited, subcariniform (Fig. 4); punctures on head and pronotum conspicuously elongated in longitudinal or posterolateral directions and coalesced into irregular longitudinal grooves; tarsal claws of middle and hind legs unusually elongate and slender and sharply curved near middle in lateral aspect (Fig. 113); lateral margins of elytra with band of purplish iridescence; aedeagus as in Figs. 115, 116. Known only from Brazil ..... *E. strigella*

Pronotum slightly transverse, subquadrate or slightly elongate (only *E. costaricensis* from Costa Rica, width:length ratio = 0.95, but other characters do not apply); anterolateral angles of pronotum not prominent, obtusely rounded, not subcariniform (Figs. 1, 2, 3); punctures on head and pronotum not uniformly elongated and coalesced into irregular furrows on both head and pronotum; tarsal claws of middle and hind legs similar to those of front legs, not unusually elongate and slender and not sharply curved near middle in lateral aspect; lateral margins of elytra without purplish iridescence; aedeagus different ..... 2

2. (1) Anterior margin of submentum with a large medial spinose process ..... 3  
Anterior margin of submentum broadly rounded or truncate medially ..... 5

3. (2) Medial area of longitudinal groove on external surface of hind tibia glabrous, without scattered setae and punctures; aedeagus as in Figs. 109, 110. Known from Bolivia ..... *E. spinosus*  
Medial area of longitudinal groove of external surface of hind tibia with scattered setae and punctures, not, or at most narrowly, glabrous; aedeagus different. Known from Suriname, Peru and Brazil ..... 4
4. (3) Parameres of aedeagus with about 30–35 small black sensory spinules on each half (Fig. 39); aedeagus as in Figs. 37, 38. Known only from Suriname .....  
..... *E. falini*  
Parameres of aedeagus with about 15 small black sensory spinules on each half (Fig. 48); aedeagus as in Figs. 46, 47. Known from Peru and Brazil ..... *E. gigas*
5. (2) Most (4 of 39 available specimens of *E. guianae* do not show this character) specimens with a medial longitudinal impunctate line on pronotum, impunctate line may be complete from base to apex, or partial and impunctate area broken medially, or present only near basal border; most punctures on head (at least posteromedial area) and disk of pronotum relatively widely separated (at least in lateral comparisons), not contiguous, distance between most punctures in these areas 0.3–1.0 times average width of punctures, surface between punctures strongly shining; male sternum VII with very broad, shallow and inconspicuous medial emargination; median lobe of aedeagus with a single large medial tooth on dorsal surface (Figs. 58, 82) ..... 6  
Specimens without medial impunctate longitudinal line on pronotum; most punctures on head and disk of pronotum very close to contiguous, distance between most punctures not more than 0.1–0.2 times average width of punctures; male sternum VII distinctly and abruptly emarginate medially; medial lobe of aedeagus with 2 teeth or one or more semilunate or semicircular carinae on dorsal surface ..... 7
6. (5) Punctures on head and pronotum more or less round; punctures on mediolateral areas of disk of pronotum well separated, lateral distance between punctures 0.5–1.0 times average width of punctures; paramere of aedeagus parallel-sided and apical margin emarginate medially, with 6–7 black sensory spinules on each side (Fig. 80); aedeagus as in Figs. 78, 79. Known from Brazil ..... *E. lambae*  
Punctures on head and pronotum distinctly elongated in longitudinal or posterolateral directions; punctures on mediolateral areas of disk of pronotum less well

- separated, average lateral distance between punctures 0.3–0.5 times average width of punctures; paramere of aedeagus narrowed in apical half to acutely rounded apex, with 27–30 black sensory spinules on each side (Fig. 56); aedeagus as in Figs. 54, 55. Known from French Guiana and Suriname ..... *E. guianas*
7. (5) External surface of hind tibia with distinct longitudinal groove ..... 8  
 External surface of hind tibia without longitudinal groove (may be flattened and broadly and shallowly depressed, but not distinctly grooved) ..... 12
8. (7) Impunctate groove on external surface of hind tibia broad and deep, occupying at least 2/3 width of tibia at broadest point, and at least 3/4 length of tibia; aedeagus as in Figs. 72, 73. Known from Ecuador .....  
 ..... *E. hibbsi*  
 Groove on external surface of hind tibia more shallow and less broad, occupying not more than 1/2 width of tibia at widest point, and no more than 2/3 length of tibia; aedeagus not as above. Species from Central America ..... 9
9. (8) Apex of paramere of aedeagus deeply emarginate medially (Figs. 94, 99) ..... 10  
 Apex of paramere of aedeagus subtruncate (as in Fig. 124) or very slightly emarginate (as in Fig. 18) ..... 11
10. (9) Antenna with articles 10–11 (also article 9 in some) fully light flavate; apex of paramere expanded near apex in dorsal aspect, with broad U-shaped emargination (Fig. 99); dorsal surface of median lobe with 2 large cariniform ridges (one on each side) that parallel the lobes of the apex of the paramere (Fig. 100); aedeagus as in Figs. 97, 98. Known from Costa Rica (Patilla Biological Station) ..... *E. patillas*  
 Antenna with articles 10–11 not more than 1/2 light flavate; apex of paramere parallel-sided, not expanded near apex in dorsal aspect, with narrow V-shaped emargination (Fig. 94); dorsal surface of median lobe with V-shaped cariniform ridge that parallels emarginate shape of apex of paramere (Fig. 95); aedeagus as in Figs. 92, 93. Known from Panama .....  
 ..... *E. panamaensis*
11. (9) Pronotum distinctly longer than wide (width:length ratio = 0.95); paramere of aedeagus broad and expanded apically, apex broadly arcuate and shallowly emarginate medially, with 15–16 black sensory spinules on each side, arranged in broad band near apex and apico-laterally (Fig. 18); aedeagus as in Figs. 16, 17. Known from Costa Rica ..... *E. costaricensis*
- Pronotum subquadrate (width:length ratio = 1.01); paramere of aedeagus parallel-sided and broadly rounded apically and entire medially with about 10–14 black sensory spinules on each side arranged in a narrow band around apex (Fig. 124); aedeagus as in Figs. 122, 123. Known from Panama ..... *E. windsori*
12. (7) Paramere of aedeagus very broad and expanded apically, apex broadly arcuate and shallowly emarginate medially, with about 15–17 black sensory spinules on each side arranged in broad band near apex and apico-laterally (Fig. 25); aedeagus as in Figs. 23, 24. Known only from Ecuador ..... *E. ellassos*  
 Paramere of aedeagus more or less parallel-sided, not expanded and very broad apically, apex broadly rounded, truncate or broadly emarginate, with different arrangement of sensory setae. Known from Ecuador, Peru, and Central America ..... 13
13. (12) Paramere of aedeagus with apex broadly and shallowly emarginate; black sensory spinules arranged in a narrow transverse band across apical lobes of paramere (Figs. 30, 67) ..... 14  
 Paramere of aedeagus truncate or broadly rounded; black sensory spinules arranged in longitudinal band on each side of apical region of paramere (Figs. 12, 86) ..... 15
14. (13) Known from Central America. Paramere of aedeagus with apex broadly and shallowly emarginate, with about 10–12 moderately large sensory spinules on each side (Fig. 67); dorsal surface of median lobe with single large cariniform ridge in shape of a broadly curved U that parallels the broadly emarginate shape of apex of paramere (Fig. 68); aedeagus as in Figs. 65, 66. Known from Costa Rica .....  
 ..... *E. hanleyi*  
 Known from South America. Paramere of aedeagus with about 18–20 sensory spinules on each side (Fig. 30); dorsal surface of median lobe with slightly curved transverse carina (Fig. 31); aedeagus as in Figs. 28, 29. Known from Ecuador ..... *E. esmeraldas*
15. (13) Paramere of aedeagus truncate or broadly rounded apically with about 12–14 black sensory spinules on each side, arranged in longitudinal band on each side of paramere (Fig. 12); aedeagus as in Figs. 10, 11. Known from Ecuador ..... *E. brooksi*  
 Paramere of aedeagus broadly rounded apically with about 6–8 black sensory spinules on each side, arranged in longitudinal band on each side of apex (Fig. 86); aedeagus as in Figs. 84, 85. Known from Peru .....  
 ..... *E. lescheri*

## RECONSTRUCTION OF PHYLOGENETIC RELATIONSHIPS

The phylogenetic analysis was based exclusively on adult structure; larvae are not known for any *Elmas*, and specimens suitable for molecular studies are not available for most taxa. The ingroup taxa used in the analysis included representatives of all known species of *Elmas*. Choice of outgroups was complicated by lack of credible hypotheses about the relationships of *Elmas* within the Xanthopygina. Because *Plociopterus* and *Nordus* have been proposed to be closely related to *Elmas*, representatives of these genera were chosen as out-groups. In addition, representatives of two other common xanthopygine genera, *Xanthopygus* (*Xa. callidus*) and *Xenopygus* (*Xe. analis* Erichson) were chosen to broaden the outgroup.

Homologous suites of characters were hypothesized based on the criteria of position and special similarity (Remane, 1956; Wiley, 1981). Thirty-two characters and their hypothesized homologous states are shown in Table 1, and their distribution among species is given in the appendix. Homologous states were written into a standard character by taxon character state matrix (Appendix) with missing or inapplicable characters coded as "?". Characters were analyzed using the heuristic search option of PAUP 3.1 (Swofford, 1997). All exemplar taxa of *Plociopterus*, *Nordus*, *Xanthopygus* and *Xenopygus* were designated as outgroups. All characters were treated as unordered, and character polarities were determined in the context of the phylogenetic analysis. Character distributions and alternative tree topologies were studied using MACLAD 4 (Maddison & Maddison, 2000).

In order to further ascertain the phylogenetic pattern in the character data, characters were reweighted to the base weight of 1000 by the maximum retention index of each character, and a successive approximation analysis (Farris, 1969; Carpenter, 1988) was applied to the resulting data.

Bootstrap analysis (Felsenstein, 1985) using 1000 resampling replicates was used to study the level of character support in the dataset for hypothesized clades.

**Results of Phylogenetic Analysis.**—Heuristic search in PAUP produced 8 equally most parsimonious trees (Fig. 130) with a length of 116, consistency index of 0.491, and retention index of 0.672. A strict consensus tree of these eight equally parsimonious trees is shown in Fig. 131, and character distribution is mapped on one of the most parsimonious trees (Fig. 132).

The reconstructed phylogeny hypothesizes that the genus *Elmas* is monophyletic based on derived states of 13 characters (character argumentation based only on characters that consistently support lineages in all most parsimonious trees; these are a subset of those that support lineages in any individual most parsimonious tree, such as those in Fig. 132), 7 of which are unique to this node (9-2,

mandibles, in lateral aspect, deflexed ventrally in an angle of 25-30° about 1/4-1/3 distance from base to apex; 10-2, mandibles asymmetrical, right mandible acutely pointed, left mandible flattened and blade-like; 11-2, apical segment of maxillary palpi with numerous small setae; 12-2, apical segment of labial palpi with numerous small setae; 21-2, tarsomeres of middle and hind tarsi moderately to strongly flattened; 22-2, tarsomere 1 of middle and hind tarsi as long or longer than next 3 combined; 24-2, elytra with patch of setae on lateral margin directed medially to posteromedially). Among the species of *Elmas*, all reconstructions hypothesize that the most basal lineage is *E. strigella*. All species other than *E. strigella* are united into a single lineage based on 6 synapomorphies, only one of which (16-2, apical segment of labial palpi slightly oblique, outer length 1.1-1.3 times inner length) is unique to this lineage. *Elmas lambos* and *E. guianas*, respectively, are weakly hypothesized to be the next set of basal branches (character 1-2, postclypeus distinctly depressed in relation to frons, uniquely supports the monophyly of *E. guianas* and the lineage consisting of *E. modesta*-*E. patillas*). Support for other internal nodes is weak as indicated by a large internal polytomy. From this, only three lineages receive consistent support in all parsimonious trees.

The lineage *E. hibbsi* + *E. spinosus* + *E. falini* + *E. gigas* is united by 6 synapomorphies, only one of which (16-3, apical segment of labial palpi strongly oblique, outer length 1.4 or more times inner length) is unique to this lineage. Within this lineage *E. hibbsi* is the basal lineage, and the lineage *E. spinosus* + *E. falini* + *E. gigas* is supported by 6 synapomorphies, two of which (4-2, medial area of head between antennae depressed to form a longitudinal groove; 5-2, submentum with prominent medial spine) are unique to this lineage. The monophyly of these three species is one of the best supported in the tree. Among this latter three, *E. falini* and *E. gigas* are sister species, based on 8 synapomorphies, though none are unique to this lineage.

The lineage *E. elassos* + *E. hanleyi* + *E. esmeraldas* is weakly supported based on only 1 synapomorphy, a derived reversal (20-1, longitudinal groove of hind tibia fully setose) which is not unique to this lineage. Some of the equally parsimonious trees hypothesize that *E. modesta* is also member of this lineage, but others do not. The instability of position of *E. modesta* is probably related to the fact that all the characters related to aedeagal features (characters 26-32) are not known for this species.

The lineage *E. windorsori* + *E. costaricensis* + *E. panamaensis* + *E. patillas* is found in all equally parsimonious trees. These four species are weakly united by 1 synapomorphy (19-2, hind tibia with a narrow, short longitudinal groove), a state which is unique to this lineage. Furthermore, *E. windorsori* and *E. costaricensis* are hy-

Table 1. Characters and character states used in inferring phylogenetic relationships among species of *Elmas*<sup>1</sup>

## HEAD:

1. Postclypeus: deflexed or not
    - 1) not deflexed in comparison to frons – in same plane as frons
    - 2) distinctly deflexed in comparison to frons
  2. Postclypeus: punctation
    - 1) punctured similar to frons
    - 2) distinctly less punctured than frons
    - 3) glabrous and shining
  3. Head: middle of frons with pit or not
    - 1) frons without medial pit or depression
    - 2) frons with slight depression or pit
    - 3) frons distinctly depressed to form a pit
  4. Head: medial area between antennae
    - 1) not longitudinally depressed
    - 2) longitudinally depressed to form shallow V-shaped groove
  5. Submentum: medial spine or not
    - 1) Without medial spine
    - 2) With prominent medial spine
  6. Postmandibular carina;
    - 1) prominent and complete from near mandibular fossa to base of head
    - 2) complete anteriorly and on base of head, interrupted medially by large, irregular punctures
    - 3) complete only anteriorly near mandibular fossa
    - 4) present only basally
  7. Antenna: shape of articles 5–11
    - 1) round
    - 2) distinctly and strongly flattened
  8. Antenna: articles 5–10
    - 1) not appearing "serrate" (anterior and posterior margins of article subequal in length)
    - 2) appearing "serrate" (anterior margin longer than posterior margin)
- MOUTHPARTS:
9. Mandibles: lateral aspect
    - 1) more-or-less straight in lateral aspect
    - 2) deflexed ventrally in an angle of 25–30 degrees about 1/4–1/3 distance from base to apex
  10. Mandibles: shape in apical half
    - 1) right and left similar, mandibles more-or-less symmetrical
    - 2) mandibles asymmetrical, right mandible acutely pointed, left mandible flattened and blade-like
  11. Maxillary palpus: apical segment
    - 1) aetose
    - 2) With numerous small setae (as in Fig. 62)
  12. Labial palpus: apical segment
    - 1) aetose
    - 2) With numerous small setae (as in Fig. 107)
  13. Maxillary palpus: apical segment
    - 1) not dilated apically
    - 2) slightly dilated apically (apex less than 1.2 times wider than base)
    - 3) moderately dilated apically (apex 1.3–1.6 times wider than base)
    - 4) strongly dilated apically (apex 1.7–2.0 times wider than base or more)
  14. Labial palpus: apical segment
    - 1) not dilated apically
    - 2) slightly dilated apically (apex less than 1.3 times wider than base)
    - 3) moderately dilated apically (apex 1.4–1.6 times wider than base)
    - 4) strongly dilated apically (apex 1.7–2.0 times wider than base or more)

Table 1. Continued

15. Maxillary palpus: apical segment
    - 1) Not oblique apically; inner and outer lengths subequal
    - 2) Slightly oblique apically; outer length 1.1–1.3 times length of inner marginal length
    - 3) Strongly oblique; outer length 1.4 or greater times length of inner marginal length
  16. Labial palpus: apical segment
    - 1) Not oblique apically; inner and outer lengths subequal
    - 2) Slightly oblique apically; outer length 1.1–1.3 times length of inner marginal length
    - 3) Strongly oblique; outer length 1.4 or greater times length of inner marginal length
  17. Left mandible: apex
    - 1) sharp,
    - 2) broadly rounded (as in Figs. 5, 34, 104, 120)
    - 3) obliquely truncate (as in Figs. 42, 51, 60, 89)
- LEGS:
18. Hind tibia: flattened or not
    - 1) not flattened
    - 2) slightly flattened
    - 3) distinctly flattened
  19. Hind tibia: longitudinally grooved or not
    - 1) without longitudinal groove
    - 2) with narrow, short longitudinal groove
    - 3) with broad, long longitudinal groove
  20. Hind tibia: structure of longitudinal groove
    - 1) fully setose
    - 2) narrowly aetose
    - 3) broadly aetose
  21. Tarsomeres of middle and hind tarsi: flattened or not
    - 1) not flattened
    - 2) slightly to strongly flattened
  22. Tarsomere 1 of middle and hind tarsi: elongate or not
    - 1) Not as long as next 3 combined
    - 2) As long or longer than next 3 combined
- THORAX:
23. Prosternum: basisternum
    - 1) with pair of prominent setae
    - 2) without pair of prominent setae
  24. Elytra: setae
    - 1) without patch of setae on lateral margin directed medially to posteromedially
    - 2) with patch of setae on lateral margins directed medially to posteromedially
  25. Pronotum: medial longitudinal aetose area
    - 1) Absent
    - 2) Present
- AEDEAGUS: PARAMERE
26. Paramere: distribution of sensory spinules
    - 1) in a longitudinal row on each side (as in Figs. 12, 56, 86)
    - 2) primarily in a band along anterior margin (as in Figs. 30, 67, 124)
    - 3) in a band along anterior margin and along each side (as in Figs. 25, 74)
    - 4) uniformly distributed on disk of lobes of parameres (as in Figs. 39, 94, 100)
  27. Paramere: condition of apex in dorsal aspect
    - 1) parallel-sided or slightly converging apically (as in Figs. 12, 67, 80, 111)

Table 1. Continued

2) distinctly expanded apically (as in Figs. 25, 39, 48, 99)	
3) distinctly converging to tip (as in Figs. 56, 118)	
28. Paramere: condition of apical margin	
1) broadly rounded (as in Fig. 119)	
2) truncate or subtruncate (as in Figs. 12, 25, 30)	
3) pointed (as in Fig. 56)	
29. Paramere: apical margin emarginate or not	
1) entire (as in Figs. 56, 86, 123)	
2) slightly and broadly emarginate (as in Figs. 30, 67, 111)	
3) deeply and narrowly emarginate (as in Figs. 81, 94, 118)	
4) broadly and deeply emarginate (as in Figs. 39, 48, 99)	
30. Paramere: lateral aspect of apex	
1) narrowed or parallel-sided from base to apex (as in Figs. 14, 22, 57, 84, 119)	
2) distinctly broadened in lateral aspect (as in Figs. 26, 109)	
AEDEAGUS: MEDIAN LOBE	
31. Medial Lobe: dorsal teeth	
1) without dorsal teeth (as in Fig. 76)	
2) present as a single medial tooth or carina (as in Figs. 58, 82, 118)	
3) present as 2 widely separated teeth or carinae (as in Figs. 39, 48, 100, 112)	
4) united medially into U- or V- shaped carina (as in Figs. 68, 95)	
5) united medially into transverse semilunulate carina (as in Figs. 19, 125)	
32. Medial Lobe: apex	
1) broadly rounded (as in Fig. 118)	
2) slightly narrowed to broad sub-acute apex (as in Figs. 95, 100, 125)	
3) strongly narrowed to acute apex (as in Figs. 19, 25)	
4) subtruncate or slightly emarginate (as in Figs. 39, 48)	

<sup>1</sup> Character states within each character in this table are not listed in any particular order. Relative plesiomorphy and apomorphy of states is estimated within the context of the phylogenetic analysis, and the plesiomorphic condition is not necessarily the first state listed. We have, therefore, purposefully not labeled the first state as "0" because this designation is, by convention, usually taken to indicate the plesiomorphic state. Thus, the relative order of states within each multistate character should not be interpreted as a hypothesis of transformation direction or polarity.

hypothesized to be sister species (based on one synapomorphy, 31-3-->5, dorsal teeth of median lobe of aedeagus united into a transverse semilunulate carina), and *E. panamaensis* and *E. patillas* are sister species (based on three synapomorphies that are not unique to this lineage).

One iteration in the successive approximation analysis (characters reweighted to the base of 1000 by the reten-

tion index) produced a single tree (Fig. 132) (tree length 71852, C.I. = 0.555, R.I. = 0.744, Rescaled C.I. = 0.413) that did not change in topology or length with additional iterations. The single successive approximation tree is topologically identical to one of the eight most parsimonious trees (Fig. 130). The successive approximation tree is consistent with the lineages mentioned above for the strict consensus tree. In addition, the most important features of the successive approximation tree are that *E. modesta* and *E. brooksi* are hypothesized to be members of the lineage that includes *E. hanleyi* and *E. esmeraldas*, and *E. lescheni* is hypothesized to be the basal member of the *E. hibbsi* - *E. gigas* lineage.

The bootstrap analysis indicates that the character dataset is not robust with regard to most of the monophyletic lineages of *Elmas* hypothesized in the strict consensus tree. The only lineages that reach 50% presence in all bootstrap trees are: the genus *Elmas* as a whole (found in 100% of bootstrap trees); the basal position of *E. strigella* within *Elmas* (found in 50% of bootstrap trees); the lineage *E. spinosus* + *E. falini* + *E. gigas* (found in 63% of bootstrap trees); and the lineage *E. falini* + *E. gigas* (found in 97% of bootstrap trees). This low bootstrap support for most lineages reflects the relatively low number of characters in the matrix and the relatively high homoplasy in the tree.

**Phylogenetic Conclusions.**—The lineages of *Elmas* species are only weakly resolved by the available dataset. Few well-supported conclusions can be drawn. *Elmas* is strongly supported to be a monophyletic lineage, and *E. strigella* is probably the most basal known species. *Elmas spinosus* + *E. falini* + *E. gigas* are strongly supported to be a monophyletic group; among known species they are unique in having a strong spine medially on the submentum (character 5-2) and a longitudinally depressed area between the antennae (character 4-2). *Elmas hibbsi* is more weakly supported to be the sister group to these three species. The *E. windorsori* - *E. patillas* lineage, consisting of 2 Panamanian and 2 Costa Rican species, is found in all trees, but is not strongly supported. It is interesting that within this lineage, the Panamanian and Costa Rican species are sister species in all reconstructions (*E. windorsori* + *E. costaricensis* and *E. panamaensis* + *E. patillas*).

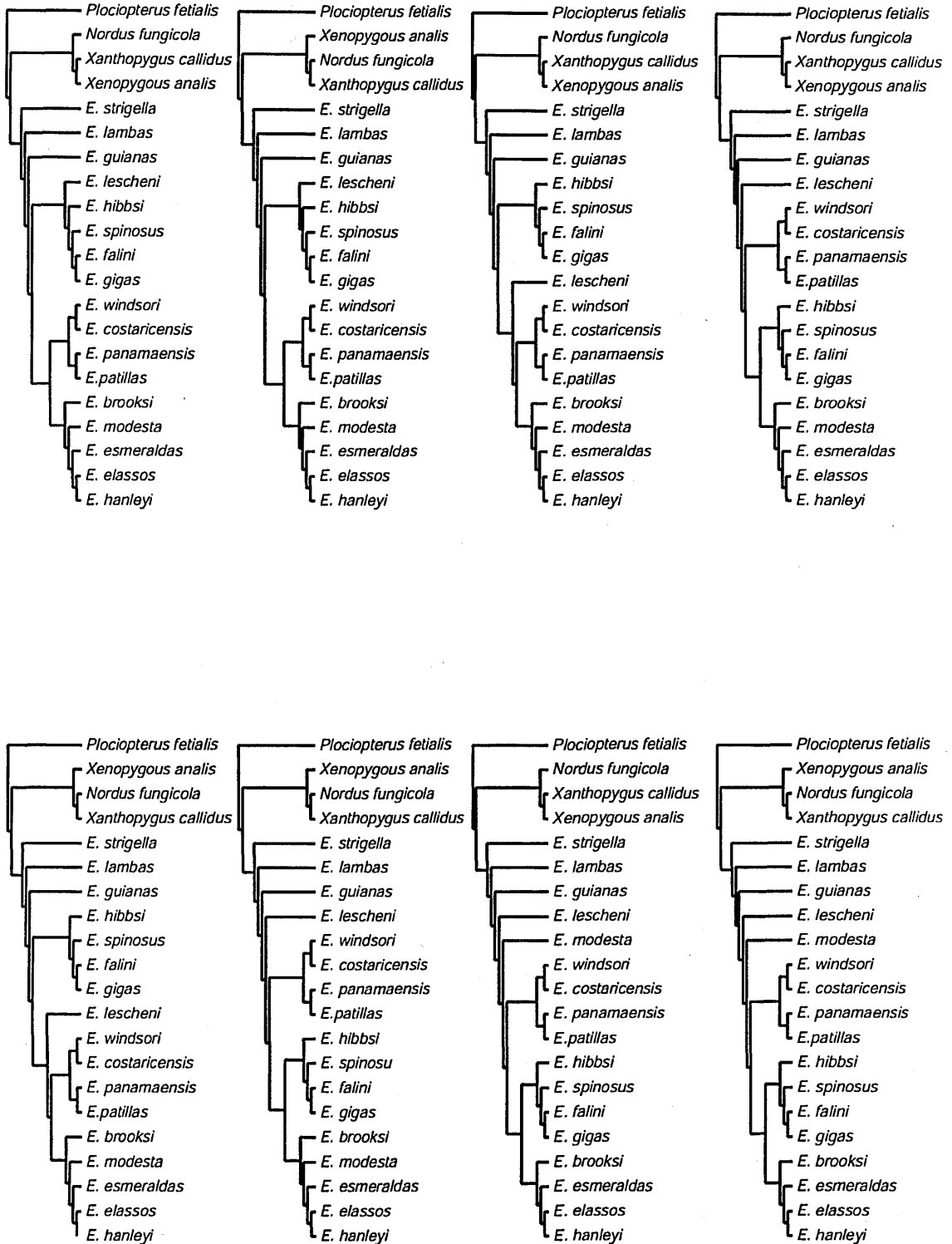


Fig. 130. The eight equally most parsimonious trees resulting from heuristic search with characters treated as unordered and equally weighted (Tree length = 116, Consistency Index = 0.491, Retention Index = 0.672).

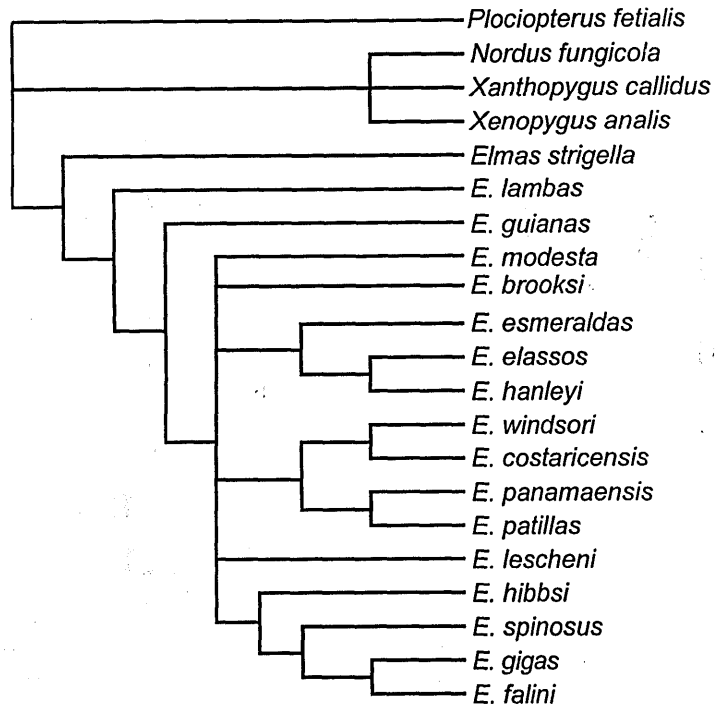


Fig. 131. Strict consensus tree of the eight equally most parsimonious trees.



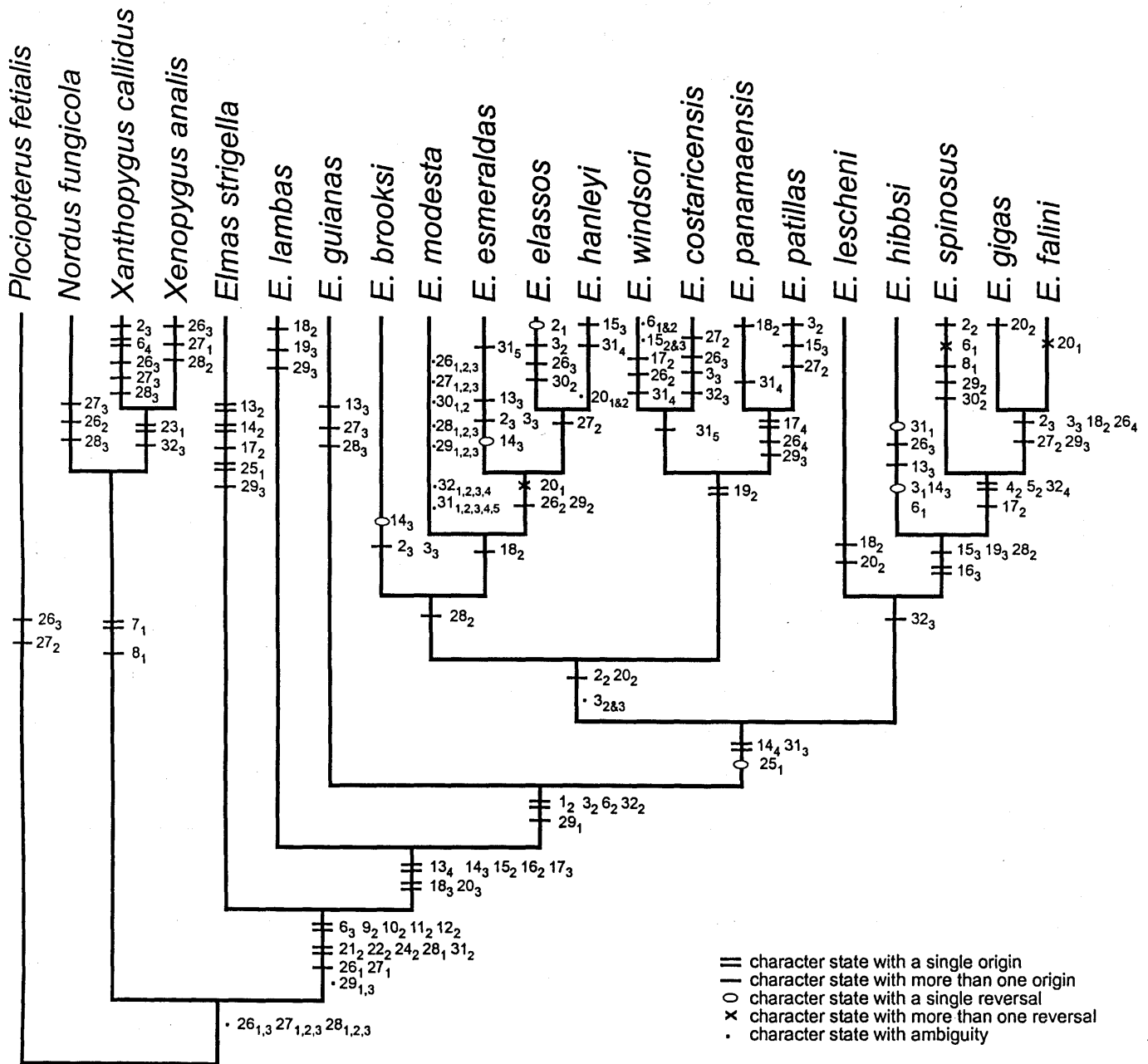


Fig. 132. Distribution of characters mapped onto one of the most parsimonious trees (topologically equal to the single tree produced by successive approximation).

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APPENDIX

Character by taxon matrix showing the distribution of character states among species of *Elmas*. Missing and inapplicable data are coded “?”.

Taxon	Character															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Plociopterus fetialis</i>	1	1	1	1	1	1	2	2	1	1	1	1	1	1	1	1
<i>Nordus fungicola</i>	1	1	1	1	1	4	1	1	1	1	1	1	1	1	1	1
<i>Xanthopygus callidus</i>	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Xenopygus analis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1
<i>E. modesta</i>	2	2	1,2	1	1	2	2	2	2	2	2	2	4	4	?	?
<i>E. strigella</i>	1	1	1	1	1	3	2	2	2	2	2	2	2	2	1	1
<i>E. spinosus</i>	2	2	2	2	2	1	2	1	2	2	2	2	4	4	1	1
<i>E. falini</i>	2	3	3	2	2	2	2	2	2	2	2	2	4	4	4	2
<i>E. gigas</i>	2	3	3	2	2	2	2	2	2	2	2	2	4	4	4	2
<i>E. lescheni</i>	2	1	2	1	1	2	2	2	2	2	2	2	4	4	1	1
<i>E. hibbsi</i>	2	1	1	1	1	1	2	2	2	2	2	2	3	3	3	1
<i>E. brooksi</i>	2	3	3	1	1	2	2	2	2	2	2	2	4	3	1	1
<i>E. elassos</i>	2	1	2	1	1	2	2	2	2	2	2	2	4	4	3	2
<i>E. guianas</i>	2	1	2	1	1	2	2	2	2	2	2	2	3	3	1	3
<i>E. windsori</i>	2	2	1,2	1	1	1,2	2	2	2	2	2	2	4	4	2	1
<i>E. panamaensis</i>	2	2	1,2	1	1	2	2	2	2	2	2	2	4	4	4	1
<i>E. hanleyi</i>	2	2	1,2	1	1	2	2	2	2	2	2	2	4	4	2	2
<i>E. costaricensis</i>	2	2	3	1	1	2	2	2	2	2	2	2	4	4	3	2
<i>E. esmeraldas</i>	2	3	3	1	1	2	2	2	2	2	2	2	3	3	2	1
<i>E. patillas</i>	2	3	2	1	1	2	2	2	2	2	2	2	4	4	4	2
<i>E. lambas</i>	1	1	1	1	1	3	2	2	2	2	2	2	4	3	1	1

Taxon	Character															
	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
<i>Plociopterus fetialis</i>	1	1	1	1	1	1	2	1	2	3	2	2	1	1	1	1
<i>Nordus fungicola</i>	1	1	1	1	1	1	2	1	2	3	3	3	1	1	1	1
<i>Xanthopygus callidus</i>	1	1	1	1	1	1	1	1	2	1	3	3	1	1	1	3
<i>Xenopygus analis</i>	2	1	1	1	3	1	1	1	1	1	1	1	1	1	1	2
<i>E. modesta</i>	?	?	?	?	?	2	2	3	2	1	2	2	2	2	2	1
<i>E. strigella</i>	1	3	1	2	1	1	1	2	1	1	1	2	2	2	2	1
<i>E. spinosus</i>	2	2	2	3	4	3	3	2	3	3	3	2	2	2	2	1
<i>E. falini</i>	2	3	1	3	4	3	3	2	2	3	1	2	2	2	2	1
<i>E. gigas</i>	2	3	1	3	4	3	3	2	2	3	2	2	2	2	2	1
<i>E. lescheni</i>	1	1	1	3?	3?	2	2	3	2	1	2	2	2	2	2	1
<i>E. hibbsi</i>	2	1	1	1	3	3	3	3	3	3	3	2	2	2	2	1
<i>E. brooksi</i>	2	1	1	3	2	2	2	3	3	1	2	2	2	2	2	1
<i>E. elassos</i>	2?	2	2	3	2	2	2	3	2	1	1	2	2	2	2	1
<i>E. guianas</i>	3	1	1	2	2	2	2	3	3	1	3	2	2	2	2	2
<i>E. windsori</i>	1	1	1	5	2	2,3	2	2	3	2	2	2	2	2	2	1
<i>E. panamaensis</i>	β1?	3	1	4	2	2	2	4	2	2	2	2	2	2	2	1
<i>E. hanleyi</i>	2	2	1	4	2	3	2	3	2	1	1,2	2	2	2	2	1
<i>E. costaricensis</i>	1	1	1	5	3	2	2	3	3	2	2	2	2	2	2	1
<i>E. esmeraldas</i>	2	2	1	5	2	2	2	3	2	1	1	2	2	2	2	1
<i>E. patillas</i>	1	3	1	3	2	3	2	4	3	2	2	2	2	2	2	1
<i>E. lambas</i>	1?	3	1	2	1	2	2	3	2	3	3	2	2	2	2	2

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