

REVIEW OF THE NEW WORLD TREEHOPPER TRIBE STEGASPIDINAE (HEMIPTERA: MEMBRACIDAE: STEGASPIDINAE): II: *LYCODERES* *GERMAR*, *OEDA AMYOT* AND *SERVILLE*, AND *STEGASPIS* *GERMAR*

JASON R. CRYAN AND LEWIS L. DEITZ

Department of Entomology, Box 7613, North Carolina State University, Raleigh, NC 27695-7613, U.S.A. (LLD e-mail: lewis_deitz@ncsu.edu); JRC current address: Department of Zoology, 574 Widtsoe Bldg., Brigham Young University, Provo, UT 84602, U.S.A. (JRC e-mail: jrc233@email.byu.edu)

Abstract.—Three genera in the treehopper tribe Stegaspidini Haupt—*Lycoderes* Germar, *Oeda* Amyot and Serville, and *Stegaspis* Germar—are redescribed and illustrated based on adult and nymphal morphology. *Lycoderes* has 36 valid species, including *L. nathanieli* Cryan, new species; *Oeda* has 4 valid species and *Stegaspis* has 2. Six previously described *Lycoderes* species are here placed to subgenus for the first time: *L. fernandezi* Strümpel, *L. luteus* Funkhouser, *L. phasianus* Fowler, and *L. serraticornis* Fowler are included in the subgenus *Lycoderides* Sakakibara; *L. capitatus* Buckton and *L. minameni* (Buckton) are included in the subgenus *Lycoderes* Germar. An updated taxonomic key and a complete species checklist, including all synonymies, are given for each genus.

Key Words: Membracidae, Stegaspidini, *Lycoderes*, *Oeda*, *Stegaspis*, taxonomy

This work, the second in a series of three publications on the treehopper tribe Stegaspidini (Hemiptera: Membracidae: Stegaspidinae), includes redescriptions of the genera *Lycoderes* Germar, *Oeda* Amyot and Serville, and *Stegaspis* Germar. The genera *Bocydium* Latreille, *Lirania* Stål, and *Smerdalea* Fowler were treated in part I (Cryan and Deitz 1999a); *Flexocentrus* Goding, *Stylocentrus* Stål, and *Umbelligerus* Deitz will be addressed in part III (Cryan and Deitz, in press). Part I also included an introduction to this review series, explanations and illustrations of relevant morphological features, a redefinition of the tribe Stegaspidini, and a taxonomic key for the identification of included genera.

MATERIALS AND METHODS

Methods used in this work were described in part I (Cryan and Deitz 1999a).

The following codens are used herein to refer to the collections in which relevant specimens are located or have been deposited. Arnett et al. (1993a) listed the full postal addresses for most of the institutions; those not found in that publication are indicated by a dagger (†) following the coden.

- AMNH: American Museum of Natural History, New York, New York, USA.
BMNH: Department of Entomology, The Natural History Museum, London, United Kingdom.
BPBM: Department of Entomology, Bernice P. Bishop Museum, Honolulu, Hawaii, USA.
CNCI: Canadian National Collection of Insects, Eastern Cereal and Oilseed Research Centre, Agriculture and Agri-Food Canada, Re-

- search Branch, Ottawa, Ontario, Canada.
- EMUS: Entomological Museum, Department of Biology, Utah State University, Logan, Utah, USA.
- INBC: Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica.
- IZAV: Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Aragua, Venezuela.
- MZLU: Museum of Zoology, Lund University, Helgonavägen, Lund, Sweden.
- NCSU: North Carolina State University Insect Collection, Department of Entomology, North Carolina State University, Raleigh, North Carolina, USA.
- QCAZ: Quito Catholic Zoology Museum, Departamento de Biología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.
- SEMC: Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA.
- SHMC†: S. H. McKamey Collection, currently at the United States Department of Agriculture, Agricultural Research Service, Systematic Entomology Laboratory, % National Museum of Natural History, MRC-168, Washington, D.C., USA.
- TKWC†: T. K. Wood Collection, currently at the Department of Entomology and Applied Ecology, University of Delaware, Newark, Delaware, USA.
- UCDC: The Bohart Museum of Entomology, University of California, Davis, California, USA.
- USNM: Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.
- ZMUH: Zoologisches Institut und Zoolo-
gisches Museum, Universität

von Hamburg, Hamburg, Germany.

Following each distribution record in the text is either a coden (see above) or a superscript number. Codens refer to a collection that includes specimens validating that record (only one collection is listed in most cases, although multiple collections may have specimens validating the distribution record); superscript numbers document records from the literature that have not been confirmed in this work—references are: ¹Metcalf and Wade 1965a, ²Ceballos-Bendezú 1980a, and ³Remes-Lenicov 1976b. Unverified distribution records from the literature should be used with caution, as some may be based on misidentified specimens.

The location and structure of suprnhumerals horns vary greatly within the tribe Stegaspidini, and even within some genera; nevertheless, the nature of these pronotal extensions usually provides excellent taxonomic features at the specific and generic levels. We consider any pronotal extensions located above the humeral angles to be suprhumeral horns. Thus, the unbranched processes of *Lycoderes* and *Oeda* spp. (Figs. 2–3, 11, 17–18), the stalked bulbs of *Bocydium* spp. (Cryan and Deitz 1999a: figs. 9, 11, 13), and the sometimes trifurcating horns of *Smerdalea* spp. (Cryan and Deitz 1995a: figs. 2, 9, 16) are homologous.

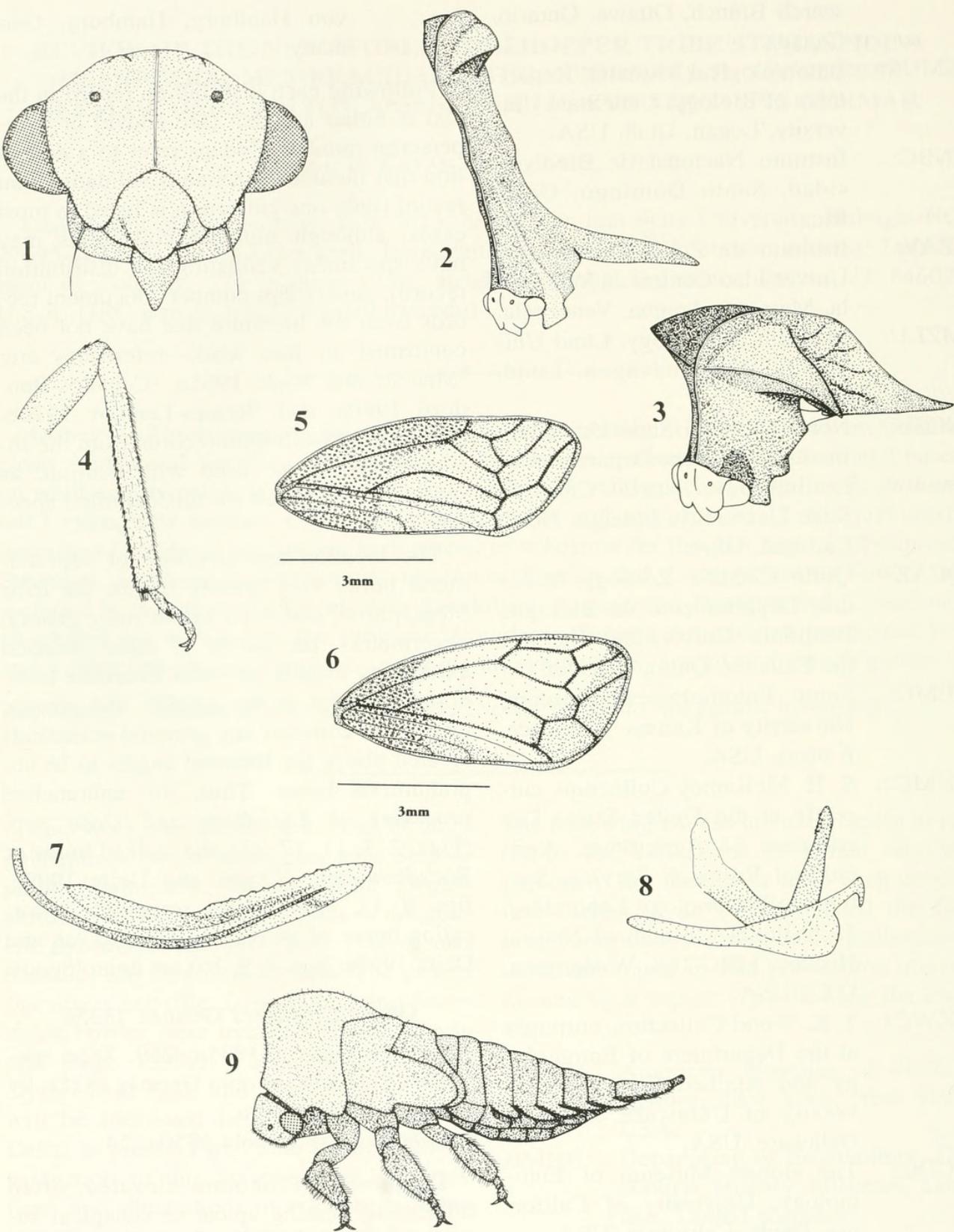
Genus *Lycoderes* Germar, 1835a

Lycoderes Germar 1835a: 259. Type species: *Centrotus ancora* Germar 1821a, by original designation.

Sycoderes [sic] Spinola 1850a: 54.

Diagnosis.—Pronotum elevated, often foliaceous, bearing apical or subapical suprhumeral horns; foliate lobes of the head not covering the postclypeus.

Adult.—*Dimensions* (mm): Total length 5.0–8.7. *Structure: Head* (Figs. 1–3): Finely setose; dorsal projections either very small or absent; ocelli on or above centro-ocular line; foliate lobes rounded; postcly-



Figs. 1-9. *Lycoderes* species. 1, *L. amazonicus*, head, anterior aspect (face). 2, *L. amazonicus*, head, pronotum, and scutellum, anterolateral aspect. 3, *L. mitratus*, head, pronotum, and scutellum, anterolateral aspect. 4, *L. mitratus*, left metathoracic femur, tibia, and tarsus, ablateral aspect. 5, *L. (Lycoderides) amazonicus*, right forewing. 6, *L. (Lycoderes) ancora*, right forewing. 7, *L. mitratus*, female second valvulae, lateral aspect. 8, *L. mitratus*, male aedeagus and left style, lateral aspect. 9, *L. marginalis*, late-instar nymph, lateral aspect.

peus usually strongly trilobed. *Thorax*: Pronotum (Figs. 2–3): Metopidium elevated into compressed anterior horn of variable length, with suprathumeral horns at (or just below) apex; suprathumeral horns always unbranched, of variable size and shape; posterior process variable (foliaceous, semi-foliaceous, or simple), completely concealing scutellum in some species (Fig. 2), not concealing scutellum in others (Fig. 3). *Pronotal surface sculpturing* (Fig. 35): Punctate; pits shallow, spaced closely together, each associated with a single long, narrow seta. *Scutellum* (Fig. 3): Relatively short, weakly produced anteriorly, with emarginate apex. *Legs* (Fig. 4): Tibiae foliaceous in some species; metathoracic femur without dorsal row of cucullate setae, tibiae with cucullate setae in enlarged setal row II (and, rarely, III); cucullate setae absent from row I. *Forewing* (Figs. 5–6): Basal $\frac{1}{3}$ coriaceous, distal $\frac{2}{3}$ either hyaline or semi-translucent; vein R_{2+3} basally fused with R_1 ; 1 r-m and 1 m-cu crossvein present (location of crossvein differs between subgenera). *Genitalia*: ♀: 2nd valvulae (Fig. 7) slightly curved dorsally, of roughly uniform width, tapered apically; dorsal ridge of distal $\frac{1}{2}$ usually with small serrations. ♂: Lateral plates fused to pygofer; aedeagus and styles (Fig. 8) relatively elongate; aedeagus tapered apically, anterior face of posterior arm with preapical area denticulate; styles of variable width, always with strongly hooked apices.

Late-instar nymph (Fig. 9).—Unknown for most species; pronotum laterally flattened, metopidium vertically produced into low median horn; tibiae foliaceous, fringed with setae; lateral lamellae, present on abdominal segments 5–9, fringed with setae.

Range.—Argentina [AMNH]; Bolivia [USNM]; Brazil [NCSU]; Peru [USNM]; Ecuador [NCSU]; French Guiana¹; Suriname [USNM]; Guyana [NCSU]; Venezuela [IZAV]; Trinidad [BMNH]; Colombia [USNM]; Panama [USNM]; Costa Rica [INBC]; Nicaragua¹; Honduras¹; Guatemala [USNM]; Mexico [USNM].

Material examined.—13 specimens from AMNH; 22 from BMNH; 8 from BPBM; 6 from CNCI; 8 from INBC; 25 from IZAV; 4 from MZLU; 67 from NCSU; 3 from QCAZ; 48 from SHMC; 15 from TKWC; 115 from USNM.

Remarks.—Sakakibara (1972b) published a major revision of *Lycoderes*, including descriptions and illustrations of most species (excluding those not occurring in Brazil), as well as a taxonomic key. We present the description of a new species, a checklist of described *Lycoderes* species (listing synonymies and new subgeneric placements), a modified translation of Sakakibara's key (originally published in Portuguese), and selected new illustrations for descriptive purposes. Several *Lycoderes* species were not examined during this work, and so we present the modified translation of Sakakibara's dichotomous key rather than a novel, comprehensive key. *Lycoderes* exhibits a relatively high degree of sexual dimorphism, often making species identification difficult; although Sakakibara's treatment alleviated much of this confusion, further work remains to determine the status of species that were omitted or new since his contribution. Reference to Sakakibara's figures (1972b) is recommended when identifying specimens of *Lycoderes* to the species level.

The subgenera *Lycoderides* and *Lycoderes* are defined by the shape of cell M_{1+2} (the fourth apical cell of the forewings; Figs. 5–6, respectively), although it is the placement of the r-m crossvein in relation to the fork of vein M that determines the cell's shape. Several species previously unplaced in the genus *Lycoderes* are here assigned to either the subgenus *Lycoderides* Sakakibara (r-m crossvein either basad of, or at, the fork of vein M) or *Lycoderes* Germar (r-m crossvein distad of the fork of vein M). Included in the subgenus *Lycoderides* are: *L. fernandezi* Strümpel (1988a: 147), *L. luteus* Funkhouser (1940a: 275), *L. phasianus* Fowler (1896e: 164), and *L. serraticornis* Fowler (1896e: 165); included in

the subgenus *Lycoderes* are: *L. capitatus* Buckton (1903a: 203) and *L. minamen* (Buckton) (1903b: 51).

The immature stages are unknown for most *Lycoderes* species; those that are known appear very similar to the nymphs of the closely related genus *Stegaspis*, differing primarily in their less foliaceous tibiae (Figs. 9, 34). Host plant information is limited to the following: Richter (1942c) reported *L. serraticornis* on *Bellucia* sp. (family Melastomataceae) and *L. petasus* from an unspecified species of the same family; Haviland (1925a) collected *L. hippocampus* on unidentified low shrubs in "shaded places," noting the absence of ant attendants; Wood (1984a) reported *L. phasianus* from *Miconia* sp. (Melastomataceae); McKamey (pers. comm.) collected *Lycoderes* from *Vismia* sp. (Guttiferae).

The Greek generic name, "*Lycoderes*," translates as "wolf neck," probably comparing the enlarged pronotal metopidium to the hackles on a canine neck. When making a generic name that refers to a feature of the prothorax, it is customary to modify the Greek noun "*dere*" to "*deres*," thereby making the name masculine (W. Kuschel, personal communication). Therefore, the names of *Lycoderes* species should have masculine endings, unless the name is a noun in opposition.

Lycoderes (Lycoderides) nathanieli

Cryan, new species

(Figs. 10–15)

Type locality.—Sierrazul, Napo Province, Ecuador.

Diagnosis.—*Lycoderes nathanieli* has enlarged suprahumeral horns extending anteriorly and curving toward the midline; the elevated posterior pronotal process bears two small pyramiform 'horns' apically; metathoracic tibia with reduced cucullate setae in rows II and III.

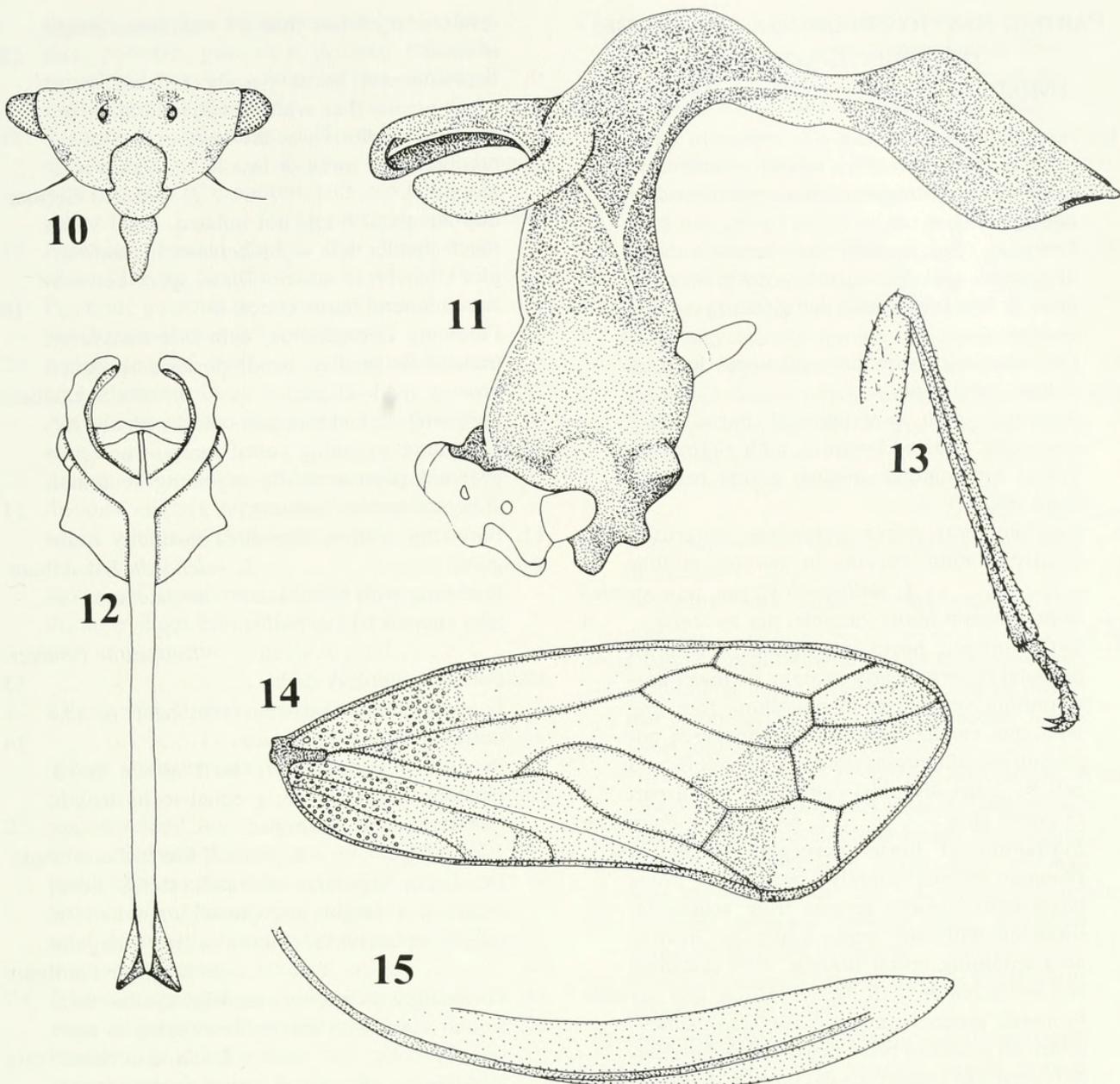
Adult (♀).—**Dimensions (mm):** Total length 9.9; width between humeral angles 2.3; pronotal length 7.2; forewing length 8.2; maximum width of head across eyes

2.1. **Coloration:** Pronotum generally dark brown with lighter metopidium; constriction in posterior pronotal process tan; scutellum with dark brown anterior base and pale apex; forewings hyaline with darker basal and apical pigmentation. **Structure:** **Head:** Face (Figs. 10–11) with fine pubescence; ocelli on centro-ocular line; dorsal projections small, nearly indistinguishable, with apices separated by a distance just shorter than the distance between ocelli. **Thorax:** **Pronotum** (Figs. 11–12): Middorsal ridge slightly produced, extending over full length of pronotum; supraocular callosities distinct; humeral angles moderately produced; pronotum raised vertically, with suprahumeral horns and posterior process well above body and a slightly raised carina on each side, extending both anteriorly and posteriorly; suprahumeral horns extending horizontally and anteriorly, curving inward, apices nearly meeting to approximate a circle; posterior process extending to end of abdomen, laterally compressed, with semi-constricted median area; apex of posterior process with one pyramiform, lateral projection on each side. **Scutellum** (Fig. 11): Relatively short; slightly produced for entire length (anterior region raised higher); apex acuminate. **Legs** (Fig. 13): Metathoracic femur lacking dorsal row of cucullate setae; metathoracic tibia with three enlarged setal rows: setal row I lacking cucullate setae, rows II and III with few, very reduced cucullate setae only on distal halves of produced ridges. **Forewing** (Fig. 14): Basal $\frac{1}{4}$ slightly thickened, punctate except for area between vein Cu and claval suture; 1 r-m and 1 m-cu crossvein. **Genitalia** (Fig. 15): 2nd valvulae relatively uniform in width and slightly curving dorsally; dorsal ridge lacking serration. ♂: Unknown.

Late-instar nymph.—Unknown.

Distribution.—Ecuador: Napo Province.

Material examined.—**Holotype:** [♀, dissected] from Escuela Politecnica Nacional, Quito, Ecuador (on indefinite loan to



Figs. 10–15. *Lycoderes nathanieli*, structures of the holotype. 10, Head, anterior aspect (face). 11, Head, pronotum, and scutellum, anterolateral aspect. 12, Head and pronotum, dorsal aspect. 13, Left metathoracic femur, tibia, and tarsus, ablateral aspect. 14, Right forewing. 15, Female second valvulae, lateral aspect.

USNM), with labels "ECUADOR: Napo Prov./Sierrazul, 2,200 m/SW of Baeza/O 40°S 77°55'W 22–30/Jan. 1996, T. J. Henry" and "Holotype / *Lycoderes/nathanieli* J. R. Cryan."

Remarks.—The pronotal structure of *L. nathanieli* is unusual in that the metopidium and posterior pronotal process are similar to those of other *Lycoderes* (and even *Stegaspis*) species, but the suprhumeral horns are reminiscent of those of *Oeda informis* and

O. hamulata, albeit much more produced. Unlike most other species of *Lycoderes*, the metathoracic tibiae of *L. nathanieli* bear reduced cucullate setae in the distal halves of setal rows II and III. Position of the r-m crossvein (basad of the fork of vein M) places *L. nathanieli* in the subgenus *Lycoderides*.

This species is named for Nathaniel Cryan, who was born during the preparation of this publication.

PARTIAL KEY TO SUBGENERA AND SPECIES
OF ADULT *LYCODERES*
(Modified from Sakakibara 1972b)

1. Forewing (Fig. 5) with r-m crossvein basad of, or at, fork of vein M; cell M_{1+2} transverse, more or less triangular; Subgenus *Lycoderes* Sakakibara
- Forewing (Fig. 6) with r-m crossvein distad of fork of vein M; cell M_{1+2} not transverse, more or less trapezoidal; Subgenus *Lycoderes* Germar
2. Pronotum with suprahumeral horns long, or at least contiguous
- Pronotum with suprahumeral horns much shortened, situated laterally, with slightly elevated longitudinal, median carina between them (Fig. 2)
3. Suprahumeral horns extending anteriorly from pronotum, curving in towards midline *L. nathanieli* Cryan, new species
- Suprahumeral horns variable, not as above 4
4. Suprahumeral horns contiguous; posterior pronotal process nearly straight, its lower basal portion very close to scutellum; forewing with one small, triangular, hyaline area adjoining costal margin, occupied by cell R_1 and cell R_{2+3} , the discoidal cell, and a small part of costal area *L. burmeisteri* Fairmaire
- Suprahumeral horns divergent; posterior pronotal process slightly sinuous, its lower basal portion more remote from scutellum; forewing with one large, triangular, hyaline area adjoining costal margin, with discoidal cell in its center *L. fuscus* Amyot and Serville
5. Pronotal process strongly elevated, subcylindrical; posterior process extending horizontally from the posteromedial portion of pronotal cylinder, curving basally and after, backwards at an angle, straight, shaped like steps of a staircase *L. gradatus* Sakakibara
- Pronotal process not much elevated, more or less constricted; slightly sinuate posterior process originating subapically or basally (on pronotal process) and extending over abdomen (Fig. 2)
6. Each suprahumeral horn, viewed from above, triangular, much longer than its basal width *L. hippocampus* (Fabricius)
- Each suprahumeral horn, viewed from above, rounded, shorter than its basal width *L. amazonicus* Sakakibara, *L. brevirostris* Sakakibara
7. Male 8
- Female 23
8. Apices of suprahumeral horns separated by a distance greater than $2 \times$ maximum length of head 9
- Apices of suprahumeral horns separated by a distance much less than $2 \times$ maximum length of head 12
9. Suprahumeral horns basally inflated, basal width greater than width between humeral angles; in anterior view, the contour line of the pronotal arch more or less in form of a half-moon *L. mitratus* Germar
- 2 - Suprahumeral horns not inflated, basal width much smaller than width between humeral angles (Fig. 3); in anterior view, space between suprahumeral horns concave 10
7. Forewing ferruginous, with one transverse, translucent median band; posterior pronotal process sickle-shaped *L. furcifer* Sakakibara
- 3 - Forewing dark chestnut in color, with one hyaline area adjoining costal margin; posterior pronotal process nearly adjoining scutellum along its outline (contour) 11
11. Forewing with hyaline area distinctly triangular *L. reichardti* Sakakibara
- Forewing with hyaline area elongate, more or less shaped like a half-moon *L. apertus* (Walker)
12. Forewing entirely dark 13
- Forewing with one transverse band or one nearly hyaline median area 14
13. Pronotum strongly elevated above head, reaching a height nearly equal to its length, in lateral view L-shaped *L. fabricii* Metcalf and Wade
- Pronotum regularly elevated above head, reaching a height just greater than half its length, in lateral view more or less triangular *L. unicolor* Fairmaire
14. Forewing with a round, median, hyaline area; frontal view with pronotum swollen at apex *L. clavatus* Sakakibara
- Forewing with a transverse hyaline band; frontal view with pronotum not swollen at apex 15
15. Base of posterior pronotal process removed from scutellum by a distance equal to or greater than its length 16
- Base of posterior process adjoining or slightly removed from scutellum 19
16. Apex of posterior pronotal process reaching inner angle of forewing; abdomen orange colored *L. ancora* (Germar)
- Apex of posterior pronotal process not reaching inner angle of forewing; abdomen ashen or chestnut colored 17
17. Apices of suprahumeral horns separated by a distance approximately equal to width between humeral angles; posterior pronotal process constricted; forewing widened at apex, with external angles straight *L. gladiator* Germar
- Apices of suprahumeral horns separated by a

- distance less than width between humeral angles; posterior process with basal half subcylindrical; forewing more or less narrowed, with external angle acute 18
18. Anterior face of pronotum elevated vertically above head *L. alvarengai* Sakakibara
- Anterior face of pronotum elevated obliquely above head *L. wygodzinskyi* Sakakibara
19. Posterior pronotal process thin, basal width about $0.2 \times$ its length *L. petasus* Fairmaire
- Posterior pronotal process compressed, basal width greater than $0.3 \times$ its length 20
20. Apical spot of forewing with small hyaline area adjoining distal margin 21
- Apical spot of forewing without small hyaline area 22
21. Apices of suprahumeral horns separated by a distance slightly greater than interocular distance; outline of pronotum slightly sinuate *L. gaffa* Fairmaire
- Apices of suprahumeral horns separated by a distance about $0.5 \times$ interocular distance; outline of pronotum slightly arched *L. foliatus* Sakakibara
22. Tibiae with 3 dark, transverse bands *L. luctans* Stål
- Tibiae without dark, transverse bands *L. turritus* Sakakibara
23. Suprahumeral horns strongly divergent, distance between their apices greater than $2 \times$ width between the humeral angles 24
- Suprahumeral horns more or less contiguous, or if divergent, distance between apices less than width between humeral angles 27
24. Posterior pronotal process sickle-shaped; suprahumeral horns V-shaped 25
- Posterior pronotal process not sickle-shaped; suprahumeral horns horizontal or slightly curved basally 26
25. Posterior pronotal process reaching apex of clavus; forewing hyaline with dark apical spot *L. ancora* (Germar)
- Suprahumeral horns not inflated, basal width approximately equal to $0.5 \times$ width between humeral angles; anterior view with pronotal outline depressed in middle *L. reichardti* Sakakibara
26. Posterior pronotal process distinctly sickle-shaped, with an average diameter of space between posterior pronotal process and scutellum greater than greatest diameter of eyes; forewing yellowish ferruginous, generally with somewhat distinct apical spot 28
- Posterior pronotal process not sickle-shaped, that is, adjoining scutellum or, when separated, with an average diameter of space less than greatest diameter of eyes; forewing dark or with very distinct apical spot 30
27. Suprahumeral horns slightly longer than interocular distance, with points slightly divergent, turning toward front in approximate horizontal plane of posterior pronotal process *L. gladiator* Germar
- Suprahumeral horns approximately $2 \times$ interocular distance, contiguous but turning out toward top, points much higher than horizontal plane of posterior pronotal process 29
28. Anterior of pronotum undulating; color generally yellowish ferruginous, with coxae, head, and anterior portion of pronotum dark chestnut; forewing with apical spot very weakened, nearly imperceptible *L. luctans* Stål
- Anterior of pronotum nearly straight; color generally chestnut ferruginous; forewing with apical spot more or less distinct *L. gaffa* Fairmaire
29. Forewing entirely dark or slightly translucent in middle 31
- Forewing with large, conspicuous hyaline area 32
30. Distance from humeral angles to bases of suprahumeral horns more than length of posterior pronotal process; suprahumeral horns short and divergent *L. fabricii* Metcalf and Wade
- Distance from humeral angles to base of suprahumeral horns less than length of posterior process; suprahumeral horns more or less long and contiguous *L. unicolor* Fairmaire
31. Posterior pronotal process long, its basal width about $0.5 \times$ its length 32
- Posterior pronotal process thin, its basal width about $0.2 \times$ its length 33
32. Pronotal outline triangular in lateral view, with dorsal angle nearly straight; dorsal outline more or less arched *L. unicolor* Fairmaire
- Pronotal outline triangular in lateral view, with dorsal angle pointed; dorsal outline slightly sinuate *L. turritus* Sakakibara
33. Color of posterior pronotal process uniform, adjoining scutellum or slightly removed, but not by more than its basal width; suprahumeral horns generally contiguous *L. petasus* Fairmaire
- Color of posterior pronotal process paler basally, removed from scutellum by a distance greater than its basal width; suprahumeral horns generally divergent 34
34. Pronotum, in lateral view, projecting obliquely anteriorly; suprahumeral horns nearly equal in length to interocular distance *L. wygodzinskyi* Sakakibara
- Pronotum, in lateral view, not projecting obliquely anteriorly, anterior portion more or less vertical; suprahumeral horns nearly equal

in length to $0.3 \times$ interocular distance
 *L. alvarengai* Sakakibara

SPECIES CHECKLIST OF *LYCODERES*

- Subgenus *Lycoderides* Sakakibara 1972b:
 92. Type-species: *Centrotus hippocampus* Fabricius 1803a, by original designation.
amazonicus Sakakibara
Lycoderes amazonica Sakakibara 1991a: 655.
brevilobus Sakakibara
Lycoderes brevilobus Sakakibara 1972b: 102.
burmeisteri Fairmaire
Lycoderes burmeisteri Fairmaire 1846b: 525.
Enchenopa laeta Walker 1851a: 494.
Enchenopa fissa Walker 1851b: 685.
Lycoderes igniventer Buckton 1903a: 200.
Lycoderes triangulata Funkhouser 1919c: 27.
culturatus Sakakibara
Lycoderes cultrata Sakakibara 1991a: 657.
***fernandezii* Strümpel, new subgeneric placement**
Lycoderes fernandezii Strümpel 1988a: 147.
fuscus Amyot and Serville
Lycoderes fuscus Amyot and Serville 1843a: 561.
Lycoderes angustata Buckton 1903a: 201.
Lycoderes fusca: Metcalf and Wade 1965a: 56.
gradatus Sakakibara
Lycoderes gradatus Sakakibara 1972b: 101.
hippocampus (Fabricius)
Centrotus hippocampus Fabricius 1803a: 20.
Lycoderes pileolum Fairmaire 1846b: 526.
Lycoderes hippocampus: Walker 1851a: 634.
Lycoderes hippocampa: Metcalf and Wade 1965a: 59.

luteus Funkhouser, new subgeneric placement

Lycoderes luteus Funkhouser 1940a: 275.

Lycoderes lutea: Metcalf and Wade 1965a: 61.

marginalis (Walker)

Membracis marginalis Walker 1851a: 479.

Stegaspis marginalis: Metcalf and Wade 1965a: 73.

Lycoderes marginalis: Sakakibara 1991a: 652.

nathanieli Cryan, new species

obtusus Sakakibara

Lycoderes obtusa Sakakibara 1991a: 657.

pennyi Sakakibara

Lycoderes pennyi Sakakibara 1991a: 653.

phasianus Fowler, new subgeneric placement

Lycoderes phasianus Fowler 1896e: 164.

Lycoderes phasiana: Metcalf and Wade 1965a: 62.

protensus Sakakibara

Lycoderes protensa Sakakibara 1991a: 659.

serraticornis Fowler, new subgeneric placement

Lycoderes serraticornis Fowler 1896e: 165.

strumpeli Sakakibara

Lycoderes strumpeli Sakakibara 1991a: 653.

Subgenus *Lycoderes* Germar 1835a.

Corythophora Stål 1869a: 53.

Lophucha Stål 1869a: 54.

Rhyparoptera Stål 1869a: 54.

alvarengai Sakakibara

Lycoderes alvarengai Sakakibara 1972b: 131.

ancora (Germar)

Centrotus ancora Germar 1821a: IV.32.

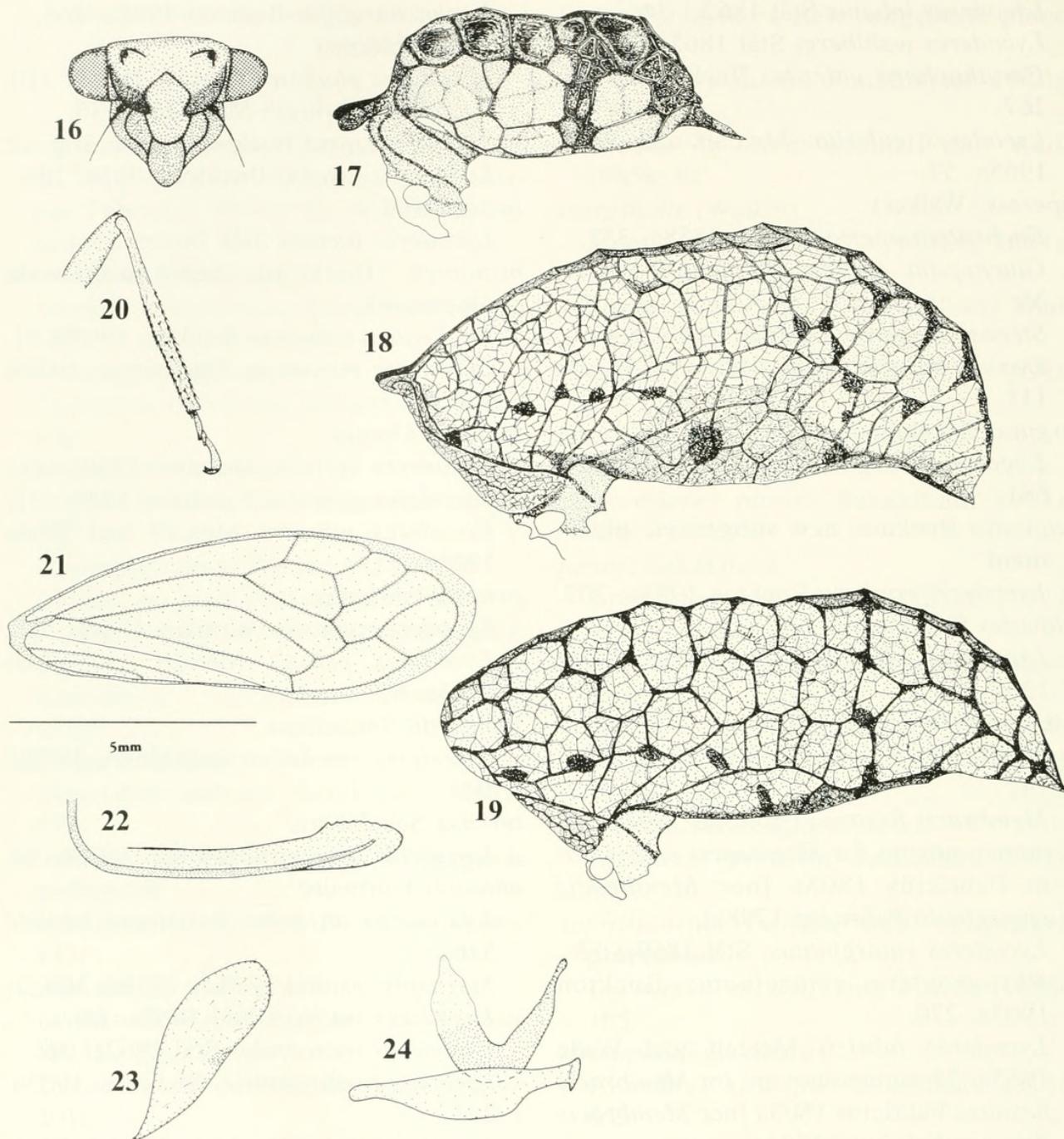
Bocydium galeritum Lesson 1832a: 56.

Lycoderes ancora: Germar 1835a: 259.

Lycoderes furca Fairmaire 1846b: 524.

Lycoderes galeritus: Fairmaire 1846b: 523.

- Lycoderes lobatus* Stål 1862e: 34.
Lycoderes wahlbergi Stål 1862e: 35.
Corythophora galerita: Buckton 1903a: 267.
Lycoderes galerita: Metcalf and Wade 1965a: 57.
apertus (Walker)
Enchenopa aperta Walker 1858c: 337.
Guayaquila aperta: Funkhouser 1927f: 36.
Stegaspis aperta: Goding 1928a: 395.
Lycoderes apertus: Sakakibara 1972b: 111.
- argutus* Sakakibara
Lycoderes arguta Sakakibara 1991a: 661.
- capitatus** Buckton, new subgeneric placement
Lycoderes capitata Buckton 1903a: 203.
- clavatus* Sakakibara
Lycoderes clavatus Sakakibara 1972b: 123.
- fabricii* Metcalf and Wade
Membracis emarginata Fabricius 1803a: 14.
Membracis flexuosa Fabricius 1803a: 16; nomen novum for *Membracis emarginata* Fabricius 1803a [nec *Membracis emarginata* Fabricius 1798a].
Lycoderes emarginatus: Stål 1869a: 53.
Rhyparoptera emarginata: Buckton 1903a: 270.
Lycoderes fabricii Metcalf and Wade 1965a: 55; nomen novum for *Membracis flexuosa* Fabricius 1803a [nec *Membracis flexuosa* Fabricius 1794a].
- foliatus* Sakakibara
Lycoderes foliatus Sakakibara 1972b: 124.
- furcifer* Sakakibara
Lycoderes furcifer Sakakibara 1970b: 25.
- gaffa* Fairmaire
Lycoderes gaffa Fairmaire 1846b: 524.
Centrotus latipennis Walker 1851a: 607.
Stegaspis bellicosa Walker 1858b: 165.
Lycoderes latipennis: Stål 1862b: 491.
Pterygia subminax Walker 1862a: 316.
Stegaspis latipennis: Buckton 1903a: 270.
- Lophucha gaffa*: Buckton 1903a: 268.
gladiator Germar
Lycoderes gladiator Germar 1835b: 310.
Lycoderes corniger Stål 1862e: 36.
Lycoderes torta Buckton 1903a: 202.
Lycoderes fuscata Buckton 1903a: 204.
luctans Stål
Lycoderes luctans Stål 1862e: 35.
minamen (Buckton), new subgeneric placement
Enchenopa minamen Buckton 1903b: 51.
Lycoderes minamen: Funkhouser 1927f: 436.
- mitratus* Germar
Lycoderes mitratus Germar 1835b: 311.
Lycoderes spinolae Fairmaire 1846c: 12.
Lycoderes mitrata: Metcalf and Wade 1965a: 62.
- petasus* Fairmaire
Lycoderes petasus Fairmaire 1846b: 526.
Lycoderes petasa: Metcalf and Wade 1965a: 62.
- reichardti* Sakakibara
Lycoderes reichardti Sakakibara 1972b: 109.
- turritus* Sakakibara
Lycoderes turritus Sakakibara 1970b: 27.
- unicolor* Fairmaire
Lycoderes unicolor Fairmaire 1846b: 526.
Stegaspis insolita Walker 1858b: 109.
Lycoderes prolixus Stål 1862e: 35.
Lycoderes truncatulus Stål 1862e: 36.
Lycoderes truncatulis Buckton 1903a: 203.
Lycoderes insolita: Metcalf and Wade 1965a: 60.
- wygodzinskyi* Sakakibara
Lycoderes wygodzinskyi Sakakibara 1972b: 129.
- Genus *Oeda* Amyot and Serville, 1843a
Oeda Amyot and Serville 1843a: 546. Type species: *Membracis inflata* Fabricius 1787a, by original designation.
Aeda [sic] Spinola 1850a: 55.
Ada [sic] Desmarest 1859a: 199.
- Diagnosis.—*Oeda* differs from other stegaspidine genera in the balloon-like infla-



Figs. 16–24. *Oeda* species. 16, *O. inflata*, head, anterior aspect (face). 17–19, Head and pronotum, antero-lateral aspect of *O. informis*, *O. hamulata*, and *O. inflata*, respectively. 20, *O. informis*, left metathoracic femur, tibia, and tarsus, ablateral aspect. 21, *O. hamulata*, right forewing. 22, *O. inflata*, female second valvulae, lateral aspect. 23, *O. informis*, male left lateral plate, lateral aspect. 24, *O. informis*, male aedeagus and left style, lateral aspect.

tion of the posterior pronotal process, which has well defined and reticulate venation.

Adult.—**Dimensions (mm):** Total length 7.5–13.8. **Structure:** **Head** (Fig. 16): Dorsal projections either absent or very small; ocelli on raised tubercles; foliate lobes extend over postclypeus. **Thorax:** **Pronotum**

(Figs. 17–19): Suprahumeral horns (if present) short, simple; posterior pronotal process long, inflated, variously reticulate. **Pronotal surface sculpturing** (Fig. 36): Metopidium punctate; pits small, spaced regularly, not associated with a seta; posterior process membranous, not punctate. **Scutel-**

lum: Short, moderately elevated anteriorly; apex broadly acuminate (rounded). *Legs* (Fig. 20): Metathoracic femur lacking cucullate setae, tibiae with cucullate setae in rows II and III. *Forewing* (Fig. 21): Apical limbus wide; vein R_{2+3} fused basally with R_1 ; 1 r-m and 1 m-cu crossvein present (crossvein r-m remotely basad of fork of vein M). *Genitalia*: ♀: 2nd valvulae (Fig. 22) basal 2/3 slender, distal 1/3 broadened with dorsal serrations. ♂: lateral plates (Fig. 23) free, without apical hook; aedeagus and styles (Fig. 24) relatively short, stout; styles hooked apically; aedeagus tapering apically, anterior face of posterior arm with preapical area weakly denticulate.

Late-instar nymph.—Unknown for all species.

Range.—Argentina³; Paraguay [NCSU]; Bolivia [USNM]; Peru [AMNH]; Ecuador [MZLU]; Brazil [AMNH]; French Guiana¹; Suriname¹; Guyana¹; Venezuela [IZAV]; Colombia [USNM]; Costa Rica [TKWC].

Material examined.—Type specimens not examined. Other specimens: *O. hamulata*: 1 ♂ from AMNH, 1 ♀ from IZAV, 4 ♀ from NCSU, 1 ♀ from SEMC, 5 ♀ from USNM (including Cryan Research #93-162a ♀), 3 ♀ from ZMUH. *O. inflata*: 1 ♀ from AMNH, 1 ♀ from MZLU, 1 ♀ from TKWC, 2 ♀ from USNM (including Deitz Research #71-293a ♀), 3 ♀ from ZMUH. Sp. possibly *O. mirandai*: 5 ♀ from ZMUH. *O. informis*: 3 ♀ from AMNH, 2 ♀ from NCSU, 1 ♀ from SEMC, 1 ♂ from SHMC (Cryan Research #94-299a ♂), 4 ♀ from USNM (including Cryan Research #94-300b ♀).

Remarks.—The genus *Oeda* was revised by Fonseca (1951a), who erected the new subgenus *Oedacanthus* and recognized four species. These species are some of the strangest, most bizarre treehoppers known. Aside from the illustrations presented in this work (Fig. 28), drawings of *O. hamulata* were given by Vignon (1930a), Seitz (1951a), Fonseca (1951a), and Richter (1955a, with a discussion of pronotal evolution theories). Schröder (1962a), Boulard

(1986a), and Klausnitzer (1987a) all published pictures of *O. hamulata* (as *O. inflata* in the figure captions). *Oeda informis* was illustrated by Vignon (1930a), Fonseca (1951a), and Richter (1955a). Wood (1984a) reported that three adults of *O. inflata* were collected from one leaf of *Cecropia* sp. (Moraceae). Nymphs of all species of *Oeda* remain unknown.

Deitz's (1975a) statement that the male lateral plates are absent in *Oeda* seems to be incorrect. The lateral plates are present and free (no apical hooks) in *O. informis* (Fig. 23) and *O. hamulata*, resembling the lateral plates of the closely related genus *Bocydium* (Cryan and Deitz 1999a). Males of *O. inflata* and *O. mirandai* were not examined, but are presumed to have lateral plates.

The type specimen of *O. mirandai* was not examined. Based on the original description, the difference between this species and *O. hamulata* seems to lie solely in the relative lengths of their balloon-like posterior pronotal processes. Some specimens examined in this work have pronota like *O. hamulata*, except the suprhumeral horns are reduced to mere nubs. If these specimens represent *O. mirandai*, then there is no doubt about that species' validity. Although *O. mirandai* is recognized here as a separate species, it may not actually be valid.

The purpose of the inflated posterior pronotal process is unknown. Rietschel (1987a) suggested that this bizarre structure serves as a "passive protecting adaptation," specialized against predators (e.g. birds and lizards) that attack the pronotum. Following this theory of autotomy, the predator grasps the inflated pronotum, which apparently breaks along a "fault-line" located at the base of the posterior process where the diameter is smallest, thus allowing the insect to escape. Unlike the pronotal fault-line visible in the genus *Anchistrotus* Buckton of the subfamily Heteronotinae (Boulard 1983a), however, the fault-line is not plainly visible in *Oeda*. Buckton (1903b) hy-

pothesized that the pronotum of *Oeda* mimics fragments of dead leaves in their yellow-orange color, their leaflike venation, and their small, dark spots that might correspond to sites where insect feeding has damaged a leaf surface. A theory proposed by Poulton (in Buckton 1903b), suggested that this structure mimics the empty pupal case of some Neotropical butterflies and moths. Finally, T. K. Wood (personal communication) has speculated that this mysterious structure may play some role in thermoregulation or in sound reverberation.

The generic name is based on the Greek noun "oidema," meaning "a swelling."

KEY TO SUBGENERA AND SPECIES OF ADULT *OEDA*

(Modified from Fonseca 1951a)

1. Swollen pronotal process sessile (Figs. 18–19) and opaque, with finely reticulate areas; posterior pronotal process unarmed apically; Subgenus *Oeda* Amyot and Serville 2
- Swollen pronotal process pedunculate (Fig. 17) and translucent, glassy, without finely reticulate areas; posterior pronotal process with spiny (thornlike) apical projection; Subgenus *Oedacanthus* da Fonseca *O. informis* (Westwood)
2. Anterior of pronotal swelling with two digitate suprahumeral horns (Fig. 18) 3
- Anterior of pronotal swelling without digitate suprahumeral horns (Fig. 19) *O. inflata* (Fabricius)
3. Posterior pronotal process extending beyond wing apices (at rest) *O. hamulata* Stål
- Posterior pronotal process not extending beyond wing apices *O. mirandai* da Fonseca

SPECIES CHECKLIST OF *OEDA*

Subgenus *Oeda* Amyot and Serville 1843a.
hamulata Stål

- Oeda hamulata* Stål 1869a: 52.
inflata (Fabricius)
Membracis inflata Fabricius 1787a: 262.
Cicada inflata: Linnaeus 1790: 2092.
Smilia inflata: Germar 1833a: 177.
Oeda inflata: Amyot and Serville 1843a: 547.
Oeda inermis: Fairmaire 1846b: 506.
Oeda frondosa: Buckton 1903a: 206.
mirandai Fonseca

Oeda mirandai Fonseca 1951a: 211.
Subgenus *Oedacanthus* Fonseca 1951a: 211. Type-species: *Smilia informis* Westwood 1842a, by original designation.
informis (Westwood)

Smilia informis Westwood 1842a: 119.
Oeda informis: Fairmaire 1846b: 507.

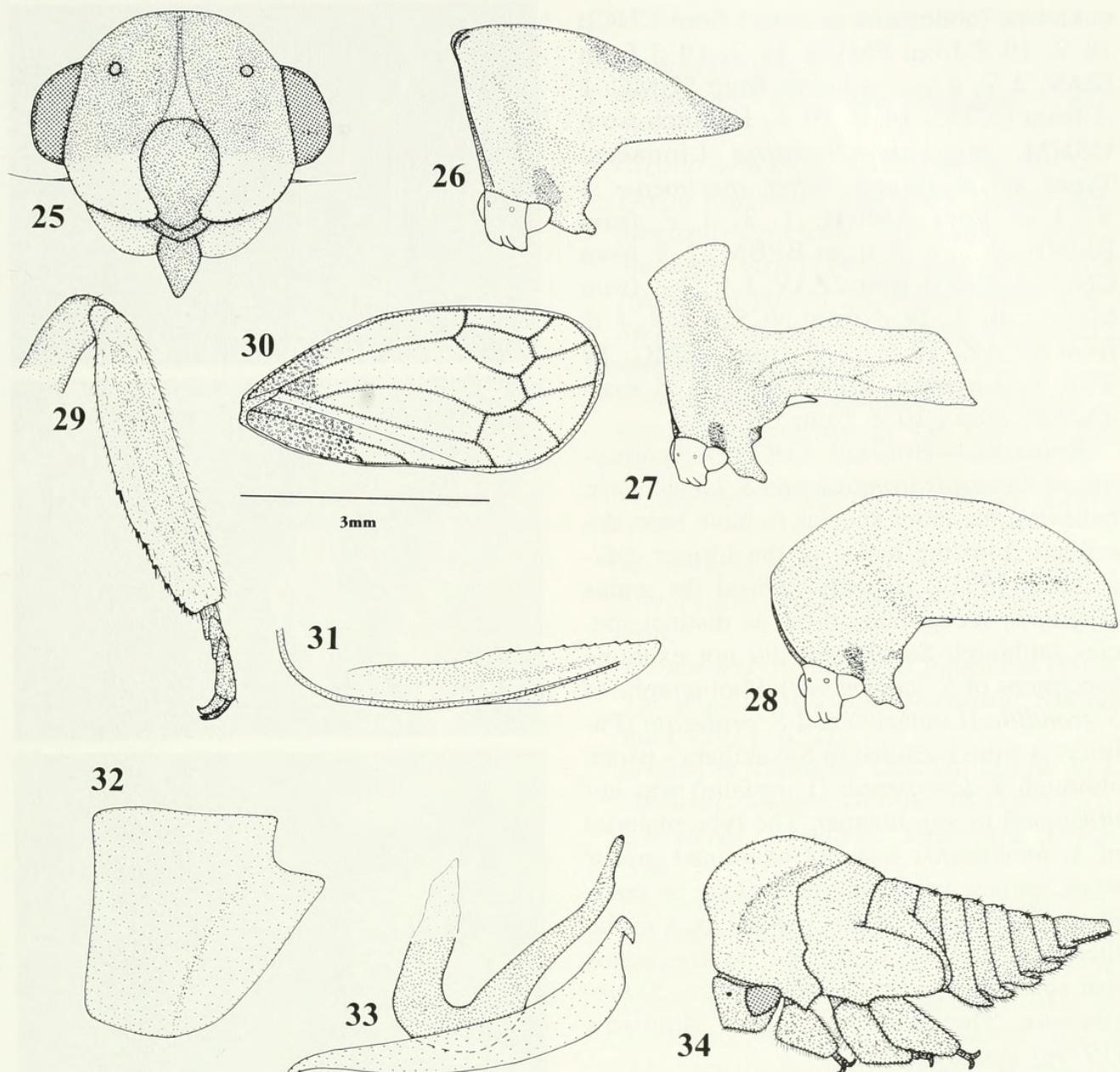
Genus *Stegaspis* Germar, 1833a

Stegaspis Germar 1833a: 177. Type species: *Cicada fronditia* Linnaeus 1758a, by subsequent designation of Kirkaldy 1901e: 219.

Membracis Fabricius: Blanchard 1840a: 180 [error].

Diagnosis.—*Stegaspis* is unique among Stegaspidini in having the foliate lobes of the head extending over the postclypeus.

Adult.—**Dimensions (mm):** Total length 5.6–7.7. **Structure: Head** (Fig. 25): Finely setose; dorsal projections absent; foliate lobes rounded, extending over unilobed postclypeus. **Thorax:** **Pronotum** (Figs. 26–28): Metopidium elevated, laterally compressed; suprahumeral horns absent (or, at most, represented by extremely small carinae at metopidial apex); posterior process foliaceous, either dorsally or completely concealing scutellum. **Pronotal surface sculpturing** (Fig. 37): Punctate; pits shallow and closely spaced, each associated with a single long, narrow seta. **Scutellum** (Figs. 27–28): Relatively short, weakly produced anteriorly, with emarginate apex. **Legs** (Fig. 29): Tibiae strongly foliaceous; metathoracic femur without dorsal row of cucullate setae, tibia with cucullate setae in row II only. **Forewing** (Fig. 30): Basal $\frac{1}{3}$ coriaceous, distal $\frac{2}{3}$ hyaline; vein R_{2+3} basally fused with R_1 ; 1 r-m and 1 m-cu cross-vein present (r-m crossvein distad of fork of vein M). **Genitalia:** ♀: 2nd valvulae (Fig. 31) roughly uniform in width, tapered apically; dorsal ridge of distal $\frac{1}{2}$ with small serrations. ♂: Lateral plates fused to pygofer (Fig. 32); aedeagus and styles (Fig. 33) elongate; aedeagus tapered apically, anterior face of posterior arm with preapical



Figs. 25–34. *Stegaspis* species. 25, *S. bracteata*, head, anterior aspect (face). 26–28, Head, pronotum, and scutellum, anterolateral aspect of *S. bracteata*, *S. fronditia* (female), and *S. fronditia* (male), respectively. 29, *S. bracteata*, left metathoracic femur, tibia, and tarsus, ablateral aspect. 30, *S. bracteata*, right forewing. 31, *S. fronditia*, female second valvulae, lateral aspect. 32, *S. fronditia*, male left lateral plate and pygofer, lateral aspect. 33, *S. fronditia*, male aedeagus and left style, lateral aspect. 34, *S. bracteata*, late-instar nymph, lateral aspect.

area weakly denticulate; styles of variable width, always with strongly hooked apices.

Late-instar nymph (Fig. 34).—Pronotum laterally flattened, metopidium vertically produced into low median horn; tibiae strongly foliaceous, fringed with setae; lateral lamellae, present on abdominal segments 4–8, fringed with setae.

Range.—Bolivia [USNM]; Peru [NCSU]; Ecuador [QCAZ]; Brazil [USNM]; French

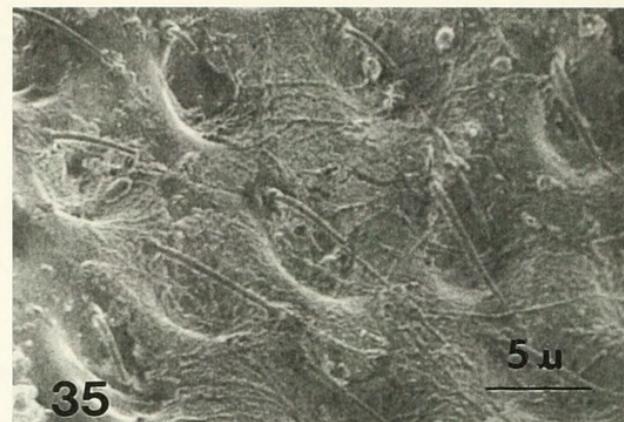
Guiana¹; Guyana [NCSU]; Suriname²; Venezuela [IZAV]; Trinidad [USNM]; Colombia [USNM]; Panama [USNM].

Material examined.—*Stegaspis bracteata* (Fabricius): Holotype of *Stegaspis viridis* Funkhouser [♀] [USNM], with labels: "Port of Spain/Trinidad, W.I./R.J. Crew," "WDFunkhouser/Collection/1962," and "TYPE/Stegaspis viridis." Other specimens: 1 ♂ from AMNH; 19 ♀, 30 ♂, 4

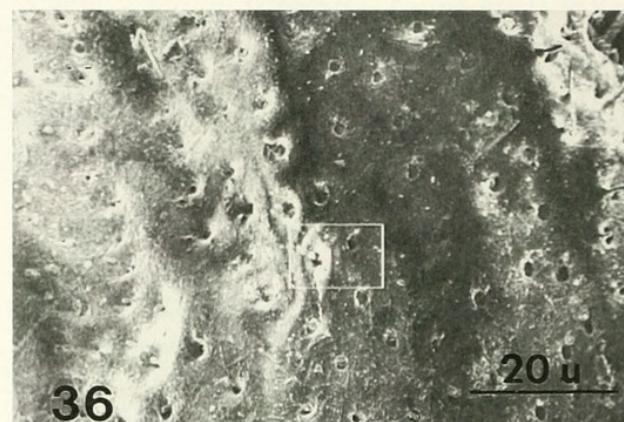
unknown (abdomens missing) from CNCI; 14 ♀, 19 ♂ from EMUS; 14 ♀, 19 ♂ from IZAV; 2 ♀, 6 ♂, 3 nymphs from SHMC; 1 ♂ from UCDC; 14 ♀, 10 ♂, 1 nymph from USNM. *Stegaspis fronditia* Linnaeus: Types not examined. Other specimens: 3 ♀, 1 ♂ from AMNH; 1 ♀, 1 ♂ from BMNH; 2 ♀, 1 ♂ from BPBM; 2 ♀ from CNCI; 8 ♀, 2 ♂ from IZAV; 1 ♀, 7 ♂ from MZLU; 46 ♀, 24 ♂ from NCSU; 4 ♀, 1 ♂ from QCAZ; 10 ♀, 2 ♂ from SEMC; 19 ♀, 6 ♂, 3 nymphs from SHMC; 1 ♂ from TKWC; 20 ♀, 10 ♂ from USNM.

Remarks.—Boulard (1979g) synonymized *Stegaspis fronditia* and *S. laevipennis*, believing the latter species to have been described from the males of the former. Sakakibara (1991a) recently revised the genus *Stegaspis*, recognizing these as distinct species (although Sakakibara did not examine specimens of *S. laevipennis*). Photographs of *S. fronditia* (Linnaeus) and *S. bracteata* (Fabricius) were included in Sakakibara's paper, although *S. laevipennis* (Fairmaire) was not illustrated in any manner. The type material of *S. laevipennis* was not examined in our work, either; no clear illustrations or complete descriptions of this species exist in the literature, and we examined no specimens that could be identified definitively as *S. laevipennis*. Therefore, we follow Boulard's (1979g) synonymy.

Haviland (1925a) reported that *S. fronditia* (as *S. galeata*) can be found with ant attendants. She hypothesized that the unusual pronotal shapes of *S. galeata* mimic bits of dead leaves, also observing that the foliaceous tibiae serve to obscure the outline of the insects as they cling to tree branches and twigs. Haviland described *S. fronditia* (as *S. galeata*) as living in colonies attended by ant mutuals, whereas *S. laevipennis* (now *S. fronditia*) is a solitary species, not ant-attended. Substrate mediated vibrational signals have been recorded from females of *S. fronditia* (R. Crocroft, personal communication). Poulton (1891a) illustrated a nymph of *Stegaspis* sp. (the illustration was later reproduced by Heikertinger [1954a]), describ-



35



36



37

Figs. 35–37. Pronotal surface sculpturing of Stegaspidini. 35, *Lycoderes* sp. 36, *Oeda informis*. 37, *Stegaspis fronditia*.

ing the nymph as a mimic of leaf-cutting ants, the pronotal shape resembling jagged pieces of leaves carried over the backs of the ants. It is probable, however, that this nymph was actually a species of the genus *Cymbomorpha*, subfamily Darninae, that was incorrectly identified (McKamey, personal communication).

Other illustrations of *Stegaspis* in previous literature include Vignon's (1930a) figure of a *Stegaspis* sp. nymph, Suchantke's

(1983a) of a *S. fronditia* adult, Strümpel's (1983a) photograph of *S. fronditia* (as "S. insignis" in the caption), and Boulard's (1979g) of *S. fronditia* adults (one male and one female). Richter (1955a) discussed the possibility that the expanded pronota of Membracidae originated as the dorsal fusion of prothoracic wings, illustrating both *Stegaspis* spp. and *Oeda* spp. as examples.

The only host records for *Stegaspis* (Haviland 1925a) describe the plants rather than identify them: *S. fronditia* [as *S. gal-eata*] was collected from unidentified green vines and shoots in "shaded places." *Stegaspis laevipennis* is reported from a "slender, straggling tree, common in open places, [and] had the twigs and undersides of the leaves covered with rusty brown powder." Haviland's host plant descriptions are apparently consistent with *Vismia* sp. (family Guttiferae), on which species of *Bocydium* and *Lycoderes* were also collected (McKamey, personal communication).

Species of *Stegaspis* can be easily separated from the morphologically similar species of *Lycoderes* by the form of the head's foliate lobes: *Stegaspis* has the foliate lobes extending over the postclypeus (Fig. 25), sometimes nearly touching each other; the foliate lobes of *Lycoderes* do not extend over the postclypeus (Fig. 1). *Stegaspis*, like *Lycoderes* and other stegaspidine genera, exhibits sexual dimorphism with respect to pronotal structure (Figs. 27–28).

The generic name is a combination of the Greek terms "steg" (from "stego," meaning "roof or cover") and "aspis" (meaning "shield"), perhaps referring to the fact that the pronota of *Stegaspis* almost entirely cover (protect) the dorsal surfaces of these insects.

KEY TO SPECIES OF ADULT STEGASPIS

1. Pronotum foliaceous, L-shaped in females (Fig. 27) and ovoid in males (Fig. 28) *S. fronditia* (Linnaeus)
- Pronotum triangular in both sexes; dorsal pronotal margin nearly straight (Fig. 26) *S. bracteata* (Fabricius)

SPECIES CHECKLIST OF STEGASPIS

bracteata (Fabricius)

Membracis bracteata Fabricius 1787a: 263.

Cicada bracteata: Donovan 1820a: 2.

Thelia bracteata: Fairmaire 1846a: 309.

Stegaspis bracteata: Stål 1869a: 54.

Stegaspis viridis Funkhouser 1915e: 104.

Lycoderes viridis Strümpel 1988a: 148.

Stegaspis viridis: Sakakibara 1991a: 652.

fronditia (Linnaeus)

Cicada fronditia Linnaeus 1758a: 435.

Cicada foliatasinuosa De Geer 1773a: 208.

Membracis fronditia: Fabricius 1781a: 316.

Membracis folium Olivier 1792a: 668.

Membracis melanopetalus Olivier 1792a: 668.

Membracis abdominalis Fabricius 1803a: 15. [equals *Stegaspis fronditia*: Sakakibara 1991a: 652].

Stegaspis fronditia: Germar 1833a: 177.

Stegaspis folium: Germar 1833a: 177.

Lycoderes fronditia: Fairmaire 1846b: 526.

Enchenopa galeata Walker 1851a: 486.

Stegaspis galeata: Walker 1858c: 341.

Stegaspis melanopetala: Stål 1869a: 54.

Hypsoprora insignis Buckton 1901a: 59.

Stegaspis insignis: Funkhouser 1922a: 34. [equals *Stegaspis fronditia*: Sakakibara 1991a: 652].

Lycoderes laevipennis Fairmaire 1846b: 527.

Stegaspis laevipennis: Walker 1851a: 635. [equals *Stegaspis fronditia*: Boulard 1979g]

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