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A REVISION OF THE NEW WORLD GENUS *ERPETOGOMPHUS* HAGEN IN SELYS (ODONATA: GOMPHIDAE)

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This revision of adult *Erpetogomphus* includes a phylogenetic assessment of all 21 species using outgroup comparison and parsimony algorithm, descriptive biogeography, keys to both sexes, synonymies, descriptions, type designations, and illustrations, including distribution maps of all species. Six new species are described: *E. agkistrodon, E. leptophis, E. elaphe, E. liopeltis, E. bothrops, E. heterodon. Erpetogomphus coluber* is considered a junior synonym of *E. compositus, E. natrix* is considered a subspecies of *E. lampropeltis*, and a neotype is designated for *E. cophias*. Phylogenetic assessment of 41 mostly somatic characters shows *Erpetogomphus* to be partitioned into three monophyletic groups: 1) six dark green species (*E. constrictor, E. sabaleticus, E. tristani, E. agkistrodon, E. schausi, E. ophibolus*) with mostly allopatric or parapatric distributions along the eastern coast of Mexico south into northern Colombia and Venezuela, 2) two species (*E. leptophis, E. eutainia*) with distributions from southern Texas south through Mexico and up the west coast to Michoacan states, and 3) 13 remaining species (*E. elaphe, E. elaps, E. liopeltis, E. bothrops, E. viperinus, E. designatus, E. sipedon, E. lampropeltis, E. crotalinus, E. heterodon, E. compositus, E. boa, E. cophias*) with distributions in the central United States south through Mexico to Costa Rica. Derived characters states were gleaned mostly from primary and secondary genitalic characters (head structure, penis, hamules, caudal appendages, vulvar lamina); but satisfactory resolution of terminal clades, especially of the third group, is difficult due to apparent character reversals.

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Key words. – Odonata; Gomphidae; *Erpetogomphus*; systematics; keys; cladistics; phylogeny; biogeography.

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INTRODUCTORY PART

Introduction

No other group of Middle American Gomphidae has been in need of revision as much as the genus *Erpetogomphus* Hagen *in* Selys. The last species were described by Williamson and Williamson (1930), and although several odonatists have since received species which are possibly undescribed, there has been a hesitancy to describe them because so many species are rare or poorly known. Several years ago, I collected a few specimens of one species I thought new, but I realized that an examination of most of the types would be necessary before I could resolve the problem.

This paper is the result of those investigations. My purpose here is to: 1) describe and figure all species currently going under the generic name *Erpetogomphus*, 2) select lectotypes and establish type localities, if possible, and 3) construct a cladogram of all the known species so that phylogenetic relationships and distribution patterns can be adduced for the genus. I have examined types for all taxa except for two species, *E. cophias* (type lost), and *E. ophibolus*. The last species is distinct, and no confusion exists about its identity or type deposition. A neotype is selected for *E. cophias*. I also provide keys for all species.

Twenty-three names (table 1) have been included in *Erpetogomphus*, but three, *E. severus* Selys, *Herpetogomphus rupinsulensis* Walsh, and *H. pictus* Needham (= *Ophiogomphus rupinsulensis* (Walsh)) have been transferred to *Ophiogomphus*. Another, *E. menetriesii* (Selys) I consider to be a *nomen dubium*, for reasons detailed below; and six new species are described. One species thought lost, *E. boa* Selys, has been rediscovered, and *E. viperinus* auctorum is really an undescribed species. I suspect that several new species will be found in Mexico and Central America, and I hope this paper will make it easier for others to describe those new species.

The difficulties I have encountered during this study have mostly been due to the paucity of specimens of various species which have been considered rare. I have successfully associated both sexes of all current species except the male of *E. agkistrodon*, which is unknown. My task of recording aspects of intraspecific variation has been made considerably easier by various museum authorities and individuals listed under acknowledgements.

History

The genus *Erpetogomphus* was described (as a subgenus) by Selys (1858) to receive two previously described species, *Gomphus menetriesii* Selys, 1850, and *Ophiogomphus crotalinus* Hagen *in* Selys (the latter originally described from a pair in 1854), as well as two new species, *Erpetogomphus elaps* Selys, and *E. cophias* Selys. In the 'Appendice' of the same paper, Hagen described *E. compositus* and *E. designatus*. Selys described *E. boa* in 1859 and *E. viperinus* in 1868. Some of these species were briefly redescribed or discussed by Selys and Hagen in 1859, 1869, 1873, and 1878. In 1879, Selys redefined the subgenus *Herpetogomphus* (an unjustified emendation of *Erpetogomphus*, see Cowley, 1934), under which were included eight species: *E. compositus*, *E. designatus*, *E. viperinus*, *E. menetriesii*, *E. elaps*, *E. boa*, *E. cophias*, and *E. crotalinus*. Calvert (1899) redescribed *E. viperinus* (now *E. bothrops* sp. n.) based on material collected in Tepic, and included a diagnosis of the females of *E. viperinus* and *E. elaps*. Kirby (1890), in a synonymic catalogue of the world Odonata, designated *Herpetogomphus crotalinus* as the type species of the genus. Calvert (1905) included a synopsis for all *Erpetogomphus* from Middle America and described *E. eutainia*, *E. ophibolus*, *E. sipedon*, and *E. diadophis*. Calvert (1912a) added *E. tristani*. Ris (1917) described *E. constrictor* and redescribed what he thought to be the second known male of *E. boa*. In 1918 Williamson described *E. sabaleticus* from a pair from Colombia, and Kennedy (1918) described *E. lampropeltis* from California. Calvert (1919) described *E. schausi* from a male from Guatemala. Finally, Williamson and Williamson (1930) described two new species from Baja California, *E. coluber* and *E. natrix*. In the same paper, they presented a synopsis of what was known for all species. Their summary makes clear that only a few common species were represented in collections, and that many others were poorly known and/or described from insufficient material.

The status of the name *Erpetogomphus menetriesii* (Selys)

This name was first applied by Selys to an incomplete male supposedly from Brazil. Selys (1850) briefly compared it to *Paragomphus genei*, as follows: 'Its colouration yellow, almost without spots, prevents confusion of this species with any other in Europe, but it resembles in this respect *G. pallidus* (Ramb.) of Southern America whose stature is stronger, and *Gomphus menetriesii* (new) from Brazil, but the feet of the last are mostly black, the ♂ abdomen is bordered by black on the two sides, etc...'. The same specimen was redescribed it in 1854 as follows: 'Head yellow, except for space between ocelli, that between the eyes and ciliated margin of the occiput black. Front of thorax yellow, with 2 median, contiguous stripes, almost obliterated, pale red, antehumeral and humeral stripe equidistant.

♂ Appendages lacking. From: Brazil?' The type is said to be in the 'Musée de St- Pétersburg'.

Table 1. Species-group names used in the genus *Erpetogomphus*

Name	Original Genus	Original Reference	Type locality	Location of type	Type status	Reference for first placement in *Erpetogomphus*	Present placement
agkistrodon	*Erpetogomphus*	This paper	Jalapa, Mexico	UNAM (♂)	Holotype	This paper	*E. agkistrodon*
boa	*Erpetogomphus*	Selys 1859	Vera Cruz, Mexico	IRSN (♂)	Lectotype	Selys 1859	*E. boa*
bothrops	*Erpetogomphus*	This paper	Rio Otapa, Veracruz State, Mexico	USNM (♂)	Holotype	This paper	*E. bothrops*
coluber	*Erpetogomphus*	Williamson & Williamson 1930	San José de Comandu, Baja Calif., Mexico	UMMZ (♂)	Holotype	Williamson & Williamson 1930	*E. compositus*
compositus	*Erpetogomphus*	Hagen *in* Selys 1858	Pecos River, Texas; corrected to vicinity of Roswell, NM[1]	MCZC (♀)	Holotype	Hagen *in* Selys 1858	*E. compositus*
constrictor	*Erpetogomphus*	Ris 1917	Misantla, Veracruz, Mexico	SMF (♂)	Lectotype	Ris 1917	*E. constrictor*
cophias	*Erpetogomphus*	Selys 1858	Mexico	MNHP (♂)	Neotype	Selys 1858	*E. cophias*
crotalinus	*Ophiogomphus*	Hagen *in* Selys 1858	Mexico	MCZC (♂)	Lectotype	Hagen *in* Selys 1858	*E. crotalinus*
designatus	*Erpetogomphus*	Hagen *in* Selys 1854	Pecos River, Texas; corrected to vicinity of Roswell, NM[1]	MCZC (♂)	Lectotype	Hagen *in* Selys 1858	*E. designatus*
diadophis	*Erpetogomphus*	Calvert 1905	Texas	BMNH (♂)	Holotype	Calvert 1905	*E. eutainia*
elaphe	*Erpetogomphus*	This paper	Costa Rica	FSCA (♂)	Holotype	This paper	*E. elaphe*
elaps	*Erpetogomphus*	Selys 1858	Mexico	MNHP (♂)	Holotype	Selys 1858	*E. elaps*
eutainia	*Erpetogomphus*	Calvert 1905	Guerrero, Mexico	BMNH (♂)	Holotype	Calvert 1905	*E. eutainia*
heterodon	*Erpetogomphus*	This paper	Aragon, New Mexico	USNM (♂)	Holotype	This paper	*E. heterodon*
lampropeltis	*Erpetogomphus*	Kennedy 1918	Fillmore, California	USNM (♂)	Holotype	Kennedy 1918	*E. l. lampropeltis*
leptophis	*Erpetogomphus*	This paper	Blue Creek, Belize	FSCA (♂)	Holotype	This paper	*E. leptophis*
liopeltis	*Erpetogomphus*	This paper	La Estanzuela, Nuevo Leon, Mexico	FSCA (♂)	Holotype	This paper	*E. liopeltis*
menetriesii	*Ophiogomphus*	Selys 1854	Brazil?	Lost		Selys 1858	*Nomen dubium*
montanus	*Herpetogomphus*	Selys 1878	Yellow Town, Montana	IRSN♂ (♂)	Holotype	Selys 1879	*Ophiogomphus severus montanus*
natrix	*Erpetogomphus*	Williamson & Williamson 1930	San Jose de Comandu, Baja Calif., Mexico	UMMZ (♂)	Holotype	Williamson & Williamson 1930	*E. lampropeltis natrix*
ophibolus	*Erpetogomphus*	Calvert 1905	Atoyac, Veracruz, Mexico	BMNH (♂)	Holotype	Calvert 1905	*E. ophibolus*
pictus	*Herpetogomphus*	Needham 1897	Ithaca, New York	CUIC (♂)	Holotype	Needham 1897	*Ophiogomphus rupinsulensis*[2]
rupinsulensis	*Herpetogomphus*	Walsh 1862	Rock Island, Illinois	Lost		Walsh 1862	*Ophiogomphus rupinsulensis*[3]
sabaleticus	*Erpetogomphus*	Williamson 1918	Cristalina, Colombia	UMMZ (♂)	Holotype	Williamson 1918	*E. sabaleticus*
schausi	*Erpetogomphus*	Calvert 1919	Purulta, Guatemala	ANSP (♂)	Holotype	Calvert 1919	*E. schausi*
severus	*Ophiogomphus*	Hagen 1874	Colorado	Lost♂ (♂, ♀)		Selys 1878[4]	*Ophiogomphus severus*[5]
sipedon	*Erpetogomphus*	Calvert 1905	Guadalajara, Mexico	BMNH (♀)	Holotype	Calvert 1905	*E. sipedon*
tristani	*Erpetogomphus*	Calvert 1912	Oricuajo, Costa Rica	ANSP (♂)	Holotype	Calvert 1912	*E. tristani*
viperinus	*Erpetogomphus*	Selys 1868	Orizaba, Veracruz, Mexico	IRSN (♂)	Lectotype	Selys 1868	*E. viperinus*

[1] See remarks under *E. designatus.*; [2] Transferred to *Ophiogomphus* by Needham (1899); [3] Transferred to *Ophiogomphus* by Hagen (1874)
[4] As *Herpetogomphus*; [5] Transferred to *Ophiogomphus* by Selys (1879)

In 1858, Selys discussed *E. menetriesii* under *E. crotalinus* (in translation):

'N.B. In the Synopsis des Gomphines, I described under the name of *Ophiogomphus? Menetriesii* an incomplete male individual, which was communicated to me a long time ago by the knowledgeable M. Menetries. Now, I am inclined to believe that this is not a species distinct from *crotalinus*.

One reason that made me suppose the species different, was its occurrence in *Brazil*, but it was still necessary that this fact be duly confirmed and that the missing anal appendages be known.

This ♂ is a little smaller than our specimens [the presently described males and female of *E. crotalinus*], the space around the ocelli is distinctly black, the appearance of the reddish antehumeral stripes more closely approaches the median [stripes], the humeral is more distinct and more elongated, the base of the abdomen is less swollen, the dorsal yellow stripe of 3rd, 4th, and 5th segments seems modified: it consists of spots of three lobes [each], whose posterior isn't visibly narrowed into a little round head. (This note is based on diagnosis and a description made a long time ago, so that I have not been able to compare the specimen since I have had *crotalinus* at hand.)

A female, same indication of origin [Brazil] from the Mus. St. Petersburg, communicated to M. Hagen by M. Menetries differs very slightly from *crotalinus* by the following: 6 cells under the pterostigma.; costa yellower, tarsi black, the first article [tarsomere] of the posterior [leg] yellow, black tibiae bilineated with yellow outside; femora yellow with a double black external line shorter and finer at the ends. Abdomen thicker, marked with black; 9th segment black above with a dorsal round spot, touching the posterior margin. [Abdominal segment] 10 and appendages light red, the end of these last [structures] pale *not marked with black* [italics are Selys']. Vertex more black. Dimensions a little more robust.

Not being certain of its identity, I fear to cause confusion later by putting the name *E. menetriesii* in true *crotalinus* from Mexico, even though I have already published this name [*menetriesii*] in speaking of another species (page 102 Revue des Odonates, 1850; and Synopsis des Gomphines, 1854).

If its identity is confirmed, it would be necessary to replace the name of *E. crotalinus* with that of *E. Menetriesii*.'.

Finally, Selys (1878) described *Herpetogomphus menetriesii* based on 'un mâle in complet [in MNHP]' and female [in IRSN] from Guatemala. He states: 'I believe it identical with the ♂ example described in Synopsis No. 20 [1854] and reported with doubt as *crotalinus* in the Monographie [1858].' Calvert (1905) pointed out the inconsistencies of the three descriptions and left open the question of what *E. menetriesii* really is.

According to the original description (Selys, 1854), *E. crotalinus* cannot be *E. menetriesii*. A supplementary male of *E. crotalinus* described in 1858 (in ZMHB, examined) is unusual in having faint antehumeral stripes, but no *E. crotalinus* I have examined fits the description of *E. menetriesii* of 1854 (with middorsal, antehumeral and humeral stripes).

The 1854 description is too brief to indicate what *E. menetriesii* is, and I cannot associate it with any known species. According to Hagen (1861), it was destroyed. I have been unable to trace the 1858 female described by Selys, but I was able to examine the 'pair' described in 1878. The two specimens, which have determination labels by Selys, are really two females of *E. eutainia* Calvert. However, I cannot be certain that these females are conspecific with Selys' original description of *E. menetriesii*. Selys and others apparently had difficulty in associating specimens of *E. eutainia*, because a male from Texas in the IRSN is given the manuscript name of *Erpetogomphus berus*, another female is identified as *Cyanogomphus ?mexicanus* (by R. Martin), and, of course, the two females, one in the IRSN, the other in the MNHP, are labelled as *E. menetriesii*.

Thus, the original description of *E. menetriesii* may refer to *E. eutainia*, but because no one can ever be sure of this, I propose that *E. menetriesii* should be considered a *nomen dubium*.

Biology

Little is known of the biology of the genus, though their habits as recorded in the literature mirror the behaviour of other Gomphidae. Adults are most commonly found near shores of streams and rivers, but they may also be found in agricultural stubble or on tree branches near streams. Many species are seldom encountered and only a few species appear to be common in collections.

Available notes taken from the literature, personal correspondence, and personal observations cited under various species accounts indicate that female *Erpetogomphus* oviposit by swiftly tapping the water's surface or by hovering motionless over moderately swift water systems. Details of copulation and copulation time are largely unknown, although the bizarre male and especially female morphological adaptations for achieving the tandem position in *E. tristani* have been detailed by Calvert (1912a).

Larvae of *E. designatus*, *E. compositus*, and *E. lampropeltis* were keyed by Needham and Westfall (1955), and illustrations and full descriptions of *E. crotalinus* and *E. lampropeltis natrix* were given by Novelo and González (1991). The larva of *E. sabaleticus* was recently described and illustrated by Belle (1992).

Table 2. Characters used in cladistic analysis of *Erpetogomphus* adults. ♂ (male) or ♀ (female) in parentheses indicates sex to which character pertains. An asterisk (*) indicates an ordered multistate character. Numbers in parentheses following character states refer to figure numbers.

Number/character	Primitive state	Derived state(s)
1. Postocciput width (♀)	tumid, convex	linear
2. Postocciput (♀)	not visible from above	visible from above
3. Occiput (♀)	semicircular	transverse
4. Vertex (♀)	with long median trough	with no trough
5. Postocellar ridge (♀)	incomplete	complete
6. Vertex:	sexually dimorphic	not sexually dimorphic
7. Frontoclypeal suture	with black	with no black
8. Hind margin of metepimeron	with black	with no black
9. Hind wing 3-celled anal loop	present	absent
10. Anterior hamule* (♂)	states 1-5 (fig. 208)	state 0 (fig. 208)
11. Posterior hamule* (♂)	states 1-4 (fig. 209)	state 0 (fig. 209)
12. Tip of posterior hamule* (♂)	states 1-5 (fig. 210)	state 0 (fig. 210)
13. Posterior lobes of penis segm. 1 (♂)	small	well developed, divided lobes
14. Penis: segment 3 dorsally (♂)	with pair of tubercles	lacking tubercles
15. Penis: segment 4 (♂)	about twice as long as wide (fig. 211)	about as long as wide (fig. 211)
16. Prepuce of penis* (♂)	states 1-3 (fig. 212)	state 0 (fig. 212)
17. Lateral lobe of penis-shape* (♂)	states 1-5 (fig. 213)	state 0 (fig. 213)
18. Membranous hood of penis (♂)	not overlapping distally	overlapping
19. Shape of cornua of penis* (♂)	states 1-6 (Fig. 214)	state 0 (fig. 214)
20. Development of cornua of penis* (♂)	reduced (1), absent (2)	present (fig. 214)
21. Length of vulvar lamellar plates (♀)	about 0.25 length of sternite	≥ 0.50 length of sternite
22. Medial margins of vulvar lamina (♀)	folded under	not folded under
23. Postlamellar ridge (♀)	Y-shaped	semicircular
24. Postlamellar ridge with juncture (♀)	posterior to plates (e.g. figs. 184, 195)	at or before margin of plates (fig. 192)
25. Ventral base of cercus (♂)	with large blunt tooth	with no tooth (fig. 94).
26. Ventral base of cercus (♂)	with no carina	with a carina
27. Distal part of cercus ventrally (♂)	with no carina	with a carina
28. Dorsal surface of cercus (♂)	with a tubercle	without a tubercle
29. Ventral surface of cercus (♂)	linear or concave	convex
30. Curvature of epiproct with tips (♂)	about parallel to base	at about 90° to base
31. Tips of epiproct (♂)	spatulate or bidentate	pointed
32. Penis segment 3 (♂)	short and stocky	longer than wide
33. Penis guard (♂)	quadrate in cross-section	circular in cross-section
34. Epiprocts (♂)	approximate and curved at distal 0.50	not approximatebarely curved
35. Spermatheca (♀)	states 1-2 (fig. 215)	state 0 (fig. 215)
36. Dorsal surface of epiproct (♂)	with dorsal spine (fig. 95)	unarmed
37. Ventral base of cercus (♂)	with pebble-like carina	otherwise (fig. 97)
38. Membranous hood of penis (♂)	partially (1) or wholly (2) exposing subcuticular membrane	completely covering subcuticular membrane
39. Ventral base of cercus (♂)	with carina ending in tooth (fig. 116)	with carina (if present) not ending in tooth
40. Postocciput (♀)	with lateral depressions (fig. 165)	with no lateral depressions
41. Occiput (♀)	with a posteriorly directed medial spine fig. 151	without a spine

PHYLOGENICS AND BIOGEOGRAPHY

Phylogenetic analysis

I have attempted to construct a cladogram based on an algorithm which infers phylogenies based on the presence of shared derived characters. Using the outgroup comparison method of Watrous and Wheeler (1981), I consider *Ophiogomphus* to be the outgroup to *Erpetogomphus*, following Carle (pers. comm.) in his assessment of gomphid dragonfly classification. In this analysis, I have used the most austral species, *O. severus* Hagen.

The genus *Erpetogomphus* has never been easily defined (Calvert 1905, Needham and Westfall 1955), these authors using a series of characters to characterize the genus. A synapomorphy apparently unique to *Erpetogomphus* is the condition of the epiprocts of the males: all have gently (at least 110°) to strongly dorsally curved, non-divergent epiprocts.

Carle (1986), in his treatment of the higher classification of the Gomphidae, included *Erpetogomphus* in the tribe Onychogomphini of the subfamily Onychogomphinae. In his key to the eight subfamilies of Gomphidae, he characterized the Onychogomphinae as follows: 1) hind femur shorter than head, 2) anal triangle typically 4-celled with small rectangular cell along inner margin, 3) anterior hamuli with shoulder and end hook forming lateral u-shaped notch, and, 4) female sternum 9 with large U- or V-shaped basal membranous area. Within this subfamily, the tribe Onychogomphini (including *Erpetogomphus*) is distinguished from the tribe Crenigomphini by the following characters (antagonistic characters for Crenigomphini in parentheses): postgenal suture present (absent), male tibial laminae

present (absent), penile segment one (= peduncle) without cuplike thin-walled hood (with bilobed cuplike thin-walled hood), female sternum 9 with dome-shaped membranous area not extending to distal half of sternum (this structure extending to distal half of sternum). None of these characters is stated by Carle (1986) to be uniquely derived for any of the above categories. Carle (pers. comm.) and I agree that *Ophiogomphus* is the most likely outgroup to *Erpetogomphus*, and we agree that both should be placed in the Onychogomphini. Three characters seem unique to the New World Onychogomphini, which include only *Ophiogomphus* and *Erpetogomphus*: 1) rami of male epiprocts contiguous along all or most of their length, 2) female sternum 8 with a well-defined costate postlamellar ridge separating the soft membranous area from the posteriorly sclerotized area (this ridge reduced in *Ophiogomphus*), 3) presence of a lateral lobe on the ventrolateral margin of the fourth penile segment (fig. 213) (reduced in *Ophiogomphus*, and not specialized in the *E. ophibolus* group). This last character seems to be a unique synapomorphy for *Ophiogomphus* and *Erpetogomphus*.

Carle (1992) further separated *Erpetogomphus* into three subgenera, two of which were new: *Calogomphus* (type species *E. eutainia*) and *Erpetocyclops* (type species *E. ophibolus*). Both Carle (pers. comm.) and I consider *Erpetogomphus* to be composed of three monophyletic groups as discussed below. While several earlier versions of my cladogram using series of characters and different states generally support a conservative grouping of the genera into three monophyletic groups, I do not think it necessary to provide subgeneric rank to those groups.

A suite of 41 characters, 7 of which are multistate (table 2), was analyzed using the HENNIG86 computer program (Farris, 1988), with the following options: The character set was first run using the ie* (guaranteed to find the most parsimonious trees) option where all characters were ordered and each was equally weighted (default options). All autapomorphies were included from this analysis. The final set of 41 characters was finally chosen from larger sets, each with different coding sequences, because this set seemed to be the most heuristic. The resultant analysis yielded six equally parsimonious trees. A Nelsen (consensus) tree (length 106, consistency index 0.62) was then generated from the six trees. The resultant characters, tree, and matrix are shown in figs. 208-216, and tables 2-3. As this manuscript was in review, Jan van Tol kindly ran the same data set on PAUP 3.1.1 for the Macintosh (Swofford 1993) using unordered as well as ordered sequence of multistate characters. His results, which he kindly communicated to me, resulted in 61 semistrict consensus trees each with a length of 94 for unordered multicharacter states. His resulting cladogram is similar to that in fig. 216 except that the entire *E. crotalinus* group (except for three sister groups: *E. elaphe* and *E. elaps*; *E. sipedon* and *E. lampropeltis*; and *E. boa* and *E. cophias*) collapses to a polytomious assemblage. (I recorded a similar cladogram when multistate characters were listed as unordered for HENNIG86.) When all multistate characters were run as ordered on PAUP 3.1.1, the resulting cladogram was the same as shown for fig. 216.

I have not been totally successful in resolving several of the terminal clades, due to high degree of apparent homoplasies. The best characters are those of the secondary genitalia of the male (hamules, penis); but, despite a thorough examination of these structures, I am still uncertain of the correct interpretation of character polarity for several of these complex, multistate character sets (figs. 208-210, 213-214). Little difficulty was encountered in assigning states to members of the *E. ophibolus* and *E. eutainia* groups, and their generalized tracks also independently supplement in understanding their phylogeny; but the same characters in males of the *E. crotalinus* group show, if my cladogram is correct, a bewildering complex of character reversals for some characters. The generalized tracks within the *E. crotalinus* group (fig. 226) also provide few clues to possible speciation events, except for that between the *E. elaps* and *E. crotalinus* (s.s.) groups.

Individual clades are numbered as shown in fig. 216, each of which is discussed below.

Clade 1.1. – ***E. ophibolus*** group (six species: ***E. constrictor, E. sabaleticus, E. tristani, E. ophibolus, E. agkistrodon, E. schausi***) = subgenus *Erpetocyclops* Carle

Character 3. – female occiput semicircular (parallel development in Clade 1.22112, *E. liopeltis*)

Character 5. – female postocellar ridge incomplete (parallel development in Clade 1.211, *E. leptophis*)

Character 6. – vertex sexually dimorphic (state not known for male *E. agkistrodon*, but probably follows for other members of this clade)

Character 11, state 1. – male with posterior hamule triangular (fig. 209)

Character 12, state 1. – male with tip of posterior hamule acuminate (fig. 210)

Character 16, state 1. – male with prepuce well-developed (fig. 212)

Character 17, state 1. – male with lateral lobe vestigial, broadly angulate with no serrations (fig. 213)

Clades 1.11 (***E. constrictor, E. sabaleticus, E. tristani, E. ophibolus***), **1.12** (***E. agkistrodon***), **1.13** (***E. schausi***). Clade 1.11 is defined by the following synapomorphies:

Character 20, state 2 - male with loss of cornuae of penis (fig. 214). Most Gomphidae (including the outgroup, *Ophiogomphus severus*), have a pair of long, strap-like cornuae. I have hypothesized the character transformation for this structure throughout the genus (fig. 214).

Character 25. – ventral base of cercus of male with large blunt tooth (fig. 94)

Character 28. – dorsal surface of cercus of male with a tubercle (fig. 94)

I have found no synapomorphy for uniting 1.12 (*E. agkistrodon*) and 1.13 (*E. schausi*). The former is known only from the holotype female, the latter by two males and a teneral female.

Clades 1.111 (*E. constrictor*), 1.112 (*E. sabaleticus*), 1.113 (*E. tristani*)

Character 29. – curvature of epiproct of male with tips completely recurved so as to lie parallel to base

Clade 1.21. – *E. eutainia* group (two species: ***E. eutainia, E. leptophis***) = subgenus *Calogomphus* Carle

Character 10, state 1. – anterior hamule with equally divided arms (fig. 52-53, 208) at distal 0.25

Character 11, state 2. – posterior hamule digit-shaped (fig. 209)

Character 14. – dorsal surface of third segment of penis of male with two tubercles

Character 16, state 2. – prepuce of male reduced, largely hidden by frill-like lateral lobe (fig. 212)

Character 17, state 2. – lateral lobe of penis of male frill-like (fig. 213)

Character 35, state 1. – spermatheca of female a single tube (fig. 215). I was only able to study this structure in *E. eutainia*, as only the allotype of *E. leptophis* is known. Due to other synapomorphies listed above, I hypothesize that *E. leptophis* will possess single, rather than paired, spermatheca.

Clade 1.22. – *E. crotalinus* group (13 species: ***E. elaphe, E. elaps, E. liopeltis, E. bothrops, E. viperinus, E. designatus, E. sipedon, E. lampropeltis, E. crotalinus, E. heterodon, E. compositus, E. boa, E. cophias***) = subgenus *Erpetogomphus* Hagen *in* Selys

Character 16, state 3. – prepuce of penis of male lacking

Character 35, state 2. – spermatheca of female paired, each forming a long, narrow sac (fig. 215)

Clade 1.221. – *E. elaps* subgroup (five species: ***E. elaphe, E. elaps, E. liopeltis, E. bothrops, E. viperinus***)

Character 17, state 3. – unique shape of lateral lobe (fig. 213)

Clade 1.2211 (*E. elaphe, E. elaps, E. liopeltis, E. bothrops*)

No satisfactory synapomorphy has been found for this clade. One character, the spatulate tip of the epiproct (fig. 129) separates *E. viperinus* from its sister species.

Clade 1.22111 (*E. elaphe, E. elaps, E. liopeltis*)

No synapomorphy has been found, but the transverse condition of the female postocciput in *E. bothrops* and in *E. viperinus* (fig. 166) split *E. bothrops* from the other three sister species.

Clade 1.221111 (*E. elaphe, E. elaps*)

Character 22. – vulvar lamina of female with margin folded under ventrally (figs. 180- 181)

Clade 1.222 (*E. designatus, E. sipedon, E. lampropeltis, E. crotalinus, E. heterodon, E. compositus, E. boa, E. cophias*)

No satisfactory synapomorphy has been found to unite the *E. crotalinus* group (*sensu stricto* [s.s.]). The one aberrant species in the group is *E. designatus*. It alone has the following characters which separate it from the other 7 species: 1) tip of posterior hamule lacking a tooth (recurrence of this state from the *E. eutainia* group) and 2) unique shape and position of the lateral lobe (fig. 82). The shape of the anterior hamule of *E. designatus* (fig. 60) is, however, like that of *E. sipedon, E. lampropeltis, E. crotalinus*, and *E. compositus*, which thus unites these species into a clade.

The widely distributed *E. designatus* has been difficult to place cladistically in this study. It combines characters of the *E. elaps* group (for example, linear condition of lateral lobe and acuminate condition of the cornua) and even apomorphic characters common to the *E. crotalinus (*s.s.*)* group as noted above.

Clade 1.2222 (*E. sipedon, E. lampropeltis, E. crotalinus, E. heterodon, E. compositus, E. boa, E. cophias*)

Character 12, state 5. – tip of posterior hamule of male with anteapical tooth

Character 17, state 5. – unique shape of lateral lobe of fourth segment of penis of male (fig. 213). The small, semicircular condition of the lateral lobe present in Clade 1.2222 is similarly developed in Clade 1.12 (*E. schausi*).

Clades 1.22221 (*E. sipedon*), 1.22222 (*E. lampropeltis*), and 1.22223 (*E. crotalinus, E. heterodon, E. compositus, E. boa, E. cophias*)

No satisfactory apomorphy has been found to dichotomize these clades. The distinctive shape of the cornuae of *E. sipedon* and *E. lampropeltis* (figs. 83-85) has separated these two species from clade 1.22223.

Table 3. Character matrix used in producing Nelsen (consensus) tree shown in Fig. 216.

Character No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oph. severus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
constrictor	1	1	1	1	1	1	1	1	0	0	1	1	1	0	0	1	1	1
sabaleticus	1	1	1	1	1	1	1	1	0	0	1	1	1	0	0	1	1	1
tristani	1	1	1	1	1	1	1	1	0	0	1	1	1	0	0	1	1	1
ophibolus	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0	1	1	1
agkistrodon[1]	0	0	1	0	1	1?	1	1	0	0?	1?	1?	1	0	0	1?	?	1?
schausi	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0	1	5	1
eutainia	0	1	1	0	0	0	1	1[2]	0	1	2	2	1	1	0	2	2	1
leptophis	1	1	0	0	1	0	1	1	0	1	2	2	1	1	0	2	2	0
elaphe	1	0	0	0	0	0	0	0	0	3	3	2	1	0	1	3	3	1
elaps	1	0	0	0	0	0	0	0	0	2	3	5	1	0	1	3	3	1
liopeltis	1	1	1	0	0	0	0	0	0	2	3	4	1	0	1	3	3	1
bothrops	0	1	0	0	0	0	0	0	0	2	3	5	1	0	1	3	3	1
viperinus	0	1	0	0	0	0	0	0	0	2	3	3	1	0	1	3	3	1
designatus	0	1	0	0	0	0	0	0	0	4	3	2	0	0	1	3	4	0
sipedon	0	1	0	0	0	0	0	0	0	4	3	5	1	0	1	3	5	1
lampropeltis	0	1	0	0	0	0	0	0	0	4	3	5	1	0	1	3	5	1
crotalinus	0	1	0	0	0	0	0	0	0	4	3	5	1	0	1	3	5	1
heterodon	0	1	0	0	0	0	0	0	0	4	3	5	1	0	1	3	5	1
compositus	0	0	0	0	0	0	0	0	0	4	3	5	1	0	1	3	5	1
boa	1	1	0	0	0	0	0	0	0	5	4	5	1	0	1	3	5	1
cophias	1	0	0	0	0	0	0	0	0	5	4	5	1	0	1	3	5	1

[1] Only the holotype ♀ is known for this species. Male characters were scored as ? (unknown), on 0? or 1?, based on affinity with rest of the *E. ophibolus* group. [2] Character prevalent in this species. [3] Basal carina weak in *E. boa*.
[4] This structure not examined for this species. Plesiomorphy/apomorphy hypothesized by examination of spermatheca in closely related species, and placement of these taxa in cladogram due to other synapomorphies.

Clades 1.222231 (*E. crotalinus*) and 1.222232 (*E. heterodon, E. compositus, E. boa, E. cophias*)

No satisfactory apomorphy has been found for clade 1.222232. *Erpetogomphus crotalinus* was separated because of the unique shape of its cornuae (fig. 86).

Clades 1.2222321 (*E. heterodon*), 1.2222322 (*E. compositus*), 1.2222323 (*E. boa, E. cophias*)

The unique shape of the cornua (figs. 87-89) has segregated *E. heterodon* and *E. compositus* from clade 1.2222323. Apomorphies for the last clade, representing the two closely related species, *E. boa* and *E. cophias*, are:

Character 10, state 5. – unique shape of the anterior hamule of male (fig. 208)

Character 11, state 4. – unique shape of the posterior hamule of male (fig. 209)

Character 19, state 6. – unique shape of the cornua of male (fig. 214)

The clades mentioned above have problems primarily within the *E. crotalinus* group (*sensu lato*, [*s.l.*]), and most dichotomies are based on one or two highly complex character states of the penis. I realize that my interpretation of the morphoclines of this character is open to reevaluation, which could result in a somewhat different shuffling of some species within the larger group. Only two species in this group, *E. boa* and *E. cophias*, are easily characterized as a monophyletic group.

A further analysis to resolve some of the difficulties described above will have to await further specimens and a proper analysis of their larvae. As stated earlier, I have not assigned formal names to subordinate clades, because further investigation may involve transfer of some monophyletic or paraphyletic groups to other clades, nor can I see any purpose in a proliferation of infrageneric names.

Cladospecies

Of the 21 species described here, seven (33%) can be defined by autapomorphies and can be termed cladospecies (Ackery and Vane-Wright, 1984). These cladospecies with their uniquely derived character states are shown below.

Clade 1.112. *E. ophibolus*. Character 36, dorsal surface of epiproct of male with a dorsal spine (fig. 95)

Clade 1.211. *E. leptophis*. Character 41, female occiput with a posteriorly directed medial spine (fig. 151)

Clade 1.212. *E. eutainia*. Character 37, ventral base of cercus of male with a pebble-like carina.

Clade 1.2211112. *E. elaphe*. Character 10, state 3,

2	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
	1	1	1	0	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0
	1	1	1	0	1	1	1	1	1	1	1	1	0[4]	0	0	0	0	0	0
	1	1	1	0	1	1	1	0	0	1	1	1	0[4]	1	0	0	0	0	0
	1	0	0?	0	1?	0?	1	0	1	1	1	1	0	0	0	0	0	0	0
	1	1	1	0	1	0	1	0	1?	1	1	1	0?	0	0	0	0	0	0
	0	1	0	0	0	0	1	0	1	1	1	1	0[4]	0	1	0	0	0	0
	0	1	0	1	0	0	1	0	1	1	1	1	1	0	0	0	0	0	1
	1	0	0	1	1	0	1	0	1[2]	1	1	1	1[4]	0	0	0	0	0	0
	1	0	0	1	1	0	1	0	1	1	1	1	2[4]	0	0	0	0	0	0
	1	0	0	1	1	0	1	0	1	1	1	1	2	0	0	0	0	0	0
	1	0	0	1	1	0	1	0	1	1	1	1	2[4]	0	0	0	0	0	0
	1	1	0	1	1	0	1	0	0	1	1	1	2	0	0	0	0	0	0
	1	0	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0
	1	0	0	0	0	0	1	0	0	1	1	1	2	0	0	2	0	0	0
	1	0	0	0	0	0	1	0	0	1	1	1	2	0	0	0	0	0	0
	1	0	0	0	0	0	1	0	0	1	1	1	2	0	0	0	0	0	0
	1	0	0	0	0	0	1	0	0	1	1	1	2	0	0	0	0	0	0
	1	0	0	0	0	0	1	0	1	1	1	1	2	0	0	1	0	0	0
	1	1	0	1[3]	1	0	1	0	0	1	1	1	2	0	0	0	0	0	0
	1	1	0	0	0	0	1	0	1	1	1	1	2[4]	0	0	0	1	1	0

unique shape of anterior hamule of male (fig. 208)

Clade 1.22221. *E. sipedon.* Character 38, state 2, membranous hood of penis of male wholly exposing subcuticular membrane.

Clade 1.2222322. *E. compositus.* Character 38, state 1, membranous hood of penis of male partially exposing subcuticular membrane.

Clade 1.22223232. *E. cophias.* Character 39, ventral base of cercus in male with carina ending in tooth (fig. 116), and Character 40, postocciput of female with lateral depression (fig. 165). These two characters are probably correlated: I hypothesize that the postoccipital depressions of the female receive the inferior carinal tooth of the cerci of the male during copulation.

I have been unsuccessful in finding autapomorphies for the 14 other species, and they can be termed paraspecies (Ackery and Vane-Wright, 1984). A further, more detailed analysis of these species may yield autapomorphies. The cladist may question the status of species recognized by single or combinations of plesiomorphic characters, but I agree with Ackery and Vane-Wright (1984: 10), who cogently argue: 'the traditional groupings often (but by no means always) turn out to be good. The cladist must, therefore, always retain respect for the 'Gestalt' approach (especially when practised by field workers), unless armed with concrete evidence for some contrary arrangement.'.

Distribution patterns

Table 4 details the distributional patterns of all New World Gomphidae according to five political regions: Canada/Alaska, U. S. A., Mexico, Central America, and South America. All speciose (*i.e.*, $N \geq 3$ species) gomphid genera in the New World have proportionally more species in the United States and in South America than *Erpetogomphus. Erpetogomphus* has the most species in Mexico (76%). Central America follows with 48%, the United States with 24%. No other genus is proportionally as speciose in Mexico. The *Gomphus* complex of genera (*Arigomphus, Gomphus* and subgenera, *Stylurus*), and *Ophiogomphus* are dominantly North American, and several genera (*Agriogomphus, Aphylla, Archaeogomphus, Cyanogomphus, Gomphoides, Neogomphus, Phyllocycla, Phyllogomphoides, Progomphus*, and *Zonophora*) are South American. *Epigomphus* is most speciose in Central America, where 46% of all described species occur, closely followed by South America.

Figure 217 shows the density and approximate overall distribution of species of *Erpetogomphus* as

shown by 150 km squares. Of the five species found in the United States, most are found in the southwestern states. The most northerly distribution for the genus is Grant County, Washington (46°50'N), for *E. compositus* (Paulson and Garrison, 1977). The greatest concentration in species is in south-central Mexico between approximately 18°-20°N with eight species (31%) of all the total number of species in the genus found in southern Veracruz alone.

Descriptive biogeography

In this section I describe the current distribution range (= tracks) of various monophyletic groups based on my cladogram. Unfortunately, the numerous problems associated with the cladistic analysis concomitant with the poorly known or spotty distributions (most of which may be due to inadequate collecting in parts of Mexico) preclude a discussion of vicariance biogeography. However, I do discuss possible speciation sequences within the *E. ophibolus* and *E. eutainia* groups.

The cladogram (fig. 216) for *Erpetogomphus* divides the 21 known species into three monophyletic groups. The generalized track for the genus is shown in fig. 218. The first two groups, the *E. ophibolus* and *E. eutainia* groups, have generalized tracks encompassing south Texas, eastern Mexico south into northern Colombia and Venezuela (figs. 219-220). The *E. ophibolus* group comprises six closely related species united by seven derived character states. Figure 221 shows that the distribution of all six species except *E. schausi* are largely allo- or parapatric. Little can be said of *E. agkistrodon* or *E. schausi* due to paucity of records. *Erpetogomphus ophibolus* occupies an area between two disjunct populations of *E. constrictor*. Further collecting may show *E. constrictor* to be sympatric or parapatric with *E. ophibolus*. Aside from *E. agkistrodon* and *E. schausi*, the track of *E. ophibolus* was probably the first to separate from the *E. ophibolus* group, a hypothesis consistent with the results of my cladogram (fig. 216). The three remaining species, *E. constrictor, E. tristani*, and *E. sabaleticus*, are closely related sister taxa whose tracks are largely parapatric. Presumably their differentiation (by allopatric speciation?) took place from a common ancestor which occupied part of the present range of all three species.

The tracks of the second monophyletic group comprises just two species, the relatively widespread *E. eutainia* and the peripheral *E. leptophis* (fig. 222). The latter, known only from the holotype and allotype from Belize, is sympatric with *E. ophibolus*, but its genealogical affinities are unquestionably with *E. eutainia* (fig. 216). *Erpetogomphus leptophis* probably arose as a peripheral isolate from *E. eutainia*, or from a common ancestor, since it is a more apomorphic species than *E. eutainia*.

The remaining 13 species comprise two monophyletic subgroups, one predominantly austral, the other more boreal. Their generalized tracks are shown in figs. 223-226. The *E. elaps* subgroup contains five species, whose somewhat limited distributions occupy the western and eastern lowlands of Mexico south along the mountainous areas into Costa Rica. *Erpetogomphus elaps* and *E. elaphe* are closely related sister species which are parapatric in Guatemala. A slight but consistent southern variant of *E. elaps* occupies the area between more northerly typical populations of *E. elaps* and *E. elaphe* (see discussion under *E. elaps*): it may be an incipient species. These two (or three?) species, like those for *E. constrictor, E. tristani*, and *E. sabaleticus*, probably arose from an *E. elaps*-like ancestor or from one another. Interpretations of the tracks of the remaining three species is problematical due to the uncertain position of *E. liopeltis* in my cladogram. It possesses characters common to *E. bothrops* and *E. viperinus*. No convincing apomorphy unites *E. liopeltis* with the sister taxa *E. elaps* and *E. elaphe*, so its genealogical relationship must remain in doubt. The two species with the greatest ranges (*E. elaps* and *E. bothrops*) are broadly sympatric; *E. liopeltis* and *E. viperinus* are allopatric.

The *E. crotalinus* (s.s.) subgroup comprises the boreal group of eight species, with at least one representative occurring throughout most of the southern half of the United States. Their complex, mostly overlapping distributions (fig. 226) and questionable phylogenetic sequence in the cladogram preclude any meaningful discussion on their biogeography. *Erpetogomphus boa* and *E. cophias* stand out because of three synapomorphies. Their limited distribution and close proximity indicate speciation, possibly by allopatric means. *Erpetogomphus sipedon* and *E. heterodon* make up the only other allopatric species pair in this complex subgroup. Although distribution of *E. heterodon* and *E. compositus* overlap, I have seen no evidence of these two species collected together.

It is obvious that a more thorough knowledge of the phylogeny of the genus will be necessary before interpretation of biogeographical events is possible. Of particular interest will be a methodological interpretation of the biogeography of the genus, for then we may be able to determine which species tracks are the result of dispersal and gene flow or vicariant events.

Characters

The best diagnostic characters for males are found in the caudal appendages, accessory genitalia, and overall body maculation. Most species are easily identified by the caudal appendages. The cerci (superior appendages) assume a wide variety of shapes (figs. 92-

Table 4. Distribution of species of New World Gomphidae. Number under each region = area of region in square miles; % directly under area = % of total land area; N = total number of species; number under each region = total number of species; number in parentheses () = percent of total number of species in genus. Phylogenetic classification is after Carle (1986). Genera are arranged alphabetically under each tribe.

Genus	N	Canada/Alaska 4,438,221 mi^2 29.5%	U.S.A.[1] 3,022,261 mi^2 20.2%	Mexico 761,530 mi^2 5.2%	Cent. Amer.[2] 208,800 mi^2 1.1%	South Amer. 6,597,386 mi^2 43.9%
Hageniinae						
Hagenini						
Hagenius	1	1 (100)	1 (100)			
Octogomphinae						
Hemigomphini						
Neogomphus	3					3(100)
Octogomphini						
Lanthus	2	1 (50)	2 (100)			
Octogomphus	1	1 (100)	1 (100)	1 (100)		
Stylogomphus	1	1 (100)	1 (100)			
Gomphinae						
Gomphini						
Arigomphus	7	3 (43)	7 (100)			
Dromogomphus	3	1 (33)	3 (100)			
Gomphus[3]	38	13 (34)	38 (100)	1 (3)		
Stylurus	13		12 (92)	4 (31)		
Epigomphinae						
Epigomphini						
Epigomphus	26	6 (23)	12 (46)	10 (38)		
Austrogomphinae						
Archaeogomphini						
Archaeogomphus	5			1 (20)	1 (20)	5 (100)
Cyanogomphini						
Agriogomphus	4			1 (25)	1(25)	3 (75)
Cyanogomphus	6					6(100)
Tibiagomphus	2					2(100)
Onychogomphinae						
Onychogomphini						
Erpetogomphus	21		5 (24)	16 (76)	10 (48)	1 (5)
Ophiogomphus	18	8 (44)	18 (100)			
Lindeniinae						
Gomphoidini						
Aphylla	19[4]		3 (16)	2 (11)	3 (16)	18 (95)
Gomphoides	3					3 (100)
Idiogomphoides	2					2 (100)
Peruviogomphus	2					2 (100)
Phyllocycla	31			3 (10)	4 (13)	27 (87)
Phyllogomphoides	43		2 (5)	12 (28)	7 (17)	27 (63)
Lindeniini						
Cacoides	1					1 (100)
Melanocacus	2					2 (100)
Mitragomphus	1					1 (100)
Progomphini						
Progomphus	59[5]		4 (7)	9 (15)	7 (12)	52 (77)
Zonophorini						
Desmogomphus	2				1 (50)	2 (100)
Diaphlebia	2					2 (100)
Perigomphus	1				1 (100)	1 (100)
Zonophora	10					10 (100)
TOTAL	329	35 (10.6)	97 (29.4)	50 (15.2)	47 (14.3)	180 (54.7)

[1] Excluding Hawaii; [2] Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama; [3] Includes subgenera *Gomphurus, Gomphus, Phanogomphus, Stenogomphurus;* [4] One species, *A. caraiba*, is endemic to Hispaniola and Cuba, not included in N; [5] Three species, *P. integer, P. serenus, P. zephyrus*, are endemic to the Greater Antilles, not included in N.

116), but they are never longer than segments 9 and 10 combined. All males of the *E. ophibolus* group, except for *E. schausi* (and possibly the unknown male of *E. agkistrodon*) have a dorsal appendage on the distal third of the cercus. The dorsal surface of the cercus may be straight as in *E. elaps*, strongly curved as in *E. schausi* and *E. viperinus*, angulate as in most species in the *E. crotalinus* group, or concave as in the *E. boa* and *E. cophias* group. The inferior third of the cercus forms a strong carina in *E. cophias* (weakly so in *E. boa*), in the *E. crotalinus* group, and in *E. eutainia*. In the lighter coloured species of the *E. crotalinus* group, the carina does not contrast with the rest of the appendage. A unique series of pebble-like structures characterizes the basal carina in *E. eutainia*. The inferior carina was used by Calvert (1905), although he wrongly placed *E. eutainia* among individuals lacking such a carina. Instead of a basal carina, the *E. ophibolus* group, *E. bothrops* and *E. viperinus* have an inferior carina on the distal third of the appendage. This structure is weak in *E. elaps*.

The epiprocts (inferior appendages) are not as varied as the cerci. In most of the *E. ophibolus* group, they are strongly curved so that their distal third is nearly parallel to the basal 0.30. The epiproct of *E. ophibolus* is unique in having an anteriorly directed projection on its dorsal surface near the middle. The epiprocts are remarkably similar throughout the remaining groups: they form a gentle curve with the tips at approximately 90° to the basal third of the appendage.

The penes of most species possess a semi-hyaline pair of flagella or cornuae best seen in dorsal view. The cornuae are considerably reduced in the *E. ophibolus* group (except for *E. schausi*). Their shape provides a useful character to differentiate among *E. designatus*, *E. compositus*, and *E. lampropeltis*. The tip of each cornua is bluntly rounded in the *E. crotalinus* group (except for *E. crotalinus*). In all others, the tip forms a sharp point.

The spiny lateral lobes of the penis are well developed and frill-like in *E. eutainia* and *E. leptophis*, primarily knife-like or pointed in *E. viperinus*, *E. liopeltis*, *E. bothrops*, *E. elaps*, and *E. elaphe*, and a protruding semicircle in most members of the *E. crotalinus* and *E. cophias* groups. When the penis is viewed laterally, the lateral lobe is on edge, because this structure rotates posteriorly with its flat portion placed mediodistally. The lateral lobes are poorly developed in *E. constrictor*, *E. tristani*, and *E. sabaleticus* (possibly also in *E. agkistrodon*), but those species and *E. schausi* have a unique ventral, arcuate prepuce.

The anterior hamules are always divided, but the posterior arm in the *E. tristani* group forms more of a shoulder than a branch. The bifurcation occupies the distal 0.25 of the hamule in the *E. ophibolus*, *E. elaps*, and *E. eutainia* groups, the distal 0.50 in the *E. crotalinus* group, and the entire length of the appendage in *E. boa* and *E. cophias*.

The posterior hamules are always more prominent than the anterior pair. They are broadly triangular in the *E. ophibolus* group, but they possess an anterior shoulder in the *E. crotalinus* group. In *E. eutainia* and *E. leptophis*, the posterior hamule forms a small finger-like appendage. All known species except *E. designatus*, *E. elaphe*, *E. leptophis*, and *E. eutainia* possess a black apical tooth. This distal tooth is rotated laterally in *E. viperinus* and in some *E. bothrops*.

The best structural characters for separating the females are those associated with the vertex, occiput, postocciput (note: my use of the term, 'postocciput' is *not* equivalent to the structure immediately surrounding the occipital foramen, but, instead refers to the medioposterior side of the head behind and below the occipital crest), and vulvar lamina. Calvert (1905) relied on the curvature of the posterior border of the occiput, but it is variable within species. I do not use it here. Better characters are the shapes of structures on the vertex. In *E. constrictor*, *E. tristani*, and *E. sabaleticus*, the median ocellus is placed within a deep longitudinal trough which accommodates the strongly curved epiproct of the male. In all other species may be found a transverse trough (figs. 145-146) or a pair of anterolateral pits (fig. 137) anterior to the median ocellus. These pits correlate with the shape of the tip of the male epiproct, and these depressions are also present on the vertex of males. Their shape is useful in distinguishing between the closely related pairs, *E. viperinus* and *E. bothrops*, and between *E. compositus* and *E. lampropeltis*. A complete postocellar ridge is present only in all members of the *E. tristani* group and *E. leptophis*. In all others, the middle part of the ridge is lacking, leaving only postocellar tubercles. Females of a few species have autapomorphic characters, such as the raised median area of the occiput of *E. designatus* (figs. 156-157), the posteriorly directed pointed protuberance on the occiput of *E. leptophis* (fig. 151) or the postoccipital depressions of *E. cophias* (fig. 165).

The vulvar laminae vary in the shape of the plates. The simple horizontal plates are bisected by a small V-shaped cleft in the *E. ophibolus* group. The plates are corrugated and more membranous in *E. boa* and *E. cophias*, often succumbing to much post mortem distortion. In the *E. crotalinus* group, each plate is a large, rectangular, planar structure which meets the other only at the anterior angle. The resulting median cleft is only a third or less the width of each plate; but the cleft is wider and U-shaped in *E. designatus*. A further widening of the cleft is evident in the *E. elaps* group. The plates form two small, widely separated, digit-like structures in *E. eutainia* and *E. leptophis*.

A Y-shaped postlamellar ridge is found posterior to the vulvar lamina. The posterior stem of the Y is absent in *E. eutainia* and *E. leptophis*, so that the ridge forms a semicircle (figs. 178-179).

I have found no structural differences between the females of *E. heterodon* and *E. sipedon*. Body pattern must be used to differentiate females of those species. *Erpetogomphus tristani* and *E. sabaleticus*, and *E. elaphe* and *E. elaps* are also closely related pairs, and their females are distinguishable only by locality.

In well-preserved specimens, body maculation provides useful characters. Dark thoracic maculation predominates in the *E. tristani* group, in *E. leptophis*, and in southernmost specimens of *E. eutainia*. All of those have a well-defined dark stripe bordering the posterior margin of the metepimeron. *Erpetogomphus cophias*, *E. crotalinus*, and most *E. elaps* have nearly immaculate body patterns. Thoracic maculation is usually stable, but there is variability in *E. lampropeltis*, *E. compositus*, *E. designatus*, *E. elaps*, and *E. eutainia*. Two formerly named species, *E. natrix* and *E. coluber*, I consider subspecies of *E. lampropeltis* and *E. compositus*, respectively: I have found no morphological characters which separate those forms. Thoracic patterns in *E. elaps* are often nearly absent (fig. 13), and more extensive dark markings characterize populations of *E. eutainia* in the north, less extensive in the south (figs. 7-9).

Abdominal patterns are characterized by a combination of light and dark banding patterns separated dorsally by pale longitudinal stripes. The least amount of black occurs in *E. cophias* and *E. crotalinus*, the most in *E. agkistrodon*.

A sharp, prominent, middorsal posterior spine on abdominal segments 8 and 9 is found in many males of *E. ophibolus*, *E. bothrops*, *E. liopeltis*, and *E. viperinus*. The spine is variable and cannot be used reliably to distinguish among species. For example, many *E. bothrops* have no indication of a middorsal spine, but it is well developed in others. The spines are also found on abdominal segment 9 in some females of the *E. ophibolus* group.

Erpetogomphus species groups

I divide the 21 species into five groups. I believe the unknown male of one species (*E. agkistrodon*) will follow those characters listed for that sex discussed below.

1. *E. ophibolus* group (= subgenus *Erpetocyclops* Carle, 1992). Males (probably so for *E. agkistrodon*, when discovered): With a distinct curved prepuce, posterior hamule forming a triangle culminating in a sharp black tooth. Females: Vulvar lamina simple, small, relatively undifferentiated postocellar ridge complete, though curved in *E. tristani*, *E. sabaleticus*, and *E. constrictor*. Six species: *E. tristani*, *E. sabaleticus*, *E. constrictor*, *E. ophibolus*, *E. agkistrodon*, *E. schausi*.

2. *E. eutainia* group (= subgenus *Calogomphus* Carle, 1992). Males: Prepuce small, obscured by lateral lobes of penis; lateral lobes of penis strongly developed, forming a spiny frill; posterior hamule finger-like, lacking an apical tooth. Reduced prepuce present. Females: Vulvar lamina small, finger-like, widely separated; post-laminar ridge semicircular, not Y- shaped. Two species: *E. leptophis*, *E. eutainia*.

3. *E. elaps* group. Males: Lateral lobe of penis knife-like. Females: Vulvar lamina connected anteriorly, but separated by a cleft 1.0 or more the width of each plate. Five species: *E. bothrops*, *E. liopeltis*, *E. viperinus*, *E. elaphe*, *E. elaps*.

4. *E. crotalinus* group. Males: Superior surface of cercus angulate (except for *E. compositus*); anterior hamule divided at distal half. Females: Vulvar lamina large, planar, rectangular, meeting at anterior margins only, resultant cleft one third the width of each plate (except for *E. designatus*). Six species: *E. crotalinus*, *E. lampropeltis*, *E. compositus*, *E. heterodon*, *E. sipedon*, *E. designatus*.

5. *E. cophias* group. Males: Anterior hamule talon-like, divided along its full length; posterior hamule broadly spatulate, surmounted by a small, black, curved anteapical tooth. Females: Vulvar lamina diagonally corrugated; distal and lateral margins with a strongly raised semicircular ridge. Two species: *E. boa*, *E. cophias*.

SYSTEMATIC PART

Introduction

Under each species, I have endeavoured to include a complete synonymy (some minor references may be lacking for *E. designatus*, a common species in the eastern United States), a full description, type data, diagnosis, remarks, biology, distribution, and material examined. For new species, I have designated allotypes when the opposite sex was available, but I have not established allotypes for syntypic material. Under comments, I have quoted older authors (Ris, Selys, Hagen), when this information contributes to the history of the species. For *E. agkistrodon*, I include a discussion of what the male should be like, based on my cladogram. Unless otherwise stated, measurements are taken from 20 males and 20 females, when available, and from as many localities as possible. Abdominal measurements include caudal appendages. Full locality data are given for all species, except for the following species where abundant material was available: *E. eutainia, E. elaps, E. viperinus, E. designatus, E. l. lampropeltis, E. l. natrix, E. crotalinus,* and *E. compositus*. For these species, I have listed states, counties, brief data, and repository. Full locality

data for these specimens are available from me. Maps represent distribution records from collections. For some common and well known species (such as *E. bothrops*, *E. compositus*, *E. crotalinus*, *E. designatus*), I include records from published sources I consider reliable.

Abbreviations for figure legends and synonymies are: abd. = illustration(s) of abdomen; app. = illustrations(s) of caudal appendages; cat. = listed in catalogue, descr. = description of male, female, larva, or all, may include keys; distr. = documents or mentions distribution of taxon; ept. = illustration(s) of epiproct; sep. = [page number of] separate (see Cowley (1937) for pagination of reprint of Selysian monographs and synopses of Odonata); thx. = illustration(s) of thorax; vl. = illustration(s) of vulvar laminae.

Abbreviations in descriptions are as follows: anx = antenodal crossveins, pnx = postnodal crossveins, cs = crossveins.

New names proposed in this paper follow the ophidian example set by Selys, Hagen, Calvert, and Williamson. All should be considered as nouns in apposition.

Most illustrations are from type material, which I believe will aid further researchers when describing new species. All illustrations were executed with the aid of a camera lucida with a Wild M-8 stereoscopic microscope.

Erpetogomphus Hagen in Selys, 1858

Erpetogomphus Selys, 1858 (Type species *Ophiogomphus crotalinus* [Hagen *in* Selys], 1854; designated by Kirby 1890: 61). – Selys 1858: 329 (69 sep.) (characters of genus); Selys 1859: 535 (9 sep.) (addition of generic characters); Hagen 1861: 98 (brief descr. of genus); Walsh 1863: 253 (comparison with other American gomphid genera); Brauer 1868: 372 (in key to genera of Gomphidae); Karsch 1890: 371 (mentioned in Gomphidae classification); Calvert 1905: 147 (key to Middle American Gomphidae); Calvert 1909: 468 (distr.); Calvert 1912a: 289 (distr. of genus); Kennedy 1917a: 544 (comments on larvae); Tillyard 1917: 296 (distr.); Ris 1921: 343 (comparison with *Mesogomphus* [= *Paragomphus*]); Garman 1927: 125 (note on genus); Needham and Heywood 1929: 78 (descr.); Byers 1930: 52 (descr.); Cowley 1934: 241 (nomenclature of *Erpetogomphus*); Tinkham 1934: 218 (comments on distr. in Tex.); Fraser 1940: 544 (possible affinities with *Onychogomphus* based on penis morphology); Needham 1941: 240 (comments on larva); Needham 1944: 172 (verification table, larva); Wright and Peterson 1944: 152 (in key to larvae of nearctic Gomphidae); Needham & Westfall 1955: 139 (treatment of genus); Pritchard & Smith 1956: 114 (key to larvae of nearctic Gomphidae, key to genera of Gomphidae); Ferguson-Beatty 1956: 369 (proventriculus of larva); Musser 1962: 13 (diagnosis of larvae); Gloyd 1963: 147 (molar structure of adult); Westfall 1984: 158 (in key to larvae of nearctic Gomphidae); Chao 1984: 79 (uncertainty of *Erpetogomphus* in subfamily Onychogomphinae); Carle 1986: 313 (characters of genus within Onychogomphini); Belle 1988: 99 (in key to neotropical genera of Gomphidae); Bridges 1991: II.17 (cat.); Novelo-G. & Peña-O. 1991: 129 (origin of *Erpetogomphus* in Mexico); Gonzalez-S. & Novelo-G. 1991: 97 (adults in Mexico); Novelo-G. & Gonzalez-S. 1991: 150 (larvae in Mexico); Belle & Quintero 1992: 93 (in key to adults and larvae of Panamanian Gomphidae); Carle 1992: 148 (key, *Erpetocyclops* subg. n. [type = *E. ophibolus* Calvert], *Calogomphus* subg. n. [type = *E. eutainia* Calvert]).

Herpetogomphus Walsh, 1862: 388 (unjustified emendation of *Erpetogomphus*). – Hagen 1875a: 42 (cat.); Selys 1879: 63 (2 sep.) (modification of generic characters); Kirby 1890: 60 (cat.); Carpenter 1897: 452 (distr.); Needham 1897: 166 (in key to nearctic Gomphidae); Needham 1899: 234 (venation); Calvert 1899: 386 (comments on Selys' classification); Needham & Hart 1901: 53 (in key to larvae of North American Gomphidae); Förster 1914: 73 (comparison with *Ammogomphus*); Seemann 1927: 19 (key to larvae, adults of western U. S. Gomphidae); Needham 1940: 389 (key, verification table).

Medium sized to small neotropical Gomphidae of slender build.

Head. – Eyes widely separated, characters of the mouth parts, clypeus, frons typical of the Gomphidae. Vertex variable, often interspecifically and, in the *E. ophibolus* group, sexually dimorphic. Anterior margin of vertex with a transverse trough, or a pair of transverse pits anterior or anterolateral to median ocellus, median ocellus anterior to lateral ocelli, or in some members of the *E. ophibolus* group, this structure at posteriormost part of deep, longitudinal trough, thus causing median ocellus to be posterior to lateral ocelli (figs. 145-146); median surface of vertex at vicinity of lateral ocelli and postoccipital tubercle mostly planar, but members of *E. ophibolus* group with a complete postocellar ridge, which may be bilobed (*E. agkistrodon*, fig. 148) or, in remainder of group, vestigial; occiput highly variable according to species and sex, *E. ophibolus* group with occiput small, semicircular, in other groups roughly trapezoidal, with posterior part broader than anterior part, its dorsal surface roughly planar to nearly vertically inclined, some species with slight to strongly tumid area medially, one species (female of *E. leptophis*) with a posteriorly projected medial spine; rest of occiput variable, semicircular, linear, weakly to strongly notched medially, or sinuate; condition of crest often variable within a few species; postocciput variable, most in the *E. ophibolus* group convexly arcuate, in others slightly convex to linear, postocciput mostly not visible from above, but conspicuously so in others (*e.g.*, female of *E. compositus*); lateral margins of one species (females of *E. cophias*) with transverse depressions.

Thorax. – Prothorax and synthorax typical of the

Gomphidae, but with great differences in maculation and colouration due to species and age differences. Pale colour pale green, apple green to vivid blue green, usually lighter ventrally and often with a slight dusting of white pruinosity ventrally and around coxae. Synthorax immaculate to heavily patterned with full complement of thoracic stripes. Legs moderately short, with femora slightly swollen and usually pale basally, with dark brown to black distally; tibiae in almost all species black, prothoracic tibiae of males with small keel occupying distal 0.15 of mesal ventral margin.

Wings (figs. 227-230) variable inter- and intraspecifically. Fore wing moderately narrow, with 11-21 antenodal crossveins, 5-16 postnodal crossveins, no subcostal crossvein; pterostigma prominent, about 4 times as long as wide, widest medially with its posterior margin slightly convex, surmounting 4-8 crossveins, the proximal a brace vein; anterior margin of costa in many species pale, becoming dark at pterostigma; arculus at vicinity of second antenodal, the sectors not stalked, separated at base by distance greater than width of each sector; supratriangular, triangular, and subtriangular crossveins absent; paranal cells variable in number, often numbering 5-7, smaller species usually with zero or few supplementary marginal cells behind paranal cells, other species with irregular row of up to 6-7 supplementary cells; no apical or medial planates, discoidal field of two rows. Hind wing with 7-14 antenodal crossveins, 7-14 postnodal crossveins; anal triangle of 2-4 cells, often with one of them in the latter condition small; anal loop absent (some specimens with a vestigial anal loop of 3 cells, but this condition rare); one paranal cell at Y interspace, two paranal cells at X interspace. Wing colouration entirely hyaline or flavescent at bases in some species. Hind wing length 21-36 mm.

Abdomen cylindrical, narrowest medially in males, transverse carinae on segments 3-7; auricles well developed in male, inner margin denticulate; auricle vestigial in female; male posterior margin of tergites 8 and especially 9 in a few species prolonged into a medial point, but this condition variable intraspecifically; segments 8-9 moderately clubbed, with moderate foliate extensions; female with apical abdominal segments hardly widened, foliar expansions small. Colour pattern and maculation variable between species and within sexes; all species with a pale green to pale orange middorsal stripe, sometimes extending full length of segment, but progressively less so on more posterior segments; dark brown to black dorsolateral stripe present on first 7 segments, usually constricted or separated medially, giving most of abdomen a serial dark and pale appearance; posterior part of segment 7, all of segments 8-10 tan to dark red brown, especially middorsally and ventrolaterally. Length of abdomen including appendages: ♂: 29-40 mm, ♀: 29-41 mm.

Abdominal appendages of male with cerci of great diversity according to species, but these structures always as long as segment 10, cercus usually gently decumbent at apical 0.30; rarely with a dorsal appendage. Ventral carina present basally, or distally, or absent, depending on species, epiprocts divided at base but contiguous along most of their length, gently to strongly curved at distal 0.50 to 0.30, depending on species; this structure lacking any accessory spines, or protuberances (except for *E. ophibolus*, fig. 95); tips of epiprocts assuming a wide variety of shapes and forms, and often variable intraspecifically (*e.g., E. bothrops*, figs. 127-128).

Vulvar lamina of female variable interspecifically, but never more than 0.50 length of segment 9, vulvar plates small, digit-like to forming large, contiguous, triangular or quadrangular plates, a moderate to large V- or U-shaped notch medially; postlamellar ridge always present, semicircular in only two species (*E. eutainia, E. leptophis*), in all others forming an inverted Y; stem of Y originating before or often at level of vulvar plates, some species with a well defined semicircular depression on each side of posterior stem.

Male genitalia variable among species: anterior lamina not prominent; anterior hamule smaller than posterior hamule, usually with the distal end hidden from view by posterior lamina; anterior lamina dark, divided at various heights according to species, but with posterior branch usually less conspicuous, smaller, and anterior branch more prominent; posterior lamina usually pale, linear in two species (*E. eutainia, E. leptophis*); in all others with a moderately wider base, its tip usually adorned with an apical or anteapical hook directed cephalad or cephalolaterad. Penis with basal (first) segment prominent, with a semicircular rim, especially so laterally, posteriorly with a pair of prominent lobes, or these lobes vestigial; second segment moderately long, third short, with a pair of small, nipple-like sclerotizations dorsally in two species (*E. eutainia, E. leptophis*); fourth segment highly variable specifically, with or without a prepuce, most species with a well defined lateral lobe; in most of the *E. ophibolus* group, lateral lobe small and pointed; membranous hood short to long and overlapping; a pair of flattened membranous cornuae of various lengths and shapes present on apical part of segment; in most of the *E. ophibolus* group, cornuae absent or vestigial; penis guard short, quadrate in cross-section.

A more complete discussion of the male and female genitalia is given under discussions of the species group accounts and in the cladistics section.

Keys

The keys should work for most specimens, but the worker may have difficulty when trying to determine poorly preserved material. I have used morphological characters for both sexes wherever possible, but some species pairs (*e.g.*, females of *E. heterodon* and *E. sipedon*, or *E. tristani* and *E. sabaleticus*) show little or no morphological differentiation. For them, I have had to rely on colour pattern. Abdomens of some females, particularly those laterally compressed, may need to be relaxed so that the vulvar lamina can be seen.

Key to *Erpetogomphus* males

1. Cercus with a prominent superior tooth at about 0.75 of appendage length (figs. 92-94) 2
– Cercus with dorsal surface convexly angulate (fig. 112), smoothly curved (fig. 103), straight (fig. 100), or with a concavity (fig. 115) 5
2 (1). Epiproct smoothly curved, with tip pointing dorsally or posterodorsally, a small, sharp, anteriorly directed superior tooth at middle of epiproct (fig. 95). Southern Mexico, Belize ..... *ophibolus*
– Epiproct strongly curved so that distal 0.30 is parallel to basal 0.30, tip of epiproct pointing anteriorly, superior surface of epiproct with no tooth 3
3 (2). Ventral margin of cercus smoothly concave (fig. 92). Northeastern Mexico to Costa Rica ..... *constrictor*
– Ventral margin with a large ventral tubercle at 0.50-0.75 length of cercus (figs. 93-94). Costa Rica south to Colombia and Venezuela 4
4 (3). In lateral view, superior tooth of cercus as long as rest of appendage, so that appendage appears to end in two equal branches (fig. 93). Panama, Colombia, Venezuela ..... *sabaleticus*
– In lateral view, superior tooth of cercus less than 0.50 as long as remainder of appendage (fig. 94). Costa Rica, northern Panama ..... *tristani*
5 (1). Metathoracic tibiae either entirely yellow externally (fig. 169), or yellow with median longitudinal black line. Western Mexico, southeastern Arizona ..... *crotalinus*
– Metathoracic tibiae entirely brown or black externally; never with any yellow (*e.g.* figs. 168, 170) 6
6 (5). Basal 0.25 to 0.30 of lower margin of cercus with a distinct longitudinal carina which may end in a small ventral tooth (*e.g.*, *E. cophias*, fig. 116) 7
– Basal part of cercus with no ventral carina, though a small tubercle may be present at basal 0.15-0.20 of appendage (*e.g.*, figs. 99, 102) 14
7 (6). With a dark stripe bordering posterior margin of metepimeron (figs. 8-9). Southern Mexico, Belize through Costa Rica ..... *eutainia* (in part)
– Without a dark stripe on posterior margin of metepimeron 8
8 (7). In lateral view, ventral margin of cercus with carina terminating in a distinct ventral tooth at basal 0.30 of appendage (fig. 116); thorax almost immaculate, at most barely an indication of a dark antehumeral stripe (fig. 27). Michoacan and Morelos states of western Mexico ..... *cophias*
– Ventral margin of cercus with longitudinal carina not terminating in a ventral tooth; thorax with well-defined dark antehumeral stripe, though it may be an elongated, isolated spot (*e.g.*, fig. 23) 9
9 (8). Dorsal surface of cercus distinctly angulate in lateral view (figs. 110, 112) 10
– Dorsal surface of cercus smoothly curved (fig. 112) 13
10 (9). Sides of thorax almost entirely green, with only a small, ill-defined dark humeral stripe; second lateral stripe incomplete, dark only below metathoracic spiracle, or absent; and third lateral stripe present only on upper 0.30 of suture (fig. 23), or absent (fig. 19) 11
– Sides of thorax green with usual complement of dark thoracic stripes; second lateral stripe may be incomplete, but humeral and third lateral stripes always present (figs. 17, 20-21) 12
11 (10). Dark antehumeral stripe incomplete, not touching humeral stripe (fig. 23); tip of cercus acute, but not gradually narrowing posteriorly (figs. 110-111); cornuae of penis without mesal lobes (fig. 87). New Mexico, western Texas, northern Mexico ..... *heterodon*
– Dark antehumeral stripe complete, usually connected to humeral stripe (fig. 19); tip of cercus drawn out into a narrow cylindrical point (figs. 105-106); cornuae with mesal lobes (fig. 83). Durango, Jalisco, Morelos, and Puebla states of central Mexico ..... *sipedon*
12 (10). Tip of cercus strongly acuminate (fig. 104), dark antehumeral stripe not connected to

collar (fig. 17) (except in some Mexican individuals), base of wings flavescent (except in some Mexican individuals, fig. 18), median area of occiput with a strongly raised tubercle (fig. 156). Eastern U.S. to Arizona, northern Mexico ..... *designatus*

– Tip of cercus blunt, not acuminate (figs. 107-108); dark antehumeral stripe always connected to collar (ssp. *natrix*, fig. 21), or largely connected to humeral stripe (ssp. *lampropeltis*, fig. 20); base of wings hyaline, median area of occiput only slightly raised (fig. 160). Southern California, Arizona, New Mexico, western Texas, Baja California, Durango state, Mexico .... *lampropeltis*

13 (9). Ventral carina at base of cercus black, contrasting with remainder of appendage; this carina usually denticulate; thorax blue-green in life; sides of posterior hamules parallel, linear (fig. 52). Southern Texas to southern Mexico ..... *eutainia* (in part)

– Ventral carina at base of cercus pale, the same colour as rest of appendage, this carina smooth; thorax pale green in life; sides of posterior hamules converging toward tip, not linear (fig. 66). Southwestern United States, Baja California ..... *compositus*

14 (6). Distal 0.5 of cercus concave dorsally, this area covered with thick, long bristles (fig. 115). Southern Veracruz state, Mexico .... *boa*

– Distal 0.5 of cercus straight or convex (*e.g.*, figs. 99, 103) 15

15 (14). Ventral margin of cercus straight (figs. 99, 100) or forming a gentle concave curve (fig. 98) so that appendage appears linear 16

– Apical 0.30 of ventral margin of cercus curved downward 18

16 (15). Thorax entirely yellow-green (fig. 13), or with only an antehumeral and faint indication of a dark middorsal and antehumeral stripe (figs. 11-12); face entirely pale. Mexico south to Costa Rica. 17

– Thorax blue-green with full complement of dark thoracic stripes (fig. 10); face blue-green with extensive dark brown frontoclypeal stripe. Belize ..... *leptophis*

17 (16). Distal branch of anterior hamule thick, as high as gap separating the two branches (fig. 54); posterior hamules with no distal tooth (fig. 54). Guatemala south to Costa Rica .... *elaphe*

– Distal branch of anterior hamule narrow, not as high as gap separating the two branches (figs. 55-56); posterior hamules with a distal tooth (fig. 55). Mexico to Guatemala ..... *elaps*

18(15). Thorax blue-green, with full complement of dark stripes, including second lateral stripe and stripe on posterior margin of metepimeron (fig. 6); face (fig. 142) predominantly dark, with a well defined blue green spot on frons. Guatemala, Costa Rica ..... *schausi*

– Thorax blue-green or yellow-green; sides lacking complete dark second lateral stripe (except in some *viperinus*; incomplete in some *bothrops*) and without dark stripe on posterior margin of metepimeron; face predominantly pale, with dark areas limited to sutures 19

19(18). Tip of epiproct in posterior view terminating in a blunt point (fig. 129); southern Veracruz state, Mexico..... *viperinus*

– Tip of epiproct in posterior view spatulate (fig. 126), broadly truncate (fig. 127), or bidentate (fig. 128) 20

20 (19). Larger species (hind wing 30-31 mm); epiprocts in lateral view curved, extending 0.50 or less the length of cerci (fig. 101), epiprocts in posterior view truncate or slightly bidentate; dark antehumeral and humeral stripes combined or nearly so (fig. 14); posterior hamular tooth prominent, directed laterocephalad or cephalad. Nuevo Leon, Michoacán, San Luis Potosí states, Mexico. (fig. 199) ..... *liopeltis*

– Smaller species (hind wing 21-28 mm); epiprocts in lateral view curved, extending 0.75- 0.90 the length of cerci (fig. 102), epiprocts in posterior view bidentate or truncate (fig. 128); dark antehumeral and humeral stripes separate (fig. 15); posterior hamular tooth not as prominent, more strongly directed cephalad. Tamaulipas, Mexico, south to El Salvador (fig. 199) .... *bothrops*

Key to *Erpetogomphus* females

1. Medial area of occiput with a posteriorly pointed protuberance (fig. 151) ... *leptophis*

– Medial area of occiput variously shaped, but never with a posteriorly directed protuberance 2

2 (1). Occiput with a shallow oval depression on each side posterior to elevated rim (fig. 165). Michoacán and Morelos, Mexico .... *cophias*

– Occipital area posterior to elevated rim entire, with no shallow depressions 3

3 (2). Outer surfaces of metathoracic tibiae entirely yellow, or yellow with a median longitudinal black line (fig. 169). Western Mexico,

southeastern Arizona ..... *crotalinus*

– Outer surfaces of metathoracic tibiae entirely black (*e.g.*, figs. 168, 170) 4

4 (3). Median ocellus posterior to lateral ocelli, the former lying within a deep longitudinal trough (figs. 145-146) 5

– Median ocellus at level of or anterior to lateral ocelli, no longitudinal trough 6

5 (4). Dorsal surface of vertex with sides of trough roughly parallel, or only slightly converging anteriorly (fig. 145). Northeastern Mexico, south to Costa Rica ..... *constrictor*

– Dorsal surface of vertex with sides of trough strongly converging anteriorly .....(fig. 146) Costa Rica, western Panama ..... *tristani* Central Panama, Colombia, Venezuela .... *sabaleticus*

6 (4). Vertex with transverse ocellar ridge bilobed behind median ocellus (figs. 148-149) 7

– Vertex with transverse ocellar ridge entire (fig. 147), low and almost vestigial (fig. 150), or absent, its lateral ends forming oval tubercles posterior to lateral ocelli (*e.g.*, fig. 150) 8

7 (6). Occiput transversally narrow, forming a shallow semicircle (fig. 148). Jalapa, Mexico ..... *agkistrodon*

– Occiput wide, forming a full semicircle (fig. 149). Guatemala, Costa Rica ..... *schausi*

8 (6). Vertex with transverse ocellar ridge entire, prominent, and concave posteriorly (fig. 147). Southern Veracruz, Mexico, Belize ....*ophibolus*

– Vertex with median area bare, or at most only slightly raised (*e.g.*, fig. 150) 9

9 (8). Vulvar lamina followed on segment 9 by distinct and prominent semicircular ridge, never with a posteriorly directed arm (fig. 178). Southern Texas, eastern Mexico, Belize to Guatemala and Costa Rica ..... *eutainia*

– Vulvar lamina followed on segment 9 by a Y-shaped ridge (e.g., fig. 195) 10

10 (9). Vulvar lamina with each plate strongly corrugated diagonally, distal and lateral margins of each plate forming a strongly raised semicircular ridge (figs. 195-196); a median tumid swelling on postocciput immediately behind occipital ridge (fig. 167) [includes *liopeltis*, but properly goes to 10']. Southern Veracruz, Mexico ..... *boa*

– Vulvar lamina with each plate entire (fig. 185) or bisected diagonally by only one groove (fig. 186); distal and lateral margins of each plate planar, not forming a strongly raised semicircular ridge; postocciput not differentiated, evenly curved (fig. 166) [tumid in *liopeltis*] 11

11 (10). Median surface of occiput with a strongly raised tubercle (fig. 156). Eastern United States west to Arizona, northern Mexico .... *designatus*

– Median surface of occiput planar or at most slightly raised (fig. 152) 12

12 (11). Lobes of vulvar lamina separated by an almost U-shaped interval 3 to 4 times as wide as either lobe (figs. 180-181) Mexico south to Guatemala ..... *elaps* Guatemala to Costa Rica ..... *elaphe*

– Lobes of vulvar lamina separated by a triangular or semicircular interval 0.5 to 1.0 the width of each lobe (*e.g.*, figs. 182, 187) ...13

13 (12). With a second complete dark lateral stripe on thorax (*e.g.*, figs. 20-21, 24) 14

– Second dark lateral stripe completely lacking or vestigial, at most extending from base to just above metathoracic spiracle (*e.g.*, fig. 36) 15

14 (13). Occiput in dorsal view narrow, its width less than width between median ocellus and occiput; postoccipital area easily visible (fig. 163); base of wings with flavescent infusion between Sc and R at least up to first anx and cubitoanal area; top of abdomen with light areas ivory or with a tinge of orange, usually not different from white on sides. Southwestern United States, Baja California ..... *compositus*

– Occiput in dorsal view wide, its width almost equal to width between median ocellus and occiput; postoccipital area not visible (fig. 160); base of wings hyaline; top of abdomen with light areas much darker than white on sides. Southwestern United States, Baja California, Durango state, Mexico .... *lampropeltis*

15 (13). Occiput narrow, vestigial, with only a small medially arched area (fig. 153); post-occiput with a median tumid area (as in fig. 167). Nuevo Leon, Michoacan, San Luis Potosí states, Mexico ..... *liopeltis*

– Occiput not especially narrow, extending full width (*e.g.*, figs. 154-155, 159, 162); post-occiput planar or, at most, only slightly convex medially (as in fig. 166) 16

16 (15). Stem of postlamellar ridge with a well defined circular or oval depression on either side; junction of Y of postlamellar ridge usually posterior to hind margin of vulvar laminar plates (fig. 183) 17

– Stem of postlamellar ridge with only a slight depression or, more often, without any circular or oval depression on either side; junc-

tion of Y of postlamellar ridge at or anterior to hind margin of vulvar laminar plates (figs. 187-188, 193) 18

17 (16). A deep pit at anterior margin of frons anterolateral to median ocellus (fig. 155); cleft between vulvar laminar plates wide, forming an obtuse arc greater than 100°; dark humeral and antehumeral stripes combined or nearly so (fig. 16); larger species (hind wing 31-34 mm). Southern Veracruz, Mexico .... *viperinus*

– Anterior margin immediately anterior to median ocellus forming a narrow V-shaped trough with base of postfrons (fig. 154); cleft between vulvar laminar plates narrow, forming a V- shaped notch of not more than 90° (fig. 183); dark humeral and antehumeral stripes separate (fig. 15); smaller species (hind wing 17-31 mm). Tamaulipas, Mexico, south through El Salvador .... *bothrops*

18 (16). Dark antehumeral stripe complete, usually connected at its upper end to narrow humeral stripe (fig. 19). Jalisco, Morelos, and Puebla, Mexico ..... *sipedon*

– Dark antehumeral stripe vestigial, forming an isolated elongate spot, not connected to vestigial humeral stripe (fig. 23). Southwestern United States, northern Mexico ..... *heterodon*

Key to *Erpetogomphus* males based primarily on characters of abdominal segments 2 and 3

I include this key for male specimens lacking the posterior abdominal segments. The key should allow a high probability of identification, though some species (*E. ophibolus, E. sabaleticus, E. tristani, E. constrictor*, for example) appear inseparable by penis structure and are distinguished only by the caudal appendages. For those species, I have added other somatic characters and/or geographic data with which to separate them. The key does not include *E. agkistrodon*, the male of which is unknown.

1. Ental surface of penis with a prepuce (*e.g.*, fig. 76), this structure reduced and partially hidden by frill-like lateral lobe in *leptophis* (fig. 76) and *eutainia* (fig. 75); thoracic pale colouration in life deep blue green, dark thoracic stripes always present on sides (*e.g.*, fig. 10) 2

– Ental surface of penis lacking a prepuce (*e.g.*, fig. 90); thoracic pale colour in life yellow green (except for *viperinus* and probably *liopeltis*); dark lateral thoracic stripes often (but not always – figs. 16, 18) reduced or absent 8

2 (1). Posterior hamule digit-shaped (figs. 52-53), its tip broadly rounded; anterior hamule divided at upper 0.30 to 0.25, its posterior branch well defined, its tip almost meeting larger anterior branch (figs. 52-53); lateral lobe of penis composed of large spinulose frill (figs. 52-53); cornuae well developed, their apices pointed 3

– Posterior hamule triangular, its tip armed with a spine (fig. 47); anterior hamule with only a posterior shoulder (*e.g.*, fig. 47); lateral lobe of penis reduced to a small, semicircular, spinulose frill (fig. 74) or vestigial (fig. 70); cornuae vestigial (fig. 74) or present (fig. 70) 4

3 (2). Membranous hood of penis about 3 times as long as wide, apices overlapping (fig. 76) [Note: this character is based on the only known specimen, the holotype; other specimens may show variability similar to *eutainia*.]; dark second and third lateral stripes connected at upper ends, forming an isolated pale spot below subalar carina; dark lateral stripe along posterior margin of metepimeron well defined (fig. 10); caudal appendages as in fig. 98; Belize ..... *leptophis*

– Membranous hood of penis reduced, less than 2 times as long as wide, though apices may overlap (fig. 75); dark second and third lateral thoracic stripes not connecting (fig. 7-9); dark lateral stripe along posterior margin of metepimeron absent (fig. 7) or present primarily in populations of central Mexico (fig. 8) south through Costa Rica (fig. 9); caudal appendages as in fig. 97 .... *eutainia*

4 (2). Cornuae of penis present; their tips divergent (fig. 74); lateral lobe a small, circular, spinulose frill (fig. 74); Guatemala and Costa Rica ..... *schausi*

– Cornuae vestigial (fig. 71); lateral lobe vestigial, forming a small, acute point (fig. 71) 5

5 (4). Appendages as in fig. 93; Central Panama south to Colombia and Venezuela ..... *sabaleticus*

– Mexico south through Costa Rica and northern Panama 6

6 (5). Epiproct smoothly curved, with tip pointing dorsally or posterodorsally, a small, sharp, anteriorly directed superior tooth at middle of epiproct (fig. 95). Southern Mexico, Belize ..... *ophibolus*

– Epiproct strongly curved so that distal 0.30 is parallel to basal 0.30, tip of epiproct

pointing anteriorly, superior surface of epiproct with no tooth 7

7 (6). Appendages as in fig. 92; Mexico south through Costa Rica ..... *constrictor*

– Appendages as in fig. 94; northern Costa Rica through northern Panama ..... *tristani*

8 (1). Anterior hamule divided at base; its branches resembling a claw; posterior hamule broadly spatulate (figs. 68-69) 9

– Anterior hamule divided at lower 0.30 to upper 0.25 posterior arm short and truncate or acute; posterior hamule broadly triangular 10

9 (8). Dark antehumeral and humeral stripes united, forming a broad, dark stripe over first lateral suture (fig. 26); southern Veracruz, Mexico ..... *boa*

– Thorax almost entirely pale, with only a vestigial antehumeral stripe (fig. 27); Michoacán and Morelos states of Mexico ... .*cophias*

10 (8). Lateral lobe of penis linear, at least 3 times longer than wide; its posterior margin spinulose (figs. 77-78, 82, etc.) 11

– Lateral lobe of penis round, about as long as wide, its margin spinulose (fig. 86) 16

11 (10). Lateral lobe of penis almost recumbent against ental margin of fourth segment (fig. 82); anterior hamule divided at distal 0.5 of segment; posterior hamule lacking a distal tooth (fig. 60); posterior margin of first segment (peduncle) of penis strongly cleft, each lobe on either side of cleft protruding well beyond posterior margin of segment; southern United States west to Arizona, northern Mexico ..... *designatus*

– Lateral lobe of penis prominent, directed almost perpendicularly to ental margin of fourth segment; anterior hamule divided at distal 0.30 of segment, posterior hamule with a distal tooth (except for *elaphe* from Guatemala south through Costa Rica); posterior margin of first segment of penis weakly bilobed, lobes on either side of emargination only slightly extending beyond posterior margin of segment; northern Mexico south through Costa Rica 12

12 (11). Distal branch of anterior hamule thick, as tall (high) as gap separating the two branches (fig. 54); posterior hamule with no distal tooth (fig. 54); Guatemala south to Costa Rica ..... *elaphe*

– Distal branch of anterior hamule narrow, not as tall (high) as gap separating the two branches (figs. 55-56); posterior hamule with a distal tooth 13

13 (12). Distal tooth of posterior hamule bent anteriorly so that it lies in same direction as the planar surface of hamule (figs. 55-56); Mexico south to Guatemala ..... *elaps*

– Distal tooth of posterior hamule bent laterally or anterolaterally so that it points distally and perpendicularly from planar surface of hamule (fig. 59) [Note: This condition appears universally only in *E. viperinus*, but variation in this condition occurs in *E. bothrops* and *E. liopeltis*; some specimens of these last two species may not be separable from *E. elaps* by this character]; Mexico south through Guatemala 14

14 (13). Base of postfrons medially with a pair of deep pits, each anterolateral to median ocellus (fig. 137). Southern Veracruz, Mexico .. ..*viperinus*

– Base of postfrons medially with a transverse arcuate trough immediately anterior to median ocellus (fig. 136) 15

15 (14). Smaller species (hind wing 21-28 mm); dark antehumeral and humeral stripes separate (fig. 15); posterior hamule with apical tooth shorter, less prominent, more strongly curved laterally over tip of hamule. Tamaulipas, Mexico, south through El Salvador (fig. 199) ..... *bothrops*

– Larger species (hind wing 30-31 mm); dark antehumeral and humeral stripes connected (fig. 14); posterior hamule with apical tooth longer, more linear, not as strongly curved laterally over tip of hamule. Nuevo Leon, Michoacan, San Luis Potosí, Mexico .... *liopeltis*

16 (10). Cornuae of penis with tips long, narrow, and attenuate; medial lobe present (fig. 86); extensor surfaces of tibiae yellow, or yellow with a median longitudinal black line; south-eastern Arizona south through central Mexico ..... *crotalinus*

– Cornuae of penis with tips bluntly rounded (figs. 87-88); medial lobe present (figs. 83-84) or absent (figs. 87-88); extensor surfaces of tibiae black, never with yellow 17

17 (16). Tips of cornuae bluntly rounded; medial lobe absent (figs. 87-88) 18

– Tips of cornuae with a well defined medial lobe (figs. 83-84) 19

18 (17). Median part of base of postfrons with a transverse arcuate trough immediately anterior to median ocellus (as in fig. 138); western United States ..... *compositus*

– Base of postfrons medially with a pair of deep pits, each anterolateral to median ocellus (as in fig. 138); western Texas, western

New Mexico, Chihuahua, Mexico .... *heterodon*

19 (17). Penis in dorsal view with membranous hood short, exposing a subcutaneous membranous hood which forms the posterior margin of segment [be sure to examine closely: rotation of penis to dorsolateral view will reveal a raised hood anterior to subcutaneous membrane], (fig. 83); Jalisco, Morelos, and Puebla, Mexico ..... *sipedon*

– Penis in dorsal view with membranous hood long, completely covering subcutaneous membrane, thus forming posterior margin of segment (figs. 84-85); western Texas, southern and central New Mexico and Arizona, southwestern California, Baja California, Durango state, Mexico .... *lampropeltis*

Erpetogomphus constrictor Ris

(figs. 1-thx, 28-abd, 97-hamules, 70-penis, 92-app, 145-♀ vertex, 171-vl, 198-distr)

Erpetogomphus constrictor Ris, 1917: 154 ('Nach 3♂, 1♀ von Misantla, Vera Cruz, Mexiko, VI 1911, die ich dem schweizerischen Sammler W. Gugelmann verdanke.'). – Williamson and Williamson 1930: 12 (summary of status); Montgomery 1973: 239 (derivation of name); Paulson 1982: 255 (Mex.); Davies and Tobin 1985: 27 (cat.); Tsuda 1986: 87 (cat.); Dunkle 1988: 46 (Honduras); Maes et al. 1988: 36 (Nicaragua); Bridges 1991: VII.51 (cat.); Tsuda 1991: 95 (cat.).

Description

Male. – Labium grey, becoming dark grey medially, labrum entirely brown to grey green with dark brown margin and large inverted medial triangular spot; base of mandibles grey green, anteclypeus grey green; postclypeus brown except for small triangular green spots above lateral lobes; ventral margin of frons brown joining brown of postclypeus, thus forming a large brown frontoclypeal stripe; remainder of frons green; extreme base of frons, vertex, and occiput dark brown; area immediately anterior to median ocellus with a shallow longitudinal trough, postocellar tumid areas prominent, a lower incomplete transverse ridge posterior to median ocellus but not continuous with each postocellar tumid area laterally; occiput planar, its crest costate, linear, fringed with dark brown hairs; postocciput brown, linear to gently concave medially; rear of head brown.

Prothorax brown, paler dorsally, anterior and posterior lobes green, some specimens with two small green midlateral spots (almost touching) on median lobes; synthorax (fig. 1) with prominent, well defined dark stripes on green background as follows: middorsal stripe narrowing anteriorly at collar, costal margins of antealar sinus and area along this structure connecting with humeral stripe; antehumeral stripe connecting with humeral basally and dorsally, but its upper end often not touching brown below antealar crest, or, if so, then isolating small area of green; second and third lateral stripes connecting at upper 0.25, isolating small green spot, second lateral stripe swollen in vicinity of metaspiracle and, in some specimens, enlarged and touching third lateral stripe; posterior margin of metepimeron, metasternum, and venter of thorax grey green to tawny. Venter of profemora grey green, remainder of femora dark brown, becoming black distally; tibiae, tarsi, armature black.

Wings hyaline, venation and pterostigma black.

Venational statistics. Fifth (rarely fourth or sixth) antenodal thickened; number of marginal cells behind fore wing paranal cells: 0-1/0-1; anx: fore wing 13-17/14-17, hind wing 10-12/10-13; pnx: fore wing 10-14/9-14, hind wing 9-12/9-13; cs under pterostigma.: fore wing 5-7/4-7, hind wing 4-7/5-7; anal triangular cells: 3- 5/3-4. Hind wing 25-30 mm.

Abdomen with segment 1 brown, green laterally and with a green middorsal stripe; segment 2 brown except for green auricles, ventral margin, and narrow middorsal stripe, annulus black; segment 3 primarily black with green middorsal stripe extending from black annulus of segment 2 and ending at distal annulus, a pale grey green anterolateral spot becoming narrower along ventral margin and disappearing at 0.25 to 0.75 of segment length; segments 4-6 similar to segment 3 but with pale middorsal stripe ending at posterior 0.10 to 0.25 of segment, segment 6 in some specimens with anterolateral white connecting dorsally with pale green middorsal stripe; segment 7 grey green on anterior 0.50 to 0.60, except for dark transverse carina, posterior part of segment brown to black; segments 8-10 red brown, becoming darker dorsally and ventrally, especially along foliate margins, posterior medial margin of segment 9 bluntly pointed or slightly so. Abdomen 31-35 mm.

Cercus (fig. 92) grey green, becoming dark brown posteriorly, arcuate with a prominent laterally compressed dorsal tubercle on distal 0.75 of cercus, extreme base with a black ventral tooth (mostly hidden by posterior margin of abdominal tergite 10), a ventral carina on distal 0.25 of cercus, tip of cercus with a black tooth; epiprocts dark brown, strongly curved at distal 0.50 so that distal 0.5 of appendage is parallel, distal 0.30 sulcate medially on exterior surface. Accessory genitalia. Hamules (fig. 47) small; anterior hamule brown, divided at distal 0.30, posterior branch a well developed shoulder; posterior hamule roughly triangular, its tip with a spine; penis (fig. 70) with cornuae slightly bilobate or transverse at base, a well developed prepuce, lateral lobe a small tooth.

Female. – Head markings similar to male but with

dark median spot on labrum larger, often connecting with ventral brown, thus separating green into two lateral spots; some specimens with an entirely brown labrum; brown on frontoclypeal suture more extensive laterally, so that entire postclypeus may be brown; brown at base of antefrons with a median extension which, in some specimens, connects with brown frontoclypeal suture, thus dividing frontal green into two spots. Morphology of vertex and occiput differs from male as follows: a large longitudinal trough on vertex with median ocellus recessed posterior to lateral ocelli (fig. 145); bottom of median furrow with longitudinal convex area; lateral margins of trough formed by median ocellar protuberances connecting posteriorly forming a semicircular ridge; occiput small, forming a narrow semicircle, crest covered with long brown hairs; postocciput brown, convex.

Pro- and synthorax as in male, but with dark areas more extensive.

Venational statistics (n = 15). Fifth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 0-5/0-3; anx: fore wing 14-17/14-17, hind wing 11-12/11-12; pnx: fore wing 11-14/11-14, hind wing 10-14/11-13; cs under pterostigma.: fore wing 5-7/5-7, hind wing 5-7/5-7. Hind wing 28-31 mm.

Abdomen (fig. 28) with segment 1 brown, a green spot posterolaterally and with a complete green middorsal stripe; segment 2 brown except for following green areas: wide middorsal stripe narrowing posteriorly, longitudinal lateral stripe connecting just anterior to auricle and narrowing slightly to posterior margin of segment, a thin pale margin at venter of segment; segment 3 similar to segment 2 but lateral pale stripe ending posteriorly at transverse carina, middorsal green narrowly acuminate posteriorly, forming a mere line on posterior 0.25 of segment; segments 4-6 similar to segment 3 but with middorsal green progressively shorter posteriorly, lateral pale stripe white and forming a small quadrangular spot at anteroventral margin of segment; segment 7 with anterior 0.50 pale green, interrupted by black transverse carina, posterior 0.50 becoming red brown; segments 8-10 all red brown, often darker dorsoposteriorly; cerci pale grey green. Vulvar lamina (fig. 171) with plates broadly connected at basal 0.75, relatively unspecialized, cleft obtusely V- or U-shaped, about as wide as each lobe; postlamellar ridge with Y-juncture posterior to plates, base of stem well defined and with oval depression laterally. Abdomen 30-35 mm.

Diagnosis

Males of *E. constrictor* are easily separated from its closest allies, *E. tristani* and *E. sabaleticus*, by the shape of the cercus. This structure is concave ventrally in *E. constrictor*, not convex as in the other two species. It superficially resembles *E. schausi* in body colouration and is diagnosed under that species.

Females seem to be separable from the same two species by the width of the median trough of the vertex. This structure is slightly divergent anteriorly in *E. constrictor* (figs. 145), but is largely parallel in the other two species (fig. 146).

Remarks

Variation. – Venational details of lectotype male of *E. constrictor*. No marginal cells behind fore wing paranal cells; anx: fore wing 15/14, hind wing 11/11; pnx: fore wing 11/12, hind wing 12/13; cs under pterostigma: fore wing 7/7, hind wing 7/6; number of anal triangular cells: 4/3. Hind wing 29 mm.

Material I examined indicates that specimens from more southerly parts of its range (Guatemala, Honduras, Nicaragua) are more melanic than those from eastern Mexico. For example, black markings on the labrum, postclypeus, and thoracic striping are generally more extensive, further reducing or isolating green areas.

Two females, one from San Luis Potosí (El Salto Falls) and the paralectotype are unusual in having 5/3 and 4/3 marginal cells behind fore wing paranal cells in right and left fore wings, respectively. All other female specimens ranged from 0-1 marginal cells.

Biology. – E. González (*in litt.*) found this species to be abundant at the Rio Huichihuayan. Males perched on leaves, vines, and snags at the edge of the river. Judging from specimens in collections, *E. constrictor* is the northern counterpart of *E. tristani*, and appears to be common in certain areas.

Erpetogomphus constrictor appears to be a lowland species of wet tropical forest habitats along the east coast of Mexico south through Costa Rica (Guanacaste Prov.: Miravalles, 26 April 1991 (C. Esquivel), 3♂, A. Ramirez, *in litt.*). Altitudes range from near sea level (70 m, San Luis Potosí, km 410) to about 550 m (Nuevo Leon, entrance to Horsetail Falls). Collection dates range from 26 April to 4 October. One specimen was collected in an ultraviolet light trap.

Distribution (fig. 198). – This species occurs along the eastern Mexican states of Nuevo Leon, Tamaulipas, San Luis Potosí, Veracruz, south through Guatemala, Honduras, and Nicaragua, to Guanacaste Prov., Costa Rica. It is apparently parapatric or allopatric with *E. tristani* in Costa Rica.

Material

Type data. – Lectotype ♂ by present designation with the following data in Ris' hand: '15098' in green ink in an unknown hand, *Erpetogomphus* / n. sp. ♂ / *constrictor* Ris 1917/ Misantla, Vera Cruz / Mexico VI 1914 / W. Gugelmann. Two paralectotype males

and one female with same data. One male is labelled '15092' in green ink, another male in poor condition (head partially fragmented, abdomen broken in several places) is labelled 'Type' probably by Ris. The left pair of wings is missing and probably served for figure 6 in the original description. The female is labelled '15096' in green ink. In SMF.

Other material (53♂, 15♀, including lectotype ♂ and paralectotypes). – MEXICO: Nuevo Leon: Cola Caballo, SW Monterrey, 6 July 1960 (W. B. Cutts), 1♀ (UMMZ); Rio Ramos, 3 km S of Allende, 500 m, 7 Sept. 1963 (T. W. Donnelly), 1♂ (RWG); south of Monterrey, Rio Elizondo, 19-20 June 1965 (O. S. Flint, Jr.), 6♂ (USNM, RWG); stream at entrance to Horsetail Falls, 550 m, 25 June 1965 (D. R. Paulson), 1♂ (DRP); Tamaulipas: Gomez Farias, Río Frio, 4 Oct. 1985 (F. Arias, L. Cervantes, M. Garcia), 'colectado en trampa U.V. en la noche', 1♂ (RWG); San Luis Potosí: El Salto, 4 June 1967 (O. S. Flint, Jr.), 1♀ (USNM); Palitla, N of Tamazunchale, 25 June 1965 (O. S. Flint, Jr.), 9♂ (USNM, RWG); Huichihuayan, rte 85, km 399, 7 Aug. 1966 (O. S. Flint, Jr.), 5♂ (USNM, CC, TWD); stream crossing Hwy 85 (1000'); 6 mi N of Tamazunchale, 4 Sept. 1957 (G. H. Beatty, III), 1♂ (FSCA); km 410, 'Sam Brown' Hacienda, 250 ft, 27 Sept. 1938 (L. J. Lipovsky), 1♂ (UMMZ); Route 85, km 399, Huehuetlán, 26 June 1965 (O. S. Flint, Jr.), 4♂, 1♀ (USNM); Rio Huichihuayan, Mpio de Huchuetlan, 100 m, 26 May 1987 (E. González-S, 2♂ (RWG); upstream Cascadas Micos just S of town N of Ciudad Valles off Hwy 85, 27 June 1990 (J. S. Daigle), 1♂ (RWG); GUATEMALA: Suchitepequez Dept., Cuyotenango, Finca San Rafael Olimpo, 1700 ft, 10-20 June 1966 (O. S. Flint, Jr., M. A. Ortiz-B.), 8♂ (USNM, RWG); HONDURAS: *Comayagua Dept.*, Rancho Chiquito, 11.8 mi SE Villa de San Antonio, 2-3 Aug. 1967 (O. S. Flint, Jr., M. A. Ortiz-B.), 3♂, 7♀ (USNM, CC, RWG); *Francisco Morazan Dept.*, 30 km E of Tegucigalpa, 13 June 1982 (Fernandez, Garcia), 1♀ (SWD); [no date], (Carlos Jaramillo), 1♀ (SWD); EL SALVADOR: *Ahuachapan Dept.*, Loma de Paya, Bosque El Impossible, San Francisco Menendez, 24 July 1987 (A. Campus), 1♂ (VH); 20 Aug. 1986 (V. Hellebuyck), 1♀ (VH) 4 Aug. 1987 (V. Hellebuyck), 1♀ (VH); NICARAGUA: *Chobales Dept.*, La Flor, rte 7, km 159, 4 mi W of Acoyapajit, 29 July 1967 (O. S. Flint, Jr., M. A. Ortiz- B.), 4♂ (USNM); *Managua Dept.*, stream along Pan American Hwy, 7 km S of Nandaime, 21 June 1962 (T. W. Donnelly), 1♂ (TWD).

Erpetogomphus sabaleticus Williamson
(figs. 2-thx, 48-hamules, 71-penis, 93-app, 172-vl, 198-distr)

Erpetogomphus sabaleticus Williamson, 1918: 1 (descr. holotype ♂, allotype ♀). – Williamson and Williamson 1930: 12 (summary of status); Paulson 1982: 255 (Panama, South America); Davies and Tobin 1985: 28 (cat.); Tsuda 1986: 87 (cat.); De Marmels 1990: 338 (Venez.); Bridges 1991: VII.184 (cat.); Tsuda 1991: 95 (cat.); Belle 1992: 32 (descr. larva); Donnelly 1992: 85 (Panama); Belle and Quintero 1992: 99 (key, Panama).

Description

A thorough comparative description of the holotype male and allotype female is given by Williamson (1918). I illustrate the thorax (fig. 2), caudal appendages (fig. 93) and details of the accessory genitalia (fig. 48) of the holotype, and the vulvar lamina of the allotype (fig. 172).

Male (n=6, including holotype). – Venational statistics. Fifth (rarely sixth) antenodal thickened; number of marginal cells behind fore wing paranal cells: 0/0; anx: fore wing 13-18/15-17, hind wing 10-12/9-12; pnx: fore wing 11-13/15-16, hind wing 11-14/11-13; cs under pterostigma: fore wing 5-6/6-7, hind wing 5-7/6-7; anal triangular cells 3-4/3-4. Hind wing 26-27 mm. Abdomen 30-33 mm.

Female (n = 4, including allotype). – Venational statistics . Fifth or sixth (rarely fourth) antenodal thickened; number of marginal cells behind fore wing paranal cells: 0-1/0-1; anx: fore wing 15-17/15-16, hind wing 11-12/9-12; pnx: fore wing 11-15/13, hind wing 10-12/11-13; cs under pterostigma: fore wing 6-7/6-7, hind wing 6-7/6-7. Hind wing 28-29 mm. Abdomen 31-32 mm.

Diagnosis

Erpetogomphus sabaleticus is diagnosed under *E. tristani.*

Remarks

Variation. – Venational details of holotype male: number of marginal cells behind fore wing paranal cells: 0/0; anx: fore wing 15/16, hind wing 11/11; pnx: fore wing 13/13, hind wing 12/11; cs under pterostigma: fore wing 6/6, hind wing 6/6; anal triangular cells: 3/3. Hind wing 26 mm.

Venational details of allotype female: number of marginal cells behind fore wing paranal cells: 1/0; anx: fore wing 16/15, hind wing 12/11; pnx: fore wing 12/13, hind wing 10/11; cs under pterostigma: fore wing 6/6, hind wing 6/7. Hind wing 29 mm.

The living colours of the holotype male were recorded by Williamson (1918).

Biology. – Williamson (1918) collected the allotype female and holotype male along the upper San Juan near Maraquita in Colombia. The male was taken along the Quebrada Sabaleticus as it rested on a flat leaf about five feet above the water. Only one other specimen of this species was seen (but not collected) during their stay in Colombia. A description of the type locality is given by Williamson (1918).

Michael May collected one male and three female larvae of the species at the Quebrada Juan Grande, along Pipeline Road in the Panama Canal Zone on 28 January 1975 and 23 January 1977. These were brought back to Gainesville, Florida, where the adults emerged about three months later.

This species, like *E. tristani*, is apparently rare. Other odonatists and I have collected along Pipeline Road in Panama, but have failed to find the species.

Distribution (fig. 198). – *Erpetogomphus sabaleticus* is the most austral of the genus and is currently known from one locality in northwestern Venezuela, one locality in northern Colombia, and Panama. It is apparently the only member of the genus found in the first two countries. Its northern limit is unknown, but it is probably parapatric with the more northerly *E. tristani*. Collection dates range from 3 February (Maraquita, Colombia) through 24 June (Panama Canal Zone).

Material

Type data. – Holotype male: COLOMBIA: Dept. Antioquia: Cristalina, 28 km on railroad above Puerto Berrio, 19 Feb. 1917 (J. H. and E. B. Williamson); allotype female: COLOMBIA: Dept. Tolima: Maraquita, 3 Feb. 1917 (J. H. and E. B. Williamson). Both specimens in UMMZ.

Other material (6♂, 4♀, including holotype ♂ and allotype ♀). – PANAMA: *Canal Zone*: Quebrada Juan Grande, Pipeline Road, 28 Jan. 1975 (M. L. May), 1♀ larva, emerged 19 June 1975 (FSCA); same data but 23 Jan. 1977 (FSCA), 1♂, 2♀ larvae, male emerged 16 May 1977, females emerged 20, 26 May 1977; Pipeline Road, 1.7-4.8 mi NW of Gamboa, 2nd bridge, 24 June 1970 (E. S. Morton), 1♂ (TWD); VENEZUELA: *Tachira Dept.*: Tachira, 11 April 1920 (J. H. and E. B. Williamson, W. H. Ditzler), 3♂ (2♂ in UMMZ, 1♂ in FSCA).

Erpetogomphus tristani Calvert

(figs. 3-thx, 49-hamules, 72-penis, 94-app, 120-ept, 146-vertex, 173,174-vl, 198-distr)

Erpetogomphus tristani Calvert, 1912a: 290 (descr. of ♂, ♀). – Calvert 1912b: 384 (mentions mating adaptations); Williamson 1918: 1 (comparison with *E. sabaleticus*); Ris 1917: 154 (Panama); Ris, 1918: 154 (Panama); Calvert 1920b: 339 (mentions mating adaptations); Williamson and Williamson 1930: 12 (summary of status); Paulson 1982: 256 (Costa Rica, Panama); Davies and Tobin 1985: 28 (cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.212 (cat.); Tsuda 1991: 95 (cat.); Belle and Quintero 1992: 100 (key, Panama).

Description

Male. – A thorough description of the holotype male and allotype female is given by Calvert (1912). I illustrate the caudal appendages of the holotype (fig. 94) and vulvar lamina of the allotype (fig. 173). In addition to Calvert's description, I add the following: A strong ventral tooth at base of cercus (plainly seen in lateral view, fig. 94), which in most specimens is partially hidden by lateroposterior margin of tergite 10; tips of epiprocts narrow in posterior view (fig. 120); anterior hamule black, divided at apical 0.25, lower branch a rounded shoulder; anterior (upper) branch well developed; posterior hamule pale, acutely triangular, with a prominent apical tooth; penis with well developed prepuce, which, when viewed laterally, is hidden by ventrolateral margin of segment 4; lateral lobe small, rudimentary, barely visible, and with spinulose margin; cornua rudimentary, forming an ental membranous plate with a quadrate margin (fig. 72). Abdomen 31-33 mm.

Venational statistics. – (n = 5, including holotype). Fifth antenodal thickened; number of marginal cells behind fore wing paranal cells: 0-1/0; anx: fore wing 13-15/14-15, hind wing 10-12/10-11; pnx: fore wing 11-13/11-13, hind wing 11-13/10-12; cs under pterostigma: fore wing 5-6/5-6, hind wing 5-6/5-6; anal triangular cells: 3/3. Hind wing 25-27 mm.

Female. – Vulvar lamina (fig. 174, allotype; 173) broadly connected, relatively unspecialized, and with a gently U-shaped notch; basal plate poorly developed; juncture of Y-shaped postlamellar ridge posterior to posterior margin of lamina; well defined arcuate depression on either side of central stem. Abdomen 31-33.5 mm.

Venational statistics. – (n = 4, including allotype). Fifth antenodal thickened; number of marginal cells behind fore wing paranal cells: 0-1/0; anx: fore wing 15-16/15-17, hind wing 11-12/10- 12; pnx: fore wing 12-14/11-12, hind wing 12-13/12-13; cs under pterostigma: fore wing 5-7/6-7, hind wing 6-7/5-6. Hind wing 29 mm.

Diagnosis

Erpetogomphus tristani, E. sabaleticus, and *E. constrictor* form a compact group which is easily separable from all other congeners by the unique shape of the epiprocts of the male (figs. 92-94, 120) and by the morphology of the vertex of the female (figs. 145-146). Males of *E. tristani* differ from the other two species only in the shape of the cerci. The ventral margin is distinctly convex at the apical 0.60-0.80 in *E. tristani* (fig. 94) and *E. sabaleticus* (fig. 93), not smoothly concave as in *E. constrictor* (fig. 92). All three species have a prominent dorsal tooth near the distal end, but the tooth in *E. constrictor* is broader in lateral view and more vertical than in *E. tristani* and *E. sabaleticus*.

Males of *E. tristani* and *E. sabaleticus* approach one another closely. Williamson (1918: 4-5) found males of both species inseparable except by the male caudal appendages. Williamson sent a pair of *E. sabalecticus* to Calvert, who also supported the statement of differences between the males of both species. Calvert was unable to separate the females of these two species. I have found the females of these three species (*E. constrictor, E. tristani* and *E. sabaleticus*) to be extremely similar, more so than their males. The sides

of the longitudinal trough of the vertex of *E. constrictor* are more parallel (fig. 145), than those of the other two species. Like Calvert and Williamson, I have not found any differences between females of the small series of *E. tristani* and *E. sabaleticus.*

Remarks

Variation. – Little variation is expressed among the small series (males, n = 5; females, n = 4, including holotype and allotype).

Venational details of holotype male: number of marginal cells behind fore wing paranal cells: 0/0; anx: fore wing 14/14, hind wing 11/11; pnx: fore wing 12/12, hind wing 13/12; cs under pterostigma: fore wing 5/5, hind wing 5/5. Hind wing 27 mm.

Venational details of allotype female: number of marginal cells behind fore wing paranal cells: 0/0; anx: fore wing 15/15, hind wing 11/11; pnx: fore wing 14/12, hind wing 13/12; cs under pterostigma: fore wing 7/7, hind wing 7/6. Hind wing 29 mm.

Biology. – The species is relatively rare in collections, despite intensive collecting in Costa Rica in recent years. Collection dates are February, June, and July. Nothing else is known of its biology.

Distribution. (fig. 198). – *Erpetogomphus tristani* is thus far known from only two northwestern provinces of Costa Rica and Panama (Lino, Chiriqui Prov. at about 1600 m, 8°48'N, 82°26'W, 1♂, 1 ♀, Ris 1917). It is replaced to the north by *E. constrictor* (fig. 198) and to the south by *E. sabaleticus. Erpetogomphus tristani* will probably be found in southern Nicaragua, but its southernmost distribution is unknown.

Material

Type data. – Holotype male with following label data (all handwritten by P. P. Calvert unless otherwise noted): 'Oricuajo,/ Costa Rica./ July, 1911/ J. F. Tristan', '*Erpetogomphus*/ *tristani*/ ♂/ Calvert/ TYPE.', 'Needham/ fig' [in Needham's hand?], red label: '9244 TYPE [printed] 944/ *Erpetogomphus*/ *tristani* ♂/ Calvert.', '2nd ham-/ ules/ sheath of/ penis.' Allotype female with same label as holotype except for following: 'Labium &/ Maxillae.', '*Erpetogomphus*/ *tristani* ♀/ Calvert'. Both specimens were originally pinned, but each has been placed in a clear envelope. Both specimens in ANSP.

Other material (5♂, 4♀, including holotype ♂ and allotype ♀). – COSTA RICA: *Guanacaste Prov.*: Nicoga, Feb. 1912 (J. F. Tristan), 1♂ (UMMZ); Quebrada Azul, 2.5 mi W of Tilaran, 24 July 1967 (O. S. Flint, Jr., and Ortiz B.), 1♂, 1♀ (USNM); Rio Santa Rosa, 3.7 mi E of Las Canas, 25 July 1967 (O. S. Flint, Jr., and Ortiz B.), 1♀ (USNM); *Puntarenas Prov.*: 8 mi WNW of Esparta, 26 June 1967 (O. S. Flint, Jr., and Ortiz B.), 1♂ (USNM); stream 8.1 mi WNW of Esparta, 26 June 1967 (O. S. Flint, Jr., and Ortiz B.), 1♂ (DRP); *San Jose Prov.*: Res. Biol. El Rodeo, 7 km W of Villa Colon, 9°54'N 84°16'W, 800 m, 10-13 July 1990 (T. W. Donnelly), 1♀ (TWD).

Erpetogomphus ophibolus Calvert
(figs. 4-thx, 29-abd, 50-hamules, 73-penis, 95-app, 121-ept, 147-vertex, 175-vl, 198-distr)

Erpetogomphus ophibolus Calvert, 1905: 163 (Mexico: Atoyac in Veracruz, H. H. Smith, 2♂). – Calvert 1909: 489 (distr., Mex.); Muttkowski 1910: 87 (cat.); Calvert 1912a: 294 (comparison with *E. tristani*); Ris, 1917: 155 (comparison with *E. constrictor*); Williamson and Williamson 1930: 489 (summary of status); Kimmins 1969: 296 (type in BMNH); Montgomery 1973: 239 (derivation of name); Paulson 1982: 255 (Mex.); Davies and Tobin 1985: 27 (cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.154 (cat.); Tsuda 1991: 95 (cat.).

Erpetogomphus (Erpetocyclops) ophibolus. – Carle 1992: 148 (key to subgenera, type species of *Erpetocyclops* subg. n.).

Description

Male. – Labium, labrum, mandibles, anteclypeus brown; postclypeus entirely brown, or with small lateral green triangular spot; frons green except for brown along frontoclypeal suture, and at base of antefrons; vertex dark brown; area anterior to median ocellus undifferentiated, postocellar tubercles well developed, connected medially by a low transverse ridge, slightly tuberculate medially; occiput planar, trapezoidal, hind margin linear or slightly concave medially, crest covered with long brown hairs; postocciput brown, transversely concave; rear of head brown.

Prothorax brown, anterior lobe green, posterior lobe green brown; synthorax (fig. 4) with prominent well defined dark stripes on green background as follows: middorsal stripe slightly narrowing dorsally, antealar sinus and area along this structure connecting to humeral stripe, antehumeral stripe of same width as humeral connecting ventrally and (but not always) dorsally, and in some specimens broadly so, antehumeral not or just touching antealar sinus; second and third lateral stripes connecting at upper 0.75, isolating round green spot below subalar carina; posterior margin of metepimeron, metasternum and venter of thorax grey brown; venter of profemora grey green, remainder of femora dark brown, becoming black distally; tibiae, tarsi, armature black. Wings hyaline, venation and pterostigma black.

Venational statistics. Fifth (rarely fourth or sixth) antenodal thickened; number of marginal cells behind fore wing paranal cells: 0/0; anx: fore wing 13-15/13-16, hind wing 10-12/10-12; pnx: fore wing 10-13/8-12, hind wing 9-12/9-12; cs under pterostigma: fore wing 4-7/5-8, hind wing 5-6/4-7; anal tri-

angular cells: 3/3. Hind wing 25-27 mm.

Abdomen (fig. 29) with segment 1 brown, green posterolaterally and with a green middorsal stripe; segment 2 brown except for green auricles, ventral margin, and narrow middorsal stripe; annulus dark brown; segment 3 primarily dark brown, becoming black distally with green middorsal stripe extending from annulus of segment 2 and narrowing posteriorly to end, a pale grey anterolateral spot becoming narrower along ventral margin and disappearing at 0.25 to 0.50 of segment length; segments 4-6 similar to segment 3 but with pale middorsal stripe ending at posterior 0.10 to 0.75 of segment and anterolateral pale spot ending at transverse carina; segment 7 grey green on anterior 0.50 to 0.60, except for dark transverse carina, posterior part of segment brown to black; segments 8-10 red brown, becoming darker dorsally and ventrally, especially along foliate margins; posterior medial margin of segment 9 bluntly pointed or slightly so. Abdomen 30-33 mm.

Cercus (fig. 95) ivory brown, becoming brown distally, arcuate with a prominent laterally compressed dorsal tubercle on distal 0.75, extreme base with a black ventral tooth (mostly hidden by posterior margin of abdominal segment 10), though not as prominent as in *E. constrictor*; a ventral carina on distal 0.30 of cercus, tip of cercus with a black tooth; epiprocts brown, gently curved at distal 0.50, tips slightly diverging, each forming a blunt point (fig. 121), a well defined anterodorsally projecting tooth at middle of medial margin of epiproct.

Accessory genitalia. Hamules (fig. 50) small; anterior hamule brown, divided at distal 0.30, posterior branch a well developed shoulder; posterior hamule roughly triangular, its tip with a spine; penis (fig. 73) with cornuae slightly bilobate or transverse at base; a well developed prepuce, lateral lobe a small tooth.

Female. – Head markings similar to male but with some green on mediolateral areas of labrum, brown at base of antefrons with a median extension connecting with frontoclypeal suture, thus dividing frontal green into two spots. Morphology of vertex and occiput similar to male with following differences: transverse postocellar ridge (fig. 147) complete, slightly arcuate medially, with a slight shallow notch laterally before resuming at postocellar tubercle; occiput a narrow planar semicircle, crest covered with long brown hairs; postocciput tumid, brown; rear of head brown.

Pro- and synthorax as in male, with dark markings in some specimens less extensive.

Venational statistics (n = 11). Fifth (rarely fourth or sixth) antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 0-1/0-2; anx: fore wing 14-16/14-17, hind wing 10-12/10-13; pnx: fore wing 10-13/9-13, hind wing 10-13/10-14; cs under pterostigma: fore wing 5-8/5-8, hind wing 5-7/4-7. Hind wing 26-29 mm.

Abdomen with segment 1 brown, a green spot posterolaterally and a complete green middorsal stripe; segment 2 brown with following areas green: wide middorsal stripe narrowing posteriorly, incomplete lateral stripe extending from just anterior to auricle to black posterior annulus, a thin pale margin at venter of segment; segment 3 similar to segment 2 but brown becoming darker; middorsal stripe narrowing posteriorly and forming a mere line on posterior 0.25 of segment; lateral pale stripe ending posteriorly at transverse carina; segments 4-6 similar to segment 3 but middorsal green becoming increasingly smaller on successive segments, so that only a small middorsal spot occupies basal 0.10-0.50 of segment 6; segment 7 with anterior 0.50 pale green white, interrupted by brown transverse carina, posterior 0.50 becoming red brown to almost black; segment 8-10 all red brown to dark brown, darker dorsoposteriorly; cerci pale grey green. Vulvar lamina (fig. 175) with plates broadly connected at basal 0.75; relatively unspecialized, cleft obtusely V- or U-shaped, about as wide as each lobe; postlamellar ridge with Y- juncture posterior to plates, base of stem well defined and with oval depression laterally. Abdomen 30-33 mm.

Diagnosis

Males of *E. ophibolus* are unique in possessing an anterodorsal spine on the mediodorsal surface of the epiproct (fig. 95). The cercus of this species is most similar to that of *E. constrictor* (fig. 92). Morphology of the vertex and occiput serve to distinguish female *E. ophibolus* from similarly marked species. The median ocellus is in line with the lateral ocelli (fig. 147), separating this species from *E. sabaleticus, E. tristani* (fig. 146), and *E. constrictor* (fig. 145). Female *E. ophibolus* more closely resemble females of *E. schausi, E. agkistrodon*, and *E. eutainia*. However, *E. schausi* and *E. agkistrodon* have a transverse postocellar ridge which is medially bilobed (figs. 148-149), while *E. eutainia* lacks any postocellar ridge and has postocellar tubercles only. The postocellar ridge in *E. ophibolus* is arcuate and entire medially (fig. 147). *Erpetogomphus ophibolus* and *E. eutainia* are often sympatric, and the females superficially resemble one another. The second and third thoracic stripes in *E. eutainia* are always separate (figs. 7-9), but are connected at their upper 0.30 in *E. ophibolus* (fig. 4). Finally, females of *E. eutainia* lack the basal stem of the postlamellar ridge (fig. 178) present in *E. ophibolus* (fig. 175).

Remarks

Variation. – Most specimens of *E. ophibolus* that I examined are from southern Veracruz, and they show little variability in maculation. The single male from Chiapas has slightly more extensive black thoracic

markings: the pale area between the dark humeral and antehumeral stripes is a narrow line. The two females from Belize have the apical dark brown on abdominal segment 7 laterally extending anteriorly separating the lateral pale area into one anterodorsal and one anteroventral spot. The acuminate condition of the posterior medial margin of abdominal segment 9 varies intraspecifically.

Biology. – This small green species often occurs with *E. eutainia* at small rivulets along the lowland Gulf of Mexico drainage systems of eastern Mexico. In 1976 I collected many by flushing them from agricultural stubble bordering trees and shrubs along the Rio Otapa in central Veracruz. Adults, when flushed, did not fly far and were consequently easy to collect. Six other gomphids collected at the same site under the same circumstances included *Phyllocycla breviphylla* Belle, *P. volsella* (Calvert), *Phyllogomphoides suasus* (Selys), *P. duodentatus* Donnelly, *Progomphus clendoni* Calvert, *Erpetogomphus eutainia*, and *E. bothrops*.

Raúl López (*in litt.*), from information given to him by Enrique González, writes that *E. ophibolus* is the most common gomphid in Veracruz, found yearround in the vicinity of the Los Tuxtlas Biological Station near Catemaco. Altitudinal range is from sea level to 615 m (Chiapas). Collection dates range from 8 June (Belize) to 13 September (Veracruz).

Distribution (fig. 198). – This species is thus far known from southern Veracruz (southeast of 19°N, 97°W), central Chiapas, Guatemala, and Belize. Tineke Boomsma (*in litt.*) collected a pair of this species in the Mountain Pine Ridge area of Belize (Cayo Distr.: Privassion Creek, 24 July 1993).

Material

Type data. Holotype male: [MEXICO] Vera Cruz, Atoyac, May (H. H. S[mith])/ Erpetogomphus ophibolus Calv. TYPE ♂. P. P. Calvert det. 1905. B. C. A. Neur., p. 164. Original of pl. 7, figs. 30-32, 46 (Kimmins 1969). In BMNH.

Other material (43♂, 12♀). – MEXICO: *Veracruz*: Rio Otapa, 8 km S of La Tinaja, 90 m, 13 Aug. 1976, (R. W. and J. A. Garrison), 18♂, 3♀, (RWG); 20 Aug. 1976, 12♂, 1♀ (RWG); Playa Escondida, 20-24 June 1981, (E. González), 1♀, (UNAM); Arroyo cerca de Playa Escondida, 17-24 July 1981, (E. González), 1♀, (UNAM); arroyo nr. Playa Escondida, about 30 km NE of Catemaco, 18°34-36'N, 95°04-09'W, 23 July-6 Aug., 9-13 Aug. 1982, (R. W. Garrison), 5♂, (RWG); Los Tuxtlas, arroyo despues de Laguna Escondida, 25 May 1980, (E. González), 1♂, (SWD); 11 June 1980, (R. Novelo), 1♂, (UNAM); Los Tuxtlas, stream nr. Jicacal Beach, 10 July 1979, (Gerado Jimenez), 1♀, (CC); Colonia Apachital, 16 km S, 10 km E of Tierra Blanca, 10 Sept. 1965, (T. W. Donnelly), 2♂, 1♀, (TWD, CC, UNAM); Rio Hondo, on rd. to 'Colonia la Apachital' 50 ft [15 m], 6 mi E of Hwy from Tierra Blanca to Cd. Aleman, 25-26 Aug. 1957, (G. H. Beatty III), 1♂, (FSCA); 3 km N of Santiago Tuxtla, 13 Sept. 1965, (T. W. Donnelly), 1♀, (CC); *Chiapas*: stream 20.1 mi N Ocozocoautla, 2000 ft [615 m], 25 Aug. 1967, (D. R. and M. L. Paulson), 1♂, (FSCA); BELIZE: *Toledo Distr.*: Blue Creek Village, EARTHWATCH Belize Expedition, 1981, 8 June 1981, (D. H. Messersmith, W.E. Steiner, *et al.*), 1♀, (USNM); *Cayo Distr.*: Mountain Pine Ridge, Rio Frio at Augustine, 16°58'N, 88°59'W, 500 m, 22-25 July 1983, (T. W. Donnelly), 1♀, (TWD); GUATEMALA: *El Progreso Dept.*: 6.5 km N of Est. de la Virgén, 29 Aug. 1965, (T. W. Donnelly), 1♂, 2♀, (TWD).

Erpetogomphus agkistrodon sp. n.
(figs. 5-thx, 30-abd, 148-vertex, 176-vl, 198-distr)

Type material. – Holotype ♀, MEXICO: Veracruz State, Parque Javier Clavijero, Jalapa, 23 Aug. 1982, 1300 m (R. López) in UNAM.

Description

Male. – Unknown.

Holotype female. – Labium pale grey, becoming dark grey medially; labrum, clypeus, base of mandible dark brown washed with dark olive green along median area of labrum, ante-clypeus, and above lateral lobes; pale green spot along lateral margin of labium; broad green stripe above frontoclypeal suture continuing to near base of vertex; antennae, vertex, occiput dark brown; transverse postocellar ridge (fig. 148) complete, emarginate medially; rear of occiput broadly semicircular; rear of head dark brown.

Prothorax entirely brown except for green anterior lobe; synthorax (fig. 5) with dark brown thoracic stripe well developed on green background; triangular middorsal stripe interrupting inverted green '7' at base, upper end of middorsal stripe connecting with antehumeral and humeral stripes, these two united leaving only pale spot below antealar sinus, and small green streak below; second lateral stripe connecting with humeral and third lateral stripes above and below, this stripe also connecting with third lateral below antealar sinus, thus isolating a green spot; metaspiracle black; posterior margin of metepisternum with a dark brown stripe; metasternum dark brown-grey. Femora red-brown, becoming black distally; remainder of legs and armature black.

Wings hyaline, venation and pterostigma black.

Venational details. Sixth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 3/2; anx: fore wing 15/17, hind wing 12/11; pnx: fore wing 14/16, hind wing 15/15; cs under pt: fore wing 6/5, hind wing 5/6. Hind wing 31 mm.

Abdomen (fig. 30) predominantly black with vestiges of a narrow green middorsal stripe on segments 2-6; anterior 0.25 of segment 7 green, becoming white laterally; broad brown midlateral stripe on segment 2 becoming darker on segment 3 and more extensive on succeeding segments, thus encircling small white anterolateral spots; auricle on segment 2 green; segments 8-10 entirely black, cercus white. Vulvar lamina as shown in fig. 176. Abdomen 31 mm.

Diagnosis

Erpetogomphus agkistrodon belongs to the *E. tristani* group because of the simple condition of the vulvar lamina and the complete postocellar ridge. This species is distinguished from females of all other species by the emarginate condition of the postocellar ridge. That of *E. ophibolus* is entire. The female of *E. agkistrodon* is similar to the only known female of *E. schausi*, and is diagnosed under the latter species.

Remarks

I suspect the male of *E. agkistrodon* will have a penis similar to that of *E. ophibolus* or *E. schausi*; it should have a prepuce and the lateral lobes should be small, semi-circular and with or without spinules.

The thickened sixth antenodal in this species is an unusual condition: the fifth antenodal is usually thickened throughout the genus. However, this may be an anomaly of the holotype.

No conspicuous depressions or pits are present anterior to the median ocellus. This area, instead, forms a shallow transverse V. Based on female morphology, I suspect the male epiprocts will be relatively thick, gently curved at posterior 0.5, forming a 90° angle, tip broadly spatulate.

Biology. – The female was collected along a shaded creek in company with *Cordulegaster diadema godmani* McLachlan. *Erpetogomphus boa* were also taken at the locale, though they were flushed from low vegetation about 50 m from the stream.

Distribution (fig. 198). – Known only from the type locality.

Erpetogomphus schausi Calvert

(figs. 6-thx, 31-abd, 51-hamules, 74-penis, 96-app, 142-face, 149-vertex, 177-vl, 198-distr)

Erpetogomphus schausi Calvert, 1919: 33 (desc. holotype ♂). – Calvert 1920a: 113 (note on type); Williamson and Williamson 1930: 13 (summary of status); Paulson 1982: 255 (Guat.); Davies and Tobin 1985: 28 (cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.187 (cat.); Tsuda 1991: 95 (cat.).

Description

Male. – A thorough description of the holotype male accompanies the original description. I illustrate the thorax (fig. 6), abdomen (fig. 31), accessory genitalia (fig. 51), penis (fig. 74), head (fig. 142), and caudal appendages (fig. 96) of the holotype. The specimen has been skewered with a bristle. The cercus of the holotype (fig. 96) is strongly curved at distal 0.30, the ventral margin has a remnant of an inferior carina at its extreme base, but is well developed again on the distal 0.50.

Venational statistics (based on holotype ♂ and one ♂ from Costa Rica): number of marginal cells behind fore wing paranal cells: 3/2-3; anx: fore wing 16-18/16-20, hind wing 12-14/12-13; pnx: fore wing 15/14-15, hind wing 13-14/13-15; cs under pterostigma: fore wing 5-6/5-6, hind wing 6/5-6; anal triangular cells: 4/4. Hind wing 29-30 mm. Abdomen 32-33 mm.

Female. – Labium grey; labrum brown with indication of green mediolaterally, ante- and postclypeus brown with possible green medially on postclypeus; frons green with brown along frontoclypeal suture and base of antefrons, especially medially, with offshoot almost touching frontoclypeal suture, thus almost separating green; base of antefrons with a slight longitudinal raised area with a slight concavity on each side; antennae, vertex brown; transverse postocellar ridge (fig. 149) complete, emarginate medially; occiput brown, semicircular crest covered with long brown hairs; postocciput brown, convex, rear of head brown.

Prothorax entirely brown, paler on anterior and posterior lobes; synthorax as in holotype male (fig. 6); femora grey brown, tibiae and tarsi darker, armature black.

Wings hyaline, venation and pterostigma black.

Venational statistics (n = 1). Fifth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 2/0; anx: fore wing 16/16, hind wing 12/11; pnx: fore wing 15/15, hind wing 14/14; cs under pterostigma: fore wing 6/5, hind wing 6/6. Hind wing 31 mm.

Abdomen compressed laterally with markings mostly unrecognizable, but probably similar to *E. agkistrodon* (fig. 30). Vulvar lamina simple (fig. 177), similar to that of *E. agkistrodon*. Abdomen about 32 mm.

Diagnosis

Erpetogomphus schausi is unique in possessing a combination of characters of the penis (with well developed prepuce) and caudal appendages (with gently decumbent cercus (fig. 96)). Although the morphology of its penis allies this species with *E. sabaleticus, E. tristani,* and *E. constrictor*, the penes of the other three species lack well developed cornuae and a spinulate lateral lobe, typical of *E. schausi*. The only known female differs from all other known species except *E.*

agkistrodon in possessing a complete transverse postocellar ridge which is notched medially. The only morphological difference that I have noted between these two species is the broader, more semicircular occiput (figs. 149) of *E. schausi*, compared with the narrower, more broadly semicircular condition found in the holotype of *E. agkistrodon* (fig. 148). The sixth antenodal crossvein is thickened in all four wings of *E. agkistrodon*, while the fifth is thickened in this female of *E. schausi*; but, as stated under *E. agkistrodon*, I suspect the condition in the holotype is atypical.

Remarks

Variation. – The male sex of this species is known from only two specimens, the holotype male described in detail by Calvert (1919), and another male from Costa Rica collected by J. Belle and loaned to me for inclusion in this paper. The Costa Rican male is slightly smaller (HW = 29 mm) than the holotype (HW = 30 mm) and differs as follows (condition for holotype in parentheses): small green triangle just lateral to medial area of anteclypeus (all dark brown); round green spot below antealar sinus of mesepisternum smaller (bigger); anterior pale abdominal spots extending well beyond transverse carina on segments 3-7 (these spots smaller and confined to anterior 0.25 of segments 4-6, to 0.5 of segment 7); sides of abdominal segments 8-10 light brown (dark brown); lateral lobe of penis more angulate (more rounded); second thickened antenodal in fore wing 5-5 (6-7) and in hind wing 5-6 (6-6).

The holotype appears to be a fully mature male: traces of pruinosity are present on the venter of its thorax. The Costa Rican male seems to be less mature: it lacks pruinosity, and the dark brown areas of the holotype are pale in this specimen. The green areas of the thorax of the Costa Rican male are slightly more restricted than for the holotype.

The teneral female described above seems to represent the female of this species. The combination of characters allying it with the *E. tristani* group and the occurrence of a male from Puntarenas Province, lead me to suspect that I have associated this specimen correctly.

Before the discovery of the two *E. schausi* from Costa Rica, I considered the possibility that *E. agkistrodon* might be the female of *E. schausi*: morphological considerations in light of the characters for other members of the *E. tristani* group (*e.g.*, vulvar lamina, shape of occiput) supported this view. However, the geographic distance (about 1700 km), coupled with the local occurrence of both forms, tend to discount this. It is possible that the morphological differences I detect in the occiput of female *E. agkistrodon* and *E. schausi*, though major, may be due to geographic variation, which would render *E. agkistrodon* a junior synonym of *E. schausi*.

Biology. – Nothing is recorded of the circumstances of capture of the holotype. Jean Belle records the following for the Costa Rican male: 'This gomphid was secured on the grass-covered bank of an almost impassable mountain rivulet where the insect alighted after a clash with a *Hetaerina* specimen. The colors when alive are as follows: compound eyes dark brown; head and thorax dark brown with light green; middorsal pale spots of abdominal segments 3 to 6 and pale spot of abdominal 7 yellow.'

Altitudinal data range from 1220 m to 1500 m; the female was collected 8-9 April, the Costa Rican male on 30 August.

Material

Type data. – Holotype male: GUATEMALA: Dept. Purulhá, Baja Vera Paz, 1220 m, forest stream (W. Schaus, J. Barns), 7 July [no date], in ANSP.

Other material (2♂, 1♀, including holotype ♂). – COSTA RICA: *Puntarenas Prov.*: Monte Verde, 1500 m, rivulet, 30 Aug. 1986 (J. Belle), 1♂ (RNHL); Rio Bellavista, *ca.* 1.5 km NW of Las Alturas (8.951 N, 82.846 W), elev. 1400 m, 8-9 April 1987 (Holzenthal, Hamilton, Heyn), 1♀ (USNM).

Distribution (fig. 198). – Known only from the type locality in Guatemala and Puntarenas Province, Costa Rica. It probably occurs in intervening Central American republics.

Erpetogomphus eutainia Calvert
(figs. 7, 8, 9-thx, 32, 33-abd, 52-hamules, 75-penis, 97-app, 122, 123, 124, 125-ept, 143, 144- face, 150-vertex, 178-vl, 199-distr)

Herpetogomphus menetriesii. – Selys, 1878: 429 (24 sep.) ('Guatemala. (Un mâle [*sic*, female] incomplet. Musée de Paris, une femelle. – Coll. Selys.')).

Erpetogomphus eutainia Calvert, 1905: 162 (1♂, Rio Papagayo in Guerrero, Mexico). – Calvert 1919: 35 (comparison with *E. schausi*); Kimmins 1969: 293 (type in BMNH); Paulson 1982: 255 (U.S., Mex., Guat.); Davies and Tobin 1985: 27 (cat.); Tsuda, 1986: 87 (cat.); Bridges 1991: VII.72 (cat.); Tsuda 1991: 95 (cat.).

Erpetogomphus diadophis Calvert, 1905: 167 (2♂, Texas). – Muttkowski 1910: 87 (cat.); Needham and Heywood 1929: 79 (descr.); Needham and Westfall 1955: 147 (descr.); Borror 1963: 104 (common name); Montgomery 1968: 133 (distr.); Kimmins 1969: 293 (type in BMNH); Paulson, 1982: 266 (synonymy of *E. diadophis* and *E. eutainia*); Bridges 1991: VII.60 (cat.).

Erpetogomphus ? diadophis. – Calvert 1919: 36 (Guat., possible conspecificity with *E. diadophis*)

Herpetogomphus diadophis. – Byers 1928: 5 (larva unknown).

Erpetogomphus (Calogomphus) eutainia. – Carle 1992 (key to subgenera, type species of *Calogomphus* subg. n.).

Description

Male. – Labium grey to dark grey, labrum all green with a small medial spot on anterior margin (fig. 144) to entirely brown with large central green spot (fig. 143), base of mandibles green, tips becoming black, anteclypeus all green to largely brown; postclypeus green with brown medially along frontoclypeal suture and descending laterally along lateral lobes, thereby isolating medial green spot; in more southerly specimens, brown expanding so that green confined to lateral margins; frons green with brown along frontoclypeal suture and at extreme base of antefrons; vertex brown with medial transverse area at postocellar tubercles green, to entirely brown; occiput brown, transverse triangular pits anterolateral to medial ocellus, postocellar tubercles low, incomplete medially; occiput trapezoidal, largely planar except for medial swelling; crest costate, linear to slightly concave, rimmed with long brown hairs; postocciput green medially to all brown, concave; rear of head brown.

Prothorax brown along middle lobe, remainder green or becoming entirely brown except for pale anterior lobe; synthorax (figs. 7-9) with prominent, well-defined dark brown stripes on green background as follows: middorsal stripe expanding toward collar, divided by pale middorsal thoracic carina, not touching collar, medial 0.5 or entire antealar crest, linear antehumeral, not touching upper margin; humeral, second and third lateral stripes, medial area of mesinfraepisternum; more southerly specimens with these stripes becoming thicker (figs. 8-9) so that antehumeral and humeral connect at lower and upper ends; a vestigial stripe along posterior margin of metepimeron; venter of thorax and metasternum pale grey green to grey. Coxae, trochanters pale green, venter of profemora green, remainder of profemora black; metafemora dark brown to black except for pale area ventrally; basal 0.40 to 0.60 of metafemora pale green to dark grey, becoming black apically; tibiae, tarsi and armature black.

Wings hyaline, venation and pterostigma black; more northerly specimens with pale, narrow line along costa disappearing proximal to pterostigma.

Venational statistics. Fifth, rarely fourth, antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 0-1/0-1; anx: fore wing 11-15/11-15, hind wing 8-11/8-10; pnx: fore wing 8-11/8-12, hind wing 8-11/8-11; cs under pterostigma: fore wing 4-6/4-6, hind wing 4-6/4-6; anal triangular cells: 3-4/3-4. Hind wing length 23-25 mm.

Abdomen (fig. 32) with segment 1 green and a pale brown dorsolateral stripe on each side; segment 2 brown except for green auricles, ventrolateral margin, and middorsal stripe; segment 3 with lateral brown stripe, interrupted medially just posterior to transverse carina, and with an irregular pale spot within anterior brown spot, posterior brown more prominent posteriorly and meeting dorsally on posterior 0.10 of segment; more southerly specimens with lateral brown not interrupted medially and with pale anterolateral spot reduced or almost absent; incomplete middorsal stripe blue green, pale areas becoming white laterally; segments 4-6 similar to segment 3 but with dark brown more prominent posteriorly and with anterolateral white spot confluent with ventral margin; segment 7 pale blue green on anterior 0.50-0.60, except orange brown transverse carina, posterior part of segment dark red brown; segments 8-10 red brown, becoming darker dorsally and ventrally, especially along foliate margins; posterior medial margin of segment 9 smoothly carinate, or with a moderately blunt point. Abdomen 29-32 mm.

Cercus (fig. 97) ivory, becoming brown distally, gently arcuate at distal 0.30, with a small black tooth, a ventral costate carina on basal 0.35-0.40 of cercus, often ending in a small, isolated, pebble-like tooth; in other specimens, the posterior part of this carina may be pebble- like; epiprocts (figs. 122-123) brown, moderately curved along posterior 0.50, tip of epiproct in lateral view thick, bluntly pointed, with lateral costate margin; tips in posterior view (figs. 124-125) planar, roundly divergent.

Accessory genitalia. Hamules (fig. 52) small, anterior hamule brown, distal 0.25 divided, the superior branch meeting the inferior branch, thus enclosing an oval space; posterior hamule small, digit-shaped, no apical hook; penis (fig. 75) with long pointed cornuae; dorsal membranous hood prominent, its ends parallel; lateral lobes large, frill-like, their margins with spinules; dorsal area of membranous third segment with a pair of mediolateral blunt chitinized tubercles.

Female. – Head as in male with following differences: brown at base of antefrons projecting anteriorly, partially isolating dorsal green; vertex morphology similar to male, postoccipital tubercles small, isolated medially, occiput trapezoidal as in male, planar with faintly convex arcuate crest; postocciput brown, planar.

Thorax as in male.

Venational statistics. Fifth, rarely sixth, antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 0-2/0-3; anx: fore wing 13-16/13-16, hind wing 9-11/8-11; pnx: fore wing 8-12/8-11, hind wing 8-12/8-13; cs under pterostigma: fore wing 4-7/4-7, hind wing 4-7/4-7. Hind wing 25-28 mm.

Abdomen (fig. 33) with segment 1 green with a brown dorsolateral stripe; segment 2 similar to segment 1, but with wash of brown along ventral margin of tergite; segment 3 with dorsolateral stripe darker, expanding posteriorly and connecting above at posterior 0.10 to 0.20 or separated by thin hairline of

green, ventral margin with brown interrupted by white below brown dorsolateral stripe; in more northerly specimens, connecting above with middorsal green stripe; posterior part of brown connecting with dorsolateral stripe posteriorly, transverse carina dark brown; segments 4-6 similar to segment 3 but brown darker, more definite, connecting posterodorsally on 0.25-0.50 on progressive segments, lateral white confined to spots, one at anteroventral margin, another ventromedially, these two spots sometimes connected by narrow line of white ventrally; more northerly specimens with medioventral white connecting with middorsal green stripe; segment 7 with anterior 0.50 white except for darkened transverse carina, posterior 0.50 dark brown; segments 8-10 dark brown; cerci white, their tips black. Vulvar lamina (fig. 178) with plates small, almost digit-shaped; U-shaped cleft about as wide as or wider than each plate; postlamellar ridge with a costate semicircular ridge. Abdomen 29-33 mm.

Diagnosis

The characteristically shaped posterior hamules (fig. 52) and penile structures (short prepuce, wide spinulate lateral lobe [fig. 75]) separate males of this species from all others except *E. leptophis*. *Erpetogomphus eutainia* possesses a straight or pebble-like ventral carina on the basal 0.25 of the cercus (fig. 97); no such carina is present in *E. leptophis* (figs. 98).

Females of *E. eutainia* and *E. leptophis* are unique in possessing a semicircular postlamellar ridge; in all other congeners, this structure is a Y-shaped ridge. The posteriorly pointed occipital protuberance in *E. leptophis* (fig. 151) is distinct from the relatively unmodified condition present in *E. eutainia* (fig. 150).

Remarks

Variation. – Venational details of holotype male of *E. eutainia*. No marginal cells behind fore wing paranal cells; anx: fore wing 14/14, hind wing 10/10; pnx: fore wing 10/9, hind wing 10/10; cs under pterostigma: fore wing 5/5, hind wing 5/6; number of anal triangular cells: 4/4. Hind wing 24.5 mm.

Venational details of holotype female of *E. diadophis*: number of marginal cells behind fore wing paranal cells: 0/1; anx: fore wing 13/14, hind wing 10/10; pnx: fore wing 10/9, hind wing 10/11; cs under pterostigma: fore wing 6/7, hind wing 6/5. Hind wing 28 mm.

This small species has a widespread distribution and, consequently, exhibits some degree of clinal variation north to south. Specimens from southeastern Texas and northern Mexico are the palest: the dark transverse markings of the face are narrower, and green is often present medially on the vertex and occiput. The labrum is mostly green (fig. 144), the dark thoracic stripes are narrow, and none is present on the posterior margin of the metepimeron (fig. 7). Medial bands of white encircle abdominal segments 3-6 in both sexes. The dark somatic markings are darker, broader, and more definite in specimens from southern Veracruz. Vestiges of a stripe on the posterior margin of the metepimeron can be seen (fig. 8), and the pale white medial abdominal bands are obscured, entirely or almost entirely interrupted by the dorsolateral brown stripe. Specimens from Costa Rica are the most melanic (figs. 9, 143); no green is present on the vertex or occiput, and the middorsal green stripe of abdominal segments 3-6 is always separate from the medioventral white.

The ventral carina of the cercus is also variable. Some specimens have a continuous costate carina with a small, isolated, pebble-like tooth distally; but others may have several antepenultimate pebble-like teeth in addition to the longer ultimate one. The tips of the epiproct may also be variable. In most specimens, these structures are posteriorly flattened (fig. 122) with the outer margin slightly to strongly concave (fig. 123). The male from El Progreso, Guatemala, has the epiprocts similar to the condition described above, but they are narrower (fig. 125).

The clinal differences described above probably led Calvert (1905) to interpret the female of *E. diadophis* as a separate species from *E. eutainia*. Calvert (1919) later received another female from Guatemala, which he postulated may be the same as the paratype of *E. diadophis*; he made no mention of *E. eutainia*.

The large series of males and females examined from various parts of its range convince me that Paulson (1982) was correct in synonymizing the two names. The status of the two females (not male and female) described by Selys (1878) as *Herpetogomphus menetriesii* is discussed under the status of *E. menetriesii*. I also examined a female labelled '*Cyanogomphus*? / *mexicanus*/ n. sp. / coll. R. Martin / ♀', from Honduras, in the MNHP.

Biology

I collected this small, colourful species in southeastern Texas over several years. They were flushed from stubble bordering agricultural fields next to the Gonzales River. They were sympatric with the larger *E. designatus*, and were about as common. However, the former species behaved more like a damselfly, for they never flew far, rested on tips of stubble or barbs of barbed-wire fences, and were always easy to take with a net. I collected one male which was the prey of a robber fly (Asilidae); another, I rescued from an orb-weaver spider web. I was able to photograph a pair in copula in the late afternoon.

In southern Veracruz at the Rio Otapa, *E. eutainia* had similar habits, as described under *E. ophibolus*.

The female from El Salvador (Rio Palio) has the following by V. Hellebuyck: 'on bushes along a fast running river, clear water, rocky bottom & shady banks'. Altitudinal ranges are from near sea level (20 m, Medina Bank, Belize) to 615 m (Oaxaca). Collection dates range from 19 May (Costa Rica) through October (Veracruz, La Gloria; Guerrero, Rio Papagaio).

Distribution (fig. 199). – This species occurs southeast of the Edwards Plateau in southern Texas, south along the lowlands and foothills of the Sierra Madre Oriental in northern and central Mexico. The farthest western locality is El Sabino in Michoacan state. Specimens have been collected sporadically in Belize, Guatemala, Honduras, El Salvador, and northern Costa Rica.

Material

Type data. – Holotype male of *E. eutainia* [labels all printed unless otherwise stated]: 'R. Papagayo, / Guerrero, 1200 ft. / Oct. H. H. Smith.', 'Brit. Mus. / 1911-339.', 'ERPETOGOMPHUS/ *eutainia* Calvert [written]/ P. P. Calvert, det. 1905 [written]/ B. C. A. Neur., p. 162 [written]/ Original of Pl. 7, f. 24-27, 39 [all written]', small round label with red border: 'Holo-/ type', in BMNH. Holotype female (not male, as erroneously stated by Kimmins, 1969) of *E. diadophis*: [labels all printed unless otherwise stated]: 'Texas [written by an unknown hand]', pale violet label: 'McLachlan Coll./ B. M. 1938-674.', 'ERPETOGOMPHUS ♀ [written]/ *diadophis* Calv. TYPE [written]/ P. P. Calvert, det. 1905 [written]/ B. C. A. Neur., p. 167 [written]/ original of Pl. VII, ff. 35, 47 [all written]', in BMNH.

Material examined (74♂, 42♀, including holotypes of *E. eutainia* and *E. diadophis*). – U. S. A.: TEXAS: *Caldwell Co.*: San Marcos R. at Luling, (FSCA, CC); *Gonzales Co.*: Guadalupe River, 4 mi S of Gonzales, (CC, RWG); near Otting, Palmetto State Park, (FSCA); Palmetto State Park, 6 mi S of Luling, (RWG); MEXICO: *Michoacan*: El Sabino, 20 mi SSE of Uruapan (UMMZ, RWG); *Oaxaca*: La Escondida, route 190, km 727, 2000', (USNM); *San Luis Potosí*: Tamazunchale, (USNM); *Tamaulipas*: 3 mi S of Ciudad Victoria, (USNM); *Veracruz*: Cardel, La Gloria, (USNM); pond 2.7 mi S of La Tinaja, 300 ft., (DRP); Rio La Palma, 25 km N of Catemaco, (RWG); Rio Otapa, 8 km S of La Tinaja, 90 m, (RWG); Sontecomapan, Coscoapan, (UNAM); BELIZE: *Toledo Dist.*: Medina Bank, 20 m, (TB); GUATEMALA: *El Progreso Dept.*: San Agustin Ac., (FSCA); *Zacapa Dept.*: Zacapa, (FSCA); unknown locality and date ('Rodig.' [illegible]) [labelled as *Herpetogomphus menetriesii*], (IRSN); unknown locality, date, and collector [labelled '*E. menetriesii*? Selys'], (MNHP); HONDURAS: Unknown locality, date, and collector [labelled '*Cyanogomphus*?/ *mexicanus*/ n. sp./ (Coll. R. Martin/ ♀'], (MNHP); EL SALVADOR: *La Libertad Dept.*: Rio Palio, San Juan Opico, 400 m, (VH); COSTA RICA: *Alajuela Prov.*: Quebrada Mina 0.2 mi S Hwy. 11 on Hwy, (FSCA); *Guanacaste Prov.*: Hda. Taboga, 100 ft., (DRP); Rio Santa Rosa, 3.5 mi N of Cañas, 300 ft (DRP).

Erpetogomphus leptophis **sp. n.**
(figs. 10-thx, 34, 35-abd, 53-hamules, 76-penis, 98-app, 151-vertex, 179-vl, 200-distr)

Type material. – Holotype male. BELIZE: Toledo District, I. Z. E. field station, Blue Creek, 25 June 1983 (M. L. May) (FSCA). Allotype female. BELIZE: Toledo District, Blue Creek Village (Earthwatch) Belize Expedition 1981, 8 June 1981 (D. H. Messersmith, W. H. Steiner, *et al.*) (USNM).

Description

Holotype male. – Labium light grey, becoming dark grey medially; labrum green with dark brown margin and medial line almost separating green into two spots; base of mandibles grey-green, anteclypeus green, postclypeus brown except for small green spots above lateral lobes; ventral margin of frons brown, joining brown of postclypeus, thus forming a large frontoclypeal stripe; remainder of frons green; a large transverse furrow at base of antefrons, this area with a pair of deeper pits, each anterolateral to median ocellus; postocellar ridge complete, but with medial part lower and at level of lateral ocelli; extreme base of frons, entire vertex, and occiput dark brown, occiput tumid medially, hind margin mostly straight but peaked medially so that hind margin seems slightly angularly convex; rear of head dark brown.

Prothorax entirely brown except for following green areas: anterior lobe, and two small midlateral spots (almost touching) on median lobe; synthorax (fig. 10) with dark brown thoracic stripes well developed on green background; dark middorsal stripe triangular, its wide base touching collar but not connecting with antehumeral; antehumeral and humeral connected along upper 0.25, thus isolating small green spot; second lateral as shown in fig. 10, a posterior branch connecting with third lateral along upper 0.30, isolating a green spot; posterior margin of metepimeron brown, all thoracic stripes connected by brown along antealar sinus; metasternum grey-brown. Venter of profemora grey-green, remainder of legs dark brown; tibiae, tarsi, armature black.

Wings hyaline, venation and pterostigma black.

Venational details. Fifth antenodal thickened in all wings; no supplementary marginal cells behind fore wing paranal cells; anx: fore wing 14/13, hind wing 10/10; pnx: fore wing 10/11, hind wing 10/10; cs under pterostigma: fore wing 6/5, hind wing 5/5; anal triangular cells: 4. Hind wing 29 mm.

Abdomen as in fig. 34. Segment 1 brown, green laterally and with a green middorsal spot; segment 2 brown except for green auricles, ventral margin, and narrow middorsal spot with a cordate expansion in the middle; segment 3 black with green middorsal stripe ending at basal 0.30 of segment and grey ante-

rolateral spot; segment 4 black with anterior 0.2 white laterally, becoming green dorsally; segments 5-6 like segment 4; segment 7 with anterior 0.5 white laterally, becoming green dorsally, posterior 0.5 of segment dark red-brown; segments 8-10 red-brown, posterior medial margins of segments 8-9 slightly pointed. Abdomen 31 mm.

Cercus (fig. 98) light green, simple, with no ventral carinae, slightly arcuate, tip black; epiprocts brown, gently curved at distal 0.5, tips viewed posteriorly with parallel sides, forming bluntly rounded tips.

Accessory genitalia. Hamules (fig. 53) small; anterior hamule brown, distal 0.25 divided, the superior branch meeting the inferior branch, thus enclosing an oval space; posterior hamule small, finger-like, no apical hook; penis (fig. 76) with long, pointed cornuae, dorsal membranous hood long, its ends crossing (fig. 76); lateral lobes large, frill-like, their margins with spinules.

Allotype female. – Head as in male except on labrum, brown medial line separating green into two spots; base of antefrons as in male (fig. 151) with a raised bilobed ridge between lateral ocelli; posterior margin of occiput with a prominent, posteriorly directed, pointed protuberance, its base tumid so that entire raised area assumes shape of a plumbob.

Thorax as in male.

Wings hyaline, similar to male.

Venational details. No supplementary marginal cells behind fore wing paranal cells; anx: fore wing 14/16, hind wing 9/11; pnx: fore wing 11/13, hind wing 10/11; cs under pterostigma: fore wing 5/4, hind wing 5/6. Hind wing 25 mm.

Abdomen (fig. 35) with segment 1 brown, becoming dark green-brown laterally; segment 2 brown with a narrow green middorsal stripe and green lateral stripe encircling auricle and extending entire length of segment; segment 3 like segment 2, but brown becoming darker and green lateral stripe abbreviated, forming an elongate spot along basal 0.5 of segment; segments 4-6 all black with white basal band, extending ventroposteriorly along ventral margin of tergites; segment 7 with anterior 0.30 white, remainder dark red-brown; segments 8-10 dark red-brown, cercus white. Vulvar lamina (fig. 179) with plates connected anteriorly, plates wider than in *E. eutainia*; postlamellar ridge semicircular as in *E. eutainia*. Abdomen 30 mm.

Diagnosis

The structure of the hamules and penis ally *E. leptophis* with *E. eutainia*, but the superior appendages easily distinguish the two species (figs. 97-98). *Erpetogomphus eutainia* has a pebble-like ventral carina on the basal 0.25 of the cercus; but no such structure is present in *E. leptophis*. The posteriorly directed pointed occipital protuberance easily identifies the female of *E. leptophis*. The female shares with *E. eutainia* the semicircular postlamellar ridge, but *E. leptophis* possesses a bilobed ridge between the lateral ocelli. This surface is planar in *E. eutainia*.

Remarks

Although the types were taken by different collectors two years apart, the female characters indicate it is the female of *E. leptophis*.

Biology. – Michael May collected the male along a creek in the forest.

Distribution (fig. 200). – Known only from the type locality.

Erpetogomphus elaphe sp. n.

(figs. 11-thx, 54-hamules, 77-penis, 99-app, 180-vl, 200-distr)

Erpetogomphus elaps. – Calvert 1907: 398 (Costa Rica, figures anterior hamules).

Erpetogomphus sp. n. near *elaps*. – Dunkle 1988: 46 (Honduras).

Description

Holotype male. – Labrum pale grey green; anteclypeus, labrum, base of mandibles pale green, tips of mandibles dark brown; postclypeus and frons pale green, a slight wash of brown on lateral margins of frontoclypeal suture, antefrons pale green, slightly darker at base, vertex dark brown; a deep transverse trough in front of median ocellus; pedicel, scape, and flagellum brown; occiput trapezoidal, pale green, mostly planar, slightly tumid medially, crest slightly prominent, slightly emarginate medially and covered with long brown hairs; postocciput green, transverse when viewed dorsoposteriorly; rear of head yellow brown.

Prothorax green, becoming brown on middle lobe laterally and anteromedially. Synthorax (fig. 11) apple green with following dark areas: poorly defined middorsal stripe not extending to collar and interrupted medially by middorsal thoracic carina and antealar crest, well defined antehumeral stripe narrowing dorsally but touching antealar crest and extending ventrally to mesinfraepisternum, a small posterior offshoot from antehumeral stripe at upper 0.10 connecting with vestigial first lateral stripe which is abbreviated to upper 0.50; venter of synthorax green, coxae and trochanters grey green, femora pale green becoming dark brown on distal extensor surfaces, these dark markings occupying distal 0.80 of profemora, about distal 0.60 of mesofemora, and distal 0.30 of metafemora; tibiae and tarsi black; armature black.

Wings hyaline, anterior margin of costa yellow to pterostigma, thereafter black; yellow at base of costa darkening to brown at costal triangle, pterostigma

brown, veins bordering it black.

Venational details. Fifth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 1/1; anx: fore wing 13/13, hind wing 10/10; pnx: fore wing 9/9, hind wing 9/10; cs under pt: fore wing 6/5, hind wing 4/6; anal triangular cells: 4/3. Hind wing 26 mm.

Abdomen with segment 1 yellow green with a wash of brown dorsolaterally; segment 2 yellow green dorsally and ventrally, with a brown midlateral stripe expanding ventrally behind auricle, anterior 0.5 of this stripe poorly defined, annulus dark brown; segment 3 light yellow green dorsally interrupted laterally by a longitudinal brown stripe well marked at transverse carina, expanding again at posterior 0.25 of segment and connecting dorsally at black annulus; inferior margin of tergite probably ivory (post mortem preservation has partially obscured this area); segments 4-6 similar to segment 3, with anterior 0.10 of dark midlateral interrupted and with gradual dorsolateral expansion of stripe so that inverted dorsal pale green wedge-shaped middorsal stripe disappears at distal 0.40 of segment 6; segment 7 pale green brown becoming tawny on posterior 0.10 of segment; segments 8-10 red brown becoming darker dorsolaterally on segment 8; foliate expansion and denticles black. Abdomen 33 mm.

Cercus (fig. 99) pale ocher becoming dark brown at tip; linear, gradually narrowing distally, tips roundly pointed, a weakly defined ventral carina on distal 0.50 of cercus; epiprocts brown, gently curved at 90° angle; tips spatulate when viewed posteriorly.

Accessory genitalia (fig. 54). Anterior hamule green basally, becoming dark brown distally, branched at distal 0.50; superior (upper) branch greatly enlarged, as long as stem of hamule with resulting interval between branches small, semicircular; posterior hamule (fig. 54) almost digit-shaped, wider at base, with a poorly developed anterior shoulder, tip broadly rounded, without an apical tooth; penis with a prominent knife-like serrated lateral lobe; membranous hood well developed but lobes not overlapping, cornua pointed but with median shoulder as in fig. 77.

Allotype female. – Similar to male in markings and colouration. Head with transverse trough anterior to median ocellus as in male, but occipital region differing as follows: occiput small, erect, barely visible in dorsal view, convex medially; postocciput with median tumid area. Thoracic, leg, and abdominal patterns as in male, but dark areas more restricted; middorsal and antehumeral stripes faint, first lateral stripe vestigial, confined to upper 0.20 of thorax.

Venational details. Fifth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 1/2; anx: fore wing 14/15, hind wing 10/10; pnx: fore wing 10/11, hind wing 11/12; cs under pterostigma: fore wing 6/5, hind wing 5/6. Hind wing 29 mm.

Vulvar lamina (fig. 180) with basal plate prominent, lobes narrow with medial margins distinctly concave, their bases not touching; distal part of lobe with a ventral flap bent under; its costate rim visible externally and disappearing medially near base of lobe (fig. 180); with resultant cleft forming a wide, U-shaped interval; Y-shaped juncture of postlamellar ridge not extending beyond posterior margin of plate, stem with diagonally ovaloid depression on each side. Abdomen 34 mm.

Diagnosis

Erpetogomphus elaphe males differ from males of the more northerly *E. elaps* by only two morphological characters (contrasting characters for *E. elaps* in parentheses): 1) The superior branch of the anterior hamule is robust and is as high as the basal 0.5 of the hamule so that the resulting gap between upper and lower branches is small (fig. 54), (superior branch less robust, thinner; resultant gap between hamular branches wider [figs. 55-56]), and 2) The tip of the posterior hamule is rounded, (tip of posterior hamule with a cephalad directed tooth). The posterior hamule of *E. elaphe* appears to be more digit-shaped and is reminiscent of those of *E. eutainia* and *E. leptophis*. The same structure appears more triangular in *E. elaps*. However, this last character is subtle and is best detected when specimens of both species are in hand: I do not consider it a good diagnostic character. I have found no significant differences in the penis or caudal appendages between the closely related and allopatric *E. elaphe* and *E. elaps*. I have been unable to find any differences between females of the two species.

Differences between *E. elaphe* and other similar species parallel those of *E. elaps* and are discussed under that species.

Remarks

Variation. – *Erpetogomphus elaphe* does not show as great variation in thoracic markings as does *E. elaps*. The holotype male is the most boldly marked of the series. All paratype males (n = 15), two of which are teneral, have an antehumeral stripe, although it is obscure in one male from Costa Rica. The humeral stripe in all but one of the paratypes is restricted to the upper 0.20 of the humeral suture, and the middorsal stripe is vestigial or absent.

Female paratypes of *E. elaphe* are similar in maculation to the allotype, although one female from Costa Rica has a poorly defined antehumeral stripe. The small humeral stripe is reduced to the upper 0.20 and barely visible.

Venational statistics for paratype males (n = 18); number of marginal cells behind fore wing paranal

cells: 0-2/0-3; anx: fore wing 12-15/12-15, hind wing 9-11/9-11; pnx: fore wing 8-11/9-11, hind wing 9-11/9-11; cs under pterostigma: fore wing 3-6/4-7, hind wing 4-6/4-7; anal triangular cells: 3-5. Hind wing 25-28 mm. Abdomen 30-34 mm.

Venational statistics for paratype females (n = 6); number of marginal cells behind fore wing paranal cells: 0-4/0-3; anx: fore wing 11-17/14-16, hind wing 10-12/10-12; pnx: fore wing 9-12/10-12; hind wing 9-12/9-13; cs under pterostigma: fore wing 4-6/4-5, hind wing 5-6/4-6. Hind wing 27-30 mm. Abdomen 33-34 mm.

Biology. – Little is known of the biology of this species, though its habits probably mirror those of *E. elaps*. The female from Cartago Province was collected in a 'marshy area by grassy hillside'. Altitudinal gradients for *E. elaphe* range from about 900 m (nr. Camotán, Guatemala) to about 1700 m (SE of Cartago, Costa Rica). Collection dates range from 2 June (Agua Caliente, Guatemala) to 5 August (San Jose, Costa Rica).

Distribution (fig. 200). – *Erpetogomphus elaphe* is known only from Guatemala, Honduras, and Costa Rica, but it probably exists in El Salvador and Nicaragua. Its distribution is allopatric (or possibly parapatric) with the form of *E. elaps* with thin anterior hamules.

Material

Type data. – Holotype male: GUATEMALA, Guatemala Dept., El Fiscal, 6 June 1909 (E. B. Williamson). Allotype female: same data, but 4 June 1909. Both in UMMZ.

Paratypes examined (18♂, 7♀): GUATEMALA: *Chiquimula Dept.*: Alda dos Quebradas nr. Camotán, 900 m (T. W. Donnelly) , 1♀ (TWD); *Guatemala Dept.*: Agua Caliente, 2 June 1909 (E. B. Williamson), 1♀; El Fiscal, 4 June 1909 (E. B. Williamson), 1♂, 1♀; 5 June 1909 (E. B. Williamson), 1♂; 6 June 1909, 2♂ (all UMMZ); Finca El Rosario, 36.5 km SE of Guatemala City, 15 June 1975 (J. E. Hafernik, Jr.), 2♂ (RWG); HONDURAS: *Francisco Morazan Dept.*: 30 km ESE Tegucigalpa, 29 June 1985 (Pinto and Ranch), 1♀ (SWD); 24 July 1983 (L. Cordoba), 1♂ (SWD); COSTA RICA: [no locality data], 1920 (Paul Serre), 3♂ (MNHP); *Cartago Prov.*, 5 mi SE Cartago, 5500 ft, 14 June 1963 (F. G. Thompson), 1♀ (DRP); *San José Prov.*: (all collected by H. Schmidt), San José, 18 June [no year stated], 1♂ (H. Kahl Coll'n, Acc. 12676); 24 June, 1♂; 4 July, 1♂; 5 July, 2♂; 17 July, 1♂, 1♀; 18 July, 1♀; 21 July, 1♂; 5 August, 1♂ (FSCA).

Erpetogomphus elaps Selys
(figs. 12, 13-thx, 55, 56-hamules, 78-penis, 100-app, 152-vertex, 181-vl, 200-distr)

Erpetogomphus elaps Selys, 1858: 330 (70 sep.) (♂ descr. 'Le Mexique, d'après un exemplaire unique du Museum de Paris, rapporté par M. Sal[l]e.'). – Selys 1859: 538 (12 sep.) (descr. ♂); Selys 1869: 175 (12 sep.) (descr. ♂, ♀); Selys 1873b: 519 (75 sep.) (list); Calvert 1905: 163 (localities in Mex.); Calvert 1907: 399 (comparison with *E. boa*); Calvert 1909: 481 (distr. in Mex.); Muttkowski 1910: 87 (cat.); Ris 1917: 153 (mentions Calvert's [1907] comments on comparison with *E. boa*); Williamson and Williamson 1930: 13 (summary of status); Montgomery 1973: 239 (derivation of name); Paulson 1982: 255 (Mex., Guat., Costa Rica); Davies and Tobin 1985: 27 (cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.68 (cat.); Tsuda 1991: 95 (cat.).

Gomphus elaps. – Hagen, 1861: 100 (descr. ♂)

Herpetogomphus elaps. – Hagen 1875a: 42 (cat.); Selys 1879: 64 (note on classification); Kirby 1890: 60 (cat.); Needham 1897: 182 (name mentioned); Calvert 1899: 386 (descr. ♂, comparison with *E. viperinus* auct.), 415 (gizzard); Higgins 1901: 128 (mentions Calvert, 1899).

Description

Male. – Labrum grey white with wash of brown around margin of median lobe; anteclypeus, labrum, base of mandibles pale grey green, tips of mandibles dark brown; postclypeus and frons light green, some specimens with brown at base; vertex dark brown; a deep transverse trough in front of median ocellus, a small tubercle behind each lateral ocellus; pedicel, scape and flagellum brown; occiput trapezoidal, light green, mostly planar; crest slightly prominent, straight, slightly notched medially, and covered with long brown hairs; postocciput green, transverse when viewed dorsoposteriorly; rear of head yellow brown, paler laterally.

Prothorax and median lobe red brown becoming pale apple green medially, especially on anterior and posterior lobes. Synthorax ranging from entirely apple green (fig. 13) with slight hint of dark antehumeral stripe to having following brown areas (fig. 12): poorly defined middorsal stripe divided by pale middorsal thoracic carina, well-defined antehumeral stripe just touching antealar crest dorsally and not touching mesinfraepisternum ventrally; a vestigial first lateral stripe confined to upper 0.30-0.40 of suture and sometimes with a small anterior offshoot touching antehumeral; venter of synthorax, coxae, trochanters, grey green; femora pale green, becoming dark brown on distal extensor surfaces; these dark markings occupying distal 0.80 of profemora, distal 0.50 of mesofemora, and distal 0.20 to 0.40 of metafemora; tibiae and tarsi dark brown to black; armature black.

Wings hyaline, anterior margin of costa yellow to pterostigma, thereafter black; yellow at base of costa darkening to brown costal triangle; pterostigma dark brown, veins bordering it black.

Venational statistics. Fifth antenodal (occasionally fourth or sixth) thickened in all wings; number of marginal cells behind fore wing paranal cells: 0-2/0-3;

anx: fore wing 11-15/12-15, hind wing 9-11/8-11; pnx: fore wing 8-11/8-11, hind wing 8-11/8-11; cs under pt: fore wing 4-6/4-7, hind wing 4-6/4-7; anal triangular cells: 3-5. Hind wing 24-29 mm.

Abdomen with segment 1 yellow green with a wash of brown dorsolaterally; segment 2 yellow green dorsally with a large midlateral brown spot dorsoposteriorly to auricle, or, in well- marked specimens, a distinct dark brown midlateral stripe expanding ventrally behind auricle, annulus dark brown; segment 3 broadly light yellow green dorsally interrupted laterally by a longitudinal brown stripe well-marked at transverse carina and flaring again at posterior 0.25 of segment to annulus; in palely marked specimens, brown midlateral stripe interrupted behind transverse carina; in well-marked specimens, midlateral stripe broad and meeting dorsally on posterior 0.10 of segment; inferior margin of tergite ivory, in heavily marked specimens limited to a triangular spot an anterior 0.10 of segment; segments 4-6 similar to segment 3, but some specimens with dark midlateral stripe more prominent and not interrupted behind transverse carina; in heavily marked specimens, midlateral stripe almost black and covering entire segment, except for basal pale annulus at basal 0.10 of segment and dorsal inverted pale green wedge- shaped middorsal stripe gradually narrowing posteriorly and disappearing at distal 0.20 of segment 4; these dorsal pale areas lacking on segment 5 and 6; segment 7 pale green, becoming tawny on posterior 0.10 of segment, or with posterior 0.20 dark brown, becoming black dorsally, transverse carina brown; segments 8-10 generally red brown becoming darker dorsally; in darkly marked specimens becoming almost black dorsally; foliate expansion and denticles black. Abdomen 29-38 mm.

Cercus (fig. 100) pale ocher to light brown, linear, gradually narrowing distally, the tips roundly pointed, a weakly defined ventral carina on distal 0.50 of cercus; epiprocts brown, gently curved at a 90° angle, tips when viewed posteriorly slightly spatulate, broadly rounded, or obliquely truncate.

Accessory genitalia (fig. 55). Anterior hamule dark brown to black, branched at distal 0.30, superior branch larger than inferior branch; superior branch moderately thickened in specimens from northern Mexico south to Chiapas, Mexico; specimens south of Chiapas (fig. 56) with superior arm of hamule more slender (see remarks); posterior hamule (figs. 55-56) pale, roughly triangular, with an anterior shoulder, tip with a tooth pointed cephalad; penis with prominent, knife-like serrated lateral lobe; membranous hood well developed but lobes not overlapping, cornua pointed but with median shoulder as shown in fig. 78.

Female. – Similar to male in markings and coloration; head with transverse trough anterior to median ocellus as in male, but occipital region differing as follows: occiput small, planar, encompassed posteriorly by arcuate (convex) crest (fig. 152); postocciput with median tumid area. Thoracic, leg, and abdominal patterns as in male, but dark areas more restricted, especially on femora and abdomen; cerci pale. Abdomen 30-36 mm.

Venational statistics. Fifth (rarely sixth) antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 0-3/0-3; anx: fore wing 12-16/13-16, hind wing 9-12/9-12; pnx: fore wing 8-11/9-12, hind wing 8-12/9-12; cs under pt: fore wing 5-6/5-7, hind wing 5-7/5-7. Hind wing 26-30 mm.

Vulvar lamina (fig. 181) with basal plate prominent, lobes narrow with medial margin distinctly concave, their bases not touching, with resultant cleft forming a wide, U-shaped interval; apical 0.30 of plate with mesal margin folded ventrally, beneath main plate, the costate rim sometimes visible along lateral margin of plate (fig. 181); Y-shaped juncture of postlamellar ridge not extending beyond posterior margin of plate, stem with diagonally ovaloid depression on each side.

Diagnosis

Erpetogomphus elaps and *E. elaphe* are closely related species which are diagnosed under *E. elaphe*. In males, the linear cercus of *E. elaps* (fig. 100) easily distinguishes it from the decumbent cercus (fig. 102) of *E. bothrops*. Body colouration is similar in *E. elaps* and *E. bothrops*, but all *E. bothrops* have well-marked antehumeral and humeral stripes (fig. 15). Many specimens of *E. elaps* have these markings poorly developed or nearly absent (fig. 13).

With the exception of *E. elaphe*, whose females appear indistinguishable, females of *E. elaps* are most similar to *E. bothrops*. The differences in the vulvar lamina as discussed by Calvert (1899) are an easy way to distinguish them. Secondly, the occiput of *E. elaps* is small and convexly arcuate (fig. 152); in *E. bothrops*, this structure is wider (fig. 154) and not nearly as arcuate.

Remarks

Variation. – The description is based on 49 males and 21 females. The holotype is in fair condition, although most of dorsum of the prothorax and part of the mesepisternum have been eaten away by dermestids. It has a completely pale thorax and the black midlateral stripes on abdominal segments 3-6 are interrupted only on the basal 0.10 of each segment. The hamules (fig. 55) and cerci (fig. 100) show that this specimen is the apple-green species ranging from northern Mexico south through Guerrero and into southern Veracruz.

Venational details of holotype male: number of marginal cells behind fore wing paranal cells: 0/0; anx: fore wing 12/12, hind wing 9/10; pnx: fore wing 9/8, hind wing 8/9; cs under pt: fore wing 4/4, hind wing 5/5; anal triangular cells: 3/4. Hind wing 24 mm. Abdomen 31 mm.

I consider *E. elaps* to be the most variable of any species in the genus. Calvert (1907) figured three forms of the anterior hamules of this species when he examined a male from San Jose, Costa Rica (= *E. elaphe*). His fig. 31 (Guerrero, Rincon) and fig. 32 (Morelos, Cuernavaca) correspond to the holotype of *E. elaps* (fig. 55), which is characterized by possessing a moderately thickened anterior branch whose tip almost overlaps the posterior branch when viewed laterally. Calvert's fig. 30 (Guerrero, Rincon) is typical of specimens I have seen from Chiapas, Mexico, and northern Guatemala (fig. 56). The anterior branch forms a slender hook which rarely overlaps the posterior branch when viewed posteriorly. Figures 33 and 34 of Calvert (1907) represent *E. elaphe* and are discussed under that species. Calvert (1907) stated that he was unable to find any other characters which varied correlatively, and I have found no other characters to separate *E. elaps* and the narrow hamular form. I have not found any intermediate conditions in the shape of the anterior hamule. Their distributions appear to be largely allopatric, although Calvert (1907) figures both forms from Rincon in Guerrero.

Interestingly, the distribution of the form with the thin anterior hamular branch lies between typical *E. elaps* and *E. elaphe*. Because I have been unable to find any other diagnostic characters, I am inclined to treat the Rincon male and others from Chiapas and northern Guatemala as a variant of *E. elaps*. The divergent morphology of southernmost *E. elaps* may represent character displacement between *E. elaps* and *E. elaphe*.

Both males and females show remarkable range in size and maculation patterns throughout its range. The smallest specimens examined are from Morelos (HW: males 23 mm, females 26 mm), the largest from the Rio Metlac region of Veracruz (HW: males 29 mm, females 31 mm).

Specimens collected at 1220 m in Sinaloa State are melanic, characterized by pale areas of abdominal segments 4-6 reduced to basal 0.10 laterally; pale areas on dorsum of segments 3-6 reduced laterally, this pale area a thin hairline on segment 5, a basal ring on segment 6.

I find no correlation of presence or absence of the dark thoracic stripe to locality. A series of specimens from Palapita, Nayarit, ranges from an entirely pale thorax to possessing antehumeral and humeral stripes. All specimens from Veracruz that I have examined lack dark thoracic stripes, but all southern variants with the thin anterior hamular branch from Chiapas and northern Guatemala possess them.

Biology. – This small species has habits similar to those described for *E. bothrops*. The following field notes accompany specimens collected by E. B. Williamson: Nov. 6 (Tepic): '♀ Gomphine – from brushy vegetation between road and river at rapids above mill'; Nov. 7: 'Gomphine ♂ – Have seen these only in bushes along bank of Rio de Tepic – usually not over foot above ground – resting or flying. One ♀ was ovipositing in rather still water below the rapids'; Nov. 14 (Jalisco: San Diego Rancho): 'Very hard to catch in net. Sits tight on rock and lets it [net] pass over and then flies. Easily approached and I finally began catching them by dropping the net over their rock & letting them rise into the bag.'; and Nov. 16 (Jalisco: San Diego Rancho): '[♂, ♀] caught in grass in banana patch early in AM, sluggish'.

López (*in litt.*) records it as one of the most common members of the genus in Mexico, having a wide tolerance for diverse stream habitats. I have seen no records of this species taken near sea level, unlike *E. bothrops*. Altitudinal records range from 670 m (Nayarit, Palapita) to about 1500 m (Cuernavaca), dates of capture from 9 June (Veracruz, Teocelo) to 23 November (Jalisco, San Diego Rancho).

Distribution (fig. 200). – Both this species and *E. bothrops* appear to be the most widespread members of this genus in Mexico. *Erpetogomphus elaps* occurs in mesic areas on either side of the Sierra Madre Oriental and Occidental. It has been collected as far north as Nuevo León in the east, and southern Sinaloa in the west, southward through Jalisco, Morelos, Guerrero, and Veracruz.

Material

Type data. – Holotype male with following data: small round white label with handwritten '2/44'; rectangular manila label with handwritten (in R. Martin's hand) 'Ophiog. elaps/ ♂ De Selys/ Mexique? a renvoyer.'; large green label with black border with handwritten 'E. elaps, Selys/ Mexique'; small white label with printed 'MUSEUM PARIS'; narrow red label with printed 'HOLOTYPE'; white printed label with '*E. elaps* HOLOTYPE/ Det. J. Belle, 1977/ No. 2, 1844. Insects [sic] de/ [reverse side] differents Ordres envoyes/ de Mexique par/ *Mr. Ghresbreght*!' and in lower right hand corner 'ne pas/ Sal[l]e!' In MNHP. The caudal appendages and accessory genitalia are shown in figs. 55, 78, 100.

Other material (49♂, 21♀). – MEXICO: *Chiapas*: Pacific slope, 800-1000 m), (USNM); stream 20.1 mi NE Tapanatepec, Oaxaca, 2700 ft., (FSCA); San Geronimo, Volcan Tacana, 450 m (UMMZ); Distrito Soconusco, Finca Juarez, (UMMZ); Guerrero: Chilpancingo, 4600', (FSCA, BMNH); Tepetlapa, 3000 ft., (BMNH); Jalisco: San Diego Rancho nr. Cocula,

(UMMZ); 15 mi on road to Tequila, (UMMZ); Michoacan: El Sabino, 20 mi SSE of Uruapan, (UMMZ); Morelos: Alpuyeca, S of Cuernavaca on Rt. 95, (FSCA); Cerro de Higuerón, Jojutla, (UNAM); Cuautla, (UMMZ); Cuernavaca, ca. 1200-1500 m, (UMMZ, USNM, RWG); 5 mi S of Cuernavaca, (UMMZ); 16 mi S of Cuernavaca, (UMMZ); Itzamatitlan, 5 km SW of Yautepec, (RWG); Nayarit: Acaponeta, (BMNH); Jumatán, (UNAM); Tepic, (UMMZ, USNM); Jalisco: Palapita, 670 m (UNAM); Nuevo León: Municipio de Monterrey, Cerro El Mirador, (FSCA); Sinaloa: stream 27.9 mi NE of Concordia, 4000 ft., (DRP, FSCA, CC, RWG); Veracruz: Barranca de Cayoapa, Teocelo, (UNAM); Jalapa, (USNM); 4.9 km N of Coscomatepec by Mex. Hwy 156 (RWG); Rio Metlac, 2 km WNW of Fortin, 900 m, (RWG); GUATEMALA: Suchitepequez Dept.: Finca Moca Grande, Rio Bravo, (FSCA).

Erpetogomphus liopeltis sp. n.
(figs. 14-thx, 36-abd, 57-hamules, 79-penis, 101-app, 117-cercus, 126-ept, 140, 141-occiput, 153-vertex, 182-vl, 201-distr, 227-wings)

Erpetogomphus elaps. – Novelo & Peña, 1991: 130 (misidentification).

Type material. – Holotype male: MEXICO: Nuevo Leon State, Municipio de Monterrey, La Estanzuela, 2 July 1987 (M. J. Westfall, Jr., H. Quiróz, A. Contreras). In FSCA. Allotype female: Nuevo Leon State, Monterrey, El Diente, 5 mi SE, 2 July 1960 (W.B. Cutts). In UMMZ.

Paratypes examined (15♂, 3♀, including holotype ♂ and allotype ♀). – MEXICO: *Hidalgo*: Pemuxtitla, Rio Zacuala, 1000 m, 22 April 1984 (R. Novelo), 1♂ (RWG); *Michoacán*: 12 km W Apatzingán, 369 m (1200 ft.), 4th Hoogstraal Mexican Biological Expedition, 12 Aug. 1941 (Harry Hoogstraal), 1♀ (UMMZ); *Nuevo Leon*: Chipingue, 12 July 1960 (W.B. Cutts), 1♀ (RWG); Municipio de Monterrey, Cerro El Mirador, 9 Aug. 1984 (A. Contreras), 2♂ (IORI); same data as holotype, 3♂ (FSCA); Municipio de Santiago, El Cercado, Arroyo Dolores, 17 Aug. 1984 (A. Contreras), 2♂ (IORI); Municipio de Santiago, Rancho Los Pinos, 3 July 1987 (M. J. Westfall, Jr., Jr., G. Luna, A. Contreras), 5♂ (FSCA, RWG); *San Luis Potosí*: La Conchita (Camino a Xilitla), 7 May 1950 (no collector), 1♂ (CC).

Description

Holotype male. – Entire head pale green, labrum dull grey green, base of mandible, anteclypeus dull green, tip of mandible black; basal 0.25 and all of vertex brown, a transverse trough at anterior margin of vertex at juncture of base with antefrons, this trough with two slightly deeper pits, one each anterolateral to median ocellus; occiput with slightly medial tumid area, occipital crest distinctly emarginate medially (figs. 140-141), dark brown, rimmed with long dark brown hairs; postocciput green, becoming black laterally, concave medially; rear of head brown, becoming yellow brown laterally; antennae dark brown.

Prothorax brown, anterior and posterior lobes and small dorsolateral area of median lobe pale green. Thorax (fig. 14) entirely green (probably blue green in life) with following dark brown: obscure middorsal stripe ending before collar, becoming darkest near middorsal thoracic carina, lateral margins of this stripe gradually fading to green on mesepisternum; posterolateral rim of antealar crest; lateral 0.40 of mesepisternum except for dorsal emargination, with no indication of pale green separating coalesced humeral and antehumeral stripes; this stripe narrowing slightly ventrally but connecting with lateral margin of collar and anterior 0.50 of mesinfraepisternum; rim below subalar carina at obsolete second lateral suture; narrow partial third lateral stripe extending ventrally to 0.50 of suture before merging with green. Metasternum pale grey brown, tawny anteriorly. Coxae, trochanters grey; base of femora brown, becoming black distally; tibiae and armature black.

Wings hyaline, anterior margin of costa dark brown at base, becoming yellow distally to proximal level of pterostigma, remainder of venation and pterostigma black.

Venational details. Fifth antenodal thickened in all wings; no supplementary marginal cells behind fore wing paranal cells; anx: fore wing 14/15, hind wing 10/10; pnx: fore wing 8/9, hind wing 9/9; cs under pterostigma: fore wing 7/6, hind wing 6/5; anal triangular cells: 4/3. Hind wing 31 mm.

Abdomen (fig. 36) with segment 1 green dorsally, paler laterally with a midlateral stripe of brown expanding anteriorly at base and darkening posteriorly at articulation point; segment 2 similar to segment 1 but with a ventral stem of brown behind auricle from dark midlateral stripe, midlateral brown becoming wider and darker along posterior 0.50 of segment, annulus black; segment 3 with pale green middorsal stripe acuminate and disappearing at posterior 0.10 of segment, black midlateral stripe expanding slightly at transverse carina and again widening at posterior 0.10 of segment, this area with a ventral offshoot terminating anteriorly at 0.20 of segment; segments 4-6 similar to segment 3, but with middorsal pale green stripe shorter and narrower on each succeeding segment, thus black midlateral stripe connecting dorsally at posterior 0.40 of segment 6, these midlateral stripes interrupted at anterior 0.10 of each segment with small longitudinal wedge-shaped white area along ventral margin of tergite behind transverse cari-

na; segment 7 with basal 0.60 pale grey green, except for irregular diffuse black spot at transverse carina, remainder of segment red brown, becoming black dorsally; segments 8-10 red brown, becoming darker dorsally; carinae and lateral foliations black, posterior medial margin of segment 9 pointed.

Cercus (fig. 101) pale ocher, decumbent at posterior 0.30, largely parallel in lateral view except for distal 0.20, tip with a shiny black tooth; black inferior carina on distal 0.25; epiproct brown, about 0.45 as long as cercus, U-shaped in lateral view, tip of epiproct when viewed posteriorly (fig. 126) broadly truncate. Abdomen 40 mm.

Accessory genitalia (fig. 57). Anterior hamule dark brown, branched at distal 0.30, superior branch larger than inferior branch; posterior hamule pale, roughly triangular with a well developed anterior shoulder, distal 0.75 curved posteromedially with a well developed black tooth twisted laterally from broad axis of hamule; penis with cornuae acuminate as shown in fig. 79, lateral lobe prominent, knife-like, serrated posteriorly.

Allotype female. – Similar to male with following differences: labrum slightly darker (possibly due to post mortem effects); transverse trough at juncture of antefrons and vertex well defined with slightly larger and deeper pit anterolateral to median ocellus; occiput strongly reduced to a small, gently convex, largely perpendicular medial arch; postocciput tumid medially, dark middorsal stripe vestigial, with only a wash of brown on either side of lower arms of antealar sinus, a narrow poorly defined incomplete green stripe separating dark brown antehumeral and humeral stripes up to dorsal 0.75. Abdominal segment 3 with acuminate black spot posterolateral to black dorsolateral stripe projecting anteriorly to black transverse carina; dorsolateral black stripes on segments 4-7 more extensive; pale middorsal stripe reduced to basal 0.75 (segments 4-5) to basal 0.50 (segment 7), and anteriorly touching annulus on each segment; segments 8-9 black dorsally, red brown laterally. Abdomen 38 mm.

Vulvar lamina (fig. 182) small, cleft larger than each plate, each plate connected basally, each with a raised shelf occupying anterior 0.5, postlamellar ridge with Y-shaped juncture posterior to hind margin of lamina, central stem with a well defined circular depression on either side.

Venational details. Fifth antenodal thickened in left fore wing; the sixth in remaining wings; Number of marginal cells behind fore wing paranal cells: 2/3; anx: fore wing 16/17, hind wing 13/11; pnx: fore wing 10/12, hind wing 12/11; cs under pterostigma: fore wing 6/7, hind wing 6/7. Hind wing 34 mm.

Diagnosis

This remarkable species approaches *E. viperinus* in size, colour, and maculation, but is most closely related to *E. bothrops* in morphology. Males of *E. liopeltis* and *E. bothrops* are similar in possessing epiprocts with broadly truncate tips (figs. 126-128); but those of *E. bothrops* are usually, but not always, bidentate (fig. 128). In lateral view, the epiprocts of *E. liopeltis* are more strongly curved and extend about 0.5 or less the length of the cercus; the same structures in *E. bothrops* extend 0.75 or more the length of the cercus (fig. 102). The apical tooth of the posterior hamule of *E. liopeltis* is longer and not as tightly recurved as in *E. bothrops* (figs. 57-58). Abdominal segments 1-3 in *E. liopeltis* (fig. 36) are more heavily marked than in *E. bothrops* (fig. 37); and the dark thoracic markings are also more extensive (fig. 14) than in *E. bothrops* (fig. 15).

In size and overall colouration, *E. liopeltis* seems indistinguishable from *E. viperinus*; but differences in the tips of the epiproct (figs. 126, 129) and structure of the area anterior to the vertex in both sexes (figs. 136 [as for *E. bothrops*], 137) easily distinguish the two species. Subtle differences between these two species exist in the morphology of the distal 0.5 of the cercus. In *E. liopeltis*, these structures are thicker and more cylindrical when viewed dorsally (fig. 101) and mediodorsally (fig. 117). The cercus of *E. viperinus* is more laterally compressed (fig. 119). The tip of the cercus in *E. liopeltis* terminates in a sharp black tooth; this tooth is lacking in *E. viperinus*.

Females of *E. liopeltis* and *E. bothrops* can be separated by overall size (*E. liopeltis* hind wing 32-34 mm; *E. bothrops* hind wing 28-31 mm) and thoracic maculation and colouration, as stated for males. Structural differences of the occiput and postocciput easily distinguish these species. The occiput of *E. liopeltis* is rudimentary, with only a gently rounded vertical medial crest. The medially tumid postocciput is easily visible in dorsal view (fig. 153). In *E. bothrops*, the occiput is narrow, but the anterior and posterior margins are roughly parallel except for the angulate lateral margins (fig. 154). In *E. bothrops*, the crest is vertical and the exposed postocciput is easily visible; but its posterior margin is planar or only slightly tumid. Receptacles for the tips of the male cerci differ slightly between the females. The transverse trough located anterior to the median ocellus narrows laterally in *E. bothrops* (fig. 136); but the lateral area of the greater U-shaped trough tends to curve lateroposteriorly around the anterior margin of the median ocellus in *E. liopeltis* (as in fig. 139).

Like males, females of *E. liopeltis* and *E. viperinus* can show striking similarities, but greater morphological differences manifest themselves in structures of the head and vulvar laminae. The trough anterior to the median ocellus of *E. liopeltis* is unlike the antero-

lateral pits of *E. viperinus* (fig. 137). The occiput of *E. viperinus* (fig. 155) is much broader, and the anterior margin of the occiput and curvilinear occipital crest are roughly parallel. The median postoccipital swelling of *E. liopeltis* is absent in *E. viperinus*. The vulvar laminae of the two species are similar, but the Y-shaped postlamellar ridge generally arises at or just before the posterolateral margins of the lamellar plates in *E. liopeltis*; the postlamellar ridge usually surpasses the vulvar lamina in *E. viperinus*. The median cleft between the vulvar lamellae is more obtuse in *E. viperinus* (fig. 184) than in *E. liopeltis* (fig. 182).

Erpetogomphus liopeltis and *E. viperinus* are allopatric and *E. viperinus* generally has more dense venation, despite wing lengths (*E. liopeltis* hind wing 29-31 mm [n = 13 males, 3 females], *E. viperinus* hind wing 29-31 mm [n = 20 males, 20 females]). The number of marginal cells behind fore wing paranal cells in male *E. liopeltis* ranges from 0-2 (only one wing has 3), compared with 1 (in 4 wings only) to 4 in *E. viperinus*.

Both sexes of *E. liopeltis* and *E. elaps* are easily diagnosed in the key by differences in body colouration, shape, and position of the posterior hamular tooth and shape of the cercus (males) and shape of the vulvar laminae (females). The occiput of females of *E. elaps*, *E. elaphe*, and *E. liopeltis* are similar in being reduced to a perpendicularly raised medial area (figs. 152-153) and a medial tumid area on the postocciput.

Remarks

Variation. – I found little variation among the 12 paratype males and 2 paratype females. The hind margin of the occiput (crest) is medially concave in the holotype (fig. 140), but ranges to almost linear (fig. 141) in other specimens. A poorly defined narrow green stripe is present between the coalesced dark antehumeral and humeral thoracic stripes in 7 males, but this condition varies from a short, narrow mark to one occupying the medial 0.50 of the lateral margin of the mesepisternum.

Wing variation among paratypes: Males: anx: fore wing 13-15/13-16, hind wing 9-12/10-12; pnx: fore wing 8-10/8-10, hind wing 9-13/9-12; cs under pterostigma: fore wing 5-7/4-6, hind wing 4-6/5-7; anal triangular cells: 3-4/3-4. Hind wing 29-31 mm. Abdomen 37-40 mm.

Females: Anx fore wing 16/14-15, hind wing 10/10; pnx fore wing 8-10/9-10, hind wing 11/9-11; cs under pterostigma fore wing 6-7/6, hind wing 6-7/7-8.

Other aspects of wing venation variability are characterized under the diagnosis for *E. liopeltis* and *E. viperinus*.

Some (n = 5) males have no marginal cells behind fore wing paranal cells, while two others (fig. 227) have one marginal cell in only one wing. All females have at least two such cells, except for the left fore wing of the Chipingue female. The fifth antenodal is almost always thickened; but the sixth is thickened in two males from La Estanzuela and in the right fore wing of the Apatzingan female.

One male from La Estanzuela has aberrant hind wing venation and was not included in the measured samples. Most specimens, including the holotype, had been preserved in acetone; and their resultant preservation leads me to believe that the pale colouration is similar to the blue green of *E. viperinus*.

Biology. – Novelo (pers. comm.) misidentified this species as *E. elaps* in Novelo and Peña (1991). They collected *E. liopeltis* in Hidalgo state from 22 April to 25 July (Rio Zacuala, Pemuxtitla) and 27 July (Calnali). They were taken as they perched on rocks along narrow, shaded, shallow, rocky streams. *Erpetogomphus liopeltis* was collected at Cerro El Mirador with *E. elaps*. Data for the female collected in Michoacan indicate that it was collected on 'side of stream'. Collection dates range from 22 April (Rio Zacuala) to 17 August (Arroyo Dolores).

Distribution (fig. 201). – *Erpetogomphus liopeltis* is only known from the states of Hidalgo, Michoacan, Nuevo Leon, and San Luis Potosi in northeastern Mexico.

Erpetogomphus bothrops sp. n.
(figs. 15-thx, 37-abd, 58-hamules, 80-penis, 102-app, 118-cercus, 127, 128-ept, 136-base of postfrons, 154-vertex, 183-vl, 201-distr, 228-wings)

Erpetogomphus viperinus. – Calvert 1899: 385 (described as *E. viperinus* Selys); Calvert 1905: 163 (described as *E. viperinus* Selys); Calvert 1909: 35 (misidentified as *E. viperinus*, compared with *E. schausi*); Muttkowski 1910: 87 (in part, cat.); Williamson & Williamson 1930: 11 (in part, refers to true *E. viperinus* but specimens in E. B. Williamson Coll. misidentified); Calvert 1947: 608 (status of Tepic specimens); Paulson 1982: 256 (in part, as *E. viperinus* from Mex., Guat.); Davies and Tobin 1985: 28 (in part, cat.); Tsuda, 1986: 87 (in part, cat.); Maes *et al.* 1988: 36 (as *E. viperinus* from Nicaragua); Tsuda 1991: 95 (in part, cat.).

Type material. – Holotype male: MEXICO: Veracruz: Rio Otapa, 8 km S of La Tinaja, elev. 90 m, 13 Aug. 1976 (R. W. Garrison). Allotype female: same data, but 20 Aug. 1976. In USNM.

Paratypes examined (61♂, 28♀). – MEXICO: *Guerrero*: Dos Arroyos, 1000 ft., Sept. 1888 (H. H. Smith), 1♀ (BMNH); *Jalisco*: San Diego Rancho near Cocula, 14 Nov. 1923 (J. H. Williamson), 1♂ (BMNH); *Michoacan*: El Sabino, 20 mi SSE of Uruapan, 27 July, 1 Aug. 1936 (H. Devlin Thomas), 8♂, 3♀ (UMMZ, FSCA); *Morelos*: Puente de Ixtla, 3

July 1900 (C.C. Deam), 1♀ (UMMZ); Cerro del Higuerón-Jojutla, July 1983 (C. Deloya), 1♂ (UNAM); *Nayarit*: Acaponeta, 1-2 Nov. 1923 (J. H. Williamson), 9♂, 1♀ (UMMZ); Tepic, 7 Nov. 1923 (J. H. Williamson), 1♂ (UMMZ); Jumatán, 10 Sept. 1980 (G. Jiménez), 2♂ (UNAM); *San Luis Potosí*, Cascadas Micos nr. aqueduct, 27 June 1990 (K. J. Tennessen), 1♂ (KJT); El Salto, 400 m, 6 Sept. 1963 (T. W. Donnelly), 1♂, 1♀ (TWD); Huichihuayan, km 410, S of Valles, 'Sam Brown' Hacienda, 25 Sept. 1938 (L. J. Lipovsky), 1♂, 2♀ (UMMZ); *Tamaulipas*: Rio Corona, 20 mi N of Ciudad Victoria, nr. Mex. Hwy 101, 1000 ft., 26 July 1968 (R. W. Garrison), 1♂, 2♀ (RWG); *Veracruz*: Atoyac, 400 m, (Schumann), 1♀ (BMNH); 16.5 mi S of Catemaco, by Hwy 180, 25 June 1985, (I. S. Askevold), 2♂ (CC); Cordoba 12-25 July 1964 (E. Fisher, D. Verity), 1♀ (LACM); Isla, 17 July 1969 (R. Wind), 1♂ (CC); K375-390 Cordoba Rd., 11 Aug. 1961 (R. and K. Dreisbach), 1♂ (USNM); 4.9 km N of Coscomatepec, by Mex. Hwy 156, 11 Aug. 1976 (R. W. and J. A. Garrison), 1♀ (RWG); Rio Otapa, 8 km S of La Tinaja, 90 m, 13, 20 Aug. 1976 (R. W. and J. A. Garrison), 10♂, 2♀ (RWG); Rio Hondo, on road to 'Colonia la Apachital' (50'), Soteapan, 500 m, July-Aug. 1990, (collector unknown), 6♂, 4♀ (PM, RWG); 6 mi E of Hwy from Tierra Blanca to Ciudad Aleman, 25-26 Aug. 1957 (G. H. Beatty, III), 1♂ (FSCA); Salto Eyipantla, 8 km S of San Andres Tuxtla and Mex. Hwy 180, 15 Aug. 1976 (R. W. and J. A. Garrison), 2♂ (RWG); Tierra Colorada, nr. Veracruz, 17 July 1932 (H. M. Smith), 1♀ (UMMZ); *Oaxaca*: Candelaria Loxicha, 500 m, 7 Sept. 1973, (E. C. Welling-M.), 1♂ (CC); 5 July 1974, (E. C. Welling-M.), 1♂ (SWD); *Chiapas*: river 26.1 mi NE Tapanatepec, 2100 ft., 2 Aug. 1965 (D. R. Paulson), 1♂ (DRP); stream 15.4 mi NE Arriaga on Mex. 195, 2300 ft., 24 July 1965 (D. R. Paulson), 2♂ (DRP); El Aguacero, nr. Ocozocoautla, 26 Oct. 1986 (E. Fisher), 1♂ (RWG); GUATEMALA: *Baja Vera Paz Dept.*: San Geronimo, 1879-80 (G. C. Champion), 1♂ (BMNH); *Chiquimula Dept.*: streams vic. Tierra Colorado, 800 m, 20 July 1962, (T. W. Donnelly), 1♂, 2♀ (TWD); small stream vic. Veguitas, 600 m, 10 July 1962 (T. W. Donnelly), 1♂, 1♀ (TWD); *Dept. Zacapa*: Gulan, 16-17 June 1909 (E. B. Williamson), 2♂ (UMMZ); La Union, 850 m, 31 Aug. 1972 (E. C. Welling M.), 1♀ (UMMZ); EL SALVADOR: *Anuachopan Dept.*: (all collected by V. Hellebuyck): Bosque El Imposible, San Francisco Mendez, 16 Aug. 1987, 3♂ (VH, RWG); May 1987, 1♂, 1♀ (VH); 12 July 1987, 2♂ (VH); 25 July 1987, 1♂, 1♀ (VH); 16 Aug. 1987, 1♂ (VH); 3 Sept. 1987, 3♂, 1♀ (1 pair in copula) (VH); El Coyolar, El Imposible, 2 Aug. 1987, 2♂ (VH); Valle de la Puerta, Bosque El Imposible, 3 Sept. 1987, 3♂ (VH).

Description

Holotype male. – Labium grey-white with wash of brown around margin of median lobe; entire face including vertex and occiput yellow green, a transverse trough in front of median ocellus, lateral ends slightly deeper than medial area; a small tubercle behind each ocellus; pedicel, scape, flagellum brown; occiput yellow green, mostly planar, slightly tumid medially, crest green, slightly prominent, straight, slightly notched medially and covered with long brown hairs; postocciput green, transverse when viewed dorsoposteriorly; rear of head yellow brown, paler laterally; lateral margins of labrum and base of mandible ocher; rear of head yellow brown.

Prothorax yellow green except for brown on anterior margin of median lobe and posterior area of anterior lobe. Synthorax (fig. 15) entirely yellow green except for following brown areas: slight vague stripe lateral to middorsal carina; antehumeral stripe; spot on upper end of humeral suture connected anteriorly to antehumeral, and gradually disappearing basally toward mesinfraepisternum; line bordering antealar crest; metasternum pale yellow green. Coxae, femora pale yellow green, becoming dark brown dorsodistally; tibiae, tarsi and armature black.

Wings hyaline, anterior margin of costa yellow, remainder of venation black, pterostigma brown.

Venational details. Fifth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 1/3; anx: fore wing 15/15, hind wing 11/11; pnx: fore wing 11/13, hind wing 13/13; cs under pterostigma: fore wing 6/6; hind wing 7/6; anal triangular cells: 4. Hind wing 27 mm.

Abdomen (fig. 37) with segment 1 yellow green with a wash of brown dorsally; segment 2 yellow green with diffuse brown spot posterodorsally to auricle; segment 3 broadly light green dorsally, interrupted laterally by a longitudinal brown stripe flaring at transverse carina, inferior margin of tergite ivory; segments 4-6 similar to segment 3, but lateral brown stripes progressively more extensive and each meeting its neighbor dorsally at posterior end of segment; segment 7 with anterior 0.66 pale green white except for black transverse carina, posterior 0.30 of segment red brown; segments 8-10 red brown, darker dorsally, carinae and lateral foliations black; posterior medial margin of 9 pointed. Abdomen 35 mm.

Cercus (fig. 102) pale ocher, gently decumbent at posterior 0.30, gradually narrowing toward end, tip with a shiny black tooth; epiproct brown, gently curved as is characteristic for the genus, tip of epiproct when viewed posteriorly (fig. 128) bidentate.

Accessory genitalia. Anterior hamule dark brown, branched at distal 0.30, superior branch larger than inferior branch; posterior hamule (fig. 58) pale, roughly triangular with an anterior shoulder, tip with

a black tooth twisted laterally from broad axis of hamule; penis with cornuae pointed but each with median shoulder as shown in fig. 80; lateral lobe prominent, knife- like, serrated posteriorly.

Allotype female. – Similar to male with following differences: synthorax with definite dark triangular middorsal stripe, its base not touching collar; broad, diffuse brown dorsolateral stripe on abdominal segment 2, brown lateral stripes on segments 3-6 with their anterior ends ending at basal 0.20 of each segment so that lateral white connects with dorsal yellow-white middorsal stripe; cercus pale.

Vulvar lamina (figs. 183) small, cleft about as large as each plate; each plate connected basally, each with a raised shelf occupying anterior 0.5; postlamellar ridge with Y-shaped juncture posterior to hind margin of lamina; central stem with a well defined circular or oval depression on each side. Abdomen 32 mm.

Venational details. Fifth antenodal thickened in all wings; no marginal cells behind fore wing paranal cells; anx: fore wing 12/13, hind wing 9/9; pnx: fore wing 8/9, hind wing 10/10; cs under pterostigma: fore wing 4/5, hind wing 5/5. Hind wing 27 mm.

Diagnosis

Selys' (1868) description of *Erpetogomphus viperinus* was too brief and inexact for Calvert (1899) to detect a specific difference between his specimens of *E. viperinus* (= *E. bothrops*) and the true *E. viperinus*. Examination of the lectotype male and female of *E. viperinus* shows that the *Erpetogomphus viperinus* of Calvert and all subsequent authors is referable to the new species *E. bothrops*.

E. bothrops is most similar to *E. liopeltis* and is diagnosed under that species. *Erpetogomphus bothrops* also resembles *E. viperinus*, but in life, the pale colouration of *E. bothrops* is yellow green (deep green in *E. viperinus*). *Erpetogomphus viperinus* is generally larger (hind wing male 29-31 mm) and darker. In males, the cercus of *E. bothrops* is pale with a distinct black tooth; while in *E. viperinus* this structure is dark red brown with no apical tooth. In *E. bothrops*, the distal 0.5 of the cercus gradually narrows, so the distal 0.5 of the cercus in lateral view is not as thick or robust as the base (fig. 102). In *E. viperinus*, the distal 0.5 of the appendage is robust and is as thick as its base (fig. 103). In dorsoposterior view, the posterior 0.30 of the cercus of *E. bothrops* gradually narrows (fig. 118), and is not as laterally compressed as in *E. viperinus* (fig. 119). The inferior distal margin of the cercus of *E. viperinus* is strongly carinate, not so in *E. bothrops*. The tip of each epiproct of *E. bothrops* in posterior view is bidentate (fig. 128) or truncate (fig. 127), not bluntly pointed as in *E. viperinus* (fig. 129). Other characters are given in the key.

Females of these species are easily distinguished by overall body colouration in life, and thoracic maculation. Two structural characters separate *E. bothrops* from *E. viperinus*: the anterior margin of the vertex of *E. viperinus* contains two well defined pits, each dorsolateral to the median ocellus. Each pit is the receptacle for the bluntly pointed tip of the male epiproct when in copulation. In *E. bothrops*, these pits are replaced by a continuous groove deepest medially, which accommodates the explanate tips of the male epiprocts. Secondly, the V-shaped notch of the vulvar lamina in *E. bothrops* is more acute (fig. 183) than the more widely divergent notch of *E. viperinus* (fig. 184). The shape of the vulvar lamina of *E. bothrops* (fig. 183) distinguishes it from similarly marked females of *E. sipedon* (figs. 187, 188) and *E. elaps* (fig. 181).

Remarks

Variation. – Venational variation among the paratype series of males (fig. 228): number of marginal cells behind fore wing paranal cells: 0-3; anx: fore wing 14-16/13-16, hind wing 9-12/10-12; pnx: fore wing 9-11/8-13, hind wing 10-13/10-13; cs under pterostigma: fore wing 5-7/5-7, hind wing 5-7/5-7; number anal triangular cells: 3-4. Hind wing 21-28 mm.

Variation exists in the direction of the apical tooth of the posterior hamule. It is present in all males and, in most, is twisted so that its tip is directed laterally (*i.e.*, distally) to the direction of the planar surface of the hamule. In a few males, the tooth, though rotated, points in a more lateroanterior direction.

The tip of the epiproct, when viewed posteriorly, is planar and bidentate (*e.g.*, fig. 128); but in some, the distal and mesal teeth are reduced. In rare cases, the tip is almost straight (fig. 127); variations link these extremes. I have found no correlation of the posterior hamular condition with the epiproct condition; nor do these conditions seem to vary according to altitude or locality. For example, of 5 males from Nayarit, Jamatan, only one has hamular teeth pointing predominantly cephalad. This same specimen has a bidentate condition of tips of the epiprocts. Another male has a bidentate condition, another has an intermediate condition, and two others have truncate tips. Of another series of 9 males (including holotype) from the Veracruz, Rio Otapa, two have the hamular tooth pointing predominantly cephalad. These two specimens have bidentate epiprocts, although the right epiproct of one male is intermediate. The remaining 7 males have bidentate epiprocts, but one has an intermediate condition of its right epiproct.

The membranous hood of the penis is variable among and within populations. Most specimens, including the holotype, possess a short hood, exposing a subcutaneous membrane (fig. 80); but a male from

San Luis Potosi, Cascadas Micos, has a long, acute, non-overlapping hood. Another two males, one from Guatemala (Dept. Chiquimula, small stream, vic. Veguitas), and all specimens I examined from El Salvador (Dept. Anuachopan, Bosque El Imposible, San Francisco Mendez), have long, overlapping hood membranes similar to that illustrated for the holotype male of *E. leptophis* (fig. 76). With the exception of the San Luis Potosí male, specimens with long, acuminate hoods seem to typify most southerly specimens. I can find no other characters differentiating these specimens from others.

Venational variation among the paratype series of females (n = 18): number of marginal cells behind fore wing paranal cells: 1-3; anx: fore wing 12-16/12-16, hind wing 9-11/8-11; pnx fore wing 8-12/9-12, hind wing 9-13/9-13; cs under pterostigma: fore wing 4-7/5-7, hind wing 5-8/5-7. Hind wing 27-31 mm.

Biology. – I have often seen this species along margins of cut agricultural fields bordering streams and canals. Its apple green colouration renders it difficult to detect among vegetation, but when disturbed, it does not fly far. The type locality is a wide, shallow stream bordered by trees in extensively cultivated farmland. I collected *E. bothrops* next to cut fields along with six other gomphids: *Erpetogomphus eutainia*, *E. ophibolus*, *Phyllocycla breviphylla* Belle, *P. volsella* (Calvert), *Phyllogomphoides duodentatus* Donnelly, and *Progomphus clendoni* Calvert. Twenty-five other species of Odonata were collected there.

R. Novelo (pers. comm.) observed a pair in copula in Morelos state (Cerro del Higuerón) at 1250 m at 18.20 hr on 14 Sept. 1988.

Williamson records the following on two Acaponeta males: 'Eas[il]y caught while sitting in brushy weed patch on bank of river, sun behind cloud,' and 'Quite common flying over water just above the real rapids and lighting on willow-like stems and twigs along the bank. Saw no ♀ gomphine today.' López (*in litt.*) writes that they perch along sides of streams or on exposed rocks in the middle of streams. He states that they do not remain long at a spot, moving constantly along the length of the stream.

Elevation gradients range from near sea level (50 m, Veracruz, Agua Caliente) to 1250 m (Morelos, Cerro del Higuerón). Collection dates range from May (El Salvador) to November (Mexico, Jalisco).

Distribution (fig. 201). – This species and *E. elaps* are the most widely distributed species in Mexico and Guatemala. *Erpetogomphus bothrops* ranges from Tamaulipas in eastern Mexico (24°N) south to El Salvador (14°N). It also occurs in mesic areas in western Mexico from Nayarit (22°N) south. Its distribution indicates an avoidance of the xeric areas in northwestern Mexico and the high mountain plateau in northern Mexico.

Erpetogomphus viperinus Selys

(figs. 16-thx, 38-abd, 59-hamules, 81-penis, 103-app, 119-cercus, 129-pet, 137-base of postfrons, 155-vertex, 166-postocciput, 184-vl, 201-distr, 229-wings)

Erpetogomphus viperinus Selys, 1868: 68 (3 sep.) (descr. of ♂, ♀, 'D'Orizaba'). – Selys 1869: 176 (13 sep.) (redescription of ♂ and ♀ from Orizaba); Selys 1873b: 519 (75 sep.) (list); Muttkowski 1910: 87 (in part, cat.); Williamson & Williamson 1930: 14 (summary of status); Paulson 1982: 256 (Mex.); Davies and Tobin 1985: 28 (cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.220 (cat.); Tsuda 1991: 95 (cat.).

Herpetogomphus viperinus. – Hagen 1875a: 42 (cat.); Selys 1879: 64 (2 sep.) (status of classification); Kirby 1890: 60 (cat.).

Description

Male. – Entire head pale green (blue green in life), slightly darker on anterior of ante- and postclypeus and labrum, lateral margins of labrum ocher, base of mandible and labium dull grey green; basal 0.25 of postfrons and all of vertex brown, a pair of pits at anterior margin of vertex at juncture of base of antefrons (fig. 137), one each anterolateral to median ocellus; antennae dark brown; occiput with well developed medial tumid area, green, occipital crest slightly emarginate medially, dark brown to black, rimmed with long dark brown hairs; postocciput brown, green medially, transverse, with a slight vertical depression medially; rear of head yellow brown.

Prothorax brown, anterior and posterior lobes green. Synthorax (fig. 16) entirely green (blue green in life) with following dark brown: obscure middorsal stripe ending before collar, becoming darkest at base of antealar crest and extending as narrow wash of brown below rim of antealar crest and joining wide stripe along lateral 0.30 of mesepisternum; this stripe coalescing with normal humeral stripe; often with a narrow isolated stripe of green separating these two stripes; combination antehumeral and humeral stripe reaching collar; all of mesinfraepisternum and ventral part of thorax; rim below subalar carina, often with small extension on obsolete second lateral suture, which in some specimens may form an indistinct second lateral stripe; narrow but well defined third lateral stripe. Metasternum pale grey green. Coxae, trochanters grey, becoming brown exteriorly; base of femora brown, becoming black distally; tibiae and armature black.

Wings (fig. 229) hyaline, anterior margin of costa dark brown at base, becoming yellow distally to proximal level of pterostigma, remainder of venation and pterostigma black.

Venational statistics. Fifth (occasionally sixth) antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 1-4/1-4; anx: fore

wing 13-18/13-18, hind wing 9-12/10-13; pnx: fore wing 8-13/10-12, hind wing 10-14/10-13; cs under pterostigma: fore wing 5-7/4-7, hind wing 5-7/5-7; anal triangular cells: 4 (rarely 5). Hind wing 29-31 mm.

Abdomen (fig. 38) with segment 1 green with brown dorsolaterally except for green on posterior dorsal 0.50 of segment; segment 2 with middorsal green stripe; brown dorsolaterally surrounding green auricle; ventrolateral area pale green, annulus black; segments 3-6 primarily black with following pale areas: basal 0.10 of each segment, dorsally forming an incomplete blue green middorsal stripe extending to posterior 0.20 of each segment; ventrolateral wedge shaped white spot at middle of each segment, connecting in some specimens to basal pale ring; segment 7 with dorsal 0.50 light green, posterior 0.50 red brown, black along transverse carina; segments 8-10 predominantly red brown, darker dorsally, denticulated posterior margin of these segments black; posterior margin of segment 9 often forming a posteriorly directed point. Abdomen 36-40 mm.

Cercus (fig. 103) pale ocher, slightly darker ventrally, robust and strongly curved at posterior 0.30, inner margin of posterior 0.30 of cercus planar (fig. 119); same structure in posterodorsal view narrow, inferior carina along posterior 0.30 of cercus; epiproct brown, becoming black posteriorly, gently curved as is characteristic for the genus; tip of epiproct, when viewed posteriorly (fig. 129) forming a narrow, blunt point.

Accessory genitalia. Anterior hamule (fig. 59) black, divided at distal 0.30; smaller posterior branch almost as large as anterior branch, its pointed tip almost meeting tip of anterior (larger) branch; posterior hamule (fig. 59) pale, roughly triangular, swollen at distal 0.25 to 0.50 of appendage, tip with a black tooth twisted laterad from broad axis of hamule; penis with cornuae pointed but each with well developed median shoulder (or median lobe in some specimens), as shown in fig. 59; lateral lobe prominent, knife-like, arcuate laterally, its outer margin strongly serrated.

Female. – Similar to male, with following differences: Vertex (fig. 155) without postocellar ridge, a well defined pit anterolaterad to median ocellus as in male; occiput green, narrow, mostly planar, or with only a slight tumid area medially, hind margin slightly sinuate, barely emarginate at middle; postocciput green, transverse; synthorax with no vestige of second lateral stripe; abdomen with dorsolateral dark stripe on segment 1 reduced or vestigial, middorsal dark stripe on segments 2-6 narrower, anteriorly touching black annulus, widened at transverse carina, constricted near center and widening at distal 0.25 of each segment, ventral white narrow but expanded near center of segment, sometimes a longitudinal wedge-shaped spot isolated by narrow posterior and anterior lateral offshoots of black dorsolateral stripe, white lateral wedge- shaped spots largest on segments 2 and 3, dividing or partially dividing dorsolateral brown stripe; segment 7 similar to segment 6, but dorsal pale orange green connecting anteriorly with lateral white at basal 0.10 of segment; segments 8-10 dark brown, becoming black dorsally and posterolaterally to all black with ill-defined white lateral spot on each segment; cercus, paraproct brown. Abdomen 37-41 mm.

Vulvar lamina (fig. 184) small, cleft as large as each plate; each plate broadly connected basally, each with a well developed raised shelf occupying anterior 0.50; medial margin of each plate slightly concave, its tip falcate; postlamellar ridge with Y-suture posterior to hind margin of lamina; central stem short with a well-defined circular or oval depression on each side.

Venational statistics. Anx: fore wing 15-20/15-21, hind wing 10-14/11-14; pnx: fore wing 10-13/10-15, hind wing 10-15/9-14; cs under pterostigma: fore wing 5-8/5-8, hind wing 5-8/6-7. Hind wing 31-34 mm.

Diagnosis

Erpetogomphus viperinus is most closely related to *E. bothrops*, and is diagnosed under that species. It is also superficially similar to *E. liopeltis* and is diagnosed under that species. The thoracic pattern of *E. viperinus* is superficially similar to that of *E. sipedon*, but is easily separated by characters listed under that species and in the key.

Remarks

Variation. – The description is based on 49 males and 38 females from Veracruz State, Mexico. The lectotype and paralectotype are in reasonably good condition, but post mortem preservation is poor and would yield an inadequate description. Venation characters for this pair are as follows:

Lectotype male: number of marginal cells behind fore wing paranal cells: 3/1; anx: fore wing 16/17, hind wing 12/12; pnx: fore wing 13/12, hind wing 11/13; cs under pterostigma: fore wing 6/6, hind wing 6/5; anal triangular cells: 4/4.

Paralectotype female: number of marginal cells behind fore wing paranal cells: 4/3; anx: fore wing 15/18, hind wing 12/11; pnx: fore wing 10/12, hind wing 12/13; cs under pterostigma: fore wing 7/8; hind wing 7/6.

Examination of 20 males shows variability is some venational characters. All specimens have marginal cells behind the fore wing paranal cells, ranging from 1-4 cells. The fifth antenodal is most often thickened, but rarely the fourth (one wing) or sixth (7 wings). The sixth antenodal is thickened on both wings of the lectotype.

Little variation exists in body colouration. The second lateral thoracic stripe is incomplete or vestigial in most males. It is complete on only one male from Rio Metlac. Females show a greater tendency toward a dense venation than do males. Marginal cells behind the fore wing paranal cells were present in all 20 females I examined, ranging from 1 (one wing) to 8 (two wings). The fifth antenodal is generally thickened, but it is the fourth on the left wing of the paralectotype, sixth in 17 wings (including right wing of paralectotype) and seventh in four wings.

Biology. – Although of restricted distribution, *E. viperinus* can be common during certain years. I collected a few specimens of both sexes in the mostly shaded understory at the Rio Metlac. The locality consists of a fast running river in a steep canyon. The narrow valley contained many coffee plants. I flushed various specimens, and they alit on low vegetation, where their deep blue green colour made them difficult to detect unless the eye followed closely where each specimen landed. Once approached they were easy to take with a net. Other Odonata taken at the same site were *Hetaerina cruentata* Rambur, *Argia* sp. nr. *fissa* Selys, *Argia extranea* Hagen *in* Selys, *Aeshna psilus* Calvert, *Brechmorhoga pertinax* (Hagen), *B. vivax* Calvert, *Cannaphila vibex* Hagen, *Erythrodiplax fusca* (Rambur), and *E. umbrata* (Linnaeus).

The species has been collected more frequently farther north at Teocelo under similar circumstances. The Odonata assemblage there is more varied and consists of *Palaemnema* sp. n., *Paraphlebia zoe* Selys, *Argia extranea*, *Argia* sp. n., *Brechmorhoga pertinax*, *B. rapax* Calvert, *B. tepeaca* Calvert, *Cannaphila vibex*, *Libellula herculea* Karsch.

This species has been taken at elevations of 800-1300 m (Teocelo and vicinity). Collection dates range from 6 June through 18 September (Teocelo and vicinity).

I have abstracted the following biological notes from López (*in litt.*): Tenerals and adults travel far from the stream, hiding in vegetation in open areas, where they feed by making short sallies from perches. They capture primarily small flies and butterflies (Lycaenidae) passing by. Copulation takes place in open fields away from streams, as males grab females which fly by. The copulating pair then retires to the dense forest. Females oviposit while flying above water, dropping their eggs from about 30 cm. At dusk, males return to feeding sites, often in considerable numbers, where threat display patterns among males and females have been observed when two or more individuals try to occupy the same perch. Specimens are often preyed upon by spiders (Araneidae).

Distribution (fig. 201). – *Erpetogomphus viperinus* is apparently restricted to central Veracruz. As stated under the species account for *E. bothrops*, all published records of this species since Calvert's redescription of *E. viperinus* refer to the widespread *E. bothrops*. I examined one male from the Paris Museum with a handwritten label, 'N. Carolina', but I have seen no specimens of *E. viperinus* from the United States. I believe that locality is in error.

Material

Type data. – Lectotype male by present designation with following data: small green handwritten label 'Mex/B[ouchard]'; white handwritten label '*Herp. / viperinus* /S.[elys]/ ♂'; two manila coloured labels each with '26' handwritten in pencil in an unknown hand; rectangular red label with printed 'LECTOTYPE'/and handwritten: '*Erpetogomphus/ viperinus* Selys 1869/ ♂/des. [printed] R. W. Garrison 1984'. The caudal appendages are shown in fig. 103. Paralectotype female: small green handwritten label 'Mex./B[ouchard]'; white handwritten label '*Herp./ viperinus/* S[elys]/ ♀', two manila coloured labels, each with '28' handwritten in pencil in an unknown hand; rectangular white label with printed 'LECTOTYPE'/ and handwritten '*Erpetogomphus/ viperinus* Selys 1869/ ♀/ des. [printed] R. W. Garrison 1984'. Both specimens in IRSN.

Other material (48♂, 32♀, including lectotype ♂ and paralectotype ♀). – MEXICO: *Veracruz*: nr. Municipio Teocelo at Puente Teocelo, *ca.* 1150 m, (UNAM, RWG); Barranca de Cayoapa, Teocelo, 750-890 m, (UNAM, JB, CE, PSM, DALD); Barranca de Cayoapa, Tejeria-Teocelo, 800 m, (UNAM); road to Monte Blanco, Teocelo, (UNAM); El Trapiche, Teocelo, 1100 m (UNAM); road to Santa Rosa, Teocelo, (UNAM); Santa Rosa, Teocelo, (UNAM); Cascada de Xico, Teocelo, 1100 m, (UNAM); Cascada Texolo, (UNAM); Parque Javier Clavijero, Jalapa, 1300 m (UNAM); Fortín de las Flores, 1010 m (RWG); Rio Metlac, *ca.* 3.5 km WNW of Fortín de las Flores, 900 m (RWG); km 327 W of Cordoba, (FSCA); Cordoba, (USNM).

Erpetogomphus designatus Hagen *in* Selys
(figs. 17, 18-thx, 60-hamules, 82-penis, 104-app, 130, 131-ept, 156, 157-vertex, 185, 186-vl, 202-distr)

Erpetogomphus designatus Hagen in Selys, 1858: 661 (401 sep.) (descr. ♂, ♀, 'Pecos River, Texas'). – Hagen in Selys 1859: 536 (10 sep.) (descr. ♂, ♀); Selys 1873b: 519 (75 sep.) (list); Calvert 1899: 386 (mentioned); Calvert 1905: 166 (Ohio, Ind., Mexico); Muttkowski 1910: 86 (cat.); Calvert 1912a: 289 (Mex., distr.); Hine 1913: 96 (Ohio); Williamson 1914b: 447 (Tex.); Kennedy 1917a: 544 (larva, notes); Williamson 1917: 8 (Ind.): Kennedy 1917b: 137 (Kans.); Kennedy 1918: 298 (notes); Williamson 1923: 8 (Kentucky); Montgomery 1925: 386 (Ind., habits); Montgomery 1927: 289 (Ind.);

Kennedy 1928: 373 (seasonal distribution); Montgomery 1929: 340 (Ind.); Needham & Heywood 1929: 80 (key, descr.); Byers 1930: 53 (Fla. Key, descr., habits); Williamson & Williamson 1930: 12 (summary of status); Byers 1931: 51 (Tenn.); Bird, 1932: 51 (Okla.); Williamson 1932: 23 (Mo., habits); Tinkham 1934: 216 (Tex.); Montgomery 1935: 234 (Ind.); Borror 1935: 453 (Ohio); Borror 1937: 186 (Ohio); Montgomery 1937: 207 (Ind., habits); Ahrens 1938: 11 (Mo., predation); Wright 1938: 27 (Tenn.); Ferguson 1940: 5 (Tex.); Montgomery 1940: 289 (S. C.); La Rivers 1940b: 63 (Nev.); Montgomery 1941: 230, 238 (Ind.); Ferguson 1942: 146 (Tex.); Montgomery 1947: 165 (distr.); Bick 1951: 179 (Okla.); Montgomery 1951: 207 (Ind.); Needham and Westfall 1955: 146 (key, descr.); Cross 1955: 11 (S. C.); Montgomery 1955: 133 (Ind.); Cross 1956: 4 (Fla.); Bick and Bick 1957: 2 (Okla.); Kormondy 1957: 108 (Tenn.); Bick 1957: 80 (La.); Gloyd 1958: 8 (Tex.); Bick and Bick 1958: 240 (Okla.); Bick 1959: 131 (Ark.); Donnelly 1961: 7 (Md. Va., D. C.); Alrutz 1961: 23 (Ohio); Borror 1963: 104 (common name); Macklin and Cook 1967: 120 (Ky.); Montgomery 1967: 127 (distr.); Roback & Westfall 1967: 114 (water quality data); Montgomery 1968: 134 (distr.); Pinhey 1969: 189 (tandem linkage); Resener 1970: 37 (Ky.); Huggins *et al.* 1976: 16 (Kans.); Harp & Rickett 1977: 50 (Ark.); Huggins 1978: 2 (Kans.); Young & Bayer 1979: 90 (larva, key, Tex.); Carle 1979: 322 (status in Virginia); White *et al.* 1980: 26 (S. C.); Carle 1982: 339 (W.Va.); Dunkle & Westfall 1982: 32 (status in Fla.); Paulson 1982: 255 (U.S., Mex.); Huggins & Brigham 1982: 4: 39 (N. C., S. C.); Harp & Rickett 1985: 132 (Ark.); Davies & Tobin 1985: 27 (cat.); Tsuda 1986: 87 (cat., attributes authorship to Selys); Bridges 1991: VII.60 (cat.); Tsuda 1991: 95 (cat.); Dunkle 1992: 39 (Fla).

Gomphus designatus. – Hagen 1861: 99 (descr. ♂, ♀).

Gomphus sp.. – Cabot,1872: 4 (descr. larva as *Gomphus* sp. No. 6, Poles Creek, Tex.).

Herpetogomphus designatus. – Walsh 1862: 389 (compared with *Ophiogomphus rupinsulensis*); Hagen 1875a: 42 (cat.); Selys 1879: 64 (2 sep.) (characters of genus); Hagen 1885: 255 (larva of Cabot identified); Kirby 1890: 60 (cat., attributes authorship to Selys); Banks 1892: 179 (Kans.); Calvert 1899: 386 (characters of genus); Adams 1900: 622 (Ark.); Williamson 1903: 226 (Tenn.); Van der Weele 1906: 177 (mentioned); Tucker 1907: 79 (Kans.); Tucker 1908: 99 (Tex.); La Rivers 1938: 76 (Nev., habits); La Rivers 1940a: 112 (Nev.).

Description

Male. – Entire face pale green, more vivid on postclypeus and frons, vertex with wash of brown around ocelli or entirely dark brown, scape dark brown, pedicel light brown, flagellum dark brown; anterior margin of vertex forming a trough at junction of antefrons, this trough with a pair of deeper pits anterolateral to median ocellus; occiput green, wide, tumid medially, crest slightly sinuate, barely emarginate medially or straight, its hind margin covered with long brown hairs; postocciput not visible dorsally, green; rear of head brown, darker toward occipital foramen.

Prothorax predominantly brown, becoming green dorsally; anterior and posterior lobes green; synthorax (fig. 17) green with following dark brown: well defined middorsal stripe widening to collar, its upper end extending along antealar sinus connecting with narrow humeral stripe; an isolated antehumeral stripe not touching dorsal or ventral margin (except in specimens from Durango and Chihuahua – see remarks); lower part of humeral stripe extending posteriorly to form a fragmented second lateral stripe, though in some specimens a vestige of a complete stripe exists; narrow third lateral stripe. Coxae, trochanters pale green, femora green becoming brown posterolaterally at distal 0.20; distal 0.05 of metafemora green with narrow brown line extending distally from subapical brown area; tibiae dark brown with yellow along lateral carinae of basal 0.5 of mesotibiae, a vestige of yellow or none on metatibiae; tarsi dark brown, armature black.

Wings hyaline with wash of yellow basally, venation dark brown, basal wing venation light brown, especially anteriorly, anterior margin of costa yellow, except for anterior margin of pterostigma; pterostigma dark brown, veins bordering it black.

Venational statistics. Fifth (rarely fourth) antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 2-5/1-4; anx: fore wing 11-14/11-14, hind wing 8-11/8-11; pnx: fore wing 7-10/8-11, hind wing 7-11/8-12; cs under pterostigma: fore wing 5-7/5-7, hind wing 4-7/4-7; anal triangular cells: 3-5/3-4. Hind wing 28-31 mm.

Abdomen. Segment 1 green with dorsolateral brown stripe occupying basal 0.75 of segment; segment 2 similar to segment 1, but dark brown expanding ventrolaterally behind auricle, contracting again and connecting with dark brown annulus; segment 3 similar to segment 2 but dark brown dorsolateral stripe interrupted at anterior 0.25 and again at distal 0.50 to 0.75 of segment, dark brown prominent at transverse carina, posterior 0.25 to 0.30 of segment with dorsolateral brown expanding laterally to encircle segment at posterior 0.10 of segment; segments 4-6 similar to segment 3 but dorsolateral brown interrupted only at anterior 0.25 to 0.30 of segment and expanding abruptly at transverse carina; segment 7 with narrow dark brown on transverse carina and poorly defined brown on lateral 0.50 of segment; segments 8-10 yellow brown with dorsolateral red brown occupying basal 0.40 to 0.75 of segments; pale areas of segments 2-6 orange green dorsally, becoming white below. Abdomen 35-37 mm.

Cercus (fig. 104) yellow brown, strongly angulate near middle; tip of cercus beyond angulation narrow, drawn out into a fine point; ventral margin with inferior carina at basal 0.45. Epiprocts yellow brown, gently curved dorsally at 90°, tips obliquely truncate (fig. 130) or spatulate (fig. 131).

Accessory genitalia (fig. 60). Anterior hamule black, divided at upper 0.50; lower branch forming a small, posteriorly directed truncate appendage; posterior hamule pale green, triangular, with anterior basal shoulder, tip evenly round, black; penis with long, decumbent lanceolate lateral lobe, its posterior end serrated; cornuae separated, tips narrowly rounded, with no medial lobe; membranous hood moderately long but usually with ends not overlapping.

Female. – Head as in male, but median swelling of occiput more prominent; prothorax and synthorax as in male; wings with yellow at base more extensive, often with markings at base of arculus, to cubitoanal crossvein; abdomen with definite pale orange dorsally, white to orange white laterally, these areas separated by brown dorsolateral stripes as in male; these stripes on each segment may be narrower, especially so between transverse carina and posterior 0.20 to 0.30 of segment; segments 8-9 mostly dark brown dorsally, sides tawny, annulus pale; segment 10 yellow brown, cercus ocher. Abdomen 33-36 mm.

Vulvar lamina (figs. 185-186) with prominent basal plates; quadrangular laminar plates acuminate posteriorly, meeting at medioanterior margin; cleft between plates broadly U-shaped; juncture of Y-shaped postlamellar ridge at or before level of posterior margin of lamina. Abdomen 33-36 mm.

Venational statistics: number of marginal cells behind fore wing paranal cells: 2- 5/1-5; anx: fore wing 12-15/11-15, hind wing 8-12/8-11; pnx: fore wing 7-12/7-12, hind wing 8-12/7-12; cs under pterostigma: fore wing 5-7/5-7, hind wing 4-8/5-7. Hind wing 28-32 mm.

Diagnosis

Little difficulty should be encountered in identifying either sex of this species. The strongly angulate cercus superficially allies it with *E. sipedon, E. heterodon*, and *E. lampropeltis*, but the structure of the occiput and the penile characters easily separate males of these species. The broadly defined occiput, with the large medial tumid area characteristic of *E. designatus*, is not present in the other three species. Male *E. lampropeltis* have a broad occiput, as do male *E. designatus*, but the medial area of the occiput is only slightly tumid.

The long, recumbent lateral lobe of the penis is unique to this species (fig. 82). In *E. lampropeltis* and *E. sipedon*, this structure forms a spinulose semicircle (figs. 83-85).

As in males, females of *E. designatus* are distinguished from all other similar species by the tumid median area of the occiput (fig. 156). The vulvar lamina in *E. designatus* (figs. 185- 186) more closely approaches that of *E. bothrops* (fig. 183) than of *E. sipedon* (figs. 187-188), *E. heterodon* (fig. 193), or *E. lampropeltis* (figs. 189-190). Each lamellar plate of *E. designatus* is smaller and the notch in the medial margin is more concave than in the other species.

Remarks

Variation. – Calvert (1907) described a specimen from San Pedro, Coahuila, Mexico, which differed from typical *E. designatus* in the following characters (typical condition in parentheses): 1) dark antehumeral stripe reaching down to mesinfraepisternum (lower part of stripe isolated), and 2) darker, more pronounced markings on abdominal segments as follows: segment 7 with a black spot on each side of posterior 0.50 of segment (like area red brown, blending anteriorly with ocher pale area); segment 8 with a black stripe on each side for almost its entire length (this area red brown); segment 9-10 with black at basal dorsolateral 0.50 to 0.75 (this area red brown with some black on dorsal 0.50 of segment). Calvert (1907) considered the San Pedro male to represent *E. designatus*. This specimen is indicated as in the ANSP, but it could not be found (Azuma *in litt.*, 1984). However, I have seen three males (Durango and Chihuahua) and a female (Durango) whose markings agree with Calvert's San Pedro male. I also find the following other differences: 1) no wash of yellow present on wing bases, 2) dark thoracic stripes thicker and more pronounced (fig. 18), 3) a black spot anteroventrally to auricle of abdominal segment 2, and 4) tip of epiproct, viewed posteriorly, is spatulate (fig. 131), not obliquely truncate (fig. 130) as is typical of other specimens. The single female has a more arcuate occiput (fig. 157) than typical *E. designatus* (fig. 156), but the dark anteroventral spot on segment 2 is small and inconspicuous.

Specimens from Durango, Chihuahua, and Coahuila could be a well-defined subspecies characterized by overall darker colouration and slight morphological modification of the female occiput (if typical for this form) and male epiproct. I detect no morphological differences in the penes, hamules, or cerci and, like Calvert, I am inclined to treat these specimens as *E. designatus*. Further evidence to support their conspecificity comes from a male from Nuevo Leon (in foothills of the northernmost range of mountains) in which the antehumeral stripe extends to the mesinfraepisternum but is in all other characters typical of *E. designatus*.

One male from McLennan Co., Texas, has the tips of the posterior hamules with a small, anteriorly recurved hook. This male and another from the same locality have vestiges of an anteroventral dark spot on abdominal segment 2.

I have not seen sufficient material of this species throughout eastern parts of its range to render any conclusions about geographic variability. Numerous

specimens, primarily from Gonzales and Williamson counties, Texas, show little variability.

Although the type locality for *E. designatus* and many other species collected by Capt. John Pope of the Smithsonian Institution and described by Hagen, is said to be the Pecos River in western Texas (32°N, 104°W), Needham and Cockerell (1903), citing Scudder and Cockerell (1902), argue that the type locality was probably at or near Roswell, Chaves Co., New Mexico, as follows (Needham and Cockerell 1903: 138-139): 'In Proc. Davenport Acad. Sci. vol. 9 (1902), p. 51, it is inferred that Pope collected his material at very different localities above the river, since he obtained both *Melanoplus bivittatus* and *M. differentialis*, which inhabit different life-zones. However, in 1902 it was observed that these two grasshoppers do actually occur together at Roswell. As it is not very likely that their ranges overlap very much, it thus seems likely that Pope's collections, if all from one place, were from the vicinity of the present town of Roswell, rather than from Lat. 32° (the present boundary between New Mexico and Texas), as Hagen indicates. In all probability, however, the collections were made in several places.'

No year is indicated on the data of any of the type material, nor have I found any reference to the year of Capt. Pope's expedition. However, a public display on the recent human history of the caverns at the visitor center at Carlsbad Caverns National Park, Eddy Co., New Mexico, states that Pope's expedition occurred in 1854-1855.

Venational details of lectotype male: number of marginal cells behind fore wing paranal cells: 1/2; ; anx: fore wing 12/13, hind wing 10/10; pnx: fore wing 8/9, hind wing 9/9; cs under pterostigma: fore wing 6/6, hind wing 7/6; anal triangular cells: 3/4.

Biology. – The synonymy indicates that more is known about this species than any other congener. *Erpetogomphus designatus* seems to be a species of mesic deciduous forests where there are clear streams and rivers. Montgomery (1925) writes of its habits in Indiana: 'This species was common in a well-cultivated orchard near Vincennes on August 7, 1924, resting on the ground with wings spread out against the soil but taking flight so readily that only three specimens were taken in two hours although I saw 20 or more.' In Hamilton Co., Indiana, Montgomery (1937) records it as '...rather numerous at ripples in the river, flying just above the surface of the water, and alighting on rocks. However, it was exceedingly difficult to capture...'. Williamson (1932) observed this species flying back and forth near the surface over ripples in Missouri. Others alighted on vegetation or on tips of mullein heads. La Rivers (1938) described the flight of *E. designatus* at Hiko Springs in the Pahranagat Valley, Nevada, as 'low, swift, and change of position rapid...' Ahrens (1938) describes the capture of a male along with a male *Hagenius brevistylus* Selys near Lebanon, Missouri: 'The *H. brevistylus* had struck and seized the *designatus* with such force that both were carried into the water. Both were dipped from the river an instant after they struck the surface.'

Dunkle and Westfall (1982) assign *E. designatus* as 'threatened' in Florida, because it is thus far known only from Liberty and Gadsden counties in the panhandle. In 1975 and 1977, I found this species abundant along cultivated stubble bordering trees next to the Guadalupe River in Gonzales County, Texas. It was more abundant than *E. eutainia*; and both species were easily flushed from low or cut vegetation. Members of both sexes did not fly far, and I could easily photograph and capture specimens.

Collection dates range from 6 May in Texas (Williamson, 1914b) to 5 October in Tennessee (Wright, 1938).

The larva has been described by Cabot (1872), Needham and Heywood (1929) and Needham and Westfall (1955).

Distribution (fig. 202). – *Erpetogomphus designatus* and *E. compositus* are the most boreal of the genus, with *E. designatus* generally replacing the western *E. compositus* in the eastern United States. *Erpetogomphus designatus* occurs as far north as Maryland and Washington, D. C., west through West Virginia, Ohio, Indiana, Missouri, Kansas, southeastern Colorado, eastern New Mexico, into western Texas. Sidney Dunkle (*in litt.*, 1991) mentions one female from South Dakota (Fall River Co., 9.7 mi SW Hot Springs, 29 July 1976, G. and J. Bick, L. Hornuff), erroneously published as *Stylurus intricatus* (Selys) (Bick *et al.*, 1977: 151), which is the northernmost record for this species. It occurs generally throughout the southeastern United States, but does not penetrate peninsular Florida (Dunkle and Westfall, 1982). Farthest western records include Hiko Springs, Lincoln Co., Nevada (La Rivers, 1938) and Arizona (Maricopa Co., Salt River at Corn Bluff Campground, 15 mi NE of Mesa). *Erpetogomphus designatus* is found as far south as Nuevo Leon (24-26°N, 100°W) and west to Coahuila (Calvert, 1907), Durango, and Chihuahua, Mexico.

It is partially sympatric with *E. compositus* in Arizona, Nevada, New Mexico, and western Texas. I collected it with *E. eutainia* in Gonzales Co., Texas.

Material

Type data. – Lectotype male by present designation with following data: 'July/ 16' [handwritten], '*designatus*' [handwritten], 'Hagen' [printed], small white label with printed 'Type' with red label glued to lower edge with handwritten '1864'; red rectangular label with printed 'LECTOTYPE'/ and written

'*Erpetogomphus designatus*/ Hagen ♂/ des. [printed] R. W. Garrison 1984'. Another ♂, a paralectotype, has the handwritten labels, '*Erp. designatus*/ ♂/ Pecos River' [in Hagen's hand] and 'Pecos River/ Uhler 1860.' in an unknown hand. A female paralectotype, collected 'July/ 15' has the additional label: [all printed unless otherwise stated] 'ERPETOGOMPHUS/ DESIGNATUS HAGEN [stamped] / P. P. Calvert, det [written] 1905/ B. C. A. Neur., p. [written] 166.' Type locality herein restricted to vicinity of Roswell, Chaves Co., New Mexico (see remarks).

Other material (84♂, 53♀, including lectotype ♂ and ♂ ♀ paralectotypes). – U. S. A.: FLORIDA: *Gadsden Co.*, Apalachicola River, Aspalaga Landing, Hwy I-10 (JD, RWG); GEORGIA: *Houston Co.*, Ocmulgee River at 96, (RWG); VIRGINIA: *Louisa Co.*, South Anna River, Rte 657, (CSUC); North Anna River, Rte 601, (CSUC); KANSAS: *Chatauqua Co.*, Big Caney River, 1 1/2 mi W of Elgin, (CSUC); TEXAS: *Caldwell Co.*, Plum Creek at US Hwy 90 (RWG); *Goliad Co.*, 3 mi N of Goliad, (RWG); *Gonzales Co.*, Guadalupe River, 4 mi S of Gonzales (RWG); Palmetto State Park, 6 mi S of Luling, nr. US Hwy 183, (RWG); *Hidalgo Co.*, Bentsen, Rio Grande State Park, (CSUC); *McLennan Co.*, Hog Creek, (RWG); *Real Co.*, Nueces River at Tex Hwy 55, S of Barksdale, (RWG); *Reeves Co.*, roadside irrigation ditch W of Balmorhea (RWG); *Williamson Co.*, 3 mi SW of Taylor, (RWG); Mustang Creek by Carlos G. Parker Blvd (= Loop 427), Taylor, (RWG); COLORADO: *Las Animas Co.*, Purgatory River, Bent Cyn nr. Delphi (CSUC, RWG); NEW MEXICO: *Guadalupe Co.*, Santa Rosa, 4600 ft. (UMMZ); ARIZONA: *Maricopa Co.*, Salt River at Corn Bluff Campground, 15 mi NE Mesa, (FSCA); MEXICO: *Nuevo Leon*: in foothills of the northernmost range of mountains, (UMMZ); Apodaca, just NE of Monterrey, near course on Instituto farm, (UMMZ, RWG); Chihuahua: La Cruz, (RWG); Naica (UMMZ); Durango: 3.7 mi NW of Gomez Palacio on Hwy 49, 3700 ft., (UMMZ); 8.2 mi N of Gomez Palacio on Hwy 49, (UMMZ); Rio Nazas at Mex. Hwy 49, 3.4 mi S Ciudad Leon Guzman, 4200 ft. (DRP).

Erpetogomphus sipedon Calvert

(figs. 19-thx, 39, 40-abd, 61-hamules, 83-penis, 105, 106-app, 158, 159-vertex, 168-leg, 187, 188-vl, 203-distr)

Erpetogomphus sipedon Calvert, 1905: 165 (descr. ♀ Jalisco: Guadalajara). – Calvert 1907: 399 (♀ 'Las Bocas in Durango...'); Calvert 1908c: xxx (*Erpetogomphus sipedon*, type ♀, Guadalajara, found by Schumann); Calvert 1909: 481 (Cuernavaca, Mexico); Williamson and Williamson 1930: 13 (summary of status); Kimmins 1969: 297 (type in BMNH); Paulson 1982: 256 (Mex.); Davies and Tobin 1985: 28 (cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.195 (cat.); Tsuda 1991: 95 (cat.).

Description

Male. – Entire face light green; this colour more vivid on frons, post- and anteclypeus; base of mandible, labrum light green, vertex with brown around and on ocellar prominences, remainder light green; antennal pedicel dark brown dorsally, light green ventrally; second segment and flagellum dark brown; occiput light green, crest slightly emarginate medially, its hind margin covered with long brown hairs; rear of head brown, darker toward occipital foramen, becoming light green laterally.

Prothorax predominantly dark brown, becoming light green dorsally; anterior and posterior lobes light green. Synthorax entirely light green (probably a vivid apple green in life) with following dark brown: antehumeral stripe ending dorsally before antealar sinus, narrow stripe along humeral suture, this stripe widening at dorsal 0.30 of suture and with anterior margin just touching upper part of antehumeral stripe, anterior 0.50 of mesinfraepisternum. Coxae, trochanters ivory, femora light green with black along external surfaces, more so on mesofemora; most of lateral surface of mesofemora dark brown, these markings more restricted and limited to apical 0.30 of metafemora; tibiae black with small lateral ivory stripes along basal 0.30; tarsi and armature black.

Wings hyaline, venation dark brown, basal wing venation brown, anterior margin of costa yellow; pterostigma brown, black along margins.

Venational statistics (n = 13). Fifth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 1; anx: fore wing 12-13/12-15, hind wing 9-10/9-10; pnx: fore wing 7-10/7-9, hind wing 9-11/8-10; cs under pterostigma: fore wing 5-6/5-6, hind wing 5-6/6; anal triangular cells: 4. Hind wing 28-31 mm.

Abdomen (fig. 39). Segment 1 light green with dorsolateral brown stripe; segment 2 similar to segment 1 but dark brown expanding posteriorly behind auricle, contracting again and interrupted just before brown annulus; segment 3 similar to segment 2 but with dark brown at transverse carina, anterior end of dorsolateral not on or just touching segment 2, its posterior end broadly connecting with dark brown annulus; segments 4-6 similar to segment 3 with posterior 0.40 wider than anterior 0.60; segment 7 largely pale except for brown along transverse carina, becoming red brown posteriorly, especially so laterally; segment 8 largely red brown with ill-defined light yellow brown middorsal and ventrolateral stripes; segment 9 similar to segment 8; segment 10 red brown basally, becoming pale yellow brown distally. Abdomen 33-37 mm.

Cercus (figs. 105-106) ivory, strongly angulate near middle; tip of cercus beyond angulation narrow, drawn out to a fine point; ventral margin with inferi-

or carina at basal 0.30. Epiprocts yellow brown, typical of genus.

Accessory genitalia (fig. 61). Anterior hamule black, divided at upper 0.30, lower branch forming a small, truncate appendage; posterior hamule white, triangular, with anterior basal shoulder, tip with small, anteriorly recurved tooth; penis with small serrated lateral lobes, membranous hood short, exposing a subcutaneous membrane which forms posterior margin of segment (fig. 83); cornuae (fig. 83) moderately long, widely separated, medial lobe present, usually 0.5 to 1.0 length of outer lobe.

Holotype female. – Face entirely pale except for small black area at base of mandible, occiput (fig. 159) dark brown around ocelli, remainder pale. Prothorax mostly pale, darker along pleura. Synthorax (fig. 19) mostly pale except for brown margin around antealar sinus and incomplete antehumeral stripe, its upper end joined with narrow humeral stripe. Coxae, trochanters, and femora pale with apical 0.30 black, especially mesofemora, metathoracic legs with black less extensive (fig. 168), forming black streaks externally; tibiae entirely black except for pale line laterally, tarsi and armature black.

Abdomen (fig. 40) similar to male but with dark brown dorsolateral stripe of uniform width on segment 2, segments 8-9 mostly black dorsally, sides tawny, annulus pale, cerci lacking. Abdomen 35 mm.

Venational details: number of marginal cells behind fore wing paranal cells: 2/2; anx: fore wing 13/13, hind wing 9/11; pnx: fore wing 9/9, hind wing 10/12; cs under pterostigma: fore wing 6/7, hind wing 7/6. Hind wing 31 mm.

Vulvar lamina (fig. 187) with broadly rectangular flaps meeting at anterior margin; juncture of Y-shaped postlamellar ridge at level of posterior margin of lamina.

Diagnosis

Males of *Erpetogomphus sipedon* are most similar to *E. heterodon* but are easily distinguished by the structure of the penis and cercus. The cornua in *E. sipedon* has a medial lobe (fig. 83), which is lacking in *E. heterodon* (fig. 87), and the tip of the cercus in *E. sipedon* are slender and finely attenuate (figs. 105-106), not robust and short as in *E. heterodon* (figs. 110-111). *Erpetogomphus heterodon* and *E. sipedon* are the only two species of the *E. designatus* group which share a similar thoracic design. However, *E. sipedon* lacks any dark thoracic stripes on the second and third lateral sutures; a vestigial incomplete second lateral stripe and complete narrow third lateral stripe exist on *E. heterodon*. The thoracic pattern of *E. boa* is also similar to *E. sipedon*, but *E. boa* is well differentiated by genital characters given in the keys. Although the difference in somatic patterns between *E. lampropeltis* and *E. sipedon* is great, these two species are separable by the structure of the penis. In *E. sipedon*, the hood is abbreviated, exposing a subcutaneous membrane, which latter forms the posterior margin of the segment. In *E. lampropeltis*, the hood is of normal length and it forms the posterior margin of the segment.

Although females of *E. sipedon* are easily differentiated from all other similar species by differences in colour and pattern, their separation from the same species using only structural characters is more difficult. Species morphologically similar to *E. sipedon* include *E. crotalinus, E. compositus, E. viperinus, E. bothrops*, and *E. heterodon*.

The occiput of *E. sipedon* is straight or, at most, weakly notched, (notch in *E. crotalinus* not clearly seen in the paralectotype female, [fig. 161]). The longitudinal distance of the occiput (hereafter called width) is narrower in *E. sipedon* than in *E. crotalinus*, and the posterolateral ocellar tubercle is less pronounced in *E. sipedon* than in *E. crotalinus*.

The occipital crest of *E. compositus* is sinuous (mostly linear in *E. sipedon*) and the postocciput is easily visible in dorsal view (fig. 163); the same structure is barely visible in *E. sipedon* (fig. 159).

The structure of the postlamellar ridge provides the best means of separation between *E. sipedon* and sister taxa *E. bothrops* and *E. viperinus*. In *E. sipedon*, this Y-shaped structure is short: the juncture of the lateral arms meets at or near the hind margin of each vulvar plate. The longitudinal stem also does not possess any circular or oval depressions on either side (figs. 187-188). In *E. bothrops* and *E. viperinus*, the juncture of the Y-stem is well posterior to the hind margin of each vulvar plate, and a well-defined oval or circular depression exists on either side of the longitudinal ridge (figs. 183-184).

I have been unable to find any morphological differences between females of *E. sipedon* and *E. heterodon*. Body pattern (figs. 19, 23) and distribution (figs. 201-204) will serve to separate females of these closely related species.

Remarks

Variation. – The male description is based on 11 males from Jalisco, Morelos, and Durango states, Mexico. The four from Durango are slightly larger (hind wing 30-31 mm); and their thoracic pattern is similar to that of the holotype female (fig. 19). The other seven males are smaller (hind wing 28-29 mm), and the lower 0.60 of the dark humeral stripe is narrower. The Durango males, though larger, have a sparser venation. For example, three have no marginal cells behind fore wing paranal cells, one has one marginal cell in both wings; and all other specimens have one marginal cell, except for the left fore wing of one Acatlipa male, which has no marginal cells. Two

of the Durango males have a 3-celled anal triangle in both hind wings, while all others possess 4 cells. The cerci of the Durango males are less angulate and the tips more robust (fig. 106) than the other males, but other characters of the body and penis leave no doubt that they represent *E. sipedon*.

Variability for females is less pronounced than for males, and I can find no overall differences in venational patterns among the 12 females examined.

Female venational statistics (n = 12, including holotype): number of marginal cells behind fore wing paranal cells: 1-3/0-3; anx: fore wing 12-14/12-15, hind wing 9-12/9-11; pnx: fore wing 8-10/8-10, hind wing 9-11/8-12; cs under pterostigma: fore wing 5-7/5-7, hind wing 5-7/4-6. Hind wing 30-34 mm. Abdomen 36-37 mm.

When Calvert (1905) described this species, he had only 6 females available; and he noted differences in the condition of the occiput between the holotype and a paratype from Matamoros, Puebla (figs. 158-159). Both forms were represented in his key. I cannot consider the differences noted by Calvert as useful, as much variation seems to exist in the shape of the occipital ridge in females of this and other species.

At the time of the original description, Calvert (1905) postulated that the female of *E. sipedon* could be *E. boa*, which was then known only from one incomplete teneral male. The discovery of more specimens of both species, and especially the capture of both males and females of *E. sipedon* in Durango, leaves no doubt that both are valid species.

Biology. – González (*in litt.*) collected this species at Palo Bolero, where adults perched on herbaceous vegetation on the banks of the Rio Sabinos. Its known distribution suggests that it is more widely distributed, but specimens are rare in collections. Specific ecological requirements may restrict its occurrence to certain sites, but a more likely answer to its apparent rarity is a lack of thorough collecting within its range. Collection dates range from 21 May (Cuernavaca) to 13 August (Nombre de Dios).

Distribution (fig. 203). – *Erpetogomphus sipedon* is known from northern Durango (Las Bocas [Calvert, 1907] settlement on the Rio Florida in extreme northern Durango near Villa Ocampo, approx. 26°25'N 105°25'W, [Selander and Vaurie 1962]) south through Morelos and Puebla (approx. 18°50'N, 99°W) and seems restricted to the highland area of central and western Mexico from altitudes of 1000 m (Palo Bolero) to about 2073 m (Las Bocas). González (*in litt.*) collected this species in Mexico state (Tonatico) during July, 1992.

Material

Type data. – Holotype female: white printed label: '[Mexico] Guadalajara,/Jalisco,/July. Schumann:', white, partially printed label: '*Erpetogomphus* ♀/*sipedon* Calv. TYPE /P. P. Calvert, det. 1905/B. C. A. Neur., p. xxx, 166/orig. of Pl. VIII, ff. 34, 40' with '(form/*a*)' handwritten on left side; printed label 'Brit. Mus./1911-339.'; small round label with red margin: 'Holo-/type'.

Other material (11♂, 12♀, including holotype ♀). – MEXICO: *Durango*: Nombre de Dios, just SE of Durango on Mex. Hwy 45 (23°51'N, 104°14'W), 5900 ft. (1800 m), 13 Aug. 1947 (W. Gertsch, M. Cazier), 4♂, 7♀ (AMNH, RWG); Morelos: Cuernavaca, 21 May 1898 (no collector), 1♀ (CUIC); Cuernavaca, 7 July 1900 (C.C. Deam), 2♀ (UMMZ); Palo Bolero, km. 18.3, route 95, 5 km. S. Acatlipa, 1000 m (approx. 18°45'N, 99°15'W), 26 June 1985 (E. González), 2♂ (UNAM); 18 June 1986 (E. González), 2♂ (UNAM), 12 July 1986 (E. González, V. Garcia), 3♂ (RWG); Morelos: Pueblo Cocyotla, Hwy 421, about 30 km SW of Cuernavaca, 23 July 1992 (J. Daigle), 1♂ (JD); Puebla: Matamoros, no date, (Otis W. Barrett), 1♀ (ANSP).

Erpetogomphus lampropeltis Kennedy

Description

Male. – Face entirely pale with dark markings as follows: along basal margin of labium, along frontoclypeal suture (less developed in *E. l. natrix*), base of antefrons; vertex all dark brown; antennae dark brown; anterior margin of vertex with an arcuate pit, one each anterolaterad to median ocellus; area between these pits tumid (fig. 138), occiput white green, wide, slightly tumid medially, crest entirely black, slightly raised, linear or slightly convex posteriorly, some with a small median notch, its hind margin covered with pale brown hairs; postocciput slightly concave, pale; rear of head dark brown.

Prothorax largely brown with pale green or grey green areas on anterior and posterior lobes, and with two small median spots on median lobe; contrasting dark/pale areas more prominent in nominotypic subspecies; pale colours of synthorax grey or grey green (*E. l. lampropeltis*) to green (*E.l. natrix*) with following dark brown areas: middorsal stripe, widening basally to collar, its upper end covering antealar sinus, extending posteriorly and connecting with broad, well defined antehumeral and humeral stripes; well defined sinuate second lateral stripe; third lateral stripe. Coxae, trochanters pale grey green with slight wash of brown posteriorly; tibiae pale grey green with defined superior surfaces brown, becoming dark brown distally; tibiae black with narrow strip of pale grey green along basal 0.30 to 0.50 of lateral margin; base and armature black.

Wings hyaline, basal wing venation brown; anterior margin of costa yellow up to pterostigma; pteros-

tigma black; fifth antenodal thickened in all wings (with rare exceptions).

Abdomen. Abdominal segment 1 pale grey green to green with basal 0.25 brown and with dorsolateral brown stripe; segment 2 with dorsolateral stripe sending a ventral stem posterior to auricle and (often) an isolated spot on anteroventral margin of segment, dorsolateral stripe often connecting with black annulus or ending just before; segment 3 with isolated black dorsolateral spot surrounding lateral carina; its anterior end tapering and sometimes touching anterior margin of segment, distal 0.25 of segment with dorsolateral black increasing in width posteriorly and touching dorsally near black annulus; segment 4 similar to segment 3, but two black spots broadly connected forming a continuous dorsolateral stripe occupying distal 0.80 of segment, this stripe often constricted in middle; segments 5 and 6 similar to segment 4, but with middorsal pale areas becoming darker; segment 7 with anterior 0.50 pale, except for black transverse carina, becoming entirely tawny to black posteriorly; segments 8-10 yellow brown, becoming black dorsally in most specimens; foliar extensions dark brown to black.

Cercus (figs. 107-108) ocher, in lateral view slightly concave dorsally near base, posterior 0.25 moderately angulate, the short tips slightly recumbent; cercus enlarged ventrally at basal 0.40 to 0.50 with inferior carina along same area, remainder slightly concave with tip forming a blunt point. Epiprocts yellow brown, gently curved dorsally at 90°, tips (fig. 132) dorsoventrally flattened and divergently bluntly pointed.

Accessory genitalia (figs. 62-63). Anterior hamule dark brown, divided at basal 0.50, lower branch forming a small, posteriorly directed truncate appendage; posterior hamule grey white, triangular, with anterior basal shoulder, tip bluntly rounded and armed with a small anteriorly directed tooth on posterior border; penis with lateral lobe small, roughly semicircular, serrate; cornuae (figs. 84-85) moderately widely separated, tips broadly rounded with well developed median lobes.

Female. – Head as in male, but with crest of occiput slightly more erect and convexly arcuate; posterior margin of postocciput slightly concave; prothorax and thorax as in male, but with pale areas generally more extensive; wings hyaline or with saffron infusion at base in some *E.l. natrix*; abdomen in well preserved specimens with pale colours primarily white with dull orange dorsally; black dorsolateral stripes and spots more reduced than in male, these stripes sometimes separated or greatly constricted on segments 4 and 5; cercus ocher.

Vulvar lamina (figs. 189-190) with prominent basal plates, quadrangular laminar plates acuminate posteriorly, meeting at anteromedial margin; cleft between plates forming a 90° angle; V juncture of Y-shaped postlamellar ridge at level of posterior margin of lamina.

Diagnosis

This species is most similar to its congeneric relatives, *E. sipedon* and *E. compositus*, and is diagnosed under those species.

Remarks

The original description of *E. lampropeltis* is brief and is based on an unspecified number of males and females from Sespe Creek, Fillmore, Ventura County, California. Williamson and Williamson (1930) originally described *E. natrix* in detail from 21 males and two females from Baja California, Mexico. An abstract of their diagnosis of males *E. natrix* from *E. lampropeltis* is as follows:

> 'The head and thorax of *lampropeltis* are duller and paler than in *natrix*.... the rear of the head is brown in *lampropeltis* and black in *natrix*; the thoracic brown is paler in *lampropeltis* and the pale areas are grayer, giving much less contrast in the thoracic pattern; the two lateral dark stripes are always joined, often very broadly in *lampropeltis*, and are not joined in.....*natrix*,....the femora are brown in *lampropeltis*.....black in *natrix*; and the inferior dilated edge of abdominal segments 8 and 9 is black in *lampropeltis* and, in *natrix*, is colored light vivid brown like the sides of the segment adjacent to the edge.....'

The apparent differences in morphology described above fall well within the latitude of individual and geographic variation and do not, in my opinion, constitute specific differences. Further, several specimens of *E. natrix* from various parts of its range have maculation patterns more closely approaching those of *E. lampropeltis*. For example, the antehumeral and humeral stripes are briefly connected, the dorsum of abdominal segments 7-10 have black as in *E. lampropeltis*, and the inferior dilated margin of abdominal segments 8 and 9 is black. I can also detect no differences in the shape of the vulvar lamina between females of *E. lampropeltis* and *E. natrix*.

The forms are allopatric, separated by the Colorado Desert. The large series of *E. lampropeltis* (mostly topotypes) that I examined does show consistent differences in pale thoracic colouration and minor differences in thoracic maculation. I consider the forms to represent subspecies separable as follows:

1. Pale thoracic colouration grey green, antehumeral and humeral stripes broadly connected on dorsal 0.25, after isolating a small pale spot below antealar sinus; second lateral stripe about twice as wide on dorsal 0.5 and often connecting with narrow third lateral stripe; dark thoracic stripes,

especially second and third, often not well defined (fig. 20); Ventura, San Diego, Los Angeles, and western San Bernardino counties, California ..... *E. lampropeltis lampropeltis*

– Pale thoracic colouration vivid green, antehumeral and humeral stripes not connected, or only narrowly so; second lateral stripe narrower than in *E. l. lampropeltis*, not connecting with third lateral stripe (fig. 21); central Baja California, Arizona, New Mexico, western Texas, south through Durango, Mexico ..... *E. lampropeltis natrix*

Erpetogomphus lampropeltis lampropeltis Kennedy (figs. 20-thx, 62-hamules, 84-penis, 107-app, 132-ept, 138-base of postfrons, 160-vertex, 189-vl, 204-distr)

Erpetogomphus lampropeltis Kennedy, 1918: 297 (descr. ♂ Sespe Creek, Fillmore, Ventura Co., California). – Needham and Heywood 1929: 80 (descr. ♂, ♀); Williamson and Williamson 1930: 13 (summary of status); Needham and Westfall 1955: 147 (descr.); Pritchard and Smith 1956: 116 (key); Musser 1962: 14 (notes on larva); Borror 1963: 104 (common name); Montgomery 1968: 133 (distr.); Paulson and Garrison 1977: 157 (Calif.); Paulson 1982: 255 (U.S.); Davies and Tobin 1985: 27 (cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.115 (cat.).

Herpetogomphus lampropeltis. – Byers 1928: 5 (larva unknown).

Erpetogomphus lampropeltis lampropeltis. – Tsuda 1991: 95 (cat.).

Description

Male. – Colouration and maculation as given under species account, key and in fig. 20.

Venational statistics: number of marginal cells behind fore wing paranal cells: 0-3/1-3. – anx: fore wing 9-14/10-14, hind wing 8-10/8-10; pnx: fore wing 7-9/5-10, hind wing 7-12/7-12; cs under pterostigma: fore wing 4-5/4-5, hind wing 3-5/3-6; number of anal triangular cells: 3-4/3-5. Hind wing 28-31 mm. Abdomen 34-37 mm.

Female. – Venational statistics (n = 6): number of marginal cells behind fore wing paranal cells: 0-4/1-3; anx: fore wing 13-15/12-16, hind wing 9-11/9-11; pnx: fore wing 9-11/9-10, hind wing 9-12/9-12; cs under pterostigma: fore wing 5-6/5-6, hind wing 5-6/5-6. Hind wing 32-36 mm. Abdomen 33-36 mm.

Diagnosis

See account under *E. compositus* and key to subspecies of *E. lampropeltis*.

Remarks

Variation. – Venational details of holotype male: number of marginal cells behind fore wing paranal cells: 1/2; anx: fore wing 12/12, hind wing 9/9; pnx: fore wing 8/9, hind wing 9/9; cs under pterostigma: fore wing 5/5, hind wing 5/4; number of anal triangular cells: 4/5. Hind wing 28 mm.

The large series of specimens primarily from the type locality shows little somatic colour and/or pattern variation, due, possibly, to its limited distribution. The fifth antenodal in the fore wings is generally thickened, but 7 of 40 wings of 20 males examined have the fourth antenodal thickened; and one wing has the sixth antenodal thickened. A 3-celled anal triangle is common in this subspecies, as almost half (19/40) of the wings possess this condition.

The female from Matillija Hot Springs has flavescent wing bases.

Biology. – At the type locality, this species was abundant during early September, 1982. I collected 54 males within about two hours. All preferred to sit on exposed rocks and were easily collected with a net. Hundreds of cast skins were attached to the exposed rocks. I did not find the species in smaller rivulets emptying into Sespe Creek. The only female I saw and collected was found dead in the water.

I returned to the locality in September, 1984, but the entire area had been fenced off. Five males were collected in the general vicinity, below Matillija Hot Springs, but they were rare and more wary.

This is a late summer species: the specimens from San Bernardino Co. collected in June are all teneral. Flight dates for specimens from Ventura Co. range from 10 July to 8 September.

Distribution (fig. 204). – The nominotypic subspecies has been collected only at three localities in Ventura County one in San Bernardino County, one in Los Angeles County, and one in San Diego County, California. It has the most restricted distribution of any Odonata form in southern California.

Material

Type data. – Holotype male: CALIF: Ventura Co., Sespe Creek, Fillmore, 7 Aug. 1915 (C. H. Kennedy); in USNM. I have illustrated the thorax (fig. 20), caudal appendages (fig. 107), and penis (fig. 84) of the holotype.

Other material (70♂, 6♀, including holotype ♂). – U. S. A.: CALIFORNIA: Los Angeles Co., San Gabriel Mtns., jct of N and W Fork of San Gabriel River, E of Hwy 39, 11 Aug. 1986 (D. Swinney), 1♂ (RWG), *Ventura Co.*, Sespe Creek, 4.0 mi N of Fillmore, 600 ft., 8 Sept. 1971 (D. Paulson), 2♂ (CC, RWG); 5 Sept. 1982 (R. W. and J. A. Garrison), 54♂, 1♀ (RWG); Matillija Hot Springs, 14 Aug. 1927 (T. Craig), 1♂, 1♀ (FSCA); just below Matillija Hot Springs, 1400 ft., 2 Sept. 1984 (R. W. and J. A. Garrison), 5♂ (RWG); Wheeler Hot Springs, 10 July 1927 (T. Craig), 4♂, (FSCA); *San Bernardino Co.*, Deep Creek Public

Camp, 15 June 1957 (A. Menke, L. Strange), 1♂, 4♀ (LACM); *San Diego Co.*, La Jolla, La Jolla Indian Res. Campground, San Luis Rey River, 25 Aug. 1991 (W. F. Mauffray), 1♂ (RWG).

Erpetogomphus lampropeltis natrix Williamson and Williamson **stat. n.**
(figs. 21-thx, 63-hamules, 85-penis, 108-app, 1990-vl, 204-distr)

Erpetogomphus natrix Williamson & Williamson,1930: 19 (- descr. ♂, ♀ Baja Calif. Sur, Purissima, 12 October 1923). – Byers 1939: 50 (quotes Williamson & Williamson, 1930); Fraser 1940: Pl. 6 (penis); Needham & Westfall 1955: 148 (descr. ♂); Borror 1963: 104 (common name); Montgomery 1968: 133 (distr.); Paulson 1982: 255 (U.S., Mex.); Davies and Tobin 1985: 28 (cat.); Tsuda 1986: 87 (cat.).

Erpetogomphus lampropeltis. – Tinkham 1934: 215 (Tex.), Needham & Westfall 1955: 147 (Tex.); Gloyd 1958: 8 (Tex.); Kormondy 1960: 122 (Ariz.); González & Novelo 1991: 97 (Mex.); Novelo & González 1991: 154 (descr. larva, Mex.).

Erpetogomphus lampropeltis natrix. – Bridges 1991: VII.144 (cat.); Tsuda 1991: 95 (cat.). [Demotion of *E. natrix* to subspecies status was advised by me *in litt.* to Bridges and Tsuda.]

Description

Male. – Colouration and maculation as given under species account, key, and fig. 21.

Venational statistics: number of marginal cells behind fore wing paranal cells: 0-3/0-2; anx: fore wing 11-15/11-14, hind wing 9-11/9-11; pnx: fore wing 6-11/7-10, hind wing 8-14/7-12; cs under pterostigma: fore wing 4-6/4-6, hind wing 4-6/4-6; number of anal triangular cells: 3-4/2-4. Hind wing 24-33 mm. Abdomen 30-37 mm.

Female. – Venational statistics (n = 17, including allotype): number of marginal cells behind fore wing paranal cells: 0-6/0-5; anx: fore wing 12-15/12-15, hind wing 9-11/9-11; pnx: fore wing 7-11/7-12, hind wing 9-12/9-12; cs under pterostigma: fore wing 4-6/4-7, hind wing 4-7/5-7. Hind wing 30-35 mm. Abdomen 36-41 mm.

Diagnosis

See comments under *E. compositus* and key to subspecies of *E. lampropeltis.*

Remarks

Venational details of holotype male: number of marginal cells behind fore wing paranal cells: 2/1; anx: fore wing 13/13, hind wing 9/9; pnx: fore wing 9/9, hind wing 10/9; cs under pterostigma: fore wing 4/4, hind wing 5/4; number of anal triangular cells: 4/3. Hind wing 30 mm.

Venational details of allotype female: number of marginal cells behind fore wing paranal cells: 2/1; anx: fore wing 13/13, hind wing 9/10; pnx: fore wing 7/8, hind wing 10/9; cs under pterostigma: fore wing 6/5, hind wing 5/5. Hind wing 30 mm.

Variation. – Intrapopulational variation of body maculation appears to be as great as interpopulational variation. The antehumeral and humeral stripes may be connected or separate in any small series from a given locality: 1 of 3 specimens from Cane Springs, Mojave Co., 3 of 12 specimens from Cave Creek, Maricopa Co. (4 have these stripes barely connected), and 2 of 11 specimens from 15 mi E of Douglas, Cochise Co., Arizona, all have connected antehumeral and humeral stripes. Similar degrees of variation exist for the dorsal and dorsolateral darkening of abdominal segments 7-10. Some specimens have little black on these segments (as noted by Williamson and Williamson, 1930, for their type series of *E. natrix*), but others have various degrees of darkening, and some specimens are as dark as I have observed for nominotypic *E. lampropeltis.*

A male I collected at Las Parras, Baja California, has the posterior 0.5 of the dorsum of abdominal segments 7 and all of segments 8-9 with black. The male from 'Corralitos' is unusual in having narrow second and third lateral thoracic stripes. The upper 0.5 of the second lateral stripe is also lacking, but in all other aspects, this specimen is *E. lampropeltis natrix* by morphology and overall body colouration and maculation.

Biology. – Williamson and Williamson (1930) described the type locality. González (*in litt.*) collected this subspecies with *E. crotalinus* in Durango state (La Michiliá). I collected one male of the species at Las Parras in September, 1985 (Garrison, 1986) as it sat upon an exposed rock in the middle of the small stream. It was the only individual I saw.

This subspecies can be common at certain sites in Arizona and New Mexico. Jo A. Garrison and I collected *E. lampropeltis natrix* on the East Fork of the Gila River at Grapevine Campground, where it was equally as common as *E. heterodon.* Adults landed on exposed rocks, exposed bleached logs in the center of the stream, or on the gravel shores. I have also taken it on sandy-bottomed desert streams, often in company with *E. compositus.* Novelo (pers. comm.) found this subspecies with the more common *E. crotalinus* in Durango state (La Michiliá).

I observed oviposition on 1 August 1992 at the Agua Fria River, Yavapai County, Arizona. Females appeared over the stream surface in the late afternoon (about 6: 15 p.m.), and flew rapidly over the water, dispersing their eggs by dipping the abdomen briefly into the water. This behaviour continued until sundown (about 7: 30 p.m.). A few males were still

present, sitting on emergent rocks near oviposition sites. No copulations were observed.

Altitudinal gradients for the species range from near 923 m (Tangle Creek, Yavapai Co., Ariz.) to 1754 m in New Mexico and southeastern Arizona (W of Portal). Like *E. l. lampropeltis*, *E. l. natrix* is primarily a late summer to autumn species. Flight dates range from 27 June to 10 October.

Distribution (fig. 204). – Though originally described from Baja California, *E. lampropeltis natrix* is widely distributed throughout the southwestern United States. It has been collected as far east as western Texas (Tinkham, 1934, Gloyd, 1958) and Durango and Chihuahua, Mexico. The most northerly records are from northcentral Arizona. I have seen no specimens from central or eastern New Mexico, although it probably occurs in those areas. The species apparently does not penetrate north of the Mogollon Rim in Arizona northwest into the Colorado Desert.

Material

Type data. – Holotype male: MEXICO: Baja California Sur: Purissima, 12 Oct. 1923 (J. H. Williamson); allotype female, same data but 6 Oct. 1923 (both examined), in UMMZ. I have illustrated the thorax (fig. 21), hamules (fig. 63), caudal appendages (fig. 108), and penis (fig. 85) of the holotype, and vulvar lamina (fig. 190) of the allotype.

Other material (101♂, 22♀, including holotype ♂ and allotype ♀). – U. S. A.: ARIZONA: *Cochise Co.*: Bear Creek, Rte 61, 6 mi SE Parker Lake, Coronado National Forest (CSUC); mouth Miller Canyon, Huachuca Mtns., (FSCA, UMMZ), pond N of Slaughter Ranch, 15 mi E of Douglas, 3800 ft, (RWG); springs just E of Slaughter Ranch, 17 mi E of Douglas, (RWG); Bear Creek, Rte 61, 6 mi SE Parker Lake, Coronado Nat'l Forest, (CSUC), San Pedro River at Hwy 90 (FSCA); San Pedro River, jct. Charleston Rd., (BYUC); San Pedro River, 9 mi SW of Tombstone (BYUC); San Pedro River at Hereford Rd., (RWG); Southwestern Research Station, 5 mi W of Portal at John Hands Picnic Grounds, 5400 ft, (FSCA); *Gila Co.*, Tonto Natural Bridge (RWG); Webber Creek at Camp Geronimo, 8 mi ENE of Payson, (RWG); *Maricopa Co.*, Cave Creek by Ocotillo Rd, Cave Creek, (RWG); Camp Creek by Cave Creek Rd., 12 mi NE of Scottsdale Rd., 2700 ft., Tonto Nat'l. Forest, (RWG); Sycamore Cyn., 3.3 mi WNW of Hwy 87 (RWG); *Mojave Co.*, irrigation ditches E of Cave Springs, (DRP); *Pima Co.*, Sabino Cyn, N of Tucson (FSCA); Lower Sabino Cyn, (RWG); Upper Sabino Cyn, *ca.* 3 mi N of visitor center, N of Tucson (RWG); *Santa Cruz Co.*, Sonoita Creek Ranch (on way to Salero Cyn), along Santa Cruz River, along Ariz. Hwy 82, 2 mi SW of Patagonia, (RWG); White Rock Campground, Peña Blanca Lake, 4200 ft, (RWG, JD); *Yavapai Co.*, Agua Fria River at Black Canyon City, (RWG); Tangle Creek, nr Tangle Creek cabin, *ca* 33 mi N of Carefree, T9N-R5E, sec. 1, 2800 ft (RWG); on limestone rim of Montezuma's (*sic*) Well (National Monument) (RWG); Sycamore Canyon, Atasco Mtns (LACM); NEW MEXICO: *Catron Co.*, Gila Cliff Dwellings, (RWG); West Fork Gila River at Gila Cliff Dwellings Nat'l Mon., 5700 ft, (RWG); *Grant Co.*, Gila River at Cliff (FSCA); Mangus Springs Creek, Hwy 180, Mangus Springs, (RWG); Grapevine Campground, East Fork of Gila River at N. Mex. Hwy 15, 5600 ft, (RWG); TEXAS: *Jeff Davis Co.*, Ft. Davis, (FSCA); Limpia Creek, 2-3 mi N of Ft. Davis, (UMMZ); Musquiz Creek, 6 1/2 mi SE Ft. Davis (FSCA); MEXICO: Chihuahua: Cascada de Basaseachic National Park, (CSUC, BYUC); San Diego Canyon, (BYUC); Durango: Arroyo El Temazcal (camino a El Aleman), Reserva de la Biosfera La Michiliá, (UNAM); km 21 Camino Suchil-Reserva de la Biosfera La Michiliá, 'Corralitos', (UNAM); Sonora: Maycoba River, (BYUC); Maycoba River, W of Maycoba, (BYUC); 8 mi W of Maycoba River, (CSUC); Maycoba River, Hwy 16, 13 mi W of Maycoba at San Francisco Bridge, (CSUC); Rio Magdalena, Hwy 15 S of Immuris, (BYUC, CSUC); small river W of Vecora, Rte 15, (CSUC, BYUC); Baja California Sur: Purissima (FSCA); Las Parras, about 18 km W of Hwy 1 on route to San Javier, SW of Loreto, (RWG).

Erpetogomphus crotalinus (Hagen *in* Selys)

(figs. 22-thx, 41-abd, 64-hamules, 86-penis, 109-app, 133-ept, 161-vertex, 169-leg, 191, 192-vl, 205-distr)

Ophiogomphus crotalinus Hagen *in* Selys, 1854: 40 (21 sep.) (♂, ♀ descr. from Mexico).

Erpetogomphus crotalinus. – Hagen *in* Selys 1858: 332 (72 sep.) (descr. ♂, ♀, relationship with *E. menetriesii*); Walsh 1863: 253 (mentioned); Selys 1869: 174 (11 sep.) (Mex., attributes authorship to Selys); Selys 1873b: 519 (75 sep.) (list, attributes authorship to Selys); Kirby 1890: 61 (cat., attributes authorship to Selys); Calvert 1899: 38 (Tepic, Mex.); Calvert 1905: 165 (Mex.); Calvert 1907: 399 (Mex.), Calvert 1909: 481 (distr. in Mexico); Muttkowski 1910: 86 (cat.); Ris 1917: 153 (comparison with *E. boa*); Kennedy 1918: 298 (comparison with *E. lampropeltis*); Byers 1939: 50 (quotes Calvert 1907); Williamson and Williamson 1930: 12 (summary of status); Montgomery 1968: 133 (distr.); Paulson 1982: 255 (cat.); Davies and Tobin 1985: 27 (cat.); Tsuda 1986: 87 (cat., attributes authorship to Selys); Bridges 1991: VII.54 (cat.); Tsuda 1991: 95 (cat.); Cannings and Garrison 1991: 478 (Mex.); González and Novelo 1991: 97 (Mex.); Novelo and González 1991: 150 (descr. larva, Mex.).

Herpetogomphus crotalinus. – Hagen 1875a: 43 (cat.); Selys 1879: 64 (2 sep.) (characters of genus); Kirby 1890: 61 (cat.).

Description

Male. – Labium grey white, base of mandibles pale green becoming red brown distally, lips black, remainder of face pale green except for narrow wash of brown at base of antefrons, vertex mostly dark brown with green medially behind postoccipital tubercles; antennae dark brown; anterior margin of vertex with two lanceolate pits, each anterolateral to median ocellus; occiput bright green, broad, gently tumid medially, crest black, linear to emarginate medially, its rim covered with row of long brown hairs; postocciput green, smoothly concave or somewhat angulate medially, rear of head light green with brown near occipital foramen.

Prothorax predominantly green, most of middle lobe and posterior of frontal lobe marked with dark brown, a small middorsal green spot longitudinally divided by narrow dark brown line medially on middle lobe. Synthorax (fig. 22) entirely green with brown along margins of antealar crest in a few specimens with a hint of a dark brown antehumeral stripe. Coxae, trochanters pale green, femora green with streak of dark brown becoming wider distally, these streaks restricted to lateral surface of femora (fig. 169) and brown reduced to apical 0.50 of metafemora; a supplementary narrow, linear streak of dark brown more posteriorly placed on femora and, in some specimens, touching lateral streaks of brown distally; tibiae ranging from all yellow green except dark brown laterally, to all brown with yellow on lateral carinae; tarsi and armature black or with some yellow on exterior surfaces of second and third tarsomeres.

Wings hyaline, venation dark brown, anterior margin of costa yellow to base of pterostigma, this structure brown, veins bordering it black.

Venational statistics. Fifth, rarely fourth or sixth, antenodal thickened in all wings; marginal cells behind fore wing paranal cells: 1-3/1-3; anx: fore wing 11-13/11-13, hind wing 8-9/8-10; pnx: fore wing 7-10/7-10, hind wing 8-10/8-10; cs under pterostigma: fore wing 4-6/4-7, hind wing 4-7/4-6; anal triangular cells: 3-4/3-5. Hind wing 26-31 mm.

Abdomen (fig. 22). Segment 1 green, slightly fuscous basally, with small line of black at posterior articulation point; segment 2 all green with narrow dorsolateral streak of black above auricle and with poorly defined dorsolateral brown spot on posterior 0.25 of segment, dorsal 0.75 to 0.50 of annulus black; segment 3 pale green, becoming white ventrally with black along transverse carina and elongate black dorsolateral spot on posterior 0.25 of segment connecting to black annulus; segments 4-7 similar to segment 3, but with narrow anterior offshoot of black laterally on transverse carina and with posterior midlateral black occupying posterior 0.50 of segments, middorsal pale area of these segments becoming progressively more tawny posteriorly, especially so on posterior 0.50 of segment 7; segments 8-9 ocher yellow with well defined dark brown dorsolateral stripe; segment 10 ocher becoming red brown at basal 0.50. Abdomen 31-36 mm.

Cercus (fig. 109) yellow, strongly to moderately angulate dorsally at distal 0.50-0.30; tip of cercus beyond angulation attenuate, drawn out to a blunt point, ventral margin with inferior carina at basal 0.40 to 0.50. Epiprocts yellow brown, gently curved dorsally at 90°, extending to distal 0.25 or almost to level of tip of cercus, tips forming divergent points, dorsoventrally flattened (fig. 133).

Accessory genitalia (fig. 64). Anterior hamule black, divided at upper 0.50, lower branch forming small posteriorly directed truncate appendage; posterior hamule pale green, triangular, with anterior basal shoulder, tip rounded with a small anteriorly directed tooth on posterior margin; penis with semicircular spinose lateral lobe, cornuae separated; with medial lobe, and a long narrow flap at outer distal margin, membranous hood present but not overlapping. Abdomen 31-37 mm.

Female. – Head as in male but with crest of occiput (fig. 161) more emarginate medially, in some specimens with lateral margin arcuate; prothorax and synthorax as in male; legs with black areas more reduced than in male; wings with slight wash of yellow at base (more so in tenerals); abdomen as in male but with black areas more reduced on abdominal segments 1-3; dorsolateral brown stripes almost complete on segments 4-7 except for basal 0.05 of each segment, these stripes complete on segments 8-9; cercus ocher. Abdomen 30-36 mm.

Vulvar lamina (figs. 191-192) with broadly rectangular flaps meeting at anterior margin, juncture of Y-shaped postlamellar ridge at level of posterior margin of lamina.

Venational statistics: number of marginal cells behind fore wing paranal cells: 1-4/1-3; anx: fore wing 11-13/11-13, hind wing 8-10/8-10; pnx: fore wing 7-10/7-9, hind wing 8-10/8-10; cs under pt: fore wing 4-7/4-6, hind wing 4-6/4-6. Hind wing 26-32 mm.

Diagnosis

Erpetogomphus crotalinus is unique in having the extensor surfaces of the tibiae yellow (fig. 169). Some specimens have largely brown tibiae, but the lateral costate ventral margins are always yellow; all other congeners have dark brown to black tibiae. The almost immaculate synthorax is shared by only two other species: *E. cophias* (fig. 27) and some *E. elaps* (fig. 13), but the male cerci of these two species (figs. 100, 116) are never angulate as in *E. crotalinus* (fig. 109). The cornua of the penis (fig. 186) has a well developed median lobe and a long, acuminate tip, a condition unique to this species. This species is superficially similar to *E. heterodon* and is diagnosed under that species.

Females of *E. crotalinus* differ from other species by three characters of the head, the presence of anterolateral pits at the base of the frons, the relatively broad occiput, and the medial notch of the crest. The vulvar lamina (figs. 191-192) provides no discriminatory characters, and is similar to those of *E. lampropeltis* (figs. 189-190), *E. compositus* (fig. 194), *E. heterodon* (fig. 193), and *E. sipedon* (figs. 187-188).

Remarks

The description is based on 91 males and 43 fema-

les. The lectotype male is reasonably well preserved, although it lacks the accessory genitalia. I illustrate the cercus (fig. 109) and right hind leg (fig. 169) of the lectotype, and the vertex, occiput (fig. 161), and vulvar lamina (fig. 191) of the paralectotype.

Venational details for lectotype male: number of marginal cells behind fore wing paranal cells: 2/3; anx: fore wing 13/13, hind wing 9/8; pnx: fore wing 10/10, hind wing 10/10; cs under pt: fore wing 6/6, hind wing 6/6; anal triangular cells: 4/5. Hind wing 31 mm. Abdomen 36 mm.

Venational details for paralectotype female: number of marginal cells behind fore wing paranal cells: 1/1; anx: fore wing 11/11, hind wing 9/9; pnx: fore wing 9/9; hind wing 9/9; cs under pt: fore wing 5/4, hind wing 4/5. Hind wing 29 mm. Abdomen 33 mm.

Variation. – Two teneral males of *E. crotalinus* reared in Arizona are superficially similar to *E. heterodon* in the blunt shape of the cercus, the vestige of an isolated antehumeral stripe in one specimen, and the fuscous condition of the extensor surfaces of the metafemora. However, the penis structure of both specimens is unmistakably that of *E. crotalinus*. Because the two Arizona specimens are teneral, I cannot determine if dark thoracic stripes similar to those of *E. heterodon* would have developed, or whether the maculation would have been the same as observed when mature.

The male described by Hagen *in* Selys (1858) has the darkest and most distinct antehumeral stripes that I have seen for any specimen of this species. The tibiae of a majority of specimens I examined are entirely dark brown with the lateral costae yellow; others, including the lectotype, have the entire ventral margin yellow.

Biology. – Specimens are apparently common at favored localities. Boris Kondratieff (*in litt.*, 1990) states that adults of this species were 'on every [exposed] rock [in Rio Macoba] – hundreds and hundreds of them.' During a two-day stay at Ajijic near Laguna Chapala, Oliver S. Flint, Jr., and M. A. Ortiz collected 28 males and 23 females. Calvert (1907) records the following concerning its habits: '[*Progomphus borealis*] and *Erpetogomphus* were found on sand- or mud-banks, hardly above water-level, along sides of an irrigating ditch into which the water from the baths of Santa Rosalia empties. On alighting on these banks, *P. obscurus borealis* held its abdomen slanting upward to form an angle of 45°-60° with the bank, while *E. crotalinus* held it nearly horizontal.' The male collected at Lago de Patacuaro in Michoacan is noted as taken on 'stream flowing into lake', the two males and one female from the pyramids at S. Juan Teotihuacan as 'on high grassy plains far from water'. González and Novelo (1991) record the following about *E. crotalinus* (in translation): 'This is the most abundant gomphid in the area [the Biosphere Reserve of La Michiliá, Durango]. Like other members of the family, the adults of *E. crotalinus* have a seasonal flight pattern that, although it has not been exactly established, apparently is restricted to the months of May to October. The individuals of this species are characteristic inhabitants of both seasonal and permanent streams, easily recognized in the field by the bright green colour of the thorax. Males have the habit of resting on emergent rocks, a position they defend aggressively from other conspecific males.'

Erpetogomphus crotalinus has been collected with *E. designatus, E. lampropeltis*, and *E. heterodon*. Collection dates range from May through October (Calvert 1905).

Distribution (fig. 205). – *Erpetogomphus crotalinus* is restricted to the higher xeric areas of central and western Mexico. The species was reared from larvae collected by Minter Westfall, Jr., from the Slaughter Ranch, 15 mi W of Douglas, Cochise Co., Arizona; but no other collectors have encountered it there. I have also seen a pair from New Mexico (Eddy Co., Sitting Bull Falls), which may be strays from Mexico; its occurrence in the southwestern United States appears sporadic, and other odonatists have failed to find the species during their work in Arizona and New Mexico. Altitudinal data show a range of 1225 m (Mexico: Chihuahua: Santa Rosalia Springs) to 2290 m (Mexico: Mexico: Pyramids, S. Juan Teotihuacan). In the Paris Museum is a male labelled, 'Veracruz', which is probably in error.

Material

Type data. – Lectotype male by present designation with following data: white handwritten label by Hagen, '*G. lineatus* / Mexico'; white handwritten label, '*crotalinus*' in an unknown hand; white, black-bordered printed label: 'Mus. Berol.'; two small printed labels, 'Hagen'; red label with 'Type [printed]/12334' (written by N. Banks); rectangular label [all printed unless otherwise stated]: 'ERPETOGOMPHUS / CROTALINUS HAGEN [stamped]/ P. P. Calvert, det. 1905 [written]/ B. C. A. Neur. p. 165 [written]'. In MCZC. The penis and hamules are missing and probably served as the basis for the free-hand illustrations of these structures for Hagen *in* Selys (1858). Paralectotype female with following data: green printed label: 'Mexico/ Deppe.'; red printed label 'Typus'; yellow printed label, 'Zool. Mus./ Berlin', on reverse side written in ink, 'cat nr./ 2314; white label: 'syntypus ♀ von: / *Ophiogomphus* / *crotalinus* Hagen' [written in an unknown hand]; yellow label (handwritten except as noted), 'PARALECTOTYPE [printed] ♀/ *Ophiogomphus* / *crotalinus* Hagen/ des.

[printed] R. W. Garrison 1984'. In ZMHB.

There is a male in the ZMHB with the same data as the paralectotype female, except as follows: green label, 'Mexico Deppe'; green label, '*crotalinus* / Hag.' [both handwritten by Selys]; printed label, '2314'; and 'Syntypus ♂ von / *Ophiogomphus* / *crotalinus* Hagen'. Although the specimen is labelled as a type, I believe it is not a syntype and, in fact, that it represents the second male described by Hagen *in* Selys, 1858. I decided that the male in the MCZC and the female in the ZMHB represent the original syntypes for the following reasons: The original (1854) description of *Ophiogomphus crotalinus* is brief and was based on a male and female. Hagen gave measurements for both sexes (abdomen: male 36 mm, female 33 mm; hind wing male 31 mm, female 29 mm). These measurements and the description of the male ('Front of thorax yellow, with indication of two median stripes and a pale red humeral stripe...') correspond to the MCZC male and the ZMHB female. Hagen *in* Selys (1858) described this species in greater detail and had access to a second, smaller male (abdomen 33 mm, hind wing 29 mm). He stated, 'In the other specimen [*i.e.*, the second male], the stripes are brown and straight, quite visible...' The original male is again characterized as follows, 'Thorax yellow green without spots and...one can scarcely see the appearance of two median stripes and a thick antehumeral stripe...', which tallies with the earlier description of 1854. The male from the ZMHB corresponds with the smaller of the two measurements given by Hagen in 1858; and it also has a pair of easily visible antehumeral stripes, an apparently rare feature for this species. The ZMHB male is unique in this respect. Even though the original description by Hagen gives 'Musée de Berlin' as the repository of the types, I strongly suspect that Hagen took the male with him when he was invited to join the faculty at the Museum of Comparative Zoology in 1867.

Other material (97♂, 44♀, including lectotype ♂ and paralectotype ♀). – U. S. A.: ARIZONA: *Cochise Co.*, San Bernardino Ranch, 15 mi E of Douglas (FSCA); NEW MEXICO: *Eddy Co.*, Sitting Bull Falls, Guadalupe Mtns., (RWG, WM); MEXICO: Chihuahua: Chihuahua Creek, 4 mi SW of Col. Juarez, (CSUC); Rio Pacheco, (CSUC); Santa Rosalia Springs, 1219 m, (ANSP); Durango: Durango City, (ANSP); Rio Dalita and marshes, 6 mi E of Durango, 1890 m, (DRP); Jalisco: Jopopau, 1667 m, (ANSP); Guadalajara, (ANSP, MCZC); Laguna de Chapala (nr. Mex. Hwy 15), 75 mi SE of Guadalajara, (RWG); Ajijic nr. Laguna Chapala (USNM, CC, TWD); Ajijic, (FSCA); Rio La Sanguijuela, Degollado, (UNAM, RWG); route 15, km 206, San Lorenzo, 9 mi W Tuxpan, (USNM, CC); Jalisco [no other locality], (BMNH); Michoacan: Arrollo W of La Piedad, (UNAM); Lago de Patzcuaro, 2.6 mi W of Quiroga, 2042 m, (FSCA); Route 15, km 206, San Lorenzo, 8 mi W of Tuxpan, (USNM); Route 15, km 431, Carapan, (USNM); Route 15, km 291, near Morelia, Parque Nacional Insurgente Morelos, (USNM); stream 0.5 mi S of Tuxpan, 1798 m, (DRP); Hidalgo: ditches around Tasquillo, 1700 m, (DRP); Rio Tula at Puente Tasquillo, (USNM); Tecozautla, Rio San Juan, 1710 m, (RWG); Tecozautla, Rio Tecozautla, 1750 m (RWG); Tecozautla, arroyo San José del Desierto, 1730 m (RWG); Mexico: Route 15, km 125, El Salitre, (USNM); Pyramids, S. Juan Teotihuacan, 2290 m, (FSCA, CUIC); Morelos: Cuernavaca (BMNH, ANSP, CUIC); Puebla: ditch just NW of Tehuacan, 1700 m, (DRP, TWD); Veracruz: Veracruz [probably erroneous locality], (MNHP); MEXICO [no other locality], (ZMHB).

Erpetogomphus heterodon sp. n.

(figs. 28-thx, 42, 43-abd, 65-hamules, 87-penis, 110, 111-app, 162-vertex, 170-leg, 193-vl, 206-distr, 230-wings)

Type data. – Holotype male. U. S. A.: New Mexico: Catron Co., Tularosa River just E of Aragon on N. Mex. Hwy 12, 28 July 1984 (R. W. and J. A. Garrison). Allotype female. Same data as male. Both in USNM.

Paratypes (36♂, 2♀). – NEW MEXICO: *Catron Co.*, same data as holotype and allotype, 27-28 July 1984, 22♂, 1♀ (RWG); same data, 23 August 1964 (Clifford Johnson), 3♂, 1♀ (DRP, FSCA); Gila Cliff Dwellings, 30 July 1983 (John E. Hafernik, Jr.), 4♂ (RWG); *Grant Co.*, Grapevine Campground, East Fork of Gila River at N. Mex. Hwy 15, 5600 ft., 27 July 1984 (R. W. and J. A. Garrison), 11♂ (RWG); TEXAS: *Jeff Davis Co.*, Limpia Canyon in Davis Mtns. State Park, 23 June 1958 (M. J. Westfall, Jr.), 1♂ (FSCA); Limpia Creek at Tex. Hwy 17, 3.4 mi NE of Ft. Davis, 4500 ft., 24 August 1977 (Dennis Paulson, Susan Hills), 1♂ (DRP); *Reeves Co.*, Balmorhea State Park, 13 Sept. 1983 (S. W. Dunkle), 1♂ (SWD); MEXICO: Chihuahua: 6 mi NNE of Boquilla, 16 July 1960 (Scheibner), 1♂ (RWG); Chihuahua Creek, 4 mi S of Col. Juárez, 25 Aug. 1986 (B. C. Kondratieff), 1♂ (CSUC); 'Bosuchel [probably Basuchi]', 18 Aug. 1950 (R. F. Smith), 2♂ (AMNH, RWG).

Description

Holotype male. – Entire face pale light green, slightly darker on postclypeus and anterior of frons; labrum, base of mandibles, labium ivory; vertex and antennae black; base of antefrons with transverse furrow, tumid medially, laterally with a pair of pits; postocellar tubercles small, no postocellar ridge; occiput pale green, slightly tumid medially, hind margin fringed with long hairs, crest with black along lateral margin, slightly emarginate medially; postocciput green, transverse; rear of head dark brown, becoming pale green laterally.

Prothorax light green with dark brown on middle lobe extending laterally to pleura, two adjacent laterodorsal small green spots on medial lobe. Synthorax

(fig. 23) light green with following dark brown: inverted wedge-shaped middorsal stripe, its ventral end not touching collar, its dorsal end forming a narrow stripe below antealar carina and meeting narrow humeral stripe; small isolated antehumeral stripe; vestigial second lateral stripe extending from metacoxa to metaspiracle; upper end of third lateral stripe. Coxae, trochanters ivory, femora ivory with black external surfaces spreading to lateral areas at distal 0.25 (fig. 170), tibiae black with small lateral ivory stripes along basal 0.5; tarsi and armature black.

Wings (fig. 230, paratype) hyaline, venation dark brown, basal wing venation brown; anterior margin of costa yellow; pterostigma brown, darker around margin.

Venational details. Fifth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 2; anx: fore wing 14/12, hind wing 9/9; pnx: fore wing 9/8, hind wing 10/10; cs under pterostigma: fore wing 4/6, hind wing 6/4; anal triangular cells: 4. Hind wing 33 mm.

Abdomen (fig. 42). Segment 1 pale orange-yellow dorsally with narrow black lateral stripe, white laterally; segment 2 similar to segment 1 but with black along anterior margin of segment laterally; segment 3 similar to segment 2 but with black along transverse carina and posterior annulus; segments 4-7 similar to segment 3 but black dorsolateral stripe incomplete anteriorly so that dorsal orange-yellow merges with lateral white and with black along transverse carina, expanding ventrally, and with a similar mark posteriorly just before black annulus; segments 8-9 predominantly yellow-orange with black denticles dorsally, incomplete black dorsolateral stripe extending from anterior margin of segment but ending just before posterior margin; segment 10 yellow-orange posteriorly, orange-brown anteriorly. Abdomen 40 mm.

Cercus (fig. 110) yellow brown, strongly angulate near middle, ventral margin with inferior carina at basal 0.30. Epiprocts curved at distal 0.75, tips darkened, bluntly pointed, slightly divergent.

Accessory genitalia (fig. 65, paratype). Anterior hamule black, divided at upper 0.30, lower branch forming a small, truncate appendage; posterior hamule white, triangular, with anterior basal shoulder, tip with small, anteriorly recurved tooth; penis with small serrated lateral lobes, cornuae (fig. 87, paratype) moderately long, widely separated tips broadly rounded.

Allotype female. – Overall colouration similar to male but with more extensive pale areas on abdomen and legs; furrow anterior to medial ocellus as in male; vertex (fig. 162) with postocellar tubercles not connected but with small remnant of ridge extending medially; occiput simple, posterior margin raised with row of hairs; postocciput green, transverse.

Venational details. Fifth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 3/2; anx: fore wing 13/12, hind wing 10/10; pnx: fore wing 7/8, hind wing 9/10; cs under pterostigma: fore wing 6/6, hind wing 6/6. Hind wing 36 mm.

Abdomen (fig. 43) as in male, but with black dorsolateral stripe reduced, with black extending anteriorly before transverse carina. Abdomen 37 mm.

Vulvar lamina (fig. 193) with broadly planar rectangular flaps meeting at anterior margin; juncture of Y-shaped postlamellar ridge at level of posterior margin of lamina.

Diagnosis

This species is related to *E. crotalinus* and *E. sipedon*. *Erpetogomphus crotalinus* lacks the dark thoracic stripes present in *E. heterodon* (fig. 22); the extensor surfaces of the tibiae of *E. heterodon* are black (fig. 170) (yellow in *E. crotalinus*); and the cornuae of the penis in *E. heterodon* are broadly rounded (fig. 87) (long and acutely pointed in *E. crotalinus* [fig. 86]).

Males of *E. heterodon* are most similar to *E. sipedon*, but they differ in thoracic maculation shape of the epiprocts, and structure of the penis. In *E. sipedon*, the antehumeral stripe is long and joined with the humeral stripe (fig. 19); in *E. heterodon*, this stripe is vestigial and disjunct. In *E. sipedon*, the tips of the superior appendages are slender and acuminate (figs. 105-106), not obtusely acuminate as in *E. heterodon* (figs. 110-111). The cornua of the penis in *E. sipedon* (fig. 83) possess a mesal lobe absent in *E. heterodon* (fig. 87).

Structurally, the females of *E. crotalinus, E. heterodon*, and *E. sipedon* approach one another closely. The latter two species have a relatively narrow occiput with the width across the crest about 4 times as long as its greatest length. The occiput in *E. crotalinus* is wider, about 3 times the width. I have been unable to detect morphological differences between females of *E. heterodon* and *E. sipedon*. Body maculation must be used to separate females.

Remarks

Variation. – Slight variation occurs in males within the type series. The dark dorsolateral stripe on abdominal segment 3 may be broken in the middle. In the male from Mexico (6 mi NNE Boquilla), this stripe is reduced to an isolated spot on the basal 0.30 of the segment. Similarly, the extent of black markings on abdominal segments 8-10 may be reduced.

Venational statistics for type series. Males: Number of marginal cells behind fore wing paranal cells: 0-3; anx: fore wing 11-14/11-15, hind wing 8-11/8-11; pnx: fore wing 7-11/7-11, hind wing 8-12/8-11; cs under pterostigma: fore wing 4-7/4-6, hind wing 4-7/4-7; anal triangular cells: 3-4. Hind wing 32-34

mm. Abdomen 36-40 mm.

Females: Number of marginal cells behind fore wing paranal cells: 1-4; anx: fore wing 13/12-13, hind wing 8-10/9-10; pnx: fore wing 7-9/8-9, hind wing 8-10/8-10; cs under pterostigma: fore wing 5-6/5-6, hind wing 5-6/5-6. Hind wing 34-36 mm. Abdomen 36-37 mm.

Biology. – Adult males were taken along sandy margins of the Tularosa River in New Mexico. They often sat on the bank facing the river and were easy to approach. I collected one female as it hovered over the river ovipositing. Another teneral female was flushed from nearby vegetation. At the East Fork of the Gila River, males sat on emergent rocks in the stream or by the river's edge. They occasionally made swift sorties, usually to chase another male. At this locale, *E. heterodon* was sympatric with *E. lampropeltis natrix*. Altitudinal data show *E. heterodon* to occupy high, mostly xeric areas of the southwestern United States and northern Mexico. Collection dates are from 23 June to 13 September at elevations of 1370 m (Limpia Creek, Texas) to 1700 m (Grapevine Campground, New Mexico).

Distribution (fig. 206). – *Erpetogomphus heterodon* is known only from western Texas, New Mexico, and northern Mexico. It has been collected with *E. crotalinus* in at least one locality in Mexico (Chihuahua state, Rio Pacheco, 27 Aug. 1986, B. Kondratieff, S. Dunkle, pers. comm.), and is apparently allopatric with *E. sipedon*.

Erpetogomphus compositus Hagen *in* Selys

(figs. 24, 25-thx, 66, 67-hamules, 88, 89-penis, 112, 113-app, 145-ept, 139-base of postfrons, 163-vertex, 194-vl, 206-distr)

Erpetogomphus compositus Hagen *in* Selys, 1858: 660 (400 sep.) (♀, 'Rivière Peros [*sic*: Pecos] (*Texas occidental*)'). – Hagen *in* Selys 1859: 536 (10 sep.) (descr. ♀); Hagen *in* Selys 1873a: 740 (12 sep.) (descr. ♂, ♀, 'Le nord de la Californie"); Selys 1873b: 519 (75 sep.) (list); Calvert 1905: 166 (Ariz.); Calvert 1908a: 45 (Ariz.); Muttkowski 1910: 86 (cat.); Calvert 1912a: 289 (mentioned); Williamson 1914a: 226 (Ariz.); Kennedy 1917a: 544 (Calif.); Seemann 1927: 22 (Calif.); Byers 1928: 51 (larva unknown); Needham and Heywood 1929: 80 (descr.); Williamson and Williamson 1930: 12 (summary of status); Tinkham 1934: 215 (W. Tex.); Ahrens 1938: 11 (Ariz., Utah); Fraser 1940: pl. 5 (penis); Ferguson 1940: 5 (Tex.); Needham and Westfall 1955: 144 (descr.); Pritchard and Smith 1956: 116 (key); Gloyd 1958: 8 (W. Tex.); Musser 1961: 54 (larva, Utah); Musser 1962: 14 (larva, Utah); Borror 1963: 104 (common name); Cruden 1964: 81 (Calif.); Montgomery 1968: 133 (distr.); Paulson and Garrison 1977: 151 (Washington); Molnar and Lavigne 1979: 130 (Wyo.); Paulson 1982: 255 (distr.); Paulson 1983: 67 (Wash.); Davies and Tobin 1985: 27 (cat.); Tsuda 1986: 87 (cat., attributes authorship to Selys); Bick 1990: 3 (Idaho); Bridges 1991: VII: 49 (cat.); Tsuda 1991: 5 (cat.).

Gomphus compositus. – Hagen 1861: 99 (desc. ♀, Tex.).

Gomphus (Herpetogomphus)? viperinus. – Hagen, 1873 (misidentification, Yellowstone).

Herpetogomphus compositus. – Hagen 1874: 597 (Yellowstone, Tex.); Hagen 1875a: 42 (Tex.); Hagen 1875b: 918 (N. Mex.); Selys 1879: 64 (2 sep.) (characters of genus); Kirby 1890: 60 (cat., attributes authorship to Selys); Calvert 1899: 386 (characters of genus); Currie 1903: 303 (Ariz.); Osburn 1905: 186 (mentioned); Byers 1928: 5 (larva unknown); La Rivers 1938: 85 (Nev.); La Rivers 1940a: 112 (Nev.); La Rivers 1941: 177 (Nev.).

Erpetogomphus coluber Williamson and Williamson, 1930: 17 (♂, San José de Comandu, Baja Calif. Sur). – Needham and Westfall 1955: 143 (desc.); Borror 1963: 104 (common name); Montgomery 1968: 133 (distr.); Montgomery 1973: 239 (comment on name); Paulson 1982: 255 (distr.), 266 (synonymy with *E. compositus*); Bridges 1991: VII: 49 (cat.).

Description

Male. – Entire face pale grey green with dark markings as follows: along basal margin of labium and median extension ending before distal margin (almost absent in some specimens), frontoclypeal suture, base of antefrons; vertex all dark brown or with pale median area extending posteriorly from median ocellus to anterior margin of occiput; antennae dark brown; anterior margin of vertex forming a trough at junction of postfrons, this trough with a pair of deeper pits anterolateral to median ocellus (fig. 139); occiput white green, wide, planar with slight tumid median area, crest barely convex, slightly to broadly emarginate medially, its hind margin covered with pale brown hairs; postocciput white green, transverse, not visible dorsally, rear of head dark brown.

Prothorax pale green with brown dorsolaterally on middle lobe; synthorax (fig. 24) predominantly pale green with following dark brown: well defined middorsal stripe widening to collar, its upper end extending along antealar sinus connecting with well defined humeral stripe; antehumeral stripe widened dorsally and connected basally at mesinfraepisternum; lower part of humeral stripe extending posteroventrally but not connecting with well defined sinuate second lateral stripe; lower 0.50 of this stripe encompassing metaspiracle, constricted along posterior margin at 0.50 and abruptly widening dorsally before turning anterodorsally toward subalar carina; complete third lateral stripe ending behind posterior margin of metacoxa. Pale colour of thorax light green with lighter tone almost becoming white in areas between antehumeral and humeral stripes, and between second and third lateral stripes. Coxae, trochanters white grey with slight wash of brown, tibiae pale grey green with defined superior surfaces black, basal 0.40 of metafemora with streaks of grey green or with basal 0.60 of this area largely pale, tibiae black with narrow stripe of pale grey green along basal 0.30 of lateral margin in

some specimens; tarsi and armature black.

Wings hyaline with slight wash of yellow at extreme base (more so on teneral specimens), basal wing venation brown, especially anteriorly, anterior margin of costa yellow white except for anterior margin of pterostigma, costa beyond pterostigma white or darkened, but contrasting with black of pterostigma; pterostigma black.

Venational statistics. Fifth antenodal thickened in all wings; marginal cells behind fore wing paranal cells: 0-4; ; anx: fore wing 10-15/10-15, hind wing 7-11/7-11; pnx: fore wing 6-11/6-10, hind wing 7-11/7-11; cs under pterostigma: fore wing 3-6/3-6, hind wing 3-6/3-6; anal triangular cells: 2-5. Hind wing 25-32 mm.

Abdomen. Segment 1 pale grey green with broad basal semicircle of brown laterally, its posterior end touching lateral articulated area; segment 2 white with dorsolateral brown stripe sending a ventral stem posterior to auricle, and connecting with black annulus, a small brown spot at anteroventral margin of segment; segment 3 with isolated black dorsolateral spot surrounding lateral carina, distal 0.25 of segment with dorsolateral black increasing in width posteriorly and touching dorsally near black annulus; segment 4 similar to segment 3, but isolated black of transverse carina longer and touching or connecting with distal black, thus forming an incomplete midlateral stripe occupying distal 0.75 of segment and isolating ventral longitudinal wedge of white; segments 5 and 6 like segment 4, but with middorsal white becoming fuscous; segment 7 with anterior 0.5 white, except for tawny transverse carina, becoming entirely tawny posteriorly, some specimens with varying degrees of lateral black on posterior 0.25 of segment or in specimens from Baja California (*E. coluber*) with tawny areas becoming black; segments 8-10 yellow brown with darker red brown dorsally, in Baja California specimens this dark red brown replaced with well defined black on segments 8 and 9, and dark brown on segment 10. Abdomen 32-39 mm.

Cercus (figs. 112-113) ocher, in lateral view slightly concave dorsally near base and with tips slightly recumbent, cercus enlarged ventrally at basal 0.45 with inferior carina along this same area, remainder slightly concave with tip forming a blunt point. Epiprocts yellow brown, gently curved dorsally at 90°, tips (fig. 134) dorsoventrally flattened and truncate or obliquely truncate.

Accessory genitalia (figs. 66-67). Anterior hamule dark brown, divided at basal 0.5; lower branch forming a small, posteriorly directed truncate appendage; posterior hamule grey white, triangular; with anterior basal shoulder, tip bluntly rounded and armed with a small anteriorly directed tooth on posterior border; penis with lateral lobe small, roughly semicircular, serrate; cornuae (figs. 88-89) moderately long, widely separated, tips broadly rounded.

Female. – Head as in male but pale areas more extensive, especially on vertex, where dark brown may be reduced to areas around ocelli and postocellar protuberances; occiput narrower than in male, with erect curvilinear occipital crest separating easily visible postocciput (fig. 163), posterior margin of postocciput slightly concave; prothorax and thorax as in male, but with pale areas more extensive; wings with yellow at base more extensive, often with markings within second series of antenodals to level of arculus and cubitoanal area in both wings.

Abdomen in well preserved specimens with pale colours primarily white with pale orange dorsally, black dorsolateral stripes reduced and separated in their middle on segments 3-6; segment 7 similar to male but with posterior 0.25-0.30 darker laterodorsally; segments 8-10 tawny, with varying amounts of dark brown, especially dorsally, on segments 8-9; cerci ocher. Abdomen 31-37 mm.

Vulvar lamina (fig. 194) with prominent basal plates, quadrangular laminar plates acuminate posteriorly, meeting at anteromedial margin; cleft between plates forming a 90° angle; stem of Y-shaped postlamellar ridge at level of posterior margin of lamina.

Venational statistics: number of marginal cells behind fore wing paranal cells: 1-6/0-5; anx: fore wing 12-15/12-14, hind wing 8-11/9-11; pnx: fore wing 7-11/8-10, hind wing 9-11/8-11; cs under pterostigma: fore wing 3-5/4-6, hind wing. Hind wing 30-32 mm.

Diagnosis

This common, distinctive species is easily separated from its nearest ally, *E. lampropeltis*, by several structural and maculation characters. Males of *E. compositus* differ from *E. lampropeltis* in lacking the characteristic middorsal angulation of the cercus. The tip of the epiproct in *E. compositus* is truncate (fig. 134), but this structure in *E. lampropeltis* is obliquely and bluntly pointed (fig. 132). Depressions in male and female anterolateral to median ocellus will also separate the species: in *E. compositus*, an arcuate trough has more pronounced pits anterolateral to the median ocellus (fig. 139). In *E. lampropeltis*, the anterolateral pits are deeper and the intervening area directly anterior to the median ocellus is not as depressed (fig. 138). This structure in *E. lampropeltis* more closely approaches the condition found in *E. viperinus* (fig. 137).

Erpetogomphus compositus, though a boldly marked species, is lighter than *E. lampropeltis*. The occipital crest in *E. compositus* is largely pale, though there may be some darkening along the lateral 0.30 of margins in specimens from Baja California. In *E. lampropeltis*, the occipital crest is entirely dark brown and provides

a striking contrast to the pale occiput. The thoracic patterns of the two species are different (figs. 20-21, 24-25), and the dorsolateral black stripes of abdominal segments 4-6 of *E. lampropeltis* are more extensive.

In the field, pale thoracic colouration will easily separate both species. *Erpetogomphus compositus* is unique in having a pale green thorax with intervening grey white areas between the antehumeral and humeral stripes and second and third lateral stripes. In *E. lampropeltis*, the thoracic colouration is grey green (*E. lampropeltis lampropeltis*) or dark green (*E. lampropeltis natrix*).

Females of *E. compositus* differ from *E. lampropeltis* in the shape of the occiput. In *E. compositus*, the occiput is narrow and the postocciput is clearly visible in dorsal view (fig. 163). In *E. lampropeltis*, the occiput is broad and the postocciput is not visible dorsally (fig. 160). Secondly, the area in front of the median ocellus mirrors the condition stated for males above. The vulvar laminae of the two species appear indistinguishable.

Remarks

Williamson and Williamson (1930) described in detail *Erpetogomphus coluber*, comprising 31 males from San José de Comandu, Baja California. In comparing *E. coluber* with other species, they stated that *E. coluber* would, in Calvert's (1905) key to the genus '...run to AA, page 160, and if the individual be one with the facial dark markings reduced, it will run to *H. compositus*. Drs. Calvert and Kennedy regard *coluber* as distinct from any described species.' The Williamsons sent two males to Calvert, who commented, 'No special reason for thinking it *diadophis* [= *E. eutainia*]; like a small *compositus*; differs in size; has broader metepisternal dark stripe; brown on [abdominal segments] 3-7 more extended; brown on 8-10 much darker; darker lines or stripes on the frontoclypeal and clypeo-labral sutures'. Finally, the Williamsons commented on the affinities of *E. coluber* to *E. compositus* as follows: '*Compositus* is certainly its closest relative and the derivation of *coluber* from *compositus*, through geographical isolation in Baja California, is almost certain and is a case exactly parallel, so far as speciation goes, to that of certain species, of several genera, endemic in Florida. *Coluber* is separated from *compositus* by its darker color, especially of the last four abdominal segments and by venational characters, especially the two-celled anal triangle and the single row of cells posterior to A in the front wing.'

I have seen the holotype and 15 paratypes of *E. coluber* and believe, as did Paulson (1982), that they represent diminutive, melanic examples of *E. compositus*. The specific differences ascribed to *E. coluber* are those of venation only, and I believe these to be correlated to their smaller size. I have found no differences in body morphology, including the accessory genitalia.

Variation. – Two specimens from San Diego County appear intermediate to *E. coluber* and *E. compositus* s.s. These males have more pronounced dark thoracic stripes, but the dorsum of abdominal segments 8-10 lacks dark brown markings typical of *E. coluber*. However, other *E. compositus* have varying amounts of dark brown on these segments. The hind wing anal triangle in 3 of 16 specimens of *E. coluber* has 3 anal triangular cells instead of 2, and a 2-celled anal triangle, though rare, does exist in *E. compositus* (s.s.). For example, of 21 males I measured from California, Arizona, and another from northern Baja California, one of the San Diego males and another from Riverside, California, had one wing each with two cells. These two specimens had shorter hind wings (26 mm and 28 mm, respectively) than is typical for *E. compositus* (s.s.). Statistics for the number of anal triangular cells show it to be variable within *E. compositus* (s.s.). The number of wings with range of stated conditions is (number of wings follows in parentheses): 3 (19), 4 (19), 5 (2). Hind wing lengths from the San Diego males are 25-26 mm, well within the range for *E. coluber*. The next smallest specimen is a male from Riverside (28 mm), the same male with two anal triangular cells in one hind wing.

Most wings of *E. coluber* which I have examined have no marginal cells behind the fore wing paranal cells, but 6 of 32 (19%) did. Eight of 42 (19%) wings of *E. compositus* (s.s.) had no marginal cells.

Williamson and Williamson (1930) warned of fallibility of some of their characters among the paratypes they examined: 'The face markings are very pronounced in some and scarcely discernible in others; there is considerable variation in the extent of the dark thoracic markings [fig. 25] and this variation occurs independently on the mesepisternum and metepisternum, so an individual may have the dark humeral and antehumeral relatively extensive and the two dark lateral stripes relatively reduced and *vice versa*.'

With the exception of specimens from Baja California and the two specimens from San Diego, body colouration appears remarkably constant throughout its range. The male from Baja California Norte (Guadalupe Hot Springs) is more like typical *E. compositus*, but it has no marginal cells behind the fore wing paranal cells. The hind wing length (29 mm) and other venational characters indicate a closer relationship to more northerly populations.

The female holotype was collected with the type series of *E. designatus* and was probably collected in the vicinity of Roswell, New Mexico in 1854-1855. See

remarks under *E. designatus* for further details.

Venational details. Holotype female of *E. compositus*: number of marginal cells behind fore wing paranal cells: 2/4; anx: fore wing 13/13, hind wing 9/10; pnx: fore wing 8/9, hind wing 9/8; cs under pterostigma: fore wing 5/6, hind wing 5/6. Holotype male of *E. coluber*: number of marginal cells behind fore wing paranal cells: 0/0; anx: fore wing 12/12, hind wing 9/9; pnx: fore wing 7/7, hind wing 9/9; cs under pterostigma: fore wing 2/2, hind wing 4/4.

Biology. – This species and *Progomphus borealis* McLachlan *in* Selys are the two most conspicuous gomphid elements along most desert streams and irrigation ditches in the southwestern United States. In Arizona, this species occurs commonly in the Lower Sonoran Zone, and in ecotonal fingers into the Upper Sonoran Zone. Kennedy (1917a), who collected *E. compositus* at certain sites in the northern Central Valley of California, writes: 'One female, a teneral, was taken on the irrigating ditch across the river from Oroville.' Collecting along the lower Truckee River south of Pyramid Lake, Nevada, Kennedy (1917a) mentions that 'This widely spread species occurred sparingly on the riffles of the lower Truckee. The males appeared to be more nervous and more touchy, flying farther for conflict with passing males than the males of *Ophiogomphus morrisoni nevadensis*.'

The two males collected at the Boyce Thompson Southwestern Arboretum in Pinal County, Arizona, had the following annotation by H. K. Gloyd: '[in] Creek, arboretum. Canyon, after rain and run-off almost over. between 5 & 7: 00 p.m., water low, few dragonflies seen'. Williamson and Williamson (1930) provided a lengthy account of the type locality and assemblage of Odonata present with *Erpetogomphus coluber*. In August, 1972, I collected several *E. compositus* with *Stylurus plagiatus* (Selys) at Riverside Park, Yuma, Arizona. Adults were taken in the late afternoon on grassy areas shaded by trees. Adults of this species and *Progomphus borealis* were abundant along Big Chico Creek in Chico, Butte County, California in June and July of 1974, 1976, and 1978. They sat on exposed sand bars near the edge of the creek, and both were difficult to approach. *Progomphus borealis* was the more wary. In the late afternoon, I have collected *E. compositus* away from water, resting on dry desert scrub. Collection dates range from 24 May (Nevada: Clark Co.) to 13 Dec. (Calif.: San Bernardino Co.).

Distribution (fig. 206). – *Erpetogomphus compositus* is a desert species found commonly in the southwestern United States. It has been taken as far east as Dallas (Hagen, 1875a), but most records from Texas are from the western portion of the state. It occurs in eastern New Mexico and is common in low desert regions of Arizona, especially southwest of the Mogollon Rim. It is common in the arid regions of southern California and penetrates north through the Central Valley to Chico. Paulson and Garrison (1977) list it from south central Washington. The species was listed from Oregon by Hagen (1875a, 1875b) with no specific locality); but specimens were recently collected from the John Day River, Deschutes Co., Oregon (Valley 1993). *Erpetogomphus compositus* occupies river systems in the Great Basin of Nevada, but its most easterly distribution is unknown. Bick (1990) lists a specimen from Owyhee Co., Idaho. Hagen (1874) records it from the Yellowstone, but it was probably taken in a more arid environment around what is present-day Yellowstone National Park. Molnar and Lavigne (1979) also cite it without specific locality from Wyoming, based on previous records given by Needham and Heywood (1929), Needham and Westfall (1955), and Pritchard and Smith (1956). All of these records probably originated from the original Hagen (1874) citation. In Utah, the species apparently penetrates only the southwesternmost part of the state. The most southerly distribution for *E. compositus* is also unknown. Except for *E. coluber*, the only records I have observed from mainland Mexico are two males collected by J. H. Williamson in Hermosillo, Sonora. The distribution of *E. compositus* in Texas, New Mexico, and Arizona indicates that it must be further widespread in northern Mexico.

Material

Type data. – Of *E. compositus*: Holotype female with following label data: 'Aug/ 16' [handwritten], 'Hagen' printed [two of these labels attached], '*compositus*' written in an unknown hand; red label 'HOLOTYPE [printed] / *Erpetogomphus compositus* / Hagen 1857 [*sic*, should be 1858] '♀' handwritten by RWG. In MCZC. Of *E. coluber*: Holotype male dry in envelope with following data: '*E. coluber*' written in pencil by E. B. Williamson, 'Mexico/ State of Baja California/ San Jose de Comandu/ J. H. Williamson/ Oct 10 1923' [all stamped]/ ♂214.' handwritten by EBW, 'Type' handwritten in pencil by EBW on side of label. In UMMZ.

Type locality of *E. compositus* herein restricted to vicinity of Roswell, Chaves Co., New Mexico (see remarks under *E. designatus*).

Other material (151♂, 46♀, including holotype ♀ *E. compositus* and holotype ♂ *E. coluber*). – U. S. A.: ARIZONA: *Cochise Co.*, Miller Cyn., Huachuca Mtns., (CC); pond at Slaughter Ranch, San Bernardino Valley, 15 mi E of Douglas, 1169 m, (RWG); 5 mi E of Hereford (CC); San Pedro River, 9 mi SW of Tombstone, (BYUC); San Pedro River, at Hereford Rd., (RWG); *Coconino Co.*, Havasu Canyon, 3 mi N of Supai, 923m, (RWG); Supai, (CDFA); *Graham Co.*, 3 mi SE of Bylas, valley of the Gila, 2000 ft., (UMMZ); Roper Lake, 5 mi S of Safford (RWG); *Maricopa*

Co., Granite Reef Dam, (UMMZ); Mesa, (UMMZ); Phoenix, (RWG); slough ponds by Verde River, by Ariz. Hwy 87, Ft. McDowell Indian Reservation (RWG); Tempe (UMMZ); *Mohave Co.*, spring, Hwy 15 bridge, Littlefield, (BYUC, RWG); Virgin River, Big Bend, (BYUC); *Pima Co.*, Organ Pipe Cactus Nat'l. Mon., Quitobaquito, (Long Beach State Univ.); Quitobaquito Springs, 15 mi S of Lukeville, Organ Pipe Cactus Nat'l. Mon., (RWG); *Pinal Co.*, Boyce Thompson Southwestern Arboretum, 4 1/2 mi SW of Superior, (UMMZ); 8 mi NW of Florence, (UMMZ); *Santa Cruz Co.*, Santa Cruz River, Sonoita Creek Ranch (on way to Salero Cyn.), *ca.* 2 mi W of Patagonia, by Ariz. Hwy 82, (RWG); *Yavapai Co.*, Oak Creek at Cornville, 1077 m, (CSUC); *Yuma Co.* Ave 3E at Co. 14 St., SE of Yuma, (RWG); Riverside Park, nr. Colorado River, Yuma, (RWG); N. R. Adair Park, McPhaul Bridge, by Gila River, *ca.* 15 mi ENE of Yuma, (RWG); CALIFORNIA: *Butte Co.*, Bidwell City Park, by Big Chico Creek, Chico, 61 m, (RWG); Oroville, (UMMZ); *Fresno Co.*, Friant, San Joaquin River, (UMMZ); *Imperial Co.* Calexico, (BYUC); canal 8 mi E of Holtville, sea level, (DRP); ditch 4.7 mi E of Bond's Corner, (DRP); Hot Mineral, (LACM); irrigation canal 7.3 mi E of Holtville, (DRP); irrigation canal at Winterhaven, (DRP); *Inyo Co.*, Hunter Cyn., Salino Valley, (LACM); Laws, Owens River, (UMMZ); Lone Pine, Owens River, (UMMZ); *Los Angeles Co.*, Tanbark Flat, (CDFA); *Mono Co.*, 5 mi N of Benton Station, 5300 ft., (UMMZ, LACM); *Riverside Co.* Blythe, (CC); Coachella Valley Preserve, NE of Thousand Palms, (J. Cole); Palm Springs, (LACM); Whitewater River nr. Salton Sea, (DRP); *San Bernardino Co.*, Colorado River at Moabi Rd., S of Needles, (RWG); Lost Palm Cyn., Joshua Tree N. Mon., (Long Beach State Univ.); Parker Dam, (RWG); *San Diego Co.*: T14S, R5E, (CASC); San Felipe Creek, 13.8 mi E of Julian, 615 m, (DRP); San Felipe Creek at Scissors Crossing, 11.9 mi E of Julian, 738 m, (DRP, RWG); Sentenac Cyn., (LACM); Vallecito, (LACM); *Yolo Co.*, Cache Creek at William H. 'Bill' Davis Memorial Picnic Area, by Calif. Hwy 16, 6 mi N of Rumsey, 132 m, (RWG); NEVADA: *Clark Co.*, Logandale, (BYUC); *Elko Co.*, Carlin, Humboldt River, (UMMZ); 8.5 mi NW of Currie, (UMMZ); *Humboldt Co.*, Can Spring, 3 mi S of Pahuhe Meadows, (UMMZ); *Lincoln Co.*, 6 mi S of Alamo, (UMMZ); *Nye Co.*, Amargosa R., 2 mi below Beatty, (UMMZ); *Pershing Co.*, Lovelock, Humboldt River, (UMMZ); *Washoe Co.*, Pyramid Lake, Truckee River, (UMMZ); *White Pine Co.*, 2 mi NW of Preston, (UMMZ); TEXAS: *Brewster Co.*, Big Bend Nat'l Park, 1 mi N of Rio Grande Village, (RWG); Boquillas Cyn., Big Bend Nat'l. Park, (CSUC); Rio Grande Village, Big Bend Nat'l. Park, (CSUC); *Maverick Co.*, Quemado, (LACM); UTAH: *Washington Co.*, St. George, (CC); Beaver Dam Wash, Terry Ranch, (BYUC); Beaver Dam Wash, Lytle Ranch, (BYUC); Gunlock, W of Veyo, (BYUC); Virgin River, Virgin, (BYUC); MEXICO: *Baja Calif. Norte*: Guadalupe Hot Spgs., Guadalupe Cyn., Sierra Juarez, (CSUC); *Baja Calif. Sur*: San José de Comandu, 10 Oct. 1923 (J. H. Williamson), 15♂ (all paratypes of *E. coluber*) (UMMZ, RWG, FSCA, USNM); *Sonora*: Hermosillo, (UMMZ).

Erpetogomphus boa Selys
(figs. 26-thx, 44, 45-abd, 68-hamules, 90-penis, 114, 115-app, 135-ept, 164-vertex, 167-postocciput, 195, 196-vl, 207-distr)

Erpetogomphus boa Selys, 1859: 37 (11, sep.) (descr. ♂ 'Vera Cruz, Mexique. Par M. Salle. (Collect. Selys.)'). – Walsh 1863: 253 (mentioned); Selys 1873b: 519 (75, sep.) (list); Calvert 1905: 165 (notes); Calvert 1907: 399 (possible identity with *E. elaps*); Muttkowski 1910: 86 (cat.); Ris 1917: 153 (notes and descr. of 2nd known ♂); Williamson and Williamson 1930: 11 (summary of status); Paulson 1982: 255 (Mex.); Davies and Tobin 1985: 27 (cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.31 (cat.); Tsuda 1991: 95 (cat.).

Erpetogomphus crotalinus, nec Hagen *in* Selys, 1854. – Selys 1859: 537 (11, sep.) (♀ descr. 'Vera Cruz, Mexique. Par M. Salle. (Collect. Selys.)' = *E. crotalinus* Hagen *in* Selys, 1858.

Gomphus boa. – Hagen 1861: 100 (descr. from Selys).

Herpetogomphus boa. – Walsh 1862: 389 (mentioned); Hagen 1875a: 42 (cat.); Selys 1879: 64 (2, sep.); Calvert 1899: 386 (list, English translation of Selys, 1879); Calvert 1908b: 693 (mentioned).

Description

Male. – Labrum, clypeus, and frons light blue green, paler along sides of labrum and lateral lobes of postclypeus; base of mandibles pale green, tips black; base of antefrons anterior to median ocellus with narrow, arcuate, V-shaped sulcus, shallower medially; vertex dark brown with usual postocellar tubercles, occiput tumid medially, pale green brown, its posterior margin ciliated, transverse to slightly concave, slightly emarginate in the middle, or more rarely smoothly curved, postocciput green, tumid; rear of head red brown.

Prothorax red brown, synthorax (fig. 26) predominantly green, area around middorsal carina washed with brown, often appearing as a faded middorsal stripe; antehumeral and humeral stripes dark brown, united into one large stripe; most of this stripe occupying posterior 0.30 of mesepisternum, metastigma black, a wash of brown between metepisternum and metepimeron often forming an obscure, narrow thoracic stripe, subalar carina darkened with brown, mesinfraepisternum and metinfraepisternum brown; metasternum green-brown. Coxae pale grey- brown with some green on exterior surfaces, trochanters grey brown, femora tawny at base, becoming dark brown distally, tibiae and tarsi black.

Venational statistics (n = 13, including lectotype ♂). Fifth antenodal (occasionally fourth, sixth, or seventh) thickened in all wings; marginal cells behind fore wing paranal cells: 0- 4/0-4; anx: fore wing 13-15/13-16, hind wing 9-11/10-12; pnx: fore wing 9-12/9-11, hind wing 10-13/10-13; cs under pterostigma: fore wing 5-7/5-7, hind wing 5-7/5-7; anal triangular cells: 4-5. Hind wing 33-34 mm.

Abdomen (fig. 44). Segment 1 brown dorsally, becoming green laterally; segment 2 with blue green middorsal stripe, with dorsolateral stripe of brown surrounding green auricle, lateral margin near hamules pale greenish white; segment 3 with green middorsal stripe bounded on sides by dorsolateral stripes of brown, lateral areas of tergites pale green becoming white posteriorly, anterior transverse carina edged

with black expanding laterally interrupting white lateral areas of segment, thus forming two pale spots, posterior transverse carina also black, expanding laterally so that posterior 0.2 of segment is black; segments 4-6 similar to segment 3, but with middorsal brown stripe narrowed anteriorly so that whitish green side almost touches middorsal green; segment 7 with anterior 0.5 dull white, conspicuously traversed by black anterior transverse carina, posterior 0.5 of segment red brown; segments 8-10 red brown with ventral and posterior borders of each segment black. Appendages red brown with apices becoming black. Abdomen 37-40 mm.

Cercus (fig. 115) nearly straight, swollen anteriorly, apical 0.5 abruptly concave dorsally and covered with thick series of strong black bristles. Epiprocts about 0.5 the length of superiors, strongly curved dorsally; tips slightly divergent, each a thick, blunt point (fig. 135).

Accessory genitalia (fig. 68). Anterior hamule black, glabrous, deeply forked with posterior branch slightly longer than anterior, the whole structure resembling a talon; anterior branch of hamule with a small semi-oval planar surface on outer side, this area covered with small hairs. Posterior hamule pale green or white, becoming brown near tip; in lateral view, tip obtusely pointed with posterior margin gently convex. Penis (fig. 90) with lateral lobes poorly developed posteriorly, almost circular, its margin serrated.

Female. – Overall colouration as in male, but with pale areas on abdomen and legs more extensive. On abdomen (fig. 45), brown on terminal segments extending anteriorly so that green middorsal and dorsolateral brown stripes become ill-defined. Lateral margins of abdominal segments mostly white and similar to male except that white extends posteriorly to segment 8. abdomen 37-40 mm.

Vertex with slightly tumid, oval areas posterior to lateral ocelli; posterior margin of occiput (fig. 164) elevated and nearly straight; postocciput green, tumid medially (fig. 167).

Venational statistics. Fifth antenodal (occasionally fourth, sixth, or seventh) thickened in all wings; anx: fore wing 13-16/13-16, hind wing 10-12/10-11; pnx: fore wing 9-13/9-12, hind wing 10-13/10-14; cs under pt: fore wing 5-7/5-8, hind wing 5-8/5-8. Hind wing 34-37 mm.

Vulvar lamina (fig. 195) membranous, diagonally corrugated, outer margin of plate with strong costate ridge, area immediately mesal to ridge furrow-like, with a smaller tumid area occupying the center, medial area tumid, posterior margin of each plate a thin, membranous ridge, postlamellar ridge long, greatly surpassing hind margin of lamina, its Y-shaped juncture at distal 0.30 of sternum. Abdomen 37-40 mm.

Diagnosis

Erpetogomphus boa is most similar to *E. cophias*, but is easily distinguished by the thoracic pattern and the male caudal appendages. A well-defined combined antehumeral and humeral stripe is present in *E. boa*, but no such stripe is present in *E. cophias*. The superior appendages of *E. cophias* possess a large ventral ridge which ends in a prominent tooth 0.30 the length of the appendage (fig. 116). This structure is lacking in *E. boa* (fig. 115). Dorsally, the apical 0.30 of the superior appendages of *E. cophias* contains a few strong bristles, not as many or as stout as in *E. boa*.

The females of these two species are similar morphologically, but may be distinguished by the thoracic pattern. The postocciput of *E. boa* (fig. 164) does not have the posterior depressions on each side found in *E. cophias* (fig. 165).

Females of *E. boa* superficially resemble females of *E. viperinus*, but the latter have a pair of circular depressions on abdominal sternite 9 posterior to the juncture of the postlamellar ridge which are absent in *E. boa*. The vulvar lamina of *E. viperinus* (fig. 184) is totally unlike that of *E. boa* (figs. 195-196).

Remarks

This species has been known from only two specimens: Selys' type and an incomplete male described by Ris (1917). The lectotype is a teneral male with the apical 0.5 of the cerci missing (fig. 114), but it was apparently complete at the time of the original description. The original description of the male is as follows (translated from the French): 'Pterostigma light yellow brown. Head and thorax yellow, femora yellow, with an external brown stripe, short, the anterior four tarsi brownish black.

'[male]. Superior appendages swollen at their base, with an obtuse tooth above at the end of the swelling; their points rounded, slightly bent inwards, hairy. Inferior appendage divided, branching a little distance, attaining 1/2 length of the superior. Occiput nearly straight. Tibiae brown.'

Selys' (1859) description of the female led Calvert (1905) to believe that it was really a specimen of *E. crotalinus*; and my examination of this female confirms Calvert's assertion. *Erpetogomphus crotalinus* appears to be restricted to the Pacific side of Mexico, and I doubt that the locality ('Vera Cruz') is correct for this specimen. In the supplement to the Biologia (Calvert, 1907), Calvert received drawings of the incomplete abdominal appendages of the type which led him to remark that *E. boa* seemed hardly different from *E. elaps*. Ris (1917) provided a history of the type male of *E. boa* and remarked (translated from the German): 'I examined a long time ago in the Hamburg Museum an old male that was different

from *elaps* and corresponds with the description of *boa*, that its identity [with *boa*] seemed likely. The locality is, unfortunately, uncertain, the label reads 'Agua Caliente' without further information. Its preservation is fair, the tip of the inferior appendages are missing about the distal fourth as shown in the figure...'

Examination of the hamules of the lectotype verifies the identity of a series of *E. boa* all collected in southern Veracruz; and the Agua Caliente specimen of Ris is also *E. boa*.

Calvert (1905) postulated that *E. sipedon* might be the female of *E. boa*. Although I have not seen a pair of *E. boa* in copula or in tandem, I am confident in ascribing these females to *E. boa*. The similarity of the vulvar laminae in *E. boa* and *E. cophias* (whose males are closely related) further strengthens my conviction that *E. sipedon* does not represent the female of *E. boa*. López (*in litt.*) has observed tandem pairs, confirming the female sex of this restricted species.

The male epiprocts, which are robust and form a sharp point, are apparently responsible for structural damage to the vertex of many females during mating. Of the 26 females I examined, 14 (54%) had two holes medially to the postoccipital tubercles. Some of these specimens had encrusted haemolymph surrounding the wounds. Dunkle (1984, 1991) reviews cases of traumatic mating among other anisopteran Odonata, but their negative effect, if any, is unknown. Of the remaining 12 females, which were uninjured, 5 were teneral and had not yet mated.

Venational details of lectotype male: fifth antenodal thickened in fore wings, fourth in hind wings; marginal cells behind fore wing paranal cells: 1?/2; anx: fore wing 14/14, hind wing 10/10; pnx: fore wing 10/10, hind wing 10/11; cs under pterostigma: fore wing 5/6, hind wing 5/5; anal triangular cells: 4. Hind wing 34 mm.

Biology. – Most specimens were obtained at a city park near Jalapa. Individuals were found by flushing them from low vegetation about 50 m from a small stream. Adults spent most of their time resting and were difficult to detect among the green foliage. Its habits are similar to those reported for *E. viperinus*. Adults prefer parts of small, low volume sandy-bottomed streams where banks are often covered by trees. Reproductive maturation continues through July. Copulation apparently occurs primarily in open areas near streams. Ensuing pairs fly some distance from these sites. Some males settle at the edge of the stream, but passing females are unreceptive there. Females, like other members of this genus, oviposit unattended, flying over the water, stopping briefly to drop eggs from a height of about 40 cm. López has observed *E. boa* captured by spiders (Araneidae) and robber flies (Asilidae).

Collection dates are July and August. Altitudes of capture range from 1150 m (Orizaba) to 1300 m (Jalapa).

Distribution (fig. 207). – *Erpetogomphus boa* has been taken only in central Veracruz between 18°50'N and 19°30'N along the eastern foothills of the Sierra Madre Oriental.

Material

Type data. – Lectotype male by present designation with following data: small green label 'Vera Cruz/Salle', yellow rectangular label: 'ERPET. BOA / ♂' [this last label probably added by Selys during or after 1879], all in Selys' hand; two pencilled labels on red tags: 'No. 100'; and two pencilled white labels: '28', all in an unknown hand. The caudal appendages and accessory genitalia are shown in fig. 114. The female specimen originally described as the female of *E. boa* is actually *E. crotalinus* and possesses the following labels: small green label: 'Vera Cruz/Salle'; and white label: '*Herp. boa* S. / ♀', both in Selys' hand. Both specimens in IRSN.

Other material (13♂, including lectotype ♂; 26♀). – MEXICO: *Veracruz*: Parque Javier Clavijero, Jalapa, 1300 m, 21 June 1980 (Raul López), 1♂ (RWG); (same data), 11 Aug. 1980 (A. Garcés), 1♂ (UNAM); (same data), 13 Aug. 1980 (R. López), 1♂ (UNAM); (same data), 16 Aug. 1980 (A. Garcés), 1♂ (UNAM); (same data), 20 Aug. 1980, 1♀ (UNAM); (same data), 5 Aug. 1981, (R. López), 2♂, 6♀ (RWG); (same data), 6 Aug. 1981, 1♂ (UNAM); (same data), 1 Aug. 1982, 3♂, 1♀ (RWG); (same data), 9 Aug. 1982, 1♀ (UNAM); (same data), 19 Aug. 1982, 3♀ (UNAM); (same data), Bosque Mesofilo de Montaña, 12 June 1981 (R. López), 1♀ (UNAM); Barranca de Cayoapa, Teocelo, (no collector), 1♀ (RWG); 4.8 mi N of Coscomatopec, (M. A. Ortiz, O. S. Flint), 1♂, 2♀ USNM); 2.5 mi S of Huatusco, 23 July 1966 (M. A. Ortiz, O. S. Flint), 1♀ (USNM); 4.7 mi N of Huatusco, Puente Ruiz Cortines, 31 July 1966 (M. A. Ortiz, O. S. Flint), 3♀ (USNM); Orizaba, Ojo de Agua, 3800 ft. (D. R. Paulson), 1♂, 5♀ (DRP, FSCA).

Erpetogomphus cophias Selys
(figs. 27-thx, 46-abd, 69-hamules, 91-penis, 116-app, 165-vertex, 197-vl, 207-distr)

Erpetogomphus cophias Selys, 1858: 332 (72 sep.) (descr. ♂ 'Le Mexique, d'après un mâle du Museum de Paris'). – Selys 1859: 537 (11 sep.) (descr. ♂); Selys 1869: 175 (12 sep.) (descr. ♀); Selys 1873b: 519 (75 sep.) (list); Calvert 1899: 386 (mentioned); Calvert 1905: 164 (descr. ♂, ♀); Calvert 1907: 398 (mention of new figure); Calvert 1909: 481 (seasonal distr.); Muttkowski 1910: 86 (cat.); Williamson and Williamson 1930: 12 (summary of status); Montgomery 1973: 239 (comment on name); Paulson 1982: 255 (Mex.); Davies and Tobin 1985: 27

(cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.52 (cat.); Tsuda 1991: 95 (cat.).

Gomphus cophias. – Hagen 1861: 100 (descr. ♂).

Herpetogomphus cophias. – Walsh 1862: 389 (mentioned); Hagen 1875a: 42 (cat.); Selys 1879: 64 (2 sep.) (characters of genus); Kirby 1890: 60 (cat).

Description

Neotype male. – Entire face pale green; base of mandibles pale green, tips black; antefrons pale green with wash of brown at base; vertex brown, with some green on tubercle behind each lateral ocellus; two prominent cone-shaped pits anterolateral to median ocellus; scape and pedicel dark brown, flagella missing; occiput broad, its dorsal surface evenly convex, especially medially, its posterior margin slightly arcuate; crest with long brown hairs; postocciput light green, evenly concave, rear of head red brown.

Prothorax primarily brown, with light green medially on anterior, median, and posterior lobes; synthorax entirely pale green with wash of brown ventrally above coxae. Coxae and trochanters pale grey green, femora pale grey green becoming tawny distally, a dark brown streak on lateroextensor surfaces of femora occupying almost all of profemora, about 0.60 of mesofemora, and distal 0.30 of metafemora; tibiae, tarsi, and armature black. Wings hyaline, venation dark brown basally, black distally; anterior margin of costa pale yellow to proximal end of pterostigma; pterostigma brown, veins bordering it black.

Venational details. Fifth antenodal thickened in all wings; no marginal cells behind fore wing paranal cells; anx: fore wing 13/13, hind wing 9/9; pnx: fore wing 7/7, hind wing 7/9; cs under pterostigma: fore wing 5/5, hind wing 5/4; anal triangular cells: 4 . Hind wing 29 mm.

Abdomen predominantly pale with following dark brown markings: vestige of midlateral stripe on segment 1; this stripe more defined on segment 2, especially behind auricle; annulus; midlateral stripe on segment 3, transverse carina and darker annulus; segments 4-6 similar to segment 3 but stripes darker, each beginning at a little beyond beginning of segment, enlarging at transverse carina, narrowing and then widening, especially posteriorly, but not touching dorsally; segment 7 with transverse carina and posterior 0.40 of segment laterally; segment 8 pale yellow brown with ill-defined dorsolateral dark stripe; segment 9 similar to segment 8, but with a longitudinal lateral middorsal spot on posterior 0.75 of segment; segment 10 pale ocher with dark red brown along anterior 0.20 of segment. Pale areas of segments 1-7 primarily pale olive dorsally and ventrally; pale areas of segments 8-10 red brown dorsally and ventrally. Abdomen 35 mm.

Cercus yellow brown, linear, slightly concave dorsally beyond basal 0.30, tip smoothly rounded, ventral margin with inferior carina at basal 0.30, terminating in a distinct ventral tooth; dorsal concave area of cerci with scattered thick bristles. Epiprocts yellow brown, distal 0.50 curved dorsally at 90°, as is typical of genus, tips slightly divergent, each with a thick, blunt point.

Accessory genitalia. Anterior hamule black, glabrous, deeply forked, with posterior branch slightly longer than anterior, the whole structure resembling a talon; distal 0.20 of anterior branch with a longitudinal, obtuse V-shaped area. Posterior hamule spatulate, pale green, becoming brown near tip; in lateral view, tip obtusely pointed with a small, blunt cephalad directed tooth on rear margin. Peduncle of penis with prominent rounded foliate erect lateral lobes, its posterior margin not prominent, forming a gentle bilobed area; penis with lateral lobes poorly developed posteriorly, forming a serrated semicircle; membranous hood not overlapping; cornuae well developed, parallel sided, their tips evenly rounded.

Female. – Overall colouration as in male, head with prominent conical pits anterolateral to median ocellus as in male; vertex with tumid oval area posterior to lateral ocelli; occiput narrow, crest prominent, straight to slightly sinuate along medial 0.30, lateral arms bent posteriorly; prominent transverse postoccipital pit (fig. 165) immediately behind lateral arms of crest, medial area of postocciput tumid.

Pro- and synthorax as in male, femora with brown areas reduced with little brown on extensor surface of metafemora.

Venational statistics (n = 2): number of marginal cells behind fore wing paranal cells: 2-4/1-3; anx: fore wing 13/13, hind wing 9-11/9-10; pnx: fore wing 9/8-9, hind wing 9-10/10; cs under pterostigma: fore wing 5/4-5, hind wing 4-6/4-5. Hind wing 32-34 mm.

Abdomen with brown dorsolateral stripe more reduced than male, more prominent and expanded around lateral carinae; segments 8-9 tawny, cercus pale ocher. Vulvar lamina (fig. 197) membranous, diagonally corrugated; posterior margin of each plate gently curved, a prominent ridge along its border, a prominent long diagonal depression immediately anterior to posterior margin; plates meeting medially at tumid area; cleft between plates a small notch; juncture of Y-shaped postlamellar ridge well posterior to vulvar laminar plates; area on each side of central stem of postlamellar ridge darkened, with a slight depression. Abdomen 35-37 mm.

Diagnosis

Erpetogomphus cophias is most similar to *E. boa* and is diagnosed under that species. The characteristic ventral tooth of the cercus in the male and the postoccipital depressions in the female are autapomorphic characters.

Remarks

This is apparently a rare species. Williamson and Williamson (1930) stated that there were only 10 known specimens. Only one other specimen from Michoacan, collected in 1941, has come to my attention. I have examined only 3 males and 4 females, of which one male and one female are teneral and in poor condition. I can see no noticeable differences among the few specimens examined.

Variation. – Venational details of one additional male: number of marginal cells behind fore wing paranal cells: 3/2; anx: fore wing 11/12, hind wing 9/8; pnx: fore wing 9/8, hind wing 9/10; cs under pterostigma: fore wing 5/5, hind wing 5/5; number of anal triangular cells 3/3. Hind wing 30 mm.

Biology. – Nothing is known of the biology of this species.

Distribution (fig. 207). – Like *E. boa, E. cophias* has a restricted distribution and apparently replaces *E. boa* in the highlands of west-central Mexico south of 20°N and west of 100°W. Records indicate an elevational gradient of 1525 m (Cuernavaca) to 2438 m (Omilteme) and flight during June and July.

Material

Type data. According to Dr. J. Legrand (*in litt.* 11 May 1984), the holotype male from 'Le Mexique, d'après un mâle du Museum de Paris', is missing, there remaining only a large rectangular green label with [handwritten] '*E. cophias*, Selys' which was originally attached to the specimen. Dr. Legrand was kind enough to send a male of which he states, '...we have from ex Martin's collection a specimen called *O. cophias* Selys (determined by Selys himself, according to Martin...),' which he suggested I designate as neotype. This I now do. The neotype male contains the following data: white label in R. Martin's hand: '*Ophiogomphus* / *cophias* Selys/ Det. De Selys/ Mexique', small green label printed: 'MUSEUM PARIS / Coll. R. MARTIN 1920', and red rectangular label handwritten: '*Erpetogomphus* / *cophias* Selys ♂ / NEOTYPE / des./ R. W. Garrison 1986'. The abdomen is detached and is in a triangular envelope pinned beneath the specimen.

Other material (3♂, 4♀, including neotype ♂). – MEXICO: *Guerrero*: Omilteme, 8000 ft., July 1888 (H. H. Smith), 1♀, (BMNH); *Michoacan*: Tancítaro, 6000 ft. (1846 m), 4th Hoogstraal Mexican Biological Expedition, 28 July 1941 (H. Hoogstraal), 1♂ (UMMZ); *Morelos*: Cuernavaca, June 1897 (O. W. Barrett), 1♂, 1♀ (ANSP); June 1888 (H. H. Smith), 1♂ (BMNH); 8 July 1900 (C.C. Deam), 2♀ (UMMZ).

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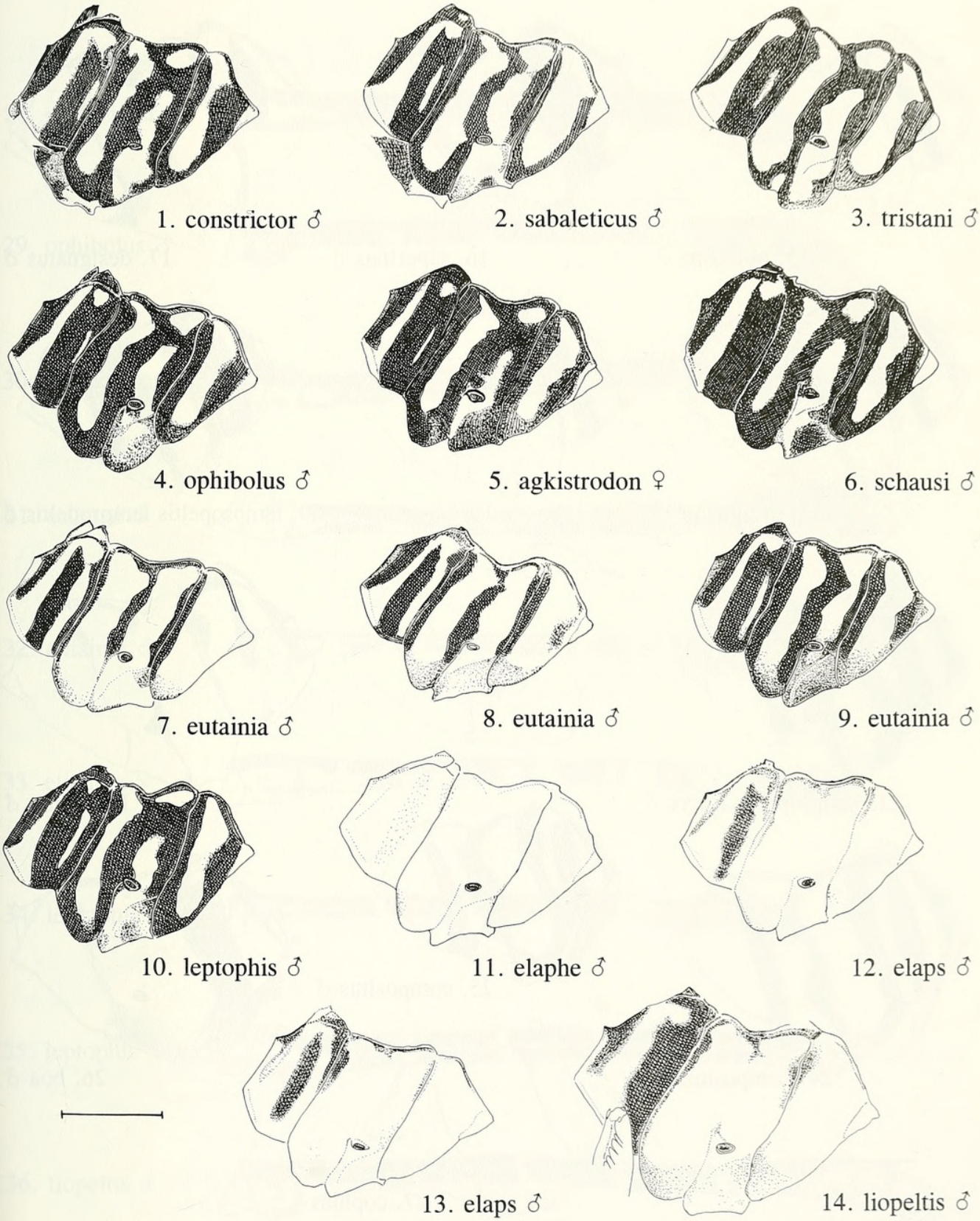
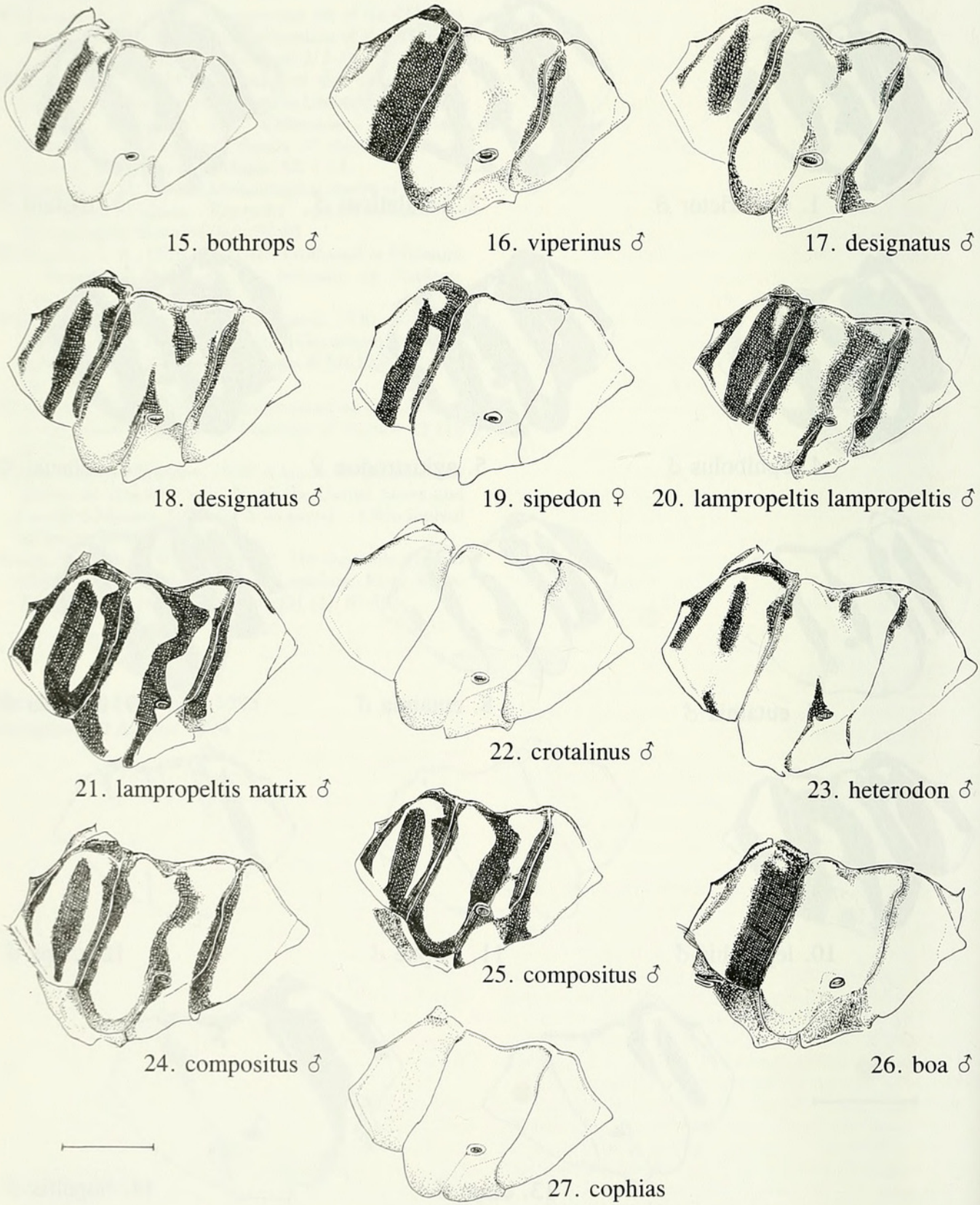


Figs. 1-14. Synthorax of *Erpetogomphus* species, lateral view (males, except given otherwise). – 1, *constrictor* (Honduras); 2, *sabaleticus* (holotype); 3, *tristani* (Costa Rica); 4, *ophibolus* (Mexico: Veracruz State); 5, *agkistrodon* (female holotype); 6, *schausi* (holotype); 7, *eutainia* (Texas: Gonzales Co.); 8, *eutainia* (Mexico: Veracruz State); 9, *eutainia* (Costa Rica); 10, *leptophis* (holotype); 11, *elaphe* (holotype); 12, *elaps* (Mexico: Sinaloa State); 13, *elaps* (Mexico: Morelos State); 14, *liopeltis* (holotype). Scale line: 3 mm.



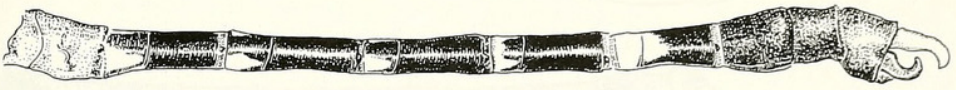
Figs. 15-27. Synthorax of *Erpetogomphus* species, lateral view (males, except given otherwise). – 15, *bothrops* (holotype); 16, *viperinus* (Mexico, Veracruz State); 17, *designatus* (lectotype); 18, *designatus* (Mexico, Durango State); 19, *sipedon* (female holotype); 20, *l. lampropeltis* (holotype); 21, *lampropeltis natrix* (holotype); 22, *crotalinus* (lectotype); 23, *heterodon* (holotype); 24, *compositus* (California, Yolo Co.); 25, *compositus* (paratype of *coluber*); 26, *boa* (Mexico: Veracruz State); 27, *cophias* (Mexico: Morelos State). Scale line 3 mm.

28. constrictor ♀

29. ophibolus ♂

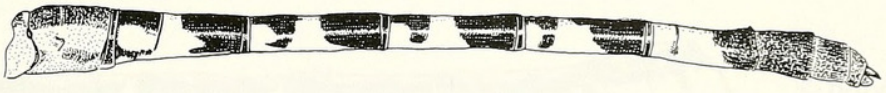
30. agkistrodon ♀

31. schausi ♂



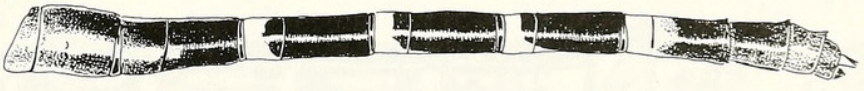
32. eutainia ♂

33. eutainia ♀



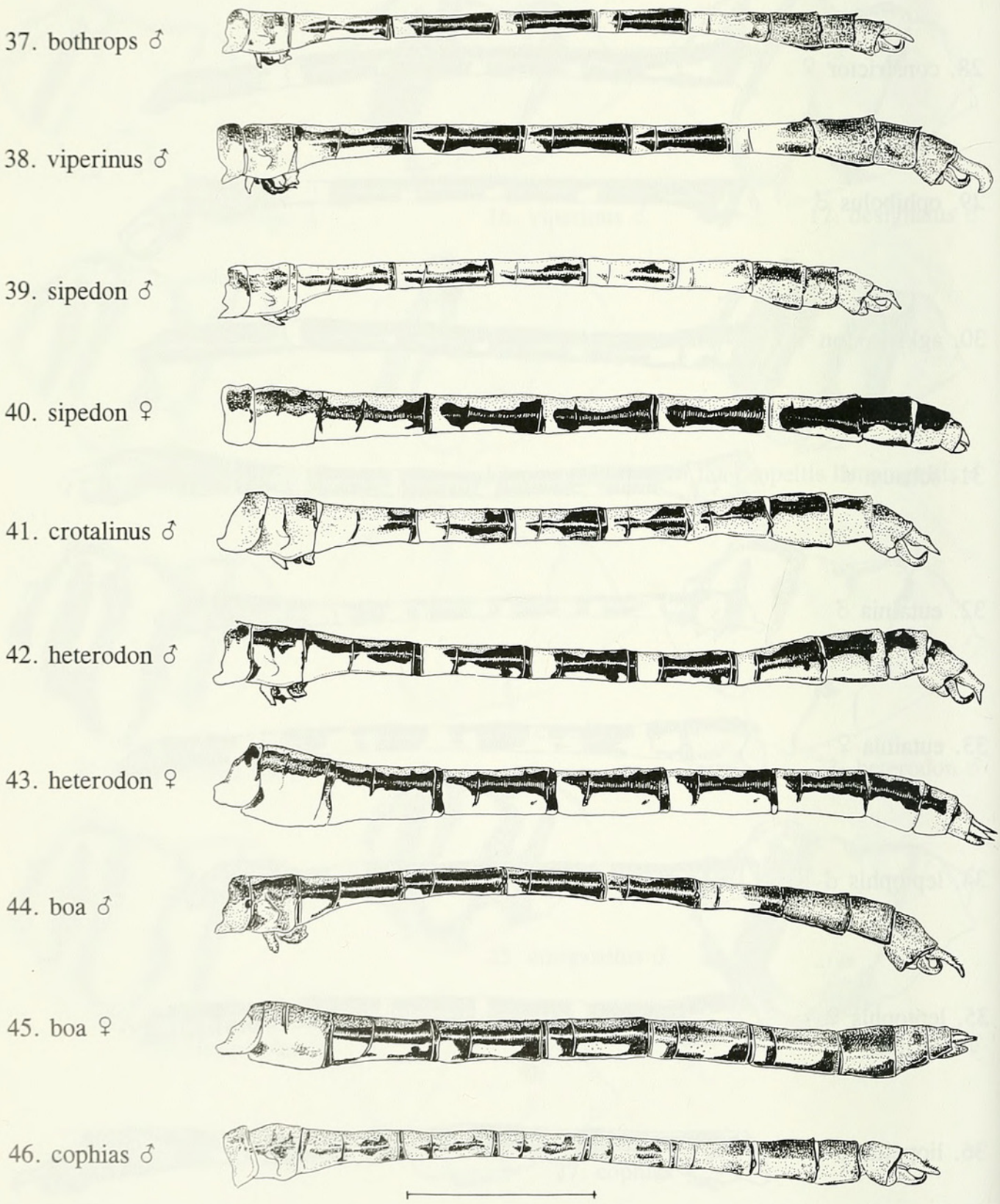
34. leptophis ♂

35. leptophis ♀

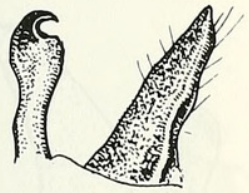


36. liopeltis ♂

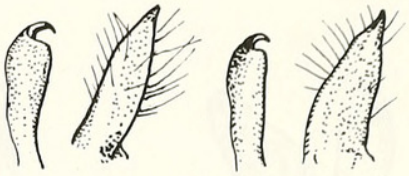
Figs. 28-36. Abdomen, lateral view. – 28, *constrictor* ♀ (Honduras); 29, *ophibolus* ♂ (Mexico: Veracruz State); 30, *agkistrodon* ♀ (holotype); 31, *schausi* ♂ (holotype); 32, *eutainia* ♂ (Texas: Gonzales Co.); 33, *eutainia* ♀ (idem); 34, *leptophis* ♂ (holotype); 35, *leptophis* ♀ (allotype); 36, *liopeltis* ♂ (holotype). Scale line 10 mm.



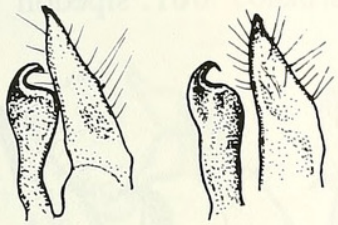
Figs. 37-46. Abdomen, lateral view. – 37, *bothrops* ♂ (holotype); 38, *viperinus* ♂ (Mexico: Veracruz State); 39, *sipedon* ♂ (Mexico: Morelos State); 40, *sipedon* ♀ (holotype); 41, *crotalinus* ♂ (Mexico: Jalisco State); 42, *heterodon* ♂ (holotype); 43, *heterodon* ♀ (allotype); 44, *boa* ♂ (Mexico: Veracruz State); 45, *boa* ♀ (idem); 46, *cophias* ♂ (Mexico: Morelos State). Scale line 10 mm.



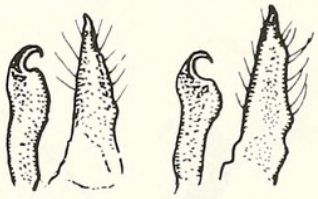
47. constrictor



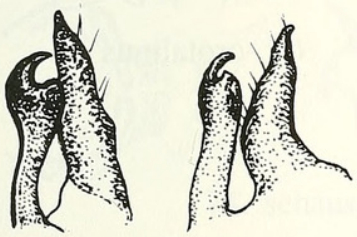
48. sabaleticus



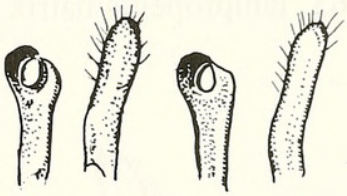
49. tristani



50. ophibolus

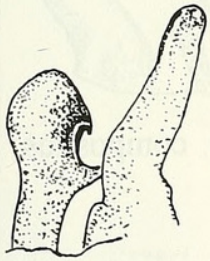


51. schausi

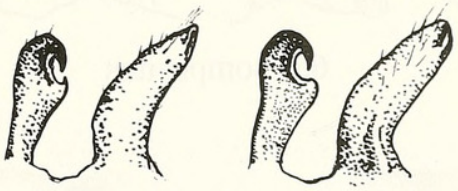


52. eutainia

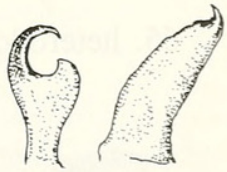
53. leptophis



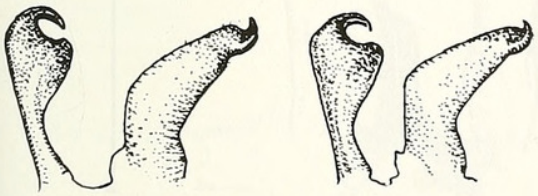
54. elaphe



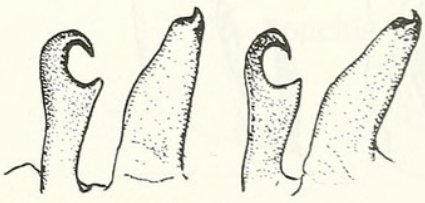
55. elaps



56. elaps

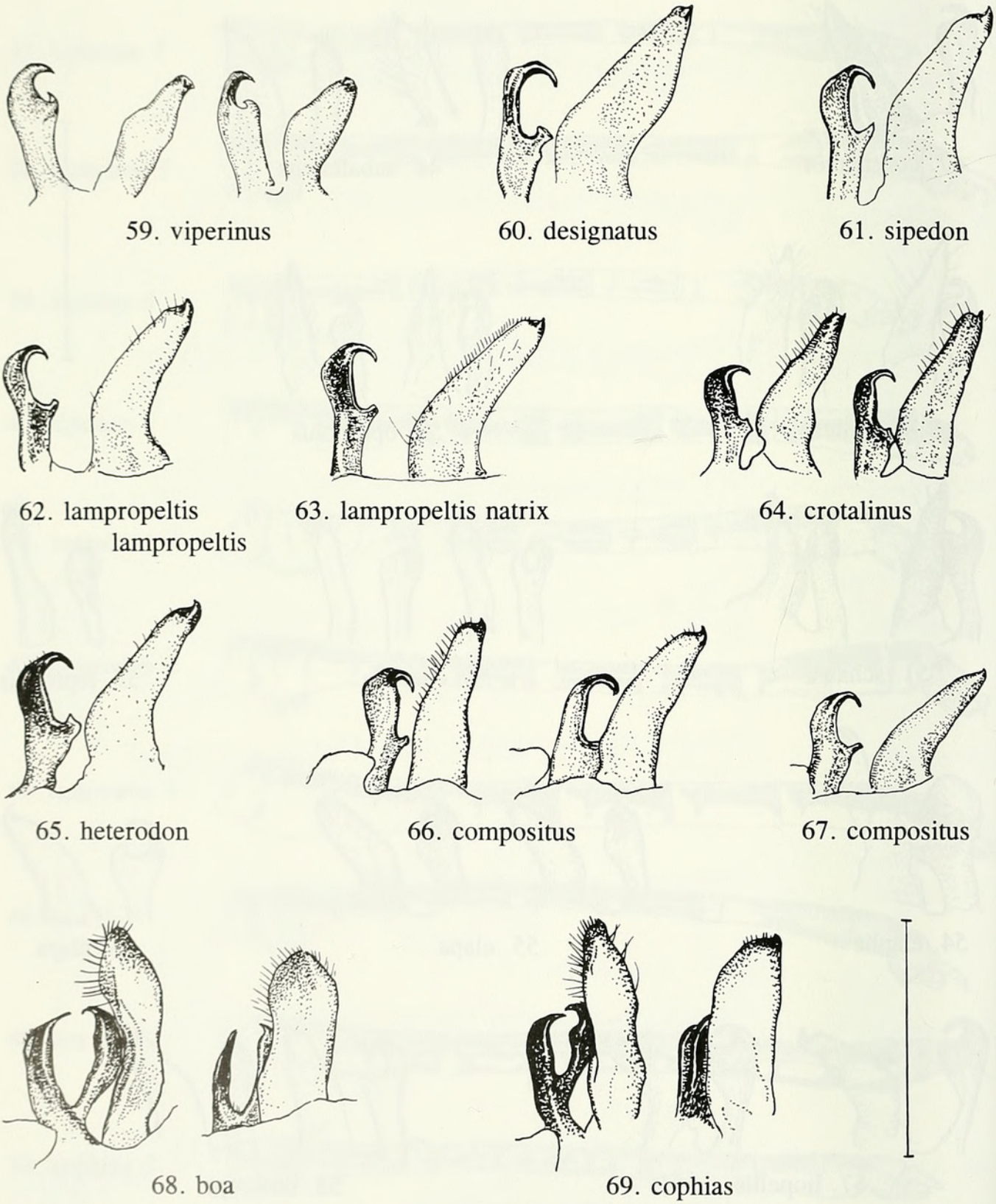


57. liopeltis

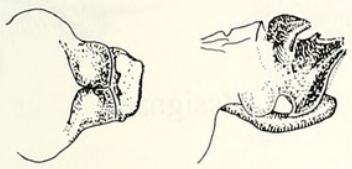


58. bothrops

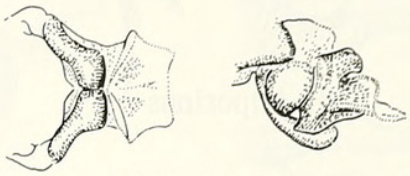
Figs. 47-58. Anterior and posterior hamules. First view is anterolateral view showing profile of anterior hamule; second view (when shown) is lateral view showing profile of posterior hamule. – 47, *constrictor* (Mexico: San Luis Potosi State); 48, *sabaleticus* (holotype); 49, *tristani* (Costa Rica); 50, *ophibolus* (Mexico: Veracruz State); 51, *schausi* (holotype); 52, *eutainia* (Texas: Gonzales Co.); 53, *leptophis* (holotype); 54, *elaphe* (Costa Rica); 55, *elaps* (holotype); 56, *elaps* (variant) (Mexico: Chiapas State); 57, *liopeltis* (paratype); 58, *bothrops* (paratype). Scale line 2 mm.



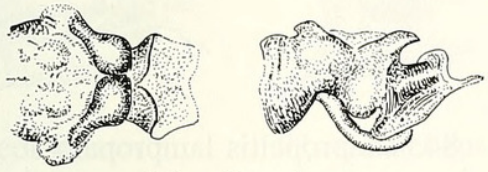
Figs. 59-69. Anterior and posterior hamules. First view is anterolateral view showing profile of anterior hamule; second view (when shown) is lateral view showing profile of posterior hamule. – 59, *viperinus* (Mexico: Veracruz State); 60, *designatus* (lectotype); 61, *sipedon* (Mexico: Morelos State); 62, *l. lampropeltis* (California: Ventura Co.); 63, *l. natrix* (holotype); 64, *crotalinus* (Mexico: Michoacan State); 65, *heterodon* (New Mexico: Catron Co.); 66, *compositus* (Arizona: Pima Co.); 67, *compositus* (paratype of *coluber*); 68, *boa* (lectotype); 69, *cophias* (Mexico: Morelos State). Scale line 2 mm.



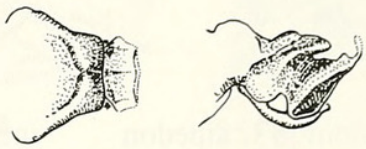
70. constrictor



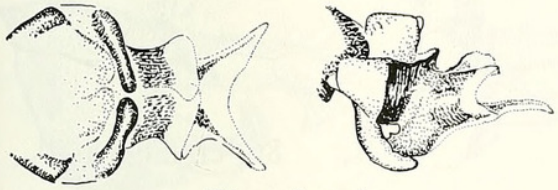
71. sabaleticus



72. tristani



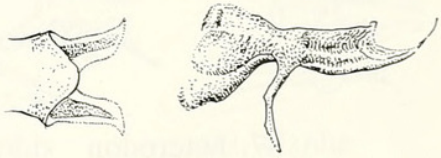
73. ophibolus



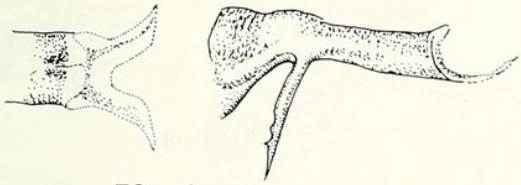
74. schausi

75. eutainia

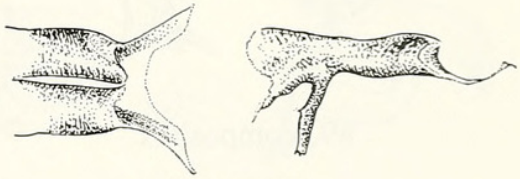
76. leptophis



77. elaphe



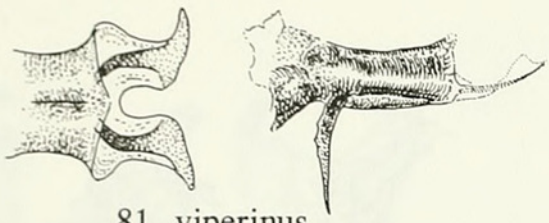
78. elaps



79. liopeltis

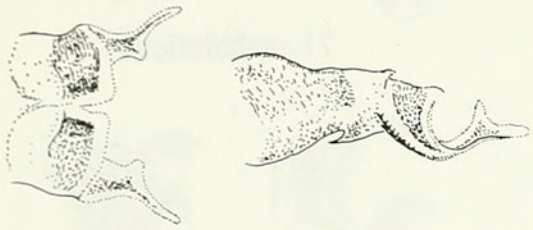
80. bothrops

Figs. 70-80. Penis segment 4, left: dorsal view, right: lateral view. – 70, *constrictor* (Mexico: San Luis Potosi State); 71, *sabaleticus* (holotype); 72, *tristani* (Costa Rica); 73, *ophibolus* (Mexico: Veracruz State); 74, *schausi* (holotype); 75, *eutainia* (Texas: Gonzales Co.); 76, *leptophis* (holotype); 77, *elaphe* (Costa Rica); 78, *elaps* (holotype); 79, *liopeltis* (paratype); 80, *bothrops* (Mexico: Tamaulipas State). Scale line 1 mm.

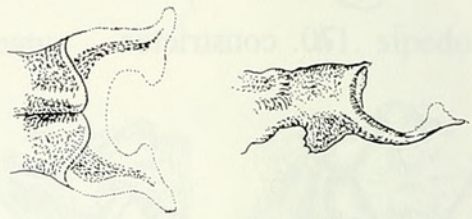


81. viperinus

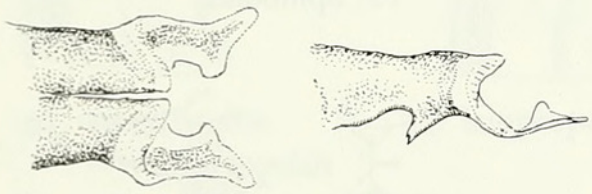
82. designatus



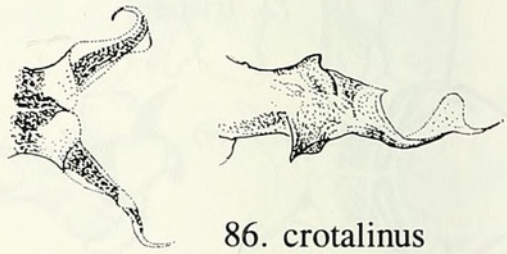
83. sipedon



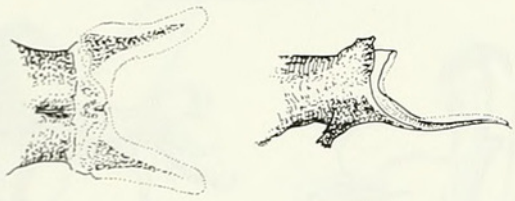
84. lampropeltis lampropeltis



85. lampropeltis natrix



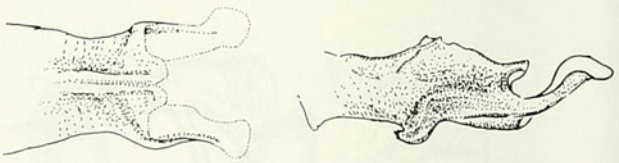
86. crotalinus



87. heterodon

88. compositus

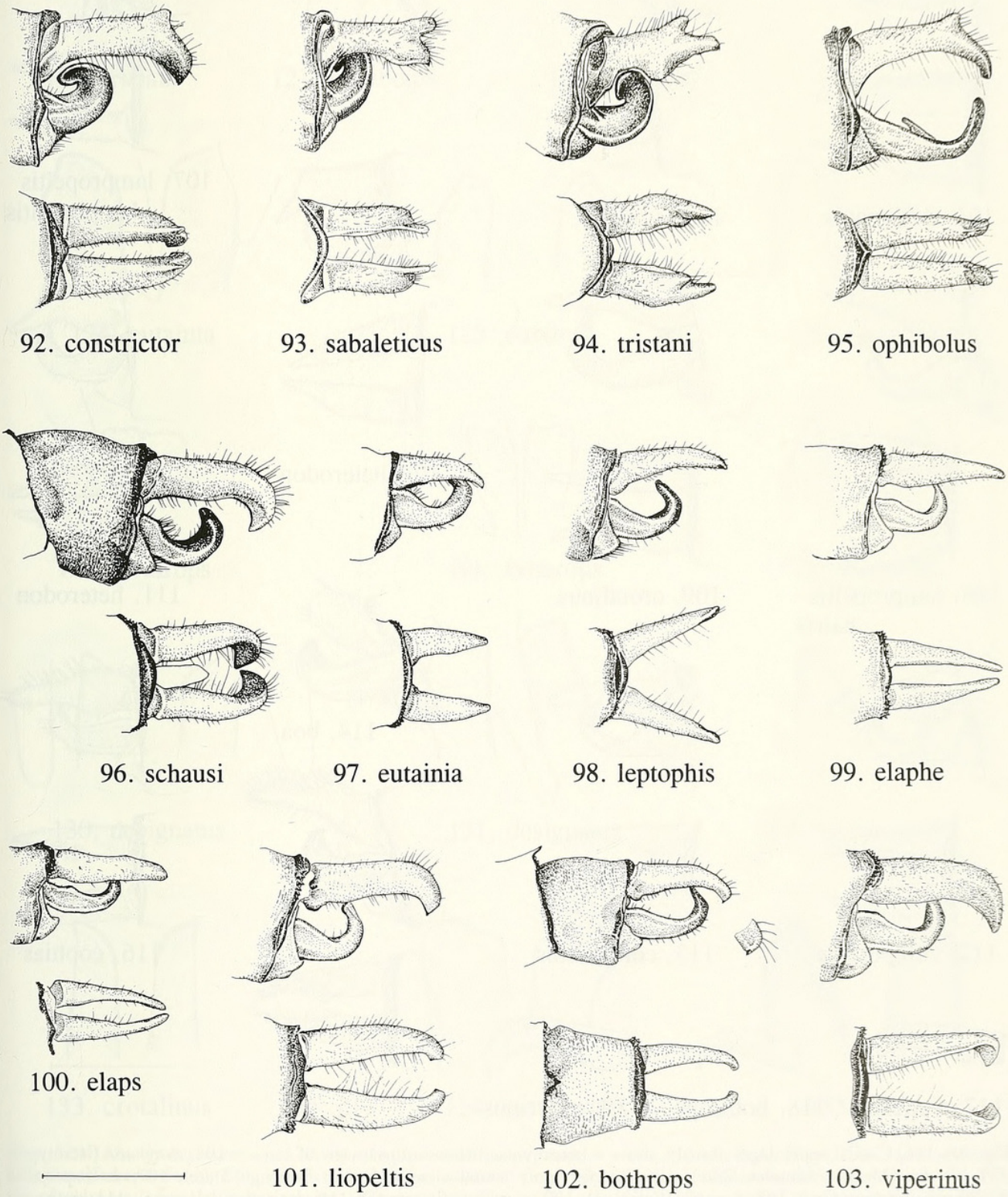
89. compositus



90. boa

91. cophias

Figs. 81-91. Penis segment 4, left: dorsal view, right: lateral view. – 81, *viperinus* (Mexico: Veracruz State); 82, *designatus* (Texas: Gonzales Co.); 83, *sipedon* (Mexico: Morelos State); 84, *l. lampropeltis* (California: Ventura Co.); 85, *l. natrix* (Arizona: Cochise Co.); 86, *crotalinus* (Mexico: Michoacan State); 87, *heterodon* (New Mexico: Catron Co.); 88, *compositus* (CA: Yolo Co.); 89, *compositus* (paratype of *coluber*); 90, *boa* (lectotype); 91, *cophias* (Mexico: Morelos State). Scale line 1 mm.



Figs. 92-103. Caudal appendages of male, above = lateral view, below = dorsal view of cerci. – 92, *constrictor* (Mexico: Tamaulipas State); 93, *sabaleticus* (holotype); 94, *tristani* (holotype); 95, *ophibolus* (Mexico: Veracruz State); 96, *schausi* (holotype); 97, *eutainia* (Texas: Gonzales Co.); 98, *leptophis* (holotype); 99, *elaphe* (Costa Rica); 100, *elaps* (holotype); 101, *liopeltis* (holotype); 102, *bothrops* (holotype); 103, *viperinus* (lectotype). Scale line 5 mm.

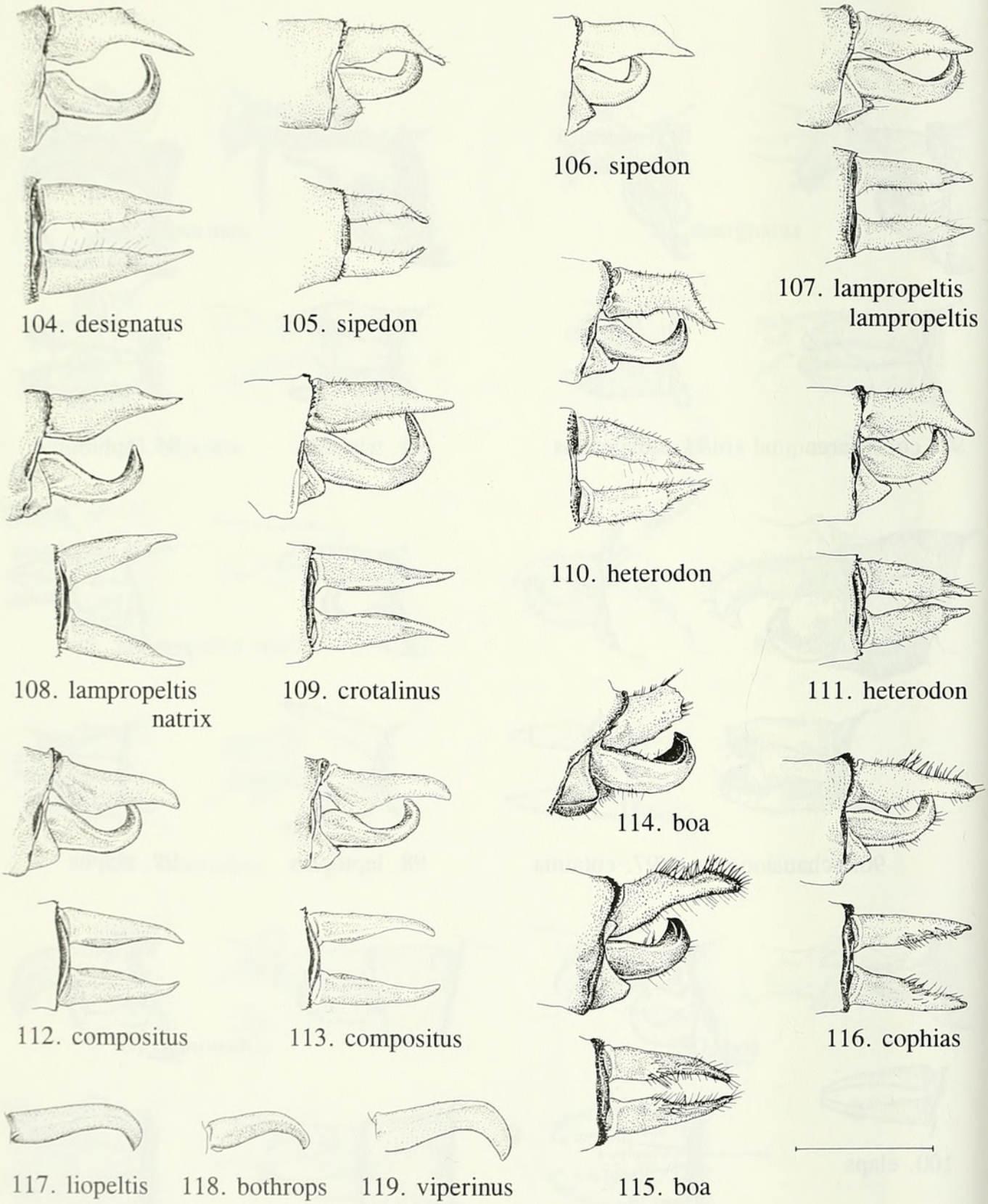
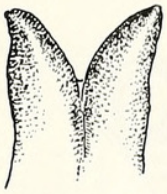
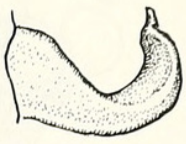


Fig. 104-116. Caudal appendages of male, above = lateral view, below = dorsal view of cerci. – 104, *designatus* (lectotype); 105, *sipedon* (Mexico: Morelos State); 106, *sipedon* (only lateral view) (Mexico: Durango State); 107, *l. lampropeltis* (California: Ventura Co.); 108, *l. natrix* (holotype); 109, *crotalinus* (lectotype); 110, *heterodon* (holotype); 111, *heterodon* (Mexico: Durango State); 112, *compositus* (California: Yolo Co.); 113, *compositus* (paratype of *coluber*); 114, *boa* (only lateral view) (lectotype); 115, *boa* (Mexico: Veracruz State); 116, *cophias* (Mexico: Morelos State). Figs. 117-119. Right cercus, mediolateral view. – 117, *liopeltis* (Mexico: Nuevo Leon State); 118, *bothrops* (Mexico: Nayarit State); 119, *viperinus* (Mexico: Veracruz State). Scale line 5 mm.

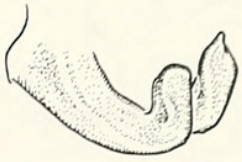
120. tristani



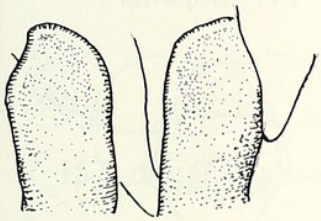
121. ophibolus



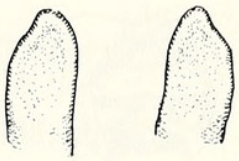
122. eutainia



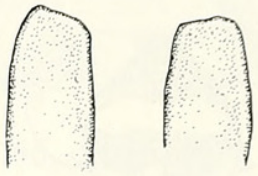
123. eutainia



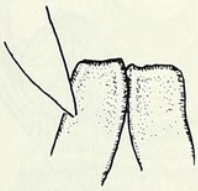
124. eutainia



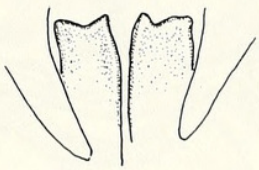
125. eutainia



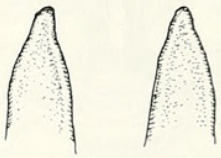
126. liopeltis



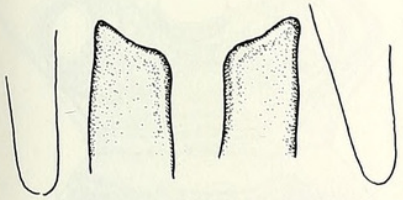
127. bothrops



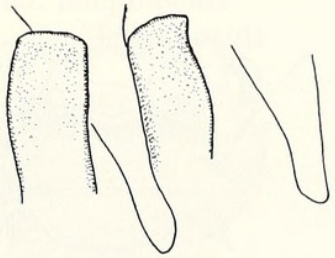
128. bothrops



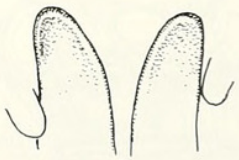
129. viperinus



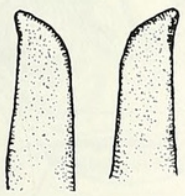
130. designatus



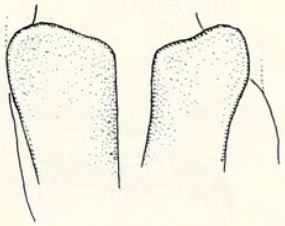
131. designatus



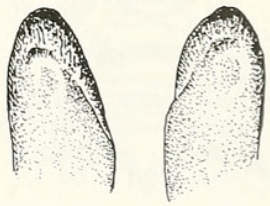
132. lampropeltis lampropeltis



133. crotalinus



134. compositus



135. boa

Figs. 120-135. *Erpetogomphus*. – 120, tip of epiproct of male, posterior view, *tristani* (Costa Rica); 121, idem, *ophibolus* (Mexico: Veracruz State); 122, epiproct, lateral view, *eutainia* (Texas: Gonzales Co.); 123, idem, dorsolateral view; 124-135, tip of epiprocts of male, posterior view, 124, *eutainia* (Texas: Gonzales Co.); 125, *eutainia* (Guatemala); 126, *liopeltis* (Mexico: Nuevo Leon State); 127, *bothrops* (Mexico: Nayarit State); 128, *bothrops* (holotype); 129, *viperinus* (Mexico: Veracruz State); 130, *designatus* (Texas: Gonzales Co.); 131, *designatus* (Mexico: Durango State); 132, *l. lampropeltis* (California: Ventura Co.); 133, *crotalinus* (Mexico: Jalisco State); 134, *compositus* (Arizona: Coconino Co.); 135, *boa* (Mexico: Veracruz State). Scale line 2 mm (figs. 122-123), 1 mm (figs. 120-121, 124-135).

136. bothrops

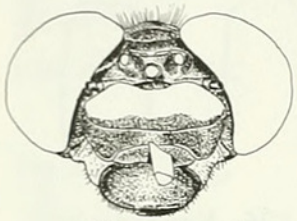
137. viperinus

138. lampropeltis lampropeltis ♂

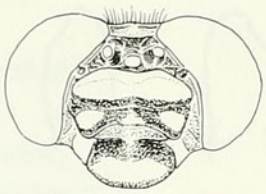
139. compositus ♂

140. liopeltis

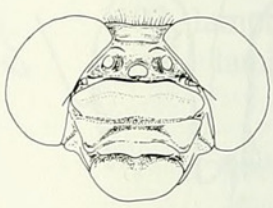
141. liopeltis



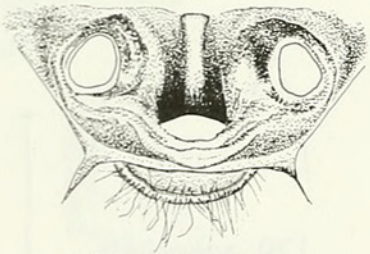
142. schausi



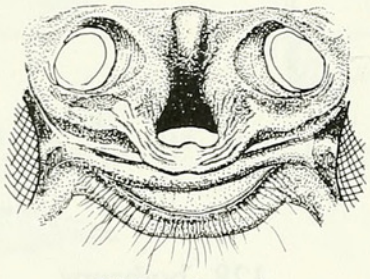
143. eutainia



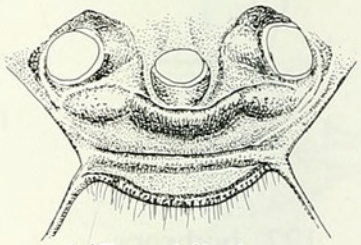
144. eutainia



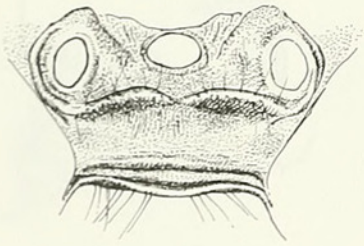
145. constrictor



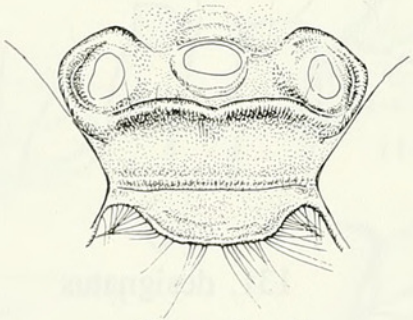
146. tristani



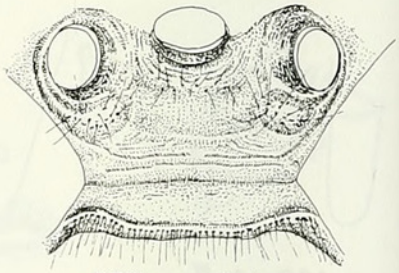
147. ophibolus



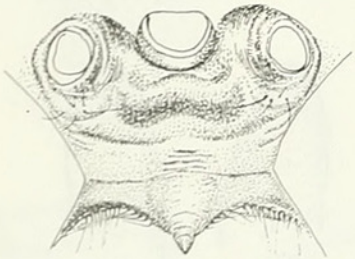
148. agkistrodon



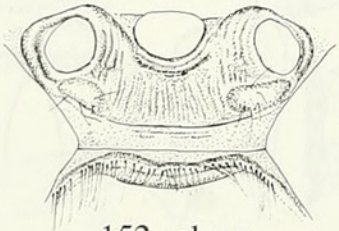
149. schausi



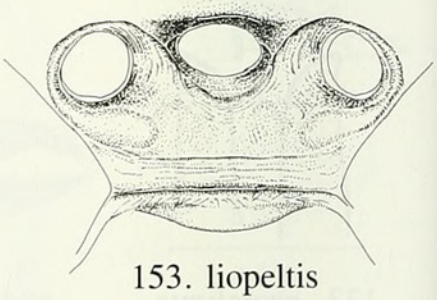
150. eutainia



151. leptophis

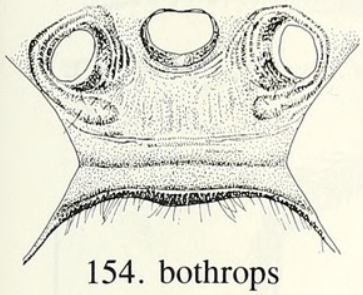


152. elaps

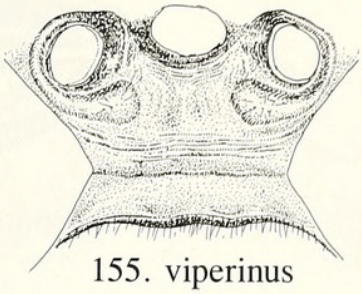


153. liopeltis

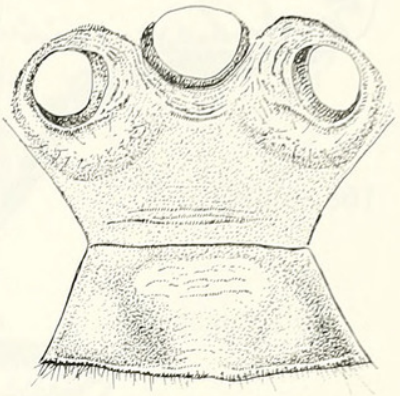
Figs. 136-153. *Erpetogomphus*. – 136-139. Anterior part of frons, dorsal view. 136, *bothrops* ♀ (Mexico: San Luis Potosi State); 137, *viperinus* ♀ (Mexico: Veracruz State); 138, *l. lampropeltis* ♂ (California: Ventura Co.); 139, *compositus* ♂ (AZ: Maricopa Co.). – Figs. 140-141. Crest outline of occiput, dorsal view. 140, *liopeltis* (holotype), 141, *liopeltis* (Mexico: Nuevo Leon State). – Figs. 142-144. Head, anterior view. 142, *schausi* (holotype); 143, *eutainia* (Costa Rica); 144, *eutainia* (Texas: Gonzales Co.). – Figs. 145-153.Vertex, occiput of female, dorsal view. 145, *constrictor* (Honduras); 146, *tristani* (Costa Rica); 147, *ophibolus* (Mexico: Veracruz State); 148, *agkistrodon* (holotype); 149, *schausi* (Costa Rica); 150, *eutainia* (Texas: Gonzales Co.); 151, *leptophis* (allotype); 152, *elaps* (Mexico: Morelos State); 153, *liopeltis* (allotype). Scale line 4 mm (figs. 142-144); 1 mm (136-141, 145-153).



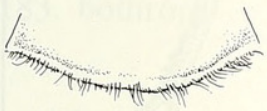
154. bothrops



155. viperinus

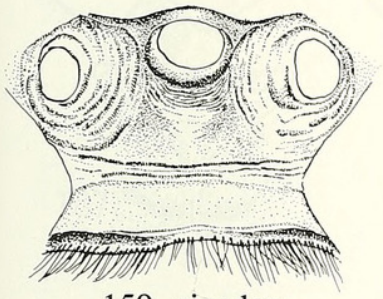


156. designatus

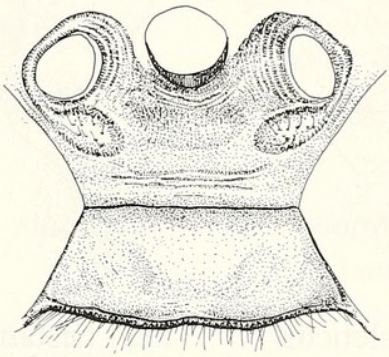


157. designatus

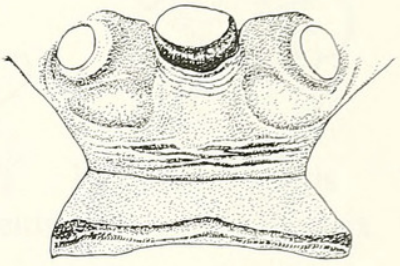
158. sipedon



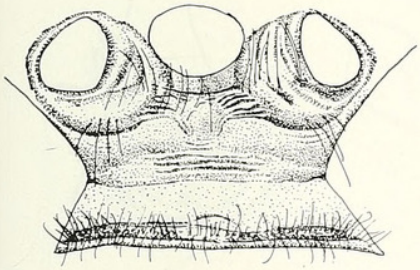
159. sipedon



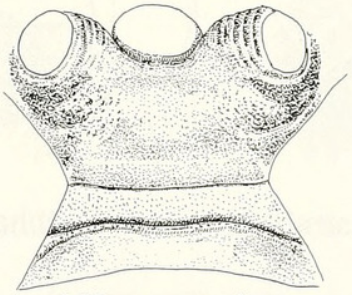
160. lampropeltis lampropeltis



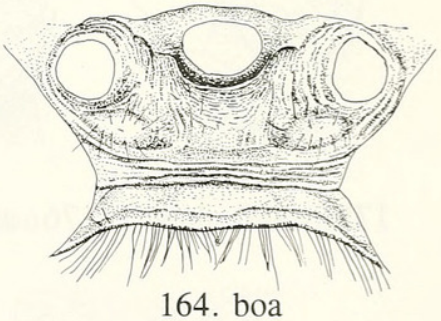
161. crotalinus



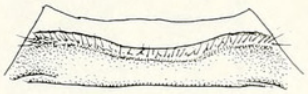
162. liopeltis



163. compositus

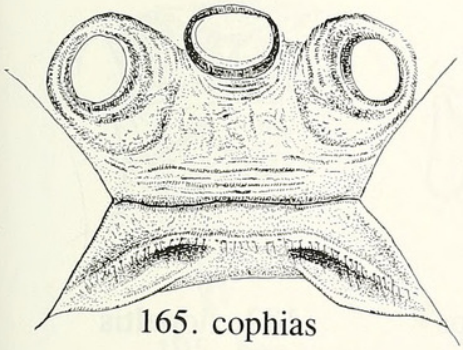


164. boa



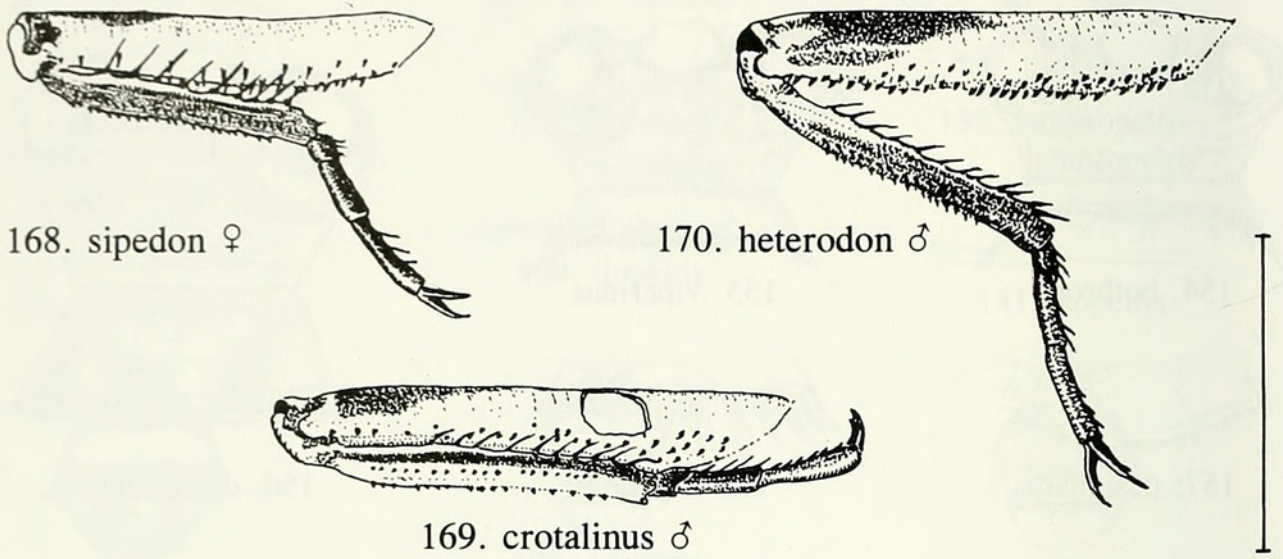
166. viperinus

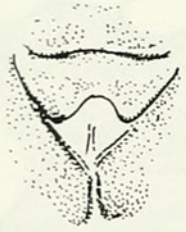
167. boa

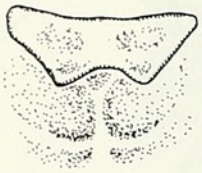


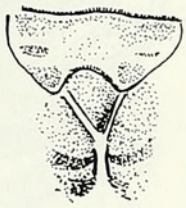
165. cophias

Figs. 154-165. Vertex, occiput of female, dorsal view. 154, *bothrops* (allotype); 155, *viperinus* (Mexico: Veracruz State); 156, *designatus* (paralectotype); 157, *designatus* (Mexico: Durango State); 158, *sipedon* (form 'b') (Mexico: Puebla State); 159, *sipedon* (holotype); 160, *l. lampropeltis* (California: Ventura Co.); 161, *crotalinus* (paralectotype); 162, *heterodon* (allotype); 163, *compositus* (holotype); 164, *boa* (Mexico: Veracruz State); 165, *cophias* (Mexico: Guerrero State). – Figs. 166-167. Crest and part of rear of head (postocciput) of female, dorsal view. 166, *viperinus* (Mexico: Veracruz State); 167, *boa* (Mexico: Veracruz State). Scale line 1 mm.

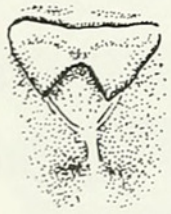



171. constrictor

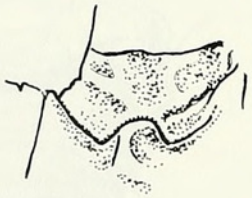

172. sabaleticus


173. tristani


174. tristani

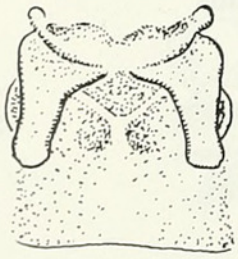

175. ophibolus

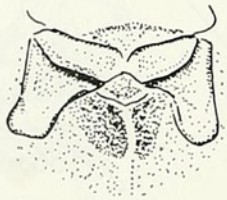

176. agkistrodon


177. schausi


178. eutainia

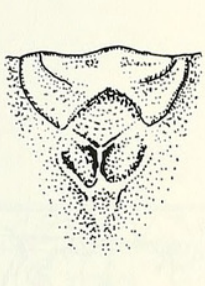

179. leptophis


180. elaphe


181. elaps

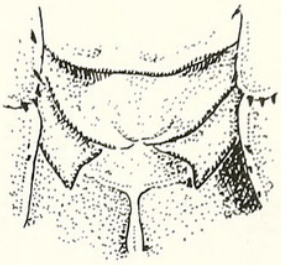

182. liopeltis

Fig. 168-170. Metathoracic leg, lateral view. – 168, *sipedon* ♀ (holotype); 169, *crotalinus* ♂ (lectotype); 170, *heterodon* ♂ (holotype). – Figs. 171-182. Vulvar lamina, dorsal view. – 171, *constrictor* (Honduras); 172, *sabaleticus* (allotype); 173, *tristani* (allotype); 174, *tristani* (Costa Rica); 175, *ophibolus* (Mexico: Veracruz State); 176, *agkistrodon* (holotype); 177, *schausi* (Costa Rica) (distorted on right side); 178, *eutainia* (Mexico: Veracruz State); 179, *leptophis* (allotype); 180, *elaphe* (Costa Rica); 181, *elaps* (Mexico: Morelos State); 182, *liopeltis* (Mexico: Nuevo Leon State). Scale line 4 mm (figs. 168-170), 2 mm (figs. 171-182).

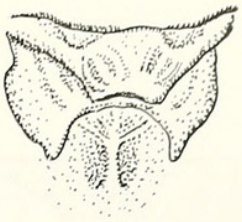


183. bothrops

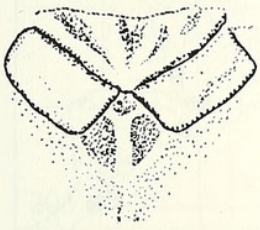
184. viperinus



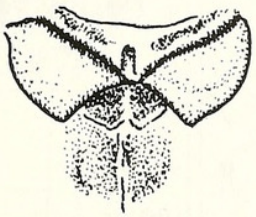
185. designatus



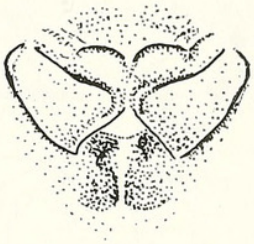
186. designatus



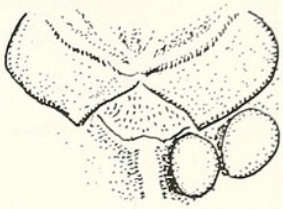
187. sipedon



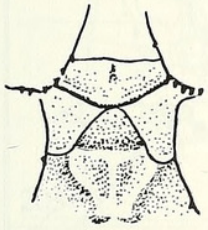
188. sipedon



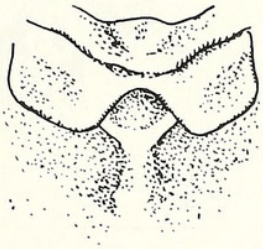
189. lampropeltis lampropeltis



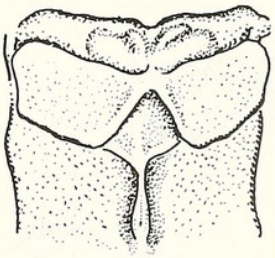
190. lampropeltis natrix



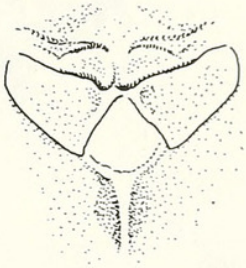
191. crotalinus



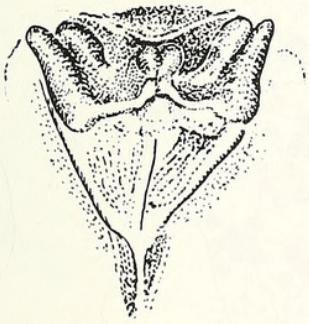
192. crotalinus



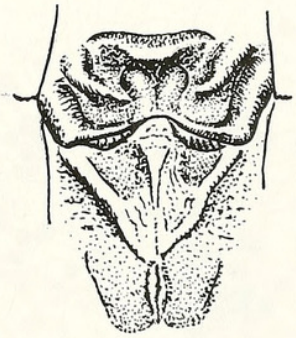
193. heterodon



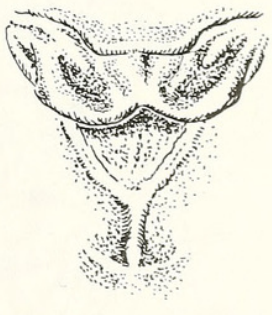
194. compositus



195. boa

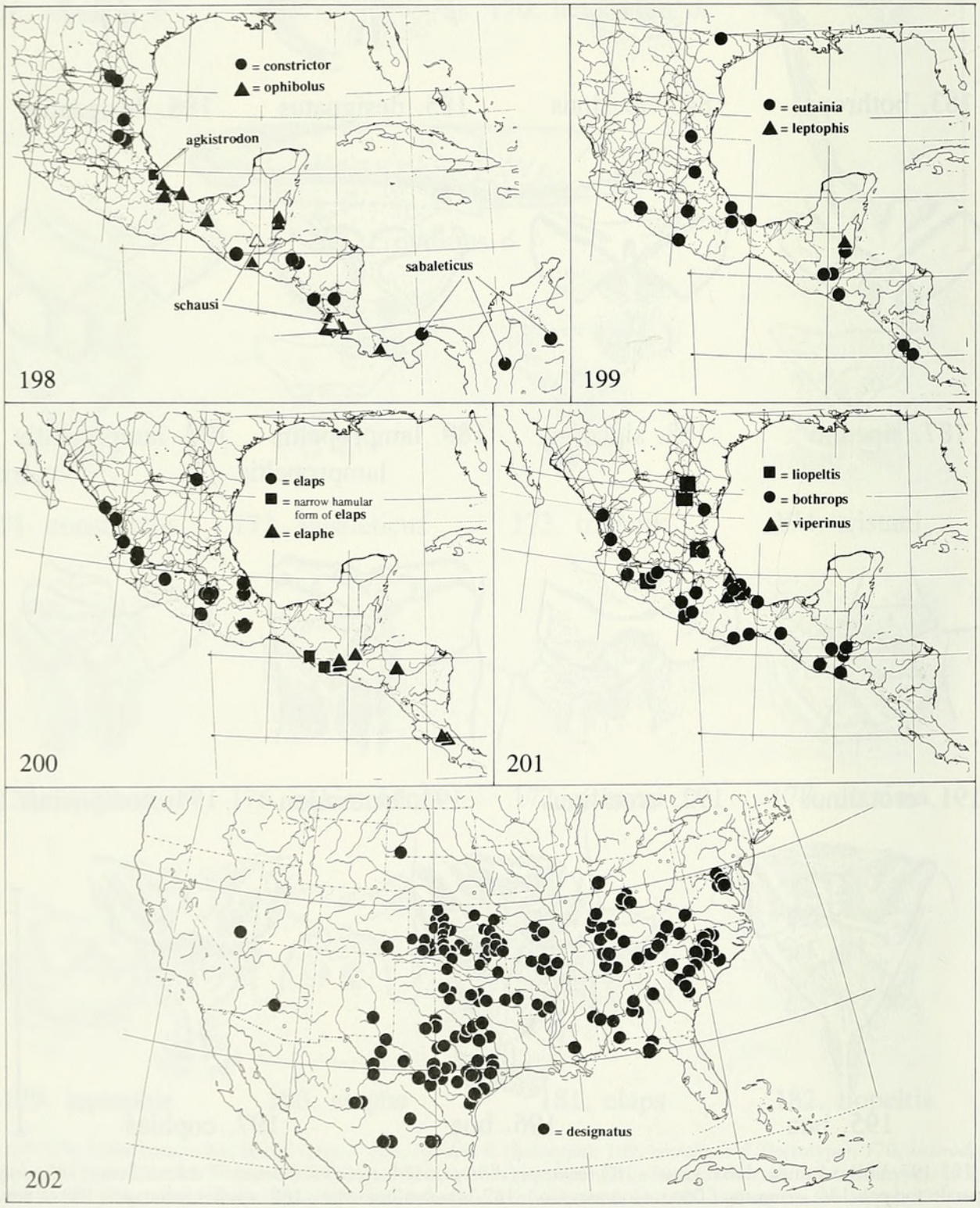


196. boa

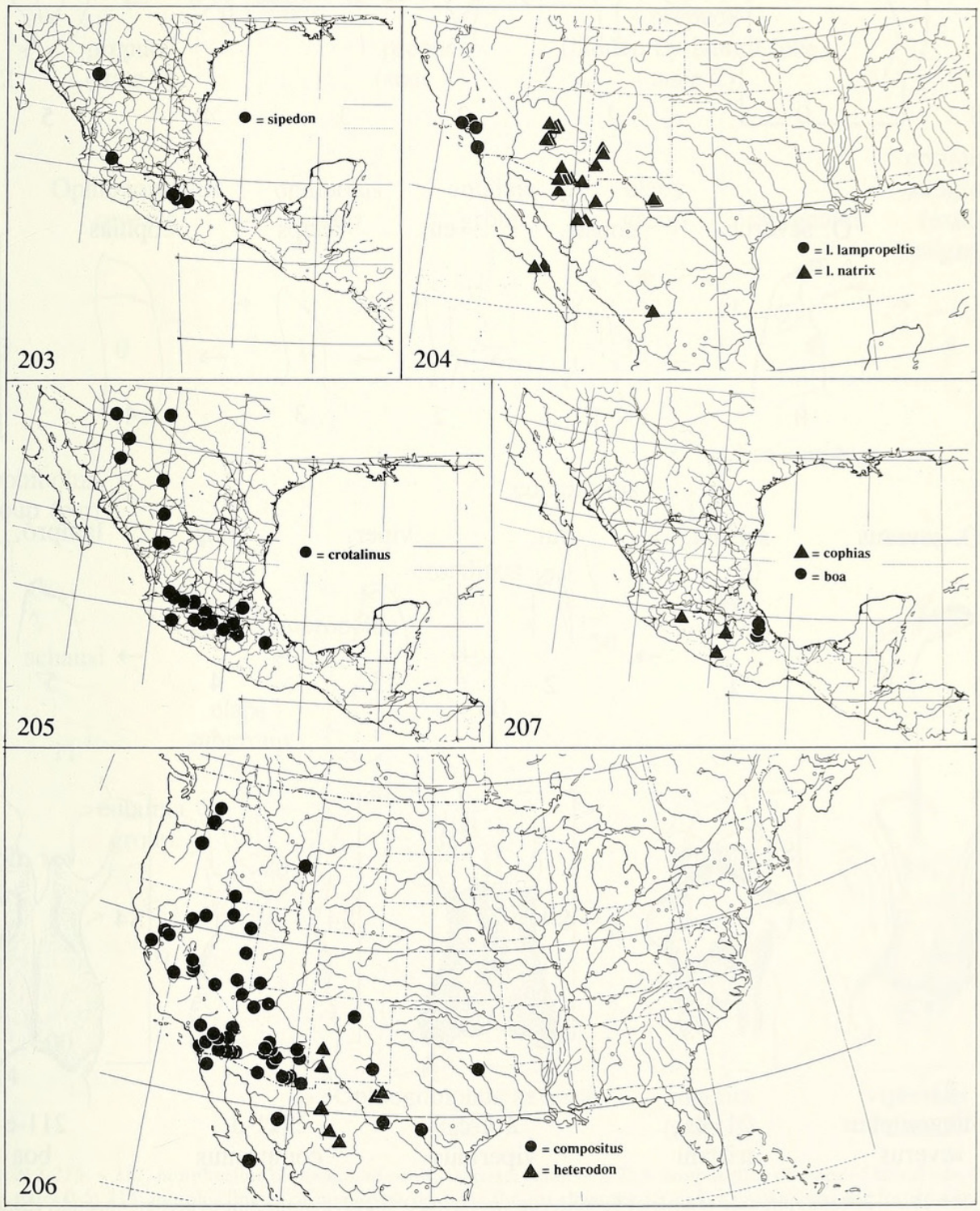


197. cophias

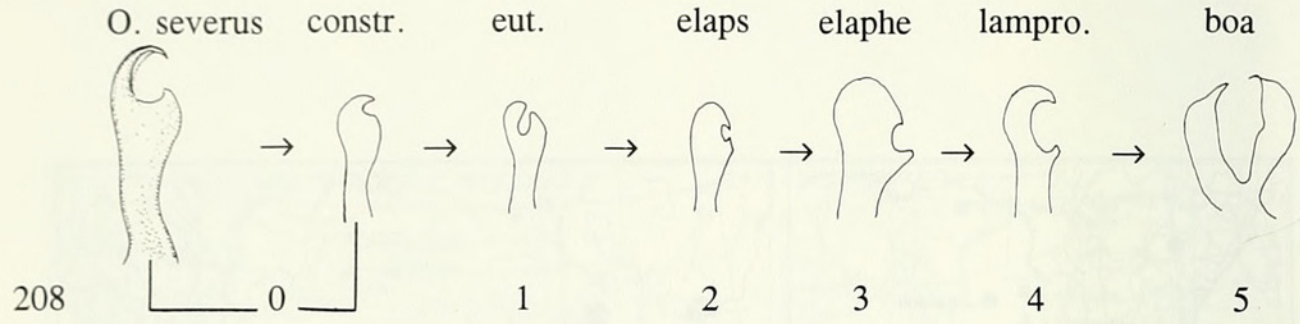
Figs. 183-197. Vulvar lamina, dorsal view. – 183, *bothrops* (allotype); 184, *viperinus* (Mexico: Veracruz State); 185, *designatus* (paralectotype); 186, *designatus* (Texas: Gonzales Co.); 187, *sipedon* (holotype); 188, *sipedon* (paratype); 189, *l. lampropeltis* (California: Ventura Co.); 190, *l. natrix* (allotype); 191, *crotalinus* (paralectotype); 192, *crotalinus* (Mexico: Jalisco State); 193, *heterodon* (allotype); 194, *compositus* (Arizona: Maricopa Co.); 195, *boa* (Mexico: Veracruz State); 196, *boa* (Veracruz State); 197, *cophias* (Mexico: Guerrero State). Scale line 2 mm.

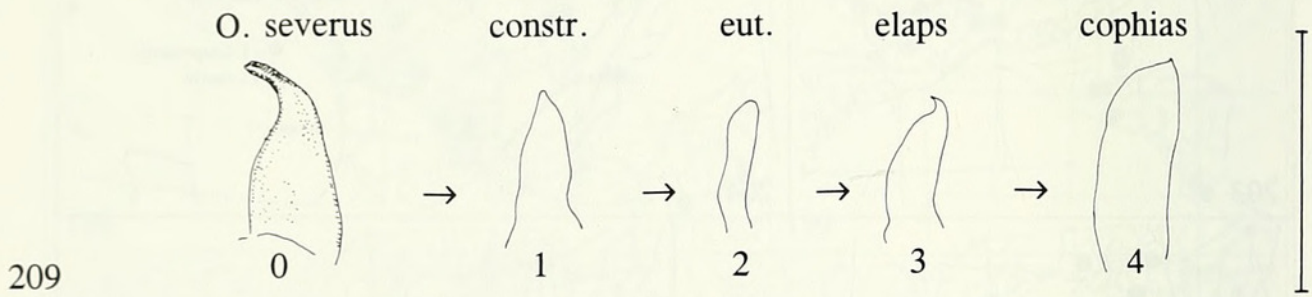


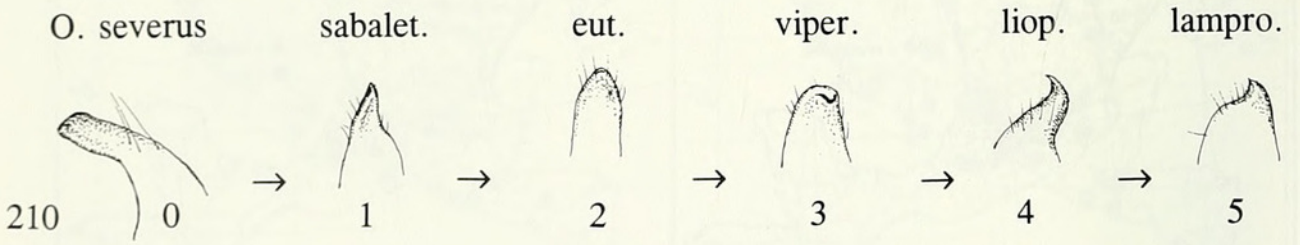
Figs. 198-202. Distribution patterns. – 198, *E. ophibolus* group; 199, *E. eutainia* group; 200, *E. elaps* group (in part); 201, *E. elaps* group (in part); 202, *E. designatus*.

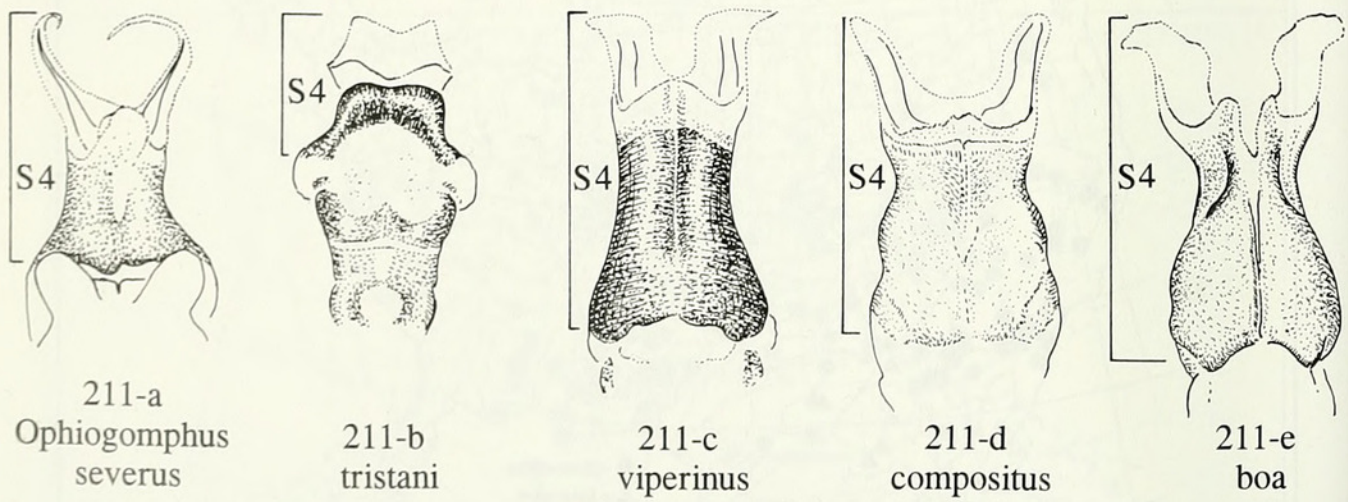


Figs. 203-207. Distribution patterns. 203, *E. sipedon*; 204, *E. lampropeltis*; 205, *E. crotalinus*; 206, *E. heterodon* and *E. compositus*; 207, *E. boa* and *E. cophias*.

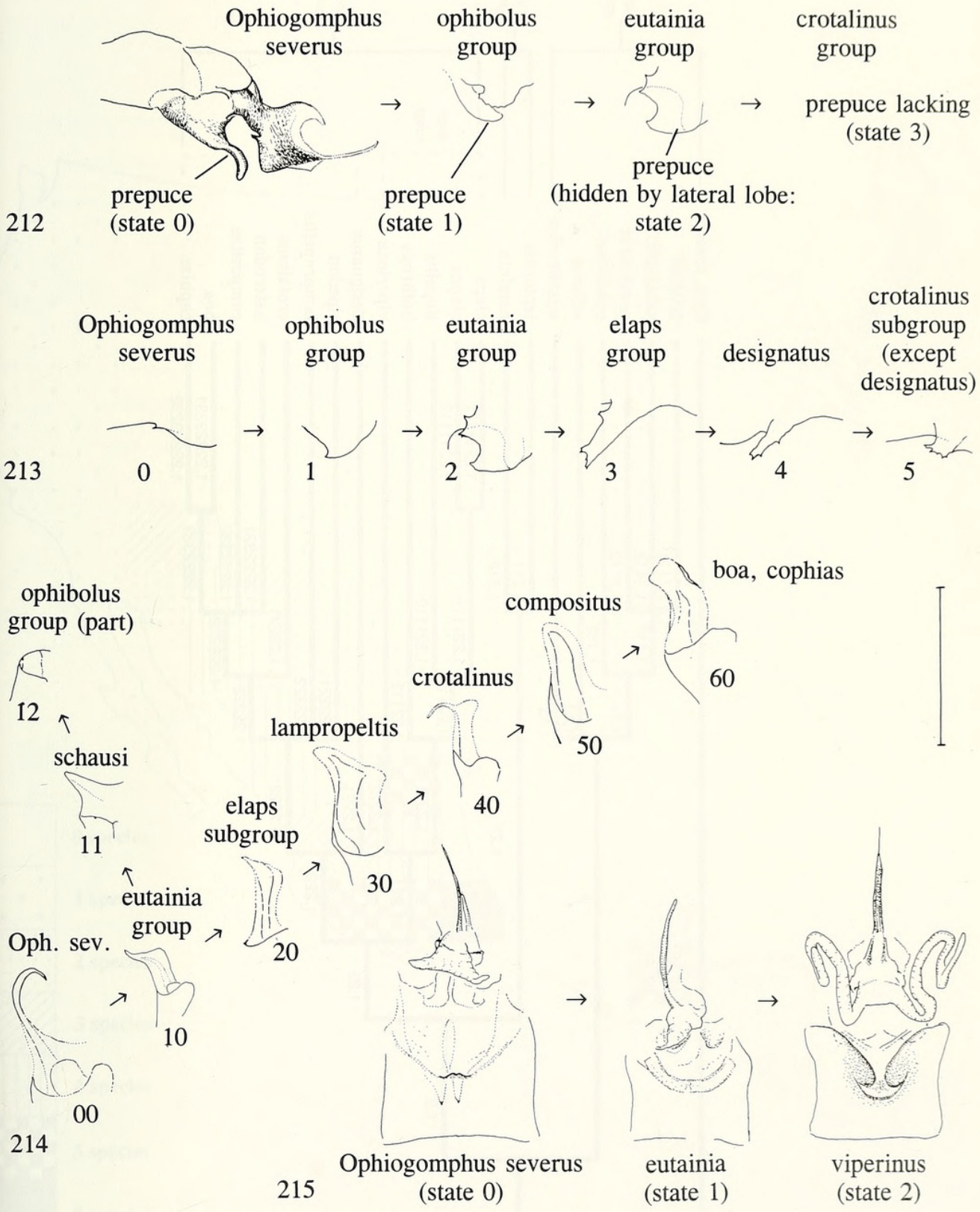








Figs. 208-211. – 208, morphocline of anterior hamule, character states 0-5; 209, morphocline of posterior hamule, character states 0-4; 210, morphocline of tip of posterior hamule, character states 0-5; 211, dorsal view of fourth segment of penis (S4); figs. 211a and 211b have 4th segment about as long as wide, figs. 211c-e about twice as long as wide. Scale line 2 mm (figs. 208-209); 1 mm (figs. 210-212).



Figs. 212-215. – 212, morphocline of prepuce of penis, character states 0-3; 213, morphocline of shape of lateral lobe, character states 0-5; 214, morphocline of cornua: character states 0-6 for character 19 and character states 0-2 for character 20; 215, morphocline of spermatheca in dorsal (internal) view character states 0-2 (figures show dorsal (internal) view of sternum 9 (including postlamellar ridge). Spematheca is dorsad of vulvar lamina). Scale line 1 mm (figs. 212, 215); 0.5 mm (figs. 213-214).

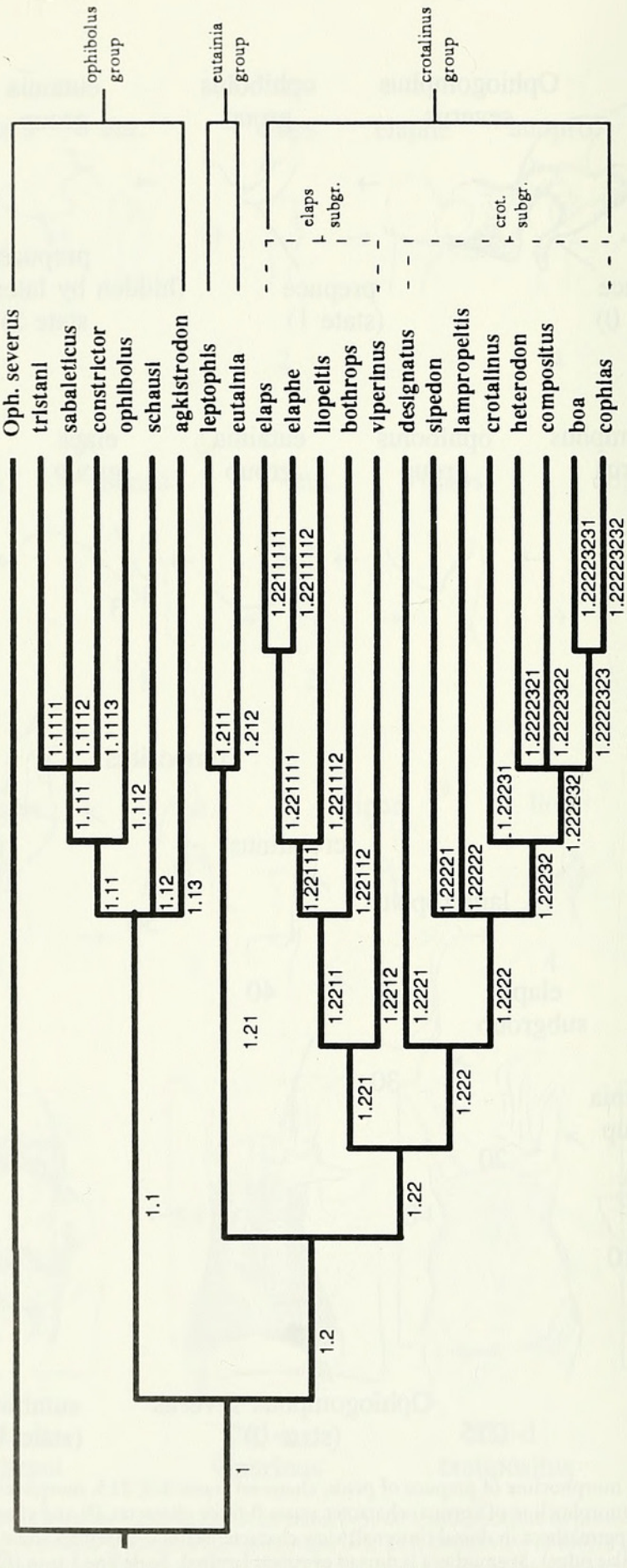


Fig. 216. cladogram.

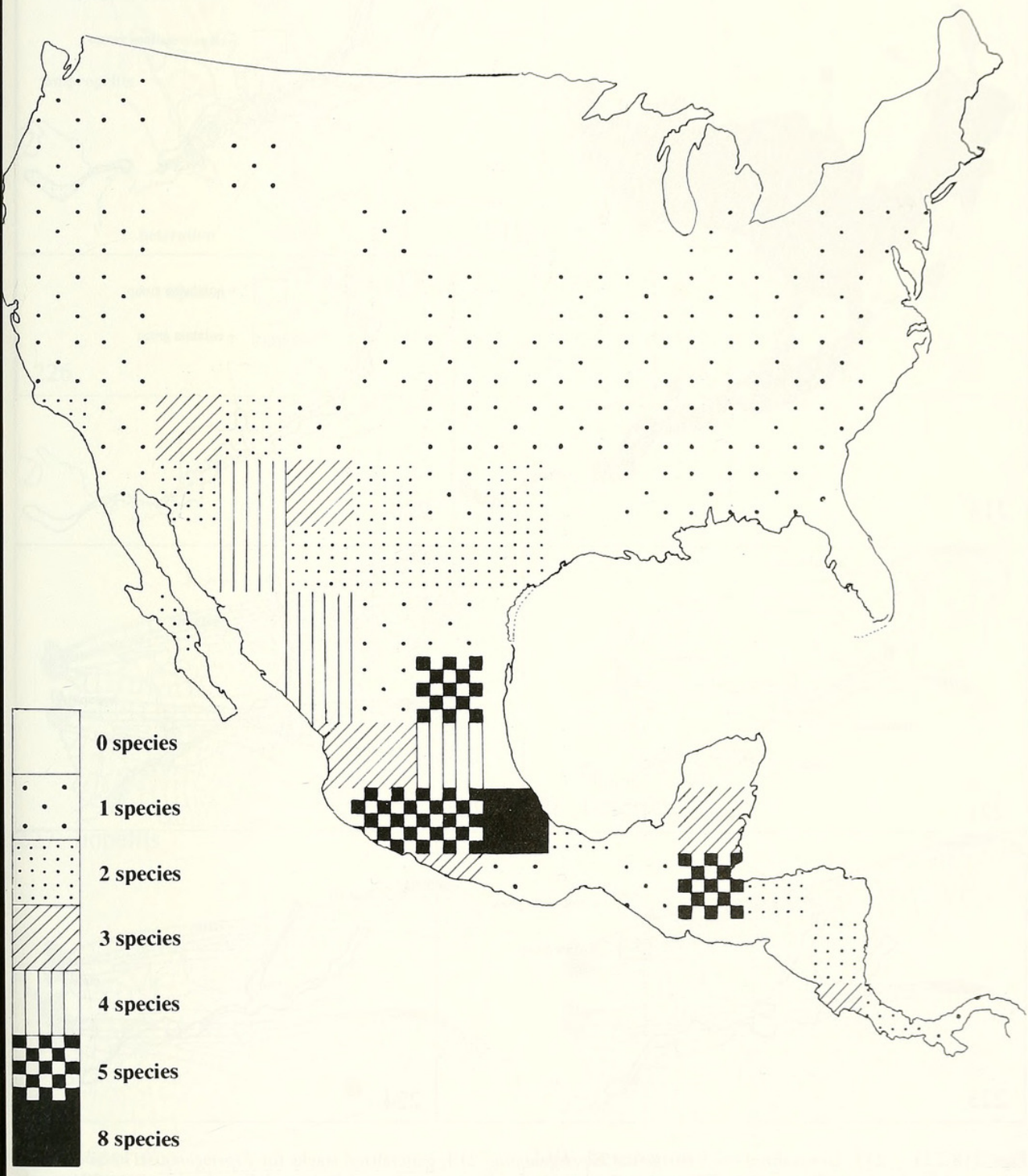
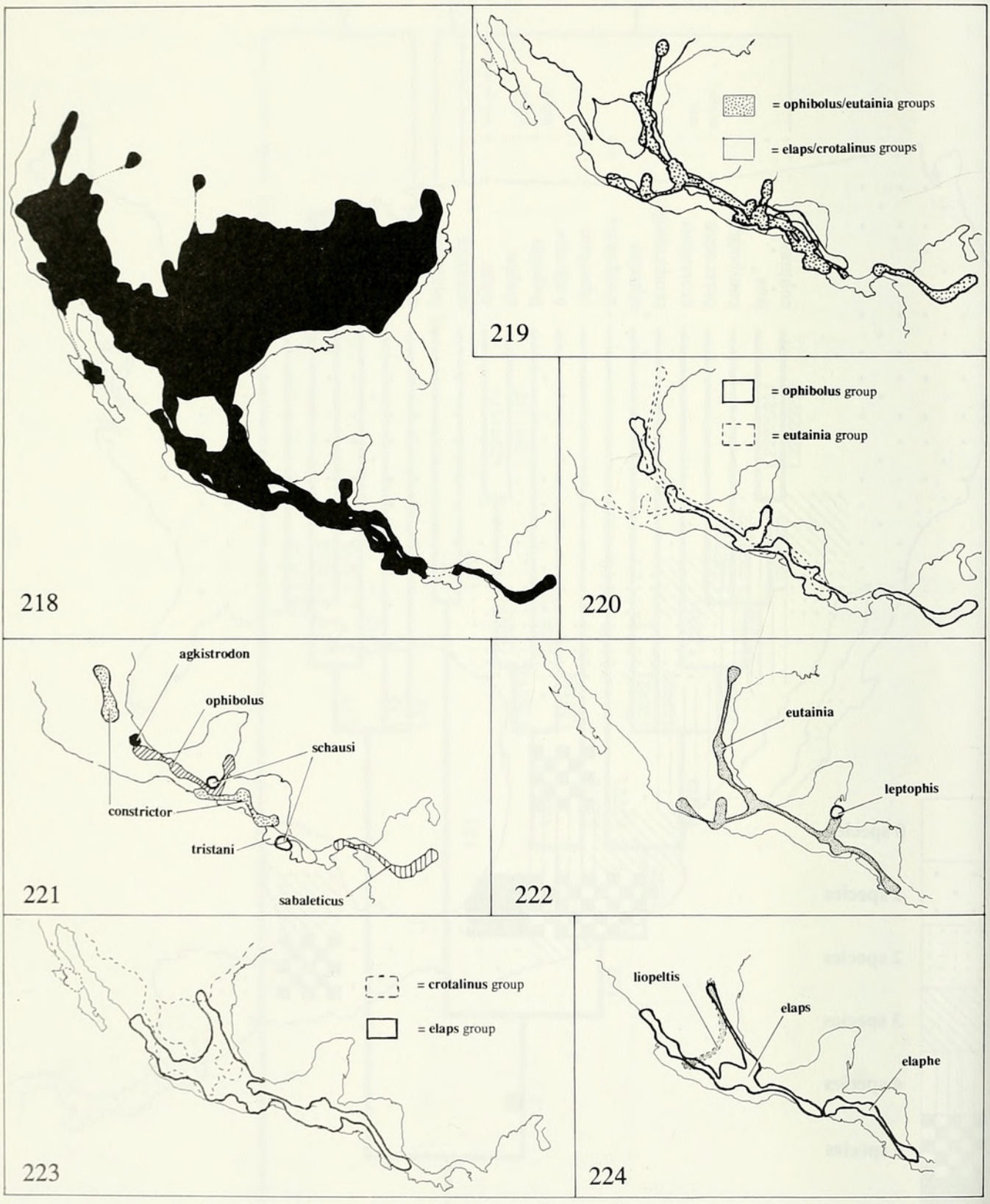
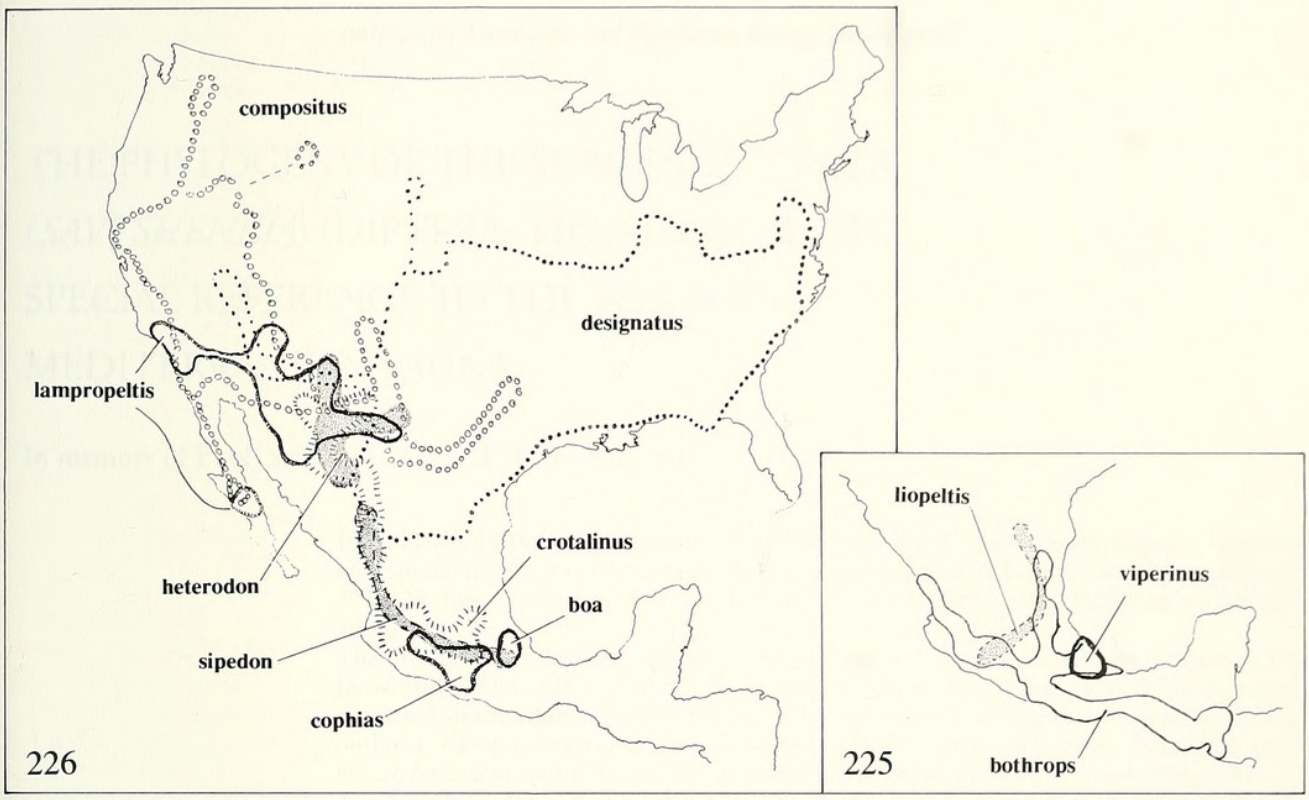
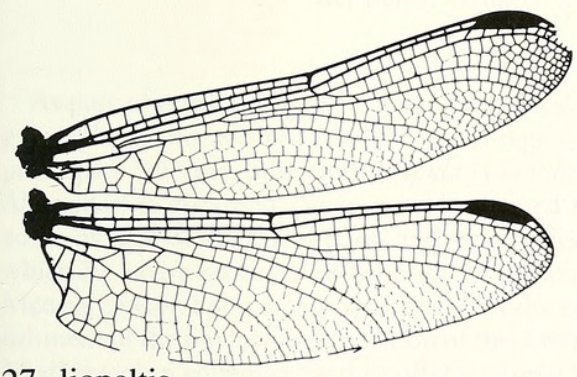


Fig. 217. geographic distribution of *Erpetogomphus* collected in the U. S. A., Mexico, and Central America. Each square is approximately 150 kilometers square.

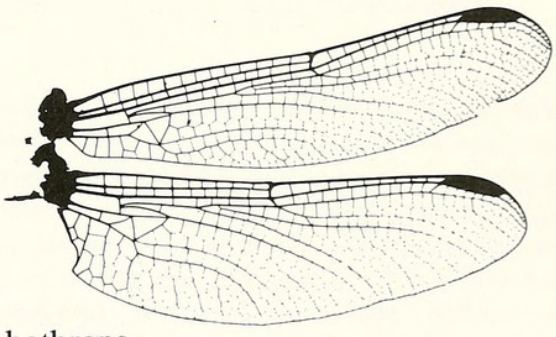


Figs. 218-224. – 218, Generalized track for genus *Erpetogomphus*; 219, generalized tracks for *Erpetogomphus ophibolus* / *eutainia* and *E. elaps* / *crotalinus* groups; 220, generalized tracks for *Erpetogomphus ophibolus* and *E. eutainia* groups; 221, tracks of species within the *Erpetogomphus ophibolus* group; 222, tracks of species within the *Erpetogomphus eutainia* group; 223, generalized tracks for *Erpetogomphus crotalinus* and *E. elaps* groups; 224, tracks of species within the *Erpetogomphus elaps* group (in part).

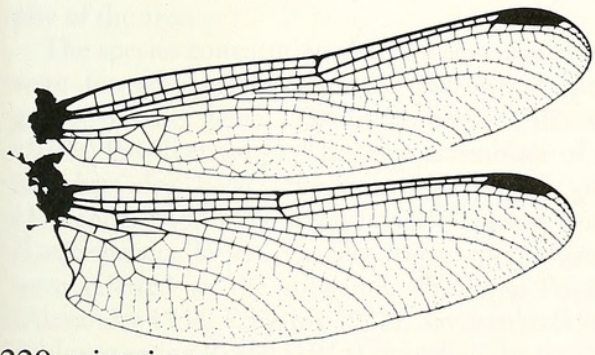




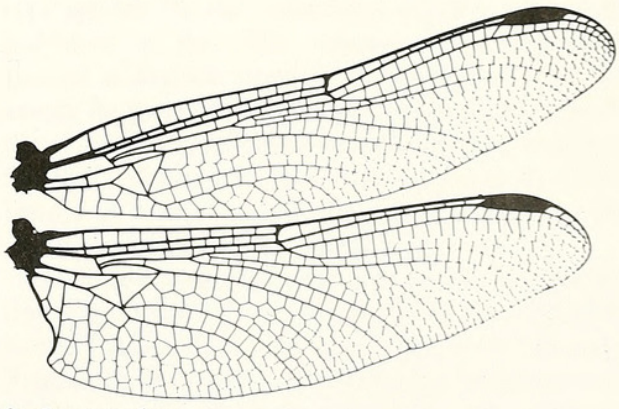
227. liopeltis



228. bothrops



229. viperinus



230. heterodon

Figs. 225-230. – 225, tracks of species within the *Erpetogomphus elaps* group (in part); 226, tracks of species within the *Erpetogomphus crotalinus* group; 227, pair of wings of *liopeltis* ♂ (Mexico: Nuevo Leon State); 228, idem, *bothrops* ♂ (Mexico: Nayarit State); 229, idem, *viperinus* ♂ (Mexico: Veracruz State); 230, idem, *heterodon* ♂ (N. Mexico: Grant Co.)