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R. E. CRABILL, JR.

*Tracheotaxy as a  
Generic Criterion in  
Himantariidae, with  
Proposal of Two New  
Bothriogastrine Genera  
(Chilopoda: Geophilomorpha)*



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## ABSTRACT

Two new Bothriogastrine genera are proposed and based upon three species, two of them new, thereby recording for the first time the presence of the subfamily in the New World. The characterizations utilize a new intertaxic criterion, tracheotaxy, the study of tracheal configurations and patterns, which is introduced herein and described. Some evolutionary inferences are suggested. Additionally, other new criteria are employed, e.g., the nature of the pretarsal parungues. A key to all known Bothriogastrine genera is appended.

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### Introduction

The Himantariidae, a family of persisting ancient habitus, is properly divisible into two subfamilies: Himantariinae, occurring widely but almost exclusively in the northern hemisphere; Bothriogastrinae,<sup>1</sup> heretofore known only from Greece and the adjacent Near East, including northern Africa and Asia. The most useful and reliable (but not the only) feature distinguishing the two is the second maxillary isthmus, anteromedially strongly diastemate in the nominate group, but somewhat protracted and not at all diastemate in the Bothriogastrinae. In terms of genera and species the Himantariinae is much the larger.

To date several dozen species and more than a dozen himantariid genera have been described from North America including Mexico, chiefly by R. V. Chamberlin.<sup>2</sup> Over a period of many years and until recently all of the specimens that I had examined from North America were plainly referable to Himantariinae. Chamberlin, for his part, neither in publication nor in letters to me ever suggested any reason for supposing that his forms were not similarly assignable. So it was with some surprise that I discovered the presence recently of unquestioned bothriogastrines in Mexico and California. My surprise was not total, however, for considering chilopod distributional patterns between eastern Asia and the North American west coast, it would not have been unreasonable to predict the

<sup>1</sup> As used here, exactly equal to Attems' Bothriogastrini (1929, p. 46) and to Verhoeff's Bothriogastrinae and Mesocanthinae (1925, p. 548).

<sup>2</sup> For a detailed systematic summary, see Crabill (1959, pp. 117-126, 154-159).

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presence of bothriogastrines in this part of the New World.

The Mexican Bothriogastrinae that I have examined so far are divisible into two new genera and three species, two of them new. All are described below, and a revised key to all of the genera of Bothriogastrinae is appended.

One of the chief generic characteristics that I rely upon in this study makes use of what I have termed *tracheotaxy*,<sup>3</sup> utilizing kinds of criteria that have never before been employed diagnostically below the rank of Order. Because it is a new and unexplored departure, a few words of explanatory orientation are needed. The reader's attention is directed to Figures 22 and 23, which show semischematically, respectively for *Geoballus* and *Straberax*, three typical segments with their dorsal tracheal divisions and spiracles. Both are in dorsal aspect, cephalic ends uppermost.

In Figure 22 the segments' spiracles (A) are indicated; from each there arises a single tracheal trunk that soon bifurcates to give rise to a posterior ramus (B) and an anterior ramus (C). Each posterior ramus passes directly to a nodus (E) which receives nearly all of the various tracheal components. Note that there is one nodus posteriorly in each segment. In all Geophilomorpha known to me the connections of the posterior ramus, which directly connects the spiracular trunk with the nodus, are unvarying; as we shall see, it is the anterior ramus that is variable.

In *Geoballus* the anterior ramus (C) does not pass directly to the next segment's nodus, although in most non-himantariids it does pass directly to it. Rather, it connects in the preceding segment with an internodal

<sup>3</sup> Tracheotaxy, a new term: the study of tracheae as systematic criteria.

connective (D) at a point just anterior to the nodus of that segment. The internodal connectives pass from one nodus to the next down the full length of the body where they may function as a direct intersegmental carrier of air, as an air storage reservoir, or as both.

Comparing Figure 23 (of *Straberax*) with the foregoing (of *Geoballus*), it may be seen that in the former the posterior ramus has exactly the same connections as it has in the latter; the internodal connectives, however, are very different. In *Straberax*, in effect, each anterior ramus terminates not in the preceding segment, but in the pre-antecedent segment at the nodus. Therefore, this type of connection might be described as *saltate*, whereas the former kind could be termed *seriosaltate*. In most Geophilomorpha the anterior ramus connects directly with the nodus of the antecedent segment, and internodal connectives are absent; this simplest of all arrangements I term *serial*. The rear terminus of each internodal connective has detached, but the interior terminus has remained intact, so that the anterior division of the system is in fact composite, consisting of the continuous anterior ramus and internodal connective. It seems clear that the dorsal tracheal system of the *Straberax*-type represents a derivative of that of the *Geoballus*-type.

I have encountered both tracheal types or their proximate variations throughout the family; of the two the *Geoballus*-type is by far the more common and in both subfamilies. But the uncommon *Straberax*-type has also been discovered in both subfamilies, where the anterior ramus' extension may skip up to five segments before terminating at a nodus. From these studies, whose elaboration transcends the scope of this paper, I have drawn several hypotheses. (1) In himantariid evolution there was no single point-of-departure at which the saltate *Straberax*-type of tracheation arose once and only once from the seriosaltate *Geoballus*-type. I believe that the saltate type has arisen many times in different evolving lines (independently in the two subfamilies) from the common and antecedent seriosaltate type. (2) A given tracheal configuration seems constant at least throughout a genus, and it seems often, though not always, constant throughout a group of related genera.

This study was undertaken with the aid of a grant from the National Science Foundation. I would like to thank Dr. G. E. Ball, Jr., and Mr. D. R. Whitehead of the University of Alberta, Dr. W. T. Keeton of Cornell University, and Dr. B. D. Valentine of the

Ohio State University for the material that they have so generously placed at my disposal.

#### *Geoballus*, new genus<sup>4</sup>

Comparable with both *Bothriogaster* and *Straberax*, this genus appears to resemble *Bothriogaster* more closely in what I take to be the more fundamental features. They differ conspicuously as follows: In *Bothriogaster*—(1) Certain sternites, usually anterior to mid-body length, with deep fovea-like sternobothria. (2) The legs at least of the foregoing segments with hypertrophied parungues that equal or exceed their claw lengths. In *Geoballus*—(1) No sternites with sternobothria. (2) No parunguis equal to or exceeding its claw; the former always much shorter.

Antennae: The more proximal articles slightly dorsoventrally flattened, those remaining terete, not flattened; distally slightly attenuate. Bucca: Mesal margins not sclerotized and pigmented.<sup>5</sup> Labral embayment shallow; labral sides not completely divisive. First maxillary coxosternal lappets absent; telopodite lappets present or absent. Second maxillary claw without basal bristles or filaments; isthmus anteromedially without diastema, protracted. Tarsungula without basal denticle, other articles unarmed; presentation dorsomesal. Prosternal pleurograms present and complete to condyles. Tergites without paramedian sulci. Major paratergites absent. Tracheation seriosaltate type. Sternites without sternobothria; anterior and posterior body sternites wider than long. Porefields strongly transverse, very wide, subreniform; present on 1 through penult without interruption. Ultimate pretergite bilaterally fissate, the pleurites discrete; presternite divided; sternite wider than long, posteriorly embayed. Each coxopleuron with one dorsal and one ventral glandular fossa bordering the tergite and sternite. Telopodite relatively short, in the male slightly clavate. Anal pores absent.

Two species are referable to the genus.

TYPE-SPECIES.—*Geoballus caputalbus*, new species. Original designation.

<sup>4</sup> *Geoballus*, dedicated with gratitude to George Ball, carabid connoisseur and esteemed old friend, who for more than 20 years has generously sent me wonderful Chilopoda from wherever his coleopterous safaris took him.

<sup>5</sup> Throughout the Himantariinae and in some Bothriogastriine genera, these margins are heavily sclerotized and pigmented: a new character.

*Geoballus caputalbus*, new species<sup>6</sup>

The type-species is, of course, most like the genus' only other species, *bebelus*, new species, differing notably as follows: In *caputalbus*—(1) Leg pairs 91. (2) Telopodite lappets absent. (3) Final porefields straight, slightly shorter. In *bebelus*—(1) Leg pairs 61. (2) Telopodite lappets present. (3) Final porefields somewhat bent, slightly longer.

**HOLOTYPE**.—Male. Mexico, Oaxaca, 21.8 miles north of Tuchatengo. 18 August 1966; G. E. Ball, Jr., and D. R. Whitehead, legg. Deposited in the United States National Museum.

**GENERAL CHARACTERS**.—Length 45 mm. Leg pairs 91. Shape: Dorsoventrally flattened; of essentially uniform width. Color sordid yellow. Vestiture extremely sparse and short.

**DETAILED DESCRIPTION**.—*Antennae*: Not attenuate; dorsoventrally only slightly flattened. All articles except 14th wider than long. Articles (4–5)–14 finely densely setose; 1–(3–4) with fewer and longer setae. 14th article setosensoria ectally and mesally, located slightly distad of midlength. *Cephalic plate*: Greatest width to length = 11:8. Shape: anteriorly rostrate; sides slightly excurved; rear straight. Cephalic suture not apparent. *Clypeus*: Without plagulae or antero-central fenestra. Paraclypeal sutures nearly straight, complete to outer ends of fulcra. With 30–40 short weak setae on anterior half; posterior half glabrous. *Labrum*: Deeply embayed, teeth 6+7; entirely demarcated from clypeus by hyaline suture. *Mandible*: Shaft long, flat, proximally curved. Corpus with 7 pectinate lamellae and 1 dentate lamella having 10 teeth. *First maxillae*: Coxosternum medially deeply incised; lappets absent. Medial lobes relatively long, subtriangular. Telopodite lappets absent; unipartite, not demarcated from coxosternum. *Second maxillae*: Isthmus deep anteroposteriorly, medially protracted, not diastemate. Weak postmaxillary sclerites present. Telopodite: Both basal condyles present, strong; articles 1 and 2 wider than long; claw robust, without basal bristles and filaments, shallowly excavate within.

*Forcipular segment*: Tarsungula relatively long and relatively little curved; edges smooth, not serrulate; presentation dorsomesal. Poison calyx linear, not subspherical. Prosternal pleurograms present but weak, complete to condyles. Antero-central denticles absent.

<sup>6</sup> Named in honor of D. R. Whitehead, who with G. E. Ball collected these and plethorous other excellent specimens.

*Tergites*: Essentially glabrous. Paramedial sulci absent. *Pleurites*: Paratergites absent. Spiracles subcircular. *Legs*: Sparsely shortly setose, robust. Pretarsi: Robust and very long, not excavate beneath; parungues equal, about one-fourth as long as claws. *Sternites*: All wider than long. Very shortly, sparsely setose. Without *carpophagus*-structures, foveae, stigmoid, or virgiform structures. Porefields: On 1 through penult without interruption, on anterior body subcentral in position, on rear body posterior in position; transversely wide and straight to exceedingly wide, anteroposteriorly short, each posteriorly slightly embayed or subreniform.

*Ultimate pedal segment*: Pretergite bilaterally fissate, the pleurites discrete. Tergite much wider than long, 17:8. Presternite medially separated. Sternite: Greatest width to length, 12:7; sides straight and convergent, rear slightly incised. Coxopleuron: Moderately inflated, encroaching slightly upon penult; gland canals opening into fossae along edges of sternite and tergite, hence glands not in subsurface pockets. Telopodite: Slightly longer than penult; dorsoventrally slightly flattened and distally slightly clavate; with two tarsalia; pretarsus absent.

*Postpedal segments*: Syntergum densely hirsute. Female gonopods long, well separated, each biarticular. Anal pores absent.

*Geoballus bebelus*, new species

*Geoballus bebelus* most resembles *caputalbus*; their diagnostic differences are summarized under the latter's description.

**HOLOTYPE**.—Male. Mexico, Veracruz, San Andres Tuxtla, Vulcan San Martin, 3,500'. 1 August 1959; W. T. Keeton and B. D. Valentine, legg. Deposited in the United States National Museum.

**GENERAL CHARACTERS**.—Length 40 mm. Leg pairs 61. Shape: Dorsoventrally flattened; body essentially uniform in width front to rear. Color sordid yellow.

**DETAILED DESCRIPTION**.—*Antennae*: Not attenuate, only slightly flattened dorsoventrally. Each article except 14th very slightly wider than long. Articles 6–14 finely densely setose, 1–5 with fewer but longer setae. 14th article setosensoria ectally and mesally, located far distad of midlength. *Cephalic plate*: Greatest width to length 19:17. Shape: anteriorly rostrate; sides excurved, rear straight. Cephalic suture not apparent. *Clypeus*: Without plagula or fenestra. Paraclypeal



sutures nearly straight, complete to outer ends of fulcra. Setae about 30, on anterior third of clypeus, the rest glabrous. *Labrum*: Relatively shallowly embayed. Teeth 6+7. Demarcated from clypeus by a hyaline suture. *Mandible*: Shaft long and flat, proximally curved. Corpus with 7 pectinate and 1 lamellate lamellae, the latter with 9 teeth. *First maxillae*: Coxosternum medially deeply incised; lappets absent; medial lobes relatively long and subtriangular. Telopodites small, lappets present; unipartite, not discernibly demarcated from coxosternum. *Second maxillae*: Isthmus deep anteroposteriorly, medially protracted, not diastemate. With weak postmaxillary sclerites. Telopodite: Dorsal and ventral condyles present; claw robust, without basal bristles or filaments, shallowly cochlear. *Forcipular segment*: Tarsungula relatively long, relatively little curved; edges smooth, not serrulate; poison calyx linear; presentation mesodorsal. Prosternal pleurograms present, complete to condyles, weak; anteromesal denticles absent. *Tergites*: Essentially glabrous. Paramedial sutures absent. *Pleurites*: Paratergites absent. Spiracles subcircular. *Legs*: Sparsely, shortly setose, robust. Pretarsi: Robust and very long, not excavate beneath; parungues equal, about one-fifth as long as claw. *Sternites*: All much wider than long. Very shortly, sparsely setose. Without *carphagus*-structures, foveae, stigmoid or virguliform structures. Porefields: On 1 through penult without interruption; on anterior body subcentral in position, on rear body posterior in position; transversely wide to exceedingly wide and slightly arched, anteroposteriorly short, somewhat reniform.

*Ultimate pedal segment*: Pretergite bilaterally fissate, the pleurites discrete. Tergite: Much wider than long, 15:10. Presternite medially separated. Sternite: Greatest width to length 18:13; sides straight and convergent, rear strongly incised. Coxopleuron: Moderately inflated; encroaching slightly upon penult; gland canals opening into fossae along edges of sternite and tergite, hence not in subsurface pockets. Telopodite: Slightly longer than penult; dorsoventrally flattened, not notably clavate; densely finely hirsute; with two tarsalia; pretarsus absent.

*Postpedal segments*: Syntergum densely hirsute. Male gonopods long, biarticular. Anal pores absent.

#### *Straberax*, new genus<sup>7</sup>

*Straberax* seems most like *Geoballus*; the two differ most conspicuously as follows: In *Geoballus*—(1) Tracheation is, like that of *Bothriogaster*, serialsaltate as in

Figure 22. (2) Coxopleural glands in deep, subcircular crypts. (3) Second maxillary telopodite lappets, if present, normal, not amalgamated with telopodites. In *Straberax*—(1) Tracheation is saltate as in Figure 23. (2) Coxopleural glands in shallow elongate fossae. (3) Second maxillary telopodite lappets present but curiously amalgamated with telopodites.

Antennal proximal articles dorsoventrally slightly flattened, the more distal articles not flattened, terete; distally slightly attenuate. Buccae: Mesal margins not sclerotized and pigmented. Labral embayment deep, completely divisive. First maxillary coxosternal lappets absent; telopodite lappets present but amalgamated with telopodites. Second maxillary claw without basal bristles or filaments; isthmus anteromedially without diastema, protracted. Tarsungula without basal denticles, all articles unarmed; presentation dorsoventral; article 1 basomesally with a prominent pigmented macula. Prosternal pleurograms strong and complete to condyles. Tergites without paramedian sulci. Major paratergites absent. Tracheation saltate. Sternobothria absent. Anterior body sternites wider than long; posterior sternites longer than wide or rectilinear. Porefields transversely not notably wide; present on 2 through penult without interruption. Ultimate pretergite bilaterally fissate, pleurites discrete; presternite divided, sternite wider than long, posteriorly embayed. Each coxopleuron with one dorsal and one ventral glandular crypt, these deep, subcircular, heterogeneous. Telopodite relatively short, clavate in male, not so in female, dorsoventrally slightly flattened; tarsalia 2, without pretarsus. Anal pores absent.

The genus is known to contain one species.

TYPE-SPECIES.—*Gosiphilus morelos* Chamberlin (= *Straberax morelos* (Chamberlin)). Monotypic and original designation.

*Straberax morelos* (Chamberlin), new combination  
*Gosiphilus morelos* Chamberlin, 1943, p. 11.

GENERAL CHARACTERS.—Length to 56 mm. Leg pairs 77–97. Shape: Dorsoventrally flattened; essentially uniform in width front to rear. Color sordid yellow.

DETAILED DESCRIPTION.—*Antennae*: Length to head length (2–2.5):1. Proximal 3–4 articles slightly flattened, the remainder terete; distally slightly attenuate; all articles except 14th wider than long. Articles 6–14 more setose than 1–7. Article 14 ectally and mesally with a setosensorium immediately proximad of mid-

<sup>7</sup> A name of arbitrary coinage.



length. *Head*: Greatest width to length, 9:7. Anteriorly rostrate, sides excurved, rear straight. Cephalic suture weakly indicated. *Clypeus*: Fenestra and plagula absent. Paraclypeal sutures straight, slightly oblique, complete, ending at ectal third of the fulcra. Setae numerous, short, about 40 on each side of the glabrous midline; prelabrals absent. Buccae without deeply pigmented sclerotic margins. *Labrum*: Protuberant and dependent; deeply medially embayed, there with some 14–18 teeth. *Mandible*: Proximal half of shaft slightly curved, expanded. Corpus with 4 pectinate and 1 dentate lamellae, the latter with 10–11 teeth. *First maxillae*: Coxosternum essentially divided medially into right and left halves, i.e., deeply, widely cleft, lappets absent. Medial lobes short. Telopodites: Weakly demarcated from coxosternum, not discernibly biarticular; evidently broadly amalgamated with lappets. *Second maxillae*: Isthmus anteroposteriorly deep; anteromedially protracted, not diastemate. Postmaxillary sclerites present, atrophied. Telopodite: Articles 1 and 2 wider than long; both basal condyles present; terminal claw short, robust, evidently cochlear, without basal bristles or filaments.

*Forcipular segment*: Prehensors: Claw relatively short and but slightly curved; smooth, not serrulate, presentation mesodorsal; poison calyx linear, elongate; all articles without denticles; article 1 posteromesally with a prominent, dark macula. Prosternum: Without anterior denticles; pleurograms strong, complete to condyles.

*Tergites*: Paramedial sulci not discernible. *Pleurites*: Paratergites absent. Spiracles subelliptical, vertical. *Legs*: Robust, essentially glabrous; each pretarsus with two equal parungues, these about one-

third as long as claw. *Sternites*: On anterior half of body wider than long; on rear of body essentially rectilinear. Porefields: On 2 through penult without interruption; on anterior body subcentral in position, transversely subelliptical, thereafter becoming smaller in size and more posterior in position. Without foveae, stigmatic, and virgiform structures.

*Ultimate pedal segment*: Pretergite laterally fissate, the pleurites discrete. Tergite much wider than long. Presternite medially separated. Sternite: Greatest width exceeds length, 8:7; sides essentially straight, rear slightly embayed. Each coxopleuron: Inflated but not encroaching upon penult; with one dorsal and one ventral heterogeneous, multicanalicate glandular cavity, opening respectively along tergite and sternite margins. Telopodite: In the female as long as penult and no more robust, in the male as long as penult but notably more robust and slightly clavate; with two tarsalia; pretarsus absent.

*Postpedal segments*: Female gonopods medially contiguous but not fused, each distinctly biarticular. Anal pores absent.

**SPECIMENS STUDIED.**—I have studied seven specimens from three Mexican states; all agree closely with each other. All are deposited in the collection of the U.S. National Museum. Their leg-pair dispersion is as follows: 77 leg-pairs, 1; 89, 5; 95, 1. Locality data is as follows: *Morelos*: 9.1 miles east of Cuernavaca, Canon de Lobos at 4,300', 24.VII.66, Ball and Whitehead; Cuatla, 24.IV.63, Whitehead. *Oaxaca*: 18.4 miles south of Suchixtepec at 4,500', 20.III.66, Ball and Whitehead. *Veracruz*: 5.8 miles west of Ojazarco at 5,400', 10.VII.59, Keeton and Valentine.

### Key to BOTHRIOGASTRINAE

1. Coxopleura entirely without glands and their associated cavities, fossae, canals, and pores (Africa, Asia) . . . . . *Mesocanthus* Meinert  
Coxopleura with glands in cavities or fossae, with associated canals and pores . . . . . 2
2. Each coxopleuron with only one dorsal gland cavity, this exiting along tergite; ventral glands absent. Second maxillary claw with robust basal bristles. (Africa, Asia) . . . . .  
. . . . . *Polyporogaster* Verhoeff  
Each coxopleuron with dorsal and ventral glands, these exiting via one dorsal and one ventral gland cavity or fossa. Second maxillary claw basally unarmed . . . . . 3
3. Tracheal anterior rami saltate as in Figure 23. Second maxillary telopodite lappets present but amalgamated with telopodites (Mexico) . . . . . *Straberax*, new genus  
Tracheal anterior rami seriosaltate as in Figure 22. Second maxillary telopodite lappets, if present, normal, not amalgamated with telopodite . . . . . 4
4. Certain sternites (usually anterior to midbody length) with prominent, deep sternobothria. Legs, at least of foregoing segments, with hypertrophied parungues equal to or exceeding their claw length (Africa, Asia) . . . . . *Bothriogaster* Selivanoff  
Sternites without sternobothria. Parungues not hypertrophied, always much shorter than their claws (Mexico) . . . . . *Geoballus*, new genus

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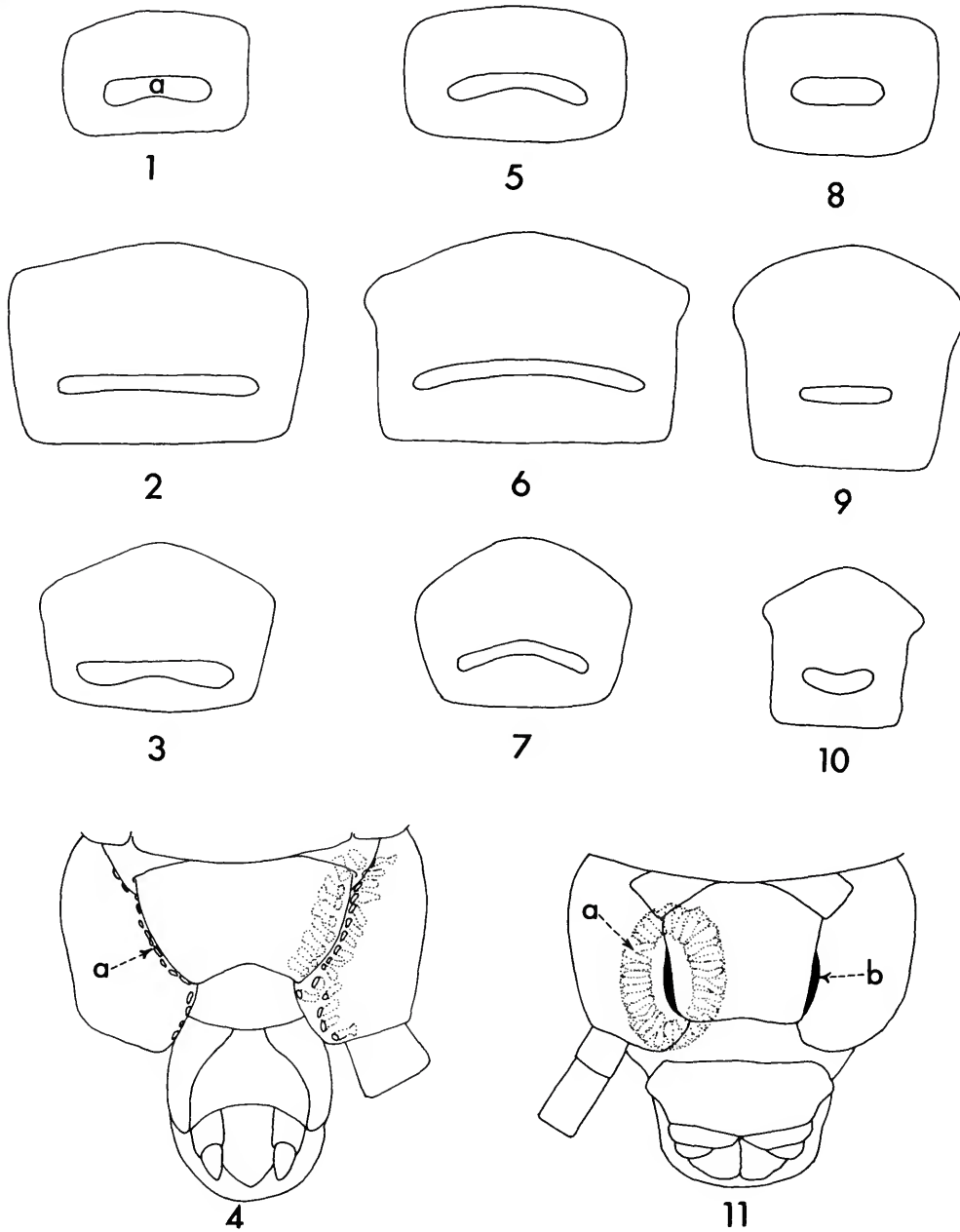
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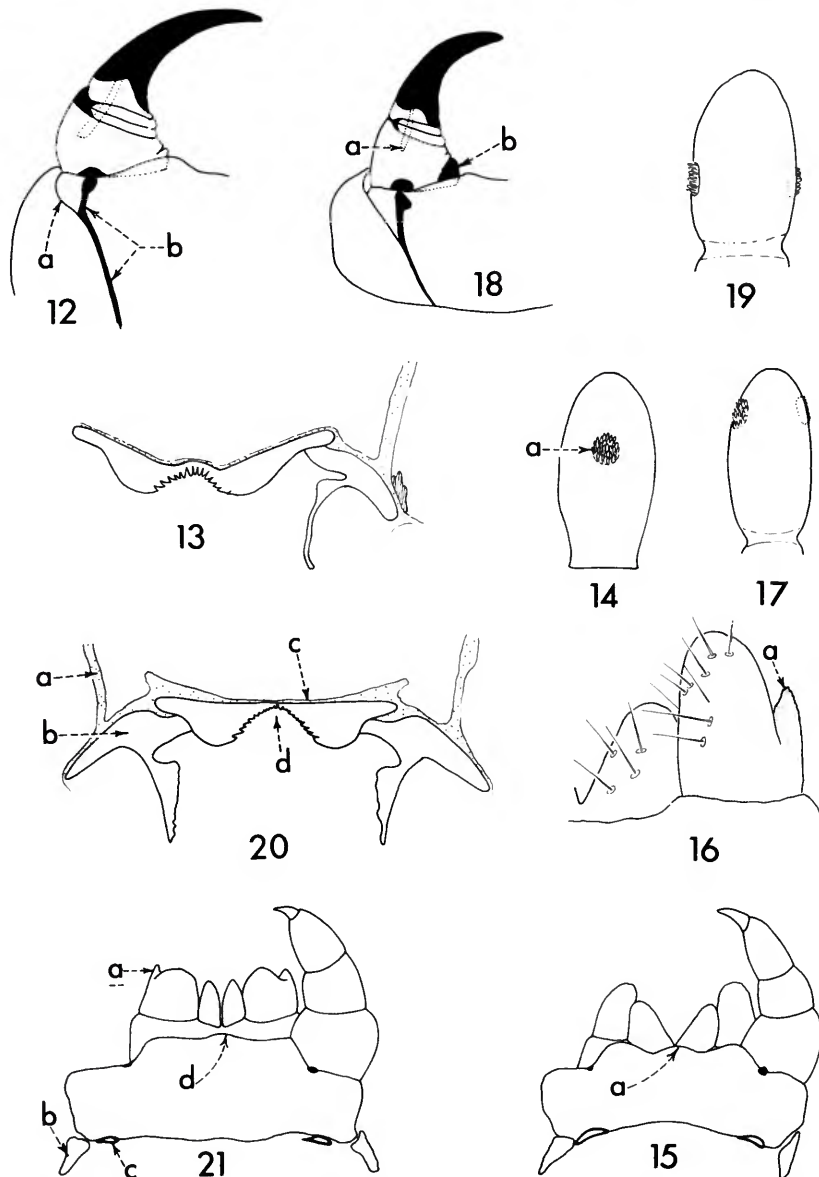
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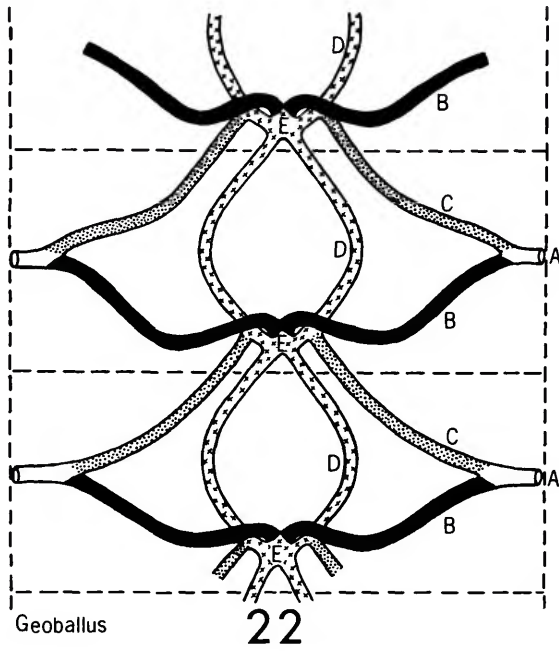


FIGURES 1-11.—*Geoballus caputalbus*, holotype: 1, 5th sternite (a=porefield); 2, ultimate sternite minus 8; 3, penult sternite; 4, ultimate pedal and postpedal sternites (a=pores in coxopleural fossa). *Geoballus bebelus*, holotype: 5, 8th sternite; 6, ultimate sternite minus 8; 7, penult sternite. *Straberax morelos* (Chamberlin): 8, 10th sternite; 9, ultimate sternite minus 10; 10, penult sternite; 11, ultimate pedal and postpedal sternites (a=concealed gland canals in crypt, b=crypt opening).





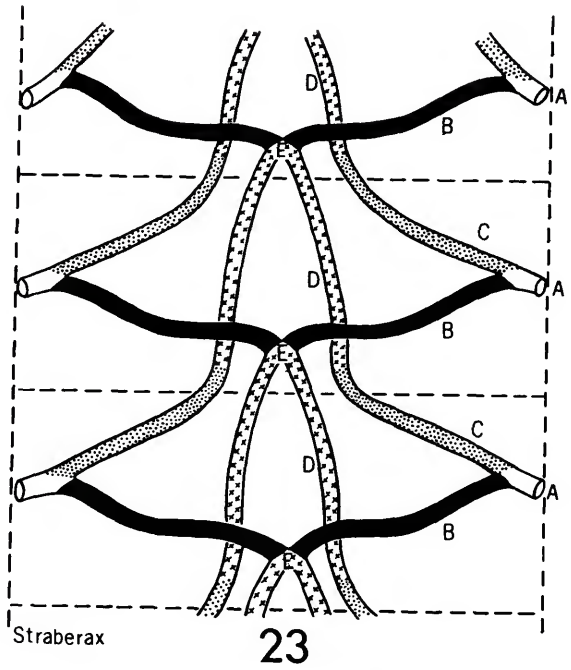
FIGURES 12-21.—*Geoballus caputalbus*, holotype: 12, right side of prosternum with prehensor (a=pleuroprosternal suture, b=pleurogram); 13, labrum with left fulcrum and paraclypeal suture, 14, ultimate antennal article (a=setosensorium); 15, first and second maxillae (a=protracted medial portion of isthmus). *Geoballus bebelus*, holotype: 16, first maxillae, left telopodite with medial lobe (a=lappet); 17, ultimate antennal article showing both setosensoria. *Straberax morelos* (Chamberlin): 18, right side of prosternum with prehensor (a=poison calyx, b=macula); 19, ultimate antennal article showing both setosensoria; 20, labrum with both fulcra and adjacent areas (a=right, paraclypeal suture, b=right fulcrum, c=clypeolabral suture, d=labral embayment); 21, first and second maxillae (a=right lappet, b=postmaxillary sclerite, c=salivary pore, d=protracted portion of isthmus).



Geoballus

22

FIGURE 22.—*Geoballus caputalbus*, holotype, semischematic (A=spiracle; B=posterior ramus; C=anterior ramus; D=internodal connective; E=nodus).



Straberax

23

FIGURE 23.—*Straberax morelos* (Chamberlin) (A=spiracle; B=posterior ramus; C=anterior ramus; D=internodal connective; E=nodus).





## Publication in *Smithsonian Contributions to Zoology*

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The *title* should be complete and clear for easy indexing by abstracting services. Taxonomic titles will carry a final line indicating the higher categories to which the taxon is referable: "(Hymenoptera: Sphecidae)." Include an *abstract* as an introductory part of the text. Identify the *author* on the first page of text with an unnumbered footnote that includes his professional mailing address. A *table of contents* is optional. An *index*, if required, may be supplied by the author when he returns page proof.

Two *headings* are used: (1) text heads (boldface in print) for major sections and chapters and (2) paragraph sideheads (caps and small caps in print) for subdivisions. Further headings may be worked out with the editor.

In *taxonomic keys*, number only the first item of each couplet; if there is only one couplet, omit the number. For easy reference, number also the taxa and their corresponding headings throughout the text; do not incorporate page references in the key.

In *synonymy*, use the short form (taxon, author, date, page) with a full reference at the end of the paper under "Literature Cited." Begin each taxon at the left margin with subsequent lines indented about three spaces. Within a taxon, use a period-dash (:—) to separate each reference. Enclose with square brackets any annotation in or at the end of the taxon. For *references within the text*, use the author-date system: "(Jones, 1910)" or "Jones (1910)." If the reference is expanded, abbreviate the data: "Jones (1910, p. 122, pl. 20: fig. 1)."

Simple *tabulations* in the text (e.g., columns of data) may carry headings or not, but they should not contain rules. Formal *tables* must be submitted as pages separate from the text, and each table, no matter how large, should be pasted up as a single sheet of copy.

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In the *bibliography* (usually called "Literature Cited"), spell out book, journal, and article titles, using initial caps with all words except minor terms such as "and, of, the." (For capitalization of titles in foreign languages, follow the national practice of each language.) Underscore (for italics) book and journal titles. Use the colon-parentheses system for volume, number, and page citations: "10(2):5-9." Spell out such words as "figures" and "plates" (or "pages" when used alone).

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