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Millipeds from Dominican Amber, with the Description of Two New Species (Diplopoda: Siphonophoridae) of Siphonophora

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ABSTRACT Representatives of 11 genera (*Lophoproctus*?, *Glomeridesmus*, *Epinanolene*, *Siphonophora*, *Siphonotus*, *Docodesmus*, *Iomus*, *Lophodesmus*?, *Psochodesmus*, *Dasyodontus*, and *Inodesmus*?) are reported from Dominican amber, most of them constituting the first or oldest fossils of their corresponding higher taxa. Extant species of *Iomus* and *Inodesmus* have not been reported from Hispaniola; a chelodesmid seems more closely related to South American genera than to present-day Caribbean diplopods. *Siphonophora hoffmani* spec. nov. and *S. velezi* spec. nov. are described from adults embedded in Dominican amber.

KEY WORDS Diplopoda, systematics, *Siphonophora* spp., Hispaniola

ALTHOUGH THE OLDEST EXTINCT ORDERS of millipeds are known from the Late Silurian (421-408 mya), none of the extant orders is known from an epoch preceding the Oligocene (36-24 mya; Tertiary, Cenozoic) (Hoffman 1969, Kraus 1974, Shear & Kukulova-Peck 1990). In most cases, millipeds from Dominican amber belong to extant genera of the Greater Antilles myriapodofauna.

Siphonophora Brandt (1837) is a predominantly tropical American genus (Attems 1951), with 12 described species in the Caribbean (Loomis 1936, 1937, 1941, 1970), all from the extant fauna. *Siphonophora hoffmani* spec. nov. and *S. velezi* spec. nov. are the second and third (respectively) reported fossil species of the Siphonophoridae from Dominican amber; *Siphonocybe* sp. was the first (Shear 1981).

Materials and Methods

All fossils discussed in this study are believed to have come from amber mines located in the Cordillera Septentrional between Santiago and Puerto Plata in northern Dominican Republic. These mines are in the Altamira facies of the El Mamey Formation (Upper Eocene), which is estimated to range in age from 23 to 40 million yr (Lower Miocene to Upper Eocene) (Lambert et al. 1985).

In the description of the new species of *Siphonophora*, parenthetical statements, where present, refer to the allotype and to other paratypes, respectively. Nomenclature and descriptions usually follow those of Loomis (1970). Unless otherwise mentioned, supraspecific diagnoses follow Vélez (1965) with some modifications. Abbreviations of depositories are as

follows: GOP, George O. Poinar, Jr., collection of Dominican amber housed at the University of California, Berkeley; PC, Patrick Craig private collection of Dominican amber. Specimens are available for study by consulting G.O.P.

Milliped Taxa from Dominican Amber Fig. 1-17

Hoffman's (1980) classification of the Diplopoda is used. The following code is used: **, new fossil record for the Diplopoda; *, new milliped record for Hispaniola.

Subclass Psephalognatha

Order Polyxenida

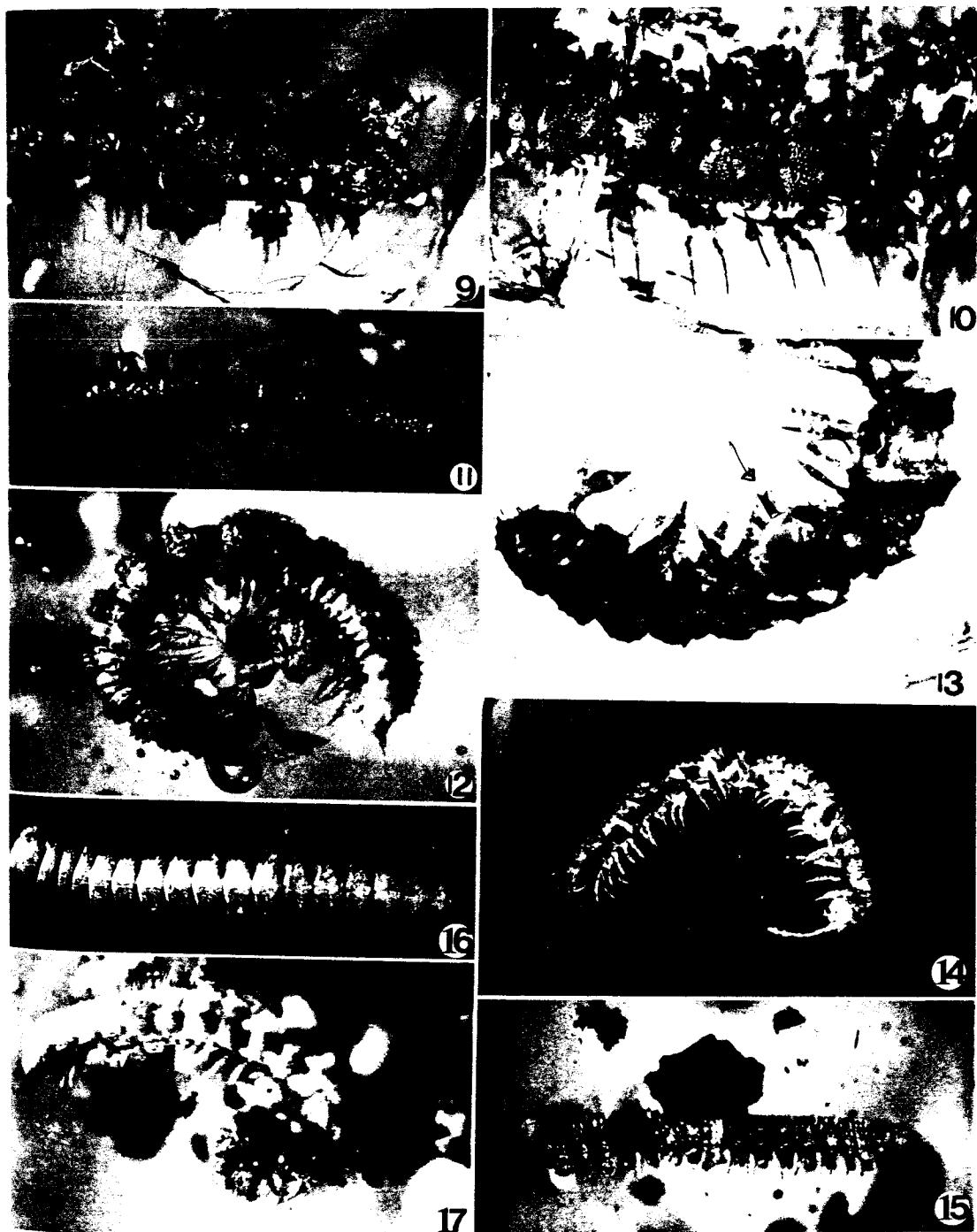
**Family Lophoproctidae (?), *Lophoproctus* ? (Fig. 1)

Diagnosis. Body surface not highly chitinized, bearing numerous barbed setae disposed in radiating tufts; with 11 body segments; 2 distalmost antennal segments (segments 7 and 8) elongated, subequal, with minute sensory cones on terminal segment; lateral cones of gnathochilarium and ocelli absent; with 13 pairs of simple, clawed legs.

Comments. Three adults were examined: one female (PC) \approx 2 mm long with 10-11 segments; 2 unsexed adults, one (GOP DC-3-14) \approx 3 mm with 11 segments, another (PC) about 1.6 mm with 11 segments. All specimens have pilosity almost complete.



Figs. 1-8. (1) *Lophoproctus* ? sp. adult, ventrolateral view. (2-3) *Glomeridesmus* sp., adult female (2) Ventrolateral view. (3) Ventrolateral view (arrowhead points to Tömösvary's organ, arrow points to extruded ovipositors). (4-5) Stemmiulid adult female. (4) Overall ventrolateral view. (5) Large, apposed legs characteristic of this family, ventral view. (6) *Epinannolene* sp. immature, dorsolateral view. (7) Siphonotid immature, lateral view. (8) Chelodesmid sp. adult (sex undetermined), overall dorsolateral view.



Figs. 9-17. (9-10) *Chelodesmid* sp. (sex undetermined). (9) Epiproct, ventrolateral view. (10) Tergum (arrowhead points to large metazonite projection). (11) *Docodesmus* sp. adult male, dorsal view. (12,13) *Iomus* sp. (12) Adult female, dorsolateral view. (13) Arrowhead points to greatly expanded gonocoxa of adult male, lateral view. (14) *Lophodesmus* ? sp. adult male, lateral view. (15) *Psochodesmus* sp. adult male, dorsolateral view. (16) *Dasyodontus* sp. female, dorsal view. (17) *Inodesmus* ? sp. Adult female, dorsolateral view.

Subclass Pentazonia

Order Glomeridesmida

Family Glomeridesmidae, *Glomeridesmus* (Fig. 2)

Diagnosis. Head not covered by collum; mentum divided mesally by 2 plates; tergites smooth, with a few small setae and transverse sutures that are bent posteroventrally on lateral sides.

Comments. The specimen studied (GOP DC-3-4) is an adult female (≈ 3.5 mm long) with 21 trunk segments, extruded ovipositor, and an evident Tömösvary's organ (Fig. 3).

Subclass Helminthomorpha

Order Stemmiulida

**Family Stemmiulidae (Fig. 4, 5)

Diagnosis. With ≥ 39 trunk segments; body laterally compressed; tergites with fine striae; ozopores on segments beyond 4; with 1 or 2 ocelli; no pronotum.

Comments. One headless adult female (GOP DC-3-13) ≈ 7 mm long with at least 35 trunk segments was studied. Several species of *Prostemmiulus* are represented in the extant Hispaniolan myriapodofauna (Loomis 1941), including an extinct form (Shear 1987); *Scoliozonus* also occurs in Puerto Rico (Loomis 1941). Other genera may have been present in the Hispaniolan Miocene.

**Order Spirostreptida

Family Pseudonannolenidae, *Epinannolene* sp. (Fig. 6)

Diagnosis. Laterally narrowed collum; no paranota; ozopores on all segments beyond 4; with ocelli; anal valves slightly surpassing epiproct.

Comments. One immature specimen (GOP DC-3-12) ≈ 13 mm long, with ≈ 36 trunk segments was studied. The previous placement of a fossil milliped in this order is questionable (Hoffman 1969).

Order Siphonophorida

Family Siphonophoridae, *Siphonophora* sp.

Diagnosis. Long and slender, almost cylindrical, with body covered with numerous tiny setae; head produced anteriorly into narrow, elongated beak; eyes absent; antennae stout, densely setose; gnathochilarium consisting of a single, undivided plate.

Comments. Three females were studied: one adult (GOP DC-3-9A) ≈ 15 mm long with at least 35 trunk segments, and 2 immatures (PC), one > 5 mm long, with at least 19 segments; the other 11 mm long, with at least 30 trunk segments. The distally gradual widening of the adult body and the conspicuous, regularly placed setae distinguishes the adult female from *S. hoffmani* and *S. velezi* spp. nov. *Siphonocybe* was reported by Shear (1981).

**Order Polyzonida

Family Siphonotidae, *Siphonotus* sp.

Diagnosis. With strongly depressed body; dorsum arched, venter generally flat or slightly concave; tergite surface generally smooth; head with acute, conical beak.

Comments. An immature (GOP DC-3-15) (Fig. 7) (Mauriès & Silva 1971) with remarkable resemblance (because of position of the fossil) to Silurian-Devonian kampecarids (Almond 1985, Peach 1882) was studied. The specimen has a scarcely sclerotized body with a single spiracle anterior to each leg, 25 pairs of legs, a small head with reduced mouthparts, the first 4 trunk segments cover 3 pairs of legs, the 12 following segments cover two pairs of legs each, the last large diplosegment is legless, and legs are with long, thin tarsi.

Order Polydesmida

**Suborder Chelodesmidea

Family Chelodesmidae

Diagnosis. One adult female (GOP DC-3-11) > 18 mm long, with head mostly lost but otherwise in nearly complete condition (Fig. 8).

Comments. In many peripheral features (e.g. broadened and somewhat concave epiproct [Fig. 9], granulose metaterga, slender legs, laterally dentate paranota without trace of peritremata [Fig. 10]), the specimen strongly resembles extant species of the tribe Batodesmini (Hoffman 1982). Regrettably, the definitive apomorphy of this taxon (several macrosetae at apex of gonopod prefemur) cannot be affirmed because of the sex of the milliped. At present, batodesmines are confined to Panama and the northern Andes to Peru. If the specimen at hand could be confirmed as a batodesmine, previous land connections over the present Antillean region would be implied. At the present time, we know no modern species with these facies in the West Indies.

Suborder Polydesmidae

Family Pyrgodesmidae

Docodesmus sp. (Fig. 11) (see Shear 1981)

Diagnosis. Collum smooth or slightly scalloped, with 12 radiating anteromarginal areas concealing head completely; tergites usually with 2 longitudinal rows of tubercles mesally; paranota broad, nearly horizontal, tri- or tetralobed; ozopores very small.

Comments. Three adults were studied: two females (PC), one ≈ 9.5 mm long with 17 trunk segments, the other about 6.4 mm long with 18 trunk segments; the male (GOP DC-3-3) is ≈ 6.5 mm long and has 18 segments.

Iomus sp.

(Fig. 12, 13)

Diagnosis. Collum with 10 radiating anteromarginal areas; all free margins of paranota with deep, wide incisions; tergites with 4 prominent rows of tubercles; ozopores located on posterolateral elevations of paranota 12, 13, and 15-18; anal region concealed.

Comments. Two specimens were studied: an adult female (GOP DC-3-6) ≈ 5 mm long with 18 trunk segments (Fig. 12), and an adult male (GOP DC-3-5) ≈ 7 mm long with 19 trunk segments showing greatly expanded gonocoxae (Fig. 13) characteristic of the Pyrgodesmidae and two other diplopod families. An *Iomus* sp. was reported by Shear (1987).

Lophodesmus sp.

(Fig. 14)

Diagnosis. According to Pocock (1894), fifth antennal segment the longest and thickest; collum as wide as second trunk segment, laterally expanded and completely covering head; remaining segments with strongly developed, subcontiguous, depressed keels that cover legs; each trunk terga with 2 longitudinal rows of tubercles and additional, scattered tubercles; ozopores on segments 5, 7, 9, 10, 12, 13, 15, and 16, located on posterior angles of paranota and raised on a tubercle.

Comments. The specimen studied (PC) is an adult male ≈ 5 mm long with 19 trunk segments.

Pschodesmus sp.

(Fig. 15)

Diagnosis. According to Loomis (1936), trunk terga with four subcontiguous transverse rows of distinct tubercles; ozopores on segments 5, 7, 9, 10, 12, 13, and 15.

Comments. The specimen studied GOP DC 3-20 is an adult male ≈ 5 mm long with 19 trunk segments.

Polydesmidea of uncertain status and family position

Dasyodontus sp.

(Fig. 16)

Diagnosis. According to Loomis (1936), overall body size < 10 mm long; trunk segments with abundant, long, suberect, and scattered tergal setae; segments 1-18 with 2 pointed or conical tubercles on each side of tergum, near paranota projecting beyond its posterior margin.

Comments. The specimen studied (GOP DC-3-10) is an adult female ≈ 6 mm long with 19 trunk segments. This specimen differs from *Dasyodontus hispaniolus* Loomis (1941) by being slightly larger and lacking the posteriormost pairs of strong conic teeth on the first three segments.

Inodesmus? sp.

(Fig. 17)

Diagnosis. Millipedes 6-10 mm long, with 19-20 body segments; head not concealed by collum; metatergites elevated and densely covered by setae, indistinct paranota; ozopores on segments 5, 7, 9, 10, 13, and 15-19.

Comments. Six specimens were studied: three adults, both females (GOP DC-3-2 and PC) with 19 trunk segments, one ≈ 8 mm long, the other 4.1 mm long, the male (PC) ≈ 5 mm long with 19 body segments; three immatures, one a male and one of undetermined sex (GOP DC-3-1), the other (PC) a female 2.1 mm long with 17 body segments.

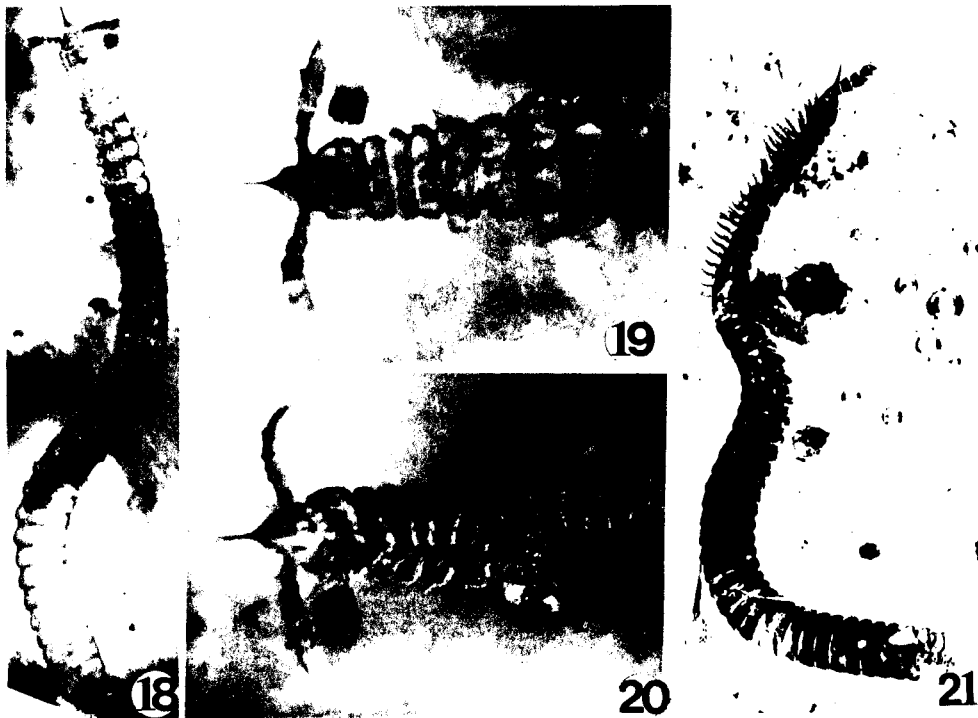
Inodesmus, a genus present in Jamaica, has not yet been reported for the extant Hispaniolan myriapodofauna, suggesting that it may have become extinct there. An undescribed new family of polydesmoids was reported by Shear (1987). We are puzzled by the relative abundance of most of these leaf litter Diplopoda in amber and can conclude only that resin was also exuded from basal portions of the tree.

Family Siphonophoridae Newport, 1844

Siphonophora hoffmani Santiago-Blay & Poinar, spec. nov.

(Fig. 18-20)

Description. Body ≈ 7 mm long (≈ 11 , > 12) with 41 (54, > 55) trunk segments; variegated brown and pale brown dorsally; male as wide as females at trunk segment 4, 0.7 mm (0.8, 0.8), all trunk segments but distalmost ones widening very slightly posteriorly. Unretracted portion of head, including beak, 0.4 mm long (not taken).



Figs. 18–21. (18–20) *Siphonophora hoffmani* spec. nov. adult male. (18) Overall dorsal view. (19) Head and anterior trunk segments, dorsal view. (20) Head and anterior trunk segments, ventral view. Arrowhead points gonopods. (21) *Siphonophora velezi* spec. nov., adult male.

0.6), ≈ 1.5 times longer than wide; beak as long as unretracted head portion; antennae 0.6 mm long (0.6, 0.7), clavate, surpassing apex of beak by 2 apical segments; antennal segment 1 slightly shorter than 2. Trunk tergites slightly convex transversally, anterior margin of 1 deeply concave. Prozonites smooth, slightly thinner than metazonites; metazonites abundantly granulated, slightly slanted anterodorsally, slightly elevated over prozonites, anterior interangle, posterior interangle, and anterior–posterior distances of 4 as follows, 0.3:0.3:0.1 (not taken; 0.5, 0.5, 0.1); metazonite setae scarce, usually less than half metazonite length, irregularly distributed. Head and first trunk segments as in Fig. 18 and 19. Gonopods podiform, length subequal as in Fig. 20.

Diagnosis. *Siphonophora hoffmani* sp. nov. will run to couplet 11 in Loomis (1970) and can be distinguished from the extant Cuban species *S. cubana* Karsch (1881) and *S. senaria* Loomis 1937 by its beak length, head length proportions, and body length.

Type Data. Holotype (complete adult male), allotype (complete adult female), and another adult female paratype (missing distal segments). Dimensions of the pieces are as follows: holotype

δ (GOP DC-3-9) 4 by 2.8 by 1.2 cm; allotype δ (GOP DC-3-8) 2.9 by 1.6 by 1.0 cm; paratypes δ (GOPDC-3-7) 2.5 by 1.4 by 1.1 cm (measured), δ (PC) 2.7 by 2.0 by 0.4 cm (not measured).

Etymology. This taxon is named after Richard L. Hoffman for his monumental contributions to myriapodology and for mentoring J.A.S.B. in diplopodology.

***Siphonophora velezi* Santiago-Blay & Poinar.
spec. nov.
(Fig. 21)**

Description. Body ≈ 15 mm long (7.7), with >48 (40) trunk segments; brown with tergal margins dark brown, all trunk segments but distal-most ones widening very slightly posteriorly. Unretracted portion of head, including beak, 0.7 mm long (not taken); beak as long as unretracted head portion; antennae 0.8 mm long (not taken), strongly clavate, surpassing apex of beak by ≈ 2 apical segments; antennal segment 1 half as long as 2. Trunk tergites convex transversally, anterior margin of 1 shallowly concave. Prozonites smooth, slightly thinner than metazonites; metazonites abundantly and finally granulated, slightly slanted anterodorsally, slightly elevated

over prozonites, metazonite setae abundant, less than half metazonite length. Head and first trunk segments as in Fig. 21. Gonopods podiform, lengths subequal.

Diagnosis. *Siphonophora velezi* sp. nov. will run to couplet 11 in the key by Loomis (1970) and can be readily distinguished from the extant Cuban species *S. cubana* Karsch (1881) and *S. tenaria* Loomis (1937) by its abundant, small, fine metazonotal pilosity and granulation.

Type Data. Holotype (incomplete adult male), allotype (complete adult female). Dimensions of the pieces are as follows: holotype ♀ (PC) 1.4 by 1.0 by 0.4; allotype ♀ (PC) 3.2 by 1.6 by 1.1 cm.

Etymology. This taxon is named after Manuel J. Vélez, Jr., for his contributions to the study of terrestrial and freshwater invertebrates of Puerto Rico and for exemplifying a true scientific partnership with J.A.S.B. during his time as major professor and thereafter.

Comment. As Loomis (1970) indicated, the taxonomy of this genus is in need of further revision and precludes us from developing phylogenetic or biogeographic inferences.

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