SYSTEMATICS, MORPHOLOGY AND PHYSIOLOGY

New Fossil *Stylops* (Strepsiptera: Stylopidae) from Dominican Amber

Marcos Kogan[1], George Poinar Jr[2]

[1]Integrated Plant Protection Center and Dept of Horticulture; [2]Dept of Zoology. Oregon State Univ, Corvallis, Oregon, 97331, USA; koganm@science.oregonstate.edu; poinarg@science.oregonstate.edu

Edited by Roberto A Zucchi

Neotropical Entomology 39(2):227-234 (2010)

ABSTRACT - Description of a new species of the genus *Stylops* from Dominican amber expands the number of families of this order represented by fossils of the mid-Eocene in the Neotropical region. The specimen described herein is reasonably well preserved, except for the tip of the abdomen that hampered observation of the aedeagus. The specimen fits definition of the comtemporary genus *Stylops* and differs from a related species, *Jantarostylops kinzelbachi* Kulicka, from Baltic amber, by the larger number of ommatidia, relative proportion of antennal segments, and venation of hind wings. The specimen differs from other contemporary species of Nearctic *Stylops* in, among other characters, the smaller size, sub-costa detached from costa and maxillary structure. Discovery of this fossil species of *Stylops* provides evidence of a possibly more temperate climate in the Antilles, since most contemporary species of the genus occur predominantly in the temperate zones of the Nearctic, Palearctic, and Oriental regions. All known species of the genus parasitize bees of the genus *Andrena* (*sensu lato*). Existence of a fossil andrenid, *Protandrena eickworti* Rozen Jr, of the same Dominican amber, offers evidence of a potential host for this new species of *Stylops*.

KEY WORDS: Fossil insect, Neotropical Strepsiptera, *Jantarostylops*, *Protandrena*

For a relatively rare group of insects, Strepsiptera are well represented in the Dominican amber (Table 1). The first species described from that Neotropical amber, based on a single specimen, was the Elenchidae, *Protelencholax schleei* Kinzelbach. A new species of Myrmecolacidae, *Myrmecolax glaesi* Kinzelbach, was described and two specimens are known to exist (Pohl & Kinzelbach 1995). In their review of fossil Strepsiptera, Kinzelbach & Pohl (1994) reported having examined four specimens of Myrmecolacidae that seemed to be very close to the complex defined by *Stichotrema beckeri* (Oliveira & Kogan 1959). The complex includes *S. trilobulata* (Brailowski), and *S.* aff. *beckeri* Kinzelbach. In addition they described *S. dominicanum* Kinzelbach & Pohl and *Bohartilla joachimscheveni* Kinzelbach & Pohl. Another closely related species was described the year before as *B. kinzelbachi* Kathirithambi & Grimaldi. A second specimen included in the Kathirithamby & Grimaldi (1993) paper, was found to be closely related to the contemporary species *B. megalognatha* Kinzelbach. Poinar & Poinar (1999) illustrated a species of *Caenocholax* (Myrmecolacidae) possibly close, if not identical, to the contemporary *C. fenyesi* Pierce. Grimaldi *et al* (2005) reported much older Strepsiptera from Cretaceous amber including a probable strepsipteran triungulinid from Manitoba, Canada.

Poinar (2004) offered fossil evidence of parasitism by Strepsiptera in the form of a male puparium in a halictid bee (Hymenoptera: Halictidae) and a female cephalothorax and male puparium in planthoppers of two families: Delphacidae and Achilidae (Homoptera: Fulgoroidea), in 15-45 million year old Dominican amber. The halictid bee, *Augochloropsis* sp., contained an empty male puparium. The achilid planthopper contained two male puparia, one of them empty. The delphacid had two female cephalothoraces and 25 first stage larvae observed on the ventral side of the host's abdomen. Based on these finds, which include the first fossil record of Strepsiptera larvae associated with a host insect, it was possible to establish a minimum age for parasitism of halictid bees and planthoppers by Strepsiptera.

In this paper we describe a first species of *Stylops* from Dominican amber. The identification of a stylopid in this amber inclusion is of interest because, up until now, fossil records from this neotropical region have been restricted to the Myrmecolacidae, Elenchidae and Bohartillidae. This relatively limited representation of the other Strepsiptera families led Kinzelbach & Pohl (1994) to question whether it was "only by chance that neither the widespread Stylopidae and Halictophagidae nor the tropical Corioxenidae have been found in amber inclusions". With this finding we may answer with a cautious 'yes' to their question. The chance for an adult male strepsipteran to be caught in the resin of the *Hymenaea protera* Poinar tree probably was not very great so it is not surprising that we still have an incomplete record of all the extant Strepsiptera families in the fossil record. It seems, however, reasonable to assume that the presently

Table 1 Species of Strepsiptera recorded from Dominican amber and number of specimens from each species known to exist.

Family	Species	Nº of specimens	References
Elenchidae	*Protelencholax schleei* Kinzelbach	1	Kinzelbach & Pohl (1994); Pohl & Kinzelbach (1995); Kulicka (2001)
Myrmecolacidae	*Myrmecolax glaesi* Kinzelbach	2	Dito
	Coenocholax brodzinskyi Kathirithamby & Grimaldi	2	Dito
	Coenocholax dominicensis Kathirithamby & Grimaldi	1	Dito
	Stichotrema beckeri (Oliveira & Kogan)	4	Dito
	Stichotrema dominicanum	1	Dito
	Coenocholax aff. *fenyesi* Pierce	1	Poinar & Poinar (1999)
Bohartillidae	*Bohartilla joachimscheveni* Kinzelbach and Pohl	4	Pohl & Kinzelbach, 1994
	Bohartilla kinzelbachi Kathirithamby & Grimaldi	1	Pohl & Kinzelbach (1995)
	Bohartilla sp.	1	Kinzelbach & Pohl (1994) based on a photo published by Poinar (1992)

recognized families of the order already were established by the mid-Eocene and discovery of representatives of the other families may be a matter of time and more diligent search in the most promising Dominican amber mines (Poinar & Poinar 1999).

Material and Methods

The amber piece was polished and prepared using standard procedures (Poinar & Poinar 1999, cf. pp. 189-191). The specimen was examined under a Leica-Wild M32 stereo- microscope and a Leica DME compound microscope, both capable of receiving a Spot Insight, model 3.2.0 digital camera. To minimize diffraction, the specimen was immersed in vegetable oil for microscopic observation of more inconspicuous morphological features. Black and white prints of the digital photos were retouched by hand when necessary to enhance visualization of details; the retouched figures were rescanned to produce digital images. Some images were enhanced by removing unwanted background using Photoshop tools.

Genus *Stylops* Kirby

Type species: *Stylops melitae* Kirby, 1802: 112
Synonymy after Kinzelbach (1971) and Luna de Carvalho (1972):
Triungulinus Dufour, 1828: 63
Katastylops Pierce, 1918: 455
Neostylops Pierce, 1918: 455
Prostylops Pierce, 1918: 455
Afrostylops Fox & Fox, 1967: 754 (pro parte)

At least 114 species have been described so far in the genus *Stylops*, making it probably the most numerous of the Strepsiptera. All described species are parasitic of *Andrena* (*sensu latu*) (Hymenoptera: Andrenidae), a group of solitary bees with a predominant temperate zone distribution.

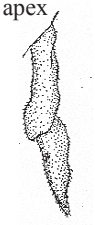
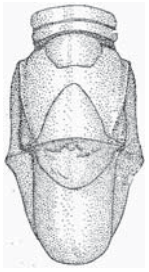
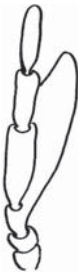
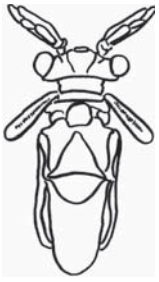
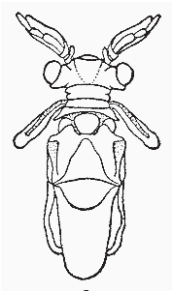
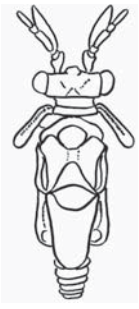
The males of the genus are characterized by six-segmented antennae with flabellum extended from the 3rd segment at least to the base of 6th; eyes usually with more than 20 small, round ommatidia; mandibles slender, lanceolate; maxillary palpi robust generally bisegmented; tarsi four-segmented with first segment sub-equal to or longer than any of the distal three segments; postlumbium oval or semi-circular; aedeagus 'pick-axe' shaped with main stem often sinuous with a mild angular protrusion on the external margin; hind wings with R_2 and R_3 well developed and longer than half the length of R_4. The known Nearctic species of *Stylops* of which male specimens have been described are listed in Table 2.

Stylops neotropicallis sp.n.
(Figs 1-12)

Type material: **Holotype –** Male specimen designated D-1-11 in the George Poinar Collection, Corvallis, Oregon, USA. The specimen is almost perfectly set in an oboval amber piece (Fig 1) about 26 mm x 15 mm, and 4 mm at the thickest point. The specimen is set near the edge of the amber piece, with most anatomical features apparent, except for the tip of the abdomen with the aedeagus blocked from view by a refractive flaw in otherwise generally well structured amber. The strepsipteran specimen has a 3.62 mm wing span and the body is 1.52 mm long from tip of head to tip of last discernible abdominal sclerite (Figs 2-3).

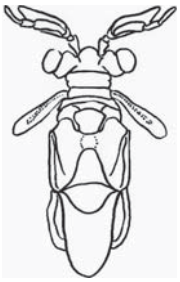
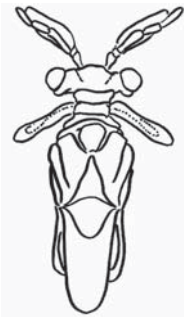
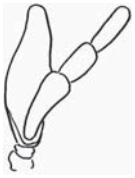
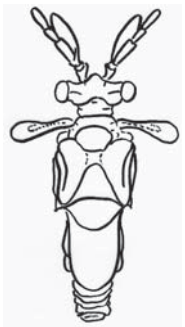
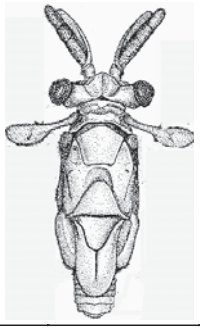
Description: **Head** – Eyes protruded from narrow occipital lateral plates, with at least 30 discernible small ommatidia (Fig 4). Width at edges of eyes 590 μm. Clypeus not distinguished dorsally; post-frons rounded frontad, 230 μm at widest line. Antennae 6-segmented (Fig 5). Length of antennal segments: I – 32.2 μm, II – 55.8 μm, III (base) – 41.2 μm, IV – 148.7 μm, V – 95.7 μm, VI – 276.5 μm. Flabelum of segment III hidden in dorsal view; length at 160 μm (probably under-estimated due to distortion in ventral view); barely reaching base of

Table 2 Summary of main available descriptive characters of Nearctic *Stylops* spp. males.

Species	Length	Head W	Ant. L	Ant. 3-6 ratio**	Palpi	Oedeagus	Dorsal view	Antenna
1. *Stylops crawfordi* Pierce 1909 Host: *Andrena crawfordi* Dist: USA (Texas)	4.50	1.05	1.36	65:36:18:21	Base> apex 			
2. *Stylops cuneiformis* Bohart 1936 Host: *Andrena* sp. Dist.: USA (California)	2.50	0.76	0.61	56:28:13:21	//			
3. *Stylops duboisi* Bohart 1937 Host: *Andrena* sp. USA (California)	3.22	0.77	0.80	49:17:15:22	//			
4. *Stylops elongata* Bohart 1937 Host: *Andrena* sp. near *blaisdelli* *Andrena oenothera* Dist.: USA (California)	3.05	0.80	0.79	50:23:10:19	//	Not illustrated		
5. *Stylops leechi* Bohart 1941 Host: *Andrena advarians* Dist.: Canada (British Columbia)	3.00	0.82	0.80	49:23:11:19	//		Not illustrated	

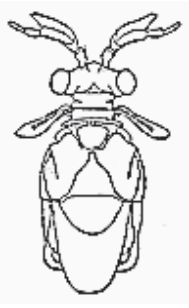
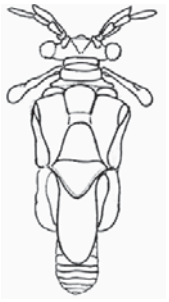
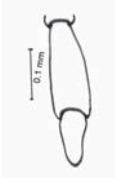
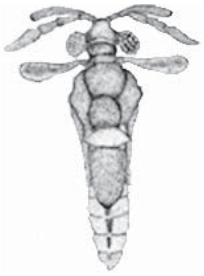
Continue

Table 2 Continuation.

Species	Length	Head W	Ant. L	Ant. 3-6 ratio**	Palpi	Oedeagus	Dorsal view	Antenna
6. *Stylops medionitans* Pierce 1918 Host: *Andrena medionitans, A. scurra, A.* sp. USA (California, Oregon)	3.07	0.77	0.69	50:29:15:19	//			
7. *Stylops pacificus* Bohart 1936 Host: *Andrena complexa, A. suavis, A. cuneilabris, Panurginus melanocephalus* Dist.: USA (California)	2.75	0.85	0.75	83:44:26:29	//			
8. *Stylops packardi* Pierce 1909 (= *S. childreni* Packard, 1864) Host: *Andrena placida* Dist.: USA (Massachusetts)	//	//	//	//	//	Not illustrated	Not illustrated	Not illustrated
9. *Stylops salicifloris* Pierce 1909* (= S. centroclarus Bohart, 1937a) Host: *Andrena salicifloris, A. quintiliformis* Dist: USA (California, Washington)	3.35	0.99	0.97	49:22:14:20	//			
10. *Stylops shannoni* Pierce 1918 Host: Unknown Dist.: USA (Maryland)	//	//	//	//	base>apex	Not illustrated		

Continue

Table 2 Continuation.

Species	Length	Head W	Ant. L	Ant. 3-6 ratio**	Palpi	Oedeagus	Dorsal view	Antenna
11. *Stylops solidulae* Pierce 190 9 Host: *Andrena solidula* Dist.: USA (Washington)	3.25	//	//	//	Base>apex		Not illustrated	Not illustrated
12. *Stylops timberlakei* Bohart 1936 Host: *Andrena macrocephala* Dist.: USA (California)	3.50	0.95	0.95	49:29:15:16	//			
13. *Stylops vandykei* Bohart 1936 Host: *Andrena perimelas* *A. carliniformia* Dist.: USA (California, Oregon)	3.70	0.82	0.81	83:41:30:50	//			
14. *Stylops neotropicallis* sp. n. Host: Unknown Dist.: Dominican Republic	1.52	0.59	0.68	67:37:24:69		Not visible		

Abbreviations: Head W = head width; Ant. L = length of antenna; // = missing data.

* Descriptive data for *S. salicifloris* based on Bohart's (1937) description of *S. centroclarus* considered a synonym of the former by Kinzelbach (1971).

** Antennal ratios: Pierce and Bohart used this expression in the description of *Stylops* antennae. Although we could not find a definition of what they meant by 'ratios' we assumed that it was the divison of segmental lengths by the largest common denominator of the lengths of the four antennal segments (III-VI) considered.

segment VI; width of flabellum not greater than that of segment VI. Mandible (Figs 6-7) lanceolate, 145 μm long, pointed at tip, arising from "socket-like" structure near frontal margin of head and extending forward (partially prognathe). Maxillary palp robust, longer than mandible, bisegmented, arising from socket-like structure; distal segment (maxillary palp) almost as thick at base as basal segment (stype+cardo), about 1/3 as long (Figs 8-9).

Thorax – Prothorax extending frontad appearing to intrude between bases of eyes. Mesothorax reduced; front wing narrow at base, club-shaped at tip. Metathorax (Fig 10) with prescutum about as long as scutellum; scutum angularly expanded laterally; postlumbium with frontal and caudal sections rounded and with frontal and caudal lines meeting laterally into a sharp angle. Postnotum about as long as praescutum+scutellum combined. Sternal features of thorax not clearly discernible. Hind wings (Figs 12-13) about 1.85 mm from tip of wing to axillary region; wing venation consisting of C clearly running along 2/3 of front wing margin; an apparent SC running parallel to distal 1/2 of R1; R2 slightly curved, longer than R3; R4 and MA running full distance from axilla to margin of wing; CuA1 fading distally, CuA2 present, CuP and ANL probably hidden by fold of wing (venation nomenclature following

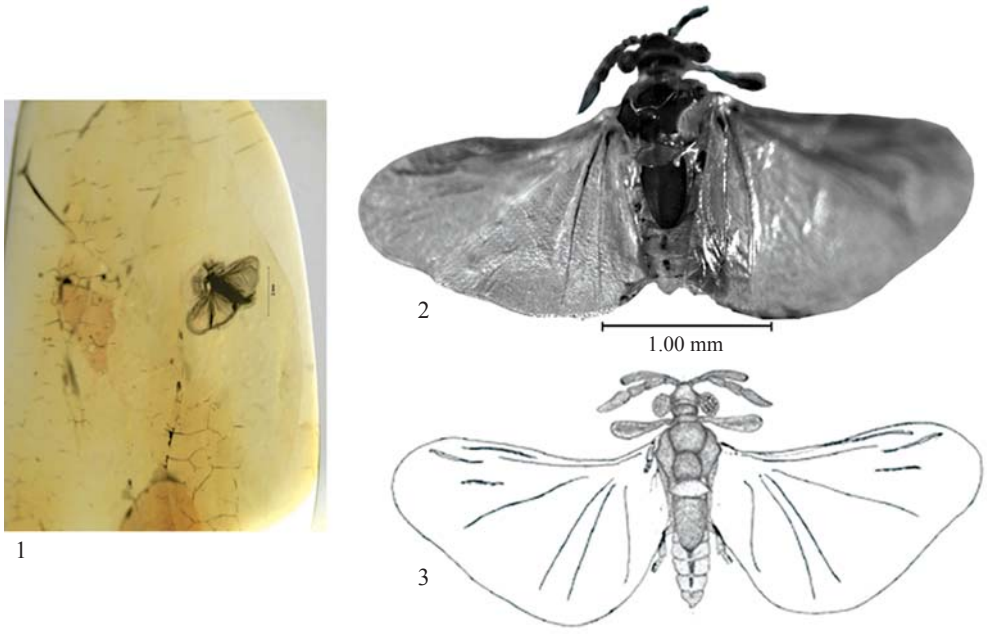


Plate I - *Stylops neotropicallis* sp.n., holotype. Fig 1) quadrant of the amber piece showing position of the specimen; Fig 2) dorsal view with background removed by Photoshop; Fig 3) drawing reconstituting dorsal view based on digital photos of body components.

Kinzelbach 1971). Legs: femur and tibia of fore-and mid-legs short and stout; tarsi sub-equal in length and width, appearing ventrally clad with short pulvillus; coxae of front legs global, robust (Fig 11).

Abdomen – Eight tergites visible dorsally, segments 3-5 with narrow sclerotized band in middle. Terminalia not visible.

Discussion

Table 2 offers a listing of the main male diagnostic characters of the species of Nearctic *Stylops* in comparison to those of *S. neotropicallis* sp.n. *S. neotropicallis* seems to differ from all known Nearctic male *Stylops* by its

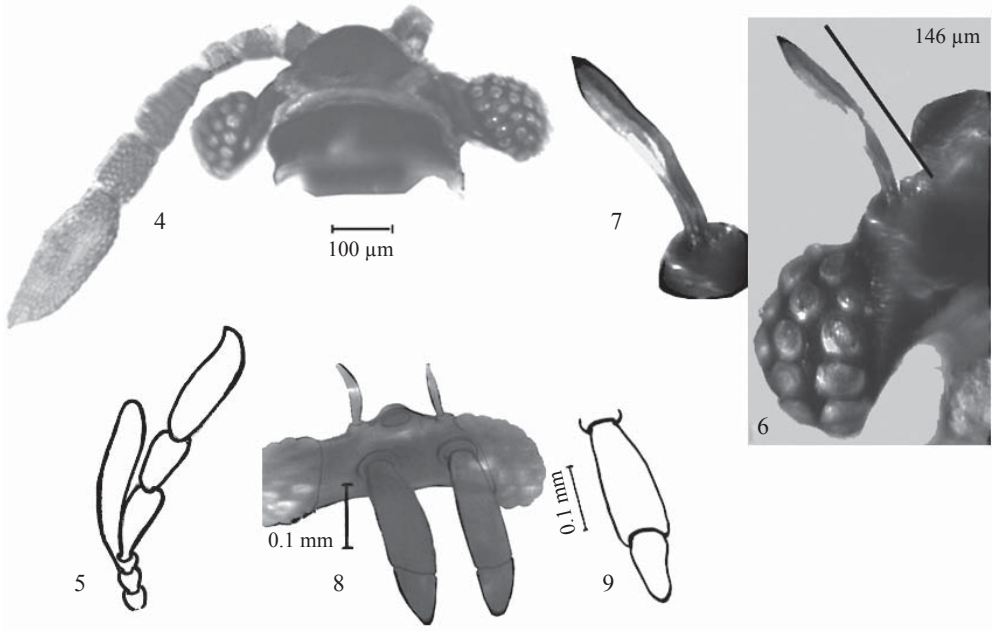


Plate II - *Stylops neotropicallis* sp.n., holotype. Fig 4) dorsal view of head and left antenna - flabellum of 3rd segment hidden behind segments 4 & 5; Fig 5) drawing of right antenna; Fig 6) ventral view of right side of head showing insertion of the mandible and detail of the eye; Fig 7) detail of right mandible and insertion in socket-like structure; Fig 8) ventral view of head showing mandibles and maxillae; Fig 9) drawing of right maxilla.

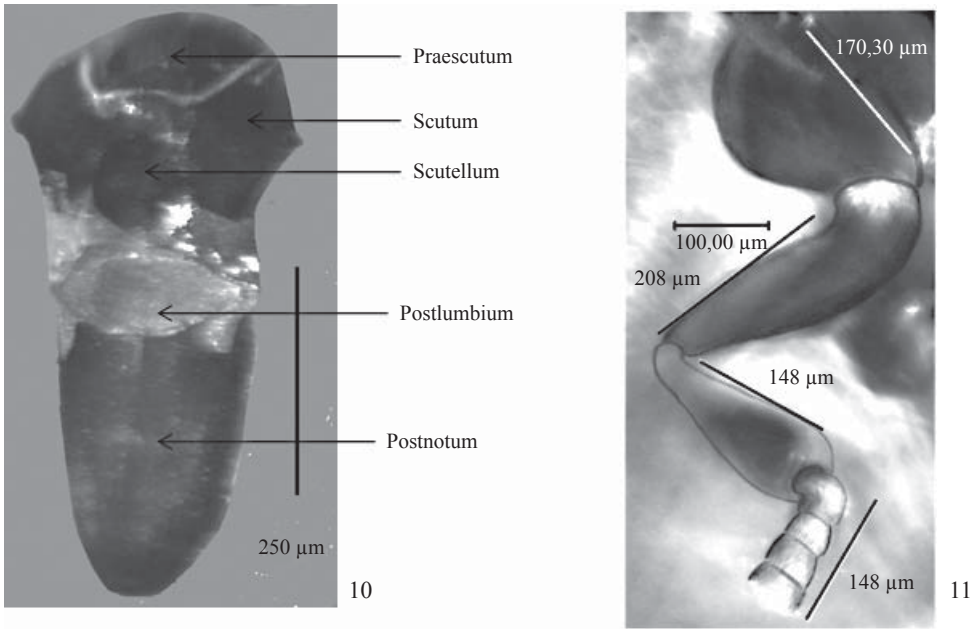


Plate III - *Stylops neotropicallis* sp.n., holotype. Fig 10) dorsal view of metanotum. Background removed by Photoshop; Fig 11) detail of right front leg.

smaller size, structure of maxillary palps and mandibles, placement of eyes with base reaching below the front margin of prothorax, and detached SC vein in the hind wing. The impossibility to discern the shape of the aedeagus removes this character from a more complete diagnostic definition. The small size of this species suggests that it may be associated with an andrenid host which is also of a small size. Studies of large series of *Coenocholax fenyesi*, parasitizing *Solenopsis invicta* in Texas showed a correspondence of the range of host sizes to male *C. fenyesi* sizes (Kathirithamby & Johnston 1992). Description of *Protandrena eickworti* Rozen Jr 1997, a panurgine bee from Dominican amber, provides evidence of a contemporary potential host for *S. neotropicallis*.

Kulicka (2001) described the genus *Jantarostylops* for a specimen found in the Baltic amber. The diagnostic characters offered by Kulicka include the following: antennal segments 2-5 structurally similar, lateral process of the 3rd segment reaching middle of 6th; eyes with 12-15 ommatidia; hind wings with R_4, R_5 and M_1 veins present. The specimen described here, however, seems to fit within the definition of extant *Stylops* particularly in the number of ommatidia and the absence of R5 in the hind wings. The current study of this specimen does not warrant erection of a new genus or its inclusion under *Jantarostylops*. This view, however, may change if further study of the morphology of the species reveals additional distinguishing features from extant *Stylops*.

The finding of *S neotropicallis* is of interest not only from the stand point of the fossil record, but also from the aspect of the zoogeography of the genus. The vast majority of the extant *Stylops* species occur in the temperate zones of

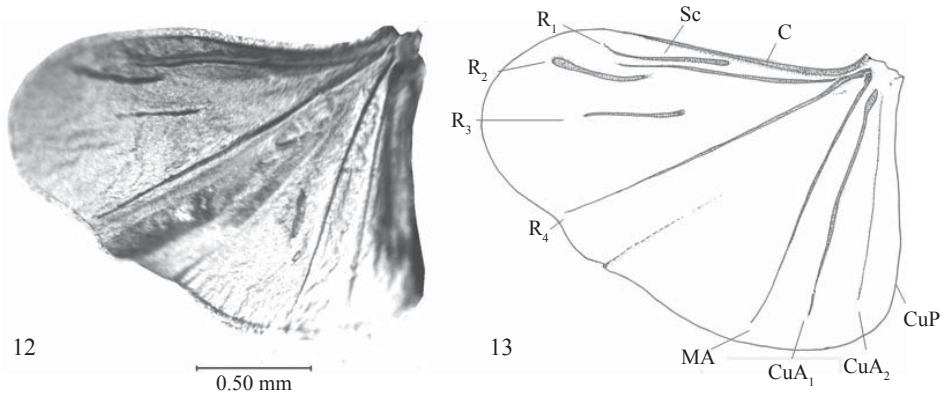


Plate IV - *Stylops neotropicallis* sp.n., holotype. Fig 12) cropped photo of left hind wing; Fig 13) drawing of wing based on Fig 12, showing nomenclature of venation according to Kinzelbach (1971): C = costa, Sc = sub-costa, R1-4 = radius, MA = media anterior, CuA1-2 = cubitus anterior, CuP = cubitus posterior.

the Holoarctic (Paleartic 45.6% of all species and Nearctic 35.1%) and Oriental (19.3%) regions. The present record is the first from the Neotropics, suggesting, perhaps, that the climate in the Antilles in that mid-Eocene period was more temperate than it is today.

References

Bohart R M (1936) A preliminary study of the genus *Stylops* in California (Part 1). Pan-Pac Entomol 12: 9-18.

Bohart R M (1937) A preliminary study of the genus *Stylops* in California (part II). Pan-Pac Entomol 13: 49-57.

Bohart R M (1941) A revision of the Strepsiptera with special reference to the species of North America. University of California, Publications in Entomology, University of California Press, Berkeley 7: 91-160.

Grimaldi D, Kathirithamby J, Schawaroch V (2005) Strepsiptera and triungula in Cretaceous amber. Insect Syst Evol 36: 1-20.

Kathirithamby J, Grimaldi D (1993) Remarkable stasis in some Lower Tertiary parasitoids: descriptions, new records and review of Strepsiptera in the Oligo-Miocene amber of the Dominican Republic. Entomol Scand 24: 31-41.

Kathirithamby J, Johnston J S (1992) Stylopization of *Solenopsis invicta* (Hymenoptera: Formicidae) by *Coenocholax fenyesi* (Strepsiptera: Myrmecolacidae) in Texas. Ann Entomol Soc Am 85: 293-297.

Kinzelbach R K (1971) Morphologische Befunde an Fächerflüglern und ihre phylogenetische Bedeutung (Insecta: Strepsiptera). Zoologica: Originalabhandlungen aus dem Gesamtgebiet der Zoologie 119, Hälfte 1: 1-128, Hälfte 2: 159-256.

Kinzelbach R K (1979) Das erste neotropische Fossil der Fächerflügler (Stuttgarter Bernsteinsammlung: Insecta, Strepsiptera). Stuttgarter Beit Natur Ser B 52: 1-14.

Kinzelbach R K (1983) Strepsiptera from the Dominican amber (Insecta: Strepsiptera: Myrmecolacidae). Verhand NaturwissVer Hamburg 26: 29-36.

Kinzelbach R, Pohl H (1994) The fossil Strepsiptera (Insecta: Strepsiptera). Ann Entomol Soc Am 87: 59-70.

Kulicka R (2001) New genera and species of Strepsiptera from the Baltic amber. Prace Muzeum Ziemi 46: 3-16 + 7 plates.

Luna de Carvalho E (1972) Contribuição para o estudo dos *Stylops* da Península Ibérica. EOS Ver Esp Entomol 48: 301-365.

Pierce W D (1909) A monographic revision of the twisted winged insects comprising the order Strepsiptera Kirby. Proc US Nat Mus, Smithsonian Institute, Washington 66: 1-232.

Pierce W D (1918) The comparative morphology of the order Strepsiptera together with records and descriptions of insects. Proc US Nat Mus, Smithsonian Institute, Washington 54: 391-501.

Poinar G (2004) Evidence of parasitism by Strepsiptera in Dominican amber. Biocontrol 49: 239-244.

Poinar G, Poinar R (1999) The amber forest: a reconstruction of a vanished world. Princeton University Press, Priceton, 239p.

Pohl H, Kinzelbach R (1995) Neufunde von Fächerflüglern aus dem Baltischen und Dominikanischen Bernstein (Strepsiptera: Bohartillidae, Myrmecolacidae). Mit Geol-Paläontolog Inst Univ Hamburg 78: 197-209.

Pohl H, Beutel R G, Kinzelbach R (2005) Protoxenidae fam. nov. (Insecta, Strepsiptera) from Baltic amber — a 'missing link' in strepsipteran phylogeny. Zool Scripta 34: 57-69.

Rozen Jr JG (1997) A new species of the bee *Heterosarus* from Dominican amber (Hymenoptera: Adrenidae: Panurginae) J Kansas Entomol Soc 69: 346-352.

Received 24/I/09. Accepted 30/III/09.