The oldest records of Polyxenida (Myriapoda, Diplopoda): new discoveries from the Cretaceous ambers of Lebanon and France

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ABSTRACT
Electroxenus jezzinensis n. gen., n. sp. and *Libanoxenus hammanaensis* n. gen., n. sp. are described from the Lower Cretaceous amber of Lebanon. These are the oldest known records of Penicillata because *Phryssonotus burmiticus* (Cockerell, 1917), from Burmese amber, is dated as being from upper Albian. They belong to the family Polyxenidae. This family contains the recent genus *Polyxenus* Latreille, 1803, which is known from Eocene Baltic amber. *Electroxenus* n. gen. and *Libanoxenus* n. gen. are very close to the recent genera of Polyxenidae. The first French fossil Penicillata, discovered in the Cretaceous amber of Haute-Provence, is also described and referred to the genus *Phryssonotus* Scudder, 1885 (sole genus of the family Synxenidae). The recent polyxenid families Polyxenidae and Synxenidae therefore already existed during the Cretaceous.

KEY WORDS
Myriapoda,
Diplopoda,
Penicillata,
Polyxenidae,
Synxenidae,
Early and Late Cretaceous,
fossil,
amber,
Electroxenus jezzinensis n. gen., n. sp.,
Libanoxenus hammanaensis n. gen., n. sp.,
Phryssonotus,
new genera,
new species.

RÉSUMÉ

Les plus anciens Polyxenida (Myriapoda, Diplopoda), découverts récemment dans l'ambre crétacé du Liban et de France.

Electroxenus jezzinensis n. gen., n. sp. et *Libanoxenus hammanaensis* n. gen., n. sp. sont décrits de l'ambre du Liban datant du Crétacé inférieur. Ce sont les Penicillata fossiles les plus anciens connus actuellement puisque *Phryssonotus burmiticus* (Cockerell, 1917), de l'ambre birman, date de l'Albien supérieur. Ils appartiennent à la famille des Polyxenidae. Cette famille comprend le genre actuel *Polyxenus* Latreille, 1803, qui est aussi connu de l'ambre éocène balte. *Electroxenus* n. gen. and *Libanoxenus* n. gen. sont très proches des genres de Polyxenidae actuels. Le premier Penicillata fossile découvert en France dans l'ambre crétacé supérieur de Haute-Provence, est également décrit et attribué au genre *Phryssonotus* Scudder, 1885 (unique genre de la famille des Synxenidae). Notre étude confirme que deux des familles actuelles de Penicillata, Polyxenidae et Synxenidae, existaient déjà au cours du Crétacé.

MOTS CLÉS
Myriapoda,
Diplopoda,
Penicillata,
Polyxenidae,
Synxenidae,
Crétacé inférieur et supérieur,
fossile,
ambre,
Electroxenus jezzinensis
n. gen., n. sp.,
Libanoxenus hammanaensis
n. gen., n. sp.,
Phryssonotus,
nouveaux genres,
nouvelles espèces.

INTRODUCTION

The first six fossils of Penicillata were described from the Eocene Baltic amber in Koch & Berendt (1854); five of them belong to the family Polyxenidae and to the genus *Polyxenus* Latreille, 1803 (*P. conformis* Koch & Berendt, 1854, *P. ovalis* Koch & Berendt, 1854, *P. caudatus* Menge, 1854, *P. colurus* Menge, 1854, and *P. lophurus* Menge, 1854). The sixth fossil, *Phryssonotus hystrix* (Menge, 1854), belongs to the family Synxenidae (Scudder, in 1885, replaced the genus name *Lophonotus* diagnosed by Menge *in* Koch & Berendt, 1854 by *Phryssonotus* because the former name was preoccupied). Later Cockerell (1917) described from the Lower Cretaceous Burmese amber *Polyxenus burmiticus*, which was thought to belong to the family Synxenidae by Condé & Jacquemin (1963), but was more recently assigned to *Phryssonotus* by Rasnitsyn & Golovatch (2004). Finally, Bachofen von Echt (1942) described from Baltic amber representatives of both these families, *Polyxenus* sp. and *Schindalmonotus hystrix*; the latter, according to Condé (1954), most probably being a synonym of *Phryssonotus hystrix*. For all these amber fossils the identification criteria of the species are poorly known, particularly in the family Synxenidae represented by the sole genus *Phryssonotus*, resulting in synonymies and inaccuracies in descriptions (Nguyen Duy-Jacquemin & Geoffroy 2003). In this work, two new genera and species of Penicillata (*Electroxenus jezzinensis* n. gen., n. sp. and *Libanoxenus hammanaensis* n. gen., n. sp.) are described from the Lower Cretaceous amber of Lebanon, constituting the oldest records of Penicillata to date. A specimen from the Cretaceous amber of France, attributable to *Phryssonotus* Scudder, 1885, is also reported.

SYSTEMATICS

Lebanese amber

Order POLYXENIDA Lucas, 1840
Superfamily POLYXENOIDEA Lucas, 1840
Family POLYXENIDAE Lucas, 1840

Genus *Electroxenus* n. gen.

TYPE SPECIES. — *Electroxenus jezzinensis* n. sp., by present designation.

FIG. 1. — *Electroxenus jezzinensis* n. gen., n. sp., holotype adult body length: 3.10 mm (JS 231/1), Acra collection; **A**, lateral view; **B**, dorsal view.

ETYMOLOGY. — A combination of electron, meaning amber in Greek and xenus, suffix used in polyxenids.

DIAGNOSIS. — Head: six to eight ocelli; antenna with eight articles; three sensilla basiconica or more on the seventh antennal article, four or more on the sixth. Lateral expansion of gnathochilarial palp with at least 17 sensilla. Trunk: tergal trichomes grouped into two separate, oval clusters with an additional posterior row, subdivided in its middle. Presence of a spine on tarsus II. Telotarsus with posterior lamellate process. Telson: two dorsolateral penicils of hooked trichomes, joined side by side, dorsally.

Electroxenus jezzinensis n. sp.
(Figs 1; 2)

"Polyxenid millipede" – Grimaldi 1996: 36.

TYPE MATERIAL. — Holotype: one adult specimen, number JS 231/1, Acra collection, provisionally deposited in the Muséum national d'Histoire naturelle, Paris (MNHN).

ETYMOLOGY. — After Jezzine, the type locality.

TYPE LOCALITY AND TYPE HORIZON. — Jouar Es-Sous locality, Jezzine area, Caza of Jezzine, Mouhafazit Loubnan El-Janoubi, South Lebanon; Lower

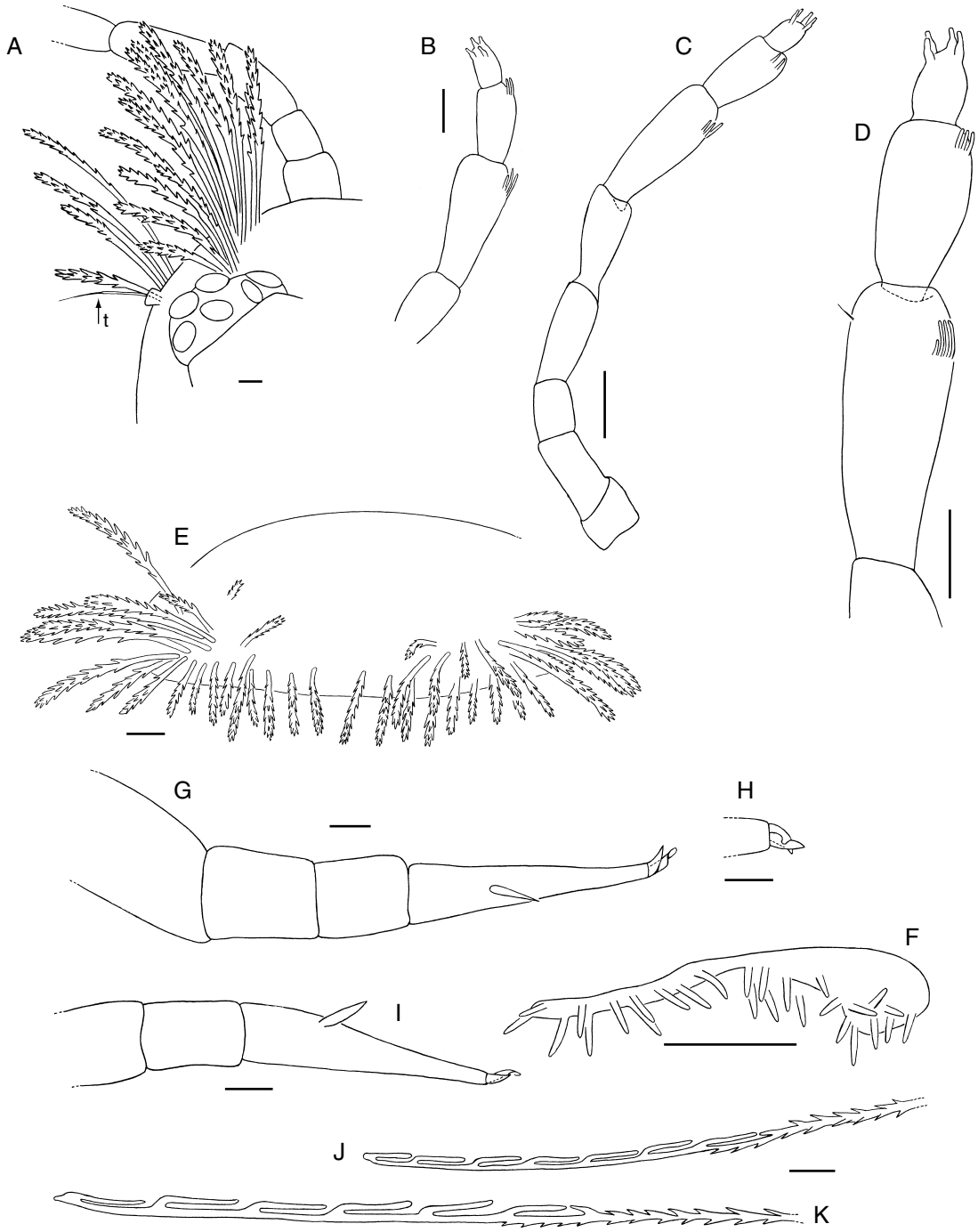

FIG. 2. — *Electroxenus jezzinensis* n. gen., n. sp., holotype adult (JS 231/1), Acra collection; **A**, right latero-dorsal part of head with ocelli group and five basal antennal articles; **B**, distal articles of left antenna; **C**, right antenna; **D**, three distal articles of right antenna; **E**, trichomes on tergite II; **F**, right palpus of gnathochilarium; **G**, right leg III from femur to telotarsus; **H**, right telotarsus leg IV; **I**, distal right leg I; **J**, **K**, hooked caudal trichomes. Abbreviation: **t**, trichobothria. Scale bars: A, E, G, I-K, 20 µm; B-D, 40 µm; F, 50 µm; H, 25 µm.

Cretaceous, Valanginian-Hauterivian (135-125 million years). The amber piece is mounted on a microscope slide in Canada balsam medium.

DIAGNOSIS. — As for genus.

DESCRIPTION

Adult (Figs 1; 2)

Grimaldi (1996: 36) figured the habitus of the same specimen without giving a description. The sexual organs, penis or vulvae, normally located at the base of the second pairs of legs are not preserved; in addition the state of preservation of the coxae does not allow observation of the absence or the presence of coxal glands, hence the sex cannot be determined.

Measurements. Body length = 2.25 mm; penicil length = 0.70 mm; head trichomes length = 0.18 mm; total length = 3.10 mm.

Head. Six visible ocelli (Fig. 2A), but more might be present. The longer anterior trichomes of vertex are 200 µm long. Eight antennal articles. Length of right sixth article 2.5 times the diameter. Three or four sensilla basiconica observed on the seventh article, more visible on the right antenna. Three (perhaps four) thin sensilla basiconica visible on right article VI: two or three long and a third that seems shorter than the two others (Fig. 2B-D). Elongated lateral expansion of palp with at least 17 sensilla, but perhaps more (Fig. 2F). Labrum not visible.

Trunk. The long, thin trichomes of the tergites are grouped into two, separate, oval clusters with an additional posterior row, subdivided in its middle (Fig. 2E). The longer lateral trichomes of tergites reach 150 to 160 µm; the trichomes of posterior row are only 70 to 95 µm long. Only 12 pairs of legs are visible. Some pubescent cylindrical setae visible on coxae. Spine of tarsus II longer than the claw (Fig. 2G, I). Telotarsus with well visible posterior lamellate process longer than claw (Fig. 2G-I) and one anterior spinous denticle seen on several telotarsi. Telson with caudal penicil not of same type as *Polyxenus* Latreille, 1803 and *Propolyxenus* Silvestri, 1948 (Condé 1969); trichomes of caudal penicil with five, six (Fig. 2K) or seven (Fig. 2J) aligned hooks).

Genus *Libanoxenus* n. gen.

TYPE SPECIES. — *Libanoxenus hammanaensis* n. sp., by present designation.

ETYMOLOGY. — A combination of Lebanon and xenus.

DIAGNOSIS. — Head: eight ocelli; antenna with eight articles. Labrum entirely covered with small dense setae. A dozen sensilla on outer palpus of gnathochilarium. Trunk: two rows of short tergal trichomes. Presence of a seta on tarsus II. Telotarsus with posterior lamellate process. Telson: caudal penicil with two groups of hooked trichomes joined side by side, dorsally.

Libanoxenus hammanaensis n. sp.
(Figs 3; 4)

TYPE MATERIAL. — Holotype: adult specimen number 633, Azar collection, provisionally deposited in the MNHN.

ETYMOLOGY. — After Hammana, the type locality.

TYPE LOCALITY AND TYPE HORIZON. — Mdeirij/Hammana locality, Caza of Baabda, Mouhafazit Jabal Loubnan, Central Lebanon; Early Cretaceous, Valanginian-Hauterivian to lower Aptian (135-125 million years). The amber piece is mounted on a microscope slide in Canada balsam medium.

DIAGNOSIS. — As for genus.

DESCRIPTION

Adult (Figs 3; 4A-J)

The trunk of the holotype is open over all its length along the axis of symmetry, hence the tergites are not seen entirely.

Measurements. Body length = 2.50 mm; penicil length = 0.30 mm; head trichomes length = 0.10 mm; total length = 2.90 mm.

Head. Eight ocelli (Fig. 4A). Left antenna with eight articles (Fig. 4A). Length to diameter ratio of the sixth antennal article = 1.80. Only the end of one sensillum basiconicum is visible on articles VI and VII (Fig. 4B); some setiform sensilla are seen on article III, V, VI and VII; right antenna with four articles, the article V is broken. Labrum with numerous small setae (Fig. 4C). Outer right palp of gnathochilarium with 12 or 13 sensilla (Fig. 4D); it is more than twice as long as the diameter of the middle palp.

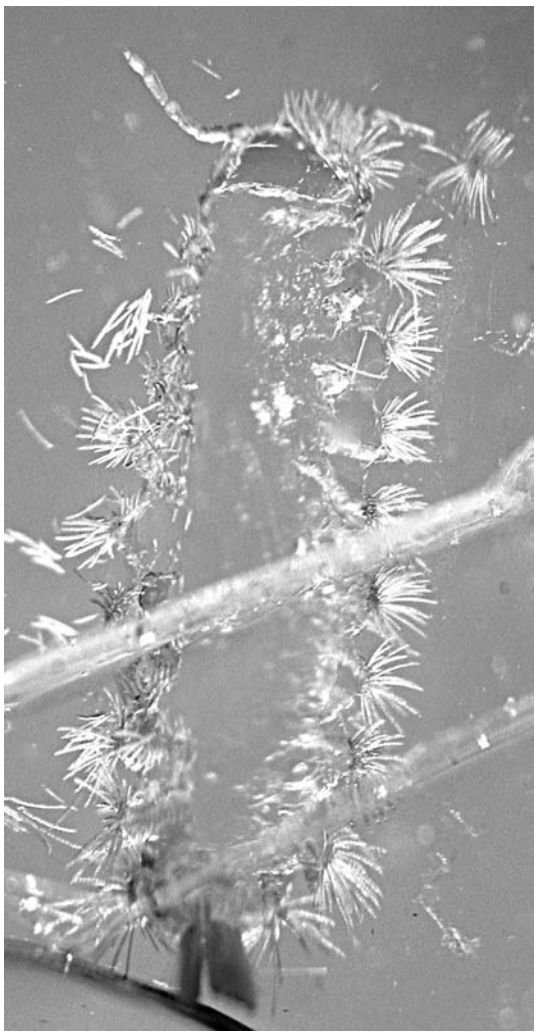

FIG. 3. — *Libanoxenus hammanaensis* n. gen., n. sp., holotype adult body length: 2.90 mm (633), Azar collection, dorsal view.

Trunk. The tergal trichomes (seen only on the lateral part of tergites), are short (Fig. 4E, F); the longer lateral trichomes of tergite reach 120 to 130 µm while in the middle of the tergite the trichomes measure 50 to 53 µm. They seem to be arranged in two rows: one anterior row with trichomes directed anteriad and one posterior row with trichomes directed caudal (Fig. 4F). One clearly visible seta on tarsus II (Fig. 4G, I), nude setae (Fig. 4H) observed on other article (coxa, trochanter, prefemur, femur and tibia). Telotarsus with clearly visible posterior lamellate process longer than claw (Fig. 4G). Dorsal face of telson with an anterior row including three to four visible barbate trichomes. Telson is not of *Polyxenus* and *Propolyxenus* type (latter with trichomes ended by multiple hooks: Fig. 4K); trichomes of caudal penicil with three or four aligned hooks (Fig. 4J).

French amber

Superfamily SYNXENOIDEA Silvestri, 1923
Family SYNXENIDAE Silvestri, 1923
Genus *Phryssonotus* Scudder, 1885

Phryssonotus sp.
(Figs 5; 6)

MATERIAL EXAMINED. — Immature female, specimen number SA 5.1, deposited in the MNHN.
Locality and horizon: from the amber of Salignac (Haute-Provence, France). Albo-Cenomanian period (100-95 million years). The amber piece is mounted between coverslips in Canada balsam medium.

DESCRIPTION

Immature female (Figs 5; 6)

The posterior part of body is lacking; only the head, seven tergites and 10 pairs of legs are present; only the tarsus II and telotarsus of the eleventh pair remain (Fig. 6A) because the posterior part of the body is broken. The slightly elongated vulval sacs demonstrates that the specimen is not an adult; it is probably an immature female with 12 or 14 pairs of legs (adults have 17 pairs of legs), the stage with 11 pairs of legs does not exist in Synxenidae.

Measurements. Body length up to eleventh pair of legs = 2.40 mm.

Head. Only four right ocelli are visible, the remaining ocelli cannot be observed; left antenna with eight articles; only some setiform sensilla are visible on the articles. Right antenna with only three basal articles. Labrum not visible. Lateral

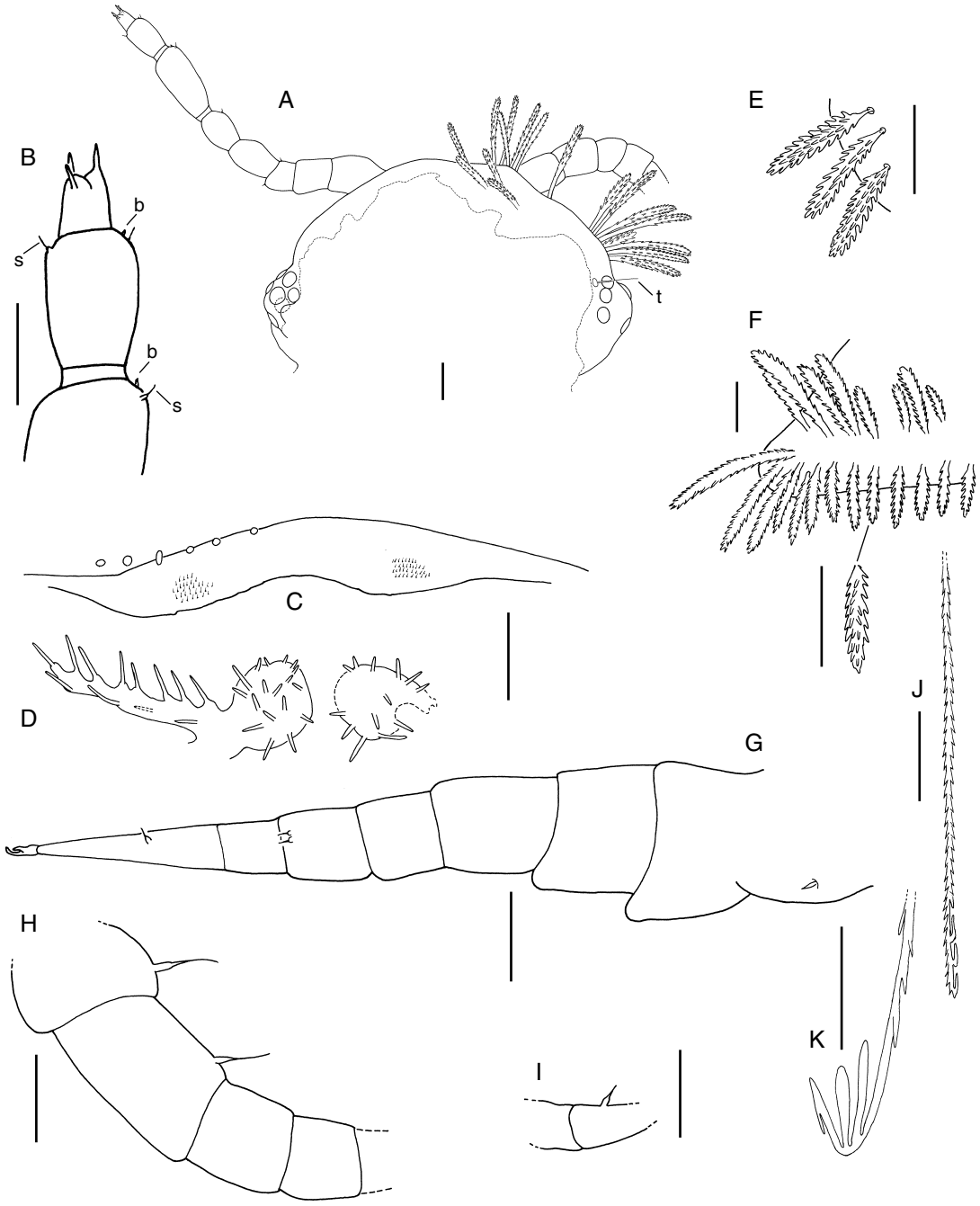

FIG. 4. — **A**-**J**, *Libanoxenus hammanaensis* n. gen., n. sp., holotype adult (633), Azar collection; **A**, head, dorsal face, dotted line indicates the missing part; **B**, detail of left antenna; **C**, labrum, only the visible cuticular spines are represented in two areas; **D**, right palpus and left middle palpus of gnathochilarium; **E**, left lateral posterior part of tergite IV; **F**, left lateral part of tergite III with detail of a trichome; **G**, right leg IX; **H**, trochanter, prefemora, femora and tibia of right leg XIII; **I**, part of tarsus of left leg VIII showing the seta; **J**, hooked caudal trichome; **K**, *Polyxenus lagurus*, distal part of crooked caudal trichomes. Abbreviations: **b**, sensillum basiconicum; **s**, setiform sensillum; **t**, trichobothria. Scale bars: 50 µm.

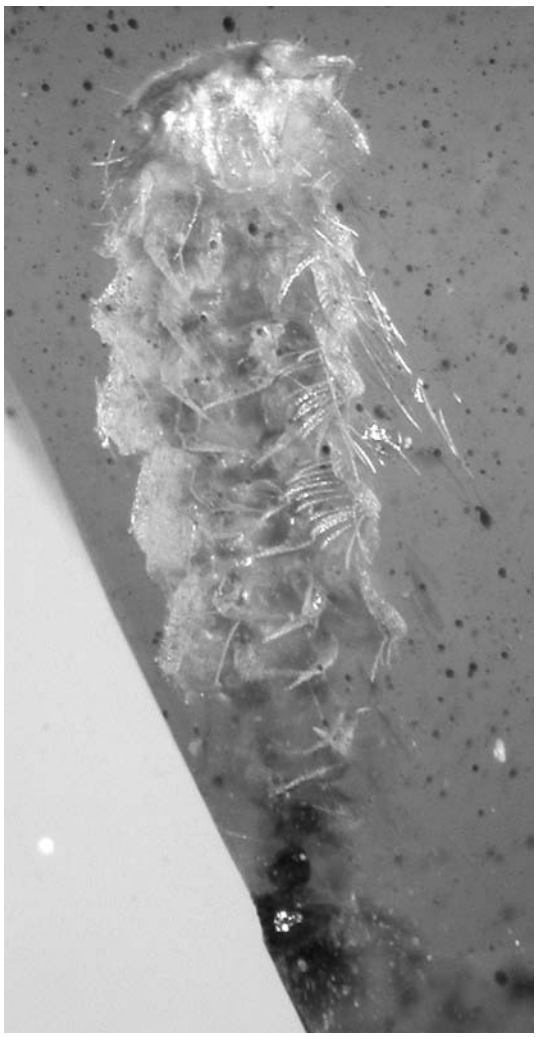

FIG. 5. — *Phryssonotus* sp., immature female without posterior part of body, length: 2.40 mm (SA 5.1), ventral view.

expansion of gnathochilarial palp very long (200 µm), with 16 visible sensilla on right palp and 18 on left palp (Fig. 6B).

Trunk. The scale-shaped trichomes of the tergites are often lacking or detached from their insertion (Fig. 6C). One easily visible seta on tarsus II longer than telotarsus and one seta on the posterior edge of each article (Fig. 6D). The caudal penicil is unknown because the posterior part of the body is missing.

DISCUSSION

The specimens studied here do not allow the observation of all the essential characters used for systematics and identification. The number and position of the sensilla basiconica of the sixth and eleventh antennal articles, the ornamentation of the external surface of the labrum, the structure of the claws with accessory processes, and the insertion and the shape of the trichomes on the tergites play an important role in the systematics of the group. All these characters are either only partially visible or not at all in our specimens.

POLYXENIDAE

The two specimens in Lebanese amber were identified by comparison with recent genera. Their telson is not of the *Polyxenus* and *Propolyxenus* type, which is easily recognizable by the end of the hooked trichomes having aligned hooks (with point directed towards base: Figs 2J, K; 4J) and not terminated with multiple hooks (Fig. 4K) as in *Polyxenus* and related genera. Their gnathochilarial sensilla do not seem pseudoarticulated at their end as in *Afraustraloxenodes* Nguyen Duy-Jacquemin, 2003, *Macroxenodes* Silvestri, 1948, *Macroxenus* Brölemann, 1917 and *Chilexenus* Silvestri, 1948. Consequently we eliminate these genera in our comparison with those of Polyxenidae, together with the genera *Apoxenus* Chamberlin, 1947 and *Mesoxenontus* Silvestri, 1948, which are insufficiently described and doubtful.

Electroxenus jezzinensis *n. gen., n. sp.*

If we consider the other polyxenid genera (other than those quoted previously) that have a spine on the tarsus II, none has six ocelli; some have less (five in *Pauropsxenus* Silvestri, 1948, three in *Typhoxenus* Condé, 1955) or none (*Anopsxenus* Condé & Jacquemin, 1963). On the other hand, *Mauritixenus* Verhoeff, 1939 and *Monographis* Attems, 1907 have eight ocelli. The fossil adult in amber may have eight ocelli: it is possible that the two ventral ones are not visible. From the length of the trichomes and their mode of insertion on the tergites, *Electroxenus jezzinensis* n. gen., n. sp.

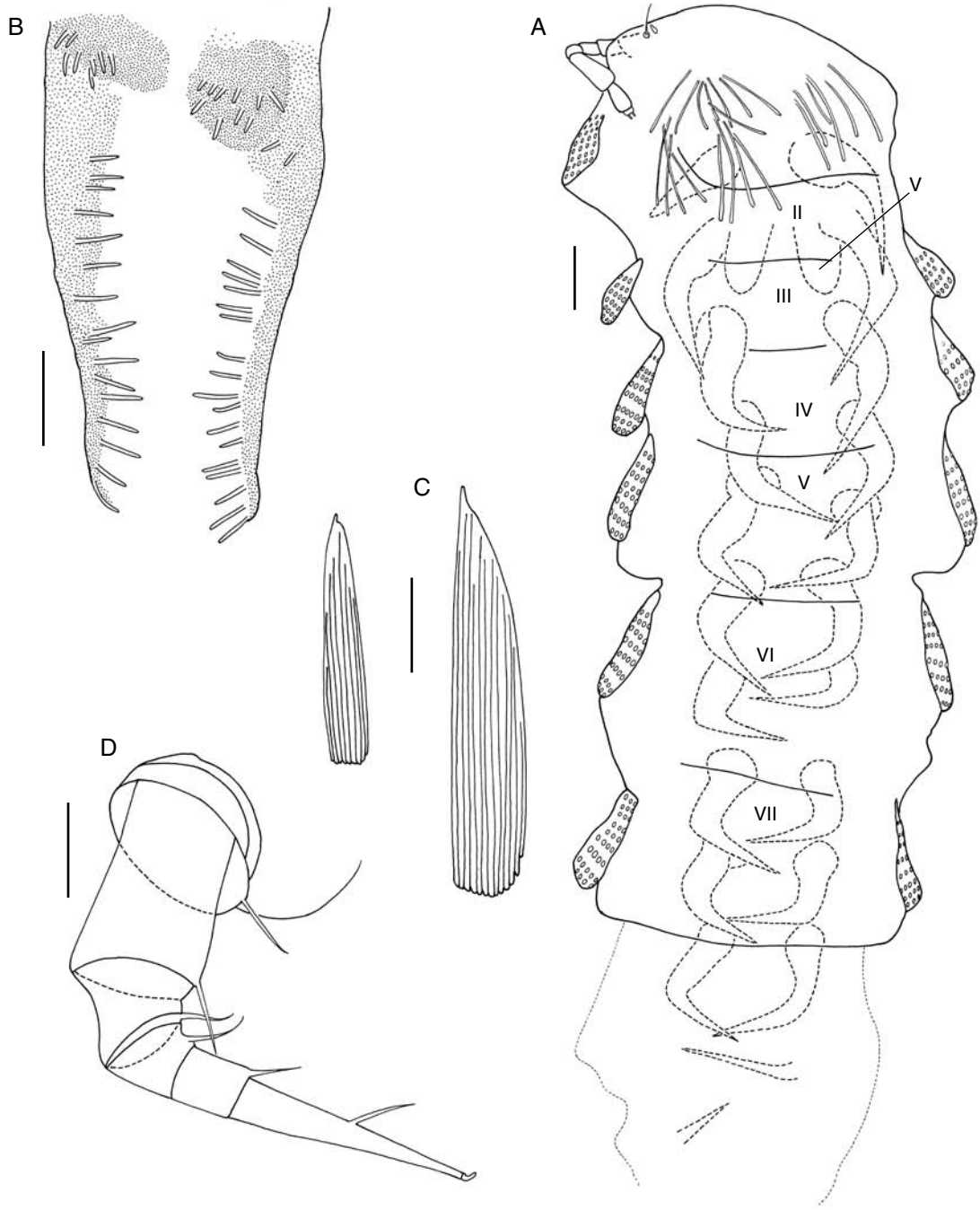

FIG. 6. — *Phryssonotus* sp., immature female (SA 5.1); **A**, habitus, dorsal face, ventral legs and vulval sacs shown with dotted lines; **B**, palpi of gnathochilarium; **C**, scale-shaped trichomes of tergites, detached from their insertions; **D**, right leg V. Abbreviations: **V**, vulval sac; **II-VII**, tergite II to VII. Scale bars: A, 0.1 mm; B-D, 50 µm.

seems closer to the genus *Mauritixenus* than to *Monographis* which, moreover, has a spine on the tarsus 1, unlike our specimen. However these two extant genera have only two sensilla basiconica on the seventh antennal article, whereas *E. jezzinensis* n. gen., n. sp. has at least three sensilla basiconica on its seventh antennal article. *Electroxenus* n. gen., *Polyxenus* and *Propolyxenus* are the only genera of Polyxenidae with more than two sensilla basiconica on the seventh antennal article; however *Polyxenus* and *Propolyxenus* have a very different telson.

Libanoxenus hammanaensis *n. gen., n. sp.*
If we compare *Libanoxenus* n. gen. to the genera that have a seta on tarsus II and eight ocelli, we can eliminate the genus *Ankistroxenus* Attems, 1907, of which the type species, *A. minutus*, was insufficiently described by Attems (1907); the other species, *A. aethiopicus* (Chalande, 1908), attributed to this genus by Ribaut (1922), has pleural trichomes, reaching one third or one half the length of the body, thus much longer than those of *Libanoxenus* n. gen. In the four other Polyxenid genera – *Eudigraphis* Silvestri, 1948, *Saroxenus* Cook, 1896, *Silvestrus* Jones, 1937 and *Unixenus* Jones, 1944 – the insertion or the size of the tergal trichomes is different.

SYNXENIDAE
Phryssonotus
Immature female from French amber.
The genus *Phryssonotus* is characterized by tergal trichomes that are striated scale-shaped (Fig. 6C), 11 segments (telson excluded) instead of 10 in Polyxenidae, and 17 pairs of legs, the last two pairs terminated by palettes rather than claws. The females have subconical vulval sacs elongated and named ovipositors by Silvestri (1923). These unusual characters render the identification of the genus very easy and justified the creation of the family Synxenidae for this genus. On the other hand, the differentiation of species is very difficult because of the great homogeneity of the genus. The immature female from French amber belongs to *Phryssonotus*, but it cannot be compared with the two insufficiently described fossil species (type species *P. hystrix* Menge, 1854, and *P. burmiticus* Cockerell, 1917), nor with any of the six living species which Silvestri diagnosed (1923, 1948). The differentiation of these species is mainly based on the presence of trichomes (named setae *A* and *B* by Silvestri [1923]), aligned near the short anterior trichobothria, the number and size of which are variable, as well as on the number of ocelli (see key in Silvestri [1923]). These setae are not visible on our specimen, except a long one that could be *A.*

CONCLUSIONS

Previously described Penicillata from Tertiary Baltic amber and Cretaceous Burmese amber belong to two recent genera: *Polyxenus* and *Phryssonotus*. This is not the case for the two specimens from Lebanon, which belong to genera not previously observed in the fossil record. They are currently the oldest known records of Penicillata because *Phryssonotus burmiticus* from Burmese amber is dated as upper Albian (Rasnitsyn & Golovatch 2004). Two of the recent polyxenid families, Polyxenidae and Synxenidae, already existed during the Cretaceous and the order is probably even older if we consider the phylogenetic relationship between Penicillata and the other groups of diplopods (Wilson & Shear 2000; Kraus & Brauckman 2003). As yet, no fossil belonging to the family Lophoproctidae Silvestri, 1897 – supposed to be more advanced in evolution because of the reduction of the palps, and, in one species, the disappearance of a tergite and two pairs of legs (Condé 1969: 48) – has been found; their endogean habitat may explain why they were not included in the resin. All fossil Penicillata have been in amber, which is undoubtedly the best medium for preserving these small Myriapoda with soft teguments, in which adults never measure more than 7 mm. The Lebanese amber is the oldest in the World containing numerous biological inclusions. *Electroxenus* n. gen. and *Libanoxenus* n. gen. are very close to the extant genera of Polyxenidae and

their ancestors are likely to remain unknown to us for a long time. The representative of the genus *Phryssonotus*, the first fossil Penicillata discovered in France, reminds us that Synxenidae, which currently live in southernmost Europe (Catalonia, Sicily), Africa, South America and Australia, were present during the Cretaceous in Laurasia; indeed representatives of this family were described from Baltic amber (Menge *in* Koch & Berendt 1854; Scudder 1885) and from Burmese amber (Cockerell 1917; Rasnitsyn & Golovatch 2004).

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