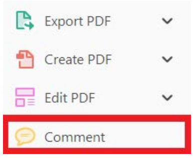
USING e-ANNOTATION TOOLS FOR ELECTRONIC PROOF CORRECTION

Required software to e-Annotate PDFs: Adobe Acrobat Professional or Adobe Reader (version 11 or above). (Note that this document uses screenshots from Adobe Reader DC.)
The latest version of Acrobat Reader can be downloaded for free at: http://get.adobe.com/reader/

Once you have Acrobat Reader open on your computer, click on the Comment tab (right-hand panel or under the Tools menu).

This will open up a ribbon panel at the top of the document. Using a tool will place a comment in the right-hand panel. The tools you will use for annotating your proof are shown below:

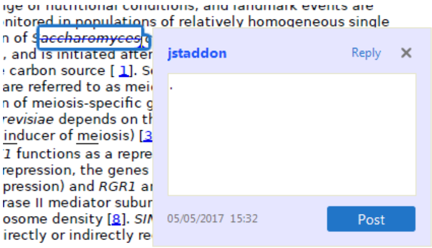


1. Replace (Ins) Tool – for replacing text.

Strikes a line through text and opens up a text box where replacement text can be entered.

How to use it:

- Highlight a word or sentence.
- Click on .
- Type the replacement text into the blue box that appears.



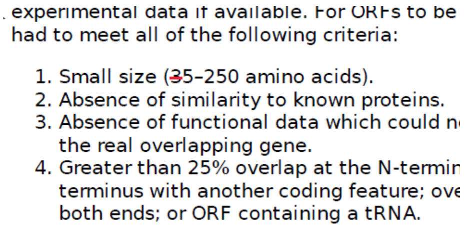
nitored in populations of relatively homogeneous single
n of ~~Saccharomyces~~
, and is initiated after
carbon source [1]. S
are referred to as mei
n of meiosis-specific g
revisiae depends on th
inducer of meiosis) [3
1 functions as a repre
repression, the genes
pression) and RGR1 ar
rase II mediator subur
osome density [8]. SIN
irectly or indirectly re

2. Strikethrough (Del) Tool – for deleting text.

Strikes a red line through text that is to be deleted.

How to use it:

- Highlight a word or sentence.
- Click on .
- The text will be struck out in red.



experimental data if available. For ORFs to be
had to meet all of the following criteria:

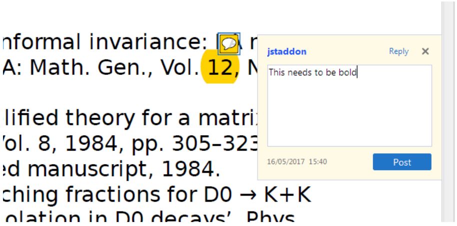
1. Small size (~~3~~5–250 amino acids).
2. Absence of similarity to known proteins.
3. Absence of functional data which could n
the real overlapping gene.
4. Greater than 25% overlap at the N-termin
terminus with another coding feature; ove
both ends; or ORF containing a tRNA.

3. Commenting Tool – for highlighting a section to be changed to bold or italic or for general comments.

Use these 2 tools to highlight the text where a comment is then made.

How to use it:

- Click on .
- Click and drag over the text you need to highlight for the comment you will add.
- Click on .
- Click close to the text you just highlighted.
- Type any instructions regarding the text to be altered into the box that appears.



nformal invariance:
A: Math. Gen., Vol. 12, N

lified theory for a matri
ol. 8, 1984, pp. 305–323
d manuscript, 1984.
ching fractions for D0 → K+K

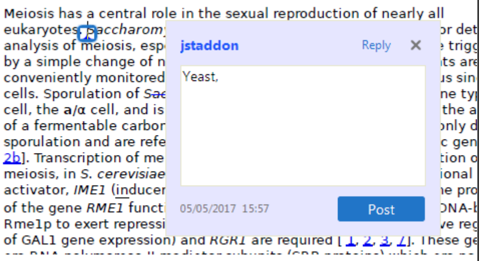
This needs to be bold

4. Insert Tool – for inserting missing text at specific points in the text.

Marks an insertion point in the text and opens up a text box where comments can be entered.

How to use it:

- Click on .
- Click at the point in the proof where the comment should be inserted.
- Type the comment into the box that appears.



Meiosis has a central role in the sexual reproduction of nearly all
eukaryotes. Saccharomy
analysis of meiosis, esp
by a simple change of n
conveniently monitored
cells. Sporulation of Sac
cell, the a/α cell, and is
of a fermentable carbor
sporulation and are refe
2b]. Transcription of me
meiosis, in S. cerevisiae
activator, IME1 (inducer
of the gene RME1 functi
Rme1p to exert repressi
of GAL1 gene expression) and RGR1 are required [1, 2, 3, 7]. These ge

Yeast,

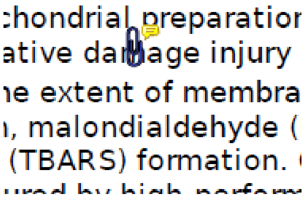
5. Attach File Tool – for inserting large amounts of text or replacement figures.

Inserts an icon linking to the attached file in the appropriate place in the text.

How to use it:

- Click on .
- Click on the proof to where you'd like the attached file to be linked.
- Select the file to be attached from your computer or network.
- Select the colour and type of icon that will appear in the proof. Click OK.

  The attachment appears in the right-hand panel.



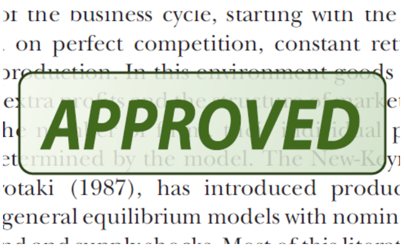
chondrial preparatior
ative damage injury
ıe extent of membra
ı, malondialdehyde (
(TBARS) formation.

6. Add stamp Tool – for approving a proof if no corrections are required.

Inserts a selected stamp onto an appropriate place in the proof.

How to use it:

- Click on .
- Select the stamp you want to use. (The Approved stamp is usually available directly in the menu that appears. Others are shown under *Dynamic*, *Sign Here*, *Standard Business*).
- Fill in any details and then click on the proof where you'd like the stamp to appear. (Where a proof is to be approved as it is, this would normally be on the first page).

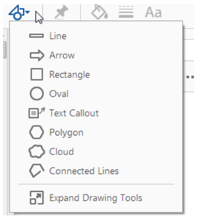


of the business cycle, starting with the
on perfect competition, constant ret
otaki (1987), has introduced produc
general equilibrium models with nomin

7. Drawing Markups Tools – for drawing shapes, lines, and freeform annotations on proofs and commenting on these marks.

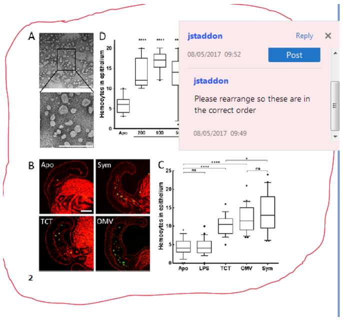
Allows shapes, lines, and freeform annotations to be drawn on proofs and for comments to be made on these marks.

Drawing tools available on comment ribbon



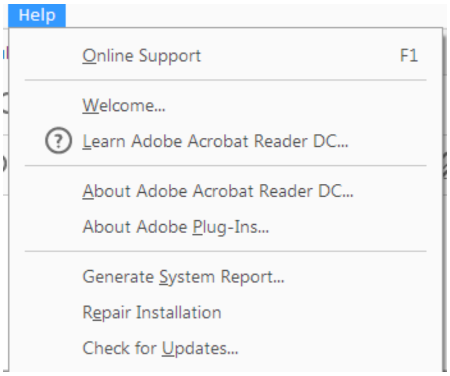
How to use it:

- Click on one of the shapes in the Drawing Markups section.
- Click on the proof at the relevant point and draw the selected shape with the cursor.
- To add a comment to the drawn shape, right-click on shape and select *Open Pop-up Note*.
- Type any text in the red box that appears.



jstaddon
08/05/2017 09:52
jstaddon
Please rearrange so these are in the correct order
08/05/2017 09:49

For further information on how to annotate proofs, click on the Help menu to reveal a list of further options:



WILEY

Author Query Form

Journal: SPP2

Article: 1261

Dear Author,

During the copyediting of your manuscript the following queries arose.

Please refer to the query reference callout numbers in the page proofs and respond to each by marking the necessary comments using the PDF annotation tools.

Please remember illegible or unclear comments and corrections may delay publication.

Many thanks for your assistance.

Query reference	Query	Remarks
1	**AUTHOR: Please verify that the linked ORCID identifiers are correct for each author.**	
2	**AUTHOR: Please confirm that given names (blue) and surnames/family names (vermilion) have been identified correctly.**	
3	**AUTHOR: Please check that authors and their affiliations are correct.**	
4	**AUTHOR: Please check software hyperlinks that have been added.**	
5	**AUTHOR: Repetition of Zhang et al.reference? or refers to the species described?**	
6	**AUTHOR: In the naming of the new taxon above, you refer to Dr Bach de Roca as Prof.; please correct one for consistency.**	
7	**AUTHOR: Sturm and Bach de Roca (1993) has not been cited in the text. Please indicate where it should be cited; or delete from the Reference List.**	

Funding Info Query Form

Please confirm that the funding sponsor list below was correctly extracted from your article: that it includes all funders and that the text has been matched to the correct FundRef Registry organization names. If a name was not found in the FundRef registry, it may not be the canonical name form, it may be a program name rather than an organization name, or it may be an organization not yet included in FundRef Registry. If you know of another name form or a parent organization name for a "not found" item on this list below, please share that information.

FundRef name	**FundRef Organization Name**
Spanish Ministry of Economy and Competitiveness	
European Community Research Infrastructure Action (SYNTHESIS Project)	

S P P 2	1261	WILEY	Dispatch: 6.3.19	CE: Geetha M
Journal Code	Manuscript No.		No. of pages: 19	PE: Raymond Appavoo M.

[Papers in Palaeontology, 2019, pp. 1–19]

JUMPING BRISTLETAILS (INSECTA, ARCHAEOGNATHA) FROM THE LOWER CRETACEOUS AMBER OF LEBANON

by ALBA SÁNCHEZ-GARCÍA[1], ENRIQUE PEÑALVER[2], XAVIER DELCLÒS[1] *and* MICHAEL S. ENGEL[3,4]

[1]Departament de Dinàmica de la Terra i de l'Oceà & Institut de Recerca de la Biodiversitat (IRBio), Facultat de Ciències de la Terra, Universitat de Barcelona, Martí i Franquès s/n, 08028, Barcelona, Spain; sanchez.garcia.alba@gmail.com
[2]Museo Geominero, Instituto Geológico y Minero de España, Cirilo Amorós 42, 46004, Valencia, Spain
[3]Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA
[4]Division of Entomology, Natural History Museum, & Department of Ecology & Evolutionary Biology, University of Kansas, 1501 Crestline Drive, Lawrence, KS 66045-4415, USA

Typescript received 14 September 2018; accepted in revised form 4 February 2019

Abstract: Jumping bristletails (order Archaeognatha), the basalmost order of extant insects, include some of the earliest fossil records among hexapods, yet their overall geological occurrence remains sparse and has provided little insight into their evolution. The earliest representatives of crown-group bristletails are those in Lebanese amber (Cretaceous), hitherto known only from a single species. Here we significantly expand the known fossil record of Archaeognatha, and from the prolific Lower Cretaceous (Barremian) deposits of Lebanon. One new genus and species, *Glaesimeinertellus intermedius* gen. et sp. nov., and one new species, *Macropsontus bachae* sp. nov., are described and figured from Hammana amber, whereas one additional *Macropsontus* species, *M. azari* sp. nov., and one meinertellid morphotype are described and figured from Al-Rihan amber. The new taxa are compared with their modern and fossil relatives. Collectively, the new taxa render the Archaeognatha fauna from Lebanese amber the earliest with sufficient preservation to provide character data comparable to modern forms, highlighting the considerable morphological conservatism within the order.

Key words: Hexapoda, Archaeognatha, bristletails, amber, fossils, Cretaceous.

INSECTS have an extensive history that stretches back to, at least, the earliest Devonian, over 410 Ma (Engel & Grimaldi 2004; Grimaldi & Engel 2005; Engel 2015). Accordingly, as the most plesiomorphic lineage of living insects, one presumes that the jumping bristletails (Archaeognatha = Microcoryphia) are similarly archaic. Historically, Archaeognatha were grouped with the silverfish (Zygentoma) in the order Thysanura, which contained those families of primitively wingless insects (Remington 1954, 1955). This assemblage was at times enlarged as the Apterygota, which also included the orders of non-insect hexapods (i.e. the Entognatha: Diplura, Protura and Collembola) (Börner 1904; Verhoeff 1905). Abundant phylogenetic evidence reveals that apterygotes are an unnatural grouping, and that even the Thysanura are paraphyletic (Hennig 1969, 1981). Unlike the Zygentoma, Archaeognatha retain a long, slender, monocondylar mandible and lack a gonangulum at the base of the ovipositor. These features not only help to distinguish the two orders but also reveal the affinity of the former group to the winged insects, or Pterygota (Hennig 1969, 1981; Mendes 2002; Grimaldi & Engel 2005; Engel *et al.* 2013). The separation of bristletails and silverfish into two orders is today universally accepted, the 'thysanurans' forming a grade to the pterygotes.

There is much about bristletails that is plesiomorphic, such as the primitive absence of wings, presence of three terminal filaments (two cerci and a median caudal filament), monocondylar mandibles, and lack of a gonangulum. Species range in length from 6 to 20 mm and have an overall cylindrical habitus, with the second and third thoracic nota hunched in profile. Archaeognatha are generally defined by a slew of anatomical traits: integument generally covered with scales, typically arranged in distinctive patterns; large and contiguous compound eyes, and three well-developed ocelli (the two last traits putatively owing to their nocturnal habits); long, flagellate antennae; long maxillary palpi, with seven palpomeres; head skeleton composed of paired anterior and posterior sclerotic plates; meso- and metapleura consisting of a

doi: 10.1002/spp2.1261

single sclerite, with large pleural apodemes; legs with coxal styli on meso- and metacoxae, on metacoxae only or completely absent; tarsi with two or three rigidly united tarsomeres; pretarsi with paired claws and lacking empodia; abdominal coxosternites with styli and eversible vesicles; and the aforementioned, three posteriorly directed caudal filaments (Sturm & Machida 2001; Grimaldi & Engel 2005). Bristletails are also distinctive for their particular jumping mechanism which is the result of a sudden flexion of the abdomen that propels the insect into the air and is partially made possible by the arched thoracic segments. Species occur in a wide variety of climates, from the tropical rain forest, living on the forest litter around the bases of living or fallen trees, to the rocky areas of dry regions, where they are principally petrophilous and live in stone crevices (Mendes 1990). Many bristletails feed on green algae, lichens and detritus of decaying leaves (Sturm & Machida 2001). Sturm & Machida (2001) and Mendes (1990, 2002) have provided general overviews regarding the biology and systematics of Archaeognatha. Extant Archaeognatha consist of about 500 species in two families – the putatively more plesiomorphic Machilidae (itself organized into the subfamilies Machilinae, Petrobiinae and Petrobiellinae), and the more derived Meinertellidae (Sturm & Machida 2001). The former family is mostly distributed in the Northern Hemisphere, with few exceptions in Africa and Asia, while the latter is principally found in the Southern Hemisphere (Sturm & Machida 2001; Mendes 2002).

Unfortunately, the fossil record of Archaeognatha is sparse. Fragments of cuticle from the mid-Devonian of Gilboa, New York, USA, may represent an early bristletail (Shear *et al.* 1984), while a head and thorax of a definitive bristletail recovered from fissures in the Gaspé fossil beds of Quebec, Canada, may represent a more recent contaminant rather than a later Devonian record of the order (Labandeira *et al.* 1988; Jeram *et al.* 1990). Unfortunately, these fragments provide little information on the Devonian record of Archaeognatha. Several Carboniferous and Permian species placed in the extinct family Dasyleptidae are apparently stem-group Archaeognatha, recognized earlier as the Monura and sometimes as an order or suborder (Sharov 1957; Kukalová-Peck 1987, 1991, 1997). These fossils are larger than most modern Archaeognatha and appear to be represented by juveniles, frequently shed exuviae (Bitsch & Nel 1999; Rasnitsyn 1999; Grimaldi 2001; Rasnitsyn *et al.* 2004; Engel 2009). Bechly & Stockar (2011) described a fossil species from the mid-Triassic of Meride Limestone of Monte San Giorgio, Switzerland as a dasyleptid, and considered the family to be a plesiomorphic suborder, sister to all Recent bristletails. An earlier Triassic fossil, *Triassomachilis uralensis* Sharov, was originally described as an archaeognathan (Sharov 1948), but its identity has been questioned (Bitsch 1994; Grimaldi & Engel 2005), with several authors regarding it as a nymphal mayfly (Bitsch & Nel 1999; Sinitshenkova 2000; Bechly & Stockar 2011). Aside from body fossils, various trace fossils have been described putatively representing the movement of dasyleptids across various substrates (Benner *et al.* 2015).

Apart from dasyleptids and the controversial fossils, the record of Archaeognatha is almost entirely restricted to several Cretaceous and Cenozoic ambers, and to the extant families Machilidae and Meinertellidae. The oldest Mesozoic meinertellid described and unquestionably placed in the Machiloidea is an individual of *Cretaceomachilis libanensis* Sturm and Poinar from the Lower Cretaceous amber of Lebanon (Sturm & Poinar 1998). Further Cretaceous amber Archaeonatha are known from the Albian of Spain (Peñalver & Delclòs 2010), Cenomanian of Myanmar (Burma) (Grimaldi *et al.* 2002; Mendes & Wunderlich 2013; Zhang *et al.* 2018), and Turonian of New Jersey (Grimaldi *et al.* 2000; Sturm & Machida 2001), although only a fraction of these have been thoroughly documented. The Cenozoic record is not much better, where jumping bristletails are described exclusively in amber, and from the Eocene of the Baltic region (Koch & Berendt 1854; Gadeau de Kerville 1893; Olfers 1907; Silvestri 1912; Haug *et al.* 2015), the Miocene of Mexico (Wygodzinsky 1971; Riquelme *et al.* 2015), and the Miocene of the Dominican Republic (Sturm & Poinar 1997). There is also a published record of a meinertellid from Venezuelan copal (Mendes 1997*a*). Zygentoma have a similarly sparse fossil record that is analogous richest during the Cenozoic and Cretaceous, although hitherto silverfish are known from Burmese, Baltic, Mexican and Dominican ambers (Silvestri 1912; Mendes 1997*b*, 1998; Sturm & Mendes 1998; Mendes & Poinar 2004, 2008, 2013; Mendes & Wunderlich 2013).

Although a single species has previously been described from the amber of Lebanon (Sturm & Poinar 1998), there is additional Lebanese material from a variety of different deposits and spanning the Barremian (Al-Rihan and Hammana outcrops). Although not abundant, this material provides new morphotypes and collectively represents the earliest fauna of Archaeognatha with sufficient preservation as to obtain character data comparable to modern forms. We therefore provide here an account of this diversity, aiming to build a body of data to allow future interpretations on the Cretaceous evolution of the Archaeognatha.

MATERIAL AND METHOD

Locality and stratigraphy

Lebanese amber represents one of the most important fossil Konservat-Lagerstätten from which to learn about life during the Early Cretaceous, and it remains as the earliest fossiliferous resin providing abundant biological inclusions (Azar 2007; Azar *et al.* 2010). Amber has been recorded from more than 450 fossil localities throughout Lebanon and spanning from the Late Jurassic (Kimmeridgian) to the Early Cretaceous (Albian) in age (Maksoud *et al.* 2017), although only the Barremian outcrops have yielded arthropods, mostly insects, as bioinclusions (Azar *et al.* 2010). The Lower Cretaceous amber-bearing outcrops are found in three intervals at the upper part of the 'Grès du Liban' (Sandstone of Lebanon); the middle and upper intervals recently dated as early and late Barremian, respectively, and the lower interval dated as early Barremian or possibly older. Nevertheless, it has been noted that amber pieces with inclusions from the middle and upper intervals could be reworked from the lower interval (Maksoud *et al.* 2017). The present amber pieces originate from two outcrops: Hammana (belonging to the upper interval) and Al-Rihan (belonging to the lower interval), together these have yielded most of the known Lebanese arthropod inclusions (Azar *et al.* 2010). Based on geological and palaeontological data, these deposits correspond to siliciclastic coastal and estuarine environments, where amber is always associated with levels of dark shales with lignite and other fossil plant remains from the three intervals (Maksoud *et al.* 2014, 2017; Granier *et al.* 2015). The localities have been recently mapped by Maksoud *et al.* (2014, 2017) (Fig. 1).

Specimens 1222 and 1565 (Figs 2–7) were found at the outcrop of Hammana, Baabda District, Mount Lebanon Governorate, in central Lebanon, which has yielded thousands of arthropod inclusions of about 20 different orders (Azar *et al.* 2010). Specimens RIH-2A and RIH-4A (Figs 8–10) were found at the outcrop of Al-Rihan, Jezzine Department, South Lebanon Governorate, in southern Lebanon, and where *c.* 40 inclusions have been discovered to date. The Al-Rihan outcrop has so far yielded the specimens of Archaeognatha reported herein as well as arthropod inclusions of the following clades: Acariformes, Araneae, Orthoptera, Blattaria, Mantodea, Psocoptera, Thysanoptera, Hemiptera, Hymenoptera, Neuroptera, Coleoptera and Diptera (Azar & Nel 2013; Delclòs *et al.* 2016).

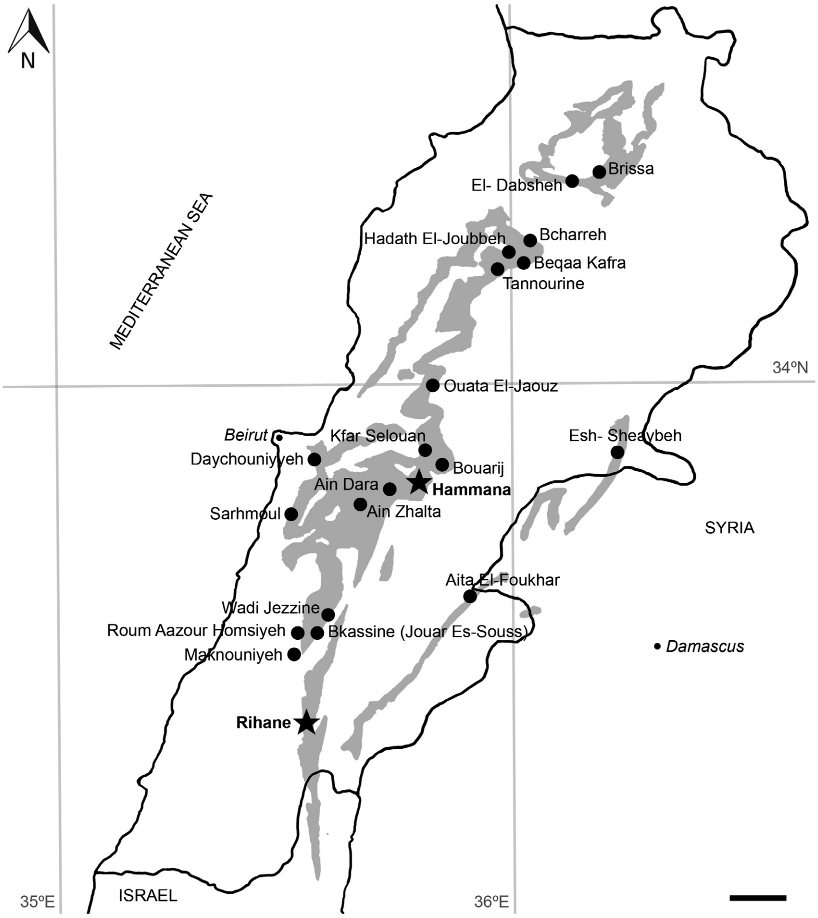


FIG. 1. Map of Lebanon with locations of the Lower Cretaceous amber outcrops. Modified after Maksoud *et al.* (2017). Grey areas indicate the distribution of the amber localities. Black circles indicate the outcrops with fossil inclusions, and stars those outcrops preserving Archaeognatha studied in this paper. Scale bar represents 10 km.

Preparation and descriptive method

Lebanese amber is highly mature and fractures easily, so the amber pieces containing the inclusions were stabilized in a medium of Canada balsam and then mounted between glass coverslips (Azar *et al.* 2003). The individual fossils were examined with Nikon SMZ 1500 and Olympus SZX12 stereomicroscopes and a BX41 compound microscope using reflected and transmitted light. Measurements were taken using ImageJ software (https://imagej.nih.gov/ij) and recorded in millimetres. Microphotography was performed with an AmScope MU900 digital camera attached to a Nikon SMZ 1500 stereomicroscope with AmScope ToupView 3.5 software (http://www.touptek.com), at the Muséum national d'Histoire naturelle (Paris, France), and a Moticam 2500 digital camera attached to a Motic BA310 compound microscope with Motic Images Plus 2.0 software (https://www.motic.com/As_Support_Download), at the Universitat de Barcelona (Barcelona, Spain). Helicon Focus software was used to combine photographs of a given inclusion at different focal depths (https://www.heliconsoft.com/heliconsoft-products/helicon-focus). Camera lucida drawings were prepared with a drawing tube attached to an Olympus CX41 compound microscope at the Universitat de Barcelona. The images were arranged in Adobe Photoshop CS3.

Morphological terminology used throughout is namely that widely employed in the systematics of Archaeognatha (Sturm & Machida 2001), although in the descriptions we have abbreviated the specific palpomeres of the maxillary and labial palpi as 'P_n', where *n* refers to a specific palpomere as numbered from base to apex (e.g. P_3 would indicate the third palpomere). All of the material reported herein is deposited in the amber collection of the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon.

SYSTEMATIC PALAEONTOLOGY

Order ARCHAEOGNATHA Börner, 1904
Family MEINERTELLIDAE Verhoeff, 1910

Genus GLAESIMEINERTELLUS nov.

LSID. urn:lsid:zoobank.org:act:854FC159-20A4-4DBE-9753-ED0A02EB6569

Derivation of name. The generic name is a combination of the Latin *glaesum* (meaning, 'amber'), and *Meinertellus* Silvestri, type genus of the family. The gender of the name is masculine.

Type species. Glaesimeinertellus intermedius sp. nov.

Diagnosis (female). Maxillary P_2 without a hook-like process; labial P_2 without a protrusion; labial P_3 slightly widened distally, with numerous sensilla basiconica (type D: Sturm & Machida 2001); compound eyes large and rounded; frons slightly protruding; profemora not wider than meso- and metafemora; only hindleg with coxal styli; spiniform setae present on legs; tarsi trimerous, without scopula; apical spine of abdominal styli thin and long.

Glaesimeinertellus intermedius sp. nov.
Figures 2–4

LSID. urn:lsid:zoobank.org:act:FB36EFDC-C236-41DA-B129-3233C46FEB83

Derivation of name. The specific epithet is derived from the Latin *intermedius*, meaning, 'in the middle', and in reference to the mixture of primitive and derived characters of the species.

Type specimen. 1222 (coll. Azar), holotype; juvenile or sub-adult specimen, female; partially preserved and observable dorsally and ventrally; the cuticle is highly damaged, but details of the antennae (incomplete), maxillary palpi, labial palpi, legs and abdominal styli are visible; preserved in a thin section of transparent yellow amber together with several loose fragments of a flagellum in close association; no syninclusions.

Diagnosis. As for genus (see above).

Description. Female. Body (Figs 2, 3) length as preserved 3.97 mm (without appendages), covered with scales (scale pattern indiscernible). Appendages (antennae, maxillary and labial palpi, legs, and styli) devoid of scales.

Head (Fig. 4A) orthognathous; frons slightly protruding, with few short setae; posterodorsal surface of head partly preserved. Compound eyes partly preserved, large, flattened, round-shaped, holoptic (i.e. in contact along median tangent), and composed of many ommatidia (average diameter of ommatidia 0.02 mm); exact ocular ratios (length/width of compound eye, and length of contact line/length of compound eye) not measurable due to nature of preservation, but length of contact line almost reaching entire length of compound eyes. Ocelli not accessible. Antenna (Fig. 3) incomplete, length as preserved 3.14 mm; scape robust, length 0.26 mm, width 0.14 mm; pedicel length 0.10 mm, width 0.10 mm; flagellum subdivided into numerous elements, with distinct breakpoints (with a narrowed diameter and lack of setae: Fröhlich & Lu 2013) separated by 7–8 flagellomeres; each flagellomere bearing one or two whorls of long, slender, curved, acuminate setae. Maxillary palpus (Fig. 4A) 7-segmented, fairly stout, with abundant, simple setae; P_1 with a pronounced triangular process dorsally; P_2 without a hook-like process; P_7 conical, distinctly shorter than P_6 (P_7/P_6 length ratio (0.07/0.17) 0.41), although measurements possibly underestimated due to foreshortened position; P_5 without spines; P_6 and P_7 with dorsal hyaline spines

Colour online

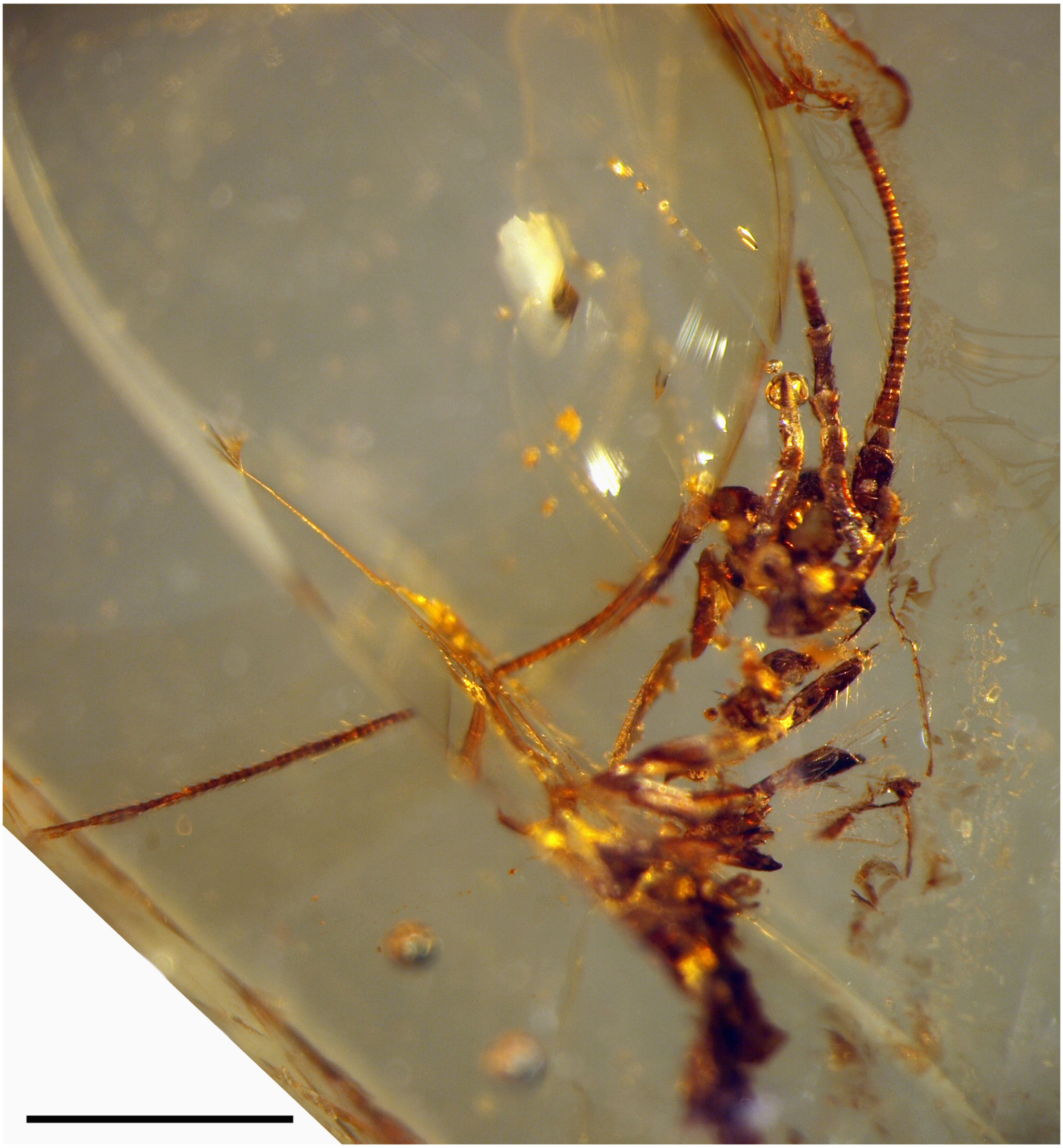


FIG. 2. Microphotograph of *Glaesimeinertellus intermedius* gen. et sp. nov. (holotype 1222, female), in ventral habitus, in Barremian amber from Hammana. Scale bar represents 1 mm. Colour online.

distributed as follows: P_6 with four spines along its length plus three spines distally, P_7 with five distal spines around its apex. Labial palpus (Fig. 4A) 3-segmented, elongate, lengths of palpomeres (P_1–P_3) 0.13, 0.14, and 0.20 mm, respectively; P_2 simple, without a protrusion; P_3 only slightly widened distally (greatest width 0.08 mm), with numerous distal sensilla basiconica (type D: Sturm & Machida 2001) (Fig. 3) that are distinctly thicker than the surrounding setae; sensilla basiconica micro-denticulate at apex. Mandible not discernible.

Thoracic cuticle poorly preserved, proportions not measurable due to preservation. Legs with coxal styli present only on metacoxae (Fig. 3); metacoxal styli (Fig. 4B) fairly stout, length 0.16 mm, width 0.04 mm, with numerous elongate setae; forelegs not modified (e.g. not crassate), similar in form to mid- and hindlegs; femur, tibia and tarsus with ventral spiniform setae intermixed among thin, simple setae, those on the tarsus (Fig. 4C) shorter and thicker than those on the femur and tibia; tarsus length 0.32 mm, with three tarsomeres (Fig. 4C); pretarsus with

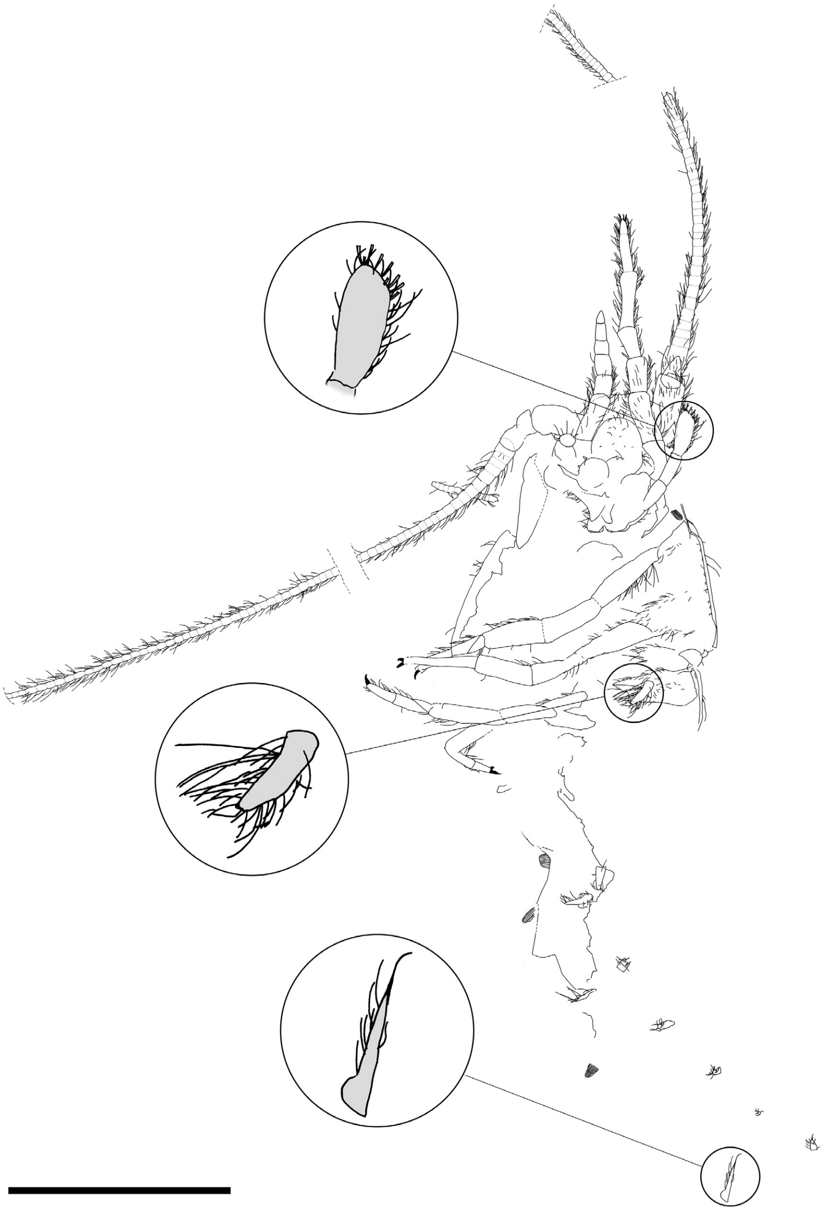


FIG. 3. Camera lucida drawing of *Glaesimeinertellus intermedius* gen. et sp. nov. (holotype 1222, female), in ventral habitus, showing details of labial P_3, metacoxal stylus and abdominal stylus (see top, middle, and bottom magnified areas, respectively). Scale bar represents 1 mm.

simple, paired claws (Fig. 4C); tarsal scopula (i.e. a brush-like patch of dense, often apically sinuate, specialized setae) absent.

Abdominal cuticle poorly preserved; abdominal coxites as well as corresponding sternites, and eversible vesicles not accessible as preserved; six pairs of abdominal styli visible (Fig. 3); all visible styli (Fig. 4D) of similar form, rather slender, width 0.02 mm, with several fine, long setae more or less disposed in a longitudinal row; styli terminating in a distinct spine longer and thicker than neighbouring setae; length of stylus (without spine) 0.12 mm; length of spine 0.06 mm. Terminalia (genitalia, cerci, and median caudal filament) not preserved.

Male. Unknown.

Remarks. The new genus *Glaesimeinertellus* is readily distinguished from the other genera of Meinertellidae by the simple maxillary and labial palpi, the shape of the compound eyes, the slightly protruding frons, the not modified forelegs, the coxal styli only present on hindlegs, the presence of spiniform setae on legs, the trimerous tarsi without scopula, and the apical spine of abdominal styli thin and long.

Among the genera of Meinertellidae, only the fossil *Unimeinertellus* Zhang *et al*., and the modern *Hypomachiloides* Silvestri, *Praemachilellus* Sturm and Bach (both of the *Hypomachiloides*-group), and *Machilontus* Silvestri (*Machilontus*-group) have coxal styli restricted to the metacoxae (Sturm & Machida 2001). However, the new fossil specimen can be distinguished from *Unimeinertellus* and *Machilontus* by the presence of a trimerous tarsi (vs dimerous) (Sturm & Bach de Roca 1988).

Colour online

FIG. 4. Microphotographs of *Glaesimeinertellus intermedius* gen. et sp. nov. (holotype 1222, female). A, detail of head in ventral view, showing the maxillary and labial palpi. B, detail of metacoxal stylus. C, detail of tarsus, showing the three tarsomeres (arrows); D, detail of abdominal stylus. *Abbreviations*: 1–6, maxillary palpomeres; lp, labial palpus; tp, triangular process. Figures made with consecutive pictures taken at successive focal planes. Scale bars represent: 0.5 mm (A); 0.2 mm (B, C); 0.1 mm (D). Colour online.

Conversely, *Glaesimeinertellus* shares with the genera *Hypomachiloides* and *Praemachilellus* the trimerous tarsi, but can be distinguished from them in its forelegs similar to mid- and hindlegs (vs stronger than mid- and hindlegs in both males and females) (Bach de Roca & Sturm 1988; Sturm & Bach de Roca 1992; Packauskas & Shofner 2010). Other differences worthy of mention relate to several secondary sexual characters. Indeed, males of both extant genera have the distal labial palpomeres distinctly and greatly widened (less markedly in females) (Bach de

Roca & Sturm 1988; Sturm & Bach de Roca 1992; Sturm & Machida 2001), while this condition is poorly developed in *Glaesimeinertellus*. Additionally, males of *Hypomachiloides* have the second article of the labial palp with a large apophysis on the inner border (reduced to a slight protrusion in females) (Bach de Roca & Sturm 1988; Packauskas & Shofner 2010), while the fossil lacks any protrusion.

Although present knowledge of bristletail ontogeny remains incomplete, the available data reveal that nearly all changes concern the postembryonic growth of some parts of the body largely resulting in the change of the relative proportions of some structures or the appearance of mature traits (e.g. labial palpus, coxal styli, eversible abdominal vesicles, terminalia), and leading gradually and qualitatively to the adult stage (Bach de Roca & Gaju-Ricart 1987; Sturm & Machida 2001). However, comparable data on the growth of the different parts and duration of the early stages are scarce. Taking into consideration the body length (*c.* 4.0 mm) of the fossil, the holotype of *G. intermedius* might correspond to a scaled juvenile or a sub-adult (Sturm & Machida 2001). The form of the labial palpi (with P_2 lacking any process and P_3 only slightly widened) and the maxillary palpi (with P_2 lacking any process) raise the question as to whether these are plesiomorphic absences in an adult, or whether they are absent owing to the individual representing a non-adult stage. However, the presence of a well-developed metacoxal stylus (a trait that also tends to correlate with ontogenetic stage), supports the conclusion that the simple labial and maxillary palpi are true characters for *Glaesimeinertellus*, it is likely that it corresponds to a female.

Occurrence. Lower Cretaceous (Barremian; Maksoud *et al.* 2017), Hammana outcrop, Caza Baada (Baabda District), Mouhafazit Jabal Libnen (Mount Lebanon Governorate), central Lebanon.

Genus MACROPSONTUS Silvestri, 1911

Macropsontus bachae sp. nov.

Figures 5–7

LSID. urn:lsid:zoobank.org:act:F1DAE74C-25DD-4BBB-AD7F-02D59B15D49F

Derivation of name. The specific epithet honours Prof. Carmen Bach de Roca, Universitat Autònoma de Barcelona (Bellaterrra, Spain), for her outstanding contributions to our knowledge of the Archaeognatha.

Type specimen. 1565 (coll. Azar), holotype; juvenile of indeterminate sex; virtually complete except for the antennae and terminalia, and observable dorsally and ventrally; preserved in a thin section of transparent yellow amber together with several coprolites and plant remains (syninclusions).

Diagnosis (sex unknown, juvenile). Maxillary P_2 without a hook-like process, bearing two setae 2× longer than greatest palpomere diameter; labial P_2 without a protusion; labial P_3 slightly widened distally, with numerous sensilla basiconica (type D); compound eyes large and rounded; ocelli sole-shaped; frons slightly protruding; profemora not wider than meso- and metafemora; all legs without coxal styli; spiniform setae present on legs; tarsi dimerous, without scopula; second abdominal sternite enlarged; 1 + 1 eversible vesicles on abdominal segments; apical spine of abdominal styli thin and long.

Description (sex unknown, juvenile). Sex unknown (juvenile). Body (Figs 5, 6) nearly complete, length as preserved 2.66 mm, covered with scales (scale pattern indiscernible); appendages devoid of scales.

Head (Fig. 7A) orthognathous, rounded in dorsal view, length 0.30 mm, about 0.11× total body length as preserved, width 0.30 mm; frons slightly protruding, with few short setae. Compound eyes (Fig. 7C) large (length 0.18 mm), flattened, round-shaped, holoptic, and composed of many ommatidia (average diameter of ommatidia 0.01 mm); ratio length/width of compound eyes close to 1 (i.e. isodiametric); ratio length of contact line/length of compound eye close to 1. Ocelli sole-shaped. Antenna (Fig. 7A) incomplete, length as preserved 0.81 mm; scape not robust, length 0.11 mm, width 0.07 mm; pedicel length 0.06 mm, width 0.06 mm; flagellum with distinct break-points separated by seven flagellomeres; each flagellomere bearing one or two whorls of long, slender, curved, acuminate setae. Maxillary palpus (Fig. 7B) 7-segmented, thin, with abundant, simple setae; P_1 obscured as preserved (triangular process not discernible); P_2 without a hook-like process, bearing two setae 2× longer than greatest palpomere diameter; P_7 conical, somewhat shorter than P_6 (P_7/P_6 length ratio (0.04/0.06) 0.66), although measurements possibly underestimated due to foreshortened position; P_5–P_7 with dorsal hyaline spines distributed as follows: P_5 with two distal spines, P_6 with three distal spines, and P_7 with three distal spines. Labial palpus (Fig. 7B) 3-segmented, elongate, lengths of palpomeres (P_1–P_3) 0.05, 0.06, and 0.09 mm, respectively; P_2 without a protusion, P_3 only slightly widened distally (greatest width 0.03 mm), with numerous distal sensilla basiconica (type D) that are distinctly ticker than surrounding setae; sensilla basiconica micro-denticulate at apex. Labium (Fig. 7B) with bilobed endites (two glossae and two paraglossae).

Thorax (Figs 5A, 7A) 0.64 mm in length, about 0.24× the total body length as preserved; pronotum length 0.13 mm, width 0.35 mm; mesonotum length 0.34 mm, width 0.39 mm; metanotum only slightly shorter than mesonotum, length 0.30 mm, width 0.38 mm; spiniform setae not present on lateral margins of terga. Legs (Fig. 6) without coxal styli; forelegs not modified, similar in form to mid- and hindlegs; femur and tibia subequal in length; tarsus longer than tibia, with ventral spiniform setae

Colour online

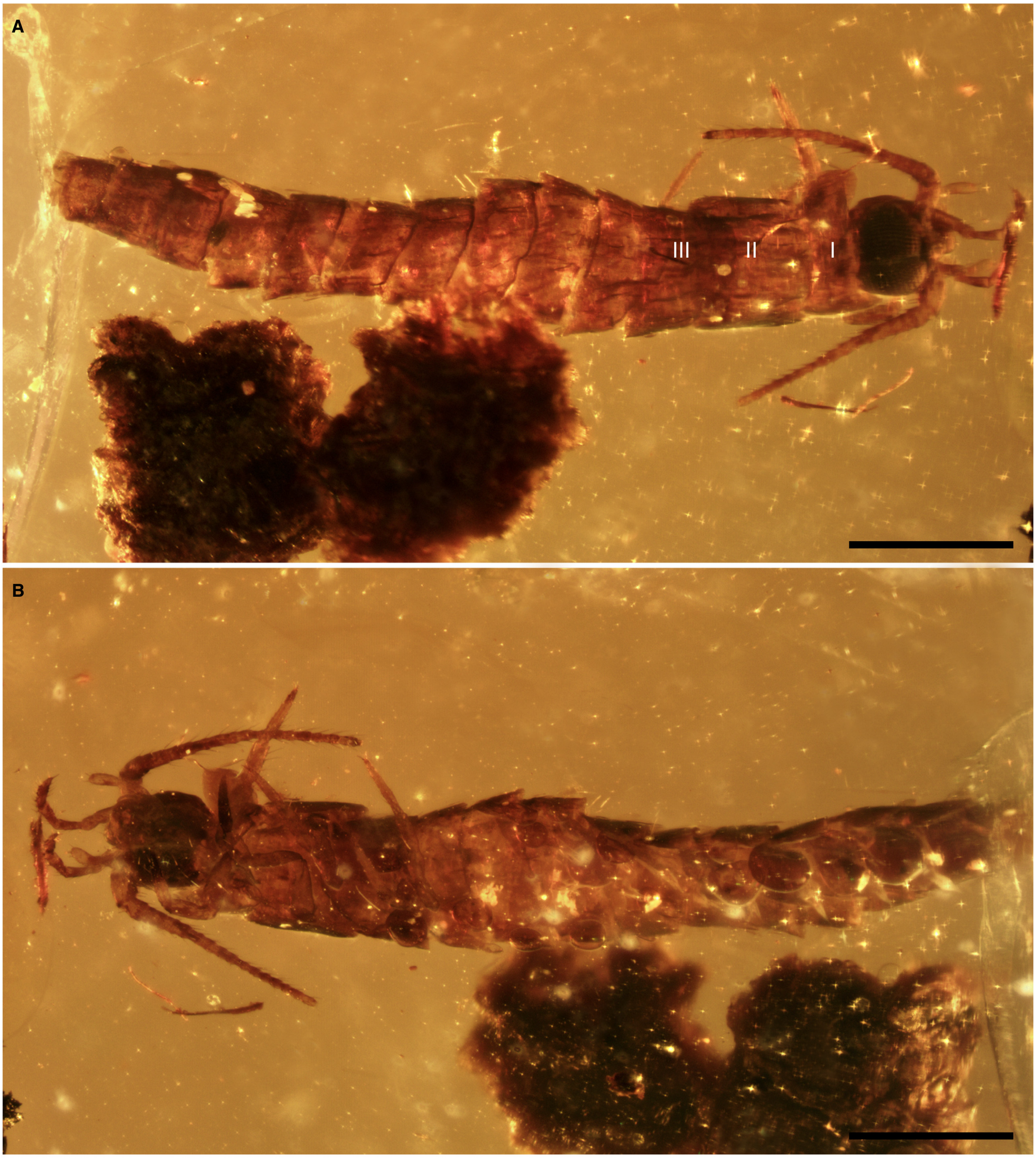


FIG. 5. Microphotographs of *Macropsontus bachae* sp. nov. (holotype 1565), in Barremian amber from Hammana. A, dorsal habitus (thoracic terga have been tagged with Roman numerals). B, ventral habitus. Figures made with consecutive pictures taken at successive focal planes. Scale bars represent 0.5 mm. Colour online.

intermixed among thin, simple setae; tarsus length 0.18 mm, with two tarsomeres (Fig. 7D); pretarsus with simple, paired claws (Fig. 7D); tarsal scopula absent.

Abdomen 1.84 mm in length, about 0.69× the total body length, with seven pairs of abdominal styli visible on coxites III–IX (Fig. 6); all visible styli (Fig. 7E) of similar form, rather slender, width 0.02 mm, with several fine, long setae more or less disposed in a longitudinal row; styli terminating in a distinct spine longer and thicker than neighbouring setae; length of stylus (without spine) 0.10 mm, length of spine 0.04 mm;

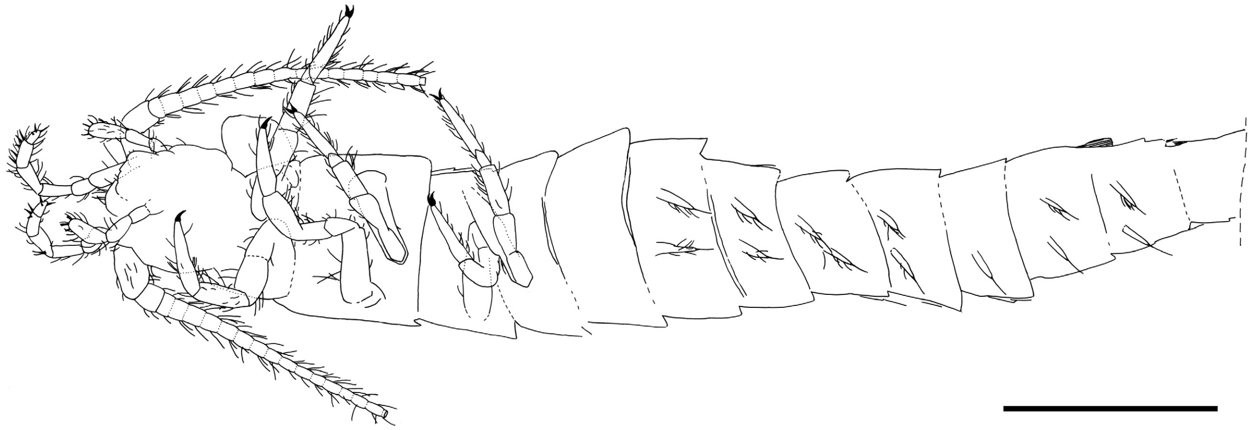


FIG. 6. Camera lucida drawing of *Macropsontus bachae* sp. nov. (holotype 1565), in ventral habitus. Scale bar represents 0.5 mm.

abdominal sternite II enlarged; 1 + 1 eversible vesicles (Fig. 7E) visible on some abdominal segments; length and width of abdominal segments I–X (in mm): I: 0.22, 0.42; II: 0.19, 0.44; III: 0.19, 0.43; IV: 0.16, 0.34; V: 0.18, 0.31; VI: 0.19, 0.31; VII: 0.18, 0.31; VIII: 0.20, 0.29; IX: 0.18, 0.25; X: 0.14, 0.20. Genitalia not accessible as preserved (probably not developed). Cerci and median caudal filament not preserved.

Remarks. Dimerous tarsi only occur in four genera of Meinertellidae (the extant *Hypermeinertellus* Paclt, *Macropsontus* Silvestri, and *Machilontus* Silvestri, and the fossil *Unimeinertellus* Zhang *et al.*), and this has been widely interpreted to be a derived feature among Archaeognatha (Sturm & Machida 2001; Mendes & Wunderlich 2013). Unlike *Hypermeinertellus*, *Macropsontus bachae* lacks a tarsal scopula (highly developed in *Hypermeinertellus* and related taxa in the *Meinertellus*-group of genera except *Neomachilellus* Wygodzinsky) (Sturm & Machida 2001). As for the genera *Macropsontus* and *Machilontus* (both of the *Machilontus*-group) *Macropsontus bachae* shares the very large compound eyes, lateral ocelli sole-shaped, terminal labial palpomeres only moderately widened distally, spiniform setae present on legs, tarsi lacking scopulae, and enlarged second abdominal sternite (Sturm & Machida 2001). However, the absence of meso- and metacoxal styli is in accordance with *Macropsontus* and contradicts its inclusion within *Machilontus* as well as the fossil *Unimeinertellus*. Indeed, the genus *Macropsontus* is principally differentiated from *Machilontus* by the aforementioned absence of meso- and metacoxal styli (while metacoxal styli are present in *Machilontus*), and the presence of a hook with a long cylindrical base on the male maxillary P_2 (if present, the cylindrical base is shorter than half the length of the hook in *Machilontus*) (Sturm & Bach de Roca 1988). Admittedly, the present fossil lacks the maxillary P_2 hook (a secondary sexual feature in adult males) and one might interpret that feature could exclude the species from *Macropsontus*. However, the small size of the specimen suggests that it was juvenile, and therefore would have lacked the secondary sexual traits of the adult or it may have been a female, and thus the absence of the maxillary P_2 hook is not greatly informative in this case. *Macropsontus* also differs from the fossil in the tendency to protrusion on the second labial palpomere (Sturm & Bach de Roca 1988). Thus, in the absence of further data, we have conservatively placed the present fossil within *Macropsontus*. It is possible that if other features were discernible (e.g. details of the genitalia), then this Lower Cretaceous species might be better classified in a separate genus, but this must await more completely preserved material.

Occurrence. Lower Cretaceous (Barremian; Maksoud *et al.* 2017), Hammana outcrop, Caza Baada (Baabda District), Mouhafazit Jabal Libnen (Mount Lebanon Governorate), central Lebanon.

Macropsontus azari sp. nov.

Figures 8, 9

LSID. urn:lsid:zoobank.org:act:0181426F-FB84-4FCA-9D5C-0BA755E94D53

Derivation of name. The specific epithet honours Dr Dany Azar, Lebanese University (Beirut, Lebanon), whose work has given renewed vitality to the study of the numerous and significant amber-bearing deposits of Lebanon and their palaeobiological content.

Type specimen. RIH-2A (coll. Azar), holotype; juvenile of indeterminate sex; virtually complete, and observable in lateral view; preserved in a thin section of transparent yellow amber; the piece also contained a coccid male (RIH-2B) as syninclusion.

FIG. 7. Microphotographs of *Macropsontus bachae* sp. nov. (holotype 1565). A, anterior part of the body in ventral view. B, magnified view of mouthparts from A. C, anterior portion of the body in dorsal view. D, magnified view of tarsus from A, showing the two tarsomeres (arrows). E, abdomen showing the sternite development, abdominal eversible vesicles (arrows) and styli. *Abbreviations*: ast, abdominal styli. Figures made with consecutive pictures taken at successive focal planes. Scale bars represent: 0.3 mm (A, C); 0.2 mm (B, D, E). Colour online.

Diagnosis (sex unknown, juvenile). Maxillary P_2 without a hook-like process, with no special setae; labial P_3 slightly widened distally, with numerous sensilla basiconica (type D); compound eyes large and rounded; frons slightly protruding; profemora not wider than meso- and metafemora; all legs without coxal styli; spiniform setae present on legs; tarsi dimerous, without scopula; apical spine of abdominal styli thin and long; cerci very short, ending

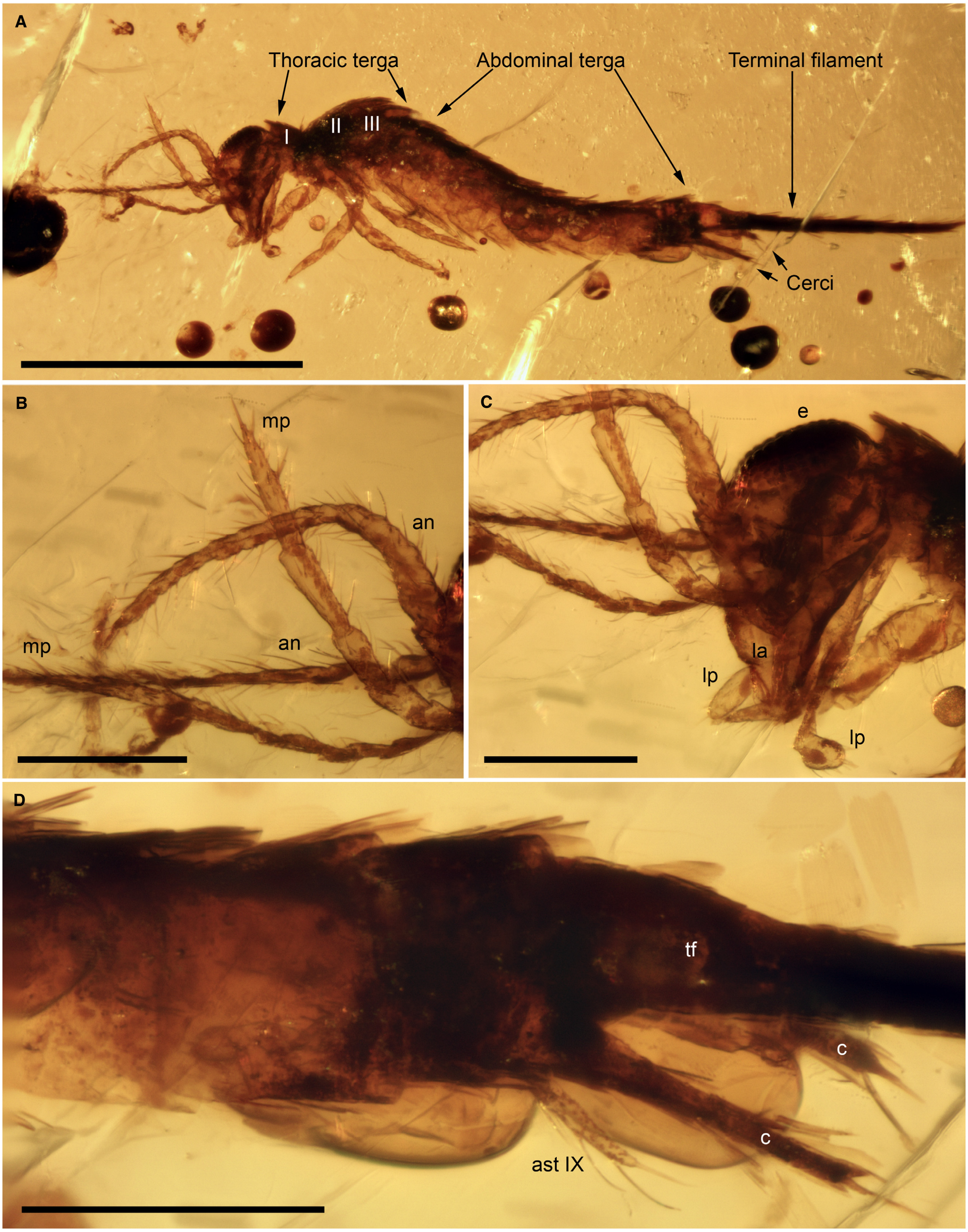


FIG. 8. Microphotographs of *Macropsontus azari* sp. nov. (holotype RIH-2A), in Barremian amber from Al-Rihan. A, lateral habitus. B, detail of maxillary palpi and antennae. C, detail of head. D, detail of posterior part of abdomen, cerci, and median caudal filament. *Abbreviations*: an, antenna; ast IX, abdominal stylus IX; c, cercus; e, compound eye; la, lacinia; lp, labial palpus; mp, maxillary palpus; tf, terminal filament. Figures made with consecutive pictures taken at successive focal planes. Scale bars represent: 1 mm (A); 0.2 mm (B–D). Colour online.

FIG. 9. Camera lucida drawing of *Macropsontus azari* sp. nov. (holotype RIH-2A), in lateral habitus. Scale bar represents 0.5 mm.

with an apical spine and two longer subapical setae on each side of the spine.

Description (sex unknown, juvenile). Body (Figs 8A, 9) length 1.70 mm, with elongate habitus, transverse section rounded along body length; abundant scales on all terga (scale pattern indiscernible), abdominal coxites, cerci, and median caudal filament, but scales absent on appendages; some pigmentation detectable on dorsal part of head and body.

Head (Fig. 8C) shape subtriangular in lateral view due to elongate mouthparts, orthognathous; cephalic diagonal 0.42 mm, length 0.24 mm, about 0.14× the total body length; frons slightly protruding, with at least two long setae and several short setae. Compound eyes (Fig. 8C) large (length 0.19 mm), flattened, apparently round-shaped (although width not measurable), holoptic, and composed of many ommatidia (average diameter of ommatidia 0.01 mm); exact ocular ratios (length/width of compound eye, and length of contact line/length of compound eye) not measurable due to nature of preservation (dorsal and frontal views are not possible as preserved). Ocelli not accessible. Antenna (Fig. 8B) incomplete, length as preserved 0.79 mm; scape poorly visible, length *c.* 0.09 mm, width 0.06 mm; pedicel length 0.07 mm, width 0.05 mm; breakpoints of flagellum not discernible; each flagellomere bearing one or two whorls of long, slender, curved, acuminate setae. Maxillary palpus (Fig. 8B) 7-segmented, thin, with abundant, simple setae; P_1 obscured as preserved (triangular process not discernible); P_2 without a hook-like process, with setae similar to those of the others palpomeres (never longer than greatest palpomere diameter); P_7 conical, somewhat shorter than P_6 (P_7/P_6 length ratio (0.07/0.10) 0.70); P_5–P_7 with dorsal hyaline spines distributed as follows: P_5 with one distal spine; P_6 with three distal spines; P_7 with three distal spines (one terminal). Labial palpus (Fig. 8C) 3-segmented, elongate; P_1 and P_2 poorly visible as preserved; P_3 length 0.10 mm, only slightly widened distally (greatest width 0.03 mm), with numerous distal sensilla basiconica (type D) that are distinctly thicker than surrounding setae; sensilla basiconica micro-denticulate at apex. Mandible (Fig. 8C) with several teeth (precise number not discernible as preserved).

Thorax (Fig. 8A) 0.32 mm in length, about 0.19× the total body length, strongly arched; spiniform setae not present on lateral margins of terga. Legs (Fig. 9) without coxal styli (although the coxa and trochanter are poorly visible due to preservation); forelegs not modified, similar in form to mid- and hindlegs, the left profemur and protibia compressed and taphonomically altered giving a crassate appearance; femur and tibia subequal in length; tarsus longer than tibia, with ventral spiniform setae intermixed among thin, simple setae; tarsus length 0.15 mm, with two tarsomeres (Fig. 9); pretarsus with simple, paired claws (Fig. 9); tarsal scopula absent.

Abdomen (Fig. 8A) 1.15 mm in length, about 0.68× the total body length; abdominal coxites as well as corresponding sternites, and eversible vesicles not accessible as preserved; abdominal styli poorly visible (Fig. 9); all visible styli (Fig. 8D) of similar form, rather slender, width 0.02 mm, with several fine, long setae more or less disposed in a longitudinal row; styli terminating in a distinct spine longer and thicker than neighbouring setae; length of stylus (without spine) 0.09 mm; length of spine 0.05 mm. Genitalia not accessible as preserved (probably not developed). Cerci and median caudal filament complete; median caudal filament (Figs 8A, 9) length 0.97 mm, about 0.57× of total body length, with dense scales and sparsely scattered, long, sensory, spine-like setae; cerci (Fig. 8A, D) very short, scarcely exceeding abdominal apex, length 0.23 mm, about 0.24× the length of median caudal filament, densely covered by scales, ending with an apical spine and two longer subapical setae on each side of the spine.

Remarks. As already noted (refer to remarks for *Macropsontus bachae* sp. nov., above), the presence of dimerous tarsi is not common among Archaeognatha. For many of the same reasons outlined for the specimen from Hammana outcrop, the present fossil can also be placed within the extant genus *Macropsontus*. Indeed, the absence of tarsal scopulae excludes the dimerous *Hypermeinertellus* and the absence of coxal styli excludes the dimerous *Machilontus*. The setation of the second maxillary palp, immediately distinguishes *M. azari* from the other *Macropsontus* species described in this paper. While *M. azari* has setae never longer than the greatest palpomere diameter and uniformly distributed along the maxillary palp, *M. bachae* has a second maxillary palp with two setae twice longer than the greatest palpomere diameter. Unfortunately, other diagnostic characters of *M. bachae* are not preserved or are poorly visible in *M. azari* (i.e. labial P_2 without a protusion; ocelli sole-shaped; second abdominal sternite enlarged; 1 + 1 eversible vesicles on abdominal segments), meaning that it is impossible to establish if they differ in the two species. In the case of the specimen of *M. azari*, the small body size and the absence of secondary sexual traits is in agreement with the exceptionally reduced cerci (scarcely exceeding the

Colour online

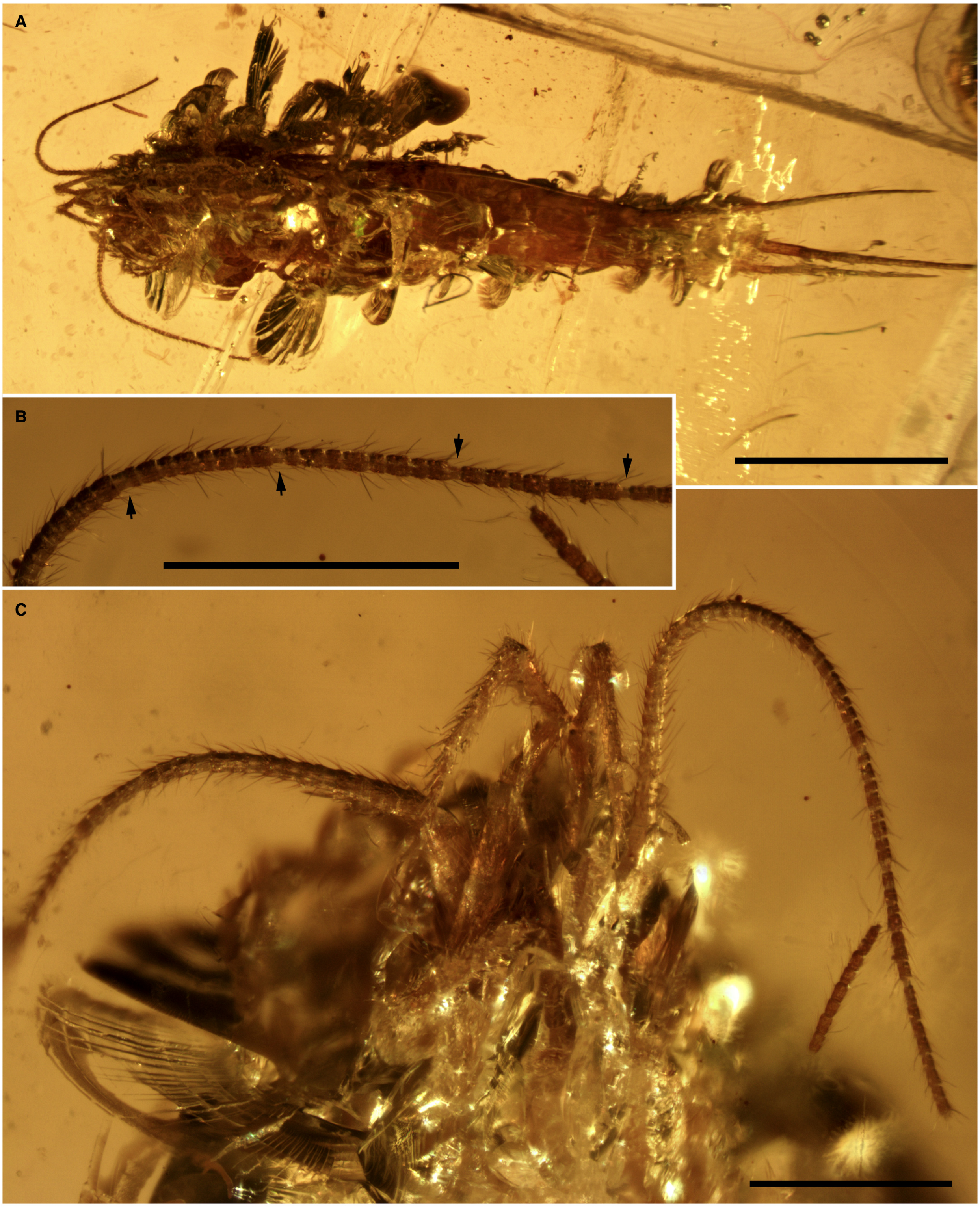


FIG. 10. Microphotographs of meinertellid specimen RIH-4A, in Barremian amber from Al-Rihan. A, ventral habitus. B, detail of antennae showing the breakpoints along the flagellum (arrows); note that the breakpoints are easily recognizable by their narrowed diameter and lack of setae. C, detail of head in ventral view. Scale bars represent: 2 mm (A); 0.5 mm (B, C). Colour online.

abdominal apex), and the specimen most likely corresponds to a juvenile.

Occurrence. Lower Cretaceous (Barremian; Maksoud *et al.* 2017), Al-Rihan outcrop, Caza Jezzine (Jezzine Department), Mohafazat Loubnan El-Janoubi (South Lebanon Governorate), southern Lebanon.

Gen. et sp. indet.
Figure 10

Material. Specimen RIH-4A (coll. Azar); the amber piece originally contained a spider (RIH-4B), an unidentified ceratopogonid (RIH-4E), and a mite and an undetermined brachyceran fly (both as RIH-4CD) as syninclusions.

Descriptive notes. Specimen observable in dorsal and ventral views, preserved in brittle amber with multiple internal fractures that hinder examination (Fig. 10A), only with antennae, maxillary palpi, and terminalia partly visible with some detail. Body (Fig. 10A) length 5.91 mm, greatest width as preserved 1.10 mm. Antenna (Fig. 10B, C) incomplete, length as preserved 2.08 mm, devoid of scales; scape and pedicel poorly visible; flagellum with distinct breakpoints (Fig. 10B), these separated by stretches of 7–8 flagellomeres; each flagellomere bearing one or two whorls of long, slender, curved, acuminate setae. Maxillary palpus (Fig. 10C) thin, densely setose; maxillary P_5–P_7 with dorsal and apical spines. Median caudal filament (Fig. 10A) incomplete, length as preserved 2.76 mm; cercus length 2.16 mm; median caudal filament and cerci (Fig. 10A) with dense scales and sparsely scattered, long, sensory, spine-like setae.

Remarks. The above specimen is too poorly preserved to permit conclusive assignment to any particular genus or species but the observable details (e.g. antennae and maxillary and labial palpi devoid of scales) are indicative of a meinertellid.

Occurrence. Lower Cretaceous (Barremian; Maksoud *et al.* 2017), Al-Rihan outcrop, Caza Jezzine (Jezzine Department), Mohafazat Loubnan El-Janoubi (South Lebanon Governorate), southern Lebanon.

DISCUSSION

The fauna of Archaeognatha preserved in Lebanese amber is, at present, the earliest documented source of the group with sufficient preservation to provide character data comparable to modern forms. All the specimens can be placed within the extant superfamily Machiloidea. Apomorphies of machiloids (summarized by Sturm & Machida 2001) include the presence of lateral cranial lobes that include the mandibular condyle (mandibular overhang); large and contiguous compound eyes; hypertrophic maxillary palpi, with seven palpomeres typically longer than the mesothoracic appendages; maxillary P_1 with a dorsal triangular process; bilobed labial endites; metacoxae, and sometimes also mesocoxae, with styli that cannot be actively moved; and caudal appendages with scales. Most of these characters are easily observed in the studied material. Furthermore, the newly described specimens can be placed within the Meinertellidae, a family characterized by having small abdominal sternites, a longitudinal projection on the base of maxillary palp, the maxillary P_1 with two inner humps, the male maxillary P_2 with a hook-like process dorsoapically, the absence of paramera, and the absence of scales on the antennae, palpi, legs and styli (Sturm & Machida 2001; Zhang *et al.* 2018). Currently, there are four informal, suprageneric groups recognized within Meinertellidae (the *Machiloides*-, *Hypomachiloides*-, *Machilontus*- and *Meinertellus*-groups), as well as the unplaced genus *Machilinus* Silvestri (Sturm & Machida 2001). It is not clear to what degree these might represent natural groups, and there is considerable need for a revision of extinct phylogenetic concepts among meinertellids. The differences between the genera of Archaeognatha are rather subtle, and most of the taxa show a distressingly confusing mosaic of conserved and highly labile features (i.e. plesiomorphies and homoplasies), whose combinations are used to characterize the groups, but necessitating various exceptions. Overall, the pattern of relationships is rather opaque, further emphasizing the need for greater investigation and perhaps the application of genomic data.

Despite preservation in comparatively clear amber and the fine preparations available to us, many details commonly examined among living Archaeognatha were simply not preserved (e.g. terminalia), or were not visible due to concealed positions in the fossils (e.g. the hooks of the maxillary palpi or the genitalia). Nonetheless, diagnostic characters from the general shape of the body and proportions of segments, structure of the antennae and maxillary and labial palpi, as well as coxal styli and tarsal configurations, are informative and allow the comparison between fossil and modern forms.

Cretaceomachilis libanensis, also in Lebanese amber (Jouar Es-Souss outcrop in Bkassine, southern Lebanon; Azar *et al.* 2010), was reported to be related to the *Machiloides*-group (currently including the genera *Machiloides* Silvestri, *Nesomachilis*, and the recently synonymized *Allomachilis* Silvestri and *Kuschelochilis* Wygodzinsky) (Mendes *et al.* 2009), based on the presence of meso- and metacoxal styli (Sturm & Poinar 1998). More specifically, *C. libanensis* was considered a relative of *Machiloides* based on the moderately protrudent frons, sole-shaped lateral ocelli, apical labial palpomere that is not distinctly broadened, and the trimerous tarsi (Sturm & Poinar 1998). Lately, Zhang *et al.* (2018) described one more species of *Cretaceomachilis*, *C. longa* Zhang *et al.*, based on a female specimen in Cenomanian amber from Myanmar, allowing the redescription of the genus. Therefore, the list of Lebanese Archaeognatha increases to four species in two genera.

The considerable anatomical homogeneity of the order and the subtle differences among seemingly homoplastic features, while posing a considerable challenge for the study of extant groups, are even more problematic when dealing with fossil material of varying degrees of completeness. The generalized appearance of living and fossil Archaeognatha has apparently remained little changed over at least the last 129 or more million years. This bradytely is much like that of other arthropods with similar subcortical, litter, or crevice habitats (Engel & Grimaldi 2002; Cognato & Grimaldi 2009; Chatzimanolis *et al.* 2013; Engel *et al.* 2016; Sánchez-García & Engel 2016*a*, *b*), and perhaps reflects a long-term consistency of the microenvironment in which they pass out their lives (Hamilton 1978). It is not until the Palaeozoic, or perhaps the mid-Triassic, that there may be found taxa that deviate sufficiently as to fall outside of crown-group Machiloidea (i.e. the previously discussed Dasyleptidae). From this, it seems clear that glimpses into the basal divergences among Archaeognatha must await Palaeozoic material with sufficient preservation as to permit fine comparisons with the modern and Cretaceous taxa.

CONCLUSION

The study of Archaeognatha has been generally hampered by their overall morphological conservatism and the lack of robust phylogenetic estimates from which to determine the polarity and consistency of traits often used in bristletail systematics. There are apparently repeated losses and appearances of suites of characters, and it is unclear to what degree these are valid in supporting particular clades (Sturm & Machida 2001). Added to this is a limited understanding of intraspecific variability among ontogenetic stages, with only the tiniest fraction of species having been examined and yet large swaths of palaeontological material are of sundry juvenile instars (e.g. Dasyleptidae: Rasnitsyn 1999). This reality certainly poses problems when attempting to consider fossil Archaeognatha, with varied forms of and degrees of completeness in preservation. Even among some of the most well understood fossil insects, there is rarely a strong understanding of potential sexual dimorphism or changes among life stages. Despite these setbacks, incremental progress can be made through the continued documentation of available fossil material and their unique character combinations in comparison with modern counterparts. As such, fossil Archaeognatha, even immature stages, should not be ignored and while taxonomic uncertainties may persist, as is true for any lineage, it is only through the discovery and description of new material that resolution of long-standing questions in bristletail evolution may be achieved (Haug *et al.* 2015). Here we have provided an overview of bristletail diversity in the Lebanese amber fauna, building and expanding upon the body of data available for understanding the Cretaceous evolution of this basal insect order.

Acknowledgements. We are grateful to Dr Dany Azar, Lebanese University (Beirut), for the preparation and loan of the specimens presented herein; to Dr André Nel, Muséum national d'Histoire naturelle (Paris), for his advice during a research stay at the MNHN; and to Dr Carmen Bach de Roca, Universitat Autònoma de Barcelona (Bellaterra), for aid with discussions regarding the new fossil specimens. Partial support for this work was provided by the SYNTHESYS Project (FR-TAF-3362), financed by the European Community Research Infrastructure Action under the FP7 'Capacities' Program. This study is a contribution to the Spanish Ministry of Economy and Competitiveness Projects AMBERIA CGL2014-52163, and AEI/FEDER, UE Grant CGL2017-84419 CRE; and to the Division of Entomology, University of Kansas Natural History Museum. We thank Sally Thomas and three anonymous referees for their helpful comments on an earlier draft.

DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: http://zoobank.org/References/D38B891F-4713-4FC9-8B42-EBF4578BB291

Editor. Andrew Smith

REFERENCES

AZAR, D. 2007. Preservation and accumulation of biological inclusions in Lebanese amber and their significance. *Comptes Rendus Palevol*, **6**, 151–156.

—— and NEL, A. 2013. A new beaded lacewing from a new Lower Cretaceous amber outcrop in Lebanon (Neuroptera: Berothidae). 111–130. *In* AZAR, D., ENGEL, M. S., JARZEMBOWSKI, E., KROGMANN, L. and SANTIAGO-BLAY, J. (eds). *Insect evolution in an amberiferous and stone alphabet*. Brill, Leiden.

—— PERRICHOT, V., NÉRAUDEAU, D. and NEL, A. 2003. New psychodid flies from the Cretaceous ambers of Lebanon and France, with a discussion about *Eophlebotomus connectens* Cockerell, 1920 (Diptera, Psychodidae). *Annals of the Entomological Society of America*, **96**, 117–126.

—— GÈZE, R. and ACRA, F. 2010. Lebanese amber. 271–298. *In* PENNEY, D. (ed.) *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester.

BACH DE ROCA, C. and GAJU-RICART, M. 1987. A study of the post-embronic development of *Promesomachilis hispanica* Silvestri, 1923 (Apterygota, Microcoryphia). 611–618. *In Proceedings of the 9th International Colloquium on soil Zoology*. Nauka Press, Moscow.

—— and STURM, H. 1988. Description of the male *Hypomachiloides texanus* Silvestri, 1911 (Microcoryphia: Meinertellidae). *Entomologica Scandinavica*, **19**, 193–198.

BECHLY, G. and STOCKAR, R. 2011. The first Mesozoic record of the extinct apterygote insect genus *Dasyleptus* (Insecta: Archaeognatha: Monura: Dasyleptidae) from the Triassic of Monte San Giorgio (Switzerland). *Palaeodiversity*, **4**, 23–37.

BENNER, J. S., KNECHT, R. J. and ENGEL, M. S. 2015. *Tonganoxichnus*: a revision of the ichnogenus with new material from Massachusetts. 31–43. *In* McILROY, D. (ed.) *Ichnology: papers from ICHNIA III*. Geological Association of Canada, Miscellaneous Publication, **9**.

BITSCH, J. 1994. The morphological groundplan of Hexapoda: critical review of recent concepts. *Annales de la Société Entomologique de France*, **30**, 103–129.

—— and NEL, A. 1999. Morphology and classification of the extinct Archaeognatha and related taxa (Hexapoda). *Annales de la Société Entomologique de France*, **35**, 17–29.

BÖRNER, C. 1904. Zur Systematik der Hexapoden. *Zoologischer Anzeiger*, **27**, 511–533.

CHATZIMANOLIS, S., NEWTON, A. F., SORIANO, C. and ENGEL, M. S. 2013. Remarkable stasis in a phloeocharine rove beetle from the Late Cretaceous of New Jersey (Coleoptera, Staphylinidae). *Journal of Paleontology*, **87**, 177–182.

COGNATO, A. I. and GRIMALDI, D. A. 2009. 100 million years of morphological conservatism in a bark beetle (Coleoptera: Curculionidae: Scolytinae). *Systematic Entomology*, **34**, 93–100.

DELCLÒS, X., PEÑALVER, E., ARILLO, A., ENGEL, M. S., NEL, A., AZAR, D. and ROSS, A. 2016. New mantises (Insecta: Mantodea) in Cretaceous ambers from Lebanon, Spain, and Myanmar. *Cretaceous Research*, **60**, 91–108.

ENGEL, M. S. 2009. A new Lower Permian bristletail from the Wellington Formation in Kansas (Archaeognatha: Dasyleptidae). *Transactions of the Kansas Academy of Science*, **112**, 40–44.

—— 2015. Insect evolution. *Current Biology*, **25**, R845–R875.

—— and GRIMALDI, D. A. 2002. The first Mesozoic Zoraptera (Insecta). *American Museum Novitates*, **3362**, 1–20.

—— —— 2004. New light shed on the oldest insect. *Nature*, **427**, 627–630.

—— DAVIS, S. R. and PROKOP, J. 2013. Insect wings: the evolutionary developmental origins of Nature's first flyers. 269–298. *In* MINELLI, A., BOXSHALL, G. and FUSCO, G. (eds). *Arthropod biology and evolution: molecules, development, morphology*. Springer Verlag, Berlin.

—— BREITKREUZ, L. C. V., CAI, C., ALVARADO, M., AZAR, D. and HUANG, D. 2016. The first Mesozoic microwhip scorpion (Palpigradi): a new genus and species in mid-Cretaceous amber from Myanmar. *The Science of Nature*, **103**, 19.

FRÖHLICH, A. and LU, Z. 2013. Built to break: the antenna of a primitive insect, *Petrobius brevistylis* (Archaeognatha). *Arthropod Structure & Development*, **42**, 95–106.

GADEAU DE KERVILLE, H. 1893 [1894]. Note sur les Thysanoures fossiles du genre *Machilis* et description d'une espèce nouvelle du succin (*Machilis succini* G. de K.). *Annales de la Société Entomologique de France*, **62**, 463–466.

GRANIER, B., AZAR, D., MAKSOUD, S., GÈZE, R. and HABCHI, R. 2015. New fossiliferous sites with Barremian Charophyta in the "Grès du Liban" *auct.* (Lebanon), with a critical perspective regarding the nature of *Munieria* Deecke, 1883. *Carnets de Géologie*, **15**, 199–229.

GRIMALDI, D. 2001. Insect evolutionary history from Handlirsch to Hennig, and beyond. *Journal of Paleontology*, **75**, 1152–1160.

—— and ENGEL, M. S. 2005. *Evolution of the insects*. Cambridge University Press, Cambridge, 755 pp.

—— SHEDRINSKY, A. and WAMPLER, T. P. 2000. A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey. 1–76. *In* GRIMALDI, D. (ed.) *Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey*. Backhuys Publishers, Leiden.

GRIMALDI, D. A., ENGEL, M. S. and NASCIMBENE, P. C. 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates*, **3361**, 1–72.

HAMILTON, W. D. 1978. Evolution and diversity under bark. 154–175. *In* MOUND, L. A. and WALOFF, N. (eds). *Diversity of insect faunas*. Blackwell Scientific, Oxford.

HAUG, J. T., HÄDICKE, C. W., HAUG, C. and HÖRNIG, M. K. 2015. A possible hatchling of a jumping bristletail in 50 million years old amber. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **278**, 191–199.

HENNIG, W. 1969. *Die Stammesgeschichte der Insekten*. Kramer, Frankfurt, 436 pp.

—— 1981. *Insect phylogeny*. Wiley and Sons, Chichester, 514 pp.

JERAM, A. J., SELDEN, P. A. and EDWARDS, D. 1990. Land animals in the Silurian: arachnids and myriapods from Shropshire, England. *Science*, **250**, 658–661.

KOCH, C. L. and BERENDT, G. C. 1854. Die im Bernstein befindlichen Crustaceen, Myriapoden, Arachniden und Apteren der Vorwelt. 1–124. *In* BERENDT, G. C. (ed.) *Die im Bernstein befindlichen Organischen Reste der Vorwelt. Erster Band. II. Abtheilung*. Nicolaischen Buchhandlungen, Berlin.

KUKALOVÁ-PECK, J. 1987. New Carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the role of thoracic side lobes in the origin of wings (Insecta). *Canadian Journal of Zoology*, **65**, 2327–2345.

—— 1991. Fossil history and the evolution of hexapod structures. 141–179. *In* NAUMANN, I. D. (ed.) *The insects of Australia: A textbook for students and research workers* 2nd edn, Vol. 1. Cornell University Press.

—— 1997. Arthropod phylogeny and 'basal' morphological structures. 249–268. *In* FORTEY, R. A. and THOMAS, R. H. (eds). *Arthropod relationships*. Chapman & Hall, London.

LABANDEIRA, C. C., BEALL, B. S. and HUEBER, F. M. 1988. Early insect diversification: evidence from a Lower Devonian bristletail from Québec. *Science*, **242**, 913–916.

MAKSOUD, S., AZAR, D., GRANIER, B. and GÈZE, R. 2017. New data on the age of the Lower Cretaceous amber outcrops of Lebanon. *Palaeoworld*, **26**, 331–338.

—— GRANIER, B., AZAR, D., GÈZE, R., PAICHELER, J.-C. and MORENO-BEDMAR, J. A. 2014. Revision of "Falaise de Blanche" (Lower Cretaceous) in Lebanon, with the definition of a Jezzinian regional stage. *Carnets de Géologie*, **14**, 401–427.

MENDES, L. F. 1990. *An annotated list of generic and specific names of Machilidae (Microcoryphia, Insecta) with identification keys for the genera and geographical notes*. Instituto de Investigação Científica Tropical, Estudos, Ensaios e Documentos, **155**. Lisbon. 127 pp.

—— 1997*a*. On a new fossil Microcoryphia (Insecta: Apterygota) from South-American copal. *Boletim da Sociedade Portuguesa de Entomologia*, **6**, 245–251.

—— 1997*b*. First contribution to the study of the Dominican amber Zygentoma (Insecta). Family Ateluridae. *Pedobiologia*, **41**, 40–43.

—— 1998. Second contribution to the study of the Dominican Republic amber Zygentoma (Insecta): family Lepismatidae. *Canadian Entomologist*, **130**, 899–904.

—— 2002. Taxonomy of Zygentoma and Microcoryphia: historical overview, present status and goals for the new millennium. *Pedobiologia*, **46**, 225–233.

—— and POINAR, G. O. JR 2004. A new fossil Nicoletiidae (Zygentoma, "Apterygota") in Dominican amber. *Proceedings of the Entomological Society of Washington*, **106**, 102–109.

—— —— 2008. A new fossil silverfish (Zygentoma: Insecta) in Mesozoic Burmese amber. *European Journal of Soil Biology*, **44**, 491–494.

—— and POINAR, G. JR 2013. Description of two new fossil Zygentoma from Mexico and the Dominican Republic. *Soil Organisms*, **85**, 1–9.

—— and WUNDERLICH, J. 2013. New data on thysanurans preserved in Burmese amber (Microcoryphia and Zygentoma Insecta). *Soil Organisms*, **85**, 11–22.

—— GAJU-RICART, M., MOLERO-BALTANÁS, R. and BACH DE ROCA, C. 2009. On the genera *Allomachilis* Silvestri, 1906, and *Kuschelochilis* Wygodzinsky, 1951 (Insecta: Microcoryphia). *Pesquisa Agropecuária Brasileira*, **44**, 984–987.

OLFERS, E. W. M. VON. 1907. Die "Ur-Insecten" (Thysanura und Collembola im Bernstein). *Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg*, **48**, 1–40.

PACKAUSKAS, R. J. and SHOFNER, R. M. 2010. A new species of jumping bristletails from Kansas (Microcoryphia: Meinertellidae: *Hypomachiloides* Silvestri, 1911). *Journal of the Kansas Entomological Society*, **83**, 340–346.

PEÑALVER, E. and DELCLÒS, X. 2010. Spanish Amber. 236–270. *In* PENNEY, D. (ed.) *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester.

RASNITSYN, A. P. 1999. Taxonomy and morphology of *Dasyleptus* Brongniart, 1885, with description of a new species (Insecta: Machilida: Dasyleptidae). *Russian Entomological Journal*, **8**, 145–154.

—— ARISTOV, D. S., GOROCHOV, A. V., ROWLAND, J. M. and SINITSHENKOVA, N. D. 2004. Important new insect fossils from Carrizo Arroyo and the Permo-Carboniferous faunal boundary. *Bulletin of the New Mexico Museum of Natural History & Science*, **25**, 215–246.

REMINGTON, C. 1954. The suprageneric classification of the order Thysanura (Insecta). *Annals of the Entomological Society of America*, **47**, 277–286.

—— 1955. The "Apterygota". 495–505. *In* KESSEL, E. L. (ed.) *A century of progress in the natural sciences (1853–1953)*. California Academy of Sciences, San Francisco.

RIQUELME, F., MONTEJO-CRUZ, M., LUNA-CASTRO, B. and ZUÑIGA-MIJANGOS, L. 2015. Fossil jumping-bristletail from the Chiapas amber: *Neomachilellus* (*Praeneomachilellus*) *ezetaelenensis* sp. nov. (Microcoryphia: Meinertellidae). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **275**, 93–106.

SÁNCHEZ-GARCÍA, A. and ENGEL, M. S. 2016*a*. Long-term stasis in a diverse fauna of Early Cretaceous springtails (Collembola: Symphypleona). *Journal of Systematic Palaeontology*, **15**, 513–537.

—— —— 2016*b*. Springtails from the Early Cretaceous amber of Spain (Collembola: Entomobryomorpha), with an annotated checklist of fossil Collembola. *American Museum Novitates*, **3862**, 1–47.

SHAROV, A. 1948. Triassic Thysanura from the Ural forelands. *Doklady Akademii Nauk, SSSR*, **61**, 517–519. [In Russian]

—— 1957. Distinctive Paleozoic wingless insects of a new order Monura (Insecta, Apterygota). *Doklady Akademii Nauk, SSSR*, **115**, 795–798. [In Russian]

SHEAR, W. A., BONAMO, P. M., GRIERSON, J. D., ROLFE, W. D., SMITH, E. L. and NORTON, R. A. 1984. Early land animals in North America: evidence from Devonian age arthropods from Gilboa, New York. *Science*, **224**, 492–494.

SILVESTRI, F. 1911. Contributo alla conoscenca dei Machilidae dell' America settentrionale. *Bolletino del Laboratorio di Zoologia Generale e Agraria Della Facoltà Agraria in Portici*, **5**, 324–350.

—— 1912. Die Thysanuren des baltischen Bernsteins. *Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg*, **53**, 42–66.

SINITSHENKOVA, N. D. 2000. A review of Triassic mayflies, with description of new species from western Siberia and Ukraine (Ephemerida = Ephemeroptera). *Paleontological Journal*, **34**, S275–S283.

STURM, H. and BACH DE ROCA, C. 1988. Archaeognatha (Insecta) from the Krakatau Islands and the Sunda Strait area, Indonesia. *Memoirs of the Museum of Victoria*, **49**, 367–383.

—— —— 1992. New American Meinertellidae (Archaeognatha, Machiloidea). *Pan-Pacific Entomologist*, **68**, 174–191.

—— —— 1993. On the systematics of the Archaeognatha (Insecta). *Entomologia Generalis*, **18**, 55–90. 7

—— and MACHIDA, R. 2001. Archaeognatha. 1–213. *In* KRISTENSEN, N. P. and BEUTEL, R. G. (eds). *Handbuch der Zoologie, Band IV, Arthropoda: Insecta, Teilband 37*. Walter de Gruyter, Berlin.

—— and MENDES, L. F. 1998. Two new species of Nicoletiidae (Zygentoma, "Apterygota", Insecta) in Dominican amber. *American Museum Novitates*, **3226**, 1–11.

—— and POINAR, G. O. JR 1997. A new *Neomachilellus* species from Miocene amber of the Dominican Republic and its phylogenetic relationships (Archaeognatha: Meinertellidae). *Entomologia Generalis*, **22**, 157–170.

—— —— 1998. *Cretaceomachilis libanensis*, the oldest known bristle-tail of the family Meinertellidae (Machiloidea, Archaeognatha, Insecta) from the Lebanese amber. *Deutsche Entomologische Zeitschrift*, **45**, 43–48.

VERHOEFF, K. W. 1905. Über vergleichende Morphologie des Kopfes niederer Insekten mit besonderer Berücksichtigung der Dermapteren und Thysanuren, nebst biologisch-physiologischen Beiträgen. *Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum [Abhandlungen der Kaiserlichen Leopoldinisch– Carolinischen Deutschen Akademie der Naturforscher]*, **84**, 1–126.

—— 1910. Dber felsenspringer, Machiloidea IV. systematik und orthomorphose. *Zoologischer Anzeiger*, **36**, 425–438.

WYGODZINSKY, P. 1971. A note on a fossil machilid (Microcoryphia) from the amber of Chiapas, Mexico. *University of California Publications in Entomology*, **63**, 101–102.

ZHANG, W., LI, H., SHIH, C., ZHANG, A. and REN, D. 2018. Phylogenetic analyses with four new Cretaceous bristletails reveal inter-relationships of Archaeognatha and Gondwana origin of Meinertellidae. *Cladistics*, **34**, 384–406.