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Geodiversitas is a fast track journal published by the Museum Science Press, Paris

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diff.pub@mnhn.fr / <http://sciencepress.mnhn.fr>

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ISSN (imprimé / *print*): 1280-9659/ ISSN (électronique / *electronic*): 1638-9395

A 100-million-year-old ensiferan with unusual mouthparts and comments on the evolution of raptorial appendages within Polyneoptera

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Submitted on 7 August 2019 | accepted on 19 September 2020 | published on 27 January 2022

urn:lsid:zoobank.org:pub:CAF128F4-1301-4620-8BB1-17A668A32723

Haug J. T., Hörnig M. K., Kiesmüller C., Pazinato P. G., Baranov V. & Haug C. 2022. — A 100-million-year-old ensiferan with unusual mouthparts and comments on the evolution of raptorial appendages within Polyneoptera. *Geodiversitas* 44 (4): 57-73. <https://doi.org/10.5252/geodiversitas2022v44a4>. <http://geodiversitas.com/44/4>

ABSTRACT

Myanmar amber is known to provide fossils of the group Insecta with surprising morphologies. Here we present fossils of the new species *Gryllobencain patrickmuelleri* n. gen., n. sp. from Myanmar amber that possess an overall “orthopteroid” morphology, hence resemble crickets. Unlike in most crickets, thorax appendages 1 and 2 (“legs”) are large and prominent, even in comparison to thorax appendage 3. Furthermore, thorax appendages 1 and 2 are able to fold against themselves and are armed with prominent spine-like setae, indicating that these legs were originally used for grasping prey. Most prominent is a large spine on the tibia of both appendages distantly reminding of the tibial spur or claw of praying mantises. Comparable prey-catching apparatuses have evolved repeatedly in the group Polyneoptera: gladiators (Mantophasmatodea), three ingroups of bush-crickets (Saginae, Austrosaginae, Listrosceledinae) as well as one species of fossil mantises (*Santanmantis axelrodi* Grimaldi, 2003) appear to have used thorax appendages 1 and 2 for prey catching. The new fossils do not seem to be closely related to any of these groups. They differ especially by prominent cerci equipped with numerous, probably mechano-sensorial setae. In the other five groups, the cerci are significantly smaller, often indistinct. The fossils furthermore have prominent maxillae with sickle-shaped proximal parts and well-armed large palps, indicating that the maxillae played an important role in processing the prey. While the thorax appendages hence represent a case of clear convergent evolution, the uniqueness of the feeding apparatus leads us to recognise the fossils as a highly specialised new species.

KEY WORDS

Orthoptera,
Ensifera,
Myanmar amber,
Burmese amber,
predatory cricket,
bush-crickets,
Cretaceous,
new genus,
new species.

RÉSUMÉ

Un ensifère vieux de 100 millions d'années avec des parties inhabituelles de la bouche et commentaires sur l'évolution des appendices préhensibles chez les polynéoptères.

L'ambre du Myanmar est connu pour fournir des fossiles du groupe Insecta avec des morphologies surprenantes. Nous présentons ici des fossiles de la nouvelle espèce *Gryllobencaïn patrickmuelleri* n. gen., n. sp. provenant de l'ambre du Myanmar, qui possèdent une morphologie générale « orthoptéroïde », et ressemblent donc aux grillons. Contrairement à la plupart des grillons, les appendices 1 et 2 du thorax (« pattes ») sont grands et proéminents, même en comparaison avec l'appendice 3 du thorax. De plus, les appendices 1 et 2 du thorax sont capables de se replier sur eux-mêmes et sont armés de setae proéminentes ressemblant à des épines, ce qui indique que ces pattes étaient à l'origine utilisées pour saisir des proies. La plus importante est une grande épine sur le tibia des deux appendices qui rappelle de loin l'éperon tibial ou la griffe des mantes religieuses. Des dispositifs comparables de capture de proies ont évolué à plusieurs reprises dans le groupe des polynéoptères : les gladiateurs (Mantophasmatodea), trois groupes de grillons des bois (Saginae, Austrosaginae, Listrosclidinae) ainsi qu'une espèce de mantes fossiles (*Santanmantis axelrodi* Grimaldi, 2003) semblent avoir utilisé les appendices 1 et 2 du thorax pour attraper leurs proies. Les nouveaux fossiles ne semblent pas être étroitement liés à l'un de ces groupes. Ils diffèrent surtout par des cerques proéminents équipés de nombreuses setae, probablement mécanosensorielles. Chez les cinq autres groupes, les cerques sont nettement plus petits, souvent indistincts. Les fossiles présentent en outre des maxillaires proéminents avec des parties proximales en forme de faucille et de grands palpes bien armés, ce qui indique que les maxillaires jouaient un rôle important dans la transformation des proies. Alors que les appendices du thorax représentent un cas clair d'évolution convergente, le caractère unique de l'appareil alimentaire nous amène à reconnaître les fossiles comme une nouvelle espèce hautement spécialisée.

MOTS CLÉS

Orthoptera,
Ensifera,
ambre du Myanmar,
ambre de Birmanie,
grillon prédateur,
grillons des buissons,
Crétacé,
genre nouveau,
espèce nouvelle.

INTRODUCTION

Insecta is an extremely species-rich group of organisms. While the general statement that it represents the most successful group of animals is logically false (see Haug *et al.* 2016), its myriads of representatives, from silverfish to butterfly, indeed dominate our modern-day terrestrial ecosystems. Naturally, they fulfil numerous different ecological roles. Some forms, such as the iconic praying mantis, have specialised in catching and consuming their relatives, i.e. other representatives of Insecta, and hence are fierce predators.

Our modern-day fauna is also unsurprisingly dependent on the diversity of the myriad representatives of Insecta. Hence an apparent decline of this diversity has become recognised even by non-specialists. To better understand processes of loss and gain of diversity, the fossil record in principle offers a valuable data set to tackle questions of changes in diversity over time. Luckily, we have especially exquisite types of fossil preservation for the many forms of Insecta in certain time slices. One hot spot in this aspect is Myanmar amber (also known as Burmese amber or Burmite) which is about 100 million years old. This amber site has provided so far quite astonishing findings, including rather modern appearing forms such as different types of hymenopterans (recent review in Zhang *et al.* 2018) or butterflies (Mey 2011; Zhang *et al.* 2017), quite old appearing forms such as certain types of damselflies (e.g., Bechly & Poinar 2013; Zheng *et al.* 2017) or cicadas (Jiang *et al.* 2019) (and also non-insectans, such as the spider *Chimerarachne yingi* Wang, Dunlop, Selden, Garwood, Shear, Müller & Lei, 2018; Wang *et al.* 2018), and

unusual and unexpected “experimental” forms such as different neuropteran larvae (e.g., Badano *et al.* 2018; Haug *et al.* 2019a, b) or different species of Dictyoptera (*Manipulator modificaputis* Vršanský & Bechly, 2015; Vršanský & Bechly 2015; *Alienopterus brachyelytrus* Bai, Beutel, Klass, Zhang, Yang & Wipfler, 2016; Bai *et al.* 2016; *Caputoraptor elegans* Bai, Beutel, Zhang, Wang, Hörnig, Gröhn, Yan, Yang & Wipfler, 2018; Bai *et al.* 2018).

Among the various species of Insecta preserved in Myanmar amber there are also numerous forms that can be identified as predatory species, revealing also parts of their original ecological function (examples: representatives of Dictyoptera: Vršanský & Bechly 2015; Delclòs *et al.* 2016; Bai *et al.* 2016, 2018; representatives of Neuroptera: Badano *et al.* 2018; Haug *et al.* 2019a). Recognising a fossil individual as predatory can be based on several arguments (which also apply to other forms of behaviour in fossil animals, e.g., parasitism, see criteria in Nagler *et al.* 2016 and Serrano-Sánchez *et al.* 2016):

Argument 1: An ingroup position of a species in a group that has modern representatives that exclusively show predatory behaviour (see also ‘phylogenetic bracketing’ concept; Witmer 1995). Important in this aspect are the details of relationship, or if it is a true ingroup position: species branching off a lineage towards the modern forms (often termed “stem-group” forms, but see ambiguities of this term in Donoghue 2005) might not yet show the highly specialised behaviour of its modern representatives. One tricky example is the case of Alienoptera, a group exclusively known from Myanmar amber closely related to praying mantises (Bai *et al.* 2016). These forms might have been predatory, but the phylogenetic

signal is unclear in this aspect. Deeper ingroup positions, on the other hand, provide a rather robust indication. Certain forms found in Myanmar amber have a deep ingroup position and hence are easier to interpret in this aspect, such as numerous larvae of lacewings and their relatives (e.g., Wang *et al.* 2016; Badano *et al.* 2018; Haug *et al.* 2019a) or praying mantises (Delclòs *et al.* 2016).

Argument 2: A fossil “caught in the act”. This means nothing less than a specimen being trapped in amber while directly stinging, grabbing or chewing on another specimen. Such cases have only been extremely rarely reported. Yet, they represent the most direct case of indication of a predatory lifestyle (Arillo 2007; Boucot & Poinar 2010; Poinar & Buckley 2012). On the contrary, examples of parasitism seem relatively common (e.g., Weitschat & Wichard 1998; Arillo 2007; Gröhn 2015).

Argument 3: A fossil “caught in the act”, but still on its way. This case is related to the last one but is one step more indirect. Hence such cases are preserved situations that precede the true act of predation. An example preserved in Myanmar amber is a larva of a mantis lacewing climbing onto a spider (Haug *et al.* 2018). In modern forms the larva later on will prey on the eggs produced by the spider.

Argument 4: Functional morphology. This means that a fossil possesses a specific morphology that is indicative of a predatory lifestyle. This is the most indirect type of indication, nevertheless an important one. The true challenge for such a case is if it cannot be easily combined with another aspect. As mentioned above, lacewing larvae in amber are identified as predators based on their systematic position, yet this is furthermore supported by the morphology of their massive mouthparts. Related, but less strict, are cases of forms further down the tree, i.e. branching off a lineage towards the modern forms (see above). Yet, if we find morphological indications for a predatory lifestyle in such forms the case also is quite sound. Truly challenging are forms that are in a more isolated position or possess (at first) strange appearing structures that are not easy to interpret in which way they might have functioned (e.g., Hörnig *et al.* 2017; Bai *et al.* 2018).

Here we report some new fossils from Myanmar amber which possess structures that appear to have been used in predatory actions. We discuss which aspects of the morphology indicate a predatory lifestyle, possible relationships, and the implications on the evolution of raptorial appendages within Polyneoptera.

MATERIAL AND METHODS

MATERIAL

In the centre of this study are four specimens preserved in Myanmar amber. Two specimens are deposited in the collection of the Palaeo-Evo-Devo (PED) Research Group, Ludwig-Maximilians-Universität München, Germany, under repository number PED 0147 (Figs 1-3) and PED 0178 (Fig. 4). Two additional specimens come from the collection of Patrick Müller, Zweibrücken (Figs 5; 6).

METHODS

The specimen has been documented with different imaging techniques. In all cases distilled water was used as immersion liquid, and a cover slip was placed on top of the amber piece to create an even surface, further reducing distortions.

Overview images were recorded with a Keyence VHX-6000 digital microscope, either with ring light illumination or cross-polarised co-axial illumination (as e.g., in Haug *et al.* 2018, 2019a; inspired by Schaarschmidt 1973; Bengtson 2000). All images are composite images; each image detail was documented with a stack of images (frames) of differing focal planes which were fused to a single sharp image (e.g., Haug *et al.* 2011; Kerp & Bomfleur 2011) with the built-in software. Several adjacent image details were stitched to a large panorama image with the built-in software, resulting in a high-resolution image. Additionally, the HDR function was employed (cf. Haug *et al.* 2013), i.e. each single frame is a composite from several images under different exposure times; the resulting image contains all information without too dark or too bright regions in the image.

The description follows the concepts of describing the animal segment by segment, structure by structure (Haug *et al.* 2012). Insectan terminology is provided in combination with the more general euarthropodan terminology (the latter in squared brackets); if the correspondence to euarthropodan terminology is not entirely clear, a question mark is added. This will allow also non-expert readers to follow and is thought to form a basis for larger-scaled approaches, following earlier attempts (e.g., Haug *et al.* 2018, 2019b).

RESULTS

POLYNEOPTERA Martynov, 1938

ORTHOPTERA Olivier, 1789

ENSIFERA Chopard, 1920

REMARK

Due to the rather unique morphology of the new specimens it is currently not possible to provide a more accurate systematic interpretation. Long antennae and prominent cerci are consistent with interpreting them as representatives of Ensifera.

Gryllobencain n. gen.

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TYPE SPECIES. — *Gryllobencain patrickmuelleri* n. sp.

DERIVATIO NOMINIS. — ‘Gryllo’ for cricket; ‘ben’ is Hebrew for ‘son of’ and provides connection to the next part of the name; ‘cain’ for the biblical figure. According to some legends, the children of Cain became the vampires. The name hence means ‘vampire cricket’ in reference to the prominent sickle-shaped proximal parts of the maxilla, distantly reminding of vampire teeth.

DIAGNOSIS. — As for the species.

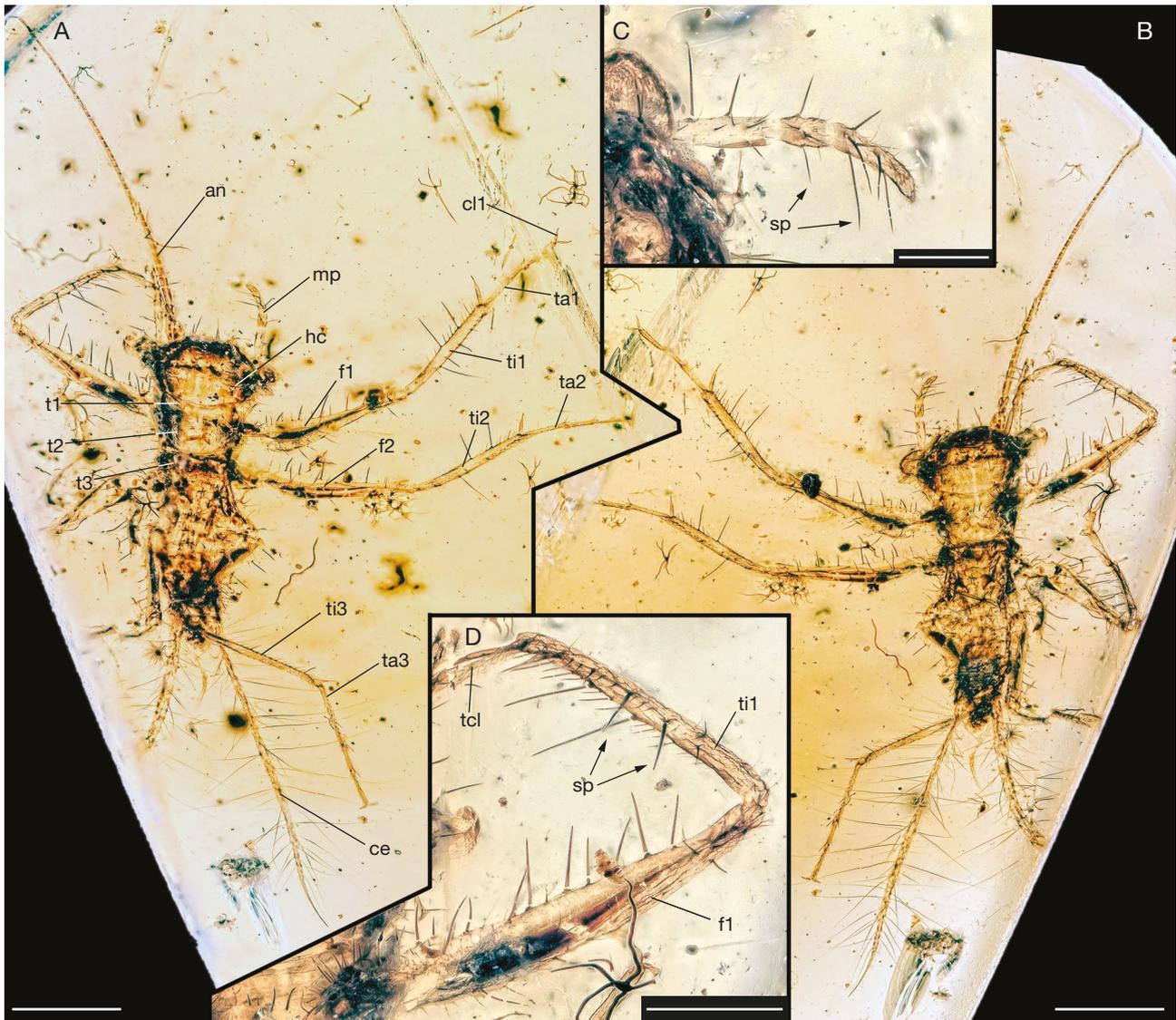


FIG. 1. — Holotype of *Gryllobencain patrickmuelleri* n. gen., n. sp., PED 0147: **A**, overview in dorsal view; **B**, overview in ventral view; **C**, close-up on maxillary palp, distal part; **D**, close-up on thorax appendage 1. Abbreviations: **an**, antenna; **ce**, cercus; **cl1**, claw of thorax appendage 1; **f1-2**, femur of thorax appendage 1-2; **hc**, head capsule; **mp**, maxillary palp; **sp**, spine-like seta; **t1-3**, thorax segment 1-3; **ta1-3**, tarsus of thorax appendage 1-3; **tcl**, tibia claw; **ti1-3**, tibia of thorax appendage 1-3. Scale bars: A, B, 1 mm; C, 0.25 mm; D, 0.5 mm.

REMARK

The current version of the International Code of Zoological Nomenclature demands that a newly described species is assigned to a genus. Due to the uncertainty of relationship and the apparent unique combination of characters of the new fossils we cannot assign them to any known genus. We therefore must erect a new one. While it is in principle possible to avoid creating this factually unnecessary additional category and we generally support the idea to not erect a new genus in such a case, we here provide a classical approach for the convenience of readers used to this approach. We still want to point out that the uncertainty concerning relationship could much better be expressed with the combination of the next higher group (in this case '*Ensifera patrickmuelleri*', see for this approach discussion in Haug & Haug 2016 and references therein; Wagner *et al.* 2019).

Gryllobencain patrickmuelleri n. gen., n. sp.

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HOLOTYPE. — PED 0147.

PARATYPE. — PED 0178.

ADDITIONAL MATERIAL. — BUB 3072, 3073, from the collection of Patrick Müller.

DERIVATIO NOMINIS. — In honour of Patrick Müller and his effort for research, especially on Myanmar amber.

DIAGNOSIS. — Specimen with prominent maxillae [maxillulae]; medio-proximal part prominent sickle-shaped; palp prominent with long and strong setae; foreleg and mid leg [thorax appendages 1 and 2] with many long and strong setae mostly medially, on femur and

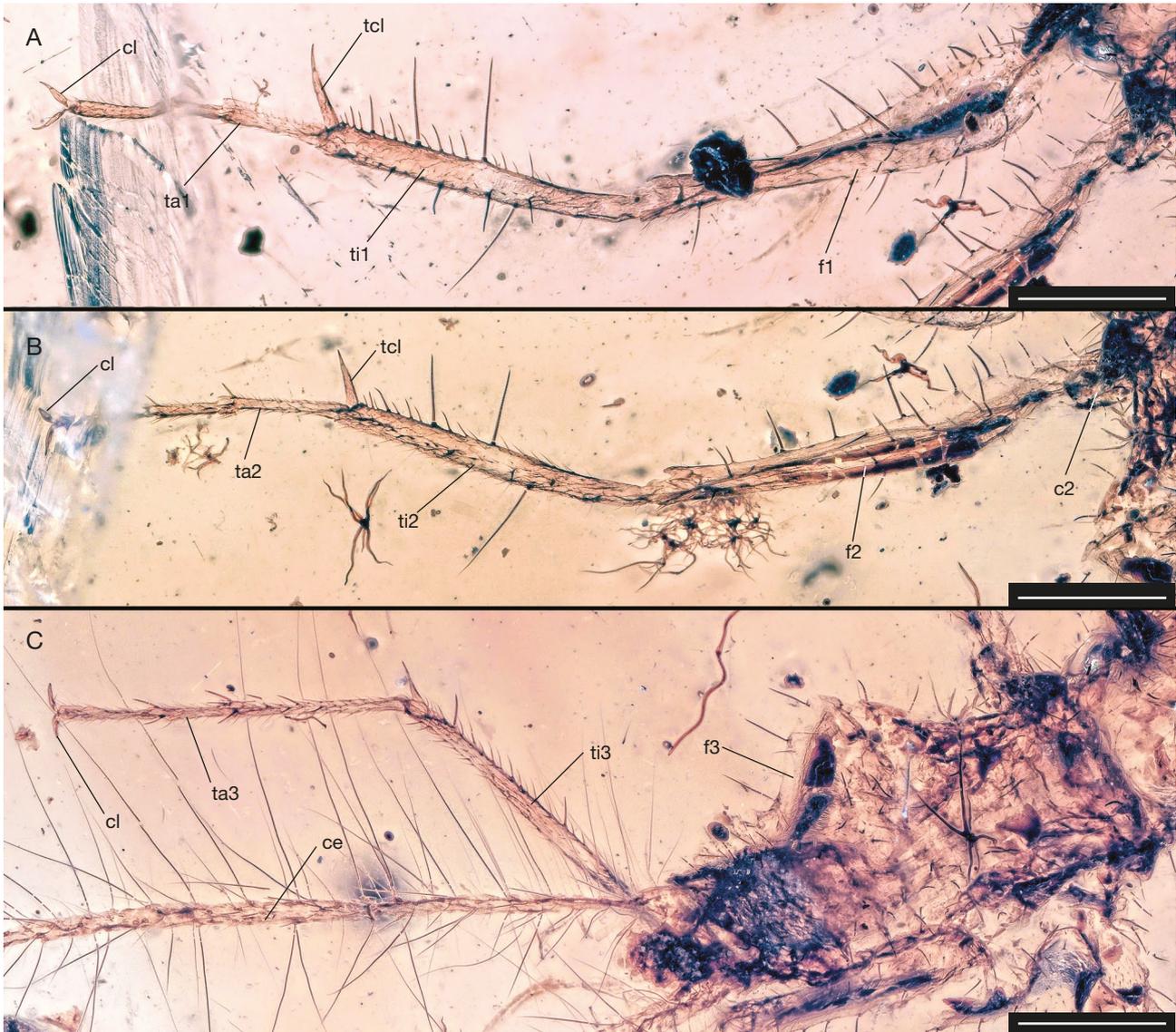


FIG. 2. — Holotype of *Gryllobencain patrickmuelleri* n. gen., n. sp., PED 0147, close-up on thorax appendages: **A**, thorax appendage 1; **B**, thorax appendage 2; **C**, thorax appendage 3. Abbreviations: **c2**, coxa of thorax appendage 2; **ce**, cercus; **cl**, claw of thorax appendage; **f1-3**, femur of thorax appendage 1-3; **ta1-3**, tarsus of thorax appendage 1-3; **tcl**, tibia claw; **ti1-3**, tibia of thorax appendage 1-3. Scale bars: 0.5 mm.

tibia. Tibia additionally with strong disto-medial spur-like spine. Cerci prominent with numerous very long and strong setae.

DESCRIPTION

General

Body organised into head and trunk, the latter subdivided into thorax and abdomen (Figs 1A, B; 4A, C; 5A, C; 6A, C), presumably with 20 segments, ocular segment plus 19 post-ocular segments.

Head

Ocular segment and post-ocular segments 1-5 forming distinct capsule (head capsule) (Figs 1A; 4A; 5A; 6A). Head capsule oval in dorsal (or ventral) view; about 1.6× wider than long. Surface of head capsule dorsally with prominent Y-shaped moulting suture (epicranial suture) (Fig. 5A). Lateral edges of head capsule rounded with few setae.

Ocular segment recognisable by prominent compound eyes laterally projecting from the head capsule; additionally, three ocelli present [median eyes] (Fig. 5B). Compound eyes with numerous facets; difficult to count, at least 40 rows of facets (Fig. 7A, B). Ocelli arranged in a triangle; central ocellus dorsal to lateral ones. Appendage derivative of ocular segment (clypeo-labrum complex) [hypostome-labrum complex] well developed (Fig. 7D). Clypeus [hypostome] rectangular, about 2× wider than long. Labrum lobe-like, about as large as clypeus, anterior edge gently rounded.

Post-ocular segment 1 recognisable by its appendage, antenna [antennula]. Antenna arising from head capsule antero-dorsally; lateral to the clypeus; very long, longer than main body, with numerous elements (antennomeres), more than 40 (Figs 1A, B; 5A, C); some elements are longer and possess a distinct constriction (indication of future subdivision?); length of

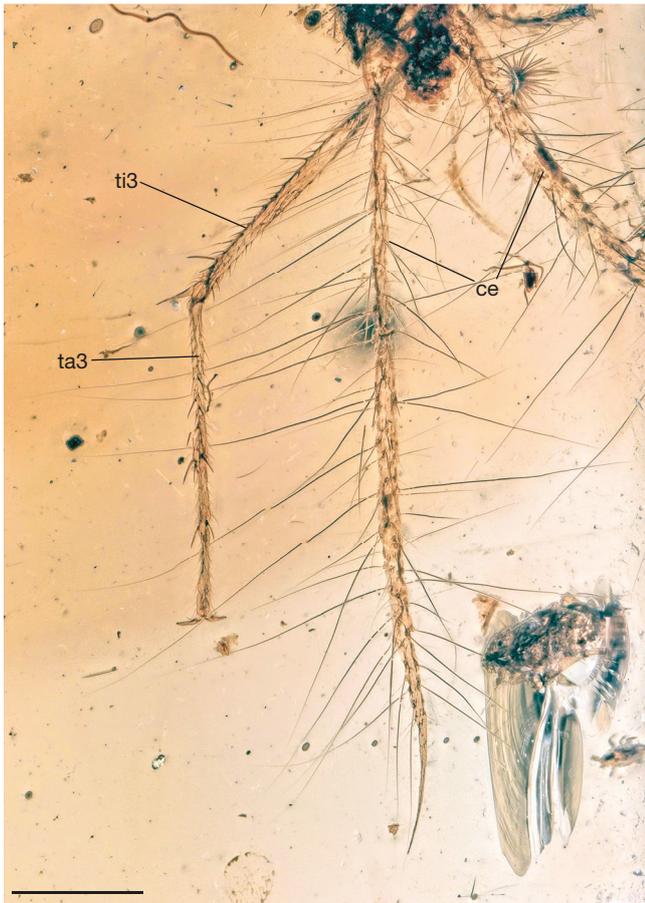


FIG. 3. — Holotype of *Gryllobencaïn patrickmuelleri* n. gen., n. sp., PED 0147, close-up on posterior end with thorax appendage 3 and cerci. Abbreviations: **ce**, cercus; **ta3**, tarsus of thorax appendage 3; **ti3**, tibia of thorax appendage 3. Scale bar: 0.5 mm.

elements strongly varying; proximal elements with few, but prominent setae. More distal elements with numerous, but shorter setae. Post-ocular segment 2 (intercalary segment) not recognisable externally.

Post-ocular segment 3 recognisable by its appendage, mandible (Fig. 7A-D). Mandibles prominent, curved, bearing teeth on inner surface.

Post-ocular segment 4 recognisable by its appendage, maxilla [maxillula] (Fig. 7A-F). Proximal part of maxilla (cardo) [basipod?] medially drawn out; cardo distally carrying palp [endopod]. Drawn out part (cardo? stipes? both?) prominent, sickle-shaped; laterally with at least three setae. Palp with five elements (Figs 1C; 6D; 7F). Element 1 (most proximal one) short, as long as wide (diameter). Element 2 sub-similar to element 1. Element 3 elongate, at least 4.5× longer than wide (diameter); with at least two strong spine-like setae and numerous smaller setae of varying sizes. Element 4 shorter than preceding element, elongate, at least 2.8× longer than wide (diameter); with at least two strong spine-like setae and numerous smaller setae of varying sizes. Element 5 (most distal one) elongate, about 4× longer than wide (diameter); with at least six strong spine-like setae and numerous smaller setae of varying sizes.

Post-ocular segment 5 recognisable by its appendage, labium [maxilla] (Fig. 7E, F); only distal parts, palp [endopod], apparent. Palp mostly concealed, with numerous setae.

Thorax [anterior trunk]

Post-ocular segments 6-8 differentiated from posterior ones, forming a distinct unit, thorax (Fig. 5A). Tergite of post-ocular segment 6 (tergite of thorax segment 1; pronotum) about 0.55× narrower than head; about 1.6× wider than long; rectangular-shaped in dorsal view; with six smaller setae medio-anteriorly. Post-ocular segment 6 (thorax segment 1; prothorax) ventrally with a pair of prominent appendages (foreleg) [thoracopod 1] (Figs 1D; 2A; 4B, D; 5D); basically cylindrical, composed of five elements.

Element 1 (coxa) [basipod?] about as long (proximal-distal axis) as wide (diameter); with at least three smaller, thin setae posteriorly. Element 2 (trochanter) [endopod element 1?] slightly longer than wide, slightly longer than coxa; with more than nine small, thin setae medially. Element 3 (femur) [endopod element 2?] very elongate; about 10× longer than coxa, similar width at proximal part, tapering towards distally to about 0.48× of maximum width; with more than ten small, thin setae proximo-medially and disto-laterally; also with more than ten strong spine-like setae arranged in two rows (Fig. 4D), the majority of which is located proximally, with one exception disto-laterally. Element 4 (tibia) [endopod element 3?] elongate, about 0.75× the length of the femur; about as wide as the femur, though slightly less proximally; covered with smaller setae, more distally than proximally; with three strong spine-like setae disto-medially of varying size and one strong spine-like seta laterally, more towards proximal than distal; with one very strong spine very medio-distally. Element 5 (tarsus) [endopod element 4?] slightly shorter than preceding element, more than 0.8× of the length and about half of the width; with numerous smaller, thin setae throughout its surface; distally with a pair of claws, possible attachment structure between claws not apparent; tarsus subdivided into three sub-elements (tarsomeres) which are of mostly similar length (0.3× of total length) and similar width, most proximal element has three stronger spine-like setae distally.

Post-ocular segment 7 (thorax segment 2; mesothorax) about half as long as prothorax and about as wide as the latter, but slightly tapering posteriorly; trapezoid-shaped; with one small seta on each side respectively (antero-laterally), close to the coxa. Ventrally with a pair of prominent appendages (mid leg) [thoracopod 2] (Fig. 2B); basically cylindrical, composed of five elements; as a whole slightly longer than foreleg [thoracopod 1].

Element 1 (coxa) [basipod?] about as long (proximal-distal axis) as wide (diameter); with two smaller setae medially. Element 2 (trochanter) [endopod element 1?] slightly longer than wide, but as wide as the coxa; with one small, thin seta and two stronger, spine-like setae medio-distally. Element 3 (femur) [endopod element 2?] very elongate; about 10× longer than coxa, almost similar width at proximal part, then widening to 1.5× width at about 30 % of total femur length,

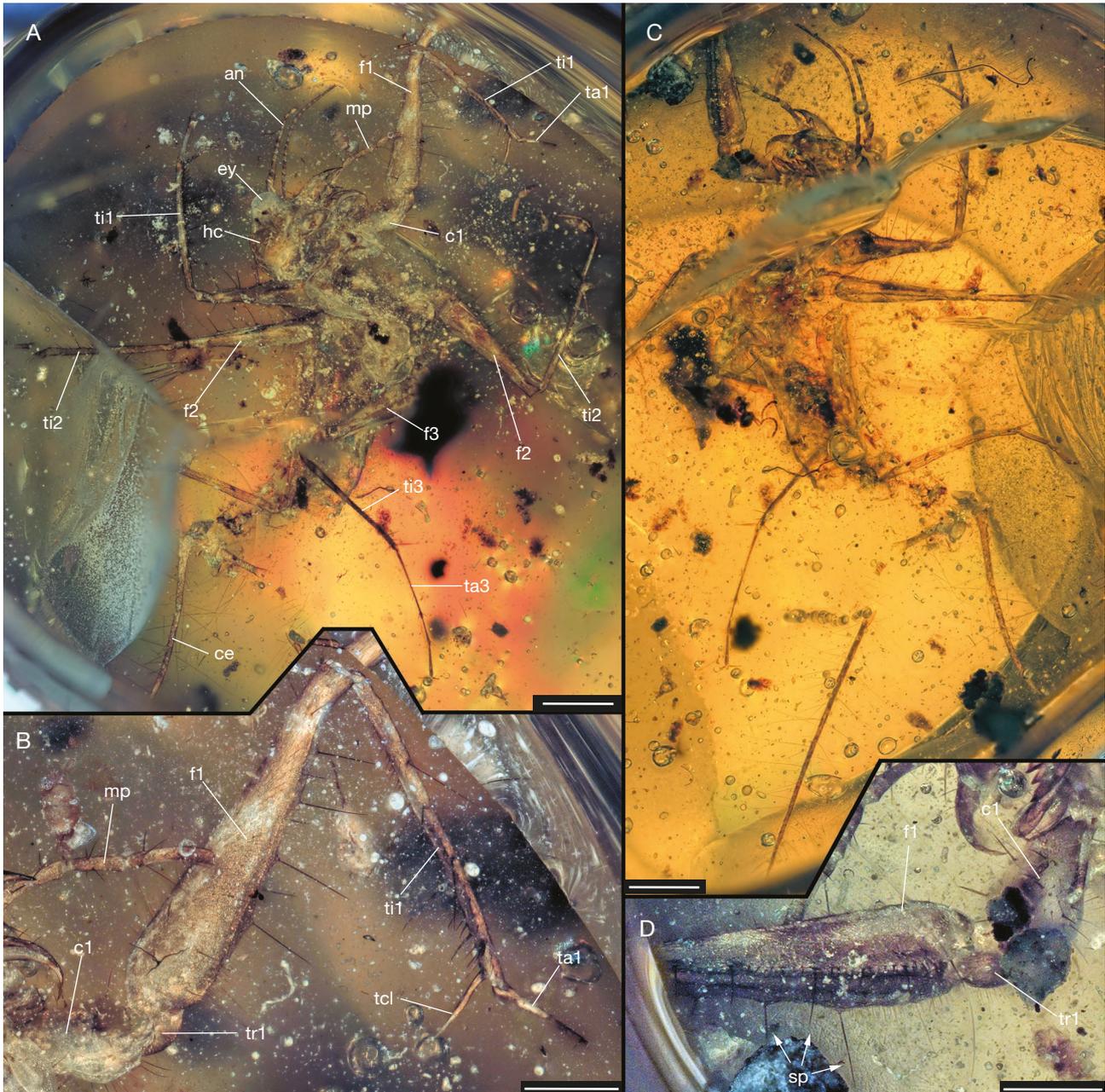


FIG. 4. — Paratype of *Gryllobencain patrickmuelleri* n. gen., n. sp., PED 0178: **A**, overview in dorso-lateral view; **B**, detail of thorax appendage 1 in posterior view; **C**, overview in ventro-lateral view; **D**, detail of thorax appendage 1 in anterior view. Abbreviations: **an**, antenna; **c1**, coxa of thorax appendage 1; **ce**, cercus; **ey**, compound eye; **f1-3**, femur of thorax appendage 1-3; **hc**, head capsule; **mp**, maxillary palp; **sp**, spine-like seta; **ta1, 3**, tarsus of thorax appendage 1, 3; **tcl**, tibia claw; **ti1-3**, tibia of thorax appendage 1-3; **tr1**, trochanter of thorax appendage 1. Scale bars: A, C, 1 mm; B, D, 0.5 mm.

then tapering towards distally to about 0.67× of maximum width; with more than ten small, thin setae laterally throughout its surface; also with more than ten strong spine-like setae with varying sizes, the majority of which located medially, with one exception laterally. Element 4 (tibia) [endopod element 3?] elongate, slightly shorter than femur; about as wide as femur, though slightly less so proximally; covered with smaller setae, more distally than proximally; with two strong spine-like setae and more than five smaller spine-like setae disto-medially; also with one strong spine-like seta laterally, more towards proximal than distal, and one very strong spine

very medio-distally. Element 5 (tarsus) [endopod element 4?] slightly shorter than tibia, more than 0.8× of the length and about half of the width; with numerous smaller, thin setae throughout; distally with a pair of claws, possible attachment structure between claws not apparent; tarsus subdivided into three sub-elements which are of mostly similar length (0.3× of total length) and similar width.

Post-ocular segment 8 (thorax segment 3; metathorax) about 1.4× longer than preceding segment and about as wide as that as well; rectangular shaped. Ventrally with a pair of prominent appendages (hind leg) [thoracopod 3] (Figs 2C; 3); basically



FIG. 5. — *Gryllobencain patrickmuelleri* n. gen., n. sp., BUB 3073: **A**, overview in dorsal view; **B**, close-up in anterior head area with ocelli; **C**, overview in ventral view; **D**, close-up on distal part of thorax appendage 1. In A and C background was desaturated to enhance contrast. Abbreviations: **an**, antenna; **ce**, cercus; **cl**, claw of thorax appendage; **f1-3**, femur of thorax appendage 1-3; **mp**, maxillary palp; **oc**, ocelli; **ta1**, tarsus of thorax appendage 1; **ti1-3**, tibia of thorax appendage 1-3. Scale bars: A, C, 0.5 mm; B, D, 0.1 mm.

cylindrical, composed of supposedly five elements; slightly longer than mid leg [thoracopod 2].

Element 1 (coxa [basipod?]) not differentiable from next element, i.e. element 2 (trochanter) [endopod element 1?]. Proximal region (coxa + trochanter?) slightly longer than wide. Element 3 (femur) [endopod element 2?] very elongate; about 8× longer than proximal region, similar width as preceding element, but tapering slightly distally; with four strong spine-like setae laterally. Element 4 (tibia) [endopod element 3?] elongate, but about 0.8× shorter than femur; about 0.67× the width of the femur, tapering slightly distally;

covered with smaller setae and stronger spine-like setae; no very strong spine very medio-distally, but with one strong spine-like seta on a similar position as on the tibia of fore and mid legs, but shorter than in the latter. Element 5 (tarsus) [endopod element 4?] as long as tibia and slightly less wide than that as well; with numerous smaller, thin setae throughout; distally with a pair of claws, possible attachment structure between claws not apparent; tarsus subdivided into three sub-elements which are of similar width, but with varying length (from proximal to distal: 0.52×, 0.22× and 0.26× of total length).

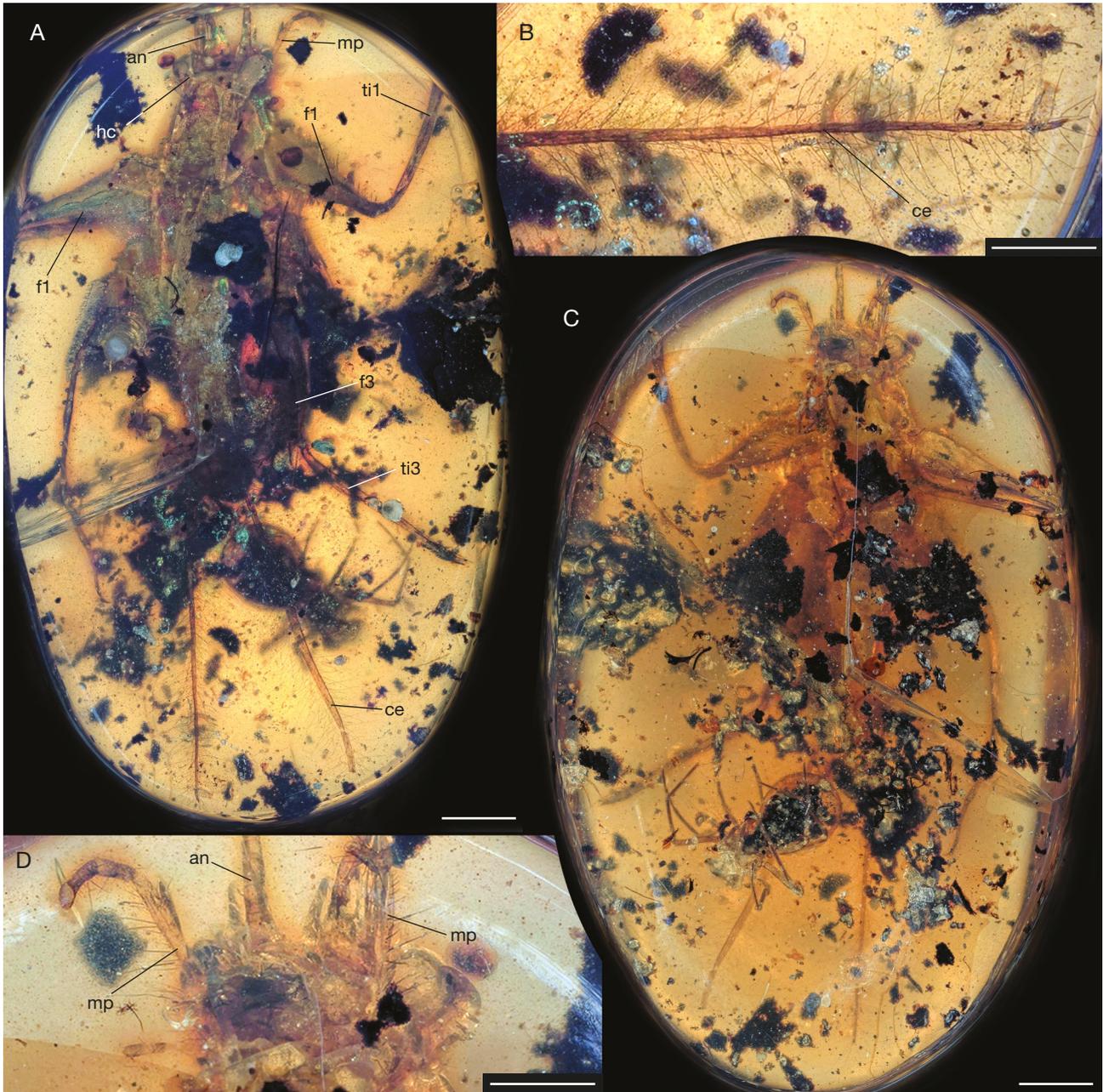


FIG. 6. — *Gryllobencain patrickmuelleri* n. gen., n. sp., BUB 3072: **A**, overview in dorsal view; **B**, close-up on cercus; **C**, overview in ventral view; **D**, close-up on head. Abbreviations: **an**, antenna; **ce**, cercus; **f1**, **3**, femur of thorax appendage 1, 3; **hc**, head capsule; **mp**, maxillary palp; **ti1**, **3**, tibia of thorax appendage 1, 3. Scale bars: A, C, 1 mm; B, D, 0.5 mm.

Abdomen [posterior trunk]

Post-ocular segments 9-19 differentiated from further anterior ones, forming distinct unit (abdomen; not corresponding to abdomen in other crustacean groups) (Figs 1A, B; 5A, C).

Only eight distinct units differentiable, first seven probably corresponding to abdominal segments 1 to 7, rectangular-shaped. Last unit most likely corresponding to several abdomen segments (8-11?), triangular-shaped.

Post-ocular segment 9 (abdomen segment 1) about 1.4× longer than metathorax; but less wide, about 0.67× of metathorax width; one spine-like seta postero-laterally on each side.

Post-ocular segment 10 (abdomen segment 2) similar to preceding segment, but very slightly shorter and slightly wider posteriorly (widening posteriorly); one spine-like seta postero-laterally on each side.

Post-ocular segment 11 (abdomen segment 3) about half as long, but as wide as the preceding segment; one spine-like seta postero-laterally respectively.

Post-ocular segment 12 (abdomen segment 4) slightly longer and wider than preceding segment; two spine-like setae postero-laterally respectively, one slightly longer than the other.

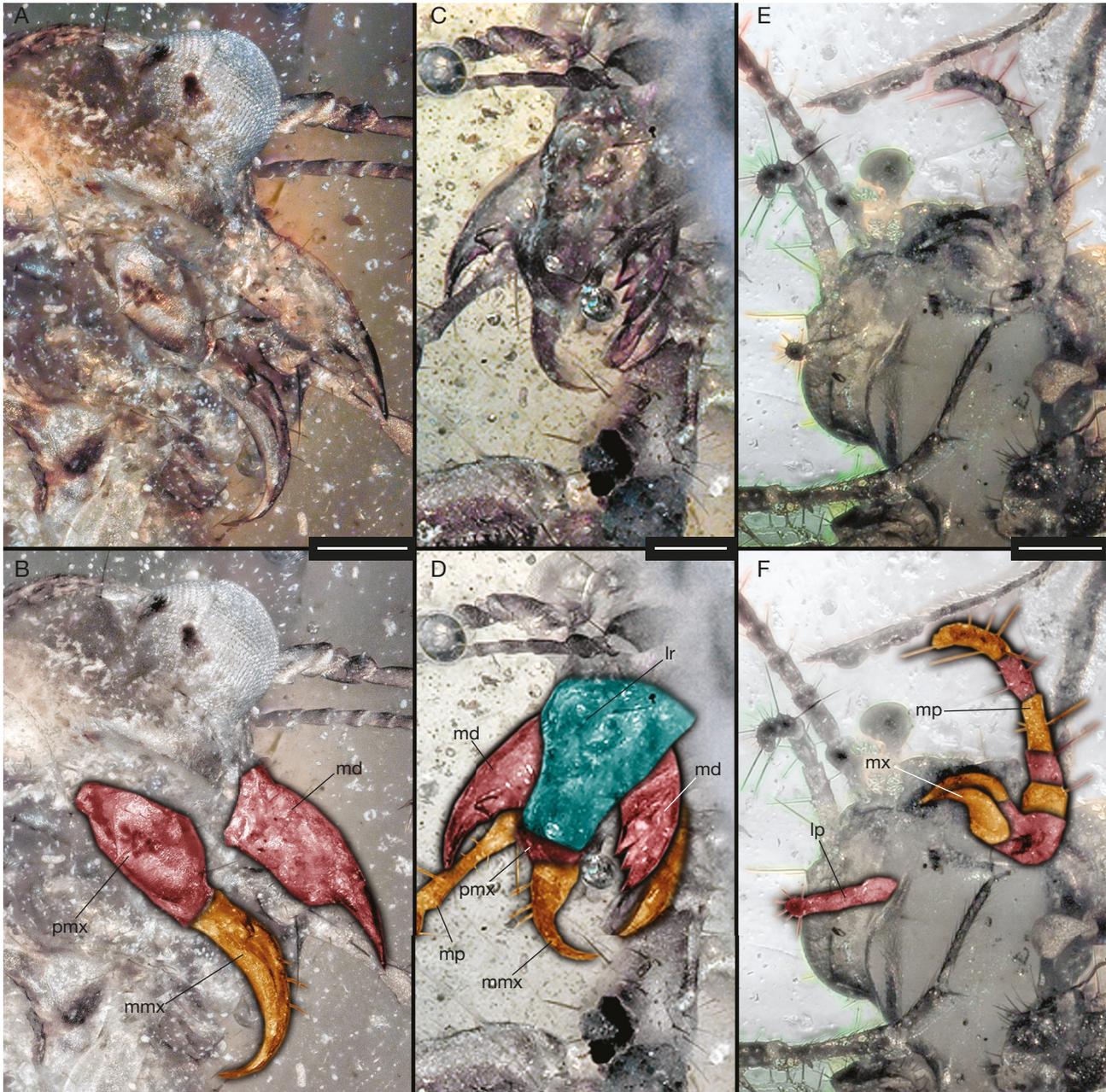


FIG. 7. — Close-ups on head area in different specimens of *Gryllobencain patrickmuelleri* n. gen., n. sp. as normal versions (A, C, E) and colour-marked (B, D, F): A–D, PED 0178; A, B, latero-posterior view; C, D, mostly anterior view; elements of maxillary palp difficult to differentiate; E, F, BUB 3073, ventral view. Abbreviations: lp, labial palp; lr, labrum; md, mandible; mmx, median part of maxilla; mp, maxillary palp; mx, maxilla; pmx, proximal part of maxilla. Scale bars: A–D, 0.3 mm; E, F, 0.2 mm.

Post-ocular segment 13 (abdomen segment 5) similar to preceding segment, but slightly longer and very slightly tapering posteriorly; two spine-like setae postero-laterally on each side, one slightly longer than the other.

Post-ocular segment 14 (abdomen segment 6) slightly shorter and less wide than preceding segment, tapering slightly posteriorly; one spine-like seta postero-laterally on each side.

Post-ocular segment 15 (abdomen segment 7) similar to preceding segment, but less wide and tapering posteriorly; one spine-like seta postero-laterally on each side.

Trunk end (post-ocular segments 16–19?; abdomen segments 8–11?) as long as first abdomen segment; anteriorly as wide as preceding segment, but tapering drastically posteriorly. Ventrally with a pair of prominent appendages (cerci) (Figs 1A, B; 3; 5A, C; 6B); basically cylindrical, not subdivided; about 0.8× the length of the antenna; as wide as the tibia of the hind leg proximally and tapering slightly until about 70% of its length, then strongly tapering towards tip; bearing numerous spine-like setae of varying sizes, mostly strong and very long (compared to similar structures elsewhere); also with a few smaller, shorter setae throughout.

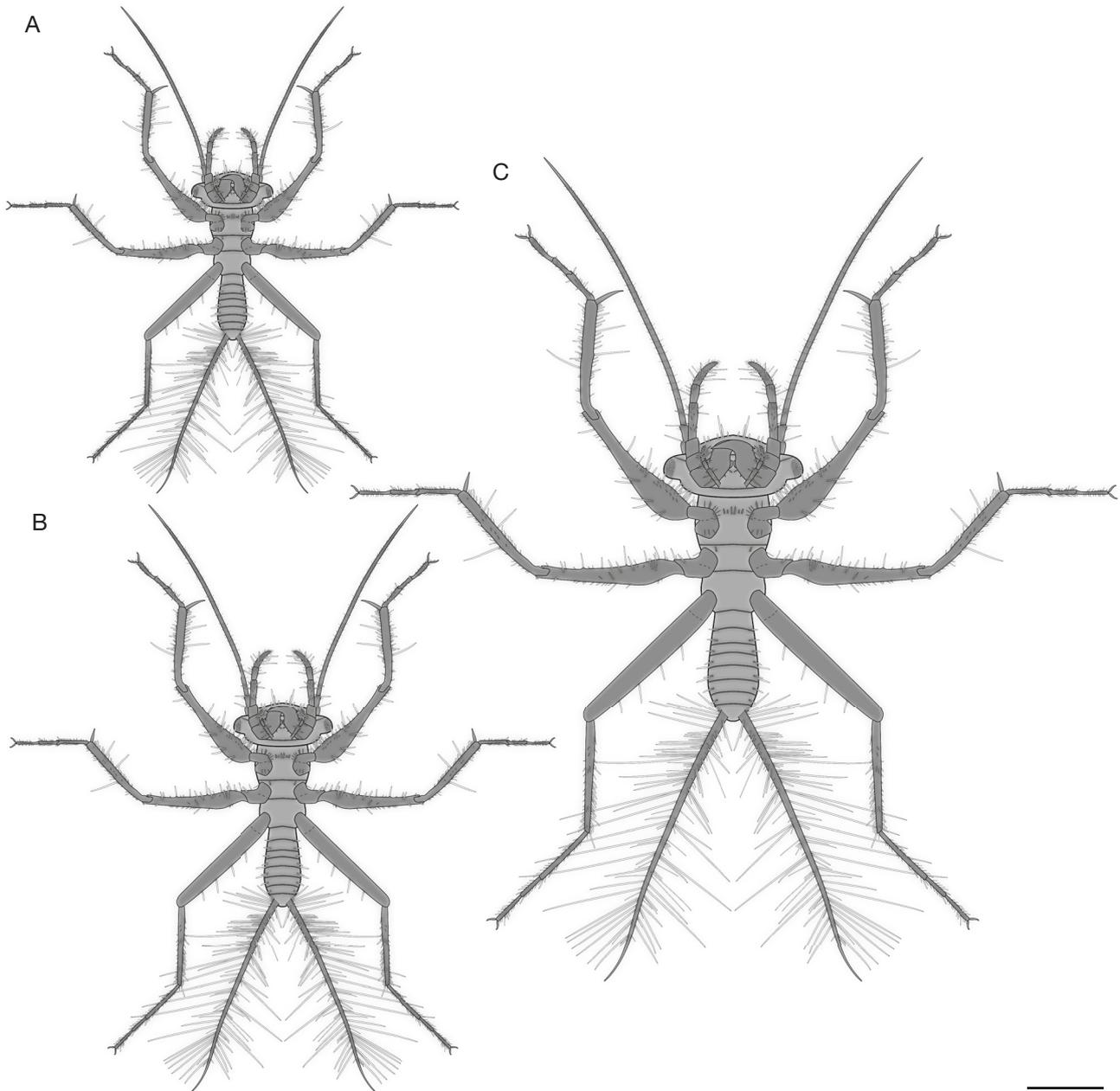


FIG. 8. — Reconstructed growth series of *Gryllobencain patrickmuelleri* n. gen., n. sp. based on specimens investigated in this study: **A**, BUB 3073; **B**, PED 0147; **C**, PED 0178 + BUB 3072. Scale bar: 1 mm.

Size of specimens

While the specimens are very similar in overall appearance, they differ in size. Though it remains difficult to measure, it appears that the four specimens fall into three size classes (Fig. 8). It seems likely that these represent three successive stages. It remains unclear whether the largest size class corresponds to the adult stage.

DISCUSSION

THE COMPARATIVE FRAME: POLYNEOPTERA

The new specimens have an overall “orthopteroid”-type morphology (Fig. 9A). This indicates that the new specimens represent a species that is an ingroup of Polyneoptera. The anterior two pairs of thorax appendages of the fossils have quite prominent spines. Similar morphologies are known in several modern-day representatives of Polyneoptera; also, some fossil representatives are known to possess such a morphology. We shortly summarise these forms as a basis for further comparisons.

1) *Mantodea – praying mantises*

Praying mantises are the most iconic predatory forms of Polyneoptera. They are known also by many non-experts, and almost everyone will have an idea how these creatures look like. Mantodea is an ingroup of Dictyoptera, the group additionally including cockroaches in the strict sense, termites and cockroach-like extinct forms. In praying mantises, the first thorax appendage or foreleg, forms a sub-chelate scissoring device allowing to effectively grab prey (Wieland 2013). The most proximal element of the appendage, the coxa, is elongated (a trait inherited from its cockroach-like ancestors; Hörnig *et al.* 2017: fig. 5); elements 3 and 4, femur and tibia, fold against each other. Especially the tibia is armed with numerous prominent spines, the most prominent distal one is often referred to as the tibial spur.

One fossil representative from the Cretaceous Crato Formation (about 110 million years old), *Santanmantis axelrodi* Grimaldi, 2003, additionally has prominent spines on thorax appendage 2 (Hörnig *et al.* 2017: fig. 9D). In this aspect, it resembles the new fossils and numerous other polyneopterans (see below). It is interesting to note that it has been assumed that *S. axelrodi* could not have used its second thorax appendage in catching prey, as it could not “rotate” its leg forward (Brannoch & Svenson 2017). However, this statement is flawed as it ignores the basic mechanics of euarthropodan appendages as well as the fact that numerous representatives of Polyneoptera (as discussed in the following) do indeed involve thorax appendage 2 in prey catching and immobilisation.

Praying mantises possess well-developed cerci at the posterior end of the abdomen. These are of the typical dictyopteran type, rather short and subdivided into about a dozen ringlets.

Also, some non-mantodean ingroups of Dictyoptera have been supposed to be predatory (e.g., Raphidiomimidae; Vishniakova 1973; Alienoptera; Bai *et al.* 2016). Yet, most of them do not possess prominent spines on the anterior thorax appendages and are therefore not further considered here.

2) *Mantophasmatodea – heel walkers or gladiators*

Gladiators (Fig. 9E) resemble grasshoppers on a first glimpse, but their hind leg is not enlarged as a jumping leg. They also resemble some phasmatodeans, and for a long time have been misidentified as such (see Zompro *et al.* 2002). The name of the group ‘heel walkers’ is based on the unusual position of the terminal tarsus element on the thorax appendages: in normal condition they are held upwards and the animal rests on the large attachment structures of the more proximal tarsal elements (Klass *et al.* 2003; Eberhard *et al.* 2009).

The fore and mid legs of gladiators form a distinct sub-chelate grasping device. Femur and tibia are armed with prominent spines allowing them to grasp prey (Roth *et al.* 2014). Cerci appear to be present, but rather small (but varies in different species in exact morphology; Klass *et al.* 2003). Even adult forms remain non-winged.

3) *Saginae, Listroscelidinae, Austrosaginae (Tettigoniidae) – predatory bush-crickets*

Predatory bush-crickets (representatives of Ensifera; Fig. 9B, C, F) may appear just like normal bush-crickets, but only on first sight to the untrained eye. Body shape and the large hind legs appear “normal” for a bush-cricket. Yet, on a second glimpse, massive spines on the fore and mid legs become apparent. With these massive appendages, predatory bush-crickets entrap prey and consume it, although it remains unclear how the spines are exactly involved (Gangwere 1967; Marshall & Hill 2009).

Also, the mandibles are extremely prominent (e.g., Isely 1944; Fialho *et al.* 2014). While many crickets have rather long cerci, lacking subdivisions, those of bush-crickets including predatory ones are quite short and often inconspicuous (Fialho *et al.* 2014).

A recent phylogenetic analysis indicates that predatory bush-crickets do not form a monophyletic group (Mugleston *et al.* 2018). Therefore, the specific morphology, as well as the predatory behaviour, appears to have evolved at least two or even three times within Orthoptera.

COMPARISON TO THE NEW FOSSILS

The new fossils show some characteristics indicating an ingroup position within Orthoptera (compare Fig. 9). The cerci are not subdivided in ringlets. This seems also to be the case in representatives of Phasmatodea (e.g., Bradler 2009 and references therein). Yet, the very prominent size and the very long and dense armature with setae resembles the condition in the orthopteran ingroup Ensifera. The new fossils hence differ from mantises and gladiators in their cerci morphology. The new fossils lack the elongated coxae of mantises and also the specialised tarsi of gladiators. Also, the quite long and highly subdivided antenna show similarities to those in ensiferans (Grimaldi & Engel 2005: 202ff).

In summary, we see many similarities with ensiferans. The femur of the hind leg in the new fossils is only slightly longer than that of the two anterior ones; although not as extremely enlarged as in many other crickets, this morphology is still very well compatible with an interpretation of the new specimens as representatives of Ensifera.

The absence of wings in the new specimens and even wing pads could indicate that the specimens are early immature instars. This is further supported by the condition of the antennae: there are some elements that appear to show indications of future subdivisions in the form of constrictions (Fig. 5C), as it would be expected for immatures (e.g., Hockman *et al.* 2009: fig. 4B).

It would now be tempting to simply suggest that the fossils are predatory bush-crickets, especially as the mouthparts in predatory bush-crickets are dominated by the enlarged mandibles (e.g., Fialho *et al.* 2014), and also the new fossils possess relatively large mandibles. Another similarity is the prominent spination on the fore and mid legs (e.g., Fialho *et al.* 2014). Yet, there are some significant differences:

1) The maxillae differ in two aspects. The medially drawn out part (lacinia?) is very prominent and sickle shaped. This

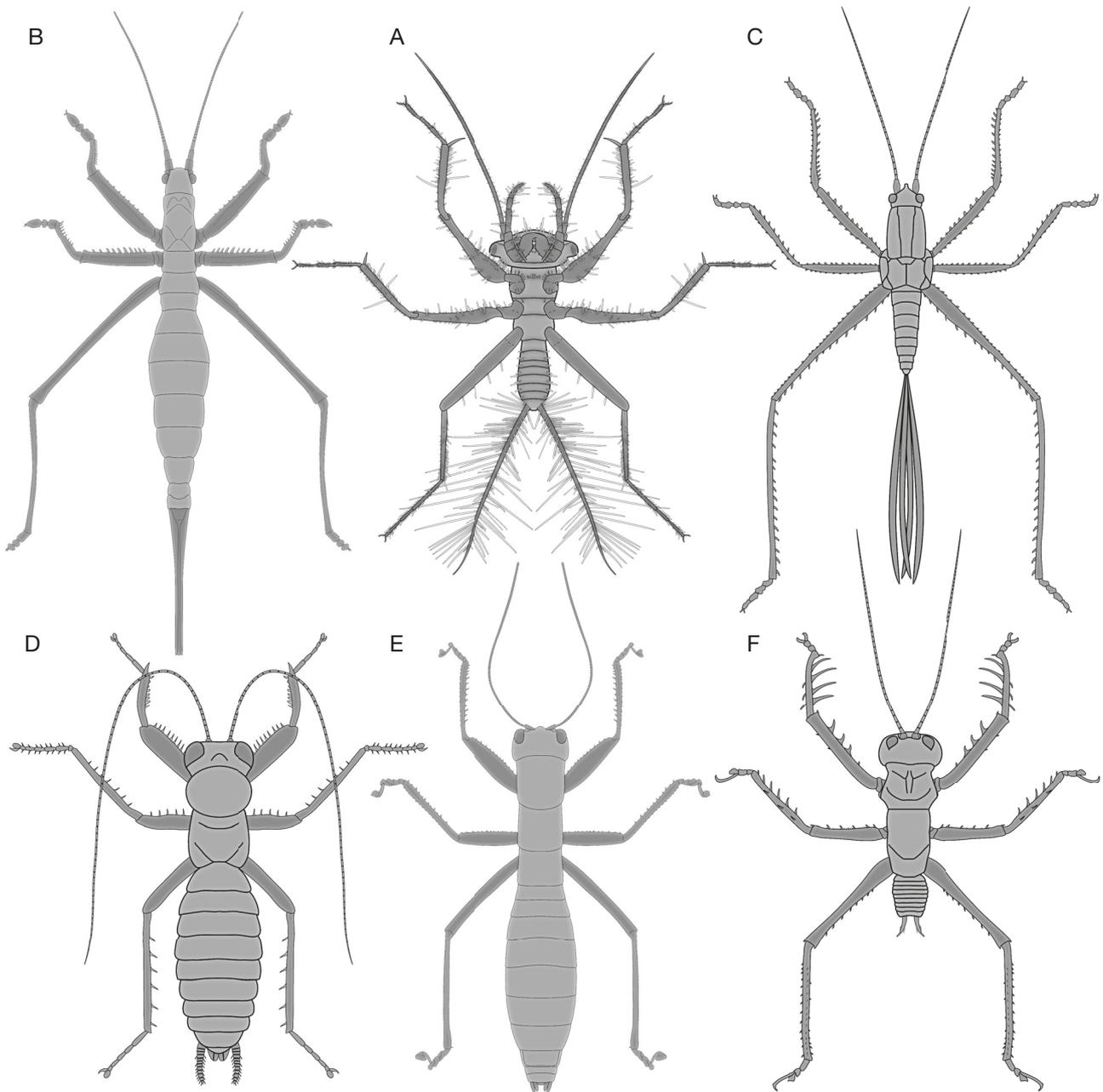


FIG. 9. — Comparison of the new species with other groups; all drawings idealised concerning posture: **A**, *Gryllobencain patrickmuelleri* n. gen., n. sp.; **B**, *Saga pedo* (Pallas, 1771) (Saginae; drawn from photo, sample ID 01DRAGO_H11, CC BY-NC-SA 3.0, license holder IBER, Sofia, Bulgaria, Centre for Biodiversity Genomics); **C**, *Psacadonotus seriatus* Redtenbacher, 1891 (Austrosaginae; modified after Karny 1912); **D**, *Santanmantis axelrodi* Grimaldi, 2003 (Mantodea; modified after Hörnig *et al.* 2017: fig. 4, wings omitted); **E**, female of undetermined species (Mantophasmatodea; modified after Klass *et al.* 2003: fig. 3A); **F**, male of *Cerberodon viridis* Perty, 1832 (Listroscelidinae; modified after Fialho *et al.* 2014: fig. 9B, wings omitted).

morphology resembles that of the mandibles of bush-crickets, but not that of their maxillae (e.g., Fialho *et al.* 2014: figs 9C, 10C, 15C). Also, the maxillary palps of the fossils appear unusually prominent and are armed with spines resembling those on fore and mid legs, including the principal arrangement (Fig. 7F). In predatory bush-crickets palps appear to largely lack armature, at least it appears not to be prominent (e.g., Fialho *et al.* 2014); 2) The fore and mid legs of the fossils resemble those of predatory bush-crickets in overall arrangement of spines, yet the spines in predatory bush-crickets appear

stronger (Fialho *et al.* 2014). This might be related to the fact that the new fossil specimens are immatures; also nymphs of predatory bush-crickets appear to have less prominent spines (e.g., Hemp 2001: fig. 6 vs fig. 7). An additional difference is the single, very prominent spine distally on the tibiae of the new fossils. This is distantly reminding of the tibial spur in praying mantises. This morphology is different from that in predatory bush-crickets; and 3) The cerci are very prominent and elongated in the new fossil (Fig. 3), also carrying numerous elongated and prominent, supposedly sensorial,

setae. In predatory bush-crickets, the cerci are rather short (e.g., Fig. 9F).

These characters could be interpreted in a way that the new fossils are closely related to at least one of the groups of predatory bush-crickets and simply retaining numerous plesiomorphies. Yet, also the more closely related forms to bush-crickets appear to possess shorter cerci (e.g., Muggleston *et al.* 2018). This makes a closer relationship of the fossils to predatory bush-crickets not very likely.

Within Ensifera, the tarsal morphology appears to be an important character: the tarsus of Tettigoniodea (katydid or bush-crickets) consists of four sub-elements, whereas that of Grylloidea consists of three sub-elements (the middle one often being significantly shortened). In the new fossils, the tarsus consists of three sub-elements with the middle one being the shortest (Fig. 2). Together with the very prominent cerci, this makes it very likely that the fossil is a representative of Grylloidea.

CONVERGENT EVOLUTION OF SUB-CHELATE THORAX APPENDAGES IN POLYNEOPTERA

Predatory bush-crickets and gladiators show clear similarities representing convergencies: sub-chelate fore and mid legs with prominent spines, and very short and inconspicuous cerci. The sub-chelate thorax appendages 1 and 2 with prominent spines additionally occur in the fossil praying mantis *Santanmantis axelrodi* (Grimaldi 2003; Hörnig *et al.* 2013, 2017) and also in the new fossils. Given that predatory bush-crickets evolved this feature at least twice, it means that this morphology evolved at least five times independently within Polyneoptera. This is important to note concerning the suggestion that the mid legs could not be involved in prey catching (Brannoch & Svenson 2017).

The new fossils show a further convergency, the tibial spur-like spines (Fig. 2). These resemble the tibial spurs in praying mantises.

Besides the similarities, representing convergencies, the new fossils show unique features. The presence of a spur-like spine on thorax appendage 2 is, in fact, unique but is well known on the next anterior appendage.

More special seem to be the long cerci (Fig. 3). All discussed groups have rather inconspicuous cerci, making the long cerci so far unique in combination with two pairs of sub-chelate appendages. Yet, long cerci are well known in many orthopterans and are hence not unexpected.

More unusual is the morphology of the maxillary palps (Fig. 7). These possess the same type of setae as the fore and mid legs. As the hind legs and also the cerci possess different types of setae, the presence of these setae on the palps cannot be explained by the general presence of such setae all over the body. This armature indicates that the maxillary palps may have been involved in the process of handling the prey. This appears so far unique.

Many representatives of Insecta use their walking legs for trapping prey (such as Tettigoniidae, Mantodea, Mantophasmatodea, Odonata (adult), Mantispidae, Reduviidae, e.g., Redborg 1998; Marshall & Hill 2009; Leipelt *et al.* 2010;

Weirauch *et al.* 2011; Wieland 2013; Roth *et al.* 2014). Yet, some also use their mouthparts. Examples for the use of the mandibles for trapping prey include ants or beetles (e.g., Pearson 1988; Larabee *et al.* 2017), mandibles in combination with maxillae are used in lacewing larvae (e.g., Canard 2001), and larvae of dragonflies and damselflies use their labium (e.g., Pritchard 1965).

Combining thorax and head appendages for trapping prey is yet quite unusual. A comparable arrangement of one smaller and two larger pairs of appendages forming a feeding apparatus is, for example, present in some larvae of Trichoptera (pers. obs.), but in that case all these appendages are that of the thorax.

If we widen the view to (other) crustaceans, the feeding apparatus of representatives of Remipedia and Thylacocephala is formed by the two posterior head appendages and the first trunk appendages (e.g., Yager & Carpenter 1999; Haug *et al.* 2014). While these are termed maxillula, maxilla and maxilliped, they correspond to maxilla, labium and thorax appendage 1 in Insecta. Hence, in principle a prey-catching apparatus combining the maxillary palps and thorax appendages 1 and 2 would appear so far unique but fits well into the range of known types of prey-catching apparatuses. Together with the prominent mouthparts, we interpret the new fossil as a predatory cricket.

COMPARISON TO OTHER ORTHOPTERANS FROM MYANMAR AMBER

Gorochov (2010a, b) described several orthopteran species based on Myanmar amber. Most of these forms differ significantly from the here presented fossils in overall morphology: the species reported by Gorochov (2010a, b) are mostly characterised by a very prominent femur on the hind legs and rather slender fore and mid legs, while the fossils presented here have rather massive fore and mid legs, but a rather slender femur of thorax appendage 3.

The rather slender femur on the hind legs is overall rather unusual for a representative of Orthoptera. Yet, in some species of predatory bush-crickets males also have a rather slender femur (e.g., Hemp 2001: figs 1, 6; Hemp 2006: fig. 6), while it is more prominent in the female (Hemp 2001: figs 2, 10). It can hence not be excluded that the specimens at hand all represent male forms, although it seems that they are still immature.

Some species described by Gorochov (2010a) appear more similar to the specimens reported here, as for example *Protomogoplistes asquamosus* (his fig. 1A). Yet, also here the morphology of the appendages differs in the same way as described above. Also, the specimens here reported bear much more armature than the ones reported by Gorochov (2010a, b).

A fossil orthopteran from Cretaceous amber showing a comparably strongly developed armature is *Hispanelcana arilloi* Peñalver & Grimaldi, 2010, described by Peñalver & Grimaldi (2010: fig. 2). Yet, the armature of this specimen is distributed more around the appendages instead of mostly along the median side on the forelegs. Also, as for other cases, the forelegs do not appear stronger and the femur of the hind

legs is quite massive. An additional difference in armature also indicates a significant distance concerning relationship. *H. arilloi* bears prominent scale-like spines on the tibia of the hind legs. This feature characterises the group Elcanidae (e.g., Fang *et al.* 2015). As the specimens reported here lack such spines, a closer relationship to Elcanidae and the ingroup species *H. arilloi* is unlikely.

It therefore seems that the specimens reported here are representatives of a so far not formally named species. Still, specimens similar to the ones described here have been reported, but not dealt with in detail, in Xia *et al.* (2015) and Zhang (2017).

CONCLUSIONS

The new fossils represent a new type of, most likely, predatory crickets. They represent the (at least) fifth case of convergent evolution of a raptorial apparatus formed by sub-chelate thorax appendages 1 and 2.

Yet, the specimens are also highly special, as:

1) they present a unique character combination (as is the case also in other fossils from Myanmar amber; Haug *et al.* 2019a); and 2) they present a so far unique mechanism for trapping prey (as assumed also for other Myanmar fossils, e.g., discussed for *Caputoraptor elegans*, Bai *et al.* 2018).

Acknowledgements

We are grateful to Sven Bradler, Göttingen, and Pedro Souza-Dias, Rio de Janeiro, for helpful comments on the manuscript. We would like to thank Patrick Müller, Zweibrücken, for providing specimens for this study. JTH was kindly funded by the Volkswagen Foundation with a Lichtenberg professorship. CK is currently funded by the Landesgraduiertenförderung MV. MKH and CK thank Steffen Harzsch, Greifswald, for his continuous support. PGP was supported by Capes/Dctoral Program (CAPES/DAAD/CNPQ, Notice n°. 15-2017/Process n° 88887.161379/2017-00).

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Submitted on 7 August 2019;
accepted on 19 September 2020;
published on 27 January 2022.