Palaeoentomology 005 (5): 439–444
https://www.mapress.com/j/pe/

Article

ISSN 2624-2826 (print edition)
PALAEOENTOMOLOGY
ISSN 2624-2834 (online edition)

https://doi.org/10.11646/palaeoentomology.5.5.4
http://zoobank.org/urn:lsid:zoobank.org:pub:80808B4C-60D3-4CA8-8573-21C91F883AAF

A proctotrupid wasp in Lebanese Lower Cretaceous amber (Hymenoptera: Proctotrupidae)

MICHAEL S. ENGEL[1, 2, 3], HOLLISTER W. HERHOLD[3] & PHILLIP BARDEN[3, 4, *]

[1]*Division of Entomology, Natural History Museum, University of Kansas, 1501 Crestline Drive- Suite 140, Lawrence, Kansas 66045-4415, USA*
[2]*Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045-4415, USA*
[3]*Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192, USA*
[4]*Department of Biological Sciences, New Jersey Institute of Technology, Dr Martin Luther King Jr Boulevard, Newark, New Jersey 07102, USA*

msengel@ku.edu; https://orcid.org/0000-0003-3067-077X
hherhold@amnh.org; https://orcid.org/0000-0002-6377-4711
barden@njit.edu; https://orcid.org/0000-0001-6277-320X
**Corresponding author*

Abstract

The first fossil proctotrupid wasp in Lower Cretaceous Lebanese amber is described and figured. *Astarteserphus grimaldii* **gen. et sp. nov.** is distinguished from all other living and fossil Proctotrupidae and placed into its own subfamily, Astarteserphinae **subfam. nov.** A key is presented to the living and fossil subfamilies and tribes of Proctotrupidae, and a brief discussion is provided on the unique features and diminutive size of the fossil.

Keywords: amber, Barremian, Lebanon, Proctotrupoidea, Proctotrupomorpha, taxonomy

Introduction

The parasitoid wasp family Proctotrupidae is one of modest diversity, with about 350 described extant species, although Masner (1995) has estimated the total world diversity to be closer to 1,200 species. While less species-rich than many other parasitoid lineages, Proctotrupidae are the most diverse and widely-distributed lineage within the Proctotrupoidea, a superfamily with close phylogenetic affinities to several proctrupomorphan lineages (Sharkey *et al*., 2012). Recent transcriptomic data suggest that Proctotrupoidea are putatively sister to Diaprioidea in a clade that is itself sister to chalcidoid wasps (Peters *et al*., 2017). The family consists of primary endoparasitoids of polyphagan and adephagan beetle larvae, primarily Carabidae, Staphylinidae, and Elateridae, although some alternative hosts have been confirmed from among the Mycetophilidae, Sciaridae, and Oecophoridae (a dubious mid-19th Century record from Lithobiidae is in need of corroboration), and are most diverse across the Holarctic (Kozlov, 1970; Townes & Townes, 1981; Masner, 1968, 1995; Grimaldi & Engel, 2005).

Species are typically solitary but many cases of gregarious endoparasitism do exist, and a single species may be either gregarious or solitary dependent on the host. Williams *et al*. (1992) demonstrated that females are sensitive to the host's food source in a reared colony, and will persistently probe through the food substrate to locate and sting host larvae. The ovipositor can extend to about twice the length of the abdomen and a single sting can result in multiple ovipositions; multiple stings are also known. After development, the larvae emerge from the venter of the host and pupate with the apical segments of the pupal metasoma embedded within the host's carcass. The pupa does not form a cocoon, completing development within a thin membrane before eclosing as an adult. High rates of parasitism by species of Proctotrupidae have inspired possible use as a biological control agent against agriculturally important insects such as sap beetles and wireworm, though with mixed success (Knodel & Shrestha, 2018).

The fossil record of Proctotrupidae is meager and the most well understood fauna is that preserved in Eocene amber from the Baltic and Rovno regions (Brues, 1923, 1940; Kolyada & Mostovski, 2007; Kolyada & Perkovsky, 2011). Proctotrupidae are also known as compression fossils from the Early Cretaceous deposits of China, Russia, and Mongolia (*e.g*., Rasnitsyn, 1980, 1986; Zhang & Zhang, 2001). Many of these taxa are likely stem groups to Proctotrupidae given the more developed wing venation and less greatly enlarged syntergum (*e.g*., *Saucrotrupes* Zhang & Zhang) or may even be misplaced, such as *Ocnoserphus* Zhang & Zhang, which has metasomal segment I enlarged, lacks a syntergum, and has a comparatively enriched forewing venation (Zhang &

Submitted: 8 Jul. 2022; accepted by D.-Y. Huang: 5 Sep. 2022; published: 22 Sep. 2022

Zhang, 2001). Additionally, there is a species described from Kachin amber of the extant tribe Disogmini (Rasnitsyn *et al*., 2022). Here we report the first proctotrupid wasp in Lower Cretaceous amber from Lebanon, representing the earliest definitive member of the family preserved as an amber inclusion and thus offering a greater range of character information than what has been available from compression fossils of comparable ages. The fossil is represented by an exceptionally well-preserved female (Fig. 1) and is described, figured, and compared with its extant relatives.

Material and methods

Morphological terminology employed herein is generally that presented by Huber & Sharkey (1993), with the tribal and generic classification of Proctotrupidae largely following an intermingling of those of Kozlov (1970), Townes & Townes (1981), and Masner (1995). Photographs of the inclusion were taken with an Olympus SZX16 stereoscope fitting with an Olympus DP28 digital camera. Measurements were taken an Olympus SZX12 stereomicroscope and ocular micrometer. The holotype is deposited in the amber fossil collection of the Division of Invertebrate Zoology, American Museum of Natural History, New York, New York, USA. The age, origin, and biodiversity of Lebanese amber has been reviewed by Azar *et al*. (2010) and Maksoud & Azar (2020).

Systematic palaeontology

Family Proctotrupidae Latreille, 1802

Astarteserphinae subfam. nov.

Type genus. *Astarteserphus* **gen. nov.**

Diagnosis. The subfamily is diagnosed by the following combination of characters: Females with head broad, slightly wider than long; antennal toruli separated from clypeal base by about 3× torular diameter; scape short; flagellomere XI enlarged; compound eyes short, occupying upper portion of lateral head surface, hirsute, inner ocular margins roughly parallel; malar space elongate, nearly as long as compound eye and longer than mandible; mandible simple, without subapical teeth; maxillary palpus tetramerous; labial palpus trimerous; occipital carina wholly lacking (neither present dorsally nor laterally). Mesoscutum with notauli present as shallow furrows extending to posterior margin of mesoscutum; metepisternum without demarcated smooth polished area. Forewing with only Sc+R, pterostigma, and r-rs as sclerotized veins; C absent, thus costal cell open along entire anterior length (marginal cell only closed cell); 3Rs nebulous, short, straight, forming short marginal cell shorter than pterostigma. Metasoma with metasomal tergum I and sternum I short, fused, forming short petiole, petiole visible from above; terga II–IV fused to form syntergum, with two faint furrows running transversely across syntergum indicating points of fusion between original terga II, III, and IV.

Key to subfamilies and tribes of Proctotrupidae

1. Forewing with 3Rs typically short to of modest length, forming short marginal cell, marginal cell along anterior wing margin typically shorter than pterostigma, if as long as pterostigma, then pterostigma comparatively narrow and distinctly less than 1.75× width of costal cell; sclerotized spot (medial sclerite) absent; preoccipital carina present (either complete or present only dorsally) or absent; ovipositor decidedly downcurved; syntergum at most with setae laterally, lateral margins short largely or entirely covering synsternum.....2
–. Forewing with 3Rs elongate, forming long marginal cell, marginal cell along anterior wing margin about as long as pterostigma, which itself is large, about 2× width of costal cell; sclerotized spot (medial sclerite) present at juncture of where M+Cu and 1M would meet; preoccipital carina scarcely evident; ovipositor not downcurved, projecting caudally in line with longitudinal axis of metasoma; syntergum hirsute, with lateral margins short and thus exposing synsternum [type genus: *Heloriserphus* Masner; couplet serves as diagnosis].....Heloriserphinae **subfam. nov.**
2(1). Forewing C present, at least as pigmented trace, enclosing distinct costal cell; preoccipital carina present, at least dorsally if not fully; notauli typically absent or if present, then incomplete, faint, or represented by anterolateral pits or depressions.....3
–. Forewing C wholly absent, thus costal cell open along entire anterior margin; preoccipital carina absent, area wholly rounded; notauli present and complete [type genus: *Astarteserphes* **gen. nov.**].....Astarteserphinae **subfam. nov.**
3(2). Forewing without M+Cu and 1A; scape without dorsoapical spine or process [Proctotrupinae Latreille].....4
–. Forewing with M+Cu and 1A present as distinct nebulous veins; scape with distinct dorsoapical spine or process [type genus: *Austroserphus* Dodd].....Austroserphinae Kozlov
4(3). Forewing 2Rs absent or present as short tubular or nebulous stub; preoccipital carina typically complete, extending laterally; notauli variable, but absent to virtually absent aside from pits or shallow grooves; metepisternum typically with smooth, polished area of integument of variable size, but sometimes absent; metasoma subsessile or petiolate; ovipositor variable.....5
–. Forewing 2Rs nearly complete as nebulous vein; preoccipital carina present only dorsally; notauli present, typically extending beyond mesoscutal midlength; metepisternum without smooth, polished area of integument; metasoma petiolate; ovipositor long and slender [type genus: *Disogmus* Förster].....Disogmini Kozlov
5(4). Metepisternum with large area of smooth, polished, and glabrous integument; notauli typically short and represented by anterolateral pits or weakly impressed grooves; metasoma typically subsessile [type genus: *Cryptoserphus* Kieffer].....Cryptoserphini Kozlov
–. Metepisternum lacking smooth, glabrous area or, if present, then area small; notauli absent or represented by broadly shallow impressions but never as grooves; metasoma petiolate [type genus: *Proctotrupes* Latreille].....Proctotrupini Latreille

***Astarteserphus* gen. nov.**

Type species. *Astarteserphus grimaldii* **sp. nov.**

Etymology. The new genus-group name is a combination of the Ancient Greek name for the Near Eastern goddess *Ἀστάρτη* / *Astártē* (particularly worshipped among the Phoenicians) and *Serphus* Schrank (from Ancient Greek *σέρφος* / *sérphos*, meaning, "small winged insect" and at the time likely referring to gnats), the latter a historical name for *Proctotrupes* Latreille. The gender of the name is masculine.

Diagnosis. As for the subfamily (*vide supra*).

***Astarteserphus grimaldii* sp. nov.**
(Fig. 1)

Holotype. ♀, AMNH LB-AE-137, deposited in the amber collection, Division of Invertebrate Zoology, American Museum of Natural History, New York, New York, USA.

Etymology. The specific epithet honors our dear friend and colleague, David A. Grimaldi, for his decades of collaboration, friendship, and breadth of important contributions to the study of living and fossil insects.

Diagnosis. As for the genus (*vide supra*).

Locality and horizon. Lebanon: Bcharreh District, Bcharreh Mountains, Lower Cretaceous, A. Estephan coll.

Description. ♀: Total body length (as preserved) 1.08 mm; forewing length 0.75 mm, maximum width 0.32 mm (length about 2.34× width). Integument dark brown to black throughout except palpi light brown. Head apparently slightly wider than long (direct frontal view not possible as preserved), integument apparently smooth with dense

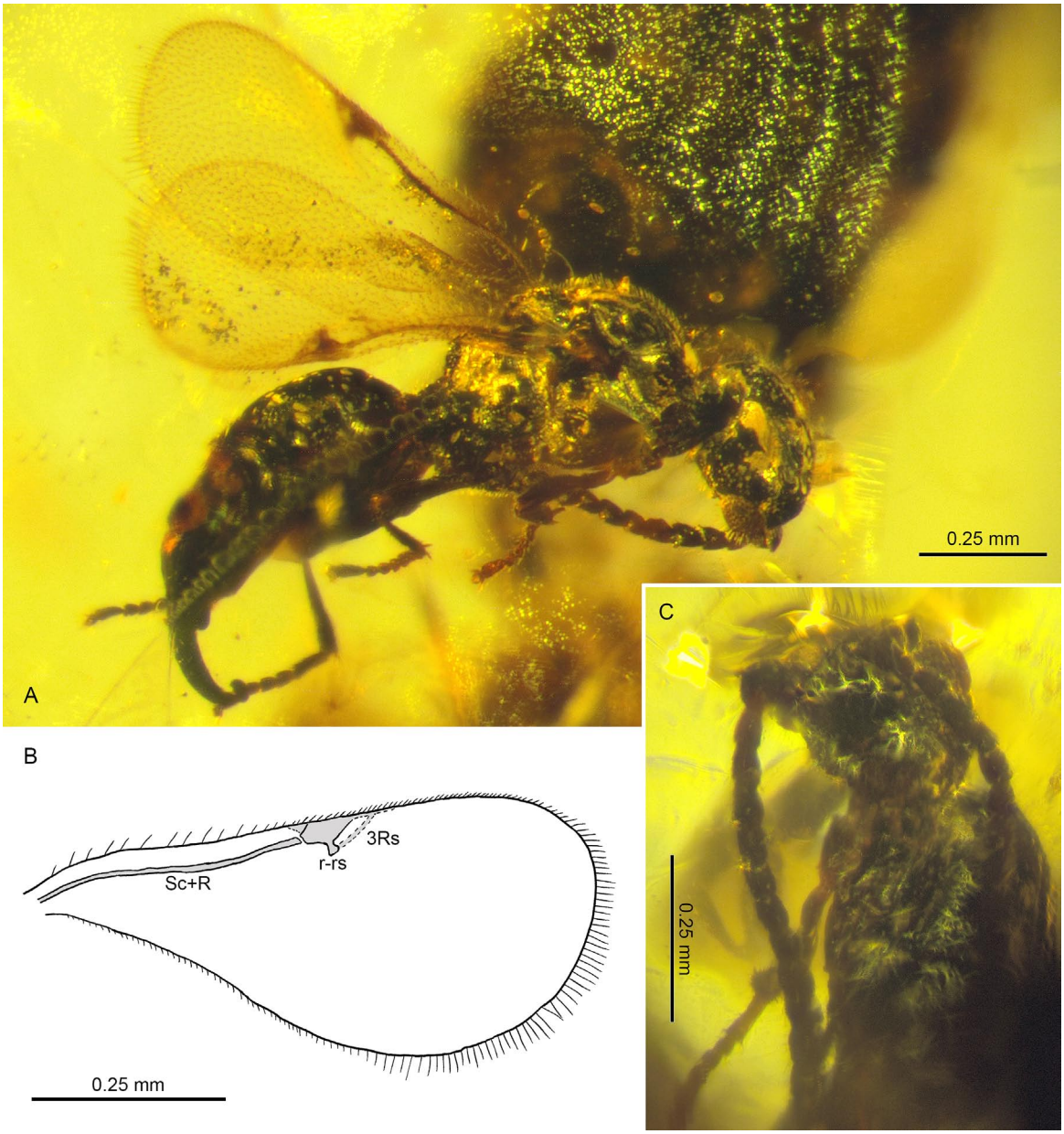

FIGURE 1. *Astarteserphus grimaldii* **gen. et sp. nov.** (Proctotrupidae), holotype (AMNH LB-AE-137), in Lower Cretaceous amber from Bcharreh, Lebanon. **A**, Photograph of lateral habitus. **B**, Line drawing of forewing venation. **C**, Ventral view of head.

setigerous punctures, head with abundant, fine, short setae although apparently less abundant on lower face; compound eyes comparatively small, occupying only about 50% of lateral head surface, hirsute, ocular setae about as long as setae of remainder of head, inner ocular margins roughly parallel; malar space elongate, almost as long as compound eye and longer than mandible, with faint indication of malar sulcus at margin; mandible short, triangular, with acute apical tooth, without subapical teeth, upper margin slightly concave; maxillary palpus tetramerous; labial palpus trimerous; clypeus short, half-moon shaped, apical margin straight, width subequal to mandible length; antenna long, apex extending in repose to petiole; antennal toruli separated from clypeal base by about 3× torular diameter; scape short, robust, length 1.7× apical width; pedicel short, length 1.1× apical width and about 0.5× length of scape; flagellomeres I–VII each slightly longer than wide, flagellomeres VIII–X each about as long as wide, flagellomere XI enlarged, length 1.8× its maximum width; flagellomere I longer than pedicel and slightly longer than flagellomeres II–X, flagellomeres II–VII subequal in lengths, flagellomeres VIII–X subequal in lengths; flagellomeres I–VII of subequal widths, flagellomeres VIII–IX of subequal widths and slightly wider than preceding flagellomeres; flagellomere XI slightly wider than all preceding flagellomeres and about as wide as scape; flagellomeres with fine, short, subdecumbent to suberect setae; vertex gently arched above upper tangent of compound eyes, ocelli in small triangle at about upper tangent of compound eyes.

Mesosoma longer than high, length 1.5× height; propleura producing a short neck; mesoscutum smooth, with scattered minute punctures, with notauli present as shallow furrows extending to posterior margin of mesoscutum, furrow more deeply impressed in anterior half, notauli simple (not areolate or foveolate), surface of mesoscutum gently arched and tapering anteriorly to meet pronotal posterior margin without defined anterior declivity; mesoscutum with abundant, short (of similar lengths to ocular setae), fine, suberect, posteriorly sloped setae; mesoscutellum comparatively flat, sculptured as on mesoscutum, length approximately 0.5× mesoscutal length; metanotum not visible as preserved; dorsal surface of propodeum comparatively short, seemingly about as long as mesoscutellum, sculpturing of dorsal surface not visible as preserved, lateral surface apparently finely and irregularly areolate (ridges of individual areolae low); mesepisternum largely smooth with minute punctures although appearing faintly imbricate above; metepisternum as on mesepisternum, without demarcated area of smooth, polished, shiny integument compared to remainder of metepisternal surface.

Forewing length about 2.3× maximum width, with venation reduced, with only Sc+R, pterostigma, and r-rs sclerotized, 3Rs nebulous and darkly pigmented, all other veins, inclusive of C, lacking (not even present as spectral veins); pterostigma of modest size, triangular, length about 1.5× depth; r-rs originated at about pterostigmal midlength, length less than pterostigmal width; 3Rs short, straight, forming short marginal cell, apical margin of marginal cell distinctly shorter than pterostigmal length, pterostigmal length 1.8× marginal cell length along anterior wing margin; wing membranes hyaline and clear, with modest abundance of microtrichia, wing margins with marginal microtrichia numerous and short along anterior margin from pterostigma to apex, such setae longer along apex and rounded apex of posterior margin, then shorter again along posterior wing margin, anterior wing margin proximal to pterostigma with scattered, fine setae longer than marginal microtrichia but not as long as apical setae. Hind wing with only Sc+R present, with marginal microtrichia numerous along anterior wing margin, becoming elongate setae at apex and along apical third of posterior margin, then reducing in size again for remaining proximal portion of posterior wing margin.

Legs generally slender and with scattered erect to suberect, fine setae, those of tibiae more numerous than femoral setae; tibiae and femora long and slightly widening apically; trochantellus lacking; tibiae about as long as corresponding femora; tibial spur formula 1-2-2, spurs simple, outer metatibial spur distinctly shorter than inner metatibial spur; metafemur slightly swollen medially; basitarsi longer than each remaining tarsomere's individual lengths, basitarsi about as long as combined lengths of tarsomeres II–IV, basitarsal lengths about 1.4–1.5× corresponding tarsomere V lengths; pretarsal claws simple and thin; arolium present, large.

Metasoma with metasomal tergum I and sternum I short, fused, forming short petiole, petiole shorter than metacoxa and visible from above, sculpturing distorted as preserved but apparently longitudinally striate; remaining terga smooth and largely glabrous; terga II–IV fused to form syntergum although two faint furrows run transversely across syntergum likely indicating points of fusion between original terga II, III, and IV; terga V–VII roughly subequal in length, not as high as syntergum, tergum VII shortening in height apically to meet tergum VIII; tergum VIII reduced, shorter than preceding segment and approximately 0.5× as high as base of tergum VII; sterna I–IV seemingly fused; ovipositor sheaths downcurved and gently arched apically, with scattered, long, erect, fine setae ventrally, without evident sculpturing.

♂: *Latet*.

Discussion

Assignment of the Lebanese fossil to Proctotrupidae is undeniable given the large swath of traits indicative of the family (Kozlov, 1970; Townes & Townes, 1981; Naumann

& Masner, 1985; Masner, 1993): antennal toruli separated from clypeus by more than torular diameter; antennae not positioned on antennal shelf; antenna not geniculate, with scape short and thick, 0.65–1.5× length of flagellomere I; 13 antennomeres (*i.e.*, 11 flagellomeres); inner ocular margins not converging below; wing venation reduced, only costal and marginal cells delimited (albeit open anteriorly in the fossil); forewing 3Rs simple, Rs+M absent (in extant taxa this is at most represented by a faint nebulous trace); pterostigma present; syntergum composed of terga II–IV; ovipositor downcurved; thick, heavily sclerotized ovipositor sheaths. Nonetheless, there remain several peculiar attributes of the fossil that make it quite distinctive among all living and fossil Proctotrupidae. The notauli are complete and consist of a pair of longitudinal furrows, shallower in the posterior half, that converge slightly posteriorly but remain separated where they meet the transscutal sulcus. The notauli lack any areolae, foveae, or other ornamentation, but are distinct. Interestingly, the metasomal syntergum is traversed by faint furrows that appear to represent the original boundaries of the three terga composing the combined segment. The three terga are certainly fused in the fossil and form a continuous structure, as well as a continuous margin laterally, and the faint furrows fade by the laterally downturned portion of the syntergum.

While the complete notauli and presence of transverse lines on the syntergum are assuredly plesiomorphic relative to other proctotrupids, the loss of the occipital carina, the loss of the costal vein, the markedly elongate malar space, and the ocular setae are likely apomorphic and their combination is unique among living and fossil Proctotrupidae, when taken in conjunction with the other features of wing venation and metasomal structure. Of note as well is the minute nature of the fossil. Extant proctotrupid species commonly range between 3–6 mm in total size (*e.g.*, Park & Lee, 2021) and, while some species reach sizes below 2 mm (Choi *et al*., 2012), to our knowledge this is the smallest described member of Proctotrupidae at just over 1 mm in length. It seems unlikely that such diminutive sizes would be plesiomorphic for the family, and a good null hypothesis for the moment would be that this miniaturization is an apomorphic condition, perhaps associated with the size of the host.

There remains no robust molecular divergence estimate for the family Proctotrupidae. Estimates from mitochondrial genomes suggest that proctotrupids diverged from the monogeneric family Vanhorniidae in the Early Cretaceous (Tang *et al*., 2019); however, this result was based on single exemplar terminals for each lineage and thus likely suffers from insufficient sampling. Fossil taxa with clear synapomorphies such as *Astarteserphus grimaldii* and *Cresogmus grimaldii* Rasnitsyn & Kolyada (Rasnitsyn *et al*., 2022) are likely to serve as impactful calibration points in the temporal reconstruction of the most conspicuous of the putatively relict lineages within Proctotrupoidea.

Dedication. No words are sufficient to express our admiration and gratitude to Dave Grimaldi, the world's authority on insect evolution, drosophilid systematics, and amber studies. It has been our great pleasure to know Dave for many years, working alongside him in the field and museum, and benefitting from his charm, wit, artistic talents, and broad scope of knowledge in evolution, entomology, and biology writ large. This small contribution fails to truly embody our gratitude and love for this paragon of scholarly achievement, but we hope it serves to convey in some form our joy at the celebration of his birthday. We look forward to decades of further enjoyment and enlightenment. Happy birthday, Dave!

Acknowledgements

H.W.H is supported by an AMNH Richard Gilder Graduate Fellowship. We thank Dany Azar and Diying Huang for the opportunity to contribute to this issue honoring David Grimaldi, and two anonymous referees for their helpful comments. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

References

Azar, D., Gèze, R. & Acra, F. (2010) Lebanese amber. *In*: Penney, D. (Ed.), *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester, pp. 271–298.

Brues, C.T. (1923) Some new fossil parasitic Hymenoptera from Baltic amber. *Proceedings of the American Academy of Arts and Sciences*, 58 (8), 327–346. https://doi.org/10.2307/20025999

Brues, C.T. (1940) Serphidae in Baltic amber, with the description of a new living genus. *Proceedings of the American Academy of Arts and Sciences*, 73 (9), 259–264. https://doi.org/10.2307/25130185

Choi, M.-B., Kolyada, V.A. & Lee, J.-W. (2012) Description of two new species from South Korea and Russian Far East with a key to the Palearctic species of the genus *Brachyserphus* Hellén (Hymenoptera, Proctotrupidae). *Animal Cells and Systems*, 16 (3), 237–244. https://doi.org/10.1080/19768354.2011.644402

Grimaldi, D. & Engel, M.S. (2005) *Evolution of the insects*. Cambridge University Press, Cambridge, xv + 755 pp.

Huber, J.T. & Sharkey, M.J. (1993) Structure. *In*: Goulet, H. & Huber, J.T. (Eds), *Hymenoptera of the world: an identification guide to families*. Agriculture Canada, Ottawa, pp. 13–59.

Knodel, J.J. & Shrestha, G. (2018). Pulse crops: pest management of wireworms and cutworms in the Northern Great Plains

of United States and Canada. *Annals of the Entomological Society of America*, 111 (4), 195–204.
https://doi.org/10.1093/aesa/say018

Kolyada, V.A. & Mostovski, M.B. (2007) Revision of Proctotrupidae (Insecta: Hymenoptera) described by Ch.T. Brues from Baltic amber. *Zootaxa*, 1661 (1), 29–38.
https://doi.org/10.11646/zootaxa.1661.1.3

Kolyada, V.A. & Perkovsky, E. (2011) A new species of the genus *Disogmus* Förster (Hymenoptera, Proctotrupoidea, Proctotrupidae) from the Eocene Rovno amber. *ZooKeys*, 130, 455–459.
https://doi.org/10.3897/zookeys.130.1560

Kozlov, M.A. (1970) Suprageneric groups of the Proctotrupoidea (Hymenoptera). *Entomological Review*, 49, 115–127.

Latreille, P.A. (1802) *Histoire naturelle, générale et particulière des crustacés et des insectes. Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par C.S. Sonnini, membre de plusieurs sociétés savantes. Familles naturelles des genres.* Tome troisième. Dufart, Paris, xii + 467 pp.
https://doi.org/10.5962/bhl.title.15764

Maksoud, S. & Azar, D. (2020) Lebanese amber: latest updates. *Palaeoentomology*, 3 (2), 125–155.
https://doi.org/10.11646/palaeoentomology.3.2.2

Masner, L. 1968. The fungus gnats (Dipt., Mycetophiloidea) as potential hosts of proctotrupid wasps (Hym., Proctotrupoidea). *Acta Entomologica Bohemoslovaca*, 65, 464–466.

Masner, L. (1995) The proctotrupoid families. *In*: Hanson, P.E. & Gauld, I.D. (Eds), *The Hymenoptera of Costa Rica*. Oxford University Press, Oxford, pp. 209–246.

Naumann, I.D. & Masner, L. (1985) Parasitic wasps of the proctotrupoid complex: a new family from Australia and a key to world families (Hymenoptera: Proctotrupoidea *sensu lato*). *Australian Journal of Zoology*, 33 (5), 761–783.
https://doi.org/10.1071/ZO9850761

Park, B. & Lee, J.-W. (2021) Seven new records of the family Proctotrupidae (Hymenoptera: Proctotrupoidea) from South Korea. *Animal Systematics, Evolution and Diversity*, 37 (1), 39–51.
https://doi.org/10.5635/ASED.2021.37.1.082

Peters, R.S., Krogmann, L., Mayer, C., Donath, A., Gunkel, S., Meusemann, K., Kozlov, A., Podsiadlowski, L., Petersen, M., Lanfear, R., Diez, P.A., Heraty, J., Kjer, K.M., Klopfstein, S., Meier, R., Polidori, C., Schmitt, T., Liu, S., Zhou, X., Wappler, T. Rust, J., Misof, B. & Niehuis, O. (2017) Evolutionary history of the Hymenoptera. *Current Biology*, 27 (7), 1013–1018.
https://doi.org/10.1016/j.cub.2017.01.027

Rasnitsyn, A.P. (1980) Origin and evolution of Hymenoptera. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, 174, 1–192. [In Russian]

Rasnitsyn, A.P. (1986) Vespida (= Hymenoptera). *Trudy Sovmestnoy Sovetsko-Mongol'skoy Paleontologicheskoy Ekspeditsii*, 28, 154–164. [In Russian]

Rasnitsyn, A.P., Kolyada, V.A., Vorontsov, D.D. & Öhm-Kühnle, C. (2022) The first Proctotrupidae (Hymenoptera) in Burmese amber, with description of a new genus and species. *Palaeoentomology*, 5 (5), 445–451 .

Sharkey, M.J., Carpenter, J.M., Vilhelmsen, L., Heraty, J., Liljeblad, J., Dowling, A.P., Schulmeister, S., Murray, D., Deans, A.R., Ronquist, F., Krogmann, L. & Wheeler, W.C. (2012) Phylogenetic relationships among superfamilies of Hymenoptera. *Cladistics*, 28 (1), 80–112.
https://doi.org/10.1111/j.1096-0031.2011.00366.x

Tang, P., Zhu, J.C., Zheng, B.Y., Wei, S.J., Sharkey, M., Chen, X.X. & Vogler, A.P. (2019) Mitochondrial phylogenomics of the Hymenoptera. *Molecular Phylogenetics and Evolution*, 131, 8–18.
https://doi.org/10.1016/j.ympev.2018.10.040

Townes, H.K. & Townes, M. (1981) A revision of the Serphidae (Hymenoptera). *Memoirs of the American Entomological Institute*, 32, 1–541.

Williams, R.N., Fickle, D.S. & Galford, J.R. (1992) Biological studies of *Brachyserphus abruptus* [Hym.: Proctotrupidae], a nitidulid parasite. *Entomophaga*, 37 (1), 91–98.
https://doi.org/10.1007/BF02372977

Zhang, H.C. & Zhang, J.F. (2001) Proctotrupoid wasps (Insecta, Hymenoptera) from the Yixian Formation of western Liaoning Province. *Acta Micropalaeontologica Sinica*, 18 (1), 11–28. [In Chinese with English abstract]