The First Mantidfly (Neuroptera: Mantispidae) from the Early Eocene Green River Formation

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Abstract

Protonolima mantispinoformis gen. et sp. nov. (Neuroptera: Mantispidae) is described from the early Eocene Green River Formation. It likely belongs to Calomantispinae, on the basis of the very distal origin of posterior radius and the basal crossvein between media and cubitus (1m-cu) connecting radius + media and anterior cubitus; if so, it would be the only fossil representative of the subfamily. *Protonolima* gen. nov. is probably most closely related to the extant American genus *Nolima*.

Keywords

Neuroptera, Mantispidae, Calomantispinae, Drepanicinae, Ypresian, new genus, new species

Introduction

The Mantispidae, or mantidflies, are remarkable for the raptorial forelegs and elongate tubular prothorax that most possess. The family currently comprises more than 400 species, and is distributed nearly worldwide except for northern parts of Europe, Asia, and North America (Ohl 2004).

The oldest known genus of Mantispidae is from the Early Jurassic (early Toarcian) (Ansorge and Schlüter 1990; Wedmann and Makarkin 2007). Thirteen species of Mesozoic mantispids are known, mostly belonging to the extinct subfamily Mesomantispinae (Panfilov 1980; Makarkin 1990, 1997; Poinar and Buckley 2011; Jepson et al. 2013, 2018a, 2018b; Khramov 2013; Jepson 2015). Recently, a first-instar larva of Mantispidae was described from mid-Cretaceous Burmese amber (Haug et al. 2018). However, only seven species have been described from the Cenozoic (see below), including two from the Eocene: *Symphrasites eocenicus* Wedmann and Makarkin, 2007 from the mid-Eocene Messel, Germany, and *Vectispa relicta* (Cockerell 1921) from the latest Eocene Bembridge Marls, England, both represented by incomplete specimens (see Cockerell 1921; Jarzembowski 1980; Wedmann and Makarkin 2007). Additionally, four first-instar larvae of Mantispinae were reported from late Eocene Baltic amber (Ohl 2011).

Here, a new genus and species of Mantispidae is described based on an incomplete and poorly preserved fossil from the Green River Formation, likely belonging to the Calomantispinae, a subfamily unknown in the fossil record. It is the oldest Cenozoic record of Mantispidae.

Materials and Methods

The specimen was collected by Jim Barkley at a quarry 2 miles (approx. 3 km) west of the Rio Blanco store and 2,179 masl in Rio Blanco County, Colorado, USA, known as Gus' Pit and as "Site B" of Dayvault et al. (1995) (Antell and Kathirithamby 2016). The specimen was photographed, both dry and wetted by ethanol, with a Leica M205 C stereo microscope and Leica DMC 4500 camera attachment (Leica Microsystems; https://www.leica-microsystems.com) using Leica Application Suite X, Version 3 (Leica Microsystems 2018). The line drawings were prepared from camera images with Adobe Photoshop CS3 (Adobe Systems 2007).

Gus' Pit in Rio Blanco County and localities of the Anvil Points area in Garfield County, Colorado, are stratigraphically equivalent; all are from

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the so called "B-Groove" layer (see Young 1995:9, fig. 4) in the upper part of the Parachute Creek Member (D. Kohls, pers. comm.). Gus' Pit is located approximately 150 ft (45 m) below the Magomany bed (Dayvault et al. 1995). The Green River Formation is considered to be 53.5 to 48.5 million years old on the basis of ^{40}Ar/^{39}Ar dating (Smith et al. 2003, 2008). The Parachute Creek Member was deposited during approximately 2.5 million years of the Ypresian, from about 51.3 to about 48.5 Ma, and localities in the "B-Groove" layer are estimated to be approximately 49 million years old (see Smith et al. 2008:57, fig. 2), that is, late Ypresian.

Venational terminology in general follows Kukalová-Peck and Lawrence (2004) as interpreted by Yang et al. (2012, 2014). Terminology of wing spaces and details of venation (e.g., veinlets) follows Oswald (1993). Abbreviations used: Cu, cubitus; CuA, anterior cubitus; CuP, posterior cubitus; M, media; MA, anterior branch of media; MP, posterior branch of media; R, radius; RA, anterior radius; RP, posterior radius; ScP, posterior subcosta. Crossveins are designated by the longitudinal veins to which they connect, and are numbered in sequence from the wing base, for example, 1m-cu, basal crossvein connecting M/MA and Cu/CuA.

Systematic Paleontology

Order Neuroptera Linnaeus, 1758
Family Mantispidae Leach, 1815
Subfamily Calomantispinae Navás, 1914
Protonolima Makarkin gen. nov.

Type and only species. *Protonolima mantispinoformis* sp. nov.

Etymology. From the Greek *protou*, before, and *Nolima*, a genus-group name. Gender feminine.

Diagnosis. Postocular lobe very narrow. Prothorax elongate, about 3.5 times as long as wide. Profemur rather broad; its major (longest) spine long, nearly perpendicular to axis of profemur, and located at approximately 0.34 of its length; first to fourth protarsomeres ventrally with short prostrate setae. Protibia plus protarsus slightly shorter than profemur. Forewing narrow; its costal space moderately broad proximally; RP originates very far from wing base (at approximately 0.44 of estimated complete length); crossvein 1m-cu connects R+M and CuA.

Remarks. The new genus may be distinguished from other genera of Calomantispinae by the narrow postocular lobe, the narrowed costal space, and the longer ScP.

Protonolima mantispinoformis Makarkin sp. nov.
Figures 1, 2, 3, and 4

Type material. Holotype (YPM IP 586369), a poorly preserved male specimen in lateral aspect, housed in the Division of Invertebrate Paleontology of the Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. Collected by Jim Barkley in a quarry known as Gus' Pit (39°43′38.10″N, 107°58′34.14″W), 2 miles (approx. 3 km) west of Rio Blanco store, at 2,179 masl, Rio Blanco County, Colorado, USA (Parachute Creek Member of the Green River Formation). Early Eocene (late Ypresian).

Etymology. From Mantispinae, and the Latin suffix *formis*, having the form of, referring to its resemblance to Mantispinae species.

Diagnosis. As for the genus.

Description. Male. Body 12.2 mm long.

Head. Head with large eyes; vertex appears moderately domed; postocular lobe very narrow; face appears elongate.

Thorax. Prothorax elongate, approximately 2.6 mm long, approximately 0.75 mm maximum width (in lateral view), slightly dilated near head; not appearing rugose dorsally and ventrally. Procoxa very long, approximately 2.6 mm; covered short setae. Profemur approximately 2.9 mm long, 0.8 mm wide, relatively broad; major (longest) spine approximately 0.65 mm long (Figure 2A and C; msp), nearly perpendicular to axis of profemur, located approximately at 0.34 its length; at least two to three smaller spines discernible distad it (Figure 2B; sp). Protibia fragmentarily preserved, appears terminating at longest spine (not clearly discernible); with rather short terminal spurs (one discernible). Protarsi very poorly preserved in both legs, but one pair of short ventral prostrate setae on second to fourth tarsomeres, possibly two pairs (or three setae) on first tarsomere, clearly discernible in right protarsus (Figure 4B; ts). Protibia plus protarsus slightly shorter than profemur. Structures of meso-, metathorax unclear. Mid-legs poorly discernible, probably incompletely preserved. Hind legs with elongate metafemur, approximately 0.9 mm long; metatibia narrow, relatively short, less than or equal to 1 mm; metatarsus not discernible.

Forewing narrow, approximately 7.3 mm long as preserved (estimated complete length approximately 8.5 mm), approximately 1.8 mm wide; venation fragmentarily preserved. Costal space moderately dilated in proximal portion; subcostal veinlets very poorly discernible except one, simple. ScP approaching to costal margin, but unclear if fused with it or not (poorly discernible), curved toward RA immediately before pterostigma. RA running far from costal margin, nearly parallel to it distally. Subcostal space dilated toward pterostigma, at least in right wing. Pterostigma incompletely preserved (distal part not preserved); incorporated veinlets not discernible, but numerous setae distinct. RP originates very far from wing base (at approximately 0.44 of estimated complete length). Space between RA and RP rather narrow; crossvein not discernible. Basal part of CuA distinct. Basal crossvein 1m-cu rather long, connecting fused R+M and CuA. Other venation poorly discernible.

Hind wing venation not discernable.

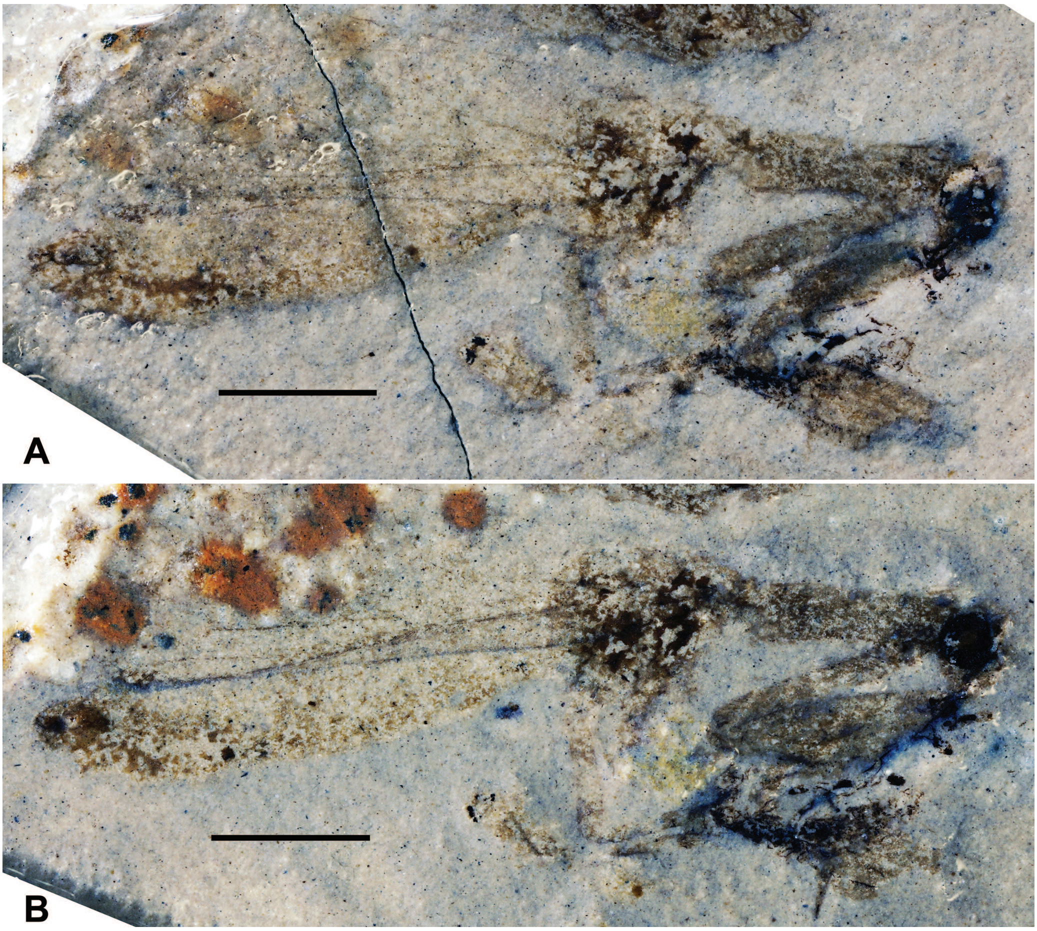

FIGURE 1. *Protonolima mantispinoformis* gen. et sp. nov., holotype (YPM IP 586369). **A.** Part (converted to standard right view). **B.** Counterpart. Both wetted by ethanol. Scale bars equal 2 mm.

Abdomen. Abdomen long, approximately 6.8 mm, rather stout; segmentation of proximal segments not discernible. Terminal segments (most reasonable interpretation): presumable tergite 9 relatively long; ectoproct elongate, broad; presumable sternite 8 large, elongated; presumable sternite 9 short, nearly quadrate in lateral view, extending beyond ectoproct (alterative interpretation: sternite 9 [S8 and S9 in Figure 4C] large, very long, extending beyond ectoproct).

Remarks. Dayvault et al. (1995:105) reported a "mantidfly" from the same locality ("Site B") without details. Unfortunately, the location of this specimen is unknown, and therefore it is impossible to verify this family assignment.

Discussion

Subfamily Placement of Protonolima mantispinoformis

The holotype and only known specimen of *Protonolima mantispinoformis* is poorly preserved. Its wings provide only a few characters that can be used in the determination of its subfamily. The prothorax and foreleg provide more characters, although these are also poorly preserved. The structure of the terminal segments of the male abdomen is hard to interpret due to poor preservation. Therefore, determination of its subfamily is problematic.

Five subfamilies of Mantispidae are currently recognized: Mesomantispinae (Middle Jurassic to Early Cretaceous), Drepanicinae (Late Cretaceous to Recent), Symphrasinae and Mantispinae (both Eocene to Recent), and Calomantispinae (Recent) (Jepson 2015; Liu et al. 2015). The profemora of Mesomantispinae and Symphrasinae bear no long spines (at least the major spine is absent), and therefore these subfamilies may be excluded from consideration. Three other subfamilies possess

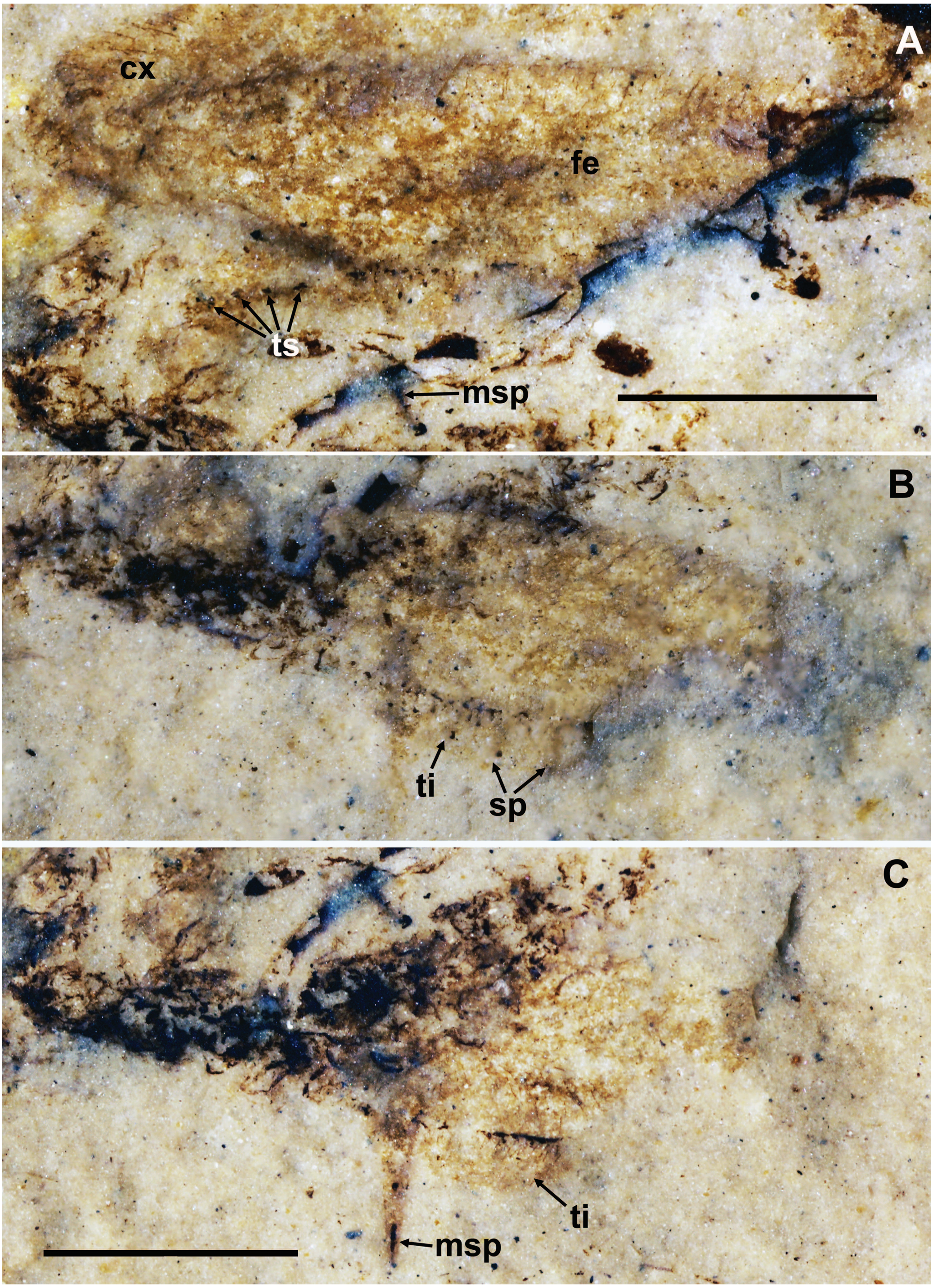

FIGURE 2. *Protonolima mantispinoformis* gen. et sp. nov., femora of the holotype (YPM IP 586369) (wetted by ethanol). **A.** Right profemur, counterpart. **B.** Left profemur, part (converted to standard right view). **C.** Left profemur, counterpart. *Abbreviations:* cx, coxa; fe, profemur; msp, major spine; sp, minor spines; ti, protibia; ts, tarsal prostrate setae. Scale bars equal 1 mm (B, C to same scale).

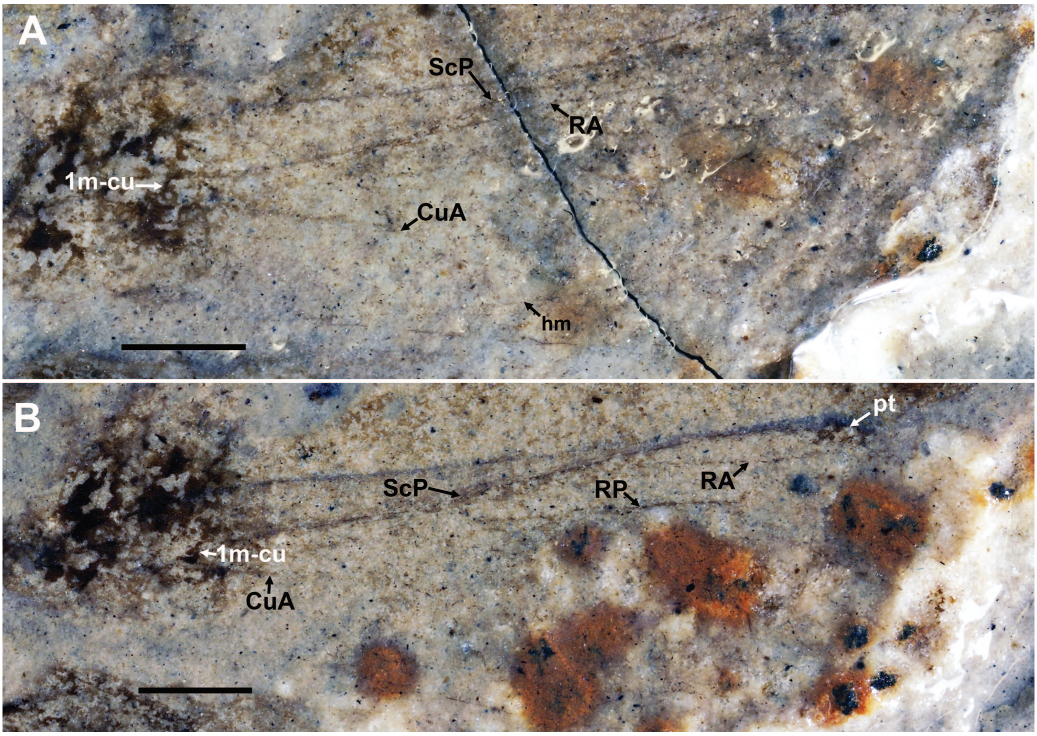

FIGURE 3. *Protonolima mantispinoformis* gen. et sp. nov., holotype (YPM IP 586369), forewings (wetted by ethanol). **A.** Left forewing, part (converted to standard right view). **B.** Right forewing, counterpart. *Abbreviations:* CuA, anterior cubitus; hm, hind margin; pt, pterostigma; RA, anterior radius; RP, posterior radius; ScP, posterior subcosta; 1m-cu, basal crossvein between media and cubitus. Scale bars equal 1 mm.

several elongate spines with the proximal-most being longest (i.e., the major spine is present).

Protonolima mantispinoformis superficially resembles some species of Mantispinae. Of these, its venation is most similar to that of those genera (e.g., *Climaciella* Enderlein, 1910, *Entanoneura* Enderlein, 1910, *Pseudoclimaciella* Handschin, 1960) in which RA runs parallel to and far from the costal margin in the pre-pterostigmal area after the apparent termination of ScP (RA is very close to the costal margin in this area in other Mantispinae). The subcostal space of these genera is not dilated distally; however, and the major spine is strongly inclined toward the femoral apex and located more distally than in *Protonolima mantispinoformis*. These character states are characteristic of all species of Mantispinae (see Lambkin 1986b; Machado and Raphael 2010; Snyman et al. 2012, 2018; Ardila-Camacho and García 2015; Ardila-Camacho et al. 2018). Also, the mantispine protarsomeres lack prostrate setae. Additionally, the protibia plus protarsus is markedly shorter than is the profemur in Mantispinae; this condition is considered an apomorphy of the subfamily (Liu et al. 2015). Therefore, although this specimen resembles some species of Mantispinae, it certainly does not belong to it.

The presence of tarsal prostrate setae in the foreleg of *Protonolima mantispinoformis* suggests that this genus belongs to either Drepanicinae or Calomantispinae.

Drepanicinae

The extant Drepanicinae comprise five genera and 39 species: *Drepanicus* Blanchard in Gay, 1851 and *Gerstaeckerella* Enderlein, 1910 (both from South America), *Ditaxis* McLachlan, 1867 and *Theristria* Gerstaecker, 1885 (both from Australia), and *Allomantispa* Liu et al., 2015 from southeastern Asia (Liu et al. 2015; Oswald 2018). Fossil representatives of the subfamily are restricted to the Mesozoic. The Jurassic genera *Liassochrysa*

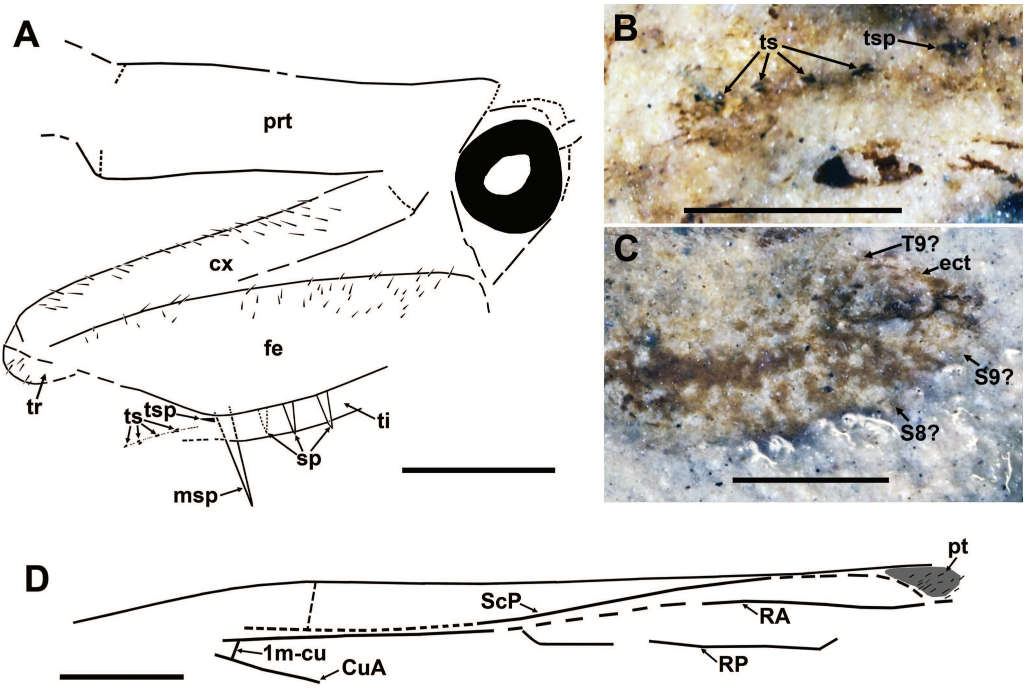

FIGURE 4. Details of the holotype of *Protonolima mantispinoformis* gen. et sp. nov. (YPM IP 586369). **A.** Anterior part of the body. **B.** Right protarsus (wetted by ethanol). **C.** Terminal segments of abdomen in lateral view (wetted by ethanol). **D.** Venation of the anterior part of the right forewing. *Abbreviations:* CuA, anterior cubitus; cx, procoxa; ect, ectoproct; fe, profemur; hm, hind margin; msp, major spine; prt, prothorax; pt, pterostigma; RA, anterior radius; RP, posterior radius; ScP, posterior subcosta; sp, minor spines; S8, 8th sternite; S9, 9th sternite; ti, protibia; tr, protrochanter; ts, tarsal prostrate setae; tsp, tibial spur; T9, 9th tergite; 1m-cu, basal crossvein between media and cubitus. Scale bars equal 1 mm (A, D, C) and 0.5 mm (B).

Ansorge and Schlüter, 1990 from Dobbertin (Germany) and *Promantispa* Panfilov, 1980 from Karatau (Kazakhstan) were assigned to Drepanicinae by Liu et al. (2015), but both are represented only by forewings, which in this case is problematic, as they differ from the forewings of typical Drepanicinae. *Gerstaeckerella asiatica* Makarkin, 1990 from the Late Cretaceous (early Turonian) of southern Kazakhstan is probably the only fossil species that unquestionably belongs to this subfamily; although it is only represented by a hind wing, this bears character states typical of the subfamily (see Makarkin and Khramov 2015:412, fig. 4C).

Protonolima mantispinoformis is dissimilar to most extant Drepanicinae by their robust prothorax and relatively broad forewings and costal space. The exception is most species of *Theristria*, for example, *T. discolor* (Westwood, 1852), *T. delicatula* (Westwood, 1852), and *T. pallida* Lambkin, 1986. Their prothorax is elongate, the major spine is perpendicular to axis of the profemur, the forewing is narrow, and the venation is similar to the preserved venation of *P. mantispinoformis* (see Lambkin 1986a:100, fig. 78). But in this genus, the profemur is not as dilated as in *P. mantispinoformis*, and the major spine is often located closer to its base. It is more important that in Drepanicinae (1) RP originates much closer to the wing base than in *P. mantispinoformis*, and (2) M is not fused with R, only approaching it proximad 1m-cu, and the crossvein 1m-cu connects M and CuA (M is apparently fused with R for a considerable distance, and therefore 1m-cu connects R+M and CuA in *P. mantispinoformis*). Therefore, based on these latter two character states, assignment of the new genus to Drepanicinae is rather unlikely.

Calomantispinae

The extant Calomantispinae comprise only two genera: *Calomantispa* Banks, 1913 with three

Australian species, and *Nolima* Navás, 1914 with three species distributed from the southern United States to Guyana (Oswald 2018). No fossil species have been reported.

The shape of the profemur of *Protonolima mantispinoformis* is very similar to that of all Calomantispinae (e.g., see Lambkin 1986b:71, fig. 434; Reynoso-Velasco and Contreras-Ramos 2008:707, fig. 21). Their major (longest) spine is located at approximately one-third profemur length, that is, similar to its location in *P. mantispinoformis*. The prothorax of *Calomantispa* is much shorter and stouter than in *P. mantispinoformis*, but the prothorax of *Nolima* is at least twice as long as wide, and it is especially elongate in *N. infensa* Navás, 1924. The general shape of the profemur and the arrangement of its spines in *P. mantispinoformis* are very similar to those of *Nolima* (see Reynoso-Velasco and Contreras-Ramos 2008:704, 707, figs. 1, 21).

The very distal origin of RP is characteristic of *Nolima*. For example, it originates at 0.48 of complete forewing length in *N. infensa*, that is, nearly in the middle (estimated based on fig. 544 in Hoffman 2002:421). By this condition, *P. mantispinoformis* is most similar to *Nolima*; its RP originates at 0.44 of estimated complete forewing length. In other Mantispidae, RP originates more proximally, even in Mantispinae.

In *Nolima*, M is fused with R for a considerable distance, and therefore crossvein 1m-cu connects CuA and R+M. Such character states are found in *P. mantispinoformis*.

Only two character states contradict assignment of the new genus to Calomantispinae: the forewing costal space is strongly dilated, and ScP joins the costa far from the pterostigma in all Calomantispinae (e.g., Lambkin 1986b:71, fig. 435; Hoffman 2002:421, fig. 544), contrary to the wing of *P. mantispinoformis*. However, ScP is relatively long in *Nolima victor* Navás, 1914, but it is still fused with the costa well before the pterostigma (Navás 1914:101, fig. 14). Also, the distal part of ScP is poorly discernible in *P. mantispinoformis*, and this vein may possibly be fused with the costa before the pterostigma.

The male terminalia of *Protonolima* appear to be similarly constructed to those of *Nolima* and *Calomantispa*. In the latter two genera, sternite 9 is large and very long, far extending beyond the ectoproct, and tergite 9 is narrow (very reduced in *Nolima*). Although the terminalia of *Protonolima* allow similar interpretation (see above, and Figure 4C), these are too poorly preserved to come to unambiguous conclusion.

Therefore, the new genus likely belongs to Calomantispinae, mainly on the basis of (1) the distal origin of RP and that (2) the crossvein 1m-cu connects R+M and CuA. The structure of the prothorax and forelegs as found in *P. mantispinoformis* may occur in both Calomantispinae and Drepanicinae. The relatively narrow costal space and the presumably long ScP of *P. mantispinoformis* should be regarded as plesiomorphic in Calomantispinae.

Protonolima is probably most closely related to the extant American genus *Nolima*, as its prothorax, forelegs, and forewing are most similar to those of *N. infensa*.

Cenozoic Mantispidae

Eight fossil species of Mantispidae are currently described from the Cenozoic, including *Protonolima mantispinoformis*. The new species likely represents the first record of Calomantispinae. It is the first Eocene Mantispidae with a preserved body. The mid-Eocene *Symphrasites eocenicus* from Messel (Germany) is represented by an incomplete forewing belonging to Symphrasinae, its only fossil record (Wedmann and Makarkin 2007). All other known species of the family from the Cenozoic belong to Mantispinae; of these, its oldest record is of first-instar larvae from late Eocene Baltic amber (Ohl 2011). Therefore, possibly three subfamilies are now known from the Eocene.

The latest Eocene *Vectispa relicta* from the Bembridge Marls (United Kingdom) is represented by two specimens: the holotype is a small wing fragment (see Cockerell 1921:478, fig. 46; Jarzembowski 1980:254, fig. 29), and the second specimen (In.24597) is a nearly compete forewing (see Jarzembowski 1980, fig. 30). These specimens may belong to different taxa, as the holotype has no specific character states (i.e., this wing fragment may belong to different genera of Mantispidae and even Chrysopidae). When *Vectispa relicta* has been discussed by authors, the second specimen (In.24597) has been meant, not the holotype.

Prosagittalata oligocenica Nel, 1989 from the early Oligocene of Cereste (France) is a small mantispine species; its body is 8.6 mm long. The relative length of its prothorax is nearly equal to that of *Protonolima mantispinoformis* (its prothorax/body length ratio is 0.22 in the former, 0.21 in the latter). The major spine of the profemur is located at 0.66 its length, that is, far distad its middle, a condition that rarely occurs in Mantispinae, where this spine is usually located slightly proximad the middle.

The other four fossil Cenozoic species are rather typical mantispines: *Climaciella*? *henrotayi* Nel, 1989 from the Early Oligocene of Dauphin (France); *Feroseta priscus* Poinar, 2006 from Miocene Dominican amber; *Dicromantispa moronei* Engel and Grimaldi, 2007 from Dominican amber; and *D. electromexicana* Engel and Grimaldi, 2007 from Miocene Mexican amber. These taxa were critically considered by Wedmann and Makarkin (2007) and by Jepson (2015).

Conclusion

The discovery of *Protonolima mantispinoformis*, the first mantispid species from the early Eocene Green River Formation is important. It is highly likely that this is the only fossil representative of the subfamily Calomantispinae, and is most similar to the southern North American to Mesoamerican genus *Nolima*. Previously, only two species of Neuroptera belonging to Berothidae and Myrmeleontidae have been described from this formation (Makarkin 2017a, 2017b). Of these, the myrmeleontid *Epignopholeon sophiae* Makarkin, 2017 is also most similar to taxa that are currently distributed in southern North America.

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