UNIWERSYTET RZESZOWSKI

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WYDZIAŁ BIOLOGICZNO-ROLNICZY

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EWOLUCJA NADRODZINY ANISOPODOIDEA KNAB, 1912 (DIPTERA, NEMATOCERA)

EVOLUTION OF SUPERFAMILY ANISOPODOIDEA KNAB, 1912 (DIPTERA, NEMATOCERA)

PRACA DOKTORSKA WYKONANA
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SPIS TREŚCI

1. STRESZCZENIE W JĘZYKU POLSKIM

MACIEJ WOJTOŃ – „Ewolucja nadrodziny Anisopodoidea Knab, 1912 (Diptera, Nematocera)”

STRESZCZENIE

Muchówki (Diptera), obejmujące obecnie około 160 tysięcy gatunków, pojawiły się na Ziemi około 245 mln lat temu, w triasie. W mezozoiku nastąpił ogromny wzrost tempa radiacji ewolucyjnej doprowadzając do zwiększenia różnorodności gatunkowej Diptera. Muchówki zgrupowane w nadrodzinie Anisopodoidea Knab, 1912 (Diptera: Nematocera) to współcześnie kosmopolityczna, lecz stosunkowo nieliczna grupa owadów, która przetrwała od triasu.

Kluczowe znaczenie dla poznania potencjalnych ścieżek ewolucji Anisopodoidea, miały materiały badawcze zachowane w jurajskich osadach i żywicach kredowych. W jurze i kredzie Anisopodoidea były znacznie zróżnicowane pod względem gatunkowym.

W trakcie badań zrealizowanych w ramach niniejszej pracy doktorskiej, wskazano i opisano 15 nowych dla nauki taksonów, dokonano redeskrypcji gatunku *Mycetobia connexa* Meunier, 1899, potwierdzono synonimikę tego gatunku z *Mycetobia callida* Meunier, 1904 zaproponowaną przez Edwardsa w 1928 r. Sporządzono dodatkowe opisy znanych już gatunków kopalnych: *Sylvicola splendida* Meunier, 1780, *Sylvicola thiriona* Meunier, 1907. Przesunięto zasięg stratygraficzny rodzaju *Mycetobia,* z eocenu (priabon, 37,2-33,9 Ma) na późną kredę (wczesny cenoman, 99,7-94,3 Ma). Wykonane analizy porównawcze kopalnych i współczesnych Anisopodoidea z wykorzystaniem elektronowego mikroskopu skaningowego umożliwiły wskazanie istotnych pod względem taksonomicznym cech struktur morfologicznych w materiale kopalnym. Określono potencjalne kierunki zmian ewolucyjnych Anisopodoidea, jakie zaszły od okresu jurajskiego.

2. STRESZCZENIE W JĘZYKU ANGIELSKIM

MACIEJ WOJTOŃ – „Evolution of superfamily Anisopodoidea Knab, 1912 (Diptera, Nematocera)"

ABSTRACT

Diptera, currently comprising about 160,000 species, appeared on the Earth about 245 million years ago, in the Triassic. In the Mesozoic there was a huge acceleration in evolutionary radiation, leading to increment of Diptera species diversity. Flies grouped in the superfamily Anisopodoidea Knab, 1912 (Diptera: Nematocera) is a contemporary cosmopolitan but relatively small group of insects that survived from the Triassic.

The research materials preserved in the Jurassic sediments and Cretaceous resins have been of key importance for understanding the potential pathways of Anisopodoidea evolution. In the Jurassic and the Cretaceous, Anisopodoidea were significantly differentiated in terms of species numbers.

During the research carried out as part of this doctoral thesis, 15 new taxa species were identified and described − *Mycetobia connexa* Meunier was redescribed and its formerly prosed by Edwards in 1928 synonymy with *Mycetobia callida* Meunier, 1904 was confirmed. Additional descriptions of the already known fossil species were presented − *Sylvicola splendida* Meunier, 1780, *Sylvicola thiriona* Meunier, 1907. The stratigraphic range of the genus *Mycetobia,* from Eocene (Priabonian, 37.2-33.9 Ma) for late Cretaceous (early Cenomanian, 99.7-94.3 Ma). Comparative studies of fossil and modern Anisopodoidea performed with the use of scanning electron microscopy enabled the identification of taxonomically significant features of morphological structures in fossil material. Potential directions of Anisopodoidea evolutionary changes that have occurred since the Jurassic period were determined.

SYNTEZA ROZPRAWY DOKTORSKIEJ

3. SYNTEZA ROZPRAWY DOKTORSKIEJ

3.1. WSTĘP

Muchówki (Diptera) obecnie zasiedlają niemal wszystkie kontynenty. Najczęściej owady te występują w środowiskach wilgotnych i ciepłych, o małej rocznej amplitudzie temperatur, a ich największą różnorodność obserwuje się w strefach klimatu tropikalnego oraz śródziemnomorskiego. Liczbę opisanych gatunków muchówek na całym świecie określa się na około 160 tysięcy (Marshall, 2012), przy czym w Polsce występuje ponad 7 tysięcy gatunków. W obrębie rzędu Diptera wyróżniamy dwa podrzędy: Nematocera (długorogie) i Brachycera (krótkorogie). Liczba gatunków przedstawicieli pierwszego z nich sięga 50 tysięcy (Szadziewski i in., 2012), a w Polsce znanych jest około 3300 – 3500 gatunków (Wiedeńska, 2007).

Muchówki są grupą siostrzaną wojsiłek (Mecoptera) – owadów, o charakterystycznie wydłużonym rostrum, wywodzą się od Mecopterida. Oba te rzędy owadów wraz z pchłami (Siphonaptera) mają wspólnego przodka i należą do grupy Anthliophora (Grimaldi i Engel, 2005). W zapisie kopalnym wojsiłki są znane już od dolnego permu, ale to w mezozoiku przeszły fazę największego rozkwitu. W mezozoiku nastąpił również ogromny skok radiacji ewolucyjnej doprowadzając do zwiększenia różnorodności gatunkowej Diptera.

Muchówki zgrupowane w nadrodzinie Anisopodoidea Knab, 1912 (Diptera: Nematocera) to współcześnie kosmopolityczna, lecz stosunkowo nieliczna grupa owadów o niewielkich rozmiarach. Należą tu rodziny Protorhyphidae Handlirsch, 1906, Anisopodidae Knab, 1912 i Siberhyphidae Kovalev, 1985 (Krzemiński i Krzemińska, 2003). Formy imaginalne Anisopodoidea spotykane są na ogół w siedliskach wilgotnych, w pobliżu butwiejących pni. Dorosłe osobniki odżywiają się zwykle nektarem kwiatów, zaś larwy tych owadów są saprofagiczne, najczęściej spotykane są w miejscach wzbogaconych w butwiejącą materię organiczną, w rozkładających się pniach drzew, szczątkach gnijących liści, a nawet w pobliżu oborników. Najstarsze Anisopodoidea znane są z triasu, z odcisków utrwalonych w osadach jeziornych (Blagoderov i in., 1993; Krzemińska i Krzemiński, 2003). Muchówki te znane są również z żywic kopalnych, w postaci inkluzji zachowały się w mioceńskim bursztynie dominikańskim, eoceńskim bursztynie bałtyckim, a także kredowym bursztynie birmańskim (Kania i in., 2019).

Głównym celem pracy doktorskiej było prześledzenie trendów ewolucyjnych muchówek z nadrodziny Anisopodoidea od okresu jurajskiego, momentu kiedy w zapisie kopalnym pojawiają się jedni z pierwszych przedstawicieli tej grupy owadów.

3.2. HIPOTEZY BADAWCZE

- Przedstawiciele Anisopodoidea wykazują zróżnicowanie morfologiczne i taksonomiczne;
- Podrodzina Mycetobiinae należy do rodziny Anisopodidae (weryfikacja rangi taksonomicznej grupy);
- Różnorodność morfologiczna i zróżnicowanie taksonomiczne Anisopodoidea (Diptera, Nematocera) pozwala na prześledzenie ich relacji filogenetycznych (rekonstrukcja dróg ewolucyjnych).

3.3. CELE BADAWCZE

- określenie i opis zróżnicowania morfologicznego oraz taksonomicznego kopalnych muchówek z nadrodziny Anisopodoidea Knab, 1912;
- ustalenie rangi badanych okazów, weryfikacja dotychczasowej przynależności do gatunków, rodzajów i rodzin w obrębie Anisopodoidea od okresu jurajskiego;
- redeskrypcje niektórych znanych już kopalnych gatunków w obrębie Anisopodoidea;
- wskazanie i opis taksonów nowych dla nauki;
- morfologiczna analiza porównawcza Anisopodoidea zachowanych w różnowiekowych żywicach kopalnych i skałach osadowych w odniesieniu do przedstawicieli tej grupy owadów występujących w współczesnej faunie światowej;
- określenie kierunków zmian ewolucyjnych u Anisopodoidea jakie zaszły od początków okresu jurajskiego.

3.4. Materiał i metody

Materiał badawczy stanowiły okazy kopalnych muchówek z grupy Anisopodoidea, zachowane w zarówno w postaci inkluzji w różnowiekowych żywicach kopalnych, jak i w postaci odcisków w skałach osadowych. Przeprowadzono badania ponad 100 okazów, ze względu na zróżnicowany stan zachowania okazów w publikacjach uwzględniono 47 z nich. Opracowano odciski w jurajskich osadach, jak i inkluzje w najstarszych żywicach kopalnych, w których zachowały się inkluzje zwierzęce, jak bursztyn birmański datowany na późną kredę (wczesny cenoman, 98.79 ± 0.62 Ma (Shi i in., 2012)) oraz młodszych, eoceńskich, jak bursztyn bałtycki (priabon, 37,2 – 33,9 Ma) (Grimaldi i Ross, 2017) czy bursztyn biterfeldzki (priabon, 37,2 – 33,9 Ma).

Materiał do badań pozyskano z kolekcji różnych jednostek naukowych na całym świecie: Instytutu Systematyki i Ewolucji Zwierząt Polskiej Akademii Nauk w Krakowie, Muzeum Inkluzji w Bursztynie Uniwersytetu Gdańskiego, Instytutu Geologii i Paleontologii Chińskiej Akademii Nauk w Nankinie (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences), Uniwersytetu w Pekinie (Capital Normal University), Muzeum Geologicznego Uniwersytetu w Getyndze (Museum for Geological Sciences of the University of Göttingen) oraz z kolekcji prywatnych: Christel i Hansa Wernera Hoffeinsów zdeponowanej w Niemieckim Instytucie Entomologicznym w Senckenberg (Senckenberg Deutsches Entomologisches Institut), kolekcji Andrzeja Górskiego, Bielsko-Biała, Polska - holotypy zdeponowane w ISEZ PAN w Krakowie.

Zastosowane metody i techniki badania okazów nie odbiegały od stosowanych powszechnie w badaniach paleoentomologicznych. Wykonano fotografie z wykorzystaniem mikroskopu stereoskopowego Nikon SMZ 1500 oraz kamery Nikon DS-Fi1. Część zdjęć została wykonana w Muzeum Geologicznym Uniwersytetu w Getyndze podczas pracy w kolekcji, w ramach stażu naukowego. W każdym przypadku wykorzystywano dodatkowe oświetlenie, dostosowane indywidualnie do poszczególnych inkluzji. Po obróbce komputerowej fotografie drukowano, większość z nich posłużyła do sporządzenia rysunków metodą dokładnego odwzorowania. Wykonano kilkaset rycin całych okazów, jak i poszczególnych części morfologicznych, takich jak przydatki głowowe (czułki, głaszczki), skrzydła, męskie i żeńskie aparaty kopulacyjne, bardzo istotne pod względem cech taksonomicznych w przypadku tej grupy owadów. Sporządzono także rekonstrukcje rysunkowe przedstawicieli poszczególnych rodzajów. Część fotografii i rycin zamieszczono w publikacjach. Podobnie w przypadku odcisków w osadach, zastosowano metodę dokładnego odwzorowania wykonując rysunki na wydrukach fotografii w oparciu o cechy widoczne bezpośrednio na okazie. Zarówno w pierwszym, jak i drugim przypadku niezmiernie ważne było zastosowanie odpowiedniego oświetlenia, istotny jest bowiem kąt padania światła oraz zastosowanie odpowiednich filtrów. Odciski Anisopodoidea w jurajskich skałach osadowych były fotografowane z wykorzystaniem kamery i odpowiedniego oprogramowania. Pomiary poszczególnych części ciała badanych okazów wykonano za pomocą programu NIS-Elements D 3.0. na cyfrowo zapisanym obrazie.

Do szczegółowej analizy morfologii Anisopodoidea wykorzystano okazy współczesne. Wykonano kilkaset zdjęć z wykorzystaniem elektronowego mikroskopu skaningowego Hitachi SU 8010 SEM w Centrum Innowacyjno-Badawczym Środowiska Uniwersytetu Rzeszowskiego.

Przyjęto system klasyfikacji Anisopodoidea z wyróżnieniem rodzin Protorhyphidae, Anisopodidae oraz Siberhyphidae za Krzemiński i Krzemińska (2003).

Klasyfikację Anisopodidae z wyróżnieniem czterech podrodzin: Anisopodinae, Mycetobiinae, Olbiogastrinae i Teginae (Shcherbakov i in., 1995; Lukashevich, 2012), przyjęto za Edwards'em (Edwards, 1928) oraz Michelsenem (1999) i Thompsonem (2006).

Analizę filogenetyczną przeprowadzono z wykorzystaniem oprogramowania Mesquite wersja 3.6 (Maddison i Maddison, 2011), TNT 1.1. (Goloboff i in., 2008), z algorytmem "New Technology Search" (Goloboff i in., 2008; Congreve i Lamsdell, 2016), WinClada v. 1.00.08 (Nixon, 2002). Do analizy filogenetycznej wykorzystano nowy zestaw cech, zarówno w przypadku eoceńskich Anisopodoidea, jak i kredowych przedstawicieli grupy.

3.5. WYNIKI

Rozprawa doktorska obejmuje cykl publikacji pt.:

"EWOLUCJA NADRODZINY ANISOPODOIDEA KNAB, 1912 (DIPTERA, NEMATOCERA)"/ "EVOLUTION OF SUPERFAMILY ANISOPODOIDEA KNAB, 1912 (DIPTERA, NEMATOCERA)"

[1] WOJTOŃ, M., KANIA, I., KOPEĆ, K. 2018. *Sylvicola* Harris, 1780 (Diptera: Anisopodidae) in the Eocene Resins. *Annales Zoologici* 68(4): 849–866. doi: 10.3161/00034541ANZ2018.68.4.009.

[2] WOJTOŃ M., KANIA I., KRZEMIŃSKI W., 2019. Review of *Mycetobia* Meigen, 1818 (Diptera, Anisopodoidea) in the Eocene ambers. *Zootaxa* 4544 (1): 001–040. https://doi.org/10.11646/zootaxa.4544.1.1

[3] KANIA I., WOJTOŃ M., LUKASHEVICH E., STANEK-TARKOWSKA J., WANG B., KRZEMIŃSKI W. 2019. Anisopodidae (Insecta: Diptera) from Upper Cretaceous Amber of Northern Myanmar, *Cretaceous Research* 94: 190–206. https://doi.org/10.1016/j.cretres.2018.10.013.

[4] KANIA I., WOJTOŃ M., KRZEMIŃSKI W. 2019. The oldest *Mycetobia* Meigen, 1818 (Diptera, Anisopodoidea) from Upper Cretaceous amber of northern Myanmar. *Cretaceous Research* 95: 302–309. https://doi.org/10.1016/j.cretres.2018.11.014.

[5] WOJTOŃ M., KANIA I., KRZEMIŃSKI W., DONG R. 2019. Phylogenetic relationships within the superfamily Anisopodoidea (Diptera: Nematocera), with description of new Jurassic species. *Palaeoentomology* [in press]

Prace wchodzące w skład rozprawy doktorskiej stanowią szczegółowe opracowanie kopalnych muchówek z grupy Anisopodoidea Knab, 1912 zachowanych w materiałach kopalnych pochodzących z eocenu, kredy, a także jurajskich przedstawicieli tej grupy owadów. Na okres jurajski przypada bardzo wczesny etap ewolucji Anisopodoidea, jednych z najstarszych przedstawicieli tej grupy owadów znamy właśnie z tego okresu. Materiały badawcze zachowane w postaci odcisków w jurajskich osadach pochodzących z Chin, to materiały bardzo cenne i znaczące przy analizie kierunków zmian całej grupy.

Liczne skamieniałości muchówek pochodzą z okresu kredowego i co najważniejsze, z tego przełomowego okresu znane są inkluzje w żywicach kopalnych. Szczególnie ważny jest bursztyn birmański, bogaty w inkluzje zachowanych w doskonałym stanie ciał owadów. Po raz pierwszy można obejrzeć wszystkie szczegóły morfologiczne owadów sprzed około 100 mln lat, z dużą dokładnością, porównywalną do tej z jaką oglądamy pod mikroskopem części ciała współczesnych owadów.

Szczegółowe analizy morfologiczne i taksonomiczne są elementem koniecznym i niezbędnym przy opisywaniu nowych dla nauki taksonów różnej rangi. W ramach realizacji pracy doktorskiej dokonano selekcji okazów i wykonano dokumentację wszystkich badanych okazów, w tym okazów wymienianych w pracach Meuniera z 1904 i 1909 roku. Niektóre gatunki opisane na początku XX wieku, wymagały redeskrypcji. Nowoczesne techniki badawcze umożliwiają szczegółową analizę morfologiczną i taksonomiczną okazów, nawet tych, których stan zachowania jest słaby. W pracach Meuniera (1904, 1907) i Scuddera (1890) autorzy podali jedynie bardzo krótkie, ogólne opisy gatunków, nie uwzględniające wzoru użyłkowania skrzydeł, jak również morfologii tak ważnych w taksonomii tych owadów aparatów kopulacyjnych, a także przydatków głowowych. Rewizja materiałów muzealnych oraz przebadanie nowych materiałów z wykorzystaniem zaawansowanych technik badawczych pozwoliła przede wszystkim na uszczegółowienie opisów znanych już taksonów, a także wyznaczenie i opisanie nowych dla nauki taksonów z określeniem ich pozycji systematycznej. Przeprowadzone badania pozwoliły na poznanie szczegółów morfologicznych kopalnych Anisopodoidea. Na tej podstawie określono i opisano potencjalne kierunki ewolucyjne tej nadrodziny. Dzięki przeprowadzonym badaniom możliwe było wyjaśnienie również wielu problemów związanych z wewnętrzną klasyfikacją grupy Anisopodoidea oraz momentu pojawienia się poszczególnych rodzin czy rodzajów.

Kluczowe znaczenie dla realizacji celów pracy miały materiały jurajskie. Z jury znane są jedne z najstarszych Anisopodoidea, w tym przedstawiciele rodziny Protorhyphidae, jedynie kilka gatunków znanych jest z triasu. Duże znaczenie miały również inkluzje Anisopodoidea zachowane w kredowym bursztynie birmańskim (ok. 100 mln lat). Zróżnicowany wiek materiałów badawczych i położenie geograficzne stanowisk, z których pochodziły, dały okazję do interesujących studiów porównawczych.

W trakcie badań uzyskano następujące wyniki:

1. Wskazano i opisano **nowy dla nauki rodzaj:** *Cretolbia* Kania, Wojtoń, Lukashevich, Wang i Krzemiński, 2019.
2. Wskazano i opisano **15 nowych dla nauki gatunków**: *Sylvicola baltica* Wojtoń, Kania i Kopeć, 2018; *Sylvicola hoffeinsorum* Wojtoń, Kania i Kopeć, 2018; *Sylvicola punctata* Wojtoń, Kania i Kopeć, 2018; *Cretolbia hukawnga* Kania, Wojtoń, Lukashevich, Wang i Krzemiński, 2019; *Cretolbia burmitica* Kania, Wojtoń, Lukashevich, Wang i Krzemiński, 2019; *Cretolbia zhoudei* Kania, Wojtoń, Lukashevich, Wang i Krzemiński, 2019; *Mesorhyphus blagoderovi* Wojtoń, Kania, Kopeć i Dong, 2019; *Mycetobia christelae* Wojtoń, Kania i Krzemiński, 2019; *Mycetobia hansi* Wojtoń, Kania i Krzemiński, 2019; *Mycetobia myanmara* Kania, Wojtoń i Krzemiński, 2019; *Mycetobia silvia* Wojtoń, Kania i Krzemiński, 2019; *Mycetobia szwedoi* Wojtoń, Kania i Krzemiński, 2019; *Mycetobia perkovskyi* Wojtoń, Kania i Krzemiński, 2019; *Protorhyphus lukashevichae* Wojtoń, Kania, Krzemiński i Dong, 2019; *Protorhyphus jurassicus* Wojtoń, Kania, Krzemiński i Dong, 2019.
3. Dokonano **redeskrypcji** *Mycetobia connexa* Meunier, 1899, gatunku znanego z eoceńskiego bursztynu bałtyckiego.
4. Sporządzono **dodatkowe opisy** znanych już gatunków kopalnych: *Sylvicola splendida* Meunier, 1780, *Sylvicola thiriona* Meunier, 1907.
5. Podjęto następujące decyzje taksonomiczne:

   - potwierdzono synonimikę kopalnych gatunków *Mycetobia connexa* Meunier, 1899 i *Mycetobia callida* zaproponowaną przez Edwardsa w 1928 r.;

   - Taksony: *Mycetobia longipennis* Meunier, 1899; *Mycetobia platyuroides* Meunier, 1899; *Mycetobia terricola* (Scudder, 1878) uznane zostały za *nomina dubia*, taksony *Mycetobia unicalcarata*: Keilbach, 1982, *Mycetobia parallela*: Keilbach, 1982 uznane zostały za *nomina nuda*, przyjęto również za Keilbachem (1982), że gatunek *Mycetobia defectiva* Loew, 1850 zaklasyfikowany został do innego rodzaju jako *Symmerus defectivus* (Loew, 1850), a gatunek *Mycetobia macrocera* Meunier, 1899 jako *Paleoplatyura macrocera* Meunier, 1899.

6. Przesunięto zasięg stratygraficzny rodzaju *Mycetobia* z eocenu (priabon, 37,2 – 33,9 Ma) na późną kredę (wczesny cenoman, 99,7 – 94,3 Ma).
7. Wykonane analizy porównawcze kopalnych i współczesnych Anisopodoidea z wykorzystaniem elektronowego mikroskopu skaningowego umożliwiły porównanie i wskazanie istotnych pod względem taksonomicznym cech struktur morfologicznych w materiale kopalnym.
8. Przeprowadzono analizę filogenetyczną i wskazano blisko powiązane ze sobą taksony w obrębie Anisopodoidea.
9. Określono potencjalne kierunki zmian ewolucyjnych Anisopodoidea, jakie zaszły od okresu jurajskiego.

Pierwsza praca z cyklu [1] obejmuje szczegółowe opracowanie kopalnych muchówek z rodzaju *Sylvicola* Harris, 1780 z eoceńskich żywic kopalnych. Szczegółowa analiza morfologiczna inkluzji pozwoliła na uzupełnienie opisów dwóch gatunków opisanych w 1907 roku *Sylvicola splendida* Meunier, 1907 i *Sylvicola thiriona* Meunier, 1907 oraz deskrypcje trzech nowych dla nauki gatunków *Sylvicola baltica* Wojtoń i in., 2018, *Sylvicola hoffeinsorum* Wojtoń i in., 2018, *Sylvicola punctata* Wojtoń i in., 2018. W pracy zamieszczono klucz do oznaczania gatunków z rodzaju *Sylvicola* znanych z eoceńskich żywic kopalnych oparty o nowy zestaw cech diagnostycznych, jak również dyskusję nad szczegółami morfologii ciała gatunków kopalnych i współczesnych w obrębie rodzaju *Sylvicola*. Analizy porównawcze przeprowadzono z wykorzystaniem elektronowego mikroskopu skaningowego.

W drugiej pracy z cyklu [2] ujęto wyniki rewizji rodzaju *Mycetobia* Meigen, 1818, zachowanych w formie inkluzji w eoceńskich żywicach kopalnych. Dzięki badaniom, przeprowadzonym w ramach pracy doktorskiej, kopalnych okazów muchówek z rodzaju *Mycetobia*, opisywanych wcześniej przez Meunier'a (1899, 1904) zdeponowanych w Muzeum Geologicznym Uniwersytetu w Getyndze możliwa była weryfikacja ich dotychczasowej przynależności do gatunków. W pracy ujęto diagnozę oraz dodatkowy opis gatunku *Mycetobia connexa* Meunier, 1907 oraz pięciu gatunków nowych dla nauki *Mycetobia christelae* Wojtoń i in., 2019, *Mycetobia hansi* Wojtoń i in., 2019 (Ryc. 2B), *Mycetobia silvia* Wojtoń i in., 2019, *Mycetobia szwedoi* Wojtoń i in., 2019, *Mycetobia perkovskyi* Wojtoń i in., 2019, a także porównanie charakteru użyłkowania skrzydeł eoceńskich przedstawicieli rodzaju *Mycetobia*. W wyniku przeprowadzonej rewizji wyjaśniono pozycję taksonomiczną pozostałych eoceńskich gatunków opisanych w obrębie rodzaju. Praca obejmuje również dyskusję na temat zróżnicowania gatunków wymarłych i współczesnych w obrębie rodzaju *Mycetobia* oraz ich występowaniu na Ziemi w odniesieniu do warunków klimatycznych.

Trzecia praca z cyklu [3] obejmuje opis nowego dla nauki rodzaju *Cretolbia* Kania i in., 2019 należącego do rodziny Anisopodidae, podrodziny Olbiogastrinae oraz trzech nowych dla nauki gatunków w obrębie rodzaju *Cretolbia*: *Cretolbia hukawnga* Kania i in., 2019, *Cretolbia burmitica* Kania i in., 2019, *Cretolbia zhuodei* Kania i in., 2019. Przedstawicieli rodzaju *Cretolbia* odkryto wśród inkluzji muchówek w kredowym bursztynie birmańskim (RYC. 2C). Rodzaj ten różni się on od pozostałych rodzajów w obrębie Anisopodoidea głównie takimi cechami jak: budowa oczu - oczy samców rodzaju *Cretolbia* są holoptyczne, podczas gdy oczy samic dichoptyczne, bez dodatkowych szczecinek, przyoczka tworzą równoboczny trójkąt, zaś 16-członowe czułki nie są dłuższe od tułowia, poszczególne człony biczyka są cylindryczne, długości równej dwukrotnej szerokości każdego z członów, głaszczek zbudowany jest z pięciu członów, ze znacznie zredukowanym członem nasadowym, skrzydła są szerokie bez wyraźnych plam barwnych z wyjątkiem bardzo ciemno ubarwionej pterostigmy otaczającej dystalną część żyłki R_1. Szczegółowy opis cech diagnostycznych dla rodzaju w zestawieniu z cechami charakterystycznymi pozostałych rodzajów w obrębie Anisopodoidea zamieszczono w publikacji.

W czwartej pracy z cyklu [4] zamieszczono opis najstarszego gatunku z rodzaju *Mycetobia* (RYC. 1). Odkrycie pierwszego przedstawiciela rodzaju *Mycetobia* w kredowym bursztynie birmańskim (98.79 ± 0.62 Ma (Shi i in., 2012)) to niepodważalny dowód na to, iż owady te występowały na Ziemi znacznie wcześniej niż dotychczas sądzono. Najstarsi przedstawiciele rodzaju *Mycetobia* znani byli do tej pory z eocenu (około 40 mln lat).

Ostatnia praca z cyklu [5] stanowi część podsumowującą, syntetyczne opracowanie i wskazanie potencjalnych dróg ewolucji Anisopodoidea od okresu jurajskiego. Opisano dwa nowe gatunki jurajskich Protorhyphidae: *Protorhyphus lukashevichae* Wojtoń i in., 2019, *Protorhyphus jurassicus* Wojtoń i in., 2019 oraz nowy gatunek przedstawiciela Anisopodidae z jury: *Mesorhyphus blagoderovi* Wojtoń i in., 2019 (RYC. 2A, D).

3.6. Dyskusja

Przeprowadzone rewizje oraz nowe materiały badawcze pozwoliły na określenie i opis zróżnicowania morfologicznego oraz taksonomicznego kopalnych muchówek z nadrodziny Anisopodoidea, jak również umożliwiły wyjaśnienie pozycji taksonomicznej niektórych taksonów. Dzięki przeprowadzonym analizom porównawczym Anisopodoidea zachowanych w różnowiekowych żywicach kopalnych i skałach osadowych w odniesieniu do przedstawicieli współczesnych tej grupy owadów możliwym stało się również wskazanie oraz opis nowych dla nauki taksonów.

Mimo, iż zapis kopalny nie jest kompletny, możliwe jest wskazanie tendencji ewolucyjnych Anisopodoidea. Szczególnie wyraźnie widać to w zmieniającym się w drodze ewolucji użyłkowaniu skrzydeł tej grupy owadów. Najstarsze wśród Anisopodoidea Protorhypidae charakteryzują się obecnością pięciu żyłek radialnych, natomiast u Anisopodidae obecne są cztery żyłki radialne. Rodzaj *Brachyrhyphus* Blagoderov i Grimaldi, 2007 jest najprawdopodobniej formą pośrednią pomiędzy Protorhyphidae i Anisopodidae, co było dyskutowane już przez Blagoderova i Grimaldiego (2007). Ten unikatowy triasowy rodzaj charakteryzuje się występowaniem skróconej żyłki radialnej R_4, a u wszystkich pozostałych Protorhypidae żyłka ta jest wyraźnie wydłużona, natomiast u Anisopodidae obserwuje się wyraźne zlanie tej żyłki z żyłką R_5 w R_{4+5}. Natomiast u przedstawiciela Siberhyphidae występują jedynie dwie żyłki radialne.

Najstarsze Protorhyphidae znane są z triasu. Liczne gatunki reprezentowane są w jurajskim zapisie kopalnym (Krzemiński i Krzemińska, 2003). Nie ma dowodów na to, że grupa ta przetrwała na Ziemi dłużej niż do okresu kredowego. Pierwsze pojedyncze gatunki Anisopodidae znane są z okresu jurajskiego, ta grupa owadów jest licznie reprezentowana w zapisie późnojurajskim i wczesnokredowym. Do dnia dzisiejszego przetrwały nieliczne rodzaje, dwa z nich *Sylvicola* i *Olbiogaster* pojawiły się we wczesnej kredzie, dwa pozostałe, pojawiły się później, wśród nich *Mycetobia* – najstarsza znana z późnej kredy i blisko spokrewniona z nią *Mesochria* – najstarsza znana z eocenu. W holocenie pojawiają się rodzaje takie jak *Lobogaster* czy *Carreraia* znane jedynie współcześnie i nie ma dowodów na to, iż występowały one wcześniej.

3.7. Wnioski

- Najstarszą grupą w obrębie Anisopodoidea (*sensu* Krzemiński and Krzemińska, 2003: Protorhyphidae, Siberhyphidae, Anisopodidae) są Protorhyphidae.
- Protorhyphidae to wymarła grupa rodzina muchówek najliczniej reprezentowana w triasowym i jurajskim zapisie kopalnym.
- Anisopodidae pojawiły się na Ziemi w okresie jurajskim, zapis kopalny dowodzi, iż były one najbardziej zróżnicowane pod względem taksonomicznym na przełomie jury i kredy.
- Spośród rodzajów w obrębie Anisopodidae, reprezentowanych w materiale kopalnym, jedynie cztery przetrwały i występują w faunie współczesnej.
- Rodzaje *Carreraia* i *Lobogaster* (Anisopodidae) reprezentowane są jedynie w faunie współczesnej, nie ma dowodów na występowanie przedstawicieli ww. rodzajów wcześniej na Ziemi.
- W obrębie Anisopodoidea można wyróżnić klady obejmujące rodziny: Protorhyphidae i Anisopodidae.
- Blisko spokrewnione w obrębie Anisopodoidea są rodzaje *Mycetobia* i *Mesochria*, a także rodzaje *Cretolbia*, *Olbiogaster* i *Lobogaster*.

3.8. Podsumowanie

Dzięki badaniom różnowiekowych materiałów kopalnych w odniesieniu do współczesnych materiałów badawczych możliwe stało się wykazanie potencjalnych dróg ewolucji Anisopodoidea. Informacje jakie niesie zapis kopalny dostarczył cennych wskazówek dotyczących przebiegu ewolucji grupy.

3.9. PIŚMIENNICTWO

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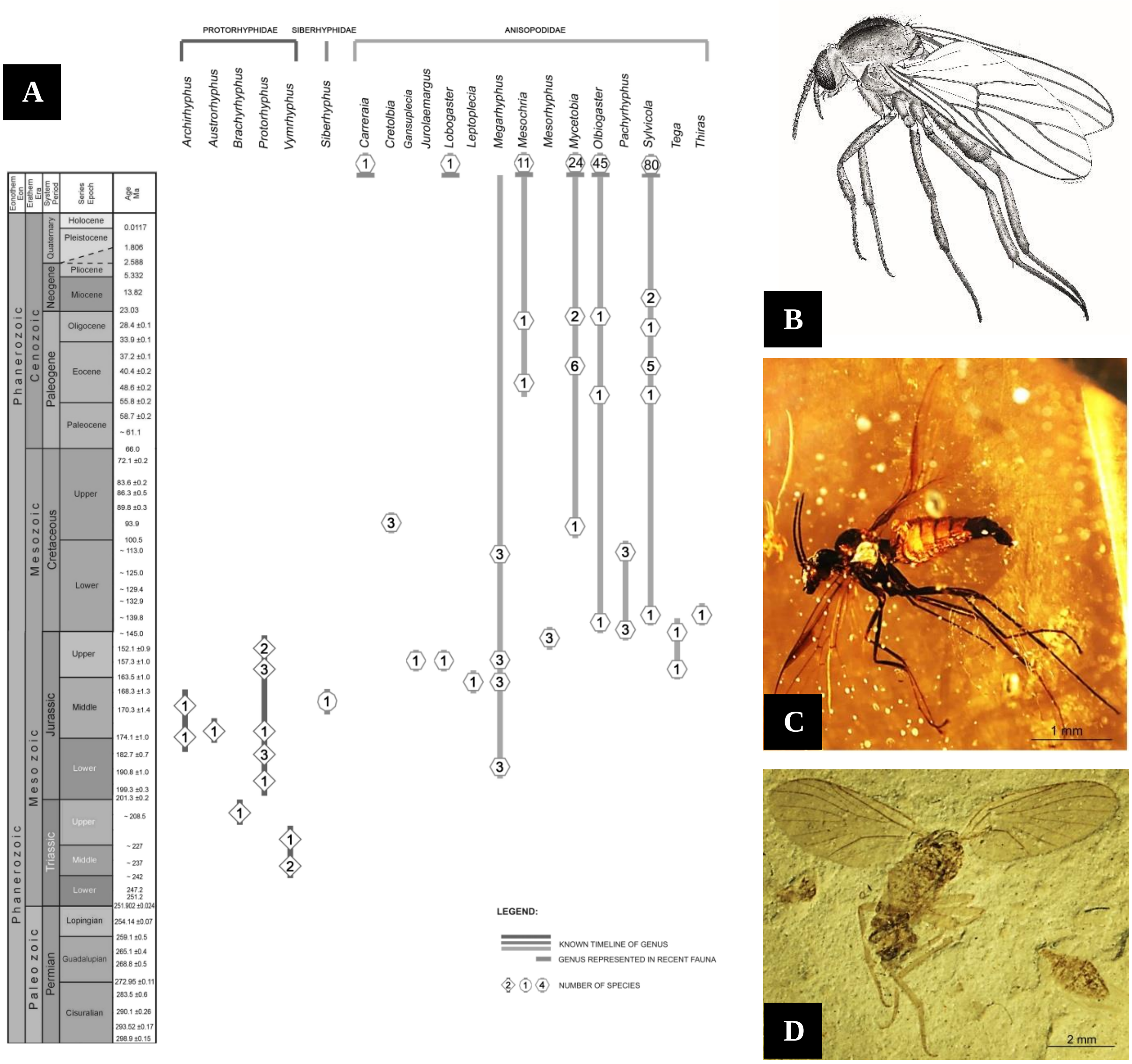
RYCINA 1. Najstarszy przedstawiciel rodzaju *Mycetobia*, gatunek opisany na podstawie inkluzji w kredowym w bursztynie birmańskim (za Kania i in., 2019).



RYCINA 2. A. Zasięg stratygraficzny przedstawicieli Anisopodoidea z podaną liczbą gatunków (za Wojtoń i in., 2019); B. *Mycetobia hansi* Wojtoń i in., 2019, gatunek reprezentowany w eoceńskim bursztynie bałtyckim, rekonstrukcja; C. Inkluzja przedstawiciela nowego dla nauki rodzaju w kredowym bursztynie birmańskim (za Kania i in., 2019); D. Muchówka z rodzaju *Protorhyphus* zachowana w triasowych osadach pochodzących z Chin (za Wojtoń i in., 2019).

WYKAZ PUBLIKACJI NAUKOWYCH WCHODZĄCYCH W SKŁAD ROZPRAWY DOKTORSKIEJ

4. WYKAZ PUBLIKACJI NAUKOWYCH WCHODZĄCYCH W SKŁAD ROZPRAWY DOKTORSKIEJ

1. WOJTOŃ, M., KANIA, I., KOPEĆ, K. 2018. *Sylvicola* Harris, 1780 (Diptera: Anisopodidae) in the Eocene Resins. *Annales Zoologici*. 68(4): 849–866. doi: 10.3161/00034541ANZ2018.68.4.009.

   IF = 0,732/pkt. MNiSW $_{2013\text{-}2016}$ = 25*

2. WOJTOŃ M., KANIA I., KRZEMIŃSKI W., 2019. Review of *Mycetobia* Meigen, 1818 (Diptera, Anisopodoidea) in the Eocene ambers. *Zootaxa*. 4544 (1): 001–040. https://doi.org/10.11646/zootaxa.4544.1.1

   IF = 0,931/pkt. MNiSW $_{2013\text{-}2016}$ = 20*

3. KANIA I., WOJTOŃ M., LUKASHEVICH E., STANEK-TARKOWSKA J., WANG B., KRZEMIŃSKI W. 2019. Anisopodidae (Insecta: Diptera) from Upper Cretaceous Amber of Northern Myanmar. *Cretaceous Research*. 94: 190–206. https://doi.org/10.1016/j.cretres.2018.10.013.

   IF = 2,196/pkt. MNiSW $_{2013\text{-}2016}$ = 40*

4. KANIA I., WOJTOŃ M., KRZEMIŃSKI W. 2019. The oldest *Mycetobia* Meigen, 1818 (Diptera, Anisopodoidea) from Upper Cretaceous amber of northern Myanmar. *Cretaceous Research*. 95: 302–309. https://doi.org/10.1016/j.cretres.2018.11.014.

   IF = 2,196/pkt. MNiSW $_{2013\text{-}2016}$ = 40*

5. WOJTOŃ M., KANIA I., KRZEMIŃSKI W., DONG R. 2019. Phylogenetic relationships within the superfamily Anisopodoidea (Diptera: Nematocera), with description of new Jurassic species. *Palaeoentomology* [in press]

   IF /pkt. MNiSW – nie dotyczy

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pkt. MNiSW: 25; IF: 0,732

Sylvicola Harris, 1780 (Diptera: Anisopodidae) in the Eocene Resins

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ANNALES ZOOLOGICI (Warszawa), 2018, 68(4): 849-866

SYLVICOLA HARRIS, 1780 (DIPTERA: ANISOPODIDAE) IN THE EOCENE RESINS

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Abstract.— New information on the genus *Sylvicola* Harris, 1780 from the Eocene is presented. Additional descriptions of *Sylvicola splendida* Meunier, 1907 and *Sylvicola thiriona* Meunier, 1907 known from Baltic amber are given. Descriptions of three new species of *Sylvicola* from Eocene resins are stated: *Sylvicola baltica* **sp. nov.**, *Sylvicola hoffeinsorum* **sp. nov.**, *Sylvicola punctata* **sp. nov.** Analyses of the morphological structures and taxonomical differences among representatives within the genus *Sylvicola* have been carried out. Key to the species of Sylvicola known from the Eocene resins is given.

Key words.— fossil insects, inclusions, morphology, taxonomy, *Sylvicola*, new species

Introduction

The representatives of the genus *Sylvicola* Harris, 1780 (Diptera, Anisopodidae) are characterized by hyaline membrane or with pattern of dark markings, pterostigma is present or absent, membrane is densely covered with microtrichia, macrotrichia are present on veins (McAlpine, 1981) (Fig. 1).

In recent fauna there are ca. 80 species which occur on all continents except Antarctica. The first information on fossil *Sylvicola* were given by Heer (1849) and Scudder (1890). The oldest representative of *Sylvicola* is known from Lower Cretaceous of England – *Sylvicola prisca* Westwood, 1845. A few species are known from earlier periods. Heer (1849) described two species from Miocene of Croatia: *Sylvicola lugubris* Heer, 1849, *Sylvicola maculata* Heer, 1849 previously classified as *Rhyphus*. Lewis (1969) also described species from Miocene – *Sylvicola carolae* Lewis, 1969. One unidentified species but classified to genus *Sylvicola* was ascribed by Guérin-Méneville, 1838 from Miocene of Sicily (Table 1). Another unidentified species of *Sylvicola* is known from Oligocene of France (Serres, 1829). There are four known species from Eocene or from fossil materials dated on the border of Eocene and Oligocene like *Sylvicola cadaver* Scudder, 1890 (USA) or *Sylvicola hooleyi* Cockerell, 1921 (England), amongst which were only two species known from Baltic amber: *Sylvicola splendida* Meunier, 1907 and *Sylvicola thiriona* Meunier, 1907 (Evenhuis, 1994, 2014) (Table 2). New research on Eocene inclusions of *Sylvicola* have enabled us to find three new species.

Material and methods

The study was based on material (16 inclusions) in Baltic amber aged on Eocene, Lutetian–Priabonian (Grimaldi and Ross, 2017) and Bitterfeld amber also aged for Eocene. From the collection of Institute of Systematics and Evolution of Animals Polish Academy of

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Sciences (ISEA PAS) (four specimens); collection of Museum of Amber Inclusions, University of Gdańsk (MAIG) (one specimen); collection of Christel and Hans Werner Hoffeins – ten specimens deposited in Senckenberg Deutsches Entomologisches Institut (SDEI), Müncheberg, Germany and one specimen from the collection of Andrzej Górski (Bielsko-Biała, Poland), deposited in ISEA PAS. Specimens were studied using a Nikon SMZ 1500 stereomicroscope equipped with a Nikon DS–Fi1 camera and the measurements were taken with NIS–Elements D 3.0 software in University of Rzeszów. The drawings for the analysis were based on the specimen and photographs. The drawings of wings and reconstruction of habitus were made by Maciej Wojtoń. The measurements of specimens were taken with NIS–Elements D 3.0 software in University of Rzeszów. The measurements were made as follow: the length of head—length of head capsule; measurements were made at widest point and maximum length. The measurements were given only in case where relevant structures were not distorted. The nomenclature of male genitalia, thorax and structures which occur on thorax were used after Grimaldi, 1991, nomenclature of wing venation is given after Krzemińska *et al.*, 2009. The paper strictly follows the International Code of Zoological Nomenclature.

Results

Systematic palaeontology

Order: **Diptera** Linnaeus, 1758

Suborder: **Nematocera** Duméril, 1805

Infraorder: **Bibionomorpha** Hennig, 1954

Superfamily: **Anisopodoidea** Knab, 1912

Family: **Anisopodidae** Knab, 1912

Genus: ***Sylvicola*** Harris, 1780

Type species: *Sylvicola brevis* Harris, 1780 [= *Tipula fenestralis* Scopoli, 1763], by subsequent designation of Coquillett (1910: 610).
Phryne Meigen, 1800: 16. Suppressed by I.C.Z.N. (1963: 339).
1803 *Anisopus* Meigen, p. 264.
Type species: *Anisopus fuscus* Meigen, 1804 [= *Tipula fuscata* Fabricius, 1775], by subsequent designation of Coquillett (1910: 507).
1804 *Rhyphus* Latreille, p. 188.
Type species: *Tipula fenestralis* Scopoli, 1763 [as "fenestrarum"], by monotypy.
1856 *Bria* Giebel, p. 226.
Type species: *Rhyphus priscus* Westwood, 1845 (as "*priscus* Brodie"), by monotypy.
1890 *Asarcomyia* Scudder, p. 567.
Type species: *Asarcomyia cadaver* Scudder, 1890, by monotypy.

Key to species of the genus *Sylvicola* Harris, 1780 from Eocene resins

1. Antenna as long as head or shorter .... ***Sylvicola thiriona*** Meunier, 1907
–. Antenna longer than head **2**
2. Tarsus with very small empodium, much smaller than claws; ocelli form equilateral triangle .... ***Sylvicola splendida*** Meunier, 1907
–. Tarsus with large empodium; ocelli form scalene triangle **3**
3. All flagellomeres longer than they are wide; last flagellomere elongated, approximately 6× as long as it is wide; last palpomere very elongated, approximately 7× as long as it is wide .... ***Sylvicola baltica*** sp. nov.
–. At least one flagellomere shorter than it is wide; last flagellomere elongated, but up to 3× as long as it is wide; last palpomere elongated, but up to 3× as long as it is wide **4**
4. Cross vein m-m is as long as m'-m'; the distance between Sc and R_1 apices approximately 3× the distance between R_1 and R_{2+3} apices; additional, dark spot beyond stigmal area .... ***Sylvicola punctata*** sp. nov.
–. Cross vein m-m is longer than m'-m'; the distance between Sc and R_1 apices approximately 1.5× the distance between R_1 and R_{2+3} apices; wing without additional, dark spot beyond stigmal area .... ***Sylvicola hoffeinsorum*** sp. nov.

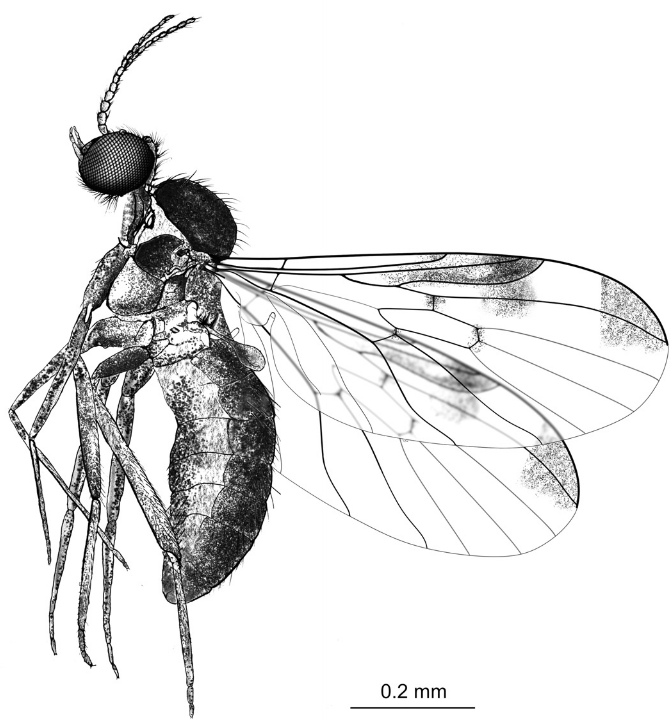

Figure 1. *Sylvicola punctata* sp. nov., reconstruction by Maciej Wojtoń.

Table 1. List of species of the genus *Sylvicola* known so far.

Species	Origin	Period
Sylvicola carolae Lewis, 1969	Imprint, USA	Miocene
Sylvicola lugubris Heer, 1849	Imprint, Croatia	Miocene
Sylvicola maculata Heer, 1849	Imprint, Croatia	Miocene
Unidentified sp.	Sicilian amber	Miocene
Sylvicola hooleyi Cockerell, 1921	Imprint, UK	Eocene/Oligocene
Unidentified sp.	Imprint, France	Oligocene
Sylvicola splendida Meunier, 1907	Baltic amber	Eocene
Sylvicola thiriona Meunier, 1907	Baltic amber	Eocene
Sylvicola cadaver Scudder, 1890	Imprint, USA	Eocene
Sylvicola prisca Westwood, 1845	Imprint, UK	Cretaceous

Sylvicola splendida Meunier, 1907
(Figs 2–4)

Diagnostic characters. Ocelli form equilateral triangle; antenna longer than head, flagellomeres 1–7 as long as they are wide or wider than long; 8–14 longer than they are wide, last flagellomere approximately 2× as long as it is wide; last palpomere 3.5× as long as it is wide, as long as the second one; the distance between Sc and R_1 apices approximately twice the distance between R_1 and R_{2+3} apices; cross vein m-m longer than m’-m’; the distance between M_3 and M_4 apices shorter than the distance between M_1 and M_2, M_2 and M_3 apices; width between M_4 and Cu up to 2× the width between M_3 and M_4 in widest place; d-cell elongated, approximately 3.5× to 4× as long as it is wide; empodium small, claw large, longer than empodium.

Material examined. No. 787-1 (female), No. 923-1 (male), No. 664-1 (sex unknown), (SDEI), coll. Ch. & H.W. Hoffeins; No. MP/1425 (female); MP/1426 (sex unknown); coll. Institute Systematics and Evolution, Polish Academy of Sciences (ISEA PAS).

Additional description. Body (Fig. 3A, F) 3.14–4.07 mm long, brown with brown legs. Head width (Fig. 3B, G) 0.72–1.06 mm, 0.49–0.66 mm high. Head and thorax combined 1.53–2.17 mm. Dichoptic eyes occupying

Table 2. List of species of the genus *Sylvicola* revised and described herein.

Species	The number of specimen	Material examined	Sex	Age	Collection
S. splendida Meunier, 1907	787-1	addit. mat.	female	Baltic amber	SDEI/coll. Ch. & H.W. Hoffeins
	923-1	addit. mat.	male	Baltic amber	SDEI/coll. Ch. & H.W. Hoffeins
	664-1	addit. mat.	unknown	Bitterfeld amber	SDEI/coll. Ch. & H.W. Hoffeins
	MP/1425	addit. mat.	female	Baltic amber	ISEA PAS
	MP/1426	addit. mat.	unknown	Baltic amber	ISEA PAS
S. thiriona Meunier, 1907	644-4	addit. mat.	unknown	Baltic amber	SDEI/coll. Ch. & H. W. Hoffeins
S. baltica sp. nov.	1258-1	holotype	male	Baltic amber	SDEI/coll. Ch. & H. W. Hoffeins
S. hoffeinsorum sp. nov.	773a	holotype	male	Baltic amber	MAIG
	189-2	addit. mat.	male	Baltic amber	SDEI/coll. Ch. & H.W. Hoffeins
	1789-2	addit. mat.	male	Baltic amber	SDEI/coll. Ch. & H.W. Hoffeins
	664-2	addit. mat.	female	Bitterfeld amber	SDEI/coll. Ch. & H.W. Hoffeins
	70-3	addit. mat.	female	Baltic amber	SDEI/coll. Ch. & H.W. Hoffeins
	MP/1287	addit. mat.	male	Baltic amber	ISEA PAS
	MP/1427	addit. mat.	male	Baltic amber	ISEA PAS
	MP/3726	addit. mat.	male	Baltic amber	ISEA PAS/coll. Andrzej Górski
S. punctata sp. nov.	1117-1	holotype	female	Baltic amber	SDEI/coll. Ch. & H.W. Hoffeins

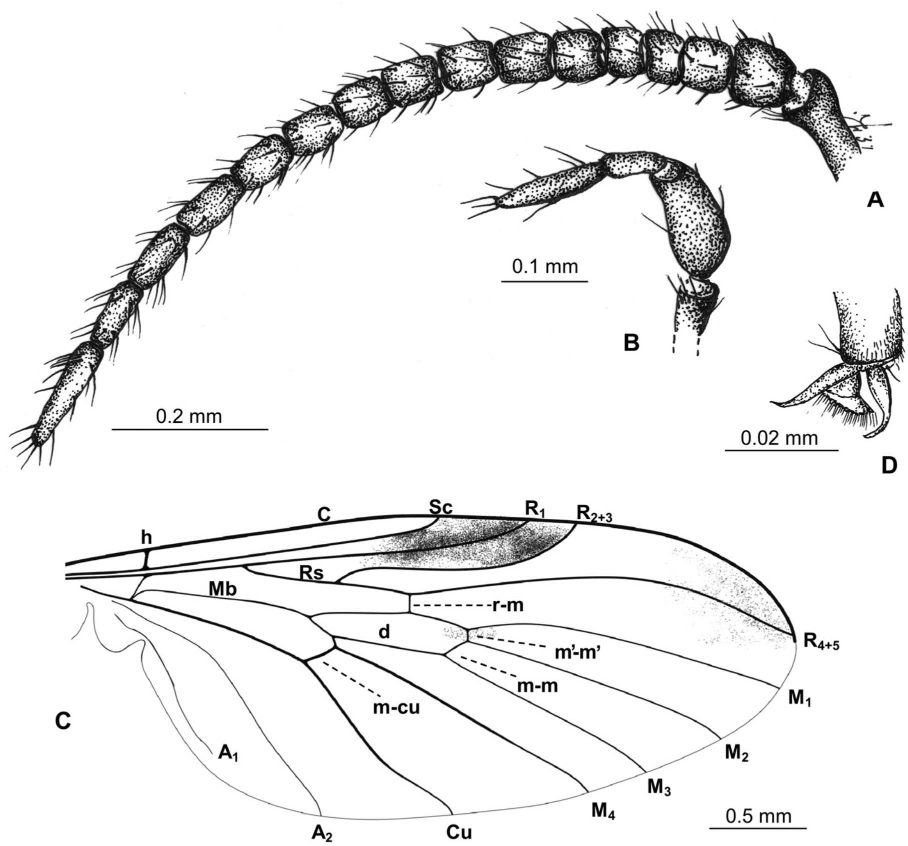

Figure 2. *Sylvicola splendida* Meunier, 1907. (A–B): No. 787-1 (female), coll. Ch. & H. W. Hoffeins: (A) antenna; (B) palpus maxillaris; (C, D): No. 923-1 (male), coll. Ch. & H. W. Hoffeins, (C) wing; (D) apical part of tarsus, redrawing after Meunier, 1907.

most of the head in lateral view, in frontal and dorsal view eyes are separated by a distance wider to diameter of ocellus; raised ocelli form equilateral triangle (Fig. 3 D, G, H). Antenna 1.15–1.59 mm long (Figs 2A; 3A, B), longer than head, became slender to the apex, with 14 cylindrical flagellomeres, more or less elongated, scapus not very elongated 1.5× as long as it is wide; pedicel wider than it is long, last flagellomere longer than penultimate one; all flagellomeres with comparatively elongated and thick setae, but shorter than segments bearing them and rather sparse; additionally very short setae on all flagellomeres, last flagellomere with a few not very elongated setae at apex, palpus maxillaris 4-segmented, 0.24–0.38 mm long (Figs 2B; 3E), first palpomere rather cylindrical, not very elongated; second thick and widened, twice as long as it is wide, third palpomere very short and rather tiny, last one very small and elongated, twice as long as penultimate one, tapered at apex with a few elongated setae at apex; additionally elongated, not numerous and short setae on all palpomeres.

Thorax (Fig. 3C): prescutellar setae and apical scutellar setae not very elongated; acrostichal setulae not very elongated; wing (Figs 2C; 4A–C): 3.34–3.84 mm long, 1.34–2.13 mm, approximately twice as long as it is wide; Sc comparatively elongated, slightly arched, ending opposite m-m level, R_1 almost straight; R_{2+3} strongly waved; Rs not very elongated, as long as the distance between Mb bifurcation and connection of r-m with d-cell; R_{2+3} slightly arched; the distance between M_1 and M_2 apices and between M_2 and M_3 apices equal, longer than the distance between R_{4+5} and M_1 and between M_3 and M_4 apices; d-cell approximately 3.5× as long as it is wide, r-m behind half of d-cell; A_1 well developed, A_2 comparatively elongated, waved; halter not very elongated with elongated stem and widened knob. Legs (Figs 2D; 3A, F): coxa of fore leg elongated, longer than coxa of middle and hind legs; tarsus of all legs with very elongated and massive claw and small empodium (Figs 2D; 4D, E). Apical comb well visible on fore and hind legs. Coxa of fore leg 0.43–0.65 mm, trochanter 0.12–0.20 mm, femur 0.69–1.17 mm, tibia 0.78–1.15 mm, tarsus 1.36–1.71 mm long (0.56–0.71/ 0.35–0.44/0.19– 0.23/0.14–0.18/0.12–0.15). Coxa of middle leg 0.67–0.75 mm, trochanter 0.15–0.19 mm, femur 0.90–1.21 mm, tibia 0.86–1.41 mm, tarsus 1.42–2.10 mm

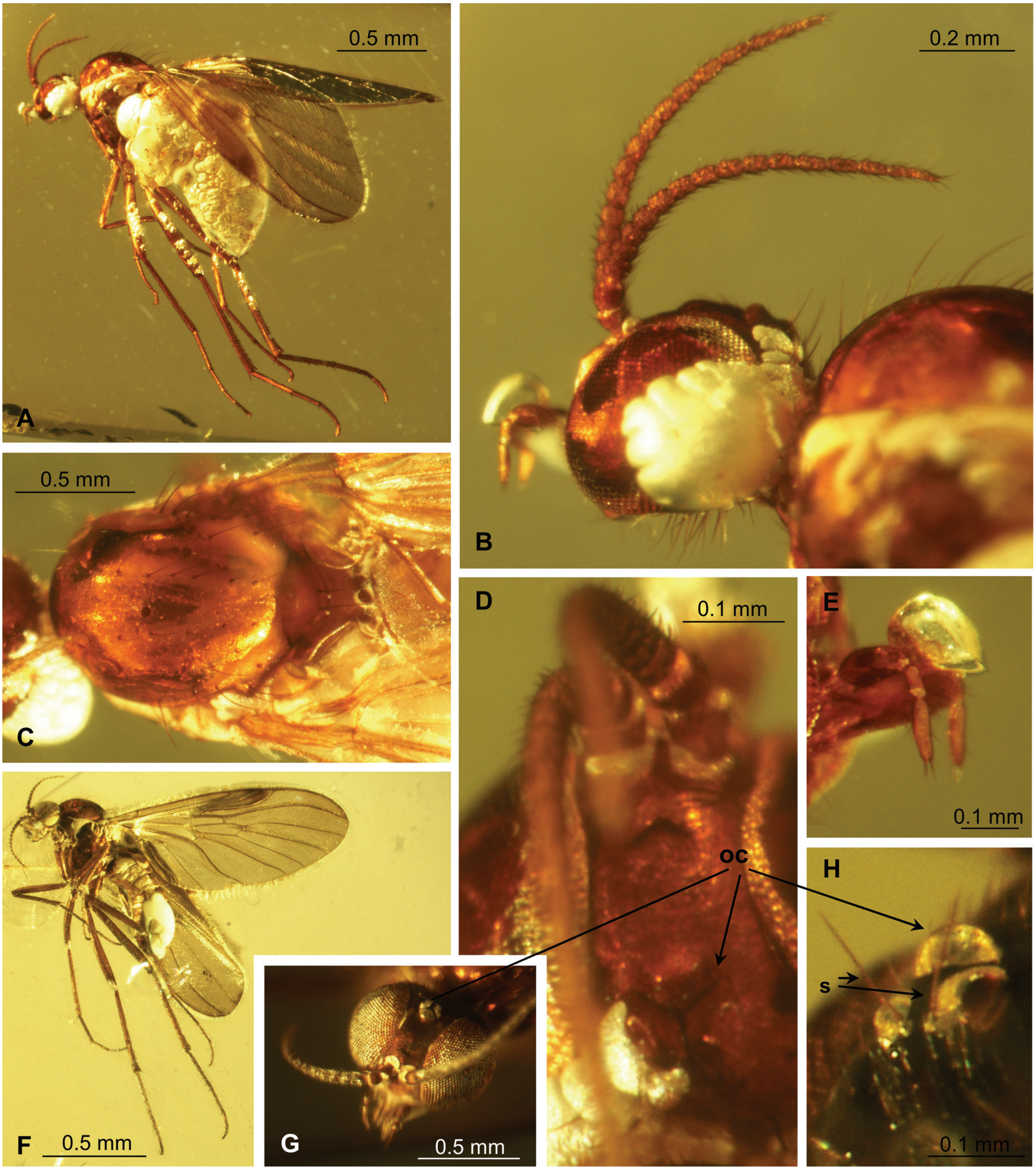

Figure 3. *Sylvicola splendida* Meunier, 1907. (A–E): No. 787-1 (female), coll. Ch. & H. W. Hoffeins, (A) body, lateral view; (B) enlarged view of head with antenna and palpi visible, lateral view; (C) thorax, dorsal view; (D) ocelli; (E) palpus maxillaris; (F–H) No. 923-1 (male), coll. Ch. & H. W. Hoffeins, (F) body, latero-ventral view; (G) head with ocelli well visible; (H) ocelli. Abbreviations: oc – ocelli, s – elongated setae.

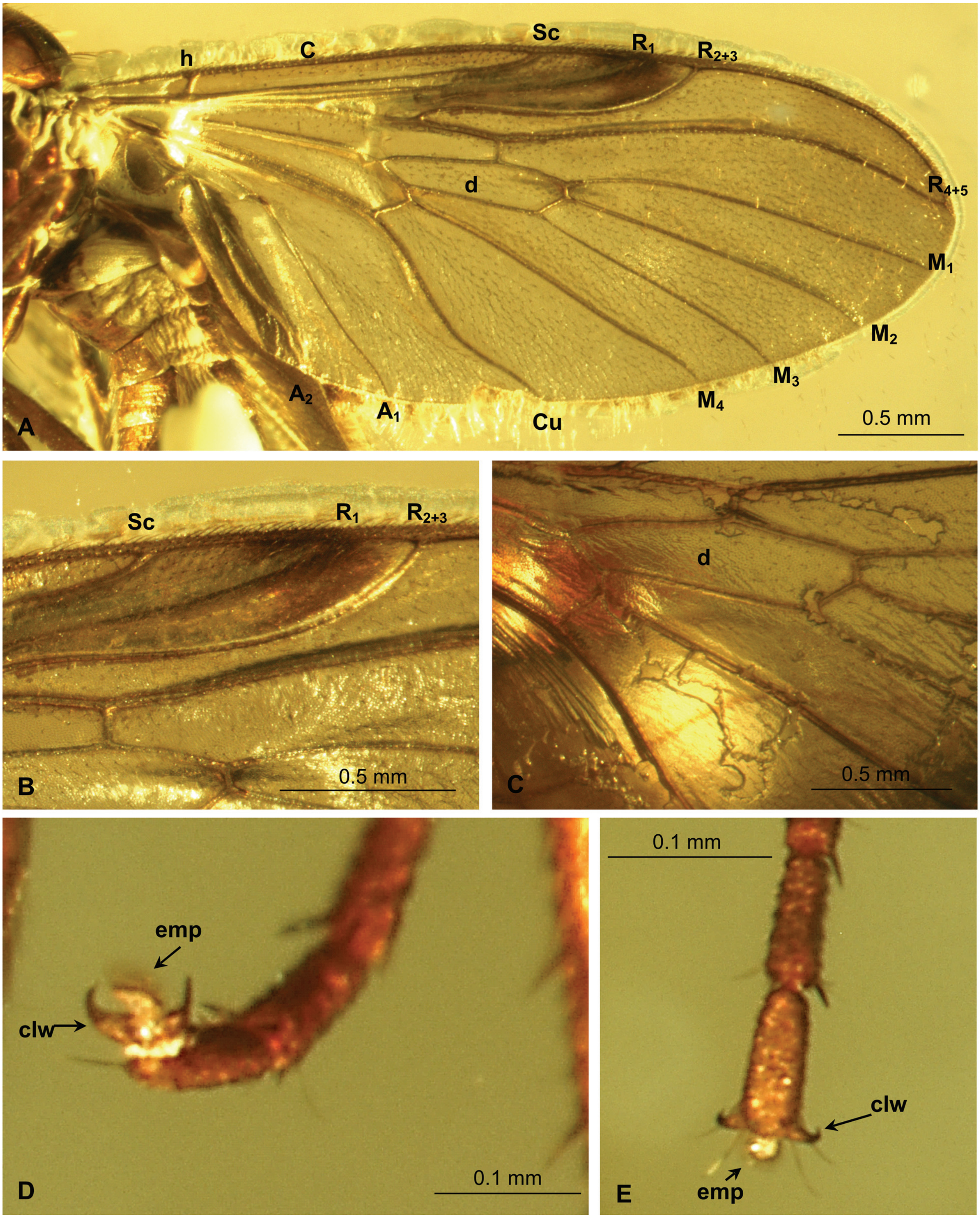

Figure 4. *Sylvicola splendida* Meunier, 1907. (A–C): No. 923-1 (male), coll. Ch. & H. W. Hoffeins, (A) wing; (B) enlarged view of Sc, R_1 and R_{2+3} apices; (C) enlarged view of d-cell; (D, E) No. 787-1 (female), coll. Ch. & H. W. Hoffeins, claw and empodium, (D) ventral view; (E) dorsal view. Abbreviations: clw – claw, emp – empodium.

long (0.59–0.81/0.38–0.50/0.20–0.33/0.13–0.24/0.12–0.22). Coxa of hind leg 0.51–0.87 mm, trochanter 0.20–0.21 mm, femur 1.57–1.87 mm, tibia 1.34–1.91 mm, tarsus 1.48–2.43 mm long (0.74–1.00/0.32–0.58/0.18–0.34/0.13–0.27/0.11–0.24).

Abdomen (Fig. 3F): female terminalia rather small, cerci not very elongated; male terminalia not very large.

Comparison. Small empodium and large claw, longer than empodium, this feature differs *Sylvicola splendida* Meunier, 1907 from other species known from Eocene resins.

Sylvicola thiriona Meunier, 1907
(Figs 5–6)

Diagnostic characters. Ocelli form scalene triangle; antenna as long as head or shorter, all flagellomeres longer than they are wide; last flagellomere approximately 3× as long as it is wide; last palpomere 3× as long as it is wide, as long as the second one; the distance between Sc and R_1 apices approximately 1.5× the distance between R_1 and R_{2+3} apices; cross vein m-m only slightly longer than m'-m'; the distance between M_2 and M_3 apices is shorter than the distance between M_1 and M_2, and shorter than the distance between M_3 and M_4 apices; width between M_4 and Cu up to 2× the width between M_3 and M_4 in widest place; d-cell approximately 3× as long as it is wide; empodium large, longer than claw, claw large.

Material examined. No. 644-4 (sex unknown), (SDEI), coll. Ch. & H. W. Hoffeins.

Additional description. Body (Fig. 6A): 4.18 mm long, pale brown, head (Fig. 6B) 0.91 mm wide, wider than thorax, 0.92 mm long, head and thorax combined 1.81 mm; holoptic eyes, raised large ocelli form scalene triangle, antenna (Figs 5A; 6B) 0.91 mm long, 14 flagellomeres, scape elongated, cylindrical, pedicel comparatively elongated, longer than wide, first flagellomere twice as long as wide, elongated, longer than other flagellomeres except the last one; flagellomeres 2–13 cylindrical, longer than wide, approximately the same length, twice as long as wide; became more slender to the apex of antenna, last flagellomere elongated tapered at apex, approximately 3× as long as wide with a few comparatively elongated setae at apex; all flagellomeres with a few elongated setae, but shorter than segments bearing them; additionally short and dense setae are visible on all segments of antenna; palpus maxillaris (Figs 5B; 6B) 4-segmented, 0.34 mm long; first palpomere elongated, cylindrical, second palpomere elongated, approximately 3× as long as wide; third palpomere short, tiny, shorter than other palpomeres; last palpomere elongated, twice as long as penultimate one.

Thorax (Fig. 6A): prescutellar setae not very elongated, wing (Figs 5C; 6C) approximately 3× as long as wide (Fig. 6C, D): 3.85 mm long, 1.47 mm wide; the distance between Sc and R_1 apices longer than the distance between R_1 and R_{2+3} apices (Fig. 6D); Sc ending

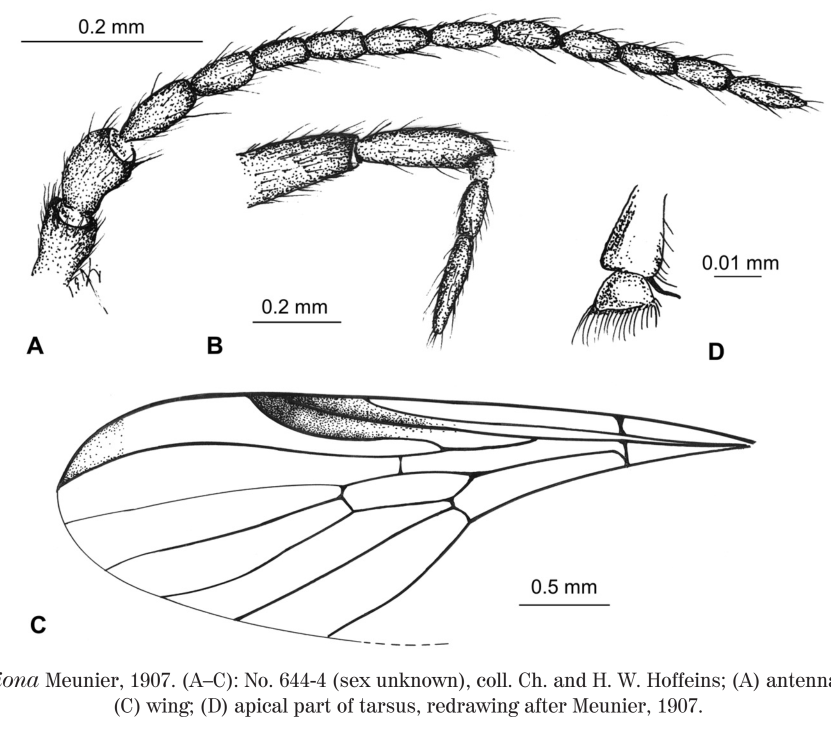

Figure 5. *Sylvicola thiriona* Meunier, 1907. (A–C): No. 644-4 (sex unknown), coll. Ch. and H. W. Hoffeins; (A) antenna; (B) palpus maxillaris; (C) wing; (D) apical part of tarsus, redrawing after Meunier, 1907.

before m-m level; R_1 almost straight, R_{2+3} strongly waved; R_1 apex in about $^2/_3$ of wing length; Rs separate Rb in $^2/_5$ of wing length from wing base. Legs: fore coxa elongated, longer than middle and hind coxa; tarsus comparatively elongated with last segment only slightly longer than penultimate one and not very elongated, not very large claw and large empodium (Figs 5D; 6E). Coxa of fore leg 0.54 mm, trochanter 0.16 mm, femur 0.86 mm, tibia 0.70 mm, tarsus 1.24 mm long (0.53/0.34/0.14/0.12/0.11).

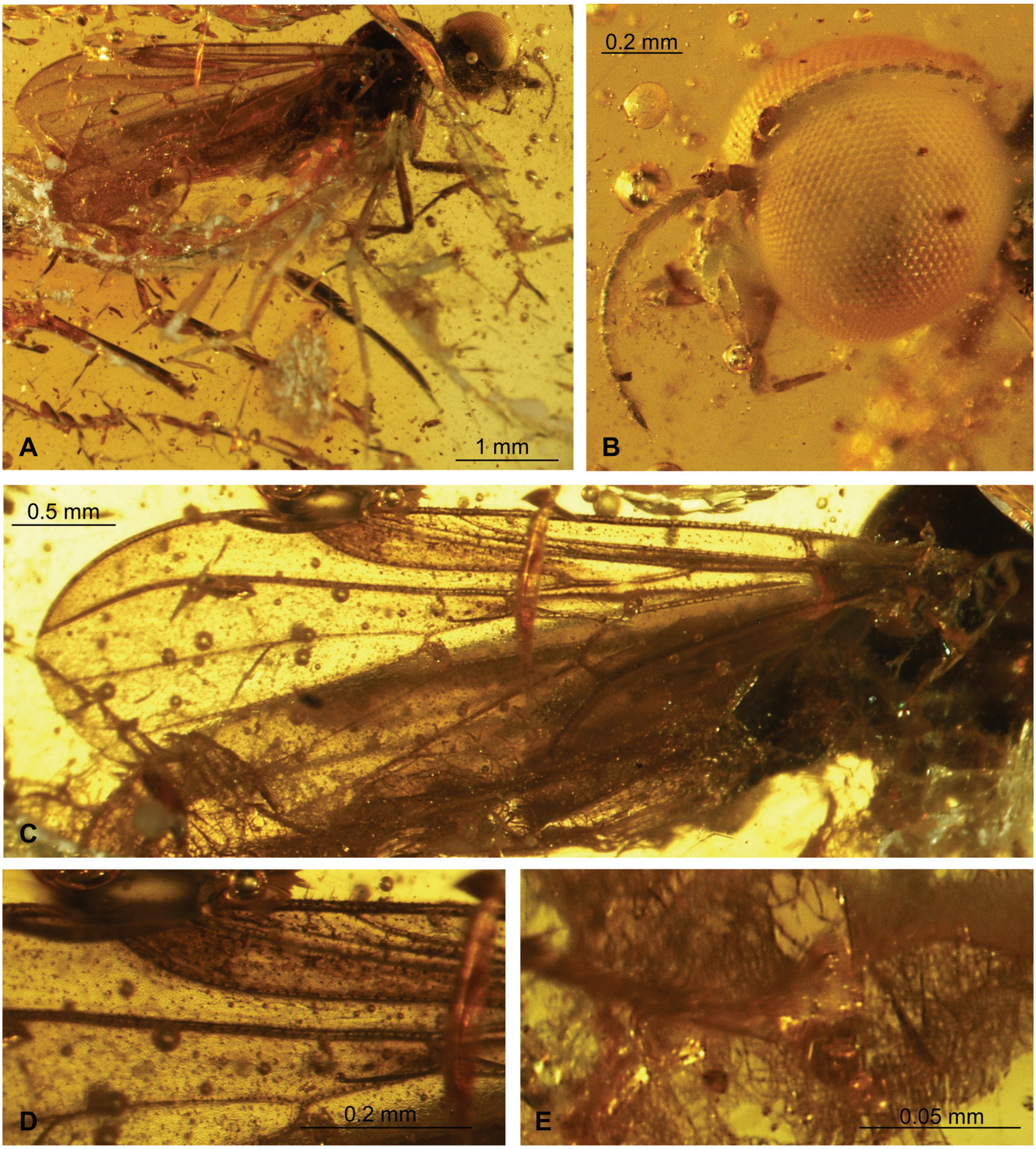

Figure 6. *Sylvicola thiriona* Meunier, 1907, (A–E): No. 644-4 (sex unknown), coll. Ch. and H. W. Hoffeins; (A) body, latero-ventral view; (B) head, lateral view; (C) wing; (D) enlarged view of Sc, R_1 and R_{2+3} apices; (E) apical part of tarsus.

Comparison. Large empodium and not very large claw, there is a feature which differ *Sylvicola thiriona* Meunier, 1907 from *Sylvicola splendida* Meunier, 1907, where empodium is very small and claws are massive. Moreover, short antenna, as long as head differ *Sylvicola thiriona* Meunier, 1907 from other species known from Eocene resins.

Sylvicola baltica sp. nov.
(Figs 7–9)

Diagnosis. Ocelli form scalene triangle; antenna longer than head, flagellomeres longer than they are wide, last flagellomere approximately 6× as long as it is wide; last palpomere 7× as long as it is wide, longer than second one; the distance between Sc and R_1 apices approximately 1.5× the distance between R_1 and R_{2+3} apices; cross vein m-m only slightly longer than m'-m'; the distance between M_2 and M_3 apices approximately as long as the distance between M_1 and M_2, M_3 and M_4 apices; width between M_4 and Cu up to 2× the width between M_3 and M_4 in widest place; d-cell elongated, approximately 4.5× as long as wide; empodium large, longer than claw, claw large.

Etymology. Species epithet after “Baltic amber”.

Type material. Holotype: No. 1258–1 (male), (SDEI), coll. Ch. & H. W. Hoffeins.

Description. Body (Fig. 8A): 5.71 mm long, brown, head darkest 0.72 mm high, 1.09 mm wide, head and thorax combined 2.31 mm; holoptic eyes (male), large ocelli form scalene triangle (Figs 8D, E), antenna (Figs

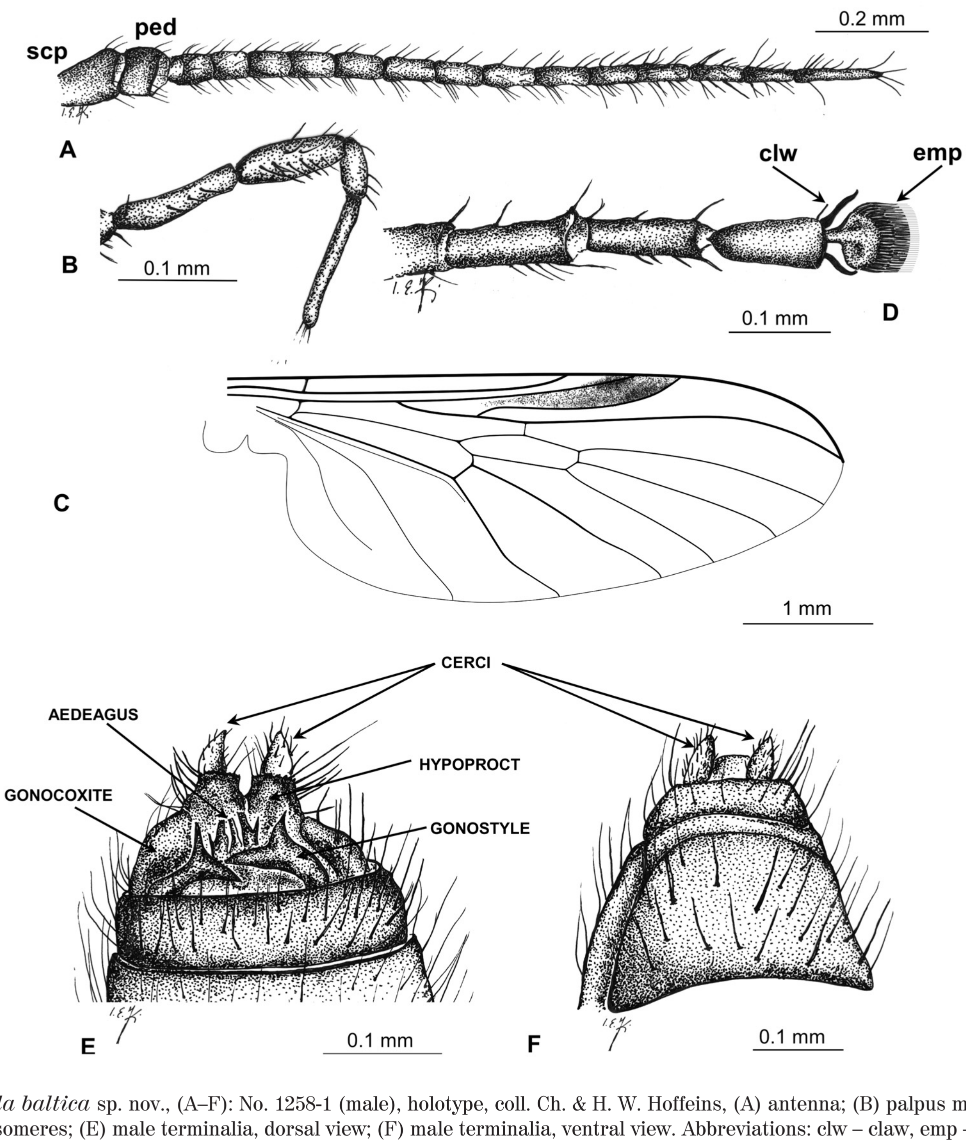

Figure 7. *Sylvicola baltica* sp. nov., (A–F): No. 1258-1 (male), holotype, coll. Ch. & H. W. Hoffeins, (A) antenna; (B) palpus maxillaris; (C) wing; (D) last tarsomeres; (E) male terminalia, dorsal view; (F) male terminalia, ventral view. Abbreviations: clw – claw, emp – empodium.

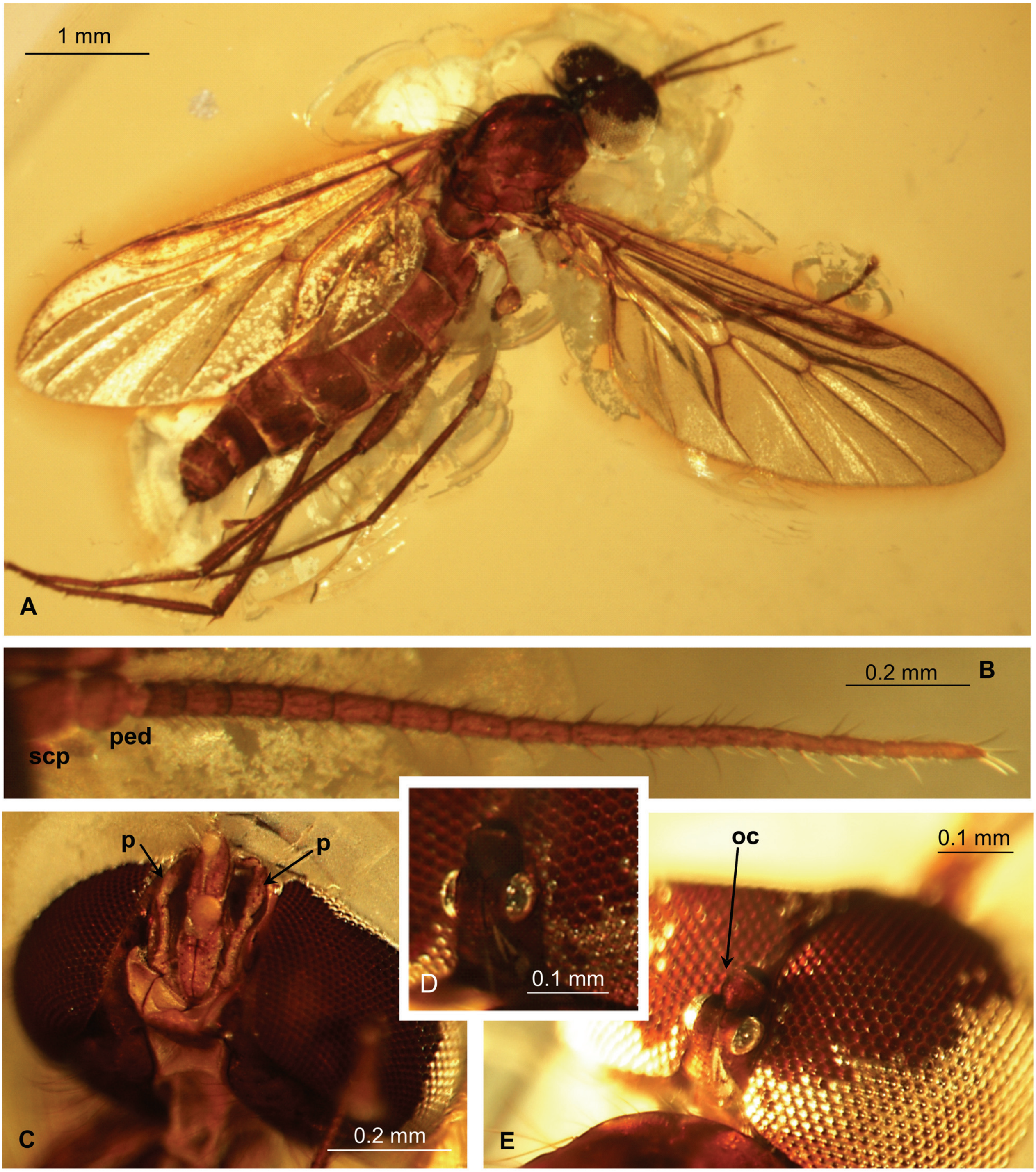

Figure 8. *Sylvicola baltica* sp. nov., (A–E): No. 1258-1 (male), holotype, coll. Ch. & H. W. Hoffeins, (A) body, dorsal view; (B) antenna; (C) head, ventral view; (D) ocelli, dorsal view; (E) head, dorsal view. Abbreviations: oc – ocelli; p – palpus maxillaris; ped – pedicel; scp – scape.

7A; 8B) 1.48 mm long, longer than head, 14 flagellomeres, scape elongated, cylindrical, pedicel shorter than scape, wide, approximately as long as it is wide, squat; flagellomeres cylindrical, elongated, became longer and slender to the apex of antenna, 1.5× as long as it is wide or longer; last flagellomere elongated tapered at apex, approximately 6× as long as it is wide with four comparatively elongated setae at apex; all flagellomeres with a few elongated setae, but shorter than segments bearing them; additionally short and dense setae are visible on all segments of antenna; palpus maxillaris (Figs 7B; 8C) 4-segmented, 0.34 mm long, first palpomere cylindrical, elongated, second one widened, third palpomere short, last palpomere very elongated, much longer than penultimate one.

Thorax (Fig. 8A): prescutellar setae not very elongated, wing (Figs 7C; 9A) approximately 3× as long as it is wide (Fig. 9A): 4.94 mm long, 1.77 mm wide; the distance between Sc and R_1 apices longer than the distance between R_1 and R_{2+3} apices (Fig. 9B); Sc ending opposite m-m level; R_1 apex in about $^2/_3$ of wing length from wing base; Rs separate Rb in $^2/_5$ of wing length from wing base; crossvein r–m as long as m–m. Legs (Figs 8A; 9C, D): fore coxa elongated, longer than

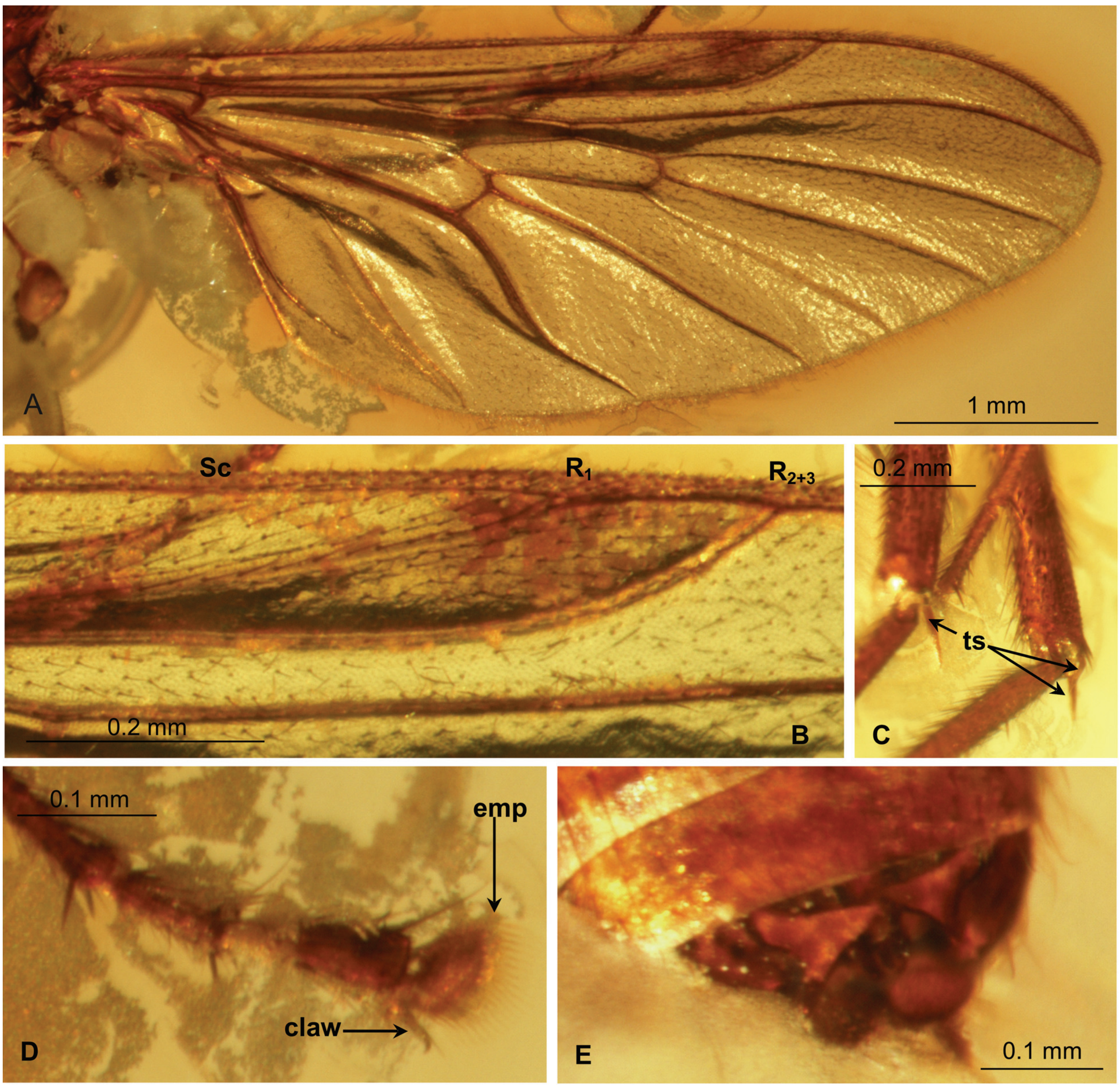

Figure 9. *Sylvicola baltica* sp. nov., (A–E): No. 1258-1 (male), holotype, coll. Ch. & H. W. Hoffeins, (A) wing; (B) Sc, R_1 and R_{2+3} apices; (C) tibial spurs; (D) last tarsomeres; (E) male terminalia. Abbreviations: claw – clawus; emp – empodium; ts – tibial spurs.

middle and hind coxa; tarsus comparatively elongated with last segment only slightly longer than penultimate one and not very elongated, massive claw and large empodium (Fig. 7D). Apical comb is well visible on fore and hind legs; coxa of fore leg 0.59 mm, trochanter 0.19 mm, femur 0.84 mm, tibia 0.84 mm, tarsus 1.75 mm long (0.73/0.42/0.24/0.20/0.16). Femur of middle leg 1.45 mm, tibia 1.50 mm long. Coxa of hind leg 0.43 mm, trochanter 0.23 mm, femur 1.74 mm, tibia 1.75 mm, tarsus 1.44 mm long (0.66/0.32/0.21/0.13/0.12). All tibia with dense, not very elongated setae.

Abdomen: male terminalia (Figs 7E, F; 9E) not large, 0.28 mm long, cerci pale brown, not very elongated, tapered at apex; hypoproct with short teeth on fore edge; gonostyle comparatively triangular.

Comparison. In *Sylvicola baltica* sp. nov. all flagellomeres are longer than they are wide, while in *S. splendida* and these species described herein are characterized by at least a few flagellomeres as long as they are wide. Moreover, last flagellomere in *Sylvicola baltica* sp. nov. is elongated, approximately 6× as long as it is wide and last palpomere is 7× as long as it is wide while in other species both last flagellomere and last palpomere are distinctly shorter, last flagellomere or last palpomere are up to 3.5× as long as they are wide.

Sylvicola hoffeinsorum sp. nov.
(Figs 10–12)

Diagnosis. Ocelli form scalene triangle; antenna longer than head, flagellomeres 2–4 as long as they are wide, flagellomeres 5–14 longer than they are wide, last

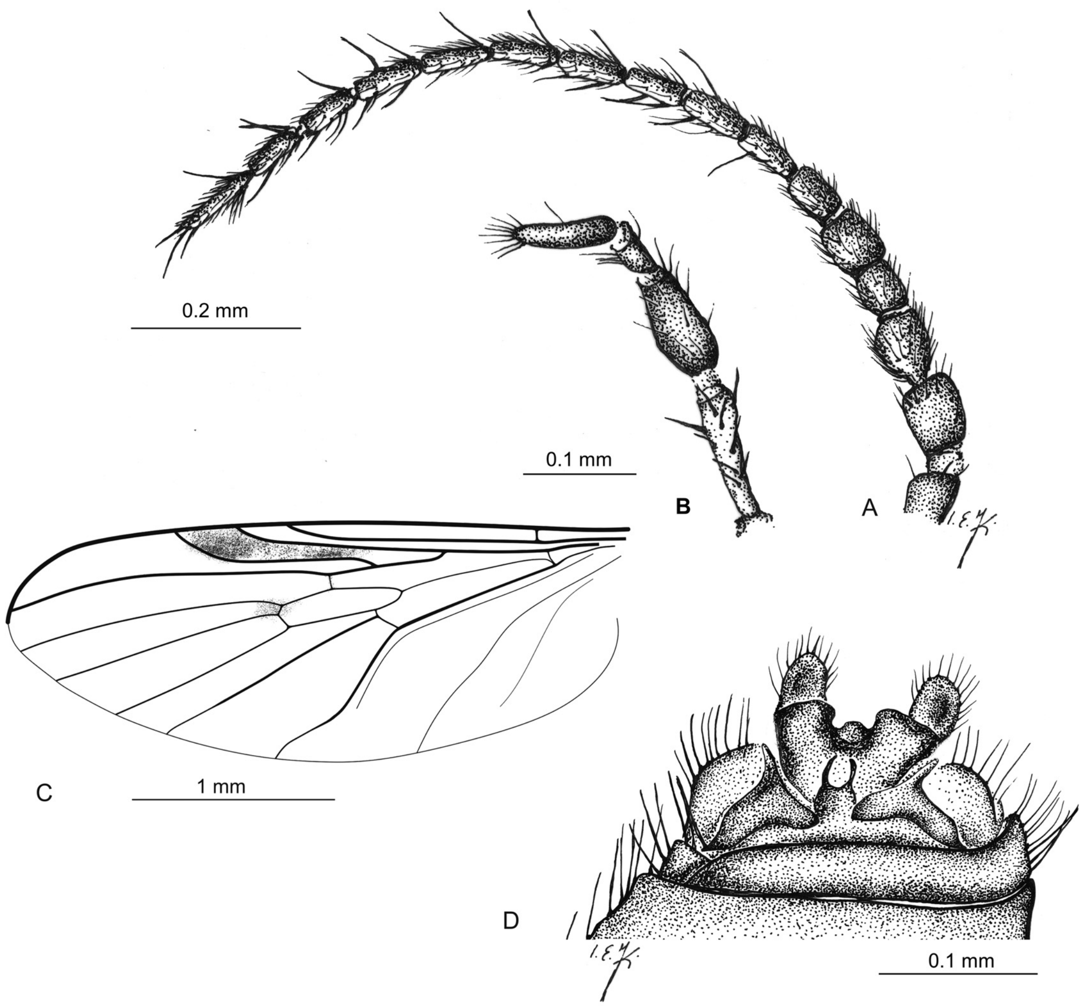

Figure 10. *Sylvicola hoffeinsorum* sp. nov., (A, C, D): No.773a (male), holotype, MAIG: (A) antenna; (B) No. 644-2 (female), Ch. & H. W. Hoffeins, palpus maxillaris; (C) wing; (D) male terminalia.

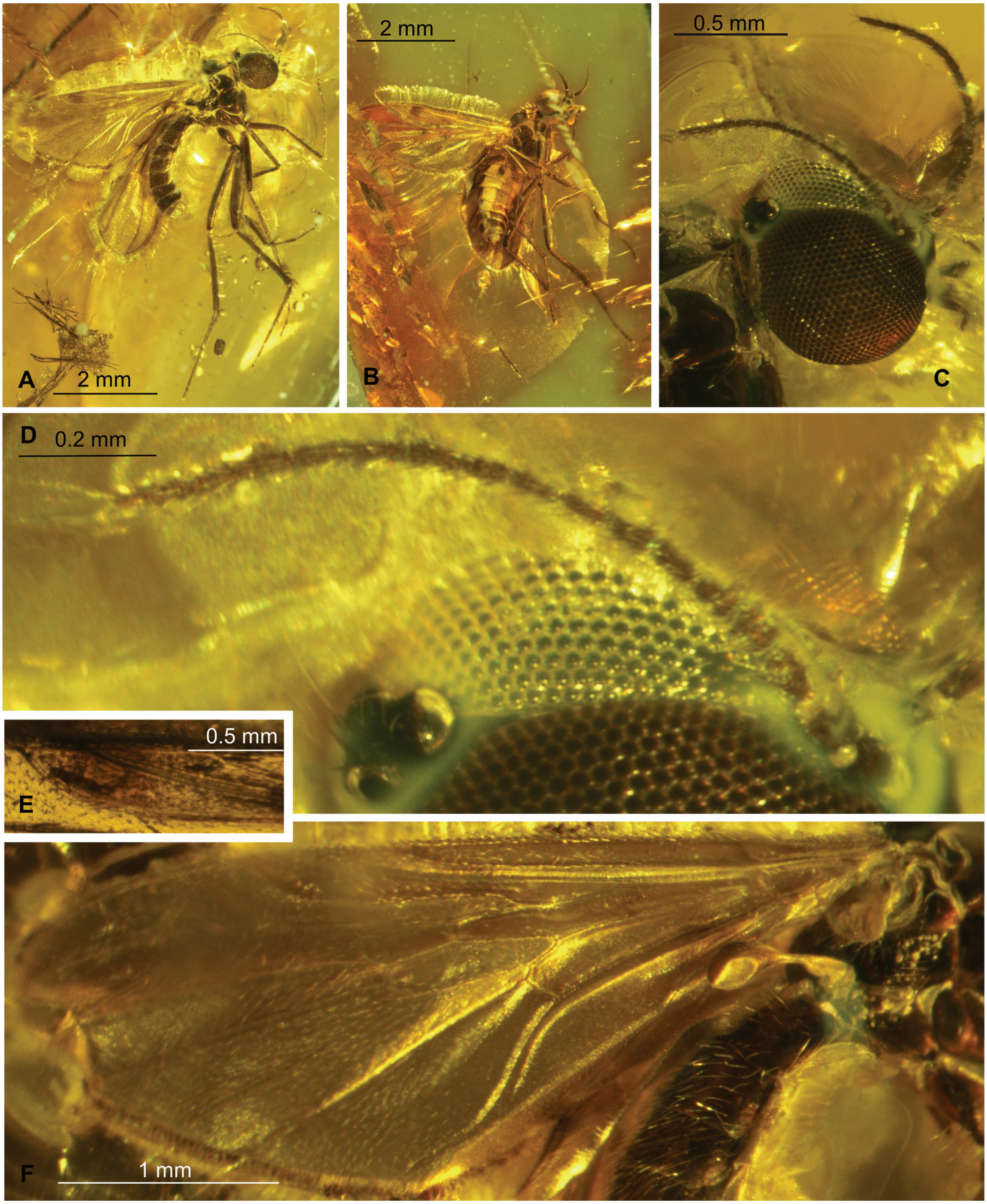

Figure 11. *Sylvicola hoffeinsorum* sp. nov., (A, C–F). No. 773a (male), holotype, MAIG: (A) body, lateral view; (B) No. 664-2 (female), coll. Ch. & H. W. Hoffeins, body, latero-ventral view; (C) head, latero-dorsal view; (D) antenna and ocelli, latero-dorsal view; (E) Sc, R_1 and R_{2+3} apices; (F) wing.

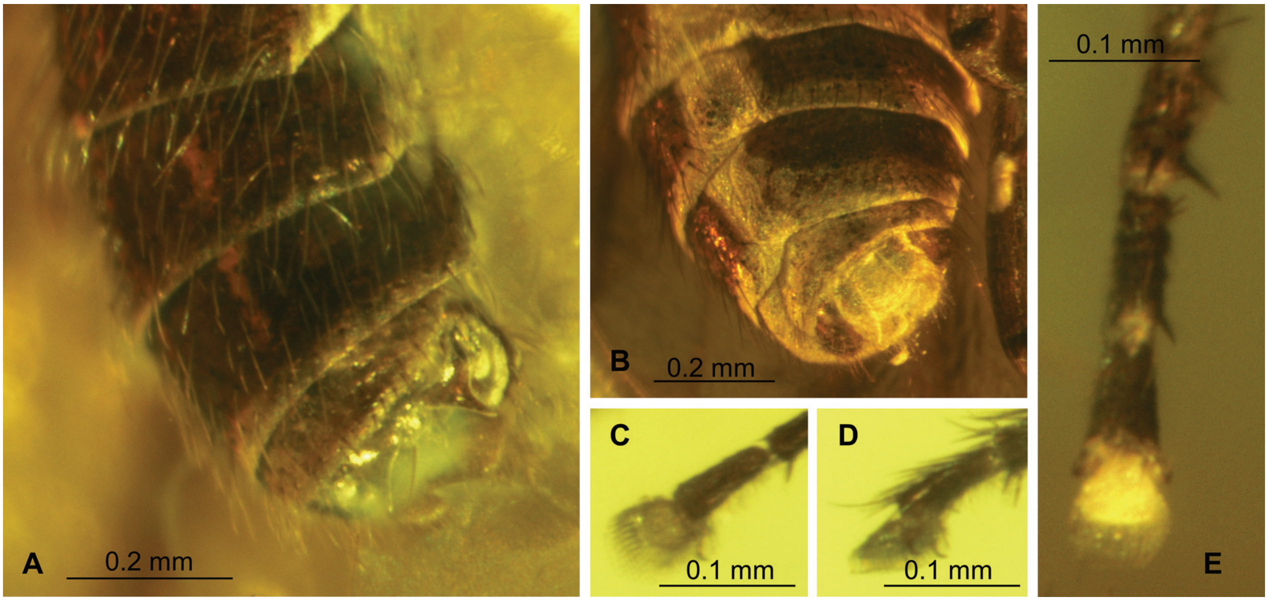

Figure 12. *Sylvicola hoffeinsorum* sp. nov., (A, C–E). No. 773a (male), holotype, MAIG: (A) male terminalia; (B) No. 664-2 (female), coll. Ch. & H. W. Hoffeins, female terminalia; (C–E) last tarsomeres: (C) dorsal view; (D) lateral view; (E) ventral view.

flagellomere approximately 3× as long as it is wide, last palpomere 3× as long as it is wide, longer than the second one; the distance between Sc and R_1 apices approximately 1.5× the distance between R_1 and R_{2+3} apices; cross vein m-m only slightly longer than m'-m'; the distance between M_2 and M_3 apices wider than the distance between M_1 and M_2, M_3 and M_4 apices; d-cell elongated, approximately 3.5× as long as it is wide; width between M_4 and Cu 2.5× the width between M_3 and M_4 in widest place; empodium large, longer than claw, claw large.

Etymology. The species name is dedicated to Christel and Hans Werner Hoffeins from Hamburg, Germany, the collectors of amber inclusions and the expert in Baltic amber inclusions.

Material examined. Holotype: No. 773a (male), coll. Museum of Amber Inclusions, University of Gdańsk (MAIG); additional material: No. 189-2, (male), No. 1789-2 (male), No. 664-2 (female), No. 70-3 (female), (SDEI), coll. Ch. & H.W. Hoffeins, No. MP/1287 (male), MP/1427 (male), coll. Institute Systematics and Evolution, Polish Academy of Sciences (ISEA PAS); No. MP/3726 (male), (ISEA PAS), coll. Andrzej Górski.

Description. Body (Fig. 11A, B) 3.43–4.90 mm long, pale brown with pale brown legs and dark brown last and penultimate tarsomeres and the apex of third tarsomere. Head width (Fig. 11C) 0.58–0.92 mm, 0.58–0.92 mm high. Head and thorax combined 1.67–2.38 mm. Holoptic eyes in male and female occupying most of head in lateral view; raised ocelli form scalene triangle (Fig. 11C, D). Antenna 1.20–1.34 mm long (Figs 10A; 11A–D), longer than head, became slender to the apex, with 14 cylindrical, more or less elongated flagellomeres, last flagellomere longer than penultimate one; all flagellomeres with comparatively elongated and thick setae, longer than segments bearing them and rather sparse; additionally short setae on all flagellomeres, last flagellomere with a few elongated setae at apex, palpus maxillaris 4-segmented, 0.27–0.35 mm long (Figs 10B; 11C), first palpomere elongated, longer than second and the last one, very pale, second palpomere elongated, widened in the midlength, third short, cylindrical, fourth palpomere not very elongated, twice as long as the penultimate one, shorter than first and the second one; last one tapered at apex with a few elongated setae at apex; additionally short setae on all palpomeres.

Thorax (Fig. 11A, B): prescutellar setae and apical scutellar setae not very elongated; acrostichal setulae not very elongated; wing (Figs 10C; 11E, F): 3.51–4.41 mm long, 1.28–1.74 mm wide, approximately twice and half as long as wide; Sc comparatively elongated, slightly arched, ending opposite m-m level, R_1 almost straight; R_{2+3} strongly waived; Rs not very elongated, as long as the distance between Mb bifurcation and connection of r-m with d-cell; d-cell approximately 3.5× as long as wide, r-m behind half of d-cell; A_1 well developed, A_2 comparatively elongated, waved; halter not very elongated with elongated stem and widened knob. Legs (Figs 11A, B; 12C–E): coxa of fore leg elongated, longer than coxa of middle and hind legs. Coxa of fore leg 0.36–0.57 mm, trochanter 0.12–0.18 mm, femur

0.71–0.96 mm, tibia 0.80–0.95 mm, tarsus 1.26–1.58 mm long (0.50-0.60/0.35–0.41/0.16–0.28/0.12–0.15/0.13–0.14). Coxa of middle leg 0.43–0.58 mm, trochanter 0.14–0.15 mm, femur 0.97–1.14 mm, tibia 0.95–1.21 mm, tarsus 1.56 mm long (0.62/0.38/0.24/0.15/0.17). Coxa of hind leg 0.44 mm, trochanter 0.14–0.16 mm, femur 1.26–1.63 mm, tibia 1.10–1.40 mm, tarsus 1.42–1.73 mm long (0.66–0.74/0.30–0.40/0.21–0.31/0.13–0.14/0.12–0.14).

Abdomen: female terminalia (Figs 10D; 12B) with rather elongated cerci; male terminalia (Fig. 12A) not very large, cerci comparatively wide, rounded at apex, hypoproct wide, gonostyle triangular.

Comparison. In *Sylvicola hoffeinsorum* sp. nov. in contrast to other species known from Baltic amber the distance between M_4 and Cu is comparatively wide and over twice the distance between M_3 and M_4 measured in widest area, while in other species this width is up to 2× the width between M_3 and M_4.

Sylvicola punctata sp. nov.
(Figs 1; 13–14)

Diagnosis. Ocelli form scalene triangle; antenna longer than head, flagellomeres 2–4 as long as they are wide, flagellomeres 5–14 longer than they are wide, last flagellomere approximately 3× as long as it is wide, the distance between Sc and R_1 apices approximately 3× the distance between R_1 and R_{2+3} apices; cross vein m-m as long as m'-m'; the distance between M_2 and M_3 apices wider than the distance between M_1 and M_2, M_3 and M_4 apices; width between M_4 and Cu up to 2× the width between M_3 and M_4 in widest place; d-cell elongated, approximately 3.5× as long as it is wide; empodium large, longer than claw, claw large.

Etymology. The species name is derived from Latin: "punctum", English: "point".

Material examined. Holotype: No. 1117-1 (female), (SDEI), coll. Ch. & H.W. Hoffeins.

Description. Body (Figs 1; 14A) 3.84 mm long, brown. Head (Fig. 14B) width 0.50 mm, 0.59 mm high. Head and thorax combined 1.60 mm. Dichoptic eyes occupying most of head in lateral view, in frontal and dorsal view eyes separated by a distance wider to diameter of ocellus; raised ocelli form scalene triangle. Antenna 1.12 mm long (Figs 13A; 14B) shorter than head and thorax combined, became slender to the apex, with 14 cylindrical, more or less elongated flagellomeres, last flagellomere longer than penultimate one; all flagellomeres with comparatively elongated and thick, dense setae, but shorter than segments bearing them; additionally very short setae on all flagellomeres, last flagellomere with a few elongated setae at apex; palpus maxillaris 4-segmented, 0.27 mm long (Figs 13B; 14B), first palpomere rather cylindrical, elongated; second elongated, twice as long as it is wide, third palpomere short, last one very small and elongated, twice as long as the penultimate one, tapered at apex with a few elongated setae at apex; additionally elongated, not numerous and short setae on all palpomeres.

Thorax (Fig. 14A): prescutellar setae and apical scutellar setae not very elongated; acrostichal setulae

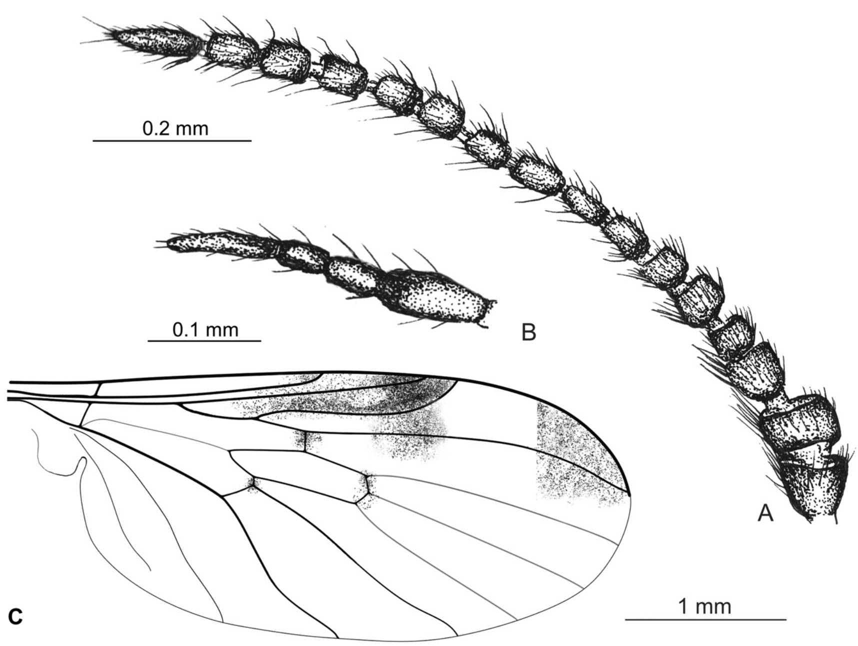

Figure 13. *Sylvicola punctata* sp. nov., (A–C): No. 1117-1 (female), holotype, coll. Ch. & H. W. Hoffeins. (A) antenna; (B) palpus maxillaris; (C) wing.

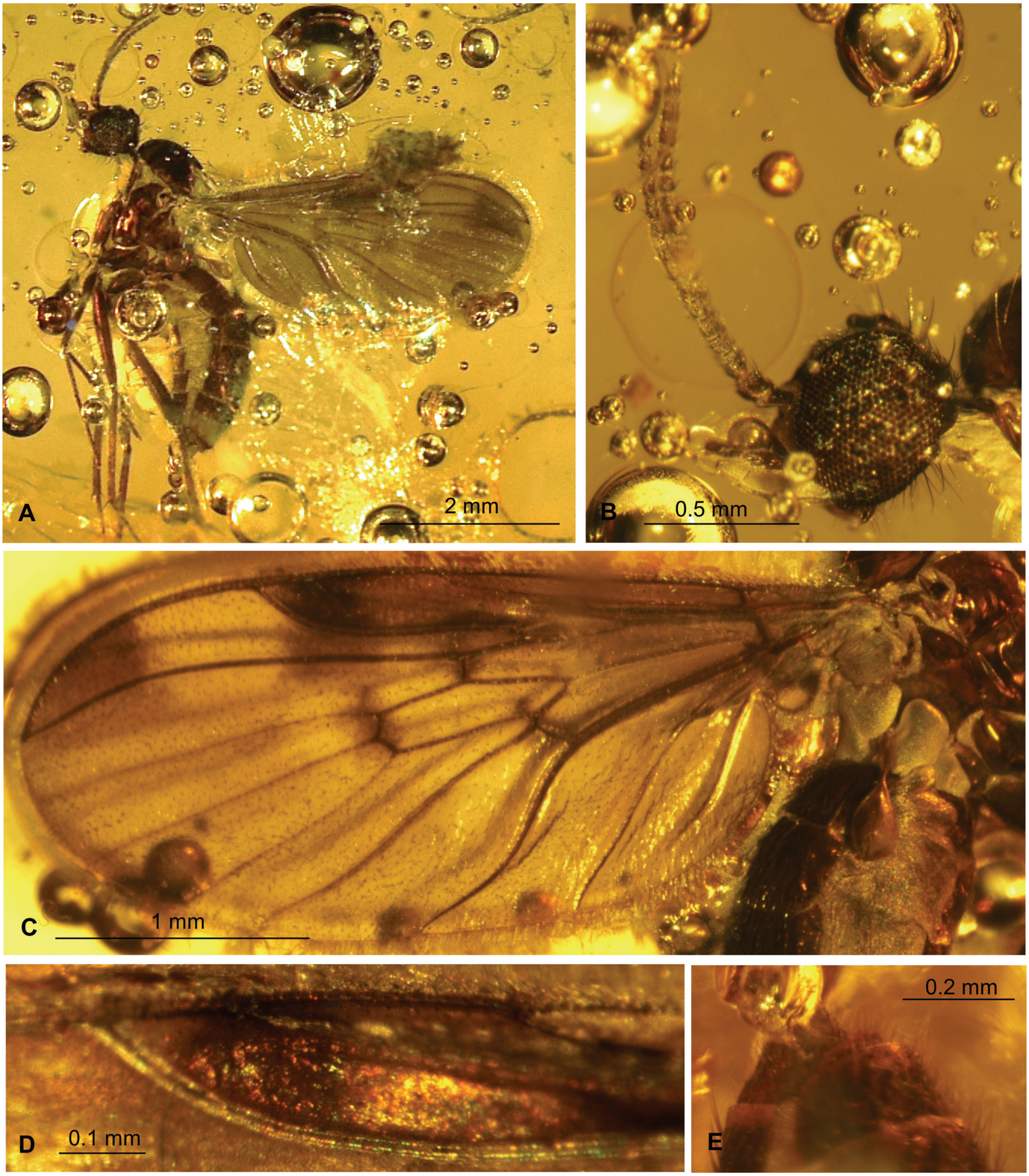

Figure 14. *Sylvicola punctata* sp. nov., (A–E): No. 1117-1 (female), holotype, coll. Ch. & H. W. Hoffeins. (A) body, lateral view; (B) enlarged view of head, lateral view; (C) wing; (D) enlarged view of Sc, R_1 and R_{2+3} apices; (E) female terminalia.

not very elongated; wing (Figs 13C; 14C): 3.35 mm high, 1.30 mm wide, with dark spots, approximately twice as long as wide; Sc comparatively elongated, slightly arched, ending before m-m level, R_1 almost straight; R_{2+3} strongly waved (Fig. 14D); Rs not very elongated, longer than the distance between Mb bifurcation and connection of r-m with d-cell; d-cell approximately 3× as long as wide, r-m at half of d-cell; A_1 well developed, A_2 comparatively elongated, waved; halter not very elongated with elongated stem and widened knob. Legs (Fig. 14A): coxa of fore leg elongated, longer than coxa of middle and hind legs; tarsus of all legs with elongated claw and large empodium. Apical comb well visible on fore and hind legs. Coxa of fore leg 0.57 mm, trochanter 0.13 mm, femur 0.75 mm long. Coxa of middle leg 0.65 mm, trochanter 0.14 mm, femur 0.92 mm, tibia 1.10 mm long. Coxa of hind leg 0.47 mm long.

Abdomen (Fig. 14E): female terminalia rather small, 0.36 mm long.

Comparison. In *Sylvicola punctata* sp. nov. in contrast to other species known from Baltic amber wing is comparatively rounded at apex, in other species known from Eocene resins wing is comparatively elongated, not rounded in apical part. Moreover, additional dark spots, especially large spot beyond stigmal area and waved vein M_4 differ this species from other representatives of *Sylvicola* known from Eocene resins.

Discussion

All species of *Sylvicola* differ by morphology of male and female terminalia. Despite being obvious, some morphological differences of antenna, palpus, wing venation or topography of tarsus of particular species are quite distinct to distinguish these species. *S. splendida* as suggests Meunier, 1907 differ from other species by morphology of tarsus, with all other species known from Eocene resins, being characterized by comparatively large empodium, with not so massive claws. All species of *Sylvicola* known form Eocene resins and described herein are characterize by antenna distinctly longer than the head, in *S. thiriona* antenna is shorter, is as long as the head. Some other differences are visible also in eyes position and arrangement of ocelli. In fossil representatives of *Sylvicola* eyes are holoptic or dichoptic, e.g. in *S. hoffeinsorum* sp. nov., both females and male have holoptic eyes. To compare female and male of some recent species like *Sylvicola cinctus* (Fabricius, 1787) or *Sylvicola fenestralis* (Scopoli, 1763) showed lack of distinct differences in morphology of the head. Moreover, ocelli of fossil species of *Sylvicola* seems to arrange in three morphological groups, those that form equilateral triangle and those in which central ocellus is positioned more closely to the front of the head in comparison to the first type. An intermediate form is also observed.

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Review of *Mycetobia* Meigen, 1818 (Diptera, Anisopodidae) in the Eocene ambers

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Abstract

A revision of the genus *Mycetobia* Meigen, 1818 from the Eocene is presented. Redescription of *Mycetobia connexa* Meunier, 1899 known from the Baltic amber is given and documented by photographs and drawings. Five new species of *Mycetobia* from Eocene resins are described, four from Baltic amber: *Mycetobia christelae* sp. nov., *Mycetobia hansi* sp. nov., *Mycetobia silvia* **sp. nov.**, *Mycetobia szwedoi* **sp. nov.** and one from the Ukrainian amber: *Mycetobia perkovskyi* **sp. nov.** Key to the species of *Mycetobia* known from the Eocene is provided.

Key words: fossil insects, inclusions, Eocene, morphology, taxonomy, *Mycetobia*, new species

Introduction

Representatives of the genus *Mycetobia* Meigen, 1818 (Diptera, Anisopodoidea) are characterized by not very elongated antenna, shorter than head and thorax combined, wing venation with vein M 3-branched and absence of discal cell. Dark markings of wing and macrotrichia on wing membrane do not occur in this genus (Fig. 2). The first information on fossil *Mycetobia* were given by Loew (1850) and Meunier (1899, 1904). One species was described from the Green River Formation, Wyoming, U.S.A. by Scudder in 1878 as *Diadocida* (?) *terricola* Scudder, 1878. It was originally placed in Mycetophilidae, later transferred to the genus *Mycetobia* by Edwards in 1928. One of the oldest descriptions of the *Mycetobia* species from the Baltic amber is to be found in the works of Meunier (1899). *Mycetobia longipennis* Meunier, 1899 was ascribed by Meunier to Loew, but this name was probably taken from label or unpublished notes or manuscript, as it had not been published elsewhere before Meunier's work. Edwards (1928) treated this taxon and another species, *Mycetobia platyuroides* Meunier, 1899 as *nomina dubia*. Nomenclatorial chaos gained in intensity with two specific names: *Mycetobia paralella* (Loew, 1850) and *Mycetobia unicalcarata* (Loew, 1850) being ascribed to Loew by Keilbach (1982a, b). These names were introduced probably from data on the labels (Spahr, 1985). Evenhuis (1994, 2014) stated that these names are *nomina nuda*. Unidentified species of *Mycetobia* was mentioned from the Pleistocene Mizunami amber, Japan (Saigusa, 1974). It was also listed in Anisopodidae, in "copal Diptera" section by Spahr (1985) and in Evenhuis' catalogues (1994, 2014), Arillo and Ortuño (2005), and in Perez-Gelabert (2008). Moreover, species described as *Mycetobia defectiva* Loew, 1850 was transferred to the genus *Symmerus* by Evenhuis (1994) as *Symmerus defectivus* (Loew, 1850) in the family Ditomyiidae. Species *Mycetobia macrocera* (Meunier, 1899) was transferred to *Paleoplatyura* by Meunier in 1917 as *Paleoplatyura macrocera* Meunier, 1899.

More recent data about fossil representatives of *Mycetobia* were covered in studies by Grimaldi who described two species from Miocene (Chattian) of Dominican Republic (Fig. 1): *Mycetobia antillea* Grimaldi, 1991 and *Mycetobia cryptambra* Grimaldi, 1991 and mentioned one unidentified species of *Mycetobia* from Dominican amber. The first descriptions of fossil *Mycetobia* come from nineteenth century (Meunier, 1899), hence, the systematic revision of *Mycetobia* from Eocene inclusions were needed. The holotypes of *M. longipennis* and *M. platyuroides* were not listed in original publication and the specimens studied by Meunier in 1899 were not found. The descriptions of these species in Meunier's papers (1989, 1907) are short or absent, without information about

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the morphology of species. The drawings were not enough to enable the detailed study of the features of species. We decided to consider *M. longipennis* and *M. platyuroides*, as well as *M. terricola* as *nomina dubia* (Table 1). New material gives us new possibilities of view on *Mycetobia* in Eocene.

TABLE 1. List of species of the genus *Mycetobia* revised and described herein.

Species	The number of specimen	Material examined	Sex	Age	Collection
Mycetobia connexa Meunier, 1899 = *Mycetobia callida* Meunier, 1904*	GZG.BST 03400 [Z 6457][1]	addit. mat.	female	Baltic amber	GMUG
	GZG.BST 03401 [Z 2304]	addit. mat.	male	Baltic amber	GMUG
	GZG.BST 03402 [Z 211]	addit. mat.	female	Baltic amber	GMUG
	GZG.BST 03403 [Z 3299]	addit. mat.	female	Baltic amber	GMUG
	GZG.BST 03408 [G 659]	addit. mat.	female	Baltic amber	GMUG
	GZG.BST 03409 [G 674]	addit. mat.	male	Baltic amber	GMUG
	GZG.BST 03410 [G 664]	addit. mat.	unknown	Baltic amber	GMUG
	4226	addit. mat.	female	Baltic amber	MAIG
	MP/3695	addit. mat.	female	Baltic amber	ISEA PAS
	70-2	addit. mat.	female	Baltic amber	Ch. & H. W. Hoffeins
	1258-2	addit. mat.	female	Baltic amber	Ch. & H. W. Hoffeins
	1737-3	addit. mat.	female	Baltic amber	Ch. & H. W. Hoffeins
	804-1	addit. mat.	female	Baltic amber	Ch. & H. W.Hoffeins
	804-2	addit. mat.	female	Baltic amber	Ch. & H. W. Hoffeins
Mycetobia christelae **sp. nov.**	1258-3	holotype	male	Baltic amber	Ch. & H. W. Hoffeins
	MP/3694	addit. mat.	female	Baltic amber	ISEA PAS
	838-1	paratype	male	Baltic amber	Ch. & H. W. Hoffeins
Mycetobia hansi **sp. nov.**	1258-4	holotype	female	Baltic amber	Ch. & H. W. Hoffeins
Mycetobia longipennis Meunier, 1899	*nomina dubia***				
Mycetobia paralella: Keilbach, 1982	*nomina nudi***				
Mycetobia perkovskyi **sp. nov.**	872	holotype	unknown	Ukrainian amber	NAS of Ukraine
Mycetobia platyuroides Meunier, 1899	*nomina dubia***				
Mycetobia silvia **sp. nov.**	1345(a)	holotype	unknown	Baltic amber	Scheele
	1345(b)	paratype	female	Baltic amber	Scheele
Mycetobia szwedoi **sp. nov.**	MP/3693	holotype	male	Baltic amber	ISEA PAS
Mycetobia terricola (Scudder, 1878)	*nomina dubia***				
Mycetobia unicalcarata: Keilbach 1982	*nomina nudi***				
taxa from the Eocene removed from *Mycetobia*					
Mycetobia defectiva Loew, 1850	as *Symmerus defectivus* (Loew, 1850)				
Mycetobia macrocera, Meunier, 1899	as *Paleoplatyura macrocera* Meunier, 1899				

* synonymy after Edwards (1928)
** see the text
[1]old/previous number is given in bracket

FIGURE 1. Geographical distribution of fossil species of the genus *Mycetobia.* A. Location of recent amber area with localities of *Mycetobia*; B. Location of amber area with localities of *Mycetobia* in Eocene.

Material and methods

The study was based on material (22 inclusions) in Baltic amber dated Eocene, Lutetian-Priabonian (Grimaldi and Ross, 2017) and Ukrainian amber, also Eocene. Material comes from the following collections: University of Göttingen (GMUG), seven specimens; Institute of Systematics and Evolution of Animals Polish Academy of Sciences (ISEA PAS), three specimens; Museum of Amber Inclusions, University of Gdańsk (MAIG), one specimen; collection of Scheele, two specimens; collection of Christel and Hans Werner Hoffeins; eight specimens;

all in the Baltic amber; and one specimen in the Ukrainian amber, collection of National Academy of Sciences of Ukraine, I. I. Schmalhausen Institute of Zoology (NAS of Ukraine). The holotypes of new described species herein from the collection of Christel and Hans Werner Hoffeins will be deposited in Senckenberg Deutsches Entomologisches Institut (SDEI), Müncheberg, Germany. Specimens were studied using a Nikon SMZ 1500 stereomicroscope equipped with a Nikon DS-Fi1 camera, the measurements were taken with NIS-Elements D 3.0 software in University of Rzeszów and in Göttingen. The drawings for the analysis were based on the specimens and photographs. The drawings were made by Maciej Wojtoń; drawings of male terminalia of *Mycetobia* were made by Iwona Kania. The measurements of specimens were taken with NIS-Elements D 3.0 software in University of Rzeszów. The measurements were made as follow: the length and width of head capsule; measurements were made at widest point and maximum length. The measurements are given only in case when relevant structures were not distorted. The nomenclature of male genitalia, thorax and structures which occur on thorax were used after Grimaldi (1991) nomenclature of wing venation is after Krzemińska *et al.*, 2009.

Results

Systematic palaeontology

Order: Diptera Linnaeus, 1758

Suborder: Nematocera Duméril, 1805

Infraorder: Bibionomorpha Hennig, 1954

Superfamily: Anisopodoidea Knab, 1912

Family: Anisopodidae Knab, 1912

Subfamily: Mycetobiinae Crampton, 1924

Genus: *Mycetobia* Meigen, 1818

Type species: *Mycetobia pallipes* Meigen, 1818, by subsequent designation of Westwood (1840: 127).
1861 *Micltoica*: Rondani, p. 12 [unjustified emendation of *Mycetobia*]
Type species: *Mycetobia pallipes* Meigen, 1818; automatic.
1882 *Micetobia* (Meigen) Rondani = *Mycetobia* Meigen): Scudder, p. 210
1940 *Micetoica*: Neave, p. 144 [unjustified emendation of *Micltoica*]
Type species: *Mycetobia pallipes* Meigen, 1818; automatic
1995 *Neomesochria* Amorim & Tozoni, p. 533
Type species: *Mycetobia stonei* Lane & d'Andretta, 1958

Key to species of the genus *Mycetobia* Meigen, 1818 from Eocene

1. Flagellomeres 8–13 elongated, 2x or more longer than wide; Sc ending distally of Rs bifurcation level; R_1 apex distally of M_{1+2} bifurcation level; fork of M_{1+2} narrow, M_{1+2} short, approximately half the length of M_1, last palpomeres approximately 8x as long as wide. . . . . *M. silvia* **sp. nov.**
- Flagellomeres 8–13 up to 2x as long as wide; Sc ending proximally of or opposite Rs bifurcation level; R_1 apex proximally of M_{1+2} bifurcation level; fork of M_{1+2} wide, M_{1+2} elongated, longer than half the length of M_1, last palpomeres at most 3x as long as wide. . . . . 2.
2. R_{2+3} three times as long as Rs or longer; last palpomere rounded at apex. . . . . *M. christelae* **sp. nov.**
- R_{2+3} two and half times as long as Rs or shorter; last palpomere thinned at apex . . . . 3.
3. M_{1+2} shorter than M_1; tarsus of fore leg distinctly shorter than 0.3 the length of entire leg including coxa . . . . *M. hansi* **sp. nov.**
- M_{1+2} as long as M_1 or longer; tarsus of fore leg 0.3 the length of entire leg including coxa or longer . . . . 4.
4. The distance between M_2 and M_{3+4} apices approximately twice longer the distance between M_1 and M_2 apices. . . . .

. . . . *M. connexa* Meunier, 1899

- The distance between M_2 and M_{3+4} apices at most 1.5x than the distance between M_1 and M_2 apices . . . . 5.

5. Sc ending before Rs bifurcation level; the distance between M_1 and M_2 apices equal the distance between R_{4+5} and M_1 apices; R_{2+3} ending before bifurcation of M_{1+2} level; R_{2+3} ending before half the length R_{4+5} level; thorax with sparse and not very thick setae; the distance between R_1 and R_{2+3} apices approximately 3x as long as the distance between Sc and R_1 apices. . . . . *M. perkovskyi* **sp. nov.**

- Sc ending opposite Rs bifurcation level; the distance between M_1 and M_2 apices shorter the distance between R_{4+5} and M_1 apices; R_{2+3} ending beyond bifurcation of M_{1+2} level; R_{2+3} ending beyond half the length R_{4+5} level; very elongated, thick and dense setae on thorax; the distance between R_1 and R_{2+3} apices approximately 5x as long as the distance between Sc and R_1 apices . . . . *M. szwedoi* **sp. nov.**

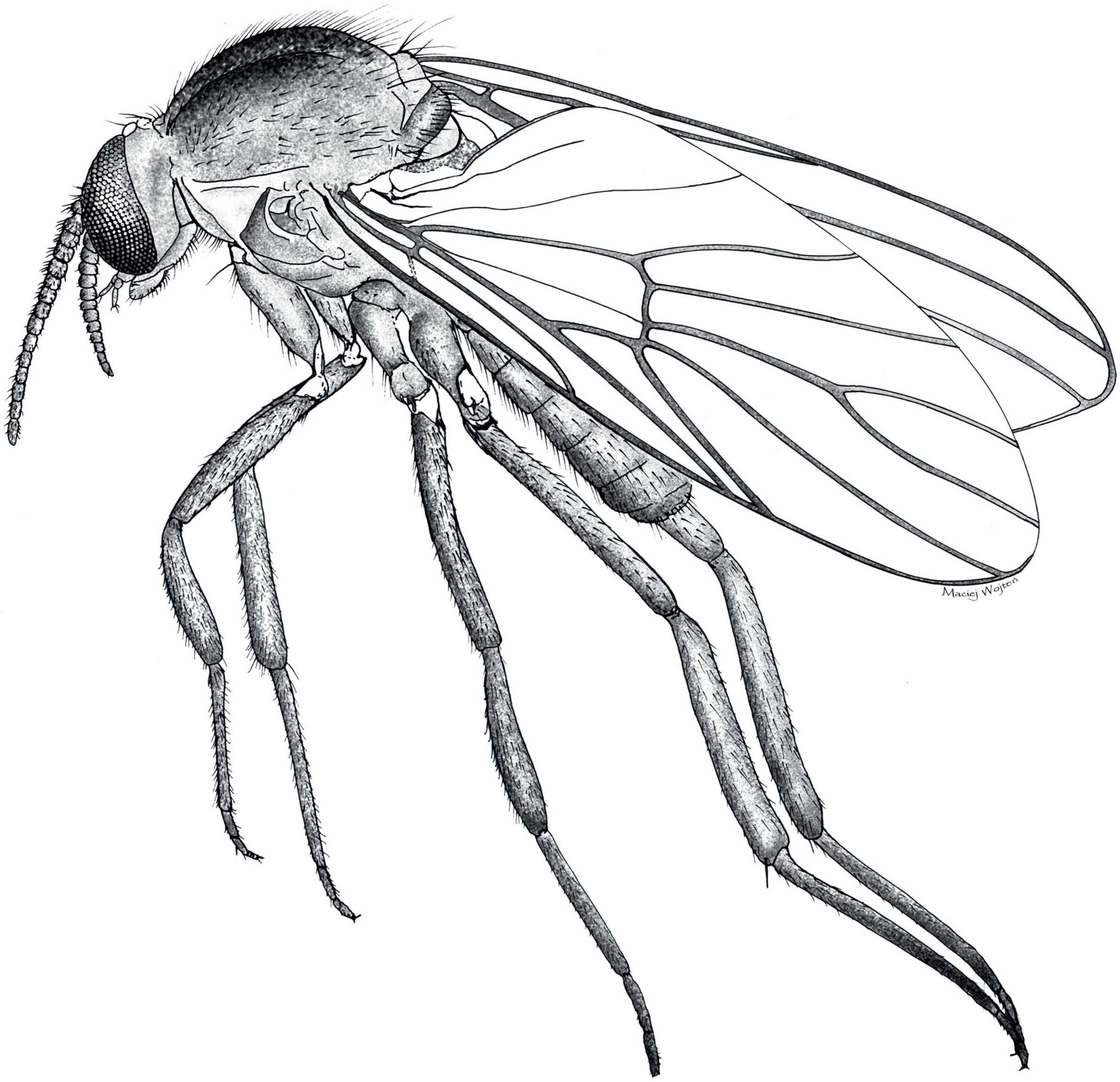

FIGURE 2. *Mycetobia hansi* **sp. nov.** reconstruction.

Mycetobia connexa Meunier, 1899
(Figs 3–9)

*1899 *Mycetobia connexa*, Loew: Meunier, p. 163, pl. I, fig. 8)—N^{os} 14550. VI. 8390. [1]
1899 *Mycetobia connexa*, Loew, p. 163—N^{os} 14557. VI. 8397. [2]

*1904 *Mycetobia callida*: Meunier, p. 101 [p. 90], p. 94 [p. 83], p. 97 [p. 86], p. 271 [p. 260] pl. VIII, fig. 1 (Nº 211.), 2 (Nº 3299.)
1907 *Mycetobia callida* Meunier: Handlirsch, p. 934
1907 *Mycetobia connexa* Loew (Meunier): Handlirsch, p. 934 [3]
1928 *Mycetobia callida* Meunier: Edwards, p. 25 [4]
1928 *Mycetobia connexa* (Loew) Meunier: Edwards, p. 25
1982b *Mycetobia callida* Meunier, 1904: Keilbach, p. 330 [5]
1982b *Mycetobia connexa* Meunier, 1899: Keilbach, p. 330 [6]
1985 *Mycetobia callida* Meunier, 1899: Spahr, p. 8
1985 *Mycetobia connexa* Meunier, 1899: Spahr, p. 8
1994 *Mycetobia connexa* Meunier, 1899: Evenhuis, p. 204
1994 *Mycetobia callida* Meunier, 1904: Evenhuis, p. 205
2014 *Mycetobia connexa* Meunier, 1899: Evenhuis, http://hbs.bishopmuseum.org/fossilcat/fossanisopod.html
2014 *Mycetobia callida* Meunier, 1904: Evenhuis, http://hbs.bishopmuseum.org/fossilcat/fossanisopod.html

Remarks.

[1] Figured specimen probably comes from Loew collection, and probably was labeled (as manuscript name) under this name, but never published.

[2] Meunier mentioned that the venation characters of this specimen are less distinct, but it probably belongs to the genus *Mycetobia* based on comparison of the characters. It could represent another species.

[3] Handlirsch listed *M. connexa* in Mycetophilidae, he mentioned under this name also "*Mycetobia* (spec.), Loew, Bernsteinfauna. 35. 1850.", probably referring to one of the 5 species mentioned by Loew as belonging to this genus.

[4] Edwards proposed to synonymise these species, but he gave neither reasons for this action no information if he examined the specimens, but it seems possible.

[5] Keilbach listed *M. callida* in Mycetophilidae, refers to specimens mentioned by Meunier, 1904. These are preserved in the amber collection of Georg-August-Universität Göttingen.

[6] Following Handlirsch statement Keilbach refers also to "*Mycetobia* sp. Loew, 1850, p. 35. Meunier, 1899, p. 163, Taf. I, Abb. 8." under *M. connexa*. He also mentions the specimens with acquisition number "Balt. B. Coll. GPIK No. 14556 VI 8396, 14557 VI 8397." following Meunier. These specimens were not found.

Diagnosis. Flagellomeres short, shorter than head and thorax combined, 1–9 wider than long; 10–13 as long as wide or slightly longer than wide, tapered to the apex of antenna, last palpomere not very elongated, approximately 2x as long as wide, tapered at apex, shorter than second one; Sc ending before Rs bifurcation level; R_1 apex before M_{1+2} bifurcation level; R_{2+3} 2.5x as long as Rs; the distance between R_1 and R_{2+3} apices approximately 6x as long as the distance between Sc and R_1 apices; M_{1+2} longer than M_1; fork of M_{1+2} wide; the distance between M_1 and M_2 apices as wide as the distance between R_{4+5} and M_1 apices; the distance between M_2 and M_{3+4} apices one and half the distance between M_1 and M_2 apices; R_{2+3} ending before bifurcation of M_{1+2} level, before half the length R_{4+5} level; thorax with sparse setae, prescutellar and postalar setae thick, not very elongated, apical scutellar setae very thick, very elongated.

Material examined. (*M. connexa*): No. 4226 (female), Baltic amber, (MAIG); MP/3695 (female), Baltic amber, (ISEA PAS); No. 804-2 (female), Baltic amber, (coll. Ch. & H. W. Hoffeins); No. 70-2 (female), Baltic amber, (coll. Ch. & H. W. Hoffeins); No. 1258-2 (female), Baltic amber, (coll. Ch. & H. W. Hoffeins); No. 1737-3 (female), Baltic amber, (coll. Ch. & H. W. Hoffeins); No. 804-1 (female), Baltic amber, (coll. Ch. & H. W. Hoffeins); No. GZG.BST 03403 [Z 3299] (female), Baltic amber, (GMUG); No. GZG.BST 03402 [Z 211] (female), Baltic amber, (GMUG); No. GZG.BST 03400 [Z 6457] (female), Baltic amber, (GMUG); No. GZG.BST 03401 [Z 2304] (male), Baltic amber, (GMUG); No. GZG.BST 03408 [G 659] (female), Baltic amber, (GMUG); No. GZG.BST 03409 [G 674] (male), Baltic amber, (GMUG); No. GZG.BST 03410 [G 664] (sex unknown), Baltic amber, (GMUG).

Old/previous numbers are given in square brackets.

Remarks: The specimens mentioned by Meunier in 1899 were not found, these mentioned in Meunier's publication in 1904: No. Z 6457 (new number GZG.BST 03400), No. Z 2304 (new number GZG.BST 03401), No. Z 211 (new number GZG.BST 03402), No. Z 3299 (new number GZG.BST 03403) are housed in the Göttingen (GMUG) collection. The holotype of neither *M. connexa* nor *M. callida* was specified by Meunier (1899, 1904).

Additional description. Body (Figs 6A; 7A–H) 2.07–5.02 mm long, pale brown with pale brown legs. Head width (Figs 6A; 8A, B, D) 0.77–0.86 mm, 0.69–0.84 mm high. Head and thorax combined 0.46–0.57 mm. Eyes occupying most of head in lateral view, in frontal view eyes separated by a distance about equal to diameter of ocellus; raised ocelli form equilateral triangle (Fig. 8B, D). Antenna 0.42–0.86 mm long (Figs 3A; 6A; 8A, D) with 14 cylindrical, but short flagellomeres, more or less elongated, scape and pedicel short and wide, wider than long, last flagellomere longer than penultimate one; all flagellomeres with comparatively numerous to *Mycetobia*, elongated and thick setae, shorter than segments bearing them and rather sparse; additionally short setae on all flagellomeres, last flagellomere tapered at apex with a few not very elongated setae at apex, shorter than segment bearing them; palpus maxillaris 4-segmented, 0.14 mm long (Fig. 8A, C), first palpomere rather cylindrical, not very elongated; second thick and widened in distal part, elongated, twice as long as wide, third short; last one elongated, longer than penultimate one, elongated, not numerous and short setae on all palpomeres.

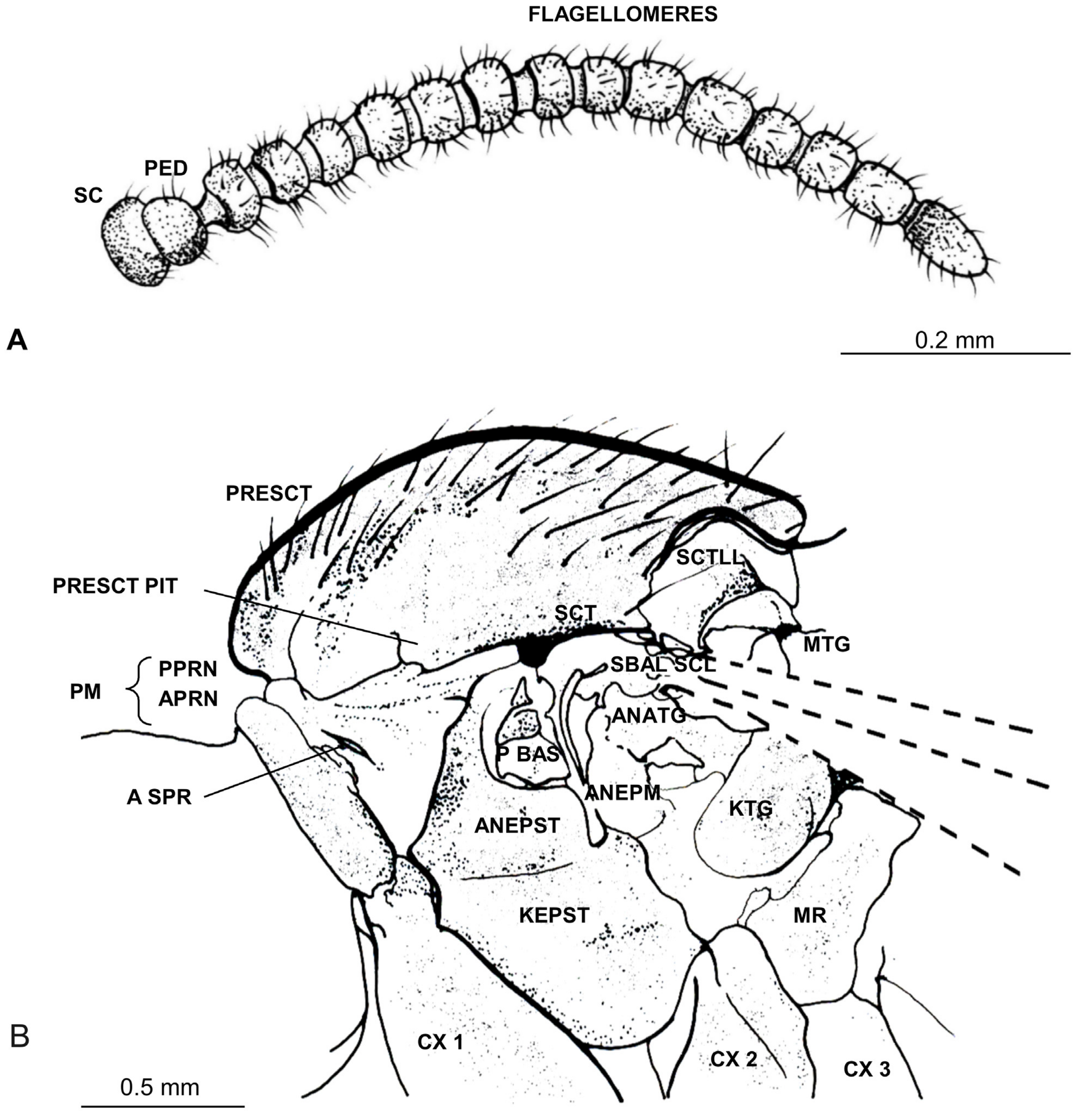

FIGURE 3. *Mycetobia connexa* Meunier, 1899, No. 804-2 (female), (coll. Ch. & H. W. Hoffeins). A. antenna; B. thorax, lateral view. Abbreviation: ANATG—anatergite; ANEPM—anepimeron; ANEPST—anepisternum; APRN—antepronotum; A SPR—anterior spiracle; CX—coxa; KEPST—katepisternum; KTG—katatergite; MR—meron; MTG—mediotergite; P BAS—posteriori basalare; PED—pedicel; PPRN—postpronotum; PRESCT—prescutum; PRESC PIT—prescutal pit; PM—pronotum; SBAL SCL—subular sclerite; SCT—scutum; SCTLL—scutellum; SC—scape.

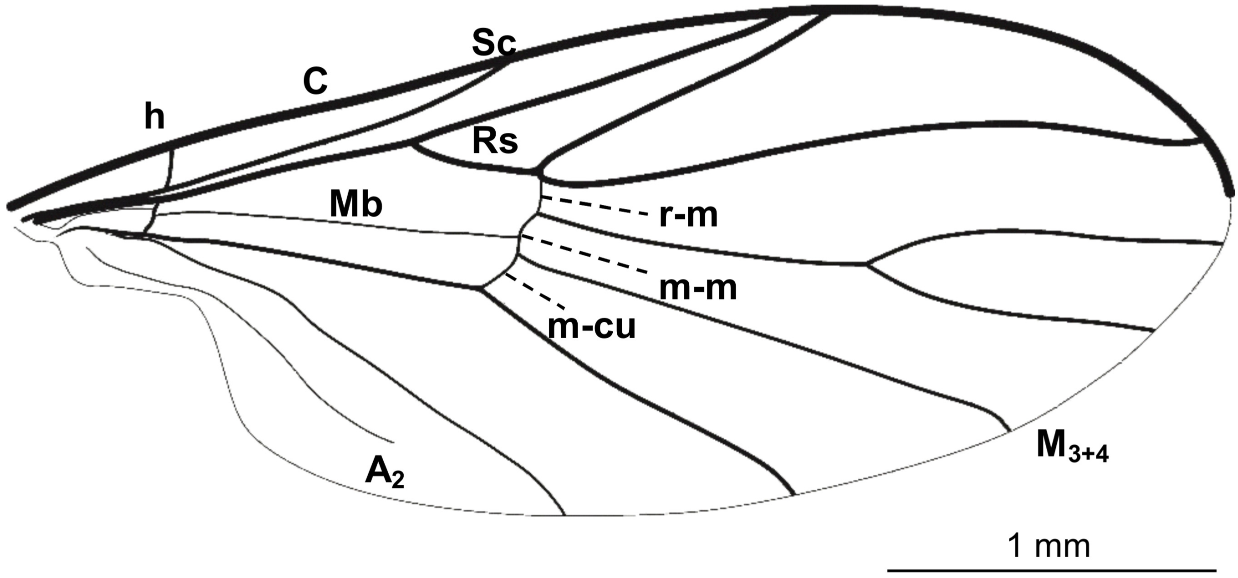

FIGURE 4. *Mycetobia connexa* Meunier, 1899, No. 1258-2 (female), (coll. Ch. & H. W. Hoffeins), wing venation.

Thorax (Figs 3B; 6B, C): prescutellar setae and apical scutellar setae very elongated; acrostichal setulae not very elongated, Sc ending opposite A_1 apex; wing (Fig. 4): 2.25–4.03 mm long, 0.93–1.11 mm wide; Sc comparatively elongated, slightly arched, R_{2+3} slightly arched at apex; A_1 well developed, A_2 comparatively elongated, waved; halter not very elongated with elongated stem and widened knob. Legs (Figs 5A–C; 9A–D): coxa of fore, middle and hind coxa with very rare elongated bristles; fore, middle and hind tibia with two unequal tibial spurs; tarsus with last segment only slightly longer than penultimate one and not very elongated, rather slender claw and almost invisible empodium (Fig. 9D). Tarsus of fore leg 0.3 the length of entire leg including coxa or longer (Fig. 5D). Apical comb well visible on fore and hind legs (Fig. 9A, C). Coxa of fore leg 0.50–0.69 mm, trochanter 0.10–0.26 mm, femur 0.65–0.92 mm, tibia 0.66–0.89 mm, tarsus 0.84–1.47 mm long (0.41/0.16/0.10/0.09/0.11). Coxa of middle leg 0.38–0.70 mm, trochanter 0.13–0.15 mm, femur 0.75–0.96 mm, tibia 0.65–0.86 mm, tarsus 0.95–1.48 mm long (0.48/0.17/0.11/0.09/0.10). Coxa of hind leg 0.41–0.73 mm, trochanter 0.11–0.17 mm, femur 0.68–1.17 mm, tibia 0.82–1.28 mm, tarsus 0.98–1.75 mm long (0.56/0.13/0.10/0.09/0.10).

Abdomen (Figs 6A; 7A–H; 9F): female terminalia rather small cerci not very elongated; male terminalia not very large.

Comparison. In contrast to *M. christelae* **sp. nov.** in *M. connexa*, last segment of palpomere is elongated, but approximately 2x as long as wide, tapered at apex, while in *M. christelae* **sp. nov.** last palpomere is very elongated, approximately 3x as long as wide and rounded at apex. Setae on thorax in *M. connexa* are sparse, in *M. szwedoi* **sp. nov.** are dense. Flagellomeres in *M. connexa* are short, 1–9 wider than long; 10–13 as long as wide or slightly longer than wide, tapered to the apex of antenna, in *M. silvia* **sp. nov.** flagellomeres are distinctly longer, flagellomeres 8–13 are elongated, 2x as long as wide or longer. Other differences in morphology of antenna and wing venation between *M. connexa* and other species of *Mycetobia* from Eocene are provided in Table 2.

Mycetobia christelae sp. nov.

(Figs 10–13)

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Diagnosis. Flagellomeres 1–6 short, distinctly wider than long, flagellomeres 7–13 longer than wide, up to 2x as long as wide; last flagellomeres longer than penultimate one, tapered at apex; last palpomere elongated, 3x as long as penultimate one, 3x as long as wide, rounded at apex, longer than second one; Sc ending before Rs bifurcation level; R_1 ending just before M_{1+2} bifurcation level; R_{2+3} elongated, 3x as long as Rs; the distance between R_1 and R_{2+3}

apices approximately 10x as long as the distance between Sc and R_1 apices; M_{1+2} longer than M_1; fork of M_{1+2} wide; the distance between M_1 and M_2 apices slightly longer than the distance between R_{4+5} and M_1 apices; the distance between M_2 and M_{3+4} apices as long as the distance between M_1 and M_2; R_{2+3} ending before bifurcation of M_{1+2} level, just beyond half R_{4+5}; dense setae on thorax, praescutellar and postalar setae not very elongated, pronotal setae thick and elongated; male terminalia large, approximately 0.25 the body length with cerci very elongated, massive, blunt ended and gonostyles shovel-shaped.

Etymology. The species name is dedicated to Christel Hoffeins from Hamburg, Germany, the owner of amber inclusions collection and the expert in Baltic amber inclusions.

Type material. Holotype: No. 1258-3 (male), Baltic amber, (coll. Ch. & H. W. Hoffeins); **Paratype:** No. 838—1 (male), Baltic amber, (coll. Ch. & H. W. Hoffeins); **Additional material:** No. MP/3694 (female), Baltic amber, (ISEA PAS).

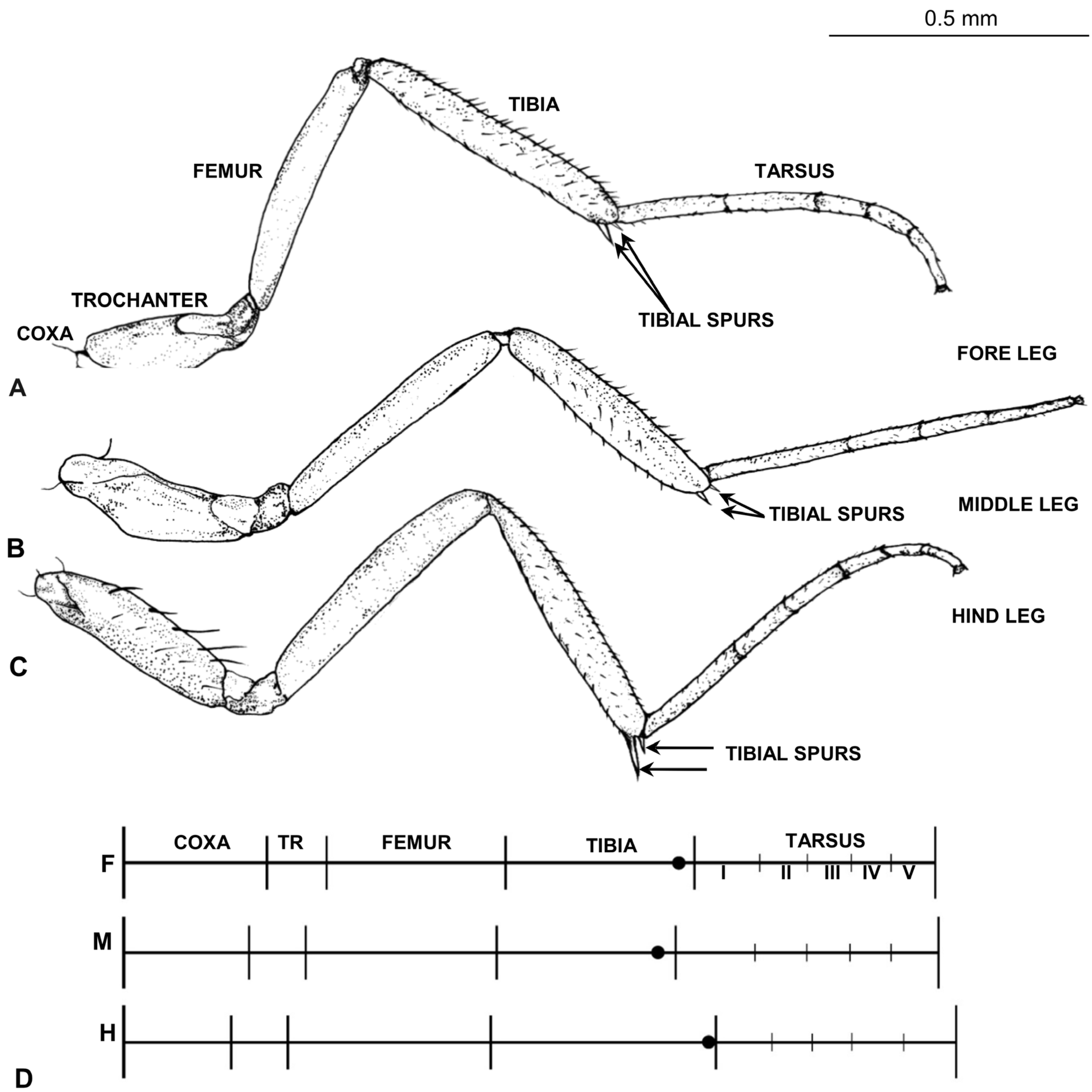

FIGURE 5. *Mycetobia connexa* Meunier, 1899. A.–C. No. 804-2 (female), (coll. Ch. & H. W. Hoffeins). A–C. drawing of leg with two tibial spurs: A. fore leg; B. middle leg; C. hind leg; D. diagram of relation between the length of legs: fore leg (F), middle leg (M), hind leg (H); point indicate position of tibial spurs. Abbreviations: I–V—numbers tarsomeres.

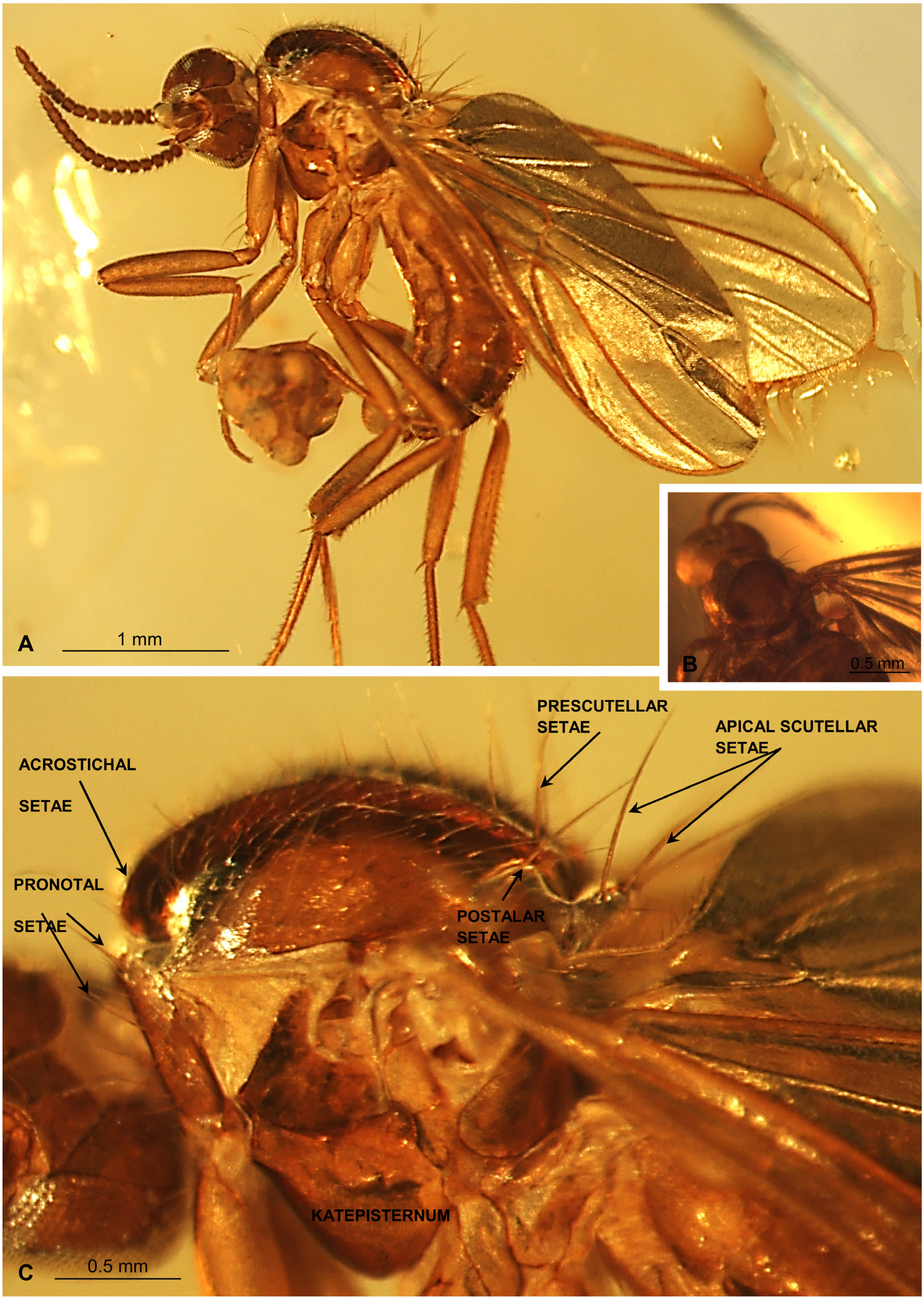

FIGURE 6. *Mycetobia connexa* Meunier, 1899. A., C. No. 804-2 (female), (coll. Ch. & H. W. Hoffeins). A. habitus, lateral view; B. No. GZG BST 03402 (female) (GMUG), head and thorax, dorsal view; C. thorax, lateral view.

FIGURE 7. *Mycetobia connexa* Meunier, 1899, the body. A. No. GZG BST 03402 (female) (GMUG), dorsal view; B. No. GZG BST 03403 (female) (GMUG), dorsal view; C.; D. No. GZG BST 03401 (male) (GMUG), lateral view; E. No. GZG BST 03400 (female) (GMUG), ventral view; F. No. GZG BST 03409 (male) (GMUG), latero-ventral view; G. No. GZG BST 03408 (female) (GMUG), lateral view; H. No. GZG BST 03410 (sex unknown) (GMUG), lateral view.

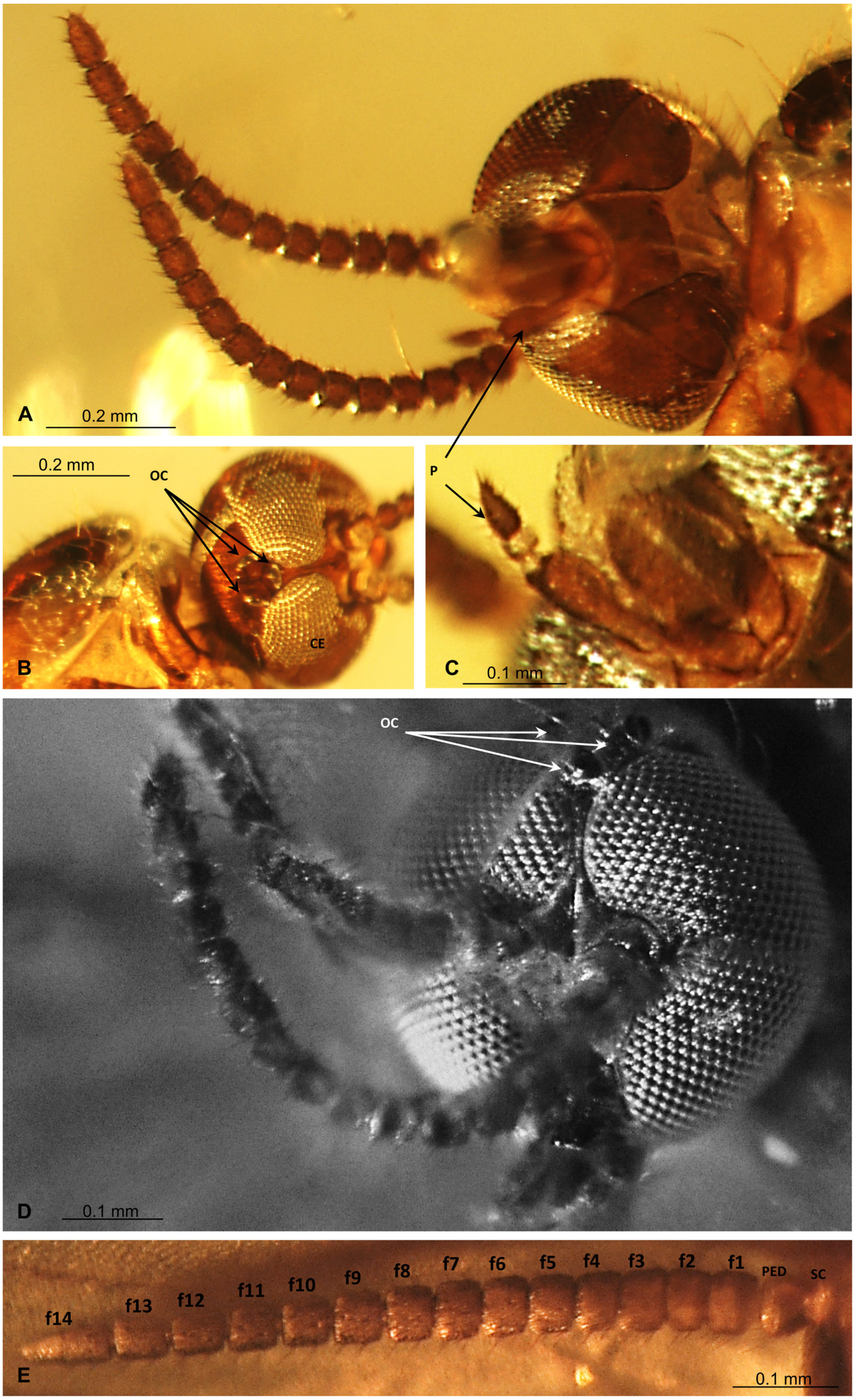

FIGURE 8. *Mycetobia connexa* Meunier, 1899. A.–C. No. 804-2 (female), (coll. Ch. & H. W. Hoffeins): A. head with palpus maxillaris and antenna visible, ventral view; B. head with ocelli, scape and pedicel visible, dorsal view; C. palpus maxillaris; D. No. GZG BST 03400 (female), (GMUG), head, frontal view; D. No. GZG BST 03401 (male), (GMUG), antenna. Abbreviations: CE—compound eyes; f1–f14 flagellomeres; OC—ocelli; P—palpus maxillaris; PED—pedicel; SC—scape.

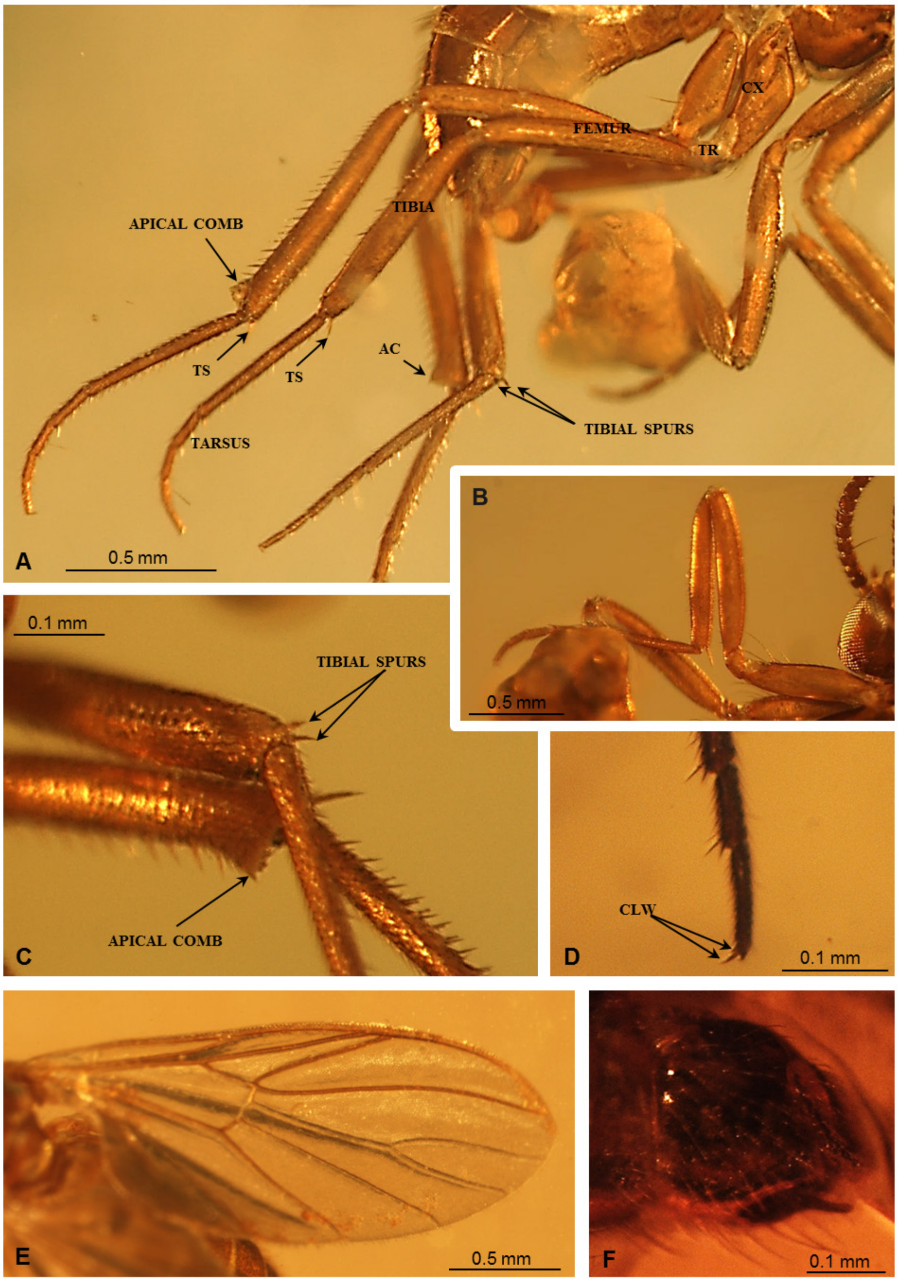

FIGURE 9. *Mycetobia connexa* Meunier, 1899, No. 804-2 (female), (coll. Ch. & H. W. Hoffeins). A.–C. legs: A. middle and hind legs; B. fore leg; C. tibial spurs of middle and hind leg, apical combs of hind leg; D. No. GZG BST 03401 (male), (GMUG), last tarsomeres of middle leg; E. No. 1258-2 (female), (coll. Ch. & H. W. Hoffeins), wing; F. No. GZG BST 03409 (male), (GMUG), male terminalia. Abbreviations: AC—apical comb; CLW—claw; CX—coxa; TR—trochanter; TS—tibial spurs.

Description. Body (Fig. 11A–F) 2.68–3.06 mm long. Head, thorax and legs brown. Head: antenna (Figs 10A; 12A–C), 1.10 mm long, 14 flagellomeres with elongated sparse setae, shorter to width of segments bearing them; additionally very short setae on all flagellomeres; last flagellomere 0.11 mm long, penultimate one 0.03 mm; palpus maxillaris 4-segmented, the second palpomere 0.10 mm long, penultimate one 0.04 mm, last palpomere 0.14 mm long.

Thorax (Fig. 12D, E): prescutellar setae not very elongated, wing (Figs 10C; 12F): 3.18 mm long, 1.06–1.14 mm wide; Sc ending opposite A_1 apex; R_1 apex in about 0.6 of wing length; Rs separate Rb in 0.4 of wing length from wing base; Rs 0.27 mm long; cross-vein r-m shorter than m-m.

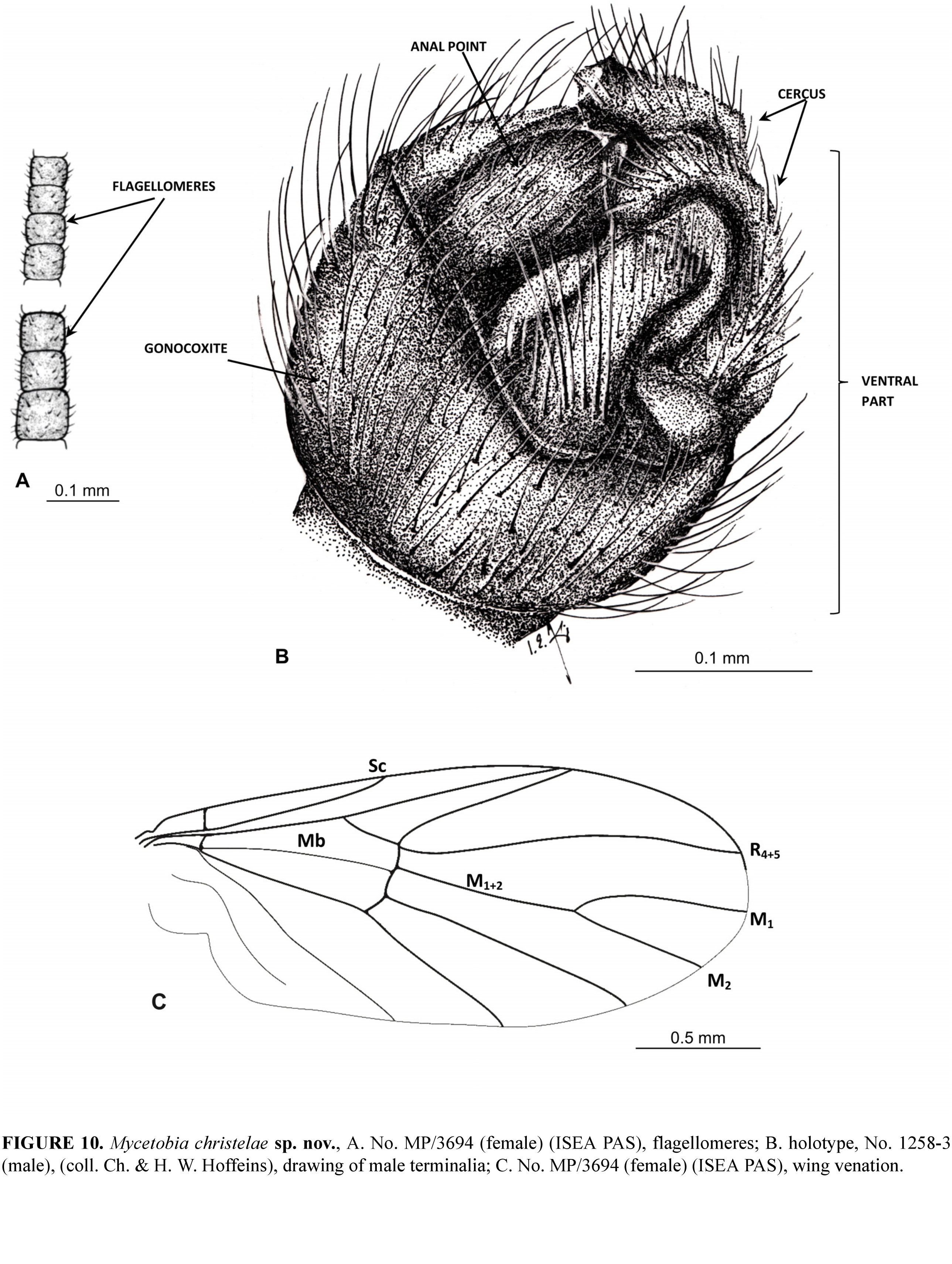

FIGURE 10. *Mycetobia christelae* **sp. nov.**, A. No. MP/3694 (female) (ISEA PAS), flagellomeres; B. holotype, No. 1258-3 (male), (coll. Ch. & H. W. Hoffeins), drawing of male terminalia; C. No. MP/3694 (female) (ISEA PAS), wing venation.

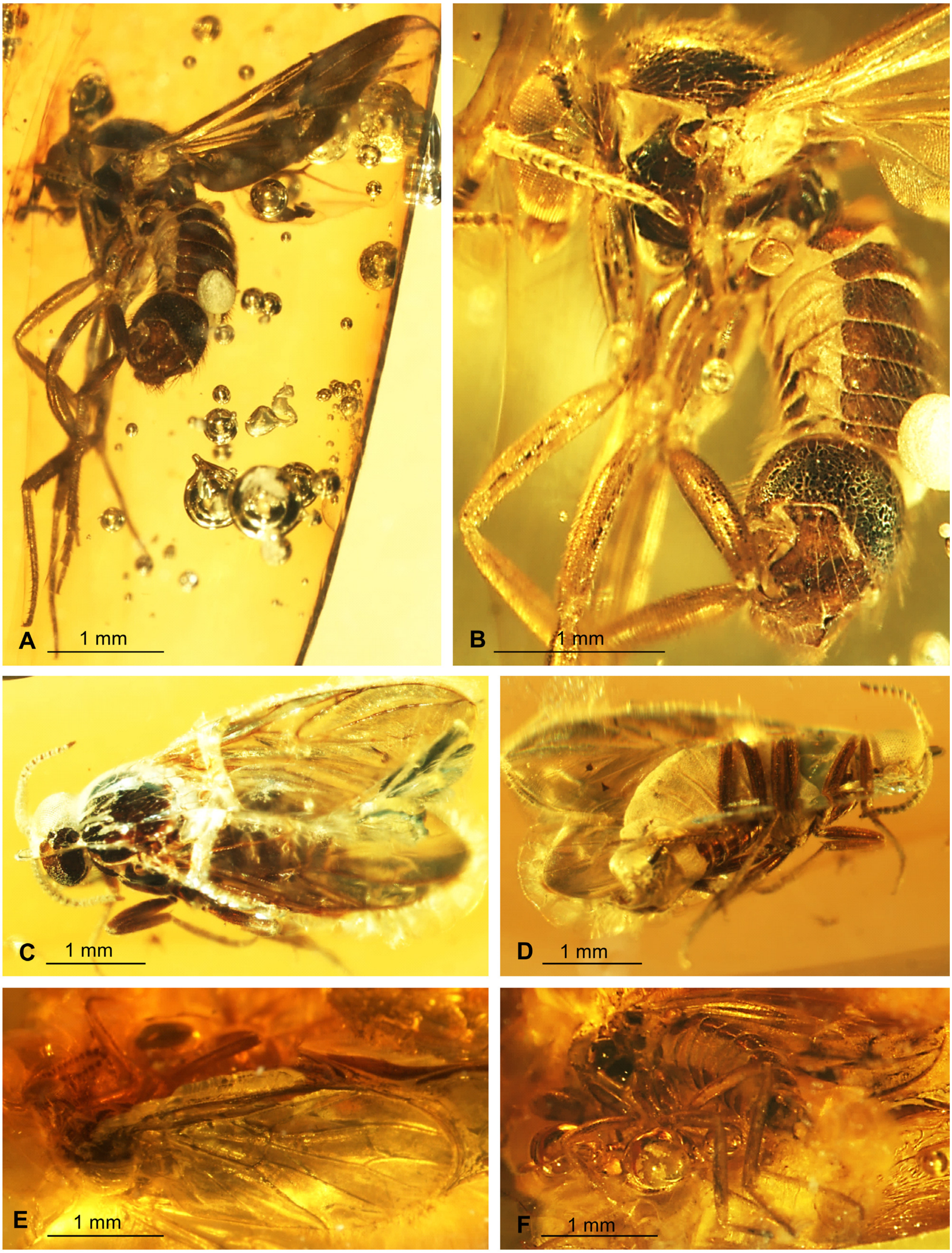

FIGURE 11. *Mycetobia christelae* **sp. nov.** A, B. holotype, No. 1258-3 (male) (coll. Ch. & H. W. Hoffeins). A. habitus, latero-dorsal view; B. enlarged view of head, thorax and abdomen, latero-dorsal view; C., D. paratype, No. 838-1 (male) (coll. Ch. & H. W. Hoffeins); C. habitus, dorsal view; D. habitus, ventral view; E., F. No. MP/3694 (female) (ISEA PAS), habitus. E. lateral view; F. latero-ventral view.

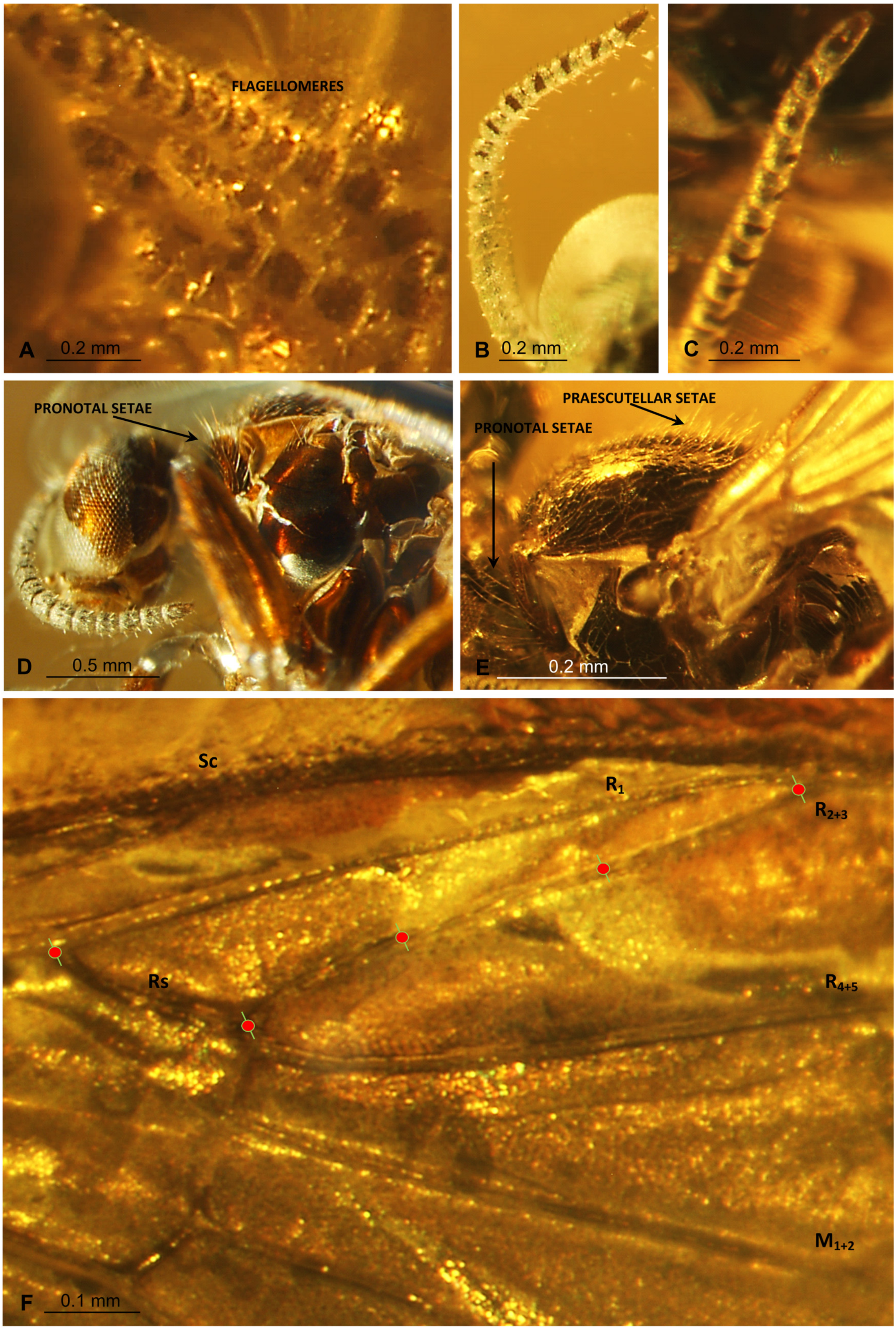

FIGURE 12. *Mycetobia christelae* **sp. nov.** A.–C. flagellomeres: A. No. MP/3694 (female) (ISEA PAS); B. No. 838-1 (male) (coll. Ch. & H. W. Hoffeins), antenna; C. holotype, No. 1258-3 (male) (coll. Ch. & H. W. Hoffeins), enlarged view of flagellomeres; D. holotype, No. 838-1 (male) (coll. Ch. & H. W. Hoffeins), head and thorax, latero-ventral view; E., F. holotype, No. 1258-3 (male) (coll. Ch. & H. W. Hoffeins), E. thorax, lateral view; F. enlarged view of Sc, R_1 and R_{2+3} apices. Remark and abbreviations: red points—the distance between red points is equal to Rs length.

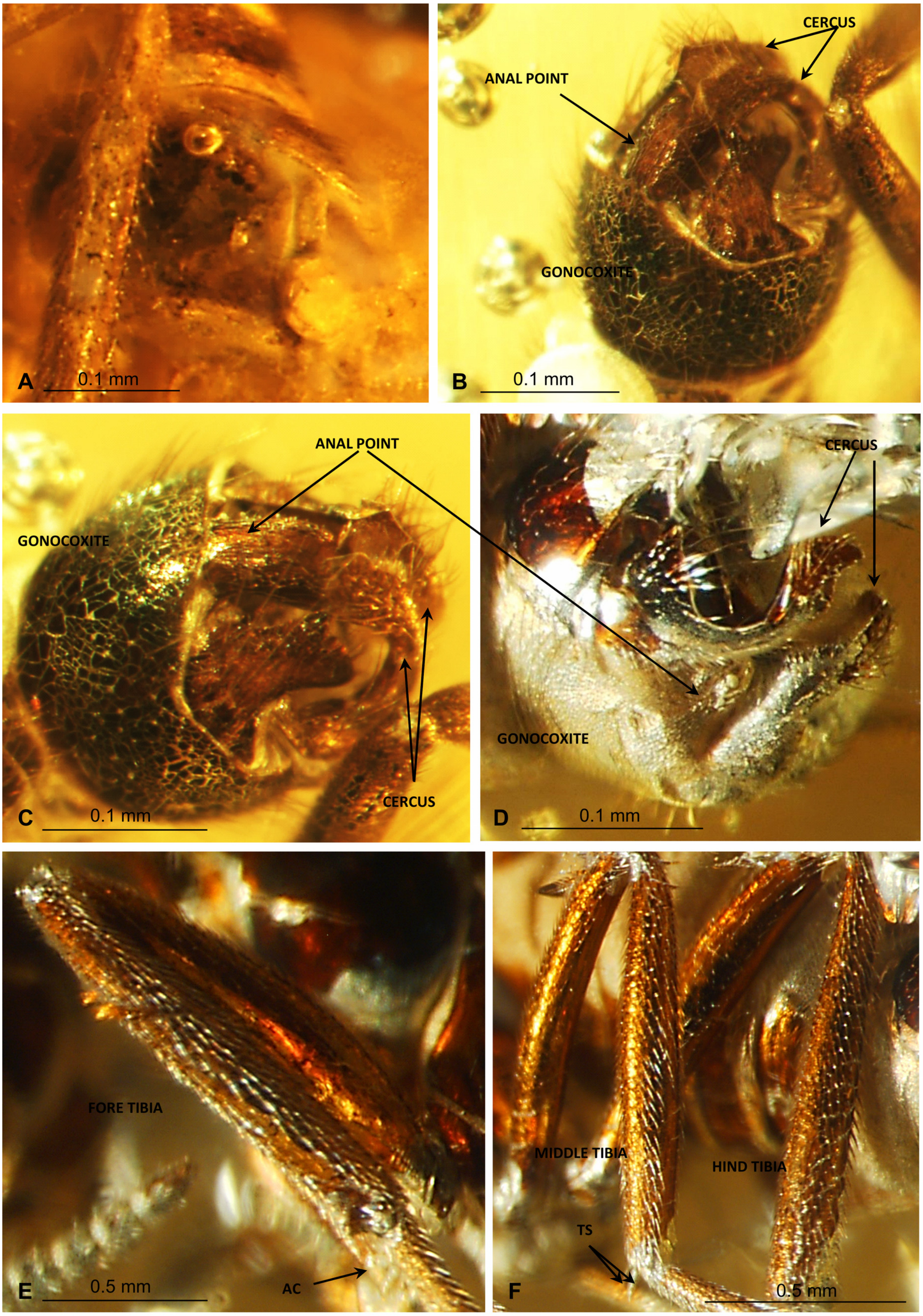

FIGURE 13. *Mycetobia christelae* **sp. nov.** A. No. MP/3694 (female) (ISEA PAS), female terminalia; B, C. holotype, No. 1258-3 (male) (coll. Ch. & H. W. Hoffeins), male terminalia: B. lateral view; C. dorso-lateral view; D.–F. No. 838-1 (male) (coll. Ch. & H. W. Hoffeins): D. male terminalia, latero-ventral view; E. fore tibia with dense setae visible; F. middle and hind tibia with dense setae visible.

Legs (Figs 13E, F): fore, middle and hind tibia with two unequal tibial spurs; tarsus comparatively elongated with last segment only slightly longer than penultimate one and not very elongated, rather slender claw and almost invisible empodium. Apical comb well visible on fore and hind legs; coxa of fore leg 0.62 mm, trochanter 0.13 mm, femur 0.86 mm, tibia 0.80 mm, tarsus 1.05 mm long (0.58/0.13/0.10/0.09/0.15). Tarsus of fore leg 0.3 the length of entire leg including coxa. Longer tibial spur of fore leg 0.07 mm long. Coxa of middle leg 0.60–0.70 mm, trochanter 0.10–0.12 mm, femur 0.77–0.93 mm, tibia 1.01–1.02 mm, tarsus 1.13–1.28 mm long (0.64–0.77/0.15–0.17/0.12–0.13/0.09–0.11/0.11–0.12). Coxa of hind leg 0.81 mm, trochanter 0.09–0.10 mm, femur 1.06–1.07 mm, tibia 1.10–1.22 mm, tarsus 1.05–1.28 mm long (0.59–0.77/0.11–0.19/0.11–0.12/0.09–0.10/0.11–0.13). All tibia with dense, not very elongated setae.

Abdomen (Figs 11A–F; 13A–D): male terminalia (Figs 10B; 13B–D) very large, 0.79–0.80 mm long, dense, thick and elongated setae on anal point, gonocoxite, cerci and gonostyles, anal point wide, with many, dense setae, blunt ended; gonocoxite almost black with very elongated setae; female terminalia (Fig. 13A) comparatively massive.

Remarks: There are no differences in wing venation between males and females.

Comparison. *M. christelae* **sp. nov.** differ from other known from Baltic amber species by elongated last palpomere, which is 3x as long as penultimate one and is rounded at apex, not tapered as in other species of *Mycetobia* known from Eocene or described herein. This species also differ from other species in structure of male genitalia, e.g. in *M. szwedoi* **sp. nov.** additional structures are hooked, while in *M. christelae* they are shovel-shaped. Moreover, *M. christelae* **sp. nov.** differs distinctly from *M. silvia* **sp. nov.** in shape of flagellomeres. In *M. silvia* **sp. nov.** flagellomeres are cylindrical, as long as wide up to twice longer than wide or even longer; in *M. christelae* **sp. nov.** flagellomeres 1–6 are much wider than long. Differences in wing venation are provided in Table 2.

Mycetobia hansi sp. nov.

(Figs 14–15)

urn:lsid:zoobank.org:act:B8B4B962-E5C4-4989-8256-2C6F348154C0

Diagnosis. Flagellomeres 1–7 wider than long, flagellomeres 8–13 longer than wide, became more elongated to the apex of antenna, up to 2x as long as wide; last flagellomere at most 2x as long as wide; last palpomere elongated 3x as long as wide, tapered at apex, longer than second one; Sc ending before Rs bifurcation level; R_1 apex before M_{1+2} bifurcation level; the distance between R_1 and R_{2+3} apices approximately 4x as long as the distance between Sc and R_1 apices; R_{2+3} 2.5x as long as Rs; the distance between Sc and R_1 apices approximately 4x as long as the distance between R_1 and R_{2+3} apices; M_{1+2} shorter than M_1; fork of M_{1+2}; the distance between M_1 and M_2 apices slightly wider than the distance between R_{4+5} and M_1 apices; the distance between M_2 and M_{3+4} apices longer than the distance between M_1 and M_2; R_{2+3} ending opposite bifurcation of M_{1+2} level, before half the length R_{4+5} level; only prescutellar and apical scutellar setae thick, but not very elongated.

Etymology. The species name is dedicated to Hans Werner Hoffeins from Hamburg, Germany, the owner of amber inclusions collection and the expert in Baltic amber inclusions.

Type material. Holotype: No. 1258-4 (female), Baltic amber, (coll. Ch. & H. W. Hoffeins).

Description. Body (Fig. 15A) 3.28 mm long, pale brown with dark brown thorax. Head (Figs 15A, B): 0.62 mm high; ocelli present and form equilateral triangle. Antenna 1.06 mm long (Figs 14A; 15A, B), 14 flagellomeres, more or less elongated, scape and pedicel comparatively short and wide, wider than long, with a few very elongated setae in distal part, sometimes longer than segments bearing them; last flagellomere tapered to the end, longer than penultimate one, approximately twice as long as wide; flagellomeres covered by comparatively elongated sparse and thick setae, but setae much shorter than segments bearing them; additionally very short setae on all flagellomeres, last flagellomere with a few not very elongated apical setae; palpus maxillaris 4-segmented, slender, first palpomere 0.04 mm long cylindrical, second palpomere not very elongated, 0.09 mm long, only slightly longer than wide, widened in the midlenght, third small, short, 0.03 mm long, approximately as long as wide, last one elongated, 0.10 mm long, tapered at apex (Figs 14B; 15B) elongated and short setae on all palpomeres.

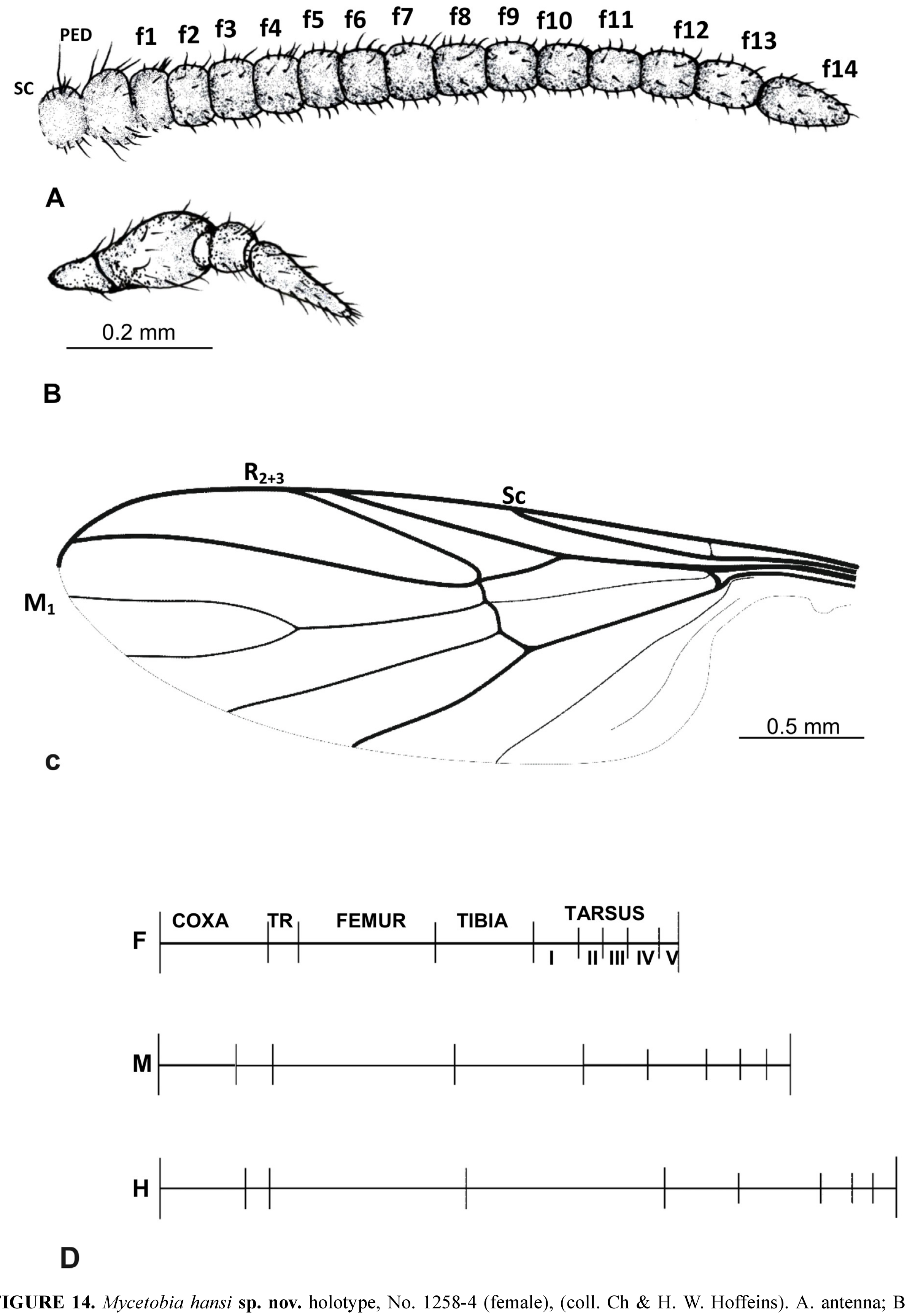

FIGURE 14. *Mycetobia hansi* **sp. nov.** holotype, No. 1258-4 (female), (coll. Ch & H. W. Hoffeins). A. antenna; B. palpus maxillaris; C. wing venation; D. diagram of relation between the length of legs: fore leg (F), middle leg (M), hind leg (H); point indicate position of tibial spurs. Abbreviations: SC—scape; PED—pedicel; f1–f14—flagellomeres; I–IV numbers of tarsomeres.

FIGURE 15. *Mycetobia hansi* **sp. nov.** holotype, No. 1258-4 (female), (coll. Ch & H. W. Hoffeins). A. habitus, latero-dorsal view; B. enlarged view of head with antenna and palpus maxillaris, latero-ventral view; C. wing.

Thorax: prescutellar setae and apical scutellar setae very elongated; acrostichal setulae not very elongated; wing (Figs 14C; 15C): 3.08 mm long, 1.03 mm wide; Sc comparatively short, slightly arched, ending at 1/2 of Rs level, Rs 0.33 mm long; Rs not very short, R_{2+3} 0.66 mm long; R_1 ending before midlength, at R_{4+5} level; M_{1+2} approximately as long as M_2 and shorter than M_1, M_{1+2} 0.74 mm long, A_1 well developed, connected with wing edge; A_2 short and slender. Halter not very elongated with elongated stem and widened knob. Legs (Figs 15A; 14D): fore, middle and hind tibia with two unequal tibial spurs; tarsus comparatively elongated with last segment only slightly longer than penultimate one and not very elongated, rather slender claw and almost invisible empodium. Apical comb well visible on fore and hind legs. Tarsus of fore leg shorter than 0.3 the length of leg. Fore coxa 0.59 mm, trochanter 0.08 mm, femur 0.89 mm, tibia 0.80 mm, tarsus 1.96 mm long (0.38/0.12/0.11/0.01/0.02). Middle coxa 0.42 mm long, trochanter 0.12 mm long, femur 0.57 mm long, tibia 0.79 mm, tarsus 0.95 mm (0.55/0.15/0.09/0.09/0.09). The length of hind coxa 0.42 mm, trochanter 0.12 mm, femur 1.02 mm, tibia 0.88 mm, tarsus 1.22 mm (0.67/0.18/0.13/0.11/0.13).

Abdomen: female terminalia not very elongated, cerci not very large

Comparison. In contrast to other species known from the Baltic amber and described herein vein M_{1+2} in *M. hansi* **sp. nov.** is distinctly shorter than M_1. There are also some other differences in wing venation; in contrast to *M. silvia* **sp. nov.**, where Sc ending beyond Rs bifurcation level, R_1 apex is positioned beyond M_{1+2} bifurcation level, in *M. hansi* **sp. nov.** Sc ending before Rs bifurcation level and R_1 apex is positioned before M_{1+2} bifurcation level. Moreover, in contrast to *M. christelae* **sp. nov.**, where R_{2+3} is 3x as long as Rs, R_{2+3} ending beyond half the length

R_{4+5} level, in *M. hansi* **sp. nov.** R_{2+3} is 2.5x as long as Rs, R_{2+3} ending before half the length R_{4+5} level. More differences of wing venation is given in Table 2. *M. hansi* **sp. nov.** differ distinctly from *M. silvia* **sp. nov.** by morphology of antenna. In *M. hansi* **sp. nov.** flagellomeres 1–7 are wider than long, flagellomeres 8–13 are longer than wide, became more elongated to the apex of antenna, the last one is at most 2x as long as wide, while in *M. silvia* **sp. nov.** flagellomeres are cylindrical, becoming narrowed and more elongated to the apex of antenna, only flagellomeres 1–3 are as long as wide, flagellomeres 4–7 are more than 1x to 1.5x as long as wide, flagellomeres 8–13 are elongated 2x or more longer than wide, the last one is 3x as long as wide. Prescutellar and apical scutellar setae are thick, but not very elongated in *M. hansi* **sp. nov.**, not like in *M. szwedoi* **sp. nov.** where are very elongated and thick.

Mycetobia perkovskyi **sp. nov.**
(Figs 16–18)
urn:lsid:zoobank.org:act:5451D820-E169-450E-A9EF-9A946AB86595

Diagnosis. Flagellomeres short, wider than long or slightly longer, tapered to the apex of antenna, last flagellomeres at most 1.5x as long as wide, up to 2x as long as wide; last palpomere 3x as long as wide, tapered at apex; Sc ending before Rs bifurcation level; R_1 apex fare before M_{1+2} bifurcation level; the distance between R_1 and

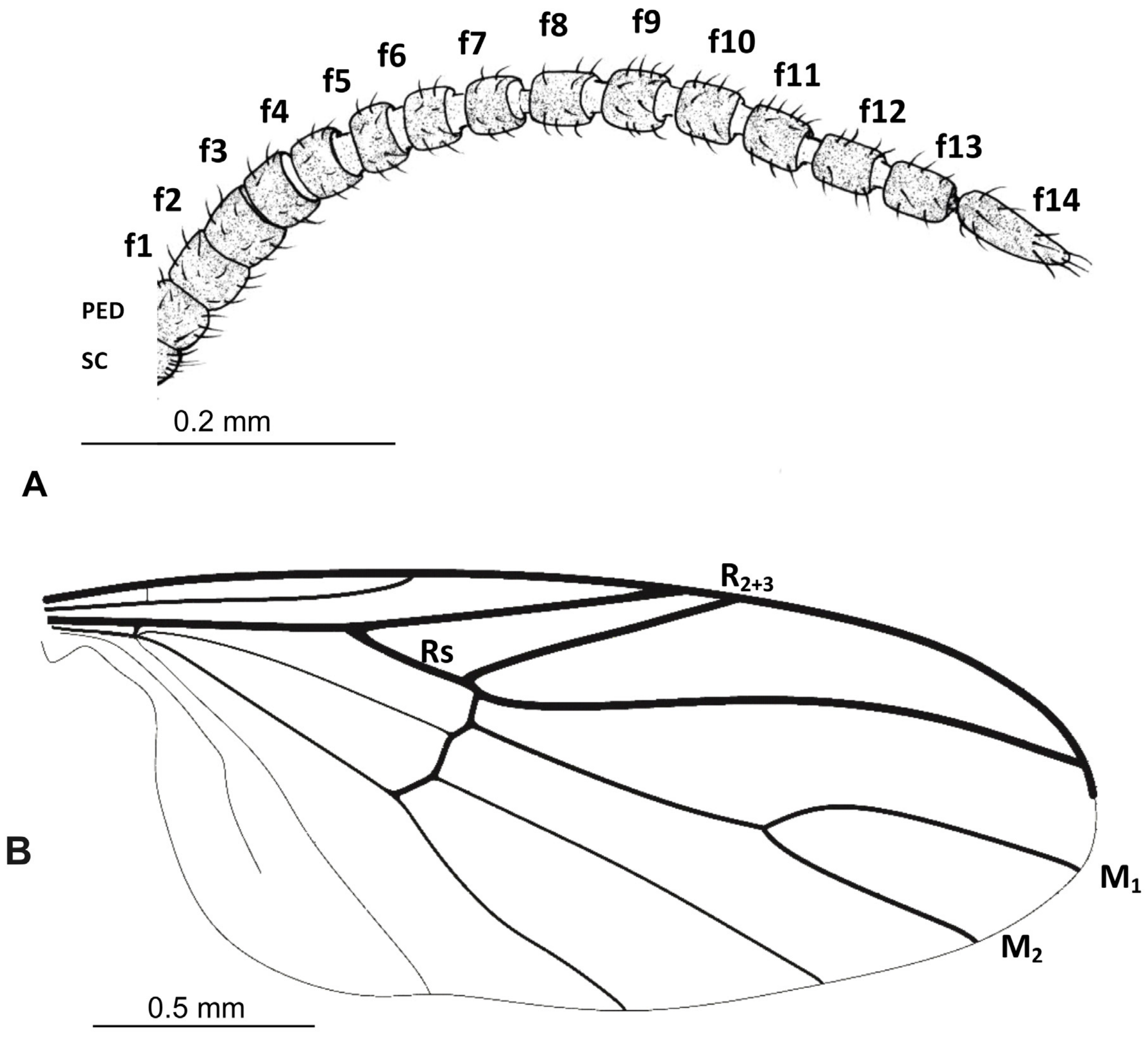

FIGURE 16. *Mycetobia perkovskyi* **sp. nov.** holotype, No. 872 (sex unknown), (coll. NAS of Ukraine). A. antenna; B. wing venation. Abbreviations: SC—scape; PED—pedicel; f1–f14—flagellomeres.

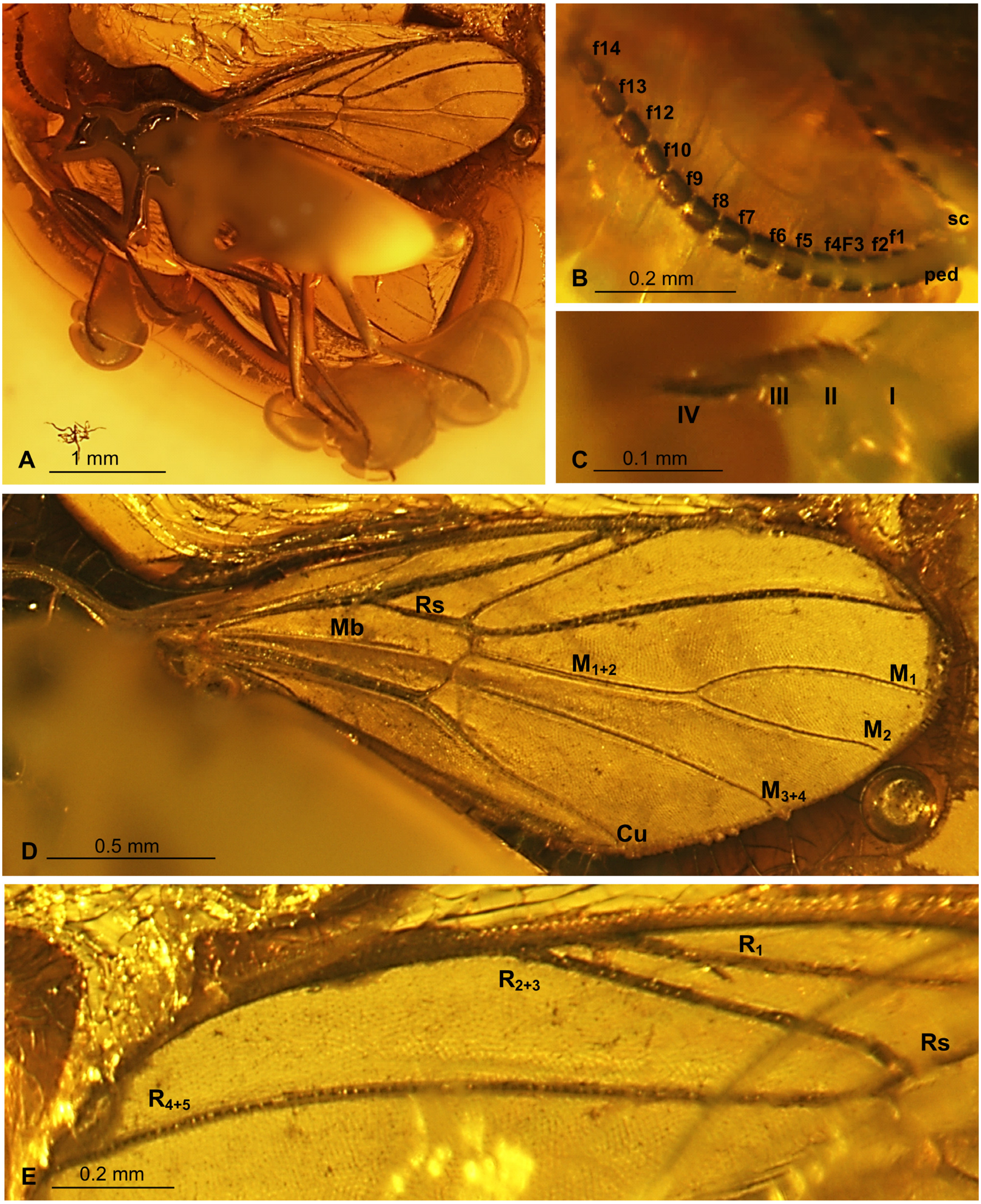

FIGURE 17. *Mycetobia perkovskyi* **sp. nov.** holotype, No. 872 (sex unknown), (coll. NAS of Ukraine). A. habitus, lateral-view; B. antenna; C. palpus maxillaris; D. wing; E. enlarged view of R_1, R_{2+3}, R_{4+5} apices. Abbreviations: f1–f14—flagellomeres; PED—pedicel; SC—scape; I–IV palpomeres I–IV.

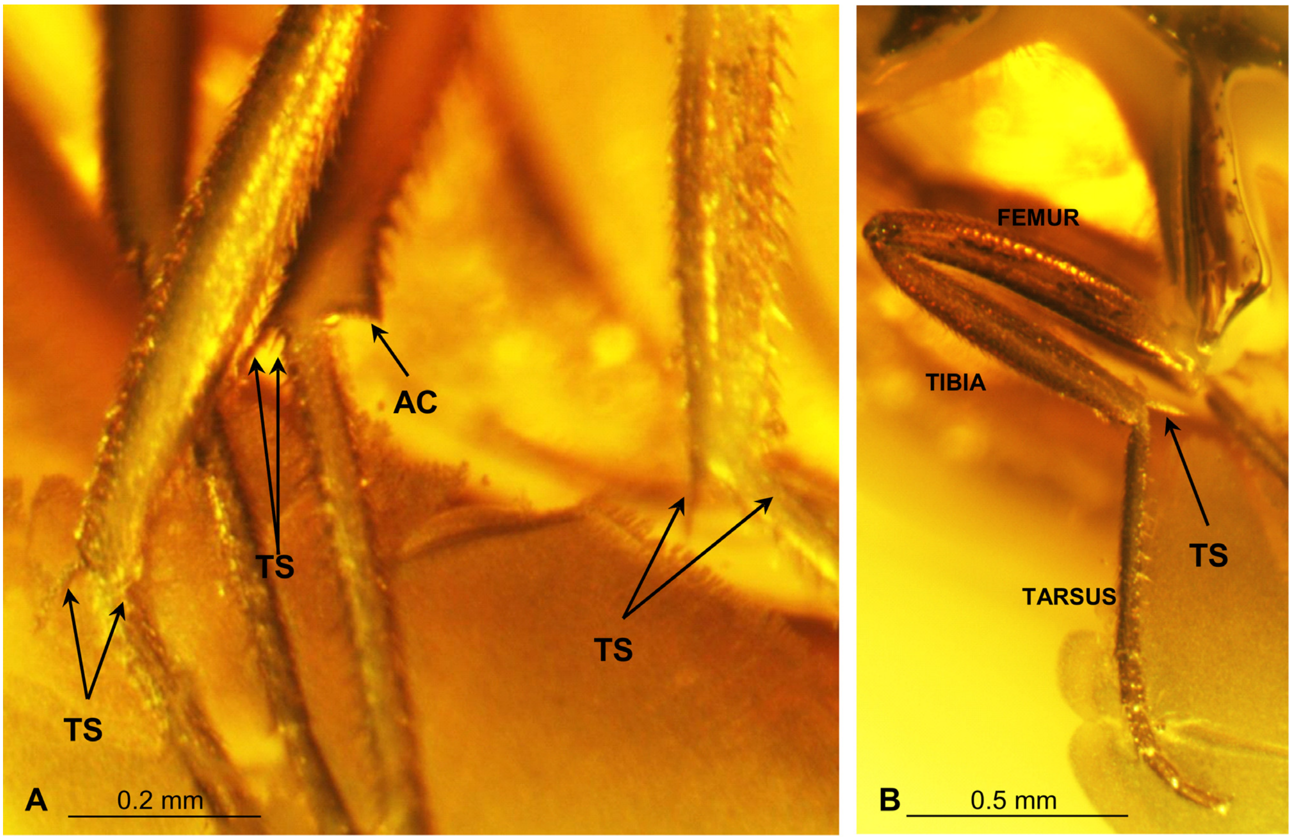

FIGURE 18. *Mycetobia perkovskyi* **sp. nov.** holotype, No. 872 (sex unknown), (coll. NAS of Ukraine). A. tibial spurs and apical combs of middle and hind legs; B. fore leg. Abbreviations: AC—apical comb; TS—tibial spurs.

R_{2+3} apices approximately 3x as long as the distance between Sc and R_1 apices; R_{2+3} 2.5x as long as Rs; M_{1+2} as long as M_1; fork of M_{1+2} wide; the distance between M_1 and M_2 apices as long as the distance between M_1 and R_{4+5} apices and shorter than the distance between M_2 and M_{3+4}. R_{2+3} ending before bifurcation of M_{1+2} level, before half R_{4+5}; thorax with not very thick, not very elongated and sparse setae.

Etymology. The species name is dedicated to Professor Evgeny Perkovsky, National Academy of Sciences of Ukraine; I. I. Schmalhausen Institute of Zoology, eminent specialist on extinct and extant Diptera.

Type material. Holotype: No. 872 (sex unknown), Ukrainian amber, (Ukrainian Amber Museum, National Academy of Sciences of Ukraine; I. I. Schmalhausen Institute of Zoology, (NAS of Ukraine)).

Remarks: Head, thorax and abdomen are partially covered by "white milk".

Description. Body (Fig. 17A) 3.41 mm long, brown; head and thorax combined 1.39 mm long, head high 0.37 mm. Antenna (Figs 16A; 17A, B), comparatively elongated, 1.09 mm long; pedicel very short, approximately as long as wide; last flagellomere longer than penultimate one, tapered at apex; all 14 flagellomeres with not very elongated sparse setae, shorter than width of segments bearing them; additionally very short setae on all flagellomeres; palpus maxillaris (Fig. 17C) with terminal palpomere elongated; sparse short setae on all palpomeres.

Thorax: Wing (Figs 16B; 17A, D, E): 2.79 mm long, 1.17 mm wide; Sc comparatively short, ending in proximal part of wing, approximately in one third from base, before half the length of Rs; Rs 0.36 mm long; R_1 apices in about 0.6 of wing length. Rs separate Rb in 0.3 of wing length from wing base; Rs stem shorter than half R_{2+3}; R_{2+3} 0.77 mm long.

Legs (Fig. 18A, B): fore, middle and hind tibia with two unequal tibial spurs; tarsus comparatively elongated with last segment only slightly longer than penultimate one and not very elongated, rather slender claw and almost invisible empodium. Apical comb well visible on fore and hind legs. Elongated bristles in distal part of femurs; tarsus comparatively elongated with last tarsomere longer than penultimate. Tarsus of fore leg 0.3 the length of entire leg including coxa or longer. Fore coxa 0.65 mm, tibia 0.60 mm, tarsus 0.94 mm long (0.51/0.27/0.13/0.07/0.09). Hind tarsus 1.13 mm long (0.62/0.18/0.11/0.09/0.13).

Comparison. In contrast to *M. szwedoi* **sp. nov.** setae on thorax in *M. perkovskyi* **sp. nov.** are sparse, not very elongated, last flagellomere is at most 1.5x as long as wide, in *M. szwedoi* **sp. nov.** flagellomeres are short, wider than long or slightly longer, in *M silvia* **sp. nov.** flagellomeres 8–13 are elongated 2x as long as wide or longer, the last one 3x as long as wide. Differences in wing venation between *M. perkovskyi* **sp. nov.** and other are provided in Table 2.

Mycetobia silvia **sp. nov.**
(Figs 19–23)
urn:lsid:zoobank.org:act:73DF6194-7EC9-4028-8C2D-F1321A5A188C

Diagnosis. Flagellomeres cylindrical, becoming narrowed and more elongated to the apex of antenna, flagellomeres 1–3 as long as wide, 4–7 more than 1x to 1.5x as long as wide, 8–13 elongated 2x as long as wide or longer, the last one 3x as long as wide, tapered at apex, last palpomere elongated, 8x as long as wide, tapered at apex, longer than second one; Sc ending behind Rs bifurcation level; the distance between R_1 and R_{2+3} apices approximately 5x as long as the distance between Sc and R_1 apices; R_1 apex beyond M_{1+2} bifurcation level; R_{2+3} 2.5x as long as Rs; M_1 and M_2 narrowly bifurcated, M_{1+2} distinctly shorter than M_1; the distance between M_1 and M_2 apices approximately one and half the distance between R_{4+5} and M_1; the distance between M_1 and M_2 apices shorter than the distance between M_2 and $M_{3+4;}$ R_{2+3} and R_1 ending behind bifurcation of M_{1+2} level, R_{2+3} ending before half R_{4+5} level; only prescutellar and apical scutellar setae thick and very elongated.

Etymology. The species name is dedicated to Sylwia Wojtoń, wife of Maciej Wojtoń.

Type material: Holotype: No. 1345(a) (sex unknown), Baltic amber, (coll. Scheele); **Paratype:** No. 1345(b) (female), Baltic amber, (coll. Scheele).

Remarks: two specimens are preserved in one piece of amber.

Description. Body (Fig. 20A) 4.85–4.90 mm long, dark brown with pale brown basal part of tibia and all segments of tarsus of all legs 4.84–5.03 mm long. Head width 0.77–0.87 mm, 0.69–0.84 mm high. Head and thorax combined 2.12 mm–2.20 mm. Eyes occupying most of head in lateral view, in frontal view eyes separated by a distance about equal to diameter of ocellus; raised ocelli present and form equilateral triangle (Fig. 21A). Antenna 1.72 mm long (Figs 19A; 21A–E) with 14 cylindrical flagellomeres, more or less elongated, scape and pedicel comparatively short and wide; all flagellomeres with comparatively elongated and thick setae, but setae much shorter than segments bearing them and rather sparse; additionally short setae on all flagellomeres, tapered at apex last flagellomere with a few not very elongated setae at apex, last segment of antenna longer than penultimate one; palpus maxillaris 4-segmented (Figs 19B; 21F, G) 0.35–0.36 mm long, second palpomere 0.14 mm, third 0.08 mm, fourth 0.14 mm long. palpomere comparatively elongated, second palpomeres cylindrical, third palpomere widened, 2x as long as wide; third palpomere not very elongated; last one elongated and tapered at apex, longer than penultimate one; not numerous and short setae on all palpomeres.

Thorax (Figs 20A, B): prescutellar setae and apical scutellar setae very elongated; acrostichal setulae not very elongated; wing (Figs 19D; 20A; 22A–D): 4.00 mm–4.20 mm long, 1.69 mm wide; Sc comparatively elongated, slightly arched; Rs very short, 0.34 mm long, vein R_{2+3} short, 0.98 mm, twice as long as Rs; R_1 apex before midlength of R_{4+5} level; R_{4+5} arched; M_1 and M_2 approximately twice the length of M_{1+2}, A_1 well developed, connected with wind edge; Halter not very elongated with elongated stem and widened knob. Legs (Figs 19C, E; 23A–F): coxa of fore, middle and hind coxa with elongated bristles; coxa, trochanter and femur of all legs dark brawn, fore tibia pale brown with darkened dorsal edge, middle and hind tibia darkened in distal part; tarsus of all legs with first tarsomere pale brown, distal part of second and third tarsomere darkened, fourth and last segment of tarsus dark brown; fore, middle and hind tibia with two unequal tibial spurs; tarsus comparatively elongated with last segment only slightly longer than penultimate one and not very elongated, rather slender claw and almost invisible empodium. Apical comb well visible on fore and hind legs. Tibial spurs of fore legs unequal 0.09 mm and 0.11mm long, middle equal 0.12 mm, hind 0.12 mm long. Fore leg 4.74–4.88 mm long, middle leg 4.96–5.34 mm long, hind legs 5.18–5.76 mm long. Fore coxa 0.84–0.89 mm long, trochanter 0.20–0.21 mm, femur 1.13–1.17 mm, tibia 1.04–1.10 mm, tarsus 1.50–1.51 mm long (0.69–0.77/0.22–0.26/0.21/0.14–0.15/0.17). Middle coxa 0.78–0.93 mm long, trochanter 0.18–0.22 mm long, femur 1.05–1.20 mm long, tibia 1.23–1.27 mm, tarsus 1.72 mm (0.86/0.27/0.28/0.18/0.18). The length of hind coxa 0.67–0.71 mm, trochanter 0.17 mm, femur 1.19–1.49 mm, tibia 1.27–1.51 mm, tarsus 1.88 mm (0.87/0.30/0.23/0.18/0.20).

Comparison. In contrast to other species of *Mycetobia* from Eocene, in *M. silvia* **sp. nov.** flagellomeres 8–13 are elongated, 2x as long as wide or longer. Moreover, in *M. silvia* **sp. nov.** R_1 apex is positioned beyond M_{1+2} bifurcation level and Sc ending beyond Rs bifurcation level, while in other species R_1 apex is positioned before M_{1+2} bifurcation level and Sc ending before or opposite Rs bifurcation level, like in *M. szwedoi* **sp. nov.**

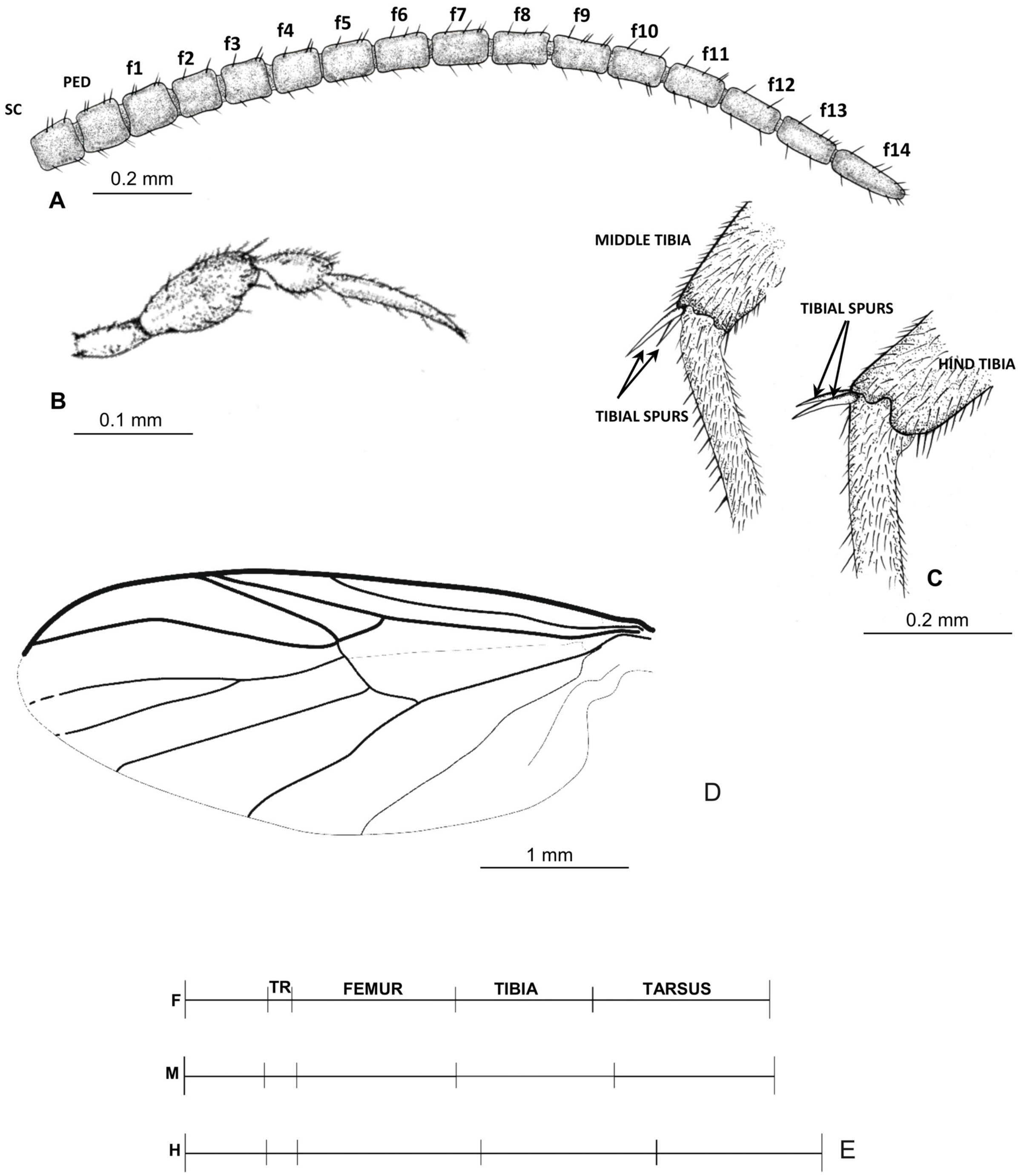

FIGURE 19. *Mycetobia silvia* **sp. nov.** holotype, No. 1345(a) (sex unknown) (coll. Scheele). A. antenna; B. palpus maxillaris; C. tibial spurs of hind and middle legs; D. wing venation; E. diagram of relation between the length of legs: fore leg (F), middle leg (M), hind leg (H).

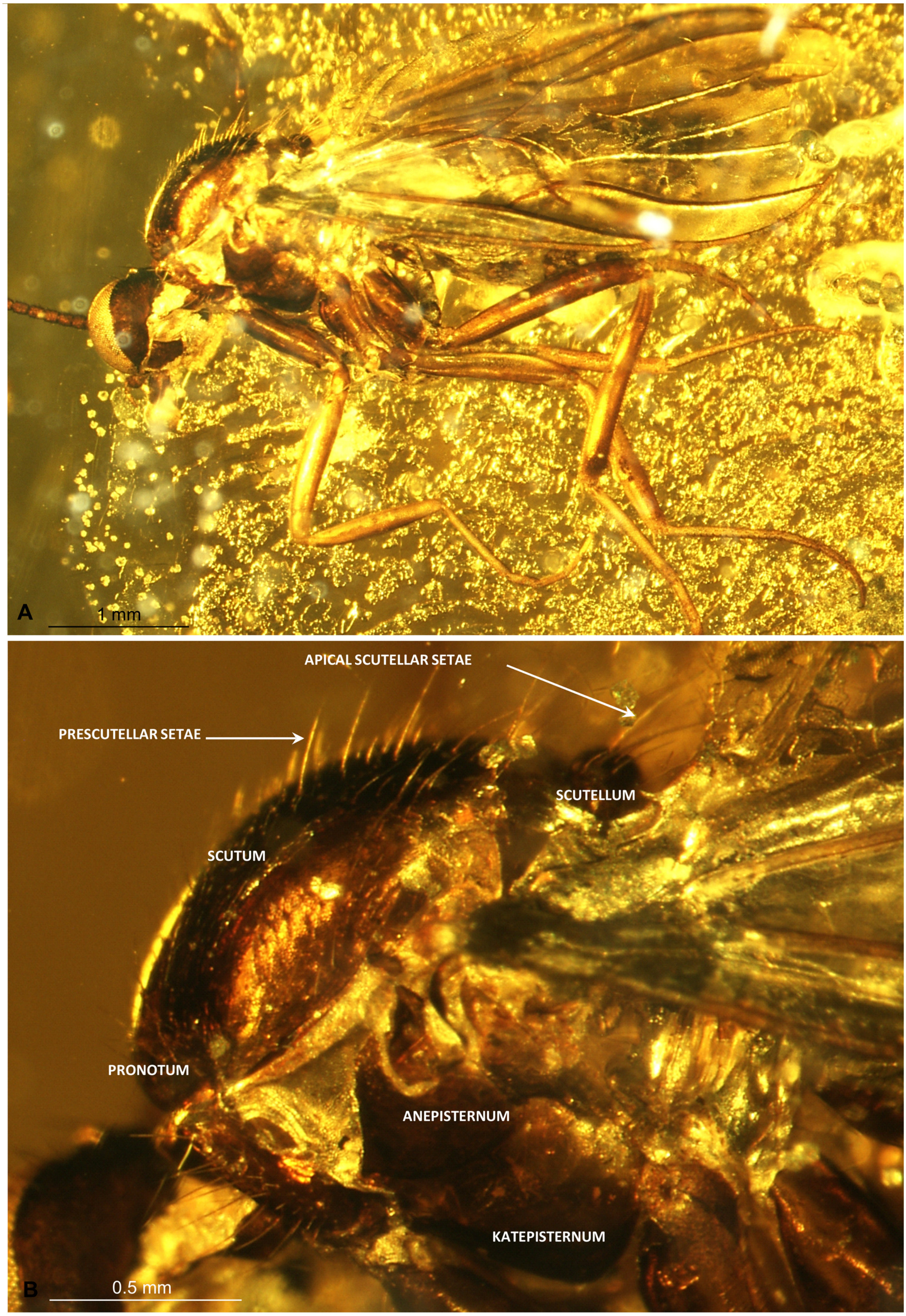

FIGURE 20. *Mycetobia silvia* **sp. nov.** holotype, No. 1345(a) (sex unknown) (coll. Scheele). A. habitus, latero-ventral view; B. head and thorax, lateral view.

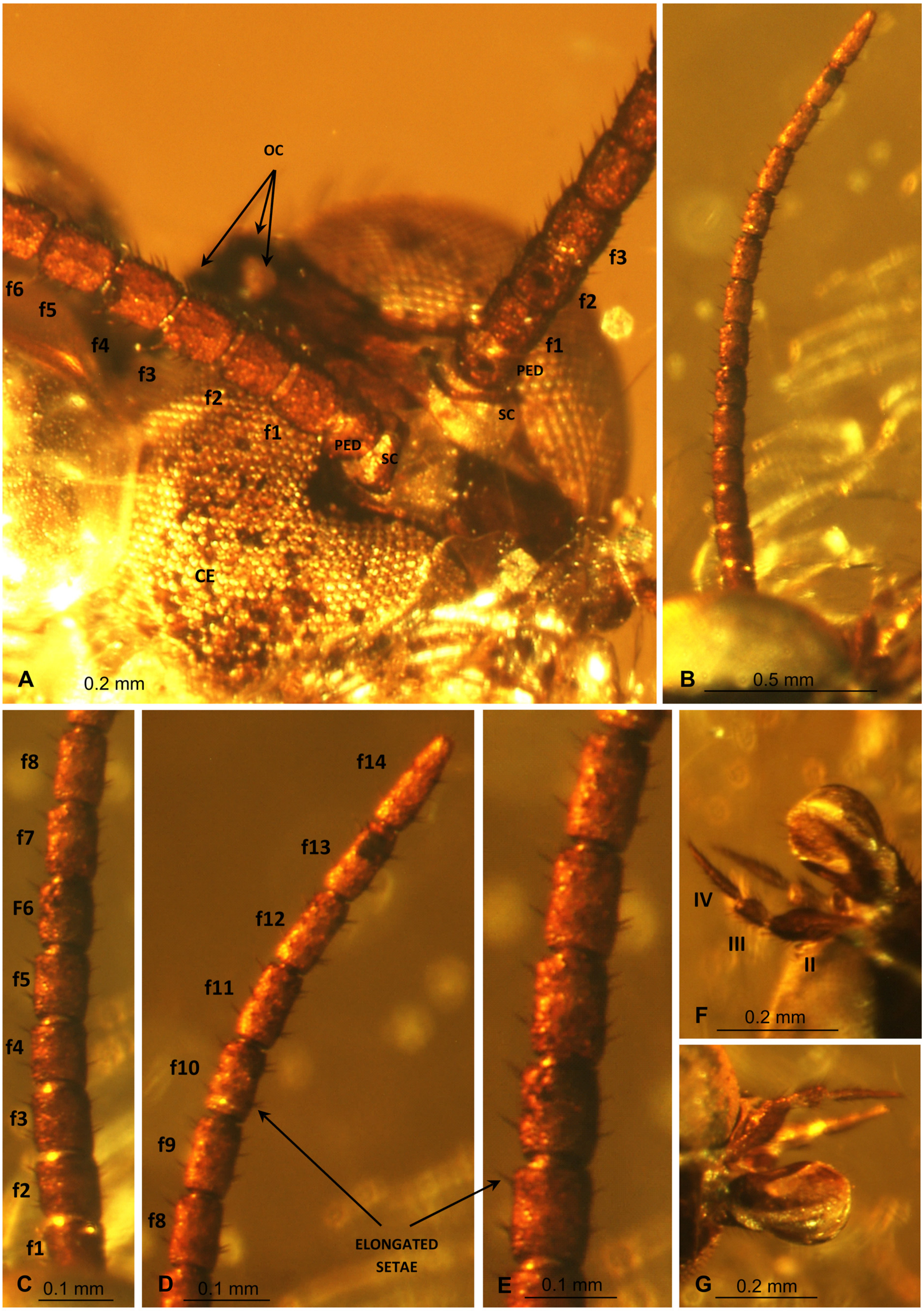

FIGURE 21. *Mycetobia silvia* **sp. nov.** holotype, No. 1345(a) (sex unknown), (coll. Scheele). A. head, frontal view; B. antenna; C.–E. enlarged view of flagellomeres; F.–G. palpus maxillaris. Abbreviations: CE—compound eyes; f1–f14—flagellomeres; OC—ocelli; PED—pedicel; SC—scape; II–IV—palpomeres II–IV.

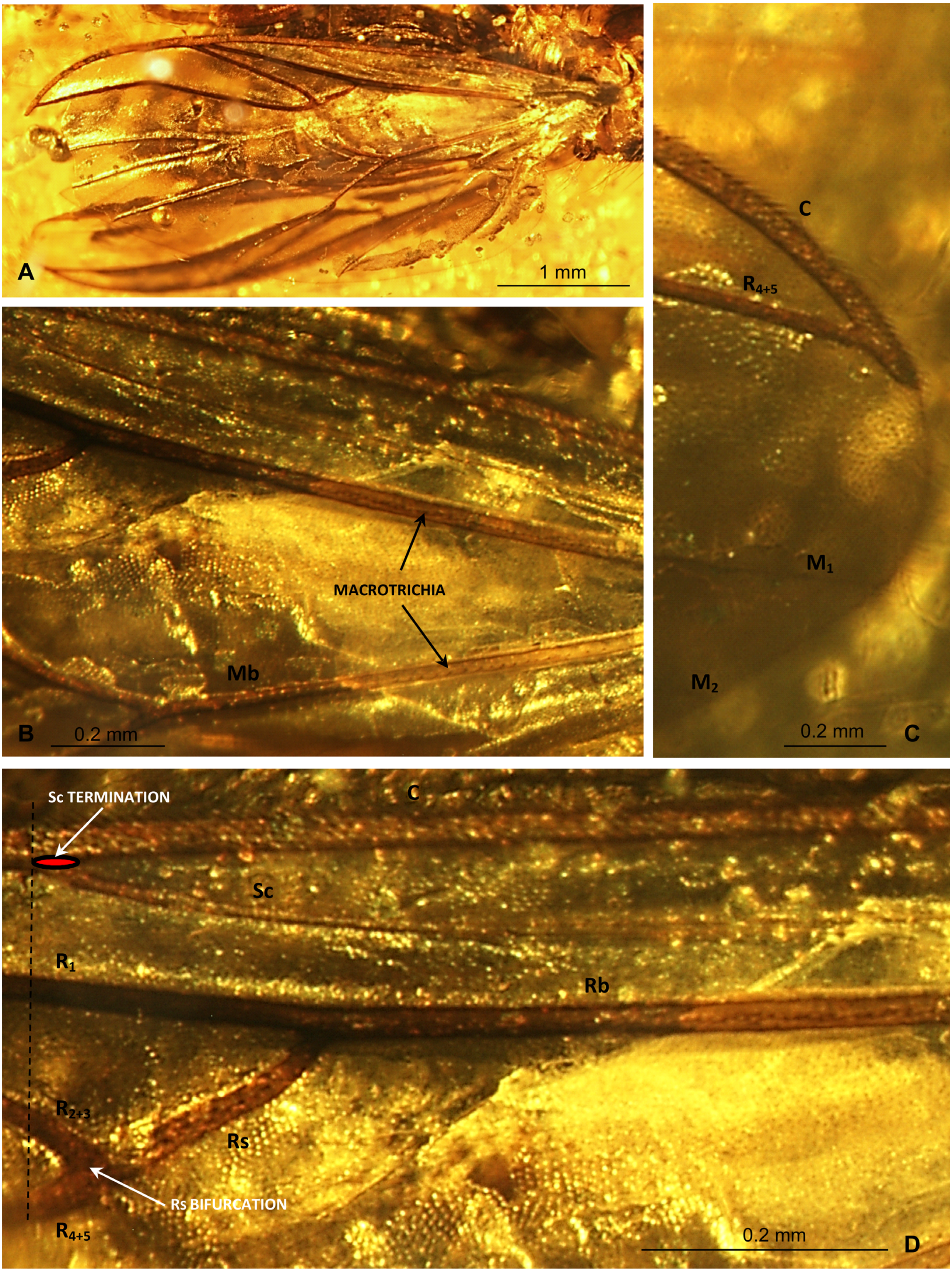

FIGURE 22. *Mycetobia silvia* **sp. nov.** holotype, No. 1345(a) (sex unknown), (coll. Scheele). A. wing venation; B. macrotrichia on wing venation; C. apex of wing with C apex visible; D. enlarged view of Sc apex and bifurcation of Rs.

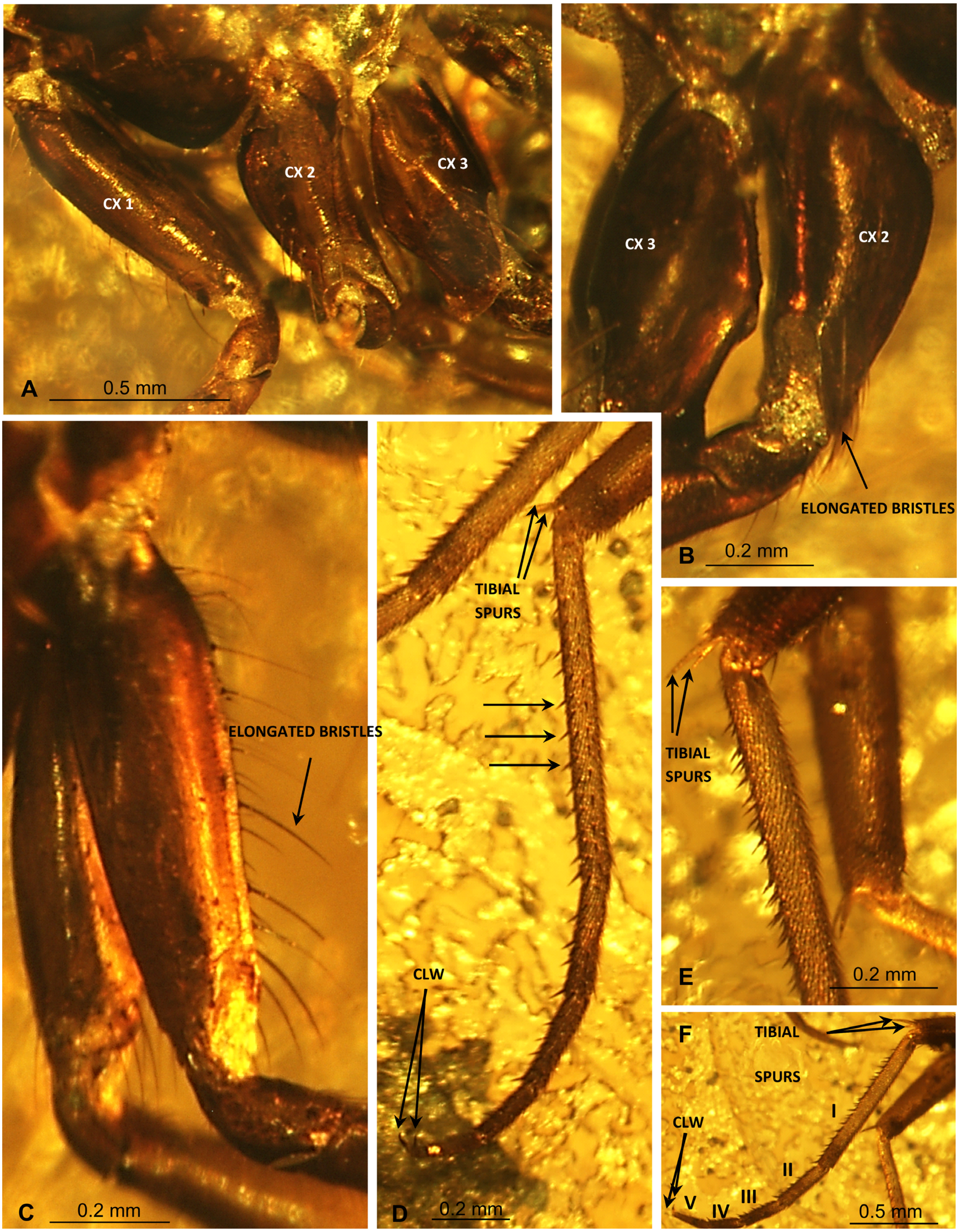

FIGURE 23. *Mycetobia silvia* **sp. nov.** holotype, No. 1345(a) (sex unknown), (coll. Scheele). A. coxa of fore, middle and hind legs; B.–C. enlarged view of elongated bristles on middle coxa visible; D. tarsus of middle leg; E. tibial spurs of middle and hind legs; F. tarsus of hind leg. Abbreviations: CLW—claw; CX 1–CX 3—coxa of fore and hind legs; I–V—tarsomeres I–V; arrows without abbreviations point thick setae on tarsus.

TABLE 2. Wing venation characters of *Mycetobia* from Eocene.

	M. connexa Meunier, 1899	*M. christelae* **sp. nov.**	*M. hansi* **sp. nov.**	*M. perkovskyi* **sp. nov.**	*M. silvia* **sp. nov.**	*M. szwedoi* **sp. nov.**
Sc ending before Rs bifurcation level	+	+	+	+	- (beyond)	opposite
R_1 apex before M_{1+2} bifurcation level	+	+	+	+	- (beyond)	+
R_{2+3} 2.5x as long as Rs	+	- (3x)	+	+	+	+
M_{1+2} longer than M_1	+	+	- (shorter)	- (equal)	- (shorter)	+
the distance between M_1 and M_2 apices equal the distance between R_{4+5} and M_1 apices	+	- (longer)	- (longer)	+	- (longer)	- (shorter)
the distance between M_2 and M_{3+4} apices equal the distance between M_1 and M_2 apices	- (longer)	+	- (longer)	- (longer)	- (longer)	- (longer)
R_{2+3} ending before bifurcation of M_{1+2} level	+	+	- (opposite)	+	- (beyond)	- (beyond)
R_{2+3} ending before half the length R_{4+5} level	+	- (beyond)	+	+	+	- (beyond)
the distance between R_1 and R_{2+3} apices approximately 5x as long as the distance between Sc and R_1 apices	- (6x)	- (10x)	- (4x)	- (3x)	+	+

Mycetobia szwedoi **sp. nov.**
(Figs 24–26)
urn:lsid:zoobank.org:act:A84B5185-7BA0-46C0-B2C6-CA11DAA7FA64

Diagnosis. Flagellomeres wide, 1–10 wider than long; becoming narrowed and more elongated to the apex of antenna, the last one 3x as long as wide, tapered at apex; last palpomere elongated 3x as long as wide, tapered at apex; Sc ending opposite Rs bifurcation level; the distance between R_1 and R_{2+3} apices approximately 5x as long as the distance between Sc and R_1 apices; R_1 apex before M_{1+2} bifurcation level; R_{2+3} 2.5x as long as Rs; fork of M_{1+2} wide, M_{1+2} slightly longer than M_1; the distance between M_1 and M_2 apices shorter than the distance between R_{4+5} and M_1; the distance between M_1 and M_2 apices shorter than the distance between M_2 and M_{3+4}; R_{2+3} and R_1 ending behind bifurcation of M_{1+2} level, R_{2+3} ending beyond half R_{4+5} level; very elongated and thick setae on thorax; male terminalia approximately one third of the body length; cerci large, gonostyles arched with elongated process, anal point huge with elongated process at apex.

Etymology. The species name is dedicated to Professor Jacek Szwedo (University of Gdańsk), the eminent specialist on recent and fossil insects.

Type material. Holotype: No. MP/3693 (male), Baltic amber, (ISEA PAS).

Description: Body (Fig. 25A, B) 3.17 mm long, brown. Head: antenna (Figs 24A; 25A–C), 0.68 mm long; last flagellomere 0.12 mm long, penultimate one 0.06 mm; 14 flagellomeres with dense, elongated setae, short setae very dense.

Thorax (Fig. 25A, D): wing (Figs 24C; 25E): 2.32 mm long, 0.99 mm wide, Rs 0.24 mm long; R_{2+3} 0.73 mm long; M_{1+2} 0.67 mm long; the length of M_1 0.61 mm.

Legs (Fig. 25A, F): fore, middle and hind tibia with two unequal tibial spurs; tarsus comparatively elongated with last segment only slightly longer than penultimate one and not very elongated, rather slender claw and almost invisible empodium. Apical comb well visible on fore and hind legs (Fig. 25F). Tarsus of fore leg 0.3 the length of entire leg including coxa or longer. Fore coxa 0.46 mm, trochanter 0.12 mm, femur 0.65 mm, tibia 0.69 mm, tarsus

1.96 mm long (0.54/0.11/0.10/0.10/0.11); longer tibial spur of fore leg 0.09 mm long. Middle coxa 0.42 mm long, trochanter 0.10 mm long, femur 0.74 mm long, tibia 0.90 mm, tarsus 0.95 mm (0.53/0.14/0.12/0.10/0.13); longer tibial spur of middle leg 0.05 mm long. The length of hind coxa 0.41 mm, trochanter 0.12 mm, femur 0.83 mm, tibia 0.92 mm, tarsus 1.22 mm (0.55/0.40/0.12/0.09/0.13); longer tibial spur of hind leg 0.09 mm long. Last tarsomere longer than penultimate one. Apical comb of fore leg not very huge, apical comb of hind leg well developed, massive.

Abdomen (Figs 24B; 25A; 26A, B): male terminalia very large, 0.96 mm long, cerci large, not tapered at apex, small processes on apex of anal point.

Comparison. In contrast to *M. christelae* **sp. nov.**, in *Mycetobia szwedoi* **sp. nov.** small processes on apex of anal point is visible. Sc ending opposite Rs bifurcation level, while in other species R_1 apex is positioned before or beyond M_{1+2} bifurcation level (Table 2).

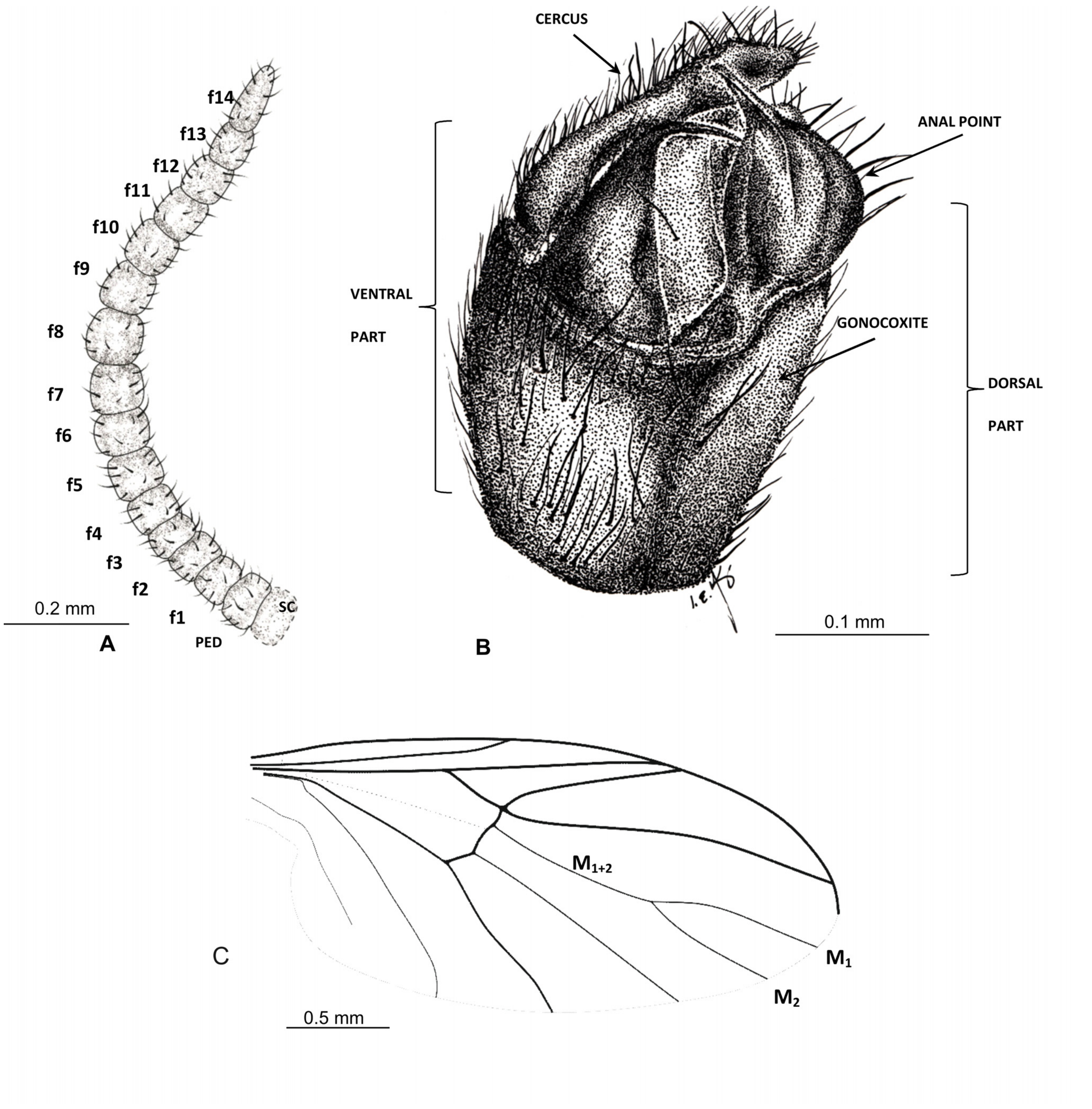

FIGURE 24. *Mycetobia szwedoi* **sp. nov.** holotype, No. MP/3693 (male), (ISEA PAS). A. antenna; B. male terminalia C. wing venation. Abbreviations: PED—pedicel; SC—scape; f1–f14—flagellomeres.

FIGURE 25. *Mycetobia szwedoi* **sp. nov.** holotype, No. MP/3693 (male), (ISEA PAS). A. habitus, lateral view; B. habitus, dorso-lateral view; C. flagellomeres; D. enlarged view of part of thorax with praescutellar setae; E. enlarged view of macrotrichia on wing venation; F. enlarged view of apical comb of hind leg.

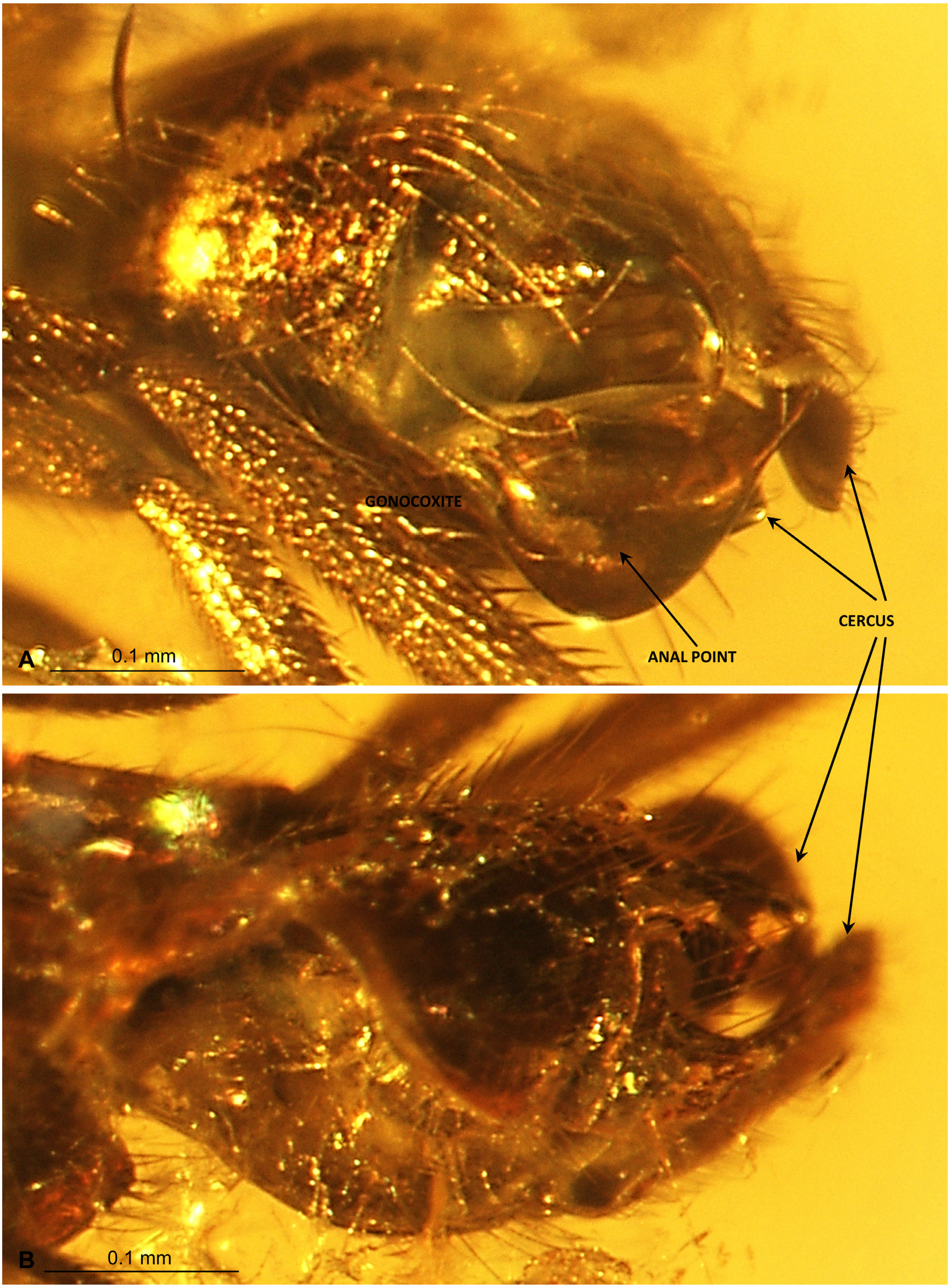

FIGURE 26. *Mycetobia szwedoi* **sp. nov.** holotype, No. MP/3693 (male), (ISEA PAS). A., B. male terminalia. A. latero-ventral view; B. latero-dorsal view.

Unplaced taxa

Mycetobia longipennis Meunier, 1899, *nomen dubium*

*1899 *Mycetobia longipennis*, Loew: Meunier: p. 163 [1]
1907 *Mycetobia longipennis* Loew (Meunier): Handlirsch, p. 935 [2]
1928 *Mycetobia longipennis* (Loew) Meunier: Edwards, p. 25 [3]
1982b *Mycetobia longipennis* (Loew, 1850): Keilbach, p. 330 [4]
1985 *Mycetobia longipennis* Meunier, 1899 [nicht: Loew 1850!]: Spahr, 8 [5]
1994 *Mycetobia longipennis* Meunier, 1899b: Evenhuis, p. 205
2014 *Mycetobia longipennis* Loew (Meunier): Evenhuis, http://hbs.bishopmuseum.org/fossilcat/fossanisopod.html

Remarks:

[1] Meunier ascribed this species to Loew, but this name is probably label or manuscript name, as it was not published before Meunier's work.

[2] Handlirsch mentioned under this name also "*Mycetobia* (sp.), Loew, Bernsteinfauna. 35. 1850.", probably referring to one of the 5 species mentioned by Loew as belonging to this genus.

[3] Edwards treated this taxon as unrecognisable and probably not belonging to *Mycetobia*.

[4] Keilbach listed *M. longipennis* in Mycetophilidae, he ascribed this name to Loew (1850), referring to specimen number following Meunier: "*Mycetobia longipennis* Loew, 1850, p. 35. Meunier, 1899, p. 163. Balt. B. Coll. GPIK No. 14553 VI 8393". The specimen was not found.

[5] Listed in Anisopodidae. Corrects authorship.

Mycetobia platyuroides Meunier, 1899, *nomen dubium*

*1899 *Mycetobia platyuroides*, Loew: Meunier, p. 164 [1]
1907 *Mycetobia platyuroides* Loew (Meunier): Handlirsch, p. 935 [2]
1928 *Mycetobia platyuroides* (Loew) Meunier: Edwards, p. 25 [3]
1982 *Mycetobia platyuroides* (Loew 1850): Kielbach, p. 330 [4]
1985 *Mycetobia platyuroides* Meunier, 1899 [nicht: Loew 1850!]; Spahr, p. 8 [5]
1994 *Mycetobia platyuroides* Meunier, 1899: Evenhuis, p. 205
2014 *Mycetobia platyuroides* Meunier, 1899: Evenhuis, http://hbs.bishopmuseum.org/fossilcat/fossanisopod.html

Remarks:

[1] Meunier doubts in correct assignment of this species by Loew, stating that detailed studies of venation of this specimen are almost impossible and that it will be better leave it not named, however, he stated that he agreed with Loew, that male genital structures are appreciable. Meunier gave the acquisition number N^{os} 14554, VI. 8394. The species was never figured and the specimen is not found. *[I would not dare, as Loew did, to give a generic name to this little Mycetophilian, because one can not make, even at a high magnification, the detailed study of the veins of the wings. It is preferable, for the case which occupies us to confess its ignorance, to give it this problematic determination of this dipteran. Like Loew, we find that male genitalia are appreciable.]*

[2] Handlirsch mentioned under this name also "*Mycetobia* (sp.), Loew, Bernsteinfauna. 35. 1850.", probably referring to one of the 5 species mentioned by Loew as belonging to this genus.

[3] Edwards treated this species as unrecognisable and probably not belonging to this genus.

[4] Keilbach ascribed this name to Loew (1850), referred it to Meunier (1899) paper, but did not gave the acquisition number. Wrong page (163) of description given.

[5] Listed in Anisopodidae. Corrected authorship and page of description.

Mycetobia terricola (Scudder, 1878), *nomen dubium*

*1878 *Diadocidia*? *terricola*: p. 750 [1]
1890 *Diadocidia*? *terricola*: Scudder, p. 598, Pl. 10, Figs. 10, 11 [2]
1891 5304. *Diadocidia* (?) *terricola*: Scudder, p. 622
1907 *Diadocidia*? *terricola* Scudder: Handlirsch, p. 934 [3]
1928 *Mycetobia terricola* (Scudder, 1878): Edwards, p. 25 [4]

1991 *Diadocidia* (?) *terricola* Scudder, 1878: Lewis & Heikes, p. 446 [5]
1991 *Diadocidia terricola* Scudder 1890: Lewis & Heikes, p. 464 [6]
1994 *Mycetobia terricola* (Scudder, 1878): Evenhuis, p. 205
2014 *Mycetobia terricola* (Scudder, 1878): Evenhuis, http://hbs.bishopmuseum.org/fossilcat/fossanisopod.html

Remarks:

[1] Originally placed in Mycetophilidae.
[2] Placed in Mycetophilidae.
[3] Listed in Mycetophilidae.
[4] Edwards gave no explanation for change of generic placement of this species.
[5] Eocene—Green River Formation; locality: Petrified Fish Cut, 6 miles west of Green River, near Green River Station, Sweetwater County, Wyoming.
[6] Eocene—Green River Formation; Unidentified locality Green River, Wyoming of Eocene age locality.

Taxa *nomina nudi*

Mycetobia parallela: Keilbach, 1982

1982b *Mycetobia parallela* (Loew, 1850): Keilbach, p. 330 [1]
1985 „*Mycetobia parallela*": Spahr, . 8 [2]
1994 *Mycetobia parallela* Keilbach, 1982b: Evenhuis, p. 205 [3]
2014 *Mycetobia parallela* Keilbach, 1982b: Evenhuis, [4]

Remarks:

[1] Listed in Mycetophilidae. Specific name ascribed to Loew. Keilbach listed this name probably based on data from labels: "Balt. B. Coll. Berendt NPB „*Mycetobia* sp. 2 ♀ Original Dr. B." +."
[2] Nomenclaturally non-binding label-name.
[3] Evenhuis stated that *M. parallela* is *nomen nudum*.
[4] Evenhuis stated that *M. parallela* is *nomen nudum*.

Mycetobia unicalcarata: Keilbach 1982

1982b *Mycetobia unicalcarata* (Loew, 1850): Keilbach, p. 330 [1]
1985 „*Mycetobia unicalcarata*": Spahr, p. 8 [2]
1994 *Mycetobia unicalcaratus* [sic!] Keilbach, 1982b: Evenhuis, p. 205 [3]
2014 *Mycetobia unicalcaratus* [sic!] Keilbach, 1982b: Evenhuis, http://hbs.bishopmuseum.org/fossilcat/fossanisopod.html [4]

Remarks:

[1] Listed in Mycetophilidae. Specific name ascribed to Loew. Keilbach listed this name probably based on data from labels: "Balt. B. Coll. Berendt NPB „*Mycetobia* sp. 3 *unicalcarata* ♂ I C E Original Dr. B." + ."
[2] Nomenclaturally non-binding label-name.
[3] Evenhuis stated that *M. unicalcaratus* is *nomen nudum*.
[4] Evenhuis stated that *M. unicalcaratus* is *nomen nudum*.

Unnamed specimens of *Mycetobia*

Mycetobia sp. [1]

1895 Meunier, p. 9 [1]
1907 *Mycetobia* sp., Meunier: Handlirsch, p. 935 [2]

Remarks:

[1] Listed in Mycetophilidae, no other details given

[2] Listed in Mycetophilidae; refers to note in Meunier.

Mycetobia sp. [2]

1850 Loew, p. 35 [1]
1885 Scudder, p. 811 [2]
1886 Scudder, p. 93 [3]
1891 Scudder, p. 637 [4]
1985 Spahr, p. 8 [5]

Remarks:

[1] Listed as belonging to *Tipularia fungicola*. Five recognized but unnamed by Loew species mentioned.

[2] Listed in Mycetophilidae. Five unidentified species mentioned, most probably following Loew.

[3] Scudder mentioned (following Loew) five species belonging to this genus from Baltic amber.

[4] Scudder mentioned 4 unnamed species following Loew data.

[5] Listed in Anisopodidae. Data refers to specimens mentioned by Loew (1850: 35).

Taxa from the Eocene removed from *Mycetobia*

Symmerus defectivus (Loew, 1850)

*1850 *Mycetobia defectiva*: Loew: p. 35 [1]
1891 5452. *Mycetobia defectiva* Loew, 1850: Scudder, p. 637 [1]
1907 *Mycetobia defectiva* Loew: Handlirsch, p. 934 [2]
1921 *Mycetobia defectiva* Loew: Edwards, p. 435 [3]
1928 *Mycetobia defectiva* Loew: Edwards, p. 25 [4]
1982b *Mycetobia defectiva* (Loew, 1850): Keilbach, p. 330 [5]
1985 *Mycetobia defectiva* Loew, 1850: Spahr, p. 8 [6]
1994 *Symmerus defectivus* Loew, 1850 (*Mycetobia*): Evenhuis, p. 137 [7]
1997 *Symmerus defectivus* Loew, 1850 (*Mycetobia*): Evenhuis, http://hbs.bishopmuseum.org/fossilcat/fossditomy.html [8]

Remarks:

[1] The description is giving no details except the mention that “additional vein” is absent.

[2] Listed in Mycetophilidae.

[3] Suggests that this species, mentioned by Meunier, could belong to the genus *Symmerus* Walker, 1848 (Ditomyiidae), and possibly could be even identical with *S. balticus* Edwards, 1921.

[4] Proposed that *M. defectiva* is belonging to the genus *Symmerus*.

[5] Keilbach listed *M. defectiva* in Mycetophilidae and gave the acquisition number of the specimen: “Balt. B. Coll. Berendt NPB „*Mycetobia* sp. 1 *defectiva* ♀ Original Dr. B.” +.”

[6] Listed in Anisopodidae.

[7] Listed in Ditomyiidae.

[8] Listed in Ditomyiidae.

Paleoplatyura macrocera Meunier, 1899

1899 *Mycetobia macrocera*, Loew: Meunier, p. 163, Pl. II, fig. 9 [1]
1899 *Paleoplatyura macrocera*: Meunier, p. 164 [2]
1907 *Mycetobia macrocera* (Loew) Meunier: Handlirsch, p. 935 [3]
1909 *Palaeoplatyura macroneura* [sic!] (*Mycetobia*), Loew: Johannsen, p. 10.
1909 *Palaeoplatyura macroneura* [sic!] (Loew), Meunier: Johannsen, p. 10

1913 *Paleoplatyura* Meun. (3): Meunier, p. 167 [4]
1917 *Palaeoplatyura macrocera*[1] Loew (Meun.): Meunier, p. 90, 104, Pl. 12, Figs. 48–50, Pl. 13, Fig. 51 [5]
1917 *Mycetobia macrocera* Loew: Meunier, p. 90
1928 *Mycetobia macrocera* (Loew): Edwards, p. 25 [6]
1982b *Palaeoplatyura macrocera* Meunier, 1917 [sic!]: Keilbach, p. 333 [7]
1982b *Mycetobia macrocera* Loew, 1850: Keilbach, p. 333
1982b *Palaeoplatyura macrocera* Meunier, 1899d: Keilbach, p. 333 [8]
1985 *Mycetobia macrocera* Meunier, 1899: Spahr, p. 8 [9]
1985 *Palaeoplatyura macrocera* Meunier, 1899: Spahr, p. 8
1994 *Paleoplatyura macrocera* Meunier, 1899: Evenhuis, p. 141
1997 *Paleoplatyura macrocera* Meunier, 1899: 163 (*Mycetobia*): Evenhuis: http://hbs.bishopmuseum.org/fossilcat/fosskero.html
2006 *Paleoplatyura macrocera* Meunier, 1899: Evenhuis, p. 94 [10]
2006 *Mycetobia macrocera* Meunier, 1899: Evenhuis, p. 94
2006 *Palaeoplatyura macroneura*: incorrect subsequent spelling of *macrocera* (Johannsen, 1909: 10): Evenhuis, p. 94

Remarks:

[1] Acquisition number: N^{os} 14555. VI. 8395.
[2] Generic name *Paleoplatyura* proposed here for this species
[3] Handlirsch listed the species in Mycetophilidae, mentioned under this name also "*Mycetobia* (sp.), Loew, Bernsteinfauna. 35. 1850.", probably referring to one of the 5 species mentioned by Loew as belonging to this genus.
[4] Indirect reference to the species—index (3) refers to Meunier (1899) work; listed in chresonymy under full name by Keilbach (1982b).
[5] Meunier listed *P. macrocera* in Keroplatidae
[6] Edwards placed the species in "*Palaeoplatyura*" [incorrect subsequent spelling of *Paleoplatyura* Meunier, 1899], genus placed within Keroplatidae.
[7] Keilbach listed the species in Mycetophilidae. He ascribed the species name to Loew. In the list of chresonyms he refers to works of Meunier (1917).
[8] Keilbach listed the species in Mycetophilidae. Incorrect subsequent spelling of *Paleoplatyura* Meunier, 1899.
[9] Placed in Keroplatidae.
[10] Evenhuis stated that two male syntypes should be found, but type depository is unknown or unable to trace in his study. Probably this results from wrong interpretation of Meunier acquisition numbers, as in original paper only single specimen is mentioned.

Discussion

The Eocene was the geological epoch from which we have a very rich and well documented fossil record for insects (Nicholson *et al.*, 2015), while numerous older fossil deposits have been destroyed by constant subduction, faulting, erosion, and other earth processes. The Eocene Baltic amber was formed over millions of years (probably at least Lutetian to Priabonian), across vast geographical area of Fennoscandia, under very diverse environmental conditions, at various geographical latitudes, varied altitudes above sea level, insolation, precipitation etc. (Grimaldi and Engel, 2005; Weitschat and Wichard, 2010; Szwedo and Kania, 2015). The most productive and extensive amber deposits in the world from the Eocene—Baltic amber, covering the Gulf of Gdańsk area, in "Blue Earth" deposits, easiest to reach and commercially exploited in Samland Peninsula (Szwedo and Kania, 2015). Other findings come from Denmark, Sweden, Lithuania, Germany and Poland (secondary deposits along coast, layers moved to south through glaciers, and recently identified area in South-east Poland). Amber from Bitterfeld (Germany, Saxony) and Ukraine (Rovno) also belong to Baltic amber group of resins, and succinite is to be found as far as Spitsbergen and Axel Heiberg Island in Canadian Arctic (Szwedo and Sontag, 2013, Wolfe *et al.*, 2009, 2016). About 50% of insect genera from the Eocene are modern ones as exemplified by the well-known fauna of the Baltic amber (Grimaldi and Engel, 2005).

In Recent fauna, the representatives of *Mycetobia* occur mainly in Holarctic Realm (Hancock et al., 1996), especially in the Eastern Palearctic (Mamaev, 1968, 1971, 1987). Eight species are known from Eastern Siberia and Far East; two—from Kazakhstan and Central Asia; three—from Caucasus; five—from Europe, one—from Nearctic; five—from Neotropics, and three—from New Caledonia (Pape and Thompson, 2013). One unidentified species is reported from Ethiopian Highlands (Hancock, 2018). But, the Eocene climate of northern Europe, was different from modern, temperate climate—it was distinctly hotter (periodically very hot) and more humid, cooling significantly at the terminal phase of the Eocene (Zachos *et al.*, 2008). Kosmowska-Ceranowicz (2017) following earlier thoughts of palaeobotanist Hanna Czeczott (in Kosmowska-Ceranowicz 2017) suggested that some volcanic activity, indicated by the presence of ashes, hothouse gases and more acid rains could partly be responsible for succinose, increased production of resin. If the trees of amber forests were under such kind of environmental stress, the rate of damaged ones could be higher, offering favourable havitats for saprophytic and saproxylobiontic taxa such as *Mycetobia*. So, is it possible to hypothesize that the climatic changes in Eocene affected diversification of *Mycetobia* at that time. Further interdisciplinary researches are needed to demonstrate exact climatic preferences of *Mycetobia* and to proffer answers to this question.

Concluding remarks

The Eocene Baltic amber hold numerous and highly diversified specimens of *Mycetobia*, preserved as an inclusions. The numerous new fossils available for study gave additional assumptions to discussion on the evolution and systematics of these insects. Simultaneously, elaboration of new material allowed to update knowledge on formerly described taxa, but also the description of the new taxa.

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Anisopodidae (Insecta: Diptera) from Upper Cretaceous amber of northern Myanmar☆

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ABSTRACT

A new genus and three new species of Anisopodidae are described from the Cretaceous Burmese amber: *Cretolbia hukawnga* gen. et sp. nov., *Cretolbia burmitica* gen. et sp. nov., *Cretolbia zhuodei* gen. et sp. nov. Analyses of the morphological structures and taxonomical differences among representatives within the Anisopodidae have been carried out. A morphological comparison with their closest recent and fossil relatives is provided with the use of light and scanning electron microscopes.

1. Introduction

The Anisopodidae (wood gnats, window-gnats) are a small cosmopolitan family of relatively primitive flies. The wood gnats are found on all continents except Antarctica, on most major islands like Indonesia or Madagascar but are rather rare on smaller, "oceanic" islands (Thompson, 2006). The adults feed on nectar and other liquids, their saprophagous larvae occur under bark of decaying trees, and are associated with fungi or rotting vegetation, fermenting sap and mammal manure (Grimaldi and Amorim, 1995; Scudder and Cannings, 2006). Anisopodidae are represented by 15 genera with about two hundred of species, in fossil record 13 genera (four of them – extant ones) and about forty species have been described. The number of genera given herein is lower than that published earlier (Pape et al., 2011; Szadziewski et al., 2016; Evenhuis, 2017) because the mentioned authors did not take into account some previous transfers and synonimizations. In result of the revisions of type material and new finds *Oligophryne* Rohdendorf, 1962 and *Valeseguya* Colless, 1990 were transferred into Brachycera and the family of its own, respectively (Ansorge and Krzemiński, 1994; Amorim and Grimaldi, 2006), *Eoplecia* Handlirsh, 1920 was synonymized under *Mesorhyphus* Handlirsh, 1920 (Ansorge and Krzemiński, 1995) whereas *Mesobrachyopteryx* Hong and Wang, 1990, *Sinorhyphus* Hong, 1983 and *Sinotendipes* Hong and Wang, 1990 were transferred into Brachycera, Protorhyphidae and Blephariceridae, respectively, based on published illustrations (Blagoderov et al., 2002; Zhang, 2007).

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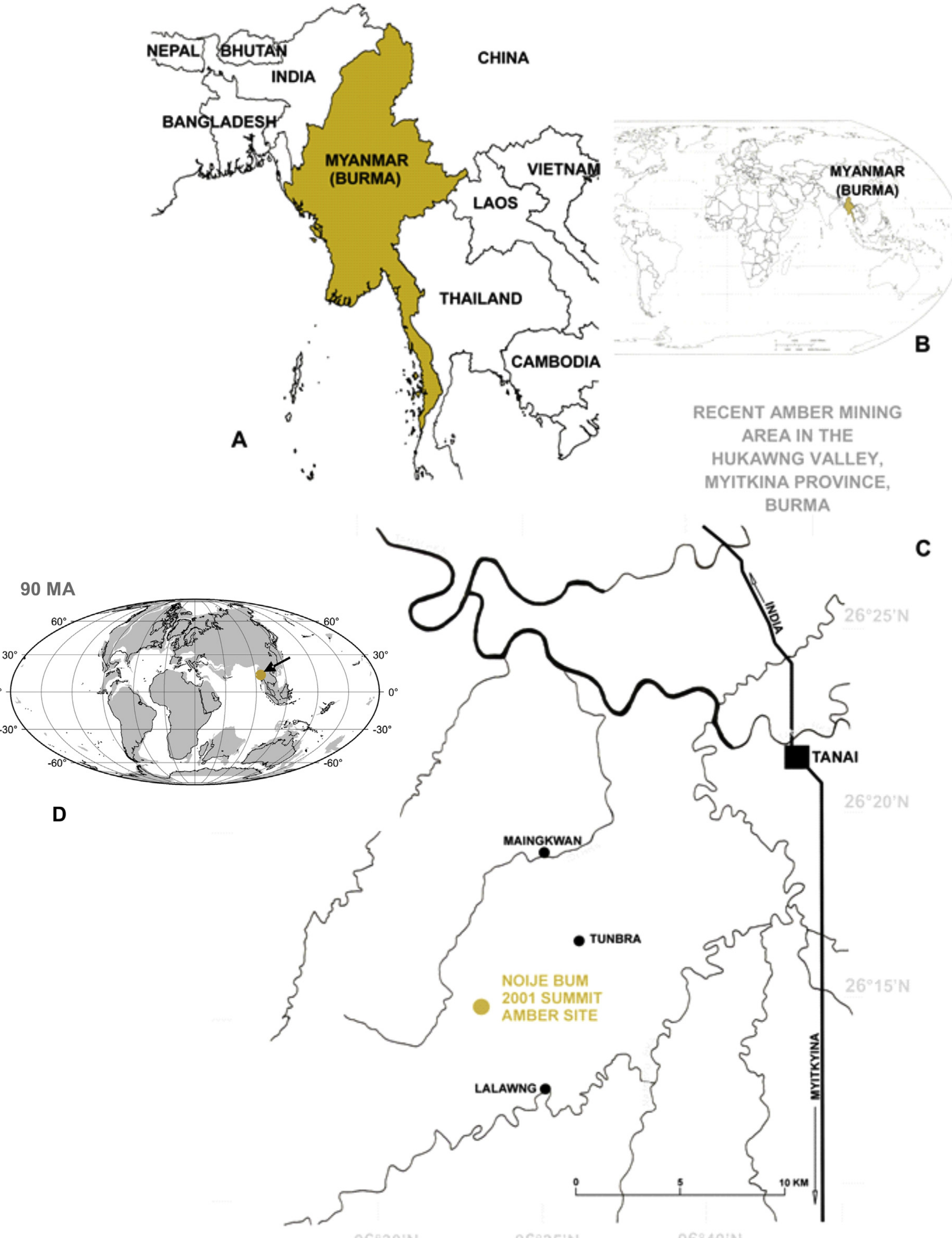

Fig. 1. A–C. Location of recent amber mining area in the Hukawng Valley, Myitkina Province, Myanmar. Compiled from data provided by Grimaldi et al. (2002), Cruikshank and Ko (2003) and Wandrey (2006), after Kania et al. (2015), modified; D. Position of Myanma on the Upper Cretaceous plate tectonics background.

The family Anisopodidae is known since the Early Jurassic: the oldest member, *Mesorhyphus rhaeticus* (Rohdendorf, 1962), was found in the Lower Jurassic of Kyrgyzstan near Lake Issyk-Kul, Sogyuty locality, Dzhil Formation, Sinemurian (Rohdendorf, 1962; Rasnitsyn and Zherikhin, 2002; Krzemińska and Lukashevich, 2018). Anisopodidae regularly occurs in the Euro-Chinese faunas of the Jurassic and Early Cretaceous age: all extinct genera (9 genera with 21 species) are known from this period but the number of extinct genera is still probably overestimated. The present consensus holds that only six extant genera exist although the classification of the Anisopodidae is still under discussion (Amorim and Tozoni, 1994; Michelsen, 1999; Thompson, 2006; Amorim et al., 2016). The extinct species of extant genera *Sylvicola* Harris, 1780, *Mesochria* Enderlein, 1910, and *Olbiogaster* Osten-Sacken, 1886 are described without hesitation only from the Cenozoic, *Mycetobia* Meigen, 1818 from the Cretaceous (Kania et al., 2018, in press), two remaining genera *Lobogaster* Philippi, 1865 and *Carreraia* Corrêa, 1947 are still unknown in the fossil record.

The three new species described herein within one new genus are the Anisopodidae from the Cenomanian Burmese amber and are classified to subfamily Olbiogastrinae which comprises also the oldest anisopodid species and most other Mesozoic members of the family.

2. Material and methods

The studied specimens are amber inclusions from the Hukawng Valley in northern Myanmar (Fig. 1) that was studied and named 'burmite' (Helm, 1892, 1893) although the only commercial source is the Hukawng Valley in the Myitkyina and Upper Chindwin districts (Zherikhin and Ross, 2000; Cruikshank and Ko, 2003; Ross et al., 2010). Shi et al. (2012) dated zircons from the amber-bearing bed which gave an age of 98.79 ± 0.62 Ma; therefore, the amber is likely to be of early Cenomanian age (Smith and Ross, 2017).

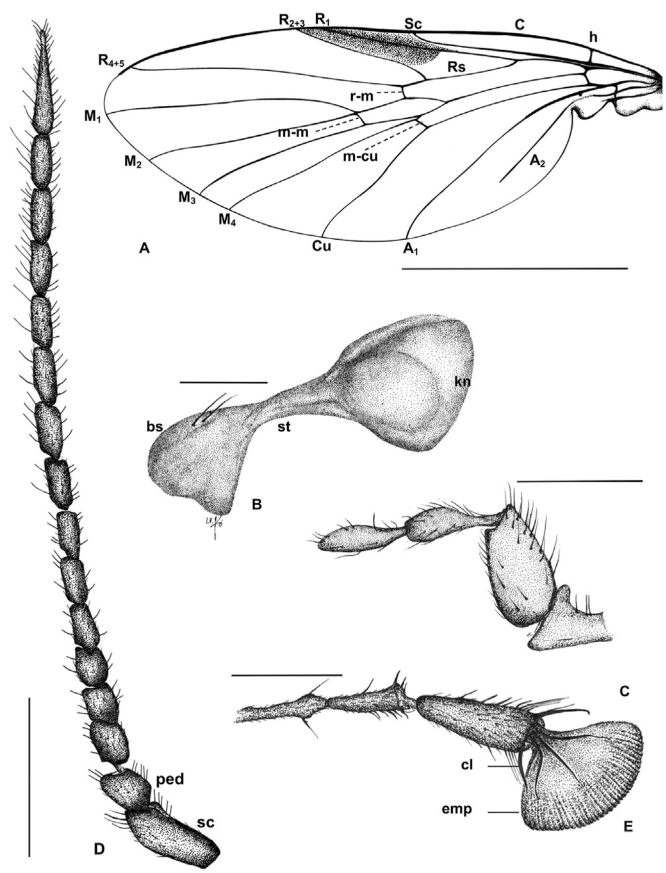

Fig. 2. *Cretolbia hukawnga* gen. et sp. nov., holotype, No. MP/3657 (male): A. wing venation; B. halter; C. palpus; D. antenna; E. last segments of tarsus. Abbreviations: bs – base; cl – claw; emp – empodium; st – stem; kn – knob; ped – pedicel; sc – scape. Scale bar = 1 mm for A; scale bar = 0.1 mm for B and E; scale bar = 0.2 mm for C and D.

The study was based on specimens from the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China (three specimens) and Institute of Systematics and Evolution of Animals Polish Academy of Sciences, Kraków, Poland (ISEA PAS) (two specimens). All five inclusions in Burmese amber were studied using a Nikon SMZ 1500 stereomicroscope equipped with a Nikon DS-Fi1 camera and the measurements were taken with NIS-Elements D 3.0 software. The drawings for the analysis were based on the specimen and photographs and were made by the first author.

Additionally, for comparison of morphology of chosen structures the recent species *Sylvicola* (*Sylvicola*) *cinctus* (Fabricius, 1787) were studied. The some structures, e.g. antenna, apical combs and tarsus of *S.* (*S.*) *cinctus* were analyzed under the scanning microscope Hitachi SU 8010 SEM at the Podkarpacie Innovative Research Center of the Environment (PIRCE) at the University of Rzeszów. For scanning electron microscope (SEM) observations, the material was attached to aluminum stubs and sputtered with 20 nm of gold using a Turbo-Pumped Sputter Coater Quorum Q 150OT ES.

The measurements were made as follow: the length of head—length of head capsule; the length of discal cell was measured from its posterior edge to the point of connection of vein m-m with vein M_3. The measurements were given only in case when relevant structures were not distorted.

The classification of Anisopodidae used here is conservative and follows mainly from Edwards' *Genera Insectorum* (Edwards, 1928) updated by Michelsen (1999) and Thompson (2006) without over splitting the wood gnats into numerous genera and tribes. The family includes 15 genera totally (six of them extant) classified in four subfamilies, three extant Anisopodinae, Mycetobiinae and Olbiogastrinae and one extinct Teginae as was adopted by one of us earlier (Shcherbakov et al., 1995; Lukashevich, 2012). In the Olbiogastrinae three extant genera *Olbiogaster*, *Lobogaster* and *Carreraia* and most of Mesozoic ones are included (except for *Tega* Blagoderov, Krzemińska and Krzemiński, 1993).

The nomenclature of wing venation follows that used in literature on Anisopodidae (e.g. Ansorge and Krzemiński, 1995; Krzemińska et al., 2010) and differs from the system of Wootton and Ennos (1989) accepted by one of the co-authors (Shcherbakov et al., 1995; Lukashevich, 2012). The terminology of the external structures of *S.* (*S.*) *cinctus* was used after Friedemann et al. (2014), Meyer-Rochow (2015), Yang and Zhang (2014).

3. Systematic palaeontology

Order: Diptera Linnaeus, 1758
Suborder: Nematocera Duméril, 1805
Infraorder: Bibionomorpha Hennig, 1954
Superfamily: Anisopodoidea Knab, 1912
Family: Anisopodidae Knab, 1912
Subfamily: Olbiogastrinae Hennig, 1973

Most of Mesozoic anisopodids have been described in this extant subfamily. In their wings, R_{2+3} is gradually approaching C, without a strong curve in the distal third; the branches of Rs are not

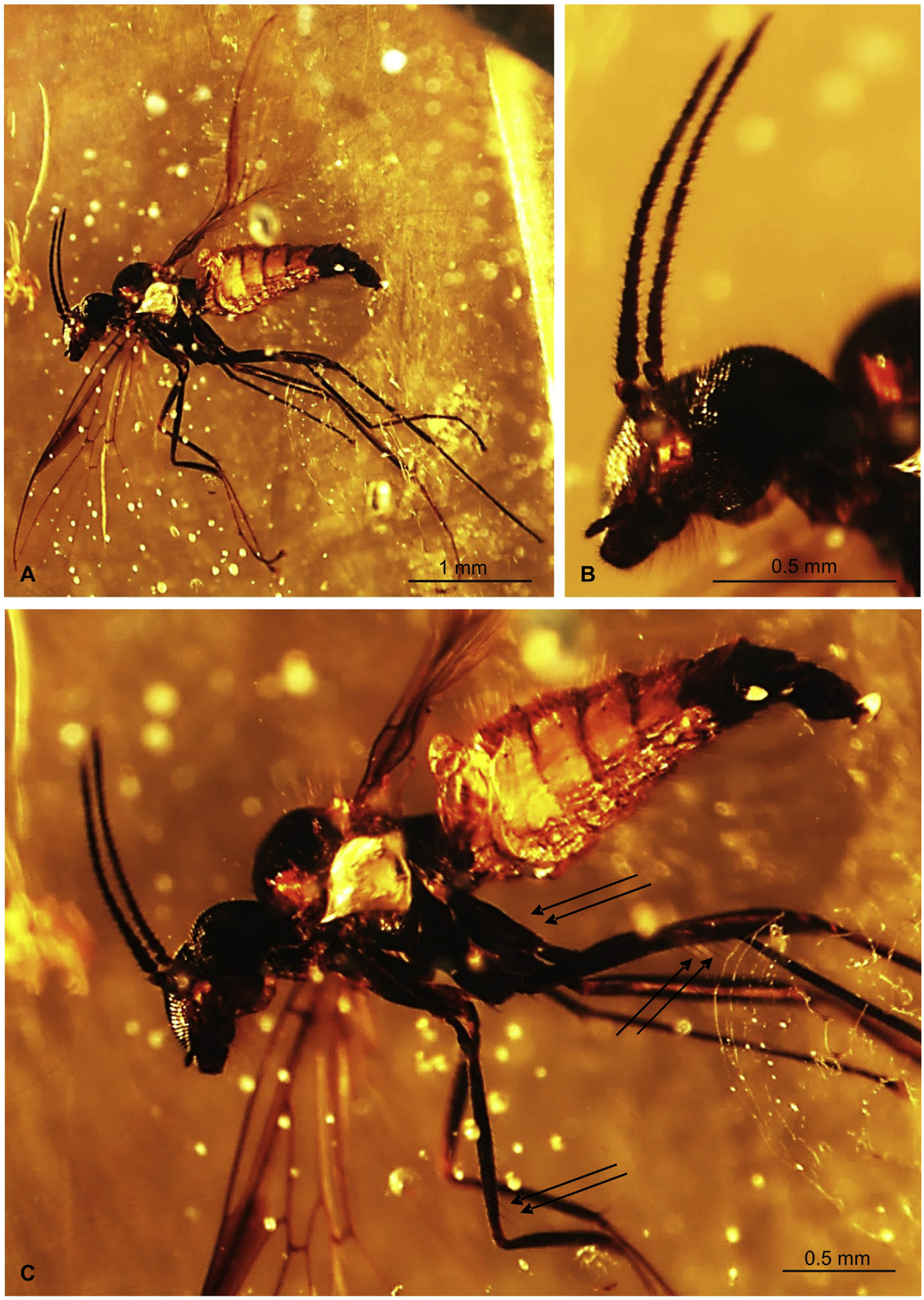

Fig. 3. *Cretolbia hukawnga* gen. et sp. nov.; holotype, No. MP/3657 (male). A. habitus, lateral view; B. head; C. enlarged lateral view of body with elongated setae on coxa and femur visible, pointed by arrows.

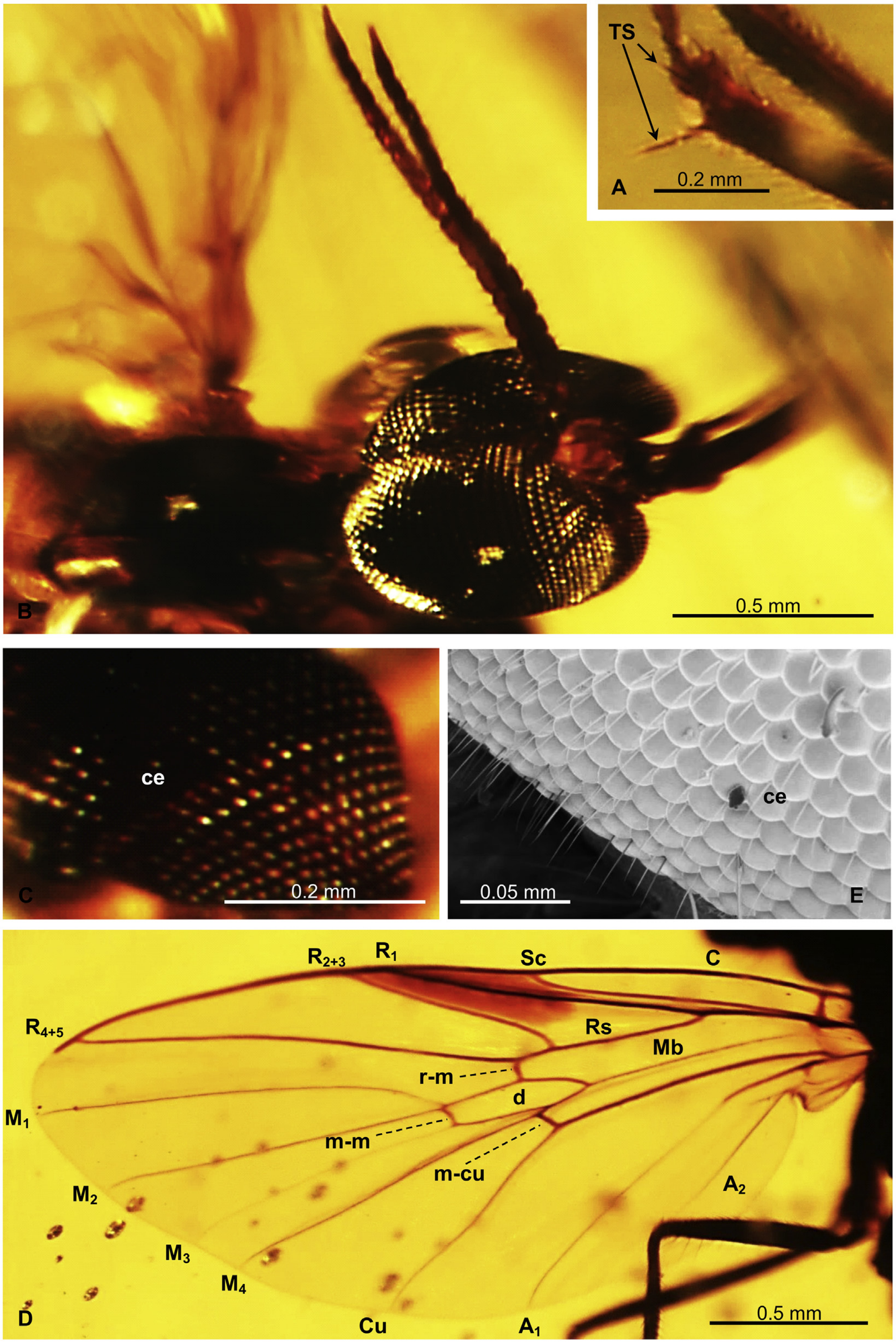

Fig. 4. A – D. *Cretolbia hukawnga* gen. et sp. nov., holotype, No. MP/3657 (male): A. tibial spurs of fore leg; B. head with holoptic compound eyes; C. compound eyes without long pilosity; D. wing venation; E. *Sylvicola* (*S.*) *cinctus* (Fabricius, 1787), ommatidia of compound eye with short microommatrichia, SEM. Abbreviations: ce – compound eye, TS – tibial spurs.

lying close to each other, both flowing into C; media has four branches; discal cell of usual size with m-m lying in the distal half of the wing (Lukashevich, 2012). In the new genus described herein one can see a main peculiarity of adults, which was used by Hennig for establishing the subfamily, absence of macrotrichia on wing membrane (Figs. 13D, 14E). In contrast to the extant members of the family, the antennae in all Mesozoic genera are much shorter than the body (not longer than head and thorax together) and the number of spermathecae is sometimes two, rather than usual three. In the new species described herein spermathecae are invisible. Anisopodid larvae (important for subfamilial attribution) are unknown in the fossil record.

***Cretolbia* gen.** nov. Kania, Wojtoń, Lukashevich, Wang and Krzemiński
(Figs. 2–15)

LSID urn:lsid:zoobank.org:act:7C7854E2-BB51-4AE9-9F23-9F624825D8CE

Type species. Cretolbia hukawnga sp. nov. Kania, Wojtoń, Lukashevich, Wang and Krzemiński.

Etymology. The species name is derived from “creta” (Latin) = Cretaceous and “olbios” (Greek) = happy. Gender: feminine.

Diagnosis. Small body; huge holoptic (male) or dichoptic (female) eyes without long pilosity (Fig. 4B, C); raised large ocelli formed equilateral triangle (Fig. 9A); antennae approximately as long as head and thorax combined or slightly shorter, 16-segmented, flagellomeres cylindrical, twice as long as wide (Figs. 2D, 10A, B); maxillary palpus longer than proboscis, 5-segmented, first palpomere greatly reduced (Figs. 6C, 9B); katepisternum bare; wing (Figs. 2A, 4D) wide, membrane hyaline without distinct coloration pattern except for very dark pterostigma surrounding apical part of R_1, C distinctly extending approximately 1/3-1/4 distance between R_{4+5} and M_1 apices; radial veins strongest; distance between R_1 and R_{2+3} apices short, only 0.25 distance between Sc and R_1 apices; R_{4+5} ending well before wing tip; Rs approximately as long as d-cell; M stem weaker than M_1 and M_2, diverging from pentagonal d-cell independently; M_{1+2} fork narrower than fork of Rs; M_3 out of d-cell weaker than other M veins; distance between M_2 and M_3 apices one and half to twice the distance between M_3 and M_4 apices; M branches with macrotrichia (at least M_1 and M_2, Fig. 8B); d-cell much longer than wide; Cu curved at m-cu, slightly S-shaped distally; reduced vein A_2 comparatively short, all veins except A_2 meeting wing margin. Maximum width of wing between Cu and A_1; anal lobe well developed, alula strongly differentiated (Figs. 8C, 12A, 14B); halter more or less elongated with very wide, rounded knob and rather short stem (Figs. 2B, 14H); all tibia slender, tibial

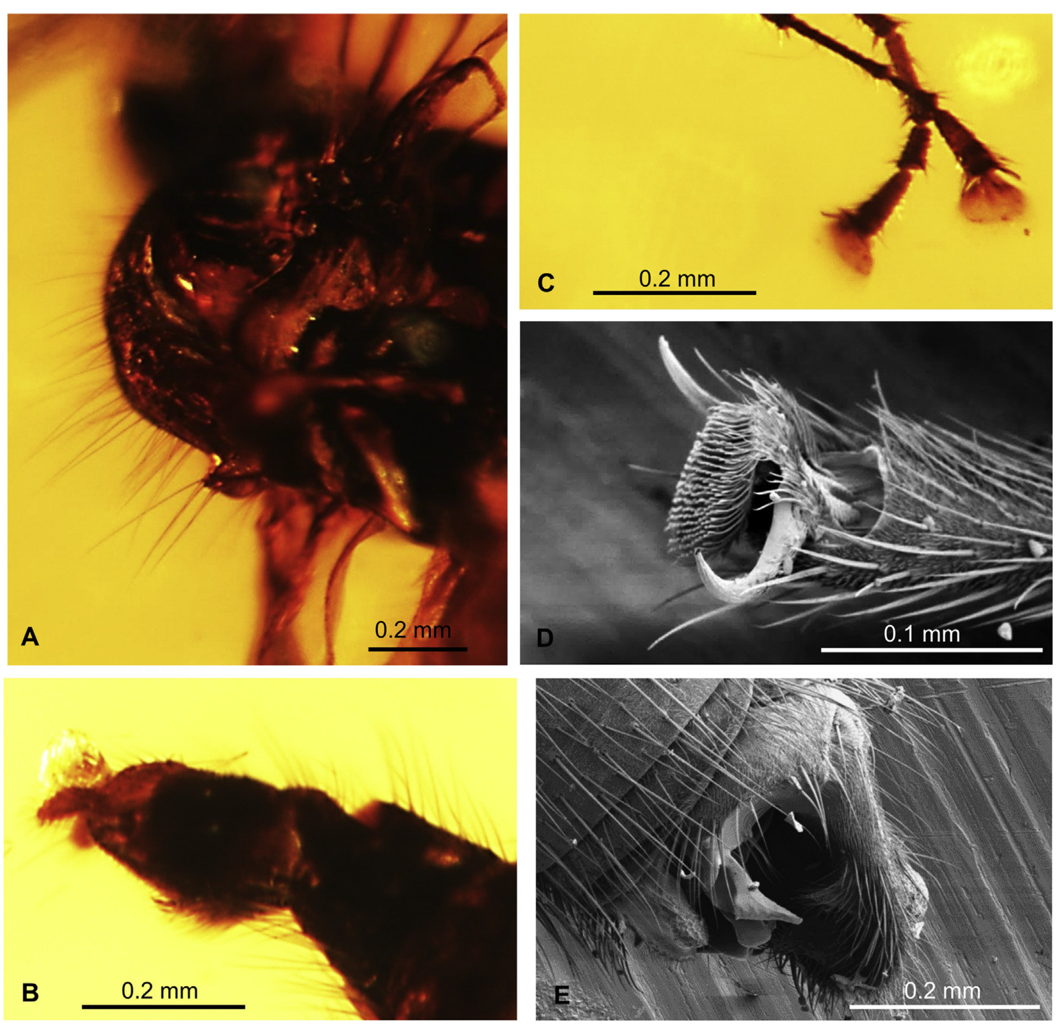

Fig. 5. A – C. *Cretolbia hukawnga* gen. et sp. nov. holotype, No. MP/3657 (male): A. thorax, latero-dorsal view; B. male terminalia, lateral view; C. last segments of tarsi; D – E. *Sylvicola* (*S.*) *cinctus* (Fabricius, 1787), SEM: D. last segment of tarsus with empodium visible; E. male genitalia, latero-ventral view.

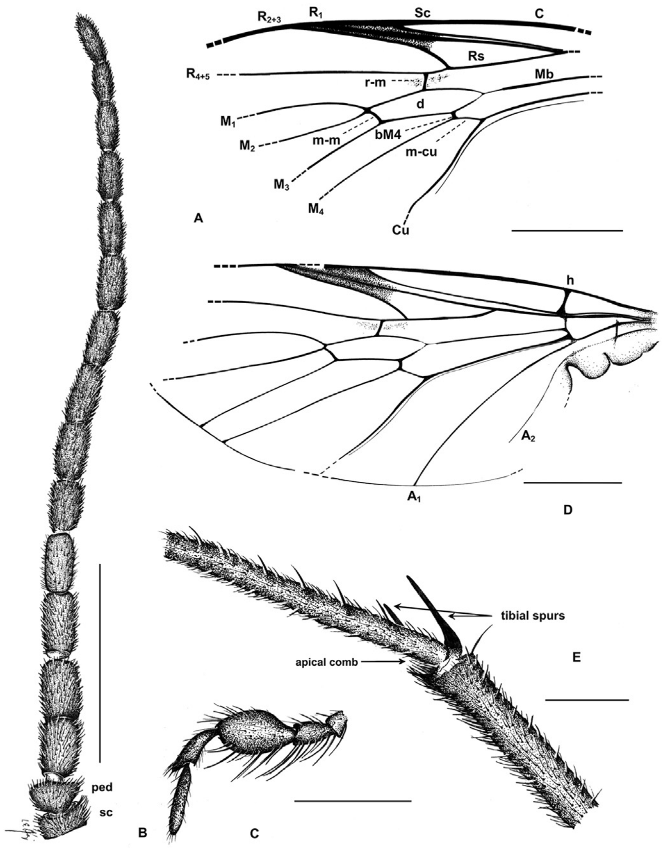

Fig. 6. A – C. *Cretolbia burmitica* sp. nov., holotype, No. NIGP168837 (female): A. wing venation; B. antenna; C. palpus; D – E. No. NIGP168838 (sex unknown): D. wing venation; E – part of middle leg with tibial spurs visible. Abbreviations: ped – pedicel, sc – scape. Scale bar = 1 mm for A and D; scale bar = 0.5 mm for B; scale bar = 0.1 mm for C; scale bar = 2 mm for E.

spur formula 2:2:2 with subequal spurs of fore legs (Fig. 11C-E); empodium large in female, very large in male (Figs. 2E, 5C); female cerci rather short (Fig. 11F); male terminalia complex, unrotated, comparatively elongated, with fleshy, somewhat conical rather short cerci (Fig. 5B).

Comparison. The new genus differs from other Euroasian Mesozoic genera with the wide distribution (*Mesorhyphus* Handlirsh, 1920, *Pachyrhyphus* Kovalev, 1986 and *Megarhyphus* Kovalev, 1990) in a slender male habitus and longer antenna which is not longer than thorax in all aforementioned genera (Kovalev, 1990). Additionally, it distinct from *Megarhyphus* in a smaller size, a bare katepisternum, wing venation (narrow M_{1+2} fork, m-m connecting with M_2, M_3 weaker than other medial veins) and maximal width of wing at level of Cu-A_1, from *Mesorhyphus* – in slender, not clavate hind tibia, from *Pachyrhyphus* – in elongated flagellomere (with length twice longer than wide) and maxilary palpi longer than proboscis.

Among extant genera *Cretolbia* gen. nov. is more similar to *Olbiogaster* (see Table 1) but differ mainly in shorter antenna, holoptic male eyes, two spurs on fore and hind tibia, a large empodium, rather short cerci of male, and presence of macrotrichia on medial veins, at least on M_1 and M_2 (Peterson, 1981; Amorim and Tonzoni, 1994). Such short antenna and holoptic male eyes are unknown among extant Olbiogastrinae.

Remarks. For comparison SEM images of eyes with short ommatrichia (Figs. 4E, 9C) and wing membrane with macrotrichia (Fig. 14F) of *Sylvicola* (*S.*) *cinctus* is given. The strongly differentiated alula, found in *Cretolbia* gen. nov. (Figs. 8C, 12A, 14B), is also known in extant *Sylvicola* (Fig. 14A) and *Olbiogaster* (Peterson, 1981) and is described in Mesozoic *Pachyrhyphus* (Lukashevich, 2012).

Cretolbia hukawnga sp. nov. Kania, Wojtoń, Lukashevich, Wang and Krzemiński
(Figs. 2–5)

LSID urn:lsid:zoobank.org:act:7A544010-1656-41C7-B128-26B5A9F14D89

Etymology. The species name is derived from Hukawng Valley in Myanmar.
Material examined. Holotype, No. MP/3657 (male), Institute of Systematic and Evolution of Animals, Polish Academy of Sciences, Kraków.
Horizon and locality. Lowermost Cenomanian, Hukawng Valley, northern Myanmar. The mining is done at a hill named Noije Bum, near Tanai Village (26°21′33.41″N, 96°43′11.88″E).
Diagnosis. Sc short, ending before r-m level; R_{4+5} almost straight; any sclerotization across r-m absent; M stem and d-cell connection

Table 1
Characters of *Cretolbia* gen. nov. compared to extant anisopodid genera (mainly based on Edwards, 1928, additional or corrected data are marked with references below [1]Peterson, 1981; [2]Amorim & Tozoni, 1994; [3]Thompson & Rogers, 1992; [4]Thompson, 2006).

Characters of *Cretolbia* gen. nov.	*Sylvicola*	*Olbiogaster*	*Lobogaster*	*Carreraia*	*Mycetobia*	*Mesochria*
Antenna not longer than head and thorax together	+	−	−		+	+
Male eyes holoptic	+ or −	−	−	−[2]	− or +[2]	+ or −[4]
Eyes with short pubescence or bare	+	+	−	+[3]	+	+
Ocelli large	+	−	+		−	− or +[4]
Palpomere I-III not fused	+	+	+	+	−	−
Katepisternum bare	+	+	−	−[3]		
Thorax with long dense setae	+	+ or −[1]	+		−	+ or −[4]
Wing without macrotrichia	−	+	+	+	+	+
R_{2+3} – in C	+	+	+	+	+	−
R_{2+3} not curved	−	+	+	+	+	+
Rs branches not closed	+	+	+	+	+	+
R_{4+5} well before apex	−	−	+		−	−
M_3 present	+	+	+	+	−	−
M_3 weaker than others	−	+ or −[2]	−		Absent	Absent
M stem distinct	+	+	+	+	−	−
d-cell present	+	+	+	+	−	−
Metatibia with apical comb	+	−/+[1]	−		+	
Empodium large	+	−	+		Absent	
Unrotated male terminalia	+	−			−	+[4]

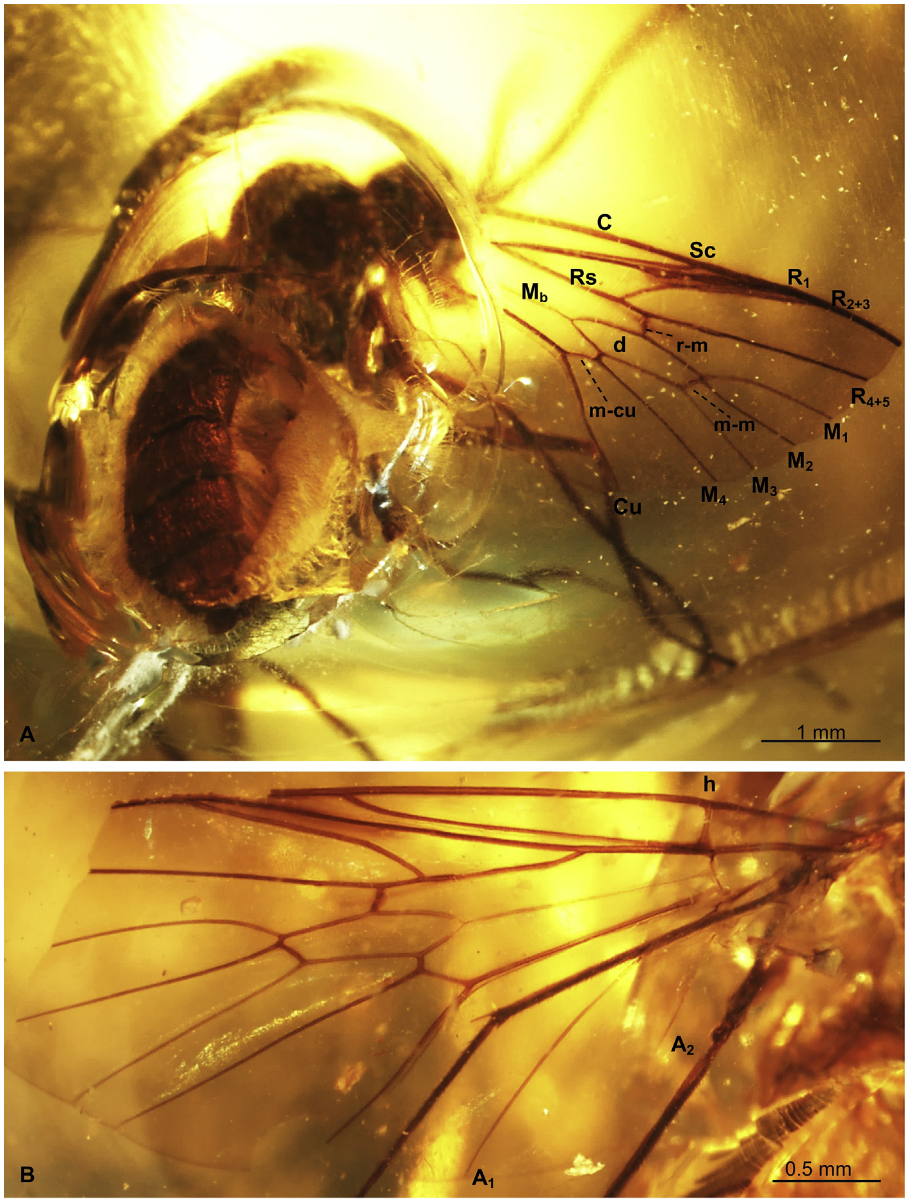

Fig. 7. *Cretolbia burmitica* sp. nov.: A. Holotype, No. NIGP168837 (female), habitus, latero-dorsal view; B. No. NIGP168838 (sex unknown): wing venation.

without desclerotization; scape cylindrical; flagellomeres with elongated sparse setae; terminal flagellomere longer than penultimate one, tapered at apex; III maxillary palpomere strongly dilated; elongated dense bristles on thorax, coxae and femora; abdomen yellow with almost black last segments; spots on femur and tibia absent.

Description. Body (Fig. 3) 2.90 mm long. Head, thorax and legs dark brown, almost black, I-V abdominal segments pale, yellow instead dark brown distal part; head and thorax combined 1.09 mm long, head width 0.69 mm. Antenna (Figs. 2D, 3B, 4B), comparatively long (1.05 mm); scape elongated, twice as long as wide; pedicel very short, approximately as long as wide; terminal flagellomere longer than penultimate one, tapered at apex; all flagellomeres with elongated sparse setae, subequal to width of bearing segments; additionally very short setae on all flagellomeres; maxillary palpus 0.5 mm (Figs. 2C, 3B) with third palpomere dilated, massive and longest, penultimate and terminal palpomeres subequal, approximately 0.30 mm, elongated and narrow; sparse short setae on all palpomeres.

Thorax: mesoscutum (Fig. 5A) with very elongated dense setae, scutellum with probably four such setae. Wing (Figs. 2A, 3A, 4D): 2.66 mm long, 0.89 mm wide; very dark pterostigma in half length of wing, surrounding apical part of R_1 to 3/5 length of R_1 from edge of wing and extending to 5/6 of R_{2+3} from edge of wing, distinctly separated from other part of wing by arched/rounded line of dark tint. Sc comparatively short, ending in proximal part of wing, approximately in 2/5 from base, beyond Rs bifurcation, but before r-m, opposite approximately 1/3 of d-cell length and A_1 apex; R_1 apices in about 3/5 of wing length, distance between R_1 and R_{2+3} apices very short, subequal to m-m, only 0.25 distance between Sc and R_1 apices. Rs separate Rb in proximal 1/5 of wing length from wing base; Rs stem longer than half R_{2+3} and as long as d-cell, constituting approximately 2/3 of R_{2+3}. D-cell pentagonal, 4× longer than wide, in proximal wing half, margins of d-cell evenly

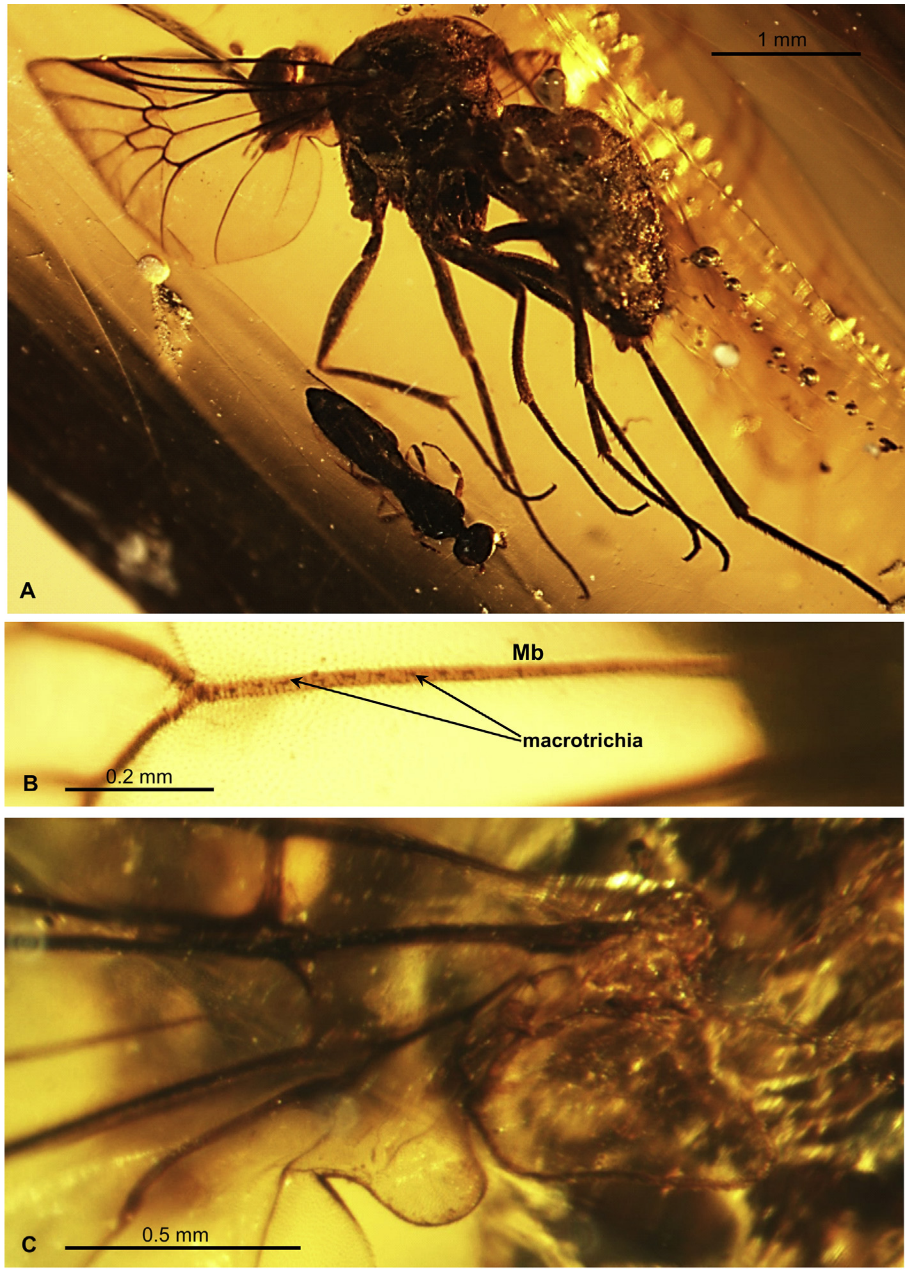

Fig. 8. *Cretolbia burmitica* sp. nov., additional material, No. MP/3682 (female): A. habitus, latero-dorsal view; B. macrotrichia on Mb stem; C. base of wing with strongly differentiated alula.

sclerotized, m-m almost straight. Segment bM_4 much shorter than m-cu, diverging from d-cell in proximal 1/3. Crossvein r-m shorter than m-m, r-m positioned just before d-cell midlength, approximately right angle to d-cell. Halter uniformly yellow, 0.39 mm long (Fig. 2B), not very elongated with short stem, shorter than knob and base of halter.

Legs (Figs. 3A, B, 4A, 5C): all coxae long, coxae and femora with very long, sparse bristles on inner surface of apical part and rare short setae. Tarsus (Figs. 2E, 5C) comparatively elongated with last tarsomere wide and longer than penultimate, simple claw shorter than very large empodium. Fore leg 3.01 mm long, middle 3.41 mm, hind leg 4.09 mm. Fore coxa 0.48 mm, trochanter 0.08 mm, femur 0.77 mm, tibia 0.61 mm, tarsus 1.07 mm long (0.51/0.27/0.13/0.07/0.09). Middle coxa 0.32 mm, trochanter 0.12 mm long, femur 1.07 mm, tibia 0.82 mm, tarsus 1.08 mm long (0.47/0.26/0.15/0.07/0.13). Hind coxa 0.45 mm, trochanter 0.14 mm, femur 1.11 mm, tibia 1.04 mm, tarsus 1.35 mm long (0.46/0.29/0.17/0.09/0.13).

Abdomen (Fig. 5B): male terminalia 0.22 mm long.

Comparison. The new species can be distinguished from other species of the genus described below in the shortest Sc, ending in proximal part of the wing and in color pattern of the body, in the shape and length of terminal flagellomere, the setation of antenna and pubescence of mesoscutum, scutellum, coxae and femora.

Remarks. For comparison scanning electron micrograph of the empodium (Fig. 5D) and male terminalia (Fig. 5E) of *Sylvicola* (*S.*) *cinctus* is given. In both genera the male terminalia are unrotated and structure of empodium is probably similar but in *Cretolbia* gen. nov. the empodium larger than in both extant species of *Sylvicola*, examined by us and previously (Peterson, 1981; Friedemann et al., 2014).

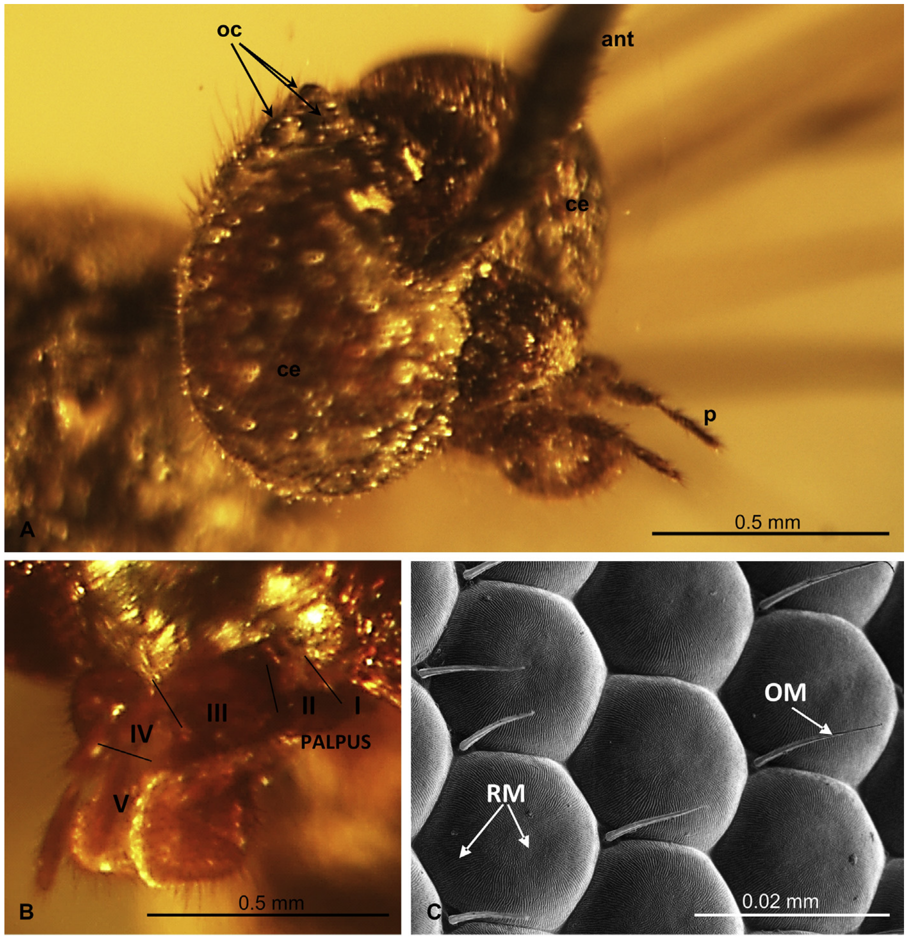

Fig. 9. A– B. *Cretolbia burmitica* sp. nov., A. additional material, No. MP/3682 (female), head with ocelli and palpi visible; B. Holotype No. NIGP168837 (female), head with palpi visible; C. *Sylvicola* (*S.*) *cinctus* (Fabricius, 1787) (female), SEM, the corneal surface with radial microridges and short ommatrichia arranged irregulary. Abbreviations: ant – antenna; ce – compound eye; oc-ocelli; p – palpus.; OM – ommatrichia; RM – radial microridges; I-V – palpomeres I–V.

Cretolbia burmitica sp. nov. Kania, Wojtoń, Lukashevich, Wang and Krzemiński
(Figs. 6–11)
LSID urn:lsid:zoobank.org:act:6B153067-8A99-46BD-9033-381448C6801E

Etymology. The species name is derived from the mineralogical name of the resin containing inclusions – burmite.
Material examined. Holotype, female, No. NIGP168837; additional material: sex unknown, No. NIGP168838, deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, P.R. China; female, No. MP/3682, Institute Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków.
Horizon and locality. Lowermost Cenomanian, Hukawng Valley, northern Myanmar. The mining is done at a hill named Noije Bum, near Tanai Village (26°21′33.41″N, 96°43′11.88″E).
Diagnosis. Sc ending just behind of r-m level, but before M_{1+2} bifurcation level; R_{4+5} almost straight; small sclerotization across r-m; M stem and d-cell connection desclerotized; scape saucer-shaped; flagellomeres without elongated sparse setae; terminal oval flagellomere subequal to penultimate one; III maxillary palpomere strongly dilated; thorax, coxae and femora without elongated dense bristles; abdomen brown; spots on femur and tibia absent.
Description. Body (Figs. 7A, 8A) uniformly pale brown, 3.85–5.54 mm long. Head (Fig. 9A): small, 0.73–1.23 mm high, 0.95–1.55 mm wide; eyes widely separated; antenna (Figs. 6B, 10A, B) comparatively massive, elongated, approximately as long as head and thorax combined, 1.65–2.22 mm long, scape and pedicel short, wider than long, both saucer-shaped, flagellomeres elongated, distinctly longer than scape and pedicel, comparatively equal in length, last oval flagellomere subequal to penultimate one; all segments of antenna densely covered by thick and very short setae only; maxillary palpus (Figs. 6C, 9A, B) 0.36–0.54 mm long, second palpomere elongated with elongated and strong setae at apex, third one strongly dilated, twice as long as wide, with strong elongated setae, fourth one short, slightly widened distally, with elongated and strong apical setae, last one twice as long as penultimate, with strong setae arranged evenly, additionally on all palpomeres short and thick setae arranged evenly.
Thorax: with not numerous, elongated setae on mesoscutum; head and thorax combined 2.01–2.40 mm; wing (Figs. 6A, D, 7A, B): 1.68–1.78 mm wide; very dark pterostigma in distal wing half, beyond Rs bifurcation, small sclerotization across r-m. Sc long, ending in distal half of wing, approximately in 2/3 from wing base, beyond Rs bifurcation and r-m, but before M_{1+2} bifurcation, just beyond d-cell midlength; Rs setose, separate Rb in distance 2/3 of its length from cross-vein h, Rs stem 0.75–0.89 mm long. R_1 terminating in 2/3 from wing base, 1.3 times longer than Rs. Crossvein r-m subequal to m-m, positioned aslant, in d-cell midlength; M stem with macrotrichia (Fig. 8B), bM_2 extremely short, almost entirely reduced, bM_4 much shorter than m-cu, diverging from d-cell in proximal part, d-cell four times longer than wide, 0.95–0.97 mm long, 0.19–0.26 mm wide,

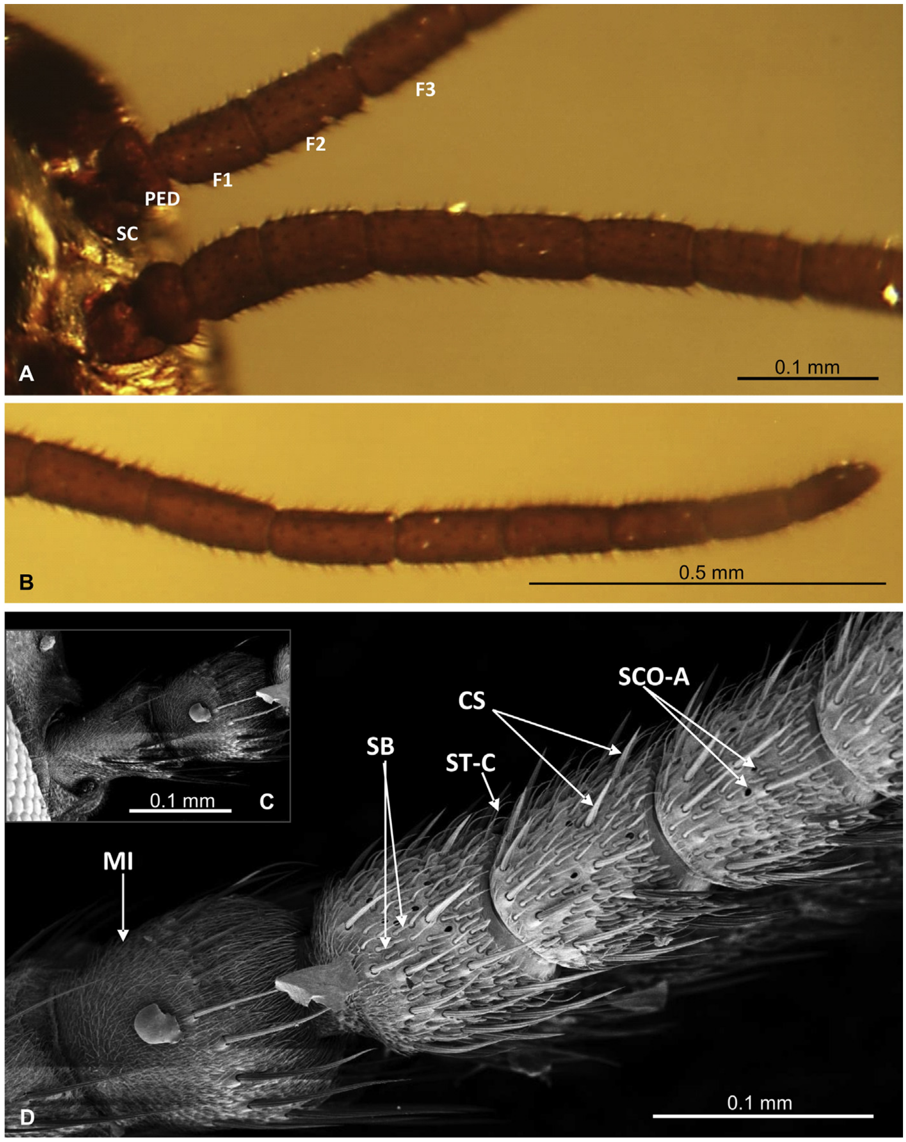

Fig. 10. A – B. *Cretolbia burmitica* sp. nov., holotype, No. NIGP168837, morphology of antenna: A. saurcer-shaped scape and pedicel, and cylindrical flagellomeres 1–3; B. elongated flagellomeres; C, D. *Sylvicola* (*S.*) *cinctus* (Fabricius, 1787) (female), SEM: D. scape and pedicel; E. comparatively short flagellomeres with stout chaetic sensilla. Abbreviations: CS – chaetic sensilla; F1-F3 – flagellomeres; PED – pedicel; SB – sensilla basiconica; SC – scape; SCO-A – sensilla coeloconica type A; ST-C – sensilla trichoidea; MI – microtrichia.

M stem and d-cell connection desclerotized. A_1 almost straight; A_2 slightly waved. Halter uniformly yellow, comparatively elongated.

Fore, middle and hind tibia (Fig. 11C-E) with two equal tibial spurs each, 0.17 mm long, middle and hind legs with apical combs (Figs. 6E, 11E). Coxa of fore leg 0.65 mm; trochanter 0.20 mm; femur 0.91–1.16 mm long, tibia 1.04–1.11 mm; tarsus 1.21 mm long. Coxa of middle leg 0.46 mm; trochanter 0.15 mm; femur 0.80 mm; tibia 0.85 mm; tarsus 1.37 mm long. Coxa of hind leg 0.51 mm; trochanter 0.17 mm; femur 0.80 mm; tibia 1.14 mm; tarsus 1.75 mm long. Empodium small, shorter than claw.

Abdomen (Fig. 11F): female terminalia not very elongated.

Comparison. The new species can be distinguished from *C. hukawnga* sp. nov. by having a saucer-shaped scape, absence of elongated sparse setae (subequal to flagellomere width) on antenna, terminal oval flagellomere subequal to penultimate one, longer Sc, desclerotization of M stem and d-cell connection.

Remarks. Holotype: female terminalia not well visible, partially destroyed, distal portion of wings absent. Specimen No. NIGP168838: antenna, palpi, wings partially cut.

For comparison scanning electron micrographs of ommatidia with ommatrichia (Fig. 9C), antenna (Fig. 10C, D), female terminalia (Fig. 11G) and apex of tibia (Fig. 11A, B) of *Sylvicola* (*S.*) *cinctus* are given. Sensilla which are visible on first flagellomere of extinct species are comparable to sensilla coeloconica of *Sylvicola* (*S.*) *cinctus*. Apical combs of bristles look similar in both extinct and extant anisopodids and differ only in the degree of development but in extant species combs are known on hind tibia only (Peterson, 1981).

Cretolbia zhuodei **sp. nov. Kania, Wojtoń, Lukashevich, Wang and Krzemiński**
(Figs. 12–15)

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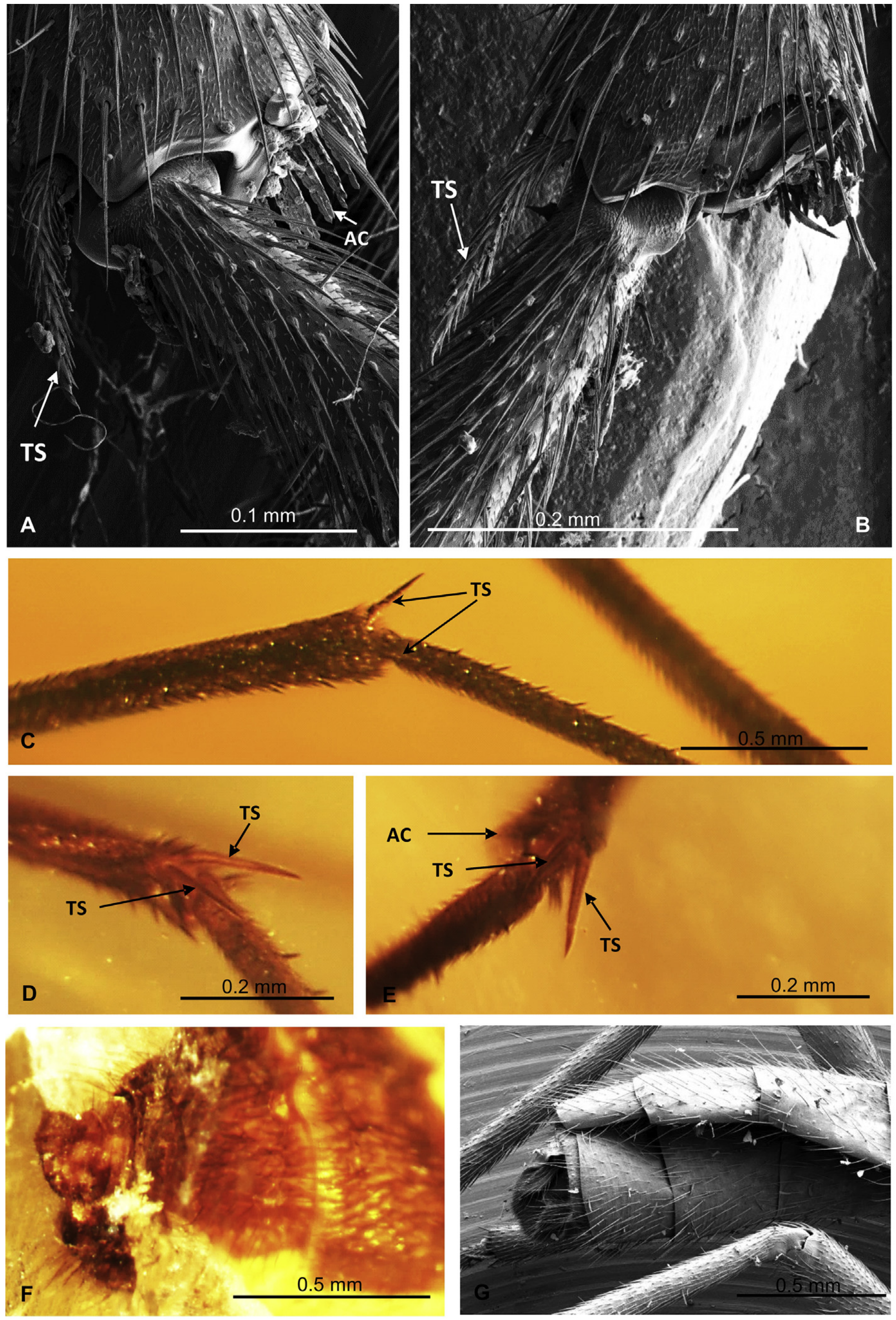

Fig. 11. A, B, G. *Sylvicola* (*S.*) *cinctus* (Fabricius, 1787), SEM: A. apex of tibia with tibial spur and apical comb (female); B. apex of tibia with tibial spur and apical comb (male); G. female terminalia; C – F. *Cretolbia burmitica* sp. nov., additional material, No. MP/3682: C. tibial spurs of fore leg; D. tibial spurs of middle leg; E. tibial spurs of hind leg; F. female terminalia. Abbreviations: AC – apical comb; TS – tibial spurs.

Etymology. The species name is dedicated to private collector Zhuo De.
Material examined. Holotype, female, No. NIGP168839, deposited in the collections of Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, P.R. China.
Horizon and locality. Lowermost Cenomanian, Hukawng Valley, northern Myanmar. The mining is done at a hill named Noije Bum, near Tanai Village (26°21′33.41″N, 96°43′11.88″E).
Diagnosis. Sc long, ending before M_{1+2} bifurcation level; R_{4+5} sinuous; small sclerotization across r-m; short and very thick setae on all flagellomeres; terminal flagellomere slightly narrowed in distal part, subequal to penultimate one; uniform, slender maxillary palpomeres; thorax, coxae and femora without elongated dense bristles; abdomen brown; small dark spots on femur and tibia.
Description. Body (Fig. 13A) 4.15 mm long, uniformly pale brown, with dark small spots on femur and tibia (Fig. 15B). Head: not very small, 0.92 mm high, 0.58 mm wide; antennae comparatively massive (Fig. 12B), elongated, as long as head and thorax combined, 1.48 mm long, flagellomeres elongated, subequal in length; all flagellomere covered by very thick and short uniform setae, almost perpendicular to surface of bearing flagellomere; elongated sensilla not visible on flagellomeres; maxillary palpus (Fig. 12C) with

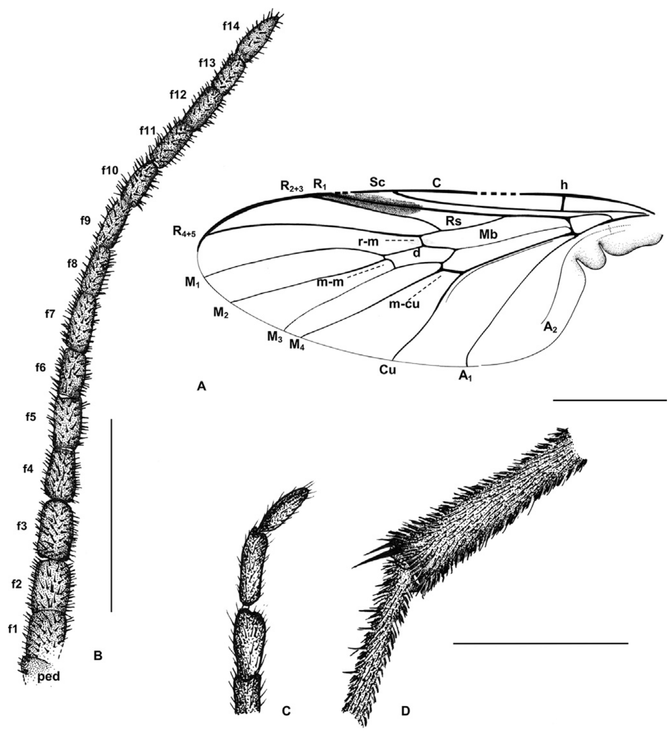

Fig. 12. *Cretolbia zhuodei* sp. nov., holotype No. NIGP168839: A. wing venation (reconstruction); B. antenna; C. palpus; D. part of fore leg with tibial spurs. Abbreviations: f1-f14 – flagellomeres; ped – pedicel. Scale bar = 0.5 mm for A and D; scale bar = 0.2 mm for B and C.

uniform slender palpomere, third one only slightly widened apically, twice as long as wide, with not very elongated setae, fourth one smooth, three times as long as wide; last one shortest.
Thorax: wing (Figs. 12A, 13A-D, 14B-E): 4.05 mm long, 1.65 mm wide; very dark pterostigma surrounding apical part of R_1 to 5/6 of R_{2+3}, distinctly separated from other part of wing by arched/rounded line of dark tint. Sc ending approximately in 3/5 from wing base, distal to r-m, and before M_{1+2} bifurcation level; r-m positioned aslant, directed to wing apex; Rs separate Rb at distance equal of its length from cross-vein h, Rs short, half of R_{2+3}, 0.53 mm long. R_1 about 4/6 of wing length. R_{4+5} sinuous. Crossvein r-m shorter than m-m, just before d-cell midlength, with small sclerotization across r-m. D-cell (Fig. 13D) 0.60 mm long, approximately 3.5× longer than wide, m-m arched to wing base. Distance between M_3 and M_4 apices about half of that between M_2 and M_3 apices (Figs. 13C, 14D). Vein bM_4 much shorter than m-cu, diverging from d-cell proximal 1/4; A_1 slightly arched at end, reduced A_2 comparatively short, waved. Halter (Fig. 14H) uniformly yellow, 0.62 mm long, with elongated sensilla.
Legs: Apical combs invisible. Subequal tibial spurs of fore legs 0.18 mm long (Figs 12D, 15C). Fore trochanter 0.19 mm, femur 0.92, tibia 1.11 mm long. Middle trochanter 0.23 mm, femur 0.84 mm, tibia 1.20 long. Hind trochanter 0.21 mm, femur 1.27 mm long.
Abdomen: female terminalia not very elongated (Fig. 15D).
Comparison. The species is distinguished from both other species described here in wing venation with extremely long Sc and sinuous R_{4+5}, thick setae on flagellomeres, uniform, slender maxillary palpomeres and small dark spots on femur and tibia.
Remarks. For comparison scanning electron micrograph of base, membrane of wing (Fig. 14A, F), halter (Fig. 14G) and part of leg (Fig. 15A) of *Sylvicola* (*S.*) *cinctus* is given. Allula (Fig. 14B) and sensilla on halter of new species (Fig. 14H) are comparable to those of *Sylvicola* (*S.*) *cinctus.*

4. Discussion

The taxonomic system of the family is still under current discussion but it is widely acknowledged that extant wood gnats "can be partitioned into three primary subgroups as follows: (1) a widespread group of *Sylvicola* only, (2) a pantropical group of *Olbiogaster* and some smaller genera, and (3) a widespread group of *Mycetobia* and some smaller genera" (Michelsen, 1999). Edwards (1930: 115) had already proposed a possibility of division of the family into three parts *Anisopus* (now–*Sylvicola*)/*Mycetobia* and *Mesochria*/*Olbiogaster* and *Lobogaster* (*Carreraia* wasn't described yet) but he did not discuss the characters. He wrote: "The five known genera of the family may be arranged in three groups, which are so distinct in various ways as almost to be deserve sub-family rank". Hennig (1954) supported only the erection of Olbiogastrinae and later (1973) suggested several diagnostic features: lateral position of spiracles on segment VIII and absence of torma in larva, absence of macrotrichia on wing membrane and apical comb on hind tibia in imago. The latter was shown to be of little value in classification because this character appears in most, if not all, species of the family and differs only in the degree of development of the pectinate bristles (Peterson, 1981).

Edwards (1928) considered that members of the genus *Olbiogaster,* or at least flies with a practically identical venation, are known from as far back as the Early Jurassic. Kovalev (1990) followed this opinion and included all Mesozoic members of Anisopodidae into Olbiogastrinae thought their shorter antennae (unknown in extant members) had been described long time ago. Probably the main reason for such consideration is the absence of macrotrichia on the wing membrane of Cretaceous anisopodids.

The species of the extant genera are distinguished mainly by color pattern of wing and body (Edwards, 1928; Tozoni, 1993) hence at the first glance, the significant differences of three new species worth to be erected up to a generic rank. Moreover, if we follow Kovalev (1990) and consider the short Sc as a genus level character, then *Cretolbia hukawnga* sp. nov. should probably be separated into its own genus (Sc is the shortest among species described herein ending in proximal part of the wing).

However, as one can see in Table and, for example in the two species of *Mesochria* from Fiji (Thompson, 2006), the intraspecific variation is considerable and male eyes may be holoptic or dichoptic, bristles on scutum weak or distinct, tibial spurs on hind tibia one or two and vein M_4 setose or bare. Unfortunately, nobody paid attention on the length of Sc in extant species, but we can estimate a variation of the character based on published figures of wings. This character varies significantly among Palearctic species of one subgenus of *Sylvicola*: in *S.* (*S.*) *cinctus* Sc ends just before r-m level, in *S.* (*S.*) *oceanicus* Frey, 1949 beyond r-m level, in *S.* (*S.*) *zetterstedti* (Edwards, 1923) Sc ends much more distally, level with M_{1+2} bifurcation (Krivosheina, 1998). Therefore, the recent variation of this character is comparable with the one discovered in anisopodids from Burmese amber, described herein. Therefore we prefer to include all species under discussion in one genus, in spite of the differences in pilosity of body, shape of terminal flagellomere, structure of pubescence and size of empodium in male and females. Some of these differences can be sexual, others – specific peculiarities and only

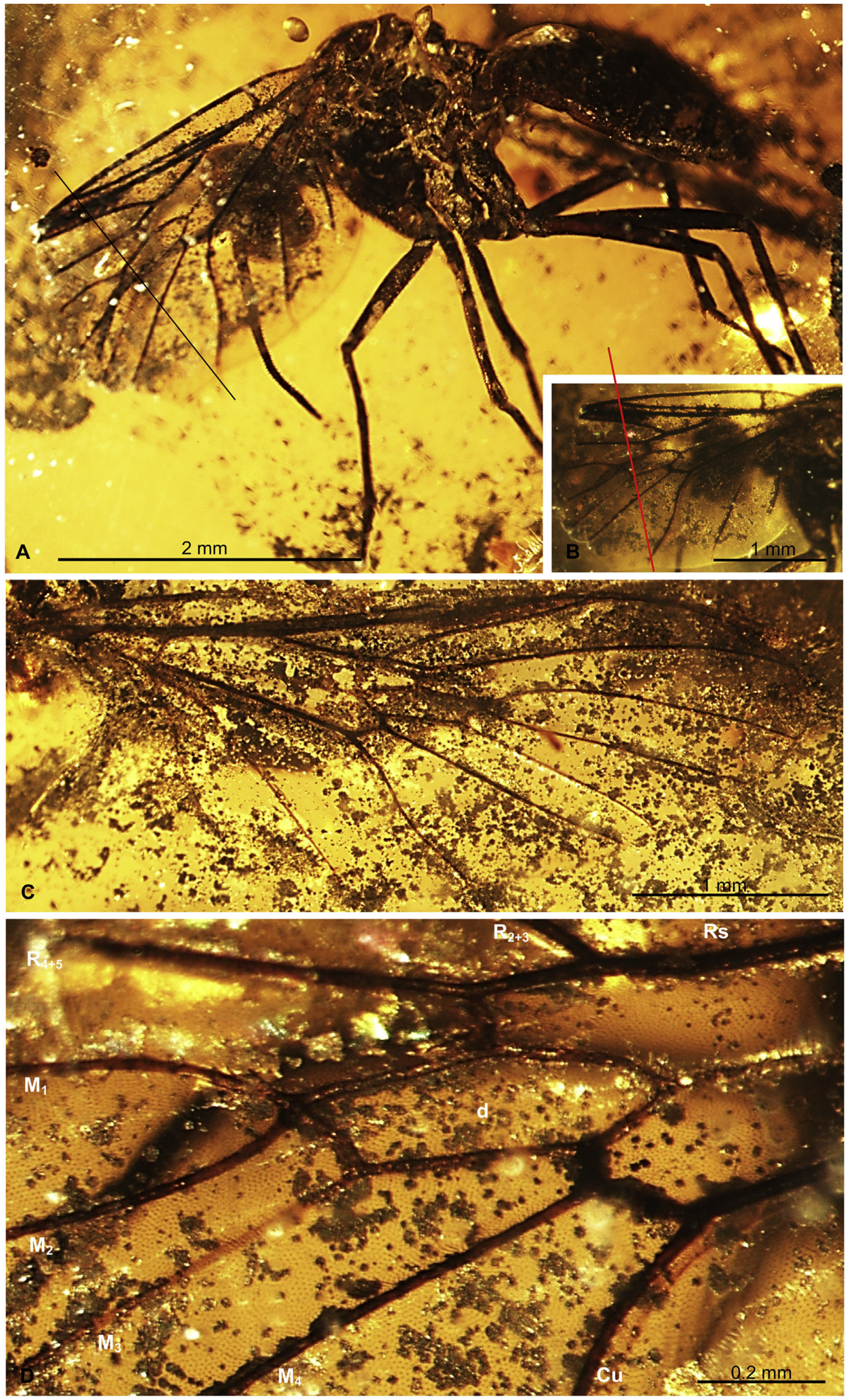

Fig. 13. *Cretolbia zhuodei* sp. nov., holotype No. NIGP168839: A. habitus, latero-dorsal view; B. wing venation with Sc long, ending just behind M_{1+2} bifurcation level, pointed by red line; C. right wing; D. part of left wing. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

new data (and new anisopodid males) can elucidate the problem.

It is worth to mention that plesiomorphic (shorter antenna) as well as apomorphic (holoptic eyes of male) characters distinguish the new genus from extant Olbiogastrinae. Both characters (and large empodium) are known in *Sylvicola* but the new genus differs from the latter also in the absence of macrotrichia and color pattern on the wing membrane and R_{2+3} not curved (all probably plesiomorphic states) as well as M_3 weaker than other medial veins (an undobtely apomorhic state) which are typical olbiogastrine

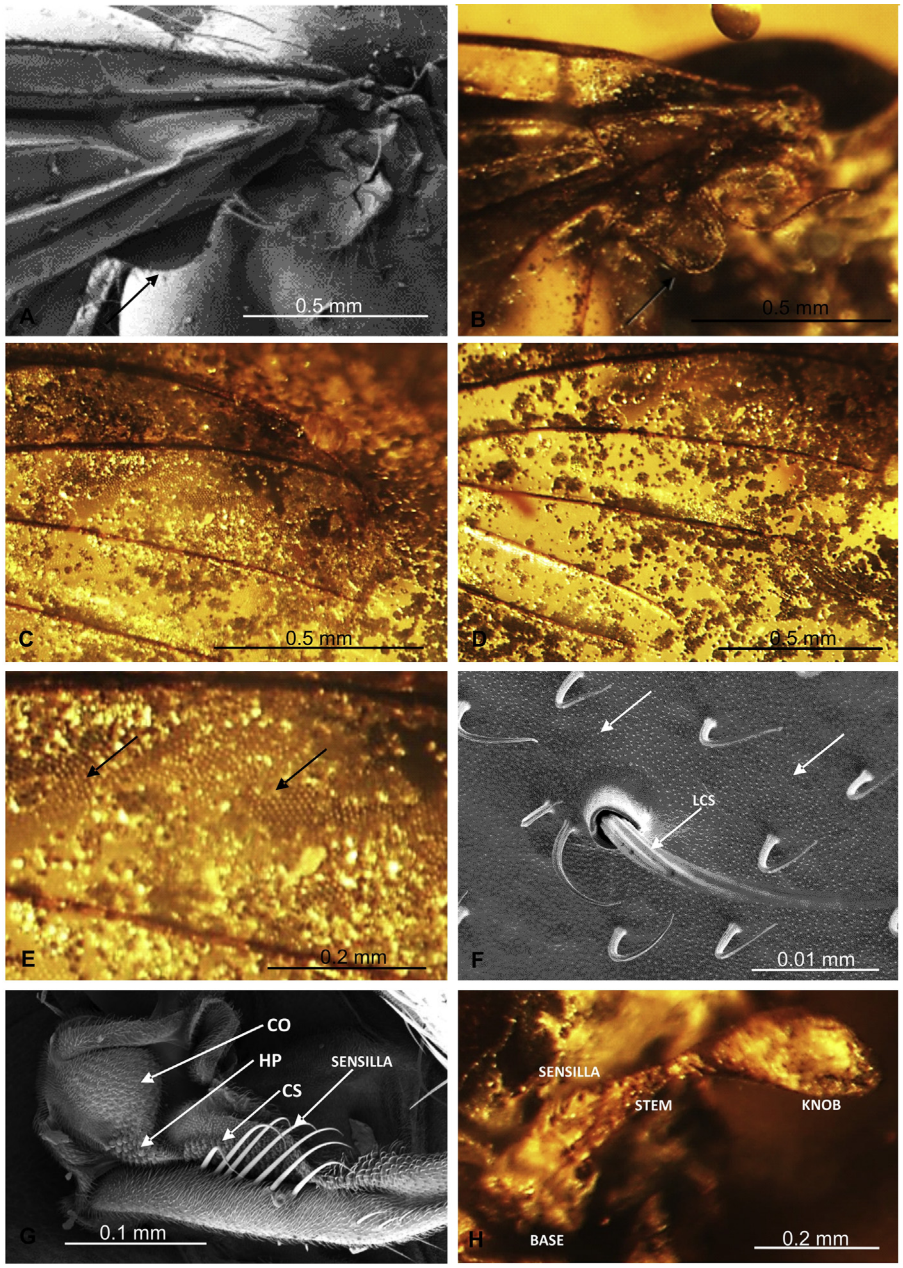

Fig. 14. Morphology of wings. A, F, G: *Sylvicola* (*S.*) *cinctus* (Fabricius, 1787), SEM: A. base of wing with strongly differentiated alula (pointed by arrow), F. membrane of wing; G. base and stem of halter with differentiated sensilla visible; B – E, H: *Cretolbia zhuodei* sp. nov., holotype, No. NIGP168839: B. – base of wing with strongly differentiated alula (pointed by arrow); C. apex of wing; D. edge of wing; E. microstructure of wing membrane (pointed by arrows); H. halter with differentiated sensilla visible. Abbreviations: CO – chordotonal organ; CS – campaniform sensilla; HP – Hicks' palpillae; LCS – long chaetic sensilla (long grooved setae).

peculiarities. The only undoubted apomorphic state (holoptic eyes) which connected the new genus with Anisopodinae (and Mycetobiinae) is so common in numerous nematocerous families that it is of little value for the understanding of relationships.

The general morphology of Anisopodidae has not changed since Cretaceous and *Cretolbia* gen. nov. is distinguished by the unique combination of known characters. The system of very differentiated microtrichia or sensory organs in these insects is quite complicated, it is especially obvious in morphology of antenna or palpi. Many differentiated structures are better visible under scanning electron microscope, but sometimes we can observe these details on amber inclusions and even on compressions (Kania and Wegierek, 2008). For example, very similar elongated sensilla are visible on stem of halter of *Sylvicola* (Fig. 14G) and *Cretolbia zhuodei* gen. et sp. nov. (Fig. 14H). There is a strong possibility that this is the same type of sensilla. Long sensilla also occur on legs of *Sylvicola* (Fig. 15A) but they are probably absent on *Cretolbia zhuodei* gen. et sp. nov. (Fig. 15B). This kind of comparison is the base for further studies of fossil and recent Anisopodidae for a better understanding of the morphology of these insects.

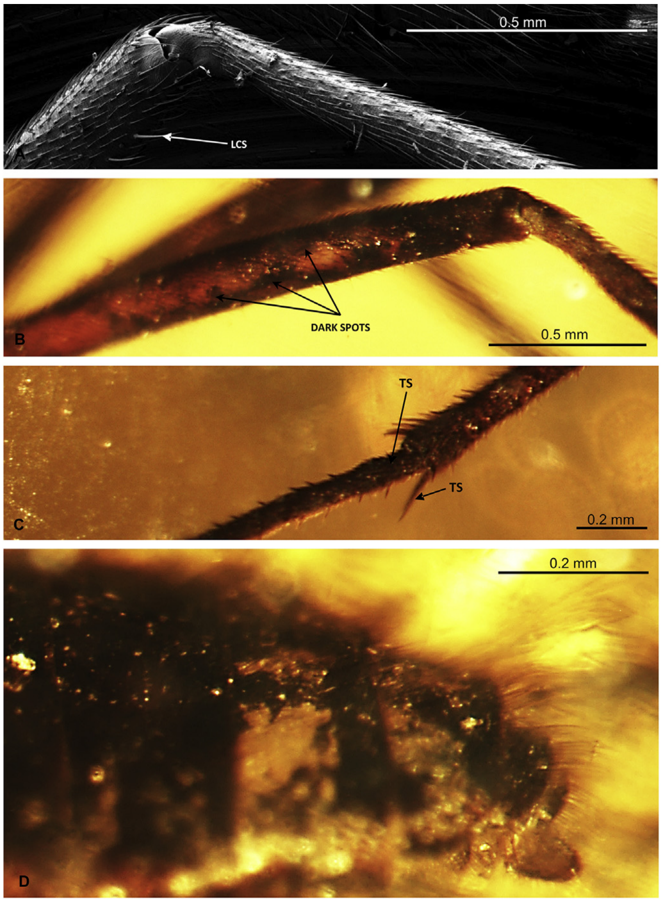

Fig. 15. A. *Sylvicola* (*S.*) *cinctus* (Fabricius, 1787), SEM, femur and tibia with long chaetic sensilla; B. – D. *Cretolbia zhuodei* sp. nov., holotype, No. NIGP168839: B. femur and tibia without long chaetic sensilla; C. tibial spurs of fore leg; D. female terminalia. Abbreviations: LCS – long chaetic sensilla (long grooved setae); TS – tibial spurs.

5. Conclusions

The study of inclusions in Burmese amber gives us the inside view of life in the Cretaceous, an epoch when the dinosaurs existed with many groups of insects. This is a very important period to study the evolution of many groups of animals, also the insects. The discovery of the new genus of Anisopodoidea which existed about 140 million years ago provides us with new information about this group of insects.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2018.10.013.

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Short communication

The oldest *Mycetobia* Meigen, 1818 (Diptera, Anisopodoidea) from Upper Cretaceous amber of northern Myanmar

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ABSTRACT

The oldest known representative of the genus *Mycetobia, Mycetobia myanmara* sp. nov., is described from Upper Cretaceous Burmese amber.

1. Introduction

The representatives of the genus *Mycetobia* Meigen, 1818 (Diptera, Anisopodoidea) are characterized by the vein Mb 3–branched, absence of discall cell, the wing membrane free of dark markings and of macrotrichia. These insects are not numerous in recent fauna, such as *Mycetobia pallipes* Meigen, 1818, *Mycetobia gemella* Mamaev, 1968 or *Mycetobia obscura* Mamaev, 1968, known from the United Kingdom (Palearctic region) (Hackston, 2013), *Mycetobia limanda* Stone, 1966, and *Mycetobia downiei* Hancock, 2016, from the Neotropical region, and *Mycetobia stonei* Lane and d'Andretta, 1958, from the Nearctic region. The fossil record of this genus is comparatively scarce and comprises only a few species (Evenhuis, 2017). Up to this date the oldest representatives of *Mycetobia* were known from the Eocene. The first fossil *Mycetobia* (*M. terricola* Scudder, 1878), was described by Scudder (1878) from the Eocene of USA, whereas other Eocene species are known from Baltic amber (Meunier, 1899, 1904). Moreover, three species, *Mycetobia antillea* Grimaldi, 1991, and *Mycetobia cryptambra* Grimaldi, 1991, and one unidentified species, are known from the Miocene of the Dominican Republic, and one unidentified species is known from the Pleistocene of Japan (Table 1). The present discovery of the oldest representative of *Mycetobia* is evidence that the genus existed for over 100 myrs, at a period of rapid changes of flora and fauna, thus giving us a new view on all groups of the Anisopodoidea.

2. Material and methods

The study was based on material from the Institute of Systematics and Evolution of Animals Polish Academy of Sciences, 31-016 Kraków, Poland (ISEA PAS). The specimen described here was found in amber deposits of Noije Bum in the Hukawng Valley in Kachin State, northern Myanmar (Fig. 1). Burmese amber was dated by Cruickshank and Ko (2003) to the middle–late Albian, but Grimaldi et al. (2002) estimated the age of this resin to the Turonian–Cenomanian based on arthropod inclusions. Shi et al. (2012) based on U–Pb dating of zircons from the volcaniclastic matrix of the amber estimate the age of Burmese amber at 98.79 ± 0.62 Ma (earliest Cenomanian).

The specimen was studied using a Nikon SMZ 1500 stereomicroscope equipped with a Nikon DS-Fi1 camera. The measurements were taken with the NIS-Elements D 3.0 software; only the undistorted structures were measured. The drawings (made by IK) were based on photographs and supplemented

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Table 1
A list of species of *Mycetobia* known from fossil record (after Evenhuis, 2017).

Species	Age	Locality
Unidentified sp. Saigusa, 1974	Pleistocene	Japan
Mycetobia antillea Grimaldi, 1991	Miocene	Dominican Republic
Mycetobia cryptambra Grimaldi, 1991	Miocene	Dominican Republic
Unidentified sp. Grimaldi, 1991	Miocene	Dominican Republic
Mycetobia terricola Scudder, 1878	Eocene	USA
Mycetobia connexa (Meunier, 1899) = *Mycetobia callida* Meunier, 1904	Eocene	Baltic Region
Mycetobia longipennis Meunier, 1899	Eocene	Baltic amber
Mycetobia platyuroides Meunier, 1899	Eocene	Baltic amber

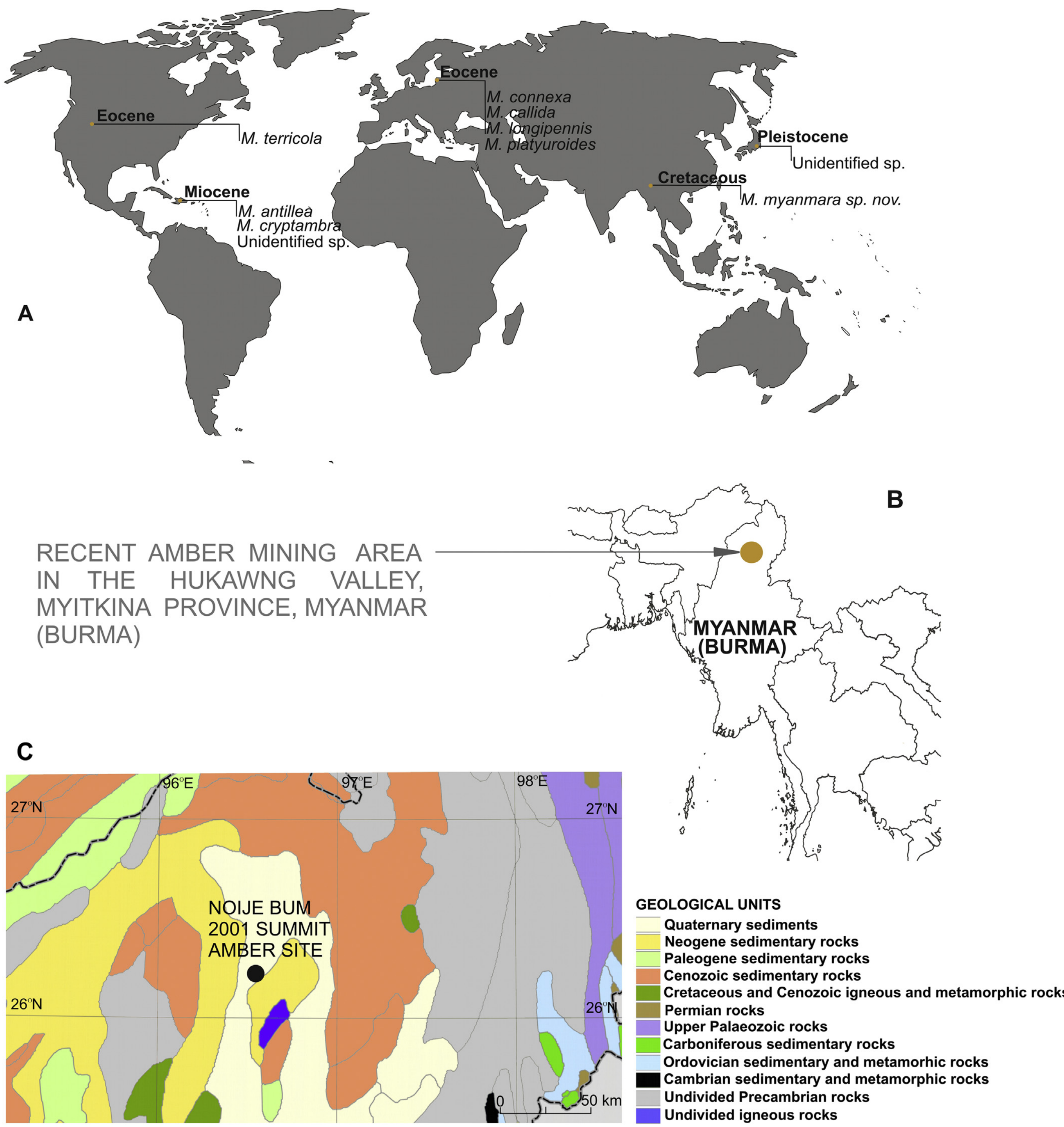

Fig. 1. A. Geographical distribution of fossil species of the genus *Mycetobia*; B. Location of recent amber mining area in the Hukawng Valley, Myitkina Province, Burma/Myanmar; C. Geological units of recent amber mining area in the Hukawng Valley compiled from data provided by Grimaldi et al. (2002), Cruikshank and Ko (2003), Wandrey (2006) and Kania et al. (2015).

Fig. 2. *Mycetobia myanmara* sp. nov., holotype, No MP/3683 (male) (ISEA PAS). Enlarged view of habitus, lateral view.

with details observed under the microscope. The terminology pertaining to male genitalia is according to Grimaldi (1991), while some terms of wing venation are after Krzemińska et al. (2009).

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID for this publication is: LSIDurn:lsid:zoobank.org:pub:9A1BB5AE-229F-4725-B10F–F78176DEB314.

3. Systematic Palaeontology

Order: Diptera Linnaeus, 1758.
Suborder: Nematocera Duméril, 1805.
Infraorder: Bibionomorpha Hennig, 1954.
Superfamily: Anisopodoidea Knab, 1912.
Family: Anisopodidae Knab, 1912.
Subfamily: Mycetobiinae Crampton, 1924.

Genus *Mycetobia* Meigen, 1818: 229.
Type species: *Mycetobia pallipes* Meigen, 1818, by subsequent designation of Westwood, 1840, p. 127.

Mycetobia myanmara sp. nov.
(Figs 2–8).

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Diagnosis. Sc terminates before Rs bifurcation level; veins R_1 and R_{2+3} straight with apices very close to each other, the distance between Sc and R_1 approximately eight times the distance between R_1 and R_{2+3}; apex of R_{2+3} beyond level of bifurcation of M_{1+2} into M_1 and M_2. Flagellomeres cylindrical with sparse, thick setae, shorter than segments bearing them; cerci massive with two spatula-shaped appendices, external one with sharp apex.
Etymology. The species name is derived from Myanmar (Burma).
Material examined. Holotype, No. MP/3683 (male), Institute of Systematic and Evolution of Animals, Kraków (ISEA PAS) (see Fig. 3).
Description. Body 2.20 mm long, pale brown with dark brown head, pale brown antenna, legs and proboscis (Figs 2 and 3A–D). Ocelli (Fig. 4 A–C) raised, but not on tubercle, arranged in an equilateral triangle. Wing hyaline (Fig. 5A–C), male genitalia pale brown (Fig. 6A–E).
Head. Eyes, 0.18 mm diameter in lateral view, dorsally contiguous, occupying most of the head whose diameter is 0.22 mm in lateral view. Antenna (Fig. 7A) elongated, 0.90 mm long, shorter than head and thorax combined, composed of 14 flagellomeres, scape 0.04 mm long and cylindrical, approximately 1.5 times as long as it is wide, and the pedicel 0.08 mm long, approximately 1.5 times as long as it is wide. All flagellomeres are rather short and thick; first flagellomere, is 0.07 mm long, flagellomeres 2–13 are 0.05 mm long, approximately as long as they are wide or slightly shorter, distal segments are slightly longer; last flagellomere is 0.08 mm long, approximately 2.5 times as long as it is wide and longer than penultimate one, tapered at the apex; all flagellomeres with sparse setae, shorter than the segments bearing them. Palpus short and rather small, slender.
Thorax. mesoscutum with sparse and not very long setae, praescutellar setae and apical scutellar setae long and rather delicate; katepisternum pale brown, remainder of pleuron pale brown. Wing (Fig. 7B) 2.15 mm long, 0.59 mm wide with veins C, Sc, R_1, R_{2+3}, R_{4+5} and basal portion of Cu, vein r-m, m-cu thick and very dark. C extended to slightly beyond R_{4+5}, in 0.2 the distance from R_{4+5} to M_1. Wing membrane with dense microtrichia. One row of macrotrichia on R_{4+5}, m-cu and r-m is visible. Veins Mb and M_{1+2}, M_1, M_2 very pale, only slightly sclerotized. R_1 and R_{2+3} straight; R_{2+3} apex beyond level of bifurcation of M_{1+2}. Sc not very long, terminates just before of Rs bifurcation level, distance between apices of R_1 and R_{2+3} very short, convergent within a distance of about the width of the veins, but not touching apically. Rs shorter than half R_{2+3}, R_{2+3} about 2.5 times the length of Rs. Stem M_{1+2} shorter than M_1; M_1 and M_2 narrowly separated. The distance between R_{4+5} and M_1 apices about 1.5 times the distance between M_1 and M_2, the distance between apices of M_1 and M_2 comparable to the distance between apices of M_2 and M_{3+4}; R_{2+3} longer than M_{1+2}. Cross vein r-m shorter than cross vein m-cu. The distance between apices of R_{2+3} and R_{4+5} approximately 2.5 times the distance between apices of M_1 and R_{4+5}. A_1 sinuate. Halter 0.39 mm long, pale brown.
Legs. two tibial spurs on fore, middle and hind legs, tibial spurs pattern as for genus *Mycetobia*: 2:2:2. Fore coxa 0.19 mm long, trochanter 0.08 mm, femur 0.39 mm, tibia 0.39 mm, tarsus 0.49 mm long. Middle coxa 0.19 mm long, trochanter 0.08 mm long, femur 0.54 mm long, tibia 0.29 mm, tarsus 0.40 mm. The length of hind coxa 0.26 mm, trochanter 0.10 mm, femur 0.57 mm, tibia 0.45 mm, tarsus 0.67 mm.
Abdomen. tergites and sternites pale brown, cerci pale brown; male genitalia 0.43 mm long (Fig. 8A, B) rotated at 180°: anal point well developed, bifid at apex; gonocoxite massive; aedeagus rather tiny, comparatively elongated, strongly sclerotized; cercus massive with two elongated, comparatively wide and sharp-shaped appendices.
Comparison. In *M. cryptambra* vein Sc terminates beyond bifurcation of Rs, veins R_1 and R_{2+3} are slightly curved, apices of these veins are widely separated, in *M. myanmara* sp. nov. the vein Sc

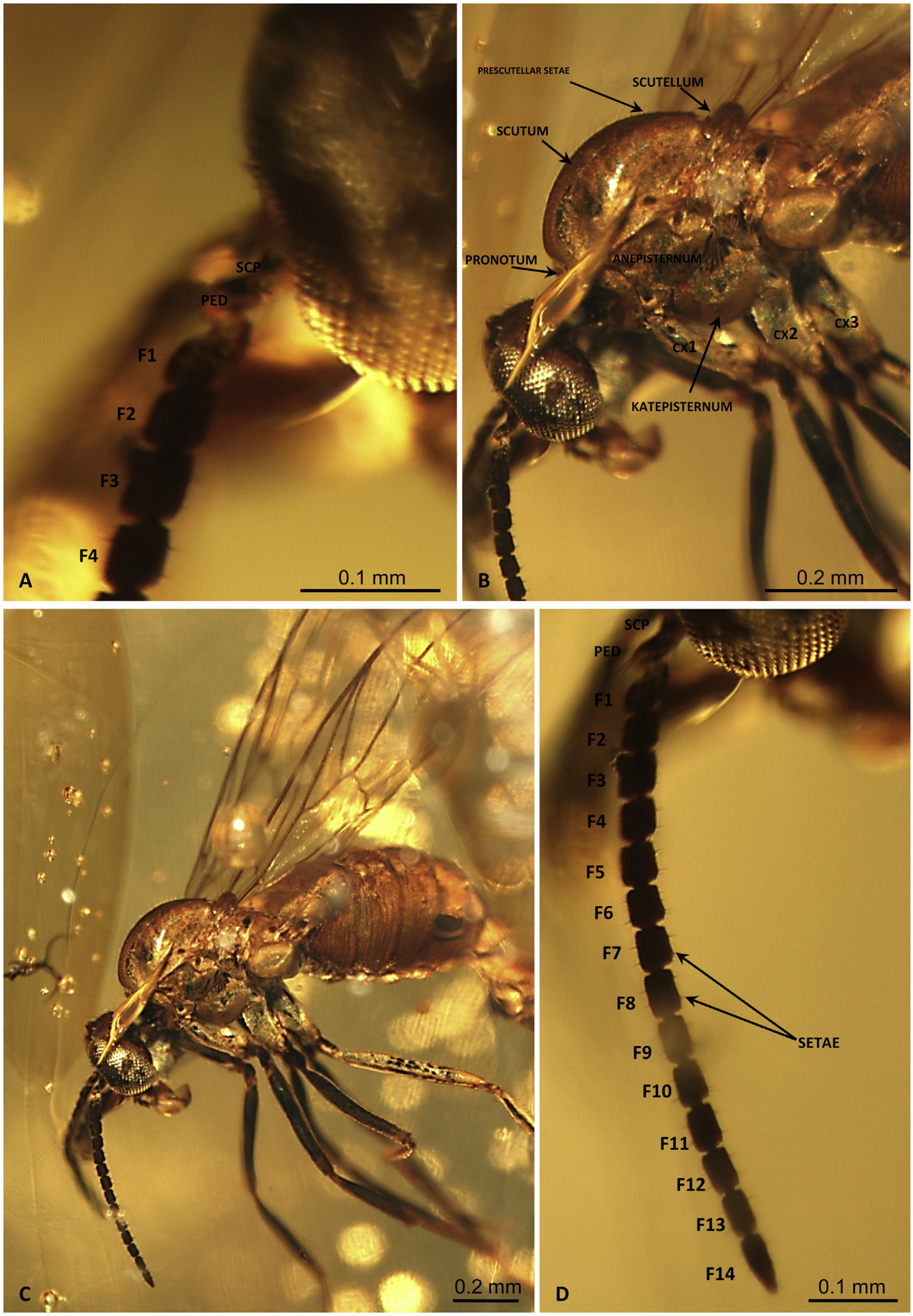

Fig. 3. *Mycetobia myanmara* sp. nov., holotype, No MP/3683 (male) (ISEA PAS). A. scapus and pedicel, flagellomeres 1–4; B. head and thorax, lateral view; C. habitus, lateral view; D. antenna; Abbreviation: CX1-CX3 – coxa 1–3; F1–F14 – flagellomeres; PED – pedicel; SCP – scape.

terminates before bifurcation of Rs, veins R_1 and R_{2+3} are straight and apices of these veins are separated but close to each other. Male terminalia in a newly described species differs from other fossil representatives of *Mycetobia* especially by large appendices on the cercus. In *M. connexa* the apices R_1 and R_{2+3} are widely separated.

4. Discussion

The Cretaceous was a period of dramatic changes and transitions towards the modern world (Grimaldi, 1991). Diptera, which appeared in the Triassic (Krzemiński et al., 1994), in the Cretaceous existed in a variety of environments and relied on a

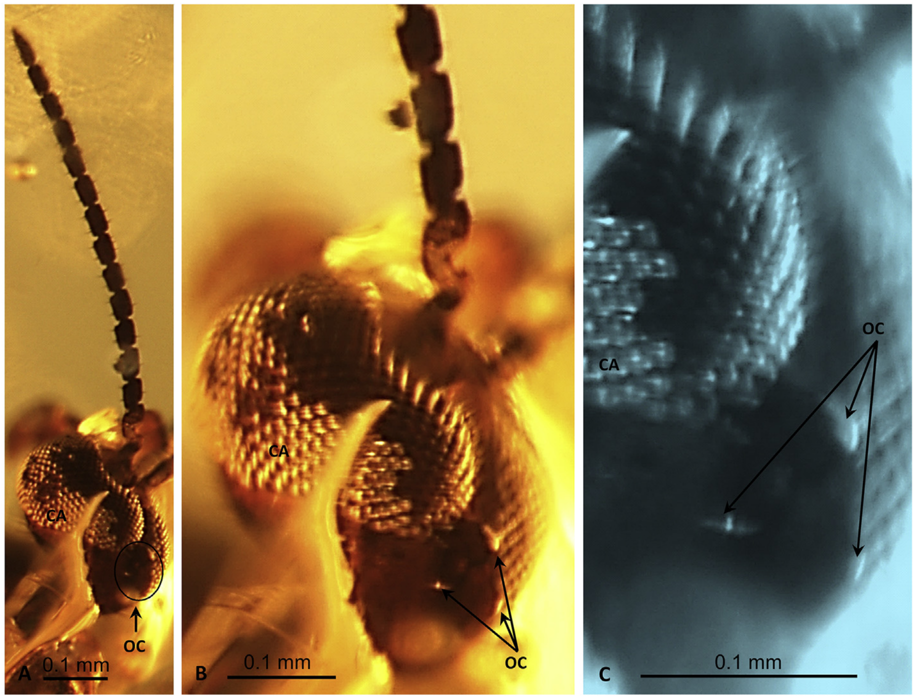

Fig. 4. *Mycetobia myanmara* sp. nov., holotype, No MP/3683 (male) (ISEA PAS). A. head with antenna and ocelli visible; B. enlarged view of head with ocelli visible; C. enlarged view of ocelli. Abbreviation: CA – compound eyes; OC – ocelli.

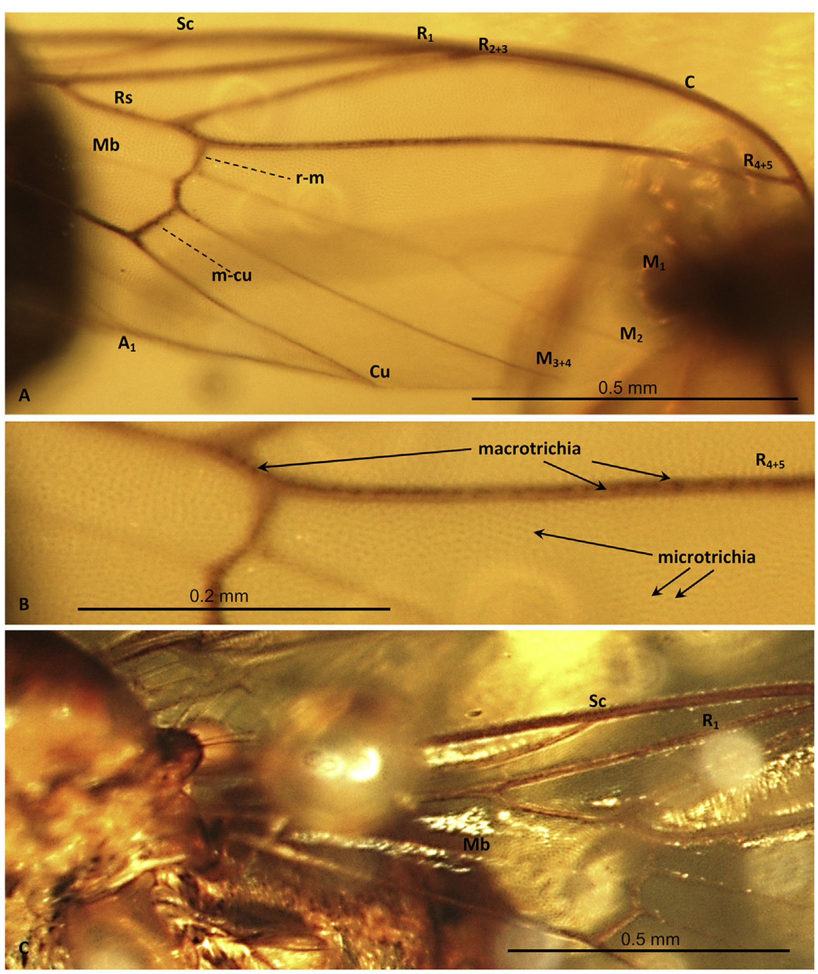

Fig. 5. *Mycetobia myanmara* sp. nov., holotype, No MP/3683 (male) (ISEA PAS). A. wing venation; B. R_{4+5} with macrotrichia and membrane with microtrichia visible; C. part of wing with Mb well visible; Abbreviation: wing venation: C – costal vein; Sc – subcostal vein; Rs – sector radii; R_1 – R_{4+5} – radial veins; Mb – medial-basal vein; M_1 – M_{3+4} – medial veins; Cu – cubital vein; A_1 – anal vein; r-m – radial-medial cross vein; m-cu – medial-cubital vein cross vein.

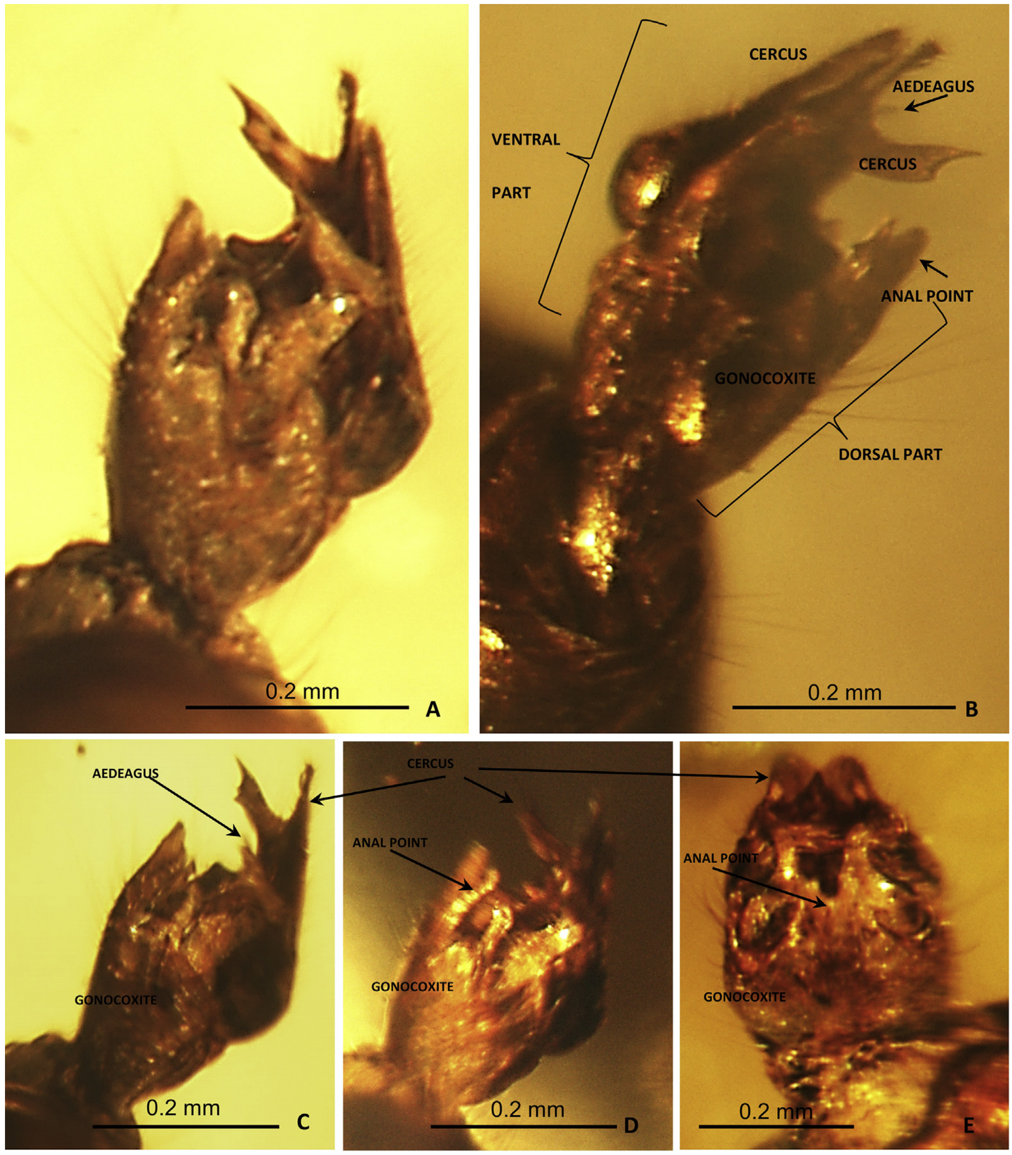

Fig. 6. *Mycetobia myanmara* sp. nov., holotype, No MP/3683 (male) (ISEA PAS), genitalia. A. latero-dorsal view; B. latero-ventral view; C.-D. latero-dorsal view; E. dorsal view.

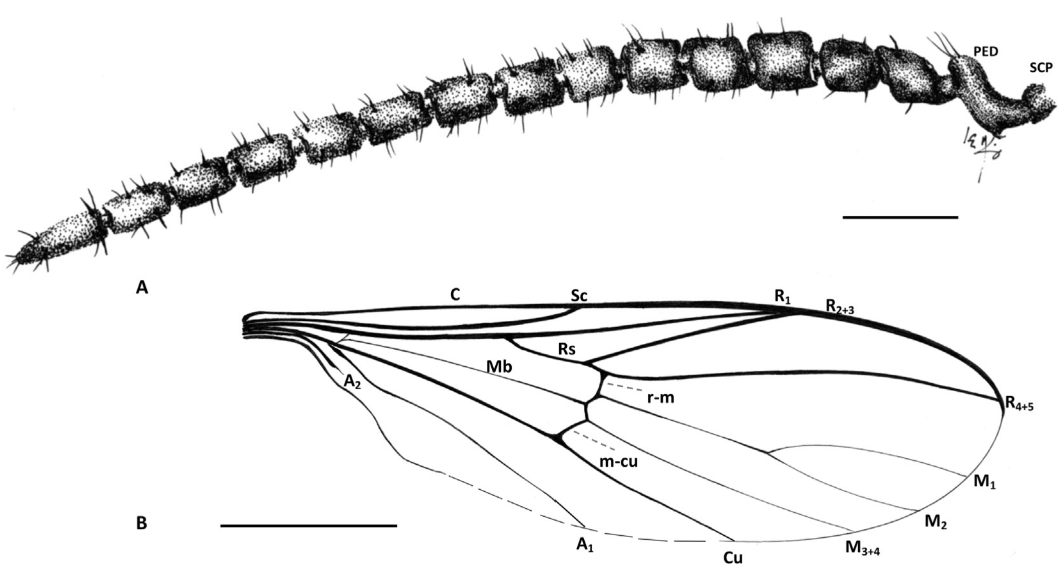

Fig. 7. *Mycetobia myanmara* sp. nov., holotype, No MP/3683 (male) (ISEA PAS). A. antenna; B. wing venation. Abbreviations: PED – pedicel; SCP – scape; wing venation: as in Fig. 5. Scale bar = 0.1 mm for A; scale bar = 0.5 mm for B.

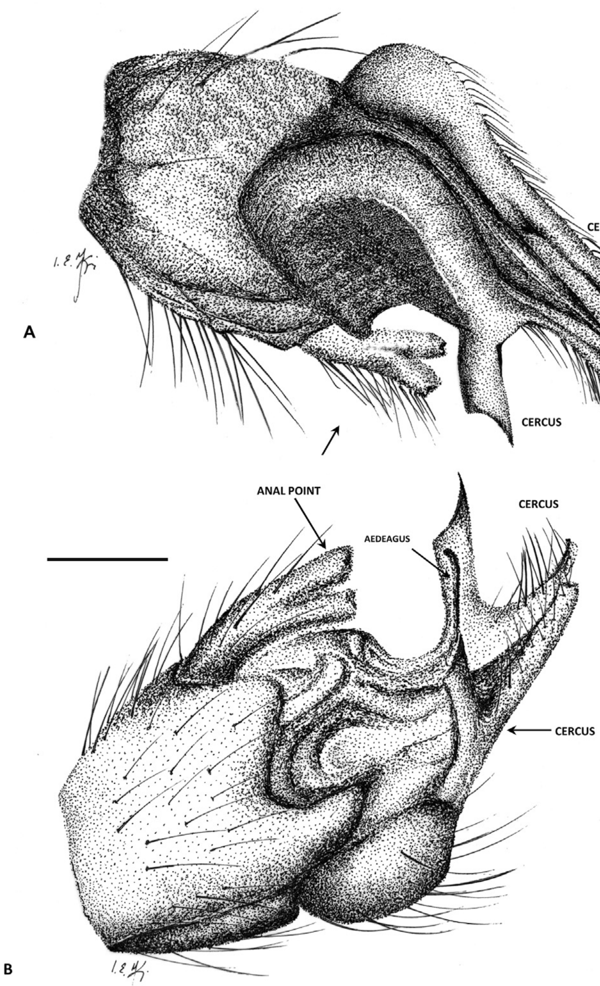

Fig. 8. *Mycetobia myanmara* sp. nov., holotype, No MP/3683 (male) (ISEA PAS), male terminalia. A. latero-ventral view; B. latero-dorsal view. Scale bar = 0.1 mm.

differentiated spectrum of food. Based on the fossil data, it is possible to say that the Nematocera fauna experienced major speciation in the Cretaceous, when probably gymnosperm trees of the family Cupressaceae exuded resins which became eventually Burmese amber (Grimaldi and Ross, 2017). Diptera has been recorded in Cretaceous fossil resins of Lebanon, Spain, Myanmar. Major fossiliferous deposits of Cretaceous amber in southeastern Asia have provided additional evidence concerning the evolution of many groups of insects, amongst which are the Diptera (Grimaldi et al., 2002; Podenas and Poinar, 2009; Guo et al., 2017; Xing et al., 2017; Jiang et al., 2018; Skibińska and Krzemiński, 2018). The data suggest that the amberiferous forests at the time of formation and deposition of Burmese amber were constituent parts of the equatorial floristic realm (Vakhrameev, 1988) with humid warm temperate climate (Cruickshank and Ko, 2003; Jiang et al., 2018) with some islands or archipelago environments (Jiang et al., 2018). Forty five families of Diptera, including 100 species are represented in Burmese amber (Ross, 2018). The oldest member of Anisopodidae – *Mesorhyphus rhaeticus* (Rohdendorf, 1962) was found in the Lower Jurrasic of Kyrgyzstan. *Mycetobia myanmara* sp. nov. is the first representative of *Mycetobia* in Burmese amber. *Mycetobia antillea* and *M. cryptambra* that were extensively described by Grimaldi (1991), which differ from *Mycetobia myanmara* sp. nov. mainly by wing venation and morphology of male genitalia. Especially noteworthy is the specific morphology of the antenna of the new species because it distinguishes this species from other congeners from both Dominican amber and Baltic amber. Comparatively short but very sparse setae do not occur in a known fossil record species of *Mycetobia*. This feature can probably be treated as a plesiomorphic feature.

5. Conclusions

The new species, *Mycetobia myanmara* sp. nov., described from Upper Cretaceous Burmese amber, demonstrates that this group of insects appeared in the Cretaceous. The new fossil record indicates that the general body structure and many morphological features of the *Mycetobia* are the same as ca. 100 Ma. Currently, *Mycetobia* is rather considered to be a relict group.

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Phylogenetic relationships within the superfamily Anisopodoidea (Diptera: Nematocera), with description of new Jurassic species

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Abstract

New species of Jurassic Protorhyphidae: *Protorhyphus lukashevichae* **sp. nov.**, *Protorhyphus jurassicus* **sp. nov.**, and Anisopodidae: *Mesorhyphus blagoderovi* **sp. nov.** from Daohugou, China, are described and illustrated. Phylogenetic relationships and evolution within the Anisopodoidea are analyzed and discussed. The oldest Anisopodoidea appeared in the Triassic and fossil record indicate that they were most numerous in Jurassic and in the Cretaceous.

Keywords: imprints, taxonomy, evolution, Protorhyphidae, Anisopodidae, Daohugou, China

Introduction

According to Krzemiński & Krzemińska (2003), superfamily Anisopodoidea Knab, 1912 is divided on three families: Protorhyphidae Handlirsch, 1906, Siberhyphidae Kovalev, 1985 and Anisopodidae Knab, 1912. The family Protorhyphidae is currently divided in five genera: *Archirhyphus* Handlirsch, 1939, *Austrorhyphus* Martin, 2008, *Brachyrhyphus* Blagoderov & Grimaldi in Blagoderov *et al.*, 2007, *Protorhyphus* Handlirsch, 1906, *Vymrhyphus* Blagoderov in Shcherbakov *et al.*, 1995 (Table 1). Other genera like *Acritorhyphus* Bode, 1953, *Eoptychoptera* Handlirsch, 1906, *Heterorhyphus* Bode, 1953 or *Brachyopteryx* Hong, 1984, which previously were assigned to this family now were excluded. *Acritorhyphus* Bode, 1953 was synonymized with the genus *Eoptychoptera* Handlirsch, 1906 by Lukashevich *et al.* 1980, *Heterorhyphus* Bode, 1953 was placed in the family Heterorhyphidae by Ansorge & Krzemiński (1995). The genus *Brachyopteryx* Hong, 1984 was considered by Zhang (2007) to fall outside the Protorhyphidae (Martin, 2008).

The oldest Anisopodoidea: Protorhyphidae are known from Triassic deposits of Europe, North America, and Asia (Table 1). The oldest known species of Protorhyphidae is *Vymrhyphus blagoderovi* Krzemińska & Krzemiński, 2003 from the Grès a Voltzia Formation of France. The youngest representatives of this extinct family are recorded at the turn of the Jurassic and Cretaceous (Table 1). The oldest known representatives of the extant family Anisopodidae are from Lower Jurassic. This latter family is rich in species placed in extinct and extant genera (Table 3). The small extinct family Siberhyphidae is known only from one species reported from Upper Jurassic of Kubekovo (Kovalev *in* Kalugina & Kovalev, 1985) (Table 1).

The purpose of this paper is to describe three new species, and to analyze the phylogenetic relationships and discuss the evolution within the taxa of the superfamily Anisopodoidea that are reported in the fossil record.

Material and methods

The study was based on three imprints collected from the Middle Jurassic Jiulongshan Formation at Daohugou, Ningchen, Inner Mongolia, China (Gao *et al.*, 2012; Gu *et al.*, 2012; Wang *et al.*, 2016; Ren *et al.*, 2019), and housed at Key Laboratory of Insect Evolution and Environmental Changes, Capital Normal University, Beijing.

Specimens were studied using a Nikon SMZ 1500 stereomicroscope equipped with a Nikon DS–Fi1 camera and the measurements were taken with NIS–Elements D 3.0 software in University of Rzeszów. The drawings for the analysis were based on the specimens and photographs. The measurements of specimens were taken with NIS–Elements D 3.0 software in University of Rzeszów. They were made at widest point and maximum length and were given only in case where relevant structures were not distorted. The nomenclature of wing venation follows that used in literature.

The phylogenetic relationships of Anisopodoidea genera and species reported from the fossil record were

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TABLE 1. A list of fossil species of Anisopodoidea. Data based on Paleobiology Database: fossilworks; Evenhuis (2019); Huang (2015; 2019); Huang *et al.* (2018); Kania *et al.* (2019); Lukashevich (2012); Martin (2008), Pape *et al*. (2011). Zhou *et al.* (2013); Xu *et al.* (2016).

Species	Age	Precise data locality*/ type material	Locality
Protorhyphidae Handlirsch, 1906			
Archirhyphus Handlirsch, 1939			
Archirhyphus asiaticus Rohdendorf, 1964	Tithonian (150.8 – 145.5 Ma) (Late Jurassic)	Shar-Teg/imprint	Mongolia
	Callovian/Oxfordian (164.7 – 145.5 Ma) (Middle – Late Jurassic)	Karatau-Galkino/imprint	Kazakhstan
Archirhyphus geinitzi Handlirsch, 1939	Early Toarcian (183.0 – 182.0 Ma) (Early Jurassic)	Dobbertin, Mecklenburg/ imprint	Germany
Austrorhyphus Martin, 2008			
Archirhyphus moryi Martin, 2008	Sinemurian/Toarcian (183.0 – 175.6 Ma) (Early Jurassic)	Hill River region/imprint	Australia
Brachyrhyphus Blagoderov & Grimaldi, 2007			
Brachyrhyphus distortus Blagoderov & Grimaldi, 2007 *in* Blagoderov *et al.*, 2007	Norian (221.5 – 205.6 Ma) (Late Triassic)	North Carolina/imprint	USA
Protorhyphus Handlirsch, 1906			
Protorhyphus arcuatus (Hong, 1983)	Callovian (164.7 ± 1.8 Ma) (Middle Jurassic)	Daohugou/imprint	China
Protorhyphus jurassicus sp. nov.	Callovian (164.7 ± 1.8 Ma) (Middle Jurassic)	Daohugou/imprint	China
Protorhyphus liaoningicus Zhang, 2007	Callovian (164.7 ± 1.8 Ma) (Middle Jurassic)	Daohugou/imprint	China
Protorhyphus lukashevichae sp. nov.	Callovian (164.7 ± 1.8 Ma) (Middle Jurassic)	Daohugou/imprint	China
Protorhyphus major Kovalev, 1990	Tithonian (150.8 – 145.5 Ma) (Late Jurassic)	Chita/imprint	Russia
Protorhyphus neimonggolensis Zhang, 2007	Callovian (164.7 ± 1.8 Ma) (Middle Jurassic)	Daohugou/imprint	China
Protorhyphus ovisimilis Bode, 1953	Early Toarcian (183.0 – 182.0 Ma) (Early Jurassic)	Grassel, Braunschweig; Niedersachsen/imprint	Germany
Protorhyphus rohdendorfi Lukashevich, 2012	Tithonian (150.8 – 145.5 Ma) (Late Jurassic)	Shar-Teg/imprint	Mongolia
Protorhyphus sibiricus Kovalev, 1985	Bajocian (171.6 – 164.7 Ma) (Middle Jurassic)	Kubekovo/imprint	Russia
Protorhyphus simplex (Geinitz, 1888)	Early Toarcian (183.0 – 182.0 Ma) (Early Jurassic)	Grimmen/imprint	Germany
Protorhyphus stigmaticus Handlirsch, 1920	Early Toarcian (183.0 – 182.0 Ma) (Early Jurassic)	Mecklenburg/imprint	Germany
Protorhyphus turanicus Rohdendorf, 1964	Hettangian (201.6 – 189.6 Ma) (Early Jurassic)	Tonskiy/imprint	Kyrgyzstan
Vymrhyphus Blagoderov *in* Shcherbakov *et al.*, 1995			

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TABLE 1 (Continued)

SPECIES	AGE	PRECISE DATA LOCALITY*/ TYPE MATERIAL	LOCALITY
Vymrhyphus blagoderovi Krzemiński & Krzemińska, 2003	Aegean (247.2 – 242.0 Ma) (Middle Triassic)	Arzviller/imprint	France
Vymrhyphus tuomikoskii Blagoderov, 1995	Carnian (235.0 – 221.5 Ma) (Late Triassic)	Osh/imprint	Kyrgyzstan
Vymrhyphus triassicus Blagoderov, 1995	Carnian (235.0 – 221.5 Ma) (Late Triassic)	Osh/imprint	Kyrgyzstan
Siberhyphidae Kovalev, 1985			
Siberhyphus lebedevi Kovalev *in* Kalugina & Kovalev, 1985	Bajocian (171.6 – 164.7 Ma) (Middle Jurassic)	Kubekovo /imprint	Russia
Anisopodidae Knab, 1912			
Anisopodinae Knab, 1912			
Gansuplecia Hong & Wang, 1990			
Gansuplecia triporata Hong & Wang, 1990	Callovian (164.7 ± 1.8 Ma) (Middle Jurassic)	Daouhugou/imprint	China
Jurolaemargus Evenhuis, 1994			
Jurolaemargus yujiagouensis Hong, 1983	Callovian (164.7 ± 1.8 Ma) (Middle Jurassic)	Daouhugou/imprint	China
Leptoplecia Hong, 1983			
Leptoplecia laevis Hong, 1983	Callovian (164.7 ± 1.8 Ma) (Middle Jurassic)	Daouhugou/imprint	China
Sylvicola Harris, 1780			
Sylvicola baltica Wojtoń *et al.*, 2018	Priabonian (37.2 – 33.9 Ma) (Eocene)	Baltic Region/Baltic amber	Baltic Region
Sylvicola cadaver Scudder, 1890	Bridgerian (50.3 – 46.2 Ma) (Eocene)	Green River/imprint	USA
Sylvicola carolae Lewis, 1969	Langhian (16.0 – 13.7 Ma) (Miocene)	Idaho/imprint	USA
Sylvicola hoffeinsorum Wojtoñ *et al.*, 2018	Priabonian (37.2 – 33.9 Ma) (Eocene)	Baltic Region/Baltic amber	Baltic Region
Sylvicola hooleyi Cockerell, 1921	Priabonian (37.2 – 33.9 Ma) (Eocene)	Isle of Wight/imprint	England, United Kingdom
Sylvicola lugubris Heer, 1849	Sarmatian (12.7 – 11.6 Ma) (Miocene)	Radoboj/imprint	Croatia
Sylvicola maculata Heer, 1849	Sarmatian (12.7 – 11.6 Ma) (Miocene)	Radoboj/imprint	Croatia
Sylvicola punctata Wojtoñ *et al.*, 2018	Priabonian (37.2 – 33.9 Ma) (Eocene)	Baltic Region/Baltic amber	Baltic Region
Sylvicola prisca Westwood, *in* Brodie 1845	Middle Berriasian (145.5 – 140.2 Ma) (Early Cretaceous)	Middle Purbeck/imprint	England, United Kingdom

......continued on the next page

TABLE 1 (Continued)

Species	Age	Precise data locality*/ type material	Locality
Sylvicola splendida Meunier, 1907	Priabonian (37.2 – 33.9 Ma) (Eocene)	Baltic Region/Baltic amber	Russian Federation
Mycetobiinae Crampton, 1924			
Mesochria Enderlein, 1910			
Mesochria fani Szadziewski & Szwedo, 2016 *in* Szadziewski *et al.*, 2016	Early-Middle Ypresian (~ 48 – 56 Ma) (Eocene)	Guchengzi/ Fushun amber	China
Mesochria neotropica Grimaldi, 1991	Burdigalian (20.4 – 13.7 Ma) (Early to Middle Miocene)	El Valle/ Dominican amber	Dominican Republic
Mycetobia Meigen, 1818			
Mycetobia antillea Grimaldi, 1991	Burdigalian (20.4 – 13.7 Ma) (Miocene)	Dominican Republic/ Dominican amber	Dominican Republic
Mycetobia connexa Meunier, 1899	Priabonian (37.2 – 33.9 Ma) (Eocene)	Baltic Region/Baltic amber	Baltic Region
Mycetobia christelae Wojtoñ *et al.*, 2019	Priabonian (37.2 – 33.9 Ma) (Eocene)	Baltic Region/Baltic amber	Baltic Region
Mycetobia cryptambra Grimaldi, 1991	Burdigalian (20.4 – 13.7 Ma) (Miocene)	Dominican Republic/ Dominican amber	Dominican Republic
Mycetobia hansi Wojtoñ *et al.*, 2019	Priabonian (37.2 – 33.9 Ma) (Eocene)	Baltic Region/Baltic amber	Baltic Region
Mycetobia myanmara Kania *et al.*, 2019	Early Cenomanian (99.7 – 94.3 Ma) (Late Cretaceous)	Hukawng Valley/ Myanmar amber	Myanmar
Mycetobia perkovskyi Wojtoñ *et al.*, 2019	Priabonian (37.2 – 33.9 Ma) (Eocene)	Baltic Region/Baltic amber	Baltic Region
Mycetobia silvia Wojtoñ *et al.*, 2019	Priabonian (37.2 – 33.9 Ma) (Eocene)	Baltic Region/Baltic amber	Baltic Region
Mycetobia szwedoi Wojtoñ *et al.*, 2019	Priabonian (37.2 – 33.9 Ma) (Eocene)	Baltic Region/Baltic amber	Baltic Region
Unidentified sp.	Pleistocene	Japan/imprint	Japan
Olbiogastrinae Hennig, 1973			
Cretolbia Kania *et al.*, 2019			
Cretolbia burmitica Kania *et al.*, 2019	Early Cenomanian (99.7 – 94.3 Ma) (Late Cretaceous)	Hukawng Valley/ Myanmar amber	Myanmar
Cretolbia hukawnga Kania *et al.*, 2019	Early Cenomanian (99.7 – 94.3 Ma) (Late Cretaceous)	Hukawng Valley/ Myanmar amber	Myanmar
Cretolbia zhoudei Kania *et al.*, 2019	Early Cenomanian (99.7 – 94.3 Ma) (Late Cretaceous)	Hukawng Valley/ Myanmar amber	Myanmar
Megarhyphus Kovalev, 1990			
Megarhyphus amberae Krzemińska *et al.*, 2010	Turneri (196.5 – 189.6 Ma) (Early Jurassic)	Lyme Regis/imprint	England, United Kingdom

......*continued on the next page*

TABLE 1 (Continued)

Species	Age	Precise data locality*/ type material	Locality
Megarhyphus rarus Zhang, 2007	Oxfordian (162.7 ± 1.8 Ma) (Late Jurassic)	Daohugou/imprint	China
Megarhyphus rectinervis Kovalev, 1990	Aptian (125.5 – 112.6 Ma) (Early Cretaceous)	Chita/imprint	Russia
Megarhyphus sophiae Kovalev, 1990	Tithonian (150.8 – 145.5 Ma) (Late Jurassic)	Chita/imprint	Russia
Mesorhyphus Handlirsch, 1920			
Mesorhyphus anomalus Handlirsch, 1939	Early Toarcian (183.0 – 182.0 Ma) (Early Jurassic)	Dobbertin, Mecklenburg/ imprint	Germany
Mesorhyphus blagoderovi sp. nov.	Oxfordian (162.7 ± 1.8 Ma) (Late Jurassic)	Daohugou/imprint	China
Mesorhyphus clavipes Kovalev, 1990	Tithonian (150.8 – 145.5 Ma) (Late Jurassic)	Chita/imprint	Russia
Mesorhyphus handlirschi Lukashevich, 2012	Tithonian (150.8 – 145.5 Ma) (Late Jurassic)	Shar-Teg/imprint	Mongolia
Mesorhyphus hennigi Lukashevich, 2012	Tithonian (150.8 – 145.5 Ma) (Late Jurassic)	Shar-Teg/imprint	Mongolia
Mesorhyphus nanus Handlirsch, 1920	Early Toarcian (183.0 – 182.0 Ma) (Early Jurassic)	Dobbertin, Mecklenburg/ imprint	Germany
Mesorhyphus rhaeticus Rohdendorf, 1962	Hettangian to Hettangian (201.6 – 189.6 Ma) (Early Jurassic)	Issyk-Kul/imprint	Kyrgizstan
Mesorhyphus zirzipanus Ansorge, 1996	Early Toarcian (183.0 – 182.0 Ma) (Early Jurassic)	Grimmen/imprint	Germany
Olbiogaster Osten Sacken, 1886			
Olbiogaster fittoni Westwood, 1845	Middle Berriasian (145.5 – 140.2 Ma) (Early Cretaceus)	Middle Purbeck/imprint	England, United Kingdom
Olbiogaster perezi Grimaldi & Amorim, 1995	Burdigalian to Burdigalian (20.4 – 13.7 Ma) (Miocene)	Dominican Republic/ Dominican amber	Dominican Republic
Olbiogaster simplex Cockerell, 1920	Bridgerian (50.3 – 46.2 Ma) (Eocene)	Colorado/imprint	USA
Pachyrhyphus Kovalev, 1986			
Pachyrhyphus jakovlevi Kovalev, 1986	Aptian (125.5 – 112.6 Ma) (Late Jurassic/Early Cretaceous)	Gurvan-Ereny-Nuruu/ imprint	Mongolia
Pachyrhyphus malus Kovalev, 1986	Aptian (125.5 – 112.6 Ma) (Late Jurassic/Early Cretaceous)	Gurvan-Ereny-Nuruu/ imprint	Mongolia
Pachyrhyphus transbaicalicus Kovalev, 1990	Tithonian (150.8 – 145.5 Ma) (Late Jurassic/Early Cretaceous)	Chita/imprint	Russia
Thiras Giebel, 1856			
Thiras westwoodi Giebel, 1856	Berriasian (145.5 to 140.2 Ma) (Early Cretaceous)	Lower Purbeck/imprint	England, United Kingdom

......continued on the next page

TABLE 1 (Continued**)**

SPECIES	AGE	PRECISE DATA LOCALITY*/ TYPE MATERIAL	LOCALITY
Teginae Shcherbakov & Lukashevich, 2012			
Tega Blagoderov *et al.,* 1993			
Tega karavatica Blagoderov *et al.*, 1993	Callovian/Oxfordian (164.7 – 145.5 Ma) (Middle – Late Jurassic)	Karatau/imprint	Kazakhstan
	Tithonian (150.8 – 145.5 Ma) (Late Jurassic)	Shar-Teg/imprint	Mongolia
Tega penna Blagoderov *et al.*, 1993	Tithonian (150.8 – 145.5 Ma) (Late Jurassic)	Shar-Teg/imprint	Mongolia

analyzed using morphological characters available for studied fossils (see below). Some of those characters were defined in previous studies (Wojtoń *et al.*, 2018 a, b; Kania *et al*., 2019 a, b). Characters used for the phylogenetic analysis have been treated as unordered. The data matrix was composed in Mesquite, version 3.6 build 917 (Maddison & Maddison, 2011), and is presented in Table 2.

In the phylogenetic analysis of genera within Anisopodoidea (excluding doubtful taxa), representatives of three families Protorhyphidae, Siberhyphidae and Anisopodidae, were included. Type species were chosen as the representative taxa of particular genera. The species *Plecia americana* Hardy, 1940 (Bibionidae) was chosen to polarize the characters. The analysis was performed using TNT 1.1. (Goloboff *et al*., 2008), by New Technology Search algorithm, with memory reserved to store 10000 trees. Equal Weighting and Implied Weighting performances (Goloboff *et al.*, 2008; Congreve & Lamsdell, 2016) with values of k-parameter between 1 to 11 were done. Strict Consensus tree and Majority Rule tree (the level cut-off 50) were analyzed. The trees received were studied under WinClada v. 1.00.08 with Unambiguous Changes, Fast Optimization and Slow Optimization procedures (Nixon, 2002). The cladograms obtained were adjusted using Corel Photo-Paint (Kania, 2015).

The classification of Anisopodomorpha used here follows Krzemiński & Krzemińska (2003). The classification of Anisopodidae used here follows mainly Edwards's Genera Insectorum (Edwards, 1928) updated by Michelsen (1999) and Thompson (2006). The family includes three extant subfamilies: Anisopodinae, Mycetobiinae and Olbiogastrinae and one extinct: Teginae (Shcherbakov *et al.*, 1995; Lukashevich, 2012).

Systematic palaeontology

Order Diptera Linnaeus, 1758
Suborder Nematocera Duméril, 1805
Infraorder Bibionomorpha Hennig, 1954
Superfamily Anisopodoidea Knab, 1912
Family Protorhyphidae Handlirsch, 1906
Genus *Protorhyphus* Handlirsch, 1906

Characters like strong Sc, shorter than half wing length, R_4 longer than R_{4+5}, stem of M thin and desclerotized, moreover M_1 and M_2 diverging from discal cell independently (Lukashevich, 2012) indicate that two of three new species described herein belong to the genus *Protorhyphus*. In this fossil genus 10 species are currently known (Table 1).

Key to species of *Protorhyphus*

1. Sc only 0.3x the length of the wing .... ***P. major***
- Sc longer than 0.3x the length of the wing ....2.
2. Sc elongate, ending opposite Rs bifurcation level.............. .... ***P. arcuatus***
- Sc rather short, ending before Rs bifurcation level ....3.
3. Sc ending opposite or beyond Mb bifurcation level, opposite d-cell level...5.
- Sc ending distinctly before Mb bifurcation level, before d-cell level...4.
4. M_1 and M_2 widely separated from d-cell ....6.
- M_1 and M_2 closely related, leaving d-cell in one point.....7.
5. R_4 distinctly arched at apex; M_1 separate d-cell in 0.83 from Mb bifurcation; crossvein r-m is positioned in the middle of stem R_{4+5} .... ***P. turanicus***
- R_4 almost straight, M_1 separate d-cell of the same level as M_3; crossvein r-m is positioned closer to R_4 than to R_{2+3}..... .... ***P. stigmaticus***
6. The distance between R_1 and R_{2+3} up to 7x the distance between Sc and R_1; R_{2+3} only slightly waved at apex; distal parts of R_1 and R_{2+3} parallel ....9.
- The distance between R_1 and R_{2+3} at least 10x the distance

TABLE 2. The data matrix.

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Plecia americana Hardy, 1940	0	3	?	0	2	2	3	3	1	2	0	0	1	0	0	0	0	1	2	2	0	1	?	0	0
Archirhyphus geinitzi Handlirsch, 1939	?	?	?	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	?	?	?
Austrorhyphus moryi Martin, 2008	?	?	?	0	1	1	0	1	0	1	1	0	0	0	?	0	0	1	0	0	0	0	?	?	?
Brachyrhyphus distortus Blagoderov & Grimaldi, 2007	?	?	?	1	1	1	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	?	?	?
Protorhyphus simplex Geinitz, 1888	?	?	?	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0	0	?	?	0
Vymrhyphus blagoderovi Krzemiñski & Krzemiñska, 2003	?	?	?	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	?	?	?
Siberhyphus lebedevi Kovalev, 1985	?	?	?	?	3	2	2	2	0	?	?	?	0	0	0	0	0	1	0	0	?	0	?	0	?
Carreraia edwardsi Carrera, 1941	?	?	?	1	2	2	2	2	0	1	1	1	0	0	0	0	0	1	0	0	0	2	?	0	0
Cretolbia burmitica Kania et al., 2019	0	0	0	1	2	2	2	2	0	1	1	1	0	1	1	0	1	1	0	0	1	0	1	0	0
Lobogaster philippii Schiner, 1868	1	?	1	1	2	2	2	2	0	1	1	1	0	1	0	0	1	2	0	0	0	0	0	0	0
Megarhyphus sophiae Kovalev, 1990	0	2	0	0	2	2	2	2	0	0	1	1	0	0	0	0	1	1	0	0	0	0	?	1	0
Mesochria scottiana Enderlein, 1910	0	3	0	1	2	2	2	2	1	2	0	1	1	2	2	0	1	1	2	2	0	0	?	0	0
Mesorhyphus nanus Handlirsch, 1920	0	1	0	1	2	2	2	2	0	1	1	1	0	0	0	0	0	1	0	0	0	0	?	0	0
Mycetobia pallipes Meigen, 1818	0	3	0	1	2	2	2	2	1	2	0	1	1	1	1	0	1	1	2	2	0	0	?	0	1
Olbiogaster simplex Cockerell, 1920	1	0	0	1	2	2	2	2	0	1	1	1	0	0	0	0	1	1	0	0	1	0	1	0	0
Pachyrhyphus jakovlevi Kovalev, 1986	0	1	0	0	2	2	2	2	0	1	1	1	0	0	0	0	0	1	0	0	0	0	?	0	0
Sylvicola cadaver Scudder, 1890	0	2	0	0	2	2	2	2	0	1	1	1	0	0	0	1	2	1	0	0	1	1	1	0	0
Tega caravatica Blagoderov et al., 1993	0	2	0	1	2	2	2	2	0	1	1	1	0	0	0	0	0	1	1	1	0	0	?	?	?

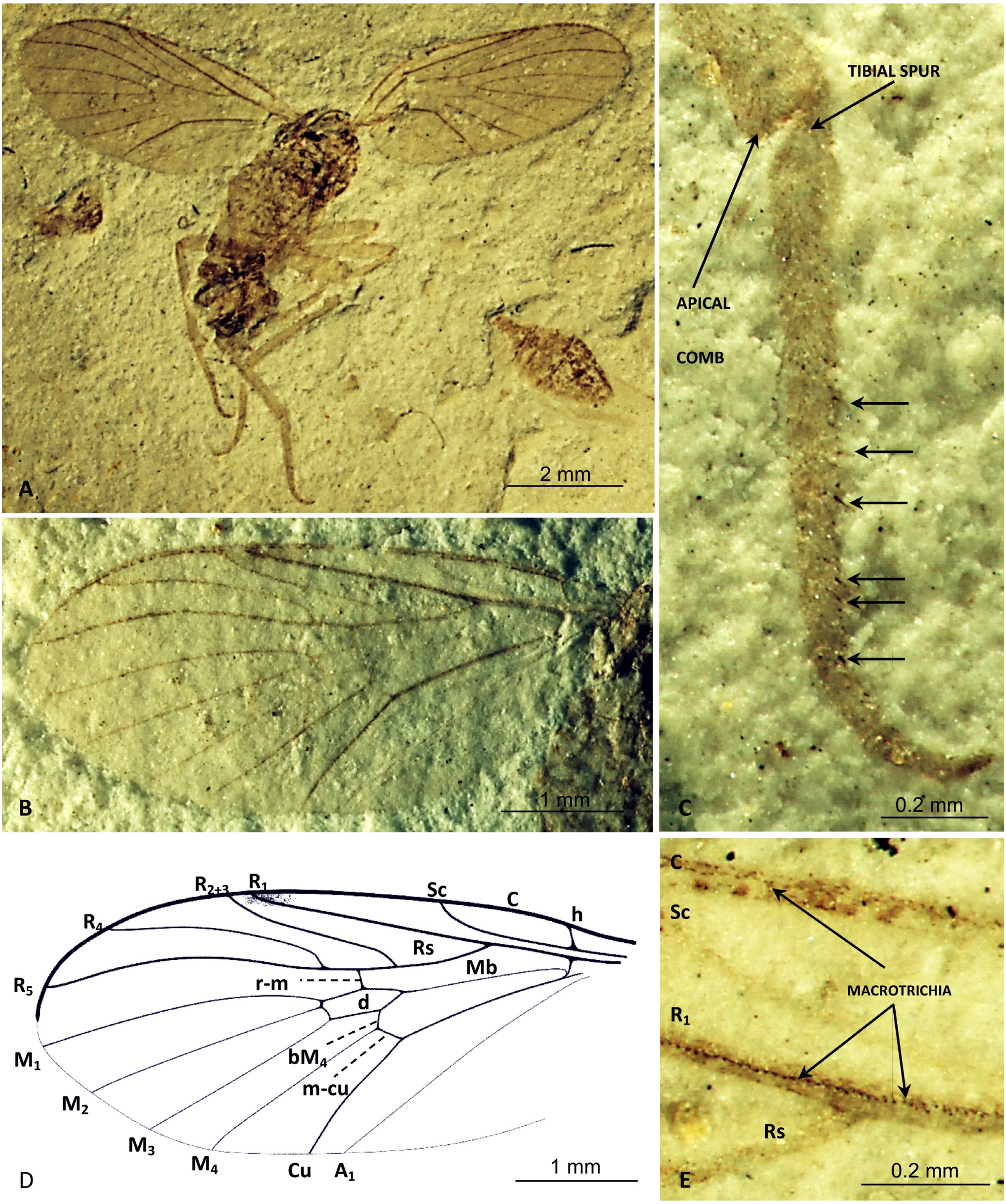

FIGURE 1. *Protorhyphus lukashevichae* **sp. nov.** CNU-DIP-NN2019001. **A**, Body, dorso-lateral view. **B**, Wing. **C**, Tarsus. **D**, Wing venation. **E**, Macrotrichia on costal and subcostal veins.

between Sc and R_1; R_{2+3} strongly waved at apex.. ***P. liaoningicus***

7. R_{2+3} elongate, 2.5x as long as Rs ...... ***P. jurassicus* sp. nov.**

\- R_{2+3} up to 2x as long as Rs..8.

8. The distance between R_1 and R_{2+3} apices 3x the distance between R_1 and Sc apices; Sc ending beyond d-cell level... ***P. neimonggolensis***

\- The distance between R_1 and R_{2+3} apices 6x the distance between R_1 and Sc apices; Sc ending distinctly before d-cell level .... ***P. simplex***

9. The length of R_{4+5} 2x the length of Rs; R_{2+3} rather short, up to 2x Rs, strongly waved; the distance between M_3 and M_4 apices narrower than the distance between M_2 and M_3 apices ....***P. sibiricus***

- The length of R_{4+5} 1.5x the length of Rs; R_{2+3} over 2x Rs, only slightly waved; the distance between M_3 and M_4 apices short, but wider than the distance between M_2 and M_3 apices .... ***P. lukashevichae*** **sp. nov.**

Protorhyphus lukashevichae **sp. nov.**
(Figs. 1A–E)

Diagnosis. Crossvein m-m meeting M_2 beyond fork of M_{1+2}; m-cu 1.5x as long as bM_4; crossvein r-m is positioned in the middle of stem R_{4+5}; vein R_{2+3} is sigmoid, convergent to R_1 terminally; Sc rather short, ending before half the length of Rs level, before r-m level, before Mb bifurcation level; Mb twice as long as d-cell; the distance between Cu and A_1 very narrow but wider than the distance between

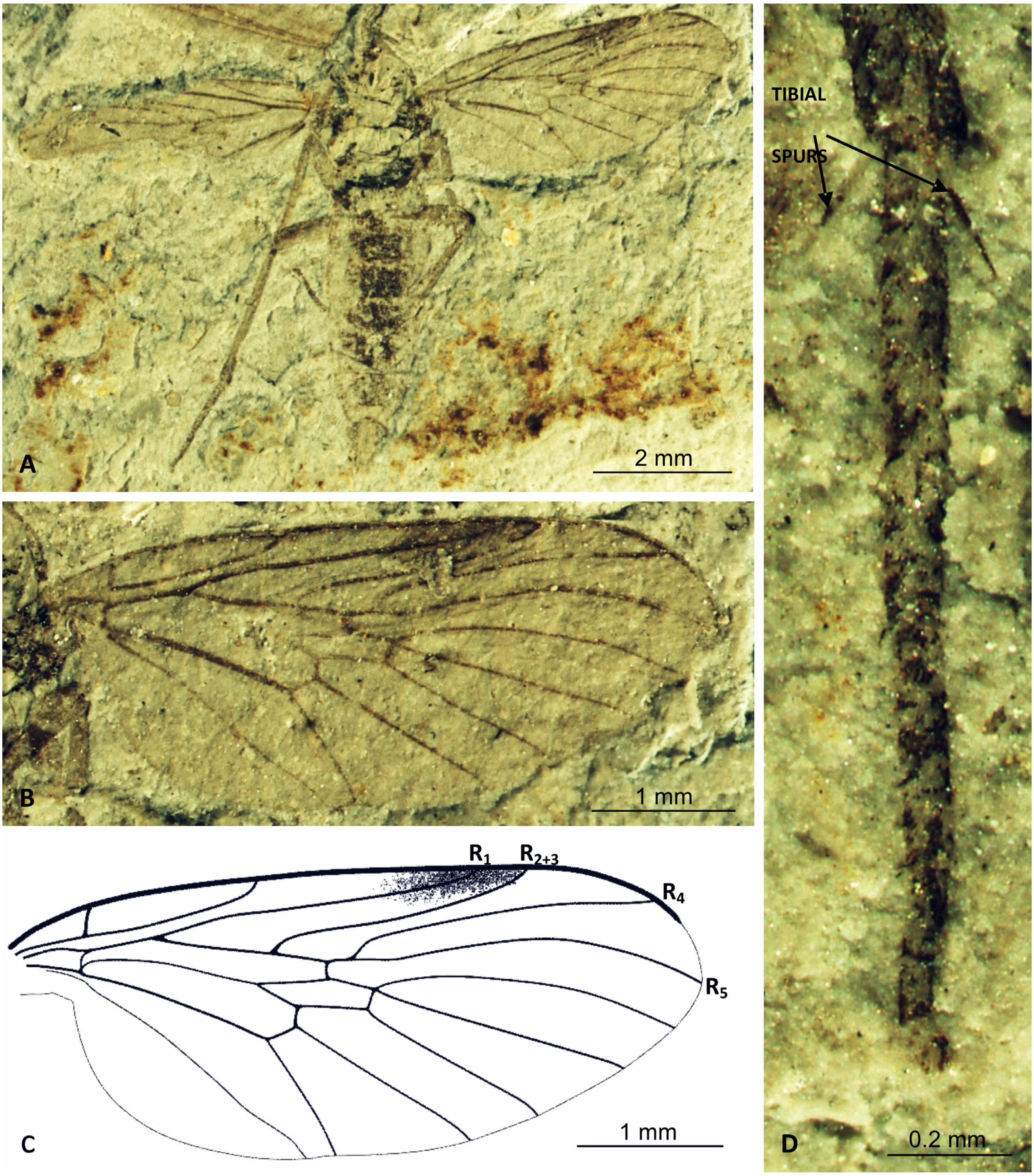

FIGURE 2. *Protorhyphus jurassicus* **sp. nov.** CNU-DIP-NN2019002. **A**, Body, ventral view. **B**, Wing. **C**, Wing venation. **D**, Wing.

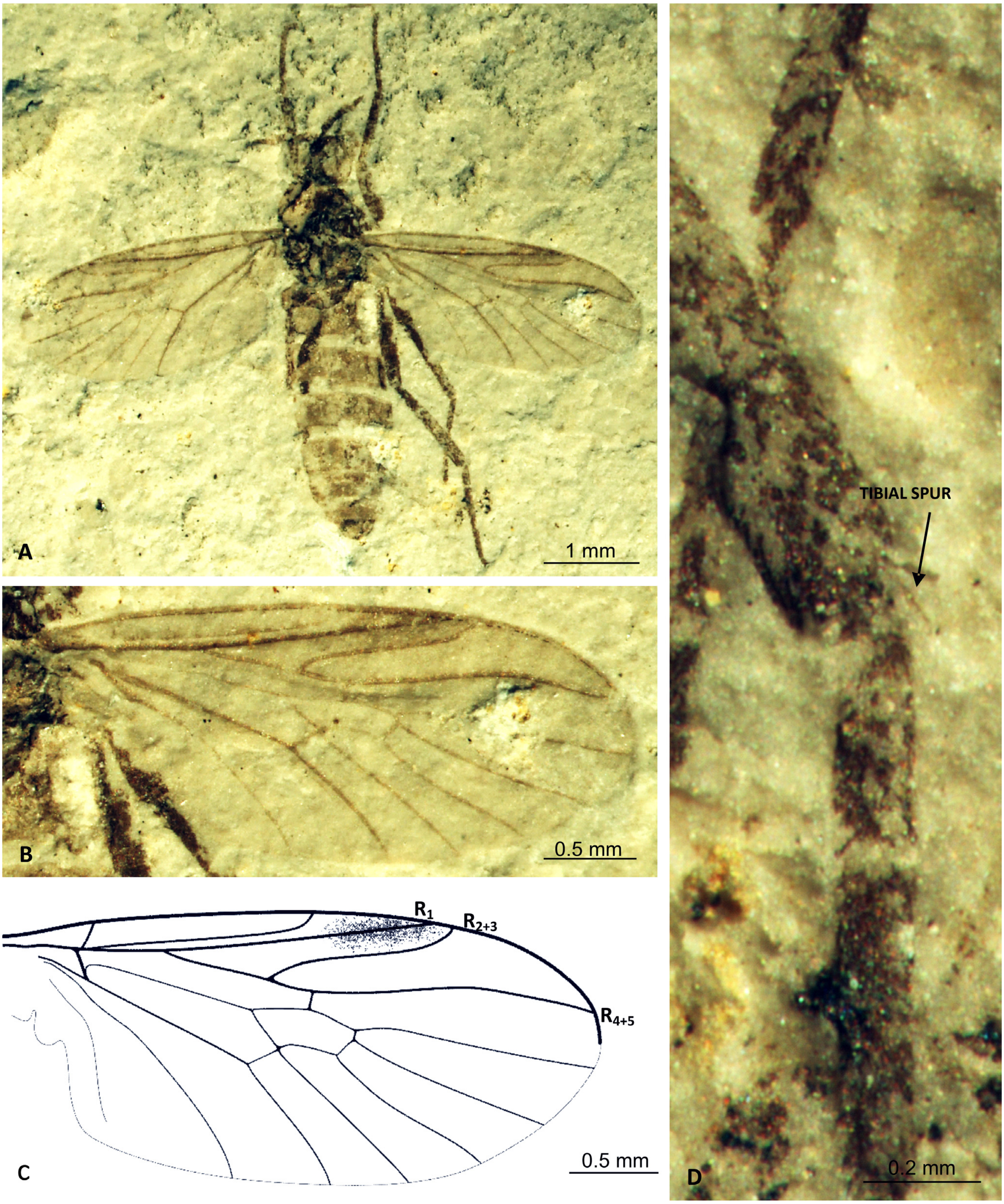

FIGURE 3. *Mesorhyphus blagoderovi* **sp. nov.** CNU-DIP-NN2019003. **A**, Body, ventral view. **B**, wing. **D**, Wing venation.

R_1 and R_{2+3} apices; R_1 shorter than 2/3 wing length. Bifurcation on R_4 and R_5 opposite bifurcation on M_1 and M_2 level. D-cell elongate, approximately 2.5x as long as wide.

Etymology. The species name is dedicated to Professor Elena Lukashevich eminent specialist on fossil and recent entomofauna.

Material examined. Holotype CNU-DIP-NN2019001 (sex unknown), Jurassic, Daohugou, Capital Normal University (CNU). Head and antennae are

TABLE 3. A list of fossil and recent genera of Anisopodoidea. Data partially based on Paleobiology Database: fossilworks; Evenhuis (2019); Kania *et al.* (2019); Lukashevich (2012); Martin (2008).

Superfamily: Anisopodoidea Knab, 1912		fossil	recent
Family: Protorhyphidae Handlirsch, 1906			
1.	*Archirhyphus* Handlirsch, 1939	+	-
2.	*Austrorhyphus* Martin, 2008	+	-
3.	*Brachyrhyphus* Blagoderov & Grimaldi *in* Blagoderov *et al.*, 2007	+	-
4.	*Protorhyphus* Handlirsch, 1906	+	-
5.	*Vymrhyphus* Blagoderov *in* Shcherbakov *et al.*, 1995	+	-
Family: Siberhyphidae Kovalev, 1985			
1.	*Siberhyphus* Kovalev *in* Kalugina & Kovalev, 1985	+	-
Family: Anisopodidae Knab, 1912			
Subfamily: Anisopodinae Knab, 1912			
1.	*Gansuplecia* Hong & Wang, 1990	+	-
2.	*Jurolaemargus* Evenhuis, 1994	+	-
3.	*Leptoplecia* Hong, 1983	+	-
4.	*Sylvicola* Harris, 1780	+	+
Subfamily: Mycetobiinae Crampton, 1924			
5.	*Mesochria* Enderlein, 1910	+	+
6.	*Mycetobia* Meigen, 1818	+	+
Subfamily: Olbiogastrinae Hennig, 1973			
7.	*Carreraia* Carrera, 1947	-	+
8.	*Cretolbia* Kania *et al.*, 2019	+	-
9.	*Lobogaster* Philippi, 1865	-	+
10.	*Megarhyphus* Kovalev, 1990	+	-
11.	*Mesorhyphus* Handlirsch, 1920	+	-
12.	*Olbiogaster* Osten Sacken, 1886	+	+
13.	*Pachyrhyphus* Kovalev, 1986	+	-
14.	*Thiras* Giebel, 1856	+	-
Subfamily: Teginae Lukashevich, 2012			
15.	*Tega* Blagoderov *et al.*, 1993	+	-

invisible on imprint. On account of its preservation it is impossible to determine the sex of the specimen.

Description. Body (Fig. 1A) approximately 4.44 mm long, pale brown with pale brown legs.

Thorax (Fig. 1A): wing approximately twice as long as wide (Fig. 1A, B, D): 4.82 mm long, 2.20 mm wide; Sc approximately in 1/3 of wing length; Rs almost straight, 1.31 mm long; before A_1 apex, is slightly arched, Rs only 1/3 longer than the stem of R_{4+5}, half the length the segment between Sc and R_1 apices; R_1 almost straight; R_{2+3} slightly waived and arched at apex, ending opposite half the length of R_4; d-cell 0.47 mm long, 0.23 mm wide, pentagonal, 3.5x as long as wide, positioned in approximately half the length of wing from its base; segment bM_4 is shorter than m-cu, m-cu is 1.5x longer than bM_4, bM_4 diverging from discal cell proximal to its middle; M_1 and M_2 widely separated; the distance between R_{2+3} and R_1 apices very short, approximately 1/7 the distance between Sc and R_1 apices; the distance between humeral vein (h) and Sc apex shorter than the distance between Sc and R_1 apices; the distance between R_5 and M_1 apices approximately as long as the distance between M_1 and M_2 apices, M_2 and M_3 apices, M_3 and M_4 apices; the distance between M_4 and Cu apices wide, comparatively as long as the distance between R_4 and R_5 apices. Numerous and dense macrotrichia arranged in one row are visible on C and R_1 vein (Fig. 1E). A_1 well developed, almost straight. Mactrotrichia are visible along all veins of wing.

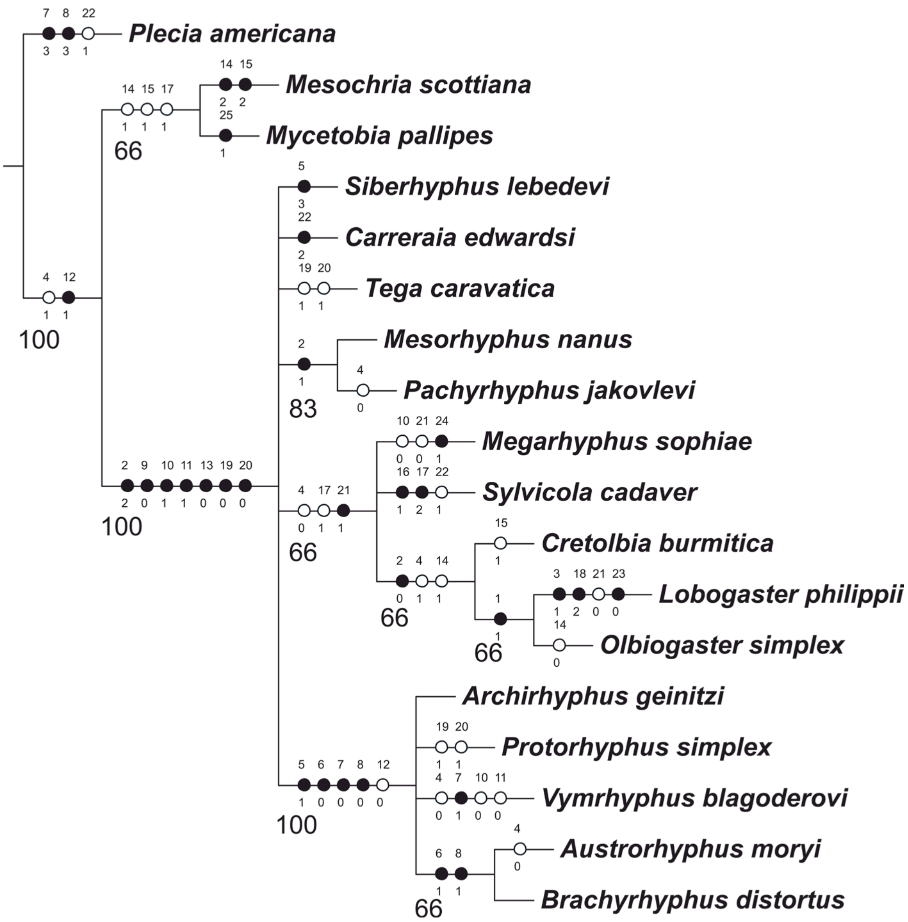

FIGURE 4. Tree of relationship of the genera within Anisopodoidea, fast optimization. Filled circles indicate synapomorphies or autapomorphies; open circles indicate plesiomorphies or homoplasies. Only type species of undebatable taxa of Anisopodoidea are mentioned. Classification of Anisopodoidea after Krzemiński & Krzemińska (2003).

Legs (Figs 1A, C): femur of hind legs longer than tibia, tarsus of hind legs with rare, thick setae, tibial comb on hind legs well developed (Fig. 1C). Tarsus of hind leg longer than tibia of hind leg (Fig. 1A).

Comparison. In contrast to the Middle Jurassic *P. neimonggolensis* Zhang, 2007 and *P. liaoningicus* Zhang, 2007 where r-m is closer to R_4 than R_{2+3}, this structure is in the middle in the new species. Vein Sc is more elongate in the two species *P. neimonggolensis* and *P. liaoningicus*, viz., in *P. neimonggolensis*, it is ending opposite or even beyond Mb bifurcation, in *P. liaoningicus* it is opposite 1/7 of Mb from wing base, while in new species it is in 1/4 of Mb from wing base. In *P. neimonggolensis* R_{2+3} is straight or nearly so and subparallel terminally to R_1, while in new species this vein is slightly waived and arched at apex, it is sigmoid and convergent terminally to R_1. Moreover, in *P. neimonggolensis* m-cu is elongate, four times as long as bM_4, in new species it is 1.5x as long as bM_4. In contrast to *P. liaoningicus* Zhang, 2007 where m-cu is 2x the length of bM_4, in new species it is 1.5x. *P. sibiricus* Kovalev, 1985 is characterized by R_1 slightly longer than 2/3 of wing length, r-m is closer to R_4 than R_{2+3}, in *P. lukashevichae* **sp. nov.** R_1 is shorter than 2/3 the wing length, r-m is in the middle between R_4 than R_{2+3}. In contrast to *P. jurassicus* **sp. nov.** in *P. lukashevichae* **sp. nov.** crossvein m-m meeting M_2 beyond fork of M_{1+2}, crossvein r-m is positioned in the middle of stem R_{4+5}, vein R_{2+3} is sigmoid, convergent to R_1 terminally, Sc is rather short, ending before half the length of Rs level, R_1 is shorter than 2/3 wing length. Bifurcation on R_4 and R_5 is opposite bifurcation on M_1 and M_2 level, d-cell is elongate, approximately 2.5x as long as wide, in *P. jurassicus* **sp. nov.** crossvein r-m is closer to R_4 than R_{2+3}, R_{2+3} is only slightly arched, subparallel to R_1 terminally, and d-cell is elongate, approximately 3x as long as wide.

Moreover, *P. lukashevichae* **sp. nov.** differs mainly by wing venation from other, younger and older known from Upper and Lower Jurassic, representatives, e.g., in contrast to *P. simplex* (Geinitz, 1888), in new species the distance between R_{2+3} apices and R_4 is wider than the distance between R_4 and R_5 apices, while in *P. simplex* the distance between R_4 and R_5 apices is as wide as between R_{2+3} and R_4 apices. Moreover, the distance between R_1 and R_{2+3} apices is about 1/7 the distance between Sc and R_1

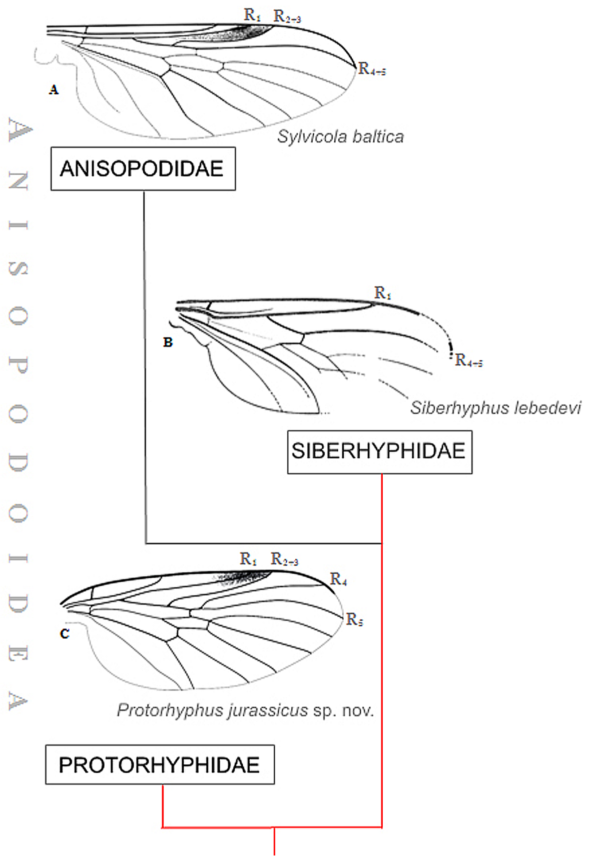

FIGURE 5. Phylogenetic relations between families of Anisopodoidea according to Krzemiński & Krzemińska (2003) (modified). Wing venation of *Sylvicola baltica* after Wojtoń *et al.* (2019). Wing venation of *Siberhyphus lebedevi* after Kalugina & Kovalev (1985).

apices, in *P. simplex* this distance is approximately 1/4. M_1 and M_2 diverging from discal cell separately, but from one point in *P. simplex*, in new species are widely separated.

Protorhyphus jurassicus **sp. nov.**
(Figs. 2A–D)

Diagnosis. Crossvein r-m closer to R_4 than R_{2+3}; pterostigma present and reach R_{2+3}; R_{2+3} slightly arched, subparallel to R_1 terminally; m-cu only slightly longer than bM_4. The distance between M_2 and M_3 apices and the distance between M_4 and Cu apices longer than the distance between M_3 and M_4 apices; R_1 approximately as long as 2/3 of wing length. Bifurcation on R_4 and R_5 before bifurcation on M_1 and M_2 level. D-cell elongate, approximately 3x as long as wide.

Etymology. The species name is derived from the Jurassic period.

Material examined. Holotype CNU-DIP-NN2019002 (female), Jurassic, Daohugou, Capital Normal University (CNU). Head and antennae of specimen are not well visible. On account of its preservation it is impossible to determinate the sex of the specimen.

Description. Body (Fig. 2A) 6.27 mm long, pale brown with pale brown legs. Antenna.(Fig. 2A) with short flagellomeres, more or less elongate.

Thorax (Fig. 2A): wing one and half as long as wide; 4.78 mm long, 1.99 mm wide; Sc ending before Rs bifurcation and opposite A_1 apex (Fig. 2B, C), Sc rather short, slightly arched, R_{2+3} slightly arched at apex. Rs 1.07 mm long, shorter than half the length of R_{2+3}. D-cell pentagonal, 3x longer than wide. The distance between R_4 and R_5 apices shorter than the distance between R_{2+3} and R_4 apices. The distance between R_5 and M_1 apices approximately equal the distance between M_1 and M_2 apices. The distance between Cu and A_1 apices very narrow, approximately 0.25 the distance between M_4 and Cu apices. A_1 well developed.

Legs (Fig. 2A, D) with elongate tibiae longer than femora; hind tibia with two equal, massive tibial spurs, large and very distinct; tarsus of hind legs comparatively short, shorter than tibia of hind legs (Fig. 2D).

Abdomen (Fig. 2A): female terminalia rather small cerci not very elongate.

Comparison. In the Middle Jurassic *P. neimonggolensis* Zhang, 2007 and *P. liaoningicus* Zhang, 2007 d-cell is approximately 2x as long as wide, while in new species it is approximately 3x as long as wide. In *P. neimonggolensis* R_{2+3} is straight or nearly so and subparallel to R_1 terminally, while in new species this vein is slightly waived and arched at apex, ~~is~~ sigmoid and convergent to R_1 terminally. Moreover, in *P. neimonggolensis* m-cu is elongate, four times as long as bM_4, in *P. liaoningicus* Zhang, 2007 m-cu is twice the length of bM_4, while it is almost as long as bM_4 in new species. *P. sibiricus* Kovalev, 1985 is characterized by R_1 slightly longer than 2/3 of wing length, in *P. jurassicus* **sp. nov.** it is approximately as long as 2/3 the length of wing. In contrast to *P. lukashevichae* **sp. nov.**, where crossvein m-m meeting M_2 beyond fork of M_{1+2}, in *P. jurassicus* **sp. nov.** crossvein r-m is positioned in the middle of stem R_{4+5}, vein R_{2+3} is sigmoid, convergent to R_1 terminally, Sc is rather short, ending before half the length of Rs level, R_1 shorter than 2/3 wing length. Bifurcation on R_4 and R_5 is opposite bifurcation on M_1 and M_2 level and d-cell is elongate, approximately 2.5x as long as wide, in *P. jurassicus* **sp. nov.** crossvein r-m is closer to R_4 than R_{2+3}, R_{2+3} is only slightly arched, subparallel to R_1 terminally, d-cell is elongate, approximately 3x as long as wide.

Moreover, *P. jurassicus* **sp. nov.** differs mainly by wing venation from other, younger and older known from Upper and Lower Jurassic representatives, e.g., in contrast to *P. simplex* (Geinitz, 1888), in new species the

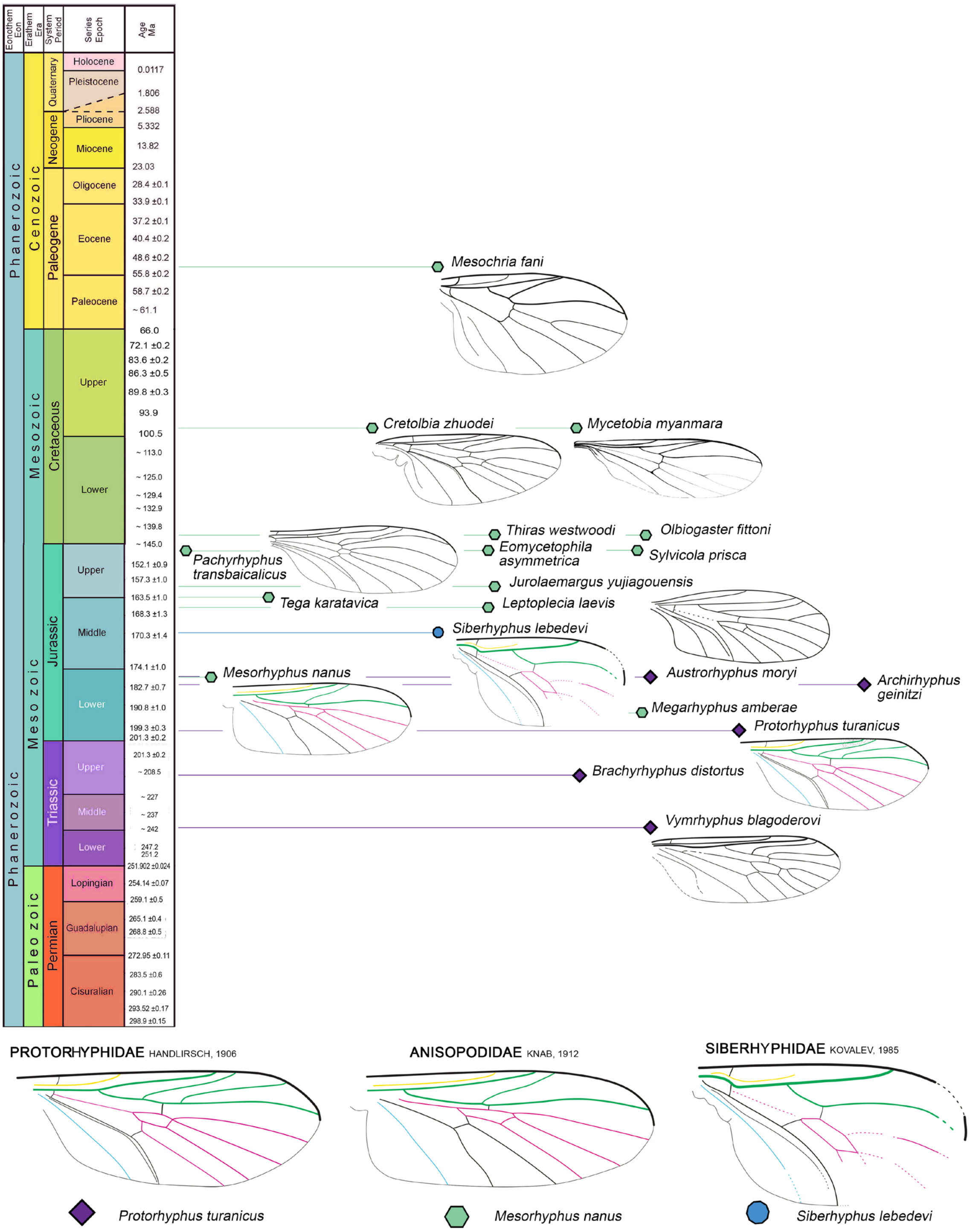

FIGURE 6. Chronostratigraphic distribution of the oldest representatives of genera of Anisopodoidea. Wing venation redrawing after Blagoderov *et al.* (1993); Handlirsch (1920); Kania *et al.* (2019); Kovalev in Kalugina & Kovalev (1985); Krzemiński & Krzemińska (2003); Martin (2008); Rohdendorf (1964); Szadziewski *et al.* (2016). Stratigraphic chart according to International Stratigraphic Chart, International Commission on Stratigraphy.

distance between R_{2+3} apices and R_4 is wider than the distance between R_4 and R_5 apices while in *P. simplex* the distance between R_4 and R_5 apices is as wide as the distance between R_{2+3} and R_4 apices.

Family Anisopodidae Knab, 1912

Subfamily Olbiogastrinae Hennig, 1973

Genus *Mesorhyphus* Handlirsch, 1920

Features like strong Sc, about half wing length, terminating

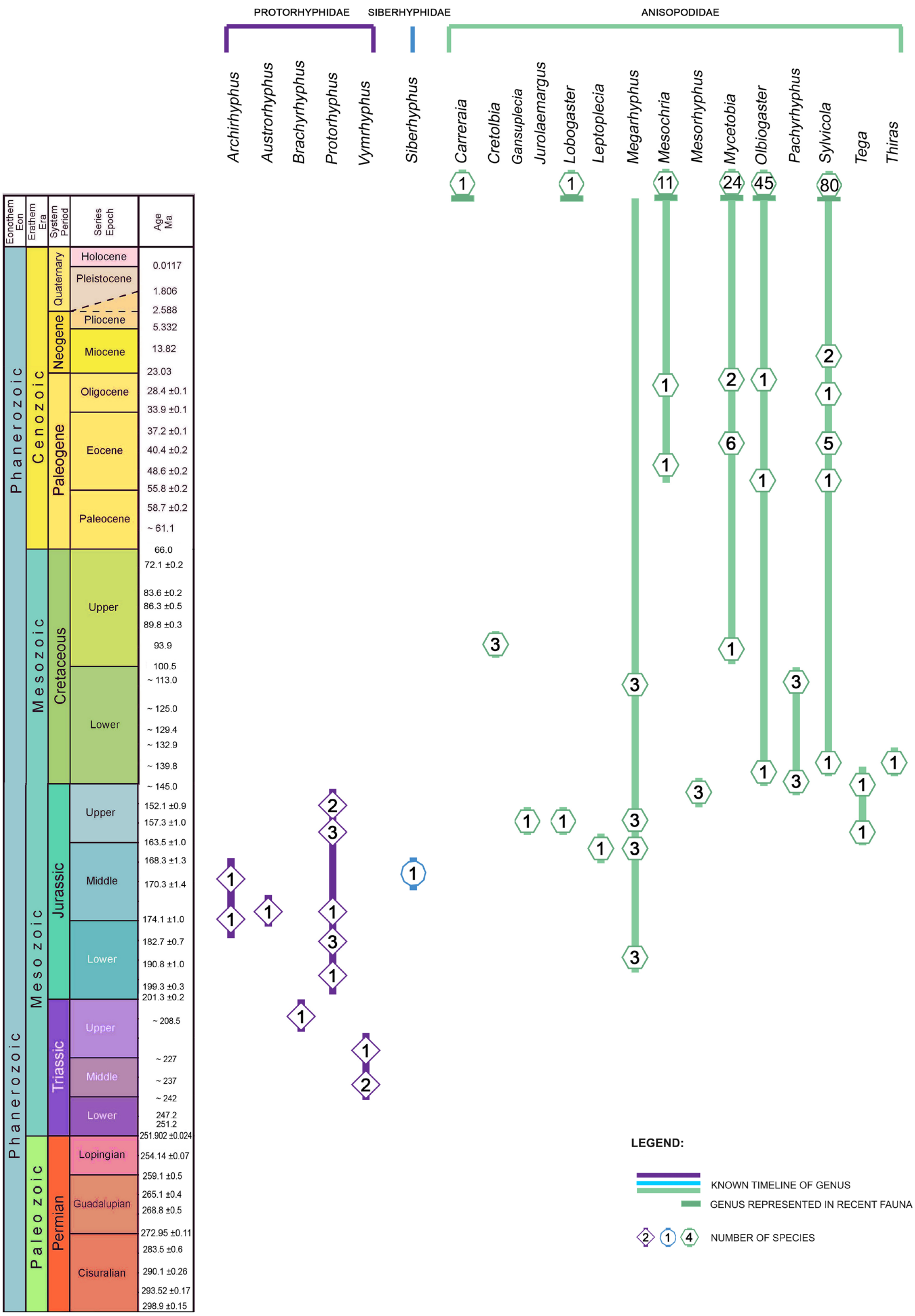

FIGURE 7. Chronostratigraphic distribution of Anisopodoidea. In white figures the number of species is given. Interrupted lines mark extinct genera. Stratigraphic chart according to International Stratigraphic Chart, International Commission on Stratigraphy.

distal to first bifurcation to Rs. Moreover, veins R_{2+3} and R_{4+5} terminating before wing apex, branches of media are visibly weaker than branches of radius, stem of M is also weaker than M_1 and M_2. Maximum width of wing area is of Cu-A_1 (Lukashevich, 2012) allow us to determine the new species described herein in the genus *Mesorhyphus*. The genus currently includes 7 known fossil species (Table 1).

***Mesorhyphus blagoderovi* sp. nov.**
(Figs. 3A–D)

Diagnosis. Crossvein bM4 very short, almost atrophied; Cu slightly curved to the base of wing; Sc apex opposite r-m level.

Etymology. The species name is dedicated to Dr. Vladimir Blagoderov, eminent specialist on fossil and recent entomofauna.

Material examined. Holotype CNU-DIP-NN2019003 (sex unknown), Jurassic, Daohugou, Capital Normal University (CNU). Antenna and legs are not well preserved. On account of its preservation it is impossible to determine the sex of the specimen.

Description. Body (Figs. 3A-C) 4.34 mm long. Head, thorax, abdomen and legs brown. Antenna (Fig. 3A), flagellomeres wider than long, last, terminal flagellomere longer than wide, tapered at apex.

Thorax: wing (Fig. 3A): 3.27 mm long, 1.65 mm wide; pale brown pterostigma beyond half the length of wing, surrounding apical part of R_1 to approximately 1/3 length of R_1 from edge of wing and extending to 2/3 of R_{2+3} from edge of wing, not distinctly separated from other part of wing. Sc elongate, ending just beyond half of wing, beyond Rs bifurcation, before fork on M_1 and M_2 and opposite Cu apex; distance between R_1 and R_{2+3} apices comparatively short, subequal to m-m, only 0.25 distance between Sc and R_1 apices. Rs separate Rb in proximal 1/3 of wing length from wing base; Rs stem 1.5 of R_{2+3} and as long as d-cell. D-cell hexagonal, 0.29 mm long, 2x longer than wide, positioned in half of wing, m-m straight. Segment bM_4 much shorter than m-cu, diverging from d-cell in proximal 2/5. Crossvein r-m as long as m-m, r-m positioned approximately at mispoint of d-cell, approximately at right angle to d-cell. A_1 well developed. Legs (Figs. 3A, D): femora and tibiae elongate, tarsus comparatively elongate, two rather tiny tibial spurs on hind legs.

Comparison. The new species can be distinguished from the congeners by the very short, almost all atrophied crossvein bM4, vein Sc ending opposite level of r-m, and Cu slightly curved toward base of wing.

Phylogenetic analysis

The matrix is based mainly on characters of wing venation, the most important for distinguishing taxa, allowing comparison of fossil and extant data, but also including characters of antenna and copulatory apparatus. The matrix of character states is given in Table 2.

Characters states are defined as follows:

1. Length of antenna
   0. – antenna as long as head and thorax combined or shorter
   1. – antenna longer than head and thorax combined

2. Shape of flagellomeres, excluding the last one
   0. – very elongate, up to twice as long as wide
   1. – elongate, approximately 1.5x as long as wide
   2. – rather short, only a little longer than wide
   3. – very short, thick, usually as long as wide or little longer than wide

3. Pilosity on eyes
   0. – not elongate or absent
   1. – very elongate (longer than diameter of single facet)

4. Length of Sc
   0. – Sc≥ 0.5x wing length
   1. – Sc<0.5x wing length

5. Number of radial branches
   0. – 5 (R_1; R_2; R_3; R_4; R_5)
   1. – 4 (R_1; R_{2+3}; R_4; R_5)
   2. – 3 (R_1; R_{2+3}; R_{4+5})
   3. – 2 (R_1; R_{4+5})

6. Vein R_4
   0. – well-developed
   1. – shortened
   2. – fused into R_{4+5}

7. Position of cross-vein r-m
   0. – between R_{4+5} stem and upper margin of d-cell if R_4 and R_5 separate
   1. – between R_5 and upper margin of d-cell if R_4 and R_5 separate
   2. – between R_{4+5} and upper margin of d-cell if R_4 and R_5 fused in R_{4+5}
   3 – between Mb and common stem of R_{4+5} and R_{2+3}

8. Veins R_4 and R_5
   0. – divergent separately, both are elongate (approximately half wing length)
   1. – divergent separately, but both are short (R_5 approximately 0.25 wing length; R_4 shorter than 0.2 wing length)
   2. – fused into R_{4+5}, elongate (approximately half wing length)
   3. – fused into R_{4+5}, short (shorter than half wing length)

9. Number of medial branches
   0. – 4 (M_1; M_2; M_3; M_4)
   1. – 3 (M_1; M_2; M_{3+4})

10. Branches of M_1 and M_2
   0. – d-cell with petiole
   1. – leaving d-cell independently
   2. – with elongate common stem

11. Length of medial veins M_1 and M_2
   0. – shorter or equal half of wing length
   1. – longer than half of wing length

12. Shape of vein Cu
0. – arched posteriorly
1. – distinctly sinuous

13. D-cell
0. – closed
1. – opened

14. Apices of R_1 and R_2 or R_{2+3}
0. – separate
1. – approximate
2. – connected

15. Stem of M
0. – well-developed or slightly desclerotized
1. – distinctly thin and desclerotized from the base of wing
2. – atrophied

16. Shape of R_2 if R_{2+3} divided into R_2 and R_3 or shape R_{2+3} if R_2 and R_3 fused
0. – almost straight or slightly arched
1. – strongly curved in the distal third

17. Position of R_2 if R_{2+3} divided into R_2 and R_3 or shape R_{2+3} if R_2 and R_3 fused
0. – parallel
1. – R_{2+3} gradually approaching C
2. – subparallel, differentiated

18. Shape of R_{4+5}
0. – divided into R_4 and R_5 and R_4 only slightly waved
1. – only slightly sinuous
2. – distinctly arched

19. Size of d-cell
0. – d-cell not very small (longer than 0.1 wing length)
1. – d-cell very small (shorter than 0.06 wing length)
2. – open distally

20. Position of d-cell
0. – located from the middle to distal wing half
1. – located in basal wing half
2. – not presented

21. Alula
0. – absent
1. – strongly differentiated

22. Coloration of wing
0. – wing without distinct coloration
1. – distinct spots or all dark wing
2. – wing apex dark colored

23. Number of tibial spurs on hind legs
0. – 1
1. – 2

24. Very long and dense setae on hind tibia
0. – absent
1. – present

25. Size of male genitalia
0.– rather small
1. – large, reaching even 1/3 of length of the body

The phylogenetic analysis yielded five (equal weighting) and five (implied weighting) most parsimonious trees, respectively. The Majority Rule consensus tree was 57 steps long, with Consistency Index (CI) = 70 and Retention Index (RI) = 69, the tree present (Fig. 4) is the Fast Optimization (ACCTRAN) tree.

Analysis revealed the Anisopodoidea as a monophyletic unit, supported by a single synapomorphy [12(1)] and a homoplastic feature [4(1)] shared with the *Cretolbia*+[*Lobogaster*+*Olbiogaster*] clade (part of Olbiogastrinae). Inside the Anisopodoidea, the clade *Mesochria*+*Mycetobia* is sister to the remaining members of the superfamily, but supported only by homoplastic character states 14(1), 15(1), and 17(1). The monophyly of the remaining Anisopodoidea is strongly supported by seven non-homoplastic shared character states, however internal relationships are not fully resolved, with a polytomy presented (Fig. 4). A few clades are revealed *Mesorhyphus*+*Pachyrhyphus* and (*Megarhyphus*+*Sylvicola*+(*Cretolbia*+(*Lobogaster*+*Olbiogaster*))), but these are not strongly supported. Well supported, by four shared characters 5(1), 6(0), 7(0), and 8(0), is a clade containing members of the Protorhyphidae. This group seems to be monophyletic but its internal relationships are not fully resolved (Fig. 4).

Discussion

The sister group of Diptera (+ Siphonaptera in some analyses) is Mecoptera which comprise representatives with two well developed pairs of wings (Grimaldi & Engel, 2005). In the venation of the fore wing of Mecopterida (this is the stem group of the clade (Mecoptera & Diptera & Siphonaptera) like *Oochorista gunderseni* Martynov, 1932 three branches of the subcostal vein, seven branches of the radial vein, six branches of the media, two cubital veins and three anal veins are present. Whereas in *Petromantis sarbalensis* Martynova, 1961 the radial branches are reduced to five and subcostal to three.

Based on fossil and recent data, it is possible to conclude that the process of evolution of Anisopodoidea is well readable, especially in morphology of wing. The comparison of morphological features of recent representatives of Anisopodoidea allow us to infer evolutionary changes since the Triassic. The oldest group within the superfamily Anisopodoidea is the family Protorhyphidae known since Lower/Middle Triassic to terminal Jurassic. The extinct family Protorhyphidae seems to be a monophyletic unit, according to the results received (Fig. 4), well supported by morphological character states 5(1), 6(0), 7(0), 8(0), 12(0). The rapid radiation of the representatives of Protorhyphidae is recorded in the Jurassic period; at the end of this period this group of Anisopodoidea became extinct. We have no information about Protorhyphidae from the younger fossil record (Fig. 7). In this small group of insects with some reduction of branches of radial veins well-visible, in comparison to the oldest fly *Grauvogelia* Krzemiński *et al*. in Krzemiński & Krzemińska, 2003. Taxa of Protorhyphidae are characterized by the occurrence of four branches of veins R_1, R_{2+3}, R_4 and R_5, four branches of the medial vein, but only a single branch of Sc and cubital vein (Cu). These features are also visible in the two above described Jurassic species. But, in Anisopodidae from Jurassic sediments, a reduction of wing venation is noted. In Anisopodidae only three branches of the radial vein are developed: R_1, R_{2+3}, and R_{4+5}. As Blagoderov & Grimaldi (2007) suggested, the genus *Brachyrhyphus* Blagoderov & Grimaldi, 2007 probably represents an intermediate condition between Protorhyphidae and Anisopodidae. This unique Triassic genus has a very short vein R_4, while all other Protorhyphidae have an elongate vein R_4. Anisopodidae have vein R_{4+5}. A distal shift and reduction of R_4 is common among Bibionomorpha and Brachycera, and probably is a result of costalization (Blagoderov *et al*., 2007).

Another point to discuss is status of Siberhyphidae, which here is supported by a single apomorphy [5(3)]. In Siberhyphidae only two branches of the radius are present. Siberhyphidae presents a highly apomorphic wing venation with advanced reduction of radial branches to only R_1 and R_{4+5} (Figs. 5, 6).

Anisopodidae appears in fossil record in the Jurassic. They are represented by 15 known genera, of which only six are present in the modern fauna (Fig. 7). The most speciose Recent genus is *Sylvicola* (over 80 species), represented in the fossil record by 11 species, with the oldest, *Sylvicola prisca* Westwood in Brodie, 1845, known from the Cretaceous. In the genus *Sylvicola* (Anisopodinae) many apomorphic features are clearly visible in the wing venation: the cubital vein is wavy, and macrotrichia occur on the costa and radial branches, sometimes on medial branches like the Cretaceous genus *Cretolbia* (Olbiogastrinae). In *Sylvicola,* the alula is present as in *Olbiogaster* (Hancock 2017). The extant genera *Olbiogaster* and *Lobogaster* are closely related to the extinct genus *Cretolbia* (all placed in Olbiogastrinae). The recently described genus *Cretolbia* from the mid-Cretaceous, is close to the modern genera *Lobogaster* and *Olbiogaster*. The clade *Mesorhyphus*+*Pachyrhypus* also placed in Olbiogastrinae is sister to the remaining genera of this subfamily, i.e. the clade (*Megarhyphus*+*Sylvicola*+(*Cretolbia*+(*Lobogaster*+*Olbiogaster*))), supported by a single synapomorphy [21(1)] [= presence of alula], which is present in *Sylvicola*, *Cretolbia* and *Olbiogaster*, but (probably secondarily) lost in *Megarhyphus* and *Lobogaster* (Fig. 4). In the Cretaceous *Cretolbia,* medio-basal vein is only slightly sclerotized, and M_4 is weaker than other veins. The genus *Lobogaster*, closely related to *Olbiogaster* and *Cretolbia*, is represented only in the Recent fauna. The genus *Carreraia*, also present only in the Recent fauna, is placed in the Olbiogastrinae, and seems to be related to the other genera of the subfamily, however it is not strongly supported by results of the analysis performed here.

Interestingly, the genera placed in the traditional subfamily Mycetobiinae are revealed as a separate clade, sister to Protorhyphidae and Anisopodidae, which puts some doubts about their placement in the Anisopodoidea as a separate family (Amorim & Tozzoni, 1994) or as a subfamily of Anisopodidae (Amorim *et al*., 2016). *Mesochria* and *Mycetobia* are extant genera with a poorly understood fossil record. The oldest *Mycetobia* is recorded in Cretaceous (Kania *et al.*, 2019), but are not numerous in fossil record, known mainly from the Eocene. The oldest species of *Mesochria* is from the Eocene (Szadziewski *et al*., 2016). In *Mycetobia,* three branches of the media are present together with an only slightly sclerotized Mb; in *Mesochria* only two branches of media occur, and Mb is atrophied. The morphology of the wing venation may indicate that these taxa represent the next stage of the venation evolution of the Anisopodoidea, viz., reduction of medial veins, open d-cell and atrophy of medio-basal vein in *Mesochria*, the clade *Mesochria*+*Mycetobia* is sister to the remaining members of the superfamily, supported by homoplastic character states 14(1), 15(1) and 17(1). A strongly supported clade uniting the genera *Mesochria* and *Mycetobia* (traditionally placed in Anisopodidae) as closest relatives of the outgroup *Plecia* (Bibionidae) and sister to the remaining Anisopodoidea, could support the opinion of Krzemiński (pers. comm.) that these two genera should be classified as separate families, and close to the bibionids.

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Oświadczenia współautorów

5. OŚWIADCZENIA WSPÓŁAUTORÓW

Rzeszów, dnia 04.04.2019R.

Imię i nazwisko/Name and surname MGR MACIEJ WOJTOŃ

Jednostka/Department UNIWERSYTET RZESZOWSKI/ UNIVERSITY OF RZESZÓW

Promotor/ Promoter DR HAB. IWONA KANIA PROF. UR

Promotor pomocniczy/ Auxiliary promoter DR AGNIESZKA SOSZYŃSKA-MAJ

OŚWIADCZENIE/DECLARATION

W związku z przygotowywaniem przeze mnie rozprawy doktorskiej w formie spójnego tematycznie zbioru artykułów, na co zezwala Ustawa **o stopniach naukowych i tytule naukowym oraz o stopniach i tytule w zakresie sztuki** z dnia 14 marca 2003, art. 13.1 (Dz. U. Nr 65, poz. 595 z późn. zm.) oraz przyjęta na mocy uchwały Rady Wydziału Biologiczno-Rolniczego z dnia 10.07.2014 rekomendacja w tej sprawie, będąca uszczegółowieniem pkt. 21 Regulaminu Postępowania w Przewodach Doktorskich na Wydziale Biologiczno-Rolniczym UR przyjętego na posiedzeniu Rady Wydziału w dniu 24.01.2013, oświadczam niniejszym, że wkład mojej pracy naukowej, a tym samym pracy pozostałych współautorów w opublikowaniu poniższych artykułów, które zamierzam przedstawić jako własną dysertację doktorską jest następujący:

In connection with the preparation of my doctoral dissertation in the form of a coherent thematic collection of articles,

in pursuant of the Act of Academic Degrees and Academic Titles as well as Degrees and Titles in the field of Arts of March 14, 2003, art. 13.1 (Journal of Laws No. 65, item 595, (with subsequent amendments) and based on the resolution of the Council of the Faculty of Biology and Agriculture of 10/07/2014, including recommendations concerning this matter, with more details provided in paragraph 21 of the Rules of Conduct for Ph.D Procedures adopted by the Faculty Board of the Faculty of Biology and Agriculture on January 24, 2013, I hereby declare that I intend to present as my doctoral dissertation the contribution of my scientific work, as well as the work of other co-authors contained in the publication of the following articles:

[publikacja nr 1/publication no. 1]

1. **Wojtoń M.**, Kania I., Kopeć K. 2018. *Sylvicola* Harris, 1780 (Diptera: Anisopodidae) in the Eocene resins. *Annales Zoologici.* 68(4): 849 – 866. doi: 10.3161/00034541ANZ2018.68.4.009

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2. Katarzyna Kopeć ....

[publikacja nr 2/publication no. 2]

1. **Wojtoń M.**, Kania I., Krzemiński W., 2018. Review of *Mycetobia* Meigen, 1818 (Diptera, Anisopodoidea) in the Eocene ambers. *Zootaxa.* 4544 (1): 001 – 040. https://doi.org/10.11646/zootaxa.4544.1.1

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2. Wiesław Krzemiński ......W. Krz......

[publikacja nr 3/publication no. 3]

1. Kania I., **Wojtoń M.**, Lukashevich E., Stanek-Tarkowska J., Wang, B., Krzemiński W. 2019. Anisopodidae (Insecta: Diptera) from Upper Cretaceous Amber of Northern Myanmar, *Cretaceous Research*. 94: 190 – 206. https://doi.org/10.1016/j.cretres.2018.10.013

- koncepcja badań/idea of research: 55%
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5. Wiesław Krzemiński ....

[publikacja nr 4/publication no. 4]

1. Kania I., **Wojtoń M.**, Krzemiński. W. 2019. The oldest *Mycetobia* Meigen, 1818 (Diptera, Anisopodoidea) from Upper Cretaceous amber of northern Myanmar. *Cretaceous Research*. 95: 302 – 309. https://doi.org/10.1016/j.cretres.2018.11.014

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2. Wiesław Krzemiński ....

[publikacja nr 5/publication no. 5]

1. Wojtoń M., Kania I., Krzemiński W., Ren D. 2019. Phylogenetic relationships within the superfamily Anisopodoidea (Diptera: Nematocera), with description of new Jurassic species. Polaeoentomology. [in press]

- koncepcja badań/idea of research: 90%
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2. Wiesław Krzemiński ....
3. Ren Dong ....

INNE OSIĄGNIĘCIA

6. INNE OSIĄGNIĘCIA

6.1. WYKAZ POZOSTAŁYCH PUBLIKACJI NAUKOWYCH

KANIA I., WOJTOŃ M., KOPEĆ K., OWSIAK A., JORDAN W. 2016. *Helius anetae* sp. nov. (Limoniidae, Diptera), a new representative of the genus from Eocene Baltic amber. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 281/1, 101–109.

KRZEMIŃSKI W., KANIA I,. WOJTOŃ M. 2018. A new Eocene *Dicranomyia* Stephens 1829 (Diptera: Limoniidae) from Baltic amber. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 107: 271–277.

6.2.WYKAZ PUBLIKACJI POPULARNO-NAUKOWYCH

KANIA I., JORDAN W., KOPEĆ K., KRZEMIŃSKI W., WOJTOŃ M. 2016. Data on the genus *Helius* Lepeletier et Serville, 1828 (Diptera, Limoniidae). *Bursztynisko* 39: 21–25.

KANIA I., WOJTOŃ M., KOPEĆ K., KRZEMIŃSKI W., JORDAN W. 2016. Data on the genus *Dicranomyia* Stephens, 1829 (Diptera: Limoniidae) in the Eocene. *Bursztynisko* 39: 25–27.

6.3 GRANTY NAUKOWE

2017–2020: grant NCN pt. „Ewolucja muchówek (Diptera, Nematocera) na tle zmian w środowisku przyrodniczym mezozoiku oraz ich znaczenie dla poznania ewolucji całego rzędu" (wykonawca; kierownik grantu: prof. dr hab. Wiesław Krzemiński PAN, Kraków).

2018: projekt badawczy "Rodzaj *Sylvicola* Harris, 1780 (Diptera, Nematocera) w eoceńskim bursztynie bałtyckim" finansowany ze środków przyznanych na naukę Wydziałowi Biologiczno-Rolniczemu Uniwersytetu Rzeszowskiego na działalność służącą rozwojowi młodych naukowców oraz uczestników studiów doktoranckich w 2018 roku.

2017: projekt badawczy "Rodzaj *Mycetobia* Meigen, 1818 w żywicach mezozoiku i kenozoiku" finansowany ze środków przyznanych na naukę Wydziałowi Biologiczno-Rolniczemu Uniwersytetu Rzeszowskiego na działalność służącą rozwojowi młodych naukowców oraz uczestników studiów doktoranckich w 2017 roku.

2016: projekt badawczy "Eoceński etap ewulucji Anisopodidae Knab, 1912 (Diptera: Nematocera)" finansowany ze środków przyznanych na naukę Wydziałowi Biologiczno-Rolniczemu Uniwersytetu Rzeszowskiego na działalność służącą rozwojowi młodych naukowców oraz uczestników studiów doktoranckich w 2016 roku.

6.4 STAŻE ZAGRANICZNE I KRAJOWE

2016 staż – Muzeum Geologiczne Uniwersytetu w Getyndze.
2016 staż – Instytut Systematyki i Ewolucji Zwierząt Polskiej Akademii Nauk w Krakowie.
2016 staż – Wydział Biologii, Uniwersytet Gdański.

6.5 ORGANIZACJA I UDZIAŁ W KONFERENCJACH NAUKOWYCH

2017: Konferencja Paleoentomologiczna i XXXIV zjazd Sekcji Paleontologicznej PTE; Gdańsk, 23.03.2016r. (konferencja o charakterze międzynarodowym)
▪ REFERAT: „Anisopodidae Knab, 1912 (Diptera) in Baltic amber"

2016: Konferencja Paleoentomologiczna i XXXIII zjazd Sekcji Paleontologicznej PTE; Gdańsk, 17.03.2016r.
▪ REFERAT: „Nowy przedstawiciel rodzaju *Helius* (Limoniidae; Diptera) z eoceńskiego bursztynu bałtyckiego"

▪ REFERAT: „Nowy przedstawiciel rodzaju *Dicranomyia* (Diptera: Limoniidae) z bursztynu bałtyckiego"

6.6. DZIAŁALNOŚĆ POPULARYZUJĄCA NAUKĘ

2016, 2017, 2018: Czynny udział w wydarzeniu „Noc Biologów"

2017: - Czynny udział w wydarzeniu „Dni Wydziału" Biologiczno-Rolniczego Uniwersytetu Rzeszowskiego.