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**Review**

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# On the identity and limits of Falsiformicidae (Insecta: Hymenoptera, Vespoidea *s.l.*)

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## Abstract

Falsiformicidae are found to belong to Vespoidea *s.l.* and not to Chrysidoidea because of sexually dimorphic antennae (12-segmented in female and 13-segmented in male) and permanently internalized female tergum 7. Eight described species in three genera are known in the family including five new species (*Siccibythus oculatus* **sp. nov.**, *S. pallidus* **sp. nov.**, *S. martynovae* **sp. nov.**, *S. ohmkuhnlei* **sp. nov.**, *S. paulus* **sp. nov.**) as well as a number of undescribed ones, all from mid-Cretaceous ambers (mostly of Kachin in Myanmar but also of Charente in France and Agapa in North Siberia). Phylogenetic affinities of Falsiformicidae within Vespoidea are left to be clarified, and biology of this family is enigmatic yet.

**Keywords:** Fossil insects, aculeate wasps, new taxa, Cretaceous, Burmese amber, Charente amber, Taimyr amber

## Introduction

The taxonomic fate of the family Falsiformicidae has varied over the years. The family was introduced by Rasnitsyn (1975) based on synincluded and putatively conspecific incomplete male and female wasps in the Cenomanian amber of Agapa (Taimyr Peninsula, North Siberia). It was questionably attributed to the superfamily Scolioidea in his understanding (including, in modern terms, also Scoliidae, Tiphiidae, Mutillidae, Bradynobaenidae, Sapygidae and Sierolomorphidae) as similar to Sierolomorphidae and ants and possibly close to ancestor of the latter. Later Rasnitsyn (1980) placed the family in Scolioidea and related it to Sierolomorphidae, and additionally he erroneously identified *Taimyrisphex* Evans, 1973 as a male of Falsiformicidae. Now we know that, unlike *Taimyrisphex*, real males of Falsiformicidae are similar to their females in wing venation and form of metasomal base. Still later, Rasnitsyn (1988, 2002) suggested Falsiformicidae to be monophyletic with Formicoidea, with Sierolomorphidae as their sister group. Ronquist *et al*. (1999: figs 12, 13) proposed more or less similar arrangements. *Taimyrisphex*, in our opinion, is either a senior synonym or a close relative of *Burmusculus* Zhang & Rasnitsyn, 2018 (Burmusculidae), based particularly on its wing venation and open belt-like metapostnotum (*cf*. Evans, 1973; Rasnitsyn, 1980: fig. 179; Zhang *et al*., 2018). The case certainly needs further study.

Recently, Perrichot *et al*. (2014) announced research (not published yet) based on the fossils in various Cretaceous ambers (Lebanese, Spanish, Burmese and French) that proposed the chrysidoid and non-scolioid relationship of Falsiformicidae. This stimulated us to reconsider the available material on the family to check the above statement. The material includes, besides the type specimens of *Falsiformica cretacea* Rasnitsyn, 1975, at least one of two genera and species identified by their authors as belonging to the chrysidoid family Scolebythidae (Cockx & McKellar, 2016) and several fossils in the mid-Cretaceous Burmese amber as specified below. Initially we intended to consider the well preserved specimen from the late Albian Charente amber of SW France presented as a MCT reconstruction but not formally described (Lak *et al*., 2008) as well, but the anonymous reviewer suggested to leave it out until the reviewer and colleagues publish an ongoing description.

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## Material and methods

The fossils used for the present study derive from various Cretaceous resins with each particular site being reviewed in Rasnitsyn *et al*. (2016) and considered there under their respective paragraphs: #2.2.2.5 for the holotype of *Falsiformica cretacea* Rasnitsyn, 1975 (Nizhnyaya Agapa, Taimyr Peninsula, N. Siberia; ?upper Cenomanian); and 2.2.2.2 for the remaining considered fossils including those described by Cockx & McKellar (2016) (Burmese amber: Myanmar, Hukawng Valley, Albian–Cenomanian boundary). For geographic and stratigraphic position of the amber localities see Rasnitsyn *et al*. (2016: fig. 1).

The material of *Falsiformica cretacea* is kept at the A.A. Borissiak Palaeontological Institute, Russian Academy of Sciences (RAS) under collection PIN, 3426/15; that of new species from the Burmese amber as follows: those with prefix NIGP at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (CAS) (Nanjing, China), PIN at A.A. Borissiak Paleontological Institute, RAS (Moscow, Russia), and SNSB at Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany).

The fossils in amber have been studied using a Leica M165C stereomicroscope with a Leica DFC 420 camera at the A.A. Borissiak Paleontological Institute, RAS. Helicon Focus Pro × 64 was used to stack photos for better depth of field. For imaging of specimens, a compound microscope Nikon E-800 with dry (4 ×, 10 ×, 20 ×) and water dip optics (40 × and 60 ×) was used. Specimens were imaged with the combination of brightfield and incident illumination. Stacks of images, comprising multiple focal planes, were obtained with an Olympus OM-D E-M10II camera. Stacks were processed with Helicon Focus software using mostly algorithm B. Line drawings were done using image-editing software (CorelDraw X7 and Adobe Photoshop CS6) based on digital photographs.

Venational terminology follows Rasnitsyn (1969) with additional names of successive sections of longitudinal veins as follows: 1-RS, 2-RS etc. for sections of RS, 1-M, 2-M etc. for those of M, and so on.

All taxonomic acts established herein have been registered in ZooBank (see below), together with the electronic publication LSID: urn:lsid:zoobank.org:pub: AFDEE42F-11CD-43DD-819C-4CB599712607

## Systematic palaeontology

### Order Hymenoptera Linnaeus, 1758
### Superfamily Vespoidea Laicharting, 1781
### Family Falsiformicidae Rasnitsyn, 1975

**Type genus.** *Falsiformica* Rasnitsyn, 1975

**Included genera.** *Falsiformica* Rasnitsyn, 1975 from Cenomanian Agapa amber (northern Siberia), *Siccibithus* Cockx & McKellar, 2016 from mid-Cretaceous Burmese amber and possibly *Cursoribythus* Cockx & McKellar, 2016.

**Diagnosis** (synapomorphies of the family are given bold)**.** Antenna 12-segmented in female, 13-segmented in male, antennal attachments open (not under frontal lobes). Pronotum plate-like, gently excised behind, loosely overlaying mesonotum behind, with posterodorsal angles reaching tegula, not inflated above spiracles. Notauli and adlateral lines (parapsides) present. Mesoventropleuron with no lobes over mesocoxal bases. Metapostnotum open, wide trough-like. Propodeum moderately long, with distinct dorsal and declivitous parts, variously carinate, sometimes with two sublateral parallel carinae but never grooves (as is characteristic of Scoliidae). Fore wing with pterostigma well developed and with **venation reduced**: at most with cells c, 1+2r (possibly 1+2r+2rm), 3r, 1rm, 1mcu, and 1cua closed with tubular veins, sometimes with only c and 1rm closed. **Hind wing with no cells closed**. Mid coxae subcontiguous, with basal orifice small. Tibiae lacking distinct spines, with spurs 1–2–2, with hind tibial spur pectinate. Claw simple or with single small preapical tooth, arolium often big, with arculus exaggerate. Metasoma elongate, with **first tergum node-like**, not fused with its sternum, with well-developed lateroterga, first sternum distinctly convex transversally, with thick hind margin, not distinctly overlapping base of second sternum, second tergum largest, not modified, second sternum with anterior margin bent upright to form collar highest medial (to close a gap between convex apex of the first sternum and base of the second sternum when metasoma is straightened at the articulation between 1st and 2nd segments, as described for *Sierolomorpha* and *Falsiformica*, *cf*. Rasnitsyn, 1980: 123–124). Otherwise male segments 2–6 and female 2–5 with no distinct modifications. No felt line present. Female tergum 7 completely internalized (never visible), sternum 6 forming a kind of laterally compressed cone with upper sides superimposed with no distinct upper lobes delimited and with round apical orifice for ovipositor. Male sternum 7 more or less elongate, and **sternum 8 visible as two upcurved teeth** (with impair base hidden, if at all). Male and female genitalia unknown except for short apex of sting visible in females.

**Remarks.** Falsiformicidae are attributed to Aculeata *sens*. *str*. (= Aculeata other than Chrysidoidea) because of antennae sexually dimorphic with 12 segments in female and 13 in males (not sexually dimorphic in Chrysidoidea) and the female metasomal tergum 7 always internalized (normally external apically in Chrysidoidea other than

Chrysididae with several apical segments tube-like modified).

It is not easy to identify a position of Falsiformicidae within non-chrysidoid aculeate wasps (Aculeata *sens. str*.) primarily because the internal structure of this group is obscure, as the current diversity of opinions witnesses ranging from collapsing of all non-apoid families into a single superfamily Vespoidea (Heraty *et al*., 2011; Klopfstein *et al*., 2013; Nieves-Aldrey, Sharkey, 2014) to splitting them into five (Peters *et al*., 2017) or eight (Braunstetter *et al*., 2017) of very different composition, or else to leaving most of families lone (out of any superfamily: Johnson *et al*., 2013; Payne *et al*., 2013), or even taking Aculeata not split into superfamilies at all (Sharkey *et al*., 2012). Here for the present study we select the most popular version of Aculeata consisting of the three monophyletic superfamilies Chrysidoidea, Apoidea and Vespoidea.

Of these three superfamilies, Falsiformicidae fall unquestionably outside of Chrysidoidea for the above reasons (sexually dimorphic antenna and internalized female 7$^{th}$ metasomal tergum, two main synapomorphies of non-chrysidoid aculeates). Equally they exclude being Apoidea because of absence of any signs of the apoid synapomorphy in having metapostnotum broadly intervening caudally into propodeum. Similarly, the propodeum structure displayed in *Siccibythus ohmkuhnlei* **sp. nov.** (Fig. 5) and *Sierolomorpha* (Leley & Mokrousov, 2015: fig. 5) is particularly convincing in that respect. Within Vespoidea *s.l*., Falsiformicidae differ clearly from most of other families (Scoliidae, Tiphiidae, Mutillidae, Bradynobaenidae, Pompilidae, Vespidae, Formicidae) in having female metasomal sternum 6 conical and sidewise compressed, with its upper sides distinctly overlapping and lacking delimited dorsal lobes. In the above listed families, however, the female sternum 6 has its sides either well separated dorsally or overlapping with clearly delimited lobes, and often distinctly depressed generally or at least above (except for Formicidae). Instead, Falsiformicidae are similar in that respect to (synapomorphous or homoplasious with) Sierolomorphidae, Rhopalosomatidae and Sapygidae. Additionally, Falsiformicidae show similarity with these three plus Vespidae and Formicidae in having mid tibiae lacking distinct spines on outer surface, and with Sierolomorphidae and Rhopalosomatidae in having a similar structure of junction of metasomal sterna 1 and 2 as specified above (all plesiomorphies). Besides the above differences, Falsiformicidae differ from Vespidae in having propodeum not shortened (plesiomorphy), from Sierolomorphidae and Rhopalosomatidae in having the first metasomal tergum node-like (synapomorphy), and from ants in having only the first metasomal tergum (not all the segment as a whole) modified node-like, with lateroterga present and with no fusion occurring between tergum and sternum (plesiomorphy). Falsiformicidae further differ from the vast majority of Vespoidea in reduced wing venation and particularly in hind wing lacking closed cells (synapomorphy).

The genus *Cursoribythus* Cockx & McKellar, 2016 may belong to Falsiformicidae because of the apparently modified metasomal base (not clearly visible in published illustrations) and 12-segmented antenna (characteristic of female Falsiformicidae and rare in Scolebythidae where the genus was originally described). Unfortunately a taxonomic position of the genus remains to be identified depending on redescription of the type and particularly until decisive features (synapomorphies) of either Falsiformicidae (node-like first metasomal segment) or Scolebythidae (large external prosternum) are demonstrated.

### Genus *Falsiformica* Rasnitsyn, 1975

**Type species.** *Falsiformica cretacea* Rasnitsyn, 1975

**Included species.** Type species.

**Diagnosis.** Fore wing with no cells closed with tubular veins in its middle and distal part, with 1m-cu tubular. Claw simple.

### Genus *Siccibythus* Cockx & McKellar, 2016

**Type species.** *Siccibythus musculosus* Cockx & McKellar, 2016.

**Included species.** Type and 6 species described below.

**Diagnosis.** Fore wing with no cells closed with tubular veins in its middle and distal part and with 1m-cu at most only partially tubular. Claws simple.

**Remarks.** The genus is considered as a member of Falsiformicidae based on its type species that demonstrates a node-like modified first metasomal tergum and a male apical metasomal sternum modified into two teeth. Both characters represent the most striking synapomorphies of the family Falsiformicidae, and both are clearly illustrated in the original publication (Cockx & McKellar, 2016, Fig. 1A, B, E).

### *Siccibythus oculatus* sp. nov.

(Figs 1–3)

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**Material.** Holotype and paratype from the same locality and horizon.

**Holotype.** Female, NIGP173799 [BA01-16315]. Well preserved complete specimen in a piece of amber filled with bubbles partially covering inclusion. Syninclusions: Coleoptera: Scydmaeninae; Diptera: Psychodidae; Collembola.




**FIGURE 1.** *Siccibythus oculatus* **sp. nov.**, female holotype. **A**, Dorsal view. **B**, Lateral right view. C, Lateral left view. Scale bars = 0.5 mm.

**Paratype (allotype).** Male, SNSB-BSPG 2020 XCIII 20. Complete specimen with upper part of head and most of both antennae cut, with integument of meso- and metasoma somewhat deteriorate and basal part of right wings distorted. Syninclusia: Coleoptera, 2 Diptera (Cecidomyioidea, Atelestidae: *Alavesia* sp.), 3 Collembola, Myriapoda (*Phryssonotus burmiticus* Cockerell, 1917, S.I. Golovatch det.), 6 Acari (Microtrombidiidae larva; Trombidiiformes; Eupodidae: *Linopodes*? sp. nymph; 2 Oribatidae (1 *Enarthronota* sp.; indet.).

**Etymology.** Species name is because of big eyes evident in female (damaged in male).

**Diagnosis.** Differs from all congeners in both sexes in combination of RS short distal of 2r-rs and 2-A not pigmented.

**Locality and horizon.** Burmese amber obtained from a mine situated in Northern Myanmar, Kachin State, Tanai Township, Hukawng Valley, SW of Tanai City; uppermost Albian–lowest Cenomanian (mid-Cretaceous).

**Description.** *Female*. Body and appendages dark except light brown prothorax, mesonotum, fore and mid coxae, all femora, metasomal terga 4–7 and sternum 6 and wide apical bands on terga 2–3; scape, pedicel, tibiae and apex of fore femur dark brown. Body smooth, short hairy, pronotal sides and metasomal terga 2–3 weakly longitudinally canaliculated (possibly because of integument degradation). Head globose, some 1.3 × as wide as long in dorsal aspect, with eyes bulging, occupying most of head sides (except for wide, convex temples), almost reaching mandibular bases, occipital carina complete, reaching hypostomal carina well below mandibular base, vertex and frons narrow, impressed between eyes, with row of long setae along inner orbits, ocelli in small acute triangle well distant from eyes, toruli open, next to clypeus, much closer to eyes than to each other, interantennal space more or less flat, clypeus short, simple, with fore margin rounded. Antenna narrow, all antennal segments several times as long as wide, scape almost as long as pedicel and first flagellomere combined, pedicel slightly shorter than first flagellomere, flagellomeres slightly shortening gradually toward apex except for longer apical segment. Labrum not visible externally, mandibles small, overlapping, with 3 small teeth visible, maxillary and labial palps not visible. Pronotum with long posterior part gently excised behind, short declivitous part delimited with transverse groove behind, and with long collar covering elongate propleura almost up to head, with posterior angles subacute, not inflated, reaching tegula, with lower corner short, obtuse. Propleura long, slender, abutting throughout, prosternum obscured. Mesoscutum convex between well impressed lines: complete notauli, incomplete adlateral lines, and lateral edges; notauli little spaced behind and widely diverging anterior; transverse mesonotal line distinct; prescutellar impression with short hind extensions laterally and short one medially; scutellum rounded triangular, weakly convex. Meso- and metapleurae smooth. Metanotum moderately short. Propodeum with clear cut dorsal and hind surfaces, dorsal one with lateral, sublateral and apical carinae, hind surface with lateral, sublateral and supracoxal carinae. Fore wing distal of basal vein (1-RS&1-M) and cu-a with no tubular veins other than pterostigma and short section of RS distal of 2r-rs, with nebulous rudiments of RS+M, distal RS, Cu and A, cu-a slightly antefurcal. Coxae elongate, particularly fore and hind ones, hind one apparently with dorsal tooth, fore trochanter short, mid- and hind ones elongate, trochantelli absent, femora moderately thick basally, narrow distally, tibiae and tarsi thin, long, tibial spurs 1-2-2, fore one short

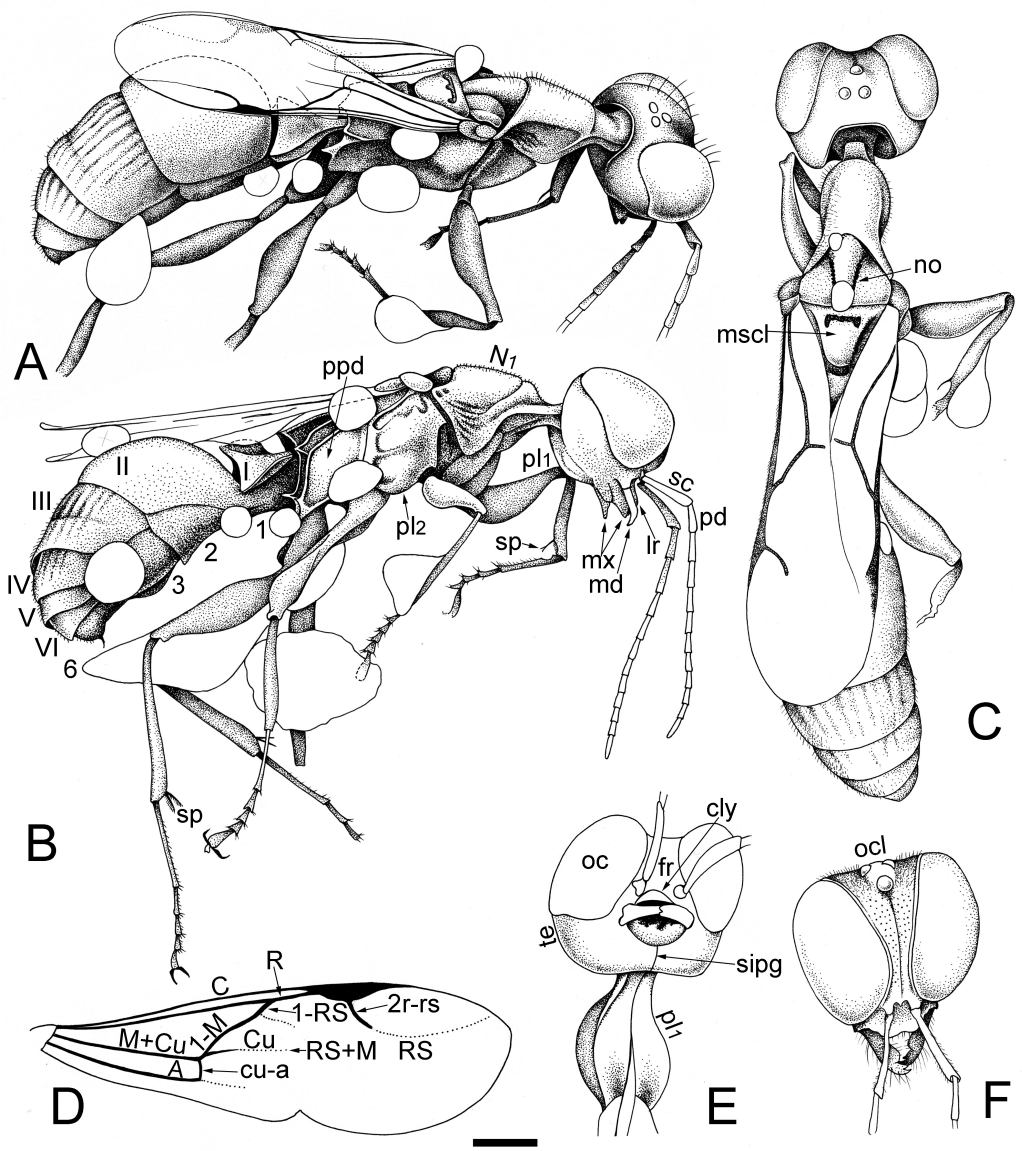



**FIGURE 2.** *Siccibythus oculatus* **sp. nov.**, female holotype, line drawing (by K.V. Martynova). **A**, Body oblique dorsal view. **B**, Lateral view. **C**, Dorsal view. **D**, Fore wing. **E**, Head and prothorax ventral. **F**, Head frontal. Symbols: cly, clypeus, fr, frons, lr, labrum, md, mandible, mscl, mesoscutellum, mx, maxilla, $N_1$, pronotum, no, notaulus, oc, eye, ocl, ocelli, pd, pedicel, $pl_1$, $pl_2$, pro- and mesopleurae, ppd, propodeum, sc, scape, sipg, interpostgenal suture, sp, spur, te, temple, I, II, II, etc., metasomal terga, 1, 2, 3, etc., metasomal sterna. Venational symbols standard. Scale bar = 0.5 mm.

and straight except for somewhat bent apex, with adaxial comb growing higher apical and forming seemingly bifid apex, hind spurs pectinate. Tarsal segments elongate, with strong setae apical and, basitarsus, below, basitarsus about as long as other tarsomeres combined, claw simple, arolium possibly small (all arolia closed). First metasomal segment short, tergum node-like, with form difficult to appreciate because of bubbles and cracks but apparently with upper surface flat triangular (acute forward), second segment longest and highest, following gradually smaller, apical sternum high, with upper sides overlapping, not modified as delimited lobes.

*Male*. Body and appendages brown, with no distinct pale markings. Body with no pronounced microsculpture, short and sparse hairy (denser at metasomal apex). Head form not clear because of damage, with eyes large and apparently bulging, occupying most of head sides except for temples at most 0.3 × as wide as width of lateral aspect of eye, distant from mandible for less than width of mandibular base, clypeus transverse, with fore margin rounded, simple. Antennal attachments simple, touching clypeus, close to eye, distant from each other. Antenna with scape long, robust, inflated basal, pedicel thin, long but apparently shorter than scape. Mandible elongate, with at least three teeth, with apical one long, acute, preapical teeth small. Maxillary palp with 3 apical segments long.




**FIGURE 3.** *Siccibythus oculatus* **sp. nov.**, paratype male, 2802. **A**, Oblique dorsal view. **B**, Ventral view. **C**, Lateral view. Scale bars = 0.5 mm.

Pronotum moderately long, with few details apparent; propleura short. Mesoscutum not much convex, with notauli impressed, distant posterior, diverging anterior, adlateral lines not apparent, transscutal line thin, complete, prescutellar fossa deep, simple, mesoscutellum small, triangular. Metanotum short, with distinct metascutellum. Meso- and metapleuron apparently simple (possibly because of integument degradation). Metapostnotum not distinct. Propodeum with posterolateral angles forming short upward teeth. Mid coxae separated, hind ones possibly contiguous, metasternum obscured. Fore wing distal of basal vein (1-RS&1-M) and crossvein cu-a with no tubular or nebulous veins other than pterostigma and short tubular section of 2r-rs&RS, with RS part being very short in left wing and a little longer than 2r-rs in right one. Coxae elongate, trochanters slightly elongate, trochantelli very short ring-like, femora moderately thick midlength (not subbasally), tibiae and tarsi moderately thin, fore tibial spur not long, rather thick, bifid apical, mid and hind tibia with 2 spurs; tarsal segments with strong setae apically and, basitarsus, below, basitarsus much longer than tarsomeres 2–4 combined, tarsomere 4 elongate but deeply excised dorsal, with dorsal length some 0.3 to 0.5 its full length (in fore and hind legs, respectively), 5th segment not enlarged, claw simple, arolium rather large. First metasomal segment short, weakly seen, second segment longest and highest, following smaller but not very small, gradually shortening rearward; sterna 2–6 ordinary, 7th forming elongate hypopygium, 8th bearing two long narrow teeth gently bent upward.

**Measurements.** Holotype female. Body length 4.3 mm, head length 0.7 mm, width 0.9 mm, height 0.52 mm, scape length 0.37 mm, pedicel length 0.23 mm, flagellum length 1.46 mm, mesosoma length 1.84 mm, height 0.82 mm, fore wing length 2.3 mm, hind femur length 0.94 mm, hind tibia length 1.1 mm, hind tarsus length 0.95 mm, metasoma length 1.8 mm, 1st metasomal segment length 0.43 mm. Paratype male. Body length *ca*. 2.8 mm, head width 0.8 mm, mesosoma length 1.2 mm, fore wing length 1.9 mm, hind femur length 0.56 mm, hind tibia length 0.63 mm, hind tarsus length 0.82 mm, metasoma length 1.4 mm, 1st metasomal segment length 0.30 mm.

**Remarks.** The male and female are putatively considered as conspecific based on similarity of several characters treated here as diagnostic of species of *Siccibythus*, particularly fore wing length (2.3 *vs*. 1.9 mm, the difference expectable for different sexes), ground color dark, wing venation (tubular RS short, RS+M, 1-Cu and 2-A not clearly pigmented), fore tibial spur short (bifid at least in female), basitarsus much longer than tarsomeres 2–4 combined, 1st metasomal segment short. There are some differences as well with scape thin in female and thicker in male, and hind tarsomere 4 having its dorsal length some 0.3 × of its total length in female and 0.5 × in male. However, these could be examples of a sexual dimorphism. In any case, association of opposite sexes is proposed here as a hypothesis aimed to be tested using additional fossil material.

***Siccibythus martynovae* sp. nov.**
(Fig. 4)
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**Material.** Holotype only.

**Holotype.** Female, PIN, 5620/22a. Well preserved complete specimen in a piece of amber filled with bubbles and cracks partially covering inclusion. Syninclusions: many Collembola, 4 Homoptera nymphs (1 Sternorrhyncha , 3 Auchenorrhyncha), Blattodea nymph, Coleoptera, many Acari.

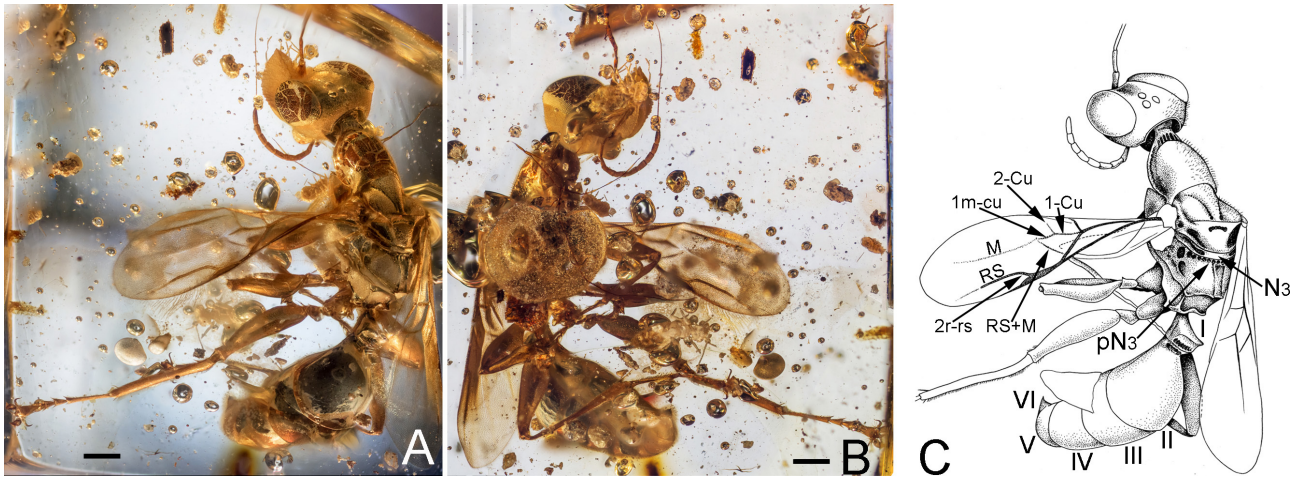



**FIGURE 4.** *Siccibythus martynovae* **sp. nov.**, female holotype. **A**, Oblique dorsal view. **B**, Oblique ventral view. **C**, Oblique dorsal view, line drawing (by K.V. Martynova). Symbols as in Fig. 2, except: $N_3$, metanotum, $pN_3$, metapostnotum. Scale bars = 0.5 mm.

**Etymology.** The species is named for Dr Kateryna V. Martynova, an entomologist and artist.

**Diagnosis.** Differs from all congeners in large size (fore wing 3.5 mm in length) and pigmented RS+M in the fore wing.

**Locality and horizon.** Burmese amber obtained from a mine situated in Northern Myanmar, Kachin State, Tanai Township, Hukawng Valley, SW of Tanai City; uppermost Albian–lowest Cenomanian (mid-Cretaceous).

**Description.** Body and appendages light brown except metasoma dark brown. Body with no pronounced microsculpture, short hairy (denser at metasomal apex). Head globose, less than 1.5 × as wide as long in dorsal aspect, with eyes bulging, occupying most of head sides (except for rather narrow temples), occipital carina complete at least dorsally, frons apparently less narrow (only visible dorsally), ocelli in small acute triangle well distant from eyes. Antenna slender, all antennal segments several times as long as wide, pedicel almost as long as scape and much longer than any flagellomere, flagellomeres slightly shortening gradually toward apex except for longer apical segment. Mouthparts invisible. Pronotum less elongate than in previous species, with long posterior part gently excised behind, short declivitous part delimited with transverse groove behind, with collar moderately long and longitudinally canaliculate. Propleura moderately long, prosternum hidden. Mesoscutum convex between and beyond notauli, notauli complete, with traces of crenulations, little spaced behind and widely diverging anterior, adlateral lines weak, incomplete; otherwise mesonotum as in *S. oculatus*. Meso- and metapleurae mainly smooth (incompletely visible). Metanotum short, with distinct metascutellum. Metapostnotum open, narrow, particularly laterally, transcarinate throughout. Propodeum with dorsal surface delimited with lateral and posterior carinae and with two submedial longitudinal carinae, hind propodeal surface carinated laterally and below. Side and lower aspect of mesosoma insufficiently visible. Fore wing distal of basal vein (1-RS&1-M) and cu-a with no tubular veins other than pterostigma and section of 2r-rs&RS far not reaching wing margin, with nebulous rudiments of RS+M, distal RS, Cu and A; cu-a interstitial. Coxae not much elongate, hind one with flat dorsal tooth, mid trochanter slightly elongate, hind one short and with posterodorsal hump, trochantelli absent, femora moderately thick basally, narrow distally, tibiae and tarsi thin, not particularly long, hind tibia with 2 spurs, larger spur apparently pectinate. Tarsal segments with strong setae apical and, basitarsus, below, basitarsus about as long as other tarsomeres combined, narrow, following segments somewhat widened, 4th one very short dorsally (with 5th one attached near its base) and much longer ventrally, 5th segment about as long as dorsal length of 3 previous ones combined, claws simple, arolium large. First metasomal tergum node-like, small, near triangular in side view, with fore surface long and hind one short, subvertical; second segment longest and highest, following smaller but not very small, subequal in length.

**Measurements.** Apparently, it is impossible to get precise measurements because of improper position of the fossil in amber block. Body length 6.4 mm, head length 1.0 mm, width 1.4 mm, scape length 0.55 mm, pedicel length 0.4 mm, flagellum length 1.8 mm, mesosoma length 2.8 mm, fore wing length 3.5 mm, hind femur length 1.35 mm, hind tibia length 1.64 mm, hind tarsus length 1.45 mm, metasoma length 2.7 mm, 1st metasomal segment length 0.6 mm.

***Siccibythus ohmkuhnlei* sp. nov.**

(Fig. 5)

LSID: urn:lsid:zoobank.org:act:F1F7B168-7719-48A2-88BA-B22AA79C1859

**Material.** Holotype only.

**Holotype.** Male, PIN, 5620/49. Complete specimen somewhat distorted (as particularly visible in dorsal aspect), with body integuments degraded. Syninclusions: 2 Diptera imagines, many Diptera (Cecidomyioidea) larvae, Acari, Fungi.

**Etymology.** The species is named in honor of Dr Christoph Öhm-Kühnle (Herrenberg, Germany) in appreciation of his donation of this and many other important fossils to the collection of Paleontological Institute, RAS.

**Diagnosis.** Differs from all congeners in combination of tubular RS long distal of 2r-rs in the fore wing and hind tarsomere 4 long dorsally (half as long as entire tarsomere).

**Locality and horizon.** Burmese amber obtained from a mine situated in Northern Myanmar, Kachin State, Tanai Township, Hukawng Valley, SW of Tanai City; uppermost Albian–lowest Cenomanian (mid-Cretaceous).

**Description.** Body and appendages dark with no distinct pale markings. Body with no pronounced microsculpture, short and sparse hairy (denser at metasomal apex). Head subglobose in side view, real

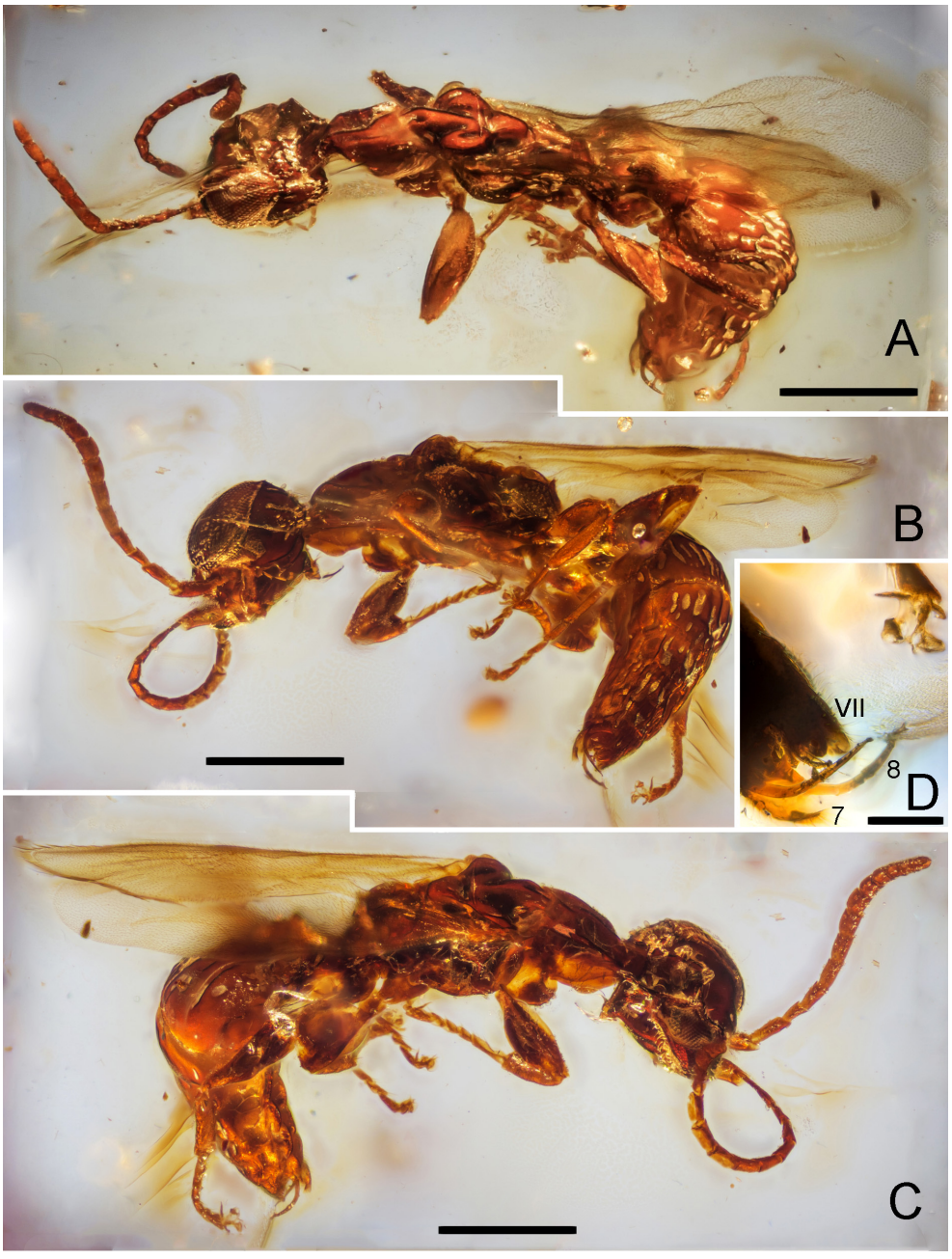



**FIGURE 5.** *Siccibythus ohmkuhnlei* **sp. nov.**, male holotype. **A**, Oblique dorsal view. **B**, Oblique ventral view. **C**, Oblique lateral view. **D**, Genitalia and hind pretarsus (claws and arolium). Symbols as in Fig. 2. Scale bars: **A–C** = 0.5 mm, **D** = 0.1 mm.

form obscure because of compression, with eyes large but not bulging (possibly because of compression), occupying most of head sides except for temples (which width difficult to measure because of deformation), distant from mandible for about width of mandibular base, clypeus somewhat thickened along midline (unless result of deformation). Antennal attachments simple, touching clypeus, close to eye, distant from each other. Antenna with scape long, robust, slightly inflated basal, pedicel thinner, long but distinctly shorter than scape, flagellar segments 2–4 longest (but distinctly shorter than pedicel), penultimate ones shortest, subquadrate. Mandible narrow, with outer surface concave, dentition not clear. Maxillary palp with 5 apical segments visible, 4 apical elongate, penultimate one shorter than both before and behind it. Pronotum moderately long, apparently smooth; propleura short. Mesoscutum convex, with notauli deeply impressed, distant posterior, diverging anterior, adlateral lines not apparent, transscutal line thin, complete, prescutellar fossa deep, simple, mesoscutellum triangular. Metanotum obscured, metapleuron apparently not delimited from propodeal side. Propodeum with lateral, sublateral and dorsoapical carinae (medial part not visible), its posterolateral angles forming upward teeth. Wing venation hardly visible (possibly much reduced) except for pterostigma and tubular 2r-rs&RS, with RS part long (not reaching wing margin for less than length of pterostigma). Legs short and thick comparing other congeners, fore coxa and all trochanters hardly elongate, trochantelli not distinct, femora thick, tibiae and tarsi not particularly thin, spurs not visible; tarsal segments with strong setae apically and, basitarsus, below, basitarsus shorter than tarsomeres 2–4 combined, tarsomere 4 elongate but deeply excised dorsal, with dorsal length some 0.2 to 0.4 its full length (fore and hind ones, respectively), 5th segment not enlarged, claw simple, arolium large. First metasomal segment short, possibly triangular in side view (not well visible), second segment longest and highest, following smaller but not very small, gradually shortening rearward; sterna 2–6 ordinary, 7th (hypopygium) possibly of complicated form (not well seen), 8th bearing two long narrow teeth bent upward, genitalia partially visible but difficult to interpret.

**Measurements.** Body length 2.7 mm, head length 0.46 mm, width 0.47 mm, scape length 0.18 mm, pedicel length 0.17 mm, flagellum length 0.82 mm, mesosoma length 1.1 mm, height 0.45 mm, fore wing length 1.5 mm, hind femur length 0.45 mm, hind tibia length 0.52 mm, hind tarsus length 0.35 mm, metasoma length 1.25 mm, 1st metasomal segment length 0.24 mm.

***Siccibythus pallidus* sp. nov.**

(Fig. 6)

LSID: urn:lsid:zoobank.org:act:91A821E7-8E2B-4FA0-8FD0-41633BE8CFDA

**Material.** Holotype only.

**Holotype.** Male, SNSB-BSPG 2020 XCIII 21. Complete specimen. Syninclusions: Acari: *cf. Speleorchestes* sp. (D. Vorontsov, pers. comm. 22.10.2020)

**Etymology.** Species name is the Latin for pale because of predominate body coloration.

**Diagnosis.** Differs from all congeners in body paler in color (metasomal tergum 3 predominantly pale dorsally) and in combination of tubular RS long distal of 2r-rs with 2–A pigmented and protibial spur long, acute.

**Locality and horizon.** Burmese amber obtained from a mine situated in Northern Myanmar, Kachin State, Tanai Township, Hukawng Valley, SW of Tanai City; uppermost Albian–lowest Cenomanian (mid-Cretaceous).

**Description.** Body and appendages pale (yellowish) with dark vertex, propodeum, lateral spots on metasomal terga 2–7, and teeth of metasomal sternum 8. Body with no pronounced microsculpture, short and sparse hairy (denser at metasomal apex). Head subglobose in side view, almost twice as wide as long in dorsal aspect, with eyes large and bulging, occupying most of head sides except for temples at most 0.3 × width of lateral aspect of eye, distant from mandible for about width of mandibular base, clypeus transverse, with fore margin rounded, simple. Antennal attachments simple, touching clypeus, close to eye, distant from each other. Antenna with scape long, robust, slightly inflated basal, pedicel thin, long but distinctly shorter than scape, flagellar segments all elongate, very gradually shortening apical except for apical segment some 1.2 × as long as penultimate one. Mandible narrow, with outer surface concave, other details not clear. Maxillary palp with 4 apical segments long, particularly last segment. Pronotum moderately long, apparently smooth; propleura short. Mesoscutum convex, with notauli deeply impressed, distant posterior, diverging anterior, adlateral lines apparently very short, transscutal line thin, complete, prescutellar fossa deep, simple, mesoscutellum small, triangular. Metapleuron apparently not delimited from propodeal side. Propodeum with lateral, sublateral and dorsoapical carinae (medial part not visible), its posterolateral angles forming strong teeth. Mid coxae possibly slightly separated, hind ones contiguous, metasternum obscured. Fore wing distal of basal vein (1-RS&1-M) and crossvein cu-a with no tubular veins other than pterostigma and short tubular section of 2r-rs&RS, with RS part some half as long as 2r-rs; dark nebulous 2-A present. Coxae elongate, fore and mid trochanters elongate, hind one not elongate, with medial hump, trochantelli very short ring-like, femora moderately thick midlength (not subbasally), tibiae and tarsi moderately thin, spurs 1-2-2, fore tibial spur long, simple, almost straight; tarsal segments with strong setae

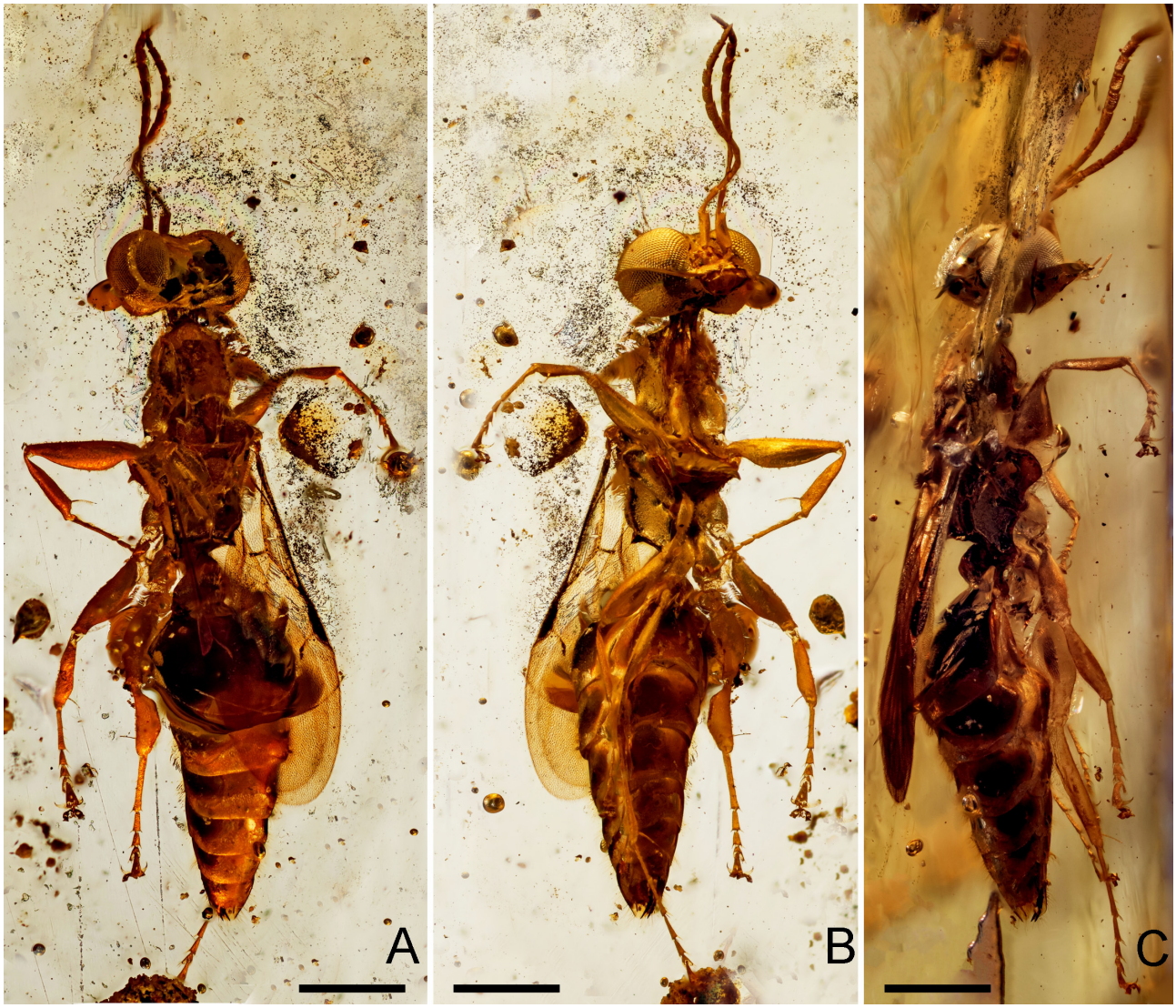



**FIGURE 6.** *Siccibythus pallidus* **sp. nov.**, male holotype. **A**, Dorsal view. **B**, Ventral view. **C**, lateral view. Scale bars = 0.5 mm.

apically and, basitarsus, below, basitarsus longer than tarsomeres 2–4 combined, tarsomere 4 elongate but deeply excised dorsal, with dorsal length some 0.2 to 0.3 its full length (fore and hind ones, respectively), 5th segment not enlarged, claw simple, arolium large. First metasomal segment short, globose, second segment longest and highest, following smaller but not very small, gradually shortening rearward; sterna 2–6 ordinary, 7th forming elongate hypopygium, 8th bearing two long narrow teeth gently bent upward.

**Measurements.** Holotype female. Body length 3.3 mm, head length 0.42 mm, width 0.69 mm, height 0.56 mm, scape length 0.18 mm, pedicel length 0.14 mm, flagellum length 0.88 mm, mesosoma length 1.18 mm, height 0.53 mm, fore wing length 1.75 mm, hind femur length 0.52 mm, hind tibia length 0.63 mm, hind tarsus length 0.7 mm, metasoma length 1.8 mm, 1st metasomal segment length 0.25 mm.

***Siccibythus paulus* sp. nov.**

(Fig. 7-9)

LSID: urn:lsid:zoobank.org:act:1169BD11-312B-4376-94DB-85E880DD816C

**Material.** Holotype and possibly male SNSB-BSPG 2020 XCIII 23, non-type specimen from of same origin as the type, with incompletely visible head and mesosoma and distorted metasomal apex (Fig. 9) which is similar to the holotype in the available diagnostic characters (runs smoothly to *C. paulus* **sp. nov.** in below key), with following measurements: body length 1.74 mm, head width 0.38 mm, mesosoma length *ca*. 0.7 mm, fore wing length 0.72, hind femur length 0.36 mm, hind tibia length 0.33 mm, hind tarsus length 0.41 mm, metasoma length as preserved 0.65 mm, 1st metasomal segment length 0.18 mm. Syninclused are Acari: Tarsonemidae, possibly Collembola.

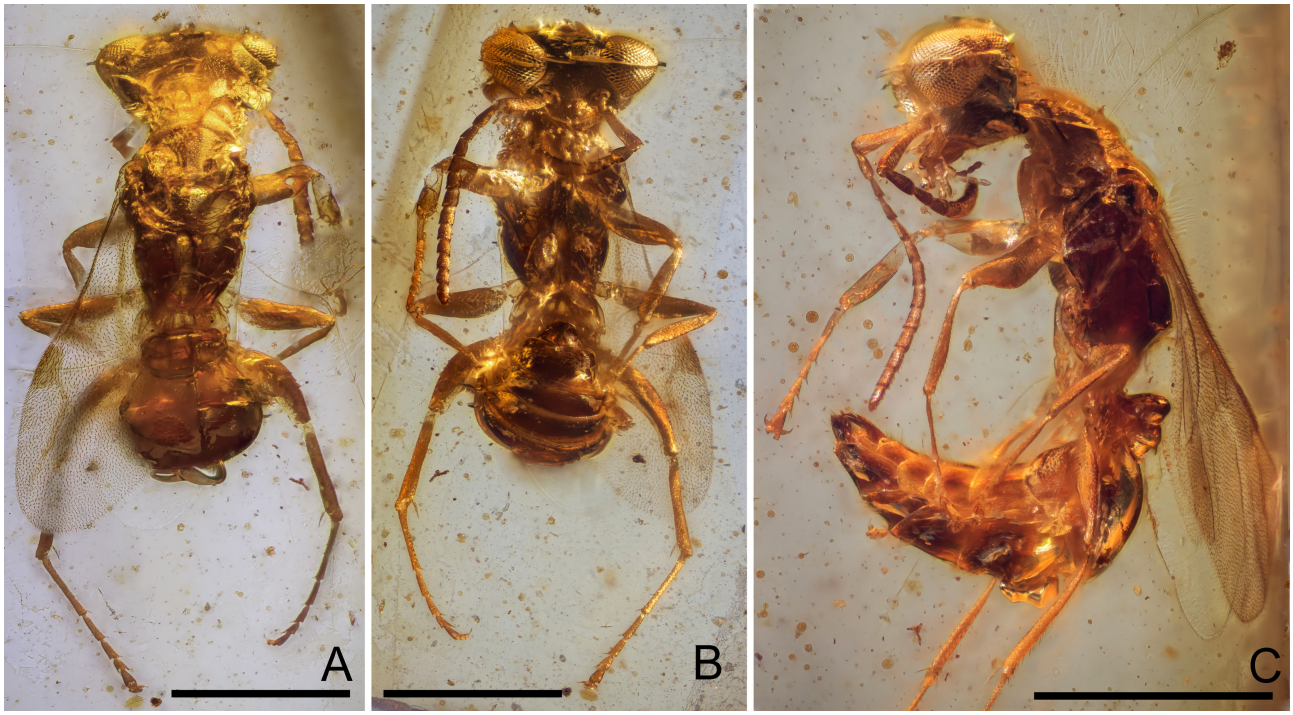



**FIGURE 7.** *Siccibythus paulus* **sp. nov.**, male holotype. **A**, Dorsal view. **B**, Ventral view. **C**, Lateral view. Scale bars = 0.5 mm.

**Holotype.** Male, SNSB-BSPG 2020 XCIII 22. Well preserved complete specimen except that integuments somewhat deteriorate in head and mesosoma. Syninclusions: spider web, plant hairs.

**Etymology.** Species name is the Latin for small.

**Diagnosis.** Differs from all congeners in smaller size (fore wing 0.75 mm long).

**Locality and horizon.** Burmese amber obtained from a mine situated in Northern Myanmar, Kachin State, Tanai Township, Hukawng Valley, SW of Tanai City; uppermost Albian–lowest Cenomanian (mid-Cretaceous).

**Description.** Body dark brown, appendages and metasomal sterna and tergal apices paler. Body with no pronounced microsculpture, short and sparse hairy (denser at metasomal apex). Head transverse, near twice as wide as long in dorsal aspect, with eyes bulging, occupying most of head sides except for temples about half as wide as lateral aspect of eye, frons as wide as scape long, clypeus transverse, with fore margin rounded, simple. Antennal attachments simple, touching clypeus, close to eye, distant from each other. Antenna slender, all antennal segments elongate, pedicel about half as long as scape and much longer than any flagellomere, flagellomeres scarcely shortening toward apex. Form of mandible not clear. Maxillary palp with 5 visible segments, with three apical ones slightly elongate, visible basal ones longer; labial palp with 3 short segments visible. Pronotum comparatively short, with few detail apparent; propleura short. Mesoscutum less convex, otherwise mesonotum similar more or less with previous species. Mesopleuron with several vertical folds probably resulted by integument degradation. Metanotum short, with distinct metascutellum. Metapostnotum open laterally, narrow or closed centrally. Propodeum with dorsal surface delimited with lateral and posterior carinae and with two submedial longitudinal carinae, hind propodeal surface with lateral, submedial and apical carinae. Mid and hind coxae separated, metasternum split for a distance. Fore wing distal of basal vein (1-RS&1-M) apparently with no tubular or nebulose veins other than pterostigma and tubular section of 2r-rs&RS; tubular RS almost twice as long as 2r-rs, far not reaching wing margin. Coxae elongate, trochanters slightly elongate, trochantelli absent or, rather, very short ring-like, femora moderately thick subbasally, narrowed distally, tibiae and tarsi thin, not long, fore tibial spur long, thin, simple, hind tibia with 2 spurs; tarsal segments narrow, with strong setae apically and, basitarsus, below, basitarsus about as long as tarsomeres 2–4 combined, following segments all elongate, 5$^{th}$ segment not enlarged, claw simple, arolium possibly large (all visible arolia are closed). First metasomal segment short, tergum node-like, its hind surface not shorter than fore one and with deep transverse impression, second segment longest and highest, following smaller but not very small, gradually shortening rearward; sterna 2–6 ordinary, sternum 7 forming elongate hypopygium, 8$^{th}$ bearing two long narrow teeth gently bent upward.

**Measurements.** Body length 1.3 mm, head length 0.21 mm, width 0.39 mm, height 0.21 mm, scape length 0.12 mm, pedicel length 0.07 mm, flagellum length 0.4

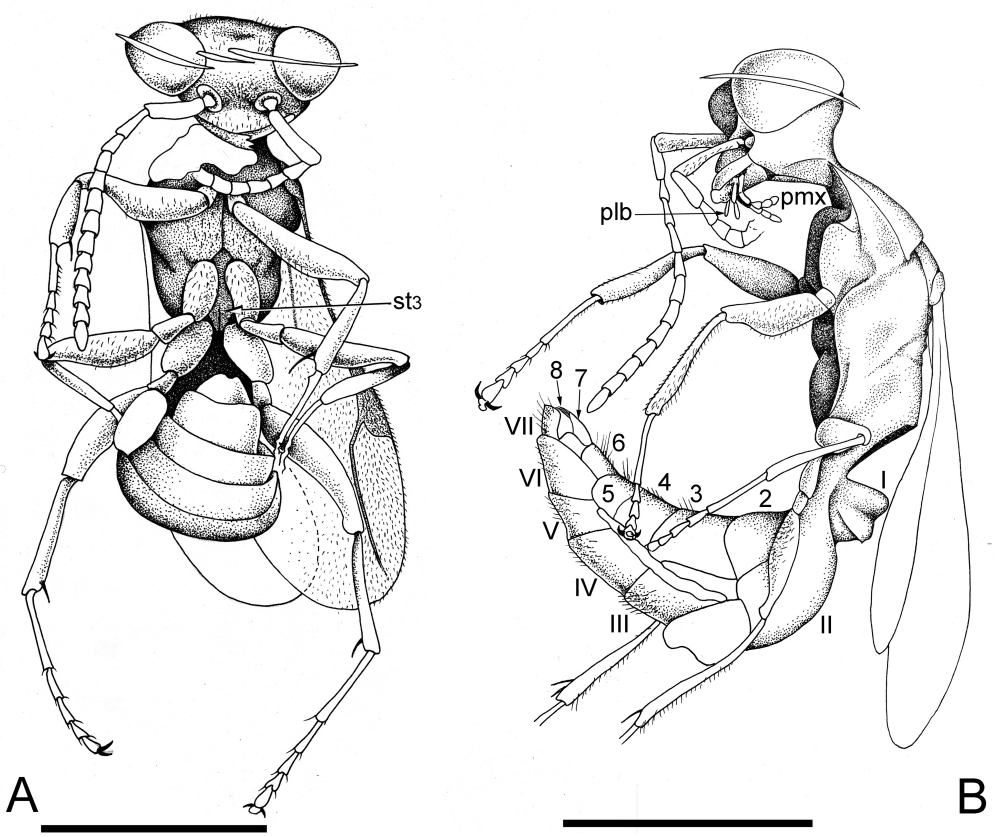



**FIGURE 8.** *Siccibythus paulus* **sp. nov.**, male holotype, line drawing (by K.V. Martynova). **A**, Ventral view. **B**, Lateral view. Symbols as in Fig. 2, except: plb, labial palp, pmx, maxillary palp, $st_3$, metasternum. Scale bars = 0.5 mm.

mm, mesosoma length 0.47 mm, fore wing length 0.74 mm, hind femur length 0.28 mm, hind tibia length 0.25 mm, hind tarsus length 0.34 mm, metasoma length 0.65 mm, 1st metasomal segment length 0.13 mm.

## Key to genera and species of described Falsiformicidae

1. Fore wing with cells 2+3rm and 3r enclosed with tubular veins. Claws with preapical tooth. Fore wing length *ca*. 2.3 mm.....(?) *Cursoribithus silvestris* Cockx & McKellar, 2016.
- Fore wing with cells 2+3rm and 3r not enclosed with tubular veins. Claws simple. ..... 2
2. Fore wing with 1m-cu tubular. Female fore wing length 2.0 mm..... *Falsiformica cretacea* Rasnitsyn, 1975
- Fore wing with 1m-cu at most partially tubular. *Siccibythus* Cockx & McKellar, 2016 ..... 3
3. RS distal of 2r-rs several times as long as 2r-rs. Basitarsus distinctly longer than tarsomeres 2-4 combined. Males ... 4
- RS distal of 2r-rs at most about as long as 2r-rs. Basitarsus not longer than tarsomeres 2-4 combined. Males and females..... 6
4. 1-Cu well pigmented. Fore tibial spur short, possibly bifid apical. 1st metasomal segment long both before and behind node. Fore wing length 1.66 mm..... .....*Siccibythus musculosus* Cockx & McKellar, 2016
- 1-Cu scarcely or not at all pigmented. Fore tibial spur long, thin and acute apical. 1st metasomal segment short ..... 5
5. Fore wing length *ca*. 0.75 mm. Dorsal length of hind tarsomere 4 0.3 × its total length ..... .....*Siccibythus paulus* **sp. nov.**
- Fore wing length 1.5 mm. Dorsal length of hind tarsomere 4 0.5 × its total length.....*Siccibythus ohmkuhnlei* **sp. nov.**
6(3). Fore wing length 3.5 mm. RS+M and 1-Cu both distinctly pigmented. Female ..... *Siccibythus martynovae* **sp. nov.**
- Fore wing length 2.5 mm or less. RS+M and 1-Cu both not pigmented. Males and females ..... 7
7. 2-A pigmented. Fore tibial spur long, acute. Metasomal tergum 3 mainly pale dorsally. Fore wing length 1.75 mm. Male..... *Siccibythus pallidus* **sp. nov.**
- 2-A not pigmented (except for very base). Fore tibial spur short, bifid apical. Metasomal tergum 2 mainly dark. Fore wing length 1.9 mm (male)—2.3 mm (female). Male and female .....*Siccibythus oculatus* **sp. nov.**

## Discussion

The present revision shows the family Falsiformicidae as a compact group of two or three described genera and seven to eight species and perhaps two or three times more expected to be discovered in the near future. Its taxonomic position in Vespoidea *s.l*. rather than in Chrysidoidea, as suggested by Perrichot *et al*. (2014), can be considered as most likely, based on sexual dimorphism in the number of antennomeres (12 in females and 13 in males) and the permanently internal metasomal tergum 7. As explained

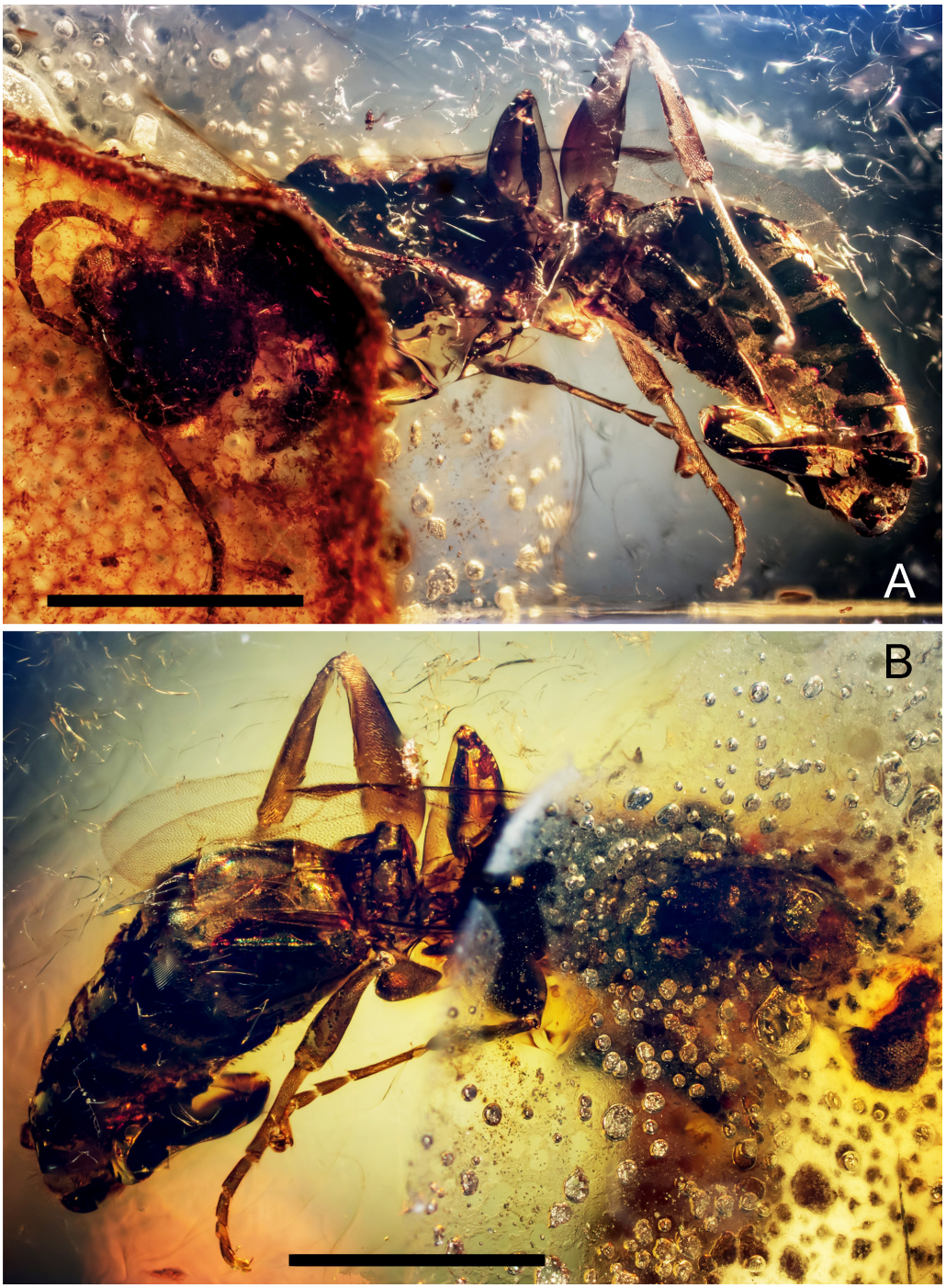



**FIGURE 9.** *Siccibythus cf. paulus* **sp. nov.**, male non-type specimen 2805. **A**, Oblique ventral view. **B**, Oblique dorsal view. Scale bars = 0.5 mm.

in introduction above, the form of the metapostnotum, first metasomal tergum and sternum and second sternum might suggest relationship of Falsiformicidae to Sierolomorphidae and Formicidae. However, precise identification of its position in the system of Vespoidea is hardly possible to assess until the phylogeny of Vespoidea is developed with any certainty. The internal structure and phylogeny of the family are also waiting for more information to be explored in detail.

Based on available material, we can hypothesize that Falsiformicidae are limited in geological distribution to the Cretaceous period and during that time they were widely distributed over eastern Laurasia (Spain, France), northern Angaraland (northern Siberia), northern Gondwana (Lebanon) and the West Burma block in the midst of the Tethys Sea south of the S. China terrain. It is the latter insular isolate that shows the center of diversity of the family and so suggests a distinct thermophily of the group. Unfortunately, this is apparently the only cue indicative of the ecology of Falsiformicidae, because their morphology gives no hint at their prey, nesting mode, and so on. Their kin, the two supposedly close lineages,

are equally of no help because the nesting biology of Sierolomorphidae is unknown, and the biology of ants is also unknown in respect to both their ground plan nesting mode and prey taxonomy.

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