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New species of *Hybristodryinus* Engel (Hymenoptera, Dryinidae) from mid-Cretaceous amber of northern Myanmar, with notes on their possible hosts

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Abstract

Two new species of *Hybristodryinus* Engel, 2005, are described from mid-Cretaceous amber of northern Myanmar: *H. castaneus* **sp. nov.** (based on one male) and *H. zaifui* **sp. nov.** (based on one female). Keys to the females and males of *Hybristodryinus* species are modified to include the two new taxa. A syninclusion, a nymph of Cixitettiginae (Perforissidae), present in the same amber piece containing *H. zaifui*, is studied. This syninclusion, together with the presence of Antennal Dorsal Organs (ADOs) in *Hybristodryinus*, suggests that Perforissidae are possible hosts of *Hybristodryinus*.

Keywords

Chrysidoidea, Cixitettiginae, host, keys, Perforissidae, taxonomy

Introduction

Dryinidae (Hymenoptera: Chrysidoidea) are parasitoids and often also predators of leafhoppers, planthoppers and treehoppers (Hemiptera, Auchenorrhyncha) (Guglielmino et al. 2013). They comprise 16 subfamilies, 50 genera and almost 1900 species worldwide (Olmi et al. 2020).

Mid-Cretaceous Kachin (Myanmar) amber (about 99 Ma) is the famous Burmese amber (Lin et al. 2019; Cao et al. 2020; Zhao et al. 2020), different from the recently discovered Campanian Tilin amber (Zheng et al. 2018) and Albian Hkamti amber (Xing and Qiu 2020). Dryinidae from Burmese amber are not common. Lists of the species known from this type of amber, reported by Perkovsky et al. (2019, 2020a) and Tribull et al. (2020), include the following subfamilies and genera: Anteoninae: *Burmanteon* Engel, 2003 (one species); Burmadryininae: *Burmadryinus* Olmi, Xu & Guglielmino, 2014 (one species); Dryininae: *Dryinus* Latreille, 1804 (13 species); *Hybristodryinus* Engel, 2005 (14 species); *Pseudodryinus* Olmi, 1991 (one species); Palaeoanteoninae: *Palaeoanteon* Olmi, 2000 (one species); Raptodryininae: *Raptodryinus* Olmi, Perkovsky, Martynova, Contarini, Bückle & Guglielmino, 2020 (one species).

The extinct genus *Hybristodryinus* is known only from Burmese amber (Perkovsky et al. 2019). With 14 described species, it is the most diverse genus of pincer wasps from that type of amber (Perkovsky et al. 2020a; Tribull et al. 2020).

In this study, we examined a small collection of dryinids from Burmese amber and recognized two additional new species, described below. In addition, we studied a syninclusion, represented by a nymph of a possible host of *Hybristodryinus*.

Material and methods

The descriptions follow the terminology used by Olmi et al. (2019) and Perkovsky et al. (2019). The measurements reported are relative, except for the body length (head to abdominal tip, without the antennae). In the descriptions, POL is the distance between the inner edges of the lateral ocelli; OL is the distance between the inner edges of a lateral ocellus and the median ocellus; OOL is the distance from the outer edge of a lateral ocellus to the compound eye.

The term “metapectal-propodeal complex” is here used in the sense of Kawada et al. (2015). It corresponds to the term “propodeum” sensu Olmi (1984).

In all monographs on Dryinidae (Olmi 1984; Xu et al. 2013; Olmi and Virla 2014; Olmi and Xu 2015; Olmi et al. 2019), different names of the cells and veins of the fore wing were used. They are here used in the sense of Azevedo et al. (2018), and Perkovsky et al. (2019). The correspondence between old and new names is the following (the first name is the old name): median cell = radial cell (R); submedian cell = first cubital cell (1Cu); marginal cell = second radial 1 cell (2R1); stigmal vein = second radial cross & radial sector (2r-rs&Rs); metacarp = poststigmal abscissa of radial 1 (PostabR1). In the text, cells and veins are named by their respective abbreviations, including costal cell (C).

The term "ADOs" (= Antennal Dorsal Organs) is here used in the sense of Riolo et al. (2016). It corresponds to the term "rhinaria" sensu Olmi (1984) and Xu et al. (2013). According to Riolo et al. (2016), ADOs are sensory structures that might mediate the antennal responses to vibratory stimuli. As far as we know, they are present only in the antennae of dryinid females attacking Fulgoromorpha (Olmi 1984). Antennae without ADOs are present mainly in species that are parasitoids of Cicadomorpha.

Because of the nature of the fossils and distortions sometimes caused by artifacts, the word "apparently" is used when describing characters for which there is slight uncertainty about the true condition or where a false impression is obtained at first sight.

The types of all fossil species of *Hybristodryinus* were examined. The type material of the new taxa studied in this paper is deposited in the collections of the Key Lab of Insect Evolution and Environmental Changes, the College of Life Sciences, Capital Normal University, Beijing, China (**CNUB**) and the Department of Agriculture and Forest Sciences (DAFNE), University of Tuscia, Viterbo, Italy (**DAF**).

Results

Generic placement

The new species described in this paper have been placed in the genus *Hybristodryinus*, because they fit the generic diagnosis reported below.

Genus *Hybristodryinus* Engel, 2005

Hybristodryinus Engel 2005: 486. Type species: *Hybristodryinus resinicolus* Engel 2005, by monotypy and original designation.

Diagnosis of the genus. Female: Macropterous; occipital carina complete; mandible quadridentate, with teeth becoming regularly progressively larger from dorsal to ventral tooth; palpal formula 6/3; antenna without tufts of long hairs; antennal ADOs present; disc of metapectal-propodeal complex with posterior corners strongly projected posteriorly; fore wing with three cells enclosed by pigmented veins (C, R, 1Cu); chela with rudimentary claw; protarsomere 5 less than twice as broad as enlarged claw; enlarged claw shorter than protibia; tibial spurs 1/1/1 or 1/1/2. Male: Macropterous; antenna with scape much broader than pedicel; palpal formula 6/3; occipital carina complete; mandible with four irregular teeth; epicnemium visible, because lateral regions of prothorax not continuous with mesopleura; mesopleuron protruding laterally; fore wing with three cells enclosed by pigmented veins (C, R, 1Cu), 2r-rs&Rs vein and pterostigma; fore wing with PostabR1 slightly shorter than pterostigma; tibial spurs 1/1/2.

***Hybristodryinus castaneus* Olmi, Guglielmino & Chen, sp. nov.**
http://zoobank.org/5CA10E8A-2DE2-4FD6-B4C4-9D3F580BA92F
Figure 1

Diagnosis. Male: macropterous, with antennomere 9 about six times as long as broad (Fig. 1E); face without long deep longitudinal furrow (Fig. 1D); posterior margin of vertex not deeply excavated medially (Fig. 1C); lateral ocelli not touching occipital carina; notauli complete, posteriorly separated (Fig. 1C).

Description. Male. Macropterous (Fig. 1A, B); length 1.4 mm. Completely dark brown. Antenna filiform, about as long as body, with setae very short. Scape about as broad as pedicel. Antennomeres in following proportions: 5:4:8:9:9:9:8:8:6:7. Antennomere 9 about six times as long as broad (Fig. 1E). Head with sculpture not visible; face without long deep median longitudinal furrow; mandible with teeth not visible; frontal line not visible; occipital carina complete, laterally not reaching eyes; ocellar ratio: POL:OL:OOL:OPL = 1:1:2:1; temple more than twice as long as OOL (5:2); greatest breadth of lateral ocellus as long as OOL; posterior margin of vertex not excavated medially (Fig. 1C); occiput deeply excavated. Palpal formula 6/3. Mesosoma much longer than head (30:10) and metasoma (30:20). Pronotum with lateral regions not protruding. Mesoscutum shiny, with sculpture not visible, slightly shorter than head (9:10), much longer than mesoscutellum (9:5). Notauli complete, posteriorly separated (Fig. 1C); minimum distance between notauli longer than OOL (3:2). Mesoscutellum shiny, with sculpture not visible. Metanotum and metapectal-propodeal complex not visible. Epicnemium not visible. Mesopleuron not visible. Fore wing hyaline, without dark transverse bands (Fig. 1F). Stigmal vein (2r-rs&Rs) with angle between proximal and distal parts, with distal part much longer than pterostigma (12:8). Second radial 1 cell (2R1) open. Pterostigma much longer than broad (9:2). Metacarpus (PostabR1) slightly shorter than pterostigma (7:9). Fore leg ratio: ? (coxa not visible, because it is hidden by an air bubble): 5 (trochanter): 16 (femur): 12 (tibia): 8 (protarsomere 1): 3 (protarsomere 2): 3 (protarsomere 3): 2 (protarsomere 4): 4 (protarsomere 5). Protrochanter more than four times as long as broad (5:1). Mid leg ratio: 7 (coxa): 4 (trochanter): 17 (femur): 15 (tibia): 9 (mesotarsomere 1): 3 (mesotarsomere 2): 2 (mesotarsomere 3): 1.5 (mesotarsomere 4): 3 (mesotarsomere 5). Mesotrochanter more than twice as long as broad (4:1.5). Hind leg ratio: 8 (coxa): 4 (trochanter): 17 (femur): 21 (tibia): 10 (metatarsomere 1): 4 (metatarsomere 2): 3 (metatarsomere 3): 2 (metatarsomere 4): 3 (metatarsomere 5). Tibial spurs 1/1/2.

Female. Unknown.

Material examined. *Holotype*: male (DAF3869), Myanmar: specimen in mid-Cretaceous Burmese amber (about 99 Ma). Obtained from a mine situated in Northern Myanmar, Kachin State, Tanai Township, Hukawng Valley, SW of Tanai City (DAF).

Etymology. The species is named *castaneus* (Latin adjective meaning "brown") because of its dark brown colour.

Remarks. *H. castaneus* is similar to *H. konbaung* Perkovsky, Olmi, Müller & Martynova, 2019, known from Burmese amber, for the following characters: face

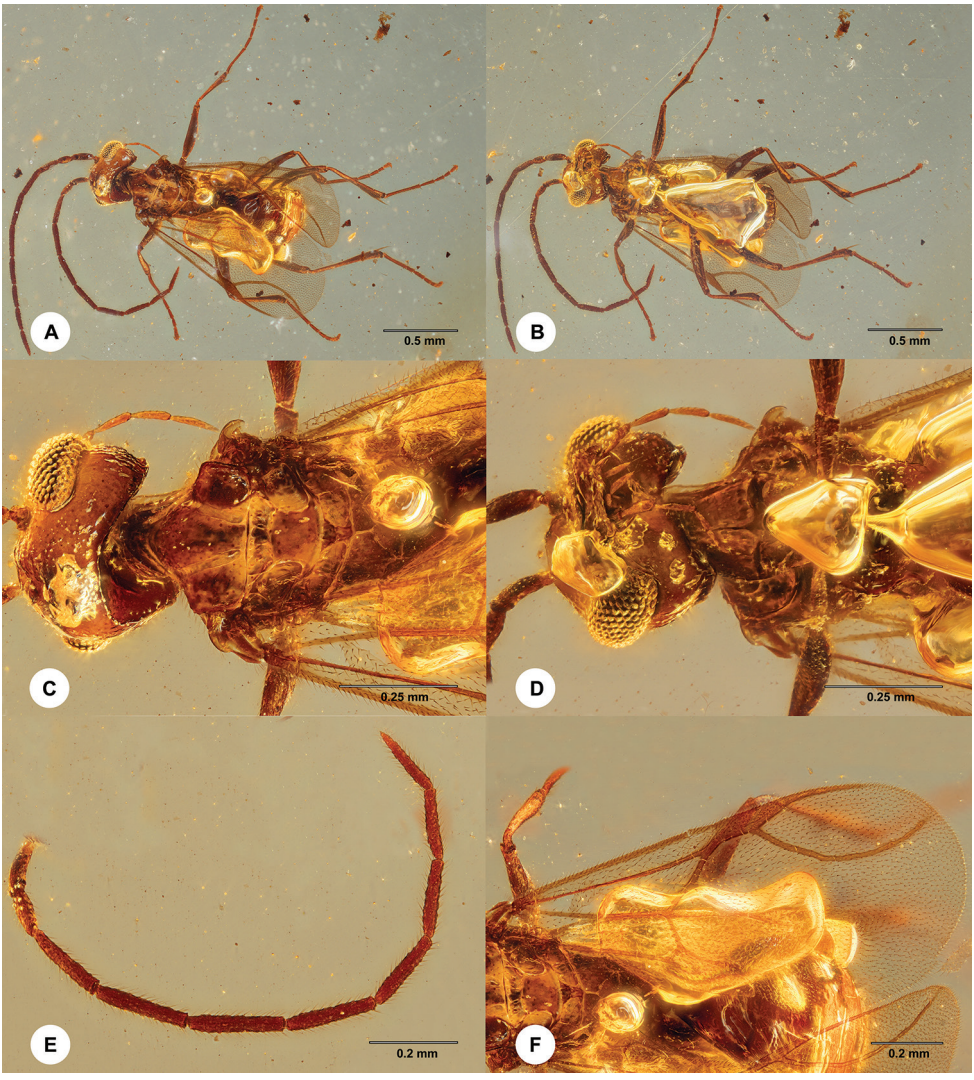

Figure 1. *Hybristodryinus castaneus* sp. nov., male, holotype **A** habitus, dorsal view **B** habitus, ventral view **C** head and mesosoma, dorsal view **D** head and mesosoma, ventral view **E** antenna **F** fore wing.

without a long deep longitudinal furrow, lateral ocelli not touching the occipital carina, posterior margin of the vertex not excised medially, notauli complete and separated posteriorly. However, the antenna of *H. castaneus* is slenderer, with antennomere 9 about six times as long as broad (less slender in *H. konbaung*, with antennomere 9 about twice as long as broad). Perkovsky et al. (2019) indicate "pronotum with lateral regions protruding" among the characters of the generic diagnosis. However, this character is not visible in all known males (as in *H. pyu* Perkovsky, Olmi, Müller & Martynova, 2019) and it is not present in *H. castaneus* sp. nov. (see description above). Except this character, *H. castaneus* meets with all other generic

diagnosis characters of *Hybristodryinus*. Therefore, we update the diagnosis of the genus by excluding this character.

Hybristodryinus zaifui Chen, Olmi & Perkovsky, sp. nov.

http://zoobank.org/6455A84B-B0A6-42E6-818E-F7B4F6586BE8
Figures 2, 3

Diagnosis. Female: macropterous, with disc of pronotum shaped as an isosceles triangle; notauli incomplete, reaching about 0.7 × length of mesoscutum (Fig. 2C).

Description. Female. Macropterous (Fig. 2A, B); length 1.8 mm. Apparently completely brown-testaceous. Antenna clavate, apparently almost hairless; antennomeres in following proportions: 6:4:5:4:4:3.5:3.5:3:3:4; antenna about three times as long as head (37:12), reaching metapectal-propodeal disc. ADOs apparently present in antennomeres 6–10 (Fig. 2E). Flagellomeres longer than wide; antennomere 9 about three times as long as broad. Head excavated, apparently unsculptured; clypeus not visible; mandible not visible; face slightly concave; occipital carina complete (Fig. 2C); vertex without two longitudinal keels connecting lateral ocelli to occipital carina; occiput deeply excavated; eye normally bulging; ocellar ratio: POL:OL:OOL:OPL = 1:2:2:1; temple about twice as long as OOL (4:2); greatest breadth of lateral ocellus longer than POL (2:1); frontal line apparently complete; palpal formula probably 6/3 (labial palpus not distinct). Pronotum crossed by anterior deep transverse impression between anterior collar and disc; disc humped, apparently isosceles triangle shaped, not deeply medially longitudinally excavated; posterior collar absent; anterior surface of pronotum not sculptured by longitudinal striae; sculpture of disc not distinct; pronotum shorter than head (6:12); anterior collar of pronotum much shorter than disc (2:4); pronotal tubercle reaching tegula. Epicnemium not visible. Mesoscutum apparently unsculptured, longer than pronotum (10:6). Notauli incomplete, reaching about 0.7 × length of mesoscutum (Fig. 2C). Mesoscutellum apparently unsculptured, shorter than mesoscutum (4:10). Metanotum shorter than mesoscutellum (2:4), with sculpture indistinct. Metapectal-propodeal complex shorter than mesoscutum (5:10), with disc reticulate rugose, with areolae very broad, with posterior corners lamina shaped, strongly projected posteriorly (Fig. 2D); propodeal declivity not visible. Fore wing (Fig. 2F) apparenly hyaline, not darkened, with the usual venation of Dryininae; pterostigma much longer than broad (10:2); second radial cell (2R1) open; stigmal vein (2r-rs&Rs) regularly curved; fore wing with usual three basal cells (C, R, 1Cu) clearly enclosed by pigmented veins. Hind wing not visible. Fore leg ratio: 7 (coxa): 5 (trochanter): 15 (femur): 9 (tibia): ? (tarsus only partly visible); enlarged claw (Fig. 3A, B) slightly shorter than protarsomere 5; protrochanter very slender and long, with long and slender proximal stalk, broadened after half-way; protrochanter less than seven times as long as broad (5:1); protarsomere 3 produced into hook; rudimentary claw not visible; arolium not visible; enlarged claw apparently with one subapical tooth, with one row of lamellae (number of lamellae uncertain). Protarsomere 5 (Fig. 3B) with inner side not visible; lamellae of protarsomere 5 not visible. Mid leg

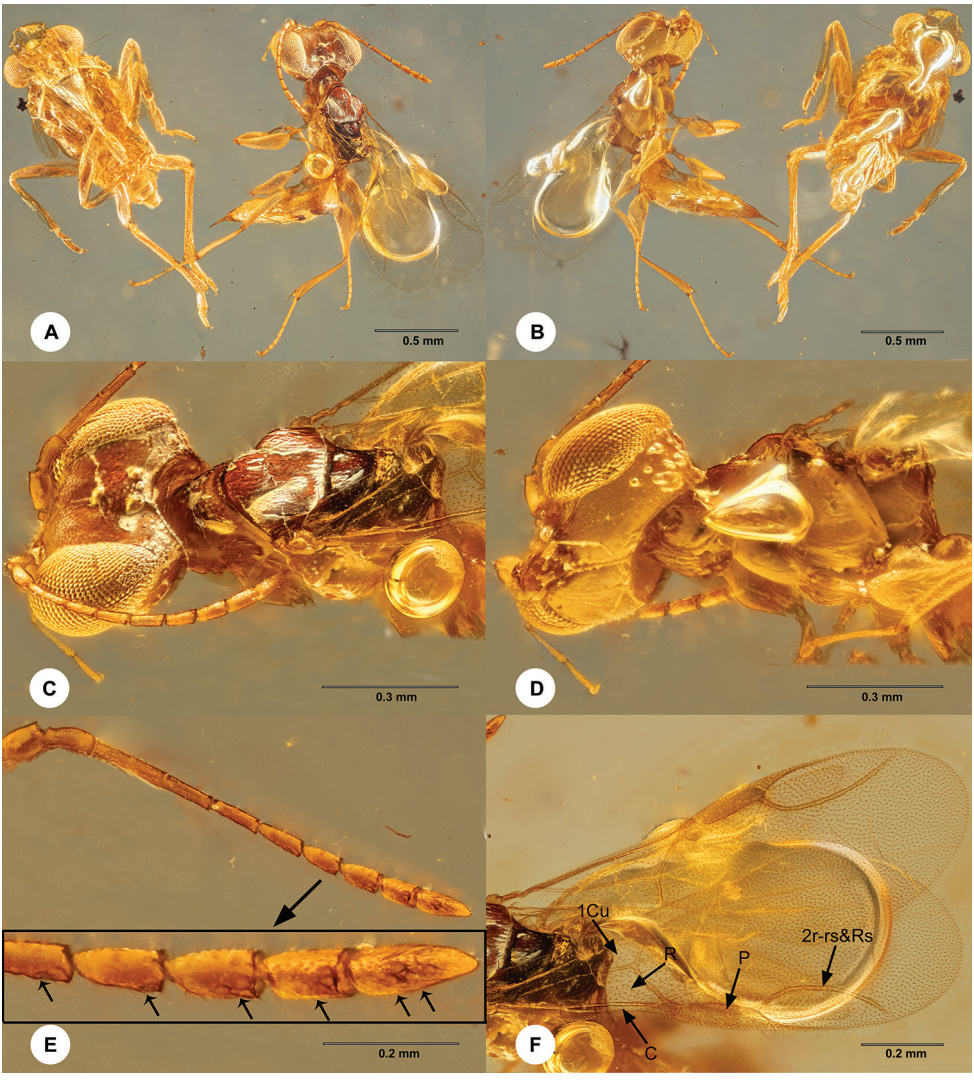

Figure 2. A right, *Hybristodryinus zaifui* sp. nov., female, holotype, habitus, latero-dorsal view; left, nymph of Perforissidae (Perforissidae), ventral view **B** left, *Hybristodryinus zaifui* sp. nov., female, holotype, habitus, latero-ventral view; right, nymph of Cixitettiginae, habitus, dorsal view **C, D** *Hybristodryinus zaifui* sp. nov., female, holotype: **C** head and mesosoma, dorsal view **D** head and mesosoma, latero-ventral view **E** antenna, arrows indicate the ADOs in the antennomeres 6–10 (one ADO per antennomere, except two ADOs in antennomere 10) **F** wings, 1Cu = cubital 1 cell, 2r-rs&Rs = stigmal vein, C = costal cell, P = pterostigma, R = radial cell.

ratio: 5 (coxa): 3 (trochanter): 13 (femur): 12 (tibia): 16 (tarsus). Mid trochanter short and broad. Hind leg ratio: 6 (coxa): 3 (trochanter): 18 (femur): 17 (tibia): 21 (tarsus). Metasomal petiole very short. Metasoma (excluding sting (Fig. 3C)) longer than mesosoma (39:27). Tibial spurs 1/1/2.

Male. Unknown.

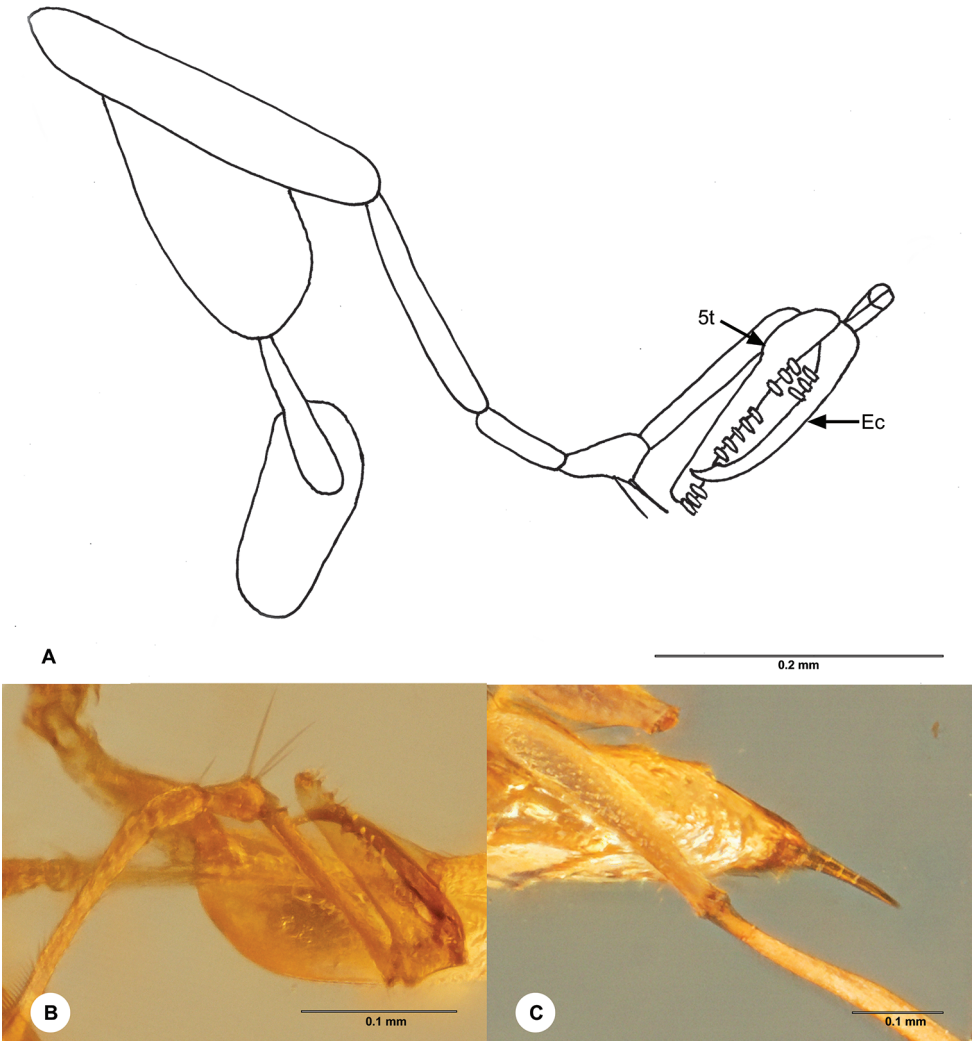

Figure 3. *Hybristodryinus zaifui* sp. nov., female, holotype **A** fore leg, 5t = protarsomere 5, Ec = enlarged claw **B** claw **C** sting.

Material examined. ***Holotype*****:** female (CNN-HYM-MA 2017087), Myanmar: specimen in mid-Cretaceous Burmese amber (about 99 Ma). Obtained from a mine situated in Northern Myanmar, Kachin State, Tanai Township, Hukawng Valley, SW of Tanai City (CNUB).

Etymology. The new species is named after the late Prof. Zaifu Xu (South China Agricultural University, Guangzhou, Guangdong, China), for his important contribution to the study of Chinese Dryinidae.

Remarks. For its isosceles triangle shaped pronotal disc, *H. zaifui* is similar to *H. nalae* Perkovsky, Olmi, Müller & Martynova, 2019, *H. concavifrons* Perkovsky, Olmi, Müller & Martynova, 2019, *H. resinicolus* Engel, 2005 and *H. ligulatus* Perko-

vsky, Olmi, Müller & Martynova, 2019. However, *H. zaifui* has incomplete notauli (Fig. 2C), reaching about 0.7 × length of mesoscutum, whereas in the other species the notauli are complete.

Partial keys to species of *Hybristodryinus*[*]

Females

1 Disc of pronotum isosceles triangle shaped (fig. 2A in Perkovsky et al. 2019)....**2**
– Disc of pronotum with normal shape, not isosceles triangle shaped (fig. 8A in Perkovsky et al. 2019) 6
2 Notauli incomplete, reaching about 0.7 × length of mesoscutum (Fig. 2C)... .....***H. zaifui* sp. nov.**
– Notauli complete, posteriorly separated (fig. 2A in Perkovsky et al. 2019)..... **3**
3 Pronotum with disc deeply excavated longitudinally..... .....***H. nalae* Perkovsky, Olmi, Müller & Martynova**
– Pronotum with disc not deeply excavated longitudinally.....**4**
4 Enlarged claw with two subapical teeth..... ..... ***H. concavifrons* Perkovsky, Olmi, Müller & Martynova**
– Enlarged claw without subapical teeth (fig. 7C in Perkovsky et al. 2019) **5**
5 Enlarged claw with distal apex sharp .....***H. resinicolus* Engel**
– Enlarged claw with distal apex spoon-shaped (fig. 7C in Perkovsky et al. 2019) .....***H. ligulatus* Perkovsky, Olmi, Müller & Martynova**

Males

2 Notauli incomplete, reaching about 0.5–0.9 × length of mesoscutum (fig. 5A in Perkovsky et al. 2019).....**3**
– Notauli complete, posteriorly separated (fig. 10A in Perkovsky et al. 2019).....**4**
3 Notauli reaching about 0.5 × length of mesoscutum ....***H. kayin* Perkovsky, Olmi, Müller & Martynova**
– Notauli reaching about 0.9 × length of mesoscutum .... ***H. karen* Perkovsky, Olmi, Müller & Martynova**
4 Lateral ocelli touching occipital carina (fig. 10A in Perkovsky et al. 2019)..... ..... ***H. pyu* Perkovsky, Olmi, Müller & Martynova**
– Lateral ocelli not touching occipital carina.....**5**
5 Antenna slenderer, with antennomere 9 about six times as long as broad (Fig. 1E) ..... ***H. castaneus* sp. nov.**
– Antenna less slender, with antennomere 9 about twice as long as broad ....***H. konbaung* Perkovsky, Olmi, Müller & Martynova**

[*] Modified from Perkovsky et al. 2019.

Discussion

Following the descriptions of the above two new taxa, the number of known *Hybristodryinus* species has increased from 14 to 16 (Perkovsky et al. 2019; Tribull et al. 2020; present paper), indicating that this extinct genus of Dryininae is the most diverse from Burmese amber, based on the known records. However, the main problem of this genus is the significant sexual dimorphism between the male and the female, so that it is impossible to associate the opposite sexes based on morphologic characters. This extreme sexual dimorphism is common to almost all pincer wasps (except the subfamily Aphelopinae, whose females are often similar to males, so that the association of the opposite sexes is less difficult). Males and females of extant species can be associated by rearing or DNA analysis, which apparently are not applicable to species in amber. Although males and females of this genus have been assigned to different new species, some of them are possibly the opposite sexes of one species. Therefore, currently there are two separate keys for *Hybristodryinus* species, one for females and one for males.

In the same subfamily Dryininae, *Dryinus* (13 species, see Martynova et al. 2020) is another relatively diverse genus in Burmese amber. However, *Dryinus* is an extant genus and has been reported not only from Burmese amber, but also from Priabonian Baltic, Scandinavian and Rovno amber (nine species, see Martynova et al. 2020; Perkovsky et al. 2020b), amber from upper Cenomanian Taimyr (Nizhnyaya Agapa River, Siberia, one species), Campanian Medicine Hat (Canada, one species) and Middle Miocene (Mexico, one species; Dominican Republic, nine species) (Martynova et al. 2020). In conclusion, there are 34 species of *Dryinus* reported from amber, much more than those of *Hybristodryinus*.

The hosts of *Hybristodryinus* are unknown, whereas the extant *Dryinus* are known to parasitize and prey on nymphs and adults of many Fulgoromorpha families: Acanaloniidae, Cixiidae, Dictyopharidae, Flatidae, Fulgoridae, Issidae, Lophopidae, Ricaniidae and Tropiduchidae (Olmi 1999; Guglielmino et al. 2013).

In Fig. 2A, B, *H. zaifui* is close to a nymph of unidentified Cixitettiginae (Hemiptera, Auchenorrhyncha, Perforissidae), a subfamily of extinct planthoppers known from Cretaceous amber (Barremian Lebanese, Barremian Jordanian, Albian Spanish, Cenomanian Burmese, Santonian Taimyr) and Aptian Bon Tsaagan Marl (Shcherbakov 2007; Petrulevicius et al. 2014; Rasnitsyn et al. 2016; Zhang et al. 2017; Perkovsky and Vasilenko 2019; Luo et al. 2020). Two genera and three species of the subfamily Cixitettiginae were described from Burmese amber (Luo et al. 2020); additional new taxa were reported, but not named (Shcherbakov 2007).

In *Hybristodryinus*, the antenna has the ADOs, which are sensorial structures present in dryinid females parasitizing Fulgoromorpha (Martynova et al. 2020). Perforissidae belong to Fulgoromorpha and therefore they could be hosts of *Hybristodryinus*. As mentioned previously, in mid-Cretaceous Burmese amber the most common dryinids were species of *Dryinus* and *Hybristodryinus*, both with antennal ADOs (Perkovsky et al. 2019; Martynova et al. 2020). *Hybristodryinus* is an extinct genus, whereas *Dryinus* is not extinct. The morphology of these two genera is similar (differences il-

lustrated in Martynova et al. 2020 and Perkovsky et al. 2019) and cannot explain why one genus is extinct and the other is not. It could be hypothesized that *Hybristodryinus* is extinct as their hosts became extinct (Perkovsky et al. 2019). From this point of view, as Perforissidae are extinct planthoppers, they are perfect as one of the hosts of *Hybristodryinus*. Finding of perforissids with a thylacium of dryinids could strengthen the above hypothesis.

The above conclusion contrasts with the hypothesis proposed by Perkovsky et al. (2019) and Martynova et al. (2020), who asserted that Perforissidae are less likely hosts of *Hybristodryinus*, because they are well known from *Baeomorpha* realm (see Perkovsky and Vasilenko 2019 and references therein), where *Hybristodryinus* is unknown, and are scarce from Burmese amber. However, already two genera and three species of Cixitettiginae (Perforissidae), were described from Burmese amber (Luo et al. 2020), indicating that Perforissidae from Burmese amber were more diverse than expected.

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