

# Burmese amber reveals a new stem lineage of whirligig beetle (Coleoptera: Gyrinidae) based on the larval stage

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Burmese amber is well known for preserving unique extinct lineages of insects. Here, we describe a new fossil beetle in its larval stage from Burmese amber. Bayesian and parsimony phylogenetic analysis of 50 morphological characters support this fossil as being sister to both the tribes Dineutini and Orectochilini, representing an extinct stem lineage in Gyrininae. It is described here as a new genus and species of whirligig beetle, *Chimerogyrus gigagalea* **gen. & sp. nov.**, a taxon that preserves remarkable intermediate features between the whirligig beetle tribe Gyrinini and the crown Orectochilini and Dineutini. This new taxon preserves key features for studying the evolution of characters within the larval stage of the Gyrinidae and highlights the importance of Burmese amber for preserving both stem and crown lineages present during the mid-Cretaceous, before the end-Cretaceous mass extinction event.

ADDITIONAL KEYWORDS: aquatic beetles – Cretaceous – fossil – larva – resin.

## INTRODUCTION

Burmese amber deposits from northern Myanmar are the richest Cretaceous amber deposits in the world, containing some of the most diverse palaeofauna known (Grimaldi & Engel, 2005; Shi *et al.*, 2012). These deposits represent the major fossiliferous Cretaceous amber known from southeast Asia and are among the most southerly located (Grimaldi *et al.*, 2002). Of further biological interest is the fact that Burmese amber was probably formed in a moist tropical palaeoenvironment, and it is known for exceptional preservation of minute structures and microscopic details affording improved interpretations of the extinct species it holds (Grimaldi *et al.*, 2002; Grimaldi & Engel, 2005; Daza *et al.*, 2016).

The age of Burmese amber has been estimated to be ~99 Myr using radiometric dating of zircons in the surrounding volcanic matrix (Shi *et al.*, 2012), thus

preserving taxa from the middle to Late Cretaceous (although the exact age of Burmese amber remains debated; Yu *et al.*, 2019). This time period is particularly interesting because it coincides with the rise and radiation of angiosperms as well as the appearance of many modern insect families and precedes the mass extinction event at the end of the Cretaceous (Grimaldi & Engel, 2005). To date, Burmese amber has revealed exceptional arthropod and entomological discoveries, such as the only known Mesozoic onychophoran (Grimaldi *et al.*, 2002), the only known Mesozoic member of Embiodea (Grimaldi & Engel, 2005) and the oldest member of the Strepsiptera (Grimaldi *et al.*, 2005), including the unlikely discovery of a minute strepsipteran larva, revealing the Mesozoic origin of parasitism in the order (Pohl *et al.*, 2018). Recently, Burmese amber has even led to the discovery of multiple new, extinct insect orders (Bai *et al.*, 2016; Poinar & Brown, 2017). Among the insects most well represented in Burmese amber are the beetles, the order Coleoptera (Grimaldi *et al.*, 2002; Grimaldi & Engel, 2005; Peris & Rust, 2020).

Whirligig beetles, the family Gyrinidae, are a relatively small aquatic beetle family in the suborder

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Adephaga, containing ~900 species (Short, 2018). Recent phylogenomic studies have supported Gyrinidae as the sister lineage to all other adephagans (Baca *et al.*, 2017). Consistent with this relationship, phylogenetic tip-dating estimates have shown Gyrinidae to be a relatively old beetle family, with an estimated origin sometime between the Late Permian and Early Triassic, ~255 Mya (Gustafson *et al.*, 2017). The family has a good fossil record spanning the Mesozoic from the Early Jurassic to the late Cenozoic (Hatch, 1927; Nel, 1989; Gustafson, *et al.*, 2017). Older fossil taxa have been attributed to the Gyrinidae, such as those from the Triassic (i.e. *Triadogyrus sternalis* Ponomarenko, 1977; by Beutel *et al.*, 2013) and from the Permian (i.e. *Tunguskagyru planus* Yan *et al.*, 2018; by Yan *et al.*, 2018), but these have been rebuked as relying upon misinterpretations of morphological characters and might not be members of Gyrinidae, stem or otherwise (Ponomarenko & Prokin, 2015; Kirejtshuk & Prokin, 2018).

Among fossil Gyrinidae, specimens are known from Baltic amber (Hatch, 1927). Most recently, a larva, *Cretogyru beuteli* Zhao *et al.*, 2019, was described from Burmese amber (Zhao *et al.*, 2019). The larvae of several extant gyrinid genera remain unknown, including key taxa, such as *Spanglerogyru* Folkerts, 1979 and *Heterogyru* Legros, 1953, representing the subfamilies Spanglerogyrinae and Heterogyrinae (Miller & Bergsten, 2012), and for some genera in the subfamily Gyrininae, such as the dineutine genus *Porrorynchus* Laporte, 1835 and the gyrinine genus *Metagyru* Brinck, 1955 (Michat *et al.*, 2017b). Recent efforts have been made not only to describe the general larval morphology of different gyrinid genera formally, but also to provide a formal system of chaetotaxy, allowing chaetotaxic analysis and improved homology across larval characters for use in future phylogenetic studies (Archangelsky & Michat, 2007; Michat *et al.*, 2010, 2016, 2017b; Michat & Gustafson, 2016; Colpani *et al.*, 2018).

Here, we describe a new late-instar gyrinid larva exquisitely preserved in Burmese amber, such that it allows the study and description of its chaetotaxy. Before the description of the new larva, we conduct phylogenetic analyses in order to infer its relationship to currently known gyrinid genera. Finally, we provide a discussion of the key morphological and chaetotaxic characters present in the new Burmese amber specimen, comparing them with the currently known extinct and extant gyrinid larvae.

## MATERIAL AND METHODS

### METHODS FOR THE STUDY OF LARVAE

Material examined in this study comes from the following institutions: Grey Gustafson research

collection, currently at the University of Kansas, Lawrence, KS, USA (GTGC); Snow Entomological Collection, University of Kansas, Lawrence, KS, USA (SEMC); and Zoologische Staatssammlung München, Munich, Germany (ZSMG).

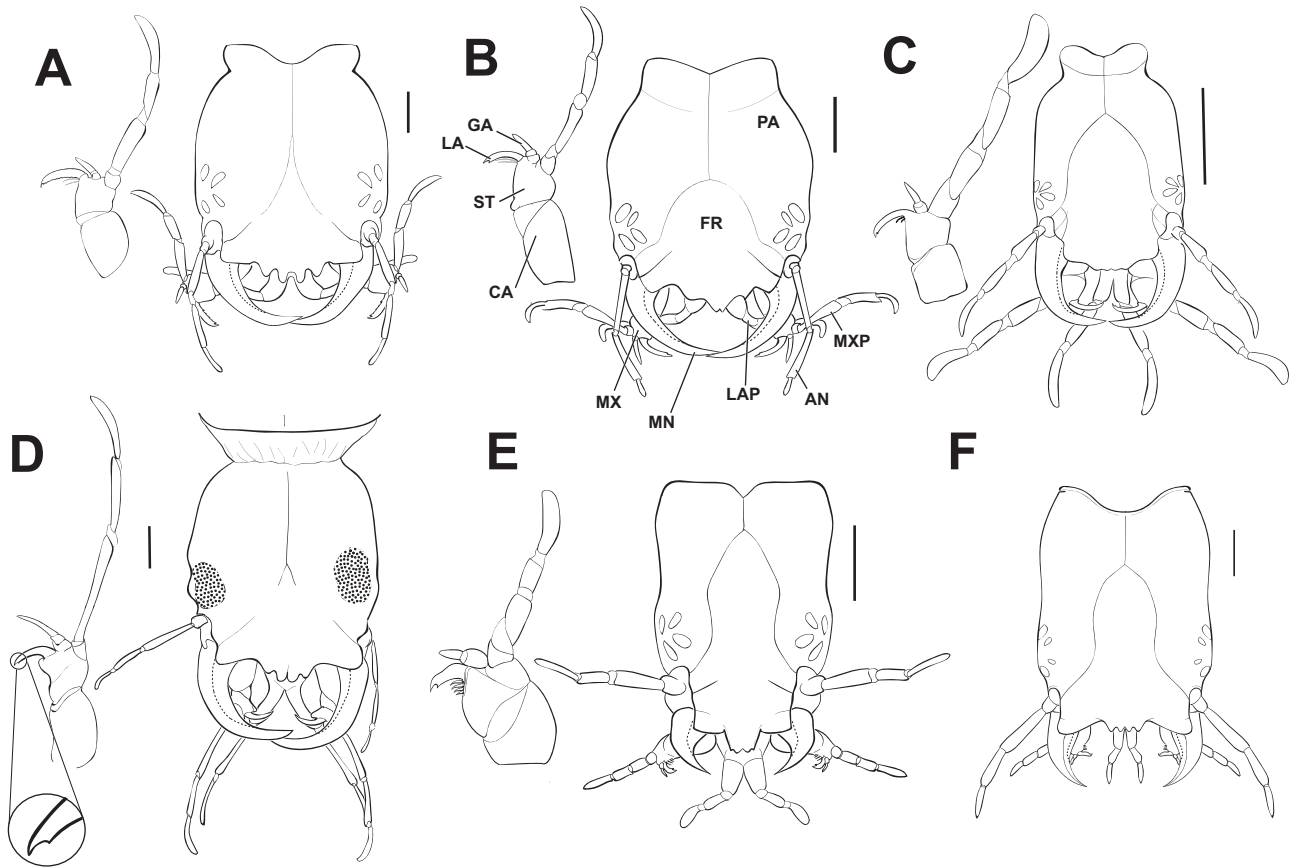
Specimens were examined using an Olympus SZX16 microscope with a 2× perfluorocarbon (PFC) ocular lens attachment. Drawings were first made using a camera lucida attached to the microscope, then scanned and digitally inked using Adobe Illustrator. Habitus and other images were obtained using a Visionary Digital BK+ light imaging system ([www.visionarydigital.com](http://www.visionarydigital.com); R. Larimer). Images were then edited using Adobe Photoshop to improve clarity and colour.

The amber specimen was examined *in situ*, whereas modern comparative larval material was examined either submerged in ~60% ethanol or in glycerin with a top layer of distilled water. Given that the amber taxon described below is not a first instar, primarily third instar larvae were selected for comparative study during the description and in order to code morphology for the species examined as part of the phylogenetic analysis. Because the larval specimen in amber is intact, larvae examined comparatively were also studied intact, rather than being cleared, dissected and mounted on glass slides, as is typically done for larval descriptive work.

Terminology follows previous papers dealing with the larval morphology of Gyrinidae (Archangelsky & Michat, 2007; Michat *et al.*, 2010, 2016, 2017b; Michat & Gustafson, 2016; Colpani *et al.*, 2018). The following abbreviations are used: AN, antennae; CO, coxa; FE, femur; FR, frontoclypeus; LA, labium; MN, mandible; MX, maxilla; PA, parietal; PT, pretarsus; TA, tarsus; TI, tibia; TR, trochanter. Because the preservation of the specimen in amber prevents full standardized views of structures, a morphometric analysis was not performed. Total body length, *L*, was measured from the mandibles to the apex of the abdominal gills on segment IX. Total body width, *W*, was taken from the widest point of the abdomen, approximately abdominal segment V.

Visible primary setae of the cephalic capsule, head appendages and legs were included in chaetotaxic analysis, but pores were not distinguishable in the amber fossil. Setae were coded using the two capital letter abbreviations corresponding to the structure on which they were located in addition to a number. Chaetotaxic coding was done in comparison to the primary chaetotaxy of prior studies on larvae of Gyrinidae (Archangelsky & Michat, 2007; Michat *et al.*, 2010, 2016, 2017b; Michat & Gustafson, 2016; Colpani *et al.*, 2018) and other adephagans (Bousquet & Goulet, 1984; Nilsson, 1988; Alarie *et al.*, 2004,

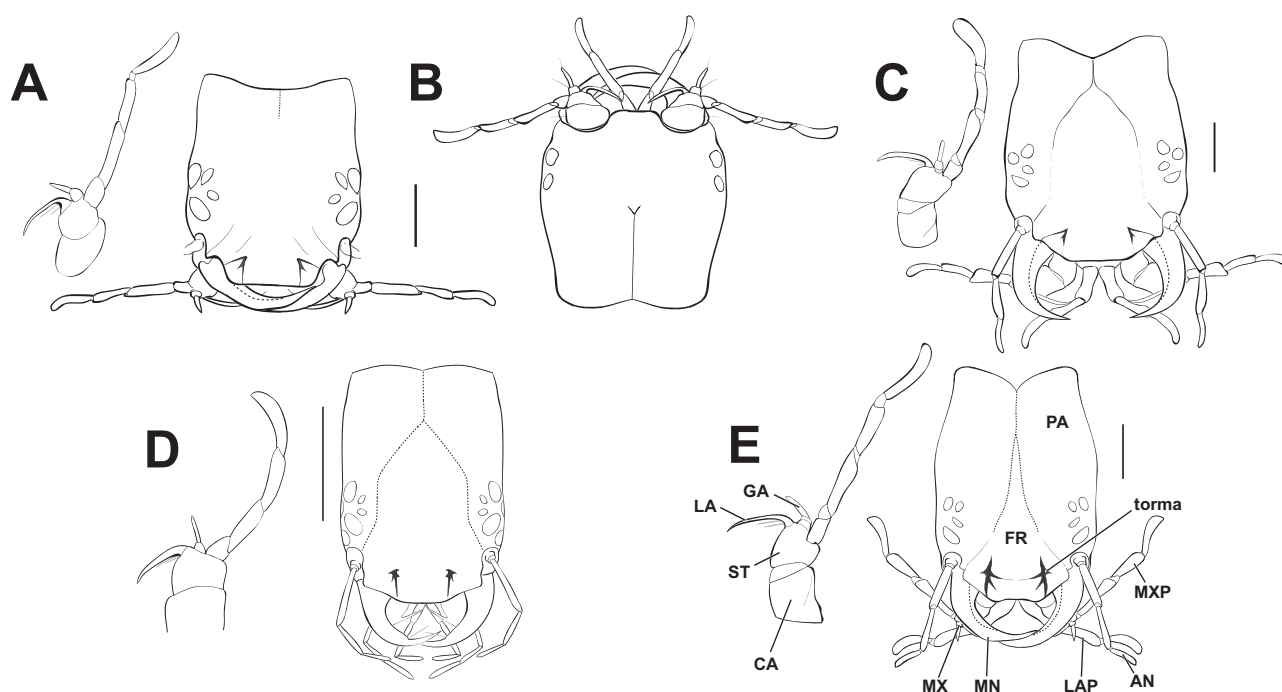




**Figure 1.** Cephalic capsule of larvae of extant genera of the Dineutini and Gyrinini in dorsal view (to scale), including left maxilla in ventral view (not to scale), except for D, dorsal view of right maxilla. A, *Macrogyrus ellipticus* (Brullé, 1836). Scale bar: 0.25 mm. B, *Dineutus* sp. from Africa. Scale bar: 0.5 mm. C, *Enhydrus sulcatus* (Wiedemann, 1821). Scale bar: 0.50 mm. D, *Cretogyrus beuteli*† Zhao *et al.*, 2019. Scale bar: 0.20 mm. Drawn from digital images provided by X. Zhao and after Zhao *et al.*, (2019). E, *Gyrinus vicinus* Aubé, 1838. Scale bar: 0.25 mm. F, *Aulonogyrus strigosus* (Fabricius, 1801). Scale bar: 0.20 mm. After Beutel & Roughley (1994). Abbreviations: AN, antenna; CA, cardo; FR, frons; GA, galea; LA, lacinia; LAP, labial palp; MN, mandible; MX, maxilla; MXP, maxillary palp; PA, parietal; ST, stipes.

- frontoclypeus, lacking teeth (Fig. 2A, C–E). This has been a proposed autapomorphy of the Orectochilini (Beutel & Roughley, 1994).
8. Frontoclypeal teeth: (0) distinct, all four widely separated and relatively large; (1) less distinct, teeth often reduced, sometimes situated on anteriorly protruding medial lobe and/or asymmetrical in form. In the gyrid larval genera retaining frontoclypeal teeth there are typically four present, either all distinct (Fig. 1A, F) or variously reduced (Fig. 1C), asymmetrical (Fig. 1B, D) and/or situated on the anteriorly protruding medial process (Fig. 1E).
  9. Tormae: (0) absent; (1) present. The tormae (Noars, 1956) are strong internal sclerotizations separating the medial lobe of the frontoclypeus from the lateral lobes (Figs 2A, C–E) and are a likely autapomorphy of the Orectochilini (Beutel & Roughley, 1994).
  10. Mandible size: (0) shorter, less than half the length of cephalic capsule; (1) longer, more than half the length of the cephalic capsule. Shorter mandibles are found in the outgroup *Halipilus* larva and in the Gyrinini (Fig. 1E, F) within Gyrinidae, whereas larvae of the Orectochilini and Dineutini have elongate and more crescent-shaped mandibles (Figs 1A–D, 2A–E).
  11. Mandible shape: (0) crescent shaped; (1) triangular in form. Crescent-shaped mandibles are found within the outgroup selected, a member of the Haliplidae and the Dineutini and Orectochilini (Figs 1A–D, 2A–E), whereas the Gyrinini appear to have a unique derived mandible that is triangular in form, rather than crescent shaped.
  12. Mandibular denticles: (0) absent; (1) present. Most larval members of the Dineutini have denticles on the inner margin of the mandible (Archangelsky & Michat, 2007; Michat *et al.*, 2016, 2017b; Michat & Gustafson, 2016).

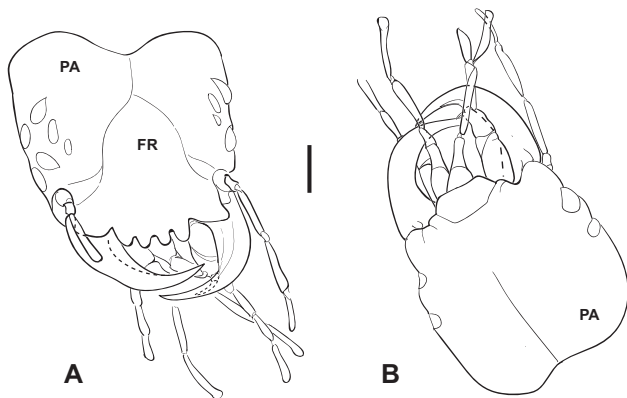




**Figure 2.** Cephalic capsule of larvae of extant genera of the Orectochilini in dorsal view (to scale), including left maxilla in ventral view (not to scale). A, *Gyretes* sp. from Texas. Scale bar: 0.25 mm. B, *Gyretes* sp. from Texas. Cephalic capsule in ventral view. C, *Orectogyrus* Régimbart, 1884 sp. '2'. Scale bar: 0.25 mm. D, *Orectochilus villosus* (Müller, 1776). Scale bar: 0.50 mm. Cephalic capsule after Noars (1956) and maxilla after Říha (1952). E, *Patrus* sp. Scale bar: 0.25 mm. Abbreviations: AN, antenna; CA, cardo; FR, frons; GA, galea; LA, lacinia; LAP, labial palp; MN, mandible; MX, maxilla; MXP, maxillary palp; PA, parietal; ST, stipes.

13. Mandibular retinaculum: (0) present; (1) absent. The presence of a mandibular retinaculum is considered to be an ancestral condition within larvae of Adephaga (Beutel, 1993). Within Gyrinidae, larvae of the Gyrinini have the retinaculum distinctly present (Beutel & Roughley, 1994), whereas most Dineutini and Orectochilini completely lack the retinaculum (Beutel & Roughley, 1994). Within *Macrogyrus*, one of the mandibular denticles could be interpreted as a vestigial retinaculum (Arndt *et al.*, 1993; Beutel & Roughley, 1994; Michat & Gustafson, 2016).
14. Mandibular channel apical opening: (0) wide; (1) narrow. The narrower apical opening of the mandibular channel of larvae of the Dineutini and Orectochilini is considered a derived feature, relative to the wide opening within the Gyrinini (Beutel & Roughley, 1994).
15. Ventral mandibular joint: (0) visible in ventral view; (1) not visible in ventral view, obscured by the cardo. Beutel & Roughley (1994) considered a visible ventral mandibular joint, i.e. not obscured by the cardo, to be a derived condition associated with an elongate cardo (character 16 below) and synapomorphic of larvae of

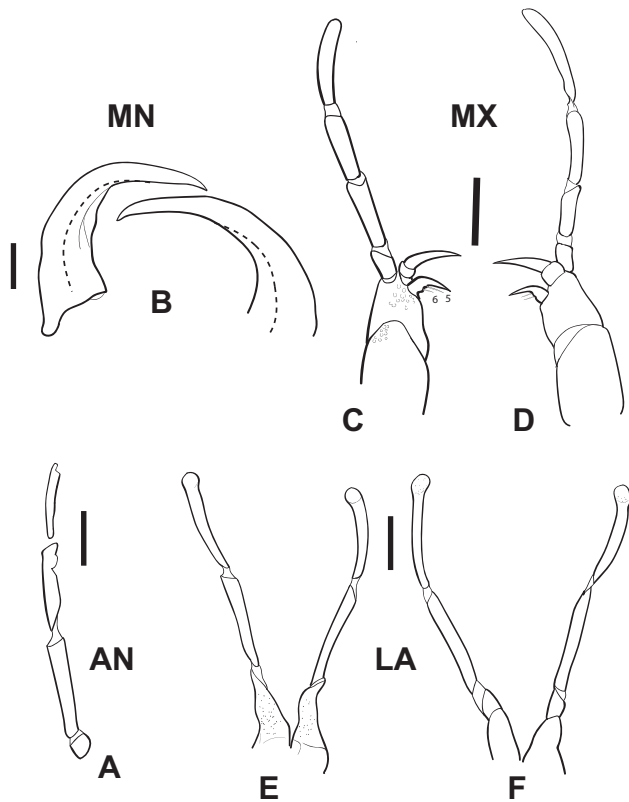
the Dineutini and Orectochilini. They considered the condition within larvae of the Gyrinini where the ventral joint is obscured by a relatively large cardo to be the ancestral condition, citing a similar state found in Haliplidae and *Trachypachus* Motschulsky, 1844. However, within the North American *Haliplus* Latreille, 1802 larva studied here, the ventral mandibular joint is visible, even without an elongate cardo. Likewise, illustrations of the ventral view of the larval head of the Palaearctic *Haliplus apicalis* (Thomson, 1868) show a visible ventral mandibular joint (Van Vondel, 2005). Illustrations of the larva of *Hygrobia* Latreille, 1804 also show a visible ventral mandibular joint (Bertrand, 1972). Furthermore, a larva of *Gyretes* from Texas examined in the present study, despite having a relatively elongate cardo (Fig. 2A), has the ventral mandibular joint obscured owing to a lateral expansion of the cardo (Fig. 2B), which appears to be an autapomorphy within *Gyretes*. Given that a visible ventral mandibular joint does not appear to be associated uniquely with the derived elongate cardo of larvae of Dineutini and Orectochilini, we here instead treat an obscured ventral mandibular joint as derived, given that it appears less commonly within



**Figure 3.** *Chimerogyrus gigagalea*† line drawings of cephalic capsule. Scale bar: 0.16 mm. A, dorsal view. B, ventral view. Abbreviations: FR, frons; PA, parietal.

Gyrinidae, and within distantly related lineages, such as the Gyrinini and *Gyretes*, which exhibit other derived features of the maxilla (see discussion under character 18).

16. Cardio of maxilla: (0) short, less than one-fifth the length of the cephalic capsule in ventral view; (1) elongate, at least one-fifth the length of the cephalic capsule in ventral view. An elongate cardo of the maxilla is considered a synapomorphy of larvae of the Dineutini (Fig. 1A–D) and the Orectochilini (Fig. 2) (Beutel, 1993; Archangelsky & Michat, 2007). Larvae of the Gyrinini (Figs 1E, F) have a relatively short and broader cardo (Crespo, 1986a, b; Beutel & Roughley, 1994; Michat *et al.*, 2010).
17. Cardio and stipes: (0) joined by a hinge; (1) without hinge, forming a functional unit (Beutel, 1993). The cardio and stipes of the maxilla of gyrinid larvae have a hinge with a mesal membrane (visible on the ventral surface; Figs 1A–E, 2C, E), a trait shared with larvae of other beetle suborders, but not with other adephagans (Beutel, 1993). Other adephagan larvae instead have the cardio and stipes fused into a functional unit, thus this feature is considered a derived synapomorphy (Beutel, 1993; Beutel & Roughley, 1994).
18. Stipes of maxilla: (0) short, length as measured from lateral margin less than the length of the lateral margin of the cardo; (1) elongate, length as measured from lateral margin approximately equal in length to lateral margin of cardo. The stipes of all currently known gyrinid genera is relatively short compared with the cardo (Figs 1A–E, 2A, C–E). Our amber specimen is unique in having an elongate stipes that is similar in length to the cardo (Figs 3B, 4C, D).
19. Small apical hook-like setae on internal margin of stipes: (0) absent; (1) present. Known larvae of the Gyrinini [i.e. *Gyrinus* Geoffroy, 1762 (Fig. 1E) and *Aulonogyrus* Motschulsky, 1853 (Fig. 1F)] have the internal margin of the stipes apically with a series of small, hook-like setae (Schjødte, 1861, 1872; Crespo, 1986b; Beutel & Roughley, 1994; Michat *et al.*, 2010). This appears to be an autapomorphy of Gyrinini, because they are absent in Dineutini and Orectochilini.
20. Maxillary palpomeres I–III: (0) relatively short and broader; (1) elongate and gracile. Elongate and slender maxillary palpomeres appear to be a unique synapomorphy uniting larvae of the Dineutini (Figs 1A–D) and the Orectochilini (Fig. 2A–E) within the Gyrinidae (Beutel, 1993). Broader and less elongate palpomeres similar to those exhibited in the Gyrinini (Fig. 1E, F) are found in other Adephagan groups (Beutel, 1993).
21. Maxillary galea: (0) relatively short, less than length of lacinia; (1) approximately equal to length of lacinia; (2) long, greater in length than lacinia. Within Gyrinidae, most larvae have the maxillary galea relatively short, being smaller in size than the lacinia (Figs 1A, C, E, F, 2) or roughly similar in size (Fig. 1B, D). Our amber specimen (Fig. 4C, D) clearly has a galea that is longer than the lacinia, a feature unique to this taxon.
22. Lacinia: (0) present and well developed; (1) absent and/or strongly reduced. All gyrinid genera have a well-developed lacinia, whereas the outgroup taxon *Haliphus* has a strongly reduced lacinia.
23. Lacinia length: (0) short, at most one-fifth the length of mandible; (1) elongate, at least one-quarter the length of mandible. The Dineutini and Orectochilini larvae exhibit an elongate lacinia, whereas the Gyrinini and our amber specimen have a short lacinia. Given that the current phylogenetic hypotheses support Gyrinini as sister to Orectochilini and Dineutini, a short lacinia is treated as the ancestral condition.
24. Lacinia form: (0) distinctly narrower; (1) broader. In addition to being relatively short in length, the lacinia of the Gyrinini is broad throughout their length (Fig. 1E). The lacinia of Orectochilini, Dineutini and our amber specimen is either narrow throughout its length (Figs 1A–D, 2) or distinctly narrowed distally (Fig. 4D).
25. Lacinal posterior margin dentation: (0) absent; (1) present only basally; (2) present along entirety of margin. The lacinia of larval *Macrogyrus* has a unique feature in that the posterior margin has dentation along its length (Fig. 1A; Arndt *et al.*, 1993; Michat & Gustafson, 2016).
26. Indentation on posterior margin of lacinia: (0) absent; (1) present. The lacinia of larval *Dineutus* (Fig. 1B; Michat *et al.*, 2017b), *Enhydrus* (Fig. 1C; Michat *et al.*, 2016), *Cretogyrus* (Fig. 1D) and *Gyrinus* (Fig. 1E; Michat *et al.*, 2010) has an indentation on the posterior margin near the apex.

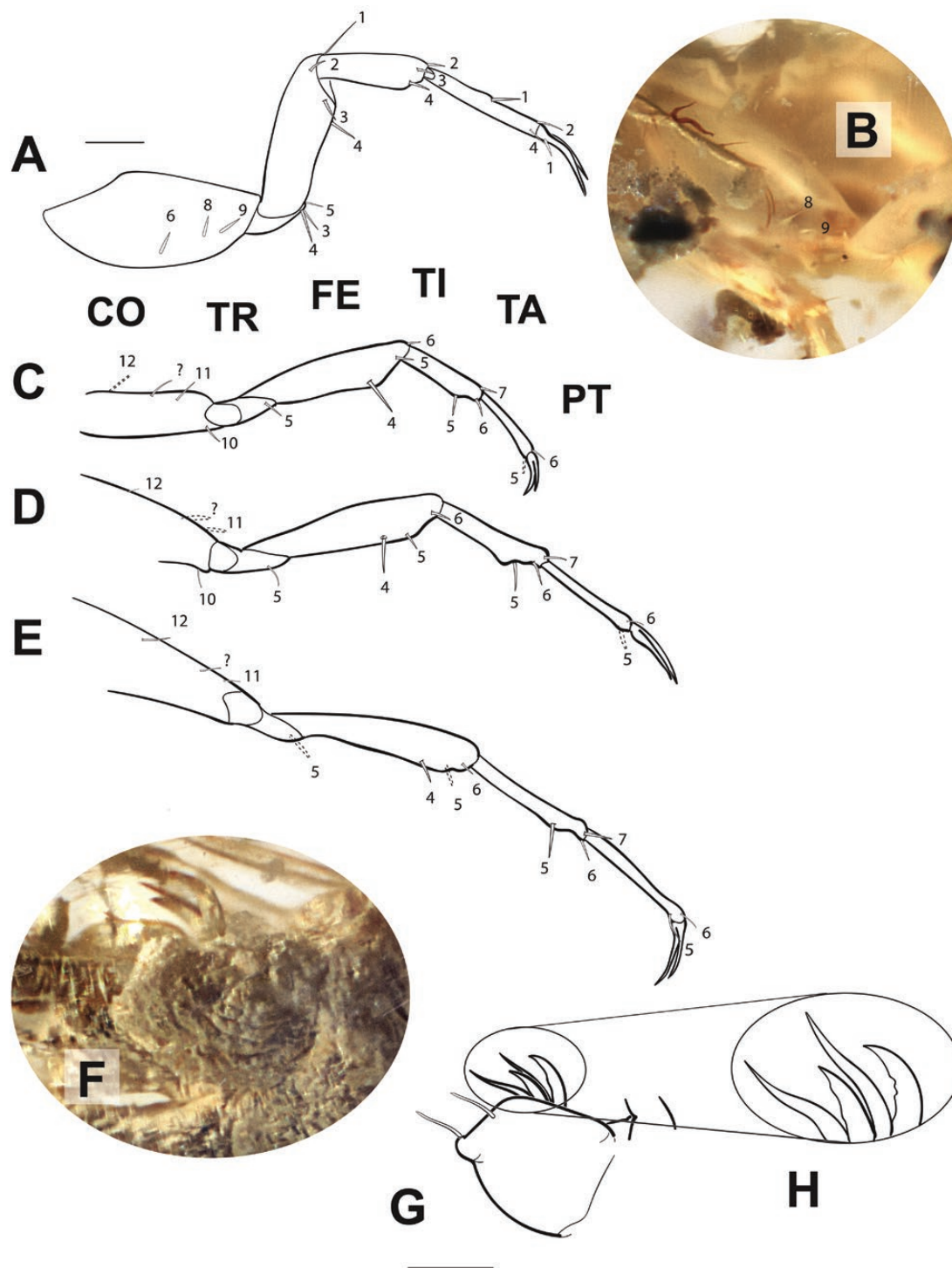


**Figure 4.** *Chimerogyrus gigagalea*† line drawings. All scale bars: 0.10 mm. A, left antenna in dorsal view. B, mandibles in dorsal view. C, D, left maxilla. C, dorsal view. D, ventral view. E, F, labium. E, dorsal view. F, ventral view. Abbreviations: AN, antenna; LA, labium; MN, mandible; MX, maxilla.

27. MX5 and MX6: (0) present; (1) absent. The setae MX5 and MX6 are present in all Orectochilini and Dineutini genera (Říha, 1952; NOARS, 1956; ARCHANGELSKY & MICHAT, 2007; Michat *et al.*, 2016, 2017b; Michat & Gustafson, 2016; Figs 1A–C, 2) and in our amber specimen (Fig. 4C, D). These are absent from their usual position in Gyrinini, probably incorporated into the row of hook-like setae (Michat *et al.*, 2010; Fig. 1E). The character state for *Cretogyrus* is currently unknown.
28. MX5 and MX6 length: (0) both long and subequal in length; (1) MX6 strongly reduced in length relative to MX5; (2) both MX5 and MX6 short.
29. Prementum: (0) divided medially; (1) fused medially. The divided prementum as found in the larvae of Gyrinidae is considered an important autapomorphy of the family (Beutel & Roughley, 1994).
30. Labial palpomeres I–II: (0) relatively shorter; (1) relatively longer and narrower in form. Presence of elongate labial palpomeres is a likely synapomorphy of the Dineutini and Orectochilini (Beutel & Roughley, 1994), including our amber specimen.

### Thorax

31. Pronotum: (0) less developed; (1) well developed and shield shaped. Larvae of all known Gyrinidae have a large sclerotized pronotum, which is more developed than the pronotum present within the Haliplidae and other ‘Hydradephaga’.
32. CO6, CO8 and CO9 form: (0) narrow and hair like; (1) stout and spine like. Our amber specimen has an autapomorphy of setae CO6, CO8 and CO9 in that they are stout and spine like (Fig. 5B) rather than narrow and hair like.
33. Femur form: (0) broadened distally, narrower proximally; (1) not noticeably broadened distally. The femur of larval *Gyrinus* (Michat *et al.*, 2010) and of our amber specimen is broadened distally (Fig. 5A–E), whereas those of Dineutini and Orectochilini are narrower and not broadened distally.
34. TI7 form: (0) spine like; (1) hair like. Seta TI7 is spine like in Haliplidae, Meruidae, Aspdytidae and several Dytiscidae (Nilsson, 1988; Alarie & Bilton, 2005; Alarie *et al.*, 2011; Michat *et al.*, 2014a, 2017a). It is also spine like in our amber specimen (Fig. 5C–E), whereas in other Gyrinidae (Michat *et al.*, 2010, 2017b) and Adephaga (e.g. Hygrobiidae, Noteridae, several Dytiscidae) it is hair like (Alarie *et al.*, 2004; Michat *et al.*, 2017a; Urcola *et al.*, 2019).
35. Tarsus form: (0) broader, less elongate and cylindrical in appearance; (1) narrower, elongate and strongly cylindrical in appearance. The tarsus of members of the Gyrinini is broader and less elongate in appearance (Crespo, 1986b; Costa *et al.*, 1988; Michat *et al.*, 2010).
36. TA1 size: (0) long; (1) short. Our amber specimen is unique in having an elongate seta TA1 (Fig. 5A), relative to other Gyrinidae, which have TA1 shortened (Crespo, 1986b; Michat *et al.*, 2017b).
37. TA1 position: (0) at tarsal mid-length; (1) situated more distally towards or at tarsal apex. In our amber specimen and other adephagan larvae (Nilsson, 1988) TA1 is situated at mid-length on the dorsal surface of the tarsus (Fig. 5A), whereas all other known gyrinid larvae, with the exception of *Dineutus* and some *Gyretes*, have TA1 positioned distally towards the tibial apex (Crespo, 1986b; Michat *et al.*, 2010, 2017b; Colpani *et al.*, 2018).
38. Pretarsal claw number: (0) two claws; (1) one claw. All Gyrinidae have two thoracic claws compared with the derived condition of a single claw found in Haliplidae (Van Vondel, 2005).
39. Pretarsal claw form: (0) narrow, weakly curved; (1) broader, more strongly curved. The claws of the Gyrinini and some Orectochilini, with the exception of *Gyretes*, are broader and more strongly curved compared with the narrow and weakly curved claws typical of Dineutini and our amber specimen (Fig. 5A–E).



**Figure 5.** *Chimerogyrus gigagalea*† line drawings and *in situ* images. A–E, thoracic legs with setae labelled. Scale bar: 0.16 mm. A, left metathoracic leg, anterior view. B, *in situ* image of left metacoxa in anterior view, showing form of CO8 and CO9. C, right prothoracic leg, posterior view. D, right mesothoracic leg, posterior view. E, right metathoracic leg, posterior view. F–H, abdominal segment X and terminal hooks. F, *in situ* image of abdominal segment X and terminal hooks. G, line drawing of abdominal segment X and terminal hooks. Scale bar: 0.16 mm. H, terminal hooks. Abbreviations: CO, coxa; FE, femur; PT, pretarsus; TA, tarsus; TI, tibia; TR, trochanter.



40. Spinulae on pretarsal claws: (0) absent; (1) present. The claws of larval Gyrinini have spinulae located along the ventral surface (Crespo 1986b; Michat *et al.*, 2010).
41. Pretarsal claw length: (0) claws equal in length; (1) anterior claw distinctly longer than posterior claw. The claws of the larvae of most Dineutini, with the exception of *Dineutus* and our amber specimen (Fig. 5D, E), are asymmetrical in length, with the anterior claw being distinctly longer than the posterior claw.
42. Prothoracic ventral sclerite: (0) absent, thorax membranous except for small sclerites associated with regions articulating with coxae; (1) present, as a large sclerite situated anteriorly. Larvae of the Dineutini (Michat *et al.*, 2016, 2017b), and the Orectochilini examined here, exhibit a prothoracic ventral sclerite that is situated anteriorly between the prothoracic legs. Our amber specimen lacks this sclerite, instead exhibiting a state similar to that found within the Gyrinini, in which there are small sclerites associated with the region of the thorax articulating with the procoxae.
43. Prothoracic ventral sclerite size: (0) smaller, at most approximately one-third the length of the pronotum; (1) Larger, greater than approximately one-third the length of the pronotum. The prothoracic ventral sclerite of *Enhydrus* (Michat *et al.*, 2016) and a few other orectochiline genera is larger in size than that exhibited by the Dineutini.
44. Abdominal tracheal gills: (0) absent; (1) present. Larvae of all known Gyrinidae have well-developed tracheal gills present on abdominal segments I–IX.
45. Tracheal gill spinulae: (0) absent; (1) present. Larvae of *Enhydrus* are unique in tracheal gill spinulae, thus appearing non-plumose (Michat *et al.*, 2016).
46. Abdominal segment X form: (0) shorter and rounder in appearance, not pygopodiform; (1) elongate and pygopodiform; (2) with long post-anal prolongation.
47. Abdominal segment X spinulae: (0) absent; (1) present. *Enhydrus* also appears unique in having spinulae on abdominal segment X (Michat *et al.*, 2016), not present in any of the other larvae examined.
48. Abdominal segment X setae: (0) absent; (1) two long setae present; (2) more than two setae present. Most gyrinid larvae have four or more setae present on abdominal segment X. Our amber specimen and most Orectochilini genera, with the exception of *Gyretes*, have two long setae present (Fig. 5G).
49. Terminal hooks on abdominal segment X. (0) absent; (1) present. All known gyrinid larvae have four terminal hooks situated apically on abdominal segment X.
50. Terminal hooks form: (0) medial and lateral hooks similar in form; (1) medial hooks different in form from lateral hooks. Most gyrinid larvae have all four terminal hooks similar in form. However, a couple of living species from the genus *Gyrinus* in the subgenus *Neogyrinus*, such as *Gyrinus (Neogyrinus) ovatus* (Crespo 1986a) and *Gyrinus (Neogyrinus) gibbus* (Costa *et al.*, 1988), have medial and lateral hooks different in form. Our amber specimen also shows this strange derived character (Fig. 5F–H).

#### PHYLOGENETIC ANALYSES

Bayesian inference (BI) and parsimony analyses (PS) recover similar tree topologies (Fig. 6; Supporting Information, Figs S1–S4) with support for the currently recognized tribes and their relationships within the Gyrininae (Gustafson *et al.*, 2017). Although all analyses place *Cretogyrus* as nested in *Dineutus*, this is likely a result of the large amount of missing data for *Cretogyrus* owing to the lack of chaetotaxic analysis in the original description (Zhao *et al.*, 2019), because this taxon was coded, in part, from the literature and from additional high-resolution images of the head provided by X. Zhao, but this did not allow the study of maxillary chaetotaxy. All phylogenetic analyses strongly support our amber specimen as being sister to both Dineutini and Orectochilini [BI without *Cretogyrus* (Fig. S1) posterior probability (pp) = 96; BI with *Cretogyrus* (Fig. S2) pp = 97; PS with and without *Cretogyrus* (Figs S3, S4) bootstrap (bs) = 90]. Both Bayesian and parsimony analysis support *Cretogyrus beuteli* as being within crown Dineutini, with parsimony strongly supporting this placement (Fig. 6).

#### SYSTEMATIC PALAEOLOGY

ORDER COLEOPTERA LINNAEUS, 1758

FAMILY GYRINIDAE LATREILLE, 1810

SUBFAMILY GYRININAE LATREILLE, 1810

STEM GROUP DINEUTINI + ORECTOCHILINI

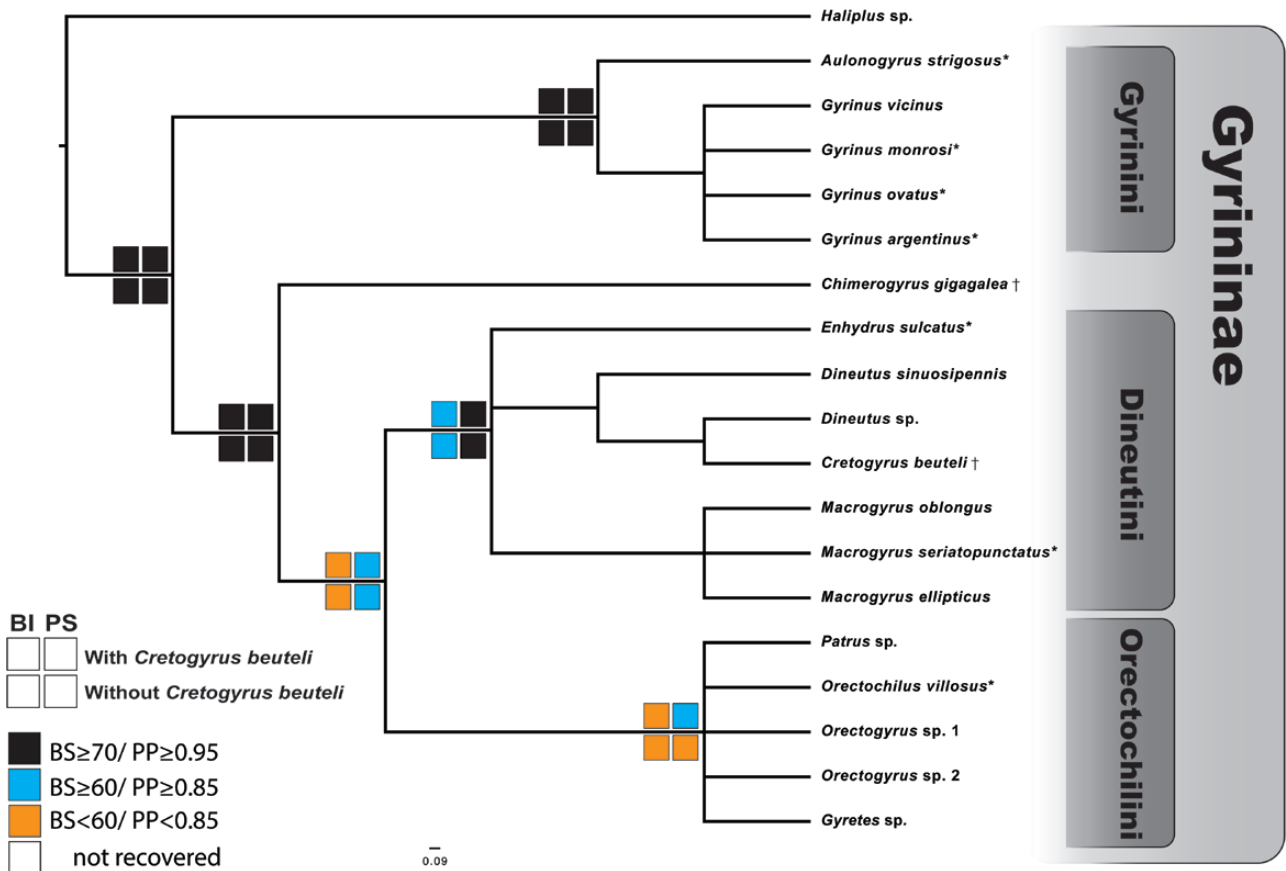
#### *CHIMEROGYRUS* GEN. NOV.

*lsid*: urn:lsid:zoobank.org:act:D7259533-80FC-44A2-B58B-FEDE654E53A5

*Type species*: *Chimerogyrus gigagalea*, by current designation, monotypic.

#### *Etymology*

The genus name is Latinized from the Greek χίμαιρα, *chimaira*, a chimera, the amalgamate monster of legend, here in reference to the strange combination of ancestral and derived features of the larval taxon being described, and γύρος, *gyros*, meaning turning or



**Figure 6.** Summary of the results of the phylogenetic analyses. Tree topology derived from Bayesian analysis including *Cretogyrus beuteli*†. Boxes at nodes indicate support values across the different analyses either with or without the inclusion of *Cretogyrus beuteli*† based on the key provided at the bottom left.

spinning, a common ending used in gyrinid names..

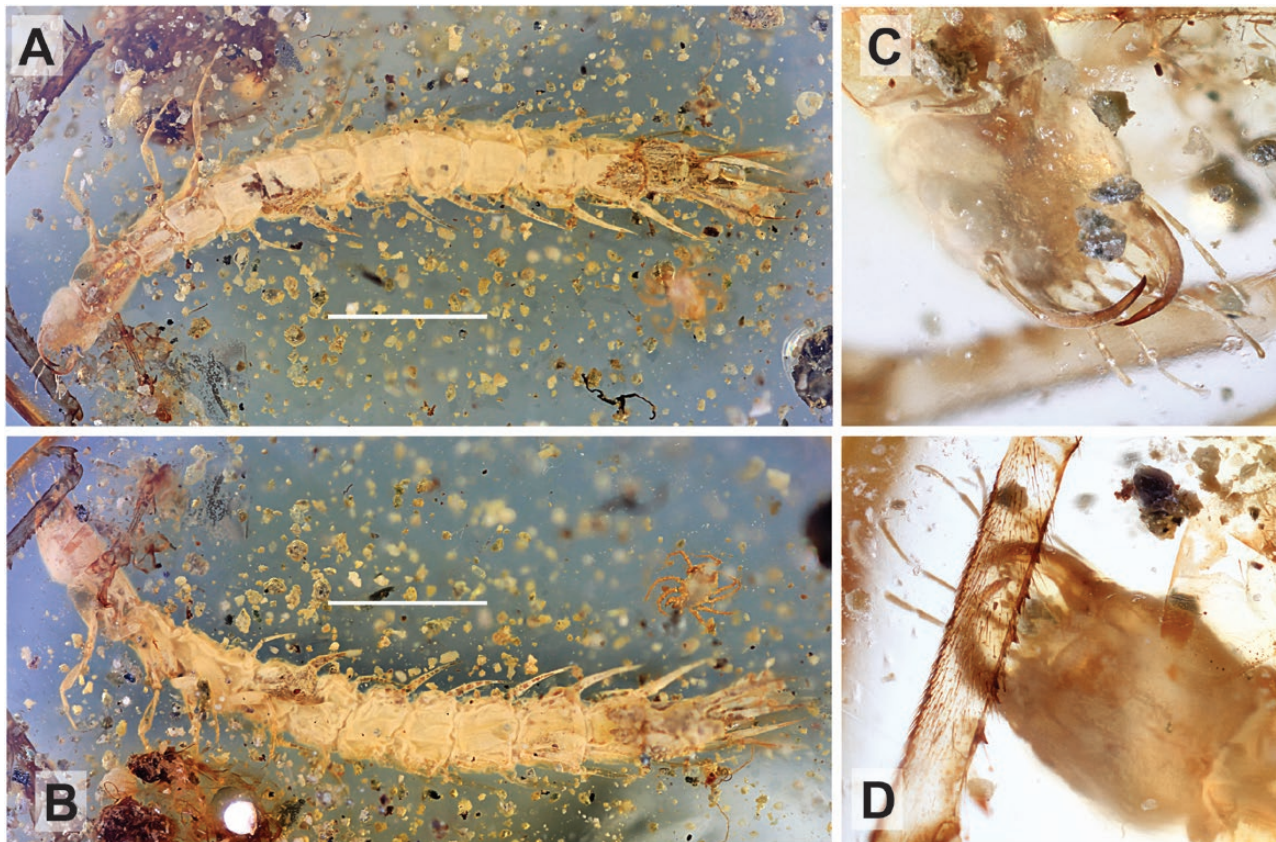
### Diagnosis

*Chimerogyrus* can be diagnosed by the following combination of characters: cephalic capsule (Figs 3, 7C, D) not constricted at level of occipital region; FR (Fig. 3A) symmetrica,l with four equally sized, well-developed teeth; tormae absent; maxilla (Fig. 4C, D) with elongate cardo and stipes; galea longer than lacinia; lacinia small and strongly curved, with inner margin straight apically and weakly dentate basally, apex without indentation; two long setae (MX5 and MX6) subequal in length at base of lacinia; anterior face of CO (Fig. 5A, B) with three large, stout, spine-like setae (CO6, CO8 and CO9); TA1 long and spine like, situated at mid-length dorsally (Fig. 5A); pretarsal claws (Fig. 5A–E) without spinulae; tracheal gills with spinulae; segment X (Fig. 5F, G) with two long, hair-like setae, spinulae absent; terminal hooks (Fig. 5F–H) asymmetrical, with lateral hooks narrower and elongate, medial hooks broader, less strongly curved.

The form of the maxilla (Fig. 4C, D) distinguishes *Chimerogyrus* from all known gyrinid genera. The maxilla of *Chimerogyrus* is most similar to that of genera of the tribes Dineutini and Orectochilini, having an elongate cardo that does not cover the ventral joint of the mandible, with the internal margin of the stipes lacking small hook-like setae dorsally. However, the stipes is longer than that of any currently known dineutine or orectochiline larva, which have relatively short stipes (Figs 1A–D, 2). Furthermore, its maxilla is unlike any known gyrinid larva in that the galea is considerably longer than the small lacinia, rather than being roughly similar in size (as in *Dineutus* Macleay, 1825; Fig. 1B) or smaller in size, as in most genera. The form of the lacinia (Fig. 4C) is also unique, being strongly curved, with a straight inner margin apically, becoming dentate proximally and possessing two long setae basally. The presence of two long setae of subequal length basal to the lacinia is similar to larvae of the Orectochilini (Fig. 2), but unlike these genera the lacinia is short, somewhat similar to the Gyrinini, but much narrower and more hook shaped. It







**Figure 7.** *Chimerogyrus gigagalea*† *in situ*. A, B, habitus images. Scale bars: 2 mm. A, dorsal view. B, ventral view. C, D, cephalic capsule. C, dorsal view. D, ventral view.

stout, spine-like setae (CO6, CO8 and CO9) situated distomedially and one small hair-like seta (CO10) distoventrally; posterior face proximally with one hair-like seta (CO12) and two hair-like setae (CO11 and one probably additional or secondary seta) distally; anterior face of TR with one short hair-like seta (TR3) and one long hair-like seta (TR4) ventrodistally; posterior face of TR with one short hair-like seta (TR5) ventrodistally; anterior face of FE distally with two short spine-like setae, one (FE2) dorsally and another (FE3) ventrally; posterior face of FE distally with one longer spine-like seta (FE4) and two small spine-like setae (FE5 and FE6); anterior face of TI with one long hair-like seta (TI1) proximally and three short spine-like setae distally (TI2, TI3 and TI4); posterior face of TI distally with one long spine-like seta (TI5) and two short spine-like setae (TI6 and TI7); anterior face of TA with one long spine-like seta at mid-length dorsally (TA1) and two short spine-like setae distally (TA2 and TA4); posterior face of TA with two short setae distally (TA5 and TA6); anterior face of PT with one short spine-like seta on basoventral portion

(PT1). *Abdomen* (Fig. 5F, G): segment X with two long hair-like setae paramedially.

#### *Differential diagnosis*

The genus is monotypic. The generic diagnosis provided above separates the species from all other known species based on larvae.

## DISCUSSION

*Chimerogyrus gigagalea* exhibits a fascinating suite of derived and plesiomorphic features. In particular, this new taxon shares several synapomorphies with larval Dineutini and Orectochilini, especially in reference to the cephalic capsule, including: (1) elongate and gracile labial and maxillary palps; (2) an elongate cardo of the maxilla; and (3) elongate and crescent-shaped mandibles. Of these, the elongate cardo of the maxilla appears to be a strong synapomorphy uniting

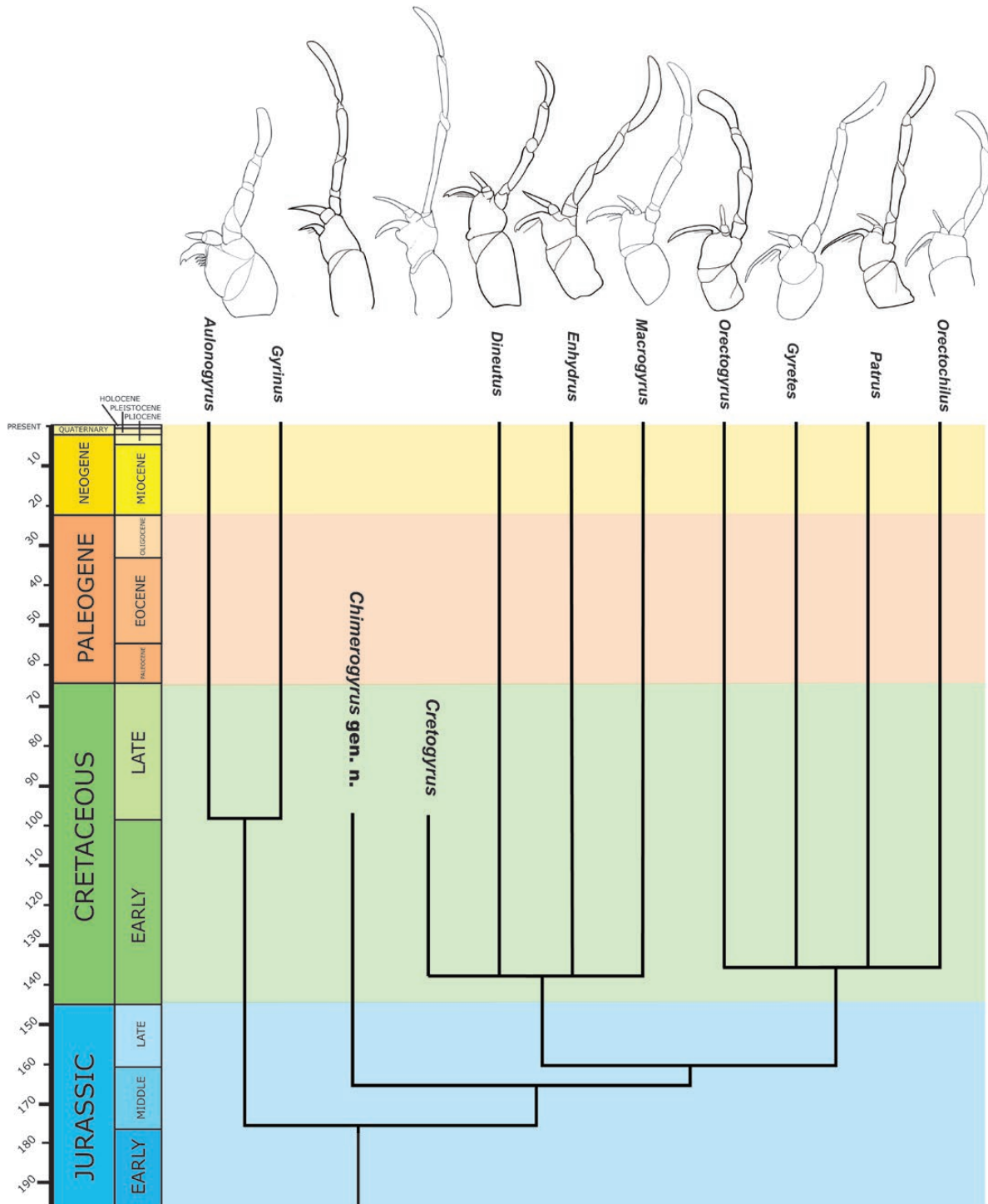


the Dineutini and Orectochilini (Beutel & Roughley, 1994), with its presence in *Chimerogyrus* supporting its close relationship to these taxa. However, unlike crown Orectochilini and Dineutini, *Chimerogyrus* does not have an elongate lacinia, instead retaining a lacinia that is similar in size to that present in the Gyrinini. Additionally, it retains other plesiomorphic features in common with the Gyrinini, such as the distally expanded femur, compared with the narrow femur exhibited by larvae of crown Dineutini and Orectochilini, and the absence of a ventral prothoracic sclerite, which is present in crown Dineutini and Orectochilini.

With regard to chaetotaxy, *Chimerogyrus* likewise exhibits an intriguing combination of plesiomorphic and autapomorphic features. In terms of plesiomorphic features, the form of TI7 is spine like, similar to that seen in other adaphagan larvae, such as Haliplidae, Aspidytidae, Meruidae and several Dytiscidae (Nilsson, 1988; Van Vondel, 2005; Alarie & Bilton, 2005, 2011; Michat *et al.*, 2014a, 2017a), whereas the known gyrenid larvae have TI7 hair like in form (Michat *et al.*, 2010, 2016, 2017b; Michat & Gustafson, 2016; Colpani *et al.*, 2018). Similarly plesiomorphic is the position of TA1 being not only situated at mid-length on the tarsus [a condition seen only in the larvae of *Dineutus* (Michat *et al.*, 2017b) and in some *Gyretes* (Colpani *et al.*, 2018)], but also dorsally as in other adaphagan beetles (Nilsson, 1988; Alarie *et al.*, 2004; Alarie & Michat, 2014; Michat *et al.*, 2014b, 2017a; Urcola *et al.*, 2019) [unlike *Gyretes* and, to a lesser degree, *Dineutus*, where TA1 is situated laterally (Michat *et al.*, 2017b; Colpani *et al.*, 2018)]. Most gyrenid larval genera have TA1 positioned apically, representing a derived condition (Archangelsky & Michat, 2007; Michat *et al.*, 2010, 2016; Michat & Gustafson, 2016). Other chaetotaxic characters appear unique to *Chimerogyrus*, such as the stout spine-like form of CO6, CO8 and CO9. Additionally, the homology of the setae on the posterior face of the coxa is difficult to assess. The setae CO11 and CO12 are clearly present, but there is another seta present between these (labelled as ‘?’ in Fig. 5C–E) whose homology is unclear. It is possible that the ‘CO?’ could be regarded as an additional or secondary seta, considering that in other gyrenids (particularly within the tribe Dineutini) there are either additional and/or secondary setae on that region of the coxa, further supporting the hypothesis of a close relationship of *Chimerogyrus* with members of this tribe. Alternatively, the position of ‘CO?’ is similar to the position of pore COd of extant larval gyrenids, particularly of larvae of *Dineutus* (Michat *et al.*, 2017b). Perhaps these two sensilla are homologous, with ‘CO?’ transitioning from a seta to pore COd in modern dineutine taxa.

Another gyrenid larva, *Cretogyrus beuteli*, was recently described from Burmese amber (Zhao *et al.*, 2019). This taxon was not placed at the tribal level despite clearly exhibiting features suggesting placement in crown Dineutini. The larva presents the following features that appear to be synapomorphic of members of the Dineutini: (1) cephalic capsule constricted at occipital region; (2) coronal suture present and elongate (at least one-third the length of cephalic capsule); and (3) lacinia elongate, with a weakly curved posterior margin (similar to Fig. 1A–C; rather than being strongly hooked in appearance, with a mostly straight posterior margin, as found in the Orectochilini; compare Fig. 1D to 2). However, the original description lacks further key information with regard to the lacinia (Zhao *et al.*, 2019). Xiangdong Zhao kindly provided us with high-resolution images of the cephalic capsule in order to allow us to study the gross morphology of the maxilla (Fig. 1D), revealing additional characters further uniting *Cretogyrus* with extant dineutine genera (Archangelsky & Michat, 2007; Michat *et al.*, 2016, 2017b), such as the indented apical margin of the lacinia. Unfortunately, neither the presence nor the form of MX5 and MX6 could be determined from the images. Derived features of the frontoclypeal teeth also suggest membership of *Cretogyrus* in crown Dineutini, having the teeth situated on an anteriorly produced medial lobe, with the lateral teeth being shorter than the medial pair, similar to the condition present in the extant genus *Dineutus* (Fig. 1B; Michat *et al.*, 2017b). In addition to the character evidence presented above, both Bayesian and parsimony phylogenetic inference placed *Cretogyrus* within the Dineutini clade with considerable support (pp = 87, bs = 78, respectively). Combined, the results of the phylogenetic analysis (Fig. 6) and the strong character evidence (Fig. 1D) make it clear that *Cretogyrus* should be regarded as a member of the crown Dineutini. However, its placement nested in *Dineutus* was weakly supported and, given the amount of missing data, the question of the relationship of *Cretogyrus* with the other dineutine genera remains open.

Our phylogenetic analysis, placing *Cretogyrus* in crown Dineutini, in combination with our description of *Chimerogyrus*, provide further evidence of the diverse entomofauna present during the middle Cretaceous, during which stem lineages existed alongside those that have persisted until the present (Badano *et al.*, 2018). The Cretaceous was an important time during the evolution of whirligig beetles, in that this period saw the origins of the crown tribes of Gyrininae (Fig. 8), with Dineutini and Orectochilini appearing during the Early Cretaceous and Gyrinini later, during the Late Cretaceous (Gustafson *et al.*, 2017). The discovery of a crown dineutine lineage in Burmese amber (Zhao



**Figure 8.** Summary tree of our current understanding regarding the timing and evolutionary relationships among the known living and extinct gyrinid genera based on the results of the present study and that of Gustafson *et al.* (2017). The maxillae associated with the known living and extinct larvae of the Gyrinidae are depicted above the tree, showing the evolution of this structure and the key intermediate morphology of *Chimerogyrus gigagalea*† Maxillae not to scale.

*et al.*, 2019) provides fossil evidence in support of these timing estimates based on phylogenetic divergences using tip-dating and the fossil record of whirligig beetles (Gustafson *et al.*, 2017). *Chimerogyrus* represents a crucial taxon for future studies on the timing and evolution of larval characters within the Gyrinidae in a phylogenetic framework, particularly for future tip-dating analyses.

#### CONCLUSIONS

Phylogenetic analysis and the suite of plesiomorphic and derived features exhibited by *Chimerogyrus gigagalea* strongly support its status as a stem lineage in Gyrininae, sister to Dineutini + Orectochilini (Fig. 6). In particular, the maxilla preserves transitional morphology between Gyrinini and crown Dineutini and Orectochilini, having a derived elongate cardo and maxillary palp accompanied by a plesiomorphically small lacinia (Fig. 8). This taxon is an important addition to the knowledge of gyrid larval morphology and provides timing for the evolution of key larval features, further highlighting the importance of Burmese amber for preserving extinct stem lineages that existed alongside crown lineages during the Middle Cretaceous.

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### SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

- Figure S1.** Results of Bayesian analysis without *Cretogyrus beuteli*†.
- Figure S2.** Results of Bayesian analysis including *Cretogyrus beuteli*†.
- Figure S3.** Results of parsimony analysis without *Cretogyrus beuteli*†.
- Figure S4.** Results of parsimony analysis including *Cretogyrus beuteli*†.