A new fossil dragonfly (Anisoptera: Corduliidae) from the Paleocene Fur Formation (Mo clay) of Denmark

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Abstract
A new fossil dragonfly genus and species, Molercordulia karinae n. gen. n. sp. (Anisoptera: Corduliidae), is described from the Paleocene Fur Formation (Mo clay) in Denmark. Considering the rarity of Paleocene odonate fossils and the stratigraphic proximity to the important K-T boundary, this fossil, even though only fragmentarily preserved, represents an interesting contribution to our knowledge of the odonate fauna in the Early Tertiary. The new taxon is identified as oldest fossil record of Corduliiidae (sensu BECHLY 2002). A new character (post-oblique-vein-gap) that seems to be quite useful in dragonfly systematics is described and is proposed as independently acquired autapomorphy in Macromiidae and Haplohamulida.

Keywords: Odonata, Anisoptera, Corduliidae, dragonfly, fossil, Tertiary, Paleocene, Moler, Mo clay, Fur Formation, Denmark.

1. Introduction
Together with the insect fauna from the Late Paleocene Maíz Gordo Formation in Argentina (PETRULEVICIUS et al. 1999) the fossil insects from the Paleocene and Early Eocene Ølst Formation and Fur Formation (Mo clay) from the Limfjord area in Denmark belong to the oldest known fossil insects from the Tertiary. Representa-
tives of most insect orders have been found in these marine sediments, including a lot of fossil damselflies (esp. Calopterygoidea) and dragonflies (esp. Gomphaeschnidae). Larsson (1975) reported 39 specimens and Rust (1999) could already study 70 specimens of fossil odonates from this locality. However, the fossil Anisoptera are much rarer than the Zygoptera and Rust (1999) could only report five specimens. Several new species remain to be described and some of described species need to be revised. The "Gomphaeschna" species have already been revised by Bechly et al. (2001). Here I describe an interesting new species of Corduliidae from the Fur Formation.

Acknowledgements

I am indebted to Mr G. Stöbener (Staufenberg, Germany), the original owner of this fossil, who kindly donated the holotype to our museum. I also thank Dr K. Wolf-Schwenninger (SMNS, Stuttgart) who made the Automontage photos of the fossil. Last but not least, I thank Prof. Dr. J. Rust (Univ. Bonn) and Dr. A. Nel (MNHN, Paris) for critical, but very helpful, comments to an earlier draft of this paper, and Dr R. Böttcher (SMNS, Stuttgart) for the careful proof-reading of this manuscript.

2. Methods

The drawing was made with a camera lucida on a Wild M5 binocular microscope by combining all details from plate and counter plate of the holotype specimen. The photos have been made with a digital camera and the Syncroscopy Automontage software. All figures have been improved with the Adobe Photoshop imaging software. The nomenclature of the dragonfly wing venation is based on the interpretations of Riek & Kukalová-Peck (1984), amended by Nel et al. (1993) and Bechly (1996). The phylogenetic classification of dragonflies is based on Bechly (1996, 2005).

3. Systematic Palaeontology

Class Insecta Linnaeus, 1758 (= Hexapoda Latreille, 1825)
Subclass Pterygota Brauner, 1885
Order Odonata Fabricius, 1793
Suborder Anisoptera Selys in Selys & Hagen, 1854
Haplohamulida Bechly, 1996
Family Corduliidae Selys in Selys & Hagen, 1850

Genus Molercordulia n. gen.

Type species: Molercordulia karinae n. sp., by present designation.
Derivation of name: Named after the geological setting (Moler) and the extant genus Cordulia.

Diagnosis. – Same as type species since monotypic.

Molercordulia karinae n. sp.

Figs 1–3

Holotype: Specimen no. SMNS 66121 at the Staatliches Museum für Naturkunde Stuttgart, Germany (ex coll. Stöbener, no. E 092 A); the counter plate (no. E 092 B) is in pri-
vate collection of Mr Gerhard Stöbener (Staufenberg, Germany), but does not show any important further details. It is the only known specimen of this new genus and species.

Type locality: Limfjord area, Denmark.

Type horizon and age: Mo clay (Moler), Fur Formation; Paleocene or lowermost Eocene, 54 mya.

Derivation of name: Named after the wife (Mrs Karin Stöbener, Staufenberg, Germany) of the former owner (Mr Gerhard Stöbener) of the holotype.

Diagnosis. – This new cordulid genus and species can be distinguished from all other fossil and extant dragonflies by the following combination of hind wing characters: basal space free; arculus straight; sectors of arculus separated at arculus; costal side of hypertriangle strongly curved; hypertriangle and triangle undivided by crossveins; hypertriangle quadrangular, because costal side of hypertriangle is ending on distal side (MAb) of discoidal triangle (autapomorphy); discoidal triangle recessed to level of arculus; Mspl strongly developed and reaching wing margin (autapomorphic reversal); gap of crossveins distal of lestine oblique vein; only three antesubnodal crossveins; only two antefurcal crossveins; four crossveins between IR2 and RP3/4 basal of level of lestine oblique vein; only one bridge crossvein that is situated distal of subnodus; small size with a wing length of only about 28 mm.

Description. – Plate and counter plate of a fossil dragonfly of unknown sex, with preservation of fragments of the basal part of a right hind wing and of parts of head, thorax, legs, and abdomen. The visible parts of the wing venation are well-preserved, especially when the fossil is submerged under alcohol. Unfortunately, some important areas of the wing are missing, such as the anal area (with the anal loop and sexual dimorphic characters like anal angle and anal triangle) and the apex of the wing (with the pterostigma, IR1, and RP1 and RP2).

Hind wing: Estimated length of wing about 28 mm (based on the assumption that the nodus is situated at 40–45% of the wing length as in most extant Anisoptera); width at nodus about 9.5 mm; distance between wing base and nodus about 12 mm.
Distance between wing base and arculus 2.7 mm; the arculus is straight (not kinked) and the origins of the sectors of arculus (RP and MA) are distinctly separated. The hypertriangle is 2.8 mm long and undivided; the anterior margin of the hypertriangle is strongly curved. The discoidal triangle is slightly elongate and undivided. Three rows of cells in basal part of posttrigonal space; two convex intercalary veins in the distal posttrigonal space (one is Mspl that is not rejoining MA but reaches the hind margin). MA and RP3/4 parallel with one row of cells in-between. Three antesubnodal crossveins and two antefurcal crossveins. Antenodal and postnodal crossveins are not preserved, as well as the pterostigma and wing apex. Base of RP2 aligned with subnodus. A single lestine oblique vein 'O' 1.6 mm distal of subnodus. There is a distinct gap of crossveins directly distal of the oblique vein. Only one bridge crossvein that is situated distal of subnodus. Rspl present and parallel to IR2 with only one row of cells between IR2 and Rspl. IR2 and RP2 slightly diverge distal of the oblique vein. Cubito-anal area and wing base not preserved.

Discussion. – Within the order Odonata this new fossil taxon can be attributed to the clade of libelluloid Anisoptera because of the following synapomorphies: arculus straight; costal side of hypertriangle strongly curved; Rspl and Mspl well-developed; triangle recessed to the level of arculus; only a single lestine oblique vein; the general pattern of the longitudinal veins.

The presence of a distinct gap of crossveins distal of the oblique vein is a remarkable derived character state, which is here described for the first time and is exclu-

Fig. 2. *Molercordulia karinae* n. gen. n. sp., complete fossil; holotype, SMNS 66121. – Scale bar: 5 mm.
sively present in Macromiidae and in most taxa of Haplohamulida, such as Oxygastridae, Corduliidae s. str. (Neurocorduliinae and Corduliinae), and Anauriculida (Hemicorduliidae, Urothemistidae/Macrodiplactidae and Libellulidae). Within Libellulidae the character is somewhat homoplastic, but it is strongly developed in most genera of the subfamilies Leucorrhininae, Sympetrinae, Trithemistinae, Onychothemistinae, Rhyothemistinae, Trameinae, Zygonychinae and many Libellulinae, but hardly in Tetrathemistinae and Brachydiplactinae (except Hemistigma and Uracis). The character state is not present in the basal libelluloid families Synthemistidae, Gomphomacromiidae, Austrocorduliidae, Idionychidae, Idomacromiidae (incl. Nesocorduliinae), and Cordulephyidae (incl. Neophyinae). Since Macromiidae is phylogenetically rather far removed from Haplohamulida according to Bechly (1996, 2005), the shared presence of this derived character state has to be considered as a convergence. Therefore, I here propose the post-oblique-vein-gap as independently acquired autapomorphy in Macromiidae and Haplohamulida.

Among those dragonflies with a post-oblique-vein-gap, an attribution of the new fossil taxon to Macromiidae can be excluded because of the non-stalked arculus (always distinctly stalked in Macromiidae), the undivided hypertriangle (always divided by 1–2 crossveins in Macromiidae), and the presence of only two antefurcal crossveins (at least four in Macromiidae). Consequently, the taxon has to be attributed to Haplohamulida.

Fig. 3. *Molercordulia karinae* n. gen. n. sp., right hind wing; holotype, SMNS 66121. – Scale bar: 2 mm.
The quadrangular hypertriangle, formed by the trigonal vein (costal side of the hypertriangle) ending on the distal side of the triangle distinctly below the distal angle, is rather unique apomorphy within Cavilabiata (only known in Macrodiplax balteata; BECHLY 1996), and among Odonata otherwise only present in the Mesozoic taxa Heterophlebioidae and Liassogomphidae, as well as in the following Mesozoic aeshnoid and gomphid species: Sinojagoria imperfecta BECHLY et al., 2001, Aeschnopsis jurassica (GIEBEL, 1856) (= Necrogomphus jurassicus), some specimens of Mesupetala koebleri (GERMAR, 1839), Pritykiniella deichmuelleri (PRI-TYKINA, 1968), Araripogomphus hansegeri BECHLY, 2000 and Cratolindenia knuep-fae BECHLY, 2000. In a few Gomphides (e.g. Archaeogomphus) and in Cordulephy-inae, Neophyinae and Theragemistinae the trigonal vein is ending on the anterior side of the hypertriangle thus above the distal angle of the triangle, so that the discoidal triangle becomes secondarily quadrangular. Anyway, this character state is here considered as an autapomorphy of this new genus and species, because a synapomorphy with Macrodiplax balteata can be excluded by the presence of at least four crossveins between RP3/4 and IR2 basal of the level of the oblique vein, because there are maximal two such crossveins in all Urothemistidae.

The presence of only three antesubnodal crossveins is a derived similarity with Hemicorduliidae, Urothemistidae, most Corduliidae, and many Libellulidae, not present in Oxygastridae, but it is a very homoplastic character. However, the recession of the hind wing triangle to the level of the arculus is a good synapomorphy with Cordulidae, Hemicordulidae, Urothemistidae and Libellulidae, that is clearly absent in Oxygastridae. Urothemistidae was already excluded above, and Libellulidae s. str. (= EuLibellulida) can also be excluded because of the distinctly separated origin of the sectors of the arculus (sectors of arculus always stalked in Libellulidae).

Consequently this new taxon can only be attributed to Hemicordulidae or Cordulidae s. str., which is confirmed by the circumstance that in Hemicordulidae and most (but not all!) Corduliidae there are also maximal two crossveins between RP3/4 and IR2 basal of the level of the oblique vein. Hemicordulidae can be excluded because of the shape of Mspl, which is not distally rejoining MA. Such a Mspl is not present in Anauriculida (Hemicordulidae, Urothemistidae, and Libellulidae), but well present as reversal in some cordulid genera like Williamsonia or Dorocor-dulia. A single bridge crossvein distal of subnodus is also unknown in Hemicordulidae but occurs within Corduliidae, e.g. in Helocordulia. Therefore, I here tentatively attribute this new genus and species to the family Corduliidae, as its oldest fossil record and thus one of the oldest fossil records (except for Palaeolibellula zherikhi-ni FLECK et al., 1999 from the Turonian of Kazakhstan) of crown group Eurypalpi-da, Neolamellida, Valvulida, Trichodopalpida, Laterocaridida, Mediocostiida, Longiansida, Liberaponsida, Haplohamulida, and Italoansida (all taxa described by BECHLY 1996).

Altogether, this fossil is another beautiful showcase for fossil insects that can deliver interesting scientific information even though they are very poorly and/or only fragmentarily preserved (compare BECHLY 1998; BECHLY & SACH 2002).
4. References


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