



# A chasmatspidid affinity for the putative xiphosuran *Kiaeria* Størmer, 1934

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## Abstract

The putative xiphosuran *Kiaeria* Størmer, 1934, from the Late Silurian (Ludlow) of Ringerike, Norway, is redescribed from the holotype and only known specimen as a chasmatspidid chelicerate arthropod. Morphological features such as the presence of a fused buckler of three opisthosomal segments clearly indicate a chasmatspidid affinity, while the size of *Kiaeria*, along with the occurrence of a raised axial region and expanded anterior articulation, suggest a close phylogenetic relationship to the Ordovician *Chasmatspis*. As such, *Kiaeria* represents the first indication that the *Chasmatspis*-type chasmatspidid morphology persisted alongside the radiation of diploaspidids. This is also only the third chasmatspidid species recorded from the Silurian.

**Keywords** Chasmatspidida · Chelicerata · *Kiaeria* · *Kiaeritia* · Ringerike

## Introduction

The Paleozoic record of Chelicerata includes numerous aquatic representatives divided between the bizarre Pycnogonida Latreille, 1810, morphologically distinctive Xiphosura Latreille, 1802, taxonomically diverse Euryp-terida Burmeister, 1843, enigmatic Chasmatspidida Caster and Brooks, 1956, and synziphosurines, which are now recognized to be a polyphyletic grouping of taxa distinct from Xiphosura (Lamsdell 2013a, 2016; Selden et al. 2015; Lamsdell et al. 2015). However, there remain a few described chelicerate species that are of uncertain affinity, often retained within Xiphosura as a legacy of when it included synziphosurines. For example, *Archaeolimulus hanusi* Chlupáč, 1965, a supposed xiphosurid from the Middle Ordovician of the Czech Republic, most likely represents a bradoriid arthropod. Probable misidentifications occur in other aquatic chelicerate groups, too; *Mycterops whitei* Schram 1984, from the Carboniferous of Iowa, USA,

is potentially a crustacean or other arthropod of unknown affinity, as is *Marsupipterus sculpturatus* Caster and Kjellesvig-Waering, 1955, which strongly resembles a phyllocarid telson. Finally, *Willwerathia laticeps* (Størmer, 1936), from the Lower Devonian of Germany, has been interpreted as a ‘synziphosurine’ chelicerate (Anderson et al. 1998), however the prosomal carapace does not bear any resemblance to other aquatic chelicerates; instead, *Willwerathia* bears a strong resemblance to the Cambrian artiopod *Falcatamacaris* Ortega-Hernández et al. 2015.

Here, I review the affinities of another chelicerate of unclear affinities, *Kiaeria limuloides* Størmer, 1934, from the Late Silurian (Ludlow) of Ringerike, Norway. Originally described as a xiphosurid, *Kiaeria* instead exhibits a number of characteristics of chasmatspidids, particularly *Chasmatspis* Caster and Brooks, 1956.

## Geological setting

*Kiaeria* is part of the diverse fauna described from the Silurian (Ludlow) Sundvollen Formation of the Ringerike Group exposed at Rudstangen, Norway, discovered by Johan Kiær (1911, 1924). The fauna is derived from a greyish-green to brownish-red schistose sandstone with occasional interbedded shales representing marine conditions within a broad coastal plain (Davies et al. 2003). The fauna includes

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numerous fish and arthropods preserved alongside *Dictyocaris* (Kiær 1911, 1924), which is now known to be a benthic marine alga (Botting 2007). Størmer (1934) described the arthropods, most of which represented eurypterids, in detail. *Kiaeria*, from the same horizon as the eurypterids and fish, represents the only supposed xiphosuran from the locality.

The specimen of *Kiaeria* is stored in the Geologisk Museum, Universitetet i Oslo, Norway (PMO). Specimens of *Chasmaspis* figured for comparative purposes are stored at the National Museum of Natural History, Washington, DC, USA (NMNH).

## Systematic palaeontology

**Arthropoda** von Siebold, 1848

**Chelicerata** Heymons, 1901

**Euchelicerata** Weygoldt and Paulus, 1979

**Chasmataspidida** Caster and Brooks, 1956

Incertae sedis

Genus *Kiaeria* Størmer, 1934

*Type species.* *Kiaeria limuloides* Størmer, 1934, by monotypy.

*Revised diagnosis.* Chasmataspidid arthropod with buckler displaying clear axial furrows; buckler anterior with expanded articulation surface; postero-lateral margins of buckler drawn out into broad projections (emended from Størmer, 1934).

*Remarks.* The genus name *Kiaeria* has previously been assigned to two arthropods: the chelicerate *Kiaeria* Størmer, 1934, and the bivalved leperditicopid *Kiaeria* Glebowski, 1949, with the leperditicopid clearly representing the junior homonym. The replacement name *Kiaeritia* Schallreuter and Hinz-Schallreuter, 1999 has been introduced as a replacement name for *Kiaeria* Glebowski, 1949; however, the original homonym *Kiaeria* Glebowski, 1949 was still in use as recently as 2016 (e.g., Johnson and Baarli 2012; Abushik et al. 2016). The history of the taxonomic revision is therefore repeated here in the hope of spreading awareness of the replacement name.

*Kiaeria* shows close affinities to the genus *Chasmaspis* Caster and Brooks, 1956, and arguably could be assigned to the family Chasmataspididae Caster and Brooks, 1956. However, as the only known specimen is represented solely by a partially complete buckler, the genus is considered *incertae sedis* within Chasmataspidida pending the discovery of further, more complete, material.

*Kiaeria limuloides* Størmer, 1934

Figure 1a, b

*Material.* PMO H 2038 (holotype), preabdominal buckler.

*Description.* PMO H 2038 preserves a largely complete preabdominal buckler comprising opisthosomal segments 2–4. The specimen is preserved as a flattened compression of grey-brown cuticle which has flaked off in places, particularly on the right of the buckler (Fig. 1a), although comparison with the figure of the specimen presented by Størmer (1934) (his pl. 12, fig. 1) shows that this damage had already occurred to the specimen prior to its initial description and has not advanced since. To the left, the specimen is truncated by the rock that hosts the specimen having broken away. Anteriorly, the expanded articulation of the buckler is damaged and absent on the right due to a small escarpment in the matrix of the specimen. The buckler is 60 mm long, from the anterior margin of the articulation to the tip of the posterior projections; along the axis, the buckler is 40 mm long. The axis is defined by narrow furrows that are likely the result of compression of an originally inflated axial region. The axis is 32 mm wide at the buckler anterior and narrows evenly posteriorly to a width of 19 mm at the posterior margin. The anterior margin of the buckler is dominated by a broad articulation that likely represents the expanded articulation facet of the first buckler tergite. The anterior margins of the articulation are rounded; it is 5 mm long at the centre of the axis (which extends on to the articulation) and narrows laterally to 3 mm in length before expanding again to a maximum preserved width of 8 mm towards the pleural margin. Posterior to the buckler articulation, the first buckler tergite (representing the second opisthosomal segment) is 9 mm long at the centre of the axis, exhibits moderate posterior curvature laterally and expands in length to 12 mm. The tergite is laterally incomplete on both sides, but has a maximum preserved width of 86 mm. The second tergite (third opisthosomal segment) has a preserved width of 80 mm, is 10 mm long at the centre of the axis, and exhibits extreme posterior curvature laterally, expanding to a maximum preserved width of 17 mm. The final buckler tergite (fourth opisthosomal segment) exhibits extreme lateral curvature, has a preserved width of 64 mm, is 16 mm long at the axis, and 11 mm long at the lateral margin. Due to the extreme curvature of the segment, the pleural margins extend some 18 mm beyond the posterior margin of the axis. Despite preserving the cuticle, no ornamentation beyond very fine granulations are present anywhere on the buckler.

*Remarks.* Siveter and Selden (1987) considered *Kiaeria* to be only questionably assigned to Xiphosura. The style of preservation (a flattened compression preserving the original

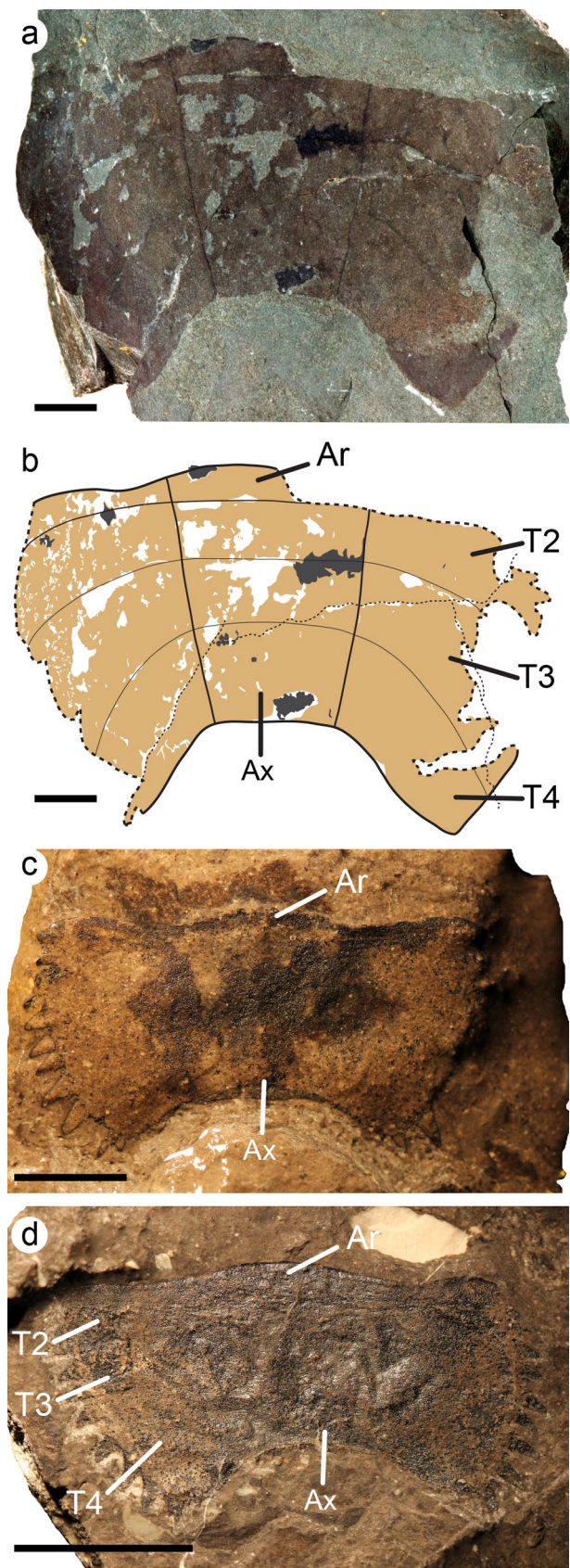
**Fig. 1** **a** PMO H 2038, *Kiaeria limuloides* (holotype), buckler. **b** Interpretive diagram of PMO H 2038. Cuticle is shown in brown, pyrite growth in grey. Natural boundaries indicated by solid lines, while dashed lines represent boundaries due to breakage. **c** USNM 125117, *Chasmataspis laurencii* (paratype), buckler. **d** USNM 125103, *Chasmataspis laurencii* (paratype), buckler. Abbreviations: Ar articulation, Ax axis, T2–T4 tergites 2–4. Scale bars = 10 mm

cuticle) does not match that of other xiphosurids, which are generally resistant to complete compression and do not preserve the cuticle (Babcock et al. 2000; Feldmann et al. 2011; Lamsdell and McKenzie 2015). The preservation of *Kiaeria* does, however, match that typical of eurypterids and chasmataspidids (see Dunlop et al. 2001; Lomax et al. 2011; Lamsdell 2013b; Marshall et al. 2014), suggesting that the affinity of *Kiaeria* lies with one of these groups rather than xiphosurans. Having a fused mesosoma consisting of only three segments is also unprecedented in Xiphosura; however, it is a synapomorphy of Chasmataspidida (Dunlop and Lamsdell 2017), and so *Kiaeria* is transferred to this rare group of chelicerate arthropods.

## Discussion and conclusions

*Kiaeria* exhibits a number of clear chasmataspidid characteristics, most notably the possession of a three-segmented fused buckler, a synapomorphy of chasmataspidids (Dunlop et al. 2004; Lamsdell et al. 2019). The xiphosurid thoracetron is composed of nine segments (Lamsdell 2013a; Dunlop and Lamsdell 2017) and is assembled by the time the group first appears in the Ordovician (Rudkin et al. 2008); the chasmataspidid buckler is not homologous to the xiphosurid thoracetron, and xiphosurids do not appear to go through a transitory stage comprising only three segments. The pattern of tagmosis in *Kiaeria*, therefore, only makes sense in light of a chasmataspidid affinity for the species. Aspects of the taphonomy also agree with a chasmataspidid identity, including the degree of compression and preservation of cuticle (Dunlop et al. 2001; Poschmann et al. 2005; Lamsdell and Briggs 2017). Chasmataspidids are also frequently found preserving only their bucklers (Marshall et al. 2014), probably a result of the prosoma and postabdomen having disarticulated during or after moulting.

Of the known chasmataspidid species, *Kiaeria* most closely resembles *Chasmataspis laurencii*, from the Ordovician of Tennessee, USA (Caster and Brooks 1956; Dunlop et al. 2004). This is in part due to its size; diploaspidids, encompassing all the previously known Silurian–Devonian chasmataspidids, attained maximum sizes of < 30 mm (Marshall et al. 2014; Lamsdell and Briggs 2017). However, *Chasmataspis* and the diploaspidid *Hoplitaspis*, both known from the Ordovician, reached body sizes in excess of 60 mm (Dunlop et al. 2004; Lamsdell et al. 2019). *Kiaeria* is also



distinct from diploaspidids in possessing a demarcated axial region on the buckler and the expanded anterior articulation (Fig. 1a, b). These traits are shared with *Chasmataspis*, the disarticulated bucklers of which clearly show an anterior articulation identical to that of *Kiaeria* (Fig. 1c, d) and also demonstrate the presence of an inflated axial region.

The available information suggests a close relationship between *Chasmataspis* and *Kiaeria*, although whether *Kiaeria* should be transferred to Chasmataspididae (which would then be a junior synonym of Kiaeriidae) or retained as a separate family within Chasmataspidida is currently uncertain. Irrespective of this, *Kiaeria* represents the first evidence that the *Chasmataspis*-type chasmataspidid morphology persisted past the Ordovician into the Silurian. *Kiaeria* is also only the third chasmataspidid recorded from the Silurian (Tetlie and Braddy 2004; Lamsdell and Briggs 2017). The determination of *Kiaeria* as a chasmataspidid confirms previous suspicions that the group is more diverse than historically recognized, and that Chasmataspididae and Diploaspididae coexisted for some time before diploaspidids radiated in the Devonian.

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