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The trigonotarbid arachnid *Alkenia mirabilis* Størmer, 1970

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ABSTRACT Contrib. Nat. Hist. 12: 489–498.

The affinities of the remarkable trigonotarbid *Alkenia mirabilis* Størmer, 1970 (Arachnida: Trigonotarbida) from the Early Devonian (Emsian) of Alken an der Mosel, Germany are discussed based on a redescription of the type material. The first reconstruction of the species is presented. *A. mirabilis* expresses a number of unique features – particularly in carapace morphology – and cannot be referred unequivocally to any of the existing trigonotarbid families. *Alkenia* Størmer, 1970 is thus treated here as a plesion genus.

Introduction

Trigonotarbids are an extinct group of Late Silurian to Early Permian arachnids resolved by Shear & al. (1987) as basal members of the so-called Pantetrapulmonata; i.e. spiders and their closest relatives. Trigonotarbids lack the spinnerets of spiders and are characterized primarily by a division of the opisthosomal tergites into median and lateral plates. Ricinuleids also express (in some fossil and all Recent taxa) such a division – and thus may also be related to trigonotarbids (Dunlop 1996) – but show a greater consolidation of the opisthosomal segments yielding a series of macrotergites. Some seventy species of trigonotarbid have been described, although recent revisions have tended to reduce the overall number of taxa (cf. Rössler 1998). Most trigonotarbids have been found in the Carboniferous Coal Measures of Europe and North America (e.g. Pocock 1911, Petrunkevitch 1949). There are, however, an increasing number of older species from the Early Devonian of Great Britain (Hirst 1923, Dunlop & Selden 2004, Fayers & al. 2005) and Germany (Størmer 1970, Shultka 1991, Brauckmann 1994). They are also known from the Middle (Shear & al. 1987) and Late (Shear 2000) Devonian of the USA. Those from

the Early Devonian remain among the oldest known examples of terrestrial arthropods.

One of the most remarkable of the Early Devonian trigonotarbids is *Alkenia mirabilis* Størmer, 1970 from Alken an der Mosel, Germany. This species (Figs. 1–3) is known from relatively complete material and has a quite unique morphology (see below) with a lobed carapace and a strongly tuberculate dorsal surface. In some respects these are characters more usually associated with younger (Carboniferous) species, but details of its morphology seem to preclude its referral to any other existing families. Here, the affinities of *A. mirabilis* are discussed in the light of Recent studies of trigonotarbids and the first reconstruction of the species is presented based on a re-examination of the type material.

Material and Methods

The type material of *A. mirabilis* is held in the Forschungsinstitut and Naturmuseum Senckenberg, Frankfurt am Main, Germany (SMF). It derives from the well-known German fossil locality of Alken an der Mosel and accounts of its geological setting and dating can be found in Dunlop & al. (2001), Poschmann & Tetlie (2004) and Poschmann & al. (2008) and references therein. Alken an der Mosel is an almost 400 million year old near-shore, perhaps lagoonal, environment which also preserves terrestrial plants and animals. The fauna includes eurypterids and chasmataspids (both of which are extinct, aquatic chelicerates), a scorpion, an arthroplurid millipede, bivalves, rarer brachiopods, tentaculites and fish. The fossils are preserved as coalified films on a dark siltstone matrix and retain a certain degree of three-dimensional surface relief (Fig. 1). The mater-ial was studied under 70% ethanol – which improves the contrast against the matrix – and digital photographs were made under the same conditions. Low-angle lighting also proved helpful to bring out the relief of the material.

Morphological interpretation

Størmer's (1970) original description and drawings are largely accurate, but it proved necessary to reinterpret some features as discussed below. The carapace (Figs. 1–2) has a subtriangular, but bluntly pointed outline – as per the original description – with a prominent median lobe and lateral flanks which widen posteriorly. There is no evidence that these lateral regions were strong-

ly subdivided as in some Carboniferous trigonotarbids; cf. Rössler (1998, various figs) for *Aphantomartus* Pocock, 1911. The median lobe in *A. mirabilis* bears the eyes sub-centrally (and perhaps a little smaller than in the original *camera lucida*), while the ornament in front of the eyes seems to form more or less regular rows of tubercles (Figs. 2–3). Tuberculation across the rest of the carapace is more random. Behind the eyes there is strong, 'Y'-shaped bilobation of the posterior carapace region with at least two further transverse (but incomplete) divisions across the median lobe in this posterior region (Figs. 2–3). While some Carboniferous trigonotarbids also have lobation of their median carapace region – typically two lobes flanking the eye tubercles and two further large lobes immediately behind them, cf. Rössler (1998, various figs.) – the specific pattern of lobation illustrated here seems to be unique to *A. mirabilis*. The mouthparts and pedipalps are equivocal, but the legs are fairly complete and indicate quite a robust morphology with a flaring of the distal margins of some articles, in particular the tibia (Fig. 3), and an ornament of rows of small tubercles along all articles preserved. Claws on the legs are equivocal.

The opisthosoma shows the typical trigionotarbid character of tergites divided longitudinally into median and lateral plates. These are ornamented with discrete, circular tubercles, as per the carapace, with a tendency to form horizontal, but slightly irregular, rows. Størmer (1970, text-fig. 7) recognized eight tergites and numbered them 1–8 accordingly. Subsequent work on well preserved and (in part) three-dimensional fossils (e.g. Shear & al 1987; Dunlop 1996; Fayers & al. 2005) has demonstrated that the trigonotarbid opisthosoma has nine dorsally visible tergites, plus two or three further segments, the last two forming a small pygidium on the ventral side. The first opisthosomal tergite in trigonotarbids is a so-called 'locking ridge' which tucks underneath the carapace and which may become reduced in some more derived forms (Dunlop 1994). Thus it is often the case that in typical compression fossils this first tergite is hidden and/or hard to resolve. The following tergites (2 and 3) are typically fused together into a diplotergite in trigonotarbids; although again there are possible exceptions among derived genera (Dunlop 1994). The anterior tergite boundaries of the part of the holotype are a little confusing (Fig. 2a), but the counterpart (Fig. 2b) reveals the morphology more clearly and shows that *A. mirabilis* had an opisthosomal segmentation pattern of fused tergites 2+3, interestingly with a possible hint of the original segment boundary within this diplotergite, and then tergites 4–9; giving the eight elements recognized by Størmer and matching patterns typically observed in other Devonian trigonotarbids (e.g. Shear & al. 1987, Fayers & al. 2005).

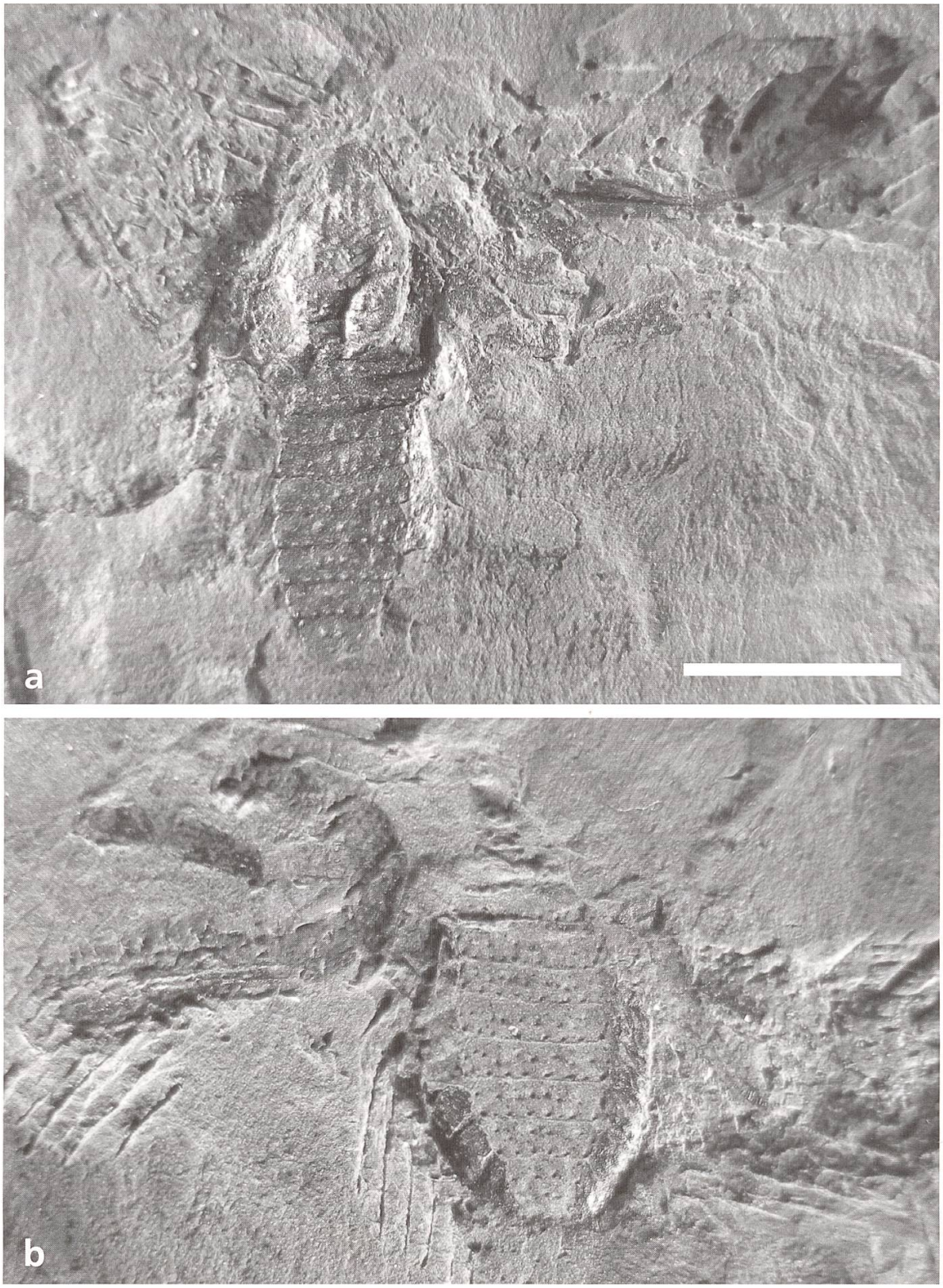

Fig. 1. The holotype of the trigonotarbid (Arachnida, Trigonotarbida) *Alkenia mirabilis* Størmer, 1970 from the Early Devonian (uppermost Lower Emsian) of Alken an der Mosel, Rhineland-Palatinate, Germany; SMF VIII 30a, b, photographed under 70% ethanol. a. Part. b. Counterpart. Scale bar equals 5 mm.

Fig. 2. Camera lucida drawings of the specimen shown in Fig. 1. – a: Part; – b: Counterpart. Abbreviations: cl = clypeus of carapace; cp = carapace; fe = femur; lf = lateral flank of carapace; lt = lateral tergite; ml = median lobe of carapace; ms = metatarsus; mt = median tergite; ot = ocular (median eye) tubercle; pt= patella; st = (superimposed) sternites; ti = tibia. Opisthosomal tergites numbered from 2+3 (a diplotergite) to 9. Scale bar equals 5 mm.

Systematic palaeontology

Order Trigonotarbida PETRUNKEVITCH, 1949
Plesion (Genus) *Alkenia* STØRMER, 1970

Type and only species: *Alkenia mirabilis* STØRMER, 1970; by original designation.

Emended diagnosis: Devonian trigonotarbid with a coarsely tuberculate dorsal surface; tubercles on median opisthosomal tergites forming horizontal, but slightly irregular, rows. Carapace subtriangular with a prominent median lobe, divided behind the eyes by a strong 'Y'-shaped suture and with further transverse divisions across this region (Emended from Shear & al. 1987).

***Alkenia mirabilis* STØRMER, 1970** (Figs. 1–3)

1969 Arachnid; Størmer, p. 1276, text-figs. 1–2.
1970 *Alkenia mirabilis;* Størmer, pp. 352–355, pls. 3, 4, 5, fig. 1, text-fig. 7.
1987 *Alkenia mirabilis* STØRMER; Shear & al., pp. 16–17.
1994 ?*Alkenia mirabilis* STØRMER; Brauckmann, pp. 171–172, fig. 2.
2004 *Alkenia mirabilis* STØRMER; Dunlop & Selden, p. 1473.

Type material: SMF VIII 30a, b (holotype) and SMF 26029 (paratype).

Type locality and horizon: Quarry in the Alkener Bach Tal, east of Alken an der Mosel, 320 m south of Dunkelsmühle (TK 25 sheet Münstermaifeld R 2603800, H 5568670), Rhineland-Palatinate, Germany. From the Nellenköpfchen Formation, upper Vallendar Group. Early Devonian (uppermost Lower Emsian).

Distribution: From the type locality and questionably from an opisthosomal fragment from the stratigraphically equivalent Klerf Beds of Waxweiler, the Eifel Hills, Germany (cf. Brauckmann 1994).

Diagnosis: As for the genus.

Description: See Størmer (1970, pp. 353–355). Deviations from Størmer's descriptions and interpretations are discussed above.

Remarks: Størmer (1970) initially assigned *A. mirabilis* to Hirst's (1923) family Palaeocharinidae – at that time including the only other trigonotarbids recorded from the Devonian. This placement seems inappropriate since detailed study of core palaeocharinids (Shear & al. 1987, Fayers & al. 2005), i.e. *Palaeocharinus* spp. (Hirst 1923), reveals a number of important differences, not least of which is the plesiomorphic retention of multi-facetted lateral eyes in palaeocharinids for which there is no evidence in *A. mirabilis*. Like the

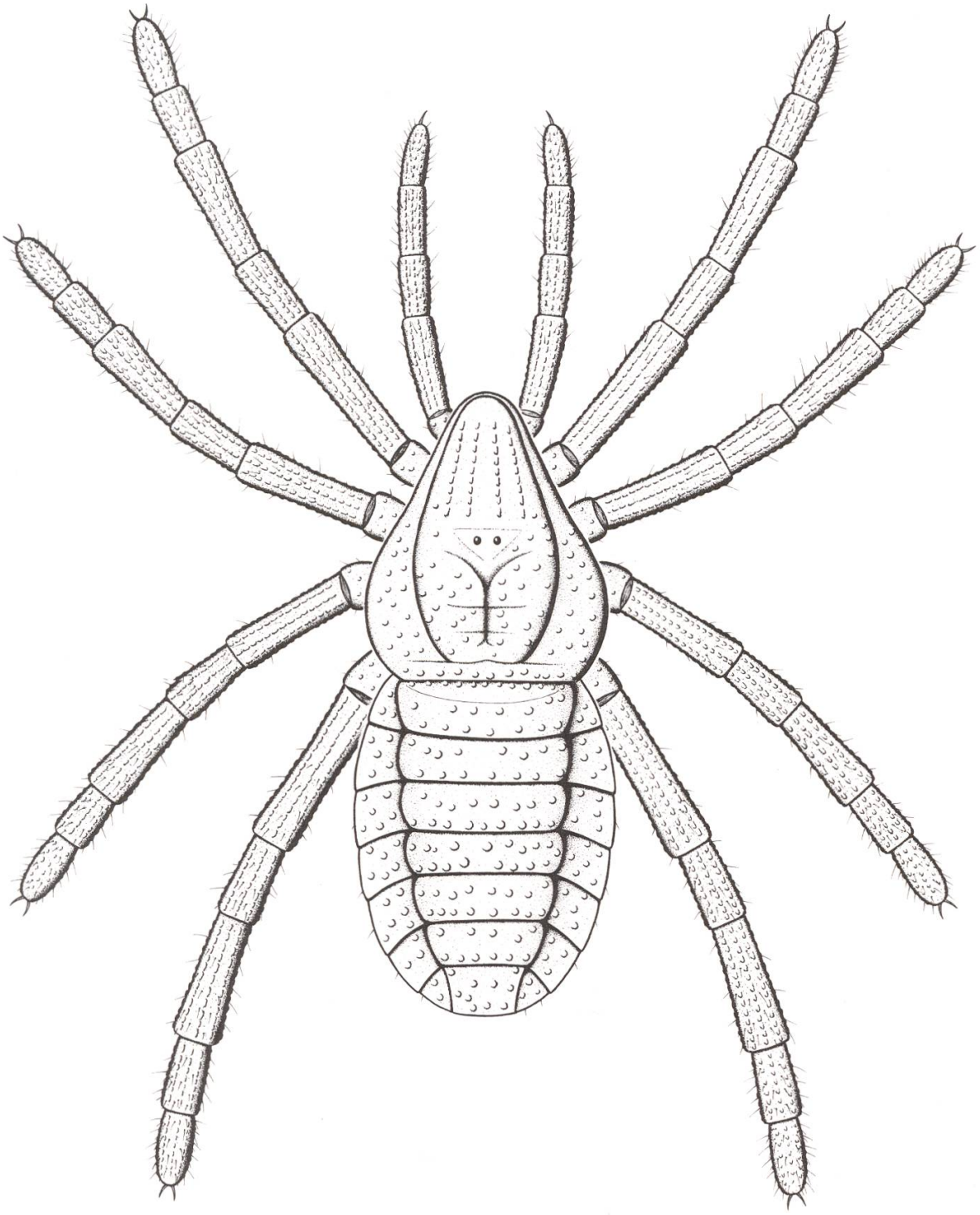

Fig. 3. Reconstruction of the possible appearance of *A. mirabilis* in life, with some details (claws, setae, etc.) taken from comparisons with better preserved Rhynie chert trigonotarbids (cf. Hirst 1923; Fayers & al. 2005) and extant arachnids. Total body length in life ca. 12.5 mm.

Alken fossil, at least one palaeocharinid has now been shown to have a tuberculate dorsal surface (Fayers & al. 2005), but the lobed carapace in *A. mirabilis* is another important difference between these forms. Shear & al. (1987) treated *A. mirabilis* as Trigonotarbida *incertae sedis*, but noted some similarities to the heavily ornamented Carboniferous genus *Aphantomartus*. Brauckmann (1994) went one stage further and tentatively referred *A. mirabilis* to

the relevant family, Aphantomartidae, based again on the strongly sclerotised body and similarities in the pattern of dorsal tuberculation. However Rössler (1998), who did not cite and may have overlooked this latter paper, did not include *A. mirabilis* in his revision of Aphantomartidae.

The rather unique morphology of *A. mirabilis* might be grounds for raising a new family, as was proposed in the taxonomically non-binding thesis of Dunlop (1994). However, a surfeit of monotypic higher taxa is generally unhelpful. A formal phylogenetic analysis of Trigonotarbida has not been carried out, but drawing on the earlier thesis work – see also Dunlop & Brauckmann (2006) – it is possible to identify some broad trends. The most obvious seems to be a division between those taxa plesiomorphically retaining semi-compound lateral eyes (Palaeocharinidae, Anthracomartidae and, perhaps, Anthracosironidae) and the rest which have reduced the lateral eyes and retain only the median ones. *A. mirabilis* appears to belong in this latter – as yet unnamed – group and is treated in the present paper as a plesion genus of uncertain familial affinity. The carapace of *A. mirabilis* is quite unique in terms of its suture patterns, but has overall a subtriangular form. It may thus resolve close to (or even among) the so-called 'triangular carapace' trigonotarbids (cf. Dunlop & Brauckmann 2006), comprising the families Trigonotarbidae, Lissomartidae, Eophrynidae, Kresicheriidae and Aphantomartidae. The last three, recently named the eophrynid–kesicheriid–apahntomartid assemblage, may also be monophyletic. They all express a heavily ornamented granular or tuberculate body; a potential synapomorphy shared with *A. mirabilis* (cf. Brauckmann 1994). However, pending formal phylogenetic analysis, this body ornament may prove to be homoplastic since the carapace morphology of *A. mirabilis* differs quite fundamentally in its details (see above) to that in the 'eophrynid assemblage'.

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