A redescription of the trigonotarbid arachnid Pseudokreischeria pococki (Gill, 1924)

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Summary

The trigonotarbid (Arachnida: Trigonotarbida) *Pseudokreischeria pococki* (Gill, 1924) from the Upper Carboniferous (Westphalian B) of Ryton-on-Tyne, Co. Durham, UK, is redescribed. The less well preserved *Pseudokreischeria varia* (Petrunkevitch, 1949) is regarded as a junior synonym of *P. pococki* and a new reconstruction of this species is presented. *Pseudokreischeria* itself is formally referred to the family Kreischeriidae Haase, 1890.

Introduction

The trigonotarbids were an abundant group of Palaeozoic spider-like arachnids, which ranged from the Silurian to the Permian (Dunlop, 1996a). Trigonotarbids are placed in the arachnid taxon Tetrapulmonata Shultz, 1990, as sister group to Araneae, Amblypygi and Uropygi (e.g. Shear et al., 1987), though Dunlop (1996b) suggested trigonotarbids may also be closely related to Ricinulei. Trigonotarbids are most abundant in the Upper Carboniferous Coal Measures of Europe and North America where a number of quite large, tuberculate species are recorded, leading some authors to refer to trigonotarbids as "armoured spiders". As part of an ongoing revision of trigonotarbid systematics, Rössler & Dunlop (1997) recently reinstated the family Kreischeriidae Haase, 1890 and provisionally referred the genus Pseudokreischeria Petrunkevitch, 1953 to this family. *Pseudokreischeria* is represented by two species, P. pococki (Gill, 1924) and P. varia (Petrunkevitch, 1949), both from the Upper Carboniferous of Ryton-on-Tyne, Co. Durham, UK. This paper redescribes the holotypes of these two species (Figs. 1–8), which are here regarded as synonyms, and presents a new reconstruction of the animal in life (Fig. 9).

Historical background

Gill (1924) described a number of arthropods collected by a Mr William Eltringham from the Phoenix Brickworks quarry at Crawcrook in the Tyne Valley. The fossils from this site were noted as coming from a band of ironstone nodules associated with a thin coal seam, known locally as the Crow Coal, which Gill regarded as Middle Coal Measures in age. Among the arthropods, Gill described *Eophrynus pococki* as a new species of trigonotarbid arachnid and compared it at some length to the type species of the genus, *Eophrynus prestvicii* (Buckland, 1837). Gill's (1924: fig. 2) figure of *E. pococki* is excellent and his description is for the most part highly accurate.

Petrunkevitch (1949) created a new species, *Eophrynus* varius, for a poorly preserved specimen, also from

*Present address: Museum für Naturkunde, Humboldt Universität Berlin, Invalidenstr. 43, 10115 Berlin, Germany. the William Eltringham collection, consisting of the posterior end of an opisthosoma and a femur. Petrunkevitch (1949) separated E. varius from other *Eophrynus* species on the possession of a last tergite with a longitudinal ridge. Petrunkevitch (1949) distinguished Gill's (1924) species, E. pococki, from other eophrynids on tergites divided by a pair of furrows and having large tubercles only on the second tergite. Subsequently, Petrunkevitch (1953) created a new genus, Pseudokreischeria, for these two species, differentiating this genus from *Eophrynus* on the characters he originally used to diagnose E. pococki, i.e. longitudinal furrows on the tergites and large tubercles restricted to the second tergite. E. varius therefore became P. varia to fit systematic conventions. Petrunkevitch's (1953) drawing of P. pococki is awful, bearing no resemblance to the specimen at all, and this same drawing was repeated in the Treatise on Invertebrate Paleontology (Petrunkevitch, 1955). In the Treatise the family Eophrynidae Karsch, 1882 was split into two subfamilies: the less heavily tuberculate Areomartinae Petrunkevitch, 1955, and the strongly tuberculate Eophryninae Karsch, 1882. Pseudokreischeria, with large tubercles restricted to segment 2, was referred to Areomartinae by Petrunkevitch (1955).

Material and methods

The type specimens of *Pseudokreischeria pococki* (In 41509) and *Pseudokreischeria varia* (In 39767) were studied from the Natural History Museum, London (BMNH) collections. Specimens were photographed whitened with ammonium chloride and drawings were prepared using a camera lucida. A superb specimen of *Eophrynus prestvicii* from the Lapworth museum, Birmingham (Specimen no. 669) was also studied as an example of the type genus of the family Eophrynidae, along with photographs of *Kreischeria wiedei* Geinitz, 1882, the type species of the type genus of Kreischeriidae. All measurements are in mm.

Preservation and geological setting

Both specimens (Figs. 1-8) comprise a part and counterpart and are preserved in sideritic, clay-ironstone concretions. Pieces of the holotype of P. pococki have broken off the main nodule at some point and were subsequently reattached. The fossils are preserved as external moulds comprising both dorsal and ventral features depending on how the nodule has split. Where part and counterpart show the same surface, the tuberculation, and other raised morphological features, are preserved in positive relief (i.e. tubercles) in the part and negative relief (i.e. depressions) in the counterpart (Figs. 1-8). This means that the part (Figs. 1, 3, 5, 7), with raised tubercles, is regarded as showing the appearance of the animal in life (Fig. 9) and also means that Petrunkevitch's (1949, 1953) claim that the last tergite is ornamented with a ridge is partly inaccurate, as this refers to the appearance of the counterpart, and it would have been a groove in life.

Both *P. pococki* and *P. varia* were cited as coming from the Middle Coal Measures of the Phoenix Brickworks at Crawcrook, near Ryton-on-Tyne, Co. Durham, i.e. Westphalian B-C (Petrunkevitch, 1953). Gill's (1924) notes on the Eltringham collection and the BMNH labels for both specimens indicate they came from near the Crow Coal. This "Crow Coal" in the Tynemouth district was cited as a synonym of the Bottom Seam (Land, 1974), which occurs just below the High Main Seam in this district. The High Main Seam itself is placed towards the base of the lower *Anthraconia similis-Anthraconia pulchra* zone, which in turn dates these fossils to the middle of the Westphalian B (Land, 1974; Ramsbottom *et al.*, 1978).



Figs. 1–4: Pseudokreischeria pococki (Gill, 1924) from the Upper Carboniferous (Westphalian B) of Crawcrook, Ryton-on-Tyne, Co. Durham, UK. 1 BMNH In 41509 (part); 2 In 41509 (counterpart); 3 In 39767 (part); 4 In 39767 (counterpart). Specimens whitened with ammonium chloride. Scale lines=0.5 cm.



Figs. 5–8: Camera lucida drawings of material shown in Figs. 1–4. **5** BMNH In 41509 (part); **6** In 41509 (counterpart); **7** In 39767 (part); **8** In 39767 (counterpart). Abbreviations: cp=carapace, cu=carbonised cuticle, fe=femur (with leg number), L=leg with number, me=median eyes, mg=median groove, Pl.fe=palpal femur, pt=patella (with leg number), py=pygidium (segments 11 & 12), S=sternite with number, Se10=tenth opisthosomal segment surrounding pygidium, Str=sternites, sp=terminal spine of opisthosoma, T=tergite (with number), Ter=tergites, ti=tibia (with leg number), tr=trochanter (with leg number). Scale line=1 cm.



Fig. 9: Reconstruction of *Pseudokreischeria pococki* based on the type material and comparisons with other trigonotarbids and extant arachnids. Distal leg podomeres poorly known and omitted. Scale line=1 cm.

Systematic palaeontology

Tetrapulmonata Shultz, 1990 Order Trigonotarbida Petrunkevitch, 1949

Diagnosis: Tetrapulmonate arachnids with tergite 1 formed into a locking ridge, reduced in some families, and tergites 2–8 (2–9 in some) divided into median and lateral plates. Tergites 2 and 3 fused into a diplotergite, tergites 4–9 not fused. Sternite 1 absent. Pedipalps and walking legs pediform. Chelicerae two-jointed and of the clasp-knife type (Dunlop, 1996a).

Remarks: Dunlop (1996a) synonymised the extinct arachnid order Anthracomartida with Trigonotarbida, both rediagnosed as above.

Family Kreischeriidae Haase, 1890

Type genus: Kreischeria Geinitz, 1882.

Included genera: Pseudokreischeria Petrunkevitch, 1953 and provisionally Anzinia Petrunkevitch, 1953, Gondwanarachne Pinto & Hünicken, 1980 and Hemikreischeria Frič, 1904.

Diagnosis: Large trigonotarbids with a subtriangular carapace and tuberculate dorsal surface. Tuberculation with a more uniform, granular pattern as opposed to discrete large tubercles in Eophrynidae and Aphantomartidae. Tergites 2 and 3 fused into a single diplotergite, as opposed to separate tergites in Eophrynidae. Terminal opisthosomal spines present in most taxa (after Rössler & Dunlop, 1997). *Remarks:* Rössler & Dunlop (1997) reinstated the family Kreischeriidae for *Kreischeria wiedei* and suggested that a number of other genera previously referred to Eophrynidae may also belong in this family. The reinstatement of Kreischeriidae negates Petrunkevitch's (1955) split of Eophrynidae into two subfamilies, Areomartinae and Eophryninae, as most of the areomartid genera, with their less robust tuberculation, probably belong in Kreischeriidae (Rössler & Dunlop, 1997). *Areomartus* Petrunkevitch, 1913 itself may not be a trigonotarbid and most eophrynid taxa require restudy before their position can be confirmed.

Genus Pseudokreischeria Petrunkevitch, 1953

Type and only known species: Pseudokreischeria pococki (Gill, 1924).

Diagnosis: Kreischeriids with cuticular ornamentation of small tubercles and single pair of large tubercles adjacent to deep grooves on diplotergite 2+3, as opposed to rows of large tubercles in *Kreischeria*. Subsequent median tergites with a pair of furrows (not seen in other kreischeriids), except for ninth tergite which has a single median groove.

Remarks: Petrunkevitch (1953) removed Gill's (1924) species from the genus *Eophrynus* and placed it into a new genus *Pseudokreischeria* (see historical background). Though resembling *Kreischeria* in its ornamentation of small tubercles, *Pseudokreischeria* is a smaller, more rounded animal and its pattern of opisthosomal tuberculation with two large tubercles restricted to diplotergite 2+3 and the furrows on the median tergites differentiates it from the type genus *Kreischeria*.

Pseudokreischeria pococki (Gill, 1924) (Figs. 1-9)

Eophrynus pococki Gill, 1924: 459, fig. 2; Petrunkevitch, 1949: 246. *Eophrynus varius* Petrunkevitch, 1949: 247–248, figs. 110, 258. Syn. nov.

Pseudokreischeria pococki: Petrunkevitch, 1953: 81–82, figs. 91–92; 1955: 110, fig. 75(1).

(?) Pseudokreischeria varia: Petrunkevitch, 1953: 82.

Pseudokreischeria varia: Petrunkevitch, 1955: 110, fig. 75(2).

Holotype: BMNH In 41509 from nodule-bearing horizon associated with Crow Coal, Phoenix Brickworks at Crawcrook, near Ryton-on-Tyne, Co. Durham, UK. Upper Carboniferous (middle Westphalian B).

Additional material: BMNH In 39767 (holotype of *Eophrynus varius*) from same locality and stratigraphic horizon as holotype. Petrunkevitch (1953) reported a specimen from Deepfields, near Bilston, UK, labelled *Eophrynus pococki*, which seemed to him to be *Pseudo-kreischeria pococki*. This specimen was reported by Petrunkevitch (1953) as being in the Lapworth Museum (Specimen no. 11), but could not be traced in the Lapworth collections during this study.

Diagnosis: As for the genus.

Description: BMNH In 41509 represents a near complete carapace and opisthosoma plus some proximal podomeres. Both part (Figs. 1, 5) and counterpart (Figs. 2, 6) essentially show dorsal views, though posterior end of counterpart shows ventral opisthosoma.

Carapace best preserved on part, length 9.5, maximum width 10.0. Carapace tuberculate, subtriangular with short anterior spine; median area raised, width 4.2, bearing a pair of median eyes and strongly divided into a pair of lobes behind these eyes; lateral areas strongly divided into four lobes on each side, with additional single frontal lobe merging into anterior spine. Legs poorly preserved. Part preserves femur of pedipalp, length 3.2, and portions of femora 2–4. Counterpart preserves portions of legs 1, 2 and 4, with leg 2 being most complete. Ornamentation of small tubercles preserved on all legs.

Opisthosoma rounded, with estimated length and width 22 mm. Bottom left portion of opisthosoma missing on part, and tergites 1 and 2+3 only preserved in counterpart. All tergites tuberculate, though tuberculation better preserved on anterior and median tergites. Tergite 1 short, length 1.4, undertucking carapace as a locking ridge and with a pair of elongate depressions. Tergites 2 and 3 fused into a single diplotergite, which is large, length 3.7, with a pair of large tubercles either side of a pair of deep grooves (ridges in counterpart), probably representing muscle apodemes. Subsequent median tergites 4-7 shorter, lengths 1.9, divided by pair of furrows. Tergites 8 and 9 poorly preserved. Posterior end of counterpart shows pygidium (i.e. segments 11 and 12), diameter 1.8, surrounded by plate-like 10th opisthosomal segment. Segment 10 ornamented with tubercles in positive relief and with median groove posterior to pygidium. Adjacent sternites 7-9 ornamented with tubercles in negative relief. Triangular, terminal spines at posterior end of opisthosoma evident.

BMNH In 39767 represents the posterior end of an opisthosoma plus the proximal podomeres of leg 4. Both part (Figs. 3, 7) and counterpart (Figs. 4, 8) show essentially dorsal views, though left side of counterpart may represent sternites. Opisthosomal portion with maximum length 13.7 and maximum width 16.7. Posteriormost tergite distinctly tuberculate and with a median groove in part (ridge in counterpart). Tuberculation present on other tergites, but less distinct. Two pairs of small, triangular spines present on terminal end of counterpart. Dark patches on part represent carbonised remnants of cuticle. Trochanter of leg 4 preserved, maximum length 4.8, along with femur, maximum length 9.1. Slight tuberculation preserved on femur.

Remarks: BMNH In 39769, the holotype of *P. varia*, shows few features of taxonomic significance and even Petrunkevitch (1953) placed a question mark by his previous assignment of this fossil to a separate species (Petrunkevitch, 1949). Petrunkevitch (1953) differentiated *P. varia* from *P. pococki* by smooth tergites 3–7 in *P. varia*, while the corresponding tergites in *P. pococki* were described as tuberculate. *P. varia* was also characterised by a longitudinal median ridge on the last tergite. When the fossils are examined closely, the holotype of *P. varia* can be seen to have some tuberculation on its "smooth" tergites (Fig. 8), while the tergites at the posterior end of the holotype of *P. pococki*

are less tuberculate, showing that the preservation of tubercles is not uniform. Petrunkevitch's tergite ridge would have been a groove in life, as discussed above. The holotypes of both *P. pococki* and *P. varia* have the same basic ornamentation of small tubercles, the same posterior spines on the opisthosoma and are of approximately the same size. Since both are from the same stratigraphic horizon at the same locality, and since there are no obvious morphological features to distinguish the fossils from each other I regard *P. varia* as a junior synonym of *P. pococki*.

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The effects of maternal nest guarding behaviour by *Eremobates marathoni* Muma & Brookhart on the survivorship of offspring (Solifugae, Eremobatidae)

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Summary

Observations on the depression burrows (nests) of Eremobates marathoni that contained eggs indicated that the clutch size ranged from 18-69 (mean 36.5 ± 5.8). The number of first-instar nymphs per nest ranged from 9-41 (mean 22.0 ± 7.7 , S.D.). Field studies were also conducted to assess the effect of maternal guarding of the nest against a naturally occurring predator, Schizocosa avida (Lycosidae), on the survivorship of first-instar solifuge nymphs. The presence of a maternal parent within the nest resulted in a significant increase in survivorship of offspring in this solifuge. Twelve of 15 adult female Schizocosa avida spiders (80%) introduced into nests containing an adult female solifuge were killed and eaten by the maternal parent. Mortality of solifuge nymphs resulting from spider predation was observed at a low frequency (5.9-15%) in only three of these 15 nests. In no case did a spider kill an adult solifuge. In unguarded nests, mortality of solifuge nymphs was significantly higher, ranging from 45-100%. Mortality was higher than 60% in 10 out of 15 unguarded nests. The results of this study indicate that nest guarding behaviour contributes in a significant way to offspring survivorship and hence to the overall fitness of E. marathoni.

Introduction

It is generally assumed that the guarding of a nest by a maternal or paternal parent will contribute in a positive way to the survivorship of their young (Reznick, 1985; Clutton-Brock, 1988). When some degree of parental care is exhibited by lower vertebrates (fish, reptiles) or arthropods it is usually confined to one parent only (Dawkins & Carlisle, 1976; Smith, 1980).

Many female spiders are known to provide assistance and protection to their brood. Lycosid females carry their egg sacs (usually attached to the abdomen) with them as they move from one location to another and will frequently assist their offspring during hatching by using their chelicerae to tear open the cocoon (Fujii, 1978). The emerging spiderlings then climb on to their mother's back and remain there for several days. Pisaurid females carry their egg sacs in their chelicerae (Foelix, 1996). In a few species of theridiid, agelenid and eresid spiders, females provide food for their young by leaving captured prey near the spiderlings, feeding them liquified food, or laying an additional batch of smaller eggs as a food source (Gundermann *et al.*, 1988, 1991; Tahiri *et al.*, 1989). Maternal guarding of the nest has also been shown to enhance the subsequent survival of juvenile scorpions (*Euscorpius flavicaudis* (De Geer)) (Benton, 1991), and spiderlings of the thomisid *Misumena vatia* (Clerck) (Morse, 1992).

Eremobates marathoni Muma & Brookhart is a common representative of the solifuge fauna of the Big Bend region of Trans Pecos Texas which lies in the northern region of the Chihuahuan Desert (Punzo, 1997a). Individuals of both sexes frequently construct a bowl-shaped depression burrow under a rock (personal observation). Females utilise these depression burrows as nests in which they lay their eggs. Females will remain in the nest and guard their eggs, as well as hatchling nymphs. First-instar nymphs remain with their mother in the nest. After moulting, the second-instar nymphs leave the nest and disperse.

During the course of field studies on several species of solifuges, including *E. marathoni*, found in this area, I have frequently observed the wolf spider, *Schizocosa avida* (Walckenaer) feeding on unguarded solifuge nymphs in their burrows (personal observation). Other than mortality resulting from cannibalism by other nymphs, this is the only predator that I have observed capturing and feeding on solifuge nymphs at this study site. In the present field study, I examined the effect of maternal nest guarding by *E. marathoni* on the subsequent survivorship of offspring. To my knowledge, no previous studies exist on the possible adaptive significance of this behaviour in solifuges.

Methods

All field experiments were conducted on solifuges found within a 3 km radius of Marathon, Texas (Brewster County), during late July and August 1995. The general topography and dominant vegetational zones have been described in detail elsewhere (Tinkam, 1948; Punzo, 1997b). I located burrows (nests) occupied by adult solifuges by turning over rocks located on the desert floodplain. Burrows containing females with firstinstar nymphs (n=86) were identified and given a number which was placed on a small wooden marker driven into the ground next to each burrow. Females