A redescription of the Carboniferous arachnid *Plesiosiro madeleyi* Pocock, 1911 (Arachnida: Haptopoda)

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**ABSTRACT.** *Plesiosiro madeleyi* Pocock, 1911, the monotypic representative of the fossil order Haptopoda Pocock, 1911 from the British Middle Coal Measures (Upper Carboniferous, Westphalian B) of Coseley, Staffordshire, is redescribed. A specimen from Sparth Bottoms, Lancashire is not a *Plesiosiro* and is referred to Arthropoda incertae sedis. *Plesiosiro* was probably a predator, having tooth-like projections on the femora for prey capture, and shows adaptations of the limbs for crawling in narrow spaces. The uncertain nature of the chelicerae, eyes and respiratory organs makes resolving the phylogenetic position of *Plesiosiro* difficult, though Haptopoda deserves its status as a separate order. *Plesiosiro* resembles both cyathopithild and trogulid opilionids. Its broad prosoma–opisthosoma junction could be interpreted as a synapomorphy for *Plesiosiro* + Opilionidae, but this character is not unique to these orders. Alternatively, *Plesiosiro* has a large, ventral opisthosomal sclerite. This is interpreted here as a genital operculum, a synapomorphy for Tetrapulmonata, and *Plesiosiro* is tentatively referred to this clade. Based on the synapomorphies of a divided sternum and subdivided telotarsi a relationship of the form: (*Plesiosiro* (Amblypygi (Thelyphonida + Schizomida))) is proposed.

**KEY WORDS:** Amblypygi, arthropod, Coal Measures, Coseley, fossil, Opilionidae, phylogeny, systematics, Thelyphonida

*Plesiosiro madeleyi* Pocock, 1911 was described in a new, monotypic arachnid order, Haptopoda Pocock, 1911. This paper recognizes nine specimens of *Plesiosiro*, all from the same Upper Carboniferous locality of Coseley near Dudley. Seven are in the collections of the British Museum (Natural History) (BMNH) and two in the collections of the Museum of the British Geological Survey (GSM). A further specimen referred to this species by Petrunkevitch (1953) and in the Manchester Museum (MM) is not a *Plesiosiro* (see 2.1). The position of *Plesiosiro* within Arachnida is currently uncertain (see 1) and this present study redescribes all apparently known material, presents a new reconstruction of this fossil and discusses the phylogenetic position of this poorly known and enigmatic arachnid. Though some important character states cannot be resolved, those that are preserved support a tentative (*Plesiosiro* (Amblypygi (Thelyphonida + Schizomida))) relationship.

### 1. Previous work

Pocock (1911) described a new, Upper Carboniferous arachnid from Coseley, near Dudley, based on material in the collections of Madeley, Hind, Priest and Eggington. Pocock (1911) named the animal *Plesiosiro madeleyi* and placed it in his own family, *Plesiosirionidae* Pocock, 1911, as the sole representative of a new, monotypic, order Haptopoda. *Plesiosiro* was described as having a broad prosoma–opisthosoma junction, an 11-segmented opisthosoma, small pedipalps and an elongate leg pair 1 with subdivided tarsi. Pocock (1911) named the order Haptopoda in recognition of the apparent tactile nature of the first pair of legs, while his choice of genus name, *Plesiosiro*, implies similarities with the extant cyathopithild genus *Siro* (Cyathopithild) are usually regarded as basal opilionids. Pocock (1911) figured only one specimen (not the holotype) and presented a reconstruction of the animal. Pocock (1911) established his new order since he was unable to fit *Plesiosiro* into any existing arachnid order. However, he noted similarities between *Plesiosiro* and Opilionidae in the broad prosoma–opisthosoma junction, between *Plesiosiro* and Uropygi in the elongate first pair of legs, and between *Plesiosiro* and Anthracomartia (= Trigonotarbida (Dunlop 1996a)) in the terminal end of the opisthosoma. Pocock (1911) concluded that the fossil orders Haptopoda, Phalangiotaebi and Anthracomartia may represent intermediates between opilionids and more primitive orders of arachnids.

Petrunkevitch (1913) briefly mentioned *Plesiosiro* and suggested that it was in fact a phalangiotaebid. Waterlot (1949) reproduced Pocock's (1911) reconstruction in *Traité de Zoologie*. Petrunkevitch (1949) redescribed *Plesiosiro* at length based on six of the BMNH specimens, figuring three of them. Petrunkevitch (1949) made some additional observations, describing the opisthosoma as having 12 segments, subdivided tarsi on legs 2–4 and a single pair of median eyes. Petrunkevitch (1949) also described three-jointed, chelate chelicerae and two pairs of book lungs opening on opisthosomal sternites 2 and 3. In the same monograph, Petrunkevitch (1949) split the existing fossil order Anthracomartia into two orders. Those originally in the family Anthracomatidae were retained as Anthracomartia and placed, with Haptopoda, in a new subclass, Stethostomatia. This was defined as arachnids with a broad prosoma–opisthosoma junction and downwards-hanging chelicerae. The rest of the Anthracomartia were placed in a new order, Trigonotarbida, in another new subclass, Soluta, defined by a prosoma–opisthosoma junction of variable width (see Shear et al. (1987) and Dunlop (1996a) for critical reviews).

Waterlot (1953), in *Traité de Paléontologie*, followed Petrunkevitch's (1949) interpretations and systematics. Petrunkevitch (1953) did not elaborate on his previous descriptions of *Plesiosiro*, but noted the presence of an additional specimen in the Museum of the Geological Survey (GSM 60169A/B) from the 1937 Hughes collection, Lower
similis-pulchra zone, Ten-foot ironstone measures, Coseley. He appears to have overlooked a further specimen in the GSM collection (60170A/B). Petrunkevitch (1953) also referred a single specimen in the Manchester Museum from the Coal Measures of Sparth Bottoms, Rochdale (MM L7097) to *Plesiosiro*. Petrunkevitch (1953, 1955) retained Haptoptoda within the Stethostomatata and Petrunkevitch (1955) reproduced some of his 1949 figures in the *Treatise on Invertebrate Paleontology* in which he also emended the order name to Haptopodida following ICZN recommendations. Subsequent authors have tended to use Haptopoda.

Since Petrunkevitch's work there has been little mention of *Plesiosiro* in the literature. Dubinin (1962) included Haptoptoda in a subclass Opiliomorpha, along with the Phalangiotarbid and Opiliones. 'Opiliomorphs' were characterised primarily by an oval body and were believed by Dubinin (1962) to have evolved from amblypygids. Savory (1964) included Haptoptoda in his general book on arachnids and accepted Petrunkevitch's descriptions. Crowson et al. (1967) included *Plesiosiro* under Haptopodida in *The Fossil Record*, but many authors on arachnid higher systematics and phylogeny have simply overlooked or ignored *Plesiosiro*. Grasshoff (1978) placed Stethostomatata as a relatively early derivative arachnid group of a similar grade of organisation to Amblypygi, Uropygi and Phalangiotarbid. Meanwhile, Firstman (1973) and van der Hammen (1977) both tentatively placed Haptoptoda within the group of arachnids with two book lung pairs, a taxon now recognised as comprising Trigotonotarbid, Araneae, Amblypygi, Thelyphonida and Schizomida (e.g. Shear et al. 1987). Unusually among arachnids, this clade, including spiders and their closest relatives, appears to be relatively stable and well supported (Selden & Dunlop 1998) and has been referred to as Megoperculata (Weygoldt & Paulus 1979), Arachnidae (Shear et al. 1987) and Tetrapelmonata (Shultz 1990). This latter name is adopted here, although tetrapelmonates' primary character, presence of two book lung pairs, may be synapomorphic for non-scorpion arachnids. In this paper I follow Shultz (1990) and Dunlop & Horrocks (1996) and use the order names Thelyphonida and Schizomida, with both orders together forming a clade Uropygi. Other authors have used Uropygi and Schizomida as order names.

Petrunkevitch's (1949) Stethostomatata was questioned by Shear et al. (1987) and formally rejected by Dunlop (1996a) as a polyphyletic grouping of one family of trigotonotarbid, Anthracomartidae, and a separate order of arachnids, Haptoptoda. With respect to the position of *Plesiosiro*, Shear et al. (1987) suggested that it was probably not one of the Arachnidea and Shear & Kukalová-Peck (1990) further suggested that *Plesiosiro* might be an opilionid, though gave no evidence in support of this. Beall & Labandeira (1990) placed Haptoptoda as sister group to phalangiotarbid, opilionids and mites (a similar model to Dubinin (1962)), but did not list the characters on which this clade was based. Delle Cave & Simonetta (1991) mentioned *Plesiosiro* as a 'very interesting' arachnid; it was included in *The Fossil Record* 2 (Selden 1993a) and mentioned by Selden (1993b) as a fossil deserving restudy. Dunlop (1996a, 1997) suggested that *Plesiosiro* belonged in Tetrapelmonata and might be a sister group of (Amblypygi + (Thelyphonida + Schizomida)) on synapomorphies of an elongate leg pair 1 and subdivided tarsi. Dunlop (1996c) figured a specimen of this fossil and new reconstructions of *Plesiosiro* were included by Dunlop (1996a, 1997) and Selden & Dunlop (1998). The latter authors noted that while comparisons can be made with both Uropygi and Opiliones, Haptoptoda does not show autapomorphies of either group and probably deserves its status as a separate order.

2. Materials and methods

All nine specimens of *Plesiosiro madeleyi* were studied: BMNH I. 7922, I. 7923, I. 15899, In 18341, In 22835, In 22837, In 31236, GSM 60169A/B and 60170A/B. This material all comes from the same locality, Coseley near Dudley, Staffordshire, UK, which is part of the British Middle Coal Measures (e.g. Petrunkevitch 1949, 1953) and which has been dated at Upper Carboniferous (Westphalian B) in age (e.g. Ramsbottom et al. 1978). All specimens are preserved either as external moulds, or more rarely as casts, in sideritic ironstone concretions. With the exception of BMNH In 18341, all specimens comprise a part and counterpart. The nodules usually split into primarily dorsal and ventral views, but in a number of specimens either part and/or counterpart show both dorsal and ventral features (section 6). Specimens were drawn using a camera lucida and photographed whitened with ammonium chloride. Specimens of representative extant arachnids were studied in association with the literature for comparative anatomy. Other Carboniferous arachnids in the BMNH, GSM and Lapworth Museum, Birmingham collections were also examined, especially those in sideritic concretions which show similar preservation and taphonomy to the *Plesiosiro* material.

2.1. The Manchester Museum specimen

MM L7097 (Figs 4d & 5d), a specimen in an ironstone concretion from the Coal Measures of Sparth Bottoms, Rochdale, Lancashire, UK, was also examined. This fossil was referred to *Plesiosiro madeleyi* by Petrunkevitch (1953). This specimen appears to be the opisthosoma (= abdomen), of an arthropod, including structures resembling leg coxae. This specimen is broadly oval and has a median ridge similar to the opisthosoma of *Plesiosiro*, but lacks transverse segmentation. There are no further characters which identify this specimen as *Plesiosiro*. It has features reminiscent of an opilionid, i.e. an opisthosoma projecting anteriorly between leg coxae, but this interpretation is speculative and MM L7097 is regarded here as Arthropoda incertae sedis. All unequivocal specimens of *Plesiosiro* therefore come from Coseley.

2.2. Abbreviations

The following abbreviations are used as standard in the *camera lucida* drawings and descriptions: ap = tergal muscle apodemes, as = anterior sclerite of sternum, bt = basitarsus, ch = chelicerae, cp = carapace, cx = coxa, fe = femur, L = leg with number, le = probable lateral eye tubercle, me = median eyes, pp = pedipalp, ps = posterior sclerite of sternum, pt = patella, py = pygidium, s = probable ring-like segment, S = sternite with number, "S2" and "S3" possible opercula, T = tergite with number, ti = tibia, tr = trochanter, ts = telotarsus. All scale bars in the figures and photographs are 4 mm and measurements in the descriptions are given in mm.

3. Morphological interpretation

The following descriptions and interpretations are based on a composite of material, with particular specimens named where appropriate. With respect to ridges, tubercles, etc., descriptions are of the appearance of the animal in life. Individual specimens are described in section 6. A reconstruction of *Plesiosiro madeleyi* is presented in Figure 1.

3.1. Carapace

The carapace of *Plesiosiro* is roughly trapezoidal in shape, dorso-ventrally flat and drawn into a small anterior projection (e.g. I. 7922, Figs 2a & 3a). The posterior margin of the carapace is straight and appears to have folded back on itself
Figure 1  Reconstruction of *Plesiosiro madeleyi* Pocock, 1911 based on a composite of the material studied and comparisons with Recent arachnids; see text for details.
to form a slight undertucking (see 3.8). The carapace bears three narrow ridges by which *Plesiosiro* can be easily distinguished from other Carboniferous arachnids (see 6). The central ridge bifurcates into an elongate oval before converging anteriorly, close to the median eyes, and merging into the anterior projection. There is a further pair of carapace ridges, one either side of the central ridge, which are angled laterally midway along their length and terminate in small, rounded tubercles at the anterior end (e.g. I. 15899, Figs 4a & 5a). The carapaces of some specimens (e.g. In 31236, Figs 6c & 7e) are covered in tiny tubercles, presumably present in all animals in life, but not preserved in every specimen.
Figure 3 Camera lucida drawings of the specimens shown in Figure 2.
3.2. Eyes

A pair of median eyes is located near the anterior margin of the carapace (e.g. I. 7922, Figs 2a & 3a) either side of the area where the bifurcate median ridges converge. Their preservation is unusual in that they occur as raised structures in the fossils, which implies they were depressions in life. In living arachnids, median eyes tend to be raised structures. However, this phenomenon is not unique to Plesiosiro and occurs in an otherwise superbly preserved specimen of the trigonotarbid Eophrynus prestisci (Lapworth Museum, no. 669) and probably represents an artefact of taphonomy in both fossils. Compaction of the sediment may have pressed the eye lens inwards resulting in its preservation as a raised structure.

The tubercles at the end of the lateral carapace ridges (e.g. I. 15899, Figs 4a & 5a) could represent lateral eyes; however, individual lenses cannot be seen and this interpretation cannot be proved unequivocally. Alternatively these structures could represent the raised openings of repugnatorial glands like those on the carapace of opilionids (W. Shear, pers. comm.), where this character is autapomorphic for the order. They
Figure 5 Camera lucida drawings of the specimens shown in Figure 4.

could simply be tubercles whose significance is unknown. The interpretation of these structures to some extent presupposes the relationships of *Plesiosiro*: if it is a tetrapulmonate they probably are lateral eye tubercles, if it is an opilionid they could well be repugnatorial glands. Clearly phylogeny cannot be determined on these structures alone. The lateral tubercles in *Plesiosiro* (labelled 'le') are in a similar position to the lateral eye tubercles of amblypygids and thelyphonids, in which each tubercle bears three main lenses, to the 'triads' of the probable spider groundplan (Kraus & Kraus 1993), and
some primitive trigonotarbid, where the tubercles tend to be larger with multiple lenses (e.g. Dunlop 1997). Significantly, if these structures in *Plesiostro* are lateral eyes then they occur on carapace ridges, which are essentially the same as ophthalmic ridges, a traditional autapomorphy of Xiphosura (e.g. Dunlop & Selden 1997). Lateral eyes associated with ridges are also seen in the carapace of many thelyphonids (Dunlop & Horrocks 1996).

Meanwhile, the cyphopthalmid *Siro* has a pair of tubercles on the carapace for repugnatorial glands, also in approximately the same position as the *Plesiostro* tubercles. Just as there are no lenses preserved, there is no obvious gland pore in these tubercles in *Plesiostro*. Position alone cannot resolve which interpretation is correct. As shown below (see 3.3, 3.7), *Plesiostro*’s coxo-ster nal region and ventral opisthosoma is more consistent with tetrapulmonates than opilionids. Presence of lateral eyes is almost certainly plesiomorphic for arachnids (e.g. Shultz 1990). On balance, since *Plesiostro* cannot be shown unequivocally to be an opilionid (see 5.1) and since lateral eyes are present in many arachnid orders, I believe it is better to interpret the tubercles in *Plesiostro* as eye tubercles (a plesiomorphic state) for lack of convincing evidence that they are repugnatorial glands (an apomorphic state). This interpretation is made with reservations, but is reflected in the labelling of the specimens and in the reconstruction (Fig. 1).

### 3.3. Coxo-ster nal region

The sternum (e.g. In 22835, Figs 6b & 7b) is an elongate, inverted triangular structure, widening anteriorly with a notch in its anterior margin and with slightly raised areas either side
of this notch forming a pair of anterior 'horns' (GSM 60169B, Figs 8b & 9b). The sternum is divided into two sclerites, not three as figured by Petrunkevitch (1949), the posterior one being smaller and approximately square. Petrunkevitch (1955) figured the mouth in *Plesiosiro* just anterior to the sternum. This position is probably correct, but like a number of Petrunkevitch’s interpretations, cannot be demonstrated from the fossils. Comparisons with other arachnids suggest that *Plesiosiro* would have had a labrum, and perhaps also a labium, forming the lips of the mouth. In 22835 (Figs 6b & 7b) has a structure anterior to the sternum preserved as a series of three transverse depressions and which is not obviously a chelicera. This is in the right position to be either a labrum and/or labium, but it is not seen in other specimens and its interpretation remains uncertain.

The coxae of the pedipalps and walking legs are subtriangular and become larger going from anterior to posterior (GSM 60169B, Figs 8b & 9b). There are no gnathobases, endites or...
other projections from either the palp or leg coxae, which also appear to lack tuberculation. The palpal coxae are noticeably smaller than the leg coxae (e.g., 1, 7922, Figs 2b & 3b) and project slightly out from under the carapace. The leg 1 and 2 coxae also appear to project slightly beyond the margin of the carapace (e.g., 1, 7923, Figs 2c & 3c). Coxae 1, 2 and 3 are in contact with the sternum, while coxae 4 attach behind the sternum and are in contact with the first opisthosomal sternite (see 3.7).

The character states seen in the Plesiosiro coxo-ster nal region are primarily plesiomorphic. There are no endites forming a preoral cavity (as in the opilionid stomatheca), no enlargement and fusion of the palpal coxae (as in the uropygid camerostome) and no highly reduced sternum (as in ambly-
Figure 9 Camera lucida drawings of the specimens shown in Figure 8.
3.4. Chelicerae

The chelicerae of *Plesiostro* are small and poorly preserved. Petrunkevitch (1949) interpreted them as three-jointed, chelate structures supposedly hanging down underneath the carapace; one of his diagnostic characters for Stethostomata (see 1). Subsequently, Petrunkevitch (1955) could only interpret the presence of the third cheliceral podomere from an ‘articulating surface’. Like his mouth position, this evidence is not at all convincing. I. 7922, undoubtedly one of the best specimens, has chelicerae which project out in front of the carapace (Figs 2a & 3a). As such, they appear rather like the chelicerae of mygalomorph spiders, amblypygids, uropygids and opilionids, and this was reconstructed as the life position by both Pocock (1911) and Petrunkevitch (1949). It is not clear how Petrunkevitch reconciled this position with his diagnosis of Stethostomata having downward-hanging chelicerae, though such discrepancies between the text and figures are by no means uncommon in his work. Determining cheliceral morphology would help resolve the position of *Plesiostro*. Three-jointed, chelate chelicerae would support an affinity with opilionids, though outgroup comparison with xiphosurans and eurypterids suggests that this is the plesiomorphic character state. Alternatively, two-jointed, so-called ‘clasp-knee’ chelicerae have been proposed as a tetrapulmonate synapomorphy (e.g. Shear et al. 1987).

Forward-pointing chelicerae are not seen in the two other specimens of *Plesiostro* where the chelicerae are known (I. 7923, Figs 2d & 3d and GSM 60170, Figs 8d & 9d). In these fossils, the chelicerae are retained wholly beneath the carapace and project down into the nodule, as would be expected for structures hanging beneath the animal. Meanwhile in I. 7922 the back of the sternum no longer lies close to the first opisthosomal sternite (Figs 2b & 3b) and compared to other specimens, has clearly been displaced forwards. This implies that all the anterior ventral structures, i.e. the anterior coxae and the chelicerae, have also been displaced and would explain why the chelicerae in this specimen have moved forwards relative to their life position. Downward-hanging chelicerae, indicated by the other two specimens, are interpreted here as the position in life. In fact, in anthracomartids, Petrunkevitch’s other stethostomatan group, and many other trigonotarbid preserved in nodules, the chelicerae are often preserved in a similar way, i.e. as depressions located entirely beneath the carapace and going down into the nodule. Studies of much better-preserved Rhynie Chert trigonotarbid (Dunlop 1997, fig. 4) showed that these animals did indeed have paraxial, downward-hanging chelicerae, an orientation which Dunlop (1997) termed ‘palaeognathy’ and suggested as a possible groundplan for tetrapulmonate arachnids. *Plesiostro* is here interpreted as probably having palaeognath chelicerae too and this is shown in the reconstruction (Fig. 1).

None of the three specimens shows whether the chelicerae comprise two or three podomeres and whether or not they are chelate or clasp-knee structures. In I. 7922 (Figs 2b & 3b) it is possible to interpret the ventral counterpart of this specimen as showing a pair of clasp-knee chelicerae displaced obliquely onto their side with the fangs pointing backwards, and as such there is better evidence for clasp-knee chelicerae in *Plesiostro* than the chelate appendages figured by Petrunkevitch (1949, 1955). This clasp-knee interpretation is shown in the reconstruction (Fig. 1), but remains tentative and cannot be used as a reliable character to place *Plesiostro*.

3.5. Pedipalps

The pedipalps of *Plesiostro* are small and pediform with all podomeres approximately the same length (e.g. In 18341, Figs 4c & 5c). The palpal coxae were discussed above (see 3.3). The coxa-trochanter joint is slightly oblique (I. 7922, Figs 2b & 3b). The femur, patella and tibia of the pedipalp are ornamented with a pair of dorsal grooves (e.g. GSM 60170B, Figs 8d & 9d). The tarsus is not preserved, but in comparison with arachnids such as trigonotarbid, it was probably a
single, unmodified podomere (not divided into a basitarsus and telotarsus), bearing a single claw (Fig. 1).

3.6. Legs

The legs of *Plesiosiro* are reasonably complete. All were fairly robust, pediform appendages, with legs 1 and 4 longest and legs 2 and 3 noticeably shorter (e.g. I. 7922, Figs 2a & 3a). The tuberculation seen on the body is not evident on the palps and legs. Typically, the legs are preserved with their prolateral (i.e. anterior) face uppermost (e.g. GSM 60169A, Figs 8a & 9a) and this probably reflects their life position. This could be a taphonomic effect of compression, but since all the legs have the same, prolateral, face uppermost, it appears less likely to be random compression of unmodified limbs, but an accentuation of the life position where the legs were held close to the body in a latigrade position. This leg orientation is seen in some other arachnids and appears to be functionally significant (see 4).

The leg coxae were discussed above (see 3.3). The trochanters have a narrow proximal region which slots into the coxae, but widen distally with a slight marginal flange (e.g. I. 7923, Figs 2d & 3d). In all legs the femur is the longest podomere. Each femur has a row of small, tooth-like projections on the ventral surface of the podomere (e.g. I. 7923, Figs 2c & 3c), though these are not clearly preserved in every specimen. Because of the orientation of the legs with the prolateral side uppermost, these projections are generally angled forwards, especially in the anterior legs, and if this was their life position then a role in prey capture seems likely (see 4). The femora, patellae and tibiae are ornamented on their prolateral face with a pair of shallow ridges separated by a broad groove (e.g. In 18341, Figs 4c & 5c). The retrolateral limb ornamentation consists of a single, distally curving ridge on the femur with a more central single ridge on the patella and tibia (e.g. GSM 60169, Figs 8b & 9b). All patellae are narrow proximally, but widen distally. The leg 1 tibia is distinctly inflated (e.g. I. 7922, Figs 2a & 2b) and has a more complex pattern of prolateral grooves and ridges, while the tibiae of the remaining legs are shorter podomeres which widen distally. This inflated leg 1 tibia perhaps contained strong muscles for flexing the tibia—basitarsus joint during prey capture. Unlike the palps, the arachnid leg tarsus is divided into a basitarsus and telotarsus (alternatively metatarsus and tarsus). The basitarsus in *Plesiosiro* is a small podomere about as long as wide in leg 1, but relatively longer in legs 2–4 (e.g. In 18341, Figs 4c & 5c). In all legs the telotarsi are subdivided into small podomeres about as long as wide. The leg 1 tarsi are subdivided into six podomeres (I. 7922, Figs 2a & 3a), those of the other legs into four podomeres (e.g. GSM 60169A, Figs 8a & 9a). Claws have not been preserved in any of the specimens, though would be predicted in comparison with extant arachnids. However, amblypygids and thelyphonids have antenniform leg 1 tarsi which lack claws. This is similar to the antenniform end of the *Plesiosiro* leg 1 and claws were omitted here in the reconstruction. Setae are included in the reconstruction (Fig. 1) based on their distribution in Recent arachnids.

3.7. Opisthosoma

The *Plesiosiro* opisthosoma apparently consists of 12 segments, as described by Petrunkevitch (1949), not the 11 noted by Pocock (1911). Only 10 or 11 tergal elements are clearly visible dorsally (e.g. I. 7922, Figs 2a & 3a). The opisthosoma as a whole widens slightly and then narrows anteriorly. The posteriormost tergites are longest and have straight posterior margins, but moving posteriorly the tergites become shorter and slightly curved. A median ridge runs along the length of the tergites (e.g. GSM 60170B, Figs 8d & 9d), but becomes less pronounced posteriorly. Two specimens indicate paired muscle apodemes on each tergite (GSM 60169A, Figs 8a & 9a and In 22835, Figs 6a & 7a) located at the anterior margin on all tergites except the first clearly expressed one, where they appear to be more central. As observed on the carapace, a fine ornament of tubercles is preserved in some material (In 31236, Figs 6e & 7e) and was probably present on all specimens in life (Fig. 1).

The best evidence for 12 opisthosomal segments comes from the specimen showing the most complete ventral surface (I. 7922, Figs 2b & 3b). This shows a triangular plate between the coxae of leg 4, as does GSM 60169B (Figs 8b & 9b), which is interpreted here as opisthosomal sternite 1. An almost identical, and probably homologous, structure is seen in this position in thelyphonids and was traditionally interpreted as a prosomal sclerite, the metasternum. Shultz (1993) argued convincingly from the musculature that this thelyphonid metasternum is in fact the first opisthosomal sternite. Irrespective of whether *Plesiosiro* is related to thelyphonids, this sclerite in *Plesiosiro* is interpreted here as opisthosomal segment 1, occurring posterior to the prosomal legs and not obviously sutured off from the sternum immediately in front of it.

Accepting this interpretation, there then follows a division before the next sclerite. This morphology again argues against including *Plesiosiro* in Opiliones, where from this position there is a continuous sclerite projecting forwards between the leg coxae and bearing the gonopore. In fact, the next two sclerites in *Plesiosiro* are a huge, curving plate, followed by a much shorter plate, also with a curving posterior margin (I. 7922, Figs 2b & 3b). Both again resemble what is seen in thelyphonids and there is weak evidence for respiratory organs opening here (see 3.9). Indeed Weygoldt & Paulus (1979), and more recently Weygoldt (1998), made reference to a large sclerite in the same position as the one in *Plesiosiro* in recognising their taxon Megoperula (literally 'big plate'). They argued that this large plate evolved in response to having to carry both the genitalia and a pair of book lungs (see 5.3 for further discussions). This large sclerite is an unequivocal character in *Plesiosiro* which could be used to resolve its phylogenetic position.

First though, in thelyphonids Shultz (1993) demonstrated that 'sternites' 2 and 3 really are opercula, i.e. appendage-derived elements homologous with the gill opercula in xiphosurans and which continue to bear the appendage-derived book lungs. The true sternites 2 and 3 in thelyphonids are highly reduced and hidden above these opercula. Shultz (in press) has also demonstrated the presence of these opercula in amblypygids. Does *Plesiosiro* have opercula or sternites? Again this cannot be determined directly from a fossil preserved in a concretion, and the interpretation of these structures as opercula implies accepting that they are tetrapulmonates *a priori*. As such, this large sclerite and the one immediately following it are tentatively retained and labelled as 'sternites' 2 and 3, though there is indirect evidence for interpreting them as opercula.

Posterior to these two sclerites *Plesiosiro* has at least seven segments, i.e. sternites 4 to 10 (I. 7922, Figs 2b & 3b). There are no obvious muscle apodemes or opisthosomal appendages, e.g. spinnerets, on the ventral sternites. The posteriormost sternites, 5 to 10, have a median groove (e.g. In 31236, Figs 6f & 7f). This is interpreted as a genuine structure, rather than a taphonomic impression into the corresponding dorsal ridge, as the dorsal ridge runs the length of the opisthosoma, while the ventral groove is more restricted. At the posterior end of the opisthosoma the number of segments becomes more difficult to interpret (hence the uncertainty about the total
number of segments) and it is also not clear whether the posteriormost segments are ring-like or divided into tergites and sternites. There are at least two segments (11 and 127), the last of which is plate-like, and which together appear to form a small postabdomen or pygidium (e.g. In 31236, Figs 6f & 7f). This is located ventrally, again similar to the anal operculum of Siro and other opilionids, and also like the pygidium of trigonotarbidis (e.g. Shear et al. 1987). There is no evidence for a postanal telson.

3.8. Prosoma–opisthosoma junction
It is relatively straightforward to match up tergites and sternites (Fig. 1) for segments 2 to 9, and it becomes apparent that the lateral margins of ‘sternites’ 2 and 3 correspond, respectively, to the first and second visibly expressed tergites. This means that if the triangular ventral sclerite in Plesiosiro is opisthosomal segment 1, then there should be an additional tergal element corresponding to it. The evidence for this in the fossils is difficult to interpret, though both I. 7923 (Figs 2c & 3c) and GSM 60169 (Figs 8b & 9b) clearly show a dorsal sclerite with a broken anterior margin, anterior to what is interpreted as tergite 2. This sclerite is probably tergite 1, although it is not seen in every specimen and even within a specimen it is present in the counterpart of GSM 60169, but not the part. This specimen further suggests that the tergal median ridge is also present on what I believe to be tergite 1 (Figs 8b & 9b).

Meanwhile, a number of carapaces where this tergite 1 is not preserved instead show a clear ridge along the posterior carapace margin, e.g. I. 7922 (Figs 2a & 3a), In 18341 (Figs 4c & 5c) and In 22835 (Figs 6a & 7a). This ridge is continuous with the lateral edges of the carapace and clearly belongs to the carapace rather than the opisthosoma, i.e. it is not a narrow tergite 1. This first tergite is interpreted here as a relatively large structure, but one which probably lay mostly beneath the posterior margin of the carapace in life, while the carapace itself had some sort of posterior fold or undertucking to accommodate this first opisthosomal tergite (Fig. 1). Something very similar is seen in both trigonotarbidis and ricinuleids, where the first opisthosomal tergite is specifically modified into a locking ridge which tucks under the posterior margin of the carapace (e.g. Dunlop 1996b). However, the Plesiosiro material is equivocal as to whether tergite 1 in Haptopoda was modified into a locking ridge. This interpretation is difficult to confirm in material compressed dorso-ventrally, with no one specimen showing both tergite 1 and the carapace ridge unequivocally, but it is consistent with observed morphology. It is also worth noting that in chelicerates in general the first opisthosomal tergite is often reduced or modified in some way, and that in thelyphonids the first tergite slightly undertucks the carapace, as does the anterior dorsal sclerite of the spider pedicel (Wilson 1965).

3.9. Respiratory organs
Petrunkevitch (1949, 1955) described and figured book lungs on ‘sternites’ 2 and 3 in Plesiosiro. Lungs are fragile structures and unlikely to be preserved in a siderite nodule, although possible gills have been reported in a eurypterid preserved in a phosphatised nodule (Manning & Dunlop 1995). Petrunkevitch’s observations of actual lungs could not be substantiated here. There are, however, two slight depressions visible on the right side of the ‘sternites’ 2 and 3 of I. 7922 (Figs 2b & 3b). These structures occur on the posterior margin of the sclerites on the same segment, and in approximately the same position, as the book lung spiracles of tetrapalmate arachnids. However, the evidence for corresponding spiracles on the left side of the opisthosoma is weak.

External spiracles in Plesiosiro might not be expected. In thelyphonids and amblypygidis the spiracles are not clearly visible externally; this also applies to Carboniferous fossils of these animals preserved in nodules (Dunlop & Horrocks 1996). The actual spiracles open beneath the opercula (e.g. Shultz 1993), though in some thelyphonids there is a slight depression in the sclerite immediately posterior to the spiracle (pers. obs.). Spiracles can only be seen in spiders because of their extreme reduction of the opercula to sclerotised plates in front of the spiracle. The respiratory organs of Plesiosiro should be interpreted as unknown and Petrunkevitch’s observation of book lungs cannot be used to place this fossil, as Firstman (1973) and van der Hammen (1977) did. By way of comparison, opilionids have a single pair of tracheal spiracles opening in the middle of a sclerite in this anterior, ventral position. There is no evidence for such spiracles, or of tracheal respiration in general, in Plesiosiro.

4. Mode of life

With the exception of some mites and opilionids (Savory 1964), most arachnids are primarily predators and it seems reasonable to interpret Plesiosiro as a predator too. The presence of tooth-like projections on the leg femora, which could be used to grab and immobilise prey, supports this interpretation. The dorso-ventrally flattened body and disposition of the legs, preserved with the prolateral surface uppermost (Fig. 1), suggests that Plesiosiro could hold its legs close over the body. A similar leg arrangement is seen in various Recent arachnids, e.g. scorpions, and enables them to crawl into narrow spaces, usually for protection. The first pair of legs in Plesiosiro could have been used like the first leg pair in amblypygids and uropygids, to probe in front of the animal and to detect prey. The first pair of legs is robust in Plesiosiro, but as Pocock (1911) noted in naming the order Haptopoda, the long, subdivided tarsi appear delicate and sensitive.

5. Phylogeny

5.1. Haptopoda is a valid order

This study supports Pocock’s (1911) creation of a separate arachnid order, Haptopoda, for Plesiosiro. The characters identified in this study do not include autapomorphies which would place Plesiosiro in any of the known arachnid orders, living or extinct. Petrunkevitch (1913) suggested that Plesiosiro was a phalangiotarbid, but this was evidently based only on Pocock’s (1911) figures and in later work (Petrunkevitch 1949, 1953, 1955) he retained Haptopoda as a distinct order. Dunlop & Horrocks (1997) gave a recent account of phalangiotarbid morphology and recognised a number of significant phalangiotarbid characters not seen in Plesiosiro: e.g. six eyes on a single tubercle, short anterior tergites, longitudinally divided sternites, tiny pedalpals and a dorsal anal operculum.

More recently, Shear & Kukalová-Peck (1990) suggested Plesiosiro might be an opilionid. Plesiosiro does resemble the opilionid Siro and Pocock (1911) was presumably aware of this when he named the genus. There are also similarities in overall shape and ornamentation between Plesiosiro and troglobid opilionids, although in troglobids, unlike Plesiosiro, leg 2 is longest, a derived character within opilionids. Opiliones is characterised by a number of autapomorphies, e.g. a pair of tracheae, prosomal repugnatorial glands and a penis (Shultz 1990). None of these can be convincingly demonstrated in Plesiosiro. Opiliones have only nine opisthosomal segments plus their anal operculum, lack strong tagmatisation at the prosoma–opisthosoma junction and have coxal endites forming
a stomathec (e.g. van der Hammen 1989). *Plesiosiro* apparently has 12 segments, some degree of tagmatization and lacks a stomathec (Fig. 1). Apart from the questionable interpretation of the carapace tubercles as repugnatorial glands, there are no fossilised characters which support the referral of *Plesiosiro* to Opiliones, though the possibility of a *Plesiosiro + Opiliones* relationship is discussed below (see 5.2).

Though *Plesiosiro* does not belong in any other arachnid order, it is difficult to identify convincing autapomorphies for Haptopodopa itself. Its most immediately diagnostic feature, the carapace ridges (see 6) could be homologous with the xiphosuran ophthalmic ridges, although this assumes that the tubercles at the anterior end are lateral eyes. Alternatively, *Plesiosiro’s* pattern of tarsal subdivision, six on leg 1, four on legs 2–4, is a possible autapomorphy if treated as a single character complex. Haptopodopa mostly presents a unique combination of characters: a divided sternum, a ventral ‘megoperculum’, pediform appendages, an elongate leg pair 1, spinose femora, etc. Other characters shown in the reconstruction (Fig. 1), e.g. lateral eyes, clasp-knife chelicerae and 12 opisthosomal segments, are probably correct, but cannot be taken directly from the fossils and should not be used to resolve the position of *Plesiosiro*.

5.2. *Plesiosiro + Opiliones?*

If *Plesiosiro* is not an opilionid, could it still be a sister taxon to Opiliones? The position of the opilionids is controversial. Weygoldt & Paulus (1979) placed them as highly derived arachnids, van der Hammen (1989) placed them in a taxon with scorpions and xiphosurans rendering Arachnida paraphyletic, while Shultz (1990) and Wheeler & Hayashi (1998) placed them as quite basal within a monophyletic Arachnida. The only unequivocal character which could support *Plesiosiro + Opiliones* is the broad prosoma–opisthosoma junction, and this character is not unique to opilionids, being present in scorpions, pseudoscorpions and mites. Divided telotarsi are seen in *Plesiosiro* and many opilionids, but represent a poor synapomorphy as the telotarsi of cyathophthalmid are undivided, suggesting this is a derived state within the opilionid clade. The terminal segment of the *Plesiosiro* opisthosoma resembles the opilionid anal operculum, but homology cannot easily be proved. Pocock’s (1911) suggestion that *Plesiosiro* is an intermediate between opilionids and more primitive arachnid orders is intriguing, a relationship with Opiliones and Tetrapulmonata is not necessarily mutually exclusive, but the balance of evidence supports referral of *Plesiosiro* to Tetrapulmonata.

5.3. *Plesiosiro is probably a tetrapulmonate*

Shear & Selden (1986) and Shear et al. (1987) were the first authors to determine the relationships of an extinct arachnid order, the trigonotarbids, based on synapomorphies rather than overall resemblances. Shear et al. (1987) recognised a clade: (Trigonotarbida (Araneae (Amblypygi (Uropygi + Schizomida))) and this model was supported with additional characters by Selden et al. (1991). These authors also noted that a few of the animals they had previously described as trigonotarbids (Shear et al. 1987) did not belong to that order and might represent a radiation of Devonian ‘pulmonate’ (i.e. tetrapulmonate) arachnids which did not fit into existing recognised groups. A recently described, but incomplete, Devonian arachnid, *Xenarachne* Dunlop & Poschmann (1997), could not be placed in a known order and was interpreted as one of these predicted pulmonate fossils.

Is *Plesiosiro* a Carboniferous survivor from Selden et al.‘s (1991) Devonian radiation of ‘pulmonate’ arachnids? *Plesiosiro* has a large plate posterior to the first opisthosomal sternite. This is also seen in Amblypygi, Thelyphonida and Schizomida, where it covers both the gonopore and the first pair of book lungs. It is also present in trigonotarbids (e.g. Dunlop 1996b, fig. 4) and a single plate covers the anterior book lungs in mesothelie spiders, the most basal spider clade containing living taxa. A ‘megoperculum’ is not seen in other arachnid orders, though Dunlop (1996b) indicated a possible homology in Riciulue. This large *Plesiosiro* sclerite cannot be proved to be an appendicular operculum, but morphology is so similar to that in thelyphonids, amblypygids and trigonotarbids that it is proposed here as a character supporting the inclusion of *Plesiosiro* in the Tetrapulmonata clade.

Despite using Megoperculata to name their clade, Weygoldt & Paulus (1979) did not actually code this character of a large genital operculum into their analysis. Shultz (1990) did in a modified form, recognising an apomorphic state of ‘genital sternite overlapping third opisthosomal sternite’, a character also adopted by Wheeler & Hayashi (1998). A strict interpretation of Shultz’s character cannot be applied to *Plesiosiro* since its preservation in a nodule prevents us from seeing whether or not it had both a ‘genital sternite’, i.e. an operculum, and a ‘third opisthosomal sternite’, a true sternal element. A wider definition of this character as a large plate covering the genital region could still be coded as synapomorphic for *Plesiosiro* and the other tetrapulmonates.

One character that provides evidence against this model is the broad prosoma–opisthosoma junction in *Plesiosiro*. This region is, to a greater or lesser extent, restricted in other tetrapulmonates, though in the fossil trigonotarbids this constriction is not so strongly expressed. This is reflected in Petrunkevitch’s (1949) placement of at least some trigonotarbids in Stethostomata, defined on a broad prosoma–opisthosa junction. Furthermore, the polarity of this character should be treated with caution. All the cladistic studies of arachnids considered a restriction of the prosoma–opisthosoma junction as apomorphic, yet even in an outgroup such as *Lamulus* the first tergite is reduced and the ‘broad’ junction is mostly made up of a wide hinge between the carapace and thoracoteron, while the actual proportion of it carrying the internal anatomy is relatively small, as in a spider pedicel.

5.4. *Plesiosiro + Pedipalpi*

If *Plesiosiro* does belong in Tetrapulmonata, can it be placed within this clade with any confidence? One interpretation would be to place it as sister group to all other tetrapulmonates, in which case the narrow pedicel could still be interpreted as a synapomorphy for this latter clade. A first opisthosomal tergite underrusting the carapace (see 5.8) could be synapomorphic with Trigonotarbida, although the *Plesiosiro* structure is equivocal as a locking ridge. Alternatively, *Plesiosiro* has divided tarsi and a divided sternum, two unequivocal characters, which can be used as synapomorphies to place it as sister group to (Amblypygi (Thelyphonida + Schizomida)), all three of which together form a clade, Pedipalpi. The Pedipalpi themselves are supported by a number of synapomorphies (e.g. Shultz 1990, in press), primarily an antenniform first pair of legs and their large, subchelate pedipalps which give the clade its name. Dunlop (1996a, 1997) suggested that an elongate first leg pair could be synapomorphic for *Plesiosiro + Pedipalpi* too, though I now consider this a less appropriate character. The first legs of *Plesiosiro* are long relative to adjacent leg pairs, but they are not the whip-like, antenniform leg pair I seen in Pedipalpi.

It should, however, be added that in a recent and comprehensive ‘total evidence’ approach to chelicerate phylogeny, Wheeler & Hayashi (1998) concluded that Pedipalpi was not a valid clade and placed Amblypygi as sister group.
to Araneae in a clade Labellata (also supported by Weygoldt & Paulus (1979) and van der Hammen (1989)). Wheeler & Hayashi (1998) noted that Amblypygi+Araneae was supported primarily by their molecular data, not the morphologically characters, which in general support the Pedipalpi clade. Whilst it is beyond the scope of this paper to comment on their model in detail, it is worth noting that Wheeler & Hayashi's (1998, fig. 6) best supported tree using molecular data alone did group most taxa within an order together, but produced an unorthodox cladogram of relationships between orders. This raises concerns about the reliability of their molecular data in overturning a clade such as Pedipalpi which has strong morphological support. Furthermore, Shultz (in press) has recently proposed a list of 31 morphological synapomorphies for Pedipalpi which appear more convincing than the evidence supporting Labellata.

In summary, the position of *Plesiosiro* is difficult to determine with confidence because it is only known from fossil material and relatively few characters of phylogenetic significance have been preserved. Its original locality is no longer workable for fossil material and so the chances of discovering new material, at least of *Plesiosiro madeleyi*, are uncertain. However, simply to regard *Plesiosiro* as Arachnida incertae sedis ignores the characters we do know. These suggest that *Plesiosiro* does belong to a distinct arachnid order and that there are two main phylogenetic hypotheses: that it relates to Opiliones, or that it is one of the Tetrapulmonata. *Plesiosiro*+Opiliones is supported by *Plesiosiro*’s broad prosoma–opisthosoma junction. Alternatively, *Plesiosiro* does have a large sclerite consistent with it being a genital operculum and which is synapomorphic for Tetrapulmonata. Other ventral morphological features are more consistent with Tetrapulmonata as opposed to Opiliones. Within Tetrapulmonata, *Plesiosiro* can be tentatively placed as sister group to Pedipalpi on the synapomorphies of divided telotarsi and a divided sternum. This hypothesis is summarised in Figure 10.

6. Systematic palaeontology

**TETRAPULMONATA** Shultz, 1990

Order HAPTOPODA Pocock, 1911

**Emended diagnosis.** Arachnids with an entire carapace, ornamented with a distinctive pattern of ridges: a median ridge, bifurcate along most of its length, and two lateral ridges each of which terminates anteriorly in a tubercle. Median eyes present. Pedipalps small and pediform, leg 1 elongate, with telotarsi subdivided into six joints, legs 2–4 with telotarsi subdivided into four joints. Prosoma–opisthosoma junction broad. Genital plate massive. (Emended from Dunlop (1996a).)

**Family Plesiosironidae Pocock, 1911**

**Diagnosis.** As for the order.

**Genus Plesiosiro Pocock, 1911**

**Diagnosis.** As for the order.

**Plesiosiro madeleyi** Pocock, 1911

(Figs 1–3, 4a–c, 5a–c & 6–9)

1911 *Plesiosiro madeleyi* Pocock, pp. 41–4; text-figs 15–16, pl. 2, fig. 5.
1913 *Plesiosiro madeleyi* Pocock: Petrunkevitch, p. 112.
1949 *Plesiosiro madeleyi* Pocock: Waterlot, p. 900; fig. 679.
1953 *Plesiosiro madeleyi* Pocock: Waterlot, pp. 569–70; figs 6–7, 22.
1953 *Plesiosiro madeleyi* Pocock: Petrunkevitch, p. 58.
1957 *Plesiosiro madeleyi* Pocock: Petrunkevitch, p. 58, L7097 from Sparth Bottoms.
1955 *Plesiosiro madeleyi* Pocock: Dubinin, pp. 726–9; fig. 1366.
1962 *Plesiosiro madeleyi* Pocock: Dunlop, pp. 180–82; fig. 2d.
1996b *Plesiosiro madeleyi* Pocock: Dunlop, pp. 83, 91; fig. 3b.
1997 *Plesiosiro madeleyi* Pocock: Dunlop, p. 77; fig. 5c.
1998 *Plesiosiro madeleyi* Pocock: Selden & Dunlop, pp. 303–31; fig. 7.1.

**Diagnosis.** As for the order.

**Material.** Holotype, BMNH I. 7923, from the Coal Measures of Coseley near Dudley, Staffordshire, UK. Upper Carboniferous (Westphalian B). Exact locality and horizon not recorded. Paratypes, BMNH In 22835 and In 31236, from the same locality as the holotype. Additional specimens, BMNH I. 7923, I. 15899. In 18341, In 22837, GSM 60169A/B and 60170A/B, all from the same locality as the holotype. The BMNH labels give no locality details, although Schram (1979) stated that his crustaceans from Coseley probably came from the Lower *similis–pulchra* zone of the Claycroft Openworks. GSM 60169A/B specifically recorded from Lower *similis–pulchra* zone, Ten-foot ironstone measures at Coseley. Not MM L7097 from the Westphalian B of Sparth Bottoms, Rochdale.

**Description of I. 7923 (Holotype).** Relatively complete specimen showing both dorsal and ventral surfaces (Figs 2a–b & 3a–b). Body length 12.6 mm, carapace length 5.1 mm, basal width 4.8 mm. Carapace ridges and median eyes distinct, tubercles at ends of the lateral ridges less so. Sternum indistinct. Coxae well preserved. Chelicerae at least 1.1 mm long, interpreted as displaced anteriorly. Pedipalps partially complete. Podomere lengths: fe, 0.7 mm; pt, 0.6 mm; ti, 0.6 mm. Pedipalpal femur and patella with paired grooves. Leg 1 complete. Podomere lengths: tr, 1.1 mm; fe, 4.0 mm; pt, 1.7 mm; ti, 3.2 mm; mt, 0.4 mm; ts, 1.3 mm. All six segments of subdivided telotarsus preserved. Leg 2 partially complete. Podomere lengths: tr, 1.0 mm; fe, 1.6 mm; pt, 1.2 mm. Leg 3 almost complete. Podomere lengths: tr, 1.1 mm; fe, 2.9 mm; pt, 1.1 mm; ti, 1.3 mm; mt, 0.5 mm. Leg 4 partially complete. Podomere lengths: tr, 1.1 mm; fe, 4.1 mm; pt, 1.3 mm; ti, 2.4 mm. Legs with prolateral surface uppermost. Femora of legs 1 and 2 with tooth-like projections. Opisthosoma length 7.5 mm dorsally, maximum width 4.5 mm. Tergite lengths: 2, 1.1 mm; 3, 1.0 mm; 4, 0.9 mm; 5, 0.7 mm; 6, 0.7 mm; 7, 0.7 mm; 8, 0.8 mm; 9, 0.6 mm; 10, 0.4 mm; 11, 0.2 mm. Tergites with median ridge. Tergite 1 indistinct, leaving gap between carapace and tergite 2. Sternite lengths: 1, 1.1 mm; ‘2’ (genital plate), 2.6 mm; ‘3’, 0.3 mm; 4, 0.5 mm; 5, 0.9 mm; 6, 6.7 mm; 7, 0.6 mm; 8, 0.6 mm; 9, 0.3 mm; 10, 0.2 mm. Segments 11 and 12 ring-like. Diameters 1.5 mm and 0.9 mm respectively. Median groove preserved on sternites 4 to 10. Posterior margins of ‘sternites’ 2 and 3 strongly curved, genital plate bearing a pair of curving ridges originating on posterior margin either side of midline and diverging anteriorly.

**Description of I. 7923.** Reasonably well-preserved specimen showing both dorsal and ventral views (Figs 2c–d & 3c–d). Opisthosoma and whole of ventral surface slightly distorted, probably from lateral compression. Body length 12.4 mm, carapace length 5.6 mm, basal width 4.6 mm. Carapace ridges and median eyes distinct, tubercle on right lateral ridge
distinct. Sternum indistinct. Coxae on left side quite well preserved. Paired chelicerae preserved as narrow, paraxial depressions Projecting down into matrix. Pedipalps with trochanter and femur lengths of 0.8 mm and 0.6 mm, respectively. Femur with paired grooves. Legs reasonably complete, anterior coxae projecting beyond carapace margin. Leg 1 with podomere lengths: tr, 0.7 mm; fe, 4.3 mm; pt, 1.6 mm; ti, 3.1 mm. Leg 2 partially complete. Podomere lengths: tr, 0.9 mm; fe, 2.5 mm; pt, 1.4 mm; ti, 1.7 mm. Leg 3 trochanter only preserved, length 1.1 mm. Leg 4 partially complete. Podomere lengths: tr, 1.1 mm; fe, 4.1 mm; pt, 1.4 mm; ti, 2.1 mm. Legs with prolateral surface uppermost, trochanter shape clearly seen. Legs 1 and 3 with similar proportions. Opisthosoma length dorsally 7.4 mm, maximum width 4.7 mm. Tergite lengths: 2, 0.9 mm; 3, 0.6 mm; 4, 0.9 mm; 5, 0.9 mm; 6, 0.9 mm; 7, 0.8 mm; 8, 0.7 mm; 9, 0.6 mm; 10, 0.4 mm. First tergite distinct, but anterior margin broken. Anteriormost sternites poorly preserved. Featureless area 'S2' may represent genital operculum. Sternite lengths: 4, 0.7 mm; 5, 0.7 mm; 6, 0.8 mm; 7, 0.6 mm; 8, 0.7 mm. Pygidium preserved, composed of at least two segments, total diameter 0.8 mm.

**Description of I. 15899.** Reasonably complete specimen, mostly in dorsal view, but ventral prosoma preserved in counterpart (Figs 4a–b & 5a–b). Body length 10.9 mm, carapace length 4.5 mm, basal width 4.1 mm. Carapace ridges and median eyes clearly preserved, as are both tubercles at anterior end of lateral ridges. Carapace with fine tuberculation. Sternum well preserved, length 1.85 mm. Anterior notch flanked by 'horns' and clearly divided into anterior and posterior sclerites with respective lengths: 1.4 mm and 0.4 mm. Coxae quite well preserved, but chelicerae and pedipalps missing. Legs reasonably complete. Leg 1 with podomere lengths: tr, 1.0 mm; fe, 3.6 mm; pt, 1.3 mm. Leg 2 with podomere lengths: tr, 0.6 mm; fe, 2.2 mm; pt, 0.9 mm; ti, 1.3 mm. Leg 3 with podomere lengths: tr, 0.7 mm; fe, 2.1 mm; pt, 1.2 mm; ti, 1.4 mm; bt, 0.7 mm. Leg 4 with podomere lengths: tr, 1.2 mm; fe, 2.4 mm; pt, 1.2 mm; ti, 2.1 mm. Legs preserved with prolateral face uppermost. Femora 1–3 with tooth-like projections. Opisthosoma length dorsally 6.4 mm, maximum width 4.5 mm. Tergite lengths: 2, 0.7 mm; 3, 0.8 mm; 4, 0.6 mm; 5, 0.8 mm; 6, 0.7 mm; 7, 0.7 mm; 8, 0.8 mm; 9, 0.5 mm. Tergite 1 not preserved. Tergites with median ridge. Stermites and pygidium not preserved.

**Description of I. 18341.** Specimen comprising part only (Figs 4c & 5c). Preserved body length 11.5 mm, carapace length 5.2 mm, basal width 4.8 mm. Carapace ridges and median eyes well preserved, clearly showing lateral ridges widening into tubercles anteriorly. Coxo-sternal region unknown. Appendages reasonably complete. Leg 4 on left side folded over dorsal surface of opisthosoma and visible through breaks in opisthosoma. Patella and tibia of pedipalps with lengths of 0.5 mm and 0.6 mm, respectively. Leg 1 complete. Podomere lengths: tr, 1.0 mm; fe, 4.3 mm; pt, 1.6 mm; ti, 3.7 mm; mt, 0.7 mm; ts, 2.1 mm. Teleotarsus with all six divisions. Leg 3 almost complete. Podomere lengths: tr, 0.9 mm; fe, 2.2 mm; pt, 1.6 mm; ti, 2.4 mm; mt, 0.6 mm. Leg 4 partially complete. Podomere lengths: fe, 3.8 mm; pt, 1.3 mm; ti, 2.1 mm. Legs with prolateral surface uppermost. Projections on femur 3 particularly well preserved. Opisthosoma incomplete. Maximum width 4.5 mm. Tergite lengths: 2, 0.9 mm; 3, 0.9 mm; 4, 1.0 mm; 5, 0.9 mm; 6, 1.0 mm; 7, 0.9 mm. Carapace with clear infolded posterior margin. Median ridge on dorsal surface of opisthosoma faint.

**Description of I. 22835 (Paratype).** Specimen reasonably well preserved, though part split by large crack through anterior opisthosoma (Figs 6a–b & 7a–b). Body length 11.2 mm, carapace length 4.8 mm, basal width 4.8 mm. Carapace well preserved with pattern of ridges and both median eyes and lateral tubercles present. Carapace with ornament of fine tubercles. Coxo-sternal region reasonably well preserved. Sternum present, clearly divided into anterior and posterior sclerites, respective lengths: 1.0 mm and 0.5 mm. Subtriangular leg coxae arranged around sternum, but palpal coxae and chelicerae not preserved. Enigmatic structure present anterior to sternum, possibly representing a labrum and/or labium. Femur, patella and tibia of right pedipalp preserved, femur and patella showing dorsal grooves. Legs poorly preserved. Leg 1 with podomere lengths: tr, 0.8 mm; fe, 3.5 mm; pt, 1.5 mm; ti, 2.5 mm; bt, 0.4 mm; ts, 0.8 mm. Leg 3 femur length 2.3 mm. Leg 4 femur length 3.1 mm, of which has rostral 'horn'. Opisthosoma length 6.1 mm, maximum width 4.2 mm. Tergite lengths: 2, 0.8 mm; 3, 0.8 mm; 4, 0.8 mm; 5, 0.7 mm; 6, 0.8 mm; 7, 0.8 mm; 8, 0.6 mm; 9, 0.5 mm; 10, 0.3 mm. Median tergite ridge and tergal apodemes preserved. Anterior sternites obscured by superimposed tergites which complicates interpretation of more posterior sternites. Sternite lengths: 4, 0.7 mm; 5, 0.7 mm; 6, 0.7 mm; 7, 0.6 mm; 8, 0.5 mm; 9, 0.4 mm; 10, 0.3 mm. Ventral longitudinal impression not on midline, probably superimposed from tergites. Pygidium clearly preserved, diameter 1.0 mm, and composed of two segments.

**Description of I. 22837.** Poorly preserved specimen, part showing dorsal surface anteriorly and ventral surface posteriorly, counterpart showing dorsal surface only. Anterior region of carapace missing (Figs 6c–d & 7c–d). Body length 12.6 mm, carapace length 4.8 mm, basal width 4.6 mm. Outline of carapace distinct, but carapace ridges faint. Eyes, coxo-sternal region and appendages not preserved. Opisthosoma length 7.8 mm, maximum width 4.9 mm. Tergite lengths: 2, 1.2 mm; 3, 1.0 mm; 4, 0.7 mm; 5, 0.9 mm; 6, 0.7 mm; 7, 0.9 mm; 8, 0.6 mm; 9, 0.5 mm. Anteriormost sternites obscured by superimposed tergites. Lengths of sternites: 4, 0.5 mm; 5, 0.7 mm; 6, 0.6 mm; 7, 0.7 mm; 8, 0.6 mm; 9, 0.4 mm; 10, 0.2 mm. Terminal segments not clearly preserved. Longitudinal lineations on left opisthosomal margin of part obscure segmentation, perhaps indicative of a folded pleural membrane between tergites and sternites in life.

**Description of I. 31236 (Paratype).** Smallest specimen showing dorsal surface on part and dorsal prosoma, anterior tergites and most of ventral opisthosoma on counterpart (Figs 6f–g & 7e–f). Body length 9.6 mm, carapace length 3.9 mm, basal width of 3.5 mm. Margins of carapace indistinct, but median eyes and carapace ridges well preserved. Fine tuberculatation present on carapace of part. Coxo-sternal region not preserved. Leg 4 partially complete. Podomere lengths: tr, 1.1 mm; fe, 3.1 mm; pt, 1.1 mm; ti, 1.7 mm; mt 1.0 mm. Fragments of appendages on right side of part preserved. Opisthosoma length 5.7 mm, preserved maximum width 3.2 mm. Right side of part missing. Tergite lengths: 2, 0.6 mm; 3, 0.6 mm; 4, 0.7 mm; 5, 0.6 mm; 6, 0.7 mm; 7, 0.6 mm; 8, 0.6 mm; 9, 0.4 mm; 10, 0.3 mm. Median ridge and tergal apodemes distinct. Lengths of preserved sternites: 5, 0.6 mm; 6, 0.7 mm; 7, 0.6 mm; 8, 0.5 mm; 9, 0.3 mm; 10, 0.1 mm. Median groove evident on sternites. Pygidium well preserved, diameter 0.7 mm.

**Description of I. 31236 (Paratype).** Smallest specimen showing dorsal surface on part and ventral prosoma on counterpart, though ventral opisthosoma of counterpart obscured by superimposed tergites (Figs 8a–b & 9a–b). Body length 12.5 mm, carapace length 5.2 mm, basal width 5.3 mm. Carapace ridges clearly preserved, but eyes and lateral tubercles less distinct. Coxo-sternal region excellent, showing sternum divided into two sclerites, respective lengths 1.0 mm and 0.7 mm, anterior of which has paired 'horns'. Shape and position of leg coxae and first opisthosomal sternite in relation
to sternum clearly shown, but both chelicerae and pedipalps and their coxae not preserved. Legs almost complete. Leg 1 with podomere lengths: tr, 0.7 mm; fe, 3.6 mm; pt, 1.6 mm; ti, 3.6 mm; bt, 0.5 mm; ts, 1.4 mm. Leg 2 with podomere lengths: tr, 0.7 mm; fe, 2.8 mm; pt, 1.3 mm; ti, 1.5 mm; bt, 0.8 mm; ts, 0.6 mm. Leg 3 with podomere lengths: tr, 0.9 mm; fe, 3.0 mm; pt, 1.1 mm; ti, 1.7 mm; bt, 0.8 mm; ts, 1.0 mm. Leg 4 with podomere lengths: tr, 1.6 mm; fe, 4.0 mm; pt, 1.4 mm; ti, 2.4 mm; bt, 1.0 mm; ts, 1.1 mm. Legs 3 and 4 with all four podomeres of subdivided telotarsus. Right femur 3 with tooth-like projections. All legs have prolateral surface uppermost, except for displaced right leg 1. Opisthosoma length 7.1 mm, maximum width 4.6 mm. Tergite lengths: 2, 1.1 mm; 3, 1.0 mm; 4, 0.9 mm; 5, 0.9 mm; 6, 0.8 mm; 7, 0.9 mm; 8, 0.7 mm; 9, 0.5 mm; 10, 0.3 mm. Median ridge and tergal apodemes distinct. Anteriormost sclerite with broken anterior margin probably represents tergite 1. Sternites mostly obscured, but pygidium clearly preserved, diameter 1.0 mm, and comprised of two segments.

**Description of GSM 60170A/B.** Reasonably well-preserved specimen, part and counterpart mostly in dorsal view, but carapace broken to reveal some ventral prosomal structures (Figs 8c–d & 9c–d). Body length approximately 11 mm, carapace basal width 4.6 mm. Carapace poorly preserved, broken anteriorly. Carapace ridges preserved, but eyes and lateral tubercles missing. Coxae preserved anteriorly and on left side of counterpart. Chelicerae preserved as pair of depressions projecting down into matrix. Appendages reasonably complete. Pedipalp femora clearly show pattern of dorsal grooves. Leg 1 with podomere lengths: tr, 0.9 mm; fe, 4.0 mm; pt, 1.6 mm; ti, 3.1 mm; bt, 0.5 mm; ts, 1.6 mm. Leg 2 with podomere lengths: tr, 0.9 mm; fe, 2.4 mm; pt, 1.1 mm. Leg 3 with podomere lengths: tr, 0.7 mm; fe, 2.8 mm; pt, 1.4 mm; ti, 1.5 mm; bt, 0.7 mm. Leg 4 poorly preserved, podomere lengths indistinct. All legs with prolateral surface uppermost. Ventral surface of legs 2 and 3 with tooth-like projections. Opisthosoma length 6.3 mm, maximum width 4.0 mm. Full width of opisthosoma not preserved. Tergite lengths: 2, 1.0 mm; 3, 0.9 mm; 4, 0.8 mm; 5, 0.8 mm; 6, 0.8 mm; 7, 0.8 mm; 8, 0.7 mm; 9, 0.6 mm. Median ridge on tergites preserved along with less clear tergal apodemes. Ventral opisthosoma unknown.

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8. References


REDESCRIPTION OF PLESIOSIRO


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