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THE FIRST FOSSIL CYPHOPHTHALMID (ARACHNIDA, OPILIONES) FROM BITTERFELD AMBER, GERMANY

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ABSTRACT.   The first fossil cyphophthalmid harvestman, *Siro platypedibus* new species (Arachnida, Opiliones, Cyphophthalmi), is described from Bitterfeld amber, Sachsen-Anhalt, Germany. The age of this amber is in dispute. Geological studies support a Miocene (20–22 Ma) date for the deposit, but the presence of insect species identical to those in Baltic amber (dated at ca. 35–40 Ma) has led other authors to suggest that the Bitterfeld amber comprises older, redeposited material, contemporary with Baltic inclusions. Two features in this harvestman fossil are consistent with the Recent genera *Siro*, *Paramiopsalis* and *Tranteeva*: (a) smooth tarsi and metatarsi in legs 1 and 2 and (b) the apparent absence of a dorsal crest on the basal article of the chelicera. Unequivocal autapomorphies of any one of these genera are not clearly preserved in this fossil, but *Paramiopsalis* is a monotypic Iberian genus, and *Tranteeva* is a monotypic genus from Bulgaria, while *Siro* is more diverse and widely distributed, including living representatives in Central Europe relatively close to the Bitterfeld type locality. For this reason we assign the fossil to *Siro*.

Keywords: Cyphophthalmi, Sironidae, *Siro*, taxonomy, paleontology, new species

Fossil harvestmen are rare and their fossil record is currently restricted to a few Paleozoic and Mesozoic examples together with a more diverse Tertiary record based principally on the Florissant Formation and on Baltic and Dominican ambers; see e.g., Petrunkevitch (1955), Cokendolpher & Cokendolpher (1982) and Selden (1993) for reviews. The majority of the fossil harvestmen have been referred to, or strongly resemble members of, the Eupnoi and Dyspnoi clades. Among those specimens which have not been formally described there is a very old (c. 340 Ma), but remarkably modern-looking, phalangioid harvestman (Wood et al. 1985), which implies for this group a high degree of morphological conservatism over geological time. Laniatores is currently known only from Tertiary ambers, and all of the Dominican amber harvestmen described thus far are Laniatores (Cokendolpher & Poinar 1998). The remaining suborder, Cyphophthalmi, has not previously been recorded in the fossil record. Petrunkevitch (1949) claimed that some of the Pennsylvanian Coal Measures harvestmen distinctly resembled cyphophthalmids, but his arguments are unconvincing. These Coal Measures fossils lack autapomorphies of Cyphophthalmi and are relatively large with long, slender legs in at least some specimens.

Cyphophthalmi are small to medium-sized, inconspicuous, almost mite-like, creatures with short, stubby legs which typically live in soil, leaf litter or caves (Shear 1980). They are often regarded as primitive harvestmen and recent phylogenetic studies (Shultz 1998; Giribet et al. 1999, 2002) have consistently placed them in a basal position, as sister-group to the remaining opilionids. The fossil record provides minimum divergence times for clades, thus the recently published cladograms predict that the cyphophthalmid lineage should go back to at least the mid-Paleozoic, the age of the oldest recorded harvestman (see above). The systematics of the Recent cyphophthalmids have been summarized by the catalogue of Giribet (2000), who recognized 113 extant species in 26 genera, and the cladistic analysis of generic relationships by Giribet & Boyer (2002). We refer to these publications for additional background literature on the group. In this paper we describe the first fossil

cyphophthalmid, a specimen discovered in the Berlin collection of inclusions from the Bitterfeld amber deposit of eastern Germany.

METHODS

The holotype, and only specimen, was informally recognized as a cyphophthalmid in 1989 by Manfred Moritz, the then Curator of Arachnids in the Zoology Department of the Museum für Naturkunde, Berlin. It was thus discovered too late to be listed in the summary paper of Schumann & Wendt (1989) on Bitterfeld inclusions. The fossil was not subsequently formally described. The specimen is held in the Arthropod Section of the Paleontology Department of the Museum für Naturkunde Berlin (MB.A.) under the repository number 1086. Drawings were prepared with the aid of a camera lucida attachment and the fossil was compared to all extant genera of Cyphophthalmi and to most species of Sironidae (see e.g. Giribet & Boyer 2002, Appendix 2). Digital photographs (Figs. 1–2) were taken using a JVC Digital Camera KY-F70B mounted on a Leica MZ 12.5 stereomicroscope. Series of ca. 20 images were taken at different focal planes and assembled with the dedicated software package Auto-Montage 4.01.0085 by Synoptics Ltd. All measurements are in mm.
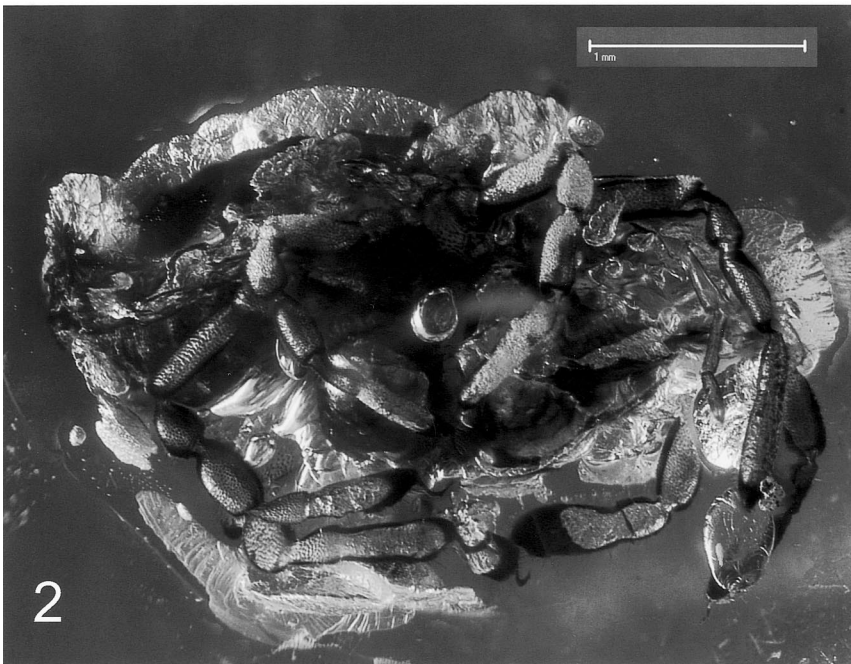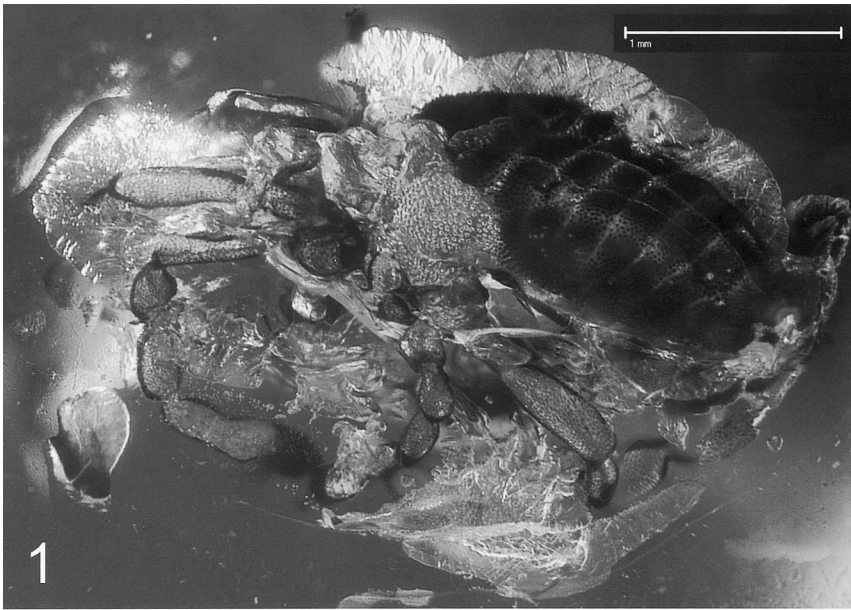
BITTERFELD AMBER

Amber from the Bitterfeld region of Germany has been known since at least the mid 17th century; see Kosmowska-Ceranowicz & Krumbiegel (1989) for a review. This Bitterfeld, or Saxon (=Saxonian), amber is not as well known as Baltic or Dominican amber. The locality was originally kept secret by the German Democratic Republic on the suspicion that it was associated with uranium deposits (M. Barthel, pers. comm., 2003), but in recent years it has seen increased activity from amateur collectors. It nevertheless contains a diverse range of inclusions, provisionally listed by Schumann & Wendt (1989). Although there have been numerous papers on the plants, fungi and, especially, the insect fauna (e.g. Röschmann 1997; Wagner et al. 2000), the arachnids remain quite poorly studied with only a few formal species descriptions (e.g. Wunderlich 1993). The first concerted study of the inclusions was by Barthel & Hetzer (1982). These authors figured a number of

taxa, including some spiders and a well-preserved phalangiid harvestman, and provided an overview of the geological setting. Further geological details can be found in Führmann & Borsdorf (1986) and Kosmowska-Ceranowicz & Krumbiegel (1989).

Geological setting.—Historically, amber has been recovered from a number of sites in the vicinity of Bitterfeld and the adjacent Mulde river in the Sachsen-Anhalt region of eastern Germany (see e.g. Kosmowska-Ceranowicz & Krumbiegel 1989, fig. 1). Since 1955 the principal source of amber, almost certainly including the specimen described here, has been the now disused, open-cast Braunkohl mine of Goitsche near Bitterfeld. The amber-producing horizon consists of a series of massive, sandy-clay lenses which, according to the local geological terminology, lie between the Bitterfeld main coal seam and the Breitenfeld seam (Kosmowska-Ceranowicz & Krumbiegel 1989, fig. 3). The sand and clay have been interpreted as representing a period of marine ingression which was dated on spore evidence to sporomorph zone IIIA according to the German Democratic Republic stratigraphic scale for the Tertiary (Krutsch in Barthel & Hetzer 1982). This spore zone correlates to a lower Miocene (lower Aquitanian) age.

Age of the amber.—Amber is notoriously difficult to date precisely and the Bitterfeld inclusions have been assigned to anything between an Eocene and a Miocene age. Barthel & Hetzer (1982) interpreted Bitterfeld amber as younger than Baltic amber, dating the former at lower Miocene (ca. 22 Ma) based on a combination of the regional geology and microbotany (see above). The inclusion-bearing pieces unequivocally lie in situ in strata associated with the Miocene coal seams (M. Barthel, pers. comm., 2003). Wunderlich (1983) suggested that the Bitterfeld amber was merely part of the Baltic amber complex and thus implicitly late Oligocene/Eocene (ca. 35–40 Ma) in age. He derived these conclusions from a (very provisional) survey of similar faunal (spider) and floral elements in both ambers. Fuhrmann & Borsdorf (1986) supported the Miocene age and rejected this redeposition hypothesis. These authors presented a detailed physico-chemical analysis in which they argued that the composition of mineralogical species in Bitterfeld amber dif-

Figures 1–2.—*Siro platypedibus* new species; the first fossil cyphophthalmid. MB.A. 1086 from Bitterfeld amber, Sachsen-Anhalt, Germany. 1. Dorso-lateral aspect; 2. Ventro-lateral aspect. Scale bars = 1 mm.

fered significantly from that of Baltic amber. Kosmowska-Ceranowicz & Krumbiegel (1989) analyzed the heavy mineral composition in the amber-bearing sediments and compared them to strata of known age in the same region. Their main conclusion was that an Eocene age for the amber-bearing sediments could be ruled out, but that the sediments could represent redeposited Oligocene material. Note that these results apply to the sedi-

ments and not the amber itself. These authors also noted a degree of color variation in the Bitterfeld amber which is not seen in Baltic amber, again implying that these ambers come from different sources.

However, Röschmann (1997, and references therein) has challenged the assumption that the Baltic and Bitterfeld ambers are fundamentally different, based on a detailed comparison of insect faunas; particularly Diptera. In this study, 14 species of fossil Sciaridae were found to be common to both ambers and, in general, the Baltic and Bitterfeld fly faunas score similarly on various ecofaunistic indices. The longevity of arthropod species has been estimated at 2.5–7 million years, thus if there really is an age difference of at least 13 million years between the Baltic and Bitterfeld ambers then, assuming these longevity estimates are accurate and widely applicable, we would not expect to find identical species in them. Röschmann thus implied an older age and redeposition of the Bitterfeld material and suggested that the Baltic and Bitterfeld amber-producing forests were of a rather similar age; unlike the host sediments of the amber pieces.

It should be added that Wagner et al. (2000) gave an Eocene (50 Ma) date for both Bitterfeld and Baltic amber, but the two papers they cite in support of this (Noonan 1986, 1988) are essentially biogeographical studies, one of which mentions a date for Baltic amber of 30 Ma and neither of which mention the Bitterfeld deposit! This illustrates the danger of poorly-justified dates becoming perpetuated in the literature. It is beyond the scope of the present paper to resolve the problems of dating the Bitterfeld fossils. Rikkinen & Poinar (2000) used the younger, Miocene age of around 20–22 Ma, but Poinar (pers. comm., 2002) now accepts the idea that Bitterfeld amber could be equivalent to Baltic amber, but perhaps originating from a different geographical source to the Baltic amber forest. Our fossil can thus be constrained to, at best, an age of between 20–40 Ma.

MORPHOLOGICAL INTERPRETATION

The fossil is preserved in an oval piece of relatively clear and translucent amber. Its orientation makes it primarily visible from both sides in a dorso-lateral and ventro-lateral view respectively, thus details of the legs are easier to see than those of the body (Figs. 1–4). Un-fortunately there is a series of internal fractures in the matrix around the body, which, along with numerous bubbles, obscures some details. There also appears to be some sort of foreign body (a spore?) directly underneath the animal which partly covers the coxo-sternal region and ventral surface of the opisthosoma. Grinding the amber would not clearly reveal the entire ventral surface without damaging the legs. Some parts of the legs are encrusted with a refractant substance, but the underlying morphology is still visible. The fossil is undoubtedly a cyphophthalmid and, like modern examples, it has a small, compact and densely tuberculate body (Murphree 1988), short, stubby legs with somewhat swollen and rounded podomeres, and a tarsus which ends in a single claw. The animal is complete and the body is c. 2 mm long, which is within the range of modern species. There is no projecting adenostyle on the fourth tarsus; therefore, since the specimen looks mature due to the degree of sclerotization, we interpret it as a female.

The carapace is mostly hidden in the matrix. There is no evidence for the presence of eyes. Ozopores on a pair of raised tubercles are characteristic for cyphophthalmids (Giribet et al. 2002) and one of these paired, raised, horn-like structures, sometimes termed ozophores, can be seen on one side of the fossil (Figs. 2, 4). It is deep within the matrix and details of morphology are lacking. Its apparently dorso-lateral position is consistent with the 'type 2' orientation (cf. Juberthie 1970; Giribet & Boyer 2002). On the other side (Figs. 1, 3) the ozophore region is obscured, almost as if a secretion from it has formed an ill-defined bubble in the matrix over the antero-lateral corner of the carapace. The opisthosoma expresses at least seven tergites dorsally, each densely tuberculate with circular tubercles and separated from adjacent tergites by a narrow band of non-tuberculate cuticle.

The chelicerae are mostly obscured behind other limbs, but the dorsal surface of the basal article can be seen. Proximally, there is no evidence for a dorsal crest (= dorsal ridge) which is characteristic of many living cyphophthalmids (e.g. Giribet & Boyer 2002, Figs. 1–3). Characters relating to the ventral surface of the second article or the movable finger of the chela are equivocal. The pedipalps are

slender with elongate podomeres which are distally densely setose. The legs are robust and tend to converge distally beneath the animal. Like the body, the legs are densely tuberculate. The leg tuberculation tends to be formed from more elongate, oval tubercles, especially on the dorsal surface of the articles in legs 3 and 4. Significantly, this tuberculation is not apparent on the metatarsus and tarsus of legs 1 and 2 (Figs. 1–4). The leg formula is, from longest to shortest: 1 2 4 3. The patellae and tibiae of leg 4 are notably swollen and ovate in appearance. The legs preserve a number of setae, which become more numerous on the more distal articles. There is a particular concentration of setae on the ventral surface of the distal tarsus near the origin of the claw, but not forming a distinct solea. All legs end in a single, smooth, hook-shaped tarsal claw.

SYSTEMATIC PALEONTOLOGY

Suborder Cyphophthalmi Simon 1879
Family Sironidae Simon 1879
Genus *Siro* Latreille 1796
Siro platypedibus new species
Figs. 1–4

Type and only material.—MB.A. 1086. Holotype and only known specimen. Bitterfeld amber. From the site of the Goitsche (or Goitzsche) Mine, near Bitterfeld, Sachsen-Anhalt, Germany (c. 51°36′N, 12°22′E). Tertiary (?Oligocene–Miocene) in age. Specimen also bears the identification number ''Ser. 15/4''.

Etymology.—From the tall, flattened patella and tibia in leg 4.

Diagnosis.—Ornamentation of legs as in the genera *Siro*, *Paramiopsalis* and *Tranteeva* with all tarsi and metatarsi 1 and 2 lacking the normal pattern of granulation seen in the other podomeres. Articles of legs compressed laterally with patella and tibia 4 becoming enlarged and flattened. Claws large. The appendages of this specimen are of particular interest and may indicate some special type of habitat.

Description.—Complete female cyphophthalmid. Total body length c. 2, but anterior obscured in matrix. Body with tuberculate ornament, darker than legs with at least seven clearly defined opisthosomal tergites. Prosoma with anterolateral ozophore. Chelicerae mostly obscured, but basal article 0.65 long. Pedipalps slender, podomere lengths: patella 0.33,

tibia 0.29, tarsus 0.27. Leg article lengths as follows. Leg 1: femur 0.75, patella 0.32, tibia 0.56, metatarsus 0.30, tarsus 0.55; total length c. 2.5. Leg 2: femur 0.65, patella 0.32, tibia 0.41, metatarsus 0.29, tarsus 0.50; total length c. 2.2. Leg 3: femur 0.45, patella 0.33, tibia 0.33, metatarsus 0.30, tarsus 0.47; total length c. 1.9. Leg 4: femur 0.58, patella 0.30, tibia 0.38, metatarsus 0.26, tarsus 0.53; total length c. 2.1. Legs tuberculate like body, but tuberculation absent on distal articles of legs 1 and 2. All legs end in single, smooth, hook-shaped claw, c. one-third the length of the tarsus.

Remarks.—This specimen represents the first, and so far only, fossil record of Cyphophthalmi. Their rarity as fossils is undoubtedly due to a combination of their unmineralized cuticle, small size and cryptic, soil-living habits; all of which reduce their chances of preservation. Amber nevertheless has the potential to trap soil or leaf-litter organisms. Schumann & Wendt's (1989) faunal list for Bitterfeld amber includes various elements of the soil meso- and macrofauna such as nematodes, isopods, oribatid mites, collembollans and myriapods.

Although there has been some northward drift of continental Europe by a few degrees over the last 40 million years, our fossil still probably represents the most northerly record of European Sironidae, c. 51–52° N. The most northerly distributed extant species in Europe is *Siro carpaticus* Rafalski 1956 which occurs in the Carpathian mountains of south-eastern Poland (c. 40°08′N). The amber fossil suggests that *Siro* was at one stage more widespread in Europe and previously occurred further north than its present geographical range. Two other sironid species occur at high latitudes in North America, *S. acaroides* (Ewing 1923) in Washington, up to 47°50′N, and *S. kamiakensis* (Newell 1943) in Washington and Idaho, c. 47°50′N.

AFFINITIES

The specimen described here lacks ventral teeth on the claw of leg 2, a character which excludes placement in the following genera: *Neogovea* Hinton 1938, *Huitaca* Shear 1979, *Metagovea* Rosas Costa 1950, *Paragovia* Hansen 1921, *Troglosiro* Juberthie 1979 and *Metasiro* Juberthie 1961 (see Giribet & Boyer 2002). Two preserved features (Figs. 1–4) are of particular interest: (a) the absence of tubercular ornament on the metatarsus and tar-
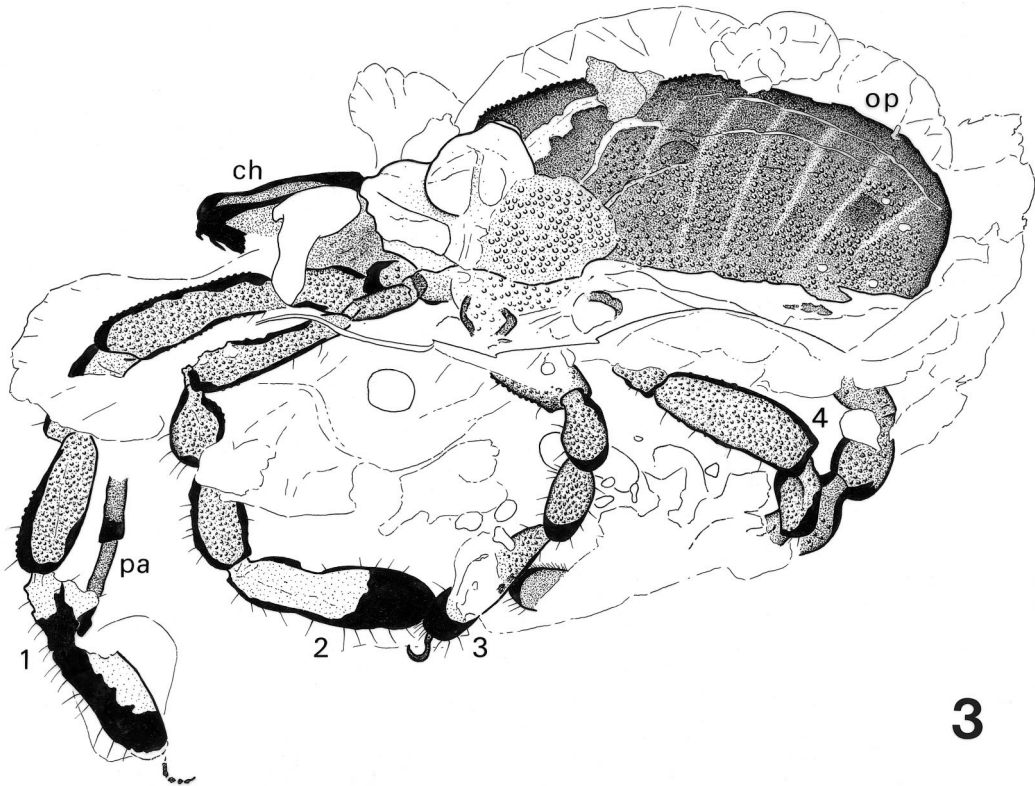
Figures 3–4.—Interpretive drawings of the specimens shown in Figs. 1, 2. Abbreviations: ch = chelicera, cx = coxae, in = unidentified inclusion beneath the animal, op = opisthosoma, oz = ozophore, pa = pedipalp, pt = patella, ti = tibia. Legs numbered from 1 to 4. Note the lack of tuberculation at the distal ends of legs 1 and 2 and the shape of the patella and tibia on leg 4. Scale bar = 0.5 mm.

sus of legs 1 and 2 and (b) the apparent absence of a dorsal crest on the basal article of the chelicera. Both of these characters are consistent with the extant genera *Siro*, *Paramiopsalis* Juberthie 1962 and *Tranteeva* Kratchovíl 1958 (see e.g. Juberthie 1970, 1991; Giribet & Boyer 2002) all of which belong to the Laurasian family Sironidae. The distinct lack of ornamentation on metatarsi 1 and 2 is also found in the Japanese genus *Suzukielus* Juberthie 1970, but it has a dorsal crest on the basal article of the chelicera. The type 2 position of the ozophore is also consistent with these taxa, although this character is seen in other genera too. However, it indicates that the fossil does not belong to the sironid genera *Parasiro* Hansen & Sørensen 1904 or *Odontosiro* Juberthie 1961, which have type 1 ozophores inserted in the margin of the carapace. Resolving the position of the fossil between the genera *Siro*, *Paramiopsalis* and *Tranteeva* is difficult based on the preserved morphology. They are differentiated from each other on characters relating to the corona analis at the posterior end of the opisthosoma, fusion of the coxae of legs 2 and 3 (in *Paramiopsalis*), the shape of the palpal trochanter, the length of the appendages, and the type of adenostyle. All these characters are either absent or equivocally preserved in the fossil and further preparation by grinding the amber is unlikely to reveal them. The appendages of *S. platypedibus* are of particular interest because they have long claws as in some of the troglobiontic species of *Siro* and *Tranteeva*, but the legs in the fossil, instead of being elongated, are compressed laterally. This is reminiscent in a certain way of the appendages of the equatorial African genus *Ogovea* Roewer 1923 which may show fossorial behavior.
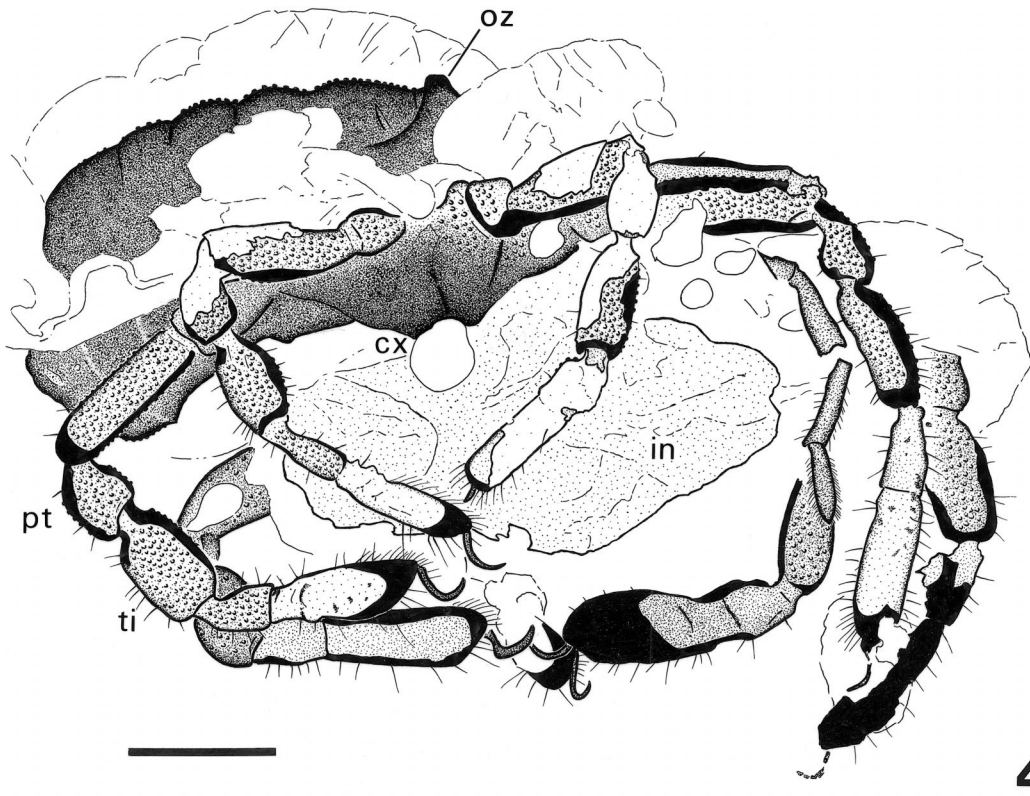
Figure 4.—Same as Fig. 3.

Paramiopsalis is a monotypic genus, currently restricted to the north-west Iberian Peninsula (Juberthie 1962; Giribet 2000). *Tranteeva* is also monotypic and restricted to some caves in Bulgaria (Kratochvíl 1958; Juberthie 1991), although there are doubts about the validity of the genus, which seems to be an apomorphic form of the Balkan sironid clade (Juberthie 1991). By contrast, *Siro* is more diverse and widely distributed, containing 23 extant species spread across Europe, Turkey and the USA. These records include Central European taxa (Austria, Slovakia, Poland) whose, albeit often localized, distribution is relatively consistent with the type locality of the Bitterfeld amber in eastern Germany. We see no characters in the fossil which would justify the creation of a new genus and for biogeographical reasons we tentatively assign our fossil to the more widespread *Siro* and suggest that this genus may have inhabited Central Europe since at least the mid-Tertiary.

While most members of the Laurasian Sironidae are smaller than 1.8 mm, a few species are reported to measure between 2.0 and 2.5 mm. Among the European species, *Siro gjorgjevici* Hadži 1933, *S. teyrovskyi* Kratochvíl 1938 and *Tranteeva paradoxa* Kratochvíl 1958 measure between 2.0 and 2.5 mm in length.

ACKNOWLEDGMENTS

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