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The pseudoscorpion genus *Centrochthonius* (Pseudoscorpiones: Pseudotyrannochthoniidae) from central Asia and description of a new species from Nepal

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Abstract. The pseudotyrannochthoniid genus *Centrochthonius* Beier, 1931 is one of the rarest and most poorly understood pseudoscorpion genera in the world. Only a handful of specimens are presently known, all from high-altitude habitats in China, Kyrgyzstan and Nepal. The inaccessibility of specimens has resulted in major taxonomic difficulties such as a poor generic diagnosis, but also a lack of understanding of evolutionary patterns in this psychrophilic fauna. Herein we diagnose *Centrochthonius* for the first time since its original description and include four Holocene species: one from Kyrgyzstan, two from China, and *C. anatonus* sp. nov. from Nepal. A fifth fossil species from Bitterfeld amber (Oligocene-Miocene) in central Europe highlights significant range retraction and continental extinction in this genus since the Neogene, leading us to suggest a climatic relict hypothesis for this fauna. Biogeographically, the genus provides further evidence for significant range shifts and extinction events in the Holarctic invertebrate biota during the Cenozoic. Close relatives of *Centrochthonius* are found in subterranean habitats throughout eastern Asia and warm temperate forests in the western U.S.A. which highlights the magnitude of range retraction caused by climatic cycling in an ancient fauna since at least the Paleogene. The subgenus *Allochthonius* (*Urochthonius*) Morikawa, 1954 from caves in Japan has been largely defined by the presence of troglomorphic features such as eye loss, which are here regarded as insufficient to retain as a separate clade from other species of *Allochthonius*. Therefore, *Allochthonius* (*Urochthonius*) is treated as a junior synonym of *Allochthonius* (**syn. nov.**).

Keywords: Tibetan Plateau, biogeography, psychrophilic, relict, systematics.

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ZooBank Registration: http://zoobank.org/References/EA145CBA-772B-404A-8D2D-0DB400B4BCB5

The pseudoscorpion genus *Centrochthonius* Beier, 1931 is amongst the rarest pseudoscorpion genera in museum collections and only a handful of specimens have ever been reported since the first species was described in the early 20th century. This rarity reflects the elusive nature of these leaf-litter dwelling pseudoscorpions that have been collected from several countries (China, Kyrgyzstan and Nepal) throughout central Asia. Apart from rarity, the genus is interesting for three main reasons. It belongs to the earliest branching pseudoscorpion lineage – the Pseudotyrannochthoniidae – and shares with all members in this family a plesiomorphic morphology that includes the absence of venom glands in the chelal fingers, a trichobothrial pattern of the chela that matches the oldest known pseudoscorpion fossils from the Devonian (Judson 2012), and a small tubercle between the coxae of leg III that may be a remnant of the sternum that is otherwise lost in higher pseudoscorpions. From a biological perspective the genus is interesting because most of the species have been collected from high altitude habitats with harsh climatic conditions that include regular frost and snow as well as long winters; habitats that are too cold for most other pseudoscorpions. Biogeographically, the genus seems to belong to an ancient Laurasian radiation of pseudotyrannochthoniids with 16 setae on the carapace, as its closest morphological relatives occur either in the warm temperate forests of western North America (Oregon, Washington, California and Utah) (Muchmore 1967; Benedict & Malcolm 1970) or are exclusively confined to caves in Japan and Korea (You et al. 2022; also Fig. 1).

Research on *Centrochthonius* has been hampered by an extremely confusing taxonomy that includes a poorly defined original generic concept (Beier 1931). Most pseudoscorpion taxonomists have subsequently ignored this genus, probably because the inaccessibility of specimens prevented proper documentation and interpretation of characters. Originally, *Centrochthonius* had been proposed by Beier (1931) for *Chthonius kozlovi* Redikorzev, 1918 from western China (Redikorzev 1918) and a short descriptive diagnosis was provided. This diagnosis includes several errors, such as a setation count for the carapace that is given as 20 setae although only 16 setae are actually present (Fig. 11). Interestingly, Beier was probably the only worker since Redikorzev (1918) who had access to the original specimens from the Museum in St. Petersburg (then Leningrad) and provided details that were not mentioned in the original description, including the number of carapaceal setae, the positions of the trichobothria, coxal blades, and details of the intercoxal tubercle. The following year, Beier (1932a) provided more information on the genus and its only included species, and provided an illustration of the left pedipalp, presumably from one of the syntypes. The major feature that Beier (1931, 1932a) used to separate *Centrochthonius* from the only other genera of the tribe Pseudotyrannochthoniini known at the time, *Pseudotyrannochthonius* Beier, 1930 and *Afrochthonius* Beier, 1930, was the presence of an intercoxal tubercle. This

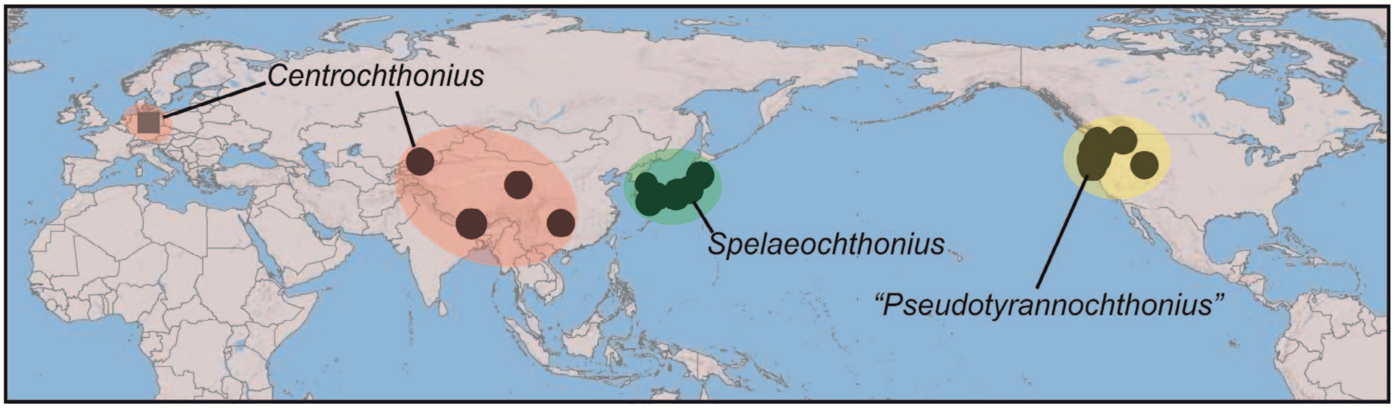


Figure 1.—Distribution of Holarctic Pseudotyrannochthoniidae genera with 16 setae: *Centrochthonius* from central Asia (red), presently misplaced specimens of "*Pseudotyrannochthonius*" from western U.S.A. (yellow), and *Spelaeochthonius* from caves in Korea and Japan (green). The black square denotes the locality of fossil †*Centrochthonius bitterfeldicus* from Bitterfeld amber (Bitterfeld, Germany).

tubercle, which is found in many, but not all chthonioids, has since been found to be present in most species of *Pseudotyrannochthonius* (e.g., Beier 1964, 1966; Harms 2013, 2018; Harms & Harvey 2013), including the type species *P. silvestrii* (Ellingsen, 1905) from Santiago de Chile, and can no longer be used to distinguish *Centrochthonius* and *Pseudotyrannochthonius*.

Centrochthonius was later expanded by the inclusion of *Chthonius* (*Centrochthonius*) *schnitnikovi* Redikorzev, 1934 from Kyrgyzstan (Redikorzev 1934a), *C. ussuriensis* Beier, 1979 from eastern Russia (Beier 1979) and *C. sichuanensis* Schawaller, 1995 from Sichuan Province, China (Schawaller 1995). A specimen from Nepal was attributed to *C. kozlovi* by Schawaller (1991, 1995). Two of these species have since been transferred to the genus *Allochthonius* Chamberlin, 1929: *C. ussuriensis* by Schwarze et al. (2022), and *C. sichuanensis* by Hu & Zhang (2011), who noted that they possessed all the major features of the genus *Allochthonius,* including the shape of the coxal blades [grooming organs for the leg claws and pedipalps on the coxae of the first pair of legs (Judson 1990; Schwarze et al. 2022; Figs. 5–8)] that vary greatly in pseudotyrannochthoniids.

Amongst the three pseudotyrannochthoniid genera known to occur in Asia today, the speciose and morphologically diverse genus *Allochthonius* includes species in which these spines sit on a common protuberance (a "spray" or "fan" according to Chamberlin 1929a) at the apical margin of the leg coxa, with each spine being tripartite, relatively short and with

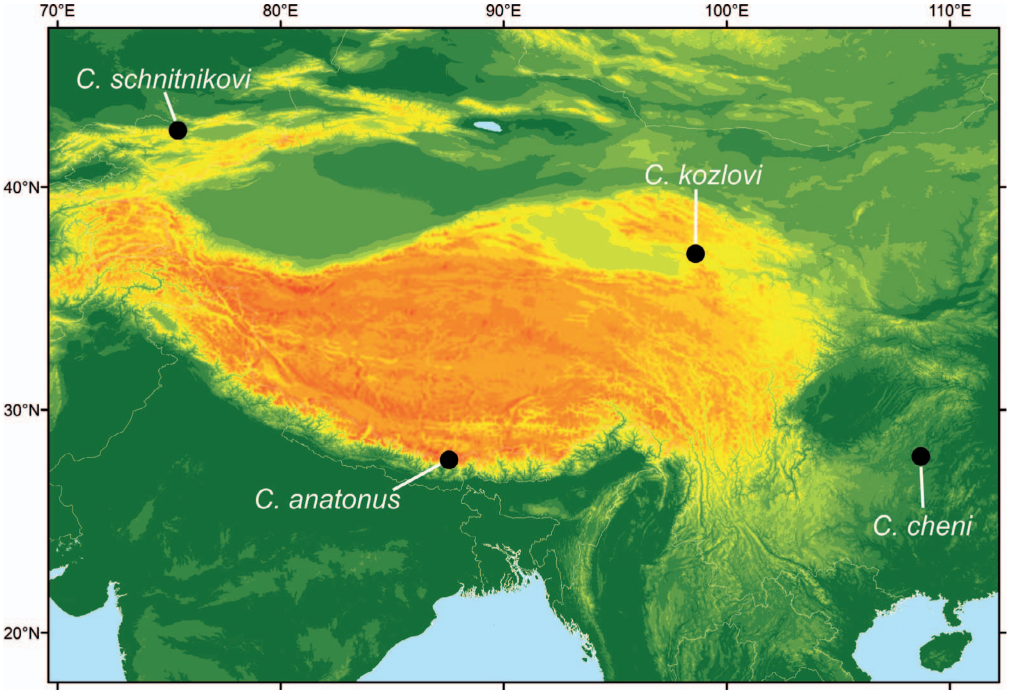
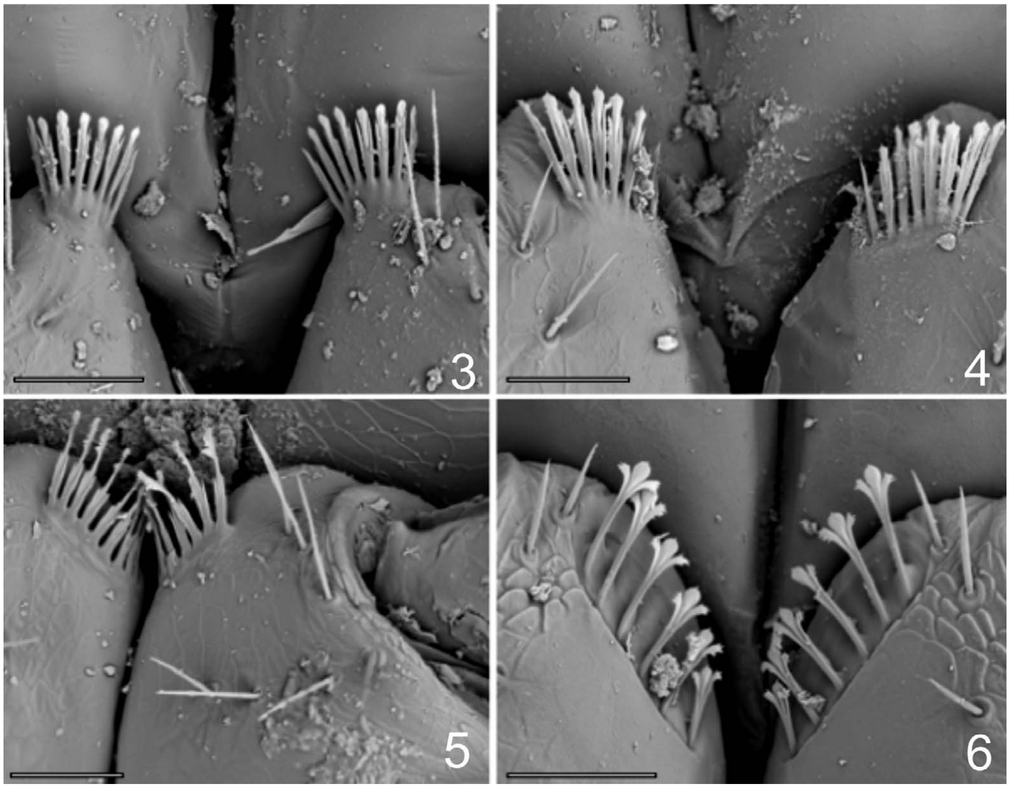


Figure 2.—Topographic map of the eastern Palearctic, showing the distribution of the four species of *Centrochthonius* in central Asia, with the Tibetan Plateau highlighted.

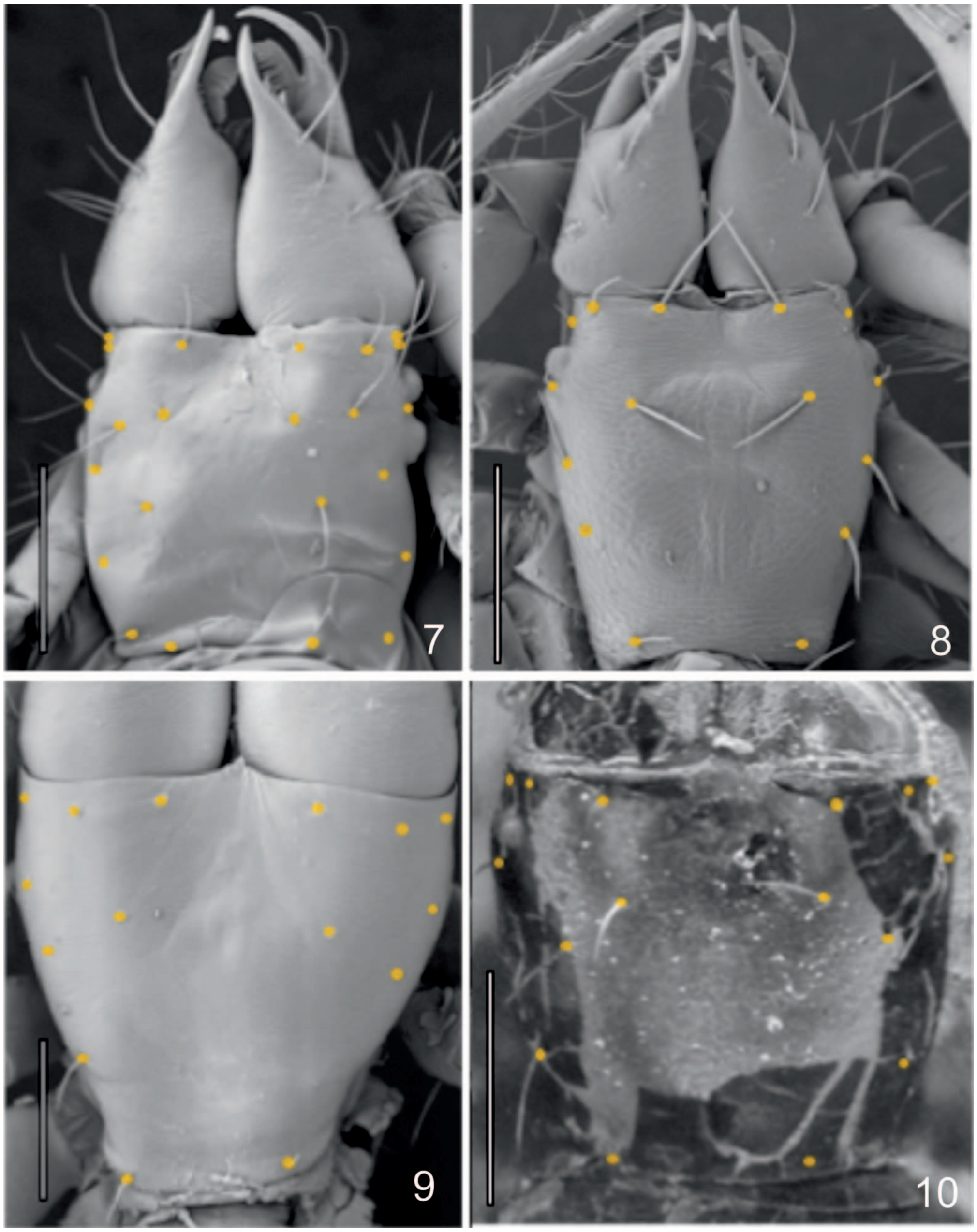


Figures 3–6.—Scanning electron micrographs showing the coxal blade morphology of some Pseudotyrannochthoniidae genera: 3, *Allochthonius ussuriensis* from Russia (WAM T146405); 4, "*Pseudotyrannochthonius*" *gracilis* from the U.S.A. (WAM T146426); 5, *Spelaeochthonius dentifer* from South Korea (WAM T146409); 6, *Pseudotyrannochthonius* sp. from Chile (WAM T146417). Scale bars = 50 µm.

a spatulate apical end (Fig. 3). The newly reinstated genus *Spelaeochthonius* Morikawa, 1954 from caves in Japan and Korea has 9–11 coxal blades that are inserted directly on the subapical margin of the pedipalp coxa, never sit on a common protuberance, and each spine is rather long and has plumose or tassel-shaped tips (e.g., Morikawa 1954, 1956, 1960; You et al. 2022; Fig. 5). The coxal blade morphology in *Centrochthonius* was reported by Redikorzev (1918, fig. 9C) who illustrated five short and acute coxal blades for the type species *C. kozlovi* and this configuration has since been found in the recently discovered *C. cheni* from high altitude habitat in central Asia (Gao et al. 2016), and a fossil species *C. bitterfeldicus* Schwarze et al., 2022 from Bitterfeld amber in Germany (Schwarze et al. 2022). It should be noted here that *C. cheni* had initially been described in *Pseudotyrannochthonius* following the generic arrangements proposed by Muchmore (1967) who had synonymised *Spelaeochthonius* with *Pseudotyrannochthonius* and also placed all pseudotyrannochthoniid species from the western U.S.A. in this genus, which was originally described from Chile (Beier 1930). We emphasize that all species from Chile differ in several important details from any of the Asian pseudotyrannochthoniids, including the number of carapaceal setae and coxal blade morphology that was discussed by Muchmore (1967) based on the literature but without having seen any specimens from either Asia or Chile. Muchmore (1967) did not mention *Centrochthonius* or any of the literature pertaining to this genus, and the synonymy of *Spelaeochthonius* with *Pseudotyrannochthonius* – suggested as provisional by Muchmore (1967) himself – was abandoned by Schwarze et al. (2022) who rediagnosed *Centrochthonius* for species with only 4–5 coxal blades that are situated subapically on the antero-mesal margin of leg coxa I, and individual spines that are short, tripartite and have an acute tip. Schwarze et al. (2022) also emphasized the importance of the number of carapaceal setae in Holarctic pseudotyrannochthoniids and noted the presence of only 16 setae on the carapace in *Centrochthonius*, a similar configuration to *Spelaeochthonius* from caves in Japan and Korea [currently with nine valid species, see You et al. 2022], and to the three species from western U.S.A. that presently remain misplaced in *Pseudotyrannochthonius* but are rather related to *Centrochthonius* and *Spelaeochthonius*.

Based primarily on coxal blade morphology, we here redefine *Centrochthonius* and include four Holocene species from central Asia as well as a fossil species from Europe. With the removal of *C. sichuanensis* and *C. ussuriensis* to *Allochthonius* (Hu & Zhang 2011; Schwarze et al. 2022), this leaves only species that are endemic to high altitude regions (2,000 m above sea level or higher; Fig. 2) of the eastern Palearctic, as well as the extinct *C. bitterfeldicus* from Europe, that offers an exciting avenue to interpret the evolutionary history of this fauna.

To understand more fully the morphology and diversity of this genus and its constituent species, we have examined the type specimens of both *C. kozlovi* and C. *schnitnikovi* decades after their first description, as well as the specimen referred to *C. kozlovi* by Schawaller (1991, 1995). The results include a revised diagnosis for the genus, and the first detailed



Figures 7–10.—Scanning electron micrographs showing carapaceal setae patterns in Holarctic Pseudotyrannochthoniidae: 7, *Allochthonius opticus* from Japan (WAM T146482); 8, "*Pseudotyrannochthonius*" *gracilis* (WAM T146426) from the U.S.A.; 9, *Spelaeochthonius kobayashii* from Japan (WAM T146408); 10, †*Centrochthonius bitterfeldicus* from Bitterfeld amber (GZG.BST.23850). Scale bars = 250 µm.

description of the type species *C. kozlovi*. This study concludes that the genus can be defined by the presence of only 16 setae on the carapace including the absence of seta *Mm*, a highly unusual feature in chthonioid pseudoscorpions, the distinct morphology of the coxal blades with four to five short and acute spines on the antero-mesal margin of the coxa I, an intercoxal tubercle that is small in comparison with *Allochthonius*, and biological attributes of the Holocene fauna that is psychrophilic and exclusive to high-altitude habitats in central Asia.

METHODS

The specimens examined in this study are lodged in the following institutions: Geowissenschaftliches Museum, Universität Göttigen, Germany (GZG); Muséum d'histoire naturelle, Geneva, Switzerland (MHNG); Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS); Western Australian Museum, Perth, Australia (WAM); and Zoological Institute of the Russian Academy of Sciences, St Petersburg (ZISP).

Some of the type specimens of *C. schnitnikovi* are permanently mounted on microscope slides. The specimens stored in ethanol were examined by preparing temporary slide mounts by immersing specimens in 75% lactic acid at room temperature for one to several days, then mounting them on microscope slides with 10 mm coverslips supported by small sections of 0.25 mm or 0.50 mm diameter nylon fishing line. Specimens were examined with a Leica MZ16 dissecting microscope and an Olympus BH–2 compound microscope, and illustrated with the aid of a drawing tube. Measurements were taken at the highest possible magnification using an ocular graticule. After study, the specimens were rinsed in water and returned to 75% ethanol with the dissected portions and placed in 12 × 3 mm glass genitalia microvials (BioQuip Products, Inc.).

The species treated here are arranged alphabetically, except for the type species *C. kozlovi* which is described first. Terminology and mensuration largely follow Chamberlin (1931) with the exception of the nomenclature of the pedipalps, legs and with some minor modifications to the terminology of the trichobothria (Harvey 1992), chelicerae (Harvey & Edward 2007; Judson 2007) and faces of the appendages (Harvey et al. 2012). The notations of the setae on the carapace are adopted from the terminology initially proposed by Gabbutt & Vachon (1963), Heurtault-Rossi (1963) and Vachon (1963) and modified by Zaragoza (2017) for chthoniid pseudoscorpions. Five discrete rows occur in most members of the Chthonioidea, except for Tridenchthoniinae which have numerous setae (e.g., Chamberlin & Chamberlin 1945); also see Wreidt et al. (2021) for a discussion in fossil chthonioids). These rows are termed anterior (*A*), ocular (*O*), median (*M*), intermediate (*I*) and posterior (*P*). To facilitate the identification of homologous setae, each setal pair is provided with notation based on its position: the median pair termed *m*, the lateral pair termed *l*, and the seta slightly anterior to the ocular region termed *o*. The standard formation in most Chthonioidea is three pairs in the anterior row, two pairs in the ocular row, two pairs in the median row, one pair in the intermediate row, and one pair in the posterior row. This pattern is displayed with the notation 6: 4: 4: 2: 2 (= 18).

Coordinates for the collection localities were calculated using Google Earth or obtained from various other online resources.

SYSTEMATICS

Family Pseudotyrannochthoniidae Beier, 1932

Genus *Centrochthonius* Beier, 1931

Centrochthonius Beier, 1931: 56.

Type species.—*Chthonius kozlovi* Redikorzev, 1918, by original designation.

Diagnosis.—*Centrochthonius* differs from all other pseudotyrannochthoniids by a unique arrangement of only 4–5 coxal blades that are short, tripartite, distally acute, and positioned subapically on the antero-median margin of the leg coxa (Figs. 15, 22). It shares with *Spelaeochthonius* and all species of "*Pseudotyrannochthonius*" from western U.S.A. the presence of only 16 setae on the carapace and the absence of seta *Mm* in the median row of setae (Figs. 11, 27) (occasionally 18 are present, see Fig. 19) but differs from these in coxal blade morphology (7–10 coxal blades in *Spelaeochthonius* that are longer and distally plumose or end as a feathered tassel; see Morikawa (1954); see also Fig. 5 as another reference) more than 6 spines in "*Pseudotyrannochthonius*" that are also short but have spatulate tips. The genus is further distinguished from *Allochthonius*, a genus occurring in eastern Asia, by a smaller intercoxal tubercle (Figs. 16, 24), coxal blades arranged on a small mound in *Allochthonius* (see Fig. 3), and niche-differentiation that includes a dependence on high-altitude habitats for *Centrochthonius* whereas *Allochthonius* is known from lowland and moderate elevation forest habitats (usually not higher than 1500 m) and some caves in Japan (Morikawa 1960).

Description (adults).—*Chelicera:* hand with 5, but occasionally 4 or 6, acuminate setae; movable finger with 1 medial seta.

Pedipalp: setae acuminate. Fixed chelal finger and hand with 8 trichobothria plus duplex trichobothrium (*dt*), movable chelal finger with 4 trichobothria (Figs. 14, 26, 30): *ib* and *isb* situated close together sub-distally on dorsum of chelal hand; *eb*, *esb* and *ist* in a row sub-laterally at base of fixed chelal finger, *ist* either slightly basal to *esb* or slightly distal to *esb*; *it* and *est* situated sub-medially; *et* situated distally, much closer to *dt* than to *it*; *dt* situated distal to *et*, each seta shorter than those of other trichobothria; dorsum of chelal hand and fixed finger without dorsal microsetae; trichobothrium *st* of movable finger situated sub-basally; *sb*, *b* and *t* situated sub-distally, equidistant from each other. Chelal teeth homodentate and diastemodentate.

Cephalothorax: carapace (Figs. 11, 19, 27) subquadrate; 2 pairs of eyes present; epistome broad and serrate (Figs. 12, 20, 28); with 16 setae arranged 6: 4: 2: 2: 2 or 18 setae arranged 6: 4: 2: 3: 3; seta *m1* absent; furrows absent; the pre-ocular seta about half the length of other setae in anterior row; with 3 pairs of small lyrifissures, first and second pairs situated in ocular row, third pair situated lateral to setae of posterior row. Manducatory process with 2 acuminate distal setae, lateral seta about half length of medial seta; pedipalpal coxa with other 3 setae arranged in triangle; median maxillary lyrifissure straight; coxae I with several coxal blades on each side, set in transverse row near anterior coxal margin (Figs. 15, 22); intercoxal tubercle small with 2 setae (Figs. 16, 24).

Abdomen: tergites and sternites undivided; setae acuminate and arranged in irregular uniseriate rows. Tergite I with 2 setae (*C. cheni*, *C. kozlovi* and *C. schnitnikovi*) or 4 setae (*C. anatonus*); tergite XII with 0 setae; sternite XI absent.

Genitalia: male genitalia with small ejaculatory atrium; lateral genital sacs small; glandular genital setae in 2 parallel rows of 4; sternite III with V-shaped opening. Female genitalia: not studied.

Legs: femur I much longer than patella I; heterotarsate (i.e., metatarsi and tarsi of legs I and II fused, metatarsi and tarsi of legs III and IV separate); tarsi with one elongate gland opening along dorsal surface with non-crenulate margins; arolium slightly shorter than claws, claws simple and with ventral striations.

Remarks.—The main distinctive feature of this genus is the morphology of the coxal blades but also the ecological dependence on cold habitats with regular frost that is now becoming apparent. We emphasize again that the presence of 16 carapace setae is a synapomorphy for a clade containing three genera of Holarctic pseudotyrannochthoniids: *Centrochthonius* from central Asia with four Holocene species and a Cenozoic species based on a single fossil; *Spelaeochthonius* from eastern Asia with nine valid species (You et al. 2022); and "*Pseudotyrannochthonius*" from western U.S.A with three valid species (Benedict & Malcolm 1970). We also note that there are interesting cases of convergent evolution of this character in *Allochthonius*: *A. brevitus* Hu & Zhang, 2012 from high altitudes in Níngxià Autonomous Region China (Mt. Liupan) has only 16 carapace setae but still shares the typical coxal blade morphology of *Allochthonius* (Hu & Zhang 2011, fig. 4f).

Allochthonius montanus Sakayori, 2000 from Mt. Kohshin in Japan (830–1700 m alt.) has a coxal blade morphology that is reminiscent of *Centrochthonius* (Sakayori 2000, fig. 6). We were initially tempted to include the latter species in *Centrochthonus* but specimens suitable for DNA sequencing became available recently and the genetic data (M. Hillyer & J. Huey, unpubl. data) clearly align this species with other *Allochthonius* species from Japan. The species has 18 carapaceal setae on the carapace, including four setae in the posterior row (Sakayori 2000). It is interesting that some high-altitude *Allochthonius* seem to reduce the carapaceal setae but too little is known about the nexus between ecological adaptation and morphological evolution to conclude anything other than the phenotypic observation.

We also note that trichobothrium *ist* varies in position between the different species of *Centrochthonius*. It is slightly basal to *esb* in *C. cheni* and *C. bitterfeldicus* (Gao et al. 2016; Schwarze et al. 2022) but is distal to *esb* in the three species from the Tibetan Plateau, *C. anatonus*, *C. kozlovi* and *C. schitnokovi* (Figs. 14, 26, 30). The basal position also occurs in species of *Spelaeochthonius* (Morikawa 1954; You et al. 2022) and the North American species attributed to *Pseudotyrannochthonius* (Muchmore 1967; Benedict & Malcolm 1970).

Centrochthonius kozlovi (Redikorzev, 1918)

ZooBank LSID: http://zoobank.org/NomenclaturalActs/
132AF726-E4DF-4E20-AF67-A0186A691901
(Figs. 11–18)

Chthonius kozlovi Redikorzev, 1918: 100–101, figs. 9, 10, 10a–c.
Centrochthonius kozlovi (Redikorzev): Beier, 1931: 56; Beier, 1932a: 70, fig. 84.
Not *Centrochthonius kozlovi* (Redikorzev): Schawaller, 1991: 772–773, figs. 1, 7–10; Schawaller, 1995: 1046, fig. 6 (misidentifications; see *Centrochthonius anatonus*, sp. nov.).

Type material.—*Syntypes*. CHINA: *Qinghai*: 1 ♂, 1 ♀ (slide), 1 ♀ (ethanol), "Dulon-kit" [now Dulansi, 37°01′N, 98°37′E], "11,000 a. h.", August 1901, Expédition au Thibet, 1899–1901 (ZISP, no. 3–1902).

Diagnosis.—*Centrochthonius kozlovi* differs from other species of *Centrochthonius* by its larger size, e.g., chela length 1.64 (♂), 1.71 mm (♀) in *C. kozlovi*, 1.20 mm (♀) in *C. anatonus*, 1.01 mm (♀) in *C. schnitnikovi*, 1.21 mm (♀) in *C. cheni*, and 0.70 mm in *C. bitterfeldicus* (♀).

Description (adult).—*Color:* apparently light yellow brown (but any color pattern may have been lost).

Chelicera: hand with 5 (♂) 4–5 (♀) acuminate setae (Fig. 17); movable finger with 1 medial seta; fixed finger with 4 (♂, ♀) large and ca. 8 (♂), 4 (♀) small teeth, movable finger with ca. 17 (♂), 12 (♀) small teeth; lyrifissures not visible; galea absent; rallum consisting of 11 (♂, ♀) bipinnate blades (Fig. 18).

Pedipalp: all setae acuminate (Fig. 13); trochanter 1.64 (♂), 1.76 (♀), femur 6.14 (♂), 5.89 (♀), patella 2.22 (♂), 2.36 (♀), chela 5.86 (♂), 5.50 (♀), hand 2.07 (♂), 1.95 (♀) × longer than broad; moveable finger 1.77 (♂), 1.80 (♀) × longer than hand. Patella with 1 mediodorsal lyrifissures. Fixed chelal finger and hand with 8 trichobothria plus duplex trichobothrium (*dt*), movable chelal finger with 4 trichobothria (Figs. 13, 14): *ib* and *isb* situated close together sub-distally on dorsum of chelal hand; *eb*, *esb* and *ist* in a row sub-laterally at base of fixed chelal finger; with *ist* situated slightly distad to *esb*; *it* and *est* situated sub-medially about 2 areolar diameters apart; *et* situated distally, much closer to *dt* than to *it*; *dt* situated distal to *et*, each seta shorter than those of other trichobothria; dorsum of chelal hand and fixed finger without dorsal microsetae; trichobothrium *st* of movable finger situated sub-basally; *sb*, *b* and *t* situated sub-distally, equidistant from each other. Chelal teeth homodentate and diastemodentate: fixed finger with ca. 24 (♂), 23 (♀) teeth; movable finger with ca. 15 (♂), 14 (♀) teeth.

Cephalothorax: carapace (Fig. 11) 0.87 (♂), 0.92 (♀) × longer than broad; with 4 corneate, widely separated eyes; epistome broad and serrate (Fig. 12); with 16 setae arranged 6: 4: 2: 2: 2; furrows apparently absent; the pre-ocular seta about half the length of other setae in anterior row; lyrifissures not visible. Chaetotaxy of coxae: ♂, 2 + 3: 7: 5–6: 5: 5, ♀, 2 +3: 6–7: 4–6: 5: 5; manducatory process with 2 acuminate distal setae, lateral seta about half length of medial seta; pedipalpal coxa with other 3 setae arranged in triangle; median maxillary lyrifissure slightly curved; coxae I with 4 or 5 coxal blades on each side, set in transverse row near anterior coxal margin (Fig. 15); intercoxal tubercle present, with 2 setae (Fig. 16).

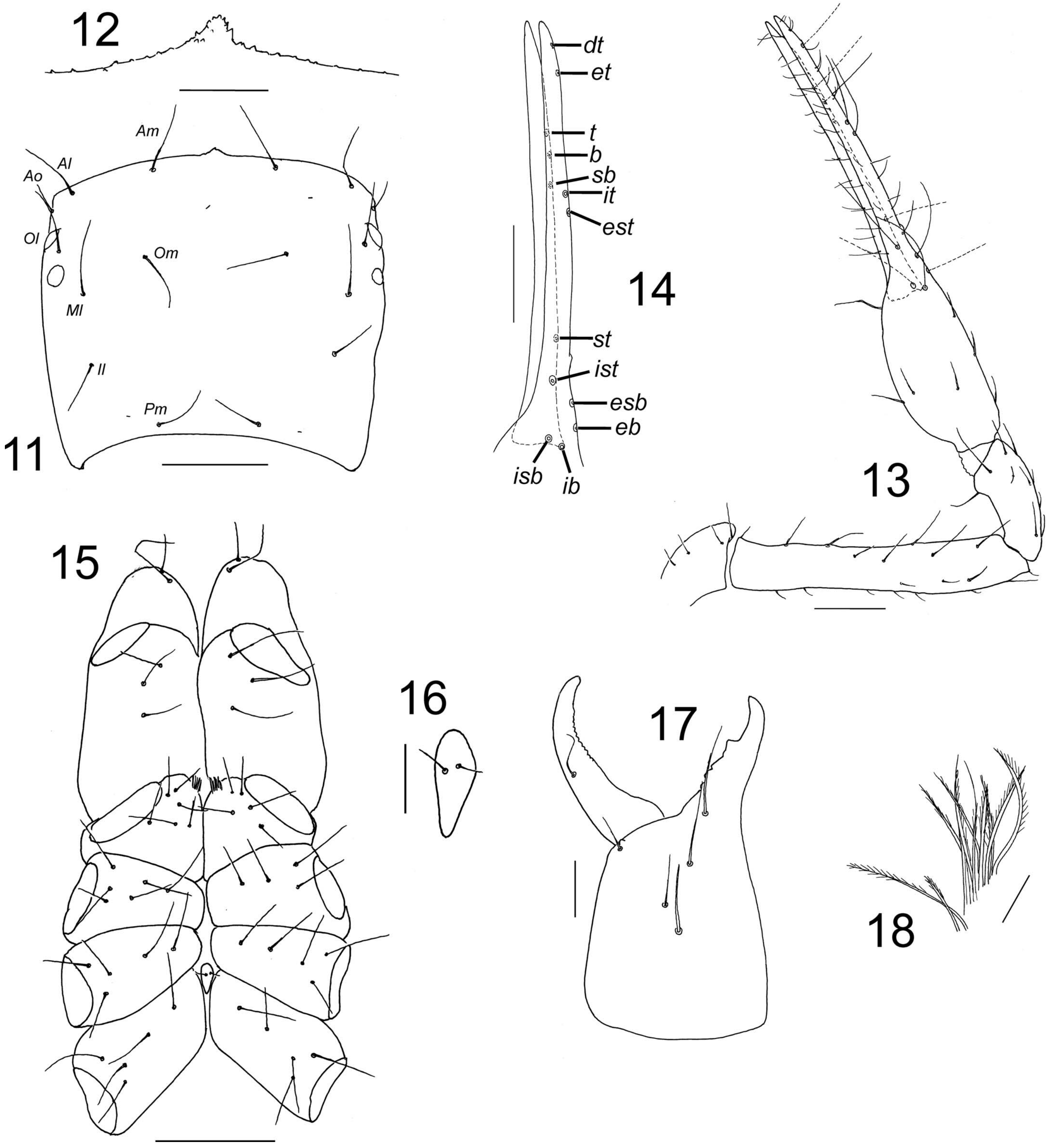
Abdomen: Tergites and sternites undivided; setae acuminate and arranged in irregular uniseriate rows. Tergal chaetotaxy: ♂, 2: 6: 6: 6: 6: 7: 7: 7: 5: 4: 2: 0; ♀, 2: 6: 6: 6: 6: 6: 7: 7: 6: 4: 2: 0. Sternal chaetotaxy: ♂, 10: (2) 15 [4 + 4] (3): (3) 8 (3): 12: 12: 11: 10: 10: 6: –: 2; ♀, 6: (2) 9 (2): (3) 8 (3): 12: 11: 10: 9: 9: 8: –: 2.

Genitalia: male genitalia with small ejaculatory atrium; lateral genital sacs small; glandular genital setae in 2 parallel rows of 4; sternite III with V-shaped opening. Female genitalia not visible.

Legs: arolium shorter than claws; claws simple.

Dimensions (mm): male syntype: Body length ca. 2.5. Pedipalps: trochanter 0.36/0.22, femur 1.105/0.18, patella 0.455/0.205, chela 1.64/0.28, hand length 0.58, movable finger length 1.025. Chelicera 0.655/0.325, movable finger length 0.335. Carapace 0.68/0.78; anterior eye diameter 0.05, posterior eye diameter 0.05. Leg I: femur 0.61/0.105, patella 0.35/0.095, tibia 0.355/0.075, tarsus 0.64/0.07. Leg IV: femur + patella 0.91/?, tibia 0.735/0.13, metatarsus 0.325/0.095, tarsus 0.66/0.07.

Female syntype: Body length ca. 2.46. Pedipalps: trochanter 0.37/0.21, femur 1.09/0.185, patella 0.46/0.195, chela 1.705/



Figures 11–18.—*Centrochthonius kozlovi* (Redikorzev), syntype female, unless stated otherwise: 11, carapace, dorsal; 12, epistome, dorsal; 13, right pedipalp, dorsal; 14, right chelal fingers, setae omitted, dorsal; 15, coxal region, ventral; 16, intercoxal tubercle; 17, left chelicera, dorsal, male syntype; 18, rallum, male syntype. Scale lines = 0.25 mm (Figs. 11, 13–15); 0.1 mm (Fig. 17); 0.05 mm (Figs. 12, 16, 18).

0.31, hand length 0.605, movable finger length 1.09. Chelicera 0.735/0.37, movable finger length 0.37. Carapace 0.76/0.83; anterior eye diameter 0.065, posterior eye diameter 0.065. Leg I: femur 0.615/0.095, patella 0.36/0.09, tibia 0.34/0.085, tarsus 0.70/0.07. Leg IV: femur + patella 1.17/?, tibia 0.28/?, metatarsus 0.30/?, tarsus 0.67/?.

Remarks.—*Chthonius kozlovi* was described by Redikorzev (1918) from a male and two females collected from "environs de Dulon-kit" in "Thibet". "Dulon-kit" is now known as Dulansi, and is situated at 37°01′N, 98°37′E on the Tibetan Plateau (Fig. 2). The site is upstream of Dulan-gol (river), and NNE of Dulan-nor (lake) (V. Dubatolov and D. Logunov, in litt., 2010). Dr. Logunov kindly supplied a copy of a map from Kozlov (1906) that shows the location of Dulon-kit. The collection data states "11,000 a. h.", which is interpreted as an elevation in feet, with "a. h." an abbreviation of the French expression "l'altitude haut" (the entire manuscript was in French) (Dr. D. Logunov, in litt., April 2021). This height corresponds to 3,350 meters which is consistent with the type locality on the Tibetan Plateau.

The description of *C. kozlovi* included an outline illustration of the body including the left appendages, and more detailed drawings of the right pedipalp, left chela, epistome and the coxal blades. Beier (1932a) provided a short redescription and an illustration of the left pedipalp, which was most likely based on one of the syntypes. We examined the type specimens which were used for the redescription. The ethanol preserved female is missing its left pedipalp and is quite faded. The other two specimens are mounted on a single microscope slide.

Schawaller (1991) recorded a specimen of *C. kozlovi* from Nepal and suggested it might represent a tritonymph. He later suggested that the specimen was in fact an adult male (Schawaller 1995), but our examination of the specimen shows that it is in fact an adult female. As it has several substantial differences to the syntypes of *C. kozlovi* and to the other species of the genus, we regard it as a new species, *C. anatonus*, that is described below.

Centrochthonius anatonus sp. nov.

ZooBank LSID: http://zoobank.org/NomenclaturalActs/45BC7C62-2066-4891-A01B-126618D3158B
(Figs. 19–26)

Centrochthonius kozlovi (Redikorzev): Schawaller, 1991: 772–773, figs. 1, 7–10 (misidentification); Schawaller, 1995: 1046, fig. 6 (misidentification).

Type material.—*Holotype female*. NEPAL: *Eastern District*: Thudam [27°45′N, 87°33′E], 3,550–3,650 m, 25–27 May 1988, Mischwald mit *Betula* und *Rhododendron*, J. Martens, W. Schawaller (SMNS 2825).

Etymology.—The specific epithet refers to the presence of this species in the Himalayan Mountains (*anatonus*, Latin, stretching or extending upward) (Brown 1956).

Diagnosis.—*Centrochthonius anatonus* differs from all Recent species of *Centrochthonius* as follows: from all other species by the presence of 4 setae on tergite I (2 setae in other species); from *C. kozlovi* by its smaller size, e.g., chela length 1.20 mm (♀) compared with 1.64 (♂), 1.71 mm (♀) in *C. kozlovi*; from *C. schnitnikovi* by its larger size, e.g., chela length 1.01 mm (♀) in *C. schnitnikovi*; and from *C. cheni* by the presence of 22 teeth on the movable chela finger (Fig. 26), compared with only 16 teeth in *C. cheni*, and less robust chela appendages, e.g., chela 5.11 x longer than broad, compared with 4.65 x in *C. cheni*.

Description (adult female).—*Color:* uniformly light yellow brown (but faded in ethanol).

Chelicera: hand with 5 acuminate setae (Fig. 25); movable finger with 1 medial seta; fixed finger with ca. 8 teeth, the distalmost teeth the largest becoming progressively smaller basally, movable finger with 18 very small teeth; with 1 dorsal and 1 ventral lyrifissure; galea absent; rallum consisting of 10 bipinnate blades.

Pedipalp: all setae acuminate (Fig. 21); trochanter 1.87, femur 4.15, patella 2.12, chela 5.11, hand 1.55 × longer than broad; moveable finger 2.11 × longer than hand. Patella with 1 large and 1 small mediodorsal lyrifissures. Fixed chelal finger and hand with 8 trichobothria plus duplex trichobothrium (*dt*), movable chelal finger with 4 trichobothria (Fig. 26): *ib* and *isb* situated close together sub-distally on dorsum of chelal hand; *eb*, *esb* and *ist* in a row sub-laterally at base of fixed chelal finger, with *ist* situated slightly distad to *esb*; *it* and *est* situated sub-distally about half-way between *et* and *ist*, and about 2 areolar diameters apart; *et* situated distally, closer to *dt* than to *it*; *dt* situated distal to *et*, each seta shorter than those of other trichobothria; dorsum of chelal hand and fixed finger without patch of lanceolate setae; trichobothrium *st* of movable finger situated sub-basally; *sb*, *b* and *t* situated sub-distally, ca. equidistant from each other. Chelal teeth homodentate and diastemodentate: fixed finger with 22 triangular teeth; movable finger with 22 acuminate teeth (Fig. 26).

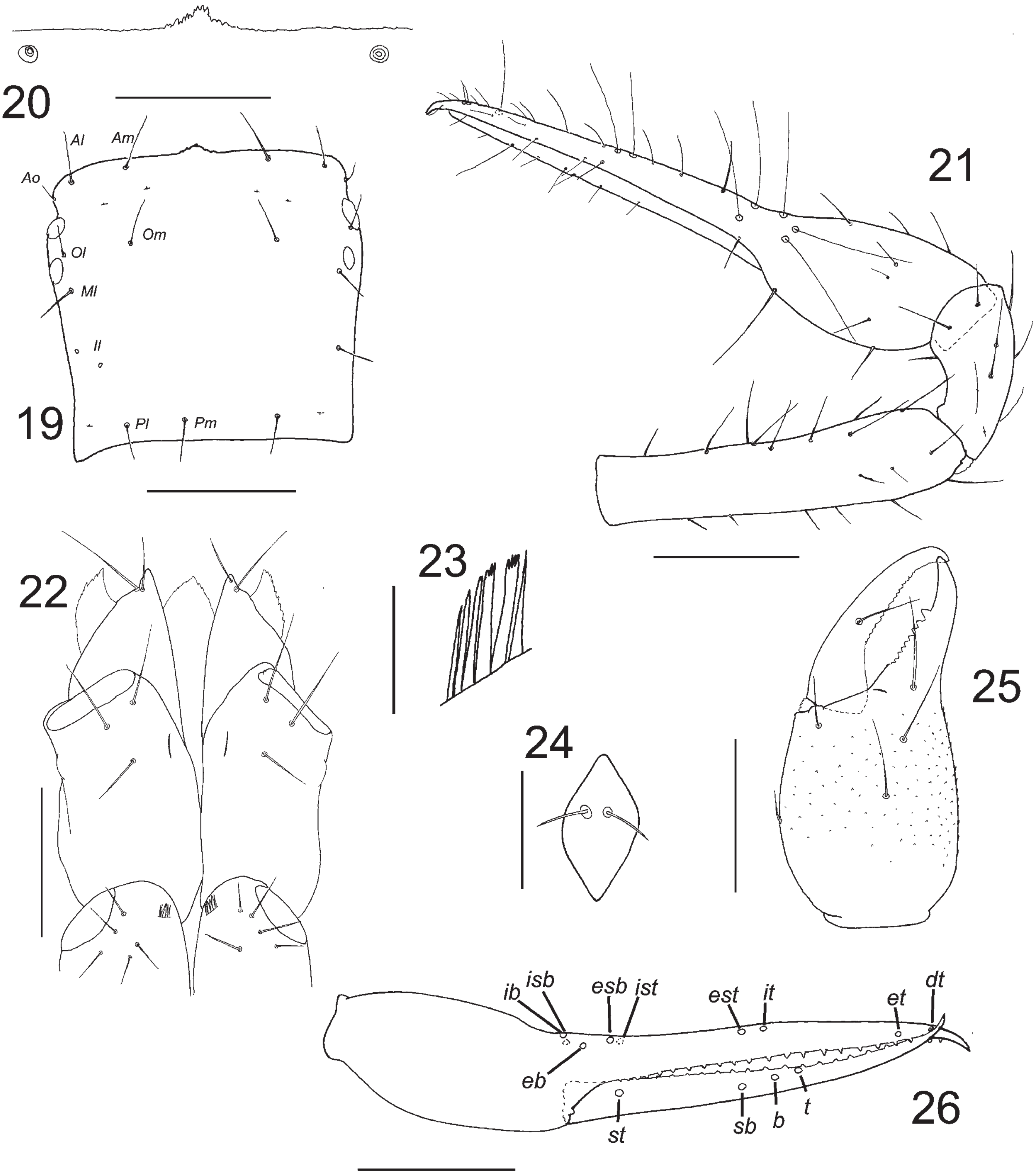
Cephalothorax: carapace (Fig. 19) 0.99 × longer than broad; with 4 corneate eyes; epistome low but distinctly serrate (Fig. 20); with 18 setae arranged 6: 4: 2: 3: 3; seta *Mm* absent; furrows absent; the pre-ocular seta about half the length of other setae in anterior row; 3 anterior and 1 pair of posterior lyrifissures present. Chaetotaxy of coxae: 2 + 3: 5–6: 4: 5: 5–6; manducatory process with 2 acuminate distal setae, lateral seta about half length of medial seta; pedipalpal coxa with other 3 setae arranged in triangle; median maxillary lyrifissure slightly curved; coxae I with 5 coxal blades on each side, set in transverse row near anterior coxal margin (Fig. 22), not set on mound, detailed morphology not readily visible, but apparently most blades tripartite with central lobe only slightly longer than lateral lobes (Fig. 23); intercoxal tubercle present, large, with 2 setae (Fig. 24).

Abdomen: tergites and sternites undivided; setae acuminate and arranged in irregular uniseriate rows, except for sternite II which are arranged in 2 triangles. Tergal chaetotaxy: 4: 7: 7: 7: 8: 8: 9: 10: 7: 7: 4: 0. Sternal chaetotaxy: 6: (1) 8 (1): (1) 9 (1): 13: 12: 12: 12: 11: 9: –: 2.

Genitalia: not visible.

Legs: arolium shorter than claws; claws simple with faint striations.

Dimensions (mm): Female holotype: Body length 2.22. Pedipalps: trochanter 0.290/0.155, femur 0.705/0.170, patella 0.350/0.165, chela 1.200/0.235, hand length 0.365, movable finger length 0.770. Chelicera 0.500/0.415, movable finger length 0.375. Carapace 0.605/0.610; anterior eye diameter 0.060, posterior eye diameter 0.050. Legs: not measured.



Figures 19–26.—*Centrochthonius anatonus*, sp. nov., holotype female: 19, carapace, dorsal; 20, epistome, dorsal; 21, right pedipalp, dorsal; 22, anterior coxal region, ventral; 23, coxal blades; 24, inter-coxal tubercle; 25, left chelicera, dorsal; 26, left chela, setae omitted, retrolateral. Scale lines = 0.25 mm (Figs. 19, 21, 22, 26); 0.2 mm (Fig. 25); 0.1 mm (Fig. 20); 0.05 mm (Figs. 23, 24).

Remarks.—The specimen from Nepal (Fig. 2) identified as *C. kozlovi* by Schawaller (1991, 1995) differs significantly from the type specimens of that species, and is here described as a new species. The specimen was originally regarded as a tritonymph (Schawaller 1991) and then as an adult male (Schawaller 1995) but is in fact an adult female. The illustration of the carapace by Schawaller (1991) was depicted with 18 setae arranged in a pattern of 6: 4: 2: 2: 4, but we detected a pattern of 6: 4: 2: 3: 3, also with a total of 18. While the presence of 18 setae is higher than in other species of *Centrochthonius*, we believe that its placement in *Centrochthonius* can be justified by the morphology of the coxal blades (Fig. 23) which are short and terminally incised, and by the absence of setae *Mm* on the carapace (Fig. 19). Curiously, the specimen has a duplication of *Il* on the left side and has three setae in the posterior row (Fig. 19). The two extra setae appear to be abnormalities and the authors have observed a duplication of these posterior setae in large series of other species such as *Pseudotyrannochthonius giganteus* (Beier, 1971) from Western Australia, the only species in this family that has been studied extensively both for morphology and genetic structure (Harms 2018; Harms et al. 2019; Michalski et al. 2022). Note that in *Allochthonius*, the most common East Asian pseudotyrannochthoniid genus, the posterior row frequently comprises four carapaceal setae, although the cave or soil-adapted species in this genus usually have only two setae, and all setae are usually arranged in a pattern 8–10: 4–6: 4–6: 2 (rarely 4): 4 (= 22–28) (= 22–28) (e.g., Morikawa 1956, 1970; Chamberlin 1962; Lee 1982; Sato 1984; Schawaller 1995; Sakayori 1999, 2002, 2014a, b; Hu & Zhang 2011, 2012; Gao & Zhang 2013; Zhang & Zhang 2014; Gao et al. 2016). Four species of *Allochthonius* have fewer than 22 setae: *A. brevitus* has 6: 4: 2: 2: 2 (= 16) (Hu & Zhang 2012); *A. yoshizawai* has 6: 6: 2: 2: 2 (=18) (Viana & Ferreira 2021); *A. montanus* has 6: 4: 2: 2: 4 (=18) (Sakayori 2000) and three of the four subspecies of *A. ishikawai* have a total of 18 or 20 setae including eight setae in the anterior row and two setae in the posterior row but without any details regarding the number of setae in the other rows (Morikawa 1954).

†***Centrochthonius bitterfeldicus*** Schwarze, Harms, Hammel & Kotthoff, 2022

ZooBank LSID: http://zoobank.org/NomenclaturalActs/a4ddf2f9-4b0c-4556-b209-6501e5de1daf
(Fig. 10)

Centrochthonius bitterfeldicus Schwarze, Harms, Hammel & Kotthoff, 2022: pages 17-21, figs. 4B, 4D, 8–10.

Type material.—Holotype female (in amber). GERMANY: *Sachsen-Anhalt:* "Braunkohle" mine, Goitzsche, Bitterfeld, ca. 51°37′N, 12°20′E, M. Kutscher (GZG.BST.23850).

Description.—See Schwarze et al. (2022).

Remarks.—The presence of pseudotyrannochthoniid inclusions in European succinite ambers was first noted by Ahrens et al. (2019) who illustrated an unidentified specimen from Bitterfeld amber. The specimen was recently described (Schwarze et al. 2022) and attributed in *Centrochthonius* based on the presence of four coxal blades that are short, tripartite and with acute tips on the inner subapical margin of leg coxa I, 16 setae on the carapace, and the presence of a small but bisetose intercoxal tubercle. The species is unusually small (0.89 mm) but does not deviate otherwise from the diagnosis proposed here for *Centrochthonius*. The finding has major implications for our understanding of biogeography in this fauna (but see discussion). The age of Bitterfeld amber is still being debated because it is embedded in coal deposits of Miocene age but likely reworked and probably older (but see Dunlop et al. 2018 for a full discussion on arachnids in this type of amber). Some authors suggest that this is a more southern deposit of Baltic amber and in this case, it would be of late Eocene age (Sadowski et al. 2017).

Centrochthonius cheni (Gao, Zhang and Zhang, 2016)

ZooBank LSID: http://zoobank.org/NomenclaturalActs/AFE6941B-6C4A-4268-ABD7-D04913E730ED

Pseudotyrannochthonius cheni Gao, Zhang and Zhang, 2016: 119 –123, figs 1–3.

Centrochthonius cheni (Gao, Zhang and Zhang): Schwarze et al., 2022.

Type material.—*Holotype female*. CHINA: *Guizhou Province:* Fanjingshan National Nature Reserve, Jiangkou County, 27°54.494′N, 108°41.859′E, alt. 2,214 m, 12 October 2014, Z. Gao (MHBU, Ps.-MHBU-GZ14101201) (not examined).

Diagnosis.—*Centrochthonius cheni* differs from the other Holocene species of *Centrochthonius* as follows: from *C. kozlovi* and *C. schnitnikovi* by its intermediate size, e.g., chela length 1.21 mm (♀) in *C. cheni*, 1.64 (♂), 1.71 mm (♀) in *C. kozlovi*, and 1.01 mm (♀) in *C. schnitnikovi*; and from *C. anatonus* by the presence of only 16 teeth on the movable chelal finger, compared with 22 in *C. anatonus* (Fig. 26), and more robust chelal appendages, e.g. chela 4.65 x longer than broad, compared with 5.11 x in *C. anatonus*.

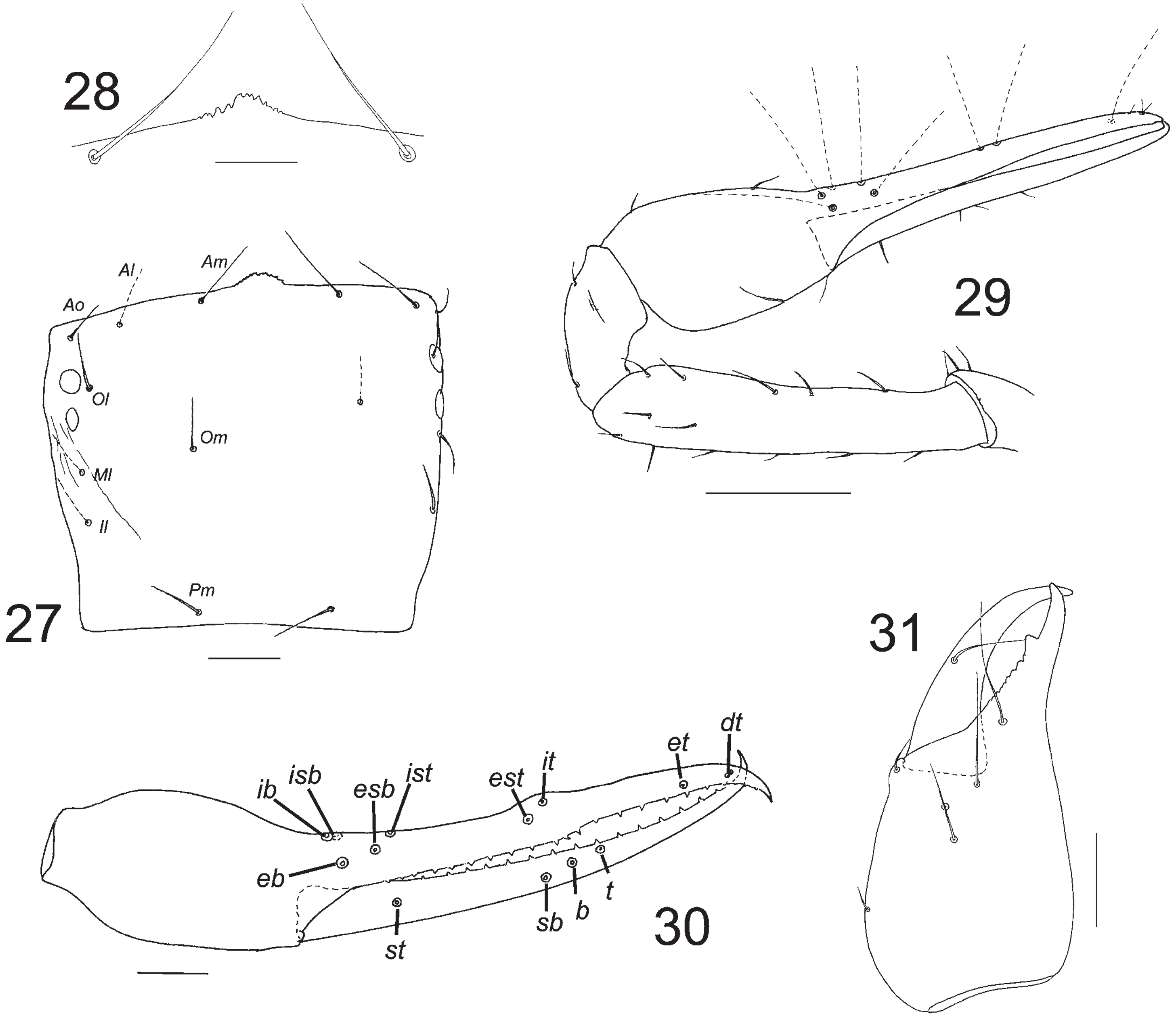
Description (adult).—See Gao et al. (2016).

Remarks.—This species was described from a single female collected from Guizhou Province (Fig. 2), China (Gao et al. 2016) and initially assigned to *Pseudotyrannochthonius*. The description of this species has all of the distinctive features of *Centrochthonius*, including only 16 carapace setae and the morphology of the coxal blades. The initial assessment as "*Pseudotyrannochthonius*" is based on Muchmore (1967) who had revised the pseudotyrannochthoniid fauna of the U.S.A. and placed all species in the Northern Hemisphere with 16 carapace setae in *Pseudotyrannochthonius* although the type species of this genus is from Chile and differs both in coxal blade morphology and number of carapace setae [18 are present in the type species *P. silvestrii* (Ellingsen, 1905) from Santiago]. Schwarze et al. (2022) discussed this taxonomic confusion and, based on the comparison with *C. kozlovi* and †*C. bitterfeldicus*, transferred *P. cheni* to *Centrochthonius*, resulting in the new combination *Centrochthonius cheni*. As usual for the genus, the species is from high altitude habitats (2,214 m) with extensive cold periods.

Centrochthonius schnitnikovi (Redikorzev, 1934)

ZooBank LSID: http://zoobank.org/NomenclaturalActs/7A812113-38DB-4CFA-8B18-6D282FA6CBBB
(Figs. 27–31)

Chthonius (Centrochthonius) schnitnikovi Redikorzev, 1934a: 439–440, fig. 19.



Figures 27–31.—*Centrochthonius schnitnikovi* (Redikorzev), holotype female: 27, carapace, dorsal; 28, epistome, dorsal; 29, left pedipalp, dorsal; 30, right chela, setae omitted, lateral; 31, left chelicera, dorsal. Scale lines = 0.25 mm (Fig. 29); 0.1 mm (Figs. 27, 30, 31); 0.05 mm (Fig. 28).

Centrochthonius schnitnikovi (Redikorzev): Roewer, 1937: 241.

Type material.—*Holotype female*. KYRGYZSTAN: *Chüy*: Schlucht des Flusses Tujuk [=Tuyuk Vostochnyy, 42°32′N, 75°24′E], Alexander-Gebirge [=Kirghizsky Mountain Ridge], 25 July 1931, Moos unter *Juniperus*-Busch, V. Schnitnikov (ZISP No. 1078).

Diagnosis.—*Centrochthonius schnitnikovi* differs from the other species of *Centrochthonius* by its smaller size, e.g., chela length 1.01 mm (♀) in *C. schnitnikovi*, 1.20 mm (♀) in *C. anatonus*, 1.21 mm (♀) in *C. cheni*, and 1.64 (♂), 1.71 mm (♀) in *C. kozlovi*.

Description (adult female).—*Color:* uniformly light yellow brown (but any color pattern may have been lost).

Chelicera: hand with 5 (or 6, see Remarks) acuminate setae (Fig. 31); movable finger with 1 medial seta; fixed finger with ca. 8 teeth, the distalmost teeth the largest, movable finger without teeth; with 2 dorsal and 1 ventral lyrifissures; galea represented by very low swelling; rallum consisting of 11 bipinnate blades.

Pedipalp: all setae acuminate (Fig. 29); trochanter 1.88, femur 4.62, patella 2.00, chela 4.81, hand 1.71 × longer than broad; moveable finger 1.81 × longer than hand. Patella with 1 large and 1 small mediodorsal lyrifissures. Fixed chelal finger and hand with 8 trichobothria plus duplex trichobothrium (*dt*), movable chelal finger with 4 trichobothria (Fig. 30): *ib* and *isb* situated close together sub-distally on dorsum of chelal hand; *eb*, *esb* and *ist* in a row sub-laterally at base of fixed chelal finger; with *ist* situated slightly distad to *esb*; *it* and *est* situated sub-medially about 2 areolar diameters apart; *et* situated distally, much closer to *dt* than to *it*; *dt* situated distal to *et*, each seta shorter than those of other trichobothria; dorsum of chelal hand and fixed finger without dorsal microsetae; trichobothrium *st* of movable finger situated sub-basally; *sb*, *b* and *t* situated sub-distally, equidistant from each other. Chelal teeth homodentate and diastemodentate: fixed finger with 20 triangular teeth; movable finger with 19 triangular teeth (Fig. 30).

Cephalothorax: carapace (Fig. 27) 0.86 × longer than broad; with 4 corneate, widely separated eyes; epistome broad and serrate (Fig. 28); with 16 setae arranged 6: 4: 2: 2: 2; furrows apparently absent; the pre-ocular seta about half the length of other setae in anterior row; lyrifissures not visible. Chaetotaxy of coxae: 2 + 3: 4: 5: 4: 5; manducatory process with 2 acuminate distal setae, lateral seta about half length of medial seta; pedipalpal coxa with other 3 setae arranged in triangle; median maxillary lyrifissure slightly curved; coxae I with ca. 6 coxal blades on each side, set in transverse row near anterior coxal margin, each coxal blades apparently tripartite; intercoxal tubercle present, with 2 setae.

Abdomen: Tergites and sternites undivided; setae acuminate and arranged in irregular uniseriate rows. Tergal chaetotaxy: 2: 6: 6: 6: 6: 6: 6: 6: 6: 4: 4: 0. Sternal chaetotaxy: ?: (2) 6 (2): (?) ? (?): 8: 8: 9: 8: 6: 4: –: 2.

Genitalia: not visible.

Legs: arolium shorter than claws; claws striated.

Dimensions (mm): Female holotype: Body length ca. 1.92. Pedipalps: trochanter 0.235/0.125, femur 0.67/0.145, patella 0.29/0.145, chela 1.01/0.21, hand length 0.36, movable finger length 0.65. Chelicera 0.47/0.23, movable finger length 0.24. Carapace 0.48/0.56; anterior eye diameter 0.035, posterior eye diameter 0.035. Legs: not positioned to enable accurate measurements.

Remarks.—*Chthonius* (*Centrochthonius*) *schnitnikovi* was described from a single female collected from "Schlucht des Flusses Tujuk" (canyon of the Tujuk River) in the "Alexander-Gebirge". Fluss Tujuk is now known as the Tuyuk Vostochnyy, and the Alexander-Gebirge is the Kirghizsky Mountain Range (Fig. 2). The original description was rather basic, and the only illustrations (body dorsal and abdomen ventral) lack sufficient detail to establish the precise identity of the species. No further specimens have been recorded in the literature. The species was first described in the subgenus *Chthonius* (*Centrochthonius*), but it is unlikely that Redikorzev intended to regard *Centrochthonius* as a subgenus of *Chthonius* C.L. Koch, 1843. It is more likely that the manuscript was drafted prior to the extensive genus-level rearrangements undertaken by Chamberlin (1929b, 1930) and Beier (1932a, b), and included revised names as subgenera for some of the taxa described in the publication (Redikorzev 1934a). Apart from *C. schnitnikovi*, he also described two species in *Chelifer* (*Chelanops*) Gervais, 1849 and another in *Garypus* (*Geogarypus*) Chamberlin, 1930, most likely without intending to synonymise *Chelanops* and *Geogarypus* with *Chelifer* Geoffroy, 1762 and *Garypus* L. Koch, 1873, respectively. Some of these species were mentioned in an erratum (Redikorzev 1934b) but *C. schnitnikovi* wasn't listed.

The female holotype is in fair condition but is now rather bleached, making some morphological features difficult to discern. For example, there are either five or six cheliceral setae, but the precise number is uncertain. The sixth seta seems to be represented by an areole, with the seta absent, on both chelicerae. The precise morphology of the coxal blades is uncertain, as the coxae are pressed against each other making it difficult to discern the fine details. However, we can confirm that they are rather short and distally incised.

The right fixed chelal of the holotype is slightly damaged near trichobothria *est* and *it*, resulting in an apparently swollen surface. This is in fact an artefact but included to accurately represent the specimen.

The presence of only 16 carapaceal setae, including the lack of seta *Mm* (Fig. 27), and the shape of the coxal blades which are rather short, clearly confirms that *Ch. (Ce.) schnitnikovi* is a species of *Centrochthonius*.

The altitude based on georeferencing is roughly 2,100 m above sea level, similar to the other species in this genus. The specimen was taken from moss under junipers, a type of conifer.

Misidentified species of *Allochthonius*

The poor generic diagnosis for *Centrochthonius* (notably the wrong count for the carapace setae) has led to a number of misidentifications and erroneous identifications in the more recent past. Morikawa (1954, 1956, 1960) omitted this genus altogether in his revisions of the Japanese and Korean pseudoscorpion faunas, including the description of many new pseudotyrannochthoniid species, and Schuster (1966), Muchmore (1967) and Benedict & Malcolm (1970) followed the omission in their revisions of the North American pseudotyrannochthoniids. Based on his own generic concept, Beier (1979) placed a species of *Allochthonius* with 20 carapace setae from deciduous lowland forests in far eastern Russia (Primorsky Kray) in *Centrochthonius*. This species shares the typical configuration of the short, tripartite and distally spatulate coxal blades that are arranged on a small protuberance (as a "spray" or "fan") that is typical for the genus (e.g., Chamberlin 1929a, 1962; Morikawa 1960; Lee 1982; Sakayori 1999, 2002, 2014b, c; Hu & Zhang 2012; Gao & Zhang 2013; Zhang & Zhang 2014; Gao et al. 2016; Viana & Ferreira 2021) and the species was recently transferred to *Allochthonius* (Schwarze et al. 2022). A second misidentification was the description of *Centrochthonius sichuanensis* Schawaller, 1995 for a species from central China with 26 carapace setae and "9–10 serrate coxal blades on a single socle" (Schawaller 1995). The description of *A. sichuanensis* is accurate and we refer the reader to Schawaller (1995) but provide the original details, agreeing with Hu & Zhang (2011) who had transferred this species to *Allochthonius*.

Genus ***Allochthonius*** Chamberlin, 1929

Allochthonius Chamberlin, 1929b: 154.

Type species.—*Chthonius opticus* Ellingsen, 1907, by original designation

Allochthonius sichuanensis (Schawaller, 1995)

ZooBank LSID: http://zoobank.org/NomenclaturalActs/81069ED5-D497-4504-AA88-A3B9D132E119

Centrochthonius sichuanensis Schawaller, 1995: 1046–1048, figs. 1–5.

Allochthonius (Allochthonius) sichuanensis (Schawaller): Hu and Zhang, 2011: 2168, fig. 25

Type material.—See Schawallwer (1995).

Description.—See Schawaller (1995).

Remarks.—Schawaller (1995) described *A. sichuanensis* from 11 specimens that were collected in the Wolong National Nature Reserve, Wenchuan, Sichuan Province, China. The specimens were collected at 1,500 m altitude, presumably in forest habitats. Schawaller (1995) used the specimen of *Centrochthonius anatonus* sp. nov. (misidentified by him as *C. kozlovi*) and *C. ussuriensis* (actually *Allochthonius*, see above) to assign his specimens to this genus, noting that it has a very high number of 26 carapace setae, coxal blades on a protuberance and distantly spaced acute teeth, altogether common and/or diagnostic features for *Allochthonius*. The recent transfer by Hu & Zhang (2011) and listing in their species key of *Allochthonius* (Hu & Zhang 2012) is correct.

Allochthonius ussuriensis (Beier, 1979)

ZooBank LSID: http://zoobank.org/NomenclaturalActs/174de433-8c21-4781-b695-76445d19056c

Centrochthonius ussuriensis Beier, 1979: 554–556, fig. 2.

Allochthonius ussuriensis (Beier, 1979): Schwarze et al. 2022: 18.

Material examined.—RUSSIA: *Primorsky Kray*: 12 ♂, 1 ♀, Gornotaezhnoye, Mountain-taiga-Station, 43°41′19″N, 132°09′09″E, 144 m, 13 June 2010, sifting leaf litter, D. Harms, M.S. Harvey, M.M. Omelko (WAM T120640, T153614); 22 ♂, 1 ♀, 2 tritonymphs, same data except 43°42′19″N, 132°07′18″E, 206 m, 14 June 2010, deciduous forest in rocky gully, sifting leaf litter (WAM T146405, T146406, T153615); 2 ♂, 1 ♀, à l'est d'Ussuriysk, village Kamenushka [43°38′N, 132°14′E], 19 June 1992, S. Kurbatov (MHNG).

Description.—See Beier (1979).

Remarks.—*Centrochthonius ussuriensis* was described from specimens collected in Primorskiy Kray, eastern Russia (Beier 1979), with additional distribution records and figures supplied by Schawaller (1989, 1995). Newly collected specimens from this region have been examined for this study that have an increased number of carapace setae (8 setae on the anterior row, 6 setae in the ocular row, and more than 4 setae in the posterior row) and coxal blades which are raised on a mound and somewhat splayed, as found in *Allochthonius*. The species was recently transferred to *Allochthonius* (Schwarze et al. 2022) because it shares all diagnostic features of the genus.

DISCUSSION

Biogeography of *Centrochthonius* and related genera.—The taxonomy of pseudotyrannochthoniid genera is still confusing and the poor generic concepts render biogeographical interpretations very difficult, although recent genetic studies (Harms 2018; Harms et al. 2019) and taxonomic revisions (You et al. 2022) are slowly leading to a better understanding of the evolutionary history of this fauna. From the data now available based on careful examination of original type series and more recent specimen collections from all over the world, it is evident that the closest relatives of *Centrochthonius* are the genera *Spelaeochthonius* from eastern Asia and the species presently attributed to "*Pseudotyrannochthonius*" from the western U.S.A. All three genera share the unique synapomorphy of the absence of carapaceal seta *Mm* and coxal blades that sit subapically near the mesal margin of leg coxa I (not apically and on a protuberance such as in *Allochthonius*, or directly on the interior margin of the coxa such as in most of the Southern Hemisphere genera). *Spelaeochthonius* is probably the closest relative of *Centrochthonius* and its nine species are exclusively found in cave systems throughout Japan and Korea (You et al. 2022). The North American "*Pseudotyrannochthonius*" species occur in warm temperate forest systems with high annual rainfall (more than 800 ml per annum) and occupy leaf litter habitats (Benedict & Malcolm 1970). They range from northern California to northern Washington, although an outlier species has been recorded from Logan Canyon in Utah (Muchmore 1967). *Centrochthonius* is the only genus that appears to be restricted to high-altitude habitats with extreme climate conditions including regular frost and snow, although the cave habitats of *Spelaeochthonius* are also permanently cool. The American "*Pseudotyrannochthonius*" follows the general pattern of Southern Hemisphere pseudotyrannochthoniids that also occur in mesic lowland forests.

Trans-pacific distributions of organisms in the Northern Hemisphere have often been explained as an outcome of dispersal between the Palearctic and Nearctic, either via Trans-Beringian or Trans-Atlantic exchange using some of the land bridges or connections that existed through time, although comprehensive meta-analyses have highlighted substantial vicariance in old lineages, with Holarctic vicariance events generally being older than Asiamerican splits and often predating the late Cretaceous (Sanmartín et al. 2001). Ancient vicariance and substantial extinction in the Northern Hemisphere is also the likely scenario to explain the present-day distribution of the three pseudotyrannochthoniid genera that lack carapaceal seta *Mm* in the Holarctic region. Phylogenomic data indicate Pseudotyrannochthoniidae is an ancient and basal lineage of pseudoscorpions with possible origins in the Carboniferous or even Devonian (Benavides et al. 2019) and the fossil record also highlights extinction across its former distribution that was likely to have spanned the entire Laurasian landmass, with present-day restriction to refugia in Asia and the western U.S.A. (Fig. 1). Pseudotyrannochthoniidae are absent in Europe today but fossil species of both *Allochthonius* and *Centrochthonius* have recently been found in European succinite amber (Baltic and Bitterfeld amber, late Eocene – Miocene in age; see (Dunlop et al. 2018; Schwarze et al. 2022)) and these ambers preserve a fauna that thrived in warm temperate forest habitats with high precipitation, similar to the warm-temperate zoobiomes of East Asia and North America today (Sadowski et al. 2017). The pseudoscorpion diversity in both Baltic and Bitterfeld amber is highly diverse at both the family and generic levels (Ahrens et al. 2019) and includes families that are today only found in North America (e.g., Pseudogarypidae), the Southern Hemisphere (e.g., Feaellidae), or the Mediterranean of Europe (e.g., various neobisiids). The recent discovery of Pseudotyrannochthoniidae in European ambers and the link to their relatives in Asia is similar to patterns found in some harvestmen (e.g., the genus *Caddo*, Dunlop & Mitov 2009) or pill millipedes (Wesener 2019) that occur in European ambers but are extinct in Europe today and found only in Asia or North America. It is obvious from the palaeobotanical data that such invertebrate lineages persist today in mesic forest habitats that were more widespread before the Late Cenozoic Ice Age and excessive glaciation in parts of the Northern Hemisphere. It is interesting in this context that the fossil *Centrochthonius bitterfeldicus* from the Eocene of Europe probably lived in lowland forest habitats similar to those in Oregon and Washington (American "*Pseudotyrannochthonius*") and eastern Asia (*Allochthonius*) today, and not in extreme high-altitude habitats such as the Holocene fauna of *Centrochthonius*. The reasons for this may be ecological (but see Ecology, below). Certainly, based on the available area cladograms for the Holarctic and the fossil record we hypothesize *Spelaeochthonius* in eastern Asia as the most likely sister genus of *Centrochthonius* in central Asia and these two genera may be divided from North American "*Pseudotyrannochthonius*" by ancient (e.g., before the late Cretaceous) vicariance. This hypothesis requires future testing using a molecular framework for which specimens of *Centrochthonius* suitable for DNA sequencing need to be obtained. We furthermore highlight *Centrochthonius* as a relict lineage that had a much wider distribution in Eurasia before the Neogene, and a distribution that once encompassed at least parts of Europe.

Ecology of *Centrochthonius*.—In our revised generic framework *Centrochthonius* emerges as a psychrophilic genus that is restricted to forest habitats at high altitudes (2,000 m or higher). All specimens have been collected from moist leaf litter in forest habitats or gorges, typically between late spring (May – C. *anatonus*) and autumn (October – *C. cheni*) (July and August for C. *kozlovi* and *C. schnitnikovi*). The animals appear to be elusive, with only six Holocene specimens available for this study: for example, Schawaller (1991) listed more than a hundred specimens in other chthonioid genera (*Ditha*, *Lechytia*, *Tyrannochthonius* in the Chthoniidae) and similarly high numbers of other litter-dwelling pseudoscorpions (e.g., taxa that are nowadays included in the neobisiid genera *Bisetocreagris* Ćurčić, 1983 and *Stenohya* Beier, 1967) but only one specimen of *Centrochthonius* in his revisions of Himalayan pseudoscorpions (Schawaller 1983, 1987, 1991). Following this pattern, *C. cheni* is also known from a single individual and attempts to recollect this species have been unsuccessful (Gao, pers. comm.). There are several possibilities to explain rarity and one of these is niche-competition with other pseudoscorpions (suggested for the elusive North American *Pseudotyrannochthonius* by Benedict & Malcolm (1970)), specifically the speciose and morphologically more diverse neobisiids. A second possibility is that the animals are just difficult to collect or have activity patterns that lie outside the spring-autumn period when most of the sampling for pseudoscorpions occurs. The exclusive occurrence of *Spelaeochthonius*, the putative sister genus of *Centrochthonius*, in caves provides a possible explanation insofar as close relatives of *Centrochthonius* are obviously capable of extensive vertical migration and colonisation of deep soil strata. Too little is known about the latter genus but is it possible that these animals can only be found in upper soil and leaf litter during a short period of a year when climate conditions are favourable. The main activity period may even lie in winter or early spring, in particular since seasonality is known in other pseudotyrannochthoniids (e.g., Benedict & Malcolm 1970; Sato 1982). Based on our own field collections, an as yet undescribed genus from Tasmania and alpine eastern Australia shows similar ecological patterns and two described species ("*Pseudotyrannochthonius*" *tasmanicus* Dartnall, 1970 and "*P.*" *typhlus* Dartnall, 1970 – also presently misplaced in the polyphyletic *Pseudotyrannochthonius*) are local endemics of caves in Tasmania whereas epigean relatives occur in high-altitude habitats and are typically collected in spring, either via pitfall traps or direct collecting from leaf litter in rocky habitats. The animals seem to migrate vertically within the soil matrix and colonise karst frequently, which has led to a rich fauna of more than 10 undescribed cave species (Eberhard et al. 1991), but a wealth of epigean specimens are present in Australian museum collections that come from subalpine or alpine habitats and have been collected primarily using pitfall traps. Both *Centrochthonius* and *Spelaeochthonius* likely share some pre-adaptations towards their life in extreme habitats (e.g., resistance to cool micro-climates, preference for rocky habitats with deep soil rather than top litter). Activity predominantly in the cooler months of the year may also help to reduce ecological competition with other pseudoscorpions but, again, our conjectures are based on the scarce data available and our own field observations.

Two other aspects of ecology deserve mention. All taxonomic studies on Pseudotyrannochthoniidae suggest that species ranges are typically small, which has been confirmed in recent genetic studies (Harms 2018; Harms et al. 2019). *Centrochthonius* is unlikely to deviate from this pattern and the species described herein are likely confined to small areas surrounding their original habitats, e.g., single gorges that are embedded into the local geomorphology.

The second aspect is ecology over time. The extinct *C. bitterfeldicus* was found in amber that likely originates from a warm temperate forest system, similar to the lowland forest habitats occupied by *Allochthonius* in eastern Asia and "*Pseudotyrannochthonius*" in the western U.S.A. today. There is no evidence for major mountain ranges in the source area of Bitterfeld amber during the Paleogene or alpine/cool habitats that match those occupied by *Centrochthonius* in modern Asia today. Other pseudoscorpions preserved in Bitterfeld amber, as well as the harvestmen and spiders (e.g., Dunlop & Mitov 2009; Dunlop & Giribet 2013), rather point to a warm temperate to Mediterranean climate for the Bitterfeld amber deposit and its constituent paleofauna. Although we cannot exclude the possibility that the amber that contains the fossil *C. bitterfeldicus* was reworked and originates in a different area than most of the remaining Bitterfeld amber invertebrates, this hypothesis is somewhat less likely than an alternative scenario that suggests a shift in occupied habitats between the fossil and Holocene faunas, or occupation of more diverse habitats by *Centrochthonius* before the Neogene.

Morphology and variability.—The morphology of many pseudotyrannochthoniid taxa remains poorly documented, in particular at the generic level, and many of the original generic descriptions contain errors or omissions. *Centrochthonius* is a prime example and was ignored by all subsequent workers following Beier (1931) because the original description was brief and erroneous, but also because no specimens were available to other prolific pseudoscorpion taxonomists such as Joseph Chamberlin, who published major monographs on this order. The genus was also ignored by Morikawa (1960), who derived his own classification systems for Asian pseudotyrannochthoniids and recognised three subgenera in the single genus *Allochthonius*: *A.* (*Allochthonius*) for ophthalmic species with many carapaceal setae and coxal blades on a "socle" (meaning protuberance); *A.* (*Urochthonius*) for similar but eyeless or nearly eyeless species; and *Allochthonius* (*Spelaeochthonius*) for species with tassel-shaped coxal spines and 16 carapaceal setae (Morikawa 1954, 1956, 1960). Although Morikawa did not mention *Centrochonius*, we have found that *Centrochthonius* has the same number of carapaceal setae as *Spelaeochthonius*.

With our redefinition of generic limits in the recently resurrected *Spelaeochthonius* (You et al. 2022) and now *Centrochthonius*, we emphasize the importance of the coxal blades that differ drastically in both overall shape and fine morphology between the genera, as well as the number and position of the carapaceal setae. It is important that neither of these character systems is useful alone but generic concepts in the Laurasian fauna become much clearer when both characters are explored in conjunction. The coxal blades are grooming organs for the legs and pedipalp tips (Judson 1990) and not subjected to sexual selection such as, for example, the pedipalps in male spiders or penis morphology in male harvestmen. Coxal blade morphology may rather be linked to species ecology and the habitat type occupied by the organisms, and therefore subjected to other evolutionary modes.

The same is true for the carapaceal setae, with the loss of seta *Mm* being conserved across the three genera we have focussed on here; there is also a certain degree of homoplasy between some high-altitude species of *Allochthonius* and *Centrochthonius* insofar as these species tend to reduce the number of setae in the anterior or median rows of setae. There are no data on the biological importance of this character system or its role in evolution. Nonetheless, the combination of both characters and the classification derived from their combination makes sense both biogeographically and ecologically. Future genetic or genomic studies could now be used to test some hypotheses beyond taxonomy, such as timing the divergences for the Laurasian pseudotyrannochthoniid genera, correlating vicariance with paleoclimatic and/or geological events, and evaluate if, for example, *Centrochthonius* and *Spelaeochthonius* are indeed the outcome of a common Mesozoic radiation of pseudotyrannochthoniids that is now confined to karstic refugia (*Spelaeochthonius*) or high altitudes (*Centrochthonius*).

Certainly, some characters that have been used extensively by taxonomists in the past appear to be of little value following character evaluation, such as the division of *Allochthonius* into subgenera based on the absence or presence of eyes. *Spealeochthonius* consistently lacks eyes or their vestiges but *Centrochthonius* and "*Pseudotyrannochthonius*" from the U.S.A. consistently retain four eyes with lenses. In *Allochthonius* the case is different and overlapping conditions occur (e.g., *A. biocularis* Morikawa, 1956 from caves in Japan has two rudimentary eyes) which is why we consider this character of little use in dividing this genus further. We reject the subgeneric concept proposed by Morikawa (1954, 1956, 1960) and retained by subsequent workers (e.g., Hu & Zhang 2011; Viana & Ferreira 2021) and formally synonymise the subgenus *Allochthonius* (*Urochthonius*) Morikawa, 1954 with *Allochthonius* (**syn. nov.**). This redefines the genus for all pseudotyrannochthoniids with coxal blades that are on a common protuberance, together forming a "spray" or "fan", and a high number of carapaceal setae that is generally (with some exceptions) in the range of 18–28 setae. This taxonomic change results in four Holarctic pseudotyrannochthoniid genera that are clearly defined morphologically and can be explored in a wider (e.g., ecological or evolutionary) framework.

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