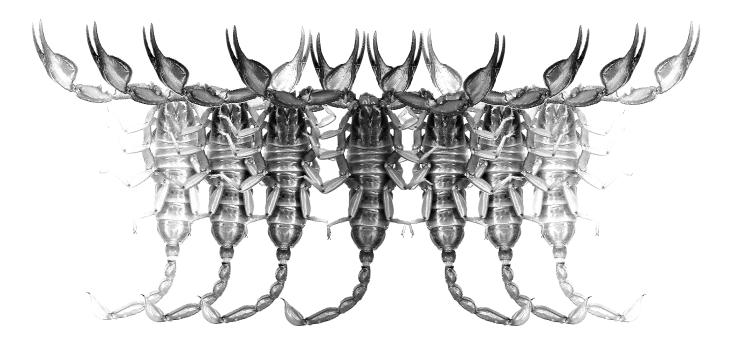
# Euscorpius

Occasional Publications in Scorpiology



Scorpions 2011

John L. Cloudsley-Thompson 90<sup>th</sup> Birthday Commemorative Volume

The First Record of Upper Permian and Lower Triassic Scorpions from Russia (Chelicerata: Scorpiones)

Victor Fet, Dmitry E. Shcherbakov & Michael E. Soleglad

## Euscorpius

### **Occasional Publications in Scorpiology**

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# The first record of Upper Permian and Lower Triassic scorpions from Russia (Chelicerata: Scorpiones)

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#### **Summary**

Several small fragments of fossil scorpions are reported from two localities in Vologda Province, Russia, representing the Upper Permian (Severodvinian, correlated to Wuchiapingian) (Isady) and Lower Triassic just above the Permian-Triassic boundary (Induan) (Nedubrovo). Most observed structures are not diagnostic at genus or family level. The Isady leg fragment possesses ungues (claws), which are both denticulated and setaceous, and resembles a Carboniferous *Eobuthus* sp. (Eobuthidae). It is the latest record of this type of ungues, which are known in some Paleozoic scorpions (extinct suborder Mesoscorpiones); all extant scorpions have smooth claws without denticulation or setation.

#### Introduction

The only record of a fossil scorpion from Russia (Fet et al., 2004) was based on a single femur fragment found in the Lower Carboniferous of the Moscow Coal Basin.

Kjellesvig-Waering (1986: 81) tentatively placed one Jurassic fossil from Ust'-Balei in Siberia in an extinct scorpion genus *Mesophonus* as "*M.* (?) *maculatus* (Brauer, Redtenbacher et Ganglbauer, 1889)" However, it is probably an immature cockroach, and indeed was described as such; see Fet et al. (2000: 595); Dunlop et al. (2007: 247).

Here, we report several scorpion fragments found in two localities in northern European Russia (Vologda Province): one Upper Permian (Severodvinian) (Isady) and another Lower Triassic (Induan), immediately above the Permian-Triassic boundary (Nedubrovo). The fossils of these two localities are separated by 8–10 Mya period.

As Dunlop et al. (2007) wrote in a recent review, "Scorpions are unusual among arachnids in that more Palaeozoic species have been described than Mesozoic and Tertiary ones." In contrast with numerous Carboniferous taxa, late Paleozoic and Mesozoic scorpion fossils are rare. Most of known Mesozoic forms are Cretaceous, which belong to the modern group Orthosterni (suborder Neoscorpiones; Carboniferous to the present) (Lourenço, 2001, 2002, 2003; Santiago-Blay et al., 2004a, 2004b; Baptista et al., 2006; Menon, 2007).

Some Cretaceous orthosterns are classified in modern families: Chaerilidae (100 Mya; Santiago-Blay et al., 2004a) and Chactidae and Hemiscorpiidae (110 Mya; Menon, 2007). Divergence of major orthostern lineages is assumed to be an early Mesozoic event (Soleglad & Fet, 2003; Baptista et al., 2006).

At the same time, very few Permian, Triassic, and Jurassic scorpions are known (Kjellesvig-Waering, 1986; Lourenço & Gall, 2004), although during this period a more ancient scorpion lineage, suborder Mesoscorpiones (Silurian–Jurassic), still co-existed with Neoscorpiones. Its last possible representative, *Liassoscorpionides*, is Jurassic (Dunlop et al., 2007). Any record of fossil scorpions from the late Paleozoic and early Mesozoic, therefore, is very important.

#### Material

The material studied was collected in 2005–2010 by expeditions of the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN). All specimen photographs were taken by D.E. Shcherbakov. See map and photographs of localities in Figure 1.

**Isady**, Sukhona River, Vologda Province, Russia, 60°37'N, 45°37'E; large lens of fluvio-lacustrine (presumably deltaic) deposits, lower part of Kalikino Member, Poldarsa Formation; latest Severodvinian Stage (correlated with the Wuchiapingian (Golubev, in press), ca. 258 Mya), Upper Permian. The insect assem-

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**Figure 1:** Geographic position of the localities yielding the scorpion remains. Isady (60°37'N, 45°37'E; photo by D. Kopylov) and Nedubrovo (60°03'N, 45°44'E; photo by E. Karasev).

blage of Isady is one of the greatest and most diverse ones for the Upper Permian (Tatarian), comprising over 2500 specimens assigned to at least 23 insect orders. Presence of scorpions in Isady deposits was mentioned by Sinitshenkova & Aristov (2010).

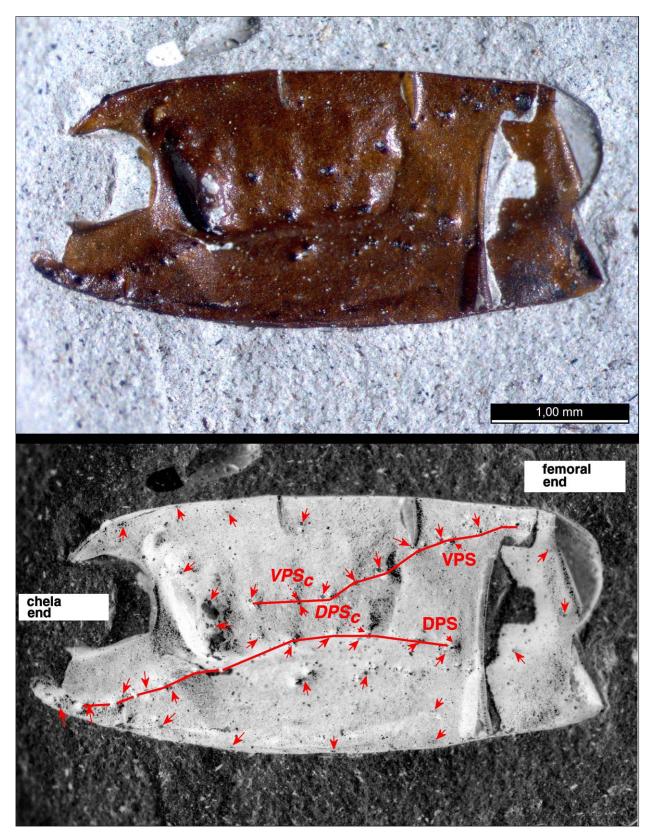
Three available scorpion fragments include: pedipalp patella (PIN 3840/986; Ó) (Fig. 2), leg tarsus with ungues (PIN 3840/2083; Ó) (Figs. 3–6), and two mesosomal tergites (one incomplete) (PIN 3840/987; Ó) (Fig. 7).

**Nedubrovo**, Kichmenga River (left tributary of the Yug River), Vologda Province, Russia, 60°03′N, 45°44′E; siltstones of lacustrine genesis, Nedubrovo Member, Vokhmian Horizon, Vetlugian Series; earliest Induan immediately above the Permian-Triassic boundary (Krassilov & Karasev, 2009), Lowermost Triassic, ca. 250 Mya.

Two fragments discussed below include: leg basitarsus (PIN 4812/46) (Fig. 8) and a metasomal segment (PIN 4812/44) (Fig. 9). Several other fragments bear no characters necessary for their interpretation.

#### **Comments on Preservation**

The exceptional and excellent preservation of scorpion cuticle (mainly in Paleozoic assemblages) is unique among arthropods, and has been described for a number of sites in Europe and North America (Bartram et al., 1987; Jeram, 2001). In some assemblages, *only* scorpion cuticles are present. Such preservation could be related to the unusual stability against biodegradation of the so-called hyaline cuticle – the upper layer of scorpion cuticle (Jeram, 2001).



**Figure 2:** PIN 3840/986, Isady, left pedipalp patella, internal view (bottom edge is dorsal surface). Fossil (top) and hypothesized interpretation of structures (bottom). Red lines outline the Dorsal Patellar Spur (*DPS*<sub>c</sub>) and Ventral Patellar Spur (*VPS*<sub>c</sub>) carinae, and red arrowheads indicate setal areolae. DPS and VPS are also indicated accompanied by setal areolae.

#### Morphology

#### Isady specimens

Pedipalp patella (Fig. 2). Length (top edge) 4.17 mm, depth (centered) 1.87 mm. The left pedipalp patella, an internal view, is illustrated in Fig. 2. The determination as a left patella is based on the shape of the two interconnecting sockets of the segment's ends as well as the slope of the proposed Dorsal Patellar Spur (DPS<sub>c</sub>) carina (for comparison see several Recent scorpion right patellae in Soleglad & Fet (2003: figs. 92-107)). The two internal carinae,  $DPS_c$  and  $VPS_c$ , are clearly visible where each granule is accompanied by a setal areola. The indicated Dorsal Patellar (DPS) and Ventral Patellar (VPS) Spurs (terminology first introduced by Soleglad & Sissom (2001: 59-62)) are determined solely by their terminal positions in the carinae, not necessarily by there increased sizes. Interestingly, as reported by Soleglad & Sissom (2001), each patellar spur is accompanied by a somewhat stout seta at its base, which makes for easy identification even if the spur is small or near obsolete. In this fossil specimen, each granule has a setal areola at its base and most are approximately of the same size; in VPSc, larger and smaller areolae alternate.

Leg tarsus (Figs. 3–6). Length (top edge including lobe) 5.55 mm, ungue (approximate) 2.21 mm. The leg tarsus (lateral view) is illustrated in Figures 3-6. The determination of which leg it is, or the perspective, internal or external, is not possible. This structure is clearly a leg tarsus, as indicated by well formed ungues (claws), the shape of the tarsus itself, and the median row of ventral spinules (there is usually some kind of spinule and/or seta formation on the ventral surface of a leg tarsus). The ventral spinule row is composed of eleven somewhat stout, short, carinate, slightly pigmented spinules curving towards the distal aspect of the segment. The distal ventral aspect of the tarsus segment appears to have a rounded lobe that extends distally towards the ungues. The lobe, presumably matched on the other lateral side, is suggestive of the lobes exhibited in Recent scorpion subfamily Diplocentrinae (family Scorpionidae). The ungues are stout, long and about one-half the length of tarsus segment itself. Of particular interest is the presence of well defined, unequal, flat, canaliculate denticles on the ventral surface of the curved edges of the two ungues, at least six, maybe seven in number. Also of interest is the presence of setal areolae on the ungues itself. A posttarsus structure (dactyl) is relatively short, acute (its apex somewhat damaged at preparation). See Discussion for more details on ungues and posttarsus.

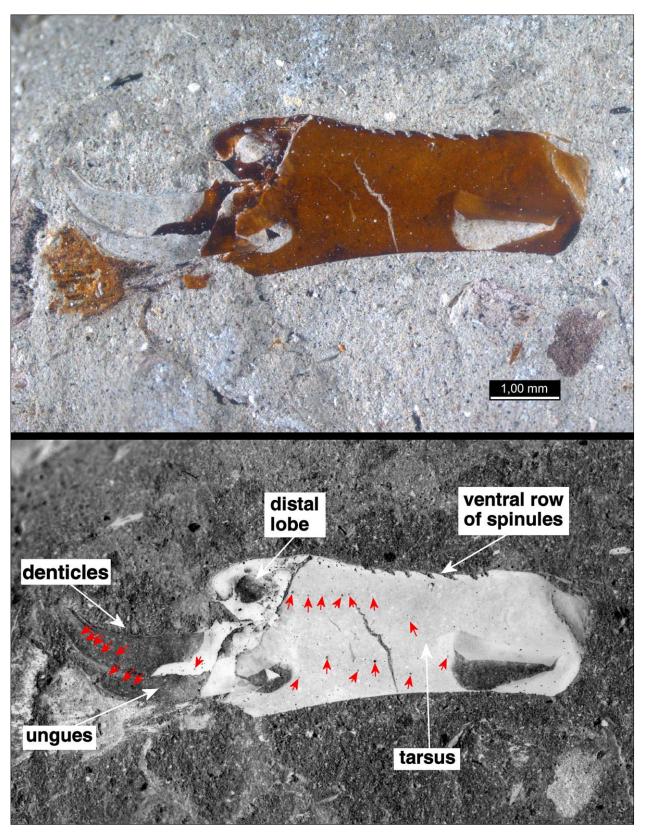
Mesosomal tergites (Fig. 7). Width (top sclerite) 3.53 mm. Two mesosomal segments are shown in Figure 7, presumably dorsal tergites. Which mesosomal segments these are, cannot be determined. These structures are somewhat smooth, lacking significant granulation or carinal structures. Interestingly, the larger sclerite (figure top) is equipped with a row of delicate closely positioned granules on its border. The smaller sclerite appears to have broken off the larger sclerite, but close examination of its edge bordering the larger sclerite reveals a smooth even sclerotized margin, which implies it is a separate sclerite. The lateral portions of both structures are absent.

#### Nedubrovo specimens

Leg basitarsus (Fig. 8). Length (centered) 3.73 mm. A lateral view of a leg basitarsus is shown in Figure 8. The determination of which leg it is, or the perspective, internal or external, is not possible. As with the other structures discussed in this paper, the basitarsus is covered with setal areolae. A row of sparsely spaced spinules is present on the external edge of this segment. These spinules are robust in form with the distal tips somewhat tapered and pigmented, darker than their base. There are four intact spinules and traces of a base of the fifth one.

At the base of basitarsus is an enlarged spinule, roughly three times the size of the other spinules. As with the line of spinules the distal tip of this enlarged spinule is slightly tapered and pigmented. We interpret this enlarged spinule as a *tibial spur* since it overlies the basitarsus, the wide, cushion-shaped, more sclerotized base visible. See Discussion for more details on tibial spurs.

Metasomal segment (Fig. 9). Length (centered, to ridge adjacent to ISC-sleeve) 5.61 mm. The carinal structure seen on this segment indicates that this is probably a portion of a metasomal segment. In particular, the intersegmental connecting sleeve (the term is introduced here) is visible (left side of the figure), which leads us to believe that this is the anterior end of the segment. For comparison, see Soleglad & Fet (2003: figs. 6-7) for several illustrations of dorsal views of metasomal segment IV of Recent scorpion families Vaejovidae and Chactidae. It is not possible to determine, which of five metasomal segments it is. As indicated by the hypothesized identification of carinae, the segment portion seen in Fig. 9 is a dorsal view with the distal end (i.e., the telson end) situated at the right of the figure. In this interpretation, we see both dorsal carinae (the upper only partially visible), the dorsolateral carina on one side, and two well developed transverse carinae connecting the two dorsal carinae at both ends. Most granules comprising the carinae are all of similar



 $\textbf{Figure 3:} \ \ PIN\ 3840/2083, Isady, leg\ tarsus, lateral\ view.\ Fossil\ (top)\ and\ hypothesized\ interpretation\ of\ structures\ (bottom).\ Red\ arrowheads\ indicate\ setal\ areolae.$ 

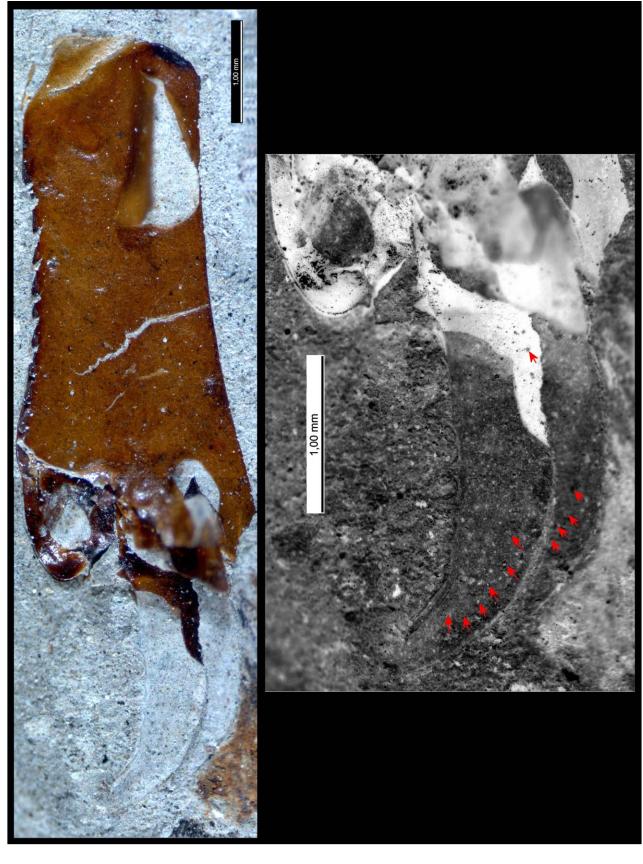
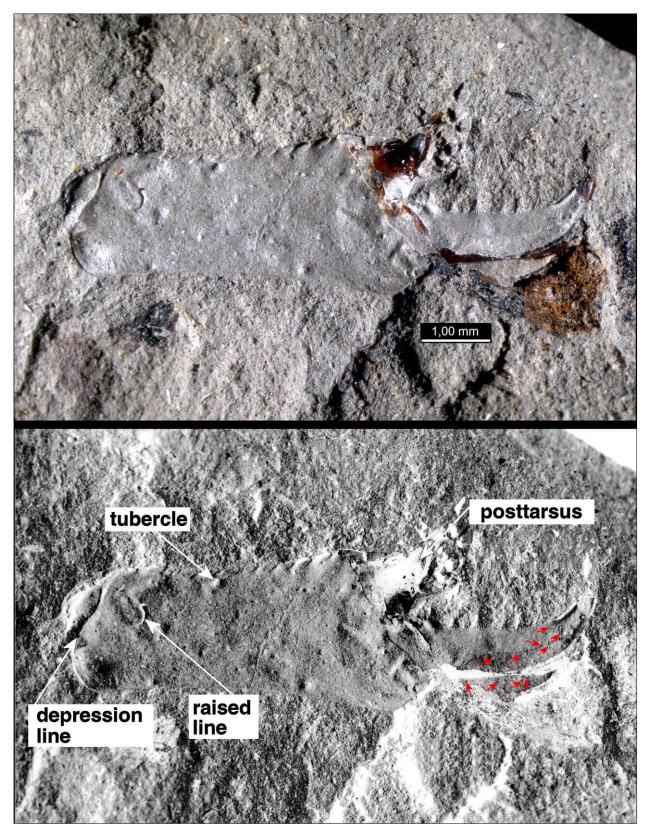


Figure 4: PIN 3840/2083, Isady, leg tarsus, lateral view. Fossil (top) and closeup of ungues (bottom). Red arrowheads indicate setal areolae.



**Figure 5:** PIN 3840-2083, Isady, leg tarsus, lateral view, counterpart. Fossil (top) and hypothesized interpretation of structures (bottom). Red arrowheads indicate setal areolae.

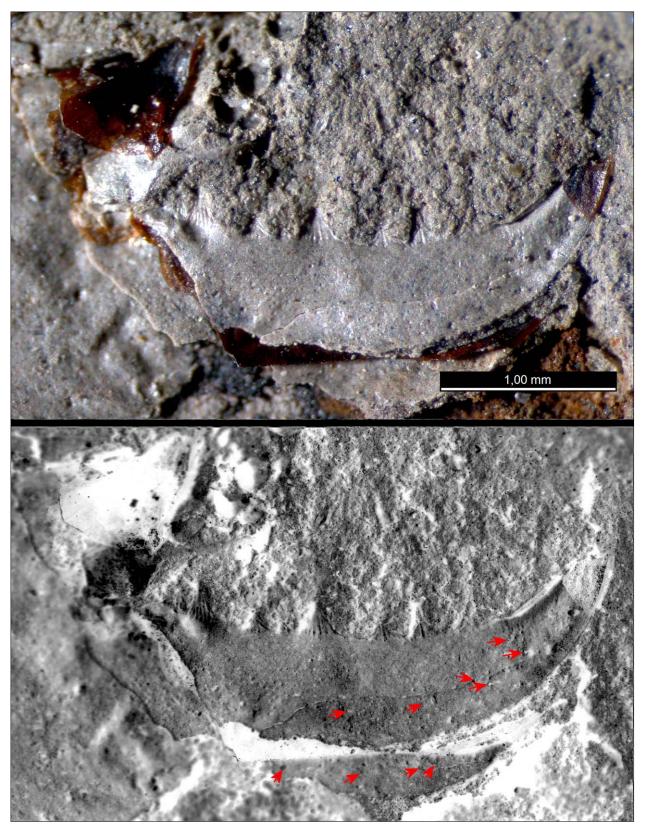
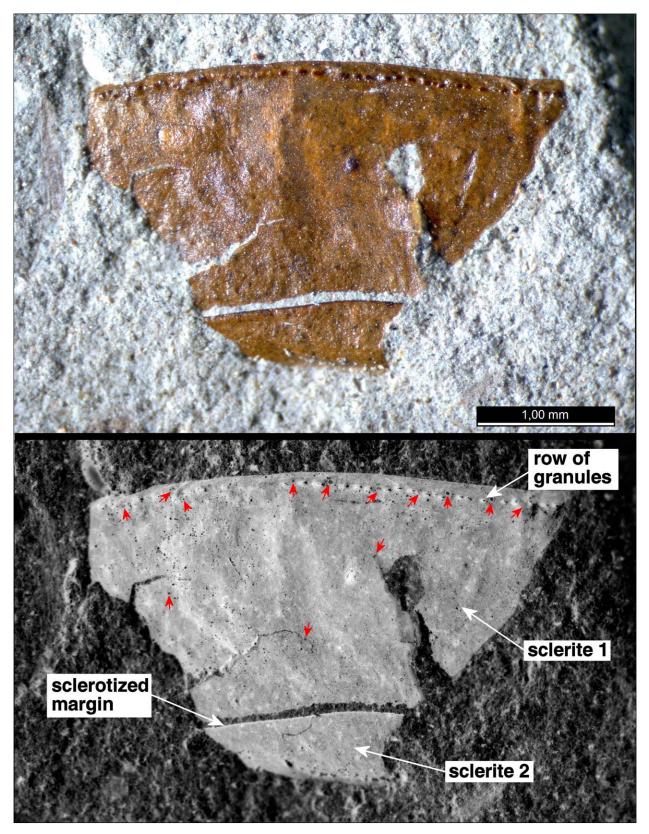


Figure 6: PIN 3840/2083, Isady, leg tarsus, lateral view, counterpart. Fossil (top) and closeup of ungues (bottom).



**Figure 7:** PIN 3840/987, Isady, two mesosomal tergites (one mostly incomplete). Fossil (top) and hypothesized interpretation of structures (bottom). Red arrowheads indicate setal areolae.

size (some approximately twice larger than others); there is no indication of an elongated terminal spine as seen in many Recent scorpions. The intercarinal area between the dorsal carinae is covered with granules of various sizes, roughly the same size as those populating the carinae.

#### **Discussion**

Our fragments do not seem to match any of the known Triassic scorpion families: Mesophonidae from England (Wills, 1947; Kjellesvig-Waering, 1986), or Protobuthidae and Gallioscorpionidae recently described from France (Lourenço & Gall, 2004). Lack of diagnostic features in discovered Russian fragments does not allow one to classify them confidently to any known genus or family; for the same reason, no new taxa can be described.

The Isady leg tarsus, judging from its ungue structure, possibly belongs to extinct suborder Mesoscorpiones, and resembles a Carboniferous *Eobuthus* sp. (Eobuthidae). Patella and tergites are not diagnostically informative. For the Nedubrovo specimens, basitarsus and metasomal segment are not diagnostic at any level.

Below, we discuss some of the structures described above as they relate to our diagnostic knowledge of extinct and extant scorpions.

#### Isady specimens

Pedipalp patella. Found already in the Carboniferous scorpion family Palaeopistacanthidae, the two internal carinae are more typical of Recent scorpions: Jeram (1994a: 535) provided detailed information on the patella carinal development for the Carboniferous scorpion Compsoscorpius elegans: "... The precise number of carinae cannot be established in the flattened fossil material, but at least seven were present. Two internal carinae bear particularly large tubercles, each carrying a single setal follicle ..." Certainly, Jeram was referring to both patellar spurs, each with a single seta. This implies that these spurs are not a recent development in the extant scorpions.

Ungues. The fragment 3840/2083 (Figs. 3–6) possesses two notable features of ungues (claws), which are both denticulated and setaceous. While all extant scorpions have smooth claws (ungues) without any denticulation and setation, one or both of these features are known from a number of Paleozoic (mainly Carboniferous) forms. Our Upper Permian fragment is the latest record of this type of ungues in scorpions.

Wills (1925: 91; text-fig. 3A; Plate 3, fig. 1) was the first to illustrate both a denticulated and setaceous ungue in a Carboniferous "Eobuthus sp." from England (see

our Fig. 10, a). He called it "a claw unlike any so far described from either fossil or living scorpions. ... The tarsus... carries a large toothed claw, near the distal end of which was a bunch of small sensory setae, that are represented by hair-facets. One seta is still in place... No such claw has been ever described from among fossil scorpions, which have always been illustrated with simple claws as in the recent forms".

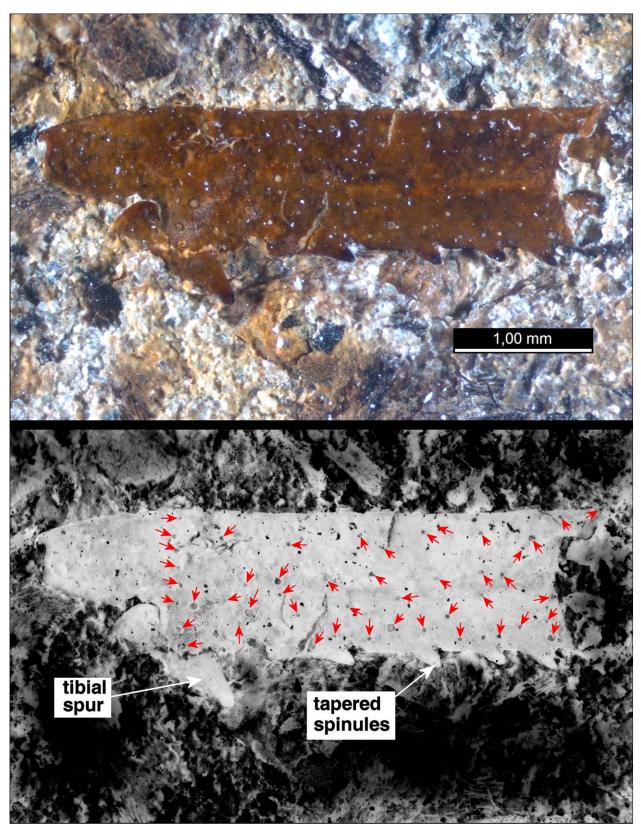
Immediately after Wills's article was published, Birula (1925: 132) discussed this remarkable structure noting: "one of the claws, probably external, and well-developed, has serrations on ventral edge, which is absent in extant scorpions" (translated from Russian). In 1926 (fig 2), Birula reproduced Wills's illustration. This specimen was finally described by Wills (1959) as *Pareobuthus salopiensis* Wills, 1959, type specimen of *Pareobuthus*. He mentions (p. 269) "claws (one only preserved) curved, with spiny teeth on inner side and a bunch of setae near tip". Kjellesvig-Waering (1986) only briefly mentioned this specimen, without any illustrations, and placed it in family Pareobuthidae.

Later, Wills (1959) studied another non-orthostern, *Lichnophthalmus pulcher* [now *Eoscorpius pulcher* (Petrunkevich, 1949), Eoscorpiidae, Upper Carboniferous, England], and gave remarkably good figures of their denticulated claws (1959, see our Fig. 10b, which also shows a spectacular "dagger" development of post-tarsus). He described (Wills, 1959: 280–281) "a pair of claws, toothed on their inner sides... [Leg I]: armed on their inner sides, the smaller with four and the larger with five teeth. They carried a few setae near their sharp, curved ends.... [Leg II]... large spines near the bases of the claws... [Leg IV]... the claws each carrying four teeth." Kjellesvig-Waering (1986) has the same species illustrated in his text-fig. 77, with text p. 180: "claw... armed with small denticles on the underside".

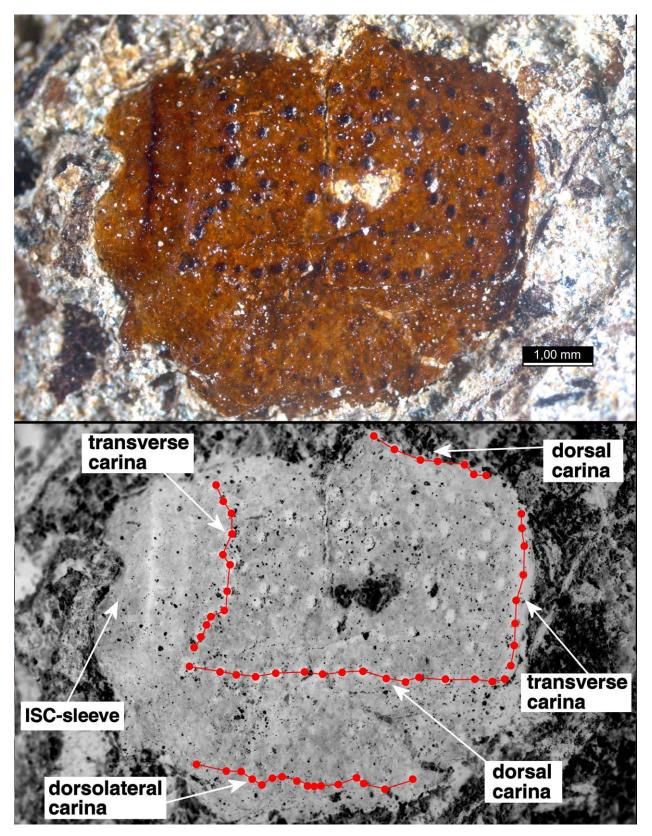
Wills (1960) also observed denticulated ungues in two other unidentified Carboniferous scorpions (text-fig. 22; Plate 54) as well as both denticulated and setaceous ungues in *Mazoniscorpio mazoniensis* Wills, 1960 (Plate 50). The latter was synonymized with *Palaeobuthus distinctus* Petrunkevitch, 1913 by Kjellesvig-Waering (1986: 138, 140), although ungues in the holotype of *P. distinctus* are not depicted as denticulated and setaceous by Kjellesvig-Waering (1986: text-fig. 55).

Five more Upper Carboniferous taxa with setaceous and/or denticulated ungues were described by Kjellesvig-Waering (1986):

- (a) *Antracochaerilus palustris* Kjellesvig-Waering, 1986 (text-fig. 63; p. 150: "the claws are ...covered with small pits, very likely setaceous");
- (b) *Boreoscorpio copelandi* Kjellesvig-Waering, 1986 (text-fig. 65; p. 156: "...two large, wide spines or serrations on the inner part of the ventral arc of the claw");



**Figure 8:** Fossil PIN 4812/46, Nedubrovo, leg basitarsus, lateral view. Fossil (top) and hypothesized interpretation of structures (bottom). Red arrowheads indicate setal areolae.



**Figure 9:** Fossil PIN 4812/44, Nedubrovo, metasomal segment, dorsolateral view; strong carinae visible. Fossil (top) and hypothesized interpretation of structures (bottom). Red dotted lines outline identified carinae. Intersegmental connecting (ISC) sleeve is situated at the segment's anterior end.

- (c) *Eobuthus cordai* Kjellesvig-Waering, 1986 (text-fig. 68, p. 160: "...ungues...are large, falcate, and with traction spines on the underside"); *Eobuthus* also has possible setae on ungues and lobe (Text-fig 68 D, E; areolae shown as punctations) (see our Fig. 10c);
- (d) Paraisobuthus duobicarinatus Kjellesvig-Waering, 1986 (text-fig. 90, p. 206: "claws...with a single row of sharp spines on the ventral side. The spines are perpendicular to the shaft of the ungues, thus assuring the greatest traction against the substrate");
- (e) *Waterstonia airdriensis* Kjellesvig-Waering, 1986 (text-fig. 99, p. 224: "the claws are straight and quite long... are covered with setal openings, revealing that they were rather hirsute").

In total, denticulation and setation on ungues is expressed in at least 10 different Carboniferous species of scorpions. The identified forms with one or both of these traits belong to eight genera and eight families: Anthracochaerilus (Antracochaerilidae), Boreoscorpio (Isobuthidae) Eobuthus (Eobuthidae), Eoscorpius (Eoscorpiidae), Palaeobuthus (=Mazoniscorpio) (Palaeobuthidae), Paraisobuthus (Paraisobuthidae), Pareobuthus (Pareobuthidae), and Waterstonia (Waterstoniidae) (family placement of Kjellesvig-Waering, 1986).

It is not clear where all these Carboniferous genera and families belong in scorpion phylogeny, since no consensus exists in high-level grouping of fossil scorpions. Stockwell (1989: 285) placed at least four of the abovelisted genera (Eobuthus, Eoscorpius, Paraisobuthus, and Pareobuthus) in his distinct (extinct??) suborder Mesoscorpionina, while listing Anthracochaerilus, Boreoscorpio, Palaeobuthus and Waterstonia as "Scorpiones incertae sedis".

Recently, Dunlop et al. (2008), in their study of *Eoscorpius* sp., noted that "Jeram (1994b) resolved relationships among the so-called orthostern genera – the most derived Palaeozoic forms – leading up to the modern scorpion crown-group. What has not been addressed in detail is the position of various putative mesoscorpion and/or palaeostern genera (including *Eoscorpius*) which represent the most frequently encountered Carboniferous scorpions."

Kjellesvig-Waering (1986: 19) speculated about denticulated ungues in fossil scorpions: "In Carboniferous times the development of the terminal joints reached its greatest diversity. Some scorpions, such as *Eoscorpius, Eobuthus, Isobuthus*, etc. developed large curved claws that were armed with small spines on the ventral side. This development, however, occurred as early as Middle Silurian, as it is present in the Wenlockian *Allopalaeophonus* (see text-fig. 17C). These claws could only be adapted for holding onto some object, such as underwater roots, leaves, stems, etc, present at swamp forests. All of these scorpions were ... water-dwellers breathing through gills. We could assume

that some of these scorpions lived among the underwater roots and trunks of trees and other plants, but were capable of excursions above water on these plans, thus occupying the same position as many crabs living today".

Assumptions on aquatic or amphibious nature of Paleozoic scorpions were based on Kjellesvig-Waering's (1986) interpretation of their respiratory system as gills. Dunlop et al. (2007), however, warn against accepting a mode of life for which the morphological evidence was largely equivocal.

At the same time, *none* of the terrestrial (lungbreathing) Orthosterni (*sensu* Jeram, 1994a, 1994b, 1998) starting from Carboniferous to extant scorpions are known to have setaceous and/or denticulated ungues. In our opinion, it is quite possible that the Isady fossil belongs to the extinct scorpion suborder Mesoscorpiones. It represents the latest record of this type of ungues.

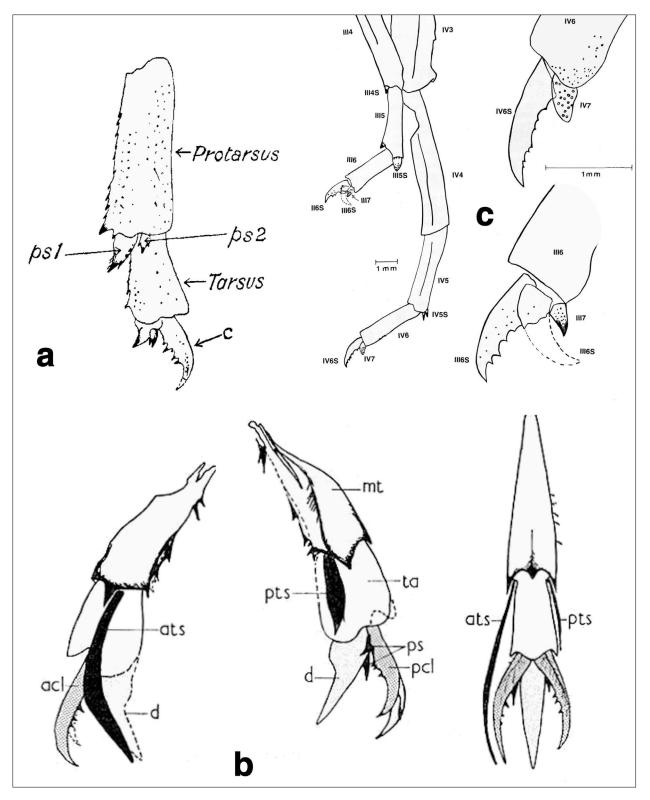
Note that Kjellesvig-Waering (1986) mentioned also denticulation in the Silurian *Allopalaeophonus*, which belongs to a more ancient scorpion lineage than all other abovelisted forms (Protoscorpiones of Stockwell, 1989; or Palaeophonidae of Jeram, 1998). Denticulation and setation of ungues appear, therefore, to be apomorphies of some extinct groups, which possibly were derived more than once. Denticulation of ungues is common in other arthropod groups; among arachnids, it is well-documented in spiders. A similar trait ("fimbriated claws") is already known in the Middle Devonian (386 Ma) *Attercopus fimbriunguis*, first described as a spider, and then placed in the order Uraraneida, a sister group to spiders (Selden et al., 2008).

Posttarsus. Extant forms have a variably shaped median claw (unguicular spine, dactyl) between ungues. This structure is well developed, often exaggerated (Fig. 10b), in many fossil scorpions, not only Orthosterni. Wills (1925, 1959, 1960) used for it a German term "Gestachel", and Kjellesvig-Waering (1986) also called it a "posttarsus, or heel" and described it e.g. as "rounded and subtriagular, and acts as a heel" (Anthracochaerilus, text-fig. 63B) or "very short, setaceous and triangular" (Eobuthus, text-fig. 68E, see our Fig. 10c).

Judging from its posttarsus and ungue structure, the Isady leg fragment resembles a Carboniferous *Eobuthus* sp. (Eobuthidae).

#### Nedubrovo specimens

*Tibial spur*. The presence of a tibial spur is generally considered a primitive trait in Recent scorpions; it is already present in many extinct taxa, not only Orthosterni, on various leg pairs. While the tibial spur is



**Figure 10:** Examples of ungues (with denticulation and setation) and posstarsus (=Gestachel, dactyl, unguicular spine, median claw) in Carboniferous scorpions: **a.** *Pareobuthus salopiensis* (after Wills, 1925, fig. 2, in part); **b.** *Eoscorpius pulcher* (after Wills, 1959, text-fig. 6, in part); **c.** *Eobuthus cordai* (after Kjellesvig-Waering, 1986, text-fig. 68, in part). See text for details.

found in many extinct orthostern scorpions, e.g., Compsoscorpius (Jeram, 1994a: text-fig. 5-D), Palaeoburmesebuthus (Santiago-Blay et al., 2004b), and Pulmonoscorpius (Jeram, 1994b), there is a great variability seen also in Recent scorpions, including loss. In the primitive parvorders, we see tibial spurs on legs III-IV in Pseudochactida (absent in a cave adapted species, Vietbocap canhi Lourenço et Pham, 2010), absent in Chaerilida, and variable in Buthida (Soleglad & Fet, 2003). In Buthida, tibial spurs are absent in most New World genera, and variable within the Old World members, although showing consistency across many genera. In certain Old World psammophilic genera (e.g., Apistobuthus, Liobuthus, etc.) we see either a reduction or the complete absence of these spurs, presumably due to habitat adaptation. Finally, we find tibial spurs on legs III-IV in the iuroid genus Calchas (Fet et al., 2009: fig. 16). We consider the Iuroidea by far the most primitive of the three superfamilies comprising parvorder Iurida; Calchas and its sister genus Iurus, in particular, are quite interesting in this context.

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#### References

- BAPTISTA, C., J. A. SANTIAGO-BLAY, M. E. SOLEGLAD & V. FET. 2006. The Cretaceous scorpion genus, *Archaeobuthus*, revisited (Scorpiones: Archaeobuthidae). *Euscorpius*, 35: 1–40.
- BARTRAM, K. M., A. J. JERAM, & P. A. SELDEN. 1987. Arthropod cuticles in coal. *Journal of the Geological Society of London*, 144: 513–517.
- BIRULA, A. 1925. (Sur la morphologie extérieure des scorpions fossiles et vivants). *Comptes Rendus de l'Académie des Sciences de l'URSS*, 10: 131–134 (in Russian).
- BIRULA, A. 1926. Zur äusseren Morphologie der fossilen und recenten Skorpione. *Zoologisher Anzeiger*, 67(1–2): 61–67
- BRAUER, F., J. REDTENBACHER & L. GANG-LBAUER. 1889. Fossile Insekten aus der Jura-

- formation Ost-Sibiriens. Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg. VIIe série, 36(15): 1–22.
- DUNLOP, J. A. 2002. Character states and evolution of the chelicerate claws. Pp. 345–354 *In*: Toft, S. & N. Scharff (eds.), *European Arachnology* 2000. Aarhus: Aarhus University Press.
- DUNLOP, J. A., C. BRAUCKMANN & H. STEUR. 2008. A Late Carboniferous fossil scorpion from the Piesberg, near Osnabrück, Germany. *Fossil Record*, 11(1): 25–32
- DUNLOP, J. A., C. KAMENZ, & G. SCHOLTZ. 2007. Reinterpreting the morphology of the Jurassic scorpion *Liassoscorpionides*. *Arthropod Structure* and *Development*, 36: 245–252.
- FET, V., W. D. SISSOM, G. LOWE & M. E. BRAUN-WALDER. 2000. *Catalog of the Scorpions of the World (1758–1998)*. New York: New York Entomological Society, 690 pp.
- FET, V., M. E. SOLEGLAD & F. KOVAŘÍK, 2009. Etudes on iurids, II. Revision of genus *Calchas* Birula, 1899, with the description of two new species (Scorpiones: Iuridae). *Euscorpius*, 82: 1–72.
- FET, V., M. E. SOLEGLAD, YU. V. MOSSEICHIK & D. E. SHCHERBAKOV. 2004. A scorpion from a peatbog: the first arthropod fossil from the Late Viséan of the Moscow Coal Basin. *Euscorpius*, 13: 1–5.
- GOLUBEV, V. K. (in press). Late Permian fossil animal and plant locality Mutovino (=Isady) at the Sukhona River, Vologda Province: historical geology. *Paleontological Journal*.
- JERAM, A. J. 1994a. Carboniferous Orthosterni and their relationship to living scorpions. *Palaeontology*, 37: 513–550.
- JERAM, A. J. 1994b. Scorpions from the Visean of East Kirkton, West Lothian, Scotland, with a revision of the infraorder Mesoscorpionina. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, 84(3–4): 283–299.
- JERAM, A. J. 1998. Phylogeny, classification and evolution of Silurian and Devonian scorpions. Pp. 17–31 in Selden, P.A. (ed.) Proceedings of the 17<sup>th</sup> European Colloquium of Arachnology, Edinburgh 1997. British Arachnological Society, Burnham Beeches, Bucks.

- JERAM, A. J. 2001. Paleontology. Pp. 370–392 in Brownell, P. H. & G.A. Polis (eds.) Scorpion Biology and Research. Oxford: Oxford University Press.
- KJELLESVIG-WAERING, E. N. 1986. A Restudy of the Fossil Scorpionida of the World. (Palaeontographica Americana, 55). Organized for publication by A. S. Caster & K. E. Caster. Ithaca, New York: Paleontological Research Institution, 287 pp.
- KRASSILOV, V. & E. KARASEV. 2009. Paleofloristic evidence of climate change near and beyond the Permian–Triassic boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 284: 326–336.
- LOURENÇO, W. R. 2001. A remarkable scorpion fossil from the amber of Lebanon. Implications for the phylogeny of Buthoidea. *Comptes Rendus de l'Académie des Science, Paris*, 332: 641–646.
- LOURENÇO, W. R. 2002. The first scorpion fossil from the Cretaceous amber of Myanmar (Burma). New implications for the phylogeny of Buthoidea. *Comptes Rendus Palevol*, 1: 97–101.
- LOURENÇO, W. R. 2003. The first scorpion fossil from the Cretaceous amber of France. New implications for the phylogeny of Chactoidea. *Comptes Rendus Palevol*, 2(3): 213–219.
- LOURENÇO, W. R. & J.-C. GALL. 2004. Fossil scorpions from the Buntsandstein (Early Triassic) of France. *Comptes Rendus Palevol*, 3(5): 369–378.
- MENON, F. 2007. Higher systematics of scorpions from the Crato formation, Lower Cretaceous of Brazil. *Palaeontology*, 50: 185–195.
- SANTIAGO-BLAY, J. A., V. FET, M. E. SOLEGLAD & S. R. ANDERSON. 2004a. A new genus and subfamily of scorpions from Lower Cretaceous Burmese amber (Scorpiones: Chaerilidae). *Revista Ibérica de Aracnología*, 9:3–14.
- SANTIAGO-BLAY, J. A., V. FET, M. E. SOLEGLAD & P. R. CRAIG. 2004b. The second Cretaceous

- scorpion specimen from Burmese amber (Arachnida: Scorpiones). *Journal of Systematic Palaeontology*, 2(2): 147–152.
- SELDEN, P. A., W. A. SHEAR & P. M. BONAMO. 1991. A spider and other arachnids from the Devonian of New York, and reinterpretation of Devonian Araneae. *Palaeontology*, 34(2): 241–281.
- SINITSHENKOVA, N. D. & D. S. ARISTOV. 2010. New Permian stoneflies of the family Palaeonemouridae (Insecta: Perlida = Plecoptera) from the Isady locality. *Paleontological Journal*, 44(1): 49–52
- SOLEGLAD, M. E. & V. FET. 2003. High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). *Euscorpius*, 11: 1–175.
- SOLEGLAD, M. E. & W. D. SISSOM, 2001. Phylogeny of the family Euscorpiidae Laurie, 1896: a major revision. Pp. 25–111 in V. Fet & P.A. Selden (eds.). *Scorpions 2001. In Memoriam Gary A. Polis.* Burnham Beeches, Bucks: British Arachnological Society.
- STOCKWELL, S. A. 1989: Revision of the Phylogeny and Higher Classification of Scorpions (Chelicerata). Ph. D. Dissertation, University of California, Berkeley. Published by University Microfilms International, Ann Arbor, Michigan.
- WILLS, L. J. 1925. The morphology of the Carboniferous scorpion, *Eobuthus* Fritsch. *Journal of the Linnean Society, Zoology*, 36 (241): 87–97.
- WILLS, L. J. 1947. A Monograph of British Triassic Scorpions. The Palaeontographical Society, London (Vols. 100 & 101), 137 pp.
- WILLS, L. J. 1959. The external anatomy of some Carboniferous 'scorpions'. Part 1. *Palaeontology*, 1(4): 261–282.
- WILLS, L. J. 1960. The external anatomy of some Carboniferous 'scorpions'. Part 2. *Palaeontology*, 3(3): 276–332.