

ARTÍCULO:

**A redescription and family placement of *Uintascorpio* Perry, 1995 from the Parachute Creek Member of the Green River Formation (Middle Eocene) of Colorado, USA (Scorpiones: Buthidae)**

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ARTÍCULO:

**A REDESCRIPTION AND FAMILY PLACEMENT OF *UINTASCORPIO* PERRY, 1995 FROM THE PARACHUTE CREEK MEMBER OF THE GREEN RIVER FORMATION (MIDDLE EOCENE) OF COLORADO, USA (SCORPIONES: BUTHIDAE)**

Jorge A. Santiago-Blay, Michael E. Soleglad & Victor Fet

**Abstract:**

The monotypic genus *Uintascorpio* Perry, 1995 from the Parachute Creek Member of the Uinta Basin in the Green River Formation, Colorado, USA (Middle Eocene; approximate age 48 Ma) is redescribed and placed in the family Buthidae (parvorder Buthida). The placement of this fossil in the Buthidae is supported by the diagnostic carination of the pedipalp, metasoma, and other morphological details. This fossil is the most ancient known record of the Buthidae in the New World and the oldest North American scorpion fossil since Carboniferous. The existence of *Uintascorpio halandrasorum* reflects a long Cenozoic history of buthid evolution in North America.

**Key words:** Scorpiones, Buthidae, *Uintascorpio*, *Uintascorpio halandrasorum*, Middle Eocene, morphology, Uinta Basin, Green River Formation, Colorado, USA.

**Redescripción y asignación familiar de *Uintascorpio* Perry, 1995 del Eoceno Medio de Colorado, EEUU (Scorpiones: Buthidae)**

**Resumen:**

El género monotípico *Uintascorpio* Perry, 1995 de Parachute Creek, en la Cuenca de Uinta, localizada en la Formación Green River, Colorado, Estados Unidos (Eoceno Medio; edad aproximada 48 Ma) se redescrive y se asigna a la familia Buthidae (parvorder Buthida). La inclusión de este fósil en los Buthidae está basada en la carinación del pedipalpo, metasoma y otros detalles morfológicos. Este fósil es el registro más antiguo de Buthidae del Nuevo Mundo y el más antiguo de escorpiones norteamericanos desde el Carbonífero. La existencia de *Uintascorpio halandrasorum* refleja una larga historia en la evolución de los bütidos en América del Norte.

**Palabras clave:** Scorpiones, Buthidae, *Uintascorpio*, *Uintascorpio halandrasorum*, Eoceno Medio, morfología, Cuenca de Uinta, Formación Green River, Colorado, EEUU.

**Introduction**

A Cenozoic fossil scorpion from Colorado was briefly described in 1995 as *Uintascorpio halandrasii* Perry, 1995. The familial placement of this genus was unclear. Perry (1995, 2003) suggested that it could be tentatively placed in the North American family Vaejovidae. Kovařík (1998) suggested, however, that the genus might belong to Buthidae and could even be a synonym of the modern New World genus *Rhopalurus* Thorell, 1876. Fet *et al.* (2000) and Soleglad & Fet (2003) listed *Uintascorpio* under “*Orthosternina Incertae Sedis*” since it is impossible to establish a definite placement from the original description and illustrations.

The publication by Perry (1995) was titled “Preliminary description of a new fossil scorpion...”, and indicated that the specimen was “...lacking in sufficient detail to apply taxonomic criteria as used for living forms” (p. 133). However, the International Code of Zoological Nomenclature (ICZN, 1999) does not distinguish between “preliminary descriptions” and any other descriptions. In our opinion, both genus and species as described by Perry (1995: 133) satisfy criteria of availability as defined by Articles 10, 11, 13, of the Code (ICZN, 1999). At the same time, the description and illustrations given by Perry (1995) are herein significantly extended. A brief overview of fossil studies of the Green River Formation is given.

## Geological Background

The Green River Formation (GRF) is a large geological entity that spans temporarily from the Lower to Middle Eocene [Wasatchian to Bridgerian; most recent estimates approximately 53–48.5 Ma (Pietras *et al.*, 2003 and Smith *et al.*, 2003 for several sites in the Lake Gosiute basin, see below); broader and sometimes older estimates have been published (58–39 Ma, Grande 1984;  $48.8 \pm 1.5$ –2.5 Ma, Machlus *et al.*, 2004)] in three of the western Rocky Mountain states of the United States: Utah, Colorado, and Wyoming (Brenes *et al.*, 1999; Caggiano, 2000; Smith *et al.*, 2003). There has been a huge interest in the GRF [e.g. close to 2000 hits were found in GeoRef (1785 to present), Biological Abstracts (1969 to present), and Zoological Record (1978 to present)] due, in part, to a vigorous interest in its potential for oil-shale exploitation (Hail, 1992) as well as for its rich fossil deposits ([http://www.coloradomtn.edu/campus\\_rfl/staff\\_rfl/kohls/eocene.html](http://www.coloradomtn.edu/campus_rfl/staff_rfl/kohls/eocene.html)). Three major lacustrine, at times extensively interdigitating (Hail, 1992), basins contribute to the GRF (approximate locations parenthesized): Fossil Lake (SW Wyoming and NE Utah), Lake Gosiute (SW Wyoming, NE Utah, and NW Colorado), and Lake Uinta (NE Utah and NW Colorado). The GRF has been variously subdivided into geological members (Calkin, 1997) one of which is the Parachute Creek, where the scorpion *Uintascorpio halandrasi* was collected. The GRF includes oolitic grindstones, packstones, and mudstones (Brenes *et al.*, 1999); the Parachute Creek Member sedimentologically “consists of gray shales with intervals of oil shale and tuff beds that formed in lake environments” (Calkin, 1997) and it is mineralogically is made out of numerous species, such as marlstone and siltstone (Cashion, 1959). The Parachute Creek Member has been recently dated to approximately  $48.66 \pm 0.12$  Ma (Smith, 2002) although older dates exist (Franczyk *et al.*, 1992). The GRF, to which the Uinta Basin belongs, had a temperate to subtropical climate (MacGinitie, 1969; Coddington, 1993; Lyon *et al.*, 1999); several hundred fossil species have been described from the shores of Lake Uinta (Colorado and Utah) (Bradley, 1931; MacGinitie, 1969; Siber, 1982; Grande, 1984; Coddington, 1993; Averett, 1995; Perry, 1995). This ancient Lake Uinta or Uintah County (Utah), both geographical features of the area, should not be confused with the Uinta Formation, a younger geological entity that overlays the GRF in some portions of its spatial range.

## Methods & Material

**Methods.** Photography was performed using two methods. Overall views (Fig. 1) were taken with a Wein Digital camera (SSHS) equipped with three fiber optic sources (Microptics) and lightly enhancing the images with PhotoShop<sup>®</sup>. Closeups (Figs. 2–5) were taken with a dissecting microscope (Olympus SZX MDU 12)

equipped with a digital camera (Olympus Q Color 5) and two fiber optics light sources (Dolan-Jener, Fiber-Lite MI-150). Measurements and terminology follow Sissom *et al.* (1990) and Soleglad & Fet (2003).

**Comparative recent scorpion material.** For confirmation of major diagnostic features, we used the following extant representatives of family Buthidae: *Alayotityus nanus* Armas, 1973, Cuba (VF); *Androctonus bicolor* Ehrenberg, 1828, Israel (MES); *Anomalobuthus rickmersi* Kraepelin, 1900, Uzbekistan (VF); *Apistobuthus pterygocercus* Finnegan, 1932, Oman (VF); *Babycurus exquisitus* Lowe, 2000, Oman (GL); *Babycurus* sp., Kenya (NMNH); *Buthacus yotvatensis* Levy *et al.*, 1973, United Arab Emirates (VF); *Butheolus gallagheri* Vachon, 1980, Oman (VF); *Buthus occitanus* Amoreux, 1789, Spain (MES); *Centruroides exilicauda* (Wood, 1863), Baja California Sur, Mexico (MES), *Centruroides hentzi* (Banks, 1910), Panama City, Florida, USA (MES); *Centruroides margaritatus* (Gervais, 1841), Panama (Fig. 7) (MES); *Compsobuthus matthiesseni* (Birula, 1905), Iraq (VF); *Grosphus hirtus* Kraepelin, 1901, Madagascar (MES); *Hottentotta minax* (L. Koch, 1875), Eritrea (VF); *Isometrus maculatus* (DeGeer, 1778), Singapore (VF); *Isometrus* sp., Papua New Guinea (MES); *Karasbergia methueni* Hewitt, 1913, South Africa (LP); *Kraepelinia palpator* (Birula, 1903), Turkmenistan (VF); *Leiurus quinquestriatus* (Ehrenberg, 1828), Saudi Arabia (VF); *Liobuthus kessleri* Birula, 1898, Kazakhstan (VF); *Lychas* sp., Viti Levu, Fiji (MES); *Lychas* sp., Indonesia (VF); *Mesobuthus caucasicus* (Nordmann, 1840), Kazakhstan (VF); *Mesobuthus eupeus* (C.L. Koch, 1839), Turkmenistan (VF); *Microbuthus* sp., Oman (GL); *Microtityus jaumei* Armas, 1974, Cuba (VF); *Odontobuthus* sp., Oman (GL); *Odonturus* sp., Tanzania (NMNH); *Orthochirus scrobiculosus* (Grube, 1873), Israel (MES); *Parabuthus* sp., Kenya (VF); *Paraorthochirus glabrifrons* (Kraepelin, 1903), Oman (VF); *Polisius persicus* Fet *et al.*, 2001, Iran (NMNH); *Razianus zarudnyi* (Birula, 1903), Iran (VF); *Rhopalurus junceus* (Herbst, 1800), Cuba (VF); *Tityus nematochirus* Mello-Leitão, 1940, Colombia (MES); *Uroplectes vittatus* (Thorell, 1876), Zimbabwe (VF); *Vachoniolus globimanus* Levy *et al.*, 1973, Oman (VF); *Zabius fuscus* (Thorell, 1876), Argentina (NMNH). This sample (33 genera) represents approximately 38 % of the 88 extant and extinct buthoid genera of the world. Detailed label data are available from the authors.

**List of depositories:** GL, Personal collection of Graeme Lowe, Philadelphia, Pennsylvania, USA; LP, Personal collection of Lorenzo Prendini, New York, New York, USA; MES, Personal collection of Michael E. Soleglad, Borrego Springs, California, USA; VF, Personal collection of Victor Fet, Huntington, West Virginia, USA; NMNH, National Museum of Natural History (Smithsonian Institution), Washington, DC, USA.

## Systematic Description

Order **SCORPIONES** C. L. Koch, 1850

Suborder **Neoscorpiones** Thorell & Lindström, 1885

Infraorder **Orthosterni** Pocock, 1911

Parvorder **Buthida** Soleglad & Fet, 2003

Superfamily **Buthoidea** C. L. Koch, 1837

Family **Buthidae** C. L. Koch, 1837

Genus ***Uintascorpio*** Perry, 1995

**TYPE SPECIES.** *Uintascorpio halandrasorum* Perry, 1995, by original designation (as *Uintascorpio halandراسي*).

### ***Uintascorpio halandrasorum* Perry, 1995**

(Figs. 1–5)

*Uintascorpio halandراسي* Perry, 1995: 131–133, Figs. 1–2.

**Incorrect original spelling** (see below).

*Uintascorpio halandراسي*: Kovařík, 1998: 7, Fig.; Fet *et al.*, 2000: 552; Perry, 2003: 22; Soleglad & Fet, 2003: 119.

**HOLOTYPE.** Deposited in Denver Museum of Nature and Science (DMNH No. 6004). Green River Formation, Rio Blanco County, Colorado, USA.

**ETYMOLOGY.** Genus, *Uintascorpio*, was named after the famous fossil-producing Eocene site of Lake Uinta (Grande, 1984; Perry, 1995). The species epithet, *halandراسي*, was explicitly given by Perry (1995) as a patronym in honor of Mr. and Ms. Gus and Christine Halandras (Meeker, Colorado, USA). According to the Article 31.1.2 of ICZN (1999), if a species-group name is derived from the family name of more than one person (a male and a female in this case), it should be declined adding the suffix “-orum”. Thus, the species name “*halandراسي*” is an **incorrect original spelling** (ICZN, 1999: Article 32.5) and is here corrected to “*halandراسorum*”.

**MATRIX.** The *Uintascorpio halandراسorum* holotype is preserved in a light gray, thinly bedded, highly compacted shale (714.12 g; maximum linear dimensions, approximately 170 mm x 100 mm x 35 mm, density roughly similar throughout).

**DESCRIPTION** (Figs. 1–5). Nomenclature of metasomal and pedipalpal carination follows that of Soleglad & Fet (2003). A minus (-) sign indicates that the structure cannot be measured with confidence. All measurements are in mm.

**Measurements.** *Carapace*: length = 4.43, anterior width (at lateral eyes) = 2.41, posterior width = 4.79, median eyes + tubercle width = 0.89, median eye (anterior edge to median eyes)/length (carapace length) formula = 167/443 (approximately 0.38). *Mesosoma*: length = 11.77, tergite widths (at widest point): I = 4.54, II = 4.68, III = 4.79, IV = 5.18, V = 5.43, VI = 5.21, VII = 4.96. *Metasoma*: segment length/width: I = 2.52/2.55, II = 3.16/-, III = 3.37/-, IV = -/-, V = -/-. *Telson*: undeterminable. *Pedipalp* (left): femur length/width = 3.37/

1.60, patella length/width = 4.11/1.95, chela length = 7.84, palm length/width = 2.98/1.67. *Leg* (IV, right): femur length/width = 3.97/0.82, patella length/width = 3.19/1.24, tibia length/width = 2.13/0.60. *Total length* (approximate; carapace + mesosoma + metasoma + telson): 25.25 + (14 = metasomal segments IV–V and telson estimated) = 39.25.

**General Appearance:** Dorsal view of the entire scorpion visible, including chelicerae and pedipalps, carapace, eight legs, mesosoma, and telson (Fig. 1). The metasoma curves in a right to left direction (from a “carapace on top” perspective), segment I visible dorsally, segments II–III visible dorsolaterally, and segments IV–V and telson curving upwards somewhat, not providing a parallel perspective to the viewing surface. In particular, the telson is positioned roughly perpendicular to metasomal segment V, so that metasomal segment V is positioned dorsolaterally while telson and aculeus are positioned laterally. The whitish areas visible in the fossil illustrations are due to the absence of rock and must be considered artifacts, not coloration patterns of the scorpion.

**Coloration:** Overall coloration of specimen is medium brown; carapace, mesosoma, and metasoma slightly darker than pedipalps and legs; carinae of carapace, mesosoma, metasoma, pedipalps, and legs dark brown; articulation mechanism on patellae of leg IV dark brown; cheliceral fingers dark brown.

**Carapace** (Fig. 1): surface covered with minute granules; anterior edge broadly concave, extreme lateral edges protruding furthest anteriorly; median eyes and ocular tubercle well developed, situated anterior of middle, at 167/443 (ca. 0.38) ratio of total length; indication of three lateral eyes on left side; posterior median carinae present, darkly pigmented; median posterior furrow widely developed.

**Chelicerae** (Fig. 1): Extend considerably from the anterior edge of carapace; palm roughly one and one-half times longer than the fingers; detailed finger structure and dentition mostly not visible.

**Legs** (Fig. 1): Femur: dorsal carinae visible, delicately crenulate; cuticle projection on external aspect of femur-patella joint visible (as described in Fet *et al.*, 2004). Patella: five finely crenulate carinae are visible on dorsal aspect of segment; articulation mechanism at patella-tibia joint conspicuously pigmented on leg IV; details of more distal leg segments not adequately visible, thus we are unable to determine presence of tibial spurs, pedal spurs, or tarsal armature. The outline of some coxae of legs, located under the carapace, is barely visible in this compression fossil but we cannot confidently discern all of them.

**Mesosoma** (Fig. 2): all tergites covered with small to medium sized granules; intersegmental membranes visible; median carinae visible, well developed and delicately granulate on segments I–VII; two pairs of well developed delicately granulate lateral and lateral median carinae clearly visible on segment VII, darkly pigmented in contrast to the lighter segment surface; lateral edges

of segment VII with delicate serrations. Ventral organs and details (sternites, stigmata, sternum, genital operculum, pectines and basal piece) not visible.

**Metasoma** (Fig. 3): Segments I–IV: dorsal and dorso-lateral carinae delicately crenulate; lateral carinae crenulate on segment I, absent on segments II–IV; ventrolateral carinae not visible on I, delicately crenulate on II–IV; ventromedian carinae not visible; intercarinal spaces covered with minute granulation. Segment V: dorsolateral carinae crenulate; lateral carinae not visible; ventrolateral and ventromedian carinae not visible; intercarinal spaces covered with minute granulation.

**Telson** (Fig. 3): Vesicle is somewhat smaller than metasomal segment V, broadly rounded, terminating in a long sweeping, large aculeus; significant subaculear tooth not detectable (small sized tooth possible); surface of vesicle appears to be covered with large granules.

**Pedipalp** (Figs. 4–5): Relatively small to medium pedipalps, chelal palms small and rounded with long thin fingers. Femur: delicately sculpted with crenulate dorso-external, dorsointernal, and ventroexternal carinae; surfaces covered with minute granulation. Patella: dorso-internal ( $DI_c$ ), dorsomedian ( $DM_c$ ) (Fig. 5), and dorsoexternal ( $DE_c$ ) carinae crenulate; Dorsal Patellar Spur ( $DPS_c$ ) carina roughly granulate, DPS small; exteromedian ( $EM_c$ ) carina crenulate; other carinae not visible (i.e.,  $VPS_c$ ,  $VI_c$ ,  $VE_c$ ); intercarinal surfaces rough. Chela: palm and fingers not exposed too well, no discernible detail is visible. Chelal finger dentition, trichobothriotaxy, and maxillary lobes not visible.

## Discussion

Soleglad & Fet (2003) diagnosed Buthidae (as well as superfamily Buthoidea and parvorder Buthida) by a number of features, most of which cannot be observed on a fossil seen from only a dorsal aspect. However, the diagnosis includes among important synapomorphies the features clearly observed in *Uintascorpio*: elongated leg coxae IV; absence of lateral carinae on metasomal segment V; and, especially, presence of pedipalp patellar  $DM_c$  carina. Additional observations, made specifically for this study, confirm the presence of the  $DM_c$  carina as a common feature (synapomorphy) in 32 genera of extant Buthidae from all over the world, namely (in alphabetical order): *Alayotityus*, *Androctonus*, *Anomalobuthus*, *Apistobuthus*, *Babycurus*, *Buthacus*, *Buthus*, *Centruroides*, *Compsobuthus*, *Grosphus*, *Hottentotta*, *Isometrus*, *Karasbergia*, *Kraepelinia*, *Leiurus*, *Liobuthus*, *Lychas*, *Mesobuthus*, *Microbuthus*, *Microtityus*, *Odonobuthus*, *Odonturus*, *Orthochirus*, *Parabuthus*, *Paraorthochirus*, *Polisius*, *Razianus*, *Rhopalurus*, *Tityus*, *Uroplectes*, *Vachoniolus*, and *Zabius*. The  $DM_c$  carina is illustrated in Figs. 6–7 for two extant buthid genera from the New World: *Rhopalurus* and *Centruroides* and should be compared to the *Uintascorpio* patella illustrated in Fig. 5

The observed features of *Uintascorpio*, in our opinion, are sufficient to diagnose the genus as belonging to the Buthidae. Lack of further diagnostic features, however, precludes us from making any statements on close relationship of *Uintascorpio* to any modern genera of

Buthidae, whether from the New World or the Old World. No characters are available which could be used to ally this genus to any specific genera or groups of genera of extant buthids, i.e. pedipalp chela dentition, trichobothrial patterns, leg setation, etc. Since Buthidae currently is not subdivided into subfamilies or tribes (Fet & Lowe, 2000; Soleglad & Fet, 2003; Coddington *et al.*, 2004), this fossil might play an important role in further systematic and biogeographic assessment of the family.

The Buthidae is the most diverse among all known scorpion families, both extant and fossil. Buthids include 78 extant genera spanning all continents except Antarctica (Fet & Lowe, 2000; for additional genera described and synonymies made since 1998, see Lourenço, 1999a, 1999b, 2000a, 2000b, 2001b, 2001c, 2003a; Fet *et al.*, 2001; Kovařík, 2001, 2003, 2004; Gantenbein *et al.*, 2003), five Baltic amber genera (see below), and a subfossil genus *Palaeogrosphus* described from the copal of Madagascar (Lourenço, 2000b). Closely allied to Buthidae is another buthoid family Microcharmidae with three additional genera (Fet, 2000; Lourenço, 2000b, 2002b, 2003b). In total, superfamily Buthoidea currently embraces 88 genera (fossil and extant; *Uintascorpio* included).

Kjellesvig-Waering (1986), in his comprehensive review of fossil scorpions, did not list any fossil Buthidae. Lourenço (2001a, 2002a) described two Cretaceous genera, which he placed in Buthoidea: *Archaeobuthus* (Lebanese amber, 135–130 Ma) (Archaeobuthidae) and *Palaeoburmesebuthus* (Burmese amber, 100–90 Ma) (family placement unclear; for extended description of an additional specimen see Santiago-Blay *et al.*, 2004a). However, Soleglad & Fet (2001, 2003) and Santiago-Blay *et al.* (2004a) doubted affiliation of these two Cretaceous genera with Buthoidea. In our opinion, the most ancient confirmed Buthidae are Cenozoic taxa, known from the Paleocene to Eocene Baltic amber (65–55 Ma). This important, diverse fauna included five extinct, monotypic genera (*Palaeolychas*, *Palaeotityobuthus*, *Palaeoprotobuthus*, *Palaeoakentrobuthus*, and *Palaeoananteris*), all described by Lourenço & Weitschat (1996, 2000, 2001). These five genera are unmistakably diagnosable as Buthidae by “trichobothrial Type A pattern” (Soleglad & Fet, 2001; Santiago-Blay *et al.*, 2004a).

On the other hand, all hitherto known fossil species of Buthidae from the New World are of Miocene to Oligocene age (26–15 Ma) and already belong to the extant genera (*Tityus*, *Microtityus*, *Centruroides*; Schawaller, 1979, 1981, 1984; Santiago-Blay & Poinar, 1988, 1993; Santiago-Blay, 1990; Santiago-Blay *et al.*, 1990); these taxa were found in Dominican and Mexican amber. The Eocene *Uintascorpio* is, therefore, the first entirely fossil, and the oldest (ca. 48 Ma), buthid genus known from the New World.

An important issue in scorpion phylogeny is evolution of toxins, especially in Buthidae which is the only scorpion family with mammal-specific neurotoxins. While Old World scorpion lineages with the most potent neurotoxic venom share separate mammal- and insect-specific neurotoxins specific for  $Na^+$  channels; at the same time, New World genera have potent toxins acting





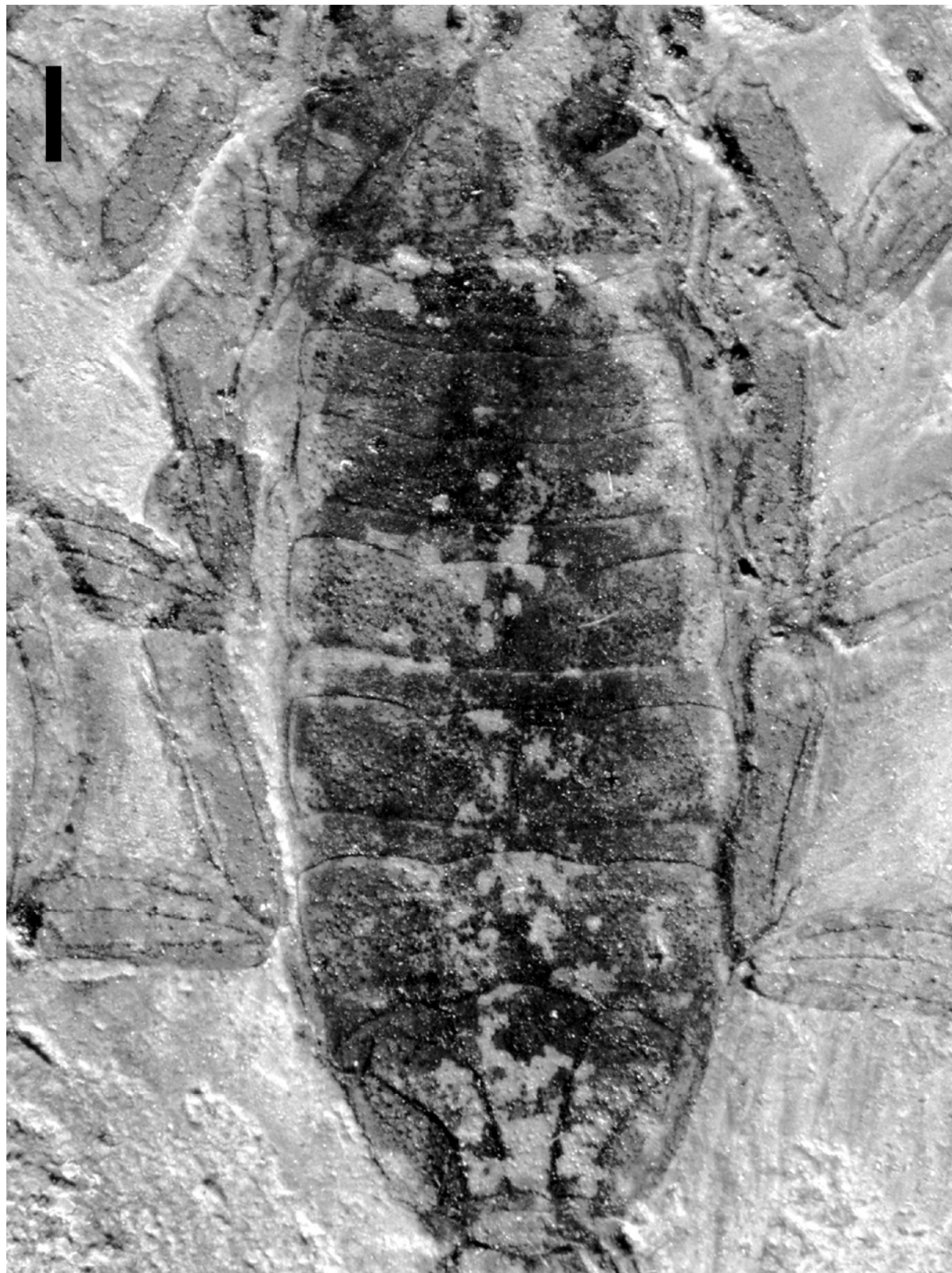
Fig. 1. *Uintascorpio halandrasorum*, dorsal view.

on both mammals and insects (Loret & Hammock, 2001; Froy & Gurewitz, 2003). Fet *et al.* (2003) provided the first, pilot molecular phylogeny of 17 genera of Buthidae and suggested several possible scenarios of the origin of New World buthids. In one of those scenarios, a few Buthidae which now inhabit deserts of North America (e.g. species of *Centruroides*) could have dispersed to the arid landscapes from the New World tropics. An alternative evolutionary scenario could include separate evolution of buthids in Laurasia and Gondwanaland after the split of Pangaea, as it was for many other groups of organisms.

Discovery of an Eocene buthid in North America suggests that both scenarios could be combined. Since

South America was completely isolated during most of the Cenozoic, the existence of Eocene buthids in temperate North America indicates that they could have evolved in North America from Pangaeian times and retreated to Mexico/Caribbean during Pleistocene glaciations only subsequently making a partial return. Similar Cenozoic extinction/dispersal events should have happened in Laurasia, signified by the extinction of "paleobuthid" genera along with the Baltic tropical forest, and recent dispersal/radiation of *Buthus* from Africa to Spain and *Mesobuthus* from Asia to the Balkans (Gantenbein & Largiadèr, 2003; Gantenbein *et al.*, 2001, 2003).

Soleglad & Fet (2003) suggested that four extant lineages (parvorders) of orthostern scorpions should



**Fig. 2.** *Uintascorpio halandrasorum*, mesosoma, dorsal view. Black bar represents 1 mm.

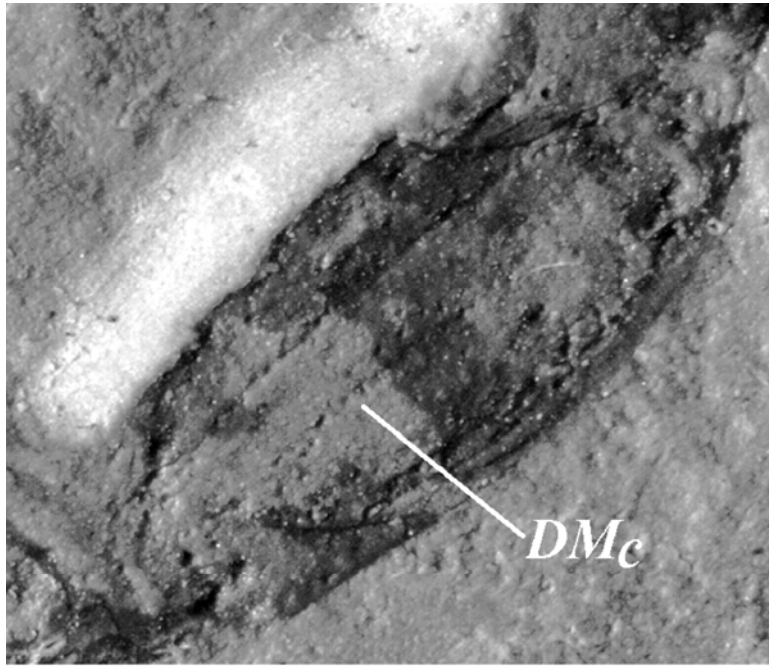
have been established already in Pangaea, during Permian to Triassic time. Lineages of scorpions which survived the K-T extinction in the end of Mesozoic undoubtedly included Buthidae; however, their origin of the New World lineages has been obscure. The Eocene genus *Uintascorpio* is the oldest buthid fossil in the New

World, and also the oldest North American orthostern scorpion fossil since Carboniferous (Soleglad & Fet, 2003). Its family placement of the Eocene in Buthidae allows adding one more important piece to the jigsaw puzzle of buthid evolution.

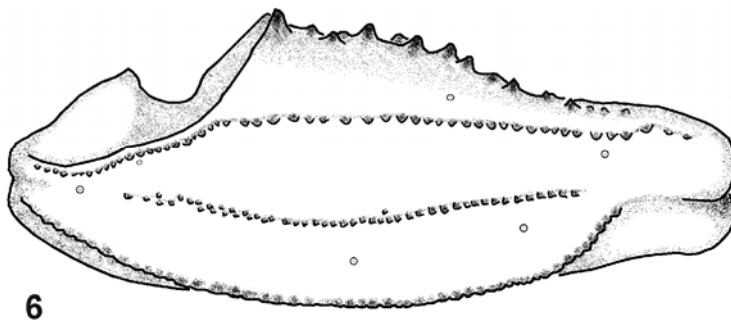




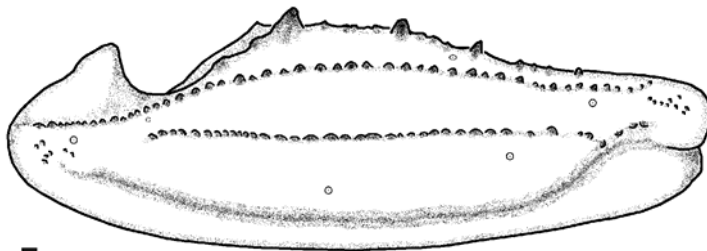
**Figs. 3–4.** *Uintascorpio halandrasorum*. 3. Metasoma and telson, dorsolateral view. 4. Left pedipalp, dorsal view. White bar represents 1 mm.



**Fig. 5.** *Uintascorpio halandrasorum*, closeup of left pedipalp patella. Note the indicated dorsomedian ( $DM_c$ ) carina.



6



7

**Figs. 6–7.** Right pedipalp patella, dorsal view, showing the dorsomedian ( $DM_c$ ) carina in Recent New World buthid genera. **6.** *Rhopalurus junceus*, male. **7.** *Centruroides margaritatus*, male.

### Acknowledgements

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searches. Zachary Jones (Bristow, VA) assisted JASB examine of the scorpion collection housed at the National Museum of Natural History (Washington, DC) looking for the dorsomedian carinae on the pedipalp patella of buthids of the world. We are grateful to Rolando Teruel for his valuable comments in reviewing this paper

### Addendum

In a paper on fossil scorpions recently published by our research group (Santiago-Blay *et al.* 2004b, p. 4, left column, second paragraph), the issue of holotype deposition in private collections was addressed. It was not the intention of Santiago-Blay *et al.* (2004b) to convey the impression that this practice is preferred by us or by the authors whose papers were cited in that paragraph.



## Bibliography

- AVERETT, W.R. (ED.). 1995. *The Green River Formation in Piceance Creek and Eastern Uinta Basins*. Grand Junction Geological Society, Grand Junction, Colorado, USA. 166 pp.
- BRADLEY, W.H. 1931. Origin and microfossils of the oil shale of the Green River Formation of Colorado and Utah. *U.S. Geological Survey, Professional Paper*, **168**: 1–58.
- BRENES, K., M. FLELING, N. RAO & L. SMITH 1999. The Green River Formation. <http://www.ucmp.berkeley.edu/tertiary/eoc/greenriver.html>
- CAGGIANO, T. 2000. The Green River Formation. <http://www.fossilnews.com/2000/gmrv/gmrv.html>.
- CALKIN, W.S. 1997. Lacustrine delta, Sunnyside Tar Sands, northeastern Utah. *AAPG (American Association of Petroleum Geologists), Rocky Mountain Section Meeting (Denver, CO, United States. Aug. 24-27. Abstracts. AAPG Bulletin*, **81**: 1220.
- CASHION, W.B. 1959. Geology and oil-shale resources of Naval Oil-Shale Reserve No. 2, Uintah and Carbon counties, Utah. *United States Geological Survey Bulletin*, pp. 753–793.
- CODDINGTON, J.A., G. GIRIBET, M.S. HARVEY, L. PRENDINI & D.E. WALTER. 2004. Arachnida. Pp. 296–318 in Cracraft, J. and M.J. Donoghue (eds.). *Assembling the Tree of Life*. New York, NY: Oxford University Press.
- CODDINGTON, L.A. 1993. *Climatic Implications of Terrestrial Arthropods from the Parachute Creek Member (Middle Eocene), Green River Formation, Garfield County, Colorado*. M. Sc. (Thesis) (Department of Geosciences) Fort Hays State University. Hays, Kansas, United States. 79 pp.
- FET, V. 2000. Family Microcharmidae Lourenço, 1996. Pp. 421–423 in Fet, V., W. D. Sissom, G. Lowe & M. E. Braunwalder. *Catalog of the Scorpions of the World (1758–1998)*. New York, NY: New York Entomological Society.
- FET, V., E.M. CAPES & W.D. SISSOM 2001. *Polisius*, a new scorpion genus from Iran (Scorpiones: Buthidae). Pp. 183–190 in: Fet, V. & P. A. Selden (eds.). *Scorpions 2001. In Memoriam Gary A. Polis*. Burnham Beeches, Bucks: British Arachnological Society.
- FET, V., B. GANTENBEIN, A.V. GROMOV, G. LOWE & W.R. LOURENÇO 2003. The first molecular phylogeny of Buthidae (Scorpiones). *Euscorpius*, **4**: 1–10.
- FET, V. & G. LOWE 2000. Buthidae. Pp. 54–286. In: Fet, V., W.D. Sissom, G. Lowe & M.E. Braunwalder. *Catalog of the scorpions of the world (1758–1998)*. New York, New York Entomological Society. 690 pp.
- FET, V., W.D. SISSOM, G. LOWE & M.E. BRAUNWALDER 2000. *Catalog of the Scorpions of the World (1758–1998)*. New York Entomological Society, New York, 690 pp.
- 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.
- FRANCZYK, K.J., T.D. FOUCH, R.C. JOHNSON, C.M. MOLENAAR & W.A. COBBAN 1992. Cretaceous and Tertiary paleogeographic reconstructions for the Uinta-Piceance Basin study area, Colorado and Utah. *United States Geological Survey Bulletin*, **1787-Q**, 37 pp.
- FROY, O. & M. GUREVITZ 2003. New insight on scorpion divergence inferred from comparative analysis of toxin structure, pharmacology and distribution. *Toxicon*, **42**(5): 549–555.
- GANTENBEIN, B., V. FET & A.V. GROMOV 2003. The first DNA phylogeny of four species of *Mesobuthus* Vachon, 1950 (Scorpiones: Buthidae) from Eurasia. *Journal of Arachnology*, **31**(3): 412–420.
- GANTENBEIN, B., C. KROPF, C.R. LARGIADÈR & A. SCHOLL 2000. Molecular and morphological evidence for the presence of a new Buthid taxon (Scorpiones: Buthidae) on the Island of Cyprus. *Revue Suisse de Zoologie*, **107**(1): 213–232.
- GANTENBEIN, B. & C.R. LARGIADÈR 2003. The phylogeographic importance of the Strait of Gibraltar as a gene flow barrier to terrestrial arthropods: a case study with the scorpion *Buthus occitanus* as model organism. *Molecular Phylogenetics and Evolution*, **28**(1): 119–130.
- GRANDE, L. 1984. *Paleontology of the Green River Formation with a Review of the Fish Fauna*. 2<sup>nd</sup> Edition: The Geological Survey of Wyoming, Bulletin, **63**, 333 pp.
- HAIL, W. J. JR. 1992. Geology of the central Roan Plateau area, northwestern Colorado. *United States Geological Survey Bulletin*. pp. R1-R26. [http://www.coloradomtn.edu/campus\\_rfl/staff\\_rfl/kohls/eocene.html](http://www.coloradomtn.edu/campus_rfl/staff_rfl/kohls/eocene.html).
- ICZN. 1999. *International Code of Zoological Nomenclature*. Fourth Edition. London: The International Trust for Zoological Nomenclature, 305 pp.
- 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. Paleontological Research Institution, Ithaca, New York. 287 pp.
- KOVAŘÍK, F. 1998. *Štíři. [Scorpions]*. Madagaskar, Jihlava. 175 pp. (in Czech).
- KOVAŘÍK, F. 2001. *Lanzatus somalicus* gen. et sp. n. (Scorpiones: Buthidae) from Somalia. *Acta Societatis Zoologicae Bohemicae*, **65**: 41–44.
- KOVAŘÍK, F. 2003. Scorpions of Djibouti, Eritrea, Ethiopia, and Somalia (Arachnida: Scorpiones), with a key and descriptions of three new species. *Acta Societatis Zoologicae Bohemicae*, **67**: 133–159.
- KOVAŘÍK, F. 2004. Revision and taxonomic position of genera *Afghanorthochirus* Lourenço & Vachon, *Balorthochirus* Kovařík, *Butholus* Simon, *Nanobuthus* Pocock, *Orthochiroides* Kovařík, *Pakistanorthochirus* Lourenço, and Asian *Orthochirus* Karsch, with descriptions of twelve new species (Scorpiones, Buthidae). *Euscorpius*, **16**: 1–33.
- LORET, E. & B. HAMMOCK 2001. Structure and neurotoxicity of scorpion toxins. Pp. 204–233 in Brownell, P. H. & G. A. Polis (Editors). *Scorpion Biology and Research*. Oxford: Oxford University Press.
- LOURENÇO, W.R. 1999a. Origines et affinités des scorpions des Grandes Antilles: le cas particulier des éléments de la famille des Buthidae. *Biogeographica* (Paris), **75**(3): 131–144.
- LOURENÇO, W.R. 1999b. Biogeography, biodiversity and old collections: a new genus and species of buthid scorpion from Congo found in the collections of the “Muséum National d’Histoire Naturelle, Paris”. *Biogeographica* (Paris), **75**(4): 187–192.
- LOURENÇO, W.R. 2000a. Un nouveau genre de Scorpion malgache, maillon possible entre les Microcharmidae et les Buthidae. *Comptes Rendus des Séances de l’Académie des Sciences, Paris, Sciences de la Vie*, **323**: 877–881.
- LOURENÇO, W.R. 2000b. More about the Buthoidea of Madagascar, with special references to the genus *Tityobuthus* Pocock (Scorpiones, Buthidae). *Revue Suisse de Zoologie*, **107**(4): 721–736.
- LOURENÇO, W.R. 2001a. A remarkable scorpion fossil from the amber of Lebanon. Implications for the phylogeny

- of Buthoidea. *Comptes Rendus des Séances de l'Académie des Science, Paris* **332**: 641–646.
- LOURENÇO, W.R. 2001b. Un nouveau genre de Buthidae, probable vicarier géographique d'*Anomalobuthus* Kraepelin (Chelicerata, Scorpiones). *Biogeographica*, **77**(1): 15–20.
- LOURENÇO, W.R. 2001c. Un nouveau genre et une nouvelle espèce de scorpion d'Algérie, avec des considérations taxonomiques sur le genre *Lissothus* Vachon, 1948 (Scorpiones, Buthidae). *Zoosystema*, **23**(1): 51–57.
- LOURENÇO, W.R. 2002a. 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. 2002b. Nouvelles données sur la morphologie et la biogéographie des *Microcharmus* Lourenço avec confirmation de la validité des Microcharmidae (Chelicerata, Scorpiones). Pp. 35–47 in LOURENÇO, W.R. & S.M. GOODMAN (eds.). *Diversité et Endémisme à Madagascar. Actes du II Colloque International Biogéographie de Madagascar. Paris, 30 août – 2 septembre 1999*.
- LOURENÇO, W.R. 2003a. Humicolous buthoid scorpions: a new genus and species from French Guiana. *Comptes Rendus Biologies*, **326** (2003): 1149–1155.
- LOURENÇO, W.R. 2003b. Humicolous microcharmidae scorpions: a new genus and species from Madagascar. *Comptes Rendus Biologies*, **327** (2003): 77–83.
- LOURENÇO, W.R. & W. WEITSCHAT 1996. More than 120 years after its description, the enigmatic status of the genus of the Baltic amber scorpion “*Tityus eogenus*” Menge, 1869 can finally be clarified. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, **79**: 189–193.
- LOURENÇO, W.R. & W. WEITSCHAT 2000. New fossil scorpions from the Baltic amber - implications for Cenozoic biodiversity. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, **84**: 247–260.
- LOURENÇO, W.R. & W. WEITSCHAT 2001. Description of another fossil scorpion from the Baltic amber, with considerations on the evolutionary levels of Cenozoic Buthoidea. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, **85**: 277–283.
- LYON, M., R. CRAIN & D.M. SMITH 1999. Food for thought; a preliminary examination of insect-mediated damage in the Green River Formation. In, *Geological Society of America, Annual Meeting (Boulder, Colorado). Abstracts with Programs*, **31**: 466–467.
- MACGINITIE, H.D. 1969. *The Eocene Green River flora of northwestern Colorado and northeastern Utah*. University of California Publications in Geological Sciences (Berkeley, California, United States), **83**, 203 pp.
- MACHLUS, M., S.R. HEMMING, P.E. OLSEN & N. CHRISTIE-BLICK 2004. Eocene calibration of geomagnetic polarity time scale reevaluated: Evidence from the Green River Formation of Wyoming. *Geology*, **32**(2): 137–140.
- PERRY, M.L. 1995. Preliminary description of a new fossil scorpion from the middle Eocene Green River Formation, Rio Blanco County, Colorado. Pp. 131–133 in Averett, W.R. (ed.). *The Green River Formation in Piceance Creek and Eastern Uinta Basins*. Grand Junction, Colorado: Grand Junction Geological Society.
- PERRY, M.L. 2003. Preliminary description of a new fossil scorpion from the Middle Eocene, Green River Formation, Rio Blanco, Colorado. In, Program 74th Annual Meeting of the Colorado-Wyoming Academy of Science. April 26, 2003. *The Journal of the Colorado-Wyoming Academy of Science*, **35**(1): 22.
- PIETRAS, J.T., A.R. CARROLL, B.S. SINGER & M.E. SMITH 2003. 10 k. y. depositional cyclicity in the early Eocene: stratigraphic and  $^{40}\text{Ar}/^{39}\text{Ar}$  evidence from the lacustrine Green River Formation. *Geology*, **31**(7): 593–596.
- SANTIAGO-BLAY, J.A. 1990. A new specimen of *Microtityus ambarensis*, fossil from Hispaniola: evidence of taxonomic status and possible biogeographic implications. *Journal of Arachnology*, **18**: 115–117.
- SANTIAGO-BLAY, J.A., V. FET, M.E. SOLEGLAD & P.R. CRAIG 2004a. A second scorpion specimen from the Burmese amber. *Journal of Systematic Palaeontology*, **2**(2): 147–152.
- SANTIAGO-BLAY, J. A., V. FET, M. E. SOLEGLAD & S. ANDERSON 2004b. A new genus and subfamily of scorpions from Cretaceous Burmese amber (Scorpiones: Chaerilidae). *Revista Ibérica de Aracnología*, **9**: 3–14.
- SANTIAGO-BLAY, J.A. & G.O. POINAR, JR. 1988. A fossil scorpion *Tityus geratus* new species (Scorpiones: Buthidae) from Dominican amber. *Historical Biology*, **1**: 345–354.
- SANTIAGO-BLAY, J.A. & G.O. POINAR, JR. 1993. First scorpion (Buthidae: *Centruroides*) from Mexican amber (Lower Miocene to Upper Oligocene). *Journal of Arachnology*, **21**(2): 147–151.
- SANTIAGO-BLAY, J.A., W. SCHAWALLER & G.O. POINAR, JR. 1990. A new specimen of *Microtityus ambarensis* (Scorpiones, Buthidae), fossil from Hispaniola: evidence of taxonomic status and possible biogeographic implications. *Journal of Arachnology*, **18**: 115–117.
- SCHAWALLER, W. 1979. Erstnachweis eines Skorpions im Dominikanischem Bernstein (Stuttgarter Bernsteinsammlung: Arachnida, Scorpionida). *Stuttgarter Beiträge zur Naturkunde, (B)*, **45**: 1–15.
- SCHAWALLER, W. 1981. Zwei weitere Skorpione im Dominikanischem Bernstein (Stuttgarter Bernsteinsammlung: Arachnida, Scorpionida). *Stuttgarter Beiträge zur Naturkunde, (B)*, **82**: 1–14.
- SCHAWALLER, W. 1984. Spinnentiere (Arachnida) im Dominikanischem Bernstein. In Bernstein-Neuigkeiten. *Stuttgarter Beiträge zur Naturkunde, (C)*, **18**: 72–78.
- SIBER, H.J. 1982. *Green River Fossilien: über ein nord-amerikanisches Fundgebiet reich an Fischfossilien und anderen Lebewesen der Eozän vor 50 Millionen Jahren*. Siber & Siber, Aathal, Switzerland. 81 pp.
- SISSOM, W.D., G.A. POLIS & D.D. WATT 1990. Field and laboratory methods. Pp. 445–461. In, Polis, G.A. (ed.) *Biology of Scorpions*. Stanford University Press, Stanford, California, 587 pp.
- SMITH, M.E. 2002.  $^{40}\text{Ar}/^{39}\text{Ar}$  Geochronology of the Eocene Green River Formation, Wyoming and Utah. M. S. Thesis. Department of Geology and Geophysics. University of Wisconsin, Madison. United States. 71 pp.
- SMITH, M.E., B. SINGER & A. CARROLL 2003.  $^{40}\text{Ar}/^{39}\text{Ar}$  geochronology of the Eocene Green River Formation, Wyoming. *Geological Society of America Bulletin*, **115**: 549–565.
- SOLEGLAD, M.E. & V. FET 2001. Evolution of scorpion orthothriotaxy: a cladistic approach. *Euscorpius*, **1**: 1–38.
- SOLEGLAD, M.E. & V. FET 2003. High-level phylogeny and systematics of the extant scorpions (Scorpiones: Orthosterni). *Euscorpius*, **11**: 1–175.