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 halandrasi has long reflected a Cenozoic history of buthid evolution in North America.

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

Introduction

A Cenozoic fossil scorpion from Colorado was briefly described in 1995 as Uintascorpio halandrasi 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. Kovář (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 temporally 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 ± 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 (Brener 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).

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 Univancorpsio haldaransi was collected. The GRF includes oolitic grindstones, packstones, and mudstones (Brener 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 ± 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®. 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: Alayotius nanus Armas, 1973, Cuba (VF); Androctonus bicolor Ehrenberg, 1828, Israel (MES); Anomalobuthus rickmersi Kraepelin, 1900, Uzbekistan (VF); Apistobuthus pterygocercus Finnegan, 1932, Oman (VF); Babycarus exquisitus Lowe, 2000, Oman (GL); Babycarus sp., Kenya (NMNH); Buthacus yoventiens 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); Compsothhus matthiesenii (Birula, 1905), Iraq (VF); Grophus hirutus Kraepelin, 1901, Madagascar (MES); Hottentotta minax (L. Koch, 1875), Eritrea (VF); Isometrus maculatus (De Geer, 1778), Singapore (VF); Isometrus sp., Papua New Guinea (MES); Karasbergia methuemii Hewitt, 1913, South Africa (LP); Kraepelinia palpat (Birula, 1903), Turkmenistan (VF); Leirurus quinquestrati (Ehrenberg, 1828), Saudi Arabia (VF); Liobuthus kessleri Birula, 1898, Kazakhstan (VF); Lychas sp., Fiji (MES); Lychas sp., Indonesia (VF); Mesobuthus caucasicus (Nordmann, 1840), Kazakhstan (VF); Mesobuthus eutepus (C.L. Koch, 1839), Turkmenistan (VF); Microbuthus sp., Oman (GL); Microtityus jaumei Armas, 1974, Cuba (VF); Odontobuthus sp., Oman (GL); Odonturus sp., Tanzania (NMNH); Orthochirinus scrobiculus (Grube, 1873), Israel (MES); Parabuthus sp., Kenya (VF); Paraothochirus glabriclinus Kraepecin, 1903), Oman (VF); Polisius persicus Fet et al., 2001, Iran (NMNH); Razians zarendiyi (Birula, 1903), Iran (VF); Rhopalurus junceus (Herbst, 1800), Cuba (VF); Tityus nematocidus Mello-Neto, 1940, Colombia (MES); Uroplectes vitatus (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 halandrasorum).

Uintascorpio halandrasorum Perry, 1995

(Figs. 1–5)

Incorrect original spelling (see below).


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, halandras, 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 “-son” (Article 32.5) and is here corrected to “halandrasorum”.

MATRIX. The Uintascorpio halandrasorum 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 segments IV–V and telson curving upwards somewhat, not providing a parallel perspective to the viewing surface. In particular, the telson is positioned roughly perpendicularly to metasomal segment V, so that metasomal segment V is positioned dorsolaterally while telson and acetabulum 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; ventro-lateral 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 metastomal segment V, broadly rounded, terminating in a long sweeping, large aculeus; significant subaculear tasomal segment V, broadly rounded, terminating in a telson.

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, dorsointerial, and ventro-external carinae; surfaces covered with minute granulation. Patella: dorso-internal (DI), dorso-median (DM) (Fig. 5), and dorso-external (DE) carinae crenulate; Dorsal Patellar Spur (DPS) carina roughly granulate, DPS small; extero-median (EM) carina crenulate; other carinae not visible (i.e., VPS, VI, VE); 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 Buthioidea 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 metastomal segment V; and, especially, presence of pedipalp patellar DM, carina. Additional observations, made specifically for this study, confirm the presence of the DM 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, Karasberga, Kraeplinia, Leirus, Liobuthus, Lychas, Mesobuthus, Microbuthus, Microtityus, Odontobuthus, Odonturus, Orthochirus, Paraclubatus, Paraor-thochirus, Polisius, Razianus, Rhopalurus, Tityus, Uroplectes, Vachoniulus, and Zabius. The DM 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; Kovarik, 2001, 2002, 2003, 2004; Gantenbein et al., 2003), five Baltic amber genera (see below), and a subfossil genus Palaeogrophus 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, superfamly Buthioidea 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 Buthioidea: 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 Buthioidea. 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 (Palaeoylocys, Palaeotityobuthus, Palaeoacrobuthus, Palaeokentobuthus, and Palaeoanteris), 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
A redescription and family placement of Uintascorpio 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 Panigean 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 & Largiadér, 2003; Gantenbein et al., 2001, 2003).

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

Fig. 2. *Uintascorpio halandrarsorum*, mesosoma, dorsal view. Black bar represents 1 mm.
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 (DMc) carina.

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

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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


