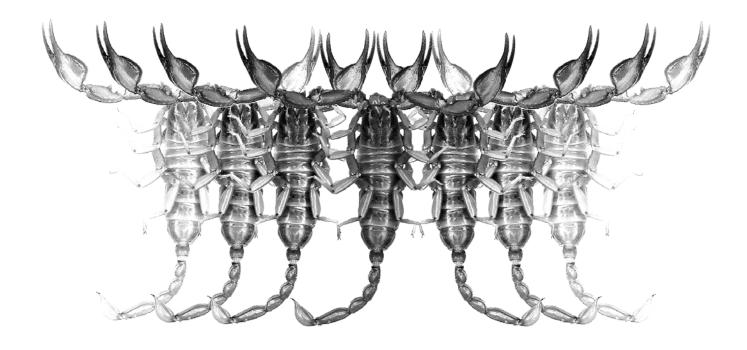
Euscorpius

Occasional Publications in Scorpiology



A New Species of *Odontobuthus* (Scorpiones: Buthidae) from Northern Oman

Graeme Lowe

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A new species of *Odontobuthus* (Scorpiones: Buthidae) from northern Oman

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Summary

The Asian buthid genus *Odontobuthus* is newly recorded from the Arabian Peninsula where is represented by *O*. *brevidigitus* **sp. nov.** from the Batínah coast and foothills of the Al Hajar mountains of northern Oman. The new species is characterized by short pedipalp fingers, long pectines with narrow basal middle lamella, 2–3 enlarged denticles on ventrosubmedian carinae of metasoma II–III, stout metasoma IV with 10 anterior transverse granules, 3 lateral anal lobes, and enlarged dentition on the ventral anal arch. A model is proposed for the speciation of *Odontobuthus* by westward dispersal of an ancestral population on the Indus floodplain, followed by vicariant tectonic events in the Miocene and Pliocene that led to divergence of four species in temporal sequence: *O. odonturus*, *O. doriae*, *O. bidentatus* and *O. brevidigitus* **sp. nov.**

Introduction

In his monograph *Études Scorpiologiques*, Thorell (1876) described Buthus doriae from Teheran in Persia (now Iran). His description of the two type specimens was lucid and detailed even by today's standards, and he noted a key diagnostic character: "segmentis caudæ 2° et 3° paribus trinis tuberculorum magnorum subter munitis". Twenty years later, Pocock was engaged in a major project, a "splendid and wholly unexpected opportunity" to study material obtained from a "collecting raid on the scorpions" of India, analyzing over 1,000 specimens. The new species he uncovered were published in a brief report in 1897 that included Buthus odonturus from the Khelat Frontier (now Pakistan). His laconic, one paragraph description emphasized a close affinity with B. doriae, both species sharing the prominent, enlarged dentition on metasomal segments II-III. The two were differentiated by numbers of denticles on transverse carinae of segments III-IV and number of lateral anal lobes. A few years later, Pocock (1900) published a more comprehensive treatise in The Fauna of British India, in which he considered these differences sufficiently minor for *B. odonturus* to be downgraded to a subspecies of *B. doriae*. Subsequently, several taxonomists have expressed conflicting opinions about the status these two forms (Fet & Lowe, 2000). In 1950, Vachon partitioned the large genus Buthus into several genera, defined primarily by differences in the form and carination of carapace, tergites and metasoma. He created the genus Odontobuthus for these two taxa, regarding them as distinct species. Recently, the genus

was reviewed by Lourenço & Pézier (2002), who confirmed the validity of *Odontobuthus doriae* and *O. odonturus* as separate species, and added a third species, *O. bidentatus*, from Iraq and western Iran. A systematic survey of the scorpion fauna of Iran yielded numerous additional records of *O. bidentatus* in western Iran (Navidpour et al., 2008a, 2008b, 2008c, 2008d; Pirali-Kheirabadi et al., 2008). Here, a fourth species is described from northern Oman, providing the first record of this distinctive Asian genus of buthid scorpions on the Arabian Peninsula.

Methods

Scorpions were collected by ultraviolet (UV) detection at night and preserved in the field by standard methods (Williams, 1968; Stahnke, 1972a; Sissom, Polis & Watt, 1990). Locality data were recorded using portable GPS units (Garmin). Specimens were examined under a dissecting microscope, either air dried or submerged in 70% isopropyl alcohol, under both white light epi-illumination and UV fluorescence (Prendini, 2003; Volschenk, 2005). Measurements were made with an ocular reticule, following biometric definitions in Lamoral (1979) and Sissom et al. (1990) with the following modifications: carapace anterior width taken between medial pair of lateral eyes; metasomal segment depths not including enlarged lobate dentition on ventrosubmedian or ventrolateral carinae; telson and vesicle lengths taken from anterior limit of vesicle to tip of aculeus, and to inflexion point on posterior slope of vesicle, respectively, with dorsal surface of vesicle level;

pedipalp chela length taken as chord length from external proximal limit of manus to apex of fixed finger; pedipalp manus width and depth measured with articular condyles level. The preocular length is defined as the distance from the center of the median ocular tubercle to the anterior margin of the carapace. Carinal terminology follows Stahnke (1970), with metasomal amendments by Prendini (2001b; 2004), but with dorsal carinae on metasoma V termed "dorsolateral" carinae, and pedipalp chelal amendments by Soleglad & Sissom (2001). Hemispermatophore terminology follows Lamoral (1979). Trichobothrial notation follows Vachon (1974, 1975). Pedipalp finger primary denticle subrows are enumerated from distal to basal (Sissom, 1994). Summary statistics for biometric data are cited as mean ± SD, ranges are given as mininum and maximum values, and cited correlation coefficient is Pearson's R.

Abbreviations

Specimen depositories: BMNH, Natural History Museum, London, UK; CAS, California Academy of Sciences, San Francisco, California, USA; FKCP, collection of František Kovařík, Prague, Czech Republic; GL, collection of the author; MEB, collection of Matt E. Braunwalder, Zürich, Switzerland; MNHN, Muséum National d'Histoire Naturelle, Paris; NHMB, Naturhistorisches Museum Basel, Basel, Switzerland; ONHM, Oman Natural History Museum, Muscat, Oman; USNM, National Museum of Natural History, Washington, D.C., USA. *Biometrics*: L, length; W, width; D, depth.

Systematics

Genus Odontobuthus Vachon, 1950

Odontobuthus Vachon, 1950: 153–154; Vachon, 1952: 325–326; Stahnke, 1972b: 132; Vachon, 1974: 906; Tikader & Bastawade, 1983: 247; Francke, 1985: 10, 16; Vachon & Kinzelbach, 1987: 92; Farzanpay, 1988: 39; Sissom, 1990: 98, 102; El-Hennawy, 1992: 102, 105, 128; Nenilin & Fet, 1992: 17; 1998: 115; Fet & Lowe, 2000: 187; Lourenço & Pézier, 2002: 116; Soleglad & Fet, 2003a: 26; Fet, Soleglad & Lowe, 2005: 3, 12, 22; Prendini & Wheeler, 2005: 481; Kovařík, 2009: 24; Lourenço & Duhem, 2009: 38, 44–45, 48; Navidpour & Lowe, 2009: 49, 58.

Type species. Buthus doriae Thorell, 1877.

Diagnosis. Carapace granular, strongly carinate; superciliary carinae well developed; central lateral carinae joined to posterior median carinae, forming lyre configuration; central median carinae joined posteriorly

with central lateral carinae which bifurcate posteriorly; median eves large, on prominent ocular tubercle in anterior half of carapace; tergites I-II tricarinate, lateral carinae curved forward, joined to transverse carinae on posterior margin; tergites III-VI tricarinate, laterally granulose; tergite VII with 5 carinae; median lateral carinae complete on metasoma I, incomplete or nearly complete on metasoma II-III, absent on IV-V; ventrosubmedian carinae of metasoma II-III armed with 4-5 enlarged conical or tuberculiform denticles; anterior ventral margin of metasoma IV bearing transverse series of 3-6 enlarged denticles; ventrolateral carinae of metasoma V with series of enlarged denticles increasing in size posteriorly; telson vesicle bulbous, lacking subaculear tubercle or spine; cheliceral fixed finger with two denticles on ventral aspect; pedipalps orthobothriotaxic, type AB (Vachon, 1974, 1975); chela fixed finger with trichobothria et and est situated between db and dt; dentate margins of chela fingers armed with 10-14 non-imbricated linear subrows of primary denticles, flanked by 9-13 external and internal accessory denticles; movable finger with two subdistal internal denticles, flanked externally by row of 3-7 external denticles; base of fingers without scalloping; legs III-IV with tibial spurs; basitarsi I-III with bristle combs; ventral surfaces of telotarsi equipped with elongate setae.

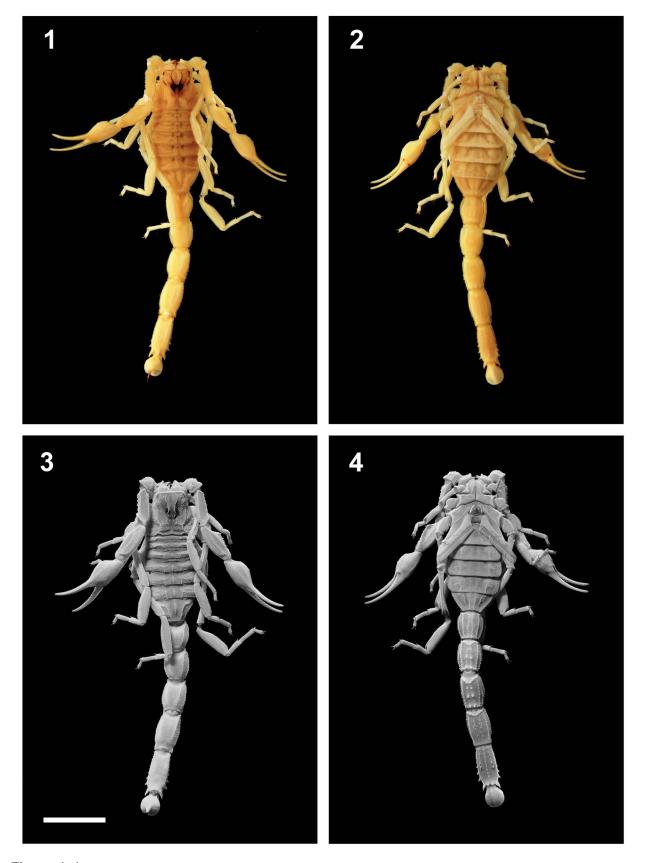
> *Odontobuthus brevidigitus* sp. nov. Figs. 1–30, 37–38, 49–50, 56–57, 60–65

Odontobuthus odonturus: Fet & Lowe, 2000: 188 (in part).

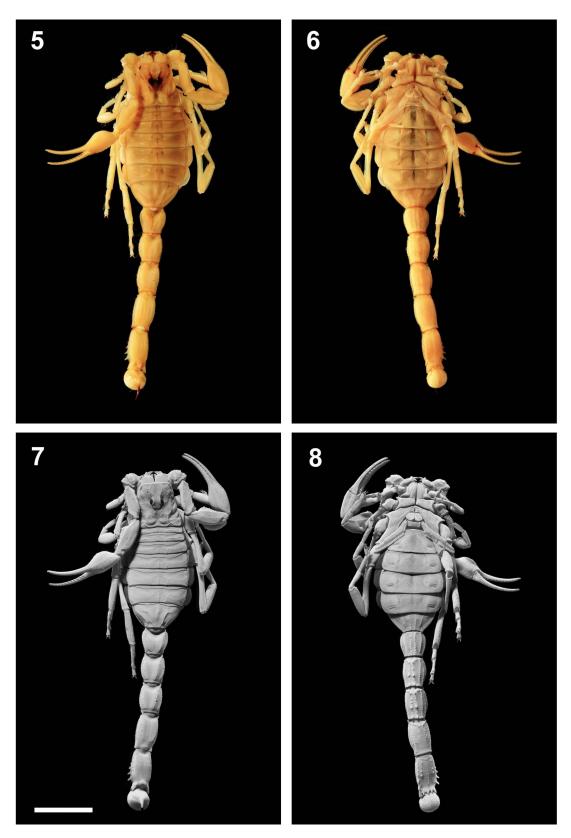
Odontobuthus sp.: Lowe, 1993: 3; Soleglad & Fet, 2003a: 5; Soleglad & Fet, 2003b: 7.

Holotype: adult ♂, **Oman**, Batinah Plain, ca. 4 km E of Seeb, UV detection, mouth of burrow in fine compacted soil/ sabkha, 23°41.39'N 58°06.93'E, 0 m a.s.l., 22 October 1993, 19:39 hrs, leg. G. Lowe, A.S. Gardner (NMB).

Paratypes: **Oman:** 2 \Diamond , 10 \bigcirc , 9 juveniles, same locality as holotype (NMB); 1 \bigcirc , same locality as holotype (GL); 2 \Diamond , near Khatmat Milahah, in and near chenopod scrub and *Prosopis* tree on dusty soil near sabkha, 24°57.36'N 56°22.33'E, 9 June 1994, 19:00-21:00 h, leg. M.D. Gallagher, MDG 8601 (ONHM); 1 \Diamond , Izki, in house, 22°56'N 57°46'E, 4 August 1994, J. Dundon (MCZ); 2 \bigcirc , between Bimmah and Fins, UV detection, on calcareous dune behind beach, between shrubs, 22°58.67'N 59°09.63'E, 5 m a.s.l., 20 February 1995, leg. M.D. Gallagher, MDG 8661 (ONHM); 3 juveniles, near Seeb, sandy area between fort roundabout and beach, at entrance to burrows, retreated into burrow at sight of UV lamp, excavated, 23°36'N 58°15'E, 15 m a.s.l., 1 June 1995, leg. J. Dundon (NMB); 4 \Diamond , 3 \bigcirc , 2



Figures 1–4: Odontobuthus brevidigitus, sp. nov., holotype male. Habitus viewed under reflected white light (1, 2) or UV fluorescence (3, 4). 1, 3. Dorsal aspect. 2, 4. Ventral aspect. Scale bar: 10 mm.



Figures 5–8: *Odontobuthus brevidigitus*, sp. nov., paratype female (from type locality). Habitus viewed under reflected white light (5, 6) or UV fluorescence (7, 8). 5, 6. Dorsal aspect. 7, 8. Ventral aspect. Scale bar: 10 mm.

juveniles, Izki area, at burrow entrance, 22°57'N 57°47'E, 590 m a.s.l., 5 June 1995, 20:00-22:00 h, leg. J. Dundon (ONHM); $2 \Diamond, 3 \Diamond, 4$ juveniles, plain SW of Seeb, UV detection, sandy area, at burrow entrance, excavated, 23°28.62'N 58°00.25'E, 15 m a.s.l., 13 August 1995, 22:30 h, leg. J. Dundon (MNHN, FKCP); 1 ♀, fragmented, Wadi Al Khawd, near Seeb, UV detection, east side of flooded wadi, 23°33.5'N 58° 06.66'E, 100 m a.s.l., 17-18 August 1995, 23:00-00:30 h, leg. J. Dundon (NMB); 5 ♂, 1 ♀, Izki area, UV detection, 22°57'N 57°47'E, 590 m a.s.l., 22 August 1995, 21:00–23:00 h, leg. J. Dundon (USNM); 1 Å, Ghubrah, on wall by door of Ministry house, under lights at night, 23°35.64'N 58°23.79'E, 10 m a.s.l, 30 September 1995, leg. G. Lowe (GL); 1 Å, Seeb area, in sandy burrow, 23°37.47'N 58°15'E, 15 m a.s.l., 26 October 1995, 21:00 h, leg. J. Dundon (MZSF); 1 immature \mathcal{Q} , 3 juveniles, Seeb airport area, UV detection, open sandy area among scattered bushes and trees, ca. 1 km from coast, 23°34'N 58°16'E, 5 m a.s.l., 19 January 1996, 0:30 h, leg. J. Dundon (114) (NMB); 1 \mathcal{Q} , near Bimah, in small 30 cm shrub, 10 cm from ground, 22°58.87'N 59°09.317'E, 17 November 1998, leg. I. Harrison (NMB); 3 ♀, Bahla Public Picnic (site F/14), daytime excavation, wadi with compact soil, powdery sand alluvium, in spiral burrows at base of or between small shrubs, 22°55.96'N 57°16.31'E, 450 m a.s.l., 04 January 1999, 12:15-17:00 h, leg. A. Winkler (NMB); 1 \bigcirc , Bahla Public Picnic (site F/14), day digging, wadi with compact soil, powdery sand alluvium; spiral burrows at base of small shrubs or between them, 22°55.96'N 57°16.31'E, 450 m a.s.l., 04 January 1999, 12:15-17:00 h, leg. A. Winkler (NMB); 1 Å, Al Ghubrah, near Muscat, 23°36'N 58°24'E, 04 June 1999, leg. D. Griffiths, ONHM 14/99 (MNHN); 1 3, Al Ghubrah, near Muscat, in house, 23°36'N 58°24'E, 03 October 1999, leg. D. Griffiths ONHM 18/99 (BMNH); 1 \bigcirc , Bahla Public Picnic (site F/5III), daytime excavation, wadi with compact soil, powdery sand alluvium, spiral burrows at base of or between small shrubs, 22°55.96'N 57°16.31'E, 450 m a.s.l., 23 January 2000, 10:00-12:30 h, leg. A. Winkler (USNM). United Arab Emirates: 1 ♀, region de Fujeira (Al Fujayrah), sandy desert with shrubs, 25°08.12'N 56°20.9'E, October 1972, leg. D.J.G. Williams, NMB 65, RS 6511 (NMB).

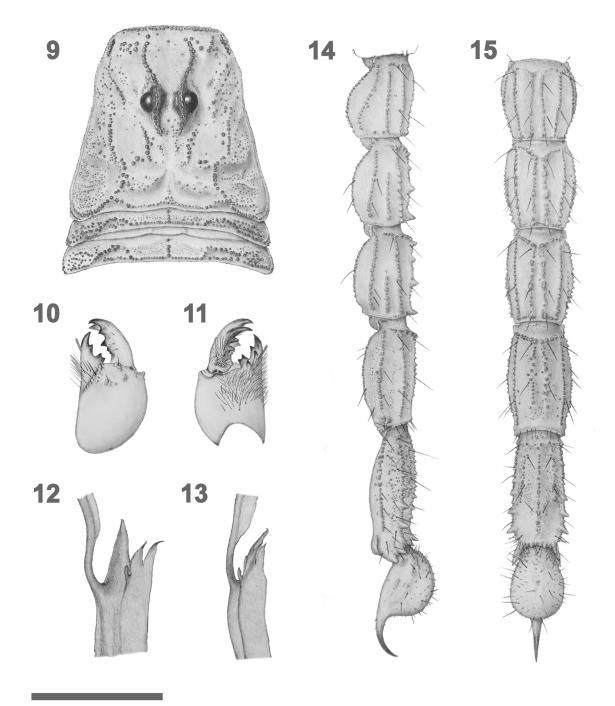
Diagnosis. A member of the genus *Odontobuthus* differentiated as follows: adults 50–65 mm in length; sternite IV of males with 4 carinae, median pair weakly developed, smooth; basal middle lamella of pectines narrow (Figs. 37–38), L/W 1.3–3.6 (males), 2.6–4.7 (females); distal tip of pectine extending past midpoint of trochanter IV in males (Fig. 4), past distal end of coxa IV in females (Fig. 8); ventrosubmedian carinae of metasoma II–III with 2–3 enlarged denticles (Fig. 14); anterior ventral margin of metasoma IV with transverse

row of 8-10 large granules (Fig. 15); males with metasoma IV stout, L/W 1.5-1.9; ventrolateral carinae of metasoma V armed with several enlarged pointed teeth; lateral anal arch divided into 3 lobes, 2 upper lobes deeply divided; ventral anal arch with 2 prominently enlarged, triangular denticles (Figs. 56–57); pedipalps robust, femur and patella short, stout; chela with swollen manus (Figs. 16-20); pedipalp femur L/W: males 2.5-3.2, females 2.5-2.9; pedipalp patella L/W: males 2.4-2.9, females 2.1-2.6; pedipalp chela L/W: males 3.7-5.4, females 2.8-4.4; ventroexternal carina of pedipalp patella with < 7 macrosetae; pedipalp fingers short, movable finger L/manus ventral L 1.4-1.75, fixed finger L/manus ventral L 1.2-1.5; movable finger straight; fixed and movable fingers with 10-12 subrows of primary denticles; primary denticles (excluding proximal subrow): 76-95 on fixed finger, 83-105 on movable finger; pedipalp patella with dorsomedian, ventromedian and ventroexternal carinae moderate to strong, granulate or dentate-granulate; dorsoexternal carina granulate in males, smooth in females.

Etymology. From Latin '*brevis*' meaning short, and '*digitus*' or finger, in reference to the relatively short pedipalp fingers compared to other species of *Odonto-buthus*.

Comparisons. *O. brevidigitus* **sp. nov.**, is differentiated from other *Odontobuthus* species by the following main characters: shorter pedipalp chela fingers relative to manus (Figs. 19, 55), corresponding reduction in primary denticle counts on fixed and movable chela fingers (Fig. 60), longer pectines (Figs. 4, 8, 46, 48), more elongate basal middle lamella (Figs. 37–44, 61), more stout metasoma IV (Figs. 1–8, 45–48, 62–63), and two enlarged triangular median denticles on ventral anal arch of metasoma V (Figs. 56–59).

O. bidentatus (Figs. 31-32, 43-48, 51-55, 58-59) differs as follows (n = 4 males, 1 female): adult length up to 85 mm; pectine with wider basal middle lamella (Figs. 43-44), male L/W 1.6-2.2, female 2.2-2.4; pectine of male shorter, distal tip not extending past midpoint of trochanter IV (Fig. 46); ventrosubmedian carinae of metasoma II-III with 2 enlarged denticles, third smaller denticle may be present (Fig. 31); anterior ventral margin of metasoma IV with transverse row of 8 large tuberculiform denticles; metasoma more elongate, male metasoma IV L/W 1.8-2.1; ventral anal arch without enlarged denticles (Figs. 58-59); ventroexternal carina of pedipalp patella with numerous macrosetae (> 10 in adults); longer pedipalp fingers, movable finger L/manus ventral L > 2.0-2.1, fixed finger L/manus ventral L 1.65-1.75; movable finger with distinct upward flexure (Fig. 55); fixed and movable fingers with 13-14 subrows of primary denticles; primary denticle count (excluding proximal subrow) 90-120 on fixed

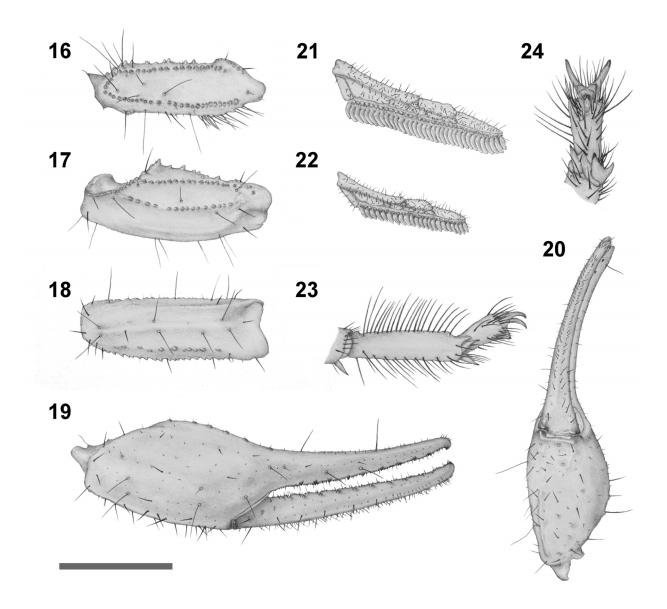


Figures 9–15: Odontobuthus brevidigitus, sp. nov. 9, 12–15, holotype male; 10–11, paratype male (Seeb). 9. Carapace, dorsal aspect. 10. Right chelicera, dorsal aspect. 11. Right chelicera, ventral aspect. 12–13. Right hemispermatophore, lobes at base of flagellum. 12 convex aspect, 13 outer aspect. 14–15. Metasoma and telson. 14. Right lateral aspect. 15. Ventral aspect. Scale bar: 9: 5 mm; 10–11: 3.8 mm; 12–13: 1.86 mm; 14–15: 7.66 mm.

finger, 105–131 on movable finger.

O. doriae (Figs. 35–36, 39–40) differs as follows (n = 8 males, 8 females): adults larger, 60–85 mm in length; sternite IV of males with two (lateral) carinae, median carinae obsolete; pectines with wider basal

middle lamella (Figs. 39–40), L/W 1.4–2.2 (males, n = 16 combs), 1.6–3.2 (females, n = 16 combs); distal tip of pectine not reaching midpoint of trochanter IV in males, and not reaching distal end of coxa IV in females; anterior ventral margin of metasoma IV with transverse



Figures 16–24: Odontobuthus brevidigitus, sp. nov. 16–18, 21, 23–24, holotype male; 19–20, paratype male (Ghubrah); 22, topoparatype female. 16. Right pedipalp femur, dorsal aspect. 17. Right pedipalp patella, dorsal aspect. 18. Right pedipalp patella, external aspect. 20. Right pedipalp chela, ventral aspect. 21. Left pectine, male, ventral aspect. 22. Left pectine, female, ventral aspect. 23. Right basitarsus and telotarsus III, retrolateral aspect. 24. Right telotarsus III, ventral aspect. Scale bar: 16–20: 4.00 mm; 21–22: 5.36 mm; 23: 3.00 mm; 24: 2.00 mm.

row of 4 large tuberculiform denticles; males with metasoma IV L/W 1.7–2.1; enlarged teeth on ventrolateral carinae of metasoma V blunt, not pointed; lateral anal arch divided into 2 lobes; ventral anal arch with 2 enlarged rounded denticles, and 2–4 smaller accessory denticles; pedipalps slender, pedipalp femur L/W: males 3.1–3.6, females 2.8–3.3; pedipalp patella L/W: males 2.7–3.3, females 2.5–2.9; pedipalp chela L/W: males 5.3–5.7, females 4.5–5.2; pedipalp fingers long, movable finger L/manus ventral L 1.8–2.2, fixed finger L/manus ventral L 1.6–1.9; fingers armed with 11–14 subrows of primary denticles; primary denticles (excluding proximal subrow) 97–118 on fixed finger (n = 31 fingers), 101– 121 on movable finger (n = 32 fingers); pedipalp patella with dorsomedian carina smooth, ventromedian and ventroexternal carinae weak to moderate, weakly granular or smooth; dorsoexternal carina smooth in males, obsolete in females.

O. odonturus (Figs. 33–34, 41–42) differs as follows (n = 3 males, 7 females): adults smaller, 35–55 mm in length; pectines with wider basal middle lamella (Figs. 41–42), L/W 1.5–2.1 (males, n = 6 combs), 1.9–3.3 (females, n = 14 combs); distal tip of pectine in females not extending beyond distal end of coxa IV; 3 enlarged denticles on ventrosubmedian carinae of metasoma II–III; anterior ventral margin of metasoma IV

with transverse row of 6 tuberculiform denticles; males with metasoma IV L/W 1.8-2.1; enlarged teeth on ventrolateral carinae of metasoma V rounded or moderately pointed; lateral anal arch divided into 3 lobes (2 upper anal lobes may be partially fused); ventral anal arch with at least 4 blunt denticles of similar size; pedipalps slender, pedipalp femur L/W: males 3.1-3.4, females 2.7-3.1; pedipalp patella L/W: males 2.7-2.9, females 2.4-2.8; pedipalp chela L/W: males 5.4-5.6, females 5.1-5.4; pedipalp fingers long, movable finger L/manus ventral L 1.9-2.3, fixed finger L/manus ventral L 1.7-2.0; pedipalp primary denticle count (excluding proximal subrow) 91–120 on movable finger (n = 13fingers), 92–115 on fixed finger (n = 14 fingers); pedipalp patella with dorsomedian carina weakly granular, smooth or obsolete, ventromedian carina weak, faintly granular distally, and ventroexternal carina obsolete; dorsoexternal carina reduced and smooth in males, obsolete in females.

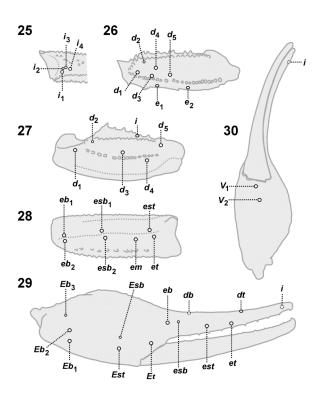
Description of holotype male (adult).

Coloration (Figs. 1–2). Base color uniform golden yellow; carapace with black pigmentation under median and lateral eyes, superciliary and anterior median carinae; underlying fuscosity around the median ocular tubercle, lateral ocular carinae, and external side of anterior median carinae; lateral interocular triangle ferruginous; tergites I–VI slightly ferruginous, with faint fuscosity along midline; metasoma V with faint underlying fuscosity on lower half of lateral surfaces; granules on carinae of pedipalps, carapace and tergites orange; articular condyles on pedipalp chela fingers and legs reddish brown; all macrosetae reddish brown; denticles on pedipalp chela fingers and aculeus of telson dark reddish brown.

Carapace (Fig. 9). Anterior margin of carapace nearly straight, with weak, finely denticulate median convexity, margin with 8 short macrosetae bordered by row of course granules; anterior median, central median, central lateral and posterior median carinae strong, studded with large polished granules; lateral ocular carinae moderate, coarsely granular; interocular triangle elevated; anterior median carinae curved outward, enclosing round, preocular depression; median ocular tubercle large, prominently elevated, with large, bulbous eyes separated by 1.4 times their diameter; superciliary carinae thick, with fused granules above eyes, separated granules posteriorly; central median carinae short; central lateral carinae bent inward posteriorly, joining with posterior median carinae; posterior median carinae outwardly curved posteriorly, bifurcating, merging with posterior marginal series of coarse granules; posterior marginal granules coarse, dentate laterally, finely granulate medially; medial intercarinal surfaces smooth or finely shagreened with scattered coarse granulation, lateral flanks with moderately dense, fine granulation; posterior median and posterior marginal furrows shallow.

Coxosternal area (Figs. 2, 4). Coxa I coarsely granular, endite with sparse granulation and coarsely granular carina on medial margin; coxae II-IV smooth, matte, with sparse, scattered fine granules; coxa II with heavy medium to coarse granulation on anterior and distal margins, endite with weakly granulose lateral marginal carina; coxa III with granulose anterior marginal carina, heavy granulation on distal margin; coxa IV narrow, elongate, distal margin smooth, anterior marginal carina finely granulose, complete, posterior marginal carina finely granulose to shagreened, obsolete in distal 1/3 of segment; macrosetae: coxa I, 2-3 distal marginal setae, 1-2 medial marginal setae on endite; coxa II, 3-4 anterior marginal setae, 2-3 distal marginal seta, 1 anterior seta on endite; coxa III, 4 anterior marginal setae, 1 distal marginal seta; coxa IV, 1 proximal anterior marginal seta, 1 distal marginal seta; sternum subtriangular, smooth, with deep, postero-median excavation; genital opercula smooth, rounded-triangular; genital papillae present; pectines elongate (Figs. 2-4, 21). tips extending well past midpoint of trochanter IV; pectines with 3 marginal lamellae, 6 middle lamellae, 1 intermediate lamella at distal end of proximal marginal lamella; basal middle lamella 3.1-3.6 times longer than wide; all lamellae with numerous reddish macrosetae, fulcra with 2-4 short reddish macrosetae; basal piece rectangular, smooth, with small anteromedian notch, 4 macrosetae; pectine teeth, left 34, right 33.

Mesosoma (Figs. 1-4, 9). Tergites: carinae on all tergites strong, armed with large tuberculate or dentate granules: tergites I-VI with 3 carinae: lateral carinae on I-II strongly anteriorly divergent, joined to transverse rows of granules extending along lateral posterior margins (Fig. 9), on III-VI weakly anteriorly divergent: median carinae on I-VI confined to posterior half of tergites; tergite VII with 5 carinae, median carina on longitudinal prominence, lateral carinae anteriorly divergent, inner lateral carinae becoming nearly transverse; all tergites with intercarinal surfaces matte or finely shagreened, I-VI with numerous tuberculate or dentate granules on lateral flanks and posterior margins, VII with lateral surfaces densely shagreened, posterior margins nearly smooth. Sternites: sternite III with 2 weak, flattened, posteriorly divergent carinae; sternites IV–VII with 4 carinae; median carinae on IV–VI weak, smooth, confined to posterior 2/3 of sclerite, strong granulate-crenulate on VII, confined to posterior 3/4 of sclerite; lateral carinae moderate, crenulate on IV-VI, confined to post-spiracular half of sclerite, bifurcated at posterior margin; lateral carinae of VII strong, crenulate, confined to anterior 2/3 of sclerite; IV-VI with trans-



Figures 25–30: Trichobothrial map of the pedipalp of *Odontobuthus brevidigitus*, sp. nov. 25–28, holotype male; 29–30, paratype male (Seeb). 25. Base of femur, internal aspect. 26. Femur, dorsal aspect. 27. Patella, dorsal aspect. 28. Patella, external aspect. 29. Chela, external aspect. 30. Chela, ventral aspect. Trichobothrial notation after Vachon (1974). Trichobothria on exposed surfaces indicated by solid circles, those on hidden surfaces indicated by dotted circles.

verse band of dense, fine granulation along anterior margins of stigmata; all sternites with pleural margins denticulate; medial intercarinal surfaces smooth or matte, lateral surfaces densely, finely shagreened.

Hemispermatophore (Figs. 12–13). Flagelliform; flagellum with wide lamina on pars recta; inner lobe at base of flagellum long, laminate; median lobe with tapered dorsal process, longer curved ventral process, fused together by wide lamina; outer lobe terminating distally in long thin, curved process; basal lobe well developed, flattened, not tapering distally.

Metasoma (Figs. 1–4, 14–15, 56–57). *Segments I–III*: with 10 carinae, dorsosubmedian, dorsolateral and median lateral carinae strong, dentate-granulate to serrate; median lateral carinae on I complete, on II confined to posterior 2/3, on III confined to posterior 1/2 of segment; ventrolateral carinae strong, on I crenulate, on II–III crenulate on anterior 3/4, granulate-dentate on posterior 1/4; ventrosubmedian carinae strong, crenulate to granulate on I, irregularly granulate on II–III with 3 nearly equally spaced, enlarged, triangular denticles,

most anterior denticle smaller than posterior two; anterior, ventral margin with prominent, arched dentategranulate carina, each side bearing 5 large granules, 3-4 small granules; carinal macrosetae on I-III: dorsosubmedian 0, 2, 3; dorsolateral 0, 2, 2; ventrolateral 2, 2-3, 2; ventrosubmedian 3, 3, 3 (third seta posterior marginal); dorsal and dorsolateral intercarinal surfaces densely, finely shagreened on I-III; ventral and lateral intercarinal surfaces smooth on I-II, smooth to lightly, finely shagreened on III; segment IV: with 8 carinae; dorsosubmedian carinae moderate, dentate-granulate anteriorly, granulate posteriorly; dorsolateral and ventrolateral carinae strong, dentate-granulate; ventrosubmedian carinae weak, with irregular large and small granules; anterior ventral margin with prominent arched carina, each side bearing 5 enlarged granules, 3–5 small granules; carinal macrosetae on IV: dorsosubmedian 4, dorsolateral 2-3, ventrolateral 2, ventrosubmedian 2; ventral posterior margin with 8 macrosetae; dorsal and dorsolateral intercarinal surfaces densely shagreened, lateral and ventral intercarinal surfaces lightly shagreened; segment V (Figs. 14-15, 58-59): with 7 carinae; dorsolateral carinae weak to moderate, strongly granular, ventrolateral carinae strong, conspicuously dentate; anterior half of carina with smaller, regular dentate granules, posterior half with 3 enlarged, triangular, bladelike denticles separated by series of 3-4 small denticles; ventrosubmedian carinae moderately developed, confined to anterior half of segment, with irregular small and large dentate granules; ventromedian carina strong, complete, with small and large dentate granules; anal arch developed into wide, dentate collar; ventral anal arch with 2 enlarged denticles; lateral anal arch deeply dissected into 3 large, triangular, dentate lateral anal lobes on each side; macrosetae: 6-7 on dorsolateral carinae. 11 on lateral surface. 2 on each ventrosubmedian carina, 2 on each concave side of posterior ventral surface; dorsal surface of segment V smooth medially, anteriorly and posteriorly, finely shagreened laterally; lateral surfaces granular; anterior half of ventral surface convex, coarsely shagreened, posterior half concave, smooth to finely shagreened.

Telson (Figs. 14–15). Vesicle bulbous, lustrous, with steeply sloped posterior face; dorsal surface smooth, lateral surface nearly smooth with shallow longitudinal furrow; ventral surface with scattered granules, more dense anteriorly; ventral and lateral surfaces bearing numerous scattered macrosetae (total 44); aculeus relatively short, stout, strongly curved.

Pedipalp (Figs. 16–20, 25–30). All segments relatively short, robust. *Femur* (Fig. 16): three times longer than wide, with 4 carinae; dorsoexternal, dorsointernal and ventrointernal carinae strong, dentate-granulate; internal carina weak, marked by 9 large dentate granules; inter-

carinal surfaces smooth; distal external macrosetae: lower cluster 20, intermediate row 2, upper row 4-5. Patella (Fig. 17-18): 2.7 times longer than wide, with 8 smooth to coarsely granular carinae; dorsointernal carina strong, dentate-granulate; dorsomedian carina moderate, weakly granulate-crenulate; dorsoexternal carina weak, faintly granular distally, smooth proximally; external carina weak, smooth; ventroexternal carina moderate, granulate; ventromedian carina strong, granulate; ventrointernal carina strong, dentate-granulate; internal carina moderate with several large dentate granules, including proximal patellar spur; intercarinal surfaces smooth. Chela (Figs. 19-20): manus swollen, fingers relatively short; ventroexternal carina moderate, smooth; dorsal secondary and dorsal marginal carinae weak, smooth; all other carinae obsolete; manus smooth except for scattered dentate granules on interior surface, fingers smooth; primary denticles subrows (including proximal subrow): fixed finger, 10 right, 12 left; movable finger, 12 left, 11 right; all subrows except proximal flanked by external accessory denticle, all except proximal two subrows flanked by internal accessory denticle; movable finger with 5 subdistal denticles, 2 internal, 3 external; trichobothrial pattern orthobothriotaxic, type AB (Vachon, 1974, 1975) (Figs. 25-30); et adjacent to denticle subrow 7 on right finger, subrow 5 on left finger; est adjacent to denticle subrow 9 on right chela, subrow 8 on left chela.

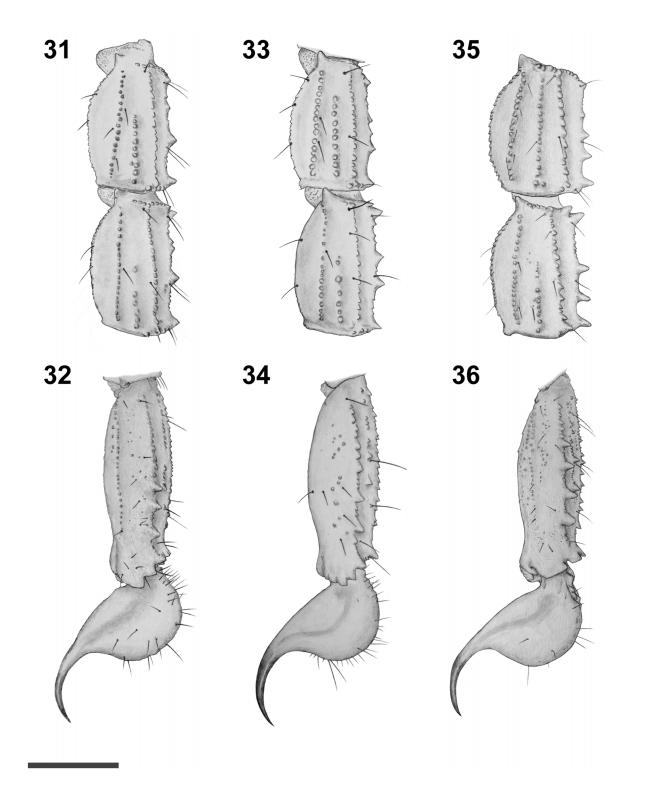
Legs (Figs 1–4, 23–24). Relatively short, robust; retrosuperior margins of tibia and basitarsus of legs I–III with bristle combs; retrosuperior setae on basitarsi: I 10, II 13–14, III 15–19; tibial spurs present on legs III–IV; tarsal spur simple on leg I, with 3 macrosetae, basally bifurcate on legs II–IV, with 4 macrosetae on II, 6–7 on III–IV; telotarsus with ventromedian row of 4–5 macrosetae, prolateral and retrolateral apical tufts of 8–10 macrosetae.

Chelicera (paratype male) (Figs. 10–11). Manus large, smooth, convex; dorsal anteromedial carina strong, with large granules; dorsal distal margin with cluster of coarse granules at base of movable finger, finer granules in transverse subdistal series; movable finger longer than fixed finger; fingers with normal buthid dentition (Vachon, 1963; Sissom, 1990): movable finger with large dorsal distal tine and ventral distal tine of equal size; dorsal margin with subdistal, large medial, and two small basal denticles in bicusp; ventral margin with 2 equal size denticles; fixed finger with subdistal denticle and large basal bicusp; ventral aspect of fixed finger with two prominent denticles, distal denticle slightly larger than proximal denticle; setation: dorsal side of manus with single dark reddish macroseta on anteromedial carina, three long pale microsetae, two on distal margin, one among subdistal granules; ventral surface of manus with numerous fine setae on anterior half; dense brush of long translucent setae on ventral and internal aspect of fixed finger; movable finger with 5 small microsetae on dorsal aspect, numerous long, fine setae on ventral aspect.

Measurements of holotype male (mm). Total L 57.00; carapace L 7.27, preocular L 2.92, anterior W 4.13, posterior W 7.30; metasoma I L 4.64, W 4.39, D 3.78; metasoma II L 5.33, W 4.13, D 3.61; metasoma III L 5.68, W 4.02, D 3.66; metasoma IV L 6.58, W 3.91, D 3.27; metasoma V L 7.74, W 3.11, D 2.67; telson L 6.46, vesicle L 4.10, W 3.14, D 2.93; pedipalp femur L 5.93, W 1.98; pedipalp patella L 6.88, W 2.58; pedipalp chela L 11.67, W 3.05, D 3.38, ventral L 5.16, fixed finger L 6.54, movable finger L 7.74; pectine L 9.03.

Measurements of paratype female (adult, same locality as holotype) (mm). Total L 60.00; carapace L 7.74, preocular L 3.11, anterior W 4.69, posterior W 8.16; metasoma I L 4.52, W 4.56, D 3.87; metasoma II L 5.33, W 4.21, D 3.96; metasoma III L 5.55, W 3.96, D 3.87; metasoma IV L 6.36, W 3.80, D 3.27; metasoma V L 7.74, W 3.35, D 2.58; telson L 6.69, vesicle L 4.17, W 3.59, D 3.20; pedipalp femur L 5.93, W 2.05; pedipalp patella L 6.71, W 2.84; pedipalp chela L 12.91, W 3.27, D 3.44, manus ventral L 4.82, fixed finger L 6.90, movable finger L 8.43; pectine L 7.22.

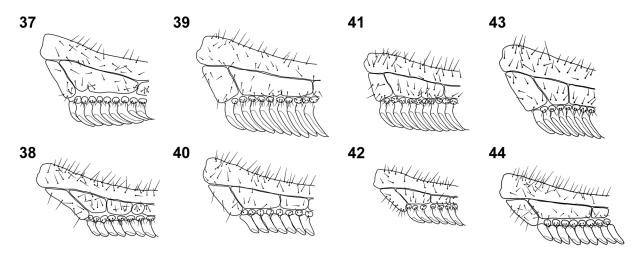
Variation. Color: dark pigmentation and fuscosity underlying the ocular tubercle and anterior interocular area is less intense in material from the Izki area, and tergites of some individuals had a faint rusty brown tinge. Size: adult body L 51-63 mm; carapace L: males 6.57-7.80 mm (n = 13); females 7.10–8.08 mm (n = 15). Sexual dimorphism: adult females differed from adult males as follows: carapace and tergites with intercarinal surfaces smoother, more minutely shagreened, carinae weaker with smaller granules: mesosoma wider: sternites: III without carinae, IV-V without median carinae, with very weak lateral carinae, VI with 4 very weak carinae, VII with four weak to moderate, crenulate carinae; all sternites smooth; pectines smaller, shorter, tips not extending past proximal 1/4 of trochanter IV, with fewer teeth; basal middle lamellae of pectines narrower; dorsal and dorsolateral surfaces of metasoma smoother; larger denticles on ventrosubmedian carinae of metasoma II-III; dorsoexternal carina of pedipalp patella smooth, nearly obsolete. Morphometrics: both sexes (n = 28)adults): median ocellus separation/carapace L 0.14–0.19; pedipalp femur L/W 2.51-3.18, pedipalp patella L/W 2.14-2.82, pedipalp movable finger L/manus ventral L 1.49–1.75; males (n = 13): pedipalp chela L/W 3.7–5.3, pedipalp manus L/W 1.45-2.25, basal middle lamella L/W 1.37–3.57 (2.36 \pm 0.44, n = 26 combs); females (n= 15): pedipalp chela L/W 2.85–4.32, pedipalp manus



Figures 31–36: Lateral views of metasoma II–III, V and telson of *Odontobuthus* species, showing carinal dentition. 31–32, *O. bidentatus* (Omidiyeh, Iran); 33–34, *O. odonturus* (Lalian, Pakistan); 35–36, *O. doriae* (Tabiz, Iran). 31, 33, 35. Metasoma II–III, lateral aspect. 32, 34, 36. Metasoma V and telson, lateral aspect. Scale bar: 31-32: 5 mm; 33-34: 3.27 mm; 35-36: 4.30 mm.

L/W 1.46-1.73, basal middle lamella L/W 2.68-4.67 $(3.70 \pm 0.53, n = 27 \text{ combs})$. Variation of selected mor-

to data from other Odontobuthus species. Meristics: pectine teeth: males 29-36 (1 comb with 29 teeth, 4 with phometric ratios is plotted in Figs. 61–63, in comparison 30, 1 with 31, 3 with 32, 7 with 33, 7 with 34, 2 with 35,



Figures 37–44: Representative basal lamellae of the pectines of *Odontobuthus* species. 37, 38. *O. brevidigitus* sp. nov.; 37, holotype male; 38, paratype female (from type locality). 39, 40. *O. doriae* (Tabiz, Iran); 39, male; 40, female. 41, 42. *O. odonturus*; 41, male (Lalian, Pakistan); 42, female (Manshera, Pakistan). 43, 44. *O. bidentatus*; 43, male (Omidiyeh); 44, female (Ahram).

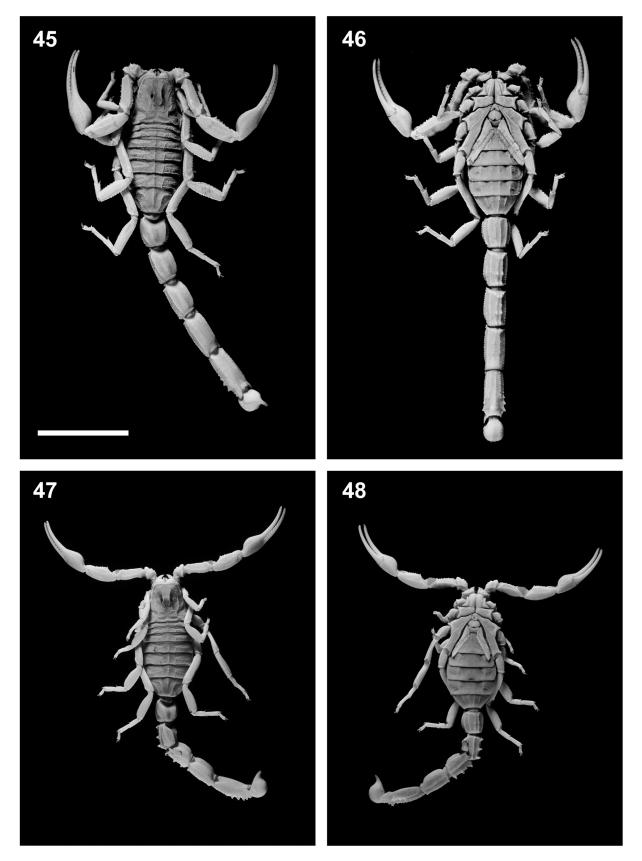
1 with 36); females 20-25 (6 combs with 20 teeth, 8 with 21, 6 with 22, 4 with 23, 3 with 24, 1 with 25); pedipalp finger primary denticles (excluding proximal subrow): movable finger 83–105 (95 \pm 4.5; n = 54 fingers), male fixed finger 81-94 (85 ± 3.6 ; n = 23 fingers), female fixed finger 80–99 (89 \pm 4.4; n = 27 fingers); pedipalp finger primary denticle subrows (including proximal): movable finger 10-12 (3 fingers with 10 subrows, 37 with 11, 15 with 12), fixed finger 10-12 (2 fingers with 10 subrows, 38 with 11, 11 with 12) (Figs. 49-50, 60); on fixed finger, trichobothrium et adjacent to subrow 5 in one finger, subrow 7 in 49 fingers; est adjacent to subrow 8 in 14 fingers, subrow 9 in 35 fingers, subrow 10 in one finger; these data exclude cases of anomalous dentition, i.e. fusion of distal subrows or irregular spacing or size of denticles; of 58 chelae examined, anomalous dentition was observed in 5 fixed fingers, 1 movable finger. Metasomal dentition: dentition on ventrosubmedian carinae of metasoma II-III was variable, with 1-4 enlarged denticles per carina, posterior two denticles always as large, or larger than, additional anterior denticles; metasoma II, 2.76 ± 0.65 enlarged denticles, n = 104 ventrosubmedian carinae (including juveniles), 2 carinae (1.9 %) with 1 denticle, 31 (29.8 %) with 2 denticles, 61 (58.7 %) with 3, and 10 (9.6 %) with 4; metasoma III, 2.84 ± 0.61 enlarged denticles, n = 104 ventrosubmedian carinae (including juveniles), 2 carinae (1.9%) with 1 denticle, 23 (21.1%)with 2 denticles, 91 (66.4 %) with 3, and 10 (9.6 %) with 4; correlation of number of enlarged denticles on left and right ventrosubmedian carinae weak on metasoma II (R = 0.26, P = 0.06), stronger on metasoma III (R = 0.37, P = 0.006); although females had larger denticles than males, number of enlarged denticles was not sexually dimorphic (P = 0.97 for metasoma II, 0.22 for metasoma

III; n = 50 female, 54 male carinae; Mann-Whitney U test); in some adults, enlarged ventrosubmedian denticles on metasoma II-III, and ventrolateral denticles on metasoma V were blunted, presumably due to wear: ventral anal arch sometimes with smaller accessory denticles between the 2 enlarged denticles. Hemi*spermatophores* (n = 4 paratype males): lobes at the base of flagellum similar to those of holotype male; differences in ornamentation included weakly bicuspid basal lobe (2 males from Izki) and small denticle in gap between flagellum and the inner lobe. Juveniles: pigmentation similar to adults, but with fuscous areas darker, more extensive, additional fuscosity on pedipalps at base of chela fingers and lateral surfaces of metasoma V; faint granular fuscosity spread over surfaces of pedipalps and tergites; compared to adults, pedipalps more slender, all carinae weakly developed without enlarged granules, all macrosetae short and pale; pattern of enlarged denticles on metasomal segments similar to that in adults; enlarged ventrolateral and circum-anal denticles on metasoma V much larger relative to the size of the segment.

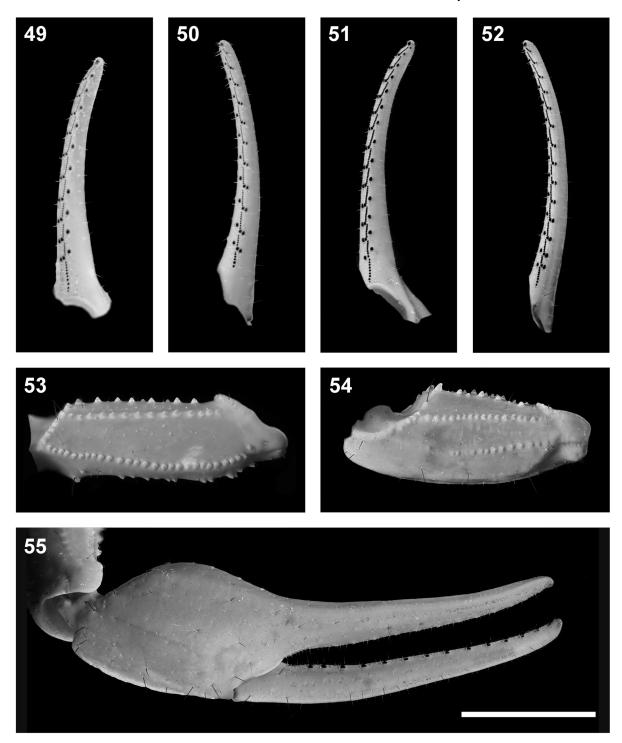
Distribution. *O. brevidigitus* **sp. nov.**, is known only from northern Oman and adjacent United Arab Emirates. It is deployed along the narrow Batinah coastal plain (Fig. 64), and also penetrates inland through the Sumail gap into the interior side of the Al Hajar Ranges. All known records are from lower elevations (< 600 m a.s.l.).

Ecology. This species is a fossorial scorpion. The robust legs and pedipalps, and enlarged denticles on the ventrosubmedian carinae of metasoma II–III and ventrolateral carinae of metasoma V, appear to be adap-

Lowe: New Odontobuthus from Oman



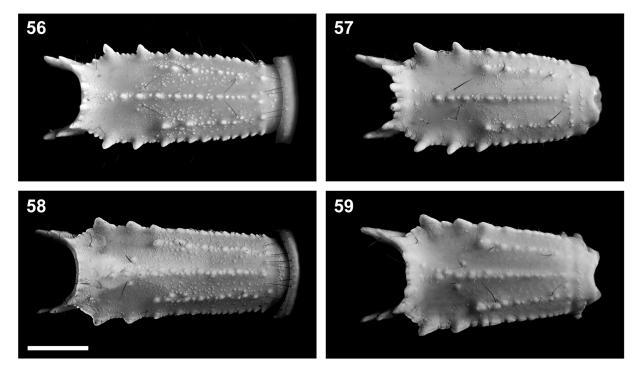
Figures 45–48: *Odontobuthus bidentatus*, habitus under UV fluorescence. 45–46, male (Omidiyeh). 45. Dorsal aspect. 46. Ventral aspect. 47–48, female (Ahram). 47. Dorsal aspect. 48. Ventral aspect. Scale bar: 20 mm.



Figures 49–55: *Odontobuthus brevidigitus* **sp. nov.**, paratype male (Seeb), right pedipalp finger dentition. **49.** Fixed finger. **50.** Movable finger. **Figures 51–55:** *O. bidentatus*, male (Omidiyeh). **51–52**, right pedipalp finger dentition. **51.** Right fixed finger. **52.** Right movable finger. **53.** Right pedipalp femur, dorsal aspect. **54.** Right pedipalp patella, dorsal aspect. **55.** Right pedipalp chela, external aspect. Scale bar: 46, 47: 3.42 mm; 48, 49: 5.70 mm; 50: 4.56 mm; 51: 5.22 mm; 52: 5.00 mm. Photographed under UV fluorescence.

tations for burrowing in compacted substrates (Lowe, 1993). Burrows are excavated in dense sandy or silty soils on alluvial plains. At the surface, burrows begin as a tube with shallow slope extending 40–60 cm, and may

include a bend or spiral, before terminating in an enlarged chamber. At night the scorpions ambush prey by stationing themselves just inside the mouth of their burrow with only their pedipalp chelae and anterior pro-



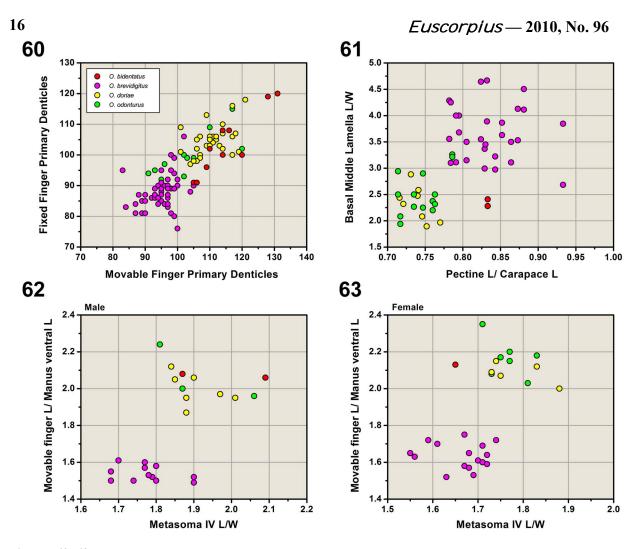
Figures 56–59: Ventral aspect of metasoma V. 56–57, *Odontobuthus brevidigitus* sp. nov. 56. Holotype male. 57. Paratype female. 58–59, *O. bidentatus*. 58. Male (Omidiyeh). 59. Female (Ahram). Scale bar: 56: 2.00 mm; 57: 2.17 mm; 58: 2.90 mm; 59: 2.40 mm. Photographed under UV fluorescence.

soma exposed. Individuals can be located by ultraviolet detection, but when approached they quickly retreat into their burrows and must then be excavated. Two specimens from the Izki area had ectoparasitic mites attached to pleural and intersternal membranes of the metasoma. The mites were purple with a white dorso-median stripe. Along the Batinah coast, populations of *O. brevidigitus* coexist closely with human settlements, and male scorpions may wander into buildings at night. However, because of its obligate burrowing habit and wary disposition, this species is probably not encountered very frequently.

Discussion

The discovery of *Odontobuthus brevidigitus* **sp. nov.**, in northern Oman represents a significant range extension for the genus into the Arabian Peninsula. Confirmed records for the three previously known species were confined to India, Pakistan, Iran and Iraq (Lourenço & Pézier, 2002). The four species display a broad, allopatric or parapatric pattern of distribution, spanning > 2,000 km across five countries (Fig. 65): *O. odonturus* in the Indus River drainage of southern Pakistan and Rajasthan desert of adjacent India; *O. doriae* in the Zagros, Elburz and Qohrud Mountains of western Iran; *O. bidentatus* in the Tigris-Euphrates River drainage of eastern Iraq and western foothills of the Zagros Mountains in Iran; and *O. brevidigitus* on the

Batinah coast and foothills of the Al Hajar Mountains of northern Oman. Character-based analysis of the phylogenetic relationships of these species poses a challenge due to their close morphological similarity and uncertainty about their nearest relatives within the buthids. However, a biogeographic hypothesis of speciation can be developed from regional paleaoclimatic and geological considerations. The range of distribution of the genus encompasses the intersection of the Arabian, Eurasian and Indian lithospheric plates, and its speciation may be linked to the Tertiary sequence of tectonic interactions between these plates. The Indus River is aligned with the suture zone of the Eurasian and Indian plates, and it appears to have formed there after collision of these plates in the early Eocene, ca. 55 Mya (Clift, 2002). Since then it has remained trapped in this zone, resulting in the accumulation of a major fan of clastic sediment derived from erosion of the Himalayas. Indus sediment transport to the Arabian Sea dates back to the mid-Eocene (ca. 45 Mya), with major flux pulses in mid-Miocene times (21 Mya, 16 Mya and 11-9 Mya). It is proposed here that alluvial deposits of the Indus delta that were accumulated during this early period provided a favorable substrate for the evolution of a fossorial, arenicolous scorpion, perhaps the ancestor of present day Odontobuthus. Presumably, this species gradually dispersed westward from the fertile plains of the Indus, eventually achieving widespread distribution across the Iranian plateau as far as the Tigris-Euphrates delta.



Figures 60–63: Scatter plots showing variation in selected meristic and morphometric data from *Odontobuthus*, comparing the new species to other members of the genus. **60.** Plot of primary denticle counts (excluding proximal subrow) of pedipalp chela fixed finger vs. movable finger. **61.** Plot of pectine basal middle lamella length/ width vs. pectine length/ carapace length, for females. **62.** Plot of Pedipalp chela movable finger length/ chela manus ventral length for males. **63.** Plot of Pedipalp chela movable finger length/ chela manus ventral length for males. **63.** Plot of Fig. 60: magenta circles, *O. brevidigitus* **sp. nov.**; red circles, *O. bidentatus*; yellow circles, *O. doriae*; green circles, *O. odonturus*.

Around 11–9 Mya, folding and uplift of the Zagros Mountains commenced after collision of the Arabian plate with the Eurasian Plate (Takin, 1972). The orogeny intensified in the mid-Pliocene (5-3 Mya) as the Arabian plate rifted from Africa, and was accompanied by sinking of central & eastern areas of the Iranian plateau, leading to the formation of the extensive gravel and sand deserts of Dasht-e-Kavir and Dasht-e-Lut. These geologic transformations may have fragmented Odontobuthus into at least three species: O. doriae, which became adapted to higher elevations in the Zagros; O. odonturus, which descended from the original lineage on the low elevation Indus delta; and O. bidentatus inhabiting alluvial plains of the Tigris-Euphrates drainage, separated from O. doriae by spectacular anticlines and peaks of the Zagros, ascending over 3,000 m a.s.l.

Key steps in the evolution and speciation of other terrestrial faunas of the Iranian plateau have been linked

to uplift of the Zagros mountains. For example, analyses of mitochondrial DNA sequences indicate major splittings in clades of the Eremia persica complex of lacertid lizards, and the Laudakia caucasia species group of agamid lizards in Iran, around 11-9 Mya (Macey et al., 1998; Rastegar Pouvani et al., 2010). Other reptile groups are thought to have achieved more rapid dispersal and speciation in the late Tertiary. Among the skinks, members of the genus Chalcides spread across North Africa and the Sahara within 7-5 Mya, and Scincus across Africa and into Arabia within 6 Mya (Carranza et al., 2008). The *Echis carinatus* group of carpet vipers has an extensive distribution ranging from northern Oman to Pakistan, India and Central Asia, comparable to the range of Odontobuthus. Genetic similarity across this range suggests rapid, recent dispersal (Arnold et al., 2009; Pook et al., 2009). Dispersal rates are expected to vary among animals with different

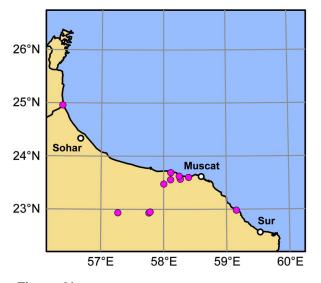


Figure 64: Plot of collection sites of *Odontobuthus brevidigitus* sp. nov., (magenta circles) in northern Oman.

adaptations. Skinks and snakes are vagile, epigean biota capable of more rapid dispersal than sessile forms with specialized substrate requirements, such as endogean, fossorial *Odontobuthus* scorpions.

A model of dispersal and vicariant speciation by Zagros orogeny is consistent with the currently known distribution of Odontobuthus in Iran. However, it should be noted that systematic surveys of scorpion fauna have not been conducted in much of central, eastern and southern Iran, and western Pakistan, so there are significant gaps in sampling of the distribution of this genus. Birula (1900, 1905) cited several records of "Buthus odonturus" from southern Iran, at longitudes and elevations intermediate between western (Zagros) sites of *O. doriae* in Iran and eastern (Indus) sites of *O.* odonturus in Pakistan (see open circles in Fig. 65). These specimens were not studied by Lourenço & Pézier (2002), so their relationship to the western and eastern species is unclear. It is possible that clinal variation along the Makran coast could link the Zagros and Indus populations into a single, variable taxon.

In conjunction with Zagros orogenic activity, the Arabian Gulf formed as a shallow tectonic depression that was flooded at the end of the Pliocene (2 Mya). This created a marine barrier that would have split off *Odontobuthus* in south eastern Arabia from the *O. bidentatus* lineage inhabiting the Tigris-Euphrates drainage and western foothills of the Zagros mountain chain, resulting in speciation of *O. brevidigitus*. Although the Gulf has been dry during subsequent Pleistocene glaciations, its surface during those epochs was probably covered by aeolian dunes composed of calcareous deposits of marine micro-organisms. This type of terrain could have presented a significant barrier to the dispersal of *Odontobuthus*, a fossorial scorpion

specialized for burrowing in firm, consolidated soils. Indeed, it was suggested that the genus Apistobuthus may have been derived from Odontobuthus by the development of psammophilous adaptations that facilitated colonization of the Rubh al-Khali dune systems on the Arabian Peninsula (Navidpour & Lowe, 2009). Marine transgression of the Arabian Gulf was probably a vicariant factor in the speciation of other animals, such as gekkonid lizards of the genus Assacus which exhibit a disjunct distribution in the Zagros mountains of Iran, and the Al Hajar mountains of northern Oman and United Arab Emirates (Arnold & Gardner, 1994; Rastegar-Pouvani, 2006). Since Assacus are lithophilic, it is unlikely that they would have crossed the sandy expanses of a dry Arabian Gulf during glacial maxima. On the other hand, vipers of the Echis carinatus group are well adapted to sandy substrates, and gene flow between Arabian and Asian populations was apparently maintained until relatively recently (0.9 Mya) (Arnold et al., 2009; Pook et al., 2009).

The biogeographic model sketched here implies a temporal ordering with *O. brevidigitus* as the most recent species, followed by *O. bidentatus* and *O. doriae*, and lastly *O. odonturus* as the oldest, direct descendent of the ancestral species. The predicted splitting events are well spaced in geologic time, and should therefore be amenable to testing by molecular phylogenetic analysis.

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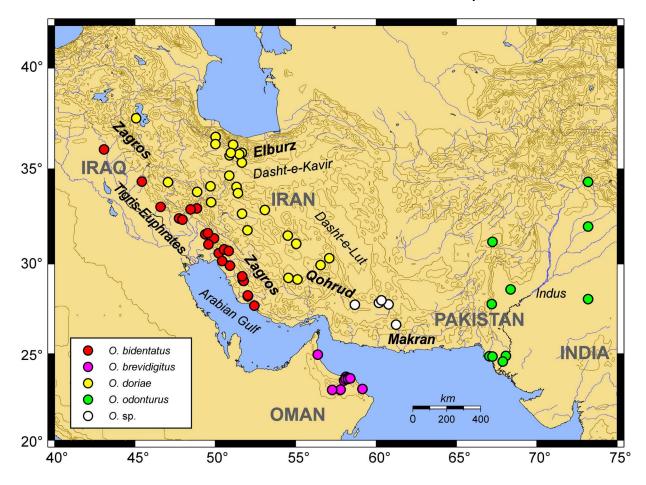


Figure 65: Plot of collection sites of all four species of *Odontobuthus* on a topographic map of the Middle East. Magenta circles, *O. brevidigitus* sp. nov.; red circles, *O. bidentatus* Lourenço et Pézier, 2002; yellow circles, *O. doriae* (Thorell, 1876); green circles, *O. odonturus* (Pocock, 1897); open circles, *O. sp.* (indeterminate) (locality data from specimens examined and literature records: Birula, 1900, 1905; Kovařík, 1997; Lourenço & Pézier, 2002; Navidpour et al., 2008a, 2008b, 2008c, 2008d; Pirali-Kheirabadi et al., 2008).

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Appendix A

Comparative material examined. Odontobuthus dor*iae*: 1 ∂, 3 ♀, Iran, Kachan, 33°35.4'N 51°21'E, RS 7827 (CAS); 1 ♂, 1 ♀, Iran, near Tabiz, 6 July 1984, leg. R. Farzanpay, MEB 107 (MEB); $2 \stackrel{?}{\ominus}, 2 \stackrel{?}{\ominus}$, Iran, ca. 5 km SE of Varamine, 27 August 1984, leg. R. Farzanpay, MEB 162 (MEB); 1 ♂, 1 ♀, Iran, ca. 2 km SE of Varamine, 27 August 1984, leg. R.Farzanpay, MEB 161 (MEB); 5 ♂, 3 ♀, Iran, Varamine, 50 km SE Tehran, 17 July 1985, leg. R. Farzanpay, MEB 242 (MEB); 3 \Diamond , 4 \bigcirc , Iran, Ghamsar, ca. 65 km E Tehran, 18 July 1985, leg. R. Farzanpay, MEB 243 (MEB). Odontobuthus odonturus: 1 3, Pakistan, Usta Mohammed, April-May 1953, leg. M. Sadiq, Zool. Survey Dept. (CAS); 1 ♀, Pakistan, Haleji Lake, Tatta District, January 1959, 59-1096 (CAS); 1 Å, Pakistan, E edge of Karachi, in modern house, 30 September 1959, leg. O. Haggem (CAS); 17 ♀, Pakistan, Pir Patho, Tatta District & nearby localities in Indus Delta, W Pakistan, before

1963, leg. S. Minton Jr. (CAS); 2 \mathcal{O} , Pakistan, Pir Patho, Tatta District & nearby localities in Indus Delta, W Pakistan, before 1963, leg. S. Minton Jr. (USNM); 1 iuvenile. Pakistan, 40 km SE Sirian, under rocks in sand. 29°25.7'N 56°00'E, 10 March 1963, leg. L.H. Herman (USNM); 1 ♀, Pakistan, Manshera, Hazara District, NW Frontier Province, 09 July 1982, leg. M.S. Khan, MEB 060 (MEB); 1 ♂, Pakistan, Lalian, District Ihang, Punjab, 30 August 1982, leg. M.S. Khan, MEB 059 (MEB). Odontobuthus bidentatus: 1 3, Iran, Khoozestan Province, Omidiyeh, 30°57'49" N 49°31'47" E, 56 m a.s.l., leg. Hayader & Bahrani (GL); 1 ♀, Iran, Bushehr Province, Ahram, Khormuj Rd, 28°45'43" N 51°17'51" E, 43 m a.s.l., leg. Masihpour, Bahrani & Hayader (GL); 3 \mathcal{E} , Iran, Bushehr Province, Tangestan, Farshanbeh, 28°52'53" N 51°18'43" E, 95 m a.s.l., leg. Masihpour, Bahrani & Hayader (GL).

Key to species of Odontobuthus.

Metasoma IV anterior ventral margin with transverse row of 6 or fewer enlarged granules; female pectine not 1 extending to distal end of trochanter IV; pectine L/ carapace L 0.77–0.95; pedipalp patella dorsomedian carina Metasoma IV anterior ventral margin with transverse row of 8 or more enlarged granules; female pectine extending to, or past, distal end of trochanter IV; pectine L/ carapace L 0.70-0.80; pedipalp patella dorsomedian Metasoma IV anterior ventral margin with transverse row of 4 enlarged granules; lateral anal arch divided into 2 Metasoma IV anterior ventral margin with transverse row of 6 enlarged granules; lateral anal arch divided into 3 lobes; found in low elevations of Indus River drainage of Pakistan, and Rajasthan desert of western India Pedipalp movable finger/ manus ventral L > 1.7 (males), > 1.9 (females); median ventral anal arch without 2 3 enlarged triangular denticles; ventroexternal carina of pedipalp patella with > 10 macrosetae; found in Tigris-Euphrates River drainage of Iraq, west foothills of Zagros mountains in Iran Pedipalp movable finger/ manus ventral L < 1.7 (males), < 1.9 (females); median ventral anal arch with 2 enlarged triangular denticles; ventroexternal carina of pedipalp patella with < 7 macrosetae; found along coast