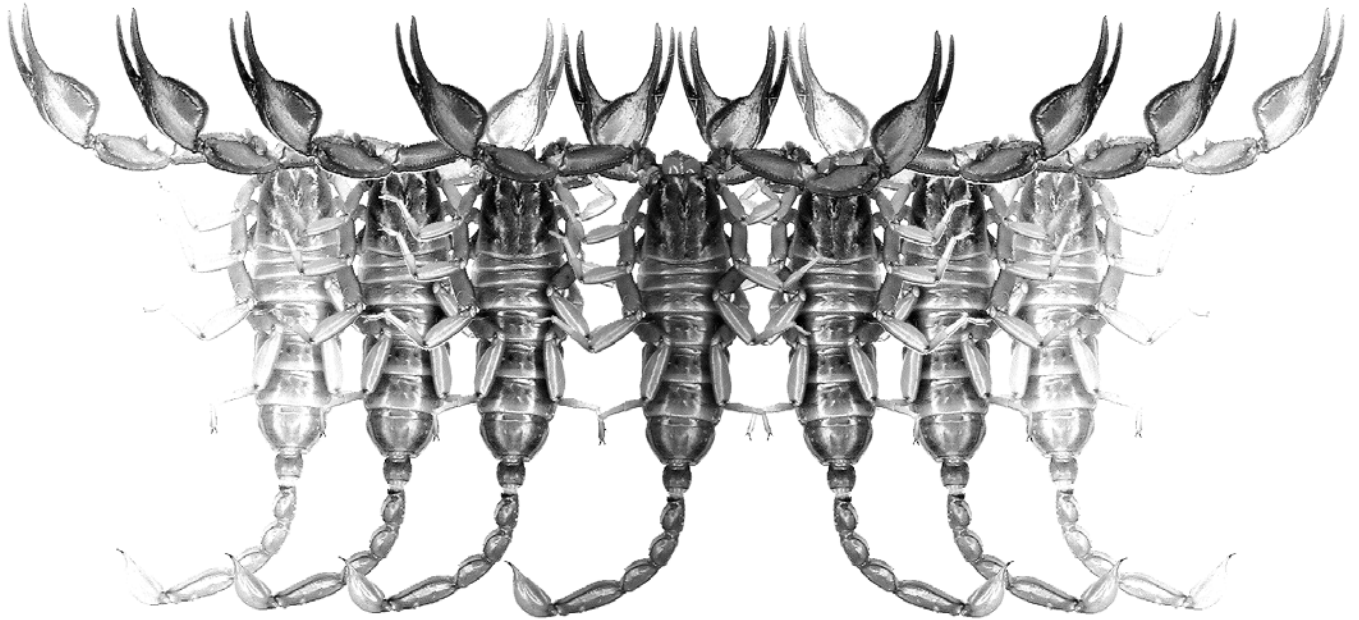


Euscorpius

Occasional Publications in Scorpiology



**The Genus *Vachoniolus*
(Scorpiones: Buthidae) in Oman**

Graeme Lowe

August 2010 – No. 100

Euscorpius

Occasional Publications in Scorpiology

EDITOR: Victor Fet, Marshall University, ‘fet@marshall.edu’

ASSOCIATE EDITOR: Michael E. Soleglad, ‘soleglad@la.znet.com’

Euscorpius is the first research publication completely devoted to scorpions (Arachnida: Scorpiones). *Euscorpius* takes advantage of the rapidly evolving medium of quick online publication, at the same time maintaining high research standards for the burgeoning field of scorpion science (scorpiology). *Euscorpius* is an expedient and viable medium for the publication of serious papers in scorpiology, including (but not limited to): systematics, evolution, ecology, biogeography, and general biology of scorpions. Review papers, descriptions of new taxa, faunistic surveys, lists of museum collections, and book reviews are welcome.

Derivatio Nominis

The name *Euscorpius* Thorell, 1876 refers to the most common genus of scorpions in the Mediterranean region and southern Europe (family Euscorpiidae).

Euscorpius is located on Website ‘<http://www.science.marshall.edu/fet/euscorpius/>’ at Marshall University, Huntington, WV 25755-2510, USA.

The International Code of Zoological Nomenclature (ICZN, 4th Edition, 1999) does not accept online texts as published work (Article 9.8); however, it accepts CD-ROM publications (Article 8). *Euscorpius* is produced in two *identical* versions: online (ISSN 1536-9307) and CD-ROM (ISSN 1536-9293). Only copies distributed on a CD-ROM from *Euscorpius* are considered published work in compliance with the ICZN, i.e. for the purposes of new names and new nomenclatural acts. All *Euscorpius* publications are distributed on a CD-ROM medium to the following museums/libraries:

- **ZR**, Zoological Record, York, UK
- **LC**, Library of Congress, Washington, DC, USA
- **USNM**, United States National Museum of Natural History (Smithsonian Institution), Washington, DC, USA
- **AMNH**, American Museum of Natural History, New York, USA
- **CAS**, California Academy of Sciences, San Francisco, USA
- **FMNH**, Field Museum of Natural History, Chicago, USA
- **MCZ**, Museum of Comparative Zoology, Cambridge, Massachusetts, USA
- **MNHN**, Museum National d’Histoire Naturelle, Paris, France
- **NMW**, Naturhistorisches Museum Wien, Vienna, Austria
- **BMNH**, British Museum of Natural History, London, England, UK
- **MZUC**, Museo Zoologico “La Specola” dell’Universita de Firenze, Florence, Italy
- **ZISP**, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia
- **WAM**, Western Australian Museum, Perth, Australia
- **NTNU**, Norwegian University of Science and Technology, Trondheim, Norway
- **OUMNH**, Oxford University Museum of Natural History, Oxford, UK
- **NEV**, Library Netherlands Entomological Society, Amsterdam, Netherlands

Publication date: 27 August 2010

The genus *Vachoniolus* (Scorpiones: Buthidae) in Oman

Graeme Lowe

Monell Chemical Senses Center, 3500 Market St, Philadelphia,
PA 19104-3308, USA; loweg@monell.org

Summary

Study of new material collected in Oman by ultraviolet detection revealed three species of *Vachoniolus*, an unusual genus of psammophilous buthid scorpion distinguished by grossly swollen male pedipalp chelae. The presence of the type species, *V. globimanus* Levy, Amitai et Shulov, 1973, in Oman is confirmed, and two new species are described: *V. batinahensis* **sp. nov.** from the Al Batinah coastal plain north of the Al Hajar mountains, and *V. gallagheri* **sp. nov.** from desert alluvial fans south and west of the Al Hajar mountains. The number of *Vachoniolus* species is thereby raised to four, including *V. iranus* Navidpour et al., 2008, from northwestern Iran. Of these four, *V. batinahensis* appears the most plesiomorphic, with 7 external patellar trichobothria, femoral trichobothrium d_5 either proximal or distal to e_2 , and complete retention of tibial spurs. It could be a relict descendent of an ancestral *Vachoniolus* population that evolved in the Tigris-Euphrates river drainage at a time when the Arabian Gulf was dry. A novel tarsal structure, the 'spine comb', is described in juvenile *Vachoniolus*, *Apistobuthus* and *Odontobuthus*. Possible mechanisms of sexual selection in the evolution of the enlarged male pedipalp chelae of *Vachoniolus* are discussed.

Introduction

In 1973, Levy, Amitai & Shulov published an important article describing several new buthid taxa from the Middle East that they had encountered while reviewing museum materials in the course of their study of the scorpion fauna of Israel and the Sinai Peninsula. Among this material was a single male specimen of a remarkable new species collected from 'Oman', distinguished by grossly swollen pedipalp chelae. The peculiar globular form of the chela manus contrasted with all other then known buthids, which typically possess slender pedipalp chelae. This unique feature, together with the absence of tibial spurs, led the authors to place this scorpion into a new monotypic genus, *Vachoniolus* (named after the renowned scorpologist Max Vachon), with type species *V. globimanus*. In many other aspects (e.g. carination and morphosculpture of the carapace, tergites and metasoma) *Vachoniolus* was quite similar to the genus *Buthacus*. Both genera have abbreviated pedipalps, reduced carination, and tarsal setation developed into bristle combs, an adaptation to life on sandy substrates. In the same paper, several new species of *Buthacus* were also described, including *B. minipectenibus* based on three females and a juvenile male collected from various sites in Saudi Arabia in the region of the Rub' al-Khali (Empty Quarter) sand system.

Shortly thereafter, Vachon (1974) published his landmark treatise on scorpion trichobothriotaxy, and observed that *Vachoniolus* could be separated from

Buthacus by additive neobothriotaxy on the external surface of the patella (8 external trichobothria, compared to the normal buthid complement of 7). Since *B. minipectenibus* had 8 external patellar trichobothria, he suggested that it might belong to *Vachoniolus*. Subsequently, Vachon (1979) analyzed six additional examples of *V. globimanus* from Abu Dhabi, including both males and females. He noted a pronounced sexual dimorphism of the pedipalps, the swollen chelae being restricted to adult males, while females and immatures had small, narrow chelae like those of *Buthacus*. The generic diagnosis of *Vachoniolus* was revised to include another trichobothrial character (distal location of femoral d_5 relative to e_2), and *B. minipectenibus* was transferred to *Vachoniolus*. Females of *V. minipectenibus* were very similar to those of *V. globimanus*, except for the absence of tibial spurs in the latter. Since males of *V. minipectenibus* were unavailable for comparison, it was not clear if these two taxa were conspecific or distinct. The issue was revisited by Hendrixson (2006), who studied three additional *Vachoniolus* males, two from Saudi Arabia and one from Dubai (United Arab Emirates). The examples from Saudi Arabia fell within the recorded geographic range of *V. minipectenibus* and exhibited variable development of tibial spurs, which could be either complete, partially reduced or totally lost. However, these males were otherwise indistinguishable from *V. globimanus* males. In the absence of stable, consistent characters to differentiate the two species, *V. minipectenibus* was

placed in synonymy with *V. globimanus*, and *Vachoniolus* once again became a monotypic genus.

The widespread distribution of the previously known records in the central and southern Arabian Peninsula suggests that *Vachoniolus* is a successful psammophile. The relatively small number of early records was probably due to the low efficiency of traditional diurnal collecting methods for sampling populations of burrowing psammophilous scorpions. Indeed, a recent survey by ultraviolet (UV) detection of the scorpion fauna of sand deserts in the Khoozestan Province of Iran revealed a new species (*V. iranus*), extending the range of the genus to beyond the northern end of the Arabian Peninsula (Navidpour et al., 2008). Here, the presence of *V. globimanus* in Oman is confirmed, and two additional new species of *Vachoniolus* are reported, that were discovered during an extensive survey of the scorpion fauna of Oman by UV detection. This raises to four the number of subordinate taxa in this unusual buthid genus.

Methods

Scorpions were collected by ultraviolet (UV) detection at night and preserved in the field by standard methods (Williams, 1968; Stahnke, 1972; Sissom, Polis & Watt, 1990). Locality data were recorded using portable GPS units (Magellan, Garmin). Specimens were examined under a dissecting microscope, either air dried or submerged in 70% isopropyl alcohol, under both white light illumination and UV epifluorescence (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 chela 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 paired dorsal carinae on metasoma V termed 'dorsolateral', and pedipalp chelal amendments by Soleglad & Sissom (2001). Trichobothrial notation follows Vachon (1974, 1975). Hemispermatophore terminology follows Lamoral (1979).

Abbreviations

Specimen depositories: BMNH, Natural History Museum, London, United Kingdom; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHMB, Naturhistorisches Museum Basel, Basel, Switzerland; ONHM, Oman Natural History Museum, Muscat, Oman; TERC, Terrestrial Environment Research Centre, Environment Agency, Abu Dhabi, UAE. *Private collections*: EV, Erich Volschenk, Western Australian Museum, Perth, Australia; FKCP, František Kovařík, Prague, Czech Republic; GL, collection of the author; VF, Victor Fet, Marshall University, West Virginia, USA. *Biometrics*: L, length; W, width; D, depth; SD, standard deviation.

Systematics

Genus *Vachoniolus* Levy et al., 1973

Vachoniolus Levy et al., 1973: 136–137; Vachon, 1974: 910, 948; Vachon, 1975: 1598; Vachon, 1979: 42, 44; Levy & Amitai, 1980: 77; Francke, 1985: 14, 16; Vachon & Kinzelbach, 1987: 92, 95, 97, fig. 4; Sissom, 1990: 102; El-Hennawy, 1992: 102, 104, 133; Nenilin & Fet, 1992: 17; Fet, Polis & Sissom, 1998: 615; Kovařík, 1998: 124; Fet & Lowe, 2000: 277; Fet, Capes & Sissom, 2001: 183; Fet et al., 2003: 2, 4, 6, 10; Soleglad & Fet, 2003a: 26, tab. 2; Soleglad & Fet, 2003b: 88, tab. 9; Santiago-Blay, Soleglad & Fet, 2004: 10; Fet & Soleglad, 2005: 11; Fet, Soleglad & Lowe, 2005: 3, 10–11, 13, 22–24, tab. 1, fig. 23–25; Prendini & Wheeler, 2005: 462, 481; Soleglad, Fet & Kovařík, 2005: 33, tab. 6; Hendrixson, 2006: 44, 47, 99–100; Prendini et al., 2006: 22, tab. 4; Dupré, 2007: 11, 14, 16; Navidpour et al., 2008: 24; Kovařík, 2009: 24; Lourenço & Duhem, 2009: 38, 44–45, 48, 50.

Type species. *Vachoniolus globimanus* Levy, Amitai et Shulov, 1973.

Diagnosis (revised). Small to medium-sized buthids, adults 30–65 mm in length; carapace smooth to finely granular, carinae indistinct or absent; median eyes large (Figs. 9, 38, 65); tergites smooth to finely granular, tergites I–VI with weak median carina, reduced or obsolete on I, obsolete lateral carinae marked by small granules near posterior margin; tergite VII with 5 carinae; metasoma elongate, with well developed carinae (Figs. 14–15, 45–46, 72–73); median lateral carinae present on segments I–III; ventrosubmedian carinae of metasoma II–III well developed, denticulate or crenulate, more strongly so in females; ventrolateral carinae of metasoma V with enlarged dentition, more strongly

developed in females; telson vesicle bulbous, lacking subaculear tubercle; aculeus long, slender, curved; pectines with fulcra; fixed finger of chelicera armed with two denticles on ventral surface (Figs. 11, 40, 67); pedipalps orthobothriotaxic type A β (Figs. 18–25), or neobothriotaxic majorante (Figs. 47–54, 74–81) (Vachon, 1974, 1975); pedipalp patella with d_3 internal to dorsomedian carina, external surface with 7–9 trichobothria (supernumerary esb_3 or em_2) (Figs. 21–22, 50–51, 77–78); fixed finger of chela with est situated between db and dt (Figs. 18, 47, 74); pedipalp segments relatively short compared to body, femur and patella shorter than carapace; chela movable finger length less than twice ventral manus length; chela manus with carinae reduced or absent; adult males with manus grossly swollen, subglobose (Figs. 18–19, 47–48, 74–75, 90, 93, 96, 99); dentate margins of chela fingers armed with 9 or fewer non-imbricated linear subrows of primary denticles (Figs. 100–105); internal and external accessory denticles present; tip of movable finger usually with 4 subdistal denticles; legs III–IV with or without tibial spurs; tibiae I–III with retrosuperior bristle combs from third instar to adult, basitarsi I–III compressed with retrosuperior and retroinferior bristle combs from third instar to adult (Figs. 16, 43, 70, 118–120); second instar juveniles with spine combs on retrosuperior margins of tibia, basitarsus and telotarsus I–III (Figs. 112–117); prolateral pedal spurs bearing macrosetae; soles of telotarsi with long macrosetae (Figs. 17, 44, 71); unguis long, curved (Figs. 16, 43, 70, 112–114, 118–120).

Vachoniolus batinahensis, sp. nov.

Figs. 1–29, 88–90, 100–101, 106–123, 136, 146–148,
Tab. 1

Vachoniolus globimanus: Fet et al., 2003: 3, tab. 1;
Soleglad & Fet, 2003a: 5; Soleglad & Fet, 2003b: 7,
149, 151–152, fig. B-1, B-2; Santiago-Blay,
Soleglad & Fet, 2004: 8.

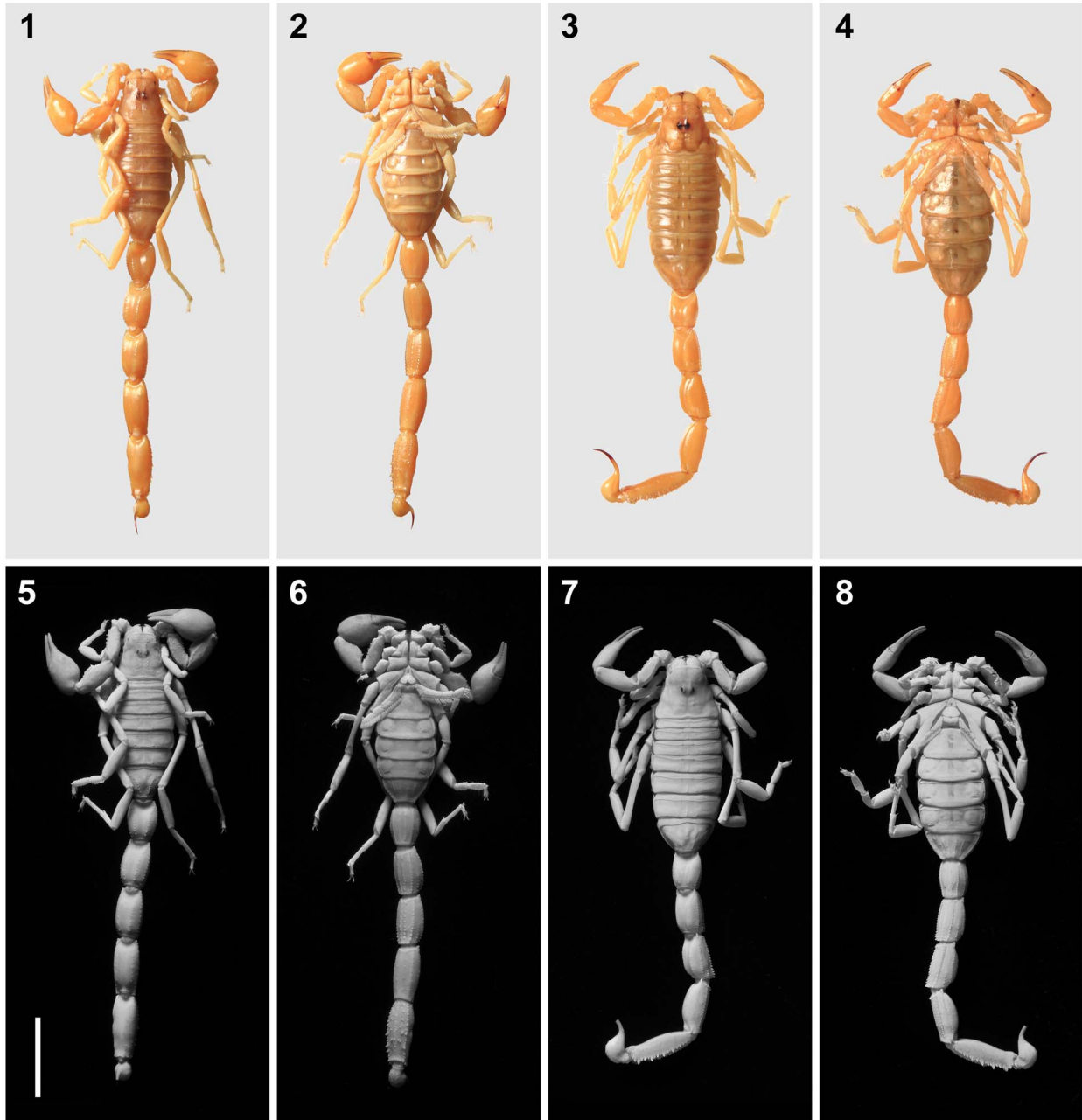
Holotype: adult ♂, **Oman**: Al Batinah plain, 10–15 km W Barka, Al Abyad pipeline road, UV detection, coastal dunes, fine sand, near shrub, 23°41.9'N 57°40.57'E, 50 m a.s.l., 13 October 1993, 22:30 h, leg. G. Lowe, A.S. Gardner & S.M. Farook, NHMB.

Paratypes: **Oman**: 23 ♂, 5 ♀, 5 juveniles, Al Batinah plain, 10–15 km W Barka, Al Abyad pipeline road, UV detection, coastal sand dunes, sand flats, scattered vegetation, *Acacia* woodland, coarser sand mostly near or at bases of vegetation, 23°40.62'N 57°45.77'E, 50 m a.s.l., 13 October 1993, 19:03 h, leg. G. Lowe, A.S. Gardner & S.M. Farook, NHMB, EV (1 ♂), FKCP (2 ♂, 1 ♀), GL (2 ♂, 1 ♀), MNHN (2 ♂, 1 ♀), VF (1 ♂); 7 ♂, 2 juveniles, Al Batinah plain, 10–15 km W Barka, Al Abyad pipeline road, UV detection, coastal

sand dunes and flats, edge of *Acacia* woodland, sparse vegetation, 23°41.16'N 57°43.61'E, 50 m a.s.l., 13 October 1993, 21:05 h, leg. G. Lowe, A.S. Gardner & S.M. Farook, NHMB; 16 ♂, 7 ♀, 9 juveniles, same locality as holotype, NHMB, ONHM (5 ♂, 2 ♀, 1 juvenile), FKCP (1 ♀); 1 ♀, near Za'faran, W side of Khawr Sallan, NW of Sohar, on earth in date garden, 24°24'N 56°42'E, 9 m a.s.l., 7 April 1994, 23:00 h, leg. K. Roberts, C.J.N. Roberts & M.D. Gallagher MDG 8597, NHMB; 2 ♂, S margins of Al Abyad dune field, 23°34'N 57°43'E, 50 m a.s.l., 14 May 1994, leg. A.S. Gardner, BMNH; 1 ♂, 2 ♀, 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, NHMB; 3 ♂, Al Hayl, Muscat, on sand, area with *Prosopis* trees, 23°37.5'N 58°15.5'E, 28 September 1994, leg. A.S. Gardner, NHMB; 3 ♂, Shinass, on fine gravel on raised beach with scattered grasses near mangrove creek, in moonlight, 24°42.9'N 56°28.62'E, 3 m a.s.l., 12 October 1995, 22:00 h, leg. M.W. Balkenohl & M.D. Gallagher MDG 8739, NHMB; 3 ♂, border post, near Khatmat Milahah, 24°55.5'N 56°21.1'E, 16 October 1999, leg. I.D. Harrison, ONHM 21,22,23/99; 1 juvenile, Al Batinah plain, W Barka, Al Abyad pipeline road (site F/1), UV detection, sand dunes and flats, in shrub, 23°41.95'N 52°44.81'E, 50 m a.s.l., 18 January 2000, 19:30–22:00 h, leg. A. Winkler, NHMB.

Diagnosis. Medium to large sized *Vachoniolus*, adults 45–65 mm; base color yellow to orange-yellow with or without weak fuscous patterns on carapace and tergites (Figs. 1–6, 136); metasoma and telson without melanic pigmentation; tergites smooth except for granules along posterior margins; positions of obsolete lateral carinae of tergites III–VI marked posteriorly by 2–3 granules; metasomal segments relatively stout (Figs. 14–15), L/W ratios: I 1.14–1.40, II 1.37–1.71, III 1.49–1.94, IV 1.85–2.38, V 2.08–2.79; metasoma I–II with dorsolateral surfaces smooth to sparsely shagreened; dorsosubmedian carinae on metasoma II–III weak, with widely spaced granules separated by two or more granule lengths; ventrosubmedian carinae of metasoma II–III crenulate to serrate with small to moderate sized, closely spaced dentate granules separated by one granule length or less, 5–9 granules on posterior half of carina; telson with moderately long aculeus, vesicle L/ telson L 0.47–0.57; pedipalp femur with trichobothrium d_5 either proximal or distal to e_2 , distance ratio $(d_5-e_2)/(e_2-e_1)$ median value 0.11 (Figs. 20, 111); pedipalp patella orthobothriotaxic with 7 trichobothria on external surface (Figs. 21–22); pedipalp chela manus smooth; tibial spurs always present on legs III–IV.

Etymology. The name derives from the Al Batinah coastal plain to which this species is endemic.



Figures 1–8: *Vachoniolus batinahensis*, **sp. nov.**, holotype male (1–4) and paratype female from 11 km W Barka (5–8). Habitus viewed under reflected white light (1–2, 5–6) or UV fluorescence (3–4, 7–8). 1, 3, 5, 7. Dorsal aspect. 2, 4, 6, 8. Ventral aspect. Scale bar: 10 mm.

Comparisons. Other species of *Vachoniolus* are differentiated from *V. batinahensis* by: neobothriotaxy (8–9 trichobothria) on the external surface of the pedipalp patella; femoral trichobothrium d_5 nearly always distal to, and usually well separated from e_2 ; often partial reduction or loss of tibial spurs on legs III–IV. In addition: *V. gallagheri* **sp. nov.**, and *V. iran* Navidpour et al., 2008, further differ in having the male

pedipalp chela manus finely granulated or shagreened; *V. gallagheri* differs in having shorter metasomal segments (relative to carapace length), stronger dentition on ventrosubmedian carinae of metasoma II–III, and more stout pedipalp segments; *V. iran* differs in its smaller size, more slender metasoma and telson, and melanic pigmentation pattern on carapace and pedipalps (Fig. 84) (Navidpour et al., 2008); *V. globimanus* differs

in having a more slender metasoma and telson, and greater numbers of posterior denticles on ventro-submedian carinae of metasoma II–III.

Description (holotype male unless otherwise specified).

Coloration (Figs. 1–2). Base color light orange-yellow with pattern of faint underlying fuscosity on carapace and tergites; superciliary carinae dark; telson with aculeus castaneous.

Carapace (Fig. 9). Subrectangular, trapezoidal, anterior interocular width 0.48 times posterior width; surface convex with lateral flanks moderately sloped; anterior margin weakly convex, posterior margin nearly straight; coarse to fine granulation of variable density present on most of carapace; coarse granules on anterior interocular area between lateral eyes, inner margins of lateral eyes, anterior margin of carapace, and superciliary carinae; positions of central median carinae marked by longitudinal series of coarse granules; area between superciliary carinae, lateral and posterior areas around median ocular tubercle smooth; lateral flanks of carapace with medium to fine granulation; other carinae obsolete; posterior median sulcus and adjacent lateral surfaces smooth; median area of posterior margin of carapace bordered by transverse band of dense, fine granulation; median eyes large, ocular tubercle prominent, wide, interocular distance exceeding two ocular diameters; 4 lateral eyes on each side, anterior 3 ocelli equal in size, 4th ocellus reduced; 8 macrosetae on anterior margin, carapace otherwise devoid of macrosetae.

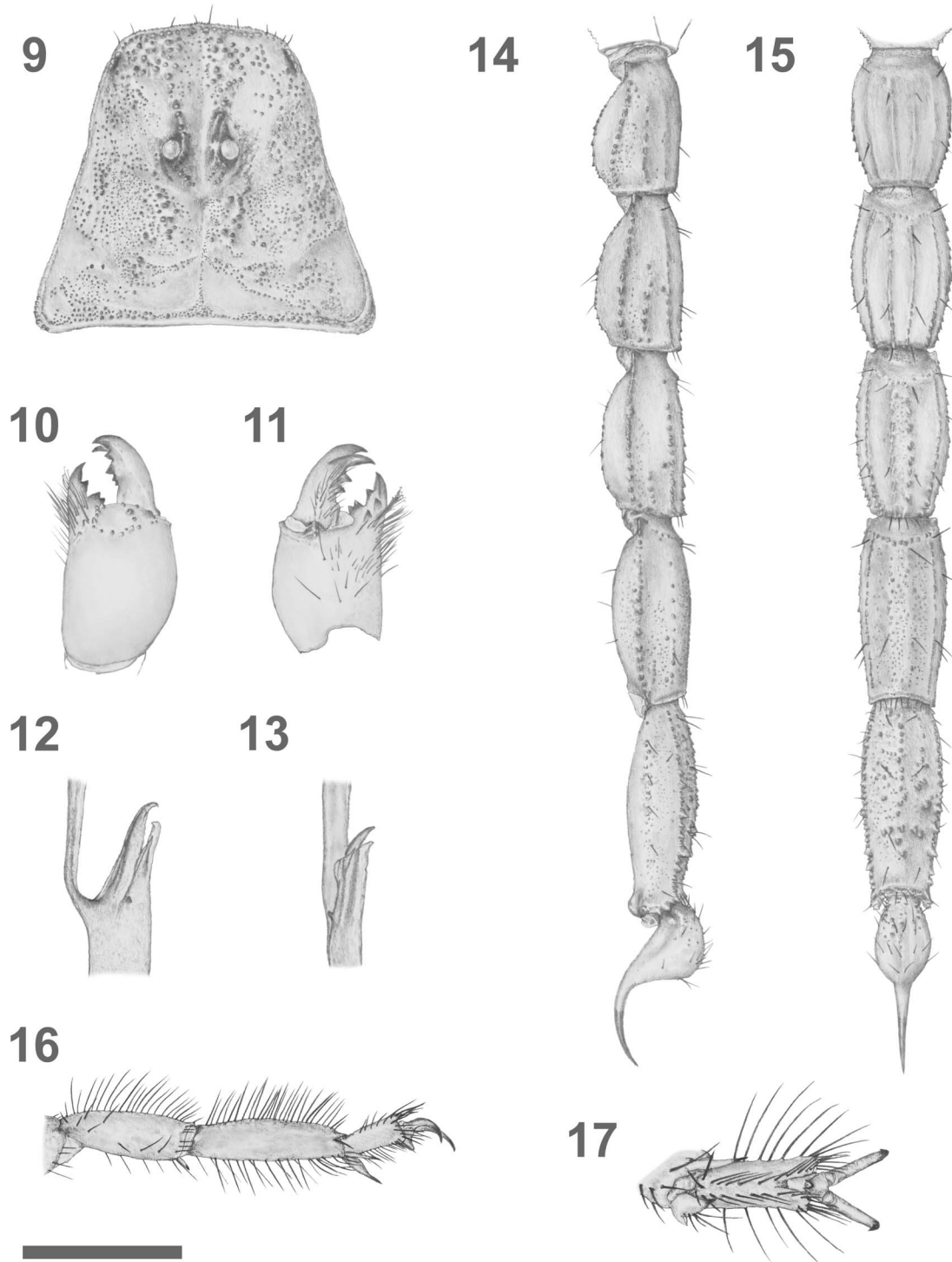
Chelicera (paratype male) (Figs. 10–11). Dorsal surface of manus smooth, convex, with medial subapical transverse series of small granules; dorsointernal carina at base of fixed finger with larger dentate granules; *chaetotaxy*: two short pale macrosetae on apical margin of manus, one on medial subapical area, amidst coarse granules; long reddish macroseta on dorsointernal carina; movable finger smooth, without macrosetae, ventral surface of manus smooth, with numerous long, fine microsetae on middle and internal surfaces, more dense on interior aspect, extending dorsally to base of fixed finger; ventral surfaces of fixed and movable fingers with dense brush of microsetae; *dentition*: fingers with normal buthid dentition (Vachon, 1963; Sissom, 1990); fixed finger with large distal tine, smaller subdistal denticle and large proximal bicuspid; two large denticles on ventral surface, proximal denticle smaller than distal; movable finger with large dorsal and ventral distal tines; dorsal margin of movable finger with two large triangulate denticles and pair of small proximal

denticles; ventral margin armed with two robust denticles of equal size.

Coxosternal area (Figs. 2, 4). Coxae smooth, lustrous, without distinct carinae; coarse granules along anterior margin of coxa II, proximal anterior margin of coxa III; anterior margin with 2–3 macrosetae on coxa II, 4 macrosetae on coxa III; coxa IV finely shagreened on posterior proximal margin and anterior surface, with single basal macroseta; sternum elongate, sub-pentagonal, angled downward anteriorly, with deep postero-median ovoid excavation; genital opercula smooth, with 3–4 macrosetae; genital papillae present.

Pectines (Figs. 2, 4, 27). Basal piece smooth, with deep anterior median sulcus, and 6 macrosetae; pectines long, tips extending to middle of trochanter IV; pectines with 3 marginal lamellae, small accessory lamella distal to first marginal lamella, 6–7 middle lamellae, 22–22 teeth; pectine teeth elongate, proximal teeth slightly shorter than middle and distal teeth; marginal lamellae, middle lamellae and fulcra with dense short, reddish macrosetae; fulcra with 7–13 setae; basal teeth not overlapping when anterior margins of pectines align with posterior margins of coxae IV.

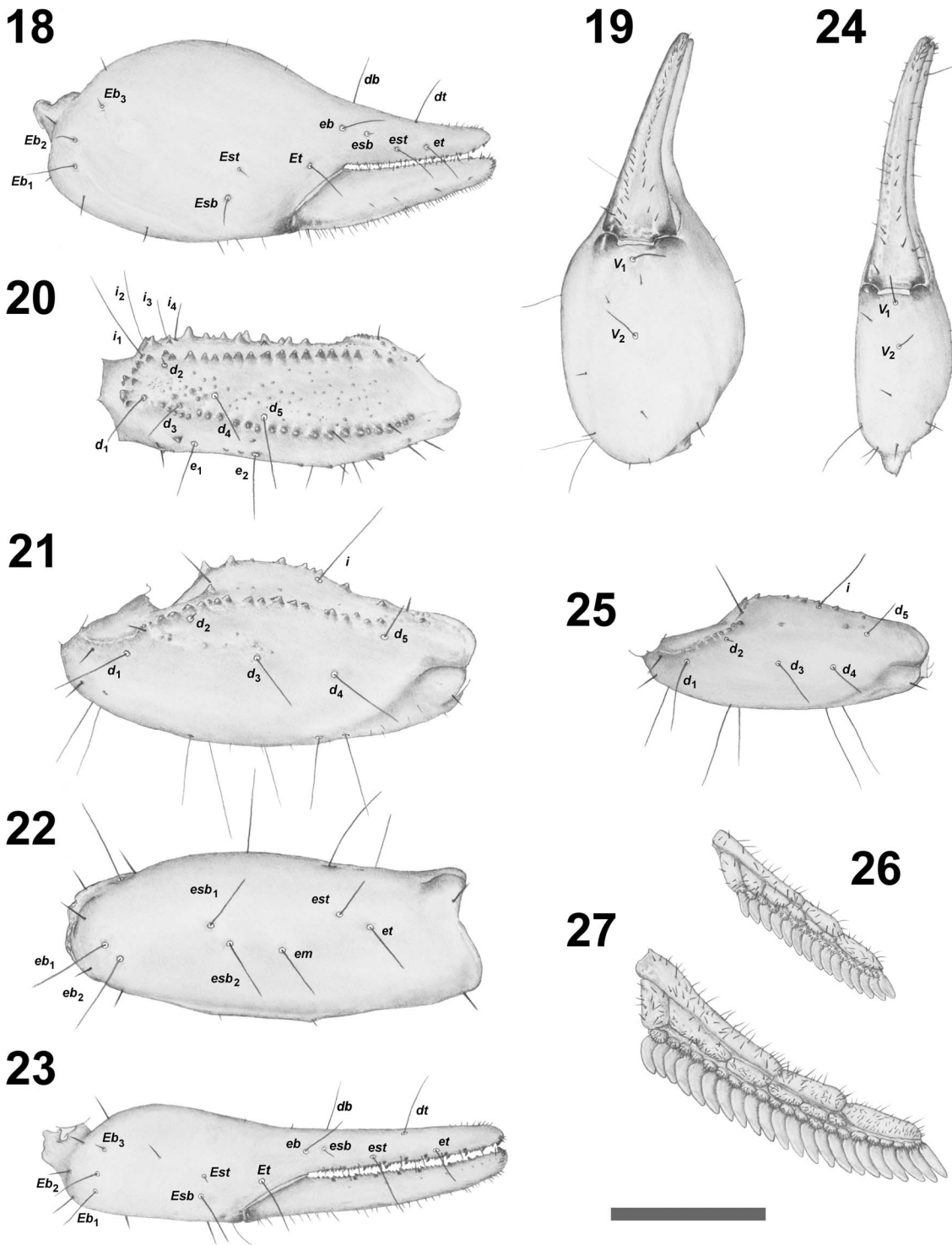
Mesosoma (Figs. 1–4). *Tergites*: pretergites smooth, lustrous; median carina nearly obsolete on tergite I, weak and granulose on II–VI; tergites I–VI with lateral carinae obsolete, marked at posterior margin by single granules on I, double granules on II–VI; tergite VII with weak median hump, and two pairs of weak granulated lateral carinae; posterior margins of all tergites nearly straight, smooth; tergites I–VI densely, finely shagreened, with coarse granules along posterior margins; tergite V finely shagreened medially, finely granulated laterally; all tergites devoid of macrosetae, lateral margins microdenticulate. *Sternites*: sternites III–VI smooth, lustrous, lacking carinae; sternite III with anterior lateral areas finely shagreened; sternite VII with smooth, nearly obsolete paired median carinae and weak, smooth paired lateral carinae, medial surfaces smooth, lateral surfaces lightly shagreened; sternites III–VI with smooth posterior margins, finely denticulate lateral margins, dentate-granulate posterolateral corners; sternite VII with smooth posterior margin, dentate lateral margins. *Chaetotaxy*: sternite III with 13 short macrosetae in medial area, IV–VI with paired medial macrosetae, VII with one pair of macrosetae on median carinae, one pair on anterior lateral surface; posterior margins of sternites with short to medium length setae on left and right sides: III–IV 7–7 (left–right), V 8–8, VI 6–3; lateral margins of sternites with well spaced macrosetae: III 2–2 (left–right), IV 9–6, V 7–6, VI 6–6, VII 1–2.



Figures 9–17: *Vachoniolus batinahensis*, sp. nov. **9, 14–17**, holotype male; **10–13**, paratype male (same locality as holotype). **9.** Carapace, dorsal aspect. **10.** Right chelicera, dorsal aspect. **11.** Right chelicera, ventral aspect. **12–13.** Right hemispermaphore, lobes at base of flagellum. **12,** convex aspect; **13** outer aspect. **14–15.** Metasoma and telson. **14.** Right lateral aspect. **15.** Ventral aspect. **16.** Right basitarsus and telotarsus III, retrolateral aspect. **17.** Right telotarsus III, ventral aspect. Scale bar: 9, 16: 3 mm; 10, 11: 1.7 mm; 12, 13: 1 mm; 14, 15: 5.7 mm; 17: 1.5 mm.

Hemispermaphore (paratype male) (Figs. 12–13). Flagelliform; trunk elongate, slender; flagellum long, filiform, pars recta 0.75 times length of trunk, pars

reflecta about equal to length of trunk; inner lobe a broad lamina, gently tapering with blunt apex; median and outer lobes shorter, laminate, partially fused, tap-



Figures 18–27: *Vachoniolus batinahensis*, sp. nov. 18–22, 27, holotype male; 23–26, paratype female (Al Abyad dune field, W of Barka). 18. Right pedipalp chela of male, external aspect. 19. Right pedipalp chela of male, ventral aspect. 20. Right pedipalp femur of male, dorsal aspect. 21. Right pedipalp patella of male, dorsal aspect. 22. Right pedipalp patella of male, external aspect. 23. Right pedipalp chela of female, external aspect. 24. Right pedipalp chela of female, ventral aspect. 25. Right pedipalp patella of female, dorsal aspect. 26. Left pectine, female, ventral aspect. 27. Left pectine, male, ventral aspect. Scale bar: 18, 23–27: 3 mm; 20–22: 2 mm. Trichobothrial notation after Vachon (1974).

ering to fine apical processes, basal lobe a short, blunt knob; measurements: trunk length (to base of flagellum) 3.4 mm, pars recta 2.5 mm, pars reflecta 3.3 mm, inner lobe (from base of flagellum) 670 μm , median lobe (from juncture with inner lobe) 280 μm , outer lobe (from juncture with median lobe) 265 μm , basal lobe 30 μm .

Metasoma (Figs. 14–15). Long, with robust segments, total length plus telson length 6.4 times carapace length. *Carination*: metasoma I with 10 complete carinae; metasoma II–III with 8 complete carinae, median lateral carinae confined to posterior 1/2 of each segment; metasoma IV with 4 carinae; metasoma V with 3 carinae; dorsosubmedian carinae weak with small, non-contiguous granules on I–III, obsolete on IV; dorso-lateral carinae moderate on I–III with large dentate granules, weak on IV with smaller granules, obsolete on V; median lateral carinae moderate, granulate on I, weak, granulate on II, obsolete and marked by row of granules on III; ventrolateral carinae on I–II moderate, smooth, weakly granulate posteriorly, on III strong, granulate with larger granules posteriorly, on IV weak, granulate, on V strong with mixed medium to large dentate granules; ventrosubmedian carinae weak, smooth on I, moderate, smooth to granulate on II, strong, regularly dentate-granulate on III, obsolete on IV; posterior half of ventrosubmedian carina with 6–7 dentate granules on II, 5–6 on III; ventrosubmedian carinae on V obsolete, marked by series of enlarged dentate granules on anterior 1/2 of segment; ventro-median carina on V moderate, studded with large dentate granules; 6 denticles on ventral anal arc, left lateral anal lobe with 3 denticles, right lobe with 4. *Granulation*: dorsal surfaces smooth on all segments, concave on I–IV, convex on V; dorsolateral surfaces smooth to sparsely shagreened on all segments, lateral surfaces smooth to lightly shagreened on I–III, shagreened IV–V; ventrolateral and ventral surfaces smooth on I–II, lightly shagreened on III, densely shagreened on IV–V. *Chaetotaxy*: carinal macrosetae (left–right) dorso-submedian: I, 0–0, II 1–2, III 3–2, IV 2–3, dorsolateral: I, 0–0, II 2–1, III 1–2, IV 2–3; ventrolateral: I 2–2, II 2–2, III 2–2, IV 3–3; ventrosubmedian: I 1–1, II 2–2, III 2–2, IV 2–2, V 3–3; intercarinal macrosetae: metasoma V 11–13 lateral setae, 1 postero-lateral pair on ventral surface.

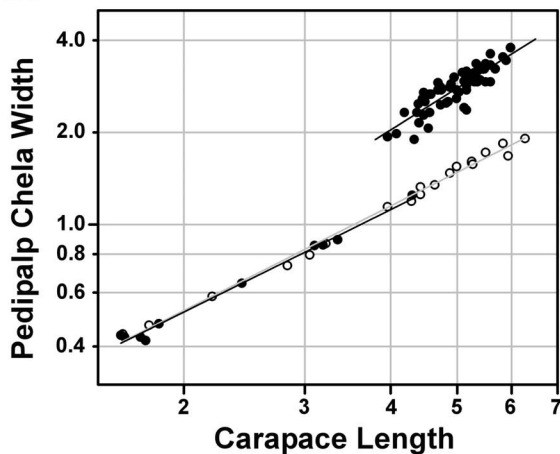
Telson (Figs. 14–15). Vesicle slim, width 0.68 times metasoma V width, dorsal and lateral surfaces smooth, lustrous, ventral surface studded with granules, bearing numerous long reddish macrosetae: 2–2 on lateral surfaces, 20 on ventral surface; aculeus slender, nearly as long as vesicle.

Pedipalp (Figs. 18–22, 88–90, 100). *Femur* (Figs. 20, 88): short, stout, 0.83 times carapace length, 2.6 times

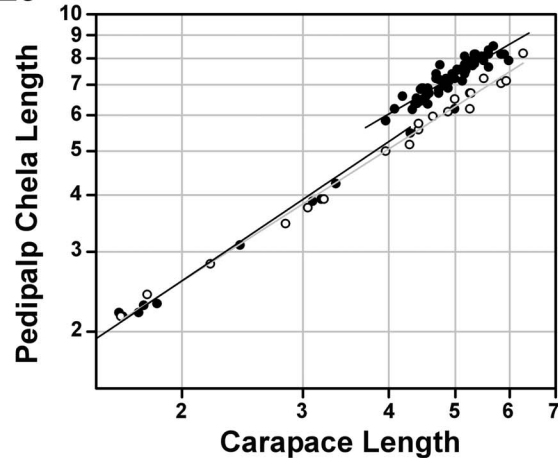
longer than wide; dorsoexternal, dorsointernal and ventrointernal carinae strong, with robust dentate granules; external surface mostly smooth with scattered small and large granules; dorsal surface flat, mostly smooth, lustrous, with scattered small and large granules, ventral surface smooth, lustrous, proximally concave, distally convex, with sparse small granules; internal surface divided by weak internal carina bearing irregular small and large conical granules, upper and lower surfaces with dispersed small granules; dorsoexternal carina with 2 distal macrosetae, external surface with 1 basal, 6–7 distal macrosetae. *Patella* (Figs. 21–22, 89): short, stout, 0.9 times carapace length, 2 times longer than wide; dorsointernal carina strong, granulose; ventrointernal carina strong, with large dentate granules; internal carina weak, marked by coarse dentate granules; other carinae obsolete; intercarinal surfaces smooth, lustrous, internal surface with sparse fine granules. *Chela* (Figs. 18–19, 90, 100–101): relatively short, 1.4 times carapace length; manus extremely swollen, subglobose, width 0.58 times carapace length, fingers short, movable finger 0.93 times ventral manus length; surfaces smooth, lustrous, all carinae obsolete; dentate margins of finger straight, without proximal scalloping; closure of fingers leaves narrow linear proximal gap, with tips of fingers apically divergent; manus mostly bare, with sparse short macrosetae; movable finger with numerous short macrosetae on ventral aspect, most dense sub-apically; 8 primary denticle subrows on fixed and movable fingers; fixed fingers with 8 internal accessory denticles, 6–7 external accessory denticles; movable fingers with 8 internal and external accessory denticles, tip of movable finger with 3 subdistal denticles (Fig. 100). *Trichobothrial pattern*: Orthobothriotaxic, type A β (Vachon, 1974, 1975); trichobothrium d_5 located slightly distal to e_2 ; femur d_2 , patella d_2 , chela Eb_3 , Esb and esb petite; db on fixed finger level with esb ; dt approximately midway between est and et .

Legs (Figs. 1–8, 16–17). Legs I–II robust, legs III–IV moderately slender; ventral carinae on femur I with large separated denticles, on femur II–III contiguously dentate, on femur IV finely denticulate; legs III–IV with tibial spurs; retrolateral pedal spurs on legs I–IV simple, without setae; prolateral pedal spurs basally bifurcate with (left–right) 4–3, 5–5, 11–14, 12–10 setae; tibiae I–III with retrosuperior bristle-combs (Fig. 16) with (left–right) 9–9, 11–13, 17–19 setae; basitarsi I–III bristle-combs present (Fig. 16) with seta counts: retrosuperior 12–11, 17–16, 26–28, retroinferior 8–9, 11–10, 16–16, ventral surfaces of telotarsi with short macrosetae on leg I, medium length macrosetae on legs II–III (Fig. 17), long macrosetae in leg IV.

28



29



Figures 28–29: Sexual dimorphism in ontogenetic scaling of the pedipalp chela of *Vachoniolus batinahensis*, sp. nov. **28.** Double logarithmic plot of pedipalp chela width versus carapace length. **29.** Double logarithmic plot of pedipalp chela length versus carapace length. Filled circles: males; open circles: females. Black lines: least squares linear regression fits to segregated subsets of male data points, showing discontinuous development of the chela during growth. Gray lines: fits to entire set of female data points, showing continuous development of the chela. Axis label units in mm.

Measurements of holotype male (mm). Total L 58.50; metasoma and telson L 38.00; carapace L 5.89, anterior W 3.10, posterior W 6.43, carapace preocular L 2.58; metasomal segments (L/W/D) I 4.99/3.83/3.27, II 5.85/3.74/3.35, III 6.19/3.61/3.10, IV 7.22/3.40/3.04, V 7.83/3.18/2.77; telson L 6.19; vesicle L 3.01, W 2.15, D 2.19; pedipalp chela L 8.17, chela manus ventral L 4.64, chela manus W 3.44, D 3.66, fixed finger L 2.92, movable finger L 4.30; pedipalp femur L 4.90, W 1.89, patella L 5.33, W 2.67; pectine L 6.62, leg III patella L 5.33, W 1.67.

Measurements of paratype female (adult from Al Abyad dune field) (mm). total L 59.00; metasoma and telson L 36.50; carapace L 6.28, anterior W 3.53, posterior W 7.80, carapace preocular L 2.89; metasomal segments (L/W/D) I 4.64/3.67/3.34, II 5.59/3.53/3.41, III 5.93/3.35/3.27, IV 6.83/3.10/2.98, V 7.57/3.39/2.77; telson L 6.54; vesicle L 3.18, W 2.41, D 2.28; pedipalp chela L 8.20, chela manus ventral L 3.35, chela manus W 1.91, D 2.15, fixed finger L 3.91, movable finger L 5.09; pedipalp femur L 4.39, W 1.81, patella L 5.33, W 2.25; pectine L 4.18, leg III patella L 5.09, W 1.88.

Variation. Biometrics were taken from 33 adults (26 males, 7 females). Adults had body length 39–62 mm (mean \pm SD 51.6 \pm 5.4 mm) and carapace length 4.4–6.3 mm (5.34 \pm 0.40 mm). Pedipalp finger primary denticle subrows for adults (Figs. 100–101): of 66 fixed fingers, there was 1 finger with 5 subrows, 7 with 6, 29 with 7, and 29 with 8; of 66 movable fingers, there was 1 finger each with 1, 3 and 4 subrows (teratological cases), 2 fingers with 5 subrows, 3 with 6, 18 with 7, 36 with 8,

and 4 with 9. Number of dentate granules on the posterior half of the ventrosubmedian carina of metasoma II–III: on II, 3 carinae with 5 granules, 17 with 6, 25 with 7, 17 with 8, 2 with 9; on III, 15 carinae with 5 granules, 32 with 6, 18 with 7 and 1 with 8. Tibial spurs were present in nearly all cases: of 93 leg III tibiae, spurs were present in 91 (97.8%), absent in 2; spurs were present in all of 93 leg IV tibiae (100%). Variation in morphometrics is summarized in Figs. 106–111, Tab. 1. A morphometric parameter of special interest is the pedipalp femur trichobothrial distance ratio $(d_5 - e_2)/(e_2 - e_1)$. The character state $(d_5 - e_2) > 0$ (i.e. d_5 distal to e_2) was previously used as a diagnostic criterion for the genus *Vachoniolus*. In *V. batinahensis*, a significant number of femora (21/122 = 17.2%) had $(d_5 - e_2) \leq 0$ (i.e. d_5 level with or proximal to e_2) (Fig. 111), and hence this character cannot be used for generic diagnosis.

Sexual dimorphism: females differed from males as follows: granulation finer, sparser on carapace; tergites smooth; pedipalp femur smooth, internal surface without large dentate granules; pedipalp patella with dorso-internal and ventrointernal carinae weaker with smaller granules, internal surface without large dentate granules (Fig. 25); pedipalp chela manus not strongly swollen (Figs. 23–24); metasoma I–IV with stronger granulation and dentition on ventrolateral and ventrosubmedian carinae; ventrolateral carinae strong, granulate on metasoma I, strong, dentate-granulate on II, strong, dentate with enlarged posterior denticles on III, moderate, granulate on IV; ventrosubmedian carinae weak to moderate, finely granulate on I, strong, dentate with enlarged posterior denticles on II–III, weak, almost

obsolete with irregular fine granules on IV; lateral surfaces of metasoma IV–V smooth; pectines much shorter (Fig. 26), tips falling well short of distal ends of coxae IV (Figs. 6, 8). Pectine teeth (including immatures): males 15–24 (of 129 combs from $n = 66$ males: 2 combs with 15 teeth, 5 with 18, 19 with 19, 32 with 20, 41 with 21, 23 with 22, 6 with 23, and 1 with 24), females 10–15 (of 40 combs from $n = 20$ females: 1 comb with 10 teeth, 1 with 11, 3 with 12, 8 with 13, 19 with 14, 8 with 15). There was significant sexual dimorphism in morphometrics (Table 1): females tended to have shorter pedipalp femur, patella, chela and metasoma I–V relative to carapace length, more slender pedipalp patella, and pedipalp chela movable finger longer relative to manus.

Juveniles: differed from adults in having weaker, less granulate carination on the pedipalp femur and patella, and fewer macrosetae on the tibiae, basitarsi and telotarsi of all legs. The manus of the pedipalp chela in sub-adult males was less swollen than in adults, and in juveniles it was not more swollen than in females of similar size. The pronounced expansion of the manus in males occurred abruptly, when the carapace attained a length of ca. 4.0–4.5 mm (Fig. 28). In the smallest juveniles (carapace L 1.58–1.75 mm, mean \pm SD 1.68 \pm 0.06 mm, $n = 7$) the tibia, basitarsus and telotarsus of legs I–III lacked macrosetae and bristle combs, bearing instead a series of elongate spiniform processes extending from their retrosuperior margins (Figs. 112–114). These processes ('spine combs') were fully sheathed with fluorescent epicuticle (Figs. 115–117). The range (mean \pm SD) for spine counts was: tibia I 0–1 (0.46 \pm 0.52, $n = 13$), basitarsus I 4–6 (5.15 \pm 0.69, $n = 13$), telotarsus I 2–3 (2.85 \pm 0.38, $n = 13$); tibia II 1–2 (1.21 \pm 0.43, $n = 14$), basitarsus II 4–8 (5.93 \pm 1.21, $n = 14$), telotarsus II 3–4 (3.21 \pm 0.43, $n = 14$); tibia III 1–3 (1.71 \pm 0.73, $n = 14$), basitarsus III 4–8 (6.14 \pm 0.95, $n = 14$), telotarsus III 3–6 (4.50 \pm 0.85, $n = 14$). In juveniles with spine combs on legs I–III, the tibial and tarsal segments of leg IV lacked such armature (although a few small marginal denticles were present), and also lacked macrosetae.

Distribution (Figs. 146–148). *V. batinahensis* is endemic to sandy areas of the Al Batinah coastal plain of northern Oman, at elevations < 50 m a.s.l.. The northernmost coastal record is at the border post of Khatmat Milahah, and it could also occur in the adjacent coastal United Arab Emirates if there were suitable dune habitats. Considering its restricted distribution, there is a concern that this species might be vulnerable to loss of habitat caused by land development along the heavily populated Batinah coast. Conservation of coastal dune habitats is recommended to protect this unique relict scorpion, which is an important part of the endemic biodiversity and evolutionary heritage of Oman.

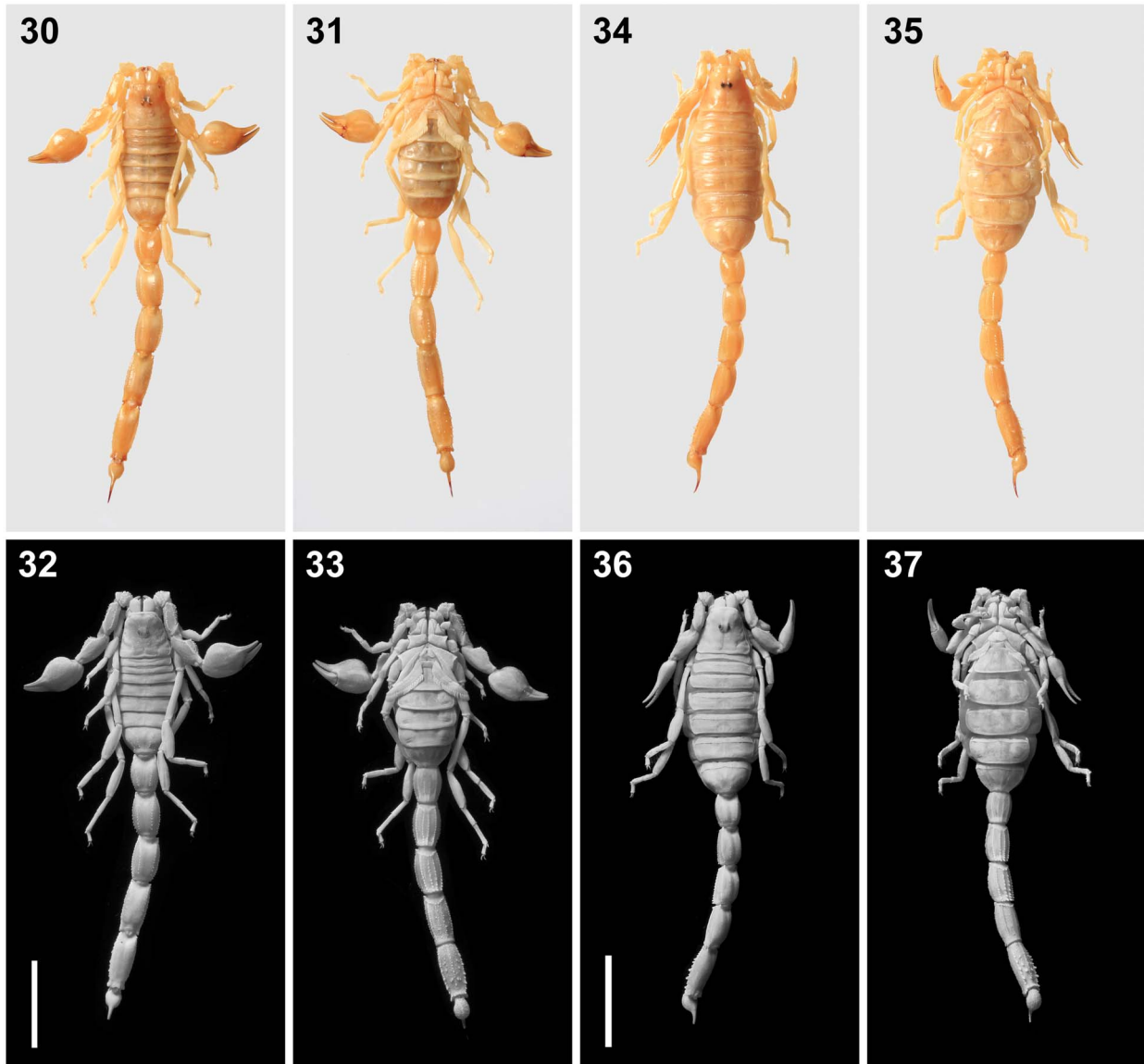
Ecology. This is psammophilous species, inhabiting aeolian dunes. It was the most numerous scorpion in *Acacia* woodlands at Al Abyad, west of Barka. Most individuals were found at night by ultraviolet detection resting at the bases of vegetation, where they excavated burrows. One individual at this site was observed being devoured by a large sparassid spider in a shrub. Other collections were made on fine sandy soils, in association with *Prosopis* trees. Two other buthid scorpions, *Androctonus crassicauda* (Olivier, 1807) and *Orthochirus innesi* Simon, 1910, were collected on sandy substrates at the type locality.

***Vachoniolus gallagheri*, sp. nov.**

Figs. 30–56, 91–93, 102–103, 106–111, 146–148, Tab. 1

Holotype: adult ♂, **Oman:** wadi N of Adam, near main road, UV detection, sandy wadi, on sandy plain, 22°31.16'N 57°31.04'E, 420 m a.s.l., 17 September 1995, 22:20 h, leg. G. Lowe, NHMB.

Paratypes: **Oman:** 1 juvenile, near Qarn Nihaydah, under stone, 21°15'N 56°55'E, 8 October 1981, leg. M.D. Gallagher MDG 6280, GL; 1 ♂, 1 ♀, 1 juvenile, ca. 57 km S of Hafit, pitfall No. 11, sand with little vegetation except *Prosopis* and *Acacia*, 23°29'N 55°52'E, 200 m a.s.l., trap collected 1 March 1994, leg. M.D. Gallagher & B.J. Tigar MDG 8592, NHMB; 2 ♂, 6 ♀, 2 juveniles, sandy wadi W of Ghabah, UV detection, low sand dunes with scrub, adjacent to sabkha, scorpions walking rapidly on sand in wind, near bases of bushes, 21°23.89'N 57°09.56'E, 185 m a.s.l., 5 October 1994, leg. G. Lowe & M.D. Gallagher, NHMB, GL(1 ♂), FKCP (1 ♀); 1 ♂, plain S of Adam, UV detection, open ground, silty gravel plain, 22°06.16'N 57°26.96'E, 250 m a.s.l., 16 September 1995, 19:00–20:00 h, leg. G. Lowe & J. Dundon, ONHM; 2 ♂, 1 juvenile, between Ghabah & Adam, UV detection on sand, sandy wadi on open gravel plain with trees and bushes, large solifuges common, 22°09.54'N 57°30.16'E, 250 m a.s.l., 16 September 1995, 22:00–23:00 h, leg. G. Lowe & J. Dundon, NHMB; 4 ♂, 1 ♀, sandy wadi S of Nizwa roundabout, near main road, UV detection, 22°44.41'N 57°33.37'E, 380 m a.s.l., 17 September 1995, 20:30 h, leg. G. Lowe, NHMB, FKCP (1 ♂); 2 ♂, same locality as holotype, NHMB; 1 ♂, Ghabah North, UV detection, active on ground, gravelly and sandy wadi, firm substrate, area of small wadis with shrubs, 21°23.63'N 57°09.64'E, 100 m a.s.l., 29 September 1995, leg. G. Lowe & M.D. Gallagher, MNHN; 1 ♀, Saiwan, rudist outcrop, 20°42.94'N 57°36.96'E, 20 February 1996, leg. A.S. Gardner, ONHM; 1 juvenile, Ghabah North area, S of Adam, in a sandy wadi, 21°45.74'N 57°17.31'E, 150 m a.s.l., 19 March 1996, 20:30–21:15 h, leg. J. Dundon 117, NHMB; 1 ♂, 15 km S of Barzaman, soft sand in grassy hollow, 22°10'N 58°03'E, 250 m a.s.l., 20 October 1997, leg. M.D. Gallagher & I.D. Harrison MDG 8887, BMNH.



Figures 30–37: *Vachoniolus gallagheri*, sp. nov., holotype male (30–33) and paratype female from N of Adam (34–37). Habitus viewed under reflected white light (30–31, 34–35) or UV fluorescence (32–33, 36–37). 30, 32, 34, 36. Dorsal aspect. 31, 33, 35, 37. Ventral aspect. Scale bars: 10 mm for both male and female.

Diagnosis. Small to medium sized *Vachoniolus*, adults 35–50 mm, uniform pale yellow without melanic pigmentation on metasoma and telson (Figs. 30–31, 34–35); tergites smooth in females, finely shagreened in males, with coarser granulation along posterior margins; positions of obsolete lateral carinae of tergites III–VI marked posteriorly by single granule; metasomal segments relatively stout (Figs. 45–46), L/W ratios: I 1.25–1.33, II 1.48–1.65, III 1.60–1.85, IV 2.00–2.31, V 2.22–2.64; metasoma I–II with dorsolateral surfaces smooth; dorsosubmedian carinae on metasoma II–III weak, with widely spaced granules separated by two or more granule lengths; ventrosubmedian carinae of metasoma II–III crenulate to dentate, armed with

moderate to large, closely spaced dentate granules, 4–8 granules on posterior half of carina; telson with moderately long aculeus, vesicle L/ telson L 0.45–0.52; pedipalp femur with trichobothrium d_5 usually distal to e_2 , distance ratio $(d_5 - e_2)/(e_2 - e_1)$ median value 0.25 (Figs. 49, 111); pedipalp patella neobothriotaxic with 8 trichobothria on external surface (Figs. 50–51); pedipalp chela manus smooth in females, finely granulated on internal, dorsal and dorsolateral surface in males; tibial spurs present or absent on legs III–IV.

Etymology. The specific epithet is a patronym honoring Michael D. Gallagher for his many enduring contributions to the natural history of Oman, including

collecting a large part of the materials for the author's study of the scorpion fauna of Oman.

Comparisons. *V. batinahensis* sp. nov., differs as follows: larger average size, 2–3 granules on lateral carinae of tergites III–VI; weaker dentition on ventro-submedian carinae of metasoma II–III; pedipalp patella with 7 trichobothria on external surface; pedipalp chela manus smooth; tibial spurs always present on legs III–IV; *V. globimanus* differs as follows: larger average size, males with shagreened tergites, finer and more dense dentition on metasomal carinae, more slender metasoma, male pedipalp chela manus smooth except for dorso-internal margin; male *V. iranus* Navidpour et al., 2008, differs as follows: melanic pigmentation on carapace, pedipalp femur and patella; 2–3 granules on lateral carinae of tergites III–VI; coarsely dentate-granulate dorsosubmedian carinae on metasoma II–III; granulate dorsal and dorsolateral surfaces on metasoma I–V; enlarged bicuspid granule on mid-internal surface of pedipalp femur; more robust dorso-internal carina on pedipalp patella.

Description (holotype male unless otherwise specified).

Coloration (Figs. 30–31). Body and appendages uniform pale yellow; melanic pigment on carapace under median and lateral eyes; denticles on fingers of chelicerae and pedipalp chelae, articular condyles of pedipalp movable finger, and telson aculeus castaneous.

Carapace (Fig. 38). Subrectangular, 1.12 times wider than long, anterior inter-ocular width 0.47 times posterior width; surface convex with lateral flanks moderately sloped; anterior margin with weak median convexity, posterior margin nearly straight; moderately coarse to fine granulation of variable density on most of carapace; coarse granules on anterior inter-ocular area between lateral eyes, inner margins of lateral eyes, along anterior margin of carapace, and behind median eyes; anterior lateral, lateral and posterior areas around median ocular tubercle smooth, lustrous; lateral flanks of carapace with medium to fine granulation; posterior median sulcus finely shagreened, adjacent lateral surfaces smooth; median posterior margin of carapace bordered by strip of dense, fine granulation; median eyes large, ocular tubercle prominent, wide, inter-ocular distance equal to two ocular diameters; 4 lateral eyes on each side, anterior 3 ocelli equal in size, 4th ocellus reduced; single median pair of short reddish macrosetae on anterior margin, carapace otherwise devoid of macrosetae.

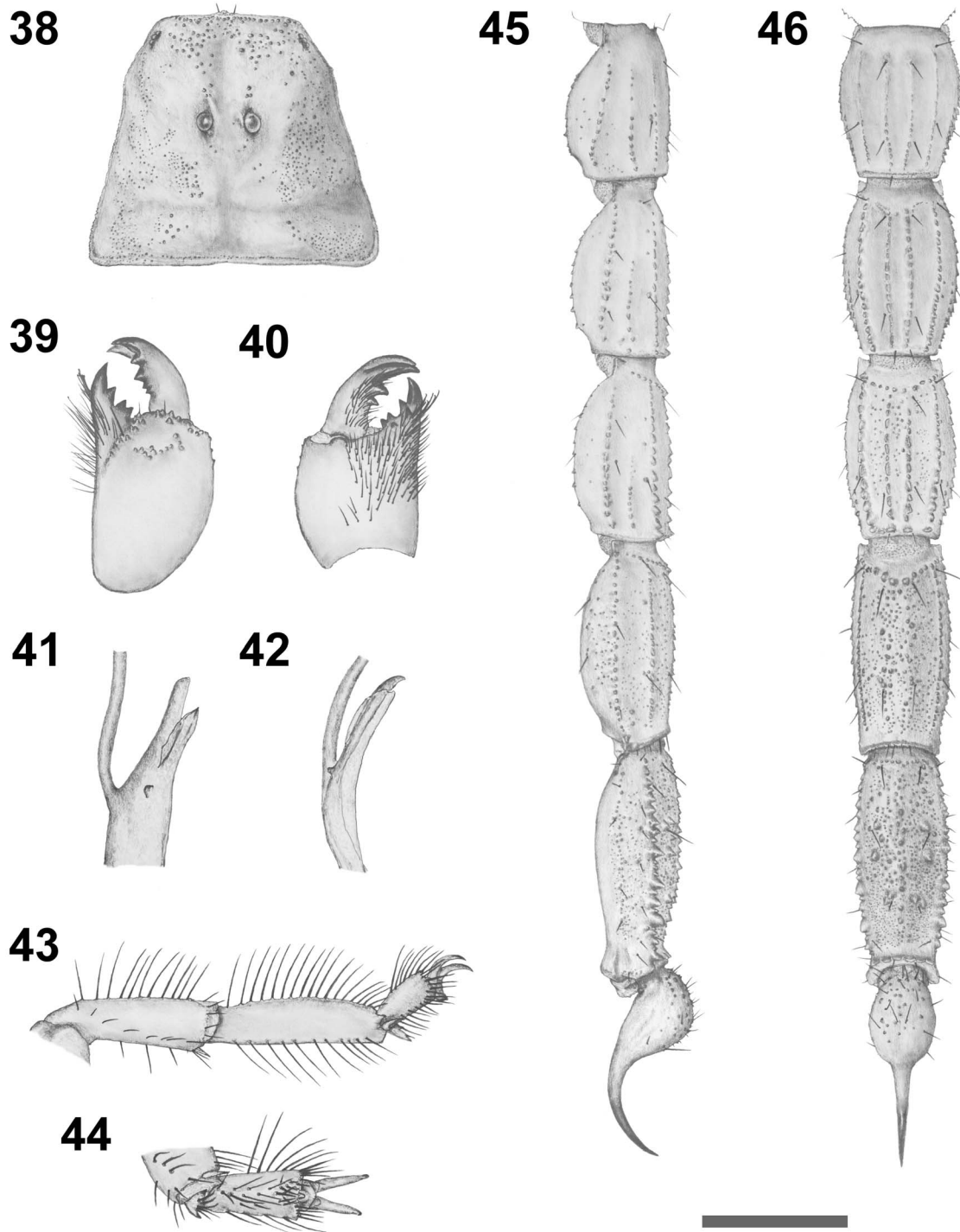
Chelicera (paratype male) (Figs. 39–40). Dorsal surface of manus smooth, convex, lustrous with dense

subapical transverse band of small granules; dorso-internal carina at base of fixed finger with larger dentate granules; *chaetotaxy*: two short pale macrosetae on apical margin of manus; long reddish macroseta on dorso-internal carina; movable finger smooth, without macrosetae, ventral surface of manus smooth, with numerous long, fine microsetae on middle and internal surfaces, more dense on interior aspect, extending dorsally to base of fixed finger; ventral surfaces of fixed and movable fingers with dense brush of microsetae; *dentition*: fingers with normal buthid dentition (Vachon, 1963; Sissom, 1990); fixed finger with large distal tine, smaller subdistal denticle and large proximal bicuspid; two large denticles on ventral surface, proximal denticle smaller than distal; movable finger with large dorsal and ventral distal tines; dorsal margin of movable finger with two large triangulate denticles and two small proximal denticles; ventral margin armed with two robust denticles, proximal smaller than distal.

Coxosternal area (Figs. 31, 33). Coxal surfaces mostly smooth, lustrous, with scattered fine granulation; coxa I with coarsely granular endite and anteromedian carina, finely granulate distal margin; coxa II with coarsely granular anterior carina, finely granular endite and distal margin; coxae III–IV with anterior carina weak, with medium to fine granules; coxa III with sparse small granules on surface, distal margin finely denticulate; coxa IV surface and distal margin smooth, posterior margin finely shagreened in basal half; anterior margin with 3 macrosetae on coxa II, 3–4 macrosetae on coxa III; coxa IV with single basal macroseta; sternum sub-pentagonal with deep postero-median excavation, sparsely shagreened, bearing 2 macrosetae; genital opercula smooth, with 3 macrosetae; genital papillae present.

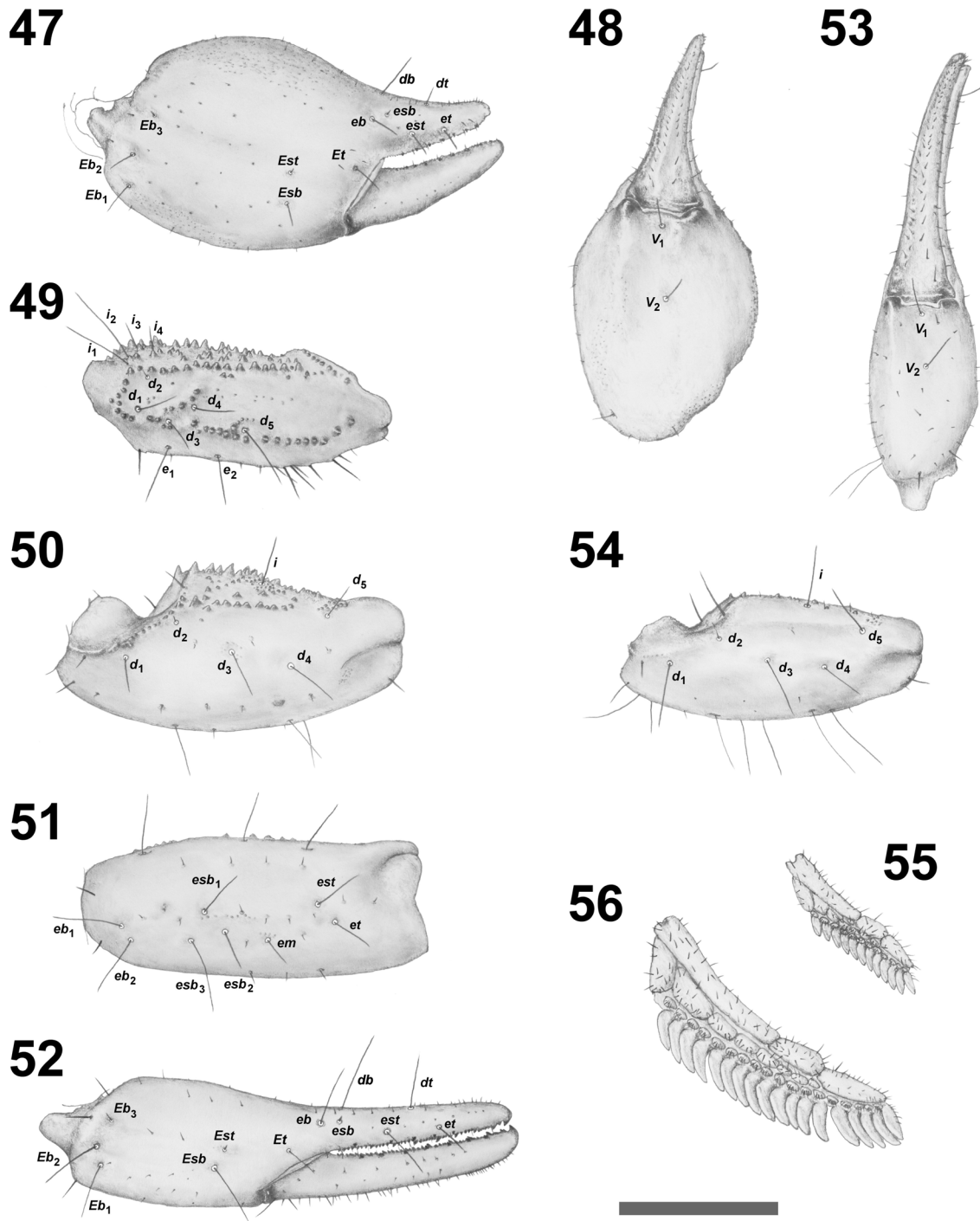
Pectines (Figs. 31, 33, 56). Basal piece smooth, rectangular, with deep anterior median notch; pectines moderately long, tips extending to basal third of trochanter IV; pectines with 3 marginal lamellae, 7–8 middle lamellae, 18–19 teeth; pectine teeth elongate, nearly uniform in size; marginal lamellae, middle lamellae and fulcra with numerous short, reddish macrosetae; fulcra with 7–11 setae; basal teeth not overlapping when anterior margins of pectines align with posterior margins of coxae IV.

Mesosoma (Figs. 30–33). *Tergites*: pretergites smooth, lustrous; median carina obsolete on tergite I, very weak on II–IV, weak on V–VI; tergites I–VI with lateral carinae obsolete, marked near posterior margin by single enlarged granule; tergite VII with weak median hump, inner lateral carinae very weak, marked by row of granules, outer lateral carinae obsolete; posterior margins of all tergites nearly straight, smooth; tergites I–VI



Figures 38–46: *Vachoniolus gallagheri*, sp. nov. 38, 43–46, holotype male; 39–42, paratype male (same locality as holotype). 38. Carapace, dorsal aspect. 39. Right chelicera, dorsal aspect. 40. Right chelicera, ventral aspect. 41–42. Right hemispermatochore, lobes at base of flagellum. 41, convex aspect; 42 outer aspect. 43. Right basitarsus and telotarsus III, retrolateral aspect. 44. Right telotarsus III, ventral aspect. 45–46. Metasoma and telson. 45. Right lateral aspect. 46. Ventral aspect. Scale bar: 38: 3.0 mm; 39–40, 44: 1.5 mm; 41–42: 1.0 mm; 43: 2.1 mm; 45–46: 4.25 mm.

densely, finely, uniformly shagreened, with series of small granules along posterior margins; tergite V finely shagreened or smooth medially, sparsely granulated laterally; all tergites devoid of macrosetae, lateral margins microdenticulate. *Sternites*: sternites III–VI smooth, lustrous, lacking carinae; sternite III with an-



Figures 47–56: *Vachoniolus gallagheri*, sp. nov. 47–51, 56, holotype male; 52–55, paratype female (S of Nizwa roundabout). 47. Right pedipalp chela of male, external aspect. 48. Right pedipalp chela of male, ventral aspect. 49. Right pedipalp femur of male, dorsal aspect. 50. Right pedipalp patella of male, dorsal aspect. 51. Right pedipalp patella of male, external aspect. 52. Right pedipalp chela of female, external aspect. 53. Right pedipalp chela of female, ventral aspect. 54. Right pedipalp patella of female, dorsal aspect. 55. Left pectine, female, ventral aspect. 56. Left pectine, male, ventral aspect. Scale bar: 47–48, 55–56: 3.0 mm; 49–54, 55–56: 2.0 mm. Trichobothrial notation after Vachon (1974).

terior lateral areas finely shagreened; sternite VII with weak, smooth, nearly obsolete paired median carinae and weak, smooth to faintly granulate paired lateral

carinae, intercarinal surfaces smooth; sternites III–VI with postero-medial margins smooth, postero-lateral and lateral margins finely denticulate; sternite VII with

nearly smooth posterior margin, denticulate lateral margins. *Chaetotaxy*: sternite III with 7 short macrosetae in medial area, IV–VI with paired medial macrosetae, VII with one pair of macrosetae on median carinae, one pair on lateral carinae, one pair on anterior lateral surface; posterior margins of sternites with short to medium length setae, III–VI with 2–3 larger posterior lateral setae, mixed with 12, 12, 19 and 11 smaller setae, arranged nearly uniformly along posterior margins with medial gap; lateral margins of sternites with well spaced macrosetae (left–right): III 2–2, IV 4–4, V 6–5, VI 4–3, VII 1–2.

Hemispermatorphore (paratype males) (Figs. 41–42). Flagelliform; trunk elongate, slender; flagellum long, filiform, proportions variable; in 3 males, pars recta 0.53, 0.71 and 0.27 times length of trunk, pars reflecta 0.65, 0.47 and 0.80 times length of trunk, respectively; inner lobe a broad lamina, gently tapering with blunt apex; median and outer lobes shorter, laminate, almost fully (1 case) or fully fused (2 cases); median lobe with outer margin curved, tapering to fine apical process, outer lobe linear, apically truncate; basal lobe a short, rounded, mediolaterally compressed knob; measurements of paratype (from N of Adam, partially fused lobes): trunk length (to base of flagellum) 3.5 mm, pars recta 2.5 mm, pars reflecta 1.7 mm, inner lobe (from base of flagellum) 900 μ m, median lobe (from juncture with inner lobe) 305 μ m, outer lobe from juncture with median lobe 120 μ m, from median lobe juncture with inner lobe 440 μ m, basal lobe 60 μ m.

Metasoma (Figs. 45–46). Long, slender, total length plus telson length 6.1 times carapace length. *Carination*: metasoma I with 10 complete carinae; metasoma II–III with 8 complete carinae, median lateral carinae confined to posterior 1/2 of segment II, posterior 1/3 of segment III; segment IV with 4 carinae, segment V with 3 carinae; dorsosubmedian carinae weak with small, separated granules on segments I–III, obsolete on IV; dorsolateral carinae moderate on segments I–III with large dentate granules, weak with smaller dentate granules on IV, obsolete on V; median lateral carinae weak with small granules on segment I, weak to obsolete on II–III with smaller anterior granules, larger posterior granules; ventrolateral carinae on segment I moderate, smooth anteriorly, coarsely granulate posteriorly, on II strong with coarse granules, on III strong, coarsely granulate-crenulate with larger posterior granules, on IV strong, coarsely granulate-crenulate, on V strong, armed with small, medium and large dentate granules; ventrosbmedian carinae on segment I weak, granulose posteriorly, obsolete anteriorly, on II moderate to strong, coarsely granular, with larger posterior granules, on III strong, coarsely granule-crenulate with enlarged posterior granules, on IV obsolete, positions marked by

scattered granules; posterior half of ventrosbmedian carina with 7–8 enlarged dentate granules on II, 6 on III; metasoma V with ventrosbmedian carinae obsolete, marked by series of enlarged dentate granules on anterior 3/4 of segment, ventromedian carina moderate, studded with small to large dentate granules; 5 denticles on ventral anal arc; lateral anal lobes split by single incision into broad dorsal lobe and dentate ventral lobe. *Granulation*: dorsal surfaces smooth on segments I–IV, smooth with scattered small granules on V, concave on I–III, convex on IV–V; dorsolateral surfaces smooth on segments I–III, with few small granules on I, finely granulate on IV–V; lateral surfaces smooth on I–III, finely granulate IV–V; ventrolateral and ventral surfaces smooth on I–II, lightly shagreened on III, densely shagreened on IV–V. *Chaetotaxy*: carinal macrosetae (left–right) dorsosbmedian: I, 0–0, II 1–0, III 2–2, IV 2–2, dorsolateral: I, 1–0, II 1–2, III 1–2, IV 2–2; ventrolateral: I 2–2, II 2–2, III 2–2, IV 2–2; ventrosbmedian: I 2–2, II 2–2, III 2–2, IV 2–2, V 3–3; intercarinal macrosetae: metasoma V 12–13 lateral setae, one posterolateral pair on ventral surface.

Telson (Figs. 45–46). Vesicle slim, width 0.69 times metasoma V width, dorsal surface smooth, lateral surface smooth with few small granules, ventral surface studded with medium to large granules, bearing numerous medium length reddish macrosetae: 1–2 on lateral surfaces, 14 on ventral surface, 2 on pedicel; aculeus slender, as long as vesicle.

Pedipalp (Figs. 47–51, 91–93, 102). *Femur* (Figs. 49, 91): short, stout, 0.73 times carapace length, 2.42 times longer than wide; dorsoexternal, dorsointernal and ventrointernal carinae strong, with robust dentate granules; external surface smooth; dorsal surface flat, mostly smooth with scattered small granules and proximal cluster of 3–4 medium granules, ventral surface smooth, proximally concave, distally convex, with few small granules; internal surface with irregular small and large conical granules, internal carina obsolete; dorsoexternal carina with 1 distal macroseta, external surface with (left–right) 0–1 basal, 8–12 distal macrosetae. *Patella* (Figs. 50–51, 92): short, stout, 0.87 times carapace length, 1.95 times longer than wide; dorsointernal carina strong, granulose; ventrointernal carina strong, with large dentate granules; internal carina weak, marked by contiguous medium to coarse granules; other carinae obsolete; dorsal surface smooth with few fine granules, external surface smooth, ventral surface smooth with sparse fine granules along internal margin; ventrointernal surface smooth with several fine granules, dorsointernal surface finely granular. *Chela* (Figs. 47–48, 93): relatively short, 1.37 times carapace length; manus extremely swollen, subglobose, width 0.65 times carapace length, fingers very short, movable finger 0.79

times ventral manus length; manus with dorsal surface densely, finely shagreened, external surface smooth to sparsely shagreened, ventroexternal surface densely, finely shagreened, ventral and ventrointernal surfaces smooth except for lightly shagreened proximal ventrointernal patch, internal surface sparsely to moderately shagreened with several small granules; all carinae obsolete; fixed and movable fingers smooth; dentate margins of finger straight, without proximal scalloping; closure of fingers leaves linear proximal gap, with tips of fingers apically divergent; ventral aspect of movable finger angled upwards near base; manus largely bare, with few short macrosetae; movable finger with numerous short macrosetae on ventral aspect, more dense apically; 7 primary denticle subrows on fixed and movable fingers; fixed fingers with 7 internal accessory denticles, 7–8 external accessory denticles; movable fingers with 7 internal accessory denticles, 6 and 8 external accessory denticles, tip of movable finger with 4 subdistal denticles (Fig. 102). *Trichobothrial pattern*: neobothriotaxic, type A β (Vachon, 1974, 1975), with supernumerary *esb*₃ on patella; trichobothrium *d*₅ located slightly distal to *e*₂; femur *d*₂, patella *d*₂, chela *Eb*₃, *Esb* and *esb* petite; *db* on fixed finger level with *esb*, at base of fixed finger; *eb* on distal manus; *dt* at middle of fixed finger, approximately midway between *est* and *et*.

Legs (Figs. 30–33, 43–44). Leg I short with stout segments; leg II moderately slender; legs III–IV very slender; ventral carinae dentate on femur I, finely denticulate on femora II–III, weak, crenulate-denticulate on femur IV; tibial spur present on right leg III, minute and vestigial on left leg III, present on both legs IV; retrolateral pedal spurs on legs I–IV simple, without setae; prolateral pedal spurs basally bifurcate on legs I–III, basally trifurcate on leg IV, with (left–right) 1–1, 0–1, 5–6, 5–4 setae; tibiae I–III with retrosuperior bristle-combs (Fig. 43) with (left–right) 6–6, 8–8, 13–11 setae; basitarsi I–III with bristle-combs (Fig. 43), retrosuperior series developed on I–III with (left–right) 9–8, 12–9, 17–16 setae; retroinferior series developed on II–III with 5–5, 11–10 setae; ventral surfaces of telotarsi with short fine macrosetae on legs I–II, medium length macrosetae on legs II–III (Fig. 17), medium to long, fine macrosetae on legs III–IV.

Measurements of holotype male (mm). Total L 49.30; metasoma and telson L 33.00; carapace L 5.40, anterior W 2.84, posterior W 6.04, carapace preocular L 2.24; metasomal segments (L/W/D) I 4.47/3.44/2.77, II 5.18/3.35/2.92, III 5.37/3.35/2.91, IV 6.24/2.92/2.75, V 6.88/2.79/2.55; telson L 5.33; vesicle L 2.75, W 1.93, D 1.81; pedipalp chela L 7.40, chela manus ventral L 4.64, chela manus W 3.48, D 3.78, fixed finger L 2.24, movable finger L 3.65; pedipalp femur L 3.96, W 1.63, patella L 4.69, W 2.41; pectine L 5.36, leg III patella L 4.64, W 1.50.

Measurements of paratype female (adult from N of Adam) (mm). Total L 47.00; metasoma and telson L 26.60; carapace L 5.03, anterior W 2.73, posterior W 5.68, carapace preocular L 2.24; metasomal segments (L/W/D) I 3.61/2.87/2.41, II 4.18/2.64/2.49, III 4.26/2.61/2.59, IV 4.99/2.41/2.28, V 5.62/2.54/2.15; telson L 4.99; vesicle L 2.41, W 1.67, D 1.72; pedipalp chela L 5.93, chela manus ventral L 2.54, chela manus W 1.46, D 1.79, fixed finger L 2.58, movable finger L 3.61; pedipalp femur L 3.18, W 1.31, patella L 4.13, W 1.72; pectine L 3.10, leg III patella L 3.78, W 1.38.

Variation. Biometric data were obtained from 17 adults or sub-adults (14 males, 3 females). The body length was 34–50 mm (mean \pm SD 41.8 \pm 4.3 mm) and carapace length 3.96–6.79 mm (5.27 \pm 0.64 mm). Pedipalp finger primary denticle subrows for adults: of 34 fixed fingers, there were 2 fingers with 6 subrows, 22 with 7, and 10 with 8; of 34 movable fingers, there was 1 finger with 5 subrows, 6 with 6, 24 with 7, and 3 with 8. The number of dentate granules on the posterior half of the ventrosubmedian carina of metasoma II and III: on II, 2 carinae with 5 granules, 13 with 6, 15 with 7, 4 with 8; on III, 5 carinae with 4 granules, 18 with 5, 11 with 6. Tibial spurs were either present or absent, and were absent more frequently on leg III than leg IV; of 30 leg III tibiae, spurs were present in 19 (63.3 %), and absent in 11 (36.7 %); of 29 leg IV tibiae, spurs were present in 25 (86.2 %), and absent in 4 (13.8 %). Variation in morphometrics is summarized in Figs. 106–111, Tab. 1. Trichobothrial distance ratio $(d_5 - e_2)/(e_2 - e_1) > 0$ (i.e. *d*₅ distal to *e*₂) for 27/28 femora (96.4 %).

Sexual dimorphism: females differed from males as follows: carapace smooth, lustrous with granulation weak to obsolete; tergites smooth, lustrous; pedipalp femur dorsally smooth, lustrous with only a few granules, internal surface mostly smooth with much smaller granules; pedipalp patella smooth, lustrous, with dorsointernal carina weak, finely granulated, ventrointernal carina weak with moderate to small granules (Fig. 54); pedipalp chela manus not strongly swollen, smooth, lustrous (Figs. 52–53); metasoma II–III with more prominent denticles on posterior half of ventrolateral and ventrosubmedian carinae; metasoma IV not as heavily granulated on lateral and ventral surfaces, with carinae weaker, more finely granular; ventrolateral and ventrosubmedian carinae on metasoma I moderate, almost smooth anteriorly, crenulate–granulate posteriorly; on II–III strong, crenulate–granulate anteriorly, dentate–granulate posteriorly; segment IV with ventrolateral carinae moderate, weakly granular; ventrosubmedian carinae obsolete; pectines much shorter (Fig. 55), terminating well short of distal ends of coxae IV (Figs. 35, 37). Pectine teeth: males 14–19 (of 28 combs from *n* = 14 males: 1 comb with 14 teeth, 4 combs with 15 teeth, 6 with 16, 7 with 17, 8 with 18, 2 with 19),

females 9–14 (of 6 combs from $n = 3$ females: 1 comb with 9 teeth, 1 with 11, 2 with 12, 2 with 14). There was significant sexual dimorphism in morphometrics (Table 1): females tended to have shorter pedipalp femur, patella, chela and metasoma I–V relative to carapace length, more slender pedipalp patella, and pedipalp chela movable finger longer relative to manus.

Juveniles: differed from adults as follows: dorso-external, dorsointernal and ventrointernal carinae on pedipalp femur weak to obsolete, with small granules; carinae on patella obsolete; chela manus not swollen in juvenile males; fewer macrosetae on the tibiae, basitarsi and telotarsi of all legs. In smallest juveniles (3 specimens, carapace lengths 1.53 mm, 1.59 mm, 1.65 mm) the tibia, basitarsus and telotarsus of legs I–III lacked macrosetae and bristle combs, and series of elongate spiniform processes (spine combs) extended from the retrosuperior margins of these leg segments (1–2 processes on tibia, 6–7 on basitarsi, 3–5 on telotarsi). Spines consisted of a short, broad basal portion and a long, fine, needle-like distal portion.

Distribution. This species is known only from arid plains of north-central Oman, south or south-west of the Al Hajar mountains, at elevations of 100–420 m a.s.l.

Ecology. All specimens were collected from sandy soils on arid, alluvial fans and wadis in the hot interior desert of north-central Oman. The development of bristle combs on the tibia and basitarsus of legs I–III is consistent with psammophilous, arenicolous specialization (Polis, 1990; Fet, Polis & Sissom, 1998; Prendini, 2001a). Compared to the more ultra-psammophilous *V. globimanus*, this species was found on more compacted sandy substrates. Burrowing in firmer soils may be correlated with the more robust development of the pedipalps and metasomal segments (Figs. 106–111), heavier carinae on the metasoma and pedipalp patella, and less elongate tarsal ungues (Fig. 43–44).

Vachoniolus globimanus Levy, Amitai
et Shulov, 1973

Figs. 57–83, 94–96, 104–111, 137–141, 146–148, Tab. 1

Vachoniolus globimanus Levy, Amitai & Shulov, 1973: 113–140, figs. 42–48; Vachon 1974: 910, 948, fig. 49; Vachon, 1979: 42–44, figs. 18–25, 28, 31, 34–36; Vachon & Kinzelbach, 1987: 100; El-Hennawy, 1992: 102, 133; Tigar & Osborne, 1997: 552, tab. 2; Tigar & Osborne, 1999: 174, 180, tab. 2; Fet & Lowe, 2000: 278; Fet, Soleglad & Lowe, 2005: 13; Hendrixson, 2006: 36, 100–102, figs. 23–24, pl. 18; Kaltsas, Stathi & Mylonas, 2008: 525; Navidpour et al., 2008: 24–26; Lourenço & Duhem, 2009: 47, fig. 29.

= *Buthacus minipektenibus* Levy, Amitai & Shulov, 1973: 128–130, figs. 27–31.

Vachoniolus minipektenibus (incorrect subsequent spelling): Vachon, 1974: 948; Vachon, 1979: 49, figs. 12–17, 27, 30, 33, 36.

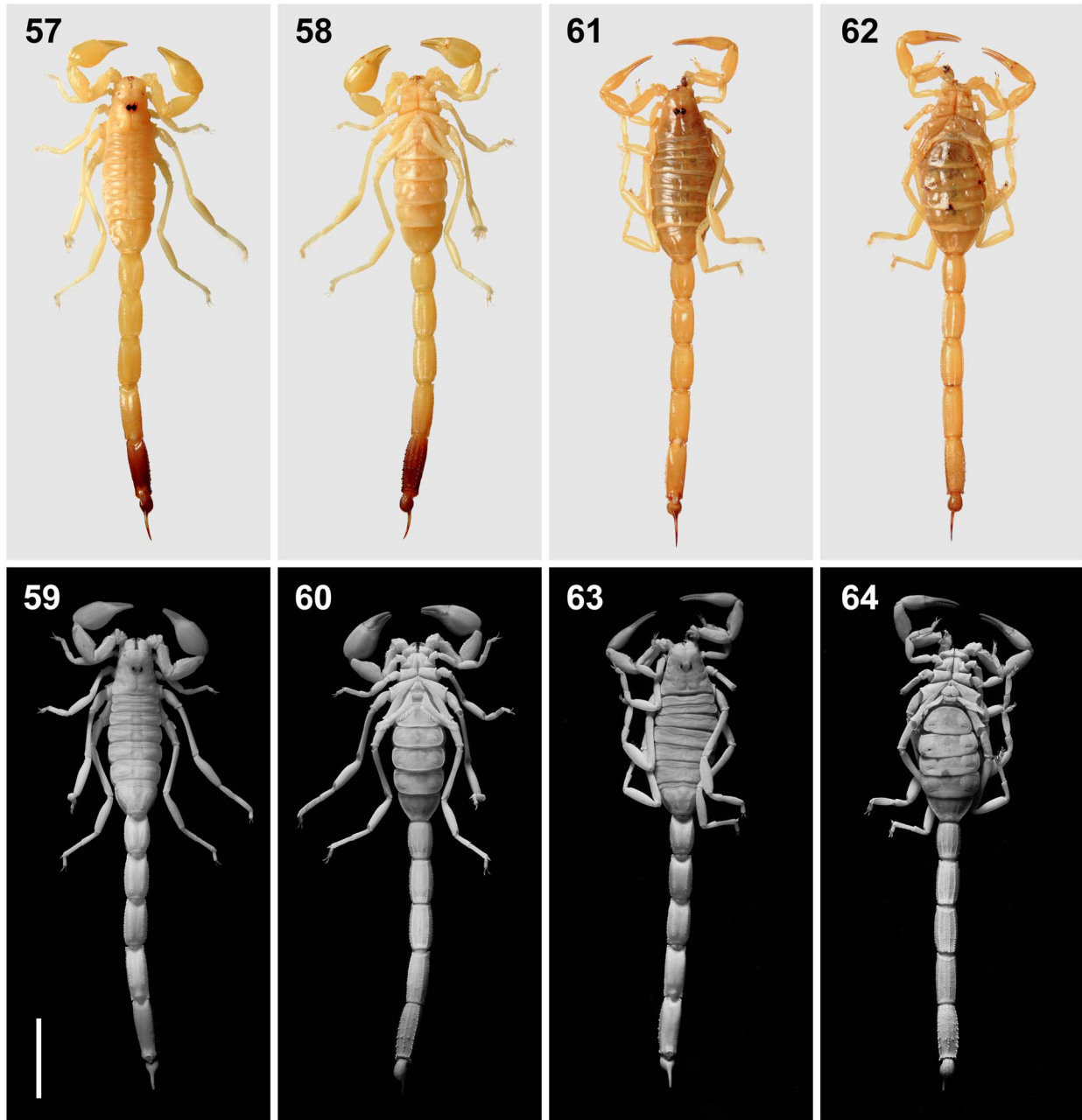
Vachoniolus minipektenibus: Kinzelbach, 1985: III; Vachon & Kinzelbach, 1987: 101; El-Hennawy, 1992: 102, 133; Tigar & Osborne, 1997: 552, tab. 2; Acosta & Fet 2005: 5–6; Fet, Soleglad & Lowe, 2005: 13.

Buthacus minipektenibus (incorrect subsequent spelling): Vachon & Kinzelbach, 1987: 100.

Vachoniolus minipektenatus (unjustified emendation): Fet & Lowe, 2000: 278; Hendrixson, 2006: 99–100.

Holotype: ♂, **Oman**: leg. Bunker, BMNH 1952.8.28.25-26 (examined).

Material examined: **Oman**: 1 juvenile, east of Ramlat as Sahmah, 20°25'N 56°05'E, 8 January 1982, leg. M.D. Gallagher MDG 6339, NHMB; 1 ♀, Wadi Tawsinat, Dhofar, on sandy plain, 17°53'N 52°57'E, 416 m a.s.l., 12–16 May 1982, leg. M.D. Gallagher MDG 6463, ONHM; 1 juvenile ♂, 1 juvenile ♀, Shariq, *Acacia* wood, Oman Eastern Sands Project, 22°28'N 58°48'E, 295 m a.s.l., 9 February 1986, leg. W. Büttiker, NHMB; 1 ♂, 1 ♀, Qitbit, behind rest house, 2 km, camping area, 19°07'N 54°27'E, 27 March 1989, leg. A.S. Gardner & S.M. Farook, NHMB 12; 1 ♀, Fasad, under car at night, sand, 18°27'N 53°06'E, 1 January 1994, leg. A. François, NHMB; 3 ♂, 1 ♀, 57 km S of Hafit, UV detection, stationary on flat and dune sand, none on nearby gravel plain, little vegetation except *Prosopis* & *Acacia*, evidence of occupation with goats, 23°28'N 55°53'E, 200 m a.s.l., 31 March 1994, 19:00 h, leg. M.D. Gallagher & B.J. Tigar MDG 8590, ONHM; 1 ♀, 57 km S of Hafit, pitfall No. 12, 23°28'N 55°53'E, 200 m a.s.l., 31 March 1994, 19:00 h, leg. M.D. Gallagher & B.J. Tigar MDG 8591, NHMB; 1 ♀, N Wahiba Sands, UV detection, eaten by *Apistobuthus*, vegetated flat between linear dune ridges, chenopods, 22°28.56'N 58°44.25'E, 340 m a.s.l., 3 October 1994, leg. G. Lowe & M.D. Gallagher, NHMB; 5 ♂, 3 ♀, Wadi Muqshin, NW of Montesar, UV detection, sandy flat in wadi, patches of dunes, *Prosopis*, *Zygophyllum*, 19°27.68'N 54°37.2'E, 195 m a.s.l., 6 October 1994, leg. G. Lowe & M.D. Gallagher, NHMB; 1 ♂, 1 juvenile, Ramlat Muqshin, edge of Rub' al-Khali, UV detection, large rounded dunes, low dune system, 19°30.86'N 54°36.71'E, 195 m a.s.l., 6 October 1994, leg. G. Lowe & M.D. Gallagher, ONHM; 1 ♂, 1 ♀, dunes NW of Montesar, S of Wadi Muqshin, UV detection on sand, humpy dunes, sparse vegetation, 19°29.17'N 54°36.89'E, 200 m a.s.l., 6 October 1994, leg. G. Lowe & M.D. Gallagher, NHMB; 1 ♀, dunes near Muqshin, UV detection on sand, open dune area with trees, 19°35.03'N 54°52.7'E, 170 m a.s.l., 6 October 1994, leg. G. Lowe &



Figures 57–64: *Vachoniolus globimanus*, male from Shigag (57–60) and paratype female from NW of Montesar (61–64). Habitus viewed under reflected white light (57–58, 61–62) or UV fluorescence (59–60, 63–64). 57, 59, 61, 63. Dorsal aspect. 58, 60, 62, 64. Ventral aspect. Scale bar: 10 mm.

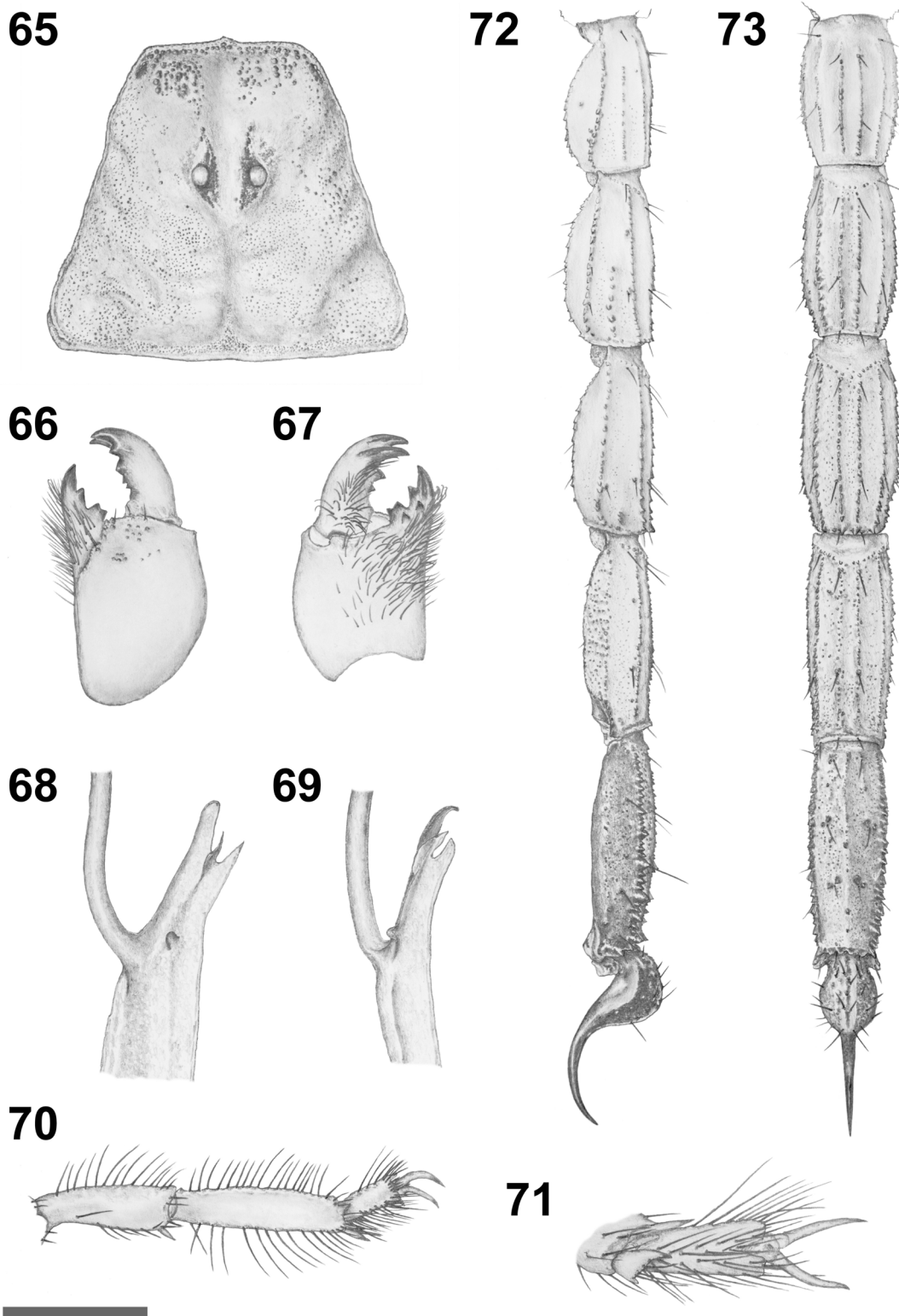
M.D. Gallagher, NHMB; 1 ♂, Ramlat as Sahmah, UV detection, coarse sandy inter-dune flat, sabkha, *Zygophyllum*, 20°13.87'N 55°54.75'E, 165 m a.s.l., 7 October 1994, leg. G. Lowe & M.D. Gallagher, BMNH; 1 ♂, Ramlat as Sahmah, UV detection, captured by *Apistobuthus pterygocercus*, sand ridge, chain of low barchan dunes, strong winds, 20°11.66'N 55°57.41'E, 170 m a.s.l., 7 October 1994, leg. G. Lowe & M.D. Gallagher, MNHN; 1 juvenile, Wadi Batha, edge of

Wahiba Sands, running on level gravelly sand, very cold night, minimum 5°C, no other scorpions found after long searches, 22°22.13'N 58°55.65'E, 200 m a.s.l., 28 December 1994, leg. M.D. Gallagher & B. Skule MDG 8651, NHMB; 2 ♀, 1 juvenile, Wahiba Sands, 22 km N of field base of 1986, UV detection, on sand dunes under *Prosopis cineraria* woodland, 21°50.43'N 59°18.83'E, 20 m a.s.l., 29 December 1994, 19:00 h, leg. B. Skule & M.D. Gallagher MDG 8655, NHMB; 1 ♂, E Wahiba

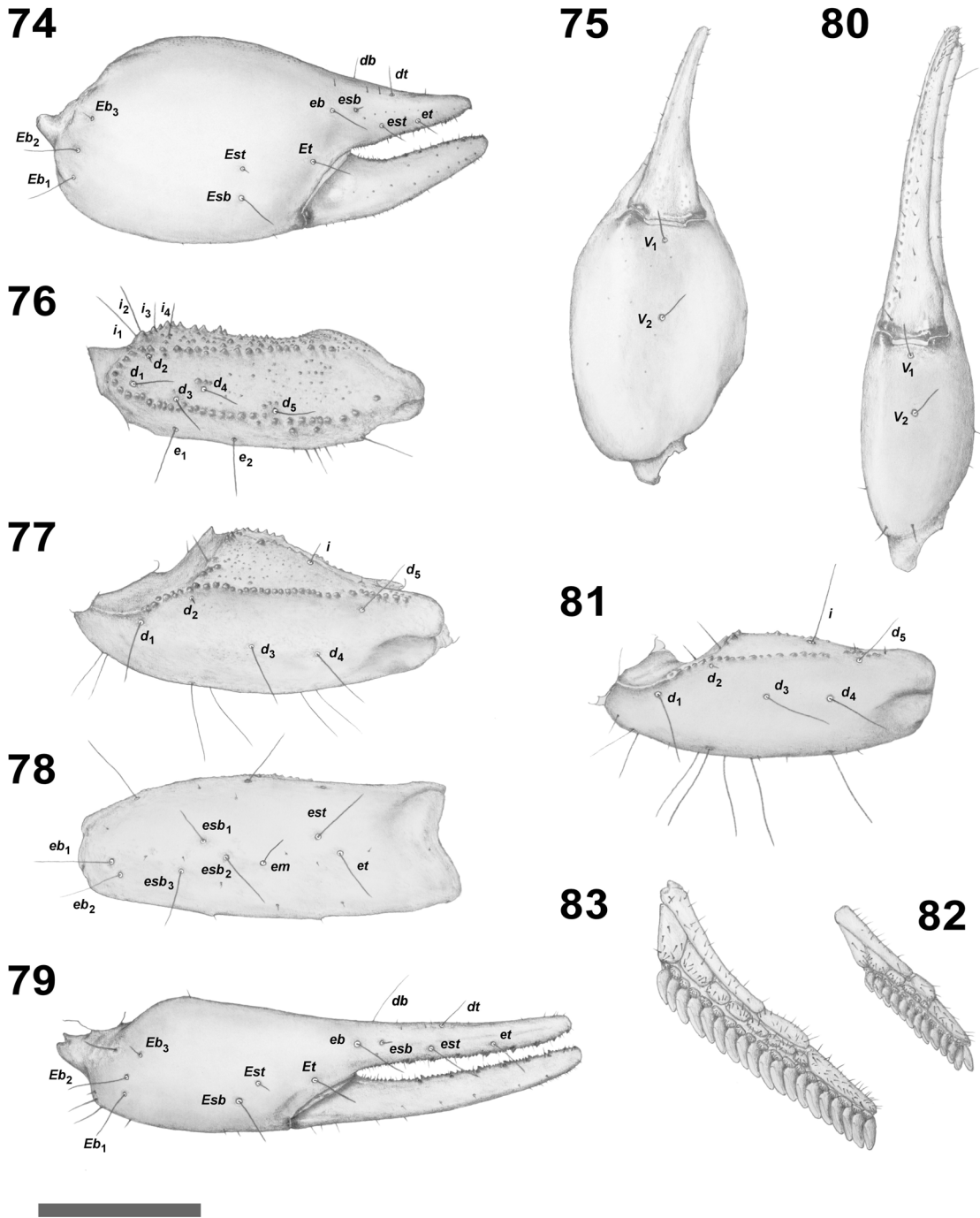
Sands, field base of 1986, on sand amongst shrubs, *Prosopis* woodland, sand dunes, 21°39.6'N 59°18.28'E, 24:00 h, 95 m a.s.l., 6 July 1995, leg. M.D. Gallagher & B. Skule MDG 8687, NHMB; 1 ♂, between Ghabah and Adam, UV detection on sand, sandy wadi on open gravel plain, trees and bushes, large *Galeodes* common, *Echis* sp. present, 22°09.54'N 57°30.16'E, 250 m a.s.l., 16 September 1995, 22:00–23:00 h, leg. G. Lowe & J. Dundon, NHMB; 2 ♀, Wadi Atiyah, UV detection on soft white sand, wide sandy wadi, low rocky ridge along dunes, 18°16.81'N 53°15.73'E, 260 m a.s.l., 28 September 1995, leg. G. Lowe, M.D. Gallagher & A. Dunsire, NHMB; 4 ♂, Empty Quarter, Uruq al Hadd, stable interdune sands, among sparse vegetation, 18°53.6'N 52°20.32'E, 11 January 1996, leg. J.N. Barnes, NHMB; 2 ♀, Wadi Muqhsin, near Montesar, level sand and some scrub, in open, 19°27.97'N 54°37.33'E, 140 m a.s.l., 12 December 1996, leg. I. Harrison & M.D. Gallagher MDG 8822, NHMB; 1 ♂, Barik, under mattress on sand near dunes, 20°59'N 56°33'E, 4 January 1997, leg. D. Willis, NHMB; 1 ♀, Wahiba Sands, 22°19.15'N 58°34.53'E, 8 February 1997, leg. I.D. Harrison & family, NHMB; 1 juvenile, Wahiba Sands, 22°19.15'N 58°34.53'E, 8 February 1997, leg. I.D. Harrison & family, NHMB; 1 ♀, 3 juveniles, 4 km N of An Nuqdah, rolling dune sand with *Halopyrum mucronatum* & *Limonium* hummocks in 500 m by 500 m area, signs of abundant lizard and rodent activity, new moon, strong south wind, 20°52.9'N 58°44.4'E, 250 m a.s.l., 22 October 1997, 18:30–20:00 h, leg. I.D. Harrison & M.D. Gallagher MDG 8891, NHMB; 1 juvenile, Fasad dunes, 18°27'N 53°06'E, 6 November 1997, leg. S. Polak, NHMB; 4 ♂, 1 juvenile, 15 km NW of Shigag, on slope of large dune, some under cover of bushes, two on level sand in front of dune, 72°F, no wind, new moon, 19°37.4'N 54°04'E, 190 m a.s.l., 30 November 1997, leg. M.D. Gallagher & I.D. Harrison MDG 8909, NHMB; 1 juvenile, mid Wahiba Sands, partly eaten specimen, 21°39.26'N 58°41.1'E, 29 January 1998, leg. I.D. Harrison, NHMB; 1 ♂, 15 km NNE Fasad (North), in high dunes and lower slopes, 18°45.2'N 53°08.9'E, 290 m a.s.l., 29–30 January 1998, leg. M.D. Gallagher & J.N. Barnes MDG 8940, GL; 2 ♀, N of An Nuqdah, low hillocks of sand with vegetation, 20°52.45'N 58°39.09'E, 30 January 1998, leg. I.D. Harrison, NHMB; 1 ♀, 5 km SE of Qitbit Rest House (site F/11), UV detection, sandy dunes near spring, base of bush, 19°09.33'N 54°30.47'E, 210 m a.s.l., 27 January 2000, 16:30–22:00 h, leg. A. Winkler & B. Winkler, NHMB; 1 ♀, north Wahiba Sands (site F/24), UV detection, plain between large dunes, burrows at base of small shrub, 22°28.36'N 58°46.8'E, 300 m a.s.l., 8 February 2000, 19:00–21:00 h, leg. A. Winkler & B. Winkler, NHMB; 1 ♀, near Marsawdad, in low sand dunes in large wadi, on open sand, 19°25.1'N 54°27.1'E, 14 February 2000, leg. I.D. Harrison, ONHM 41/20; 1 ♀, Wadi Qitbit (site F/12),

UV detection, sand dunes, near spring, on sand between shrubs, 19°09.33'N 54°30.47'E, 210 m a.s.l., 18 December 2001, 20:00–21:00 h, leg. A. Winkler, NHMB. **Saudi Arabia:** 1 ♀, Muneegger-Sanam, Great South Arabian Desert, 22°00'N 51°00'E, 198 m a.s.l., 18–19 January 1931, leg. Capt. B.S. Thomas No. 485, BMNH 1931.6.2.19, VA 1558 (paratype of *Buthacus minipectenibus*). **United Arab Emirates:** 1 ♀, Bada Zaid, Abu Dhabi, 24°27'N 55°20'E, leg. D.J.G. Williams, MNHN RS6495; 1 ♀, Madinet Zayed, 23°40.9'N 53°41.92'E, TERC; 1 ♂, Jebel Faiyah, sand dunes, 27 March 1971, leg. M.D. Gallagher MDG 737, BMNH VA1554; 2 ♂, Abu Dhabi, Bada Haza, 24°09'N 54°16.8'E, 9 November 1971, leg. D.J.G. Williams, BMNH VA 1555-1, VA1555-2; 1 ♀, Bayunna, 24°01.55'N 52°34.39'E, 9 June 1993, leg. B.J. Tigar, TERC; 1 ♀, Bayunna, 24°01.55'N 52°34.39'E, 12 November 1993, leg. B.J. Tigar, TERC; 1 ♂, Madinet Zayed, 23°40.9'N 53°41.92'E, 13 November 1993, TERC; 1 ♀, Madinet Zayed, 23°40.9'N 53°41.92'E, 18 November 1993, TERC; 1 ♂, 2 ♀, Um Az Zimul, 22°42.85'N 55°08.32'E, 16 December 1993, TERC; 1 ♀, Um az Zimul, 22°55.07'N 55°12.82'E, 6 December 1994, TERC; 1 ♀, Nahel, near Sweihan, rolling sand with vegetation, 24°27'N 55°20'E, 225 m a.s.l., 14 September 2001, leg. G. Feulner, GL; 1 ♀, Al Wathba wetland, 24°15.85'N 54°36.38'E, 14 April 2003, TERC; 1 ♂, Um Az Zimul, 22°42.85'N 55°08.32'E, 20 April 2006, leg. MAQ, TERC; 1 juvenile, western region, Abu Dhabi Emirate, pitfall trap on sand, 23°54.33'N 53°55.39'E, 17 March 2009, leg. A. Saji, NHMB.

Diagnosis. Medium to large *Vachoniolus*, adults 45–65 mm; base color yellow to orange-yellow with or without melanic pigmentation on metasoma IV–V and telson (Figs. 57–58, 61–62, 137–141); tergites smooth in females except for granules along posterior margins, finely shagreened in males; positions of obsolete lateral carinae of tergites III–VI marked posteriorly by 1–3 fine granules; metasomal segments relatively slender (Figs. 72–73), L/W ratios: I 1.37–1.60, II 1.64–1.95, III 1.76–2.09, IV 2.20–2.62, V 2.46–3.05; metasoma I–II with dorsolateral surfaces smooth in females, finely sparsely shagreened in males; dorsosubmedian carinae on metasoma II–III weak, with closely spaced, denticulate granules separated by two granule lengths or less; ventrosubmedian carinae of metasoma II–III crenulate to serrate with small to moderate sized, closely spaced, triangular dentate granules separated by one granule length or less, 5–13 granules on posterior half of carina; telson with long aculeus, vesicle L/ telson L 0.39–0.54; pedipalp femur with trichobothrium d_5 distal to e_2 , distance ratio $(d_5-e_2)/(e_2-e_1)$ median value 0.42 (Figs. 76, 111); pedipalp patella neobothriotaxic with 8–9 trichobothria on external surface (Figs. 77–78); pedipalp chela manus of males smooth to finely granular on



Figures 65–73: *Vachoniolus globimanus* Levy, Amitai et Shulov, 1973, male (65–67, 70–73: male from Shigag, 68–69 male from Fasad). **65.** Carapace, dorsal aspect. **66.** Right chelicera, dorsal aspect. **67.** Right chelicera, ventral aspect. **68–69.** Right hemispermatophore, lobes at base of flagellum. **68,** convex aspect; **69,** outer aspect. **70.** Right basitarsus and telotarsus III, ventral aspect. **71.** Right telotarsus III, retrolateral aspect. **72–73.** Metasoma and telson. **72.** Right lateral aspect. **73.** Ventral aspect. Scale bar: 65, 70: 2.8 mm; 66–67: 1.6 mm; 68–69: 1.0 mm; 71: 1.5 mm; 72–73: 1.0 mm.



Figures 74–83: *Vachoniolus globimamus* Levy, Amitai et Shulov, 1973 (74–7, 83: male from Shigag; 79–82: female from NW of Montesar). **74.** Right pedipalp chela of male, external aspect. **75.** Right pedipalp chela of male, ventral aspect. **76.** Right pedipalp femur of male, dorsal aspect. **77.** Right pedipalp patella of male, dorsal aspect. **78.** Right pedipalp patella of male, external aspect. **79.** Right pedipalp chela of female, external aspect. **80.** Right pedipalp chela of female, ventral aspect. **81.** Right pedipalp patella of female, dorsal aspect. **82.** Left pectine, female, ventral aspect. **83.** Left pectine, male, ventral aspect. Scale bar: 74–75, 82–83: 3.3 mm; 76–81: 2.5 mm. Trichobothrial notation after Vachon (1974).

dorsointernal margin, smooth elsewhere (Fig. 96); tibial spurs present or absent on legs III–IV.

Measurements of adult male (from 15 km NW of Shigag) (mm). Adult male: total L 62.50; metasoma and

telson L 40.00; carapace L 6.24, anterior W 3.18, posterior W 6.85, carapace preocular L 2.61; metasomal segments (L/W/D) I 5.50/3.70/3.05, II 6.49/3.61/3.13, III 6.84/3.59/3.01, IV 7.83/3.23/2.75, V 8.08/2.84/2.58; telson L 6.45; vesicle L 2.92, W 2.06, D 2.06; pedipalp

chela L 8.93, chela manus ventral L 5.42, chela manus W 3.90, D 4.26, fixed finger L 2.75, movable finger L 4.27; pedipalp femur L 4.73, W 1.81, patella L 5.68, W 2.58; pectine L 6.71, leg III patella L 5.63, W 1.65.

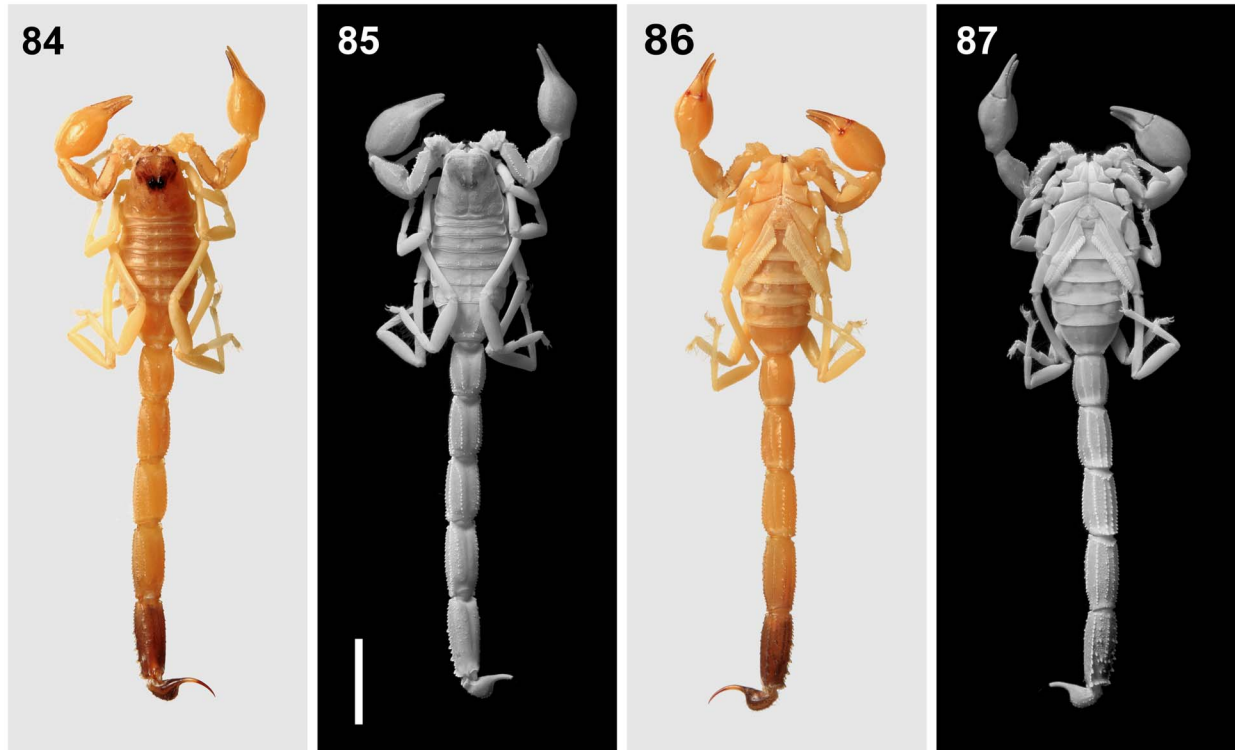
Measurements of adult female (from NW of Montesar): total L 56.50; metasoma and telson L 36.00; carapace L 5.85, anterior W 3.01, posterior W 6.49, carapace preocular L 2.54; metasomal segments (L/W/D) I 4.73/3.18/2.77, II 5.68/3.01/2.75, III 5.97/3.04/2.84, IV 6.49/2.70/2.58, V 7.01/2.74/2.61; telson L 6.11; vesicle L 2.65, W 1.96, D 1.74; pedipalp chela L 7.48, chela manus ventral L 3.18, chela manus W 1.81, D 1.98, fixed finger L 3.53, movable finger L 4.70; pedipalp femur L 4.13, W 1.55, patella L 5.07, W 2.15; pectine L 4.11, leg III patella L 4.82, W 1.58.

Variation. Coloration of the body was uniform pale yellow in some populations, while in others there was varying fuscosity on the telson, metasoma V, and posterior portion of metasoma IV. Specimens from 57 km S of Hafit had faint fuscous markings on the carapace, tergites and pedipalp patella. Biometric data were obtained from 43 adults or sub-adults (25 males, 18 females). The body length was 35–62.5 mm (mean \pm SD 49.2 ± 7.0 mm) and carapace length 3.94–5.40 mm (4.57 ± 0.46 mm). Variation in morphometrics is summarized in Figs. 106–111, Tab. 1. Pedipalp finger primary denticle subrows were variable: of 79 intact fixed fingers, there was 1 finger each with 1, 2 and 5 subrows, 2 with 4, 4 with 6, 20 with 7, 46 with 8, and 4 with 9; of 79 intact movable fingers, there was 1 finger each with 2 and 4 subrows, 2 with 5, 7 with 6, 32 with 7, 33 with 8, and 3 with 9. The number of dentate granules on the posterior half of the ventrosulmedian carina of metasoma II and III was distributed as follows: on II, 1 carina with 6 granules, 9 with 7, 20 with 8, 24 with 9, 21 with 10, 7 with 11, and 2 with 12; on III, 2 carinae with 5 granules, 9 with 6, 13 with 7, 26 with 8, 15 with 9, 8 with 10, 5 with 11, 4 with 12, and 2 with 13. Tibial spurs were either present or absent, or vestigial (< 20% of the length of fully formed spur), and were lost with similarly high frequencies on both legs III and IV: of 78 intact leg III tibiae, spurs were present in 39 (50.0 %), and absent or vestigial in 39 (50.0 %); of 77 intact leg IV tibiae, spurs were present in 43 (55.8 %), and absent or vestigial in 34 (44.2 %). Vachon (1979) found that the number of external trichobothria on the pedipalp patella varied in the range 8–9. In material examined here, 106/106 patellae (from 26 males and 24 females, including adult and juvenile samples from Oman and United Arab Emirates) bore 8 external trichobothria, always grouped in 3 clusters (2 basal, 4 middle, 2 distal). Hence, the frequency of deviation from the normal count of 8 is less than 1%. In two small juveniles (carapace lengths 1.65 mm, 1.80 mm; Ramlat as Sahmah & An

Nuqdah) the tibia, basitarsus and telotarsus of legs I–III lacked macrosetae and bristle combs, and series of elongate spiniform processes (spine combs) extended from the retrosuperior margins of these leg segments (1–5 processes on tibia, 6–9 on basitarsi, 2–4 on telotarsi). Spines consisted of a short, broad basal portion and a long, fine, needle-like distal portion.

Sexual dimorphism: females differed from males as follows: carapace and tergites smoother, lustrous (finely shagreened or finely granulose in males); pedipalp patella with weaker dorsointernal and ventrointernal carinae (Figs. 77, 81); internal surface of patella smooth (granulated in males), pedipalp chela manus not strongly swollen, smooth, lustrous (Figs. 79–80); ventrosulmedian carinae of metasoma II–III more robust, with slightly larger denticles; pectines much shorter (Figs. 82–83), tips not reaching distal ends of coxae IV (extending up to or beyond distal ends of coxae IV in males) (Figs. 58, 60, 62, 64). Pectine teeth: males 16–25 (of 56 combs from $n = 28$ males: 2 combs with 16 teeth, 3 with 17, 6 with 18, 16 with 19, 13 with 20, 8 with 21, 4 with 22, 2 each with 23 and 25), females 10–18 (of 52 combs from $n = 26$ females: 2 combs each with 10 and 12 teeth, 5 with 13, 15 with 14, 13 with 15, 8 with 16, 4 with 17, 3 with 18). There was also significant sexual dimorphism in morphometrics (Tab. 1). Females tended to have shorter pedipalp femur, patella, chela and metasoma I–V relative to carapace L, more slender pedipalp patella, and pedipalp chela movable finger was much longer relative to manus.

Wahiba Sands material: specimens from the southern and eastern margins of the Wahiba Sands tended to have higher numbers of pectine teeth compared to those from central Oman and Rub' al-Khali. Wahiba Sands females had 14–18 teeth (mean \pm SD 15.9 ± 1.5 , $n = 16$ combs), significantly higher than Rub' al-Khali females with 10–16 teeth (14.1 ± 1.5 , $n = 36$ combs) ($p = 0.0002$, t-test); Wahiba Sands males had 19–25 teeth (22.6 ± 2.1 , $n = 7$ combs), significantly higher than Rub' al-Khali males with 16–23 teeth (19.4 ± 1.4 , $n = 49$ combs) ($p = 3 \cdot 10^{-6}$, t-test). Four specimens from the northern Wahiba Sands had somewhat more stout metasomal segments and larger dentition on ventrosulmedian carinae of metasoma II–III, compared to other Wahiba Sands material. The denticles on these carinae were, however, smaller than on *V. gallagheri*, and appeared intermediate between *V. gallagheri* and *V. globimanus*. Overall, the material from the Wahiba Sands appears closest to *V. globimanus* in metasomal morphometrics and carination, and are provisionally placed here into that species. One small, apparently sub-adult male from the *Prosopis* woodlands of the eastern Wahiba Sands had swollen pedipalp chelae with the manus smooth, not granulated, also consistent with placement in *V. globimanus*. The Wahiba Sands *Vachoniolus* were smaller in body size compared to those from Rub' al-Khali, but it is unclear if



Figures 84–87: *Vachoniolus iranensis* Navidpour et al., 2008, paratype male. Habitus viewed under reflected white light (84, 86) or UV fluorescence (85, 87). 84–85. Dorsal aspect. 86–87. Ventral aspect. Scale bar: 5 mm.

this reflects a lack of adults in a limited sample. No adult males were available from the Wahiba Sands, and the status of these populations should be reviewed when such material becomes available. Although no clear morphological characters are known for separating them, it is conceivable that *Vachoniolus* in the Wahiba Sands could be isolated and genetically distinct from the Rub' al-Khali populations.

Remarks. The holotype male of *V. globimanus* was examined and confirmed to be distinct from *V. batinahensis* and *V. gallagheri*. It is smaller than the average size of adult *V. globimanus*, and it may be sub-adult. The right pectine has been lost, although it was originally intact with 18 teeth. The left pedipalp chela bears anomalous dentition on the fixed finger, with a long, fused proximal subrow. The 1950 locality reference 'Oman' is ambiguous and could also have referred to Trucial Oman, now the United Arab Emirates. However, the material collected and analyzed here unequivocally establishes the presence of *V. globimanus* in Oman.

A paratype female of *V. minipectenibus* was also examined, and comparison with the series of females analyzed in this study supports the synonymy of *V. minipectenibus* with *V. globimanus* by Hendrixson (2006). There has been some confusion about the type locality of *B. minipectenibus*, cited as 'Munegger-

Sanam' (Fet & Lowe, 2000). This compound name refers to two areas in Saudi Arabia along the route followed by Bertram Thomas on his historic camel voyage across the Rub' al-Khali: a region of sands known as As Sanam (ca. 21–23°N 51°E), and Hadh Munajjar (21°N 51°E) at the southern end of As Sanam (Thomas, 1931: 224; Thomas, 1932, foldout map). Thus, Hadh Munajjar could be the type locality of *B. minipectenibus*. Vachon (1979: 51, fig. 56) erroneously plotted 'Munegger-Sanam' at the village of Sanam, ca. 220 km southwest of Riyadh, over 800 km from the type locality.

Ecology. This species is a psammophile or ultra-psammophile, inhabiting aeolian dunes of the Rub' al-Khali and Wahiba Sands, at recorded elevations in the range 20–416 m a.s.l. (Figs. 147–148). Adaptations for life on sand include prominent bristle combs on the basitarsi and telotarsi of legs I–III (Fig. 70) and long slender tarsal ungues (Figs. 70–71) (Fet, Polis & Sissom, 1998; Prendini, 2001a; Polis, 1990). In the field, it was collected in the same areas as the common dune scorpion, *Apistobuthus pterygocercus*, but at much lower densities. It was observed to fall prey to the larger, aggressive *Apistobuthus*, suggesting that its populations might be limited by intraguild predation (Polis & McCormick, 1987).

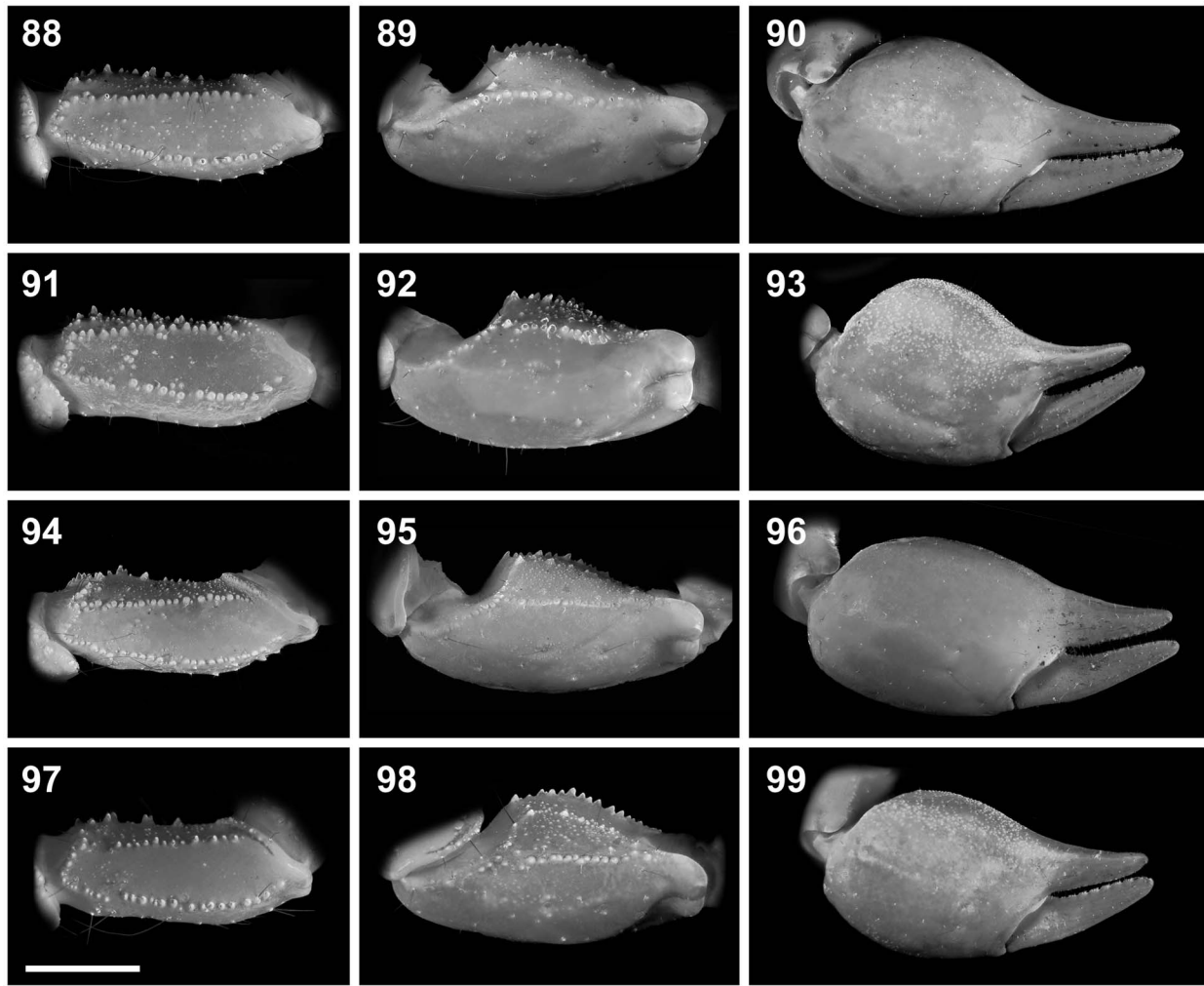
Discussion

The discovery of two new *Vachoniolus* in Oman doubles the number of known species and reveals a hidden diversity in this unusual buthid genus. All four known *Vachoniolus* are specialized psammophilous scorpions inhabiting sand deserts in the Arabian Peninsula and adjacent northern Iran. What can be deduced about their relationships and evolution? The diagnosis of *V. batinahensis* includes unique plesiomorphic characters indicating that it probably occupies a basal position in the phylogeny of the genus: (1) orthobothriotaxy of the external surface of the pedipalp patella (Fig. 22), with 7 trichobothria in the prevalent buthid configuration (Vachon, 1974; Sissom, 1990); (2) femoral trichobothrium d_5 either distal or proximal to e_2 (Figs. 20, 111), approaching the prevalent buthid configuration in which d_5 is proximal to e_2 (Vachon, 1974; Sissom, 1990); (3) complete retention of tibial spurs on legs III–IV. The polarity of these characters can be inferred by outgroup comparisons to other North African, Middle Eastern and Asian buthids, for example the similar genus *Buthacus* (Vachon, 1979). These plesiomorphic traits and the restricted distribution of *V. batinahensis* along the Al Batinah coastal plain (Figs. 147–148) suggest that it is a relict species, descended from an original ancestral population of *Vachoniolus*. Populations of *V. batinahensis* are isolated from the other species by two physiographic barriers: the rocky escarpments of the Al Hajar mountain ranges and the waters of the Arabian Gulf. Uplift of the Al Hajar mountains commenced sometime at the end of the Paleogene, or early Neogene (early Miocene, ca. 20 Mya), with the collision of the Arabian and Eurasian continental plates. The region of the Arabian Gulf was mostly dry around this time, and terrestrial substrates favorable for arenicolous or psammophilous scorpions such as *Vachoniolus* could have been made available by exposure of shallow marine sediments by tectonic movements, or accumulation of fluvial deposits on the Tigris-Euphrates delta. In the late Miocene (ca. 10 Mya), the Arabian plate began to under-thrust western Iran, initiating a process that led to uplift of the Zagros Mountains ca. 5 Mya. This resulted in sinking of the Arabian Gulf, and its eventual flooding from the Strait of Hormuz by about the late Pliocene or later (ca. < 2 Mya). If *Vachoniolus* evolved in an early Miocene to Pliocene timeframe, this marine transgression would have disrupted its populations and isolated *V. batinahensis* on the Batinah coast. However, it is also possible that *Vachoniolus* arose later in the Pleistocene, during one of the glacial maxima (< 800 kya) when sea levels were lower and the Gulf became an arid basin covered with aeolian dunes. During these periods, the Tigris-Euphrates drainage extended out to the Strait of Hormuz,

and uninterrupted sandy terrain could have connected the Batinah coast with dunes in the Arabian Gulf.

The two species *V. globimanus* and *V. gallagheri* may represent a radiation of the genus into sandy habitats of the interior Arabian Peninsula, with differential adaptation to local substrates (Prendini, 2001a). *V. globimanus* seems better adapted to soft, wind-blown sands of the Rub' al-Khali, whereas *V. gallagheri* apparently prefers to burrow in more stabilized sand deposits overlying the broad belt of alluvial fans spreading out from the interior southern and western slopes of the Al Hajar mountains (Fig. 148). In the northern sands of Khoozestan Province, Iran, speciation of *V. iranensis* may have occurred during interglacial periods when this area was isolated by flooding of the Arabian Gulf. Similar vicariance is hypothesized to have resulted in divergence of the sand scorpions *Apistobuthus susanae* and *A. pterygocercus* (Navidpour & Lowe, 2009). Speciation of the ultrasammophilous *A. pterygocercus* and *V. globimanus* was probably linked to the formation of the sands of the Rub' al-Khali. These dune systems are thought to have accumulated during late Pleistocene glaciation cycles, when sedimentary deposits of Palaeozoic and Mesozoic origin were mobilized and reworked by intensified trade winds (Glennie, 1998; Glennie & Singhvi, 2002). In Oman, *V. globimanus* is found along the south-eastern margins of the Rub' al-Khali, and its distribution extends eastward to the Wahiba Sands (Fig. 148). The Wahiba Sands were formed during the late Pleistocene and Holocene (Gardner, 1988; Pease & Tchakerian, 2002; Radies et al., 2004), and have been colonized by both *V. globimanus* and *A. pterygocercus* (Vachon, 1980).

The apparent overlap in the distributions of *V. globimanus* and *V. gallagheri* raises the question of how these two species could have diverged. The alluvial fan deposits upon which *V. gallagheri* populations reside are quite old, dating back to the early Pleistocene or Pliocene (Juyal et al., 1998). The more plesiomorphic layout of femoral d_5 trichobothrium with respect to e_2 in *V. gallagheri* (Fig. 111) is consistent with this species being descended from an earlier lineage of *Vachoniolus*. This lineage may have flourished during an early pluvial period, when the Rub' al-Khali basin was an immense subtropical savanna with gentle longitudinal dunes and interdune lakes (McClure, 1988). In those times, the substrate was probably comprised of relatively firm, stabilized sand, which would explain the predilection of *V. gallagheri* for more compacted sandy soils. In later glacial periods, intense Shamal winds and hyper-arid climate transformed the region into a vast desert with tall, mobile dunes. Such conditions would have favored the evolution of an ultrasammophilous lineage ancestral to *V. globimanus*. Although pluvial and glacial periods alternated during the Pleistocene, the Rub' al-Khali has been in a hyper-arid phase with major dune

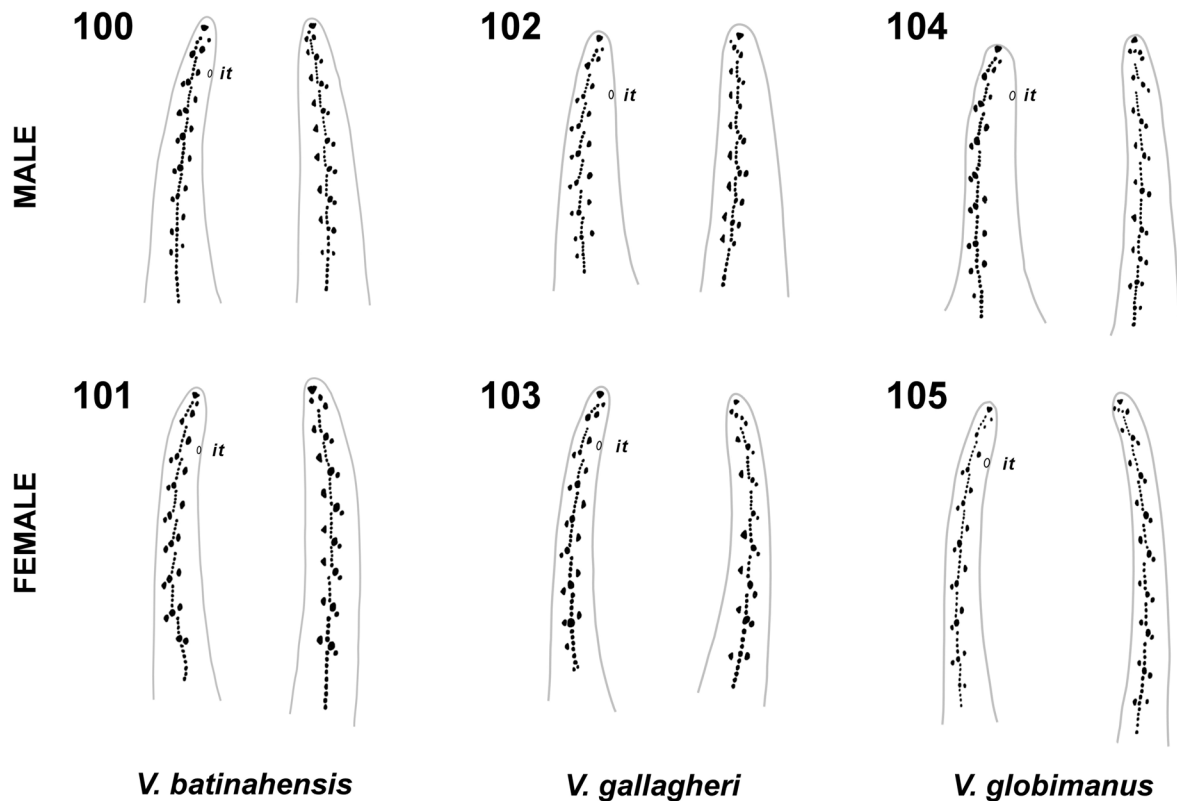


Figures 88–99: Pedipalp segments of *Vachoniolus*, species, viewed under UV fluorescence. **88–90**, *V. batinahensis*, **sp. nov.**, holotype male; **91–93**, *V. gallagheri*, **sp. nov.**, holotype male; **94–96**, *V. globimanus*, male from Barik; **97–99**, *V. iranus*, male from Iran. 88, 91, 94, 97: pedipalp femur, dorsal aspect; 89, 92, 95, 98: pedipalp patella, dorsal aspect; 90, 93, 96, 99: pedipalp chela, external aspect. Scale bar: 88–89, 99: 2.0 mm; 90: 2.4 mm; 91–92: 1.7 mm; 93, 96: 2.7 mm; 94–95: 2.1 mm; 97–98: 1.3 mm.

activity since the late Holocene (6 kYa) (Bray & Stokes, 2003; Stokes & Bray, 2005), and hence *V. globimanus* is currently the more widespread and dominant species. In the zone of overlap in north-central Oman, the two species are expected to be locally segregated by partitioning into different substrates (Williams, 1970).

The sampling of *Vachoniolus* populations by UV detection has facilitated the acquisition of significant material representing individuals of all ages, including the earliest instars which would be difficult or impossible to find and collect by any other method. Study of the smallest free-living juveniles, presumably second instar (carapace length < 2 mm), revealed a remarkable structural specialization on the distal segments of legs I–III. The retrosuperior margins of the tibia, basitarsus and telotarsus were devoid of the long, socketed macrosetae that comprise bristle combs in later instars and adults.

Instead, they were armed with a series of long spiniform processes ('spines') which appear as non-articulating extensions of the exoskeleton. This was confirmed by UV epifluorescence microscopy, which showed that the blue-green fluorescence characteristic of scorpion epicuticle (Pavan, 1954) was detectable along the length of the spines and was continuous with the fluorescent leg segment (Figs. 115–117). In contrast, the socketed macrosetae of the bristle combs of larger (presumably third or higher instar) juveniles were non-fluorescent (Figs. 118–123). These 'spine combs' were observed in juveniles of all three *Vachoniolus* species studied here, and have been included as a generic diagnostic character, with the presumption that they also occur in *V. iranus* juveniles. They could serve two functions: (i) to enhance traction on unconsolidated substrates, analogous to the role of bristle combs in later instars; and

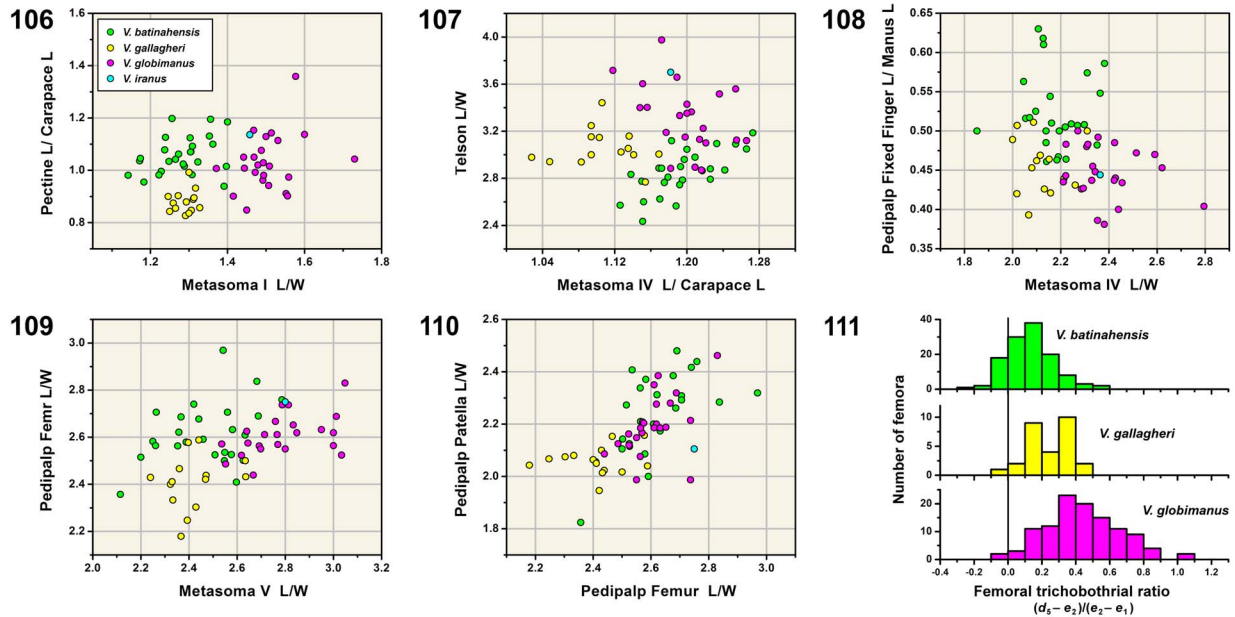


Figures 100–105: Pedipalp finger dentition of *Vachoniolus* species in Oman. Each figure shows a sketch of the denticle patterns on the dentate margins of right fixed finger (left drawing), and right movable finger (right drawing). Position of internal fixed finger trichobothrium *it* is indicated. **100.** *V. batinahensis*, **sp. nov.**, holotype male. **101.** *V. batinahensis*, **sp. nov.**, paratype female (al Abyad). **102.** *V. gallagheri*, **sp. nov.**, holotype male. **103.** *V. gallagheri*, **sp. nov.**, paratype female (N of Adam). **104.** *V. globimanus*, female (Marsawdad). **105.** *V. globimanus*, male (Shigag).

(ii) to provide internal space for the development of long, socketed macrosetae of bristle combs that will emerge after ecdysis in the third instar. In support of the latter hypothesis, spines consisted of a short, broader basal portion and a long, finer, needle-like distal portion. The distal portion was darker than the basal portion in some individuals, as expected in a precursor to the dark, hardened shafts of socketed macrosetae. The spine combs are reminiscent of ‘sand baskets’, the arrays of long spines extending from the distal dorsolateral margins of hind leg tibiae of psammophilous raphidophorid camel crickets (i.e. the ‘sand treaders’, genera *Ammobaenetes*, *Daihinibaenetes*, *Daihiniella*, *Macrobaenetes*, *Rhachocnemis* and *Utabaenetes*) (Tinkham, 1947, 1962a, 1962b, 1970; Weissmann, 1997). Spine combs were also found in very small juveniles of two other buthid scorpions: *A. pterygocercus* and *Odontobuthus brevidigitus* Lowe, 2010 (Figs. 124–135). On the other hand, neither bristle combs nor spine combs were observed on leg I–III tibiae, basitarsi and telotarsi of a very small juvenile *Leiurus* sp. from Oman (presumably second instar: carapace L 1.95 mm,

compared to mean adult carapace L 7–10 mm), a species in which well developed bristle combs do appear in later instars and adults. This implies that the second instar spine combs are not universally expressed in all sand scorpions with bristle combs, even within the Buthidae, and therefore have potential value as taxonomic characters. It is intriguing to note that *Apistobuthus* and *Odontobuthus* share some outward similarities suggestive of a closer affinity (Navidpour & Lowe, 2009), and that a clustering of *Apistobuthus* + *Vachoniolus* emerges from preliminary analysis of 16S rRNA mitochondrial DNA sequences (Fet et al., 2003). The presence of spine combs may thus be a shared derived character relating all three of these genera.

When Levy, Amitai & Shulov (1973) originally created the genus *Vachoniolus*, they relied on two key diagnostic characters: heavily swollen, subglobose pedipalp chelae and loss of tibial spurs. Later, Vachon (1974; 1979) refined the diagnosis by adding two trichobothrial characters (patellar neobothriotaxy, and femoral trichobothrium d_5 distal to e_2), and allowing for variable loss of tibial spurs. The new species *V. batinah-*



Figures 106–111: Graphical illustration of variation in selected morphometric ratios of *Vachoniolus*. **106.** Scatter plot of male variation in slenderness of metasoma I and relative length of pectine (metasoma I L/W vs. pectine L/ carapace L). **107.** Scatter plot of variation in relative length of metasoma IV and slenderness of telson (metasoma IV L/ carapace L vs. telson L/W). **108.** Scatter plot of male variation in slenderness of metasoma IV and relative proportion of pedipalp chela fixed finger (metasoma IV L/W vs. pedipalp chela fixed finger L/ manus L). **109.** Scatter plot of male variation in slenderness of metasoma V and pedipalp femur (metasoma v L/W vs. pedipalp femur L/W). **110.** Scatter plot of male variation in slenderness of pedipalp femur and patella (pedipalp femur L/W vs. pedipalp patella L/W). **111.** Histogram plots showing distributions of the trichobothrial distance ratio $(d_5 - e_2)/(e_2 - e_1)$ (data from both sexes). Vertical line is crossover point for d_5 relative to e_2 . Note: each histogram bar represents the number of cases with ratio \leq right abscissa tick mark; for *V. globimanus*, all data ≤ 0 are actually equal to 0 (i.e. no cases of d_5 proximal to e_2). The ratio distribution of *V. batinahensis* was significantly different from that of *V. gallagheri* ($P = 0.0001$), and the latter was also significantly different from that of *V. globimanus* ($P = 4 \cdot 10^{-6}$) (Mann-Whitney test). Color codes of all plots: green: *V. batinahensis*; yellow: *V. gallagheri*; magenta: *V. globimanus*; blue: *V. iranensis*. Data in 106–110 from adults, in 111 from all ages.

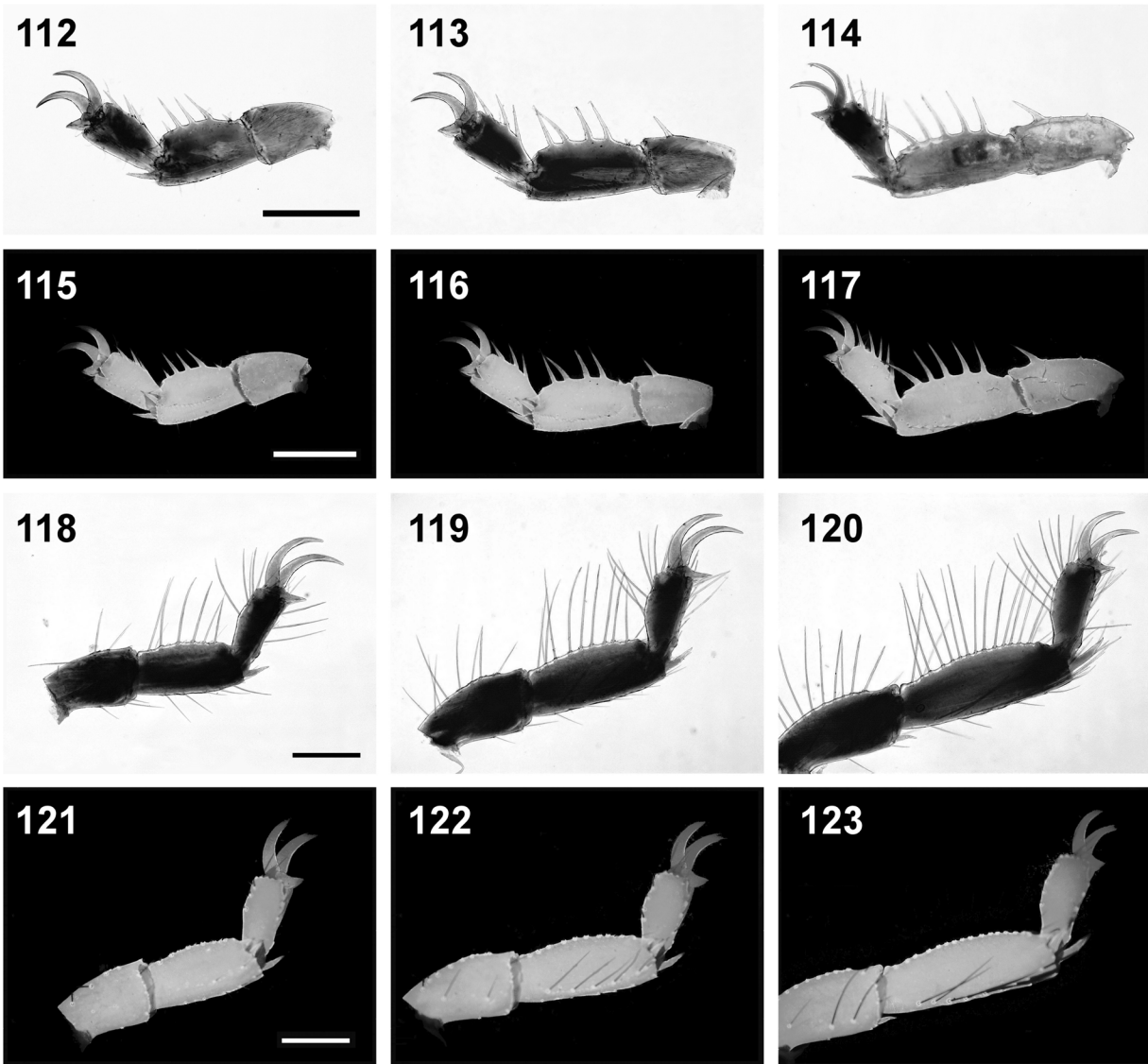
ensis has a complete set of tibial spurs, does not exhibit patellar neobothriotaxy, and can have d_5 proximal to e_2 . Thus, only one of the four key characters, i.e. the development of greatly enlarged pedipalp chelae, is still shared by all *Vachoniolus*. This chela enlargement is a secondary sexual characteristic that is only fully developed in adult males (Fig. 28), and its retention across species, and over evolutionary time, implies that it is strongly favored by selective pressures. Sexual selection can exaggerate traits used by males in the competition for females (Darwin, 1859). The evolution of enlarged male ‘weapons’ (e.g. deer antlers, beetle mandibles and horns) is driven by increased chances of success in male-male combat (Emlen, 2008). Among scorpions, male-male antagonistic behavior has been reported in *Euscorpis flavicaudis*. This is a lithophilic species that can achieve fairly high population densities, living in colonies in rock walls. Males locate and cohabit with females until they are receptive for mating. If a second male attempts to intrude, the two males will fight each other with their pedipalp chelae. In 80% of contests for females, the victor was the male with the larger pedipalp

chelae (Benton, 1992). If male *Vachoniolus* adopted a similar mate guarding strategy, then selection could drive the development of the greatly enlarged male chelae. Although population densities are relatively low in harsh environments such as the Rub’ al-Khali, male desert scorpions can probably locate female conspecifics more efficiently by following non-volatile chemical trails deposited on the substrate (Melville, Tallarovic & Brownell, 2003). Pheromone tracking could enable more than one male to find a female near or within her burrow, leading to contests for ownership of the female. This hypothesis might be tested by excavating *Vachoniolus* burrows to look for cohabitation of males and females, as occurs in *Euscorpis flavicaudis*.

Enlargement of the chelae can also be advantageous to males if they apply coercive mating methods to overcome female resistance during sexual conflict (Chapman et al., 2003). However, studies on other species of scorpions have not found evidence that males engage in forced mating behavior (Polis & Sissom, 1990). Instead, success of mating is more likely to be controlled by the female, as she ultimately decides whe-

	<i>Vachoniolus butinahensis</i> , sp. nov.		<i>Vachoniolus gallagheri</i> , sp. nov.		<i>Vachoniolus globimanus</i>	
	males	females	males	females	males	females
Carapace W/L	1.01 – 1.24, 1.12 ± 0.05 (33)		1.04 – 1.15, 1.10 ± 0.03 (17)		0.94 – 1.18, 1.09 ± 0.05 (35)	
Carapace anterior W/ posterior W	0.44 – 0.53, 0.48 ± 0.02 (33)		0.44 – 0.51, 0.49 ± 0.02 (17)		0.44 – 0.54, 0.47 ± 0.02 (35)	
Pedipalp femur L/ carapace L	0.77 – 0.85 0.81 ± 0.02 (26)	0.69 – 0.73 0.71 ± 0.02 (7)	0.71 – 0.77 0.73 ± 0.02 (14)	0.63 – 0.73 0.67 ± 0.05 (3)	0.73 – 0.82 0.78 ± 0.02 (23)	0.66 – 0.76 0.71 ± 0.03 (12)
Pedipalp patella L/ carapace L	0.89 – 1.00 0.95 ± 0.03 (26)	0.85 – 0.90 0.87 ± 0.02 (7)	0.82 – 0.92 0.88 ± 0.03 (14)	0.81 – 0.86 0.83 ± 0.03 (3)	0.86 – 0.98 0.92 ± 0.03 (23)	0.83 – 0.92 0.87 ± 0.03 (12)
Pedipalp femur L/W	2.26 – 2.97, 2.58 ± 0.14 (33)		2.18 – 2.62, 2.41 ± 0.12 (17)		2.44 – 2.83 2.61 ± 0.09 (23)	2.45 – 2.93 2.72 ± 0.14 (12)
Pedipalp patella L/W	1.82 – 2.48 2.23 ± 0.15 (26)	2.26 – 2.57 2.43 ± 0.11 (7)	1.95 – 2.16 2.06 ± 0.06 (14)	2.26 – 2.58 2.41 ± 0.16 (3)	1.99 – 2.46 2.19 ± 0.11 (23)	2.36 – 2.84 2.56 ± 0.17 (12)
Pedipalp chela L/ carapace L	1.24 – 1.57 1.45 ± 0.07 (27)	1.18 – 1.31 1.27 ± 0.05 (8)	1.28 – 1.46 1.39 ± 0.05 (14)	1.18 – 1.23 1.20 ± 0.02 (3)	1.32 – 1.53 1.44 ± 0.05 (23)	1.19 – 1.30 1.25 ± 0.04 (12)
Pedipalp chela L/manus W	2.09 – 3.16 2.59 ± 0.24 (27)	3.89 – 4.45 4.22 ± 0.16 (8)	2.12 – 2.65 2.39 ± 0.16 (14)	3.97 – 4.38 4.14 ± 0.22 (3)	2.19 – 2.66 2.45 ± 0.11 (23)	4.14 – 5.05 4.54 ± 0.28 (12)
Pedipalp chela manus W/ carapace L	0.46 – 0.65 0.56 ± 0.05 (27)	0.28 – 0.31 0.30 ± 0.01 (8)	0.54 – 0.64 0.58 ± 0.03 (14)	0.28 – 0.30 0.29 ± 0.01 (3)	0.52 – 0.65 0.59 ± 0.03 (23)	0.26 – 0.31 0.28 ± 0.02 (12)
Pedipalp movable finger L/manus ventral L	0.70 – 1.04 0.87 ± 0.07 (26)	1.33 – 1.55 1.48 ± 0.08 (7)	0.67 – 0.89 0.79 ± 0.64 (14)	1.36 – 1.42 1.40 ± 0.03 (3)	0.70 – 0.96 0.81 ± 0.07 (23)	1.14 – 1.65 1.45 ± 0.11 (12)
Metasoma I L/ carapace L	0.74 – 0.87 0.81 ± 0.03 (26)	0.72 – 0.77 0.74 ± 0.02 (7)	0.74 – 0.83 0.79 ± 0.02 (14)	0.70 – 0.75 0.72 ± 0.03 (3)	0.82 – 0.93 0.87 ± 0.03 (23)	0.73 – 0.81 0.76 ± 0.03 (12)
Metasoma II L/ carapace L	0.89 – 1.03 0.96 ± 0.04 (26)	0.83 – 0.89 0.86 ± 0.02 (7)	0.87 – 0.96 0.91 ± 0.03 (14)	0.77 – 0.90 0.83 ± 0.06 (3)	0.94 – 1.08 1.01 ± 0.03 (23)	0.84 – 0.97 0.90 ± 0.04 (12)
Metasoma III L/ carapace L	0.91 – 1.11 1.02 ± 0.04 (26)	0.89 – 0.95 0.91 ± 0.02 (7)	0.90 – 1.03 0.96 ± 0.04 (14)	0.81 – 0.90 0.85 ± 0.05 (3)	1.00 – 1.14 1.06 ± 0.04 (23)	0.89 – 1.02 0.95 ± 0.04 (12)
Metasoma IV L/ carapace L	1.13 – 1.27 1.20 ± 0.04 (26)	1.04 – 1.09 1.06 ± 0.02 (7)	1.03 – 1.17 1.11 ± 0.04 (14)	0.96 – 1.03 0.99 ± 0.04 (3)	1.12 – 1.27 1.20 ± 0.04 (23)	0.99 – 1.11 1.05 ± 0.04 (12)
Metasoma V L/ carapace L	1.20 – 1.38 1.29 ± 0.05 (26)	1.05 – 1.25 1.18 ± 0.06 (7)	1.17 – 1.27 1.21 ± 0.03 (14)	1.12 – 1.20 1.15 ± 0.05 (3)	1.21 – 1.34 1.28 ± 0.03 (23)	1.14 – 1.26 1.18 ± 0.04 (12)
Metasoma I L/W	1.14 – 1.40, 1.28 ± 0.06 (33)		1.25 – 1.33, 1.29 ± 0.03 (17)		1.37 – 1.60, 1.49 ± 0.05 (35)	
Metasoma II L/W	1.37 – 1.71, 1.56 ± 0.08 (33)		1.48 – 1.65, 1.56 ± 0.05 (17)		1.65 – 1.92 1.78 ± 0.07 (23)	1.64 – 1.95 1.83 ± 0.08 (12)
Metasoma III L/W	1.49 – 1.94, 1.73 ± 0.09 (33)		1.60 – 1.85, 1.67 ± 0.07 (17)		1.76 – 2.09 1.90 ± 0.09 (23)	1.86 – 2.08 1.98 ± 0.07 (12)
Metasoma IV L/W	1.85 – 2.38, 2.18 ± 0.11 (33)		2.00 – 2.31, 2.12 ± 0.08 (17)		2.21 – 2.62, 2.37 ± 0.10 (35)	
Metasoma V L/W	2.08 – 2.79, 2.44 ± 0.18 (33)		2.22 – 2.64, 2.40 ± 0.12 (17)		2.46 – 3.05, 2.76 ± 0.15 (35)	
Vesicle L/ telson L	0.47 – 0.57 0.51 ± 0.03 (25)	0.47 – 0.50 0.48 ± 0.01 (7)	0.45 – 0.52, 0.48 ± 0.02 (17)		0.39 – 0.54, 0.46 ± 0.03 (34)	
Vesicle W/ metasoma V W	0.64 – 0.78, 0.70 ± 0.03 (33)		0.62 – 0.77, 0.68 ± 0.04 (17)		0.61 – 0.73 0.68 ± 0.03 (23)	0.66 – 0.79 0.73 ± 0.04 (12)
Pectine L/ carapace L	0.94 – 1.20 1.06 ± 0.07 (26)	0.61 – 0.73 0.67 ± 0.04 (7)	0.83 – 0.99 0.88 ± 0.04 (14)	0.62 – 0.69 0.65 ± 0.04 (3)	0.85 – 1.36 1.03 ± 0.11 (23)	0.61 – 0.76 0.70 ± 0.04 (12)
Pedipalp femur trichobothrial distance ratio ($d_5 - e_2$)/($e_2 - e_1$)	-0.22 – 0.51 0.14 ± 0.13 (94)	-0.19 – 0.54 0.09 ± 0.16 (28)	-0.09 – 0.50, 0.24 ± 0.14 (28)		0.00 – 1.02, 0.45 ± 0.22 (112)	

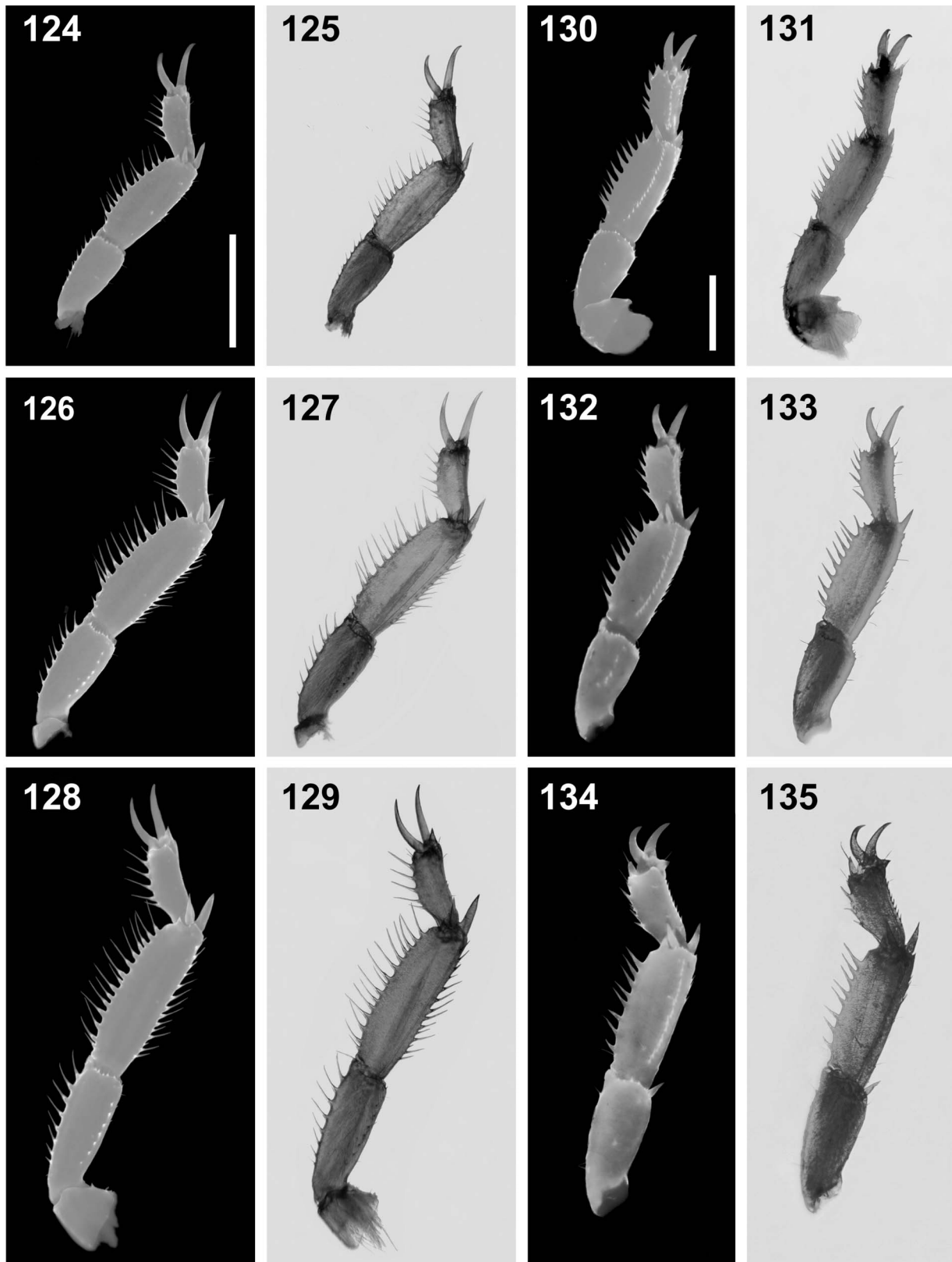
Table 1: Summary of variation in selected adult morphometric ratios of both sexes for 3 species of *Vachoniolus* (ranges, mean ± SD, sample sizes in parentheses). Ratios with no significant sexual dimorphism ($P > 0.05$, Mann-Whitney test) have been pooled for samples of both sexes. All ratios from adults, except for femur trichobothrial distance ratio, which includes immatures.



Figures 112–123: Tarsal spine combs and bristle combs on tibia, telotarsus and basitarsus of juvenile *Vachoniolus batinahensis*, sp. nov. **112–117:** left legs, juvenile female, Al Abyad, carapace length 1.68 mm. **118–123:** right legs, juvenile female, Al Abyad, carapace length 2.8 mm. **112–114, 118–120:** visible light trans-illumination; **115–117, 121–123:** UV epifluorescence. **112, 115, 118, 121:** leg I; **113, 116, 119, 122:** leg II; **114, 117, 120, 123:** leg III. Retrolateral aspect shown in all figures. Scale bars: 5 mm (across rows).

ther or not to accept male gametes packaged in a spermatophore deposited on the substrate (Peretti & Carrera, 2005). Female choice may depend on male performance during a sequence of courtship behaviors. Field observations of courtship in *V. globimanus* showed that, like other scorpions, males use their enlarged chelae to clasp the chelae of females (Figs. 140–141) while performing the classic *promenade à deux* (Maccary, 1810; Polis & Sissom, 1990). Increased muscle mass in the swollen chelae of the male could help him to keep a tight grip on the female chelae, which in *Vachoniolus* are quite small and abbreviated, with

smooth polished surfaces. This may improve his chances of sustaining the *promenade* long enough to demonstrate his fitness to the female. An extended courtship dance may also be a requirement for psammophilous scorpions to find a stable substrate upon which to deposit the spermatophore. During courtship, male *V. globimanus* displayed sand-digging behavior (Fig. 140), which could be an effort to expose a firm substrate for planting a spermatophore (Alexander, 1959). Males of many other scorpion taxa seem to have developed chelal structures to assist them in securing female chelae during the *promenade à deux*. Specialized apophyses or concavities



Figures 124–135: Tarsal spine combs of early juvenile instars of other buthids with adult tarsal bristle combs. **124–129:** *Apistobuthus pterygocercus* Finnegan, 1932, juvenile female, carapace length 2.75 mm (Wahiba Sands); **130–135:** *Odontobuthus brevidigitus* Lowe, 2010, juvenile paratype male, carapace length 2.31 mm (Seeb). 124, 126, 128, 130, 132, 134: UV epifluorescence; 125, 127, 129, 131, 133, 135: visible light trans-illumination; 124–125, 130–131: leg I; 126–127, 132–133: leg II; 128–129, 134–135: leg III. Retrolateral aspect of right leg in all figures. Scale bars: 1 mm (*A. pterygocercus*), 0.5 mm (*O. brevidigitus*).

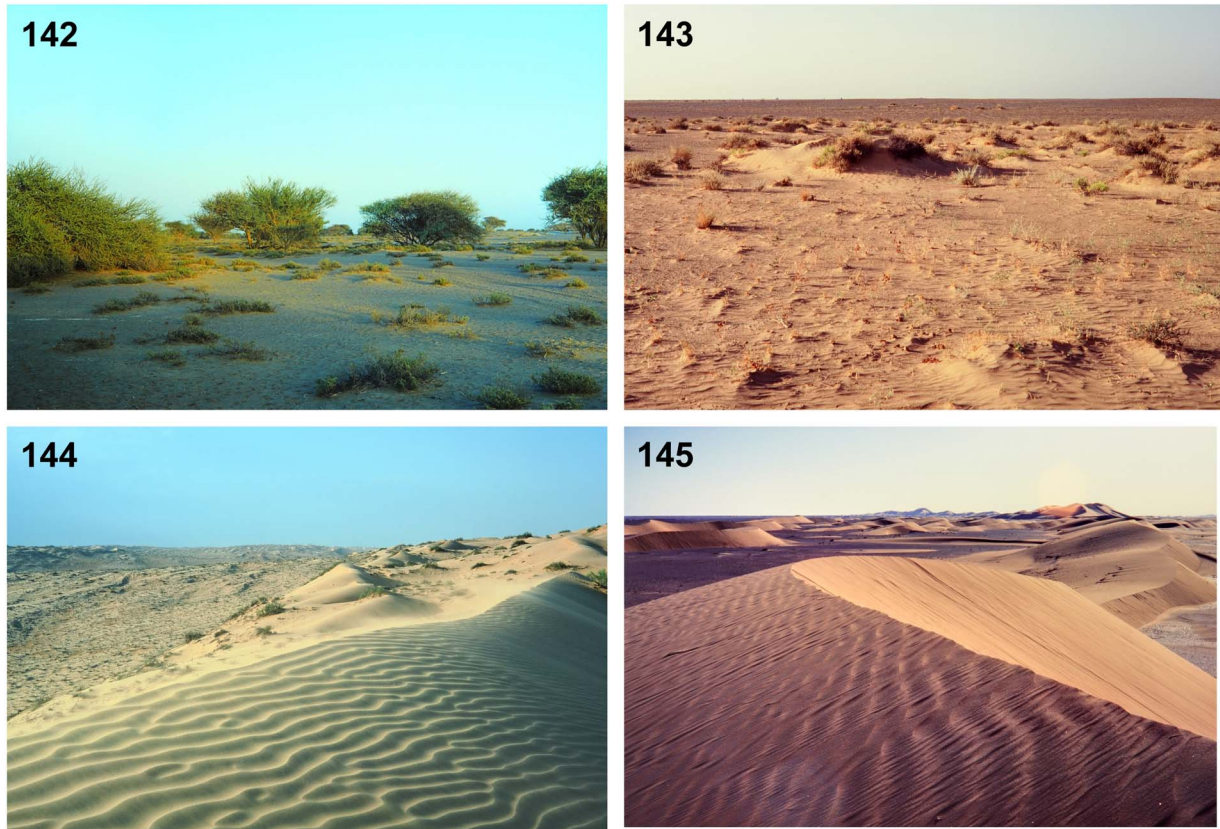


Figures 136–141: In vivo habitus and behavior of *Vachoniolus* in Oman. **136.** *V. batinahensis* sp. nov., adult male, Al Abyad dune field, W of Barka. **137–141.** *V. globimanus*, Wadi Muqshin, NW of Montesar. **137–138.** Adult males. **139.** Adult female. **140–141.** Pairs of adult males and females engaged in *promenade à deux* (photos of captured animals taken in the field, in the early morning). The male in **140** is using legs II–III to dig into the sand surface (note motion blur of sand being thrown behind his mesosoma). The pair in **141** is performing their dance in a plastic (polypropylene) tray.

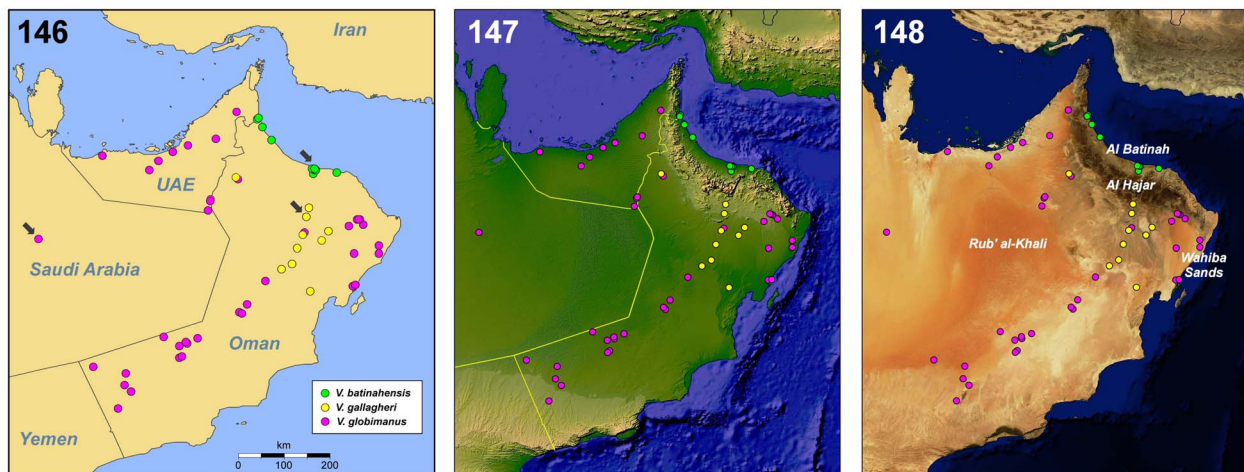
occur on the male manus of certain bothriurids (Maury, 1975), and varying degrees of enlargement of the manus and scalloping of the proximal margins of the pedipalp fingers occurs in the males of a wide variety of scorpion species in different families. Further ethological studies are needed to determine if there are unique aspects of the *Vachoniolus* mating ritual that could explain the extreme sexual dimorphism of the pedipalps of this unusual bothid genus.

Acknowledgments

The author is very grateful to: His Highness Sayyid Haitham bin Tariq Al Said, Minister of National Heritage and Culture, Sultanate of Oman, for sponsorship to study the scorpions of Oman; Khair Bin Antar Salim, Director of Museums, Said Ali Said Al-Farsi and Saddiqa Ramdhan at the Ministry of National Heritage and Culture for support during visits and field trips to



Figures 142–145: Habitats of *Vachoniolus* species in Oman. **142.** Al Abyad dune field, *Acacia* woodland, 10–15 km W of Barka on Batinah coastal plain, type locality of *V. batinahensis*, sp. nov. **143.** Sandy plains of central Oman, Wadi Andam, typical habitat of *V. gallagheri*, sp. nov. **144.** Ramlat al Wahiba (Wahiba Sands), region of high sands (Al Hibal), habitat of *Vachoniolus* sp., provisionally classified as *V. globimanus*. **145.** Ramlat as Sahmah, dunes of the Rub' al-Khali (Empty Quarter), habitat of *V. globimanus*.



Figures 146–148: Maps showing collection sites of *Vachoniolus* material examined in this study. **146.** Records plotted on geopolitical map. Arrows: type localities of *V. batinahensis* and *V. gallagheri*, and approximate type locality of *V. minipectenibus* (= *V. globimanus*). **147.** Records plotted on color topographic map with shaded relief. **148.** Records plotted on terrain map obtained by satellite imagery. Green circles: *V. batinahensis*, sp. nov.; yellow circles: *V. gallagheri*, sp. nov.; magenta circles: *V. globimanus*.

Oman to collect scorpions; Michael D. Gallagher, for his invaluable assistance in all aspects of the study of Oman scorpions; Michael Balkenohl, J. Neil Barnes, Jim Dundon, Andy Dunsire, Seyad Farook, Gary Feulner, Andrew S. Gardner, Ian Harrison, Bjarne Skule, Barbara Tigar, David Willis, Alex Winkler, and other collectors for generously contributing specimens; Shahrokh Navidpour and František Kovařík for the gift of a paratype of *Vachoniolus iranus* for comparative study; Janet Beccaloni (Natural History Museum, London) for loaning types of *Buthacus minipektenibus* and *Vachoniolus globimanus*; Matt E. Braunwalder and Ambros Hänggi for arranging scorpion loans from Naturhistorisches Museum Basel; Anitha Kumari Saji (Terrestrial Environment Research Centre, Abu Dhabi) for loaning and donating *V. globimanus* samples for study; and František Kovařík and Matthew R. Graham for critical reviews of the manuscript.

References

- ACOSTA, L. E. & V. FET. 2005. Nomenclatural notes in Scorpiones (Arachnida). *Zootaxa*, 934: 1–12.
- ALEXANDER, A. J. 1959. Courtship and mating in the buthid scorpions. *Proceedings of the Zoological Society of London*, 133(1): 145–169.
- BENTON, T. G. 1992. Determinants of male mating success in a scorpion. *Animal Behavior*, 43: 125–135.
- BRAY, H. E. & S. STOKES. 2003. Chronologies for late Quaternary barchan dune reactivation in the southeastern Arabian Peninsula. *Quaternary Science Reviews*, 22: 1027–1033.
- CHAPMAN, T., G. ARNQVIST, J. BANGHAM & L. S. ROWE. 2003. Sexual conflict. *Trends in Ecology and Evolution*, 18: 41–47.
- DARWIN, C. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: J. Murray.
- DUPRÉ, G. 2007. Conspectus genericus scorpionorum 1758–2006 (Arachnida: Scorpiones). *Euscorpius*, 50: 1–31.
- EL-HENNAWY, H. K. 1992. A catalogue of the scorpions described from the Arab countries (1758–1990) (Arachnida: Scorpionida). *Serket*, 2(4): 95–153.
- EMLÉN, D. J. 2008. The evolution of animal weapons. *Annual Review of Ecology, Evolution, and Systematics*, 39:387–413.
- FET, V., E. M. CAPES & W. D. SISSOM. 2001. A new genus and species of psammophile scorpion from eastern Iran (Scorpiones: Buthidae). Pp. 183–189 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. Family 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: The New York Entomological Society.
- FET, V., G. A. POLIS & W. D. SISSOM. 1998. Life in sandy deserts: the scorpion model. *Journal of Arid Environments*, 39: 609–622.
- FET, V. & M. E. SOLEGLAD. 2005. Contributions to scorpion systematics. I. On recent changes in high-level taxonomy. *Euscorpius*, 23: 1–13.
- FET, V., M. E. SOLEGLAD & G. LOWE. 2005. A new trichobothrial character for the high-level systematics of Buthoidea (Scorpiones: Buthida). *Euscorpius*, 23: 1–40.
- FRANCKE, O. F. 1985. Conspectus genericus scorpionorum 1758–1982 (Arachnida: Scorpiones). *Occasional Papers of the Museum, Texas Tech University*, 98: 1–32.
- GARDNER, R. A. M. 1988. Aeolianites and marine deposits of the Wahiba Sands: character and palaeoenvironments. The Scientific Results of the Royal Geographic Society's Oman Wahiba Sands Project 1985–1987. *Journal of Oman Studies Special Report*, 3: 75–94.
- GLENNIE, K. W. 1998. The desert of southeast Arabia: a product of Quaternary climate change. Pp. 279–291 in: Alsharhan, A. S., K. W. Glennie, G. L. Whittle & C. G. St. C. Kendall (eds.). *Quaternary Deserts and Climate Change*. Rotterdam: Balkema.
- GLENNIE, K. W. & A. K. SINGHVI. 2002. Event stratigraphy, paleoenvironment and chronology of SE Arabian deserts. *Quaternary Science Reviews*, 21: 853–869.

- HENDRIXSON, B. E. 2006. Buthid scorpions of Saudi Arabia, with notes on other families (Scorpiones: Buthidae, Liochelidae, Scorpionidae). *Fauna of Arabia*, 21: 33–120.
- JUYAL, N., K. W. GLENNIE & A. K. SINGHVI. 1996. Chronology and paleoenvironmental significance of Quaternary desert sediment in southeastern Arabia. Pp. 315–326 in: Alsharhan, A. S., K. W. Glennie, G. L. Whittle & C. G. St. C. Kendall (eds.). *Quaternary Deserts and Climate Change*. Rotterdam: Balkema.
- KALTSAS, D., I. STATHI & M. MYLONAS. 2008. The foraging activity of *Mesobuthus gibbosus* (Scorpiones: Buthidae) in central and south Aegean archipelago. *Journal of Natural History*, 42 (5–8): 513–527.
- KINZELBACH, R. 1985. Vorder Orient. Skorpione (Arachnida: Scorpiones). *Tübinger Atlas des Vorderen Orients (TAVO)*. Karte A VI 14.2. Tübingen.
- KOVAŘÍK, F. 1998. *Štíří (Scorpions)*. Jihlava: Madagaskar.
- KOVAŘÍK, F. 2009. *Illustrated Catalog of Scorpions*. Part I. Introductory remarks; keys to families and genera; subfamily Scorpioninae with keys to *Heterometrus* and *Pandinus* species. Prague: Clairon Production, 170 pp.
- LAMORAL, B. H. 1979. The scorpions of Namibia (Arachnida: Scorpionida). *Annals of the Natal Museum*, 23(3): 497–784.
- LEVY, G. & P. AMITAI. 1980. *Scorpiones. Fauna Palaestina*. Arachnida I. The Israel Academy of Sciences and Humanities, Jerusalem.
- LEVY, G., P. AMITAI & A. SHULOV. 1973. New scorpions from Israel, Jordan and Arabia. *Zoological Journal of the Linnaean Society*, 52: 113–140.
- LOURENÇO, W. R. & B. DUHEM. 2009. Saharo-Sindian buthid scorpions; description of two new genera and species from Occidental Sahara and Afghanistan. *ZooKeys*, 14: 37–54.
- LOWE, G. 2010. A new species of *Odontobuthus* (Scorpiones: Buthidae) from northern Oman. *Euscorpius*, 96: 1–22.
- MACCARY, A. 1810. *Mémoire sur le scorpion qui se trouve sur la montagne de Cette*, Gabon, Paris, p. 48.
- MAURY, E. A. 1975. Sobre el dimorfismo sexual de la pinza de los pedipalpos en los escorpiones Bothriuridae. *Bulletin du Muséum National d'Histoire Naturelle. 3^e série (305) Zoologie*, 215: 765–771.
- McCLURE, H. A. 1988. Late Quaternary palaeogeography and landscape evolution of the Rub' Al Khali. Pp. 9–14 in: Potts, D.T. (editor), *Araby the Blest. Studies in Arabian Archaeology*. Museum Tusulanum Press, University of Copenhagen, Njalsgade, Copenhagen.
- MELVILLE, J. M., S.K. TALLAROVIC & P. H. BROWNELL. 2003. Evidence of mate trailing in the giant hairy desert scorpion, *Hadrurus arizonensis* (Scorpionida, Iuridae). *Journal of Insect Behavior*, 16 (1): 97–115.
- NAVIDPOUR, S., F. KOVAŘÍK, M. E. SOLEGLAD & V. FET. 2008. Scorpions of Iran (Arachnida, Scorpiones). Part I. Khoozestan Province. *Euscorpius*, 65: 1–41.
- NAVIDPOUR, S. & G. LOWE. 2009. Revised diagnosis and redescription of *Apistobuthus susanae* (Scorpiones, Buthidae). *Journal of Arachnology*, 37(1): 45–59.
- NENILIN, A. B. & V. FET. 1992. Zoogeographical analysis of the world scorpion fauna (Arachnida: Scorpiones). *Arthropoda Selecta*, 1(2): 3–31 (in Russian, with English summary).
- PAVAN, M. 1954. Presenza e distribuzione di una sostanza fluorescente nel tegumento degli scorpioni. *Bollettino di Societa Italiana Biologia Sperimentale*, 30(7): 801–803.
- PEASE, P. P. & V. P. TCHAKERIAN. 2002. Composition and sources of sand in the Wahiba Sand Sea, Sultanate of Oman. *Annals of the Association of American Geographers*, 92: 416–434.
- POLIS, G. A. 1990. Ecology. Pp. 247–293 in: Polis, G. A. (ed.). *The Biology of Scorpions*. Stanford, CA: Stanford University Press.
- POLIS, G. A. & S. J. MCCORMICK. 1987. Intraguild predation and competition among desert scorpions. *Ecology*, 68(2): 332–343.
- POLIS, G. A. & W. D. SISSOM. 1990. Life history. Pp. 161–223 in: Polis, G. A. (ed.). *The Biology of Scorpions*. Stanford, CA: Stanford University Press.

- PRENDINI, L. 2001a. Substratum specialization and speciation in southern African scorpions: the effect hypothesis revisited. Pp. 113–138 in: Fet, V & Selden, P.A. (eds.). *Scorpions 2001. In Memoriam Gary A. Polis*. Burnham Beeches, Bucks.: British Arachnological Society.
- PRENDINI, L. 2001b. Further additions to the scorpion fauna of Trinidad and Tobago. *Journal of Arachnology*, 29: 173–188.
- PRENDINI, L. 2003. Discovery of the male of *Parabuthus muelleri*, and implications for the phylogeny of *Parabuthus* (Scorpiones: Buthidae). *American Museum Novitates*, 3408: 1–24.
- PRENDINI, L. 2004. The systematics of southern African *Parabuthus* Pocock (Scorpiones, Buthidae): revisions to the taxonomy and key to the species. *The Journal of Arachnology*, 32: 109–186
- PRENDINI, L., E. S. VOLSCHENK, S. MAALIKI & A.V. GROMOV. 2006. A ‘living fossil’ from Central Asia: The morphology of *Pseudochactas ovchinnikovi* Gromov, 1998 (Scorpiones: Pseudochactidae), with comments on its phylogenetic position. *Zoologischer Anzeiger*, 245: 211–248.
- PRENDINI, L. & W. C. WHEELER. 2005. Scorpion higher phylogeny and classification, taxonomic anarchy, and standards for peer review. *Cladistics*, 21: 446–494.
- RADIES, D., F. PREUSSER, A. MATTER & M. MANGE. 2004. Eustatic and climatic controls on the development of the Wahiba Sand Sea, Sultanate of Oman. *Sedimentology*, 51: 1359–1385.
- SANTIAGO-BLAY, J. A., M. E. SOLEGLAD & V. FET. 2004. 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). *Revista Ibérica de Aracnología*, 10: 7–16.
- SISSOM, W. D. 1990. Systematics, biogeography and paleontology. Pp. 64–160 in: Polis, G. A. (ed.). *The Biology of Scorpions*. Stanford, CA: Stanford University Press.
- SISSOM, W. D., G. A. POLIS, & D. D. WATT. 1990. Field and laboratory methods. Pp. 445–461 in: Polis, G. A. (ed.). *The Biology of Scorpions*. Stanford, CA: Stanford University Press.
- SOLEGLAD, M. E. & V. FET. 2003a. The scorpion sternum: structure and phylogeny (Scorpiones: Orthosterni). *Euscorpius*, 5: 1–34.
- SOLEGLAD, M. E. & V. FET. 2003b. High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). *Euscorpius*, 11: 1–175.
- SOLEGLAD, M. E., V. FET & F. KOVAŘÍK. 2005. The systematic position of the scorpion genera *Heteroscorpion* Birula, 1903 and *Urodacus* Peters, 1861 (Scorpiones: Scorpionoidea). *Euscorpius*, 20: 1–38.
- SOLEGLAD, M. E. & W. D. SISSOM. 2001. Phylogeny of the family Euscorpiidae Laurie, 1896: a major revision. Pp. 25–111 in: Fet, V. & P. A. Selden (eds.). *Scorpions 2001. In Memoriam Gary A. Polis*. Burnham Beeches, Bucks.: British Arachnological Society.
- STAHNKE, H. L. 1970. Scorpion nomenclature and mensuration. *Entomological News*, 81: 297–316.
- STAHNKE, H. L. 1972. UV light, a useful field tool. *Bioscience*, 22: 604–607.
- STOKES, S. & H. E. BRAY. 2005. Late Pleistocene eolian history of the Liwa region, Arabian Peninsula. *Geological Society of America Bulletin*, 117: 1466–1480.
- THOMAS, B. S. 1931. A camel journey across the Rub’ al Khali. *Geographical Journal*, 78: 209–242.
- THOMAS, B. S. 1932. *Arabia Felix. Across the ‘Empty Quarter’ of Arabia*. New York: Charles Scribner’s Sons.
- TIGAR, B. J. & P. E. OSBORNE. 1997. Patterns of arthropod abundance and diversity in an Arabian desert. *Ecography*, 20: 550–558.
- TIGAR, B. J. & P. E. OSBORNE. 1999. The influence of the lunar cycle on ground-dwelling invertebrates in an Arabian desert. *Journal of Arid Environments*, 43: 171–182.
- TINKHAM, E. R. 1947. New species, records and faunistic notes concerning Orthoptera in Arizona. *American Midland Naturalist*, 38(1): 127–149.
- TINKHAM, E. R. 1962a. Studies in nearctic desert sand dune Orthoptera. Part V. A new genus and two new species of giant sand treader camel crickets with keys and notes. *The Great Basin Naturalist*, 22 (1–3): 12–29.

- TINKHAM, E. R. 1962b. Studies in nearctic desert sand dune Orthoptera. Part VI. A new genus and three new species of large sand treader camel crickets from the Colorado Desert with keys and notes. *Bulletin of the Southern California Academy of Sciences*, 61(2): 89–111.
- TINKHAM, E. R. 1970. Studies in nearctic desert sand dune Orthoptera, Part XIII. A remarkable new genus and species of giant black sand treader camel cricket from the San Rafael Desert with key and notes. *Western North American Naturalist*, 30(4): 242–249.
- VACHON, M. 1963. De l'utilité, en systématique, d'une nomenclature des dents des chélicères chez les scorpions. *Bulletin du Muséum National d'Histoire Naturelle Paris*, (2) 35: 161–166.
- VACHON, M. 1974. Étude des caractères utilisés pour classer les familles et les genres de Scorpions (Arachnides). 1. La trichobothriotaxie en Arachnologie, Sigles trichobothriaux et types de trichobothriotaxie chez les Scorpions. *Bulletin du Muséum National d'Histoire Naturelle Paris*, 140: 857–958.
- VACHON, M. 1975. Sur l'utilisation de la trichobothriotaxie du bras des pedipalps des Scorpions (Arachnides) dans le classement des genres de famille des Buthidae Simon. *Comptes rendus hebdomadaires des séances de l'Académie des Sciences, Paris Ser. D Sciences naturelles*, 281(21): 1597–1599.
- VACHON, M. 1979. Arachnids of Saudi Arabia, Scorpiones. *Fauna of Saudi Arabia*, 1: 30–66.
- VACHON, M. 1980. Scorpions du Dhofar. The Scientific Results of the Oman Flora and Fauna Survey 1977 (Dhofar). *Journal of Oman Studies. Special Report*, 2: 251–263.
- VACHON, M. & R. KINZELBACH. 1987. On the taxonomy and distribution of the scorpions of the Middle East. In Krupp, F., W. Schneider & R. Kinzelbach (eds.). *Proceedings of the Symposium on the Fauna and Zoogeography of the Middle East, Mainz (TAVO)*, 28(1985): 91–103.
- VOLSCHENK, E. 2005. A new technique for examining surface morphosculpture of scorpions. *Journal of Arachnology*, 33: 820–825.
- WEISSMANN, M. J. 1997. Natural history of the giant sand treader camel cricket, *Daihinibaenetes giganteus* Tinkham (Orthoptera: Rhabdophoridae). *Journal of Orthoptera Research*, 6: 33–48.
- WILLIAMS, S. C. 1968. Scorpion preservation for taxonomic and morphological studies. *Wasmann Journal of Biology*, 26(1): 133–136.
- WILLIAMS, S. C. 1970. Coexistence of desert scorpions by differential habitat preference. *The Pan-Pacific Entomologist*, 46(4): 254–267.

Appendix A

Comparative material examined. *Apistobuthus pterygoceriscus* Finnegan, 1932, 1 juvenile ♀, Oman, Wahiba Sands, 22°12.46'N 58°51.14'E, 7 October 1993, UV detection, base of linear dune, leg. G. Lowe, M.D. Gallagher, N. Wood & S.J. Prakash (GL); *Leiurus* sp., 1 juvenile ♂, Oman, Dhofar Province, Nejd Desert, S of Thumrait, 17°30.76'N 54°02.7'E, 600 m a.s.l., 16 October 1993, leg. G. Lowe (NHMB); *Odontobuthus brevidigitus* Lowe, 2010, 1 juvenile paratype ♂, 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 h, leg. G. Lowe, A.S. Gardner (NHMB); *Vachoniolus iranus* Navidpour et al., 2008, 1 ♂, Iran, Khoozestan Province, Ahvaz–Masjedsoleyman road, 31°35'44"N 48°57'19"E, 35 m a.s.l. (GL).

Key to species of *Vachoniolus*

- 1 Pedipalp femur with trichobothrium d_5 distal or proximal to e_2 (Figs. 20, 111); pedipalp patella with 7 trichobothria on external surface (Fig. 22); legs III–IV all with fully developed tibial spurs *V. batinahensis* **sp. nov.**
 Pedipalp femur with trichobothrium d_5 distal relative to e_2 (Figs. 49, 76, 111); pedipalp patella with 8–9 trichobothria on external surface (Figs. 51, 78); tibial spurs may be reduced or absent on legs III–IV **2**
- 2 Metasoma robust, segment I L/W 1.25–1.33, segment II L/W 1.48–1.65; coarse dentition on metasomal carinae, dorsosubmedian carinae of metasoma II–III bearing 4–8 granules in posterior half of segment; male pedipalp chela manus shagreened *V. gallagheri* **sp. nov.**
 Metasoma slender, segment I L/W 1.36–1.60, segment II L/W 1.64–1.95; fine dentition on metasomal carinae, dorsosubmedian carinae of metasoma II–III bearing 5–13 granules in posterior half of segment; male pedipalp chela manus smooth or shagreened **3**
- 3 Smaller species, adults 34–43 mm; pedipalp femur and patella with melanic pigmentation; male pedipalp chela manus shagreened *V. iranus* Navidpour et al., 2008
 Larger species, adults 45–65 mm; pedipalp femur and patella pale, without contrasting dark markings; male pedipalp chela manus smooth *V. globimanus* Levy, Amitai et Shulov, 1973