

A new species of *Hyaella* from the High Andes of Ecuador (Crustacea, Amphipoda, Hyaellidae)

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Abstract

Hyaella cajasi **sp. n.** is described from high altitude shallow water lakes in southern Ecuador. This is the second representative of the genus recorded in the country after *H. meinerti*. The new species shares with nine South American species of the genus the display of a smooth, non-processiferous body, a male first uropod with a modified curved robust seta on the endopod, and six pairs of sternal gills. The new taxon can be distinguished from these species based on the presence/absence of eyes; relative length of antenna 1 with respect to antenna 2; presence/absence of short pointed robust seta distally on palp of maxilla 1; number of pappose setae proximally on medial margin of inner lobe of maxilla 2; elongation and curvature of the modified robust seta of endopod of male uropod 1; relative length of ramus of uropod 3 with respect to protopod; and armature and outline of telson, among other features. It seems to be a high-altitude endemic to the Cajas Massif in Azuay Province, being replaced in the same area at lower altitudes by *H. meinerti*.

Keywords

Crustacea, descriptive taxonomy, high altitude lakes, *Hyaella*, new species, South America

Introduction

Hyalella Smith, 1874 is the only genus of epigeal freshwater amphipod known to occur in South America. The genus is the single member of the family Hyalellidae Bulyčeva, 1957, endemic to the Nearctic and Neotropical regions, where it is broadly distributed and diversified, to a current total of about 70 species (Horton and Lowry 2013). The highest diversity is attained in Brazil, which harbours 22 species, although Lake Titicaca with 17 species—15 of which are endemic—concentrates the highest number relative to a restricted area. Here we describe *Hyalella cajasi* sp. n., a high altitude species found at Cajas National Park, near the city of Cuenca (southern Ecuador). It represents the second taxonomically substantiated record for the country after *H. meinerti* Stebbing, 1899, recorded by González and Watling (2003) at 1,500 m above sea level (a.s.l.) on the road between Guayaquil and Cuenca, thus close to the location of the new species. Other species records from Ecuador are not adequately substantiated and should not be considered in faunistic or biogeographic analyses. These include those of *H. inermis* S. I. Smith, 1875, a species known only from Colorado, U.S.A., reported by Whymper (1892), and *H. cf. dentata* reported by Gunkel and Beulker (2009), a taxon currently considered to be a junior synonym of the North American *H. azteca* (Saussure, 1858) (see Horton and Lowry 2013).

Materials and methods

Sampling was carried out during limnological surveys of 202 water bodies (lakes, lagoons and ponds) located between 3,150 and 4,460 m a.s.l. at Cajas National Park (Southern Ecuadorian Andes), in the framework of the project “Limnological Characterization of the lakes and lagoons of Cajas National Park”, funded by the University of Cuenca (Ecuador) and by Empresa Pública Municipal de Telecomunicaciones, Agua Potable, Alcantarillado y Saneamiento (ETAPA), of the municipality of Cuenca.

Samples were collected in 2015 in the littoral zone directly with a hand-held plankton net and fixed, *in situ*, in 95% ethanol. Once in the laboratory, specimens were dissected in lactic acid under the stereomicroscope, and appendages illustrated using a Leica DM2500 microscope equipped with Nomarski differential interference contrast and a drawing tube. Body measurements were derived from the sum of the maximum dorsal dimensions of body somites and exclude telson length. Type material is deposited in the Museo Ecuatoriano de Ciencias Naturales del Instituto Nacional de Biodiversidad, Quito, Ecuador [MECN].

The new species is known only from high-altitude (3,859 to 4,103 m a.s.l.) lacustrine water bodies at Cajas National Park, in the southern Ecuadorian Andes, where it is apparently endemic. It occurs both in the littoral zone of lakes and in shallow lagoons and temporary ponds. These water bodies are oligotrophic and low mineralized (Conductivity: 9.84–91.50 $\mu\text{S}/\text{cm}$), although they carry a significant amount of dissolved organic carbon (DOC) derived from adjacent terrestrial ecosystems, mainly Páramo grassland (“Pajonal”).

Taxonomy

Order Amphipoda Latreille, 1816

Family Hyaellidae Bulyčeva, 1957

Genus *Hyaella* S. I. Smith, 1874

Hyaella cajasi sp. n.

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Figs 1–5

Material examined. All collected by Henrietta Hampel at Cajas National Park (Azua Province; southern Ecuador), 5th May 2015. Laguna Togliacocha (S2°47'55.90"; W79°15'02.13"); 3,859 m a.s.l. HOLOTYPE: male 9.0 mm, preserved in formaldehyde vial. PARATYPES: Five males and 5 females in formaldehyde vial. Holotype and paratypes registered under same registration number [MECN-SI-Cal-0003]. Laguna Cardenillo (S2°46'54.32"; W79°14'50.48"); 4,103 m a.s.l. Four males and 6 females. Small laguna between Laguna Cardenillo and La Negra (S2°47'04.21"; W79°14'50.90"); 4,076 m a.s.l. Nine males and 8 females. Laguna Azul (S2°47'17.81"; W79°14'46.19"); 4,043 m a.s.l. Five males and 5 females. Small laguna close to La Larga (S2°47'35.70"; W79°14'44.08"); 3,954 m a.s.l. Ten males and 9 females. Pool close to Laguna Luspa (S2°47'54.04"; W79°15'46.94"); 3,868 m a.s.l. Ten males and 10 females. Laguna Il-lincocha (S2°46'46.59"; W79°13'51.33"); 3,986 m a.s.l. One male and 4 females.

Diagnosis. Body smooth, non-processiferous. Eyes normal. Antenna 1 much shorter than antenna 2. Incisor of mandibles multi-denticulate. Palp of maxilla 1 short, reaching to less than half distance between its insertion and distal margin of outer lobe, crowned with short robust seta. Inner lobe of maxilla 2 with two pappose setae proximally on medial margin. Coxal plate IV deeply excavated posteriorly. Six pairs of sternal gills, on pereionites II to VII. Uropod 1 sexually dimorphic, with male exhibiting a modified robust seta ("copulatory spine" *sensu* Bousfield 1996) on endopod; modified robust seta hardly curved and only just surpassing tip of endopod. Ramus of uropod 3 shorter than protopod. Telson broader than long, with distal margin evenly rounded; distal armature arranged as a single row of robust setae.

Etymology. Species name refers to Cajas National Park (Azua Province; southern Ecuador), the type locality.

Description of male. *Body* (not figured) up to 9.0 mm long, strongly pigmented, virtually black, smooth. *Head* (Fig. 1A) shorter than pereionites I and II combined; rostrum wanting; lateral lobes truncate; postantennal sinus shallow and broad. Eyes small, round, located behind insertion of antenna 1. *Epimeral plates* (Fig. 1C) each with unarmed distal margin; plates II–III posterodistally acuminate with posterodistal angle strongly produced, subacute; posterior margin of plates with several tiny tooth-like projections each provided with short setule.

Antenna 1 (Fig. 1A) much shorter than antenna 2 although longer than peduncle of latter; peduncle longer than head, segments 1–3 relative length as: 1: 1: 0.8; main

flagellum longer than peduncle; accessory flagellum absent. Pair of aesthetascs present on distomedial angle of posterior margin of middle articles of flagellum (Fig. 1B).

Antenna 2 (Fig. 1A) peduncle segments 4–5 relative length as: 0.7: 1.

Labrum (not figured) ordinary. **Paragnaths** (= lower lip; not figured) inner lobes absent.

Mandibles each with well-developed, triturative columnar molar; molar seta equally developed in both mandibles; palp lacking. **Left mandible** (Fig. 2A) incisor 7-denticulate; lacinia 5-denticulate. **Right mandible** (Fig. 2B) incisor 6-denticulate; lacinia complex, with 5 main cusps and multiple denticles, and with patch of short setules proximally on medial surface.

Maxilla 1 (Fig. 2C) inner lobe finger-like, crowned with two pappose setae; outer lobe with nine serrated stout robust setae distally; palp reduced, unsegmented, reaching to less than half distance between its insertion and distal margin of inner lobe, tapering with tiny conical robust seta on tip.

Maxilla 2 (Fig. 2D) inner lobe with two unequal pappose setae proximally on inner margin, proximal-most seta largest, hyperthrophied.

Maxilliped ordinary; basal endite (= inner plate) (Fig. 2E) subrectangular with three flattened triangular short cuspidate robust setae distally and row of pappose setae along medial margin.

Coxal gills (Figs 3E; 4A–D) on gnathopod 2 to pereopod 6, smooth, unstalked, sac-like. **Sternal gills** on pereonites II to VII, finger-like (Fig. 4F), placed antero-laterally at each side on corresponding sternite.

Gnathopod 1 (Fig. 3A–D) subchelate. Carpus longer than propodus. Propodus 1.5 times as long as broad, with concave posterior margin; palm margin evenly convex; palm angle with two short flagellate robust setae subequal in length on medial side (Fig. 3C). Dactylus with single triangular denticle subdistally on medial margin (Fig. 3D).

Gnathopod 2 (Fig. 3E–G) subchelate. Propodus massive, broadly expanded, 1.3 times as long as broad with palm length longer than carpal lobe; palm margin longer than posterior margin of segment, convex but sinuous, with continuous row of densely set robust setae along both sides of margin (only row on medial side shown in Fig. 3G); palm angle with two short, reduced flagellate robust setae on medial side. Unguis completely incorporated into dactylus (Fig. 3G).

Pereopods 3–4 (Fig. 4A, B) similar except for coxal plates. Pereopod 4 slightly shorter than pereopod 3, with coxa deeply excavated posteriorly.

Pereopods 5–7 (Fig. 4C–E) progressively longer towards posterior. Basis of pereopod 7 broadest, 1.2 times as long as broad; basis of pereopod 5 1.3 times as long as broad; basis of pereopod 6 more slender, 1.5 times as long as broad. All limbs with propodus distinctly longer than their respective carpus.

Pleopods (Fig. 1D) all similar, biramous, rami multi-annulated and provided with long plumose setae; integument of posterior face of protopod (= peduncle) and proximomedial margin of proximal article of endopod, setulose, as figured.

Uropod 1 (Fig. 1E) protopod longer than rami. Armature of protopod consisting of series of 3–4 flagellate robust setae proximally along posterolateral margin, and single flagellate robust seta at each posterodistal and posteromedial angle of segment; postero-

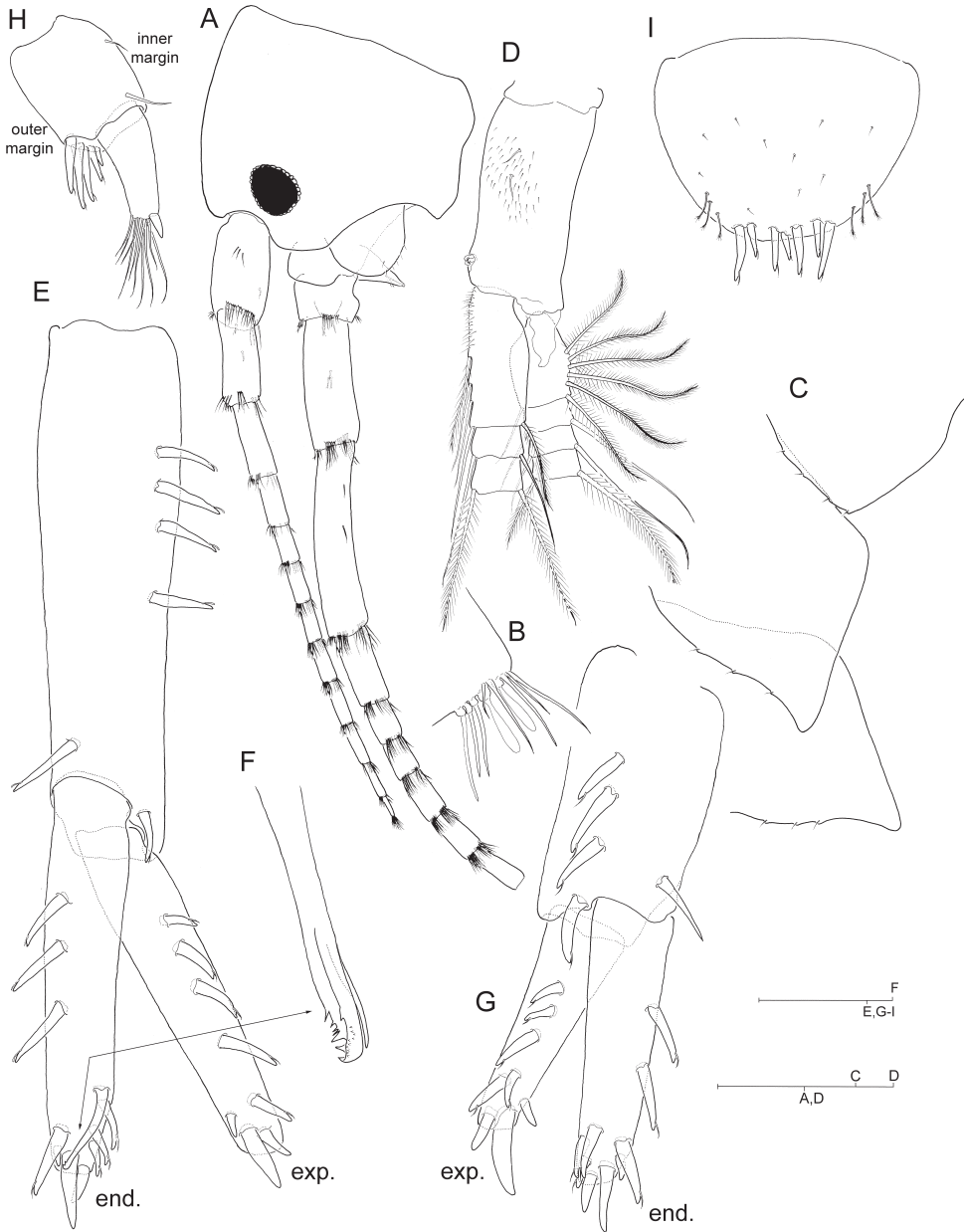


Figure 1. *Hyaella cajasi* sp. n., male. **A** head with left antenna 1 and antenna 2 attached, lateral **B** inset of distomedial armature on posterior margin of articles 3-6 of antenna 1 **C** right epimeral plates **D** right pleopod 3, posterior. Scale bars: 0.2 mm (**A, D**); 0.1 mm (**B**); 0.5 mm (**C, E, G-I**); 0.05 mm (**F**).

medial margin of segment unarmed. Exopod with series of five flagellate robust setae along lateral margin and three robust setae on tip, none of which flagellate; medial margin of segment unarmed. Endopod with four flagellate robust setae along medial margin

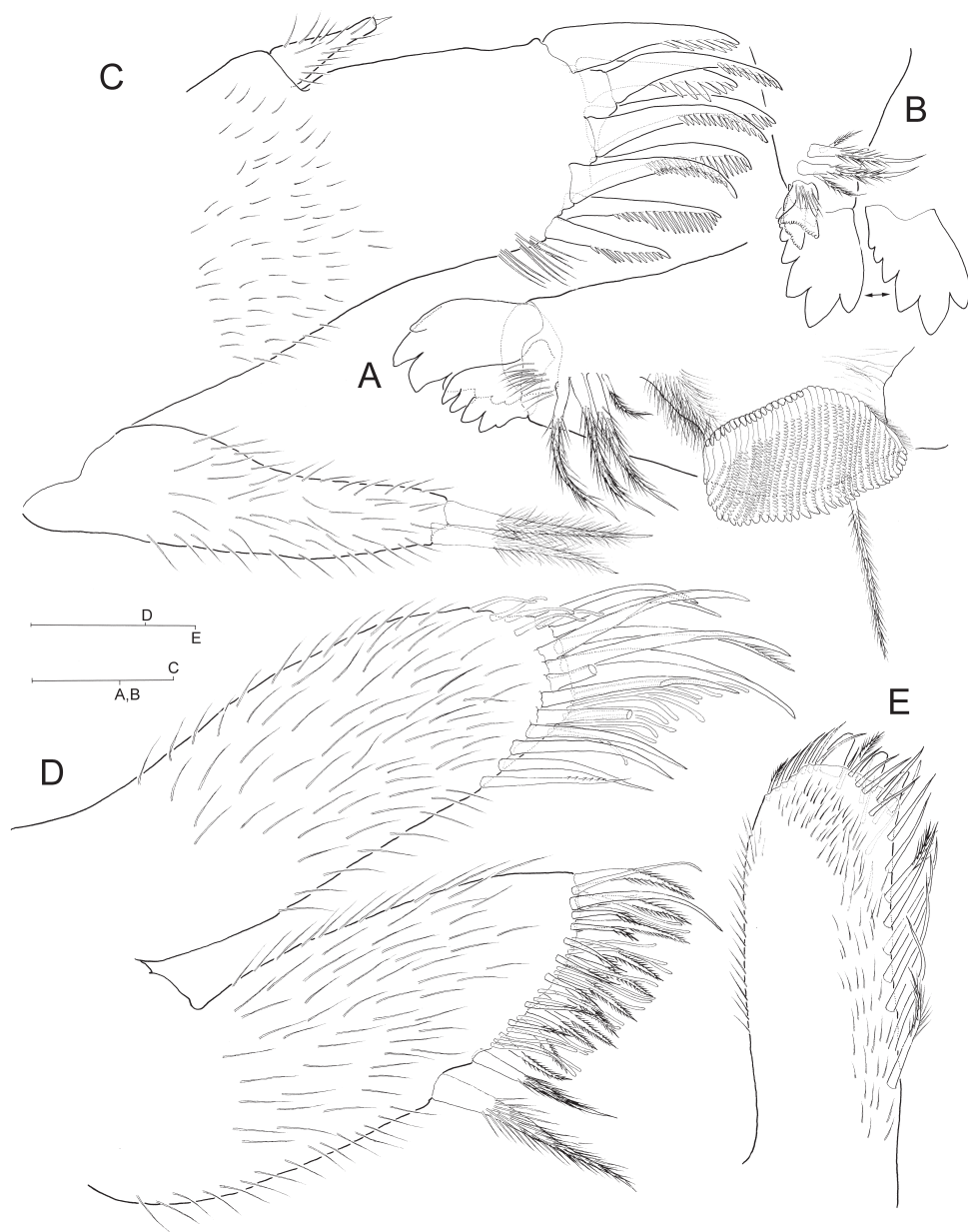


Figure 2. *Hyalella cajasi* sp. n., male. **A** left mandible **B** distal portion of right mandible **C** maxilla 1 **D** maxilla 2 **E** inset of basal endite (= inner plate) of left maxilliped, anterior view. Scale bars: 0.1 mm.

and three robust setae on tip, none of which flagellate; lateral margin of segment with series of four flagellate robust setae disposed subdistally on margin, of which proximal-most modified, longer than rest, slightly surpassing tip of endopod, slightly curved and complexly denticulate on tip (“copulatory spine” *sensu* Bousfield 1986; Fig. 1F).

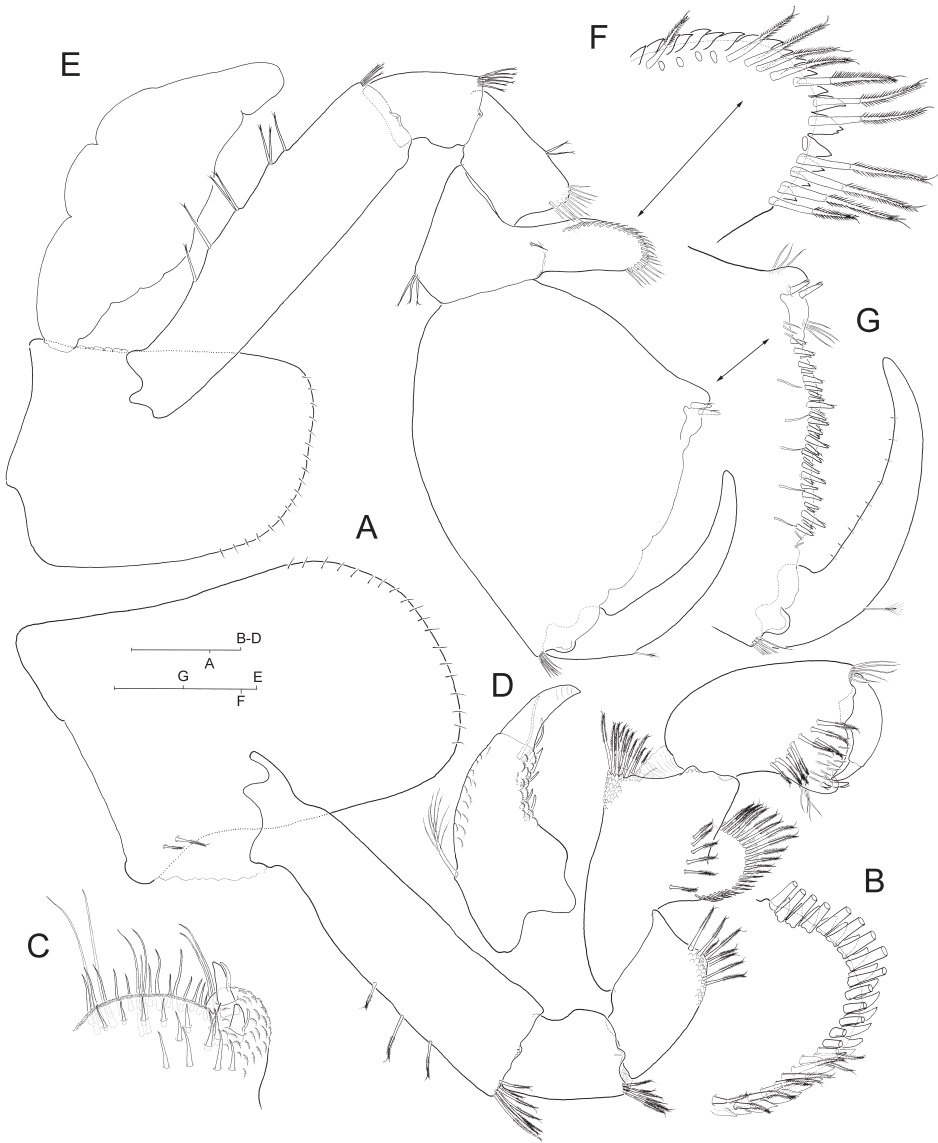


Figure 3. *Hyaella cajasi* sp. n., male. **A** left gnathopod 1, medial (armature on palm margin of propodus and on dactylus omitted) **B** inset of carpal lobe, medial **C** inset of palm margin and palm angle of propodus, medial **D** inset of dactylus, medial **E** right gnathopod 2, medial (armature on palm margin of propodus and on dactylus omitted) **F** inset of carpal lobe, medial **G** detail of palm margin and palm angle of propodus, and of dactylus, medial (submarginal armature along lateral side of palm margin omitted). Scale bars: 0.2 mm (**A**, **G**); 0.1 mm (**B–D**, **F**); 0.5 mm (**E**).

Uropod 2 (Fig. 1G) protopod about as long as rami. Protopod with three flagellate robust setae along posterolateral margin; robust seta present on each posterodistal and posteromedial angle of segment, of which that on posteromedial angle non-flagellate

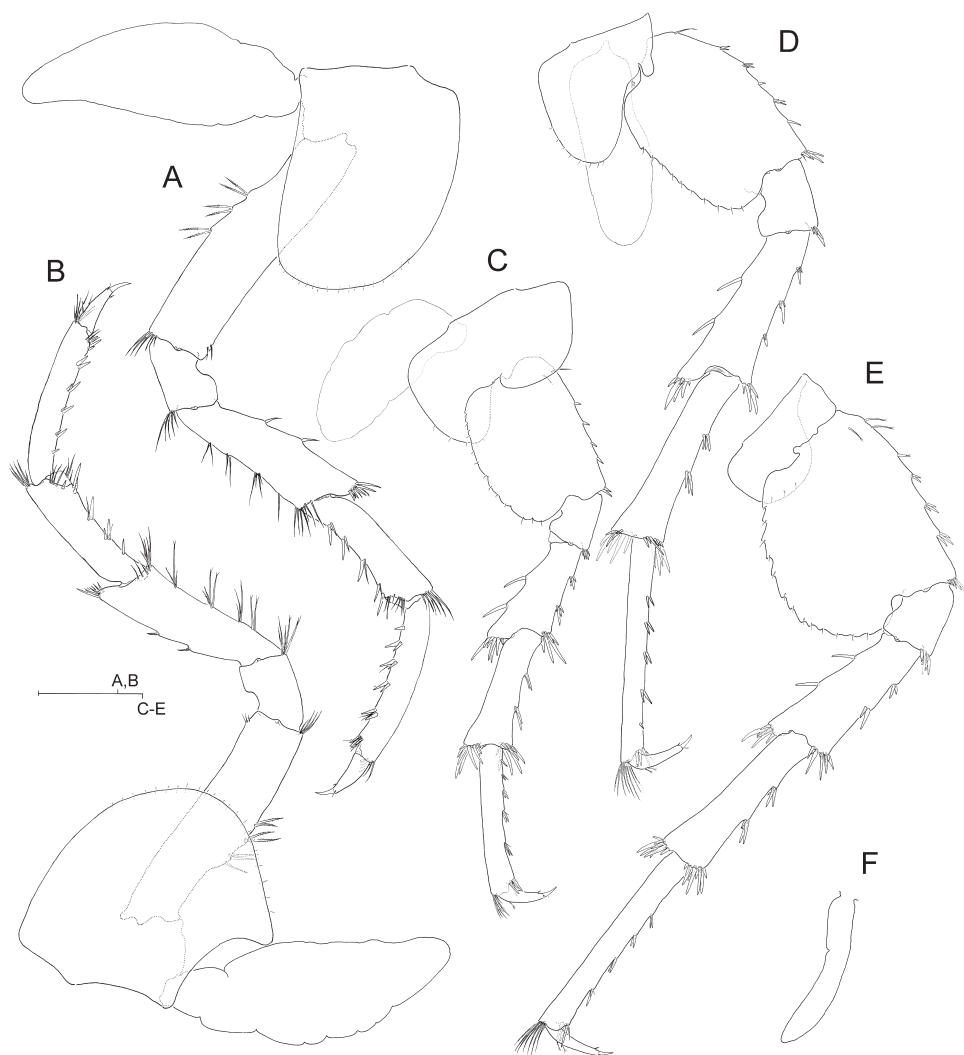


Figure 4. *Hyalella cajasi* sp. n., male. **A** right pereopod 3, lateral **B** right pereopod 4, lateral **C** right pereopod 5, lateral, coxal gill omitted **D** right pereopod 6, lateral, coxal gill omitted **E** left pereopod 7, medial **F** left sternal gill on sternite of pereonite VII. Scale bars: 0.5 mm.

and more slender than counterpart; posteromedial margin of segment unarmed. Exopod with five flagellate robust setae along lateral margin and three robust setae on tip; medial margin unarmed. Endopod with 3–4 flagellate robust setae along medial margin, three robust setae on tip, and three flagellate robust setae disposed subdistally on lateral margin.

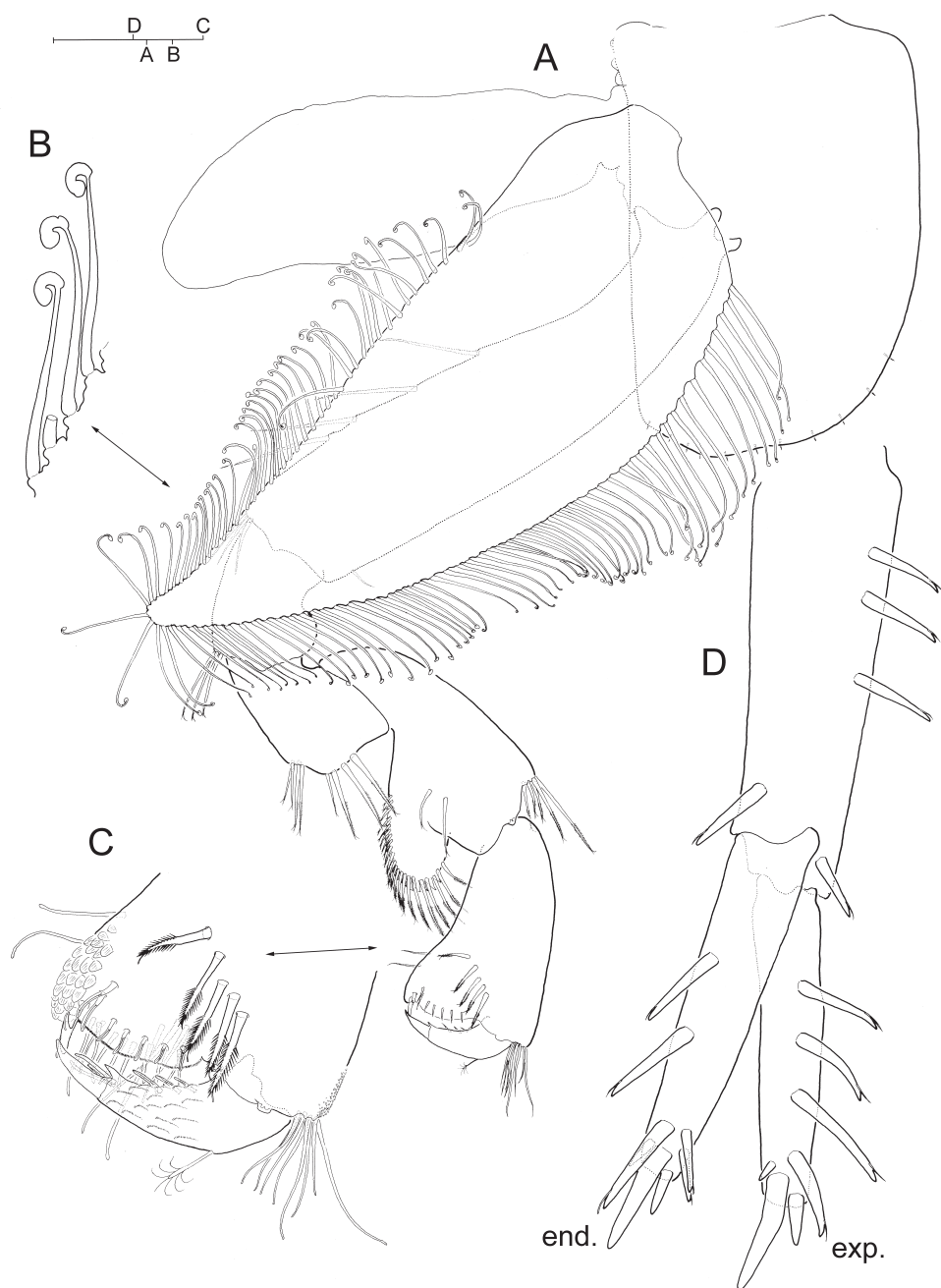


Figure 5. *Hyalella cajasi* sp. n., female. **A** left gnathopod 2, medial **B** inset of marginal setae on oostegite **C** inset of distal margin of propodus plus dactylus, medial **D** right uropod 1, posterior. Scale bars: 0.2 mm (**A**); 0.05 mm (**B**); 0.1 mm (**C**, **D**).

Uropod 3 (Fig. 1H) ramus about as long as protopod. Protopod with transverse comb of 3–6 flagellate robust setae on distolateral angle, simple seta on distomedial angle, and isolated reduced simple seta on medial margin. Ramus 2.2 times longer than broad, with short robust seta and a bunch of long simple setae on tip.

Telson (Fig. 1I) broader than long, with distal margin evenly rounded. Armature consisting of continuous marginal series of 4–7 (exceptionally only three) flagellate robust setae distally plus three tiny plumose setae disposed distolaterally at each side.

Description of brooding female. Differing from male in smaller size (body up to 6.5 mm long); presence of oöstegites on pereionites II–V (Fig. 5A, B); aspect of gnathopod 2 (Fig. 5A), which is similar to male gnathopod 1 but with a more slender propodus (1.7 times as long as broad and attaining 95% length of carpus; versus 1.5 times as long as broad and attaining 89% length of carpus in male gnathopod 1); unequal length of robust setae on palm angle of gnathopod 2 (Fig. 5C); and endopod of uropod 1 with two flagellate robust setae along distolateral margin (versus four in male), of which none modified (Fig. 5D).

Discussion

Of the approximately 70 species of *Hyalella* currently recognized (Horton and Lowry 2013), only nine (listed below) share a smooth, non-processiferous body, a male uropod 1 with a modified curved robust seta on endopod, and six pairs of sternal gills with *H. cajasi* sp. n. Nevertheless, the new taxon can be differentiated from each of them based on the presence/absence of eyes; relative length of antenna 1 with respect to antenna 2; presence/absence of a short pointed robust seta distally on palp of maxilla 1; number of pappose setae proximally on medial margin of inner lobe of maxilla 2; elongation and curvature of the modified robust seta on endopod of male uropod 1; relative length of ramus of uropod 3 with respect to protopod; and armature and outline of telson, among other features.

Thus, *Hyalella cajasi* sp. n. differs from *H. bonariensis* Bond-Buckup, Araujo & Santos, 2008, described in Santos et al. (2008) and known only from the province of Buenos Aires in Argentina, by the telson outline, which is broader than long and with the distal margin evenly rounded (versus telson as long as broad, subquadrate); by the telson marginal armature, arranged as a single row of robust setae (versus a cluster of robust setae distolaterally at each side); the sparsely setulose condition of the palp of maxilla 1 (versus palp densely setulose); and by the condition of the modified robust seta on the endopod of male uropod 1, which is hardly curved and only just surpasses the tip of endopod (versus seta elongate and strongly bowed).

Diagnostic differences between *H. cajasi* sp. n. and *H. brasiliensis* Bousfield, 1996, from Paraná State (Brazil), include the short ramus of uropod 3, which is shorter than the corresponding protopod (versus ramus longer than protopod); the comparatively shorter propodus of male gnathopod 1, which is shorter than carpus (versus propodus about as long as carpus); and the male gnathopod 2 propodus with palm margin longer

than the posterior margin (versus palm margin about as long as posterior margin) (see Bousfield 1996).

The new species differs from *H. carstica* Bastos-Pereira & Bueno, 2012, a taxon known from Minas Gerais (Brazil), by the relative length of antenna 1, which is much shorter than antenna 2 (versus antenna 1 and antenna 2 about equal in length in *H. carstica*); by the presence of two pappose setae proximally on the medial margin of inner lobe of maxilla 2 (versus only one seta); by the broader than long telson (versus telson longer than broad); by the marginal armature of robust setae on telson, comprising a distal continuous series (versus single robust seta subdistally at each side); and by the much stouter male gnathopod 2 propodus, about 1.3 times as long as broad (versus 1.6 times, with palm margin much shorter than posterior margin) (see Bastos-Pereira and Bueno 2012).

Hyalella cajasi sp. n. differs from *H. castroi* González, Bond-Buckup & Araujo, 2006, a species from Rio Grande do Sul (Brazil), in the distal robust seta present on palp of maxilla 1 (versus palp pointed but devoid of armature in *H. castroi*); in the display of two pappose setae proximally on the medial margin of inner lobe of maxilla 2 (versus only one seta); in the condition of the modified robust seta on male uropod 1 endopod, which is hardly curved and only just surpasses the tip of endopod (versus seta elongate and strongly bowed); and in the stouter condition of male gnathopod 2 propodus, which is about 1.24 times as long as broad (versus 1.32 times) (see González et al. 2006).

Hyalella curvispina Shoemaker, 1942, known from Montevideo (Uruguay) and Rio Grande do Sul (Brazil), differs from the new species in the longer-than-broad telson, which in addition displays only 1+1 robust setae on distal margin, and the unarmed but pointed palp of maxilla 1. Furthermore, the modified setae on male uropod 1 endopod (sometimes it displays two instead of only one) are more elongate and curved than in *H. cajasi* sp. n. (see Shoemaker 1942).

Hyalella formosa Cardoso & Araujo, 2014 (described in Cardoso et al. 2014), from a cave in Paraná State (Brazil), differs from the new species in being eyeless; in the elongation of antenna 1, which is longer than antenna 2; in the telson armature, reduced to two terminal simple setae; and in the large size of one of the two robust setae present on palm angle of propodus of gnathopod 1.

The new species differs from *H. paramoensis* Andres, 1988, a species known from a high altitude lake near Bogotá (Colombia), in the armature of the telson, which consists of a distal series of marginal robust setae (versus armature reduced to two long and slender robust setae in *H. paramoensis*); the presence of a robust seta on tip of the palp of maxilla 1 (versus palp unarmed); and in the relative length of the modified robust seta present on the endopod of male uropod 1 (versus seta extremely elongated in *H. paramoensis*) (see Andres 1988).

Hyalella cajasi sp. n. differs from *H. xakriaba* Bueno & Araujo, 2013 (described in Bueno et al. 2013) from Minas Gerais (Brazil), by the palp of maxilla 1 provided with a terminal robust seta (versus seta absent); by the armature of telson (reduced to 2+2 robust setae in *H. xakriaba*); and by the stouter male gnathopod 2 propodus (1.24 times as long as broad; versus 1.59 times in *H. xakriaba*).

Finally, *H. cajasi* sp. n. differs from *H. veredae* Cardoso & Bueno, 2014 (described in Cardoso et al. 2014), known from a cave in Minas Gerais (Brazil), by the non-regressed, ordinary eyes (versus eyes reduced or absent); by the relative length of antenna 1 (shorter than antenna 2; versus antenna 1 and antenna 2 about equal in length); and by the armature and outline of telson, subquadrate and with only 1+1 robust setae in *H. veredae*.

With regards to *H. meinerti*, the only representative of the genus confidently known to occur in Ecuador until now, it differs from *H. cajasi* sp. n. in the display of a non-sexually dimorphic uropod 1, a 1+1 armature arrangement on distal margin of the telson, and in the presence of only one pappose seta proximally on the medial margin of the inner lobe of maxilla 2.

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References

- Andres HG (1988) *Hyaella paramoensis* sp. n. aus dem Páramo de Chisaca (Anden) (Crustacea: Amphipoda: Talitroidea). Mitteilungen Hamburgischen Zoologischen Museum und Institut 85: 103–109.
- Bastos-Pereira R, Bueno AAP (2012) New species and new report of *Hyaella* S. I. Smith, 1874 (Crustacea: Amphipoda: Dogielinotidae) from Minas Gerais state, Southeastern Brazil. Zootaxa 3350: 58–68.
- Bousfield EL (1996) A contribution to the reclassification of Neotropical freshwater hyalellid amphipods (Crustacea: Gammaridea, Talitroidea). Bollettino del Museo Civico di Storia Naturale de Verona 20: 175–224.
- Bueno AAP, Araujo PB, Cardoso GM, Gomes KM, Bond-Buckup G (2013) Two new species of *Hyaella* (Amphipoda, Dogielinotidae) from Brazil. Crustaceana 86: 802–819. <https://doi.org/10.1163/15685403-00003205>
- Cardoso GM, Araujo PB, Bueno AAP, Ferreira RL (2014) Two new subterranean species of *Hyaella* Smith, 1874 (Crustacea: Amphipoda: Hyalellidae) from Brazil. Zootaxa 3814: 353–368. <http://dx.doi.org/10.11646/zootaxa.3814.3.3>
- González ER, Bond-Buckup G, Araujo PB (2006) Two new species of *Hyaella* from Southern Brazil (Amphipoda: Hyalellidae) with a taxonomic key. Journal of Crustacean Biology 26: 355–365. <http://dx.doi.org/10.1651/C-2599.1>

- González ER, Watling L (2003) A new species of *Hyalella* from Colombia, and the redescription of *H. meinerti* Stebbing, 1899 from Venezuela (Crustacea: Amphipoda). *Journal of Natural History* 37: 2095–2111. <http://dx.doi.org/10.1080/00222930210133255>
- Gunkel G, Beulker C (2009) Limnology of the crater lake Cuicocha, Ecuador, a cold water tropical lake. *International Review of Hydrobiology* 94: 103–125. <http://dx.doi.org/10.1002/iroh.200811071>
- Horton T, Lowry J (2013) *Hyalella* S. I. Smith, 1874. In: Horton T, Lowry J, De Broyer C, Bellan-Santini D, Coleman CO, Daneliya M, Dauvin J-C, Fišer C, Gasca R, Grabowski M, Guerra-García JM, Hendrycks E, Holsinger J, Hughes L, Jaume D, Jazdzewski K, Just J, Kamaltynov RM, Kim Y-H, King R, Krapp-Schickel T, LeCroy S, Lörz A-N, Senna AR, Serejo C, Sket B, Tandberg AH, Thomas J, Thurston M, Vader W, Väinölä R, Vonk R, White K, Zeidler W (Eds) *World Amphipoda Database*. <http://www.marinespecies.org/aphia.php?p=taxdetails&id=158104> [on 2017-02-03]
- Santos ALF, Araujo PB, Bond-Buckup G (2008) New species and new reports of *Hyalella* (Crustacea, Amphipoda, Dogielinotidae) from Argentina. *Zootaxa* 1760: 24–36.
- Shoemaker CR (1942) A new species of Amphipoda from Uruguay and Brazil. *Journal of the Washington Academy of Sciences* 32: 80–82.
- Whymper E (1892) *Travels amongst the Great Andes of the Equator*. London, John Murray. <https://doi.org/10.1037/14019-000>

Updated catalogue and taxonomic notes on the Old-World scorpion genus *Buthus* Leach, 1815 (Scorpiones, Buthidae)

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Abstract

Since the publication of the ground-breaking “Catalogue of the scorpions of the world (1758–1998)” (Fet et al. 2000) the number of species in the scorpion genus *Buthus* Leach, 1815 has increased 10-fold, and this genus is now the fourth largest within the Buthidae, with 52 valid named species. Here we revise and update the available information regarding *Buthus*. A new combination is proposed: *Buthus halius* (C. L. Koch, 1839), **comb. n.** from Portugal and Spain. *B. halius* is removed from junior synonymy with *Buthus occitanus* (Amoreux, 1789), and proposed as a senior synonym of *B. ibericus* Lourenço & Vachon, 2004, **syn. n.** Moreover, following I.C.Z.N. article 23.9.2 we propose to maintain as valid *B. ibericus* (**nomen protectum**) and to consider the disused *B. halius* as a **nomen oblitum**. *Buthus europaeus tridentatus* Franganillo, 1918 is proposed as a junior synonym of *B. occitanus* (Amoreux, 1789), **syn. n.** *Buthus sabulicola* Touloun, 2012 is proposed as a junior synonym of *Buthus bonito* Lourenço & Geniez, 2005, **syn. n.** *Buthus occitanus tunetanus neeli* Gysin, 1969 is proposed as an informal senior synonym of *Buthus tassili* Lourenço, 2002, **informal syn. n.** Two taxa are raised to species rank, *Buthus nigrovesiculosus* Hirst, 1925, **stat. n.** and *Buthus parroti* Vachon, 1949, **stat. n.** We further confirm the restricted distribution of *B. occitanus* that is confined to southeastern France and northwestern Iberian Peninsula and does not occur in North Africa. Additionally, *Androctonus barbouri* (Werner, 1932), **comb. n.** from the Agadir region of Morocco, is hereby transferred to the genus *Androctonus*. We summarize and provide a critical appraisal

of the diagnostic characters currently in use for the genus. The catalogue section considers the names for species, subspecies and varieties that have been used for *Buthus* scorpions. Information about types, including collection numbers and localities are included when available. Finally, an annotated listing of synonymies and an updated bibliography are given.

Keywords

Taxonomy, new synonymy, new combination, new status, Geographic distribution, Africa, Asia, Europe, diagnostic characters

Introduction

Members of the genus *Buthus* Leach, 1815 are medium-sized scorpions, usually yellowish in colour, with a robust metasoma that ends in a telson with a globular vesicle and a curved aculeus (Fig. 1). *Buthus* rest during the day in burrows under stones or shrubs and are active from dusk till dawn, although their activity typically peaks at the beginning of the night (Cloudsley-Thompson 1956). They are successful scorpions that, when present, tend to be the most abundant scorpion in their habitat, as for example in the Iberian Peninsula and Morocco. *Buthus* are usually described as sit-and-wait predators, although they can also actively search for prey (Skutelsky 1995, Piñero et al. 2013). *Buthus* is among the most venomous of all scorpion genera (Chippaux and Goyffon 2008). *Buthus* venom toxicity is considered much lower in Europe than in North Africa, which can be empirically corroborated by the few severe cases of scorpionism reported for Western Europe when compared to the North African countries (Chippaux and Goyffon 2008).

Buthus exhibits a wide distribution range, spanning over two biogeographic realms, the Palearctic (Western) and the Afrotropical (Udvardy 1975, Olson et al. 2001). Interestingly, none of the chorotypes proposed by Vigna Taglianti et al. (1999) satisfactorily describes *Buthus* distribution. The genus extends from the temperate Mediterranean areas of south-western Europe to the tropical and sub-tropical grasslands south of the Sahel and into the Horn of Africa, including the semi-arid and arid regions of North Africa and the Middle East (Fig. 2). Although first considered of European origin (Vachon 1952a), current data support the hypothesis that the centre of origin of the genus is North Africa (Lourenço 2002). North Africa harbours a disproportionate number of species (Fig. 2) as well as four of the five main genetic clades found in *Buthus*, as defined by mitochondrial DNA sequence variation (Sousa et al. 2012, Pedrosa et al. 2013) (Fig. 7).

Buthus species are known from 17 countries in Africa: Algeria, Cameroon, Central African Republic, Chad, Egypt, Eritrea, Ethiopia, Guinea, Libya, Mauritania, Morocco, Niger, Senegal, Somalia, South Sudan, Sudan, and Tunisia; five countries in Asia: Cyprus, Egypt (Sinai), Israel, Jordan, and Yemen; and four European countries: France, Italy (Sicily), Portugal, and Spain (Fig. 2). Unidentified *Buthus* species have also been reported from Burkina Faso, Djibouti, Gambia, Ghana, Guinea-Bissau, Ivory Coast, Nigeria, Iraq, and Lebanon (Fig. 2). No records exist for Saudi Arabia or Syria, however



Figure 1. *Buthus mariefranceae*, from south of Morocco. Photo by Arie van der Meijden.

the first might have been confused in the past with citations for the Arabian Peninsula (e.g. Vachon 1952a), although the existence of *Buthus* in either of these countries cannot be excluded. The frequently cited occurrence of *Buthus* in Iraq is based on a single specimen, deposited in the Czech National Museum of Natural History (Táborský 1934, Kovařík 1992). As such the actual distribution of the genus remains poorly delimited. Old records from mainland Greece and Turkey are highly doubtful, as these are well-studied areas with no recent *Buthus* collections (Ersen Yağmur pers. comm. for Turkey) (Fig. 2). The former records most likely refer to the genus *Mesobuthus* Vachon, 1949. As for the record for Malta, it was considered dubious by Fet and Lowe (2000), although other *Buthus* reported on islands that were previously regarded as doubtful have turned out to be correct, namely *B. kunti* Yağmur, Koc & Lourenço, 2011, from Cyprus, described from freshly collected material and *B. trinacrius* Lourenço & Rossi, 2013, from Sicily, based on 130-year-old material. Other island records include *B. occitanus* in the Columbrette islands (Castilla and Pons 2007) and *B. tunetanus* (Herbst, 1800) in the Tunisian islands of Djerba, Kerkena, and Zembra (Vachon 1952a).

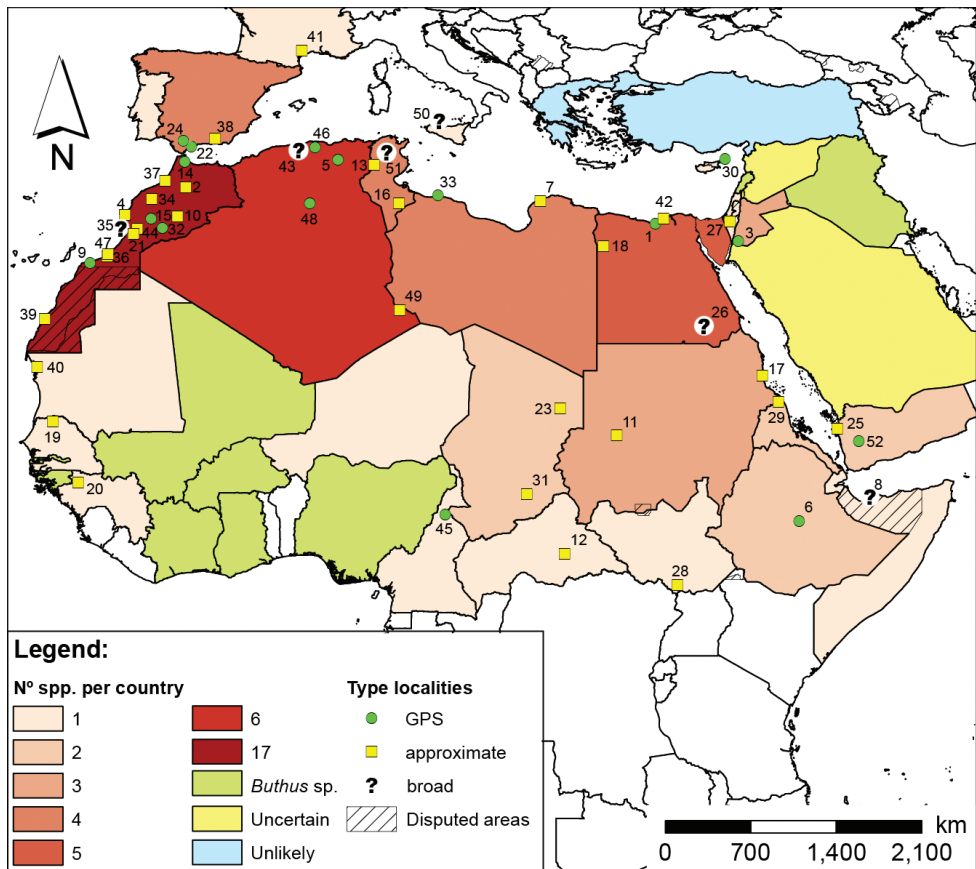


Figure 2. Map of *Buthus* species distribution, and the known number of species by country. Also depicted are the species' type localities (numbers according to the species' Catalogue and Table 2) where known or the best possible approximation. Actual distribution within each country can be much smaller, but detailed distribution information is unknown for the majority of species.

Buthus is the type genus of the Buthidae C. L. Koch, 1837 (Koch 1837, 1850), the most diverse family within Scorpiones, with almost half of all known extant scorpion species (1101 of the 2311 known species) (Rein 2016). The Buthidae also includes most of the species venomous to humans (Chippaux and Goyffon 2008). The genus *Buthus* is the second oldest valid genus of the order Scorpiones C. L. Koch, 1837, only surpassed by the single genus created by Linnaeus in 1758, *Scorpio*, to accommodate all the scorpion species he described.

Buthus was first proposed by Leach (1815), with *Scorpio occitanus* Amoreux, 1789 as its type species (Fig. 3). The only diagnostic character for the genus proposed by Leach was the presence of eight eyes "*Oculi octo*." (Leach 1815, page 391), apparently referring to the pair of central eyes and three pairs of lateral eyes. This character was mentioned as diagnostic for different scorpions early during Scorpiones taxonomy (De Geer 1778, Fabricius 1781). The same diagnostic character was used by Ehrenberg (in Hemprich

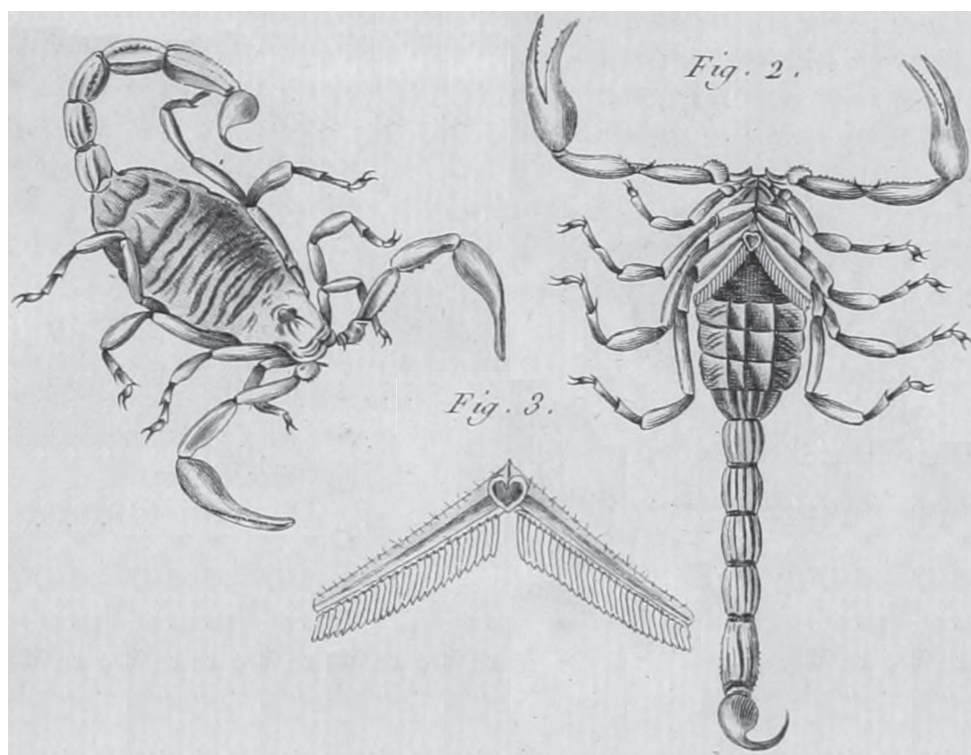


Figure 3. Original illustration of *Scorpio occitanus* (Amoreux 1789a). The work was retrieved from the Biodiversity Heritage Library and images were rearranged for compactness without re-scaling.

and Ehrenberg 1828, 1829) for defining several genera and subgenera of scorpions with a varying number of eyes, ranging from six to 12. A more detailed explanation on the usage of the number of eyes in the classification of scorpions is given in Thorell (1876).

The poor description of Leach (1815) led to a rapid increase in the number of species included in the genus, which lacked any internal coherence. This taxonomic conundrum arose through the misidentification of the number of lateral eyes of *B. occitanus* (Amoreux, 1789), originally stated by Amoreux as three pairs. Several taxonomists of that century realised that there were actually four pairs of lateral eyes (e.g. Gervais 1844b; Simon 1879), but this information was not appreciated by some later authors. It has recently been shown that most Buthidae species (including *Buthus*) have five pairs of lateral eyes, although in many species two pairs of lateral eyes are much smaller in size and require extreme care and the help of UV light to be recognised (Yang et al. 2013; Loria and Prendini 2014). Ehrenberg (in Hemprich and Ehrenberg 1828) modified the original meaning of the genus to include the species that are now part of *Heterometrus* Ehrenberg in Hemprich and Ehrenberg 1828 (Family Scorpionidae Latreille, 1802), all with five pairs of lateral eyes. Ehrenberg described several other genera that were soon synonymized with *Buthus*, at least by some taxonomists, which further exacerbated the taxonomic confusion within *Buthus*.

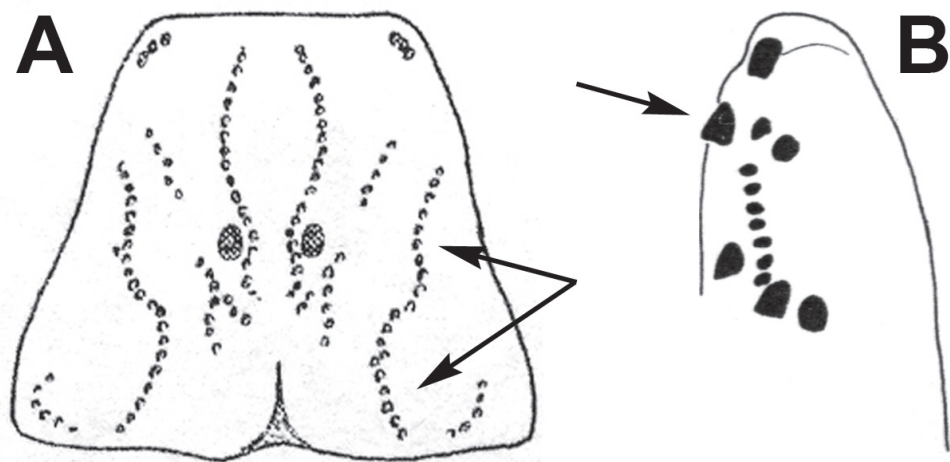


Figure 4. The two key morphological diagnostic characters of the genus *Buthus*. A- Prosoma carapace with lyra-shaped keels (Hjelle 1990); B - Tip of pedipalp movable finger highlighting the three distal granules (distal denticle not included) (Lourenço 2002).

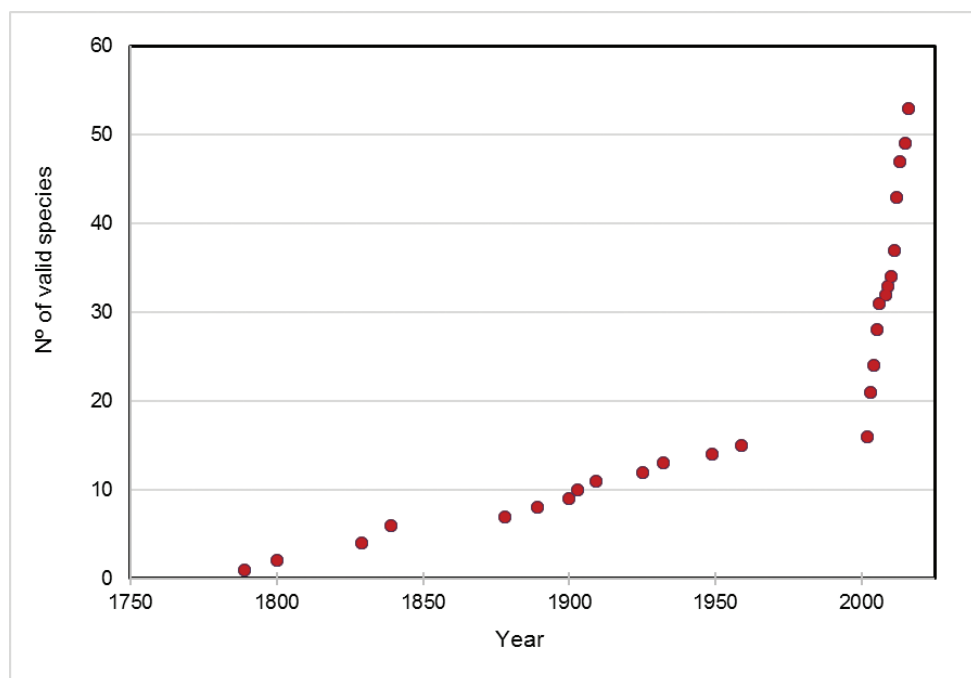


Figure 5. Cumulative number of valid named *Buthus* species. Only current valid species' names were plotted; in the year they were first described.

Because of the poor definition of the genus, many members (≈ 100 species) of the Buthidae family with no close relationship to the type species, were included in the genus *Buthus* up to the mid-20th century (Vachon 1952a, Levy and Amitai 1980, Lourenço 2002). Unfortunately, this obsolete taxonomy is still in use, for example in many toxicology and venom related papers on scorpions (*e.g.* Gopalakrishnakone et al. 2015). From 1948 to 1951, Vachon conducted a major taxonomic revision of the genus (compiled in Vachon 1952a), providing a more informative and exclusive definition, retaining only the species that were morphologically similar to the type species and hence restricting also the distribution range of the genus. He proposed two main morphological characters that in combination separate *Buthus* from all other known Buthidae genera: the central-lateral and posterior-median prosomal keels fused in a lyra shape (character shared with *Cicileiurus* Teruel, 2007, *Leiurus* Ehrenberg in Hemprich and Ehrenberg 1828, *Mesobuthus* Vachon, 1950, and *Odontobuthus* Vachon, 1950, Fig. 4A), and the presence of only three granules on the tip of the movable finger (or tarsus) of the pedipalp chela (character shared with *Androctonus* Ehrenberg in Hemprich & Ehrenberg, 1828, Fig. 4B).

While studying specimens from northwest Africa, Vachon recognized that the genus included a large amount of undescribed diversity. Vachon took a very conservative approach to *Buthus* taxonomy, recognizing only four species, further split in 12 subspecies, ten of which under *B. occitanus*, and naming four different varieties, along with other forms with no formal rank, all within *B. occitanus*. This was partly justified by Vachon's view that *Buthus* species exhibited a large morphological plasticity, at least in the characters he used to diagnose the different taxa (Vachon 1952a). Stahnke (1972), in his key to Buthidae genera, recognized 21 species and subspecies in *Buthus*, without further explanation, although this is probably an error resulting from an outdated interpretation of the genus taxonomy. In accordance with the ICZN article 45, none of Vachon's infra- subspecific varieties were included in the Catalogue of the Scorpions of the World (Fet et al. 2000). The *Buthus* Catalogue recognized as good five species and 12 subspecies, although the authors recognized that some taxa were probably not taxonomically good (Fet and Lowe 2000). Subsequently, Rossi (2015) transferred *Buthus insolitus* Borelli, 1925 to the recently erected genus *Gint* Kovařík et al., 2013. Lourenço (2003) marked a renewed interest in the taxonomy and diversity of the genus, describing six new species, some of which corresponding to Vachon's infra-subspecific varieties.

During the last 15 years, the rate of description of new *Buthus* species has increased exponentially (Fig. 5). At present, the genus is composed of 52 species, three of which were described in 2016, making it the fourth most diverse genus of Buthidae, only surpassed by the megadiverse scorpion genera *Tityus* C. L. Koch, 1836, *Centruroides* Marx, 1890 and *Ananteris* Thorell, 1891 (Rein 2016). Thirty authors have been involved in the description of recent *Buthus* species, and most species (21) have been described in collaborative studies. Wilson Lourenço is by far the most prolific author, having authored or co-authored 29 *Buthus* species, 55% of the total.

Materials and methods

Nomenclature and measurements follow Stahnke (1970), except for trichobothriotaxy (Vachon 1974, Fet et al. 2005). All diagnostic morphological characters mentioned in the text refer to adults (or large sub adults) of both sexes, unless otherwise noted.

Most references prior to 1998 cited by Fet and Lowe (2000) are confirmed, but not all original literature could be obtained, and we made some corrections following comparisons with additional sources (Vachon 1952a, Lamoral 1979, Polis 1990, Hendrixson 2006, Dupré 2013). The criteria applied by Fet and Lowe (2000) citing both taxonomic and faunistic works are broadly followed. To the best of our knowledge we cited all works that follow these criteria up to November 2016. Fet and Lowe (2000) cited approximately 180 articles pertaining to the genus *Buthus*, we added approximately 80 new articles, ten of which were published before 1998.

Whenever possible, coordinates for the type localities are provided, using information available in articles or, if not available, finding approximate coordinates with the help of Google Maps (maps.google.com) and the GEONet Names Server (geonames.nga.mil/gns/html). All coordinates are in WGS 1984 datum, in Latitude/Longitude format, in decimal degrees.

Collections abbreviation codes are listed below. Abbreviation codes follow Sabaj (2016), except for those marked with an asterisk that are not presented there.

ARPC*	Andrea Rossi Private Collection, Massa, Italy
CBGP*	Centre de Biologie pour la Gestion des Populations (UMR INRA, Cirad, IRD, Montpellier SupAgro), Montferrier-sur-Lez France, France
FKPC*	František Kovařík Private Collection, Prague, Czech Republic
MCSNB	Museo Civico di Scienze Naturali “Enrico Caffi”, Bergamo, Italy (formerly MSNB)
CRBA	Centre de Recursos de Biodiversitat Animal of the Universitat de Barcelona, Barcelona, Spain
MCVR	Museo Civico di Storia Naturale di Verona, Verona, Italy
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A.
MHNG	Muséum d'histoire naturelle de Genève, Geneva, Switzerland
MNCN	Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain
MNHN	Muséum national d'Histoire naturelle, Paris, France
MRSN	Museo Regionale di Scienze Naturali di Torino, Turin, Italy
MTAS*	Museum of the Turkish Arachnology Society, Ankara, Turkey
MZUF	Museo di Storia naturale dell'Università di Firenze, sezione di Zoologia “La Specola”, Florence, Italy
NHMK	Natural History Museum, London; England, UK (formerly BMNH, British Museum of Natural History)
UCAM*	Université Cadi Ayyad, Faculte des Sciences Semlalia, “Laboratoire Ecologie et Environnement”, Marrakech, Morocco (formerly Université Cadi

	Ayyad, Faculte des Sciences, Semlalia, Depart. BioI., Lab. Ecol. Anim. Terrestre, Marrakech, Morocco)
UGA*	University of Ghardaïa, Ghardaïa, Algeria
ZIN	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (formerly ZISP)
ZMB	Museum für Naturkunde - Leibniz-Institut für Evolutions und Biodiversitätsforschung, Berlin, Germany (formerly ZMBH)
ZMH	Biozentrum Grindel und Zoologisches Museum, Hamburg, Germany

Additional abbreviations used in the text:

a.s.l.	above sea level
ICZN	International Code of Zoological Nomenclature
IOS	incorrect original spelling
ISS	incorrect subsequent spelling
juv.	juvenile or juveniles
M	male
F	female
MIS	misidentification

The type species of the genus *Buthus*

It is worth mentioning here the taxonomic confusion that surrounded the first *Buthus* species. Leach first named the genus with *Scorpio occitanus* Amoreux, 1789 as the type species (Figs 3; 6B). Amoreux (Amoreux 1789b) described this species to accommodate a scorpion from Souvignargues, Occitanie, France. Amoreux also called the same species *Scorpio rufus*, although he, as the first reviewer, chose the name *S. occitanus* to be the correct name for the newly described species (Amoreux 1789a). Amoreux also referred to this species as Malpertius' scorpion and, in his second paper where he gave a full description of the species, included drawings from this author (Maupertuis 1731) (Fig. 6B). It is clear from observing Fig. 6A that Amoreux was well aware of the differences between *Scorpio occitanus* and *S. europaeus* Linnaeus, 1758, which he considered a member of the genus *Euscorpius* Thorell, 1876. Unfortunately, the name *S. europaeus* Linnaeus, 1758 was subsequently used to refer to three different taxa: (1) *S. maculatus* De Geer, 1778 (now part of the genus *Isometrus* Ehrenberg, 1828) (Lönnerberg 1898), (2) *S. occitanus* Amoreux, 1789 (Thorell 1876b), and (3) a *Euscorpius* species (Fet & Sissom, 2000). This taxonomical confusion was solved by ICZN decision 60 (ICZN 1957), article 1b that suppressed the name *europaeus*, Linnaeus, 1758 when used in combination with *Scorpio*, and article 4, that placed *Scorpio europaeus* Linnaeus, 1758 on the Official Index of Rejected and Invalid Specific Names in Zoology with the number 381. As such, the first author to use the name *Buthus europaeus* was Thorell in

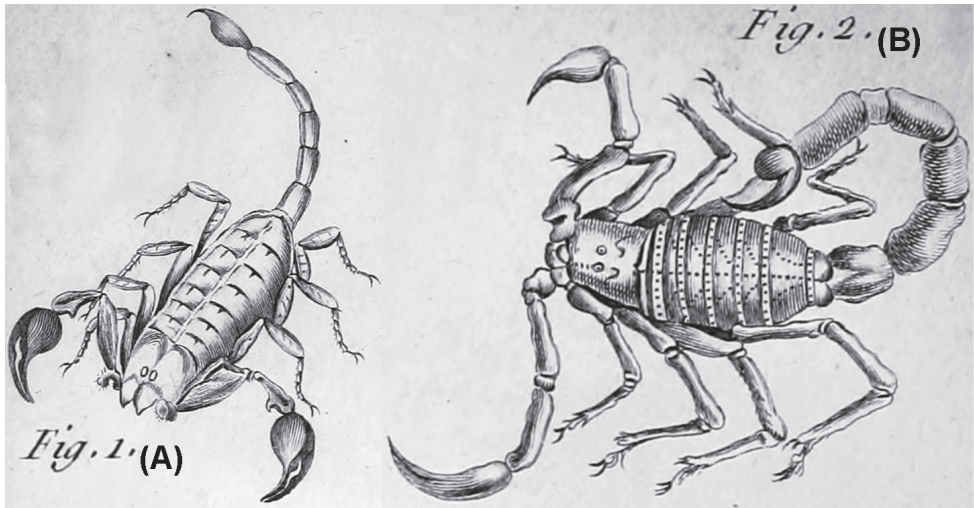


Figure 6. Original drawings of the habits of *Scorpio europaeus* Linnaeus, 1758 (A) and *S. occitanus* (B), according to Amoreux (1789b) reproduced from plate I of that work. These images are unfortunately rarely cited, as they are very informative regarding the reasoning of Amoreux while describing the new species.

1876, now a junior synonym of *B. occitanus* (Amoreux, 1789) (for further details see Braunwalder 1997, Fet et al. 2002).

Finally, although *Buthus* is considered the nominal genus of Buthidae, Koch (1837) used for the typification of the family, the species *Buthus spinifer* Ehrenberg, 1828, which is currently the type species of the genus *Heterometrus* Ehrenberg, 1828 (Scorpionidae Latreille, 1802), and as such according to ICZN Article 65.2.1. [“type genus was misidentified (that is, interpreted in a sense other than that defined by its type species)” when the family-group name was established”) we will submit to the ICZN a petition to fix the type species of the Buthidae. This was not done by Fet et al. (2000) as the authors probably interpret it as ICZN Article 65.2.3. (“type genus was, when established, based on a type species then misidentified”), which does not necessarily require a ruling by the Commission.

***Buthus* taxonomy**

The revised classification of Sharma et al. (2015) is followed, based on the first phylogenomics study on extant scorpions, which resolved most relationships between scorpion families.

Class Arachnida Lamarck, 1801

Order Scorpiones C. L. Koch, 1850

Suborder Neoscorpiones Thorell & Lindström, 1885

Infraorder Orthosterni Pocock, 1911
Parvorder Buthida Soleglad & Fet, 2003
Superfamily Buthoidea C. L. Koch, 1837
Family Buthidae C. L. Koch, 1837

There are no subfamilies in use within the Buthidae, although many have been proposed and rejected (Fet et al. 2000, 2005). Fet et al. (2005) defined six groups within the Buthidae, and placed *Buthus* in the *Buthus* group along with 38 additional genera. The phylogenomic study of Sharma et al. (2015) provided strong support for most groups (although generic level sampling was limited), including the sister group relationship of the *Buthus* group with the remaining members of the family.

Vachon (1952a) considered *Androctonus* to be the sister taxa to *Buthus*. However, the only molecular phylogenetic study addressing the relationships between Buthidae genera that includes both genera (Fet et al. 2003), recovered *Buthus* as the sister taxa to a clade formed by *Androctonus* and *Leiurus*, albeit with low support.

There are no taxonomically distinct groups within the genus *Buthus*, although two “species complexes” are generally recognised. Vachon (1952a, p. 251) suggested that “la «lignée» atlantis se sépare avec facilité de l'ensemble des autres *Buthus* par la forme élancée des appendices de la queue, de la vésicule et divers autres caractères que nos tableaux de détermination préciseront.” This distinction was retained by Lourenço (2002, 2003) who referred to *B. occitanus* as a “complexe de forms”, and subsequently also adopted it in most subsequent taxonomic works describing new *Buthus* species. According to Lourenço and Geniez (2005), the two complexes are distinguished by the level of keel development, weaker in the *atlantis* group. However, Lourenço (2005a) subsequently wrote that *B. occitanus* from Europe has a weak keel development in contradiction with the previous morphological definition. This statement has been used by subsequent authors. For example, Rossi (2012) described *B. elongatus* Rossi, 2012 as belonging to the *occitanus* complex, but if the author had applied Vachon's definition it should have included it in the *atlantis* complex because of the slender metasoma (at least its fifth segment) when compared to *B. occitanus*. None of the published molecular phylogenies of *Buthus* supports the existence of the *atlantis* complex. The results of Gantenbein and Largiadèr (2003) grouped *B. atlantis* within the species included in the *occitanus* complex. Although Lourenço and Vachon (2004) acknowledged the work of Gantenbein and Largiadèr (2003), they rejected the phylogenetic position of *B. atlantis* presented in this study.

Recently, based on the information provided by a *cox1* mtDNA tree, Sousa et al. (2012) and Pedrosa et al. (2013) have defined a series of groups, (see Table 1). These groups have been renamed to facilitate communication and have been expanded to include all available molecular data with reliable species identifications.

In Fig. 7 the current distribution of these five groups in the Maghreb, the Iberian Peninsula, and southern France is presented, based exclusively on specimens with available molecular data. The group assignment does not necessarily correspond to the species assignment in the original publications.

Table 1. Current composition of the groups proposed by Sousa et al. (2012) and Pedroso et al. (2013) based on *cox1*. To date, only 19 out of the 52 valid named *Buthus* species (37%) have been analysed. *, assignment based on Sousa (2017).

Group	Species	Group	Species	Group	Species
<i>boumalenii</i>	<i>B. boumalenii</i>	<i>occitanus</i>	<i>B. atlantis</i>	<i>rochati</i>	<i>B. bonito</i>
			<i>B. elongatus</i>		<i>B. draa</i>
<i>mardochei</i>	<i>B. elmoutaouakili</i>		<i>B. ibericus</i>		<i>B. mariefranceae</i>
	<i>B. lienhardi</i>		<i>B. malhommei</i>		<i>B. rochati</i> *
	<i>B. mardochei</i>		<i>B. maroccanus</i>	<i>tunetanus</i>	<i>B. chambiensis</i> *
	<i>B. parroti</i>		<i>B. montanus</i>		<i>B. pusillus</i> *
			<i>B. occitanus</i>		<i>B. tunetatus</i>

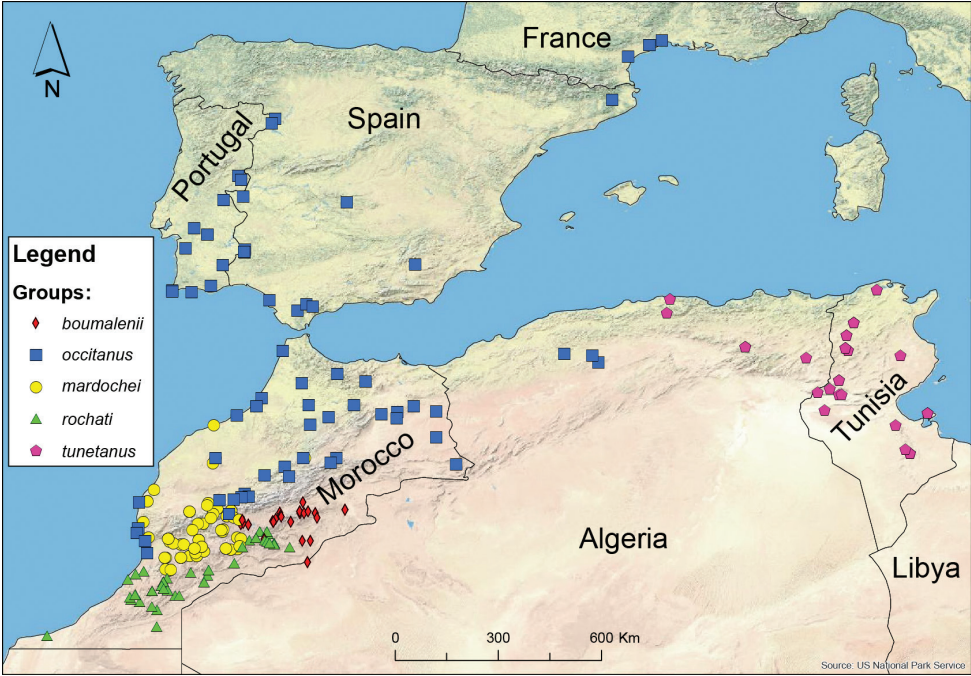


Figure 7. Map representing the five phylogenetic *Buthus cox1* groups in the Maghreb. Groups as defined by Sousa et al. (2012) and Pedroso et al. (2013), also including *cox1* sequences from Gantenbein and Largiadèr (2003), Habel et al. (2012) and Husemann et al. (2012) (redrawing of Figure 1 from Pedroso et al. 2013).

Diagnostic characters used in *Buthus* taxonomy

Several morphological traits have been used by recent authors as diagnostic characters (in the sense of Winston 1999) for *Buthus* species.

Colour is of limited utility in *Buthus* taxonomy, as the underlying colour varies in tones of yellow, orange, reddish or light brown within and between species. Only one

species has a fully dark body, *Buthus maroccanus* Birula, 1903, in some cases even black. Other species also have the mesosoma of a darker colour than the rest of the body. Of greater taxonomic use are colour patterns, such as darker marks, over a lighter background colour, that can be present on the carapace, the mesosoma or the metasoma; the latter being the more informative.

Adult size may also be diagnostic (Fig. 8). *Buthus* adult body sizes range from 38 to 90 mm (telson included) (the maximum size of 110 mm reported by Vachon (1952a) is presumably a mistake). Most species have a maximum size between 60 and 70 mm in females, and 55 to 70 mm for males (Fig. 8). On the 5% percentiles we have the smaller species of *Buthus* (less than 45 mm long), and the larger species of *Buthus* (more than 85 mm for females and 80 mm long for males).

Two additional meristic traits have been used as diagnostic characters, namely the number of rows of granules on the cutting edge of the movable finger of the pedipalp chela, and the number of pectinal teeth, a sexual dimorphic trait. Variation in the number of **rows of granules** is not very informative because species show an incremental overlap in the numbers of rows, which range from 8 to 14 (Fig. 9). **Pectinal teeth** number, although carrying a potentially greater amount of information as they have a wider range to vary from, is actually of limited usefulness because of the interspecific overlap (Fig. 10); female counts range from 18–34 and males from 24–37. Pectinal teeth number is also of limited use due to the lack of any information for several species and the unknown range of variability for many other *Buthus* species (Fig. 10). It should be noted, however, that *Buthus elizabethae* Lourenço, 2005 is unique in having male pectines that do not overlap in their proximal portion (Lourenço 2005a).

Trichobothria number and position are not useful for *Buthus* species diagnosis, as their location shows little variation and have as much intraspecific as interspecific variability (P. Sousa pers. obs.). Conversely, body **chaetotaxy** (other than trichobothria) is very useful for taxonomy. Vachon (1952a) defined three, albeit diffuse, states in *Buthus* body chaetotaxy: low (“*oligotriche*”), high (“*polytriche*”) and medium (“*mésotriche*”), and used the number of setae on the fifth segment of the metasoma as example of the ranges: low has three or fewer setae, high more than 5–6 setae and medium four setae, although this latter category was fluid. Confusion can further arise from the fact that these categories apply to the metasoma and the pedipalp, and in the same species these two body parts can have different ranges of chaetotaxy. Nevertheless, this is a useful trait, and one that needs to be explicitly stated in species descriptions to avoid misinterpretations. The chaetotaxy of the leg tarsi and mesosoma tergites is also useful.

Most other diagnostic traits in use for *Buthus* species are found in the metasoma and the pedipalp chela.

The length/width ratio of the **first metasomal** segment, which is typically square in most species but can be elongated or sturdy in certain species, is informative. This ratio is also applied to the **fifth metasomal** segment, and Vachon (1952a) further compared the ratios of the first and second segment, and sometimes even the third segment. The number of **keel rows** in the metasoma segments is also useful, with special attention paid to the presence, and in some cases the relative length (Vachon 1952a),

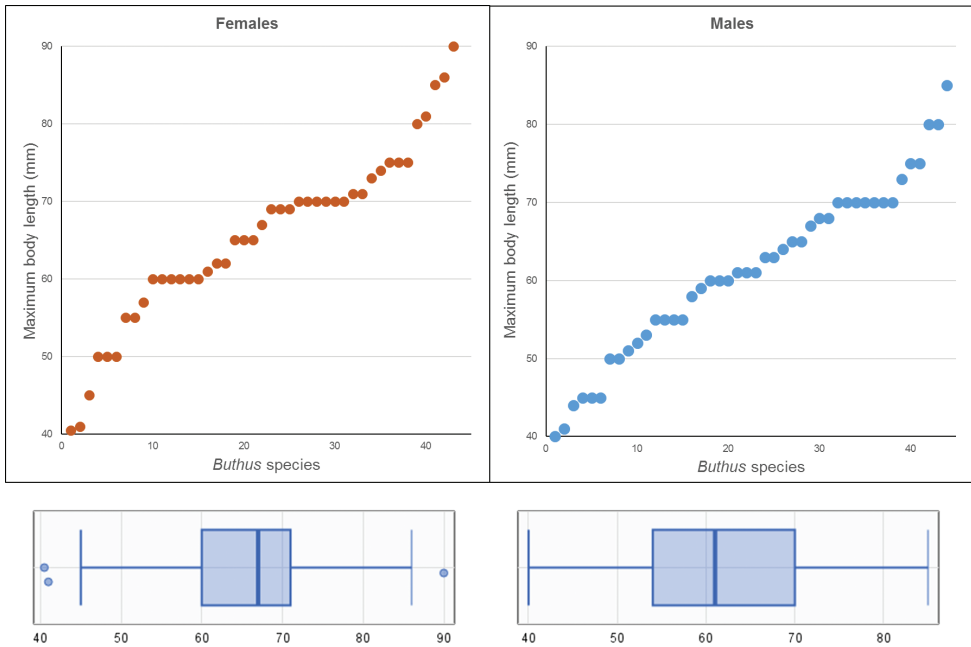


Figure 8. Chart and boxplot summary of *Buthus* species maximum sizes. Only the known maximum size per species is represented. Size information is only available for males from 44 species and females from 43 species. Some individual data might correspond to subadult specimens since this information is not always explicit in species descriptions.

of the median lateral keel in the second, third and fourth segments. Both the degree of development of the inferior median keels of the five segments (except perhaps the forth), and the existence of larger granules may also be used for taxonomic purposes. The number of lateral lobes in the **anal arch**, either two or three (the latter only in *B. atlantis* Pocock, 1889 and *B. lourencoi* Rossi, Tropea & Yagmur, 2013) may be misleading because in some species, or even specimens (Vachon 1952a), a third smaller lobe may be present between the two larger lobes, which has been interpreted as a third state (e.g. Sadine et al. 2015). For instance, Lourenço and Qi (2006) state that in *Buthus mariefranceae* Lourenço, 2003 the anal arch may sometimes have 3 lobes but this is mentioned neither in the original description nor in Vachon's descriptions. The relationship between the length of the aculeus and the length of the vesicle that form the **Telson** are also used in *Buthus* taxonomy. In most species, the aculeus is shorter than the vesicle, or as long as the vesicle at most. For a few species the aculeus is clearly shorter than the vesicle and for another handful of species, the aculeus is clearly longer. The states are defined here using a 10% difference threshold, but other authors have used a 5% difference. This ratio is correlated with the shape of the aculeus, also in use, which can be more or less curved.

species	range	08	09	10	11	12	13	14	species	range	08	09	10	11	12	13	14
<i>B. mariefranceae</i>	8-9								<i>B. albengai</i>	11-12							
<i>B. amri</i>	9-10								<i>B. aures</i>	11-12							
<i>B. brignolii</i>	9-10								<i>B. awashensis</i>	11-12							
<i>B. adrianae</i>	10								<i>B. centroafricanus</i>	11-12							
<i>B. egyptiensis</i>	10								<i>B. chambiensis</i>	11-12							
<i>B. intumescens</i>	10*								<i>B. draa</i>	11-12							
<i>B. orientalis</i>	10								<i>B. elhennawy</i>	11-12							
<i>B. trinacrius</i>	10								<i>B. hassanini</i>	11-12							
<i>B. yemenensis</i>	10								<i>B. lienhardi</i>	11-12							
<i>B. bonito</i>	10-11								<i>B. prudenti</i>	11-12							
<i>B. elmoutaouakili</i>	10-11								<i>B. pusillus</i>	11-12							
<i>B. jianxinae</i>	10-11								<i>B. tunetatus</i>	11-12							
<i>B. mardochei</i>	10-11								<i>B. ibericus</i> ^a	11-13							
<i>B. parroti</i>	10-11								<i>B. israelis</i>	11-13							
<i>B. rochati</i>	10-11								<i>B. paris</i> ^a	11-13							
<i>B. tassili</i>	10-11								<i>B. barcaeus</i>	12							
<i>B. atlantis</i>	10-12								<i>B. boumalenii</i>	12							
<i>B. malhommei</i>	10-12								<i>B. confluens</i>	12							
<i>B. tunetatus</i> ^a	10-12								<i>B. dunlopi</i>	12							
<i>B. berberensis</i>	11*								<i>B. elizabethae</i>	12							
<i>B. duprei</i>	11								<i>B. elongatus</i>	12							
<i>B. intermedius</i>	11*								<i>B. kunti</i>	12							
<i>B. karoraensis</i>	11								<i>B. labuschagnei</i>	12							
<i>B. lourencoi</i>	11								<i>B. occitanus</i>	12							
<i>B. montanus</i>	11								<i>B. ibericus</i> ^a	12-13							
<i>B. nigrovesiculosus</i>	11*								<i>B. maroccanus</i>	12-13							
<i>B. occidentalis</i>	11								<i>B. paris</i> ^a	12-14							
<i>B. saharicus</i>	11								<i>B. tunetatus</i> ^a	12-14							
species	range	08	09	10	11	12	13	14	species	range	08	09	10	11	12	13	14

Figure 9. Graphical representation of the variation in the number of rows in the movable finger of all *Buthus* species. ^a Species for which the bibliographic ranges are conflicting. * Number of rows in species identified by us from images of the type specimens may be underestimated.

The shape of the **pedipalp chelae** in *Buthus* taxonomy has gained increased usage in recent years. The shape can be approximated by using the length to width ratio of the chela, which reflects its specific robustness or slenderness. However, in many *Buthus* species the chela shape is sexually dimorphic, a trait that was first used in a species key by Kovařík (2006), although its use goes back at least to Vachon (1952a). As a measure of sexual dimorphism the pedipalp chelae has three possible states: 1) no sexual dimorphism (male = female); 2) slender chela in male (male > female); 3) chela of male more robust (male < female). There is data available for 29 species (56% of the known species), and from these we can estimate that 38% do not have sexual dimorphism (+/- 10% threshold as a cut-off point), 52% of species have males with slender chelae and only 3 species (10%) show males with more robust chelae (Fig. 11). Interestingly, although chelae play a role in mating, defense, and as a sensory organ (van der Meijden et al. 2012), their prime importance in prey capture and handling (Polis 1990) may limit the slendering of female chelae, as these may be more prone to breakage (van der Meijden et al. 2012). For three of the 39 species, the available chelae

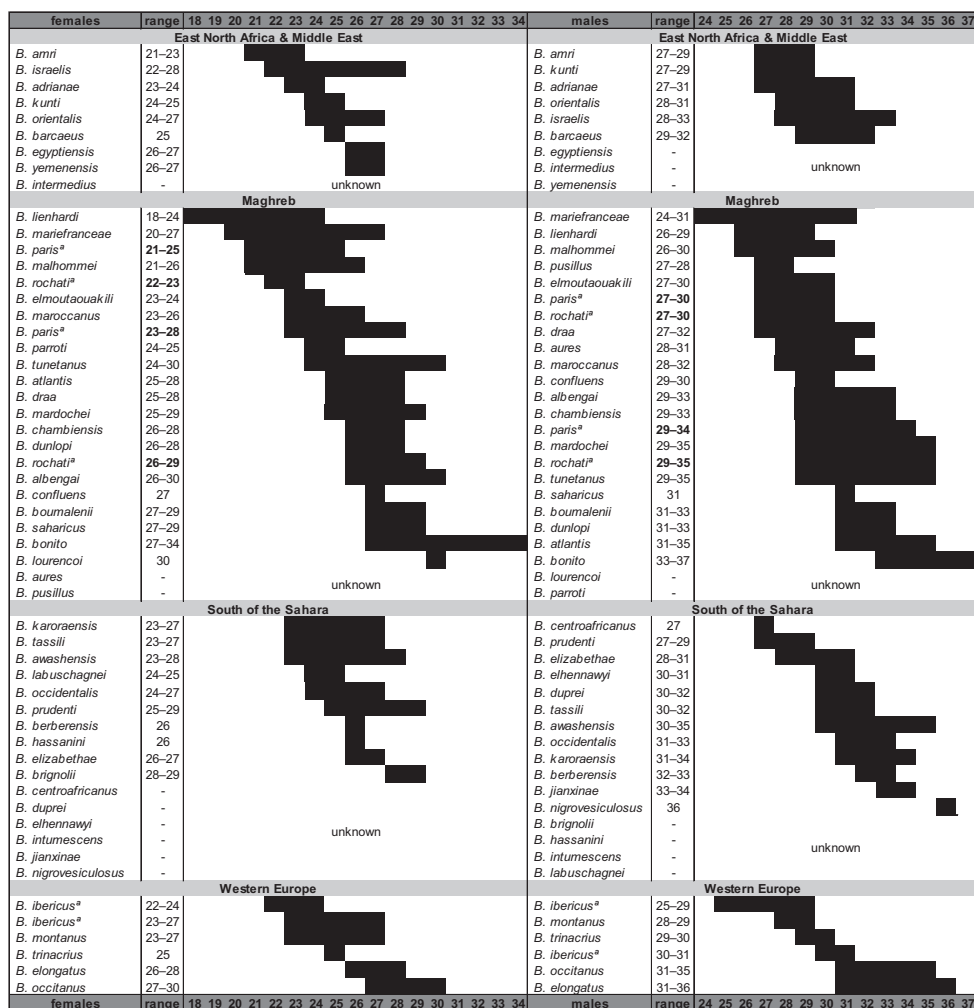


Figure 10. Graphical representation of the variation in pectinal teeth number of *Buthus* species arranged by geographical areas to facilitate comparison. All known *Buthus* species are represented, although female and male are ordered independently, from smaller to largest. ^a Species for which the bibliographic ranges are conflicting.

data was contradictory, and they are further discussed below. Another useful pedipalp trait is the interrupted dorso-median keel of the patella in *Buthus rochati* Lourenço, 2003 (Vachon 1952a).

Several partial keys have been published over the years to assist *Buthus* species identification. However, due to the high rate of new species description (Fig. 5), they have become incomplete and even outdated in their taxonomy (Birula 1903, Vachon 1952a, Lourenço 2003, Lourenço and Vachon 2004, Kovařík 2006, Rossi 2012, Rossi

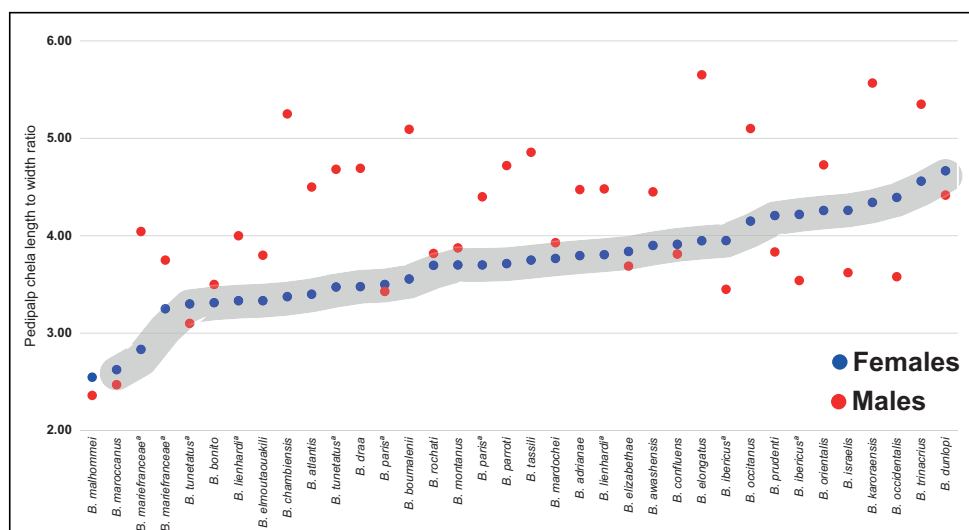


Figure 11. Graphical representation of the relation between female and male pedipalp chela aspect ratio in *Buthus* species. Only those species with available data from both sexes were plotted. The grey area represents species without perceived sexual dimorphism. Species with males above that area have slender pedipalp chela than females, while species with males plotted below have more robust pedipalp chela than females.

et al. 2013, Teruel and Melic 2015). There are keys available for Morocco and the Maghreb by Birula (1903, only four species), Vachon (1952a, ten species in the Moroccan *Buthus* key), Lourenço (2003, 10+1 species), and Kovařík (2006, Tunisia, four species); for North Africa (excluding Morocco) by Rossi et al. (2013, 13 species), and for the Iberian Peninsula by Lourenço and Vachon (2004), Rossi (2012), and Teruel and Melic (2015).

Unfortunately, the identification of the majority of *Buthus* species remains difficult, in part because of the limited number of diagnostic characters and the incomplete knowledge regarding their intraspecific variation. Sexual dimorphism of pedipalp chelae is a promising trait, but for many species the male or female is still undescribed, which limits its applicability. Authors are urged to mention the variation on all the traits mentioned here (see Rossi et al. 2013 for a nice example) in future *Buthus* species descriptions.

Confirming the fast pace of new *Buthus* species descriptions, a new species, *Buthus danyii* Rossi, 2017 was published from Ghana (Rossi 2017) while this study was under revision. As such we were unable to include this species in the present update.

It is hoped that the present catalogue will facilitate a more precise, informative and comparative description of future species. *Buthus* are an important component of the scorpions' fauna of North Africa and Western Europe, but it is only now becoming apparent that they are also diverse in the southern Sahara Desert, an area that should be prioritized in future surveys of *Buthus* scorpions.

Catalogue

Genus *Buthus* Leach, 1815

Buthus: Leach 1815: 391; Latreille 1817: 310; Gervais 1844b: 203; Peters 1861 (part): 513; Thorell 1876a (part): 82; Thorell 1876b: 7; Simon 1879: 95–96; Karsch 1886 (part): 77; Pocock 1890 (part): 122; Karsch 1891: 18; Kraepelin 1891 (part): 35–42; Pocock 1893 (part): 312; Kraepelin 1895 (part): 79–80; Laurie 1896b: 131; Lönnberg 1897b (part): 194; Kraepelin 1899 (part): 9; Pocock 1900a (part): 13; Simon 1910: 67–68; Birula 1917a (part): 20–24, 164; Birula 1917b (part): 55; Pavlovsky 1924 (part): 77; Kastner 1941 (part): 230; Vachon 1948a: 206–208; Vachon 1949a: 155–162; Vachon 1952a: 155, 241–246, fig. 579; Vachon 1963b: 164, fig. 10; Bücherl 1964: 57; Stahnke 1972: 132, fig. 20; Vachon 1974: 906; Levy and Amitai 1980: 14–15; Francke 1985: 6, 15; Sissom 1990: 101; Nenilin and Fet 1992: 17; Kovařík 1998: 106; Fet and Lowe 2000: 91; Lourenço 2016b: 3–4.

Type species (by original designation). *Scorpio occitanus* Amoreux, 1789 [= *Buthus occitanus* (Amoreux, 1789)].

Etymology. Leach did not provide an explanation for his selection of the genus name. A search on the original usage of the word may shed some light on the intended meaning. *Buthus* is the Latin form of the Greek name βοῦθος (*Bouthos*), an unusual name of a winning athlete of the ancient Pythian Games, mentioned by Hesychius and Aristotle (Müller 1848, Christesen 2007). The name was more familiar in antiquity when used in the adage “Βοῦθος περιποιτᾷ”, translated to the Latin as “*Buthus obambulat*”, which translates into “*Buthus* who wanders”, which apparently was applied to stupid and simple people (Müller 1848, Christesen 2007). In Hofmann et al. (1698) the entry for *Buthus* reads “*athleta nobilis, qui bovem integrum unô die devorare solebat; unde natum proverbium in edaces, Buthus obambulat*” which roughly translates to “a noble athlete, who used to devour a great ox in a day, and who gave rise to the proverb, *Buthus obambulat*”. Noël (1824) entry for *Buthus* also refers to an athlete that devoured an ox in a single day, and that this voracity was the origin of the proverb “*Buthus obambulat*”, which according to the author refers to gluttony. Interestingly Noël also states that *Buthus*, in combination with “βῶς, θύειν (*thuein*)”, also refers to sacrifice. This opinion shares roots with the meaning of two other words with similar etymology, *būthysīa* (used by Nero) that translates to “sacrifice of an ox” and *būthyētēs* (used by Pliny the Elder), that translates to a “sacrificed ox”, according to the Gaffiot Latin-French dictionary (Various 2016). Recently Dupré (2016) reached a similar conclusion, although he states that *Buthus* originates from the composition of the Greek word “Gr. *bous*, ox; - *thouéin* [Greek suffix?], killer”. Potentially therefore, *Buthus* refers to a stupid or voracious animal, an ox killer or to a sacrifice of an ox, from the latter two we can interpret it as a powerful and dangerous animal. In our opinion the later makes more sense and agrees well with what was known at the time about the potent venom of *Buthus* scorpions. As such, it is our opinion that *Buthus* is a singular masculine Latin word (of Greek origin), which Leach intended as homage

to an ancient hero (a trend at that time), and that refers to an animal so venomous that it could kill an ox.

Distribution. AFRICA: Algeria, Cameroon, Chad, Egypt, Eritrea, Ethiopia, Guinea, Ivory Coast, Libya, Mali, Mauritania, Morocco (including Western Sahara), Niger, Senegal, Somalia, South Sudan, Sudan, Tunisia. ?Guinea-Bissau, Nigeria, Burkina Faso, ?Gambia, Ghana, ?Djibouti. ASIA: Cyprus, Israel, Jordan, Yemen. ?Iraq, ?Lebanon, ?Saudi Arabia, ?Turkey. EUROPE: France, Italy (Sicily), Spain, Portugal. ?Malta, ?Greece (Corfu, Thessaly). All currently valid records of *Buthus* species per country are presented in Table 2. Figure 10 offers an additional zoom to the most diverse region of *Buthus* species diversity, the Maghreb.

Remarks. There are several old records of *Buthus*, marked with a question mark above, which have never been found again (independently of the material in which they were based being lost or not). As such, many have not been checked since the genus was reduced in scope by Vachon (1949), or those localities remain doubtful because no *Buthus* has been collected there since. This is of special significance in countries like Greece and Turkey that have been in recent years reasonably well prospected. Type specimens for several *Buthus* species described early on were not designated or have since become lost, but this does not necessarily represent a taxonomic problem. For example *B. occitanus* has no type specimen (Fet and Lowe 2000), but its type locality is well established and no other *Buthus* species occurs nearby. In this case the designation of a neotype is not justified under the ICZN (article 75.2). However, this is not the case for other species that have neither type specimens nor localities, and that we will further discuss below.

1. *Buthus adrianae* Rossi, 2013

Buthus adrianae: Rossi 2013: 188–191, fig. 1–2; Rossi, Tropea and Yağmur 2013: 3; 5, 8.

Type material. 1 adult M holotype (MCSNB N° 14011), El-Hamam (30.8300°, 29.3150°), Alexandria, Egypt. Paratypes: 1 adult M and 1 adult F (ARPC), same locality.

Distribution. known only from the type locality.

2. *Buthus albengai* Lourenço, 2003

Buthus albengai: Lourenço 2003: 902–904, fig. 70–74; Lourenço and Geniez 2005: 5; Aboumaâd et al. 2014: 6; Touloun et al. 2014: 76; Lourenço 2016b: fig. 3.

Type material. 1 F holotype (MHNG), Ito Plateau (approx. 33.51°, -5.3°), Ifrane, Morocco. Paratypes: 3 F, same locality; 2 juv., Ifrane (Cedars woods); 1 M, 1 F juv., region north of Kenifra (all in MHNG).

Distribution. known from an area in Morocco that extends from ifrane to Kenifra.

Remarks. It is one of the largest known *Buthus* species. Records by Habel et al. (2012) south of the High-Atlas are most likely misidentifications.

ID	Taxa	France	Italy	Portugal	Spain	Algeria	Cameroon	C.A.R.	Chad	Djibouti	Egypt	Eritrea	Ethiopia	Guinea	Lybia	Mauritania	Morocco	Niger	Senegal	Somalia	S. Sudan	Sudan	Tunisia	Cyprus	Israel	Jordan	Yemen	Total (by taxa)
27	<i>B. isradis</i>										X ¹										X							2
28	<i>B. janssinae</i>											X																1
29	<i>B. karoraensis</i>																											1
30	<i>B. kuniti</i>																						X					1
31	<i>B. labuschagnei</i>								X																			1
32	<i>B. lienhardi</i>																X											1
33	<i>B. lourençoi</i>																											1
34	<i>B. malhommei</i>														X		X											1
35	<i>B. mardochei</i>																X											1
36	<i>B. mariefraunceae</i>																X											1
37	<i>B. maroccanus</i>																X											1
38	<i>B. montanus</i>				X																							1
39	<i>B. nigrovesciculosus</i>																X ²											1
40	<i>B. occidentalis</i>															X												1
41	<i>B. octianus</i>	X																										2
42	<i>B. orientalis</i>										X																	1
43	<i>B. paris</i>					X											X						X					3
44	<i>B. parroti</i>																X											1
45	<i>B. prudenti</i>						X																					1
46	<i>B. pusillus</i>					X																						1
47	<i>B. rochati</i>																X											1
48	<i>B. sahariensis</i>					X																						1
49	<i>B. tassili</i>					X									X													2
50	<i>B. trinactius</i>		X ³																									1
51	<i>B. tunicatus</i>					X									X		X						X					4
52	<i>B. yemenensis</i>																									X		1
Total (by country)		1	1	1	4	6	1	1	2	1	5	1	2	1	4	1	17	1	2	1	1	2	4	1	1	1	2	

¹ Sinai; ² Western Sahara; ³ Sicily

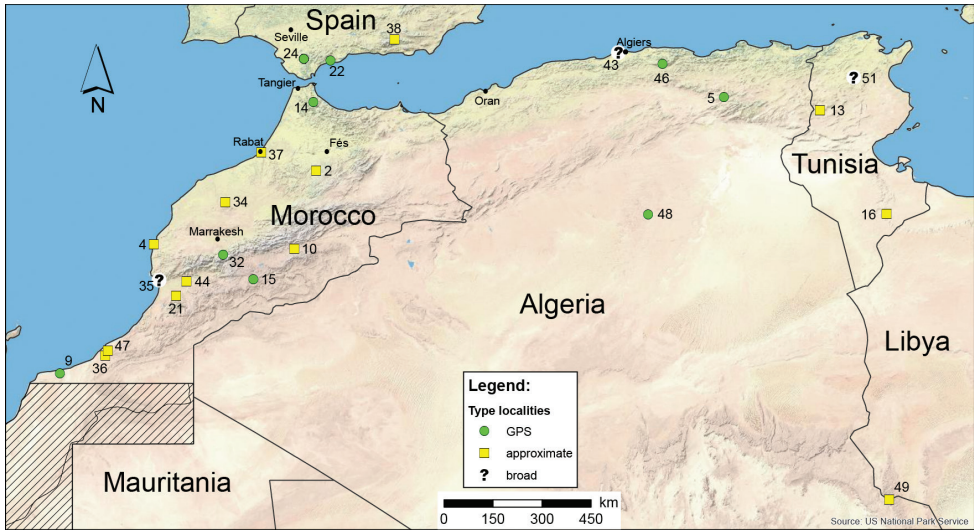


Figure 12. Map of North Africa Maghrebian *Buthus* species' type localities (numbers according to the Catalogue and Table 2) whenever known or the best possible approximation at present.

3. *Buthus amri* Lourenço, Yağmur & Duhem, 2010

Buthus amri: Lourenço, Yağmur and Duhem 2010: 96–99, fig. 1–5; Lourenço 2013: 65; Lourenço and Rossi 2013: 9; Amr 2015: 186.

Type material. 1 M holotype (MNHN), Wadi Rum Desert (29.5363°, 35.4136°), Aqaba, Jordan. Paratypes: 1 adult F (MNHN), 2 adult F, 1 subadult F, 2 subadult M, 3 juv. (MTAS), all from the same locality.

Distribution. known only from the type locality.

4. *Buthus atlantis* Pocock, 1889

= *Tityus tenuimanus* Banks 1910: 189 (synonymized by Lourenço and Francke 1984: 428). 1 F holotype (MCZ), Buena Vista Lake, California, USA (incorrect locality).

Buthus atlantis: Pocock 1889b: 340–341, pl. XV, fig. 4; Birula 1896: 244; Kraepelin 1891: 197, 199; Birula 1903: 107–108; Werner 1932: 300–305; Vachon 1949a: 162–169, fig. 345, 347, 349, 351, 354, 355, 357–362; Vachon 1952a: 254–255, fig. 345, 347, 349, 351, 354, 355, 357–362; Malhomme 1954: 25; Bücherl 1964: 57; Pérez 1974: 22; Levy and Amitai 1980: 15; El-Hennawy 1992: 98, 119; Kovařík 1998: 106; Fet and Lowe 2000: 91; Lourenço 2005a: 233–234; Lourenço and Geniez 2005: 5; Stockmann and Ythier 2010: 360–361; Stockmann 2015: fig. 5.

Buthus Atlantis (sic): Aboumaâd et al. 2014: 5.

Buthus atlantis atlantis: Vachon 1949a: 166–168; Vachon 1952a: 252, 254; Le Corroller 1967: 63; Kovařík 1995: 20; Fet and Lowe 2000: 91; Lourenço 2003: 883–885, fig. 18–22; Touloun et al. 2001: 2; Gantenbein and Largiadèr 2003: 120, 122; Touloun 2012: 43, fig. 9A.

Buthus occitanus atlantis: Kraepelin 1899: 26–27; Werner 1934b: 86–87, fig. 5; Schenkel 1949: 186–187.

Buthus (Buthus) atlantis: Birula 1910: 145; Birula 1917a: 213, 223.

Tityus tenuimanus: Cox 1921: 12; Ewing 1928: 22; Mello-Leitão 1931: 121, 140; Mello-Leitão 1939: 60, 64, 71; Comstock 1940: 27; Mello-Leitão 1945: 308; Gertsch and Sologlad 1966: 2; Hjelle 1972: 28; Lourenço and Francke 1984: 427, fig. 10–12.

Type material. 1 F holotype (NHMUK), Essaouira (formerly Mogador) (approx. 31.49°, -9.76°), Morocco.

Distribution. known to occur only in sandy dune habitats close to the Atlantic Ocean in Morocco, between Essaouira and Agadir.

Remarks. It is the largest known *Buthus* species.

5. *Buthus aures* Lourenço & Sadine, 2016

Buthus aures Lourenço and Sadine 2016: 14–17, fig. 4–13.

Type material. 1 M holotype (MNHN), Batna region (35.5319°, 5.9194°), Aurès Mountains, Algeria. 1 M paratype (UGA), same locality.

Distribution. known only from the type locality.

6. *Buthus awashensis* Kovařík, 2011

Buthus awashensis: Kovařík 2011: 1–3, 5–8, fig. 5–16.

Buthus occitanus (MIS): Kovařík and Whitman 2005 (part): 106.

Type material. 1 M holotype (FKCP), Metahara (approx. 8.900°, 39.900°), Oromia, Ethiopia. Paratypes: 34 M, 34 F, 36 juv. (FKCP), all from the same locality; 1 M (FKCP), Dire Dawa, Ethiopia.

Distribution. known only from two Ethiopian localities, more than 200 km apart.

Remarks. The pedipalp chela length-to-width ratio given by the author for the type material suggest that some animals exhibit sexual dimorphism while others do not. If this is true, the utility of this ratio as a diagnostic character in *Buthus* would be compromised. Alternatively, it may be due simply to the use of immature specimens.

7. *Buthus barcaeus* Birula, 1909

Buthus occitanus barcaeus: Birula 1909: 508–511. fig. A, C; Borelli 1914a: 155–156; Borelli 1924: 5–7; Borelli 1928: 351; Caporiacco 1932: 395; Borelli 1934: 169; Caporiacco 1937: 345; Pérez 1974: 23; Levy and Amitai 1980: 16; El-Hennawy 1992: 98, 120; Kovařík 1998: 106; Fet and Lowe 2000: 95; Kovařík 2002: 5.

Buthus (Buthus) occitanus barcaeus: Birula 1910: 156; Birula 1917a: 223.

Buthus barcaeus: Kovařík 2006: 3, fig. 6; Kaltsas et al. 2008: 215; Lourenço and Cloudsley-Thompson 2012: 15; Lourenço and Simon 2012: 11; Rossi, Tropea and Yağmur 2013: 3–5, 7.

Type material. 4 M, 1 F juv., syntypes (ZIN), Barca (approx. 32.48°, 20.83°), 5 km E from Benghazi (Cyrenaica), Libya.

Distribution. known from several localities along the Mediterranean coast of Libya.

Remarks. The specimens present in the MNHN (F n° 4896), captured in Barca and identified by Vachon in 1974, have no intermediary keel on the fourth metasomal segment, which casts doubts about the use of the character in the diagnosis of *B. barcaeus*.

8. *Buthus berberensis* Pocock, 1900

= *Buthus occitanus zeylensis* Pocock 1900b: 56–57 (synonymized by Levy and Amitai 1980: 16). 1 F holotype (NHMUK), Zeyla (northwestern Somaliland), Somalia.

Buthus occitanus berberensis: Birula 1903: 106–107; Birula 1909: 510; Birula 1910: 118; Kraepelin 1903: 558; Borelli 1904: 2–3; Giltay 1929: 196; Moriggi 1941: 84; Lamoral and Reynders 1975: 505; Levy and Amitai 1980: 16; El-Hennawy 1992: 98, 120; Kovařík 1998: 106; Fet and Lowe 2000: 95; Kovařík 2003 (part): 138.

Buthus occitanus zeylensis: Kraepelin 1903: 558–559; Borelli 1919: 363; Borelli 1931: 218; Caporiacco 1936: 137; Moriggi 1941: 84; Lamoral and Reynders 1975: 505–506; El-Hennawy 1992: 98, 121–122; Kovařík 1998: 106.

Buthus berberensis: Lourenço 2008: 46; Kovařík 2011: 4–6.

Buthus (Buthus) occitanus berberensis: Birula 1917a: 123.

Type material. 1 M holotype (NHMUK), Somaliland, Somalia.

Distribution. known from Djibouti, Eritrea, Ethiopia and Somalia, although Birula (1903) recorded toponyms that are old and difficult to map.

Remarks. Lourenço (2008) stated that *B. o. zeylensis* might be a distinct species from *B. berberensis*, but that further material was required to confirm this possibility. Kovařík (2011) considered *B. o. zeylensis* a colour morph of *B. berberensis* present in juveniles and some males.

9. *Buthus bonito* Lourenço & Geniez, 2005

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8669>

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8670>

= *Buthus sabulicola* Touloun 2012: 46, 48–58, fig.10, 13, 14 (**Syn. n.**). 1 F holotype (MNHN), Khnifiss lagoon, Tan-Tan Province, Morocco.

Buthus bonito: Lourenço and Geniez 2005: 1–5, fig. 1–8, 10; Touloun et al. 2008: 3–4, fig.1; Stockmann and Ythier 2010: 362–363; Pedroso et al. 2013: 300; Aboumaâd et al. 2014: 6; Touloun et al. 2016: 880, fig. 2D.

Type material. 1 M holotype (MNHN N° RS8669), Khnifiss lagoon (approx. 27.93°, -12.34°), Tarfaya, Morocco. Paratypes: 2 F (MNHN N° RS8670), from the same locality.

Distribution. known from the Atlantic coast of Morocco south of Tan-Tan extending almost to Dakhla in the Western Sahara (Touloun et al. 2016).

Remarks. Although the type material of *B. sabulicola* was collected in 2002 by Touloun, Stockmann and Slimani, the species was not formally described until the publication of the PhD thesis of Oulaid Touloun in 2012. The type specimens of *B. bonito* and *B. sabulicola* are from the exact same locality, the Khnifiss lagoon, and both descriptions are almost identical. Touloun et al. (2016), probably by mistake, indicated that the fifth metasomal segment and telson are darkened in *B. bonito*, but the trait does not appear in the accompanying figure.

10. *Buthus boumalenii* Touloun & Boumezzough, 2011

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8891>

Buthus boumalenii: Touloun and Boumezzough 2011a: 183–186, fig. 2–7; Pedroso et al. 2013: 300; Aboumaâd et al. 2014: 6; El Hidan et al. 2016: 4.

Type material. 1 F holotype (UCAM), Tineghir (approx. 31.366°, -5.905°), Boumalene, Morocco. Paratypes: 1 M (UCAM), 1 M, 1 F (MNHN, N° RS8891), all from the same locality.

Distribution. known only from the Boumalne region of Morocco (El Hidan et al. 2016).

Remarks. This species is the only known representative of a phylogenetic lineage present east of the High Atlas Mountains of Morocco. Because of its phylogenetic uniqueness, the conservation of this species should have top priority.

11. *Buthus brignolii* Lourenço, 2003

Buthus brignolii: Lourenço 2003: 905–907, fig. 75–79; Rossi and Tropea 2016a: 4.

Type material. 1 F holotype (MHNG), Djebel Meidob (approx. 15.21°, 26.44°), Darfur, Sudan.

Distribution. known only from the type locality.

Remarks. it is one of the four known “inland island” species of *Buthus* that have been found in the Mountainous regions in the heart of the Sahara Desert.

12. *Buthus centroafricanus* Lourenço, 2016

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs9069>

Buthus centroafricanus: Lourenço 2016a: 73–77, fig. 1–11.

Type material. 1 M holotype (MNHN), Between Bria and Yalinga (as Jalinga) (approx. 6.52°, 22.62°), Province Haute-Kotto, Central African Republic.

Distribution. known only from the type locality.

13. *Buthus chambiensis* Kovařík, 2006

Buthus chambiensis: Kovařík 2006: 1–3, fig. 2–5; Rossi, Tropea and Yağmur 2013: 3, 7.

Type material. 1 M holotype (FKCP), Djebel Chambi Mountain (approx. 35.17°, 8.56°), Kasserine Province, Tunisia. Paratypes: 1 M juv., 2 F, 1 juv., all from the same locality.

Distribution. known only from the type locality.

14. *Buthus confluens* Lourenço, Touloun & Boumezzough, 2012

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8919>

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8920>

Buthus confluens: Lourenço, Touloun and Boumezzough 2012: 22–24, fig. 1–11; Touloun et al. 2014: 76–77.

Type material. 1 M holotype (MNHN N° RS8919), Alhamra (35.39529°, -05.37181°), Tétouan, Morocco. Paratypes: 1 F (MNHN N° RS8920), 1 M (UCAM), all from the same locality.

Distribution. known from several localities in the Tingitana Pensinsula of Morocco, but also further to the south.

Remarks. Based on the colour pattern and pigmentation, the original authors suggested that *B. confluens* was the closest phylogenetic relative in Morocco to *B. ibericus*, from the Iberian Peninsula. However, because the presence of three dark bands on the metasoma is shared among several *Buthus* species, this claim should be further confirmed with additional data.

15. *Buthus draa* Lourenço & Slimani, 2004

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8694>

Buthus draa: Lourenço and Slimani 2004: 166–169, fig. 1–7; Lourenço, Sun and Zhu 2009: p. 72, fig. 2–6; Stockmann and Ythier 2010: 362–363; Touloun and Boumezzough 2011b: 186; Habel et al. 2012: 2, 4; Sousa et al. 2012: 68–69; Pedroso et al. 2013: 300; Yang et al. 2013: 2; Aboumaâd et al. 2014: 6; El Hidan et al. 2016: 4.

Buthus occitanus tunetanus neeli (MIS): Touloun et al. 1999: 1–2.

Buthus tassili (MIS): Touloun 2012: 37, 40–41, fig. 7.

Type material. 1 M holotype (UCAM), Taznakht (30.51853°, -7.02595°), Ouarzazate, Morocco. Paratypes: 1 M, 2 F (UCAM), 1 M, 1 F (ZMH), 2 M, 1 F (MNHN), all from the same locality; 1 M (ZMH), Aït Bassou; 2 F juv. (ZMH), Aït Ounzar Oulad Aissa; 1 M (ZMH), near Agdez; 1 M (ZMH), Oulad Hlal. The ZMH accession number for all paratypes is A7/03.

Distribution. *B. draa* can be found in the upper part of the Draa River, probably at elevations below 1500 m a.s.l.

Remarks. *B. draa* shares with *B. tassili* and *B. nigrovesiculosus* the presence of a darkened fifth metasoma segment and telson.

16. *Buthus dunlopi* Kovařík, 2006

Buthus dunlopi: Kovařík 2006: 2–3, 6, fig. 7–8; Rossi, Tropea and Yağmur 2013: 5, 7.

Type material. 1 M holotype (FKCP), Remada (approx. 32.31°, 10.39°), Tataouine, Tunisia. Paratypes: 1 M, 3 F (FKCP), same locality.

Distribution. known only from the type locality.

17. *Buthus duprei* Rossi & Tropea, 2016

<http://zoobank.org/86EDFE2D-B287-4DCD-BD37-8B99FC58915C>

Buthus duprei Rossi and Tropea 2016b: 25–28, fig. 1–12.

Type material. 1 M holotype (MCVR), Port Sudan (approx. 19.59°, 37.19°), Sudan. Paratype: 1 M juv. (ARPC N° 0809), same locality.

Distribution. known only from the type locality.

18. *Buthus egyptiensis* Lourenço, 2012

Buthus egyptiensis: Lourenço and Cloudsley-Thompson 2012: 12–16, fig. 1–7; Lourenço and Simon 2012: 12; Rossi 2013: 191–192; Rossi, Tropea and Yağmur 2013: 4, 7.

Type material. 1 F holotype (ZMH N° A20/12), Siwa (approx. 29.17°, 25.46°), Egypt.

Distribution. known only from the type locality.

Remarks. One of the four known “inland island” species of *Buthus* that have been found within the Sahara Desert, although in this case from an Oasis. It is also one of the largest known *Buthus* species.

19. *Buthus elhennawy* Lourenço, 2005

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8637>

Buthus elhennawy: Lourenço 2005b: 246–249, fig. 1–7; Lourenço and Leguin 2012: 8.

Type material. 1 M holotype (ZMH N° A42/05), Fété-Olé (as Félé-Olé) (16.233°, -15.099°), Ferlo, Senegal. Paratype: 1 M (MNHN N° RS8637), Rosi (as Rossi), Niger.

Distribution. this species is known from Niger and Senegal, from a single locality in each country, which are almost 2,000 Km apart.

Remarks. We used the location of Fété-Olé given in Vincke et al. (2010), a locality that has been part of long term ecological studies, to map this locality, instead of the original spelling “Félé-Olé”.

20. *Buthus elizabethae* Lourenço, 2005

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8638>

Buthus elizabethae: Lourenço 2005a: 230–235, fig. 1–12, Lourenço 2005b: 249.

Type material. 1 M holotype (ZMH N° A36/05), S.W. of Gaoual (approx. 11.71°, -13.22°), Boké, Guinea. Paratypes: 1 F (ZMH N° A37/05), same locality; 1 M, 1 F (MNHN), Niokolo-Koba National Park, Senegal.

Distribution. this species is known from Guinea and Senegal,

Remarks. Given the geographical proximity, it is possible that the *Buthus* material reported to have been found in Guinea-Bissau might very well correspond to this species. Unfortunately the Guinea-Bissau material was lost in a fire, and hence only newly collected material could confirm this possibility.

21. *Buthus elmoutaouakili* Lourenço & Qi, 2006

Buthus elmoutaouakili: Lourenço and Qi 2006: 288–291, fig. 1–11; Habel et al. 2012 (part): 2, 3; Husemann et al. 2012 (part): 2, 4–5; Touloun and Boumezzough 2011b: 11–12, fig. 2C; Aboumaâd et al. 2014: 6.

Buthus occitanus mardochei alluaudi: Vachon 1949c: 363–367, fig. 409–416; Vachon 1952a: 291–295, fig. 409–416; Le Corroller 1967: 63; Pérez 1974: 23; Touloun 2012: 39, 57.

Type material. 1 M holotype (ZMH N° A18/06), Ait Baha (approx. 30.07°, -9.15°), Chtouka Aït Baha, Morocco.

Distribution. this species seems to be widely distributed across the western portion of the Anti-Atlas, although some misidentifications with *Buthus parroti* cannot be excluded.

Remarks. According to ICZN article 45.5, Vachon's (1949) infrasubspecific name is unavailable. Although the name was published before 1961, it was only used as infrasubspecific by all subsequent authors.

22. *Buthus elongatus* Rossi, 2012

Buthus elongatus: Rossi 2012: 273–278, fig. 1–6; Teruel and Melic 2015: 5–9.

Type material. 1 adult M holotype (MZUF N° 1432), Sierra Blanca (36.533°, -4.900°), Marbella, Malaga Province, Spain. Paratypes: 1 adult F (ARPC), same locality; 1 M, 1 F (MZUF N° 875), Playa del Alicate (36.499°, -4.818), Marbella, Malaga Province, Spain.

Distribution. this species is known from the southern Iberian Mediterranean coast, close to Marbella.

Remarks. The second locality given by Rossi as Alicante (sic), had a typographic error, as the coordinates given by the author, together with their map in Fig. 7, provide sufficient evidence for the correct mapping of this locality. Both localities are under severe anthropomorphic pressure.

23. *Buthus hassanini* Lourenço, Duhem & Cloudsley-Thompson, 2012

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8927>

Buthus hassanini: Lourenço et al. 2012: 319–321, 323, fig. 35–42.

Type material. 1 F (MNHN N° RS8927), Biti Tehëc (approx. 17.187°, 22.288°), Ennedi Plateau, Chad.

Distribution. known only from the type locality.

Remarks. Another of the four known “inland island” species of *Buthus* that have been found in a Mountainous region in the heart of the Sahara Desert. The type locality was pinpointed following the map provided by the authors (fig. 90).

24. *Buthus ibericus* Lourenço & Vachon, 2004, *nomen protectum*

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8605>

= *Buthus halius* (C. L. Koch, 1839) (*nomen oblitum*) (**comb. n., syn. n.**). Holotype lost according to Fet and Lowe (2000), Portugal.

Buthus ibericus Lourenço & Vachon, 2004: 88–91, fig. 31–42, Fernández 2004: 222; Teruel and Pérez-Bote 2005: 273–276, fig. 1; Armas and González-Moliné 2009: 553–554; Fet 2010: 4; Sousa et al. 2010: 207; Rossi 2012: 274–275, 277–278; Pedroso et al. 2013: 300; Teruel and Melic 2015: 6–9.

Androctonus halius C. L. Koch 1839a: 69–70, pl.CLXIII, fig. 383; Gervais 1844a: 43; C. L. Koch 1850: 90; Simon 1879: 96.

Buthus occitanus (MIS): Berejano and Pérez-Bote 2002: 59.

Type material. 1 M holotype (MNHN N° RS8605), San José del Valle (36.6247°, -5.6646°), Cádiz, Spain. Paratypes: 2 F (MNHN, N° RS8654), 1 M, 2 F (CRBA, N° CRBA-21826), and 2 F (MNCN N° 20.02/14857), all from the same locality.

Distribution. this species seems to have a wide distribution range in the western part of the Iberian Peninsula, although the limits of its distribution remain poorly defined.

Remarks. *B. ibericus* was first described from Spain and subsequently reported for Portugal (e.g. Sousa et al. 2010, Rossi 2012). Simon (1879) synonymized *Androctonus halius* with *B. occitanus* based on its type locality, which was wrongly stated to be Spain (page 98), because Simon considered *B. occitanus* (as *B. europaeus*) to be the only good species in Spain. Koch’s original description is not by itself enough to synonymize both species. However, Koch’s fig. 383 illustration of *Androctonus halius* includes a basal lobe in the movable finger (Fig. 13a and B), which is the key diagnostic character for *B. ibericus* (Lourenço and Vachon 2004, Rossi 2012), together with its type locality (Portugal), supports this synonymy. Nonetheless, according to the I.C.Z.N. article 23.9, the junior synonym can remain valid to maintain taxonomic stability. To our knowledge the name *B. halius* has not been used since 1879 (article 23.9.1.1), and more than 25 works have been published in the past 12 years by more than 10 authors using the name *B. ibericus* (article 23.9.1.2). Not all works are cited here because they are neither taxonomic nor faunistic. As such we propose to maintain as valid the junior synonym *B. ibericus* (*nomen protectum*) according to prevailing usage (article 23.9.1), and to consider the senior synonym *B. halius* a *nomen oblitum*. Rossi, 2012 (page 278), for *B. ibericus*, states erroneously “Sexual dimorphism is not noticeable in the chela manus”, which is in contrast to the original descriptions of both Koch (1839) and Lourenço and Vachon (2004) and to the complementary description in Teruel and Pérez-Bote (2005). In both works it can be observed that the male manus is more bulbous than the female’s, which results



Figure 13. Reproduction of C. L. Koch's 1839 *B. halius* figure 382 (plate CLXIII). Right pedipalp chelae detail from three *Buthus* species published in the same work: **A** *B. paris* (as *Androctonus clytoneus*), fig. 384 (same plate) **B** *B. halius* with an arrow pinpointing the basal lobe **C** *B. paris*, fig. 352 (pl. CLI). All images were taken as provided by the pdf copy available in the BHL, which was made available by the Ernst Mayr Library of the Museum of Comparative Zoology, Harvard University.

in the males having a smaller length to width ratio. The type locality of *B. ibericus* was precisely located following the indications of Íñigo Sánchez, the original collector.

25. *Buthus intermedius* (Ehrenberg in Hemprich & Ehrenberg, 1829)

<http://www.systax.org/en/details/spm/88132>

Androctonus (Leirus) tunetanus intermedius: Ehrenberg in Hemprich & Ehrenberg, 1829: 354; Braunwalder and Fet 1998: 33–34.

Androctonus (Leiurus) tunetanus intumescens (MIS): Kovařík 2006: 10.

Androctonus (Liurus) tunetanus intermedius: Ehrenberg in Hemprich & Ehrenberg, 1831: (pages not numbered).

Androctonus occitanus intermedius: Gervais 1844a: 42.

Buthus (Buthus) occitanus intermedius: Birula 1917a: 228.

Buthus occitanus intermedius: Pérez 1974: 23.

Buthus intermedius (Ehrenberg): Lourenço 2008: 46–47.

Type material. 1 F (in bad conditions) (ZMB N° 146), Al Luhayyah (as Lohaie), Yemen.

Distribution. Known only from the type locality.

Remarks. Fet and Lowe (2000) considered the locality as probably wrong since at that time no other *Buthus* had been collected again in Yemen. However, Lourenço's (2008) *Buthus yemenensis* revalidated Ehrenberg species' by providing concrete proof

for the existence of *Buthus* species in this country. Doubts about *B. intermedius* type locality were the only evidence given by Kovařík (2006) for its synonymization with *Buthus intumescens* (Ehrenberg in Hemprich & Ehrenberg, 1829).

26. *Buthus intumescens* (Ehrenberg in Hemprich & Ehrenberg, 1829)

<http://www.systax.org/en/details/spm/88133>

Androctonus (Leiurus) tunetanus intumescens: Ehrenberg in Hemprich and Ehrenberg 1829: 354; Braunwalder and Fet 1998: 33.

Androctonus (Liurus) tunetanus intumescens: Ehrenberg in Hemprich and Ehrenberg 1831 (pages not numbered); Moritz and Fischer 1980: 316.

Androctonus occitanus intumescens: Gervais 1844a: 42.

Buthus intumescens: Kovařík 2006 (part): 10–11, 15, fig. 20; Kaltsas et al. 2008 (part): 215; Rossi 2013: 191–192; Rossi, Tropea and Yağmur 2013: 3, 6–8.

Type material. 1 (sex unknown) (in bad conditions) (ZMB N° 145), Egypt.

Remarks. known only from a single specimen.

27. *Buthus israelis* Shulov & Amitai, 1959

Buthus occitanus mardochei israelis: Shulov and Amitai 1959: 219–225, fig. 1–3.

Buthus occitanus israelis: Pérez 1974: 23; Vachon and Kinzelbach 1987: 101; Fet and Lowe 2000: 95; Skutelsky 1995: 46; Skutelsky 1996: 50

Buthus occitanus israelis (Shulov & Amitai, 1959): Levy and Amitai 1980: 16–21, fig. 25–29; El-Hennawy 1992: 101, 120; Kovařík 2006: 10; Lourenço, Yağmur and Duhem 2010: 96.

Buthus intumescens (MIS): Kovařík 2006 (part): 10–11.

Buthus israelis: Lourenço, Yağmur and Duhem 2010: 96–97; Yağmur, Koç and Lourenço 2011: 29.

Buthus israelis (Shulov & Amitai, 1959): Rossi 2013: 191–192; Rossi, Tropea and Yağmur 2013: 2–3, 6–7.

Buthus occitanus mardochei israelis: Vachon 1966: 211; Kovařík 2006: 10; Lourenço, Yağmur and Duhem 2010: 95.

Buthus occitanus typicus: Bodenheimer 1937: 235.

Type material. holotype lost (sex unknown), Mash'abbe Sade (as Mashavei Sadé) (approx. 31°, 34.78°), Negev desert, Israel.

Distribution. This species has been recorded in Egypt (the Sinai Peninsula) and Israel. Notwithstanding, Kovařík (2006) considered this species to be a junior synonym of *B. intumescens*.

Remarks. Levy and Amitai (1980) did not designate any neotype when they re-described the species. In contrast to the several infrasubspecific taxa described by Vachon that are unavailable according to the ICZN, *B. o. israelis* is an available name according to the ICZN article 45.6.4.1 (“a name that is infrasubspecific under Article 45.6.4 is nevertheless deemed to be subspecific from its original publication if, before 1985, it was either adopted as the valid name of a species or subspecies or was treated as a senior homonym”), which is the present case as Levy and Amitai redescribed this taxon before 1985, and thus articles 45.5 and 45.5.1 do not apply. Several authors wrongly report the original authors of the species in parenthesis. The use of parenthesis is only to be made when a species is changed from one genus to another (ICZN article 51.3), which is clearly not the case with *B. israelis*.

28. *Buthus jianxinae* Lourenço, 2005

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8175>

Buthus jianxinae: Lourenço 2005c: 22–23, fig. 1–12.

Type material. 1 M holotype (MNHN N° RS8175), Loka (approx. 4.21°, 30.91°), Equatoria, South Sudan.

Distribution. known only from the type locality.

29. *Buthus karoraensis* Rossi & Tropea, 2016

<http://zoobank.org/9EA2BC5A-9E0B-4457-8E32-EA3C3FAA0A74>

Buthus karoraensis: Rossi and Tropea 2016a: 4–7, fig. 1–13; Rossi and Tropea 2016b: 25.

Buthus occitanus berberensis (MIS): Kovařík 2003 (part): 138.

Buthus occitanus (MIS): Kovařík and Whitman 2005 (part): 106.

Type material. 1 M holotype (MZUF N° 610), Karora (17.703°, 38.365°) (small enclave in the Eritrean-Sudan border), Eritrea. Paratypes: 1 M, 4 F (MZUF N° 610); 1 M (MCSNB: N° 12749), 1 F (MCSNB: N° 12748), all from the same locality.

Distribution. known only from the type locality.

30. *Buthus kunti* Yağmur, Koç & Lourenço, 2011

<http://zoobank.org/96DA8302-0891-4EF8-8D5B-DA8275325908>

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8892>

Buthus kunti: Yağmur, Koç and Lourenço 2011: 29–33, fig. 1–12.

Buthus europaeus (MIS): Simon 1879: 97.

Buthus occitanus (MIS): Kraepelin 1891 (part): 199.

Buthus sp.: Levy and Amitai 1980: 21.

Type material. 1 F holotype (MTAS), Rizokarpaso (Dipkarpaz) (35.58472°, 34.42306°), Karpaz Region, Cyprus. Paratypes: 1 M juv. (MTAS), Zafer. 1 M juv. (MNHN N° RS8892), Güzelyurt.

Distribution. the species is only known from the northern portion of Cyprus.

Remarks. according to Yağmur, Koç and Lourenço (2011), this species is rare in the island.

31. *Buthus labuschagnei* Lourenço, 2015

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8992>

Buthus labuschagnei Lourenço 2015: 22–24, fig. 13–22.

Type material. 1 F holotype (MNHN N° RS8992), Zakouma (Zakouma National Park) (approx. 10.89°, 19.82°), Salamat Region, Chad.

Distribution. known only from the type locality.

32. *Buthus lienhardi* Lourenço, 2003

Buthus lienhardi: Lourenço 2003: 899–902, fig. 62–69; Stockmann and Ythier 2010: 362–363; Touloun and Boumezzough 2011a: 186; Touloun 2012: 37, fig. 5C; Aboumaâd et al. 2014: 6.

Buthus occitanus tunetatus Lepineyi: Vachon 1949: 353–359, fig. 393–400; Vachon 1952a: 281–286, fig. 393–400;

Buthus occitanus tunetatus lepineyi: Malhomme 1954: 29–30; Le Corroller 1967: 63; Pérez 1974: 22; Touloun et al. 1999: 1; Touloun et al. 2001: 2; Touloun 2012: 37.

Buthus occitanus tunetatus (MIS): Touloun 2012: 104, 108.

Type material. 1 M holotype (MHNG), Oukaimeden (approx. 31.201°, -7.861°), Marrakech, Morocco. Paratypes: 1 F, 2 juv. (MHNG), same locality.

Distribution. the species is known from a wide range across the High-Atlas Mountains.

Remarks. Vachon (1949) infrasubspecific name is not available as explained previously.

33. *Buthus lourencoi* Rossi, Tropea & Yağmur, 2013

<http://zoobank.org/82B4235D-820E-4FE2-8AFC-6E0B4E28334D>

Buthus lourencoi: Rossi et al. 2013: 2–3, fig. 3–10.

Buthus occitanus (MIS): Kovařík and Whitman 2005 (part): 106.

Type material. 1 adult F holotype (MZUF N° 783), Mellaha (approx. 32.896°, 13.285°), Tripoli, Libya

Distribution. known only from the type locality.

Remarks. The type locality is now part of the large city of Tripoli. It is fairly unlikely that the species still occur within the boundaries of the city given the level of urban development. However, Mellaha, which was originally a military airport, is now the Mitiga International Airport, where large patches of unconstructed ground that may be suitable for the species still exist.

34. *Buthus malhommei* Vachon, 1949

Buthus occitanus malhommei Vachon 1949: 376; Vachon 1952a: 304–308, fig. 433–444;

Fet and Lowe 2000: 95; Touloun et al. 2001: 2; Touloun 2012: 35, 104, 108, fig. 5A.

Buthus malhommei: Lourenço 2003: 887–889, fig. 33–38; Stockmann and Ythier 2010: 364–365 (MIS); Sousa et al. 2012: 68–69; Aboumaâd et al. 2014: 5.

Type material. 3 M, 3 F, 7 juv., syntypes (MNHN), Mechra ben Abbou (approx. 32.646°, -7.800°), Settât, Morocco.

Distribution. Touloun (2012) greatly expanded the known distribution of this species along the basin of the Oum er Rbia River.

35. *Buthus mardochei* Simon, 1878

Buthus mardoche (IOS): Simon 1878: 159–160; Simon 1879: 100; Kraepelin 1891: 199; Birula, 1896: 244

Buthus (Buthus) mardoche (IOS): Birula 1910: 145–146; Birula 1917a: 223 (“dubious species”); Werner 1932: 300–305.

Buthus occitanus mardochei: Vachon 1949c (part): 358–363, fig. 400–408; Vachon 1952a (part): 286–295, fig. 401–408; Malhomme 1954: 28–29; Pérez 1974: 22; Levy and Amitai 1980: 16; El-Hennawy 1992: 98, 120; Kovařík 1995: 20; Gantenbein et al. 1998a: 51; Gantenbein et al. 1998b: 33–39; Kovařík 1998: 106; Fet and Lowe 2000: 96; Touloun et al. 2001: 2; Gantenbein and Largiadèr 2003 (part): 120, 122.

Buthus occitanus mardochei mardochei: Le Corroller, 1967: 63; Touloun 2012: 39, 104, 108, fig. 5D.

Buthus mardochei: Lourenço 2003: 889, fig. 39; Stockmann and Ythier 2010: 364–365; Aboumaâd et al. 2014: 5.

Type material. 1 F (MNHN N° RS1771, damaged), southern Morocco.

Distribution. this species appears to have a distribution parallel to that of *B. atlantis*, between Essaouira and Agadir, but is found further inland and away from the Atlantic coast.

Remarks. Vachon (1949d: 358) corrected what he considered Simon's incorrect original spelling of “mardoche” to “mardochei”, since the form was named as a patronym after its collector, Rabbi Mardoché. Nevertheless, it is our understanding that this was an unjustified emendation, because the ICZN article 31.1 admit the use of a noun in apposition as was the case with “mardoche”, however the ICZN article 33.2.3.1 admits the prevalence of this emendation as it continues to be attributed to “the original author and date” and is “in prevailing usage” and as such we refrain from any change to the name. Vachon (1949, 1952) also established that the species occurs roughly between Essaouira and Agadir, but not near the coast where it is replaced by *B. atlantis*.

36. *Buthus mariefranceae* Lourenço, 2003

Buthus mariefranceae: Lourenço 2003: 889–893, fig. 40–46; Lourenço and Qi 2006: 291; Stockmann and Ythier 2010: 364–365; Sousa et al. 2012: 68–69; Touloun 2012: 40; Pedroso et al. 2013: 300; Aboumaâd et al. 2014: 6.

Buthus occitanus mardochei mimeuri: Vachon 1949c: 367–373, fig. 417–425; Vachon 1952a: 295–301, fig. 417–425; Le Corroller 1967: 63; Pérez 1974: 23; Touloun 2012: 40, 57.

Type material. 1 F holotype (MHNG), Tan-Tan (approx. 28.43°, -11.1°), Guelmim Region, Morocco. Paratypes: 5 M, 4 F, 2 F juv. (MHNG), Goulimine.

Distribution. this species has a large distribution in Morocco, east and south of the Anti-Atlas Mountain.

Remarks. Vachon (1949) infrasubspecific name is not available as explained above.

37. *Buthus maroccanus* Birula, 1903

= *Prionurus tingitanus*: Pallary 1928a: 350–351, fig. 4 (synonymized by Vachon 1949b: 281). Syntype, sex unknown (MNHN), Rabat, Morocco (Vachon, 1949, 1952).

Buthus occitanus maroccanus: Birula 1903: 106.

Buthus europaeus (MIS): Hirst 1925 (part): 416.

Buthus (*Buthus*) *occitanus maroccanus*: Birula 1910: 145; Birula 1917a: 223.

Buthus occitanus maroccanus: Giltay 1929: 196; Werner 1929: 31–32.

Buthus maroccanus: Werner 1932: 299; Werner 1934b: 84; Vachon 1949b: 281–287, fig. 364–371; Vachon 1952a: 255–261, fig. 364–371; Foley 1951: 33; Bücherl 1964: 57; Pérez 1974: 22; Levy and Amitai 1980: 15; El-Hennawy 1992: 98, 119; Kovařík 1995: 20; Kovařík 1998: 106; Fet and Lowe 2000: 92; Sousa et al. 2012: 68–69; Stockmann and Ythier 2010: 366–367; Aboumaâd et al. 2014: 6..

Buthus maroccanus (ISS): Le Corroller 1967: 63.

Type material. 3 M, F, syntypes (ZIN), Morocco; 1 specimen syntype (ZIN), locality unknown (Fet and Lowe 2000).

Distribution. all known specimens have been captured in the Rabat Region (approx. 28.43°, -11.10°).

Remarks. it remains the only known *Buthus* species with a uniformly darkened body.

38. *Buthus montanus* Lourenço & Vachon, 2004

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8604>

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8653>

Buthus montanus Lourenço and Vachon 2004:84, 86–87, 91, fig. 16–30; Fernández 2004: 222; Fet 2010: 4; Rossi 2012: 274, 277–278; Teruel and Melic 2015: 5–9.

Type material. 1 M holotype (MNHN N° RS8604), Sierra Nevada (between Puerto de la Ragua and Cerro Pelado) (approx. 37.11°, -3.14°), Granada Region, Spain. Paratypes: 1 M, 3 F (MNHN N° RS8653), same locality.

Distribution. known only from the type locality.

39. *Buthus nigrovesiculosus* Hirst, 1925, stat. n.

Buthus europaeus nigrovesiculosus: Hirst 1925: 416.

Buthus occitanus nigrovesiculosus: Pérez 1974: 22; Fet and Lowe 2000: 96.

Type material. 1 M (adult?), 1 juv., syntypes (NHMUK), Boste (approx. 23.79°, -15.68°), Rio de Oro (Western Sahara), now Morocco.

Distribution. known only from the type locality.

Remarks. Hirst identified this North African species as a subspecies of *B. occitanus*, but as currently circumscribed, *B. occitanus* does not occur in North Africa (Gantenbein and Largiadèr 2003, Sousa et al. 2012). The original description of *B. nigrovesiculosus* suggests morphological similarities to *B. draa* and *B. tassili* Lourenço, 2002. These three species have a dark, almost black, fifth segment of the metasoma (Fig. 14 and 15A, less clear in the male type, obvious in the juvenile, syntypes in the NHMUK). Males of these three species also show slender pedipalp chelae. The type series of *B. nigrovesiculosus* includes only two animals, and more material is necessary to correctly evaluate the relationship between these three species. Nevertheless the males of *B. nigrovesiculosus* can be distinguished from males of the other two species by a higher pectinal tooth count (Fig. 10 and 15B, 36 versus <32 in the other two species), and from *B. tassili* by having a squared first metasomal segment.



Figure 14. Photo of the syntypes of *B. nigrovesiculosus* (NHMUK). Photo by Sérgio Henriques.

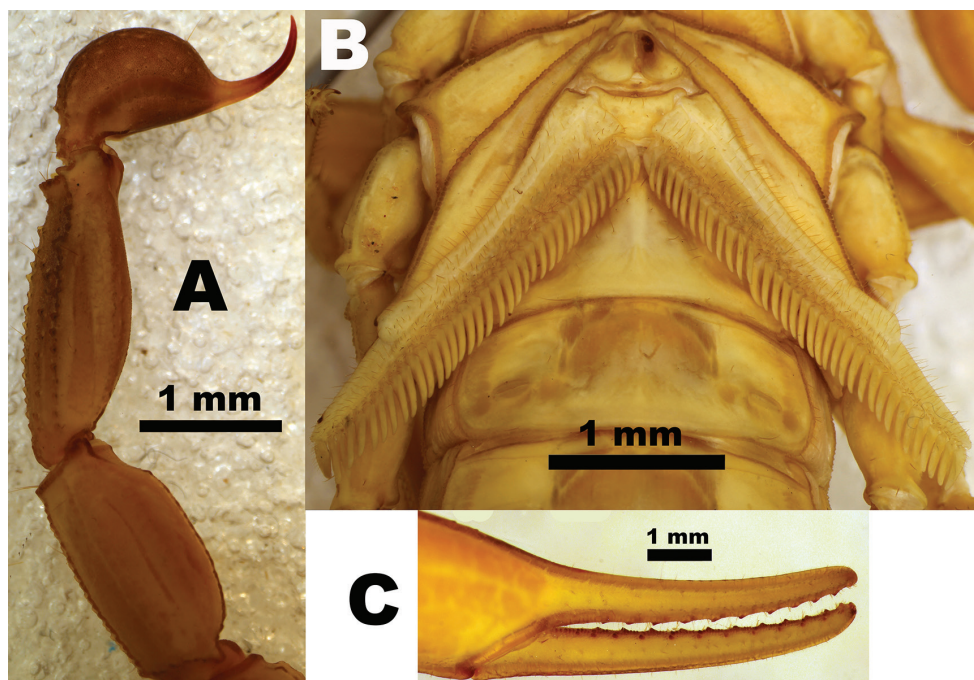


Figure 15. Detailed morphology of the larger syntype of *B. nigrovesiculosus* (NHMUK) **A** Lateral view of the telson and two terminal segments of the metasoma **B** Ventral view of the mesosoma, with pectines clearly visible **C** External lateral view of the terminal half of the right pedipalp che-la. All photos by Sérgio Henriques.

40. *Buthus occidentalis* Lourenço, Sun & Zhu, 2009

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8844>

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8845>

Buthus occidentalis: Lourenço et al. 2009: 72–74, fig. 7–19; Yang et al. 2013: 2.

Type material. 1 F holotype (MNHN N° RS8844), Dakhlet Nouadhibou Region, in the coastal area (approx. 20.28°, -16.24°), Mauritania. Paratypes: 1 M, 1 F juv. (MNHN N° 8845); 1 F, 1 M juv. (MHBU), all from the same locality.

Distribution. known only from the type locality.

41. *Buthus occitanus* (Amoreux, 1789), restricted distribution

= *Scorpio rufus*: Amoreux 1789a: 42–43 (synonymized by Amoreux 1789b, as the first revisor, ICZN article 24.2.2).

= *Androctonus ajax*: C. L. Koch 1839b: 53, pl. CXCI, fig. 467 (synonymized by Simon 1879: 96). Type lost: Spain.

= *Androctonus eurialus*: C. L. Koch 1839b: 25–27, pl. CLXXXVII (not pl. CXXXVII, as listed in the text), fig. 448 (synonymized by Simon 1879: 96). Type lost, France.

= *Androctonus eurilochus*: C. L. Koch 1839b: 27–28, pl. CLXXXVII, fig. 449 (synonymized by Kraepelin 1891: 196). Type lost, locality unknown.

= *Buthus europaeus*: Thorell 1876b: 7. Type is the lost Linnaeus (1748, 1754), specimen, purportedly from Italy (see the above “type species of *Buthus*” section and Fet et al. 2002).

= *Buthus europaeus tridentatus*: Franganillo 1918: 122–123 (**syn. n.**). Type unknown, Janvier, Navarre, Spain.

Scorpio occitanus: Amoreux 1789a: 42–43, pl. I, fig. 2; Amoreux 1789b: 10–16, pl. I, fig. 3; Herbst 1800: 73–82; Latreille 1804: 122; Latreille 1806: 132; Maccary 1810: 5–48; Audouin 1826: 172–173, pl. VIII, fig. 1; Audouin 1827: 410–411, pl. VIII, fig. 1; Dufour 1856 (part): 570.

Androctonus ajax: C. L. Koch 1850: 90.

Androctonus euryalus (ISS): C. L. Koch 1850: 90.

Androctonus eurylochus (ISS): C. L. Koch 1850: 90; Kraepelin 1891: 196.

Androctonus (Prionurus) occitanus: Lankester 1885: 380.

Buthus europaeus: Karsch 1879a: 18; Simon 1879: 96–98; Pavesi 1880: 312–313; Simon 1880c: 29; Pavesi 1884: 450; Pavesi 1885: 197, 199; Simon 1885: 51; Pocock 1889a: 116; Thorell 1893: 358–359; Birula 1896: 241–243; Birula 1900c: 9; Hirst 1925 (part): 415–416; Gadeau de Kerville 1926: 71; Bacelar 1928: 191; Hugues 1933: 487–488.

Buthus occitanicus (ISS): Dalla Torre 1905: 3; Táboriský 1934: 40.

Buthus occitanus: Leach 1815: 391; Risso 1826: 156–157; Peters 1861b: 513; Karsch 1881a: 89; Kraepelin 1891 (part): 196–199 (part), pl. I, fig. 5, pl. II, fig. 18;

- Kraepelin 1895: 80; Kraepelin 1899: 26; Kraepelin 1901a (part): 266; Werner 1902 (part): 598; Birula 1910: 118–120; Masi 1912: 101; Borelli 1914b: 460; Lampe 1917: 191; Pavlovsky 1924: 77; Pavlovsky 1925: 140; Werner 1925: 209; Werner 1936: 173; Schenkel 1938: 4; Feytaud 1940: 38–39; Vachon 1940: 242–247, 254–258, fig. 1–9, 29, 33, 61–64; Käsmer 1941: 231; Denis 1948: 155–156; Vachon 1948c: 61, fig. 5; Vachon 1949a: 156–160, fig. 331–344, 348, 372–380; Vachon 1950b: fig. 591; Vachon 1951a: fig. 641, 657, 663, 679, 687, 696; Vachon 1951b: 621–623; Vachon 1952a: 264; Vachon 1952b: 274–279; Vachon 1961: 31–32; Bücherl 1964: 57; Pérez 1974: 22; Vachon 1974: 873; Goulliart 1979: 2; Levy and Amitai 1980 (part): 15–16; Kinzelbach 1982: 53; Prost 1982: 5; Mari et al. 1987; Sissom 1990: 92, fig. 3.17C, L; Kovařík 1992a (part): 183; Reichholf and Steinbach 1992: 33, fig. 4–5; Crucitti 1993: 51; Crucitti et al. 1994: 57–66; Vincent 1994: 6; Crucitti and Chinè 1995: 15–26; Braunwalder 1997b: 3; Crucitti and Chinè 1997: 195–200; Cloudsley-Thompson and Lourenço 1998: 1–2; Kovařík 1998: 106; Kovařík 1999 (part): 39, 42, fig. 3; Fet and Lowe 2000 (part): 92–94; Lourenço 2003 (part): 884, 886–887, fig. 27–32; Lourenço and Vachon 2004: 83–85, fig. 1–15; Kovařík and Whitman 2005 (part): 106; Teruel and Pérez-Bote 2005: 276; Castilla and Pons 2007: 258; Dupré et al. 2008: (pages unnumbered); Sousa et al. 2010: 207; Colombo 2011: 1; Rossi 2012: 274–278; Pedroso et al. 2013: 300; Rossi, Tropea and Yağmur 2013: 3; Martin-Eauclaire et al. 2014: 56; Teruel and Melic 2015: 6–9; Lourenço 2016b: fig. 2.
- Buthus occitanus occitanus*: Birula 1910: 118; Hadži 1929: 31; Vachon 1949a: 156–160, fig. 331–344; Vachon 1949c: 336; Vachon 1952a (part): 264; Le Corroller 1967: 63; Fet and Lowe 2000 (part): 94–95; Gantenbein and Largiadèr 2003 (part): 120, 122.
- Buthus occitanus tridentatus*: Fet and Lowe 2000: 97; Kovařík 2001: 79;
- Buthus (Buthus) occitanus*: Birula 1909b: 507; Birula 1910: 143; Birula 1914b: 644–664; Birula 1917a: 22, 38–39, 199, 213.
- Buthus (Buthus) occitanus occitanus*: Roewer 1943: 206.
- Buthus cf. occitanus*: Piñero et al. 2013: 88.
- Scorpio australis* (MIS): Asso 1784: 146, Tab. I, fig. 2.
- Scorpio (Androctonus) occitanus*: Gervais 1844a: 42–44; pl. XXIII, fig. 4.
- Scorpio occitanicus* (ISS): Serres 1822: 65.
- Scorpion Occitanus* (ISS): Latreille 1817: 105–106.

Type material. type unknown, Souvignargues, Occitanie Region, France.

Distribution. Traditionally, the distribution of *B. occitanus* was considered to span from the Moroccan Atlantic shores in North Africa to the Middle East in Asia and to Southern-Western Europe. However, following the description of new species in the genus, the present distribution of *B. occitanus* has been restricted to NE Spain and SW France. Several molecular phylogenetic studies have demonstrated that the species range does not extend beyond Western Europe (Gantenbein and Largiadèr 2003, Sousa et

al. 2010, 2012, Pedroso et al. 2013). Lourenço and Vachon (2004) and Rossi (2012) include redescriptions of *B. occitanus* that include only European animals, but Vachon (1952a) also included material from Morocco, which was most likely not conspecific.

Remarks. All material collected outside of the range here proposed should be considered as *Buthus* sp. Only the re-examination of those specimens could reveal their appropriate identity. Vachon (1952a) included animals from the west (Atlantic) coast of Morocco, from Kenitra to El Jadida, within his definition of *B. o. occitanus*. As explained above this material is now considered not to be part of *B. occitanus* and thus remains unnamed. We opted to leave *Androctonus eurilochus* in synonymy with *B. occitanus*, despite the uncertain about the species provenance, to help to stabilise the genus' taxonomy. To further bring stability to *Buthus* taxonomy we propose Franganillo's subspecies, *B. o. tridentatus*, as a junior synonym of *B. occitanus*. Although the type specimen is not known (if it ever existed as such), its type locality is clearly stated as Javier, in Navarre, Spain. Extensive sampling on the left bank of the Ebro River (Sousa 2017) indicates that only *B. occitanus* occurs in this part of Spain and hence we here propose this new synonymy.

42. *Buthus orientalis* Lourenço & Simon, 2012

<http://zoobank.org/E408579C-9287-4EE7-9C32-E754EC925B92>

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8910>

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs6623>

Buthus orientalis: Lourenço and Simon 2012: 10–14, fig. 1–12; Rossi 2013: 191–192; Rossi, Tropea and Yağmur 2013: 5, 7.

Type material. 1 F holotype (MNHN N° RS8910), Alexandria (approx. 31.17°, 29.91°), Egypt. Paratypes: 7 M, 13 F (MNHN, N° RS6623), same locality.

Distribution. known only from the type locality.

43. *Buthus paris* (C. L. Koch, 1839)

= *Androctonus clytoneus*: C. L. Koch 1839a: 70–72, pl. CLXIII, fig. 384 (synonymized by Vachon 1949c: 380–381). Types lost; Africa.

Androctonus paris: C. L. Koch 1839a: 25–28, pl. CLI, fig. 352; C. L. Koch 1850: 90.

Androctonus clytonicus (ISS): Gervais 1844a: 43.

Androctonus clytoneus: C. L. Koch 1850: 90.

Buthus occitanus paris: Birula 1903: 107; Birula 1910: 118, 155; Giltay 1929: 196; Werner 1932: 300–305; Vachon 1949c: 380–388, fig. 356, 400, 445–455; Vachon 1951b: 621; Vachon 1952a: 308–316, fig. 356, 400 445–455; Malhomme 1954: 29; Arroyo 1961: 186–189; Le Corroller 1967: 63; Pérez 1974: 23; Levy

and Amitai 1980: 16; El-Hennawy 1992: 98, 121; Kovařík 1995: 20; Gantenbein et al. 1998a: 51; Kovařík 1998: 106; Fet and Lowe 2000: 96; Touloun et al. 2001: 2; Gantenbein and Largiadèr 2003: 120, 122; Touloun 2012: 35, 104, 108, fig.5B.

Buthus (Buthus) occitanus paris: Birula 1910. 145, 155; Birula 1917a: 223.

Buthus paris: Lourenço 2003: 896–897, fig. 52–56; Kovařík 2006: 2, 6, 8, 15, fig. 10–11; Lourenço 2013: 65–66; Rossi, Tropea and Yağmur 2013: 3, 5, 7; Aboumaâd et al. 2014: 6; Touloun et al. 2014: 77–78; Lourenço and Sadine 2016: 14–15.

Type material. Holotype lost according to Fet and Lowe (2000), Algeria. Vachon (1949c, 1952a) wrote that the types came from Alger without further explanation.

Distribution. the species is currently distributed across Algeria, Morocco and Tunisia.

Remarks. Because of the description of new species from Algeria, and the lack of both type specimen and locality (beyond the country), a neotype for *B. paris* is necessary to stabilize the taxonomy of Algerian *Buthus*, which may challenge the status of some newly described species. This is further complicated by recent diagnoses of *B. paris* (at least in part: Lourenço 2003, Kovařík 2006, Lourenço and Sadine 2016) that differ from those offered by Vachon (1952a). The differences between the different diagnoses include the number of rows in the movable finger, the aspect ratio of the first metasomal segment, the body chaetotaxie, the aculeus to vesicle length and the type of sexual dimorphism of the pedipalp chelae. Vachon (1952a) studied a large number of specimens from the entire Maghreb region, unrivalled by any subsequent study, which leads us to consider Vachon's description as the "gold standard". Vachon himself stated that most of the specimens used in his redescrptions were stored at the MNHN. If this material is ever located, it should have priority in the designation of a neotype. Although Vachon (1952a) did not formally describe any varieties within *B. paris*, he split the specimens that compose the species into three regions: 1) The typical region (from Algiers to northern Tunisia); 2) Specimens from the Oujda region (Morocco); 3) Those from northern Morocco and the Middle Atlas flanks. Interestingly the split of *B. paris* into these three regions corresponds well with the distribution of the genetic variability in the *cox1* gene (Gantenbein and Largiadèr 2003, Sousa et al. 2012, Pedroso et al. 2013), placing *B. paris* in two different groups: in *occitanus* which include all *B. paris* specimens from regions two and three, and *tunetanus*, which include *B. paris* specimens from the typical region one, along the split of the two *cox1* groups in the middle of Algeria (Fig. 7). If confirmed, this will mean that *B. paris* does not occur in Morocco. It is unclear if the variety from the third region above might correspond to *B. confluens* Lourenço, Touloun & Boumezzough, 2012, although these authors (page 22) refrained from suggesting this possibility because they could not find any of the material used by Vachon, purportedly to be in the MNHN, to describe this variety.

44. *Buthus parroti* Vachon, 1949, stat. n.

Buthus atlantis parroti: Vachon 1949a: 168–169, fig. 346, 350, 352–354, 356, 363; Vachon 1952a: 254–255, fig. 346, 350, 352, 353, 354, 356, 363; Le Corroller 1967: 63; Pérez, 1974 1974: 22; El-Hennawy 1992: 98, 119; Kovařík 1995: 20; Kovařík 1998: 106; Lourenço 2003: 883–885, fig. 23–26; Fet and Lowe 2000: 91–92; Touloun 2012: 43, fig. 9B; Pedroso et al. 2013: 300.

Type material. 1 F (MNHN N° RS1870), 1F, 12 juv., syntypes (MNHN), Forest house (approx. 30.31°, -9.33°), Ademine Forest, 40 Km S.W. of Agadir, Morocco; 2 M, 1 F juv., syntypes (MNHN), Taroudant (approx. 30.46°, -8.87°), Morocco.

Distribution. Known only from the Sous River Valley. Type localities in Fet and Lowe (2000) were mixed up.

Remarks. *B. parroti* was first described as a subspecies of *B. atlantis*. The two species occupy different habitats in Western Morocco; *B. parroti* is a forest species and *B. atlantis* is a sand dune dweller (Vachon 1952a). Furthermore, *B. atlantis* is clearly larger than *B. parroti*. Additionally, the first metasomal segment of *B. parroti* is wider than long, the aculeus is shorter than the vesicle and the anal arch has only two lobes (Vachon 1952a), while in *B. atlantis* this segment is longer than wide, the aculeus is as long as or longer than the vesicle and the anal arch has three lobes (Vachon 1952a). Three additional *Buthus* species occur in the same area of Morocco as *B. parroti*, namely *B. elmoutaouakili* Lourenço & Qi, 2006, *B. mardochei* Simon, 1878 and *B. mariefranceae*. *B. parroti* can be distinguished from all three species by the presence of macrosetae in the tergites (Vachon 1952a). Moreover, it can be distinguished from *B. mariefranceae* by its larger size and absence of a dark fifth metasomal segment. Mesosoma colour pattern is not clear for *B. parroti*; the examined specimen at the MNHN (RS1870) (Fig. 16) appears to have two very faint darker stripes, while *B. mariefranceae* has two very well marked mesosomal dark stripes. *B. parroti* males show slender pedipalp chelae than females, while there is little if any sexual dimorphism in *B. mardochei*.

45. *Buthus prudenti* Lourenço & Leguin, 2012

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8913>

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8915>

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8914>

Buthus prudenti: Lourenço and Leguin 2012: 2–6, 8, fig. 1–14; Lourenço 2016a: 76.

Type material. 1 M holotype (MNHN N° RS8913), Ouro Labaré (9.38715°, 13.83447°), Bénoué, Cameroon. Paratypes: 7 M, 8 F, same locality; 11 paratypes (MNHN N° RS8914, RS8915), 4 paratypes (CBGP).

Distribution. known only from the type locality.

Remarks. type locality toponym derived from the coordinates given in the original description, as the type locality given was only Region of Sanguéré-Djoi, Cameroon.



Figure 16. Photo of a *B. parroti* female syntype (MNHN N° RS1870), from the Ademine Forest, 04-1939, S.W. of Agadir, Morocco (Vachon 1952b).

46. *Buthus pusillus* Lourenço, 2013

Buthus pusillus: Lourenço 2013: 64–67, fig. 1–9; Lourenço and Sadine 2016: 14; Rossi, Tropea and Yağmur 2013: 5, 7.

Type material. 1 M holotype (ZMH N° A11/13), Tizi Oumalou (36.5102°, 4.3390°), Tizi Ouzou Province, Djurdjura Mountains, Algeria. Paratype: 1 M juv. (ZMH N° A12/13), same location.

Distribution. known only from the type locality.

Remarks. The locality we present here corresponds to the coordinates given in the paper, although these do not agree with the elevation also reported in the paper: 2150 m a.s.l. This is very close to the maximum altitude of the highest peaks of the Djurdjura Mountains, and much higher than the 935 m a.s.l. of Tizi Oumalou.

47. *Buthus rochati* Lourenço, 2003

Buthus rochati: Lourenço 2003: 893–896, fig. 47–51; Aboumaâd et al. 2014: 6.

Buthus occitanus mardochei panousei: Vachon 1949c: 373–376, fig. 426–432; Vachon 1952a: 301–304, fig. 426–432; Le Corroller 1967: 63; Pérez 1974: 23; Touloun 2012: 57.

Type material. 1 M holotype (MHNG), Tafnidilt Region (as Tafnidit) (approx. 28.56°, -11.03°), Guelmim Region, Morocco. Paratypes: 1 M, 1 F (MHNG); same locality; 6 F (MHNG), west of Tafnidilt Region, Draa River valley; 3 M, 1 F (MHNG), unknown locality.

Distribution. known distribution confined to the Tafnidilt region of Morocco.

Remarks. Lourenço (2003) does not mention the most remarkable diagnostic character given by Vachon (1952a), the interrupted dorso-median keel of the pedipalp patella. However Lourenço's Figure 49 illustrates this character, as it is a copy of Vachon's original drawings, and thus we consider it as part of the species diagnose and the most reliable diagnostic character for *B. rochati*. Vachon (1949) infrasubspecific name is not available as is explained above.

48. *Buthus saharicus* Saddine, Bissati & Lourenço, 2015

Buthus saharicus: Saddine et al. 2015: 47–49, fig. 6–8; Lourenço 2016b: fig. 4.

Type material. 1 F holotype (MNHN), Ghardaïa Region (approx. 32.300°, 3.833°), in Wadi bed, Algeria. Paratypes: 1 M (UGA), 1 F juv. (MNHN), same locality.

Distribution. known only from the type locality.

Remarks. Saddine et al. (2015) claimed that *B. saharicus* was the “first true deserticolous species found in Algeria”, a bold claim given that *B. tunetanus* (*sensu* Vachon 1949, part) had already been recorded for Beni Abbés by Vachon (1949, 1952), also a desert location in central west Algeria, and albeit neither localities are Erg Desert areas, Beni Abbés is in the border of the Grand Erg Occidental.

49. *Buthus tassili* Lourenço, 2002

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8501>

<https://science.mnhn.fr/institution/mnhn/collection/rs/item/rs8622>

Buthus tassili: Lourenço 2002: 113–115, fig. 10, 12, 14; Lourenço 2003: 906–909, fig. 80–86; Rossi, Tropea and Yağmur 2013: 3–5, 7.

Buthus occitanus (MIS): Pallary 1929: 134, 140; Pallary 1934: 98–99.

Buthus occitanus tunetanus neeli: Gysin 1969: 65–71, fig. 1–5; Pérez 1974: 22; Touloun 2012: 37, 40.

Buthus occitanus tunetatus, “Spécimens des régions montagneuses centrales du Sahara”: Vachon 1952a: 279.

Type material. 1 M holotype (MNHN N° RS8501), Tin Tazarif (approx. 24.466°, 10.466°), Illizi, Algeria. Paratype: 1 F (MNHN N° RS8622), same locality.

Distribution. This species is known from a wide area around the Hoggar and Tassili N’Ajjer Mountains, including at least one locality in Libya.

Remarks. The Tin Tazarif coordinates given here, standing at 880 m a.s.l., do not match the altitude given for the point by Lourenço (2002), of 1.800 m a.s.l., but correspond well to the map location given by the author in Figure 6 of the same article. Nevertheless there are several locations in the Tassili N’Ajjer Mountains at or above 1.800 m a.s.l., located closer to Jebel Azao, its highest peak. The species ranges from the Hoggar Mountains to the Tassili N’Ajjer Mountains, including Ghat in Libya. Gysin’s name, *B. o. t. neeli*, is not available under the ICZN article 10.2 and 45.5, as already stated by Fet and Lowe (2000). Therefore, it cannot enter formal synonymy. Nevertheless, because Gysin’s description (1969) brings relevant taxonomic information (figures and new localities) for *B. tassili*, we have decided to clearly state this new informal synonymy. The specimens studied of both species come from the Algerian Hoggar Mountains and share a typical darkened fifth segment of the metasoma (see *B. nigrovesiculosus* above).

50. *Buthus trinacrius* Lourenço & Rossi, 2013

Buthus trinacrius: Lourenço and Rossi 2013: 10–12, fig. 1–9.

Buthus europaeus (MIS): Simon 1879: 97; Simon 1910 (part): 69.

Buthus occitanus (MIS): Kraepelin (1901): 266.

Type material. 1 M holotype, Palermo Province? (approx. 38.05°, 13.32°), Sicily. Paratypes: 1 M, 1 F. All type material in bad conditions (MNHN N° RS3247).

Distribution. Recorded from Sicily.

Remarks. Although Lourenço and Rossi (2013) report that the collector is not mentioned in Simon’s notes, Kraepelin (1901), in his list of all the scorpion material present in the MNHN Paris, writes that Letourneur collected the *Buthus* material from Sicily and Corfu (Greece), which causes doubts regarding the correct collection locality of the specimens used to describe this species. Simon (1879) had doubts about the actual existence of *Buthus* in Sicily (when examining the specimens that would eventually be designated as type material for *B. trinacrius*): “il habite probablement aussi le midi de l’Italie et la Sicile”, and *Buthus* has never been found in mainland Italy. Furthermore, the authors also claimed that Simon (1910) “referred to the almost impossibility to distinguish *Buthus* populations from North of Africa with those from Spain and Sicily”, which is only partially correct. Simon (1910) solely referred to the distinction of *Buthus* populations of Algeria and Spain from those of Egypt, although in a subsequent paper, Simon does state that *Buthus* exist in Sicily without any further comments.

51. *Buthus tunetatus* (Herbst, 1800)

Scorpio tunetanus Herbst 1800: 68–69, pl. III, fig. 3 (not pl. II, fig. 2, as listed in the text); Latreille 1804: 122–124.

Androctonus (Leiurus) tunetanus: Ehrenberg in Hemprich and Ehrenberg 1829: 354.

Androctonus (Leiurus) tunetanus genuinus: Ehrenberg in Hemprich and Ehrenberg 1829: 354.

Androctonus (Liurus) tunetanus: Ehrenberg in Hemprich and Ehrenberg 1831 (pages unnumbered)

Androctonus (Liurus) tunetanus genuinus: Ehrenberg in Hemprich and Ehrenberg 1831 (pages unnumbered).

Androctonus tunetanus: C. L. Koch 1845: 15–19, pl. CCCCI (sic), fig. 968; C. L. Koch 1850: 90.

Buthus occitanus (MIS): Kovařík and Whitman 2005 (part): 106.

Buthus occitanus tunetanus: Birula 1903: 107; Birula 1910: 118; Borelli 1914a: 154–155; Borelli 1914b: 461; Borelli 1924: 4–5; Borelli 1928: 351; Giltay 1929: 196–197; Werner 1929: 30–31; Caporiacco 1932: 395–396; Schenkel 1932: 379–380; Werner 1932: 300–305; Pallary 1934: 99; Borelli 1934: 169; Werner 1934b: 84–85, fig. 4; Werner 1936: 173; Caporiacco 1937: 345; Schenkel 1949: 186; Vachon 1949c: 344–353, fig. 381–393; Vachon 1951a: fig. 670; Vachon 1952a: 272–281, fig. 381–393, 670; Vachon 1966: 211; Pérez 1974: 22; Levy and Amitai 1980: 16; El-Hennawy 1992: 98, 121; Kovařík 1995: 20; Kovařík 1997: 179; Gantenbein et al. 1998a: 51; Gantenbein et al. 1998b: 33–39; Kovařík 1998: 106; Fet and Lowe 2000: 97; Lourenço 2002, p. 113, 115, fig. 8–9, 11, 13; Kovařík 2002: 6; Gantenbein and Largiadèr 2003: 120, 122; Ben Othmen et al. 2004: 257; Touloun 2012: 37, 41.

Buthus (Buthus) occitanus tunetanus: Birula 1908: 123–124; Birula 1909: 507–508, fig. B; Birula 1910: 156–157; Birula 1917a: 223; Roewer 1943: 206.

Buthus tunetanus: Simon 1872: 251–252; Lourenço 2003: 897–899, fig. 57–61; Kovařík 2006: 2, 8, 10, 15, fig. 16–19.; Sadine et al. 2011: 6; Lourenço and Cloudsley-Thompson 2012: 13–16, fig. 8; Lourenço and Simon 2012: 12; Lourenço 2013: 65–66; Rossi, Tropea and Yağmur 2013: 4–5, 7

Scorpion Tunetanus (ISS): Latreille 1817: 106.

Type material. Types lost according to Fet and Lowe (2000), Tunisia.

Distribution. The species is currently distributed across Algeria, Libya, Morocco and Tunisia, and doubtfully in the island of Malta.

Remarks. Because of the description of new species from Tunisia, and the lack of both type specimen and locality (beyond the country), a neotype for *B. tunetanus* is necessary to stabilize the taxonomy of Tunisian *Buthus*. As explained for *B. paris*, this is further complicated by recent diagnoses of *B. tunetanus* that differ from those offered by Vachon (1952a), and as such if Vachon's *B. tuntetanus* material is found in the MNHN it should be given priority in the future designation of a neotype. Vachon (1952a) did not formally described any variety of *B. tunetanus*, but he again split the specimens that compose the species into four regions: 1) the typical region, cor-

responding to north and central Tunisia; 2) the southern montane region of Algeria, specimens from which have subsequently been described as *B. tassili*; 3) the Algerian Saharan Atlas and the southern region of the High Plateau; and 4) the disjunct desert regions of southern Tunisia, western central Algeria and eastern central Morocco. It is unclear whether region 3 or 4 might either correspond to *B. dunlopi* or *B. saharicus*. As explained in Fet and Lowe (2000), the name *A. (Leiurus) t. genuinus* refers to the nominotypical form of the species and as such the adjective “genuinus” is not an available subspecific name.

52. *Buthus yemenensis* Lourenço, 2008

Buthus yemenensis: Lourenço 2008: 47–50, fig. 1–7.

Type material. 1 F holotype (ZMH N° A33/08), Ma'bar (approx. 14.8°, 44.3°), Dhamar, Yemen.

Distribution. Known only from the type locality.

53. *Buthus* sp.

Buthus albengai (MIS): Habel et al. 2012: 3–4.

Buthus europaeus (MIS): Simon 1899: 85; Simon 1910 (part): 68–70, fig. 5, 8.

Buthus malhommei (MIS): Habel et al. 2012: 3–4.

Buthus occitanus (MIS): Karsch 1881b: 8 (Libya); Pocock 1899: 834 (Africa); Kraepelin 1901a (part): 266; Werner 1902 (part): 598; Chaignon 1904: 83–84 (Tunisia); Tullgren 1909: 2–3 (Egypt); Borelli 1924 (Libya): 4; King 1925: 81 (Sudan); Gough and Hirs 1927: 5, fig. 9 (Egypt); Pallary 1934: 98–99; Werner 1934a: 269, fig. 330 (Morocco); Pallary 1938: 281–282; Sergeant 1938: 519–520, pl. 49; Monard 1939: 82–83 (Guinea-Bissau); Moriggi 1941: 84; Sergeant 1941a: 355, fig. 1E, 2.7, pl. 35, fig. 7; Sergeant 1941b: 447, plate 37; Vachon 1941: 52; Frade 1947: 268 (Guinea-Bissau); Vachon 1952a (part): 262–271, fig. 331–344, 348, 372–380, 591, 641, 657, 663, 679, 687, 696; Vachon 1953: 1021–1024, fig. 12 (Mauritania); Malhomme 1954: 28 (Morocco); Belfield 1956: 44; Kinzelbach 1975: 14, fig. 1; Lamoral and Reynders 1975: 505 (Africa); Levy and Amitai 1980 (part): 15–16; Kinzelbach 1984: 100 (Asia); Kinzelbach 1985: map II (Asia); El-Hennawy 1987: 17 (Egypt); Amr et al. 1988: 374 (Jordan); Michalis and Dolkeras 1989: 265–266 (Greece); El-Hennawy 1992: 98, 101, 119–120 (Arabia); Kovařík 1992a (part): 183; Kovařík 1992b: 90 (Iraq); Amr and El-Oran 1994: 181 (Jordan); Kovařík 1997: 179 (Maghreb); Fet and Lowe 2000 (part): 92–94; Kovařík 2002: 5; Lourenço 2003: 884 (Morocco) Soleglad and Fet 2003: 7 (Morocco); Kaltsas et al. 2008: 215–216 (Libya); Sadine et al. 2012: 33; El-Hennawy 2013: 260; Aboumaâd et al. 2014: 5.

Buthus occitanus occitanus (MIS): Pocock 1895: 299 (Egypt); Vachon 1952a (part): 262–271, fig. 331–344, 372–379, 400, 554; Levy and Amitai 1980: 16 (Africa); Kovařík 1995: 20 (Morocco); Kovařík 1997: 179 (Ghana); Gantenbein et al. 1998a: 51, Fet and Lowe 2000 (part): 94–95; Gantenbein and Largiadèr 2003 (part): 120, 122.

Buthus occitanus occitanus, “Afrique occidentale française”: Vachon 1952a: 270.

Buthus occitanus occitanus, “Cote Occidentale du Maroc”: Vachon 1952a: 268–269, fig. 373–378.

Scorpio occitanus: Dufour 1856 (part): 570.

not *Buthus*: Vachon 1955: 372 (El Fâcher, Djebel Meidob, Darfur, Sudan) (Vachon said that this material was close to but not part of the genus *Buthus*).

Note. We further propose to transfer a species from the genus *Buthus* to the genus *Androctonus*.

Androctonus barbouri (Werner, 1932), **comb. n.**

Buthus barbouri: Werner 1932: 300, fig. 141; Vachon 1949b: 287–288, fig. 371; Vachon 1952a: 261–262; Perez 1974: 22; El-Hennawy 1992: 98, 119; Kovařík 1995: 20; Kovařík 1998: 106; Fet and Lowe 2000: 92.

Type material. 1 M (type probably lost), Agadir (approx. 30.43°, -9.60°), Morocco.

Distribution. known only from the type locality, Agadir, just north of the Sous River mouth, in southern Morocco.

Remarks. The species *B. barbouri* was described by Werner from Agadir, Morocco. However, this species cannot be linked to any of the *Buthus* species known from the reported type locality. This problem was already recognized by Vachon (1952a) that considered this species to have been “imperfectly described”, but then failed to make any taxonomic or nomenclatural act to fix it. *Buthus barbouri* and *B. marrocanus* are the only fully dark *Buthus* species known from Morocco. *B. marrocanus* was described from the Rabat region, 500 km distant from Agadir, and is distinguished from the former species by the shape of the inferior lateral keels of the fifth segment of the metasoma and by the number of pectinal teeth (Vachon, 1952a). Because of the chaetotaxy of the pedipalps Vachon (1952a) considered *B. barbouri* to be closer to *Androctonus mauritanicus* (Pocock, 1902). In agreement with these diagnostic characters, and Vachon’s (1952) opinion, we transfer *B. barbouri* to the genus *Androctonus*, with the new combination *Androctonus barbouri* (Werner, 1932). The relationship between *A. barbouri* and *A. mauritanicus bourdoni* Vachon, 1948, a subspecies of *A. mauritanicus* (Pocock, 1902), another black *Androctonus* species that also occurs in the Sous River valley, should be investigated.

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References

- Aboumaâd B, Iba N, Dersi N (2014) L'envenimation scorpionique au Maroc: scorpions du genre *Androctonus*, *Buthus* et *Hottentota*. Bulletin de la Société de pathologie exotique 107: 1–9. <https://doi.org/10.1007/s13149-014-0332-7>

- Amoreux P-J (1789a) Description méthodique d'une espèce de scorpion roux commune à Souvignargues en Languedoc et détails historiques à ce sujet. Observations sur la Physique, sur l'Histoire naturelle et sur les Arts. 35: 9–16. <http://biodiversitylibrary.org/page/6071194>
- Amoreux P-J (1789b) Notice des insectes de la France, réputés venimeux. Tirée des écrits des Naturalistes, des Médecins, and de l'Observation. Rue et Hôtel Serpente, Paris, 302 pp. <http://biodiversitylibrary.org/page/34452155>
- Amr ZS (2015) Scorpionism and Dangerous Species of Jordan. In: Gopalakrishnakone P, Schwartz EF, Vega RCR de la, Possani LD (Eds) Scorpion Venoms. Springer, Dordrecht, 181–200. <https://doi.org/10.1007/978-94-007-6404-0>
- Amr ZS, El-Oran R (1994) Systematics and distribution of scorpions (Arachnida, Scorpionida) in Jordan. Italian Journal of Zoology 61: 185–190. <http://dx.doi.org/10.1080/11250009409355881>
- Armas LF de, González-Moliné AL (2009) Primer registro de *Buthus ibericus* Lourenço and Vachon, 2004 (Scorpiones: Buthidae) para la provincia de Huelva, España. Boletín de la Sociedad Entomológica Aragonesa 45: 553–555.
- Arroyo H (1961) Etude sur la variété oranaise du scorpion *Buthus occitanus* (Amoreux, 1789). Archives de l'Institut Pasteur d'Algérie 39: 186–189.
- Asso IJ de (1784) CLASSIS V: INSECTA. Ordo VII APTERA. Scorpio. In: Introductio in Oryctographiam, et Zoologiam Aragoniae. Accedit Enumeratio stirpium in eadem Regione noviter detectarum. Amsterdam, 146 pp. <http://bibdigital.rjb.csic.es/spa/FichaLibro.php?Libro=80>
- Audouin V (1826) Explication sommaire des planches d'Arachnides de l'Égypte et de la Syrie, publiées par Jules-César Savigny, Membre de l'Institut; offrant un exposé des caractères naturels des genres, avec la distinction des espèces. In: Description de l'Égypte, ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée française, publié par les ordres de Sa Majesté l'empereur Napoléon le Grand. Histoire Naturelle. L'Imprimerie Impériale, Paris, 99–186. http://digi.ub.uni-heidelberg.de/diglit/jomard1809bd5_1_1?sid=b2853cf0c40b3c782fdc22a191d9050b
- Audouin V (1827) Explication sommaire des planches d'Arachnides de l'Égypte et de la Syrie, publiées par Jules-César Savigny, Membre de l'Institut; offrant un exposé des caractères naturels des genres avec la distinction des espèces. In: Description de l'Égypte ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée française. Seconde Édition, Dédiée au Roi, Histoire naturelle, Zoologie, Animaux invertébrés (suite). pp 291–430. Imprimerie de C. L. F. Panckoucke, Paris, 291–430. [http://gallica.bnf.fr/ark:/12148/bpt6k280218/f1.image.r=description de l'egypte.](http://gallica.bnf.fr/ark:/12148/bpt6k280218/f1.image.r=description%20de%20l%27egypte)
- Bacelar A (1928) Aracnídios portuguesas III Catálogo Sistemático dos Aracnídios de Portugal citados por diversos autores (1831–1926). Bulletin de la Société Portugaise des Sciences Naturelles 10: 169–203.
- Banks N (1910) The Scorpions of California. Pomona College Journal of Entomology 2: 185–190.
- Belfield W (1956) A preliminary check list of the West African scorpions and key for their identification. Journal of the West African Science Association 2: 41–47.
- Ben Othmen A, Chatti N, Ben Ali-Haouas Z, Ouldbrahim I, Said K, (2004) Allozymic differentiation of Tunisian populations of *Androctonus* species and *Buthus occitanus* (Scor-

- piones: Buthidae). Biological Journal of the Linnean Society 81: 255–265. <https://doi.org/10.1111/j.1095-8312.2003.00285.x>
- Berejano I, Pérez-Bote JL (2002) Determinación de una presa atípica en la dieta de *Buthus occitanius* (Amoreaux, 1789) (Scorpiones: Buthidae). Revista Ibérica de Aracnología 5: 59–60.
- Birula AA (1896) Miscelanea scorpologica. I. Zur synonymie der russischen Skorpione. Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de Saint-Petersbourg 1: 229–245.
- Birula AA (1900) Scorpiones mediterranei Musei Zoologici Mosquensis. Izvestiya Imperatorskogo Obshchestva Lyubitelei Prirody, Istorii, Antropologii i Etnografii 98: 8–20.
- Birula AA (1903) Bemerkungen über einige neue oder wenig bekannte Skorpionenformen Nord-Afrikas. Bulletin de l'Académie Impériale des Sciences de St-Petersbourg [Izvestiia Imperatorskoi akademii nauk] 19: 105–113.
- Birula AA (1908) Ergebnisse der mit Subvention aus der Erbschaft Treilt unternommenen zoologischen Forschungsreise Dr. F. Werner's nach dem Ägyptischen Sudan und Nord-Uganda. XIV. Scorpiones und Solifugae. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Wien 117: 121–152. http://www.zobodat.at/publikation_articles.php?id=148339
- Birula AA (1909) Scorpione und Solifugen von Tripolis und Barka. Nach der Sammlung von Dr. Bruno Klapotcz im Jahre 19-06. Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere 28: 505–522.
- Birula AA (1910) Ueber Scorpio maurus Linné und seine Unterarten. Horae Societatis Entomologicae Rossicae 39: 115–192. https://www.ntnu.no/ub/scorpion-files/Birula_1910.pdf
- Birula AA (1914) Ergebnisse einer von Prof. Franz Werner im Sommer 1910 mit Unterstützung aus dem Legate Wedl ausgeführten zoologischen Forschungsreise nach Algerien. VI. Skorpione und Solifugen. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Wien 123: 633–668. http://www.zobodat.at/publikation_articles.php?id=148652.
- Birula AA (1917a) [authored as Byalynitskii-Birulya, A. A.] Arachnoidea Arthrogastra Caucasia. Pars I. Scorpiones. Zapiski Kavkazskogo Muzeya, Seriya A [Mémoires du Musée du Caucase, Série A] 5: 1–253. [English translation: Byalynitskii-Birulya AA, 1964. Arthrogastric Arachnids of Caucasia. Part I. Scorpions. Israel Program for Scientific Translations, Jerusalem. 170 pp.]
- Birula AA (1917b) [authored as Byalynitskii-Birulya AA] Faune de la Russie et des pays limitrophes fondée principalement sur les collections du Musée Zoologique de l'Académie des Sciences de Russie. Arachnides (Arachnoidea), Petrograd, 227 pp. [English translation: Byalynitskii-Birulya AA, 1965. Fauna of Russia and Adjacent Countries. Arachnoidea. Vol. I. Scorpions. Israel Program for Scientific Translations, Jerusalem, 154 pp.]
- Bodenheimer FS (1937) Prodromus Faunae Palaestinae. Essai sur les éléments zoogéographiques et historiques du sud-ouest du sous-règne paléarctique. Mémoires p. Imprimerie de l'Institut Français d'Archéologie Orientale, Le Caire, 286 pp.
- Borelli A (1904) Di alcuni scorpioni della Colonia Eritrea. Bollettino dei Musei di Zoologia ed Anatomia Comparata della R. Università di Torino 19: 1–5.

- Borelli A (1914a) Contributo allo studio della fauna Libica. Materiali raccolti nelle zone di Misurata e Homs (1912-13). Scorpioni. Annali del Museo Civico di Storia Naturale di Genova 6: 148–159.
- Borelli A (1914b) Gli scorpioni del Museo Civico di Storia Naturale di Milano. Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano 53: 456–464.
- Borelli A (1924) Missione zoologica del Dr. E. Festa in Cirenaica. XVI. Scorpioni e Solifughi. Bollettino dei Musei di Zoologia ed Anatomia Comparata della R. Università di Torino 39: 1–16.
- Borelli A (1928) Risultati zoologici della Missione inviata dalla R. Società Geografica Italiana per l'esplorazione dell'oasi di Giarabud (1926-1927). Scorpioni e Solifughi. Annali del Museo civico di Storia Naturale Giacomo Doria 52: 346–355.
- Borelli A (1934) Scorpiones. In: Zavattari E (Ed) Prodrómo della fauna della Libia. Tipografia già Cooperativa, Pavia, 169–173.
- Braunwalder ME (1997) A note on Pierre-Joseph Amoreux (1741-1824) and his publications on *Buthus occitanus*. Newsletter of the British Arachnological Society 78: 3–4.
- Braunwalder ME, Fet V (1998) On publications about scorpions (Arachnida, Scorpiones) by Hemprich and Ehrenberg (1828–1831). Bulletin of the British Arachnological Society 11: 29–35.
- Bücherl W (1964) Distribuição geográfica dos Aracnóides peçonhentos temíveis. Memórias do Instituto Butantan 31: 55–66.
- Caporiacco L di (1932) Spedizione scientifica all'Oasi di Cufra (Marzo-Luglio 1931). Scorpioni e Solifugi. Annali del Museo civico di Storia Naturale Giacomo Doria 55: 395–408.
- Caporiacco L di (1937) Risultati scientifici della Missione del Prof. G. Scortecci nel Fezzan e sui Tassili (1936). Scorpioni e Solifughi. Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano 76: 340–354.
- Castilla AM, Pons GX (2007) Primeros datos sobre la población de escorpiones (*Buthus occitanus*) en las islas Columbretes (Mediterráneo, España). Bolletí de la Societat d'Història Natural de les Balears 50: 257–268. <http://www.raco.cat/index.php/BolletiSHNBalears/article/viewArticle/179006/0>
- Chaignon H de (1904) Contributions à l'Histoire Naturelle de la Tunisie. Bulletin de la Société d'Histoire Naturelle d'Autun 17: 1–166.
- Chippaux J-P, Goyffon M (2008) Epidemiology of scorpionism: a global appraisal. Acta Tropica 107: 71–79. <https://doi.org/10.1016/j.actatropica.2008.05.021>
- Christesen P (2007) Olympic victor lists and Ancient Greek history. Cambridge University Press, Cambridge, 580 + XX pp. <https://doi.org/10.1017/CBO9781107415324.004>
- Cloudsley-Thompson JL (1956) Studies in diurnal rhythms VI. Bioclimatic observations in Tunisia and their significance in relation to the physiology of the fauna, especially woodlice, centipedes, scorpions, and beetles. The Annals and Magazine of Natural History 12: 305–329. <https://doi.org/10.1080/00222935608655817>
- Cloudsley-Thompson JL, Lourenço WR (1998) On the meaning of the trivial name of the Scorpion *Buthus occitanus* (Amoreux, 1789) with notes on its distribution and variability. Newsletter of the British Arachnological Society 81: 1–2.
- Coelho PL, Sousa P, Harris DJ, van der Meijden A (2014) Deep intraspecific divergences in the medically relevant fat-tailed scorpions (*Androctonus*, Scorpiones). Acta tropica 134: 43–51. <https://doi.org/10.1016/j.actatropica.2014.02.002>

- Colombo M (2011) On Fabre's Traces: an Important Contributor to the Knowledge of *Buthus occitanus* (Amoreux, 1789). *Euscorpius* 117: 1–10. http://www.science.marshall.edu/fet/euscorpius/p2011_117.pdf
- Comstock JH (1940) Order Scorpionida. In: Comstock JH (Ed) The spider book, revised and edited by W. J. Gertsch. Cornell Univ. Press, Ithaca, 21–32.
- Cox FA (1921) A list of California Arachnida. III. The Scorpionida. *Journal of Entomology and Zoology*, Pomona College 14: 12–13.
- Crucitti P (1993) Problemi di conservazione degli scorpioni europei. *Ambiente Risorte Salute* 22: 51–55.
- Crucitti P, Chine A (1995) Variability and anomalies in the scorpion *Buthus occitanus occitanus* (Scorpiones, Buthidae). *Bollettino dell Associazione Romana di Entomologia* 49: 15–26.
- Crucitti P, Chine A (1997) Rapporto sessi in *Buthus occitanus occitanus* (Scorpiones, Buthidae). *Bollettino della Società Entomologica Italiana* 129: 129.
- Dalla Torre KW von (1905) Die skorpione Tirols. *Entomologisches Jahrbuch* 1905: 1–4.
- De Geer C (1778) Cinquieme Mémoire. Des Scorpions and des Faux-Scorpions. In: Mémoires pour servir à l'histoire des Insectes. Tome 7e. Imprimerie Pierre Hesselberg, Stockholm, 325–367. <https://doi.org/10.5962/bhl.title.14802>
- Denis J (1948) Le scorpion languedocien dans les Pyrénées-orientales. *Bulletin de la Société Linnéenne de Lyon* 17: 155–156.
- Dufour ML (1856) Histoire anatomique et physiologique des Scorpions. Mémoires présentés par divers savants à l'Académie des sciences de l'Institut de France 14: 561–656. doi: [ark:/12148/bpt6k3319c](https://doi.org/10.12148/bpt6k3319c)
- Dupré G (2013) Worldwide Bibliography Of Scorpions – Antiquity to nowadays (2nd edn). 968 pp. http://www.ntnu.no/ub/scorpion-files/dupre_2013.pdf
- Dupré G (2016) Dictionary of scientific scorpion names. *Arachnides* 78: 1–68.
- Dupré G, Lambert N, L'Association “Les Ecologistes D'Euzière” (2008) Le Scorpion Languedocien *Buthus occitanus* (Scorpiones, Buthidae). Sa répartition en France. *Arachnides Supplément* [not numbered].
- El Hidan, Abdelmonaim M, Touloun O, Boumezzough A (2016) New data on the diversity of scorpion fauna in the oases of south eastern Morocco. *Serket* 15: 1–7.
- El-Hennawy HK (1987) A simplified key to Egyptian scorpion species (Arachnida: Scorpionida). *Serket* 1: 15–17.
- El-Hennawy HK (1992) A catalogue of the scorpions described from the Arab countries (1758–1990) (Arachnida: Scorpionida). *Serket* 2: 95–153.
- El-Hennawy HK (2013) Preliminary list of Lebanese spiders and other arachnids (except ticks and mites). *Serket* 13: 228–275.
- Ewing HE (1928) The scorpions of the western part of the United States, with notes on those occurring in Northern Mexico. *Proceedings of the U.S. Natural Museum* 73: 1–24.
- Fabricius JC (1781) *Species Insectorum, exhibentes eorum differentias specificas, synonyma auctorum, loca natalia, metamorphosin adjectis observationibus, descriptionibus*. Tom. 1. Impensis Carol. Ernest. Bohnii, Hamburgi and Kilonii, 552 pp.
- Fernández J (2004) Noticia de nuevos táxones para la ciencia en el ámbito Íbero-Balear y Macaronésico. Nuevos táxones animales descritos en la península Ibérica y Macaronesia desde 1994 (VIII). *Graellsia* 60: 217–243.

- Fet V (2010) Scorpions of Europe. *Acta Zoologica Bulgarica* 62: 3–12.
- Fet V, Braunwalder ME, Cameron HD (2002) Scorpions (Arachnida, Scorpiones) described by Linnaeus. *Bulletin of the British Arachnological Society* 12: 176–182.
- Fet V, Gantenbein B, Gromov AV, Lowe G, Lourenço WR (2003) The first molecular phylogeny of Buthidae (Scorpiones). *Euscorpius* 4: 1–10. http://www.science.marshall.edu/fet/euscorpius/p2003_04.pdf
- Fet V, Lowe G (2000) Genus *Buthus* Leach, 1815. In: Fet V, Sissom WD, Lowe G, Braunwalder ME (Eds) *Catalog of the Scorpions of the World (1758–1998)*. The New York Entomological Society, New York, 91–97.
- Fet V, Sissom WD (2000) Family Euscorpiidae Laurie, 1893. In: Fet V, Sissom WD, Lowe G, Braunwalder ME (Eds) *Catalog of the Scorpions of the World (1758–1998)*. The New York Entomological Society, New York, 355–380.
- Feytaud J (1940) Les scorpions de France. *Revue de Zoologie Agricole et Appliquée* 39: 33–43.
- Foley H (1951) Les scorpions noirs de l'Afrique du Nord. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 42: 33.
- Frade F (1948) Trabalhos da Missão Zoológica da Guiné. X. Escorpiões, Solífugos e Pedipalpos da Guiné Portuguesa. *Anais da Junta das Missões Geográficas e de Investigações Coloniais, Lisboa* 3: 5–18.
- Francke OF (1985) *Conspectus genericus scorpionorum 1758–1982* (Arachnida: Scorpiones). *Occasional Papers of the Museum, Texas Tech University* 98: 1–32.
- Franganillo P (1918) Arácnidos nuevos o hallados por primera vez en España. *Boletín de la Sociedad Entomológica de España* 1: 120–123.
- Gadeau de Kerville H (1926) Scorpions. In: *Voyage zoologique d'Henri Gadeau de Kerville en Syrie (avril-juin 1908): tome premier, récit du voyage et liste méthodique des animaux récoltés en Syrie, par Henri Gadeau de Kerville; mémoires sur l'Éponge, les Copépodes, les Ostracodes, les Isopodes, les Opiliones, les Myriopodes, les Thysanoures, les Odonates, les Orthoptères, les Hyménoptères mellifères, les Diptères et les Oligochètes récoltés pendant ce voyage, par Émile Topsent, C. Dwight Marsh, Eugène Daday de Deés, Mme Harriet Richardson Searle, William Sørensen, le Comte Carl Attems, le Docteur Filippo Silvestri, R. Martin, Ignacio Bolivar, J. Pérez, le Docteur Joseph Villeneuve, Jacques Surcouf et le Docteur Wilhelm Michaelsen. J.-B. Baillière et fils, Paris, 71–72.*
- Gantenbein B, Braunwalder ME, Scholl A (1998) Allozyme studies on scorpions from the Aegean Region and from Morocco. *Abstracts XIV International Congress Arachnology \ 22 Annual Meeting of the American Arachnological Society, Chicago, 51.*
- Gantenbein B, Büchi L, Braunwalder ME, Scholl A (1998) The genetic population structure of *Euscorpius germanus* (C.L. Koch) (Scorpiones: Chactidae) in Switzerland. In: Selden PA (Ed.) *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh, 1997*. British Arachnological Society, Burnham Beeches, Bucks, 33–40.
- Gantenbein B, Largiadèr CR (2003) The phylogeographic importance of the Strait of Gibraltar as a gene flow barrier in terrestrial arthropods: a case study with the scorpion *Buthus occitanus* as model organism. *Molecular Phylogenetics and Evolution* 28: 119–130. [https://doi.org/10.1016/S1055-7903\(03\)00031-9](https://doi.org/10.1016/S1055-7903(03)00031-9)
- Gertsch WJ, Sologlad ME (1966) The scorpions of the *Vejovis boreus* group (subgenus *Paruroctonus*) in North America (Scorpionida, Vaejovidae). *American Museum Novitates* 2278: 1–54.

- Gervais P (1844a) Ordre III. Scorpionides. II. Scorpions. In: Walckenaer CA, Gervais P (Eds) Histoire naturelle des Insectes. Aptères. Librairie Encyclopédique de Roret, Paris, 14–74.
- Gervais P (1844b) Remarques sur la famille des scorpions et description de plusieurs espèces nouvelles de la collection du Muséum. Archives du Muséum d'Histoire Naturelle, Paris 4: 201–240.
- Giltay L (1929) Mission saharienne Augieras-Draper, 1927–1928. Scorpions. Bulletin du Muséum National d'Histoire Naturelle, Paris, 2^{me} série 1: 193–197.
- Gopalakrishnakone P, Schwartz EF, Vega RCR de la, Possani LD (Eds) (2015) Scorpion Venoms. Springer, Dordrecht, 575 pp. <https://doi.org/10.1007/978-94-007-6404-0>
- Gough HL, Hirst S (1927) Key to the identification of Egyptian scorpions. A method of identifying Egyptian scorpions from the fifth caudal segment and stings. Bulletin of the Ministry of Agriculture of Egypt, Technical Scientific Service 76: 1–7.
- Goulliart M, Frechin E (1979) Les scorpions de France. Bulletin de la Société Entomologique du Nord de la France 213: 1–3.
- Gysin J (1969) Une nouvelle variété de scorpion au Hoggar *Buthus occitanus* (Am.) ssp *tunetanus* (Herbst) var *neeli* var. nov. Archives de l'Institut Pasteur d'Algérie 47: 65–72.
- Habel JC, Husemann M, Schmitt T, Zachos FE, Honnen A-C, Petersen B, Parmakelis A, Stathi I (2012) Microallopatry caused strong diversification in *Buthus* scorpions (Scorpiones: Buthidae) in the Atlas Mountains (NW Africa). PloS One 7: e29403. <https://doi.org/10.1371/journal.pone.0029403>
- Hadži J (1929) Skorpilje Schmidtove zbirke (*Euscorpilus italicus* polytrichus n. ssp. i *ostale* nove rase). (in Slovenian). Glasnik Muzejskega Drustva za Slovenijo 10: 30–41.
- Hemprich FW, Ehrenberg CG (1828) Arachnoidea. Plates I + II. In: Symbolae Physicae seu Icones et Descriptiones Animalium Evertibratorum sepositis Insectis quae ex ilinere per Africam borealem et Asiam occidentalem. Friderici Guilelmi Hemprich et Chrisliuni Godofredi Ehrenberg, studio novae aut illustratae redierunt. Pe. Berolini ex officina Academica, Venditur a Mittlero.). <https://doi.org/10.5962/bhl.title.107403>
- Hemprich FW, Ehrenberg CG (1829) Vorläufige Uebersicht der in Nord-Afrika und West-Asien einheimischen Scorpione und deren geographischen Verbreitung, nach den eigenen Beobachtungen von Dr. Hemprich und Dr. Ehrenberg. Verhandlungen der Gesellschaft naturforschende Freunde in Berlin 1: 348–362. <https://books.google.pt/books?id=8OoTAAAAQAAJ>
- Hemprich FW, Ehrenberg CG (1831) Animalia articulata. Arachnoidea. Scorpiones africani et asiatici. In: Hemprich et Ehrenberg Symbolae Physicae. Animalia evertabrata exclusis insectis. Percensuit Dr. C. G. Ehrenberg. Series prima cum tabularum decade prima. Continent Animalia Africana et Asiatica 162. Berolini ex officina Academica, 12 (unnumbered). <https://doi.org/10.5962/bhl.title.107403>
- Hendrixson BE (2006) Buthid scorpions of Saudi Arabia, with notes on other families (Scorpiones: Buthidae, Liochelidae, Scorpionidae). Fauna of Arabia 21: 33–120.
- Herbst JFW (1800) Natursystem der ungeflügelten Insekten. Naturgeschichte der Skorpionen. Gottlieb August Lange, Berlin, 86 pp.
- Hirst S (1925) XLIII.—On some scorpions from Morocco, with the description of a new genus and species. Annals and Magazine of Natural History 15: 414–416. <https://doi.org/10.1080/00222932508633222>

- Hjelle JT (1972) Scorpions of the Northern California Coast Ranges (Arachnida: Scorpionida). Occasional Papers of the California Academy of Sciences 92: 1–59.
- Hofmann JJ, Hackius J, Boutesteyn C, Vander AP, Luchtmans J (1698) Lexicon Universale, Historiam Sacram Et Profanam Omnis aevi, omniumque Gentium; Chronologiam Ad Haec Usque Tempora; Geographiam Et Veteris Et Novi Orbis; Principum Per Omnes Terras Familiarum [...] Genealogiam; Tum Mythologiam, Ritus, Caerimonias, Omnemque. Editio abs. Hofmann JJ (Ed.) Johannes du Vivié, Leyden, 1072 pp. <http://www.uni-mannheim.de/mateo/camenaref/hofmann.html>.
- Hull-Williams V (1987) Some notes on the scorpion *Buthus occitanus* collected in Morocco, April 1987, by V. Hull-Williams and A. Smith. Journal of the British Tarantula Society 2: 12–15.
- Husemann M, Schmitt T, Stathi I, Habel JC (2012) Evolution and radiation in the scorpion *Buthus elmoutaouakili* Lourenco and Qi 2006 (Scorpiones: Buthidae) at the foothills of the Atlas Mountains (North Africa). Journal of Heredity 103: 1–9. <https://doi.org/10.1093/jhered/esr130>
- International Commission on Zoological Nomenclature (ICZN) (1957) Direction 60. Designation under the Plenary Powers of a type species for the genus *Scorpio* Linnaeus, 1758 (Class Arachnida) in harmony with accustomed usage and suppression under the same Powers of the specific name *europaeus* Linnaeus, 1758, as published in the combination *Scorpio europaeus* (amendment of a Ruling given in Opinion 104). Opinions and declarations rendered by the International Commission on Zoological Nomenclature 1E: 1–12.
- Kaltsas D, Stathi I, Fet V (2008) Scorpions of the Eastern Mediterranean. Advances in Arachnology and Developmental Biology: 209–246. <http://bozidar-curcic.bio.bg.ac.rs/PDF/16Kaltsas.pdf>.
- Karsch F (1879) Skorpionologische Beiträge. Mitteilungen des Münchener Entomologischen Vereins 3: 6–21; 97–136. <http://www.biodiversitylibrary.org/item/45585>.
- Karsch F (1881a) Uebersicht der Europäischen Skorpione. Berliner Entomologische Zeitschrift 25: 89–91.
- Karsch F (1881b) Verzeichniss der während der Rohfs'schen africanischen Expedition erbeuteten Myriopoden und Arachniden. Archive für Naturgeschichte 47: 1–14.
- Karsch F (1886) Skorpionologische Beiträge. I. Ueber einen sizilianischen Skorpion. II. Uebersicht der Gruppe Buthinae (Androctonina). III. Ueber einen neuen Opisthacanthus (Peters). Berliner entomologische Zeitschrift 30: 75–79.
- Karsch F (1891) Arachniden von Ceylon und von Minikoy gesammelt von den Herren Doctoren P. und F. Sarasin. III. Ordo Scorpiones. Berliner entomologische Zeitschrift 36: 305–307.
- Kästner A (1941) Ordnung der Arachnida: Scorpiones. In: Krumbach T (Ed.) Handbuch der Zoologie. Walter de Gruyter Verlag 3 (1): 117–240.
- King HH (1925) Notes on Sudan Scorpions. Sudan Notes and Records, Khartoum 8: 79–84. sfdas.com/IMG/pdf/sudan_notes_and_records_volume_8_-1925.pdf.
- Kinzelbach R (1975) Die Skorpione der Ägäis. Beiträge zur systematik, phylogenie und biogeographie. Zoologische Jahrbücher, Abteilung für Systematik 3 102: 12–50.
- Kinzelbach R (1982) Die Skorpionssammlung des Naturhistorischen Museums der Stadt Mainz. Teil I: Europa Und Anatolien. Mainzer Naturwissenschaftlichen Archiv 20: 49–66.

- Kinzelbach R (1984) Die Skorpionssammlung des Naturhistorischen Museums der Stadt Mainz. Teil II: Vorderasien. Mainzer Naturwissenschaftlichen Archiv 22: 97–106.
- Kinzelbach R (1985) Vorderer Orient. Skorpione (Arachnida: Scorpiones). Tübingen Atlas der Vorderen Orients (TAVO). Karte A VI 14.2. Ludwig Reichert Verlag, Wiesbaden.
- Koch CL (1837) Übersicht des Arachnidensystems. Erstes Heft. C. H. Zeh'schen Buchhandlung, Nürnberg, 39 pp. <http://www.biodiversitylibrary.org/bibliography/43744>.
- Koch CL (1839a) Die Arachniden. Getreu nach der Natur abgebildet und beschrieben. 5. C.H. Zeh'schen Buchhandlung, Nürnberg, 158 pp. <http://www.biodiversitylibrary.org/item/110884>.
- Koch CL (1839b) Die Arachniden. Getreu nach der Natur abgebildet und beschrieben. 6. C.H. Zeh'schen Buchhandlung, Nürnberg, 156 pp. <http://www.biodiversitylibrary.org/item/55838>.
- Koch CL (1845) Die Arachniden. Getreu nach der Natur abgebildet und beschrieben. 12. C.H. Zeh'schen Buchhandlung, Nürnberg, 166 pp. <http://www.biodiversitylibrary.org/item/55844>.
- Koch CL (1850) Skorpionen. Scorpiones. In: Übersicht des Arachnidensystems. Fünftes Heft. Verlag von J. L. Lotzbeck, Nürnberg, 86–92. <http://www.biodiversitylibrary.org/bibliography/43744>.
- Kovářík F (1992a) A check list of scorpions (Arachnida: Scorpiones) in the collections of the zoological department, National Museum in Prague. Acta Societas Zoologicae Bohemicae 56: 181–186.
- Kovářík F (1992b) *Buthus occitanus* (Amoreuxi, 1789) and *Orthochirus innesi* Simon, 1910 (Scorpionidea, Buthidae) from Iraq. Casopis Národního Muzea, Rada Přírodovědná 159: 90.
- Kovářík F (1995) First report of *Orthochirus innesi* (Scorpionida: Buthidae) from Morocco. Klapalekiana 31: 19–21.
- Kovářík F (1997) A check-list of scorpions (Arachnida) in the collection of the Hungarian Natural History Museum, Budapest. Annales Historico-Naturales Musei Nationalis Hungarici 89: 177–185.
- Kovářík F (1998) Štíří. Madagaskar, Jihlava, 176 pp.
- Kovářík F (1999) Review of European scorpions, with a key to species. Serket 6: 38–44.
- Kovářík F (2001) Catalog of the Scorpions of the World (1758–1998) by V. Fet, W. D. Sissom, G. Lowe, and M. Braunwalder (New York Entomological Society, 2000: 690 pp.). Discussion and supplement for 1999 and part of 2000. Serket 7: 78–93.
- Kovářík F (2002) A checklist of scorpions (Arachnida) in the collection of the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany. Serket 8: 1–23.
- Kovářík F (2003) Scorpions of Djibouti, Eritrea, Ethiopia, and Somalia (Arachnida: Scorpiones), with a key and descriptions of three new species. Acta Societatis Zoologicae Bohemicae 67: 133–159. <http://kovarex.com/scorpio/pdf/Kovarik2003c.pdf>.
- Kovářík F (2006) Review of Tunisian Species of the Genus *Buthus* with Descriptions of Two New Species and a Discussion of Ehrenberg's Types (Scorpiones: Buthidae). Euscorpius 34: 1–16. http://www.science.marshall.edu/fet/euscorpius/p2006_34.pdf.

- Kovařík F (2011) *Buthus awashensis* sp. n. from Ethiopia (Scorpiones: Buthidae). *Euscorpius* 128: 1–6. http://www.science.marshall.edu/fet/euscorpius/p2011_128.pdf.
- Kovařík F, Whitman S (2004) Cataloghi del Museo di Storia Naturale dell'Università di Firenze - sezione di zoologia «La Specola» XXII. Arachnida Scorpiones. Tipi. Addenda (1998–2004) e checklist della collezione (Euscorpiinae esclusi). *Atti della Società Toscana di Scienze Naturali, Memorie, Serie B* 111: 103–119.
- Kraepelin K (1891) Revision der Skorpione. I. Die familie der Androctonidae. *Jahrbuch der Hamburgischen wissenschaftlichen Anstalten* 8: 143–286.
- Kraepelin K (1895) Nachtrag zu Theil I der Revision der Skorpione. *Jahrbuch der Hamburgischen wissenschaftlichen Anstalten* 12: 73–96.
- Kraepelin K (1899) Scorpiones und Pedipalpi. Das Tierreich. Herausgegeben von der Deutschen Zoologischen Gesellschaft. Dahl F (Ed). Friedländer und Sohn Verlag, Berlin, 265 pp. <http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Scorpiones+und+Pedipalpi#0>.
- Kraepelin K (1901) Catalogue des Scorpions des collections du Muséum d'histoire naturelle de Paris. *Bulletin du Muséum d'Histoire Naturelle, Paris* 7: 265–274.
- Kraepelin K (1903) Skorpione und Solifugen Nordost-Afrikas, gesammelt 1900 und 1901 von Carlo Freiherrn von Erlanger und Oscar Neumann. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere* 18: 557–578.
- Lamoral BH (1979) The Scorpions of Namibia (Arachnida-Scorpionida). *Annals of the Natal Museum* 23: 497–784. <http://www.ntnu.no/ub/scorpion-files/lamoral1.pdf>.
- Lamoral BH, Reynders SC (1975) A catalogue of the scorpions described from the Ethiopian faunal region up to December 1973. *Annals of the Natal Museum* 22: 489–576.
- Lampe E (1917) Katalog der Skorpione, Pedipalpen und Solifugen des Naturhistorischen Museums der Residenzstadt Wiesbaden. *Jahrbücher des Nassauischen Verein für Naturkunde, Wiesbaden* 70: 185–208.
- Lankester ER (1885) Notes on certain points in the anatomy and generic characters of scorpions. *Transactions of the Zoological Society of London* 11: 372–384.
- Latreille PA (1804) Histoire des Scorpions. In: Histoire naturelle, générale et particulière des Crustacés et des Insectes. Ouvrage faisant suite aux oeuvres de Leclerc de Buffon, et partie de cours complet d'histoire naturelle rédigée par C. S. Sonnin, member de plusieurs Sociétés savantes. Imprimerie de F. Dufart, Paris, 110–129.
- Latreille PA (1806) Familia Tertia. Scorpionides. In: *Genera Crustaceorum et Insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata*. Amand Koenig, Parisiis and Argentorati, 130–132.
- Latreille PA (1817) Tome III. Contenant les Crustacés, les Arachnides et les Insectes. In: Cuvier G (Ed.) *Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*. Imprimerie de A. Belin, Paris, 653.
- Laurie M (1896) Further notes on the anatomy and development of scorpions, and their bearing on the classification of the Order. *Annals and Magazine of Natural History* 18: 121–133.
- Le Coroller Y (1967) Les scorpions du Maroc. *Archives de l'Institut Pasteur d'Algérie* 45: 62–71.
- Leach WE (1815) A tabular View of the external Characters of Four Classes of Animals, which Linné arranged under INSECTA; with the Distribution of the Genera compos-

- ing Three of these Classes into Orders, andc. and Descriptions of several New Genera and Species. Transactions of the Linnean Society of London 11: 306–400. <https://doi.org/10.1111/j.1096-3642.1813.tb00065.x>
- Levy G, Amitai P (1980) Fauna Palaestina. Arachnida I: Scorpiones. The Israel Academy of Sciences and Humanities, Jerusalem, 172 pp.
- Linnaeus C (1748) Systema naturae, sistens regna tria naturae, in classes et ordines, genera et species. Editio Sexta, Emendata et Aucta. Impensis Godofr. Kiesewetteri, Stockholmiae, 224 pp. <https://doi.org/10.5962/bhl.title.36934>
- Linnaeus C (1754) Museum S:ae R:ae M:tis Adolphi Friderici Regis [etc] in quo Animalia rariora imprimis, et exotica quadrupedia, aves, amphibia, pisces, insecta, vermes describuntur et determinantur, Latine et Svetice cum iconibus. E Typographia Regia, Holmiae [Stockholm], 96 pp. doi: [ark:/12148/bpt6k972707](https://doi.org/10.12148/bpt6k972707)
- Linnaeus C (1758) Scorpio. In: Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Laurentii Salvii, Holmiae [Stockholm], 624–625. <https://doi.org/10.5962/bhl.title.542>
- Lönnberg E (1897) Om Skorpionernas och Pedipalpernas geografiska utbredning. Entomologisk Tidskrift 18: 193–211.
- Lönnberg E (1898) A revision of the Linnaean type specimens of scorpions and pedipalps in the Zoological Museum of the Royal University of Upsala. The Annals and Magazine of Natural History (5th series) (7) 1: 82–89.
- Loria SF, Prendini L (2014) Homology of the lateral eyes of scorpions: A six-ocellus model. PLoS ONE 9: 1–30. <https://doi.org/10.1371/journal.pone.0112913>
- Lourenço WR (2002) Considérations sur les modèles de distribution et différenciation du genre *Buthus* Leach, 1815, avec la description d'une nouvelle espèce des montagnes du Tassili des Ajjer, Algérie (Scorpiones, Buthidae). Biogeographica 78: 109–127.
- Lourenço WR (2003) Compléments à la faune de scorpions (Arachnida) de l'Afrique du Nord, avec des considérations sur le genre *Buthus* Leach, 1815. Revue Suisse de Zoologie 110: 875–912.
- Lourenço WR (2005a) Description of a new scorpion species of the genus *Buthus* Leach, 1815 (Scorpiones, Buthidae) from Guinea and Senegal in Western Africa. Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg 14: 229–236.
- Lourenço WR (2005b) A new species of the genus *Buthus* Leach, 1815 (Scorpiones, Buthidae) from Senegal and Niger in Western Africa. Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg 14: 245–251.
- Lourenço WR (2005c) Description Of Three New Species Of Scorpion From Sudan (Scorpiones, Buthidae). Boletín de la Sociedad Entomológica Aragonesa 36: 21–28.
- Lourenço WR (2005d) Nouvelles considérations taxonomiques sur les espèces du genre *Androctonus* Ehrenberg, 1828 et description de deux nouvelles espèces (Scorpiones, Buthidae). Revue suisse de Zoologie 12: 145–171. <https://doi.org/10.5962/bhl.part.80291>
- Lourenço WR (2008) About the presence of the genus *Buthus* Leach, 1815 in the Arabian Peninsula and description of a new species (Scorpiones, Buthidae). Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg 15: 45–52.

- Lourenço WR (2013) A new species of *Buthus* Leach, 1815 from Algeria (Scorpiones, Buthidae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg* 16: 63–68.
- Lourenço WR (2015) Deux nouvelles espèces de scorpions de la famille des Buthidae C. L. Koch, 1837 collectées dans le Parc National de Zakouma au Tchad. *Revista Ibérica de Aracnología* 26: 19–24.
- Lourenço WR (2016a) A new species of the genus *Buthus* Leach, 1815 (Scorpiones: Buthidae) from dry forest formations in Central. *Serket* 15: 71–79.
- Lourenço WR (2016b) Scorpion incidents, misidentification cases and possible implications for the final interpretation of results. *Journal of Venomous Animals and Toxins including Tropical Diseases* 22: 1–25. <https://doi.org/10.1186/s40409-016-0075-6>
- Lourenço WR, Cloudsley-Thompson JL (2012) A new species of *Buthus* Leach, 1815 from Egypt (Scorpiones, Buthidae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg* 16: 11–18.
- Lourenço WR, Duhem B, Cloudsley-Thompson JL (2012) Scorpions from Ennedi, Kapka and Tibesti, the mountains of Chad, with descriptions of nine new species (Scorpiones: Buthidae, Scorpionidae). *Arthropoda Selecta* 21: 307–338. http://arthropodaselecta.britishtspiders.org.uk/articles/21_4_307_338_Lourenco_etal.pdf.
- Lourenço WR, Francke OF (1984) The identities of *Tityus floridanus* and *Tityus tenuimanus* (Scorpiones, Buthidae). *The Florida Entomologist* 67: 424–429.
- Lourenço WR, Geniez P (2005) A new scorpion species of the genus *Buthus* Leach, 1815 (Scorpiones, Buthidae) from Morocco. *Euscorpius* 19: 1–6. http://www.science.marshall.edu/fet/euscorpius/p2005_19.pdf.
- Lourenço WR, Leguin E-A (2012) A new species of the genus *Buthus* (Scorpiones: Buthidae) from northern Cameroon. *Euscorpius* 152: 1–9. http://www.science.marshall.edu/fet/euscorpius/p2012_152.pdf.
- Lourenço WR, Qi J-X (2006) A new species of *Buthus* Leach, 1815 from Morocco (Scorpiones, Buthidae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg* 14: 287–292.
- Lourenço WR, Rossi A (2013) Confirmation of a new species of *Buthus* Leach, 1815 from Sicily (Scorpiones, Buthidae). Biogeographical implications. *Revista Ibérica de Aracnología* 22: 9–14.
- Lourenço WR, Sadine SE (2016) One more new species of *Buthus* Leach; 1815 from Algeria (Scorpiones: Buthidae). *Revista Ibérica de Aracnología* 28: 13–17.
- Lourenço WR, Simon E (2012) Confirmation of a new species of *Buthus* Leach, 1815 from Alexandria, Egypt (Scorpiones, Buthidae). *Serket* 13: 8–15.
- Lourenço WR, Slimani T (2004) Description of a new scorpion species of the genus *Buthus* Leach, 1815 (Scorpiones, Buthidae) from Morocco. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg* 14: 165–170.
- Lourenço WR, Sun D, Zhu M-S (2009) About the presence of the genus *Buthus* Leach, 1815 in Mauritania, with description of a new species (Scorpiones, Buthidae). *Boletín de la Sociedad Entomológica Aragonesa* 44: 71–75. <http://www.sea-entomologia.org/PDF/BSEA44ARACNO/B44071.pdf>.

- Lourenço WR, Touloun O, Boumezzough A (2012) Un nouveau *Buthus* Leach, 1815 (Scorpiones, Buthidae) du Nord du Maroc; possible lien entre les populations Marocaines et Européennes. *Revista Ibérica de Aracnología* 21: 21–25.
- Lourenço WR, Vachon M (2004) Considérations sur le genre *Buthus* Leach, 1815 en Espagne, et description de deux nouvelles espèces (Scorpiones, Buthidae). *Revista Ibérica de Aracnología* 9: 81–94.
- Lourenço WR, Yağmur EA, Duhem B (2010) A new species of *Buthus* Leach, 1815 from Jordan. *Zoology in the Middle East* 49: 95–99. <https://doi.org/10.1080/09397140.2010.10638395>
- Maccary A (1810) Mémoire sur le scorpion qui se trouve sur la montagne de Cette, dé partement de l'Hérault, son venin, et l'usage qu'on pourrait en faire en Médecine. Imprimerie de Froullé, Paris, 48 pp.
- Malhomme J (1954) Aperçu sur la distribution des scorpions de la région de Marrakech. *Bulletin de la Société des Sciences Naturelles et Physiques du Maroc* 34: 25–30.
- Mari EG, Ferragut E, Navarro V, Laborda R, Comelles JC (1987) Nueva aportación al conocimiento de los artrópodos de las Islas Columbretes. In: Alonso Matilla LA, Carretero JL, Garcia-Carrascosa A. (Eds) Islas Columbretes. Contribución al estudio de su medio natural. Generalitat Valenciana, Valencia, 155–179. <http://www.llig.gva.es/es/1361-9788478903511.html>.
- Martin-Eauclaire M-F, Bosmans F, Céard B, Diochot S, Bougis PE (2014) A first exploration of the venom of the *Buthus occitanus* scorpion found in southern France. *Toxicon* 79: 55–63. <https://doi.org/10.1016/j.toxicon.2014.01.002>
- Masi L (1912) Note sugli scorpioni appartenenti al R. Museo zoologico di Roma. *Memorie della Società Entomologica Italiana* 3: 88–108, 120–144.
- Maupertuis PL (1731) Expériences sur les Scorpions. *Histoire de l'Académie royale des sciences, avec les mémoires de mathématique et de physique* 1731: 223–229. <http://biodiversitylibrary.org/item/86706>.
- Mello-Leitão C de (1931) Divisão e distribuição do gênero *Tityus* Koch. *Annaes da Academia Brasileira de Ciências* 3: 119–150.
- Mello-Leitão C de (1939) Revisão do gênero *Tityus*. *Physis* 17: 57–76.
- Mello-Leitão C de (1945) Escorpiões Sul-Americanos. *Arquivos do Museu Nacional, Rio de Janeiro* 40: 1–468.
- Michalis K, Dolkeras P (1989) Beitrag zur Kenntnis der Skorpione Thessaliens und Epirus (Nordgriechenland). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg* 9: 259–270.
- Monard A (1939) Résultats de la mission scientifique du Dr Monard en Guinée Portugaise. 1937-1938. IV. Scorpions. *Arquivos do Museu Bocage* 10: 81–85.
- Moriggi M (1941) Gli scorpioni dell' Africa Orientale Italiana. *Rivista di Biologia Coloniale, Roma* 4: 77–103.
- Moritz M, Fischer SC (1980) Die Typen der Arachniden-Sammlung des Zoologischen Museums Berlin. III. Scorpiones. *Mitteilungen aus dem Zoologischen Museum in Berlin* 2: 309–326.
- Müller K (1848) *Fragmenta Historicum Graecorum*. Ambrosio Firmin Didot, Paris, 630 pp.

- Nenilin AB, Fet V (1992) Zoogeographical analysis of the world scorpion fauna (Arachnida, Scorpiones). *Arthropoda Selecta* 1: 3–31.
- Noël F (1824) Dictionnaire historique des personnages célèbres de l'antiquité, princes, généraux, philosophes, poètes, artistes, artistes etc.; des dieux, héros de la fable; des villes, fleuves, etc. Seconde Éd. Le Normant Père, Paris, 581 pp.
- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'amico J a, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth. *BioScience* 51: 933–938. [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)
- Pallary P (1928) Description de quatre scorpions nouveaux de la Berbérie. *Bulletin du Muséum National d'Histoire Naturelle*, Paris, 1^{ère} série 5: 346–351.
- Pallary P (1929) Les scorpions du Sahara central. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 20: 133–141.
- Pallary P (1934) Scorpions du Sahara central. Mission du Hoggar III (Février à Mai 1928). *Mémoires de la Société d'Histoire Naturelle d'Afrique du Nord* 4: 90–100.
- Pallary P (1938) Sur des scorpions de la Berbérie, de la Syrie et du Congo. *Archives de l'Institut Pasteur d'Algérie* 16: 279–282.
- Pavesi P (1880) Studi sugli Aracnidi Africani. I. Aracnidi di Tunisia. *Annali del Museo Civico di Storia Naturale di Genova* 15: 283–388.
- Pavesi P (1884) Materiali per lo studio della fauna Tunisia raccolta da G. e L. Doria: Aracnidi. *Annali del Museo Civico di Storia Naturale di Genova* 20: 446–486.
- Pavesi P (1885) Aracnidi raccolti dal conte Bouturlin ad Assab e Massaua. *Bollettino della Società Entomologica Italiana* 17: 197–200.
- Pavlovsky EN (1924) On the morphology of the male genital apparatus in scorpions. *Trudy Leningradskogo Obshchestva Yestestvoispytatelei* 53: 17–86.
- Pavlovsky EN (1925) Zur morphologie des weiblichen Genitalapparates und zur Embryologie der Skorpione. *Annuaire du Musée Zoologique de l'Académie des Sciences d'URSS* 26: 137–205.
- Pedroso D, Sousa P, Harris DJ, van der Meijden A (2013) Phylogeography of *Buthus* Leach, 1815 (Scorpiones: Buthidae): a multigene molecular approach reveals a further complex evolutionary history in the Maghreb. *African Invertebrates* 48: 298–308. <https://doi.org/10.3377/004.048.0216>
- Pérez S (1974) Un inventario preliminar de los escorpiones de la region Palearctica y claves para la identification de los generos de la region Palearctica Occidental. *Cátedra de Artrópodos* 7: 1–45.
- Peters W (1861) Ueber eine neue Eintheilung der Skorpione und ueber die von ihm in Mosambique gesammelten Arten von Skorpionen, aus welchem hier ein Auszug mitgetheilt wird. *Monatsberichte der Königlich preussischen Akademie der Wissenschaften zu Berlin*: 507–516.
- Piñero FS, Tenorio FU, García FJM (2013) Foraging of *Buthus occitanus* (Scorpiones: Buthidae) on shrub branches in an arid area of southeastern Spain. *Journal of Arachnology* 41: 88–90. <https://doi.org/10.1636/Hi11-90.1>

- Pocock RI (1889a) Arachnida, Chilopoda and Crustacea. In “III. On the Zoology of the Afghan Commission Delimitation. by J. E. T. Aitchison [Ed.]” (p. 53–142). Transactions of the Linnaean Society of London, 2nd Ser-ies, Zoology 5: 110–121.
- Pocock RI (1889b) Notes on some Buthidae, new and old. Annals and Magazine of Natural History 3: 334–351.
- Pocock RI (1890) A revision of the genera of Scorpions of the family Buthidae with descriptions of some South-African species. Proceedings of the Zoological Society of London 10: 114–141.
- Pocock RI (1893) Notes on the classification of Scorpions, followed by some observations upon synonymy, with descriptions of new genera and species. Annals and Magazine of Natural History 6: 303–330.
- Pocock RI (1895) On the Arachnida and Myriapoda obtained by Dr. Anderson’s collector during Mr. T. Ben’s expedition to the Hadramaut, South Arabia, with a Supplement upon the Scorpions obtained by Dr. Anderson in Egypt and the Eastern Soudan. Addendum: List of the Scorpi. Zoological Journal of the Linnaean Society, London 25: 292–316.
- Pocock RI (1899) On the Scorpions, Pedipalps and Spiders from tropical West-Africa represented in the collection of the British Museum. Proceedings of the Zoological Society of London 1899: 833–885. <http://biodiversitylibrary.org/page/31572831>.
- Pocock RI (1900a) Arachnida. Fauna of British India including Ceylon and Burma. Taylor and Francis, London, 279 pp.
- Pocock RI (1900b) On a Collection of Insects and Arachnids made in 1895 and 1897, by Mr. C. V. A. Peel, F.Z.S., in Somaliland, with Descriptions of new Species. 10. General List of the Scorpions of Somaliland and the Boran Country. Philosophical Magazine series 3 32: 54–63. <https://doi.org/10.1111/j.1096-3642.1890.tb01694.x>
- Polis GA (1990) The Biology of Scorpions. Polis GA (Ed). Stanford University Press, Stanford, 587 pp.
- Prost A (1982) L’identification des scorpions de Haute-Volta. Notes et Documents Voltaïques 13: 4–10.
- Reichholf JH, Steinbach G eds. (1992) Skorpione. In: Die Grosse Bertelsmann Lexikothek. Naturezyklopädie Europas. Tome 4. Bertelsmann Verlag, 32–35.
- Rein JO (2016) The Scorpion Files. www.ntnu.no/ub/scorpion-files/buthidae.php (April 5, 2016).
- Risso A (1826) Les Scorpionides – Histoire Naturelle des principales productions de l’Europe méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes. Tome cinquième. F.-G. Levrault, Paris, 155–157.
- Roewer CF (1943) Über eine neuerworbene Sammlung von Skorpionen des Natur-Museums Senckenberg. Senckenbergiana 26: 205–244.
- Rossi A (2012) Notes on the distribution of the species of the genus *Buthus* (Leach, 1815) (Scorpiones, Buthidae) in Europe, with a description of a new species from Spain. Bulletin of the British Arachnological Society 15: 273–279.
- Rossi A (2013) A new species of the genus *Buthus* Leach, 1815 from Egypt (Scorpiones: Buthidae). Rivista del Museo Civico di Scienze Naturali “Enrico Caffi”, Bergamo 26: 187–194.

- http://www.museoscienzebergamo.it/web/images/stories/museo/Rivista_museo/26_volume/Rossi_2013_new_Buthus_from_Egypt.pdf (October 9, 2013).
- Rossi A (2017) The genus *Buthus* Leach, 1815 in the basin countries of the Gulf of Guinea with the description of a new species from Ghana (Scorpiones: Buthidae). *Onychium* 13: 9–15. <https://doi.org/10.5281/zenodo.546330>
- Rossi A, Tropea G (2016a) 1 On the presence of the genus *Buthus* Leach, 1815 in Sudan with the description of a new species from the enclave of Karora (Scorpiones: Buthidae). *Onychium* 12: 3–10. <https://doi.org/10.13156/arac.2012.15.1.273>
- Rossi A, Tropea G (2016b) A complementary study on the genus *Buthus* Leach, 1815 in Sudan with the description of a new species (Scorpiones: Buthidae). *Arachnida - Rivista Aracnologica Italiana* 8: 24–31.
- Rossi A, Tropea G, Yağmur EA (2013) A new species of *Buthus* Leach, 1815 from Libya (Scorpiones, Buthidae). *Euscorpius* 167: 1–10. http://www.science.marshall.edu/fet/euscorpius/p2013_167.pdf.
- Sabaj MH (2016) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Version 6.5 (16 August 2016). American Society of Ichthyologists and Herpetologists, Washington, DC. <http://www.asih.org/>.
- Sadílek D, Nguyen P, Koç H, Kovařík F, Yağmur EA, St'áhlavský F (2015) Molecular cytogenetics of *Androctonus* scorpions: an oasis of calm in the turbulent karyotype evolution of the diverse family Buthidae. *Biological Journal of the Linnean Society* 115: 69–76.
- Sadine SE, Alioua Y, Chenchouni H (2012) First data on scorpion diversity and ecological distribution in the National Park of Belezma, Northeast Algeria. *Serket* 13: 27–37.
- Sadine SE, Bissati S, Lourenço WR (2015) The first true deserticolous species of *Buthus* Leach, 1815 from Algeria (Scorpiones: Buthidae); Ecological and biogeographic considerations. *Comptes Rendus Biologies* 339: 44–49. <https://doi.org/10.1016/j.crv.2015.10.002>
- Sadine SE, Samia B, Ould Elhadj MD (2011) Premières données sur la diversité scorpionique dans la région du Souf (Algérie). *Arachnides* 61: 1–10.
- Schenkel E (1932) Notizen über einige Skorpione und Solifugen. *Revue Suisse de Zoologie* 39: 375–396.
- Schenkel E (1938) Spinnentiere von der Iberischen Halbinsel, gesammelt von Prof. Dr O. Lundblad, 1935. *Arkiv för Zoologi* 30A: 1–29.
- Schenkel E (1949) Mitteilungen über Spinnentiere. Skorpione aus Marokko. *Verhandlungen der Naturforschenden Gesellschaft in Basel* 60: 186–201.
- Sergeant E (1938) Iconographie des Scorpions de l'Afrique du Nord. *Archives de l'Institut Pasteur d'Algérie* 16: 513–522.
- Sergeant E (1941a) Sur le postabdomen (queue) de quelques scorpions de l'Afrique du Nord. *Archives de l'Institut Pasteur d'Algérie* 19: 353–357.
- Sergeant E (1941b) Sur le scorpion commun de l'Atlas blidéen, *Buthus occitanus* Amx. *Archives de l'Institut Pasteur d'Algérie* 19: 447–448.
- Serre M de (1822) Essai pour servir à l'histoire des animaux du midi de la France. Gabon, Paris and Montpellier, 95 pp.
- Sharma PP, Fernández R, Esposito LA, González-Santillán E, Monod L (2015) Phylogenomic resolution of scorpions reveals multilevel discordance with morphological phylogenetic

- signal. Proceedings of the Royal Society B: Biological Sciences 282: 2014295. <https://doi.org/10.1098/rspb.2014.2953>
- Shulov A, Amitai P (1959) Observations sur les Scorpions. *Buthus occitanus* ssp. *mardochei* var. *israelis* ar. nov. Archives de l'Institut Pasteur d'Algérie 37: 218–225.
- Simon E (1872) Arachnides de Syrie rapportés par M. Charles Piochard de la Brûlerie (Scorpions et Galeodes). Annales de la Société Entomologique de France, 5^{ème} série 2: 245–266.
- Simon E (1878) Études arachnologiques. 7e Mémoire. XIII. Descriptions de deux espèces de Scorpions. Annales de la Société Entomologique de France, 5^{ème} série 8: 158–160.
- Simon E (1879) 3e Ordre. Scorpion Thorell. In: Les Arachnides de France. VII. Les ordres des Chernetes, Scorpiones et Opiliones. Librairie Encyclopédique de Roret, Paris, 79–115.
- Simon E (1880) M. E. Simon montre quelques Scorpions qui lui ont été donnés par notre confrère M. Reiche, de la part de M. F. de Saulcy, qui les a reçus de Mossoul (ancienne Ninive), sur le Tigre, en Mésopotamie. Annales de la Société Entomologique de France, 5^{ème} série 10: 29.
- Simon E (1885) Étude sur les Arachnides recueillis en Tunisie en 1883 et 1884 par MM. A. Letourneux, M. Sédillot et Valéry Mayet, membres de la Mission de l'Exploration scientifique de la Tunisie. In: Exploration scientifique de la Tunisie. Zoologie – Arachnides. Imprimerie Nationale, Paris, 55 pp.
- Simon E (1899) Liste des arachnides recueillis en Algérie par M. P. Lesne et description d'une espèce nouvelle. Bulletin du Muséum d'Histoire Naturelle, Paris 5: 82–87.
- Simon E (1910) Révision des Scorpions d'Egypte. Bulletin de la Société Entomologique de d'Egypte 2: 57–87.
- Sissom WD (1990) Systematics, biogeography and paleontology. In: Polis GA (Ed.) Biology of scorpions. Stanford University Press, Stanford, 64–160.
- Skutelsky O (1995) Flexibility in foraging tactics of *Buthus occitanus* scorpions as a response to above-ground activity of termites. Journal of Arachnology 23: 46–47.
- Skutelsky O (1996) Predation risk and state-dependent foraging in scorpions: effects of moonlight on foraging in the scorpion *Buthus occitanus*. Animal Behaviour 52: 49–57. <https://doi.org/10.1006/anbe.1996.0151>
- Soleglad ME, Fet V (2003) High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). Euscorpius 11: 1–175. http://www.science.marshall.edu/fet/euscorpius/p2003_11.pdf.
- Sousa P, Froufe E, Alves PC, Harris DJ (2010) Genetic diversity within scorpions of the genus *Buthus* from the Iberian Peninsula: mitochondrial DNA sequence data indicate additional distinct cryptic lineages. Journal of Arachnology 38: 206–211. <https://doi.org/10.1636/H08-98.1>
- Sousa P, Harris DJ, Froufe E, van der Meijden A (2012) Phylogeographic patterns of *Buthus* scorpions (Scorpiones: Buthidae) in the Maghreb and South-Western Europe based on CO1 mtDNA sequences. Journal of Zoology 288: 66–75. <https://doi.org/10.1111/j.1469-7998.2012.00925.x>
- Sousa P (2017) Resilient arthropods: *Buthus* scorpions as a model to understand the role of past and future climatic changes on Iberian Biodiversity. PhD Thesis, Porto, Universidade do Porto, Portugal.

- Stahnke HL (1972) A key to the genera of Buthidae (Scorpionida). *Entomological News* 83: 121–133.
- Stockmann R, Ythier É (2010) *Scorpions of the World*. N.A.P Editions, Rodez, 572 pp. <http://www.napeditions.com/en/scorpions/20-scorpions-du-monde.html#idTab2>.
- Táborský K (1934) Sur les espèces du genre *Buthus* Leach du Muséum National de Prague (in Czech). *Sborník Zoologického Oddělení Národního Musea v Praze* [Acta Zoologica Musaei Nationalis Pragae] 1: 39–40.
- Tuerel R, Melic A (2015) Orden Scorpiones. *Revista IDE@ - SEA* 18: 1–17.
- Tuerel R, Pérez-Bote JL (2005) Complementos a la descripción de *Buthus ibericus* Lourenço and Vachon 2004 (Scorpiones: Buthidae). *Boletín de la Sociedad Entomológica Aragonesa* 37: 273–275.
- Thorell T (1876a) Études scorpiologiques. *Atti della Società Italiana di Scienze Naturali* 19: 75–272.
- Thorell T (1876b) I.— On the classification of Scorpions. *The Annals and Magazine of Natural History* (4th series) 17: 1–15. <https://doi.org/10.1080/00222937608681889>
- Thorell T (1893) Scorpiones exotici R. *Musei Historiae Naturalis Florentini. Bolletino della Società Entomologica Italiana* 25: 356–387.
- Touloun O (2012) Chapitre III. Ecologie et repartition de la scorpiofaune du Sud Ouest Marocain. In: *Les peuplements de scorpions du sud ouest marocain: Ecologie, Biogéographie et Epidémiologie des envenimations*. Éditions universitaires européennes, Saarbrücken, 30–82.
- Touloun O, Boumezzough A (2011a) 1 Une nouvelle espèce du genre *Buthus* Leach, 1815 (Scorpiones: Buthidae) du Maroc. *Boletín de la Sociedad Entomológica Aragonesa* 48: 183–187. <http://www.sea-entomologia.org/PDF/BSEA48ARACNO/B48183.pdf>.
- Touloun O, Boumezzough A (2011b) Contribution à l'inventaire et à la répartition des scorpions de la province de Sidi Ifni (Maroc). *Poiretia* 3: 8–15.
- Touloun O, Boumezzough A, Stockmann R, Slimani T (2008) Nouvelles précisions sur la biologie et le statut taxonomique de *Buthus bonito* Lourenço and Geniez, 2005 (Scorpiones, Buthidae) au Maroc. *Arachnides*: 1–30. <http://s1.e-monsite.com/2009/01/24/458084arachnides-54-pdf>.
- Touloun O, El Hidan MA, Boumezzough A (2016) Species composition and geographical distribution of Saharan scorpion fauna, Morocco. *Asian Pacific Journal of Tropical Disease* 6: 878–881. [https://doi.org/10.1016/S2222-1808\(16\)61150-7](https://doi.org/10.1016/S2222-1808(16)61150-7)
- Touloun O, Elhidan MA, Boumezzough A (2014) Inventory and distribution of scorpion fauna in eastern Morocco (Arachnida, Scorpiones). *Serket* 14: 72–79.
- Touloun O, Slimani T, Boumezzough A (1999) Découverte au Maroc de *Buthus occitanus tunetanus* var. *neeli* Gysin, 1969 (Scorpiones, Buthidae). *Arachnides* 41: 28–30.
- Touloun O, Slimani T, Boumezzough A (2001) Epidemiological survey of scorpion envenomation in southwestern Morocco. *Journal of Venomous Animals and Toxins* 7: 1–9. <https://doi.org/10.1590/S0104-79302001000200006>
- Tullgren A (1909) Solifugae, Scorpiones und Chelonethi aus Ägypten und dem Sudan. In: *Results of the Swedish Zoological Expedition to Egypt and the White Nile 1901, under*

- the direction of L.A. Jägerskiöld. Part III. The Library of the Royal University of Uppsala, Uppsala, 1–12.
- Udvardy MDF (1975) A Classification of the Biogeographical Provinces of the World. IUCN Occas. IUCN, Morges, 50 pp. <http://cmsdata.iucn.org/downloads/udvardy.pdf>.
- Vachon M (1940) Sur la systématique des scorpions. Mémoires du Muséum national d'Histoire naturelle, Nouvelle Série, Paris 13: 241–260.
- Vachon M (1941) Remarques biogéographiques sur quelques Scorpions et Pseudoscorpions pré-désertiques. Compte-rendu sommaire des Séances de la Société de Biogéographie 18: 50–53.
- Vachon M (1948a) Études sur les Scorpions. III. Description des Scorpions du Nord de l'Afrique. Archives de l'Institut Pasteur d'Algérie 26: 162–208.
- Vachon M (1948b) 3 Études sur les Scorpions. III (suite). Description des Scorpions du Nord de l'Afrique. Archives de l'Institut Pasteur d'Algérie 26: 288–316.
- Vachon M (1948c) Scorpions récoltés dans l'île de Crète par Mr le docteur Otto Von Wettstein. Annalen des Naturhistorischen Museums in Wien 56: 61–69. <http://www.jstor.org/stable/41768480>.
- Vachon M (1949a) Études sur les Scorpions. III (suite). Description des Scorpions du Nord de l'Afrique. Archives de l'Institut Pasteur d'Algérie 27: 134–169.
- Vachon M (1949b) Études sur les Scorpions. III (suite). Description des Scorpions du Nord de l'Afrique. Archives de l'Institut Pasteur d'Algérie 27: 281–288.
- Vachon M (1949c) Études sur les Scorpions. III (suite). Description des Scorpions du Nord de l'Afrique. Archives de l'Institut Pasteur d'Algérie 27: 334–396.
- Vachon M (1950a) Études sur les Scorpions. III (suite). Détermination des scorpions du Nord-Ouest de l'Afrique. Archives de l'Institut Pasteur d'Algérie 28: 152–216.
- Vachon M (1950b) Études sur les Scorpions. (suite). Description des Scorpions du Nord-ouest de l'Afrique. Archives de l'Institut Pasteur d'Algérie 28: 382–413.
- Vachon M (1951a) Études sur les Scorpions. (suite et fin). Détermination des Scorpions du Nord-Ouest de l'Afrique. Archives de l'Institut Pasteur d'Algérie 29: 46–104.
- Vachon M (1951b) Scorpions collectés au Maroc par MM. P. Strinati et V. Aellen (Mission scientifique Suisse au Maroc, août-septembre 1950). Bulletin du Muséum National d'Histoire Naturelle, Paris, 2^{ème} série 23: 621–623.
- Vachon M (1952a) Études sur les scorpions. (published 1948–1951 in Archives de l'Institut Pasteur d'Algérie, 1948, 26: 25–90, 162–208, 288–316, 441–481; 1949, 27: 66–100, 134–169, 281–288, 334–396; 1950, 28: 152–216, 382–413; 1951, 29: 46–104). Institut Pasteur d'Algérie, Alger, 482 pp. <https://www.ntnu.no/ub/scorpion-files/vachon.php>.
- Vachon M (1952b) Le Scorpion Languedocien et sa répartition en France à propos de sa présence dans le Département de l'Ardèche. Bulletin du Muséum National d'Histoire Naturelle, Paris, 2^{ème} série 24: 274–279.
- Vachon M (1953) Contribution à l'étude du peuplement de la Mauritanie. Scorpions. Bulletin de l'Institut français d'Afrique Noire 15: 1012–1028.
- Vachon M (1955) Remarques préliminaires sur la faune des scorpions du Soudan Oriental. Bulletin du Muséum National d'Histoire Naturelle, Paris, 2^e Série 27: 371–373.

- Vachon M (1958) Scorpionidea (Chelicerata) de l'Afghanistan. The 3rd Danish Expedition to Central Asia. (Zoological Results 23). Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i København 120: 121–187.
- Vachon M (1961) Le Parc national de Niokolo-Koba. III. Scorpions. Mémoires de l'Institut Français d'Afrique Noire 62: 31–32.
- Vachon M (1963) De l'utilité, en systématique, d'une nomenclature des dents de chelicères chez les Scorpions. Bulletin du Muséum National d'Histoire Naturelle, Paris, 2e Série 35: 161–166.
- Vachon M (1966) Liste des scorpions connus en Egypte, Arabie, Israeli, Liban, Syrie, Jordanie, Turquie, Irak, Iran. Toxicon 4: 209–218.
- 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, 3e Série Zoologie 104: 857–958. http://bibliotheques.mnhn.fr/medias/doc/EXPLOITATION/IFD/BMZOO_S003_1973_T140_N104/bulletin-du-museum-national-d-histoire-naturelle-zoologie.
- Vachon M (1975) Sur l'utilisation de la trichobothriotaxie du bras des pédipalpes des scorpions (Arachnides) dans le classement des genres de la famille des Buthidae Simon. Comptes rendus hebdomadaires des séances de l'Académie des sciences, Série D, Sciences naturelles 281: 1597–1599.
- Vachon M, Kinzelbach R (1987) On the taxonomy and distribution of the scorpions of the Middle East. In: Krupp F, Schneider W, Kinzelbach R (Eds) Proceeding of the Symposium on the Fauna and Zoogeography of the Middle East, Mainz, 1985. (Beihefte zum Tübingen Atls des Vorderen Orients). Reichert Verlag, Wiesbaden, 91–103.
- van der Meijden A, Kleinteich T, Coelho PL (2012) Packing a pinch: Functional implications of chela shapes in scorpions using finite element analysis. Journal of Anatomy 220: 423–434. <https://doi.org/10.1111/j.1469-7580.2012.01485.x>
- Various (2016) Félix Gaffiot. Dictionnaire Latin Français. Nouvelle édition revue et augmentée. GAFFIOT 20. Gréco G, de Wilde M, Maréchal B, Ôkubo K (Eds). http://gerardgreco.free.fr/IMG/pdf/Gaffiot_2016_-_komarov.pdf.
- Vigna Taglianti A, Audisio PA, Biondi M, Bologna MA, Carpaneto GM, De Biase A, Fattorini S, Piattella E, Sindaco R, Venchi A, Zapparoli M (1999) A proposal for a chorotype classification of the Near East fauna, in the framework of the Western Palearctic region. Biogeographia 20: 31–59.
- Vincent M (1994) Observation de *Buthus occitanus* (Amoreux, 1789) (Scorpionida, Buthidae) dans la région de Manosque (Alpes de Haute-Provence). Arachnides 22: 6–7.
- Vincke C, Diédhiou I, Grouzis M (2010) Long term dynamics and structure of woody vegetation in the Ferlo (Senegal). Journal of Arid Environments 74: 268–276. <https://doi.org/10.1016/j.jaridenv.2009.08.006>
- Volschenk ES, Mattoni CI, Prendini L (2008) Comparative anatomy of the mesosomal organs of scorpions (Chelicerata, Scorpiones), with implications for the phylogeny of the order. Zoological Journal of the Linnean Society 154: 651–675. <https://doi.org/10.1111/j.1096-3642.2008.00426.x>

- Werner F (1902) Die Skorpione, Pedipalpen und Solifugen in der zoologisch-vergleichend-anatomischen Sammlung der Universität Wien. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 52: 595–608.
- Werner F (1925) Skorpione und Solifugen aus dem östlichen und nördlichen Spanien, gesammelt von Dr. F. Haas in den Jahren 1914–1918. Senckenbergiana 7: 209–210.
- Werner F (1929) Wissenschaftliche Ergebnisse einer zoologischen Forschungsreise nach Westalgerien und Marokko. III. Scorpiones. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Wien 138: 1–34. http://www.zobodat.at/publikation_articles.php?id=169321.
- Werner F (1932) Ergebnisse einer zoologischen Forschungsreise nach Marokko. VI. Skorpione. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Wien 141: 285–306. http://www.zobodat.at/publikation_articles.php?id=180394.
- Werner F (1934a) Scorpiones, Pedipalpi. In: Bronn HG (Ed.) Klassen und Ordnungen des Tierreichs. Band 5: Arthropoda, Abteilung 4: Arachnoidea, Buch 8. Akademische Verlagsgesellschaft, Leipzig, 490 pp.
- Werner F (1934b) Über skorpione aus Marokko. Verhandlungen der Naturforschenden Gesellschaft in Basel 45: 82–88.
- Werner F (1936) Neu-Eingänge von Skorpionen im Zoologischen Museum in Hamburg. Festschrift zum 60. Geburtstage von Professor Dr. Embrik. Strand, Riga 2: 171–193.
- Winston JE (1999) Describing Species: Practical Taxonomic Procedure for Biologists. Columbia University Press, New York, 512 pp. <http://www.jstor.org/stable/10.7312/wins06824>.
- Yağmur EA, Koç H, Lourenço WR (2011) A new species of *Buthus* Leach, 1815 from Cyprus (Scorpiones, Buthidae). ZooKeys 14: 27–38. <https://doi.org/10.3897/zookeys.115.1135>
- Yang X, Norma-Rashid Y, Lourenço WR, Zhu M-S (2013) True lateral eye numbers for extant buthids: a new discovery on an old character. PloS One 8: e55125. <https://doi.org/10.1371/journal.pone.0055125>

Study on Tullbergiidae of Tibet, China I. *Metaphorura*, *Mesaphorura* and *Prabhergia* (Hexapoda, Collembola)

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Abstract

The Tullbergiidae of Tibet is studied for the first time and the genus *Metaphorura* Bagnall, 1936 is firstly recorded in China. *Metaphorura motuoensis* **sp. n.** from southeastern Tibet is described and illustrated. It is characterized by the presence of 1+1 pseudocelli on thoracic segment I, few vesicles (14–16) on PAO, pseudocellar formula as 11/111/11111, all pseudocelli of type II, setae p4 on abdominal segment V as microsetae, weakly differentiated sensory seta p3 on abdominal segment V, absence of median process on Abd VI. In addition, *Mesaphorura yosii* (Rusek, 1967), *Mesaphorura hylophila* Rusek, 1982, and *Prabhergia imadatei* Tamura & Zhao, 1996 are recorded in Tibet for the first time. The type specimens of *P. imadatei* are re-examined and errors in the original description of chaetotaxy are corrected.

Keywords

chaetotaxy, Motuo, postantennal organ, pseudocelli

Introduction

The knowledge of the taxonomy of Tullbergiidae from China is quite insufficient and only five species have been recorded to date (Rusek 1967; Tamura and Zhao 1996; Gao 2007; Bu et al. 2013; Bu and Gao 2015). There are no records of Tullbergiidae from Tibet. During an investigation of soil arthropods in southeast Tibet in November 2015,

nearly 200 specimens belonging to the family Tullbergiidae were obtained. They were identified as four species including one new species of the genus *Metaphorura* Bagnall, 1936. The new species is illustrated and described in the present paper.

Materials and methods

Specimens were collected by Berlese-Tullgren funnels and preserved in 80% ethanol. The material was mounted on slides in Hoyer's solution and dried in an oven at 60 °C for identification. Observations were done with a phase contrast microscope. Photos were taken by a digital camera installed on the microscope. The type specimens are deposited in Shanghai Natural History Museum (SNHM), Shanghai, China. In the description we use the nomenclature for morphological features following Dunger and Schlitt (2011). Pseudocellar types after Weiner and Najt (1991). Antennal chaetae notation is made following the notation of Rusek (1971). Formula of tibiotarsal chaetotaxy follows Fjellberg (1991).

Abbreviations used in the descriptions:

Th.	thoracic segment,
Abd.	abdominal segment,
Ant.	antennal segment,
Asp.	anal spine,
s	sensillum,
PAO	postantennal organ,
a	anterior setae,
m	medial setae,
p	posterior setae,
pl	pleural setae,
pso	pseudocelli.

Results

Taxonomy

Genus *Metaphorura* Bagnall, 1936

Diagnosis. Habitus more or less slender. Granulation of the integument moderately fine, with stronger granulation only on head and areas of Abd VI. Usually no crescentic ridges. A median process usually present ventrally between Asp. Antennal segment III with two large sensory clubs, bent towards one another, two small sensory rods and three protecting papillae. Postantennal organ with 14–28 vesicles in two rows. Pseudocelli clearly delimited, with two rows of parallel stripes in the centre (type II). Asp strong, distinctly longer than the claw of leg III.

Distribution. The genus *Metaphorura* includes nine species found in Holarctic regions (Dunger and Schlitt 2011; Bellinger et al. 1996–2017). It is newly recorded from China in this paper.

***Metaphorura motuoensis* sp. n.**

<http://zoobank.org/A71C4114-150F-4A47-9F13-85C7D712B1B8>

Figs 1–24, Table 1

Material examined. Holotype, female (slide no. XZ-C2015014) (SNHM), China, Tibet, Motuo county, Dexing town, extracted from soil samples in broad-leaved forest, Alt. 1100 m, 29°40'N, 95°26'E, 3-XI-2015, coll. Y. Bu & G. Yang. Paratypes, 8 females (slides nos. XZ-C2015008–XZ-C2015013, XZ-C2015015, XZ-C2015037) (SNHM), 10 males (slides nos. XZ-C2015016–XZ-C2015025), same data as holotype. Other material: 1 male (slide no. XZ-C2015095) (SNHM), China, Tibet, Linzhi, Sejila Mt., extracted from soil samples under bushes, Alt. 3500 m, 29°67'N, 95°70'E, 1-XI-2015, coll. Y. Bu & G. Yang; 17 juveniles (slides nos. XZ-C2015026, XZ-C2015027, XZ-C2015106–XZ-C2015112) (SNHM), 45 adults in alcohol, same data as holotype.

Diagnosis. *Metaphorura motuoensis* sp. n. is characterized by the presence of pseudocelli on thoracic segment I, few simple vesicles (14–16) on PAO, pseudocellar formula as 11/111/11111, all pseudocelli of type II, p4 on abdominal segment V as microsetae, less differentiated sensory setae p3 on abdominal segment V, absence of median process on Abd VI. Bisexual.

Description. Adult *body* 0.86 mm long in average (0.72–0.95 mm, $n = 19$), holotype 0.93 mm (Fig. 1). Both female and male were present. Setae well differentiated into micro- and macrosetae. Granulation of integument moderately fine (2.5–3.0 μm), with stronger granulation only on head and Abd. VI (4–5 μm). (Figs 1, 2, 23). Pseudocellar formula: 11/111/11111. All pseudocelli composed by two rows of parallel stripes in the center (type II, Figs 7–14), 7–8 μm in diameter, on Th. I between seta m2 and m3, close to hind margin; on Th. II and III between setae p3/p4, close to p3; on Abd. I–III posterior to seta p3; on Abd. IV parallel to seta p3; on Abd. V on the border of Abd. VI.

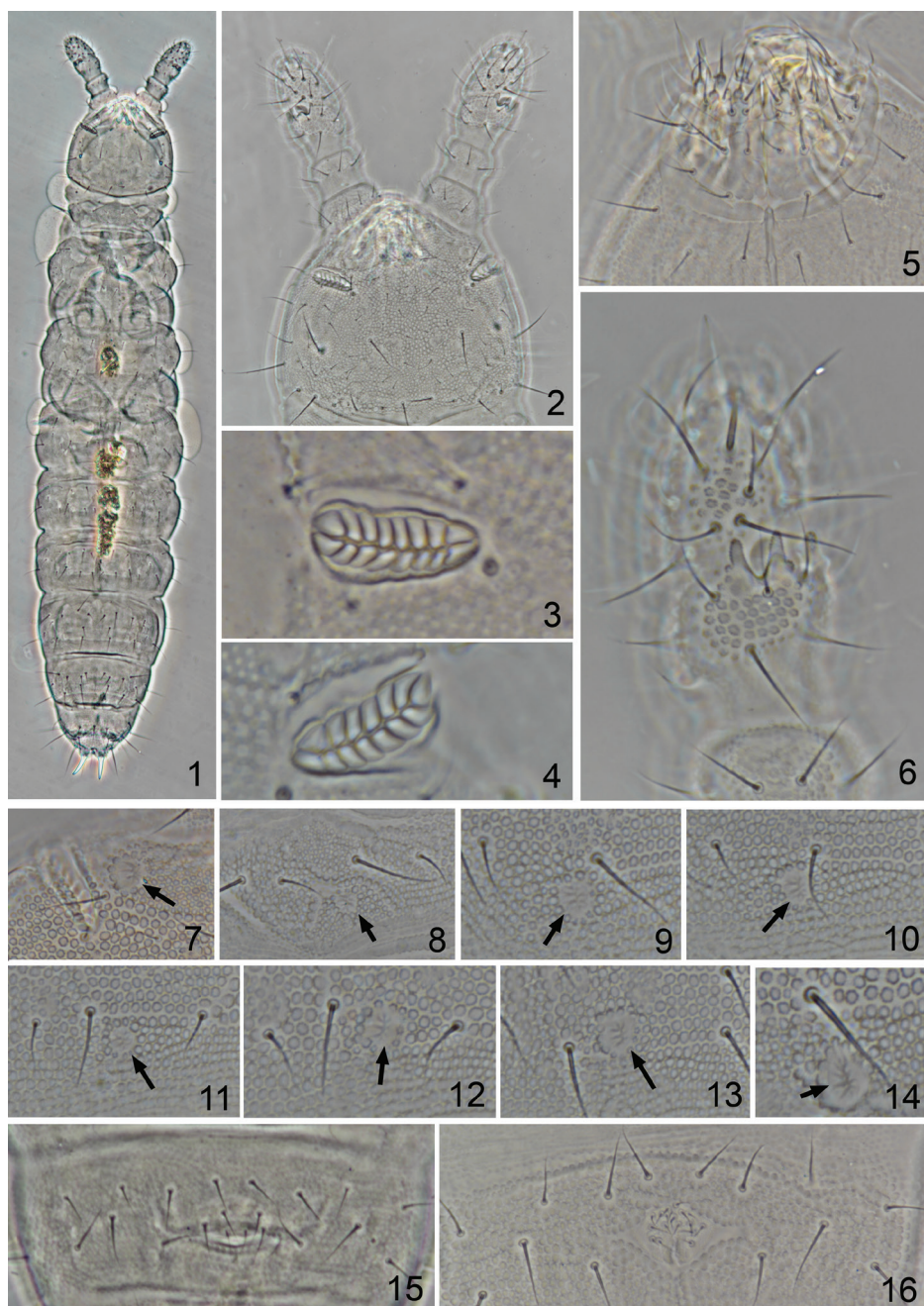
Head seta a0 present (18–20 μm), c1 absent, oc2 as macroseta (23–25 μm), sd5 as mesoseta (18–21 μm) (Fig. 2). Postantennal organ 23–26 μm long, 7–8 μm wide, composed of 14–16 elliptical vesicles arranged in two rows (Figs 2, 3), situated in a

Table 1. Dorsal Chaetotaxy of *Metaphorura motuoensis* sp. n.

Row	Thorax			Abdomen				
	I	II	III	I	II	III	IV	V
a	-	10	10	10	10	10	8 ³	10 ⁵
m	8	8	8	2 ¹	4 ²	4 ²	4 ²	-
p	-	8	8	10	10	10	8 ⁴	8 ⁶
pl	2	3	3	2	3	3	6	1

¹ seta m4 present; ² seta m3 and m4 present; ³ seta a5 absent; ⁴ seta p4 absent; ⁵ seta a2 and p4 as microseta;

⁶ sensory seta p3 slightly differentiated, seta p4 as microseta.



Figures 1–16. *Metaphorura motuoensis* sp. n. (Holotype) **1** Habitus, dorsal view **2** head, dorsal view **3** Left postantennal organ **4** Right postantennal organ (paratype XZ-C2015016) **5** Labium **6** Antenna, segments II–IV, dorsal view **7** Pseudocellus on anterior of head **8** Pseudocellus on Th. I **9** Pseudocellus on Th. II **10** Pseudocellus on Th. III **11** Pseudocellus on Abd. I **12** Pseudocellus on Abd. II **13** Pseudocellus on Abd. IV **14** Pseudocellus on Abd. V **15** Female genital plate **16** Male genital plate (paratype XZ-C2015021). Arrows in figs 7–14 indicate the pseudocelli.

deep furrow (Fig. 7). Labrum with 4/4/2 setae. Labium with five papillae, six apical guard setae, six proximal setae, four basomedian setae, and five basolateral setae (Fig. 5). Ventral head with 3+3 axial setae.

Antenna (100–115 μm) shorter than head (130–135 μm). Ant. I and II with seven and eleven setae respectively (Figs 17, 18). Ant. segment IV with five slightly thickened sensilla a–e, sensilla a, c, e long and slightly curved toward inside, b and d slightly short (Fig. 17). Small microsensillum, subapical organite and one large apical vesicle present (Fig. 17). Antennal organ III with two small sensory rods between two thick sensory clubs bent toward each other, concealed behind three papillae and four guard setae (Figs 6, 17, 18).

Legs without clavate tenant hairs (Fig. 19). Subcoxa, coxa, trochanter, femur, and tibiotarsus with 0/3/3; 3/7/7; 5/5/4; 8/8/8; 10/10/10 setae on leg I, II and III, respectively (Fig. 19), tibiotarsi each with 6+4 setae (A1 to A6, B4 to B7, and M absent). Anal lobes with setae 12' and 13' (Fig. 24). Claw 20–23 μm long, untoothed, with short empodial appendage (3–4 μm).

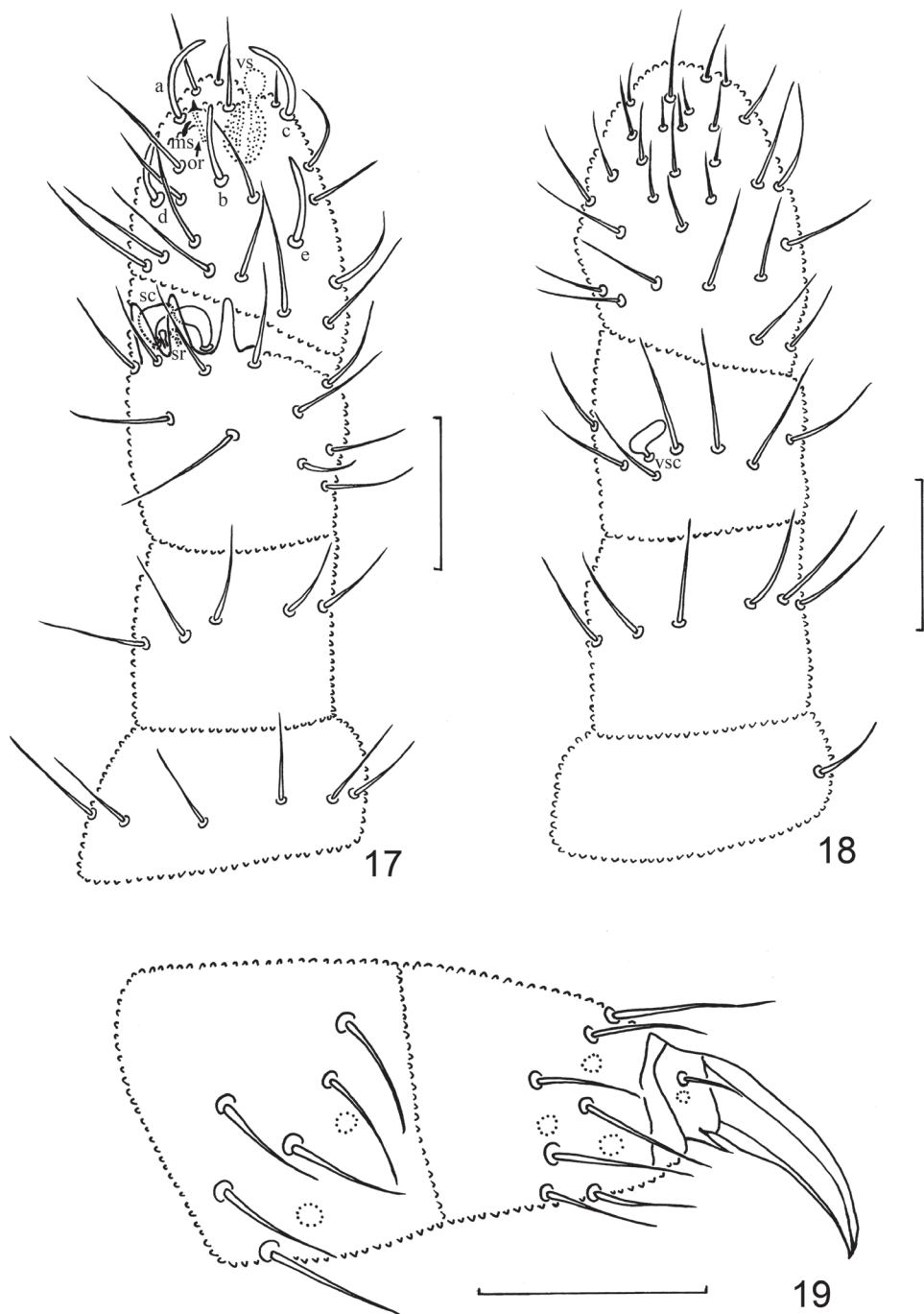
Adult chaetotaxy given in Figs 21–24 and Table 1. Setae on Th. I length as 10–13 μm for m1 and m3, 20–26 μm for m2 and m4 (Fig. 20). Microsensilla present on Th. II–III, and lateral sensory setae s 23–26 μm long (Fig. 20). Thorax with 0, 2, 2 ventral setae. Abd. I–III each with 2+2 axial setae dorsally, setae m4 present on Abd. I, setae m3 and m4 present on Abd. II–III. Abd. IV without seta px, setae m3 and m4 present. Abd. V with sensory seta p3 (24 μm) slightly differentiated; seta a2 as mesoseta (20–22 μm) and p4 as microsetae (Fig. 23). Crescentic ridges on Abd. VI present. Abd. VI with distinct dorsal secondary granulations, without median process between the anal spines (Fig. 23). Anal spines 28–32 μm long (Fig. 23).

Number of *ventral setae* on Abd. II, III and IV variable, with 18–20, 19–23, and 22–26 setae respectively (Fig. 24). Ventral tube with 4+4 apical setae and 2+2 basal setae (Fig. 24). Female genital plate with 3 pairs of pregenital setae, 2–3 pairs of circumgenital and one pair of eugenital setae (Fig. 15). Male genital plate with 3 pairs of pregenital setae, 6–9 pairs circumgenital setae and 1+1 eugenital setae (Fig. 16).

Etymology. The species is named after the Motuo county where the type specimens were collected.

Distribution. Known only from the type locality.

Remarks. There are two genera of Tullbergiidae with two anal spines, three protecting papillae, three thick sensory clubs on antennal segment III, and an elongate PAO and body longer than 0.7 mm: *Delamarephorura* and *Metaphorura*. The new species better fits *Delamarephorura* in the presence of crescent ridges on Abd. VI, which are absent in *Metaphorura*, and the presence of a “median process” on Abd. VI which is present in *Metaphorura* (present or absent in *Delamarephorura*). However, according to Janion et al (2013): “the discrimination between *Delamarephorura* and *Metaphorura* needs to be re-evaluated” for uncertainties about the state of some diagnostic characters. The new species is therefore provisionally assigned to the genus *Metaphorura*, awaiting the validation of *Delamarephorura*. Biogeographically, Tibet is part of the Holarctic region where the genus *Metaphorura* is distributed, while *Delamarephorura* is only known in Africa and in Vietnam.



Figures 17–19. *Metaphorura motuoensis* sp. n. (Holotype) **17** Antenna, dorsal view, a, b, c, d, e—large sensilla, ms—microsensillum, or—subapical organite, vs— apical vesicles, sc—sensory clubs, sr—sensory rods **18** Antenna, ventral view, vsc—ventral sensory club **19** Leg III. Scale bars 20 μ m.

Metaphorura motuoensis sp. n. has few simple vesicles (14–16) on PAO and lacks the median process on Abd. VI which clearly separate it from other congeners. It is similar to *M. affinis* (Börner, 1902) in the presence of simple vesicles on PAO and the pseudocellar formula on the body, but differs in the presence of a crescentic ridge on Abd. VI, fewer vesicles on PAO (20–25 vesicles in *M. affinis*), two pairs of m-setae m3 and m4 on Abd IV (three pairs of m-setae in *M. affinis*: m2, m3, m4), and absence of median process on Abd. VI (presence of a pointed projection in *M. affinis*) and less differentiated sensory seta p3 on abdominal segment V (flame-like p3 in *M. affinis*). It is even more similar to *Delamarephorura capensis* Janion, Deharveng & Weiner, 2013, from which it differs by seta p1 on head much longer than p2 (versus of same size in *D. capensis*).

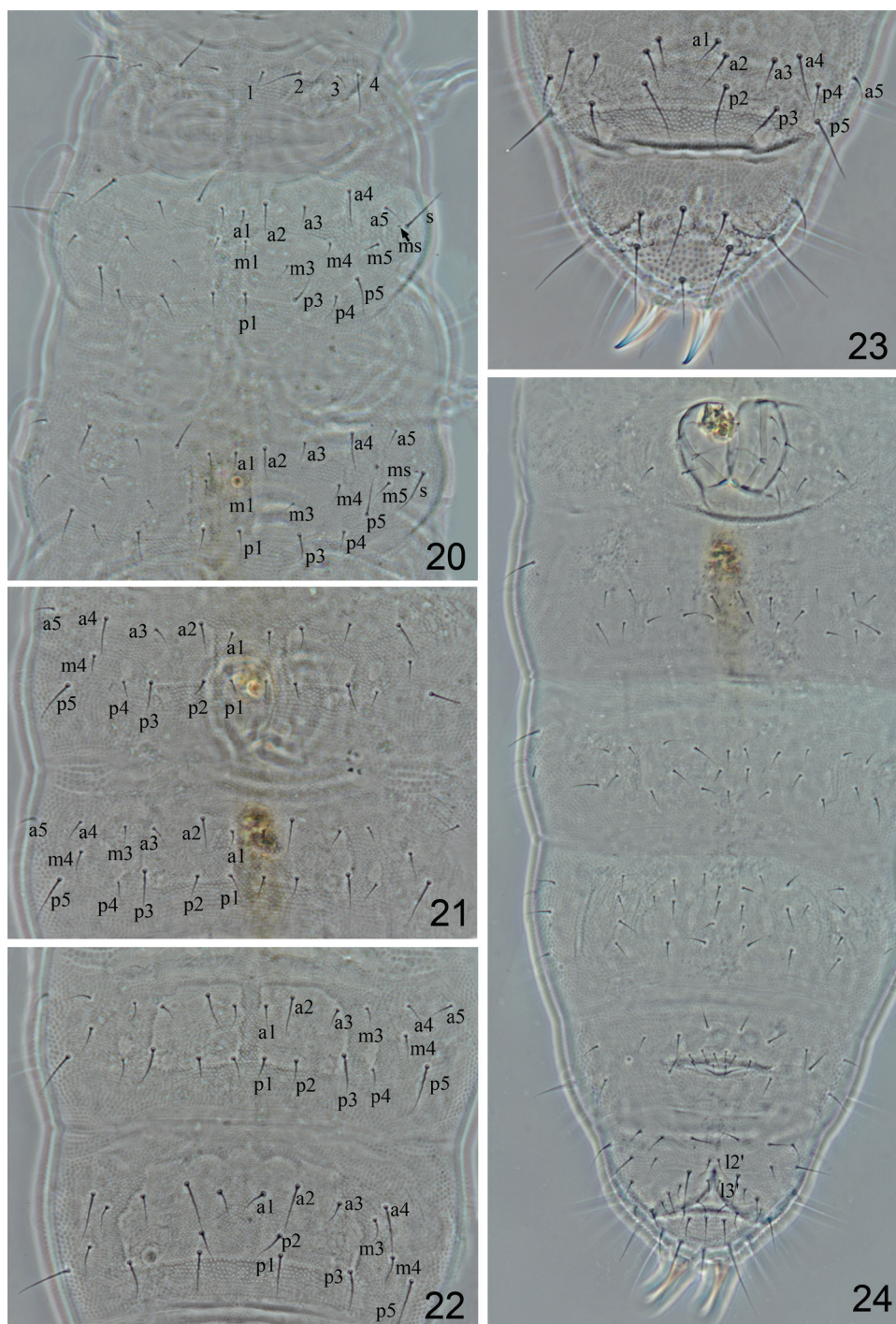
Mesaphorura yosii (Rusek, 1967)

Material examined. 2 female, 1 juvenile (slides nos. XZ-C2015064, XZ-C2015065) (SNHM), China, Tibet, Linzhi, Sejila Mt., extracted from soil samples under bushes, Alt. 3500 m, 29°67'N, 95°70'E, 1-XI-2015, coll. Y. Bu & G. Yang; 7 females (slides nos. XZ-C2015007, XZ-C2015028, XZ-C2015029, XZ-C2015038, XZ-C2015073, XZ-C2015105, XZ-C2015134), 4 juvenile (slides no. XZ-C2015030, XZ-C2015073, XZ-C2015113) (SNHM), China, Tibet, Motuo county, Dexing town, extracted from soil samples in broad-leaved forest, Alt. 1100 m, 29°40'N, 95°26'E, 3-XI-2015, coll. Y. Bu & G. Yang. 32 females (slides nos. XZ-C2015039–XZ-C2015049, XZ-C2015075–XZ-C2015077, XZ-C2015142, XZ-C2015143), 3 juveniles (slides no. XZ-C2015050, XZ-C2015076) (SNHM) and 20 adults in alcohol, China, Tibet, Motuo county, Beibeng town, extracted from soil samples in broad-leaved forest, Alt. 1500 m, 29°30'N, 95°38'E, 5-XI-2015, coll. Y. Bu & G. Yang. 18 females (slides nos. XZ-C2015051, XZ-C2015052, XZ-C2015054, XZ-C2015085, XZ-C2015168–XZ-C2015172), 1 juvenile (No. XZ-C2015053) (SNHM), China, Tibet, Linzhi City, Bomi county, Songzong town, extracted from soil samples in broad-leaved forest, Alt. 3000 m, 29°76'N, 95°96'E, 7-XI-2015, coll. Y. Bu & G. Yang. 32 females (slides nos. XZ-C2015178–XZ-C2015184) (SNHM), China, Tibet, Linzhi City, Lulang forest farm, extracted from soil samples in coniferous forest, Alt. 2459 m, 29°98'N, 95°33'E, 9-XI-2015, coll. Y. Bu & G. Yang.

Distribution. Cosmopolitan. In China the species was recorded in Fujian, Guangdong, Hunan, Shandong, Shanghai, Yunnan, Zhejiang, and for the first time in Tibet in this paper.

Mesaphorura hylophila Rusek, 1982

Material examined. 11 females (slides nos. XZ-C2015083, XZ-C2015153, XZ-C2015154, XZ-C2015171, XZ-C2015172), 1 juvenile (No. XZ-C2015053)



Figures 20–24. *Metaphorura motuoensis* sp. n. (Holotype) **20** Th. I–III, dorsal view, s–sensillum, ms–microsensillum **21** Abd. I–II, dorsal view **22** Abd. III–IV, dorsal view **23** Abd. V–VI, dorsal view **24** Abdomen, ventral view.

(SNHM), China, Tibet, Linzhi City, Bomi county, Songzong town, extracted from soil samples on broad-leaved forest, Alt. 3000 m, 29°76'N, 95°96'E, 7-XI-2015, coll. Y. Bu & G. Yang.

Distribution. Widely distributed in Palaearctic region. In China the species was recorded in Hebei (Bu and Gao 2017) and for the first time in Tibet in this paper.

Prabhergia imadatei Tamura & Zhao, 1996

Material examined. 1 female (slide no. XZ-C2015071) (SNHM), China, Tibet, Motuo county, Dexing town, extracted from soil samples in broad-leaved forest, sample 4, Alt. 1480 m, 29°45'N, 95°28'E, 3-XI-2015, coll. Y. Bu & G. Yang. Holotype (SEM). female, China, Yunnan, Mengla county, Menglun town, Xishuangbanna Tropical Botanic Garden, Alt. 550 m, 28-X-1992. Paratypes (SEM), 4 females, same data as for holotype.

Distribution. The species was only known from its type locality in Yunnan Province, southeast China. It is here recorded for the first time in Tibet.

Remarks. The description of dorsal chaetotaxy of *Prabhergia imadatei* in the original paper contains some errors, such as nominations and numbers of anterior and medial setae on Th. II and III, Abd. I–V. The type specimens were examined and a revised dorsal chaetotaxy of the species is given below in Table 2.

Table 2. Dorsal Chaetotaxy of *Prabhergia imadatei* (revised).

Row	Thorax			Abdomen				
	I	II	III	I	II	III	IV	V
a	-	10	10	10	10	10	8 ³	10 ⁵
m	8	6 ¹	6 ¹	2 ²	2 ²	2 ²	2 ⁴	-
p	-	8	8	10	10	10	10	6 ⁶
pl	2	3	3	2	2	2	6	1

¹ seta m1, m4, m5 present; ² seta m3 present; ³ seta a5 absent; ⁴ seta m4 present; ⁵ seta a2 and a4 as macroseta; ⁶ setae p2 and p4 absent, sensory seta p3 slightly differentiated.

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References

- Bellinger PF, Christiansen KA, Janssens F (1996–2017) Checklist of the Collembola of the World. <http://www.collembola.org> [Accessed 30 March 2017]
- Bu Y, Gao Y (2015) *Paratullbergia* Womersley in China: the description of a new species and a key to the genus (Collembola, Tullbergiidae). *ZooKeys* 534: 55–60. <https://doi.org/10.3897/zookeys.534.6036>
- Bu Y, Gao Y (in press) Two newly recorded species of *Mesaphorura* (Collembola, Tullbergiidae) from China. *Entomotaxonomia*.
- Bu Y, Potapov MB, Gao Y (2013) A new species and new records of Pachytullbergiidae and Tullbergiidae (Collembola: Onychiuroidea) from littoral of China, with notes on the variations of postantennal organ. *Zootaxa* 3669(2):139–146. <https://doi.org/10.11646/zootaxa.3669.2.4>
- Dunger W, Schlitt B (2011) Synopses on Palaearctic Collembola: Tullbergiidae. *Soil Organisms* 83(1): 1–168.
- Fjellberg A (1991) Tibiotarsal chaetotaxy in Tullbergiinae (Collembola: Onychiuridae). *Entomologica scandinavica* 21: 431–434. <https://doi.org/10.1163/187631290X00337>
- Gao Y (2007) Studies on the Systematics of Collembola and Soil Zooecology [Ph. D. Dissertation]. Shanghai Institutes for Biological Sciences, Chinese Academy of Sciences. Shanghai, 99 pp.
- Janion C, Deharveng L, Weiner WM (2013) Synonymy of *Spicattella* Thibaud, 2002 with *Delamarephorura* Weiner and Najt, 1999, and description of two new species (Collembola: Tullbergiidae). *Raffles Bulletin of Zoology* 61: 657–663.
- Jordana R, Arbea JJ, Simón C, Lucíañez MJ (1997) Fauna Ibérica. Vol. 8. Collembola, Poduromorpha. Museo Nacional de Ciencias Naturales, CSIC, Madrid, 807 pp.
- Rusek J (1967) Beitrag zur Kenntnis der Collembola (Apterygota) Chinas. *Acta Entomologica Bohemoslovaca* 64: 184–194.
- Rusek J (1971) Zur Taxonomie der Tullbergia (*Mesaphorura*) krausbaueri (Börner) und ihrer verwandten (Collembola). *Acta Entomologica Bohemoslovaca* 68: 188–206.
- Tamura H, Zhao L (1996) Two species of the subfamily Tullbergiinae in Xishuangbanna, southwest China (Collembola: Onychiuridae). *Japanese Journal of Entomology* 64(4): 790–794.
- Weiner WM, Najt J (1991) Collembola Poduromorpha de Nouvelle-Calédonie. 6. Onychiuridae Tullbergiinae. In: Chazeau J, Tillier S (Eds) *Zoologia Neocaledonica*, Volume 2. Mémoires du Muséum National d'Histoire Naturelle (A) 149: 119–130.

First report of the leaf-mining genus *Antispila* Hübner, [1825] from mainland China, with the description of a new species feeding on *Cornus* (Lepidoptera, Heliozelidae)

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Abstract

The genus *Antispila* Hübner, [1825] is newly recorded from mainland China. *Antispila sinensis* sp. n., the first formally named Heliozelidae species in mainland China, is described. The host plant of the new species, *Cornus walteri* Wangerin (Cornaceae), is widespread through east Asia and is used as a shade tree in city parks in Jinan City, where the moth causes damage to foliage. Morphological and molecular analyses distinguish *A. sinensis* sp. n. from its close relatives. The adult, pupa, larva, host plant, leaf-mines, and the shield of the new species are illustrated, as are male and female genitalia, venation, and larval chaetotaxy. DNA barcodes of the new species are also provided.

Keywords

Antispila, China, *Cornus walteri*, DNA barcode, Heliozelidae, Lepidoptera, new record, new species

Introduction

Leaf-mining moths, small and large (Liu and Yan 2017), are poorly investigated in China and those in the family Heliozelidae are no exception. Unlike the situation in Europe and North America, Chinese leaf-mining moths are generally known only from their capture at light and a more comprehensive investigation by rearing is required.

The family Heliozelidae comprises 125 described species in 12 genera, with the largest diversity in North America and Australia (van Nieukerken et al. 2011, 2012, 2015). Although an unidentified *Heliozela* sp. from Taiwan is listed in a checklist (Heppner and Kuroko 1992) and seven DNA barcode records of Heliozelidae from Taiwan, including *Antispila* species, are present in the BOLD database (BOLD: www.boldsystems.org), no Heliozelidae species has yet been recorded from mainland China.

The genus *Antispila* Hübner, [1825], comprising some 40 species, is widely distributed worldwide, but most diverse and best studied in the Palearctic and the Nearctic regions (Kuroko 1961, 1987, Lee et al. 2006a, Lee et al. 2006b, van Nieukerken et al. 2012). Nevertheless, it has not been recorded in mainland China until the present. Vitaceae and Cornaceae comprise the major host plant families (van Nieukerken et al. 2012, Regier et al. 2015).

During collecting trips targeting leaf-mining moths, an abundant population of *A. sinensis* sp. n. was found in Mt. Fohui Park in Jinan City, Shandong Province, where it damaged its host plant *Cornus walteri* Wangerin (Cornaceae). *Cornus walteri* is native and is frequently planted in Mt. Fohui Park, and plays an important role as a shade tree along footpaths. Another population of *A. sinensis* sp. n. was found on Mt. Baxian, Tianjin City, where less damage to its host plant was observed.

In the present paper, the new species *A. sinensis* sp. n. is described and the moth's morphology, life-history, hostplant, and DNA barcode is reported upon. The potential for this moth to damage its host plant *Cornus walteri* is described.

Material and methods

Leaves with active mines were placed in small plastic bags for rearing. After the shields had been excised and the larvae had left the mines, the larval shields were transferred into closed containers and leaves with vacant leaf-mines were dried in a plant press. The larval shields, the corresponding adults, and the vacant leaf-mines were identically coded.

Genitalia and wings were dissected and mounted according to the methods introduced by Li (2002), but stained with Eosin Y and/or Chlorazol Black. Illustrations were prepared by using a Leica DM750 microscope. Line drawings were refined in Photoshop® CS4 software. Adult photographs were taken with a Leica M205A stereo microscope and a Leica S6D stereo microscope. Photographs of host plant and leaf-mines were taken in the field using a Canon EOS camera. The larva was macerated in 10% KOH, boiling for 10 min, rinsed in water and alcohol, then stained with Chlorazol Black, and kept in

glycerin prior to examination. Measurements of shields were carried out using an ocular micrometer on an Olympus SZ11 stereo microscope.

DNA was extracted from adult specimens preserved in 95% ethanol in Shandong Normal University, Jinan, China (SDNU), with genitalia and wings preserved as vouchers (Knölke et al. 2005). Total DNA was extracted using the TIANamp Micro DNA Kit (Code: DP316, Tiangen, China). Fragments of the mitochondrial COI gene were amplified using the primer pair LEPF1/R1 and the protocol introduced by Hebert et al. (2003). The sequence data used in this study have been deposited in the public Dataset “DS-ANTISIN” in the BOLD database. Sequences were aligned using MUSCLE model and genetic distance estimation was analyzed using Kimura 2-Parameter model in the BOLD.

Terminology of adult follows van Nieukerken et al. (2012), and that of larva follows Lee et al. (2006) and Low (2008) with some modifications. Thoracic segments I–III and abdominal segments 1–10 are abbreviated as TI–TIII and A1–A10, respectively. The classification of the host plant is based on APG (2016).

The holotype of the new species is deposited in the Insect Collection of Nankai University (NKU), and paratypes are distributed in NKU and SDNU as stated in the text.

Taxonomy

Antispila sinensis sp. n.

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Figs 1–23

Diagnosis. This species can be easily separated from the two European *Cornus* feeding species, *A. treitschkiella* (Fischer von Röslerstamm, 1843) and *A. metallella* (Denis & Schiffermüller, 1775), by the forewing with the opposite basal spots separated and thus not forming a fascia, and by the vein Rs_{3+4} reaching costa near apex and the absence of the stem of vein M. *Antispila treitschkiella* has a basal fascia in the forewing, and *A. metallella* has the vein Rs_{3+4} reaching termen and has an M stem in the forewing. Specimens with the inner spots joined into a fascia, *A. sinensis* could be separated from *A. treitschkiella* reliably by genitalia. Although DNA Barcode distance analysis suggests *A. tateshinensis* Kuroko, 1987 and *A. purplella* Kuroko, 1961 to be the closest relatives (Fig. 23), morphologically, *A. sinensis* most closely resembles *A. purplella*, which feeds on *Cornus controversa* and *C. brachypoda*. These two species are similar in terms of the hooked structure of the phallus, the cusps of the ovipositor and wing venation but can be distinguished by the thin ventral tube in the distal part of the phallus, which is bifurcated in *A. purplella*. In addition, the region of the vinculum adjacent to the triangular median protrusion is almost flat in *A. sinensis*, while it is apparently concave in *A. purplella*.

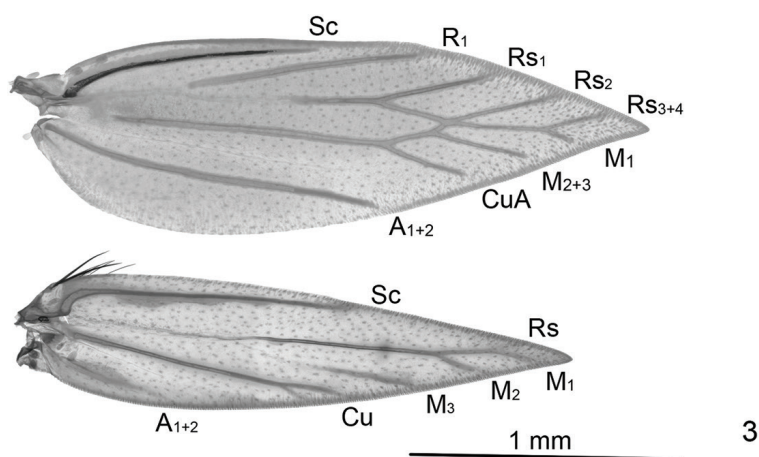
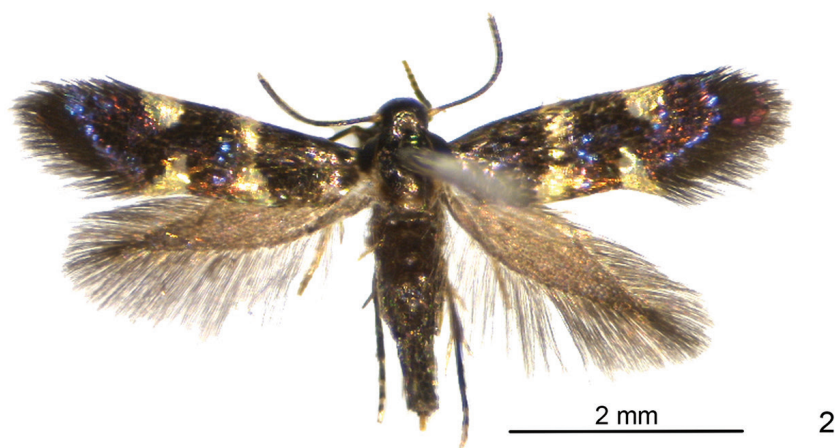
Type material. China: **Holotype** ♂, Mt. Baxian, 40.18°N, 117.55°E, 300–600 m, Ji County, Tianjin, larva coll. 5.ix.2013, emerged 9.iii.2014 (indoors), leaf-mine on *Cornus walteri*, leg. Tengteng Liu, genitalia slide No. LIU12870 (deposited in NKU).

Paratypes. Tianjin: 2♂, 1♀, larva coll. 5.ix.2013, emerged 8, 9.iii.2014, 1♂, 1♀, larva coll. 6.ix.2013, emerged 6, 12.iii.2014, 3♂, 1♀, larva coll. 9.viii.2013, 20, 25.x.2013, 10, 11.iii.2014, 5♂, 5♀, larva coll. 24.vi.2014, emerged vii–2014, other data same as holotype, genitalia slide Nos. LTT12559♀, LTT12613–4♂, LTT12866♀, LTT12867–9♂, LTT12871–3♂, LTT12874–5♀, wing slide Nos. LTT12613–4W, LTT12874W (deposited in NKU); 12♂, 12♀, Mt. Baxian, 40.194°N, 117.557°E, 300 m, Ji County, Tianjin, larva coll. 29, 30.vi, 23.vii.2015, shield made 2, 3, 5, 25, 27.vii.2015, emerged 27, 29, 31.vii, 2, 13, 20.viii.2015, leafmine on *Cornus walteri*, leg. Tengteng Liu, registered Nos. SDNU_BXS150601–05, BXS150607, BXS150608–12, BXS150615, BXS150617–19, BXS150625–27, BXS150630–31, BXS150633, BXS150701–03, BXS150704–05 (deposited in SDNU); **Shandong:** 7♂, 6♀, Mt. Fohui, Jinan, 36.633°N, 117.050°E, 260 m, leafmine on *Cornus walteri*, larva coll. 7.ix.2015, shield made 7, 10, 11, 13.ix.2015, emerged 26, 30.x.2015, 31.iii, 15, 19, 23, 24.vi.2016, leg. Tengteng Liu, genitalia slide No. LIU15003♂, registered Nos. SDNU_JN150903–04, JN150909, JN150911–14, JN150918–19, JN150926, JN150928–9, JN150939, JN150944, JN150947 (deposited in SDNU).

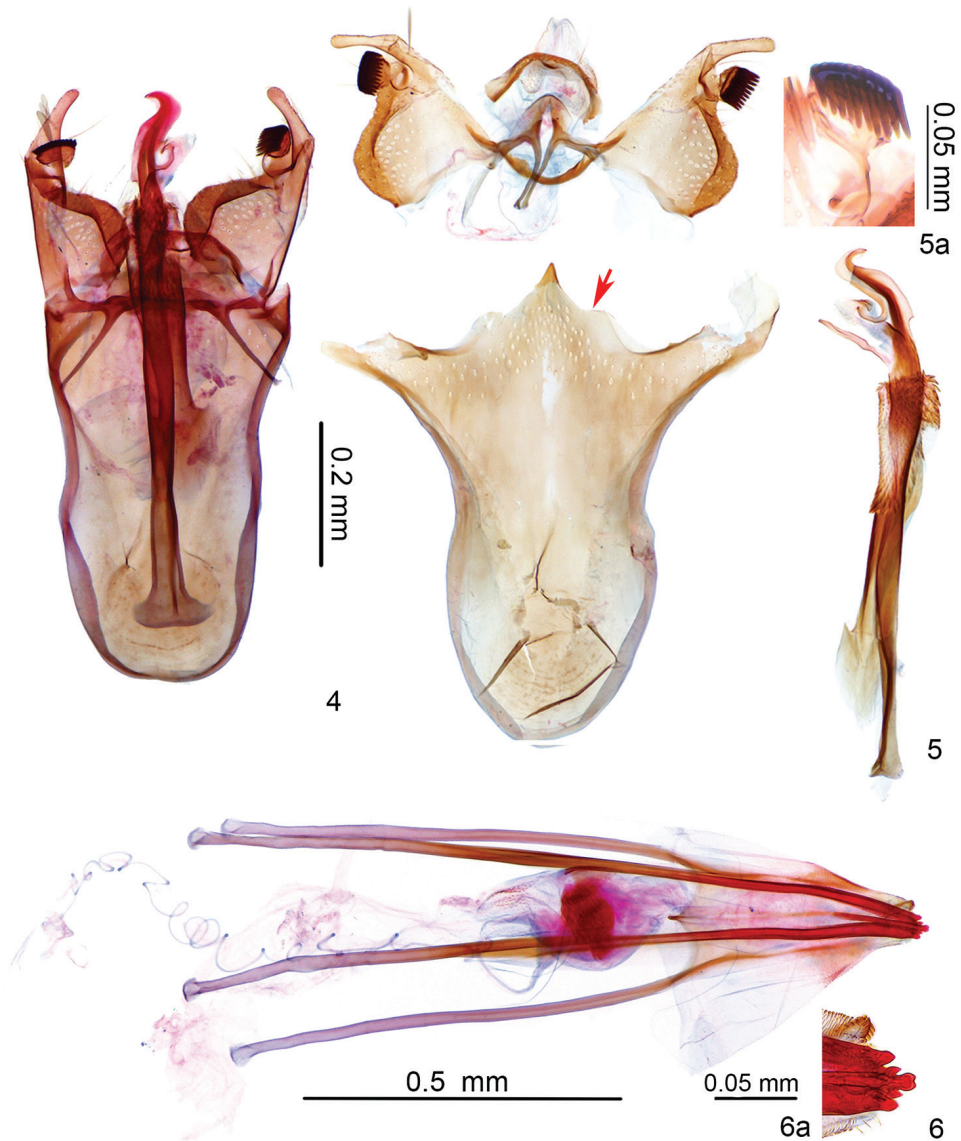
Adult (Figs 1, 2). Forewing length 2.4–3.0 mm. Head deep silvery gray, smooth. Base of proboscis covered with larger scales. Labial palpus dark gray. Antennae blackish fuscous, distal two segments grayish white. Thorax and tegula dark gray, with purplish-blue metallic reflection. Legs silvery gray to deep silvery gray, tarsi dark gray dorso-distally except last segment. Forewing black, with purplish-blue reflection; two more or less triangular silvery white spots on costa at 1/3 and 2/3; two similar spots on dorsum opposite costal spots, inner pair sometimes joined into a fascia, especially in female (Fig. 2); cilia black basally, dark gray distally. Hindwing dark gray. Abdomen dark gray dorsally, silvery gray ventrally; vestiture on external genitalia dark gray.

Venation (Fig. 3). Forewing with Sc reaching before middle on costa; R_1 from 2/5 on upper margin of cell to costal 3/5, Rs_1 from 1/7 on upper margin of cell to costal 3/4, Rs_2 from distal end of cell, Rs_{3+4} reaching costa before apex; cell triangular distally; M_1 stalked with Rs_{3+4} , to termen near apex, M_{2+3} from near distal end of cell; Cu from distal 1/7 of lower margin of cell; A_{1+2} to beyond middle of dorsum. Hindwing with Sc to costal 3/5, R+M ending in 4 branches: Rs to costa near apex, M_1 , M_2 and M_3 to dorsum; Cu ending in 2 branches; A_{1+2} weak. Male with one frenulum, female bearing two frenular bristles and several hairscales.

Male genitalia (Figs 4, 5, 5a). Uncus setose on posterior margin, with two setose sacs ventrally. Vinculum slightly shorter than phallus, anteriorly rounded, posteriorly almost even besides triangular median protrusion. Valva more or less rectangular on basal half, digitally extended distally, pecten on pedicel, with 10–14 comb teeth (Fig. 5a); transtilla almost uniform in width, sublateral processes relatively short. Juxta about half as long as phallus, densely covered with teeth on basal 2/5, anteriorly spade-shaped. Phallus long, strongly expanded at base laterally; distal part beyond base of juxta complex, curved, with small hooks distally and medio-ventrally, an incision before middle dorsally, a thin tube extruded near base ventrally.

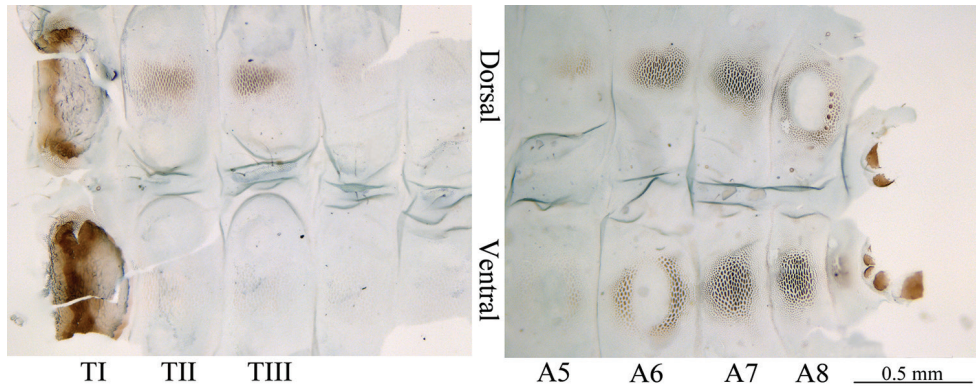


Figures 1–3. Adult and wing venation of *Antispila sinensis* sp. n. **1** Adult, paratype, male, BXS130941 **2** Adult, paratype, female, SDNU_JN150947 **3** Wing venation, female, slide No. LTT12874W, paratype.



Figures 4–6. Genitalia of *Antispila sinensis* sp. n. **4** Male genitalia *in situ*, slide No. LTT12873, paratype **5** Male genitalia unrolled, slide No. LTT12872, paratype, red arrow referring to the region of the vinculum adjacent to the triangular median protrusion **5a** Close-up of comb teeth on pecten, slide No. LIU15003 **6** Female genitalia, slide No. LTT12875, paratype **6a** Close-up of ovipositor tip, same slide as in Fig. 6.

Female genitalia (Fig. 6, 6a). Ovipositor with 3 cusps at either side (Fig. 6a). Eighth sternum medially indented posteriorly, with many papillate setal sockets, triangularly protruded on posterior margin ventrally. Vestibulum oval, covered with spines anteriorly, inner with paired wrinkled sclerotization, each with a long spine. Corpus bursae membranous.



Figures 7. Final instar larva in leaf-mine, showing sclerotized plate and granules on the body, registered No. SDNU_JN150907.

Final instar larva in mine (Figs 7–12). Body length about 5.0 mm. Two stemmata visible. Prothorax (TI) with sternum and tergum strongly sclerotized (Fig. 7). T2–3 and A5–9 with terga strongly sclerotized, covered with granules; eighth tergum with a weakly sclerotized oval zone medially, a row of sclerotized pointed bumps along posterior margin (Fig. 7). A5–9 with sternum strongly sclerotized, covered with granules, A5 and A6 with weak sclerotized zones medially (Fig. 7). Tenth tergum more or less oval, lateral and ventral plate sclerotized. Thorax legs and prolegs absent (Fig. 7).

Head (Figs 8–9). Three long setae on A-group, A1 internal to stemmata, A3 posterior to stemmata I, A2 internal to A3; Fa internal and dorsal to F1; P-group close to adfrontal area, with P1 longer than P2, two short setae lateral and ventral to P1 which might be real P setae, while P setae here designated might be AF setae; L1 posterior to A3; V-group with 2 micro-setae; O1 ventral to stemmata II, O2 and O3 ventral to stemmata I; SO1 below antennae, SO2 dorsal to SO1; G-group with three setae, G1, MG1, and MG2.

Thorax (Fig. 10). TI with D1 anterior and slightly ventral to D2, XD1 anterior and ventral to D1, near anterior margin prothoracic shield, MXD1 close to posterior margin of prothoracic shield; SD1 and SD2 on lateral margin and posterior margin respectively, SD1 longer than SD2; L-group with 3 setae, L2 ventral to SD1, L3 close to spiracle, L2 between L1 and L3; SV-group with two setae, same in length; two micro-setae on concave of lateral margin of sternum; sternum with 4 MV setae. TII similar to TI, one MD setae anterior to D1; SD2 close to SD1, with two MSD setae anteriorly; SV-group with only one seta; two MV setae exist. TIII similar to TII, except with SD2 missed.

Abdomen (Figs 11, 12). A1 with D-group and SD-group setae very short, SD1 dorsal and posterior to spiracle, SD2 next to spiracle; L-group and SV-group setae long, L1 posterior to spiracle, L2 ventral to L1, L3 posterior and ventral to L2, SV1 anterior and slightly ventral to L3. A2 similar to A1. A3 similar to A1, but with L3 shorter, SV1 moved ventrally, MV1 absent. A4–7 similar to A3, except with L3 longer on A7. A8 with D1 anterior and dorsal to D2, L-group more or less same in length, arranged in

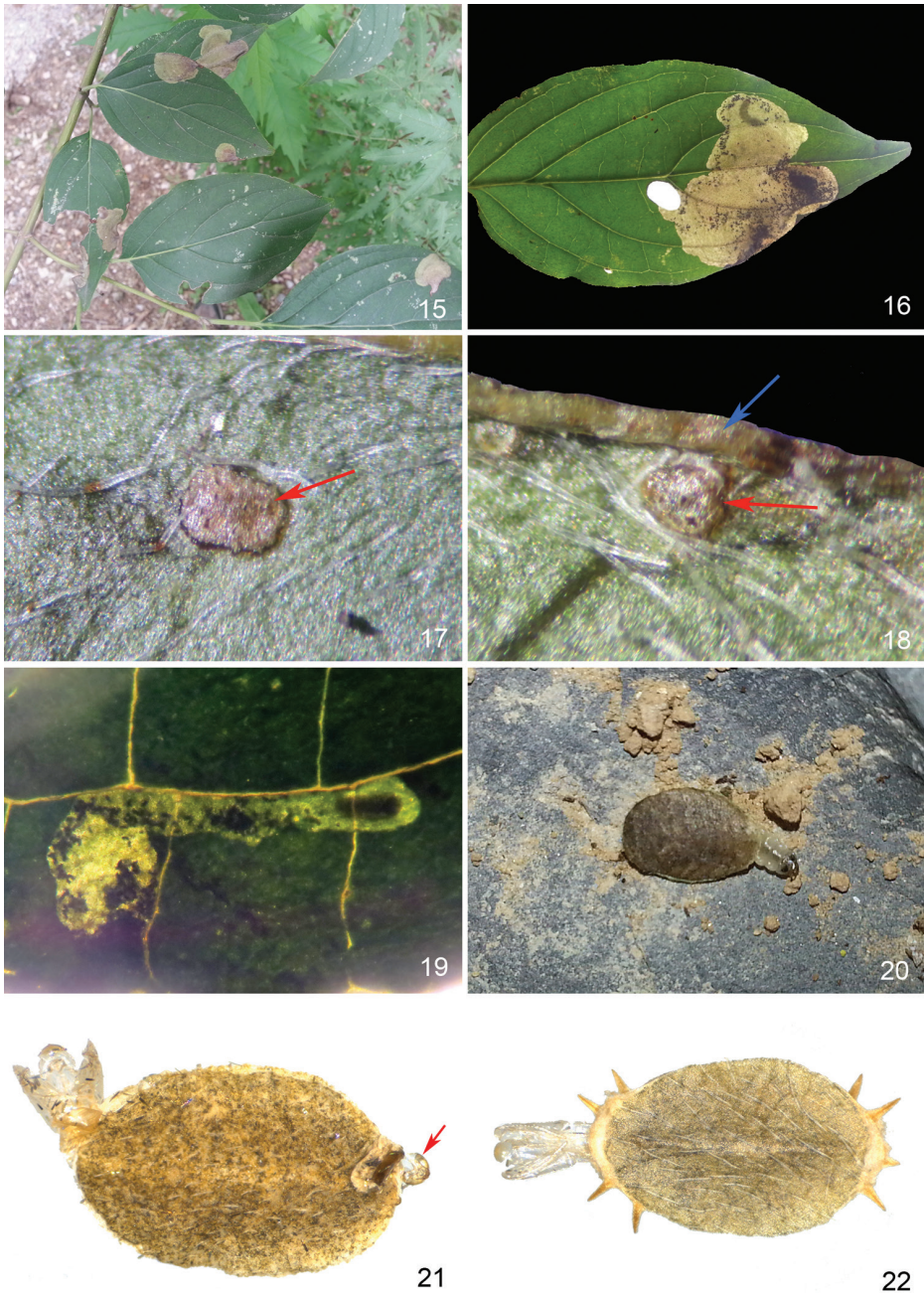


13



14

Figures 13–14. Pupa of *Antispila sinensis* sp. n. **13** a white early stage pupa **14** pupa just before emergence in ventral, lateral, and dorsal view.



Figures 15–22. Leaf mine, host plant and shield of *Antispila sinensis* sp. n. **15** Leaf mines on *Cornus walteri* **16** A large blotch mine occupied by two larvae one of which has made a cut-out **17** piercing scar on the disc of a leaf indicated by a red arrow **18** piercing scar (red arrow) near margin of a leaf where callus also occurs (blue arrow) **19** Early linear mine with an active larva **20** Larva in freshly made shield, searching for a pupation site on the ground **21** Shield without spines along margin, pupal exuviae and exuviae of prepupa (red arrow) **22** Shield with several spines along margin, pupal exuviae.

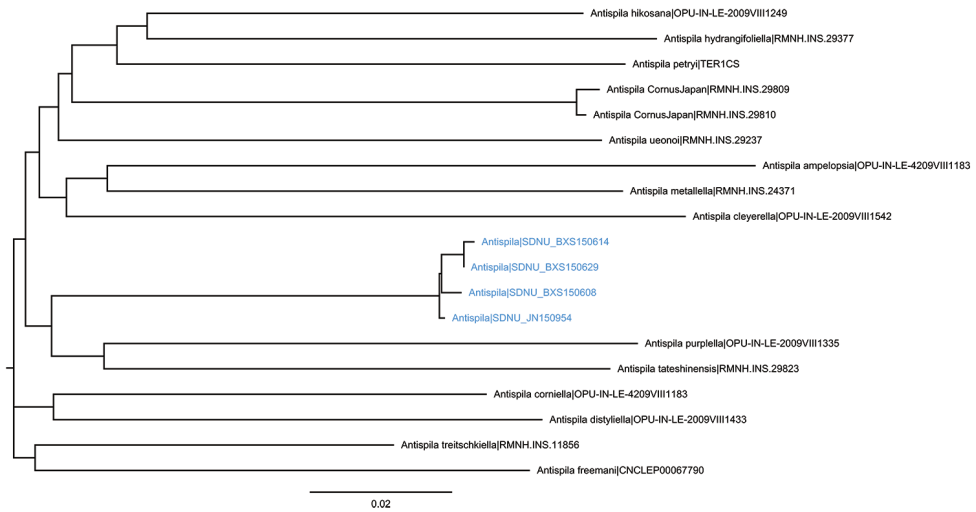


Figure 23. Neighbor-joining tree estimated from DNA barcode sequences under dataset “DS-ANTISIN”, performed by using Kimura 2-Parameter model. Clades representing *A. sinensis* sp. n. are marked blue.

line. A9 similar to A8, but with L3 absent. A10 apparently sclerotized on both sternum and tergum, with a single plate dorsally and two paired plates ventrally (Fig. 12).

Pupa and shield (Figs 13–14, 20–22). Shield 4.3 ± 0.3 mm in longitudinal diameter, 2.4 ± 0.2 mm in latitudinal diameter, with 13.2 ± 3.3 spines ($n = 23$), but also some extremes without spines (Fig. 21). Pupa changing from white to dark fuscous during maturity (Figs 13–14).

DNA barcode. Four DNA barcodes from individuals from each of the collecting sites have been submitted to BOLD under the public Dataset “DS-ANTISIN” (doi: 10.5883/DS-ANTISIN). The Barcode Identification Number is BOLD:ADG5043. A neighbor joining tree with barcodes of other *Antispila* species, particularly *Cornus* feeding species and Japanese species, is given in Fig. 23.

Host plant. *Cornus walteri* Wangerin (Cornaceae).

Distribution. China (Shandong, Tianjin).

Biology. Egg is laid on the lower side of a leaf, usually close to leaf margin and occasionally near main vein, where a darker area of callus (piercing scar) caused by piercing of the ovipositor is invariably seen (Figs 17, 18). The leaf-mine begins as a line and extends along veins if it cannot go through (Fig. 19). The mine soon enlarges to a blotch, incorporates most or all of the earlier linear mine and finally, ends in a cut-out (Fig. 16). Several mines can be found on the same leaf (Figs 15, 16). Frass primarily occupies the opposite side of the cut-out in the mine, with a small amount extending adjacent to the cut-out (Fig. 16). The newly made larval shield often falls onto the ground, after which the larva searches for a place to pupate (Fig. 20). The larva molts once in the shield before pupation and the final larval exuviae are often protruding at one end of the shield, opposite to the end where the pupal exuviae protrude (Fig. 21).

This species overwinters as a prepupa in the shield and pupates during early spring to emerge later as an adult. At least three generations occur annually.

Etymology. The specific name is derived from the country where the new species represents the first formally named Heliozelidae species.

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References

- APG (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society 181: 1–20. <https://doi.org/10.1111/boj.12385>
- Denis M, Schiffermüller I (1775) Ankündigung eines systematischen Werkes von den Schmetterlingen der Wienergegend. Augustin Bernardi, Wien, 323 pp.
- Fischer von Röslerstamm JE (1834–1843) Abbildungen zur Berichtigung und Ergänzung der Schmetterlingskunde, besonders der Microlepidopterologie als Supplement zu Treitschke's und Hübner's europaischen Schmetterlingen, mit erläuterndem., Hinrichs, Leipzig, 304 pp [pls. 1–100].
- Hebert PD, Cywinska A, Ball SL (2003) Biological identifications through DNA barcodes. Proceedings of the Royal Society of London B: Biological Sciences 270: 313–321. <https://doi.org/10.1098/rspb.2002.2218>
- Heppner JB, Kuroko H (1992) Heliozelidae. In: Heppner JB, Inoue H (Eds) Lepidoptera of Taiwan Vol 1 Introduction and Faunal synopsis, Part 2: Checklist. Scientific Publishers, 63 pp.
- Knölke S, Erlacher S, Hausmann A, Miller MA, Segerer AH (2005) A procedure for combined genitalia dissection and DNA extraction in Lepidoptera. Insect systematics & evolution 35: 401–409. <https://doi.org/10.1163/187631204788912463>
- Kuroko H (1961) The genus *Antispila* from Japan, with descriptions of seven new species (Lepidoptera, Heliozelidae). Esakia 3: 11–24. <http://catalog.lib.kyushu-u.ac.jp/handle/2324/2347/11.pdf>
- Kuroko H (1987) Three new species of the genus *Antispila* (Lepidoptera: Heliozelidae) from Japan. Tinea 12: 109–117. <http://ci.nii.ac.jp/naid/40000044288/>

- Lafontaine J (1973) Eastern North American species of *Antispila* (Lepidoptera: Heliozelidae) feeding on *Nyssa* and *Cornus*. The Canadian Entomologist 105: 991–996. <https://doi.org/10.4039/Ent105991-7>
- Lee B-W, Hirowatari T, Kuroko H (2006a) A new species of *Antispila* (Lepidoptera: Heliozelidae) from the Ryukyus, Japan, with descriptions of immature stages. Annals of the Entomological Society of America 99: 1019–1027. [https://doi.org/10.1603/0013-8746\(2006\)99\[1019:ANSOAL\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2006)99[1019:ANSOAL]2.0.CO;2)
- Lee B-W, Hirowatari T, Kuroko H, Arita Y (2006b) A new species of the genus *Antispila* Hübner (Lepidoptera, Heliozelidae), feeding on *Cleyera japonica* (Theaceae) from Japan. Transactions of the Lepidopterological Society of Japan 57: 7–12. <http://ci.nii.ac.jp/naid/110007034358/en>
- Li H (2002) The Gelechiidae of China (I) (Lepidoptera: Gelechioidea). Nankai University Press, Tianjin, China, 504 pp.
- Liu T, Yan J (2017) Review of the Palearctic *Atemelia* Herrich-Schäffer (Lepidoptera, Yponomeutoidea, Praydidae), with description of a new leafmining species. Zootaxa 4250: 327–336. <https://doi.org/10.11646/zootaxa.4250.4.3>
- Low C (2008) Seismic behaviors of a leafminer, *Antispila nysaeifoliella* (Lepidoptera: Heliozelidae). Florida Entomologist 91: 604–609. <https://doi.org/10.1653/0015-4040-91.4.604>
- Nieukerken EJ van, Geertsema H (2015) A new leafminer on grapevine and *Rhoicissus* (Vitaceae) in South Africa within an expanded generic concept of *Holocacista* (Insecta, Lepidoptera, Heliozelidae). ZooKeys 507: 41–97. <https://doi.org/10.3897/zookeys.507.9536>
- Nieukerken EJ van, Kaila L, Kitching IJ, Kristensen NP, Lees DC, Minet J, Mitter C, Mutanen M, Regier JC, Simonsen TJ, Wahlberg N, Yen S-H, Zahiri R, Adamski D, Baixeras J, Bartsch D, Bengtsson BÅ, Brown JW, Bucheli SR, Davis DR, De Prins J, De Prins W, Epstein ME, Gentili-Poole P, Gielis C, Hättenschwiler P, Hausmann A, Holloway JD, Kallies A, Karsholt O, Kawahara AY, Koster SJC, Kozlov M, Lafontaine JD, Lamas G, Landry J-F, Lee S, Nuss M, Park K-T, Penz C, Rota J, Schintlmeister A, Schmidt BC, Sohn J-C, Solis MA, Tarmann GM, Warren AD, Weller S, Yakovlev RV, Zolotuhin VV, Zwick A (2011) Order Lepidoptera Linnaeus, 1758. Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa 3148: 212–221. <http://www.mapress.com/zootaxa/2011/f/zt03148p221.pdf>
- Nieukerken EJ van, Wagner DL, Baldessari M, Mazzon L, Angeli G, Girolami V, Duso C, Doorenweerd C (2012) *Antispila oinophylla* new species (Lepidoptera, Heliozelidae), a new North American grapevine leafminer invading Italian vineyards: taxonomy, DNA barcodes and life cycle. ZooKeys 170: 29–77. <https://doi.org/10.3897/zookeys.170.2617>
- Regier JC, Mitter C, Kristensen NP, Davis DR, Nieukerken EJ van, Rota J, Simonsen TJ, Mitter KT, Kawahara AY, Yen S-H, Cummings MP, Zwick A (2015) A molecular phylogeny for the oldest (nonditrysian) lineages of extant Lepidoptera, with implications for classification, comparative morphology and life-history evolution. Systematic Entomology 40: 671–704. <https://doi.org/10.1111/syen.12129>

A new subspecies of sea snake, *Hydrophis platurus xanthos*, from Golfo Dulce, Costa Rica

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Abstract

We describe a distinctive new subspecies of sea snake from the occasionally anoxic inner-basin waters of Golfo Dulce, Costa Rica, based on combined data garnered between 2010 and 2017 for 154 specimens, 123 free-ranging and 31 museum-held. The yellow sea snake, *Hydrophis platurus xanthos* Bessesen & Galbreath, **subsp. n.**, is diagnosed by a notably smaller body size and nearly uniform yellow coloration, which contrasts with the black and yellow striae and tail spots or bands typical of the species. Within the modest geographic range (circa 320 km²), nearly all specimens possess both diagnostic character states. Bathymetrics appear to restrict genetic flow between this allopatric population and conspecifics in the broader Eastern Pacific. In perspicuous contrast to typical *H. platurus*, *H. p. xanthos* shows no association with drift lines, and feeds at night in turbulent waters, assuming a sinusoidal ambush posture never previously reported for the species. This evolutionarily significant unit (ESU) warrants taxonomic recognition and active protection.

Keywords

Golfo Dulce, Costa Rica, sea snake, yellow color morph, *platurus*, type specimens, taxonomy

Introduction

Hydrophis platurus (Linnaeus, 1766; as *Anguis platura*) is an elapid sea snake widespread in the Indo-Pacific region. The species was long classified in the monotypic genus *Pelamis*, but given molecular studies on its phylogenetic relationships (e.g. Lukoschek and Keogh 2006), it is most appropriately placed in the large genus *Hydrophis* (Sanders et al. 2013). At the ocean surface, this venomous piscivore is often associated with smooth-water drift lines (Kropach 1971a, 1975), where it opportunistically feeds on a variety of small fish from an open floating posture. Considered diurnal, it does not appear to spend time at the sea surface at night (Rubinoff et al. 1986; see our contrasting data below), preferring high light levels, which may suggest some reliance on visual cues for predation (Brischoux and Lillywhite 2011). The species has generally been found to actively avoid turbulent waters (Dunson and Ehlert 1971, Rubinoff et al. 1986, Cook and Brischoux 2014). Like many snakes, *Hydrophis platurus* is sexually dimorphic in size, with females larger on average. Individuals can reach at least 113 cm in total length (TL; Pickwell and Culotta 1980). Published population averages for adult TL include 70 cm (Cogger 1975), perhaps 60 cm (roughly extrapolated from Fig. 2A of Pfaller et al. 2012), and 72 cm for males/ 80 cm for females (Leviton et al. 2006). Weight averages in ecological studies have included 91 g (Graham et al. 1971) and 140 g (Rubinoff et al. 1986).

Hydrophis platurus is the only sea snake found off Costa Rican shores (Solórzano 2004). While variable, the majority of individuals exhibit black dorsal coloration contrasting with a yellow ventrum, and have dark spots or bands on the paddle-shaped tail (Bolaños et al. 1974; Tu 1976). Smith's (1926) seven recognized color forms of the species did not include the yellow variety and Kropach (1971b) was the first to describe yellow individuals along the Central American coast. Later, Solórzano (2011) and Bessesen (2012) reported a population in the northern waters of Golfo Dulce to be exclusively composed of xanthic (all-yellow or primarily yellow) sea snakes. A bi-seasonal distributional study across all areas of the Golfo Dulce revealed a geographically bound aquatic habitat (circa 320 km²) in which 100% of sea snakes (N = 68) possessed the diagnostic character state. See Supplementary file 1. The findings were corroborated in interviews with 82 fishermen and tour boat guides, who reported seeing only yellow sea snakes in the upper Gulf. GIS maps show the xanthic population to be spatially separated from the oceanic yellow-bellied population by a gap of about 22 km (Bessesen 2012, 2015, Fig. 1).

This distinct population of yellow sea snakes exploits warm, periodically anoxic inner-basin waters of a curved tropical embayment with tectonic origins (Hebbeln and Cortés 2001) and fjord-like features (Wolff et al. 1996). Golfo Dulce, located on the South Pacific coastline of Costa Rica, is approximately 50 km long and 10–15 km wide, and supplied with fresh water drainage from several rivers and tributaries. The bathymetry is characterized by a 215 m deep inner basin, which is held by an effective 60 m sill and a shallow valley, ≤ 80 m deep, extending southward to the mouth

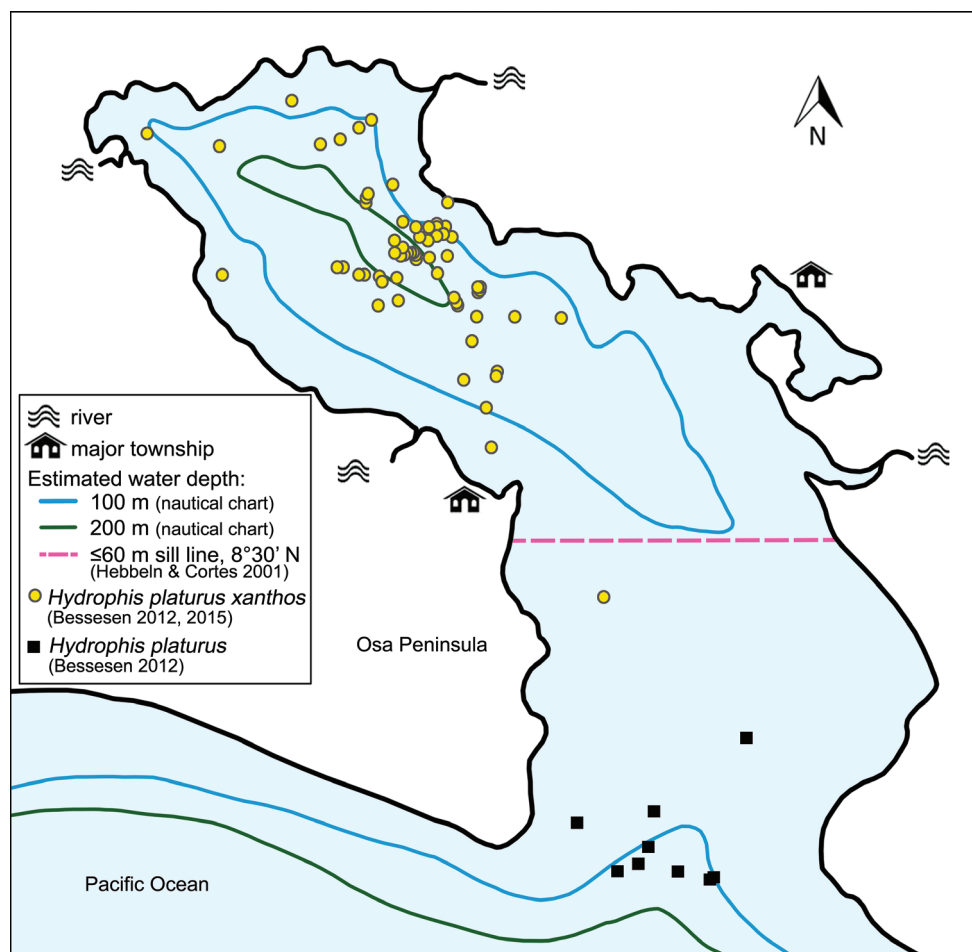


Figure 1. GPS sighting points for all sea snakes observed in Golfo Dulce during the 2010 and 2011 distribution study show *Hydrophis platurus xanthos* to reside in the inner basin, geographically divided from the broader Eastern Pacific population (Bessesen 2012, 2015).

of the Gulf. Such topography prevents free exchange between the deeper waters of the inner basin and adjacent coastal water masses (Svendsen et al. 2006). Graham (1974) showed *H. platurus* body temperature remained at or slightly above surrounding water, and found the serpent avoided surfacing when water temperatures were elevated (Graham et al. 1971). Since Dunson and Ehlert (1971) reported the species' upper lethal temperature at 33°C, and sea surface temperatures in Golfo Dulce can reach 32.5°C (Bessesen 2012), higher than other areas within the range of *H. platurus* (Hecht et al. 1974), light dorsal coloring plausibly plays a role in thermal regulation (Solórzano 2011, Bessesen 2012). Bessesen (2012) and Lillywhite et al. (2015) observed behavioral differences in the xanthic population that appeared to

have adaptive significance. Yellow sea snakes show no association with drift lines, are commonly seen in turbulent water, and most frequently surface at night, when they commonly assume a sinusoidal posture. The function of that sinusoidal posture was recently illuminated, as was smaller body size, during an investigation of morphology and behavior of the yellow sea snakes in Golfo Dulce, Costa Rica. The data from that study are reported here.

Material and methods

In January 2017, 55 free-ranging yellow sea snakes were documented in the inner-basin region of Golfo Dulce. Time and Beaufort Wind Force (BWF) were recorded at each sighting, as was the behavior of the snake: resting (floating at the surface), swimming, knotting, feeding, breeding and/or avoidance (diving). The posture of each snake was also recorded; open (elongated) versus sinusoidal. Forty-three of the specimens were captured by dip net for collection of morphological data, including total length (TL), tail length, paddle height, weight and high-resolution photos of key physical characteristics. Each snake was given an effective calming mask using 1-inch Vetrap wrapped around the head, and allowed to quiet. While resting still, TL was obtained by laying string along the mid-dorsal surface from tip of snout to tip of tail, and then measuring the string against a meter stick, taking just two measurements if the results matched exactly, or if not, averaging three measurements diverging by no more than 0.5 cm. Tail length was measured against a meter stick to nearest 0.5 cm. Paddle height was measured in 34 specimens with calipers to 0.5 mm. Weight was measured on an AWS Blade-1KG digital scale; if boat movement created a swing in readout, care was taken to wait until a proper estimate could be acquired. An additional behavioral note was made if a snake gaped its mouth or attempted to bite during handling. On-water work periods began no later than 16:30, lasting an average of 6 hr, 10 min. Sea surface temperature was measured with a floating water thermometer once per evening.

Following field work, 31 preserved specimens of *Hydrophis platurus* were examined at the Zoological Museum of University of Costa Rica; all had been captured in the upper Golfo Dulce between 2009 and 2016, and all exhibited xanthic coloration. Five particularly small specimens (<38 cm TL) were excluded from measurement to avoid possible age-related statistical bias; however, morphological data were collected for the remaining 26 specimens using the same techniques as applied in the field. TL was measured by string, although merely one precise effort was required. Tail length, paddle height, weight and photos were also collected. No additional morphological counts, such as scalation, could be practicably obtained owing to limited access to the preserved specimens.

During the research period, opportunity also arose to measure three adult yellow-bellied specimens, two preserved and one living, found along the Osa Peninsula. The same tools and techniques were applied.

Results

A total of 69 yellow sea snakes collected from the inner basin of Golfo Dulce was measured and weighed. TL ranged from 40–59 cm, with a mean of 49.1 cm. Tail length ranged from 4.3–7 cm and averaged 5.4 cm, significantly shorter than the typical 8–9 cm described by Leviton et al. (2003); Cook and Brischoux (2014) estimated mean proportionate tail length at 11.2% of TL, which held true for our samples. Weight ranged from 22–95 gm, with a mean of 46.6 g (Table 1). In comparison, the three measured yellow-bellied specimens had a TL ranging from 69–70.5 cm, with a weight average of 95 g; such findings are in accord with published size descriptions for *H. platurus* (Fig. 2A). While comparative data for paddle height is limited, we found xanthic specimens to have an average height of 9.8 mm, while the yellow-bellied specimens averaged 11.8 mm.

Several free-ranging yellow sea snakes were seen swimming (N = 13) and a few knotting (N = 3), but the most commonly observed surface behavior was resting. Recorded evening sea surface temperatures in the inner basin averaged 28.5°C, considerably cooler than the average 30.5°C previously recorded near the Puerto Jiménez marina in the dry season of 2010 (Bessesen 2012). BWF was documented at every sighting to provide specific insight into turbulence associated with xanthic snakes at the sea surface. Of the 55 live yellow sea snakes recorded, none were seen in glassy or rippled water. Only one was found in BWF2 (small wavelets), whereas the majority were recorded in BWF3 (N = 33; smooth wavelets) or BWF4 (N = 21; small wave-caps). On two nights when sea conditions calmed from BWF3 to BWF2, snakes could no longer be located. This association with rough water is in direct contrast to the behavior of typical yellow-bellied sea snakes, which strongly favor calm smooth water for surfacing. Furthermore, data reconfirmed that yellow sea snakes most commonly surface at night, at which time they often assume a tight sinusoidal posture that has never been observed during daylight hours (Fig. 2A). The first yellow sea snake sighted post-sunset was always sinusoidal, a posture observed in 80% of nocturnal sightings. Perhaps the most unexpected finding was that the sinusoidal body position appears to represent the typical ambush posture of yellow sea snakes (Fig. 2B). Six yellow sea snakes were observed in this feeding position with small prey around them, and one was captured with a larval fish in its mouth. Bunching up the body appears to create a stable buoy in turbulent water conditions while the head extends below, mouth agape. In hand, the yellow sea snakes were not overly aggressive; of the 43 brought aboard our research panga for examination, only 33% (N = 14) gaped their mouth at any point. Avoidance behavior prevented us from measuring 12 living specimens, which were seen and recorded, but not caught, before diving.

During the 2017 field work, three yellow-bellied *H. platurus* were unexpectedly found in the inner basin of Golfo Dulce. All were within close proximity (two within 400 m and another 2 km to the south). Two were juveniles, weighing only 12–22 grams. The third was an adult, which appeared to be dying, limp in the water with head drooping. Its body was emaciated, with ribs palpable, and slimy grey plaques

Table 1. Body measurements for 69 individual *Hydrophis platurus xanthos* from the inner basin of Golfo Dulce.

Specimen	TL (cm)	Tail length (cm)	Paddle height (mm)	Weight (g)
F1	49	5.5	-	28
F2	46	5.5	-	22
F3	52.5	4.5	-	50
F4	50	5	-	47
F5	48	4.5	9	35
F6	48	4.5	9.5	30
F7	46.5	5	9.5	28
F8	52	5	9	44
F9	48	4.5	9	29
F10	47	4.5	9.5	37
F11	50.5	5	9.5	42
F12	55.8	6	9.5	38
F13	47	4.5	-	32
F14	48.5	5.5	8	33
F15	47.6	4.5	9.5	39
F16	46.8	4.5	9	33
F17	55	5.5	10	52
F18	48.3	4.5	10	43
F19	46	4.5	9.5	38
F20	46	4.5	-	35
F21	49	6	9	34
F22	45.5	5.5	-	37
F23	50	5	10	52
F24	47.8	5	9.5	46
F25	45.8	5	9.5	32
F26	51.5	6	10	53
F27	45.2	5	9.5	32
F28	46.8	5	9	34
F29	48.7	5.5	9.5	41
F30	46.5	5.5	9	32
F31	54.3	6	10.5	61
F32	49.8	5.5	9.5	42
F33	49.5	6	-	38
F34	50.5	6	-	48
F35	48	5.5	8.5	40
F36	41	5	8.5	26
F37	45.3	5	9	40
F38	46	5.5	9.5	38
F39	47.7	5.5	11.5	45
F40	44	5	9.5	37
F41	48.3	5.5	9	43
F42	43	4.5	9.5	32
F43	50.8	6	10.5	48
M1	57.5	6.5	10.5	59

Specimen	TL (cm)	Tail length (cm)	Paddle height (mm)	Weight (g)
M2**	52	6	10	55
M3	59	7	11	72
M4	56	6	14	95
M5	51.5	6.5	14	73
M6	50	6.5	12	71
M7	51	6	9.5	54
M8	51	6	10	73
M9	51.5	6.5	10.5	94
M10	45	5.5	9	35
M11*	51	6	10	55
M12	42	4.5	9	26
M13	52	5	9.5	65
M14	55	6	11	78
M15	51	6	10	74
M16	55	5.5	11	94
M17	45.5	6	9.5	38
M18	54.5	5.5	10.5	80
M19	40	4.5	9.5	35
M20	50.5	5	9.5	79
M21	54	6	10	46
M22	46	5	8	35
M23	44.5	5	10	38
M24	50.5	6	9.5	40
M25	48	5	10	47
M26	50	4.5	8	36
Mean:	49.1	5.4	9.8	46.6

Notes: F specimens were free-ranging, captured during field studies, while M specimens were examined at the Zoological Museum of University of Costa Rica; **holotype; *paratype.

covered the head and speckled the skin. Strings reminiscent of thread algae also protruded along its length (Fig. 2A). Local fishermen were flummoxed by news of our finding and reiterated their experience, as reported in the 2010–2011 study: None had ever seen a yellow-bellied snake in upper Golfo Dulce.

Description of a new taxon

Hydrophis platurus xanthos subsp. n.

<http://zoobank.org/291A79DC-C871-4AE3-9628-A60AE9CF9445>

Type specimens. Holotype female from COSTA RICA: Golfo Dulce: inner basin, 08°35.76'N; 083°13.25'W; collected 13 February 2009 by A. Solórzano, and deposited in the Zoological Museum of University of Costa Rica, San Jose, Costa Rica (MZUCR:HERP:20614); body yellow with 4 black specks (<1 mm) and 5 black dots

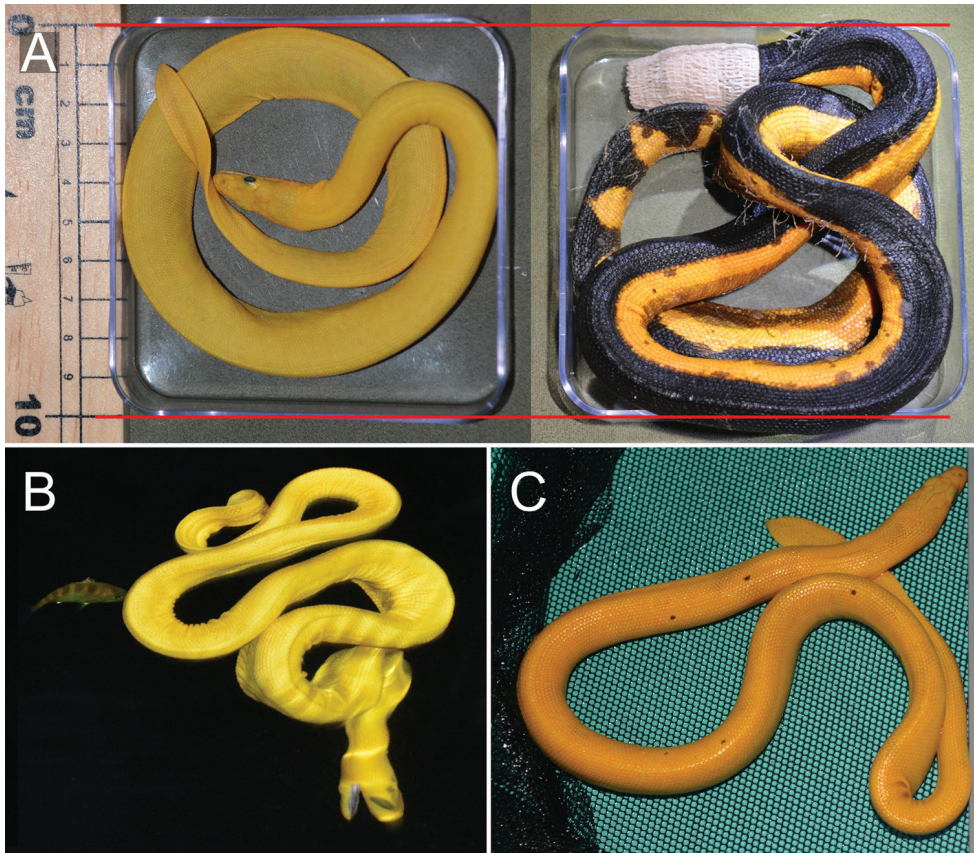


Figure 2. *Hydrophis platurus xanthos* sharply contrasts typical *H. platurus* in color, body size and behavior. **A** Scaled size comparison of yellow sea snake, TL 43 cm (left), and yellow-bellied sea snake, TL 69 cm (right; note the use of Vetrap as a calming mask and sickly condition of the specimen) **B** ambush posture of *H. p. xanthos*; floating at the sea surface at night in a sinusoidal shape, head below, mouth agape **C** although predominantly yellow, xanthic individuals often possess black spots along the dorsum.

(2–4 mm) along the dorsum, no tail markings; TL 52 cm, tail length 6 cm, paddle height 11 mm, weight 55 g. Paratype female from COSTA RICA: Golfo Dulce: inner basin, 08°35.76'N; 083°13.25'W; collected 2 September 2009 by A. Solórzano, and deposited in the Zoological Museum of University of Costa Rica, San Jose, Costa Rica (MZUCR:HERP:20836); body yellow with 4 dark-brown dorsal blotches (2–3 mm) on or just caudal to the head, 2 black specks (< 1 mm) and 2 dots (3–4 mm) farther down the dorsum, no tail markings; TL 51 cm, tail length 6 cm, paddle height 10 mm, weight 55 cm.

Diagnosis. Here we describe a new, allopatric subspecies, *Hydrophis platurus xanthos* subsp. n., or yellow sea snake, from the inner basin of Costa Rica's Golfo Dulce. The new subspecies is diagnosed based on a dramatic color character state, as well as by a marked difference in body size. Aspects of behavior also appear to be unique.

Hydrophis platurus xanthos is diagnosed as differing from other *H. platurus* by its predominantly yellow coloration and smaller size. Apparent additional behavioral diagnostic traits include a sinusoidal ambush posture, and a preference for surfacing in rough rather than smooth waters, lacking an association with drift lines. No specimens unambiguously assignable to this taxon have shown full lateral striation on head and body or prominent spots or bands on the tail. The appearance of *H. p. xanthos* starkly contrasts with the coloration of most conspecifics found in the broader Eastern Pacific, or even in the adjacent mouth of the Golfo Dulce, which evince nearly solid black pigmentation along the dorsum, breaking into spots or bands at the caudal end (Fig. 2A). *H. platurus xanthos* is also shorter in length, with an average adult TL of 49 cm, compared to about 60–75 cm for other *H. platurus* populations. Comparing our TL data for *H. p. xanthos* with those of Rubinoff et al. (1986) for *H. platurus* in the Gulf of Panama, note that the two samples do not even overlap, despite good sample sizes. The difference between the underlying distributions is significant with $P < .01$ (Wilcoxin Rank Sum Test, $N_1 = 15$, $N_2 = 69$, $T_1 = 1155$). Behavioral differences are equally pronounced between *H. platurus xanthos* and its yellow-bellied conspecifics. Drift lines, which play a critical role in the natural history of the species, supporting aggregations for feeding, reproduction and transport, are not used by *H. platurus xanthos*. Furthermore, while *H. platurus* feeds diurnally, stretched out in smooth water, *H. platurus xanthos* feeds at night, in turbulent water, assuming a sinusoidal ambush posture never previously reported for the species.

Coloration detail. Head, body and tail are bright canary-yellow. Although appearing entirely yellow at a glance, most individuals possess at least one dark, black or brown, dorsal speck or dot (Fig. 2C); such markings lack any fixed pattern, but frequently present caudal-medial to the supraocular scales. A few specimens retain larger black spots along the dorsal ridge; of the yellow sea snakes photographed by an author (BLB; $N = 120$), less than 13% ($N = 15$) exhibited a black mark longer than 2 cm.

Etymology. From Greek *xanthos*, “yellow,” to highlight a diagnostic feature of this subspecies.

Geographic distribution. The breeding population of *Hydrophis platurus xanthos* appears confined to approximately 320 km² in the northern half of the Golfo Dulce, Costa Rica, from 08°32'N to 08°44'N and 083°11'W to 083°28'W. A spatial gap up to 22 km separates the yellow sea snakes from the usually bi- or tricolored oceanic population, and appears to restrict genetic exchange (Bessesen 2012, Fig. 1).

Discussion

Hydrophis platurus xanthos constitutes a geographic isolate in which most or all specimens conform in possessing the diagnostic color state, otherwise known in very few individuals of other populations of this wide-ranging species. Sheehy et al. (2012) compared mitochondrial DNA from two Costa Rica populations, the xanthic population in Golfo Dulce, and a yellow-bellied population in Golfo de Papagayo. Four statistical

tests for difference were utilized. Two of them, Ks^* and Z^* , found significant difference at $P < .05$; two others, X^2 and Hs^* , did not. That no shared cytochrome-b haplotypes were found is intriguing, but the sample sizes were small. We concur with Sheehy et al. that any real difference in mtDNA between these populations is itself probably small and implies shallow phyletic divergence. This is not in conflict with taxonomic differentiation of the Golfo Dulce snakes, since subspecific or even specific differentiation can occur rapidly under circumstances of intense selection and/or genetic drift.

The yellow sea snake, *H. p. xanthos*, is also notably smaller in size than the yellow-bellied variety. At an adult TL of about 49 cm, weighing approximately 47 g, it measures around 10–25 cm shorter and 33–50% lighter in weight than published averages for *H. platurus*. A portion of that difference could relate to measuring technique: string versus stretching (Fitch 1987, Rivas et al. 2008). However, while typical female members of the species found in the Eastern Pacific may not commence reproductive activity until they reach a TL of 64.5–76.5 cm (Kropach 1975), no recorded individuals of the xanthic taxon even encroach into that size range. Behavioral differences suggest that the unique habitat of *H. p. xanthos* has imposed adaptive change. In Golfo Dulce, *H. platurus* has not only made a dramatic shift in tolerance—indeed, preference—for turbidity, correlated with a sinusoidal ambush posture, but appears to have shifted from diurnal to nocturnal predation. If insulated bathymetrics and restricted water currents within Golfo Dulce interrupted transit and reproductive flow with the wider oceanic population in the past, the need to avoid overheating may have selected for all-yellow coloration to reduce absorption of solar energy while surface feeding. Perhaps that same environmental pressure led to a nocturnal feeding strategy and may also explain why *H. p. xanthos* concentrate in the cooler deepest waters of the inner basin (Fig. 1).

Hydrophis platurus is very widely distributed, yet has remained largely geographically undifferentiated in morphology. That fact makes the singular xanthic population particularly intriguing. Several interesting questions are raised. For example, does the yellow color morph represent a small but normal percentage of the oceanic population in the Eastern Pacific? When 102 sea snakes were collected from five locations along the northern Pacific coastline of Costa Rica, only one (1%) was described as “yellow with a few black dorsal dots” (Bolaños et al. 1974). Of 3,077 specimens collected near Bahía de las Culebras, four (0.1%) were yellow (Tu 1976). Yet Kropach (1971b) found the variant in 9 of 278 specimens (3%) near the mouth of the Golfo Dulce. That xanthic specimens increase closer to our described population suggests the possibility that xanthic individuals in the Eastern Pacific have washed out from the inner basin of Golfo Dulce. To that point, all but one of the 154 yellow sea snake documented by an author (BLB) occurred well within habitat boundaries. However, a single xanthic specimen was observed in the outer basin in 2011 when rainy season storms and higher waves prevailed. This finding indicates that individuals of the subspecific colony occasionally cross the sill line, and might ultimately emigrate into the broader Pacific population (Fig. 1). More intriguing is our discovery of yellow-bellied specimens above the sill line; to our knowledge, no others have ever been sighted in the upper Gulf. While

cause of disease in the emaciated, algae-coated adult found dying remains unknown, sea snakes are quite sensitive to rises in water temperatures (Gillett 2015). How did the yellow-bellied snakes come to be in the inner basin? It may be relevant that their appearance occurred about seven weeks after the severe weather event of Hurricane Otto, which caused record-breaking precipitation on the Osa Peninsula. How frequently yellow-bellied snakes may be washed into the embayment or whether they can or do produce viable progeny with resident yellow sea snakes is unknown.

How do Golfo Dulce's periodically anoxic conditions impact the health, metabolic rate and/or behavior of the yellow sea snake? Despite being an air-breathing reptile, the species is reported to spend up to 99.9% of its time at 20–50 m depth, remaining submerged for up to 213 minutes per dive (Rubinoff et al. 1986). Below the water surface, *H. platurus* can absorb 12–33% of oxygen through skin respiration (Graham 1974). How might those physiological and behavioral characteristics be altered when the surrounding seawater lacks normal levels of dissolved oxygen? And, if *H. platurus* uses visual cues for predation, how does a nocturnal feeding schedule influence detection of prey?

An important unknown is the population size of *H. p. xanthos* in Golfo Dulce. Although the taxon is not at imminent risk of extirpation, it constitutes a very geographically limited population (inhabiting only circa 320 km² of aquatic habitat). This ESU is deserving of *in situ* conservation. Whether endemic to an island, mountain, lake, or gulf, any population confined to such a narrow habitat that is affected by human activity is at risk of decline and potential extirpation. Reading et al. (2010) observed that snake populations appear in global decline, and noted that populations living in unprotected habitats with increasing human influence are at greatest general risk of collapse. Golfo Dulce is not yet a Marine Protected Area, and anthropogenic impacts are already negatively affecting the marine environment (Sponberg 2004, Quesada-Alpízar and Cortés 2006, Bessesen 2015). Since the presence of yellow sea snakes in Golfo Dulce was first recognized, they appear to have become an attraction for visitors. In 2009, only one photo of a yellow sea snake was found online by an author (BLB); in 2016, there were multiple online sightings, Facebook posts, and YouTube videos. While fascination with *H. p. xanthos* is in some ways positive, it also potentially endangers the population. We note with concern, for instance, that collectors have reportedly begun removing xanthic specimens from Golfo Dulce. Conservation measures related to regulating collection of this newly recognized taxon may prove necessary. We add that, living at the upper edge of the species' temperature tolerance, there is also potential for population destruction from climate change. While it is important to recognize *H. p. xanthos* taxonomically, we have concern that taxonomic recognition without protection could lead to yet greater interest from global collectors, and urge that immediate preservation measures be considered in response to our subspecific designation.

This population has experienced genetic isolation sufficiently long to transition to an essentially monochromatic organism of notably smaller than usual stature. Major coloration and size changes evinced by *H. p. xanthos* are almost surely genetic, though

of course we cannot identify the nuclear genes involved, and these are phenotypic traits for which such major changes would presumably involve notable changes in absolute individual fitness. Adaptive aspects of the taxon's behavioral ecology may be partly or wholly a result of past natural selection on behavior; however, we do not know the relative roles of selection and drift, nor the degree of phenotypic plasticity involved.

Hopefully this globally unique population can continue to offer both scientists and conservation-conscious tourists a worthy subject of observation and study.

Conclusions

Hydrophis platurus xanthos is a well-defined evolutionary subspecies inhabiting a small area of unusual geography. Given unique aspects of its behavioral ecology, it could well represent an intrinsically genetically isolated taxon of recent origin, in which case a species designation would be appropriate. We have been appropriately conservative here, in defining it at a subspecific level. This provides footing for protective strategies, while allowing future research to refine its taxonomic rank.

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References

- Bessesen BL (2012) Geospatial and behavioral observations of a unique xanthic colony of pelagic sea snakes, *Pelamis platurus*, residing in Golfo Dulce, Costa Rica. *Herpetological Review* 43: 22–26.
- Bessesen BL (2015) Occurrence and distribution patterns of several marine vertebrates in Golfo Dulce, Costa Rica. *Revista de Biología Tropical* 63(Supl.1): 261–272.
- Bolaños R, Flores A, Taylor R, Cerdas L (1974) Color patterns and venom characteristics in *Pelamis platurus*. *Copeia* 1974(4): 909–912. <https://doi.org/10.2307/1442589>
- Brischoux F, Lillywhite HB (2011) Light- and flotsam-dependent 'float-and-wait' foraging by pelagic sea snakes (*Pelamis platurus*). *Marine Biology* 158: 2343–47. <https://doi.org/10.1007/s00227-011-1738-z>

- Cook TR, Brischoux F (2014) Why does the only 'planktonic tetrapod' dive? Determinants of diving behaviour in a marine ectotherm. *Animal Behavior* 98: 113–123. <https://doi.org/10.1016/j.anbehav.2014.09.018>
- Cogger HG (1975) Sea Snakes of Australia and New Guinea. In: Dunson WA (Ed.) *The Biology of Sea Snakes*. University Park Press, Baltimore, Maryland, 125–131.
- Dunson, WA, Ehlert GW (1971) Effects of temperature, salinity, and surface water flow on distribution of the sea snake *Pelamis*. *Limnology and Oceanography* 16(6): 845–853. <https://doi.org/10.4319/lo.1971.16.6.0845>
- Fitch HS (1987) Collecting and life-history techniques. In: Seigel RA, Collins JT, Novak SS (Eds) *Snakes: Ecology and Evolutionary Biology*. MacMillan Publishing, New York, 143–164.
- Gillett A (2015) Sea Snake Medicine and Disease. World Aquatic Veterinary Medicine Association webinar B-1008.
- Graham JB, Rubinoff I, Hecht MK (1971) Temperature physiology of the sea snake *Pelamis platurus*: An index of its colonization potential in the Atlantic Ocean. *Proceedings of the National Academy of Sciences* 68: 1360–1363. <https://doi.org/10.1073/pnas.68.6.1360>
- Graham JB (1974) Body temperatures of the sea snake *Pelamis platurus*. *Copeia* 1974: 531–533.
- Hebbeln D, Cortés J (2001) Sedimentation in a tropical fiord: Golfo Dulce, Costa Rica. *Geo-Marine Letters* 20(3): 142–148. <https://doi.org/10.1007/s003670000047>
- Hecht MK, Kropach C, Hecht BM (1974) Distribution of the yellow-bellied sea snake, *Pelamis platurus*, and its significance in relation to the fossil record. *Herpetologica* 30(4): 387–396. <https://doi.org/10.2307/1442545>
- Kropach C (1971a) Sea snake (*Pelamis platurus*) aggregations on slicks in Panama. *Herpetologica* 27(2): 131–135.
- Kropach C (1971b) Another color variety of the sea-snake *Pelamis platurus* from Panama Bay. *Herpetologica* 27(3): 326–327.
- Kropach C (1975) The yellow-bellied sea snake, *Pelamis*, in the Eastern Pacific. In: Dunson W (Ed.) *The Biology of Sea Snakes*. University Park Press, Maryland, 185–213.
- Leviton AE, Wogan GOU, Koo MS, Zug GR, Lucas RS, Vindum JV (2003) The Dangerously Venomous Snakes of Myanmar Illustrated Checklist with Keys. *Proceedings of the California Academy of Sciences* 54(24): 407–462.
- Linnaeus C (1766) *Systema Naturae per Regna tria Naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (Tomus I). Editio duodecima, reformata. Laurentii Salvii, Holmiae, 532 pp.
- Lillywhite HB, Sheehy CM III, Brischoux F, Pfaller JB (2015) On the abundance of a pelagic sea snake. *Journal of Herpetology* 49(2): 184–189. <https://doi.org/10.1670/14-004>
- Lukoschek V, Keogh JS (2006) Molecular phylogeny of sea snakes reveals a rapidly diverged adaptive radiation. *Biological Journal of the Linnean Society* 89(3): 523–539. <https://doi.org/10.1111/j.1095-8312.2006.00691.x>
- Pfaller JB, Frick MG, Brischoux F, Sheehy CM III, Lillywhite HB (2012) Marine Snake Epibiosis: A Review and First Report of Decapods Associated with *Pelamis platurus*. *Integrative and Comparative Biology* 52(2): 296–310. <https://doi.org/10.1093/icb/ics038>

- Quesada-Alpízar MA, Cortés J (2006) Los ecosistemas marinos del Pacífico sur de Costa Rica: estado del conocimiento y perspectivas de manejo. *Revista de Biología Tropical* 54(Supl.1): 101–145.
- Reading CJ, Luiselli LM, Akani GC, Bonnet X, Amori G, Ballouard JM, Filippi E, Naulleau G, Pearson D, Rugiero L (2010) Are snake populations in widespread decline? *Biology Letters* 6: 777–780. <https://doi.org/10.1098/rsbl.2010.0373>
- Rivas JA, Asconio RE, Muñoz MDC (2008) What is the length of a snake? *Contemporary Herpetology* 2008(2): 1–3.
- Rubinoff I, Graham JB, Motta J (1986) Diving of the sea snake *Pelamis platurus* in the Gulf of Panama I. Dive depth and duration. *Marine Biology* 91: 181–191. <https://doi.org/10.1007/BF00569434>
- Sanders KL, Lee MSY, Mumpuni, Bertozzi T, Rasmussen AR (2013) Multilocus phylogeny and recent rapid radiation of the viviparous sea snakes (Elapidae: Hydrophiinae). *Molecular Phylogenetics and Evolution* 66: 575–591. <https://doi.org/10.1016/j.ympev.2012.09.021>
- Sheehy CM III, Solórzano A, Pfaller JB, Lillywhite HB (2012) Preliminary insights into the phylogeography of the yellow-bellied sea snake, *Pelamis platurus*. *Integrative and Comparative Biology* 52: 321–330. <https://doi.org/10.1093/icb/ics088>
- Smith MA (1926) Monograph of the Sea-snakes (Hydrophiidae). British Museum (Natural History), London, 130 pp.
- Solórzano A (2004) Snakes of Costa Rica. Instituto Nacional de Biodiversidad, INBio, San Domingo de Heredia, Costa Rica, 792 pp.
- Solórzano A (2011) Variación de color de la serpiente marina *Pelamis platura* (Serpentes: Elapidae) en el Golfo Dulce, Puntarenas, Costa Rica. *Cuadernos de Investigación UNED* 3(1): 15–22. <https://doi.org/10.22458/urj.v3i1.211>
- Sponberg A (2004) PCB contamination in marine sediments from Golfo Dulce, Pacific coast of Costa Rica. *Revista de Biología Tropical* 52: 23–32.
- Svendsen HR, Rosland R, Myking S, Vargas JA, Lizano OG, Alfaro EJ (2006) A physical-oceanographic study of Golfo Dulce, Costa Rica. *Revista de Biología Tropical* 54(1): 147–170.
- Tu AT (1976) Investigation of the sea snake, *Pelamis platurus* (Reptilia, Serpentes, Hydrophiidae), on the Pacific Coast of Costa Rica, Central America. *Journal of Herpetology* 10(1): 13–18. <https://doi.org/10.2307/1562922>
- Wolff M, Hartman HJ, Koch V (1996) A pilot trophic model for Golfo Dulce, a tropical fjord-like embayment, Costa Rica. *Revista de Biología Tropical* 44: 215–231.

Supplementary material I

Table of localities

Authors: Brooke L. Bessesen, Gary J. Galbreath

Data type: distribution

Explanation note: *Hydrophis platurus xanthos*, COSTA RICA: Golfo Dulce: inner basin, 2010–2011.

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Sexual morphs of *Pterocomma tremulae* Börner, 1940 (Aphididae, Aphidinae) with description of male reproductive system

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Abstract

Paper presents the first description of the so far unknown sexual generation of *Pterocomma tremulae* (Aphididae, Aphidinae): oviparous female and alate male. It also provides detailed description of the male reproductive system. Discussion focuses on comparative analysis of male reproductive system with other aphid groups and possible importance of its structure in resolving phylogenetic interrelationships within the genus *Pterocomma*. A key is provided to the known males of European *Pterocomma* species.

Keywords

Aphid, phylogeny, *Populus*, reproduction, taxonomy

Introduction

Pterocommatinae have long been a somewhat problematic group within Aphididae, having been placed in most systems in close relationship with Aphidinae. The detailed history of classification has been presented in revision of Palaearctic species of Pterocommatinae made by Wojciechowski (2003). This taxon bears a set of distinct morphological traits, giving base to distinguish it from the subfamily Aphidinae. However, recent studies with application of molecular markers, both mitochondrial and nuclear, indicated the strong relationship of what was so far regarded as a subfamily Pterocommatinae, with

aphid genera belonging to the “Liosomaphidine” branch of Aphidinae, within the tribe Macrosiphini (Tang et al. 2015) or close to Macrosiphini (Papasotiropoulos et al. 2013). The current concept of systematic position of “Pterocommatines” *sensu stricto*, is that it is part of tribe Macrosiphini (Blackman and Eastop 2017).

However, within the genus *Pterocomma* itself, there are also some problems concerning the very variable morphology of a few species, making it difficult to distinguish closely related species e. g. *Pterocomma pilosum* Buckton, 1879; *P. konoi* Takahashi, 1939; *P. dubium* Börner, 1950; *P. ringdahli* Wahlgren, 1940; or various subspecies, of uncertain taxonomical status e.g. *P. pilosum sarmaticum* Szelegiewicz, 1967 (Wojciechowski 2003, Mróz and Depa 2014, Blackman and Eastop 2017). Resolution of these doubts definitely requires detailed morphological and molecular studies, but this is possible only after proper recognition of crucial morphs of each form and species, especially the sexual generation (Wieczorek et al. 2011, Wieczorek et al. 2013, Kanturski et al. 2017). Application of anatomical studies of the reproductive system, especially the male reproductive system may also shed new light on species identity and systematic relationship (Wieczorek 2006).

Pterocomma tremulae, Börner 1940 is relatively well defined in terms of its morphological characteristics. There are some accounts of its intraspecific variation, but the species as whole may be well recognized as the only *Populus*-feeding species bearing few to many secondary rhinaria on antennal segment III, a trait occurring also only in *Pterocomma kozhuchovae*, most probably an eastern Palearctic vicariant species. Here we present the first description of the sexual morphs and also provide the first description of the male reproductive system of this species.

Material and methods

Collection data of specimens applied for taxonomical description:

17.10.2014, Katowice; *Populus tremula*; leg. A. Nowińska, det. Ł. Depa, 2 oviparous females.

17.10.2014, Katowice; *Populus tremula*; leg. A. Nowińska, det. Ł. Depa, 2 alate males.

Also 29 specimens of alate males were collected from the same collection site to anatomical studies. The provisional key to males of European representatives of the genus *Pterocomma* was prepared on the basis of morphological descriptions and measurements given by Wojciechowski (2003).

Anatomical studies

Histological preparations

In order to analyse the anatomical structure of the male reproductive system of *P. tremulae*, the paraffin method was applied. The material was collected into Eppendorf

microtubes containing 70% ethanol for keeping and preserving collected specimens. Next, insects were dehydrated in increasing concentration of ethanol (90%, 96%, 100%). In order to ensure transparency, specimens were kept in methyl benzoate for one night. Then, material was consecutively transferred to benzene, benzene with paraffin (in proportions 2:3 and 1:2), paraffin I (melting point: 56°C) and finally to paraffin II (melting point: 60°C), where it was kept for the night. After this process, material was immersed in paraffin II. The bars obtained were sectioned into 5 µm strips, which were stuck on slides in a 0.5% gelatine solution at temperature 50–52°C. Then, the slides were dried in 37°C.

Slides were next deparaffined in xylene and treated with a series of ethanol solutions (100–60%). They were rinsed in distilled water, stained with Ehrlich's acid hematoxylin for about 20 minutes, rinsed again and differentiated with xylidine ponceau. After this process, preparations were treated with series of ethanol solutions (60–100%), rinsed twice in xylene and embedded in Canadian balm or DPX.

This process was applied to 17 individuals of *P. tremulae*. The following histological preparations were prepared: cross-sections from 9 individuals and longitudinal sections from 8 individuals. In total 171 microscopic slides were made, including 84 preparation of cross-section and 87 of longitudinal section.

Mounting of the whole tract

The specimens of *P. tremulae* were put into a droplet of 30% ethanol, on the microscopic glass, and with the mounting needles the whole reproductive system was extracted from the body. The extracted organs were preserved in glycerol and mounted, to make all the anatomical structures visible with the stereomicroscope. A total number of 12 preparations were made using this technique.

The documentation was prepared using Nikon Eclipse E6000, with measurements made by Lucia net program. The pictures of translucent specimens were taken with a stereomicroscope equipped with monochromatic camera Axio Cam programmed with Axio Vision.

Results

Description of sexual morphs of *P. tremulae*, Börner, 1940

Oviparous female. Body oval, 3.66–4.03 mm long (Fig. 1), grey to brightly brown, significantly convex. Head and pronotum dark and sclerotised; mesonotum with marginal sclerites, and spinal sclerites broken into smaller sclerites in the middle; metanotum with weak marginal sclerites only. Mesothoracic furca separated, but with band of dark sclerotisation between them, giving the impression of being joined. Antenna 6-segmented, brownish, with base of antennal segment III paler (Fig. 2A),

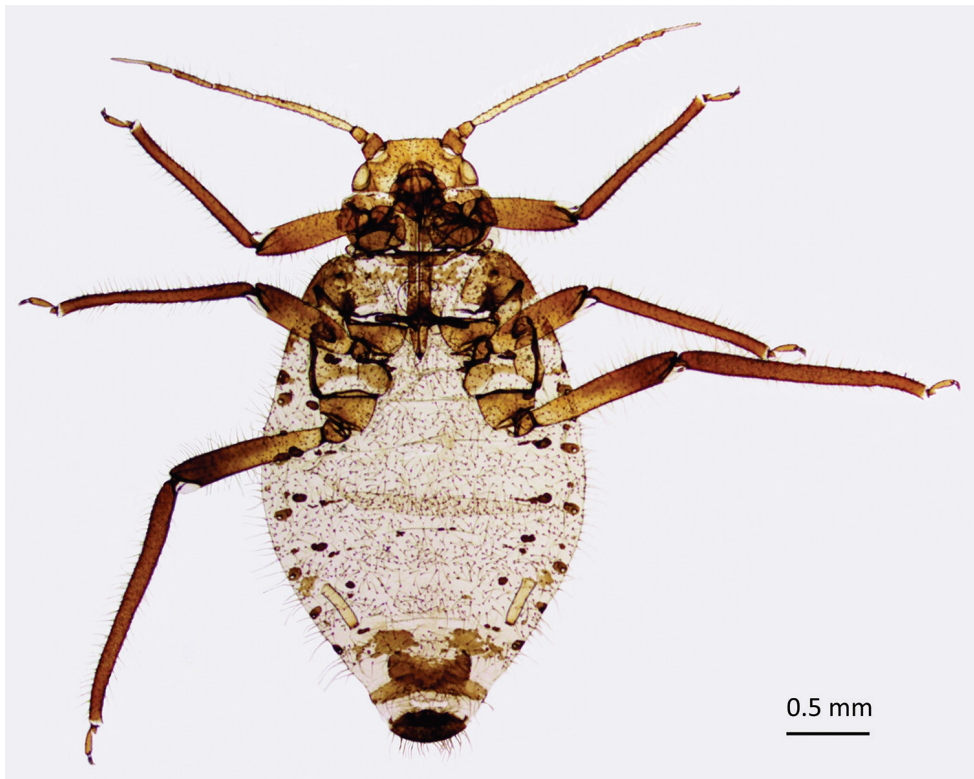


Figure 1. Oviparous female of *P. tremulae*.

1.72–1.92 mm long, 0.47–0.48 of body length. Antennal segment III 0.64–0.71, IV 0.26–0.29, V 0.26–0.31, VI 0.37–0.41 mm long; length of antennal segment III: 2.39–2.50 of the length of antennal segment IV, 2.29–2.44 of antennal segment V; processus terminalis 0.23–0.26 mm long, 1.60–1.90 of VIa. Antenna covered with long, erect hairs, 0.11–0.13 mm long. Number of secondary rhinaria on III antennal segment: 13–20 (Fig. 2), on IV antennal segment 0. Base of antennal segment VI with 6–8 erect hairs. Rostrum 0.90–1.10 mm long, 0.25–0.27 of body length, with ultimate rostral segment 0.22–0.23 mm long, 1.27–1.30 of second segment of hind tarsus, 0.33–0.34 of III antennal segment, 0.72–0.77 of siphunculus, with 12–13 accessory hairs (Fig. 1). Legs dark, with brighter bases of femora and coxae, second segment of hind tarsus 0.17–0.18 mm long; legs covered with erect hairs, their length on tibia 0.10–0.12 mm. Hind tibia swollen with ca. 150–200 scent plaques (Fig. 2B).

Abdomen membranous, covered with dense pubescence. Length of hairs on abdominal tergite V 0.17–0.19 mm. Spinal sclerites only on VI and VII segment: on VI weakly developed, broken into minute sclerites. Intersegmental sclerotic insertions dark. Marginal sclerites present on abdominal tergites I and V, sometimes also on VI but broken into smaller sclerites. Marginal tubercles present always on abdominal tergites I–IV, sometimes also on V–VII, their diameter at most as the diameter of spiracles, always

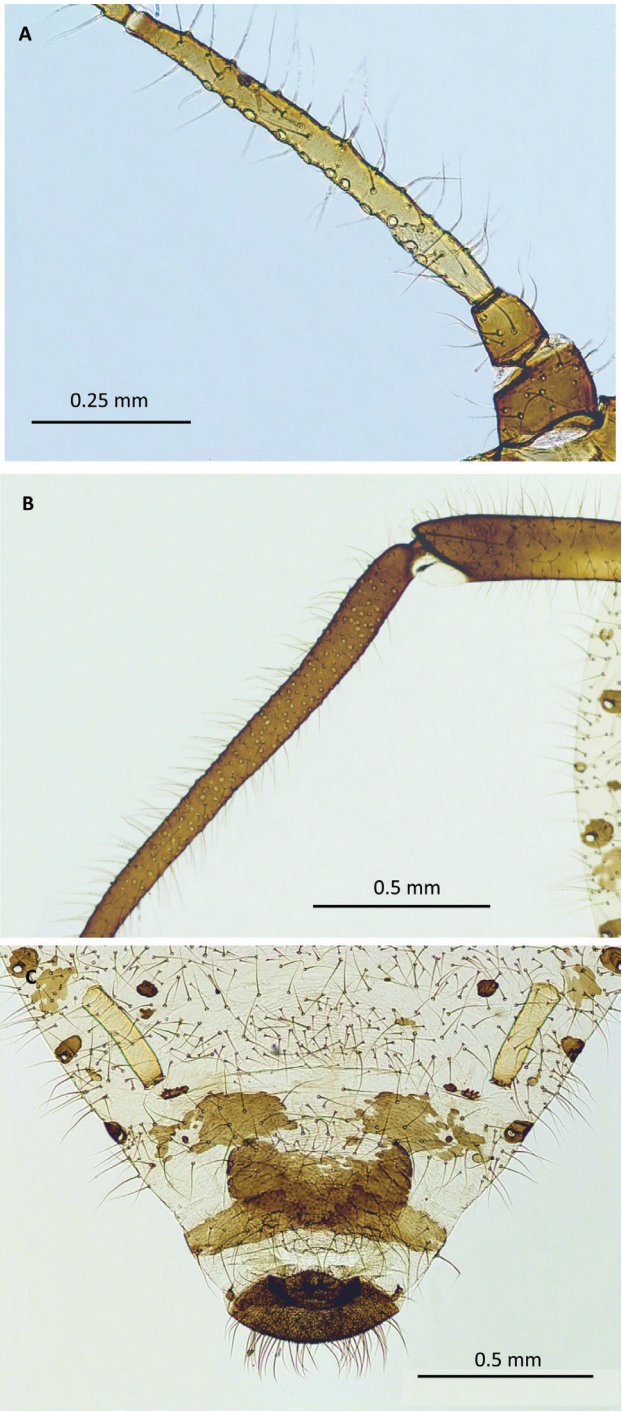


Figure 2. Morphological features of the oviparous female: **A** antennal segment III with secondary rhinaria **B** hind tibia with numerous scent plaques **C** posterior part of the abdomen, with siphunculi, cauda and genital plate.



Figure 3. Alate male of *P. tremulae*.

dark pigmented. Number of hairs on abdominal tergite VIII ca. 50, their length 0.16–0.17 mm. Cauda rounded, dark pigmented, covered with many hairs (Fig. 2C). Genital plate semicircular, dark pigmented, 0.47–0.50 mm wide, covered with many hairs. Siphunculi pale, cylindrical, but may be slightly swollen in the distal half (Fig. 2C), 0.28–0.32 mm long, slightly darker at the apex, with very delicate flange, 0.44–0.45 of the length of antennal segment III.

Alate male. Body dark, brownish, 2.87–3.03 mm long (Fig. 3); head sclerotized, with ocelli well developed and big, multifaceted eyes with triommatidium. Antennae 6 segmented (Fig. 4A), 1.74–1.92 mm long, 0.61–0.65 of body length, brownish, only slightly paler than legs. Antennal segment III 0.63–0.71, IV 0.29–0.33, V 0.29–0.33, VI 0.38–0.44 mm long; length of antennal segment III: 1.62–1.63 of the length of antennal segment IV, 2.12–2.13 of antennal segment V; processus terminalis 0.22–0.27 mm long, 1.43–1.74 of VIa. Antenna covered with long, erect hairs, 0.09–0.11 mm long. Number of secondary rhinaria on antennal segment III: 73–105 (Fig. 4A), on antennal segment IV: 27–43, V: 20–26, VI: 0–2. Base of antennal segment VI with 8–10 erect hairs. Rostrum 1.15–1.22 mm long, 0.38–0.42 of body length, with ultimate rostral segment 0.19–0.21 mm long, 1.17–1.25 of second segment of hind tarsus, 0.29–0.31 of III antennal segment, 0.94–1.00 of siphunculus, with 11–13 accessory hairs. Thorax heavily sclerotized, winged. Forewings with veins weakly sclerotized, medial vein branched twice. Legs uniformly brownish, only bases of femora slightly paler, covered with erect hairs 0.12–0.13 mm long. Second segment of hind tarsus 0.15–0.17 mm long.

Abdomen membranous, covered with hairs 0.010–0.015 mm long, with spinopleural sclerites on abdominal segments I–VII often divided in the middle, and on segment V broken into smaller sclerites. Marginal sclerites present on all abdominal

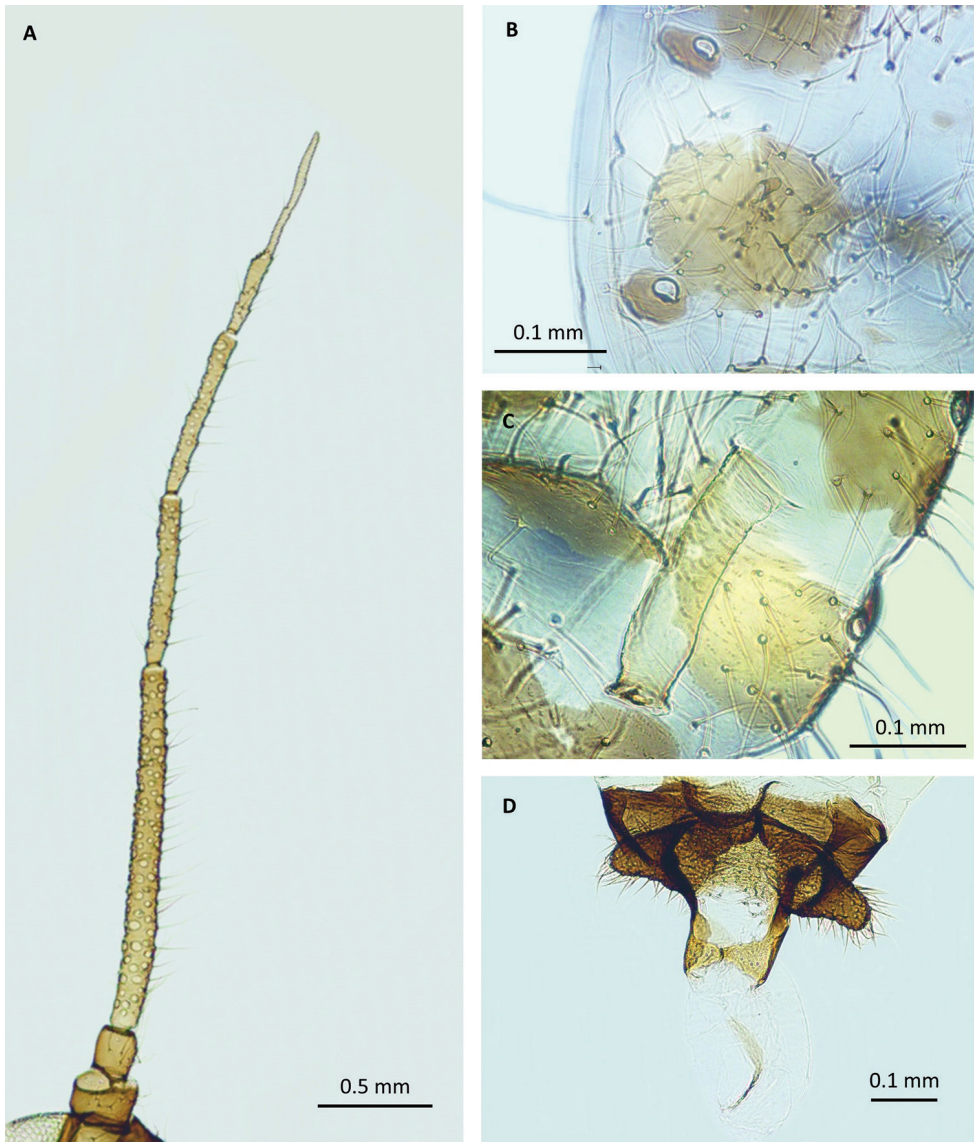


Figure 4. Morphological features of the male: **A** antenna with multiple secondary rhinaria **B** marginal plates and stigmal pores **C** siphunculus **D** genital apparatus with parameres and membranous aedeagus.

segments, with spiracles in the anterior margins of the sclerites and with conspicuous marginal tubercles (Fig. 4B), dark pigmented, on segments I–IV and VI–VII, occasionally also on V. Siphunculi pale, 0.19–0.22 mm long, 0.30–0.32 of antennal segment III, tapering, with weakly swollen apical part and small flange (Fig. 4C). Cauda small, pigmented, semicircular, sparsely covered with hairs. Genital apparatus sclerotized, parameres conspicuous, dark, densely covered by relatively short hairs; base of the membranous aedeagus less sclerotized, sparsely covered by very short hairs (Fig. 4D).

Description of the male reproductive system of *Pterocomma tremulae*

The male reproductive system of *Pterocomma tremulae* extends parallel to the longitudinal axis of the body. It consists of two testes, located in the area of abdominal segments II and III, and a pair of accessory glands (Figs 5A, B, 6A). The total length of the system is 1.12–1.36 mm. One testis is 0.34–0.82 mm long and 0.26–0.44 mm wide. Each testis

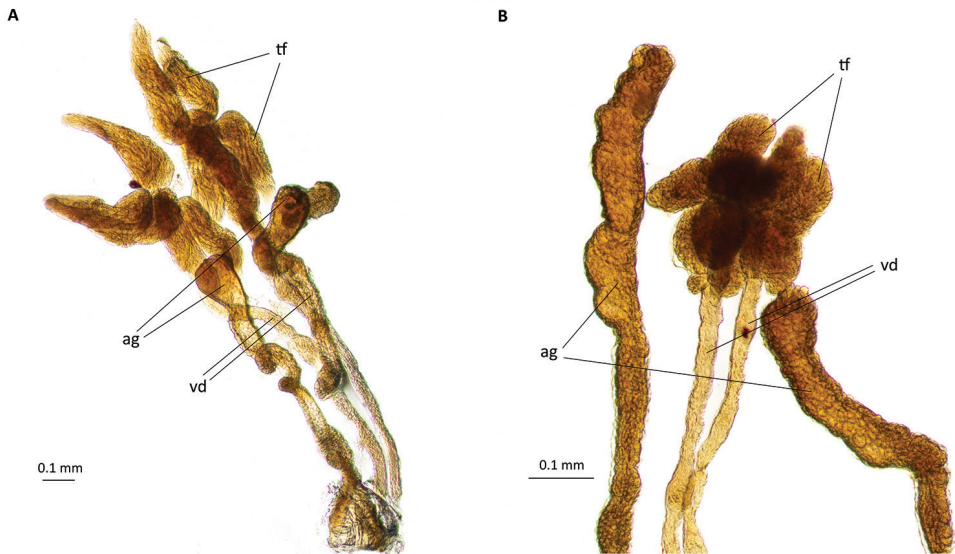


Figure 5. Morphology of the male reproductive system of *P. tremulae*: **A** young specimen **B** mature specimen; ag – accessory gland, tf – testicular follicles, vd – vas deferens.

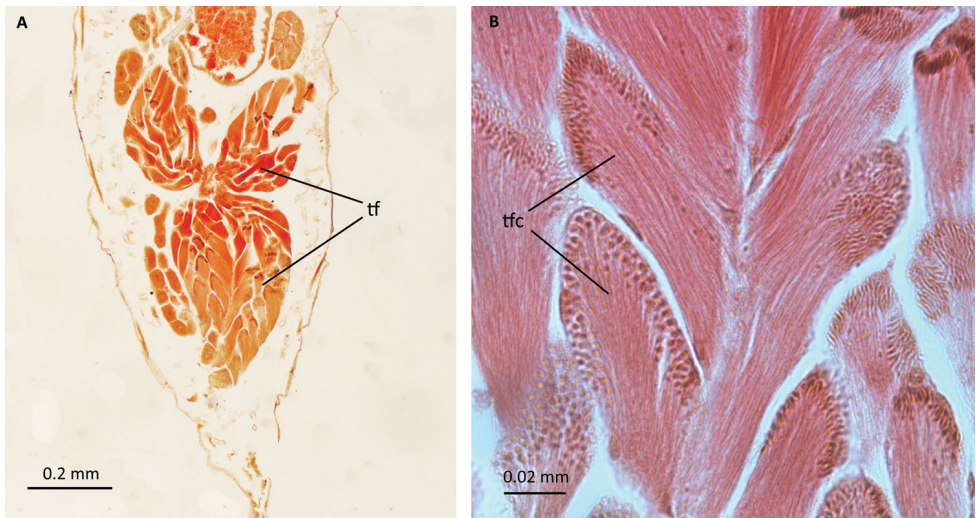


Figure 6. Male reproductive system of *P. tremulae*: **A, B** cross sections through testes; tf – testicular follicles, tfc – testicular follicle cysts.

consists of four elongated follicles with rounded tips, having a diameter of 0.03–0.2 mm each. Each follicle contains cysts with differentiating male germ cells (Fig. 6A, B). Follicles connect to each other only at the base. They are located at the top of vas deferens, which they are connected to by short efferent ducts. Follicles of both testes can be also connected to each other. The length of one vas deferens is 0.68–1.12 mm, while its diameter 0.03–0.07 mm. Over the entire length it is more or less the same width.

Accessory glands, of ectodermal origin, are 0.6–1.06 mm long. In examined species they are club-shaped or elongated. At the widest point their diameter is 0.05–0.12 mm, while at the narrowest point the diameter is 0.04–0.07 mm. Glandular wall is built of cuboidal epithelium (Fig. 7A, B). The height and width of the cells is 0.01 mm.

Depending on the age of the individual, testes and glands change their size. In younger individuals we observed testes several times larger than glands (Fig. 5A), while in older ones, testes are reduced and glands are enlarged (Fig. 5B). The vas deferens and the terminal sections of accessory glands extend next to each other independently and at the end they open to the ejaculatory duct (Fig. 7C, D).

Key to known males of European species of the genus *Pterocomma*:

- | | | |
|---|--|--------------------|
| 1 | Male apterous | <i>P. jacksoni</i> |
| – | Male alate | 2 |
| 2 | Siphunculi strongly swollen medially | <i>P. salicis</i> |
| – | Siphunculi cylindrical, at most slightly swollen distally | 3 |
| 3 | Antenna 0.6 of body length or longer | 4 |
| – | Antenna less than 0.6 of body length | 6 |
| 4 | Less than 50 secondary rhinaria on antennal segment III, on <i>Salix</i> spp. | <i>P. konoi</i> |
| – | More than 70 secondary rhinaria on antennal segment III, on <i>Populus</i> spp. | 5 |
| 5 | Less than 20 secondary rhinaria on antennal segment V | <i>P. dubium</i> |
| – | 20 or more secondary rhinaria on antennal segment V | <i>P. tremulae</i> |
| 6 | Up to 15 secondary rhinaria on antennal segment IV | <i>P. rufipes</i> |
| – | 18 or more secondary rhinaria on antennal segment IV | 7 |
| 7 | 80 or less secondary rhinaria on antennal segment III | <i>P. pilosum</i> |
| – | 80 or more secondary rhinaria on abdominal segment III | <i>P. populeum</i> |

Discussion

The male reproductive system of around 80 aphid species has been studied so far (Wieczorek et al. 2011). Compared to other insects, the characteristic features of aphids are the lack of seminal vesicles and the disordered arrangement of spermatids in the testicular follicles. The accessory glands are usually even in number, like in *Pterocomma tremulae* (Fig. 5A, B). They enter the ejaculatory duct independently of the vasa

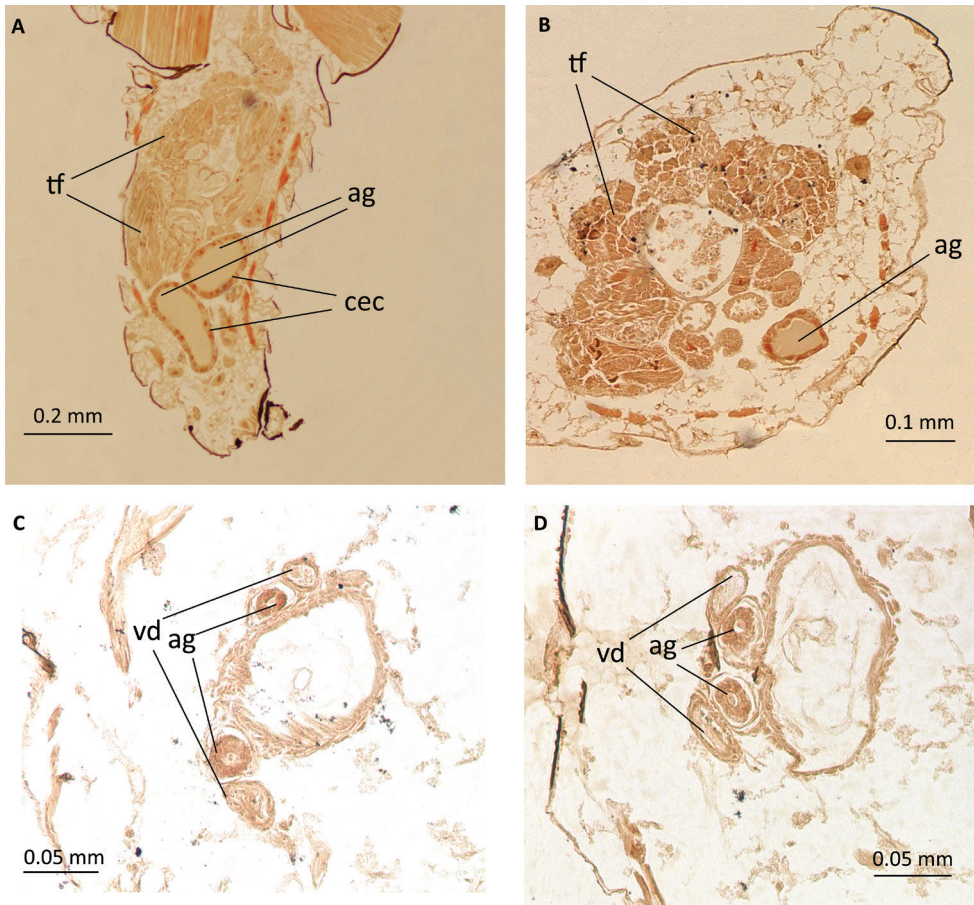


Figure 7. Male reproductive system of *P. tremulae*: **A** longitudinal section through testicles **B, C, D** cross sections through testicles; ag – accessory gland, cec – cuboidal epithelial cells, tf – testicular follicles, vd – vas deferens.

deferentia (Fig. 7B, C, D). The exception is in the Lachninae subfamily, which does not have accessory glands (Wieczorek and Świątek 2008, Wojciechowski 1977). However, in all the other studied species, accessory glands were present, entering the ejaculatory duct independently of vasa deferentia (Wieczorek 2006, Wieczorek and Świątek 2007 and 2008, Vitale et al. 2009). The ejaculatory duct is relatively short in most species, something that was also observed in *Pterocomma tremulae*. Its extremity is connected to the copulatory organ (Wieczorek and Świątek 2008).

In Aphidoidea, the number of testicular follicles varies between 2 and 7 (Szelegiewicz and Wojciechowski 1985). The number of follicles is not a feature characteristic of any one family, but has evolutionary significance. It allows the determination of the phylogenetic position of the aphid species. The smaller the number of follicles it has, the phylogenetically younger is the species (Wojciechowski 1977). The reduction of the number of testicular follicles is also related to the transfer of spermatogenesis

to early larval stages, or in some species, to the termination of that process already in embryonic development (Blackman 1987). The initial number of testicular follicles is 7, as it is the number of pregenital segments. The number of follicles is reduced during oligomerization processes that proceed independently in each family (Mróz 2007). This number can also increase during the polymerization process. In such cases, the number of testicular follicles is 8 (Mróz and Wojciechowski 2011).

There are four testicular follicles in each testicle in *Pterocomma tremulae* (Figs 5, 6A). The male reproductive system of two other species of the genus *Pterocomma* has also been studied. It has been shown that *Pterocomma populeum* has 6 testicular follicles (Wieczorek and Mróz 2006), whereas *Pterocomma salicis* (Linnaeus, 1758) has 5 (Szelegiewcz and Wojciechowski 1985). That could indicate that *P. tremulae* belongs to the youngest evolutionary line within the genus *Pterocomma*. However, due to lack of data regarding the male reproductive system of many species from this genus, it is difficult to make a more precise analysis of this theory. It is not known whether there are two developmental lines involved in the adaptation to two host genera: *Populus* and *Salix*. *P. tremulae* is associated with *Populus*, as well as *P. populeum*, which has up to 6 testicular follicles. However *P. salicis*, which has 5 follicles, feeds on *Salix*. This incongruence requires explanation by studies on the male reproductive system of more species, including *Plocamaphis* spp. as an outgroup, supported by results of molecular studies.

References

- Blackman RL (1987) Reproduction, cytogenetics and development. In: Minks AK, Harrewijn P (Eds) *Aphids: Their Biology, Natural Enemies and Control*. Elsevier, Amsterdam 2: 163–195.
- Blackman RL, Eastop VF (2017) Aphids on the World's plants. <http://www.aphidsonworld-plants.info/index.htm> [access: 19.05.2017]
- Kanturski M, Akbar ShA, Favret C (2017) The Bhutan Pine Aphid *Pseudessigella brachychaeta* Hille Ris Lambers (Hemiptera: Aphididae: Lachninae) From India Reveals the Hitherto Unknown Oviparous Female and Dwarfish Male. *Zoological Studies* 56: 12. <http://doi.org/10.6620/ZS.2017.56-12>
- Mróz E (2007) Anatomical and molecular studies of *Stenodema* Laporte genus (Heteroptera: Miridae). *Genus International Journal of Invertebrate Taxonomy* 14: 77–81.
- Mróz E, Depa Ł (2014) Description of Fundatrices of *Pterocomma tremulae* Börner, 1940 and *Pterocomma pilosum* buckton, 1879 (Sternorrhyncha: Aphididae). *Annales Zoologici* 64(1): 51–55. <https://doi.org/10.3161/000345414X680564>
- Mróz E, Wojciechowski W (2011) The systematic position the tribe Stenodemini (Heteroptera: Cimicomorpha: Miridae: Mirinae) in the light of the male internal reproductive system. *Journal of Natural History* 45(25–26): 1563–1588. <http://dx.doi.org/10.1080/00222933.2011.559595>
- Papasotiropoulos V, Tsiamis G, Papaioannou Ch, Ioannidis P, Klossa-Kilia E, Papapanagiotou A, Bourtzis K, Kiliadis G (2013) A molecular phylogenetic study of aphids (Hemiptera: Aphidi-

- dae) based on mitochondrial DNA sequence analysis. *Journal of Biological Research-Thessaloniki* 20(1).
- Szelegiewicz H, Wojciechowski W (1985) The male internal reproductive system of aphids. In: Szelegiewicz (Edt) *Evolution and biosystematics of aphids. Proceedings of the International Aphidological Symposium at Jabłonna, 5–11 April, 1981. Zakład Narodowy im. Ossolińskich, Wrocław*, 239–244.
- Tang X-J, Jiang L-Y, Chen J, Qiao G-X (2015) DNA barcoding of Pterocommatinae (Hemiptera: Aphidoidea: Aphididae) based on three molecular markers. *Acta entomologica sinica* 58: 1262–1272.
- Vitale DGM, Brundo MV, Sottile L, Viscuso R, Babbagallo S (2009) Morphological and ultrastructural investigations of the male reproductive system in aphids: observations on *Tuberculatus (Tuberculoides) eggleri* Börner (Hemiptera Aphidoidea). *Redia* 92: 195–197.
- Wieczorek K (2006) Anatomical investigations of the male reproductive system of five species of Calaphidinae (Hemiptera, Aphidoidea). *Insect Systematics & Evolution* 37(4): 457–465. <https://doi.org/10.1163/187631206788831434>
- Wieczorek K, Kanturski M, Junkiert Ł (2013) *Shenahweum minutum* (Hemiptera, Aphidoidea: Drepanosiphinae) – Taxonomic position and description of sexuales. *Zootaxa* 3731(3): 324–330. <https://dx.doi.org/10.11646/zootaxa.3731.3.2>
- Wieczorek K, Mróz E (2006) The structure of the male reproductive system of selected Hemiptera groups. *Acta Biologica Cracoviensia* 48(suppl. 1): 72.
- Wieczorek K, Płachno BJ, Świątek P (2011) Comparative morphology of the male genitalia of Aphididae (Insecta, Hemiptera): part 1. *Zoomorphology* 130(4): 289–303. <https://dx.doi.org/10.1007%2Fs00435-011-0134-z>
- Wieczorek K, Świątek P (2007) Classification of the drepanosiphine aphids (Hemiptera, Aphidoidea: Phyllaphidinae, Calaphidinae) in the light of anatomical research. *Genus International Journal of Invertebrate Taxonomy* 14: 63–65.
- Wieczorek K, Świątek P (2008) Morphology and ultrastructure of the male reproductive system of the woolly beech aphid *Phyllaphis fagi* (Hemiptera: Aphididae: Phyllaphidinae). *European Journal of Entomology* 105: 707–712. <https://dx.doi.org/10.14411/eje.2008.096>
- Wojciechowski W (1977) Procesy oligomeryzacji w budowie męskiego układu rozrodczego miodownicy (Homoptera, Lachnidae). *Prace Naukowe USI (Katowice)* 3: 140–164.
- Wojciechowski W (2003) A monograph of the Palearctic Pterocommatinae (Aphididae, Aphidinea, Hemiptera). *Wydawnictwo Uniwersytetu Śląskiego, Katowice*, 112 pp.

A new species of *Longicoelotes* (Araneae, Agelenidae) from China, with the first description of the male of *L. kulianganus* (Chamberlin, 1924)

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Abstract

A new *Longicoelotes* species is described from Jiangxi Province, China: *L. geei* sp. n. (♂♀). In addition, the male of *L. kulianganus* (Chamberlin, 1924) is described for the first time. DNA barcodes of the two species are documented for future use and as proof of molecular differences between these species.

Keywords

East Asia, description, Coelotinae, taxonomy

Introduction

The *Longicoelotes* was described by Wang (2002), with *L. karschi* Wang, 2002 from China as the type species. Wang (2003) transferred *Coelotes kulianganus* Chamberlin, 1924 from China and *C. senkakuensis* Shimojana, 2000 from Ryukyu Islands to *Longicoelotes*. Three species of *Longicoelotes* were known before the current study (World Spider Cata-

log 2017), two of which are restricted to China. This paper provides the description of a new species based on newly collected material from Jiangxi Province, China. It also redescribes *L. kulianganus* based on specimens collected from the type locality.

Material and methods

Specimens were examined and measured with a Leica M205C stereomicroscope. Images were captured with an Olympus C7070 wide zoom digital camera mounted on an Olympus SZX12 dissecting microscope. Epigynes and male palps were examined after dissection. Epigynes were cleared by boiling in 10% KOH solution before taking photos. All measurements are given in millimeters. Leg measurements are given as: total length (femur, patella + tibia, metatarsus, tarsus). Only structures (palp and legs) of the left side of the body are described and measured.

Terminology used for parts of copulatory organs in the text and figures follows Wang (2002) with some modifications. Abbreviations used in the text and figures are: ALE = anterior lateral eye; AME = anterior median eye; AME-ALE = distance between AME and ALE; AME-AME = distance between AME and AME; ALE-PLE = distance between ALE and PLE; d = dorsal; Fe = femur; Mt = metatarsus; p = prolat-eral; Pa = patella; PLE = posterior lateral eye; PME = posterior median eye; PME-PLE = distance between PME and PLE; PME-PME = distance between PME and PME; r = retrolateral; Ta = tarsus; Ti = tibia; v = ventral. References to figures in the cited papers are listed in lowercase (fig. or figs); figures from the present paper are noted with an initial capital (Fig. or Figs).

DNA barcodes were obtained for future use: a partial fragment of the mitochondrial gene cytochrome oxidase subunit I (COI) was amplified and sequenced for two species using Primers LCO1490-oono (5'-CWACAAAYCATARRGATATTGG-3') (Folmer et al. 1994; Miller et al. 2010) and HCO2198-zz (5'-TAAACTTCCAG-GTGACCAAAAAATCA-3') (Folmer et al. 1994; Zhao and Li 2016). For additional information on extraction, amplification, and sequencing procedures, see Zhao et al. (2013). All sequences were blasted in GenBank; accession numbers are provided in Table 1.

All specimens (including molecular vouchers) are deposited in the Institute of Zoology, Chinese Academy of Sciences in Beijing (IZCAS).

Table 1. Voucher specimen information.

Species	GenBank accession number	Sequence length	Collection localities
<i>L. geei</i> sp. n.	MF347606	543bp	China: Jiangxi: Wuyuan
<i>L. kulianganus</i>	MF347607	630bp	China: Fujian: Fuzhou: Guling

Taxonomy

Genus *Longicoelotes* Wang, 2002

Longicoelotes Wang, 2002: 109. Type species *Longicoelotes karschi* Wang, 2002 from Jiangsu Province, China.

Composition. Four species of *Longicoelotes* in total: they are *L. geei* sp. n. (♂♀), *L. karschi* (♂♀), *L. kulianganus* (♂♀) from China, and *L. senkakuensis* (Shimojana, 2000) (♀) from Ryukyu Islands.

Note. *Longicoelotes karschi* is very similar to *L. kulianganus* and could be its junior synonym.

Longicoelotes geei, sp. n.

<http://zoobank.org/AD46BF47-3AB3-42AD-97D9-7E4E39D83D28>

Figs 1–2, 5–6

Type material. **Holotype** ♂: China: Jiangxi Province: Wuyuan County, Lianhua Cave, N29°29'02", E117°36'53", 350 m, 4.XII.2016, X. Zhang; **Paratypes**: 3♀ 2♂, same data as holotype; 3♀, the same locality, N29°29'02", E117°36'53", 352 m, 20.V.2013, Y. Luo and J. Liu.

Etymology. The species is named after Mr. Nathaniel Gist Gee. Mr. Gee was an American biologist who lived in China about 35 years. He contributed greatly to the development of biological research and education in China, including the establishment of the first biology department in the history of university education in China (Fu 2016). He collected the holotype of *L. kulianganus*.

Diagnosis. The male can be distinguished from all other *Longicoelotes* species by its long cymbial furrow, about 1/3 length of cymbium (*vs* 1/4 or 1/5 in other species) (Figs 1, 3; Wang 2002: figs 312–314). The female differ from all other *Longicoelotes* species by the nearly heart-shaped atrium and large anterior parts of copulatory ducts, subequal to receptacles (*vs* nearly triangular atrium and small anterior parts in *L. kulianganus*, about 1/2 diameter of receptacles; nearly rounded atrium and extremely small anterior parts in *L. senkakuensis*, about 1/4 diameter of receptacles) (Figs 2, 4–5; Shimojana 2000: figs 46–49).

Description. **Male (holotype):** Total length 6.00. Carapace 2.50 long, 2.00 wide. Abdomen 3.50 long, 1.75 wide. Eye sizes and interdistances: AME 0.15, ALE 0.13, PME 0.15, PLE 0.10; AME-AME 0.05, AME-ALE 0.04, PME-PME 0.05, PME-PLE 0.06. Leg measurements: I: 12.45 (3.30, 4.00, 3.00, 2.15); II: 11.30 (3.25, 3.30, 2.75, 2.00); III: 10.65 (3.00, 3.25, 2.75, 1.65); IV: 14.65 (4.00, 4.25, 4.15, 2.25). Carapace greenish, with black lateral margins, the radial grooves distinct. Abdomen yellow, with blackish herringbone patterns. Palp as in Fig. 1: patellar apophysis long, about 2 times longer than tibia; tibia short, about 1/5 length of cym-

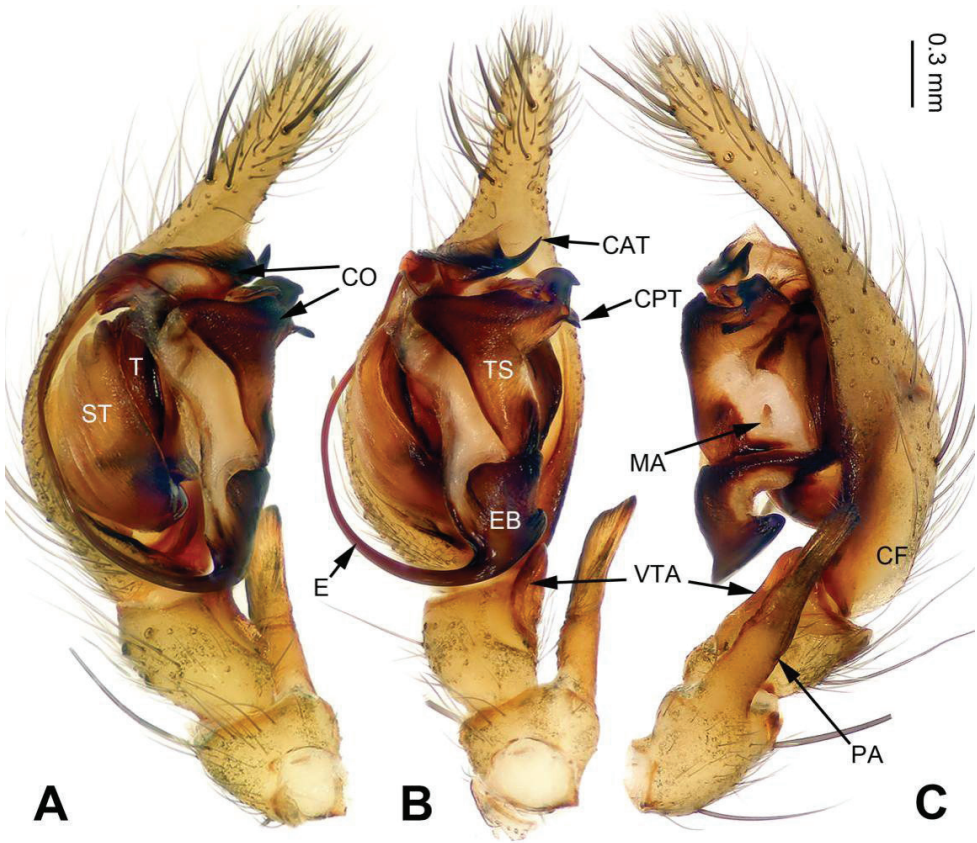


Figure 1. Palp of *Longicoelotes geei* sp. n., holotype male. **A** Prolateral view **B** Ventral view **C** Retrolateral view. CAT = anterior tip of conductor, CF = cymbial furrow, CO = conductor, CPT = posterior tip of conductor, E = embolus, EB = embolic base, MA = median apophysis, PA = patellar apophysis, ST = subtegulum, T = tegulum, TS = tegular sclerite, VTA = ventral tibial apophysis. Scale bar: equal for **A, B, C**.

bium; cymbial furrow long, about 1/3 length of cymbium; ventral tibial apophysis as long as tibia, without pointed tip, extending beyond the tibia; conductor slender and bifurcated; posterior tip of conductor bifurcated; anterior tip of conductor bifurcated, ventral part sharp, dorsal part lamellate; median apophysis reduced; embolus beginning at 5:30 o'clock position.

Leg spination in male:

	Fe	Pa	Ti	Mt	Ta
I	3d 2p 1r	-	1p 3-3v	2p 3-3v	-
II	3d 3p 2r	1d 1p	2p 3-3v	1p 3-3v	-
III	3d 2p 2r	2d 1p 1r	2d 2p 3r 3-3v	2d 5p 5r 3-3v	1p 1r
IV	3d 2p 1r	2d 1p 1r	2d 2p 2r 3-3v	5p 5r 3-3v	2p 1r

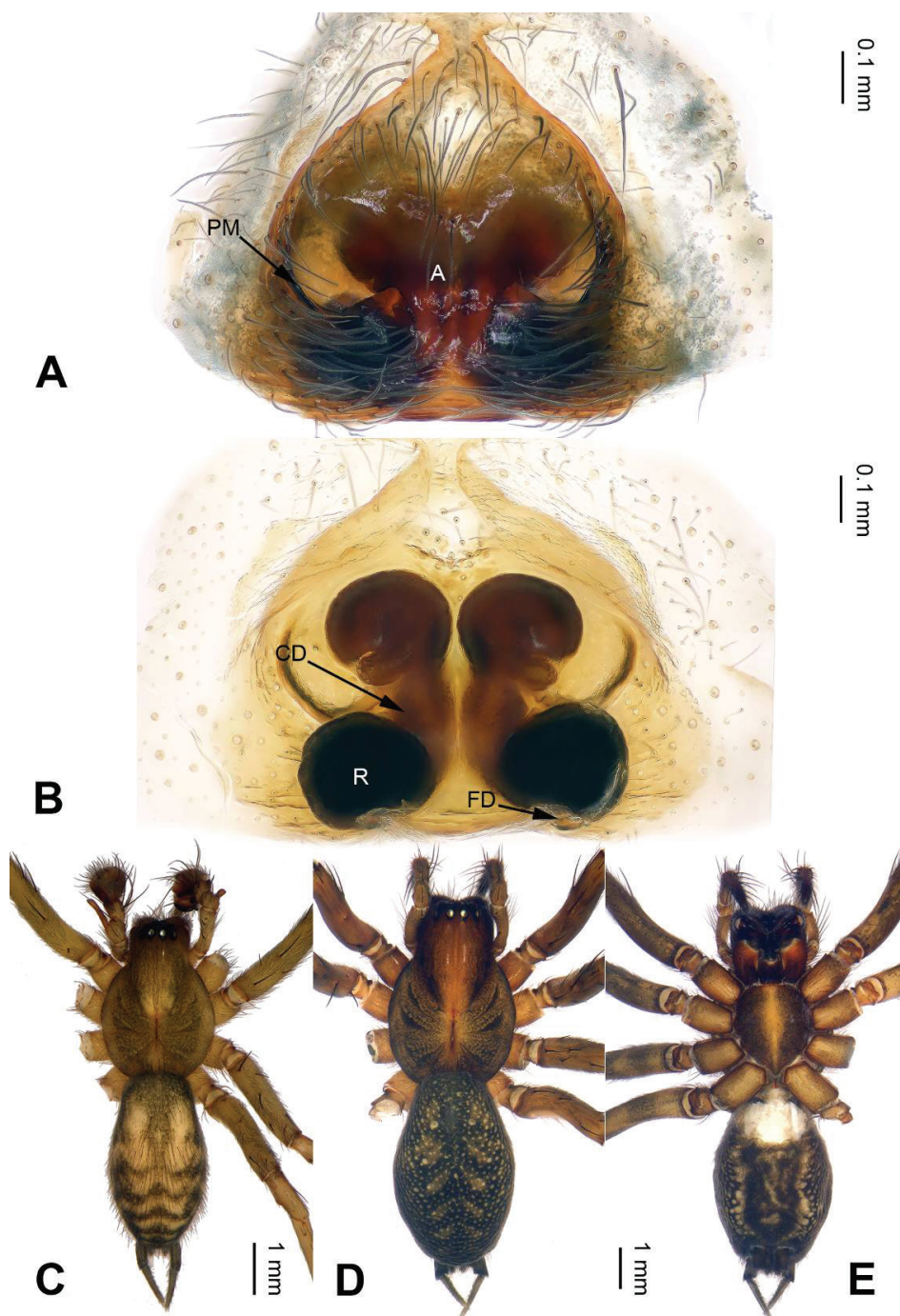


Figure 2. *Longicoelotes geei* sp. n., female paratype and male holotype. **A** Epigyne, ventral view **B** Vulva, dorsal view **C** Male habitus, dorsal view **D** Female habitus, dorsal view **E** Female habitus, ventral view. A = epigynal atrium, CD = copulatory duct, FD = fertilization duct, PM = posterior margin of atrium, R = receptacle. Scale bars: equal for **D**, **E**.

Female (paratype): Total length 8.65. Carapace 4.10 long, 3.00 wide. Abdomen 4.55 long, 2.55 wide. Eye sizes and interdistances: AME 0.20, ALE 0.18, PME 0.18, PLE 0.15; AME-AME 0.08, AME-ALE 0.05, PME-PME 0.10, PME-PLE 0.10. Leg measurements: I: 14.25 (4.00, 5.00, 3.25, 2.00); II: 12.20 (3.50, 4.00, 3.00, 1.70); III: 11.35 (3.25, 3.75, 2.75, 1.60); IV: 15.95 (4.50, 5.10, 4.25, 2.10). Carapace reddish, with black lateral margins, the radial grooves distinct; sternum with light stripes. Abdomen black, with yellow spots and herringbone patterns. Epigyne as in Fig. 2: atrium nearly heart-shaped, length subequal to width; copulatory openings indistinct; copulatory ducts long, about 1.5 times longer than diameter of receptacles, touching each other; receptacles separated, about 1/2 diameter of receptacles; hoods indistinct.

Leg spination in female:

	Fe	Pa	Ti	Mt	Ta
I	3d 2p 1r	-	1p 3-3v	1p 3-3v	-
II	3d 2p 2r	-	2p 3-3v	3p 1r 3-3v	-
III	3d 2p 2r	1d 1p	2d 2p 2r 3-3v	5p 5r 3-3v	1r
IV	3d 1p 1r	1d 1r	2d 2p 2r 3-3v	1d 5p 5r 3-3v	1p 1r

Distribution. Known only from Jiangxi Province of China (Fig. 6).

Longicoelotes kulianganus (Chamberlin, 1924)

Figs 3–6

Coelotes kulianganus Chamberlin, 1924: 24, pl. 5, fig. 40 (♀).

Longicoelotes kulianganus: Wang 2003: 560 (transferred from *Coelotes*).

Material examined. 2♀ 3♂, China: Fujian Province: Fuzhou Prefecture: Guling (new name for Kuliang), Liushanwang Park, N26°05'34", E119°23'32", 725 m, 1.XII.2016, X. Zhang; 2♀ 8♂, the same locality, Yixia Villa, N26°05'32", E119°23'32", 718 m, 1.XII.2016, X. Zhang; 5♀ 3♂, the same locality, swimming pool, N26°05'33", E119°23'30", 684 m, 2.XII.2016, X. Zhang.

Diagnosis. The male can be distinguished from other *Longicoelotes* species by indistinct median apophysis and short cymbial furrow, about 1/5 length of cymbium (*vs* 1/3 in *L. geei* sp. n.) (Figs 1, 3; Wang 2002: figs 312–314). The female can be separated from other congeners by its nearly triangular atrium and rounded anterior parts of copulatory ducts (*vs* nearly rounded atrium and extremely small anterior parts of copulatory ducts in *L. senkakuensis*) (Figs 4–5; Shimojana 2000: figs 46–49).

Description. Male: Total length 8.00. Carapace 3.50 long, 2.75 wide. Abdomen 4.50 long, 2.50 wide. Eye sizes and interdistances: AME 0.20, ALE 0.18, PME 0.19, PLE 0.15; AME-AME 0.05, AME-ALE 0.05, PME-PME 0.08, PME-PLE 0.08. Leg measurements: I: 14.75 (4.25, 4.75, 3.50, 2.25); II: 12.35 (3.50, 4.00, 3.00, 1.85); III: 11.80 (3.30, 3.50, 3.25, 1.75); IV: 16.25 (4.50, 5.00, 4.50, 2.25). Carapace greenish,

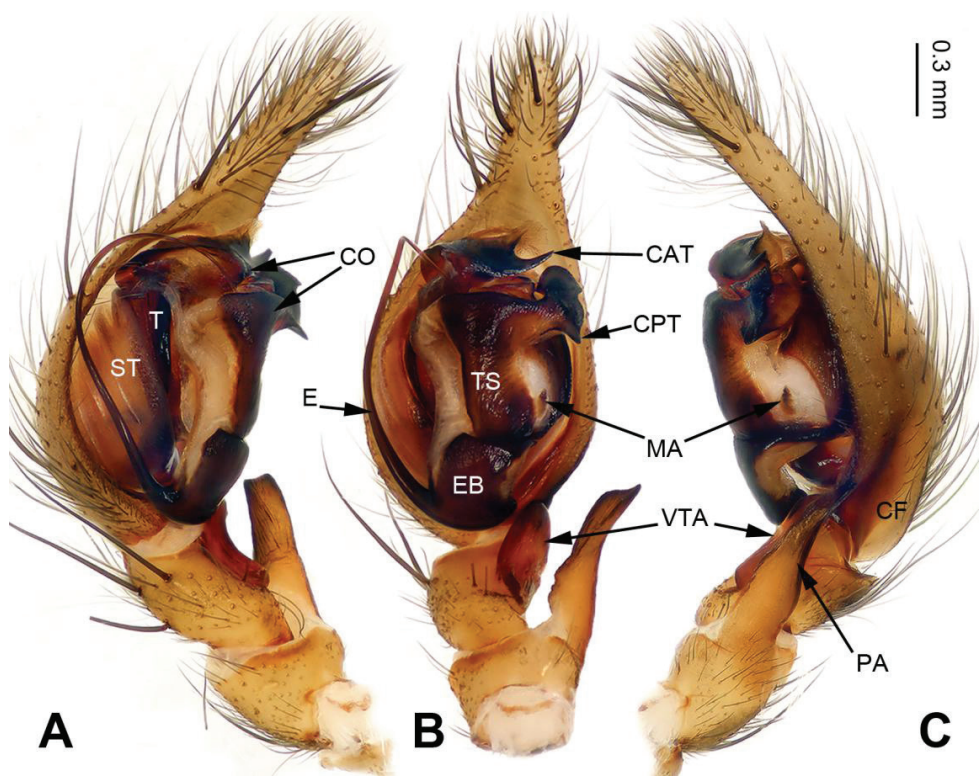


Figure 3. Palp of *Longicoelotes kulianganus*, specimen from Guling. **A** Prolateral view **B** Ventral view **C** Retrolateral view. CAT = anterior tip of conductor, CF = cymbial furrow, CO = conductor, CPT = posterior tip of conductor, E = embolus, EB = embolic base, MA = median apophysis, PA = patellar apophysis, ST = subtegulum, T = tegulum, TS = tegular sclerite, VTA = ventral tibial apophysis. Scale bar: equal for **A, B, C**.

the radial grooves indistinct. Abdomen grayish, with blackish herringbone patterns. Palp as in Fig. 3: patellar apophysis long, about 2 times longer than tibia; tibia short, about 1/4 length of cymbium; cymbial furrow short, about 1/5 length of cymbium; ventral tibial apophysis subequal to the tibial length, without pointed tip; conductor broad and bifurcated; posterior tip of conductor bifurcated; anterior tip of conductor bifurcated, ventral part nearly spine-shaped, dorsal part lamellate; median apophysis indistinct; embolus beginning at 6:00 o'clock position.

Leg spination in male:

	Fe	Pa	Ti	Mt	Ta
I	3d 2p 1r	-	3-3v	1p 3-3v	-
II	3d 1p 1r	-	2p 3-3v	3p 3-3v	-
III	3d 2p 2r	1d 1p 1r	2d 2p 2r 3-3v	5p 5r 3-3v	2p 1r
IV	3d 2p 1r	1d 1p 1r	2d 2p 2r 3-3v	5p 5r 3-3v	2p 1r

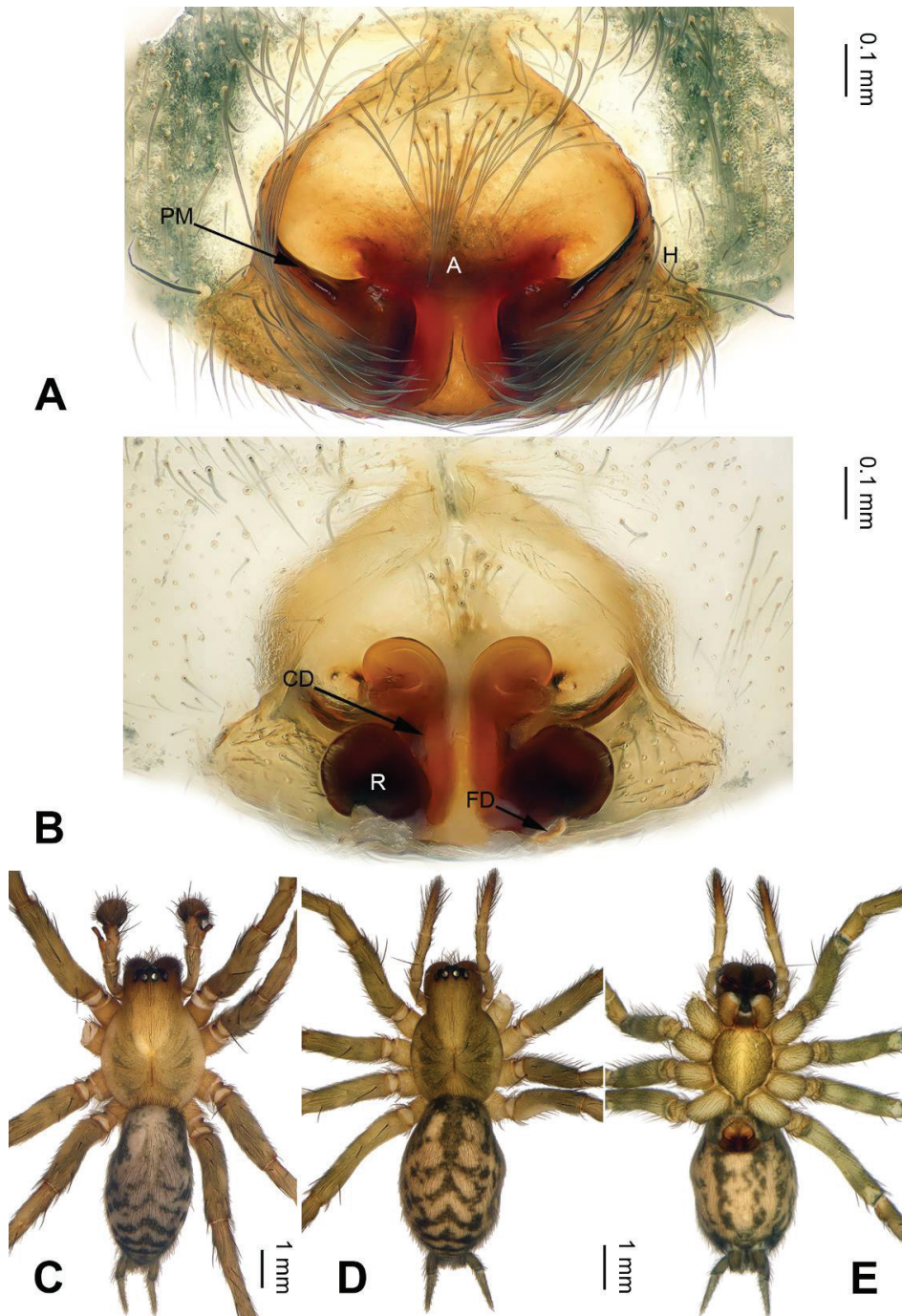


Figure 4. *Longicoelotes kulianganus*, specimen from Guling. **A** Epigyne, ventral view **B** Vulva, dorsal view **C** Male habitus, dorsal view **D** Female habitus, dorsal view **E** Female habitus, ventral view. A = epigynal atrium, CD = copulatory duct, FD = fertilization duct, H = epigynal hood, PM = posterior margin of atrium, R = receptacle. Scale bars: equal for **D**, **E**.

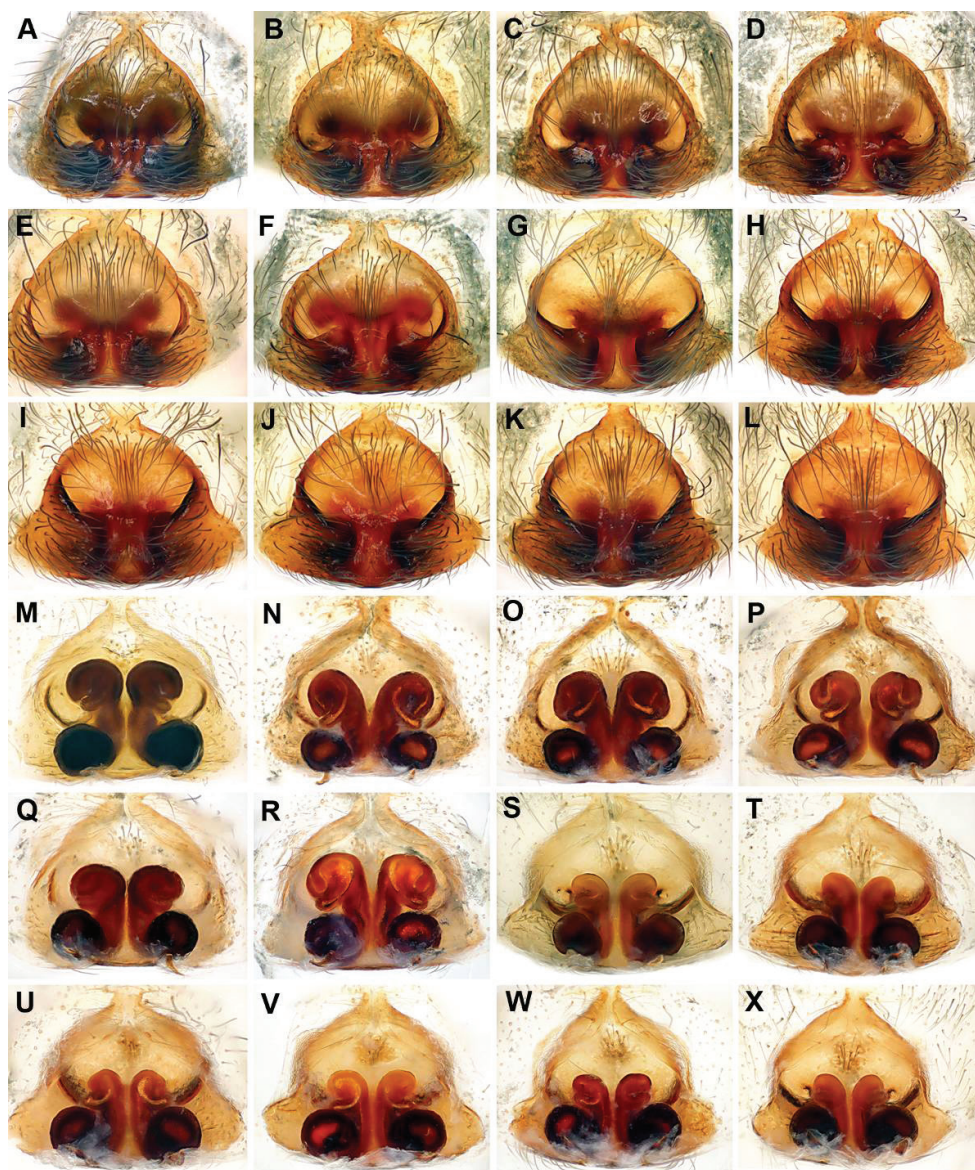


Figure 5. *Longicoelotes geei* sp. n. (A–F, M–R) and *L. kulianganus* (G–L, S–X), variations in shape of epigynal atrium and size of copulatory ducts. A–L Epigyne, ventral view M–X Vulva, dorsal view.

Female: Total length 6.75. Carapace 2.75 long, 2.15 wide. Abdomen 4.00 long, 2.25 wide. Eye sizes and interdistances: AME 0.15, ALE 0.15, PME 0.16, PLE 0.13; AME-AME 0.06, AME-ALE 0.05, PME-PME 0.10, PME-PLE 0.10. Leg measurements: I: 10.50 (3.00, 3.50, 2.50, 1.50); II: 9.20 (2.75, 3.00, 2.25, 1.20); III: 8.70 (2.50, 2.70, 2.25, 1.25); IV: 12.00 (3.50, 3.75, 3.25, 1.50). Carapace greenish, with black lateral margins, the radial grooves distinct; sternum with light stripes. Abdo-



Figure 6. Collecting localities of two *Longicoelotes* species from China. **1.** *L. geei* sp. n., **2.** *L. kulianganus*.

men black, with yellow spots and herringbone patterns. Epigyne as in Fig. 4: atrium with well delimited posterior margin, length subequal to width; copulatory openings indistinct, hidden by posterior margin of atrium; copulatory ducts long, about 2 times longer than diameter of receptacles; receptacles widely separated, subequal to diameter receptacles; hoods distinct.

Leg spination in female:

	Fe	Pa	Ti	Mt	Ta
I	3d 2p 1r	-	1p 3-3v	3-3v	-
II	3d 2p 2r	2d 1p	2p 3-3v	3p 1r 3-3v	-
III	3d 2p 2r	2d 1p 1r	2p 3r 3-3v	5p 5r 3-3v	1p 1r
IV	3d 1p 1r	1d 1p 1r	2d 2p 2r 3-3v	5p 5r 3-3v	1p 1r

Distribution. Known only from Fujian Province of China (Fig. 6).

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References

- Chamberlin RV (1924) Descriptions of new American and Chinese spiders, with notes on other Chinese species. *Proceedings of the United States National Museum* 63(13): 1–38. <https://doi.org/10.5479/si.00963801.63-2481.1>
- Fu L (2016) Nathaniel Gist Gee's contribution to biology in modern China. *Protein & Cell* 8(4): 237–239. <https://doi.org/10.1007/s13238-016-0318-x>
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3(5): 294–299.
- Miller JA, Carmichael A, Ramirez MJ, Spagna JC, Haddad CR, Řezáč M, Johannesen J, Král J, Wang XP, Griswold CE (2010) Phylogeny of entelegyne spiders: affinities of the family Penestomidae (new rank), generic phylogeny of Eresidae, and asymmetric rates of change in spinning organ evolution (Araneae, Araneoidea, Entelegynae). *Molecular Phylogenetics and Evolution* 55: 786–804. <https://doi.org/10.1016/j.ympev.2010.02.021>
- Shimajana M (2000) Description of eleven new species of the genus *Coelotes* (Araneae: Amaurobiidae) from the Ryukyu Islands, Japan. *Acta Arachnologica* 49: 165–189. <https://doi.org/10.2476/asjaa.49.165>
- Wang XP (2002) A generic-level revision of the spider subfamily Coelotinae (Araneae, Amaurobiidae). *Bulletin of the American Museum of Natural History* 269: 1–150. [https://doi.org/10.1206/0003-0090\(2002\)269<0001:AGLROT>2.0.CO;2](https://doi.org/10.1206/0003-0090(2002)269<0001:AGLROT>2.0.CO;2)
- Wang XP (2003) Species revision of the coelotine spider genera *Bifidocoelotes*, *Coronilla*, *Draconarius*, *Femoracoelotes*, *Leptocoelotes*, *Longicoelotes*, *Platocoelotes*, *Spiricoelotes*, *Tegecoelotes*, and *Tonsilla* (Araneae: Amaurobiidae). *Proceedings of the California Academy of Sciences* 54: 499–662.
- World Spider Catalog (2017) World Spider Catalog. Natural History Museum Bern. <http://wsc.nmbe.ch> [version 18.0, accessed on June 5, 2017]
- Zhao Z, Li S (2016) *Papiliocoelotes* gen. n., a new genus of Coelotinae (Araneae, Agelenidae) spiders from the Wuling Mountains, China. *ZooKeys* 585: 33–50. <https://doi.org/10.3897/zookeys.585.8007>
- Zhao Z, Su TJ, Chesters D, Wang SD, Ho SYW, Zhu CD, Chen XL, Zhang CT (2013) The mitochondrial genome of *Elodia flavipalpis* Aldrich (Diptera: Tachinidae) and the evolutionary timescale of tachinid flies. *PLoS ONE* 8:e61814. <https://doi.org/10.1371/journal.pone.0061814>

