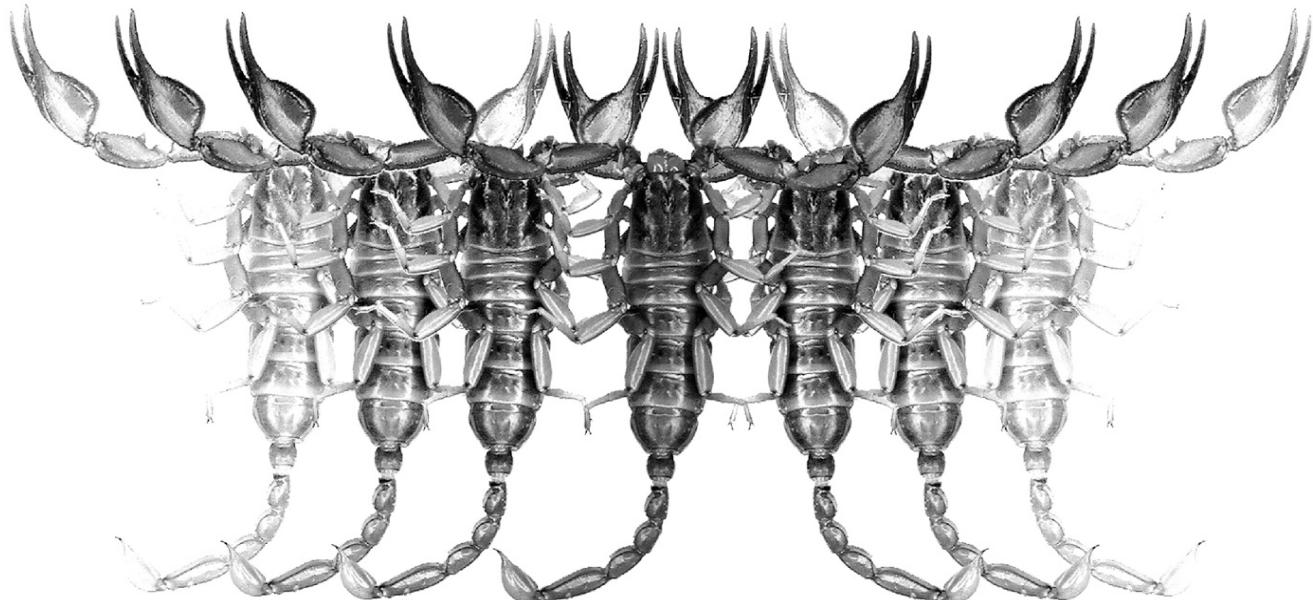


# *Euscorpius*

Occasional Publications in Scorpiology



**Two new species of the remarkable scorpion  
genus *Megacormus* Karsch, 1881  
(Scorpiones: Euscorpiidae)**

Rolando Teruel, František Kovařík, Graeme Lowe & František Šťáhlavský

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# *Euscorpius*

## *Occasional Publications in Scorpiology*

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

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Archive of issues 1-270 see also at: <http://www.science.marshall.edu/fet/Euscorpius>

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<http://zoobank.org/urn:lsid:zoobank.org:pub:E7C4D357-A2FF-4F8D-B93D-1B9B6CFE3115>

## Two new species of the remarkable scorpion genus *Megacormus* Karsch, 1881 (Scorpiones: Euscorpiidae)

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### Summary

Two new species of the very interesting euscorpiid scorpion genus *Megacormus* Karsch, 1881, are herein described from eastern Mexico. Both had been previously misidentified in the published literature, one as *Megacormus segmentatus* Pocock, 1900, the other as *Megacormus granosus* (Gervais, 1844), but the direct comparison of adults of both sexes to adult topotypes from all members of the genus currently accepted as valid taxa, revealed solid morphological characters that warrant their recognition as distinct taxa. Both new species seem also to be endemics with a small distribution area, but apparently not restricted to a single locality. This addition raises the known composition of the genus to eight species, all of them exclusively from mountain sites of eastern Mexico.

### Introduction

The genus *Megacormus* Karsch, 1881 comprises a small, relict group of New World scorpions with only six known species restricted to coastal and montane tropical forests of the Sierra Madre Oriental in southeastern Mexico (Soleglad, 1976; González-Santillán et al., 2017; Kovařík, 2019). The closely allied genus *Plesiochactas* Pocock, 1900, includes only three known species from the same region and neighboring Guatemala (Soleglad, 1976; Trujillo & Armas, 2012; Zárate-Gálvez & Francke, 2009). Remarkably, these two neotropical genera share a number of morphological features with the widespread European genera *Alpiscorpius*, *Euscorpius* and *Tetrarichobothrius*, motivating taxonomists to group them together under the same family, Euscorpiidae Laurie, 1896 (Soleglad & Sissom, 2001). Dated phylogenomic studies support the hypothesis that these New World and Old World euscorpiid genera represent sister lineages originating from a common ancestor around the time of the break-up of Laurasia in the late Mesozoic (Santibáñez-López et al., 2022; Sharma et al., 2018). Research on the systematics and biology of *Megacormus* can yield deeper insights into its relationship with its Old World sister taxa, and how it has diverged from them in adapting to neotropical environments.

Most species of *Megacormus* are small, uncommon scorpions with localized distribution. Historically, they

were seldom collected and poorly known. The type species, *Scorpio granosus* Gervais, 1843, is rare in collections, and the male, although illustrated by Pocock (1902), was described in detail only more recently (González-Santillán & Alvarez-Padilla, 2015). Pocock (1900) described a second species, *M. segmentatus*, also known only from a few females until the male was described by Sissom (1994), who also described another species, *M. grubbsi*, based only on the male holotype. A larger species, *M. gertschi* Díaz Nájera, 1966, has a wider distribution and is more frequently encountered. Its reproductive biology and has been studied (Francke, 1979; Olguín-Pérez et al., 2021) and its venom analyzed (Banerjee et al., 2018; Olguín-Pérez et al., 2021, Santibáñez-López et al., 2017). Remarkably, the venom composition differs from that of all other known scorpion venoms, with a major soluble fraction consisting of a novel low molecular weight alkaloid compound of unknown function. Recent fieldwork discovered two additional species of this unusual genus: *M. xichu* González-Santillán et al., 2017, and *M. franckei* Kovařík, 2019, both from single localities. Kovařík (2019) reviewed the genus and provided illustrations of the anatomy, in vivo habitus, and natural habitats of most species. Here, we describe two additional species, *M. orizaba*, sp. n., and *M. seductus* sp. n., clarifying the identities of some previously misidentified specimens, and further expanding our knowledge of the diversity of the genus.



1



2

Figures 1–2. *Megacormus seductus* sp. n., male holotype (1) and female paratype with a juvenile (2) in vivo habitus.

Dimensions (mm)		<i>M. orizaba</i> sp. n.	<i>M. orizaba</i> sp. n.	<i>M. seductus</i> sp. n.	<i>M. seductus</i> sp. n.
		♂ holotype	♀ paratype	♂ holotype	♀ paratype
Carapace	L / W	4.69 / 4.53	6.68 / 6.63	3.11 / 3.17	4.15 / 4.32
Mesosoma	L	9.15	14.25	5.08	9.38
Tergite VII	L / W	3.90 / 1.89	2.42 / 5.69	1.19 / 2.54	1.69 / 3.87
Metasoma + telson	L	18.08	23.76	12.23	14.28
Segment I	L / W / D	1.72 / 2.65 / 2.09	2.28 / 3.07 / 3.01	1.13 / 1.77 / 1.51	1.34 / 2.13 / 1.62
Segment II	L / W / D	1.83 / 2.27 / 1.88	2.45 / 2.70 / 2.60	1.30 / 1.57 / 1.49	1.48 / 1.76 / 1.54
Segment III	L / W / D	2.04 / 2.15 / 1.85	2.67 / 2.59 / 2.40	1.36 / 1.53 / 1.42	1.61 / 1.64 / 1.46
Segment IV	L / W / D	2.55 / 2.03 / 1.85	3.28 / 2.37 / 2.32	1.71 / 1.39 / 1.42	2.04 / 1.52 / 1.55
Segment V	L / W / D	4.52 / 1.90 / 1.85	5.99 / 2.51 / 2.44	3.13 / 1.38 / 1.41	3.58 / 1.56 / 1.47
Telson	L / W / D	5.42 / 2.10 / 1.82	7.09 / 2.84 / 2.32	3.60 / 1.33 / 1.10	4.23 / 1.36 / 1.13
Pedipalp	L	15.67	21.52	9.92	13.35
Femur	L / W	3.61 / 1.54	5.07 / 2.10	2.35 / 1.06	3.11 / 1.30
Patella	L / W	4.29 / 1.87	5.81 / 2.79	2.61 / 1.26	3.62 / 1.71
Chela	L	7.77	10.64	4.96	6.62
Manus	W / D	2.70 / 2.15	3.91 / 2.99	1.84 / 1.47	2.35 / 2.13
Movable finger	L	4.35	5.54	2.63	3.99
<b>Total</b>	<b>L</b>	<b>31.92</b>	<b>44.69</b>	<b>20.42</b>	<b>27.81</b>

**Table 1.** Morphometric data for types of *Megacormus orizaba* sp. n. and *Megacormus seductus* sp. n. Abbreviations: length (L), width (W), in carapace it corresponds to median width), depth (D).

## Methods, Material & Abbreviations

Nomenclature and measurements generally follow Stahnke (1971), Soleglad & Sissom (2001), Kovařík (2009), and Kovařík & Ojanguren Affilastro (2013), except for trichobothriotaxy (Vachon, 1974) and sternum (Soleglad & Fet, 2003a). Pedipalp patellar width excludes the dorsal patellar spur. Hemispermatophore terminology generally follows Kovařík et al. (2018), Kovařík et al. (2020a, 2020b) and Monod et al., (2017). In addition, we use the following terminology for sclerotized, or partially sclerotized, structures on the convex surface of the hemispermatophore capsule of *Megacormus* (cf. Figs. 66, 69). The *proximal transverse ridge* (*trp*) is a prominent sclerotized costate structure spanning the proximal anteroposterior width of the capsule. Anteriorly, it extends onto the distal carina and terminates in a sclerotized apophysis, the *proximal dentate process* (*dpp*), which may be dilated and plate-like, and armed with denticles or tines along its distal margin. The parallel *distal transverse ridge* (*trd*) is more weakly developed, and may be only partially sclerotized or unsclerotized. Anteriorly, it bears the *distal dentate process* (*dpd*), a sclerotized structure that may also be armed with denticles on its distal margin; posteriorly, it joins the base of the distal lamina. Previous authors labelled the proximal transverse ridge as ‘rim of dorsal trough (*dtr*)’ or ‘dorsal trough (*dt*)’, and the distal transverse ridge as ‘ventral trough (*vt*)’ (González-Santillán & Alvarez-Padilla, 2015; Sissom, 1994). The proximal dentate process was labelled as ‘dorsal spiculate process (*dsp*)’, and the distal dentate process as ‘ventral spiculate process (*vsp*)’ or ‘accessory lobes (*acc*)’. The adjectives ‘dorsal’ and ‘ventral’ refer to somatic axes of the

scorpion with hemispermatophore *in situ*. In our terminology, we decouple orientation labels from somatic axes (Kovařík et al., 2018; Monod et al., 2017). This avoids potential confusion from conflicting labels applied to homologous structures in buthids vs. non-buthids, which have opposite *in situ* orientations.

Specimens reexamined here were collected by a local collector in 2018–2019, are cited in Kovařík (2019) and are deposited in the second authors collection (FKCP). Newly examined specimens were collected in 2022 and are deposited in the first (RTOC) and the second (FKCP) authors collections. All specimens are preserved in 80% ethanol. Complete sets of anatomical photographs of the holotype and paratype of *Megacormus orizaba* sp. n. are not included here because these were already published as figs. 40–41, 51, 90–123 in Kovařík, 2019: 11, 21–27, where they were labeled as *Megacormus granosus* (misidentification).

Statistical analyses were conducted in Microsoft Excel 2019 Version 2301, MaxStat Version 3.60 and NCSS Version 23.0.1. *Morphometrics:* D, depth; L, length; W, width.

*Comparative material examined* (FKCP).

*Megacormus franckei* Kovařík, 2019

Mexico, Querétaro, Pinal de Amoles, oak-pine forest, 21°08'04"N 99° 39'50"W, 2690 m a. s. l., 1♂ (holotype) 2♂1♀2juvs.♀ (paratypes, No. 1618), (Figs. 54–55, 69, 82 and figs. 1–37, 47–49, tab. 1 in Kovařík, 2019)

*Megacormus gertschi* Díaz Nájera, 1966

Mexico, Hidalgo, Zacualtipan, pine forest, 20°40'55"N 98°40'20"W, 2117 m a. s. l., 8♂2♀ (Figs. 44–45, 67–68, 82 and figs. 38–39, 50, 55–89 in Kovařík, 2019), topotypes, Nos. 1619, 1620, 1627, 1628.

*Megacormus granosus* (Gervais, 1843)

Mexico, Veracruz/Puebla, Atotonilco, pine/oak forest, 19°08'50.3"N 97°11'47.6"W, 2180m a. s. l., 2♂2♀ (Figs. 46–47, 63, 75, 81, 82, No. 2462), 2.XI.2022, leg. R. Teruel et al.

*Megacormus grubbsi* Sissom, 1994

Mexico, Oaxaca, Huautla de Jiménez, Puerto Soledad, green mountain tropical forest, 18° 9'24.80"N 96°59'29.01"W, 2400 m a. s. l., 2019, 2♂2♀ (No. 1623, Figs. 48–49, 76–77, 82, and figs. 42–43, 52, 124–156 in Kovařík, 2019), 2♂2♀ (No. 2463,), 28.X.2022, leg. R. Teruel et al.

*Megacormus cf. segmentatus* Pocock, 1900

Mexico, Veracruz, Atoyac, green tropical forest, 18°55'11.10"N 96°46'05"W, 466 m a. s. l., 1♂ (Figs. 50, 74 80, 82 and figs. 44, 53, 157–179 in Kovařík, 2019), topotype, No. 1622; Oaxaca, San Felipe Jalapa de Diaz, south shore of Aleman Dam, green tropical forest, 18°11'15.93"N 96°36'28.92"W, 210 m a. s. l., 25.X.2022, 1♀ (Fig. 51, 82), No. 2464)

*Megacormus xichu* González-Santillán et al., 2017

Mexico, Guanajuato, Xichú, Charco Azul, El Ocotero, ca 4 km NE of Xichú, oak forest, 21°18'54"N 100°06'38"W, 2283 m a. s. l., 21.IV.2019, 5♂5♀ (Figs. 52–53 and figs. 45–46, 54, 180–214 in Kovařík, 2019), topotypes, Nos. 1617, 1626.

## Systematics

### Family Euscorpiidae Laurie, 1896

#### *Megacormus* Karsch, 1881

(Figures 1–82, Tables 1–3)

*Megacormus* Karsch, 1881: 16–18; Soleglad, 1976: 263–264; Francke, 1979: 223–230, figs. 1–6; Sissom, 1994: 265–271, figs. 1–10; Fet & Sissom, 2000: 377–378 (complete references list until 2000); Soleglad & Sissom, 2001: 25–111, figs. 10, 20, 55, 64, 81, 88, 107, 120–122, 135, 142, 153–154, 161–162, 167, 173, 182, 194, 205–215, 218, tables 2, 3, 5, 6, 9–10; Soleglad & Fet, 2003b: 7, 11, 61, 66–68, 88, 105, tabs. 3–4, 9; Kovařík, 2009: 32; Zárate-Gálvez & Francke, 2009: 342–343, fig. 15; González -Santillán & Alvarez-Padilla, 2015: 75–91, figs. 1–28; Santibáñez-López et al., 2016: 6; González-Santillán et al., 2017: 221–237, figs. 1–13, table 1; Santibáñez-López et al., 2017: 95; Kovařík, 2019: 1–46, figs. 1–215, table 1; Kovařík et al., 2020b: 30; Olgún-Pérez et al., 2021: 98–106, figs. 1–5

TYPE SPECIES. *Scorpio granosus* Gervais, 1843.

DIAGNOSIS. Carapace densely granulose, trapezoidal, anterior margin weakly emarginate; 2–4 pairs of lateral eyes, eyespot present. Dorsal dentate margin of cheliceral movable finger armed with two relatively large, subequal subdistal denticles; ventral dentate margin with 1–4 smaller, subequal denticles on its distal half, the most distal denticle always present and largest. Pedipalp patella with well-developed dorsal patellar spur, small or vestigial ventral patellar spur. Dentate margins of pedipalp chela fingers with median denticles arranged contiguously in a linear series extending the length of the finger, divided into subrows by slightly enlarged denticles; each enlarged median denticle (MD) closely flanked by one

enlarged outer denticle (OD), one enlarged inner denticle (ID), and one enlarged inner accessory denticle (IAD) (transverse denticle group of 4); numerous additional, smaller outer accessory denticles together form a sparser, secondary linear series extending the length of the finger; a smaller number of additional inner accessory denticles also present, mostly on proximal finger. Trichobothrial pattern type C, neobothriotoxic majorante on pedipalp patella: external series 17–23 (7 eb, 2 esb, 2–5 em, 3–5 est, 3–4 et); ventral series, 5–10. Legs without tibial spurs, tarsi with two pedal spurs. Sternum type 2, hexagonal in shape. Hemispermatophore lamelliform, trunk broad, with truncal flexure; convex aspect of capsule with proximal and distal transverse ridges, each terminating anteriorly in sclerotized apophyses; basal carina elongate with sclerotized crown-like structure. Sternite VII and metasoma I–V with single prominent ventromedian carina. Telson without subaculear tubercle.

#### SUBORDINATE TAXA.

*Megacormus franckei* Kovařík, 2019

*Megacormus gertschi* Díaz Nájera, 1966

*Megacormus granosus* (Gervais, 1843)

*Megacormus grubbsi* Sissom, 1994

*Megacormus orizaba* sp. n.

*Megacormus seductus* sp. n.

*Megacormus segmentatus* Pocock, 1900

*Megacormus xichu* González-Santillán et al., 2017

DISTRIBUTION. Mexico (Guanajuato, Hidalgo, Oaxaca, Puebla, Querétaro, San Luis Potosí, Tamaulipas, and Veracruz).

#### *Megacormus orizaba* sp. n.

(Figures 58–59, 61–62, 66, 82, Tables 1–2)

<http://zoobank.org/urn:lsid:zoobank.org:act:AE1641C9-4E89-4654-9375-86633841D26D>

*Megacormus granosus*: Kovařík, 2019: 1, 11–13, 21–27; figs. 40–41, 51, 90–123 (misidentification).

TYPE LOCALITY AND TYPE REPOSITORY. Mexico, border between Puebla (Tlachichuca Municipality) and Veracruz (Calcahuasco Municipality), 2 km west of Atotonilco, northeast slope of Pico de Orizaba [= Citlaltépetl], 19°08'50.3"N 97°11'47.6"W, 2,400 m a. s. l., pine forest, under rocks, 2019, 1♂ (holotype, No. 1621, figs. 40, 51, 90–91, 94–102, 106–108, 111–114, 115–117, 121 in Kovařík, 2019), FKCP, 1♂2♀ (paratopotypes, figs. 41, 51, 92–93, 103–105, 109–110, 118–120, 122 in Kovařík, 2019), FKCP, 2.XI.2022, R. Teruel et al., 2♂8♀7juvs. (paratopotypes), RTOC.

TYPE MATERIAL. Mexico, border between Puebla (Tlachichuca Municipality) and Veracruz (Calcahuasco Municipality), 2 km west of Atotonilco, northeast slope of Pico de Orizaba [= Citlaltépetl], 19°08'50.3"N 97°11'47.6"W, 2,400 m a. s. l., pine forest, under rocks, 2019, 1♂ (holotype, No. 1621, figs. 40, 51, 90–91, 94–102, 106–108, 111–114, 115–117, 121 in Kovařík, 2019), FKCP, 1♂2♀ (paratopotypes, figs. 41, 51, 92–93, 103–105, 109–110, 118–120, 122 in Kovařík, 2019), FKCP, 2.XI.2022, R. Teruel et al., 2♂8♀7juvs. (paratopotypes), RTOC.

ETYMOLOGY. The selected epithet is a Latinized noun in apposition, taken directly from the Spanish toponym of the majestic volcano inhabited by this species.



**Figures 3–6:** *Megacormus seductus* sp. n. **Figures 3–4.** Male holotype in dorsal (3) and ventral (4) views. **Figures 5–6.** Female paratype in dorsal (5) and ventral (6) views. Scale bars: 10 mm.

**DIAGNOSIS.** Adult size large for the genus (30–34 mm in males, 40–45 mm in females). Coloration entirely blackish, paler and less spotted on chelicerae, pedipalp, legs and pectines. Pedipalp patella with 22–24 external trichobothria (7 eb, 2 esb, 4–5 em, 4 est, 4 et) and 6–8 ventral trichobothria. Pedipalp fingers of adult male with undulate proximal dentate margins, lobe/notch combination moderate. Pectines with shaft clearly divided into areas and lamellae by conspicuous sulci; tooth count 5–6 in males, 4–5 in females. Metasomal segment V length/width ratio 2.37–2.40 in males, 2.38–2.40 in females. Telson elongate, narrower than metasomal segment V in both sexes.

**SEXUAL DIMORPHISM.** Female differing from male by: **1)** size larger; **2)** coloration darker and more densely infuscate; **3)** pedipalps, legs and metasoma slightly longer and slenderer; **4)** mesosoma much wider and more convex-sided; **5)** pedipalps, carapace, tergites and metasoma with granulation sparser and finer; **6)** genital papillae absent; **7)** pectines conspicuously smaller, with lower tooth counts (4–5).

**DESCRIPTION** (male holotype; Figs. 58, 62, 66 and figs. 40, 51, 90–91, 94–102, 107–108, 111–114, 115–117, 121 in Kovařík, 2019; Table 1).

**Coloration.** Base color light brown, paler on chelicerae, pedipalp manus, legs and pectines, pedipalp chelae and telson with a reddish hue. Cheliceral manus finely and irregularly reticulate with dark brown, denser distally; fingers deeply infuscate. Pedipalps very densely and irregularly marbled with blackish brown, but sparser distally (much denser on femur, sparser on manus), with all carinae deeply infuscate and the base of most trichobothria much paler (yellowish); fingers blackish, with distal third much paler progressively (becoming yellowish at the tip). Carapace symmetrically and very densely marbled with dark to blackish brown, anterior and lateral margins largely infuscate; eyes and ocular tubercles black. Tergites symmetrically and very densely marbled with dark to blackish brown, without any conspicuous pale spots that could suggest a striped pattern. Pectines with shaft heavily and irregularly infuscate, but teeth essentially immaculate. Sternites colored and patterned similarly to tergites. Legs irregularly and very densely marbled with blackish brown, with few pale areas. Metasoma concolorous throughout (i.e., no segments conspicuously darker), irregularly and very densely marbled with blackish brown and with carinae deeply infuscate. Telson vesicle densely and irregularly marbled with dark to blackish brown, with four faint pale stripes corresponding to longitudinal furrows; aculeus orange, with distal third blackish. In general, the dark pattern is so dense that the entire scorpion looks dull black to the unaided eye, especially when still alive.

**Chelicerae.** Dentition typical for the genus, teeth short but sharp. Tegument smooth and glossy. Setation very dense ventrally, but essentially lacking dorsally, i.e., reduced to a few macrosetae distally in manus and also along movable finger. Fingers short, robust, evenly curved and subequal in length.

**Pedipalps.** Size and shape standard for the genus. Trichobothrial pattern C, neobothriotoxic majorante: femur with all three trichobothria (*d*, *e*, *i*) in positions standard for the genus (at basal-most part of segment); patella with 2 dorsal trichobothria (*d*), one internal trichobothria (*i*), 21–22 external trichobothria (7/7 eb, 2/2 esb, 4/5 em, 4/4 est, 4/4 et) and 6/7 ventral trichobothria (*V*); chela manus with 2 dorsal trichobothria (*Db*, *Dt*), 11 external trichobothria (4 Eb, 1 Esb, 1 Est, 5 Et, with Et displaced to ventral surface), and 4 ventral trichobothria (with *V* displaced to external surface); fixed finger with 4 dorsal trichobothria (*db*, *dsb*, *dst*, *dt*), two internal trichobothria (*ib*, *it*) and 4 external trichobothria (*eb*, *esb*, *est*, *et*).

**Femur** robust (length/width ratio = 2.34), almost bare, with all surfaces essentially flat to shallowly convex. Dorsointernal, dorsoexternal, ventrointernal and ventroexternal carinae complete (moderate, coarsely granulose). Tegument coriaceous, with abundant fine to medium-sized granules scattered all over, plus abundant medium-sized to coarse, glossy granules irregularly scattered on dorsal surface.

**Patella** robust (length/width ratio = 2.29), almost bare, with dorsal and ventral surfaces essentially flat, external and internal surfaces markedly convex. Dorsointernal, dorsoexternal, external median, ventrointernal and ventroexternal carinae complete (strong to very strong, coarsely granulose to crenulate). Tegument finely, densely and evenly granulose on internal surface, coriaceous on dorsal, external and ventral surfaces, with abundant medium-sized to coarse, glossy granules evenly scattered all over dorsally and abundant fine and rough granules irregularly scattered all over externally and ventrally. Inner dorsal spur large, sharp and straight; inner ventral spur vestigial, reduced to a conical denticle.

**Chela** large and robust, standard for the genus (length/width ratio = 2.87). Manus incrassate-oval in dorsal view, medially wider and narrow-oval in lateral view, sparsely setose and prismatic in cross-section; dorsal internal, dorsal marginal, dorsal secondary, digital, external secondary, ventroexternal and ventrointernal carinae complete (strong, coarsely granulose to crenulate); tegument coriaceous, with a clearly defined reticulate pattern of small, glossy granules scattered all over. Fingers somewhat longer than standard for the genus, shallowly curved and sparsely setose, dentition standard for the genus, basal lobe/notch combination moderate (long and not too deep).

**Carapace.** Almost as long as wide (length/width ratio = 1.03), paraboloid in dorsal view. Anterior margin shallowly bilobed, with 2–3 pairs of white macrosetae plus several minor setae; median notch very shallowly U-shaped. Tegument finely and densely granulose, with abundant medium-sized to coarse granules scattered all over. All carinae indistinct or absent, except for the superciliaries, central medians and posterior medians (weakly, finely granulose and not fused). Furrows: anterior median, central median, posterior median and posterior marginal narrow and moderately deep, fused altogether; posterior laterals narrow and moderately deep; other furrows either absent or undefined. Median ocular



**Figures 7–16:** *Megacormus seductus* sp. n., male holotype, pedipalp chela dorsal (7), external (8) and ventral (9) views, patella dorsal (10), external (11) and ventral (12) views, femur and trochanter dorsal (13) and ventral (14) views, movable (15) and fixed (16) fingers dentition. Movable finger (15) is under UV light, other figures are under white light.

tubercle moderately raised, with eyes large and separated by less than one ocular diameter; two pairs of large lateral eyes.

**Sternum.** Standard for the genus: type 2, large, longer than wide and hexagonal in shape. Tegument densely and finely granulose.

**Genital operculum.** Medium-sized and prominent, remarkably rhomboidal in shape. Halves neither separated nor fused and almost triangular in shape; tegument smooth and glossy. Genital papillae medium-sized, well-protruding, with tips blunt, round. Pre-pectinal plate apparently absent.

**Pectines.** Size and shape standard for the genus: not reaching coxa-trochanter joint of leg IV, subrectangular and moderately setose, anterior area with 3/2 lamellae, median area with 3/3. Tooth count 6/6, teeth swollen, straight and basally not separated; fulcra entirely absent. Basal plate wider than long; anterior margin essentially straight, posterior margin widely convex; tegument smooth, glossy to coriaceous.

**Mesosoma.** Tergites almost bare, anterior margin shallowly sinuose, posterior margin straight to very shallowly produced in the median part; median carina very weak and finely subcrenulate to crenulate on I–VI, submedian and lateral carinae strong and finely serratocrenulate on VII; tegument coriaceous, with abundant small to medium-sized, glossy granules scattered all over (denser posterolaterally). Sternites sparsely setose (largely along posterior and lateral margins), posterior margin shallowly convex to widely bilobed; III–VI acarinate, VII with only ventral median carinae perfectly defined, finely granulose to subcrenulate; tegument on III–VI glossy and minutely punctate, on VII coriaceous, with abundant medium-sized, glossy granules scattered all over; spiracles small and elongate-oval; V with smooth patch large, paraboloid in shape, translucent, glossy and not bulky.

**Metasoma.** Size and shape standard for the genus (length/width ratio of segments I–V = 0.65, 0.81, 0.95, 1.26 and 2.37), moderately narrower distally and moderately setose; segment I–III wider than long, IV–V longer than wide; all segments wider than deep. Segments I–IV with seven complete to almost complete carinae, V with five: all strong, irregularly and coarsely dentate to serrate, with distalmost denticles not conspicuously enlarged; lateral inframedians entirely absent or undefined from surrounding granulation on all segments; ventral submedians entirely absent; ventral median carina perfectly defined all along I–V; anal arc weakly granulose; laterodistal lobes of V obsolete, blunt-triangular. Intercarinal tegument coriaceous, with abundant minute and fine granules scattered all over. Dorsal furrow complete, moderately narrow and shallow.

**Telson.** Sparsely setose. Vesicle oval and somewhat depressed; tegument coriaceous, with abundant minute and fine granules scattered all over and four very shallow longitudinal furrows; distal end of vesicle well-defined by a shallow annular ring and weak laterodistal shoulders. Aculeus moderately long, sharp and shallowly curved, with tegument glossy.

**Legs.** Somewhat longer and slenderer than standard for the genus, with all carinae weakly granulose to subcrenulate; tegument smooth coriaceous, with dorsal surface of femur sparsely granulose. Prolateral pedal spurs standard-sized to

large, thick but sharp. Claws standard-sized (at least one-third the length of its respective telotarsus) and well-curved.

**Hemispermatophore.** (Figs. 62, 66). Lamelliform. Overall proportions of distal lamina, capsule, truncal flexure, trunk and pedicel standard for the genus. Distal lamina relatively narrow, nearly uniform in width, with straight anterior margin, lacking a basal constriction. Capsule with moderately broad proximal transverse ridge; proximal dentate process elongate or spatulate, slightly broadened, armed with 7–9 irregular, short, blunt or sharp denticles. Distal dentate process moderately broad, laminate, armed 6–7 irregular, small to large, sharp denticles. Basal carina with crown-like structure bearing 6–8 tines. Terminal membrane of sperm duct with numerous fine spicules.

**AFFINITIES.** The described features distinguish *Megacormus orizaba* sp. n. from all other species of the genus (see the key below). The validity of *M. orizaba* sp. n. is confirmed also by DNA analysis implemented by Charles University in Prague (manuscript in preparation).

*M. orizaba* sp. n. inhabits the same locality as *M. granosus*, with which it has been confused in the past (see Kovařík, 2019), but it can be easily distinguished by its larger size (30–34 mm in males, 40–45 mm in females versus 14–18 mm in males, 18–23 mm in females in *M. granosus*) and mainly by the presence of a pedipalp lobe/notch in adult males of *M. orizaba* sp. n. (Fig. 58) which is absent in adult males of *M. granosus* (Fig. 46). The hemispermatophore of *M. granosus* has a broad distal lamina with basal constriction (Fig. 63, 75), similar to that of *M. seductus* sp. n. (Figs. 64–65), contrasting with the narrow distal lamina without basal constriction in *M. orizaba* sp. n. (Figs. 62, 66).

**DISTRIBUTION** (Fig. 82). *M. orizaba* sp. n. is currently known only from the type-locality. Nevertheless, a potential additional locality record may have been given misidentified as *M. gertschi* by González-Santillán et al. (2017), also from Veracruz State (see below, in Remarks section).

**ECOLOGICAL NOTES.** The type-specimens were all collected under rocks of various sizes (usually small to medium), in somewhat humid places inside pine forest (fig. 123 in Kovařík, 2019: 27). The scorpions were usually found on the ground, inside short scrapes excavated by themselves, but as an unusual finding, not less than 10 individuals (mostly juveniles and subadults) were found hanging to the underside of the rocks, frequently at the edges. After the rocks were turned, all scorpions played dead and remain motionless (thanatosis or catalepsy).

At the single known locality, this species lives syntopically with *M. granosus*, but we observed a very interesting trend. On one hand, *M. granosus* is widespread throughout the area and occurs in similar numbers both in oak and pine forests, but most commonly in the less densely vegetated areas of the oak forest. On the other hand, *M. orizaba* sp. n. is entirely restricted to the pine forest and becomes more and more

abundant towards its densest core, while at the edge of the pure pine forest (without any oak trees), both species are found together, even under the same rocks.

This is the first time that two species of *Megacormus* are confirmed to occur together in a same locality. No other scorpion species were found there during the two field trips conducted by the authors to this site.

**REMARKS.** This species was formerly misidentified as *M. granosus* by Kovařík (2019). During the previous field trips (2018–2019) that yielded the specimens used by him for that paper, both species were actually found, but unfortunately, all small specimens (including the authentic *M. granosus*) were mistaken for early immatures and not collected. Only during the last field trip (2022), was it noted that there were in fact two distinct species living together and the mistake was discovered.

Conversely, it is odd that González-Santillán & Álvarez-Padilla (2015) redescribed *M. granosus* from exactly the same locality, but they did not record the existence of the second, much larger species there. González-Santillán & Álvarez-Padilla (2015: 75, 77) explicitly stated that their specimens were collected exclusively in the oak forest, where according to our data *M. orizaba* sp. n. seems not to occur, thus, it apparently went undetected by them.

There is one locality record published as *M. gertschi* by Soleglad (1976) and González-Santillán et al. (2017), which could well actually belong to its closest-relative *M. orizaba* sp. n.: 11.2 km southeast of Las Vigas de Ramírez, in Veracruz State. This site is located roughly 55 km to the north of Atotonilco, in the same mountain system (eastern tip of the Trans-Mexican Neovolcanic Belt) and at similar altitude (2,420 m); even the reference to a “subadult male” (Soleglad, 1976: 284; González-Santillán et al., 2017: 237) suggests one of the main diagnostic features of *M. orizaba* sp. n., i.e., the weaker development of the pedipalp finger lobe/notch combination.

Incidentally, there is some confusion in the previous literature about this character, i.e., it has been incorrectly assumed that a weak lobe/notch combination indicates a subadult male (see, e.g., Soleglad, 1976: 285). Nevertheless, by rearing dozens of specimens from birth to adulthood in captivity, we have confirmed that in all *Megacormus* species whose male has pedipalp fingers with lobe/notch combination developed, this character state appears only with the terminal ecdysis to adult, i.e., subadult males entirely lack such combination and its fingers resemble those of adult and juvenile females.

### *Megacormus seductus* sp. n.

(Figures 1–43, 56–57, 60, 64–65, 72–73, 78–79, 82, Tables 1–3)  
<http://zoobank.org/urn:lsid:zoobank.org:act:4A7487B6-78AF-4823-A0F5-58580EF8D89B>

*Megacormus segmentatus*: Sissom, 1994: 265, 268, 270  
 (misidentification: specimen and record from Los Tuxtlas).

**TYPE LOCALITY AND TYPE REPOSITORY.** Mexico, Veracruz, Catemaco Municipality, Los Tuxtlas, Estación de Biología Tropical UNAM, 18°35'02.7"N 95°04'15.7"W, 200 m a. s. l., FKCP.

**TYPE MATERIAL.** Mexico, Veracruz, Catemaco Municipality, Los Tuxtlas, Estación de Biología Tropical UNAM, 18°35'02.7"N 95°04'15.7"W, 200 m a. s. l., broadleaf rainforest on volcanic soil, inside rotten logs and stumps, 23.X.2022, leg. R. Teruel et al., 1♂ (holotype, No. 2460), FKCP, 1♂1♀ (paratotypes, No. 2461), FKCP, 1♂2♀1juv.♀ (paratotypes), RTOC; Dos Amates, 18°29'39.2"N 95°03'47.6"W, 400 m a. s. l., broadleaf rainforest on volcanic soil, inside rotten stump, 22.X.2022, leg. R. Teruel et al., 3♂1♀ (paratypes), FKCP.

**ETYMOLOGY.** The selected epithet is a Latin word that literally means “one who lives isolated, apart from others”, and highlights the singular geographical occurrence of this species in Los Tuxtlas Massif, removed from the main distribution area of the genus.

**DIAGNOSIS.** Adult size small for the genus (20–22 mm in males, 24–28 mm in females). Coloration with base light orange to yellowish brown, densely variegated with dark to blackish brown, paler and less spotted on chelicerae, pedipalp, legs and pectines. Pedipalp patella with 22–23 external trichobothria (7 eb, 2 esb, 5 em, 4–5 est, 4 et) and 6–8 ventral trichobothria. Pedipalp fingers with straight proximal dentate margins, without lobe/notch combination in adults of both sexes. Pectines with shaft clearly divided into areas and lamellae by conspicuous sulci; tooth count 5–6 in males, 4–5 in females. Metasomal segment V length/width ratio 2.26–2.29 in males, 2.29–2.32 in females. Telson elongated, narrower than metasomal segment V in both sexes.

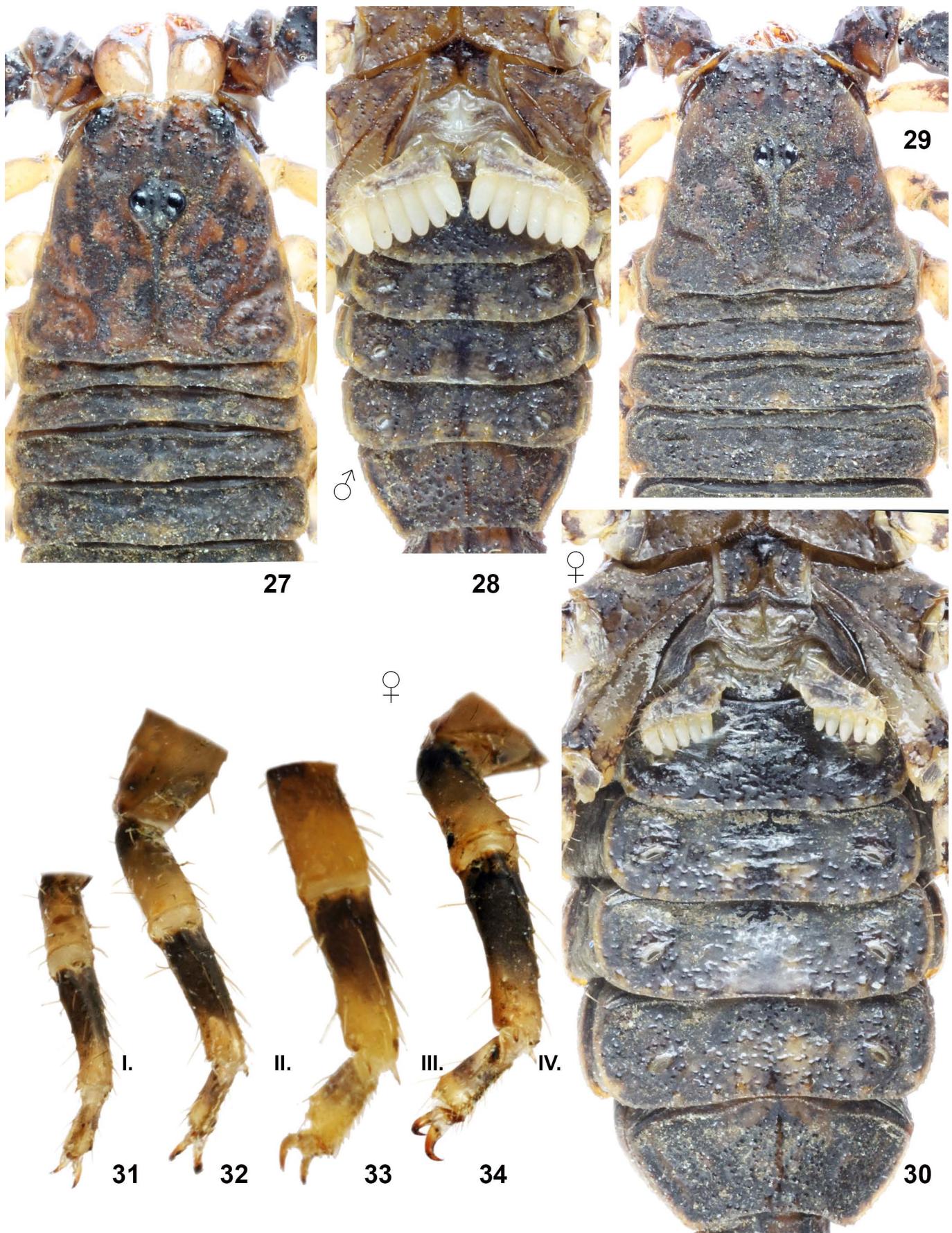
**SEXUAL DIMORPHISM.** Female differing from male by: 1) size larger (23.9–27.8 mm); 2) coloration darker and remarkably more densely infuscate (especially on chelicerae); 3) pedipalps, legs and metasoma slightly longer and slenderer; 4) mesosoma much wider and more convex-sided; 5) sternum larger and parallel-sided; 6) genital papillae absent; 7) pectines much smaller, with teeth shorter, narrower and fewer in number (4–5).

### DESCRIPTION (male holotype).

**Coloration** (Fig. 1) Base color light orange to yellowish brown, paler on chelicerae, pedipalp, legs and pectines, pedipalp chelae and telson with a reddish hue. Cheliceral manus finely and irregularly reticulate with dark brown, denser distally; fingers deeply infuscate. Pedipalps densely and irregularly marbled with blackish brown, but sparser distally (much denser on femur, sparser on manus), with all carinae deeply infuscate and the base of most trichobothria much paler (yellowish); fingers blackish, with distal third much paler progressively (becoming yellowish at the tip). Carapace symmetrically and densely marbled with dark to



**Figures 17–26:** *Megacormus seductus* sp. n., female paratype, pedipalp chela dorsal (17), external (18) and ventral (19) views, patella dorsal (20), external (21) and ventral (22) views, femur and trochanter dorsal (23) and ventral (24) views, movable (25) and fixed (26) fingers dentition.



**Figures 27–34:** *Megacormus seductus* sp. n. **Figures 27–28.** Male holotype, carapace and tergites I–IV (27) and coxosternal area and sternites (28). **Figures 29–34.** Female paratype, carapace and tergites I–IV (29), coxosternal area and sternites (30), and left legs I–IV, retrolateral aspect (31–34).

blackish brown, anterior and lateral margins mostly pale; eyes and ocular tubercles black. Tergites symmetrically and densely marbled with dark to blackish brown, with a large orange spot along midline that defines a pale dashed line all along I–VI, plus a pair of much smaller and fainter posterolateral pale spots on each side that suggest a dark four-striped pattern for the tergites. Pectines with shaft heavily and irregularly infuscate, but teeth essentially immaculate. Sternites colored and patterned similarly to tergites, but with a solid, narrow black stripe along midline (below ventral median carinae). Legs irregularly marbled with blackish brown, with pale and dark areas distributed in about the same proportion. Metasoma concolorous throughout (i.e., no segments conspicuously darker), densely and irregularly marbled with dark to blackish brown and with carinae deeply infuscate. Telson vesicle densely and irregularly marbled with dark to blackish brown, with four faint pale stripes corresponding to longitudinal furrows; aculeus orange, with distal third blackish.

**Chelicerae** (Fig. 27). Dentition typical for the genus, teeth short but sharp. Tegument smooth and glossy. Setation very dense ventrally, but essentially lacking dorsally, i.e., reduced to a few macrosetae distally in manus and also along movable finger. Fingers short, robust, evenly curved and subequal in length.

**Pedipalps** (Figs. 7–16). Slightly shorter and slenderer than standard for the genus (3.19 times longer than carapace). Trichobothrial pattern C, neobothriotoxic majorante: femur with all three trichobothria (*d, e, i*) in positions standard for the genus (at basal-most part of segment); patella with 2 dorsal trichobothria (*d*), one internal trichobothria (*i*), 21–22 external trichobothria (7/7 *eb*, 2/2 *esb*, 4/4 *em*, 4/5 *est*, 4/4 *et*) and 7/7 ventral trichobothria (*V*); chela manus with 2 dorsal trichobothria (*Db, Dt*), 10 external trichobothria (3 *Eb*, 1 *Esb*, 1 *Est*, 5 *Et*, with *Et* displaced to ventral surface), and 4 ventral trichobothria (with *V<sub>4</sub>* displaced to external surface); fixed finger with 4 dorsal trichobothria (*db, dsb, dst, dt*), two internal trichobothria (*ib, it*) and 4 external trichobothria (*eb, esb, est, et*).

**Femur** short and robust (length/width ratio = 2.22), almost bare, with all surfaces essentially flat to shallowly convex. Dorsointernal, dorsoexternal, ventrointernal and ventroexternal carinae complete (moderate, coarsely granulose). Tegument densely, roughly and irregularly granulose on dorsal and internal surfaces, coriaceous on external and ventral surfaces. **Patella** short and robust (length/width ratio = 2.07), almost bare, with dorsal and ventral surfaces flat, external and internal surfaces markedly convex. Dorsointernal, dorsoexternal, external median, ventrointernal and ventroexternal carinae complete (moderately strong, finely granulose to crenulate). Tegument coriaceous, with abundant fine to medium-sized, rough granules scattered all over (coarser and denser dorsally). Inner dorsal spur large, sharp and curved forwards; inner ventral spur small and sharp.

**Chela** short and robust, but slenderer than standard for the genus (length/width ratio = 3.37). Manus subtriangular in dorsal view (length/width ratio = 1.25, distally narrower) and oval

in lateral view, sparsely setose and prismatic in cross-section; dorsal internal, dorsal marginal, dorsal secondary, digital, external secondary, ventroexternal and ventrointernal carinae complete (moderately strong, finely granulose to crenulate); tegument coriaceous, with a poorly defined reticulate pattern of small, glossy granules scattered all over. Fingers standard for the genus (movable 1.79 times longer than underhand), shallowly curved and sparsely setose, dentition standard for the genus, basal lobe/notch combination entirely absent.

**Carapace** (Fig. 27). Slightly wider than long (length/width ratio = 0.98), paraboloid in dorsal view. Anterior margin shallowly bilobed, with 2–3 pairs of white macrosetae plus several minor setae; median notch very shallowly V-shaped. Tegument coriaceous, with abundant small granules scattered all over. All carinae indistinct or absent (even the superciliaries). Furrows: anterior median, central median, posterior median and posterior marginal narrow and moderately deep, fused altogether; posterior laterals narrow and moderately deep; other furrows either absent or undefined. Median ocular tubercle moderately raised, with eyes large and separated by slightly less than one ocular diameter; two pairs of large lateral eyes.

**Sternum** (Fig. 28). Standard for the genus: type 2, large, longer than wide and hexagonal in shape. Tegument coriaceous, with some medium-sized, round granules irregularly scattered.

**Genital operculum** (Fig. 28). Medium-sized and prominent, remarkably rhomboidal in shape. Halves neither separated nor fused and almost triangular in shape; tegument smooth and glossy. Genital papillae medium-sized, well-protruding, with tips blunt, round. Pre-pectinal plate apparently absent.

**Pectines** (Fig. 28). Size and shape standard for the genus: not reaching coxa-trochanter joint of leg IV, subrectangular and moderately setose, anterior area with 4/4 lamellae, median area with 5/6. Tooth count 6/6, teeth swollen, straight and basally not separated; fulcra entirely absent. Basal plate wider than long; anterior margin widely and deeply V-notched medially, posterior margin essentially straight; tegument smooth, glossy to coriaceous and sparsely granulose.

**Mesosoma** (Figs. 27–28). Tergites almost bare, anterior margin shallowly convex, posterior margin shallowly produced in the median part; median carina very weak and finely subcrenulate on I–VI, submedian and lateral carinae strong and finely serratocrenulate on VII; tegument coriaceous, with abundant small granules scattered all over. Sternites sparsely setose (largely along posterior and lateral margins), posterior margin shallowly concave to widely bilobed; III–VI acarinate, VII with only ventral median carinae perfectly defined, finely granulose to subcrenulate; tegument coriaceous, with abundant coarse and glossy granules; spiracles small, elongate-oval to short slit-like; V with smooth patch large, paraboloid in shape, translucent to yellowish, glossy and slightly bulky.

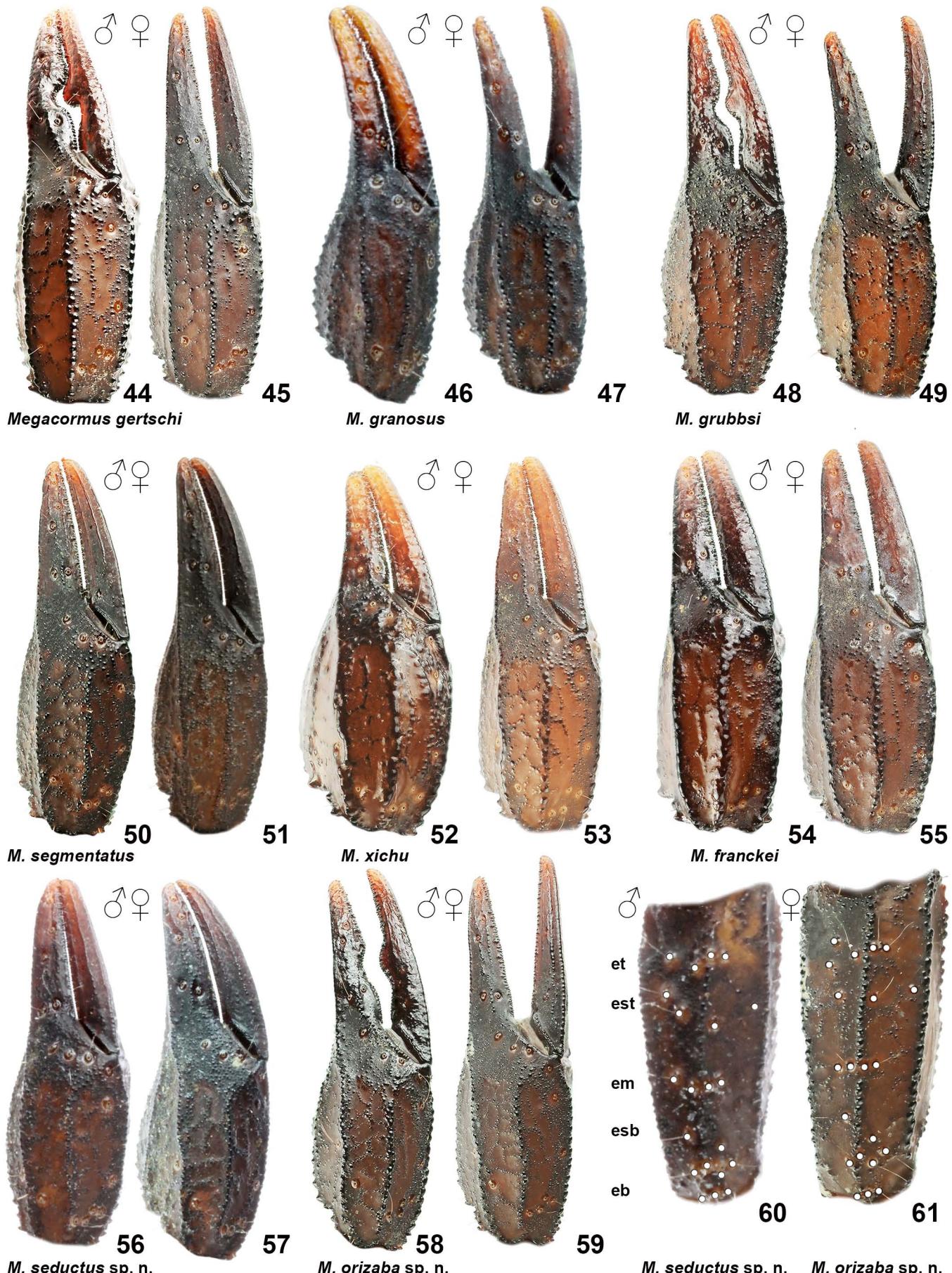
**Metasoma** (Figs. 37–39). Size and shape standard for the genus (2.77 times longer than carapace, length/width ratio of segments I–V = 0.64, 0.83, 0.89, 1.23 and 2.27), moderately narrower distally and moderately setose; segments I–III wider than long, IV–V longer than wide; I–III wider than deep, IV–V



**Figures 35–42.** *Megacormus seductus* sp. n. **Figures 35, 37–39.** Male holotype, telson in lateral (35), metasoma and telson in lateral (37), dorsal (38) and ventral (39) views. **Figures 36, 40–42.** Female paratype, telson in lateral (36), metasoma and telson in lateral (40), dorsal (41) and ventral (42) views. Scale bars: 10 mm (37–39, 40–42).



Figure 43. *Megacormus seductus* sp. n., habitat at type locality.



**Figures 44–61.** *Megacormus*, external pedipalp chela of males (44, 46, 48, 50, 52, 54, 56, 58) and females (45, 47, 49, 51, 53, 55, 57, 59), and external patella of male (60) and female (61). **Figures 44–45.** *M. gertschi*. **Figures 46–47.** *M. granosus*. **Figures 48–49.** *M. grubbsi*. **Figures 50–51.** *M. segmentatus*. **Figures 52–53.** *M. xichu*. **Figures 54–55.** *M. franckei*. **Figures 56–57, 60.** *M. seductus* sp. n. **Figures 58–59, 61.** *M. orizaba* sp. n. (44–45, 48–50, 52–55, 58–59, 61 from Kovařík, 2019).

deeper than wide. Segments I–IV with seven complete to almost complete carinae, V with five: all weak, irregularly and finely granulose to crenulate, with distalmost denticle conspicuously enlarged; lateral inframedians entirely absent or undefined from surrounding granulation on all segments; ventral submedians entirely absent; ventral median carina perfectly defined all along I–V; anal arc weakly granulose; laterodistal lobes of V obsolete, blunt-triangular. Intercarinal tegument coriaceous, with abundant minute and fine granules scattered all over. Dorsal furrow complete, moderately narrow and shallow.

**Telson** (Fig. 35). Sparsely setose, oval (2.71 times longer than wide, 1.21 times wider than deep); tegument coriaceous, with abundant moderately coarse but weak granules scattered all over and four very shallow longitudinal furrows; distal end of vesicle poorly defined by an obsolete annular ring and vestigial laterodistal shoulders. Aculeus moderately long, sharp and shallowly curved, with tegument glossy.

**Legs.** Size and slenderness standard for the genus, with all carinae weakly granulose to subcrenulate; tegument smooth coriaceous, with dorsal surface of femur sparsely granulose. Prolateral pedal spurs standard-sized, thick but sharp. Claws standard-sized (at least one-third the length of its respective telotarsus) and well-curved.

**Hemispermatophore.** (Figs. 64–65, 72–73). Lamelliform. Overall proportions of distal lamina, capsule, truncal flexure, trunk and pedicel standard for the genus. Distal lamina broad with angulate anterior margin, tapering in distal half; excluding crest, lamina width at basal constriction greater than half maximum lamina width. Capsule with moderately broad proximal transverse ridge; proximal dentate process expanded, either subrectangular with 7–9 blunt denticles (No. 2460; both left and right capsules), or lanceolate with 7–10 sharp triangular denticles (No. 2461; both left and right capsules). Distal dentate process broad, laminate, strongly serrated with 13–14 (No. 2460) or 18 (No. 2461) triangular denticles. Basal carina with crown-like structure bearing 4–6 tines. Terminal membrane of sperm duct with numerous fine spicules.

**AFFINITIES.** The described features distinguish *Megacormus seductus* sp. n. from all other species of the genus (see the key below). The validity of *M. seductus* sp. n. is confirmed also by DNA analysis implemented by Charles University in Prague (manuscript in preparation).

By the combination of very small adult size and absolute lack of pedipalp lobe/notch combination in adult males, this species resembles only *M. granosus* and *M. segmentatus*, and in fact, it was formerly misidentified as the latter taxon by Sissom (1994). However, *M. seductus* sp. n. occurs in isolated localities (Fig. 82). The most morphologically similar species can be regarded as *M. granosus*, which differs in the following morphological characters that are standard in the species-level taxonomy of the genus: 1. Size smaller (14–18 mm in males, 18–23 mm in females). 2. Entire body and appendages densely covered by very short, rigid, white microsetae in addition to ordinary setae. 3. Pectines with shaft not clearly divided into anterior and median areas and lamellae, all fused altogether into a single triangular sclerite (at most with faint incomplete

vestiges of sulci). 4. Pectinal tooth count lower (males 3–4, females 1–4). 5. Entire body and appendages with intercarinal granulation noticeably finer and more even. 6. Adults with mesosoma, metasoma and telson remarkably wider and heavier (more conspicuously so in males).

**DISTRIBUTION.** (Fig. 82). *M. seductus* sp. n. was found in two localities about 10 km apart from each other, but it may be widespread across Los Tuxtlas area, at least in the relict forest patches. The primary forest has been largely degraded or eliminated all over the area, but several such relicts still persist in the places with steepest slopes and/or privately controlled lands. Los Tuxtlas represents an isolated branch of the Trans-Mexican Neovolcanic Belt, actually its easternmost tip.

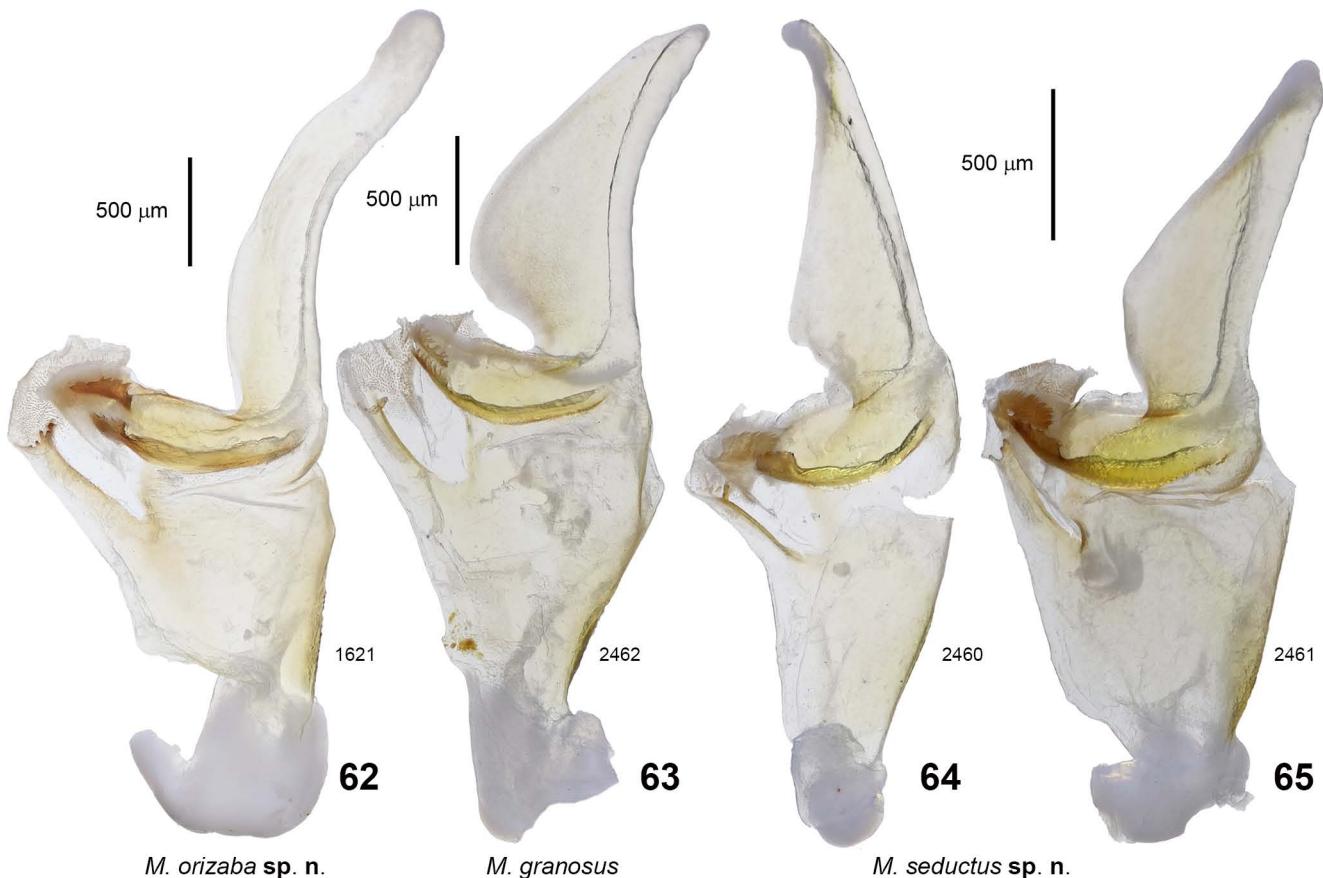
**ECOLOGICAL NOTES.** The types were all collected inside very old, moist, rotten stumps, in very humid places inside low to mid altitude broadleaf tropical rainforest (Fig. 43). Each inhabited stump housed a group of 3–5 individuals of *M. seductus* sp. n., mostly adults, which after discovery always played dead and remain motionless to confuse a potential predator (a behavior known as thanatosis or catalepsy). It is noteworthy to mention here that live individuals fluoresced very weakly under UV light, to the point that they were barely distinguishable from the background. A similar observation was reported by Soleglad (1976: 286) for live and preserved specimens of *M. gertschi*. Nevertheless, old exuviae and carcass remains did fluoresce as brightly as many other scorpions, and were readily found while searching in the soil; this allowed us to note that this species also inhabits leaf litter and occurs under rocks partially buried in the litter.

Two females were found carrying litters of young, one at each locality.

In both known localities, *M. seductus* sp. n. lives sympatrically with the buthid *Centruroides gracilis* (Latreille, 1804). At the type locality, it also occurs together with *Centruroides flavopictus* (Pocock, 1898) and *Centruroides catemacoensis* Goodman, Prendini, Francke & Esposito, 2021. In Dos Amates, it also lives sympatrically with the diplocentrid *Diplocentrus perezi* Sissom, 1991.

#### Key to species of *Megacormus*

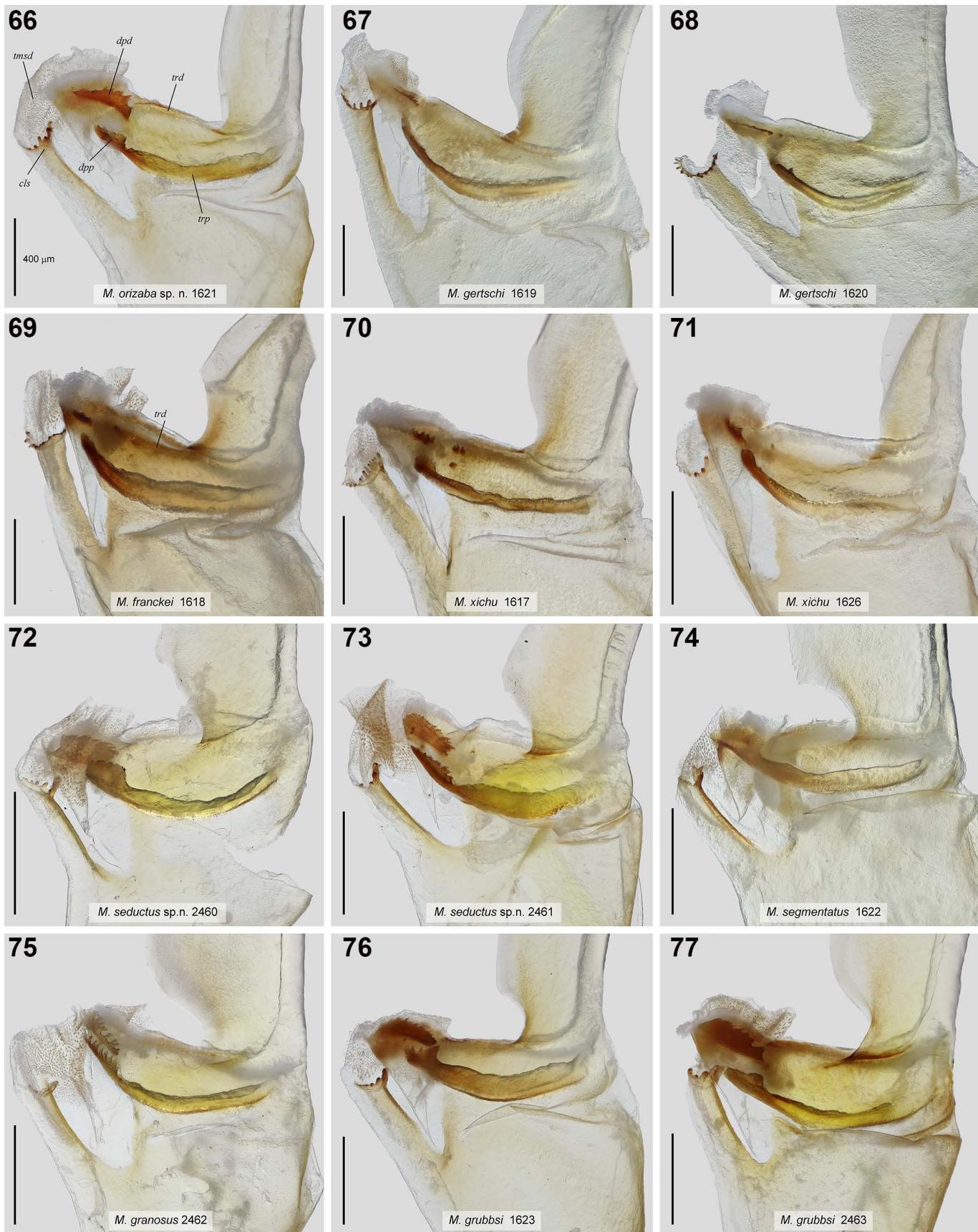
1. Adult male with basal lobe/notch combination of pedipalp fingers well-developed, absent in adult females and juveniles of both sexes (Figs. 44–45, 48–49, 58–59). ..... 2
- Adult and juveniles of both sexes with basal lobe/notch combination of pedipalp fingers entirely absent (figs. 46–47, 50–57). ..... 4
2. Pedipalp patella with 3 *et* trichobothria in distal external series; patella ventral surface granulose, with small to medium granules that are more sparse in the female ..... *M. grubbsi* Sissom, 1994
- Pedipalp patella with 4 *et* trichobothria in distal external series; patella ventral surface smooth in female, smooth or almost smooth in male with only very fine, sparse granules (shagreened) in some areas ..... 3



**Figures 62–65.** Hemispermatophores of *Megacormus* spp. **Figure 62.** *M. orizaba* sp. n. 19MD (holotype, No. 1621). **Figure 63.** *M. granosus* (No. 2462). **Figures 64–65.** *M. seductus* sp. n. 22MA (holotype and paratotype, Nos. 2460, 2461). Convex views of left hemispermatophores (62, 63) and right hemispermatophores shown in mirror image (64, 65). Scale bars: 500 µm.

3. Adult male pedipalp chela with dorsal marginal carina coarsely granulose, distal ventral surface of manus sparsely, finely granulose (figs. 59, 61 in Kovařík, 2019: 15); metasoma V with dorsolateral carina only very slightly elevated (figs. 80, 83 in Kovařík, 2019: 18) ..... *M. gertschi* Díaz Nájera, 1966
- Adult male pedipalp chela with dorsal marginal carina more finely granulose, distal ventral surface of manus densely, finely granulose (figs. 94, 96 in Kovařík, 2019: 22); metasoma V with dorsolateral carina distinctly elevated (figs. 115, 118 in Kovařík, 2019: 25). ..... *M. orizaba* sp. n.
4. Adult size medium for the genus, over 30 mm. Adult male pedipalp chelae robust and with intercarinal tegument glossy. ..... 5
- Adult size small for the genus, less than 30 mm. Adult male pedipalp chelae slender and with intercarinal tegument entirely matt. ..... 6
5. Adult male with pedipalp manus and metasoma slenderer, metasomal segment V length/width ratio 2.60–2.80. ..... *M. franckeai* Kovařík, 2019
- Adult male with pedipalp manus and metasoma more robust, metasomal segment V length/width ratio 1.94–2.13. ..... *M. xichu* González-Santillán et al., 2017
6. Pectines with shaft not clearly divided into areas and lamellae, all fused together into a single triangular sclerite, at most with faint incomplete vestiges of sulci. Entire body and appendages densely covered by very short, rigid, white microsetae in addition to ordinary setae. ..... *M. granosus* (Gervais, 1843)
- Pectines with shaft clearly divided by deep sulci into well-defined areas and lamellae. Entire body and appendages either lacking or with only a few very short, rigid, white microsetae in addition to ordinary setae. ..... 7
7. Adult male carapace with central median and posterior median carinae well-defined from surrounding granulation, finely granulose. Metasoma slenderer and with carinae stronger, composed of sharper granules. ..... *M. segmentatus* Pocock, 1900
- Adult male carapace with central median and posterior median carinae missing, not distinguishable from surrounding granulation (Fig. 27). Metasoma more robust and with carinae weaker, composed of blunter granules (Figs. 37–39). ..... *M. seductus* sp. n.

**REMARKS ON HEMISPERMATOPHORES.** The taxonomic utility of hemispermatophore characters of *Megacormus* has been questioned. González-Santillán & Alvarez-Padilla (2015) hypothesized that “the capsular region of the hemispermatophore



**Figures 66–77.** Hemispermophore capsules of *Megacormus*. **66.** *M. orizaba* sp. n. (holotype, No. 1621). **67–68.** *M. gertschi* (Nos. 1619, 1620). **69.** *M. franckei* (paratype, No. 1618). **70–71.** *M. xichu* (Nos. 1617, 1626). **72–73.** *M. seductus* sp. n. (holotype and paratopotype, Nos. 2460–2461). **74.** *M. segmentatus* (No. 1622). **75.** *M. granosus* (No. 2462). **76.** *M. grubbsi* (No. 1623). **77.** *M. grubbsi* (No. 2463). Convex views of left capsules (66, 68–71, 73–75 and 77), and right capsules shown in mirror image (67, 72 and 76). Abbreviations: *dpd*, distal dentate process; *dpp*, proximal dentate process; *cls*, crown-like structure; *trd*, distal transverse ridge; *trp*, proximal transverse ridge; *tmsd*, terminal membrane of the sperm duct. Scale bars: 400 μm.

species	DNA No.	locality	left <i>cls</i> tines	right <i>cls</i> tines
<i>M. franckei</i>	1618	19MB	12	7
<i>M. gertschi</i>	1619	19MC	11	11
<i>M. gertschi</i>	1620	19MC	12	10
<i>M. gertschi</i>	1627	19MC	12	13
<i>M. gerstchi</i> <sup>1</sup>			13	
<i>M. granosus</i>	2462	22MD	6	7
<i>M. granosus</i> <sup>2</sup>			6–8	
<i>M. grubbsi</i>	1623	19MF	7	6
<i>M. cf. grubbsi</i>	2463	22MC	7	7
<i>M. grubbsi</i> <sup>3</sup>				6
<i>M. segmentatus</i>	1622	19ME	6	5
<i>M. orizaba</i> sp. n.	1621	19MD	7	7
<i>M. seductus</i> sp. n.	2460	22MA	5	6
<i>M. seductus</i> sp. n.	2461	22MA	4	4
<i>M. xichu</i>	1617	19MA	13	11
<i>M. xichu</i>	1626	19MA	7	7
<i>M. xichu</i> <sup>4</sup>			7–8	

**Table 2.** Variation in number of tines on the crown-like structure (*cls*) of the hemispermatophore of *Megacormus* species. Data with DNA No. and locality code were obtained from examined hemispermatophores. Other data were obtained from published descriptions or illustrations (<sup>1</sup>Francke, 1979; <sup>2</sup>González-Santillán & Alvarez-Padilla, 2015; <sup>3</sup>Sissom, 1994: fig. 8; <sup>4</sup>González-Santillán et al., 2017).

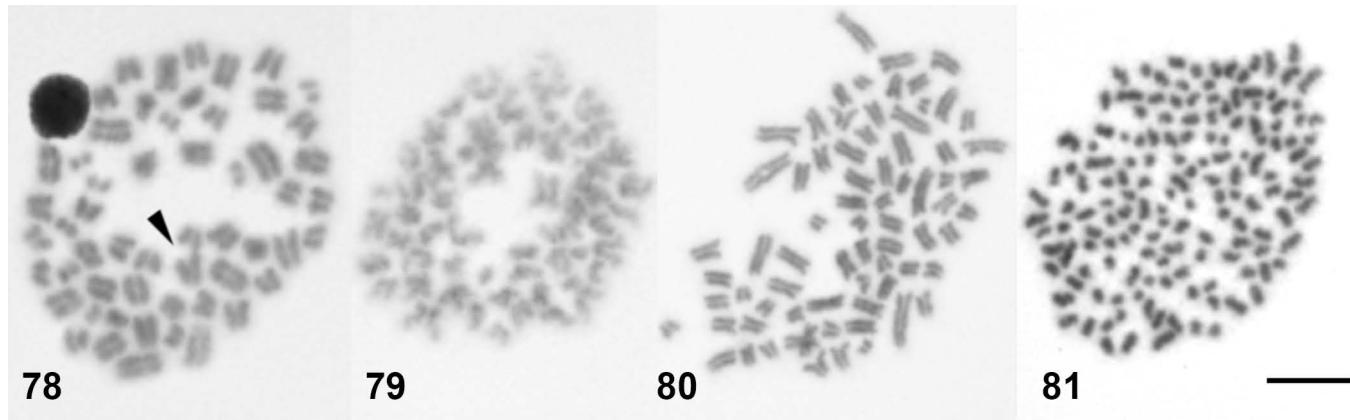
	<i>M. gerstchi</i>	<i>M. granosus</i>	<i>M. grubbsi</i>	<i>M. seductus</i> sp. n.	<i>M. xichu</i>
<i>M. gerstchi</i>	0.0000	0.0253	0.0060	0.0253	0.0670
<i>M. granosus</i>	2.2534	0.0000	0.4033	0.0806	0.4118
<i>M. grubbsi</i>	<b>2.9011</b>	0.4268	0.0000	0.0360	0.1446
<i>M. seductus</i> sp. n.	<b>4.0326</b>	1.5771	1.2356	0.0000	0.0363
<i>M. xichu</i>	1.4018	0.9799	1.5173	2.7075	0.0000

**Table 3.** Pairwise two-sided non-parametric tests of equality of tine counts of crown-like structure (*cls*) of hemispermatophores between five different *Megacormus* species. Below diagonal values: z-values from Dunn's test; thresholds for significantly different medians were: 1.9600 (regular, shaded), 2.8070 (Bonferroni correction, bold). Above diagonal values: P-values from likelihood ratio tests ( $P < \alpha = 0.05$  shaded; without family-wise correction).

of *Megacormus* might carry little information to diagnose species of the genus". To test this hypothesis, we examined both left and right hemispermatophores ( $N = 26$ ) of 13 male *Megacormus*, representing the following species: *M. franckei* (1), *M. gertschi* (1), *M. granosus* (1), *M. grubbsi* (2), *M. segmentatus* (1), *M. orizaba* sp. n. (1), *M. seductus* sp. n. (2), and *M. xichu* (2). Additional data from hemispermatophores of *M. gertschi* (3), *M. granosus* (1), *M. grubbsi* (1) and *M. xichu* (1), were compiled from published sources (Francke, 1979; González-Santillán & Alvarez-Padilla, 2015; González-Santillán et al., 2017; Sissom, 1994). Figures 66–77 show examples of capsules from 12/13 examined males. A visual comparison reveals some consistency of characters. For example, the proximal dentate process (*dpp*) was narrow and tapering, with only one or a few short denticles in *M. gertschi* ( $N = 8$ ). In contrast, the *dpp* was spatulate with variable dentition in *M. xichu* ( $N = 5$ ) and *M. grubbsi* ( $N = 5$ ). On the other hand, the shape of the *dpp* was significantly different in two conspecific males assigned to *M. seductus* sp. n. on the basis of external morphology and DNA sequences, being

either spatulate and weakly denticulate (No. 2460) or elongate and strongly denticulate (No. 2461).

As a quantitative test of the hypothesis, we analyzed intra- and interspecific variation in the number of tines on the crown-like structure (*cls*) of the capsular basal carina. The available data are listed in Table 2. The data suggested potentially significant differences, e.g., *M. gertschi* had a higher range of tine counts compared of those of most other species. We applied statistical tests to the following tine counts: *M. gertschi*: 10, 11, 11, 12, 12, 13, 13; *M. granosus* 6, 7, 7, 8; *M. grubbsi* 6, 6, 7, 7, 7; *M. seductus* sp. n.: 4, 4, 5, 6; and *M. xichu*: 7, 7, 7, 8, 11, 13. Left and right *cls* counts were assumed independent, in the absence of evidence of intraspecific correlation. Normality of residuals was rejected ( $\alpha = 0.2$ ) by Shapiro-Wilk ( $P = 0.03456$ ) and Anderson-Darling ( $P = 0.11835$ ) tests, and homogeneity of variance was rejected by Levene test ( $P = 0.00310$ ). We applied the Kruskal-Wallis test, as a non-parametric rank test of equality of median tine counts. Medians  $\pm$  interquartile ranges were: *M. gertschi*:  $12.0 \pm 2.0$ ; *M. granosus*:  $7.0 \pm 4.5$ ; *M. grubbsi*:  $7.0 \pm 1.5$ ; *M. seductus* sp. n.:  $4.5 \pm 1.0$ ; and *M. xichu*:  $7.50 \pm$



**Figures 78–81.** Chromosomes of *Megacormus* species. **78–79.** *M. seductus* sp. n. (No. 2461) ( $2n=109$ ). **80.** *M. segmentatus* (No. 1262) ( $2n=144$ ). **81.** *M. granosus* (No. 2462) ( $2n=148$ ). Postpachytene (78 and 80), one sister metaphase II (79), ane mitotic metaphase (81). Arrowhead shows trivalent in postpachytene. Scale bar: 10  $\mu$ m.

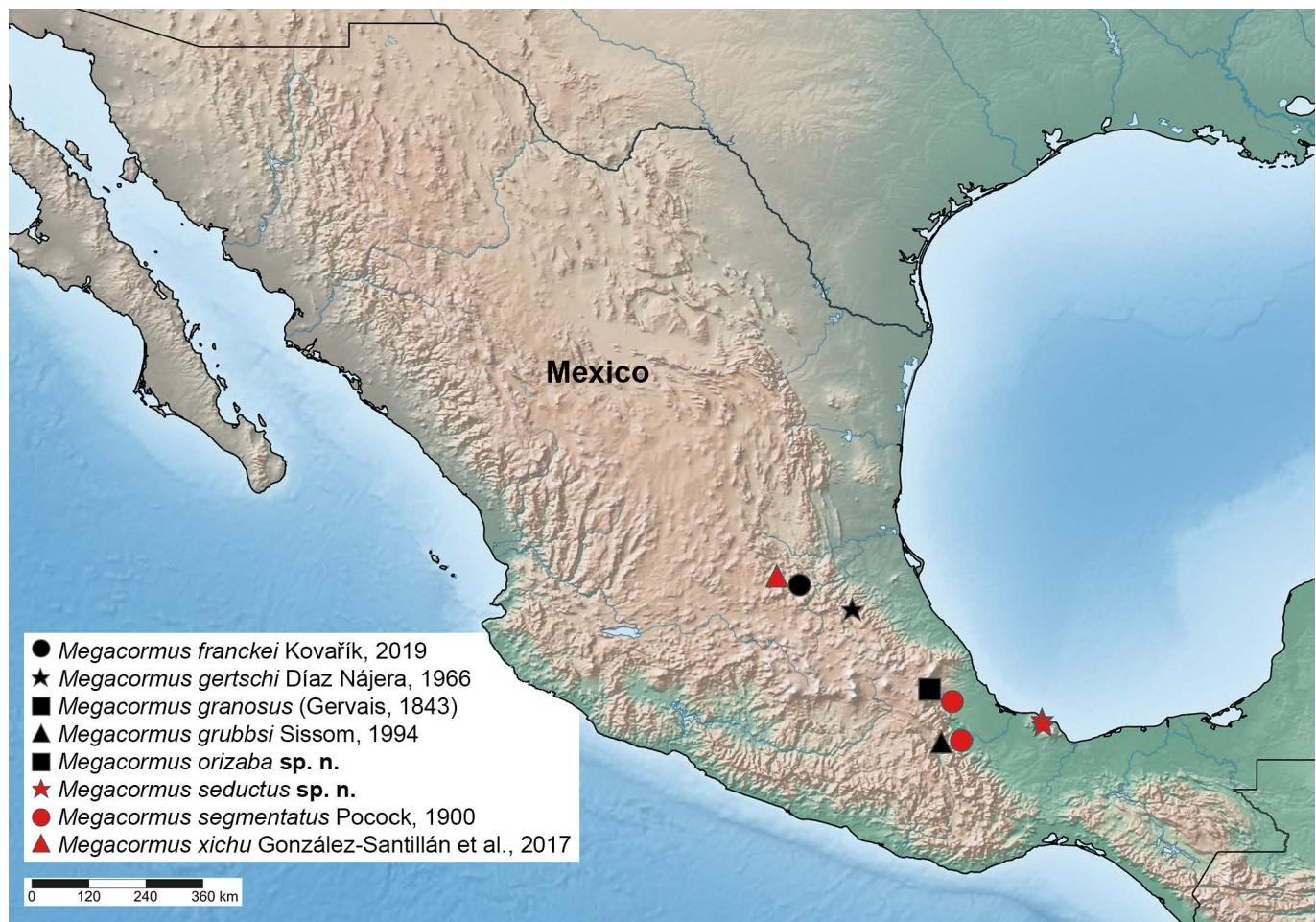
1.75. After correcting for ties,  $P = 0.00065$ , rejecting the null hypothesis that median tine counts are independent of species ( $\alpha = 0.05$ ). Accuracy of this test may be influenced by tine count being a discrete variable with a small number of recorded values. As a further test, we analysed a contingency table of species  $\times$  counts, using the likelihood ratio statistic, and obtained:  $\chi^2 = 46.358$ ,  $P = 0.0484$ , again leading to (weaker) rejection of the null hypothesis ( $\alpha = 0.05$ ). Post hoc paired comparisons identified significant differences between some species (Table 3). In particular, *M. gertschi* differed from three of four others, consistent with the gap between low and high count ranges. On the other hand, *M. xichu* did not differ from three of four others, consistent with its overlap with both low and high count ranges (see also: Kovařík et al., 2020b: 30). These results suggest that some hemispermatophore structures may contain phylogenetic signal relevant for taxonomy. However, their diagnostic utility depends on the degree of intraspecific variation and interspecific overlap, factors that will need to be addressed further by more extensive sampling.

**REMARKS ON THE KARYOTYPES (FIG. 78–81).** We analyzed chromosomes of three *Megacormus* species using the spreading technique, which has been successfully used in scorpions (e. g. Plíšková et al., 2016). The analyzed species were specifically: *M. seductus* sp. n. (sample No. 2461), *M. segmentatus* (sample No. 1262), and *M. granosus* (sample No. 2462). The chromosomes of these species (Figs. 78–81) exhibited cytogenetic characteristics known to be typical of the Old World members of the family Euscorpiidae, such as monocentric chromosomes, achiasmic meiosis in males, and higher number of chromosomes (e. g. Štundlová et al., 2019). In observed *Megacormus* species, the diploid numbers ranged from  $2n=109$  in *M. seductus* sp. n. (Fig. 78) to  $2n=148$  in *M. granosus* (Fig. 81). Unfortunately, the quality of observed chromosomes did not allow us to specify the morphology of the chromosomes very precisely. However, from the documented postpachytenes (Figs. 78 and 80) and metaphases II (Fig. 79) it is evident that the karyotypes included all of the morphological types of chromosomes with the predominance of one-armed chromosomes (i.e., subtelocentric and acrocentric). It is also evident that the karyotypes of different *Megacormus*

species differ considerably from each other, and that cytogenetics is useful in the taxonomy of this genus, as it is for Old World euscorpiid genera (e.g., Štundlová et al., 2019, Kovařík et al., 2019). It can further be proposed that centric fusions/fissions are the main mechanisms of karyotype differentiation in *Megacormus* species. These rearrangements can be deduced since a number of larger chromosomes of the species are bi-armed (metacentric or submetacentric), and in addition, a trivalent was found in *M. seductus* sp. n. (Fig. 78). This heterozygous state is also frequently found in other scorpions with monocentric chromosomes (e. g., Štundlová et al., 2019).

## References

- BANERJEE, S., E. GNANAMANI , S. R LYNCH, F. Z. ZUÑIGA, J. M. JIMÉNEZ-VARGAS, L. D. POSSANI & R. N. ZARE. 2018. An alkaloid from scorpion venom: chemical structure and synthesis. *Journal of Natural Products*, 81: 1899–1904.
- FET, V. & W. D. SISSOM. 2000. Family Euscorpiidae C. L. Koch, 1837. Pp. 355–380 in Fet, V., W. D. Sissom, G. Lowe & M. E. Braunwalder. *Catalog of the Scorpions of the World (1758–1998)*. New York: The New York Entomological Society, 689 pp.
- FRANCKE, O. F. 1979. Observations on the reproductive biology and life history of *Megacormus gertschi* Diaz. *The Journal of Arachnology*, 7: 223–230.
- GONZÁLEZ-SANTILLÁN E. & F. ALVAREZ-PADILLA. 2015. The male of *Megacormus granosus* (Gervais, 1844) with comments on its hemispermatophore (Scorpiones, Euscorpiidae). *ZooKeys*, 504: 75–91.
- GONZÁLEZ-SANTILLÁN E., J. M. GONZÁLEZ-RUÍZ & L. A. ESCOBEDO-MORALES. 2017. A new species of *Megacormus* (Scorpiones, Euscorpiidae) from an oak-pine forest in Guanajuato, México with an identification key to the species in the genus. *Zootaxa*, 4299(2): 221–237.



**Figure 82.** Distribution of *Megacormus* specimens examined for this review (see Comparative material examined in Methods, Material & Abbreviations section).

KARSCH, F. 1881. Ueber eine neue Gattung Scorpione. *Archiv für Naturgeschichte*, 47(1): 16–18.

KOVAŘÍK, F. 2009. *Illustrated catalog of scorpions. Part I. Introductory remarks; keys to families and genera; subfamily Scorpioninae with keys to Heterometrus and Pandinus species*. Prague: Clairon Production, 170 pp.

KOVAŘÍK, F. 2019. Review of *Megacormus* Karsch, 1881, with description of a new species (Scorpiones: Euscorpiidae). *Euscorpius*, 296: 1–46.

KOVAŘÍK, F., G. LOWE, M. BYRONOVÁ & F. ŠTÁHLAVSKÝ. 2020a. *Euscorpius thracicus* sp. n. (Scorpiones: Euscorpiidae) from Bulgaria. *Euscorpius*, 326: 1–17.

KOVAŘÍK, F., G. LOWE, P. JUST, A. I. AWALE, H. SH A. ELMI & F. ŠTÁHLAVSKÝ. 2018. Scorpions of the Horn of Africa (Arachnida: Scorpiones). Part XVI. Review of the genus *Gint* Kovařík et al., 2013, with description of three new species from Somaliland (Scorpiones, Buthidae). *Euscorpius*, 258: 1–41.

KOVAŘÍK, F., G. LOWE, M. STOCKMANN & F. ŠTÁHLAVSKÝ. 2020b. Revision of genus-group taxa in the family Scorplopidae Kraepelin, 1905, with description of 15 new species (Arachnida: Scorpiones). *Euscorpius*, 325: 1–140.

KOVAŘÍK, F. & A. A. OJANGUREN AFFILASTRO. 2013. *Illustrated catalog of scorpions. Part II. Bothriuridae; Chaerilidae; Buthidae I. Genera Compsobuthus, Hottentotta, Isometrus, Lychas, and Sassanidotus*. Prague: Clairon Production, 400 pp.

KOVAŘÍK, F., J. ŠTUNDLOVÁ, V. FET & F. ŠTÁHLAVSKÝ. 2019. Seven new Alpine species of the genus *Alpiscorpius* Gantenbein et al., 1999, stat. n. (Scorpiones: Euscorpiidae). *Euscorpius*, 287: 1–29.

LOWE, G. & F. KOVAŘÍK. 2019. Review of *Groshus* Simon, 1880, with description of *Teruelius* gen. n., a new buthid genus from Madagascar (Scorpiones: Buthidae). *Euscorpius*, 281: 1–128.

- MONOD, L., L. CAUWET, E. GONZÁLEZ-SANTILLÁN & S. HUBER. 2017. The male sexual apparatus in the order Scorpiones (Arachnida): a comparative study of functional morphology as a tool to define hypotheses of homology. *Frontiers in Zoology*, 14: 51: 1–48.
- OLGUÍN-PÉREZ, L., O. F. FRANCKE & A. CARBAJAL-SAUCEDO. 2021. Evidence of piercing and sexual differences in venom composition in a sexual stinging scorpion (Scorpiones: Euscorpiidae). *Journal of Arachnology*, 49: 98–107.
- PLÍŠKOVÁ, J., F. KOVÁŘÍK, O. KOŠULIČ & F. ŠTÁHLAVSKÝ. 2016. Description of a new species of *Heterometrus* Ehrenberg, 1828 (Scorpiones: Scorpionidae) from Thailand with remarks about the utilization of cytogenetic data in taxonomy of the genus. *Annales Zoologici (Warszawa)*, 66(3): 467–476.
- POCOCK, R. I. 1900. Some new or little-known neotropical scorpions in the British Museum. *Annals and Magazine of Natural History*, (7), 5: 469–478.
- POCOCK, R. I. 1902. Arachnida, Scorpiones, Pedipalpi and Solifugae. *Biologia Centrali-Americana*. Taylor and Francis, London.
- SANTIBÁÑEZ-LÓPEZ, C. E., S. AHARON, J. A. BALLESTEROS, G. GAINETT, C. M. BAKER, E. GONZÁLEZ-SANTILLÁN, M. S. HARVEY, M. K. HASSAN, A. H. ABU ALMAATY, S. M. ALDEYARBI, L. MONOD, A. OJANGUREN-AFFILASTRO, R. PINTO-DA-ROCHA, Y. ZVIK, E. GAVISH-REGEV & P. P. SHARMA. 2022. Phylogenomics of scorpions reveal contemporaneous diversification of scorpion mammalian predators and mammal-active sodium channel toxins. *Systematic Biology*, 71 (6): 1281–1289. doi: 10.1093/sysbio/syac021.
- SANTIBÁÑEZ-LÓPEZ, C. E., J. I. CID-URIBE, F. Z. ZAMUDIO, C. V. F. BATISTA, E. ORTIZ & L. D. POSSANI. 2017. Venom gland transcriptomic and venom proteomic analyses of the scorpion *Megacormus gertschi* Díaz-Najera, 1966 (Scorpiones: Euscorpiidae: Megacorminae). *Toxicon*, 133: 95–109.
- SANTIBÁÑEZ-LÓPEZ, C. E., O. F. FRANCKE, C. URETA & L. D. POSSANI. 2016. Scorpions from Mexico: from species diversity to venom complexity. *Toxins*, 8: 1–18. *Toxins* 8, 1–18. doi.org/10.3390/toxins8010002.
- SHARMA, P. P., C. M. BAKER, J. G. COSGROVE, J. E. JOHNSON, J. T. OBERSKI, R. J. RAVEN, M. S. HARVEY, S. L. BOYER & G. GIRIBET. 2018. A revised dated phylogeny of scorpions: phylogenomic support for ancient divergence of the temperate Gondwanan family Bothriuridae. *Molecular Phylogenetics and Evolution*, 122: 37–45.
- SISSOM, W. D. 1994. Systematic studies on the genus *Megacormus* (Scorpiones, Chactidae, Megacorminae), with descriptions of a new species from Oaxaca, Mexico and of the male of *Megacormus segmentatus* Pocock. *Insecta Mundi*, 8: 265–272.
- SOLEGLAD, M. E. 1976. A revision of the scorpion subfamily Megacorminae (Scorpionida, Chactidae). *Wassmann Journal of Biology*, 34 (2): 251–303.
- SOLEGLAD, M. E. & V. FET. 2003a. The scorpion sternum: structure and phylogeny (Scorpiones: Orthosterni). *Euscorpius*, 5: 1–34.
- SOLEGLAD, M. E. & V. FET. 2003b. High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). *Euscorpius*, 11: 1–175.
- SOLEGLAD, M. E. & W. D. SISSOM. 2001. Phylogeny of the family Euscorpiidae Laurie, 1896 (Scorpiones): a major revision. Pp. 25–111 in: Fet, V. & P. A. Selden (eds). *Scorpions 2001. In Memoriam Gary A. Polis*. British Arachnological Society, Burnham Beeches: Bucks, 404 pp.
- STAHNKE, H. L. 1971. Scorpion nomenclature and mensuration. *Entomological News*, 81: 297–316.
- ŠTUNDLOVÁ, J., J. ŠMÍD, P. NGUYEN & F. ŠTÁHLAVSKÝ. 2019. Cryptic diversity and dynamic chromosome evolution in Alpine scorpions (Euscorpiidae: *Euscorpius*). *Molecular Phylogenetics and Evolution*, 134: 152–163.
- TRUJILLO, R. E. & L. F. DEARMAS. 2012. Nueva especie de *Plesiochactas* Pocock, 1900 (Scorpiones: Euscorpiidae) de Guatemala. *Boletín de la Sociedad Entomológica Aragonesa*, 50: 263–266.
- VACHON, M. 1974. Études des caractères utilisés pour classer les familles et les genres des scorpions (Arachnides). 1. La trichobothrioxie en arachnologie. Sigles trichobothriaux et types de trichobothrioxie chez les Scorpions. *Bulletin du Muséum national d'Histoire naturelle*, 3e série, 140 (Zoologie, 104): 857–958.
- ZÁRATE-GÁLVEZ, K. & O. F. FRANCKE. 2009. Redescription of *Plesiochactas mitchelli* (Scorpiones: Euscorpiidae): a rare scorpion from Central America. *Journal of Arachnology*, 37: 338–345.