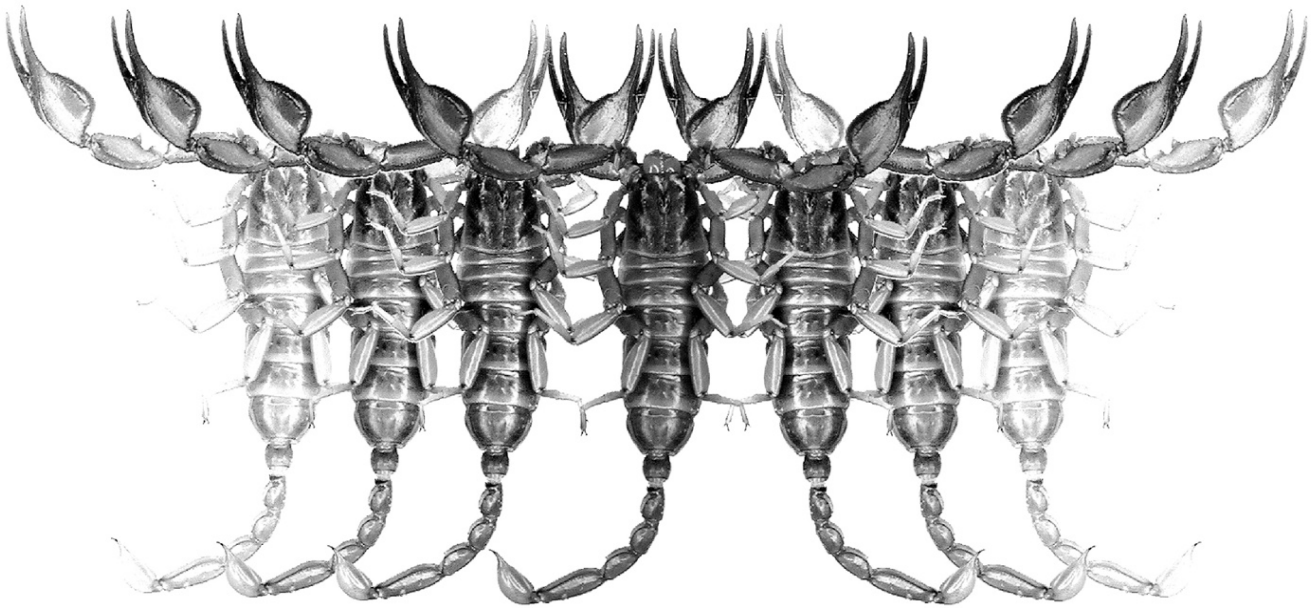


# *Euscorpius*

Occasional Publications in Scorpiology



**Neotype designation for *Pectinibuthus birulai*  
Fet, 1984 (Scorpiones: Buthidae) from  
Turkmenistan, with remarks on pectine teeth  
of psammophile scorpions**

**Victor Fet, František Kovařík & Graeme Lowe**

**August 2019 — No. 286**

# *Euscorpius*

## *Occasional Publications in Scorpiology*

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

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# Neotype designation for *Pectinibuthus birulai* Fet, 1984 (Scorpiones: Buthidae) from Turkmenistan, with remarks on pectine teeth of psammophile scorpions

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## Summary

A neotype is designated for a very rare Central Asian scorpion, *Pectinibuthus birulai* Fet, 1984, the sole species of the genus *Pectinibuthus* Fet, 1984. It is the only currently known specimen, collected by Victor Fet in July 1985, and deposited in ZISP (St. Petersburg, Russia). The original types are considered lost. Detailed photographs of the neotype are provided, as well as comments on this unique psammophile buthid. We also discuss and compare pectinal tooth counts of psammophile scorpions relative to other scorpions.

## Methods, Material & Abbreviations

Nomenclature and measurements follow Stahnke (1971), Kovařík (2009), and Kovařík & Ojanguren-Affilastro (2013), except for trichobothriotaxy (Vachon, 1974). Biometric data on pectinal tooth count and adult carapace length were compiled mostly by data mining taxonomic literature, although a few measurements were taken directly from unpublished specimens in the authors collections. If adult carapace lengths of several specimens were published, we calculated the mean value for our analyses. Plotting and statistical analyses were performed in Origin 7.0 (<http://www.originlab.com>) and MaxStat 3.60 (<http://www.maxstat.de>).

*Specimen depositories*: ZISP, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia; ZMMSU, Zoological Museum of Moscow State University, Moscow, Russia.

## Systematics

Family Buthidae C. L. Koch, 1837

Genus *Pectinibuthus* Fet, 1984

<http://zoobank.org/urn:lsid:zoobank.org:act:3B645472-F2F2-462E-8844-A0DACE767568>

*Pectinibuthus* Fet in Orlov & Vasilyev, 1984: 9.

TYPE SPECIES: *Pectinibuthus birulai* Fet, 1984, by monotypy.

DISTRIBUTION. Turkmenistan: East Karakum desert.

*Pectinibuthus birulai* Fet, 1984

(Figs. 1–21, 24, Table 1)

<http://zoobank.org/urn:lsid:zoobank.org:act:009DDF1F-25D2-4B9C-9A0B-100E1618C7EF>

*Pectinibuthus birulai* Fet in Orlov & Vasilyev, 1984: 15, fig. 8; Fet, 1987: 443–446, figs. 1–5; Fet, 1988: 24–28, figs. 1–7; Fet, 1989: 118–119; Fet, 1994: 531; Fet, 1997: 247; Fet, Polis & Sissom, 1998: 612; Fet & Lowe, 2000: 213 (full list of references before 1998); Capes & Fet, 2001: 300; Fet, Capes & Sissom, 2001: 185; Soleglad & Fet, 2005: 13.

TYPE MATERIAL (LOST; SEE COMMENTS): HOLOTYPE: ♂ (ZISP 1795), Turkmenistan: Lebap Velayati (former Chardzhou Region), Repetek Nature Reserve, leg. A. Yu. Tselarius. PARATYPES (3♀): 2♀ (ZISP 1796), same locality, 23 April 1974, leg. V. I. Kuznetsov; 1♀ (ZISP 1797), same locality, 16 June 1974, leg. V. I. Kuznetsov.

NEOTYPE (designated here): juvenile ♂ (ZISP 1796), Turkmenistan: Lebap Velayati (former Chardzhou Region), Repetek Natural Reserve, 21 July 1985, leg. V. Fet.

NEOTYPE DESIGNATION. In accord with the ICZN Article 75.3, we declare that there is an exceptional need to designate the neotype of *Pectinibuthus birulai* Fet, 1984 with the express purpose of clarifying the taxonomic status and identity of this species. No other specimen is known to us to exist of this sole species of a monotypic psammophile genus, while the study



Figures 1–3: *Pectinibuthus birulai*, neotype juvenile, dorsal (1) and ventral (2) views and original label (3). Scale bar = 10 mm (1–2).

of Turkmenistan psammophile buthids has been considerably advanced in the last decade, including DNA phylogeny data (Graham et al., 2012; Fet et al., 2018). We have strong reasons for believing that the holotype male of *Pectinibuthus birulai* Fet, 1984 (ZISP 1795) is lost along with the rest of the type series (three paratype females, ZISP 1796–1797). We have taken steps to trace these specimens by personally examining the ZISP scorpion collection in St. Petersburg (F.K. and Ersen Aydin Yağmur, 2019, see Kovařík et al., 2019) with the help of Dr. Viktor Krivokhatsky who is a curator of this collection. The neotype is consistent with what is known of the former name-bearing type from the original description, and comes from the original type locality, Repetek Nature Reserve in East Karakum, Turkmenistan. The neotype is the property of ZISP, which is a venerable scientific institution

that maintains a research scorpion collection, with proper facilities for preserving name-bearing types, and that makes them accessible for study.

DIAGNOSIS (see also Fet, 1987). Adult size medium for the family (the only known adult male 56 mm long). Cheliceral dentition modified from most common buthid pattern (Vachon, 1963): both fixed and movable finger ventrally with a single denticle. Pedipalps very slender, with chelae narrower than patella; trichobothrial pattern orthobothriotaxic A-β, patellar trichobothrium  $d_3$  located between dorsomedian and dorsointernal carinae,  $Eb_1$ - $Eb_2$ - $Eb_3$  collinear ( $\lambda$ ); fingers without lobe/ notch combination, with 9–10 principal rows of denticles (division of basal-most rows usually poorly defined), all arranged in a straight line, external accessory



denticles entirely absent, internal accessory denticles absent from basal-most rows, movable finger with 1–2 accessory denticles basal to the terminal denticle. Carapace essentially without carinae, with anterior margin almost straight; median eyes very large and raised, five pairs of much smaller lateral eyes (three same-sized and aligned along each anterolateral corner, plus two tiny and offset above the former). Tergites I–VI vestigial to obsoletely tricarinate. Sternum type 1, relatively small, and triangular to subpentagonal in shape; posterior depression very large and deep. Pectines very long, with 39–46 teeth in both sexes (neotype 40–40); fulcra well-developed; lamellae and basal plate unmodified. Legs very long and slender, adapted to psammophily: tibia and tarsi of I–III short, curved, flat, and paddle-like, with setation heavily modified into bristle-combs, telotarsi with two rows of long setae on ventral surface, claws long, asymmetrical, and weakly curved; tibial spurs highly reduced, tarsal spurs well-developed, with complex armature (bifurcate, with setae and spines). Sternites with spiracles slit-like; V without a well-defined smooth patch. Metasoma slender, sparsely hirsute with long macrosetae, with carination present but dorsal carinae partly reduced; dorsal lateral and lateral supramedian carinae of segments I–IV with 1–2 conspicuously enlarged posterior terminal denticles; ventral lateral carinae of segment V flared, with sharp denticles; intercarinal spaces rather smooth. Telson extremely elongate, subaculear tubercle absent.

**COMMENTS.** In 1983, Victor Fet shared an unpublished description of this new genus and species with Nikolay Vasilyev (Gorky, Russia). In the following year, Orlov & Vasilyev (1984) published (in Russian) this description and figures in their key to the scorpions of the USSR. This was done in good faith and under Fet's name as the author, but without his knowledge and with several errors. A formal description was published by Fet (1987) in Russian and appeared in English translation in 1988.

There is a confusion in the literature regarding the composition of the type specimen series and its accession numbers. The work of Orlov & Vasilyev (1984) does not mention type specimens. The original paper by Fet (1987, in Russian) lists only four ZISP specimens, all collected in Repetek in 1974: male holotype (collected 16 October 1974, with 43–43 pectinal teeth), and three paratypes (two females, 23 April 1974; one female, 16 June 1974). Fet (1987) did not assign any ZISP accession numbers to the type series. In the English translation of the same paper (Fet, 1988, by an anonymous translator with a rather poor knowledge of scorpion morphology), one of the paratypes was not mentioned (the female, 16 June 1974, with 45–46 pectinal teeth) although its morphometrics were listed on p. 25. Later, Fet (1989: 119; reproduced in Fet & Lowe, 2000: 213), using unpublished data, listed the ZISP type series accession numbers as ZIN–1795 (holotype), ZIN–1796 (two females, 23 April 1974), and ZIN–1797 (one female, 16 June 1974). At the same time, Fet (1989: 119) erroneously added, as a part of paratype series, a new

juvenile specimen (our current neotype), collected by himself (V. F.) in Repetek on 21 July 1985. Fet (1989) labeled this specimen as ZM–Tb–357, which indicated his intention to deposit this scorpion to ZMMSU (Moscow). This, however, was never done since V.F. emigrated to the USA in March 1988. The absence of any *P. birulai* specimens in ZMMSU was confirmed for us by Dr. Kirill Mikhailov (ZMMSU) in 2019. The label of the current juvenile male neotype (in V.F.'s handwriting, Fig. 3) says, in Russian, “ZIN–1796, *Pectinibuthus birulai* Fet, 1987 Turkm. SSR, Repetek, 21.07.1985 (V. Ya. Fet)”. The same accession number was assigned in Fet (1989) to two female paratypes collected 23 April 1974. Since the 1974 type series cannot be found, the only reasonable solution is to keep the 1985 neotype label under its current number, ZISP–1796, in the ZISP collection.

The neotype specimen has been loaned from ZISP and studied by W. David Sissom (Texas, USA) who corrected the original statement of Fet (1987) regarding neobothriotaxy (missing trichobothria) and confirmed that the species is orthobothriotaxic (see our Figs. 13, 15–17, 19). This information on *Pectinibuthus* was included in a brief comparative survey of psammophile genera of Asian deserts published by Capes & Fet (2001) and Fet, Capes & Sissom (2001).

**DISTRIBUTION:** ASIA. Turkmenistan: East Karakum desert. Known only from the type locality.

### **Pectinal tooth count (PTC) as an ecomorphotypic character**

*Pectinibuthus birulai* displays several distinctive characters that closely match the psammophilous or ultrapsammophilous ecomorphotype (Prendini, 2001): #1) long, slender legs; #2) strong compression of leg I–III tibiae, basitarsi and telotarsi; #3) leg I–III tibiae and basitarsi with retrosuperior and retroinferior series of macrosetae forming expansive bristle-combs; #4) unguis elongate, almost as long as telotarsus; and #5) a slender, elongate metasoma and narrow telson. These features can be understood as functional adaptations to life on sandy substrates. Character #1 presumably improves accuracy of prey localization by the sensing of surface waves in soft sand (Brownell, 1977). Longer legs increase the diameter of the circle formed by 8 basitarsal compound slit sensilla, producing longer delays of signal arrival between tarsi. This may optimize the response of neurons tuned to detect input delays (Brownell & Farley, 1979). Characters #2 – #4 together serve to increase the area of substrate contact of tarsi, which is presumed to increase traction during movement on sand (Fet et al., 1998). Character #5) is shared with a number of other psammophilous scorpions. For example, in the buthids *Apistobuthus* Finnegan, 1932, *Buthacus* Birula, 1908 and *Vachoniolus* Levy et al., 1973 the metasoma is quite elongate and the telson vesicle is small with a long aculeus (Kovařík et al., 2016b; Lowe, 2010, Lowe et al., 2019; Navidpour & Lowe, 2009). The psammophilous vaejovid, *Vejovoidus longiunguis* (Williams, 1969), also has a slender metasoma and the telson is remarkably elongated. This was hypothesized to be a

		<i>Pectinibuthus birulai</i>
Dimensions (MM)		juv., neotype
Carapace	L / W	2.451 / 2.532
Mesosoma	L	5.281
Tergite VII	L / W	1.408 / 2.373
Metasoma + telson	L	14.045
Segment I	L / W / D	1.795 / 0.940 / 0.924
Segment II	L / W / D	2.120 / 0.838 / 1.014
Segment III	L / W / D	2.188 / 0.813 / 0.905
Segment IV	L / W / D	2.612 / 0.754 / 0.787
Segment V	L / W / D	2.578 / 0.641 / 0.750
Telson	L / W / D	2.752 / 0.596 / 0.495
Pedipalp	L	8.431
Femur	L / W	2.279 / 0.433
Patella	L / W	2.487 / 0.676
Chela	L	3.665
Manus	W / D	0.517 / 0.591
Movable finger	L	2.202
<b>Total</b>	<b>L</b>	<b>21.777</b>

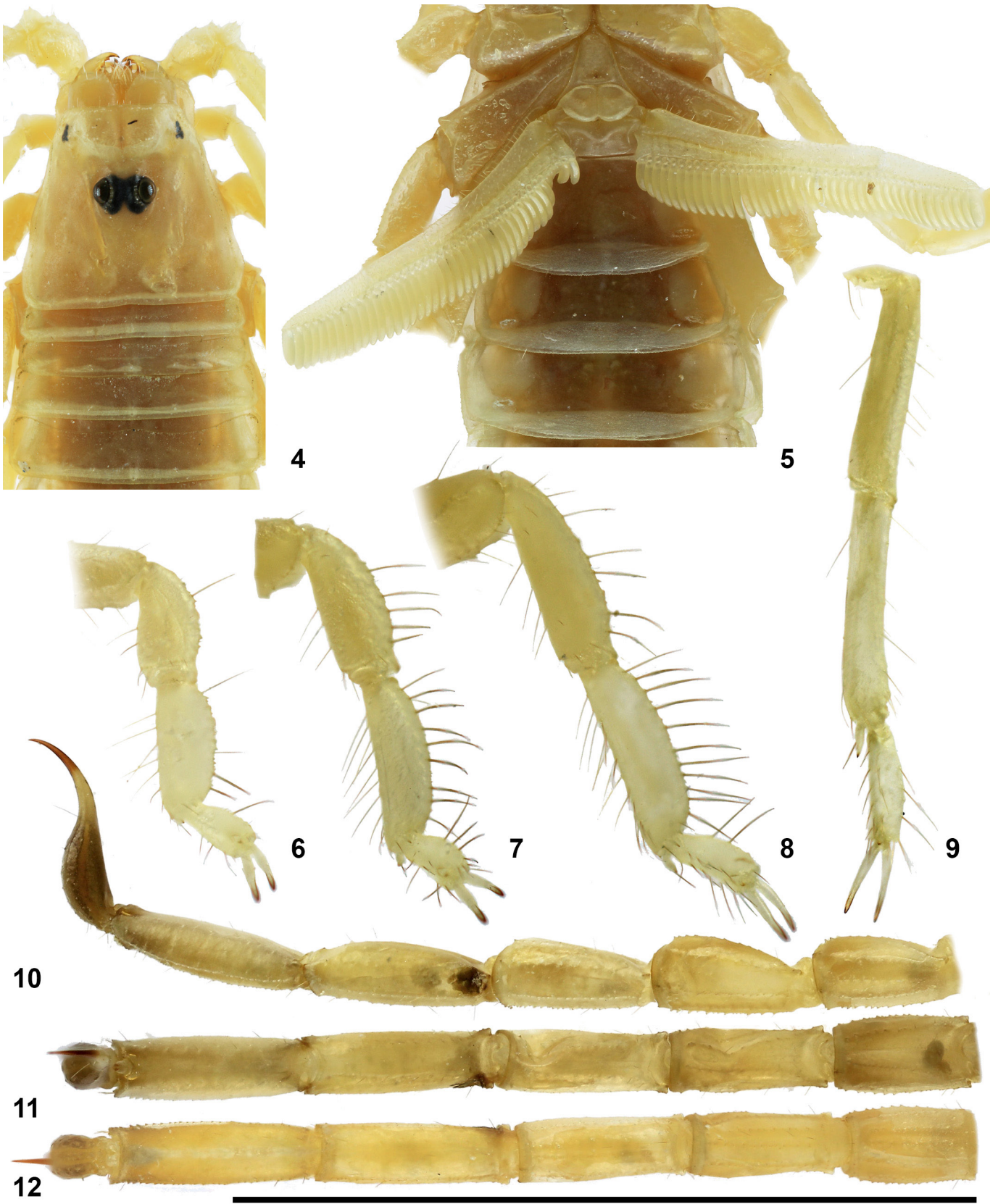
**Table 1.** Comparative measurements of *Pectinibuthus birulai* neotype. Abbreviations: length (L), width (W, in carapace it corresponds to posterior width), depth (D).

streamlining adaptation for movement when the animal is covered by sand, a likelihood in aeolian dunes (Williams, 1969).

The genus *Pectinibuthus* owes its name to the long pectines whose combs bear an unusually large number of teeth compared to most other buthids. A high PTC has also been recorded in several other psammophilous scorpions, e.g. *Apistobuthus pterygocercus* Finnegan, 1932, *A. susanae* Lourenço, 1998, *Plesiobuthus paradoxus* Pocock, 1900 and *Brachistosternus multidentatus* Maury, 1984 (the latter species also acquiring its name from this character). We therefore asked whether this could be another character of the psammophilous ecomorphotype. The definition of high PTC is complicated by Soleglad's Law which describes an allometric scaling relation of PTC with respect to body size. The exponent and scale factor in the power law can vary between sexes, and between different taxonomic groups (Kovářik et al., 2015, 2016a; Soleglad, 1973; Soleglad & Fet, 2003), so magnitude of PTC must be evaluated in the context of body size, sex and phylogenetic position. Lowe & Kovářik (2019) approached this by generating logarithmic scaling plots of PTC vs. carapace length for specific groups. The PTC scaling plots are typically rather broad, with points scattered above

and below the mean regression line. Taxa that were positioned consistently above the regression line were considered to have higher PTCs, and those that fell below it to have lower PTCs. Here, we apply this criterion to PTCs of psammophilous taxa.

Fig. 22 shows a logarithmic plot of PTC vs. carapace length (CL) for a sample of 815 male buthids encompassing all major genera and most described species (ca. 70%; gray symbols). The gray line is the corresponding fit by linear least squares regression, with slope, intercept and Pearson's correlation coefficient (R) indicated. The slope is the power law exponent,  $b$ , and the intercept the logarithm of the constant scale factor,  $a$ , in the allometric equation:  $PTC = a \cdot (CL)^b$ . On this plot, psammophilous buthids (*Anomalobuthus* 4 spp., *Apistobuthus* 2 spp., *Buthacus* 20 spp., *Parabuthus* 1 sp., *Pectinibuthus* 1 sp., *Vachoniolus* 4 spp.) are highlighted as orange symbols. Most orange symbols are positioned above the main (gray) regression line, showing that male psammophilous buthids are mostly characterized by high PTCs relative other male buthids. The linear regression fit to the psammophiles (orange line) is nearly parallel to the gray line (i.e., has the same exponent) but is displaced above it (i.e., a higher intercept and hence higher PTC). The same analysis applied to female buthids (Fig. 23) showed that essentially



**Figures 4–12:** *Pectinibuthus birulai*, neotype juvenile, chelicerae, carapace and tergites I–IV (4), sternopectinal region and sternites III–V (5), distal segments of legs I–IV (6–9), retrolateral view, and metasoma and telson, lateral (10), dorsal (11), and ventral (12). Scale bars = 10 mm (10–12).





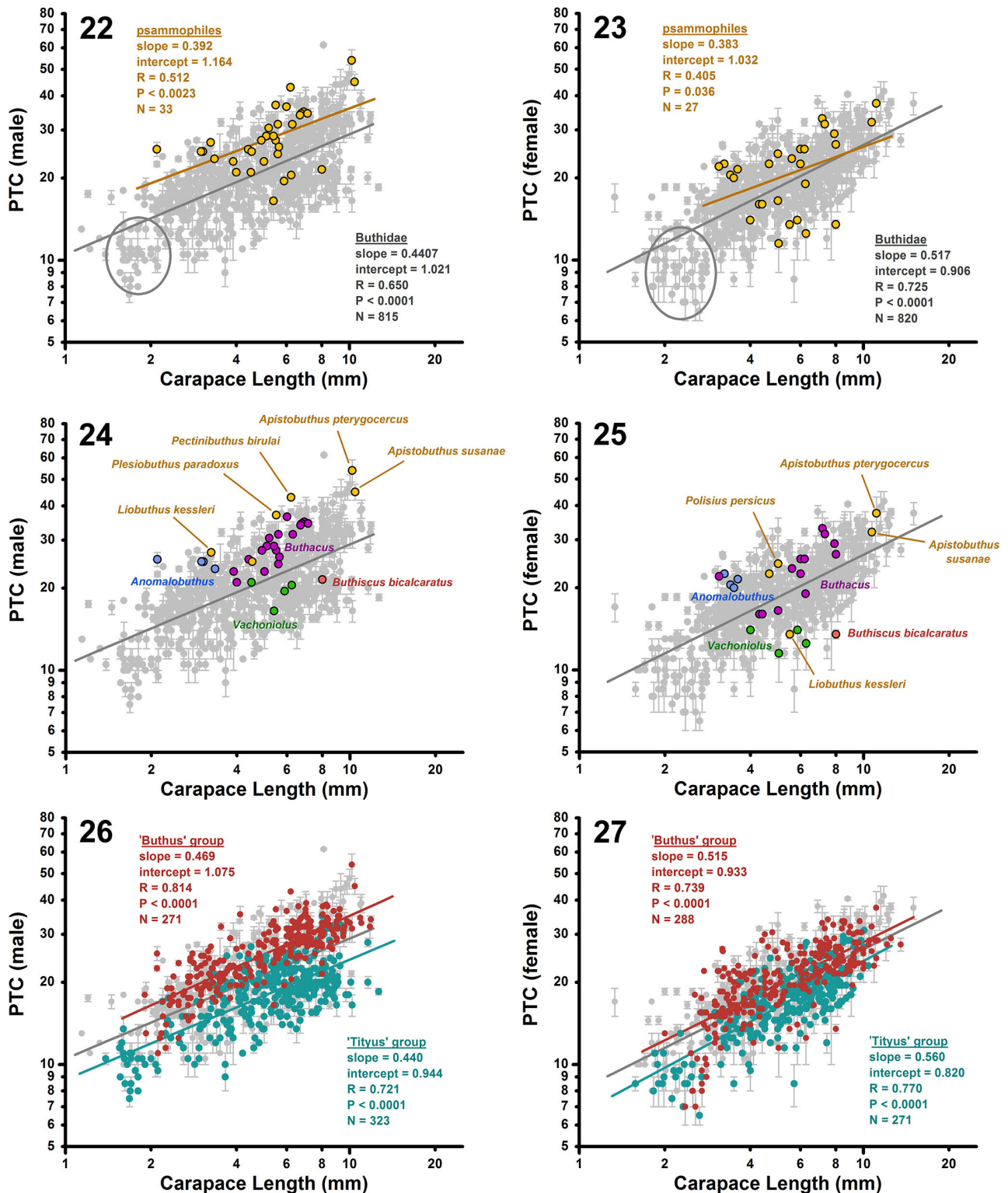
**Figures 13–21:** *Pectinibuthus birulai*, neotype juvenile, pedipalp segments. Pedipalp chela dorsal (13), external (14), and ventral (15) views, patella dorsal (16), external (17) and ventral (18) views, femur and trochanter dorsal (19) and ventral (20), movable finger (21). The trichobothrial pattern is indicated in Figures 13, 15–17, 19.

the same set of psammophilous species was split nearly equally above and below the gray line (regression line for a sample of 820 female buthids). The orange line had slightly shallower slope and was close to and intersected the gray line. Thus, psammophilous male, but not female, buthids have higher average PTCs as a group. Figs. 24 and 25 show the positions of different genera or species of psammophiles on the scatter plots. In males, most ultrapsammophilous species (orange and blue symbols) were placed near the upper limits of the distribution, and all male *Buthacus* were located above the gray line. Most species on or below the gray line belong to the Arabian psammophile genus *Vachoniolus*, which is characterized by unusually low PTCs (Lowe, 2010). The other low PTC species was the Algerian psammophile, *Buthiscus bicalcaratus* Birula, 1905, whose males bear a swollen pedipalp manus, similar to males of *Vachoniolus*. It is curious that these two genera exhibit strong sexual dimorphism in their

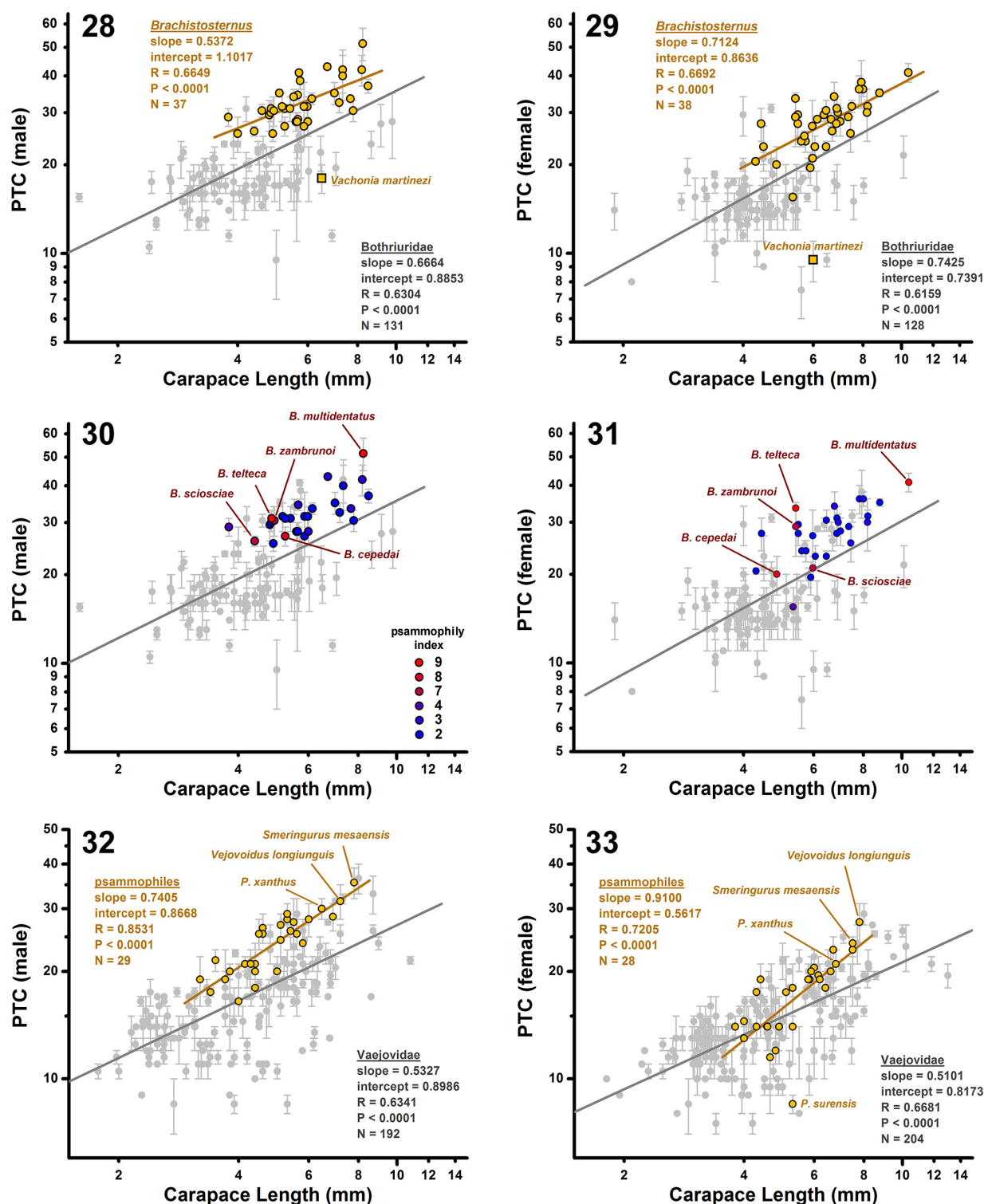
pedipalp chelae, but not in the high PTC condition that exists in other psammophile buthids. In Fig. 25, we see that among females, the ultrapsammophiles and many *Buthacus* spp. do sit above the gray line, so they have relatively high PTCs. Thus, if we restrict attention to these ultrapsammophilous species, and the more psammophilous members of *Buthacus*, then high PTC becomes an ecomorphotypic character, that in males is more pronounced due to sexual dimorphism.

Can high PTC be understood as a functional adaptation to life on sandy substrates? The musculature and innervation of pectines suggested to Brongniart & Gaubert (1891) a tactile substrate-sensing function. About pectines, Pocock (1893) wrote: “it is highly probable that they are useful organs of touch .... enabling their possessor to learn the nature of the surface over which it is walking”. More recently, Gaffin & Brayfield (2017) hypothesized that scorpion navigation is guided primarily by tactile and olfactory cues associated

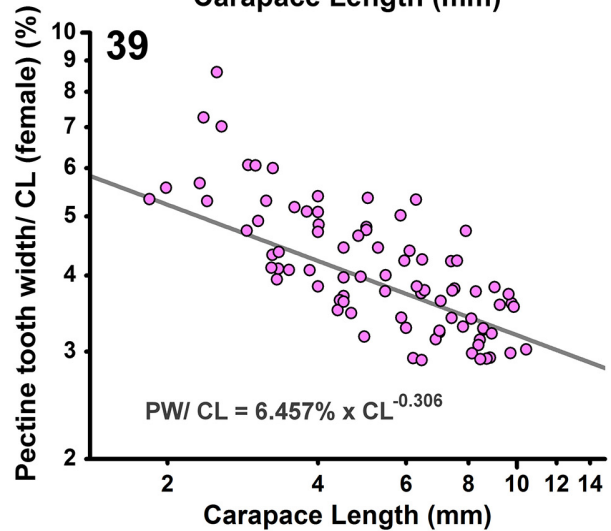
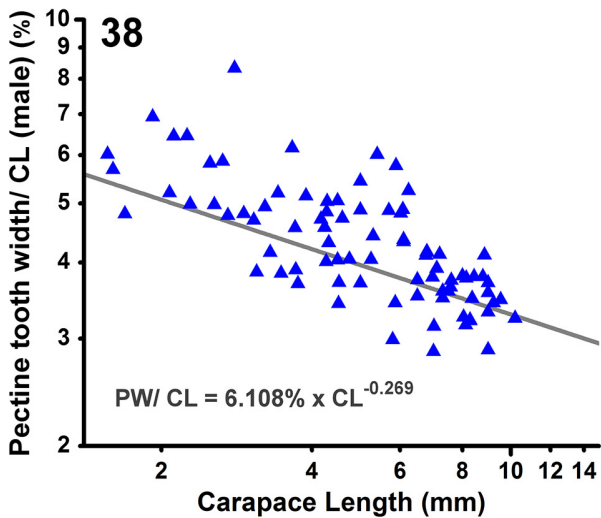
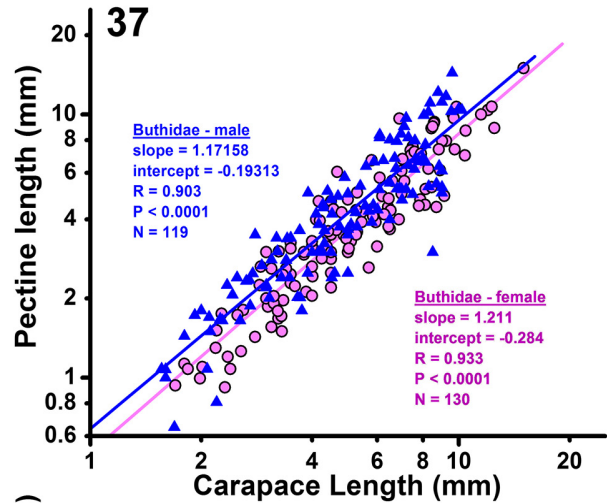
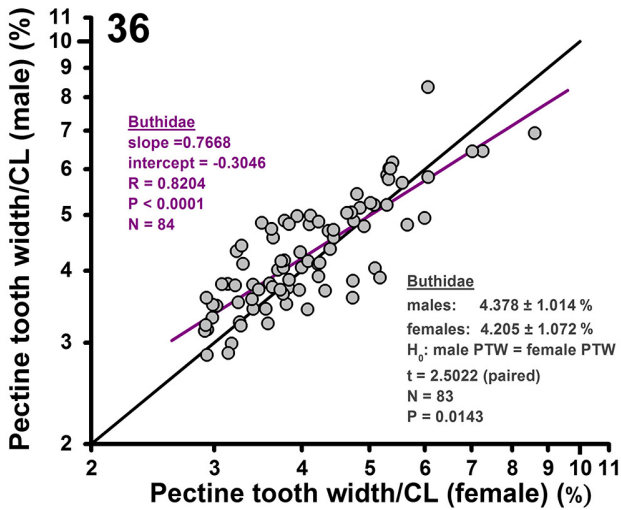
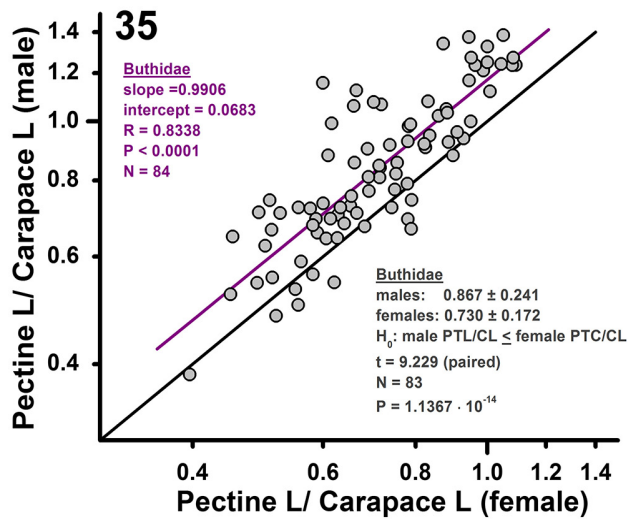
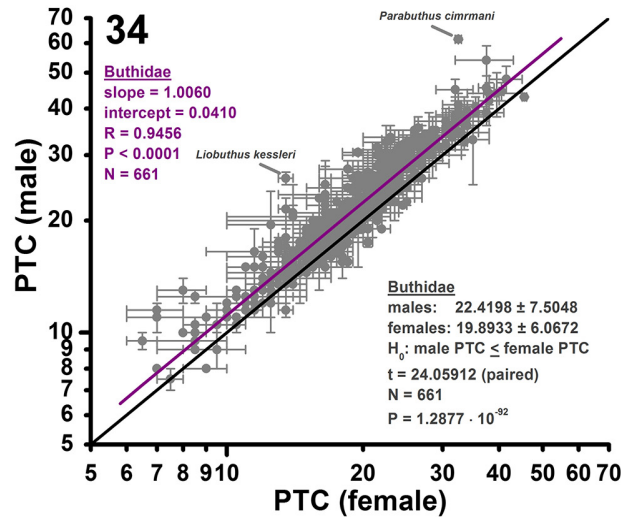




**Figures 22–27: Biometric scaling of pectinal tooth count (PTC) in buthid scorpions. Figures 22–23:** Logarithmic scatter plots of PTC vs. carapace length for 815 species of male buthids (22) and 820 species of female buthids (23). Gray symbols are mid-range PTCs of individual species, vertical error bars the ranges (minimum, maximum). Gray line is linear least squares regression of log variables, with slope, intercept, Pearson's correlation coefficient (R), P value and sample size indicated in the lower right. Gray elliptical areas on lower left indicate that most very small buthids have below average PTCs. Orange symbols highlight psammophile buthids belonging to 8 genera, orange line is regression fit to psammophiles; fit parameters are indicated in the upper left. **Figures 24–25:** Logarithmic scatter plots of buthids in Figs. 22–23 shown with different psammophile taxa highlighted by colored symbols. **Figures 26–27:** Logarithmic scatter plots of buthids in Figs. 22–23 shown with two different major clades highlighted by colored symbols and regression lines. Red: 'Buthus' group; Blue: 'Tityus' group. Corresponding fit parameters are indicated in the upper left and lower right.



**Figures 28–33:** Biometric scaling of pectinal tooth count (PTC) in bothriurid (28–31) and vaejovid (32–33) scorpions. **Figures 28–29:** Logarithmic scatter plots of PTC vs. carapace length for 131 species of male bothriurids (28) and 128 species of female bothriurids (29). Gray symbols, error bars and regression line as in Figs. 22–23, but representing the bothriurids. The psammophile genus *Brachistosternus* (38 spp.) is represented by orange circles and regression line. The orange square represents the psammophile, *Vachonia martinezi*. Corresponding fit parameters are indicated in the upper left and lower right. **Figures 30–31:** Logarithmic scatter plots of bothriurids in Figs. 28–29 shown with a subset of 30 *Brachistosternus* species highlighted by colored symbols coding for the psammophily index of Ojanguren–Affilastro et al (2016) (color key shown in lower right of Fig. 30). **Figures 32–33:** Logarithmic scatter plots of PTC vs. carapace length for 192 species of male vaejovids (32) and 128 species of female vaejovids (33). Gray symbols, error bars and regression line as in Figs. 22–23, but representing the vaejovids. The psammophile taxa *Paruroctonus* (29 spp.), *Smeringurus mesaensis* and *Vejovoidus longiunguis* are represented by orange circles and regression line. Corresponding fit parameters are indicated in the upper left and lower right.



**Figures 34–39:** Sexual dimorphism of pectinal biometrics and size scaling of pectine tooth width in buthid scorpions. **Figures 34–36:** Sexual dimorphism of PTC (34), pectine length/ carapace length (35) and estimated pectine tooth width/ carapace length (36) shown in male vs. female logarithmic scatter plots. Regression lines are purple, with corresponding fit parameters in the upper left. Parameters and results of hypothesis testing (paired t-test) of sexual dimorphism (means, null hypothesis, t value, sample size, P value) in the lower right. Estimated pectine tooth width = pectine length/ PTC. **Figures 37–39:** Size scaling of pectine tooth width. **Figure 37.** Logarithmic scatter plot of pectine length vs. carapace length for male (119 species; blue symbols and regression line) and female (130 species; pink symbols and regression line). Corresponding fit parameters are indicated in the upper left and lower right. **Figures 38–39.** Logarithmic scatter plots of pectine tooth width vs. carapace length for 83 species of male (38) and female (39) buthids. Gray lines are estimated buthid scaling relations obtained from the ratios of regression lines of Fig. 37 to the regression lines of Figs. 22–23, divided by carapace length (allometric equations indicated in gray).



with the substrate. They suggested that information about the physical texture and spatial patterns of substrate-bound chemical stimuli is captured when pectinal combs are swept over the substrate. During forays away from its burrow, a scorpion may store this sensory data in memory in a timestamped format, as a historical record of its path. This could be the basis for a homing system allowing the animal to find its way back to its burrow. A single pectine tooth was proposed to be the elementary spatial encoding unit for texture mapping, analogous to a pixel in a digitized visual image. We also considered that a single tooth may function as a pixel for scanning pheromone trails, in a discussion of the possible significance of Sologlad's Law (Kovářik et al., 2016a). If this is the case, then the resolution of substrate stimulus perception will be related to the number of pectine teeth per comb. To test this hypothesis, we compared PTCs of taxonomic groups of scorpions with different ecological niches and substrate preferences. Fig. 26 shows the PTC–CL allometric scaling plot of male buthids, in which we color-highlighted two major clades (Fet et al., 2005). The ‘Buthus’ group, comprising a dominant scorpiofauna of Palaearctic deserts, has relatively higher PTCs (red symbols). The corresponding regression line (red) runs parallel, and is shifted upwards relative to the overall buthid regression line (gray). The ‘Tityus’ group, comprising mostly Neotropical taxa, has relatively lower PTCs (blue symbols). The regression line (blue) runs parallel, and is shifted downwards from the gray line. These results agree with a prediction of the Gaffin-Brayfield hypothesis, that scorpions inhabiting more finely granular substrates, such as loose sand, sandy soils, and weathered rocks of desert environments, would evolve pectines with more dense arrays of teeth, enabling higher resolution texture perception. Indeed, the highest PTCs belong to the ultrapsammophiles (Figs. 24–25), all members of the ‘Buthus’ group that live on soft aeolian sands, the most finely textured of terrestrial surfaces. In contrast, humid, tropical forest microhabitats of many ‘Tityus’ group scorpions probably have smoother substrates than deserts (e.g., humus, leaf litter, moist logs, foliage, tree trunks, etc.), and this correlates with their lower PTCs. In females (Fig. 27), the ‘Buthus’ group PTCs were not significantly higher than the average trend, similar to female psammophiles (Fig. 23) which all belong to the ‘Buthus’ group. However, female ‘Tityus’ group were similar to males in having lower PTCs. Apparently, the ecomorphotypic sexual dimorphism is not expressed in all phylogenetic groups. This could reflect differences in behavior or pheromone tracking strategies by males in different environments.

Another example of ecological correlation of buthid PTCs can be found in the Madagascar genera *Grosphus* Simon, 1880 and *Teruelius* Lowe & Kovářik, 2019. We showed previously that *Teruelius* has higher PTCs, and *Grosphus* lower PTCs, based on Sologlad's Law scaling plots of the buthids (Lowe & Kovářik, 2019: 18, figs. 32–35). Most *Teruelius* species are distributed across the more arid southwestern regions of Madagascar, and many *Grosphus* species occur in humid, tropical northern and eastern regions.

Thus, the ecomorphotypic dichotomy of PTCs described here for ‘Buthus’ vs. ‘Tityus’ groups is directly mirrored in a pair of unrelated taxa from a different biogeographic region, further supporting a texture perception model.

Does substrate texture perception predict PTC scaling trends in non-buthid scorpions? In Figs. 28–29, we show PTC–CL scaling plots for 131 male and 128 female bothriurids (gray symbols and regression line; ca. 82% of described species). On this plot, the psammophilous genus *Brachistosternus* Pocock, 1893 (orange circles and regression line) is positioned well above the gray line for all males and nearly all females. A single psammophile outlier is the peculiar genus *Vachonia* (orange square symbol), with very low PTCs in both sexes, reminiscent of the outliers *Vachoniolus* and *Buthiscus* among buthids. In Figs. 30–31, we use color mapping (blue to red) to show values of the ‘psammophily index’, a numerical measure of sand adaptation based on pigmentation and tarsal characters that was used by Ojanguren-Affilastro et al (2016) in their phylogenetic study. Although this index does not seem well correlated overall with vertical deviation from the gray line, we note that the ultrapsammophiles (*B. multidentatus* and *B. telteca* Ojanguren Affilastro, 2000, index = 9) do exhibit the highest relative PTCs. Both male and female *Brachistosternus* species have average PTCs higher than the overall means (orange lines above gray lines). This differs from the sexual dimorphism of psammophile buthids (Figs. 22–23), further demonstrating phylogenetic variation in this trait. In Figs. 32–33, we show the PTC–CL scaling plots for 192 male and 204 female vaejovids (gray symbols and regression line; including ca. 90% of described species). The psammophiles (orange symbols and line) include all *Paruroctonus* Werner, 1934 species, and two others: *Smeringurus mesaensis* (Stahnke, 1957), *Vejevovoidus longiunguis*. In the male plot, most psammophiles are placed well above the gray line, as is their orange regression line. The distribution of females is different, with a steeper slope (= higher exponent) due to high PTCs for larger species and average PTCs for smaller species. A female outlier was the very low PTC in *Paruroctonus surensis* Williams & Haradon, 1980, a species with strong sexual dimorphism of pectines. These data indicate complex relationships for elevated PTCs in psammophiles of different phylogenetic groups, sexes and body sizes. Although a major factor, perception of substrate texture is probably not the sole determinant of pectinal tooth count. The smallest buthids (carapace length < ca. 2 mm; e.g., *Femtobothus* Lowe, 2010, *Microbothus* Kraepelin, 1898, *Microcharmus* Lourenço, 1995, *Microtityus* Kjellesvig-Waering, 1966, *Picobuthus* Lowe, 2010) have PTCs of ca. 10 or less, and these mostly fall below the main regression line, as indicated by the elliptic area drawn in lower left of plots of Figs. 22–23. A pectinal sensor grid with so few elements has limited spatial resolution, and pectines of tiny buthids might not be used for stimulus texture coding.

Although scorpion taxonomists are anecdotally familiar with sexual dimorphism of PTCs, objective quantitative analyses have not been published, except for a few species (e.g., Brown, 1996; Francke & Jones, 1982). In Fig. 34, we

show a scatter plot of male PTC vs. female PTC for 661 species of buthids. Most points sit above the black diagonal line, confirming that males tend to exhibit higher PTC than females. The regression line (purple) is parallel to, and above the diagonal line. On the plot we labeled two interesting species with pronounced sexual dimorphism among buthids: *Liobuthus kessleri*, an ultrapsammophile with typically high PTC in males (Fig. 24), but remarkably low PTC in females (Fig. 25) (Vachon, 1958); and *Parabuthus cimrmani* Kovařík, 2012, a species of unknown ecology, whose males exhibit the highest PTC of any known scorpion (Kovařík, 2004). In a paired t-test, male buthid PTC exceeded female buthid PTC with very high statistical significance. PTC distributions deviated from normality, so we confirmed the result by non-parametric tests ( $P < 0.0001$ , medians: ♂ 29, ♀ 25; Mann-Whitney  $U = 46260.5$ ,  $U' = 18255.5$ ; paired Wilcoxon signed-rank  $T = 490.5$ ). Males also typically bear relatively longer pectines than females. In Fig. 35, pectine lengths of 83 species are normalized to carapace length and the sexes are compared in a male vs. female scatter plot. Again, most points are above diagonal, as is the regression line, and the dimorphism was statistically highly significant. Does sexual dimorphism of pectine length explain sexual dimorphism of PTC, i.e. are individual teeth of similar width for both sexes, and males merely have more because their combs are longer? This is indeed the case. In Fig. 36, pectine widths, estimated by dividing PTCs into measured pectine lengths, are expressed as a percentage of carapace length, and the sexes are compared in a male vs. female scatter plot. The points are arranged mainly about the diagonal line, and no clear sexual dimorphism is apparent. A statistical test indicated males may have slightly wider teeth than females (male teeth are usually longer), although the significance level was weak. Both pectine length and width data sets analyzed here passed Anderson-Darling normality tests ( $P > 0.05$ ). Sex invariance of tooth width implies that the texture-sensing resolution is similar in the two sexes. This is certainly consistent with the fact that they share the same habitat.

Kovařík et al. (2016a) remarked that values of buthid scaling exponents (estimates revised here as 0.4407 in males, 0.517 in females; i. e., approximately a square root power law) implied that as carapace length increases, pectine teeth do not remain at a fixed size, but increase in width. However, this increase is slower than body size increase, i.e., less than direct proportionality. It was suggested that larger scorpions may require a somewhat finer spatial encoding of substrate features than smaller scorpions, relative to their absolute body size. This assumes isometric scaling of pectine length with carapace length and body size. To test this assumption, we plotted pectine length vs. carapace length (Fig. 37). The regression slopes of both sexes exceeded unity (1.1716 in males, 1.211 in females), showing that pectines of large scorpions are slightly longer than expected from simple isometric scaling. We divided the fitted power laws in Fig. 37 by the power laws in Figs. 22–23 to estimate how pectine tooth width actually varies as a function of carapace length. There was a steady reduction in average relative width, from ca. 6% of carapace length in the smallest scorpions to ca. 3% in the largest scorpions (gray lines in Figs. 38–39). This shows that large scorpions could resolve about twice the relative spatial detail of small scorpions. The scatter

plots in Figs. 38–39 are actual data showing the trend for 83 species. The points are distributed slightly higher than the gray lines derived from all buthids. This may reflect the bias of a small sample bias because pectine lengths for both sexes were seldom reported in species descriptions ( $< 10\%$  of the total sample, mainly from the publications of L. de Armas, M. A. González-Sponga and G. Lowe).

The need for an effective long-range homing mechanism in desert scorpions was appreciated by one of us (G. L.), on an expedition to the Rub' al-Khali (Empty Quarter) in Oman. During nocturnal UV detection, a large adult *Apistobuthus pterygocercus* was observed perched on a steep dune slope, consuming a scarabaeid beetle (Ramlat Muqshin, 19°30.86'N 54°36.71'E, 195 m a.s.l., 6.X.1994). The footprints that it left in soft fine sand were traced back to its home burrow entrance, a crescent-shaped opening at the base of a small bush. The integrated distance between scorpion and burrow was estimated to be ca. 50 m, roughly 550 body lengths. Suppose that pectine combs acquire sequential one-dimensional images or scenes of substrate texture and odor profile, and that the longitudinal span of each snapshot is the length of the sensillar surface of a pectine tooth (ca. 0.5 mm in an adult female *A. pterygocercus*). A continuous 50 m track will be segmented into a maximum of  $50 / 0.0005 = \sim 100,000$  non-overlapping images. With 50 teeth per comb, there will be 100 pixels per image, and approximately 10 million pixels in the entire record. Each pectine tooth bears tens to hundreds of peg sensillae each containing about a dozen sensory neurons (Wolf, 2008) that transduce either olfactory or tactile stimuli (Gaffin & Brownell, 1997; Gaffin & Walvoord, 2004; Hoffmann, 1964). Additional, potentially topographic mechanosensory input derives from numerous macrosetae covering marginal and middle lamellae, and fulcra. Pectinal primary afferents project to a complex neuropil in the subesophageal ganglion with heterogeneous glomerulus-like structures (lobuli), laminar organization, and a somatotopic mapping of comb teeth (Brownell, 1998; Wolf, 2008, 2017). The anatomy suggests multidimensional coding of substrate scenes via multiplexing of parallel olfactory and tactile inputs. This will increase afferent bandwidth, placing higher demands on neural circuits to store and retrieve data in a Gaffin-Brayfield model of homing navigation. We suggest that this could be avoided by a much simpler homing mechanism. Instead of memorizing fine texture and odor details of the entire path, *Apistobuthus* merely needs to use its pectine tactile senses to feel and recognize its own tracks made in the sand, and follow them back to its burrow, as was done by a human arachnologist using vision. This hypothesis can be tested directly by infrared study of psammophile behavior in the field. Obviously, only sand scorpions can do this, but they are the species with highest PTCs. Regardless of homing algorithm, the high PTCs of psammophiles probably provide benefits of high resolution substrate perception.

## Biogeography

The dynamic biogeographic history of Central Asian sand deserts likely had a profound impact on the diversification of numerous psammophilic animal taxa, including remarkable scorpion genera *Anomalobuthus* Kraepelin, 1901 and *Liobuthus* Birula, 1898 (Graham et al., 2012; Teruel et al., 2018) as well as psammophile species of *Mesobuthus* (Fet et al., 2018). The fauna, flora and geology of the sand deserts of Turkmenistan have been thoroughly studied (Fet & Atamuradov, 1994) but most of the literature was published in Russian, thus remaining largely inaccessible to the global research community. The most comprehensive biogeographic review was published for Coleoptera (Kryzhanovsky, 1965), while the remaining data on the fauna and biogeography of Central Asia are scattered in Russian journals as dozens of papers covering specific taxa and regions. After the demise of the USSR in 1991, the rate and quality of zoological research from the region has decreased markedly. Our research group and its collaborators were the first to use molecular phylogenetics (based on mitochondrial DNA sequence data) to study the biogeography of scorpions from the Central Asian deserts (Graham et al., 2012; Fet et al., 2018). The first DNA-based analysis of Graham et al. (2012) confirmed that both great waterways of Central Asia, especially Amu Darya and (in part) Syr Darya, acted as biogeographic barriers in vicariant speciation of *Anomalobuthus*. Our most recent DNA-based revision of the “*Mesobuthus caucasicus* complex” (Fet et al., 2018) revealed existence of diverse species across the deserts of Central Asia, again with Amudarya as an important boundary. This is also relevant in the case of *Pectinibuthus*, which is so far only south of Amu Darya, and represents the only endemic scorpion genus in the East Karakum. Morphologically, this unique genus most resembles the sympatric *Anomalobuthus*, and a future DNA study will hopefully reveal whether this resemblance is due to phylogenetic affinity or to convergent evolution of psammophile habitus.

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Incidentally, the neotype was the first scorpion specimen in the USSR (and Central Asia) collected with the help of a blacklight. This old Coleman Safari unit, a precious gift to V.F. by Gary Polis (who used it in Baja California), has traveled from Nashville, Tennessee to Aidere, Turkmenistan in 1985, kindly hand-carried via Germany by Sergei Golovatch and via Russia by Nadezhda Skalon.

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