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## A NEW SPECIES OF *EUSCORPIUS* FROM TINOS ISLAND, GREECE (SCORPIONES: EUSCORPIIDAE)

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**Abstract:** The scorpion genus *Euscorpius* has been insufficiently studied on the Aegean Islands of Greece. We describe a new species from the Western Cyclades, *E. kritscheri* sp. n., from Tinos Island. The species-level status of this form is confirmed by a phylogenetic study based on multiple DNA markers. In addition, a population from nearby Andros Island is characterized as *E. cf. kritscheri*, which could be potentially a separate species

**Key words:** Scorpiones, Euscorpiidae, *Euscorpius kritscheri*, sp. n., Tinos Island, Cyclades, Greece.

### Una especie nueva de *Euscorpius* de la isla de Tinos, Grecia (Scorpiones: Euscorpiidae)

**Resumen:** El género *Euscorpius* está insuficientemente estudiado en las islas egeas de Grecia. Se describe una especie nueva de las Cícladas occidentales, *E. kritscheri* sp. n., de la isla de Tinos. Se confirma el estatus específico de esta forma por medio de un estudio filogenético basado en marcadores de ADN múltiples. Por otra parte, se caracteriza una población de la cercana isla de Andros como *E. cf. kritscheri*, que podría resultar una especie diferente.

**Palabras clave:** Scorpiones, Euscorpiidae, *Euscorpius kritscheri*, sp. n., isla de Tinos, Cícladas, Grecia.

**Taxonomy / Taxonomía:** *Euscorpius kritscheri*, sp. n.

## Introduction

The total number of species belonging to the genus *Euscorpius* Thorell, 1876 in Greece, was recently raised to 11 (*E. avcii*, *E. candiota*, *E. corcyraeus*, *E. erymanthius*, *E. hadzii*, *E. koschewnikowi*, *E. italicus*, *E. naupliensis*, *E. ossae*, *E. scaber*, and *E. sicanus*) (Fet *et al.*, 2013; Tropea *et al.*, 2013). Our investigation of many populations from Greece using multiple DNA markers (Parmakelis *et al.*, 2013a) allowed revealing a diverse set of species, many of them undescribed. As part of the ongoing study, we describe here a new species from the western Aegean island of Tinos.

## Material and Methods

### Abbreviations

NHMW, Naturhistorisches Museum Wien, Vienna, Austria;

NMHC, Natural History Museum, University of Crete, Heraklion, Crete, Greece;

ZMB, Zoologisches Museum Berlin, Humboldt Universität, Berlin, Germany.

### Material Studied

We studied 12 specimens of *E. kritscheri* sp.n. from Tinos Island, and, in addition, 13 specimens of *E. cf. kritscheri* from nearby Andros Island. Detailed list of material with label data is given below.

### DNA Analysis and Species Validation

Validity of *E. kritscheri* sp.n., was supported by our molecular phylogenetic study of *Euscorpius* populations across

Greece (Parmakelis *et al.*, 2013a). All DNA work was performed in the University of Athens by P.K. and A.P. Several methods of species delimitation and a species validation method were employed in Parmakelis *et al.* (2013a) based on the phylogeny inferred using sequence data from one nuclear and three mtDNA loci.

For *E. kritscheri* sp.n., Parmakelis *et al.* (2013a) analyzed DNA markers of one specimen from Tinos. In a resulting phylogeny, the new species *does not* form a part of the traditional (nominotypic) subgenus *Euscorpius* s.str., therefore further confirming the latter's paraphyly (Tropea, 2013). In addition to Tinos, a specimen from Andros Island was also analyzed, which formed a sister clade to Tinos population (see Notes).

## Systematics

### *Euscorpius kritscheri* Fet, Soleglad, Parmakelis, Kotsakiozi et Stathi, sp. nov.

Fig. 1–16; Table I.

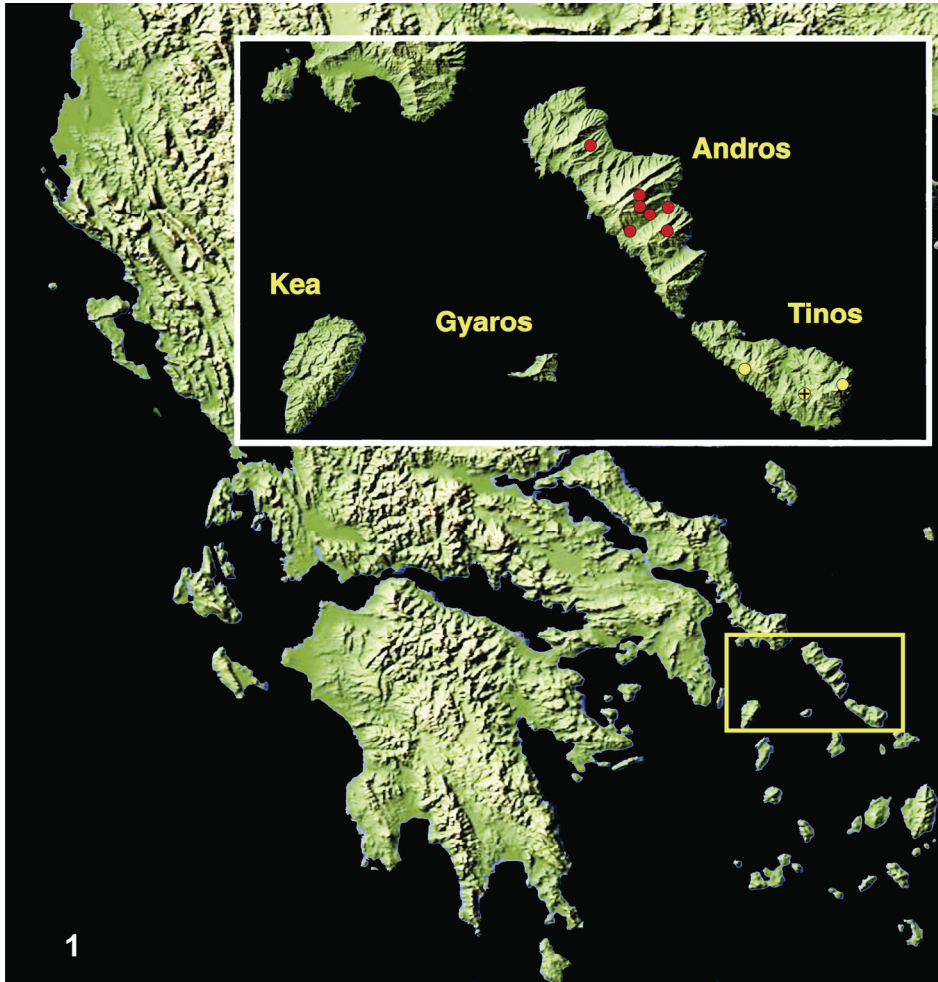
### REFERENCES:

*Euscorpius germanus*: Werner, 1902: 605 (in part: Tinos).

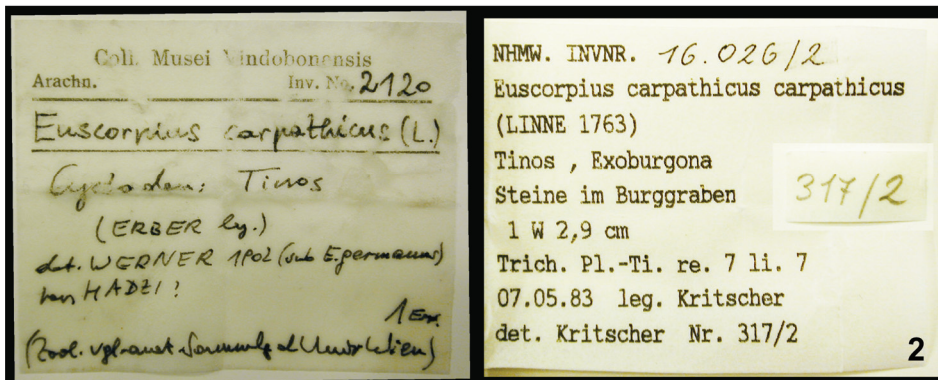
*Euscorpius germanus mingrelicus*: Kinzelbach, 1975: 27–28 (in part: Tinos).

*Euscorpius carpathicus carpathicus*: Kritscher, 1993: 384 (in part: Tinos), 387.

*Euscorpius carpathicus*: Stathi & Mylonas, 2001: 289 (in part: Tinos).



**Fig. 1:** Map showing known distribution of *Euscorpius kritscheri*, **sp. n.** on Tinos Island (yellow icons, type locality marked with '+'). Distribution of *Euscorpius* sp. specimens from Andros Island examined and discussed in this paper are also shown (red icons). Foreground map area showing Tinos and Andros Islands is indicated with a yellow box in background map of Greece.



**Fig. 2:** Original type series labels of *Euscorpius kritscheri*, **sp. n.** The label on the left is of a female paratype NHMW 2120, collected on Tinos in 1863 by J. Erber, and misidentified as *E. germanus* by F. Werner (1902). The label on the right is of the female holotype, collected on Tinos in 1983 by E. Kritscher, NHMW 16026/2.

**TYPE MATERIAL:** **Holotype** ♀, GREECE, *Central Greece*: Tinos Island, Exoburgo (“Exoburgon”, “Exoburgona”), 7 May 1983, leg. E. Kritscher (NHMW 16026/2). **Paratypes**: same label as holotype, 4 ♂, 1 ♀ im. (NHMW 16026/1, 16026/3-6); 1 ♀, Tinos (NHMW 2120); Tinos, road to Faneromeni Church, 12 January 1979, leg. M. Mylonas, 3 ♂ (NHMC, Eus80); Tinos, road Isternia to Kardiani, spring, 350 m, 26 September 2002, leg. S. Simaiakis, 2 ♂ (NHMC 4457, Eus63; used for DNA); Tinos, 1 ♀ (ZMB 15255).

**ETYMOLOGY.** Named after Erich Kritscher (1927–2010) (Vienna, Austria), a prominent Austrian zoologist who over many years of enthusiastic travels compiled one of the greatest museum collections of *Euscorpius* from Greek mainland and islands. See Sattmann & Hörweg (2011) for a detailed account of Dr. Kritscher’s life and work.

**GEOGRAPHIC RANGE.** Known only from Western Cycladic island of Tinos (see map on Fig. 1).

**HISTORY OF STUDY.** *Euscorpius* from Tinos are very rare in collections. Werner (1902: 605) misidentified a single specimen from Tinos as *E. germanus* (C. L. Koch, 1837), listing six pectinal teeth (*Dp*) and six ventral patellar trichobothria (*Pv*). Kinzelbach (1975: 27) mentioned this specimen as *E. germanus mingrelicus* (Kessler, 1874). Erich Kritscher (1993: 387) collected a series of specimens on Tinos in 1983, in the stone wall of the old Venetian fortress of Exoburgo. While Kritscher did not study Werner’s specimen, he doubted its placement and correctly suggested that the Tinos population belongs to “*Euscorpius carpathicus*” (i.e. modern subgenus *Euscorpius*). We found the specimen studied by Werner (1902) (♀, NMHW 2120, formerly from the collection of the

**Table I:** Morphometrics (mm) of *Euscorpium kritscheri*, sp. n. Exoburgo, Tinos Island, Greece \* Patella width is the widest distance between the dorsointernal and exteromedial carinae. \*\*DPS height is from tip of spine to dorsointernal carina centered. \*\*\* Measurement is an estimate.

	♀ Holotype (NHMW 16026/2)	♀ Paratype (NHMW 2120)	♂ Paratype (NHMW 16026/1)	♂ Paratype (NHMW 16026/5)
Total length	31.90	32.25	33.00***	30.05
Carapace length	4.95	4.45	4.55	4.30
Mesosoma length	11.75	13.60	11.85***	12.20
Metasoma length	11.30	10.60	12.15	10.20
Segment I: length/width	1.45/1.65	1.40/1.50	1.50/1.60	1.40/1.50
Segment II: length/width	1.80/1.45	1.65/1.30	1.95/1.45	1.55/1.35
Segment III: length/width	1.95/1.40	1.85/1.25	2.10/1.30	1.85/1.25
Segment IV: length/width	2.25/1.25	2.15/1.15	2.50/1.35	2.05/1.15
Segment V: length/width	3.85/1.35	3.55/1.20	4.10/1.35	3.35/1.25
Telson length	3.90	3.60	4.45	3.35
Vesicle length	3.15	2.70	3.65	2.55
width/depth	1.35/1.35	1.25/1.25	1.55/1.85	1.25/1.25
Aculeus length	0.75	0.90	0.80	0.80
Pedipalp length	16.80	16.20	16.35	14.10
Femur: length/width	4.00/1.50	3.90/1.45	3.90/1.40	3.40/1.40
Patella				
length/width*	4.15/1.60	4.00/1.45	4.00/1.60	3.65/1.50
DPS height**	0.50	0.45	0.50	0.40
Chela length	8.65	8.30	8.45	7.05
Palm length	4.65	4.55	4.45	3.80
width/depth	3.20/3.25	2.75/2.90	3.10/3.35	2.60/2.75
Fixed finger length	3.55	3.35	3.65	2.85
Movable finger length	4.85	4.85	4.95	4.00
Sternum: length/width	1.40/1.60	1.40/1.60	1.60/1.55	1.45/1.40
Pectines				
teeth	7/6	7/6	7/7	7/7
middle lamellae	4/3	7/3	4/4	3/4

Zoologisch-Botanischen Gesellschaft in Wien), identifiable by collector's name, Erber, on its label (Fig. 1). Werner (1902) mentions "leg. Erber", and the Austrian naturalist Joseph Erber (1824–1882) collected on Tinos in 1863 (Erber, 1868). This female, in fact, has  $Dp = 7/6$  and  $Pv = 7/7$ , miscounted by Werner (1902). Number of  $Pv$  (usually 7) and especially  $Dp$  (usually 7 in males and 6 to 7 females) is reduced in Tinos population, indeed overlapping with numbers in subgenus *Alpiscorpius*.

**DIAGNOSIS.** Medium-sized (about 32 mm) *Euscorpium*, carapace and pedipalps mahogany colored, otherwise yellowish-brown in color, no patterns. Dorsal patellar spur (DPS) well developed. Most metasomal carinae are obsolete; only on segment V, ventrolateral carinae bear small granules and single ventromedian carina is rounded and smooth. Number of trichobothria on ventral aspect of pedipalp patella 7 or 8; number of external terminal trichobothria usually 6, rarely 5. Pectinal tooth counts in male usually 7, in female 7 or 6. Key diagnostic characters of this species are reduced number of ventral patellar trichobothria, and somewhat reduced sexual dimorphism in pectinal tooth number.

#### DESCRIPTION.

The following description is based on the holotype female from Exoburgo, Tinos Island, Greece. Measurements of the holotype plus three other paratype specimens are presented in Table I. See Figure 2 for dorsal and ventral views of the female holotype and male paratype.

**Coloration.** Carapace and pedipalps mahogany in color; mesosoma, metasoma, telson, and legs yellowish-brown; genital operculum, pectines, and basal piece light yellow. Pedipalp carinae dark brown to reddish-brown; aculeus and leg articulation spots dark brown. Scorpion essentially devoid of patterns.

**Carapace** (Fig. 4). Anterior edge essentially straight with a very narrow slight median indentation; entire surface smooth and lustrous, lacking any indication of carinae. There are two lateral eyes. Median eyes and tubercle are small to medium in size, positioned anterior of middle with the following length and width ratios: 0.408 (anterior edge to medium tubercle middle / carapace length) and 0.158 (width of median tubercle including eyes / width of carapace at that point).

**Mesosoma.** Tergites I–VII essentially smooth; tergite VII lacking lateral and median carinal pairs. Sternites III–VII smooth and lustrous; VII lacking lateral and median carinae. Stigmata are small in size and close to circular in shape.

**Metasoma** (Fig. 11, paratype male). Segment I wider than long. Segments I–IV: all carinae are obsolete, the segments surfaces are very smooth. The dorsolateral carinae termini are visible, however, slightly flared and pigmented. Segment V: dorsolateral and lateral carinae obsolete; ventrolateral carinae with small granules and single ventromedian carinae rounded and smooth. Anal arch with 16+ small serrated granules. Segments I–V with 2–6 scattered short setae on ventral aspects.

**Telson** (Fig. 5, paratype male Fig. 14). Vesicle elongated, with short highly curved aculeus. Vesicle essentially void of granules, very lustrous; distal half of ventral surface with scattered setae; base of aculeus with scattered setation ventrally and dorsally. Vesicular tabs rounded to obsolete and smooth.

**Pectines** (Fig. 6, paratype male Fig. 13). Medium-developed segments exhibiting length / width ratio 1.6 (length taken at anterior lamellae / width at widest point including teeth). Sclerite construction complex, three anterior lamellae and 3/4 middle lamella; fulcra of medium development. Teeth number 7/6. Sensory areas developed along distal aspect on all teeth,



**Fig. 3:** Dorsal and ventral views of *Euscorpium kritscheri*, **sp. n.**, Exoburgo, Tinos Island, Greece. **Top,** Female holotype, **Bottom,** male paratype, (note, tergite VII, metasoma, and telson are detached).

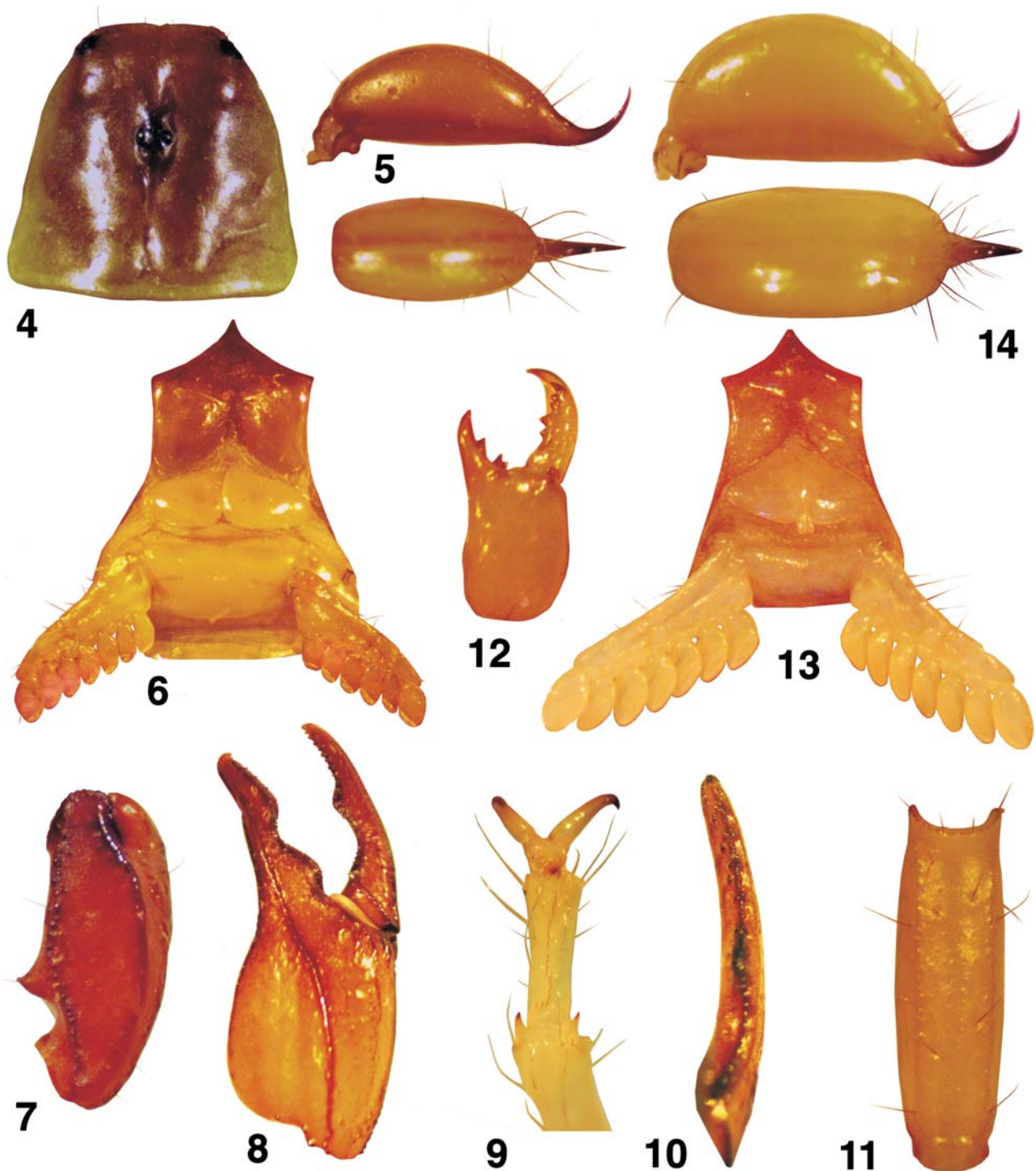


Fig. 4-14: *Euscorpium kritscheri*, sp. n., Exoburgo, Tinos Island, Greece. 4-7. Female holotype. 8-14. Male paratype. 4. Carapace. 5. Telson, lateral and ventral views. 6. Sternopectinal area. 7. Patella, dorsal view. 8. Chela, lateral view. 9. Leg tarsus, ventral view. 10. Chelal movable finger dentition. 11. Metasomal segment V, ventral view. 12. Chelicera, dorsal view. 13. Sternopectinal area. 14. Telson, lateral and ventral views.

including basal tooth. Basal piece large, with subtle shallow indentation along anterior edge, length / width ratio 0.518.

**Genital Operculum** (Fig. 6, paratype male Fig. 13). Sclerites rounded and triangular, wider than long; posterior median area rounded, separated at these rounded edges only (see discussion on male below for genital papillae).

**Sternum** (Fig. 6). Type 2, posterior emargination present, moderately convex lateral lobes, apex visible but not conspicuous; wider than long in ratio 0.875; anterior and posterior width the same.

**Chelicerae** (paratype male Fig. 12). Dentition of female holotype blunted and worn down, following description is based on paratype male. Movable finger dorsal edge with two small subdistal (*sd*) denticles; ventral edge smooth; serrula not visible. Ventral distal denticle (*vd*) conspicuously longer than dorsal (*dd*). Fixed finger with four denticles, median (*m*) and basal (*b*) denticles conjoined on common trunk; no ventral accessory denticles present.

**Pedipalps** (Fig. 7, 15, paratype male Figs. 8, 10). Well-developed chelae, with short fingers, moderately carinated,

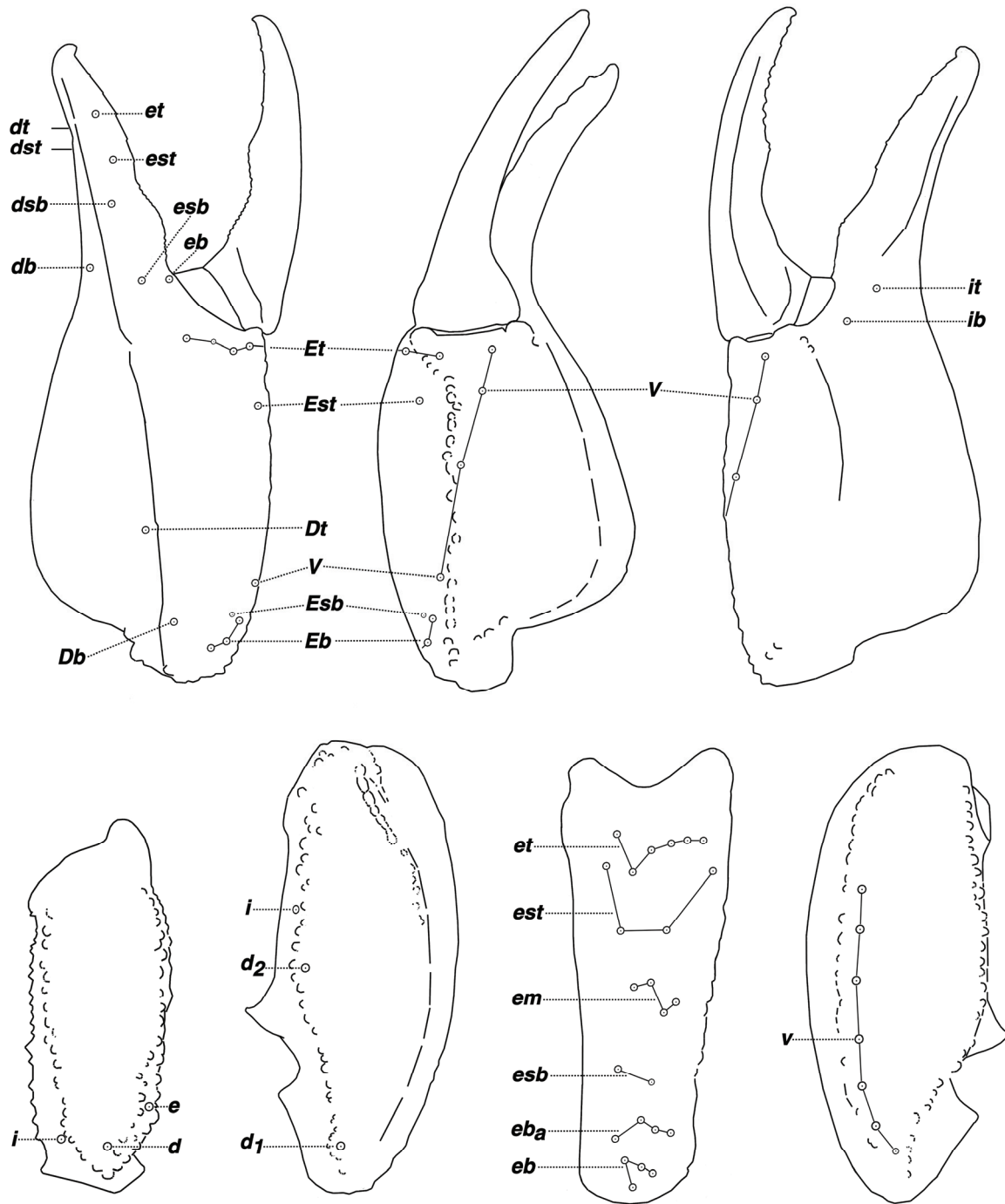


Fig. 15: *Euscorpium kritscheri*, sp. n., female holotype, Exoburgo, Tinos Island, Greece. Trichobothrial pattern.

medium scalloping on chelal fingers. **Femur:** Dorsointernal and ventrointernal carinae serrated, dorsoexternal irregularly crenulated, ventroexternal irregularly granulated on proximal half. Dorsal surface is smooth but rough at high magnification, ventral surface scattered with minute granules, internal and external surfaces rough with serrated rows of 11 and 10 granules, respectively. **Patella:** Dorsointernal and ventrointernal carinae crenulated, dorsoexternal smooth to irregularly rough, ventroexternal irregularly granulated, and extero-median carina essentially obsolete with scattered granulation distal to median area. Dorsal and ventral surfaces smooth and lustrous; external surface rough with some granulation; internal surface smooth with well-developed DPS and obsolete

VPS. **Chelal carinae:** Complies with the “10-carinae configuration”. Digital (*D1*) carina strong, smooth, and with subtle flat granules basally; sub-digital (*D2*) essentially obsolete, represented by 1–2 small granules; dorsosecondary (*D3*) essentially obsolete in very low profile; dorsomarginal (*D4*) rounded, with large low profile granulation; dorsointernal (*D5*) highly rounded and smooth; ventroexternal (*V1*) strong with flat low-profile granules, continuing in a straight line to trichobothrium *V*<sub>2</sub> and then curving externally, terminating at external condyle of movable finger; ventromedian (*V2*) obsolete; ventrointernal (*V3*) rounded and smooth; external (*E*) weak, rounded, and rough. **Chelal finger dentition** (Fig. 10): Median denticle (*MD*) row groups in straight line; 6/6 *ID*s

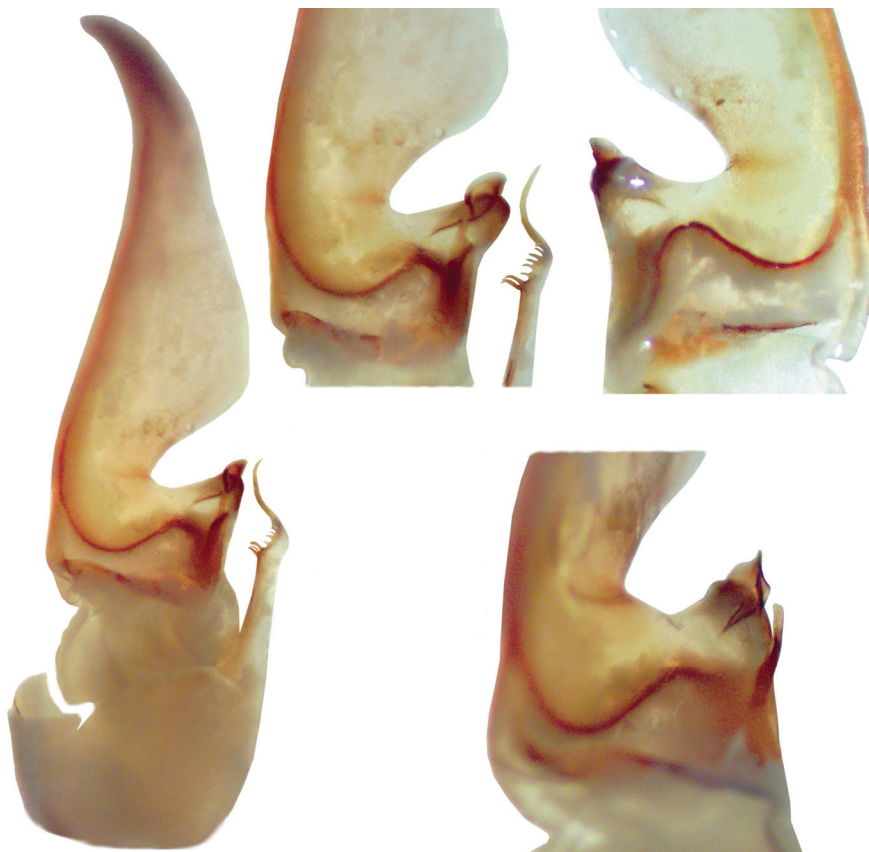
fixed finger and 7/7 on movable finger; 7/7 ODs on fixed and movable fingers; 4/4 and 5/5 IADs on fixed and movable fingers, respectively. **Trichobothrial patterns** (Fig. 15): Type C, neobothriotoxic: chela ventral = 4/4; patellar  $eb = 4/4$ ,  $eb_a = 4/4$ ,  $esb = 2/2$ ;  $em = 4/4$ ,  $est = 4/4$  (conspicuously angled at  $est_2$ - $est_3$ - $est_4$  juncture),  $et = 6/6$ ; patellar ventral = 7/7.

**Legs** (paratype male Fig. 9). Both pedal spurs present on all legs, lacking spinelets; tibial spurs absent. Tarsus with delicate single row of spinules on ventral surface, terminating distally with two offset darkened spinules. Unguicular spine well-developed and pointed.

**Hemispermatothore** (Fig. 16). Typical of subgenus. Lamina with a conspicuous basal constriction, terminus highly tapered, curving towards the external edge. A well-developed truncal flexure is present. Median projection with both primary and secondary acuminate processes. Primary acuminate process, a complex structure, has three irregular shaped lobes visible from the exteroventral perspective, the median lobe, which extends out the furthest, appears flat from this view. The secondary process, whose profile is visible from the externodorsal view, is simple and reduced to a single pointed spine. The internal lobe exhibits ten irregularly sized tines in its crown, the most ventral elongated and curved.

**SEXUAL DIMORPHISM.** The adult female exhibits a subtle proximal gap and movable finger lobe on the chela, whereas they are well developed in the male; the genital operculum sclerites in the female are connected along the middle, not separated as in the male; genital papillae are absent in the female, present in the male. The pectinal tooth counts are slightly smaller in the female, 6-7 (6.63) as compared to 6-7 (6.94) in the male. The metasoma in the female is not as slender as in the male, the mean differences when the length is compared to the width ranged 0.9 to 12.5 %. The telson vesicle in the female is not as swollen as it is in the male; the telson length compared to its depth is 2.884 in the female and 2.405 in the male, exhibiting a 19.9 % difference. The chelal palm in the female is not as swollen as it is in the male, the chelal length compared to its depth is 2.762 in the female, and 2.522 in the male, a 9.5 % difference. Finally, the carapace is relatively longer in the female, dominating in all possible morphometric ratios when compared to 24 other morphometrics, the largest difference, when the carapace is compared to the vesicle depth, exhibited a 50.2 % mean value difference.

**VARIATION.** We examined 12 type specimens of *E. kritscheri* sp.n. from Tinos (9 ♂, 4 ♀). Variation was as follows: Pectinal teeth number in males, 7/6 (1), 7/7 (8), in total: 6 (1), 7 (17); mean 6.94, SD 0.24 [n=18]. Pectinal teeth number in females, 6/7 (1), 7/6 (2), 7/7 (1), in total: 6 (3) and 7 (5); mean



**Fig. 16:** *Euscorpius kritscheri*, sp. n., male paratype, Istermia to Kardiani, Tinos Island, Greece. Right hemispermatothore (photographed submerged in alcohol). **Left**, dorsal view (note, basal portion of trunk not shown). **Upper Center**, close-up of the median area, dorsal view, showing the median projection and internal lobe with ten tines in its crown. **Upper Right**, closeup of the median area, ventral view (internal lobe is not shown). **Lower Right**, close-up of the median projection, externodorsal view, showing profile of primary and secondary acuminate processes (internal lobe is not shown). Note, due to the translucency of the hemispermatothore, the dorsal and ventral trough edges are each visible from the opposite view.

6.63, SD 0.51 [n=8]. Number of ventral patellar trichobothria ( $P_v$ ) was 7/8 (1), 7/7 (5), 8/8 (6), in total: 7 (11), and 8 (13); mean 7.54; SD 0.51 [n=24]. Number of external terminal patellar trichobothria ( $et$ ) was 5/5 (1), 5/6 (1), 6/6 (10), in total: 5 (3) and 6 (21); mean 5.88; SD 0.34 [n=24].

***Euscorpius cf. kritscheri***  
(Andros Island, Greece)

**REFERENCES:**

*Euscorpius carpathicus*: Stathi & Mylonas, 2001: 289 (in part; Andros).

**MATERIAL STUDIED:** GREECE, *Central Greece:* **Andros Island.** 13 specimens (3 ♂, 10 ♀): Andros, 1 ♀ (ZMB 15251); Andros, Paleopoli, Pigi, 9 November 1978, leg. M. Mylonas, 1 ♂ juv. (NHMC); Andros, Chora, harbor, N37°50', E24°56', 9 November 1978, leg. M. Mylonas, 2 ♀ (NHMC 1128, Eus74); Andros, Vitali, N37°55', E024°48', 3 September 1979, leg. M. Mylonas, 1 ♀ (NHMC 1134, Eus72); Andros, Vourkoti dirt road to Profitis Ilias peak, W of the village, 730 m, N37°51', E24°53', 23 April 2011, leg. S. Simaiakis, 1 ♂ (NHMC 13220); Andros, Evrousies, dry wall along the stream, east of springs, 590 m, N37°50', E24°53', 24



April 2011, leg. S. Simaiakis, 3 ♀, 1 ♂ (NHMC 13221, Eus7); Andros, Dypotamata, 2 km S from crossroad to Syneti, N37°48', E24°56', 25 April 2011, leg. S. Simaiakis, 1 ♀ (NHMC 13240, Eus6); Andros, Menites, 300 m, dense phrygana, N37°49', E24°54', 1 May 2002, leg. S. Simaiakis, 1 ♂, 1 ♀ (NHMC 4422; Eu73; used for DNA); Andros, Pitrofos, in yard, 425 m, N37°48', E024°52', leg. S. Simaiakis, 1 ♀ (NHMC 13239, Eus4);

**GEOGRAPHIC RANGE.** Western Cycladic island of Andros (see map on Fig. 1).

**VARIATION.** We examined 13 specimens of *Euscorpium* cf. *kritscheri* population from Andros (3 ♂, 10 ♀). Variation was as follows: Pectinal teeth number in males, 7/7 (1), 8/8 (2), in total: 7 (2) and 8 (4), mean 7.67, SD 0.52 [n=6]. Pectinal teeth number in females, 6/6 (1), 7/7 (8), 8/8 (1), in total: 6 (2), 7 (16) and 8 (2), mean 7.00, SD 0.46 [n=20]. Number of ventral patellar trichobothria (*Pv*) was 7/6 (2), 7/7 (8), 7/8 (1), 8/7 (1), 8/8 (1), in total: 6 (2), 7 (20) and 8 (4), mean 7.08, SD 0.48 [n=26]. Number of external terminal patellar trichobothria (*et*) was 5/5 (11), 6/5 (1), 5/6 (1), in total 5 (24) and 6 (2); mean 5.08, SD 0.27 [n=26].

#### NOTES:

1. Species delimitation and species validation methods based on multiple DNA markers (Parmakelis *et al.*, 2013a) show that Tinos and Andros populations form a common, basal clade and could potentially represent two distinct species. However, lack of adult material from Andros for further analysis of morphological data at this moment does not allow us to describe Andros population as a new species. It is addressed here as *Euscorpium* cf. *kritscheri* based on DNA phylogeny data.

2. Comparison of Andros and Tinos meristic data show that number of external terminal patellar trichobothria (*et*) appears to be a relatively fixed phenotypic marker for Tinos (usually “standard” 6; mean 5.88) and Andros (usually 5; mean 5.08). This trend is observed in unrelated clades of the genus in some isolated *Euscorpium* species in Greece and adjacent areas indeed have *et* number reduced from 6 to 5, such as *E. avcii* Tropea *et al.*, 2012 (Parmakelis *et al.*, 2013b) or *E. ossae* Di Caporiacco, 1950 (Fet *et al.*, 2013). In subgenus *Alpiscorpius* (“*mingrelicus* complex”), *et*=5 is a standard number, which is further reduced to *et*=4 in “*germanus* complex”.

3. A peculiar, derived feature of *Euscorpium kritscheri* sp.n. from Tinos is somewhat reduced sexual dimorphism in pectinal teeth number between males (mean 6.94) and females (mean 6.63), which has not been previously observed in *Euscorpium* or in family Euscorpiidae. In most scorpions, males always have higher, often considerably higher number of pectinal teeth. In *Euscorpium*, males usually have one pectinal tooth more than females (see e.g. Fet & Soleglad, 2002). Absence of sexual dimorphism in pectinal teeth number is extremely rare; it has been recorded for *Superstitionia*, a monotypic genus of another chactoid family, Superstitioniidae (North America) where both males and females have 6 pectinal teeth (Gertsch & Allred, 1965: 15).

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