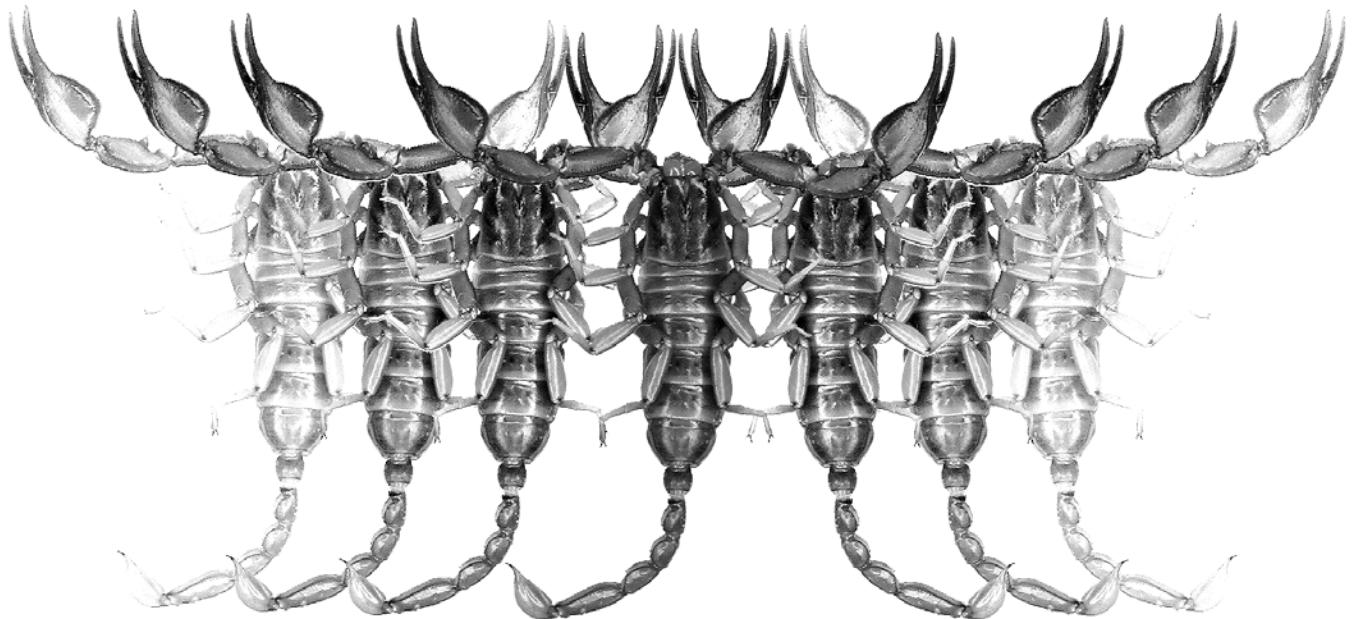


Euscorpius

Occasional Publications in Scorpiology



**Etudes on Iurids, I. The Orthobothriotaxic Pattern of
Iuridae, with Observations on Neobothriotaxy in Genus
Iurus (Scorpiones: Iuroidea)**

Michael E. Soleglad, František Kovařík & Victor Fet

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- **NTNU**, Norwegian University of Science and Technology, Trondheim, Norway

Etudes on iurids, I. The orthobothriotoxic pattern of Iuridae, with observations on neobothriotaxy in genus *Iurus* (Scorpiones: Iuroidea)

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Summary

A unique orthobothriotoxic pattern of family Iuridae is examined and illustrated. Significant positional differences in this pattern between two monotypic iurid genera, *Calchas* and *Iurus*, are presented. With the analysis of over 100 specimens of genus *Iurus*, representing many localities in Greece and Turkey, several unique occurrences of neobothriotaxy involving both the chela and patella are discussed and illustrated, representing the first report of neobothriotaxy in family Iuridae.

Introduction

The impetus for Francke & Soleglad's (1981) resurrection of family Iuridae Thorell, 1876 (in the scope that corresponds to modern superfamily Iuroidea) was based on a couple of independent events: 1) Soleglad, circa 1970s, concluded that the North American genus *Hadrurus* Thorell, 1876 was closely related to the South American genera *Hadruroides* Pocock, 1893 and *Caraboctonus* Pocock, 1893. In particular, this relationship was based on the unusual large solitary denticle found on the ventral edge of the cheliceral movable finger and the oblique alignment of the chelal finger median denticle rows; 2) Vachon (1974: figs. 212–219) presented illustrations of the trichobothrial patterns of monotypic genera *Calchas* Birula, 1899, at the time a member of family Chaetidae, and *Iurus* Thorell, 1876, then a member of family Vaejovidae. Soleglad (1976: 253) stated clearly the importance of these patterns:

“... Recently Vachon (1973) pointed out the close similarity of the trichobothrial patterns of *Calchas* and *Iurus*. The pattern shared by these two genera is very unusual in scorpions in general yet is essentially identical in all aspects across the two genera. This important observation is ramified further by the dentition of the chelicerae and ... chelae ... Both genera ... have a large basal denticle on the ventral edge of this finger ... chelal finger dentition ... median denticle row broken up into small groups. ...”

The latter observations made by Soleglad (1976), concerning the chelicerae and chelal finger dentition, formed an important nexus to the New World genera

Hadrurus, *Hadruroides*, and *Caraboctonus*. Since Francke & Soleglad's (1981) taxonomic act, Fet et al. (2004) further solidified the close relationships of iuroid genera with their study of the leg tarsus demonstrating that all had one form or another of clustered spinules on the ventral surface. Currently, six genera of Iuroidea (including *Hoffmannihadrurus* Fet et Soleglad, 2004) are grouped in two families, Iuridae and Caraboctonidae (Soleglad & Fet, 2003; Fet & Soleglad, 2005, 2008).

In this study, several populations of the genus *Iurus* were examined across the entire geographic range of this genus. Several unique types of neobothriotaxy were discovered on both the chela and patella, reported for the first time in this paper.

In order to describe the various instances of neobothriotaxy, we thought it important and necessary first to present the unique orthobothriotoxic pattern exhibited in this interesting scorpion family. In doing so, we also discuss and illustrate differences in this unique trichobothrial pattern between the genera *Calchas* and *Iurus*, the only current members of Iuridae (Soleglad & Fet, 2003; Fet & Soleglad, 2005).

Methods & Material

Abbreviations

List of depositories: FKCP, Personal collection of František Kovařík, Prague, Czech Republic; HNHM, Hungarian Natural History Museum, Budapest, Hungary; MES, Personal collection of Michael E. Soleglad, Borrego Springs, California, USA; MNHN, Muséum national d'Histoire naturelle, Paris, France; NMW, Natur-

historisches Museum Wien, Vienna, Austria; RK, Personal collection of Ragnar Kinzelbach, Rostock, Germany; VF, Personal collection of Victor Fet, Huntington, West Virginia, USA; ZMB, Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany.

Material examined

The following material was examined for analysis and/or illustrations provided in this paper.

Calchas nordmanni Birula, 1899. TURKEY (34 specimens): 1 ♂, 1 ♀, Belkis (Aspendos), near the ruins, under stones [Antalya Province], 16 May 1965, F. Ressl coll. (NMW 0848); 1 ♂, 1 ♀, mountains N of Antalya, 19 May 1969, F. Koller & F. Ressl coll. (together with *Iurus*) (NMW 0838/VF; specimens partially dismembered and used for SEM studies); 1 ♂, 2 ♀, Anamur, Mamuriye-Kalesi, Mersin Province, under stones, 15 May 1969, F. Ressl coll. (NMW 0847); 1 ♂, 1 ♂ juv., 15 km by road W of Anamur, Mersin Province, 18 May 1969, G. Pretzmann coll. (NMW 0841); 4 ♂, 3 ♀, Mardin, Mardin Province, 6 May 1966, J. Eiselt et al. coll. (NMW 0843); 1 ♀, Sakçagözü, Gaziantep Province, 26 April 1966, J. Eiselt et al. coll. (NMW 0844); 1 ♂, 1 ♀, Kavurma Köyü, 10 km NE Ergani, 1400 m a.s.l., 39°41' E, 38°19' N, Diyarbakir Province, 27 April 1989, G. Fabian, G. Ronkay, & L. Ronkay coll. (HNHM); 3 ♂, 2 ♀, 20 km S Urfa [now Şanlıurfa], Şanlıurfa Province, 1 May 1966, J. Eiselt et al. coll. (NMW 0840); 1 ♂ subad., 1 ♂ juv., 2 ♀ subad., 1 ♀ juv., Halfeti, Şanlıurfa Province, 1990, G. Ronkay coll. (HNHM); 1 ♂ subad., 2 ♂ juv., Halfeti, Şanlıurfa Province, valley of Euphrates, 500 m a.s.l., 15–22 April 1990, B. Herzig & G. Ronkay coll. ((HNHM); 1 ♂, road Siirt–Kurtalan, Siirt Province, 16 May 1966, J. Eiselt et al. coll. (NMW 0842); 1 ♀, Baykan (between Siirt and Bitlis), Siirt Province, 15 May 1966, J. Eiselt et al. coll. (NMW 0846).

Iurus difforeius (Brullé, 1832): GREECE (30 specimens): Peloponnese: 2 ♀ (VF), Nedontas River, between Artemisia and Kalamata, 29 July 1995, P. Crucitti coll. (VF); 1 ♂, Nedontas River, 13 km from Kalamata, 10 August 1995, P. Crucitti coll. (VF); 1 ♂, 1 ♀, Kastriti, Likosoura, 31 July 1995, P. Crucitti coll. (VF); 1 ♂, 13 August 1995, 1 ♂, 20 August 1995, Kourtaina (near Kalidona), P. Crucitti coll. (VF); 1 ♂, 30 July 1995, 1 ♂, 1 ♀, 3 August 1995, 1 ♀, 9 August 1995, Sparti, Gythio, Selinitsa, P. Crucitti coll. (VF); 2 ♀, Mystras, Kalivia Sochas, 10 August 1995, P. Crucitti coll. (VF); 1 ♂, 1 subad ♂, 2 ♀, 14 August 1995, 1 ♀, Gythio, Krini, 16 August 1995, P. Crucitti coll. (VF); 1 ♀, 1 juv. ♂, Sparti, Anavriti, 17 August 1995, P. Crucitti coll. (VF); 2 juv. ♀, Mystras, 18 September 1983 (FKCP), 2 subad., 2 juv., July 1990, (FKCP). 1 ♂,

Areopolis, 30 April 1991, (FKCP); 1 juv., Meropolis, June 1992, (FKCP). Crete: 1 ♀, Viano, 25 April 1887, von Oertzen coll. (ZMB 8701). Rhodes: 1 ♂, Kastelo, May 1887, von Oertzen coll. (ZMB 8069). Samos, 1 ♀, Aghios Nikolaos, 3 km west of Karlovasi, 27 June 2003, (FKCP). TURKEY (71 specimens): 2 ♂, 5 ♀, Narli Kioi near Smyrna [now Izmir], 1900 (NMW 11318); 1 subad. ♂, Köyceğiz, Sultanye spring [Muğla Province], 26 April 1991, E. Neubert coll. (RK 1053); 1 ♀, Kidirak, S of Fethiye [Muğla Province], 24–28 May 1988 R. Kinzelbach coll. (RK 1055); 1 ♂, 1 juv., Belkis (Aspendos), near ruins [Antalya Province], 16 May 1965, F. Ressl coll. (NMW 2067); 1 ♂, 2 ♀, Aspendos [Antalya Province] (NMW 11319); 1 ♂, Antalya, 15 May 1965, F. Ressl coll. (NMW 2066); 1 ♂, Antalya, 19 May 1969, F. Ressl coll. (NMW 11323); 1 ♀, Alanya, Antalya Province, 10 October 1998, E. Caraca coll. (NMW 19131); 2 ♂, “Güllük-Dagh” [Güllük Dagi, Antalya Province], A. Gaheis coll. (NMW 11320); 4 ♂, 5 ♀, “Gölbakticke, Lykien” [Gölbaşı, Kaş District, Antalya Province], May 1882, V. Luschan coll. (NMW 11321); 1 ♂, 2 ♀, “Gjölbanchi, Lykien” [Gölbaşı, Kaş District, Antalya Province], July 1882, V. Luschan coll. (NMW 11322); 1 ♂, 3 subad. ♂, 1 subad. ♀, Taurus Mts. [“Taurien”!] (ZMB 15218); 1 ♂, “Cilicien” (ZMB 8315); 1 ♀, Taurus Mts., P. Niedieck coll. (ZMB 15219); 4 ♂, 4 ♀, 4 juvs., 12 km S of Akseki, 11–12 May 2006, (FKCP); 1 ♂, Akseki, Taurus Mts., Antalya Province, 8–9 June 1993, (FKCP); 2 ♀ imm., Irmasan Geçidi, Akseki, Antalya Province, 1300 m, 2 June 1996, (FKCP); 1 ♀, 3 juv., Avlanbeli Geçidi, 1200 m a.s.l., 25 km S Elmali, 36°32' N 29°59' E, Antalya Province, 13–16 May 2006, (FKCP); 1 ♀, 1 juv., Kinik (Xanthos), Antalya Province, 15–16 April 1990, (FKCP); 1 juv., Catallar, 26 km N Finike, Antalya Province, 14–15 May 2006, (FKCP); 1 ♀, Cennet Cave [=Corycian Cave], NE Silifke, [Mersin Province], 11 April 1981, Heinz coll. (RK 367); 2 specimens (gender unknown; remnants), Corykos [near Silifke, Mersin Province] (MNHN RS 5619); 1 ♂, Silifke, Göksu Valley, [Mersin Province], 29 April 1967, F. Ressl coll. (NMW 11324); 1 ♂, near Gülnar, Mersin Province, July 2000, (FKCP); 1 ♀, Aydincik, Anamur, Mersin Province, 19 April 1990, and 1 ♂, 9 April 1990, (FKCP); 1 juv., 20 km from Anamur [Mersin Province], 22 April 1990, (FKCP); 1 ♀ juv., Antakya, July 1996, (FKCP); Antakya, Adana, south Mersin, May 1991, 1 ♀, 1 juv., 1 ♂, (FKCP); 1 ♂, 1 ♀, Fethiye, Mersin Province, May 1989 (FKCP); 1 imm. ♀, 50 km NW Tarsus, near Çamlıayala village, 1100–1200 m, Mersin Province, 9 May 1998 (FKCP); 1 ♂, Çamlıayala [Namrun], [Mersin Province], 16 May 1967, F. Ressl coll. (NMW 11325); 1 ♂, Uzuncaburg [Mersin Province], 26 July 1986, (RK 0732); 2 ♂, 2 ♀, Bademli, Konya Province, pasture, July 1998 (FKCP); 1 ♂, 1

imm. ♀, Dalyan, Muğla Province, May 1999 (FKCP); 1 ♂, “Turquie” [“Turkey”] (MNHN RS 3007).

Orthobothriotaxy in Iuridae: A Very Unusual Pattern

The trichobothrial pattern of an iurid species was first published by Vachon (1966: figs. 1–12) when he questioned the validity of genus *Chaerilomma* Roewer, 1943 (a junior synonym of *Iurus*), by comparing it to *Iurus*. This illustration predates Vachon’s (1974) monumental contribution where he defined his three “standard” types of orthobothriotaxy, Type A, Type B, and Type C (Soleglad & Fet, 2001, defined the fourth orthobothriotaxic type, Type D). The pattern of *Calchas* was first illustrated by Vachon (1971: figs. 2–7), in his detailed redescription of *C. nordmanni*. It is interesting that in both illustrations, *Iurus* (Vachon, 1966) and *Calchas* (Vachon, 1971), the homologies established for these two genera were consistent, but did *not* comply exactly with Vachon’s (1974) Type C pattern defined in 1974. Although the trichobothrial patterns designated by Vachon (1966, 1971) were close to the Type C pattern he designated in 1974 (Vachon, 1974: figs. 151–153, 166, 180, 212–219), there were two significant differences in the designation of trichobothria. In the earlier patterns, the five trichobothria positioned on the ventral surface of the palm were designated as V_1 – V_5 while the dorsal trichobothrium Dt was not designated. Although 26 chelal trichobothria were accounted for by the creation of an “accessory” trichobothrium, V_5 , and the “loss” of an orthobothriotaxic trichobothrium, Dt , this suggested set of homologies was different from the “standard” set that Vachon eventually established in 1974. Specifically, for all future Type C orthobothriotaxy designations, all 48 trichobothria are identified for the pedipalp using Vachon’s (1974) established terminology, without hypothesizing the gain of accessory trichobothria or losses of orthobothriotaxic trichobothria, even in those patterns where homology was not obvious (e.g., *Chactopsis*, *Hadruroides*, *Caraboctonus*, etc.). In Vachon’s (1974) “standard” pattern, only four ventral trichobothria are designated and trichobothrium Dt is identified.

Iuridae trichobothrial pattern

Figures 1–2 illustrate the “standard” set of orthobothriotaxic designations for family Iuridae as defined by Vachon (1974). As is evident from these illustrations, many unusual features are present, which makes this pattern quite unique within Type C scorpions (i.e., parvorder Iurida as defined by Soleglad & Fet, 2003).

Unique trichobothria topology

The unusual orthobothriotaxic pattern shared by *Calchas* and *Iurus* is encountered both on the chela and patella; only the femur, in general, reflects a more typical pattern as found in Type C scorpions.

Chela. The trichobothrial series *e* and *d* of the fixed finger are located on the distal half of the finger, even in the stockier genus *Calchas* (see exception below). This is unusual in Type C scorpions, though not exclusive to this family. For example, these eight trichobothria are also found distally in Caraboconidae (the sister family of Iuridae), which is considered a synapomorphy for superfamily Iuroidea (Soleglad & Fet, 2003). Other, less related taxa with distally placed fixed finger trichobothria are *Chactopsis* (family Euscorpiidae), *Sotano-chactas* (*db* is an exception) and *Alacran* (family Superstitioniidae), and *Akrav* (family Akravidae).

The fixed finger *i* series alignment is quite unusual in Iuridae. Trichobothria *ib* and *it* are not grouped together as typically found in Type C scorpions, but are considerably separated, *ib* located on the palm proximally of the fixed finger base and *it* is located at least at the fixed finger midpoint, if not more distally. As pointed out by Fet & Soleglad (2008), this topology is also found in the Type B genus *Chaerilus* (family Chaerilidae), suggesting this may be a plesiomorphic character for Iuridae. In other Type C scorpions this configuration is found in genus *Chactopsis* (family Euscorpiidae), *Alacran* (family Superstitioniidae), and *Nebo* (family Scorpionidae).

The chelal palm trichobothrium *Et₁* is positioned on the external surface of the palm in Iuridae, not on the ventral surface where it occurs in other Type C scorpions. [Note that Stockwell (1989) suggested a different homology scheme for these two genera which affects this trichobothrium; see below.]

The distal placement and overall configuration of the chelal palm *V* series is quite unique in Iuridae. The most proximal trichobothrium, *V₄*, is located on the distal third of the palm, considerably more distally than in other Type C scorpions. [Note that Stockwell (1989) suggested a different homology scheme for these two genera which affects this trichobothrium; see below.] The alignment of these four trichobothria is also unusual, with the very close proximity of trichobothria *V₁* and *V₂*. A short *V* series is also exhibited in many chaetid scorpions where *V₂* angles towards the internal edge.

The alignment of the *Eb* and *Esb* series in Iuridae is quite unusual, with *Esb* directly in line with the *Eb* series, not distally. In addition, *Eb₁* is located on the ventral edge, not on the external surface. [Note, Stockwell (1989) suggested a different homology scheme for these two genera which affects this tricho-

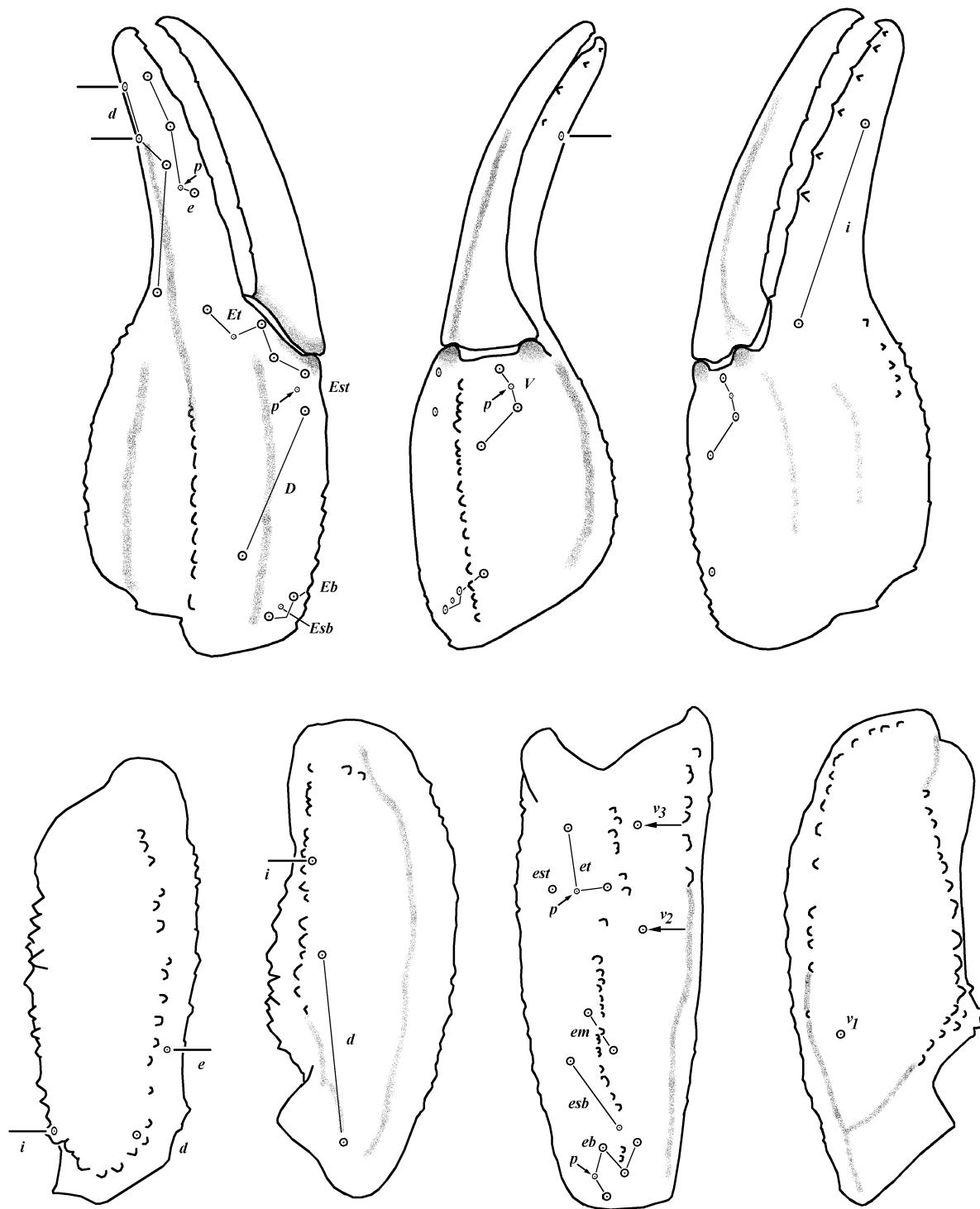


Figure 1: Trichobothrial pattern of *Calchas nordmanni*, female, Anamur, Turkey. Trichobothrial series identified by the first letter: **femur**, *i* = internal, *d* = dorsal, *e* = external; **patella**, *i* = internal, *d* = dorsal (*d*₁–*d*₂), *eb* = external basal (*Eb*₁–*Eb*₃), *esb* = external suprabasal (*esb*₁–*esb*₂), *em* = external median (*em*₁–*em*₂), *est* = external subterminal, *et* = external terminal (*Et*₁–*Et*₃), *v* = ventral (*v*₁–*v*₃); **chela**, *Eb* = external basal (*Eb*₁–*Eb*₃), *Esb* = external suprabasal, *D* = dorsal (*D*_b–*D*_t), *Est* = external subterminal, *Et* = external terminal (*Et*₁–*Et*₅), *V* = ventral (*V*₁–*V*₄), *e* = external (*eb*–*et*), *d* = dorsal (*db*–*dt*), *i* = internal (*ib*–*it*); special petite trichobothria indicated by “*p*”, three on the chela and two on the patella.

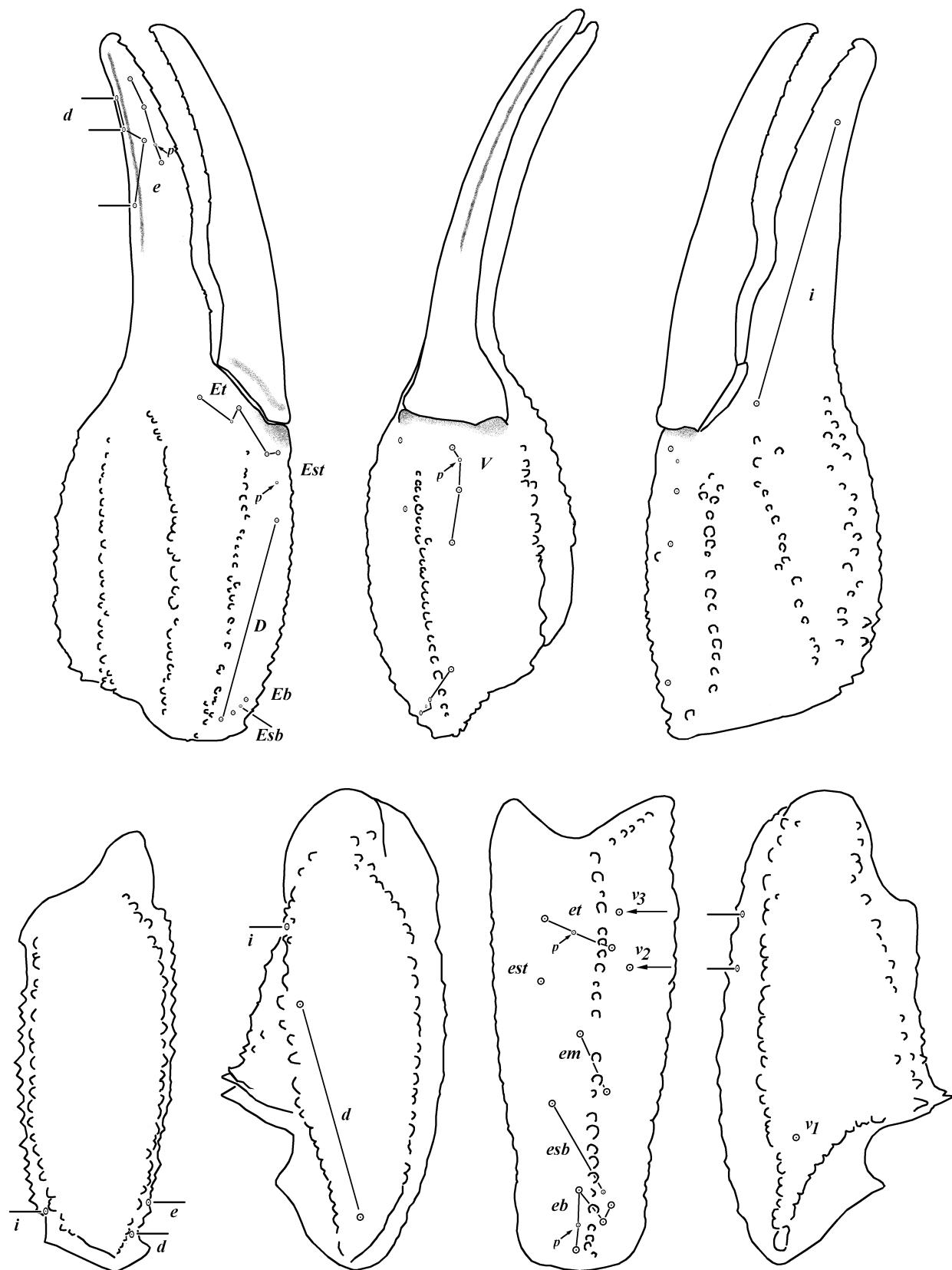


Figure 2: Trichobothrial pattern of *Iurus dusourei*, female, Nedontas River, between Artemisia and Kalamata, Greece. Trichobothrial series identified by the first letter: see Fig. 1 for definition of these series; special petite trichobothria indicated by “*p*”, three on the chela and two on the patella.

bothrium; see below.] The ventral placement of Eb_1 is also commonly found in many chaetid scorpions.

The alignment of chelal palm trichobothria Db and Dt is very unusual in Iuridae, unprecedented in Type C scorpions. The position of Db is variable in Iuridae, depending on the genus (see below), but is located essentially basal on the palm. Dt is located distally on the palm, quite close to the VI carina in close proximity to Est . This position of Dt is not found in any other Type C scorpion. [Note that Stockwell (1989) suggested a different homology scheme for these two genera which affects this trichobothrium; see below.] In addition, the angle between Db and Dt is quite unusual, slanting drastically in a medial to ventral direction. Typically, these two trichobothria slant in a dorsal direction, although there is a slight vertical slant in *Superstitionia*, *Troglotayosicus*, and in some *Typhlochactas* species (family Superstitioniidae).

Patella. Unique in Type C scorpions is the external placement in family Iuridae of ventral trichobothria v_2 and v_3 . Placement of patellar ventral trichobothria is important in scorpion systematics. For example, the placement of v_3 on the external surface is a synapomorphy for family Vaejovidae (Soleglad & Fet, 2003, 2008) and subfamily Superstitioniinae, genera *Superstitionia* and *Troglotayosicus* (Soleglad & Fet, 2003: fig. 80); and the external placement of v_2 in *Typhlochactas* and *Sotanochactas* is derived in these superstitioniid genera.

Special petite trichobothria

Standard Type C patterns exhibit three petite trichobothria, Et_4 and Esb on the chelal palm and esb_2 on the external surface of the patella. These trichobothria are also petite in *Calchas* and *Iurus*. In addition to these three petite trichobothria are the presence of five additional petite trichobothria in *Calchas* and *Iurus*, three on the chela and two on the patella. These are found exclusively in family Iuridae. In Figs. 1–2 these additional petite trichobothria are identified not only by their smaller size but are indicated by a “*p*” in the illustrations. The chela exhibits three additional petite trichobothria, esb on the fixed finger, Est on palm external surface, close to the VI carina, and V_2 on the ventral surface of the palm. On the patella external surface trichobothria et_2 and eb_2 are petite.

The presence of these additional petite trichobothria may have significance in scorpion evolution. Soleglad & Fet (2001: 31) wrote:

“... Since the iurids [now iuroids] are proving to be basal in Recent scorpions (Soleglad & Sissom, 2001), these curious petite trichobothria might represent an early form of the Type C pattern. If this

is the case, then we have an example of petite trichobothria that have not yet become full trichobothria as seen in other Type C scorpions. On the other hand, these orthobothrioxic trichobothria may be autapomorphic to Iurinae [now Iuridae], and therefore we have an example of full orthobothrioxic trichobothria becoming petite. ...”.

We might add here that, since this observation by Soleglad & Fet, the superfamily Iuroidea (Iuridae + Carabocionidae) has been demonstrated to be the most primitive superfamily in parvorder Iurida by Soleglad & Fet (2003: fig. 114). This result was further supported by Fet & Soleglad (2008) in their recent cladistic analysis of Iuroidea.

Alternative interpretations: Stockwell (1989)

Stockwell (1989: figs. 173–174), in his unpublished PhD dissertation, presented a very interesting alternative to Vachon's (1974) homology hypothesis of Iuridae orthobothriaxy (see Figure 3). In his scheme, Stockwell (1989) declared the ventral series of the palm to exclude Vachon's (1974) V_1 and include his Eb_1 , thus maintaining four trichobothria in this series. By making this change in homology, several perturbations in homology assignments are necessary: on the basal aspect of the palm, what Vachon (1974) designated as Db is reassigned to Eb_3 , Eb_3 becomes Eb_2 , and Eb_2 becomes Eb_1 . On the distal aspect of the palm, now that we no longer require an Et_1 (i.e., which is located on the ventral surface in Stockwell's scheme), the homology mappings of three of the four Et trichobothria change: Et_1 to Et_2 , Et_2 to Et_3 , and Et_3 to Et_5 . This in turn frees up what Vachon (1974) called Et_5 to become Dt in Stockwell's (1989) scheme, forcing Vachon's Dt to become Db .

This change in trichobothria designations has many attractive aspects and some negative ones as well. First, the Eb series is now contiguous on the external surface of the palm, which is more consistent with typical Type C patterns. Second, Et_1 is now located on the ventral surface, where it is located in all other Type C scorpions. A negative aspect of Stockwell's (1989) scheme is the strange alignment of trichobothria Et_4 and Et_5 , the latter being more ventrally positioned than the petite Et_4 . Although the strange alignment of Db and Dt in Vachon's (1974) scheme is quite unorthodox, the alignment in the alternative scheme is not much of an improvement, though it does now slant dorsally. The position of Eb_3 in genus *Calchas* in Stockwell's (1989) scheme is placed distally of the other Eb trichobothria (see below), unusual in Type C scorpions, though it is prevalent in euscorpiid subfamily Scorpiopsinae (see Soleglad & Sissom, 2001: figs. 113–118).

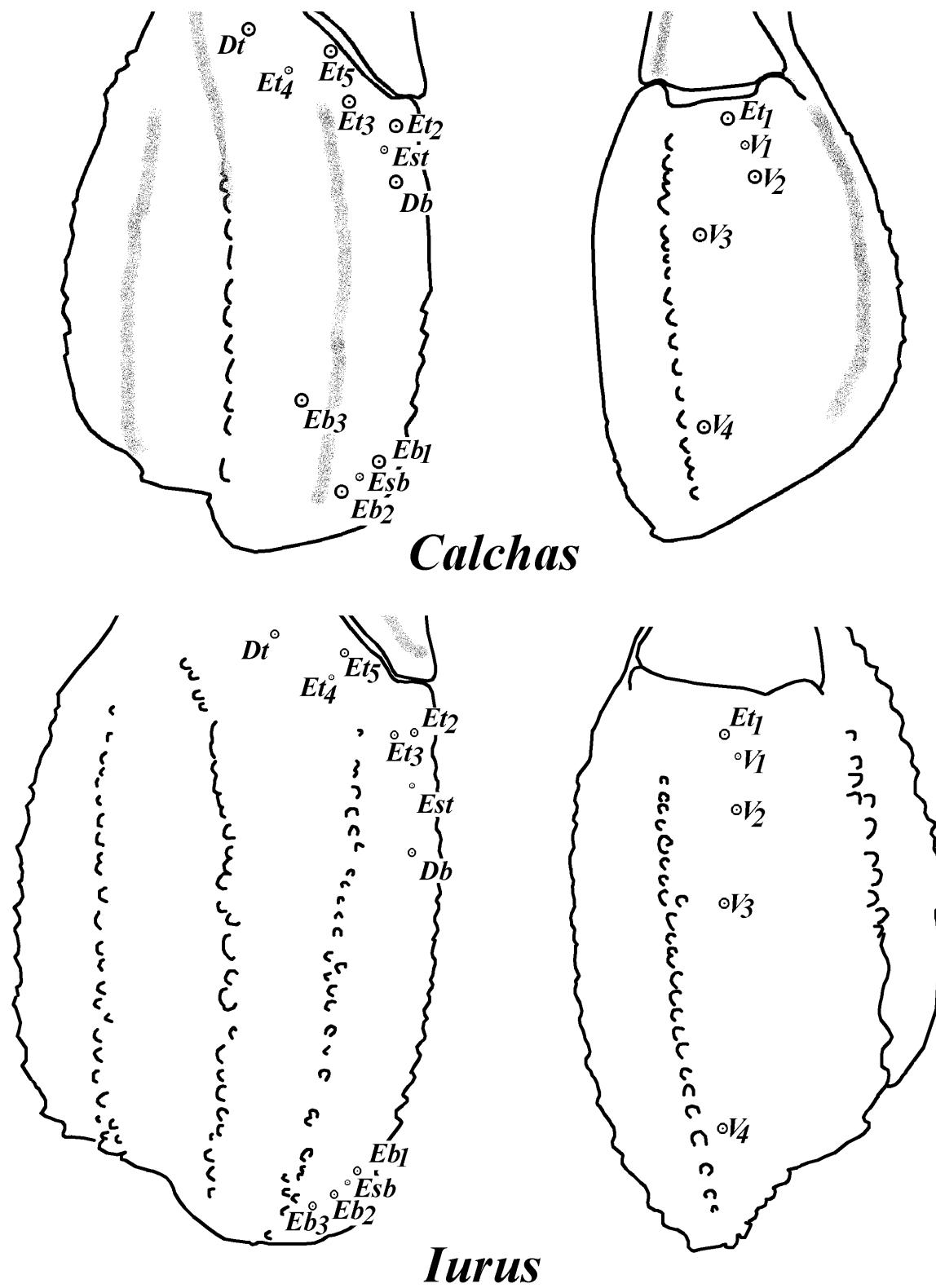


Figure 3: Stockwell's (1989) interpretation of trichobothria homology in family Iuridae.

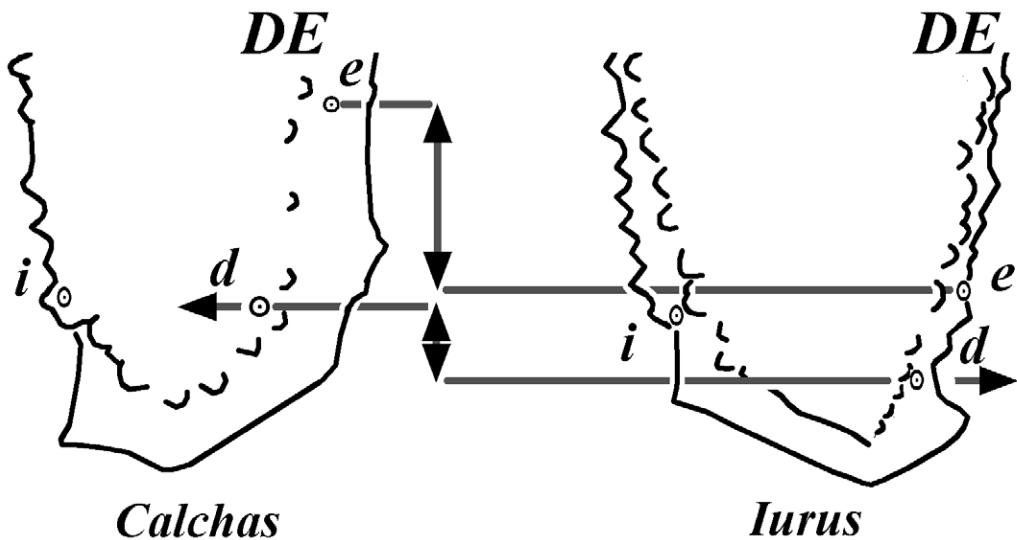


Figure 4: Positional differences in femoral trichobothria between *Calchas* and *Iurus*. Trichobothrium *e* is positioned significantly more distally in *Calchas* than in *Iurus*, trichobothrium *d* is located on dorsal surface in *Calchas*, whereas in *Iurus* it is positioned slightly lower and on the external surface. *DE* = dorsoexternal carina.

We consider the pros and cons of this alternative scheme to be interesting and definitely should be revisited in any study that considers the evolution of trichobothria positions. In fact, Soleglad & Fet (2003: 35–36, fig. 65) and Fet & Soleglad (2008: 263–265) adopted Stockwell's (1989) alternative homology assignments for subfamily Caraboctoninae (now family Caraboctonidae; see the first reference for a detailed discussion). In this case, the new mappings represented consistent improvements as compared to Vachon's (1974) original designations.

Trichobothria Positional Differences in *Calchas* and *Iurus*

Although genera *Calchas* and *Iurus* share a very distinct Type C pattern as discussed in detail above (Figs. 1, 2), there are significant differences in the position of some of these trichobothria, differences occurring in all three pedipalpal segments. Many of these positional differences between the two genera involve trichobothria occurring on different segment subsurfaces as established by carinae. Below we describe seven such differences in trichobothria locations.

Femur. In type C scorpions, only three trichobothria are present on the femur. Therefore it is remarkable that of these three trichobothria, positional differences exist in no less than two in *Calchas* and *Iurus*, trichobothria *d* and *e*. In Figure 4, we see that trichobothrium *d* is located on the dorsal surface close to the dorsoexternal (*DE*) carina in *Calchas*, where it is found in a large majority of Type C scorpions. However, in *Iurus* trichobothrium *d* is located on the external

surface, somewhat unusual for Type C scorpions. This unique position of trichobothrium *d* was first commented on by Soleglad & Sissom (2001: 47, fig. 73), though illustrated much earlier by Vachon (1966: figs. 4, 10). Though probably of less importance, we also see that trichobothrium *d* is proximal of *i* in *Iurus* whereas in *Calchas* they are located almost at the same level.

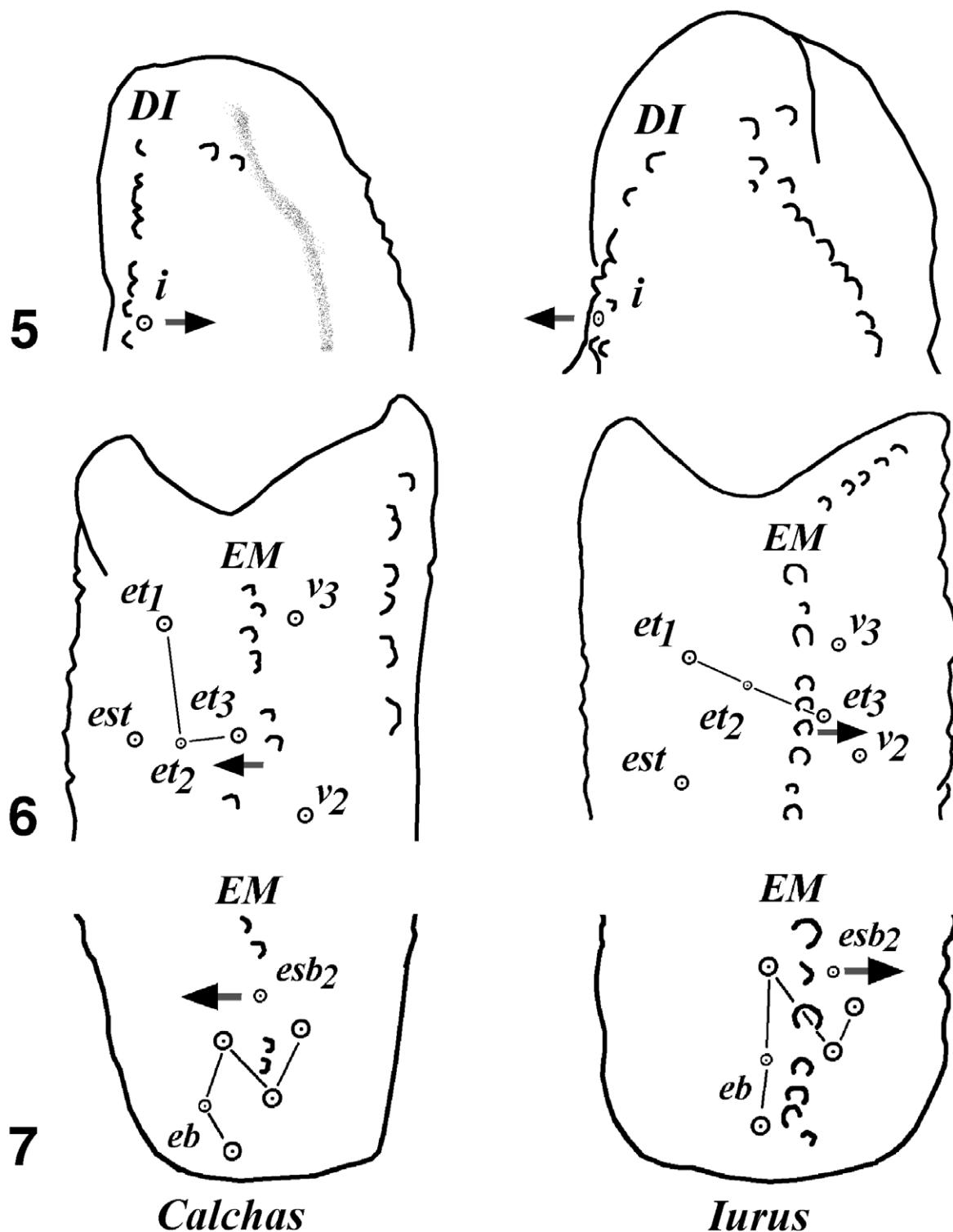
External trichobothrium *e* is clustered somewhat close to trichobothria *i* and *d* in *Iurus*, only slightly distally of *i*. In *Calchas*, *e* is considerably distal to the other two trichobothria, apparently showing some consistency with the more distally placed trichobothrium *d*.

Patella. For the patella, we see no less than three positional differences in trichobothria involving both the external and internal surfaces. In Fig. 5 the internal trichobothrium *i* is located on the dorsal surface in *Calchas* as indicated by the dorsointernal (*DI*) carina. This dorsal location of *i* is unusual in type C scorpions and was first illustrated by Vachon (1971: fig. 5). In *Iurus*, trichobothrium *i* is located on the internal surface, close to the *DI* carina.

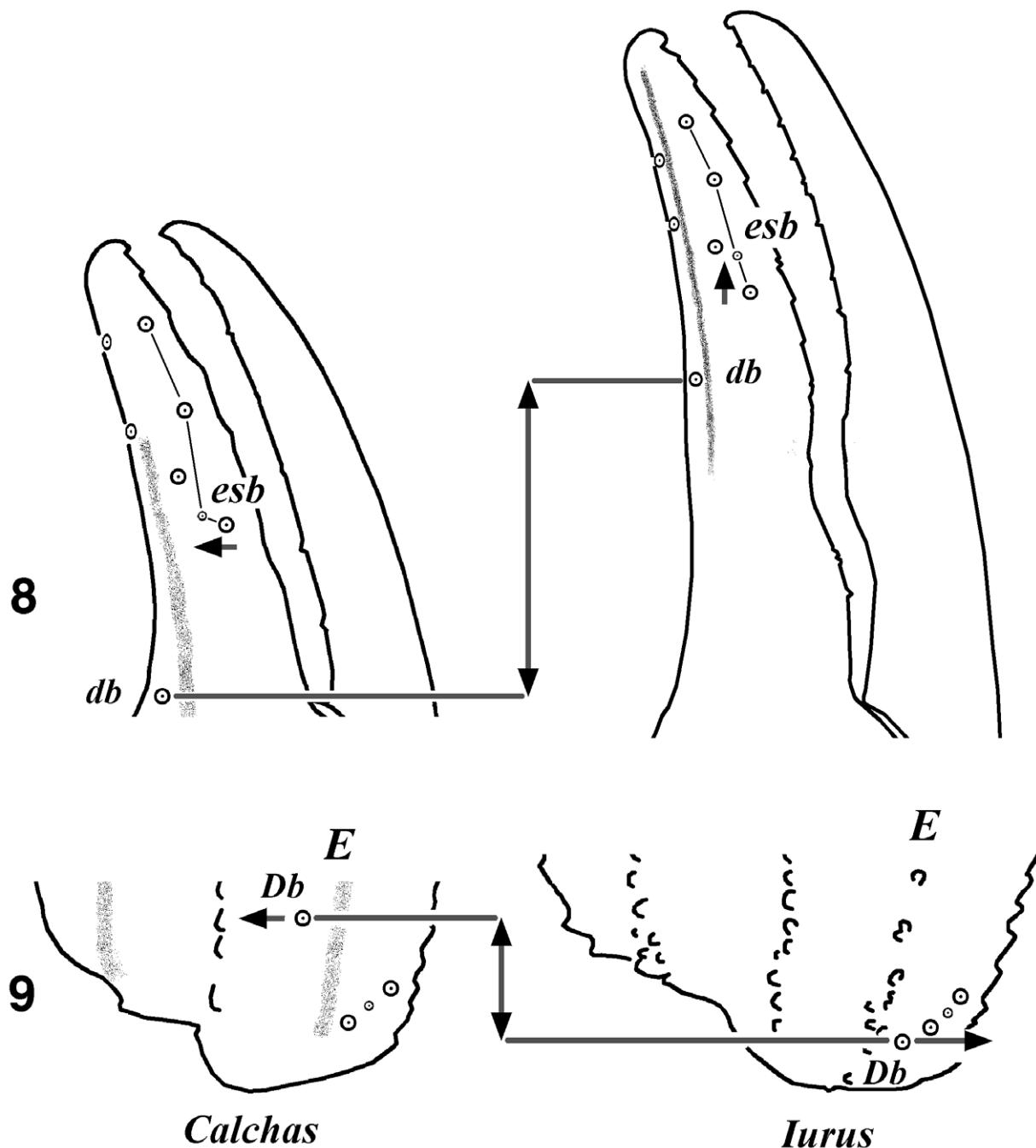
In Figures 6–7, two external trichobothria locations are of note, both involving their alignment to the somewhat well developed exteromedian (*EM*) carina which bisects the external surface vertically, creating dorsal and ventral subsurfaces:

Figure 6 illustrates the location of the *et₃* trichobothrium where it is situated on the dorsal half of the external surface in *Calchas*. In *Iurus*, this trichobothrium is located on the ventral half, quite close to the two ventral trichobothria *v₂* and *v₃*.

Figure 7 illustrates the position of petite trichobothrium *esb₂* where it is located on the dorsal half of the external surface in genus *Calchas*. In *Iurus*, *esb₂* is



Figures 5–7: Positional differences in patellar trichobothria between genera *Calchas* and *Iurus*. **5.** Trichobothrium *i* is positioned external (i.e., right in the figure) of dorsointernal carina (*DI*) in *Calchas* on the dorsal surface whereas, in *Iurus* *i* is positioned internal of *DI* carina (i.e., left in figure). **6.** Trichobothrium *et₁* is positioned dorsal (i.e., left in the figure) of exteromedian carina (*EM*) in *Calchas*, whereas in *Iurus* *et₃* is positioned ventral of *EM* carina (i.e., right in figure). **7.** Trichobothrium *esb₂* is positioned dorsal (i.e., left in the figure) of the exteromedian carina (*EM*) in *Calchas*, whereas in *Iurus* *esb₂* is positioned ventral of the *EM* carina (i.e., right in figure).



Figures 8–9: Positional differences in chelal trichobothria between *Calchas* and *Iurus*. **8.** Trichobothrium *esb* is not positioned inline with the other external trichobothria in *Calchas*, whereas in *Iurus*, *esb* is inline with these trichobothria; trichobothrium *db* is positioned significantly more basal, at fixed finger base, in *Calchas*, whereas in *Iurus* *db* is positioned distally, midfinger. **9.** Trichobothrium *Db* is positioned more distal and dorsal (i.e., left in the figure) of the external carina (*E*) in *Calchas*, whereas in *Iurus* *Db* is positioned considerably basal and ventral of the *E* carina (i.e., right in figure).

positioned on the ventral half of the patellar external surface, closer to trichobothrium *eb₅*.

Chela. In Figure 8, we see that most of the *d* and *e* series trichobothria are positioned on the distal half of the fixed finger in both genera. However, trichobothrium *db* is an exception: in *Calchas*, *db* is located at the base

of the fixed finger, not on the distal half as seen in *Iurus*. This significant location difference in the two genera may be caused, in part, by the differences in the morphometrics between the two genera, *Iurus* having longer fingers than *Calchas* as compared to the palm (see Figs. 1, 2). Also shown in Fig. 8 is the difference in the

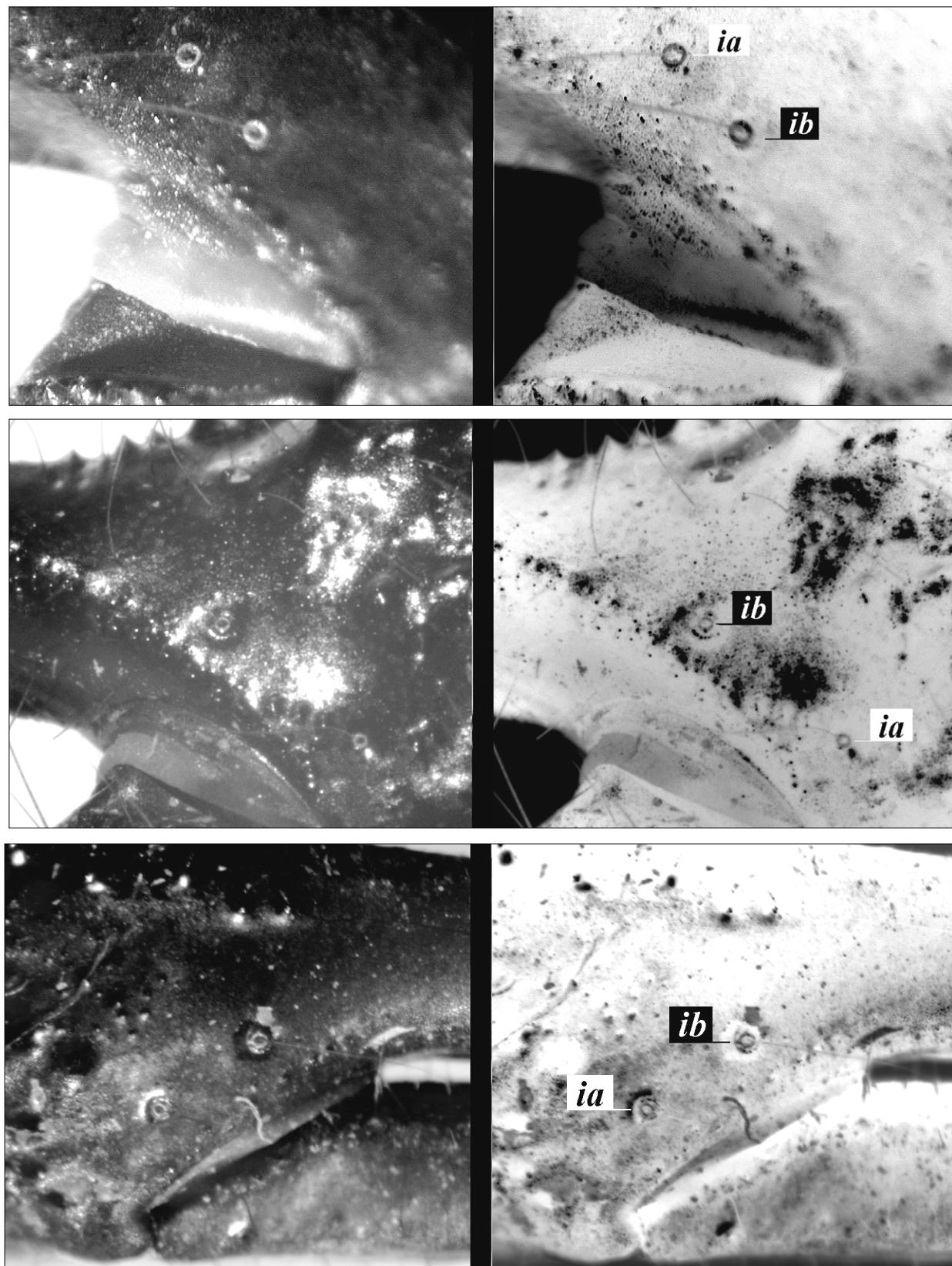


Figure 10: Examples of neobothriotaxy (*ia*, black text on white) in chelal *ib* series in *Iurus*, shown in photo on left and annotated in photo on right (note, orthobothriotaxic trichobothrium *it* is located on the distal half of the fixed finger). **Top.** Juvenile female from the Taurus Mts. in Turkey, showing a distally placed full sized accessory trichobothrium. **Middle.** Subadult female from Irmasan Gecidi, Akseki, Turkey, showing a petite *ia* basal to *ib*. **Bottom.** Subadult female from Sparti, Greece, exhibiting a petite *ia* suprabasal to *ib* (left chela).

	Chela <i>ib-it</i> Series	Chela <i>Et & Est</i> Series	Chela <i>V</i> Series	Patella <i>e</i> series
Greece (30 specimens)				
Sparti, SA ♀	1 suprabasal <i>ia</i> , one chela	-	-	-
Sparti, A ♀	-	-	-	1 <i>ea</i> (vent1), one patella
Turkey (71 specimens)				
Akseki, A ♂	-	1 <i>ea Et</i> , both chelae	-	-
Akseki, J ♂	-	1 <i>ea Et</i> , both chelae	-	-
Akseki, A ♀	-	1 <i>ea Et</i> , both chelae	-	-
Akseki, A ♂	-	1 <i>ea Et</i> , both chelae	-	-
Akseki, Irmasan Geçidi, SA ♀	1 basal <i>ia</i> , one chela	1 <i>ea Et</i> , both chelae	-	-
Akseki, Irmasan Geçidi, SA ♀	-	1 <i>ea Et</i> , both chelae	-	-
Antalya, SA ♂	1 distal <i>ia</i> , both chelae	2 <i>ea Et</i> , both chelae (one petite)	-	-
Antalya, A ♂	1 distal <i>ia</i> , both chelae	1 & 2 <i>ea Et</i> , both chelae	1 <i>va</i> (petite), both chelae	-
Belkis, SA ♂	-	1 <i>ea Et</i> , both chelae	-	2 <i>ea</i> (dor), both patella
Belkis, J ♂	-	1 <i>ea Et</i> , both chelae	-	2 <i>ea</i> (dor), both patella
Belkis, A ♀	-	1 & 2 <i>ea Et</i> , both chelae	-	-
Belkis, J ♂	-	1 <i>ea Et</i> , both chelae	-	2 <i>ea</i> (dor), both patella
Cennet, A ♀	-	-	-	1 <i>ea</i> (dor), one patella
Güllük Dagi, A ♂	-	2 <i>ea Et</i> , both chelae (one petite)	-	-
Güllük Dagi, SA ♂	-	2 <i>ea Et</i> , both chelae	-	-
Gölbasi, J ♂	-	1 <i>ea Et</i> , both chelae	-	-
Bademli, Konya Province, A ♀	-	1 <i>ea Et</i> , both chelae	-	-
Bademli, Konya Province, A ♀	-	1 <i>ea Et</i> , both chelae	-	-
Bademli, Konya Province, A ♂	-	1 <i>ea Et</i> , both chelae	-	-
Izmir (Narli-Kioi), A ♀	-	1 <i>ea Est</i> (petite), both chelae	-	1 <i>ea</i> (vent2), one patella
Izmir (Narli-Kioi), SA ♀	-	-	-	1 <i>ea</i> (vent2), one patella
Izmir (Narli-Kioi), SA ♀	-	1 <i>ea Est</i> (petite), one chela	-	-
Izmir (Narli-Kioi), A ♀	-	-	-	1 <i>ea</i> (vent2), one patella
Izmir (Narli-Kioi), SA ♀	-	1 <i>ea Est</i> (petite), one chela	-	1 <i>ea</i> (vent2), one patella
Taurus Mts., A ♂	1 distal <i>ia</i> , one chela	1 <i>ea Et</i> , both chelae	-	-
Taurus Mts., A ♂	-	1 <i>ea Et</i> , one chela	-	-
Taurus Mts., SA ♀	1 distal <i>ia</i> , both chelae	1 <i>ea Et</i> , both chelae	-	-
Taurus Mts., SA ♂	1 distal <i>ia</i> , one chela	1 <i>ea Et</i> , both chelae	-	-
Taurus Mts., SA ♂	1 distal <i>ia</i> , both chelae	2 <i>ea Et</i> , both chelae	-	-
Taurus Mts., J ♀	1 distal <i>ia</i> , one chela	1 & 2 <i>ea Et</i> , both chelae	-	-

Table 1: Neobothriotaxy in genus *Iurus* based on the examination of 101 specimens originating from mainland Greece, Crete, Rhodes and Turkey. Neobothriotaxy was detected in 32 specimens as listed in table, spanning nine different forms: three on the chelal internal surface, two on the chelal external surface, one on the chelal ventral surface, and three on the patellar external surface.

relative location of the petite trichobothrium *esb*. In *Calchas*, *esb* is not inline with the other external trichobothria, positioned more dorsally on the fixed finger. In *Iurus*, *esb* is inline with the other external trichobothria.

Figure 9 shows the position of trichobothrium *Db* with respect to the external (*E*) carina of the chelal palm. In *Calchas*, *Db* is located between the digital (*DI*) and *E* carinae, somewhat removed from the *Eb* series trichobothria. In *Iurus*, the *Db* trichobothrium is located between the *E* and ventroexternal (*VI*) carinae, quite close to and in line with the *Eb* series trichobothria. In addition to significant positional differences in *Db* location, involving palm carinae, we see that *Db* is situated more distally on the palm in *Calchas*, not on the extreme basal aspect as exhibited in *Iurus*.

Neobothriotaxy in *Iurus*

Based on the examination of 101 specimens of *Iurus*, spanning localities in mainland Greece, Crete, Rhodes, and Turkey, no less than nine *distinct types* of neobothriotaxy have been detected (note, an *instance* equals a single pedipalp):

three types of neobothriotaxy are found on the basal aspect of the chela internal surface,

- 1) suprabasal *petite* accessory trichobothrium (one instance),
- 2) basal *petite* accessory trichobothrium (one instance),
- 3) distal accessory trichobothrium (11 instances);

two types were detected on the external surface,

- 4) one or two accessory trichobothria are present in the *Et* series (47 instances),
- 5) one *petite* accessory trichobothrium in the *Est* series (four instances);

one type in the ventral surface of the chela,

- 6) a *petite* trichobothrium in the *V* series (one instance);

and three types of neobothriotaxy on the patella external surface,

- 7) one to two accessory trichobothria on the dorsal half of the surface (seven instances),
- 8) one accessory trichobothria on the ventral surface in the *em* series (one instance),
- 9) one *petite* accessory trichobothria on the ventral surface in the *et* series (four instances).

Many specimens exhibit combinations of several abovementioned types of neobothriotaxy. See Table 1 for a list of specimens, their localities, and neobothriotoxic type(s).

Neobothriotaxy on chelal internal surface

Figure 10 illustrates all three types of neobothriotaxy encountered on the internal surface of the chelal palm. The neobothriotaxy is limited to a single accessory trichobothrium and it is always positioned close to trichobothrium *ib*. The majority of instances exhibiting neobothriotaxy on the internal surface has the *ia* (internal accessory) trichobothrium positioned distally and slightly dorsally of *ib*. For this type of neobothriotaxy, *ia* is a full size trichobothrium and can occur on just one pedipalp or both. Of the seven specimens with this distal *ia*, four of them exhibited it on both chelae. These specimens were all collected from the south-central area of Turkey.

The second type of neobothriotaxy has an *ia* considerably basal to trichobothrium *ib*, adjacent to the internal condyle of the movable finger. This *ia*, petite in size, was encountered on one chela only in a solitary specimen from the high mountain locality (1300 m) of Irmasan Geçidi, Akseki, Turkey.

The third type of neobothriotaxy was found on one chela only, a female from Sparti, Greece. The *ia* is located suprabasal to *ib* and is petite in size.

Neobothriotaxy on chelal external surface

Two types of neobothriotaxy were detected on the external surface of the chela: one or two accessory trichobothria occurring in the *Et* series, and one accessory trichobothrium in the *Est* series. In Figures 11–12, we illustrate several examples of accessory trichobothria occurring in the *Et* series. In all instances the accessory trichobothria (one or two) are located in the triangular area formed by trichobothria *Et*₃, *Et*₄, and *Et*₅. In a couple instances where two *ea* are present, one is petite in size. This type of neobothriotaxy is the most prevalent in the material examined, 47 instances, and in almost all cases, found on both chelae. All specimens were collected in the south-central area of Turkey.

Presence of accessory trichobothria in the *Est* series was encountered in an isolated population from Izmir (Narlı-Kioi), Turkey. Figure 13 illustrates this solitary petite *ea* trichobothrium. The *ea* is positioned close to the *VI* carina and is proximal to trichobothrium *Dt*. This type of neobothriotaxy was found in three specimens (from a total of seven), both chelae in one specimen and on a single chela in three specimens. In all cases, the *ea* is petite.

Neobothriotaxy on chelal ventral surface

Figure 13 illustrates the only occurrence of neobothriotaxy encountered on the chelal ventral surface. The solitary *ia* is petite and is located slightly external to and between trichobothria *V*₁ and *V*₃. This

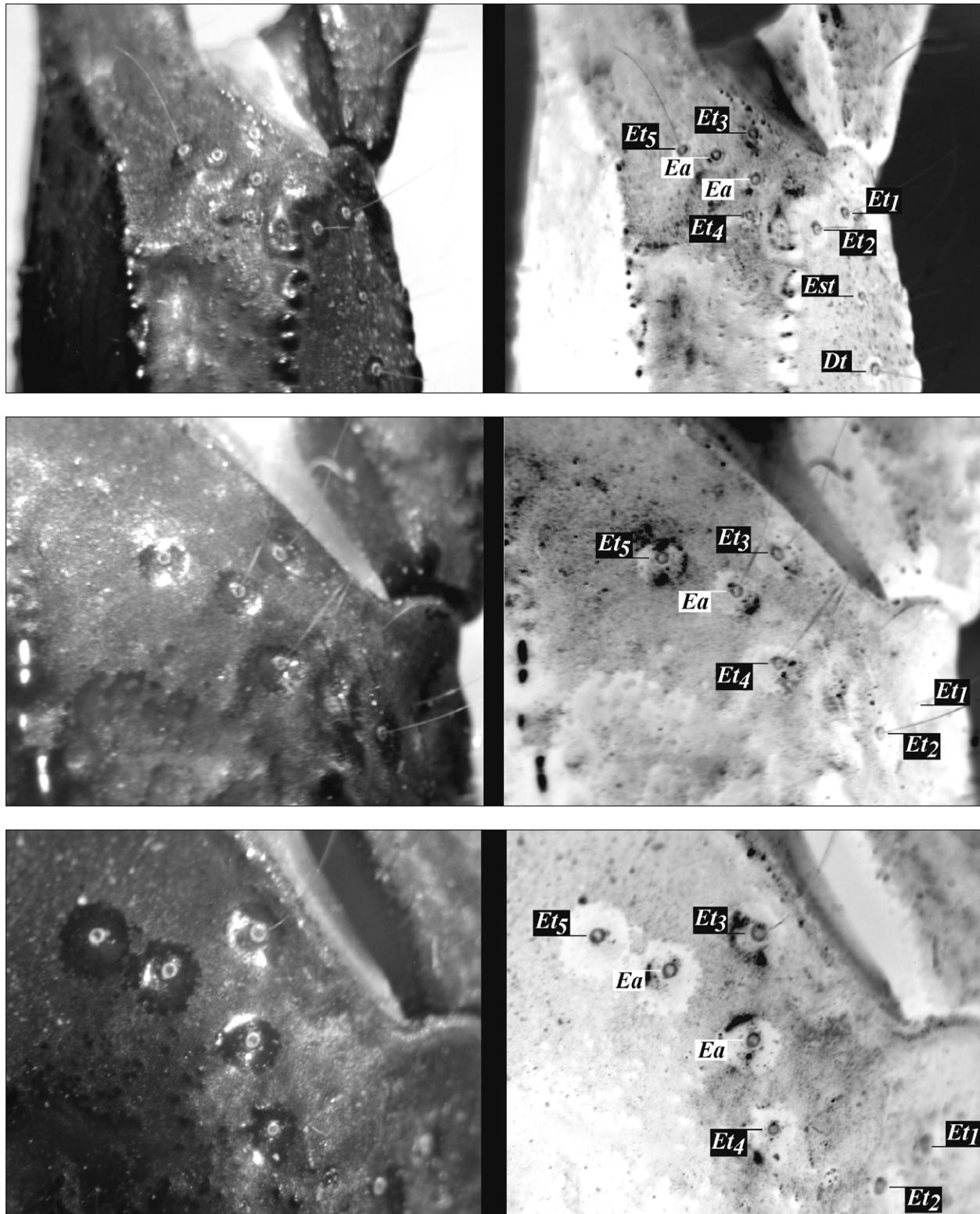


Figure 11: Examples of neobothriotaxy (*Ea*, black text on white) in chelal *Et* series in *Jurus*, shown in photo on left and annotated in photo on right. **Top.** Juvenile female, Taurus Mts., Turkey, showing two accessory trichobothria. **Middle.** Subadult male, Taurus Mts., Turkey, showing one accessory trichobothria. **Bottom.** Subadult male, Antalya, Turkey, showing two accessory trichobothria, one petite.

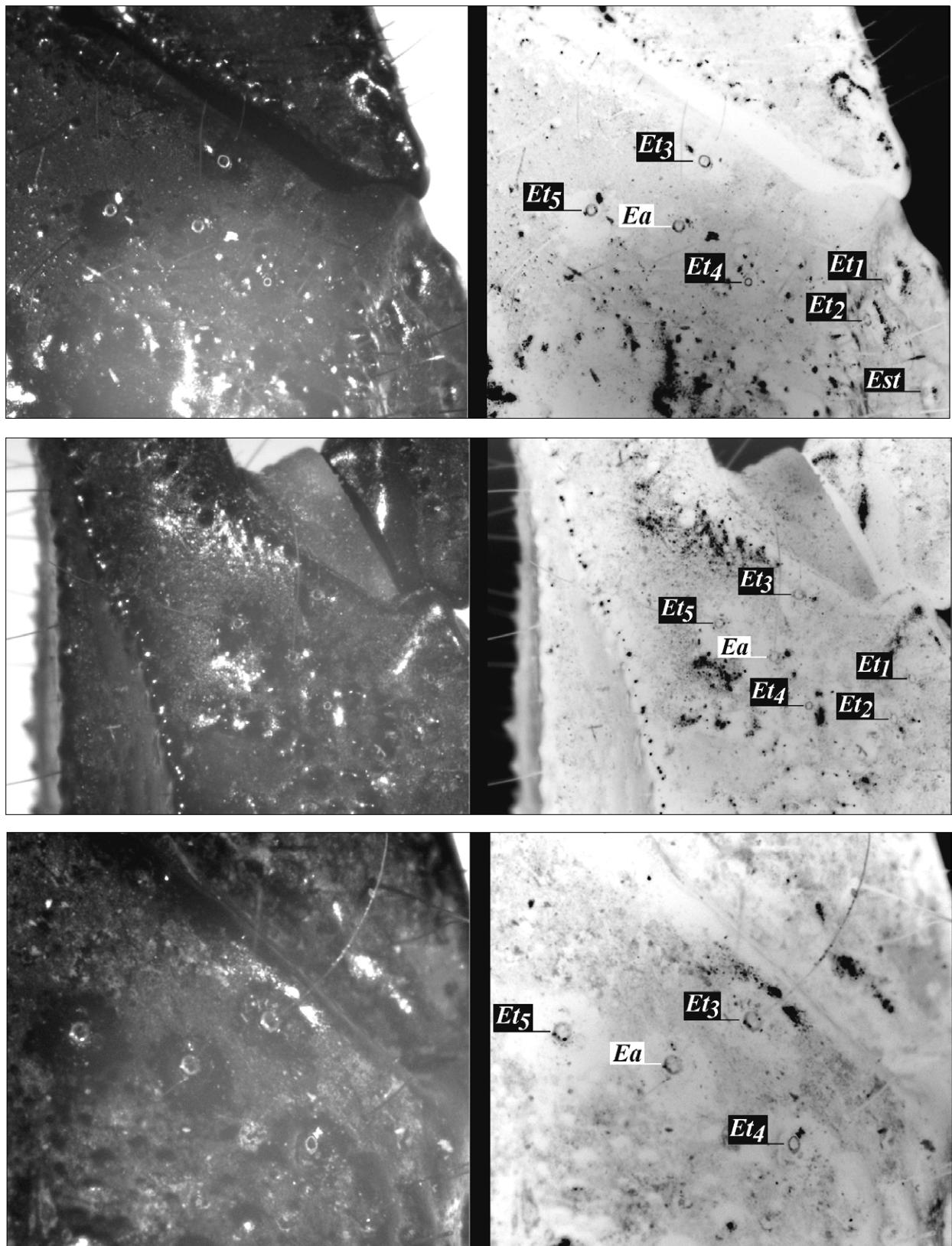


Figure 12: Examples of neobothriotaxy (*Ea*, black text on white) in chelal *Et* series in *Iurus*, shown in photo on left and annotated in photo on right. **Top.** Female, Bademli, Turkey, showing one accessory trichobothrium. **Middle.** Subadult female, Irmasan Gecidi, Akseki, Turkey, showing one accessory trichobothrium. **Bottom.** Female, Bademli, Turkey, showing one accessory trichobothrium.

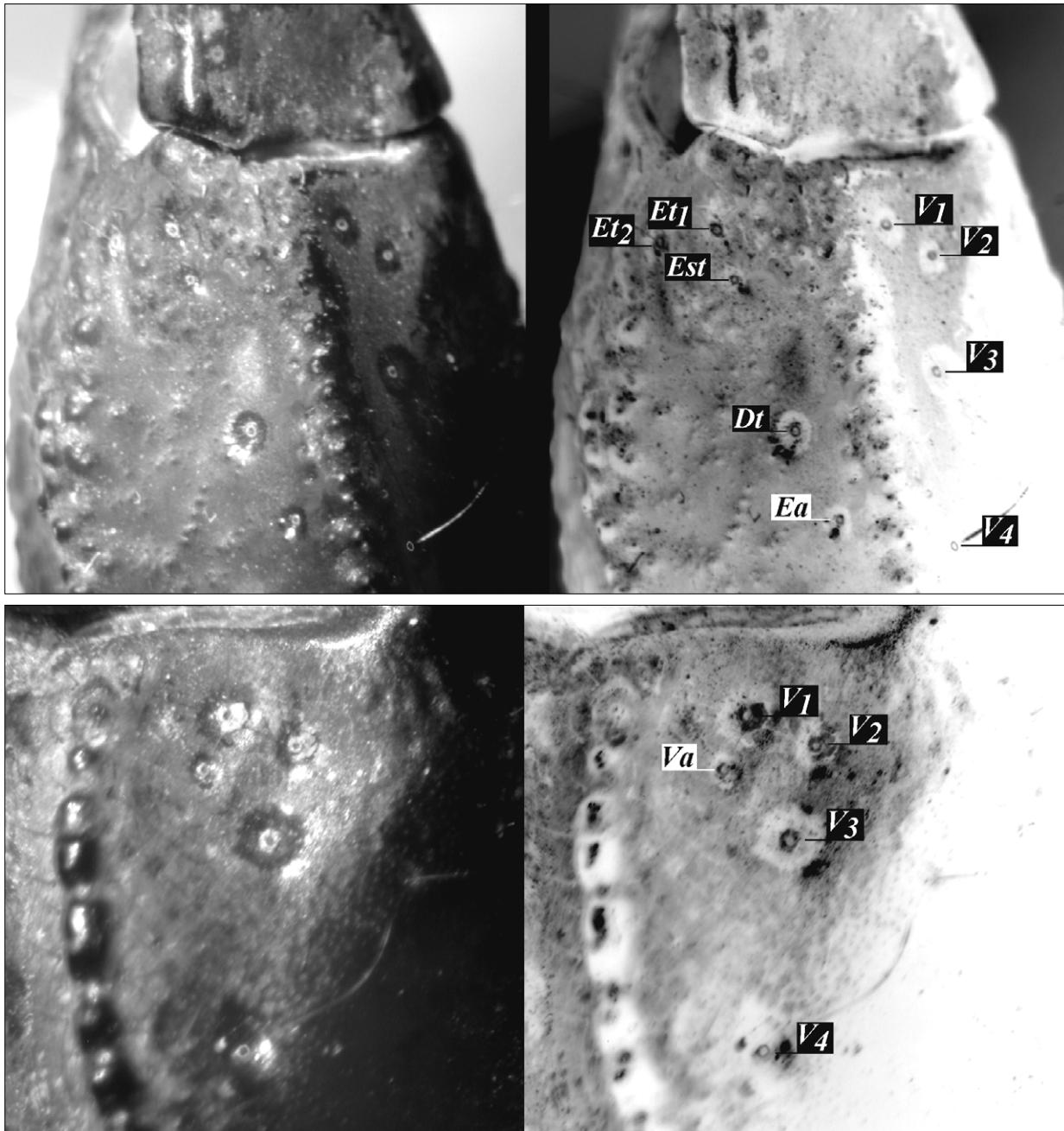


Figure 13: Examples of neobothriotaxy (*Ea* and *Va*, black text on white) in chelal *Est* and *V* series in *Iurus*, shown in photo on left and annotated in photo on right. **Top.** Female, Narli Kioi, Turkey, showing petite external accessory trichobothrium. **Bottom.** Male, Antalya, Turkey, showing petite ventral accessory trichobothrium.

petite accessory trichobothrium is quite small, slightly smaller than the special petite V_2 trichobothrium. This type of neobothriotaxy was detected on one chela of a solitary specimen from Antalya, Turkey. It is interesting to point out that this particular specimen also exhibited neobothriotaxy on both the chelal internal and external surfaces (see Tab. 1).

Neobothriotaxy on patellar external surface

In our analysis of the patellar trichobothrial patterns we have partitioned the patellar external surface into two areas. For these genera, especially *Iurus*, a well defined exteromedian (EM) carina is present which is usually heavily granulated. We use this carina to bisect the

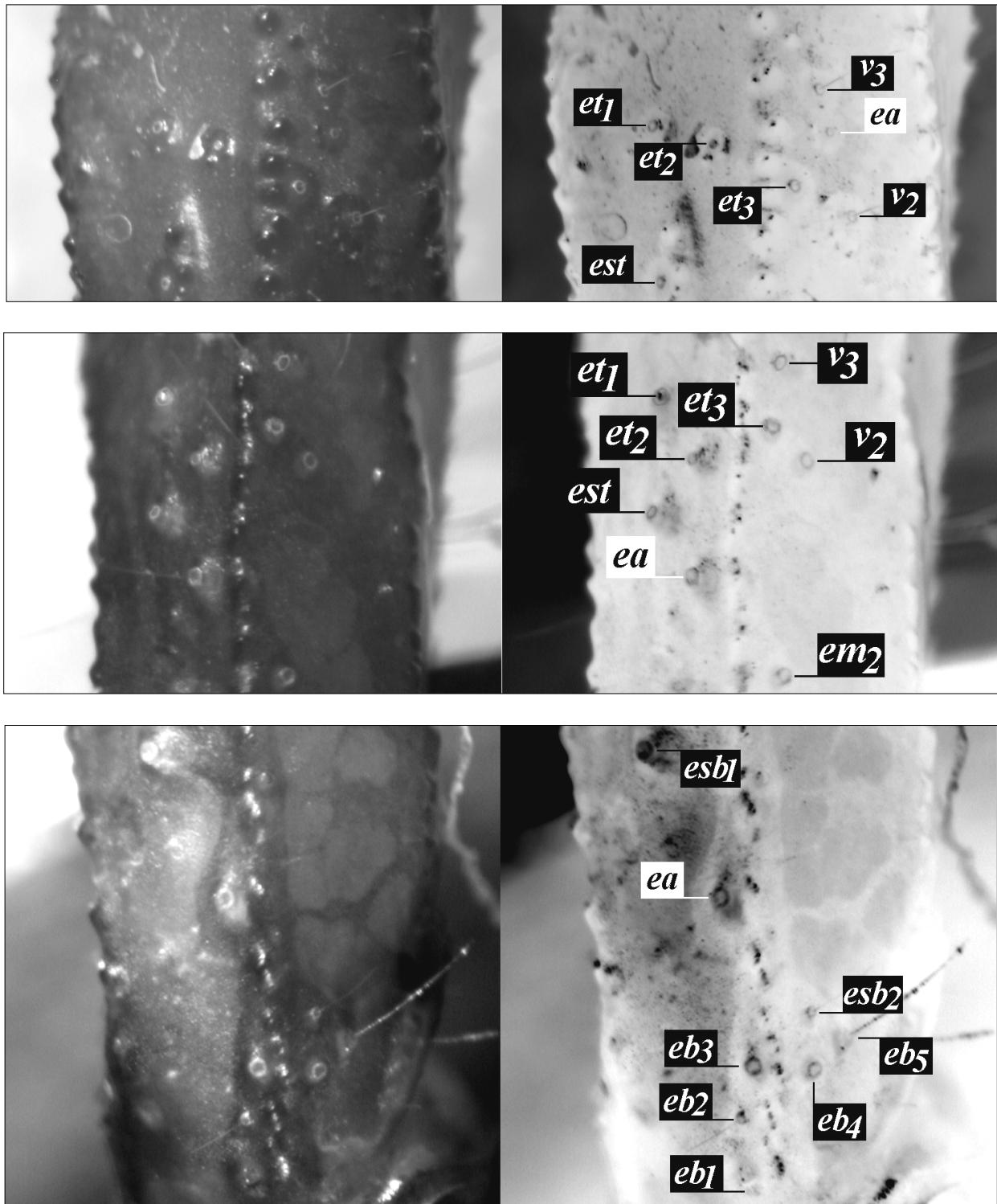


Figure 14: Examples of neobothriotaxy (*ea*, black text on white) on patella external surface in *Iurus*, shown in photograph on left and annotated in photograph on right. **Top.** Izmir (Narlı-Kioi), Turkey, subadult female, showing *petite* accessory trichobothrium in *et* series on ventral half of external surface. **Middle.** Belkis, Turkey, juvenile male, showing accessory trichobothria on the dorsal distal half of external surface. **Bottom.** Belkis, Turkey, juvenile male, showing accessory trichobothria on the dorsal basal half of external surface. See Fig. 15 for a diagrammatic pattern of the patellar external surface showing these accessory trichobothria.

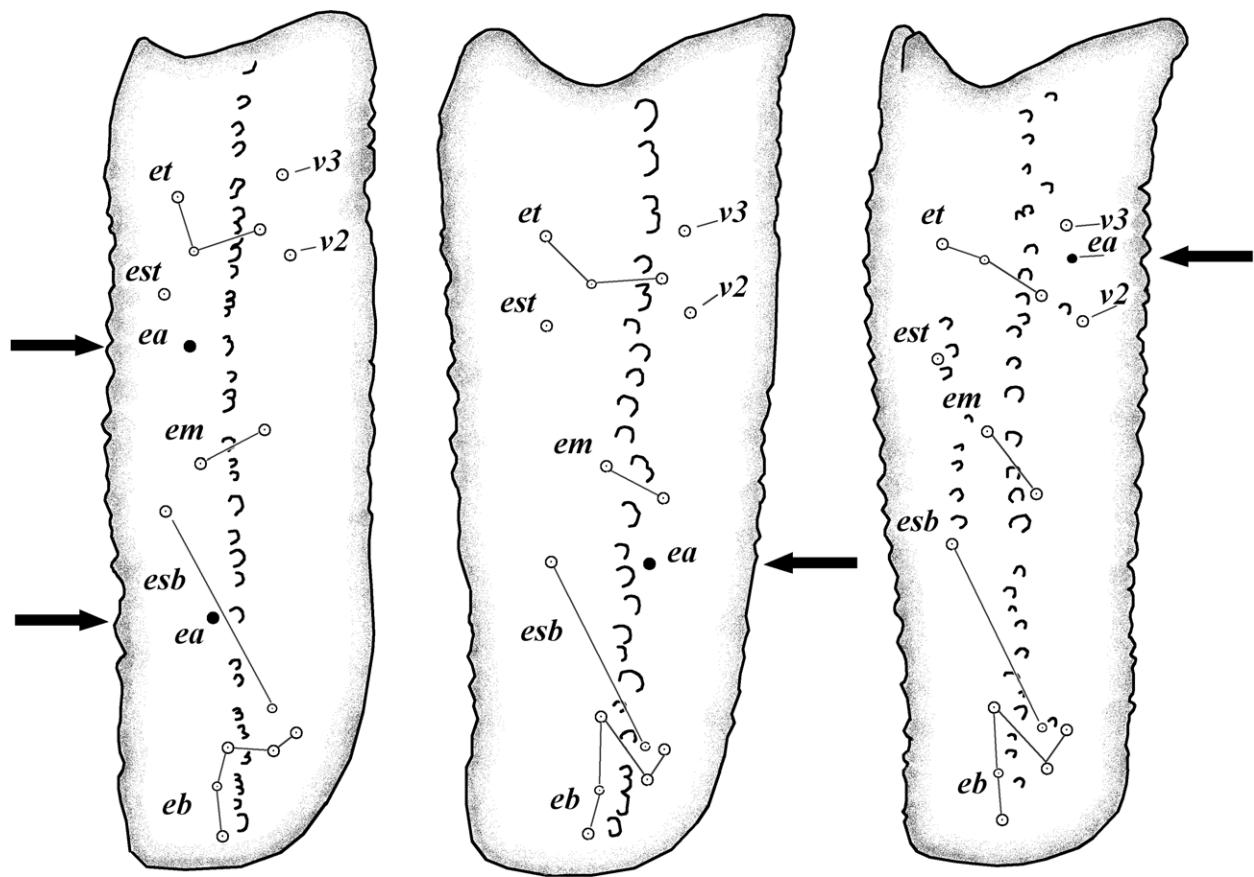


Figure 15: Neobothriotaxy (closed circles, indicated by arrow) on patella external surface in *Iurus*. **Left.** Belkis, Turkey, juvenile male, showing two accessory trichobothria on dorsal half of external surface. **Center.** Sparti, Greece, adult female, showing one accessory trichobothrium in *em* series on ventral half of external surface (from left pedipalp, figure is reversed). **Right.** Izmir (Narli-Kioi), Turkey, subadult female, showing a petite accessory trichobothrium in *Et* series on ventral half of external surface.

external surface into dorsal and ventral areas. It is interesting to point out that neobothriotaxy present in *Iurus*, three specific types, occurs both on dorsal and ventral areas of the external surface but never on both areas at the same time.

Figures 14–15 illustrates each of the neobothriotaxic types found on the patella external surface. The most frequent type encountered in our analysis, primarily in a population from Belkis, Turkey, exhibits two accessory trichobothria on the dorsal aspect of this surface. These accessory trichobothria are full size trichobothria, the most distal *ea* positioned close but proximally to *est*, and the proximal *ea* is located approximately equidistant between *esb*₁ and *esb*₂. These locations of *ea* were fairly consistent in the Belkis population (six instances). External accessory trichobothria in the chelal *Et* series is also present on the Belkis specimens for this neobothriotaxic type (see Tab. 1).

The second neobothriotaxic type is found in a solitary specimen from Sparti, Greece and only occurred on one pedipalp. Shown in Figure 15 is a single *ea*,

located on the ventral aspect of the external surface close to the *EM* carina in close proximity of trichobothrium *em*₂. This accessory trichobothrium is full size. This example of neobothriotaxy is one of only two occurrences in populations examined from Greece.

The third example of neobothriotaxy found on the pedipalp is from an isolated population from Izmir ("Narli Kioi", an old name of one of Izmir suburbs), Turkey. As shown in Figures 14–15, this neobothriotaxy is represented by a single petite *ea*. This accessory trichobothrium is located on the ventral aspect of the external surface, between *v*₃ and *v*₂. It should be pointed out that this unique neobothriotaxy occurring in this population was detected in four specimens out of seven and only on one pedipalp. In addition, two of these specimens also exhibited neobothriotaxy in the chelal *Est* series (see Tab. 1).

Discussion

It is important to note, based on the examination of 30 specimens representing a number of varied localities

in the Peloponnese, that neobothriotaxy in Greek *Iurus* appears to be quite rare. Only two instances of neobothriotaxy were detected and in each case it occurred on only one pedipalp. In addition, and important (see below), its neobothriotoxic types are unique, not matched in the Turkey populations.

Iurus occurring in the south-central area of Turkey exhibit neobothriotaxy quite frequently spanning several types, the *Ei* series being the most common (47 instances). The isolated population from Izmir ("Narli Kioi"), Turkey is proving to be very interesting: here we see that five out of seven specimens exhibit two types of neobothriotaxy, not encountered in other Turkey populations. A male specimen from Antalya, Turkey had the most types, neobothriotaxy on the chelal internal and ventral surfaces as well as on the patella, six accessory trichobothria in all (see Tab. 1).

The presence of neobothriotaxy on the internal and external surfaces of the chela is rare in Type C scorpions, only found *together* in one other genus, *Hadrurus* (Caraboctonidae, the sister family to Iuridae). Finally, as of now, neobothriotaxy has not been detected on the ventral surface of the patella, an area where neobothriotaxy commonly occurs in other Type C scorpion groups. We can also report, based on the examination of over 30 specimens from multiple localities, that neobothriotaxy has not yet been detected in *Calchas*. Therefore, if this observation holds true when other specimens are examined, then *Calchas* is the only genus in superfamily Iuroidea lacking some type of neobothriotaxy: *Hadruroides* and *Caraboctonus* exhibit consistently (ten species in all) a single accessory trichobothrium on the external surface of patella (see Vachon, 1974: fig. 139; Francke & Soleglad, 1980: figs. 13, 31); *Hadrurus* and *Hoffmannihadrurus* exhibit major neobothriotaxy on the patellar external and ventral surfaces, the chelal ventral surface, and in some genera/species groups, on the chelal internal and/or external surfaces (see Soleglad, 1976: figs. 2–25; Fet & Soleglad, 2008).

Evolutionary significance

Soleglad & Fet (2004: 102–106) and Fet & Soleglad (2008: 273–277, fig. 27) described in great detail their hypothesis concerning neobothriotaxy in Type C scorpions. Their hypothesis of accessory trichobothria loss as it relates to species dispersal and speciation in general, involved studies of large populations of *Hadrurus*, *Anuroctonus* (family Chactidae), and *Euscorpius* (family Euscorpiidae) where the number of accessory trichobothria was closely correlated to species and their geographic distribution. The assumption of this hypothesis is that accessory trichobothria are being *lost* during speciation and dispersal of a species. Clearly, the material of *Iurus* examined in this study, though

considerable, does not represent enough contiguous geographic areas or number of specimens per area to conduct similar analyses as referenced above. In addition, though nine distinct types of neobothriotaxy were detected in *Iurus*, none of these would be classified as "major neobothriotaxy" (since within each type there are only one or two accessory trichobothria present). Therefore, the observation and calibration of gradual accessory trichobothria loss as it relates to geographic distribution is probably not feasible in these cases.

However, we can make some general observations as to the presence or absence of neobothriotaxy in *Iurus* from a general geographic perspective. First we see the highest concentration of neobothriotaxy in south-central Turkey, many populations exhibiting two types. We also see this neobothriotaxy is somewhat constant in its configuration within the small populations sampled. For example, out of the nine types of neobothriotaxy described in this paper, five occur exclusively in the south-central area of Turkey. Two other types are both found in an isolated population from Izmir ("Narli Kioi"), on the western edge of the Anatolian Peninsula (Turkey). Populations from mainland Greece (Peloponnese), where only two instances of neobothriotaxy were detected, both represented distinct types, which did not match any of the types found in Turkey. Thus, we see a partitioning of these neobothriotoxic types based on geography: south-central Turkey, extreme western Turkey, and Greece.

We also take note that neobothriotaxy is much more prevalent in Turkey than in Greece: out of 77 occurrences of neobothriotaxy, only two were detected in Greek populations (2.5 %), whereas among the specimens examined, 30 % were from Greece. If we apply the accessory loss hypothesis (Soleglad & Fet, 2004; Fet & Soleglad, 2008), could these sparse data indicate that the Greek populations may be more derived (i.e. more recent), and reverting to orthobothriotoxic condition? Since *Calchas*, the sister genus of *Iurus*, is found primarily in the Anatolian Peninsula (=Turkey), does this also imply that *Iurus* could have spread to Greece from Turkey, complementing the loss hypothesis? Only the accumulation of larger and systematically collected material can tell us whether the accessory trichobothria loss is occurring in genus *Iurus*. Even in this situation, as stated above, testing of this hypothesis may not be feasible due to the relatively small numbers of accessory trichobothria involved. Additional information could come from detailed studies of *Iurus* populations on Greek islands (Karpathos, Rhodes, Crete, Kythira, etc.). A recent study of *Iurus* phylogeography using DNA markers (Parmakelis et al., 2006) indicates that evolutionary history of this genus in the Aegean region is quite ancient (estimated at more than 8 Mya), and that *Iurus* has been differentiating within Aegean landmass at least since middle Miocene.

Since Parmakelis et al. (2006) recovered only two major DNA clades of *Iurus*, and no close sister groups (of which, in fact, only *Calchas* exists) were used, it is impossible at this moment to judge from the existing phylogeny whether Greek populations are more derived or ancestral than the Anatolian ones.

Finally, it is important to mention the occurrence of *petite accessory trichobothria*. In total, we isolated 13 instances of petite accessory trichobothria out of 77. Of special importance, petite accessory trichobothria were consistently found in five neobothrioxic types: the *ia* in the Greek specimen (one instance), the *ia* in the Akseki specimen (one instance), the *ea* in the *Et* and *Est* series (six instances), *va* in *V* series (one instance), and ventral *ea* in patellar series (four instances). As stressed by Fet & Soleglad (2008), it is not unusual to encounter petite accessory trichobothria. Soleglad & Fet (2001) suggested that petite trichobothria in general are intermediate in development, and in many cases could represent trichobothria that are in the process of being lost, which is congruent with their accessory trichobothria loss hypothesis. This clearly seems to be the case in subfamily Hadrurinae where we see increasingly small petite internal accessory trichobothria extending from *ib* in *Hadrurus*, which are completely absent in *Hoffmannihadrurus* (Fet & Soleglad, 2008). If we assume that the same process is happening in *Iurus*, where we find the most concentration of neobothrioxys in south-central Turkey, many of the accessory trichobothria here being full in size, then this idea has merit since we find four other neobothrioxic types occurring in western Turkey and Greece that involve *only* petite trichobothria in three of the four cases.

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