

Figure 13: Right chelicera (35x), ventral view, of *lurus kinzelbachi*, adult male, Dilek Peninsula, Aydın, Turkey. Note that serrula is not present, only the *back* (indicated).



Figure 14: Cheliceral movable finger, ventral view, showing vestigial development of serrula in *Iurus*. **Top Left.** *I. kraepelini*, juvenile male (150x), Akseki, Antalya, Turkey. **Top Right**. *I. asiaticus*, adult female (200x), 4 km east of Kaşlıca Village, Adıyaman, Turkey. **Bottom Left**. *I. dufoureius*, subadult female (150x), Krini, Gythio, Laconia, Greece, showing worn vestigial serrula. **Bottom Right**. *I. dufoureius*, subadult female (150x), Mystras, Laconia, Greece, with vestigial serrula and conspicuous large ventral accessory denticle (*va*) indicated.



Figure 15: Distal external view of right chelal palm (35x) of *Iurus kraepelini*, juvenile male, Akseki, Antalya, Turkey, showing *neobothriotaxy*. Trichobothrial series Et_1 - Et_5 , Est, and Dt are shown as well as the solitary accessory trichobothrium, Ea, which is indicated. Note that trichobothria Et_3 and Est are petite, the latter unique to family Iuridae.

ders (see close-up in Figs. 8, 9). The pectinal **basal piece** is well-developed in *Iurus*, longer than the genital operculum in the female. Its anterior edge exhibits a somewhat narrow and shallow emargination.

The lung **stigmata** (spiracles) in *Iurus* are somewhat large, slit-like in shape (Fig. 10). They are angled roughly 45° toward anterointernal direction. The fine structure of the posterior spiracle margin (Kamenz, Dunlop & Scholtz, 2005) can be seen in Fig. 10. The stigmata of all five species are illustrated in the individual species descriptions.

Comparison to *Calchas. Iurus* differs from *Calchas* in the following. The sternum membraneous plug exhibited in *Iurus* females is considerably reduced in *Calchas*; the sternum is wider than long in *Calchas*, whereas in *Iurus* it is noticeably longer than wide in both genders (*I. dufoureius* an exception). The unique prepectinal plate conspicuous in *Calchas* females is absent in *Iurus*. The anterior emargination on pectinal basal piece in *Calchas* is generally well-developed and somewhat wide, whereas in *Iurus* it is subtle and narrow. The stigmata in *Iurus* are large, elongated and slit-like in shape, whereas in *Calchas* they are small and sub-oval.

Chelicerae

In Figures 11–12, the dorsal and ventral aspects of the *Iurus* chelicera are illustrated for *I. dufoureius* and *I.* kraepelini. This chelicera conforms to the definitive form as described for superfamily Iuroidea: ventral edge equipped with a large denticle (va), hypothesized as synapomorphic by Soleglad & Fet (2003b; character 42, state=2) and Fet & Soleglad (2008; character 9, state=1). The dorsal edge has a single large subdistal (sd) denticle, classified as symplesiomorphic (Soleglad & Fet, 2001; Fet & Soleglad, 2008). In addition, a characteristic of the chelicerae specific to Iurus within the Iuridae is the midfinger position of the large ventral denticle on the ventral edge (in *Calchas*, it is located basally). Weak to vestigial serrula is present on the ventral edge of the movable finger (Figs. 13-14), composed of at most 12-14 irregularly developed tines in juveniles and small subadults. In adults, serrula presence is dependent on the wear of the chelicerae. For example, in the adult I. kinzelbachi, sp. nov. shown in Fig. 13 only the serrula back is visible, whereas in the adult *I. asiaticus* (Fig. 14), some well defined tines are still present. Serrula in *Iurus* was first mentioned by Francke & Soleglad (1981: fig. 19). See Graham & Fet (2006: 7) for the review of serrula observations; note that fig. 2 in Graham & Fet (2006) was quoted erroneously as a serrula of a juvenile Iurus dufoureius from Crete; it in fact belongs to Calchas gruberi from Megisti.

The cheliceral fixed finger is typical of Recent scorpions, with four denticles, median (m) and basal (b)

denticles conjoined on common trunk. Ventral accessory (*va*) denticles are not present.

The ventral surface of the cheliceral palm is covered with a heavy growth of setae (Figs. 11–13) extending along the ventral edge of the movable finger and the inner surface of the fixed finger where it is the heaviest.

Comparison to *Calchas.* The chelicera of *lurus* differs from that of *Calchas* as follows. The *va* denticle of the movable finger ventral edge is much larger in *lurus* and is located midfinger whereas in *Calchas* it is located basally on the finger. The ventral distal denticle (*dd*) in *lurus* does not extend beyond its dorsal counterpart as much as in *Calchas*, where the dorsal *dd* is much shorter than the ventral *dd*. The serrula in *Calchas* is well-developed, in adults as well as in juveniles, whereas in *lurus* it is only vestigial in juveniles and small subadults, and essentially absent in adults.

Pedipalps

The trichobothrial pattern of *lurus* was illustrated and discussed in detail by Soleglad, Kovařík & Fet (2009: fig. 2) where it was contrasted with its sister genus Calchas. Therefore, we will not discuss it here in any detail except to note that the full trichobothrial patterns of the five species of *Iurus* are illustrated in this paper under their individual discussions below (Figs. 86, 119, 120, 158, 191, and 211). We will point out, however, that although a very unusual pattern in itself, representative of the family Iuridae, the pattern seen in Iurus does exhibit significant differences in individual trichobothrial positions from that found in Calchas, involving the femur, patella, and chela. At the species level, however, we did not uncover any significant positional differences in trichobothria deemed diagnostic between the five species of Iurus. Neobothriotaxy was detected in genus *Iurus*, spanning four of the five species recognized in this paper. These occurrences of neobothriotaxy, organized into 13 unique types across four species, were considerably rare in two of the species, *I*. dufoureius and I. asiaticus, common but occurring erratically in I. kraepelini, and diagnostic for I. kinzelbachi, sp. nov. In our Fig. 15, we illustrate a single accessory trichobothrium (Ea) in the Et series in I. kraepelini. Neobothriotaxy is discussed in detail in Appendix B.

The **dorsal patellar and ventral patellar spurs** (**DPS/VPS**) were illustrated by Soleglad & Fet (2003b: fig. 96) for *Calchas*, with a detailed analysis of these structures. In our Figs. 16–17 we show significantly developed DPS/VPS for *I. dufoureius* and *I. kraepelini*, illustrating two large spurs both dorsally and ventrally. In the femoral view of these spurs, shown in Fig. 17, their size and development are emphasized. We refer to these as "doubled" DPS/VPS. Accompanying the two spur sets is a large seta, represented in our figures only



Figure 16: Pedipalp patella, internal view (15x), *Iurus kraepelini*, juvenile male, Akseki, Antalya, Turkey. Note well developed *doubled* Dorsal (DPS) and Ventral (VPS) Patellar Spurs. *s* = seta areolae.



Figure 17: *Doubled* Dorsal (*DPS*) and Ventral (*VPS*) Patellar Spurs. **Top.** Femoral (50x) views, *Iurus kraepelini*, juvenile male, Akseki, Antalya, Turkey. **Middle & Bottom.** Dorsal (15x) and femoral (50x) views *I. dufoureius*, subadult female, Krini, Gythio, Laconia, Greece.





as enlarged areola (Fig. 16). There is no evidence of the DPSc or VPSc carinae in *Iurus*.

The **chelal carinae** configuration in *Iurus* complies with the "eight-carinae" configuration as identified in Soleglad & Sissom (2001: 41–44; figs. 43–72). As illustrated in our Figure 18, which shows a diagrammatic view of the chela from the fingers, this configuration excludes the ventromedian (*V2*) and subdigital (*D2*) carinae. Soleglad & Sissom (2001: character 20, state=0) characterized genus *Iurus* as conforming to this carinal configuration. Fet & Soleglad (2008: character 6, state =0) showed that this configuration, as reflected in family Iuridae, is symplesiomorphic, being present in other presumably more primitive parvorders, whereas in family Caraboctonidae the "ten-carinae" configuration is present, a demonstrated synapomorphy (state=1).

The chelal finger dentition is very distinctive in *Iurus* and is used, in part, to separate its species. The fixed and movable finger dentition is shown in Figs. 19–20 for *I. kraepelini* and *I. dufoureius*. Common to all *Iurus* species, and considered a symplesiomorphy for superfamily Iuroidea, are the oblique highly imbricated median denticle (*MD*) groups, occurring in the three other parvorders, Pseudochactida, Buthida, and Chaerilida. Interestingly, the *MD* denticle groups in sister family Caraboctonidae, though oblique, are not imbricating, which is considered a synapomorphy by Fet & Soleglad (2008: character 5, state=1). The distribution of inner (*ID*) and outer (*OD*) denticles is presented on Fig. 19. As common to most scorpions, two *ID*s are grouped

at the movable finger distal tip close to the distal denticle (DD), the remaining IDs are positioned at the beginning of MD groups distally and moving slightly more proximally in basal groups. The last two to four MD groups in either finger are not accompanied by an ID (species dependent). All MD denticle groups terminate with a slightly enlarged OD denticle, except for the basal MD group which terminates with increasingly smaller MD denticles. The most distal MD denticle group is much shorter on the movable finger, exhibiting roughly half the number of denticles than found on the fixed finger. This overall MD, ID and OD distribution is found in all five Iurus species, only the number of ID and MD denticle groups is speciesspecific, as described in detail below under species descriptions.

Fet et al. (2006) first reported the occurrence of a very unique array of minute sensilla located on the extreme distal external tip of the chelal fixed finger, termed the **constellation array**. Based on current surveys, this array is assumed to be present in one form or another in all Recent scorpions, Fet et al. (2006) having examined all four parvorders and six superfamilies. We have investigated the constellation array in all five *Iurus* species (Figs. 21–25). Interestingly, we find that each species has a different number of sensilla, ranging from two to nine, implying that this array is species-specific. In *I. asiaticus*, we detected variability, with the number of sensilla from two to four (based on two specimens).



Figure 19: Right chelal finger dentition (fixed left, movable right, 35x), *Iurus kraepelini*, juvenile male, Akseki, Antalya, Turkey. Note that the median denticle (*MD*) groups are oblique and *highly imbricated*. Bottom figure shows close-up of a movable finger distal aspect with distal denticle (*DD*), median denticles (*MD*), outer denticles (*OD*), and inner denticles (*ID*) identified (350x).



Figure 20: Right chelal finger dentition (fixed left, movable right), *Iurus dufoureius*, subadult female, Krini, Gythio, Laconia, Greece. Note movable finger is equipped with 16 inner denticles (*ID*), the largest number encountered in *Iurus* (35x).

Comparison to *Calchas.* The trichobothrial pattern in *Iurus* differs from *Calchas* as follows. Femoral trichobothrium d is located on the external surface (not dorsal); e located slightly distally of d (not significantly distally); chelal trichobothrium db is positioned at fixed finger midpoint (not basally); Db is located ventrally of external (E) carina, in line with Eb series (not dorsally of E and distally of Eb series); patellar trichobothrium i is located on the internal surface, adjacent to DI carina (not on dorsal surface). The doubled DPS/VPS are significantly developed in *Iurus*, whereas in *Calchas* they are weakly developed. Both genera comply with the "eightcarinae" configuration, but the palm is more vaulted in *Iurus*, and the vertical distance between carinae D4 and V3 is greater than the distance between carinae E and I. In *Calchas*, where palm is not vaulted and somewhat flat, the distance between D4 and V3 is less than that between E and I. In *Iurus*, the chelal finger MD rows are highly imbricated and number 14 to 16 on the movable finger, whereas in *Calchas* the MD rows are slightly



Figure 21: Constellation array in *lurus dufoureuis* showing six sensilla, subadult female, Mystras, Laconia, Greece. **Top.** Distal tip of pedipalp fixed finger showing orientation of sensilla (200x). **Bottom.** Close-up of sensilla.



Figure 22: Constellation array in *Iurus kraepelini*, showing five sensilla, male, Akseki, Antalya, Turkey. Top. Distal tip of pedipalp fixed finger showing orientation of sensilla (150x). Bottom. Close-up of sensilla (350x).



Figure 23: Constellation array in *lurus asiaticus*, showing *two* to *four* sensilla, female, Kaşlica, Adıyaman, Turkey. **Top.** Distal tip of left pedipalp fixed finger showing two sensilla (50x). **Bottom.** Right fixed finger showing four sensilla (75x).



Figure 24: Constellation array in *Iurus kadleci*, **sp. nov.**, showing nine sensilla, male, Akseki, Antalya, Turkey. **Top.** Distal tip of pedipalp fixed finger showing orientation of sensilla (50x). **Bottom.** Close-up of sensilla (150x).



Figure 25: Constellation array in *Iurus kinzelbachi*, **sp. nov.**, showing six sensilla, subadult female, Dilek Peninsula, Aydın, Turkey. **Top.** Distal tip of pedipalp fixed finger showing orientation of sensilla (100x). **Bottom.** Close-up of sensilla (350x). Note two sensilla lack a seta and the areolae are partially formed. s = sensilla, a = areolae.

imbricated and number 7 to 8. In both genera, the number of constellation array sensilla are species-specific (of eight total species of Iuridae this character is unknown only for *C. nordmanni*).

Legs

Iurus has a pair of **pedal** (tarsal) **spurs** located on the ventral surface at the juncture of the basitarsus and tarsus (Figs. 26, 28). These spurs are typical for Recent scorpions; they are smooth, neither exhibiting spinelets as in *Hadrurus* and *Hoffmannihadrurus* (family Caraboctonidae), nor showing morphometric differences between the spurs as seen in some environmentally adapted scorpions such as psammophiles. The **tibial spur** found in *Calchas* is not present in *Iurus*.

Fet et al. (2004) presented a detailed analysis of the iuroid leg tarsus. In this important study, it was shown that all six iuroid genera had some form of spinule clusters on the ventral surface of the leg tarsus. The variety and overall manifestation of this spination, however, is considerable across the six genera. In Iurus, the individual spinules are exceptionally small and form actual clusters ("tufts") of dense spinules in a medial line along the tarsus, terminating in a pair of enlarged clusters (Figs. 27, 29-31). These clusters are significantly developed in adults, with individual spinule counts exceeding 200 (Fet et al., 2004: tab. I), whereas in juveniles individual spinule clusters may exhibit as few as 3 or 4 spinules (Fig. 31). The leg basitarsus also has spinule clusters in two elongated rows on the ventral surface (Fig. 28).

Soleglad & Fet (2003b: character 57, state=3) and Fet & Soleglad (2008: character 4, state=1) demonstrated that the ventral aspect of the tarsus with heavy spination is a synapomorphy for superfamily Iuroidea.

Comparison to *Calchas. Iurus* lacks the tibial spur found on legs III–IV in *Calchas.* The spination of the leg tarsus is considerably different between *Iurus* and *Calchas.* In *Iurus*, highly populated spinule clusters are found on ventral surface of the tarsus and the basitarsus, whereas in *Calchas* irregular spinule groups exist on the base of the tarsus, only occurring along the entire length of the tarsus in juveniles and small subadults. In addition, two large rows of setae with large sockets are found on the ventral aspect of the tarsus in *Calchas*; these rows are absent in *Iurus*.

Metasoma and telson

The **metasomal** structure of *lurus* is typical for many scorpions of the parvorder Iurida (Fig. 32). Segments I–IV become narrower and longer beginning from the basal segment, with segment IV usually the narrowest and longest of the four segments. Segment V is considerably longer than segment IV, 1.60 to 1.80 times longer. Segments I-IV exhibit dorsal, dorsolateral, lateral, ventrolateral, and ventromedian carinal pairs, the lateral being complete on segment I, and decreasing in size to obsolete on segments II-IV. These carinae are well-developed and usually granulated or crenulated; in particular, the dorsal carinae are highly serrated. The dorsal and dorsolateral carinae do not terminate in an enlarged denticle. The dorsolateral carinae of segment IV are not flared distally, but terminate at the condyle. Segment V has dorsolateral, lateral, ventrolateral, and ventromedian carinae, the latter singular. The lateral carinae are present on the anterior two-thirds of the segment. As with the other carinae, segment V carinae are granulated to serrated. The single ventromedian carina is usually straight, but can terminate in an irregular bifurcation.

The **telson** in *Iurus* is somewhat elongate with a long vesicle, roughly twice as long as the aculeus (Figs. 35–40). The vesicle ventrally is covered with dense setation. The vesicle/aculeus juncture is not abrupt, but instead gradually narrowing to the aculeus base. The **subaculear setal pair** (SSP) is located on the base of the aculeus, their areolae forming a slight raised area. This area is more noticeable on juvenile and subadult specimens (Figs. 33–34).

Comparison to Calchas. The metasoma in Iurus is much thinner than in Calchas. All segments are longer than wide except for segment I in *Iurus (I. kadleci*, sp. nov., is a noted exception where all segments are longer than wide), whereas in Calchas segments I-II are wider than long, and in two species, segment III is also wider than long. In Iurus, segment V is 3.00-4.25 times longer than wide in males and 2.95-3.85 in females, whereas in Calchas it is 2.10-2.55 times longer in males and 2.03-2.41 in females. The telson vesicle is thinner in *Iurus*, the telson length 3.60–4.10 times longer than deep: ventrally it is densely covered with setae. In Calchas, the vesicle is heavier, telson length 2.65-3.05 times longer than deep: ventral setation is not as dense, being irregularly scattered on ventral surface. In all Iurus species and two Calchas species (C. gruberi the only exception), the SSP is located on the aculeus base.

Hemispermatophore

The terminology used in this discussion is derived, in part, from Lamoral (1979: 520–527), Stockwell (1989: figs. 186, 189–203), Hjelle (1990: 59–62), and Soleglad & Fet (2008: 29–40). In some cases, new terminology was instituted for the simplistic but unusual hemispermatophore found in family Iuridae. The four views of this structure are addressed here as dorsal, internal, ventral, and external.

Morphology. The hemispermatophores dissected in this study were, in almost all cases, enclosed in a membraneous sac (Fig. 41). The paraxial organ seminal



Figure 26: Left leg I, ventral view, *Iurus kraepelini*, juvenile male, Akseki, Antalya, Turkey.



Figure 27: Leg I tarsus (35x) and its closeup (top, 200x), ventral view, showing characteristic spinule clusters. *Iurus asiaticus*, male, Kaşlica, Adıyaman, Turkey.