ABSTRACT. Five scorpion genera of superfamily Iuroidea exhibit ancient disjunct ranges (South America, North America, Mediterranean), and are an important object in the study of scorpion phylogeny. They have an exceptional variety of tarsal leg setation/spination (Soleglad & Fet 2003). New SEM data from all five genera and two families: Caraboctonidae (*Caraboctonus*, *Hadruroides*, *Hadrurus*) and Iuridae (*Iurus*, *Calchas*) are characterized in detail. We demonstrate two major patterns: (1) an irregular median row of grouped spinule clusters, found in juvenile to subadult but reduced in adult (*Calchas*); or (2) a median row of highly concentrated spinule clusters. Pattern (2) is either forming "spinule tufts" (*Caraboctonus*, *Hadruroides*, *Iurus*), or individual "spinule-looking" protuberances (*Hadrurus*). We suggest that the latter are a derived feature as a result of fusion of separate spinules into a solid structure.

Tarsal Spinule Clusters and Evolution of the Superfamily Iuroidea (Scorpiones)

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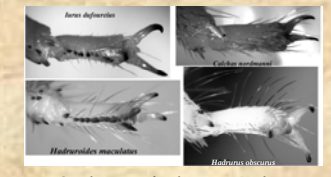
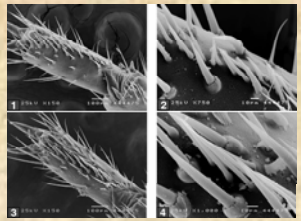
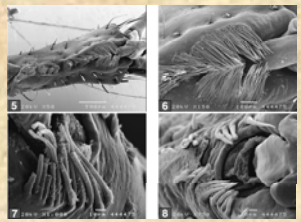


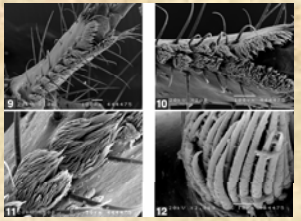
General appearance of tarsal armament in Iuroidea



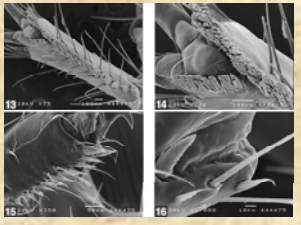
Figs. 1-4. Lateral-ventral view of leg tarsus of juvenile *Calchas nordmanni*, Megisti Island, Greece. **1.** full tarsus, leg I. **2.** closeup of spinule clusters and socketed setae, leg I. **3.** full tarsus, leg III. **4.** closeup of spinule clusters and socketed setae, leg III.



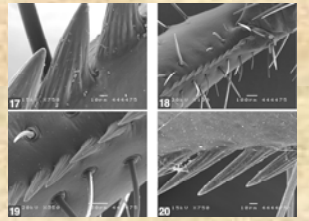
Figs 5-8. Lateral-ventral view of leg tarsus of adult (Turkey) and juvenile *Iurus dufourelus* (Crete, Greece). **5.** full tarsus of leg III, adult. **6.** Closeup of distal aspect of tarsus of leg III, adult. **7.** closeup of distal aspect of tarsus of leg IV, juvenile (seven month instar). **8.** closeup of distal aspect of tarsus of leg III, juvenile (three month instar).



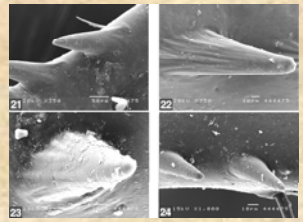
Figs. 9-12. Lateral-ventral view of leg III tarsus of adult *Carabocton us keyserlingi* (Chile). **9.** full tarsus, showing blunted unguicular spine. **10.** closeup of distal aspect of tarsus. **11.** closeup of spinule clusters. **12.** closeup of single spinule cluster showing the delicate striations on individual spinules.



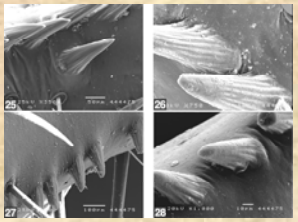
Figs. 13-16. Lateral-ventral view of leg tarsus of *Hadru*roides species. Figs. **13** and **14.** *H. maculatus*, adult (Huancayo, Peru). Figs. **15** and **16.** *H. charcausus*, instar 2 (Peru). **13.** full tarsus, leg III. **14.** closeup of distal aspect showing blunted unguicular spine, leg III. **15.** full tarsus, leg I. **16.** Closeup of spinule clusters on basitarsus, leg I.



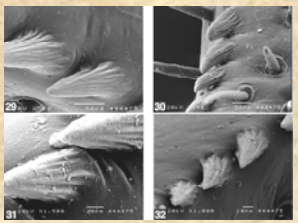
Figs. 17-20. Lateral-ventral view of leg III tarsus of *Hadrurus a. arizonensis*. **17.** Closeup of fused spinule cluster of adult (carapace length = xx.x mm). Borrego Springs, California. **18.** Medium view of fused spinule clusters of subadult, Arroyo Salado, ABDSP, California. **19.** Closeup of fused spinule cluster of subadult. **20.** Closeup of fused spinule cluster of juvenile (carapace length = 3.9 mm), Arroyo Salado, ABDSP, California.



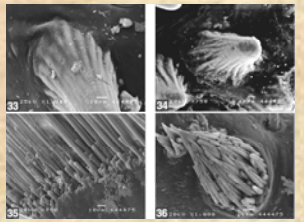
Figs. 21-24. Lateral-ventral view of leg III (leg IV in Fig. 24) tarsus of Mexican *Hadrurus* species. **21.** Closeup of fused spinule cluster of adult *H. gertschi*, Iguala, Guerrero, Mexico. **22.** Closeup of fused spinule cluster of adult *H. aztecus*, Tehuacan, Puebla, Mexico. **23.** Closeup of fused spinule cluster of subadult *H. aztecus* (carapace = 9.1 mm). **24.** Closeup of fused spinule cluster of juvenile *H. aztecus* (carapace length = 4.6 mm), Tehuacan, Puebla, Mexico.



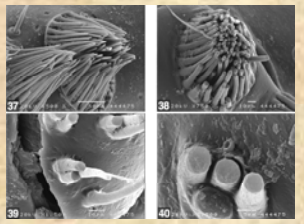
Figs. 25-28. Lateral-ventral view of leg III tarsus of Baja California *Hadrurus* species. **25.** closeup of fused spinule cluster of adult *H. hirsutus*, Cabo San Lucas, Baja California Sur, Mexico. **26.** closeup of fused spinule cluster of adult *H. concolor*, Santa Rosalia, Baja California Sur, Mexico. **27.** closeup of fused spinule cluster of adult *H. pinteri*, Oakies Landing, Baja California Norte, Mexico. **28.** closeup of fused spinule cluster of subadult *H. pinteri* (carapace = 7.0 mm), Oakies Landing, Baja California Norte, Mexico.



Figs. 29-32. Lateral-ventral view of leg III tarsus of *Hadrurus* species. **29.** closeup of fused spinule cluster of adult *H. spadix*, Nevada. **30.** closeup of fused spinule cluster of adult *H. obscurus*, ABDSP, California. **31.** closeup of fused spinule cluster of subadult *H. obscurus* (carapace = 7.5 mm), Split Mountain, ABDSP, California. **32.** closeup of fused spinule cluster of juvenile *H. obscurus* (carapace = 4.0 mm), Split Mountain, ABDSP, California.



Figs. 33-36. Comparison of setal clusters for caraboctonid genera. **33.** Closeup of fused spinule cluster of adult *Hadrurus pinteri*, Oakies Landing, Baja California Norte, Mexico. **34.** Closeup of fused spinule cluster of adult *Hadrurus obscurus*. ABDSP, California. **35.** Closeup of spinule cluster of adult *Hadruroides charcausus*, Peru. **36.** Closeup of spinule cluster of adult *Hadruroides maculatus*, Huancayo, Peru.



Figs 37-40. Lateral-ventral view of leg III tarsus of adult male (Turkey), and adult female and juvenile (seven month instar; Crete, Greece) *Iurus dufoureius*. **37.** Closeup of spinule cluster of male adult. **38.** Closeup of spinule cluster of adult female showing flathead spinules. **39.** Closeup of spinule cluster of juvenile showing three spinules. **40.** Closeup of spinule cluster of juvenile showing four flathead spinules.

Introduction

Soleglad & Fet (2003), in their revision of high-level phylogeny of extant scorpions presented five basic patterns for the armature of the ventral aspect of the leg tarsus:
(1) two median rows of spinules, parvorder Pseudochactida;
(2) two or more rows of irregularly positioned setae with medium to large sockets, spinules variable, as follows: (2a) no spinules, parvorder Buthida; (2b) medium row of spinules present, parvorder Chaerilida;
(3) medially oriented row of spinule clusters, parvorder Iurida, superfamily Iuroidea;
(4) paired lateral rows of rigid "spinoid" setae with large limbated sockets, spinules optional, parvorder Iurida, superfamily Scorpionoidea; and
(5) paired lateral rows of small to medium setae with small sockets and a median row of spinules, parvorder Iurida, superfamily Chactoidea.

In this study, we present further detailed analysis of leg tarsus armature for superfamily Iuroidea. In particular, multiple species and various development stages were studied (in genus *Hadrurus*, all eight species were studied).

Iuroid Tarsus Armature

As reported by Soleglad & Fet (2003), significant ontogenetic differences are detected in the development of the highly unusual tarsal spinule clusters on legs throughout the scorpion superfamily Iuroidea (families Iuridae and Caraboctonidae). In general, with the notable exception of genus *Calchas*, the spinule clusters and/or fused spinule clusters become more developed as the individual grows with subsequent molts, showing considerable developmental differences between early ontogenetic stages and the adult. Before we discuss these differences, the case with *Calchas* will be addressed. In *Calchas* (found only in Asian Turkey and on a couple of Greek islands, Samos and Megisti, off Anatolian coast), the ventral aspect of leg tarsus in adults is equipped with a significant display of irregularly placed large socketed setae, very similar to those seen in the genus *Chaerilus* (Chaerilioidea). Essentially, except for the basal and suprabasal areas of the tarsus, spinule clusters are absent in the *Calchas* adult. However, in subadults and, in particular, in juveniles, medially a significant number of irregularly placed spinule clusters span the entire leg tarsus, with a heavier emphasis on the basal aspects (Figs. 1-4). Thus, phenotypic expression of spinules disappears in adult *Calchas*.

Exhibited in *Calchas*'s sister genus, *Iurus* (found in Turkey and Greece), we see in the adults highly concentrated spinule clusters extending from the base of the tarsus to the enlarged pair of clusters situated distally on the tarsus segment (Figs. 5-6). Individual clusters contain as many as 100+ spinules, the distal cluster pair considerably more. However, the juveniles have significantly lower number of spinules per cluster. In juveniles seven months of age, the individual cluster contains as few as 3 spinules (Fig. 39), and the distal cluster pairs contain as little as 14 spinules in a seven month old specimen (Fig. 7), and only 11-12 in a three-month old specimen (Fig. 8). Also of interest is the development of the individual spinule in the cluster: for genus *Iurus*, we see that the cluster itself is truncated distally (Figs. 5, 37-38), and, in general, each spinule is squared off distally (Figs. 38-40). Also of importance, and also seen in Caraboctoninae (see below), the length of spinules located on the outer ring of the cluster are shorter than the more centrally oriented spinules (Figs. 37-38). We hypothesize here that these spinules are new, not fully developed. That is, in each molt, the spinule cluster gains new outer spinules, short initially, and then grow in length on successive molts. Finally, each spinule cluster base is surrounded by a low profile ring, providing a base for the outer spinules (Figs. 37-38).

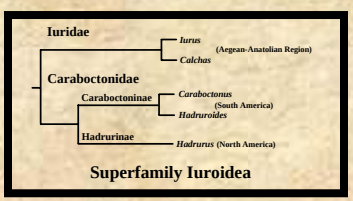
In two genera of South American iuroids (subfamily Caraboctoninae), we see the same configuration as that described above for the Old World genus *Iurus*. Adults have highly concentrated spinule clusters extending the entire length of the tarsus, including, exactly as in *Iurus*, a pair of distal spinule clusters (Figs. 9-12, *Caraboctonus*; Figs. 13-16, *Hadruroides*); we see individual clusters on adults approaching the same numbers of spinules as that seen in *Iurus*, and, as well, in the distal cluster pair. Also as in *Iurus*, the number of spinules within a cluster is considerably less in juvenile specimens. This is illustrated in a dramatic fashion for an instar-2 specimen of *Hadruroides charcausus* (Figs. 15-16), where we see individual spinules clusters with a considerably smaller number of spinules. However, the structure of the spinule cluster in this subfamily is different from that in *Iurus*: individual spinule clusters taper distally, forming a "point" at their extremity (i.e., not truncated distally as in *Iurus*). In addition, the individual spinules are also pointed (Fig. 11 and 36), not "squared off" as in *Iurus* (Figs. 38-40). As in *Iurus*, the outer spinules within a cluster are shorter than the more centrally oriented spinules, again supporting our suggestion that new spinules are acquired during each molt, shorter initially, and then becoming longer on successive molts. Again, as in *Iurus*, the outer perimeter of a spinule cluster is seen with a low profile base (Figs. 11 and 36).

The North American iuroid subfamily Hadrurinae exhibits an amazing difference in the spinule cluster configurations compared to all other iuroids. As reported in Soleglad & Fet (2003), genus *Hadrurus* has a single median row of "spinules", typical in size and overall configuration as those found in the Chactoidea. However, under high magnification we see that the individual "spinule" is composed of high definition ridges on the basal two-thirds of the structure; each ridge, at the extreme basal aspect, appearing to originate separately, as, for example, "roots of a tree" (Figs. 17, 22, 25-26, 29-30, and 33). To one degree or another, this configuration is found in all eight species of *Hadrurus*, especially in the species comprising the "hirsutus" group (Soleglad, 1976; Fet et al. 2001). As suggested in Soleglad & Fet (2003), we hypothesize here that this highly convoluted "spinule" is in fact, *a fused spinule cluster*, presumably evolved from the highly concentrated spinule cluster found in its sister subfamily Caraboctoninae. This is readily apparent when one compares Figs. 34 (*Hadrurus obscurus*) and 36 (*Hadruroides maculatus*): the two clusters are of the same basic shape, both are pointed, many individual spinules are visible, and each have a low profile base at the extreme proximal aspect of the structure (albeit more irregular in *Hadrurus*).

In *Hadrurus*, the number of ridges is less than that in subfamily Caraboctoninae (this is to be expected, however, if we trace the complete evolution of derivations proposed in this paper). As in *Iurus* and Caraboctoninae, the number of ridges of the fused spinule cluster is lower in subadult and juvenile specimens. If an adult *Hadrurus arizonensis* (Fig. 17) is compared to a juvenile (Fig. 20), we can see a reduction of approximately 50 % in the number of ridges. This can be seen also in species *H. obscurus* (Figs. 34 and 32). Of particular importance, is the reduction of these ridges in the "aztecus" group (Figs. 21-24). In these Mexican species we see that in an adult *H. gertschi* only a subtle trace of the ridges are visible on the extreme base of the fused spinule; in *H. aztecus*, a well developed set of ridges ois present in an adult, comparable to that exhibited in the "hirsutus" group, but in the subadult the definition and number of ridges is considerably lower; in the juvenile, they are absent altogether. We consider this trend in the "aztecus" group phylogenetically important.

Importance for the Phylogeny of Hadrurinae

Since we see definite fused spinule clusters in all *Hadrurus* species, except for the "aztecus" group, where this configuration is either nonexistent or inconsistently exhibited with different stages of a specimen's development, we can conclude that the "hirsutus" group (found in the United States and Baja California, Mexico) is more primitive than its sister "aztecus" group (distributed in southern mainland Mexico). This conclusion is based on the hypothesis that the fused spinule cluster seen throughout the "hirsutus" group is derived directly from the highly concentrated spinule clusters seen in *Hadrurus*'s sister subfamily, Caraboctoninae. Therefore, the "aztecus" group is more derived, as the evidence of the fused spinule cluster becoming less developed, if not obsolete altogether. This conclusion is also supported by examining the accessory trichobothria on pedipalp found in this genus. For the "hirsutus" group, we see 2-7 internal accessory trichobothria on the distal fixed finger, and in the "aztecus" group, internal accessory trichobothria are absent. The underlying foundation for this hypothesis is that the accessory trichobothria are being lost during speciation, and, even within a species geographic radiation, as documented by extension statistical analyses of *Hadrurus* trichobothria patterns (Soleglad, 1976; Fet et al., 2001). Although one may conclude that, since the "aztecus" group is geographically closer to its sister subfamily, distributed in South America, possibly it is the more primitive of the two groups. However, since we see significant disjunction in the distribution of the iuroids in general, implying a relatively ancient lineage within parvorder Iurida, we suggest that the disjunct distribution of the genus *Hadrurus*, and its split from its South American sister group, Caraboctoninae, occurred far back enough in time such that one cannot necessarily imply phylogenetic relationships alone based on geographic proximity. In addition, *H. pinteri*, presumably the most primitive of all *Hadrurus* species (fig. 27), occurs sympatrically in Baja California with two other species, and this fact, coupled with the recent split of Baja California from mainland Mexico (estimate 5 Ma), indicates that one must be careful in making the phylogenetic associations based on modern geographic distribution alone.



Phylogeny of superfamily Iuroidea (after Soleglad & Fet, 2003)

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