

ARTÍCULO:

Tarsal armature in the superfamily luroidea (Scorpiones: lurida)

Victor Fet

Department of Biological Sciences,
Marshall University,
Huntington, West Virginia 25755,
USA. fet@marshall.edu

Michael E. Soleglad

P.O. Box 250, Borrego Springs,
California 92004, USA

David P.A. Neff

Department of Chemistry,
Marshall University,
Huntington, West Virginia 25755,
USA

Iasmi Stathi

Natural History Museum of Crete
University of Crete
P.O. Box 2208
71409 Irakleio, Crete, Greece

Revista Ibérica de Aracnología

ISSN: 1576 - 9518.

Dep. Legal: Z-2656-2000.

Vol. 10, 31-XII-2004

Sección: Artículos y Notas.

Pp: 17-40.

Edita:

Grupo Ibérico de Aracnología (GIA)

Grupo de trabajo en Aracnología de la
Sociedad Entomológica Aragonesa
(SEA)

Avda. Radio Juventud, 37

50012 Zaragoza (ESPAÑA)

Tef. 976 324415

Fax. 976 535697

C-elect.: amelic@telefonica.net

Director: A. Melic

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ARTÍCULO:

TARSAL ARMATURE IN THE SUPERFAMILY LUROIDEA (SCORPIONES: LURIDA)

Victor Fet, Michael E. Soleglad,
David P.A. Neff & Iasmi Stathi

Abstract:

Six scorpion genera of the superfamily luroidea 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 armature (setation / spination) on the leg tarsus (Soleglad & Fet, 2003). New SEM data from all six genera of both iuroid families: Caraboctonidae (*Caraboctonus*, *Hadrurides*, *Hadrurus*, and *Hoffmannihadrurus*, **gen. nov.**) and luridae (*Iurus* and *Calchas*) are characterized in detail. We demonstrate two major patterns: (1) an irregular median row of grouped spinule clusters, found in juveniles to subadults but reduced in adults (*Calchas*); and (2) a median row of highly concentrated spinule clusters. Pattern (2) appears either as "spinule tufts" (*Caraboctonus*, *Hadrurides*, *Iurus*), or as individual "spinule-looking" protuberances (*Hadrurus* and *Hoffmannihadrurus*). We suggest that the latter structure is a derived feature resulting from the fusion of separate spinules into a solid structure. In addition, based on this analysis as well as differences in the trichobothrial patterns, we establish a new genus in the subfamily Hadrurinae, *Hoffmannihadrurus*, **gen. nov.**, which includes both species in the former "aztecus" group of *Hadrurus* (Mexico): *Hoffmannihadrurus aztecus*, **comb. nov.**, and *H. gertschi*, **comb. nov.** The genus *Hadrurus* is now restricted to six species in the former "hirsutus" group (United States and Baja California, Mexico).

Key words: Scorpiones, luroidea, luridae, Caraboctonidae, Hadrurinae, tarsal armature.

Taxonomy: *Hoffmannihadrurus*, **gen. nov.**

Hoffmannihadrurus aztecus, **comb. nov.**

Hoffmannihadrurus gertschi, **comb. nov.**

La armadura tarsal en la superfamilia luroidea (Scorpiones: lurida)

Resumen:

Seis géneros de escorpiones de la superfamilia luroidea presentan distribuciones disjuntas antiguas (Sudamérica, Norteamérica, Mediterráneo), y son un importante objeto de estudio en relación con la filogenia de los escorpiones. Tienen una variedad excepcional de armaduras (sedas / espinas) en los tarsos de las patas (Soleglad & Fet, 2003). Se comentan en detalle datos nuevos, obtenidos con microscopio de barrido electrónico, referentes a los seis géneros de las familias iuroideas, Caraboctonidae (*Caraboctonus*, *Hadrurides*, *Hadrurus* y *Hoffmannihadrurus*, **gen. nov.**) y luridae (*Iurus* y *Calchas*). Se han constatado dos estructuras importantes: (1) una hilera central irregular de grupos de espinulas reunidos, presente en juveniles y subadultos pero reducida en los adultos (*Calchas*); y (2) una hilera central de grupos de espinulas muy concentradas. La estructura (2) aparece, o bien como "mechones de espinulas" (*Caraboctonus*, *Hadrurides*, *Iurus*), o como protuberancias individuales "con aspecto de espinulas" (*Hadrurus* y *Hoffmannihadrurus*). Sugerimos que la segunda estructura es un carácter derivado procedente de la fusión de espinulas individuales para formar una estructura sólida. Por otra parte, según este análisis y también en atención a las diferencias en las estructuras trichobotriales, establecemos un nuevo género dentro de la subfamilia Hadrurinae, *Hoffmannihadrurus*, **gen. nov.**, que incluye las dos especies del antiguo grupo "aztecus" de *Hadrurus* (Méjico): *Hoffmannihadrurus aztecus*, **comb. nov.**, y *H. gertschi*, **comb. nov.** El género *Hadrurus* queda ahora restringido a las seis especies del antiguo grupo "hirsutus" (Estados Unidos y Baja California, Méjico).

Palabras clave: Scorpiones, luroidea, luridae, Caraboctonidae, Hadrurinae, armadura tarsal.

Taxonomía: *Hoffmannihadrurus*, **gen. nov.**

Hoffmannihadrurus aztecus, **comb. nov.**

Hoffmannihadrurus gertschi, **comb. nov.**

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 scorpion leg tarsus:

1. two median rows of spinules, parvorder Pseudochactida

2. two or more rows of irregularly positioned setae with medium to large sockets; expression of spinules variable, as follows: (2a) no spinules, parvorder Buthida; (2b) median row of spinules present, parvorder Chaerilida

[Note: in this study we have verified the presence of this median spinule row

in five species of *Chaerilus* (as that illustrated in Soleglad & Fet, 2003: Fig. 13); in addition, Pocock (1900: 53) used the presence of this row as a diagnostic character of the family Chaerilidae. Consequently, we can conclude that the median spinule row in all probability is present in all species of *Chaerilus* and therefore, consider this configuration separate from that exhibited in buthoids, delineated here as 2a and 2b.]

3. medially oriented row of spinule clusters, parvorder Iurida, superfamily Iuroidea

4. two lateral rows of rigid “spinoid” setae with large limbed sockets, spinules optional, parvorder Iurida, superfamily Scorpionoidea

5. two 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 based on SEM microscopy of leg tarsus armature for all genera of the superfamily Iuroidea. Multiple species and various developmental stages were studied. In subfamily Hadrurinae, we studied all eight species spanning both genera. In addition, preliminary information is also provided for the armature of the leg basitarsus.

Based on results of this analysis, as well as trichobothrial pattern differences, we have divided the subfamily Hadrurinae into two genera, *Hadrurus* (= “hirsutus” group) and *Hoffmannihadrurus*, **gen. nov.** (= “aztecus” group). See Soleglad (1976) and Fet et al. (2001) for definitions of these groups. This emendation is followed throughout the remainder of this paper and is officially established in the section on phylogeny, where diagnoses, a key, and a species list are provided.

Methods & Material

SEM microscopy

To investigate the leg tarsal armament, legs (usually III or IV) were removed from the preserved or freshly frozen animals and fixed for 12 hours in 0.1 M sodium cacodylate with 2.5 % glutaraldehyde (freshly prepared). After rinse/soak for 12 hours in plain 0.1 M sodium cacodylate, specimens were post-fixed for 2 hours in freshly prepared 1 % osmium tetroxide again in sodium cacodylate. Specimens were rinsed three times with distilled water and dehydrated in an ethanol series (50, 75, 95, and two changes of 100 %) before being dried and coated with gold/palladium (ca. 10 nm thickness) in a Hummer sputter coater. Digital SEM images were acquired with a JEOL JSM-5310LV at Marshall University, West Virginia. Acceleration voltage (10–20 kV), spot size, and working distance were adjusted as necessary to optimize resolution, adjust depth of field, and to minimize charging.

Spinule count estimates

The number of spinules estimated in individual clusters is calculated as follows: Each cluster is arranged essentially in an irregular cone, the base forming somewhat between an ellipse and a circle. We count the visible spinules occurring in the outer ring of the cone (i.e., the

base of the spinule cluster) for 180°, i.e., approximately one-half its base. From this number we can calculate, in general, the number of spinules contained in the cluster. For the fused spinule clusters exhibited in subfamily Hadrurinae, we calculate only the number of ridges circumscribing the cone-shaped spinule base. For the distal spinule cluster occurring in genera *Iurus*, *Caraboctonus*, and *Hadruidoidea*, we only count the number of visible spinules on the external outside of the cluster. These gross spinule counts are used to generally quantify the differences across species as well as determining the increase in spinule number with age.

Material examined

The following scorpion material was examined for this study (more detailed label data are available from the authors):

SUPERFAMILY CHAERILOIDEA

FAMILY CHAERILIDAE: *Chaerilus celebensis* Pocock, 1894, Luzon, Philippines, ♀ (WDS); *Chaerilus chapmani* Vachon & Lourenço, 1985, Palawan Island, Philippines, ♀ (FK); *Chaerilus tichyi* Kovařík, 2000, Pahang, Malaysia, ♀ paratype (FK); *Chaerilus tryznai* Kovařík, 2000, Bomi, Tibet, ♀ paratype (FK); *Chaerilus variegatus* Simon, 1877, Indonesia, ♂ (MES), Bogor, Java, Indonesia ♀ (FK).

SUPERFAMILY IUROIDEA

FAMILY CARABOCTONIDAE: *Caraboctonus keyserlingi* Pocock, 1893, Chile, ♂ adult (MES); *Hadruidoidea charcasus* (Karsch, 1879), Peru, adult ♀ and instar-2 juveniles (MES); *Hadruidoidea maculatus* (Thorell, 1876), Huancayo, Peru, adult ♂, ♀, and juvenile (MES); *Hadrurus arizonensis arizonensis* Ewing, 1928, Borrego Springs, California, USA, adult ♂ (MES), Arroyo Salado, ABDSP, California, USA, subadult ♂ and juvenile (MES); *Hadrurus concolor* Stahnke, 1969, Santa Rosalia, Baja California Sur, Mexico, adult ♀ (MES); *Hadrurus hirsutus* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico, adult ♀ (MES); *Hadrurus obscurus* Williams, 1970, Split Mountain, ABDSP, California, USA, adult ♂, subadult, and juvenile (MES); *Hadrurus pinteri* Stahnke, 1969, Oakies Landing, Baja California Norte, Mexico, adult ♀ and subadult (MES); *Hadrurus spadix* Stahnke, 1940, Nevada, USA, adult ♀ (VF); *Hoffmannihadrurus aztecus* (Pocock, 1902), Tehuacan, Puebla, Mexico, adult ♂, subadult, and juvenile (MES); *Hoffmannihadrurus gertschi* (Soleglad, 1976), Iguala, Guerrero, Mexico, adult ♀ (MES).

FAMILY IURIDAE: *Calchas nordmanni* Birula, 1899, Megisti (=Kastelorizo) Island, Greece, juveniles (NHMC, VF), Anamur, Turkey, ♀ and ♂ (NHMW), Baykan, Turkey, ♀ (NHMW), Antalya, Turkey, ♀ (NHMW); *Iurus dufourei* (Brullé, 1832), Turkey, ♂ (MES), Crete, adult ♀, juveniles (NHMC, VF).

Abbreviations

List of depositories: FK, Personal collection of František Kovařík, Prague, Czech Republic; NHMC, Natural History Museum of Crete, Irakleio, Crete, Greece; MES,

Table I. Leg tarsus spinule cluster statistics for scorpions of superfamily Iuroidea. Leg III is assumed, unless otherwise specified (e.g., (I), (IV)). *Spinule counts only include external edge of cluster. **Spinule counts only include outer circumference of cluster.

	Adult	Subadult	Juvenile			
			7 month	3 month	Instar-2	unknown
Calchas						
Basal	6+, 22 (I)					10, 9 (I)
Sub-basal	3 (I)					8, 7 (I)
Sub-distal						6, 10 (I)
Distal						6, 2 (I)
Iurus						
Terminal cluster*	36-45		14 (IV)	11-12		
Cluster	130-250		3-4			
Caraboctonus						
Terminal cluster*	44					
Cluster	232					
Hadruroides						
H. maculatus						
Terminal cluster*	50					
Cluster	130					
H. charcasus						
Terminal cluster*						18 (I)
Cluster						6-11 (I)
Hadrurus**						
H. a. arizonensis	22-28	22				12
H. spadix	20-24					
H. obscurus	18-28	18				12-14
H. hirsutus	24					
H. concolor	22					
H. pinteri	22-26	14-20				
Hoffmannihadrurus**						
H. gertschi	10					
H. aztecus	26	14				0

Personal collection of Michael E. Sologlad, Borrego Springs, California, USA; NHMW, Naturhistorisches Museum, Vienna, Austria; VF, Personal collection of Victor Fet, Huntington, West Virginia, USA; WDS, Personal collection of W. David Sissom, Canyon, Texas, USA.

Other: ABDSP, Anza-Borrego Desert State Park, San Diego County, California, USA.

Iuroid Tarsus Armature

As reported by Sologlad & Fet (2003: 19, Figs. 19-25), significant ontogenetic differences are detected in the development of highly unusual spinule clusters throughout the Iuroidea superfamily (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 special 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 the tarsus in adults is equipped with a significant display of irregularly placed

large socketed setae, very similar to those seen in the genus *Chaerilus* (superfamily Chaeriloidea): in Sologlad & Fet (2003), compare Figures 13 and 19. In general, except for the basal and suprabasal areas of the tarsus, spinule clusters are absent in adult *Calchas*. However, in subadults and, in particular, juveniles, a significant number of irregularly placed spinule clusters can be observed medially on the entire leg tarsus, with a heavier emphasis on the basal aspects. We illustrate this for legs I and III of a juvenile specimen (Figs. 1-4). Table I shows the difference in spinule count distribution in adult and juvenile specimens in the genus *Calchas*.

In *Iurus* (a sister genus of *Calchas*, found in Greece and Turkey), we see in the adult 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 200+ spinules, the distal cluster pair considerably more. However, juveniles have significantly lower number of spinules per cluster. In juveniles seven months of age, some individual clusters contain as few as three spinules (Fig. 39). The distal cluster pairs contain as few as 14 spinules in a seven month old specimen (Fig. 7), and only 11-12 in a three month old specimen (Fig. 8). These data are tabulated in Table I. Also of interest is the development of an 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. 37-40). In addition, spinules located on the outer ring of the cluster are shorter than the more centrally located spinules (Figs. 37-38); this is also observed in Caraboctoninae (see below). We hypothesize here that these outer spinules are new, not fully developed. That is, in each molt, a spinule cluster gains new outer spinules, short initially, which then increase in length during successive molts. Finally, we see that each spinule cluster base is surrounded by a low-profile ring, providing a base for the outer spinules (Figs. 37-38). In the juveniles, a somewhat gnarled base of each spinule emanates from the cuticle (Figs. 7-8), very similar to the base of individual ridges exhibited in the fused spinules found in subfamily Hadrurinae.

In the South American iuroids (subfamily Caraboctoninae), we see the same structure in adults as that described for the Old World genus *Iurus*—a row of highly concentrated spinule clusters (“tufts”) extending over the entire length of the leg tarsus and including, as in *Iurus*, a pair of distal spinule clusters (see Figs. 9-12, genus *Caraboctonus*; Figs. 13-16, genus *Hadruroides*). Individual clusters in adults approach the same numbers of spinules as that seen in *Iurus*; the same is observed for the distal cluster pair. Also, as in *Iurus*, the number of spinules within a cluster is considerably lower in juvenile specimens. This is illustrated in dramatic fashion for an instar-2 specimen of *Hadruroides charcasus* (Figs. 15-16), where spinule clusters exhibit a considerably lower number of spinules: individual tufts contain as few as 6-11 spinules, the distal tufts, only 18 spinules. However, the structure of the spinule cluster in this subfamily is different from that seen in *Iurus*; in Caraboctoninae, individual spinule clusters taper distally, forming a “point” at their extremity (Figs. 11 and 36) (i.e., are not truncated distally as in *Iurus*). In addition, the individual spinules are also pointed, not “squared off” as in *Iurus* (Figs. 37-40). As shown in a close-up of a spinule cluster of *Caraboctonus* (Fig. 12), individual spinules are marked by delicate, closely grouped striations along the entire spinule length. As in *Iurus*, the outer spinules within a cluster are shorter than the more centrally located spinules, again supporting our suggestion that new spinules are acquired during each molt, shorter initially, and then becoming longer with successive molts. Again, as in *Iurus*, the outer perimeter of a spinule cluster has a low profile base (Figs. 11 and 36).

Of a special interest in subfamily Caraboctoninae is the fact that the unguicular spine is conspicuously blunted in both its genera, *Caraboctonus* (Fig. 9) and *Hadruroides* (Figs. 13-14). This unique reduction of the tarsomere I (= epitarso) spur is unprecedented in Recent scorpions and is considered a synapomorphy for the family Caraboctonidae. The unguicular spine is well developed and pointed in all other four iuroid genera.

The North American iuroid subfamily Hadrurinae exhibits an amazing difference in the spinule cluster structure compared to all other iuroids. As reported in Soleglad & Fet (2003), genus *Hadrurus* has a single median row of “spinules”, superficially similar in size

and overall configuration to those found in the Chactioidea. However, under high magnification we see that the individual “spinule” is composed of irregular, highly defined ridges on the basal two-thirds of the structure; each ridge, at the extreme basal aspect, appearing to originate separately, in a gnarled fashion, as the “root of a tree” (Figs. 17, 22, 25-26, 29-30, and 33). The bases of these ridges are very similar in structure to those shown in the spinule cluster of a juvenile *Iurus* (Figs. 7-8). Under still higher magnification, the individual ridges show at their base remnants of striations as those seen on individual spinules in the *Caraboctonus* cluster (compare *Hadrurus obscurus*, Figs. 31-32, to *Caraboctonus*, Fig. 12). This structure, expressed to some degree, is found in all eight species comprising *Hadrurus* and *Hoffmannihadrurus*, especially in the genus *Hadrurus*. All species of *Hadrurus* and *Hoffmannihadrurus* are illustrated herein, showing the unique fused tarsal spinule cluster with its irregular ridges circumscribing the spinule cluster base: the United States species *Hadrurus arizonensis* (Figs. 17-20), *H. obscurus* (Figs. 30-32, 34), and *H. spadix* (Fig. 29); the Baja California species *H. pinteri* (Figs. 27-28, 33), *H. concolor* (Fig. 26), and *H. hirsutus* (Fig. 25); and mainland Mexican species *Hoffmannihadrurus gertschi* (Fig. 21) and *H. aztecus* (Figs. 22-24). As we suggested earlier (Soleglad & Fet, 2003), it is hypothesized here that such a highly ridged, convoluted “spinule” in Hadrurinae is, in fact, a fused spinule cluster, presumably evolved from the highly concentrated spinule cluster as seen in the sister subfamily Caraboctoninae. This is readily apparent when one compares Fig. 34 (*Hadrurus obscurus*) and Fig. 36 (*Hadruroides maculatus*): the two clusters are of the same basic shape, both are pointed, many individual spinules are visible, and each has a low profile base at the extreme proximal aspect of the structure (albeit more irregular in *Hadrurus*). The presence of striations at the base of individual ridges further endorses the hypothesis that these ridges correspond to individual spinules. In subfamily Hadrurinae, the number of ridges (Table I) is less than the number of spinules in Caraboctoninae—this is to be expected, however, if we trace the complete evolution of derivations proposed in this paper. As in the number of spinules in *Iurus* and Caraboctoninae, the number of ridges of the fused spinule cluster in Hadrurinae is lower in juvenile and subadult specimens, and increases with age. Comparison of a juvenile *Hadrurus arizonensis* (Fig. 20) with an adult of the same species (Fig. 17) shows an increase of approximately 50 % in the number of ridges. This is true also for *H. obscurus* (Figs. 34 and 32). Of particular importance in this subfamily, is the reduction of these ridges in genus *Hoffmannihadrurus* (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 species *H. aztecus*, we see a well developed set of ridges in an adult, comparable to that exhibited in *Hadrurus*, but in the subadult, and in particularly the juvenile, the definition and number of ridges is considerably less; in the juvenile they are absent altogether. We consider this trend in the genus *Hoffmannihadrurus* an important diagnostic character.

Iuroid Basitarsus Armature

In this present analysis we noted that the three iuroid genera exhibiting highly concentrated spinule clusters on the tarsus (i.e., *Iurus*, *Caraboctonus*, and *Hadruroides*) also exhibited a limited number of spinule clusters on the distal ventral aspect of the leg basitarsus (this was first reported by Soleglad & Sissom, 2001: 63, for genus *Iurus*). Based on these observations, we decided to analyze the distal aspect of the basitarsus in all six iuroid genera (Figs. 41-52).

On the ventral aspect of the basitarsus of genus *Calchas* we see two well developed rows of closely grouped spinules on legs I and II in juveniles (Figs. 41-42). As with the ventral median row of spinules found on the tarsus, the individual spinules on the basitarsus are tightly grouped and somewhat irregular in their location, not perfectly set in a straight line (Fig. 42). On legs III and IV, *Calchas* juveniles have only limited clusters of spinules. In the genus *Iurus* (Figs. 43-44), we see small spinule clusters on the extreme distal ventral aspect of the basitarsus, aligned into two irregular rows. This spinule clusters are somewhat small in diameter, similar to the basal clusters found on the tarsus, but are composed of the same individually truncated spinules.

Genera *Caraboctonus* (Fig. 45) and *Hadruroides* (Figs. 46-48) also exhibited spinule clusters on the distal ventral aspect of the leg basitarsus. As in *Iurus*, these clusters are irregularly grouped into two rows, where the individual clusters become reduced in size on the supradistal aspect of the segment (Fig. 46). As was the case for the leg tarsus, the number of individual spinules per cluster is much lower in juvenile specimens, as seen in an instar-2 *Hadruroides charcasus* (Fig. 48).

In the genera *Hadrurus* (Figs. 51-52) and *Hoffmannihadrurus* (Figs. 49-50), we find fused spinule clusters on the basitarsus, but they are located on the distal half of the dorsolateral aspect of the segment. These fused spinule clusters form a single row. As in tarsus, we see the fused spinule ridges are somewhat reduced in *Hoffmannihadrurus aztecus* (Fig. 50), as contrasted to two species of *Hadrurus*, *H. concolor* (Fig. 51) and *H. spadix* (Fig. 52).

In agreement with what was reported by Soleglad & Sissom (2001: Tables 6-7) for the family Euscorpidae, the spination of the leg basitarsus in superfamily Iuroidea is most developed on legs I and II, becoming reduced in legs III and IV.

Phylogenetic Considerations and Taxonomic Emendations

Phylogeny

Soleglad & Fet (2003) presented a high-level phylogenetic revision of extant scorpions. In this revision, family Iuridae was elevated to superfamily status, Iuroidea, and its two subfamilies were raised to family status, Iuridae and Caraboctonidae. Soleglad & Fet (2003: 110) identified several synapomorphies for superfamily Iuroidea, four of primary significance: (1) a large denticle is situated on the ventral edge of the cheliceral movable finger; (2) ventral surface of leg tarsus equipped with a

median row of spinule clusters; (3) chelal finger trichobothria series *db-dt* and *eb-et* are found on the distal half of the finger; and (4) patella ventral trichobothrium *v₃* is situated on the external surface. An important symplesiomorphy, shared by all six iuroid genera, was also identified by Soleglad & Fet (2003): the oblique alignment of the chelal finger median denticle (MD) row. The plesiomorphic state of this character implies that it is directly inherited from the common ancestor of parvorder Iurida and more primitive Recent scorpions (i.e., parvorders Pseudochactida, Buthida, and Chaerilida), and therefore firmly establishes Iuroidea as the most primitive superfamily in parvorder Iurida (Scorpionoidea and Chactoidea are the other two superfamilies).

Since we can trace a definite fused spinule clusters in all *Hadrurus* species, and, in contrast, in *Hoffmannihadrurus* this feature is either non-existent or inconsistently expressed within different developmental stages, we can assume that *Hadrurus* (found in the United States and Baja California, Mexico) is more primitive than its sister genus *Hoffmannihadrurus* (distributed in southern mainland Mexico). This conclusion is based on the hypothesis that the fused spinule cluster observed throughout *Hadrurus* is derived directly from the ancestral, highly concentrated spinule clusters like those observed in Hadrurinae's sister subfamily Caraboctoninae. Therefore, *Hoffmannihadrurus* is more derived than *Hadrurus*, with 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 the pedipalp chela found in these genera. In *Hadrurus*, we see two to seven internal accessory trichobothria located on the chelal fixed finger, and in *Hoffmannihadrurus*, internal accessory trichobothria are absent—this is considered the primary diagnostic character separating these two genera (Figs. 59-64). The underlying foundation for this hypothesis is the observation that accessory trichobothria are being lost during speciation, and even within a species' geographic radiation, as documented by extensive statistical analyses of *Hadrurus* and *Hoffmannihadrurus* trichobothria patterns involving well over 650 samples (Soleglad, 1976; Fet *et al.*, 2001). This important observation, the loss of accessory trichobothria, is also endorsed by the petite nature of the more basal accessory trichobothria, the most basal trichobothrium being quite small, as illustrated in Figures 60-64. Soleglad & Fet (2001: Appendix A: 33, Table A-2) discussed this issue as part of the evidence supporting their hypothesis that petite trichobothria are an intermediate state between full size trichobothria and the complete loss or gain of trichobothria.

Therefore, our data originating both from chela trichobothria and fused tarsal/basitarsal spinule clusters, support an opinion that the genus *Hadrurus* is more primitive than *Hoffmannihadrurus*. This may appear counter-intuitive to the geographic distribution of Hadrurinae, if we consider that its sister subfamily Caraboctoninae is found in South America, and that Caraboctoninae appear to be more primitive than Hadrurinae (judging from non-fused spinule clusters, a primitive charac-

ter found also in *Iurus*). However, since there is a significant disjunction in the distribution of the iuroids in general (Caraboctonidae vs. Iuridae), implying existence of relatively ancient lineages within superfamily Iuroidea, we suggest that the disjunct distribution of the subfamily Hadrurinae, and its split from its South American sister group, Caraboctoninae, occurred far back enough in time such that one cannot necessarily imply phylogenetic relationships between its two disjunct modern genera based on their geographic distribution (i.e. more southern distribution of *Hoffmannihadrurus*). In addition, *Hadrurus pinteri*, presumably the most primitive of all hadrurine species, occurs sympatrically in Baja California, which has been separate from mainland Mexico only since Miocene. Thus, it is likely that Hadrurinae underwent a considerable evolution within the southern part of North America since its divergence from Caraboctoninae. On a larger scale, the spectacular geographic disjunction between Caraboctonidae and Iuridae also testifies for a very ancient age of Iuroidea (Francke & Soleglad, 1981; Soleglad & Fet, 2003). We can add that the Mediterranean Iuridae appear to be more primitive than Caraboctonidae, since Iuridae exhibit single subdistal denticles and “8-carinae” configuration in the chela, both being primitive characters found in parvorders Pseudochactida, Buthida, and Chaerilida. Also, within Iuridae, the genus *Calchas* appears to be more primitive than *Iurus* judging from its tibial spurs, its heavy socketed (*Chaerilus*-like) setal pairs and reduced median spinule clusters on tarsus, presumably the precursors of tarsal spinule clusters found in all other iuroid genera.

Taxonomic Emendations

Based on the observations and conclusions stated above, we officially establish here a new genus in subfamily Hadrurinae: *Hoffmannihadrurus* Fet & Soleglad, **gen. nov.** which includes the former “aztecus” group of *Hadrurus* (Soleglad, 1976; Fet et al., 2001). Genus *Hadrurus* is restricted to species in its former “hirsutus” group. Following are diagnoses of these two genera.

GENUS. *Hadrurus* Thorell, 1876

DIAGNOSIS. Chelal fixed finger with 2-7 internal accessory trichobothria; trichobothrial series *ib-it* situated on suprabasal aspect of fixed finger (Figs. 60-64); ridges of fused spinule clusters of leg tarsus and basitarsus well defined, even in early developmental stages (Figs. 17-20, 25-34, 51-52).

TYPE SPECIES. *Buthis hirsutus* Wood, 1863 [= *Hadrurus hirsutus* (Wood, 1863)].

DISTRIBUTION. Western United States (Arizona, California, Idaho, Nevada, Oregon, and Utah); Mexico: Baja California (with adjacent islands), northwestern Sonora (south to Guaymas).

SPECIES. *H. arizonensis* Ewing, 1928; *H. concolor* Stahnke, 1969; *H. hirsutus* (Wood, 1863); *H. obscurus* Williams, 1970; *H. pinteri* Stahnke, 1969; and *H. spadix* Stahnke, 1940.

GENUS. *Hoffmannihadrurus* Fet & Soleglad, **gen. nov.**

DIAGNOSIS. Chelal fixed finger *without* internal accessory trichobothria; trichobothrial series *ib-it* situated on basal aspect of fixed finger (Fig. 59); ridges of fused spinule clusters of leg tarsus and basitarsus not well defined, essentially obsolete in early developmental stages (Figs. 21-24, 49-50).

ETYMOLOGY. Genus name *Hoffmannihadrurus* is established in honor of the late Mexican scorpologist Carlos C. Hoffmann (1876-1942) whose contributions to our knowledge of Mexican scorpions provided an inspiration to many future scorpion students. In particular, the species *H. aztecus* assigned to this new genus was illustrated and given a detailed description by Hoffmann (1931: 340-346, Figs. 20-21, the latter figure is actually of *H. gertschi*) in his monumental monograph on Mexican scorpions.

TYPE SPECIES. *Hadrurus aztecus* Pocock, 1902 [= *Hoffmannihadrurus aztecus* (Pocock, 1902)].

DISTRIBUTION. Mexico (Guerrero, Oaxaca, Puebla, and Veracruz).

SPECIES. *H. aztecus* (Pocock, 1902), **comb. nov.** and *H. gertschi* (Soleglad, 1976), **comb. nov.**

The characters used to diagnose the small but highly diverse set of genera in superfamily Iuroidea include trichobothrial patterns, cheliceral and chelal finger dentition, chelal carination, leg tarsus armature, tibial spines and pedal spur armature, and the structure of the carapace. References to trichobothrial patterns take into account Stockwell's (1989: Figs. 175-176) alternative interpretation of chelal trichobothria designations for family Caraboctonidae as discussed in Soleglad & Fet (2003: 35-36, Fig. 65). Other structural references for superfamily Iuroidea can be found in Francke & Soleglad (1981), for all genera; Vachon (1974: Figs. 154-156, 212-219), for *Caraboctonus*, *Calchas* and *Iurus*; Vachon (1966) and Francke (1981) for *Iurus*; Vachon (1971) for *Calchas*; Francke & Soleglad (1980) for *Hadruroides*; Lourenço (1995) for *Caraboctonus*; and Wood (1863), Pocock (1902), Hoffmann (1931), Stahnke (1940, 1969, 1974), Williams (1970a, 1970b), Soleglad (1976), and Fet et al. (2001), for *Hadrurus* and *Hoffmannihadrurus*. Following is a phylogenetic key to all above-species taxonomic components of superfamily Iuroidea.

Phylogenetic key to families, subfamilies, and genera of the superfamily Iuroidea

1. Dorsal edge of cheliceral movable finger with a *single* subdistal (*sd*) denticle; serrula present on ventral edge of cheliceral movable finger; denticle groups of chelal finger median row (MD) oblique and *imbricating*; chelal carinae conform to the “8-carinae” configuration, internal (I) present, subdigital (D2) and ventromedian (V2) absent; patellar trichobothria v_2 and v_3 located on external surface; orthobothriotaxic, chelal trichobothria *est*, *Est*, and V_2 and patellar trichobothria *et_2* and *eb_2* petite in size; chelal finger trichobothria *ib-it* grouping disjoint, *ib* located suprabasally while *it* located on medial to distal aspect of fixed finger; chelal trichobothrium Et_1 situated on external surface of palm; chelal trichobothrium Et_5 grouped with Et_4 , situated on palm; carapace anterior edge with subtle to deep indentation, lateral ocular carinae well developed (Figs. 53-54)..... (family **Iuridae**) **2**
 - Dorsal edge of cheliceral movable finger with *two* subdistal (*sd*) denticles; serrula absent on ventral edge of cheliceral movable finger; denticle groups of chelal finger median row (MD) oblique but *not imbricating*; chelal carinae conform to the “10-carinae” configuration, internal (I) absent, subdigital (D2) and ventromedian (V2) present; patellar trichobothrium v_3 located on external surface and v_2 located on ventral surface; neobothriotaxic, chelal trichobothria *est*, *Est*, and V_2 and patellar trichobothria *et_2* and *eb_2* full size; chelal finger trichobothria *ib-it* grouping close, *ib* and *it* situated on basal to suprabasal aspect of fixed finger; chelal trichobothrium Et_1 situated on ventral surface of palm; chelal trichobothrium Et_5 considerably removed from Et_4 , situated on fixed finger; carapace anterior edge highly convexed, lateral ocular carinae inconspicuous (Figs. 55-58)..... (family **Caraboctonidae**) **3**
2. Ventral aspect of leg tarsus without conspicuous setae, where present, sockets are quite small; ventral median aspect of leg tarsus with conspicuous highly concentrated spinule clusters (Figs. 5-8, 37-40); tibial spur absent on legs III and IV; chelal trichobothrium *db* located at the midpoint of fixed finger; large denticle on ventral edge of cheliceral movable finger located medially; carapace anterior edge with conspicuous indentation (Fig. 53) genus **Iurus**
 - Ventral aspect of leg tarsus with conspicuous large socketed setae; ventral median aspect of leg tarsus with irregularly grouped spinules, but never in conspicuous isolated clusters (Figs. 1-4); tibial spur present on legs III and IV; chelal trichobothrium *db* located at the base of fixed finger; large denticle on ventral edge of cheliceral movable finger located basally; carapace anterior edge with subtle indentation (Fig. 54) genus **Calchas**
3. Ventral median aspect of leg tarsus with conspicuous highly concentrated spinule clusters (Figs. 9-16, 35-36); unguicular spine reduced and blunted in development (Figs. 9, 13-14); minor neobothriotaxy limited to single accessory trichobothrium in patellar external *em* series; chelal trichobothria *Db-Dt* positioned on extreme distal aspect of palm; leg pedal spurs smooth, lacking spinelets; chelal movable finger with *seven* internal denticles (ID); genital papillae present in the male (subfamily **Caraboctoninae**) **4**
 - Ventral median aspect of leg tarsus with *fused* spinule clusters (Figs. 17-34); unguicular spine sharp and well developed; major neobothriotaxy exhibited on chelae, and ventral and external aspects of patellae; chelal trichobothria *Db-Dt* positioned on basal aspect of palm; leg pedal spurs with conspicuous spinelets; chelal movable finger with *nine* internal denticles (ID); genital papillae absent in the male .. (subfamily **Hadrurinae**) **5**
4. Inner accessory (IAD) and outer accessory (OAD) denticles absent on chelal fingers; chelal trichobothrium Et_5 situated on basal aspect of fixed finger; large denticle on ventral edge of cheliceral movable finger located basally genus **Caraboctonus**
 - Inner accessory (IAD) and outer accessory (OAD) denticles present on chelal fingers in adults; chelal trichobothrium Et_5 situated on suprabasal aspect of fixed finger; large denticle on ventral edge of cheliceral movable finger located suprabasally genus **Hadruroides**
5. Chelal fixed finger with 2-7 internal *accessory* trichobothria; chelal fixed finger trichobothria *ib-it* located suprabasally on fixed finger (Figs. 60-64); leg tarsus and basitarsus with well developed ridges on fused spinule clusters (Figs. 17-20, 25-34, 51-52) genus **Hadrurus**
 - Chelal fixed finger *without* internal *accessory* trichobothria; chelal fixed finger trichobothria *ib-it* located basally on fixed finger (Fig. 59); leg tarsus and basitarsus with weak or obsolete ridges on fused spinule clusters (Figs. 21-24, 49-50) genus **Hoffmannihadrurus**, **gen. nov.**

Interestingly, the existence of two genera in subfamily Hadrurinae as introduced here, and also, in part, implied in Fet *et al.* (2001), is consistent with the key provided by Soleglad (1976). In Soleglad's original key, the primary couplet, which separated the two Mexican species from the United States and Baja California species, corresponded to the two genera we recognize in this paper. In addition, the absence of internal accessory trichobothria exhibited in *Hoffmannihadrurus*, was first reported for species *H. aztecus* by Gertsch & Soleglad (1972: 564, Fig. 111).

List of valid taxa in the superfamily Iuroidea(after Sissom & Fet, 2000; Fet *et al.*, 2001; Soleglad & Fet, 2003, with emendations)

Parvorder Iurida Soleglad & Fet, 2003

Superfamily Iuroidea Thorell, 1876

Family Iuridae Thorell, 1876

Genus *Calchas* Birula, 1899*Calchas nordmanni* Birula, 1899Genus *Iurus* Thorell, 1876*Iurus dufourei* (Brullé, 1832) [with two subspecies: *I. d. dufourei* (Brullé, 1832), and *I. d. asiaticus* Birula, 1903]

Family Caraboctonidae Kraepelin, 1905

Subfamily Caraboctoninae Kraepelin, 1905

Genus *Caraboctonus* Pocock, 1893*Caraboctonus keyserlingi* Pocock, 1893Genus *Hadruioides* Pocock, 1893*Hadruioides aguilari* Francke & Soleglad, 1980*H. carinatus* Pocock, 1900*H. charcasus* (Karsch, 1879)*H. galapagoensis* Maury, 1975*H. leopardus* Pocock, 1900*H. lunatus* (L. Koch, 1867)*H. maculatus* (Thorell, 1876)*H. mauryi* Francke & Soleglad, 1980*H. udvardyi* Lourenço, 1995

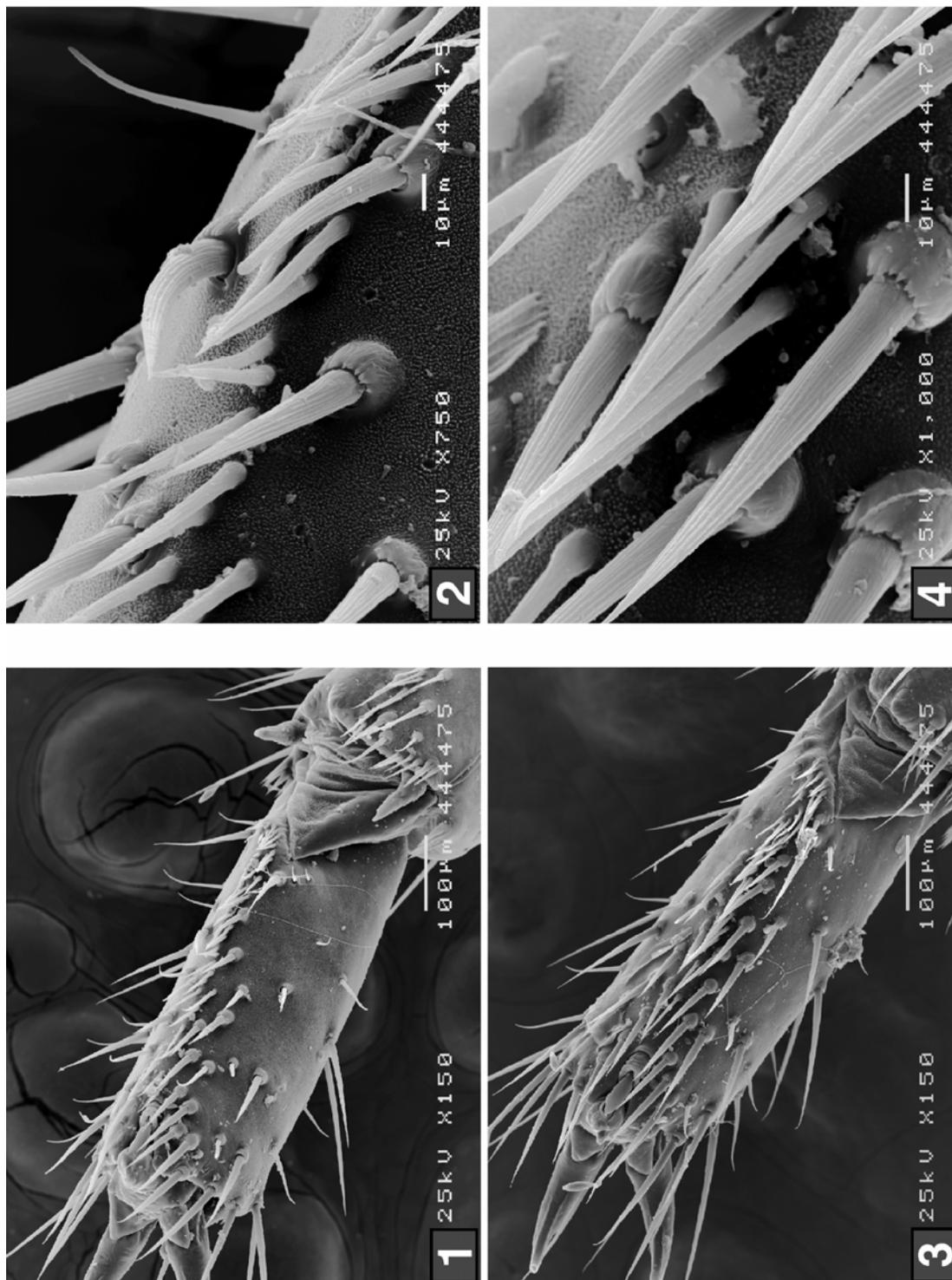
Subfamily Hadrurinae Stahnke, 1974

Genus *Hadrurus* Thorell, 1876*Hadrurus arizonensis* Ewing, 1928 (with two subspecies: *H. a. arizonensis* Ewing, 1928, and *H. a. austrinus* Williams, 1970)*H. concolor* Stahnke, 1969*H. hirsutus* (Wood, 1863)*H. obscurus* Williams, 1970*H. pinteri* Stahnke, 1969*H. spadix* Stahnke, 1940Genus *Hoffmannihadrurus* Fet & Soleglad, **gen. nov.***Hoffmannihadrurus aztecus* (Pocock, 1902), **comb. nov.***H. gertschi* (Soleglad, 1976), **comb. nov.****Acknowledgements**

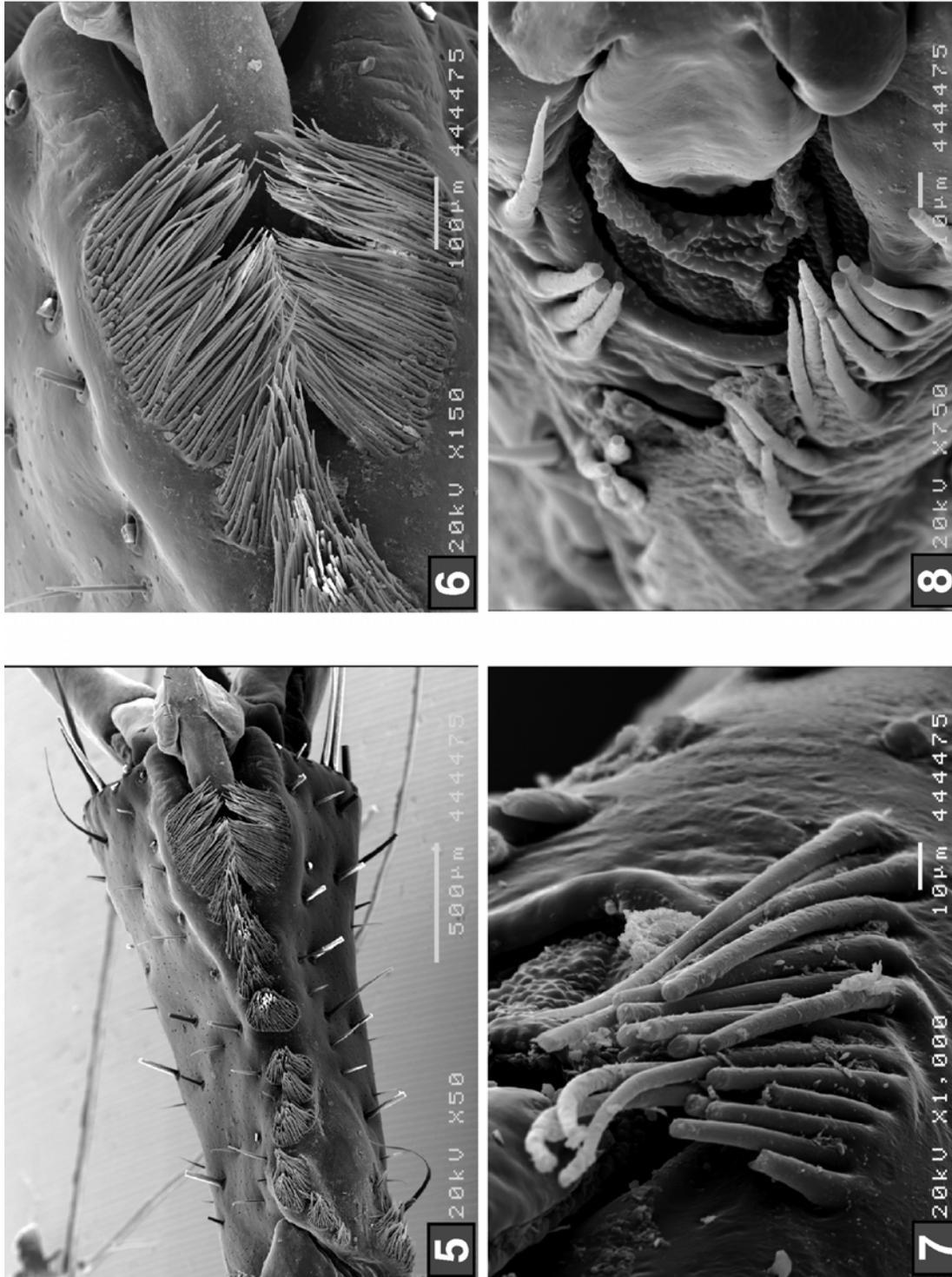
We thank David Gaban for the gift of *Hadruioides charcasus*; Dan Estabrooks for the gift of *Hadrurus spadix*; Mark Jorgensen, Anza-Borrego Desert State Park, Colorado Desert District, for providing MES a permit to collect scorpions there; and Jorge Santiago-Blay and H. Don Cameron for etymological and taxonomic comments. We are grateful to Jürgen Gruber (NMW) for the loan of *Calchas* from Turkey. František Kovařík and W. David Sissom kindly loaned specimens of *Chaerilus* mentioned in this study. Help and support of Gary A. Polis (1946-2000) allowed VF his first-hand acquaintance with *Hadrurus* in Baja California in 1991-1994, partially under the NSF grant DEB 9307855.

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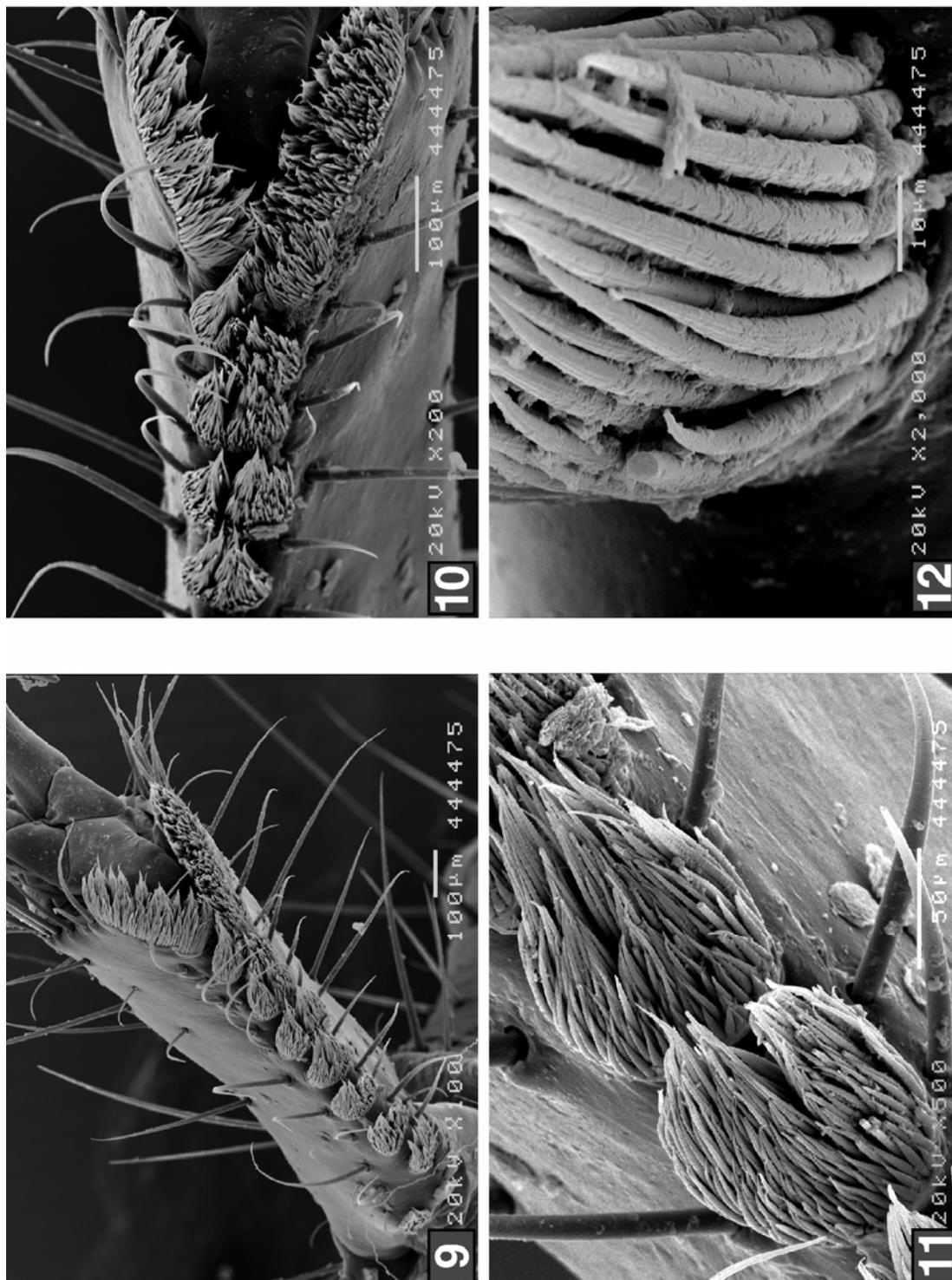
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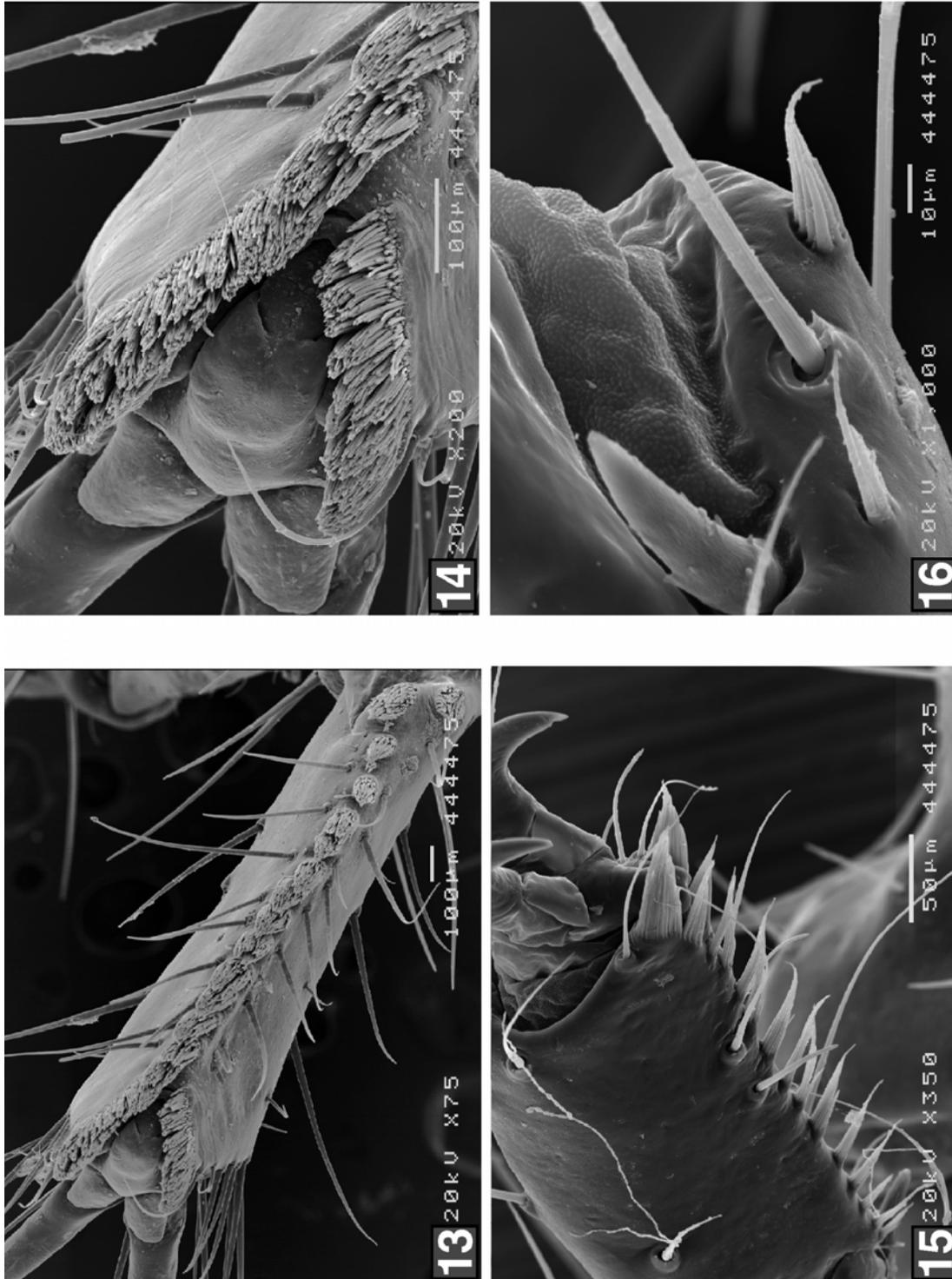
Figs. 1-4. Ventrolateral view of leg tarsus of juvenile *Calchas nordmanni*, Megisti, Greece. **1.** full tarsus, leg I. **2.** close-up of spinule clusters and socketed setae, leg I. **3.** full tarsus, leg III. **4.** close-up of spinule clusters and socketed setae, leg III.



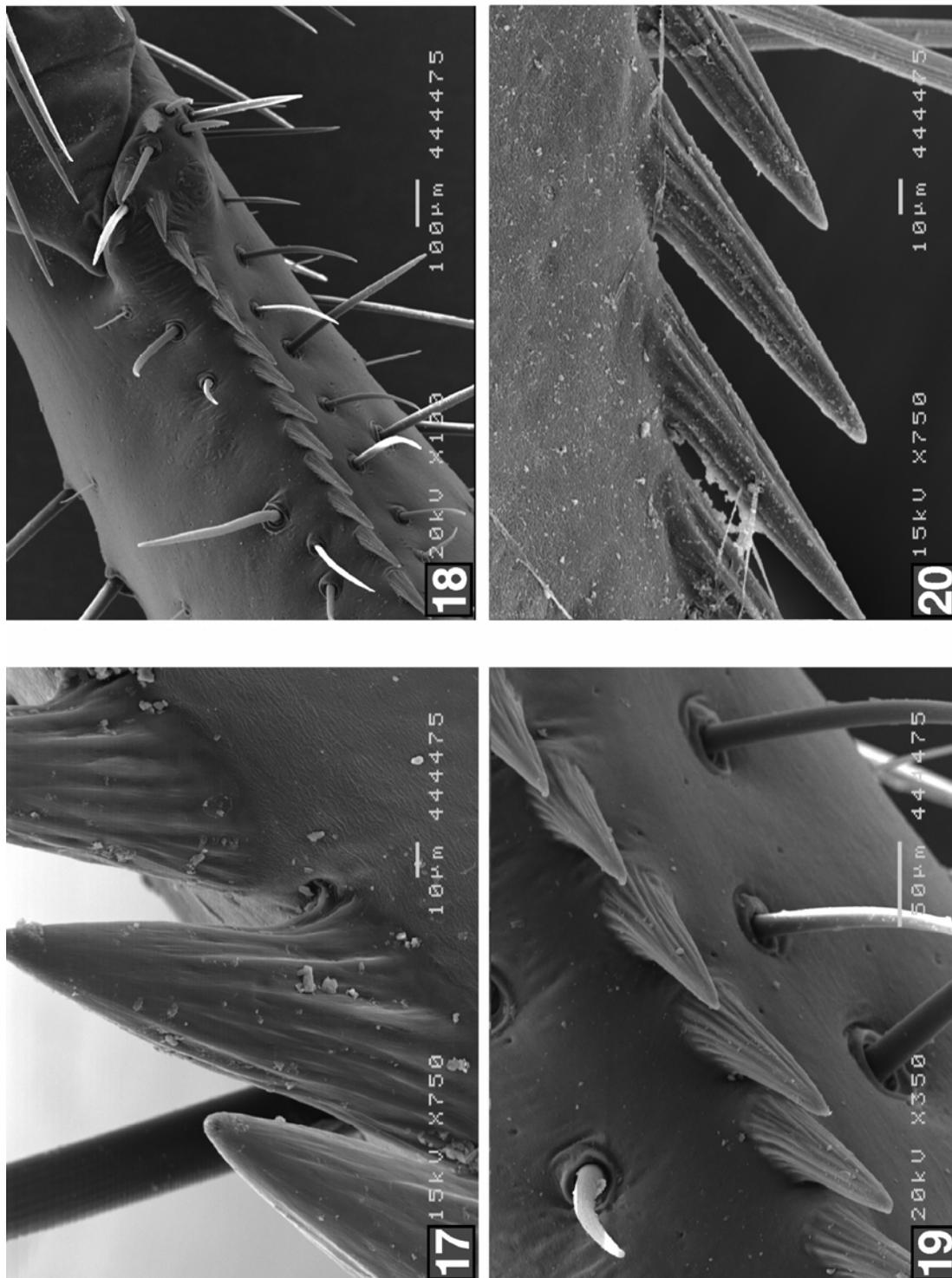
Figs 5-8. Ventrolateral view of leg tarsus of adult (Turkey) and juvenile (Crete) *Iurus difoureus*. **5.** full tarsus of leg III, adult. **6.** close-up of distal aspect of tarsus of leg III, adult. **7.** close-up of distal aspect of tarsus of leg IV, juvenile (three month instar). **8.** close-up of distal aspect of tarsus of leg III, juvenile (seven month instar).



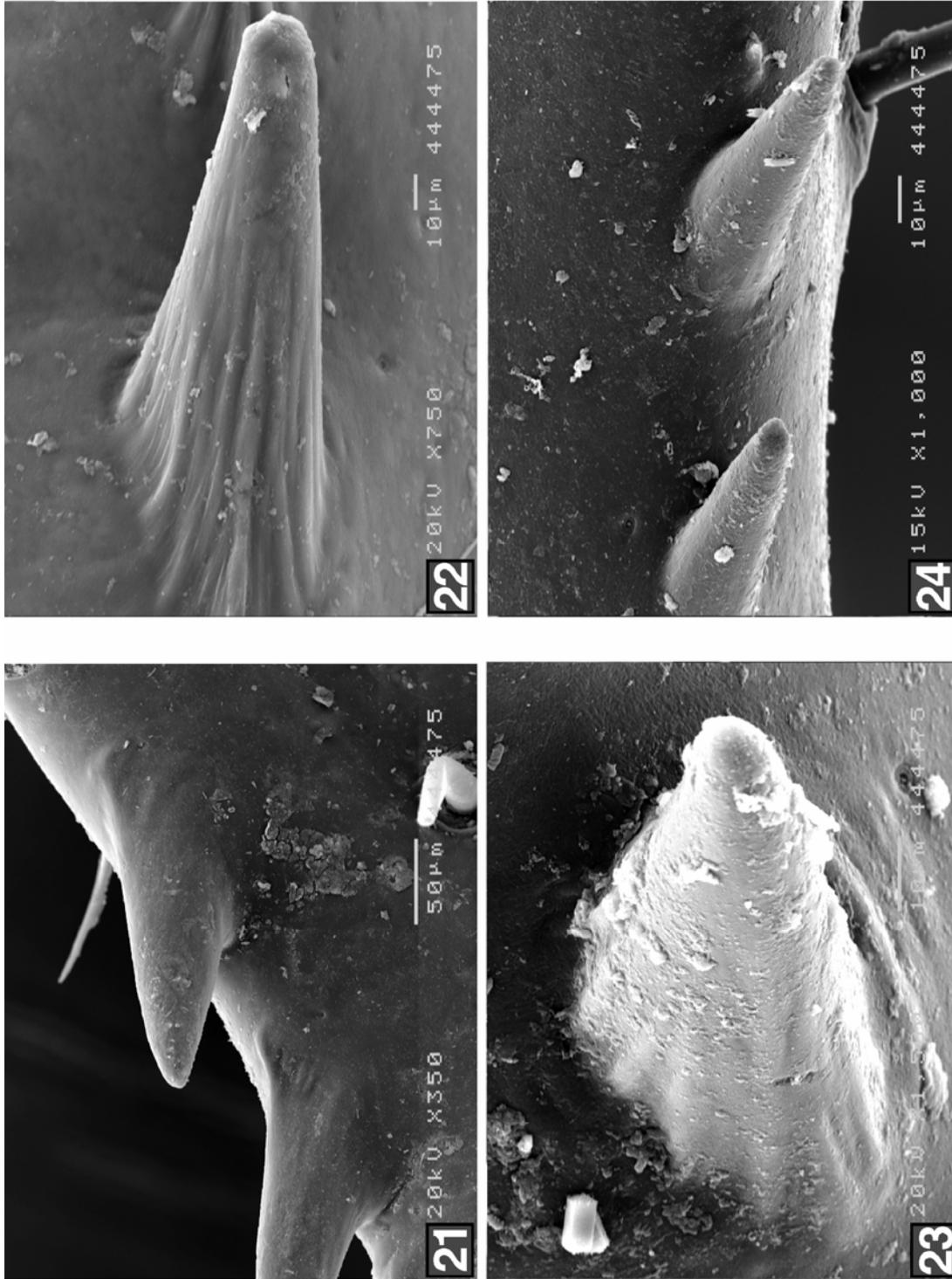
Figs. 9-12. Ventrolateral view of leg III tarsus of adult *Caraboctonus keyserlingi*, Chili. 9, full tarsus, showing blunted unguicular spine. 10, close-up of distal aspect of tarsus. 11, close-up of spinule clusters. 12, close-up of single spinule cluster showing the delicate striations on individual spinules.



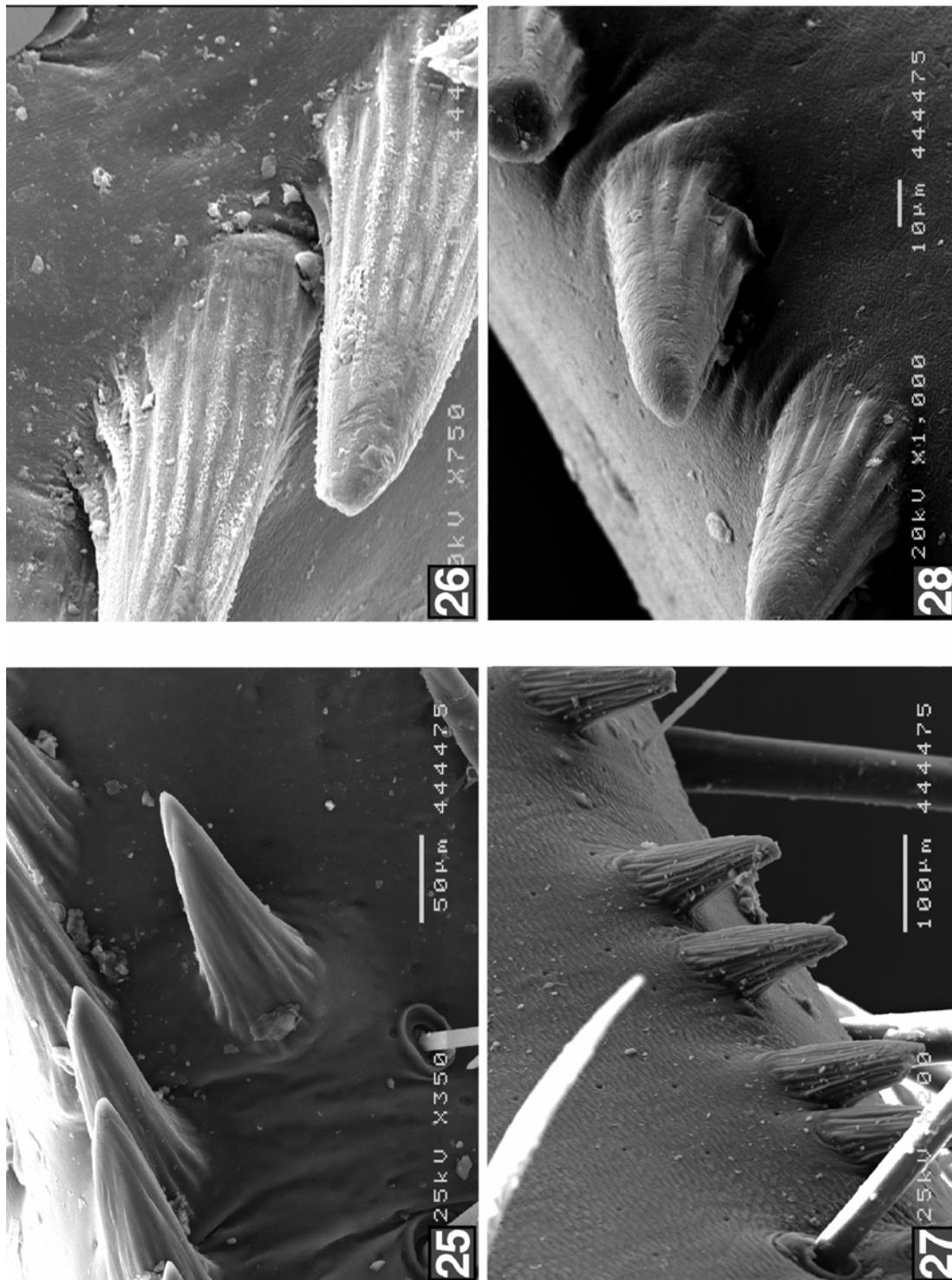
Figs. 13-16. Ventrolateral view of leg tarsus of *Hadruiroidea* species. **Figs. 13 and 14.** *H. maculatus*, adult, Huancayo, Peru. **Figs. 15 and 16.** *H. charcastus*, instar-2, Peru. **13.** full tarsus, leg III. **14.** close-up of distal aspect showing blunted unguicular spine, leg III. **15.** full tarsus, leg I. **16.** close-up of spinule clusters on basitarsus, leg I.



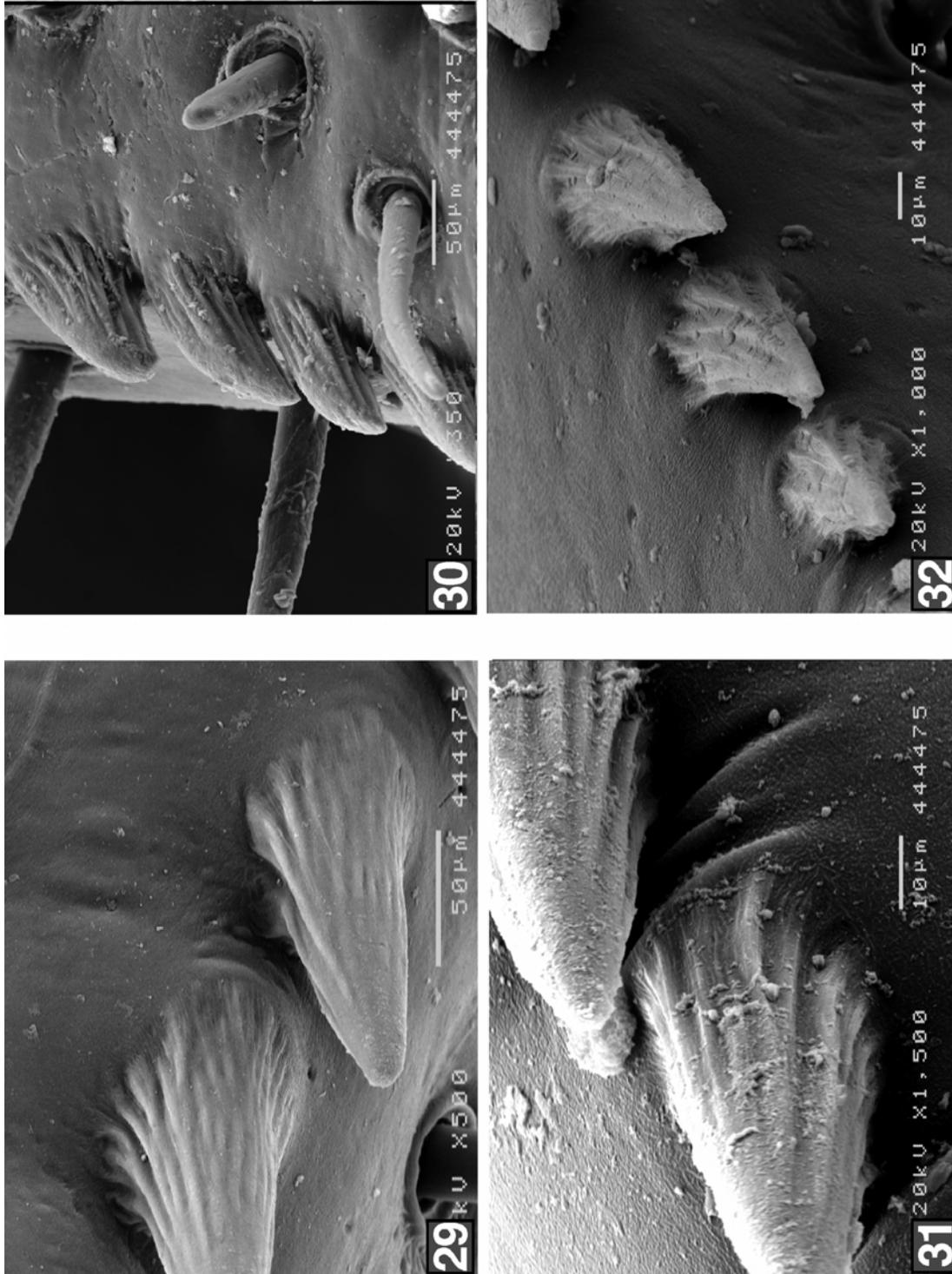
Figs. 17-20. Ventrolateral view of leg III tarsus of *Hadynurus a. arizonensis*. **17.** close-up of fused spinule cluster of subadult (carapace length = 9.3 mm), Arroyo Salado, ABDSP, California, USA. **18.** close-up of fused spinule cluster of subadult. **19.** close-up of fused spinule cluster of juvenile (carapace length = 3.9 mm), Arroyo Salado, ABDSP, California, USA. **20.** close-up of fused spinule cluster of adult, Borrego Springs, California, USA.



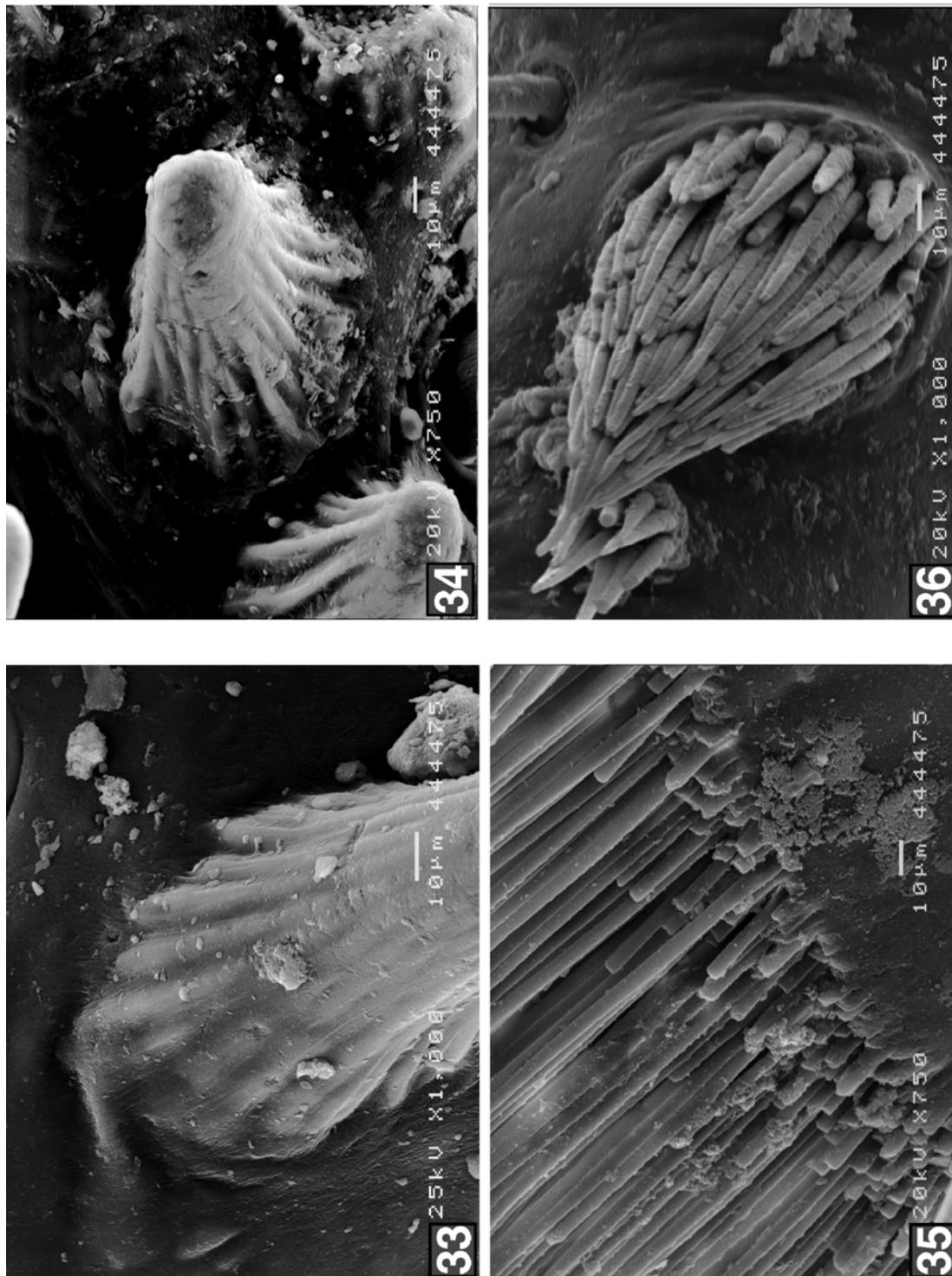
Figs. 21-24. Ventrolateral view of leg III (leg IV in Fig. 24) tarsus of Mexican *Hoffmanniadrurus* species. **21.** close-up of fused spinule cluster of adult *Hoffmanniadrurus gerisehi*, Iguala, Guerrero, Mexico. **22.** close-up of fused spinule cluster of adult *H. aztecus*, Tehuacan, Puebla, Mexico.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



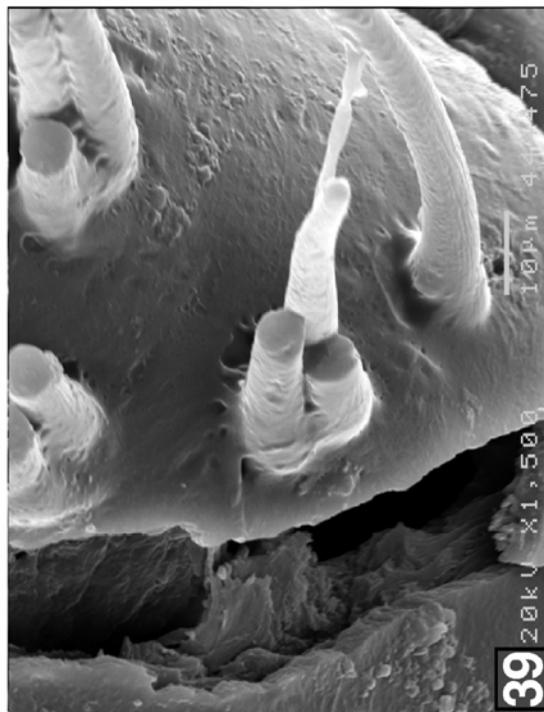
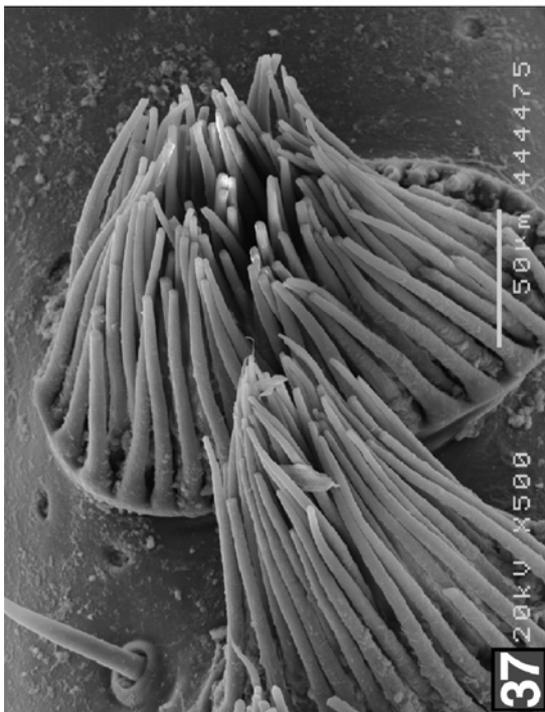
Figs. 25-28. Ventrolateral view of leg III tarsus of Baja California *Hadrurus* species. **25.** close-up of fused spinule cluster of adult *H. hirsutus*, Cabo San Lucas, Baja California Sur, Mexico. **26.** close-up of fused spinule cluster of adult *H. concolor*, Santa Rosalia, Baja California Sur,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



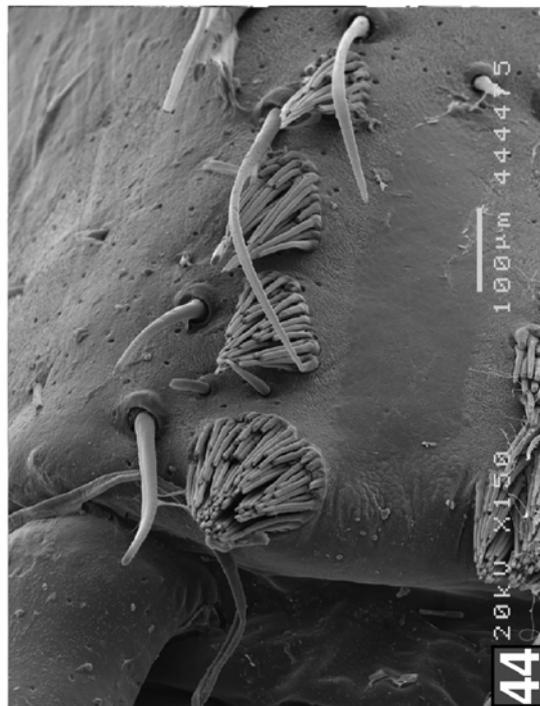
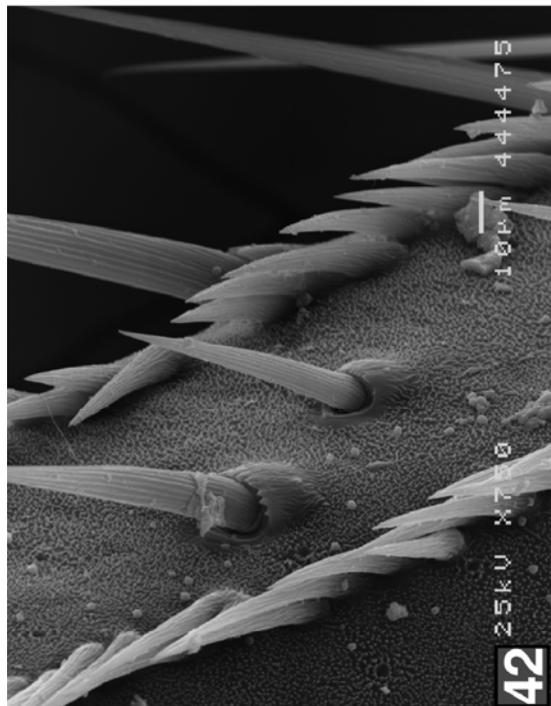
Figs. 29-32. Ventrolateral view of leg III tarsus of *Hadririus* species. **29.** close-up of fused spinule cluster of adult *H. spadix*, Nevada. **30.** close-up of fused spinule cluster of adult *H. spadix*, Nevada. **31.** close-up of fused spinule cluster of subadult *H. obscurus* (carapace = 7.5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



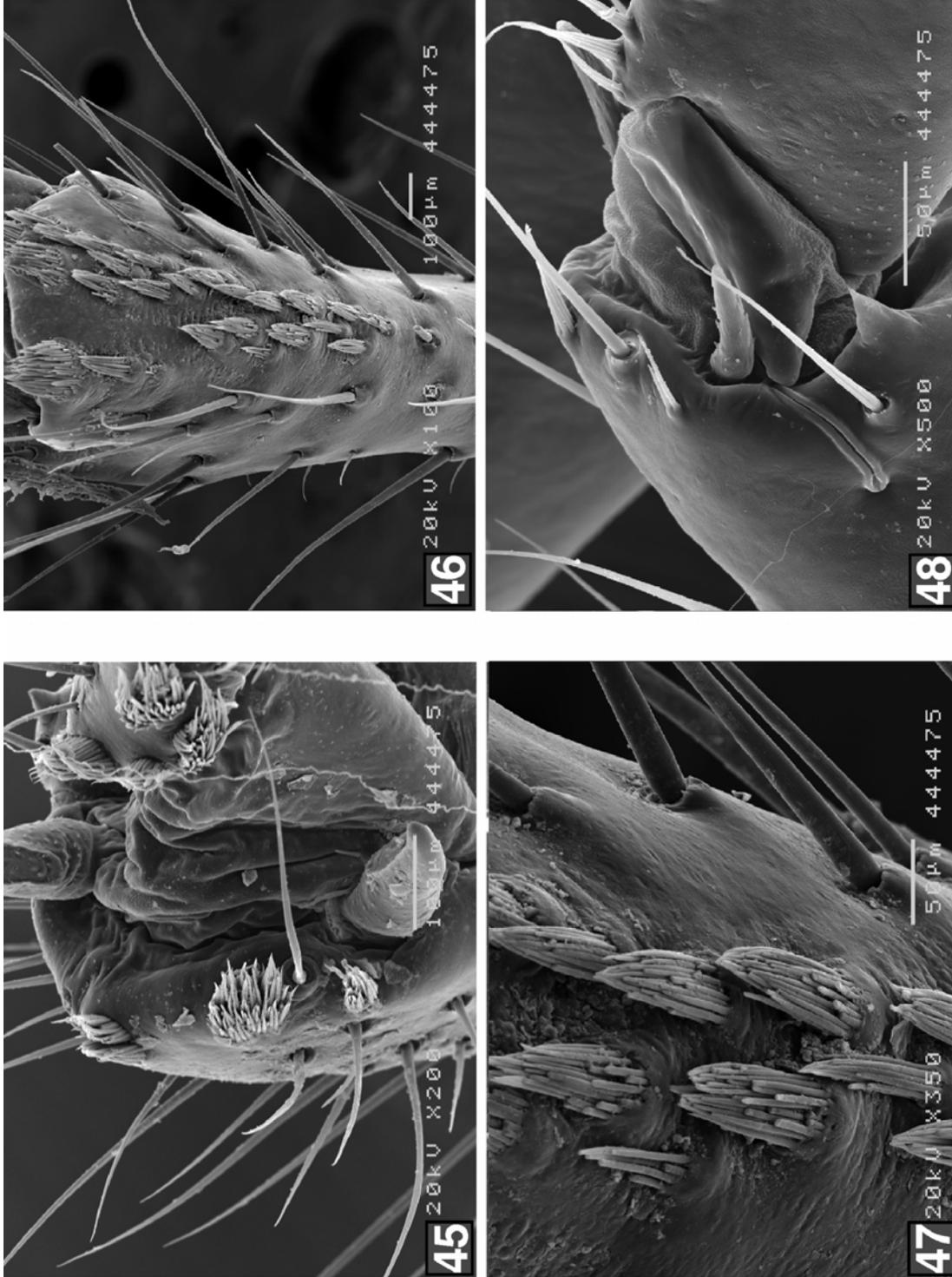
Figs. 33-36. Comparison of spinule clusters for carabocionid genera. **33.** close-up of fused spinule cluster of adult *Hadrurus pinteri*, Oakies Landing, Baja California Norte, Mexico. **34.** close-up of fused spinule cluster of adult *Hadrurus obscurus*, ABDSP, California. **35.** close-up of spinule cluster of adult *Hadruidoidea maculatus*, Huancayo, Peru. **36.** close-up of spinule cluster of adult *Hadrurus pinteri*, Oakies Landing, Baja California Norte, Mexico.



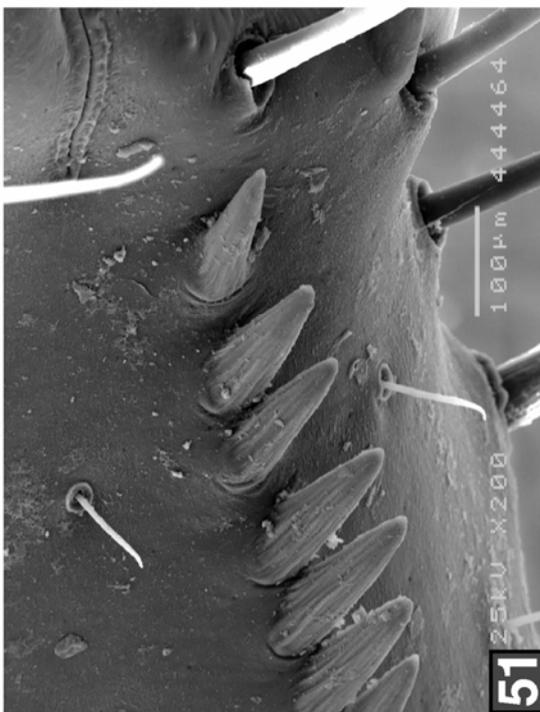
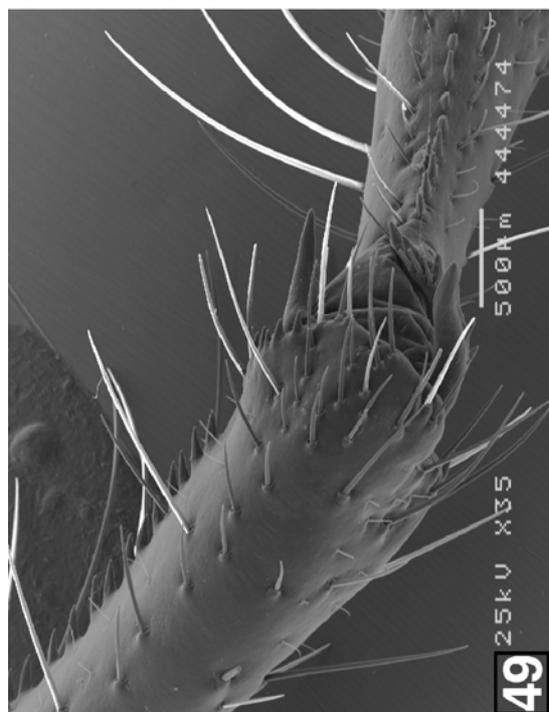
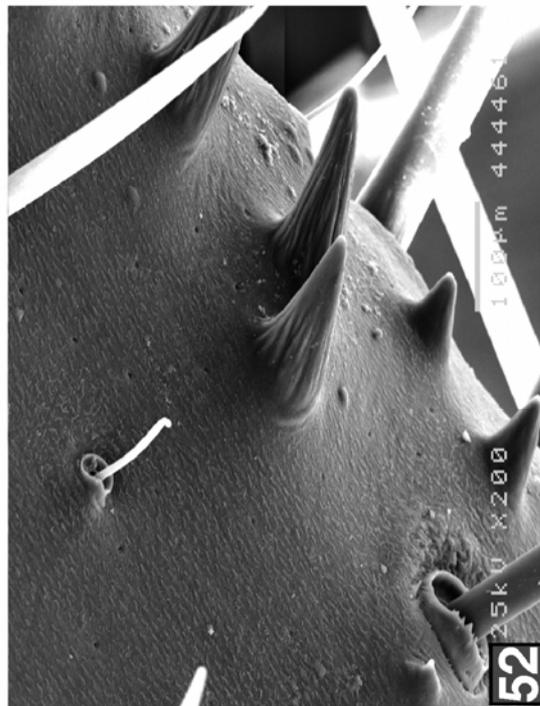
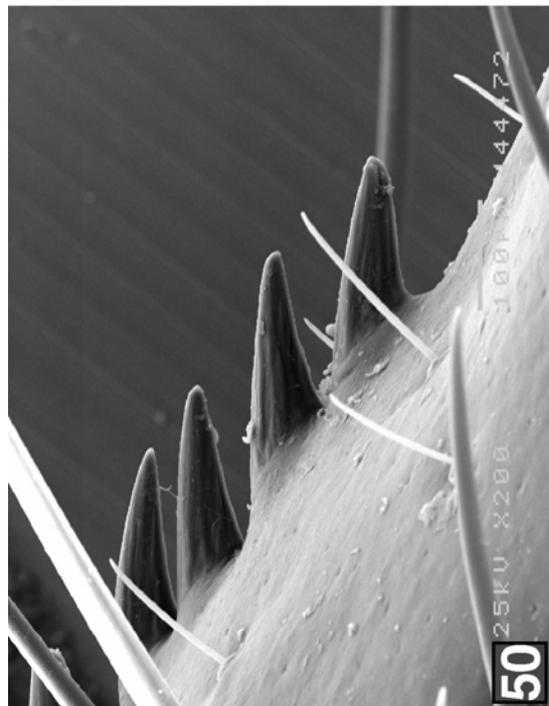
Figs 37-40. Ventrolateral view of leg III tarsus of adult male (Turkey), and adult female and juvenile (seven month instar) (Crete) *Iurus dufourieus*. **37.** close-up of spinule cluster of male adult. **38.** close-up of spinule cluster of adult female showing flathead spinules. **39.** close-up of spinule cluster of juvenile showing three spinules. **40.** close-up of spinule cluster of juvenile showing four flathead spinules.



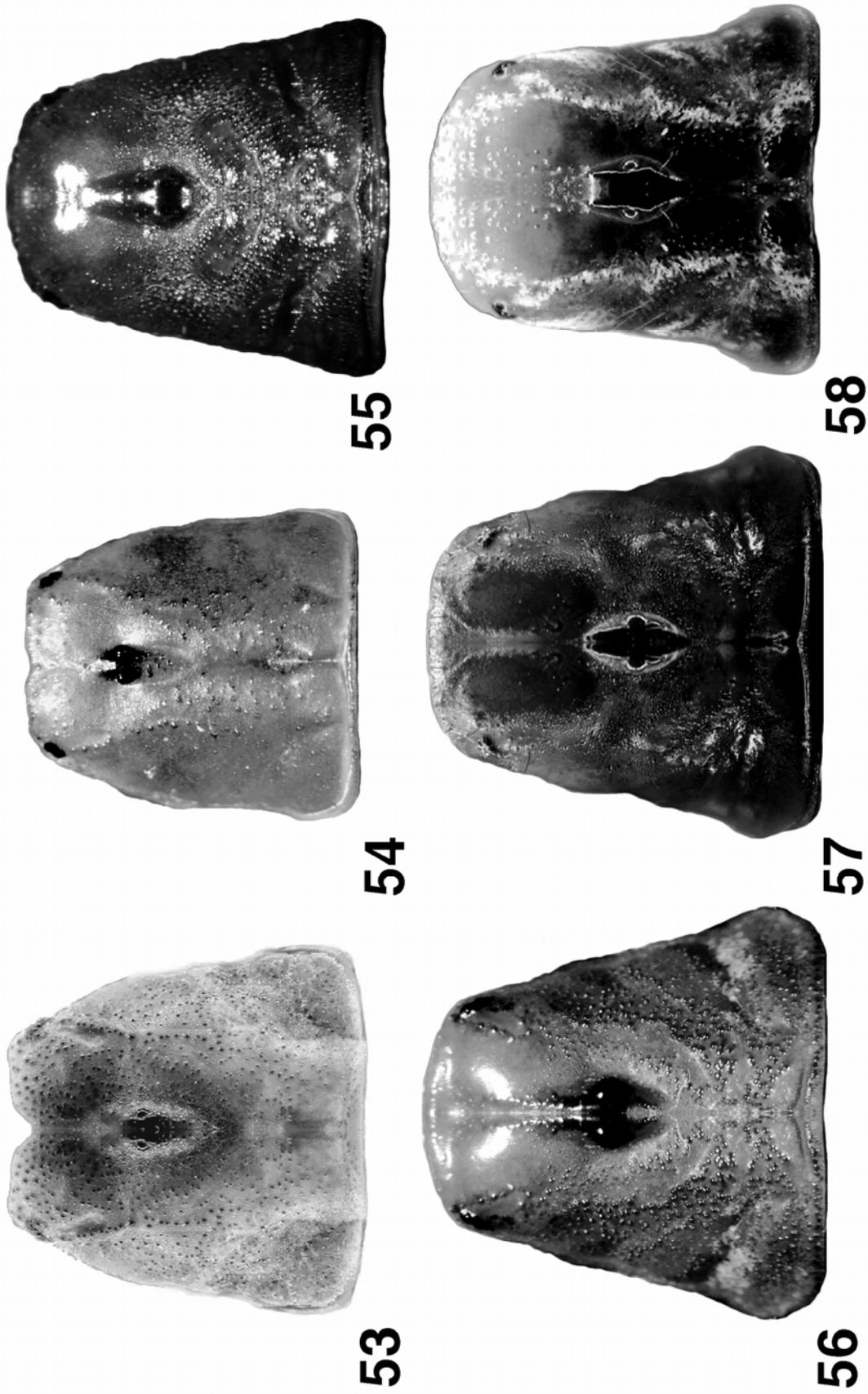
Figs 41-44. Basitarsus of juvenile *Calchas nordmanni*, Megisti, Greece, **41** and **42**, and adult *Jurus difoureus*, **43** and **44**. **41**, ventral view of basitarsus, leg I, showing two spinule rows. **42**, close-up of two spinule rows on leg I. **43**, close-up of spinule cluster of basitarsus, adult male, Turkey, leg III. **44**, close-up of spinule cluster of distal aspect of basitarsus, adult female, Crete, leg III.



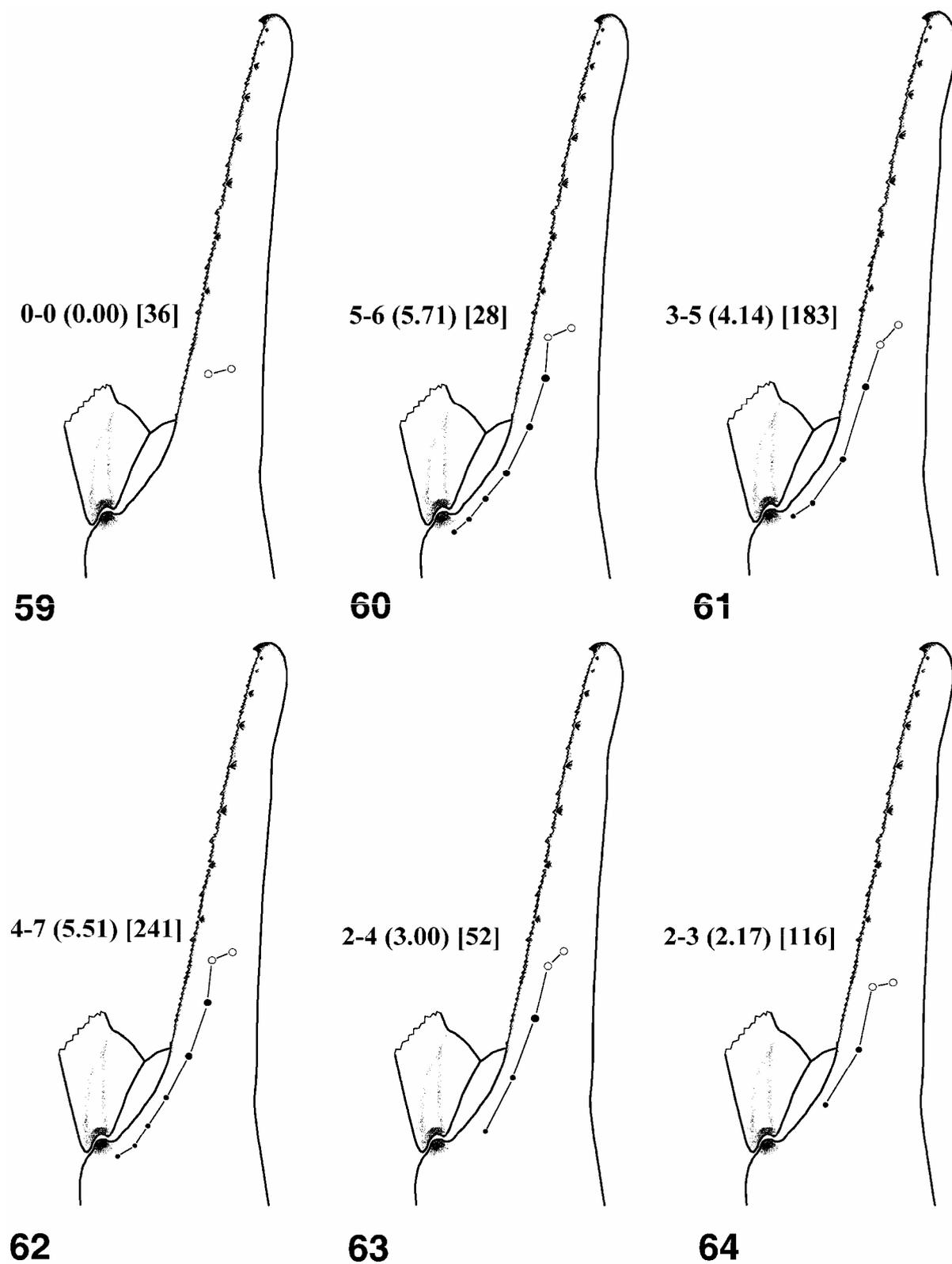
Figs 45-48. Distal ventral aspect of basitarsus showing spinule clusters. **45.** *Caraboctonus keyserlingi* male, Chile. **46** and **47.** *Hadruroides maculatus* female, Huancayo, Peru. **48.** *Hadruroides charcasus*, instar-2, leg I, Peru.



Figs 49-52. Dorsolateral view of basitarsus, leg III, of adult *Hoggiananthomyia ruscus*, Toluacan, Puebla, Mexico, 49 and 50, and *Hoggianthomyia* sp. 51 and 52. 49, general view of basitarsus and tarsus. 50, close-up of fused spumule cluster on basitarsus. 51, close-up of fused spumule cluster on basitarsus of *H. concolor*, Santa Rosalia, Baja California Sur, Mexico. 52, close-up of fused spumule cluster on basitarsus of *H. spadei*, Nevada, U.S.A.



Figs. 53–58: Carapaces of luroid genera contrasting the indented anterior edges exhibited in family Luridae with that of the highly convex anterior edges in family Caraboctonidae. Note also the well developed *lateral carinae* in family Luridae, which are inconspicuous in Caraboctonidae. 53, *Burza difformis*; 54, *Catolites noreibumii*; 55, *Caraboctonus kochelbergi*; 56, *Haeburnella maculata*; 57, *Haeburnella strabus*; 58, *Haeburnella strabus*.



Figs. 59-64: Diagrammatic depiction of internal trichobothria of the chelae for genera *Hoffmanniadrurus* and *Hadrurus*. **59.** *Hoffmanniadrurus aztecus* and *H. gertschi*. **60.** *Hadrurus pinteri*. **61.** *H. hirsutus* and *H. concolor*. **62.** *H. arizonensis*. **63.** *H. obscurus*. **64.** *H. spadix*. Open circles depict orthobothriotaxic series *ib-it*; closed circles depict accessory trichobothria. Statistical data show the number of accessory trichobothria: minimum – maximum (mean) [number of samples].