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CONSTELLATION ARRAY: A NEW SENSORY STRUCTURE IN SCORPIONS (ARACHNIDA: SCORPIONES)

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"…Striking modifications of the cuticle have turned much of its surface into an information-gathering device."
(Shear, 1999, p. 5)

Abstract: A peculiar constellation-shaped microscopic array of several chemosensory sensilla is described for the first time in scorpions. This sensillar array is located on the external aspect of the distal portion of the fixed finger of pedipalp. We present data on the constellation array across four parvorders, six superfamilies, 12 families, 23 genera, and 28 species of extant (orthostern) scorpions. The constellation array was observed in all scorpion taxa. Observed number of sensilla in the constellation array varied from one (*Vejovoidus*) to 15 (*Calchas*), on average 6 ± 3; the size of the sensillum is 5-10 µm, their shape varying from conical to hair-like. The sensilla are socketed, and appearance of their "button-like" socket areola differs from other mechanosensory and chemosensory setae common on the scorpion's body and appendages. As observed in *Calchas nordmanni* (Iuridae) and *Euscorpius tergestinus* (Euscorpiidae), there was no difference in number of sensilla between juveniles and adults. The constellation array size (maximal distance between two sensilla) usually varied between 100 to 300 µm, with Buthidae arrays markedly smaller in size. There was no apparent correlation between the size of a species and constellation array size. This ultrastructural character can be potentially of diagnostic use in scorpion systematics at family and genus levels. We suggest that the constellation array could be a chemosensory organ.
Key words: Scorpiones, pedipalp, fixed finger, sensory setae, constellation array.

Material and Methods

MATERIAL. (taxonomy after Soleglad & Fet, 2003; Soleglad et al. 2005; Fet & Soleglad, 2005). Parvorder Buthida, superfamily Buthoidea, family Buthidae: *Centruroides hentzi* (Banks, 1910), female, Alachua Co., Florida, USA; *Lychas mucronatus* (Fabricius, 1798), female, Hanoi, Vietnam; *Mesobuthus caucasicus* (Nordmann, 1840), female, Repetek, Karakum Desert, Turkmenistan; *Mesobuthus eupeus* (C.L. Koch, 1839), female, Repetek, Karakum Desert, Turkmenistan. Parvorder Chaerilida, superfamily Chaeriloidea, family Chaerilidae: *Chaerilus celebensis* Pocock, 1894, juvenile, Mapur Island, Indonesia. Parvorder Iurida, superfamily Chactoidea, family Chactidae: *Belisarius xambeui* Simon, 1879, female, Fogars de Monclus, Barcelona Province, Spain; *Brotheas gervaisii* Pocock, 1893, female, Kaw, French Guiana; *Nullibrotheas allenii* (Wood, 1863), female, Cabo San Lucas, Baja California Sur, Mexico; *Uroctonus mordax* Thorell, 1876, male, Kalmiopsis Wilderness, Siskiyou National Forest, Oregon, USA; family Euscorpiidae: *Euscorpius gamma* (Caporiacco, 1950), male and female, Planinsko Polje, Slovenia; *Euscorpius italicus* (Herbst, 1800), male, Epirus, Greece; *Euscorpius tergestinus* (C. L. Koch, 1837), female and juvenile, Sežana, Slovenia; family Superstitioniidae: *Superstitionia donensis* Stahnke, 1940, female, San Diego, California, USA; family Vaejovidae: *Serradigitus gertschi gertschi* (Williams, 1968), female, San Diego, California, USA; *Serradigitus joshuaensis* (Soleglad, 1972), female, Anza-Borrego Desert State Park, California, USA; *Serradigitus subtilimanus* (Soleglad, 1972), female, Anza-Borrego Desert State Park, California, USA; *Smeringurus mesaensis* (Stahnke, 1957), female, Anza-Borrego Desert State Park, California, USA; *Vaejovis carolinianus* (Beauvois, 1805), *Vaejovis eusthenura* (Wood, 1863), female, Cabo San Lucas, Baja California Sur, Mexico; *Vejovoidus longiunguis* (Williams, 1969), female, Vizcaino Desert, Baja California Sur, Mexico; superfamily Iuroidea, family Caraboctonidae: *Hadruroides charcasus* (Karsch, 1879), female, Peru; *Hadrurus obscurus* Williams, 1970, male, Anza-Borrego Desert State Park, California, USA; family Iuridae: *Calchas nordmanni* Birula, 1899, juvenile, Megisti (=Kastelorizo) Island, Greece; female, Anamur, Turkey; superfamily Scorpionioidea, family Bothriuridae: *Centromachetes pocockii* (Kraepelin, 1894), Lebu, Chile; family Hemiscorpiidae: *Hadogenes bicolor* Purcell, 1899, female, South Africa; family Scorpionidae: *Bioculus comondae* Stahnke, 1968, male, La Paz, Baja California, Mexico. Parvorder Pseudochactida, superfamily Pseudochactoidea, family Pseudochactidae: *Pseudochactas ovchinnikovi* Gromov, 1998, juvenile female, Akmachit, Babatag Mountains, Surkhandarya Region, Uzbekistan.

MICROSCOPY. Scorpions were preserved in 70% or 96% ethanol. Chelae were removed from the animals and sonicated for 1 minute in 50% ethanol, after which they were dehydrated in an ethanol series (75, 95, and two changes of 100 %) before being air dried and coated with gold/palladium (ca. 10 nm thickness) in a Hummer sputter coater. SEM images were acquired with a JEOL JSM-5310LV at Marshall University, West Virginia, USA. 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. Digital SEM images were taken at magnifications from 75x to 10,000x.

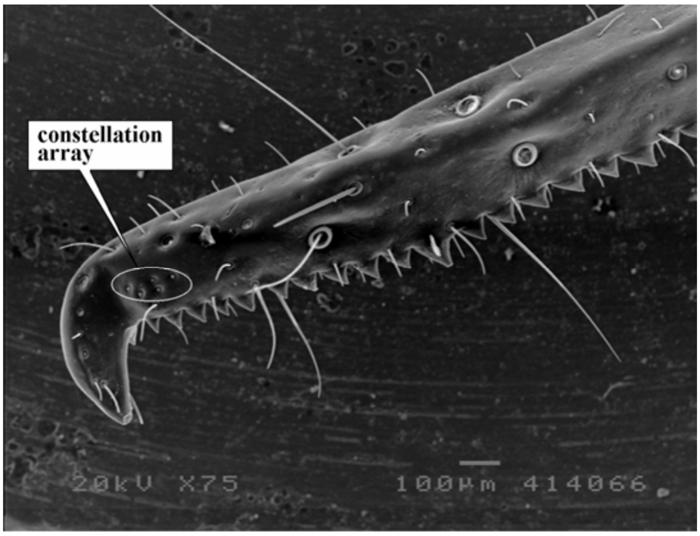

Fig. 1. *Constellation array* (enclosed in ellipse) on chelal fixed finger, external view, in *Serradigitus g. gertschi* showing five sensilla.

Results

We conducted a pilot SEM survey of pedipalp fixed fingers across four parvorders, six superfamilies, 12 families, 22 genera, and 27 species of extant (orthostern) scorpions (Table I). In addition, data on *Isometrus garyi* Lourenço et Huber, 2002 (Buthidae) from Sri Lanka were obtained from literature (see Discussion). The external aspect of the distal portion of the fixed finger of pedipalp as observed under SEM is illustrated in Figs. 1-25 for representative 22 species of scorpions belonging to 20 genera and 12 families.

In ***all*** species, we observed a peculiar constellation-shaped microscopic array of several chemosensory sensilla. This microstructure, which we will further address as a "constellation array" is always located on the *external distal aspect of the fixed finger* (both in left and right pedipalps, which were sampled randomly). No matching structures were found on the internal aspect of the fixed finger, or on either external or internal aspects of the movable finger.

Observed number of sensilla in the constellation array varied from one (*Vejovoidus*, Vaejovidae) to 15 (*Calchas*, Iuridae), most commonly being four to seven (Table I); the size of a sensillum is 5 to 10 µm, its shape varying from conical to hair-like. The sensilla are socketed, and appearance of their "button-like" socket areola differs from other mechanosensory and chemosensory setae common on scorpion's body and appendages.

As a pilot observation shows for *Calchas nordmanni* (Iuridae, 15 sensilla) and *Euscorpius tergestinus* (Euscorpiidae, six sensilla), there was *no difference in number of sensilla* between first instar juveniles and adults. We did not conduct a study of sexual dimorphism but instead, for comparative purposes, sampled mostly females. However, we surveyed both males and females for *Euscorpius tergestinus* and *E. gamma* (Euscorpiidae), and did not find any difference in number of sensilla.

The size of constellation array was estimated as the distance between the two most distant sensilla. It ranged from 18 µm (juvenile *Isometrus garyi*, Buthidae; Lourenço & Huber, 2002, fig. 18) to ca. 500 µm (*Euscorpius italicus*, Euscorpiidae) (Table I); there was no apparent correlation between scorpion's size and constellation array size. Indeed, the dwarf *Superstitionia donensis* (Superstitioniidae) had the same size constellation array (356 µm) as the giant *Hadogenes bicolor* (Hemiscorpiidae) (344 µm) (Table I). It can be observed, however, that all three representative species of Buthidae belonging to three systematically distant genera (*Centruroides*, *Lychas*, *Mesobuthus*) all had extremely small constellation arrays (30 to 50 µm), while the number of sensilla was average to high (5 to 10). Juvenile specimens had smaller sized constellation arrays than adults of the same species (142 µm and 263 µm, respectively, for *Calchas nordmanni* juvenile and adult female; 200 µm and 432 µm, respectively, for *Euscorpius tergestinus* juvenile and adult female). This growth factor could explain the very small size of the constellation array in the abovementioned juvenile of *Isometrus garyi*, since adult specimens of Buthidae species also have a relatively small constellation array size.

Discussion

Scorpions are famous for a remarkable contact chemoreception by pectinal organs, with thousands of peg sensilla (up to 120,000 per male; Gaffin & Brownell, 2001). In addition, short, curved chemosensory setae are known to be scattered all over the animal's body (Foelix & Mueller-Vorholt, 1983; Foelix & Schabronath, 1983; Farley, 1999, 2001; Brownell, 2001a, 2001b; Gaffin & Brownell, 2001). Observations of these setae were sporadic, concentrating largely on leg tarsi which bear contact chemosensory setae. Several types of very large chemosensory sensilla ("macrochaetae") were observed by San Martín (1968) on the metasoma of *Microtityus rickyi* (Buthidae) and Lamoral (1976) on the body of *Akentrobuthus leleupi* (Buthidae). Fet et al. (2003) described a sizable (over 1,000) concentration of chemosensory setae on the ventral aspect of the metasoma in *Orthochirus* (Buthidae) as one of the possible events of "antennalization" (Brownell, 2001b) in scorpions.

The SEM micrographs of scorpion pedipalp chela published in the recent several years usually depicted the diagnostic dentition of the *movable* finger (e.g. Lourenço, 2001a: figs. 15-17; Lourenço, 2001b: fig. 12; Lourenço, 2002a, fig. 13-14; Lourenço, 2002b: fig. 1-2; Lourenço, 2003a: fig. 22-23; Lourenço, 2003b: fig. 1-2; Lourenço & Huber, 2002: fig. 13-14, 17; Lourenço & Pézier, 2002: fig. 10; Lourenço & Goodman, 2003: fig. 5, 7-8). Our observations show, however, that the constellation array is present

Table I. Number of sensilla and size of constellation array in scorpions (a pilot survey).
Data on *Isometrus garyi* calculated from fig. 18 in Lourenço & Huber (2002).

Family	Species	Number of sensilla	Size of constellation Array (maximal distance between sensilla), µm	Image / reference
Buthidae	*Centruroides hentzi*	5	32	
	Isometrus garyi juvenile	6	18	Lourenço & Huber (2002, fig. 18)
	Lychas mucronatus	10	50	Fig. 5
	Mesobuthus caucasicus	5	58	Fig. 4
	Mesobuthus eupeus	5	36	
Bothriuridae	*Centromachetes pocockii*	4	338	Fig. 13
Caraboctonidae	*Hadruroides charcasus*	8	294	Fig. 8
	Hadrurus obscurus	4	238	Fig. 9
Chactidae	*Belisarius xambeui*	4	200	Fig. 18
	Broteas gervaisii	14	364	
	Nullibrotheas allenii	2	50	Fig. 19
	Uroctonus mordax	4	144	Fig. 20
Chaerilidae	*Chaerilus celebensis* juvenile	6	138	Fig. 3
Euscorpiidae	*Euscorpius gamma* female	6	240	
	Euscorpius gamma male	6	281	Fig. 17
	Euscorpius italicus	5	517	Fig. 16
	Euscorpius tergestinus female	6	432	
	Euscorpius tergestinus juvenile	6	200	Figs. 14-15
Hemiscorpiidae	*Hadogenes bicolor*	7	344	Fig. 10
Iuridae	*Calchas nordmanni* female	15	263	Fig. 6
	Calchas nordmanni juvenile	15	142	Fig. 7
Pseudochactidae	*Pseudochactas ovchinnikovi*	4	173	Fig. 2
Scorpionidae	*Bioculus comondae*	4	188	Fig. 12
Superstitioniidae	*Superstitionia donensis*	4	356	Fig. 21
Vaejovidae	*Serradigitus g. gertschi*	5	100	Fig. 1
	Serradigitus joshuaensis	5	113	Fig. 24
	Serradigitus subtilimanus	5	162	
	Smeringurus mesaensis	2	308	Fig. 22
	Vaejovis carolinianus	4	138	
	Vaejovis eusthenura	5	183	Fig. 25
	Vejovoidus longiunguis	1	not applicable	Fig. 23
Mean ± SD		**~ 6 ± 3**	**203 ± 127**	

only on fixed finger. The only clear picture of constellation array we could discover in the literature is found (without any comment) in fig. 18 in Lourenço & Huber (2002: 272) in a juvenile male paratype of *Isometrus garyi* (Buthidae). It is a compact, almost hexagonal group of six sensilla in a very small array 18 µm in size (pictured at magnification 750x). Another, less clear formation of possibly three sensilla is seen in *Tityobuthus dastychi* Lourenço, 1997 (Buthidae) (Lourenço & Goodman, 2003, fig. 6; magnification 200x). Also, a very unclear constellation array on the fixed finger can be discerned on fig. 9 in Lourenço & Pézier (2002) (magnification 190x) in *Tityus adisi* Lourenço & Pézier, 2002 (Buthidae). Prior to our study, there were no published detailed SEM photographs of fixed fingers for non-buthid scorpions.

Armas (1977) and Cruz & Armas (1980), using light microscopy, described a specialized matching cluster of "digitoterminal macrochaetae" (spatulated and filiform) present on the tips of both fixed and movable pedipalp fingers. These groups were found in 28 species and nine genera of Buthidae, mainly in New World genera *Alayotityus*, *Microtityus*, *Centruroides*, *Rhopalurus*, and *Tityus*, but also in *Ananteris*, *Buthus*, *Isometrus*, and *Uroplectes*. This prominent group of macrochetae was also recently documented (without discussion) on SEM images by W. R. Lourenço and coauthors for the following species of Buthidae: *Ananteris sabineae* Lourenço, 2001 (Lourenço, 2003b: fig. 2); *Buthacus clevai* Lourenço, 2001 (Lourenço, 2001b: fig. 12); *Charmus minor* Lourenço, 2002 (Lourenço, 2002b: fig. 2); *Grosphus ankarafantsika* Lourenço, 2003 (Lourenço, 2003a: fig. 23); *Isometrus garyi* (Lourenço, 2002b: figs. 14, 18); *Tityobuthus dastychi* (Lourenço & Goodman, 2003: figs. 6-8); *Tityus adisi* (Lourenço & Pézier, 2002: fig. 10). Our SEM survey also detected digitoterminal cluster of macrochetae in Buthidae. We did *not*, however, find digitoterminal macrochaetae in any of the inspected non-buthid families.

At the same time, we see consistent presence of **constellation arrays** across *all* scorpion families. Table I documents number of sensilla and size of sensory field in studied scorpions. As there was no visible change of sensillar number with scorpion age, this sensory field appears to be a conserved feature, probably functional already in young instars. It is also a very localized sensory field, reaching maximal observed size (in *Euscorpius italicus*) of 517 µm, and never present in multiple copies further basad on the fixed finger.

The observed number of sensilla was clearly variable within taxonomic groups of various ranks. For example, the chactoid family Vaejovidae exhibited the lowest number of one (*Vejovoidus*, Fig. 23) and two (*Smeringurus*, Fig. 22), and four to five sensilla in other studied species; three studied species of *Serradigitus* all had five sensilla, positioned in a jagged row (Figs. 1, 24). Other chactoid families exhibited variation from two to 14 (Chactidae, Euscorpiidae, Superstitioniidae). The highest number of sensilla (15) was recorded in the relict Mediterranean genus *Calchas* (Iuridae), while related New World caraboctonids (*Hadrurus* and *Hadruroides*) had four to seven sensilla, respectively. Thus, this ultrastructural character can be potentially of diagnostic use in scorpion systematics at family and genus levels.

Brownell (2001b) wrote: "...terrestrial arachnids can claim some of the most elaborate chemosensory organs among the Arthropoda. ...Taken together, the Arachnida reveal an evolutionary trend toward specialization of chemosensory appendages in arthropods, one that begins with gustation by leg-like appendages contacting the substrate [in scorpions and solpugids] and ends with olfaction by antenna directed into the air [in amblypygids, uropygids, and solpugids]." The constellation array appears to be a chemosensory field. Tips of pedipalps, the most distal spot in scorpion's body, are a very appropriate location for an additional sensory organ, analogous to palpal organ and Haller's organ on tarsi I in ticks (Evans, 1992, figs. 3.9, 3.10; Coons & Alberti, 1999, figs. 123, 129). Moreover, full development of the constellation array in juveniles suggests an important general function of this putative organ.

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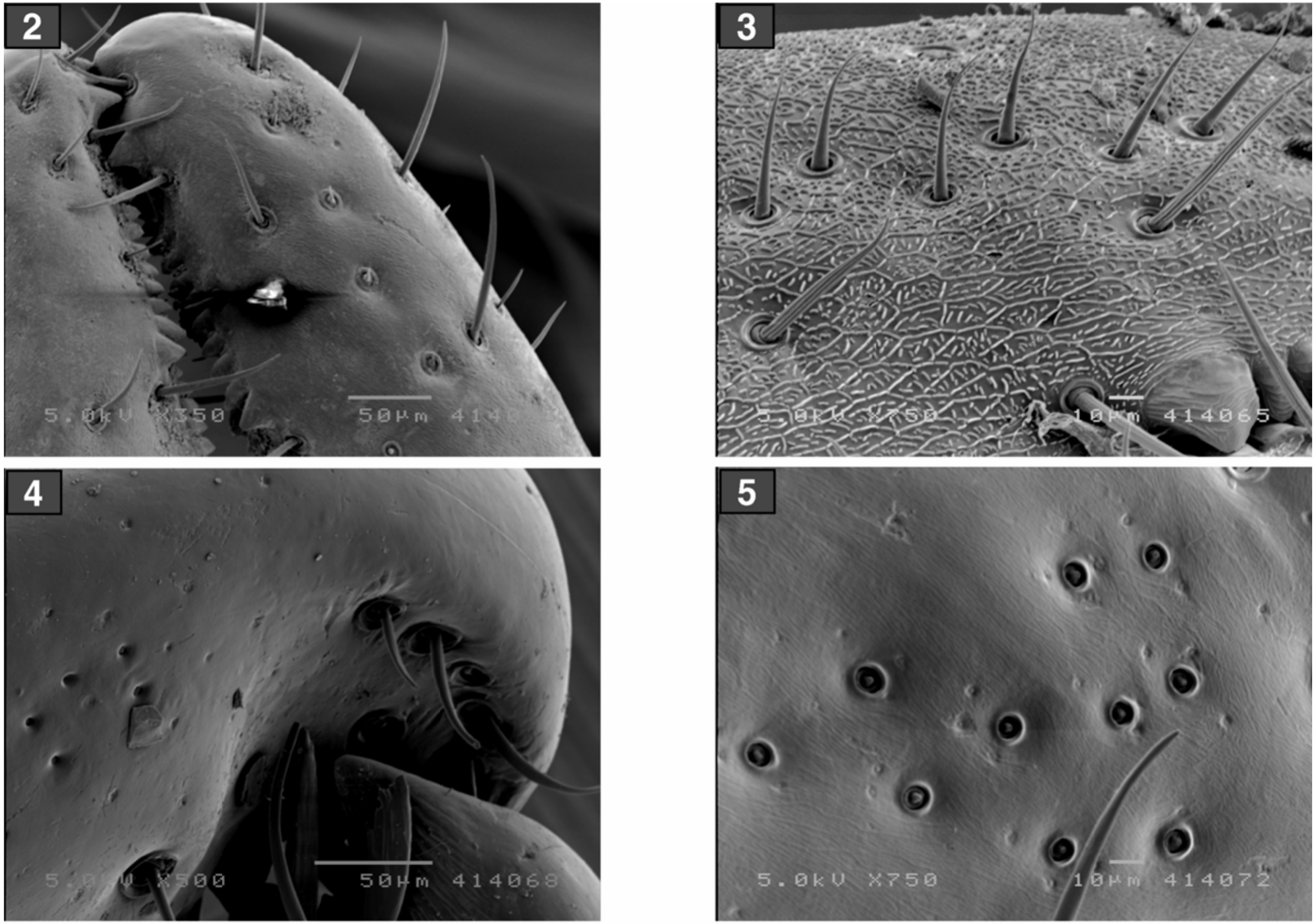

Fig. 2-5. Constellation array in parvorders Pseudochactida, Chaerilida, and Buthida. **2.** *Pseudochactas ovchinnikovi*, juvenile, showing four sensilla. **3.** *Chaerilus celebensis*, juvenile, showing six sensilla with elongated bristles lacking striations. **4.** *Mesobuthus eupeus* showing five sensilla. **5.** *Lychas mucronatus* showing ten sensilla.

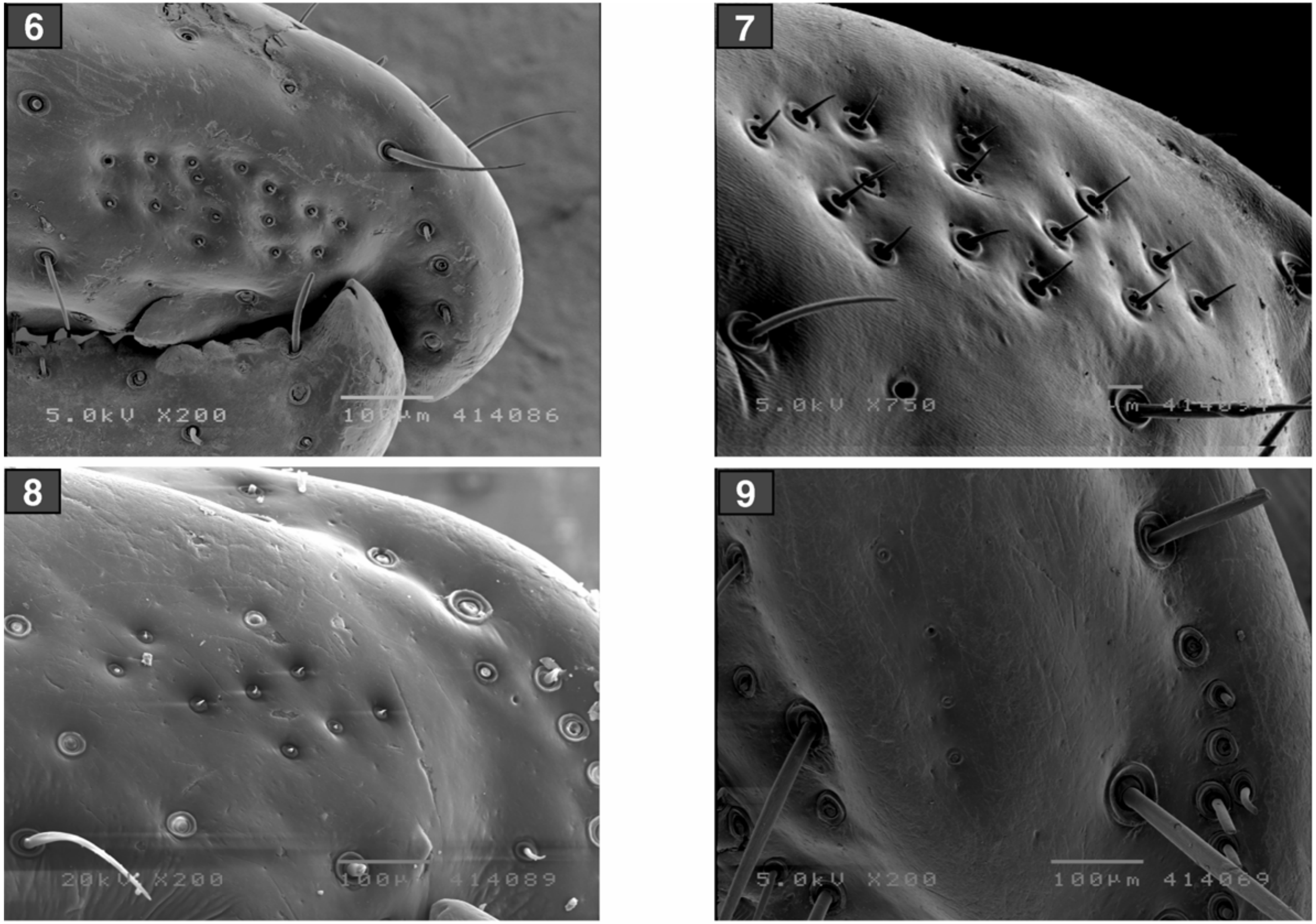

Fig. 6-9. Constellation array in parvorder Iurida, superfamily Iuroidea. **6.** *Calchas nordmanni*, adult, showing 15 sensilla. **7.** *Calchas nordmanni*, juvenile, showing 15 sensilla. **8.** *Hadruroides charcasus* showing eight sensilla. **9.** *Hadrurus obscurus* showing four sensilla.

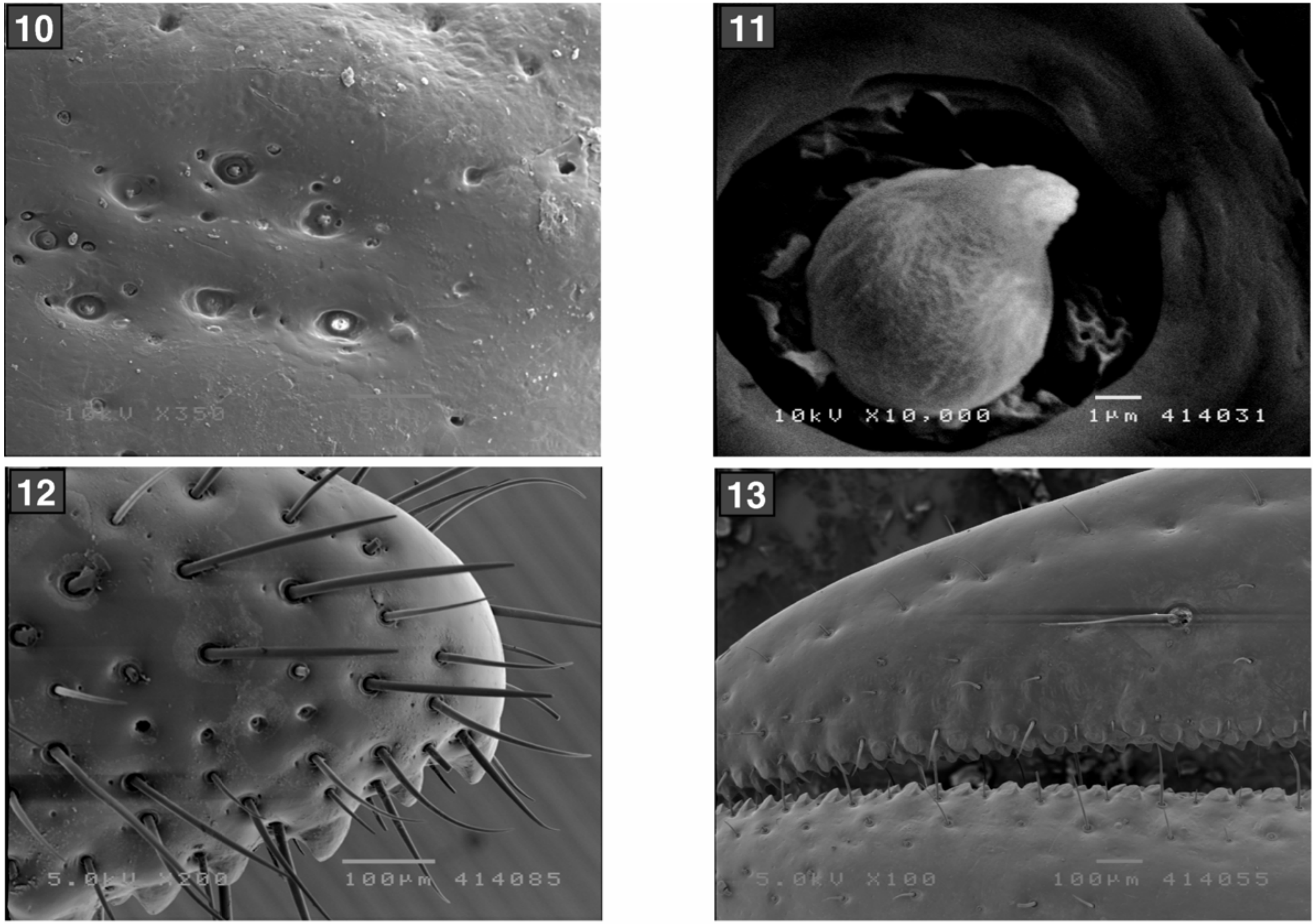

Fig. 10-13. Constellation array in parvorder Iurida, superfamily Scorpionoidea. **10.** *Hadogenes bicolor* showing seven sensilla. **11.** *Hadogenes bicolor* showing closeup of a single sensillum. **12.** *Bioculus comondae* showing four sensilla. **13.** *Centromachetes pocockii* showing four sensilla.

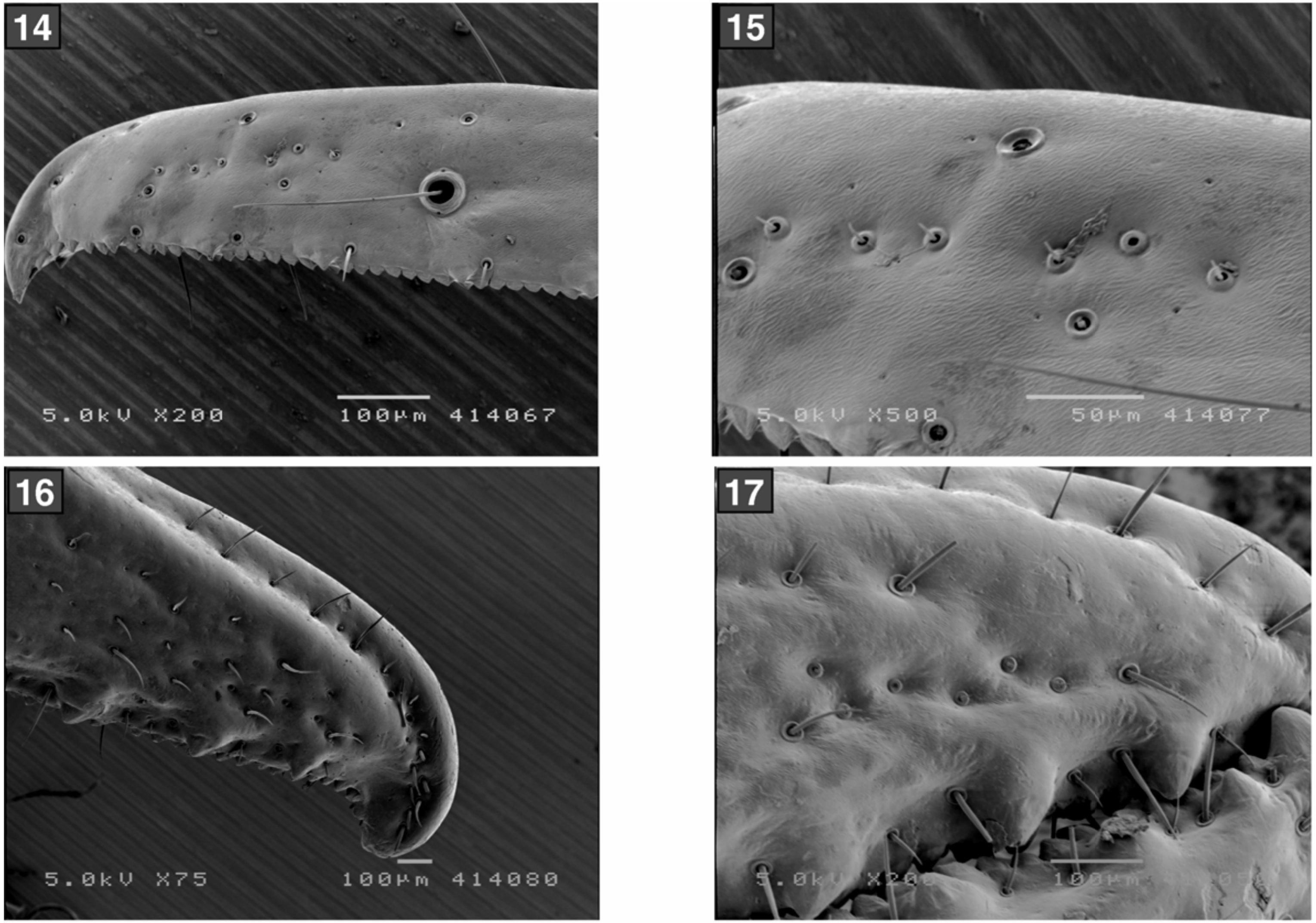

Fig. 14-17. Constellation array in parvorder Iurida, superfamily Chactoidea, family Euscorpiidae. **14 & 15.** *Euscorpius tergestinus*, juvenile, showing six sensilla. **16.** *Euscorpius italicus* showing five sensilla. **17.** *Euscorpius gamma* showing six sensilla.

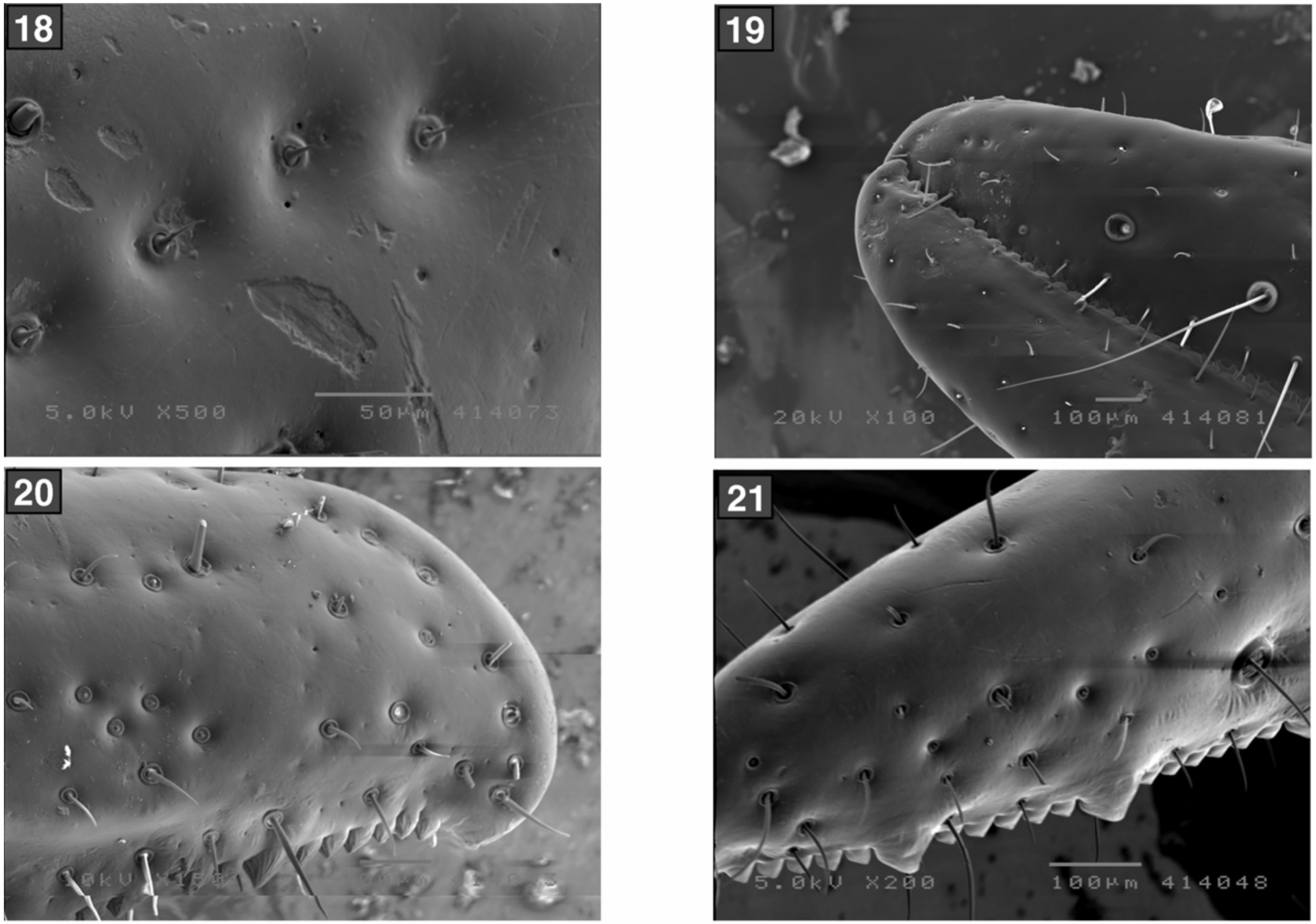

Fig. 18-21. Constellation array in parvorder Iurida, superfamily Chactoidea, families Chactidae and Superstitioniidae. **18.** *Belisarius xambeui* showing four sensilla. **19.** *Nullibrotheas allenii* showing two sensilla. **20.** *Uroctonus mordax* showing four sensilla. **21.** *Superstitionia donensis* showing four sensilla.

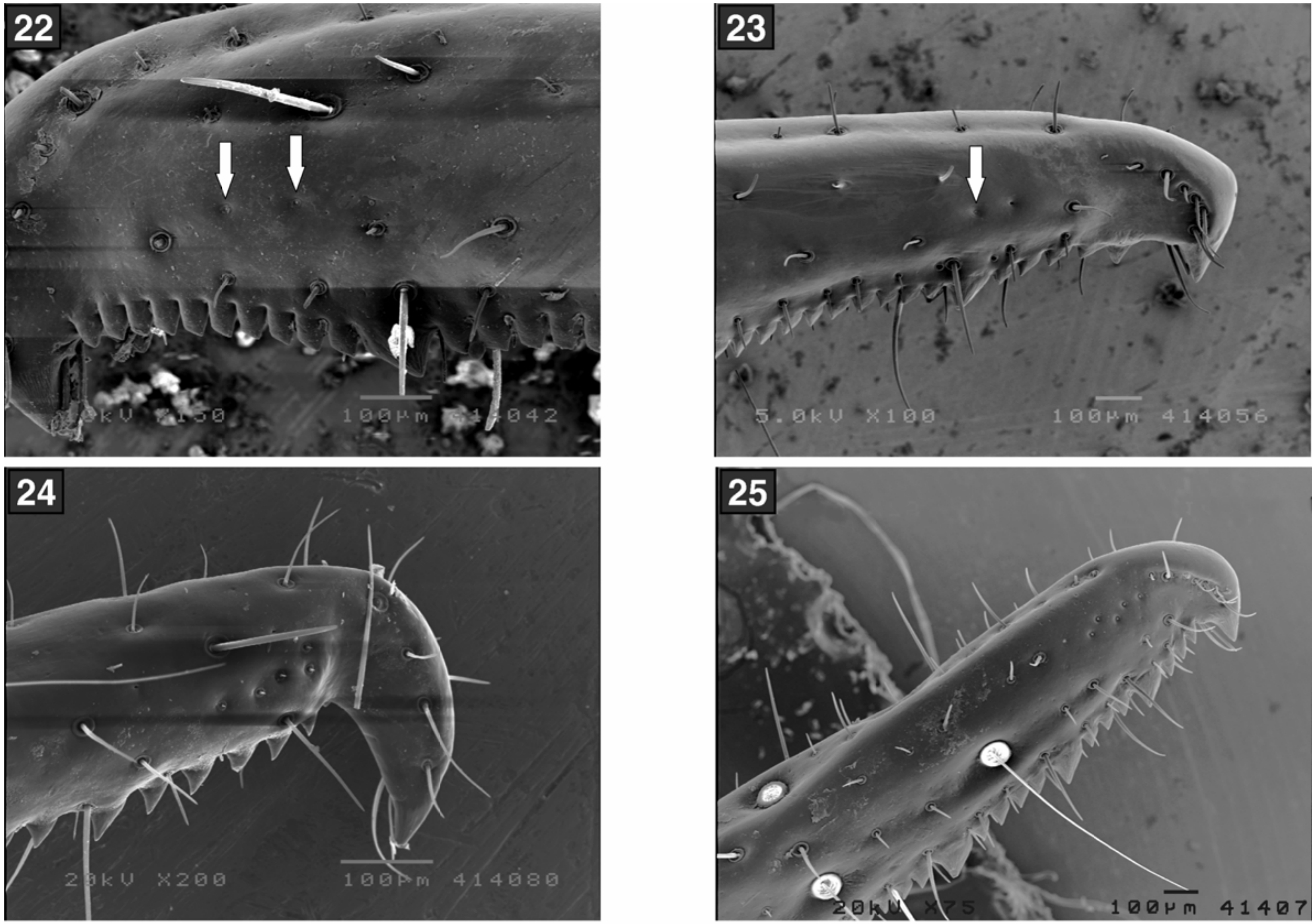

Fig. 22-25. Constellation array in parvorder Iurida, superfamily Chactoidea, family Vaejovidae. **22.** *Smeringurus mesaensis* showing two sensilla (indicated with white arrows). **23.** *Vejovoidus longiunguis* showing one sensillum (indicated with white arrow). **24.** *Serradigitus joshuaensis* showing five sensilla. **25.** *Vaejovis eusthenura* showing five sensilla.