Euscorpius

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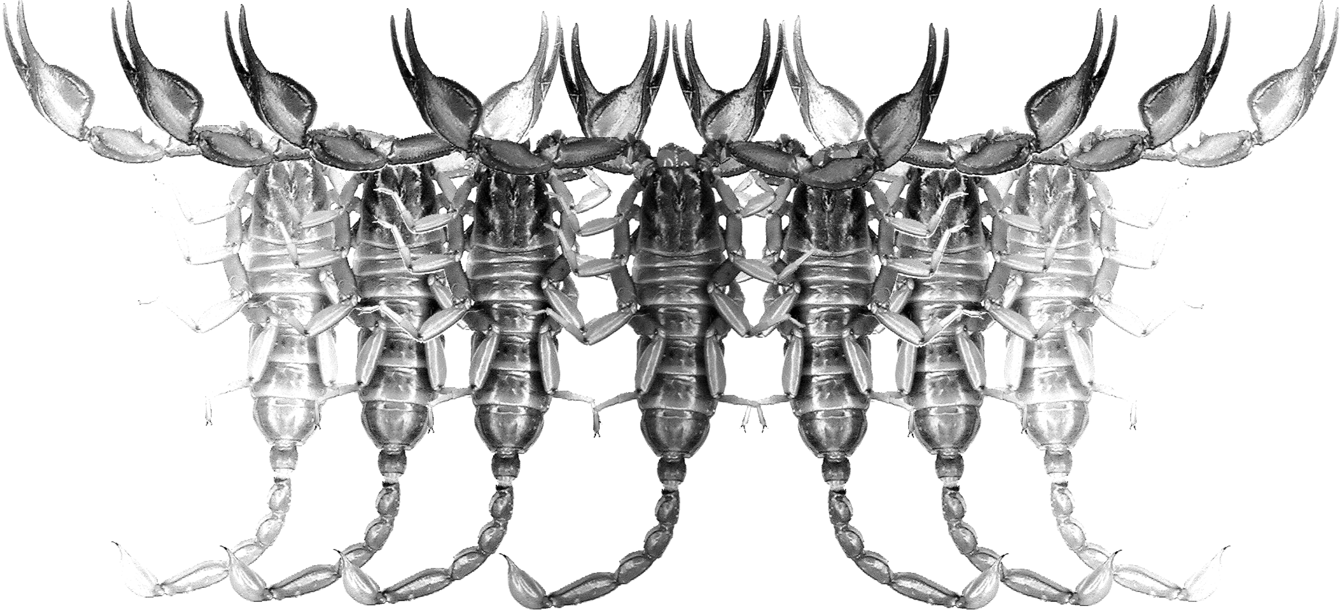

The Genus *Akrav* Levy, 2007 (Scorpiones: Akravidae) Revisited

Victor Fet, Michael E. Soleglad & Sergei L. Zonstein

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Akrav israchanani, Ayyalon Cave, Israel. Dorsal view showing a dead specimen lying on cave surface. Photo courtesy of Israel Na'aman.

Euscorpius — Occasional Publications in Scorpiology. 2011, No. 134

The genus *Akrav* Levy, 2007 (Scorpiones: Akravidae) revisited

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Summary

Akrav israchanani, a relict chactoid scorpion from the famous Ayyalon Cave in Israel, is analyzed for the first time since its original description by Gershom Levy (2007). All scorpions found in this cave (20 specimens) were dead, represented by exoskeletons; they are mostly fragmented during collection, many incomplete, but extremely well preserved, and have no evidence of fossilization. Time and cause of death are unknown. Diagnostic characters described by Levy are largely confirmed, and some are further clarified. An exhaustive set of microscopic images is published, encompassing data from all best preserved specimens. Previously unpublished morphological details are illustrated such as exact pattern of trichobothria, finger dentition, structure of pectinal organs, etc. Measurements of type series are provided. Presence of mites (Acari) in the Ayyalon Cave is not confirmed: the only specimen tentatively identified as a mite proved to be a late-stage scorpion embryo found inside one of the females; it is described and illustrated. Phylogenetic placement of *Akrav* within Recent scorpions is discussed, and its affinity to New World Chactoidea (Superstitioniidae: Typhlochactinae) is demonstrated. Biogeographic and ecological observations are provided. Unusual structure of pedipalp fingertips is suggested to be a device for foraging on aquatic crustaceans abundant in the cave's pool.

Introduction

An unusual scorpion from the Ayyalon Cave in Israel made headlines across the world in spring 2006. It was formally described a year later as a new species, genus, and family, *Akrav israchanani* Levy, 2007 (Akravidae). The most interesting and bizarre aspect of this find was that, unlike other aquatic and terrestrial organisms found in Ayyalon Cave, all scorpion specimens found in the cave were ***dead.***

Levy (2007) wrote: "The presumption that the Ayyalon Cave scorpions are extinct derives from the endless, fruitless quests with intensive use of UV lights for a live or at least a recently dead specimen. Nevertheless, a similar secluded subterranean ecosystem that sustains a live population of these scorpions may still exist somewhere along the same stratum that houses the Ayyalon underground spaces." Additional exhaustive search in the cave, using UV light, did not reveal any live scorpions (Israel Na'aman, pers. comm.). Therefore, we do not know at the present moment if Akravidae is an extant family – but it well may be.

The Cave and Its Amazing Ecosystem

In March 2006, a team of speleologists, headed by Israel Na'aman, a M.Sc. student in the Geology Department of the Hebrew University of Jerusalem, explored a karstic complex named the "Ayyalon Cave" in the famous Valley of Ayyalon (Ajalon, Aijalon) of the Old Testament (Joshua 10:12). Its previously sealed entrance was accidentally exposed by bulldozers digging in a limestone quarry about 4 km SE of Ramla, Israel (31º54' N 34º55'E), on the inner coastal plain, 24 km from the Mediterranean Sea. The team revealed an amazing and highly specialized ecosystem.

A completely isolated subterranean space is located in a quarry deep below the surface, which precludes the permeability of water or organic matter from the outside. The cave includes galleries of winding passages and a large chamber with warm, small, brackish groundwater pool having high H_2S levels (Frumkin & Gvirtzman, 2006).

The Ayyalon Cave ecosystem belongs to an autonomous aquatic subterranean biome, which Prof. Francis Dov Por (2007) named *Ophel*, the Hebrew word for

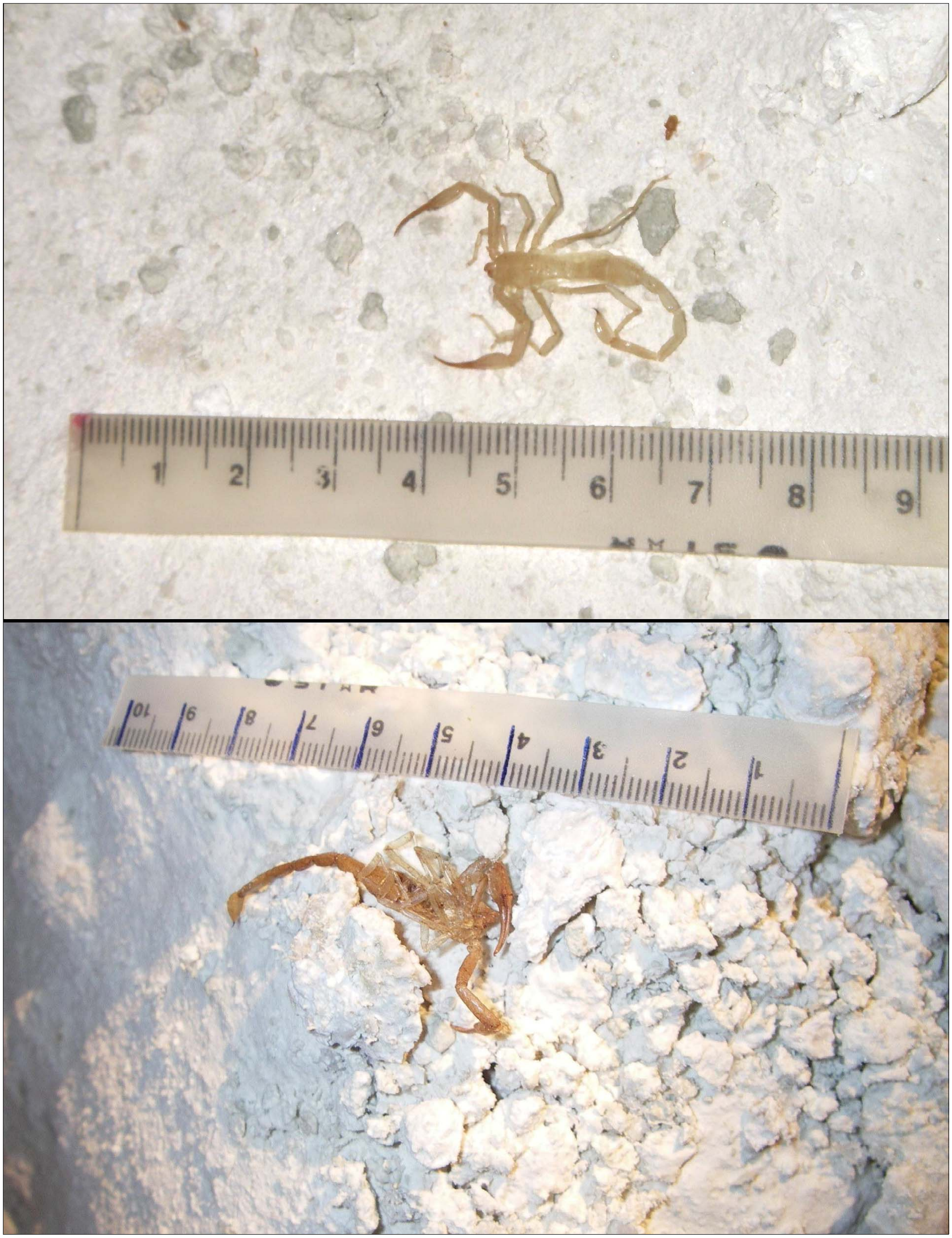

Figure 1: *Akrav israchanani*, dead specimens on cave surface, Ayyalon Cave, Israel. Photos courtesy of Israel Na'aman.

Figure 2: *Akrav israchanani*. **Top.** Dorsal view showing a dismembered specimen on cave surface. **Bottom.** Segments from a fragmented specimen. Photos courtesy of Israel Na’aman.

"darkness" and "netherworld". Before this discovery, only Movile Cave (Romania) was known to have "a diversified subterranean community feeding mainly on autochthonous films of sulfur bacteria" (Negrea, 2009).

In this ecosystem, energy and biomass come solely from chemoautotrophic sulfide-oxidizing, mat-forming bacteria *Beggiatoa* sp., found in great masses in a warm (28.5ºC), sulfidic (H_2S 4.5 ppm), pH 6.8, slightly brackish (490 mg Cl/l) underground pool (Por, 2007, 2008, 2011a, 2011b; Tsurnamal, 2008). These chemosynthetic bacteria nourish a variety of Protozoa. The pool also contains a burgeoning stygobiontic crustacean fauna, dominated by "immense populations" (Por, 2007) of a tiny thermosbaenacean peracarid *Tethysbaena* sp.; two cyclopid copepods, *Metacyclops longimaxillis* Defaye et Por, 2010, and *M. subdolus* Kiefer, 1938; and hundreds of large (~20-27 mm), blind palaemonid prawns, *Typhlocaris ayyaloni* Tsurnamal, 2008 (Por, 2007, 2008, 2011a; Tsurnamal, 2008; Defaye & Por, 2010). "Ciliate and amoeboid protozoans also accompany the bacterial growths; bacterial films are obviously the sole food basis of this isolated system; the gut of *Tethysbaena* specimens was gorged with bacterial cells." (Ćurčić, 2008).

Unlike its aquatic community, the terrestrial biota of the Ayyalon Cave is impoverished, and includes only *three* confirmed invertebrates. They are:

(a) a unique species, genus, and family of chactoid scorpions, *Akrav israchanani* Levy, 2007; (b) a unique species, genus, and tribe of chthoniid pseudoscorpions, *Ayyalonia dimentmani* Ćurčić, 2008; and

(c) an undescribed species of springtails, *Troglopedetes* sp. (Collembola: Paronellidae) (Ch. Dimentman, pers. comm.; Por, 2011b; tentative identification of L. Deharveng, Paris).

A single reported record of a thysanuran could be a contamination (Ch. Dimentman, pers. comm.). Reported presence of *mites* (Acari) is demonstrated below to be an error.

Detailed information on the Ayyalon Cave and its amazing ecosystem can be found in several recent publications (Levy, 2007; Por, 2007, 2008, 2011a, 2011b; Ćurčić, 2008; Tsurnamal, 2008; Negrea, 2009; Defaye & Por, 2010; Wagner, in press).

Material and Methods

Material and its preservation

We analyzed all scorpion specimens from the Ayyalon Cave deposited in the collection of the Hebrew University, Jerusalem, Israel (HUJ). The scorpion specimens, when found in the cave, were dead. They were represented by hollow exoskeletons, mainly with all segments in place, as seen on the photographs made in the cave (Figs. 1–5). We counted, in total, fragments of exoskeletons belonging to 20 specimens, some complete or almost complete, others represented only by fragments (see Fig. 3). All of them belong to the same species, described as *Akrav israchanani* Levy, 2007.

Levy (2007: 92) did not report the total number of discovered scorpions; his description was based on the type series that includes seven specimens (the holotype Sc. 2673, and six paratypes, Sc. 2674–Sc. 2679, as listed in the original paper). In fact, *Akrav* specimens in HUJ collection are represented by 14 lots (each stored separately under a closed plastic lid in a plastic film can), and contain dry remnants of no less than 20 specimens (see the detailed list below). Most of the specimens are highly fragmented, which allowed us to easily handle disparate body parts, especially pedipalp and leg segments, without a risk of further breaking them. Many specimens are incomplete and presented only by a few body parts such as carapace and pedipalps. See Table 1 for a correlation of the HUJ *Akrav* collection with the archived photos presented in this paper.

All specimens except one were collected in April 2006. Only one specimen (Sc. 2684) was collected later than all others, 8 May 2007. All specimens were found sitting on the rock surface in the cave (Levy, 2007; Israel Na'aman, pers. comm). Many were fairly intact, judging from the original photographs taken by Israel Na'aman (frontispiece and Figs. 1–2). Fragmentation of the specimens happened mostly as speleologists collected the exoskeletons (Israel Na'aman, pers. comm). The specimens were easily fragmented since the weakly chitinized membranes between segments (especially those of legs, pedipalps, metasoma) have been decayed, and possibly consumed by detritivores (see below).

These exoskeletons are well-preserved, hollowed out scorpion cuticles. Levy (2007: 92) wrote about "brittle, crumbled remnants" and "dry, very brittle cuticular remains", which is, however, somewhat misleading. We expected superdry specimens that would fall apart on touch. Instead, while many fragments were filmy and very light, they were not especially brittle, i.e. did not fall apart when touched and carefully moved around with a fine brush. To call them "crumbled" is an overstatement, as can be seen from our photographs.

It also would be not entirely correctly to call them dry, or mummified, in a regular sense of these words. Even in the last five years, since specimens were removed from the cave, and were kept in closed plastic vials at ambient humidity and temperature, they did not dry out the way a scorpion exoskeleton would when air-dried. We could see, for example, that all trichobothrial shafts are not only preserved but *move freely* in their areolar sockets at the slightest air movement (breathing of the operator). In an air-dried scorpion (e.g. in a dried and pinned collection) trichobothrial shafts are commonly broken off, but in *Akrav* we could not find a single broken trichobothrium!

Lot #	Number of Specimens	Type Status	Images Available, Archive #
HUJ Sc. 2673	1	Holotype	0249-0294
HUJ Sc. 2674	1	Paratype	0298-0336
HUJ Sc. 2675	1	Paratype	0337-0366
HUJ Sc. 2676	1	Paratype	0367-0401, 28125109-28133426
HUJ Sc. 2677	1	Paratype	0232-0239
HUJ Sc. 2678	1	Paratype	0295-0297, 0437-0443, 28133658-28142631
HUJ Sc. 2679	1	Paratype	0214-0231
HUJ Sc. 2680	2	not in type series	not filmed
HUJ Sc. 2681	1	not in type series	0181-0213
HUJ Sc. 2682	2	not in type series	0006-0180, 28143506-28145936
HUJ Sc. 2683	1	not in type series	not filmed
HUJ Sc. 2684	1	not in type series (coll. 8 May 2007)	not filmed
Embryo (no number)	1	not in type series	0401-0436
A vial (no number) with "residual" remnants	approximately 5 specimens	not in type series	not filmed

Table 1: *Akrav israchanani*: HUJ collection and archived photo images available, filmed in November 2010 (0006-0436, V.F. & S.Z.) and July 2011 (28125109-28145936, S.Z.).

Several of the specimens were fairly well preserved without being dismembered into segments (Figs. 1, 4), and they are soft and flexible. According to Dr. Chanan Dimentman (pers. comm., 2010), humidity inside the cave, before it was opened, reached 100 %, the source of it being the underground water pool; temperature probably also was not low. A considerable concentration of H_2S in the cave's atmosphere, combined with high humidity (and possibly warm temperature) could contribute to slow "curing" of exoskeletons to their present condition. We do not have an analogy in known cases of mummification, which commonly include dry conditions. No significant bacterial or fungal decay of the cuticles was detected.

The time of these scorpions' death is unknown. It is impossible to estimate how long these specimens spent in a completely closed underground cave, especially if no chitin-decaying bacteria or fungi were present.

Many specimens are covered with caked mineral crud, indicating that they have been covered by mineralized solution, likely precipitating from the 100% humid air (or, possibly, also from the rising and falling water level in the pond?). Inside several segments, we found some mineral accumulation, consistent with inundation by a mineralized solution, and consequent precipitation of mineral material after specimens' death. Our Fig. 26 shows a soft sandy "cast" found inside one of the pedipalp segments. This can be seen as the very first step to further fossilization. Otherwise, the exoskeletons show no sign of modification that could be interpreted as incipient fossilization.

All *Akrav* specimens exhibited typical scorpion *fluorescence* of epicuticle in UV light. As Levy (2007) noted, "…these desiccated but not fossilized cuticular remains which retain their bright fluorescence under UV light". This is consistent with their modern age, i.e. absence of chemical modification that would change cuticular chemistry involving fluorochromes responsible for fluorescence (for details on fluorochromes see e.g. Frost et al., 2001). However, we do not know how old a cuticle has to be to cease to fluoresce, especially in the uniform conditions of the cave. Dried scorpions in 150 to 200 year-old museum collections still fluoresce. Very old fossil cuticles are chemically modified, and *do not* fluoresce; this is known for Carboniferous scorpion cuticles (Jeram, 2001), as well as for late Permian-early Triassic fossils (D. Shcherbakov, pers. comm.)

It would be hard to imagine that the age of these exoskeletons is thousands, let alone millions of years: they look perfectly preserved, and are in a much better condition than any dried scorpions in a 100 year-old museum collection.

The cause of the scorpions' death is also unknown. There is no visible damage to scorpion covers that could

Figure 3: *Akrav israchanani*. Various scorpion parts from four specimens: paratypes Sc. 2674 (298), Sc. 2675 (340), Sc. 2676 (368, 370), and non-type specimen Sc. 2677 (232, 233).

result from a predation of other scorpions (no other potential predators are found in the cave). (This also probably excludes death from hunger, for if its food resources were in shortage, *Akrav* could turn to cannibalism as scorpions customarily do). Dr. Chanan Dimentman (pers. comm. 2010) suggests that death could result from a momentary release of H_2S. This is consistent with the condition of studied exoskeletons as well as with their age: the observed "necropolis" is represented by several adults and other, smaller, subadult specimens. No younger juveniles were collected but presence of an embryo inside one of the females (see below) indicates a reproducing population. The overall condition of specimens is consistent with their simultaneous death; i.e. are no indications that they could have died at different times and accumulate in the cave over generations.

There is ample evidence that, after scorpions died, the soft tissue inside *Akrav* exoskeletons has been consumed by necrophagous detritivores. Levy (2007) commented that "the internal contents of the scorpions' carcasses have been completely cleared out" but suggested that it was done by mites, due to finding of what appeared to be a mite inside one of the hollowed-out scorpions. We demonstrate (see below) that what Levy thought to be a mite is in fact a scorpion embryo, and so there is no evidence of mites resident in the Ayyalon Cave. However, we discovered numerous small piles of dark material that pepper all found specimens, mainly from inside (Fig. 25), and were not mentioned by Levy. These piles clearly are not a feature of scorpion cuticle, and are instead consistent with feces of small animals. The only candidate detritivore in the impoverished ecosystem of the Ayyalon Cave is the above-mentioned *Troglopedetes* sp., a resident, undescribed species of springtails (Collembola: Paronellidae), primitive hexapods with an unclear phylogenetic position (formerly considered basal insects). The putative feces are consistent in their size with Collembola (which measure ca. 1 mm). Also, some exoskeletons have been clearly torn (chewed through), especially in the soft sternopectinal area and behind it, which is consistent with the activity of detritivores.

Terminology and conventions

The systematics adhered to in this paper follows the classification as established in Fet & Soleglad (2005) and as modified in Fet & Soleglad (2008). In particular, the systematics of Superstitioniidae (*sensu* Soleglad & Fet, 2003b) is followed in this paper. The recent systematics suggested by Vignoli & Prendini (2009) and Prendini et al. (2010) is ignored here due to its heavy dependence on "placeholders" to determine trichobothria homology, a highly suspect hypothesis (see below). Terminology describing pedipalp chelal finger dentition follows that described and illustrated in Soleglad & Sissom (2001), that of the sternum follows Soleglad & Fet (2003a), and the metasomal and pedipalp carination, and leg tarsus armature follows Soleglad & Fet (2003b). Cheliceral dentition follows that of Vachon (1963) as further developed by Soleglad & Fet (2003b). Trichobothrial nomenclature and hypothesized homologies are those described and illustrated in Vachon (1974), in particular his interpretations presented in his figs. 183, 199-201.

Methods

All photographic images of *Akrav* were obtained with the help of Nikon AZ100 zoom stereoscope and Nikon Eclipse 80i stereoscope, two digital cameras: Nikon DS-2MBW (monochrome) and Nikon DS-Fi1 (color), and the Nikon DS-L2 control unit. The use of equipment was kindly allowed, and guided by, Dr. Ariel Chipman. A number of images of *Akrav* were acquired by UV epifluorescence imaging on Nikon Eclipse 80i in 400 nm emission spectrum.

Systematics

Family **Akravidae** Levy, 2007

Akravidae Levy, 2007: 94. Type genus *Akrav* Levy, 2007 (by original designation)

RECORDS:

Akravidae: Lubin & Gavish-Regev, 2008: 135; Volschenk & Prendini, 2008: 236 (Table I); Kovařík, 2009: 17; Lubin, 2009: ii; Soleglad, Kovařík & Fet, 2009: 3; Vignoli & Prendini, 2009: 3 (Table I).

Family diagnosis. The original diagnosis of the family Akravidae by Levy (2007: 94) is as follows: "Pedipalpi with type C trichobothrial pattern; orthobothriotaxy. Sternum pentagonal. Slits of spiracles crescent-shaped. Fingers of chelicerae smooth, without serrula on ventral surface; movable finger with one subdistal denticle; median and basal denticles of fixed finger not conjoined on a common trunk. Pectines equipped with fulcra and only with a few large teeth. Tibial spur absent. Basitarsi with two distinct pedal spurs. Tarsi bearing paired ventral setae without a median row of spinules. Metasomal segment V with single ventromedian carina. Stinger without subaculear tubercle."

We have one correction to this diagnosis: only the prolateral pedal spur is present. Possible relationships of Akravidae with related families are discussed below, and its affinity to New World Chactoidea (Superstitioniidae: Typhlochactinae) is demonstrated. While we suggest that status of Akravidae as a family is hardly justified, we refrain here from formal synonymization and rank change pending a formal phylogenetic analysis (Soleglad & Fet, in progress).

Genus ***AKRAV*** Levy, 2007

Akrav Levy, 2007: 92. Type species *Akrav israchanani* Levy, 2007 (by original designation).
No other species known.

RECORDS:
Akrav: Lubin & Gavish-Regev, 2008: 135; Soleglad, Kovařík & Fet, 2009: 3; Vignoli & Prendini, 2009: 3 (Table I).

Akrav israchanani Levy, 2007

Akrav israchanani Levy, 2007: 92–95, figs. 1–17.

Type series: Holotype: Israel, Ayyalon Cave, April 2006, leg. Israel Na'aman, HUJ Sc. 2673 (labeled "Holotype"); six paratypes (same data as for holotype); three paratypes labeled "Paratype" (Sc. 2674, Sc. 2675, Sc. 2676); three specimens *not* labeled as paratypes in HUJ collection but listed as such in Levy (2007: 92) (Sc. 2677, Sc. 2678, Sc. 2679), which therefore are paratypes as published. Gender of these and other specimens cannot be determined confidently.

Additional material (not type series): 13 specimens: three lots (Sc. 2681, Sc. 2683 and Sc. 2684) contain one specimen each; lots Sc. 2680 and Sc. 2682 are each a mixture of two specimens; one more lot (no accession number) contains a mixture of fragments from at least five specimens; and one dry embryo (no accession number). All data as for holotype, except for the specimen Sc. 2684, which was collected separately, on 8 May 2007 (not 2006). Most of the specimens are dismembered and fragmented.

RECORDS:
Akrav israchanani: Por, 2007: 3; Ćurčić, 2008: 332; Lubin & Gavish-Regev, 2008: 135; Negrea, 2008: 87; Volschenk & Prendini, 2008: 236 (Table I); Por, 2011a: 61; Por, 2011b: 452.
Akrab (misspelling) *israchanani*: Por, 2008: 107.

Genus/species diagnosis. The original diagnosis of the genus *Akrav* (and also of the species *Akrav israchanani*) by Levy (2007: 91) is as follows: "Eyeless troglobite. Chelicerae without serrula on ventral edge. Fine elongated fingers of pedipalpi equipped with a nearly contiguous median row of denticles, a straight parallel row on their basal half, and inner and outer accessory denticles. Trichobothria *ib-it* positioned on fixed finger; series *Vl-V4* extending to entire length of palm with little or no angling at the *V2* juncture. Patella (tibia auct.) with all three ventral trichobothria positioned on ventral surface, and femur with trichobothrium *d* located slightly proximal to trichobothrium *i*. Metasomal segments longer than wide and bearing ventral carinae."

We have two important corrections to this diagnosis: the pedipalp fingers are equipped with oblique median denticle (*MD*) groups along the entire length of the fingers; of the three patellar ventral trichobothria, v_3 is in fact found on the external surface, v_2 found on the ventroexternal carina, and v_1 is located on the ventral surface (see Figs. 13 and 15).

Morphology

The main goal of our study was to provide additional information to the original concise description by Levy (2007), and to illustrate the described morphology of *Akrav* by detailed photographic images. Below, we give a detailed description of all studied structures, commenting on their interpretation by Levy (2007), and augmenting his original description to correct errors and/or supply additional data. Extra detail and in-depth discussions on proposed taxonomically important structures are provided further below.

Levy's description appears to be a composite one and does not refer to a specific type series specimen. It gives no measurements of any type specimens, and no photographic images except one, of a rather poorly reproduced original photograph by Israel Na'aman (Levy, 2007, fig.1; see also our Fig. 1). Our description is based mainly on seven representative adult or subadult specimens: the holotype (Sc. 2673), four paratypes (Sc. 2674, 2675, 2678, 2679) and two specimens that do not belong to the type series (Sc. 2681, 2682), all of which were photographed by us.

Size. "Medium-sized troglobite about 50 mm in body length" (Levy, 2007). The original description has no other measurements of the holotype or paratypes. We measured the type series (holotype and six paratypes) (Table 2). In addition, measurements were taken of pedipalp chela of all other specimens (Table 3). We can see variation in size, reflecting age differences.

This species is quite slender in overall proportions, all metasomal segments considerably longer than wide; even the basal two segments are more than twice as long as wide, L/W = 2.163, 2.245 (here and below, for the holotype). The pedipalp is also slender, the femur, patella, and chela are much longer than wide, L/W 3.646, 4.323, 5.579; the fingers are long and tenuous, the movable finger longer than both the carapace and metasomal segment V, in ratios 1.533 and 1.070. The sternum is longer than wide, in a ratio 1.24.

Coloration. Levy (2007) says that *Akrav* is "brown coloured".

Prosoma. "…completely eyeless without any lenticel remnants." (Levy, 2007). We confirm complete anophthalmy – absence of median and lateral eyes; even under high magnification we find no trace of eyes. In some scorpions, smaller lateral eyes can be confused with numerous round granules covering the carapace, but granulation in *Akrav* is very minimal.

"Carapace encircled by fine raised edges; anterior margin notched by a moderate concavity, and a narrow,

Figure 4: *Akrav israchanani*. Partial ventral (top) and dorsal (bottom) views. Non-type specimen Sc. 2678 (296-297).

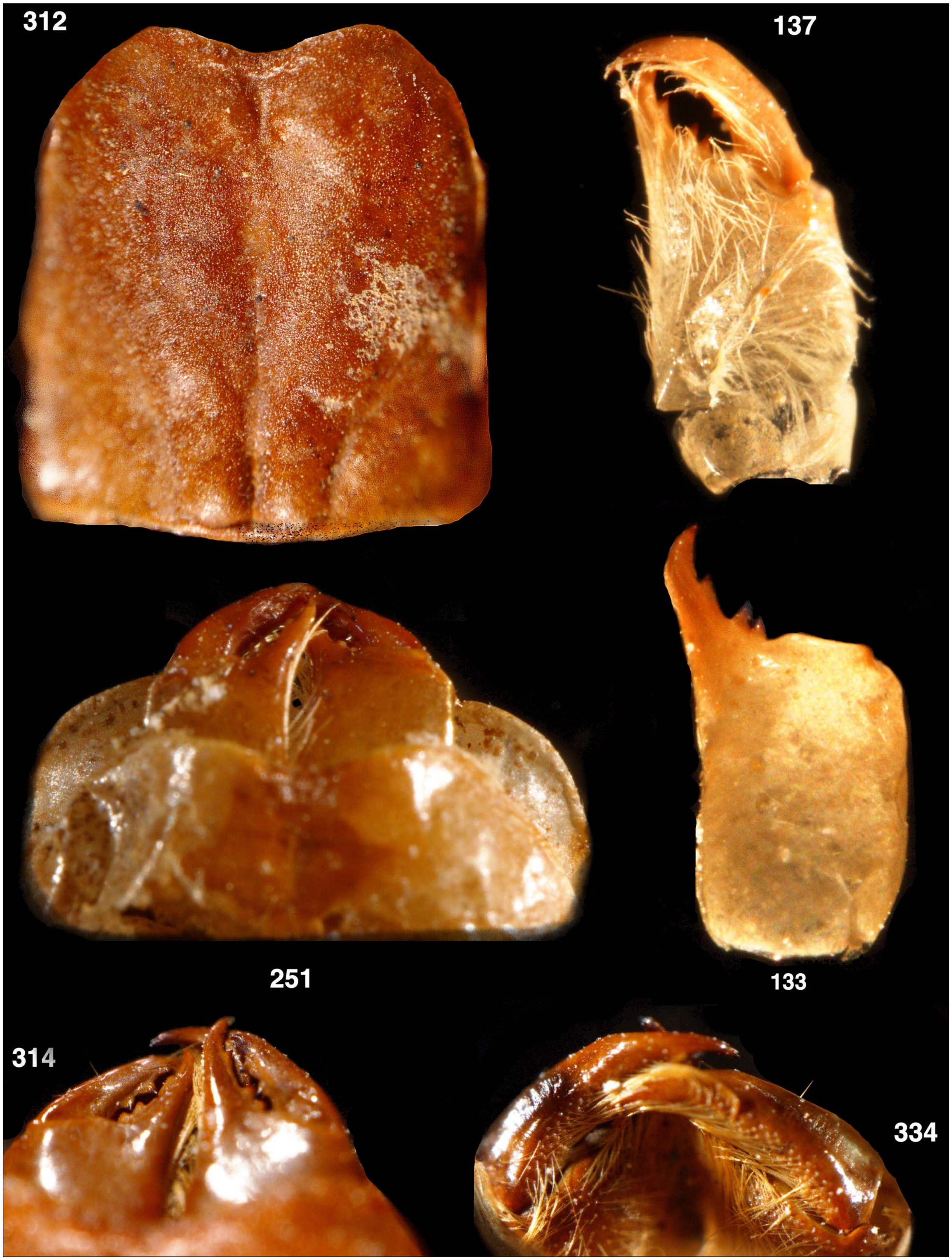

Figure 5: *Akrav israchanani*. Carapace from paratype Sc. 2674 (312), and various chelicerae from three specimens: holotype Sc. 2673 (251), paratype Sc. 2674 (314, 334), and non-type specimen Sc. 2682 (133, 137).

Figure 6: *Akrav israchanani*. Partial ventral view showing maxillary lobes, pedipalp and leg coxae, and sternopectinal area. Non-type specimen Sc. 2681 (201).

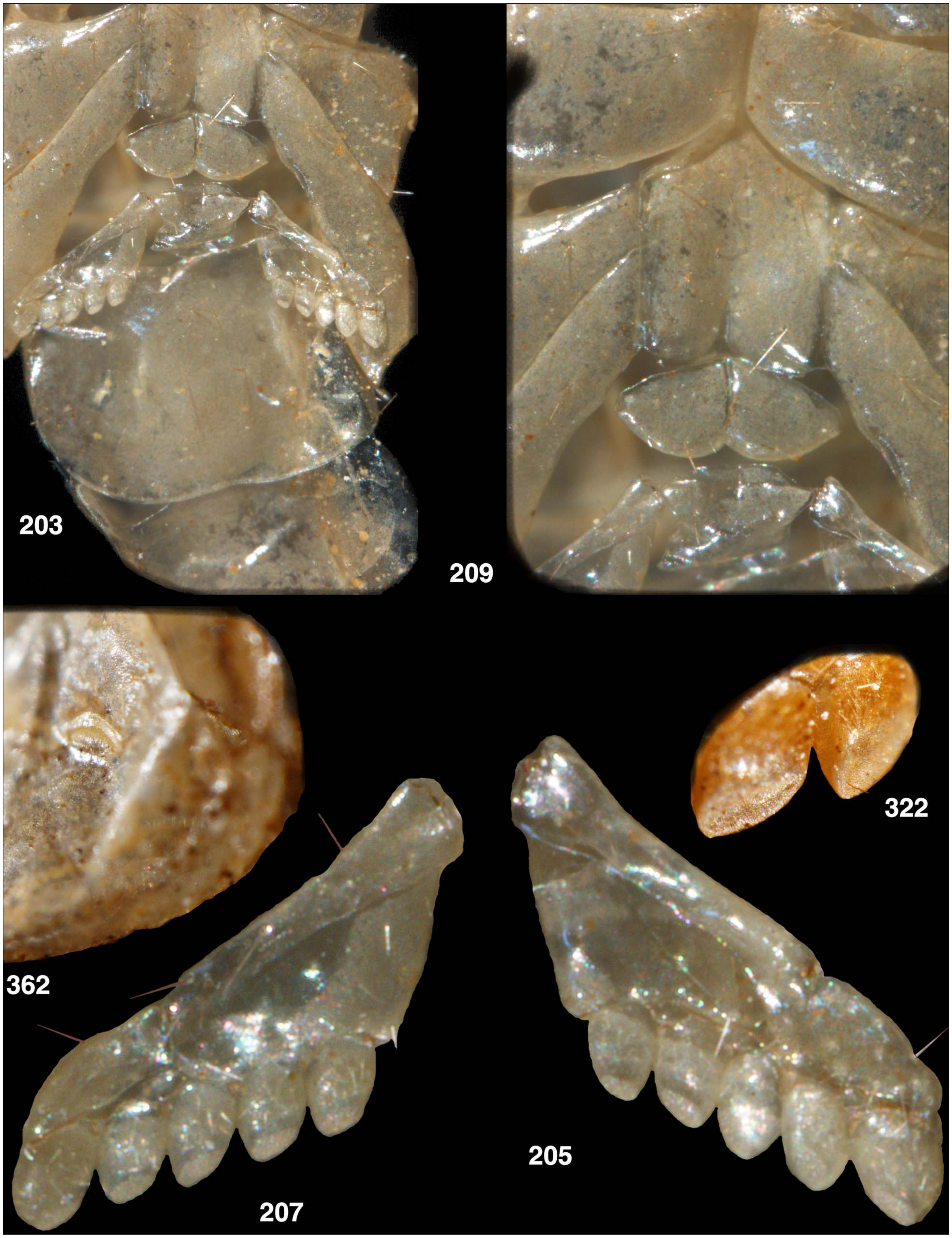

Figure 7: *Akrav israchanani*. Partial ventral view showing sternopectinal area (203), close-up of the sternum and genital operculum (209) and close-up of pectines (205, 207) of a non-type specimen Sc. 2681. Also, a partial pectine (two distal teeth) of paratype Sc. 2674 (322); and a partial sternite with a spiracle of paratype Sc. 2675 (362). Sensorial areas are visible on all five teeth of each pecten as well as in the close-up of two partial teeth.

Figure 8: *Akrav israchanani*. Right pecten, showing five teeth (basal tooth is out of focus). Sensorial areas are visible on distal tips of teeth. Paratype Sc. 2676.

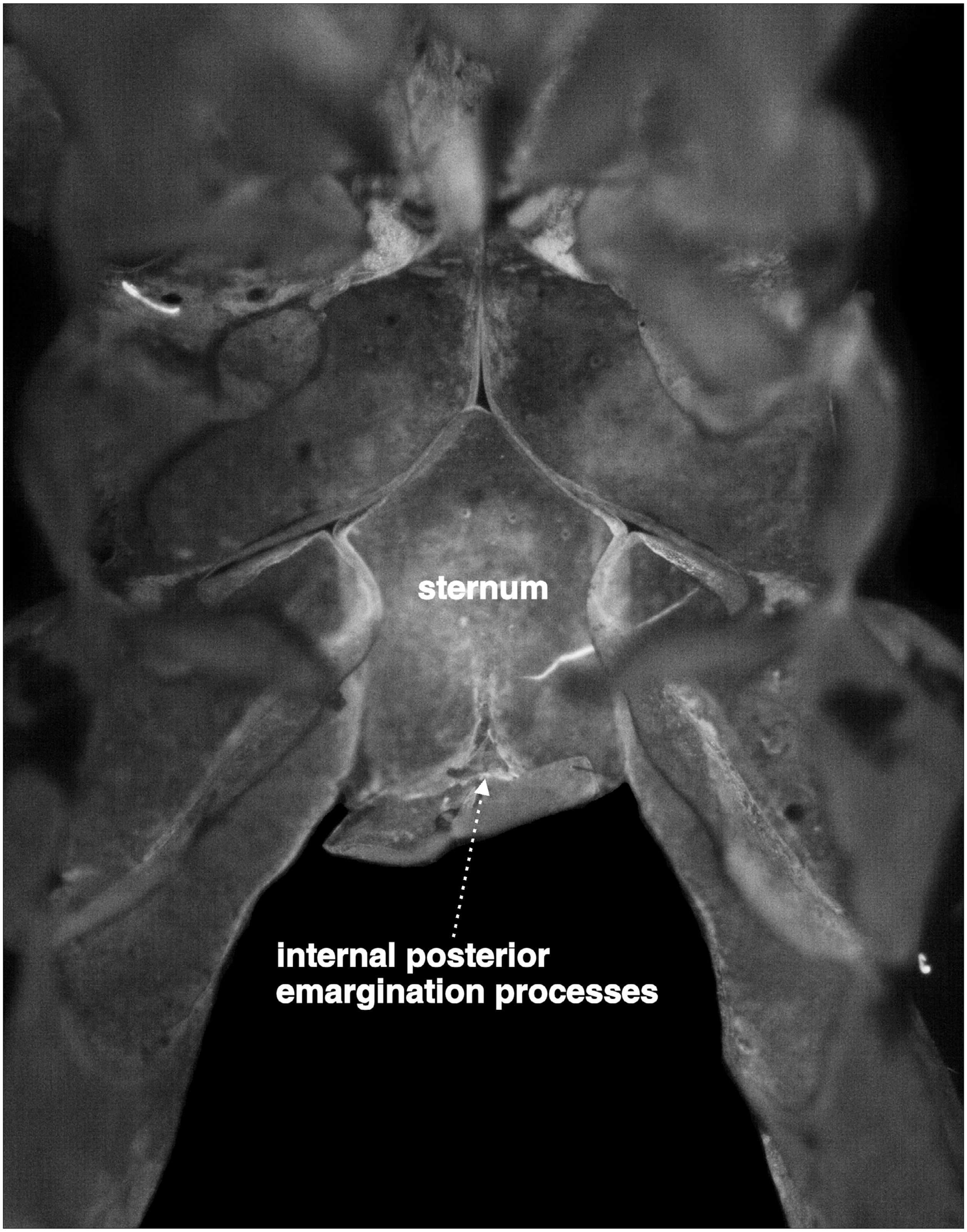

Figure 9: *Akrav israchanani*. Internal view of the sternum showing the two posterior emargination processes, diagnostic of the type 2 sternum (see Soleglad & Fet, 2003: 9). The genital operculum, somewhat folded over, is seen just posterior of these processes. "Non-type" specimen Sc. 2682.

Figure 10: *Akrav israchanani*. Miscellaneous metasomal segments and telson from six specimens. Last mesosomal segment and metasomal segment I: Paratype Sc. 2675 (344). Metasomal segments: paratypes Sc. 2674 (317-318), Sc. 2675 (354, 358), non-type specimen Sc. 2682 (163). Telson: holotype Sc. 2673 (283), non-type specimen Sc. 2682 (164). Telson and metasomal segment V: paratype Sc. 2676 (372-373), non-type specimen Sc. 2678 (442-443).

Figure 11: *Akrav israchanani*. Legs from three specimens: holotype Sc. 2673 (286, 292), and non-type specimens Sc. 2678 (440), Sc. 2682 (140, 142, 175). *pps* = prolateral pedal spur, *is* = intersegment membrane.

Akrav israchanani Levy, 2007 Ayyalon Cave, Israel							
Type series	**Sc. 2673**	**Sc. 2674**	**Sc. 2675**	**Sc. 2676**	**Sc. 2677**	**Sc. 2678**	**Sc. 2679**
	Holotype	**Paratype**	**Paratype**	**Paratype**	**Paratype**	**Paratype**	**Paratype**
Total length	45.16	n/a	n/a	n/a	43.99	30.98	n/a
Carapace length/width	5.38 / 4.99	5.85 / 4.93	5.68 / 4.80	n/a	5.50 / 4.84	4.42 / 3.64	5.33 / 3.80
Mesosoma length	12.40	n/a	11.72	11.32	10.94	10.30	10.84
Sternum length/basal width	1.84 / 1.32	1.82 / 1.32	1.80 / 1.28	1.69 / 1.30	1.76 / 1.24	1.29 / 1.04	1.50 / 1.16
Metasoma length	27.38	n/a	n/a	n/a	27.55	16.26	n/a
Metasoma Segment I length/width	4.50 / 2.08	n/a	4.28 / 2.23	n/a	4.60 / 2.12	2.64 / 1.68	4.54 / 2.08
Metasoma Segment II length/width	4.67 / 2.08	n/a	n/a	n/a	4.64 / 1.96	2.66 / 1.42	4.40 / 1.80
Metasoma Segment III length/width	4.83 / 1.92	4.85 / 1.80	4.75 / 1.90	n/a	4.86 / 1.92	2.70 / 1.28	4.54 / 1.74
Metasoma Segment IV length/width	5.67 / 1.75	4.80 / 1.85	4.95 / 1.95	n/a	5.62 / 1.84	3.34 / 1.50	n/a
Metasoma Segment V length/width	7.71 / 1.71	n/a	5.95 / 1.85	7.46 / 1.68	7.78 / 1.84	4.92 / 1.28	n/a
Telson length	5.79	n/a	n/a	5.08	5.58	4.14	n/a
Vesicle length	3.99	n/a	n/a	3.40	3.64	2.70	n/a
Vesicle width/depth	2.25 / 2.13	n/a	n/a	2.06 / 2.02	2.40 / 2.32	1.48 / 1.42	n/a
Aculeus length (= TL-VL)	1.80	n/a	n/a	1.68	1.92	1.44	n/a
Pedipalp length	26.71	27.43	n/a	24.83	25.30	18.96	24.36
Femur length/width	6.38 / 1.75	7.00 / 1.70	7.10 / 1.70	6.40 / 1.56	6.48 / 1.74	4.94 / 1.24	6.34 / 1.80
Patella length/width	6.83 / 1.58	6.88 / 1.70	n/a	6.38 / 1.66	6.52 / 1.80	4.90 / 1.28	6.36 / 1.54
Chela length (left/right)	-- / 13.50	-- / 13.55	13.00 / --	11.97 / 12.13	12.25 / 12.33	9.08 / 9.16	11.66 / --
Palm length	5.83	5.34	4.98	5.04	5.06	3.38	4.94
Palm width/depth	2.42 / 2.83	2.38 / 3.34	2.24 / 3.12	2.06 / 2.86	2.50 / 3.05	1.60 / 2.06	1.96 / 2.88
Movable finger length	8.25	8.35	8.10	7.34	7.83	5.60 / 5.78	7.16
Pectinal teeth number	5 / 5	n/a	5 / --	-- / 5	n/a	5 / 5	5 / 5

Akrav israchanani Levy, 2007 Ayyalon Cave, Israel												
Non-type specimens	**Sc. 2680 (1)**	**Sc. 2680 (2)**	**Sc. 2681**	**Sc. 2682 (1)**	**Sc. 2682 (2)**	**Sc. 2683**	**Sc. 2684**	**no accession number (mixed remnants of at least 5 specimens)**				**embryo**
Carapace length	5.60	n/a	3.83	n/a	n/a	5.12	5.20	5.24	n/a	n/a	n/a	n/a	n/a
Chela length (left / right)	-- / 9.88	8.02 / 8.22	8.33 / 8.33	9.75 / n/a	8.67 / 8.92	-- / 9.96	11.04 / --	12.08 / --	9.78 / -	9.36 / -	-- / 10.24	-- / 12.50	n/a
Pectinal teeth number	n/a	n/a	5 / 5	n/a	n/a	n/a	5 / 5	-- / 5	n/a	n/a	n/a	n/a	5 / 5

Tables 2–3: Morphometrics (mm) of *Akrav israchanani* Levy, 2007. **Top.** Type series (holotype and six paratypes). **Bottom.** 13 non-type specimens.

deep median groove running along posterior part; carinae absent" (Levy, 2007, fig. 2).

Mesosoma. "Sternum pentagonal, longer than wide, with angular anterior margin and posteriorly with a narrow depression flanked by slightly distended sides" (Levy, 2007, fig. 3; "type-2 of Soleglad & Fet, 2003a"). The length to width ratio of the sternum is 1.24.

"Internal bifurcated process projecting from posterior median edge of sternum" (Levy, 2007, fig. 3a). This is also illustrated in our Figure 9, which shows the internal view of the sternum where the two posterior emargination processes are visible.

"Genital opercula fused along median indentation" (Levy, 2007, figs. 3–4). The sclerites are wider than long and are quite rounded on their inner posterior edges.

"Tergites of mesosoma without carinae" (Levy, 2007). Tergites I–VI are generally smooth as reported by Levy, but there are slight traces of the lateral pair of carinae visible on tergite VII (see Fig. 10).

"Spiracle slits on sternites slightly crescent-shaped" (Levy, 2007).

Pectines. "Pectines consisting of basal dilated, long anterior marginal and middle lamellae, a terminal piece, four distinct fulcra, and five relatively large teeth (fig. 5). Ventral surface of anterior two-thirds of each pectinal tooth covered by short setae, and posterior third perforated by fine dense pores." (Levy, 2007).

The number of pectinal teeth (five) given by Levy does not refer to a particular specimen. We confirm, however, that all analyzed specimens in which pectinal organs were found, had exactly five pectinal teeth; in total, we counted 17 pectines (including the embryo, which also had five teeth). Such a fixed value of this meristic trait could be expected in the completely isolated and inbred population of *Akrav*; it would be more surprising to find variation in number.

Metasoma. "Metasomal segments longer than wide and bearing, in part, low tuberculated carinae or carina-like embossments. Segment V bearing a pair of ventrolateral carinae and a single, partly indicated, ventromedian (axial) carina" (Levy, 2007, species description). At the same time, Levy's genus diagnosis says, somewhat differently, "Metasomal segments longer than wide and bearing ventral carinae", and the family diagnosis mentions "Metasomal segment V with single ventromedian carina." We observe the following: segments I–IV with granulated dorsal and dorsolateral carinae; ventrolateral carinae are smooth on I to granulated to crenulated on IV; ventromedian carinae are obsolete to smooth. Segment V: we observe a granulated to crenulated dorsolateral carinae, granulated ventrolateral carinae, and weak to granulated single ventromedian carina. Also, all Recent scorpions, with the sole exception of *Pseudochactas*, have a single ventromedian carina on segment V, so it not clear why this was mentioned by Levy as a diagnostic character of the genus.

Telson. "Stinger without subaculear tubercle (fig. 6)" (Levy, 2007). The vesicle is large and globular in shape, considerably longer than the short highly curved aculeus (see Fig. 10).

Chelicerae. "Chelicerae with a fixed finger armed with two separate basal-most teeth, and a movable finger with five teeth and smooth dorsal and ventral edges without comb-like serrula" Levy, 2007, fig. 7). In addition, the family diagnosis states: "movable finger with one subdistal denticle; median and basal denticles of fixed finger not conjoined on a common trunk."

Pedipalps. "Pedipalpi with trichobothriotaxy conforming to type C pattern (Figs 12–16; see also diagnosis of genus)" (Levy, 2007). The genus diagnosis says: "Fine elongated fingers of pedipalpi equipped with a nearly contiguous median row of denticles, a straight parallel row on their basal half, and inner and outer accessory denticles. Trichobothria *ib-it* positioned on fixed finger; series *V1–V4* extending to entire length of palm with little or no angling at the *V2* juncture. Patella (tibia auct.) with all three ventral trichobothria positioned on ventral surface, and femur with trichobothrium *d* located slightly proximal to trichobothrium *i*." Our detailed discussion of trichobothria pattern is given below.

"Long, slender, slightly bent fingers of pedipalpi terminating with curved tips" (Levy, 2007, figs. 12–14). The illustrations of chelal fingers by Levy in his figs. 12–14, especially fig. 13, exaggerate the distal curvature of these fingers. In addition, the distal tip of the fixed finger overlaps the movable on its internal edge, not external as shown by Levy. See our Figs. 17–18, 20.

"Fingers with a median row of denticles arranged in a straight contiguous line, partly broken up at distal part into a few groups, and basal half armed with two straight parallel rows of denticles. Inner and outer denticles distributed alongside median row" (Levy, 2007, fig. 15). We see that the chelal finger median denticle (*MD*) row groups are not continuous but are oblique and imbricated the entire length of the finger; see more details below. Of special interest is the fact that we also see inner accessory denticles (*IAD*) on both the fixed and movable fingers; see discussion below (see Fig. 21).

Constellation array on fixed finger of pedipalp chela, not reported by Levy, and barely visible without SEM, can be distinguished at the highest magnification (Fig. 19) and appears to include five or six sensilla, close to numbers known in chactoids (Fet et al., 2006).

Legs. "Legs bearing two sclerotic basitarsal (pedal) spurs: a dilated white retrolateral spur and a brown spine-like prolateral spur" (Levy, 2007, figs. 16–17). These observations seem problematic, since Levy's depiction of two spurs is schematic, and they are described as unusually different in shape and color. As it

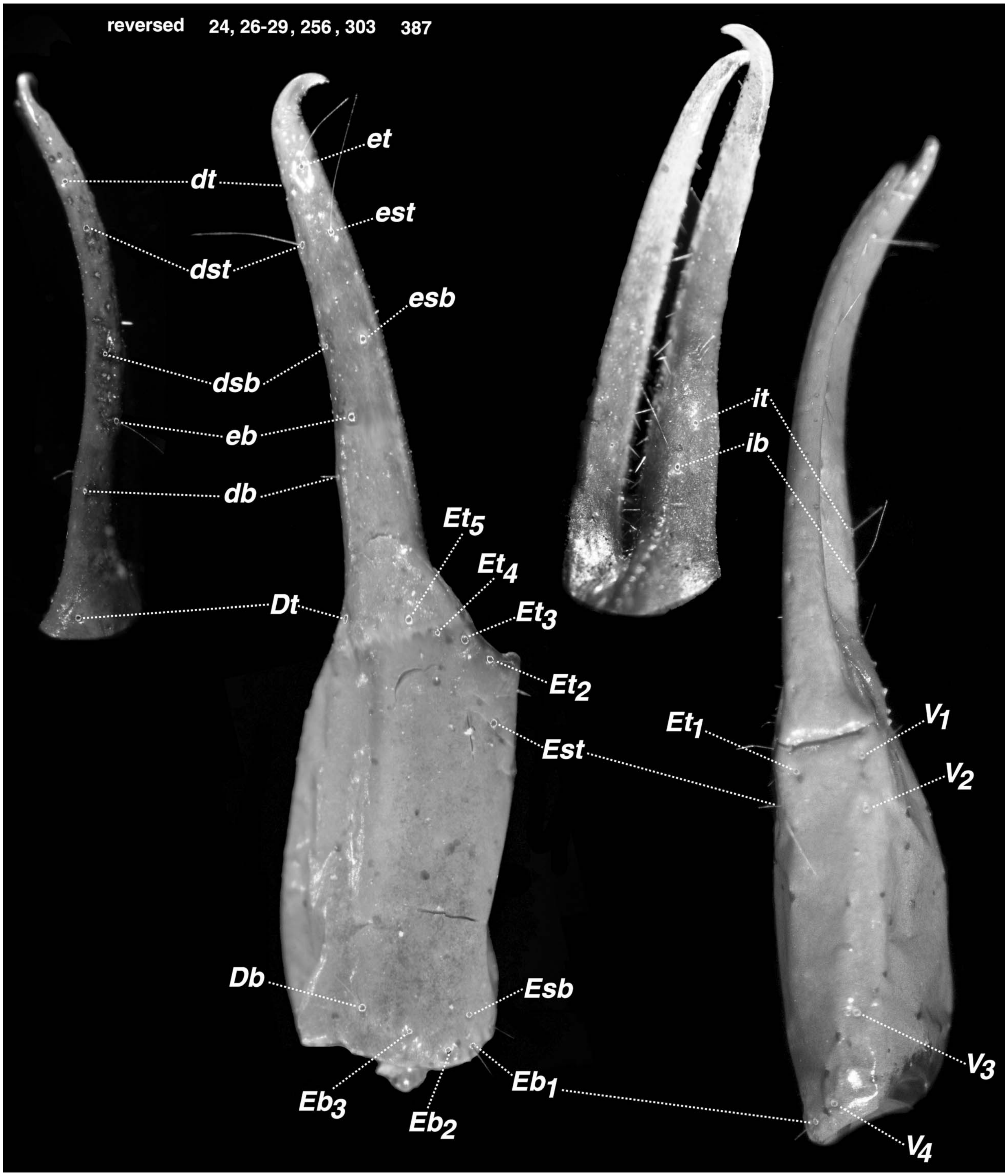

Figure 12: *Akrav israchanani*. Chelal trichobothrial pattern. Composite of four specimens: non-type specimen Sc. 2682 (24, 26-29), holotype Sc. 2673 (256), paratype Sc. 2674 (303), and paratype Sc. 2676 (387). Of particular interest, we see that trichobothrium *Dt* is located at the base of the fixed finger, the large gap between V_2 and V_3, and trichobothria Eb_3, *db*, and *dsb* are petite in size.

turns out, the retrolateral spur is indeed *missing*, and the unusual "dilated white" spur described by Levy is a swollen intersegment membrane. Its "spine point" is formed by the triangular-shaped cuticle of the basal ventral portion of the tarsus.

"Tarsi bearing paired ventral setae." (Levy, 2007,

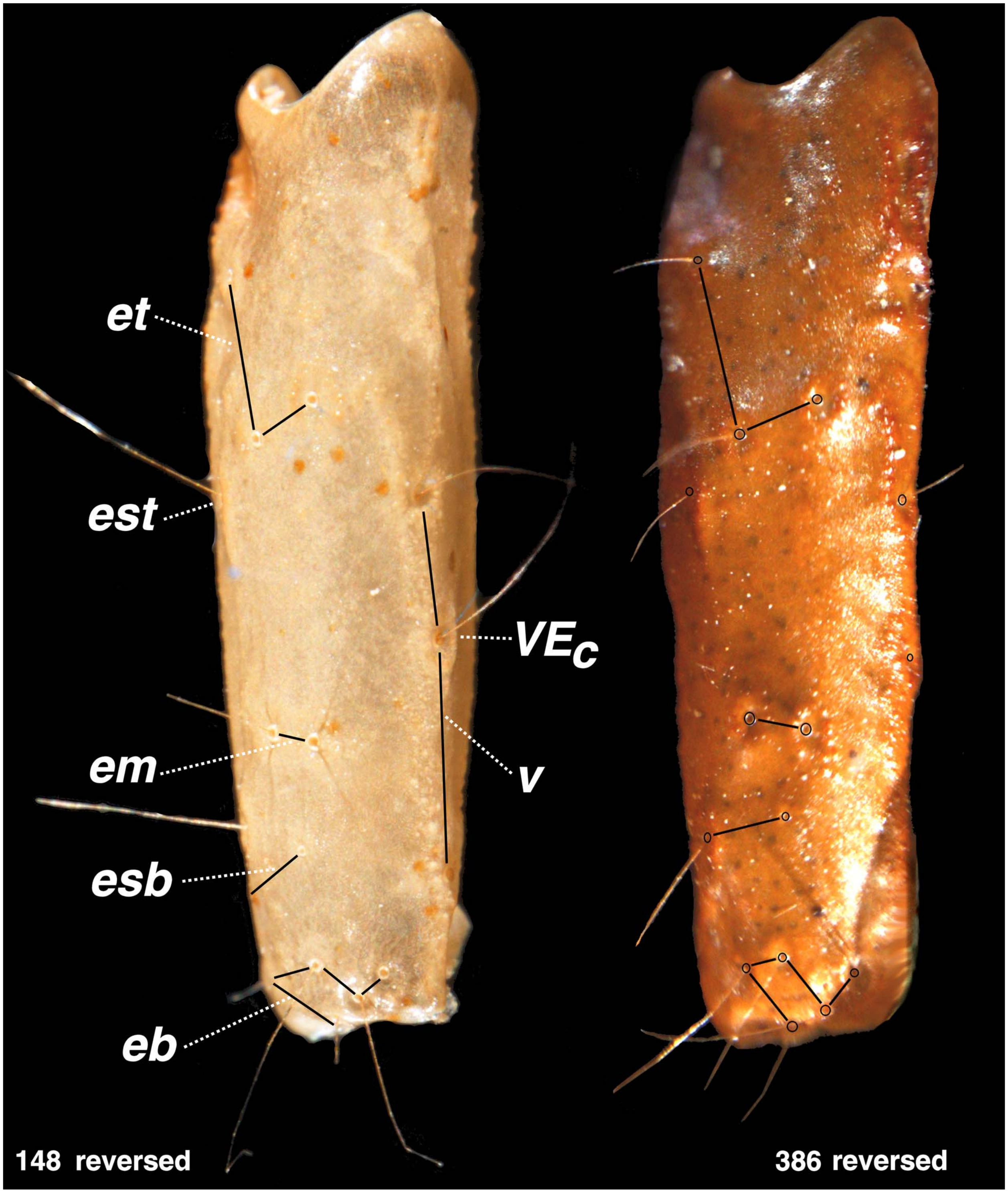

Figure 13: *Akrav israchanani*. Pedipalp patella, external view. Note, all standard 13 external orthobothriotaxic trichobothria are visible. In addition, the three ventral trichobothria are also shown on the left image. Of particular interest, the *esb* series slants "upwards" towards the distal aspect of the patella. Also of note, ventral trichobothrium v_2 is located directly on the ventroexternal carina (VE_c), and v_3 is located on the external surface of the patella. See Fig. 15 for additional images of these trichobothria. Paratype Sc. 2676 (386) and non-type specimen Sc. 2682 (148).

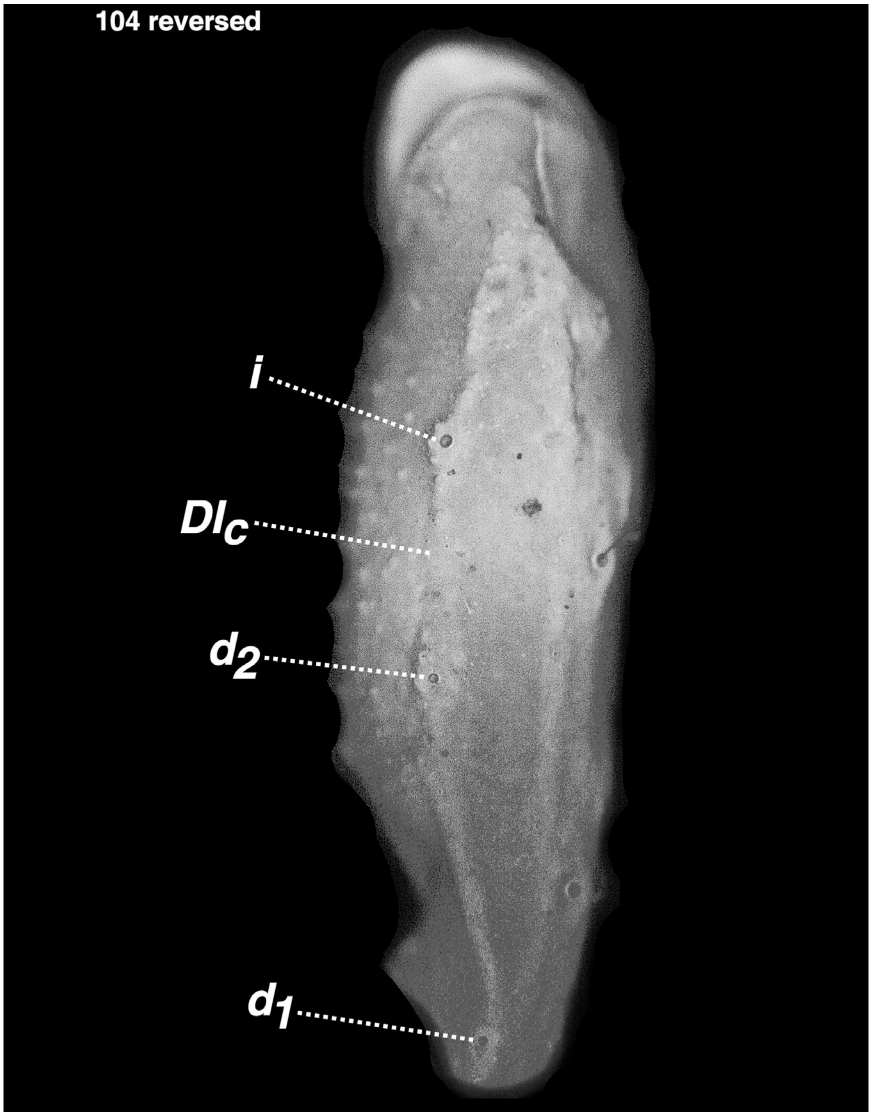

Figure 14: *Akrav israchanani*. Pedipalp patella (UV photo), dorsal view, where the two dorsal trichobothria and one internal trichobothrium are identified. Note that the internal trichobothrium, *i*, is located directly on the dorsointernal carina (*DIc*). Non-type specimen Sc. 2682.

figs. 16–17). Levy's depiction of tarsal setation is schematic, and proves to be imprecise. His figures show 9 pairs of socketed setae, with setae of each pair very widely removed from each other. In fact (Fig. 11), two rows of setae are positioned in a more usual, submedian formation and with less than 9 pairs (see below).

An Embryo

Levy (2007: 91) wrote: "The internal contents of the scorpions' carcasses have been completely cleared out. This may have been carried out by mites, as the remains of an unidentified mite were found inside a dry carcass." Presence of mites is also mentioned by Por (2007: 3; "… as yet unidentified mites") and Negrea (2008: 87, "some unidentified species of mites"). Ćurčić (2008: 331) even talks about "living populations of … mites". In fact, all this information about Ayyalon mites comes from the sole "unidentified mite" mentioned by Levy. As it happens, however, this specimen was misidentified.

We analyzed the specimen labeled "Mite (Acari)", taken from inside of one of the *Akrav* specimens, and deposited in the same box in HUJ collection. A close examination proved that this specimen is a late-stage *scorpion embryo*. It is unequivocally recognized by a combination of unique scorpion features, absent in all other arthropods: well-developed pectinal organs and a long metasoma, as well a typical late-stage embryonic setation.

As mentioned by Levy, this specimen was found *inside* a dry scorpion exoskeleton, which would indicate a gravid female. There are several adult females in the collection, but we cannot match one of them with the embryo. This dried *Akrav* embryo is illustrated here (Figs. 22–24), and its morphology is addressed below.

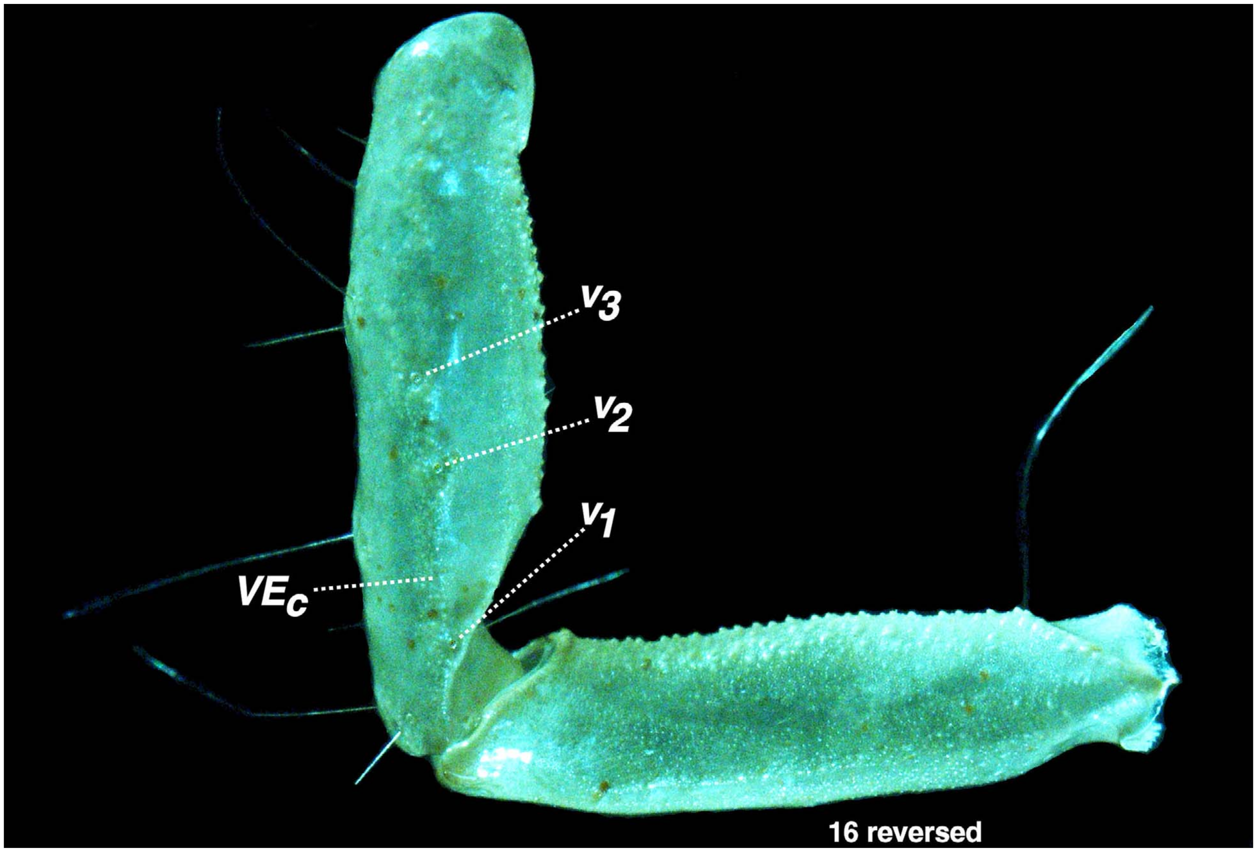

Figure 15: *Akrav israchanani*. Pedipalp femur and patella (UV photo), ventral view, where three ventral trichobothria of the patella are identified. Note that the ventral trichobothrium v_2 is located on the ventroexternal carina (VE_c) and v_3 is located on the external surface of the patella. See Fig. 13 for additional images of these trichobothria. Non-type specimen Sc. 2682.

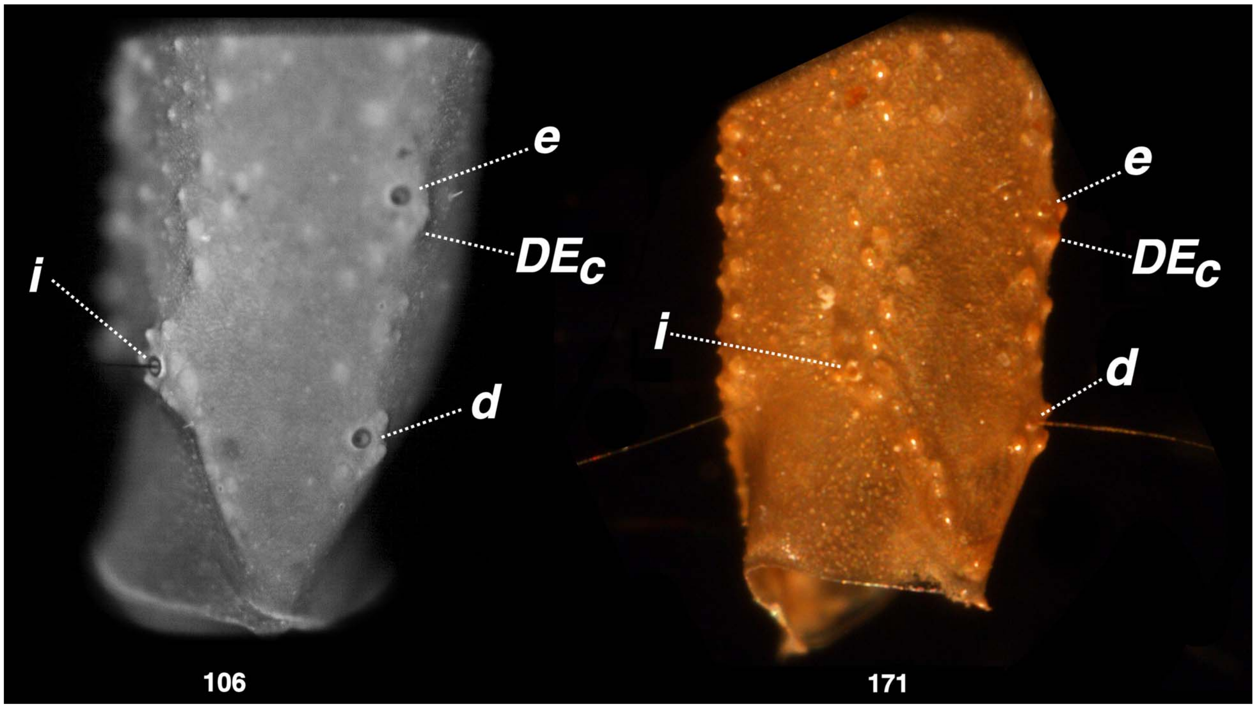

Figure 16: *Akrav israchanani*. Pedipalp femur, basal area. Left (UV photo), dorsal view showing three standard orthobothriotaxic trichobothria. Right, internodorsal view. Of particular interest, trichobothrium *e* is located on the dorsal surface of the femur as indicated by the dorsoexternal carina (DE_c). Non-type specimen Sc. 2682 (two pedipalps, one reversed).

Figure 17: *Akrav israchanani*. Chela, three basic views, showing trichobothria. Views from two paratypes, Sc. 2676 and Sc. 2678.

Morphology of late embryonic stages is not well documented in chactoid scorpions. The overall arrangement of the *Akrav* embryo and detail of structure development is similar to late-stage embryos of the apoikogenic chactoid *Smeringurus mesaensis* (Vaejovidae) illustrated by Farley (1999, 2001a). For the general information on scorpion embryonic development, see the most recent reviews by this author (Farley, 1999, 2001a) and his other important works (Farley, 2001b, 2005, 2008). Recently, our research group (Kovařík et al., 2010) published a detailed description, based on 16 late-stage embryos, of the apoikogenic iuroid *Iurus dufoureius* Brullé (Iuridae). While only remotely related to chactoids, this description illustrates some rarely observed late embryonic features in scorpions also discernable in *Akrav* embryo.

The late-stage embryo in scorpions is generally very similar to the newborn animal. As confirmed and discussed by Farley (2005), a newborn scorpion (also called a first stadium, first instar, pronymph, or pullus)

Figure 18: *Akrav israchanani*. Various images of the chelal fingers from six specimens, showing the unusual curvature of the finger distal tips and finger dentition. See Figs. 20–21 and 27–28 for further discussion on finger dentition. Holotype (265), paratypes Sc. 2674 (302, 303, 324-326), Sc. 2675 (352), Sc. 2676 (393), and non-type specimens Sc. 2679 (220), Sc. 2682 (48).

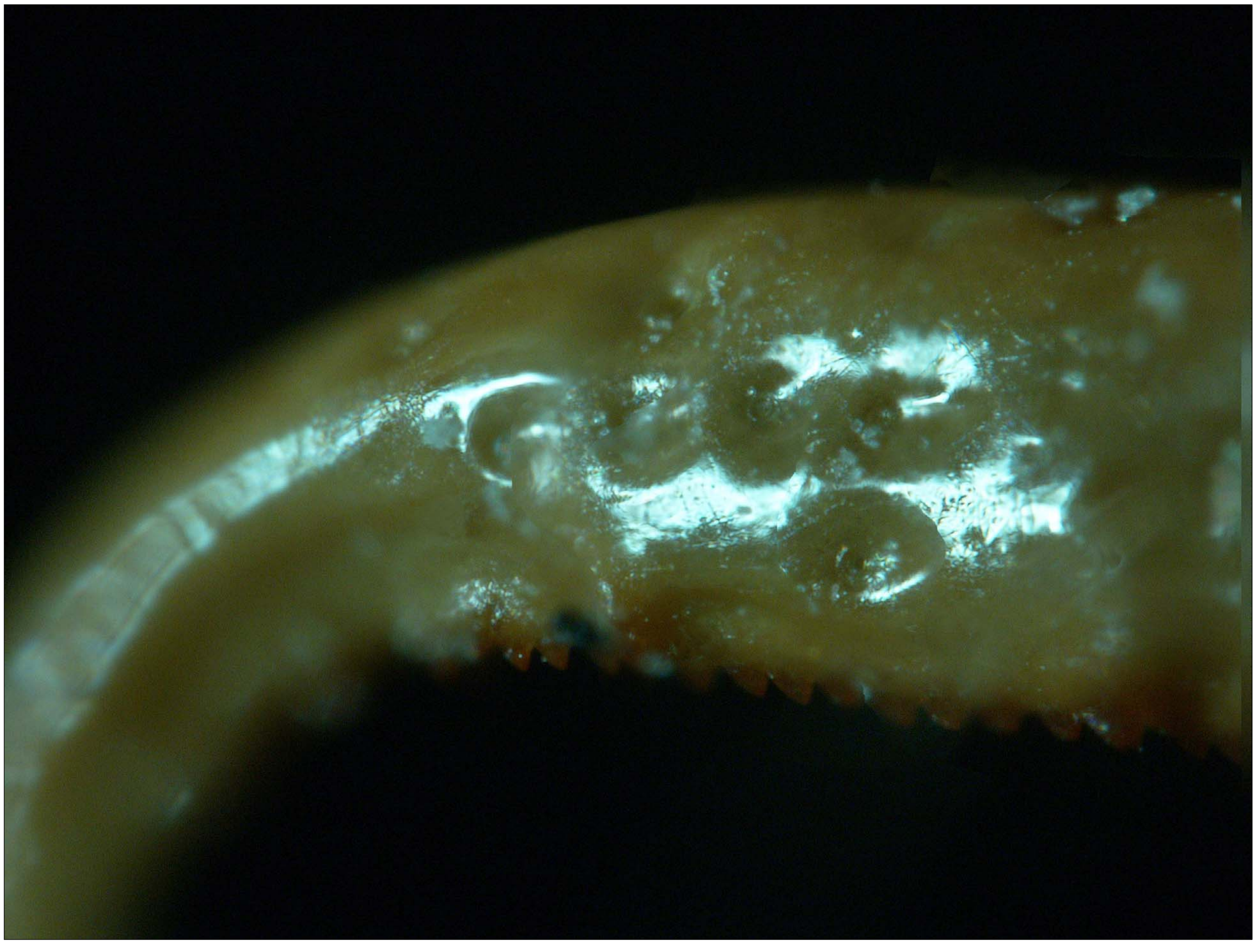

Figure 19: *Akrav israchanani*. External view of chelal fixed finger distal area showing the constellation array. Non-type specimen Sc. 2682.

represents continuation and extension of embryological development. The newborn are kept on mother's dorsum, and possess a number of distinct embryonic features. The first ecdysis (molt) of this first instar results in a drastic transformation of an embryo-like newborn to an adult-like second instar (= second stadium, nymph); see Farley (2005: figs. 9–10).

The *Akrav* embryo was preserved in a typical "supine position" (such as depicted for iuroids *Hadrurus arizonensis* in Farley, 1999, fig. 23, and *Iurus dufoureius* by Kovařík et al., 2010, figs. 235–236); i.e., when the metasoma and telson as well as the legs and pedipalps were folded over the ventral aspect of the mesosoma.

The size of the embryo (without metasoma) is 3.60 mm, i.e. ~ 8 % of the adult's size of 44–45 mm (Table I). (Compare to *Iurus*, where a late embryo without meta-soma was 14.55 mm long, while an adult female size was ca. 90 mm; Kovařík et al., 2010) Although the embryo is dry and distorted, and some structures are missing (notably pedipalps), many typical scorpion structures are clearly visible from ventral aspect (Figs. 22–24). We can easily distinguish prosoma (sternopectinal area), with both well-developed pectines visible, each having five teeth. Remnants of basal plate, genital operculum and pentagonal sternum are clearly visible, as well as remnants of all four right legs and four left legs (some leg segments are well preserved). Coxosternal area is preserved, with all coxae of legs and pedipalps. We also observe ventral view of mesosoma with attached tapering metasoma (telson is not formed), folded under posterior edge of mesosoma toward left side of the body. Left and right lung spiracles visible on mesosomal sternites III and IV. Large embryonic setae (lost after first molt) are clearly visible on metasomal sternites II, III, IV, on legs (including coxae), as well as on sternum and genital opercula. An interesting morphological feature of this stage (Farley, 2005) is a marked heterochrony: advanced embryonic development of some structures combined with the delayed development of others. In *Akrav*, as in other scorpions, we see advanced development of pectines compared to telson and metasomal segmentation.

Figure 20: *Akrav israchanani*. Three chelae showing the curvature of the fingers and the distinct overlap of the enlarged highly curved fixed finger distal denticle (*DD*). Non-type specimen Sc. 2682.

Figure 21: *Akrav israchanani*. Chelal finger dentition. Fixed finger on the left (non-type specimen Sc. 2682; UV photo) and movable finger on the right (paratype Sc. 2674).

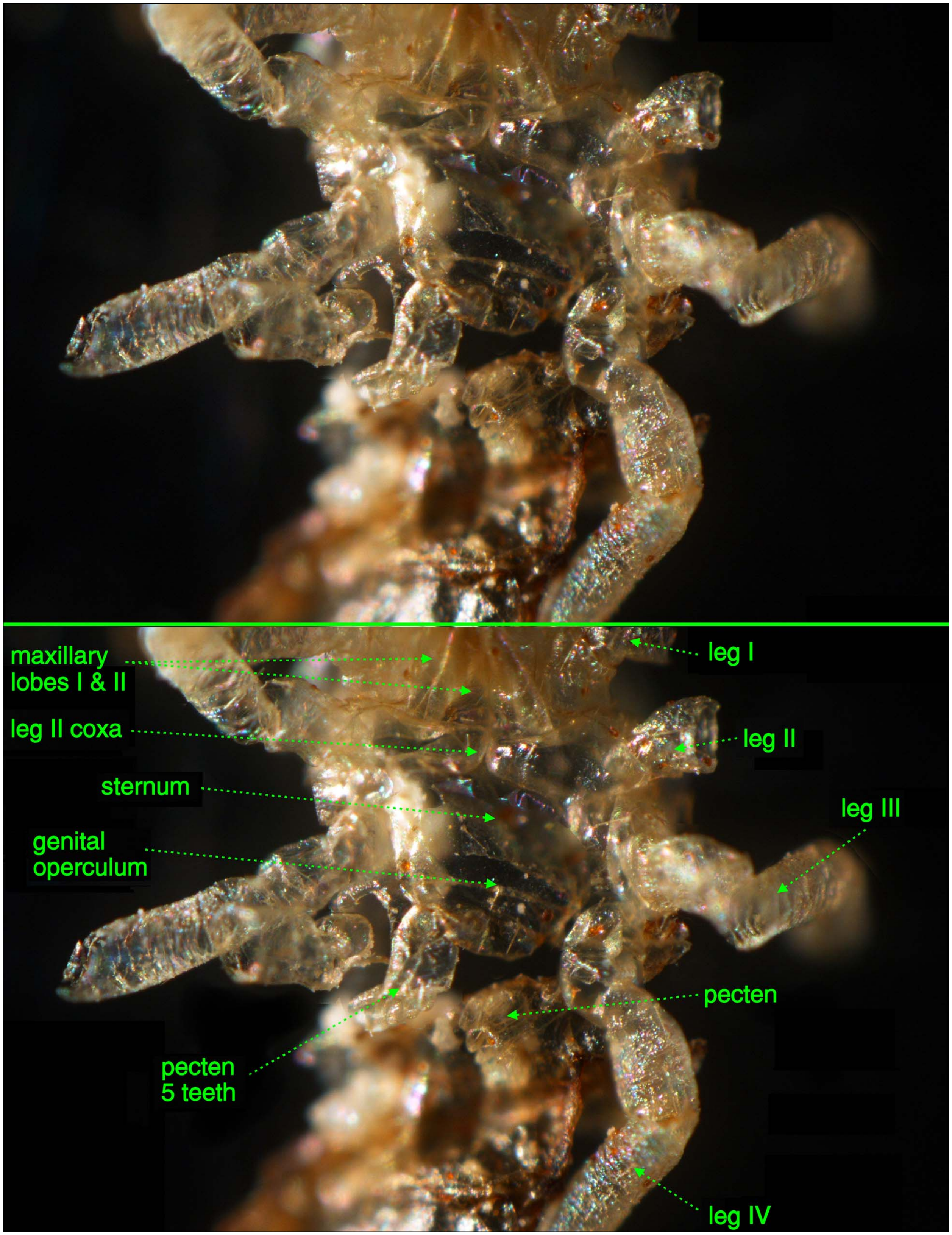

Figure 22: *Akrav israchanani*, Ayyalon Cave, Israel. Embryo, ventral view showing sternopectinal area. Note both pectines are visible, the right pecten (left side) exhibits five teeth, the distal teeth 4 and 5 are somewhat out of focus.

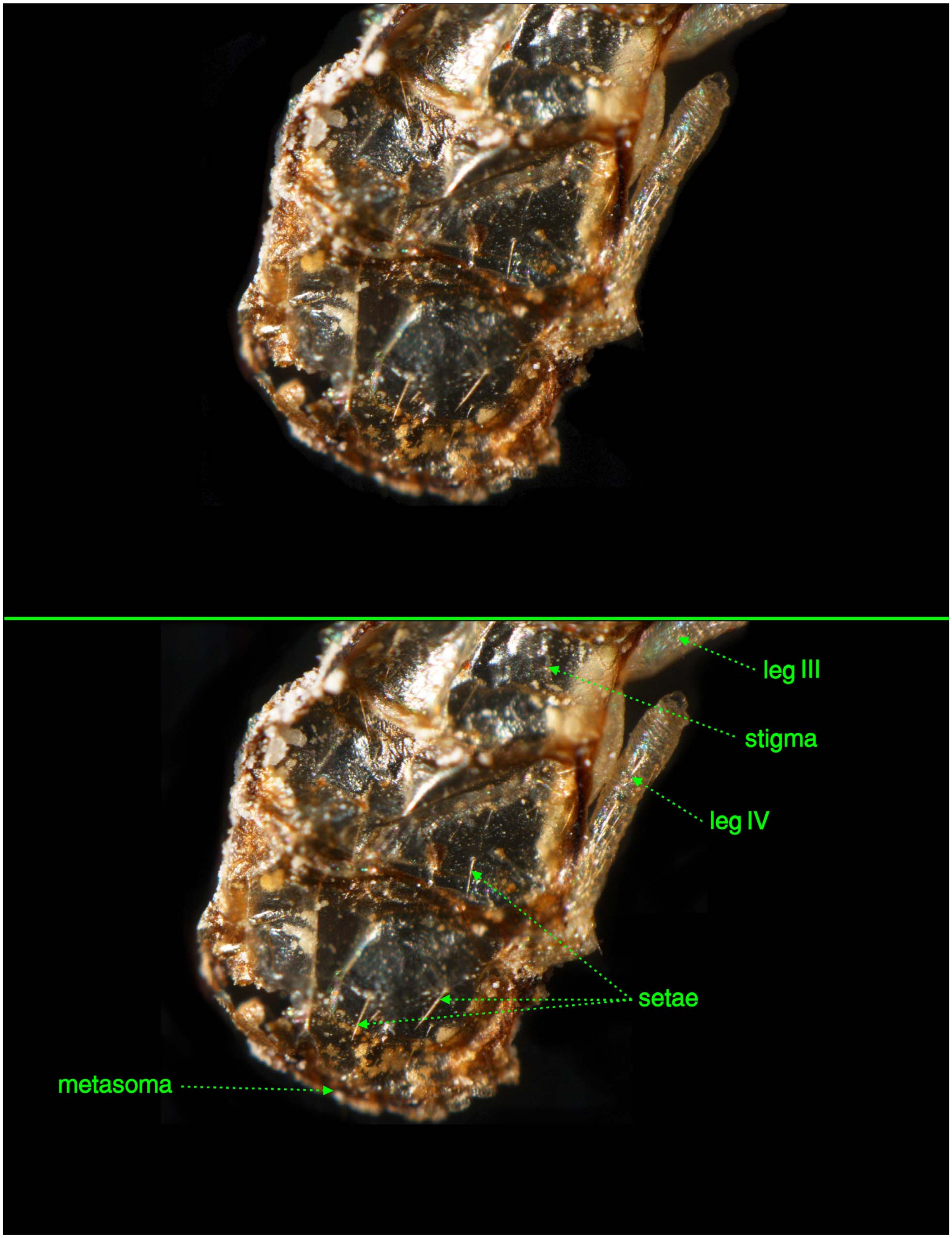

Figure 23: *Akrav israchanani*, Ayyalon Cave, Israel. Embryo, ventral view showing sternites II, III and IV. Stigma, embryonic setae, legs III and IV, and metasoma are indicated.

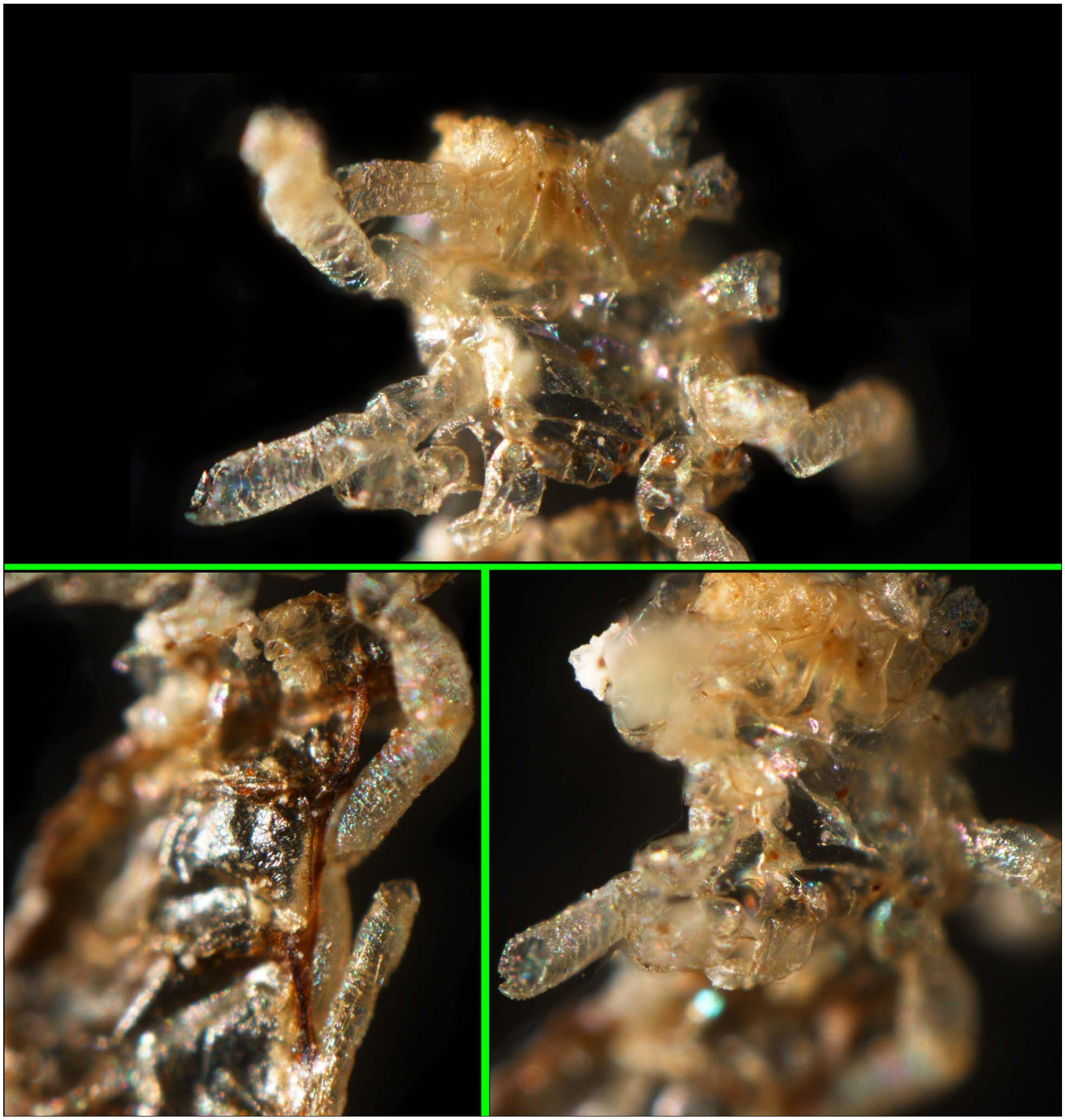

Figure 24: *Akrav israchanani*, Ayyalon Cave, Israel. Embryo, ventral view of prosoma showing various angles. **Top.** Sternopectinal area. **Bottom, Left.** Left side of prosoma. **Bottom, Right.** Sternopectinal area, right angled view.

Phylogenetic Considerations

In this section, we discuss the phylogenetic position of genus *Akrav* among the Recent scorpions. Key to this discussion is the determination of which characters are of phylogenetic importance and which characters may be the product, in part, of cave adaptation (troglomorphism).

Troglomorphic characters

In the most recent review of cave scorpions, Volschenk & Prendini (2008) discussed troglomorphic adaptations in scorpions, and came to a conclusion that only about 20 scorpion species can be called truly troglobitic. Prendini et al. (2010) suggest that troglomorphism is not a dead-end in itself and that troglo-

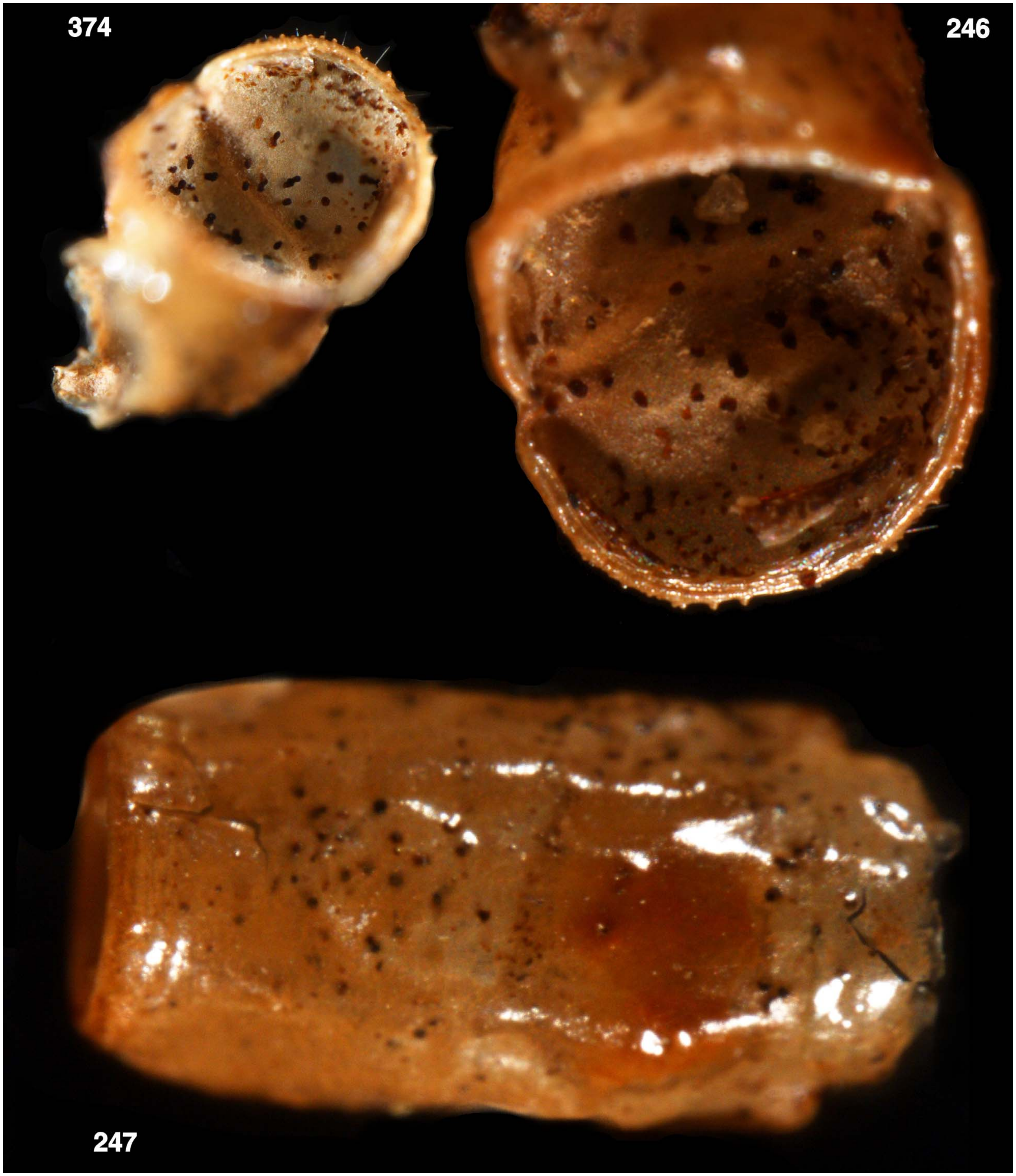

Figure 25: Possible detritivore (springtail?) excrements inside and outside scorpion's metasomal segments.

morphic features can be acquired and lost again. The same research group recently produced a series of important papers that includes some of the most interesting and specialized New World cave scorpions (Francke, 2009; Francke et al., 2009; Vignoli & Prendini, 2009; Prendini et al., 2010). Interestingly, the Chactoidea contain the predominant number of troglomorphic taxa, which are less represented in other scorpion superfamilies. We should note, however, that two of three known species (monotypic genera) of the

Figure 26: Sand deposit "cast" formed inside scorpion's pedipalp segment.

very ancient, relict scorpion family Pseudochactidae are found only in caves (Lourenço, 2007; Lourenço & Pham, 2010).

Volschenk & Prendini (2008: 248-250, tab. 1) formally distinguished *troglobitic* and *troglomorphic* scorpions. In their definition, "troglobitic" scorpions are those scorpions found exclusively in caves (i.e., cavernicolous) and exhibit high degree of cave adaptation (i.e., troglomorphism). "Troglomorphic" scorpions are those scorpions that are not found exclusively in caves, if at all, but also exhibit some degree of cave adaptation. Based on these two overlapping definitions, it appears that troglobitic scorpions would in most cases be the most cave adapted (i.e., exhibit the most troglomorphism), though there are many examples of scorpions exhibiting high troglomorphism and not technically classified as troglobitic (e.g., *Belisarius*, *Typhlochactas mitchelli*, *T. sylvestris*, etc.).

The list of scorpion troglomorphic adaptations given by Volschenk & Prendini (2008) includes: anophthalmy (loss or reduction of median and⁄or lateral ocelli); depigmentation; reduction of sclerotization and carination; attenuation of appendages (legs, pedipalps); loss of (pro- and retrolateral pedal) spurs and spinules on legs; modifications of pectinal organs (loss of fulcra, fusion of lamellae and reduction in number of teeth); and enlargement of telson.

Volschenk & Prendini (2008, table 1) classified *Akrav* as troglobitic (i.e., found exclusively in a cave). They list five structural characteristics classified as troglomorphic and assign these (yes/no) to *Akrav*: loss of both the median and lateral eyes (yes), absence of coloration and sclerotization (yes), attenuation of the pedipalps and legs (yes), loss of one or more pedal spurs (no), and telson vesicle enlarged (no). We take exception to three of these assignments: (a) *Akrav* does exhibit some weak coloration and sclerotization; (b) the retrolateral pedal spur is missing (established for the first time in this paper), and (c) the telson vesicle is enlarged in this species.

There are other characters not listed by Volschenk & Prendini (2008) that *Akrav* shares with the largest taxonomic group of troglobitic/troglomorphic scorpions, the Superstitioniidae. These features do not generally occur in scorpions that are not cave-adapted.

One such feature is simplification of the cheliceral dentition. In many species of Superstitioniidae (see Table 4), the median (*m*) and basal (*b*) denticles of the fixed finger are not formed into a bicuspid but instead are aligned evenly on the fixed finger edge. *Akrav* agrees with this condition. Several species exhibit only a single subdistal denticle (*sd*) on the movable finger, *Akrav* also agrees with this condition. In two of the smallest superstitioniid species, *Typhlochactas mitchelli* and *T. sylvestris*, additional cheliceral denticles are absent, the fixed finger *sd* in both species and the movable finger *b* in *T. mitchelli*. Therefore, *T. mitchelli* is missing no less than three cheliceral denticles.

It also appears that a simplification of the pectines occurs as a troglomorphism. For example, a large majority of species in Superstitioniidae lack fulcra; however, in this single case, *Akrav* does exhibit well developed fulcra. Roughly half the species in Superstitioniidae only have two anterior lamellae on the pectines, a condition also found in *Akrav*.

Another interesting condition found in many species of Superstitioniidae is the lack of a median spinule row on the ventral aspect of leg tarsus, a condition also exhibited by *Akrav*. In general these species, including *Akrav*, have two parallel rows of long setae along the ventral surface of the leg tarsus.

Finally, it appears that troglomorphism also causes some reduction in the size of trichobothria; i.e., normal full-sized trichobothria becoming “petite” (see Table 5). Based on the detailed data provided by Vignoli & Prendini (2009) and repeated in Prendini et al. (2010), we see that a large majority of species of Superstitioniidae have reduced trichobothria on both the pedipalp patella (usually four) and chela (usually five). *Akrav* also exhibits additional petite trichobothria, but on the chela only, trichobothria *db*, *dsb*, and *Eb*$_3$. Only trichobothrium *db* is petite in a majority of superstitioniids. It should also be pointed out that troglomorphism does not affect actual orthobothriotaxic patterns; that is, no derived trichobothrial types are known based on cave adaptation.

Based on the above discussion, we hypothesize here that two important taxonomic structure sets are *not* affected by cave adaptation (i.e., show no troglomorphism): chelal finger dentition alignment and basic trichobothrial positions on the pedipalp. These phylogenetically important structures are used, in part, along with other structures in determining the taxonomic position of *Akrav* within Recent scorpions.

Trichobothria homology and “placeholders”

Prendini et al. (2010: 15) state “…The assumption of trichobothrial ‘‘migration’’, invoked by Vachon (1974) to account for positional differences between putatively homologous trichobothria, is increasingly questioned (Prendini and Volschenk, 2007). ….”. This statement is highly misleading, since the only people really questioning “trichobothria migration” as suggested by Vachon are these authors alone; also see Vignoli & Prendini (2009) and Ochoa et al. (2010). Disagreements as to what trichobothria are homologous can be debated by systematists, especially for the unusual Type C patterns such as that found in superfamily Iuroidea (see Soleglad et al., 2009, for a detailed discussion), or in the euscorpiid genus *Chactopsis*, etc. At the same time, it is generally agreed to by a large majority of scorpion systematists that whatever the homologies are established, they reflect the standard set of orthobothriotaxic trichobothria defined by Vachon (1974). However, these authors insist on hypothesizing independent loss of one trichobothrium and a gain of another, “new” trichobothrium if it occurs at a different position, consequently, creating many “new” trichobothria outside Vachon’s (1974) original scheme (see below).

In their analysis of superstitioniid subfamily Typhlochactinae (*sensu* Soleglad & Fet, 2003b), Vignoli & Prendini (2009) and Prendini et al. (2010) hypothesize no less than 37 characters using “placeholders” to establish the existence of 37 “new” trichobothria—four on femur, ten on patella, and 23 on chela! Out of a total of 61 non-suppressed trichobothria characters, 37 hypothesize “new” trichobothria. These “new” trichobothria account for 61 % of their trichobothria-based cladistic analysis and 26 % of their total analysis. Based on this alone, we consider the results of their cladistic analysis highly suspect. Therefore, any reference in this paper to the phylogeny of Superstitioniidae will be based on Soleglad & Fet (2003b). Incidentally, we (Soleglad & Fet, in progress) will demonstrate several examples in Type C patterns where the only explanation for established trichobothria homology is *migration* (i.e. development of the same trichobothrium in a different position).

Aside of “placeholders” criticism, the papers of Vignoli & Prendini (2009) and Ochoa et al. (2010) are very thorough in their scorpion descriptions. Therefore, we depend on them, in part, in compiling our Tables 4 and 5.

Discussion of important phylogenetic structures

In this section we discuss a set of characters that will be used in the consideration of *Akrav*’s taxonomic position. Special diagrammatic line drawings accompany these discussions (Figs. 27–32), many annotated to highlight important substructures. Actual photographs of these structures of *Akrav* are also provided throughout this paper.

Chelal fingers (Figs. 17–21, 27–28)

One of the most notable characteristics of *Akrav* is its exaggerated curved distal tips of the chelal fingers (see several examples in Fig. 18). In particular, the distal tip of the fixed finger is highly curved and overlaps the inner edge of the movable finger when the fingers are

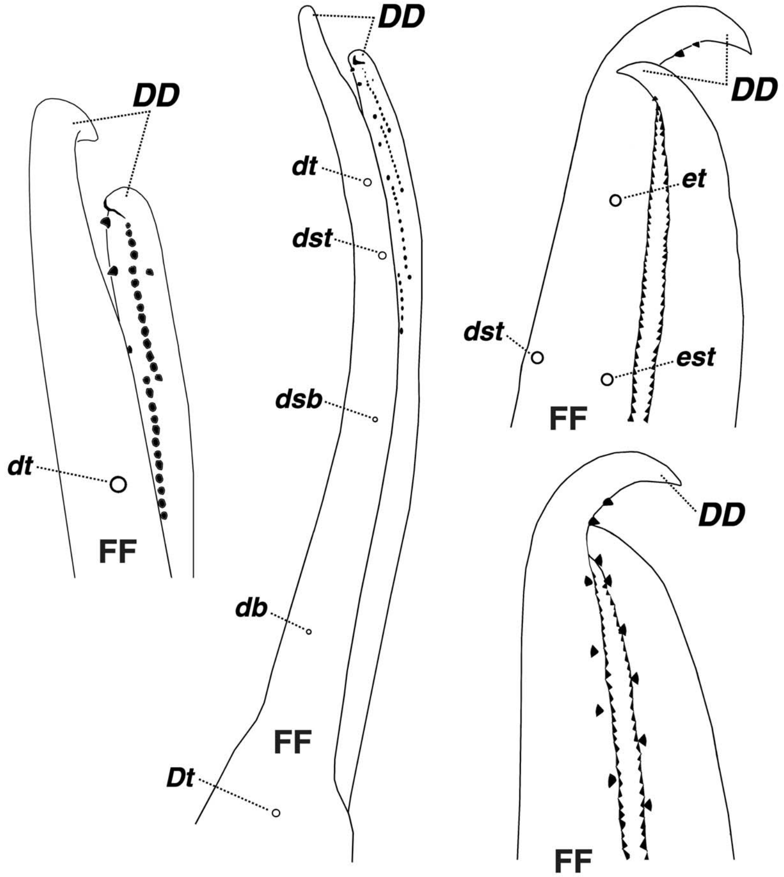

Figure 27: *Akrav israchanani*, Ayyalon Cave, Israel. Diagrammatic drawings of the right pedipalp chelal fingers showing their curvature and the distinct overlap of the enlarged highly curved fixed finger distal denticle (*DD*). Dorsal views (left and center), external view (upper right), and internal view (lower right). In particular, note that the *DD* of the fixed finger overlaps the movable finger on its inner edge. Trichobothria are identified where appropriate. FF = fixed finger.

closed, exhibiting a gap between the finger denticle edges. Two inner denticles are present on the curved tip of the fixed finger, which is highly unusual in Recent scorpions (a similar configuration is seen in the highly specialized, very small "picobuthoid" scorpions (fam. Buthidae; Lowe, 2010)). Species of *Serradigitus* and *Stahnkeus* (family Vaejovidae) exhibit elongated distal denticles (*DD*), presumably an adaptation to their lithophilic habitat, but these denticle tips are not adorned with other denticles as seen in *Akrav*.

Of taxonomic importance in *Akrav* are the oblique imbricating median denticle (*MD*) rows on the chelal fixed and movable fingers. This denticle organization is found in parvorders Pseudochactida, Buthida, and Chaerilida, but is limited in Iurida to superfamily Iuroidea (in family Caraboctonidae, the *MD* rows are oblique but not imbricating) and chactoid family Superstitioniidae (only oblique, *sensu* Soleglad & Fet, 2003b, in part). In Figure 28, we present a diagrammatic drawing of the denticle organization of the movable finger. The number of *MD* rows are large in this genus, nine occurring on the movable finger and eight on the fixed. They are aligned obliquely and are imbricated, the proximal edge of one row overlapping one or more distal *MD* denticles of the adjacent row, the overlapping more exaggerated basally. Nine and eight inner denticles (*ID*) and eight and seven outer denticles (*OD*) are present on the movable and fixed fingers, respectively. Of great interest, we also see several inner accessory denticles (*IAD*) on both fingers of the chela. The movable finger has at least 15 *IAD* and the fixed finger exhibits nine or more. These denticles becoming increasingly difficult to discern basally on each finger due to the increasing imbrication of the *MD* rows.

Trichobothria (Figs. 12–16, 29)

The trichobothrial pattern of *Akrav* is Type C, orthobothriotaxic, as illustrated diagrammatically in Fig 29 (drawing based on pedipalp segments from several specimens). In general, the pattern illustrated by Levy (2007, figs. 8–14) is accurate. However, there are a few subtle but important omissions involving trichobothria positions in Levy's pattern which we will discuss in detail.

Femur. In the three trichobothria found on the femur the dorsal trichobothrium *d* is positioned the most proximal, slightly lower than *i*. The external trichobothrium *e* is located distally of the other two trichobothria, roughly at one-quarter of the femur's length. Of particular interest we see that *e* is located on the *dorsal* surface, not on the external surface where it

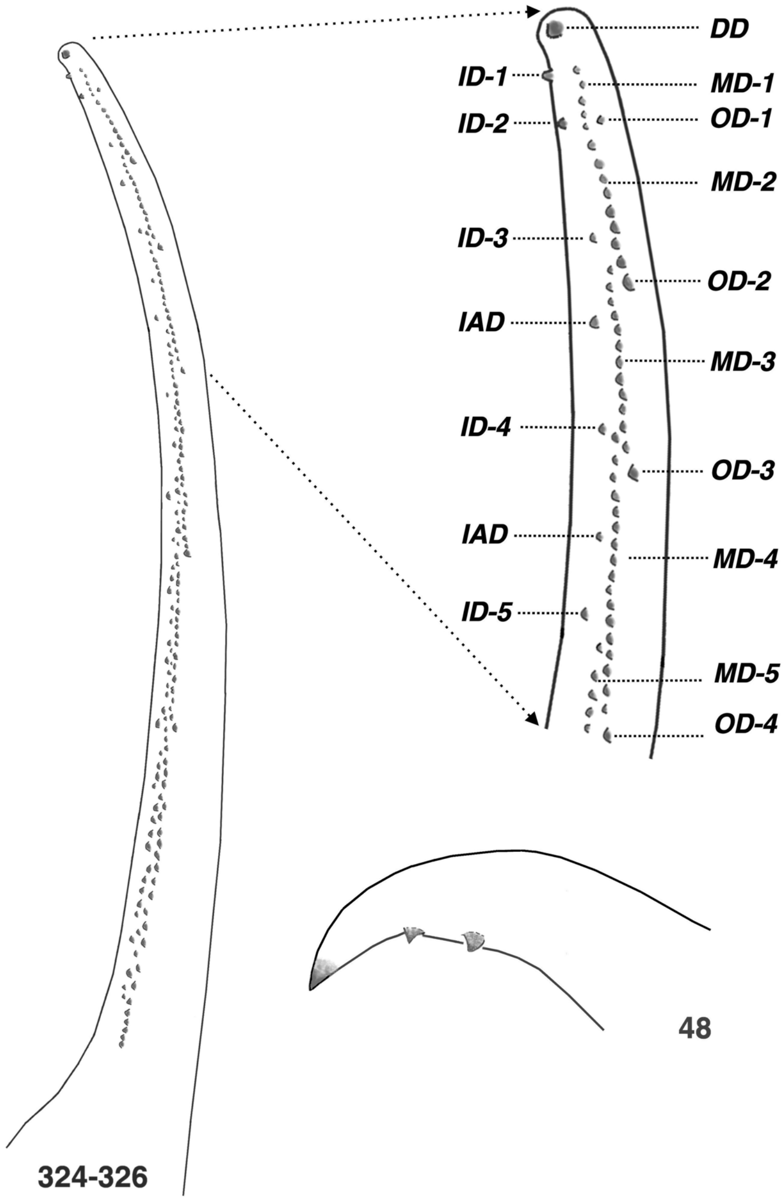

Figure 28: *Akrav israchanani*. Chela movable finger dentition (paratype Sc. 2674, 324-326) showing eight median denticle (*MD*) rows that are oblique and imbricating. Inner accessory denticles (*IAD*), outer denticles (*OD*), and distal denticle (*DD*) are also indicated. Bottom right (48, "non-type" specimen Sc. 2682) shows close-up of fixed finger with inner denticles (*ID*) occurring on the curvature of the distal tip.

normally occurs. This is clear in the two photographs of two femurs (both belonging to the same specimen, Sc. 2682) shown in Fig. 16, where the dorsoexternal carina (DE_c) is indicated.

Patella. The nineteen patellar trichobothria are positioned as follows. *Dorsal/internal surface.* Fig. 14 shows a photograph of the patella's dorsal surface. Visible are the two dorsal trichobothria, d_1 and d_2, and the solitary internal trichobothrium *i*. Interestingly, we see that *i* is located on the *dorsal* surface, next to the dorsointernal (DI_c) carina, not at its usual location at the internal surface. *Ventral surface*. The location of the patellar ventral trichobothria (three in number, v_1–v_3) is quite interesting and unique. In Figs. 13 and 15, we show photographs of these trichobothria from three perspectives: In Fig. 15, a ventral view, we definitely see that v_1 is positioned on the ventral surface, next to the ventroexternal (VE_c) carina. In this photograph we can also see that v_2 is located on VE_c and v_3 is located on the external surface. These trichobothria positions are also confirmed in Fig. 13. *External surface*. All thirteen external trichobothria are present, in addition to v_3 on the external surface and v_2 situated on the VE_c as discussed above. Trichobothrium esb_2 is petite, as it is in most Type C scorpions. The basic configuration of the thirteen external trichobothria is somewhat typical except for the distally slanting *esb* series, where esb_2 is located distally of esb_1. Generally, this series is either

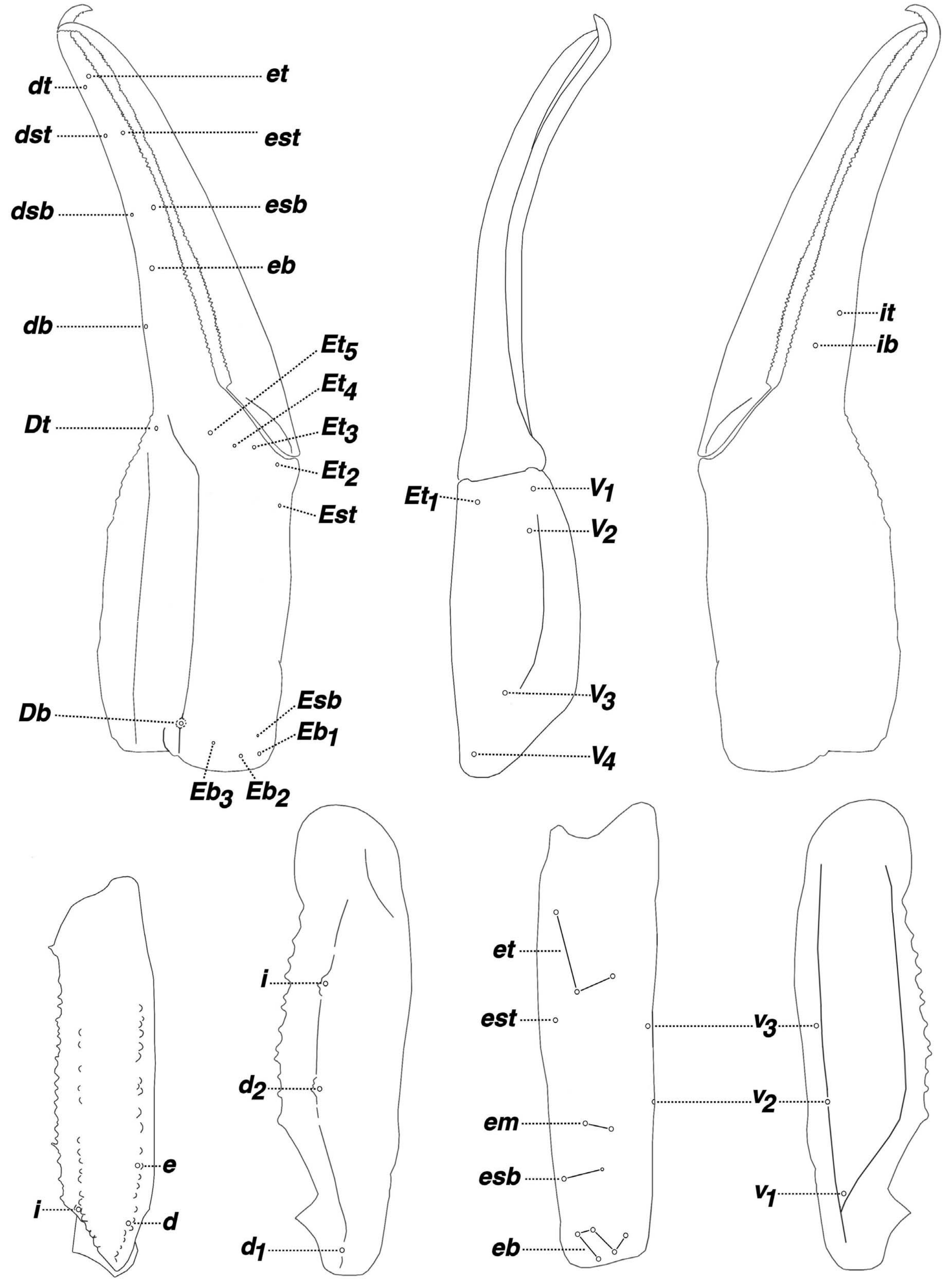

Figure 29: *Akrav israchanani*. Trichobothrial pattern.

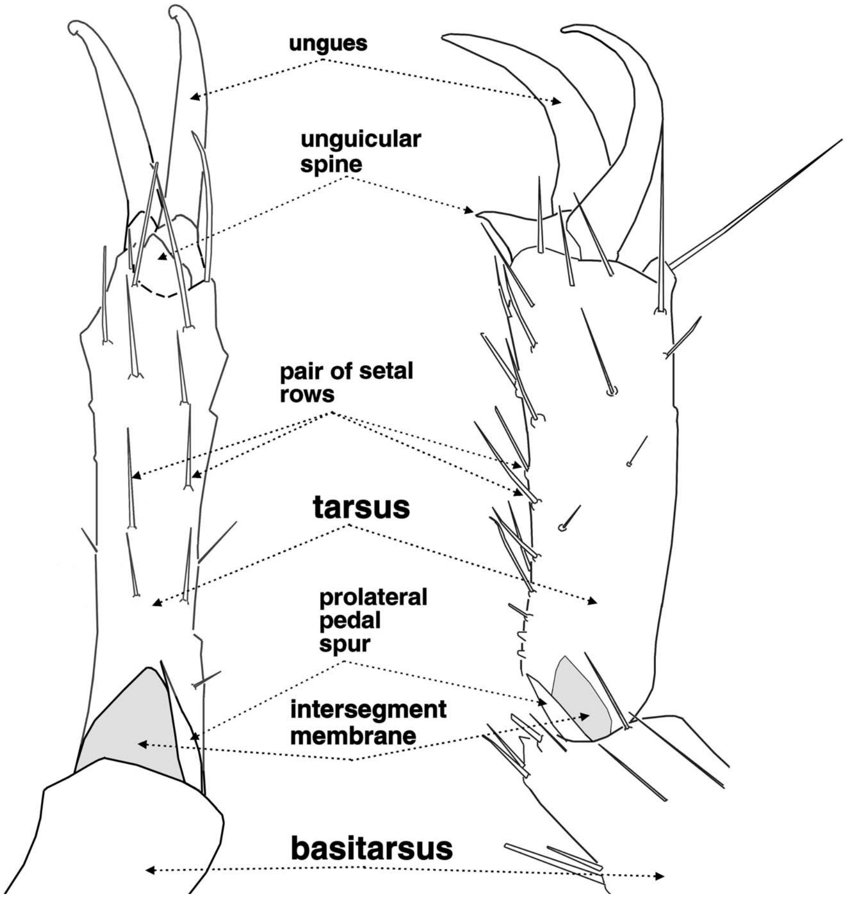

Figure 30: *Akrav israchanani*. Leg tarsus, ventral (left) and lateroventral (right) views, showing prominent spination and setation. Of particular interest, note the *absence* of a median row of spinules, the well developed socketed setal pairs aligned along the ventral surface, and the absence of the retrolateral pedal spur, only the prolateral spur is present.

roughly parallel to the edge or slants basally, *esb*$_2$ situated proximally to *esb*$_1$. Also of interest, *v*$_3$ is located significantly proximally to the *et* series.

Chela. The 26 orthobothriotaxic trichobothria are present, five of which are petite. This includes the two normal petite trichobothria *Et*$_4$ and *Esb* (which are usually petite in most Type C scorpions). Three other trichobothria are petite in size as well, *Eb*$_3$, *db*, and *dsb* on the fixed finger. These are visible in the photographs presented in Fig. 12.

Internal surface. The two internal trichobothria, *ib* and *it*, are situated somewhat basal on the fixed finger but well removed from the movable finger articular membrane. Trichobothrium *it* position compared to the fixed finger length is 0.224.

Ventral surface. Trichobothria *V*$_1$–*V*$_4$ are distributed over the entire length of the chelal palm. *V*$_1$ and *V*$_2$ are positioned considerably closer to each other, where the distance between *V*$_2$ and *V*$_3$ is more than three times the distance between *V*$_1$ and *V*$_2$. The *V*$_1$–*V*$_2$–*V*$_3$ juncture is straight, not angling towards the internal edge. The external trichobothrium *Et*$_1$ is located on the external edge of the ventral surface of the palm, the usual location for this trichobothrium.

External/dorsal surfaces. Trichobothrium *Db* is located quite basally on the palm whereas *Dt* is located distally on the palm/fixed finger juncture on the dorsal surface, considerably removed from the former, almost the complete length of the palm. Palm trichobothria *Esb*$_1$–*Esb*$_3$ and *Esb* are located at the basal edge of the palm; *Et*$_2$–*Et*$_5$ are aligned in an irregular line distally at the palm's edge with *Est* located slightly proximal. Fixed finger trichobothria, *db*–*dt* and *eb*–*et*, are all positioned well on the finger, the *eb*–*et* series located on the distal two-thirds of the finger. The *eb*–*esb*–*est* juncture points towards the fixed finger denticle edge with *eb* angling towards the finger's dorsal edge.

In summary, interesting attributes of *Akrav*'s trichobothrial pattern are the additional three petite trichobothria, the dorsal location of the femoral external trichobothrium *e*; for the patella, the dorsal location of the internal trichobothrium *i*, the external position of *v*$_3$, and the distal slanting of the *esb* series; for the chela, the distal placement of *Dt*, the alignment of *V*$_1$–*V*$_4$, and the placement of *ib*–*it* on the fixed finger.

Leg (Figs. 11, 30)

The leg tarsus is moderately armed with setation. On the ventral surface we have two submedian rows of elongated small socketed setae, five or six in number in each row. There is no spination, a ventral median spinule

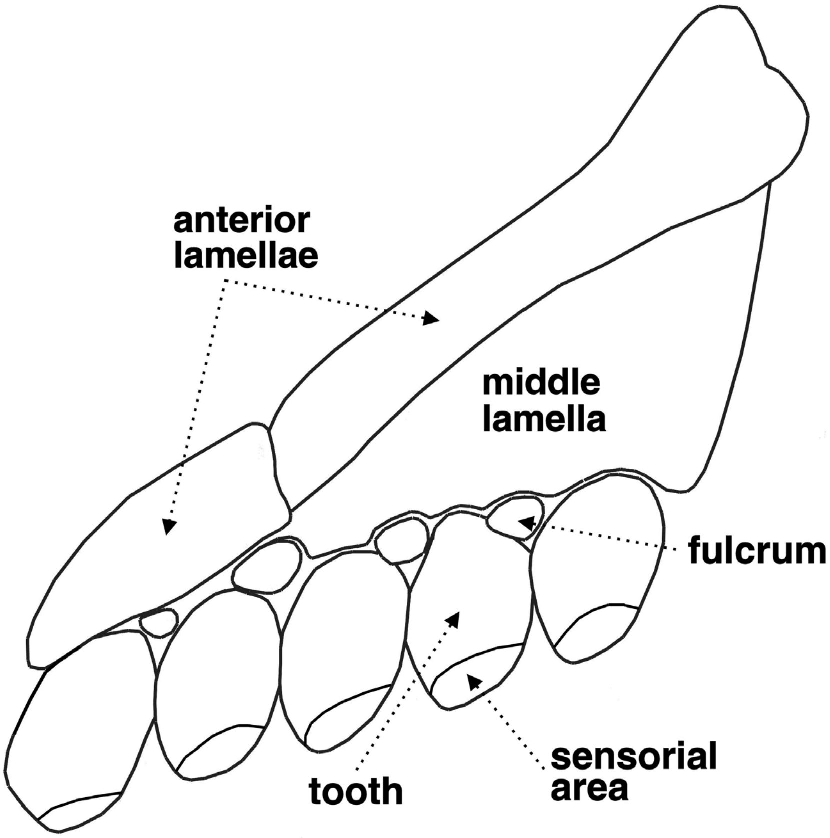

Figure 31: *Akrav israchanani*. Diagrammatic view of pecten. Note the presence of fulcra and only two anterior lamellae.

row is absent. The ungues are long, curved, and sharp and the unguicular spine (dactyl) is well developed and pointed. Only a prolateral pedal spur is present, the retrolateral spur is missing. The retrolateral pedal spur reported by Levy (2007) turns out to be a swollen intersegment membrane between the tarsus and basitarsus juncture, the triangular-shaped base of the tarsus cuticle contributing to this confusion, forming the "point" of the "spur". The basitarsus is armed with a few heavy, elongated setae on the ventral surface; a tibial spur is absent.

Pectines (Figs. 7–8, 31)

The pectines in *Akrav* are small and simply developed (see diagrammatic drawing in Fig. 31). The anterior lamellae are represented only by two plates, the basal roughly twice as long as the anterior sclerite. The middle lamella is formed into a single triangular sclerite. Well developed fulcra are present, however, positioned between the short rounded teeth. The anterior tips of each pectinal tooth exhibit a sensorial area. Out of 20 specimens, only nine had one or both preserved pectines (total of 15 pectines), and in all, five pectinal teeth were present. Scattered, sparsely distributed reddish setae are found on the lamella and fulcra, smaller whitish setae found on the teeth.

Chelicerae (Figs. 5, 32)

The distal tines of the movable finger (*dd* and *vd*) are unequal in size, *vd* considerably longer than its dorsal counterpart *dd* (see diagrammatic drawing in Fig. 32). A single, well developed subdistal (*sd*) denticle is present on the dorsal edge of the movable finger, slightly smaller than the median (*m*) denticle. The ventral edge of the movable finger is smooth. All four denticles of the fixed finger are present with the median (*m*) and basal (*b*) denticles *not* formed in a bicuspid. The fixed finger's ventral surface lacks ventral accessory (*va*) denticles. The ventral surfaces of the movable finger and palm base are covered with a heavy brush of elongated setae (see photograph in Fig. 5). No traces of serrula are detected.

Akrav's place within Recent scorpions

Based on the detailed character descriptions discussed above, we now consider *Akrav*'s position within Recent scorpions.

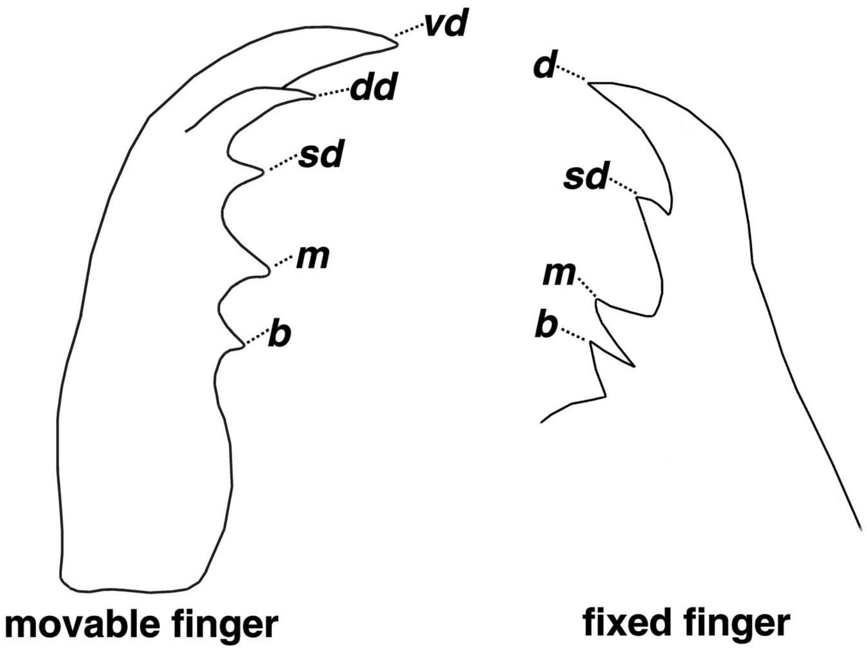

Figure 32: *Akrav israchanani*. Diagrammatic dorsal views of cheliceral fingers showing prominent dentition. Of particular interest note the single subdistal (*sd*) denticle on the dorsal edge of the movable finger and the non-cojoined median (*m*) and basal (*b*) denticles of the fixed finger (i.e., they don't form a bicuspid).

Parvorder and superfamily

Parvorder: This genus complies with orthobothriotaxy type C (Vachon, 1974), exhibiting 48 trichobothria, 3 on the femur, 19 on the patella, and 26 on the chela (see Fig. 29 for a diagram of this pattern). The sternum is type 2 (Soleglad & Fet, 2003a: fig. 7), it has a posterior emargination and internally, the internal process is bifurcated into two processes (see Figs. 7 and 9). These two characters are found exclusively in the parvorder **Iurida** Soleglad et Fet, 2003b. The hemispermatophore is not known for *Akrav*, but we suspect it is most likely lamelliform (Stockwell, 1989: figs. 218–219, 228), another exclusive character of Iurida. Based on this data we place *Akrav* in Iurida.

Superfamily: *Akrav* lacks any dentition on the cheliceral ventral edge of the movable finger. There is no trace of ventral median spinules on the leg tarsus. These two conditions exclude superfamily Iuroidea which exhibits a large solitary cheliceral *va* denticle on the movable finger and some form of ventral spinule clusters on the leg tarsus (see Soleglad & Fet, 2003b: figs. 19–22, 52–53). *Akrav* chelal *MD* denticle row is singular and is formed in oblique imbricating *MD* groups, excluding it from superfamily Scorpionoidea whose primary denticle rows number one or more and the *MD* groups are inline (see Stockwell, 1989: characters 45, 46, table 6). [It should be noted however, that *Akrav* does exhibit a single subdistal (*sd*) denticle on the cheliceral fixed finger and only possesses a prolateral pedal spur on the legs, characters which are associated with the scorpionoids. We, however, consider these characters in *Akrav* to be products of cave adaptation, and therefore, are not of any particular phylogenetic importance (see discussion elsewhere)]. This leaves superfamily Chactoidea as the only option for *Akrav* inclusion. Based on these observations, we can conclude that *Akrav* is a member of superfamily Chactoidea.

Family

Levy (2007) did not compare his new family to other chactoids. We will now attempt to establish placement of *Akrav* among four families that comprise superfamily Chactoidea: Chactidae, Euscorpiidae, Superstitioniidae, and Vaejovidae (Soleglad & Fet, 2003b).

The Euscorpiidae can be defined by their unique chelal finger dentition and the presence of major neobothriotaxy found on the pedipalp patella (Soleglad & Sissom, 2001: characters 28, 31, 51, 52: fig. 211). The primary denticle row of *MD* groups is configured in a straight line, not oblique as in *Akrav*. The outer denticles (*OD*) of the fingers are located external of the *MD* groups, not inline with the groups as in *Akrav*. *Akrav* is orthobothriotaxic, whereas the euscorpiids show significant neobothriotaxy in both the external and ventral surfaces of the pedipalp patella. Based on these differences, we can exclude Euscorpiidae as a family choice for *Akrav*.

In the family Vaejovidae, the chelae fingers have the *MD* row of denticles oriented in a straight line, chelal trichobothrium *Dt* is located from the suprabasal area to the middle of the palm, and the telson aculeus is equipped with a lateral aculear serration (LAS) (see Fet et al., 2006). *MD* denticle groups are oblique and highly imbricated in *Akrav*, trichobothrium *Dt* is located at the base of the fixed finger beyond the external condyle, and

Akrav does not exhibit a LAS on the telson, thus excluding Vaejovidae as a family choice. Similarly, *Akrav* is not consistent with family Chactidae where *MD* denticle groups are oriented in a straight line. In addition, the chelal trichobothria *ib–it* series are located on the palm next to the movable finger articular member in the chactids and the V_1–V_4 series is usually shortened and the V_1–V_2–V_3 juncture angling conspicuously towards the internal aspect of the palm. In *Akrav*, *ib–it* is located on the fixed finger base and V_1–V_4 extends the entire length of the palm not angling at the V_1–V_2–V_3 juncture.

At the same time, *Akrav* shares with family Superstitioniidae the most important taxonomic character in our opinion: the oblique orientation of the chelal finger *MD* groups. This character within parvorder Iurida is only found in the superfamily Iuroidea; it is also present in the other three parvorders, Pseudochactida, Buthida, and Chaerilida. Soleglad & Fet (2003b: 74, figs. 114, 116) hypothesized that the oblique orientation of the *MD* denticle groups found in Superstitioniidae is derived for this family (secondary character 48, state = 1). The oblique orientation found in the three basal parvorders as well as in superfamily Iuroidea was considered plesiomorphic (primary character 47, state = 0), a condition found as far back as the Carboniferous Palaeopisthacanthidae (Soleglad & Fet, 2003b). The clade formed by superfamilies Scorpionoidea and Chactoidea exhibits a straight orientation of the *MD* denticle groups, considered a synapomorphy (character 47, state = 1). Therefore, the oblique orientation of the *MD* denticle groups seen in Superstitioniidae is derived from a straight orientation. The derivation history of *MD* orientation, as suggested by Soleglad & Fet (2003b), can be represented by the following character state transforms: (47, state = 0 [oblique - primitive]) → (47, state = 1 [straight - derived]) → (48, state = 1 [oblique - derived]). Based on this character alone, we suggest here that *Akrav* is a member of family Superstitioniidae.

Two trichobothrial locations in *Akrav* also imply a close affinity to the Superstitioniidae: The esb_1–esb_2 series of the patella slants distally in *Akrav* as it does in all members of Superstitioniidae (note, this condition is not determinable in *Alacran* due to neobothriotaxy). This orientation of esb_1–esb_2 is unusual among scorpions: it normally slants towards the base of the patella. Chelal palm trichobothrium *Dt* is located distally on the palm at the base of the fixed finger, as the same in species of Superstitioniidae with the only exception being *Alacran* where it is located at the palm base. Finally, we see that the cheliceral fixed finger in *Akrav* has denticles *m* and *b* formed in a non-bicuspid, which is unusual in Recent scorpions. All Superstitioniidae also lack a bicuspid, except for genera *Superstitionia* and *Stygochactas*.

Subfamily

Soleglad & Fet (2003b: fig. 116) divided Superstitioniidae into two subfamilies, Superstitioniinae and Typhlochactinae. Of those, Superstitioniinae includes genera *Superstitionia* and *Troglotayosicus*, and Typhlochactinae includes *Typhlochactas*, *Sotanochactas*, *Stygochactas* (a new genus, described by Vignoli & Prendini, 2009), and *Alacran*, the latter considered *remotely* related to the other genera. This topology is quite similar to that derived by Vignoli & Prendini (2009) in a revision of their family Typhlochactidae (subfamily Typhlochactinae in our classification). They used genera *Superstitionia* and *Troglotayosicus* (our Superstitioninae) as outgroups. Except for ladderization between *Superstitionia* and *Troglotayosicus* (a group considered non-monophyletic by Vignoli & Prendini, 2009), the two cladograms are identical (see Fig. 33 for a comparison).

Major characters separating the two subfamilies of Superstitioniidae according to Soleglad & Fet (2003b) are the external position of patellar trichobothrium v_3 and the enlarged chelal finger *ID* denticles found in Superstitioniinae. In Typhlochactinae, v_3 is located on the ventral surface of the patella and the *ID* denticles are small. The sternum is also structured differently in these two subfamilies. The sternum is considerably wider than long with well developed lateral lobes and apex in Superstitioniinae whereas in Typhlochactinae the sternum is longer or equal than wide and is somewhat flat without conspicuous lateral lobes and apex (see Soleglad & Fet (2003a: figs. 9–13). *Akrav* complies with the Superstitioniinae in one of these characters only, the ventral placement of the patellar v_3 trichobothrium. Otherwise, *Akrav* is closer to Typhlochactinae with normal sized *ID* denticles and having a very elongate sternum (length to width ratio 1.24) with a modest to obsolete apex and low profiled lateral lobes (see Fig. 7). Interestingly, patellar v_2 trichobothrium in *Akrav* is located on the ventroexternal (*VE*) carina of the patella whereas, if one follows Vachon's (1974, figs. 167, 183) homology assignments, v_2 is located on the external surface in Typhlochactinae (*Alacran* is the sole exception). The setation and spination of the ventral surface of the leg tarsus in *Akrav* show a close affinity to subfamily Typhlochactinae with the absence of the median spinule row and the presence of a delicate pair of submedian parallel setal rows. In Superstitioniinae, we see dense spinule clusters in *Superstitionia* (see Soleglad & Fet, 2003b: fig 26) and two coarsely developed setal rows in *Troglotayosicus*.

Trichobothrial positions can be used to further narrow down a subfamily choice for *Akrav* (refer to Table 5). On the femur, trichobothrium *e* is located on the dorsal surface in *Akrav* (see Fig. 16). This unusual placement for *e* is also found in most superstitioniids ex-

	Telson	Chelicerae					Chelae			Sternopectinal Area			Leg Tarsus		Carapace	
	Vesicle Enlarged	**Movable Finger number of *sd***	**Movable Finger, *b* present**	**Fixed Finger, *sd* present**	**Fixed Finger, *m,b* orientation**	**Serrula**	***MD* rows**	***IAD***	***ID***	**Fulcra**	**Number of Anterior Lamellae**	**Stigma**	**Ventral Surface**	**Pedal Spurs**	**Lateral Eyes**	**Median Eyes**
Akrav israchanani	yes	1	yes	yes	Non-bicusp	no	obl-imb	yes	reg	yes	2	oval	Setal-pair	pro	no	no
Alacran chamuco	yes	2	yes	yes	Non-bicusp	?	obl	no	reg	no	3	circular	Setal-pair	pro	no	no
Alacran tartarus	yes	2	yes	yes	Non-bicusp	yes	obl	no	reg	no	3	circular	Setal-pair	pro	no	no
Sotanochactas elliotti	no	1	yes	yes	Non-bicusp	yes	obl	no	reg	no	2	circular	Setal-pair	none	no	no
Stygochactas granulosus	yes	1	yes	yes	Bicusp	yes	obl	no	reg	no	2	circular	Setal-pair	none	no	no
Superstitiionia donensis *	no	2	yes	yes	Bicusp	yes	obl	no	enlarged	yes	?	?	Spin/ brush	pro/ret	2	yes
Troglotayosicus vachoni	no	2	yes	yes	Non-bicusp	yes	?	no	enlarged	no	3	circular	Setal/ brush?	pro/ret	2	no
Troglotayosicus humiculum	no	2	yes	yes	Non-bicusp	yes	obl	no	enlarged	no	3	circular	Setal-pair	pro	2	no
Typhlochactas cavicola	yes	1	yes	yes	Non-bicusp	yes	?	no	reg	no	2	circular	?	none	no	no
Typhlochactas mitchelli	yes	1	no	no	Non-bicusp	yes	obl	no	reg	no	3	circular	Setal-pair + spines	pro	no	no
Typhlochactas reddelli	yes	2	yes	yes	Non-bicusp	yes	obl	no	reg	no	2	circular	Setal-pair	pro	no	no
Typhlochactas rhodesi	yes	2	yes	yes	Non-bicusp	yes	obl	no	reg	no	2	oval	Setal-pair	none	no	no
Typhlochactas sissomi	yes	2	yes	yes	Non-bicusp	yes	obl	no	reg	no	2	circular	Setal-pair	pro	no	no
Typhlochactas sylvestris	yes	1	yes	no	Non-bicusp	yes	obl	no	reg	no	3	circular	Setal-pair	pro	no	no

Table 4: Comparison of *Akrav* to all species in family Superstitioniidae. * Non-cave adapted.

	Femur	**Patella**					**Chela**			
	e	***esb* series**	v_2	v_3	*i*	**Additional petites**	***Dt***	**Additional petites**	**V_1–V_4 alignment**	***ib-it***
Akrav israchanani	dor	slant distally	VE_c	ext	dor	none	Fixed finger/palm juncture	*db*, *dsb*, Eb_3	Complete palm length, V_2 inline, V_2 & V_3 separated	Suprabasal, fixed finger
Alacran chamuco	dor?	?	ven	ven	dor?	?	palm base	?	?	Separated, fixed finger
Alacran tartarus	ext	?	ven	ven	dor?	?	palm base	?	?	Separated, fixed finger
Sotanochactas elliotti	dor	slant distally	ext	ven	int	d_1, *d2*, *et2*, *eb2*	Fixed finger/palm juncture	V_1, *Db*, Et_5, *db*, *esb*	Complete palm length, V_2 angles internally, V_2 & V_3 separated	Palm, base of fixed finger
Stygochactas granulosus	dor	slant distally	ext	ven	dor	d_1, *d2*, *et2*, *eb2*	Fixed finger/palm juncture	V_1, *Db*, Et_5, *db*, *esb*	Complete palm length, V_2 angles internally, V_2 & V_3 separated	Palm, base of fixed finger
Superstitiionia donensis *	ext	slant distally	ven	ext	int	none	palm distal	none	Distal 2/3 palm length, V_2 angles internally, V_2 & V_3 not separated	Palm, base of fixed finger
Troglotayosicus vachoni	ext	slant distally	ven	ext	dor?	?	Fixed finger/palm juncture	?	Distal 2/3 palm length, V_2 angles internally, V_2 & V_3 not separated	Palm, base of fixed finger
Troglotayosicus humiculum	ext?	slant distally	ven	ext	dor?	et_2	Fixed finger/palm juncture	*Db*, *Dt*	Distal 2/3 palm length, V_2 angles internally, V_2 & V_3 not separated	Palm, base of fixed finger
Typhlochactas cavicola	dor	slant distally	ext	ven	dor	d_1, d_2, et_2, eb_2	palm distal	V_1, *Db*, Et_5, *db*, *esb*	Complete palm length, V_2 angles internally, V_2 & V_3 separated	Palm, base of fixed finger
Typhlochactas mitchelli	dor	slant distally	ext	ven	dor?	d_1, d_2, et_2, eb_2	Fixed finger/palm juncture	V_1, *Db*, Et_5, *db*, *esb*	Distal 2/3 palm length, V_2 angles internally, V_2 & V_3 not separated	Palm, base of fixed finger
Typhlochactas reddelli	dor	slant distally	ext	ven	dor	d_1, d_2, et_2, eb_2	Fixed finger/palm juncture	V_1, *Db*, Et_5, *db*, *esb*	Complete palm length, V_2 angles internally, V_2 & V_3 separated	Palm, base of fixed finger
Typhlochactas rhodesi	dor	slant distally	ext	ven	dor	d_1, d_2, et_2, eb_2	Fixed finger/palm juncture	V_1, *Db*, Et_5, *db*, *esb*	Complete palm length, V_2 angles internally, V_2 & V_3 separated	Palm, base of fixed finger
Typhlochactas sissomi	dor	slant distally	ext	ven	ext?	d_1, d_2, et_2, eb_2	Fixed finger/palm juncture	V_1, *Db*, Et_5, *db*, *esb*	Complete palm length, V_2 angles internally, V_2 & V_3 separated	Base of fixed finger
Typhlochactas sylvestris	dor	slant distally	ext	ven	dor	d_1, d_2, et_2, eb_2, v_3	Fixed finger/palm juncture	V_1, *Db*, Et_5, *db*, *esb*	Complete palm length, V_2 angles internally, V_2 & V_3 separated	Palm, base of fixed finger

Table 5: Comparison of trichobothrial patterns of *Akrav* to all species in family Superstitioniidae. Data from observations of material, original description papers, Vignoli & Prendini (2009), and Prendini et al. (2009). * Non-cave adapted.

cept for the subfamily Superstitioniinae and the genus *Alacran*. Trichobothrium *Eb_1* on the chelal palm is found well on the palm base on *Akrav*, as it is for subfamily Typhlochactinae. This trichobothrium is located either on the ventral surface in *Troglotayosicus* or on the *V1* carina as in *Superstitionia*, both members of Superstitioniinae. Chelal ventral trichobothria V_1–V_4 in *Akrav* are aligned along the entire length of the palm with a noticeable gap between trichobothria V_2 and V_3, as is the case with most species in subfamily Typhlochactinae (again, *Alacran* being a notable exception). In subfamily Superstitioniinae, the ventral trichobothrial series does not extend the entire length of the palm and there is no large gap between V_2 and V_3. Finally, the fixed finger trichobothrium *db* is petite in *Akrav* as it is in all species in Typhlochactinae (again, except *Alacran*). In contrast, *db* is not petite in subfamily Superstitioniinae.

Based on the above discussion, we can conclude that the best subfamily fit for *Akrav* is Typhlochactinae.

Position within subfamily Typhlochactinae

It is clear from the above discussion that *Alacran* is remotely related to the other genera of this subfamily. It is also clear that *Akrav* shows a much closer affinity to *Typhlochactas* and its two related genera (*Sotanochactas* and *Stygochactas*) than to *Alacran*.

Typhlochactas, *Sotanochactas*, and *Stygochactas* are very closely related, and form a monophyletic clade (as suggested by Vignoli & Prendini, 2009). We hypothesize that this "*Typhlochactas* clade" is more closely related to *Akrav* than it is to *Alacran*. Therefore, we will concentrate on comparing *Akrav* to this group of genera.

Chelal finger dentition in *Akrav* is quite distinct, although complying with Typhlochactinae in the most important aspect, the obliqueness of the *MD* denticle groups. In *Akrav*, unlike in the "*Typhlochactas* clade" the *MD* groups are imbricated. Also, *Akrav* exhibits several *IAD* on the chelal fingers, also not found in the other clade. We consider these differences in the chelal finger dentition significant. In the "*Typhlochactas* clade" pectinal fulcra are absent, in *Akrav* they are present. Similarly, *Akrav* exhibits no serrula whereas it is well developed in the "*Typhlochactas* clade." Chelal internal trichobothria are located suprabasally on the fixed finger in *Akrav* whereas they are located on the chelal palm at the base of the fixed finger in the "*Typhlochactas* clade". It is clear from these several character differences that *Akrav* is phylogenetically distinct from the "*Typhlochactas* clade."

From the above discussion, and based on the original analysis conducted by Soleglad & Fet (2003b) augmented by new data discussed herein, the subfamily Typhlochactinae should most likely be divided into two tribes. One of them would be represented only by *Alacran* (concurring with topology of Vignoli & Prendini, 2009, who established a subfamily Alacraninae within their family Typhlochactidae). Another tribe would include *Typhlochactas*, *Sotanochactas*, and *Stygochactas*, forming a monophyletic clade, and *Akrav* as its sister clade. These two clades would correspond to two subtribes. Under this scheme, family Akravidae would be demoted to a subtribe status (see suggested phylogram in Fig. 33). However, we refrain from making formal taxonomic rearrangements here, pending a detailed phylogenetic analysis (Soleglad & Fet, in progress). Whatever the status of *Akrav* would be, it is already quite clear that this relict Old World genus is nested within New World taxa – a remarkable but in fact not unusual biogeographic pattern.

Levy's Taxonomic Decision

Our observations above should be compared to those of Levy (2007) who wrote: "…The Superstitioniidae, with the exception of *Alacran*, which displays neobothriotaxy, also have two ventral trichobothria on the patella of the pedipalpi rather than three as in Akravidae; the third "ventral" trichobothrium in Superstitioniidae is located on the external surface of patella… The crescent-shaped spiracle slits unlike the circular stigmata of the Superstitioniidae, and the peculiar basitarsal retrolateral spur of the Akravidae rather than the ordinary-shaped retrolateral spurs present only in *Superstitionia* and *Troglotayosicus*, place the Akravidae further apart from the Superstitioniidae. The trichobothrial alignment on the Akravidae pedipalpi differs distinctly from the configuration found in all the Chactoid families…". While Levy correctly placed *Akrav* in Chactoidea, his distinction between Akravidae and Superstitioniidae was clearly overstated since it includes two misinterpreted features as well as one completely ignored: position of ventral patellar trichobothria and presence of two pedal spurs are misinterpreted. We do not confirm Levy's statement that *Akrav*'s "trichobothrial alignment… differs distinctly from the configuration found in all the Chactoid families…". In fact, the only diagnostic character remaining from Levy's Akravidae is the spiracle shape, which is often variable within a family in scorpions. The most important character misstated and then ignored is the complete obliqueness (and imbricated) alignment of the chelal finger *MD* denticle groups, a condition found in all Superstitioniidae and lacking in any other Chactoidea. This further confirms our suspicion that Akravidae is not justified as a family-rank taxon.

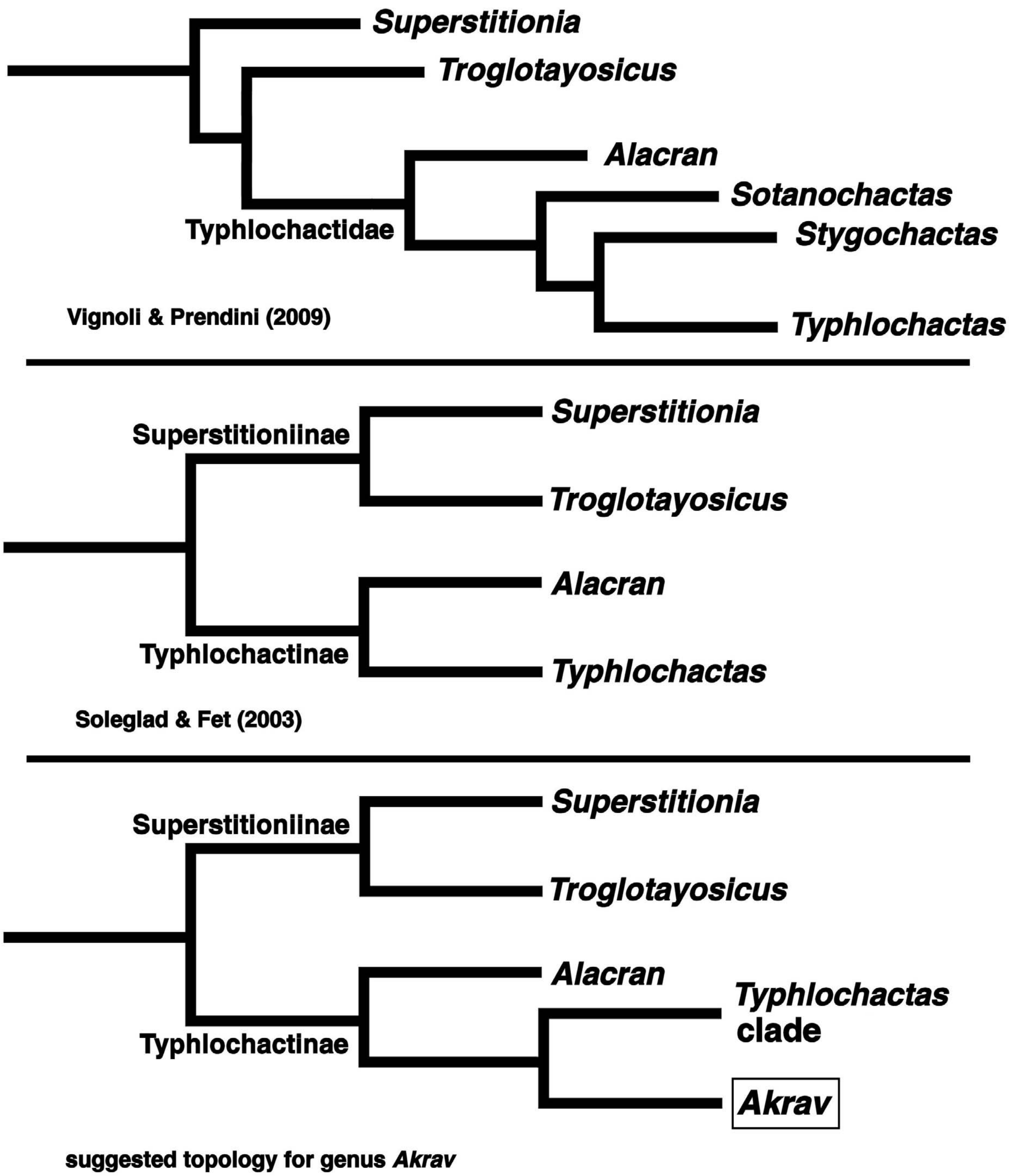

Figure 33: Phylogenetic topologies for family Superstitioniidae showing suggested placement of genus *Akrav*. Note "*Typhlochactas* clade" = *Typhlochactas* + *Sotanochactas* + *Stygochactas*.

Biogeography

Por (2008: 109) mentions that "The presence of the new high-rank taxa of arachnids in Ayyalon speak also for a very old evolutionary specialization." Can we elaborate on what "very old" means in our case?

First, we are talking about a clear affinity of *Akrav* to New World rather than to the Old World chactoid taxa, as discussed above. There are two chactoid groups in the Old World: family Euscorpiidae widespread from the Mediterranean to Southeast Asia, and a relict Pyrenean genus *Belisarius* (placed in Chactidae by Soleglad

& Fet, 2003b); neither appear to be closely related to *Akrav*. The time of divergence of *Akrav* and its New World relatives from their common ancestor cannot be confidently estimated. Our only fossil-based dating of chactoid families comes from a single Cretaceous genus *Araripescorpius* (Crato Formation, Brazil), which is classified in modern Chactidae (Menon, 2007). This at least indicates that some modern chactoid families already existed in late Mesozoic. Thus, clade divergence within Superstitioniidae and Typhlochactinae could span any time over the Cenozoic Era.

Second, we need to address the currently observed *range disjunction* among *Akrav* and its New World relatives – an amazing but not unique phenomenon among scorpions. Former continuous ranges with subsequent extinction has been hypothesized for such spectacular disjunctions as that of sister families Iuridae (Mediterranean) and Caraboctonidae (New World); of subfamily Diplocentrinae (Scorpionidae), with its range disjunct between Middle East and New World; or of the abovementioned genus *Belisarius*, which we (Soleglad & Fet, 2003b) consider to be a sister group to South American tribe Brotheini (Chactidae). In all these cases, it is reasonable to assume that the vicariance resulted from extinction under Cenozoic, or even earlier, climate changes, often by aridization. Modern distribution of chactoid families, in particular, appears to be a complex pattern with many range disjunctions (Nenilin & Fet, 1993; Soleglad & Fet, 2003b). In addition, one should never discount a possibility of dispersal: scorpions are large animals perfectly capable of active movement!

One could hypothesize that the Cenozoic aridization of the Middle East drove *Akrav*'s ancestors to underground habitat that provided a stable, non-arid environment. This pattern has been observed in many relict troglomorphic taxa. In fact, the very same pattern is suggested for the pseudoscorpion *Ayyalonia dimentmani* described from Ayyalon Cave by Ćurčić (2008). This species, placed in a new genus and a new tribe, is interpreted as a relict of an old circumtropical pattern of distribution, "either of early Miocene or late Mesozoic age and origin" (Ćurčić, 2008).

Aquatic fauna of the Ayyalon Cave also appears to be relict but possibly captured in the Cenozoic. Levy (2007: 92) wrote that "the distribution of the subterranean crustaceans living in the Ayyalon Cave is considered to be a relict of the Late Miocene circumtropical Tethys Ocean." The Late Miocene (ca. 15 Mya) is the upper age of the shrinking Tethys, and such Cenozoic date could precede *Akrav*'s troglobitization. Thus, notwithstanding possible deep antiquity of the aquatic Ophel biota based on its remarkable chemoautotrophic bacteria (Por, 2007, 2008, 2011a, 2011b), terrestrial Ayyalon Cave animals higher on the trophic chain are likely to be Cenozoic relicts.

Ecology

Absence of food items suitable for scorpions in the Ayyalon Cave puzzled Levy (2007) who wrote: "No traces of any of the scorpions' prey animals have yet been found. Could their disappearance have caused the presumed extinction of the scorpions?"

One *very* unusual feature for scorpions, immediately noticeable in *Akrav*, is asymmetric development of chela fingertips: the fixed finger terminal curvature is exaggerated, not matched by that of the movable finger (Figs. 18, 20). This arrangement resembles a beak of a raptor bird. Such asymmetry has not been observed in any other scorpion groups (Vachon, 1974; Polis, 1990). Also, an unusual arrangement of subterminal denticles (Fig. 18) could provide an additional gripping capacity.

The pedipalps are scorpion's only hunting appendages; but what are the objects at which such a unique gripping adaptation is directed? Springtails (Collembola) found in the Ayyalon Cave (~1 mm in length) probably are the food object for the blind pseudoscorpion *Ayyalonia*, the only other terrestrial predator in the cave (1.6–1.7 mm long). However, *Akrav* is a large animal, and its highly modified fingertips do not seem to be an adaptation to handle tiny springtails.

We want to offer a more speculative but plausible hypothesis: that the strangely beak-shaped fingers of *Akrav* are an adaptation for catching *aquatic crustaceans*, abundant in the cave's pool. Some of those (palaemonid prawns *Typhlocaris*, 20–27 mm long) appear to be a suitable catch for *Akrav* (whose chela length is 13.5 mm in the large holotype). Exaggerated fixed finger tip in *Akrav* is somewhat reminiscent of modified, attenuated chelicerae of *Dysdera* spiders (Řezáč et al., 2008, figs. 1e-f) that specialize in preying on Crustacea (woodlice, Isopoda) with thick, armored cuticle (kindly brought to our attention by Dr. Yael Lubin).

All scorpion exoskeletons in the Ayyalon Cave were collected within a small distance from the water edge (Israel Na'aman, pers. comm, 2010). Levy (2007) says that they "were found firmly attached to rocks at various levels corresponding to the levels attained by the rise and fall of the underground water inside the voids." Many scorpions are found in, and forage at, the very edge of water bodies where they are daily submerged (Kinzelbach, 1970; Polis, 1990). A very common *Serradigitus littoralis* (Vaejovidae) in Mexico preys, among other arthropods, on crustaceans in the tidal zone of the Gulf of California (Due & Polis, 1985), where its density reaches up to 12+/m^2 along the drift line marked by *Sargassum* algae. Aquatic crustaceans such as *Ligia* (Isopoda) are a common prey item of *S. littoralis.*

There is also an intriguing evidence that the Mexican cave chactoid scorpion *Alacran* (Superstitioniidae: Typhlochactinae) is amphibious. According to

Vignoli & Prendini (2009: 28), "*Alacran* appears to be amphibious: the second specimen [of *A. tartarus*] from Cueva de Escorpión was collected on a wet flowstone wall (fig. 3E, F) and the specimen from Te Cimutaá Cave was found underwater in a small stream (A. G. Gluesenkamp and P. Sprouse, personal commun.)." The latter record refers to a holotype and the only known specimen of recently described *Alacran chamuco* Francke, 2009.

Stable isotope composition of Ayyalon Cave biota components has been analyzed by Dr. Elisabetta Boaretto (unpublished data). In ecology, table isotopes are used as markers of foraging ecology and food webs (Rundel et al., 1988). Levy (2007: 92) mentions (as a personal communication of Dr. Boaretto) that analysis of the [stable] carbon isotope composition of the scorpions' remains resulted in a value around -36‰, "denoting diet sources that thrive in the atmosphere of an ecosystem that deviates markedly from values like -25 to -18‰ that are found in organic terrestrial organisms living in the common global atmosphere". Dr. Boaretto confirmed to us (pers. comm., March 2011) that "the carbon stable isotopes ratio in the scorpion material indicate a diet which is based on organic matter that must have their origin inside the cave."

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