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A new anophthalmous species of *Paranemastoma* from Bulgaria (Opiliones: Nemastomatidae)

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Abstract. A new, eyeless species of harvestman, *Paranemastoma beroni*, collected from the Stoykova Dupka 1 Cave in the Slavyanka Mountains (south-western Bulgaria) is described and illustrated. A character combination of the form of the penis, the form of the pedipalps and absence of scutum armament, distinguish the new species from all other *Paranemastoma* species. The closest morphological relative, and the only other eyeless example, is the troglobiont *P. bureschi* (Roewer 1926), which is allopatric (north-western Bulgaria) and clearly differs in the presence of scutum armament and lack of cheliceral apophysis and opening of the cheliceral gland. Characterization and comparison of sculpture in non-troglobiont and troglobiont *Paranemastoma* species and SEM illustrations are included. A case of cuticular neoteny in troglobionts is also reported.

Keywords: Taxonomy, troglobite species, *Paranemastoma beroni* sp. nov., microsculpture, cuticular neoteny, caves, Balkan

The nemastomatid fauna of Bulgaria currently comprises 11 species, distributed among five genera: *Nemastoma* C.L. Koch 1836 (two species), *Pyza* Staręga 1976 (one species), *Paranemastoma* Redikorzev 1936 (three species with three subspecies), *Mitostoma* Roewer 1951 (two species), *Carinostoma* Kratochvíl 1958 (two species), and *Mediostoma* Kratochvíl 1958 (one species) (c.f. Staręga 1976; Mitov 2002). Only one of them, *P. bureschi* (Roewer 1926), belongs to the Bulgarian speleofauna. This troglobite is common in caves of the Western Stara Planina Mountains (Balkan Range), and is known from 33 Bulgarian caves (Beron & Mitov 1996) and some East Serbian caves (Jezava and Samar cave systems; Mountain Kalafat and Odorovačko polje near Dimitrovgrad, see Karaman 1995b; Nešić et al. 2006).

During biospeleological investigations in the Slavyanka (= Ali Botush) Mountains in south-western Bulgaria between 2004 and 2009, the zoologists Petar Beron and Boyan Petrov collected about 12 invertebrate species in the Stoykova Dupka 1 Cave (Figs. 1, 2), some of them undescribed (B. Petrov, pers. comm.; Guéorguiev 2005). One of these undescribed taxa is recognized here as a new member of the troglobiont harvestmen fauna of Bulgaria (Fig. 3). This species can be accommodated within the genus *Paranemastoma* and is morphologically similar to the likewise troglobiont *P. bureschi*. The present paper therefore provides a complete description of this new species, separates it from *Paranemastoma bureschi* and discusses further discriminating characters within the Balkan representatives of *Paranemastoma*.

METHODS

The following abbreviations are utilized: BFS = Bulgarian Federation of Speleology, Sofia, Bulgaria, L = body length, mts = number of metatarsal segments on left/right leg, ps = number of pseudarticulations on left/right leg femora, ts = number of tarsal segments on left/right leg, v. = village. The specimens examined are lodged in the following institutions: Muséum d'Histoire naturelle, Geneva, Switzerland (MHNG); National Museum of Natural History, Sofia, Bulgaria (NMNHS); Plamen Mitov Collection (PMC).

Material examined.—*Paranemastoma titaniacum* (Roewer 1914): MONTENEGRO: *Province Crkvice*: massif Krivošije, ''Vilina pećina u Napode'', 17 July 1973, C. Deeleman, 1 ♀, 1 juvenile (L: 2.3, for SEM study), (MHNG). ALBANIA: *Shkodër District*: Mt. Prokletije, v. Bogë, cave No. 25, 23 May 1993, P. Beron, B. Petrov, 1 ♂ (for SEM study), 1 ♀, 1 juvenile (NMNHS:400).

Paranemastoma bureschi (Roewer 1926): BULGARIA: West Stara Planina Mountains: *Montana District*: cave Beljar, 7 November 1970, V. Beshkov, 1 ♂, (NMNHS:220); *Vratsa District*: v. Bistrets, cave Haydushka Dupka, 26 April 1970, P. Beron, 1 ♂ (for SEM study), (NMNHS:59); *Sofia District*: near v. Gintsi, cave Dinevata Pesht, 24 October 2005, P. Mitov, 1 juvenile (L: 1.8, for SEM study), (PMC); v. Bov, cave Mecha Dupka, 17 February 1975, P. Beron, 2 ♂♂ (1 ♂ for SEM study), 2 ♀♀, (NMNHS:286).

Paranemastoma radewi (Roewer 1926): BULGARIA: Stara Planina Mountains: *Sofia District*: near v. Gintsi, cave Dinevata Pesht, 24 October 2005, P. Mitov, 1 juvenile (L: 1.8, for SEM study), (PMC); *Lovech District*: near v. Lesidren, cave Mechata Dupka, 5 October 1994, R. Pandurska, 1 ♂, 1 ♀, 3 juveniles (1 juvenile, L: 2.1, for SEM study), (PMC); Vitosha Mountains: above Dragalevtsi, 1100 m elev., 20 May 1988, P. Mitov, 1 ♀ (for SEM study), (PMC).

Methods.—I made measurements and drawings using a MBS-9 stereoscopic microscope and Zeiss microscope equipped with a dissecting microscope ocular micrometer and a drawing tube. Harvestmen were photographed under an Olympus BX41 SZ61 stereo microscope and Olympus BX41 microscope with a mounted Olympus Color View 1 digital camera. I assembled digital images captured at different focal planes using the application Combine ZM. The detailed morphological study of adult and juvenile specimens was carried out using a scanning electron microscope Jeol JSM-5510. The SEM study was conducted at 10–20 kV at high vacuum mode. Specimens were air-dried, mounted on an aluminum stub, and sputtered with a 300–400 Å gold layer (Jeol JFC-1200 sputter). The author followed Shear & Gruber (1983), who used the prefix ''micro-'' preceding terms

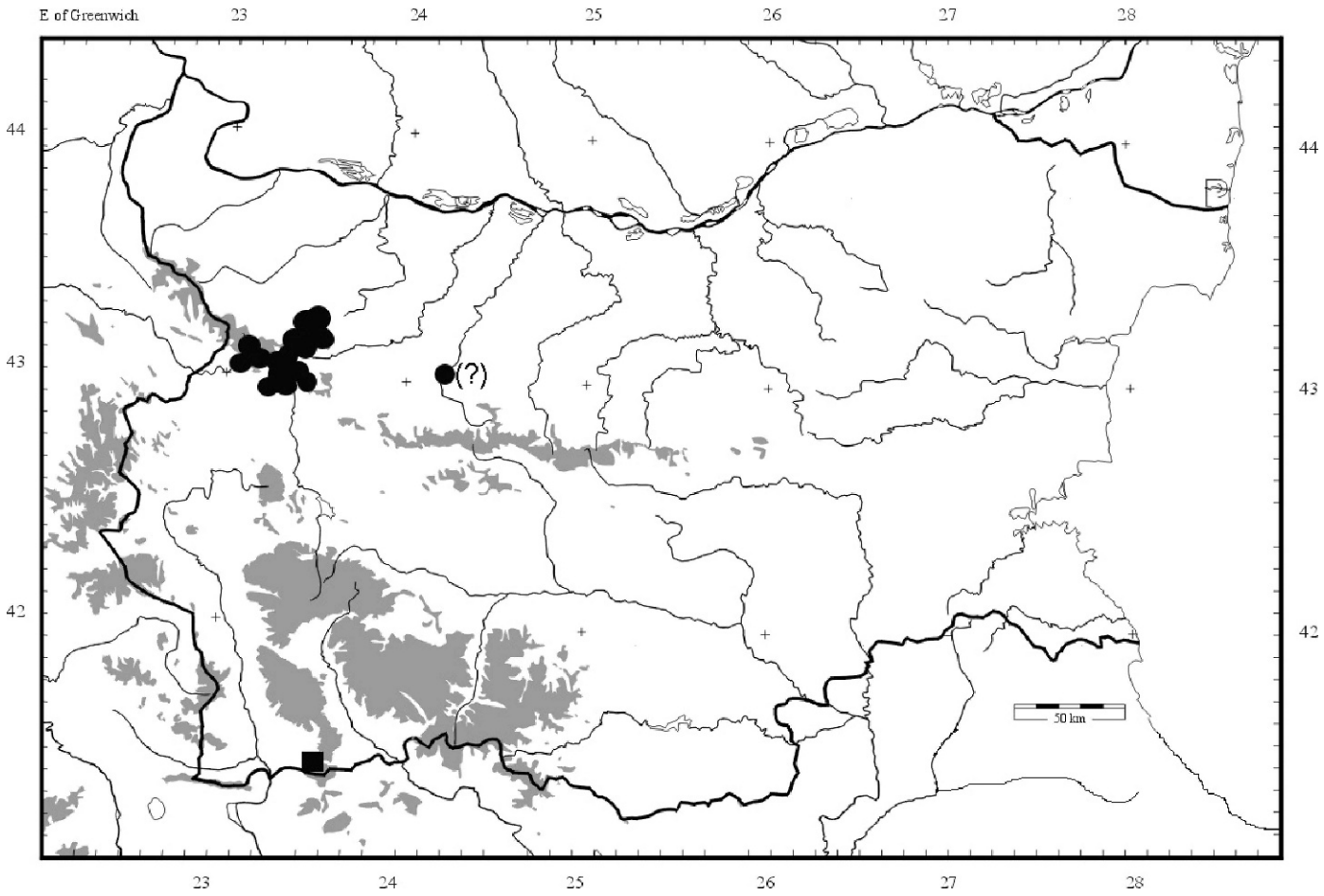


Figure 1.—Bulgaria, showing the distribution of: *Paranemastoma bureschi* (●, after Roewer 1926; Starega 1976; Beron & Mitov 1996; "?", the locality "Saeva Dupka – Lv18" Cave, seems doubtful, Beron & Mitov 1996), and *P. beroni* sp. nov., (■). Altitudes above 1200 m in gray.

describing features which measure 0.01 mm or less in size. All measurements are in mm.

TAXONOMY

Family Nemastomatidae Simon 1872
Genus *Paranemastoma* Redikorzev 1936

Paranemastoma Redikorzev 1936:40

Type species.—*Paranemastoma superbum* Redikorzev 1936, by original designation.

Paranemastoma beroni sp. nov.
Figs. 3–9, 11, 13, 15, 17–20, 22, 24–27, 29, 30, 35, 38, 46, 47, 51

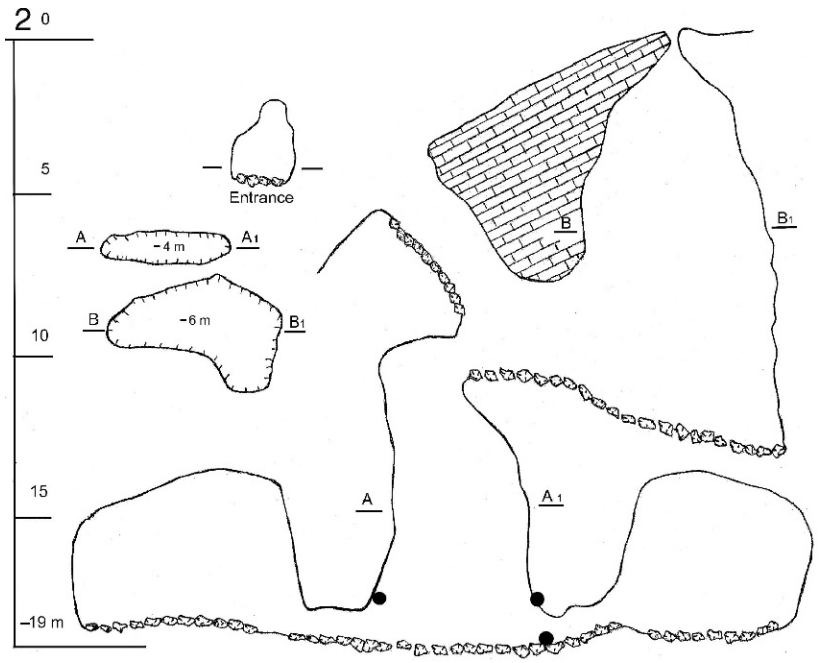
Type material.—*Holotype male*: BULGARIA: *Sandanski District*: Slavyanka (= Ali Botush) Mountains, Goleshevo Village, locality Suhomel, precipice cave Stoykova Dupka 1 (= Stoykina Dupka), BFS registration cave No. 309, 41°24′11.4–7″N, 23°35′42.8–9″E (41.40268°N, 23.59366°E, WGS 84), hand-collected from the base of cave gallery wall, 14 November 2005, P. Beron, B. Petrov (NMNHS, without registration number); *Paratype*: 1 male, same locality as holotype, hand collected from the base of cave gallery wall, 10 October 2009, B. Petrov (NMNHS, without registration number; mounted on SEM stub).

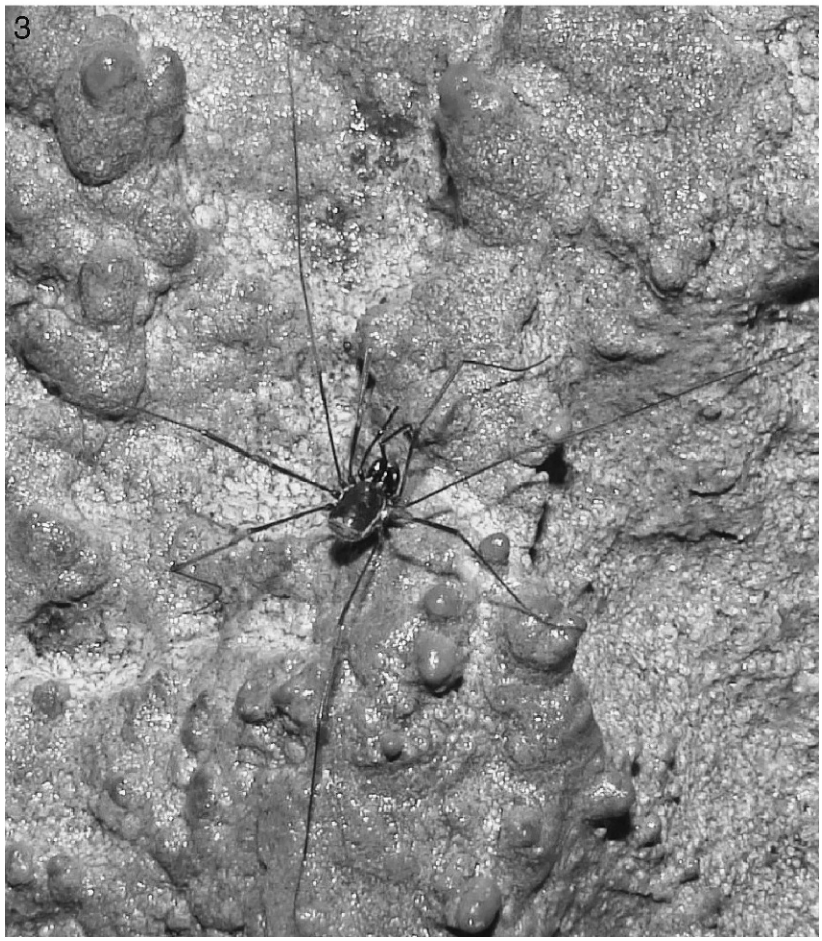
Additional material examined.—BULGARIA: 3 juveniles (1 juvenile L: 1.2 mounted on SEM stub), collected with holotype, hand collected between and under stones on cave bottom, 14 November 2005, P. Beron, B. Petrov (NMNHS, without registration numbers); 2 juveniles (1 juvenile L: 1.75 mounted on SEM stub, Figs. 30, 35, 47), collected with paratype, hand collected between stones on cave bottom, 10 October 2009, B. Petrov (NMNHS, without registration numbers).

Etymology.—This species is named in honor of Dr Petar Beron (Sofia) in recognition of his extensive contributions to speleology, arachnology, and dedicated for the occasion of his 70th birthday.

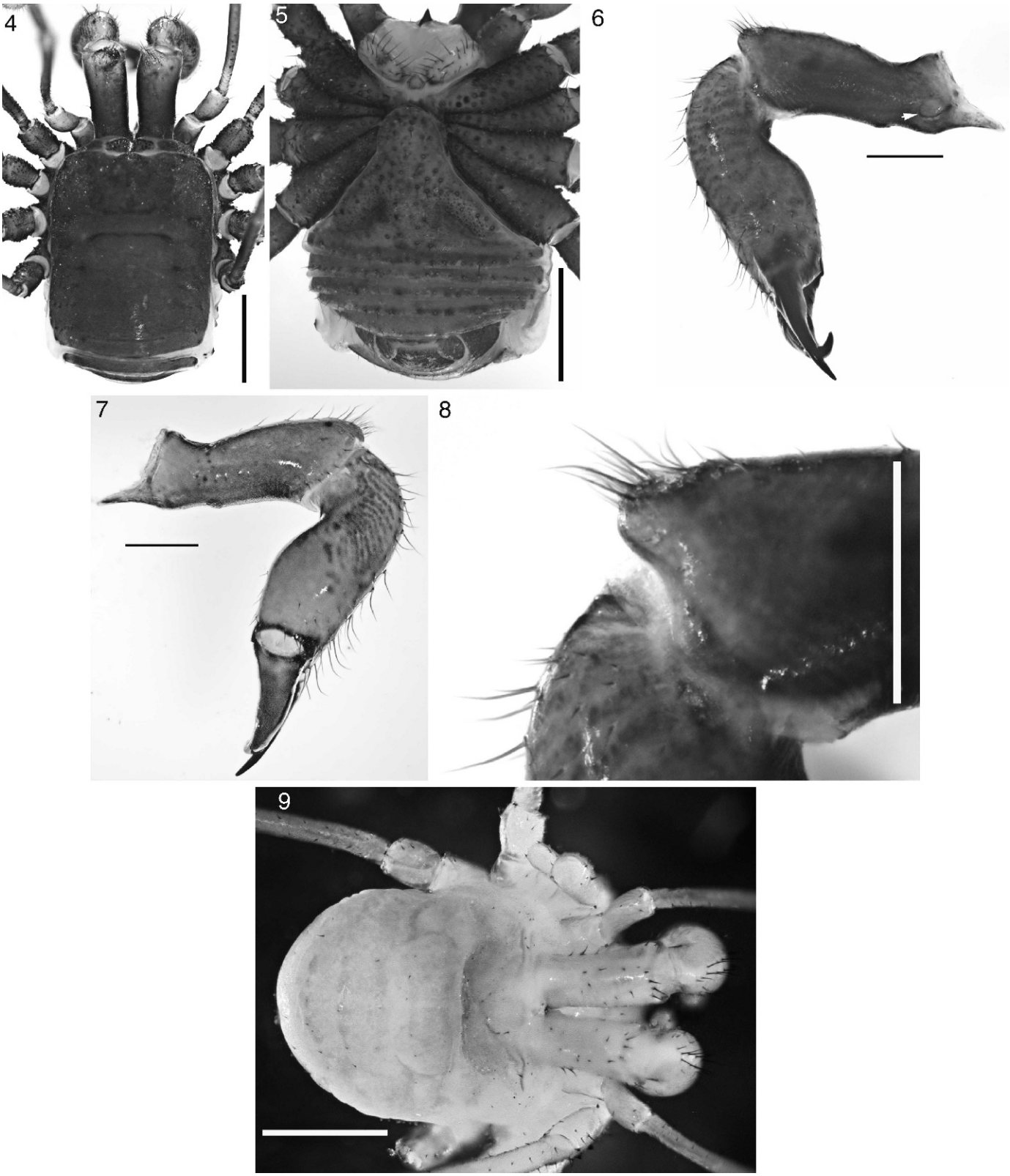
Diagnosis.—An eyeless *Paranemastoma* species with black-brown body, without scutum armament (with two pairs of weakly expressed pustules only visible under SEM) and without golden (silver) spots; integument with fine granulation, body sculpture in the form of sharp granules and conical microdenticles; ocularium reduced; supra-cheliceral lamellae bear rugged granules. Cheliceral basal segment with small ellipsoidal, fissure-like opening of the cheliceral gland, and with a very small cheliceral apophysis. Distinct form of the glans penis.

Description.—*Male holotype* (measurements of paratype in parentheses): Dorsal body (Figs. 3, 4, 11): Total length

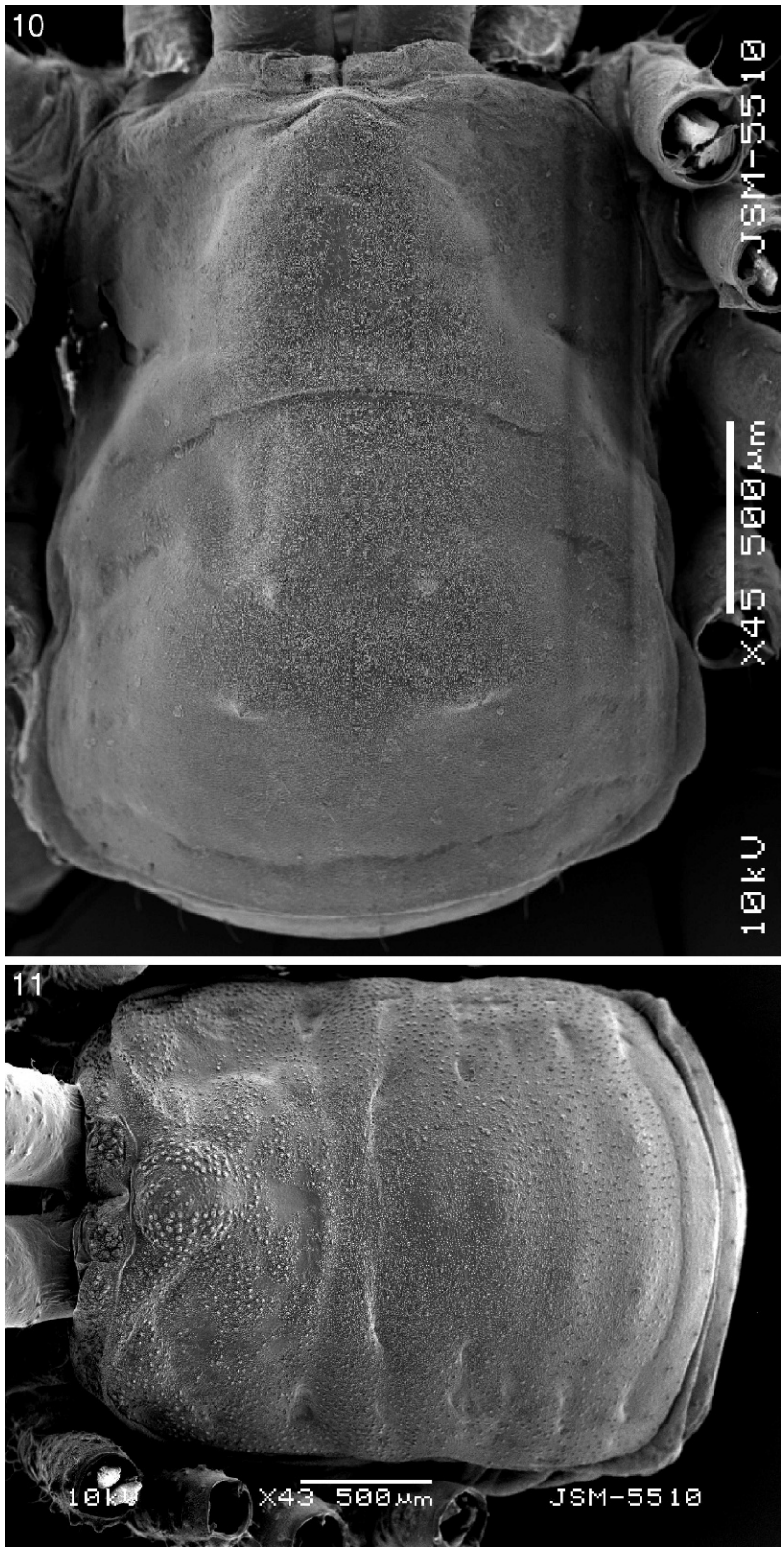




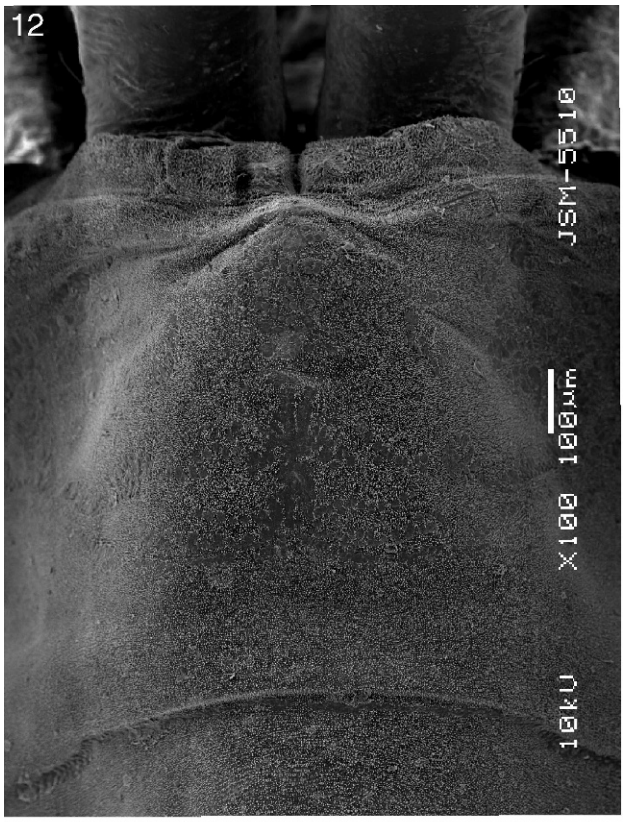
Figures 2, 3.—The type locality of *Paranemastoma beroni* sp. nov.: 2. Map of Stoykova Dupka 1 Cave (vertical section). From cave-map archive of Bulgarian Federation of Speleology, Sofia, with special permission of Mr. Alexey Zhalov, (authors: A. Iliev, R. Petrov & A. Kavaldzhiev, 1990, unpublished). (Black dots indicate the cave zones where the new species has been collected); 3. *P. beroni* sp. nov. (paratype) on the cave wall. (Photo: B. Petrov).

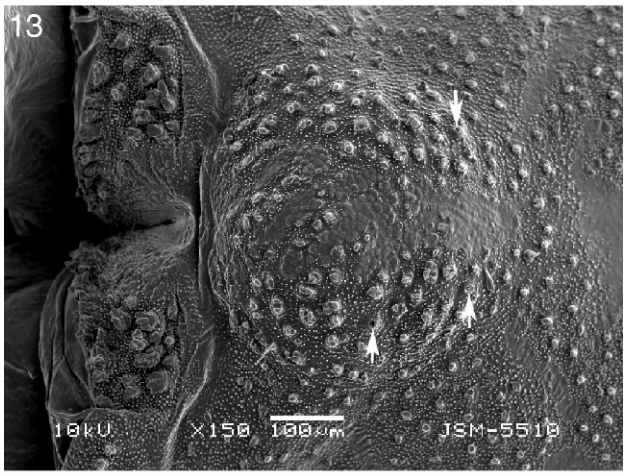


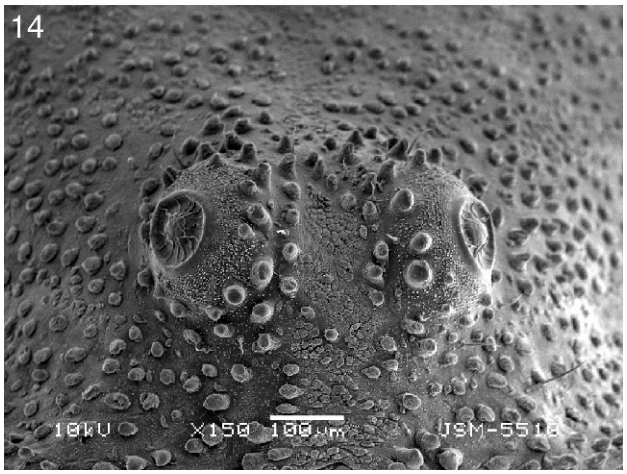
Figures 4–9.—*Paranemastoma beroni* sp. nov.: 4–8. Male holotype: 4. Dorsal view; 5. Ventral view; 6. Right chelicera, medial view (ectobasal knob arrowed); 7. Right chelicera, lateral view; 8. Right chelicera, distal part of basal segment, medial view; 9. Dorsal view, juvenile. Scale lines: 1 mm (4, 5, 9), 0.5 mm (6, 7, 8).



Figures 10, 11.—Males, habitus, SEM: 10. *Paranemastoma bureschi*, with abnormal scutum armament – the third pair of tubercles are missing, dorsal view; 11. *P. beroni* sp. nov., paratype, dorsal view.







2.7 (2.75); Total length, including supracheliceral lamellae, 2.9 (2.9). Prosoma 2.05 (2.05) wide; opisthosoma 2.1 (2.2) wide; scutum magnum length 2.55 (2.55); coloration: dorsal black-brown, prosoma darker than opisthosoma, without golden or silver spots; propeltidium with stronger granulation, consisting of tiny stumps, scutum sculpture in the form of sharp granules and conical microdenticles (Figs. 46, 51); abdominal Areas I and II medially convex; dorsal scutum with 5 rows of setae on edges of abdominal Areas I–V. Scutum armament absent, strongly reduced, with only 2 paramedian pairs of pustules of Area III, IV (only visible under SEM, Figs. 11, 17). Position of pustules marked by slit-sensilla (compare Mitov 1995, p. 157, fig. 9) (Fig. 51). Supra-cheliceral lamellae dark brown and granular, with fairly broadly separated rugged granules (Figs. 4, 11, 13, 38). Ocularium (Figs. 11, 13) reduced and low, without eyes, with three pairs of setae on the lateral and rear slopes, length = 0.45 (0.518), width = 0.56 (0.448) height = 0.126 (0.140). Ventral body dark brown; free sternites with posterior rows of setose tubercles (Fig. 5). Appendage lengths: chelicerae: basal segment 1.85, distal segment 2.40 (2.25), movable digit 1.125 (1.25); palpus: 8.025 (7.871) (trochanter 0.75 (0.75), femur 2.70 (2.65), patella 2.10 (2.05), tibia 1.60 (1.525), tarsus 0.875 (0.896)); leg I: 17.0 (16.90) (trochanter 0.5 (0.5), femur 4.10 (4.15), patella 0.95 (1.0), tibia 2.80 (2.80), metatarsus 5.50 (5.25), tarsus 3.15 (3.20)); leg II: 29.30 (28.71) (trochanter 0.5 (0.5), femur 6.30 (6.20), patella 1.20 (1.20), tibia 4.70 (4.40), metatarsus 11.10 (10.55), tarsus 5.50 (5.60)); leg III: 18.05 (17.75) (trochanter 0.5 (0.5), femur 4.35 (4.30), patella 0.90 (1.00), tibia 2.75 (2.75), metatarsus 6.05 (5.8), tarsus 3.50 (3.40)); leg IV: 23.45 (22.85) (trochanter 0.5 (0.5), femur 6.00 (5.70), patella 1.05 (1.10), tibia 3.35 (3.40), metatarsus 8.05 (7.75), tarsus 4.50 (4.40)); ps I–IV: 3/3 (2/3), 7/6 (7/6), 3/3 (4/4), 6/6 (5/7); mts I–IV: 4/5 (5/5), 11/13 (11/11), 4/5 (4/3), 5/5 (5/4); ts I–IV: 19/21 (21/20), 31/25 (29/29), 20/19 (18/20), 21/19 (19/18). Chelicerae (Figs. 6–8, 17–19): basal segment medial with ectobasal knob (Fig. 6), distal with short, black apophyses (visor like), 0.07 in length (Figs. 8, 18, 19), and with small ellipsoidal, fissure-like opening of cheliceral gland (Fig. 20); basal segment coloration black-brown; distal segment width (frontal) 0.575 (0.60), brown with black-brown spots. Digits black-brown. Pedipalps (Fig. 22) thin: patella and tibia 0.168 (0.154) in diameter; femur and tarsus 0.154 (0.140) in diameter, femur to tarsus covered with clavate setae; trochanter, femur, patella brown, tibia and tarsus yellow-brown; tarsus/tibia = 0.547 (0.587). Legs: femora black-brown; patella and tibia brown; metatarsus and tarsus are light brown (yellow-brown); claw length 0.225. Pseudoarticulations in middle of leg femora; coxae with rows of long setose tubercles (Fig. 5). Penis (Figs. 24–27, 29) typical for *Paranemastoma*, with asymmetric and bilobed glans penis, bearing setae, penial basis with lobes, brown (Fig. 27); penis length 2.17 (2.11); truncus width 0.050 (0.050); glans penis width 0.0475 (0.0425), stylus length 0.045 (0.045),

←

Figures 12–14.—Scanning electron micrographs of male ocularium: 12. *Paranemastoma bureschi*, dorsal view; 13. *P. beroni* sp. nov., paratype, dorsal view, plus part of supra-cheliceral lamellae, (broken setae position arrowed); 14. *P. titaniacum*, dorso-frontal view.

Table 1.—Diagnostic characters between males of *Paranemastoma beroni,* sp. nov. and *Paranemastoma bureschi.*

	Paranemastoma beroni sp. nov.	*Paranemastoma bureschi*
Body	Color: black-brown; max. width: 2.2; without scutum armament (with two paramedian pairs of weakly expressed pustules on abdominal Areas III, IV– only visible under SEM) (Figs. 4, 5, 11)	Color: brown to black; max. width: 1.8; with scutum armament (three (rare two) paramedian pairs of small sharp tubercles on abdominal Areas II, III, IV) (Fig. 10)
Ocularium	Broader and round (Fig. 13)	Ellipsoidal (Fig. 12)
Genital operculum	With pointed apex (Fig. 15)	With rounded apex (Fig. 16)
Supracheliceral lamellae	Granulate (with fairly broadly separated rugged granules) (Figs. 13, 38)	Smooth to weakly granulate (Figs. 32, 39, 40)
Chela	More massive (Figs. 6, 7, 17–19); basal segment: many setae on distal end; with short apophysis and opening of cheliceral gland (Fig. 20).	Slender (Fig. 21); basal segment: only 4 setae on distal end; without apophysis and opening of cheliceral gland.
Palp	More massive (Fig. 22) Patella (2.05–2.10 long) and tarsal segment (0.840–0.896 long) shorter. Tibia almost cylindrical, widest at its distal end. This shape is characteristic for epigean and neotroglobiont species. Tarsal segment almost straight (slightly curved). Ta:Ti = 0.547–0.587	More slender (Fig. 23) Patella (2.3–2.425 long) and tarsal segment (1.125–1.275 long) longer. Tibia spindle-shaped, widest at its proximal end; a typical shape for the old troglobite nemastomatids (compare with *Nemaspela* Šilhavý 1966 in Martens 2006 and Chemeris 2009) and *Mitostoma* Roewer 1951 (Martens 1978; Dunlop & Mitov 2009). Tarsal segment spindly and conspicuously curved. Ta:Ti = 0.75–0.81
Legs	Tibia I–IV without pseudarticulations.	Only Tibia II with pseudarticulations.
Scutum microsculpture	Wide, consisting of sharp granules plus conical microdenticles (Figs. 46, 51)	Dense/thickset, consisting of oval and sharp granules plus microspines and globular microgranules (Fig. 48, 49)
Penis	Apex of the stylus – narrow (pad-shaped) (Figs. 25, 26, 29). Short arm of glans penis equipped with 5 massive setae and one sharp papilla (Figs. 25, 26, 29).	Apex of the stylus – broad (fan-shaped) (Fig. 28 and Staręga 1976:fig. 36). Short arm of glans penis equipped with 10 setae, only (Fig. 28).

stylus base width 0.01375 (0.015); length (height without setae) 0.02 (0.0175) and width 0.0200 (0.0225) of short arm of glans penis; short arm equipped with 5 (5) setae and one sharp papilla (Fig. 26, see arrow); stylus equipped with 2 (4) setae.

Variation: Difficult to estimate upon the small material. The number of leg femoral pseudarticulations and metatarsal and tarsal leg segments appear variable.

Juveniles: The associated juveniles are early instars with a depigmented integument: white to yellow-white, with slight brownish yellow pigmentation on the propeltidium; the caudal borders of areas I–V weakly sclerotized, light yellow-brown in color (Fig. 9). Movable and fixed cheliceral fingers black-brown. Palps and microsculpture similar with these in adults; scutum without strong granulation, see Figs. 30, 35, 47. Measurements: L: 1.2–2.15 mm, body width 0.9–1.7.

Female: Unknown.

Differences from other *Paranemastoma* species.—*Paranemastoma beroni* is easily distinguished from most other species within the genus by the lack of eyes. This character is only shared with *Paranemastoma bureschi*, from which *P. beroni* can be discriminated by the lack of dorsal spines and the presence of a marked cheliceral apophysis and opening of the cheliceral gland in males, lacking in *P. bureschi*. Furthermore, the two species are allopatric. A comprehensive list of discriminating characters of the two morphologically similar species is given in Table 1.

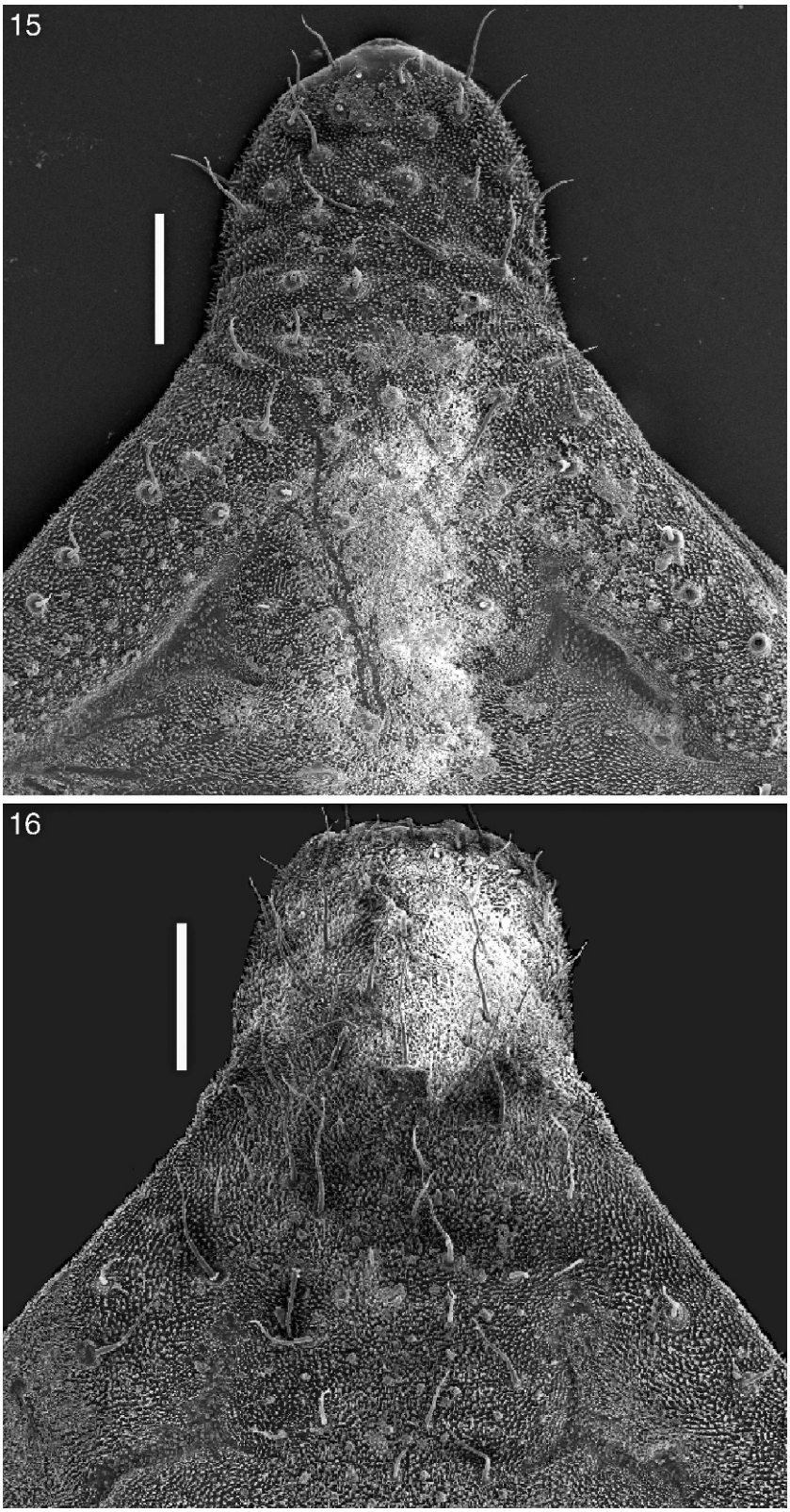
Distribution and habitat.—The type locality of *P. beroni*, cave Stoykova Dupka 1 (Figs. 1, 2), is situated on the northern slope of the Slavyanka (Ali Botush) Mountains, 1150–1160 m elev., in thin *Fagus* forest, mixed with *Carpinus, Cornus* and *Crataegus*. This precipice cave (length 39–40 m, displacement 19–35 m) formed in proterozoan metamorphic limestone and marble (Fig. 2, Nikolov & Yordanova 1997), and has its bottom covered with soil and piled stones. The temperature at the bottom of the cave lies between 4.0° and 7.0° C (4.5° C, 18 May 2004; 6.0° C, 14 November 2005; 7.0° C, 10 October 2009; all data of B. Petrov, pers. comm.).

The new species is currently known only from the type locality, where it was found at the bottom of the cave gallery walls and between stones on the ground of the cave (Figs. 2, 3).

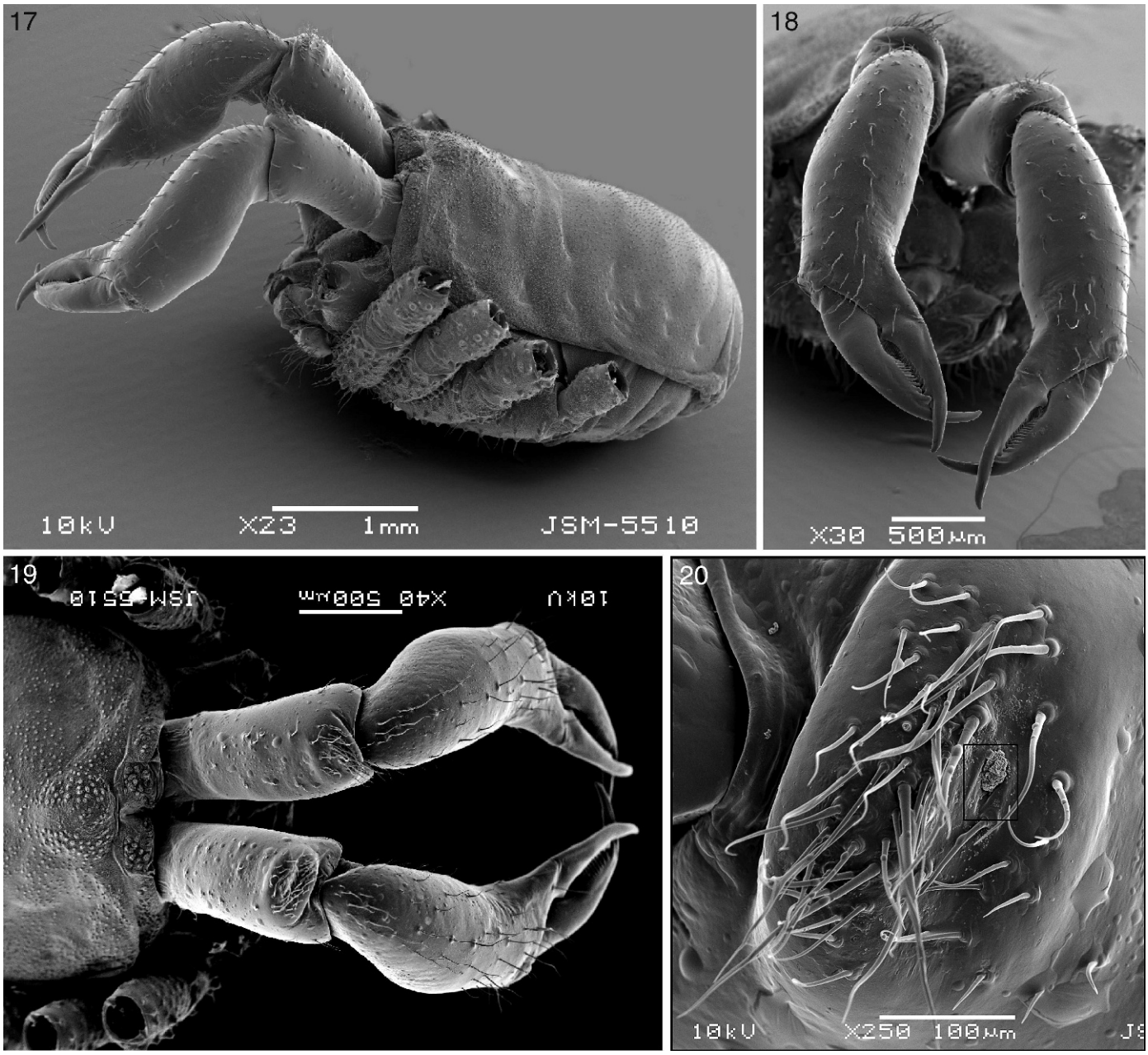
DISCUSSION

Relationships within *Paranemastoma*.—The penis type (Figs. 24–27, 29) of the new species clearly indicates that the latter is a member of genus *Paranemastoma*. The distal part of the penis is similar to that of *P. bicuspidatum* (C.L. Koch 1835), especially in the pad-shaped stylus end and setation (compare Fig. 25 with fig. 163 in Martens 1978).

On the one hand, the new species shows affinities to the only known troglobiont species – *P. bureschi* - in a number of characters, including the reduced ocularuim without eyes, lack of golden (silver) spots, scutum sculpture (consisting predominantly of long and pointed elements), a similar habitus and elongated appendages. All of the characters listed here, however, can be interpreted as modifications to cave life (see also Curtis & Machado 2007), rather than having a systematic value. These may represent convergences and could not serve



Figures 15, 16.—Male genital operculum, SEM: 15. *Paranemastoma beroni* sp. nov., paratype; 16. *P. bureschi*. Scale lines: 200 μm, × 60.



Figures 17–20.—*Paranemastoma beroni* sp. nov., paratype male, SEM: 17. Body and chelicerae, lateral view, palps and legs removed; 18. Chelicerae, frontal view; 19. Chelicerae, dorsal view; 20. Cheliceral apophysis with cheliceral gland opening (black frame); the drop-like structures on the cheliceral tegument are artifacts.

as delineating characters. On the other hand (and in contrast to *P. bureschi*) the new species is not so extremely troglomorphic, because it is more similar to the epigean and neotroglobiont members of the genus *Paranemastoma* (c.f. Staręga 1976; Martens 1978, 2006) due to its stronger chelicerae with apophyses (although short), the opening of the cheliceral gland, round ocularium, and granulate suprachelicerал lamellae, stronger granulation (consisting of tiny stumps, similar to *P. titaniacum* - Figs. 14, 37, 41), on the propeltidium and the abdominal part of the scutum, as well as the shape of the palpal tibial and tarsal segment.

It is noteworthy that the lack or the strong reduction of the golden (silver) spots and the scutum armament (reduction of the number and height of spines) are not only typical for the species restricted to caves (*P. bureschi, P. beroni, P. titaniacum*). This phenomenon can also be observed in epigean species adapted to living in the high mountains, most possibly as a response to the higher UV radiation in combination with lower temperatures; e.g., *P. bicuspidatum* (C.L. Koch 1835), *P. mackenseni* (Roewer 1923), *P. aurigerum ryla* (Roewer 1951). It is possible that the scutum spots, in combination with the black body color of the *Paranemastoma* and other nemastomatid species, facilitate heat

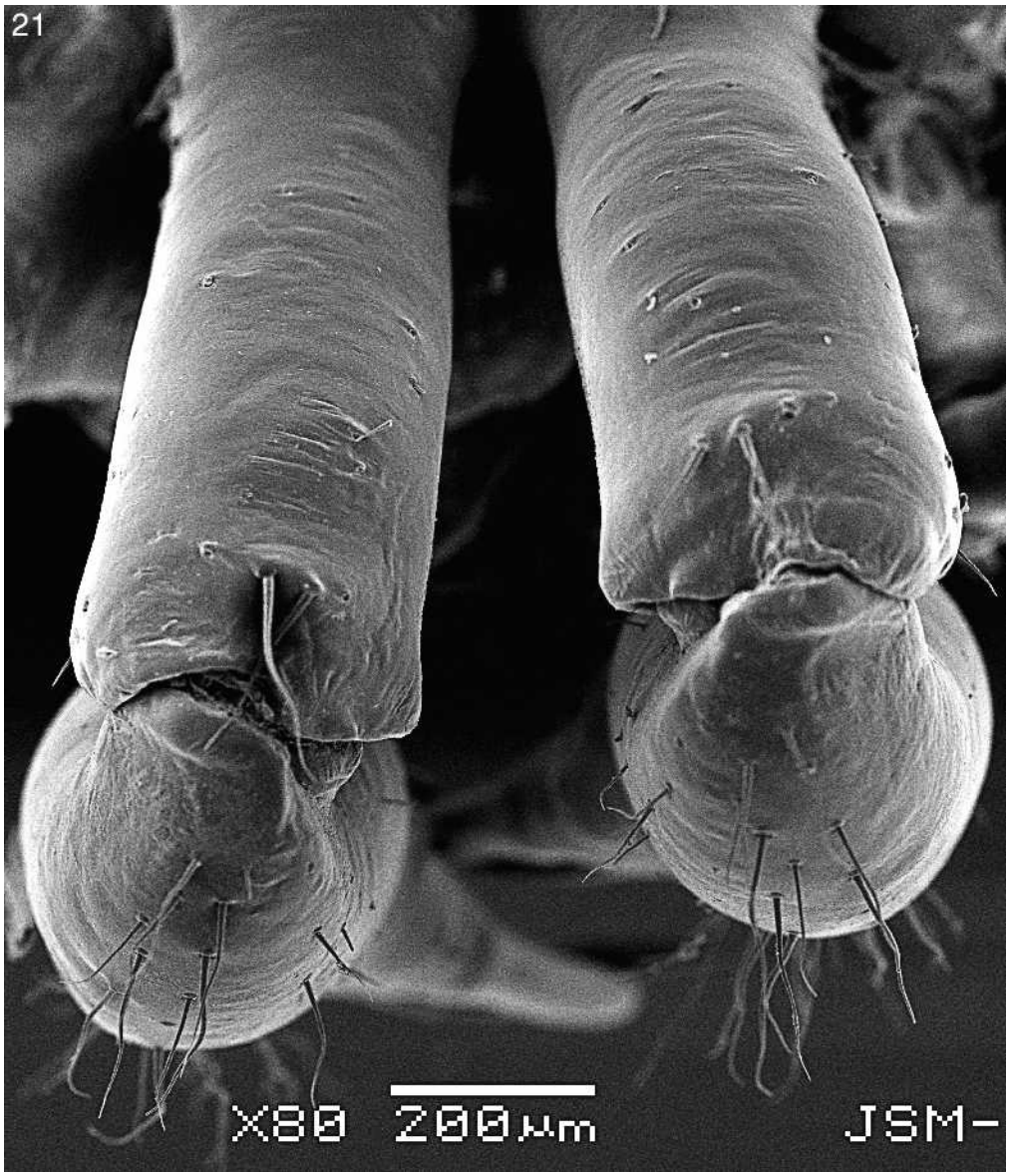
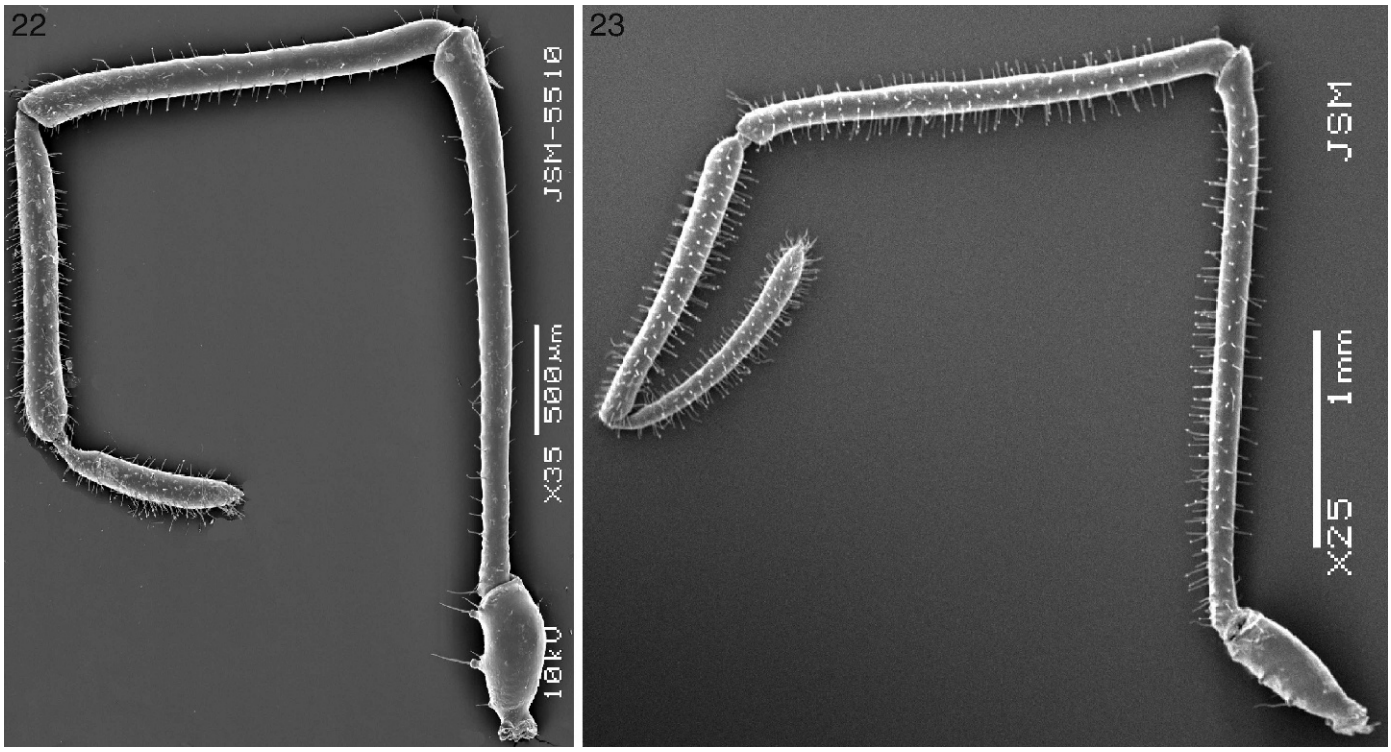


Figure 21.—*Paranemastoma bureschi*, male chelicerae, dorsal view, SEM.

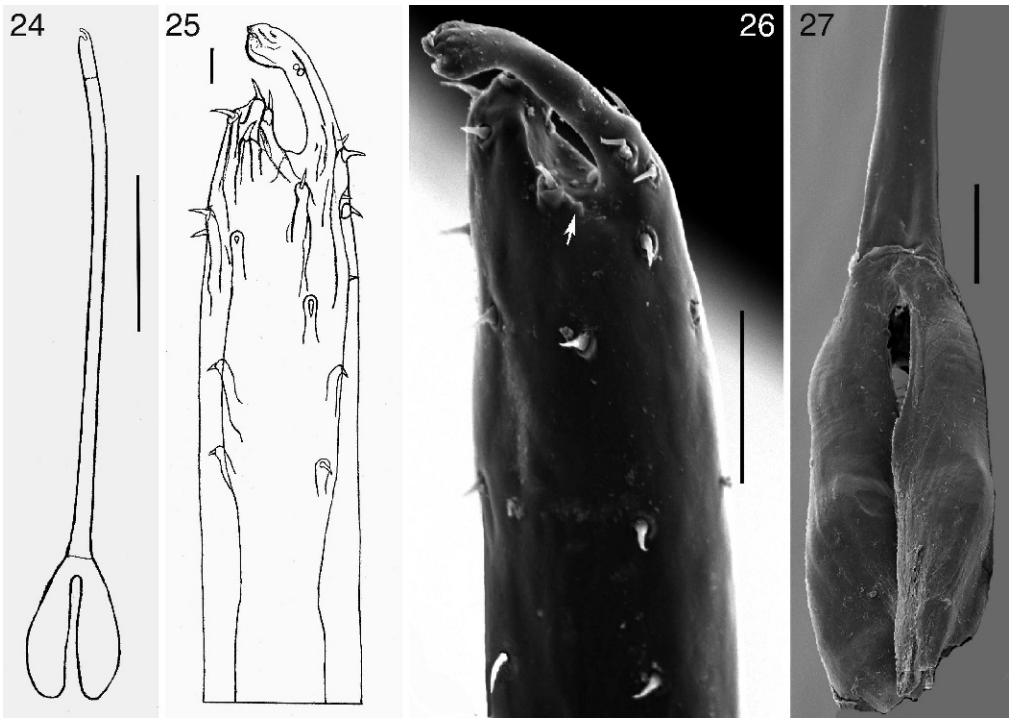
accumulation, and their development might be directly connected to the light intensity.

Comparative sculpture morphology.—The sculpture of adults and juveniles of the following Balkan *Paranemastoma* species was compared using SEM: 1) *P. radewi*, the most common surface and troglophile species in Bulgaria (Staręga 1976; Beron & Mitov 1996), 2) *P. titaniacum*, a neotroglobite and a species with lesser degrees of troglomorphism - a pigmented harvestman with reduced cornea and one pair of spines on the scutum and without golden (silver) spots known from caves in Montenegro, Bosnia, Herzegovina and Albania (Roewer 1914; Karaman 1995a; Mitov 2000) - and 3) the old troglobionts *P. bureschi* and *P. beroni*.

The comparison showed that the sculpture of adult *P. bureschi* and *P. beroni* consists of sharp and oval granules, conical microdenticles, globular microgranules and microspines (Figs. 46, 48, 49, 51), and thus clearly differs from that of other *Paranemastoma* species, in which it is mushroom-shaped or forms tiny stumps (Figs. 41, 43) (c.f. Eisenbeis & Wichard 1987, Plate 18 c, d, f; Mitov 1995, fig. 9). The comparison also showed a clear similarity in the microsculpture among the juveniles (Figs. 33–36, 42, 45, 47, 50) and the old troglobiont species – a phenomenon possibly related to the need for a hydrophobic type of surface and easier removal of clay particles, the cuticle being thin and soft (Figs. 30–32, 46–51). Such a sculpture most probably helps to prevent the animal from getting wet, as individuals shelter in narrow fissures (under stones, in deep accumulations of rotten plant material) in a very humid and dark environment, where possibilities for locomotion are strongly limited and the danger of inundation exists. A similar type of sculpture elements can be seen in *Ischyropsalis* spp. (Šilhavý 1956, figs.



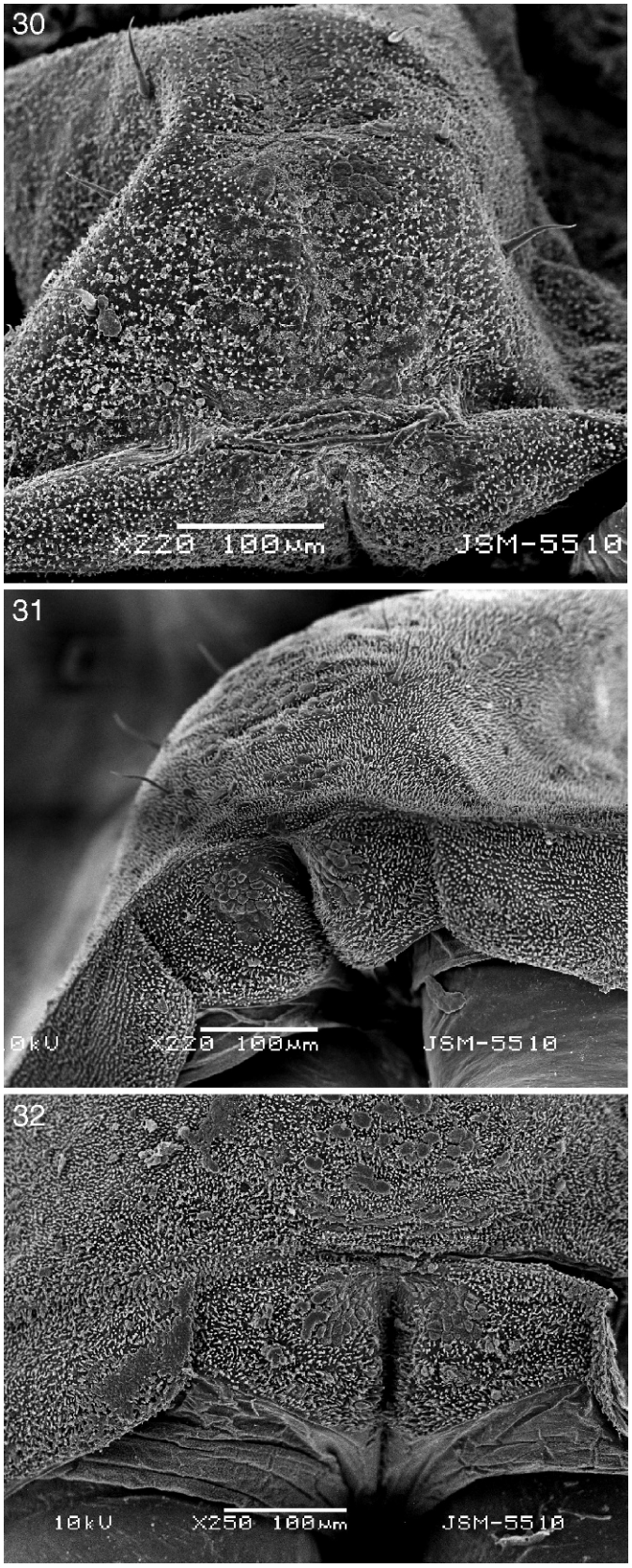
Figures 22, 23.—Pedipalps, SEM: 22. *Paranemastoma beroni* sp. nov., paratype male, left pedipalp, lateral view; 23. *P. bureschi*, male, right pedipalp, medial view.



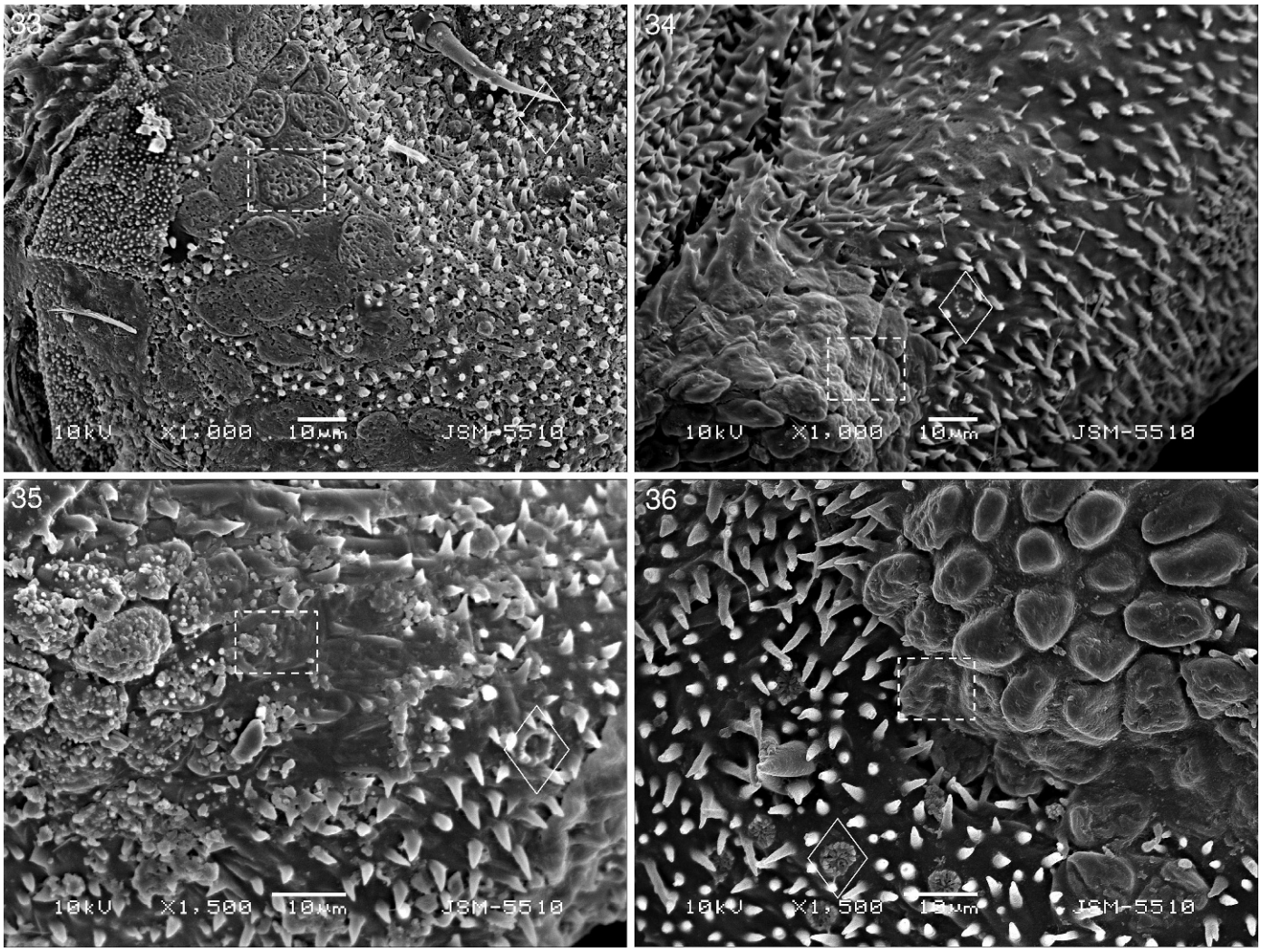
Figures 24–27.—*Paranemastoma beroni* sp. nov., male genitalia: 24. Penis, holotype, ventral view; 25. Penis, distal end, holotype, ventral view; 26. Penis, distal end, paratype, ventral view, SEM (arrow show the sharp papilla); 27. Penis, basal part, paratype, ventral view, SEM. Scale lines: 0.5 mm (24), 0.01 mm (25), 0.02 mm (26), 0.1 mm (27).

Figures 28, 29.—Male genitalia, SEM: 28. *Paranemastoma bureschi,* penis, distal end, dorsal view; 29. *P. beroni* sp. nov., paratype, penis, distal end, dorsal view. Scale lines = 0.02 mm.

3, 8), which also prefers permanently humid environments. Adis & Messner (1991), Adis et al. (1999), Hebets & Chapman (2000), and literature therein, discuss the hydrophobic type of cuticle in invertebrates. Most probably, an important role for the development of such a sculpture (microsculpture) type in the environments inhabited by juvenile *Paranemastoma* and the troglobiont species is the lack of factors selecting for ''normal'' non-troglobiont adult habit (strongly sclerotized integument). For example, adults of epigean *Paranemastoma* occur in resource rich environments under the influence of diverse abiotic factors where they are much more accessible to predators (c.f. Cokendolpher & Mitov 2007), and where there are conditions for a much higher locomotor activity mainly connected to reproduction (Mitov 1996). Also, it seems that in troglobiont members of the genus *Paranemastoma*, this type of microsculpture, characteristic of juvenile *Paranemastoma*, is retained in the adults, which also maintain a relatively thin cuticle (Figs. 30–32, 35, 36, 38–40, 46–51). This case of cuticular ''softening'' (juvenification) is perhaps related to specialization to subterranean habitats and a subterranean way of life (Curtis & Machado 2007) and could be defined as cuticular neoteny (pedomorphosis) in troglobiont *Paranemastoma* species. This simplification of the cuticle in troglobionts, driven by neotenic factors, probably facilitates their adaptation to subterranean habitats, protects the species against



Figures 30–32.—Frontal body part, detail, reduced ocularium and supra-cheliceral lamellae, sculpture, SEM: 30. *Paranemastoma beroni* sp. nov., juvenile; 31. *P. bureschi*, juvenile; 32. *P. bureschi,* male.



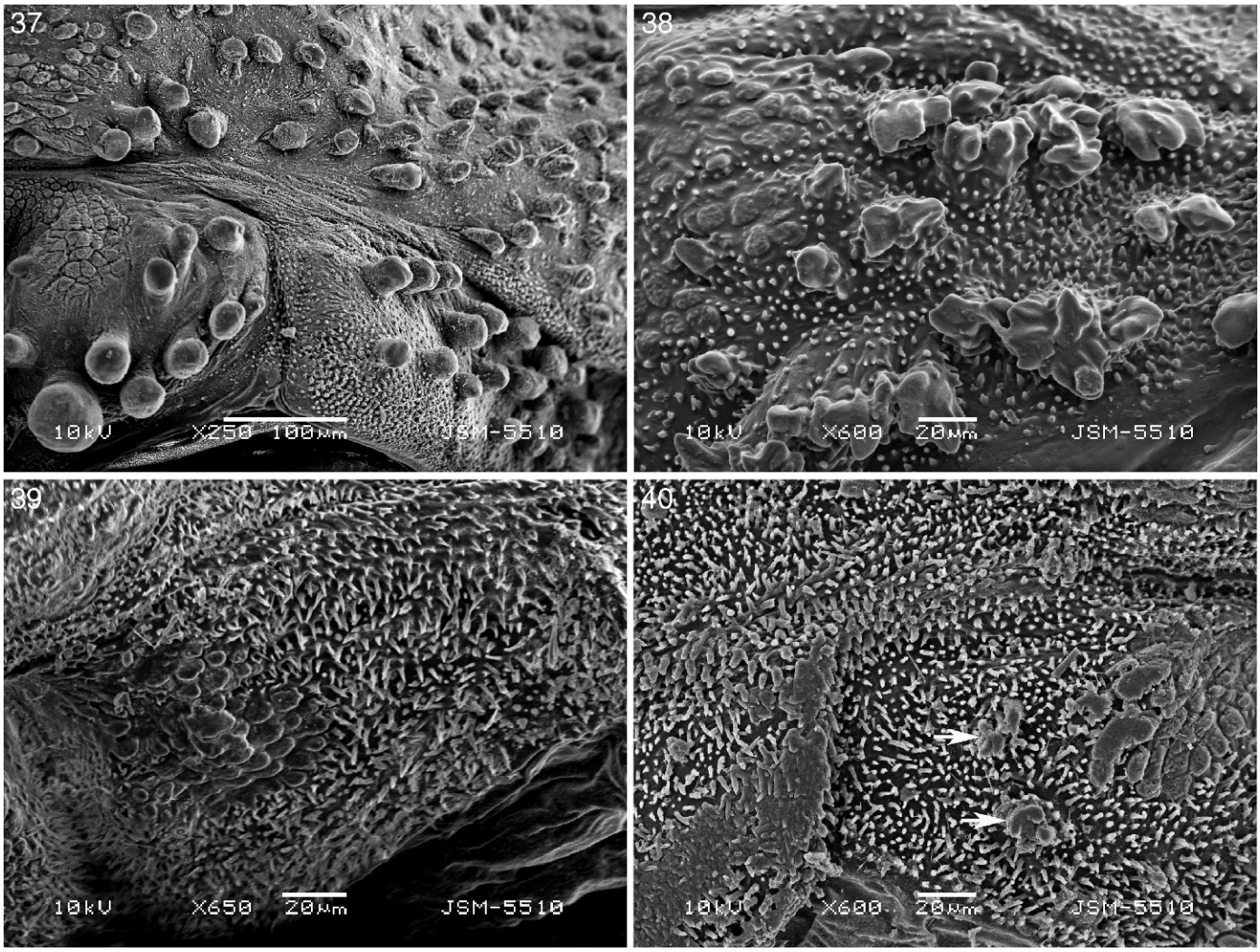
Figures 33–36.—*Paranemastoma* juveniles; supra-cheliceral lamellae, microsculpture, SEM: 33. *Paranemastoma radewi*; 34. *P. titaniacum*; 35. *P. beroni* sp. nov.; 36. *P. bureschi.* Diamond indicates glandular openings; dashed frame indicates glandular pore plates/fields.

over-specialisation and enhances the evolutionary plasticity of the group (see also Rambla 1980; Shear 1974, 1996).

By contrast, in the epigean and neotroglobiont species of the genus *Paranemastoma,* the adult cuticle is differently armed, presumably yielding additional cuticle strength and durability (Figs. 14, 37, 41, 43). Furthermore, the cuticular sculpture in epigean species is very similar (Eisenbeis & Wichard 1987; Mitov 1995, pers. obs. on *P. aurigerum* ssp. sculpture), and because of this it could not serve as a delineating character. One possible morphological adaptation to the troglobiont way of life of these species may thus be the type of sculpture elements, and in particular their transition in adults from mushroom-shaped structures (in surface and troglophile species) and stumps (in neotroglobites) to cone-like structures and ultimately to granule- and spine-like structures (in old troglobites) (Figs. 41, 43, 46, 48, 49, 51).

In summary, it can be noted that the thickness and sculpture of the cuticle among different stages in the different species of *Paranemastoma* is probably an adaptive feature. The sculpture type in *Paranemastoma* (and possibly in other opilionid groups) can be used only as a measure of troglomorphism and can be added to the list of cave adaptations.

Zoogeographical remarks.—The predecessors of *Paranemastoma* species were probably widely distributed throughout north Egeida during the Tertiary. Inundations, mountain uplifts and aridification during the late Tertiary, as well as glaciations and the following xerophytization might have caused the isolation of populations and subsequent speciation within this hygrophilic taxon. Similar to other members of the genus; e.g., *P. bicuspidatum*, *P. aurigerum ryla*, *P. kalischevskyi* (Roewer 1951), *P. titaniacum*; *P. beroni* possesses typical features of mountaneous forms such as reduction of spots and armament on the scutum, psychrophilicity and a frigostable, mountain distribution. It probably originated in the mountains at the end of the Tertiary (Pliocene-Pleistocene), when uplifts were a significant occurrence (Mandov 1986) (after Gruev 1990). Gruev (1988) argued that the troglobiont *P. bureschi* is probably a Tertiary relict. The species' predecessor, as well as that of *P. beroni*, might have entered the caves between the Pliocene and the Quaternary, when the climate



Figures 37–40.—Supra-cheliceral lamellae, sculpture, males, SEM: 37. *Paranemastoma titaniacum*; 38. *P. beroni* sp. nov., paratype; 39. *P. bureschi* (''smooth'' type); 40. *P. bureschi* (granulate type, granules arrowed).

became cooler and drier and when many other forms are thought to have entered caves in the Balkan Peninsula (Guéorguiev 1977). It is possible that the adaptation to subterranean way of life in these two tertiary relicts has taken place with a different pace and duration. This is supported by the fact that the reduction of all characters in *P. bureschi* is more advanced, and that the western Stara Planina (Balkan Range) cave system it inhabits features an old troglobiontic fauna including the laniatorids *Paralola buresi* Kratochvíl 1951 and *Trojanella serbica* Karaman 2005. It is quite possible that the predecessor of *P. bureschi* was relatively more thermophilous and entered the caves sooner than the predecessor of *P. beroni*, with the first signs of climate drying and cooling. In the latter species, features such as the cheliceral gland, which can be reduced in cave taxa of Nemastomatidae (see Martens 2006), are still present, and the ocularium is not completely reduced. Therefore it is suggested that *P. bureschi* is an older troglobite than *P. beroni*.

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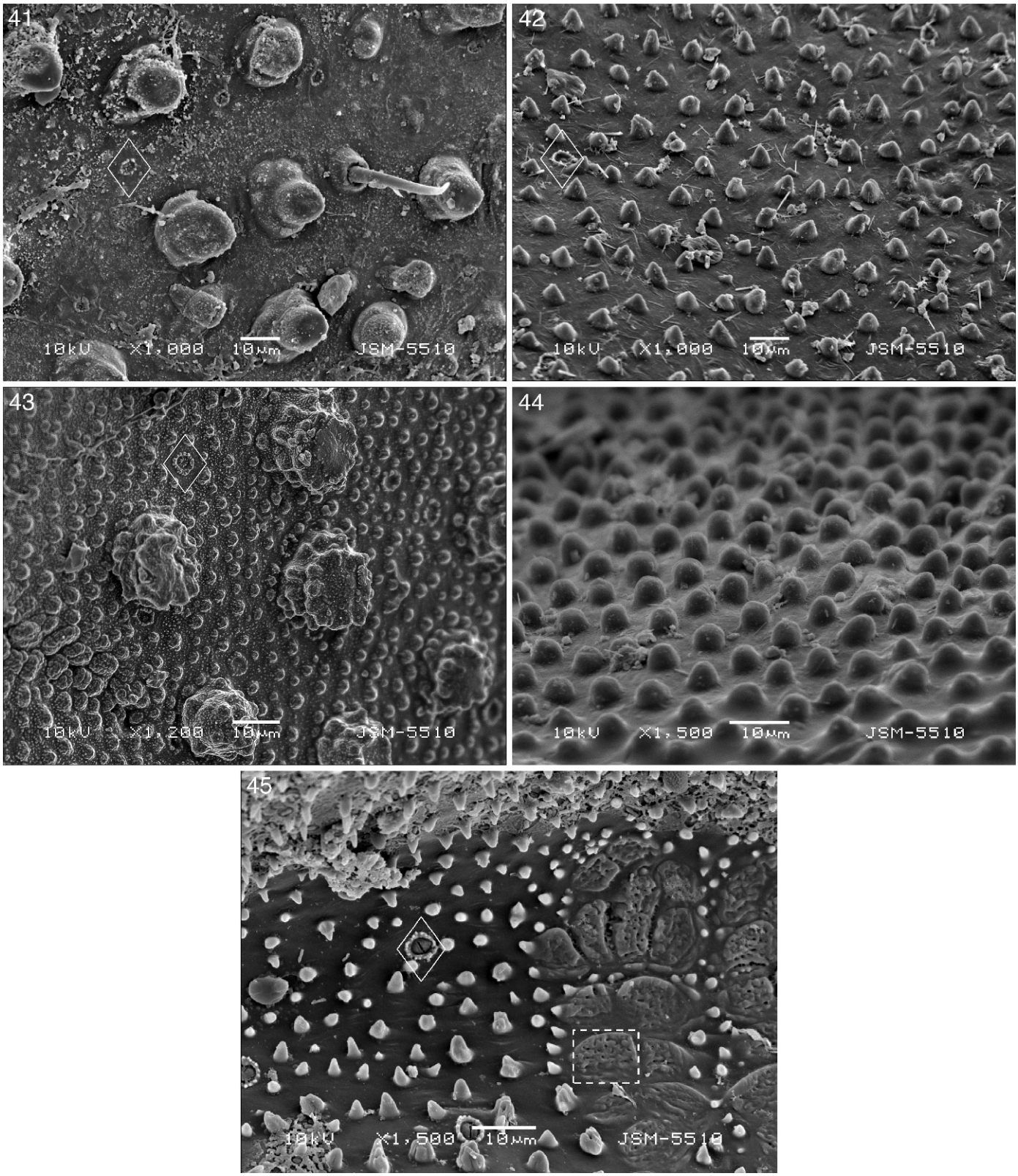
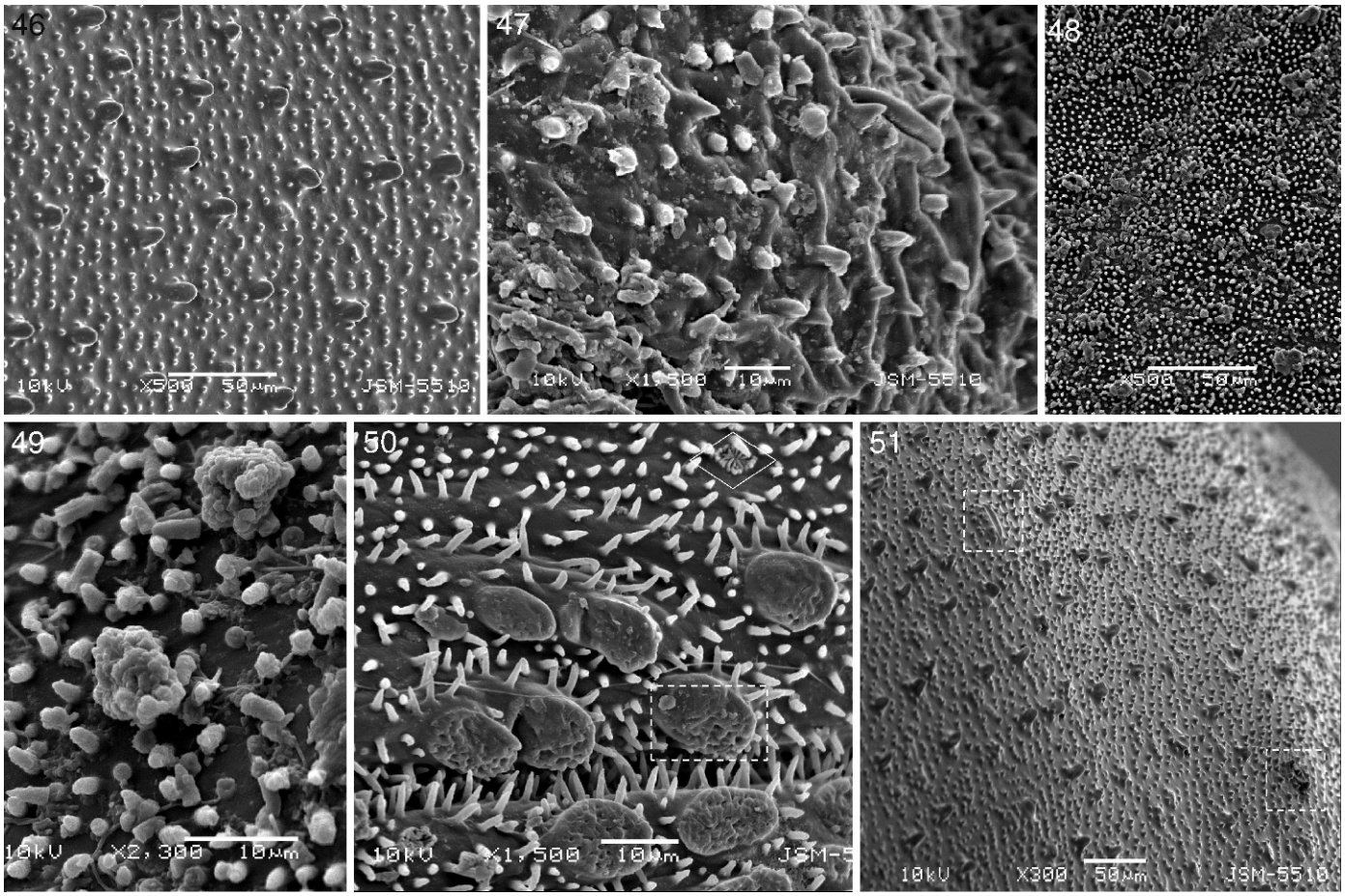


Figures 41–45.—Scutum sculpture: 41. *Paranemastoma titaniacum*, male, Area I; 42. *P. titaniacum*, juvenile, Area I; 43. *P. radewi*, female, Area I; 44. *P. radewi*, juvenile, Area I; 45. *P. radewi*, juvenile, behind ocularium, plus rear slope of ocularium. Diamond indicates glandular opening; dashed frame indicates glandular pore plate.



Figures 46–51.—Scutum microsculpture: 46. *Paranemastoma beroni* sp. nov., paratype male, Area III–IV; 47. *P. beroni* sp. nov., juvenile, Area I–II; 48. *P. bureschi,* male, Area III–IV; 49. Same, magnified; 50. *P. bureschi,* juvenile, plus part of ocularium (= the area with glandular pore plates) (diamond indicates glandular opening; dashed frame indicates glandular pore plate); 51. *P. beroni* sp. nov., paratype male, Area III-IV, left side (dashed frame indicates slit-sensilla).

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