Linzer biol. Beitr.	28/2	953-966	31.12.1996

Morphological characters of *Ceramius palaestinensis* (GIORDANI SOIKA 1957) GUSENLEITNER 1992 (Hymenoptera, Vespidae, Masarinae) and considerations about its phylogenetic position

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Abstract: Morphological characters of the exoskeleton and the male genitalia of *Ceramius palaestinensis* are described and figured. Morphometric data of the exoskeleton are presented. All known distribution records are summarized. *C. palaestinensis* is a member of species group 7 of *Ceramius*, but possesses a number of autapomorphies especially in the male genitalia. Within species group 7 *C. palaestinensis* is probably closely related to *C. hispanicus* and the *C. spiricornis*-complex. *C. palaestinensis* seems to be restricted to the Middle East, whereas the remaining members of group 7 occur in the West Mediterranean region.

Key words: male genitalia, morphology, Masarinae, pollen wasps, Ceramius, phylogeny, biogeography

Introduction

Ceramius palaestinensis was described from a single female from Israel by GIORDANI SOIKA (1957). He regarded the species as a close relative of *Ceramius lusitanicus* KLUG and placed it within the genus *Paraceramius* SAUSSURE. RICHARDS (1962: 83) preferred to retain all species of *Ceramius* LATREILLE in one genus which he divided into 8 species groups. By excluding all afrotropical species he subjectively synonymized *Paraceramius* SAUSSURE with his species group 7. But inasmuch as he had not seen the type, RICHARDS (1962: 118) was not able to place *C. palaestinensis* into any species group with certainty. In 1971 the male was formally described by BYTINSKY-SALZ (BYTINSKY-SALZ & GUSENLEITNER 1971), but the sketchy description did not give any reasons for placing it into *Paraceramius* and not even for regarding it as the male of *C. palaestinensis*. The author mentioned that RICHARDS supposed *C. palaestinensis* to be more closely related to *C. hispanicus* DUSMET than to *C. lusitanicus*, after he had examined the specimen, again without giving any reasons for this suggestion. GUSENLEITNER (1992) published the finding of a *Ceramius* male from Turkey which he supposed erroneously to be the first record of a male of *C. palaestinensis* and noted that it has spirally rolled antennae. The

form of the antennae may indicate that *C. palaestinensis* is a member of group 7, but spirally rolled male antennae are also present in the ground pattern of the afrotropical species groups 5 and 8. Therefore this character may be plesiomorphic within species group 7 and cannot be used as a criterion for membership of the group. However, the clarification of the phylogenetic position of *C. palaestinensis* is the indispensable prerequisite for a discussion of its biogeographical significance, considering that it is remarkably geographically isolated from its potential relatives which are restricted to the West Mediterranean region. In the following, morphological characters of *Ceramius palaestinensis* are described and figured. The few distribution records are summarized in order to discuss the phylogenetic position of the species and its significance for the biogeography of the group.

Material and methods

Dry specimens were investigated under a stereo microscope (WILD M3, maximum magnification 80 times). Drawings were made with a drawing tube (camera lucida). Measurements were carried out with a calibrated ocular micrometer; distances were measured at the highest possible magnification and converted into mm. Mouthparts and male genitalia were removed after resoftening the specimens in a wet chamber and studied in 70 % ethanol. Photographs were taken with a WILD M420 macroscope.

Distribution

At present five specimens of *Ceramius palaestinensis* are known from four localities in the Middle East, the data of which are listed below:

T u r k e y : Karadag, 1♂, 25.9.1988, leg. C. Özbay (Diyarbakir); Coll. Gusenleitner; data base Mauss (dbM) No. 344 (fig. 1b)

S y r i a : Qual' at al Hisn, 55 km east of Tartus; 34°46' N 36°18' E, ca. 1000m above sea level, 1♀, 30.4.1995, leg. K. Denes jun.; Coll. Biologiezentrum Linz; dbM No. 350; (according to K.†DENES (by letter 1996) the original label on which is written "Syria: Cr. des Chevalier, 30.5.95, leg. K. Denes jun." is wrong) (fig. 1a)

I s r a e l : Ein Geb (= Ein Gev, Kibbutz on east side of Lake Tiberias; ISHAY by letter 1996), 32°47' N 35°38' E, 210 m below sea level, 2♀♀ (holotype/paratype), 5.4.1942, leg. Bytinski-Salz; holotype Coll. Giordani Soika (GIORDANI SOIKA 1957); dbM No. 351; paratype Coll. Tel Aviv University (ex coll. Bytinski-Salz); dbM No. 456

I s r a e l : Hasbani river near Qirjat Shemone (river properly named Nahal Senir, FREIDBERG by letter 1996) 33°13' N 35°36' E, 1♂ (allotype), 28.04.1947, leg. Bytinski-Salz; Coll. Tel Aviv University (ex coll. Bytinski-Salz); dbM No. 352

Morphological characters

Both sexes: The vertex bears a moderately deep, shining depression on each side of the lateral ocelli (figs. 1c, 1d) which is more pronounced in the females. The area between the depression and the lateral ocellus is nearly glabrous. Depressions themselves with close macropunctation. The postocular carina (sensu CARPENTER 1988) extends along the ventral quarter of the eye, the preoccipital carina is absent. Mandibles with three apical teeth. The labial palpi consist of 4 segments (fig. 3b), as well as the weakly developed maxillary palpi (fig. 3a). Fore tarsi and inside of fore tibiae covered with stiff hairs forming a pollen-brush which is less developed in the males. The mid tibiae have a single medial spur at the distal end. The claws bear a tooth in the middle of their ventral surface. The ventral angle of the pronotum below runs smoothly into the mesepisternum (fig. 2a; cf. Richards 1962: fig. 118), i.e. it is not produced into a rounded lobe. The pronotal lobe is well set off towards the front by a furrow. Its carina is acute in the middle. The ventral mesepisternum is moderately punctured with very shiny interstices. Parapsidal furrows and median notal suture are present, the prescutal sutures are poorly developed. The scutellum has a trapeziform, slightly convex dorsal area that falls away almost perpendicularly at the lateral and posterior edges (figs. 2b, 2c). In addition this dorsal area is raised a bit along the median axis, especially in the anterior half, where a weak longitudinal keel is formed. The scutellum exceeds the metathorax at the posterior end. The anal lobe of the hindwing is poorly developed.

Males: The antennae are long and spirally rolled (figs. 1b, 3d). A3 is dorso-ventrally flattened, especially in the proximal half. A10 and A11 are exceptionally slender compared to other species of *Ceramius* (fig. 3c). A10 has a ring-like constriction in the middle which is dorsally stronger than ventrally. Posteriorly A12 has a mainly flat central area that suddenly falls away to the sides so that a weak edge is formed. The fore trochanter is not produced into a lobe. The fore femur is strongly swollen (fig. 2d), dorsally it is widened broadly, ventrally it is narrowed into a keel-like longitudinal margin. The tarsomeres are concave on the underside, but not as strongly flattened as in members of group 8. The sternites do not have any ventral prominences. Abdominal-sternites 3 and 4 are slightly depressed in the centre. Sternite 8 is deeply emarginate posteriorly. Sternite 9 has a well set off semi-ellipsoid depression between its posterior-lateral angles (fig. 2e).

Genitalia as in figs. 4 and 5; the nomenclature of genital-morphology follows BIRKET-SMITH (1981). The aedoeagus bends ventrad distally. At the end it is broadly flattened, and the thyrso are restricted to the ventral side. The dorsal wall of the aedoeagus is formed by a weakly sclerotized membrane the edges of which interconnect the thyrso, whereas they are separated from each other on the ventral side, leaving the endophallus exposed. The thyrso are studded with short basad directed barbs arranged in irregular transverse rows. The spine-like ergot are long. Distally they curve over towards the base of the genital. The distal end of each harpide is ho-

rizontally orientated with a convex dorsal and a concave ventral side and lateral margins running parallel. Farther proximally it comes to a turn resulting in the inner edge of the harpide being directed dorso-medially, whereas the outer edge is directed ventro-laterally. Dorsally the harpides change into the stipites without any visible boundary, ventro-medially they are separated by a weakly sclerotized membrane. This membrane is enlarged and interconnects medially with the volsella. On the ventral side each stipes is united over its distal half with a large rectangular concave ventral plate which medially adjoins the corresponding plate of the other side. The foramen genitale is located basal from these ventral plates. The mainly ventral orientation of the opening and its far distal extension are noteworthy. It is nearly completely encircled by the cupula, with the exception of its dorso-anterior curve. Each volsella consist of two sclerotized parts. Firstly a medio-ventral sclerite which tapers towards the distal end (possibly homologue to the cuspis). It is completely interconnected with the weakly sclerotized membrane originating from the stipes as mentioned above. At the base this sclerite is attached to the medio-dorsad orientated second part of the volsella which forms a short conical protuberance. This is probably the digitus.

Measurements

The morphometric findings are listed in Tab.1.

Discussion

The male and female specimens studied share two convincing autapomorphies, indicating that they really belong to the same species, as was already assumed by BYTINSKY-SALZ & GUSENLEITNER 1971 and GUSENLEITNER 1992. These are the existence of a shining depression on each side of the lateral ocelli and the form of the scutellum, which exceeds the metathorax. Further autapomorphies of *C. palaestinensis* are restricted to the males, like the very slenderly built segments A10 and A11 of the antennae, the ring-like constriction of A10 and the particularly strongly swollen fore femur. The male genitalia are outstanding as well: An aedoeagus with a broadly flattened end and horizontally orientated thyrso that are restricted to its ventral side has not been described for any other *Ceramius* species (cf. GESS 1965, 1968, RICHARDS 1962, 1963). Furthermore the aedoeagus bends ventrad distally and the ergots are remarkably long. The mainly ventral orientation of the foramen genitale and its large distal extension is not known from other *Ceramius* species. Interestingly enough the specimen from Turkey was captured towards the end of September, whereas all others were collected in spring. Since no morphological distinctions were recognized between the male specimens, this phenology may be due to differences in

latitude or may indicate the existence of a second generation, but more records are necessary to provide a convincing explanation of the phenomenon.

Two characters imply that species group 7 is a monophylum (sensu AX 1984). The first potential autapomorphy is the absence of a distal process of the fore trochanter. Such a process is present in all other *Ceramius* species and also in various members of the earlier diverged Paragiina BRADLEY (cf. CARPENTER 1993, cf. RICHARDS 1962, cf. GESS 1995). This indicates that it belongs to the ground pattern of Masarini and *Ceramius* as well and was reduced in the stem-group of species group 7. The second character which is possibly autapomorphic is the small anal lobe of the hind wing. A well developed anal lobe is considered to be plesiomorphic within the Vespidae (RICHARDS 1962: 19, CARPENTER 1982). In *Ceramius* an anal lobe of moderate size occurs at least in the vast majority of the members of the remaining species groups. Therefore the size of the anal lobe probably decreased in the stem-group of group 7 and this reduction can be postulated to be an autapomorphic character of its ground pattern. Since *C. palaestinensis* shows both apomorphies it must be hypothesized to be a member of species-group 7.

Within species-group 7 the *C. lusitanicus*-complex (including *C. lusitanicus*, *C. tuberculifer* SAUSSURE, *C. vechti* RICHARDS, *C. bischoffi* RICHARDS) constitutes a monophylum (cf. RICHARDS 1962: 84, 1963) which is verified by a distinct apomorphy: The ventral angle of the pronotum is produced into a rounded lobe projecting in front of the mesepisternum (RICHARDS 1962: fig. 119). A similar situation does not occur in any other taxon of the Masarinae and not even within the Vespidae. *C. palaestinensis* is not a member of the *C. lusitanicus*-complex, because it retained the plesiomorphic condition, that is the ventral angle of the pronotum runs smoothly into the mesepisternum. This invalidates the view of GIORDANI SOIKA (1957) who regarded *C. palaestinensis* as a close relative of *C. lusitanicus*.

The relationships between the remaining taxa of species group 7 are still unresolved. Consequently, one can only look out for striking similarities between *C. palaestinensis* and some of the other species that might prove in the future to be synapomorphies. The most promising structure is probably the semi-ellipsoid depression between the posterior-lateral angles of sternite 9 of the males. It is also present in the *C. spiricornis*-complex (*C. beaumonti* (GIORDANI SOIKA) and *C. spiricornis* SAUSSURE which are very similar; MAUSS in prep.) and *C. hispanicus*, although it is modified in these taxa in addition in that the proximal edge of the depression is raised to a keel. A comparable situation has not been observed in any other *Ceramius* species. Furthermore the fore femora of the males of the latter two species are also somewhat broadened and shortened, yet this is not as pronounced as in *C. palaestinensis*. Therefore it is likely that the *C. spiricornis*-complex, *C. hispanicus* and *C. †palaestinensis* form a monophylum. At present the relationships between these species can not be resolved with certainty. The form of the scutellum shows affinities between the members of the *C. spiricornis*-complex (cf. GIORDANI SOIKA 1957: fig.

3) and *C. palaestinensis*. *Ceramius hispanicus* and the members of the *C. spiricornis*-complex share the keel on sternite 9 mentioned above and a very hairy, cone-like process on the volsella, even though it is much longer in the *C. spiricornis*-complex. A comparable structure is not present in other members of group 7. Finally there are similarities between *C. palaestinensis* and *C. hispanicus*, as already recognized by RICHARDS (BYTINSKY-SALZ & GUSENLEITNER 1971). These are spatula-like harpides which are convex on the dorsal and concave on the ventral side and the form of the stipites, especially their ventral arms. Furthermore, both species are comparatively small, and the relative proportions of the clypeus and of A3 are quite similar.

Ceramius palaestinensis seems to be restricted to the Middle East. All recognized localities are to the south of the Taurus mountain range and north-(east) of the Arabian deserts. In North Africa the remaining taxa of species group 7 do not occur further to the east than Algeria (cf. RICHARDS 1962, cf. GUSENLEITNER 1977, 1990), with the next relatives of *C. palaestinensis* occurring in Northwest Africa (*C. beaumonti*) or on the Iberian Peninsula (*C. hispanicus*, *C. spiricornis*) respectively. A†comparable distribution-pattern is shown by the members of species group 1 (cf. RICHARDS 1962, cf. GUSENLEITNER 1967, 1973, 1977, 1990).

Acknowledgements

J. Gusenleitner (Linz), F. Gusenleitner (Linz) and A. Freidberg (Tel-Aviv) were kindly lent me material from the collections in their care. K. Deneš (Budèjovice) and J.S. Ishay (Tel-Aviv) provided information about the localities. I am very much indebted to F.W. and S.K. Gess (Grahamstown) for discussions, encouragement, and their indispensable help with the English text. D. Wittmann (Bonn) made valuable comments on the manuscript.

Zusammenfassung

Morphologische Merkmale des Exoskeletts und des männlichen Genitalapparates von *Ceramius palaestinensis* werden beschrieben und abgebildet. Zusätzlich werden morphometrische Daten des Exoskeletts angegeben. *C. palaestinensis* gehört zur Artengruppe 7 von *Ceramius*. Er besitzt eine Reihe von Autapomorphien, insbesondere im Bereich des männlichen Genitals. Die nächst verwandten Taxa innerhalb der Gruppe 7 sind wahrscheinlich *C. hispanicus* und der *C. spiricornis*-Komplex. Diese Hypothese wird insbesondere durch die charakteristische Ausbildung des 9. Abdominal-Sternites der Männchen gestützt. *C. palaestinensis* ist in seinem Vorkommen wahrscheinlich auf den Nahen Osten beschränkt. Die übrigen Vertreter der Artengruppe 7 treten nur im Westlichen Mittelmeergebiet auf. Die Artengruppe 7 von *Ceramius* zeigt damit ein ähnlich disjunktes Verbreitungsmuster wie die Gruppe 1.

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Tab.1: Morphometric parameters of specimens of *Ceramius palaestinensis* (distances in mm).

Parameter	♂ dbM No. 344	♂ dbM No. 352	♀ dbM No. 350	♀ dbM No. 456
1. Distance between lateral ocelli	0.39	0.35	0.39	0.35
2. Distance between frontal and lateral ocellus	0.21	0.19	0.22	0.21
3. Minimal distance between compound eyes (dorsal)	1.96	1.90	2.13	2.10
4. Minimal distance between antennal sockets	0.83	0.79	1.00	0.99
5. length of scapus (from medial, without radicle)	0.79	0.81	0.81	0.76
6. length of A3 (dorsal, along the median axis)	0.80	0.85	0.54	0.56
7. maximum width of A3 (dorsal)	0.33	0.32	0.28	0.30
8. maximum width of clypeus (with lateral wings)	1.71	1.74	2.02	1.96
9. apical width of clypeus (between lateral edges of the medial lobe)	0.72	0.70	0.87	0.87
10. Clypeus-length (along the median axis from the basal suture to the apical margin	1.14	1.12	1.22	1.21
11. Mesonotum-width (over the tegulae cf. ECK 1978)	3.04	3.03	3.13	3.15
12. Mesoscutum-length (dorsal along median axis)	2.32	2.33	2.46	2.52
13. wing-length (from proximal end of the radius to the tip of the wing)	?	7.26	7.90	7.90
14. length of R+Sc (along the posterior margin of R+Sc from its proximal end up to the point were Rs runs into it)	4.42	4.40	4.60	4.64
15. number of hamuli	13	20	18	17
16. length of femur I (between the dorsal "edges" seen from posterior)	1.60	1.68	1.79	1.79
17. length of tibia I (from posterior, along a straight line between the proximal dorsal "edge" and the distal ventral "edge" which is a short conical spine)	1.33	1.46	1.50	1.50
18. length of metatarsus I (along the median axis of the broad posterior side between the proximal hairline and the posterior end)	0.57	0.58	0.68	0.61
19. width of abdominal-tergit II (dorsal)	2.16	2.16	2.27	2.32
20. length of abdominal- tergit II (along the median axis from the posterior margin to the anterior "edge" of the medial concavity of the dome of the tergit; orientation of the specimen: viewed from above the margin of the anterior border of the tergit to the petiolus is only just visible through the medial concavity of the dome)	0.85	0.83	0.95	0.95
21. total length (dorsal)	?	10.7	10.4	12.5

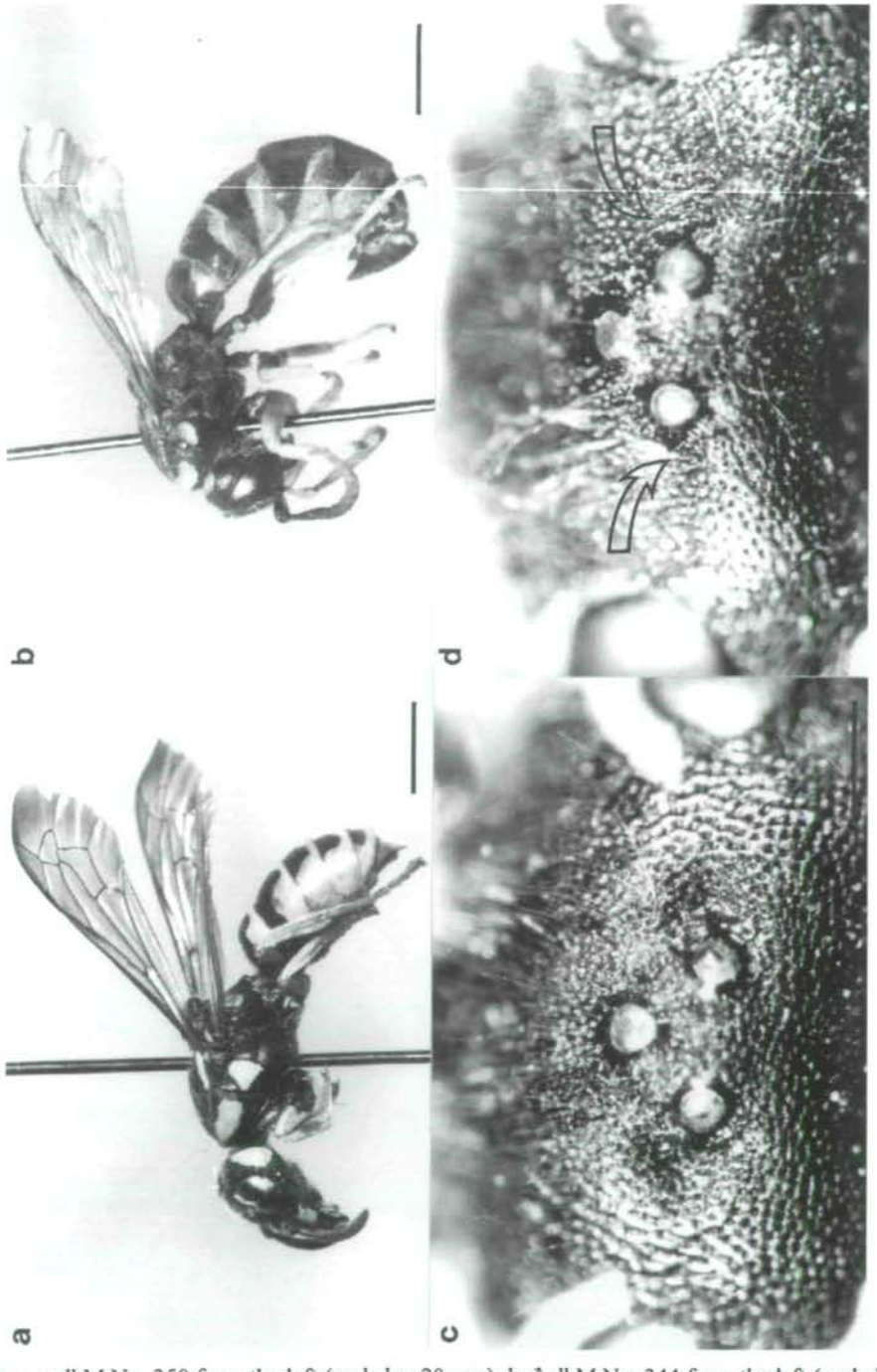

Fig. 1: a ♀ dbM No. 350 from the left (scale bar 20 mm); b ♂ dbM No. 344 from the left (scale bar 20 mm); c ♀ dbM No. 350 vertex from dorsal, showing depression on each side of the lateral ocelli (scale bar 0.4 mm); d ♂ dbM No. 352 vertex from dorsal, arrow pointing at depression on each side of the lateral ocelli (scale bar 0.4 mm).

Fig. 2: a ventral half of the thorax of ♀ dbM No. 350 from the left, arrow pointing at the ventral angle of the pronotum; b scutellum of ♀ dbM No. 350 from the left; c scutellum of ♂ dbM No. 352 from the left; d left fore leg of ♂ dbM No. 344 from posterior; e distal end of the abdomen of ♂ dbM No. 352 from ventral (s7 abdominal sternite 7); (scale bars 0.5 mm).

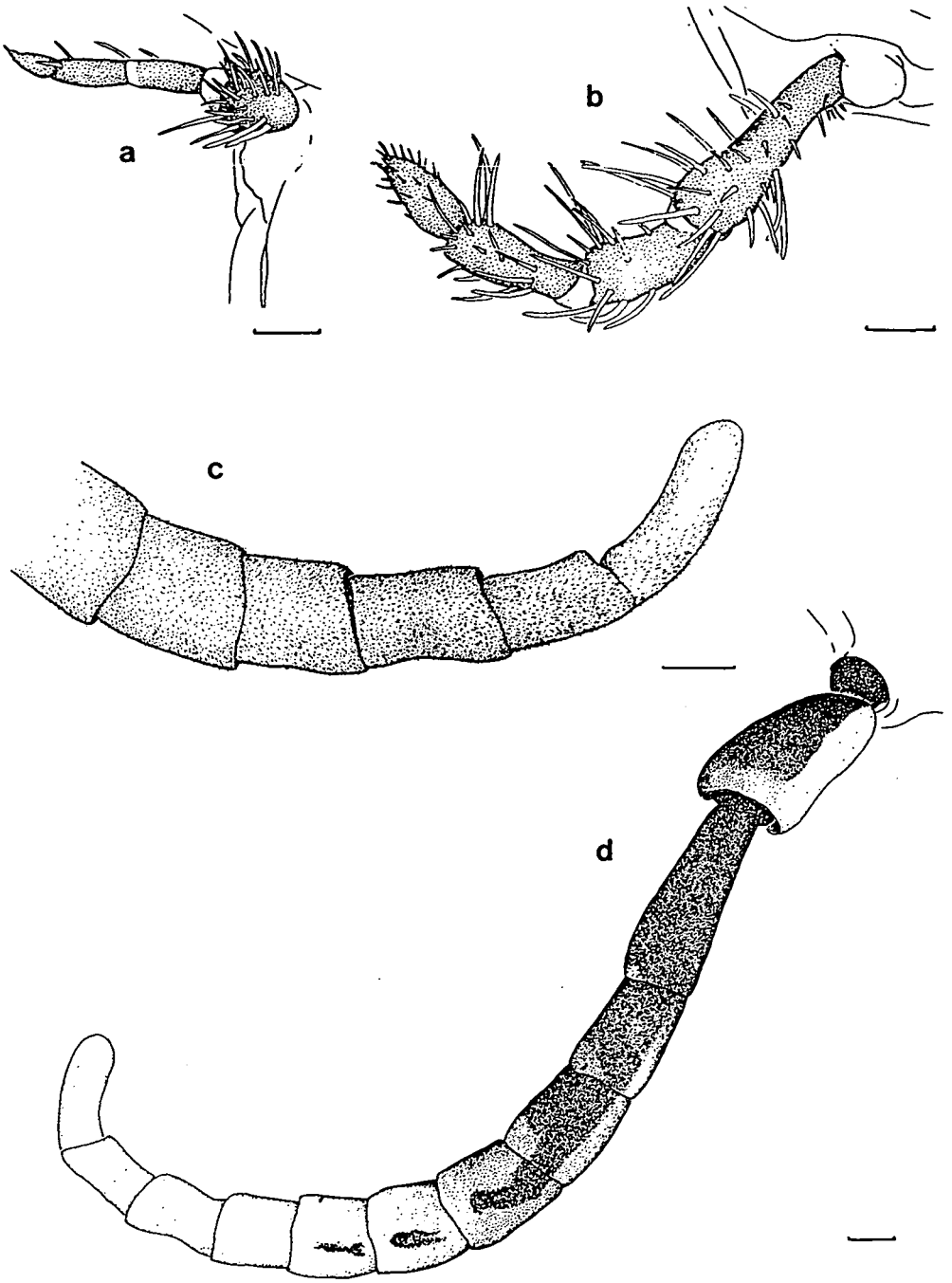

Fig. 3: a left maxillary palpus of ♀ dbM No. 350 from lateral (scale bar 0.1 mm); b left labial palpus of ♀ dbM No. 350 from dorso-lateral (scale bar 0.1 mm); c distal end (A7-A12) of left antenna of ♂ dbM No. 344 (scale bar 0.2 mm); d right antenna of ♂ dbM No. 344 from dorso-anterior (scale bar 0.2 mm).

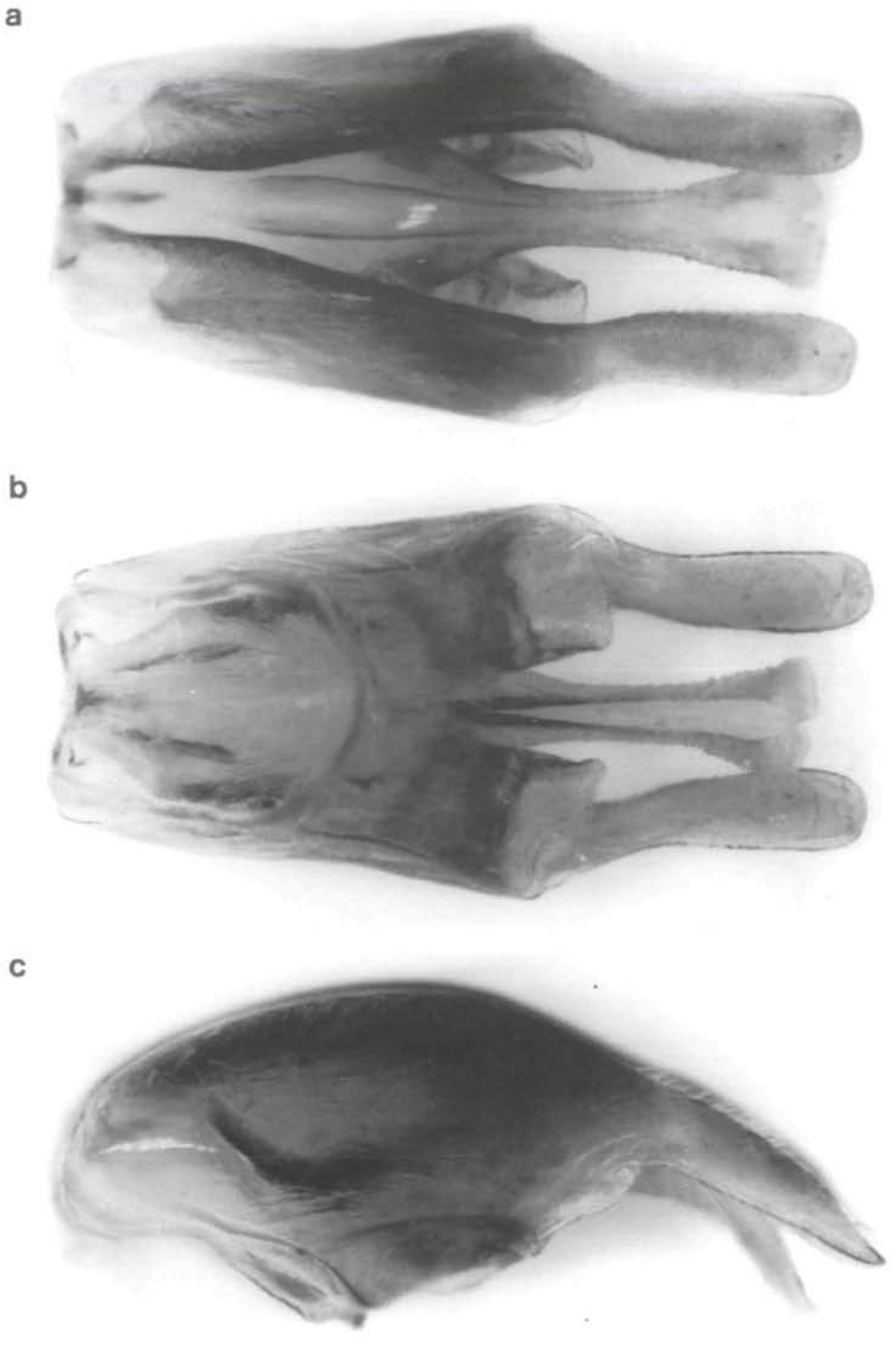

Fig. 4: male genitalia of ♂ dbM No. 344; a dorsal view; b ventral view; c lateral view (scale as in fig. 5).

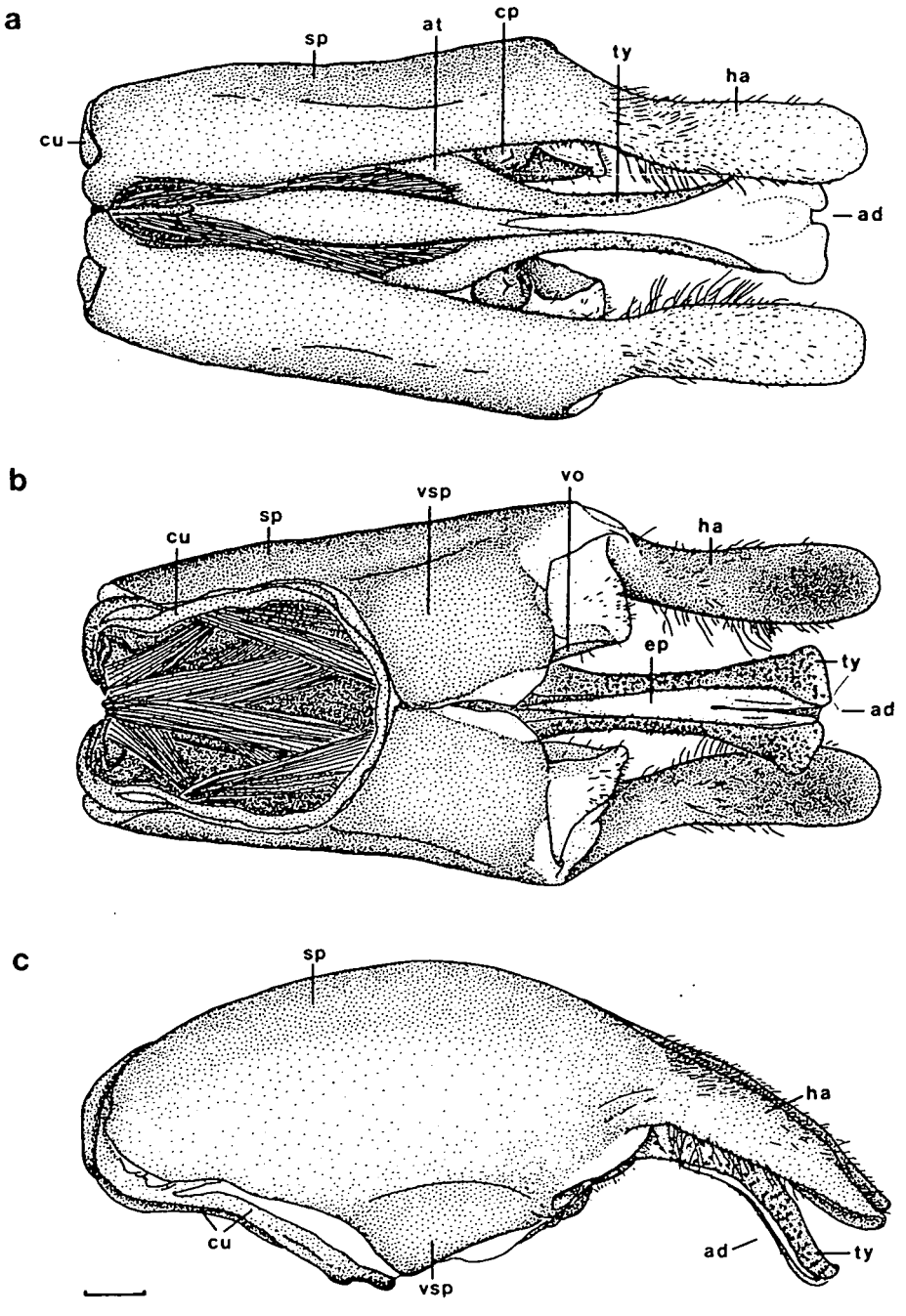

Fig. 5: male genitalia of ♂ dbM No. 344; a dorsal view; b ventral view; c lateral view (ad aedoeagus, at apodema thyrson, cp conical protuberance of volsella, cu cupula, ep endophallus, ha harpide, sp stipes, ty thyrso, vo volsella, vsp ventral plate of stipes; scale bar 0.2 mm).