ARTHROPOD SYSTEMATICS & PHYLOGENY

71 (3): 139 – 168
20.12.2013

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SENCKENBERG

Another species of European Ectobiinae travelling north – the new genus *Planuncus* and its relatives (Insecta: Blattodea: Ectobiinae)

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Accepted 21.xi.2013.
Published online at www.senckenberg.de/arthropod-systematics on 13.xii.2013.

Abstract

A new genus of Ectobiinae is described, *Planuncus* with the three new subgenera, *Planuncus*, *Margundatus* and *Margintorus*, containing species formerly belonging to the genera *Phyllodromica* (second subg.) and *Ectobius* (other subg.). New combinations: *Pl.* (*Pl.*) *tingitanus* (Bolívar, 1914), *Pl.* (*Pl.*) *finoti* (Chopard, 1943), *Pl.* (*Pl.*) *vinzi* (Maurel, 2012); *Pl.* (*Margundatus*) *baeticus* (Bolívar, 1884), *Pl.* (*Margundatus*) *agenjoi* (Harz, 1971), *Pl.* (*Margundatus*) *erythrurus* (Bohn, 1992), *Pl.* (*Margundatus*) *intermedius* (Bohn, 1992), *Pl.* (*Margundatus*) *krausei* (Bohn, 1992), *Pl.* (*Margundatus*) *maculosus* (Bohn, 1992), *Pl.* (*Margundatus*) *paludicolus* (Bohn, 1992), *Pl.* (*Margundatus*) *princisi* (Fernandes, 1962), *Pl.* (*Margundatus*) *striolatus* (Bohn, 1992); *Pl.* (*Margintorus*) *nicaeensis* (Brisout de Barneville, 1852). A new *Ectobius* species from Morocco is described: *E. hipposiderus*. The new genus and its subgenera are compared with the Ectobiinae genus *Capraiellus* and the newly described *E. hipposiderus*. The morphological phylogenetic analysis suggests the following relationships: *E. hipposiderus* + (*Capraiellus* + (*Margintorus* + (*Margundatus* + *Planuncus*))). The appearence of a new cockroach species belonging to the subgenus *Planuncus* in Germany and Great Britain is reported; the hitherto known distribution of the subgenus encompasses Algeria, Morocco, southern Spain, and France. Species affiliation and provenance of the immigrant remain doubtful due to difficulties to separate the three known species. The possible reasons for the recent areal expansion of the species are discussed.

Key words

Planuncus, *Margundatus*, *Margintorus*, *Capraiellus*, Blattodea, Ectobiinae, new genus, new subgenus, new species, phylogeny, areal expansion.

1. Introduction

Cockroach species diversity in the Palaearctic region is predominantly due to three closely related genera assigned to the subfamily Ectobiinae of Blaberoidea, *Ectobius* with three subgenera (*Capraiellus*, *Ectobiola*, *Ectobius*) and ca. 50 species in this region, *Phyllodromica* with four subgenera (*Arbiblatta*, *Lobolampra*, *Phyllodromica*, *Turanoblatta*) and ca. 110 species, and *Luridiblatta* with only 3 species. The present classification is highly unsatisfying: The definitions of most genera and subgenera are solely based on few characters concerning the wings and their reduction. The definitions don't allow a clear separation of the taxa and the characters are highly suscepti-

ble for homoplasies since wing reductions have certainly occurred many times independently during the evolution of the Blattodea. The system, therefore, hardly reflects the phylogenetic relationships.

The first step on the way to a better, phylogenetically founded system is to outline monophyletic species groups, as was initiated by M.C. Failla and A. Messina and later continued by H. Bohn and Ľ. Vidlička. As a result of the revisionary work of these authors a series of undoubtedly monophyletic groups were established: *sylvestris*-group of *Ectobius* (Failla & Messina 1987; Bohn 1989, 2004), *erythronotus*-goup of *E.* (Failla & Messina 1987), *kraussianus*-group of *E.* (Failla & Messina 1987), *baetica*-group of *Phyllodromica* (Bohn 1992), *carpetana*-group of *P.* (Bohn 1999), *maculata*-group of *P.* (Bohn & Chládek 2011), *megerlei*-group of *P*. (Vidlička & Majzlan 1997), *panteli*-group of *P.* (Bohn 1993), and *subaptera*-group of *P*. (Knebelsberger & Bohn 2003). To these can be added *Capraiellus*, subgenus of *Ectobius*, and the genus *Luridiblatta*. So far, the revised groups only contain a small fraction of the species of the two larger genera, much more species should be studied in this way.

The second step would be to analyse the phylogenetic relationships between the various species groups in order to be able to group them to higher categories (subgenus, genus, etc). A first attempt in this direction was tried in the revision of the *carpetana*-group (Bohn 1999). In the present paper the phylogenetic relationships between the *tingitanus*-group of *Ectobius* and some other species and species groups are studied.

The majority of the Palaearctic species are endemic to very small geographic areas, while a few species are widely distributed. For some of the latter, changes in the geographic distribution during recent decades have become known. The present composition of the European Fauna (and Flora) was strongly molded by the activities of the Pleistocene glacial and interglacial periods. After the end of the last glacial period many species showed a dramatic areal expansion or shift from their southern refugia mainly towards the North.

Changes in the geographic distribution of a species are, of course, not restricted to the past history of life but expected to occur steadily thanks to the steadily fluctuating abiotic and biotic environmental conditions – maybe only to a scarcely measurable extent. During the last decades, however, an increasing number of cases could be observed in which species have been expanding at an unexpectedly high rapidity into regions not inhabited before.

Among the European cockroaches the species *Ectobius vittiventris* (Costa, 1847) has to be mentioned in this connection. Its distribution area is southeastern Europe, from Switzerland and Italy eastwards as far as to the Caucasus. The northern limit of its distribution in central Europe was Tessin in southern Switzerland. Beginning at about 1985, the species expanded into northern Switzerland and southern Germany (Landau et al. 2000; Landau Lüscher et al. 2003; Baur et al. 2004) and has meanwhile reached Middle Germany (Thüringen, Jena: Köhler 2006; Rheinland-Pfalz, Landau: Pfeifer 2012).

The story of a further new cockroach appearing in Germany started in 2007 with the finding of a male cockroach in the cellar of a habitation almost in the center of the city of Mainz (federal state Rheinland-Pfalz), on the shoulders of a resident working there. It was sent by Carsten Renker (Naturhistorisches Museum Mainz) to the first author for identification. The animal revealed as belonging to the *tingitanus*-group of *Ectobius*, which consists of two species described from North Africa: *Ectobius tingitanus* Bolívar, 1914, from Tanger (Morocco), and *E. finoti* Chopard, 1943, from Ghazaouet (Algeria); the distribution of the group encompasses – according to material collected by the first author – furthermore southern Spain (material collected mainly 1984) and southern France (Dpts. Lot-et-Garonne, Tarn-et-Garonne, material collected 1995 and 1996). Since the residents of the habitation in Mainz had just returned from a stay in Morocco, it was first assumed that they had brought the animals with them. But few years later representatives of the *tingitanus*-group were again and at various localities found in Rheinland-Pfalz (Mainz-Finthen, 2010, 2011; Worms and its further environment, 2011, 2012; Ludwigshafen and environment, 2012) and in the neighbouring federal state Baden-Württemberg (Heidelberg, 2012), exclusively in green areas of villages and towns (material collected by W. Dorow and M.A. Pfeifer). The size of the populated area, about 75 km in diameter, suggests that the species had arrived already much earlier in this region. Most surprisingly, representatives of the *tingitanus*-group were recently found in Great Britain (Hythe, near Dover, 2010, 2011; collected by G. Beccaloni).

The question from where the immigrants were coming, from France, Spain or North Africa, cannot be answered at the moment due to unresolved problems in the taxonomy of the group, which don't allow a clear-cut species separation. The structure of the glandular pit in males, the most important character for species identification in the Ectobiinae, is almost invariable throughout the whole range of distribution of the group. Morales-Agacino (1948) had already suspected that *E. finoti* might be a synonym of *E. tingitanus*.

The difficulties with the group were unnecessarily aggravated by Maurel (2012), who erected a new species, *Ectobius vinzi*, for the French population. The author did not give distinguishing features to the two known species from North Africa; he did not even mention them, indicating that he did not know of their existence. Moreover, the description of several characters is inadequate and needs revision.

The present paper serves to prepare a solid base for the urgently necessary taxonomic revision of the *tingitanus*-group; it contains a detailed description of the characteristics of the group and the listing of all localities where representatives of the group were found. The group is in its features compared with some other species and species groups assumed to be closely related: the *baetica*-group of *Phyllodromica*, *Ectobius nicaeensis*, the (sub-)

genus *Capraiellus* (of *Ectobius*), and a so far undescribed *Ectobius* species from Morocco. As a result, a new genus *Planuncus* with three subgenera is erected, with the *tingitanus*-group becoming the subgenus *Planuncus*. The phylogenetic relations between the treated taxa are discussed as well as some aspects of the recent areal expansion in the distribution of representatives of the subgenus *Planuncus*.

2. Materials, methods, abbreviations

Preservation and preparation of microscopical slides. The collected cockroaches were mostly preserved in 2% formol or 80% alcohol. For the microscopical preparations of cuticular structures soft tissues were removed with KOH and the cleared exoskeletal parts mounted in Canada Balsam or Euparal.

Figures. Photographing was done with a Jenoptic camera (ProgRes SpeedXTcore5) on a Leica microscope (DM 5000B) using softwares ProgRess CapturePro v.2.8.0 and Helicon Focus 5.3. The phase contrast images were taken with a Zeiss camera (Ikon) and microscope (Photomikroskop II).

In the figures the orientation of the structures is with the anterior end on top; dorsal tegumental structures (tergites) are shown in dorsal view, ventral ones (sternites) in ventral view. Deviations from this pattern are mentioned explicitly.

Abbreviations used in text. L = larva, nymph; **ex L** = bred from larva; **O** = ootheca; **Pt** = paratergite; **S** = sternite; **S7** = sternite 7, subgenital plate of female; **S9** = sternite 9, subgenital plate of male; **T** = tergite; **T10** = tergite 10, supraanal plate.

Example for abbreviations of locality and specimen identification: **Ma 1/2** Ma = country Morocco, 1 = locality number, 2 = individual number of a specimen used for a slide preparation, the latter number is underlined when the specimen was bred from a larva.

3. Descriptions

3.1. *Planuncus* Bohn, gen. nov.

Type species
Planuncus tingitanus (Bolívar, 1914), **comb. nov.**
– *Ectobius perspicillaris tingitanus* Bolívar, 1914: 165.
– *Ectobius tingitanus:* Princis 1971: 1086.

Etymology. The genus name refers to the flattend (Latin *planus*) hooklike (hook = *uncus* in Latin) claw of the male genital hook.

Diagnosis. Male subgenital plate strongly vaulted, boat-shaped, symmetrical; genital hook with strongly flattened and broadened sickle-shaped claw; T7 with glandular pit often containing a knoblike structure covered with bristles; wings fully developed or variously reduced, tegmina in the most reduced state transversely cut, reaching about T2, tegmina of both sides touching each other along the midline; early larval stages often coloured black with white transversal band on the metanotum.

3.1.1. Subgenus *Planuncus* Bohn, subgen. nov.

Planuncus (*P.*) *tingitanus*-complex

Figs. 1A,B,O, 2A,B,I–K, 3A, 4A,F,I, 5E,G, 6G,H,K,L, 7A–I, 9A–F, 10B

Type species
Planuncus (*Planuncus*) *tingitanus* (Bolívar, 1914).

Other species
Planuncus (*Planuncus*) *finoti* (Chopard, 1943), **comb. nov.**
– *Ectobius finoti* Chopard, 1943: 21, figs. 15, 17.
Planuncus (*Planuncus*) *vinzi* (Maurel, 2012), **comb. nov.**
– *Ectobius vinzi* Maurel, 2012: 11, figs. 2–9.

Material studied
***Type material of Planuncus (P.) tingitanus* (Bolívar, 1914)**. Morocco: 3♂ (Paralectotype, Cotype and Allotype), Tanger, M.Escalera. (Museo Nacional de Ciencias Naturales, Madrid).
***Type material of Planuncus (P.) finoti* (Chopard, 1943)**. Algeria: 1♂ (Holotype), Nemours [Ghazaouet], Juin 1887. (Muséum National d'Histoire Naturelle, Paris).
***Additional material of Planuncus (P.) tingitanus*-complex**. Great Britain: ex L: 1♂, England, C. Kent, Hythe, 4.IX.2011, leg. G. Beccaloni (slide: ♂, GB 3/1); 1♀, 1L, England, C. Kent, Hythe, 2.X.2011, leg. G.Beccaloni (GB 3a). (Collection H.Bohn). – Germany: 16♂, 26♀, 19L, 7O + ex L: 7♂, 5♀, 7L, Rheinland-Pfalz, RB Rheinhessen-Pfalz, SK Mainz, Mainz-Finthen, Uhlerbornstraße, 200 m, 28.VIII.2011, leg. H.Bohn (slides: ♂, D 235/1–5; ♀, D 235/6–8; L, D 235/11,12); 2♂, Ludwigshafen, Merziger Straße, Trassenwald, 49°29′29″N 8°24′07″E, 29.IX.20112, leg. M.A.Pfeifer (D 236). (Collection H.Bohn). – 1♂, D, RP, Mainz-Finthen, Terrasse, Steubenstr. 38, 49.986°N 08.170°E, 2.Hälfte VIII, leg. De Vries & Herrmann (slide: Bo 1271) (Collection Dorow). – Rheinland-Pfalz, Ludwigshafen-Friesenheim, Merziger Straße, Trassenwald, 49°29′29″N 08°24′07″E, leg. M.A.Pfeifer: 1♂, 1♀, 6L, 93 m, 30.VII.2012; 2♀, 110 m, 29.IX.2012; Rheinland-Pfalz, Bobenheim-Roxheim, leg. M.A.Pfeifer: 1♂, Bahnhofsplatz 5, 92 m, 49°35′20″N 08°21′07″E, 18.VII.2012; 1♀, Bahnhofsstraße,

92 m, 49°35′21″N 08°21′13″E, 30.IX.2012; 2♀, Bahnhofsplatz 5, X.2012; 1♂, 2♀, 1L, 1O, Rheinland-Pfalz, Worms, auf Gebüsch, 49°37′12″N 08°21′40″E, leg. M.A.Pfeifer; 1♂, Rheinland-Pfalz, Hassloch, Gottlieb-Wenz-Str. 19, Garten, 49°22′01″N 08°15′38″E, 113 m, Sommer 2011, leg. O.Röller; 1♂, Rheinland-Pfalz, Ludwigshafen, östl. Zentralfriedhof, auf Balkon, 93 m, 49°28′56″N 08°25′38″E, IX.2012, leg. S.Tillack; 1♀, Rheinland-Pfalz, Flörsheim-Dalsheim, am Haus, 49°39′17″N 08°12′53″E, 13.IX.2011, leg. G.Reder; 1L, Baden-Württemberg, Heidelberg-Wieblingen, Garten in Ortslage, 49°25′16″N 08°38′40″E, 29.VII.2012, leg. G.Reder. (Collection M.A. Pfeifer). – 1♂, Rheinland-Pfalz, Stadt Mainz, Eduard-Frank-Str. 12, im Keller einer Wohnung, 21.VIII. 2007, K.&M.Grimm (slide: Bo 1142). (Naturhist. Museum Mainz). – **France**: 4♀, Dept. Lot-et-Garonne, 2 km NW Hautefage-la-Tour (ca. 27 km NE Agen), 200 m, IX.1995, leg. M.Faas (F 65); 12♂, 8♀, 4L + ex L: 2♂, 1♀, 2L, Dept. Lot-et-Garonne, 2 km NW Hautefage-la-Tour (ca. 27 km NE Agen), 200 m, 2.VIII.1996, leg. B.&H.Bohn (slides: ♂, F 65a/1,4–6); 2♂, 3♀, 1L + ex L: 4♂, 2♀, 2L, 1O, Dept. Lot-et-Garonne, 2 km NE Frespech (ca. 23 km NE Agen), 150 m, 2.VIII.1996, leg. B.&H.Bohn (slide: ♂, F 87/1); 3♂, 2♀ + ex L: 1♀, 2L, Dept. Lot-et-Garonne, 2 km SSW Tournon-d'Agenais, 200 m, 2.VIII.1996, leg. B.&H.Bohn (slide: ♂, F 88/1); 2♂, 2L, Dept. Tarn-et-Garonne, St. Romain (ca. 13 km WSW Lauzerte), 150 m, 3.VIII.1996, leg. B.&H.Bohn (slide: ♂, F 94/1). (Collection H.Bohn). – **Spain**: 5♂, 2♀, Prov. Albacete, Sa. de Alcaraz, near Riópar (SW Pto. de las Crucetillas), 1200 m, 18.VIII.1983, leg. B.&H.Bohn (slides: ♂, Sp 15/1,4,6,8); 3♂, 5♀, Prov. Jaén, Sa. de Cazorla, Emb. del Tranco, near Bujaraiza, 700 m, 19.VIII.1983, leg. B.&H.Bohn (slides: ♂, Sp 17/1,2); 5♂, 12♀, 4O, Prov. Jaén, Sa. de Cazorla, Pto. de las Palomas (NE Cazorla), 1300 m, 19. VIII.198, leg. B.&H.Bohn 3 (slides: ♂, Sp 18/1,6); 1♂, 1♀, Prov. Jaén, Sa. de Cazorla, 5 km S Puente de las Herrerías, 1300 m, 20.VIII.1983, leg. B.&H.Bohn (slide: ♂, Sp 19/1); 1♂, 3♀, 2O, Prov. Granada, Sa. del Campanario, 5 km W Pto. de Zegri, 1000 m, 26.VIII.1983, leg. B.&H.Bohn (slide: ♂, Sp 37/1); 1♀, 1O, Prov. Córdoba, Sta. María de Trassierra (near Córdoba), 600 m, 28. VIII.1983, leg. B.&H.Bohn (Sp 39); 1♀, 1O, Prov. Cádiz, 5 km E Arcos de la Frontera, 200 m, 1.IX.1983, leg. B.&H.Bohn (Sp 45); 7♂, 23♀, 3O, Prov. Cádiz, 15 km SSW Ubrique, 700 m, 1.IX.1983, leg. B.&H.Bohn (slides: ♂, Sp 46/1,2,5,6,9; ♀, Sp 46/7,8); 3♂, 4♀, Prov. Cádiz, Pto. del Boyar (near Grazalema, NE Ubrique), 1100 m, 2.IX.1983, leg. B.&H.Bohn (slides: ♂, Sp 47/1,4); 4♂, 18♀, 1L, 1O, Prov. Málaga, 3 km SW Gaucin (50 km SW Ronda), 600 m, 10.IX.1984, leg. B.&H.Bohn (slides: ♂, Sp 77/5,7,8; ♀, Sp 77/3,4). (Collection H.Bohn). – **Morocco**: 4♂, 10♀, 2L + ex L: 5♂, 3♀, Rif, btw. Ceuta & El-Biutz, 400 m, 10.VIII.1984, leg. B.&H.Bohn (slides: ♂, Ma 1/5; ♀, Ma 1/3,6); 3♂, 3L + ex L: 9♂, 10♀, Rif, Benzou (6 km W Ceuta), 20 m, 10.VIII.1984, leg. B.&H.Bohn (Ma 2); 8♂, 11♀, 2L, 4O, Rif, Oued Laou, 5 km SW Es-Sebt-de-Saïd, 200 m, 11.VIII.1984, leg. B.&H.Bohn (slides: ♂, Ma 3/4; ♀, Ma 3/2); 16♂, 6♀, 7L, Rif, 5 km S Chefchaouèn, 500 m, 13.VIII.1984, leg. B.&H.Bohn (Ma 4); 36♂, 20♀, 14L + ex L: 15♂, 26♀, 9O, Rif, 15 km W Bab-Berred, 1300 m, 13.VIII.1984, leg. B.&H.Bohn (Ma 5); 18♂, 4♀, 1L + ex L: 13♂, 19♀, Rif, Bab-Besen (15 km W Ketama), 1600 m, 14.VIII.1984, leg. B.&H.Bohn (Ma 6); 7L + ex L: 9♂, 1♀, 5 km S Souk-el-Had-de-Ikauen (38 km S Ketama), 800 m, 14.VIII.1984, leg. B.&H.Bohn (Ma 7); 18♂, 2♀ + ex L: 20♂, 23♀, 3O, Rif, btw. Bab-Sidi-Kebat & Boured, 1000 m, 15. VIII.1984, leg. B.&H.Bohn (slides: ♂, Ma 8/3; ♀, Ma 8/1); 9♂, 7♀ + ex L: 8♀, 6O, Moyen Atlas, Tazzeka Mountains, near Grottes du Chiker (23 km SSE Taza), 1400 m, 15.VIII.1984, leg. B.&H.Bohn (Ma 9); 3♂, 14♀, Moyen Atlas, Tazzeka Mountains, near Grottes du Chiker (23 km SSE Taza), 1400 m, 16.VIII.1999, leg. H.Bohn (Ma 9b); 30♂, 4♀, 5L + ex L: 10♂, 12♀, 1O, Moyen Atlas, S slope of Jbel Tazzeka (SW Taza), 1500 m, 16.VIII.1984, leg. B.&H.Bohn (Ma 10); 20♂, 13♀ + ex L: 4♂, 27♀, 18O, Moyen Atlas, Jbel Tazzeka (SW Taza), 1900 m, 16.VIII.1984, leg. B.&H.Bohn (Ma 11); 13♂, 4♀, 1L, Moyen Atlas, 11 km N Merhraoua (S Taza), 1200 M, 17.VIII.1984, leg. B.&H.Bohn (Ma 12); 22♂, 13♀, 1L, 1O + ex L: 2♀, Moyen Atlas, near M. F. Tamtroucht (S Tizi-Oulmou, S Taza), 1700 m, 17.VIII.1984, leg. B.&H.Bohn (Ma 13); 63♂, 19♀, 1L, 4O + ex L: 1♂, 14♀, 9O, Moyen Atlas, Dayèt Iffer (NE Ifrane), 1600 m, 18.VIII.1984, leg. B.&H.Bohn (Ma 14); 3♂, 5♀, Moyen Atlas, Dayèt Iffer (NE Ifrane), 1600 m, 16.VIII.1999, leg. H.Bohn (Ma 14b); 2♀, Moyen Atlas, Dayèt Iffer (NE Ifrane), 1600 m, 22.IX.2000, leg. B.&H.Bohn (Ma 14c); 8♂, 6♀, 1L, Moyen Atlas, Dayèt Hachlaf (E Ifrane), 1700 m, 19.VIII.1984, leg. B.&H.Bohn (Ma 15); 1♂, 6♀, Moyen Atlas, Tizi-n-Âït-Ouirra (NE Beni-Mellal), 1300 m, 28.VIII.1984, leg. B.&H.Bohn (slides: ♂, Ma 23/10; ♀, Ma 23/11); 1L + ex L: 1♀, 1L, Moyen Atlas, Tizi-n-Âït-Ouirra (NE Beni-Mellal), 1300 m, 31.V.1989, leg. B.&H.Bohn (Ma 23a); 3♂, 5♀, 2L, Moyen Atlas, Tizi-n-Âït-Ouirra (NE Beni-Mellal), 1300 m, 14.VIII.1999, leg. H.Bohn (Ma 23b); 1♀, Moyen Atlas, Tizi-n-Âït-Ouirra (NE Beni-Mellal), 1300 m, 25.IX.2000, leg. B.&H.Bohn (Ma 23c); 15♂, 13♀, 1L, 1O, Moyen Atlas, Tizi-n-Ifar (NE Beni-Mellal), 1800 m, 28.VIII.1984, leg. B.&H.Bohn (Ma 24); 7♂, 8♀, Moyen Atlas, Tizi-n-Ifar (NE Beni-Mellal), 1800 m, 14.VIII.1999, leg. H.Bohn (Ma 24a); 2♀, Moyen Atlas, Tizi-n-Ifar (NE Beni-Mellal), 1800 m, 26./27.IX.2000, leg. B.&H.Bohn (Ma 24b); 27♂, 32♀, 3L, 3O, Moyen Atlas, M. F. Tafechna (14 km E Khénifra), 1300 m, 31.VIII.1984, leg. B.&H.Bohn (Ma 27); 4♂, 5♀, 1L, Moyen Atlas, M. F. Tafechna (14 km E Khénifra), 1300 m, 15.VIII.1999, leg. H.Bohn (Ma 27b); 3♀, Moyen Atlas, Aguelmame Azigza (E Khénifra), 1600 m, 31.VIII.1984, leg. B.&H.Bohn (Ma 28); 34♂, 33♀, 8O, Moyen Atlas, 15 km S Âïn-Leuh (S Azrou), 1700 m, 31.VIII.1984, leg. B.&H.Bohn (Ma 29); 15♂, 20♀, 6O, Moyen Atlas, Âïn-Leuh (S Azrou), 1500 m, 1.IX.1984, leg. B.&H. Bohn ((Ma 30); 5♂, 4♀, 1O, Moyen Atlas, 7 km SW Ifrane, 1700 m, 1.IX.1984, leg. B.&H.Bohn (Ma 31); 1♂, Moyen Atlas, Dayèt Âaoua (17 km N Ifrane), 1500 m, 1.IX.1984, leg. B.&H.Bohn (Ma 32); 11♂, 11♀, 1L, Jbel Zerhoun (N Meknès), 1000 m, 3.IX.1984, leg. B.&H.Bohn (Ma 34); 20♂, 17♀, 3L, 1O, Rif, 15 km ESE Ouazzane, 500 m, 4.IX.198 4, leg. B.&H.Bohn (Ma 36); 1♂, 1♀, Rif, 5 km N Zoumi (E Ouazzane), 600 m, 5.IX.1984, leg. B.&H. Bohn (Ma 37); 25♂, 7♀, 6L, Rif, 4 km SW Derdara (S Chefchaouèn), 400 m, 5.IX.1984, leg. B.&H.Bohn (Ma 39); 14♂, 11♀, 6L, Rif, 10 km NW Derdara (S Chefchaouèn), 500 m, 5.IX.1984, leg. B.&H.Bohn (Ma 40); 3♂, 5♀, Rif, Jbel Tisouka (near Chefchaouèn), 1800 m, 6.IX.1984, leg. B.&H.Bohn (Ma 42); 3♂, 3♀, 1O, Rif, Bge. Sedd-en-Nakhla, near Zinat (12 km S Tetouan), 450 m, 7.IX.1984, leg. B.&H.Bohn (Ma 43); 5♂, 5♀, 1L, Rif, El-Fendek (22 km W Tetouan), 300 m, 8.IX.1984, leg. B.&H.Bohn (Ma 44); 19♂, 27♀, Rif, Dar Chaoui (33 km W Tetouan), 100 m, 8.IX.1984, leg. B.&H.Bohn (slides: ♂, Ma 45/5–9,13–15; ♀, Ma 45/10–12); 1♂, 5♀, Pont Mohammed V (30 km SW Tanger), 50 m, 9.IX.1984, leg. B.&H.Bohn (Ma 46); 2♂, 4♀, 1L, Rif, Cap Spartel (near Tanger), 200 m, 9.IX.1984, leg. B.&H.Bohn (Ma 47); 4♀, Melilla Peninsula, Mt.Gourougou (S Melilla), 500 m, 15.IX.2000,

leg. B.&H.Bohn (Ma 70b); 1♂, 5♀, Monts des Beni-Snassèn, E above Gorges du Zegze, 750 m, 15.IX.2000, leg. B.&H.Bohn (Ma 73b); ex L: 1♂, Moyen Atlas, Imouzzèr-des-Marmoucha, 1800 m, 21.IV.1998, leg. B.&H.Bohn (Ma 82a); 2♂, 12♀, 1O, Haut Atlas, Pays Glaoua, E slope of Jbel Ifirouane (S Âït Barka, ca. 70 km ESE Marrakech), 1500 m, 12.VIII.1999, leg. H.Bohn (Ma 86b); 1♀, Haut Atlas, Pays Glaoua, E slope of Jbel Ifirouane (S Âït Barka, ca. 70 km ESE Marrakech), 1500–2200 m, 3.X.2000, leg. B.&H.Bohn (Ma 86c); 5♂, 5♀, Moyen Atlas, Jbel R. Nim, Pass btw. Ouaouizarht & Timoulilt (SW Beni-Mellal), 1400 m, 13.VIII.1999, leg. H.Bohn (Ma 92a); 11♂, 6♀, 2L, Moyen Atlas, ca. 3 km W Souk-el-Arba-Ouakbli (E Beni-Mellal), 1400 m, 13.VIII.1999, leg. H.Bohn (Ma 94a); 3♀, Moyen Atlas, ca. 3 km W Souk-el-Arba-Ouakbli (E Beni-Mellal), 1400 m, 27.IX.2000, leg. B.&H.Bohn (Ma 94b); ex L: 1♂, Moyen Atlas, 1–4 km E Azrou, 1500 m, 2.VI.1989, leg. B.&H.Bohn (Ma 98); 7♂, 8♀, 5L, 2O, Haut Atlas, near Âït Khlouf (10 km S Imi-n-Ifri, near Demnate), 1650 m, 12.VIII.1999, leg. H.Bohn (Ma 161a); 9♂, 10♀, 2O, Moyen Atlas, 4 km W Tizi-n-Ifar (ESE El-Ksiba), 1600 m, 14.VIII.1999, leg. H.Bohn (Ma 167a); 1♂, 3♀, 2O, Moyen Atlas, 5 km S Tizi-n-Isly (ESE El-Ksiba), 1400 m, 15.VIII.1999, leg. H.Bohn (Ma 168a); 4♀, Moyen Atlas, S slope of Jbel Tazzeka (SW Taza), 1600–1800 m, 19.IX.2000, leg. B.&H. Bohn (Ma 185a); 14♂, 7♀, Rif, E slope of J. Kouine, 1700–1800 m, 18.IX.2000, leg. B.&H.Bohn (Ma 225a); ex L: 1♀, Mts. des Beni-Snassèn, M.F. d'Âïn -Âlmou, 950–1200 m, 16.IV.1998, leg. B.&H.Bohn (Ma 235); 2♀, Mts. des Beni-Snassèn, M.F. d'Âïn-Âlmou, 950–1200 m, 17.VIII.1999, leg. H.Bohn (Ma 235a); 1♂, 3♀, Mts. des Beni-Snassèn, M.F. d'Âïn-Âlmou, 950–1200 m, 15. IX.2000, leg. B.&H.Bohn (Ma 235b); 1♂, 2♀, 5 km E Debdou, 1200 m, 17.IX.2000, leg. B.&H.Bohn (Ma 241a); ex L: 2♂, 1♀, Moyen Atlas, 6 km S Col du Zad (ca. 15 km N Itzèr), 1900 m, 25.IV.1998, leg. B.&H.Bohn (Ma 253); ex L: 1♀, Moyen Atlas, 2 km N Tizi-Abekhnanes (ca. 40 km S Sefrou), 1750 m, 26.IV.1998, leg. B.&H.Bohn (Ma 256); 2♂, 1♀, Moyen Atlas, 2 km N Tizi-Abekhnanes (ca. 40 km S Sefrou), 1750 m, 16.VIII.1999, leg. H. Bohn (Ma 256a); 2♀, Moyen Atlas, 10 E Imouzzèr-Kandar, 1650 m, 22.IX.2000, leg. B.&H.Bohn (Ma 257a); 2♂, 2♀, Moyen Atlas, road P33 near M.F. Âït-Azrou (5 km SW El Kebab), 1400 m, 15. VIII.1999, leg. H.Bohn (Ma 278); 8♂, 6♀, 2L, Moyen Atlas, 13 km S Âïn-Leuh, 1700 m, 15.VIII.1999, leg. H.Bohn (Ma 279); 2♂, 2♀, Moyen Atlas, Forêt de Cèdres, ca. 10 km SSE Azrou, 1700 m, 16. VIII.1999, leg. H.Bohn (Ma 280); 2♀, Rif, 2–4 km E Taïneste (ca. 65 km NNW Taza), 1300 m, 19.IX.2000, leg. B.&H.Bohn (Ma 302); 5♀, Moyen Atlas, Jbel bou Iblane, N slope of Tizi-Oulmou, 1650 m, 20.IX.2000, leg. B.&H.Bohn (Ma 304); 7♀, Moyen Atlas, Khénifra -Itzèr, 3.5 km S M.F. de Arhbalou-n'Irhaouen, 1700 m, 24.IX.2000, leg. B.&H.Bohn (Ma 305); 3♀, Moyen Atlas, 12 km SSE Dechra-el-Oued (ca. 46 ENE Kashba-Tadla), 1400 m, 24. IX.2000, leg. B.&H.Bohn (Ma 306); 1♂, 1♀, Moyen Atlas, 20 km SSE Dechra-el-Oued (ca. 46 ENE Kashba-Tadla), 1800 m, 25. IX.2000, leg. B.&H.Bohn (Ma 307); 5♀, Moyen Atlas, 25 km SSE Dechra-el-Oued (ca. 46 ENE Kashba-Tadla), 1750 m, 25.IX.2000, leg. B.&H.Bohn (Ma 308). (Collection H.Bohn).

Description. ***Wings*** (Fig. 6G,H). Well developed, almost reaching the abdominal end, in females slightly shorter; hindwings in both sexes considerably shortened, by far not reaching the tips of the tegmina, apical triangle missing, veinal pattern reduced.

Colouration. *Imagines* (Fig. 9A–C): Mainly pale yellowish, head with a darker interocular band, pronotum disk yellowish, without darker markings, male abdomen dorsally uniformly yellowish or with double series of indistinct darker patches, abdomen of female usually darker, with variously broad dark transversal bands, sometimes completely dark. *Juveniles:* First larval stages black with a broad white stripe across the metanotum (Fig. 9F). In later stages the white transversal stripe of the metanotum and its dark anterior and posterior limitations are maintained, the colour of notal surface anteriorly may vary between yellowish and very dark (Figs. 6K,L, 9D,E).

Male abdomen. *Tergite bristles* (Fig. 1O): Surface of tergites only with small normal bristles. *Tergite 5*: Posterior border straight or slightly concave. *Tergite 6* (Fig. 1A, 7A,B): Posterior border mesally with a very deep angular or angularly rounded excavation. *Tergite 7* (Figs. 1A,B, 7A–I): In the center with a slight elevation bearing the glandular pit, posterior border with a moderately deep, obtuse-angular or broadly rounded concavity. *Glandular pit*: Opening obtusely cordiform, mesal part of anterior border and complete posterior border not sharply delimited, pit wall from there gradually declining towards a knob arising from the bottom of the pit; knob densely covered with bristles having longitudinal furrows and a curved tip. Anterior-lateral corners of the opening with a sharp edge, wall of the pit below the edges anteriorly deepening to two pouches fairly reaching the anterior border of the tergite. Bottom of pit on both sides often with a sharp-edged ridge reaching from the bristled knob till far into the pouch (Fig. 7B,C,G,H). Immediately anteriorly and posteriorly of the pit opening with a field of dispersed straight bristles pointing towards the pit opening, anteriorly much longer than posteriorly.

Sternite 9, subgenital plate (Fig. 3A): Posterior part ventrally deeply vaulted to a longitudinal gutter, deepest anteriorly and gradually fading away towards the tip, thus forming a boatlike structure with rounded keel; in preparations with stretched lateral walls the subgenital plate forms a symmetrical acute-angled triangle with a tiny stylus at the tip; cuticula very weakly sclerotized, only along the keel with a narrow band of stronger sclerotization, towards the lateral borders membraneous, rim very thin forming a sharp edge. *Stylus* (Fig. 5G): Tiny, specialized, but only with few scalelike microtrichia (not always well visible).

Left phallomere, genital hook (Fig. 2A,B,I–K): Weakly sclerotized, shaft long, with a longitudinal, towards the base strongly narrowing trough; apical end of the shaft at the frontal margin (below the claw tip) with a right- or protruding acute-angled edge (e in Fig. 2D,K), towards the opposite side (back) suddenly narrowing to a rather slender neck; claw strongly flattened in the plain of its curvation, in full length more or less regularly curved, together with the neck forming an ovally rounded sicklelike structure, claw largely membraneous except for a strongly sclerotized band running along the frontal margin of the neck and then turning over to the back side of the claw, tip of claw more or less broadly rounded; velum

forming an acutely triangular lobe or cone arising from the back of the neck. *Apodemal ruff* (Fig. 3A, 5E): Base of the endophallus apodeme ensheathed by membranes densely covered with scalelike microtrichia, forming a kind of a ruff around the base of the apodeme.

Right phallomere (Fig. 3A): Cleft sclerite and R3 sclerite well developed, not remarkably differing from those of most other Palearctic Ectobiinae.

Paraprocts: Not remarkably differing from the structures as described for the *sylvestris*-group of *Ectobius* (Bohn 2004).

Preparaprocts: Left preparaproct similar as in the *sylvestris*-group, right one only consisting of a short sclerite bracelet not surpassing the ventral margin of Pt10.

Since the five taxa treated herein do not show significant differences in the three last-mentioned characters these are not listed any more in the following descriptions.

Female abdomen. *Genital sclerites, dorsal complex* (Fig. 4A): Dorsal basivalvular sclerites of both sides apically converging but not fused, broadly subcrescent-shaped, broadest about in the middle, very weakly sclerotized, surface in the apical half slightly verrucous (Fig. 4F). Ventral basivalvular sclerites weakly developed, apically strongly narrowing, closely adjoining and following the lateral borders of the dorsal basivalvular sclerites, not reaching the apical end of the dorsal sclerites; remarkable is an at places very strong and massive but narrow sclerotization of the sclerites. *Ventral complex* (Fig. 4I): Central part of the laterosternal shelf circular or slightly transversely oval, with a pair of diverging posterior arms.

Ootheca. Surface with about 17 longitudinal ridges per side.

Life cycle. One year (univoltine development). The larvae hatch from the overwintering ootheca in spring or early summer and complete their development within few months with the imaginal moult in late summer or early autumn. The imagines die after mating and deposition of oothecae in late autumn.

Distribution (Fig. 10B)**.** Algeria, Morocco, Spain, France, Germany (at least since 2007), Great Britain (at least since 2011).

Remarks. The description of *E. vinzi* by Maurel (2012) needs correction in two important characters. (1) The claw of the hook is described and depicted (fig. 7 therein) as being narrow and ending in an acute tip. The description obviously only refers to the more strongly sclerotized parts of the claw, the characteristic broadening was not noticed. (2) The glandular pit of T7 according to Maurel (2012: fig. 8) is longitudinally oval; the differentiation into a fairly transversely oval open part and two internal anterior pouches is not specified.

The structure of the glandular pit of T7 in *Ectobius* and related genera usually shows great interspecific variation and, therefore, forms a very important means for the distinction of species. But the specimens of *Planuncus* from the various localities in Morocco, Algeria, Spain, France, Germany, and Great Britain show little variation in the structure of the pit; the differences between specimens from different localities don't seem to be greater than those beween specimens from the same locality (Fig. 7A,B). The great similarity in the structure of the glandular pit might indicate that all representatives of the subgenus *Planuncus* hitherto found belong to only one species, *P. tingitanus*, as already suspected by Morales Agacino (1948) with respect to the Northafrican members. At least, the descriptions of Chopard (1943, *P. finoti*) and Maurel (2012, *P. vinzi*) don't contain any information about how their newly established species can be distinguished from the previously described *P. tingitanus*.

Nevertheless, we hesitate to synonymize *P. finoti* and *P. vinzi* with *P. tingitanus*. Apart from the glandular pit some other characters should also be studied in more detail. Variations can be found in the shape of T6 (compare Figs. 1A, 7A,B), in the length of the wings, in the expression of the anal furrow of the tegmina, and in the three dimensional structure of the terminal tergites. But the structural differences did not appear to be strong and consistent enough to allow a clearcut separation in various species, and a molecular analysis was not possible since the material collected in Morocco, Spain, and France has been treated with formol. The matter is additionally complicated by the fact that characters like wing length and colouration may show an extremely high variability even within a local population as has been observed in the newly colonized area in Great Britain (Fig. 9B,C).

The unsatisfying situation in the taxonomy of the subgenus should be resolved by a new thorough study of various characters including molecular analysis, with freshly collected material from the type localities of the three described species and from a large series of localities in Algeria, Morocco, Spain, France, Germany and Great Britain. Till then all representatives of the subgenus should preferably be designated as members of the *Planuncus tingitanus*-complex.

3.1.2. Subgenus *Margundatus* Bohn, subgen. nov.

baetica-group of *Phyllodromica*, Bohn 1992: 319–345

Figs. 1C–E,P, 2 C,D,L,M, 3B, 4B,J,G, 5F

Type species

Planuncus (*Margundatus*) *baeticus* (Bolívar, 1884), **comb. nov.**

– *Aphlebia baetica* Bolívar, 1884: CV.
– *Phyllodromica baetica*: Princis 1971: 1105.

Other Species

Planuncus (*Margundatus*) *agenjoi* (Harz, 1971), **comb. nov.**

– *Phyllodromica agenjoi* Harz, 1971.

Planuncus (*Margundatus*) *erythrurus* (Bohn, 1992), **comb. nov.**

– *Phyllodromica erythrura* Bohn, 1992.

Planuncus (*Margundatus*) *intermedius* (Bohn, 1992), **comb. nov.**
– *Phyllodromica intermedia*, Bohn, 1992.
Planuncus (*Margundatus*) *krausei* (Bohn, 1992), **comb. nov.**
– *Phyllodromica krausei* Bohn, 1992.
Planuncus (*Margundatus*) *maculosus* (Bohn, 1992), **comb. nov.**
– *Phyllodromica maculosa* Bohn, 1992.
Planuncus (*Margundatus*) *paludicolus* (Bohn, 1992), **comb. nov.**
– *Phyllodromica paludicola* Bohn, 1992.
Planuncus (*Margundatus*) *princisi* (Fernandes, 1962), **comb. nov.**
– *Phyllodromica princisi* Fernandes, 1962.
Planuncus (*Margundatus*) *striolatus* (Bohn, 1992), **comb. nov.**
– *Phyllodromica striolata* Bohn, 1992.

Material studied. Same material as listed in Bohn (1992).

Etymology. The name of the subgenus refers to the undulate (Latin *unda* = wave) posterior margin (Latin *margo*) of T6.

Description. ***Wings***. Tegmina shortened, not surpassing T2; hindwings strongly reduced, lobiform, lateral, not surpassing the metanotum.
Colouration. *Imagines*: Mainly dark, posterior margin of abdominal tergites whitish, pronotum variously coloured, plain light to plain dark or maculose, with dispersed darker dots, but the latter inconspicuous in animals with lightly coloured disk, no dark lyrate pattern. *Juveniles*: Dark, without contrasting pattern.
Male abdomen. *Tergite bristles* (Fig. 1P): Surface of tergites only with normal bristles of various size. *Tergite 5*: Posterior border shallowly concave. *Tergite 6* (Fig. 1C): Latero-posterior corners posteriorly produced, rounded, posterior border in between with a sinusoidal concavity, surface near the latero-posterior corners often with a small elevation (hump). *Tergite 7* (Fig. 1D,E): Posterior border with a shallow obtuse-angled or rounded excavation. *Glandular pit*: Opening variously shaped, anterior border mesally usually with a posteriorly directed process, posterior border mesally with a dense, sometimes bipartite tuft of long bristles directed anteriorly; pit either without pouches, or with a pair of short anterior (and posterior, Fig. 1D) pouches, or pit below the opening extended to a large, anteriorly deeply bilobed pouch (Fig. 1E).

Sternite 9, subgenital plate (Fig. 3B): Very similar as in subgen. *Planuncus*, but sclerotizations more extended: area left of the keel slightly sclerotized, keel sclerotization anteriorly broadening to a large central area with lateral extensions. *Stylus*: missing.

Left phallomere, genital hook (Fig. 2C,D,L,M): Similar to the hook of the subgen. *Planuncus*, but neck usually broader and less rapidly narrowing, claw still broader, its tip less broadly rounded, frontal margin (facing the base of the hook) behind the tip with a concavity measuring about half of the claw length, velum small, visible as continuation of the frontal margin of the claw; in some of the species the similarities with the preceding subgenus are still more pronounced (shape of the neck and curvation of the sickle, Fig. 2C,L). *Apodemal ruff* (Fig. 3B, 5F): Similar to subgen. *Planuncus*, but structure usually more compact, almost scleritelike, and microtrichia more elongated, almost hairlike.
Female abdomen. *Genital sclerites, dorsal complex* (Fig. 4B,G): Dorsal basivalvular sclerites of both sides apically converging but not not fused, broad, in the apical half not narrower than in the basal half, apical half with numerous verrucous elevations with groups of poruslike perforations on the top; sclerite in the middle usually lighter coloured or complete anterior half weakly or not sclerotized; ventral basivalvular sclerites as in the subgen. *Planuncus* weakly developed, by far not reaching the apical end of the dorsal sclerites, at places with very strong but narrow sclerotization. *Ventral complex* (Fig. 4J): As in subgenus *Planuncus*.
Ootheca. Surface without longitudinal ridges, smooth.
Life cycle. Two years (semivoltine development). Larvae hatch in spring or early summer from overwintering oothecae, grow till the end of the first year up to a middle or a slightly later instar; after overwintering they complete the larval development and moult to imagines, which after mating and deposition of oothecae die in autumn.

Distribution. Sierras of southern Spain.

3.1.3. Subgenus *Margintorus* Bohn, subgen. nov.

Figs. 1F–H,Q, 2E,N, 3C, 4C,K, 5A,H, 6E,F

Type species
Planuncus (*Margintorus*) *nicaeensis* (Brisout de Barneville, 1852), **comb. nov.**
– *Blatta nicaeensis* Brisout de Barneville, 1852: LXVIII.
– *Ectobius nicaeensis*: Princis 1971: 1052.
Apart from the type species no other species known, subgenus monotypic.

Material studied
France: 4♀, 4O, Dept. Alpes-de-Haute-Provence, above Les Mées (25 km WSW Digne), 750 m, 7.VI.1982, leg. B.&H.Bohn (F 15); 1♀, 1O, Dept. Alpes-de-Haute-Provence, near Châteauredon (12 km S Digne), 600 m, 10.VI.1982, leg. B.&H.Bohn (F 18); 4♂, 23♀, 3O, Dept. Alpes-de-Haute-Provence, Grand Canyon du Verdon, La Maline, 550–700 m, 10.VI.1982, leg.B.&H.Bohn (slides: ♂, F 19/1,2,6; ♀, F 19/7–10); 6♂, 7♀, Dept. Alpes-de-Haute-Provence, Grand Canyon du Verdon, La Maline, 550–700 m, 28.V.1998, leg. B.&H.Bohn (slides: ♂, F 19a/2,8–10; ♀, F 19a/3,4); 2♂, 16♀, 3O, Depts. Drome/Alpes-de-Haute-Provence, Col de Pigiere (3 km SE Séderon), 970 m, 29.V.1998, leg. B.&H.Bohn (slide: ♂, F 99/1); 1♀, Dept. Alpes-de-Haute-Provence, Jausiers – Col de la Bonnette, near La Chalannette, 1500 m, 13.VII.2006, leg. B.&H.Bohn (F 147). (Collection H.Bohn).

Etymology. The name of the subgenus refers to the bulged (Latin *torus* = bulge) posterior margin (Latin *margo*) of T6.

Description. ***Wings*** (Fig. 6E,F). Well developed, fairly reaching the abdominal end; hindwings in both sexes slightly shortened, not reaching to the tips of the tegmina, apical triangle strongly reduced.
Colouration. *Imagines* (Fig. 5A): Mainly brownish, pronotum lightly coloured, with dispersed dark dots of various size extending also into the transparent lateral margins, disc additionally with larger markings forming in the center a lyrate pattern, in males often, in females sometimes completely covered by darker colour. *Juveniles*: Mainly lightly coloured, yellowish, nota with dispersed dark dots, pronotum disk with scarcely visible lyrate pattern.
Male abdomen. *Tergite bristles* (Fig. 1Q): Spatular bristles present on T(5)6–9, especially well developed and numerous on T6. *Tergite 5*: Posterior border shallowly concave. *Tergite 6* (Fig. 1F): Posterior border deeply concave, margin with a dorsal bulging, without sharp edge. *Tergite 7* (Fig. 1G,H): Posterior border shallowly concave or obtuse-angularly excised. *Glandular pit*: Opening transversely oval or subcordate, pit partly divided by a sagittal ridge having its summit posteriorly about at the level of the opening, descending form there towards ventro-anteriorly; pit on both sides of the ridge towards ventro-posteriorly deepened to two wide but short pouches; tergite surface mesally behind pit opening with a dense field of small bristles; anterior wall of pit above the ridge with dispersed long bristles.

Sternite 9, subgenital plate (Fig. 3C): Boatlike, but not as strongly symmetrical as in the preceding groups, left half of the subgenital plate largely membraneous with a very thin rim forming a sharp edge, right half with extended sclerotizations, rim thicker, rounded. *Stylus* (Fig. 5H): Inserted at the tip of T9, small, specialized, distally with tiny scalelike microtrichia.

Left phallomere, genital hook (Fig. 2E,N): More strongly sclerotized than in the preceding groups, apical end of shaft without angled edge at the frontal margin, shaft gradually narrowing into the neck, claw similarly broad and sclerotized as in the subgenus *Margundatus*, velum missing. *Apodemal ruff*: Absent, the apodeme is surrounded by loosely arranged membranes covered with dispersed short denticlelike structures, but a consistent three dimensional structure is not recognizable.
Female abdomen. *Genital sclerites, dorsal complex* (Fig. 4C): Dorsal basivalvular sclerites anteriorly converging but not fused, off the base rather narrow, well sclerotized throughout, smooth; ventral sclerites broader than the dorsal ones, slightly surpassing the apical ends of the latter. *Ventral complex* (Fig. 4K): Central part of the laterosternal shelf rather broad, transversely oval.
Ootheca. Surface without longitudinal ridges, smooth.
Life cycle. Two years (semivoltine development).

Distribution. Southern France (Provence).

3.2. Genus *Capraiellus* Harz, 1976

Figs. 1I–K,R, 2F,O, 3D, 4D,H,L, 5B,C,I, 6J, 10B

Type species
Capraiellus panzeri (Stephens, 1835).
– *Ectobius panzeri* Stephens, 1835: 47.

Other species
Capraiellus tamaninii (Galvagni, 1972).
– *Ectobius tamaninii* Galvagni, 1972: 4, numerous figs.
Capraiellus haeckeli (Bolívar, 1876).
– *Ectobius haeckeli* Bolívar, 1876: 118. **Nomen dubium**.

Material studied
Capraiellus panzeri. France: 8♂, 7♀, 7O, Dept. Pyrénées-Orientales, Prieuré de Serrabonne, 500 m, 8.VIII.1983, leg. B.&H. Bohn (slides: ♂, F 27/2–5; ♀, F 27/1); 11♂, 10♀, 1L, 6O, Dept. Pyrénées-Orientales, above Fetges (near Mont-Louis), 1600 m, 10.VIII.198 3, leg. B.&H.Bohn (slides: ♂, F 30/2,3); 1♀, 2L + ex L: 1♂, 1♀, Dept. Aude, Montagne de Tauch (near Tuchan), Tour de Géographes, 870–900 m, 18.VII.2005, leg. B.&H.Bohn (slide: L, F 43b/3); 2♂, 1♀, 4L + ex L: 6♂, 3♀, 6L, Dept. Var, near Col de Gratteloup (10 km N Le Lavandou), 190 m, 5.VIII.1996, leg. B.&H. Bohn (slide: ♂, F 96/1); 11♂, 3♀, Dept. Herault/Gard, 3.5 km N Le Caylar, 800 m, 20.VII.2005, leg. H.Bohn (F 105); 1♂, 6L, Dept. Gard, Val de la Dourbie, Les Laupiettes, 1000 m, 20.VII.2005, leg. H.Bohn (F 107); 5♂, Dept. Gard, Val de la Dourbie, 2 km E Les Laupies, 1080 m, 20.VII.2005, leg. H.Bohn (F 108); 1♂, 2L, Dept. Gard, Val de la Dourbie, 3 km SW l'Espérou, 1150 m, 20.VII.2005, leg. H.Bohn (F 109); 5♂, 2♀, 3L, Dept. Lozère, Mont Lozère (near Florac), Finiels, 1260 m, 21.VII.2005, leg. H.Bohn (F 113); 6♂, 2♀, 1L, Dept. Lozère, Mont Lozère (near Florac), Col de Finiels, 1540 m, 21.VII.2005, leg. H.Bohn (F 114); 7♂, 1♀, 2L, Dept. Gard, Mont Lozère (near Florac), Plateau de la Croix de l'Eremite, 1450 m, 21.VII.2005, leg. H.Bohn (F 115). – Morocco: 2♂ + ex L: 4♂, 4♀, Rif, Bab-Besen (15 km W Ketama), 1600 m, 14.VIII.1984, leg. B.&H.Bohn (slides: ♂, Ma 6/1,2,3,8). – Spain: Numerous specimens from many localities throughout Spain, not listed here.
Capraiellus tamaninii. France: 2♂, 1♀ + ex L: 11♂, 6♀, 1L, Dept. Alpes-Maritimes, SE slope of Col de Tende, 1450 m, 3.VIII.2005, leg. B.&H.Bohn (slides: ♂, F 119/1,3). – Switzerland: 1♀ + ex L: 1♀, Kanton Wallis, Hohtenn, 900 m, 7.VIII.1996, leg. B.&H. Bohn (He 5a); 5♂, 4♀, 1O + ex L: 6♂, 3♀, 4L, Kanton Wallis, Außerberg, 1100 m, 13.VII.1997, leg. B.&H.Bohn (slide: ♂, He 24/1); ex L: 6L, Kanton Wallis, Außerberg, 1350–1500 m, 13.VII.1997, leg. B.&H.Bohn (He 25). – Italy: 12♂, 16♀, Umbria, Appennino Umbro-Marchigiano, Monti Sibillini, W slope of Mt. Ventosola, il Muraglione - Rif. Perugia, 1000–1500 m, 16.VIII.1986, leg. B.&H.Bohn (slide: ♂, It 40/1); 4♂, 9♀, Abruzzo, Appennino Abruzzese, Gran Sasso d'Italia, Lago di Campotosto, E slope of Mt. Il Castellano, 1450 m, 21./22.VIII.1987, leg. B.&H. Bohn (It 56); 5♂, 1♀, Abruzzo, Appennino Abruzzese, Gran Sasso d'Italia, 'Piede il Cavallo', 2 km N Assergi (NE L'Aquila), 1000 m, 22.VIII.1987, leg. B.&H.Bohn (It 57); 28♂, 12♀, 2O, Abruzzo, Appennino Abruzzese, Gran Sasso d'Italia, SW slope of Monte Cristo, 1500 m, 22.VIII.1987, leg. B.&H.Bohn (It 58); 5♂, 1♀,

Abruzzo, Appennino Abruzzese, Gran Sasso d'Italia, Monte Cecco d'Antonio, 1600 m, 22.VIII.1987, leg. B.&H.Bohn (It 60); 2♂, 5♀, Abruzzo, Appennino Abruzzese, "Marsica", Forca Caruso (E Celano), 1100 m, 23.VIII.1987, leg. B.&H.Bohn (It 61); 2♂, 2♀, Abruzzo, Appennino Abruzzese, "Marsica", Goriano Sicoli (7 km SW Raiano), 800 m, 23.VIII.1987, leg. B.&H.Bohn (It 62). – **Bosnia-Herzegovina**: 9♂, 3♀, 2L, Dinara-Kamešnica, Trnova-Poljana, 900–1100 m, 12.VIII.1988, leg. B.&H.Bohn (Yu 33); 3♂, 4♀, Hrvatska-Bosna-Hercegovina Gora, Orjen Planina, near Jablan Do, 700–800 m, 15.VIII.1988, leg. B.&H. Bohn (Yu 41). – **Macedonia**: 2♀, Pletvar (11 km E Prilep), 990 m, 11.XI.1982, leg. B.&H.Bohn (Yu 12). – **Montenegro**: 11♂, 11♀, 1L, Dolovi, 1400 m, 17.VIII.1988, leg. B.&H.Bohn (Yu 46). – **Greece**: 4♂, 2♀, Nom. Kastoriá, Vérnon Óros, 3 km NW Apóskepos (near Kastoriá), 950 m, 3.IX.1977, leg. B.&H.Bohn (slide: ♂, Gr 5/4); 1♂, 1♀, Nom. Ioánnina, Smólikas Óros, above Pades, 1600 m, 21.VIII.1982, leg. B.&H.Bohn (Gr 20); 12♂, 7♀, Nom. Tríkala, Píndos Óros, above Malakásion (Katára-Pass), 1300 m, 27.VIII.1982, leg. B.&H.Bohn (slides: ♂, Gr 27/1,2); 6♂, 14♀, Nom. Lefkas, Insel Lefkas, Óros Kalokerinó, 1000 m, 2.IX.1982, leg. B.&H.Bohn (slide: ♀, Gr 32/1); 1♂, 3♀, Nom. Kastoriá, Vérnon Óros, Polikérasson, 1400 m, 7./8.IX.1982, leg. B.&H.Bohn (Gr 39). (Collection H.Bohn).

Description. ***Wings***. Male fully winged, wings reaching or surpassing the abdominal end, hindwings slightly surpassing the tegmina, apical triangle well developed; female with strongly shortened wings, tegmina transversely cut, reaching up to T2, hindwings rudimentary, lobiform, lateral, considerably shorter than the metanotum.

Colouration. *Imagines* (Fig. 5B): Male pale yellowish, usually with a double series of darker patches of various extension and intensity along both surfaces of the abdomen, female darker; pronotum of both sexes with dispersed dark dots, disk additionally with larger markings in the center forming a lyrate pattern, the latter sometimes very weak or missing. *Juveniles*: First larval stages black with a broad white stripe across the metanotum (compare with Fig. 9F). Later stages anteriorly of the white transversal stripe with a broadly black outlined triangle, outline anteriorly sometimes interrupted (Figs. 5C, 6J).

Male abdomen. *Transversal ridge of tergites 2–6*: Only laterally well developed, mesally only indicated by darker pigmentation. *Tergite bristles* (Fig. 1R): Numerous strong spatular bristles on T6, occasionally also some on T5. *Tergite 5*: Posterior border weakly concave. *Tergite 6* (Fig. 1I): Posterior border with a broad, moderately deep sinusoidal concavity. *Tergite 7* (Fig. 1J,K): Posterior border with a variously shaped and deep concavity. *Glandular pit*: Small and shallow, almost circular in outline, diameter between 1/4 and 1/5 of the tergite breadth; posteriorly with an anteriorly directed bristled knob distally either narrowing (*C. panzeri*, Fig 1J) or broadening (*C. tamaninii*, Fig. 1K), densely covered by bristles with slightly curved tip; along the anterior border of the pit opening with a series of long straight bristles.

Sternite 9, subgenital plate (Fig. 2D): Posterior lobe boat-shaped, in dorsal view forming an acute-angled, almost symmetrical triangle, fully but not very strongly sclerotized, rim rounded. *Stylus* (Fig. 5I): Moderately long, curved, fairly conical, specialized, distal half densely covered with scalelike microtrichia.

Left phallomere, genital hook (Fig. 2F,O): Apical end of shaft without angled edge at the frontal margin, shaft gradually narrowing into a relatively broad neck, claw throughout its length very narrow, massive, almost cylindrical, weakly and regularly curved; velum variable, in Fig. 2O appearing as a broad mound at the neck. *Apodemal ruff*: Absent.

Symmetry: Terminalia (S9 with stylus and phallomeres, paraprocts and preparaprocts) with reverse right-left-symmetry; the originally 'left' structures at the right side and mirror-image.

Female abdomen. *Genital sclerites, dorsal complex* (Fig.4D,H): Dorsal basivalvular sclerites very short, basally strongly sclerotized, dark, apically broadening and lightening, not verrucous, membraneous area in between conspicuously folded, with hairy surface (Fig. 4H); ventral basivalvular sclerites by far surpassing the apical end of the dorsal sclerites. *Ventral complex* (Fig. 4L): As in subgenus *Planuncus*.

Ootheca. Surface without longitudinal ridges, smooth.

Life cycle. One year (univoltine development; Ragge 1965; Morvan 1972).

Distribution. *C. panzeri*: England, Denmark, Germany, Netherlands, Belgium, Luxemburg, France, Spain, Portugal, Madeira, Morocco (new; Fig. 10B). *C. tamaninii*: France (new), Switzerland (new), continental Italy, Sicily, Croatia (new), Bosnia-Herzegovina (new), Macedonia (new), Montenegro (new), Greece.

Taxonomical remarks. *Capraiellus* was erected by Harz (1976) as a subgenus of *Ectobius*. The great number of important autapomorphies – in the male the reverse right-left-symmetry, the shape of the subgenital plate and of the genital hook, in the female the genital sclerites – in our eyes justify the rise to the state of a genus.

Besides *C. panzeri* and *C. tamaninii* a third species of the genus was described from Spain, *C. haeckeli* (Bolívar, 1876). But the structure of the glandular pit on T7 of this species, indispensible for an equivocal identification, is not known and not analysable since the abdomen of the singular type specimen has been lost. The species name *haeckeli*, therefore, has to be considered as a "nomen dubium". *C. panzeri* shows great variability, especially on the Iberian peninsula (Fernandes 1973), suggesting a composition of several species; a thorough revision should clarify this question.

Faunistic remarks. *C. tamaninii* was hitherto known from continental Italy, Sicily and Greece (Failla & Messina 1979; Galvagni 1991). Earlier reports of *C. panzeri* from the former Yugoslavia were assumed also to refer to this species. The new material listed above shows the occurrence of *C. tamaninii* in most of the Balkan countries, in Switzerland (Wallis; reported as

C. panzeri by Ramme 1923), and in France. The so far singular locality in France is situated in the Dept. Alpes-Maritimes immediately beyond the Italian frontier. It would be interesting to know how far westwards the distribution of the species reaches, and whether it could meet *C. panzeri*.

The finding of *C. panzeri* in Morocco, though at only one locality in the Rif, considerably extends the known distribution southwards beyond the Mediterranean Sea. The new report has some relevance to the phylogenetic hypothesis developed in the discussion below since it connects the distribution areas of species or species groups concerned in the phylogenetic considerations (*Ectobius hipposiderus – Capraiellus*).

3.3. *Ectobius hipposiderus* Bohn, spec. nov.

Figs. 1L–N,S, 2G,P, 3E, 4E,M, 5D,J, 6A,B,I, 7J–N, 8A–I, 10B

Material studied

Type material. **Morocco**: ♂ holotype, Haut Atlas, Tizi-n-Test-TV station, 2100–2400 m, 24.VIII.1984, leg. B.&H.Bohn (completely on two slides: Ma 18/27). (Zoologische Staatssammlung München).

Additional material. **Morocco**: 29♂, 44♀, 4L, 10O + ex L: 2♂, 6♀, Haut Atlas, Tizi-n-Test-TV station, 2100–2400 m, 24.VIII.1984, leg. B.&H.Bohn (slides: ♂, Ma 18/1–3,28,29,33–35; ♀, Ma 18/18,30–32); 1♂, 2♀, same data, but 7.X.2000 (Ma 18b); 6♂, 11♀, 1O + ex L: 1♀, Haut Atlas, Tizi-Ousla, 7 km E Tougramane (60 km S Marrakech), 1050 m, 25.VIII.1984, leg. B.&H.Bohn (slide: ♂, Ma 19/1); 1♂, 2♀, Haut Atlas, Tizi-Ousla, 7 km E Tougramane (60 km S Marrakech), 1050 m, 6.X.2000, leg. B.&H. Bohn (Ma 19a); 1♂, 6♀, 1O, Haut Atlas, 10 km N Tounfite (36 km SW Boumia), 2000 m, 29.VIII.1984, leg. B.&H.Bohn (slide: Ma 25/1); 1♂, Monts des Beni-Snassèn, 1 km S Taforalt, 800 m, 15.IX.2000, leg. B.&H.Bohn (slide: ♂, Ma 72a/1); ?2L, Moyen Atlas, Jbel bou Iblane, NW above Timezraï (Tighza–Tamjilt), 1800 m, 20.IV.1998, leg. B.&H.Bohn (Ma 79a); 1♀, Haut Atlas, Tizi-n-Talrhemt (SE Midelt), 1900 m, 23.IX.2000, leg. B.&H. Bohn (Ma 85d); ?2L, Pays Zaër Zaïane, Jbel Tafernennt (ca. 30 km E Ez-Zhiliga), 950 m, 5./6.V.1997 (Ma 135); ex L: 3♀, 2L, Pays Chiadma, J. Hadid (ca. 50 km NE Essaouira), 700 m, 7./8.V.1997, leg. B.&H.Bohn (slides: L, Ma 140/2,3); 1♀, Pays Chiadma, J. Hadid (ca. 50 km NE Essaouira), 700 m, 7.VIII.1999, leg. H.Bohn (Ma 140b); ex L: 1♂, W slope of Haut Atlas, Haha, J. Amsittene, 900 m, 8./9.V.1997, leg. B.&H.Bohn (slide: ♂, Ma 141/1); 2L, W slope of Haut Atlas, 3 km S Immoussèr-des-Ida-Outanane (50 km NE Agadir), 1100–1200 m, 10.V.1997, leg. B.&H.Bohn (Ma 142); 21♂, 5♀, 3L + ex L: 8♂, 2♀, 7L, W slope of Haut Atlas, 3 km S Immoussèr-des-Ida-Outanane (50 km NE Agadir), 1100–1200 m, 8.VIII.1999, leg. H.Bohn (slide:♂, Ma 142b/1); 1♀, W slope of Haut Atlas, 11 km NE Immoussèr-des-Ida-Outanane (50 km NE Agadir), 1600 m, 8.VIII.1999, leg. H.Bohn (Ma 143a); ex L: 1♂, W slope of Haut Atlas, ca. 20 km NE Immoussèr-des-Ida-Outanane (50 km NE Agadir), 1550 m, 10./11.V.1997, leg. B.&H. Bohn (Ma 144); 3♂, 1♀ + ex L: 2♂, 1♀, 1L, W slope of Haut Atlas, ca. 20 km NE Immoussèr-des-Ida-Outanane (50 km NE Agadir), 1550 m, 8.VIII.1999, leg. H.Bohn (slide: ♂, Ma 144a/1); 2♀,1O, W slope of Haut Atlas, ca. 20 km NE Immoussèr-des-Ida-Outanane (50 km NE Agadir), 1550 m, 8.X.2000, leg. B.&H.Bohn (Ma 144b); 2♂, 1♀, Haut Atlas, W above Zinit (N Tizi-n'Tabgourt, SE Imi-n-Tanoute), 1700–1900 m, 7.VIII.1999, leg. H.Bohn (slide: Ma 145a/1); 1♂, Haut Atlas, Ti-n-Mellili (near Tanefacht, NNE Taroudannt), 1200 m, 14.V.1997 (slide: Ma 147/1); ex L: 1♂, 2♀, Haut Atlas, Islane (near Tasguinnt, NNE Taroudannt), 1900–2100 m, 14.V.1997, leg. B.&H.Bohn (Ma 148); 3♂ + ex L: 2♂, 3♀, 3L, Haut Atlas, Islane (near Tasguinnt, NNE Taroudannt), 1900–2100 m, 9.VIII.1999, leg. H.Bohn (slide: ♂, Ma 148a/1); ex L: 1♀, Haut Atlas, S slope of Tizi-n-Test, 1500 m, 15.V.1997, leg. B.&H.Bohn (Ma 150); 3♂ + ex L: 2♂, 3♀, 1L, Haut Atlas, S slope of Tizi-n-Test, 1500 m, 10.VIII.1999, leg. H.Bohn (slide: ♂, Ma 150a/1); ex L: 1♂, 1♀, Haut Atlas, S slope of Tizi-n-Test, 1900 m, 15.V.1997, leg. B.&H.Bohn (slide: ♂, Ma 151/2); 1♀, Haut Atlas, Ruines Iguer (ca. 8 km NE Tizi-n-Test), 2050 m, 7.X.2000, leg. B.&H.Bohn (Ma 152a); ex L: 1♂, Haut Atlas, Tizi-n-Oulaoune (S Ijoukak), 2100 m, 17.V.1997, leg. B.&H.Bohn (Ma 153); 6♂, 2♀, 3L + ex L: 3♂, 5♀, 4L, Haut Atlas, Tizi-n-Oulaoune (S Ijoukak), 2100 m, 10.VIII.1999, leg. H.Bohn (slide: ♂, Ma 153a/1); 1♂, 10♀, Haut Atlas, Tizi-n-Oulaoune (S Ijoukak), 2100 m, 6.X.2000, leg. B.&H.Bohn (Ma 153b); ?1L, Haut Atlas, btw. Taghbart & Tizi-n-Oulaoune (S Ijoukak), 1500 m, 17.V.1997, leg. B.&H. Bohn (Ma 154); 1♂, 1♀, 4L, Haut Atlas, 9 km SW Asni, 1000 m, 17.V.1997, leg. B.&H.Bohn (Ma 155); 11♂, 2♀, Haut Atlas, 9 km SW Asni, 1000 m, 11.VIII.1999, leg. H.Bohn (slide: ♂, Ma 155a/1); 4♀, Haut Atlas, ca. 10 km SE Tahanaoute (S Marakech), 1400 m, 11.VIII.1999, leg. H.Bohn (Ma 157a); ?1L, Haut Atlas, ca. 15 km SE Tahanaoute (S Marakech), 1650 m, 18.V.1997, leg. B.&H.Bohn (Ma 158); ex L: 3♀, 1L, Haut Atlas, Tizi-n'Outfi (ca. 45 km S Demnate), 2100 m, 20.V.1997, leg. B.&H.Bohn (Ma 162); ex L: 2♀, Haut Atlas, ca. 3 km NE Cirque de Jaffar (SW Midelt), 2000–2150 m, 23.V.1997, leg. B.&H.Bohn (Ma 173); 2♂, 2♀ + ex L: 1♀, 1L, Mts. des Beni-Snassèn, M.F. d'Âïn-Âlmou, 950–1200 m, 17.VIII.1999, leg. H.Bohn (slide: ♂, Ma 235a/1); 3♂, 1♀, Mts. des Beni-Snassèn, M.F. d'Âïn-Âlmou, 950–1200 m, 15.IX.2000, leg. B.&H.Bohn (Ma 235b); 2♂, 2♀, 1O, S slope of Jbel Bou Keltoum (ca. 46 km SSW Oujda), 1400 m, 16.IX.2000, leg. B.&H. Bohn (slide: ♂, Ma 237b/1); 2♂, 1♀, 5 km E Debdou, 1200 m, 17.IX.2000, leg. B.&H.Bohn (Ma 241a); 4♀, Haut Atlas, 2.5 km S Âït-Tamlil (ca. 55 km S Demnate), 1600 m, 1.X.2000, leg. B.&H. Bohn (Ma 317); 6♀, Haut Atlas, 6 km S Tizi-n-Tichka, 2000 m, 3.X.2000, leg. B.&H.Bohn (Ma 322); 1♂, 2♀, Haut Atlas, Tizi-Ghourane (SE Amizmiz, ca. 60 km SSW Marrakech), 1700 m, 4./5.X.2000, leg. B.&H.Bohn (slide: ♂, Ma 324/1). (Collection H.Bohn).

Etymology. The species name refers to the dark marking on the pronotum resembling the shape of a horse (Grecian *hippos*) shoe (Grecian *sideros* = iron).

Description. ***Size***. Length of pronotum in male 1.73–1.95 (mean 1.86) mm, in female 2.05–2.24 (mean 2.12) mm; length of tegmina in male 7.54–8.71 (mean 8.14) mm, in female 7.47–8.06 (mean 7.70) mm (N = 10–12).

Wings (Fig. 6A,B). In both sexes fully developed, surpassing the abdominal end, tegmina narrow, with narrowly rounded tip, hindwings slightly surpassing the tegmina, with well developed apical triangle.

Colouration. *Imagines*: Male mainly lightly coloured, pale yellowish, with some darker, brown markings. Head with broad dark interocular stripe and triangular marking on the frons. Pronotum with a dark horseshoe-shaped marking (Fig. 8I). Tegmina (Fig. 6A) mottled by the darker interveinal spaces, occasionally fusing to larger patches, at the base of the anal field with a short dark stripe as continuation of the horseshoe marking of the pronotum; dark dots along the anterior branches of the radius. Legs with partly darkened basal sclerites, dorsal side of femur dark. Abdominal tergites and sternites near the lateral border – sometimes also mesally – with a darker variously shaped and often quite indistinct patch giving rise to two or three longitudinal stripes on both surfaces of the abdomen. Colouration of female as in male, but dorsal darkenings of abdomen more extended, dorsal surface sometimes almost completely dark; ventral surface with very distinct lateral patches connected by a transversal stripe along the anterior part of the sternites. *Juveniles*: First larval stages black with a broad white stripe across the metanotum (compare with Fig. 9F). Later stages anteriorly of the white transversal stripe with a broadly black outlined triangle (Figs. 5D, 6I).

Male abdomen. *Tergite bristles* (Fig. 1S): T6 with numerous strong spatular bristles, sometimes few spatular bristles also on T5 and T7. *Tergites 2–4* (Fig. 8A): Posterior border straight. *Tergite 5* (Fig. 8B): Posterior border minimally concave. *Tergite 6* (Fig. 8C): Posterior border angularly excised, sides of the excision convex. *Tergite 7* (Figs. 7J–N, 8D,E): Posterior border shallowly concave. *Glandular pit*: Rather small, scarcely broader than 1/5 of segment breadth; opening rounded trapezoidal, posterior border mesally usually with slight anterior protrusion; pit rather flat, anterior wall in the anterio-lateral corners deepened to rather shallow pouches, which may have extensions up to the posterior border of the pit (Fig. 7N); bottom of the pit near the posterior border elevated to a knob densely covered with strongly curved bristles, bottom anteriorly of the knob with a field of bristles aligned towards the knob; along the anterior border of the opening with a row of long straight bristles, behind the posterior border with a field of shorter straight bristles. *Tergite 8* (Fig. 8F): Posterior border minimally concave, lateral borders convexly curved. *Tergite 9* (Fig. 8G): Posterior border broadly rounded convex, with short lateral lobes, right one larger. *Tergite 10* (Fig. 8H): Posterior lobe (posteriorly of insertion of cerci) moderately long, broadly rounded. *Cerci*: Relatively long and slender.

Sternite 9, subgenital plate (Fig. 3E): Posterior lobe not boat-shaped, rather forming a slightly concave plate, asymmetrical, left border straight or weakly concave, right border strongly curved, convex, with a thick rounded rim. *Stylus* (Fig. 5J): moderately long, conical, curved, specialized, distal half densely covered with small scale-like microtrichia.

Left phallomere, genital hook (Fig. 2G,P): Apical end of the shaft at the frontal margin broadly rounded, suddenly narrowing to a slender neck, claw relatively narrow, distal third angularly curved and narrowed to a massive, almost cylindrical, nose- or trunklike structure, tip slightly thickened, velum not forming a notable protrusion. *Apodemal ruff*: Absent.

Female abdomen. *Genital sclerites, dorsal complex* (Fig. 4E): Basivalvular sclerites of both sides very long, apically strongly converging and approaching, but not fused; dorsal sclerites very narrow, at about two thirds of their length transiently broadening; ventral sclerites broader than the dorsal ones, but not reaching their apical end; between the basivalvular sclerites with an unusually large broadly tongue-shaped sclerite arising from the anterior arch of the second valvifer (compare with Fig.4C). *Ventral complex* (Fig. 4M): As in the subgenus *Planuncus*.

Ootheca. Surface without longitudinal ridges, smooth.

Life cycle. One year (univoltine development).

Distribution (Fig. 10B)**.** Morocco along the High Atlas and its western foothills, and eastern part of the Rif; more or less southernly adjacent to the distribution of the *Planuncus tingitanus*-complex, only at one locality (Ma 235, Fig. 10A,B) both taxa found together.

Remarks. Species with a similar striking dark horseshoe marking on the pronotum are also found among the Centralasiatic Ectobiinae, namely *Ectobius delicatulus* Bey-Bienko, 1950, *E.* (*Ectobiola*) *duskei* Adelung, 1906, *E. pusillus* Bey-Bienko, 1967, and *E. tadzhicus* Bey-Bienko, 1935. One of these species, *E. duskei*, also agrees with *E. hipposiderus* in having a similar univoltine development (Bey-Bienko 1969). But there is no agreement in other characters: The tegmina of the females are strongly shortened being either transversely cut or lobiform, lateral; the structure of glandular pit of T7 (not yet known from *E. pusillus*) is different, without a bristled knob; the colouration of the juveniles of *E. duskei* – dark horseshoe marking on the pronotum and three dark longitudinal stripes (Adelung 1919) – shows no similarity with *E. hipposiderus.* A close relationship of these species with *E. hipposiderus*, therefore, would appear unlikely. It should, however, be pointed out that many of the characters important for phylogenetic considerations – male and female genital sclerites, structure of stylus – are still not known.

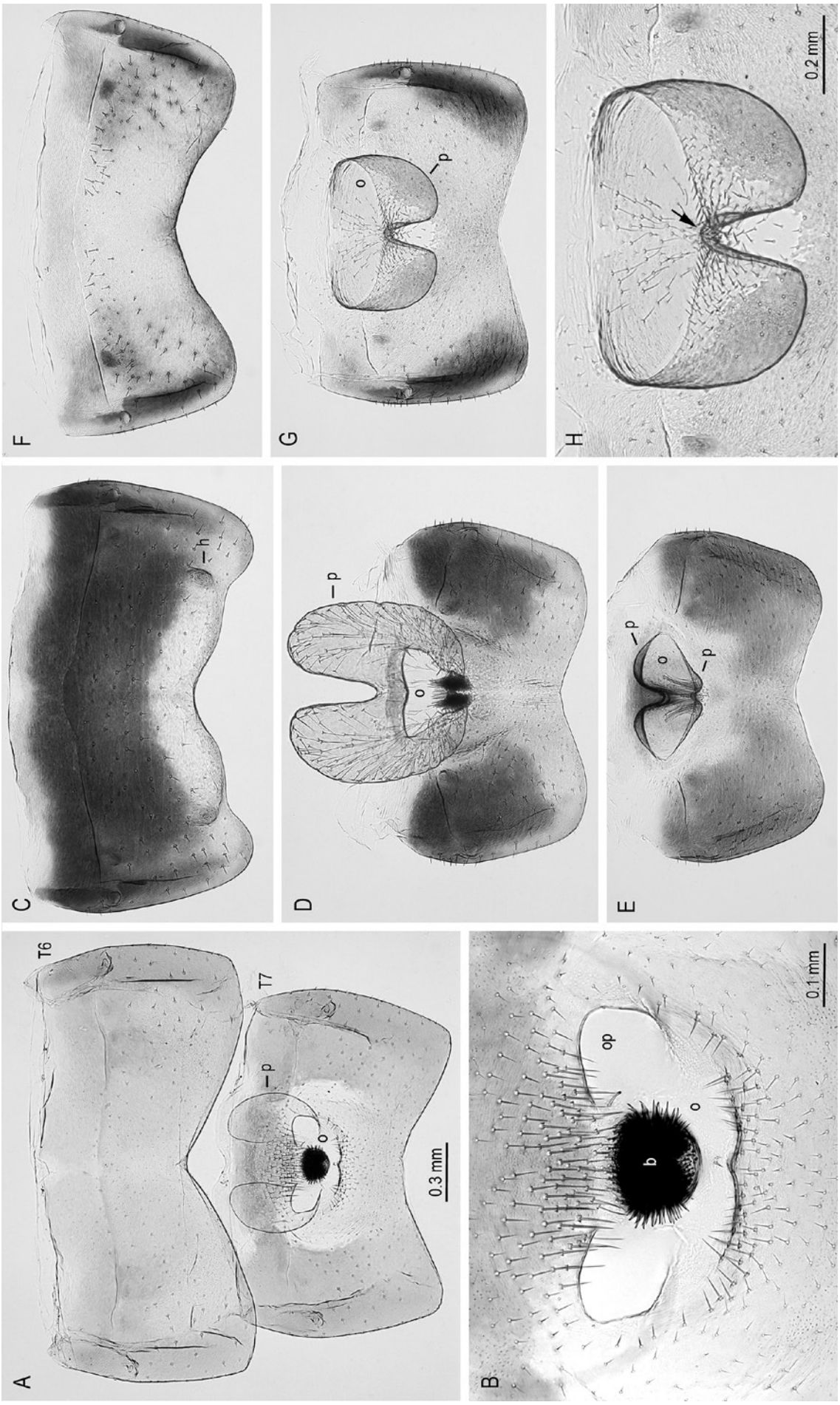
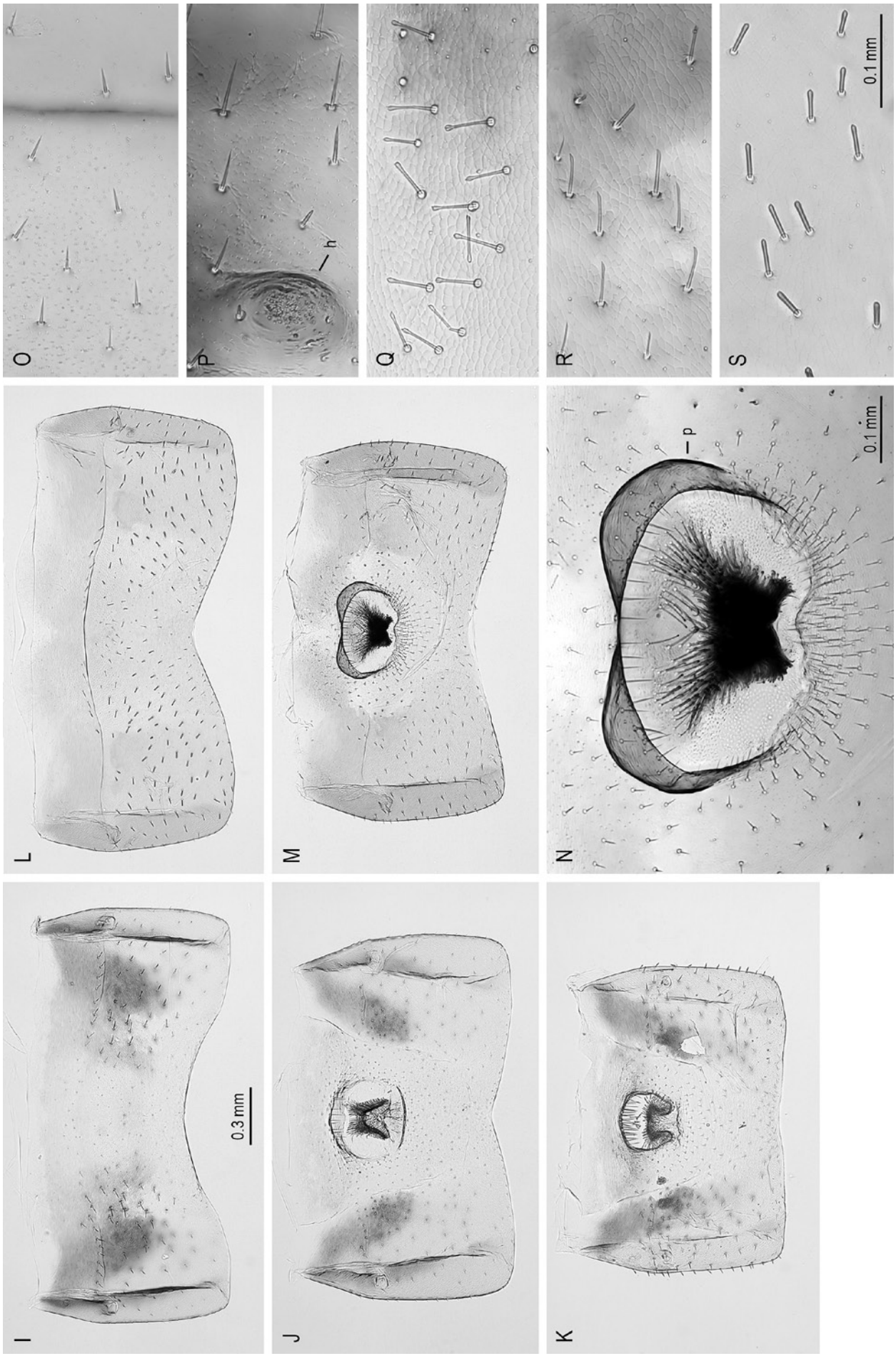


Fig. 1. (↑↓) Male abdominal tergites T6 and T7, and glandular pit of T7; O–S: bristles from surface of T6, details from A,C,F,I. **A**,**B**,**O**: *Planuncus tingitanus*-complex, T6+7 (A), glandular pit (B), bristles of T6 (O). **C**,**D**,**P**: *Margundatus agenjoi*, T6 (C), T7 (D), T6 bristles (P). **E**: *Margundatus princisi*, T7. **F**,**G**,**H**,**Q**: *Margintorus nicaeensis*, T6 (F), T7 (G), glandular pit (H; arrow points to the longitudinal ridge), T6 bristles (Q). **I**,**J**,**R**: *Capraiellus panzeri*, T6 (I), T7 (J), T6 bristles (R). **K**: *Capraiellus tamaninii*, T7. **L**,**M**,**N**,**R**: *Ectobius hipposiderus*, T6 (L), T7 (M), glandular pit (N), T6 bristles (R). – Abbreviations: **b** bristled knob, **h** hump, **o** opening of the T7 glandular pit, **op** opening of an internal pouch (**p**) of the pit. – Enlargements: same scale for A,C–G, for I–M, and for O–S. – Specimen identification: Sp 15/8 (A,B,O), Sp 66/2 (C,D,P), Sp 251/4 (E), F 99/1 (F,G,H,Q), F 27/3 (I,J,R), F 119/1 (K), Ma 18/29 (L,M,N,S).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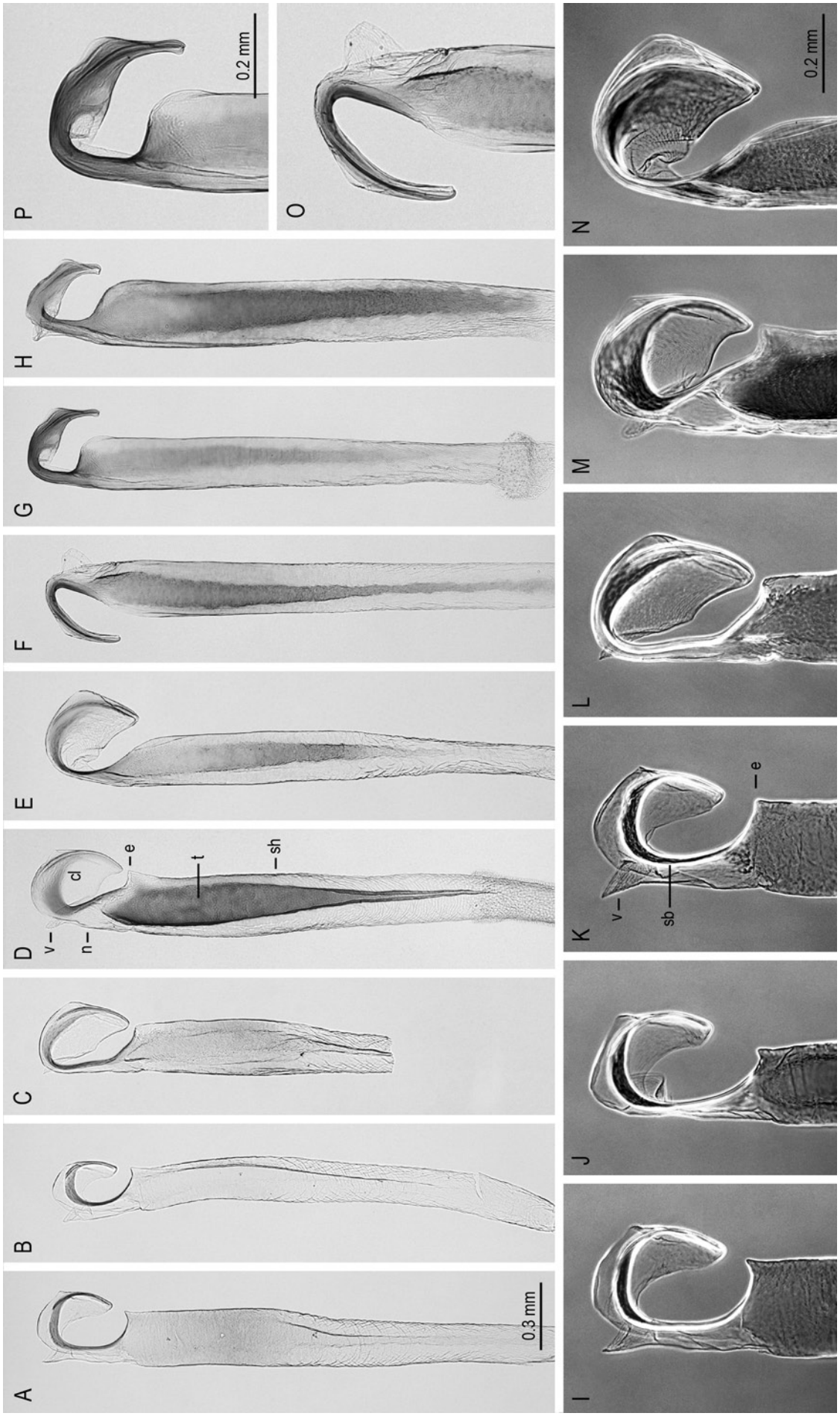


Fig. 2. Male genital hook; A–H: in almost full length; I–P: apical part enlarged (I–N phase contrast). **A**,**B**,**I**,**J**,**K**: *Planuncus tingitanus*-complex, from Morocco near type locality of *P. tingitanus* (A,I,J), from France (B), and from Germany (K). **C**,**L**: *Margundatus maculosus*. **D**,**M**: *Margundatus agenjoi*. **E**,**N**: *Margintorus nicaeensis*. **F**,**O**: *Capraiellus panzeri* (with reversal of right-left symmetry). **G**,**P**: *Ectobius hipposiderus*. **H**: *Ectobius lapponicus*. – Abbreviations: **cl** claw, **e** edge, **n** neck, **sh** shaft, **sb** sclerotization band, **t** trough, **v** velum. – Enlargements: same scale for A–H, for I–N, and for O–P. – Specimen identification: Ma 45/6 (A,I), F 94/1 (B), Sp 260/1 (C,L), Sp 252/2 (D,M), F 99/1 (E,N), F 27/5 (F,O), Ma 18/28 (G,P), Ru 3/3 (H), Ma 45/5 (J), D 235/2 (K).

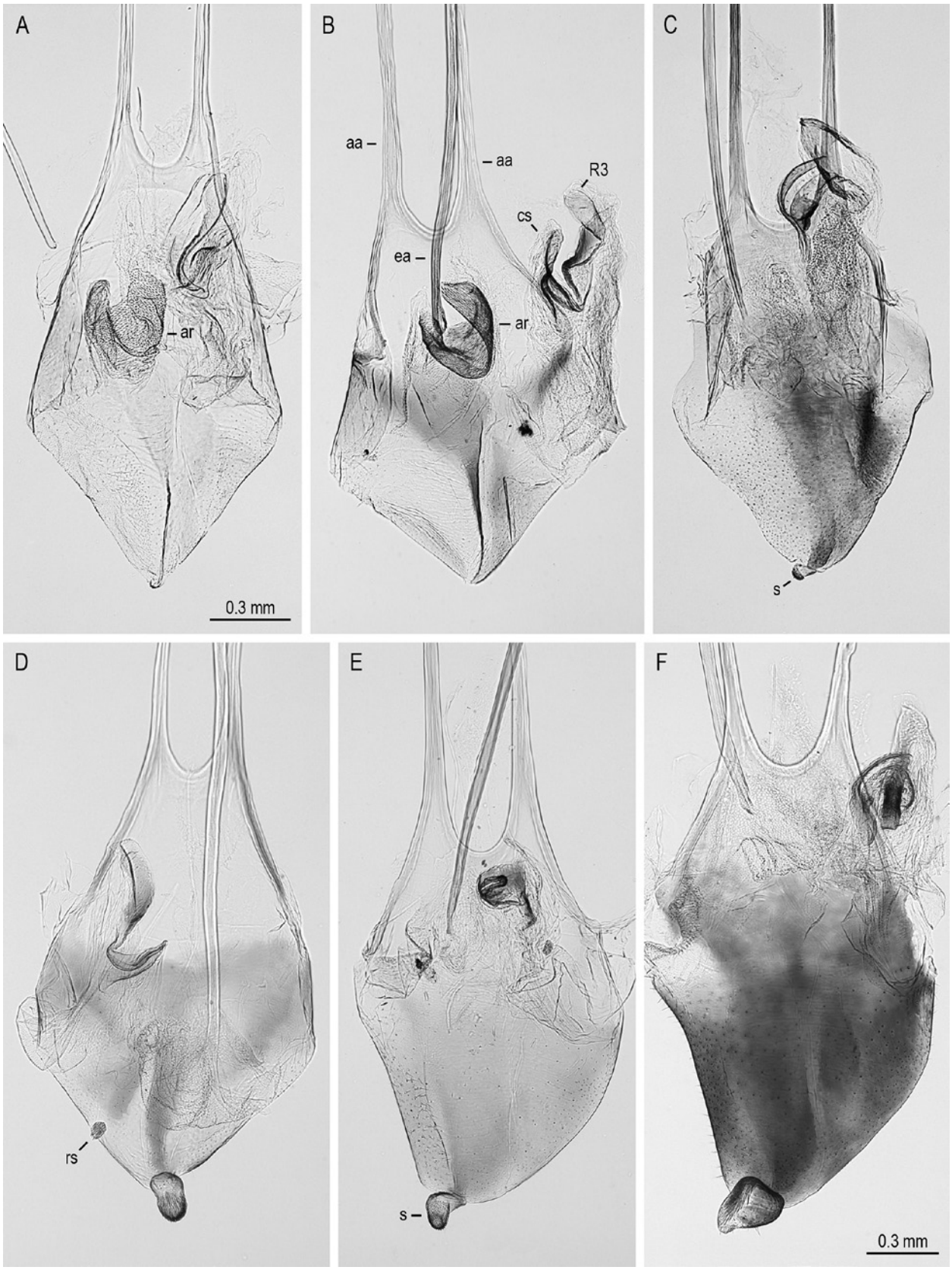


Fig. 3. Male subgenital plate (S9) and phallomeres, part of left phallomere (hook) removed; dorsal view. **A**: *Planuncus tingitanus*-complex. **B**: *Margundatus agenjoi*. **C**: *Margintorus nicaeensis*. **D**: *Capraiellus panzeri*, notice reversal of right-left symmetry. **E**: *Ectobius hipposiderus*. **F**: *Ectobius lapponicus*. – Abbreviations: **aa** anterior apodemes of subgenital plate, **ar** apodemal ruff, **ea** endophallic apodeme (left phallomere), **cs** cleft sclerite and **R3** (right phallomere), **s** stylus (in B missing, in D exceptionally with a second rudimentary stylus: **rs**). – Enlargements: same scale for A–E. – Specimen identification: F 65a/5 (A), Sp 36a/2 (B), F 19a/10 (C), F 27/2 (D), Ma 18/29 (E), Ru 3/3 (F).

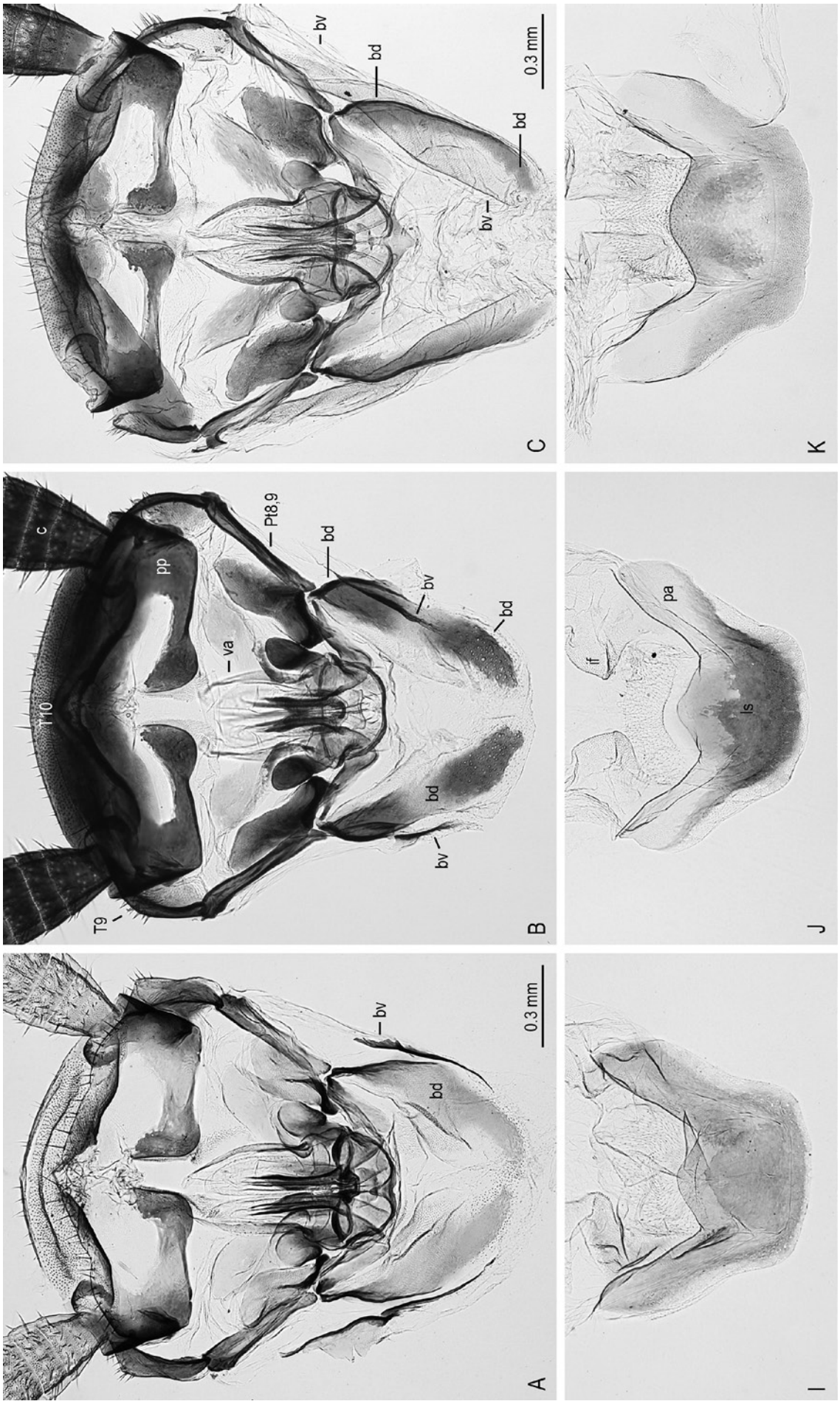
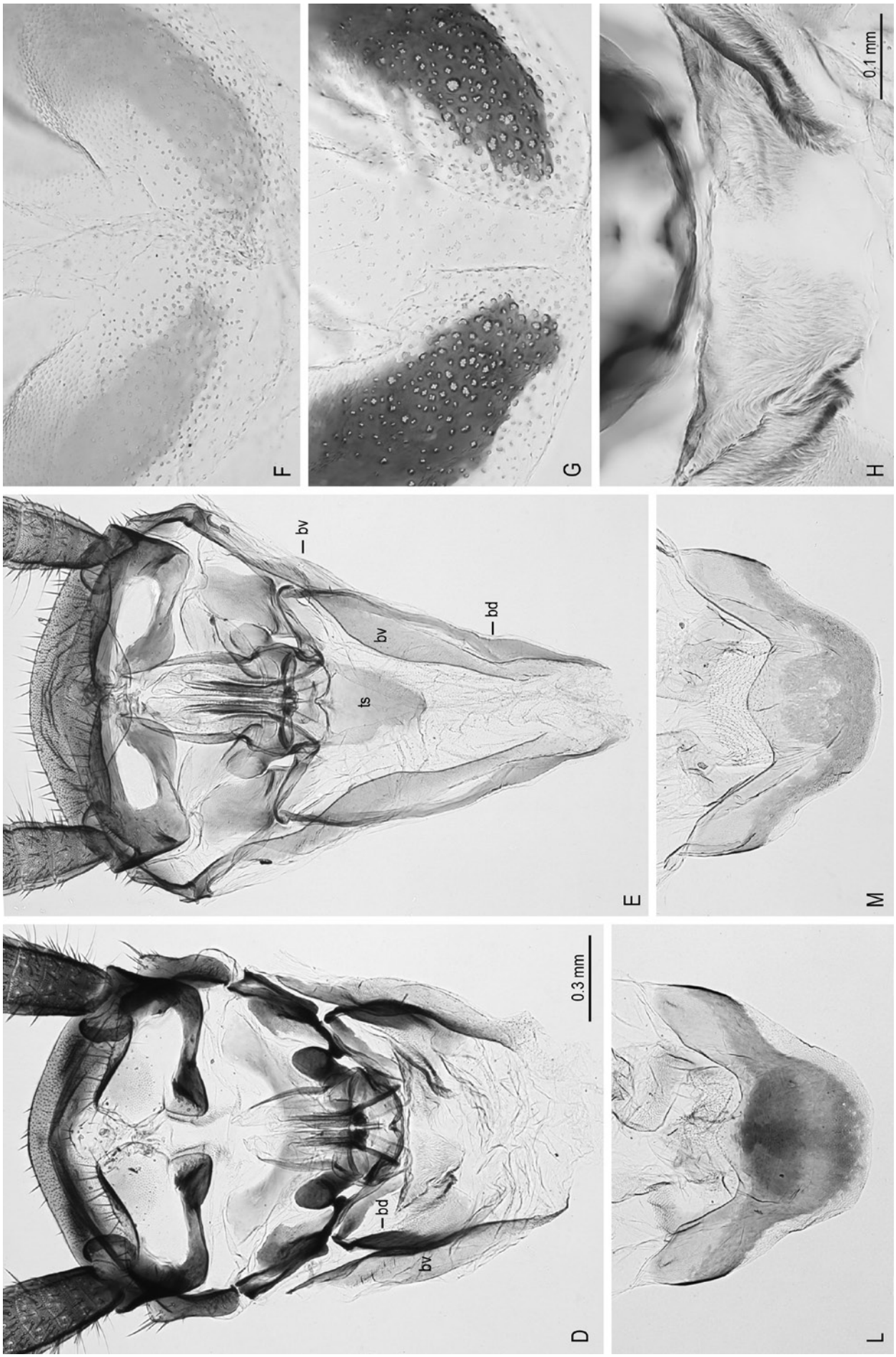


Fig. 4. (↑↓) Female terminalia with genital sclerites; A–E: complete dorsal complex; F–H: details of dorsal complex showing anterior ends of the dorsal basivalvular sclerites (F,G), the hairy surface structure posteriorly between the dorsal basivalvular sclerites (H); I–M: ventral complex. **A**,**F**,**I**: *Planuncus tingitanus*-complex. **B**,**G**: *Margundatus erythrurus*. **J**: *Margundatus princisi*. **C**,**K**: *Margintorus nicaeensis*. **D**,**L**,**H**: *Capraiellus panzeri*. **E**,**M**: *Ectobius hipposiderus*. – Abbreviations: **bd, bv** dorsal and ventral basivalvular sclerite, **c** cercus, **if** intersternal fold, **ls** laterosternite, **pa** posterior arm of laterosternite, **pp** paraproct, **s** stylus, **ts** tongue-shaped process of second valvifer, **va** valves of ovipositor. – Enlargements: same scale for A,B,I,J, for C,E,K,M, for D,L and for F–H. – Specimen identification: Ma 1/6 (A,F,I), Sp 156/4 (B,G), F 19/10 (C,K), F 27/1 (D,H,L), Ma 18/32 (E), Ma 18/31 (M).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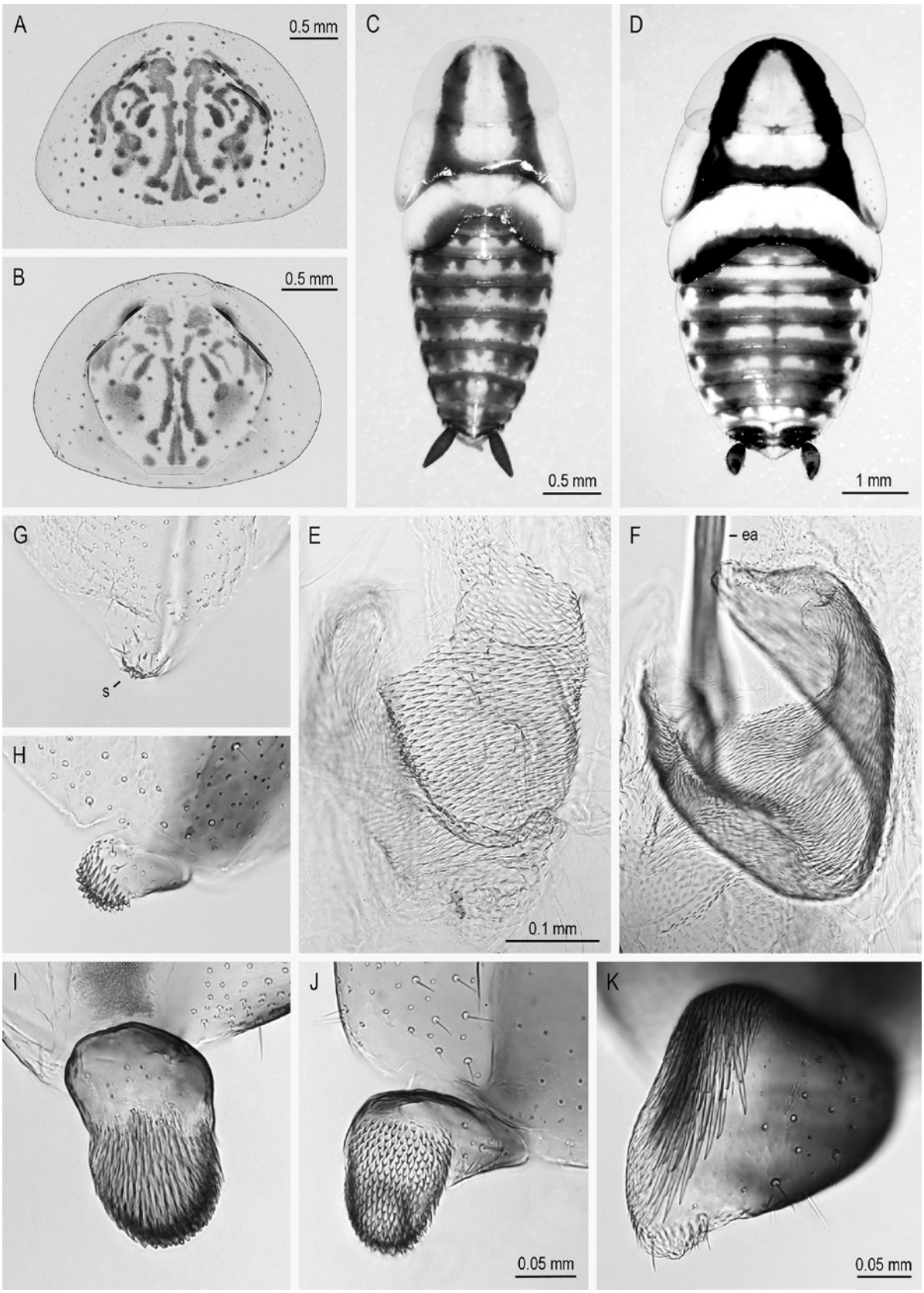


Fig. 5. A,**B**: Colouration pattern of pronotum, female of *Margintorus nicaeensis* (A), male of *Capraiellus panzeri* (B). **C**,**D**: Colouration of last instar larvae, male of *Capraiellus panzeri* (C), female of *Ectobius hipposiderus* (D). **E**,**F**: Male apodemal ruff, details from Figs. 3A,B, notice the scalelike microtrichia, *Planuncus tingitanus*-complex (E), *Margundatus erythrura* (F, with endophallic apodeme **ea**). **G**–**K**: Styli bearing scalelike microtrichia, details from Figs. 3A,C–F, *Planuncus tingitanus*-complex (G, with strongly reduced stylus **s**), *Margintorus nicaeensis* (H), *Capraiellus panzeri* (I), *Ectobius hipposiderus* (J), *Ectobius lapponicus* (K). – Enlargements: same scale for E,F, and for G–J. – Specimen identification: F 19/7 (A), F 27/4 (B), Sp 7/4 (C), Ma 142b/5 (D), F 65a/5 (E,G), Sp 36a/2 (F), F 19a/10 (H), F 27/2 (I), Ma 18/29 (J), Ru 3/3 (K).

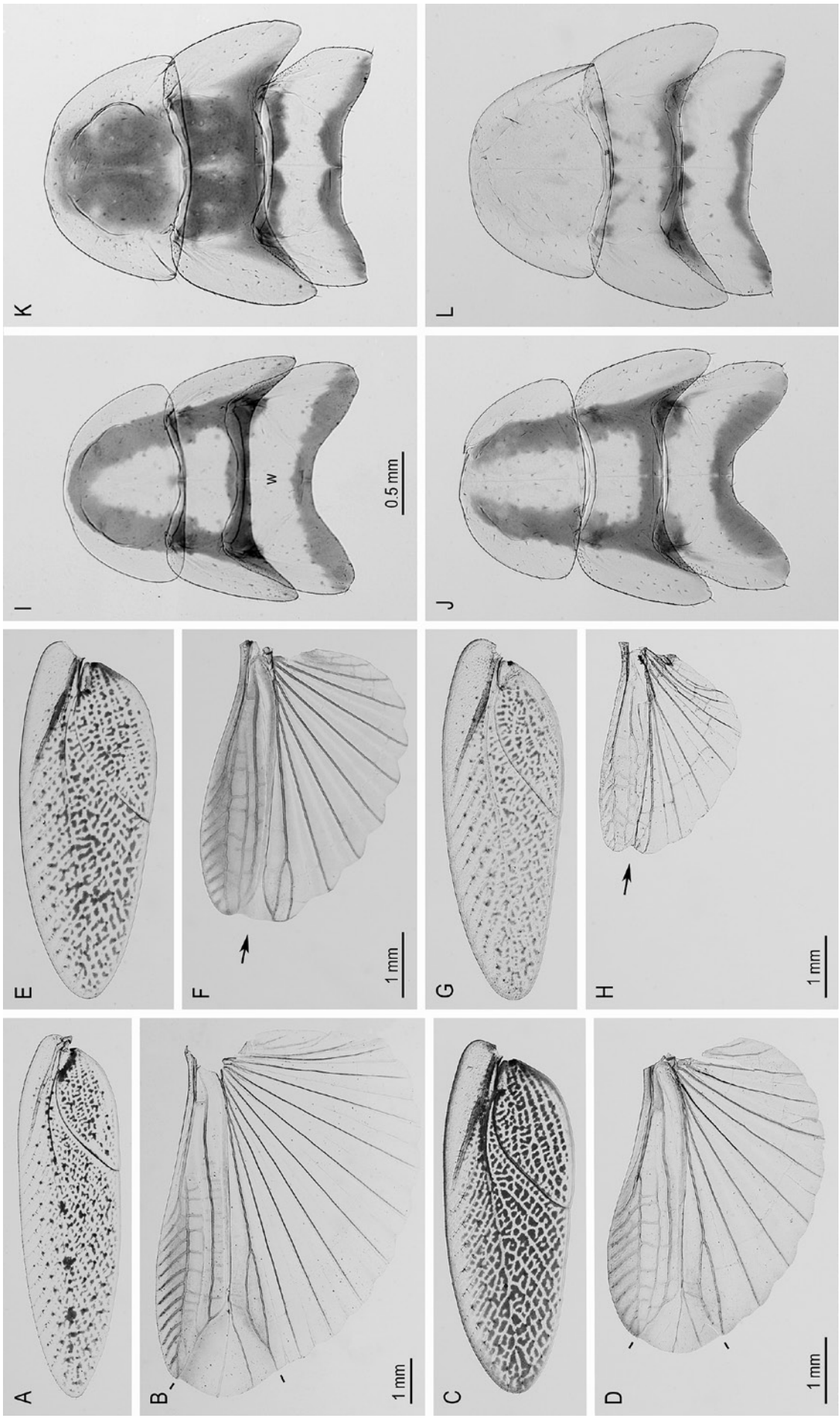


Fig. 6. A–H: Tegmina and hindwings, *Ectobius hipposiderus* (A,B), *Ectobius albicinctus* (C,D), *Margintorus nicaeensis* (E,F), *Planuncus tingitanus*-complex (G,H); apical triangle between the two markings at the wing margins in B,D, strongly reduced or missing in F,H, indicated by the arrows. **I–K**: Thoracal colouration of last instar larvae, *Ectobius hipposiderus* (I), *Capraiellus panzeri* (J), *Planuncus tingitanus*-complex, dark (K) and light (L) modification, the originally white metathoracal transversal band (**w**) appearing transparent by treatment with KOH (compare with Fig. 5C,D). – Enlargements: same scale for tegmina and hindwings, and for I–L. – Specimen identification: Ma 18/2 (A,B), Hr 11/2 (C,D), F 19a/2 (E,F), D 235/16 (G,H), Ma 140/2 (I), F 43b/3 (J), D 235/11 (K), D 235/12 (L).

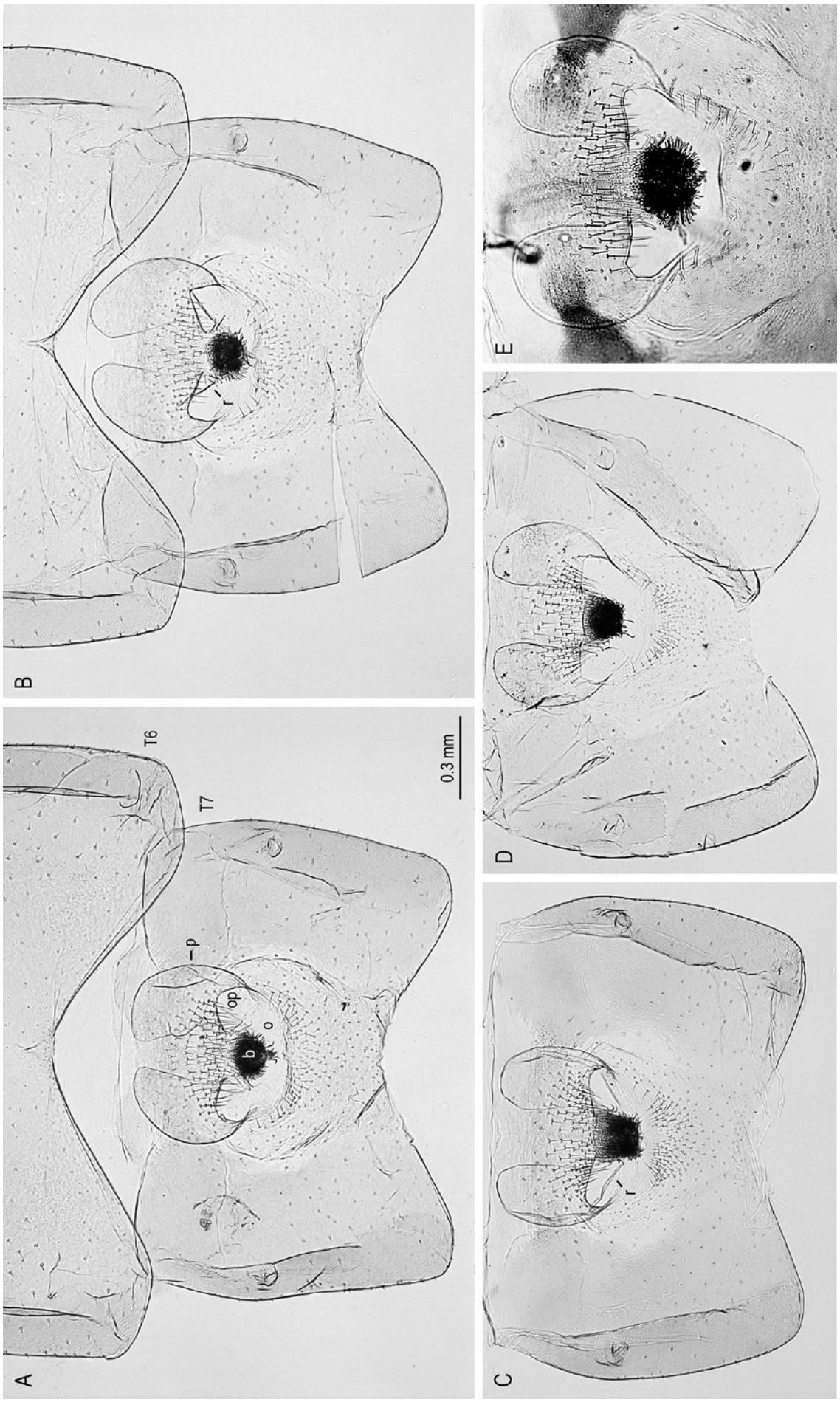
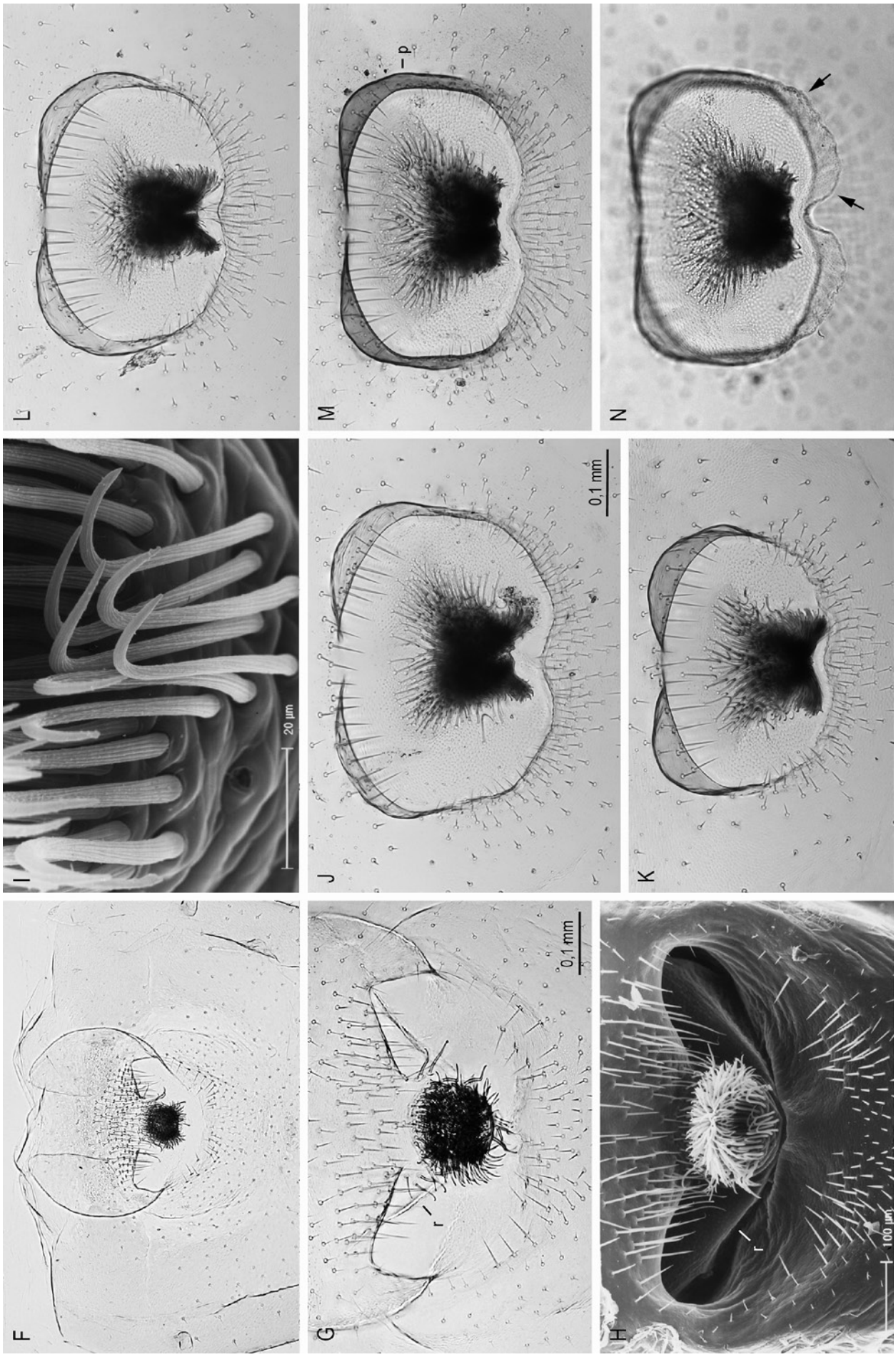


Fig. 7. (↑↓) T7 and its glandular pit, SEM pictures in H,I. **A–I**: *Planuncus tingitanus*-complex from various countries and localities; France (A,B,G) (G is a detail of B), Germany (F), Morocco near type locality of *P. tingitanus* (C,H,I) (I showing hairs of bristled knob is a detail of H), allotype of *P. tingitanus* from Morocco (D), type of *P. finoti* from Algeria (E). **J–N**: Glandular pit of *E. hipposiderus* from various localities in Morocco, M and N showing pit of same specimen in different focus to show the posterior extension of the pouches (arrows). – Abbreviations: **b** bristled knob, **o** opening of the pit, **op** opening of an internal pouch (**p**) of the pit, **r** ridge. – Enlargements: same scale for E–D,F and for J–N. – Specimen identification: F 65a/5 (A), F 65a/6 (B,G), Ma 45/15 (C), allotype of *P. tingitanus* (D), type of *P. finoti* (E), D 235/3 (F), Ma 45/2 (H,I), Ma 142b/1 (J), Ma 72a/1 (K), Ma 148a/1 (L), Ma 324/1 (M,N).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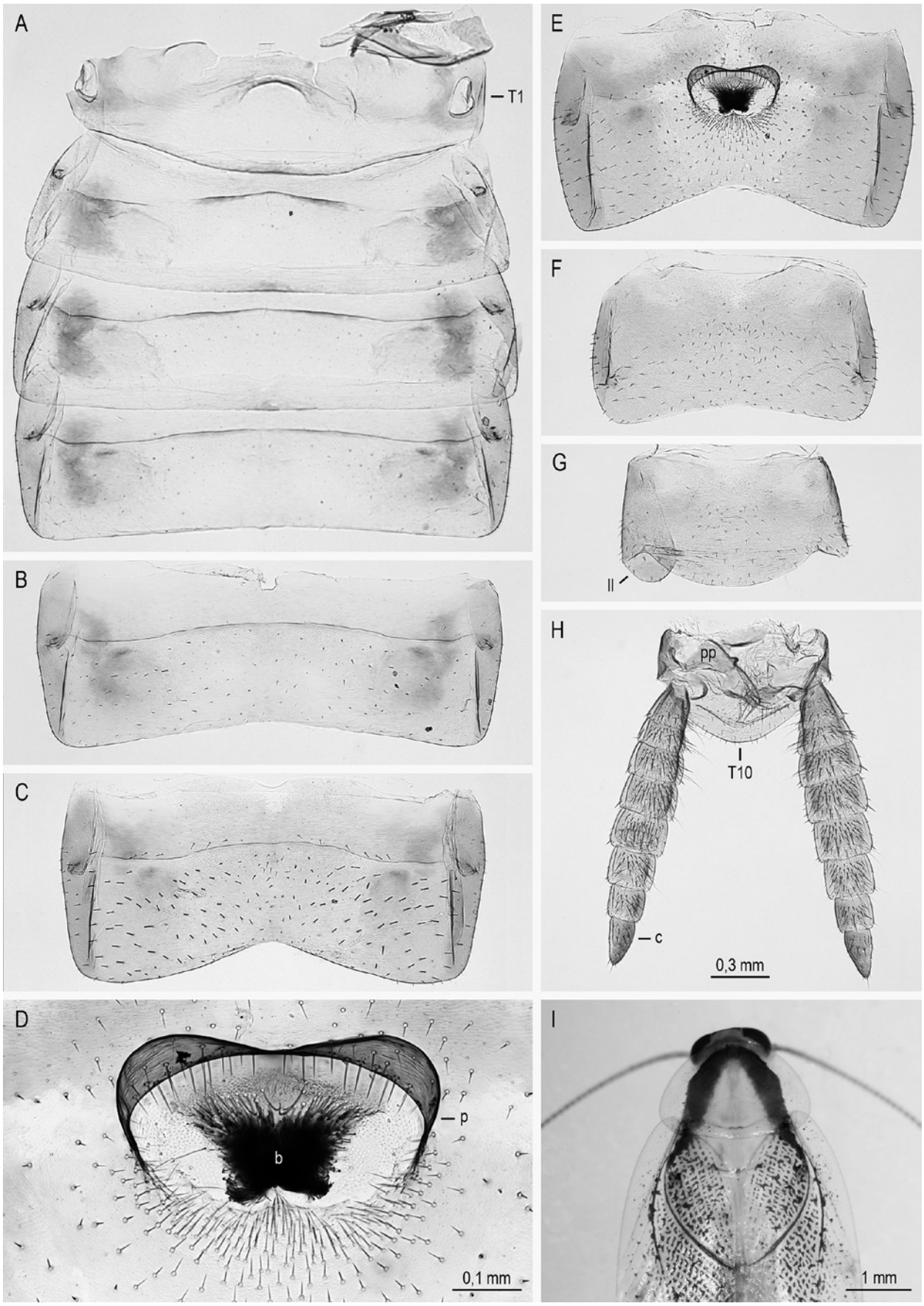


Fig. 8. Male structures of *E. hipposiderus*. **A**: T1–4; **B**: T5; **C**: T6; **D**,**E**: T7, complete (E) and glandular pit in more detail (D); **F**: T8; **G**: T9; **H**: T10 (ventral view); **I**: pronotum (with head and base of tegmina). – Abbreviations: **b** bristled knob, **c** cercus, **ll** lateral lobus of T9, **p** pouch of glandular pit, **pp** right paraproct. – Enlargements: same scale for A–C,E–H. – Specimen identification: Ma 18/27, holotype (A–G), Ma 18/29 (H), Ma 142b/6 (I).

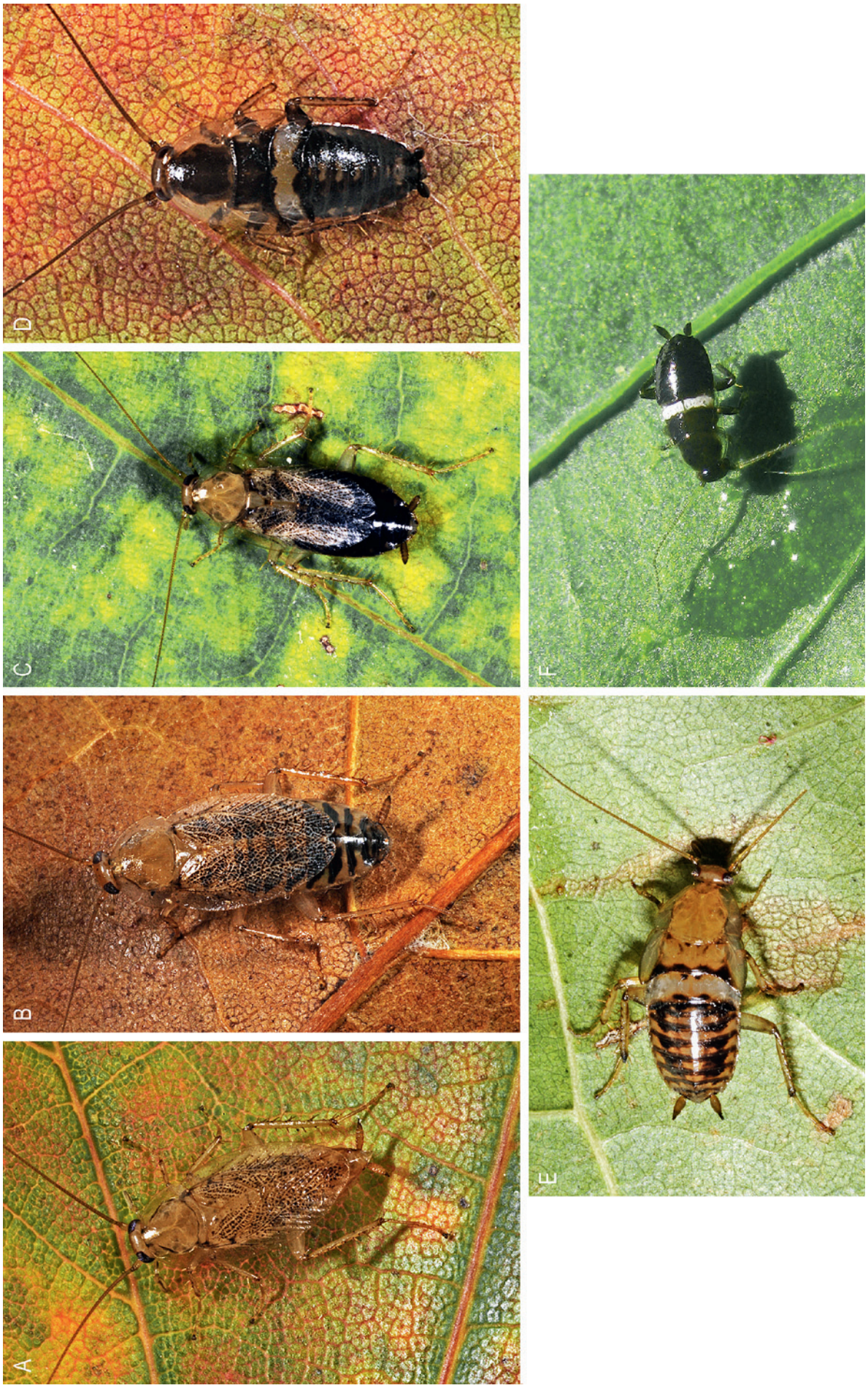


Fig. 9. Colour images of living *Planuncus tingitanus*-complex specimens, A–E from Hythe, England, F from Charente-Maritime, France. **A**: male; **B**,**C**: females (C: very dark specimen); **D**,**E**: late instar larvae; **F**: early instar larva.

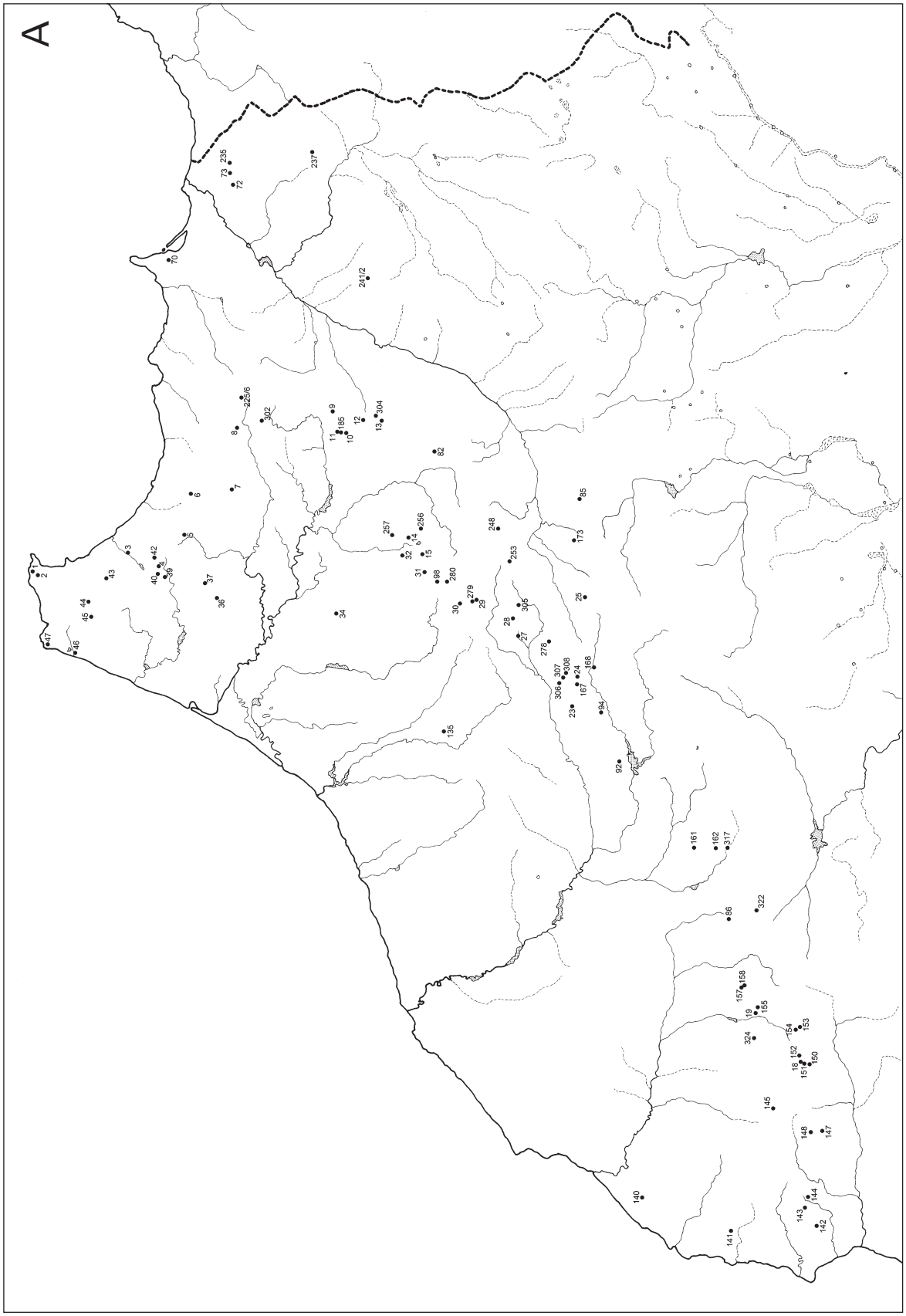
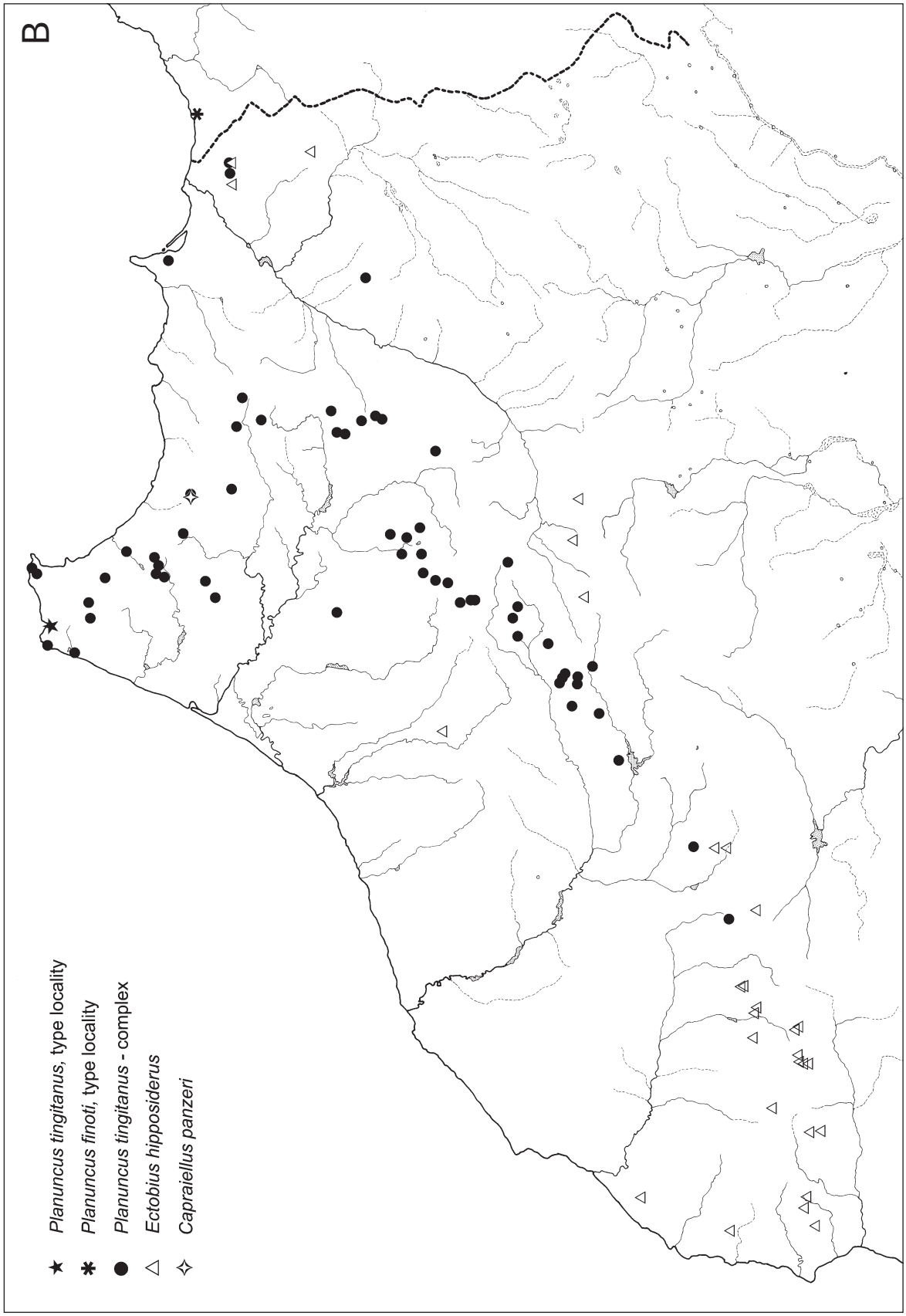


Fig. 10. (↑↓) Map of northern Morocco and adjacent Algeria. **A**: showing collecting localities with their numbers; **B**: showing distribution of species.


B
Planuncus tingitanus, type locality
Planuncus finoti, type locality
Planuncus tingitanus - complex
Ectobius hipposiderus
Capraiellus panzeri

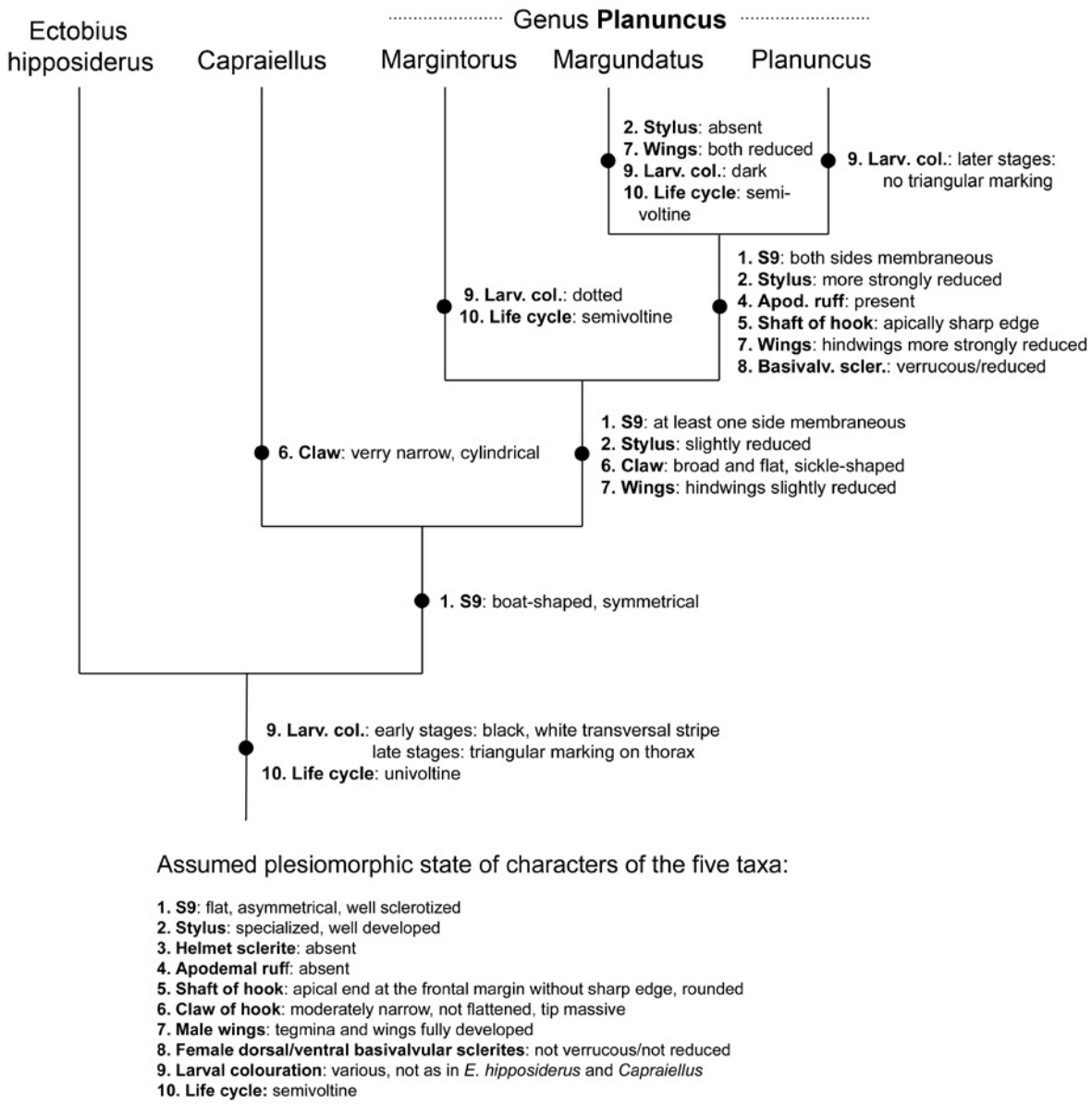


Fig. 11. Phylogenetic reconstruction of the relationships between the five taxonomic groups studied, using 10 characters. The assumed plesiomorphic state of the characters is listed at the bottom. In the tree only (syn)apomorphies important for the phylogenetic reconstruction are indicated; for autapomorphies of the terminal groups, mainly concerning structures of male tergites T6 and T7 and of female genital sclerites, see the descriptions.

4. Discussion

4.1. Taxonomic and phylogenetic considerations

Fig. 11

The species combined in the genus *Planuncus* share two notable characteristics: the strongly flattened, sickle-shaped claw of the male genital hook (Figs. 2A–E,I–N), and the symmetrical, boat-shaped male subgenital plate that towards one or both lateral borders gets very thin, almost membraneous, forming a thin, sharply edged rim (Figs. 3A–C).

The claw is in most other representatives of the Palearctic Ectobiinae (Figs. 2G,H) not as regularly curved, its terminal part is usually angularly set off from the more proximal parts, and it is not flattened but relatively massive up to the tip. There are two other groups of the Palearctic Ectobiinae having unusually shaped genital hooks, the *panteli*-group of *Phyllodromica* (Bohn 1993) and the genus *Luridiblatta* (H. Bohn, unpublished results); but the modifications in these groups are completely different from *Planuncus* and do not include a shared apomorphy.

A similarly boat-shaped subgenital plate is also present in the species of the genus *Capraiellus*, but it is fully, though not very strongly sclerotized and has a rounded rim all around (Fig. 3D). In the remaining Palearctic Ectobiinae the subgenital plate is rather strongly asymmetrical, not boat-shaped and only minimally vaulted to a shallowly concave plate (Fig. 3E,F).

The two characters mentioned above appear complex and special enough to justify their consideration as synapomorphies of the species assembled in *Planuncus*, implying the monophyly of the taxon. Monophyly is further supported by a wing character shared by the two subgenera with well developed tegmina (not assessable in *Margundatus* with its reduced tegmina): the shortening of the hindwings and – correlated with it – the reduction of apical triangle and veinal pattern in the males of the subgenera *Margintorus* and *Planuncus*, weak in the former, much stronger in the latter. The males of other Ectobiinae with well developed tegmina have longer hindwings and a prominent apical triangle, which slightly surpasses the tegmina at rest position, as is the case in *E. hipposiderus* (male and female, Fig. 6A,B) and in *Capraiellus* (male). However, the two examples are not fully comparable, the tegmina there are longer, surpassing the abdominal end; in *Margintorus* and *Planuncus* they scarcely reach the abdominal end. But another species of *Ectobius*, *E. albicinctus* (Fig. 6C,D), shows that a slight shortening of the tegmina – they reach about the abdominal end in this species – is not necessarily correlated with a reduction of the apical triangle, not to mention the relatively strong reduction of the hindwings in *Planuncus*.

In the evolution of the Blattodea, wing reductions have certainly often occurred independently with very similar results. It may, therefore, be doubtful to use the reduction of hindwings for phylogenetic argumentations. Since, however, no other case is known among the Palearctic *Ectobius* species in which the hindwings are reduced independently from the tegmina, it appears justified to include this character into phylogenetic considerations, though with lower weight.

It should be mentioned that there are several groups among the genus *Phyllodromica* and its subgenera showing a similar situation as in *Margintorus* and *Planuncus*, with tegmina almost reaching the abdominal end and strongly reduced hindwings (*maculata*-group, *megerlei*-group, *tyrrhenica*-group, etc). But they all differ by having a reduced venation system in the tegmina.

Apart from the shared apomorphies discussed above, the species of the genus *Planuncus* strongly differ in other characters relevant in the systematics of Ectobiinae: in the male the shape of tergites T6 and T7, the structure of the glandular pit of T7, the development of the stylus; in the female the structure of the genital basivalvular sclerites; and in both sexes the length of the wings. According to these differences three clearly separated groups of species crystallize, each supplied with a number of distinct autapomorphies. The number of autapomorphies, among which the respective similarities in the structure of the female genital sclerites certainly appear as most convincing, strongly argue for the monophyletic state of the respective species assemblage and justify the erection of three subgenera. The mutual relationships of the subgenera will be discussed further below.

The great similarities in the shape of the subgenital plate between *Planuncus* and *Capraiellus* can be considered as a synapomorphy suggesting a sistergroup relationship between the two genera. But there are two characters in which the two genera differ strongly and which might cast some doubt on the proposed sistergroup relationship: the reverse right-left symmetry in the terminalia of the males of *Capraiellus* and the different shape of the male genital hook.

The reverse symmetry of the male terminalia in *Capraiellus* is not a severe obstacle for the assumption of a sistergroup relationship with the genus *Planuncus* if we suppose that the reversion has taken place after the splitting of the two lines. Reversion of the symmetry has occurred several times independently in the evolution of the Blattodea; occasionally, reversed male genitalia can even be found in singular individuals of a species usually having the normal symmetry (*Phyllodromica carpetana*, Bohn 1999). Another genus of the Ectobiinae with reversed symmetry is *Dziriblatta* (H. Bohn, in prep.) which, however, is not closely related to *Capraiellus* in view of the remaining characters, indicating that both genera have developed the symmetry reversion independently.

The shape of the hook in *Capraiellus* (Figs. 2F,O) is – with its throughout massive, almost cylindrical claw – not only different from the hook of *Planuncus*, but also from the hooks of other Palearctic Ectobiinae studied in this respect (Figs. 2G,H,P). With respect to the suggested sistergroup relationship we would have to assume that the common ancestors of both genera still had the usual shape of the hook which, after splitting into the two branches, developed into diametrically opposed directions. At best, some similarity between the hooks of *Planuncus* and *Capraiellus* may be seen in the fairly even (i.e. non-angular) claw curvature, indicating that this character may already have been present in the last common ancestor of the two genera.

Looking for still deeper relationships the herein newly described species *Ectobius hipposiderus* from Morocco is of particular interest. Its early larval stages are in colouration almost identical with the respective stages of species of the genus *Capraiellus* and of the subgenus *Planuncus* (Fig. 9F). The remarkable change of the colouration pattern in later stages of *E. hipposiderus* (Figs. 5D, 6I) is similarly occurring in *Capraiellus* (Figs. 5C, 6J), but not in *Planuncus* (Figs. 6K,L, 9D,E). These colour patterns are unique among the Palearctic Ectobiinae and the occurrence in the three taxa scarcely explainable but by common descent. In the other two subgenera of *Planuncus* (*Margundatus* and *Margintorus*) this kind of juvenile colouration should have been lost and replaced by more general and among the Ectobiinae widely distributed larval patterns: overwhelmingly dark, or lightly coloured with dispersed dark dots.

In this connection the similarity of the colour pattern – dispersed dark dots and spots and a central lyra-shaped marking (Figs. 5A,B) – on the pronotum of imagines of *Capraiellus* and *Margintorus* should be mentioned. It could be seen as an additional support for the assumed sistergroup relationship between the genera *Capraiellus* and *Planuncus*. Since, however, similar patterns are widely distributed in Blattodea and even, at least in indications, not seldom found in Ectobiinae, the shared occurrence of the colour pattern in the two taxa is of little significance for phylogenetic considerations.

The proposed sistergroup relationship between *Ectobius hipposiderus* and *Capraiellus* + *Planuncus* is further supported by a partly common phenological feature: *E. hipposiderus* and the species of *Caprailleus* and of the subg. *Planuncus* have a life cycle of one year (univoltine). Among the Palearctic Ectobiinae a one-year-cycle is only found in one other, certainly not closely related genus, *Luridiblatta*; among the Centralasiatic species at least one also has a one-year-cycle: *Ectobius* (*Ectobiola*) *duskei* (Bey-Bienko 1969). The life cycle is certainly strongly dependent on the ecological constraints of the respective habitat and therefore of restricted value for phylogenetic considerations. Bey-Bienko considers the one-year-cycle of *E. duskei* as an adaptation to the strong winters of the steppe region in Central Asia, where the species lives. This certainly does not apply to *E. hipposiderus* and the species of *Capraiellus* and *Planuncus* living in Morocco and western Europe under Mediterranean or temperate climatic conditions. The possible advantages of the univoltine life cycle in these regions remain unclear as long as our knowledge of the biology of the animals is that scanty. It is striking that in the two subgenera, *Margintorus* and *Margundatus*, the same two of the assumed synapomorphies of the group have been changed: the larval colouration and the life cycle. The change from univoltine to semivoltine in *Margundatus* can be seen as an adaptation to the ecological conditions of the habitat. All species of the subgenus live in altitudes higher than 1000 m; the comparably short vegetation period at this altitude presumably would not allow the full development from egg to adult within few months.

At this point the relationships between the subgenera of *Planuncus* should be discussed. A number of synapomorphies of *Planuncus* and *Margundatus*, in *Margintorus* present in plesiomorphic state, strongly support the assumption of a sistergroup relationship. Presumable synapomorphies are, in the male: S9 on both sides membraneous, apodemal ruff present, stylus strongly reduced or missing, hook shaft at the apical end with a right- or acute-angled edge, in the female: apical end of dorsal basivalvular sclerites verrucous, ventral basivalvular sclerites weakly developed, partially with narrow strikingly strong sclerotizations. The absence of spatular tergite bristles could also be considered as a synapomorphy of the two subgenera. But the change from the one to the other state of the character seems to occur very easily: in some species the ratio of normal and spatular bristles is highly variable, and very closely related members of a species group may have different types of bristles. The value of this character for phylogenetic considerations, therefore, is very restricted. In some characters *Margintorus* is intermediate between plesiomorphic conditions in *Capraiellus* and more derived ones in *Margundatus* + *Planuncus*, for instance in the length of stylus and wings, and in S9 being membraneous on only one side.

The fact that the new genus *Planuncus* unites species which were hitherto distributed to two different genera (*Ectobius* and *Phyllodromica*) is not surprising. *Phyllodromica* and its subgenera (*Phyllodromica*, *Lobolampra*, *Arbiblatta*, *Turanoblatta*) are solely defined by various wing reductions and, thus, hardly supported as monophyletic entities.

The study of the taxonomy and phylogeny of Ectobiinae suffers from a want of characters allowing the recognition of deeper relationships. The variability in the structures of the male tergites T6 and T7 including the glanudular pit and of male and female genitalia is well suited for distinguishing species and species groups, but usually not appropriate for the recognition of relationships between the species groups or genera. A tentative division of the Palearctic Ectobiinae into two categories was proposed (Bohn 1989), one for species having a specialized stylus but no helmet sclerite (a structure located in the endophallus, in unexposed state situated at the left on the dorsal surface of S9, fairly below the basal part of the endophallic apodeme), the other containing species with unspecialized stylus and a helmet sclerite. The species treated herein belong to the first category, which, among others, also contains the *erythronotus*-, *kraussianus*-, *pallidus*-, and *vittiventris*-groups of *Ectobius* and the genus *Luridiblatta*. The specialized stylus is well visible in *E. hipposiderus*, *Capraiellus* and *Margintorus*; in the subgenus *Planuncus* the stylus is strongly reduced but still recognizable as specialized, and it is completely missing in the imaginal stage of the subgenus *Margundatus*.

One might have doubts, whether the second characteristic of the category, the missing of a helmet sclerite, does really apply in this case. The apodemal ruff, present in the subgenera *Planuncus* and *Margundatus*, has in some species of the latter a scleritelike appearance and thus resembles the helmet sclerite, which is similarly covered with scalelike microtrichia and has a similar position, ventrally of the basal part of the endophallic apodeme. But the helmet sclerite does not show the intimate contact and connection with the apodeme as is typical for the ruff, and since the ruff is found only in the presumably most derived of the taxa studied we assume that the two structures are not homologous though they might have developed from the same area of the exoskeleton.

Another character possibly suited for the elucidation of deeper relationships is the structure of the preparaprocts. The taxa treated herein agree in that the right preparaproct is short, only consisting of a sclerite bracelet not surpassing the paratergites of T10. In the *sylvestris*-group of *Ectobius* (Bohn 2004) and in the *maculata*-

group of *Phyllodromica* (Bohn & Chládek 2011), which both have an unspecialized stylus and a helmet sclerite, the right preparaproct is club-shaped, with a more or less membraneous terminal swelling, and it is longer, almost reaching the ventral midline of the segment. So far, this character has only been studied in very few cases; many additional species-groups and genera should be examined in this respect in order to test the utility of the preparaprocts for systematic and phylogenetic considerations.

4.2. The phenomenon of areal extension

The presently unsolved taxonomic problems in the subgenus *Planuncus* don't allow a clear decision in the question from which of the four countries – Algeria, Morocco, Spain or France – the immigrants in Germany and England have been coming. Most likely, the origin is in the neighbouring France, especially since it seems that the species there shows a similar behaviour, the colonizing of human settlements not or not to that extent observed before.

The prerequisite for the successful establishment of a species in a previously unoccupied area are appropriate conditions; this means for species coming from more southern, perhaps Mediterranean regions, primarily a warm climate. This might explain, why the immigrants were found only in human settlements, which usually have a milder climate than the open land (Klausnitzer 1982). The localities with earlier findings of *Planuncus* species in Morocco (1984–2000), Spain (1984), and France (1995–1996) are all situated in the open land. The localities reported by Maurel (2012, dating from 2005–2012, all for SW-France) include, as it seems, both open land and human settlements.

The apparent fixation of German and English populations to human settlements might be suspected to be a collecting artefact since most reports are accidental findings rather than the result of a systematic search. However, this aspect was tested at the locality Mainz-Finthen (D 235), where the *Planuncus* specimens were found in large numbers in the hedges seaming streets and gardens. Searching in a neighbouring village with similar hedges and in a nearby nature reserve with a xerotherm flora comparable to the habitats at the French localities in the Dept. Lot-et-Garonne were unsuccessful. A similar observation was also made at the English locality Hythe (GB 3). More studies of this kind are necessary to reassure these preliminary conclusions.

The preferred occurrence of the immigrants in human settlements might also be a consequence of the means of locomotion that the animals use for their migration. The shortened hindwings scarcely allow more than short flights between the twigs of a shrub. It is very unlikely that the animals could have moved actively over such large distances within few years, even if we assume their origin in France; the crossing of the Strait of Dover between France and England in this way appears impossible. In the recent migration of *Planuncus* species the passive component by human transportation played certainly a decisive role. The exchange of materials in and between cities and countries has increased at such a rate that it appears astonishing that there are not more species showing migrations into former unpopulated regions. Materials to be considered are especially those used for gardening, as are mixed manure, bark mulch, plant pots filled with humus earth, etc. The overwintering ootheca, deposited into the earth in autumn, appears as an ideal vehicle for transportation.

The apparently sudden trend to extend the distribution range might also have internal reasons, for example mutations of genes controlling behaviour or reaction to environmental conditions. Indications for this may be seen in an obviously greater plasticity of some characters as are length of wings and colouration within the expanding population. A similar phenomenon could also be observed in *Ectobius vittiventris*: specimens from newly colonized areas in northern Switzerland and Germany had often a much darker colouration than those from southern Switzerland.

5. Acknowledgements

The authors are much obliged to the following persons for their generous help: The curators M. Donskoff (Muséum National d'Histoire Naturelle, Paris) and Mercedes Paris (Museo Nacional de Ciencias Naturales, Madrid) provided important type material; Roland Melzer and Bernhard Ruthensteiner (Zoologische Staatssammlung, München, Germany) allowed the use of their microscopical and photographic equipment; T.M. Saks (München, Germany) made the SEM images (Fig. 7H,I) during her employment as technical assistant in the laboratory of the first author; Arp Kruithof (Hengelo, Netherlands) contributed Fig. 9F; Barbara Bohn, wife of the first author, was a great help in collecting cockroaches; Klaus-Dieter Klass (Senckenberg Naturhistorische Sammlungen Dresden, Germany) made valuable suggestions for the improvement of the manuscript.

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Jahr/Year: 2013

Band/Volume: 71

Autor(en)/Author(s): Bohn Horst, Beccaloni George, Dorow Wolfgang H. O., Pfeifer Manfred Alban

Artikel/Article: Another species of European Ectobiinae travelling north – the new genus Planuncus and its relatives (Insecta: Blattodea: Ectobiinae) 139-168