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Steps towards a revision of the *Perla bipunctata* Pictet, 1833 species complex (Plecoptera: Perlidae)

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Abstract
The traditional view of the species *Perla bipunctata* Pictet, 1833 and *Perla grandis* Rambur, 1842 as widely distributed taxa in the West Palaearctic does not stand up to a more thoroughgoing taxonomical examination. In the present study, we demonstrate that these taxa belong to unresolved species complexes, whose members are disjunctly distributed over different, often isolated, geographical areas and mountain ranges. In the first part of this study, based upon the review of specimens labelled *Perla bipunctata*, *Perla grandis* and (obsolete) *Perla maxima* (Scopoli, 1763), collected by the Italian plecopterologists Elisabetta Ravizza Dematteis and Carlalberto Ravizza, between 1970 and 1994 in rivers Nure, Staffora, Stura di Demonte, Stura di Ala, Soana and Tanaro, we show, by a morphological analysis of the penial armature and the sclerotized aedeagus of adult males, that these taxa fall into three distinct groups: a taxon found in the upper course of these rivers, then a second one present in their middle section and finally a third one living only in the very low reaches. The taxonomical problems related to the identification of these three alpine taxa are discussed, and a new species, named *Perla ravizzaorum* **sp. n.**, is described. This same tripartite species cluster within the *Perla grandis* / *bipunctata* species group is then shown to be replicated also in other alpine and perialpine regions, and only in these. Putative specimens of *Perla bipunctata* or *Perla grandis* collected in extra-alpine regions, such as the British-Irish Isles, the Pyrenees, the Cantabrian Cordillera, the Baetic System, and North Africa, are established as taxa belonging to different species, which are in need to be re-described and renamed. Two additional new species, *Perla andalusiaca* **sp. n.**, from Andalusia, and *Perla pyrenaica* **sp. n.**, from the Pyrenees, are described from adults and nymphs. The species name *Perla carlukiana* Klapálek, 1907, is finally re-instated for specimens from the British-Irish Isles.

Key words: *Perla bipunctata* species complex*, Perla ravizzaorum* **sp. n.**, *Perla grandis*, *Perla carlukiana*, *Perla andalusiaca* **sp. n.**, *Perla pyrenaica* **sp. n.**, alpha taxonomy, revision, Ravizza's collection.

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Introduction

The preservation of abundant material of both adult and nymphal specimens, labelled *Perla bipunctata* Pictet, 1833, *Perla grandis* Rambur, 1842 and (now obsolete) *Perla maxima* (Scopoli, 1763), in the collection of the Italian plecopterologists Elisabetta Ravizza Dematteis and Carlalberto Ravizza, deposited in the Department of Zoology of the Muséum cantonal des sciences naturelles, Lausanne, Switzerland (MZL), offers a unique opportunity for a renewed study of this challenging species complex. The exemplary handling of the collection (storage, labelling and digitalisation) by the staff of the MZL has by now enormously facilitated its access and enabled the present revision. Moreover, the everted penial armatures of many specimens of the Ravizza's collection pave the way for an accurate comparison with the taxa described in the literature (Despax 1942; Illies 1955; Aubert 1949, 1959; Konar 1997; Fochetti & Tierno de Figueroa 2008) and with related material from other faunistic regions. The examined specimens from the Ravizza's collection belong to the *Perla bipunctata* / *grandis* species group and have been collected mainly in the Italian Alps and Apennines, in the northern part of the country, by Elisabetta Ravizza Dematteis and Carlalberto Ravizza. Of particular interest are the specimens from the rivers Nure, Staffora, Stura di Demonte, Stura di Ala, Soana and Tanaro. The analysis of adults and nymphs collected in these rivers shows that these specimens fall into three distinct morphological types: a first one found in their upper course, then a second one present in their middle section and finally a third one living only in their very low reaches near the confluence with River Po. These findings raise the problem of the correct species assignment for each of these taxa, since the identification of specimens of *Perla* Geoffroy, 1762 from alpine regions that are neither *Perla abdominalis* Burmeister 1839, nor

Perla marginata (Panzer, 1799), is severely hampered by taxonomical uncertainties. Moreover, the now obsolete (Consiglio 1967a, 1967b) taxon name *Perla maxima* (Scopoli, 1763), found on the labels of older specimens from the Ravizza's collection, had to be reassigned.

Material and Methods

The collection of the Italian plecopterologists Elisabetta Ravizza Dematteis and Carlalberto Ravizza has been deposited in the MZL in 2016. Adults and nymphs labelled *Perla bipunctata*, *Perla grandis* and *Perla maxima*, collected between 1970 and 1994 in the Italian Alps and Apennines, are preserved in ethanol and stored in containers CB-18627 (*Perla maxima*), CB-18628 (*Perla bipunctata*) and CB-18633 (*Perla grandis*) in MZL. The material is listed in the Appendix 1. In addition, many specimens from other alpine and extra-alpine locations were examined. This material is also listed in the Appendix 1. Terminology for adults follows that of Sivec et al. (1988). Terminology and description technique for nymphs follows Reding (2020). The abdomens of many adult males were removed and soaked in 10% NaOH overnight and rinsed with HCl prior to dissection. Illustrations of the specimens were produced by the author with the help of different Canon® and Nikon® cameras attached to a Leica® S8-APO stereomicroscope. The final illustrations were postprocessed using Adobe® Photoshop® software. By principle, no focus stacking software was used.

The following abbreviations are used: ♂ = macropterous adult males; ♂b = brachypterous adult male; ♀ = macropterous adult females; L = nymphs; L♂ = macropterous male nymphs; L♂b = brachypterous male nymphs; L♀ = macropterous female nymphs; MZL = collections of the Department of Zoology of the Muséum cantonal des sciences naturelles, Lausanne, Switzerland (formerly Museum of Zoology, Lausanne); INRAE = collections of the Institut national de recherche pour l'agriculture, l'alimentation et l'environnement, Villeurbanne, France; TDF = collection of José Manuel Tierno de Figueroa; GVC = collection of Gilles Vinçon; PZC = collection of Peter Zwick; RC = collection of Jean-Paul G. Reding.

Results

The penial armatures of the adult males from the *Perla bipunctata* / *grandis* species group of the Ravizza's collection belong to three different types:

Type A: sclerotized apex of aedeagus elongated and ogive-shaped, terminated by two tiny, pointed extensions (Figs A.1, A.2, A.3, A.4, A.8); aedeagal tube cylindrical (Figs A.5, A.6, A.7).

Type B: sclerotized apex of aedeagus of medium length, ovoid-shaped in its upper part and terminated by two distinctly separated triangular extensions (Figs B.1, B.2, B.3, B.4, B.5); aedeagal tube cylindrical (Fig. B.6).

Type C: sclerotized apex of aedeagus short and cordiform, without pointed extensions (Fig. C.1); aedeagal tube shaped like a truncated cone (Fig. C.2).

Adult males and females of all three types are macropterous. The examination of the corresponding nymphal material yields similar results, and falls into three distinct categories matching with those of the adults listed above:

Type A: cerci with a dense fringe of basal mediodorsal setae (Fig. A.14). Yellow markings on tergites dot-like or forming a narrow elliptical design (*cf.* Figs A.17, A.18).

Type B: cerci with a sparse fringe of basal mediodorsal setae (Figs B.16, B.17). Yellow markings on tergites III to V lenticular (Fig. B.20).

Type C: cerci without basal mediodorsal setae (*cf.* Figs C.7, C.10). Yellow markings on tergites III to V continuous, covering the entire distal edge of the corresponding segments (Fig. C.8).

These three types of adult males and nymphs from the Italian Alps and Northern Apennines are consistently distributed over three different altitudinal gradients: type C is very rare and is only to be found at lower altitudes (< 110 m) in torrente Nure. Type B occupies the middle reaches of rivers, above 200 m. Type A occurs in higher locations. We present first an illustrated description of the adults and nymphs of each of these three types A, B and C, before attempting to provide corresponding species assignments. In addition, by comparing the material of the Ravizza's collection with specimens from other faunistic regions, we attempt to show that the presence of these three types A, B and C is not limited to the Italian Alps and Apennines, but that all of them also occur in other alpine and perialpine regions, and only in these. Specimens from the British-Irish Isles, the French and Spanish Pyrenees, the Cantabrian Cordillera, Andalusia and North Africa correspond to different taxa, presently only partially identifiable to species-level for lack of material (see discussion below).

Description of the examined material

Preliminary notes.

Adults. Adult males of the *Perla bipunctata* / *grandis* species group are identifiable only by their penial armature and by their sclerotized aedeagus. Female adults offer little distinctive criteria, since the subgenital plates of all examined females are more or less trapezoidal in shape (Figs A.12, A.13, B.14, C.6; Illies 1955, his Fig. 114D; Aubert 1959, his Fig. 249; Kis 1974, his Fig. 119D; Fochetti & Tierno de Figueroa 2008, their Fig. 55).

Nymphs. The main identification criteria for nymphs are, for one, the aspect of the markings on abdominal tergites III to V (Figs A.17, A.18, B.18, B.19, B.20, B.23,

C.8, C.12) and the design on the pronotum (Figs A.16, B.22, B.23, C.9, C.11, C.13), and, for other, the mediodorsal setation on the basal part of the cerci (Figs A.14, A.15, B.16, B.17, C.7, C.10). Three types of setation are present on the basal part of the cerci: small thorns (always present; *cf.* Fig. A.15), clothing hairs (always present; *cf.* Fig. C.7) and a dense (Fig. A.15), sparse (Fig. B.17) or absent (Fig. C.10) mediodorsal setal fringe. Only this latter type of setation can be used for taxonomical purposes. Exuviae are of limited use for taxonomical purposes, since the nymphal chaetotaxy is not always preserved invariable on these specimens. Immature nymphs (less than 12 mm) are likewise not suitable for identification to species level.

Type A

Morphological diagnosis. Males and females macropterous. Body length of males 18–26 mm; of females 20–34 mm. Body colour dark brown. Head yellow with tawny markings (Fig. A.11). Pronotum pale yellow, with a dark central band and with a symmetrical darker design on both sides (Fig. A.11). Inner half of the two lower ocelli circled by a narrow black band (Fig. A.11).

Male adults. Sclerotized apex of aedeagus elongated, narrow and lanceolate (Figs A.1, A.2, A.3, A.4, A.5, A.8, A.20). Proximal part of aedeagus with a strong row of aligned brush-like setae (Figs A.3, A.4, A.20); distal part terminated by two tiny and pointed extensions (Figs A.3, A.4, A.20). Aedeagal tube cylindrical (Figs A.6, A.7, A.20). Tergite IX with mesal field of strong, spiny projections, randomly distributed, distally undivided (Fig. A.9). Apex of hemitergal lobes of tergite X narrow, finger-like, and rounded, in dorsal view, with rows of small, blunt spines (Figs A.9, A.10) and spatulate in lateral view (Figs. A.7, A.10).

Female adults. Distal edge of female subgenital plate trapezoidal in shape (Figs A.12, A.13).

Nymphs. Length: 24 to 36 mm. Cerci with a dense and continuous fringe of basal mediodorsal setae extending beyond segment XV (Figs A.14, A.15). Yellow markings on tergites III to V dot-like or forming a narrow elliptical design, and separated by a dark central stripe (Figs A.17, A.18). Pronotum with a large, dark, central stripe flanked by two irregularly shaped dark bands connected to the upper and to the lower edges of the pronotum (Fig. A.16). Dorsal faces of femora of middle and hind legs with an indistinct dark area connected to the dorsal edge of the femora (Fig. A.19). Apex of paraprocts triangular, or with pointed apex, in ventral view.

Ecology. High altitude species (800–1900 m). Small brooks and torrents. Merovoltine. Eurythermous. Occasionally found also in the middle sections of perialpine rivers, where it lives in in near syntopy with specimens of type B, in zones disconnected from the main river channel (Fig. M.1). Flight period: May to August. The examined material is listed in the Appendix 1, under type A.

Type B

Morphological diagnosis. Males and females macropterous. Body length of males 18–26 mm; of females 20–34 mm. Body colour dark brown. Head yellow with tawny markings (Figs B.13, B.15). Pronotum pale yellow, with a large dark central band flanked with a symmetrical darker design (Fig. B.13). Inner half of the two lower ocelli circled by a narrow black band (Fig. B.13).

Male adults. Sclerotized apex of aedeagus of medially slightly enlarged, ovoid-shaped in its upper part and terminated by two triangle-shaped extensions (Figs B.1, B.2, B.3, B.4, B.5, B.10, B.11, B.12). Aedeagal tube cylindrical (Fig. B.6, B.7, B.10, B.11). Tergite IX with mesal field of spiny projections, distally divided into two sharp edges (Figs B.5, B.9). Apex of hemitergal lobes of tergite X narrow, finger-like in dorsal view (Figs B.5, B.9), with rounded apex, in lateral view (Fig. B.8).

Female adults. Distal edge of female subgenital plate slightly rounded (Fig. B.14).

Nymphs. Length: 24 to 31 mm. Cerci with a sparse fringe of basal mediodorsal setae, not extending beyond segment XV (Figs B.16, B.17). On specimens preserved in ethanol for over 40 years, this mediodorsal setation is often hardly distinguishable, since these fine setae are procumbent and completely attached to the base of the cercus, and have the aspect of a tiny white film (Fig. B.16). Yellow markings on tergites III to V lenticular (Figs B.18, B.19, B.20). Dorsal faces of femora of middle and hind legs with a dark central oval stripe (Fig. B.21). Pronotum with a large, dark, central stripe flanked by two short dark bands connected only to the upper edge of the pronotum (Figs B.22, B.23). Apex of paraprocts rounded, in ventral view (Fig. B.24).

Ecology. Main channel of larger alpine and perialpine rivers, up to ca. 900 m (Fig. M.1). Merovoltine. Cold stenothermous. Flight period: May, June. The examined material is listed in the Appendix 1, under type B.

Type C

Morphological diagnosis. Males and females macropterous. Body length of males 17–25 mm; of females 20–34 mm. Body colour dark brown. Head yellow with tawny markings and well-developed M-line (Fig. C.5). Pronotum pale yellow, with a narrow dark central band and with two small dot-like darker patches on both sides (Fig. C.5). Inner half of the two lower ocelli circled by a narrow black band (Fig. C.5).

Male adults. Sclerotized apex of aedeagus cordiform, distally without pointed extensions (Fig. C.1). Aedeagal tube shaped like a truncated cone (Fig. C.2). Mesal field of tergite IX with wide stripes of spiny projections, distally divided (Fig. C.3). Apex of hemitergal lobes of tergite X distinctly projecting downwards (Figs. C.3, C.4).

Female adults. Distal edge of female subgenital plate trapezoidal in shape (Fig. C.6).

Nymphs. Length 24 to 29 mm. Cerci without basal mediodorsal setae (Figs C.7, C.10). Yellow markings on tergites III to V continuous, wider in the middle than on the sides, and covering the entire distal edge of the corresponding segments (Figs C.8, C.12). Dorsal faces of femora of middle and hind legs with a dark central oval mark (Fig. C.17), not visible anymore on older specimens (> 40 years) preserved in ethanol. Pronotum with a large, dark, central band flanked by two dark, dot-like markings not connected to the lower edge of the pronotum and only loosely connected to the upper edge (Figs C.9, C.11, C.13, C.16). Tergites, in lateral view, with sparse mediodorsal flexible setae (Fig. C.14). Apex of paraprocts flattened (Fig. C.15).

Ecology. Low altitude, potamal species. Flight period: June. The examined material is listed in the Appendix 1, under type C.

It has to be noted that none of these three types A, B and C, adults as well as nymphs, from alpine regions, corresponds to specimens variously identified as *Perla bipunctata* or *Perla carlukiana* Klapálek, 1907, 1923, and coming from the British-Irish Isles (Hynes 1941; Feeley *et al.* 2016; Macadam *et al.* 2022). Although basal mediodorsal setae are also lacking on the cerci of their nymphs, they stand apart by the different shape of the sclerotized apex of the aedeagus and the brachypterism of their adult males. We shall label these specimens type D. The following description of type D is made after specimens from Ireland and Scotland.

Type D

Morphological diagnosis. Males brachypterous (Fig. D.4), much smaller in size (14–18 mm) than the corresponding macropterous females (30–33 mm) (Macadam 2016). Body colour dark brown. Head yellow with tawny markings (Figs D.5, D.6). Pronotum pale yellow, with a dark central band and with a large symmetrical dark design on both sides (Figs D.5, D.6). Inner half of the two lower ocelli circled by a large dark band in males as well as in females (Figs D.5, D.6).

Male adults. Sclerotized apex of aedeagus short and ovoid, with slightly angulous lower edges, and with a brush-like apex (Figs D.1, D.2). Aedeagal tube shaped like a truncated cone (Fig. D.2). Tergite IX with mesal field of stripes of spiny projections, distally divided (Figs D.3, D.4). Apex of hemitergal lobes of tergite X wide and with slightly folded apical lobes (Figs D.3, D.4).

Female adults. Distal edge of female subgenital plate trapezoidal in shape (Fig. D.7).

Nymphs. Males much smaller in size (14–21 mm) than the corresponding females (25–33 mm), with wing pads prefiguring brachypterism (Fig. D.12). Cerci without basal mediodorsal setae (Fig. D.8). Yellow markings on tergites III to V dot-like or near elliptical, and separated by a dark central stripe (Fig. D.9). Dark oval mark in the centre of the femora of all three legs (Fig. D.10). Pronotum with a dark, central band flanked by two dark, elliptical markings connected to the upper edge of the pronotum and only loosely connected to the lower edge (Figs D.11, D.12). Apex of paraprocts triangular, in ventral view.

Ecology. Merovoltine life cycle, lasting three years (Feeley et al. 2009). Small, stony rivers (Hynes 1977; Feeley et al. 2016; Macadam et al. 2022). Flight period: April to July. The examined material is listed in the Appendix 1, under type D.

Discussion

Since presently only the names *Perla bipunctata* and *P. grandis* are available for identifying members of the *Perla bipunctata* / *grandis* species group (DeWalt et al. 2023), and even only *P. grandis* for alpine regions when following Sivec & Stark (2002), the occurrence of three distinct morphospecies from this group evidently raises the problem of the adequate species assignments for each of these three morphotypes A, B and C, and accessorily also for extra-alpine specimens of type D. The main problem related to the present investigation hence is that there are more morphospecies to identify than species names available. Moreover, we also lack precise descriptions associated with the various names given to the members of the *Perla bipunctata* / *grandis* species group.

Perla bipunctata is one of the most enigmatic and also problematic taxa of the West Palaearctic. Originally described by Pictet (1833) from nymphs and later from adults (Pictet 1841/1842) collected in River Rhône near Geneva, it had never been captured again at its type locality (Aubert 1946). Moreover, no true type material is extant in the Pictet collection in the Muséum d'Histoire Naturelle de Genève (Aubert 1947; Zwick 1971; Sartori & Bauernfeind 2020). Pictet's (1833, 1841, 1842) description and illustrations (Figs L.1, L.2, L.3), as is usual in 19th century works, are not very precise, and leave much room for interpretation. The validity of the taxon name *Perla bipunctata* had already been questioned in the 19th century. *Perla bipunctata* had been considered as a synonym of *Perla maxima* by Newman (1839), McLachlan (1870) and Albarda (1889b, 1889c). At first, Klapálek (1900b, 1901, 1907) had also considered Pictet's *Perla bipunctata* as being a synonym of *Perla maxima*, which he believed to be a lowland species, and introduced consequently the new species *Perla alpicola* Klapálek, 1900b, 1901 for headwater specimens from the Austrian Alps, curiously ignoring the *Perla grandis* of Rambur (1842). Later, Klapálek (1915, 1923: 39) changed his position, considered *Perla maxima* as an upland species, and re-established the validity of the species name *Perla bipunctata* for lowland specimens. Klapálek (1923), therefore, also declared the names *Perla alpicola* and *Perla grandis* as being synonyms of *Perla maxima*. These views

were followed by Schoenemund (1925b), Illies (1955) and Aubert (1946, 1949, 1959). Finally, Scopoli's (1763) name *Perla* (*Phryganea*) *maxima* was declared invalid (Consiglio 1967b), and the name *Perla grandis* became generally adopted for specimens formerly considered as *Perla maxima sensu* Klapálek 1923 (Consiglio 1967a; Zwick 1971; Zwick 1973; Kis 1974; Ravizza & Ravizza Dematteis 1979; Fochetti & Tierno de Figueroa 2008). As a result of these repeated nomenclatural shifts, older synonymies cannot always be formally restored.

More recently, Sivec & Stark (2002) have refused to recognize a specific difference between specimens labelled *Perla grandis* and *P. bipunctata* from alpine regions and proposed to group together all the species of this latter region that are neither *P. marginata* nor *P. abdominalis*, under the single name *P. grandis* and apply the species name *Perla bipunctata* only to specimens with brachypterous males from Belgium and the British-Irish Isles (formerly named *Perla maxima* ssp. *carlukiana* Klapálek, 1907 or *Perla carlukiana* Klapálek, 1923). These recommendations by Sivec & Stark (2002), based exclusively on ootaxonomical considerations, are now widely followed (for example, Lubini et al. 2012; Roesti 2021), but not universally accepted, at least not by authors recognizing the presence of two distinct species of alpine *Perla* in the *bipunctata* / *grandis* complex (Konar & Köstenberger 2002; Ravizza et al. 2022), or considering *Perla bipunctata* as a single, widely distributed species, in alpine as well as in extra-alpine regions, with brachypterous and macropterous populations (Illies 1953; Fochetti & Tierno de Figueroa 2008; Graf et al. 2009; Fochetti 2020; DeWalt et al. 2023). The discovery of even three morphospecies of the *Perla bipunctata* / *grandis* group in alpine regions now renders the position of Sivec & Stark (2002) highly disputable.

According to the original description (Figs L.1, L.2) Pictet (1833: plate 5, his Fig. 12; 1842: plate 11, his Fig. 1) provides for his *Perla bipunctata* nymphs, this taxon is assignable to either type B or type C above, to judge from the pattern on the abdominal tergites (*cf.* Figs L.1, L.2 with Figs B.18, B.19, B.20, B.23, C.8, C.12) and by the dark oval median bands on the femora (*cf.* Fig. L.1 with Figs B.21, C.17). Note that by this latter aspect, Pictet's species also offers some resemblances with specimens of type D (*cf.* Fig. L.1 with Fig. D.10), but the markings of the tergites on type D (Fig. D.9) differ notably from the ones on types B and C, and from Pictet's illustrations of his *Perla bipunctata* (Figs L.1, L.2). Whereas the anal gills (Fig. L.2) are well visible in Pictet's later illustrations (1842: plate 11, his Figs 1 and 5), the presence or absence of a fringe of basal mediodorsal setae on the cerci, however, cannot be ascertained. Despite this, there are some hints pointing to a correspondence of Pictet's *Perla bipunctata* with our type C. The name of the species described by Pictet (1833) refers to the particular markings on the pronotum of the nymph: whereas *Perla marginata* has three vertical dark bands on the pronotum (Pictet 1833: 56; Pictet 1842: plate 17, his Fig. 3), *P. bipunctata* has only one central dark band flanked by two dark dot-shaped spots on its pronotum, from where Pictet (1833) derived the vernacular name "Perle à deux points" (*two-dotted Perla*) of his new species (Figs L.1, L.2; Pictet 1842: plate 11, his Figs 1 and 5). This criterion of the two dark dots on the pronotum is indeed only present in nymphs of type C (Figs C.9, C.11, C.13, C.16). Specimens of type A, B and D exhibit different patterns on their pronotum (Figs A.16, B.22, B.23, D.11, D.12; Hynes 1977, his Fig. 46). Extra-alpine nymphs of the *Perla bipunctata* / *grandis* species group with two dots on the pronotum have so far only been found in Spain, but these specimens are obviously brachypterous, as will be shown below. We hence dare equate Pictet's macropterous *Perla bipunctata* (Fig. L.3; 1842: plate 12, his Fig. 3) with our type C, not only for the morphological reasons enumerated above, but also for the concordance in the indication of its potamal biotope, since Pictet (1833: 56) mentions the species only from River Rhône. In the past, *Perla bipunctata* had indeed also been mentioned further downstream from River Rhône by Bocquet (1944), together with other, now rare or even extinct, typical potamal species, such as *Brachyptera braueri* Klapálek, 1900a, *Isogenus nubecula* Newman, 1833 and *Isoperla obscura* (Zetterstedt 1840). It must be reminded, however, that Pictet also considered specimens from higher locations in the Swiss Alps as belonging to his *Perla bipunctata* (Pictet 1841: 189–191), whereas his illustrations are made after specimens from River Rhône in the Greater Geneva region. The revision of several collections by the present author has shown that adult and nymphal material from alpine regions belonging to type C is extremely rare, and the only specimens extant in the MZL, in addition to those from the Ravizza's collection, are a few adults and nymphs collected by Aubert in the 1940s in Switzerland from Rivers Aare and Emme (Swiss Plateau), and preserved in the collections of the MZL (container CB-13203). These specimens, which have the typical two dots on their pronotum (Figs C.9, C.11, C.13, C.16), as well as continuous yellow markings on tergites III to V (Figs C.8, C.12) and lack basal mediodorsal setae on their cerci (Figs C.7, C.10), were also considered by Aubert himself as true specimens of *Perla bipunctata* as considered by Pictet, 1833 (Aubert 1949). Aubert (1946) also reports on a specimen of *Perla bipunctata* from River Emme, mentioned by Meyer-Dür (1874) under the name of *Perla pallida* Guérin-Méneville, 1838.

At the time Pictet issued his seminal treatise (1841 for the text; 1842 for the plates), another important work was published by Rambur (1842), who also described a new species of alpine *Perla*. The description of Rambur's *Perla grandis* (1842: 454) is not very precise, compared to modern standards, and supplies only general information on its

coloration and a few morphological proportions, without any illustrations. Moreover, Rambur's description is based on a single adult female type specimen, formerly preserved in the Selys-Longchamp collection (Albarda 1889b; Klapálek 1923: 40). No description of the corresponding nymph is provided. Rambur (1842) describes his *Perla grandis* from the upper course of River Arve near Chamonix (France, Haute-Savoie). Curiously, these two so problematic taxa *Perla bipunctata* and *P. grandis* thus have not only been described within a couple of years, but also from the very same drainage basin (Arve, Rhône). Since Rambur (1842) was acquainted with the work of Pictet (1841/1842), and thus knew the *Perla bipunctata* of this author, he must have been well aware of the differences between this species and his *Perla grandis*, and did obviously not describe the same taxon as Pictet (1833, 1841, 1842). Moreover, Rambur (1842) describes his new species *Perla grandis* from the upper reaches of River Arve: « Habite les Alpes, vallée de Chamounix [i.e. Chamonix] » (Rambur 1842: 454), whereas Pictet's *P. bipunctata* is a lowland taxon.

Presently, there are still two vicariant morphospecies of *Perla* present in the Arve drainage system: type A in the upper reaches of River Giffre (tributary to Arve River) and type B in the lower reaches of Rivers Giffre and Arve in the Greater Geneva region. Whereas we can equate Rambur's *Perla grandis* with some confidence to our type A, the taxonomical identity of our type B is more difficult to ascertain. Nymphs of type B are separable from those of type C by the presence of sparse basal mediodorsal setae on the cerci of the former (Figs B.16, B.17), and their absence in the latter (Figs C.7, C.10), and by yellow markings on tergites III to V which are continuous in type C (Figs C.8, C.12) and lenticular in type B (Figs B.18, B.19, B.20). Nymphs of type B have also been collected in several other places, chiefly in the middle reaches of alpine and perialpine rivers such as the Sense in Switzerland, the Valserine in France or the Drau in Austria, whereas there are no recent reports of nymphs of type C. Nymphs of type A, recognizable by a dense row of basal mediodorsal setae on the cerci (Figs A.14, A.15) and circular or slightly elliptic light dots on tergites III to V (Figs A.17, A.18), can be found in many other, higher locations, in the Swiss, French and Italian Alps, and can be safely identified as *Perla grandis* (*sensu* Illies 1955 and Aubert 1949, 1959, *nec* Sivec & Stark 2002).

From the point of view of adult morphology, the situation is less clear, since adult males of *Perla* from the *bipunctata* / *grandis* group are identifiable only by their penial armatures. A significant taxonomical advance had been made by Despax (1942), who used in a systematic manner the shape and structure of the everted penial armature to delineate different species of *Perla*. Despax (1942, his fig. 11) was the first to provide an illustration of the everted penial armature of an adult male of putative *Perla bipunctata* (Fig. F.1), based on brachypterous specimens from the Aude and Garonne rivers, from the foothills of the French Pyrenees. By the cone-shaped base of the aedeagal tube (Fig. F.1), this illustration is akin to either type C (Fig. C.2) or D (Fig. D.2). The brachypterism of the adult males (Despax 1951), however, precludes the possibility of ranging them with the macropterous alpine specimens of type C (Fig. L.3). The wings of adult males of *Perla bipunctata* from alpine regions are, in general, slightly shorter than those of the corresponding females (Aubert 1959: 88), but the species is never brachypterous, like those from the British-Irish Isles (*cf.* Fig. D.4). The adult male of *Perla bipunctata* illustrated by Pictet (1842, plate 12, his Fig. 3; Fig. L.3) is clearly macropterous. The brachypterous adult male depicted by Despax (1942, his Fig. 11; 1951, his Fig. 86; Figs F.1, F.2) is similar to our type D, represented by specimens from the British-Irish Isles (Figs D.1, D.2, D.4), but the sclerotized apex of its aedeagus, as represented by Despax (1942, his Fig. 12; Fig. F.1) is notably different from the one of type D (Fig. D.1), and also from type C (Fig. C.1). One has to admit, therefore, that the putative *Perla bipunctata* of Despax (1942, 1951; Figs F.1, F.2) corresponds to an undescribed species.

When comparing our illustrations of types C and D (Figs C.2, D.2), as well as those of Despax (1942, his Fig. 11; Fig. F.1) with the drawings of *Perla bipunctata* provided by Illies (1955), it becomes evident that the aedeagal tube of the former all have a truncated cone-shaped base, whereas this base is represented as cylindrical by Illies (1955, his Fig. 115B) and also by Konar (1997, his Fig. 2). Since the cylindrical-shaped aedeagal tube corresponds only to our types B or A, Illies does not provide an illustration of *Perla bipunctata* corresponding to our type C (Fig. C.2), but rather to our type B (Figs B.6, B.7). The large black rims circling the inner half of the two lower ocelli (Illies 1955, his Fig. 115A), however, illustrate specimens of type D (Figs D.5, D.6), and not type C (Figs C.5, L.3) nor B (Figs B.13). In his illustrations of the nymphal material, Illies (1955, his Figs 153A, 153B) simply reproduces the drawings of Aubert (1949, his Figs 2 and 3), which further complicates the issue, since Aubert provides illustrations of nymphs of types A and C, but not of type B. We therefore may suspect that Illies' illustrations (1955, his Figs 115A, 115B, 153A, 153B) represent a conflation of types B, C and D, which is somehow understandable, since Illies (1953; 1955: 112) considered *Perla bipunctata* as a single, widely distributed species, in alpine as well as extra-alpine regions, with brachypterous or macropterous populations. This conclusion becomes patent also from the drawing of the sclerotized apex of the aedeagus ("titillator") provided by Illies (1955, his Fig. 115B), which corresponds to our type D (Fig. D.1), and not to type B (Fig. B.1, B.2, B.3, B.4), nor to type C (Fig. C.1). Since Illies (1955, his Fig. 114C) also provides an illustration of the sclerotized apex of the aedeagus of *Perla grandis* (under *Perla maxima*), which corresponds to our type A (Figs A.1, A.2, A.3, A.4), he recognizes at least the presence of two distinct species from the *Perla bipunctata* / *grandis* group in alpine regions, but does

apparently not separate types B and D, which he believes to be one and the same species, with macropterous populations in alpine regions and brachypterous ones in other regions, and has apparently not considered, or perhaps not even seen, unlike Aubert, specimens of type C.

The illustrations found in Aubert's studies are also somewhat ambiguous. In Aubert (1959, his Figs 254, 255), we find plain reproductions of Illies' (1955, his Figs 114C, 115B) drawings for adults of *Perla bipunctata* and *P. grandis* (under *Perla maxima*), whereas Aubert provides different, original, illustrations of the sclerotized apex of the aedeagus of *Perla bipunctata* (Fig. C.18), and also of *Perla grandis* (Fig. A.21), from alpine regions in an earlier publication (1949: 225, his Figs 4 and 5). A single, unfortunately damaged, male adult specimen of type C is indeed still extant in the Aubert collection in the MZL (container 7096), and we suspect that the drawing of the sclerotized apex of the aedeagus of *Perla bipunctata* by Aubert in this earlier publication (Aubert 1949: 225, his Fig. 5; Fig. C.18), was made after this specimen, which had been captured in River Aare, in Melchenbühl, near Berne, in 1938 or 1940 (Schneider collection, Berne Museum; one specimen in MZL, catalogue number: GBIFCH01204544), not far from the place where also nymphs of *Perla bipunctata* corresponding to our type C had been captured by Aubert in the 1940's (see above). The drawing of the sclerotized apex of the aedeagus of *Perla bipunctata* by Aubert in this earlier publication (Aubert 1949: 225, his Fig. 5; Fig. C.18) neatly corresponds to the one of our type C (Fig. C.1) and is clearly different from the one depicted in 1959 (Aubert 1959, his Fig. 255, reproduced from Illies 1955, his Fig. 115B).

Whereas Aubert's and Illies' illustrations of *Perla grandis* (under *Perla maxima*) hence coincide with our type A, both are found to conflate types B, C and D for their *P. bipunctata*. Since Illies' illustrations were adopted by nearly all subsequent authors (Illies 1955, his Fig. 115B = Aubert 1959, his Fig. 255 = Tierno de Figueroa et al. 2003, their Fig. 38 = Fochetti & Tierno de Figueroa 2008, their Fig. 52 = Teslenko & Zhiltzova 2009, their Fig. 334), the confusion between types B, C and D became almost inevitable.

Another criterion, sometimes adduced to separate adults of *Perla bipunctata* from those of *P. grandis*, relies on the large black rims circling the inner half of the two lower ocelli of the former, and its absence in the latter (Klapálek 1923: 38, his Fig. 20; Despax 1951, his Fig. 86A; Illies 1955, his Fig. 115A; Aubert 1959: 86, his Fig. 243; Kis 1974: 201, his Fig. 120A). This criterion was already found to be ineffective for separating alpine material by previous authors (Konar & Köstenberger 2002) and is again invalidated by the present investigation. Significantly larger black rims circling the inner half of the two lower ocelli are only found on specimens from the British-Irish Isles (Fig. D.5, D.6), but not on alpine material (Figs A.11, B.13, C.5). Pictet's illustrations (Fig. L.3) of *Perla bipunctata* (1842, plate 12, his Figs 1, 2, 3) likewise do not show this aspect. It is also not seen on specimens of putative *Perla bipunctata* from North Africa (Figs J.8, K.8) and Spain (Fig. G.3), as will be shown below, but is present on some specimens from higher locations in the Pyrenees (Fig. E.2).

For the identification of nymphal material from the Pyrenean region, Berthélemy & Laur (1975) had stated that the absence of a fringe of basal mediodorsal setae on the cerci was typical of *Perla bipunctata*, whereas the presence of such setae was characteristic of *Perla grandis*. Aubert (1946, 1949, 1959), Illies (1955), Raušer (1980) and Zwick (2004) do not provide any information on this feature. Schoenemund (1925a) mentions the presence of setae on the cerci, but does not specify their position. Berthélemy & Laur (1975: 278, their Fig. 9) provide a drawing of this feature made after extra-alpine specimens of putative *Perla bipunctata* which may be interpreted as showing the absence of basal mediodorsal setae at the base of the cerci, but the corresponding text of the description states that there are "one or two fine isolated setae" (1975: 279). Relying on the drawing of Berthélemy & Laur (1975: 278, their Fig. 9), Membiela (1990), Konar & Köstenberger (2002) and Tierno de Figueroa et al. (2003) use this criterion to separate *Perla grandis* from *P. bipunctata*. However, nymphal specimens labelled *Perla bipunctata* from the British-Irish Isles (type D), the Cantabrian Cordillera and North Africa also lack mediodorsal setae at the base of their cerci (Figs D.8, H.5, H.6, J.5, K.5). The criterion of Berthélemy & Laur (1975), therefore, separates at best only groups of species, but may also induce confusions with nymphs of other Perlidae, such as the genus *Marthamea* Klapálek, 1907, which also lack mediodorsal setae on their cerci (Lamine et al. 2019).

The taxonomical issues pertaining to the *Perla bipunctata* / *grandis* species group have, above all, been blurred by two questionable decisions:

a) the refusal to recognize *Perla bipunctata* as a valid species for alpine regions (Sivec & Stark 2002), by considering all the taxa from this region, that are neither *P. marginata* nor *P. abdominalis*, as belonging to the single species *P. grandis* and by applying the species name *Perla bipunctata* only to brachypterous specimens from Belgium and the British-Irish Isles and possibly also to specimens from the Pyrenees;
b) the synonymisation of *Perla carlukiana* with *P. bipunctata* by Illies (1953, 1966), followed by many authors (DeWalt et al. 2023). Note, however, that Despax (1951), Illies (1955, 1966: 286) and also Graf et al. (2009) are not in agreement with Sivec & Stark (2002) over the zoogeographical status of *Perla bipunctata* by considering this taxon as a single, widely distributed species, in alpine as well as extra-alpine regions, with brachypterous or macropterous populations, where-

as, according to Sivec & Stark (2002), *P. bipunctata* does not occur in alpine regions: "[…] *the name [Perla bipunctata] has been applied rather consistently to a species which may never have occurred there*" (Sivec & Stark 2002: 3).

Since the four different types of *Perla* from the *bipunctata* / *grandis* group, labelled A, B, C and D in the present study, are separable from one another by their penial armatures and by their nymphal morphology, we propose to consider all of them as valid species and recommend the following taxonomical rearrangements:

1. The species name *Perla carlukiana* Klapálek, 1907, 1923 should be restored (= type D, present study) and removed from synonymy with *Perla bipunctata* (Illies 1966; DeWalt *et al.* 2023), and applied to brachypterous specimens from the British-Irish Isles, in place of the now currently used *Perla bipunctata* (Feeley et al. 2016; Macadam et al. 2022). Whereas *Perla carlukiana* is still widespread in the British-Irish Isles, the species seems to be extinct in Belgium, from where it was formerly cited (Lestage 1920). However, according to Sivec & Stark (2002: 3), specimens from Belgium differ slightly from those of the British-Irish Isles by their chorionic reticulation, so that "*two species may be involved*". Klapálek (1923: 39) considers specimens from Belgium as belonging to his *Perla carlukiana*.
2. We propose to accept the name *Perla bipunctata* as considered by Pictet (1833, 1841, 1842) and *sensu* Aubert (1949), *nec* Illies (1955), *nec* Aubert (1959) only for specimens with macropterous males from lowland rivers in alpine and peri-alpine regions (= type C, present study). We consider the specimens of type C as corresponding to the "true" alpine *Perla bipunctata* of Pictet (1833). This species, formerly abundant in Italy (Mendl 1972; Ravizza 1974; Ravizza & Ravizza Dematteis 1979; Ravizza et al. 2022), is now very rare and could even be extinct in the West Palaearctic, like so many other potamal species (Zwick 1992; Ravizza & Nicolai 1983), and its nymphal niche, if still present, is now probably occupied by specimens from type B.
3. We propose to keep the name *Perla grandis* as considered by Illies (1955), Aubert (1949, 1959), *nec* Sivec & Stark (2002) only for specimens from higher locations in the Alps (= type A, present study). *Perla grandis* is still widespread in alpine regions and is not to be considered as a threatened species. The distribution of type A (Figs A.7, A.8) in Italy extends as far as Calabria in the Southern Apennines, and even reaches the Madonie mountain in Sicily (Aubert 1957; MZL, catalogue number: GBIFCH00913209).
4. For specimens from the middle reaches of alpine and perialpine rivers (= type B, present study), we propose the new name *Perla ravizzaorum*. To our knowledge, this type has remained undescribed, or has been conflated with the one of type C (Konar 1997; Konar & Köstenberger 2002) or type A (Lubini et al. 2012). *Perla ravizzaorum* **sp. n.** is found in the middle reaches of larger, undisturbed peri-alpine rivers, and must be considered as potentially threatened.

***Perla ravizzaorum* sp. n.**

(Figs B.1–B.24). Described above under the label "type B". urn:lsid:zoobank.org:act:4107F110-B37D-4A16-A058-1E60C7AFEFEB

Perla bipunctata (adults); Illies 1955, his Fig. 115B; Aubert 1959, his Fig. 255; Konar 1997, his Fig. 2
Perla grandis, sensu Sivec & Stark (2002), *pro parte*
Perla bipunctata / *grandis* group, type B (present study)

Type material. Holotype male: **ITALY**. Emilia-Romagna, Piacenza. Tra Ponte dell'Olio e Bettola, torrente Nure, 200 m, 27 Jun 1977, 1♂ (holotype), leg. E. Ravizza Dematteis & C. Ravizza (MZL, catalogue number: GBIFCH00899223). Paratypes: same location and date, 2♂, 4♀, leg. E. Ravizza Dematteis & C. Ravizza; MZL, catalogue number: GBIFCH00899223).

Additional material is listed in the Appendix 1, under type B.

Distribution. Main channel of larger, alpine and peri-alpine rivers, up to ca. 900 m (Fig. M.1).

Derivation nominis. This species is dedicated to the Italian plecopterologists Drs. Elisabetta Ravizza Dematteis and Carlalberto Ravizza, in recognition for their important contributions to the exploration of the Italian Plecoptera fauna.

Morphological affinities. Adult males of *Perla ravizzaorum* **sp. n.** are separable from those of all other species by the medially enlarged, ovoid-shaped sclerotized apex of their aedeagus (Figs B.1, B.2, B.3, B.4, B.5). Nymphs of *Perla ravizzaorum* **sp. n.** are characterized by the presence of sparse mediodorsal setae at the base of their cerci (Fig. B.17), in contrast to specimens of *P. bipunctata*, which lack these setae (Fig. C.10), and of *P. grandis*, whose cerci exhibit a dense row of mediodorsal setae (Figs. A.14, A.15).

By recognizing three different species (*Perla grandis* s.str. = type A; *Perla ravizzaorum* **sp. n.** = type B and *Perla bipunctata* = type C) within the *Perla bipunctata* / *grandis* group from alpine regions, instead of two, if not only one (Sivec & Stark 2002), and by restoring the species name *Perla carlukiana* (= type D), most taxonomical problems of this group may be disentangled. The separation of types A, B, C and D into different species now also clears the path for recognizing taxa from the Pyrenees, Spain and North Africa, that were formerly identified as *Perla bipunctata*, *P. grandis* or *P. maxima*, as hitherto undescribed species.

The problem of the taxonomical identity of specimens of the *Perla bipunctata* / *grandis* group mentioned from the French (Berthélemy & Laur 1975; Despax 1942, 1951)

and the Spanish Pyrenees (Bertrand & Aubert 1952, 1955; Aubert 1963; Oscoz & Durán 2004) is presently unsolved. By the shape of the sclerotized apex of its aedeagus (Fig. F.1), the putative *Perla bipunctata* of Despax (1942, 1951) from River Garonne near Toulouse differs from all other examined types A, B, C and D, and corresponds most certainly to an undescribed, but now apparently extinct, species, with brachypterous males (Despax 1951). Putative specimens of *Perla grandis* are also mentioned from both slopes of the Pyrenees (Berthélemy & Laur 1975; Oscoz & Durán 2004). Since adult males and nymphs of this morphospecies were available, and proved to be separable from alpine specimens of *Perla grandis* (Type A), and also from putative specimens of *Perla bipunctata* as considered by Despax (type F), they are described here from both adults and nymphs under type E, and named *Perla pyrenaica* **sp. n.** These two types from the Pyrenees are distributed according to altitudinal gradients: whereas type E (putative *Perla grandis*) is a high-altitude species, type F (putative *Perla bipunctata*) is only found at lower altitudes.

Type E

***Perla pyrenaica* sp. n.**

(Figs E.1–E.15)

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Perla maxima; Despax 1951: 190; Bertrand & Aubert 1952: 96; 1955; Aubert 1963: 79.

Perla grandis; Berthélemy & Laur 1975: 278; Oscoz & Durán 2004: 188; Tierno de Figueroa et al. (2003: 112; 2015b; 2018)

Morphological diagnosis. Males and females macropterous. Body length of males 18–26 mm; of females 20–36 mm. Body colour dark brown. Head mostly yellow with tawny markings; M-line clearly delineated (Fig. E.1). Pronotum pale yellow, with a large dark central band flanked with a symmetrical darker design (Fig. E.1). Inner half of the two lower ocelli circled by a narrow black band (Fig. E.1) on most, and by a large black band (Fig. E.2) on some specimens. This type corresponds to putative *Perla grandis* from the Pyrenees.

Type material. Holotype male: **FRANCE**. Occitania. Hautes-Pyrénées; tributary to Estaragne, cote 2193, 2240 m, 21 Jun 2022, 1♂, leg. B. Launay (MZL).

Paratypes: **FRANCE**. Occitania. Ariège, Albiès, Gargante brook, 790 m, 21 Jul 1986, 1♂ with separated aedeagus, leg. J. Aubert (MZL, catalogue number: GBIFCH00913253). **SPAIN**. Lleida. Bono, Noguera Ribagorzana, 1100 m, Jul 1951, 1♂ microscopic preparation, leg. H. Bertrand (MZL, catalogue number: GBIFCH00913240).

Additional material is listed in the Appendix 1, under type E.

Male adults. Sclerotized apex of aedeagus slightly bulging out in its middle section (Fig. E.3). Proximal part of aedeagus with a strong row of aligned brush-like setae (Fig. E.3); distal part terminated by two narrow blunt ends, medially interrupted (Fig. E.3). Length of aedeagus: 0.65 mm; width: 0.30 mm. Aedeagal tube with parallel sides (Fig. E.4) and covered by a dense grid of short setae (Fig. E.5). Mesal field on tergite IX short and narrow, with few spiny projections, and shallow distal division (Figs E.6, E.7). Distal side of hemitergal lobes of tergite X apically enlarged, in lateral view (Fig. E.8). Apex of hemitergal lobes with very strong spines (Fig. E.8).

Morphological affinities. Adult males of types E and F are separable by the shape of the sclerotized apex of their aedeagus. Whereas the one of *Perla pyrenaica* **sp. n.** ends into two blunt extensions (Fig. E.3), putative specimens of *Perla bipunctata* from the Pyrenees (type F) have a much shorter, and distally indented aedeagus (Fig. F.1). *Perla pyrenaica* **sp. n.** (Fig. E.3) differs from alpine *P. grandis* (Figs. A.4, A.8) by its much shorter and medially enlarged apex of its aedeagus.

Female adults. Subgenital plate with two distinct triangular extensions (Fig. E.9).

Nymphs. Length: 24 to 36 mm. Pronotum with a large, dark, central stripe flanked by two irregularly shaped dark bands loosely connected to the upper and to the lower edges of the pronotum (Figs. E.10, E.11). Rim of pronotum with a wide, half-circled dark band (Fig. E.10). Lateral edges of pronotum yellow (Fig. E.10). Yellow markings on tergites III to V dot-like, medially separated by a dark stripe (Fig. E.12). Dorsal faces of femora of middle and hind legs with an indistinct dark area connected to the dorsal edge of the femora (Fig. E.13). Cerci with separated bunches of basal mediodorsal setae (Fig. E.14). Tergites with long mediodorsal flexible setae, in lateral view. Paraprocts with conical apex (Fig. E.15).

Morphological affinities. Nymphs of *Perla pyrenaica* **sp. n.** are characterized by the presence of separated bunches of basal mediodorsal setae on their cerci (Fig. E.14), whereas *P. grandis* nymphs exhibit a continuous row of long, mediodorsal setae (Figs. A.14, A.15).

Distribution. This species is known from high altitude brooks and springs on both slopes of the Pyrenees. The material is listed in the Appendix 1, under type E.

Derivation nominis. This species is named after the region which it inhabits. The adjective *pyrenaica* is to be treated as a feminine Latin adjective in the nominative case combined with *Perla*.

Type F

This type corresponds to putative *Perla bipunctata* (*sensu* Despax 1942, 1951; Bertrand & Aubert 1952, 1955) from the Pyrenees (Figs F.1 – F.8).

Morphological diagnosis. Males brachypterous; females macropterous (Despax 1942, 1951).

Male adults. Known only from descriptions in the literature (Despax 1942, 1951). Sclerotized apex of aedeagus short, cordiform, with a brush-like apex (Fig. F.1). Sides gently rounded; distal part with a shallow median indentation (Fig. F.1). Aedeagal tube shaped like a truncated cone (Fig. F.1). Mesal field on tergite IX long, with distally divided sensilla (Fig. F.2). Hemitergal lobes spatulate, slightly enlarged apically (Figs F.1, F.2).

Female adults. Unknown.

Nymphs. Pronotum with two dots, not connected to the upper or lower edge of the pronotum (Fig. F.3; Oscoz & Durán 2004, their Fig. 2). In dorsal view, tergites with continuous yellow markings, not interrupted by a dark central stripe (Fig. F.4) or with only a small stripe in the upper half of the tergites (Fig. F.5; Oscoz & Durán 2004, their Fig. 2). Proximal part of each abdominal tergite with a narrow, dark band (Figs F.4, F.5). In lateral view, tergites with sparse mediodorsal flexible setae. Femora with a dark, central oval marking (Fig. F.6). Paraprocts slightly bent sideward, with flattened apex (Fig. F.7). Cerci without basal mediodorsal setae (Fig. F.8).

Morphological affinities. The nymphs of types E and F are separable from one another by the absence of mediodorsal setae at the base of the cerci of the latter (*cf.* Figs E.14 and F.8; Berthélemy & Laur 1975). Nymphs of type E have dot-like markings on their tergites (Fig. E.12), whereas those of type F have continuous yellow markings (Fig. F.4).

Distribution and ecology. Large and medium-sized rivers of the piedmont of the French and Spanish Pyrenees. The material is listed in the Appendix 1, under type F.

Conservation status. Apparently a very rare taxon, of which only a single nymphal specimen was captured in 2004 (Oscoz & Durán 2004). Since there are no recent records of this species, it has to be considered as critically endangered, if not extinct.

Since adequate material of an additional, undescribed species from the Sierra de Castril and the Sierra Nevada in Andalusia (Spain) was also available, we describe these specimens here from adult males and females, as well as mature nymphs, under type G.

Type G

***Perla andalusiaca* sp. n.**

(Figs G.1–G.15).

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Perla maxima; Aubert (1956a: 255); Aubert (1963:79); Picazo Muñoz (1995), in: Sánchez-Ortega et al. (2003)

Perla bipunctata; Tierno de Figueroa et al. (2005, 2015a, 2018); Bo et al. (2008); López-Rodríguez et al. (2012); Luzón-Ortega et al. (2013) Sanz et al. (2014, 2017).

Morphological diagnosis. Males and females macropterous. Body length of males 18–26 mm; of females 20–34 mm. Body colour dark brown. Head mostly yellow with tawny markings; M-line not clearly delineated (Figs G.1, G.2). Pronotum pale yellow, with a large dark central band flanked with a symmetrical darker design (Figs G.1, G.2). Inner half of the two lower ocelli circled by a narrow black band (Fig. G.2).

Type material. Holotype male: **SPAIN**. Granada province, River Castril, Sierra de Castril, 1220 m, 37° 54' 25.0560'' N, 2° 44' 51.4788'' W, 16 Jun 2005, holotype, 1♂ (with penial armature detached), leg. J. M. Tierno de Figueroa & M. J. López-Rodríguez (MZL). Paratypes: same location, 16 Jun 2005, 1♂ (with penial armature detached), (MZL); 1♀ (MZL); 14 Dec 2004, 1L♂ (MZL); leg. J. M. Tierno de Figueroa & M. J. López-Rodríguez. Additional material is listed in the Appendix 1, under type G.

Male adults. Sclerotized apex of aedeagus slightly enlarged medially in specimens with *de vivo* everted aedeagus (Fig. G.4) and with nearly parallel sides in dissected specimens (Figs. G.3, G.5), distally terminated by two triangle-shaped extensions (Figs G.4, G.5, G.6), and with a brush-like apex (Figs. G.3, G.5). Aedeagal tube cylindrical (Fig G.4). Mesal field on tergite IX distally with a very small medial incision (Figs G.6). Apex of hemitergal lobes of tergite X blunt, wide and short, apically enlarged, in lateral view (Fig. G.7). Aedeagal tube covered by a dense field of setae with alternating lengths and densities (Fig. G.8).

Morphological affinities. Adult males of *Perla andalusiaca* **sp. n.** are close to those of *Perla pyrenaica* **sp. n.** (type E) by the sclerotized apex of their aedeagus (*cf.* Figs. G.5 and E.3). The distal side of the hemitergal lobes of tergite X is not enlarged apically in specimens of *Perla andalusiaca* **sp. n.** (Fig. G.7), whereas we find a hammer-like extension in specimens of *Perla pyrenaica* **sp. n.** (Fig. E.8).

Female adults. Subgenital plate with two distinct median triangular extensions (Fig. G.9).

Nymphs. Head mostly yellow, with narrow, darker coloured M-line (Fig. G.10). Pronotum with a large, dark, central band flanked by two dot-like dark patches loosely connected only to the upper edge of the pronotum (Fig. G.10). Rim of pronotum with a narrow, half-circled band (Fig. G.10). Lateral edges of pronotum yellow (Fig. G.10). Yellow markings on tergites III to V continuous, covering the entire distal edge of the corresponding segments (Fig. G.11). Tergites with long mediodorsal flexible setae, in lateral view (Fig. G.12). Dorsal faces of femora of middle and hind legs with a dark central oval mark (Fig. G.13). Paraprocts with conical apex (Fig. G.14). Cerci with a sparse fringe of long, basal mediodorsal setae, not extending beyond segment XV (Figs. G.14, G.15).

Morphological affinities. Nymphs of *Perla andalusiaca* **sp. n.** are separable from those of *Perla pyrenaica* **sp. n.** (type E) by the presence of a sparse and short

fringe of basal mediodorsal setae on the cerci of the former (Figs. G.14, G.15) and by a much longer fringe on the latter (Fig. E.14). The yellow markings on tergites III to V are continuous, and covering the entire distal edge of the corresponding segments in *Perla andalusiaca* **sp. n.** (Fig. G.11), whereas they are dot-like in *Perla pyrenaica* **sp. n.** (Fig. E.12).

Distribution. This species is presently known only from the Sierra de Castril and the Sierra Nevada, but is likely to have a wider distribution in Andalusia. The material is listed in the Appendix 1, under type G.

Derivation nominis. This species is named after the region which it inhabits. The adjective *andalusiaca* is to be treated as a feminine Latin adjective in the nominative case combined with *Perla*.

Note. *Perla hagenii* Pictet, 1865, described after a single female from the outskirts of Granada (pp. 12–13; plate 2, Figs 1–3 in Pictet 1865), could correspond to *Perla andalusiaca* **sp. n.**, since the female subgenital plate and the markings on the head are similar to it (Figs G.16, G.17). *Perla hagenii* has been later synonymized with *P. marginata* (DeWalt et al. 2023), referring to Illies (1966: 292), who in turn refers, erroneously, to Aubert (1956a). Aubert (1956a), indeed, considers *Perla hagenii* as a synonym of *Perla maxima* (*Perla grandis*), not *P. marginata*, as did also Navás (1901). Later, however, Aubert (1963) considered the species as a synonym of *Perla marginata*. To judge from Pictet's (1865) illustrations (Figs G.16, G.17), this taxon could, however, also correspond to *Perla madritensis* Rambur, 1842. Since no holotype had been designated by Pictet (1865), and since his description is based on a single female specimen, it is safer to designate *Perla hagenii* as a *nomen dubium*, and not as a synonym of *Perla marginata* (DeWalt et al. 2023).

Specimens of the *Perla bipunctata* / *grandis* group are also mentioned from the Cantabrian Cordillera (Vinçon & Pardo 2004; González del Tánago 1984) and Asturias. Navás (1917) had described a brachypterous species labelled *Perla bicaudata L. (maxima* auct*.)* var. *asturica* from Río de Nueva, a low altitude river in Asturias, and indicates in his description "*Alae apicem abdominis haud attingentes*" (The wings not reaching the tip of the abdomen). This brachypterous species is presently ranked as a *nomen dubium* (DeWalt et al. 2023), whereas Aubert (1952: 249) considered it as a valid species, endemic to the Cantabrian Cordillera, and Illies (1966: 293, 498) listed it as a synonym of *Perla maxima* (*Perla grandis* or *Perla bipunctata*, uncertain synonymy, see above). By its brachypterism, this species corresponds to an extra-alpine taxon of the group, but is neither identical with brachypterous *Perla carlukiana* (type D) (Navás 1917: 5 "*Similis var. carlukianae Klap., obscurior*"), nor with macropterous *Perla bipunctata* as considered by Pictet, 1833 (type C). Brachypterous male nymphs probably belonging to this taxon have been collected by M. González del Tánago and D. García de Jalón (González del Tánago 1984) and Aubert (1956a: 255, under *Perla maxima*) in the Cantabrian Cordillera. Since adults of this taxon were not available, and the type specimen being lost (Aubert 1952: 249), the taxonomical status of *Perla asturica* Navás, 1917 cannot be ascertained at the time of writing. The putative nymphs of this morphospecies with brachypterous males are easily separable from those of all other known species, except specimens of type F (putative *Perla bipunctata*) from the Pyrenees. We informally describe these nymphal specimens from the Cantabrian Cordillera, possibly identical with the *Perla asturica* of Navás (1917), and with the putative *Perla bipunctata* from the Pyrenees (type F) described by Despax (1942), under type H below.

Type H.

Nymphs. Mature male nymphs (23–24 mm) with prefigured brachypterism (Fig. H.1), but not significantly smaller in size than the corresponding females (23–27 mm). Head mostly yellow, with well-marked, darker M-line (Fig. H.2). M-line laterally interrupted by a small, yellow stripe on both sides (Fig. H.2). Pronotum yellow, with a dark, central band flanked by two dark elliptic patches loosely connected to the upper edge of the pronotum (Fig. H.2). Rim of pronotum with a narrow, half-circled dark band (Fig. H.2). Lateral edges of pronotum yellow (Fig. H.2). Yellow markings on tergites III to V lenticular, separated by a dark stripe in their middle (Fig. H.1). Tergites with long mediodorsal flexible setae, in lateral view (Fig. H.5). Dorsal faces of femora of middle and hind legs with a dark central oval mark (Fig. H.3). Apex of paraprocts straight, not rounded, in both sexes (Fig. H.4). Cerci without fringe of basal mediodorsal setae (Figs H.5, H6).

Morphological affinities. The nymphs of type H (Cantabrian Cordillera) are not separable from those of the piedmont of the Pyrenees (type F).

Distribution and ecology. Cantabrian Cordillera and Asturias, in rivers below ca. 950 m. The material is listed in the Appendix 1, under type H.

In the nymphal material collected by M. González del Tánago and D. García de Jalón in the Cantabrian Cordillera (González del Tánago 1984), we discovered a second, macropterous morphospecies, from River Carrión near Triollo (1300 m). Since the nymphs of this morphospecies are separable from those of type H, we informally describe this taxon under type I below. Adults were not available.

Type I.

Nymphs. Length: 24 to 36 mm. Mature male nymphs with prefigured macropterism (Fig. I.2). Head mostly yellow, with well-marked, darker M-line (Fig. I.1). Pronotum yellow, with a dark, central band flanked by two dark elliptic patches connected to the upper edge of the pronotum (Fig. I.1). Rim of pronotum with a narrow, half-circled band

(Fig. I.1). Lateral edges of pronotum yellow (Fig. I.1). Yellow markings on tergites III to V elliptical, separated by a dark stripe in their middle (Fig. I.2). Tergites with long mediodorsal flexible setae, in lateral view (Fig. I.3). Dorsal faces of femora of legs with a wide, dark area connected to the lower edge of the femora (Fig. I.4). Apex of paraprocts bent sideward, and with flattened apex (Fig. I.5). Cerci with separated bunches of mediodorsal setae, distributed over the whole length of the cercus (Fig. I.6).

Distribution and ecology. High altitude morphospecies (ca. 1300 m), presently known only from the Cantabrian Cordillera and Asturias. The material is listed in the Appendix 1, under type I.

Morphological affinities. The nymphs of types H and I are separable from one another by the absence of mediodorsal setae at the base of the cerci of the former (Figs H.5, H.6) and their presence on the latter (Fig. I.6). Both types H and I, however, are not separable from types E and F, from the adjacent Pyrenees.

The taxonomical identity of specimens provisionally identified as *Perla bipunctata* or *Perla maxima* from the Atlas Mountain of Morocco and Algeria by Aubert (1956b, 1960 [publ. 1961]), is even more difficult to ascertain. The perlid stoneflies (brachypterous males and nymphs) from different massifs of the Atlas Mount (M'Goun, M'Corn and Toubkal), collected by Vaillant (Aubert 1956b) and Aubert (1960 [publ. 1961]), and stored under the taxon name *Perla bipunctata* in the MZL (container CB-18143), were revised by the present author, but could not be apparently attributed to any of the types A, B, C, D, E, G or I outlined above. We have, therefore, grouped these specimens under types J and K. As far as we can conclude from this scanty material, two different morphospecies are involved, to judge from the shape of the sclerotized apex of the aedeagus (*cf.* Figs J.1, K.1), the mesal field on tergite IX (*cf.* Figs J.2, K.2) and the apex of the hemitergal lobes of their adults (*cf.* Figs J.3, K.3). Two types of nymphs were also discovered within the material from the High Atlas Mountains: one type with rounded, conical paraprocts (Fig. J.4) and another one with pointed paraprocts (Fig. K.4). All examined nymphs lacked basal mediodorsal setae on their cerci (Figs J.5, K.5). Since only exuviae with rounded paraprocts (Fig. J.4) were found in the M'Corn Massif, we have grouped the male adult (Fig. J.1) from this sampling station with type J. In the M'Goun Massif, two types of nymphs were collected, but only one adult male, with an aedeagus (Figs K.1, K.9) different from the one of type J (Fig. J.1). We hence assumed that the nymph with pointed paraprocts (Fig. K.4) also corresponded to adults of type K. Since this material had been collected in various massifs and at different altitudes in the Atlas Mountains, the presence of more than one species within the examined material could indeed be expected. Whereas both types, J and K, were present in the material from the M'Goun Massif, those from the M'Corn Massif yielded only specimens of type J; both "types" are informally described below.

Type J.

Morphological diagnosis. Males brachypterous; wing length of females unknown, but most probably macropterous, as can be inferred from female nymphs. Body length of male 21 mm. Body colour light brown and yellow. Head mostly yellow with tawny markings; M-line not clearly delineated (Fig. J.8). Pronotum pale yellow, with a narrow tawny central band, flanked by two light brown areas (Fig. J.8). Inner half of the two lower ocelli circled by a narrow black band (Fig. J.8).

Male adults. Sclerotized apex of aedeagus short, cordiform, with a brush-like apex (Fig. J.1). Width of apex 0.35 mm. Sides gently rounded; distal part with a shallow median incision (Fig. J.1). Shape of aedeagal tube unknown. Mesal field on tergite IX short, with distally divided sensilla (Fig. J.2). Hemitergal lobes slender, apically enlarged (Fig. J.3).

Female adults. Unknown.

Nymphs. Paraprocts rounded, with conical apex, in ventral view (Fig. J.4). Cerci without mediodorsal flexible setae (Fig. J.5). In lateral view, tergites with sparse mediodorsal flexible setae (Fig. J.9). Tergites with elliptical yellow dots (Fig. J.6). Head mostly yellow, with a tawny band encircling the interocellar area and well-developed M-line (Fig. J.7). Pronotum with a central, tawny band, and two stripes linking its upper edge to the lower (Fig. J.7). Pronotum circled by a tawny band; lateral edges of pronotum yellow (Fig. J.7). Marks on dorsal faces of femora not discernible anymore.

Distribution. Presently known only from the High Atlas M'Corn Massif of Algeria and M'Goun Massif of Morocco. The material is listed in the Appendix 1, under type J.

Type K.

Morphological diagnosis. Males brachypterous (Fig. K.2); wing length of females unknown, but most probably macropterous, as can be inferred from the female nymphs collected from the same sampling station (Fig. K.7). Body length of male 20 mm. Body colour light brown and yellow. Head mostly yellow with tawny markings; M-line not clearly delineated (Fig. K.8). Pronotum pale yellow, with a narrow tawny central band, flanked by two light brown areas (Fig. K.8). Inner half of the two lower ocelli circled by a narrow black band (Fig. K.8).

Male adults. Sclerotized apex of aedeagus short, cylindrical, with a brush-like apex (Figs K.1, K.9). Sides nearly parallel (Figs K.1, K.9). Shape of aedeagal tube cylindrical (Fig. K.1). Mesal field on tergite IX wide, distally with a deep central incision (Fig. K.2). Hemitergal lobes blunt, apically not enlarged (Fig. K.3).

Female adults. Unknown.

Nymphs. Length: 23 to 27 mm. Paraprocts with pointed apex, in ventral view (Fig. K.4). Cerci without mediodorsal flexible setae (Fig. K.5). In lateral view, tergites with a long and dense row of mediodorsal flexible setae (Fig. K.5). In dorsal view, tergites with narrow, nearly square-shaped yellow dots (Fig. K.6). Head mostly yellow, with a V-shaped design between the two lower ocelli (Fig. K.7). Pronotum with a central, tawny band, and two stripes linking its upper edge to the lower (Fig. K.7). Marks on dorsal faces of femora not discernible anymore.

Distribution. Known only from the High Atlas M'Goun Massif of Morocco. The material is listed in the Appendix 1, under type K.

Morphological affinities. Brachypterous male specimens from the M'Corn Massif (Algeria) have a short cordiform apex of their aedeagus (Fig. J.1), whereas some from the M'Goun Massif have a short cylindrical apex (Figs K.1, K.9). In type J, the mediodorsal setation on tergites is sparse (Fig. J.9), whereas it is denser on specimens of type K (Fig. K.5). By their brachypterism and by the short, sclerotized apex of their aedeagus (Fig. J.1), as well as by the sensilla of their mesal field on tergite IX (Fig. J.2) and the shape of the apex of their hemitergal lobes (Fig. J.3), the specimens from the M'Corn Massif are close to those of type F, described by Despax (1942, 1951) from the Pyrenees under the name *Perla bipunctata* (*cf.* Figs F.1, J.1).

Further undescribed species of the *Perla bipunctata* / *grandis* group probably exist in Central and Eastern Europe (Hlebec et al. 2022). Specimens of *Perla bipunctata* previously reported from East Germany by Braasch & Odrich (1974) and Braasch (1975) are now believed to belong to an undescribed species (Hohmann & Küttner 2018). Kis (1974) quotes *Perla bipunctata* from Romania, where both sexes are macropterous, but does not illustrate the penial armature of the species, the only distinctive trait separating it from *Perla grandis* being the large black rim around the inner half of the two lower ocelli (Kis 1974: 201, his Fig. 120A). Note, however, that this aspect might simply have been taken over from Klapálek (1923: 38, his Fig. 20), since Kis, following Illies (1953, 1966: 286), considers *Perla bipunctata* as a single species with a disjunct distribution in the West Palaearctic. The species is also mentioned from the Tisza in Hungary (Kovács et al. 2001). Doubtful records of *Perla bipunctata* in Eastern Europe are mentioned by Despax (1933), Karaouzas et al. (2016) and Arkhipova et al. (2022). The drawings provided by Raušer (1980, his Figs 27/5, 27/6, 27/9) for nymphs of putative *Perla bipunctata* from the Carpathians correspond partly to those of our type B (Figs B.18, B.19). One macropterous adult male with everted aedeagus, sent to J. Aubert by J. Raušer, and preserved in the MZL (catalogue number: GBIFCH01143925, Slovakia, Low Tatras, River Štiavnica, 700 m, 26.07.1956), could provisionally be identified as belonging to type B (*Perla ravizzaorum* **sp. n.**). The apex of the hemitergal lobes of this specimen does not show any apical curvature, a feature typical of type C (Figs C.3, C.4), and the sclerotized apex of its aedeagus corresponds to the one of type B (Figs B.1, B.2, B.3). These features preclude any identification of this specimen as corresponding to *Perla bipunctata* (type C).

Conclusions

Zoogeographical perspectives. It is necessary to say here that a more accurate and stable picture of the entire taxonomic situation could be probably traced only by analysing also molecular data on the different taxa and the different populations distributed in Europe and North Africa (but several of the taxa examined here could be probably extinct). However, following the evidence presented in this preliminary revision, available morphological data at least allow all specimens examined, thus far labelled *Perla bipunctata* or *P. grandis* by number of authors, to be allocated to several, related entities, rather than to single, unequivocally identifiable, and widely distributed Palaearctic taxa (Zwick 2004). In the present investigation, we have mainly focussed on specimens from alpine regions (types A, B and C), which may be conveniently grouped into a cluster with the three species *Perla grandis*, *P. ravizzaorum* **sp. n.** and *P. bipunctata*, distributed according to altitudinal gradients. One may identify a second cluster (type D) of specimens inhabiting the rivers of the British-Irish Isles (Feeley *et al.* 2016; Macadam *et al.* 2022) and large rivers in Belgium (Lestage 1920; Klapálek 1923), once connected when both the Ancestral Thames and River Scheldt were tributaries to the Ancestral Rhine during the Early and Middle Pleistocene. The presence of only one species (*Perla carlukiana*, type D) of the *Perla bipunctata* / *grandis* group in these regions may be simply due to the fact that they lack, unlike the Alps, the Pyrenees, the Cantabrian Cordillera and the Atlas, these higher mountain ranges, that would have allowed the differentiation of additional, more orophilous taxa. The specimens from the French (Berthélemy & Laur 1975; Despax 1942, 1951) and Spanish (Oscoz & Durán 2004) Pyrenees form a third cluster (types E and F), with two morphospecies (putative *Perla bipunctata* and *Perla pyrenaica* **sp. n.**), also distributed according to altitudinal gradients. A fourth cluster, possibly identical to the preceding one, is found in the Cantabrian Cordillera (González del Tánago 1984; Vinçon & Pardo 2004) and Asturias, with two morphospecies (types H and I), again distributed according to altitudinal gradients. The position of the rather isolated, macropterous type G, from Andalusia can presently not be assessed with confidence. The two brachypterous types from the Atlas Mountain of Morocco and Algeria (types J and K) belong to an additional cluster. It cannot be excluded, however, that type J,

from North Africa, is identical to type F, from the foothills of the Pyrenees, to be judged from the shape of the sclerotized apex of their aedeagus (*cf.* Figs F.1, J.1). Several other Perlid lowland genera (*Eoperla* Illies, 1956 and *Marthamea* Klapálek, 1907) are indeed common to North Africa and the Mediterranean slopes of the Pyrenees. Exchanges between both regions were possible during the Messinian Salinity Crisis (5.96 to 5.33 Ma), when the desiccation of the Mediterranean Sea considerably extended the reaches of coastal rivers, creating faunistic meeting points at their estuaries (Lamine et al. 2019).

The outstanding feature of the alpine *Perla bipunctata* (type C), when compared to related taxa from the Pyrenees (type F), the Cantabrian Cordillera (type H), the Atlas Mountain (types J and K) and the British-Irish Isles (type D), is the presence of macropterous males in the former, and brachypterous ones in the latter. One could be tempted to admit, following the example of Despax (1951: 180) and Illies (1953, 1955: 112), that *Perla bipunctata* exists as a macropterous form in alpine regions, and as a brachypterous one in extra-alpine regions. It is indeed not uncommon, in the order of the Plecoptera, to find pairs of species within a genus whose males are macropterous in alpine regions and brachypterous in mountain ranges belonging to the remnants of the Hercynian orogenic belt. Good examples are the macropterous *Capnia vidua vidua* Klapálek, 1904 (*sensu* Aubert et al. 1996, since the topotypical specimens from the Hercynian High Tatras are brachypterous; Reding 2020) and the brachypterous *Capnia vidua collarti* Aubert, 1950; macropterous *Capnioneura nemuroides* Ris, 1905 and brachypterous *Capnioneura brachyptera* Despax, 1932; macropterous *Dinocras megacephala* (Klapálek, 1907) and brachypterous *Dinocras cephalotes* (Curtis, 1827). In all of these instances, however, two (or more) different species are recognized.

Remarkable, also, is the altitudinal stratification of the different morphospecies belonging to the *Perla grandis-bipunctata* group. Whereas we find three species, distributed according to altitudinal gradients, in alpine regions, in most other regions (Pyrenees, Cantabrian Cordillera and North Africa) only two species are present, except the British-Irish Isles, where, due to the presence of only low altitude rivers, only one species is found. The upstream-downstream succession of three different congeneric species according to altitudinal gradients is a common phenomenon in alpine Plecoptera. Good examples are the triads *Rhabdiopteryx harperi* Vinçon & Murányi, 2009, *R. alpina* Kühtreiber, 1934 and *R. neglecta* (Albarda, 1889a), or *Perlodes intricatus* (Pictet, 1841), *P. microcephalus* (Pictet, 1833) and *P. dispar* (Rambur, 1842). Noteworthy, finally, are also the morphological analogies found in the corresponding adults and nymphs. The sclerotized apex of the aedeagus of adult males of the lower altitude species (Figs C.1, D.1, F.1) is always shorter than the one belonging to high altitude species (Figs A.4, E.3). Nymphs of low altitude species lack basal mediodorsal setae on their cerci, whereas those from higher locations are always more abundant, except the brachypterous specimens from the Atlas Mountain.

Biodiversity conservation strategies. The traditional view of the species *Perla grandis* and *P. bipunctata* as widely distributed (Graf et al. 2009; DeWalt et al. 2023), and hence not endangered, taxa in the West Palaearctic, does not stand up to a more thoroughgoing taxonomical examination. We rather face partially unresolved species complexes, whose members are disjunctly distributed over different, often isolated, geographical areas and mountain ranges and which have, consequently, also different conservation statuses. The grouping of closely related species under wider taxonomical units may facilitate identification and species management, but is exposed to the drawback of neglecting issues of conservation policies (Leys et al. 2016). Adequate naming, therefore, is an essential prerequisite also for the success of conservation programs (Mace 2004; Dussex et al. 2018).

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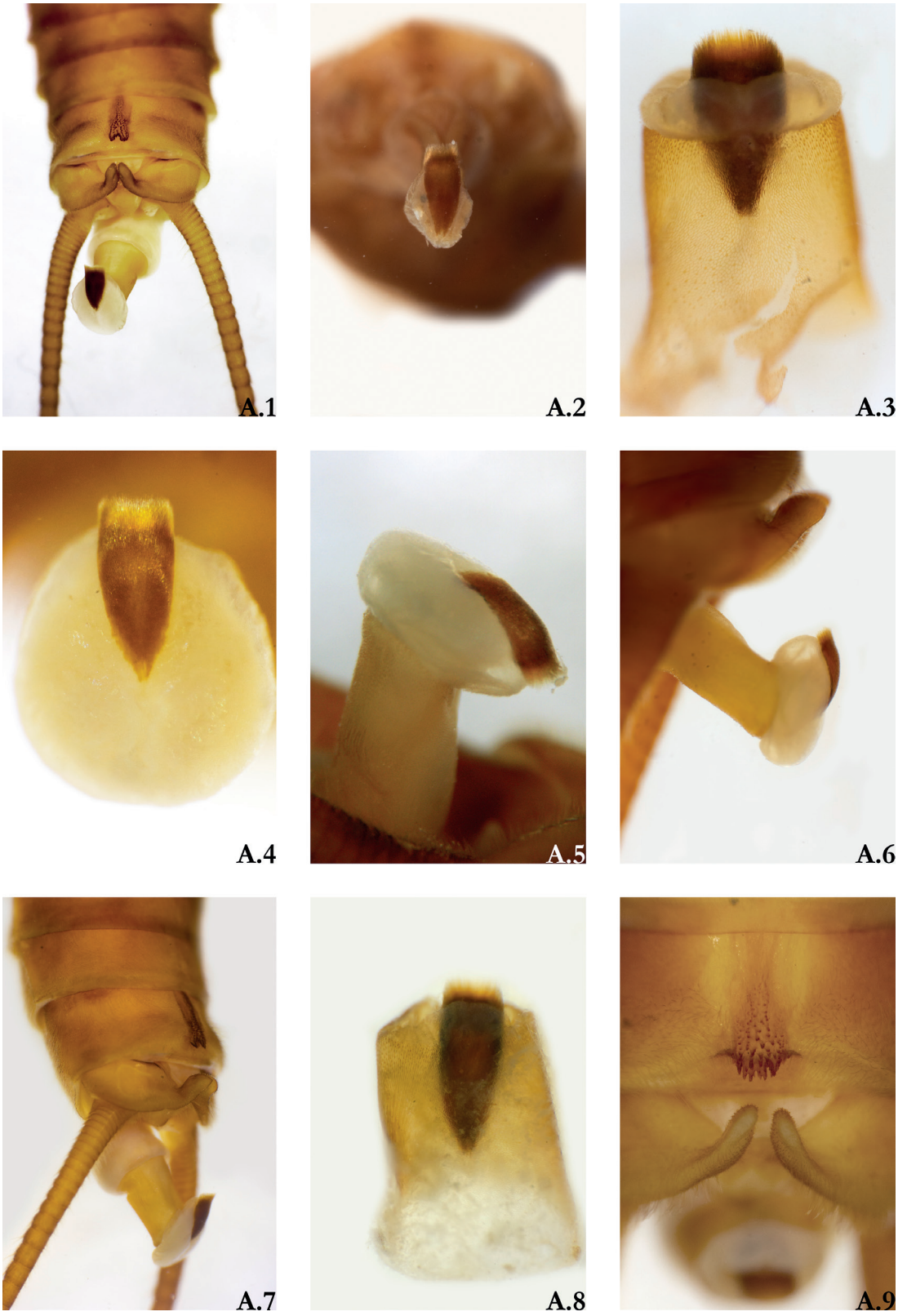


Plate I, Figs A.1–A.9 – Type A (Italian Alps and Apennines). **A.1**, hemitergal lobes, mesal field with sensilla and sclerotized apex of everted aedeagus of an adult ♂ (Soana); **A.2**, sclerotized apex of everted aedeagus of an adult ♂ (Staffora); **A.3**, sclerotized apex of extracted aedeagus of an adult ♂ (Stura di Ala); **A.4**, sclerotized apex of everted aedeagus of an adult ♂ (Soana); **A.5**, aedeagal tube of adult ♂; **A.6**, aedeagal tube and hemitergal lobes of adult ♂; **A.7**, adult ♂, hemitergal lobes and mesal field with sensilla (Southern Apennines); **A.8**, sclerotized apex of extracted aedeagus of an adult ♂ (Southern Apennines); **A.9**, adult ♂, hemitergal lobes and mesal field with sensilla, dorsal view (Stura di Demonte).

Plate II, Figs A.10–A.15 – Type A (male and female adults, nymphs). **A.10**, adult ♂, hemitergal lobes, lateral view (Southern Apennines); **A.11**, head and pronotum of an adult ♂ (Stura di Demonte); **A.12**, subgenital plate of adult ♀ (Stura di Demonte); **A.13**, subgenital plate of adult ♀ (Haute-Savoie); **A.14**, basal section of cerci of nymph (Staffora); **A.15**, basal section of cerci of nymph (Gryonne valley).

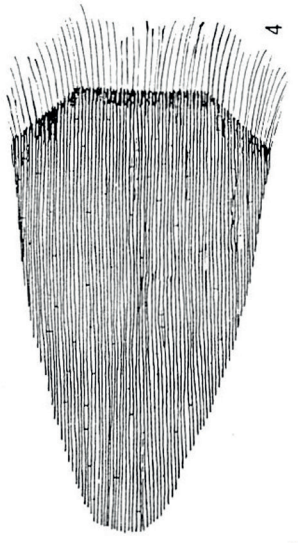


Plate III, Figs A.16–A.21 – Type A (French and Swiss Alps). **A.16**, head and pronotum of nymph (Swiss Alps); **A.17**, markings on tergites of nymph (Gryonne valley); **A.18**, markings on tergites of nymph (Sense); **A.19**, markings on the femora of legs, dorsal view (Gryonne Valley); **A.20**, sclerotized apex of extracted aedeagus of an adult ♂ (Vercors); **A.21**, sclerotized apex of aedeagus of *Perla grandis*, from Aubert 1949: 225, his Fig. 4.

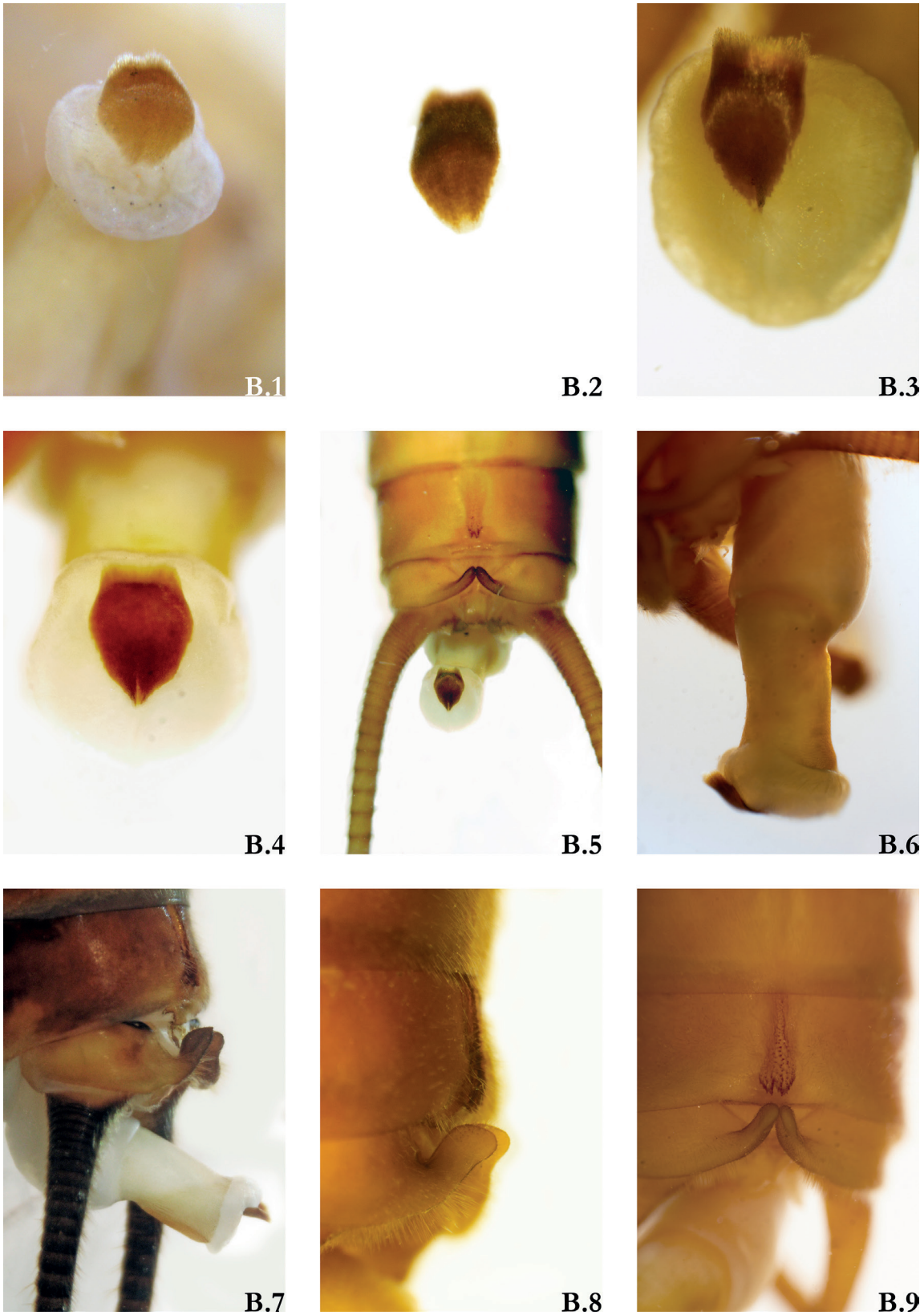


Plate IV, Figs B.1–B.9 – Type B (Italian Alps and Apennines). **B.1**, sclerotized apex of aedeagus of an adult ♂ (Nure); **B.2**, sclerotized apex of aedeagus of an adult ♂ (Stura di Demonte); **B.3**, sclerotized apex of aedeagus of an adult ♂ (Sesia); **B.4**, sclerotized apex of everted aedeagus of an adult ♂ (Tanaro); **B.5**, hemitergal lobes, mesal field with sensilla and sclerotized apex of everted aedeagus of an adult ♂ (Tanaro); **B.6**, aedeagal tube of adult ♂, in lateral view; **B.7**, aedeagal tube and hemitergal lobes of adult ♂, in lateral view; **B.8**, hemitergal lobes of adult ♂, in lateral view; **B.9**, adult ♂, hemitergal lobes and mesal field with sensilla.

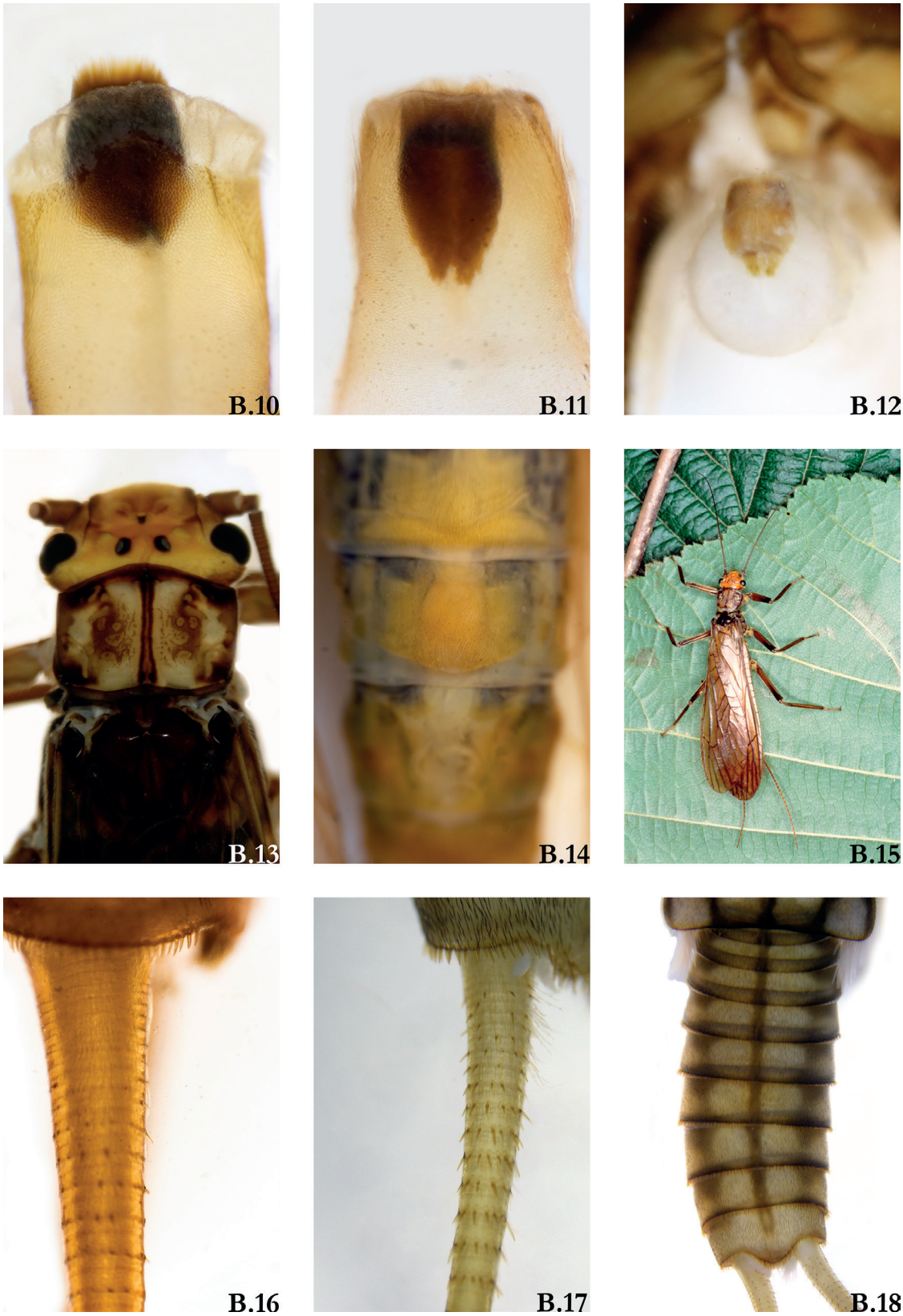


Plate V, Figs B.10–B.18 – Type B (adults and nymphs). **B.10**, sclerotized apex of aedeagus of an adult ♂ (Sense); **B.11**, sclerotized apex of aedeagus of an adult ♂ (Valserine); **B.12**, sclerotized apex of aedeagus of an adult ♂ (Drau); **B.13**, head and pronotum of an adult ♂ (Sense); **B.14**, subgenital plate of adult ♀; **B.15**, habitus of adult (Staffora; photo by Carlalberto Ravizza); **B.16**, basal section of cerci of nymph having been preserved in ethanol for nearly 50 years; **B.17**, basal mediodorsal setation on cerci of nymph (Valserine); **B.18**, markings on tergites of nymph (Valserine).

Plate VI, Figs B.19–B.24 – Type B (nymphs). **B.19**, markings on tergites of nymph (Drau); **B.20**, markings on tergites of nymph (Nure); **B.21**, markings on the femora of legs, dorsal view (Sense); **B.22**, head and pronotum of nymph (Valserine); **B.23**, head, pronotum, mesonotum, metanotum and first abdominal tergites of nymph (Sense); **B.24**, paraprocts of nymph, ventral view (Staffora).

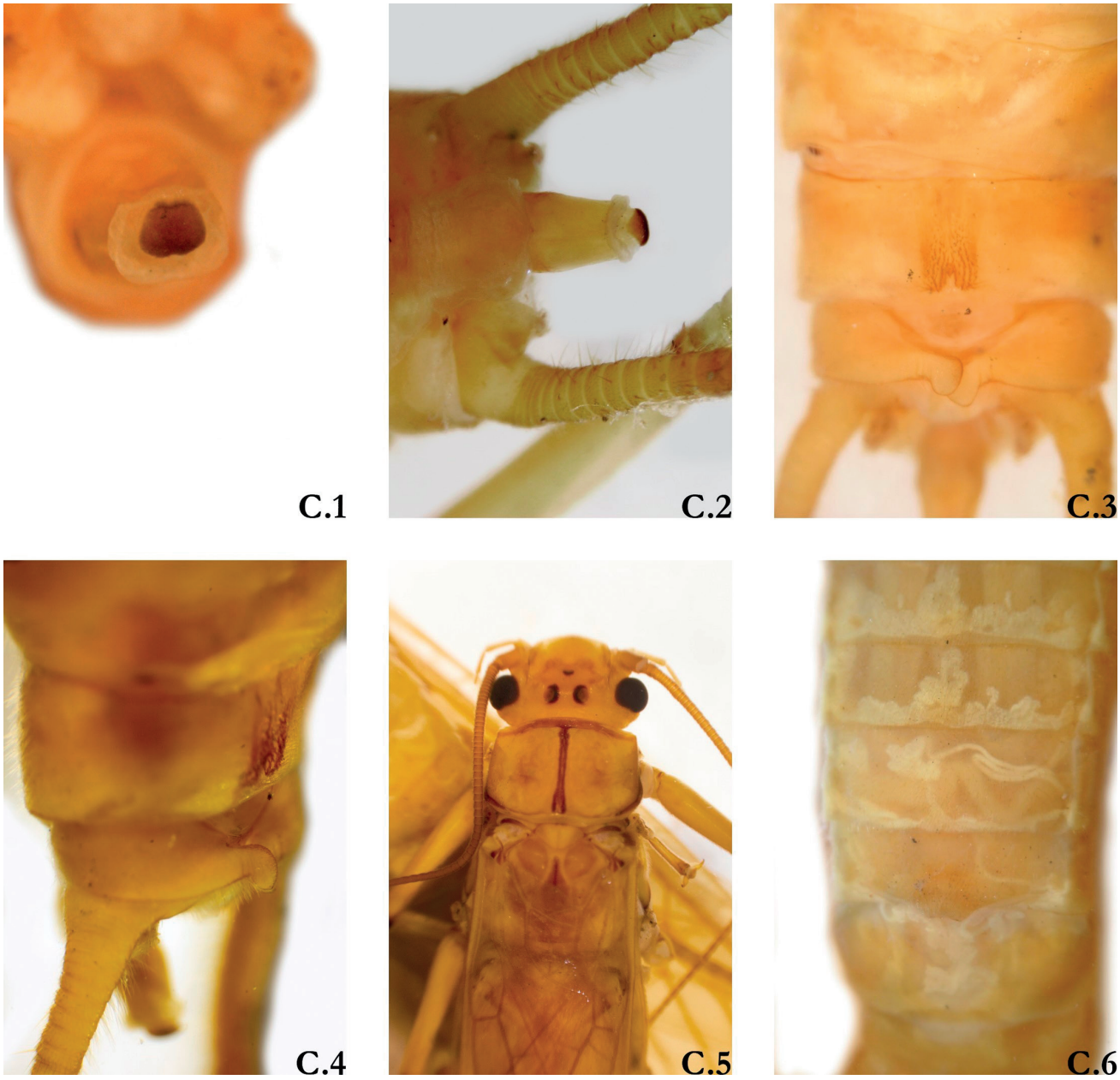
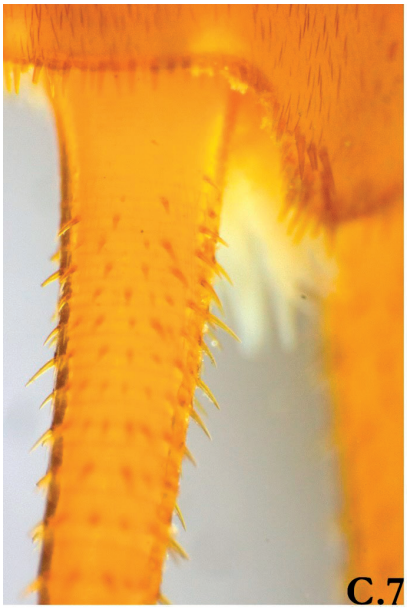


Plate VII, Figs C.1–C.6 – Type C (Italy, River Nure). **C.1**, adult ♂, sclerotized apex of aedeagus, dorso-caudal view; **C.2**, adult ♂, aedeagus and aedeagal tube; **C.3**, adult ♂, hemitergal lobes and mesal field with sensilla; **C.4**, adult ♂, hemitergal lobes, lateral view; **C.5**, head and pronotum of , adult ♂; **C.6**, subgenital plate of adult ♀.



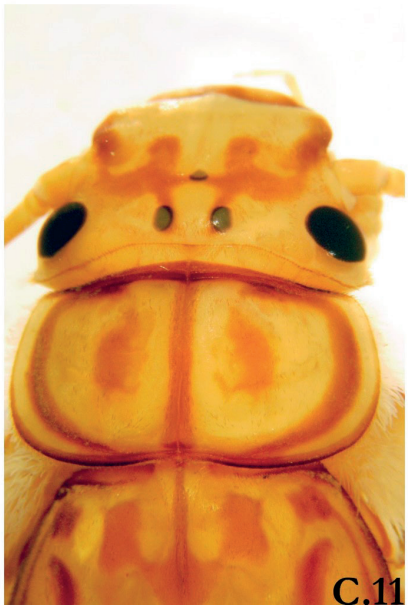


Plate VIII, Figs C.7–C.12 – Type C (nymphs, Rivers Nure, Aare and Emme). **C.7**, basal section of cerci of nymph, lateral view (Emme); **C.8**, markings on tergites of nymph (Nure); **C.9**, head, pro-, meso- and metanotum of nymph (Aare); **C.10**, basal section of cerci of nymph (Aare); **C.11**, head and pronotum of nymph (Aare); **C.12**, markings on tergites of nymph (Aare).

Plate IX, Figs C.13–C.18 – Type C (nymphs, Nure, Rivers Aare and Emme). **C.13**, head and pronotum of nymph (Nure); **C.14**, mediodorsal setation on tergites, lateral view (Nure); **C.15**, paraprocts, ventral view (Aare); **C.16**, head and pronotum of nymph (Aare); **C.17**, oval markings on femora (Emme); **C.18**, sclerotized apex of aedeagus of *Perla bipunctata*, from Aubert 1949: 225, his Fig. 5.

Plate X, Figs D.1–D.6 – Type D (British-Irish Isles). **D.1**, adult ♂b, aedeagus (Ireland); **D.2**, adult ♂b, aedeagus and aedeagal tube; **D.3**, adult ♂b, mesal field with sensilla; **D.4**, adult ♂b, hemitergal lobes, dorsal view; **D.5**, head and pronotum of adult ♀ (Scotland); **D.6**, head and pronotum of adult ♀ (Ireland).

Plate XI, Figs D.7–D.12 – Type D (British-Irish Isles). **D.7**, adult ♀, subgenital plate; **D.8**, basal section of cerci of nymph; **D.9**, tergites of ♀ nymph, dorsal view; **D.10**, marks on the femora of legs of nymph; **D.11**, pronotum and wing pads of mature ♀ nymph; **D.12**, head, pro-, meso- and metanotum of ♂b nymph.

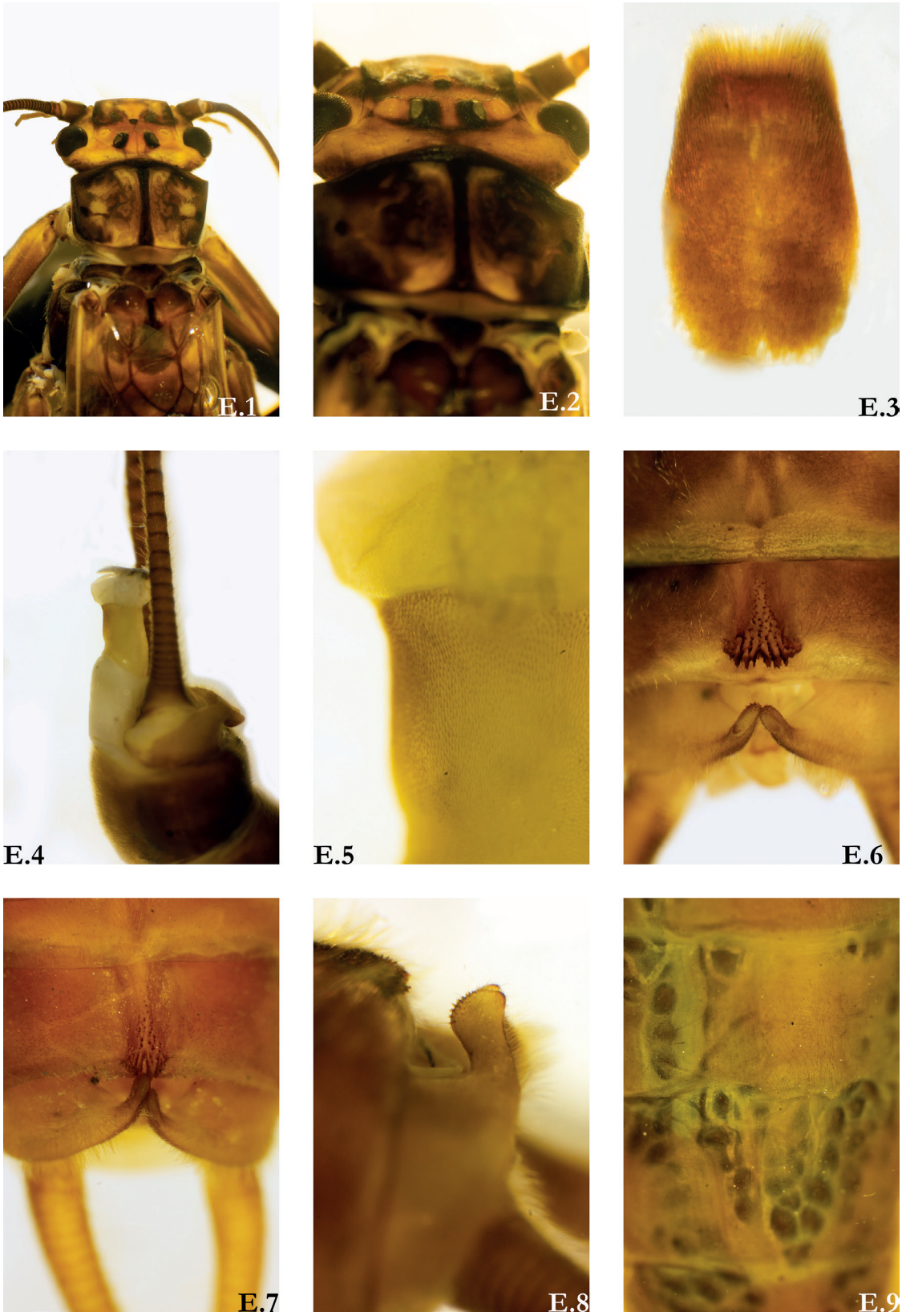


Plate XII, Figs E.1–E.9 – Type E (Pyrenees). **E.1**, adult ♂, head and pronotum; **E.2**, adult ♂, ocelli with large black rim; **E.3**, adult ♂, aedeagus (specimen from Spain); **E.4**, adult ♂, aedeagal tube (specimen from France); **E.5**, adult ♂, short setae on aedeagal tube; **E.6**, adult ♂, hemitergal lobes, dorsal view and mesal field with sensilla; **E.7**, adult ♂, hemitergal lobes, dorsal view and mesal field with sensilla; **E.8**, adult ♂, hemitergal lobes, lateral view; **E.9**, adult ♀, subgenital plate.

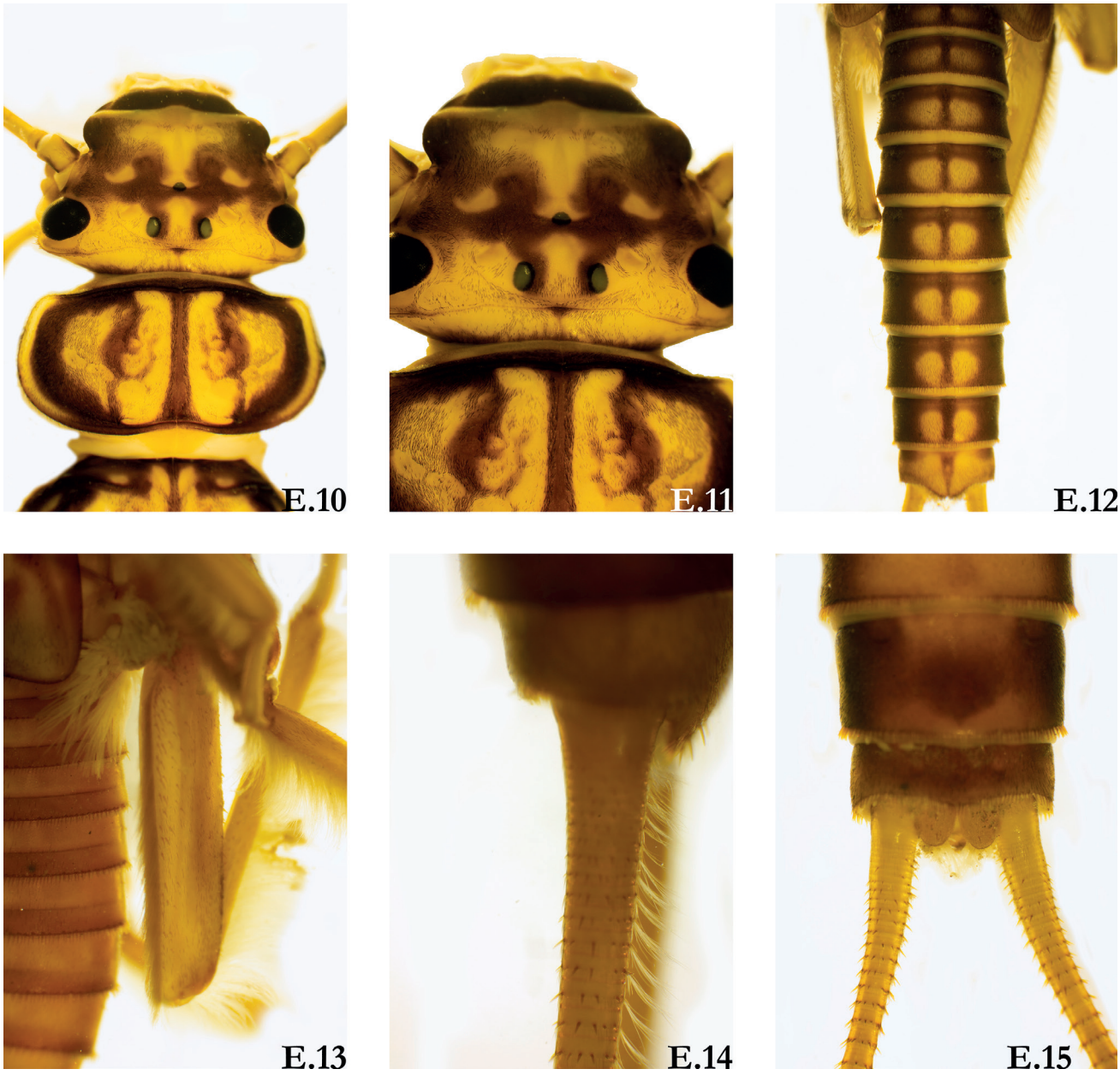
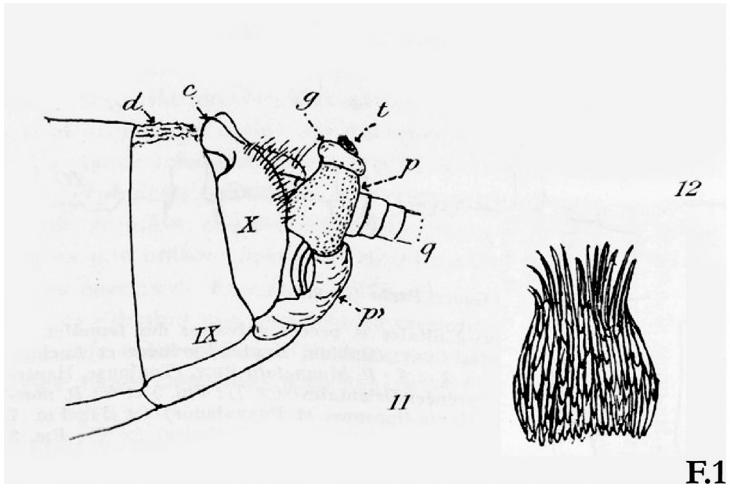
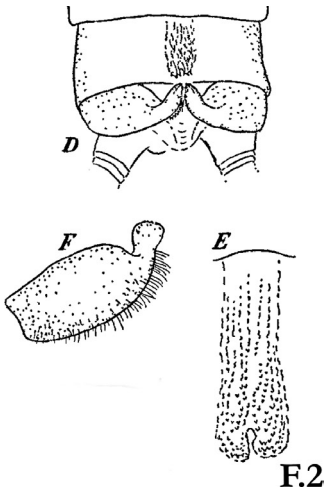


Plate XIII, Figs E.10–E.15 – Type E (Pyrenees). **E.10**, head and pronotum of nymph; **E.11**, pronotum of nymph; **E.12**, tergites of nymph, dorsal view; **E.13**, marks on the femora of leg of nymph; **E.14**, basal section of cerci of nymph; **E.15**, paraprocts of nymph, ventral view.



F.1



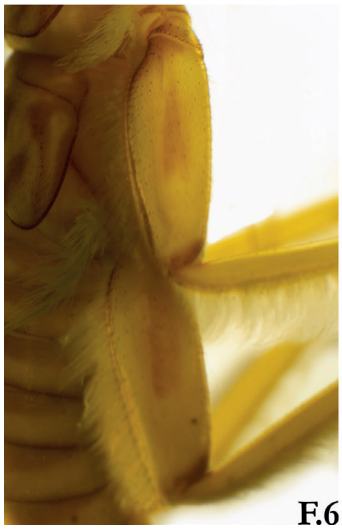
F.2

Plate XIV, Figs F.1–F.2 – Type F (putative *Perla bipunctata* from the foothills of the French Pyrenees). **F.1**, illustrations of Despax (1942, his Figs 11, 12. Fig. 11 = adult ♂b with everted aedeagus, lateral view; Fig. 12 = adult ♂b, sclerotized apex of aedeagus); **F.2**, illustrations of Despax (1951, his Fig. 86, D, E, F. D = adult ♂b, mesal field with sensilla; E = adult ♂b, mesal field; F = adult ♂b, hemitergite).

F.3

F.4

F.5



F.6

F.7

F.8

Plate XV, Figs F.3–F.8 – Type F (putative *Perla bipunctata* from the foothills of the Pyrenees, Río Aragón). **F.3**, head and pronotum of nymph; **F.4**, tergites of nymph, dorsal view; **F.5**, tergites of nymph, dorsal view; **F.6**, markings on femora; **F.7**, paraprocts of nymph, ventral view; **F.8**, cerci of nymph, lateral view.

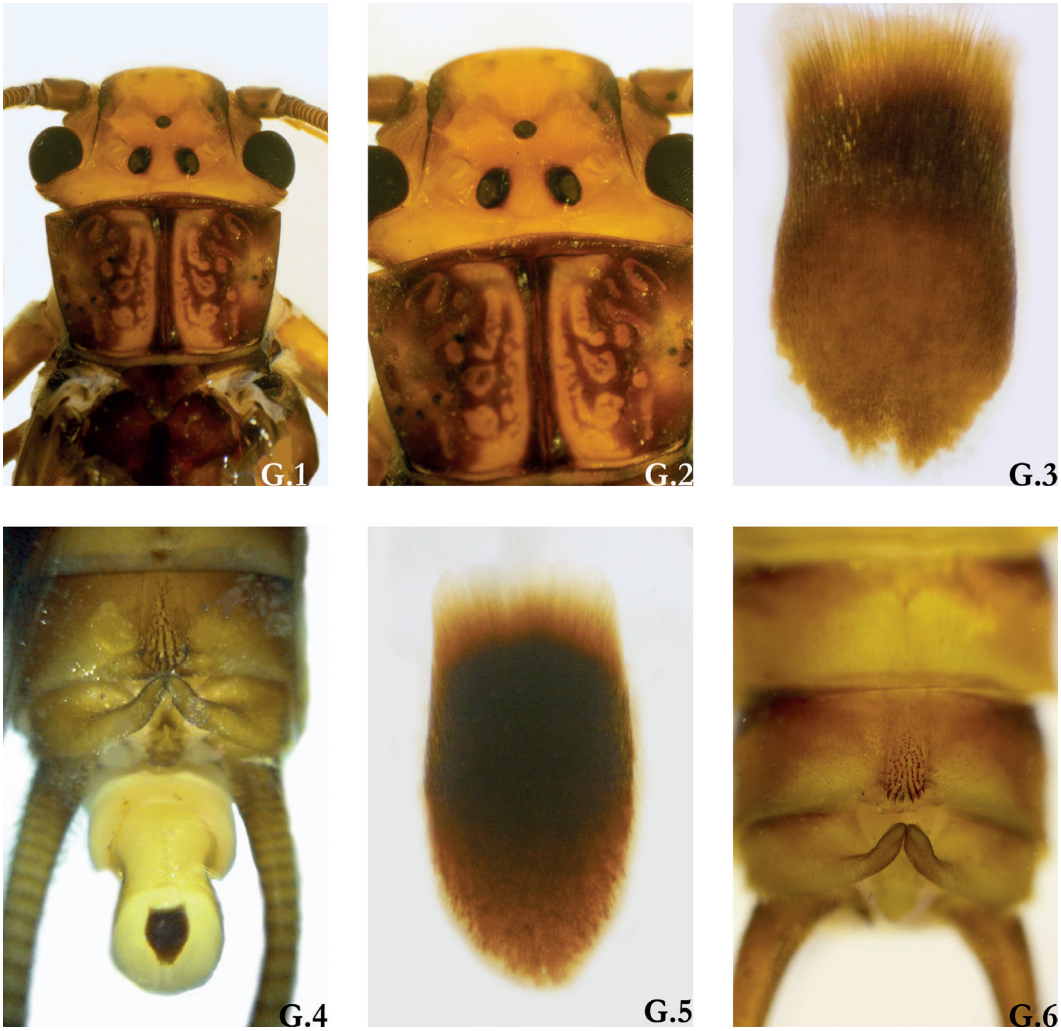


Plate XVI, Figs G.1–G.6 – Type G (Spain, Andalusia, River Castril). **G.1**, adult ♀, head and pronotum; **G.2**, adult ♀, head with ocelli; **G.3**, adult ♂, sclerotized apex of aedeagus; **G.4**, adult ♂, with everted aedeagus and aedeagal tube (photo by José Manuel Tierno de Figueroa); **G.5**, adult ♂, sclerotized apex of aedeagus; **G.6**, adult ♂, mesal field with sensilla and hemitergal lobes, dorsal view.

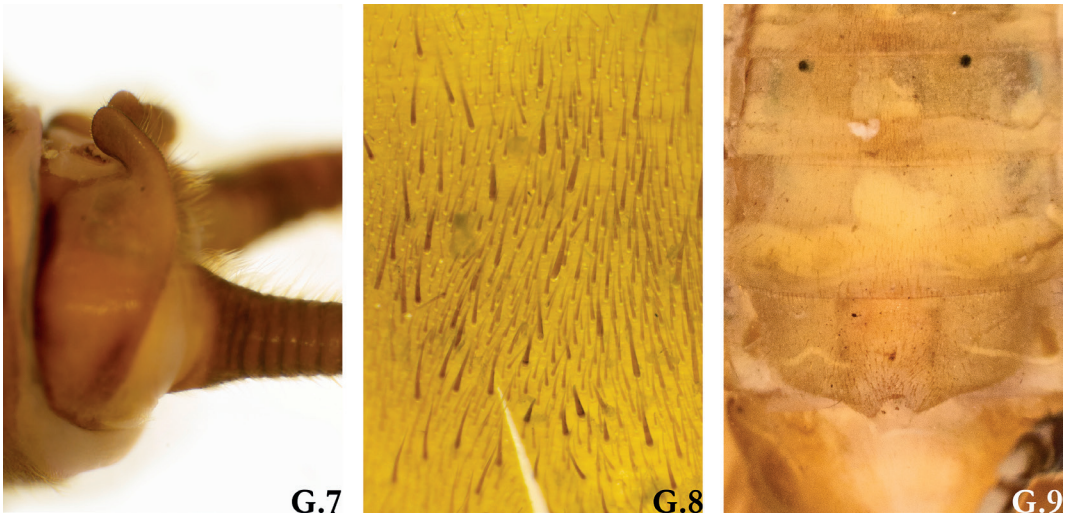


Plate XVII, Figs G.7–G.9 – Type G (Spain, Andalusia, River Castril). **G.7**, adult ♂, hemitergal lobes, lateral view; **G.8**, adult ♂, spines on aedeagal tube; **G.9**, adult ♀, subgenital plate.

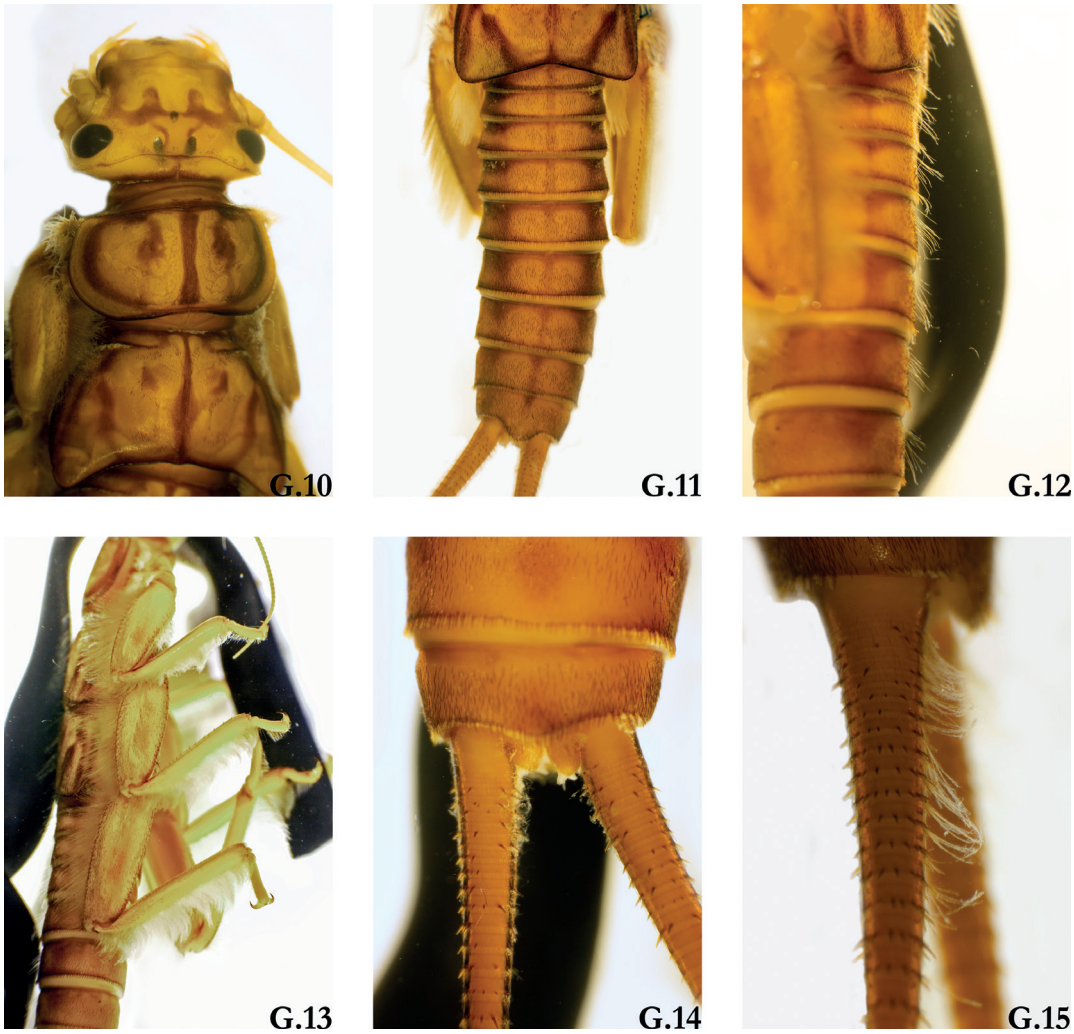


Plate XVII, Figs G.10–G.15 – Type G (Spain, Andalusia, River Castril). **G.10**, ♀ nymph, head, pronotum and mesonotum; **G11**, tergites of nymph; **G.12**, tergites of nymph, lateral view; **G.13**, femora of nymph; **G.14**, paraprocts of nymph, ventral view; **G.15**, basal mediodorsal setation on cerci of nymph.

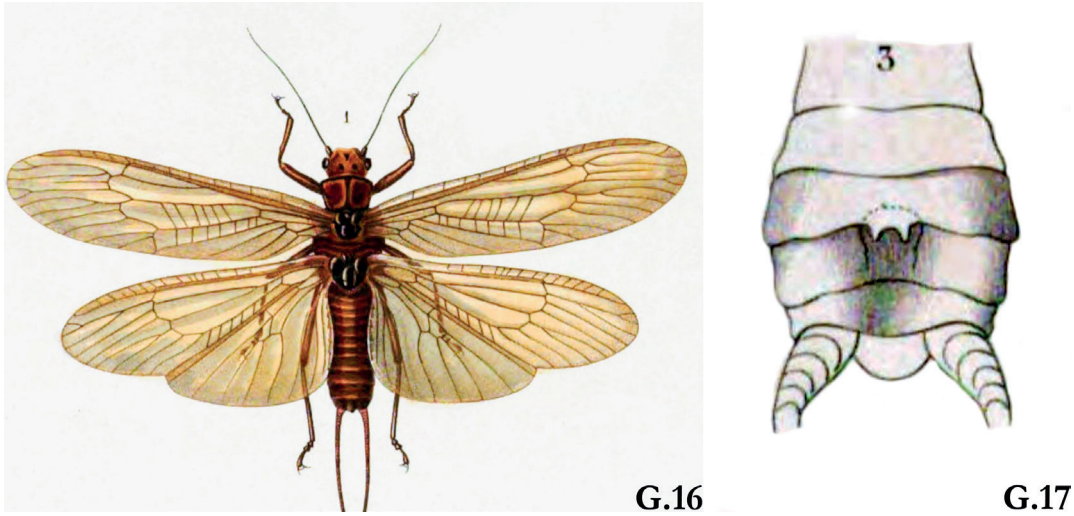


Plate XIX, Figs G.16–G.17 – *Perla hagenii* **Pictet, A**.E., 1865 (his plate 2, Figs 1, 3), from the outskirts of Granada. **G.16**, adult ♀, entire insect; **G.17**, female subgenital plate.

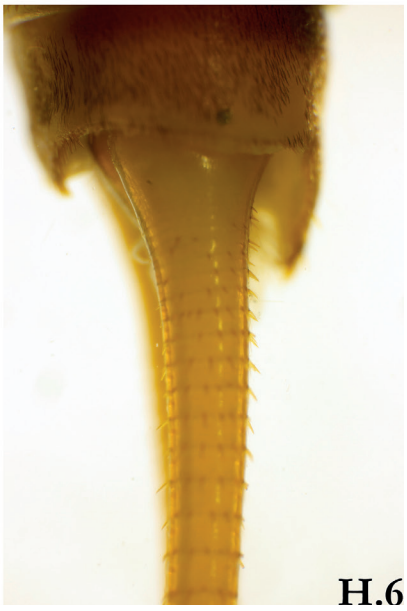


Plate XX, Figs H.1–H.6 – Type H (Spain, Cantabrian Cordillera, Asturias). **H.1**, metanotum and tergites of ♂b; **H.2**, ♀ macropterous nymph, head, pronotum, mesonotum and metanotum; **H.3**, femora of nymph; **H.4**, paraprocts of nymph; **H.5**, cerci of nymph; **H.6**, cerci of nymph.

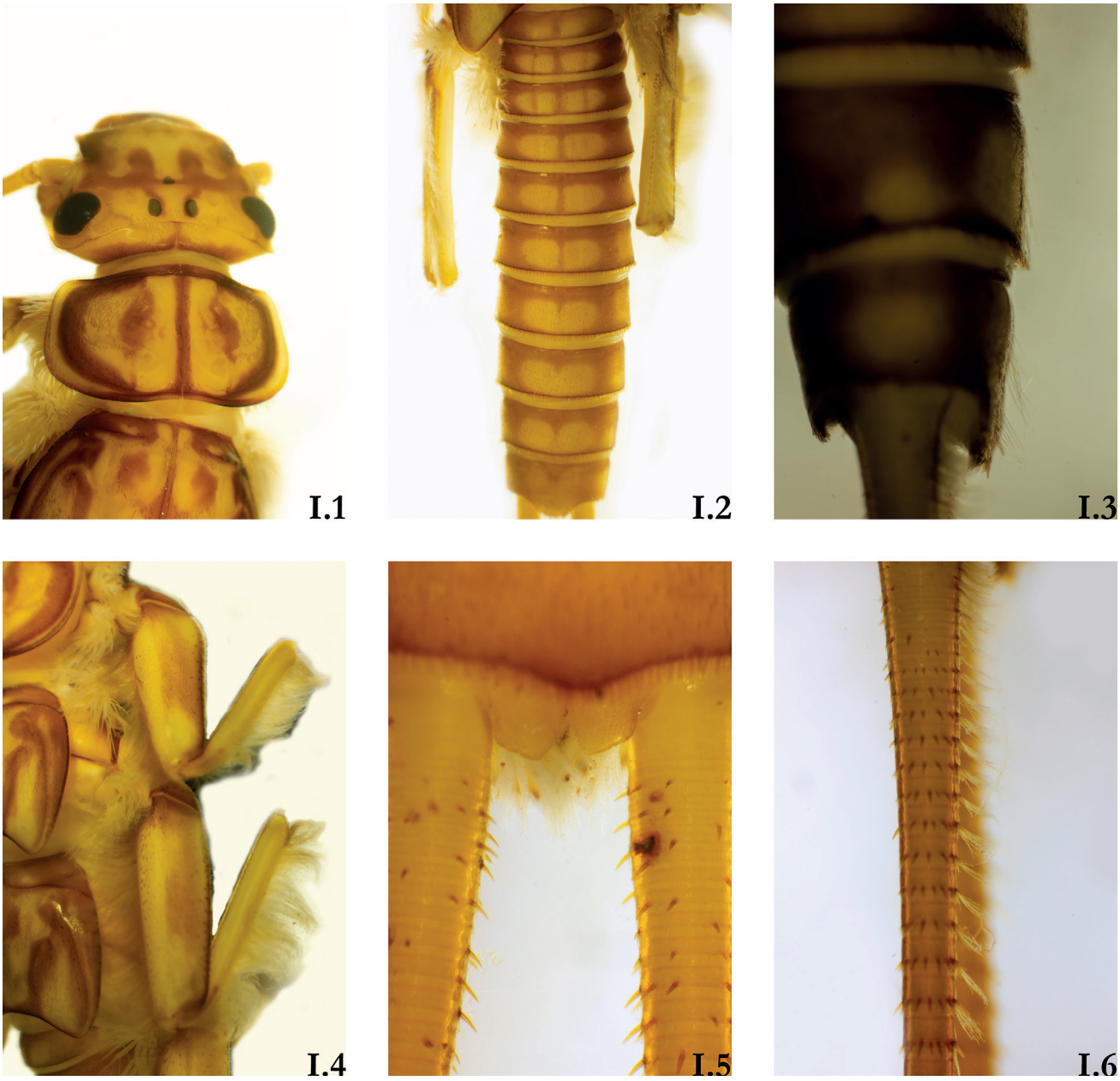


Plate XXI, Figs I.1–I.6 – Type I (Spain, Cantabrian Cordillera, Palencia province, Río Carrión, Triollo, 1300 m). **I.1**, nymph, head and pronotum; **I.2**, tergites of macropterous ♂ nymph, dorsal view; **I.3**, mediodorsal setation on tergites of nymph, lateral view; **I.4**, femora of nymph; **I.5**, paraprocts of nymph; **I.6**, cerci of nymph, mediodorsal setation, lateral view.

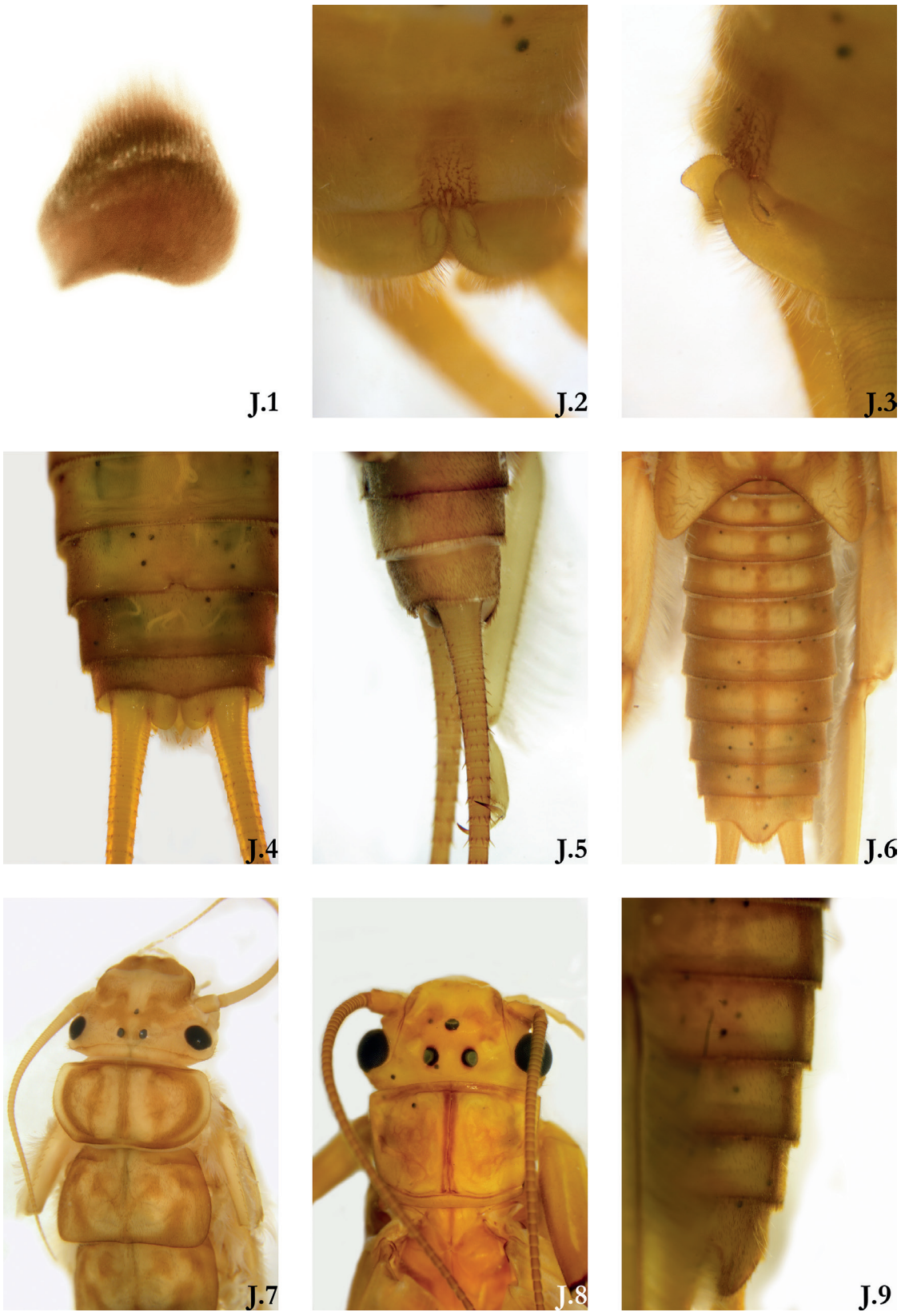


Plate XXII, Figs J.1–J.9 – Type J (High Atlas, Morocco and Algeria, M'Corn and M'Goun massifs). **J.1**, adult ♂b, sclerotized apex of aedeagus, left side damaged (M'Corn); **J.2**, adult ♂b, mesal field with sensilla (M'Corn); **J.3**, adult ♂b, hemitergal lobes, lateral view (M'Corn); **J.4**, rounded paraprocts of nymph, ventral view (M'Goun); **J.5**, cerci of nymph, lateral view (M'Goun); **J.6**, tergites of nymph, dorsal view (M'Goun); **J.7**, head, pronotum and mesonotum of ♂b nymph (M'Goun); **J.8**, adult ♂b, head and pronotum (M'Corn); **J.9**, mediodorsal setation on tergites of nymph (M'Goun).

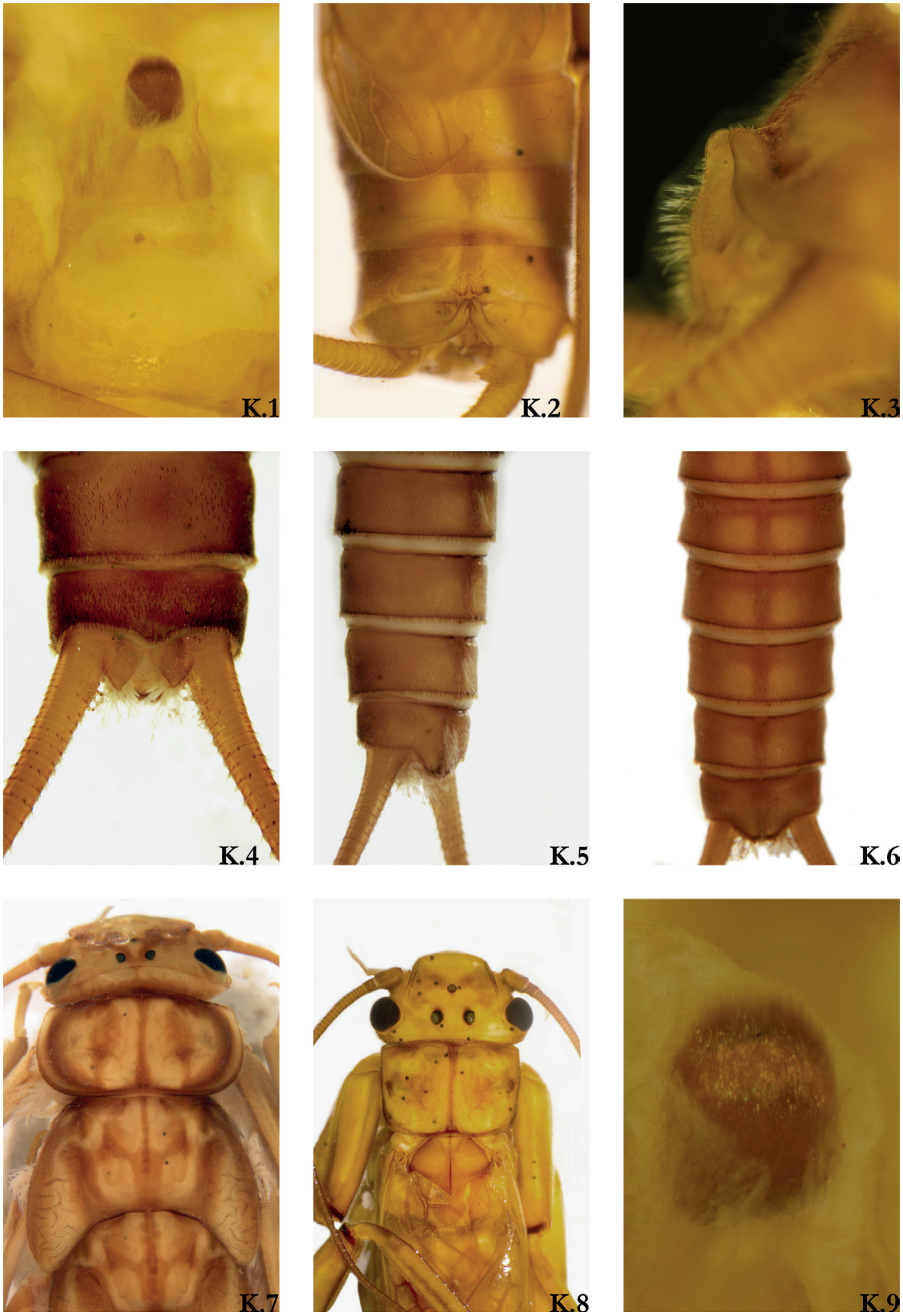


Plate XXIII, Figs K.1–K.9 – Type K (Morocco, High Atlas, M'Goun Massif). **K.1**, adult ♂b, sclerotized apex of aedeagus; **K.2**, brachypterous adult ♂b, mesal field with sensilla; **K.3**, adult ♂b, hemitergal lobes, lateral view; **K.4**, pointed paraprocts of nymph, ventral view; **K.5**, cerci of nymph, ¾ lateral view; **K.6**, tergites of nymph, dorsal view; **K.7**, head, pronotum and mesonotum of macropterous♀ nymph; **K.8**, adult ♂b, head and pronotum; **K.9**, adult ♂b, sclerotized apex of aedeagus.

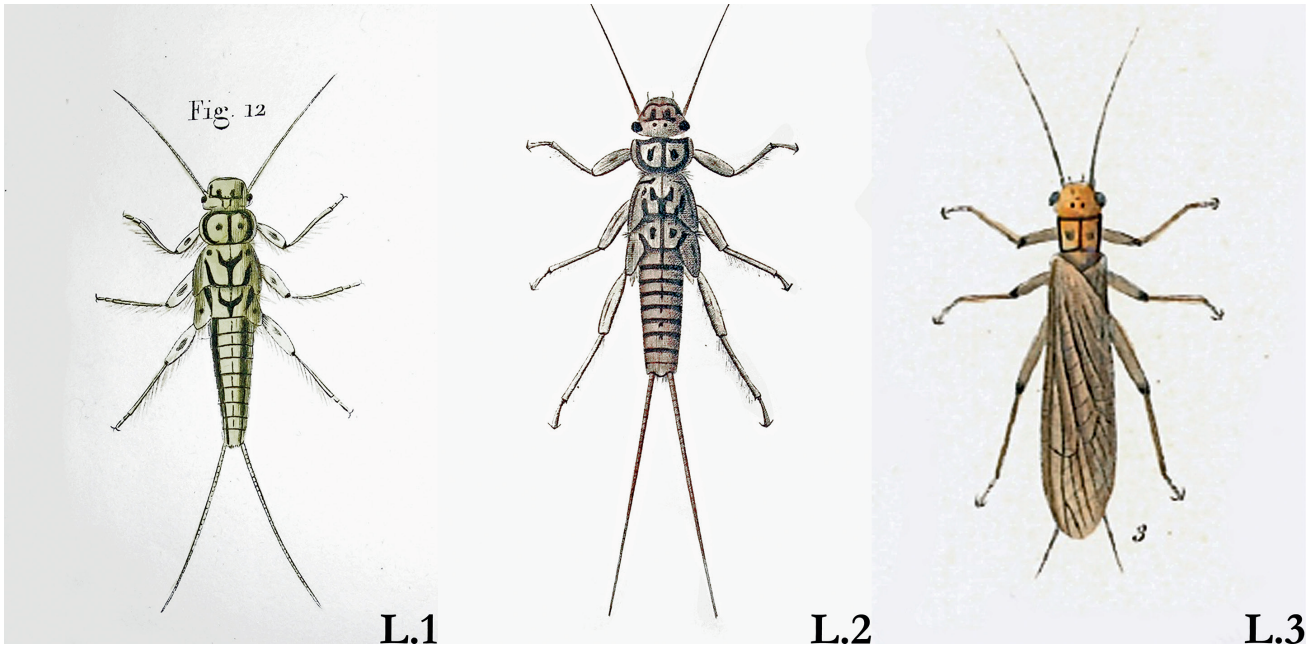


Plate XXIV, Figs L.1–L.3 – ***Perla bipunctata*** **in the works of Pictet (1833, 1842)**. **L.1**, nymph of *Perla bipunctata* (Pictet 1833: his plate 5, Fig. 12); **L.2**, nymph of *Perla bipunctata* (Pictet 1842: his plate 11, Fig. 1); **L.3**, adult ♂ of *Perla bipunctata* (Pictet 1842: his plate 12, Fig. 3).

Plate XXV, Fig. M.1 – River Cold Sense, near Zollhaus (FR), Switzerland, late March. Rare example of type A and type B in near syntopy. Black arrow: nymphal biotope of type A; white arrow: of type B.

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Appendix 1- Material examined

(see text for correspondence between capital letters and formally established and/or informally discussed taxa)

Type A:

ITALY. Pavia. Alta Valle Staffora, Casanova, Staffora, 620 m, 27 May 1973, 2♂, 2♀, 5L (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899212). Piemonte. Piamprato, Valprato Soana, 1580 m, 11 Jul 2008, 3♂, 2♀ (leg. G. B. Delmastro; GVC); Balme, Stura di Ala, 1743 m, 17 Jul 2005, 1♂ (leg. G. B. Delmastro; GVC); Valle Soana, Soana, no date, 8L (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899236); Campiglia, Soana, 1350 m, 8 Jul 1990, 8♂, 3♀ (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899229); Campiglia, Soana, 1350 m, no date, 3L (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899240); Between Valle Soana and Ronco Canavese, Soana, 850 m, 17 Jun 1990, 2♂ (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899228); Cuneo. Between Prinardo and Argentera, Stura di Demonte, 1650 m, Oct 1986, 30L (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899227); Valgrana, Grana, 1300 m, 1♂, 10♀, 7L, multiple dates between 1982 and 1984 (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899226); Valle Stura, Stura di Demonte, 1600 m, 22 Jul 1983, 2♀, 9L (leg. C. Ravizza; MZL catalogue number: GBIFCH00899232); Bagni Vinadio, torrente Corborant, 1600-1700 m, 28 Jun 1976, 1♀ with eggs (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899242); Vinadio, Stura di Demonte, 880 m, 29 May 1977, 1♂ with everted aedeagus (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899235); Demonte, Vallone dell'Arma, torrente Cant, 1300 m, 2L (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899237); between Ormea and Briga Alta, Tanaro, 950 m, 27 May 1970, 3♂, 2♀, 5L (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899213); Upega, Tanaro, 1250 m, 31 Mar 1976, 3L (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899218). Potenza. Lucania, Lagonegro, ruscello pendici Massiccio del Sirino, 1200 m, 16 Jun 1973, 1♂ with everted and detached aedeagus, 2♀ (leg. I. Bucciarelli; MZL, catalogue number: GBIFCH00899220). Calabria. Villaggio Mancuso, Sila, 1000 m, 22 May 1950, 1♂ (leg. G. Binaghi; MZL, catalogue number: GBIFCH00913205); Spezzano Albanese, Fiume Coscile, 2 Oct 1953, 1L (leg. J. Aubert; MZL, catalogue number: GBIFCH01143920); Sila, Garga 3, 28 Jun 1955, 1L (leg. J. Aubert; MZL, catalogue number: GBIFCH00913206). Sicily. Torrente di Petralia, Ponte di Brancato, 1100 m., 2 Apr 1956, 1L♂ (leg. J. Aubert; MZL, catalogue number: GBIFCH00913209). **FRANCE**. Savoie dpt. Col de Chérel, ruisseau de Chérel, 1202 m, 25 May 1992, 1♀ (leg. G. Vinçon: RC); Haute-Savoie dpt, Sous Châtel, River Giffre, 600 m, 25 Feb 2017, 1L (leg. J.-P.G. Reding; RC); Drôme dpt., Vercors, Combe Laval, Cholet, 550 m, 1♂ (leg. G. Vinçon: RC). **SWITZERLAND**. Canton of Fribourg. Zollhaus, Cold Sense, 900 m, 12 Jul 2011, 3L; 13 Aug 2011, 7L; 29 Jan 2013, 1L; 3 Jan 2016, 4L; 20 Mar 2016, 1L (leg. J.-P.G. Reding; RC). Charmey, Riau du Gros-Mont, 920 m, 13 Jul 2010, 6L; 2 Feb 2011, 1L (leg. J.-P.G. Reding; RC); Jaun, Jogne, 1000 m, 2 Feb 2011, 2L (leg. J.-P.G. Reding; RC); Charmey, Motélon, 873 m, 2 Feb 2011, 5L (leg. J.-P.G. Reding; RC). Canton of Berne. Hengstschlund, Hengstsense, 1219 m, 27 Mar 2017, 1L; Sangernboden, Hoflanderbrücke, 913 m, 12 Jul 2019, 6L; Muscherenschlund, Muscherensense, 1040 m, 8 May 2016, 1L (leg. J.-P.G. Reding; RC). Canton of Vaud. Vallée de Bonaudon, Hongrin, 1025 m, 26 Mar 2011, 2L; 21 Oct 2014, 6L; confluence Hongrin, ruisseau de Chaude, 1090 m, 12 Oct 2010, 2L; Petit Caudon, Veveyse de Fégire, 1236 m, 30 Sep 2010, 2L; Gryon, trib.

to river Gryonne, 1670 m, 2 Aug 2010, 2♀ (1♀ used for molecular studies); 14 Aug 2019, 1♀ (leg. J.-P.G. Reding; RC). Canton of Ticino. Caverno, Maggia, 465 m, 19 Aug 1989, 2L (leg. J. Aubert; MZL, catalogue number: GBIFCH01143916). **SLOVAKIA**. Bielovodská dolina, Biatka, Javorinka, 1200 m, 5 May 1965, 1L (leg. J. Aubert; MZL, catalogue number: GBIFCH00913248).

Type B:
ITALY. Emilia-Romagna, Piacenza. Farini d'Olmo, torrente Nure, 440 m, 15 May 1976, 1♀, 7L (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899224). Pavia. Alta Valle Staffora, Casanova, Staffora, 620 m, 5♂, 1♀, 1L, 11 May 1980 (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899230); 27 May 1973, 1♀ (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899216); 25 Feb 1973, 9L (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899217). Piemonte. Between Valle Soana and Ronco Canavese, Soana, 850 m, 17 Jun 1990, 11♂, 2♀ (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899228); 1♀ with eggs (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899241). Lombardia, Valle Brembana, Val Torta, torrente Stabina, 500 m, 1♀, 7 May 1973 (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899233); Val Brembana, Mezzoldo to Brembo, 700 m, 7 May 1973, 2L (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899214). Friuli (UD), torrente Pontebbana, 800 m, 15 Jun 1994, 1♂ (leg. C. Ravizza & E. Ravizza Dematteis; MZL, catalogue number: GBIFCH00899239). Vercelli. Varallo, Sesia, 430 m, May 1977, 2♂, 1♀ (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899231). Cuneo. Vinadio, torrente Stura di Demonte, 880 m, 29 May 1976, 1♂, 1♀, 21L (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899211). Emilia-Romagna, Piacenza, Farini d'Olmo, torrente Nure, 500 m, 21 May 1975, 5L (leg. C. Ravizza; MZL, catalogue number: GBIFCH00899219). **AUSTRIA**. Steinfeld, River Drau, Radlacher Brücke, 585 m, 29 Apr 2021, 2♂, 3L (leg. M. Konar; RC). **FRANCE**. Ain dpt. Chézery-Forens, Valserine, 596 m, 30 May 2014, 1♂ (leg. B. Launay; RC); La Planche, Valserine, 558 m, 4 May 2014, 1♂, 1♀, 1L (leg. B. Launay; RC); La Rivière, Valserine, 675 m, 8 May 2018, 1L (leg. J.-P.G. Reding; RC); L'Enclane aval, ruisseau de Forens, 670 m, 10 Jul 2016, 3L (leg. B. Launay; RC). Haute-Savoie dpt. Anterne, River Giffre, 461 m, 25 Feb 2017, 1L (leg. J.-P.G. Reding; RC); Taninges, River Giffre, 634 m, 25 Jun 2019, 6L (leg. J.-P.G. Reding; RC). **SWITZERLAND**. Cantons of Berne and Fribourg, Zollhaus, Cold Sense, 900 m, 29 Jan 2013, 1L; 25 Jun 2013, 1♂, 8L; Sensegraben, River Sense, 703 m, 26 Mar 2011, 1L; 12 Jul 2011, 5L; Sodbachbrücke, River Sense, 653 m, 10 Jun 2006, 1L (used for molecular studies); 5 Jun 2012, 1L (leg. J.-P.G. Reding; RC). **SLOVAKIA**. Low Tatras, River Štiavnica, 700 m, 26 Jul 1956, 1♂ (leg. J. Raušer; MZL, catalogue number: GBIFCH01143925).

Type C:
ITALY. Emilia-Romagna, Piacenza, Podenzano, torrente Nure, 110 m, 11 Jun 1977, 1♂, 3♀, 1L (leg. E. Ravizza Dematteis & C. Ravizza; MZL, catalogue number: GBIFCH00899222); Bettola, torrente Nure, 300 m, 27 Jul 1977, eggs (leg. E. Ravizza Dematteis & C. Ravizza; MZL, catalogue number: GBIFCH00899221); Parma, Langhirano, torrente Parma, 250 m, 22 May 1976, 4L, 1 reared to adult (Ravizza & Ravizza Dematteis 1977). **SWITZERLAND**. Canton of Berne. Dahlhölzli, River Aare, 540 m, 25 May 1946, 1♂ (leg. J. Aubert; MZL, catalogue number: GBIFCH01204545); Melchenbühl, near Berne, River Aare, 1938, 1940, 1♂, 1♀ (leg. Schneider; MZL, catalogue numbers: GBIFCH01204544 and GBIFCH01204549); Burgdorf, River Emme, 550 m, 3 Apr 1947, 1L (leg. J. Aubert; MZL, catalogue number: GBIFCH01143930); 2 Mar 1943, 1L (leg. J. Aubert; MZL, catalogue number: GBIFCH01143928); Berne, River Aare, 540 m, 2 Mar 1948, 1L (leg. J. Aubert; MZL, catalogue number: GBIFCH01143929); 2 Feb 1947, 1L (leg. J. Aubert; MZL, catalogue number: GBIFCH01143927); 30 Apr 1946, 10L (leg. J. Aubert; MZL, catalogue number: GBIFCH01143926).

Type D:
SCOTLAND. Co. Lanarkshire, Carluke, River Clyde, 5 May 2019, 2♂b, 3♀ (leg. C. Macadam; GVC). **ENGLAND**. Westmorland, River Rothay, 23 May 1940, 3L♂b, 3L♀; Trout Beck, 5♂b, 1♀ (leg. N. Hynes; MZL, container CB-13204). **IRELAND**. Co. Wicklow, upper River Liffey, May 2010, 8L♂b, 1L♀ (leg. H. Feeley; RC); River Liffey, below Ballyward bridge, May 2011, 2♂b (leg. H. Feeley; PZC).

Type E:
FRANCE. Occitania. Hautes-Pyrénées. Estaragne, amont confluence Lac d'Oredon, 1850 m, 20 Jul 2022, 2♂; 22 Jun 2022, 2L♂ (leg. B. Launay; INRAE). Gavarnie, Gave de Pau, 1400 m, 13 Oct 1958, 2L♀ (leg. J. Aubert; MZL, catalogue number: GBIFCH00913214); Barèges, Bastan, 1250 m, 13 Oct 1998, 1L♂ (leg. J. Aubert; MZL, catalogue number: GBIFCH00913213). Pays Basque, Saint-Engrace, Kakuetta Gorges, 1140 m, 1952, 5L (leg. R. Despax; MZL, catalogue number: GBIFCH01143923). **SPAIN**. Lleida. Bono, Noguera Ribagorzana, 1100 m, Jul 1951, 1♂ (leg. H. Bertrand; MZL, catalogue number: GBIFCH01143918); 3♂ (leg. H. Bertrand; MZL, catalogue number: GBIFCH00913259); Pobla de Ségur, Tremp, Noguera Pallarese, 540 m, 1952, 1E (leg. H. Bertrand; MZL, catalogue number: GBIFCH01143922); Tredòs, Arriu de Ruda, 1350 m, 27 Jun 1950, 1♀ (leg. F. Schmid; MZL, catalogue number: GBIFCH00913239).

Type F:
SPAIN. Aragón. Jaca, Río Aragón, 800 m, 1952, 2L (leg. H. Bertrand; MZL, catalogue number: GBIFCH01143921).

FRANCE. Coteau de Pech-David, Chemin des Etroits, Toulouse, Garonne, May 1933, 3E (leg. R. Despax; MZL, catalogue number: GBIFCH01143919); Pont St-Michel, Toulouse, Garonne, May 1942, 1E (leg. R. Despax; MZL, catalogue number: GBIFCH01143917); St-Béat, Garonne, 500 m, Aug 1946, 1♂ (leg. R. Despax; MZL, catalogue number: GBIFCH01143924).

Type G:
SPAIN. Granada province, River Castril, Sierra de Castril, 1220 m, 37° 54' 25.0560'' N, 2° 44' 51.4788'' W, 16 Jun 2005, 3♂, 1♀, leg. J. M. Tierno de Figueroa, C. Marfil Daza & M. J. López-Rodríguez (RC). River Castril, Sierra de Castril, 1040 m, 37° 52' 37.6'' N, 2° 45' 26.1'' W, 21 Jun 2012, 1L♂; 15 Mar 2013, 1L♀, leg. J. M. Tierno de Figueroa & M. J. López-Rodríguez (RC); River Castril, before Castril, 860 m, 13 Dec 1988, 1L; River Castril, El Cortijillo, 1020 m, 19 Apr 1991, 1L (Picazo Muñoz, 1995 in: Sánchez-Ortega et al., 2003). Sierra Nevada. Region of Pico del Veleta, Aug 1950, 2L♀ (leg. F. Schmid; MZL, catalogue number: GBIFCH00913246); Arroyo de San Juan, 2500 m, 5 Jul 1953, 10L (leg. J. Aubert & H. Bertrand; MZL, catalogue number: GBIFCH00913260); Río Puerto de Jerez, 2500 m, 25 Jun 1953, 12L (leg. J. Aubert & H. Bertrand; MZL, catalogue number: GBIFCH00913261); River Monachil, 2140 m, 37° 05' 24'' N, 3° 23' 59'' W, 12 Feb 1986, 1L♀, leg. C. Zamora & I. Guiasola (RC).

Type H:
SPAIN. León province. Río Órbigo, Carrizo de la Ribera, 880 m, 21 Jun 1981, 2L♀; Río Esla, Gradefes, 870 m, 16 Jun 1981, 2L♀. Burgos province. Río Arlanzón, San Millán de Juarros, 920 m, 25 Jun 1981, 1L♂b, 1L♀, leg. M. González del Tánago and D. García de Jalón (TDF).

Type I:
SPAIN. Palencia province, Río Carrión, Triollo, 1300 m, 22 Feb 1981, 1L♂, 2L♀, leg. M. González del Tánago and D. García de Jalón (TDF). Asturias. Puerto de Pajares, Río Bernesga, 1379 m, 20 May 1954, 1L♂, 1L♀ (leg. H. Bertrand; MZL, catalogue number: GBIFCH00913237); Arbas del Puerto, Río Bernesga, 1350 m, Aug 1954, 1L (leg. H. Bertrand; MZL, catalogue number: GBIFCH00913238); Villablino, Río Sil, 1000 m, 18 May 1954, 1L (leg. J. Aubert; MZL, catalogue number: GBIFCH00913236). Cantabrian Cordillera. Picos de Europa, Espinama, Río Deva, 1000 m, 17 Jul 1954, 1L (leg. J. Aubert & H. Bertrand; MZL, catalogue number: GBIFCH00913245); Espinama, Río Deva, 1300 m, 17 Jul 1953, 2L (leg. J. Aubert & H. Bertrand; MZL, catalogue number: GBIFCH00913243); Puertos de Aliva, Río Duje tributary, 1500 m, 24 May 1954, 1L (leg. J. Aubert & H. Bertrand; MZL, catalogue number: GBIFCH00913244).

Type J:
ALGERIA. High Atlas. M'Corn Massif. Asif Imdrhas, Akkendachou N'Ait Ouffi, 1700 m, 11 Jun 1954, 1♂b (aedeagus in separate vial), 2E (leg. F. Vaillant; MZL, container CB-18143). Akka Gorges, Ait Ahmed, 1900 m, 16 Jun 1954, 1E (leg. F. Vaillant; MZL, container CB-18143). **MOROCCO**. High Atlas. Toubkal Massif. Between Asni and Imlil, Oued Rerhaia, 1200 m, 29 Apr 1960, 1L♂b, 2L♀m, (leg. J. Aubert: MZL, container CB-18143).

Type K:
MOROCCO. High Atlas. M'Goun Massif. Spring of Assif M'Goun, 2500 m, 17 Jun 1954, 1♂b, 2L♂b, 4L♀ (leg. F. Vaillant; MZL, container CB-18143).