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TWO NEW SPECIES OF *DICTYOGENUS* KLAPÁLEK, 1904 (PLECOPTERA: PERLODIDAE) FROM THE JURA MOUNTAINS OF FRANCE AND SWITZERLAND, AND FROM THE FRENCH VERCORS AND CHARTREUSE MASSIFS

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ABSTRACT

Two new species of *Dictyogenus* Klapálek, *D. jurassicum* **sp. n.**, endemic to the Jura Mountains of France and Switzerland, and *D. muranyii* **sp. n.**, endemic to the French Vercors and Chartreuse Massifs, are described from adult, larva, egg characters and molecular markers. Information on the distribution, ecological preferences and conservation status of these new species is also provided. Identification keys for adults and larvae of *Dictyogenus* are proposed.

Keywords: stoneflies, *Dictyogenus jurassicum*, *Dictyogenus muranyii*, egg morphology, larval morphology, endemism, karstic springs, identification keys

INTRODUCTION

With 55 extant genera and nearly 350 species, the Perlodidae Klapálek, 1909 are one of the most genus-rich families of Palearctic, Nearctic and Oriental stoneflies (DeWalt *et al.* 2019). Whereas most of its genera are monotypic, a few of them, like *Perlodes* Banks, 1903 and *Isoperla* Banks, 1906, have proved to be prolific purveyors of new species, including many endemics (Graf *et al.* 2009, 2019, Szczytko & Kondratieff 2015). The genus *Dictyogenus* Klapálek, 1904 has received little attention up to now and only two nominal species with uncertain taxonomical status (Stark *et al.* 1986, Zwick 1971, 2004, Zwick & Weinzierl 1995, Zwick & Zwick 2010) are presently recognized: *Dictyogenus alpinum* (Pictet, F.J., 1841) and *D.*

fontium (Ris, 1896), whereas a third species, *D. gelidus* Klapálek, 1906 (redescribed by Klapálek 1912, after specimens from the Austrian Alps), is considered a *nomen dubium* (Illies 1966, DeWalt *et al.* 2019).

The genus *Dictyogenus* also has a very intricate taxonomic history. *Dictyogenus alpinum* was first described by Pictet (1841) under the name *Perla* (*Dictyopteryx*) *alpina*, and *Dictyogenus fontium* under the name *Dictyopteryx fontium* by Ris (1896). The genus *Dictyopteryx*, created by Pictet (1841), included the present genera *Perlodes*, *Dictyogenus* and *Besdolus* Ricker, 1952. Ris (1896) then separated the species arranged under the genus *Dictyopteryx* into two groups, the first corresponding to the present genus *Perlodes*, and the second, further subdivided into two branches, to *Dictyogenus* and *Besdolus*. Banks (1903) pointed out that the genus name *Dictyopteryx* was preoccupied (Stephens 1829: 189) and ranged the correspondent taxa under the newly created genus *Perlodes*. Klapálek (1904), not yet aware of these changes, proposed to restrict the scope of Pictet's *Dictyopteryx* to the present day *Perlodes* and *Diura* Billberg, 1820, whereas the genus *Isogenus* Newman, 1833 received a *sensu lato* attribution and was separated into the two subgenera *Isogenus* (*sensu stricto*) and the newly erected *Dictyogenus*, which included also the present day *Besdolus*. Kühtreiber (1934) still considered the genus *Dictyogenus* as a subgenus of *Isogenus* and Aubert (1946) used the name *Isogenus fontium* for the present day *Dictyogenus fontium*. Ricker (1952) then erected *Besdolus* as a new subgenus of *Isogenus*, restricting thereby the range of the subgenus *Dictyogenus* to *Dictyogenus alpinum* and *D. fontium*. Illies (1966) finally proposed to elevate the subgenera *Besdolus* and *Dictyogenus* to generic level. Stark *et al.* (1986), however, synonymized *Besdolus* with *Dictyogenus*. But the genus *Besdolus* was reinstated by Zwick & Weinzierl (1995) and clearly separated from *Dictyogenus* by a thorough morphological analysis. *Dictyogenus alpinum* and *D. fontium* have been re-described and illustrated more recently by Fochetti & Tierno de Figueroa (2008, Fig. 17, after drawings from Gilles Vinçon) and by Lubini *et al.* (2012a, Figs. 230–235).

The separation of the two nominal species *Dictyogenus alpinum* and *D. fontium* is difficult. Male adults of *Dictyogenus alpinum* and *D. fontium* are traditionally identified on the basis of the shape of their epiproct and lateral stylets. According to Klapálek (1912), the apex of the frontal sclerite of the epiproct is "claw-like" in *D. alpinum* (Fig. 57) and "dagger-like" in *D. fontium* (Fig. 80). Female adults are generally separated by the length and the shape of their subgenital plates (Klapálek 1912, Figs. 48, 52, Despax 1951, Figs. 76C, 77B, Fochetti & Tierno de Figueroa 2008, Fig. 17, Lubini *et al.* 2012a, Figs. 234, 235): the subgenital plate of *D. alpinum* (Figs. 60, 61) is much longer than the one of *D. fontium* (Figs. 83, 84). Larvae have been separated by the presence (Figs. 65, 71; *D. alpinum*) or by the absence (Figs. 85, 86; *D. fontium*) of a row of erect medio-dorsal setae on the pronotum (Kühtreiber 1931, 1934: 113, Fig. 80). Some criteria, however, like wing venation (Kühtreiber 1934: 22–3, Tierno de Figueroa & Fochetti 2001), the shape of the female subgenital plate (Kühtreiber 1934: 24, Fig. 12) or the chorionic structure of the eggs (Zwick 1971: 1147), are considered to be variable.

Specimens of the genus *Dictyogenus* collected in the Jura Mountains of France and Switzerland and in the French Vercors and Chartreuse Massifs (Fig. 92) could not be unambiguously identified by using the above-mentioned criteria or with the help of current taxonomic literature (Despax 1951, Illies 1955, Aubert 1959, Fochetti & Tierno de Figueroa 2008, Lubini *et al.* 2012a). Since the separation of species of *Dictyogenus* on the sole basis of adult morphology is notoriously difficult (Zwick 1971), we have resorted to additional criteria, namely egg and larval features, as well as molecular markers, for a more accurate identification of species. A review of specimens of the genus *Dictyogenus*, collected by the current authors in the Jura Mountains of France and Switzerland, and in the French Vercors and Chartreuse Massifs, analyzed with the help of these additional criteria, and compared with

Fig. 1. *Dictyogenus jurassicum* **sp. n.**, adult female habitus. Spring of River Doubs, Mouthe, Doubs dpt, France. Photo A. Ruffoni.

specimens of *Dictyogenus* from various localities in the French, Swiss, Austrian, Italian and Slovenian Alps, revealed that they belong to unknown species, the description of which is presented in this contribution. The first new species, *Dictyogenus jurassicum* **sp. n.**, is endemic to the Jura Mountains of France and Switzerland and has in the past been confused with *Dictyogenus (Besdolus) ventralis* (Pictet, 1841) by Verneaux (1971, 1973), with *D. fontium* by Reding (1998) and with *D. alpinum* by Verneaux *et al.* (2003). The second new species, *Dictyogenus muranyii* **sp. n.**, is endemic to the French Vercors and Chartreuse Massifs, and had previously been identified by Despax (1940, 1951), Aubert (1986) and Vinçon (1996) as *D. fontium*.

MATERIALS AND METHODS

Collecting. Specimens originally identified as belonging to the genus *Dictyogenus* were collected by the current authors and the late Jacques Aubert between 1986 and 2018 from karstic springs in the Jura Mountains of France and Switzerland, as well as in the French Vercors and Chartreuse massifs (Fig. 92). Adults were collected with a "Japanese umbrella" (beating screen) or with a sweep-net. Larvae were sampled either by kick sampling or by picking specimens

Figs. 2-3. *Dictyogenus jurassicum* **sp. n. 2.** Adult female, head and pronotum. Spring of River Doubs, Mouthe, Doubs dpt, France. Photo A. Ruffoni. **3.** Adult male, hemitergites, dorsal view. Karstic spring at Charabotte Mill, Ain dpt, France. Photo B. Launay.

directly from the substrate with entomological forceps. Mature larvae were reared in the laboratory. All specimens were preserved in 75% or 96% ethanol. In addition, adults of *Dictyogenus* from the collections of Jacques Aubert, Giovanni B. Delmastro, Romolo Fochetti, Wolfram Graf, Carlalberto Ravizza, Rainer Rupprecht, Ignac Sivec and Peter Zwick were revised by the last author.

Terminology and abbreviations. Terminology for adults follows that of Zwick & Weinzierl (1995) and Kovács & Zwick (2008). Terminology for larvae follows that of Stewart & Stark (1993) and Zwick (2004). Terminology for wing venation follows Béthoux (2005) and Béthoux *et al.* (2015). Terminology for egg morphology follows Stark & Szczytko (1988), Szczytko & Kondratieff (2015) and Grubbs (2016). The following abbreviations are used: L = larvae; E = exuviae; MZL = Zoological Museum of Lausanne, Switzerland; IRSTEA = Institut national de recherche en sciences et technologies pour l'environnement et l'agriculture, Villeurbanne, France; HNHM = Hungarian Natural History Museum; LEHNA = Laboratoire d'écologie des hydrosystèmes naturels et anthropisés, Villeurbanne, France; GVC = collection of G. Vinçon; RC = collection of J.-P.G. Reding; BLC = collection of Bertrand Launay; JLDC = collection of Jacques Le Doaré; ARC = collection of Alexandre Ruffoni.

Egg morphology. SEM images were produced using a Hitachi S-2600N scanning electron microscope at the Hungarian Natural History Museum, Budapest, Hungary. Specimens for SEM study were critical point dried and sputter-coated with gold-palladium alloy.

Molecular methods and phylogenetic analyses. We have used CO-1 sequences of *Dictyogenus* specimens from different origins: Swiss Barcoding of Life project on aquatic insects (Gattolliat *et al.*, 2016; SwissBOL, www.swissbol.ch), unpublished sequences made available by Alexis Reding (2011) and sequences generated by IRSTEA. For all stoneflies sequenced by IRSTEA, chromatograms were edited manually for all individuals using FinchTV (version 1.4.0, Geospiza, Inc.; Seattle, WA, USA; http://www.geospiza.com). All CO-1

Figs. 4-5. *Dictyogenus jurassicum* **sp. n.**, adult male. **4.** Hemitergal lobe, lateral view. Karstic spring at Charabotte Mill, Ain dpt, France. Photo B. Launay. **5.** Epiproct and lateral stylet, lateral view. Karstic spring at Charabotte Mill, Ain dpt, France. Photo B. Launay.

fragments used in this analysis were aligned using Seaview software (version 4.7, 1996-2018 Manolo Gouy, http://doua.prabi.fr/software/seaview) with Clustalo method. The tree building was processed with Seaview in PhyML with the Neighbor Joining method (GTR model) and the robustness of nodes was assessed by a non-parametric bootstrap test (1000 cycles) (Felsenstein 1985). *Besdolus ravizzarum* Zwick & Weinzierl, 1995 sequence data were generated by IRSTEA (accession number: MK584340) and was used as outgroup. The genetic material used for the single sequence chosen for *Dictyogenus fontium* is from a topotypical specimen from the Swiss Alps.

Morphology and depositories. Illustrations of the specimens were produced with Leica and Canon EOS DSLR cameras mounted on a Leica S8-APO microscope. Holotypes and paratypes are deposited in the Museum of Zoology, Lausanne, Switzerland (MZL).

RESULTS

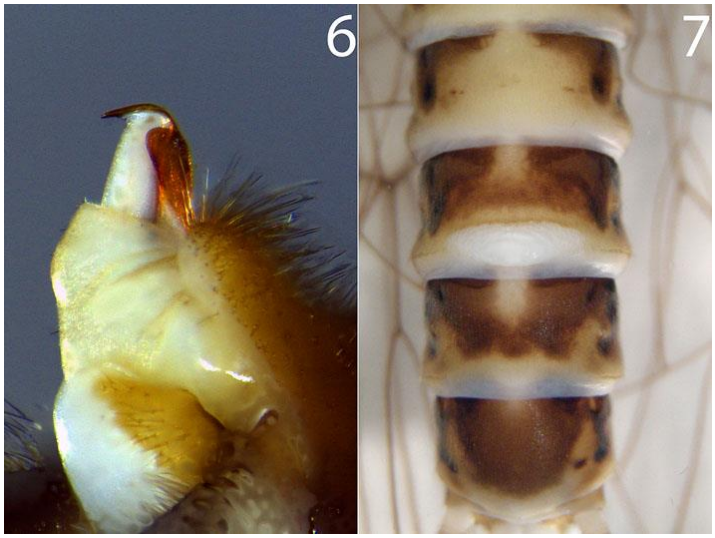
Dictyogenus jurassicum Reding, Launay, Le Doaré, Ruffoni & Vinçon, sp. n.

http://lsid.speciesfile.org/urn:lsid:Plecoptera.speciesfile.org:TaxonName:506375

(Figs. 1–25)

Dictyogenus (Besdolus) ventralis – Verneaux, J. (1973). Annales scientifiques de l'Université de Besançon, Zoologie, Physiologie et Biologie Animale, 3ème Série, 9:98.
Dictyogenus fontium – Reding, J.-P.G. (1998). Bulletin romand d'entomologie, 16:42.
Dictyogenus alpinum – Verneaux *et al.* (2003). Hydrobiologia, 490:71.
Dictyogenus fontium gr sp 5-GV sensu Gilles Vinçon (early-release DNA sequence on: www.boldsystems.org, unpublished)

Materials examined. Holotype male: SWITZERLAND, Jura Mountains, Doubs Valley, canton of Jura, Karstic spring of Côte au Bouvier, near Soubey, 47° 18.028074'N, 7° 3.595063'E, 570m a.s.l., 05.05.2009, leg. Gilles Vinçon, deposited in the MZL (catalogue number: GBIFCH00652518). **Paratypes:** same locality, 16.06.2009, 2♂, 2♀, leg. G. Vinçon, deposited in the MZL (catalogue number: GBIFCH00652530, GBIFCH00652524). Jura Mountains, canton of Jura, Karstic spring



Figs. 6-7. *Dictyogenus jurassicum* **sp. n.**, adult male. **6.** Epiproct and lateral stylet, lateral view. Karstic spring at Charabotte Mill, Ain dpt, France. Photo B. Launay. **7.** Posterior margin of sternite 7 with ventral vesicle, ventral view. Karstic spring at Charabotte Mill, Ain dpt, France. Photo J.-P.G. Reding.

near river Sorne, Blanches-Fontaines, 47° 17.338724'N, 7° 13.36608'E, 585m a.s.l., 06.04.2017, 1L, leg. J.-P.G. Reding, deposited in the MZL (catalogue number GBIFCH00652527).

Additional specimens. We examined many other specimens. These are stored in the collections of Jean-Paul G. Reding (RC), Bertrand Launay (BLC), Natural History Museum of Hungary (NHMH), Gilles Vinçon (GVC), Jacques Le Doaré (JLDC), Alexandre Ruffoni (ARC) and MZL.

SWITZERLAND

Jura Mountains

Chasseron region, Areuse river basin, canton of Vaud, Rhine tributaries:

- Small spring at Dénériaz coomb, 46° 51.180076'N, 6° 31.639395'E, 1135m, 20.09.1993, 3L; 31.07.1996, 1L; 13.10.1996, 1L; 30.08.2000, 1L; 10.05.2002, 1L; 18.07.2006, 4L; 29.06.2010, 1L (used for molecular studies by A. Reding), 1E; 04.05.2011, 1L (used for molecular studies by A. Reding); 18.05.2011, 1L; 04.07.2011, 1L; 13.12.2013, 1L; 27.08.2014, 1L (leg. J.-P.G. Reding; RC).
- Dénériaz torrent, Noirvaux, 46° 51.228685'N, 6° 30.969797'E, 1000 m, 31.03.2005, 6L (leg. J.-P.G. Reding; RC); 13.08.2017, 1L, (leg. J. Le Doaré; JLDC).
- Small spring, Poëta Raisse gorges, 46° 52.910488'N, 6° 36.307303'E, 1131m, 18.07.1997, 1E; 03.08.2011, 2L; 23.06.2012, 2L (leg. J.-P.G. Reding; RC).

Orbe River Basin, canton of Vaud, Rhine tributaries:

- Karstic spring Les Fontannets, La Mothe, 46° 49.165452'N, 6° 33.889242'E, 548m, 09.05.2014, 1L (leg. J.-P.G. Reding; MZL under catalogue number GBIFCH00284213, used for molecular studies by SwissBOL).

Doubs Valley, canton of Jura, Rhône tributaries:

- Karstic spring of Côte au Bouvier, near Soubey, 47° 18.028074'N, 7° 3.595063'E, 570m,

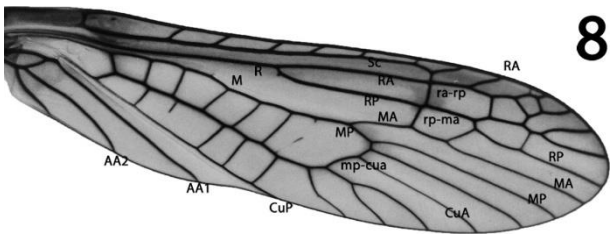


Fig. 8. *Dictyogenus jurassicum* **sp. n.**, adult male, venation of forewing (annotations by Dr. Olivier Béthoux). Karstic spring at Charabotte Mill, Ain dpt, France. Photo B. Launay.

Fig. 9. *Dictyogenus jurassicum* **sp. n.**, female, subgenital plate, ventral view. Spring of River Doubs, Mouthe, Doubs dpt, France. Photo A. Ruffoni.

26.05.1997, 1♂, 2♀, 1E; 05.05.2009, 3♂; 16.06.2009, 2♂, 10♀, 2E; 20.06.2012, 4♀, 4E (leg. G. Vinçon; GVC); 12.06.2007, 3♂, 1E; 24.06.2007, 1♂, 1E (leg. R. Rupprecht; GVC); 29.05.2010, 5L (used for molecular studies by A. Reding); 14.07.2010, 1L (leg. A. Reding; RC); 20.09.2010, 11L; 23.09.2014, 2L (leg. J.-P.G. Reding; RC).

Canton of Jura, Rhine tributaries:

- Karstic spring near river Sorne, Blanches-Fontaines, 47° 17.338724'N, 7° 13.36608'E, 585m, 10.03.2015, 1L (leg. J.-P.G. Reding; MZL under catalogue number GBIFCH00284212, used for molecular studies by SwissBOL); 06.04.2017, 1L (leg. J.-P.G. Reding; RC).

FRANCE

Jura Mountains

Doubs Department (25)

Doubs drainage basin, Rhône tributaries:

- Spring of Doubs River, Mouthe, 46° 42.295779'N, 6° 12.548421'E, 946m, 18.04.1991, 2L; 15.09.1991, 1E (leg. J. Aubert; GVC); 14.07.1996, 1♀, 7E (leg. G. Vinçon; GVC); 13.06.2007, 1L (used for molecular studies by A. Reding); 10.05.2017, 1L (leg. J.-P.G. Reding; RC).

Loue drainage basin, Rhône tributaries:

- Spring of Loue River, Ouhans, 47° 0.645115'N, 6° 17.97486'E, 529m, 10.04.2013, 1L (leg. J.-P.G. Reding; RC).
- Spring of Moulin Miguet, Nouailles Gorges, Ouhans, 47° 1.326046'N, 6° 17.934465'E, 456m, 14.05.2013, 1L; 01.04.2014, 5L; 14.04.2015, 2L (leg. J.-P.G. Reding; RC).

Ain (01) and Jura (39) Departments, Ain drainage basin, Rhône tributaries:

- Karstic spring near Albarine river, Charabotte Mill (01), 45° 57.308924'N, 5° 33.286347'E, 476m,

Fig. 10. *Dictyogenus jurassicum* **sp. n.**, larva. Spring of River Doubs, Mouthe, Doubs dpt, France. Photo A. Ruffoni.

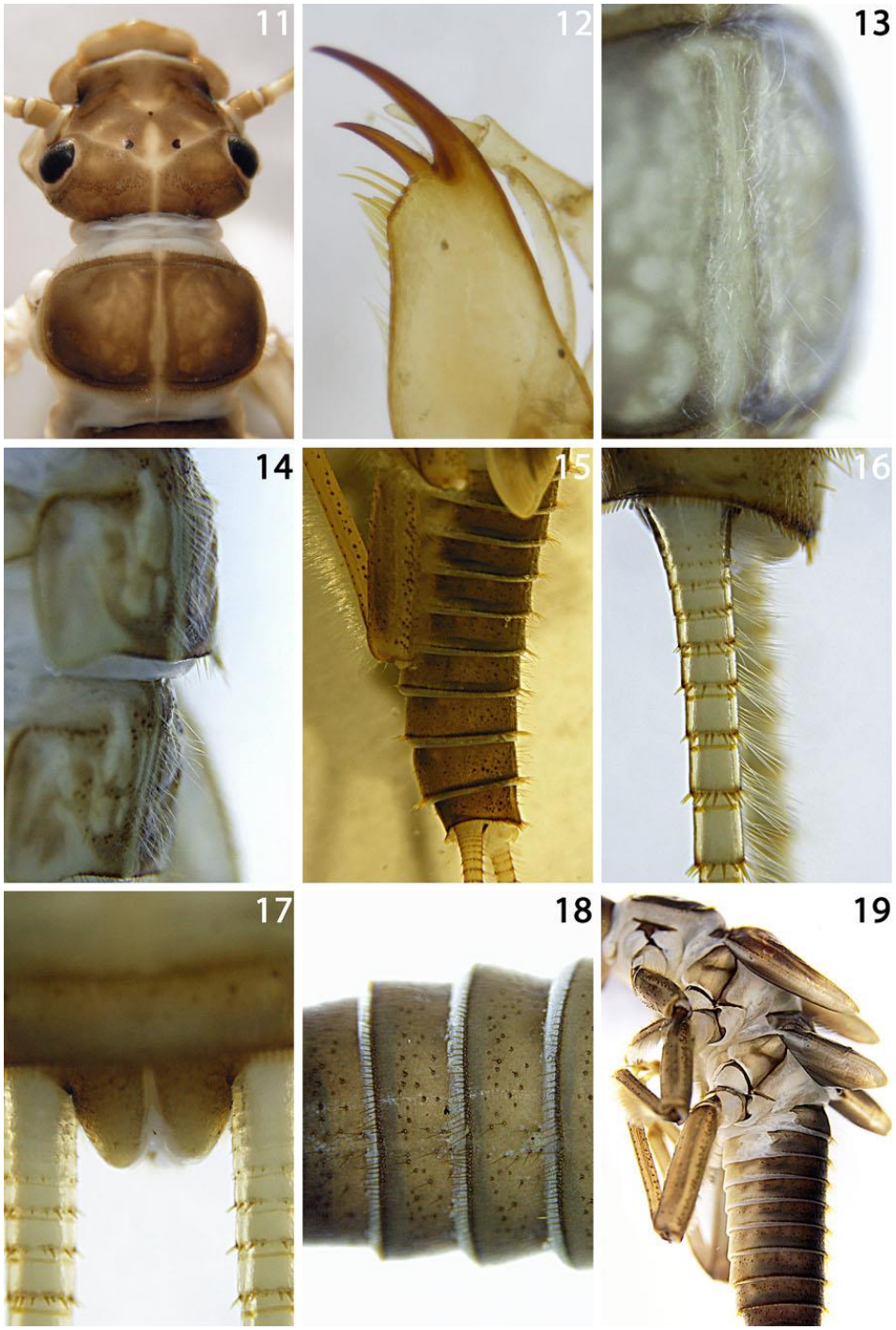
09.06.2013, 2♂, 3♀ (leg B. Launay; JLDC); 15.06.2013, 3♀; 16.02.2014, 2L; 06.05.2014, 1♂, 3♀, 1E (leg. B. Launay; RC); 13.05.2015, 4m, 1L, 2E (leg. B. Launay; BLC; used for molecular studies by IRSTEA, numbers B116 and B117).

- Valouse river near Cornod (39), bridge over road D 202, 46° 18.536086'N, 5° 32.227764'E, 310m, 12.09.2007, 1L (leg. J. Le Doaré; JLDC).
- Spring of Flumen river, near Les Moulins, Septmoncel (39), 46° 21.204252'N, 5° 54.395038'E, 800m, 24.07.2007, 9L; 28.04.2011, 1L (leg. J. Le Doaré; JLDC).
- Spring of Ravin de la Gaillarde, Tenay (01), 45° 56,078220'N, 5° 32,239020'E, 651m, 13.04.2018, 1L (leg. B. Launay; BLC).

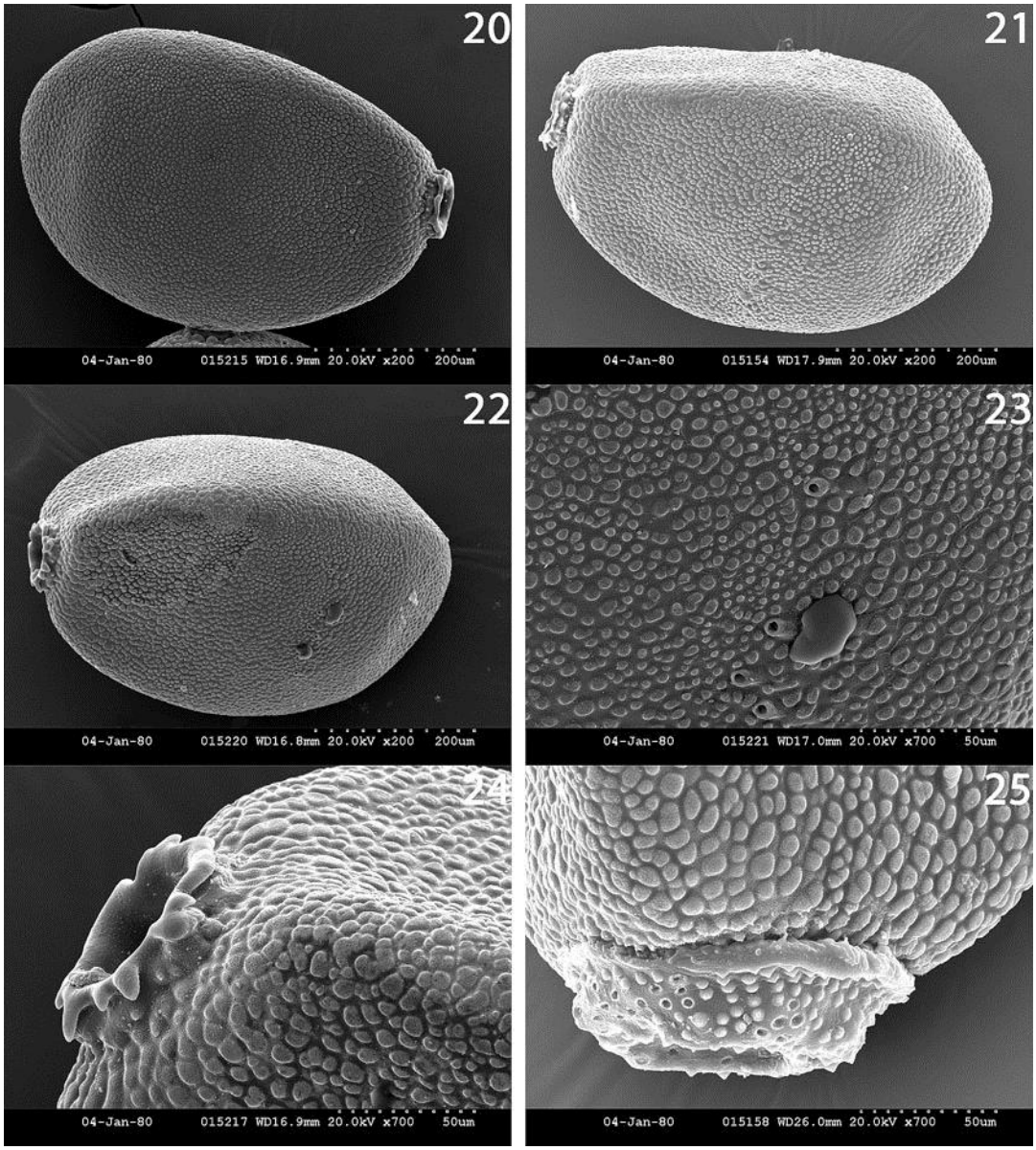
Ain Department (01), Valserine drainage basin, Rhône tributaries:

- Karstic spring at Creux-Godet, 46° 16.114284'N, 5° 54.894414'E, 879m, 13.04.1991, 1L (leg. J. Aubert; GVC); 17.03.2014, 2L; 30.05.2014, 1E (leg. B. Launay; BLC); 25.08.2014, 8L (leg. J. Le Doaré; JLDC).
- Brion waterfall, near Chézery-Forens, 46° 15.311212'N, 5° 54.032052'E, 810m, 03.02.2014, 3L; 14.02.2014, 3L; 17.03.2014, 24L (leg. B. Launay; BLC; 2L in RC); 04.05.2014, 3L; 30.05.2014, 2♂, 2E; 19.07.2014, 1♀, 1E; 22.12.2014, 2L; 11.04.2015, 1L; 22.05.2015, 2L; 13.06.2015, 2♂, 1♀, 1E; 08.06.2016, 1♀ (leg. B. Launay; BLC); 27.01.2015, 3L (leg. J.-P.G. Reding; RC).
- Karstic spring near Perissode farm, 46° 22.128147'N, 6° 0.361369'E, 1030m, 05.05.2014, 1L; 20.07.2014, 2♀; 25.08.2014, 11L (leg. J. Le Doaré; JLDC); 26.04.2015, 1L; 01.08.2015, 4L 1E (leg. B. Launay; BLC).
- Forens river tributary, Chézery-Forens, 46° 13.389054'N, 5° 51.127375'E, 700m, 03.02.2014, 1L; 14.02.2014, 2L; 30.05.2014, 1♂, 1♀, 1E; 13.06.2015, 1E (leg. B. Launay; BLC).
- Septfontaine river at Mijoux, 46° 19.277761'N, 5° 57.467904'E, 950m, 03.07.2015, 1L; 01.08.2015, 1♂, 1♀; 05.09.2015, 3L; 02.04.2016, 1L (leg. B. Launay; BLC).

Diagnosis. General color dark brown with tawny and yellow spots (Figs. 1, 2). Males and females macropterous (Figs. 1, 8). Apex of the frontal sclerite of the epiproct of adult males slightly bent downwards, in lateral view (Figs. 5, 6). Female subgenital plate covering half of the ninth sternum and exhibiting a deep median arch-shaped notch (Fig. 9). Body length of males 14–18 mm; females 15–23 mm. Anterior wings of males 15.9–17.6 mm; females 10–20.7 mm. Posterior



Figs. 11-19. *Dictyogenus jurassicum* **sp. n.**, larva. Karstic spring of Côte au Bouvier, near Soubey, canton of Jura, Switzerland. All images credited to J.-P.G. Reding. **11.** Head and pronotum, dorsal view. **12.** Lacinia. **13.** Pronotum, dorso-lateral view. **14.** Mesonotum and metanotum, dorso-lateral view. **15.** Abdominal tergites, lateral view. **16.** Medio-dorsal row of setae on base of cerci, lateral view. **17.** Paragenital lobes, ventral view. **18.** Tergites 5, 6 and 7, dorsal view. **19.** Separation of tergites and sternites, lateral view.



Figs. 20-25. *Dictyogenus jurassicum* **sp. n.**, egg characteristics. **20.** Egg, lateral view. Karstic spring of Côte au Bouvier, near Soubey, canton of Jura, Switzerland. **21.** Egg, lateral view. Karstic spring of Côte au Bouvier, near Soubey, canton of Jura, Switzerland. **22.** Egg, lateral view, with ridge and micropyles visible. Karstic spring of Côte au Bouvier, near Soubey, canton of Jura, Switzerland. **23.** Detail of egg chorion and micropyles. Karstic spring of Côte au Bouvier, near Soubey, canton of Jura, Switzerland. **24.** Egg, collar. Karstic spring of Côte au Bouvier, near Soubey, canton of Jura, Switzerland. **25.** Egg, collar and anchor. Karstic spring of Côte au Bouvier, near Soubey, canton of Jura, Switzerland.

wings of males 13.2–15.5 mm; females 13.9–20.5 mm.

Adults (Figs. 1–9). Head mostly brown, with two large lateral yellow circular spots on both sides of the clypeus and a wide, symmetric, yellow patch on the M-line, above the anterior ocellus (Fig. 2). Between the lateral ocelli, a large, tawny area delimitated posteriorly by the epicranial suture. Area between the lateral ocelli and the compound eyes pale yellow (Fig. 2). Pronotum dark brown (Fig. 2). Anterior and posterior angles of pronotum almost rectangular (Fig. 2). Presence of a yellow median band extending from the anterior margin of the pronotum to its posterior margin, widened in its middle section and gradually narrowing toward the posterior margin of pronotum (Fig. 2). A tawny area on each side of the pronotum, with dark, sculpted rugosities (Fig. 2). Abdominal sterna pale brown, with symmetrical, hyphen-like patches. Proximal part of tibiae with a dark band. Antennae and cerci blackish to dark brown (Figs. 1, 4). Wing venation as typical for the genus (Ris 1896: 308, Fig. 3). Forewing (Fig. 8) and hindwing (cf. Fig. 31) with the two cross-veins "ra-rp" and "rp-ma" nearly aligned. Numerous cross-veins forming a reticulated area between RA and RP (Fig. 8). Cross-vein "ra-rp" and subcostal area of forewing faintly infuscate (Fig. 8).

Male terminalia (Figs. 3–6). Presence of distinctly separated hemiterga (Figs. 3, 4) and an epiproct with a frontal apical sclerite ending in a single long spine and with two shorter dorso-lateral spines (Figs. 5, 6). Epiproct flanked by flat and spatulate lateral stylets (Figs. 5, 6). Tergum 10 divided into hemiterga whose lobes are covered with 20 to 25 pale long setae in which 2 to 9 darker, stronger and longer spines (half of the length of the hemitergal lobes) are embedded (Fig. 3). Hemitergal lobes long and slender, bent obliquely upwards (Fig. 3) and rearwards (Fig. 4). Apex of frontal sclerite of epiproct slightly bent downwards, in lateral view (Figs. 5 and 6). Lateral stylets large and club-shaped, widening near apex, in lateral view (Figs. 5 and 6). Abdominal sternum 7 composed of multiple plates (Fig. 7).

Females (Fig. 9). Females of *Dictyogenus* not formally identifiable to species level, except those of *D. alpinum*, whose subgenital plate covers the majority of the sternum 9 (Figs. 60, 61). Female subgenital plate of *D. jurassicum* **sp. n.** covering half of the ninth sternum and exhibiting a deep median arch-shaped notch (Fig. 9).

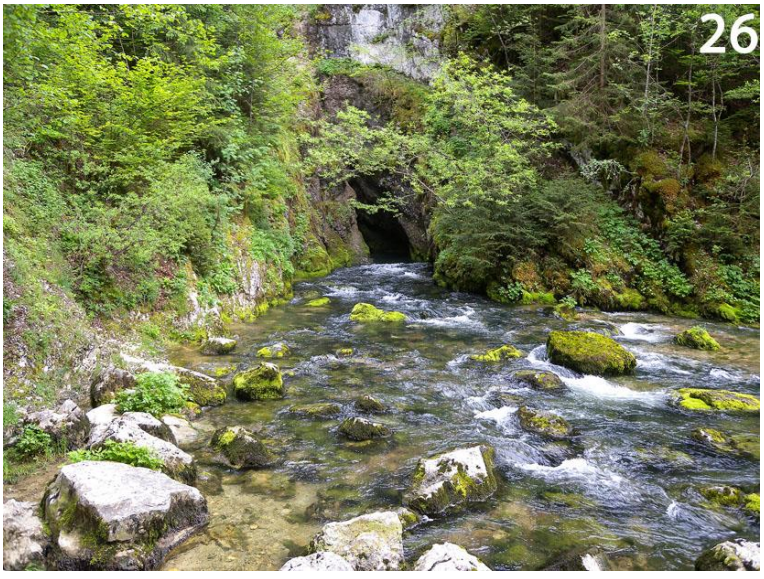


Fig. 26. *Dictyogenus jurassicum* **sp. n.**, biotope. Karstic spring of River Doubs, Mouthe, Doubs dpt, France. Photo: J.-P. G. Reding.

Fig. 27. *Dictyogenus muranyii* **sp. n.**, adult female habitus. Karstic spring of Bruyant, Isère dpt, France. Photo G. Vinçon.

Mature larvae (Figs. 10–19). Larvae <8 mm not identifiable to species-level. Immature larvae are characterized by a very dense setation on abdominal segments, legs, paragenital plates as well as cerci and live in interstitial habitats composed of loose sandy gravels. Mature larvae, on the contrary, are petricolous and this habitat shift also coincides with important chaetotactic changes, notably the reduction of length and number of setae on abdominal segments, paragenital plates and cerci.

Length of mature larvae, measured from head to end of abdomen: 9–19 mm. First two abdominal segments with abdominal terga and sterna clearly separated by a small membranous area (Fig. 19). Interocellar area with a narrow yellow patch not reaching lateral ocelli (Figs. 10, 11). Lateral ocelli without circum-ocellar yellow patch (Figs. 10, 11). A narrow elongated yellow patch above each lateral ocellus (Figs. 10, 11). M-line indistinct (Figs. 10, 11). Occipital fold and lower rim of the eyes with a conspicuous row of spines (Fig. 11; cf. also Fig. 66). Lacinia with apical and subapical tooth; marginal setae of the lacinia in a single long row (Fig. 12). Lacinia, below subapical tooth, with a shoulder-like angle (Fig. 12; cf. also Fig. 64). Shape of pronotum ovoid (Fig. 11). Medio-dorsal setae on pronotum short and scattered, arranged as several, loosely demarcated rows (Fig. 13). Medio-dorsal row of setae long and continuous on mesonotum and metanotum (Fig. 14). Medio-dorsal row of setae on abdominal terga short and sparse (Fig. 15). Posterior margins of median abdominal terga with setae of unequal lengths (Fig. 18). Tip of paragenital plates blunt, in ventral view (Fig. 17). Paragenital plates, in ventral view, with at most two unpaired spines at or near apex; generally, there is only 1 spine on one of the paragenital plates while the other is devoid of spines (Fig. 17). Numerous empty spine insertion points on the paragenital plates, in ventral view (Fig. 17). Medio-dorsal row of swimming-hairs of caudal setae sparse, with interruptions, and as long as or not much longer than the diameter of the cerci (Fig. 16). General aspect as in Fig. 10.

Egg characteristics (Figs. 20–25). General shape oblong, cross-section trilateral, smoothed (Figs. 20–22). Posterior pole of egg regularly rounded; ridges only slightly protruding (Figs. 20–22). Chorionic surface with granulose follicle cell impressions (Fig. 23). Collar short, flared

Fig. 28. *Dictyogenus muranyii* **sp. n.**, male, head and pronotum. Karstic spring of Bruyant, Isère dpt, France. Photo B. Launay.

apically with few ridges of different length (fig. 24). Anchor flat (Fig. 25). Micropyles protruding and arranged singularly near posterior ⅓ of egg (Fig. 23). Eclosion line absent.

Comparison to Congeners.

Adults. In the adult male of *Dictyogenus jurassicum* **sp. n.**, the hemitergal lobes are strongly bent upwards (Fig. 3) and rearwards (Fig. 4), whereas the hemitergal lobes of *D. alpinum* are only slightly bent upwards, pointing almost horizontally toward each other (Fig. 56). In the adult males of *Dictyogenus jurassicum* **sp. n.** (and also those of *D. muranyii* **sp. n.** and the specimens belonging to the *D. fontium* species complex), there is a wide, V-shaped membranous area between the hemitergal lobe and the inner anterior corner of the hemiterga (Figs. 3, 29, 32, 81). In the adult males of *Dictyogenus alpinum*, on the contrary, the area between the hemitergal lobe and the inner anterior corner of the hemiterga is globulous and sclerotized (Fig. 56). In *Dictyogenus jurassicum* **sp. n.**, the lateral stylets are enlarged apically (Fig. 5), whereas they are getting progressively thinner toward the apex in *D. alpinum* (Fig. 57). In the female of *Dictyogenus jurassicum* **sp. n.**, the subgenital plate (Fig. 9) covers at most the upper half of abdominal sternum 9, as is also the case for specimens of the *D. fontium* species complex (Figs. 83, 84), whereas the subgenital plate of *D. alpinum* covers ¾ of the sternum 9 (Figs. 60, 61). Adult females of *Dictyogenus jurassicum* **sp. n.** hence have more affinities with those of the *D. fontium* species complex than with those of *D. alpinum*, whereas adult males of *Dictyogenus jurassicum* **sp. n.** are closer to those of *D. alpinum* than to those of the *D. fontium* species complex, from which they differ by the much stronger curvature of the apex of the frontal epiproct sclerite in lateral view (Figs. 5, 6, 57 compared to Fig. 80).

Mature larvae. *Dictyogenus jurassicum* **sp. n.** differs from *D. fontium* by the presence of medio-dorsal setae on the pronotum (Fig. 13 compared to Fig. 86). Medio-dorsal setae on pronotum of *Dictyogenus jurassicum* **sp. n.** are short and scattered, arranged as two loosely demarcated rows (Fig. 13), whereas they are longer, but uncompacted, in *D. muranyii* **sp. n.** (Figs. 40, 41), and dense and long in *D. alpinum* (Fig. 71).

Distribution and ecology. *Dictyogenus jurassicum* **sp. n.** is the only species of *Dictyogenus* present in

Figs. 29-30. *Dictyogenus muranyii* **sp. n.**, male terminalia. **29.** Hemitergal lobes, dorsal view. Karstic spring of Bruyant, Isère dpt, France. Photo B. Launay. **30.** Hemitergal lobes, lateral view. Karstic spring of Bruyant, Isère dpt, France. Photo B. Launay.

the Jura Mountains of France and Switzerland (Fig. 92) and is distributed over all its different drainage basins. The occurrence of *Dictyogenus jurassicum* **sp. n.** is, however, restricted to karstic springs (some of them intermittent) and the initial section of their outflows in the Jura Mountains of France and Switzerland (Fig. 26). The flight period of *D. jurassicum* **sp. n.** extends from spring to early summer. Adults of both sexes emerge from the middle of April until the beginning of July. The life cycle is unknown. Our observations in the field are compatible with a semivoltine cycle, since immature larvae (3-4 mm) were generally found together with pre-emergent larvae in spring, at the end of the emergence period of adults. Half-grown larvae (6-8 mm) are present in autumn and in winter. Thus, larval growth of *Dictyogenus jurassicum* **sp. n.** extends over a period of at least two years. A possible egg diapause, as documented for a population of *Dictyogenus fontium* by Zwick & Zwick 2010, would extend its life cycle to three years.

Etymology of *Dictyogenus jurassicum* sp. n. The new species is named after the region where it was collected, the Jura Mountains of France and Switzerland.

Dictyogenus muranyii Vinçon, Launay, Le Doaré, Ruffoni & Reding, sp. n.

http://lsid.speciesfile.org/urn:lsid:Plecoptera.speciesfile.org:TaxonName:506376
(Figs. 27–51)

Dictyogenus fontium – Despax, R. (1940). Bulletin de la Société d'Histoire Naturelle de Toulouse, 75:296.
Dictyogenus fontium – Vinçon, G. (1996). Bulletin de la Société Entomologique Suisse, 69:72.
Dictyogenus fontium gr sp 3-GV sensu Gilles Vinçon (early-release DNA sequence on: www.boldsystems.org, unpublished)

Materials examined. Holotype male: FRANCE, Vercors Massif, Isère department (38), Karstic Spring of Bruyant river, above Engins, Lans-en-Vercors (38250), 45° 8.798123'N, 5° 37.049358'E, 982m a.s.l., 09.06.2017, leg. G. Vinçon, deposited in the MZL (catalogue number: GBIFCH00652534). **Paratypes:** same locality, same date, 3♂, 1♀, leg. G. Vinçon, deposited in the MZL (catalogue number: GBIFCH00652525, GBIFCH00652519); same locality, same date, 3L, leg. J.-P.G. Reding, deposited in the MZL (catalogue number: GBIFCH00652514).

Additional specimens. We examined many other specimens. These are stored in the collections of Bertrand Launay (BLC), Gilles Vinçon (GVC), Jean-Paul G. Reding (RC), Dávid Murányi (MC),

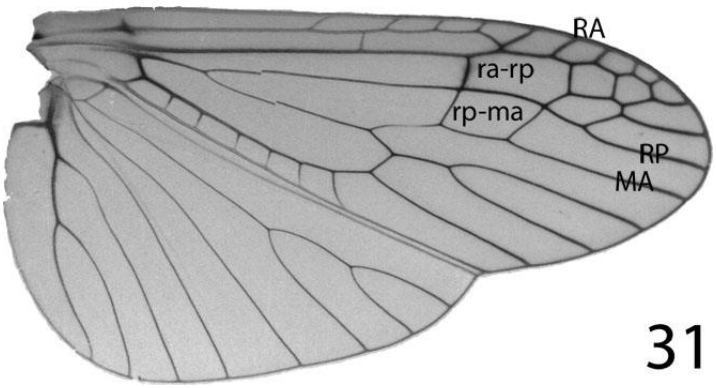


Fig. 31. *Dictyogenus muranyii* **sp. n.**, male, hindwing. Karstic spring of Bruyant, Isère dpt, France. Photo B. Launay.

Jacques Le Doaré (JLDC), Alexandre Ruffoni (ARC) and MZL.

FRANCE

Vercors Massif

Drôme department (26):

- Archiane torrent, Drôme tributary, NE Châtillon-en-Diois, Menée, Cirque d'Archiane, 44° 44.770828'N, 5° 30.214097'E, 760m, 31.07.1990, 1♂; 16.09.1990, 2♀ (leg. G. Vinçon; GVC).
- Spring at Brudour cave, Brudour River, Bourne tributary, Bouvante (26190), 44° 55.67493'N, 5° 19.257459'E, 1182m, 13.04.2016, 3L; 02.06.2016, 2♂, 2♀, 1L, 7E (leg. B. Launay; BLC; used for molecular studies by IRSTEA, numbers B079 and B080); 21.05.2017, 1E (leg. G. Vinçon; GVC); 09.06.2017, 9E (leg. J.-P.G. Reding; RC).
- Adouin river, near its spring, Vernaison and Bourne tributary, Tourtre, Saint-Martin-en-Vercors (26420), 45° 0.120928'N, 5° 27.550379'E, 793m, 21.05.2017, 1♂, 1♀ (leg. G. Vinçon, GVC); 09.06.2017, 11♀, 1E (leg. G. Vinçon; RC; 1♀ used for molecular studies by SwissBOL, MZL, catalogue number GBIFCH00280854); 2♂, 17♀ (leg. G. Vinçon; GVC).
- Cholet river, Lyonne and Bourne tributary, Combe Laval, Saint-Laurent-en-Royans (26190), 44° 59.859883'N, 5° 20.75296'E, 355m, 21.05.2017, 2♂, 6E (leg. G. Vinçon; GVC).

Isère department (38):

- Bruyant river, Furon and Isère tributary, above Engins, Lans-en-Vercors (38250), 45° 8.798123'N, 5° 37.049358'E, 982m, 06.10.1991, 1E; 25.06.1995, 7♂, 4♀; 10.05.1998, 1♂; 10.06.2007, 1♂; 22.06.2008, 1♂; 22.06.2009, 32♂, 6♀ (1♂ used for molecular studies by A. Reding); 07.07.2012, 7♂, 2♀, 1L (leg. G. Vinçon; GVC); 07.06.2015, 3♂, 2♀, 6L, 5E (leg. B. Launay; BLC); 09.06.2017, 2♂, 1♀, 17E (leg. G. Vinçon; GVC); 7♂, 1♀, 7L, 3E (leg. J.-P.G. Reding; RC; 1♂ used for molecular studies by SwissBOL, MZL, catalogue number GBIFCH00280811).
- Cuves de Sassenage strong rheocrene spring, Germe brook, Furon and Isère tributary, Sassenage (38474), 45° 12.516243'N, 5° 39.078175'E, 330m, 15.06.1991, 1♂, 2♀ strongly brachypterous (leg. G. Vinçon; MC).
- Drevenne river, Isère tributary, Pont Chabert, Saint-Gervais (38470), 45° 10.643943'N, 5° 29.885486'E, 885m, 15.06.1991, 1L (leg. G. Vinçon; GVC); 31.05.2012, 2♂; 17.07.2012, 2L; 11.07.2015, 3L (leg. J. Le Doaré; JLDC); 06.06.2015, 1E (leg. B. Launay; BLC).
- Font Noire river, Bourne tributary, Villard-de-Lans (38250), 45° 4.472474'N, 5° 33.970966'E, 1010m, 01.06.2016, 1♂, 1E (leg. B. Launay; BLC; used for molecular studies by IRSTEA, number B120).
- Fauge river, Bourne tributary, Villard-de-Lans (38250), 45° 3.373805'N, 5° 34.664105'E, 1230m, 01.06.2016, 1E (leg. B. Launay; BLC).

Figs. 32-35. *Dictyogenus muranyii* **sp. n.**, male terminalia. **32.** Hemitergal lobes, dorsal view. Karstic spring of Font Noire, Isère dpt, France. Photo B. Launay. **33.** Epiproct, lateral view. Karstic spring of Font Noire, Isère dpt, France. Photo B. Launay. **34.** Lateral stylet, lateral view. Karstic spring of Brudour, Drôme dpt, France. Photo B. Launay. **35.** Epiproct, dorso-caudal view. Karstic spring of Font Noire, Isère dpt, France. Photo B. Launay.

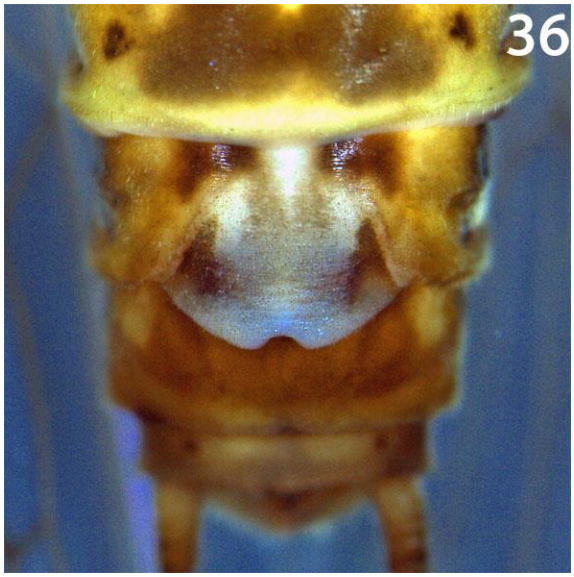


Fig. 36. *Dictyogenus muranyii* **sp. n.**, female, subgenital plate. Karstic spring of Brudour, Drôme dpt, France. Photo B. Launay.

- Spring of Furon river, Lans-en-Vercors (38250), 45° 6.304551'N, 5° 36.221224'E, 1294m, 12.07.2015, 6L (leg. J. Le Doaré; JLDC).

Chartreuse Massif

Isère (38) and Savoie (73) departments:

- Sarcenas river at Sarcenas, Isère tributary, (38700), 45° 16.829887'N, 5° 45.251584'E, 1093m, 20.04.1986, 5L; 01.06.1986, 4L; 05.10.1986, 1♂ (leg. G. Vinçon; GVC).
- Spring of Guiers-Vif river, Rhône tributary, Cirque de Saint-Même, Saint-Pierre-D'Entremont (73670), 45° 23.491629'N, 5° 53.464859'E, 1050m, 21.06.1992, 3♀; 12.09.1992, 4♀, 1E; 21.06.1992, 3♀ (leg. G. Vinçon; GVC).
- Karstic spring of Guiers Mort, Rhône tributary, Saint-Pierre-de-Chartreuse (38380), 45° 19.571976'N, 5° 51.452039'E, 1360m, 11.09.1938, stage and numbers not specified (leg. Ms. Daudin, *fide* Despax 1940).

Diagnosis. General color dark brown with tawny and yellow spots (Figs. 27, 28). Males and females macropterous; only two females were found strongly brachypterous. Apex of the frontal sclerite of the epiproct of adult males very slightly turned downwards, in lateral view (Fig. 33). Female subgenital plate covering half of the abdominal sternum 9 (Fig. 36). Body length of males 17.2 to 20.9 mm; females 18 to 23.6 mm. Anterior wings of males 15 to 19.3 mm; females 17.7 to 21.5 mm. Posterior wings of males 12.5 to 15.8 mm; females 15.3 to 17.4 mm.

Adults (Figs. 27–36). Upper side of the head brown, with large yellow spots (Fig. 28). M-line yellow, not interrupted in its middle (Fig. 28). Between the lateral ocelli, a large, ovoid, yellow area delimitated posteriorly by the epicranial suture (Fig. 28). Presence of a large, yellow, median band extending from the anterior margin of the pronotum to its posterior margin (Fig. 28). Band slightly constricted in the middle and then steadily widening toward the posterior margin (Fig. 28). A tawny area on each side of the pronotum, with dark, sculpted rugosities (Fig. 28). Anterior and posterior angles of pronotum almost rectangular (Fig. 28). Abdominal sterna 1 to 6 pale yellow, with two dark patches. Antennae dark brown; cerci light brown with basal part pale yellow (Figs. 29, 30). Wing venation as typical for the genus (Fig. 31; cf. Fig. 8). Forewing with the two cross-veins "ra-rp" and "rp-ma"

Fig. 37. *Dictyogenus muranyii* **sp. n.**, larva. Karstic spring of Brudour, Drôme dpt, France. Photo A. Ruffoni.

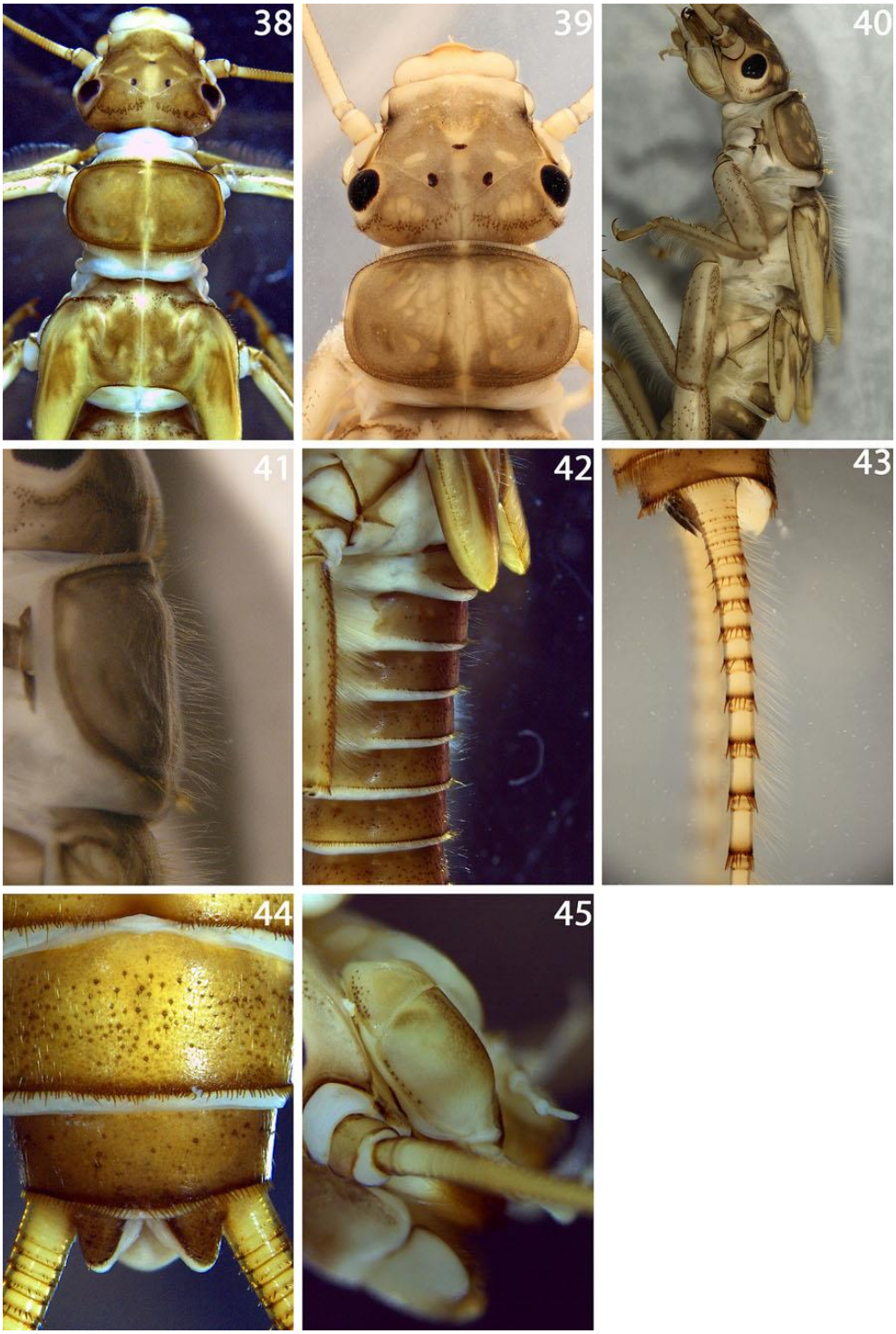
nearly aligned (like in Fig. 8). Numerous cross-veins forming a reticulated area between RA and RP (Fig. 31; cf. Fig. 8). Cross-vein "ra-rp" and subcostal area faintly infuscate (as in Fig. 8).

Male terminalia (Figs. 29, 30, 32–35). Epiproct flanked by flat and spatulate lateral stylets (Figs. 33, 34). Abdominal tergum 10 divided into hemiterga whose lobes are covered with a bunch of 20 to 25 long setae in which 3 to 6 stronger and longer spines (half of the length of the hemitergal lobes) are embedded (Figs. 29, 32). Hemitergal lobes bulb-shaped with a slight distal knob (Fig. 30), both pointing rearwards (Fig. 30) and almost horizontally toward each other (Figs. 29, 32). Apex of frontal sclerite of epiproct slightly turned downwards, in lateral view (Fig. 33). Lateral stylets long, only slightly enlarged at apex, in lateral view (Figs. 33, 34). Abdominal sternum 7 composed of multiple plates (as in Figs. 7, 59, 82).

Females (Fig. 36). Females not formally identifiable to species level. Female subgenital plate (Fig. 36) covering at most half of sternum 9. Its general shape is semi-circular with a shallow V-shaped median notch.

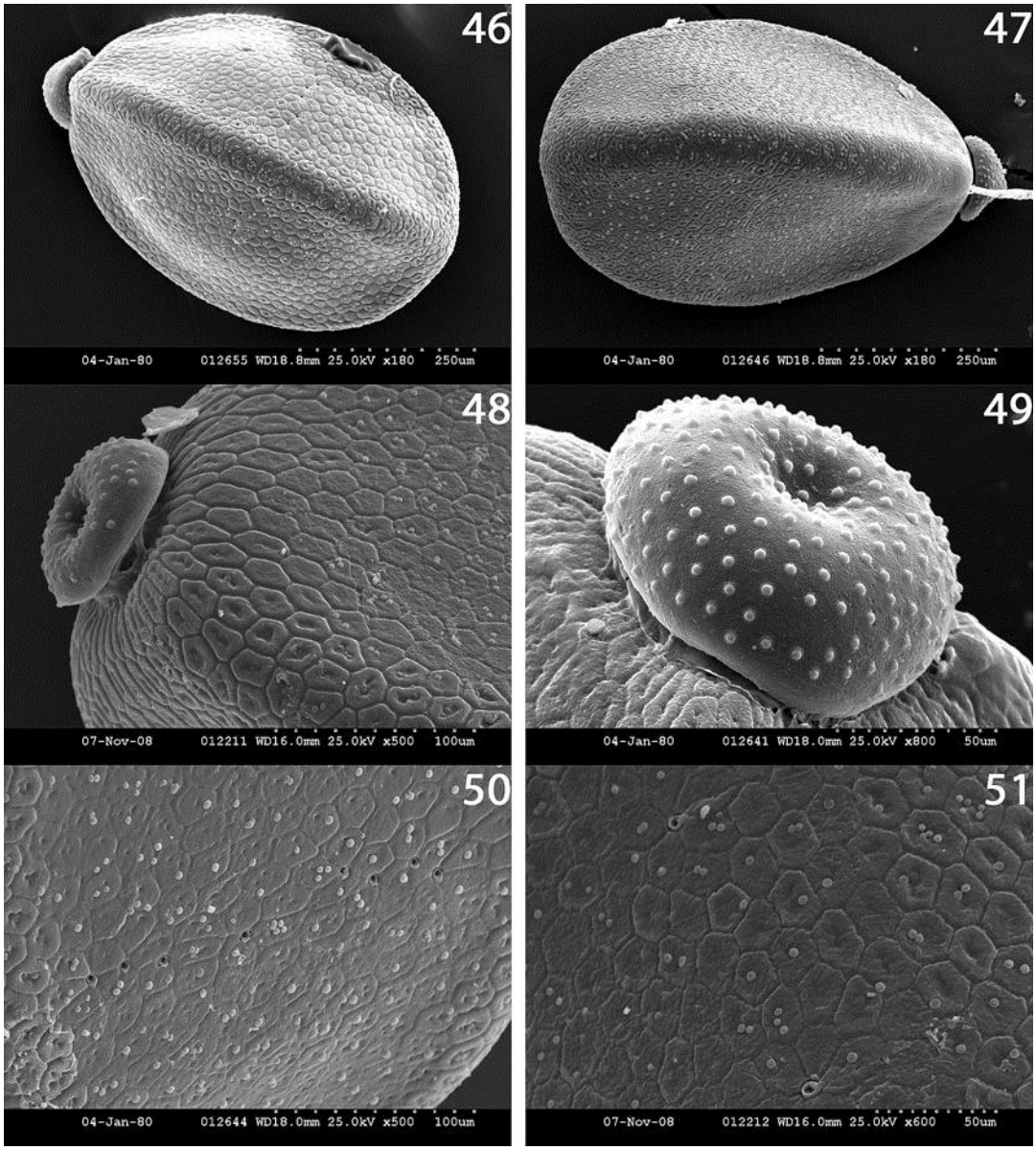
Mature larvae (Figs. 37–45). Interocellar area with a narrow yellow patch nearly reaching lateral ocelli (Figs. 37–39). Lateral ocelli with small lateral circum-ocellar yellow patch (Fig. 38). A large, elliptical yellow patch above each lateral ocellus (Figs. 37–39). M-line well visible only in its medial, crescent-shaped, section (Figs. 37–39). Pronotum wider than long (Figs. 38, 39). Medio-dorsal setae on pronotum long, but not compacted, sometimes covering only the posterior half of the pronotum (Figs. 40, 41). Medio-dorsal row of setae present on mesonotum and metanotum (Fig. 40). Abdominal terga with a row of short and sparse medio-dorsal setae (Fig. 42). Paragenital plates, in ventral view, without spines, or with only 1 spine on one of the paragenital plates, but with numerous empty spine insertion points (Fig. 44). Medio-dorsal row of swimming-hairs of caudal setae sparse, slightly longer than the diameter of the cerci (Fig. 43). General aspect as in Fig. 37.

Egg characteristics (Figs. 46–51). General shape triangular or trilateral in cross section. Posterior pole of egg regularly rounded; ridges protruding (Figs. 46, 47). Chorionic surface



Figs. 38-45. *Dictyogenus muranyii* **sp. n.**, larva. **38.** Head, pronotum and mesonotum, dorsal view. Karstic spring of Brudour, Drôme dpt, France. Photo B. Launay. **39.** Head, pronotum, dorsal view. Karstic spring of Brudour, Drôme dpt, France. Photo A. Ruffoni. **40.** Head, pronotum, mesonotum and metanotum, lateral view. Karstic spring of Bruyant, Isère dpt, France. Photo A. Ruffoni. **41.** Pronotum, lateral view. Karstic spring of Bruyant, Isère dpt, France. Photo J.-P.G. Reding. **42.** Abdominal segments, lateral view. Karstic

spring of Brudour, Drôme dpt, France. Photo B. Launay. **43.** Medio-dorsal setae on cerci. Karstic spring of Brudour, Drôme dpt, France. Photo A. Ruffoni. **44.** Paragenital plates, ventral view. Karstic spring of Brudour, Drôme dpt, France. Photo B. Launay. **45.** Stipe. Karstic spring of Brudour, Drôme dpt, France. Photo B. Launay.



Figs. 46-51. *Dictyogenus muranyii* **sp. n.**, egg characteristics. **46.** Egg, upper view from one ridge with two faces and the micropylar region visible. Bruyant, Vercors Massif, Isère dpt, France. **47.** Entire egg. Archiane, Vercors Massif, Isère dpt, France. **48.** Egg collar. Archiane, Vercors Massif, Isère dpt, France. **49.** Egg collar. Bruyant, Vercors Massif, Isère dpt, France. **50.** Detail of micropyles. Bruyant, Vercors Massif, Isère dpt, France. **51.** Detail of chorion and micropyles. Archiane, Vercors Massif, Isère dpt, France.

Figs. 52-53. *Dictyogenus muranyii* **sp. n.**, biotopes. **52.** Cave and Spring of Brudour river, Drôme dpt, France. Photo A. Ruffoni. **53.** Spring of Adouin River, Vercors Massif, Isère dpt, France, in summer. Photo J. Le Doaré.

with polygonal follicle cell impressions (Figs. 48, 50, 51). Anchor papillate, donut shaped apically with central depression (Figs. 48, 49). Micropyles not protruding and arranged regularly in a line in the middle of the egg (Figs. 47, 50). Eclosion line absent (Figs. 46, 47).

Comparison to Congeners.

Adults. In the adult male of *Dictyogenus muranyii* **sp. n.**, a wide, V-shaped membranous area between the hemitergal lobe and the inner anterior corner of the hemitergum is present (Figs. 29, 32), whereas this area is sclerotized and much narrower in *D. alpinum* (Fig. 56). The lateral stylets in *D. muranyii* **sp. n.** are slightly enlarged apically (Figs. 33, 34), intermediate in form between those of *D. alpinum* (Fig. 57) and those of the *D. fontium* species complex (Fig. 80). In the adult female of *D. muranyii* **sp. n.**, the subgenital plate (Fig. 36) covers at most the upper half of sternum 9, as is also the case for specimens of the *D. fontium* species complex (Figs. 83, 84), whereas the subgenital plate of *D. alpinum* covers ¾ of sternum 9 (Figs. 60, 61). The anterior and posterior angles of the pronotum of *Dictyogenus muranyii* ***sp. n.***, *D. jurassicum* ***sp. n.*** and *D. fontium are* almost rectangular (Figs. 2, 28, 79), whereas those of *D. alpinum* are rounded (Fig. 54). Adult males and females of *Dictyogenus muranyii* **sp. n.** hence have more affinities with those of the *D. fontium* species complex than with those of *D. alpinum*.

Mature larvae. *Dictyogenus muranyii* **sp. n.** differs from *D. fontium* by the presence of medio-dorsal setae on the pronotum (Fig. 41 compared to Fig. 86). Medio-dorsal setae on pronotum are long and sparse in *D. muranyii* **sp. n.** (Figs. 40, 41), whereas they are long and dense in *D. alpinum* (Fig. 71), and short and scattered, arranged as two loosely demarcated rows in *D. jurassicum* **sp. n.** (Fig. 13).

Distribution and ecology. *Dictyogenus muranyii* **sp. n.** inhabits karstic springs (some of them intermittent; Fig. 52) in the French Vercors and

Figs. 54-55. *Dictyogenus alpinum*, male. **54.** Head and pronotum. Vorz River, Isère dpt, France. Photo B. Launay. **55.** Hemitergal lobes, lateral view. Vorz River, Isère dpt, France. Photo B. Launay.

Fig. 56. *Dictyogenus alpinum*, male, hemitergal lobes, dorsal view. Nant Bénin River, Savoie dpt, France. Photo B. Launay.

Chartreuse massifs (Fig. 92). The localities occurring on the south western part of the Vercors Massif belong to the Drôme watershed (main Rhône tributary); those occurring on the northern and eastern part of the Vercors Massif, and on the southern part of the Chartreuse Massif belong to the Isère watershed (main Rhône tributary), and those occurring on the western

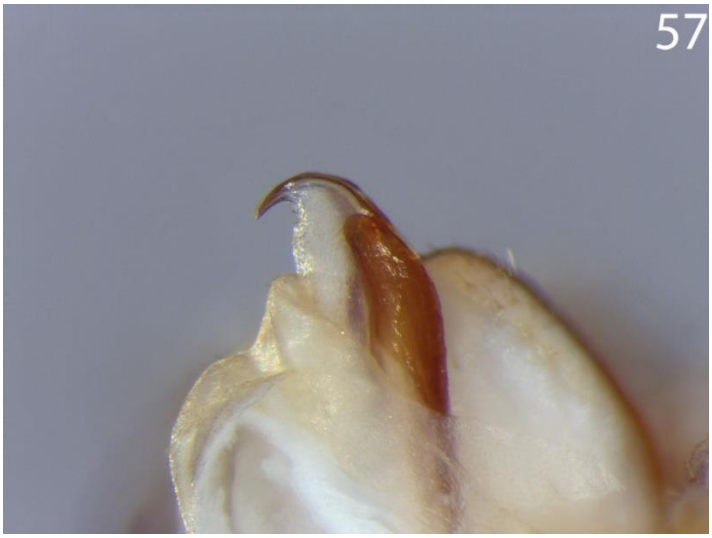


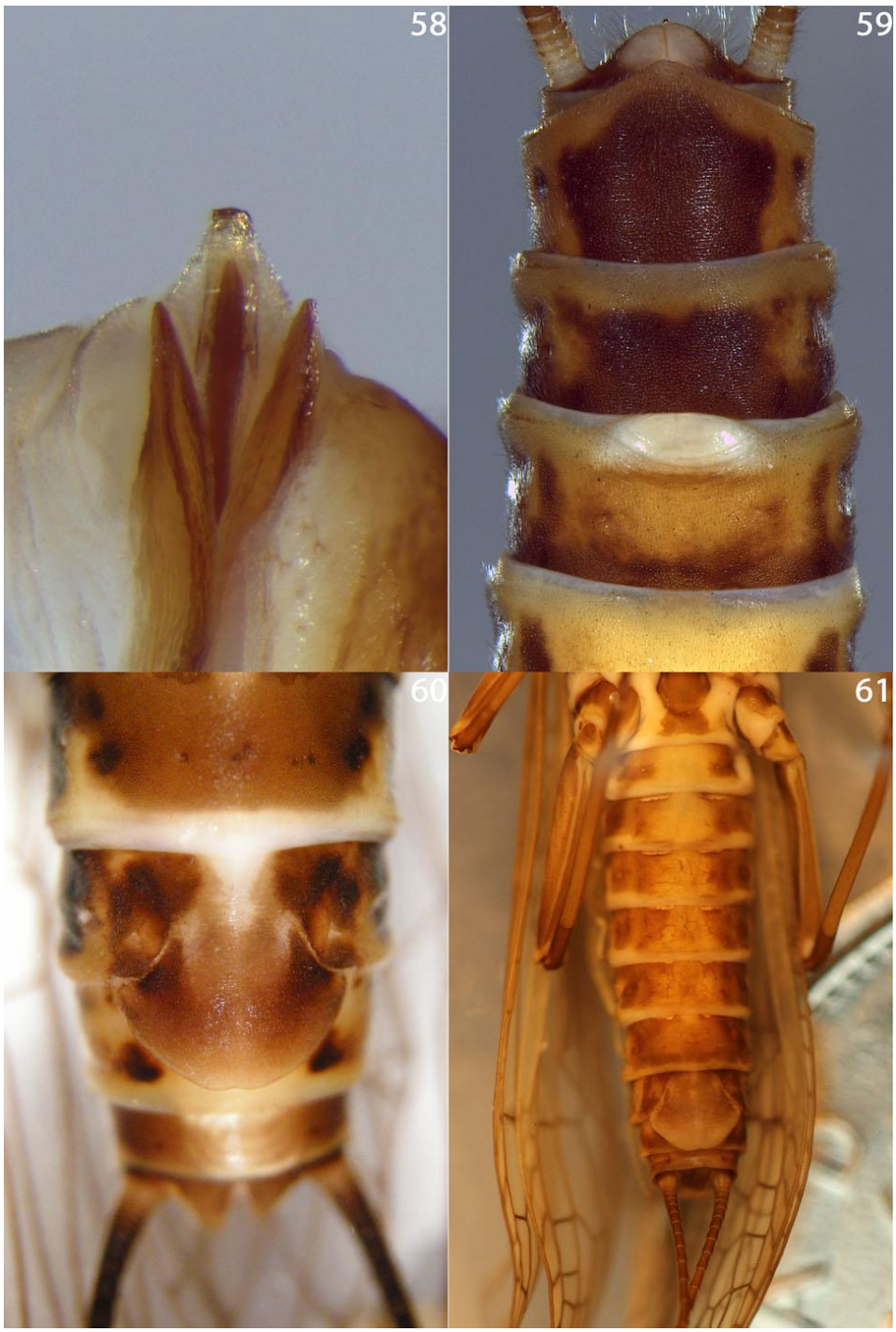
Fig. 57. *Dictyogenus alpinum*, male, epiproct, lateral view. Nant Bénin River, Savoie dpt, France. Photo B. Launay.

part of the Chartreuse Massif belong to the Guiers watershed (Rhône tributary). The life cycle of *Dictyogenus muranyii* **sp. n.** is probably similar to the one of *D. jurassicum* **sp. n.** The main emergence period of adults is in May and June, although isolated specimens occur until September. We have noted on one occasion a spectacular upstream flight of females in mid-June on the river Adouin (Fig. 53). Some of the females were ovipositing under large stones right at the spring head. Mature larvae emerge preferentially on small islets located in the middle of the river.

Etymology of *Dictyogenus muranyii* sp. n. This species is dedicated to Dr. Dávid Murányi, Hungarian Natural History Museum, Budapest, Hungary, in recognition of his outstanding contributions to the plecopteran taxonomy.

Morphological key to adults of *Dictyogenus*

1 Females ..…….. **2**
1′ Males ……..…….. **3**
2 Subgenital plate covering majority of sternum 9 (Figs. 60, 61). Macropterous (Fig. 61) ……..……. ***Dictyogenus alpinum***
2′ Subgenital plate covering at most the anterior half of sternum 9 (Figs. 9, 36, 83, 84). Macropterous or more rarely brachypterous (Fig. 78) …… ***Dictyogenus jurassicum, D. muranyii, D. fontium species complex*** **(not keyed)**
3 Hemitergal lobes separated from the inner anterior corner of each hemitergum by a wide V-shaped membranous area (Figs. 3, 29, 32, 81). Apex of frontal epiproct sclerite nearly straight in lateral view, "dagger-like" (Figs. 5, 6, 33, 80). Lateral stylets apically enlarged (Figs. 5, 6, 33, 34, 80) …….. **4**
3′ Hemitergal lobes separated from the inner anterior corner of each hemitergum by a narrow V-shaped sclerotized area (Fig. 56). Hemitergal lobes wide and bulky, hardly bent upwards, pointing almost horizontally toward each other (Fig. 56). Apex of frontal epiproct sclerite with a strong curvature in lateral view, "claw-like" (Fig. 57). Epiproct sides straight, in dorso-caudal view (Fig. 58). Lateral stylets thinning progressively toward apex (Fig. 57) …….. ***Dictyogenus alpinum***
4 Hemitergal lobes strongly bent upwards (Figs. 3, 81) …… **5**
4′ Hemitergal lobes hardly bent upwards,



Figs. 58-61. *Dictyogenus alpinum*, male and female adults. **58.** Adult male, epiproct, dorso-caudal view. Nant Bénin River, Savoie dpt, France. Photo B. Launay. **59.** Adult male, posterior margin of sternite 7 with ventral vesicle, ventral view. Nant Bénin River, Savoie dpt, France. Photo B. Launay. **60.** Female, subgenital plate, ventral view. Ristolas – Mount Viso, Queyras, Hautes-Alpes dpt, France. Photo J.-P. G. Reding. **61.** Adult female, subgenital plate, ventral view. Guiers vif, Chartreuse, Savoie dpt, France. Photo A. Ruffoni.

pointing almost horizontally toward each other (Figs. 29, 32). Hemitergal lobes more

slender, bulb-shaped with a slight distal knob (Fig. 30). Apex of frontal epiproct sclerite straight and with a median curvature, in lateral view (Fig. 33). Epiproct sides rounded, in dorso-caudal view (Fig. 35). Lateral stylets not getting thinner progressively toward apex (Figs. 33, 34) …….. ***Dictyogenus muranyii***

5 Apex of frontal epiproct sclerite straight and with a median curvature, in lateral view (Figs. 5, 6). Lateral stylets apically enlarged (Figs. 5, 6) …….. ***Dictyogenus jurassicum***

5′ Apex of frontal epiproct sclerite straight, angled posteriorly, in lateral view (Fig. 80) ……. ***Dictyogenus fontium* species complex**

Morphological key to mature larvae) (> 8 mm) of *Dictyogenus*

The larva of *Dictyogenus fontium* was first described by Kühtreiber (1931), but erroneously listed under the name of *D. alpinum*, as the same author later (1934) recognizes when providing descriptions of both species. The single major criterion used by him for separating both species hinges on the presence (*D. alpinum*) or absence (*D. fontium*) of a row of erect medio-dorsal setae on the pronotum. This criterion, however, only separates the larvae of the *Dictyogenus fontium* species complex from the group composed of *D. alpinum*, *D. jurassicum* and *D. muranyii*. As can be inferred from the descriptions of the two new species in the present contribution, the setation patterns of the medio-dorsal row of setae on the pronotum as well as on the mesonotum, metanotum and abdominal terga in the genus *Dictyogenus* are far more complex. We have also noted that early instar larvae continue to undergo important morphological changes prior to reaching 8 mm body length. Prior to this size they are impossible to identify to species.

1 Pronotum with medio-dorsal setae (Figs. 13, 40, 41, 65, 71). Postero-dorsal edge of the femora and tibiae with a fringe of dense silky hair setae (Figs. 15, 42, 70) …… **2**

1′ Pronotum devoid of medio-dorsal setae (Figs. 85, 86). Postero-dorsal edge of femora and tibiae with a fringe of sparse silky hair setae (Fig. 87) …….. ***Dictyogenus fontium* species complex (not keyed)**

2 Medio-dorsal setae on pronotum, mesonotum, metanotum and abdominal terga very long, erect, dense and continuous, extending to the occiput of the head (Figs. 65, 71). Interocellar area with a wide yellow patch, trident-shaped (Figs. 62, 63). Lateral ocelli with circum-ocellar yellow patch (Fig. 63). A large, elliptical, yellow patch above each lateral ocellus (Figs. 62, 63). M-line curved and well visible (Figs. 62, 63). Upper margin of stipes with numerous (7-25) spines arranged in several rows (Fig. 69). Pronotum markedly trapezoidal with straight sides (Fig. 63). Paragenital plates, in ventral view, with numerous spines (3-20, average 15) per side (Fig. 68). Cerci with medio-dorsal row of swimming hairs of dense and compact, twice as long as the width of the cercus (Fig. 67) …….. ***Dictyogenus alpinum***

2′ Medio-dorsal setae on pronotum, mesonotum, metanotum and abdominal terga less dense, often with interruptions (Figs. 13, 14, 15, 40, 41). Postero-medial part of head without setae, but only with a few long spines (Figs. 40, 41). Upper margin of stipes with fewer spines (1-13) arranged in a single row (Fig. 45). Paragenital plates, in ventral view, with fewer, generally unpaired, spines or else devoid of spines (Figs. 17, 44). Cerci with medio-dorsal row of swimming-hairs only slightly longer than the width of the cercus (Figs. 16, 43) …… **3**

3 Medio-dorsal setae on pronotum short and scattered, arranged as two loosely demarcated rows (Fig. 13). Interocellar area pale yellow, narrow with well demarcated contours (Figs. 10 and 11). Pronotum ovoid in shape (Fig. 11). Endemic to the Jura Mountains ..... ***Dictyogenus jurassicum***

3′ Medio-dorsal setae on pronotum longer, but dense, sometimes covering only its lower half (Figs. 40, 41). Interocellar area with wide, pale yellow, keyhole-shaped area (Fig. 37, 38).

Fig. 62. *Dictyogenus alpinum*, larva. Rioufroid, Lus-la-Croix-Haute, Drôme dpt, France. Photo A. Ruffoni.

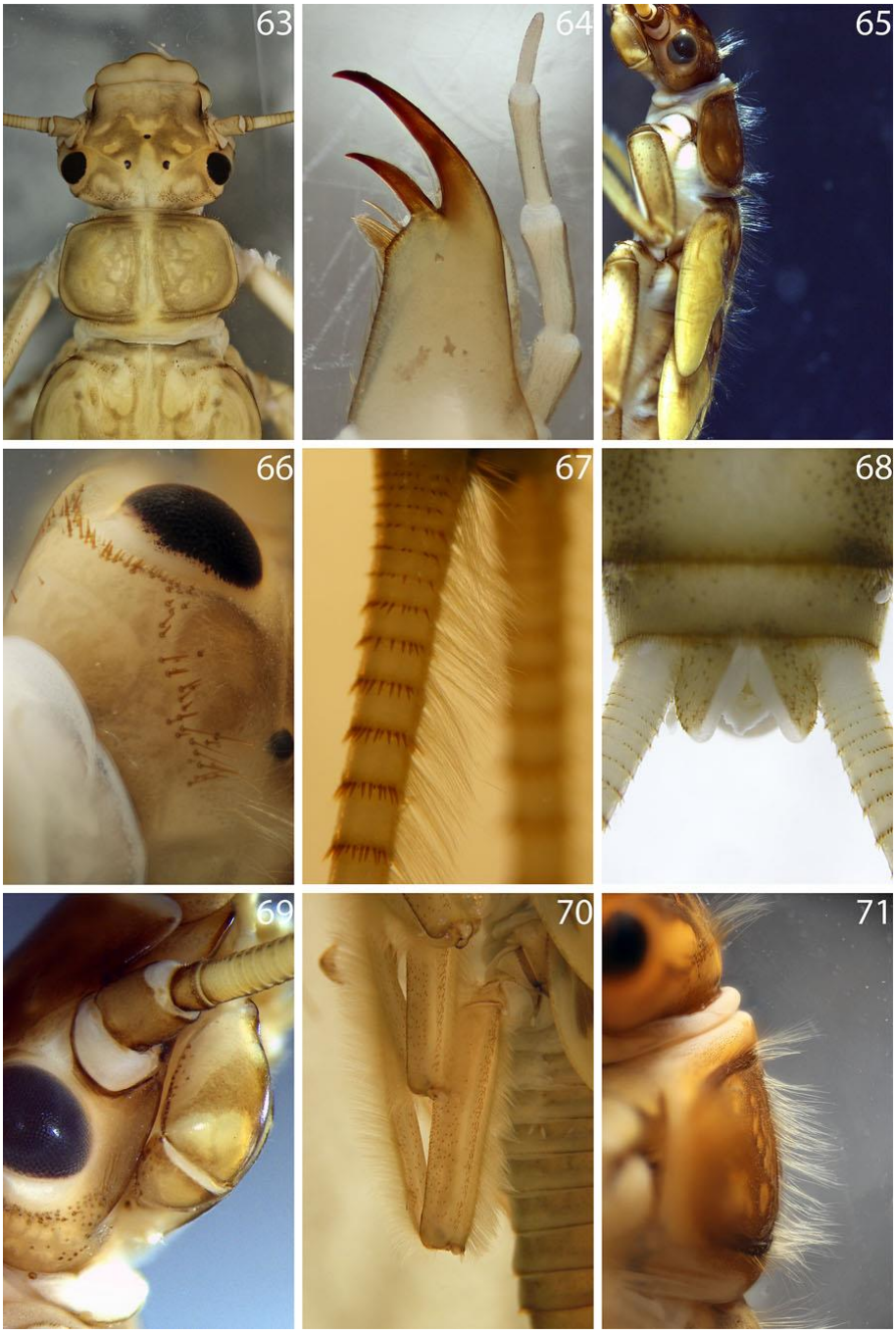
Pronotum nearly trapezoidal in shape (Figs. 37, 39). Endemic to the Chartreuse and Vercors massifs ……. ***Dictyogenus muranyii***

DISCUSSION

Egg Morphology. Eggs of *Dictyogenus* have been studied by Zwick (1971: 1147, Figs. 4b-d) and Stark *et al.* (1986: 95–96, Figs. 9–12), without aiming at a systematic intraspecific comparison. For the present study, egg characters provided the best criteria for the identification of the two new species of *Dictyogenus*. Egg ultrastructure has already been applied successfully to separate different species of *Isoperla* (Szczytko & Kondratieff 2015, Grubbs 2016, Michalik *et al.* 2017), Palearctic *Perla* (Sivec & Stark 2002) and *Perlodes* (Berthélemy 1964, Berthélemy & Laur 1975). For *Perlodes jurassicus* Aubert, 1946, it even proved to be the only reliable method for separating it from other alpine *Perlodes* (Knispel *et al.* 2002).

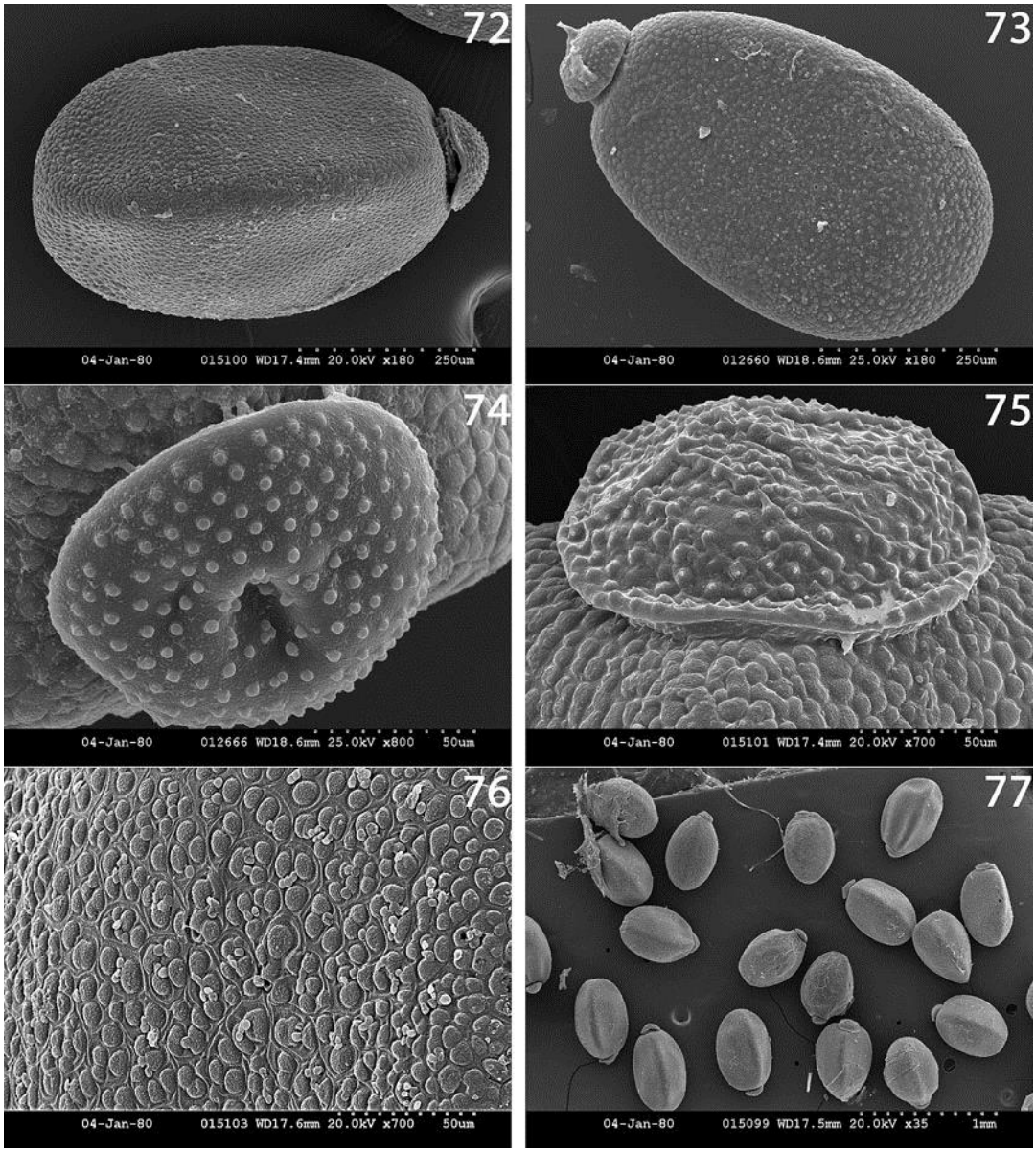
The eggs of *Dictyogenus jurassicum* **sp. n.** and *D. muranyii* **sp. n.** resemble those of *D. alpinum* by their distinct ovoid shape and their well-rounded posterior pole (Figs. 20, 21, 22, 46, 47, 72, 73, 77), but differ from those of the *D. fontium* species complex by the concave posterior pole and the cross-ridged profile of the latter (Figs. 88, 89, 90). The eggs of *Dictyogenus jurassicum* **sp. n.** are characterized by the same, grain-like aspect of the chorion (Fig. 23) as we find it also in specimens of *D. alpinum* (Figs. 73, 76; Zwick 1971: 1147, Figs. c, d), very different from the chorionic surface of *D. muranyii* **sp. n.** (Figs. 50, 51) and the one of the *D. fontium* species complex (Fig. 91). The eggs of *Dictyogenus jurassicum* **sp. n.** differ from those of all other investigated *Dictyogenus* species by their very short and flat collar (Fig. 24) and those of *D. muranyii* **sp. n.** by their polygonal follicle cell impressions (Figs. 50, 51).

Phylogeny. Maximum likelihood phylogenetic tree (Fig. 93) was run with 1000 bootstraps based on 537 base pairs of the CO-1 molecular marker. Only bootstrap values up to 50% that represent moderate to high support of nodes are shown. Phylogenetic ML tree of CO-1 mitochondrial marker strongly supports the distinctness of the two new *Dictyogenus* species and shows four separated lineages (*D. alpinum*, *D. fontium* species complex, *D. jurassicum* **sp. n.** and *D. muranyii* **sp. n.**). We used only one sequence of the *Dictyogenus fontium* species complex, from an individual



Figs. 63-71. *Dictyogenus alpinum*, larva. **63.** Head and pronotum. Rioufroid, Lus-la-Croix-Haute, Drôme dpt, France. Photo A. Ruffoni. **64.** Lacinia. Rioufroid, Lus-la-Croix-Haute, Drôme dpt, France. Photo A. Ruffoni. **65.** Pronotum, mesonotum and metanotum, lateral view. Vorz river, Belledonne massif, Isère dpt, France. Photo B. Launay. **66.** Detail of head. Rioufroid, Lus-la-Croix-Haute, Drôme dpt, France. Photo A. Ruffoni. **67.** Medio-dorsal setae on cerci. Riau du Gros Mont, Les Planeys, canton of Fribourg, Switzerland. Photo J.-P.G. Reding. **68.** Paragenital plates, ventral view. Riau du Gros Mont, Les Planeys, canton of Fribourg, Switzerland. Photo J.-P.G. Reding. **69.** Stipe. Vorz river, Belledonne massif, Isère dpt, France. Photo B. Launay. **70.** Femur and tibia of hind leg, lateral view. Riau du Gros Mont, Les Planeys, canton of Fribourg,

Switzerland. Photo J.-P.G. Reding. **71.** Pronotum, lateral view. Rioufroid, Lus-la-Croix-Haute, Drôme dpt, France. Photo A. Ruffoni.



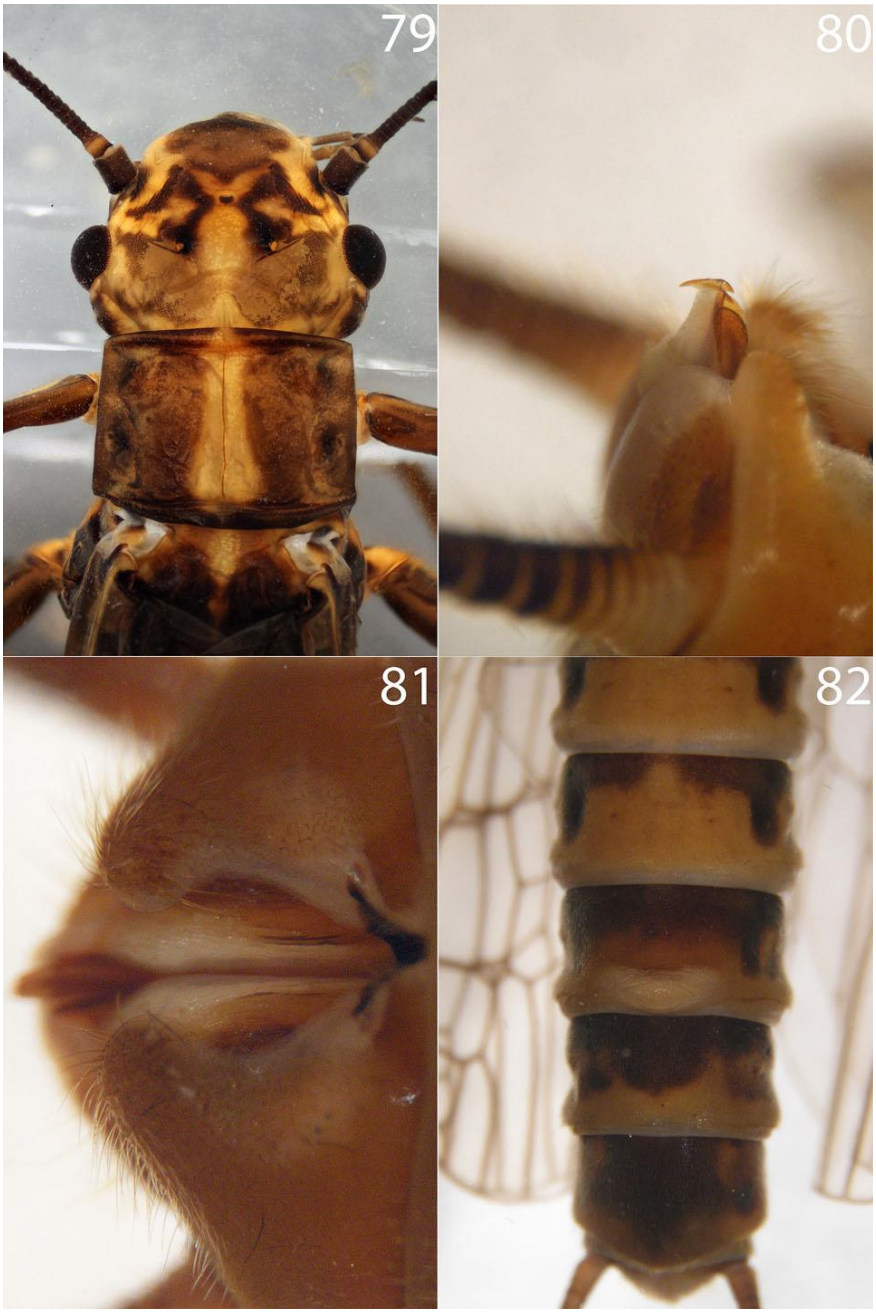
Figs. 72-77. *Dictyogenus alpinum*, egg characteristics. **72.** Egg, lateral view. Casset, Tabuc, Hautes-Alpes dpt, France. **73.** Egg, lateral view. Below Lautaret Pass, Guisanne trib., Rif torrent, 'Pont de l'Alpe', Hautes-Alpes dpt, France. **74.** Anchor. Below Lautaret Pass, Guisanne trib., Rif torrent, 'Pont de l'Alpe', Hautes-Alpes dpt, France. **75.** Anchor. Casset, Tabuc, Hautes-Alpes dpt, France. **76.** Detail of chorion and micropyles. Casset, Tabuc, Hautes-Alpes dpt, France. **77.** Eggs. Casset, Tabuc, Hautes-Alpes dpt, France.

Fig. 78. *Dictyogenus fontium* species complex, adult female habitus. Inner-alpine upper Isère Valley. Col de l'Iseran, Savoie dpt, France. Photo A. Ruffoni.

especially collected near the type locality (number GBIFCH00280144), in order to avoid confusion of with micro-endemic species in this group. The phylogenetic tree shows that *Dictyogenus alpinum* is clearly separated from the other species and supported by high bootstrap value (93%). The unique individual of the *Dictyogenus fontium* species group is also different from the two new species and separated from them with a moderate but still important bootstrap value (57%) (Douzery *et al.* 2010). The low bootstrap surely being the result of a single sequence for the species. *Dictyogenus jurassicum* **sp. n.** and *D. muranyii* **sp. n.** are clearly separated from all other species and form two monophyletic lineages, supported by high bootstraps values, respectively 88% and 77% (Hillis & Bull 1993).

Taxonomy. According to our investigations, the two new species, *Dictyogenus jurassicum* **sp. n.** and *D. muranyii* **sp. n.**, clearly stand out as two separate taxa, morphologically and genetically distinct (Fig. 93) from all other *Dictyogenus* populations examined. Whereas specimens from the northern slopes of the French and Swiss Western Alps (Fig. 92) examined by the current authors and identified as *Dictyogenus alpinum* showed only minute intraspecific morphological differences, the same was not true of those collected on the southern slopes of the Alps (Cottian, Graian, Pennine, Lepontine, Rhaetian, Julian Alps and Dolomites), and provisionally identified as *D. fontium*. From the morphological, egg ultrastructure, and also from the phylogenetic point of view, these latter specimens turned out to belong to an unresolved complex of cryptic species (unpublished research by the authors) and are presently only separable by very general traits from *Dictyogenus alpinum*, *D. jurassicum* **sp. n.** and *D. muranyii* **sp. n.**, as indicated in the proposed identification keys. The *Dictyogenus* species complex is, therefore, still in need of a general revision (already called for by Illies 1955, Zwick 1971, Zwick & Weinzierl 1995), an aim that is beyond the scope of the present work.

Distribution of the genus. Whereas *Perlodes* and *Isoperla* are widely distributed in the Palearctic ecozone, *Dictyogenus* appears to be restricted to the Alps (Illies 1955, Aubert 1963, Vinçon 1996, Zwick 2004, Zwick & Zwick 2010) and some of their foothills (Fig. 92). *Dictyogenus*, unlike *Perlodes*, *Isoperla*, *Arcynopteryx* Klapálek, 1904 or *Diura*, is absent from mountain ranges belonging to the Baltic shield or to the remains of the Hercynian orogenic belt, such as the Vosges or the Black Forest, and the genus is absent also from the Carpathian Mountains, the Pyrenees and

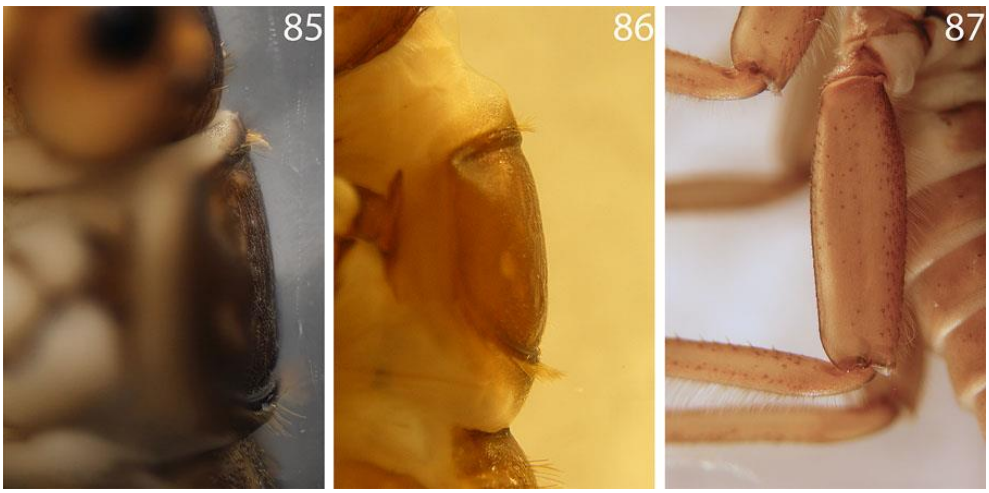


Figs. 79-82. *Dictyogenus fontium* species complex, adults. **79.** Female, head and pronotum. Inner-alpine upper Isère Valley. Col de l'Iseran, Savoie dpt, France. Photo A. Ruffoni. **80.** Adult male, epiproct with frontal apical sclerite and lateral stylet, lateral view. Julian Alps, Slovenia. Photo J.-P.G. Reding. **81.** Adult male hemitergal lobes, dorsal view. Rhaetian Alps, Switzerland. Photo J.-P.G. Reding. **82.** Adult male, posterior margin of sternite 7 with ventral vesicle, ventral view. Rhaetian Alps, Switzerland. Photo J.-P.G. Reding.

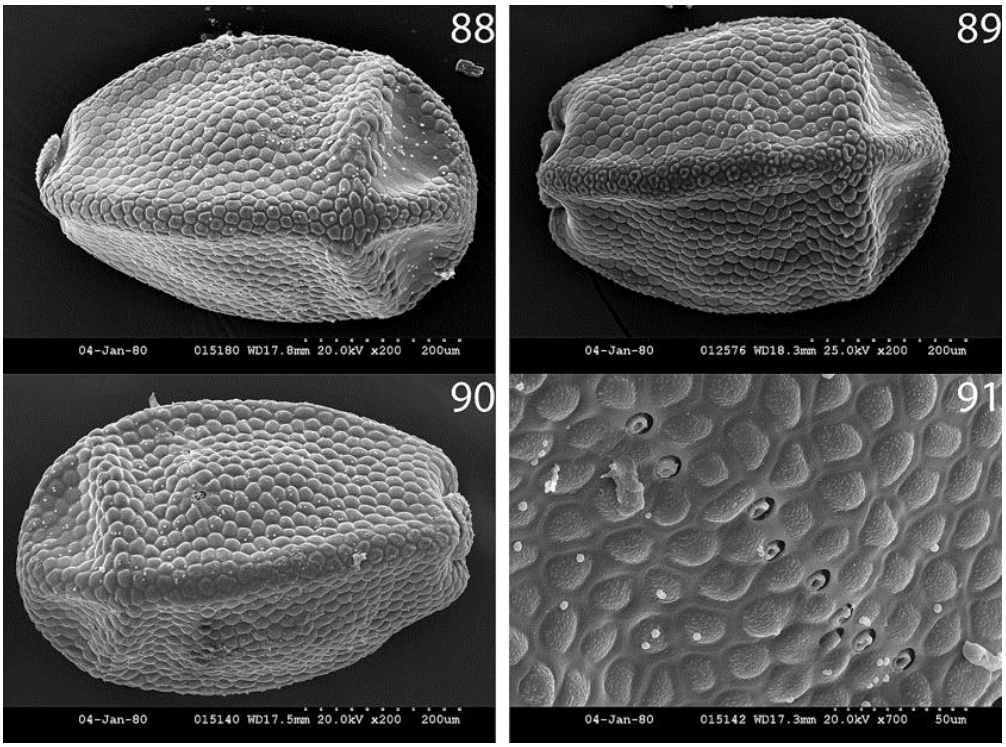
Fig. 83. *Dictyogenus fontium* species complex, female, subgenital plate. Inner-alpine upper Isère Valley. Col de l'Iseran, Savoie dpt, France. Photo A. Ruffoni.

Fig. 84. *Dictyogenus fontium* species complex, female, subgenital plate. Rhaetian Alps, Switzerland. Photo J.-P.G. Reding.

the Apennine Mountains. It is noticeable, too, that specimens belonging to the *Dictyogenus fontium* species complex are found on the southern slopes (Fig. 92) of the Alps (Cottian, Graian, Pennine, Lepontine, Rhaetian, Julian Alps and Dolomites), whereas *D. alpinum* is the only species of the genus found on the northern slopes (Fig. 92) of the Western Alps (Aubert 1989). Both taxa occur together, but not in the same biotopes, in the inner-Alpine upper Swiss Rhône and Rhine river



Figs. 85-87. *Dictyogenus fontium* species complex, larva. **85.** Pronotum, lateral view. Inner-alpine upper Isère Valley. Col de l'Iseran, Savoie dpt, France. Photo Alexandre Ruffoni. **86.** Pronotum, lateral view. Inner-alpine upper Swiss Rhône valley, Anniviers Valley, canton of Valais, Switzerland. Photo J.-P.G. Reding. **87.** Hind leg, lateral view. Inner-alpine upper Swiss Rhône valley, Anniviers Valley, canton of Valais, Switzerland. Photo J.-P.G. Reding.



Figs. 88-91. *Dictyogenus fontium* species complex, egg characteristics. **88.** Egg, upper view from one ridge with two faces and the anchor visible. Gougra, Val de Moiry, inner-Alpine upper Rhône Valley, canton of Valais, Switzerland. **89.** Egg, upper view from one ridge with two faces and the anchor visible. Campello

Monti, Verbano-Cusio-Ossola, Piedmont, Italy. **90.** Egg, upper view from one ridge with two faces and the anchor visible. Ayas Valley, tributary to Evançon torrent, Aosta, Italy. **91.** Chorionic surface and micropyles. Ayas Valley, tributary to Evançon torrent, Aosta, Italy.

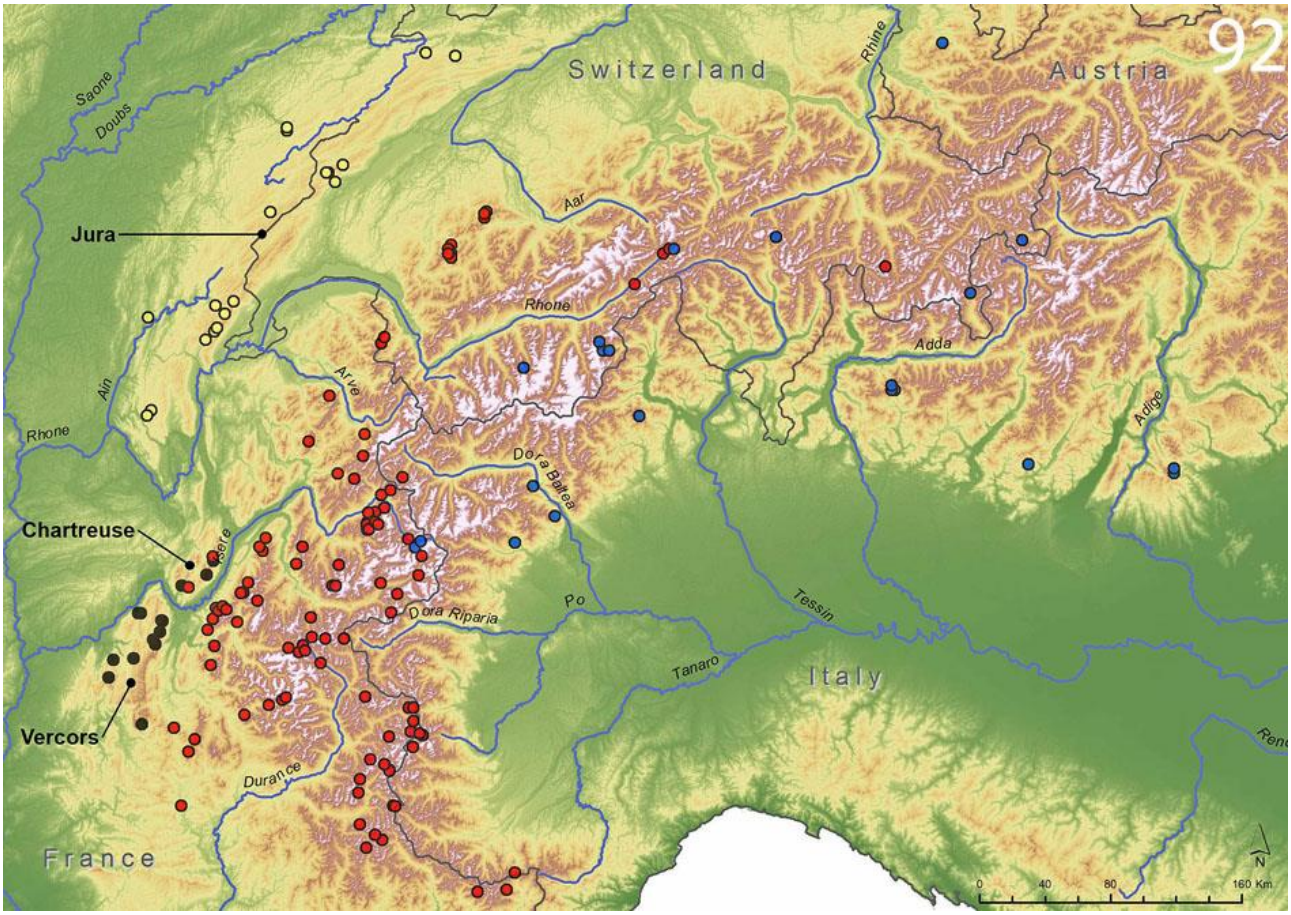


Fig. 92. Distribution map of *Dictyogenus* species in the Central and Western Alps. Legend: *Dictyogenus jurassicum*, yellow dots; *D. muranyii*, black dots; *D. alpinum*, red dots; *D. fontium* species complex, blue dots. Distribution data are those of the authors and Opie-Benthos. Map data: SRTM V4 (http://srtm.csi.cgiar.org), generated with ArcGIS version 10.3.0.4322.

valleys (Aubert 1984) and in the upper Isère valley (Aubert 1986, unpublished data of the authors). The presence of an endemic species of *Dictyogenus* in the Jura Mountains is not surprising, since this region harbors a number of other endemic species of aquatic insects, such as the ephemeropteran *Baetis nubecularis* Eaton, 1898 as well as the plecopterans *Perlodes jurassicus* and *Protonemura jurassica* Reding, Bolard & Vinçon, 2017. We have noted, furthermore, that these endemic species either preferentially or exclusively inhabit karstic springs (Fig. 26). This is also the case for *Dictyogenus jurassicum* **sp. n.** Similar observations apply to the second new species, which is also to be found in sympatry with an endemic, karstic cave-dwelling (Fig. 52), trichopteran, *Drusus spelaeus* (Ulmer, 1920).

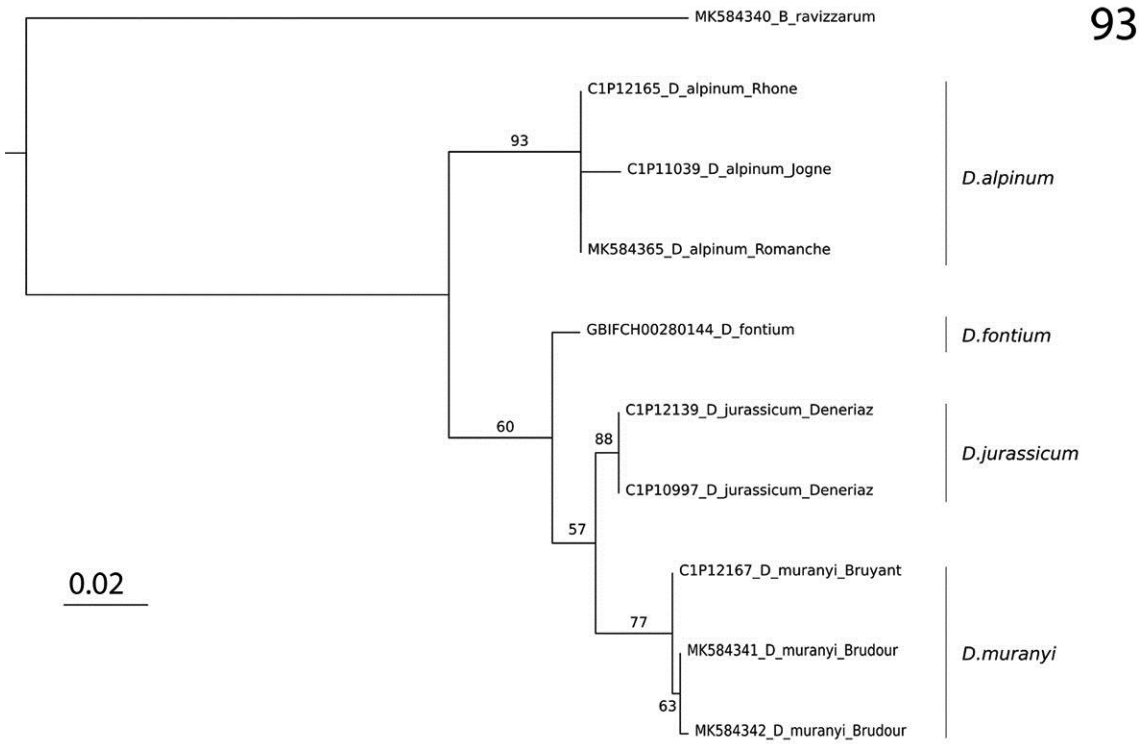


Fig. 93. Phylogenetic tree of *Dictyogenus* species. GenBank accession numbers of sequences are indicated before the code of species (start with MK).

Conservation status. Whereas *D. alpinum* and *D. fontium* are not considered as rare or threatened species (Lubini *et al.* 2012b), the same is not true of *D. jurassicum* **sp. n.** and *D. muranyii* **sp. n.** Both new species inhabit either preferentially or exclusively karstic springs (Figs. 26, 52, 53). Since the ecological integrity of karstic springs in the Jura Mountains of France and Switzerland and in the French Vercors and Chartreuse massifs is presently threatened by intensive farming and water abstraction, *D jurassicum* **sp. n.** and *D. muranyii* **sp. n.** have to be considered as facing an increased extinction risk, in spite of the fact that both the Chartreuse and the Vercors massifs have been granted the status of regional nature parks. While this article was in preparation, one of the sampling stations (Karstic spring near Albarine River, Charabotte Mill) for *Dictyogenus jurassicum* **sp. n.** has already been destroyed, due to the harnessing of the spring for water supply.

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