Published in final edited form as:

Zootaxa. 2020 June 12; 4790(3): 491–504. doi:10.11646/zootaxa.4790.3.4.

A new Drusinae species from the western Alps with comments on the subfamily and an updated key to filtering carnivore larvae of Drusinae species (Insecta: Trichoptera: Limnephilidae)

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Abstract

A new Drusinae species, *Drusus katagelastos* sp. nov., of the *Drusus chapmani* Species Complex, is described based on a male and associated larvae. Adult-larval association was achieved through DNA barcoding. The male of the new species differ from that of its congeners in the formation of the intermediate appendages and parameres. Information on the morphology of the larva is given, and important diagnostic features are discussed. In the context of filtering carnivore Drusinae, the larva of the new species can be separated from other filtering carnivore species by the dense cover of long translucent bristles within the frontal cavity surrounded by a circular corona of long bristles. *Drusus katagelastos* sp. nov. is known from only northwestern Italy (Piemonte).

Keywords

5th instar larvae; description; distribution; caddisfly

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Introduction

The limnephilid subfamily Drusinae Banks 1916 is at present presumed to comprise 177 species in two genera: *Drusus* and *Ecclisopteryx*. The genus *Drusus* purportedly contains 28 species complexes in 11 species groups, each morphologically defined based on the configuration of intermediate appendages and parameres (Oláh *et al.* 2017). Species complexes are presumed to represent distinct lineages, in which paramere structure follows a pattern of decreasing complexity. Species groups and species are defined therein based on the dorsal portion of the intermediate appendages that are conjectured to be—in combination with paramere structure—of significance for sexual selection (Oláh *et al.* 2017). Larval characters, molecular data and alternative interpretations of adult morphology on the other hand strongly support the existence of three evolutionary lineages in Drusinae (Graf *et al.* 2009; Pauls *et al.* 2008; Vitecek *et al.* 2015a). With respect to larval feeding ecology, these lineages correspond to three functional groups: shredders, grazers, and filter feeders. In contrast to net-spinning filter feeders found in annulipalpians Trichoptera families *sensu* Malm *et al.* (2013), filter-feeding Integripalpia of the genera *Allogamus* Schmid 1955, *Brachycentrus* Curtis 1834, *Drusus* Stephens 1837, and *Limnocentropus* Tsuda 1942 do not construct filtering nets, but rather employ their whole body as a filtering structure (Bohle 1983, 1987; Vitecek *et al.* 2015a). Morphological adaptations conducive to this feeding mode comprise filtering bristles on legs and sterna, elongations of leg segments, and modifications of head capsules, as observed in Drusinae. Filter-feeding Drusinae aptly make use of these organs and are reported to feed on large organic particles and drifting macrozoobenthos, such as Ephemeroptera and Chironomidae, effectively rendering them filtering carnivores (Bohle 1983, 1987).

Within Drusinae, larvae of this group are characterised by toothed mandible edges, filtering bristles on legs and abdominal sternum I, and modifications of head capsules that range from fossae to distinct concavities and may include woolly layers of flocculent-entraining hair on head and prothorax. This combination of characters delineates filtering carnivore Drusinae from omnivorous shredders and epilithic grazers that both lack filtering bristles but exhibit toothed and toothless spoon-shaped mandibles, respectively. The most recent systematic hypothesis for Drusinae ignores all larval- and molecular-based characters and transfers filtering carnivore species into two species groups based solely on paramere and intermediate appendage structure: the *Drusus discolor* Species Group *sensu* Oláh *et al.* (2017) and the *Drusus alpinus* Species Group *sensu* Oláh *et al.* (2017).

Following recent trends in Drusinae taxonomy that focus on minute differences in male terminalia, we describe a new species of the *Drusus discolor* Species Group *sensu* Oláh *et al.* (2017) together with its larva. Further, we provide an updated larval key to the species of the *Drusus discolor* Species Group *sensu* Oláh *et al.* (2017) and the *Drusus alpinus* Species Group *sensu* Oláh *et al.* (2017) that are filtering carnivores based on their morphological features.

Materials and methods

Collection and taxonomic methods

Final instar larvae were collected by one of the authors (WG) on 7 June 2013 and 20 June 2014 southwest of Fondo, Piemonte, Italy, in several springbrooks, and by authors SV and JM near Fondo (45°30' N, 07°42' E, 1584 m a.s.l.) from 11 to 18 June 2019. The larvae were collected from the substrate with forceps. A single adult male was collected by authors MS and UH on 16 April 2016 using a sweep net. This holotype will be subsequently transferred to the Insecta Varia collection of the Natural History Museum of Vienna (NHMV Holotype Number NOaS-4/2020). The material was preserved in 96% ethanol and is deposited in the collections of authors SV, WG, and JW (Lunz and Vienna, Austria). Comparative larval material of *Drusus nebulicola* (McLachlan 1867), *D. chrysotus* (Rambur 1842), *D. dudor* Oláh 2017 (in Oláh *et al.* 2017), *D. discolor* (Rambur 1842), *D. muelleri* (McLachlan 1868), *D. romanicus* Murgoci & Botosaneanu 1954, *D. puslasi* Oláh & Ibrahimi 2017 (in Oláh *et al.* 2017), *D. nigrescens* Meyer-Dür 1875, *D. macedonicus* Schmid 1956, *D. krpachi* Kucinic, Graf & Vitecek 2015 (in Vitecek *et al.* 2015b), and *D. pirinensis* Oláh & Chvojka, 2017 (in Oláh *et al.* 2017) is deposited in the collection of one of the authors (JW) (Vienna, Austria).

Nomenclature of male terminalia follows Nielsen (1957) (for *Limnephilus flavicornis* (Fabricius 1787)) using the simplifying terms “superior appendages” for the lateral processes of segment X (cerci *sensu* Snodgrass 1935), and “intermediate appendages” for the sclerite and the anterior process of segment X (paraproct *sensu* Snodgrass 1935). Illustrations were prepared according to Thomson & Holzenthal (2010) in which pencil drawings made with a drawing tube and camera lucida are digitized, edited, and “inked” in Adobe Illustrator (v. 16.0.4, Adobe Systems Inc.).

Larvae were studied and photographed using a Nikon SMZ 1500 binocular microscope with DS-Fi1 camera and NIS-elements D 3.1 image stacking software for combining 7–59 frames in one focused image. Larval morphological features and nomenclature of setal areas (= *sa*) are referred to by terminology proposed by Wiggins (1998) and Waringer and Graf (2011).

Adult-larva association

Adult larva association was achieved through sequence data of two loci fragments, one mitochondrial (mtCOI-5P, the ‘barcode’ region) and one nuclear (nuCADH), following Vitecek *et al.* (2015b). The sequence data were deposited in BOLD (SPDRU310-14).

Sequence data for the presumed sister taxa of *D. katagelastos* sp. nov. were not available.

Results

Drusus katagelastos sp. nov. Vitecek (Figures 1–5)

Material examined. Holotype. 1 male: Italy, Piemonte, Fondo; 16.iv.2016; leg. Monika Hess, Ulrich Heckes; specimen identifier: fDcm0101M.

Additional material. Four final instar larvae collected by WG on 7 June 2013 and 20 June 2014 southwest of Fondo, Piemonte, Italy; two final instar larvae collected by SV and JM near Fondo from 11 to 18 June 2019.

Diagnosis: The male of the new species is most similar to that of *Drusus letras* Oláh, 2017 (in Oláh *et al.* 2017) but exhibits (1) in lateral view a straight dorsal portion of the intermediate appendages lacking an anterior indentation, (2) in caudal view a straight dorsal section of the intermediate appendages lacking medial protuberances, (3) parameres each with a subterminal filum twice as long as the terminal spine with a somewhat dilated tip, (4) segment IX with distinct triangular medial protrusion projecting posterad, and (5) superior appendages robust and (6) shorter than inferior appendages. *Drusus letras* has an anterior indentation of the dorsal portion of the intermediate appendages in lateral view, small medial protuberances on the dorsal portion of the intermediate appendages in caudal view, parameres each with a subterminal filum that is roughly 1.5 times as long as the terminal spine, rounded posterior margins of segment IX, superior appendages slender and roughly as long as inferior appendages (Oláh *et al.* 2017).

Description. Habitus dark; head and thorax dark with pale setal areas; legs dark, somewhat lighter distally; haustellum and intersegmental integument pale, whitish with reddish sections. Wings opaque, dark, with dark setae. Length of each forewing 11.8 mm ($n = 1$), spur formula 1,2,3.

Male terminalia. Tergite VIII dark brown, glabrous; spinate area scutiform with lateral protuberances projecting posterad. Abdominal segment IX with distinct rounded and umbonal protrusion in dorsal half, projecting laterad, in caudal view about as wide dorsally as ventrally; in lateral view posterior margin on each side medially with triangular protrusion projecting posterad and preceded by indentation in the posterior half. Superior appendages in lateral view caudally elongate; length : width $\sim 2.5 : 1$, tip suboval in cross section, in dorsal view concave basomedially. Intermediate appendages in lateral view with straight, rough dorsal margin, with distinct subtriangular protrusion of caudal margin in the dorsal half, ventrolateral tips of intermediate appendages subrectangular; in dorsal view dorsal portion subtriangular with two distally diverging, rough, suboval tips; in caudal view subtriangular with straight dorsal portion. Inferior appendages in lateral view conical, robust basally, tapered to blunt apices; in ventral and dorsal views each with small median lobe separated by shallow notch from large subtriangular lateral lobe; in ventral view lateral lobe with slight elongate longitudinal groove extending from near median lobe towards tip. Parameres simple, each with crenulated terminal spine in the distal third and subterminal filum 2x as long as the terminal spine.

Etymology. From Old Greek καταγέλαστος, meaning *the absurd*, referring to the odd situation of 3 highly similar Drusinae species known from 1 male each and at most 150 km apart. The species epithet is an adjective (male/female: *katagelastos*, neutrum: *katagelaston*).

Phylogenetic placement. Phylogenetic inference through Bayesian species tree analysis suggests a nested position of *D. katagelastos* sp. nov. within filter-feeding Drusinae and a

potentially ancestral position to a clade of hirsute Drusinae filter feeders (Vitecek *et al.* 2015a).

Fifth instar larva. Body length of 5th instar larva 12.1–12.3 mm, head width 1.36–1.44 mm (n = 6).

Head. Head capsule hypognathous, mostly smooth, parietals somewhat granulate dorsally. Head capsule anteriorly concave lacking frontoclypeal median bulge, with elevated, subcircular cephalic wall formed by modified parietals and frontoclypeus (Figs 6, 7). Cephalic wall with corona consisting of more than 100 strong, straight, partly translucent, pale to brown setae 0.50–0.60 mm in length (co in Figs 6, 7). Dorsal part of frontoclypeus with dense cover of wiry, partly translucent pale to light-brown setae of 0.8 mm length and 0.01 mm thickness at their base (fs in Figs 6, 7). Two pairs of long cephalic setae present, as in all filtering carnivores (arrows in Fig. 6). Anterior portions of cephalic wall medium to dark brown, lateral parietal sections and anteroventral steep section of frontoclypeal apotome yellowish to orange brown, with dark brown muscle attachment spots. Posterior parietalia sections, ventral apotome, maxillolabial sclerites and premandibular areas yellowish to orange (Figs 6, 8). Eyes surrounded by pale ring (Fig. 6). Antennal bases (an in Fig. 6) without longitudinal carinae; each antenna consisting of one short cylindrical base and one prominent lateral seta. Ventrolateral corners of frontoclypeal apotome with eight secondary setae (ss in Fig. 6). Labrum yellowish brown, with black ventral margin and six pairs of primary setae. Ventral apotome (va in Fig. 8) cuneiform, medium brown anteriorly, yellowish brown posteriorly, postgenal suture 34% of apotome length (Fig. 8). Black mandibles fitted with three large (Fig. 6a, arrows) and two small terminal teeth (Fig. 6a, s) and with ridges in central concavity.

Thorax. Pronotum orange to medium brown and finely granulate (Figs 9, 10), its posterior margin thickened and fitted with black stripes. In lateral view, with low, evenly rounded hump in its posterior third (p in Fig. 9); two setal rows present along anterior pronotal border: i) dense fringe of short, curved, fine, yellow setae, and ii) row of widely-spaced long, straight, dark setae reaching pronotal midline (Fig. 10). Each pronotal half bearing in total 22–28 dark setae of varying lengths in addition to tiny, pale, curved, recumbent setae in low numbers. Light to median brown prosternite conspicuous, rhomboid: slightly pointed at anterior and posterior centers, with wing-like lateral sections (p in Fig. 11). Cuticle around prosternite densely covered in microspinules (Fig. 11); with pair of tiny anteroventral setae (avs in Fig. 11) and with one posteroventral seta mesal of each coxa (pvs in Fig. 11). Prosternal horn present, short (ph in Fig. 11). Mesonotal sclerites orange brown, with dark brown muscle attachment spots, black anterolateral corners and lateral and posterior borders (Fig. 9). Counts for mesonotal setae in anterior setal group *sa1*: 2–3, in posterior group *sa2*: 7–9, in lateral group *sa3*: 3–7 (*sa1*, *sa2*, *sa3* in Fig. 12). Anterior metanotal sclerites (sclerites of setal area 1, *sa1*, sensu Wiggins 1998) medium brown, with dark brown borders, large, trapezoidal, their median separation approximately as wide as their longitudinal length (*sa1* of mt in Fig. 12), each with 6–10 setae. Posteromedian sclerites (sclerites of setal area 2) medium brown, with dark brown borders, each with 6–8 setae and with 2–4 tiny setae between them (*sa2* of mt in Fig. 12). Anterior half of each lateral sclerite (sclerites of setal area 3) black, posterior half yellowish brown, with 6–9 setae concentrated in cranial section

(*sa3* of *mt* in Fig. 12); with 0–1 setae present between *sa2* and *sa3* (of *mt* in Fig. 12). Legs yellowish brown with numerous setae on coxae, trochanters, and femora, with particularly thick and elongated setae along posteroventral edges (Figs 13–15). Proximal ventral sections of trochanters with small groups of spines (e.g., Fig. 15, dotted oval). Foreleg femur much wider than those of mid- and hind legs (Fig. 13). Femora with several proximodorsal setae (e.g., Fig. 13, dotted oval), and with additional setae on anterior and posterior faces (e.g., Fig. 14, dotted oval). Forefemora each with 3 long and several short pale ventral-edge setae, mid- and hind femora each with 2 long and 2 short dark ventral-edge setae. Distal sections of foretrochanters with brushes of soft, long yellow setae (*ss* in Fig. 13). Tarsal claws sickle-shaped, pointed, with stout, yellow basal spur (Figs. 13–15).

Abdomen. Abdomen cream to white ventrally and laterally, purplish dorsally (Fig. 16). Abdominal segment I with one dorsal and pair of lateral protuberances (*dp* and *lp*, respectively in Fig. 16). Continuous transverse row of setae (some of them with small basal sclerites) present anterior of dorsal protuberance, comprising fused setal areas *sa1*, *sa2*, *sa3*, distributed to dorsal sections of lateral protuberances (Fig. 12). With small group of setae posterior of dorsal protuberance (Fig. 12). Lateral protuberances without posterior sclerites; anterior of each lateral protuberance, continuous band of anterolateral setae distributed between dorsal and ventral *sa3* setal groups (bracket in Fig. 16). Abdominal sternum I with 18–21 long, black filtering bristles with brown basal sclerites, arranged in 3 irregular transversal rows (*fb* in Figs 16, 17). Oval chloride epithelia present on sterna of abdominal segments III–VII. Abdominal segment IX with 4 ventral setae (*vs* in Fig. 18). Abdominal segments II–VIII with 2 dorsal (*ds* in Fig. 16) and 2 ventral setae (*vs* in Fig. 17), abdominal segment VIII with 2 long and 2 short posterodorsal setae (*pds* in Fig. 19). Only 1 posterolateral seta present on each half of abdominal dorsum IX (*pals* in Fig. 19). Orange brown anal prolegs of limnephilid type (Fig. 18), each lateral sclerite with 5 dark dorsal and row of 5 dark ventral setae, 4 of latter group very strong and prominent. Ventral sole plate with black dorsal stripe and single anterior seta (*sp* in Fig. 18). Anal claw orange, with 1 small dorsal accessory hook (*ac* in Fig. 18). Abdominal dorsum IX with orange brown, semicircular sclerite with medium brown muscle attachment spots; along its posterior border with 6 long and several short setae including short C setae (Fig. 19). All gills as single filaments. Dorsal gills present at most from abdominal segment II (presegmental position) to VII (postsegmental position); ventral gills present from abdominal segments II (postsegmental position) to VII (postsegmental position); lateral gills absent. Lateral fringe extending from mid-segment III (*f* in Fig. 16) to mid-segment VIII (*f* in Fig. 18) and with 1–6 forked lamellae on each of same segments.

Case. Larval case 12.7–13.9 mm long ($n = 6$) consisting mostly of mineral particles (quartz grains and mica flakes of mixed size; Fig. 20), with dorsally attached organic particles in some specimens; almost straight, slightly conical (width at anterior opening 3.5 mm and at posterior opening 2.5 mm); posterior end partly closed by silken membrane, with circular foramen 0.7 mm in diameter (Fig. 21).

Morphological separation of 5th instar larva of *Drusus katagelastos* from those of other European Trichoptera

Larvae of subfamily Drusinae are separated from those of other Trichoptera species by the following characters (Waringer & Graf 2013):

- sclerites present on pro-, meso- and metanota; mesonotum completely covered by 2 sclerites in close contact mesally, separated by straight suture; metanotum with 6 separate sclerites (Figs 9, 12);
- prosternal horn present (ph in Fig. 11);
- fleshy protuberances of abdominal segment I present dorsally and ventrally (dp, lp in Fig. 16);
- gills each consisting of single filament only;
- transverse groove (typical for other limnephilids with single filament-gills) lacking in anterior 3rd of pronotum (Fig. 9) except in *Drusus budtzi* (Ulmer, 1913).

Within the framework of the ‘Master key for main groups of larval Drusinae (final instars)’ (Key 1 of the present paper), *Drusus katagelastos* belongs to the filtering carnivore Drusinae. Information for the identification of the hitherto known ten species of this group is given in Key 2 of the present paper.

Key 1: Key to main groups of Drusinae larvae (final instars)

- 1 Mandibles with terminal teeth along edges (Fig. 6a).....
..... 2
- Mandibles lacking terminal teeth along edges (m in Fig. 22)
...
..... **epilithic grazer**
- 2 With filtering bristles on legs (dotted oval in Fig. 23) and abdominal sternum I (fb in Fig. 23); head capsules modified (Figs 26–28)
..... **filtering carnivore**
(Key 2)
- Without filtering bristles on legs and abdominal sternum I (Fig. 24); head capsules unmodified (Fig. 22)
omnivorous shredder

Key 2. Final instar larvae of Drusinae filtering carnivore species, with information on distribution

- 1 Prosternal horn absent; head with ridge forming ring anterodorsally (Fig. 26)
..... *Drusus chrysotus* (Austria, Czech Republic, Germany, Italy, Switzerland)*

- Prosternal horn present (ph in Fig. 11); head with or without ridge
.....
... 2
- 2 Head capsule with neither corona of long bristles nor flocculent hair cover (Figs 25, 28) 3
- Head capsule with corona of long bristles (Fig. 6) or flocculent hair cover (Fig. 27)
.....
.... 4
- 3 Head capsule rounded, with shallow depressions on both sides of frontal midline (d in Fig. 25)..... *Drusus nebulicola* (Austria, France, Italy, Switzerland)
- Dorsal head surface flattened (Fig. 28) *Drusus muelleri* (France, Switzerland)
- 4 Head capsule with dense cover of long translucent bristles surrounded by circular corona of long bristles; coronal bristles (co in Fig. 6) approximately half as long as sensory bristles (arrow in Fig. 6) (Figs 6, 7) .. *Drusus katagelastos* sp. nov. (Italy)
- Head capsule with flocculent cover of short hairs (Fig. 27); coronal bristles (co in Fig. 23) much shorter than sensory bristles (arrow in Fig. 23); **for further identification, remove hair cover**
..... 5
- 5 Central plate of frontoclypeal apotome (cp in Fig. 30) with two pairs of lateral arms: one pair of anterolateral arms (al in Fig. 30) and one pair of posterolateral arms (pl in Fig. 30)
..... 6
- Central plate of frontoclypeal apotome with only one pair of lateral arms (l in Fig. 33) or without lateral arms (Fig. 32)
.....
.... 8
- 6 Anterolateral arms of frontoclypeal central plate extending to parietalia (al in Fig. 29)
..... *Drusus romanicus* (Rumania)
- Anterolateral arms not extending to parietalia (al in Fig. 30)
..... 7
- 7 Central plate 1.25 X as long as wide; width at posterolateral arm base wider than at posterior arm base (dotted line angled in Fig. 30)

- *Drusus discolor*
(widespread)
- Central plate 1.4 X as long as wide; width at posterolateral arm base and
posterior arm base equal (dotted line longitudinal in Fig. 31)
..... *Drusus puskasi*
(Bosnia & Herzegovina)
- 8 Central plate of frontoclypeal apotome without lateral arms (Fig. 32)
..... *Drusus macedonicus*
(Macedonia)
- Central plate of frontoclypeal apotome with one pair of lateral arms (1 in Figs
33, 34)..... 9
- 9 Lateral arms far posterior of central constriction of frontoclypeal apotome (1 in
Fig. 33) *Drusus krpachi*
(Macedonia)
- Lateral arms close to central constriction of frontoclypeal apotome (1 in Fig. 34)
..... *Drusus pirinensis*
(Bulgaria)

**D. lapos* Oláh 2017 (in Oláh *et al.* 2017) is morphologically nearly indistinguishable from *D. chrysotus*. Its status as a distinct species is questionable.

Discussion

Systematic and geographical position of *Drusus katagelastos*

In the revision of subfamily Drusinae by Oláh *et al.* (2017), only genera *Drusus* and *Ecclisopteryx* Kolenati 1848 were retained. In the framework of that revision, based solely on male genital morphology, but ignoring molecular, larval, and other adult characters, taxa were organized into 'species groups' and 'species complexes', and former species were split into 'sibling groups.' Within this framework, *D. katagelastos* sp. nov. is sister to *D. letas* and belongs, together with the latter species and *D. chapmani* McLachlan 1901, to the *Drusus chapmani* Species Complex.

As concerns feeding ecology, characters of *D. katagelastos* larvae indicate a filtering carnivore lifestyle, an interpretation corroborated by phylogenetic reconstruction that places *D. katagelastos* among filter-feeding Drusinae (Vitecek *et al.* 2015a). Extrapolating from the high similarity in their male terminalia, it is likely that the unknown larvae of *D. letas* and *D. chapmani* follow that pattern. However, whether these larvae would in fact have distinguishing characters remains to be explored.

Unfortunately, no sequence data from neither *D. letas* nor *D. chapmani* was available for comparisons. Therefore, we cannot entirely exclude the possibility that the larva described herein could belong to either of these species. However, taking the perfectly identical partial sequence data of the *D. katagelastos* male and the larval specimen into account we are

confident that our assignment is correct. Also, we surmise that the supposedly highly localized occurrence of *D. letras* and *D. chapmani* results in a very low probability of an erroneous adult-larva association.

Species of the *Drusus chapmani* Species Complex are seemingly restricted to a small region in the Western Alps, to our current knowledge ranging from Bergamo (*D. chapmani*) to the Piemonte (*D. letras* in Viona near Biella, *D. katagelastos* in Fondo) (Oláh *et al.* 2017). The holotype locality of *D. chapmani* is in Switzerland (around Locarno), but recent faunistic data confirming its occurrence there are missing. Currently, the easternmost species is *D. chapmani*, whereas *D. katagelastos* is the westernmost known taxon in the group, comprising the historical collection site of *D. chapmani*.

Comments on the Drusinae subfamily

The Drusinae subfamily is among the best studied Trichoptera groups, with ample ecological, morphological, and genomic data available. Fernand Schmid proposed an initial set of genera that later were extended to classify Drusinae species (Schmid 1956, Sipahiler 2002). These were, in part, challenged by molecular phylogenetics and found inadequate (Pauls *et al.* 2008). In particular, all genera tested were found to be para- to polyphyletic, which was later corroborated in a broader analysis (Vitecek *et al.* 2015a). At the same time, these analyses suggested the continuance of three evolutionary lineages, each defined by morphological, molecular, and ecological traits, but no systematic hypotheses were put forward (Pauls *et al.* 2008, Graf *et al.* 2009, Vitecek *et al.* 2015a).

The systematic hypothesis proposed for Drusinae in the latest revision of the subfamily (Oláh *et al.* 2017) contrastingly focuses on two character complexes of the male genitalia: the parameres and the intermediate appendage. Based on these characters Oláh *et al.* proposed to summarize all Drusinae genera (with the exception of *Ecclisopteryx*) in the genus *Drusus*, assigned neotypes and described sets of new species based on minute deviations (Oláh *et al.* 2017). The thorough application of this approach forced us to describe *D. katagelastos*, as we could not identify an already known *Drusus* species to which our specimen could possibly correspond. This now leads to the situation that the *Drusus chapmani* Species Complex comprises three species with the same flight period (April–May), that each are known from a single male, and that they are, geographically, at most 150 km apart. Indeed, *D. letras* and *D. katagelastos* could be synonyms of *D. chapmani*. Integrating larval characters to assess species boundaries and resolve this taxonomic maze would be highly important: Our experience shows that Drusinae species are not only discernible in the adult stage, but as readily as larvae (e.g., Previšić *et al.* 2014).

It remains a terrific philosophical question whether to refrain from naming a new species while awaiting additional data (as recommended by one of the reviewers of this paper) or to name a new species now in order to stimulate future molecular, morphological, geographical, and biological research. The latter is our chosen course of action.

Acknowledgements

We are grateful to John C. Morse, Kjell A. Johanson and an anonymous reviewer for their helpful comments concerning this manuscript. This paper is part of the project “Intricate bodies in the boundary layer” (project number P31258-B29, PIs: J. Waringer, H. C. Kuhlmann) funded by the Austrian Science Fund (FWF).

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Figures 1–5.

Drusus katagelastos **sp. nov.**, male terminalia. **1**, left lateral view; **2**, caudal view; **3**, paramere (paired); **4**, dorsal view; **5**, ventral view. Abbreviations: VIII = abdominal segment VIII; IX = abdominal segment IX; X-sa = superior appendage (paired); X-ia = intermediate appendage (paired); IA = inferior appendage (paired). Scale bar: 1.0 mm. Del. Vitecek.

Figures 6–11.

Drusus katagelastos sp. nov. 5th instar larva. **6**, head, right lateral (a = antenna; co = corona; fs = felted setae; m = mandible; arrows = two sensory setae; ss = secondary setae); **6a**, detail of right mandible, lateral; **7**, head, frontal (co = corona; fs = felted setae); **8**, head, ventral (va = ventral apotome); **9**, pronotum, right lateral (p = pronotum); **10**, pronotum, dorsal (p = pronotum); **11**, pro- and mesosterna, ventral (avs = anteroventral setae; p = prosternite; ph = prosternal horn; pvs = posteroventral setae). Scale bars: 0.5 mm.

Figures 12–18.

Drusus katagelastos sp. nov., 5th instar larva. **12**, thorax and abdominal segment I, dorsal (ms = mesonotum; mt = metanotum; sa1–sa3 = setal areas 1–3; **13**, right foreleg, anterior (ss = soft setae; dotted oval = proximodorsal setae); **14**, right midleg, anterior (dotted oval = face setae on femur); **15**, right hind leg, anterior (dotted oval = ventral spines on proximal section of trochanter); **16**, metathorax and abdominal segments I–III, right lateral (ds = dorsal seta; dp = dorsal protuberance; f = beginning of lateral fringe; fb = filtering bristles; lp = lateral protuberance); **17**, sternum of abdominal segment I, ventral (fb = filtering

bristles; vs = ventral seta); **18**, abdominal segments VIII, IX, and tip of abdomen, right lateral (ac = anal claw; f = ending of lateral fringe; sp = ventral sole plate; vs = ventral setae). Scale bars: 0.5 mm.

Figures 19–24.

Drusinae, 5th instar larvae. **19–21**, *Drusus katagelastos* sp. nov. and larval case: **19**, abdominal terga VII, VIII, IX, and tip of abdomen, dorsal (c = central intermediate ‘c’ seta; ds = pair of dorsal setae of tergum VII; pds and arrows = posterodorsal setae of tergum VIII; pls = posterolateral seta of tergum IX—paired); **20**, case, right lateral; **21**, tip of case, posterior. **22**, *Drusus nigrescens* Meyer-Dür1875, head and pronotum, right anterolateral (m = mandible). **23**, *Drusus macedonicus* Schmid 1956, head, thorax and abdominal sternum I, ventral (co = corona; fb = filtering bristles on abdominal sternum I; arrow = sensory seta;

dotted oval = filtering bristles on legs). **24**, *Drusus dudor* Oláh 2017, abdominal sternum I, ventral. Scale bars: 0.5 mm.

Figures 25–30.

Drusinae, 5th instar larvae. **25–28**, heads: **25**, *Drusus nebulicola* (McLachlan 1867), right anterolateral (d = depressions on frontoclypeal apotome); **26**, *Drusus chrysotus* (Rambur 1842), right anterolateral (s = steep anterior step of frontoclypeal apotome); **27**, *Drusus discolor* (Rambur 1842), right lateral; **28**, *Drusus muelleri* (McLachlan 1868), right anterolateral. **29–30**, heads dorsal, hair cover removed: **29**, *Drusus romanicus* Murgoci & Botosaneanu 1954 (a = anterior arm; al = anterolateral arm); **30**, *Drusus discolor* (Rambur 1842) (a = anterior arm; al = anterolateral arm; cp = central plate; p = posterior arm; pl =

posterolateral arm; dotted line = decreasing central plate width in posterior direction). Scale bars: 0.5 mm.

Figures 31–34.

Heads, dorsal, hair cover removed. **31**, *Drusus puskasi* Oláh & Ibrahimi 2017 (in Oláh *et al.* 2017) (a = anterior arm; al = anterolateral arm; cp = central plate; p = posterior arm; pl = posterolateral arm; dotted line = central plate width not decreasing in posterior direction); **32**, *Drusus macedonicus* Schmid 1956; **33**, *Drusus krpachi* Kucinic, Graf & Vitecek 2015 (in Vitecek *et al.* 2015b) (l = lateral arm); **34**, *Drusus pirinensis* Oláh & Chvojka 2017 (l = lateral arm). Scale bars: 0.5 mm.