

## New ecological notes on the freshwater chrysophycean alga *Hydrurus foetidus* (Chrysophyceae, Heterokontophyta): a study from Serbia (Southeast Europe)

by

Aleksandra B. Rakonjac<sup>1,2,\*</sup>,  
Snežana B. Simić<sup>2</sup>

DOI: <https://doi.org/10.26881/oahs-2024.4.05>

Category: **Original research paper**

Received: **January 23, 2024**

Accepted: **June 14, 2024**

<sup>1</sup>Institute for Vegetable Crops, Karađorđeva 71,  
11420 Smederevska Palanka, Serbia

<sup>2</sup>University of Kragujevac, Faculty of Science,  
Department of Biology and Ecology, Radoja  
Domanovića 12, 34000 Kragujevac, Serbia

### Abstract

*Hydrurus foetidus* (Chrysophyceae, Ochrophyta) is a freshwater benthic alga that appears as a mucilaginous, filamentous thallus. It is geographically widespread but restricted to cold waters, with optimal temperatures for growth between 2°C and 12°C. The lethal temperature for this alga is 16°C. This paper reports the second occurrence of *H. foetidus* in waters with temperatures much above the recorded lethal temperature. In addition, we describe the non-obligate *Hydrurus-Paralemanea* association for the first time, with *Paralemanea* being a substrate for *Hydrurus* growth. This non-obligate association may be a strategy for the species' survival during the summer season or the species' response to climate change. Furthermore, we present co-occurring macroalgae, with special emphasis on the first finding of the rare freshwater chrysophycean alga *Phaeodermatium rivulare* in Serbian aquatic ecosystems.

**Key words:** ecology, temperature, *Phaeodermatium*, *Paralemanea*, *Hydrurus-Paralemanea*, distribution

\* Corresponding author: [aleksandra.mitrovic@pmf.kg.ac.rs](mailto:aleksandra.mitrovic@pmf.kg.ac.rs)

## 1. Introduction

Chrysophycean algae are predominantly microscopic single cells or colonial plankton, with several benthic macroscopic representatives (Kristiansen 2005; Klaveness et al. 2011; Nicholls, Wujek 2015). One of the atypical benthic macroscopic members is the freshwater alga *Hydrurus foetidus* (Villars) Trevisan, clearly visible to the naked eye and easily recognizable by its brown mucilaginous thalli (Kristiansen 2005; Klaveness et al. 2011; Nicholls, Wujek 2015; Klaveness 2017; 2019).

According to Bursa (1934), Canter-Lund & Lund (1995) and Klaveness (2017), *H. foetidus* is widely distributed in the northern hemisphere (Guiry, Guiry 2024), but restricted to cold waters. Its occurrence is associated with polar areas, periglacial, and alpine rivers (Rott et al. 2006a; Rott, Schneider 2014; Klaveness 2019), with a large number of records in glacial rheocrenic springs (Rott et al. 2000; Cantonati et al. 2012; 2016). *Hydrurus foetidus* is widely distributed in climates with defined seasons, where it can be found in late winter and early spring, the time of the year when competing algae have not yet developed (Rott et al. 2006b). The early appearance of *H. foetidus* is ecologically important as a food resource for aquatic insects and as a substrate for the growth of bacteria, protozoa, and chironomids (Milner et al. 2001; 2009; Rott et al. 2006b; Zah et al. 2001; Niedrist, Füreder 2018). As temperature increases, competing algae and macroinvertebrate predators can easily dominate over the riverbed, so *H. foetidus* can be difficult to spot during the summer season (Rott et al. 2006b). In spring environments, the seasonality of *H. foetidus* is less pronounced than in mountain streams and rivers. According to Cantonati et al. (2016), the stability of the crenon provides sustainable conditions for algal communities, resulting in the fact that *H. foetidus* never disappears in spring environments, but continuously colonizes the epilithic substrate throughout the year.

*Hydrurus foetidus* is a cold-water stenothermic species whose optimal growth temperature is between 2°C and 12°C (Bursa 1934; Kristiansen 2005; Nicholls, Wujek 2015). It has also been reported as a psychrophile, found under glacial conditions, but until recently not at temperatures above 16°C (Bursa 1934; Kann 1978; Canter-Lund, Lund 1995; Remias et al. 2013; Klaveness 2019). Although this temperature seems to be lethal for the species (Bursa 1934; Kann 1978), a recent study showed that the species can occur in water temperatures up to 19.9°C (Mašić et al. 2020). The highest temperature at which this species has been previously found in Serbia was 14°C (Simić 2002; Simić, Simić 2003; Simić et al. 2003; Krizmanić et al. 2008).

According to Bursa (1934), Kann (1978) and Canter-Lund & Lund (1995), when the water temperature rises to 16°C in the summer months, the thalli begin to decay, some cells form cysts, many probably die, and the thalli disappear. As temperatures drop in autumn, *H. foetidus* populations start to recover and can reach high abundance in a very short time (Uehlinger et al. 1998; Kristiansen 2005). *Hydrurus foetidus* is a rheophilic species resisting strong current velocities by forming mucilaginous colonies on the epilithic substrate (Traaen, Linstrøm 1983; Rott et al. 1999; Simić 2002; Krizmanić et al. 2008). According to Rott et al. (2000) and Kawecka (2003), the species is not inhibited by light, but its relative abundance drastically decreases in the shade.

It has been observed that *H. foetidus* occurs in a wide range of morphological forms (Klaveness 2019). The pronounced phenotypic plasticity, reported by many authors, may be determined by environmental parameters and may represent ecotypes, homologous or cryptic species. However, this question is still unresolved (Klaveness et al. 2011; Klaveness 2019).

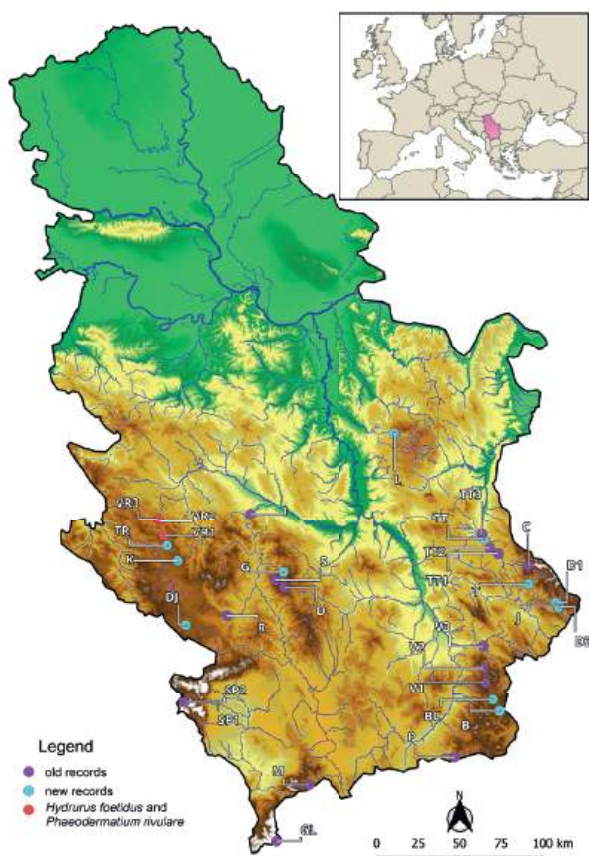
This paper aims to present the diversity in phenotypic expression of different populations of the macroscopic benthic alga *H. foetidus* in Serbian aquatic ecosystems and the ecological circumstances under which it occurs, along with notes on associated macroalgae. Special emphasis was placed on describing its growth at temperatures well above the presumed lethal temperature. Furthermore, we aimed to describe the non-obligate *Hydrurus-Paralemanea* association.

## 2. Materials and methods

### 2.1. Study area

The Republic of Serbia is a country located in Southeastern Europe (Fig. 1: A), lying between 41°N and 47°N, and 18°E and 23°E, covering an area of 88 361 km<sup>2</sup>. Serbia has an extremely complex geological structure encompassing granite, metamorphic rocks, limestone, serpentine, andesite, shells, sandstone, etc. The topographic relief of the country is predominantly mountainous: the Dinaric Alps in the west and southwest, the Carpathians in the northeast, the Balkan Mountains in the southeast, the Rila-Rhodope Mountains in the southeast corner, with the exception of alluvial plains and the isolated lowland mountains of the Pannonian Basin in the north of the country (Schmid et al. 2008). The majority of Serbia's territory, about 65%, is situated between 500 and 1000 m above sea level, with 10% exceeding 1000 m ASL and 15 mountain peaks rising above 2000 m ASL.





**Figure 1**

Geographical location of *Hydrurus foetidus* and *Phaeodermatium rivulare* sites in Serbia. • new records of *H. foetidus*: Trgoviški Timok River (TT), Lisinska River (L), Božica River (B), Božica channel (BC), Djerekarska River (DJ), Trudovačka River (TR), Gobeljska River (G), Temštica River (T), Kladnica River (K), Jelovička River (J), Dojkinačka River (D1, D2); • new records of *H. foetidus* and *Ph. rivulare*: Veliki Rzav River (VR1, VR2, VR3); • old records of *H. foetidus*: Trgoviški Timok River (TT1, TT2, TT3), Vlasina River (V1, V2, V3), Ibar River (I), Raška River (R), Pčinja River (P), Crnovrška River (C), Samokovska River (S), Duboka River (D), Muržica Brook (M), spring bellow Lake Dreljsko 1 (SP1), spring bellow Lake Dreljsko 2 (SP2), Lake Ginevodno (GL).

## 2.2. Sample collection

Field studies were performed from March 2017 to September 2023, covering 421 localities and 200 Serbian watercourses, excluding the Pannonian Basin. Benthic macroalgae were collected from various substrates at a depth ranging from 0 to 50 cm and immediately preserved with 4% formaldehyde

solution. Coverage (1–100%) was assessed visually along 100 m of a riverbed following Necchi & Moreira (1995) and Rodriguez et al. (2007). All collected samples are deposited in the collection of the Department of Biology and Ecology, Faculty of Science, University of Kragujevac, Serbia.

## 2.3. Microscopic observation and species identification

Morphological analysis of the collected algal samples was carried out under a light microscope (Motic BA310) with magnification up to 800 $\times$ , photographed using a Bresser (9MP) digital camera and MicroCamLab computer software, and identified according to John et al. (2011), Eloranta et al. (2011), Komárek (2013), Wehr et al. (2015), Necchi & Vis (2021), and Vis & Necchi (2021).

## 2.4. Ecological conditions of the environment

The type of substrate, current velocity ( $\text{m s}^{-1}$ ), water depth at which the species was found (cm), and shade degree were determined at each sampling location. Shade degree was assessed by visual analysis using the following scale: + full shade, ++ partial shade, +++ full sunlight. In addition, physical and chemical parameters of water were measured *in situ* in accordance with the American Public Health Association (2005). Water temperature ( $^{\circ}\text{C}$ ), pH, conductivity ( $\mu\text{S cm}^{-1}$ ), and water hardness ( $\text{mg l}^{-1}$ ) were measured using a Hanna Combo HI98129 portable multimeter, dissolved oxygen ( $\text{O}_2$ ) ( $\text{mg l}^{-1}$ ) was measured using a Mettler Toledo Dissolved Oxygen Electrode, while ammonium-ion ( $\text{NH}_4\text{-N}$ ) ( $\text{mg l}^{-1}$ ), nitrate-nitrogen ( $\text{NO}_3\text{-N}$ ) ( $\text{mg l}^{-1}$ ), and orthophosphate ( $\text{PO}_4\text{-P}$ ) ( $\text{mg l}^{-1}$ ) concentrations were measured using an AL400 photometer.

## 3. Results

Populations of *H. foetidus* were observed at 15 localities in 12 rivers (Fig. 1) in April (1 locality), May (4 localities), June (3 localities), July (3 localities), and August (4 localities) (Table 1). All of them represent new records for the territory of Serbia. Geographical coordinates and environmental conditions of *H. foetidus* localities are summarized in Table 1.

### 3.1. Morphological features

Variations in phenotypic expression of different populations were observed (Fig. 2A–D). Brown mucilaginous mosslike colonies were found in the

Table 1

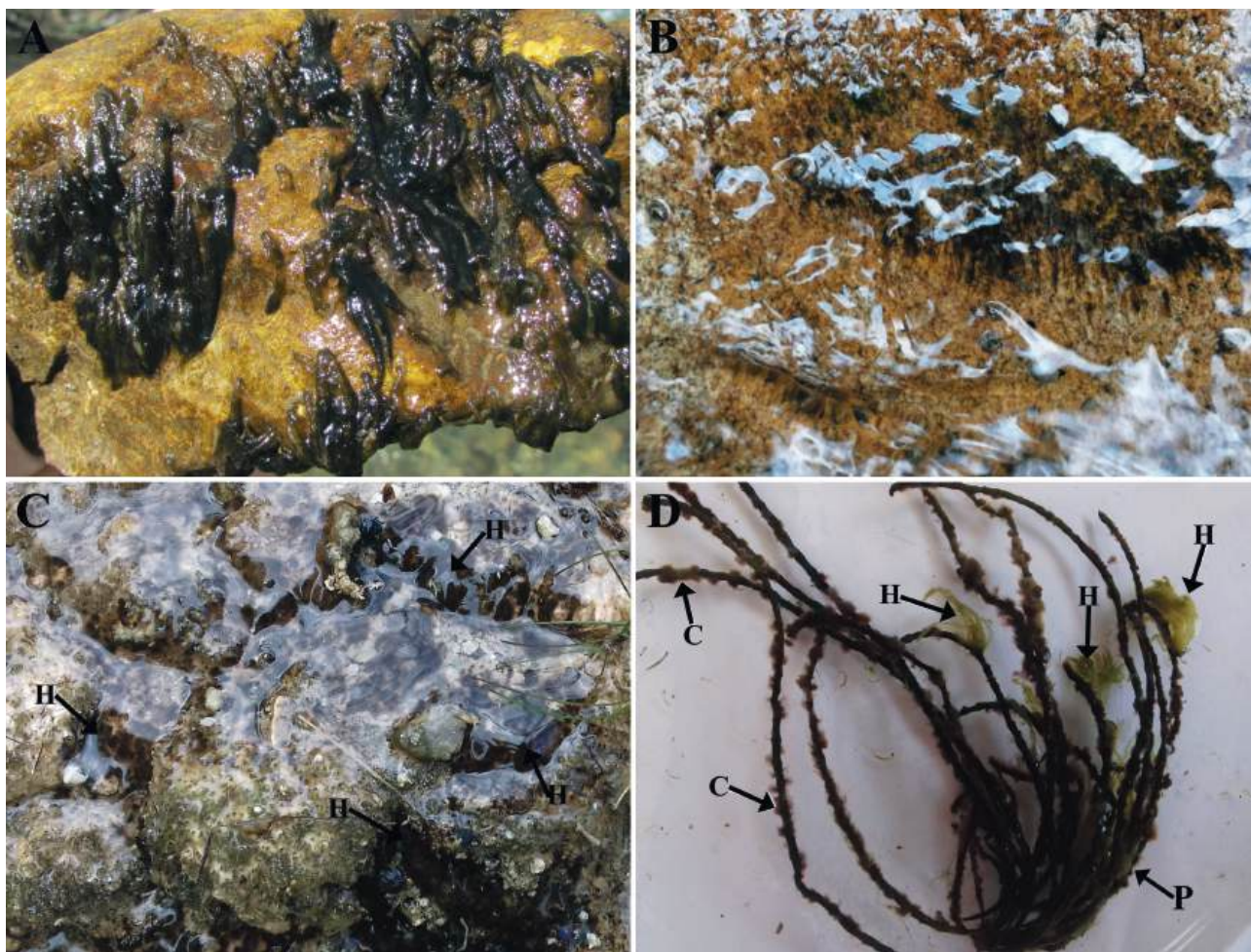
Geographical distribution and environmental conditions of *Hydrurus foetidus* localities in Serbia (2017–2022).

River/Date	Geographical coordinates	Altitude (m)	Water depth (cm)	Geological base/ Substratum type	Velocity (m s <sup>-1</sup> )	Temperature (°C)	pH	Cond. (µS cm <sup>-1</sup> )	Hardness (mg l <sup>-1</sup> )	O <sub>2</sub> (mg l <sup>-1</sup> )	NH <sub>4</sub> <sup>+</sup> (mg l <sup>-1</sup> )	NO <sub>3</sub> <sup>-</sup> (mg l <sup>-1</sup> )	PO <sub>4</sub> <sup>3-</sup> (mg l <sup>-1</sup> )	Degree of shade	Coverage (%)	Associated macroalgae
Trgoviški Timok River (TT) 1. April 2017	43°32'12.7"N 22°16'54.7"E	241	10–20	limestone/stone	1.2	14.9	7.95	200	110	11.8	< 0.03	< 4	< 0.06	+++	5	/
Lisinska River (L) 7 June 2018	44°05'41.3"N 21°37'58.6"E	353	0–10	limestone/stone	1.3	13.5	7.81	380	190	10.5	< 0.03	< 4	< 0.06	+++	10	/
Božica River (B) 27 May 2018	42°37'07.0"N 22°24'02.4"E	1038	0–10	granite/stone	1.3	13.3	7.08	80	40	9.35	< 0.03	< 4	0.21	+++	2	<i>Lemanea fluviatilis</i>
Božica channel (BC) 23 July 2019	42°40'44.8"N 22°21'02.1"E	1212	0–10	granite/stone	1.8	15.6	7.7	510	260	9.66	< 0.03	< 4	< 0.06	+++	2	<i>Lemanea rigida</i> <i>Cladophora</i> sp.
Veliki Rzav River (VR1) 22 May 2021	43°33'14.9"N 19°57'32.5"E	829	10	granite/stone	1.4	11.3	7.82	230	110	10.3	< 0.03	< 4	< 0.06	+++	5	<i>Phaeodermatium rivulare</i> <i>Cladophora</i> sp.
Veliki Rzav River (VR2) 22 May 2021	43°37'50.4"N 19°55'20.7"E	677	0–10	granite/stone	1.6	12.2	7.96	250	130	10.1	< 0.03	< 4	< 0.06	+++	5	<i>Phaeodermatium rivulare</i> <i>Cladophora</i> sp.
Veliki Rzav River (VR3) 22 May 2021	43°38'43.8"N 19°54'44.6"E	609	0–10	granite/stone	1.5	12.1	8.08	290	140	9.59	< 0.03	< 4	0.06	+++	5	<i>Phaeodermatium rivulare</i> <i>Cladophora</i> sp.
Djerekarska River (DJ) 26 June 2021	43°04'51.5"N 20°06'44.3"E	1291	0–10	limestone/stone	1.3	7.3	7.51	220	110	10.3	< 0.03	< 4	< 0.06	+++	5	<i>Microspora amoena</i>
Trudovačka River (TR) 5 July 2019	43°30'03.4"N 19°58'32.0"E	1072	0–10	limestone/tufa	1.8	11.5	7.73	300	170	11.6	< 0.03	< 4	< 0.06	+++	10	/
Gobeljska River (G) 18 June 2019	43°21'45.1"N 20°49'15.8"E	1020	surface	granite/stone	1	10.8	7.62	130	70	10.4	< 0.03	< 4	< 0.06	++	2	<i>Hildenbrandia rivularis</i>
Temštica River (T) 20 Aug. 2019	43°17'50.2"N 22°36'26.6"E	504	0–10	limestone/stone	1.5	12	7.61	230	110	10.2	< 0.03	< 4	0.21	++	2	<i>Nostoc</i> sp. <i>Paralemanea catenata</i>
Kladnica River (K) 26 July 2018	43°25'15.7"N 20°03'06.3"E	1106	0–5	limestone/tufa	0.4	9.7	7.98	360	160	10.1	< 0.03	< 4	< 0.06	+++	3	/
Jelovička River (J) 20 Aug. 2019	43°10'58.2"N 22°49'54.0"E	749	0–10	limestone/ <i>Paralemanea torulosa</i>	1.4	18.2	8.01	360	180	10.5	< 0.03	< 4	< 0.06	+++	1	<i>Paralemanea torulosa</i>
Dojkička River (D1) 18 Aug. 2019	43°12'02.8"N 22°48'25.0"E	808	surface	limestone/ <i>Paralemanea catenata</i>	1.3	18.4	7.52	180	100	9.87	< 0.03	< 4	0.11	+++	1	<i>Nostoc</i> sp. <i>Paralemanea catenata</i>
Dojkička River (D2) 18 Aug. 2019	43°10'40.1"N 22°49'38.5"E	751	surface	limestone/ <i>Paralemanea catenata</i>	1.4	18.9	7.64	350	170	9.79	< 0.03	< 4	0.32	+++	1	<i>Nostoc</i> sp. <i>Paralemanea catenata</i>

+++ full sunlight; ++ partial shade







**Figure 2**

Variation in phenotypic expression of different populations of *Hydrurus foetidus*: A – brown mucilaginous mosslike colonies; B – brown mucilaginous colonies; C – mucilaginous brown coating (H → *Hydrurus foetidus*); D – green mucilaginous colonies (P → *Paralemanea catenata*; H → *Hydrurus foetidus*; C → “*Chantransia*” stage).

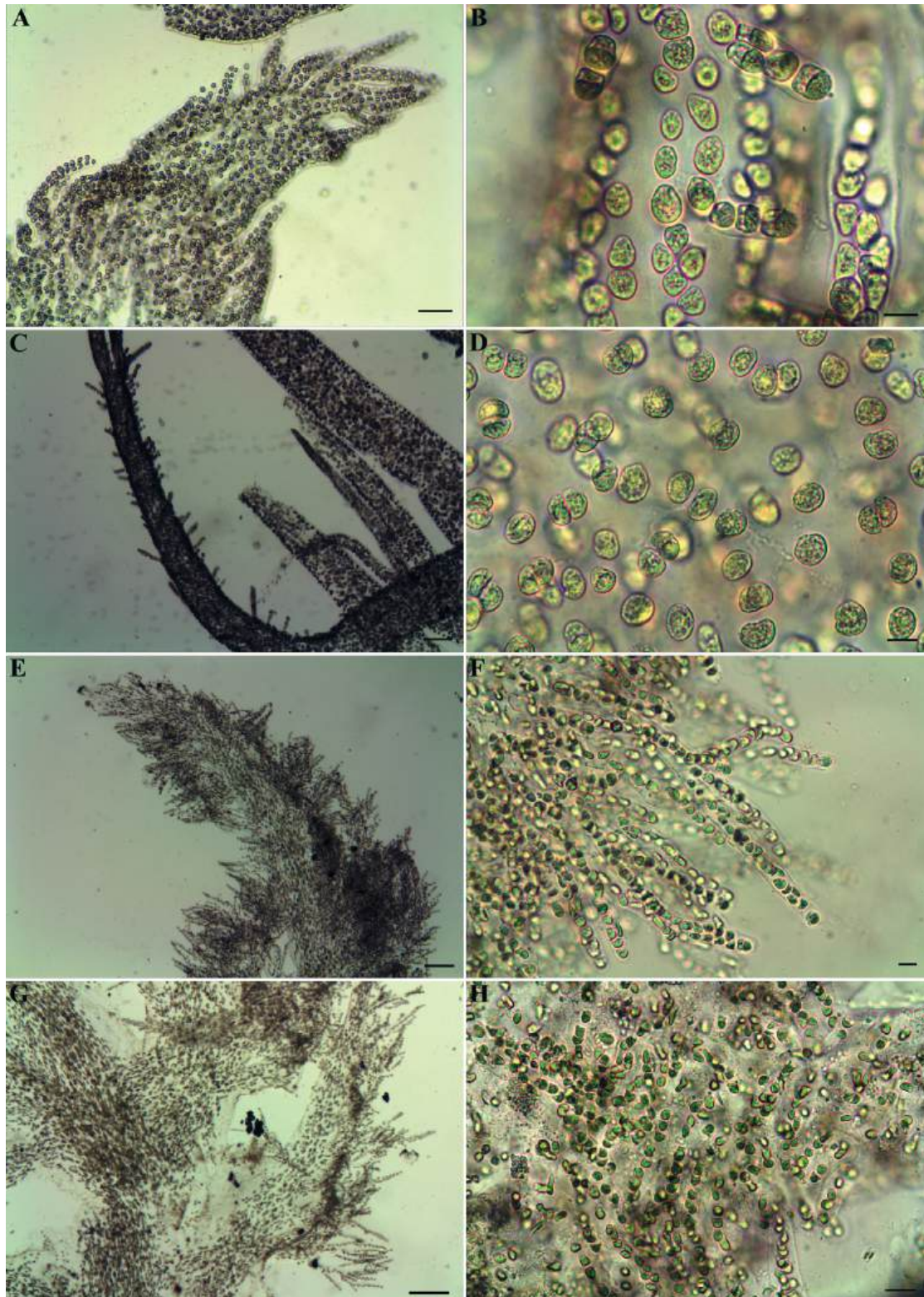
Trgoviški Timok River, the Lisinska River, the Božica River, the Božica channel, the Veliki Rzav River (three localities), the Djerekarska River and the Trudovačka River (Fig. 1). The thalli were 3 cm to 15 cm long and were clearly and abundantly branched (Fig. 2: A). Cells were spherical, subspherical to ellipsoidal, 6–12  $\mu\text{m}$  long along the longest axis, arranged peripherally in the mucilaginous matrix (Fig. 3: A–B). Tiny reddish-brown mucilaginous colonies were found in the Gobeljska and Temštica rivers. The thalli were 1 cm to 5 cm long, non clearly branched (Fig. 2: B). Small branchlets covering only a central axis were observed in microscopic analysis (Fig. 3: C). Cells were spherical, subspherical to ellipsoidal, 8–12  $\mu\text{m}$  long along the longest axis, arranged peripherally in the mucilaginous matrix (Fig. 3: C–D). A brown mucilaginous coating of *H. foetidus* was found in the source of the Kladnica

River. The thalli grew over small areas on the tufa surface (Fig. 2: C). Cells were subspherical to ellipsoidal, 6–10  $\mu\text{m}$  long along the longest axis, arranged peripherally in the mucilaginous matrix (Fig. 3: E–F). Green mucilaginous colonies were found in the Jelovička and Dojkinačka rivers (two localities). The thalli were 0.5 cm to 2 cm long (Fig. 2: D). Cells were spherical, subspherical to ellipsoidal, 8–12  $\mu\text{m}$  long along the longest axis, arranged peripherally in the mucilaginous matrix (Fig. 3: G–H).

### 3.2. Ecological data

Our results on *H. foetidus* come from the spring and summer months (April–September) in lowland, upland, and mountain Serbian aquatic ecosystems (altitudes ranging from 241 to 1291 m ASL; Table 1,





**Figure 3**

Microscopic view of *Hydrurus foetidus* thalli: A–B – brown mucilaginous mosslike colonies; C–D – brown mucilaginous colonies; E–F – mucilaginous brown coating; G–H – green mucilaginous colonies. Scale bars: 50  $\mu\text{m}$  for plate A; 10  $\mu\text{m}$  for plates B and D; 100  $\mu\text{m}$  for plates C, E and G; 20  $\mu\text{m}$  for plates F and H.



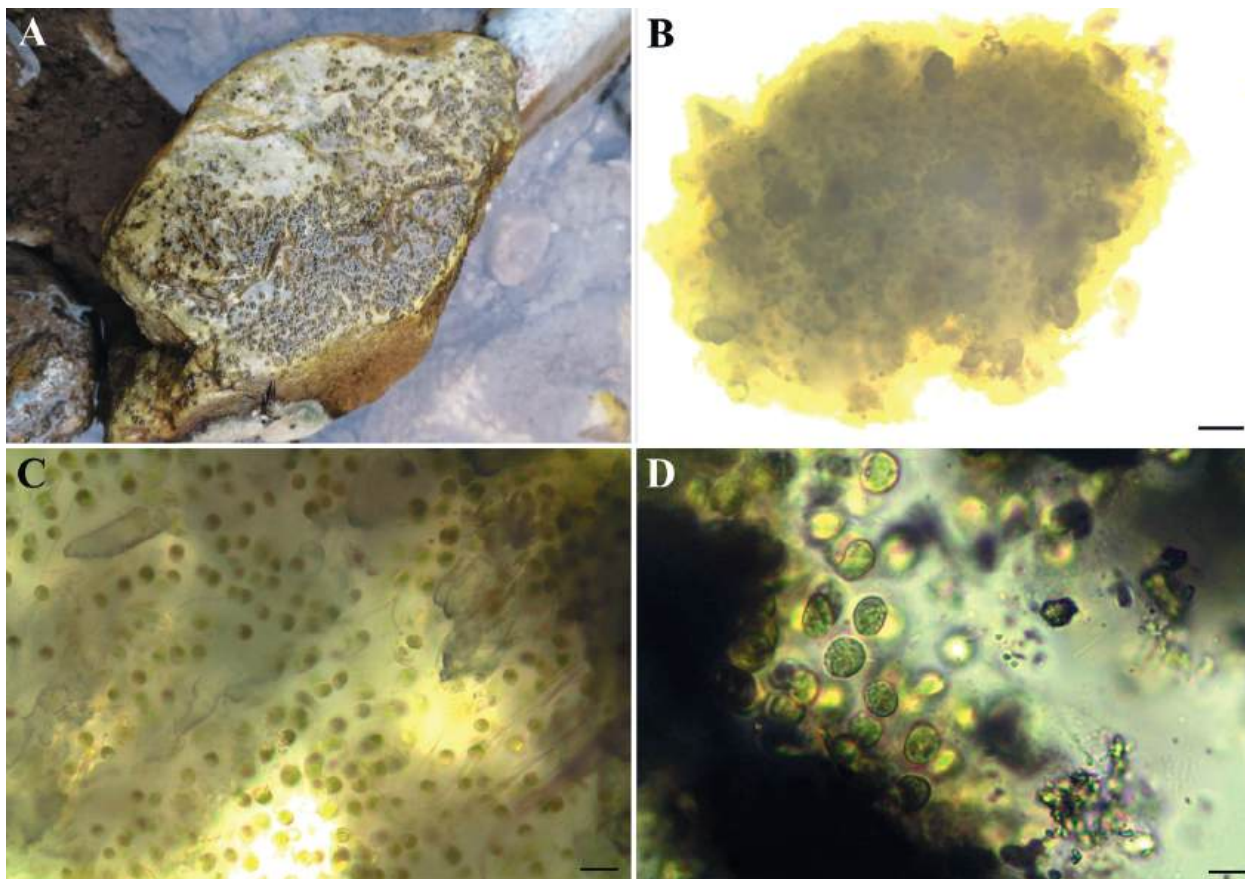


Fig. 1). The species was found in lotic water with a current velocity ranging from  $0.4 \text{ m s}^{-1}$  to  $1.8 \text{ m s}^{-1}$ , at depths ranging from 0 cm to 20 cm, attached to stony substrate, to the tufa surface or to red algae from the genus *Paralemanea*, mainly in full sunlight (Table 1). Water temperatures varied between  $7.3^{\circ}\text{C}$  and  $18.9^{\circ}\text{C}$ , conductivity from  $80 \mu\text{S cm}^{-1}$  to  $510 \mu\text{S cm}^{-1}$ , hardness between  $40 \text{ mg l}^{-1}$  and  $260 \text{ mg l}^{-1}$ , oxygen concentration ranged from  $9.35 \text{ mg l}^{-1}$  to  $11.8 \text{ mg l}^{-1}$ , and pH values from 7.08 to 8.01. Concentrations of inorganic nutrients were mainly low (Table 1), only concentrations of orthophosphates were slightly elevated in the Božica, Temštica and Dojkinačka rivers (Table 1).

*Hydrurus foetidus* was observed to co-occur with other competing benthic macroalgae, mostly representatives of Rhodophyta, such as *Hildenbrandia rivularis* (Liebmann) J.Agardh, *Lemanea fluviatilis* (Linnaeus) C.Agardh, *L. rigida* (Sirodot) De Toni, *Paralemanea catenata* (Kützinger) M.L.Vis & Sheath, and *P. torulosa* (Roth) Sheath & A.R.Sherwood. *Hydrurus foetidus* also co-occurred with cyanobacteria *Nostoc*

spp., and green algae *Cladophora* sp. and *Microspora amoena* (Kützinger) Rabenhorst (Table 1). In the Jelovička and Dojkinačka rivers, on damaged parts of *P. catenata* and *P. torulosa* thalli, *H. foetidus* grew as an epiphyte (Fig. 2: D). Also, the “*Chantransia*” stage was present in places where the thallus of *Paralemanea* species had been detached (Fig. 2: D).

At three localities of the Veliki Rzav River, we found *H. foetidus* growing together with another freshwater chrysophycean alga, *Phaeodermatium rivulare* Hansgirg. Thalli of *Ph. rivulare* were found in the form of silver-brown crusts covered with a mucilaginous coating (Fig. 4: A). The crusts were 1–2 mm in diameter, single or aggregated to cover a stony surface. Microscopically, the thalli consisted of several layers of cells (spherical, subspherical to ellipsoidal,  $7\text{--}12 \mu\text{m}$  long), respectively densely aggregated in the crustose part of the thalli and loosely in the mucilaginous coating (Fig. 4: B–D). Thalli of *Phaeodermatium rivulare* covered 20–40% of the stony bottom. This is the first finding of this rare freshwater chrysophycean alga in Serbian aquatic ecosystems.



**Figure 4**

Morphological features of *Phaeodermatium rivulare*: A – silver-brown crusts of *Ph. rivulare* growing on a rock; B–D – microscopic view of the thalli. Scale bars:  $50 \mu\text{m}$  for plate B;  $20 \mu\text{m}$  for plate C; and  $10 \mu\text{m}$  for plate D.

## 4. Discussion

In all published studies related to *H. foetidus*, the species was described as a cold-water stenotherm, or even psychrophile species, capable of growing and reproducing at very low temperatures unfavorable for most other benthic macroalgae (Rott et al. 2006a; Cantonati et al. 2006; 2016; Remias et al. 2013; Klaveness 2017). As previously mentioned, an optimal temperature for its growth is in the range of 2°C to 12°C, with a clear decline at temperatures above 16°C (Bursa 1934; Kann 1978; Canter-Lund, Lund 1995; Kristiansen 2005; Nicholls, Wujek 2015). In this study, we recorded opposite results. With the exception of the source of the Kladnica River, as well as the Gobeljska, Temštica and Djerekarska rivers (the coldest water -7.3°C), all our records come from water with temperatures above 12°C. Furthermore, we recorded *H. foetidus* in the Jelovička and Dojkinačka rivers at temperatures above 18°C. According to Kann (1978) and Canter-Lund & Lund (1995), the possible survival of *Hydrurus* in summer is limited to the resting stages or palmellae, as under these conditions the thalli become fragmented and disappear. Temperature values in the Jelovička and Dojkinačka rivers represent the second highest temperatures recorded for *H. foetidus*. The only site with a higher temperature is a mountain stream in the Vranica Mountains (Mašić et al. 2020), where *H. foetidus* was found under similar environmental conditions as in the Dojkinačka and Jelovička rivers. In Serbia, *H. foetidus* has previously been reported from watercourses with a range of thermal conditions, from cold mountainous areas of 4.6°C to warmer areas with temperatures up to 14°C (Simić 2002; Simić, Simić 2003; Simić et al. 2003; Krizmanić et al. 2008).

Some regularities in the pattern of occurrence related to environmental conditions were noted, especially with regard to water temperature, current velocity, and degree of shade. At water temperatures ranging from 7.3°C to 15.6°C, current velocity ranging from 1.3 m s<sup>-1</sup> to 1.8 m s<sup>-1</sup>, and full sunlight, *H. foetidus* grew in the form of brown mucilaginous mosslike colonies, distinctly and extensively branched (Trgoviški Timok, Lisinska, Božica, Veliki Rzav, Djerekarska and Trudovačka rivers, and the Božica channel), as described by Klaveness et al. (2011). In the Gobeljska and Temštica rivers, the thalli of *H. foetidus* were not conspicuously branched, with a reddish-brown coloration. After microscopic analysis, we found that only a central axis was covered by small branchlets, just as reported by Bursa (1934). Given the species' preference for full sunlight conditions (Rott et al. 2000; Kawecka 2003), a possible reason for this occurrence could be the growth in partial shade at these localities.

A mucilaginous brown coating of *H. foetidus* on the tufa surface described from the source of the Kladnica River is not unusual, as it was found under intermittent wetting conditions. Our results are consistent with Klaveness's (1992) findings of such a morphological form in water films with slow seeping.

In the Dojkinačka and Jelovička rivers, *H. foetidus* formed green mucilaginous colonies. These rivers are at higher altitudes, but both were characterized by warmer temperatures during the sampling period (over 18°C). In August 2019, the maximum air temperature in this region was 31.2°C, the minimum air temperature was 13.4°C, while the average monthly air temperature was 21.6°C. Precipitation was low, and water levels in the rivers were lower than usual at this time of year (Republic Hydrometeorological Institute of Serbia 2020). In the Dojkinačka River, *H. foetidus* was found growing attached to the red alga *Paralemanea catenata*, while in the Jelovička River it was found growing attached to *P. torulosa*. It has been previously documented that *H. foetidus* co-occurs with cyanobacteria, red, yellow-green, and filamentous green macroalgae (Petković 1980; Simić 2002; Kashta, Miho 2016; Stanković, Lietner 2016; Koletić et al. 2017), but never overgrows them. We describe for the first time the non-obligate *Hydrurus-Paralemanea* association. At the time of sampling, the thalli of *P. catenata* and *P. torulosa* were mainly damaged, probably due to grazing by herbivorous aquatic insects, which enabled *H. foetidus* to attach and develop on damaged parts. In this way, *H. foetidus* protects itself from insolation during the summer season by seeking shelter among the *Paralemanea* thalli. This may be the species' survival strategy during the summer season or a way to adapt to the effects of climate change. No development of *H. foetidus* on the *Nostoc* sp. thalli collected from these rivers was observed.

Our findings also represent the first record of the extremely rare chrysophycean alga *Phaeodermatium rivulare* in Serbian aquatic ecosystems. The species was found growing together with *H. foetidus* in the Veliki Rzav River. Data on the biology, ecology and distribution of *Ph. rivulare* are very scarce, as only a few collections have been made in Europe and North America (Nicholls, Wujek 2015; Kamberović et al. 2019; Guiry & Guiry 2024). However, all of the authors conclude that the species has the same habitat preferences as *H. foetidus*, as well as similar morphology (Gesierich, Rott 2004; Nicholls, Wujek 2015). As these two species have often been reported from the same localities, it has long been suspected that *Ph. rivulare* is a stage in the life cycle of *H. foetidus* (Bourrelly 1981; Jordan, Iwataki 2012; Nicholls, Wujek





2015). A study conducted by Kamberović et al. (2019) on 20 springs of Mount Konjuh revealed the presence of *Ph. rivulare* in three springs, but no *H. foetidus* was found. In our research, we recorded these two chrysophycean species growing together in May, but neither species was recorded in the subsequent sampling periods (August and September).

Some authors have argued that *H. foetidus* may be overlooked by scientists due to difficulties in distinguishing it or if scientists do not know where and when to look for it (Rott et al. 2006a,b; Klaveness 2017). We concur with this statement. Our results substantiate that *H. foetidus* can thrive in environmental conditions that are unpredictable for the species, especially with regard to temperature. The occurrence of the species in the Jelovička and Dojkinačka rivers was undoubtedly unexpected, since almost the entire riverbed was covered with competing *P. torulosa* and mosses (Jelovička River), or *P. catenata* and *Nostoc* sp. (Dojkinačka River). In addition, the temperature values were higher than those determined as lethal for the species.

In conclusion, we emphasize the importance of further, more intensive and thorough surveys and the necessity of implementing genetic methods. This will aim to resolve questions about the identity and ecology of *H. foetidus* and *Ph. rivulare*.

## Acknowledgements

The authors are grateful to their colleague Marko Arsenijević, MSc, who helped create the maps. We would also like to thank the reviewers for their useful and constructive comments and suggestions. A.B.R. was supported by the Ministry of Science, Technological Development and Innovation of the Republic of Serbia (grant No. 451-03-66/2024-03-200216). S.B.S. was supported by the Ministry of Science, Technological Development and Innovation of the Republic of Serbia (grant No. 451-03-65/2024-03/200122). Part of this research was performed within the framework of the project "Hydrobiological study of the Veliki Rzav River" implement by the Nature Conservancy and the service and trade company "Water Logist d.o.o.", funded by WWF Adria.

## References

- American Public Health Association. (2005). Standard methods for examination of Water and Wastewater (21st ed.). American Public Health Association.
- Bourrelly, P. (1981). Les Algues d'eau douce. Initiation a la systematique: Vol. II. Les Algues jaunes et brunes. Chrysophycées, Phéophycées, Xanthophycées et Diatomées. Société Nouvelle des Editions Boubée.
- Bursa, A. (1934). *Hydrurus foetidus* Kirch. w Polskich Tatrach. *Hydrurus foetidus* Kirch. in der Polnischen Tatra. I. Oekologie, Morphologie. II. Phenologie. *Bull. Int. Acad. Pol. Sci. Lett. Cl. Sci. Math. Nat. Sér. B. Science and Nature*, 1, 69–84.
- Canter-Lund, H., & Lund, J. W. G. (1995). *Freshwater Algae: Their Microscopic World Explored*. Biopress.
- Cantonati, M., Gerecke, R., & Bertuzzi, E. (2006). Springs of the Alps - sensitive ecosystems to environmental change: From biodiversity assessment to long-term studies. *Hydrobiologia*, 562, 59–96. <https://doi.org/10.1007/s10750-005-1806-9>
- Cantonati, M., Rott, E., Spitale, D., Angeli, N., & Komárek, J. (2012). Are benthic algae related to spring types? *Freshwater Science*, 31(2), 481–498. <https://doi.org/10.1899/11-048.1>
- Cantonati, M., Spitale, D., Scalfi, A., & Guella, G. (2016). Exploring the contrasting seasonal strategies of two crenic macroalgae. *Fottea*, 16(1), 133–143. <https://doi.org/10.5507/fot.2015.029>
- Eloranta, P., Kwandrans, J., & Kusel-Fetzmann, E. (2011). Rhodophyceae and Phaeophyceae. In B. Budel, G. Gartner, L. Krienitz, H. R. Preisig, & M. Schagerl (Eds.), *Freshwater flora of Central Europe* (pp. 1–155). Spectrum Akademischer Verlag.
- Gesierich, D., & Rott, E. (2004). Benthic Algae and Mosses from Aquatic Habitats in the Catchment of a Glacial Stream (Rotmoos, Ötztal, Austria). *Ber. Nat.-. Med. Verein Innsbruck*, 91, 7–42.
- Guiry, M. D., & Guiry, G. M. (2024). *AlgaeBase. World-wide electronic publication*. National University of Ireland., <https://www.algaebase.org>, Retrieved April 16, 2024, from.
- John, D. M., Whitton, B. A., & Brook, A. J. (2011). *Freshwater algal flora of the British Isles; An Identification Guide to Freshwater and Terrestrial Algae*, 2nd ed. Cambridge: Cambridge University Press.
- Jordan, R. W., & Iwataki, M. (2012). *Chrysophyceae and Synurophyceae*. John Wiley & Sons., <https://doi.org/10.1002/9780470015902.a0023690>
- Kann, E. (1978). Systematik und Ökologie der Algen österreichischer Bergbäche. *Archiv für Hydrobiologie*, 53(4), 405–643.
- Kamberović, J., Plenković-Mora, A., Kralj Borojević, K., Gligora Udovič, G., Žutinić, P., Hefner, D., & Cantonati, M. (2019). Algal assemblages in springs of different lithologies (ophiolites vs. limestone) of the Konjuh Mountain (Bosnia and Herzegovina). *Acta Botanica Croatica*, 78(1), 66–81. <https://doi.org/10.2478/botcro-2019-0004>
- Kashta, L., & Miho, A. (2016). The more frequently occurring macroalgae in Albanian running waters. *BSHN*, 21, 31–40.
- Kawecka, B. (2003). Effect of different light conditions on cyanobacteria and algal communities in Tatra Mts stream

- (Poland). *Oceanological and Hydrobiological Studies*, 32(2), 3–13.
- Klaveness, D. (1992). Ferskvanns-algene i Norge: En forskningsoppgave "for leg og lærd". *Blyttia*, 50, 121–140.
- Klaveness, D. (2017). *Hydrurus foetidus* (Chrysophyceae): An inland macroalga with potential. *Journal of Applied Phycology*, 29, 1485–1491. <https://doi.org/10.1007/s10811-016-1047-5>
- Klaveness, D. (2019). *Hydrurus foetidus* (Chrysophyceae): An update and request for observations. *Algae - Korean Phycological Society*, 34(1), 1–5. <https://doi.org/10.4490/algae.2019.34.1.15>
- Klaveness, D., Brate, J., Patil, V., Shalchian-Tabrizi, K., Kluge, R., Gislørød, H. R., & Jakobsen, K. S. (2011). The 18S and 28S rDNA identity and phylogeny of the common lotic chrysophyte *Hydrurus foetidus*. *European Journal of Phycology*, 46(3), 282–291. <https://doi.org/10.1080/09670262.2011.598950>
- Koletić, N., Alegro, A., Šegota, V., Vuković, N., Rimac, A., & Vilović, T. (2017). New sites of rare cold-water golden algae *Hydrurus foetidus* (Villars) Trevisan (Ochrophyta: Chrysophyceae) in Croatia. *Natura Croatica*, 26(2), 305–311. <https://doi.org/10.20302/NC.2017.26.22>
- Komárek, J. (2013). Cyanoprokaryota 3. Teil: Heterocytous Genera. In B. Büdel, G. Gärtner, L. Krienitz, & M. Schagerl (Eds.), *Süßwasserflora von Mitteleuropa 19/3 (1–1130)*. Springer Spektrum Verlag. <https://doi.org/10.1007/978-3-8274-2737-3>
- Kristiansen, J. (2005). *Golden Algae – A biology of Chrysophytes*. A.R.G. Gantner Verlag Kommanditgesellschaft.
- Krizmanić, J., Subakov-Simić, G., & Karadžić, V. (2008). Supplementary notes on the distribution of *Hydrurus foetidus* (Vill.) Trevisan (Chrysophyta) in Serbia. *Archives of Biological Sciences*, 60(2), 13–14. <https://doi.org/10.2298/ABS0802001K>
- Mašić, E., Barudanović, S., Žero, S., Ramić, E., Macanović, A., & Fejzić, S. (2020). New data on distribution of *Hydrurus foetidus* (Villars) Trevisan in freshwater habitats of Vranica Mountain (Bosnia and Herzegovina). *Biologica Nyssana*, 11(2), 93–101. <https://doi.org/10.5281/zenodo.4393955>
- Milner, A. M., Brittain, J. E., Castella, E., & Petts, G. E. (2001). Trends of macroinvertebrate community structure in glacier-fed rivers in relation to environmental conditions: A synthesis. *Freshwater Biology*, 46(12), 1833–1847. <https://doi.org/10.1046/j.1365-2427.2001.00861.x>
- Milner, A. M., Brown, L. E., & Hannah, D. M. (2009). Hydroecological response of river systems to shrinking glaciers. *Hydrological Processes*, 23(1), 62–77. <https://doi.org/10.1002/hyp.7197>
- Necchi, O., Jr., & Moreira, J. C. L. (1995). Longitudinal distribution of macroalgae in two tropical lotic ecosystems from southeastern Brazil. *Archiv für Hydrobiologie*, 135(1), 113–128. <https://doi.org/10.1127/archiv-hydrobiol/135/1995/113>
- Necchi, O., Jr., & Vis, M. L. (2021). Subphylum Eurhodophytina, Classes Bangiophyceae and Florideophyceae, Subclasses Corallinophycidae, Hildenbrandiophycidae, and Rhodymeniophycidae. In M.L. Vis & O.Jr. Necchi (Eds.), *Freshwater Red Algae: Phylogeny, Taxonomy, and Biogeography* (57–94). Cham: Springer Nature. [https://doi.org/10.1007/978-3-030-83970-3\\_3](https://doi.org/10.1007/978-3-030-83970-3_3)
- Nicholls, K. H., & Wujek, D. E. (2015). Chrysophyceae and Phaeothamniophyceae. In J. D. Wehr, R. G. Sheath, & J. P. Kocielek (Eds.), *Freshwater Algae of North America: Ecology and Classification* (pp. 537–586). Academic Press. <https://doi.org/10.1016/B978-0-12-385876-4.00012-8>
- Niedrist, G. H., & Füreder, L. (2018). When the going gets tough, the tough get going: The enigma of survival strategies in harsh glacial stream environments. *Freshwater Biology*, 63(10), 1260–1272. <https://doi.org/10.1111/fwb.13131>
- Petković, S. (1980). Jesenji algofloristički aspect nekih crnogorskih rijeka (prilog algološkim istraživanjima slatkih voda Crne Gore). *Poljoprivreda i Sumarstvo*, 26(1), 71–89.
- Remias, D., Jost, S., Boenigk, J., Wastian, J., & Lütz, C. (2013). *Hydrurus*-related golden algae (Chrysophyceae) cause yellow snow in polar summer snowfields. *Phycological Research*, 61, 277–285. <https://doi.org/10.1111/pre.12025>
- Republic Hydrometeorological Institute of Serbia. (2020). *Meteorological yearbook 1: Climate data 2019*. Republic Hydrometeorological Institute of Serbia.
- Rodriguez, R. R., Jiménez, J. C., & Delgado, C. M. (2007). Microhabitat and morphometric variation in two species of *Prasiola* (Prasiolales, Chlorophyta) from stream in central Mexico. *Aquatic Ecology*, 41(2), 161–168. <https://doi.org/10.1007/s10452-006-9068-9>
- Rott, E., & Schneider, S. C. (2014). A comparison of ecological optima of soft-bodied benthic algae in Norwegian and Austrian rivers and consequences for river monitoring in Europe. *The Science of the Total Environment*, 475, 180–186. <https://doi.org/10.1016/j.scitotenv.2013.08.050> PMID:24021481
- Rott, E., Pipp, E., Pfister, P., Van Dam, H., Ortler, K., Binder, N., & Pall, K. (1999). *Indikationslisten für Aufwuchsalgen in österreichischen Fließgewässern*. Teil 2: Trophieindikation (sowie geochemische Präferenzen, taxonomische und toxikologische Anmerkungen). Wasserwirtschaftskataster herausgegeben vom Bundesministerium f. Land- u. Forstwirtschaft, Wien.
- Rott, E., Walser, L., & Kegele, M. (2000). Ecophysiological aspects of macroalgal seasonality in a gravel stream in the Alps (River Isar, Austria). *Verhandlungen - Internationale Vereinigung für Theoretische und Angewandte Limnologie*, 27(3), 1622–1625. <https://doi.org/10.1080/03680770.1998.11901513>
- Rott, E., Cantonati, M., Füreder, L., & Pfister, P. (2006a). Benthic algae in high altitude streams of the Alps - a neglected component of the aquatic biota. *Hydrobiologia*, 562(1), 195–216. <https://doi.org/10.1007/s10750-005-1811-z>



- Rott, E., Füreder, L., Schütz, C., Sonntag, B., & Wille, A. (2006b). A conceptual model for niche differentiation of biota within an extreme stream microhabitat. *Verhandlungen - Internationale Vereinigung für Theoretische und Angewandte Limnologie*, 29(5), 2321–2323. <https://doi.org/10.1080/03680770.2006.11903108>
- Schmid, S. M., Bernoulli, D., Fügenschuh, B., Matenco, L., Schefer, S., Schuster, R., Tischler, M., & Ustaszewski, K. (2008). The Alpine – Carpathian – Dinaride orogenic system: Correlation and evolution of tectonic units. *Swiss Journal of Geosciences*, 101(1), 139–183. <https://doi.org/10.1007/s00015-008-1247-3>
- Simić, S. (2002). *Macroalgae in streams of hill-mountain areas of Serbia*. Unpublished doctoral dissertation, University of Belgrade, Belgrade, Serbia. (In Serbian)
- Simić, S., & Simić, V. (2003). Macroalgae and macrozoobenthos of the Pčinja River. *Archives of Biological Sciences*, 55(3-4), 121–131. <https://doi.org/10.2298/ABS0304121S>
- Simić, S., Ranković, B., & Cvijan, M. (2003). Distribution of *Hydrurus foetidus* (Vill.) Kirch. (Chrysophyta) species in highland streams of Serbia. In Third International Balkan Botanical Congress: “Plant Resources in Creation of the New Values”, 18-24 May 2003 (p. 74). Sarajevo: Bosnia and Herzegovina: University of Sarajevo.
- Stanković, I., & Leitner, P. (2016). The first record of *Hydrurus foetidus* (Villars) Trevisan (Ochromytha: Chrysophyceae) in Croatia with ecological notes. *Natura Croatica*, 25(2), 223–231. <https://doi.org/10.20302/NC.2016.25.18>
- Traaen, T. S., & Lindstrøm, E. A. (1983). Influence of current velocity on periphyton distribution. In R. G. Wetzel (Ed.), *Periphyton of Freshwater Ecosystems* (pp. 97–99). Dr W Junk Publishers. [https://doi.org/10.1007/978-94-009-7293-3\\_15](https://doi.org/10.1007/978-94-009-7293-3_15)
- Uehlinger, U., Zah, R., & Bürgi, H. R. (1998). The Val Roseg project: temporal and spatial patterns of benthic algae in an Alpine stream ecosystem influenced by glacier runoff. In K. Kovar, U. Tappeiner, N. E. Peters, & R. G. Craig (Eds.), *Hydrology, Water Resources and Ecology in Headwaters* (pp. 419–424). IAHS Publication.
- Vis, M. L., & Necchi, O., Jr. (2021). Subphylum Eurhodophytina, Class Florideophyceae, Subclass Nemaliophycidae, Order Batrachospermales. In M.L. Vis & O.Jr. Necchi (Eds.), *Freshwater Red Algae: Phylogeny, Taxonomy, and Biogeography* (129–332). Cham: Springer Nature. [https://doi.org/10.1007/978-3-030-83970-3\\_5](https://doi.org/10.1007/978-3-030-83970-3_5)
- Wehr, J. D., Sheath, R. G., & Kociolek, J. P. (2015). *Freshwater algae of North America, ecology and classification*. Academic Press.
- Zah, R., Burgherr, P., Bernasconi, S. M., & Uehlinger, U. (2001). Stable isotope analysis of macroinvertebrates and their food sources in a glacier stream. *Freshwater Biology*, 46(7), 871–882. <https://doi.org/10.1046/j.1365-2427.2001.00720.x>