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The stonefly *Taeniopteryx schoenemundi* (Mertens, 1923) (Insecta: Plecoptera) conquers Europe's busiest waterway the Lower River Rhine

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Abstract

Recent observations of winter-active Taeniopterygidae in mid-sized Central European rivers reveal that these large-river stonefly species, previously thought to have been extirpated by severe water pollution, have persisted in hidden refugia. During February and March 2024, we conducted a comprehensive survey along a 300-km section of the lower River Rhine in North Rhine-Westphalia, Germany, spanning from Bonn to the Dutch border. We recorded adults and exuviae of the stonefly *Taeniopteryx schoenemundi* (Mertens, 1923) at 13 locations along the Rhine and 2 additional sites in its tributaries, the Ruhr and Wupper rivers. These findings, together with recent records from other Rhine tributaries, suggest that colonization by *T. schoenemundi* has occurred from these tributary populations. Significant anthropogenic alterations in the river's habitat may have created conditions now favorable for *T. schoenemundi*, a species not historically observed in the Rhine. This discovery marks the first confirmed presence of a stonefly in the lower Rhine in nearly a century, representing a noteworthy milestone in the river's recovery. Furthermore, the resurgence of *T. schoenemundi* within this heavily modified waterway underscores the potential for substantial improvement in water quality, offering renewed prospects for the restoration of native biodiversity in the Rhine system.

Key words: recolonization, Plecoptera, spreading, water quality improvement

Introduction

The River Rhine is one of the longest and most prominent rivers in Europe. It has a long history of environmental degradation and pollution, particularly between 1800 and 1950 (Uehlinger *et al.* 2009). Industrialization, urbanization, and agricultural runoff severely deteriorated water quality, while straightening by the cut-off of meanders and groyne placement to secure constant deep flow in the main channel completely changed the morphology and shortened the total lengths by more than 100 km (IKSR 2024). In this sense, the travel time of water between Basel in Switzerland and Karlsruhe (appr. 210 km) was significantly reduced from 64 to 23 hours. Additionally, floodplain areas were blocked by dikes for year-round agricultural uses. The whole river between Basel and the North Sea, i.e. 884 km, was developed into a high-power freight traffic transportation belt with annual goods transportations of ca. 160 million tons (IKSR 2024) making the Rhine the world's busiest waterway. Water quality problems in the Rhine peaked in the 1980s. The severe Sandoz accident in November 1986 marked the changing point when extremely poisonous chemicals killed most of the life in the river for several hundred kilometres (Güttinger & Stumm 1992). Subsequently, the international commission for the protection of the Rhine (IKSR) formed and in all neighbouring countries water treatment plants improved effluents and thus the water quality of the Rhine.

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The deteriorated water quality of the River Rhine in the 1960s and later led to the decline of many aquatic species (Tittizer *et al.* 1991; Tittizer *et al.* 1994). Among the most affected were stoneflies. This ancient group of insects is sensitive to oxygen depletion as most of them have reduced external gills (Gaufin *et al.* 1974; Nagell 1973). Furthermore, the larger species of the family Perlidae mostly have bivoltine or even multivoltine life cycles which puts the larvae at greater risk of loss than univoltine species (Brittain 1990; Feeley *et al*. 2009; Hershkovitz *et al*. 2015). The ancient Rhine, relatively fast flowing and dominated by gravel and cobble, was an ideal habitat for many stonefly species, composed of the predacious larger Perlidae and Perlodidae and the algae and detritus eating smaller Chloroperlidae and Taeniopterygidae. Five different species of Perlidae and Perlodidae inhabited the river in the beginning of the 20th century (*Marthamea selysii* (Pictet, 1841)*, Perla abdominalis* Burmeister, 1839*, Besdolus imhoffi* (Pictet, 1841)*, Besdolus ventralis* (Pictet, 1841)*, Isogenus nubecula* Newman, 1833) (IKSR 2020). All of them disappeared from the middle and lower Rhine with no records of their presence since the 1920s (IKSR 2020) and are either extirpated or highly threatened in Germany (Reusch *et al.* 2021) and central Europe. But also, the three species of Taeniopterygidae and other smaller stonefly species (*Brachyptera trifasciata* (Pictet, 1832), *Brachyptera braueri* (Klapálek, 1900), *Oemopteryx loewii* (Albarda, 1889), *Xanthoperla apicalis* (Newman, 1836)*, Siphonoperla burmeisteri* (Pictet, 1841) (IKSR 2020), disappeared from the navigable section which is in total more than 600 km of river length.

Recently, records of Taeniopterygidae in mid-sized rivers throughout Germany (Angersbach *et al.* 2010; Kleinsteuber 2022) raised the hope that this group of large-river species were not extirpated but managed to survive in hidden refuges. The findings in tributaries to the River Rhine (Enting & Lorenz 2022; Schiffels & Enting 2015) lead to the possibility that the highly developed lower Rhine could have been recolonized by stoneflies or that some species may have survived there, too. Thus, we started a sampling campaign to search for potential recolonization signs of the ancient group of stoneflies on the banks of the lower River Rhine.

Material and Methods

Location

The River Rhine in the German federal state of North Rhine-Westphalia is a 214 km long section between the former German capital Bonn (Rhine km 651) and the border to the Netherlands (Rhine km 865) (Fig. 1). In this section the river has an average width of 340 meters and flows within an anthropogenically extremely modified riverbed featuring groins and riprap. This section of the Rhine is notable for having the highest shipping traffic of any river in Europe with on average 550 vessels per day. According to German stream typology (Pottgiesser & Sommerhäuser 2014) the upper part of the section belongs to the type “very large gravel-dominated rivers” and the lower part to the type “very large sand-dominated rivers”. Embankments and groynes significantly changed the bank structure of the river, but the bottom substrate of gravel and sand was left mainly untouched.

Survey

We conducted a comprehensive survey on 20 of the 28 bridges crossing the Rhine in the German federal state North Rhine-Westphalia between Bonn and the Dutch border in February and March 2024 (Fig. 1). Visual inspections were carried out on bridge pillars, railings, surrounding sheet pilings, and riprap. Surveys were conducted under suitable weather conditions—either sunny or cloudy, without rain, and with temperatures ranging between 5 °C and 13 °C. The survey focused on adults and exuviae.

Additionally, in the same time span a number of tributaries to the Rhine and other larger rivers in the surrounding area were surveyed for adult plecopterans and exuviae. All sampled specimens were labelled, preserved in 96% ethanol, and stored in the collections of the respective collectors (Table 1). The specimens were identified with a stereomicroscope (Leica WILD M3C) to the species level.

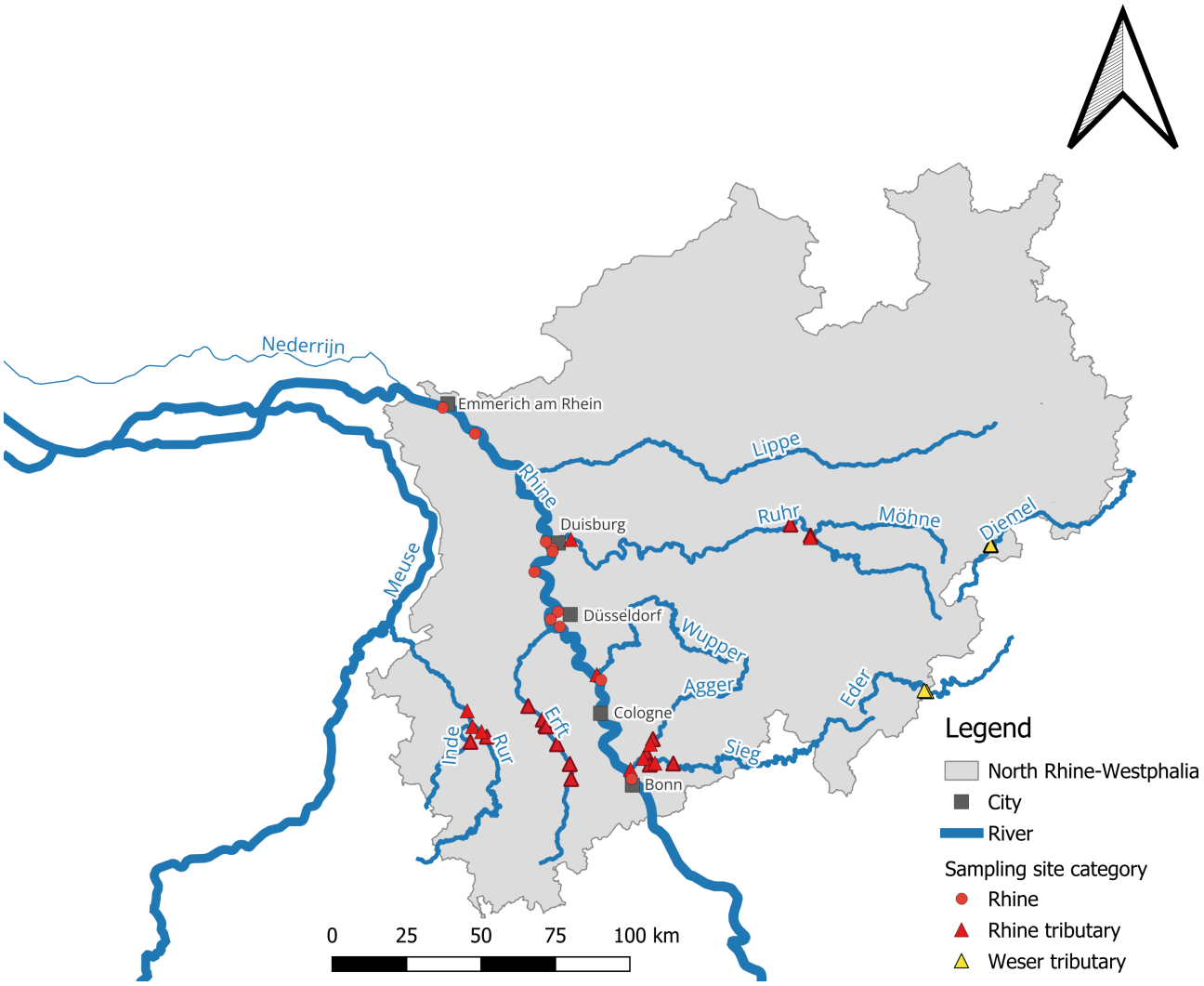

FIGURE 1. Occurrence of *Taeniopteryx schoenemundi* (circles) in the North Rhine-Westphalian section of the River Rhine between Bonn and the German-Dutch border and recent records in surrounding rivers (triangles).

TABLE 1. Dates, sampling sites and number of specimens of *Taeniopteryx schoenemundi* found in the North Rhine-Westphalian part of the River Rhine and two of its tributaries. AL = Armin Lorenz, JE = Julian Enss, KE = Klaus Enting, TH = Thomas Hörren

Date	River	n	Sampling site	Latitude	Longitude	leg
10/02/2024	Rhine	1 ♀	Krefeld, Uerdingen, Rhine bridge Krefeld-Uerdinger Brücke, on railing	51.348278	6.656389	AL
17/02/2024	Rhine	1 ♀	Kleve, Emmerich, Rhine bridge Emmerich am Rhein, on railing	51.827000	6.226000	JE
17/02/2024	Rhine	1 ♀	Kleve, Rees, Rhine bridge Rees-Kalkar, on railing	51.752000	6.377000	JE
17/02/2024	Rhine	5 ♂, 1 ♀	Duisburg, Hochfeld, footpath parallel to the Rhine	51.414333	6.742250	AL
17/02/2024	Rhine	1 ♀	Duisburg, Rheinhausen, Rhine bridge Brücke der Solidarität, on railing	51.415833	6.740417	AL
17/02/2024	Rhine	1 ♀	Duisburg, Hochfeld, Rhine bridge Hochfelder Eisenbahnbrücke, on railing	51.407417	6.741833	AL
20/02/2024	Rhine	2 ♂, 1 ♀	Duisburg, Hochfeld, Rheinpark, on railing	51.410667	6.745389	TH

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TABLE 1. (Continued)

Date	River	n	Sampling site	Latitude	Longitude	leg
23/02/2024	Ruhr	2 ♂	Mülheim an der Ruhr, Styrum, Ruhr bridge Raffelbergbrücke, on railing	51.443278	6.827694	TH
24/02/2024	Rhine	2 ♂, 1 ♀	Düsseldorf, Oberkassel, Rhine bridge Oberkasseler Brücke, on bridge piers	51.231667	6.766806	AL
24/02/2024	Rhine	1 ♀	Düsseldorf, Hamm, Rhine bridge Hammer Eisenbahnbrücke, on bridge piers	51.209028	6.732778	AL
25/02/2024	Rhine	3 ♂	Duisburg, Homberg, Rhine bridge A40 Rheinbrücke Duisburg Neuenkamp, sheet piling parallel to the Rhine	51.436694	6.709917	AL
25/02/2024	Rhine	2 ♂, 7 ♀	Düsseldorf, Flehe, Rhine bridge Fleher Brücke, on bridge piers	51.187139	6.775611	JE
03/03/2024	Wupper	2 ♂, 1 ♀	Leverkusen, Rheindorf, pedestrian bridge at the mouth of the river Wupper into the Rhine, on railing	51.046111	6.949750	AL, JE
03/03/2024	Rhine	13 Exuviae	Leverkusen, Wiesdorf, Rhine banks, concrete walls	51.030556	6.969778	AL, JE
04/03/2024	Rhine	1 ♀	Bonn Beuel downstream of Rhine bridge Kennedybrücke on right bank on a pedestrian railing	50.737556	7.113222	KE

Results

We obtained a total of 15 unique occurrence records of *Taeniopteryx schoenemundi* (Mertens, 1923), a species of the family Taeniopterygidae. These records include 31 adult specimens and 13 exuviae from the River Rhine, and 4 adult specimens from tributaries to the Rhine. The first specimens were found on 10 February and the last ones on 4 March. The specimens occurred on 11 bridges crossing the River Rhine and their surroundings (Table 1, Fig. 2). Among the collected specimens, both female and male individuals were identified though no egg-carrying females were observed. No other stonefly species were found besides *T. schoenemundi*.

In the tributaries 5 adults of *T. schoenemundi* were found. For comparative reasons we conducted a literature review of recent findings of the species *T. schoenemundi* (Table 2).

TABLE 2. Dates, sampling sites and number of specimens of *Taeniopteryx schoenemundi* found by the authors or in recent grey literature in the surrounding of the river Rhine. AL = Armin Lorenz, JE = Julian Enss

Date	River	n	Location	Latitude	Longitude	leg
18/02/2021	Ruhr	3 ♀	Wickede, Ruhr bridge, on railing	51.487146	7.859689	AL
18/02/2021	Ruhr	4 ♂, 4 ♀	Neheim, Ruhr bridge, on railing	51.455784	7.953825	AL
05/02/2023	Eder	2 ♂	Bad Berleburg, Eder bridge Ederhöhe, on railing	50.996389	8.499167	JE
05/02/2023	Eder	1 ♀	Bad Berleburg, Eder bridge Wörthstraße, on railing	50.998611	8.488500	JE
10/02/2023	Sieg	2 ♂, 6 ♀	Sankt Augustin, Sieg bridge Siegstraße, on railing	50.798361	7.166583	JE
10/02/2023	Rur	13 ♂, 9 ♀, 3 Exuvia	Jülich, Koslar, pedestrian bridge north to Hasenfelder Straße, on railing	50.939500	6.340528	JE, AL
10/02/2023	Sieg	4 ♂, 3 ♀, 3 Exuviae	Siegburg, Buisdorf, Sieg bridge Frankfurter Straße, on railing (Imagines) and bridge piers (Exuviae)	50.784389	7.222500	JE, AL
10/02/2023	Agger	3 ♂, 2 ♀	Troisdorf, Agger bridge Brückenstraße, on railing	50.841000	7.201000	JE, AL
10/02/2023	Inde	1 ♂, 2 ♀, 1 Exuvia	Düren, Inde bridge Schophovener Straße, on railing (Imago) and bridge piers (Exuvia)	50.893000	6.366000	JE, AL
10/02/2023	Rur	1 ♂, 5 ♀	Inden, Rur bridge Krauthausener Straße, on railing	50.877694	6.407806	JE, AL

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TABLE 2. (Continued)

Date	River	n	Location	Latitude	Longitude	leg
10/02/2023	Sieg	2 ♂, 7 ♀	Troisdorf, Sieg bridge L269, on railing	50.765694	7.107694	JE, AL
11/02/2023	Ruhr	4 ♂, 4 ♀	Arnsberg, Neheim, Denzbrücke, on railing	51.448806	7.952889	JE
05/02/2023	Eder	2 ♀	Bad Berleburg, Beddelhausen, Eder bridge Ederhöhe, on railing	50.996640	8.4993726	JE
05/02/2023	Eder	1 ♂, 2♀	Bad Berleburg, Beddelhausen, Eder bridge Auf d. Zäune, on railing	50.999611	8.487778	JE

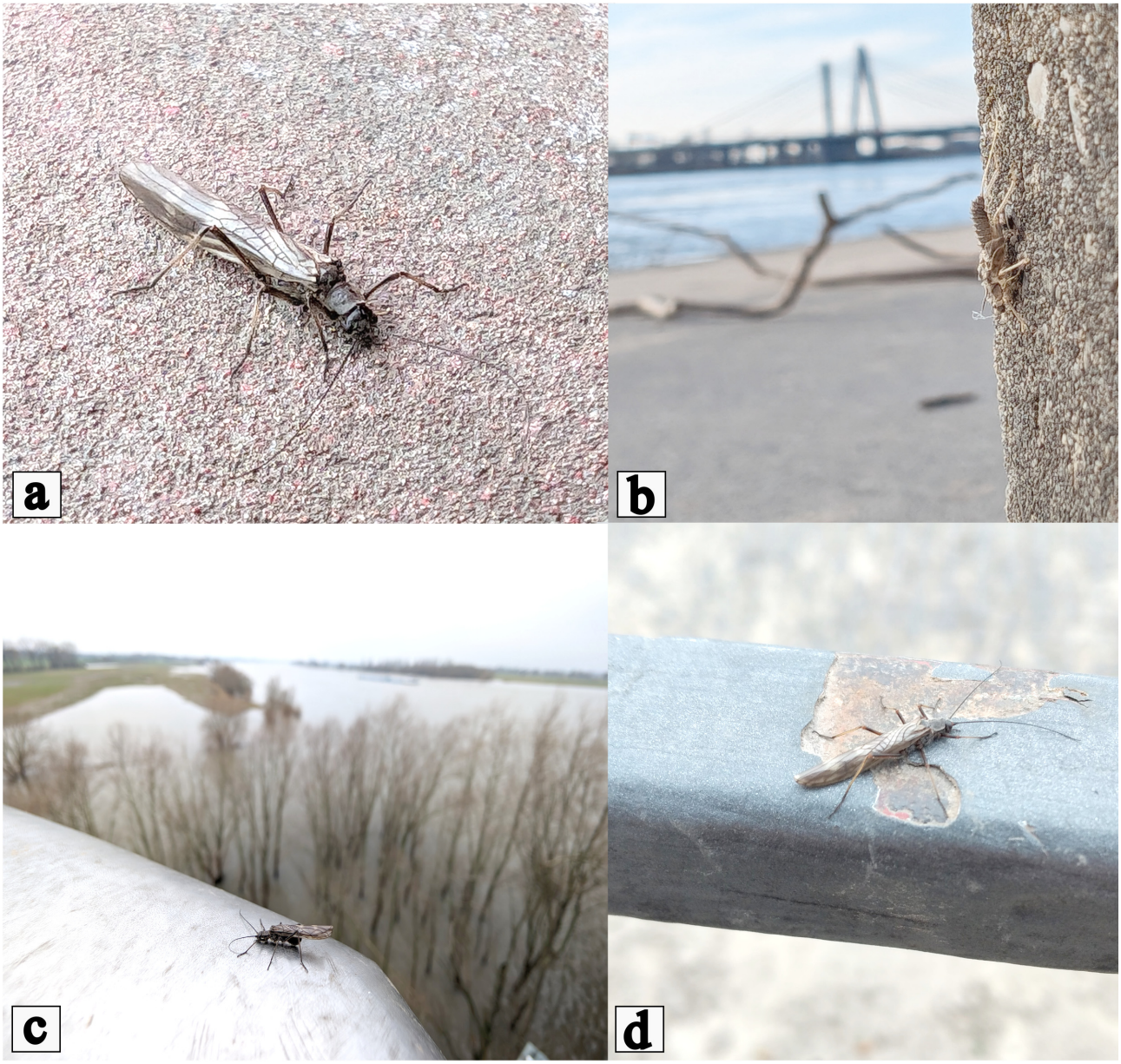

FIGURE 2. Representative findings of *Taeniopteryx schoenemundi* along the River Rhine and its surroundings. (a) Female specimen discovered on the Rhine bridge Rees-Kalkar, perched on a railing (17/02/2024). (b) One of 13 exuviae found on concrete walls along the Rhine banks at Leverkusen, Wiesdorf; the Rhine is visible in the background flowing downstream toward the Rhine-bridge Leverkusen (03/03/2024). (c) Female specimen visible in the lower left of the image, on the railing of Rhine bridge Rees-Kalkar; the background shows the Rhine flowing downstream with a large container ship in view (17/02/2024). (d) Female specimen found on the right bank of the Rhine, perched on a pedestrian railing downstream of the Kennedybrücke in Bonn-Beuel (03/03/2024). Detailed locations are provided in Table 1. (Photographs (a)–(c): Julian Enss, (d): Klaus Enting)

Discussion

We found *T. schoenemundi* on the whole lower river course in the German federal state North Rhine-Westphalia between Bonn and Emmerich am Rhein. Thus, the entire 300-kilometer stretch of the River Rhine between Bonn (Rhine km 655) and the Dutch border (Rhine km 861) appears to harbour a vital reproducing population of *T. schoenemundi*.

This discovery in the lower Rhine marks the first published records of a plecopteran in this part of the Rhine in nearly 100 years. This finding is particularly surprising given the heavily anthropogenically altered nature of the Rhine, which serves primarily as a transport highway for large vessels. The banks of the Rhine are fortified with groins and riprap to prevent lateral movement and to channel the water flow, creating an environment that is inhospitable for many indigenous aquatic species (Tittizer *et al.* 1991).

During our survey, no other stonefly species than *T. schoenemundi* were found. Although literature from the beginning of the 20th century indicates 10 different stonefly species in the lower Rhine (IKSR 2020) none of them has been found in the last 80 years. All these species are currently listed as either extirpated or highly endangered in the Red Lists of Switzerland (upper course of the River Rhine) and Germany (Lubini *et al.* 2012; Reusch *et al.* 2021). The only present stonefly in the middle course of the Rhine some 200 km upstream of our findings is the more widely distributed species *Leuctra geniculata* Stephens, 1836 which was rediscovered in the year 2018 (IKSR 2020).

Taeniopteryx schoenemundi was first described by Mertens (1923) from specimens found in tributaries to the lower Rhine (Ahr, Sieg; Klefisch 1915). Additional records comprised mountain rivers in the near surroundings (Bigge, Agger). Another historical record indicates that this species was likely present in the upper Rhine in the early 1910s (Neeracher 1910). During the early 1940s it was recorded in several mid-sized rivers across Europe (Aubert 1950; Despax 1951). However, mid-20th century water quality deterioration caused a drastic population decline, pushing this species to the brink of extirpation. By the late 1980s, *T. schoenemundi* was listed as either extirpated or highly endangered in the Red Lists of several German federal states, including North Rhine-Westphalia, as well as in Switzerland (Enting 2005; Enting & Eiseler 2011; Lubini *et al.* 2012; Wolf & Widdig 2015).

Nonetheless, the species reappeared in the beginning of the 21st century in several mid-sized mountain rivers in Germany, e.g. the River Eder (Enting 2005) and showed a notable expansion in other mid-sized rivers across Germany (Angersbach *et al.* 2010; Drescher 2018; Goertzen *et al.* 2023; Hohmann & Kleinsteuber 2023; Kleinsteuber 2022; Küttner *et al.* 2024; Mayer 2022; Wolf & Angersbach 2017) indicating a broader trend of recovery and dispersal. Despite these findings, the third version of the Red List of Stoneflies for North Rhine-Westphalia (Enting & Eiseler 2011) still showed no records of *T. schoenemundi* in the federal state after 1924. It was not until 2014 that *T. schoenemundi* was rediscovered in North Rhine-Westphalia, specifically in the Inde River (Schiffels & Enting 2015), which is a tributary to the Rur, which flows into the Maas, a tributary of the Rhine in the Netherlands. Additionally, in the lower course of the Rur (Dutch: Roer) *T. schoenemundi* was found for the first time in the Netherlands (Koese *et al.* 2014), most probably a downstream migration from the Inde population. In 2022 further records were reported for North Rhine-Westphalia from the Erft, Eifel-Rur, Hoppecke, Sieg, and Ruhr (Enting & Lorenz 2022). Some of these rivers are tributaries to the Rhine (Ruhr, Sieg, Erft). Furthermore, *T. schoenemundi* has been recorded in the upper course of the Rhine in Switzerland near Basel in 2019 and 2021 (Roesti 2021).

The appearance of *T. schoenemundi* in the lower River Rhine provokes two questions: Where does the species come from and why does the species which historically did not occur there colonize the Rhine? It is very unlikely that the (upstream) population close to Basel is the source for the newly discovered population in the lower Rhine due to the long distance—approximately 550 km from the study area—as aerial dispersal by this winter active species is thought to occur only over short distances. Downstream drift might be possible, but then recent records on this 550 km long intersect would have been highly certain. A more likely explanation would be an upstream migration from the river Meuse, a left tributary to the Rhine in the Netherlands. *Taeniopteryx schoenemundi* occurs in the tributaries of the Meuse in Germany (Inde, Rur, Fig. 1), Belgium (Lock *et al.* 2010) and the Netherlands (Koese *et al.* 2014). Nonetheless, this would have meant a travel of about 200 km downstream along the Meuse from the last known record in the Rur, and then ca. 120 km upstream in the Rhine to our most downstream record. The most probable explanation of the potential colonization sources are the mid-sized rivers which flow into the Rhine in North Rhine-Westphalia (Sieg, Erft, Ruhr, Wupper). In all these rivers the species was recorded in recent years often close to their mouth to the River Rhine, e.g. in the Wupper (Fig. 1) the record is just 200 m away from the mouth. Other

records in the Agger and the Sieg are also very close to the mouth to the Rhine and close to the historical record site from 1915 (Klefisch 1915). Thus, these tributaries might have had sustained small but viable populations during the years of heavy pollution and very recently have been the source of colonization for the Rhine.

Although the presence of a stonefly in the busiest waterway in Europe is a positive finding, the question remains why this species now prospers in the Rhine. The historical records from the late 19th and the beginning of the 20th centuries (Le Roi 1912; Klefisch 1915) indicate several stonefly species for the lower Rhine section, also encompassing winter stoneflies (e.g. *O. loewii, B. braueri*). Nonetheless, *T. schoenemundi* was only mentioned in the tributaries. Thus, historically this species seemed to have not occurred in the lower River Rhine.

The anthropogenic straightening of the River Rhine may have created conditions in the lower Rhine section that resemble those of more upstream hyporhithral and epipotamal sections – a shift called rhithralisation. The straightening increased the flow velocity and washed out the finer sediments leaving larger cobbles and the fortification of the banks with large stones additionally changed the substrate conditions. These stones and the higher current stabilized high oxygen conditions, which are favoured by most stoneflies. The current habitat conditions in the lower Rhine may now mirror those of the upper Rhine a century ago characterized by fast-flowing water and mainly gravelly substrates. Thus, this habitat change from a slower flowing, wide and sand-dominated large lowland river to a more gravelly, fast flowing river with high oxygen levels may have produced hospitable conditions for *T. schoenemundi* to colonize the Rhine from the tributaries as the habitat now resembles its preferred habitat.

Furthermore, after the extreme pollution in the 1970s and the devastating Sandoz accident (1986), the benthic invertebrate fauna of the River Rhine was extremely impoverished (Tittizer *et al.* 1994; IKSR 2020). The open ecological niches were relatively fast filled by alien invasive species particularly from the Ponto-Caspian region, which was enhanced by the opening of the Rhine-Main-Danube Canal in 1992. Since the last 30 years, waves of alien species increased in abundance then vanished again from the Rhine (IKSR 2020). Still, the different ecological niches are variable. *Taeniopteryx schoenemundi* might have colonized one of the niches. Thus, the explosive abundance increase of this stonefly along a 300 km stretch of a large river shows similarities with the behaviour of invasive species. Anyhow, it is remarkable that this small stonefly species is able to complete its life cycle despite the presence of many invasive fish (e.g. Ponto-Caspian gobies) and invertebrates species (e.g. *Dikerogammarus villosus* (Sowinsky, 1894)) which are potent predators (Leuven *et al.* 2009).

One might argue that the resurgence of *T. schoenemundi* might have been overlooked by the Bundesanstalt für Gewässerkunde (federal institute of hydrology) that conducts the standard invertebrate fauna monitoring in the Rhine. While the larvae are easily identifiable, this standard monitoring may have missed them as it is conducted in late spring when the larvae have already emerged. However, it is likely that aquatic insect researchers in Germany and the Netherlands who were actively searching for winter stoneflies in recent years would have discovered the Rhine population earlier if it would have existed. *Taeniopteryx schoenemundi* is only one of several stonefly species, particularly within the Taeniopterygidae, which reappeared in recent years in central Europe (e.g. *B. monilicornis* (Pictet, 1841), Wolf & Angersbach 2017; *B. braueri*, Wolf & Angersbach 2011) and attract attention by large range extensions in formerly devastated streams and rivers.

The discovery of *T. schoenemundi* in the River Rhine is a significant addition to the fauna of the Rhine, which is largely dominated by alien invasive species in terms of both abundance and diversity (Leuven *et al.* 2009). Given that stoneflies are highly sensitive to oxygen depletion and serve as excellent indicators of water quality (Fochetti & Tierno de Figueroa 2008; DeWalt & Ower 2019), *T. schoenemundi* strongly suggests that the water quality of the River Rhine has greatly improved in recent years (IKSR 2020). Furthermore, the presence of *T. schoenemundi* in the Rhine highlights the potential for substantial ecological recovery when water quality improves. Additionally, the appearance of a stonefly in the busiest waterway in Europe is a rare but encouraging glimpse into the ecological resilience of heavily modified rivers and raises hopes that other oxygen-demanding species might recolonize the river, too. Furthermore, it provides hope for biodiversity recovery efforts in similarly impacted rivers worldwide.

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References

Aubert, J. (1950) Note sur les Plecopteres europeens du genre *Taeniopteryx* Pictet (*Nephelopteryx* Klapálek) et sur *Capnia vidua* Klapálek. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, 13, 303–316.

Angersbach, R., Stein, U. & Wolf, B. (2010) Two new records for *Taeniopteryx schoenemundi* (Plecoptera, Insecta) in Hesse/Germany. *Lauterbornia*, 69, 51–58.

Brittain, J.E. (1990) Life History Strategies in Ephemeroptera and Plecoptera. *In*: Campbell, I.C. (Ed.), *Mayflies and Stoneflies: Life Histories and Biology*. *Vol 44. Series Entomologica*. Springer, Dordrecht, pp. 1–12. https://doi.org/10.1007/978-94-009-2397-3_1

Despax, R. (1951) *Plécoptères. Vol. 55*. *Faune de France.* P. Lechevalier, Paris, 280 pp.

DeWalt, E.R. & Ower, G.O. (2019) Ecosystem Services, Global Diversity, and Rate of Stonefly Species Descriptions (Insecta: Plecoptera). *Insects*, 10 (4), 99. https://doi.org/10.3390/insects10040099

Drescher, D. (2018) Vorkommen der Steinfliege *Taeniopteryx schoenemundi* (Mertens,1923) (Plecoptera: Taeniopterygidae) im südniedersächsischen Hügel- und Bergland – Erstnachweis für Niedersachsen. *Lauterbornia*, 85, 101–107.

Eiseler, B. & Enting, K. (2010) *Verbreitungsatlas der Steinfliegen (Plecoptera) in Nordrhein-Westfalen. LANUV-Fachbericht 23.* Landesamt für Natur, Umwelt und Verbraucherschutz NRW, Recklinghausen, 177 pp.

Enting, K. & Lorenz, A.W. (2022) Bestandsentwicklung von *Taeniopteryx schoenemundi* (Mertens, 1923) (Insecta: Plecoptera) in Nordrhein-Westfalen. Population trend of *Taeniopteryx schoenemundi* (Mertens, 1923) (Insecta: Plecoptera) in North Rhine-Westphalia/Germany. *Lauterbornia*, 88, 1–10.

Enting, K. & Eiseler, B. (2011) Rote Liste und Artenverzeichnis der Steinfliegen (Plecoptera) in Nordrhein-Westfalen 3. Fassung *In:* Landesamt für Natur, Umwelt und Verbraucherschutz NRW (Ed.), *Rote Liste der gefährdeten Pflanzen, Pilze und Tiere in NRW*, *4. Fassung*, *Band 2 – Tiere*. LANUV, Recklinghausen, pp. 535–550.

Enting, K. (2005) Aktueller Fund von *Taeniopteryx schoenemundi* Mertens 1923 (Insecta, Plecoptera) aus der unteren Eder – Erster Nachweis für Hessen seit 1984. *Hessische Faunistische Briefe*, 24, 33–40.

Feeley, H., Baars, J.R. & Kelly-Quinn, M. (2009) The life history of *Perla bipunctata* Pictet, 1833 (Plecoptera: Perlidae) in the upper River Liffey, Ireland. *Aquatic Insects*, 31 (4), 261–270. https://doi.org/10.1080/01650420903113737

Fochetti, R. & Tierno de Figueroa, J.M. (2008) Global diversity of stoneflies (Plecoptera; Insecta) in freshwater. *Hydrobiologia*, 595, 365–377. https://doi.org/10.1007/s10750-007-9031-3

Gaufin, A., Clubb, R. & Newell, R. (1974) Studies on aquatic insects to low oxygen concentrations. *The Great Basin Naturalist*, 34, 45–59.

Goertzen, D., Teichrib, A. & Hoetmer, M. (2023) Neu im Flussgebiet der Oker – Aktuelle Vorkommen von *Taeniopteryx schoenemundi* (Insecta: Plecoptera) in der Region Braunschweig. *Deutsche Gesellschaft für Limnologie (DGL) - Ergebnisse der Jahrestagung*, 2022, 5–8.

Güttinger, H. & Stumm, W. (1992) Ecotoxicology an analysis of the Rhine pollution caused by the Sandoz Chemical Accident, 1986. *Interdisciplinary Science Reviews*, 17, 127–136. https://doi.org/10.1179/isr.1992.17.2.127

Hershkovitz, Y., Dahm, V., Lorenz, A.W. & Hering, D. (2015) A multi-trait approach for the identification and protection of European freshwater species that are potentially vulnerable to the impacts of climate change. *Ecological Indicators*, 50, 150–160. https://doi.org/10.1016/j.ecolind.2014.10.023

Hohmann, M. & Kleinsteuber, W. (2023) Zur rasanten Ausbreitung von *Taeniopteryx schoenemundi* (Mertens, 1923) (Insecta: Plecoptera) in Sachsen-Anhalt. Rapid spread of *Taeniopteryx schoenemundi* (Mertens, 1923) (Insecta: Plecoptera) in Saxony-Anhalt (Germany). *Lauterbornia*, 89, 169–176.

IKSR (Internationale Kommission zum Schutz des Rheins) (2020) *Das Makrozoobenthos des Rheins 2018*. *Bericht Nr. 276d*. IKSR, Koblenz, 46 pp.

IKSR (2024) Der Rhein. Available from: https://www.iksr.org (accessed 10 October 2024)

Klefisch, T. (1915) *Beitrag zur Kenntnis der Perlidenfauna in der Umgebung Bonns. Dissertation*. Friedrich-Wilhelms-Universität Bonn, Bonn, 70 pp.

Kleinsteuber, W. (2022) Erste Nachweise der Steinfliege *Taeniopteryx schoenemundi* (Mertens, 1923) in Thüringen sowie weitere Funde der Art im benachbarten Sachsen-Anhalt (Insecta: Plecoptera: Taeniopterygidae). *Mitteilungen des Thüringer Entomologenverbandes e.V.*, 29 (1), 2–8.

Koese, B., van Maanen, B. & Boumans, L. (2014) De Negendoornige wintersteenvlieg: een nieuwe aanwinst voor de Roer en Nederland. The winter stonefly *Taeniopteryx schoenemundi*, a new species for the river Roer and the Netherlands. *Natuurhistorisch Maandblad*, 103, 217–220.

Küttner, R., Rother, A. & Plesky, B. (2024) *Taeniopteryx schoenemundi* (Mertens, 1923) (Plecoptera) erreicht Sachsen. *Entomologische Nachrichten und Berichte*, 68, 215–216.

Le Roi, O. (1912) Zur Kenntnis der Plecopteren von Rheinland-Westfalen. *Berichte über die Versammlungen des Botanischen und des Zoologischen Vereins für Rheinland-Westfalen*,1912, 25–51.

Leuven, R.S.E.W., van der Velde, G., Baijens, I., Snijders, J., van der Zwart, C., Lenders, H.J.R. & bij de Vaate, A. (2009) The river Rhine: a global highway for dispersal of aquatic invasive species. *Biological Invasions*, 11, 1989–2008. https://doi.org/10.1007/s10530-009-9491-7

Lock, K., vanden Bossche, J.-P. & Goethals, P.l.M. (2010) Checklist of the Belgian stoneflies (Plecoptera). *Bulletin de la Société Royale Belge d'Entomologie/Bulletin van de Koninklijke Belgische Vereniging voor Entomologie*, 146, 115–122.

Lubini, V., Knispel, S., Sartori, M., Vicentini, H. & Wagner, A. (2012) *Rote Listen Eintagsfliegen, Steinfliegen, Köcherfliegen. Gefährdete Arten der Schweiz, Stand 2010. Umwelt-Vollzug Nr. 1212*. Bundesamt für Umwelt, Bern, und Schweizer Zentrum für die Kartographie der Fauna, Neuenburg, 111 pp.

Mayer, J. (2022) Aktuelle Nachweise von *Taeniopteryx schoenemundi* (Mertens, 1923) (Insecta: Plecoptera) in Baden-Württemberg. Recent records of *Taeniopteryx schoenemundi* (Mertens, 1923) (Insecta: Plecoptera) in Baden-Württemberg. *Lauterbornia*, 88, 27–31.

Mertens, H. (1923) Biologische und morphologische Untersuchungen an Plekopteren. *Archiv für Naturgeschichte*, 89, 1–38.

Nagell, B. (1973) The oxygen consumption of mayfly (Ephemeroptera) and stonefly (Plecoptera) larvae at different oxygen concentration. *Hydrobiologia*, 42, 461–489. https://doi.org/10.1007/BF00047021

Neeracher, F. (1910) Die Insektenfauna des Rheins und seiner Zuflüsse bei Basel. *Revue Suisse de Zoologie*, 18, 497–590.

Pottgiesser, T. & Sommerhäuser, M. (2014) Fließgewässertypologie Deutschlands. *In:* Calmano, W., Hupfer, M., Fischer, H. & Klapper, H. (Eds.), *Handbuch Angewandte Limnologie: Grundlagen—Gewässerbelastung—Restaurierung—Aquatische Ökotoxikologie —Bewertung—Gewässerschutz.* John Wiley & Sons, Ltd., Hoboken, New Jersey, pp. 1–61. https://doi.org/10.1002/9783527678488.hbal2004005

Reusch, H., Weinzierl, A. & Enting, K. (2021) Rote Liste und Gesamtartenliste der Steinfliegen (Plecoptera) Deutschlands. *In*: Ries, M., Balzer, S., Gruttke, H., Haupt, H., Hofbauer, N., Ludwig, G. & Matzke-Hajek, G. (Eds.) *Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands. Band 5. Wirbellose Tiere (Teil 3). Naturschutz und Biologische Vielfalt 70*. Landwirtschaftsverlag, Münster, pp. 627–656.

Roesti, C. (2021) *Die Steinfliegen der Schweiz*. Haupt Verlag, Bern, 631 pp.

Schiffels, S. & Enting, K. (2015) *Taeniopteryx schoenemundi* (Mertens, 1923) (Insecta: Plecoptera) in Nordrhein-Westfalen wiedergefunden. Rediscovery of *Taeniopteryx schoenemundi* in Northrhine-Westphalia/ Germany. *Lauterbornia*, 80, 115–119.

Tittizer, T., Schöll, F., Dommermuth, M., Bäthe, J. & Zimmer, M. (1991) Zur Bestandsentwicklung des Zoobenthos des Rheins im Verlauf der letzten 9 Jahrzehnte. *Wasser und Abwasser*, 35, 125–166.

Tittizer, T., Schöll, F. & Dommermuth, M. (1994) The development of the macrozoobenthos in the River Rhine in Germany during the 20th century. *Water Science & Technology*, 29, 21–28. https://doi.org/10.2166/wst.1994.0053

Uehlinger, U.F., Wantzen, K.M., Leuven, R.S. & Arndt, H. (2009) The Rhine River Basin. *In*: Tockner, K., Uehlinger, U.F. & Robinson, C. (Eds.), *The rivers of Europe*. Elsevier Academic Press, London, pp. 199–245. [https://kops.uni-konstanz.de/handle/123456789/7202]

Wolf, B. & Angersbach, R. (2017) Wiederfund von *Brachyptera monilicornis* (Pictet, 1841) (Plecoptera, Taeniopterygidae) in Hessen. Recovery of *Brachyptera monilicornis* (Pictet, 1841) (Plecoptera, Taeniopterygidae) in Hesse/Germany. *Lauterbornia*, 84, 21–22.

Wolf, B. & Widdig, T. (2015) *Rote Liste der Steinfliegen (Plecoptera) Hessens.* Hessisches Ministerium für Umwelt, Klimaschutz, Landwirtschaft und Verbraucherschutz, Wiesbaden, 39 pp.

Wolf, B. & Angersbach, R. (2011) *Brachyptera braueri* (Klapálek, 1900) (Plecoptera, Taeniopterygidae) – neu für Hessen. *Brachyptera braueri* (Klapálek, 1900) (Plecoptera, Taeniopterygidae) – a new species for Hesse, Germany. *Lauterbornia*, 72, 59–61.