HISTORY OF RESEARCH ON *PROTEUS ANGUINUS* LAURENTI 1768 IN SLOVENIA

ZGODOVINA RAZISKOVANJA ČLOVEŠKE RIBICE (*PROTEUS ANGUINUS* LAURENTI 1768) V SLOVENIJI

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ABSTRACT

History of research on *Proteus anguinus* Laurenti 1768 in Slovenia

Olm or proteus (*Proteus anguinus* Laurenti 1768) was the first taxonomically described cave animal in the world, by J. N. Laurenti, 1768, upon a specimen that was apparently found on the famous lake Cerkniško jezero, Slovenia, yet the existence of this unusual animal in Slovenija had been known long before.

The research on *Proteus* is one of the oldest Slovenian natural history projects, a 330 year spiritual bond: from the first description by one of pioneers of karst research J. V. Valvasor in 1689, to the renowned naturalists J. A. Scopoli, who was the first researcher to actually examine proteus from the Stična area in 1762. One of the central figures of the early proteus research was Ž. Zois, the first who studied proteus behaviour, and conducted earliest physiological and ecological observations, together with Viennese zoologist Karl von Schreibers. Zois's work was continued by two researchers of proteus distribution F. J. Hochenwart and H. Freyer, and other researchers of the 19th and 20th century.

For the last 250 years, this mysterious animal has constantly raised scientific and public attention, and gradually became not only an important symbol of Slovenia's nature, but also a part of its cultural heritage. The zoologically extraordinary *Proteus* was also an important object in the history of international nature research, puzzling the minds of most prominent naturalists, from Linnaeus, Cuvier and Humboldt, to Lamarck and Darwin.

This article also presents reproductions of the earliest illustrations of proteus: a collection of ten published and unpublished work between 1752 and 1849, a forgotten heritage of the first 100 years of proteus research. *In Memoriam* Žiga Zois (1747–1819).

Key words: Olm, Proteus anguinus, history of natural history, Slovenia, Zois

IZVLEČEK

Zgodovina raziskovanja človeške ribice (*Proteus anguinus* Laurenti 1768) v Sloveniji

Človeška ribica ali močeril (*Proteus anguinus* Laurenti 1768) je bila prva taksonomsko opisana jamska žival na svetu. Laurenti jo je opisal leta 1768, po primerku, ki naj bi ga našli na Cerkniškem jezeru, vendar je bil obstoj te nenavadne dvoživke v Sloveniji že dolgo znan.

Raziskovanje človeške ribice je eden od najstarejših slovenskih naravoslovnih projektov, 330 letna duhovna vez. Od Valvasorja, enega od pionirjev raziskovanja krasa, ki je objavil prvo omembo proteusa že leta 1689, do priznanega naravoslovca Scopolija, prvega raziskovalca, ki je človeško ribico, najdeno leta 1762 v okolici Stične, dejansko prvi preučil. Ena od osrednjih osebnosti zgodnjih raziskovalcev človeške ribice, Ž. Zois, je kot prvi preučeval vedenje človeške ribice (1795), in je v sodelovanju dunajskim zoologom Karlom von Schreibersom izvedel najzgodnejše fiziološke in ekološke raziskave na tej vrsti. Zoisovo delo sta nadaljevala dva raziskovalca razširjenosti človeške ribice, muzealca F. J. Hochenwart in H. Freyer, ter drugi raziskovalci 19. in 20. stoletja, do danes.

Zadnjih 250 let je ta skrivnostna žival nenehno dvigovala pozornost znanstvenikov in javnosti, ter postopoma postala ne le pomemben simbol slovenske narave, temveč tudi del njene kulturne dediščine. Človeška ribica, je bila zaradi svojih zooloških posebnosti večkrat pomemben objekt v zgodovini razvoja mednarodne naravoslovne misli med 17. in 19. stoletjem, in je zbujala vprašanja v najpomembnejših naravoslovcih, od Linnéja, Cuvierja in Humboldta, do Lamarcka in Darwina.

V prispevku so predstavljene tudi reprodukcije najzgodnejših ilustracij človeške ribice: zbirka desetih objavljenih in neobjavljenih del med letoma 1752 in 1849, dediščina prvih 100 let raziskovanja človeške ribice. V spomin na Žigo Zoisa (1747–1819).

Ključne besede: človeška ribica, Proteus anguinus, zgodovina naravoslovja, Slovenia, Zois

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1 INTRODUCTION

Karst is a geomorphological landscape, named after the region of Kras [Italian: *Carso*, German: *Karst*], a limestone plateau above the Gulf of Trieste, on the north western corner of the Dinaric karst (Gams, 2004). Its monumental phenomena, such as the river thundering into the abyss of Škocjanske jame, fascinated antique writers and travellers along the only practicable road from Central Europe to Mediterranean (Kranjc, 2019). Around these karst features also raised early researchers (e.g., Imperato, Valvasor, Nagel, Steinberg, Hacquet, Gruber, Hochenwart), and through early international scientific cooperation the region *Karst* transformed in landscape *karst,* observed in landscapes around the world. By the end of the 19th century the understanding of karst developed into karst science (e.g., Cvijić, Kraus and Martel) (Kranjc, 1998; Gams, 2004; Kranjc, 2019).

But this journey could not be completed before the cognition that karst underground harbours unique life, which emerged through the second part of the 19th century. The birth of speleobiology was triggered by Ljubljana entomologist Ferdinand J. Schmidt (1791–1878) with his description of the first cave beetle *Leptodirus hochenwartii* Schmidt 1832 (Schmidt, 1832; Aljančič, 1991; Polak, 2005), followed soon by discoveries of other cave-adapted invertebrates in Postojnska jama (Aljančič et al., 1993; Sket, 1993A; Sket, 2012). The hotspot of karst research finally revealed the global hotspot of the subterranean biodiversity recognised today (Sket, 1993A; Sket, 1999; Culver and Sket, 2000; Culver & Pipan, 2009; Sket, 2012). An essential part of this process at the emergence of modern science was the research of the olm or proteus (*Proteus anguinus* Laurenti 1768).

2 FIRST RECORDS ON PROTEUS

In Slovenian part of the Dinaric karst (Gams, 2004), proteus spans from the regions of Kras and Vipava valley in the west, trough Notranjska and Dolenjska, to Bela krajina on its south-east, in 330 years of research documented at over 180 localities (reviews of proteus distribution in Scopoli, 1772; Hochenwart, 1838; Freyer, 1846A; Aljančič, 1962; Aljančič, 1964A; Aljančič, 1984; Sket & Arntzen, 1994; Sket, 1997; Gorički et al., 2017; Hudoklin & Aljančič, 2017). In most of these regions, proteus occasionally appears on the surface habitats (e.g., at karst spring, well, surface stream, flooded karst polje). *People knew it from their tradition and experience* (Zois, 1807), found it after floods or came across it on karst springs while collecting drinking water or watering their livestock (Michahelles, 1831; Hochenwart, 1840), such as the Virski Studenec spring near Stična, Slovenia, where this unusual animal was called in Slovenian *bela riba* [white fish] or *človeška riba* [human fish], *because of its toes and fleshy skin colour* (Zois, 1807).

In the karst landscape, where surface water is always lacking (Gams, 2004), proteus may have served as an indicator of a reliable source of drinking water, which could explain the symbolism of the depiction of two supposed protei on a stone well-head (10th century), which was once located in front of the San Nicolò church on the Venetian Lido (Vornetscher, 1972; Shaw, 2005), perhaps quarried and sculpted somewhere on the Classical karst (Aljančič et al., 1993).

It is not a surprise that proteus was for the first time shortly described 330 years ago by Janez Vajkard Valvasor (1641–1693), a Slovenian polymath and one of the pioneers of karstology, in his fundamental work *Die Ehre des Herzogthums Krain* [The Glory of the Duchy of Carniola] (Valvasor, 1689). This is the earliest known published description of any cave animal.

When Valvasor was returning from one of his many study travels around the Duchy of Carniola (today's central Slovenia), people from the area between Logatec and Vrhnika (25 km south-west from Ljubljana), told him about local curiosities, among them about the Lintvern, an unusual spring from which the water flows only twice a day. The next day, on 25 June 1684, Valvasor enquired further and visited the spring. The local guide explained the phenomenon of periodic flow by attributing it to a legend of a dragon that lives in the hill behind the spring. Namely, when the water level rises up to dragon's throat, it provokes discomfort; therefore the dragon has to move causing the water to flow from the spring. And that happens twice a day. As proof, he told Valvasor about the occasional findings of washed-out dragons. Valvasor interviewed the Vrhnika postal master Hofmann about the matter, who described the not fully grown dragon he collected two years earlier and displayed to the public. This led Valvasor to conclude, that this was, of course, not a mythological creature, but an animal *shorter than a span, similar to a lizard, in sum, an earthly reptile,*

which can be occasionally found here and there (Valvasor, 1689). Unfortunately, Valvasor never saw the animal, although visited or thoroughly explored several proteus localities (e.g., Podpeška jama; Aljančič et al., 1993).

Proteus was also recognised from the mentioning in the book of Franc Anton Steinberg (1684–1765), Slovenian geographer and one of pioneers of karst research, who described an unusual finding of *five white, four-legged fish,* caught by fisherman Primož Ziherle in 1751 in the flooded Planinsko polje near the spring of Malni (Steinberg, 1758; Freyer, 1846A; Grošelj, 1933; Aljančič et al., 1993; Shaw, 2010). It is interesting to note, that although Steinberg tried to explain how Valvasor's intermittent spring Lintvern may function, Steinberg himself never noticed the resemblance between with the animals described by him and Valvasor (Freyer, 1846A).

Both mentioning of proteus before its actual taxonomic description (Valvasor, 1689; Steinberg, 1758) were recognised already by the early researchers (Freyer, 1846A). Significance of such precious mentioning and representation was just recently recognised and evaluated by Trewor Shaw and Alenka Čuk (Shaw & Čuk, 2015), hiding on a beautiful though imaginative map, one of 12,000 units of the Moll Atlas kept at the Moravian Library in Brno (Geyer, 1752; Shaw & Čuk, 2015). Along with other seven original representations of karst features from Carniola, attributed unknown artist Geyer, the particular Map of Postojna and surroundings from 1752 (Geyer, 1752; Shaw & Čuk, 2015; Moll-0001.210; Fig. 1) has depicted a cave entrance, with an intrigues panel (translated from German after Trewor Shaw; Shaw & Čuk, 2015): "A small cave in which the peasant inhabitants here catch a lot of snakes and sell them to Venice". The cave was identified by Shaw & Čuk (2015) as being the Črna jama, where proteus has first been found in the underground (Hochenwart, 1838; Shaw & Čuk, 2015; see details below).

The artist drew at least five snake-like creatures inside this stylized cave, indeed creating a realistic sight on a group of proteus somewhere in the Postojna-Planina Cave System. This map represents the oldest known drawing of proteus (Shaw & Čuk, 2015). It is

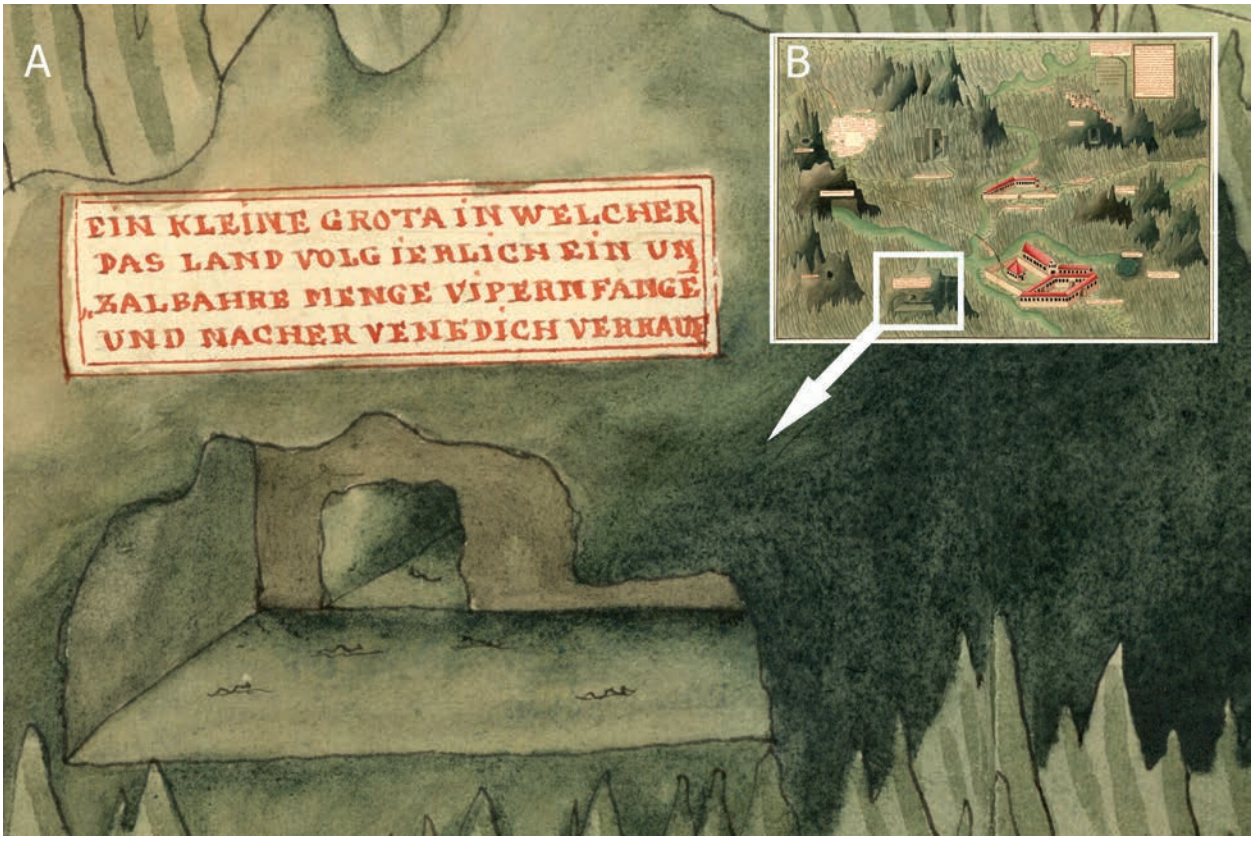

Figure 1: Geyer, 1752: Imaginative presentation of the Črna jama with several proteus (A), detail at the Map of Postojna and surroundings, 63,5 x 89 cm (B) from the Moll Atlas (Geyer, 1752; first published in Shaw & Čuk, 2015; Collection of the Moravian Library in Brno, Czech Republic, Moll-0001.210, with permission).

surprising that Steinberg, born near Postojna, did not mention such activity among the local people only six years after the map was drawn. If the stated yearly selling of proteus to Venice (or Trieste?) is correct, such traffic could be attributed rather to be used as fishing-bite, or sold as delicacy, as occasionally reported to be on sale at the fish-market in Trieste in the first half of the 19th century (Configliachi & Rusconi, 1819; Shaw, 1999). It is also worth to mention, that *bela kačica* [white snake, diminutive form] was indeed one of the documented Slovene vernacular names (Freyer, 1850; see below).

3 HOW PROTEUS WAS DISCOVERED

The first researcher to actually examine proteus was Joannes Antonius Scopoli (1723–1788), a South Tyrolean physician, between 1754 and 1769 appointed to his first post at the mercury mine in Idrija, Slovenia (Soban, 2004). There he became one of the distinguished naturalists of his time, with special dedication to fungi, plant and animal taxonomy of Carniola (Soban, 2004); among higher taxa, Scopoli introduced *Caudata* (Aljančič, 2012).

An unusual animal (perhaps two specimens; Soban, 2004) was brought to Scopoli from the area of Stična (25 km south-east of Ljubljana) by his associate botanist Franz X. Wulfen (1728–1805). In his letter to Carl Linnaeus (1707–1778), dated 3rd May 1762, Scopoli presents the animal of an unknown amphibian living in caves around Stična, with detailed taxonomic description under the name *Lacerta caeca* [*blind lacerta*] to be included in the next edition of *Systema Naturae,* and offered to send him the specimen (Scopoli, 1762; translated from Latin by Darinka Soban; in Soban, 2004):

To the distinguished and illustrious Sir
Mr. Carl Linnaeus
Knight of the North Star etc., etc.
Restorer of the Natural Sciences,
and to the most learned Assembly
of the Royal Academy of Sciences
in Uppsala.

This new Lacerta species
is presented and dedicated
by Joannes Scopoli, physician at Idrija.

Among the natural specimens which I was the first to discover in the Duchy of Carniola, this new amphibian species certainly is not of the least importance. I obtained it recently as a living animal in Ljubljana from my learned friend F. X. Wulfen, of the Society Jesu. It is worth being included in the Systema Naturae of the distinguished Knight Carl Linnaeus as

9. caeca. Lacerta [blind lizard]: *It has a short, two-sided tail, three fingers on the hands and two toes on the feet. It lives in fresh waters which emerge from the underground caves near the place Stična. Not frequent.*

Description: Body clumsy, cylindrical, bare, mucous, thicker than a human thumb.

Head rounded, partly flattened, thicker and smaller on the back, with an obtuse mouth and a shorter lower jaw; no eyes, two protruding tubercles in their place; on both sides of the throat auricular combs, composed of 3-4 fringed ramifications, cinnabar-coloured. Both jaws with teeth, the mouth opening small, only 3 lin. [6.3 mm] long. Legs: anterior with three fingers, posterior with two toes; without nails.

Variation 1º stature of standing animal, white all over, auricular comb with four ramifications.

2º stature and colour as shown in the picture, auricular comb with three ramifications. It feeds on tiny snails, abundant in our waters. I add some samples.

I keep this animal preserved in alcohol, together with Sepia sepiola. I will send it to you together with the bird Upupa muraria and the rhizomes and specimens you graciously asked me for. My only request is that you prevail upon Mr. Jacquin, whom you already know from elsewhere, to receive in Vienna the items enumerated above and forward them to you. Please kindly acknowledge the receipt of my box, filled with insects, plants and rocks, which I had sent to Mr. Jacquin in order to be forwarded to you via Mr. Gronovius, as soon as you get it. In the meantime, I wish you good health, and remain benevolent to me.

Posted at Idria on 3rd May 1762.

If you will kindly answer, please direct the letter as follows:

Vienna – Ljubljana – Idrija.

Such letters, together with its valuable supplements (e.g., specimens, seeds, drawings, new books), were practically the only way to contribute material for the growing *Systema Naturae*. Well packed for 1-18 month long post delivery from Idrija to Upsala,

the mail was first examined in Vienna (Soban, 2004). Many of these descriptions of new species from Carniola are still valid today, and Linnaeus himself named Scopoli as one of the *auctores reformatories* (Soban, 2004; Aljančič, 2012). A closer insight into the part of the early natural history science of the Linnaean period is embraced in the remaining correspondence between Linnaeus and Scopoli (1760–1775), devotedly collected, translated and interpreted by physician and botanist Darinka Soban (Soban, 1995; Soban, 2004).

The enclosed drawings of proteus were unfortunately lost; probably archived separately, or even forwarded for an opinion – perhaps not destroyed. Although Linnaeus' reply to the letter is also lost, and the discovery was never again mentioned in the preserved correspondence, we may well understand concerns of Linnaeus and his time: "Undoubtedly, it is as hard to recognise animals in their larval forms as masked people at the theatre;" (Linnaeus and Österdam, 1766; Soban, 2004). Though, the animal in question indeed belongs to a species not known before, the obvious amphibian larval characteristics of its body (e.g., external gills, flat tail fin) implied it must still be a tadpole of an unknown species. Not aware of proteus neotenic nature (Aljančič et al., 1993; Sket, 2007), Linnaeus hesitated to publish it until Scopoli finds an adult specimen as well (Scopoli, 1772; Schreibers, 1801; Hochenwart, 1838; Aljančič et al., 1993; Soban, 2004; Aljančič, 2012). The next, 12th edition of *Systema Naturae* did not contain Scopoli's *Lacerta* (Linnaeus, 1766), while Linnaeus himself was not as strict in the case of the greater siren (*Siren lacertina*) (Schreibers, 1801), another neotenic amphibian. It appears that Linnaeus has never actually saw proteus.

Finally, in 1768, Viennese physician and naturalist Joseph Nicolaus Laurenti (1735–1805) formally described the species under the name of *Proteus anguinus,* and included it in his extensive study *Sinopsis Reptilium* [An Overview of Reptiles] (Laurenti, 1768). Description of the new genus and species (translated from Latin by Darinka Soban; in Soban, 2004):

[Page 35–36, description of the new genus]
GENUS V.
PROTEUS
An amphibian that has simultaneously gills and presumably lungs. Under the surface of the water it breathes water with the gills, when on dry land it inhales air with the lungs; perhaps it can thus leave a dried-out lake and go elsewhere. The jaws and the fingers stunted. The tail ridged. It differs from some interim development stage

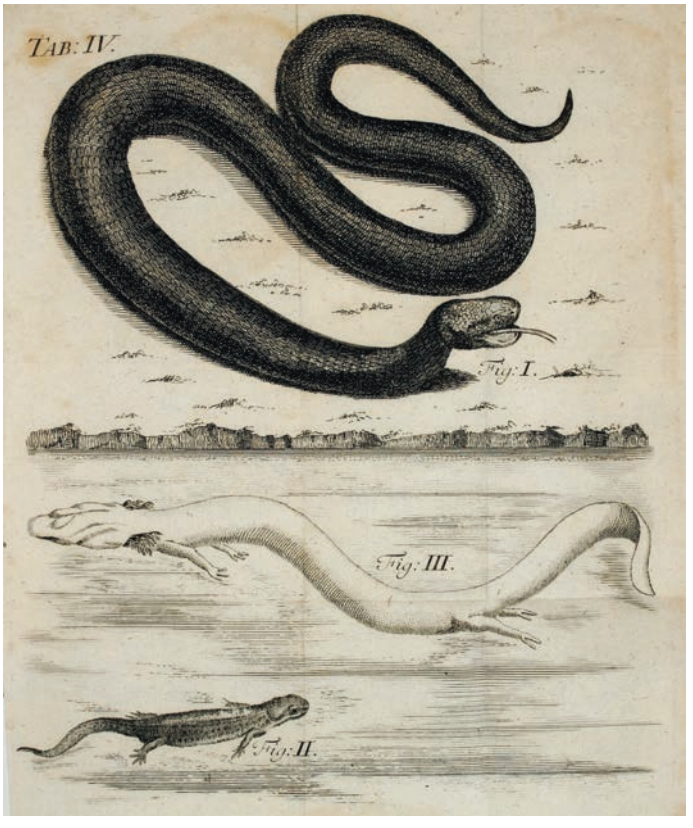

Figure 2: Joseph N. Laurenti, 1768: First accurate illustration of proteus, in a swimming position, although depicting a specimen stored in the collection of Sigismund Hohenwart (Fig. III, Laurenti, 1768; Ernst Mayr Library, Museum of Comparative Zoology, Harvard University, USA).

by its ability to use the gills and the lungs simultaneously, not successively.

[Page 37, description of the new species]
XXXVI. Proteus anguinus. Tab. IV, Fig. 3.

Diagnosis:
It walks with its hind legs. The body rounded, oblong, very pallid, without fins, with coral-red gill appendages. The tail flattened, covered with skin. It has no eyes.

It lives in Lake Cerknica in Carniola in the spring. The specimen has been kindly provided by the reverend father Hohenwarth, a Jesuit, for the purposes of research and for the drawing.

NB: Whoever pretends this is just a large larva should show the animal that grows from it, lest he lose his credibility.

The note at the end of the description was pointing at Linnaeus, indicating that some discussion on proteus may have existed even before first publication (Soban, 2004). Proteus was first mentioned in the 13th edition of *Systema Naturae* (1789), in a short comment explaining where proteus should taxonomically be placed (i.e., in Amphibia, between *genus Rana* and *Draco*; see comments on the taxonomical classification of the time in Sket, 2007), if most careful observations of more researchers would establish that no slower or later metamorphosis occurs (Gmelin, 1789; Aljančič, 2007).

The description is short, with errors due to little information Laurenti could possibly received from Hohenwart, with no opportunity to dissect it (Schreibers, 1801). The description is accompanied by an illustration of the specimen, preserved in alcohol, in a reconstructed swimming position (Fig. 2), although Fitzinger presumes that it was drawn upon a live animal (Fitzinger, 1850). The finding site indicated by Laurenti was the intermittent lake Cerkniško jezero, Slovenia, a karst polje already famous around the world (Valvasor, 1689; Steinberg, 1758; Fitzinger, 1850; Aljančič et al., 1993; Gams, 2004).

Six years after Laurenti, Scopoli finally published his description of proteus (Scopoli, 1772), although less detailed as in the letter to Linneaus. Scopoli corrected Laurenti's *terra typica*, saying that proteus is *not in the Cerkniško jezero, but in the underground cave near Stična* (translated from Latin by Darinka Soban; in Soban, 2004), occasionally washed-out in summer (Scopoli, 1772). In this short comment, he did not explain why he disagrees with Laurenti's Cerkniško jezero, and the origin remained open (Sket, 2007). Indeed, 200 years after Scopoli and Laurenti, the first case of washed-out proteus has been documented at the edge of the Cerkniško jezero (Aljančič, 1966C), and recently proteus was also found *in situ* (Drole, 2017). Although rarely, proteus does appear in the area *in spring-time* (e.g., washed-out after spring floods) as was written down by Laurenti (Sket, 2007).

Details on these earliest specimens could be found in publications of researchers, who may still had access to original unpublished information (e.g., Žiga Zois, Franc J. Hochenwart, Karl von Schreibers, Henrik Freyer; see their contributions further below). Carl Schreibers remembers that the Museum of Natural Curiosities in the University of Vienna received a specimen nearly the same time as Hohenwart, and that Scopoli received more than one specimen (Schreibers, 1801). At the beginning Henrik Freyer accepts Laurenti's Cerkniško jezero (Freyer, 1842), later explains that people of Stična raised Scopoli's attention on proteus, that Scopoli sent one specimen to Johann J. Well (1725–1787), professor at the Medical Faculty of the University of Vienna (1776–1780), and that Hohenwart received his exemplar from Scopoli (Freyer, 1847A).

The area of Stična seems to be more plausible origin of Laurenti's exemplar, if we look closer, who actually collected these very first specimens. As mentioned before, Scopoli received proteus from his associate Wulfen, of Swedish origin, at that time lecturing logic, metaphysics and Newton's physics at the Jesuit Lyceum in Ljubljana (Praprotnik, 2016).

On the other hand, Laurenti received his specimen not more than six years later from naturalist Sigismund Hohenwart (1745–1825), at that time vicar in Klagenfurt/ Celovec. Jesuit Sigismund Hohenwart was born in Celje (not to confuse with other naturalists of this old Carniolan noble family; SIC Soban, 2004), and started to accompany his teacher Wulfen at field-excursions, often together with other naturalists (Dežman, 1856). His large collection became one of foundations of the first Austrian museum, the Styrian Provincial Museum (Joanneum) in Graz/Gradec (1811).

We should not overlook the connection of Jesuits Wulfen and Hohenwart with the aincient Cistercian monastery in Stična, and the possibility that the monks from Stična draw the attention to proteus (Soban, 2004; Južnič, 2009, but check author's claims in the primary sources), but this seems to be less likely, because Scopoli would not have given the credit only to Wulfen. Nevertheless, it does appear that the monks

have kept proteus at the Stična Monastery to forcast changes in weather (Agapito, 1823; Soban, 2004).

Within the network of these Enlightenment naturalists, we may presume, Scopoli must have known the origin of the Hohenwart's specimen when correcting Laurenti, since otherwise he would simply publish his data as an additional area of proteus distribution, not as its sole. But, from which karst spring within this small area of Stična? Already from the experience of early researchers (Zois, 1807; Hochenwart, 1838; Freyer, 1846A), which we may only confirm (Bressi et al., 1999; Kordiš, 2016; Hudoklin & Aljančič, 2017), the only reliable site to see rare proteus outside caves in the area is the Virski studenec, from this point of view the most plausible *locus typicus* of Laurenti's proteus.

4 EARLY STUDIES

After a few echoes on the taxonomic description were settled, proteus seemed to be forgotten (Zois, 1807). It was Karl Franz Anton von Schreibers (1775–1852), physician and later professor of zoology at the Medical Faculty of the University of Vienna and director of the Viennese Natural History Collection, who first studied the proteus in detail. In 1795, while rearranging the museum collection, he found a jar with half dry specimen not alike any animal he knew (Aljančič, 2007). To further explore proteus anatomy, young Schreibers has asked renowned Ljubljana naturalist Žiga Zois, through his teacher Professor Peter Jordan, Zois' acquaintance, for fresh specimens.

Baron Žiga Zois (1747–1819) was the main figure of the Slovene Enlightenment, named after him the *Zois Circle*. For half a century this was the centre of scien-

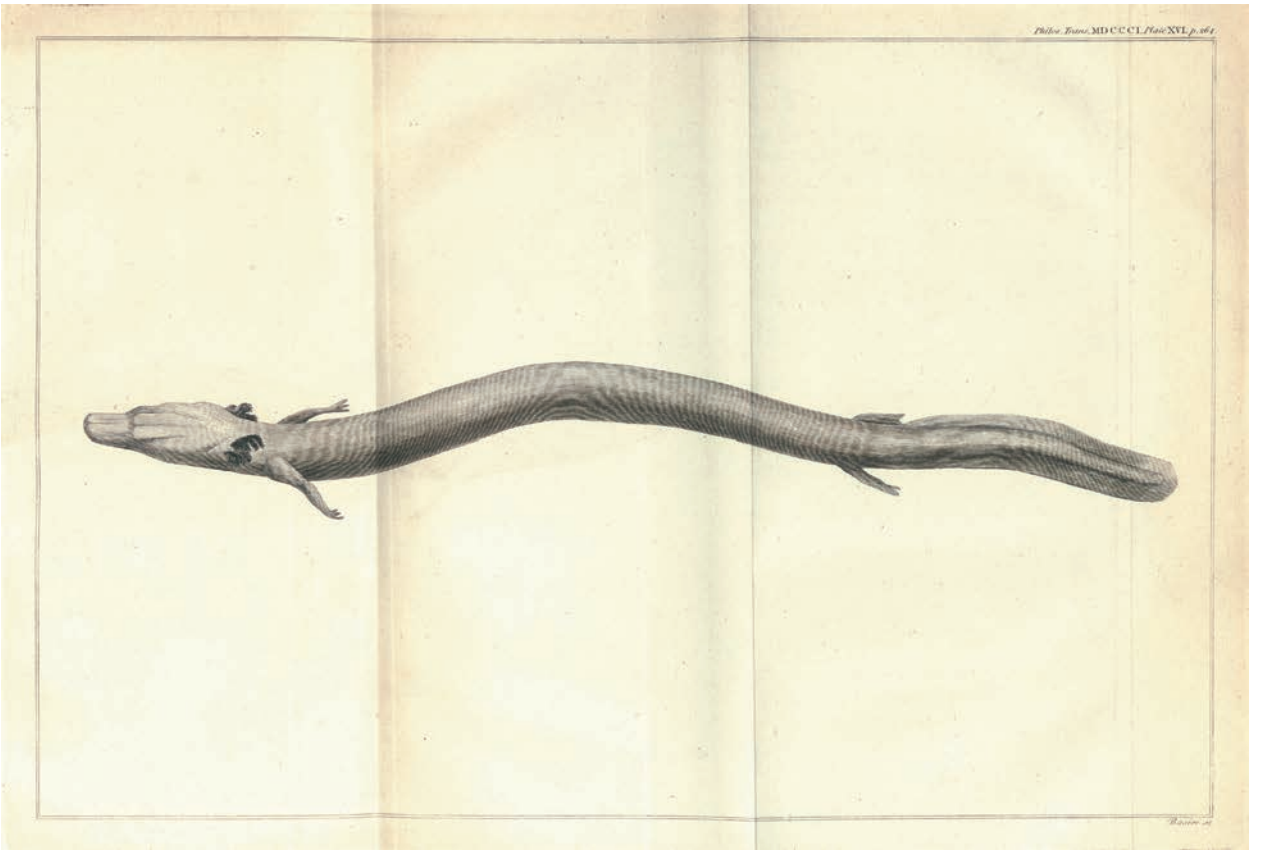

Figure 3: Karl von Schreibers, 1801: Proteus depicted in swimming position, with red external gills – *information from Zois reports on proteus behaviour, since Schreibers had not the opportunity to see a live animal during this early study (Schreibers, 1801; Library of the Royar Society, The United Kingdom).*

tific efforts in many different fields of science in Ljubljana, closely connected with similar natural history circles in cities across Europe (Aljančič, 1997; Aljančič, 2007). These fragments of the early modern science were thoroughly presented by Marko Aljančič (Aljančič, 1997; Aljančič, 2007; with Slovene translation and reprint of Zois, 1807). Among naturalists being part of the *Zois Circle*, we should mention his brother Karel Zois (1756–1799), Balthasar Hacquet (1739/40–1815), Franc J. Hochenwart (1771–1844), Valentin Vodnik (1758–1819), Rihard Ursini Blagay, and Valentin Stanič (1774–1847). Following the mountaineering steps of Scopoli, they were among the first collecting botanical, zoological, paleontological and mineralogical material in Alps of Carniola and Carinthia (Austria), during which the *circle* also accomplished some of the first documented ascents on higher peaks of Alps, from Triglav (2864 m; 1778) in Slovenia, to Grossglockner (3797 m; 1800) in Austria (Mikša & Zorn, 2016). Zois collection of minerals became one of foundations of Ljubljana Museum (Dežman, 1856).

Zois collected fresh specimens for Schreibers' anatomical research, and was the first who actually studied live proteus. He was determining the appropriate breeding parameters and was the first who researched proteus behaviour and physiology (feeding, locomotion and reaction to light, heart pulse and gill blood flow, etc.) (Aljančič, 2007). Between 1795 and 1807, Zois maintained proteus in his Ljubljana palace; long enough to first dispute the aforementioned Linnaeus' comment (Gmelin, 1789) of a possible later metamorphosis into an adult animal through long-term captivity (Zois, 1807; Hochenwart, 1838; Aljančič, 2007).

Schreibers' detailed study was also the first on the anatomy of proteus. One of main goals of Schreibers study was to demonstrate the adult stage of proteus through anatomical proof, which was supported with Zois' observations from Ljubljana and Stična (reports were submitted in three letters: 1795, 1799 and 1800) cited through the paper, published upon a lecture at the Royal Society in London (Schreibers, 1801; Fig. 3). On his travel to London and Paris (1800), Schreibers presented results of his studies, and for the first time properly introduced proteus to the science, which initiated the interest of famous naturalists Georges Cuvier (1769–1832) in France, Lorenz Oken (1779–1851) and Karl Michahelles (1807–1834) in Germany, and Pietro Configliachi (1777–1844) and Mauro Rusconi (1769–1832) in Italy.

The only Zois' (unsigned) published contribution is dedicated to proteus (Zois, 1807). There, Zois pre-

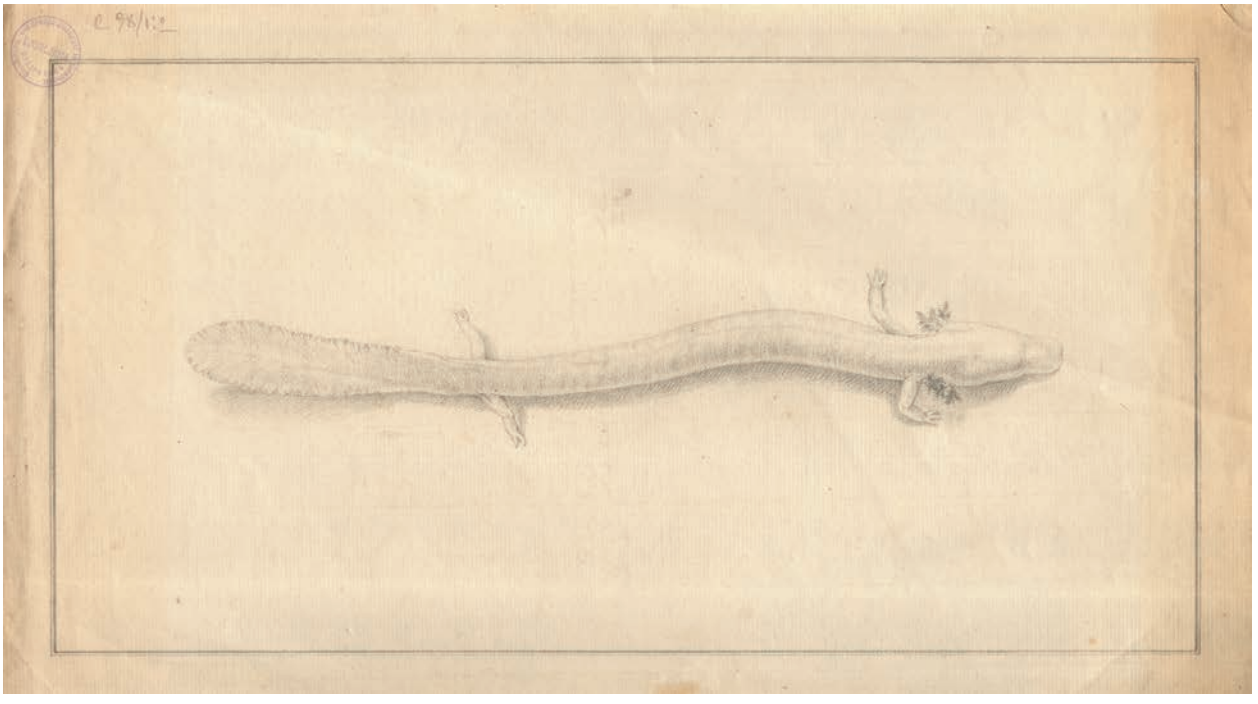

Figure 4: Vinzenz Dorfmeister, upon preparations of Žiga Zois (I), around 1805: one of three earliest drawings of proteus upon a live animal (pencil drawing, unpublished; details in Aljančič, 1998; Library of the Slovenian Academy of Sciences and Arts, Zois Legacy R 98/1, with permission).

sents proteus on high scientific level, explaining the geology of Stična, proteus distribution, history of research and review of literature, and the results of Schreibers (1801) and Zois' own research (Aljančič, 2007). Since the already explained inaccessibility and rarity of proteus, at the time known only from the Stična area, Zois rather sent accurate coloured illustrations to naturalists and museums around Europe, produced for that purpose by Vinzenz Dorfmeister, professor of drawing at the Ljubljana Lyceum (Zois, 1807; Fitzinger, 1850). Only three drawings were preserved, hidden in the archive of the Library of the Slovenian Academy of Sciences and Arts (R 98/1; legacy of Zois), where they were found in 1998 by archivist Drago Samec among the legacy of the study material of Academician Primož Ramovš (1921–1999), and firstly showed the drawings to Marjana Peterlin (Natural History Society of Slovenia), who realized their potential importance. It is not possible to describe the excitement of Marko Aljančič later the same day, when he finally saw the drawings he was searching for many years. According to Marko Aljančič, these illustrations were produced around 1805, representing the earliest preserved illustrations of proteus, drawn upon a live animal (Aljančič, 1998; Marjana Peterlin, per. comm. 8 March 2019; Figs. 4, 5 & 6).

Most unfortunately, as reported by Freyer (1849), almost all scientific material from the time of early researchers, which Schreiber gathered at the Vienna Museum, was destroyed in fire during March Revolution 1848 (Aljančič, 1991; Aljančič, 1997). Lost was the invaluable collection of early specimens, Schreibers' exhaustive notes on Scopoli's and particularly Zois' new finds, observations, illustrations, etc., including the most precious live proteus from Laze on Planinsko polje (Freyer, 1849), apparently the specimens documented by Freyer a few years earlier (Freyer, 1846B; Figs. 8, 9 & 10). One of rare objects which were not destroyed, is an accurate wax model of an particularly well grown proteus, that Zois collected at Rupe near Stična in 1806 (Aljančič, 1991). While Zois ordered illustrations of proteus to overcome the constant shortage of specimens before the presence of proteus in the Črna jama became generally known (Aljančič, 1998), Schreibers ordered such models, perhaps also to create more educative presentation of proteus at the Vienna museum (Aljančič, 1991). It is interesting to note, that both presentations appeared in about same time, perhaps created upon the same individual.

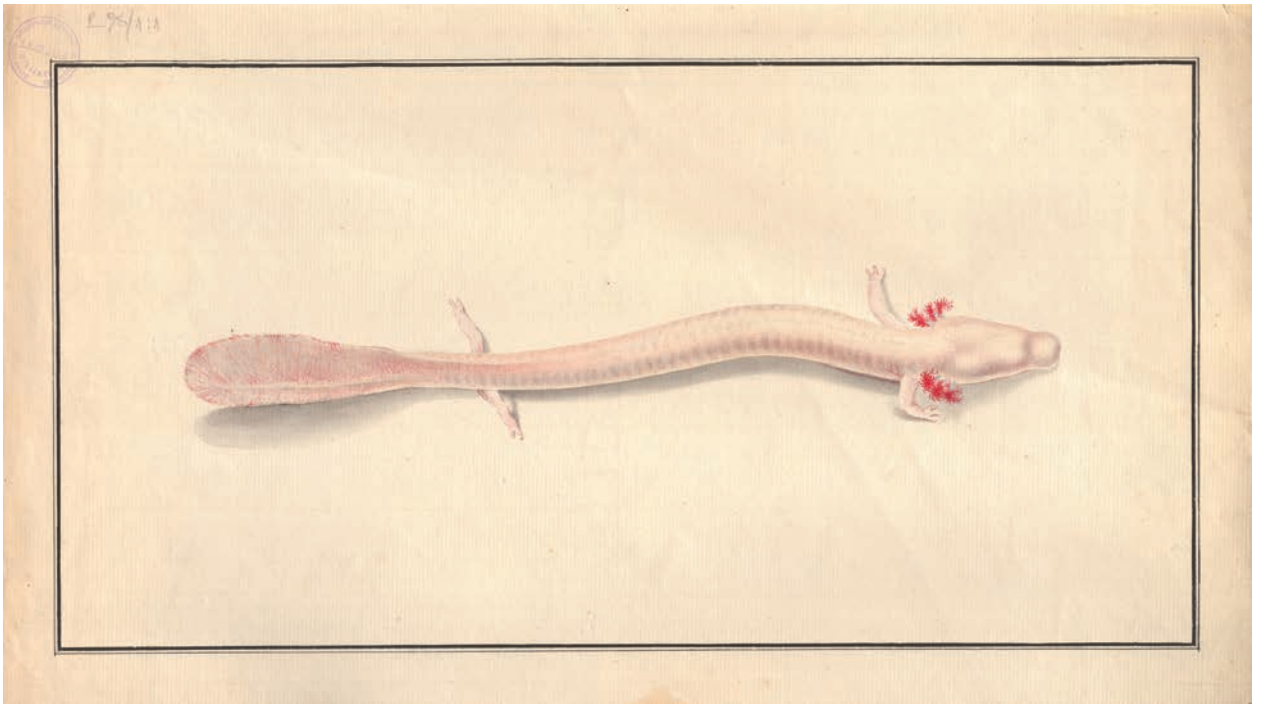

Figure 5: Vinzenz Dorfmeister, upon preparations of Žiga Zois (II), around 1805: coloured version of the same animal and position as in Fig. 4; a particularly well grown adult (coloured drawing in approx. life-size; first published in Aljančič, 1998; Library of the Slovenian Academy of Sciences and Arts, Zois Legacy R 98/1, with permission).

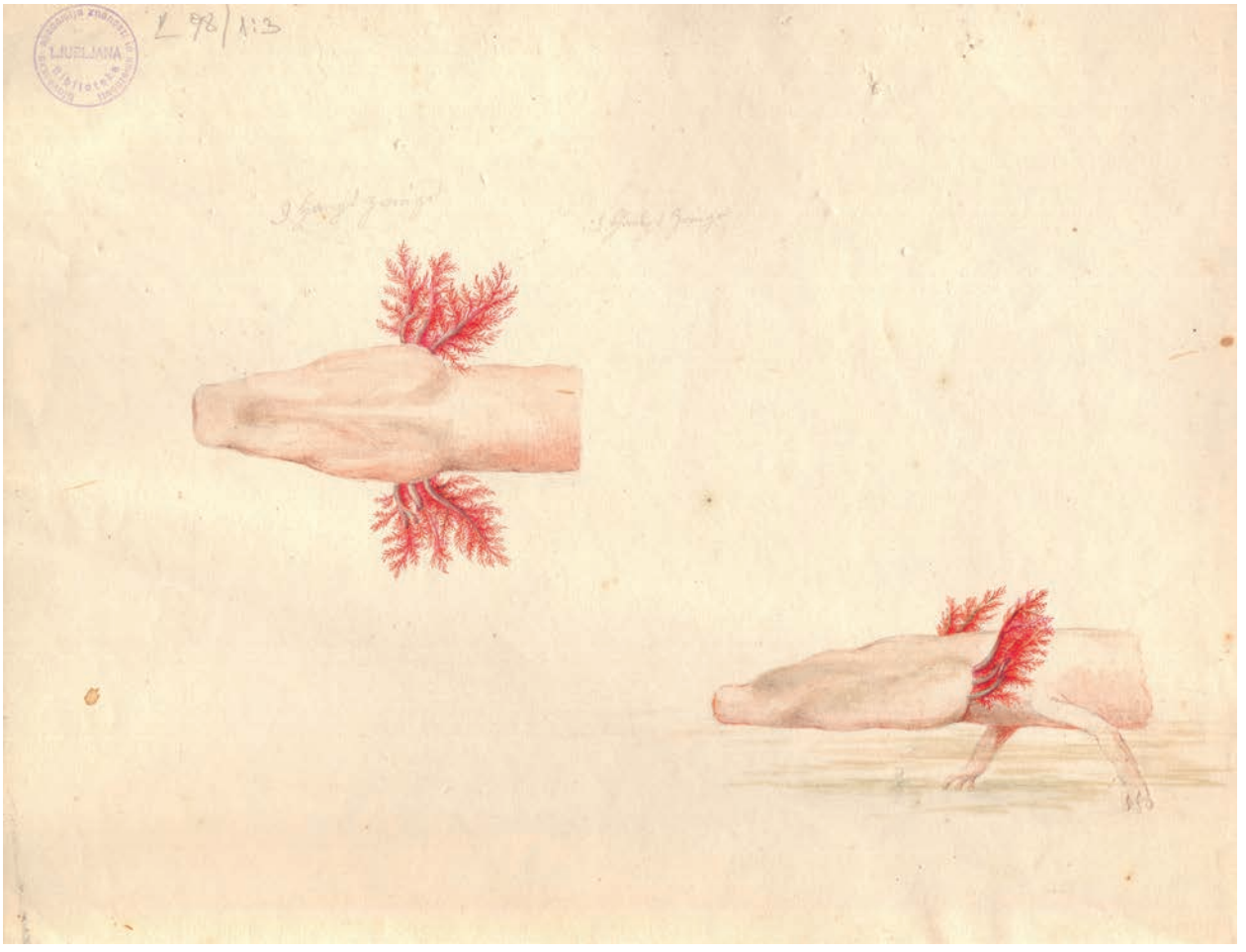

Figure 6: Vinzenz Dorfmeister, upon preparations of Žiga Zois (III), around 1805: detailed dorsal and lateral drawing of the head, external gills particularly precisely depicted (coloured drawing, unpublished; details in Aljančič, 1998*; Library of the Slovenian Academy of Sciences and Arts, Zois Legacy R 98/1, with permission).*

5 RESEARCH OF PROTEUS DISTRIBUTION

Not all proteus studies have remained as fundamentally important as they seemed to the early explorers. One of such truly long-term studies on proteus is the research of proteus distribution, by far the highest in number of researchers involved, as well as by the extent of general public involvement, since it largely depends on reports from local people. Also, search for proteus in the inaccessible subterranean habitat was always physically, materially and financially most demanding (Freyer, 1849), and thus progressing only slowly.

The distribution of proteus was first studied by Franc Jožef Hanibal Hochenwart (1771–1844), who completed Zois' initiative of foundation of the Carniolan Provincial Museum Ljubljana (Rudophinum). Hochenwart listed about ten finding sites of proteus in the Krka and Ljubljanica river basins. These localities were all revealed through finds of washed-out specimens after floods, except one - the first discovery of proteus in a cave, proteus' true habitat. Namely, in 1814, Hochenwart found proteus in Črna jama (Postojna-Planina Cave System, Slovenia), during the visit of Jožef Jeršinovič (1775–1847), later initiator of the modern cave research and tourism in Postojnska jama, who at the occasion remembered to first saw proteus there in 1797 (reported by Hochenwart; cited in Configliachi & Rusconi, 1819; Hochenwart, 1838). In Črna jama were also collected specimens studied by Con-

figliachi & Rusconi in Pavia (Fig. 7; Configliachi & Rusconi, 1819).

Hochenwart had also kept protei long-term in his apartment in Ljubljana since 1797, following Zois, all together for over 17 years (Hochenwart, 1838; Aljančič, 1984; Aljančič, 1997; Hudoklin & Aljančič, 2017).

Hochenwart's research of proteus distribution was continued more systematically by Henrik Freyer (1802–1866), the first curator of the Ljubljana Museum (1832–1852). With the support of the Schreibers fellowship, he completed a list of finding sites, which were, at the time, all limited to Carniola. He regularly invited the public to help with the gathering of valuable specimens for the collection of the Ljubljana Museum (Freyer, 1846A; Freyer; 1850; Aljančič, 1966A). Freyer visited all sites himself; in the updated list of over 30 sites, he outlined all areas of proteus distribution known today in Slovenia, with exception of Bela krajina and Kočevsko. He also documented the earliest finding sites of proteus outside of Carniola, among them proteus from the spring of Goručica near Sinj, Croatia, which was given to the museum in 1846 by Captain Joseph Appel (Freyer, 1847A).

Freyer was interested in the morphological differences of proteus between the sites, especially the shape of the head, the branching of the gills and skin colour. Based on occasional findings of washed-out proteus with prominent golden yellow patches on the flooded Planinsko polje at Laze in 1836 and 1845, Freyer described a new species *Hypochthon chrysostictus* (Freyer, 1846B). The article was accompanied by illustrations from C. F. Schmidt, upon Freyer's own drawing (Fig. 8). Probably representing one of the two proteus which (Freyer, 1846B). Animals on Figs. 8, 9 & 10 are all individuals of the nominal white proteus, washed-out onto the Planinsko polje where they were longer period exposed to sun light hence darkly pigmented (Freyer, 1842; Freyer, 1846B; Aljančič, 1966A; Božič, 2010), while the prominent golden-yellow skin

Figure 7: Faustino Anderloni, upon preparations of Mauro Rusconi, 1819: Proteus from Črna jama (Configliachi & Rusconi, 1819; Library of the Natural History Museum of Trieste, Italy, with permission; figure rotated 90° CW).

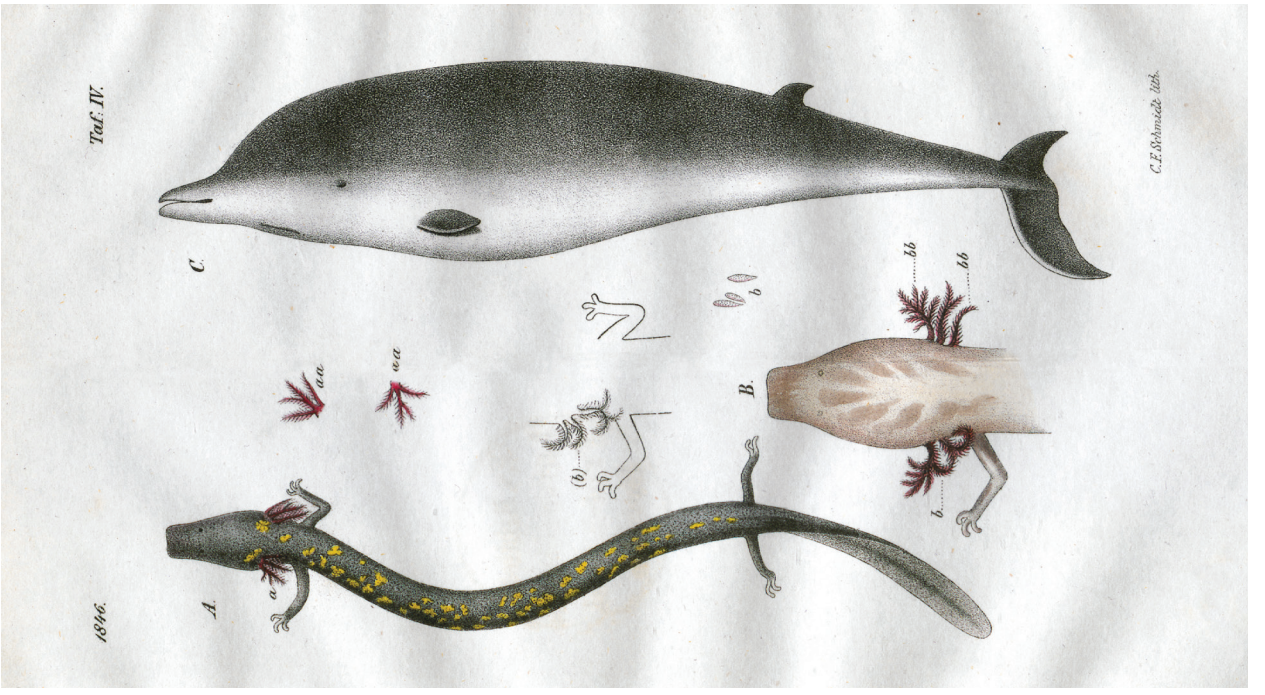

Figure 8: C. F. Schmidt, upon drawing of Henrik Freyer, 1845/ 1846: A) Hypochthon chrysostictus *sp. n., subadult proteus found on flooded Planinsko polje at Laze, beginning of July 1845; B) head of* Hypochthon Laurentii *Fitzinger, proteus washed-out in Rupe near Stična, 15 July 1845 (Freyer, 1846B; University Library at the Humboldt University of Berlin, Historical Collection, 2656:12:2:F8).*

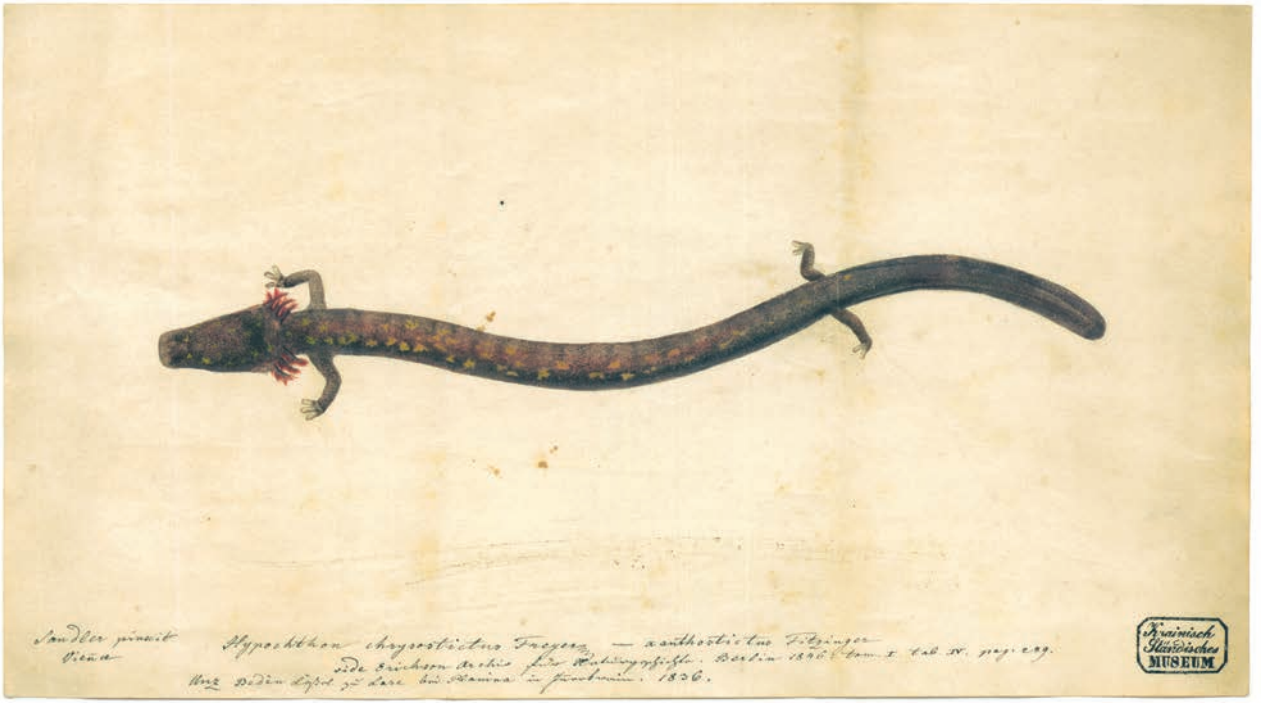

Figure 9: Michael Sandler, 1845/ 46: Hypochthon chrysostictus *Freyer /* H. xanthostictus *Fitzinger, from the flooded Planinsko polje in Bedenj, Laze; appears to be a different individual (watercolour & gouache;* Freyer, 1846B; Freyer, 1847B; *first published in* Božič, 2010; *Collection of the National Museum of Slovenia, R-2134, photodocumentation of the Graphics Cabinet of NMS, with permission).*

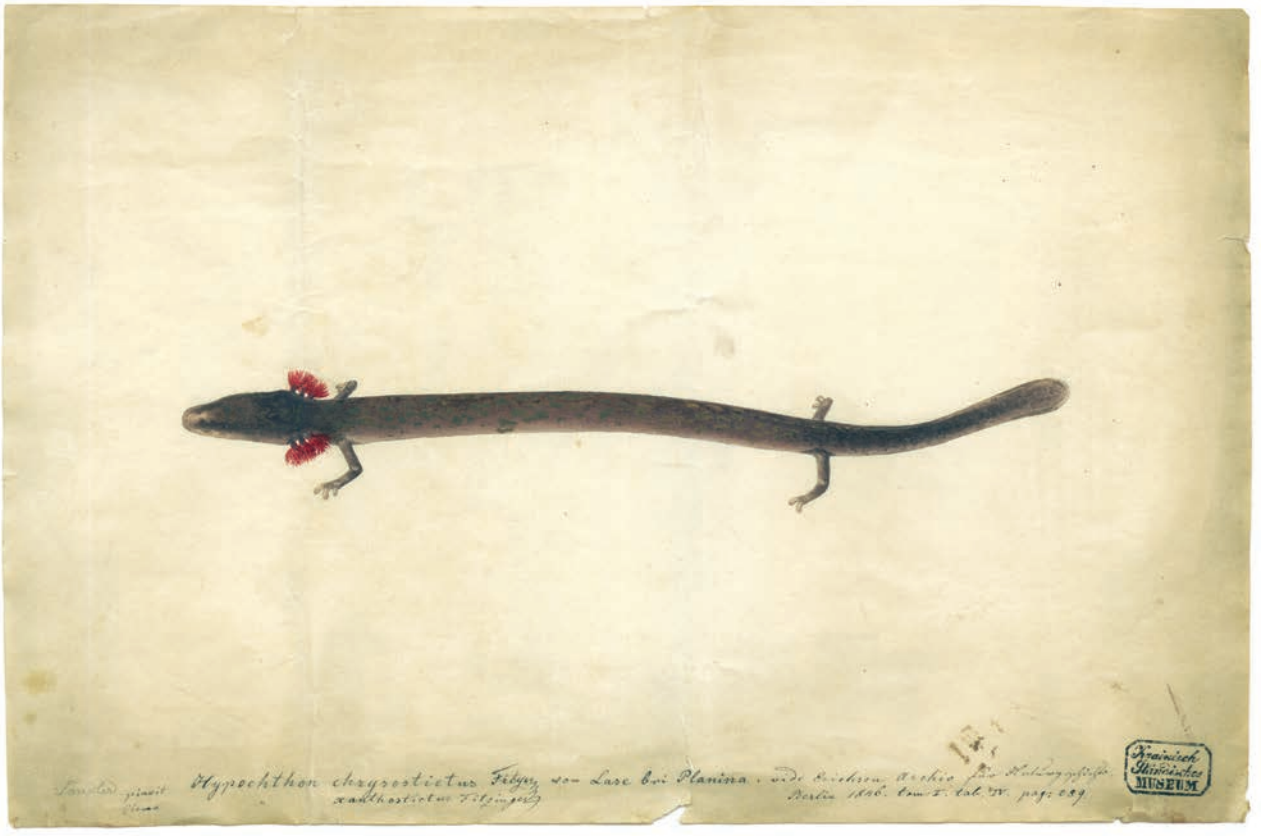

Figure 10: Michael Sandler, 1845/ 46: Hypochthon chrysostictus *Freyer* / H. xanthostictus *Fitzinger, from the flooded Planinsko polje in Bedenj, Laze; animal depicted with overdeveloped left eye? (watercolour & gouache; Freyer, 1846B; Freyer, 1847B; first published in Božič, 2010; Collection of the National Museum of Slovenia, R-2133, photodocumentation of the Graphics Cabinet of NMS, with permission).*

patches got their specific colour due to not yet explained concentrations of riboflavin (Istenič & Zigler, 1974; Simonič, 2013).

Two precious illustrations of such individuals were donated to the Ljubljana Museum in 1846 (Freyer, 1847B), but later presumably lost – until they were uncovered in 2009 by Blaženka Firs in the Graphics Cabinet of the National History Museum in Ljubljana, and described by archaeologist Prof. Dragan Božič (Božič, 2010; Figs. 9 & 10), indeed another breathtaking discovery, reminding us that more such invaluable evidence of both history of science, as well as the unique opportunity to better understand the condition of the species from pre-industrial times. Both two illustrations were painted by Michael Sandler (1790–1856), renown natural history illustrator at the Vienna Museum (Božič, 2010). By regularly sending the specimens and the data on distribution to the Viennese Museum, Freyer made a significant contribution for the taxonomic review of proteus, as prepared by Schreibers' successor Leopold Fitzinger (Fitzinger, 1850).

Here we should briefly mention curator Karel Dežman (1821–1889), who successfully succeeded Freyer at the Ljubljana Museum (1852–1889). Although Dežman's main scientific focus was not directed on proteus, he had closely studied proteus literature (Južnič, 2006; Južnič, 2009; but check author's claims in primary sources), continued to collect reports on proteus finds, and contributed to public presentations of proteus (Dežman, 1856; Dežman, 1862).

Important contribution to the search for proteus in the almost inaccessible karst underground was given by many speleologists and cavers from and around the Classical karst since the middle of the 19th century onward. Particularly extensive is the contribution of the Society for Cave Research from Ljubljana since 1910, growing into numerous caving societies of the Speleological Association of Slovenia after 1950s (overview in Novak, 1988), already documented about 13,000 caves in Slovenia (Franjo Drole, pers. comm., March 2019). The most difficultly collected was the data brought by cave divers (overview in Mlinar,

1993; Mlinar, 1996), hereafter listed in alphabetic order: Robert Anžič, Janko Brajnik, Simon Burja, Bojan Cvar, Miran Erič, Gašper Finžgar, Sašo Finžgar, Ugo Fonda, Sebastjan Gantar, Arne Hodalič, Martin Ilenič, Uroš Ilič, Franc Kljun, Marko Krašovec, Primož Krivic, Alan Levinger, Marko Matotek, Matej Mihailovski, Ciril Mlinar-Cic, Samo Morel, Janko Petkovšek, Anton Praprotnik, Martin Schweiger, Matej Simonič, Boris Sket, Rado Smerdu, Mitja Vezovnik, Igor Vrhovec, Tomo Vrhovec, Dušan Zwölf, Peter Žalec, Gregor Aljančič, and others. Here we should mention the pioneer contribtion of Ciril Mlinar-Cic & Marko Krašovec, and Arne Hodalič in underwater filming, photograpy and promotion of proteus (Aljančič et al., 1993; Mlinar, 1994; Mlinar, 2016).

From the beginning of the 1960s, data on the distribution of proteus was collected by speleobiologist Marko Aljančič (1933–2007) of the Tular Cave Laboratory (Aljančič, 1962; Aljančič, 1964A). He discerned numerous data from the already forgotten 19th century bibliography, and has carefully collected reports from locals on the findings of proteus after floods (overview in Aljančič, 1984; Sket, 1997; Hudoklin & Aljančič, 2017). Many information on finding sites and written sources along the Dinaric karst were sent to him by speleologist and entomologist Egon Pretner (1896–1982), Karst Research Institute ZRC SAZU (hereafter IZRK ZRC SAZU), one of the main experts in caves and cave animals of the Dinaric karst of his time (Aljančič, 2008; Pretner, 2016).

Distribution data were also collected at the Department of Biology (Biotechnical Faculty, University of Ljubljana) by Academician Boris Sket, who published a complete list of proteus localities across its entire range (Sket, 1997); his work is continued by Prof. Peter Trontelj and colleagues.

New localities from the area of Dolenjska and Bela krajina, were collected particularly by Andrej Hudoklin and Mira Ivanovič (Institute of the Republic of Slovenia for Nature Conservation; Hudoklin, 2003; Hudoklin, 2012; Ivanovič, 2012), Borivoj Ladišić (Speleological Society of Novo Mesto; Ladišić, 1987), Andrej Mihevc (IZRK ZRC SAZU; Mihevc, 1987), Ciril Mlinar-Cic and Marko Krašovec (Mlinar, 1986), Stanislav Klepec (Klepec, 1981) and Jože Gešelj (Bela krajina Speleological Society of Črnomelj), Martin Schweiger and others. From Notranjska by Slavko Polak (Notranjska Museum Postojna), Andrej Mihevc, Franc Malečkar, Franjo Drole and Janja Kogovšek (IZRK ZRC SAZU; Habič et al., 1990; Kogovšek, 1989; Drole, 2017) (details in Sket, 1997; Hudoklin & Aljančič, 2017); recently new localities are also reported by Tina Kirn (Kirn, 2018) and Matej Blatnik (IZRK ZRC SAZU).

6 PROTEUS RESEARCH AFTER THE FIRST AND SECOND WORLD WAR

When Ljubljana gain its full University in 1919, the newly established Zoological Institute started also with its research on cave fauna, actively from 1924 (Sket, 1993A). The first doctorate of biology was given in 1924 to the Russian immigrant Vladim Dolivo-Dobrovolsky (Wraber, 2000), for a dissertation on proteus skull (Dolivo-Dobrovolsky, 1926), who later became an assistant at the Zoological Institute.

Before the World War II, professors Albin Seliškar (1886–1973) and Hubert Pehani (1900–1995) studied the metamorphosis of tailed amphibians at the Institute of Biology (since 1971 Institute of Human Biology, and since 1991 Institute of Cell Biology) Faculty of Medicine, University of Ljubljana, and disputed the presumptions of Karoline Reis on the metamorphosis of skin grafts of protus (Pehani & Seliškar, 1941; Aljančič, 1996). Seliškar was also one of the pioneers of cave diving; in 1933 he already dived in the Štirne at Planinsko polje (Aljančič, 1996; Mlinar, 1996).

After the World War II, cave fauna was researched at the Department of Biology (Biotechnical Faculty, University of Ljubljana) from 1950s (Sket, 1993A; Aljančič, *in press*), while proteus was more actively researched from the end of the 1960s, most markedly the functional morphology of proteus, by the Research group for comparative anatomy of vertebrates, led by Prof. Lilijana Istenič, with Aleš Sojar, Boris Bulog, Danilo Musar and associates; particular attention was put on adaptations of proteus to occasional hypoxic conditions of groundwater and lung breathing, accumulation of riboflavin in skin, and studies of inner ear sensory epithelia and mechanoreceptive lateral line system (selected studies: Istenič, 1971; Istenič & Sojar, 1974; Istenič & Zigler, 1974; Istenič, 1976; Istenič & Bulog, 1976; Istenič, 1979; Istenič & Bulog, 1979; Sojar, 1980; Istenič & Bulog, 1984; Bulog, 1989A; Bulog, 1989B), continued by Prof. Boris Bulog since 1989, with Danilo Musar, Lilijana Bizjak-Mali and Marjanca Kos, with numerous students and young researchers (Katarina Mihajl-Dobrovoljec, Gregor Aljančič, Petra-Maja Prelovšek, Marjeta Konec, and others).

This research group determine proteus adaptations to its cave environment through advanced histological investigations of proteus morphology, such as the capacities of proteus sensory system (mechano- and electroreception, undeveloped eyes and pineal gland; orientation by Earth magnetic compass and hearing), in collaboration with German physiologist Prof. Peter A. Schlegel (1941–2008) (Bulog & Schlegel, 2000; Schlegel & Bulog, 1997; Schlegel et al., 2009), studies of digestive system (particularly slowed metabolism, adaptation to starvation and storage of energy) combining with the facility of their cave laboratory (see below), this research group has gathered, throughout the decades, a fundamental collection of proteus morphology (overview in Bulog, 1994; Bulog et al., 2000; Bulog, 2004; Bulog, 2007; selected studies: Bulog, 1990; Bulog, 1995; Bulog, 1996A; Bizjak-Mali & Bulog, 1996; Kos & Bulog, 1996; Kos & Bulog, 2000; Kos et al., 2001; Prelovšek & Bulog, 2003; Bizjak-Mali & Bulog, 2004; Prelovšek et al., 2008; Bizjak-Mali et al., 2013). The research group has also cooperated with Prof. Kristijan Jezernik, Institute for Biology at Faculty of Medicine (Bulog & Jezernik, 1996; Erdani-Kreft, 1996), Prof. Gorazd Avguštin, Department of Animal Science, Biotechnical Faculty (Ambrožič-Avguštin et al., 2009), and others. Lili Istenič, but in particular Boris Bulog and his colleagues introduced environmental research on accumulation of pollutants in proteus tissues, and the monitoring of pollution at selected proteus localities, focused on the threatened black proteus (Dremelj et al., 1985; Bulog, 1996B; Bulog et al., 2002; Dobrovoljc et al., 2003; Pezdirc et al., 2011; overview in Bulog, 2007; Bizjak-Mali & Bulog, 2016), with several studies in co-operation with the Department of Environmental Sciences at the Jožef Stefan Institute.

Since 2015, the programme is continued by Prof. Rok Kostanjšek with Assist. Prof. Lilijana Bizjak-Mali and associates. Since 2009, Bizjak-Mali is also focused on proteus reproductive biology (morphology of sexual organs in correlation with seasonality and animal size; cytogenetics of sexual chromosomes, currently in collaboration with Prof. Stanley K. Sessions; Bizjak-Mali & Bulog, 2010; Sessions et al., 2016; Bizjak-Mali, 2017); cultivation of proteus blood cells, and development of non-invasive methods to asses proteus physiological condition by monitor its hematological parameters, with young researcher Tajda Gredar (Gredar & Bizjak-Mali, 2017; Gredar et al., 2018). Rok Kostanjšek with associates study skin bacteriome of proteus, and the interaction of proteus with parasites and microorganisms (Kostanjšek et al., 2017, Kostanjšek et al., 2019). The special emphasis of the latter is given to determination of potential pathogens in free-living and captive proteus individuals (Bizjak-Mali et al., 2018), which are studied in collaboration with Prof. Nina Gunde-Cimerman. She and Kostanjšek, recently initiated proteus genome project, in collaboration with the Lars Bolund Institute for Regenerative Medicine, China, and University of Aarhus, Denmark, and a significant progress in research of proteus is expected from its outcomes.

In the Laboratory for Speleobiology at the Department of Biology, the biodiversity of subterranean habitats is studied mainly through taxonomy, evolution and biogeography. Academician Boris Sket, for many decades head of this group, has gathered a complete list of proteus localities across the Dinaric karst; he explained the pattern of proteus distribution as a consequence of paleogeographic development of the Dinaric karst, and corroborated his findings with the pattern of today's distribution of other cave species (Sket, 1997; Sket, 2012).

All were surprised by the discovery of an unusual dark-pigmented proteus in Bela Krajina (south-eastern Slovenia): first specimen known to the science was found in 1986 at the spring of Dobličica by karstologist Andrej Mihevc from the Karst Research Institute at the Scientific Research Centre of the Slovenian Academy of Sciences and Arts (Aljančič et al., 1986; Mihevc, 1987; Sket, 2017; Aljančič, 2017). In 1994, Boris Sket together with Dutch herpetologist Jan Willem Arntzen (Naturalis Biodiversity Center) taxonomically describes this extraordinary proteus population as *Proteus anguinus parkelj* (Sket & Arntzen, 1994; see also Sket, 1993B; Arntzen & Sket, 1996; Arntzen & Sket, 1997; Sket, 2007; Sket, 2017; hereafter: the black proteus).

Peter Trontelj and associates continued with study of proteus phylogeny. With Špela Gorički and Samo Šturm they demonstrated the sister relation between *Proteus* and the North American genus *Necturus* using molecular phylogenetic methods (Trontelj & Gorički, 2003), showed the molecular evolution of proteus by identifying several independent genetic lineages of proteus (Gorički & Trontelj, 2006; Gorički, 2012) and cryptic speciation along the Dinaric karst (Trontelj et al., 2009), and estimated a timescale of proteus evolution using molecular clock (Trontelj et al., 2007). Jure Jugovic and associates studied the predator–prey interactions (Jugovic et al., 2010). Recently, Peter Trontelj and Valerija Zakšek have focused on proteus nuclear DNA, confirming that the taxon is deeply subdivided into 6 to 9 mitochondrial DNA lineages (Trontelj & Zakšek, 2017). They are determin-

ing the conservation genetics of proteus populations (Zakšek et al., 2017), developing genetic and non-genetic monitoring methods to estimate the size and state of selected proteus populations, with Žiga Fišer, Teo Delić, and associates (Trontelj & Zakšek, 2016; Fišer et al., 2017).

Interesting pilot research at the Department of biology to be mentioned here, was an electrophysiological investigation of proteus reduced eye, performed by physiologists Academician Matija Gogala, Prof. Štefan Michieli (1933–1968) and Borut Žener (1935–1974) (Gogala et al., 1969; Žener, 1973).

7 CAVE LABORATORIES IN SLOVENIA

In research of proteus in Slovenia, special attention was given to the idea of using a cave as a laboratory. One of the earliest of such kind, with proteus from the Postojna-Planina Cave System, arranged by Armand Virè, one of the pioneers of modern speleobiology – in the catacombs of Paris, flooded by Sienna in 1910.

The earliest plans of a cave museum in Postojna came from the Cave commission in 1904, in following years thoroughly elaborated by speleologist Ivan A. Perko (1876–1941), who by 1911 raised a considerable fund, foreseeing a future Cave Research Institute (Perko, 1911). This would be the first karstological institute in the world, but the pioneer ideas were overtaken by the World War I (Shaw, 2010). However, the first cave laboratory actually built in Slovenia was active in the cave Podpeška jama (south Slovenia) between 1928 and 1931, arranged by professors Roman Kenk and Albin Seliškar at the Zoological Institute of the University of Ljubljana (Kenk & Seliškar, 1931). In 1930, after establishing the Karst institute in Postojna in 1929, Perko has finally completed his vision by building a modern Biospeleogical Station in Postojnska jama (Dudich, 1933). Albin Seliškar (Institute of Physiology at the Faculty of Medicine) started the renovation of the station in 1951 under the custody of the Slovenian Academy of Sciences and Arts, and remained in charge until 1960, when he was forced to close the laboratory due to insufficient support (Aljančič, 1996).

Marko Aljančič started to develop his interests as a keen student at the Gimansium in Kranj, where he founded school's Natural history circle (1946), gain first laboratory and fieldwork experience, and got his first opportunity to observe proteus behaviour in school tank (Aljančič, 2008; Gogala and Furlan, 2013; Aljančič, 2015). Aljančič elaborated his plans for a cave laboratory in his graduation thesis, arranged upon the Subterranean Laboratory in Moulis (Aljančič, 1960). With the support of Prof. Hubert Pehani, and the Town of Kranj, Aljančič set up a biospeleological laboratory in the Tular Cave in Kranj as a part of the Institute of Biology (Faculty of Medicine, University of Ljubljana) (Aljančič, 1961; Vandel, 1964), in order to facilitate long-term ecological and behavioural studies on proteus (Aljančič, 1961; Aljančič, 2008; Aljančič, 2015).

At the Institute of Biology, Marko Aljančič was focused mainly on morphology and physiology of proteus (e.g., erythrocyte ultrastructure, limb regeneration, skin pigmentation, stimulation of metamorphosis; selected studies: Aljančič, 1963; Aljančič & Sket, 1964; Aljančič, 1974), while at the Tular Cave Laboratory he studied proteus mainly by observation of its behaviour (Aljančič, 1964B). He was especially interested in ecology and behaviour of proteus, involved in the national project Ecology of cave animals (Prof. Janez Matjašič). In his pioneering comparison of physical-chemical parameters of groundwater ecotope in selected proteus localities (1962–1965), in collaboration with chemist Prof. Ladislav Guzelj, Marko Aljančič compared ecological conditions in selected proteus localities, but the study also alerted on high pollution of proteus habitat in the Kočevsko region (central south Slovenia) (Aljančič, 1969), where, most regretfully later proteus has locally gone extinct (Sket, 1997; Hudoklin, 2011). Findings from the nature helped in searching for adequate conditions for long-term maintenance of proteus in captivity, which were largely unknown at the time, mainly with regard to feeding, providing a semi-natural habitat and developing animal-friendly observation methods. After reorganization of the Biological Institute into the Institute of Human Biology, the Tular Cave Laboratory after 1976 continued its programme independently on the initiative and with dedication of both Marko and Marija Aljančič, biologist, active in the laboratory since 1965. After 2002, the laboratory operates under the custody of the Society for Cave Biology.

Since 2007, their son, Gregor Aljančič continues the work at the Tular Cave Laboratory, mainly by researching the distribution of proteus (Gorički et al., 2017; Hudoklin & Aljančič, 2017), its reproductive behaviour (Aljančič & Aljančič, 1998), adaptation to cave environment, e.g., proteus potential detection of

floods, with Mitja Prelovšek (Aljančič & Prelovšek, 2010); cave-related adaptations of the skull, with Ana Ivanović (Institute for Zoology, Faculty of Biology, University of Belgrade) and Jan W. Arntzen (Naturalis Biodiversity Center) (Ivanović et al., 2013); interactions between predator and prey, with Jure Jugovic (Jugovic et al., 2010). He continues with long-term observations on proteus at Tular with Magdalena Năpăruş-Aljančič (e.g., space use, reproduction and feeding behaviour, locomotion, longevity, etc.; Aljančič & Năpăruş, 2009).

In nature, their studies on proteus are conservation-oriented. Gregor Aljančič and Magdalena Năpăruş-Aljančič developed new conservation tools of monitoring proteus presence by detecting its environmental DNA along the Dinaric karst, with key experts Špela Gorički and David Stanković, and partners Prof. Matjaž Kuntner (Jovan Hadži Institute of Biology ZRC SAZU), Aleš Snoj and Prof. Peter Dovč (Department of Animal Science, Biotechnical Faculty, University of Ljubljana), Prof. William R. Jeffery (Department of Biology, University of Maryland, USA), Prof. Alberto Pallavicini (Department of Life Sciences, University of Trieste, Italy), Miloš Pavićević (Biospeleological Society of Montenegro, Montenegro), Jasminko Mulaomerović (Centre for Karst and Speleology, Bosnia and Herzegovina) and associates, revealing the presence of proteus environmental DNA at the edge of its range in Montenegro, and surveying the narrow area of actual distribution of the black proteus, and its contact with the white population in Bela krajina, Slovenia (Aljančič et al., 2014; Pennisi, 2016; Stanković et al., 2016; Gorički et al., 2016; Gorički et al., 2017). Since 2017, Špela Gorički is continuing at the Scriptorium biologorum - Biološka pisarna d. o. o., developing eDNA methods for monitoring stygobiotic species (Gorički et al., 2018).

Starting in 1964, the laboratory studies the phenomenon of proteus being occasionally washed out from its subterranean habitat during seasonal flooding. The Sanctuary for proteus was set up in 2008, with a regular veterinarian care provided for injured proteus in collaboration with veterinarian Zlatko Golob since 2013 (Aljančič et al., 2016). Both, the Sanctuary and the Laboratory operate under strict quarantine, with regular pathogene monitoring (ranaviruses, Bsal, Bd) analyzed at the Department of Biology.

The Tular Cave Laboratory is focused on conservation of the most rare and endangered populations of proteus, such as the black proteus and the Stična population of the white proteus, e.g., monitoring of distribution and GIS analysis of pollution of its groundwater habitat (Năpăruş-Aljančič et al., 2017). Since 2017, Tular Cave Laboratory is partner of the national consortium the European eScience Infrastructure of biodiversity and Ecosystem research LifeWatch-ERIC.

An important part of the laboratory's activity is dedicated to raising awareness on the vulnerability of proteus and groundwater in countries along the Dinaric karst, addressing both the public as well as the research and nature conservation organisations (Năpăruş-Aljančič et al., 2018), in the network of the biennial International meeting SOS *Proteus* (Aljančič et al., 2016; Aljančič et al., 2017; Aljančič et al., 2018).

At the Department of Biology in Ljubljana, proteus was maintained in the basement at the Faculty of Arts from the early 1960s until 1993. For the purpose of educating school children, protei were kept in the Vivarium (Borut Žener, Emerik Mezgolits, Rudi Ocepek and Dušan Vrščaj), while for the research proteus was maintained in a nearby room (France Velkovrh, Lili Istenič, Boris Sket, Milan Velikonja and associates), later Istenič arranged a special refrigerated dark chamber. For several years, Prof. Tine Valentinčič has utilized the vivarium for practical exercises in behaviour of proteus for students of biology (Emerik Mezgolits & Rudi Ocepek, pers. comm. November 2017; Lilijana Bizjak-Mali, per. comm. February 2019; Boris Sket, per. comm. March 2019; Janko Božič, per. comm. March 2019).

At the end of October 1986, Lili Istenič, Boris Sket, Boris Bulog, Tine Valentinčič, Matija Gogala, Andrej Mihevc, Marko Aljančič and associates had here the opportunity to observe the very first individual of the black proteus (Aljančič et al., 1986; Istenič, 1987; Mihevc, 1987), almost as surprised as Scopoli and Wulfen 220 years before when looking at the white proteus. Later, in the new laboratory, laying of eggs of the black proteus was recorded by Boris Bulog. Beside both subspecies of proteus, laboratory occasionally maintained several invertebrate cave species (Boris Sket, per. comm. 22 March 2019).

When Department of Biology was moved to the new building in 1993, a modern cave laboratory was arranged in a climate-controlled room upon plans of Boris Bulog and Boris Sket. A cave laboratory is now used by both, the Research group for comparative anatomy of vertebrates, and the Laboratory for Speleobiology, mainly in studies of Lilijana Bizjak-Mali, Rok Kostanjšek, Cene Fišer, Katja Zdešar-Kotnik and associates).

8 RESEARCH ON PROTEUS REPRODUCTION

More than its eyelessness and subterranean life, the researchers and the public had been giving special attention to the mysterious proteus reproduction since the very beginning (Aljančič et al., 1993; Aljančič & Aljančič, 1998), probably deriving already from the initial Linnaean search for an undoubted proof of specimens maturity. Zois, Hochenwart and Freyer had been searching in vain for females with eggs or embryos, and Schreibers has offered a reward of 25 Guldens (Hochenwart, 1839; Freyer, 1846A; Grošelj, 1933 Aljančič & Aljančič, 1998; Sket, 2007). The animals described in the following cases of reproduction derive from Slovenia, almost exclusively from the Postojna-Planina Cave System, where they were most easily accessible.

In absence of evidence, the question, whether proteus is oviparous or viviparous was stirred up the protocol of Ljubljana naturalist Joseph H. Stratil, wherein Janez Kek, municipal judge and local of Vir near Stična, witnessed in detail the viviparity of proteus, which he observed in a bottle filled with water, between 17 and 20 June 1825 (Michahelles, 1831). A supposed case of viviparity in Postojnska jama was reported by the newspaper Novice on 26 February 1862, but the Viennese comparative anatomist Joseph Hyrtl (1810–1894) showed it was only a worm, and the proteus – a male specimen (Dežman, 1862; Aljančič et al., 1993; Aljančič, 1994). Eighty years later, just before the World War I, impetus to the hypothesis of viviparity was given again by the influential, but later discredited Viennese experimental biologist Paul Kammerer (Kammerer, 1907; Kammerer 1912; van Alphen & Arnten, 2016), and another case of viviparity was also reported by Polish zoologist Józef Nusbaum (Nusbaum, 1907).

The first confirmation of oviparity came from the Postojnska jama in 1875. Beginning of May 1875, one of the animals has laid 56 eggs in a bucket that was prepared to be shown to the visitors by the cave guide Prelesnik; however, the eggs have all decayed (Schulze, 1876). Soon thereafter, animals from the Postojna-Planina Cave System laying of eggs in captivity was observed by German researcher Marie von Chauvin in 1882, and finally Ernst Zeller succeeded in growing larvae from eggs in 1886 (von Chauvin, 1883; Zeller, 1888; Aljančič & Aljančič, 1998; Sket, 2007).

The eggs of proteus were not recorded until 1958, when Prof. Albert Vandel and Michel Bouillon first succeeded with breeding of proteus at the Moulis Underground Laboratory (today Experimental Ecology Station of the CNRS at Moulis; Vandel & Bouillon, 1959; Vandel, 1965). In 1962 proteus reproduction was described in detail by Wolfgang Briegleb, who bred the animals for some years in the basement of the Zoological Institute in Munich, Germany (Vandel & Bouillon, 1959; Briegleb, 1962; Aljančič & Aljančič, 1998; Sket, 2007).

At the Tular Cave Laboratory Marko and Gregor Aljančič recorded the first young proteus in 1991, laying of eggs in 1993, and successful *ex situ* reproduction of the white proteus is monitored since 1998 (Aljančič & Aljančič, 1998; Culver & Pipan, 2009; Aljančič, 2008; Grosse et al., 2018). The endangered black proteus is maintained in Tular since 2002, though other that egg laying was not recorded.

In the touristic Postojnska jama, proteus was on public display through the 19th century on (Shaw, 2005; Shaw & Čuk, 2015), maintained by cave guides. In 2001, speleobiologist Slavko Polak (Notranjska Museum Postojna) became the first curator of proteus showed in this touristic cave. He introduced husbandry standards of the Tular Cave Laboratory in 2002, rebuilt the formal Biospeleological Station for public display and constructed a new tourist aquarium in 2010, with Ksenija Dvorščak (Postojnska jama) and associates (Aljančič, 2008; Dvorščak, 2011). In 2013, after almost 140 years, and due to improved conditions of captivity, Polak has been observing first egg laying in the tourist aquarium of Postojnska jama, in collaboration with Gregor Aljančič. However, eggs were eaten or damaged by other adults in the aquarium. The first larvae were successfully hatched there from the eggs in 2016, reared by Primož Gnezda, Sašo Weldt and Katja Dolenc-Batagelj (Postojnska jama), in cooperation with Lilijana Bizjak-Mali and Stanley K. Sessions (Bizjak-Mali et al., 2017).

Proteus from Postojna-Planina Cave System are also maintained in a touristic cave Hermannshöhle in Harz, Germany since 1931, documenting laying of eggs since 2016 (Ipsen et al., 2017; Grosse et al., 2018).

In the late 1950s and early 1960s German biologist Wolfgang Briegleb (1928–2006) built the fundaments of modern ecology of proteus, studying the species in the Postojna-Planina Cave System and captive facility arranged in the basement of the Zoological Institute in Munich, Germany, for his doctorial thesis (Briegleb, 1962; Aljančič, 1963; Aljančič, 2008). Extensive fieldwork in the Postojna-Planina Cave System was carried out together with biologist and hydrologist France Hribar (1915–1999) of IZRK ZRC SAZU (Briegleb, 1963).

The actual proof, that proteus lays eggs in nature, was shown by B. Sket and F. Velkovrh in 1976. They caught two eggs with well-developed embryos, washed-out by high groundwater at the Virski studenec (Sket

& Velkovrh, 1978). Sket later found a late embryo/hatchling of the black proteus being washed-out at the springs in Jelševnik (south-eastern Slovenia) under similar conditions (Sket & Arntzen, 1994).

Academician Jovan Hadži (1884–1972) had left an influential mark on proteus research in the period before, and especially after the World War II, mostly by directing biospeleological research (Hadži, 1965; Aljančič, 1996). His expert opinion was supporting the nature conservation permit for acquisition of the protected species from nature, which were mostly performed in the Postojna-Planina Cave System, as in case of the Underground Laboratory CNRS in Moulis (France) from 1952, as well as specimens for the Tular Cave Laboratory from 1960 (Aljančič, 2008), while the 2nd acquisition of proteus to the touristic cave Hermannshöhle (Germany) in 1956 was unlawful (Ipsen & Knolle, 2017).

9 PROTEUS IN SLOVENE NATURAL HISTORY TERMINOLOGY

We should here briefly mention an important contribution of proteus research to the development of Slovene natural history terminology in the 19th century, a subject not well studied (Aljančič, 1995).

The Slovenian vernacular name *človeška ribica* [human fish] was documented in the area of Stična (Zois, 1807; Freyer, 1842), perhaps though it was already the most common of all local synonyms, of which only a few were written down by Zois and Freyer, before this linguistic diversity was lost forever. Nevertheless, through the first half of the 19th century *človeška ribica* replaced other synonyms (i.e./ literally translated in English/ *bela riba* [white fish], *bela kačica* [white snake, diminutive form]*;* Zois, 1807; Freyer, 1850; review in Aljančič, 1989; Trontelj et al., 2017), and was probably translated in other Slavic languages (Aljančič, 1989).

During the period when Henrik Freyer was curator of Ljubljana Museum (1832–1852) (Aljančič, 1966A), Slovene natural history terminology started to developed more rapidly, following the progress of modern science, and the growing public attention, often raised through promotion of nature wonders of Carniola and cave tourism in Postojna (Aljančič et al., 1993; Shaw & Čuk, 2015). Not to be misunderstood when naming species of Slovenian flora and fauna, Freyer also searched for their exact common Slovene names and collected synonyms in the first list of amphibians of Carniola (Freyer, 1842), following the pioneer work of Žiga Zois (Jančar, 1999). He also coined Slovene binomial scientific name for proteus, the *Temnotna močerila* (Freyer, 1842; Freyer, 1849), through following years perhaps testing derivatives, such as the *Močarilec* (Freyer, 1850), to find the proper name accepted by public. Freyer's name is still use today, like the *Olm*, invention of famous German naturalist Lorenz Oken (Freyer, 1846A; Aljančič, 1989), reused from the Thuringian vernacular name for newt [*Molch*] (Trontelj et al., 2017).

Freyer is also author of the first description of proteus in Slovene language (Freyer, 1850), which is also one of the earliest Slovene natural history articles. The manuscript for this article was described and published by Marko Aljančič, although at the time he was not aware that the final version of Freyer's manuscript was indeed published (Aljančič, 1966B). Freyer was preparing the manuscript for a popular science article in a very natural history orientated Slovene language textbook, based on his public lectures, largely relying on data from his *Museum report for the year 1845* (Freyer, 1846A). This article keeps its high scientific value and rich data, largely based on Freyer's own observations (e.g., distribution of proteus, general biology and history of research).

However, the first article on proteus in Slovene language, together with an accurate drawing by A. Jurman, was published a year earlier, on 28 June 1849, in the first Slovene youth newspaper *Vedež* (published between 1848–1850) (Anon., 1849) (Fig. 11). The article is unsigned, much shorter, but the author seems to be well informed on the subject, although the text contains small mistakes. Perhaps intestinally naive for the school readers, the article contains interesting historical details of a vivid nature history community in Ljubljana (compare Hochenwart, 1838).

This short review of early authors is complete with the most popular Slovene natural history writer of the 19th century, naturalist Fran Erjavec (1834–1887), with short article on proteus included in his influential book on animals (Erjavec, 1864; Aljančič, 1995; Dular, 1995).

The Natural History Society of Slovenia, which formally arose from the Museum Society of Carniola (founded by Hochenwart and co-members in 1839), have popularise research of proteus and its conservation generations for 180 years, particularly influentially after the World War I. Since 1933, the society publishes the Proteus, Slovenia's oldest natural history

Figure 11: A. Jurman, 1849: Illustration of proteus in the Vedež, first Slovene youth newspaper, with unrealistic nostrils, perhaps to attract young reader (lithographic print by K. Egerčin; Anon, 1849). Assembled from two incomplete copies at the Slovene National and Study Library in Trieste, and the University Library Maribor (left and right edge), with permission.

magazine. With its name, the first issue of the magazine lined its mission in the often reprinted article "How proteus was discovered?" written by the initiator and first editor Prof. Pavel Grošelj (1883–1940) (Grošelj, 1933). In 80 volumes, which had a fundamental impact on the development of modern Slovene natural history terminology and writing, the magazine published about 50 articles concerning proteus.

Another fruitful promoter is the Speleological Association of Slovenia, with over 40 articles on proteus in its journal Naše jame [Our Caves], published between 1959 and 2008, for many years edited by Marko Aljančič (1977–1999) (Aljančič, 2008). Since 2008, the Association publishes its new magazine Jamar [Caver].

On proteus was discussed in about 20 scientific papers published in the journal Acta carsologica (Karst Research Institute ZRC SAZU) since 1955. Since 2016, the journal Natura Sloveniae (Biotechnical Faculty, University of Ljubljana and National Institute of Biology) published presentations from the first three International meetings SOS *Proteus* (Aljančič et al., 2018), already 32 short scientific communications on proteus.

10 BEGINNINGS OF PROTEUS CONSERVATION

In the 19th century proteus quickly became threatened by excessive collection, focused mostly on a few of the easily accessible caves of the Postojna-Planina Cave System. Much before his time, F. Hochenwart had expressed his concern for the growing vandalism already in 1838. He estimated that in the period between 1800–1838, particularly from the cave Črna jama, over 4,000 specimens were caught (Hochenwart, 1838; Aljančič, 1997; Sket, 2007), sent to the collections all over the world or sold as souvenirs to the visitors of the Postojnska jama (Aljančič, 1997; Shaw, 1999; Dvorščak, 2011). The famous cave explorer of the Classical karst, Chech speleologist Adolf Schmidl (1802–1863), had collected 500 specimens on 24 August, 1850, soon after discovering this untouched proteus population in the Pivka branch of the Planinska jama, and sent them all to Vienna, where the four survived specimens were presentated at the Academy of Sciences in Vienna (Schmidl, 1850). *In vivo,* Proteus was often presented in Ljubljana, Trieste and Vienna, and it was occasionally exhibited worldwide (Zois, 1807; Hochenwart, 1838; Schmidl, 1850; Aljančič et al., 1993; overview in Shaw, 2005), where only few animals survived for longer periods in inadequate conditions. A proteus brought in 1861, after 17 days of travel from Postojna to London, by Scottish geologist Hugh Falconer, appear to have more luck. The next day he offered it to his friend Charles Darwin, who was – like Lamarck before him – puzzled by proteus eyelessness (Darwin, 1859; Culver & Pipan, 2009). Darwin was probably well aware of the delicate care needed to keep it at home, so he rather kindly suggested letting proteus to the London Zoo, where indeed Falconer's gift was recorded on 27 June 1861 (Shaw, 1999; Shaw, 2008).

After developing into an international karst tourist attraction during the 19th century, the Postojna Cave promoted proteus as its most famous attraction (e.g., specimens exhibited at the World Exhibition in 1863 and 1873; Shaw, 2005). In the second half of the 19th century, proteus has become so rare in the Postojna-Planina Cave System, that even the guides of Postojnska jama had difficulties to purchase proteus for tourist display, while proteus became rare also in other caves of Carniola (Schulze, 1876). The high attention of the public not only encouraged poaching but also attracted researches, and Postojnska jama became an attraction for science as well (Aljančič et al., 1993; Shaw, 1999; Shaw, 2008; Dvorščak, 2011; Shaw & Čuk, 2015; Lučić, 2018). Nature conservation awareness, raised in public prior its time by F. J. Hochenwart (Hochenwart, 1838; Aljančič, 1997; Sket, 2007), has only gradually developed. First ideas to legally protect cave fauna and caves in Slovenia arose in the years before the World War I at the Museum Society of Carniola. The programme was partially achieved in 1921 with the legal protection of caves (Peterlin, 1995), though nominally proteus is protected in Slovenia since 1951.

Excessive collection of proteus has ceased after the World War I, but a new, more serious threat has already appeared – the pollution of groundwater in Slovenia. Negative anthropogenic influences derive mainly from intensive agriculture, which is not adjusted to the vulnerable karst landscape, and from non-regulated urbanisation and industry (Aljančič, 1969; Sket B., 1972; Bulog, 2007; Hudoklin, 2011; Aljančič et al., 2014; Aljančič & Aljančič, 2015; Mezga et al., 2016; Kordiš, 2016; Gostinčar, 2016; Tičar & Ribeiro, 2017; Kolar, 2018). Dolenjska and Bela krajina are the most vulnerable areas (Bulog et al., 2002; Hudoklin, 2016; Bizjak-Mali & Bulog, 2016; Prelovšek, 2016; Aljančič, 2017; Ribeiro & Tičar, 2017; Năpăruş-Aljančič et al., 2017), and in several caves proteus have already disappeared (Sket, 1997).

11 CONCLUSION

The research on proteus is one of the oldest natural history projects in Slovenia, 330 years of spiritual bond, outlined by Valvasor's pioneer studies of karst and first mentioning of proteus (Andrej Mihevc, pers. comm., Aljančič, 2008). With contributions of the early naturalists, and raised public attention, proteus gradually became not only an important symbol of Slovenia's karst nature, but also a part of its cultural heritage (Aljančič et al., 1993), which is reflected in diversity and persistence of proteus research in Slovenia. Proteus also became a myth, often presented as a dweller of the untouched karst underground. However, the reality of the growing negative pressure in karst landscape has long gave a strong motive – to proteus researchers as well as people living in the karst landscape – we need to continue studying proteus, in order to preserve the vulnerable karst ecosystems for the future.

This overview of proteus research in Slovenia, however brief and incomplete, relies particularly on the historical reviews offered by Žiga Zois, Franc J. Hochenwart, Henrik Freyer, Pavel Grošelj, Marko Aljančič, Darinka Soban, Boris Sket, Trevor Shaw, and others. Particularly Marko Aljančič devoted himself to studying and illuminating the history of proteus research, with emphasis on the contributions given by Valvasor, Scopoli, Zois, Schreibers, Hochenwart, Freyer, Seliškar and others. His popular science articles and exhibitions are one of the most fruitful contributions to the promotion of proteus as a symbol of vulnerable karst nature in his homeland and worldwide (Sket, 2007; Aljančič, 2008; Gogala and Furlan, 2013).

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