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Review

Olm sweet olm: unearthing nine species of *Proteus* hidden beneath the Dinaric Karst

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Abstract. The olm, *Proteus anguinus*, is one of the most iconic vertebrates of Europe. Since its scientific description in 1768, its extreme adaptations to subterranean life in the enigmatic underground waters of the Dinaric Karst have fascinated scholars and naturalists worldwide for more than two centuries. Yet, the evolution and taxonomic diversity of its populations remained largely unresolved, as complex patterns of phenotypic differentiation and molecular variation collide with an intricate nomenclatural history. In this work, we review recent biogeographic advances, notably based on range-wide phylogeographic analyses implementing genomic data, and combined with distributional data, species distribution modelling, red list assessment, morphological analyses and a critical species delimitation evaluation, recognize nine species in immediate danger of extinction. Based on an extensive nomenclatural search, we determined that six correspond to available names and three are newly described in this work. These species all exhibit highly restricted distributions within the Dinaric karst, collectively representing an exceptional example of subterranean microendemism among European vertebrates. Linking influential historical research with modern zoological methods, this revision provides an up-to-date science-based taxonomic framework for future studies of comparative evolution and ecology of *Proteus*, while establishing a sound basis for species-level conservation management of one of Europe's most remarkable vertebrate diversifications.

Keywords: Balkan Peninsula, microendemism, morphology, nomenclature, phylogeography, taxonomy.

Introduction

Few animals have attracted as much fascination as the olm (*Proteus anguinus* Laurenti, 1768). This paedomorphic salamander, typically blind and depigmented, is restricted to underground rivers and lakes of the Dinaric Karst in south-eastern Europe, where it has long been regarded as a flagship groundwater species (Kostanjšek et al., 2023). *Proteus* Laurenti, 1768 is the first cave-dwelling vertebrate to have been described, and the study of its natural history spans more than 350 years (Aljančič, 2019). Such prominence was already reflected in early taxonomic work, culminating in the recognition of seven species by Leopold Fitzinger (Fitzinger, 1850), and is sustained today by extensive research on its remarkable biology, including exceptional longevity (Voituron et al., 2010), a gigantic genome (Kostanjšek et al., 2022), and striking adaptations to the extreme conditions of groundwater life such as a loss of complete metamorphosis (obligate paedomorphosis; Denoël et al., 2005; Bonett et al., 2022), magnetic sensing that partly compensates for blindness (Schlegel, 2008), low metabolism (Bizjak Mali et al., 2013), arrhythmic physiology (Hervant et al., 2000) and high tolerance of de-oxygenated water (Issartel et al., 2009). Despite the olm's importance across multiple fields, establishing a coherent evolutionary framework has remained a persistent challenge, and its systematics have historically struggled to keep pace with our understanding of its diversity.

For much of its recent taxonomic history, the olm has been treated as a single species, with only the black olm – a melanistic, non-blind form known only from surface aquifer springs from south-eastern Slovenia – currently recognized as a distinct taxon, the subspecies *P. a. parkelj* (Sket and Arntzen, 1994). This apparent uniformity, whereby morphological differences noted in early descriptions (Fitzinger, 1850) were repeatedly re-examined and re-interpreted (Cope, 1866; Grillitsch and Tiedemann, 1994; Arntzen and Sket, 1997), has masked substantial phylogeographic structure. Deeply divergent lineages are associated with the complex subterranean hydrographic systems of the Dinaric Karst, as substantiated by allozyme (Sket and Arntzen, 1994), mitochondrial (Gorički and Trontelj, 2006; Gorički et al., 2017), microsatellite (Vörös et al., 2019) and genomic evidence (Recknagel et al., 2024), and further appear almost impermeable to gene flow even when occurring in close geographic proximity (Recknagel et al., 2024). Together, these patterns are consistent with the recurrent hypothesis that the olm represents a species complex, as previously suggested by biogeographic synthesis (Sket, 1997), and in this respect echo earlier taxonomic classifications (Fitzinger, 1850).

Deep divergence and absence of contemporary introgression are hallmarks of long-term isolation and reproductive barriers, and the identified phylogeographic lineages have accordingly been explicitly proposed as distinct species (Recknagel et al., 2024). However, this diversity remains unacknowledged within the Linnaean classification system, which requires the formal assignment of available names, and if necessary, the description of new taxa. Although often perceived as cumbersome, taxonomic revisions are essential, particularly as unnamed diversity remains largely invisible to conservation policy and biodiversity assessments (Garnett and Christidis, 2017; Pollock et al., 2020; Liu et al., 2022). This is particularly important for a flagship organism such as the olm, for which scientific nomenclature ensures clear and consistent communication among both the scientific community and the public. Moreover, translating evolutionary lineages into taxonomic units requires careful evaluation in the framework of species concepts and their associated criteria, while considering the evolutionary specificities of the focal organism and prevailing taxonomic practices in the region of interest.

Revising the taxonomy of the olm entails several important developments. First, reassigning known occurrence records (e.g., Sket, 1997)

using molecular and hydrogeological information will refine the distribution of each candidate species, providing a necessary basis for their future assessment in red lists. At present, the *P. anguinus* complex as a whole is classified as Vulnerable by the IUCN, primarily due to habitat fragmentation and degradation, particularly water pollution (Miaud et al., 2024; Crnobrnja-Isailović et al., 2025). In parts of its range, it is considered as Endangered (e.g., Croatia; Jelić et al., 2015), suggesting that lineages within the complex likely face an even greater risk of extinction. This must be especially the case for lineages with highly restricted distributions and low levels of genetic diversity, which may indicate demographic bottlenecks and limited adaptive potential (Spielman et al., 2004). In parallel, an updated occurrence dataset could then be used for species distribution modelling in order to predict putatively suitable areas, which has so far never been attempted for the olm.

Second, knowledge of lineage distributions and divergence provides an opportunity to assess phenotypic variation from georeferenced museum specimens within a robust evolutionary and taxonomic framework. Despite the inherent difficulties of sampling such secretive species, the longstanding scientific interest in the olm has made it relatively well represented in museum collections (Mattes, 2018), enabling re-investigation of whether morphological patterns align with phylogenetic divergence, geographic gradients or ecological habits. Such analyses may further reveal stable diagnostic criteria between the candidate species, relevant for their field identification and to understand potential adaptations.

In this article, we summarize the evolutionary history of the *P. anguinus* complex and assess the distribution, extinction risk and phenotypic variation of identified lineages, and re-examine the evidence supporting their species delimitation under different concepts. To propose a stable taxonomic revision, we then investigated the nomenclatural history of the olm, assigned available names, and provided the formal description of species that remained unnamed. By integrating centuries of Linnaean systematics with decades of phylogeographic research on *Proteus*, we build a new taxonomic foundation that will hopefully offer a deeper evolutionary and conservation perspective on one of the most emblematic vertebrates of Europe.

Historical biogeography and diversification

The olm represents an ancient Miocene-Pliocene diversification deeply shaped by the fragmented hydrography and complex geological history of the Dinaric Karst, where extant subterranean populations have persisted in long-term isolation while retaining signatures of episodic historical connectivity. This view, long anticipated from biogeographic interpretations (Sket, 1997) and molecular studies based on few loci (Sket and Arntzen, 1994; Gorički and Trontelj, 2006; Gorički et al., 2017; Vörös et al., 2017), was more recently refined by genomic analyses (Recknagel et al., 2024). Integrating mitochondrial sequences (four genes; $n = 299$) and ddRAD-seq markers (29 145 loci; $n = 32$) in what is currently the most comprehensive phylogeography of *P. anguinus*, Recknagel et al. (2024) identified nine evolutionary lineages, labelled according to geographic origins and current subspecific taxonomy: (i) Istra; (ii) Krajina; (iii) Para-littoral; (iv) Kras/Carso; (v) Lika; (vi) Stična; (vii) Dolenjska; (viii) Ljubljanica; and (ix) Parkelj, the dark form corresponding to the subspecies *P. a. parkelj* (fig. 1). Based on paleogeographic calibrations bounded by the divergence with the North-American relative *Necturus* Rafinesque, 1819, divergence times ranged from 16 Ma for the oldest lineage (Istra) to 4 Ma for the youngest pair (Stična/Dolenjska), with additional within-lineage diversity (e.g., Para-littoral, Dolenjska). Some lineages seem to have hybridized in the past, as highlighted by deep cyto-nuclear discordance among geographically adjacent lineages: the Lika lineage carries mtDNA derived from

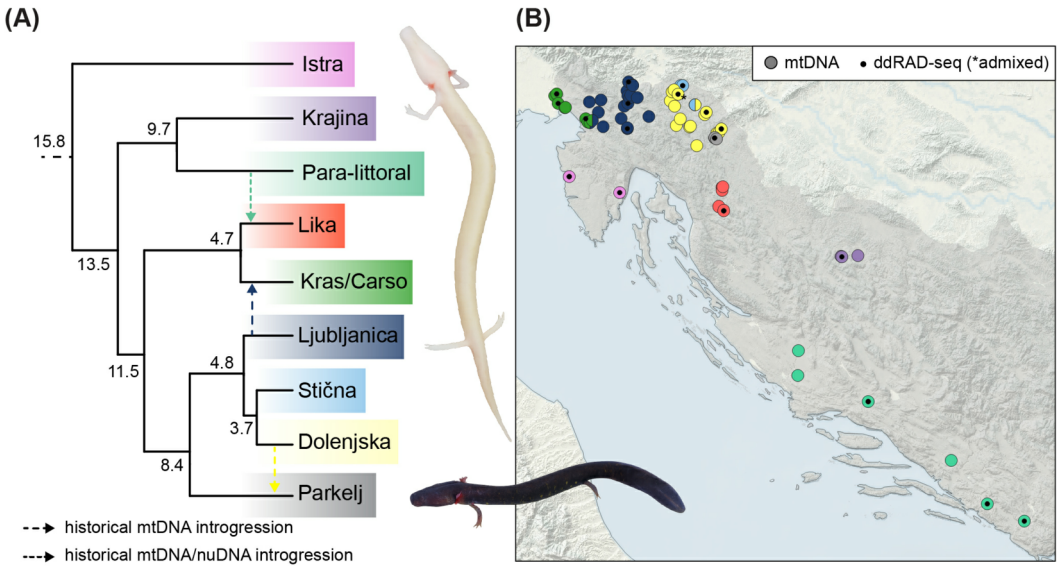

Figure 1. Diversification of *Proteus* based on genomic and mitochondrial data by Recknagel et al. (2024). (A) Phylogenomic relationships and past mitochondrial and nuclear introgression (dashed arrows). (B) Distribution of genetic samples; those analyzed by genomics are highlighted by black dots; the admixed Dolenjska sample is highlighted by an asterisk.

Para-littoral – and also incorporated nuclear alleles from that lineage; the Kras/Carso lineage carries mtDNA derived from Ljubljanica; and the Parkelj lineage carries mtDNA derived from Dolenjska. This phylogeographic picture established by Recknagel et al. (2024) is illustrated in fig. 1.

While *Necturus* is the closest extant relative of *Proteus*, a more closely related lineage according to current paleontological evidence is the extinct genus *Mioproteus* Estes and Darevsky, 1977, which is widely represented throughout the Miocene and Plio-Pleistocene fossil record of Europe (fig. 2) and comprises three described species (Macaluso et al., 2022; Syromyatnikova, 2022). Divergence between the *Necturus* and *Proteus-Mioproteus* clades has been associated with the fragmentation of widespread freshwater systems following the breakup of Laurasian land bridges during the Late Cretaceous and Paleogene (Bonett et al., 2013; Brikiatis, 2014). Furthermore, a third European proteid, *Euronecturus* Macaluso, Villa and Mörs, 2022, which branches much deeper in the proteid phylogeny, has recently been discovered in Middle Miocene sediments from Germany, suggesting additional and older Laurasian connections between European and North American proteids (Macaluso et al., 2022). Another fossil genus, *Orthophyia* von Meyer, 1845, was described from Upper Miocene deposits in Germany based on a single specimen (von Meyer, 1845). However, the holotype was subsequently lost, preventing meaningful comparisons with *Euronecturus*, *Mioproteus*, or even *Proteus*, and leaving its phylogenetic affinities (and potential synonymy) unresolved (Macaluso et al., 2022).

Unlike *Mioproteus*, the nearly complete absence of *Proteus* from the fossil record (see below) is consistent with an early restriction of the genus to the Dinarides (Sket, 1997; Recknagel et al., 2024). From the Eocene to the Early Miocene, the Dinarides and adjacent regions (Balkans, Rhodopes) formed a quasi-insular landmass surrounded by the marine and brackish waters of the Mediterranean Sea and the Peri-Tethys/Paratethys system, respectively, which constrained faunal exchanges with

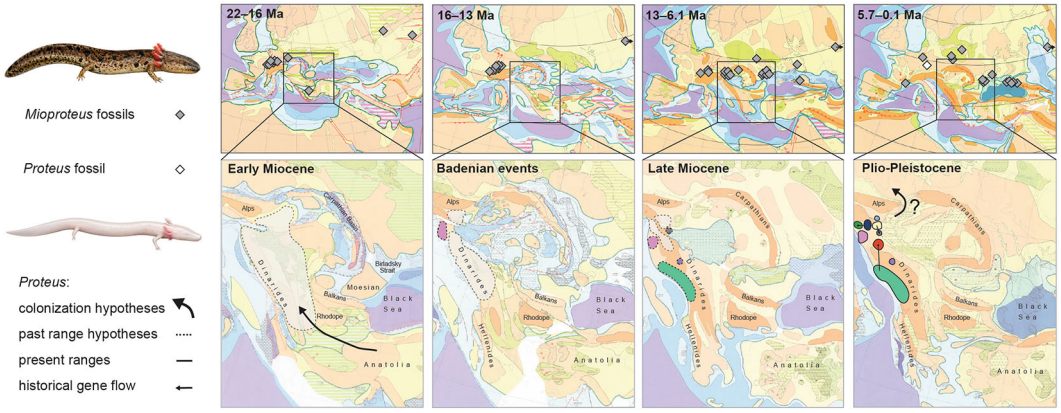

Figure 2. Biogeographic hypotheses of *Proteus* evolution and fossil record of its extinct sister genus *Mioproteus*. Geological maps were adapted from Popov et al. (2005)'s maps 4, 6, 8 and 10. Fossil records were compiled from fosFARbase (https://www.fosfarbase.org/). Ranges of *Proteus* lineages are colored as in fig. 1. Putative ranges of ancestor lineages are shown in transparent white. Arrows indicate hypotheses for the colonization of the Dinarides, and for a range expansion that would explain the occurrence of an Upper Pleistocene fossil attributed to *Proteus* in southeastern Germany.

northern and eastern Europe (Palcu and Krijgsman, 2022). Proteids likely colonized the Dinarides via Anatolia, as suggested by Burdigalian (Early Miocene, ca. 19 Ma) fossils from the northeastern Aegean (Lesvos). A northern route, either through the Moesian Platform or the proto-Alps, appears less likely, as these pathways were largely impeded by Paratethyan marine transgressions, such as the Birladsky Strait and the Alpine-Carpathian Basin (fig. 2). The generally isolated setting of the Balkan Peninsula during much of the Miocene likely promoted the divergence between *Proteus* and *Mioproteus*, either through allopatric divergence of their common ancestor or through the emergence of *Proteus* as a southern vicariant of European *Mioproteus* populations (Sket, 1997). Given that the oldest known *Mioproteus* fossils date to the Early Oligocene (Rupelian, approx. 30 Ma), the first hypothesis implies that the *Proteus-Mioproteus* split is at least this old.

The robustly built *Mioproteus* was probably an epigean, permanently aquatic freshwater salamander, perhaps ecologically more comparable to *Necturus* than to the currently troglobitic *Proteus*. Its remains accordingly occur in lacustrine deposits and in association with typical epigean amphibian assemblages, including aquatic newts and frogs (Estes and Darevsky, 1977; Młynarski et al., 1984). This was probably also true of proto-*Proteus*, as their present-day subterranean habitats were not yet available (Sket, 1997; Recknagel et al., 2024). Much of the Dinaric Karst is developed from thick Mesozoic limestone and dolomite successions deposited on extensive shallow-marine carbonate platforms, but the main development of the modern karst landscape likely followed Cenozoic, particularly Oligocene-Miocene neotectonic uplift and exposure of these carbonates to water erosion, eventually leading to major conduit expansion and underground drainage. The Dinaric Karst in its present geographic and hydrographic configuration is probably no older than approximately 20 Ma old, whereas the complex systems observed today developed and were repeatedly reorganized much more recently (Mihevc, 2007; Hrvatin et al., 2020). Early *Proteus* ancestors may thus have dispersed across the Dinarides through epigean freshwater habitats, particularly in association with the development of the Dinaride Lake System, a series of long-lived intramontane lakes that was widespread during the Early to Middle Miocene, between 18 and 13 Ma (Krstić et al., 2005; Mandic et al., 2011; de Leeuw et al., 2012). This period of expanded

surface-freshwater availability may have facilitated wider ancestral ranges and set the stage for subsequent allopatric diversification, which appears to have begun at approximately the same time, around 16 Ma.

The Middle Miocene splits within *Proteus* are plausibly attributable to a chain of paleogeographic events unfolding during the short Badenian interval (16.3-13 Ma), which drastically affected the Dinaric region. Around 16 Ma, a major marine transgression known as the Badenian Flooding connected Adriatic and Pannonian waters (fig. 2), potentially via a gateway running across present-day Slovenia, thereby re-establishing marine exchange with the brackish Paratethys (Palcu and Krijgsman, 2023). This was followed by progressive restriction of marine gateways due to tectonic reorganization, preconditioning Paratethys for the Badenian Salinity Crisis (13.8-13.4 Ma). The crisis, further triggered by a major sea-level drop (Mi3b event), was marked by evaporite deposition, elevated salinity, and severe ecological disruption (de Leeuw et al., 2010; Palcu et al., 2017). These events broadly coincide, both temporally and geographically, with the earliest divergences inferred within *Proteus* (e.g. Istra approx. 16 Ma; Krajina/Para-littoral ancestor approx. 13.5 Ma), and may have contributed to these splits by creating physical or ecological discontinuities through marine incursions, tectonically driven hydrographic shifts, and deterioration of freshwater conditions.

Later splits in the Miocene and Pliocene likely resulted from disruptive hydrogeological restructuring of karst networks and tectonic uplift (Mihevc, 2007; Špelić et al., 2021). For instance, continued orogenesis of the Snežnik-Risnjak massif was proposed to explain the separation between the Kras/Carso and Lika lineages (Recknagel et al., 2024). Another process that may have contributed to complexify the subterranean hydrographic systems is the Messinian Salinity Crisis (5.96-5.33 Ma). The dramatic lowering of Mediterranean base level likely steepened regional hydraulic gradients, forcing groundwater circulation to deeper levels and promoting conduit enlargement, deep cave development, and reorganization of major underground river systems throughout the coastal Dinaric karst (e.g. Mocochain et al., 2006). Later, climate cooling during the Pliocene and Pleistocene, notably during Quaternary glaciations, further modified cave formations and rejuvenated underground rivers, many of which do not predate the Holocene. These changes probably contributed to the present structure and compartmentalization of karst aquifers, promoting population disconnection among subterranean populations.

In parallel, it cannot be excluded that olms expanded beyond the Dinarides following the retreat of Paratethys during the Late Miocene and Plio-Pleistocene. The only fossil ever attributed to *Proteus* was accordingly discovered in Upper Pleistocene sediments of southeastern Germany (Pottenstein) and described as a distinct species, *Proteus bavaricus* (Brunner, 1956). Although the validity of this taxon has been questioned because of its limited osteological differentiation from the *P. anguinus* complex (Estes, 1981; Bailon, 1995), Bailon (1995) considered its assignment to *Proteus* plausible, based on the element used for the description (a parasphenoid). If this interpretation is correct, *Proteus* would have extended north of the Alps and occupied non-karstic habitats until the last glacial stage, long after the diversification of all extant lineages. These extinct populations may therefore represent northern relicts of either the Stična, Dolenjska and Ljubljanica lineages (which currently occupy the northern fringe of the extant distribution), or correspond to an independent north-alpine lineage that subsequently went extinct.

One difficulty in identifying recent biogeographic drivers of diversification is the uncertainty of the timing when *Proteus* lineages shifted from surface to subterranean habitats, a transition that should have profoundly influenced their ecology and phenotype. As discussed by Recknagel et al. (2024), the eight

mostly subterranean lineages could have independently and relatively recently converged from surface toward troglomorphic forms, with only Parkelj retaining ancestral surface-dwelling traits. Alternatively, if habitat transitions are reversible, a scenario involving fewer events may be invoked, namely one or a few shifts toward cave-dwelling in common ancestors, followed by a secondary transition back toward surface-associated habitats in Parkelj (Ivanović et al., 2013; Sessions et al., 2015). This scenario is not necessarily more parsimonious, however, given that (i) cave habitats were not extensively available at the time of the earliest splits (see above) (ii) specialization to either habitat may evolve repeatedly and over relatively short timescales, and (iii) the German *Proteus* fossil ("*P. bavaricus*") indicates that olms may have inhabited non-karstic (surface) environments as recently as the Pleistocene. Moreover, cave adaptation and habitat transitions may have been facilitated by paedomorphosis and associated hormonal regulation, as shown in other salamanders (Bonett et al., 2022, 2025).

In this respect, the boundary between troglomorphic and non-troglomorphic lifestyles appears less discrete than traditionally assumed. For instance, individuals of the otherwise troglomorphic Kras/Carso lineage regularly exploit surface habitats such as small pools hydraulically connected to the aquifer (Manenti et al., 2024), where they can derive trophic benefits (Barzaghi et al., 2026). Occasional surface behavior was also observed in the Dolenjska lineage (Premate et al., 2022). Olms seem generally plastic in some key traits underlying ground vs. surface life, notably the retention of basic photosensitivity despite pronounced ocular regression – depigmented specimens respond behaviorally to illumination and retain visual pigments in the degenerate retinal and pineal photoreceptors, while the integument itself also contributes to light detection (Hawes, 1945; Kos et al., 2001; Schlegel et al., 2009). Ecological transitions may therefore have occurred more readily than generally assumed, with olms alternating between surface and subterranean habitats – or even occupying both simultaneously – in response to environmental change. Supporting this view, dark epigean individuals of the Parkelj lineage are found in the same aquifer as depigmented subterranean individuals (Recknagel et al., 2022), a pattern that may reflect sympatry between Parkelj and the Dolenjska lineage (Gorički et al., 2017), and potentially also the persistence of both ecotypes within the Parkelj lineage itself. Under such scenarios, surface populations may have persisted until relatively recently before being progressively extirpated during the Pliocene desiccation and the Pleistocene glacial cycles (Gorički and Trontelj, 2006; Recknagel et al., 2024). Adapted to cold water, *Proteus* might have even thrived in surface habitat during glacial periods, and only retreated into subterranean waters as recently as the Holocene (Sket, 1997), with remaining epigean populations being eventually extirpated by post glacial expansion (or human introduction) of predatory fishes, except for the dark olm (Parkelj) – and potentially a few historical observations of abnormally pigmented individuals elsewhere (e.g. Freyer, 1846; but see below). Collectively, these hypotheses imply considerable ecological flexibility and rapid local adaptation (potentially involving pleiotropic traits and simple genetic architecture), which, together with the availability of subterranean habitats, may help explain the persistence and diversification of *Proteus* in contrast to extinct European proteids such as *Mioproteus*.

Lineage ranges and distribution modelling

Occurrence records of *Proteus* have been extensively documented in the historical literature (e.g., Freyer, 1847; Fitzinger, 1850), more recently compiled (e.g., Kranjec, 1981; Sket, 1997; Hudoklin and Aljančič, 2017), and complemented by field surveys, notably using eDNA (e.g., Gorički et al., 2017; Vörös et

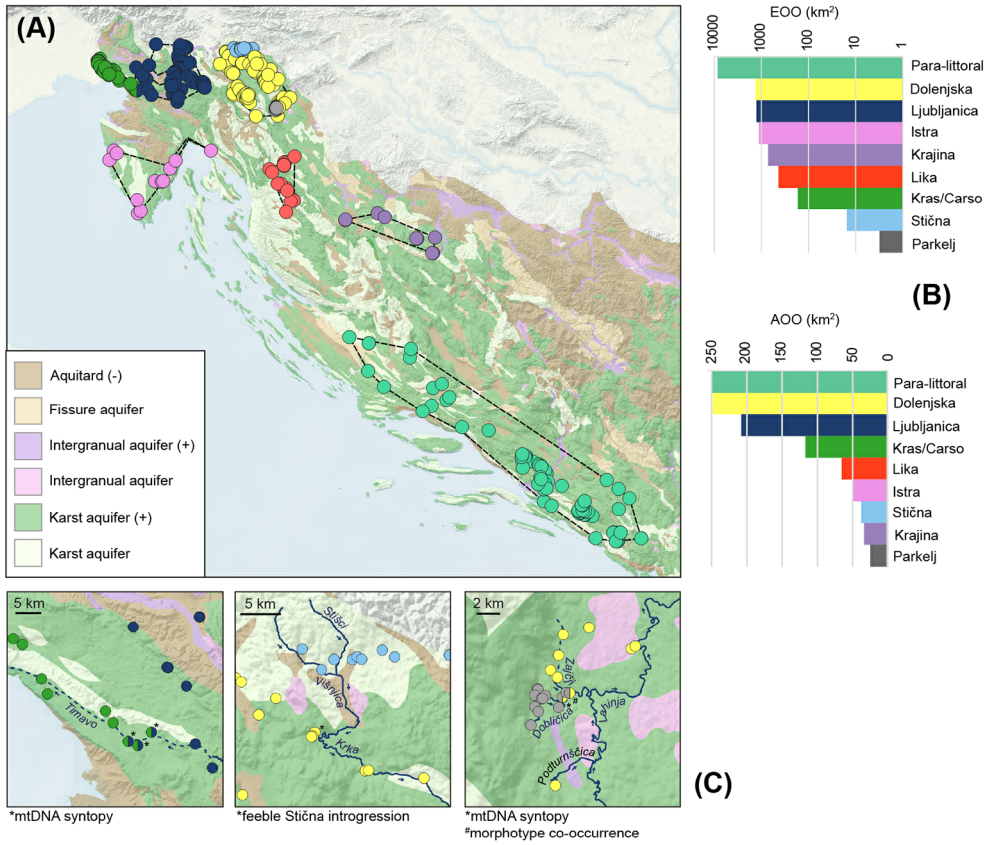

Figure 3. Occurrence and ranges of *Proteus* lineages overlayed by hydrogeology of the Dinaric Karst. (A) Localities colored by lineages with dashed lines delineating their extent of occurrence (EOO). (B) EOO, and areas of occupancy (AOO) estimates per lineages, ranked from highest to lowest. (C) Contact zones between parapatric lineages, with location of mtDNA syntopy, genomic introgression and morphotype co-occurrence. Map backgrounds show hydrogeological properties of the Dinaric karst inferred by DIKTAS; in the key, + designates increased water permeability.

al., 2017). We assembled an updated occurrence dataset that, starting from the records compiled by Sket (1997), integrates additional localities reported since then in scientific publications or the grey literature. After validation and cross-referencing, we obtained precise georeferenced information through manual searches of topographic maps and speleological databases (e.g., https://www.katasterjam.si/; https://grottomap.org/). A total of 355 verified and accurate localities were retained and assigned to species based on molecular results (fig. 1) and the hydrogeology of the karst region, as mapped by the DIKTAS initiative (http://diktas.iwlearn.org/). The inferred distributions are shown in fig. 3.

The most widespread lineages are Para-littoral, Dolenjska and Ljubljanica. The Istra lineage has a comparably extensive range but is known from far fewer localities, which may reflect limited prospection. An historical record from Rijeka, made during excavation of the refinery, is tentatively attributed to this lineage based on geographic proximity, but this requires confirmation through renewed surveys. If extant, this population could alternatively belong to peripheral extensions of the Lika or Ljubljanica lineages or even represent an undocumented lineage.

The Lika and Kras/Carso lineages have comparatively more restricted distributions but are relatively-well known across their range. Kras/

Carso has been well documented along the Isonzo River, as well as in accessible caves of the underground Timavo, notably near its mouth and north of Trieste, where the river flows up to 300 m below ground. Additional localities will almost certainly be reported between these areas as new cave systems along the Timavo are explored by speleologists. For Lika, new range extensions continue to be reported as caves are increasingly surveyed, suggesting that the present range may still be underestimated.

Two lineages – Stična and Parkelj – can be considered micro-endemics. They occur in only a few water resurgences of a single aquifer network (Višnjica and Dobličica, respectively) and unlikely extend further than their known occurrence: Parkelj is surrounded by the Dolenjska lineage, and Stična lies at the northern margin of the Dinaric Karst. For Stična, a historical record farther east (Škavba, Mačji Dol) is tentatively assigned to this lineage based on geographic proximity; however, it belongs to an entirely distinct river system (Temenica), and its identity requires genetic confirmation. Stična nuclear alleles and mtDNA were also detected further south, namely in Poltarica Jama and Bobnova Jama, likely due to recent introgressive hybridization, both localities being attributed to Dolenjska as per their main nuclear ancestry and predominant mtDNA (fig. 1).

Finally, the Krajina lineage extends over a relatively large part of northwestern Bosnia and Herzegovina, but known sites remain currently scattered, which reflects insufficient prospection – monitoring efforts, including eDNA surveys, are ongoing (D. Jelić pers. data). Surrounding areas include permeable karst aquifers that, although locally fragmented, extend more than a hundred kilometers farther south and west, reaching the range of the Para-littoral and Lika lineages. Mapping and genotyping olms across distribution gaps would be particularly informative for defining the respective limits of these lineages.

Our occurrence dataset provides an unprecedented opportunity to obtain a preliminary overview of the potential distribution of the olm through species distribution modelling (SDM). To this end, we first developed a model using all *Proteus* occurrences ($n = 295$ after removal of duplicate occurrences within 1 km^2 cells) and a random forest approach implemented in the R package *randomForest* (Liaw and Wiener, 2002), which is recognized for its strong predictive performance (Valavi et al., 2023). Four environmental variables recommended for subterranean species (Mammola and Leroy, 2018; Pavlek and Mammola, 2021) and relevant to fully aquatic organisms were selected: mean annual temperature (bio1) – an excellent proxy for mean cave temperature (Smithson, 1991; Badino, 2004, 2010); two precipitation variables describing its mean and variability, namely annual precipitation (bio12) and precipitation seasonality (bio15); soil organic carbon content (SOC), which affects the chemistry and organic matter input of groundwater ecosystems. Bioclimatic variables were obtained from CHELSA (Karger et al., 2017). SOC was obtained from the Soil Grids initiative (https://soilgrids.org/).

The modelling workflow followed published recommendations by Valavi et al. (2021, 2023). Pseudo-absences were generated at a ratio of 10:1 relative to presences within buffers located 10-100 km from occurrence records, and a down-sampling procedure was applied. Model performance was assessed using internal cross-validation, with 70% of the data used for training and 30% for testing. Random Forest parameters (the number of variables considered at each split (mtry), the number of trees (ntree), and the minimum node size (nodesize)) were optimized using the R package *caret* (Kuhn, 2008) and then used to fit the final model. Model performance was evaluated using the area under the receiver operating characteristic curve (ROC AUC, hereafter AUC), the true skill statistic (TSS), and the Boyce index. Variable importance was assessed using the Mean Decrease Accuracy (MDA), calculated by measuring the increase in classification error following the

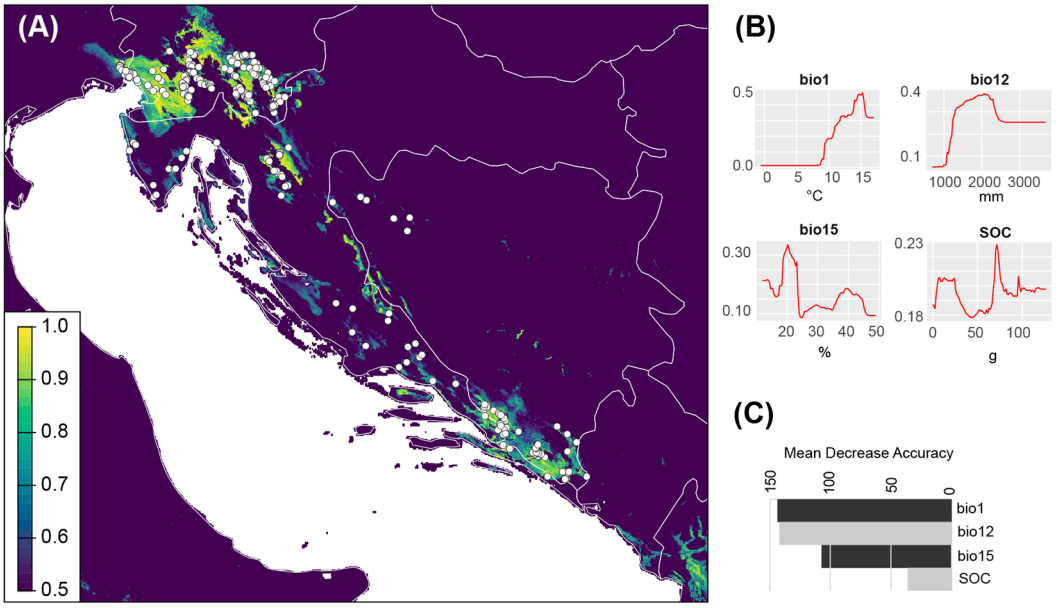

Figure 4. Species distribution modelling of the genus *Proteus*. (A) Range projection under current environmental conditions (dots show occurrence). (B) Response curves of each variable. (C) Relative importance of each variable in the model based on the MDA approach. bio1, mean annual temperature; bio12, annual precipitation; bio15, precipitation seasonality; SOC, soil organic carbon content.

removal of each predictor (Han et al., 2016). Response curves were generated by predicting across the range of each variable while holding all remaining variables at their mean values.

The model showed excellent predictive performance (Boyce index = 0.93), with bio1 and bio12 contributing most strongly to model performance (fig. 4; table S1 in the Supplementary material). The projected distribution closely matched the known range of *Proteus*, identifying the highest habitat suitability in southern Slovenia, northeastern Italy, and southern Dalmatia, where most records originate (fig. 4). Beyond these areas of known presence, the model also highlighted highly suitable habitats in northern Albania, a region without *Proteus* records but with comparatively limited survey coverage. These areas, particularly karst springs and aquifers in the Prokletije region (Dinarides), represent promising targets for future field surveys, notably using eDNA.

Environmental variation, as assessed by a PCA, varied markedly among lineages, notably between coastal and inland ones (fig. S1 in the Supplementary material), and we subsequently applied the same SDM approach to each *Proteus* lineage separately. Because these lineage-specific models were necessarily based on substantially fewer occurrence records, predictive performance was correspondingly lower (Boyce index = 0.21-0.88; table S1 in the Supplementary material). Nevertheless, most projections closely recovered the currently known distributions without predicting excessively broad areas of additional suitability, except for the Istra, Lika and Parkelj lineages (fig. S2 in the Supplementary material). Among the best-performing models (Boyce index $\geqslant$ 0.80), the Para-littoral lineage was predicted to occupy most of the karstic Adriatic coast from Istria to northern Albania, the latter being identified only for this geographically proximate lineage. In contrast, the Kras/Carso lineage was

predicted to occupy only its present distribution, suggesting relatively specific environmental requirements. Although the remaining models were less robustly supported (Boyce index $\leqslant$ 0.80), they likewise predicted comparatively restricted suitable areas, consistent with narrow environmental niches and ecological differentiation among lineages. This result highlights the importance of developing lineage-specific SDMs, particularly when sampling is imbalanced among lineages and environmentally distinctive lineages are represented by relatively few occurrence records. For example, the Krajina region appears to represent a distinct environmental space (fig. S1 in the Supplementary material), and it is predicted as largely unsuitable in the model pooling occurrences from all lineages – except in the immediate vicinity of the few known Krajina localities (fig. 4). In contrast, the Krajina-specific model correctly identifies this region (and northwestern adjacent areas) as suitable (fig. S2). Variable contribution and model fit estimates of each model are given in table S1 in the Supplementary material.

These models, the first developed for *Proteus* and among the few available for subterranean vertebrates (Mammola and Leroy, 2018), illustrate the considerable potential of SDMs for this genus. Combined with hydrogeological information, they may help prioritize future surveys for this highly secretive amphibian and provide a framework for forecasting extinction risk under future climate scenarios – especially since olms are restricted to a narrow window of cold groundwater (generally 8-12°C). Expanding species-specific occurrence datasets, particularly in under-surveyed regions such as Bosnia and Herzegovina, Montenegro, and Albania, together with the incorporation of cave-specific environmental variables (e.g. groundwater temperature, dissolved oxygen, or hydrochemical parameters) instead of indirect surface proxies, should substantially improve future models and provide new insights into the environmental processes underlying diversification within the complex.

Extinction risk assessment

The distribution data provide a basis for determining whether lineages qualify for a threatened category under IUCN Criterion B, which assesses extinction risk arising from restricted geographic range in combination with fragmentation, few locations, and continuing decline (IUCN, 2012). Under this criterion, species may be listed as Vulnerable, Endangered, or Critically Endangered when either their extent of occurrence (EOO; B1) or area of occupancy (AOO; B2) falls below defined thresholds, provided that at least two additional conditions are met. These include occurrence in a limited number of locations (subcriterion “a”) and evidence of continuing decline (subcriterion “b”), here particularly in habitat quality (subcriterion “b(iii)”).

In the case of *Proteus*, individual cave and surface river systems may each be interpreted as a single “location” in the IUCN sense, i.e., areas that could be rapidly affected by a single threatening event such as a pollution incident. Different karst systems are therefore expected to function as largely independent locations with little demographic connectivity. Moreover, the olm inhabits subterranean waters that are increasingly affected by industrial and agricultural pollution, to which it appears particularly sensitive. Trace elements, including toxic metals such as mercury and arsenic, as well as PCBs, have been detected in tissues of individuals representing different lineages (Bulog et al., 2002; Pezdirc et al., 2011). Fertilizer-derived compounds (nitrates and phosphates) have increased by up to threefold over recent decades in streams inhabited by the Parkelj lineage (Năpăruş-Aljančič et al., 2017) and can reach concentrations exceeding levels considered safe for the species (Glavan and Cvejić, 2024). Furthermore, although quantitative evidence for population declines remains scarce,

Table 1. Range estimates and IUCN assessments of the nine *Proteus* lineages.

	EOO (km^2)	B1 (EOO)	AOO (km^2)	B2 (AOO)
Istra	1115	EN	48	EN
Krajina	718	EN	32	EN
Para-littoral	8617	VU	252	EN
Lika	442	EN	64	EN
Kras/Carso	169	EN	116	EN
Ljubljanica	1297	EN	208	EN
Dolenjska	1379	EN	248	EN
Stična	15	CR	36	EN
Parkelj	3	CR	24	EN

EOO, extent of occurrence (km^2) with associated threat status under criterion B1; AOO, area of occupancy (km^2, computed from a 2 × 2 km grid) with associated threat status under criterion B2.

decreases in sightings have been reported from several localities (e.g. Postojna Cave), and local population extirpation has been documented in others (e.g. the Kočevsko region; Aljančič, 2019). We therefore infer that subcriteria "a" and "b(iii)" are met for *Proteus*, such that the final threat category primarily depends on the range parameters EOO and AOO.

Based on our data, we calculated EOO and AOO for each lineage. EOO was computed as the area (km^2) of a convex hull encompassing all occurrence points, adjusted to exclude large impermeable aquitards and the Adriatic Sea. AOO was estimated as the area covered by occupied 2 × 2 km grid cells.

The resulting estimates are summarized in table 1. All nine lineages fall below the B1 threshold for Vulnerable (EOO < 20 000 km^2), and all but the Para-littoral lineage (approx. 8600 km^2) fall below the Endangered threshold (EOO < 5000 km^2). Moreover, the Parkelj and Stična lineages, which exhibit extremely restricted distributions (EOO < 15 km^2), meet the Critically Endangered threshold under B1 (EOO < 100 km^2). All lineages also fall below the B2 threshold for Endangered (AOO < 500 km^2).

Based on these values, together with the inferred continuing decline in groundwater habitat quality and the occurrence of lineages in few independent locations, all lineages plausibly qualify as Endangered under Criterion B1ab(iii) + B2ab(iii), except the Para-littoral lineage, for which only Criterion B2ab(iii) applies. Moreover, the two most restricted lineages, Parkelj (one location) and Stična (one or two locations), plausibly qualify as Critically Endangered under Criterion B1ab(iii). Future reassessments should incorporate improved estimates of habitat degradation, demographic trends (e.g. from capture-mark-recapture studies), and population connectivity (e.g. inferred from conservation genomics) for each lineage.

Phenotypic diversification

Distinctions among olm populations were noted early on from observations of variation in morphology, skin coloration, and other anatomical features, such as the presence of eyes, providing the basis of the first revisions (Michahelles, 1830; Freyer, 1846; Fitzinger, 1850). In the past decades, multivariate analyses of museum specimen measurements have likewise emphasized some geographic patterns of differentiation, interpreted in various manners, especially in respect to their grouping in statistical analyses according to prior phylogeographic and taxonomic hypotheses (Kranjec, 1981; Grillitsch and Tiedemann, 1994; Arntzen and Sket, 1997; Gorički, 2006; Ivanović et al., 2013).

To quantify differences and test for diagnostic characters among the *Proteus* lineages, we compiled a dataset of 14 characters assessed from 259 specimens of known geographic origin representing eight lineages (Parkelj specimens were not accessible), curated in the following institutions: Muséum national d'Histoire naturelle (MNHN), Paris, France; Hrvatski prirodoslovni muzej (HPM), Zagreb, Croatia; Hrvatsko Društvo za Biološka Istraživanja (HDBI), Zagreb, Croatia; Naturhistorisches Museum Wien (NHMW), Vienna, Austria; Prirodoslovni muzej Slovenije (PMS), Ljubljana, Slovenia; Univerza v Ljubljani, Biotehniška

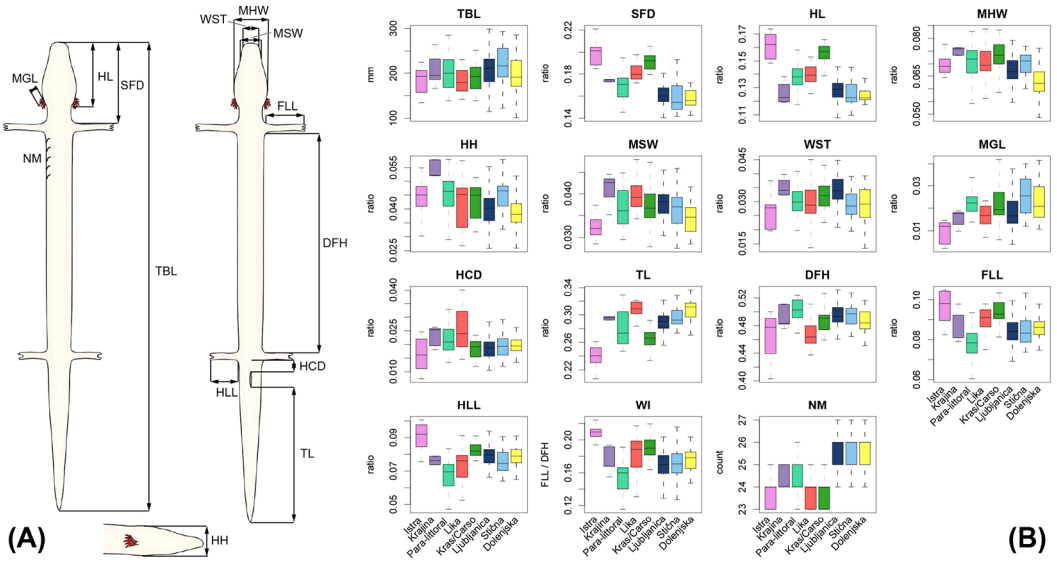

Figure 5. Measurements and variation at individual morphological traits among *Proteus* lineages. (A) Landmarks used for morphological measurements, adapted from Kranjec (1981). (B) Variation of each trait, shown in raw values or as body ratios (division by TBL). TBL, total body length; SFD, snout-forelimb distance; HL, head length; MHW, maximum head width; HH, head height; MSW, minimum snout width; WST, width of the snout tip; MGL, maximum gill length; HCD, hindlimb-cloaca distance; TL, tail length; DFH, interlimb distance; FLL, forelimb length; HLL, hindlimb length; WI, Wolterstorff Index; NM, number of myomeres.

fakulteta (ULBF), Ljubljana, Slovenia; Zemaljski muzej Bosne i Hercegovine (NMBH), Sarajevo, Bosnia and Herzegovina; Museo Civico di Storia Naturale, Trieste (MCST), Trieste, Italy; Museo Civico di Storia Naturale di Milano (MSNM), Milano, Italy. The dataset initially incorporated raw data from Kranjec (1981), and to ensure comparability, we first re-measured NHMW specimens from various series to replicate the methodology. Measurements of additional specimens were all obtained within a few weeks, thereby minimizing recording drift. To avoid bias from juveniles, only specimens above 100 mm of total body length were considered.

We considered 13 metric variables measured with a ruler (1 mm precision) or a digital caliper (0.1 mm precision): total body length (TBL), the distance between the snout tip to the tail tip (ruler); head length (HL), the distance between the base of the skull and the snout tip (caliper); tail length (TL), the distance between the posterior end of the cloaca and the tail tip (caliper); maximum head width (MHW), the maximum width between the skull edges (caliper); head height (HH), the maximum distance between the lower and upper part of the skull (caliper); minimum snout width (MSW), the minimum width of the snout (caliper); width of the snout tip (WST), the width of the rostrum (caliper); maximum gill length (MGL), the length of the longest gill from root to tip (caliper); hindlimb-cloaca distance (HCD), the distance between the anterior end of the cloaca and the posterior junction of the hindlimb (caliper); snout-forelimb distance (SFD), the distance between the anterior junction of the forelimb and the snout tip (caliper); interlimb distance (DFH), the distance between the posterior junction of the forelimb and the anterior junction of the hindlimb (ruler); forelimb length (FLL), the length of the forelimb from anterior junction to fingertip (caliper); and hindlimb length (HLL), the length of the hindlimb from the posterior junction to toetip (caliper). One meristic variable, the number of myomeres (NM) was visually counted from forelimb to hindlimb. Fig. 5A

Table 2. Average morphometric measurements of eight *Proteus* lineages based on 259 specimens.

	Istra	Krajina	Para-littoral	Lika	Kras-Carso	Ljubljanica	Stična	Dolenjska
n	10	5	27	14	15	125	30	33
TBL	191.2 ± 46.9	208.6 ± 39.1	204.2 ± 43.9	183.9 ± 29.8	191.8 ± 33.8	205.6 ± 38.7	219.9 ± 43.9	197.2 ± 50.6
HL	30.7 ± 7.1	26.2 ± 3.9	28.2 ± 6.3	25.9 ± 3.9	29.3 ± 4.7	26.4 ± 5.3	27.6 ± 5.7	24.5 ± 6.3
TL	45.5 ± 10.5	60.0 ± 7.6	58.4 ± 15.1	56.3 ± 9.5	51.7 ± 11.7	59.3 ± 11.3	65.2 ± 14.0	60.4 ± 14.9
MHW	13.3 ± 3.7	15.5 ± 2.9	14.3 ± 4.4	12.9 ± 2.3	14.0 ± 2.9	13.8 ± 3.1	15.3 ± 3.5	12.4 ± 3.8
HH	8.4 ± 3.0	11.0 ± 2.5	9.5 ± 2.9	7.7 ± 1.8	8.2 ± 2.0	8.4 ± 2.3	10.0 ± 2.7	7.7 ± 2.5
MSW	6.1 ± 1.6	8.5 ± 1.2	7.6 ± 1.9	7.4 ± 1.4	7.2 ± 1.4	7.8 ± 1.9	8.1 ± 1.8	6.6 ± 1.9
WST	5.2 ± 1.7	6.8 ± 1.1	6.2 ± 1.8	5.6 ± 1.7	5.9 ± 1.5	7.0 ± 2.1	6.5 ± 2.0	5.6 ± 2.2
MGL	1.8 ± 1.1	3.1 ± 0.7	4.6 ± 1.1	3.7 ± 2.6	4.2 ± 1.8	3.8 ± 1.7	5.9 ± 2.7	4.4 ± 1.9
HCD	3.3 ± 1.7	4.9 ± 1.5	4.5 ± 1.4	4.5 ± 1.3	3.9 ± 1.8	3.9 ± 1.2	4.3 ± 1.4	4.0 ± 1.5
SFD	38.1 ± 9.3	36.1 ± 6.3	34.3 ± 6.6	33.6 ± 4.8	36.0 ± 5.6	33.1 ± 6.2	34.5 ± 5.4	31.1 ± 7.8
DFH	88.0 ± 17.9	103.0 ± 21.4	104.0 ± 20.4	87.7 ± 15.1	93.3 ± 15.6	102.2 ± 19.8	109.5 ± 25.0	96.4 ± 25.7
FLL	18.1 ± 3.3	17.8 ± 2.3	15.9 ± 3.5	16.0 ± 2.0	17.8 ± 3.0	17.3 ± 3.4	18.5 ± 3.1	16.8 ± 3.7
HLL	17.0 ± 3.1	15.2 ± 1.8	13.8 ± 3.6	13.6 ± 2.8	15.6 ± 2.7	16.1 ± 2.8	16.6 ± 2.3	15.6 ± 3.3
WI	0.21 (0.19-0.22)	0.18 (0.15-0.19)	0.15 (0.12-0.19)	0.19 (0.13-0.22)	0.19 (0.16-0.22)	0.17 (0.13-0.25)	0.17 (0.13-0.22)	0.18 (0.13-0.25)
NM	23.8 (23-25)	24.8 (24-27)	24.4 (23-26)	23.6 (23-25)	23.7 (23-28)	25.7 (21-29)	25.6 (24-27)	25.6 (24-27)

For each lineage, mean and standard deviation are given for metric characters (in mm); mean and range are given for the ratio (WI) and meristic (NM) characters. Parkelj could not be measured. TBL, total body length; SFD, snout-forelimb distance; HL, head length; MHW, maximum head width; HH, head height; MSW, minimum snout width; WST, width of the snout tip; MGL, maximum gill length; HCD, hindlimb-cloaca distance; TL, tail length; DFH, interlimb distance; FLL, forelimb length; HLL, hindlimb length; WI, Wolterstorff Index (FLL/DFH); NM, number of myomeres.

illustrates character measurements. Finally, we computed the Wolterstorff index as the ratio between forelimb length and interlimb distance.

Analyses of the morphological datasets were conducted with the R package *groupstruct2* 1.2 (Chan and Grismer, 2026). Descriptive statistics (mean and standard deviation) for each trait are reported in table 2, and variation among and within lineages are illustrated as body ratios in fig. 5B. Statistical analyses of metric variables were conducted after scaling by TBL using the multispecies allometric growth correction of *groupstruct2*, which assumes independent allometry between pre-defined groups, while TBL was $\log_{10}$-transformed.

Lineages broadly overlap in the morphospace summarized by the first two PCA axes, with only the Istra lineage showing a relatively distinct position (fig. 6A). Nevertheless, the centroids of all but three lineage pairs (25 of 28 pairwise comparisons) differed significantly from one another (PERMANOVA on PCA scores; 10 000 permutations), while the assumption of homogeneity of multivariate dispersions was violated in only one comparison (table S2 in the Supplementary material). Accordingly, lineages significantly differed at one or more individual traits in nearly all instances (26 of 28 pairwise comparisons; Kruskal-Wallis or ANOVA tests; table S3 in the Supplementary material). Thus, although substantial within-lineage variation in body shape largely obscures among-lineage differences, these remain statistically detectable. Moreover, these differences were not randomly distributed: Euclidean distances between lineage centroids increased significantly with genomic divergence (Nei's D_{xy} computed from ddRAD-seq data; Recknagel et al., 2024), but showed no relationship with environmental divergence estimated from species distribution models (Schoener's D) (fig. 6B). This phylogenetic signal is also reflected in the number of myomeres, which is generally lower in the earliest-diverging lineages (approx. 24) than in the more recently diverged Slovenian lineages (approx. 26).

To further test whether lineages form distinct morphological groups, we performed a supervised Gaussian Mixture Model (GMM) clustering analysis. The best-supported model, based

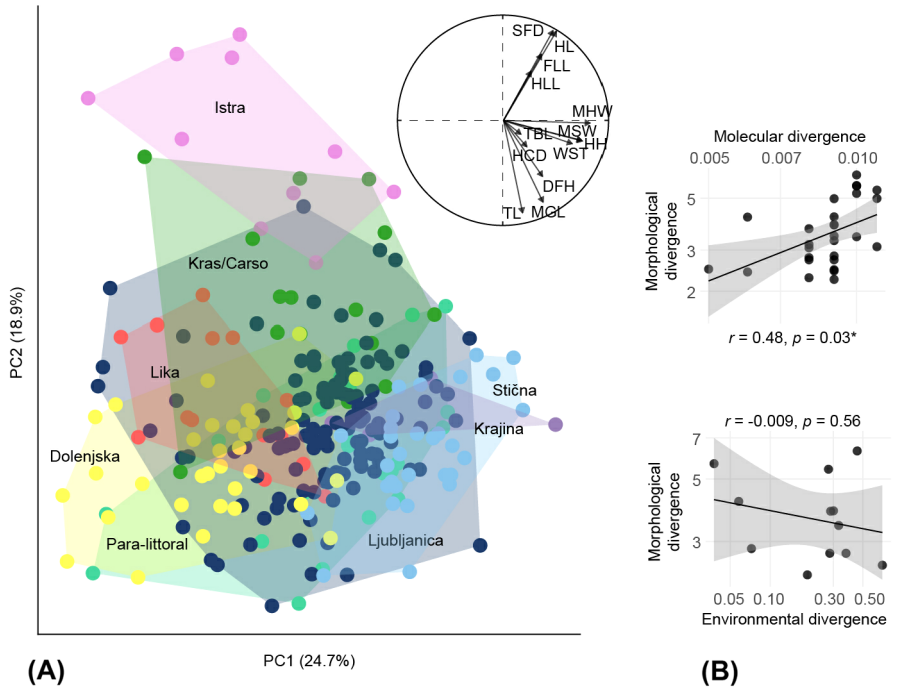

Figure 6. Multivariate morphological variation among *Proteus* lineages. (A) Principal Component Analysis (PCA) of 13 metric characters measured in 259 specimens. Polygons show convex hulls. TBL, total body length; SFD, snout-forelimb distance; HL, head length; MHW, maximum head width; HH, head height; MSW, minimum snout width; WST, width of the snout tip; MGL, maximum gill length; HCD, hindlimb-cloaca distance; TL, tail length; DFH, interlimb distance; FLL, forelimb length; HLL, hindlimb length. TBL was $\log_{10}$-transformed and other variables were transformed by allometric size correction. (B) Relationship between pairwise Euclidean distances at morphological traits and phylogenomic and niche divergence among lineages. Correlation coefficient (r) and significance (p) are assessed by a Mantel test.

on the Bayesian Information Criterion (BIC), recovered only two clusters, separating the Istra lineage from all remaining lineages. Models that included additional clusters received overwhelming support against them (Bayes factor > 10^6 relative to the best model), indicating that no further discrete groupings are supported by the morphometric data.

We next evaluated the relative importance of metric characters for discriminating *Proteus* lineages using a Random Forest machine-learning approach with the Boruta feature-selection algorithm, using default settings. All variables except total body length (TBL) consistently outperformed randomly permuted "shadow" variables, with interlimb distance (DFH) emerging as the most informative character, followed by tail length (TL), head length (HL), hindlimb length (HLL), snout-forelimb distance (SFD), maximum head width (MHW), and the remaining measurements (fig. S3 in the Supplementary material). Consistent with these results, the most distinctive lineage, Istra, is characterized by a relatively elongate head with a narrow snout, a shorter tail, longer hindlimbs, and a higher Wolterstorff Index than the remaining lineages (fig. 5).

These observations broadly corroborate previous studies of *Proteus*, which concluded that morphological differences among populations were too subtle to justify taxonomic distinction (e.g., Grillitsch and Tiedemann, 1994). However, the present analyses show that this morphological variation is not random but phylogenetically structured, indicating that phenotype evolution has tracked the historical

diversification of the complex. Such a pattern is consistent with morphological evolution proceeding within a constrained morphospace, where strong functional selection associated with subterranean life limits phenotypic divergence while mutation and genetic drift gradually generate lineage-specific differences. Morphological conservatism in *Proteus* should therefore not be interpreted as evidence against evolutionary independence, but rather as the expected outcome of diversification under persistent stabilizing selection, where subtle yet statistically detectable differences accumulate over millions of years.

Beyond its older evolutionary age, the elongated Istra phenotype may also relate to ecological specialization. Although environmental variation and species distribution models do not indicate a particularly distinct habitat, this lineage appears to be encountered more frequently in comparatively deeper groundwaters, often associated with sandy substrates rather than the rocky conduits typically occupied by the remaining species (D. Jelić pers obs.). This pattern may point to occupation of a distinct hydrological niche. Interestingly, in the Kras/Carso populations, individuals inhabiting deep cave environments tend to exhibit a more elongated and slender head profile, whereas specimens recorded from springs and other groundwater-surface ecotones generally displayed a relatively broader parietal region, giving a more expanded appearance to the head, especially posteriorly to the orbital area (R. Manenti and B. Barzaghi pers. obs.). Whether elongated head profiles convey an ecological and functional significance, and reflects phenotypic plasticity or local adaptation remains an open question.

Finally, our morphometric dataset included 47 specimens examined by Fitzinger (1850), allowing us to assess whether the morphological differences recovered here correspond to those underlying his milestone recognition of seven species of olms. Using the average values he reported for six measurements, we projected Fitzinger's species' means into the multivariate morphospace derived from our data. Several taxa showed a close correspondence (e.g. *freyeri*, *laurentii*), whereas others exhibited more pronounced deviations (e.g. *zoisii*, *schreibersii*) (fig. 7A). A detailed comparison across traits (fig. S4 in the Supplementary material) indicates that agreement is generally better for larger measurements than for smaller ones, as expected from the greater relative influence of measurement error on the latter. Moreover, Fitzinger based his diagnoses on substantially larger specimen series than those represented by the surviving museum material examined here. Likewise, the differences in head shape illustrated by Fitzinger's original drawings (published by Grillitsch and Tiedemann, 1994) broadly correspond to those observed in representative specimens of the respective lineages, although this comparison necessarily remains qualitative (fig. 7B). Given the variation in each population, it is not surprising that Fitzinger (1850) concluded on different taxa, although this assessment ultimately proved to be only partially correct (see below).

Species delimitation

Delimiting the nine phylogeographic lineages of *Proteus* as distinct species or subspecies depends on whether they meet the criteria associated with the species concept(s) adopted. Under the general lineage species concept (GLC), species are viewed as independently evolving lineages, typically identified through strong phylogenetic structure and genetic cohesion (de Queiroz, 1998, 2007). In *Proteus*, all nine lineages were statistically delimited as "species" using sequence partitioning approaches (for mtDNA) and the multispecies coalescent (for genomic loci) (Recknagel et al., 2024). In simple terms, these approaches either identify groups of sequences showing a

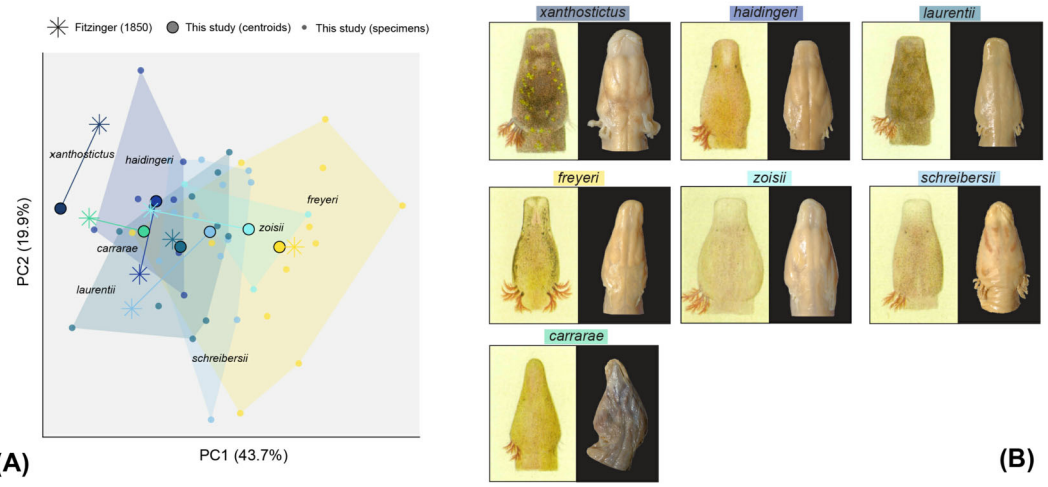

Figure 7. Re-assessment of the NHMW specimens used in Fitzinger (1850)'s taxonomic revision. (A) PCA on five body ratios (morphometric traits divided by total body length TBL) measured in 47 specimens given as "types" of the seven species delimited by Fitzinger; allometric size correction was not possible given the small sample sizes of some species. Small and large circles represent individual specimens and species centroids. Average measurements of each species given by Fitzinger (1850) are projected on the PC axes (asterisks), with lines showing deviation from the centroids of our measurements. (B) Comparison of head shape from Fitzinger's drawings (adapted from Grillitsch and Tiedemann, 1994) and photographs taken from representative specimens (credit: D. Jablonski). See fig. S4 in the Supplementary material for further assessment.

clear discontinuity between within-group variation and between-group divergence (sequence partitioning), or evaluate whether samples are better explained as belonging to a single evolutionary lineage or to distinct lineages evolving independently over time, while accounting for incomplete lineage sorting (multispecies coalescent). Although widely applied, these methods have sparked criticisms for delimiting species complexes, as they are sensitive to sampling design and may recognize recently structured populations as distinct species (Sukumaran and Knowles, 2017; Campillo et al., 2020; Dufresnes et al., 2020). This can lead to taxonomic inflation, i.e. an artificial increase in species numbers due to oversplitting of widespread and genetically diverse taxa, which is a frequent concern when molecular data form the primary basis for species delimitation (Gippner et al., 2026).

Under the more conservative biological species concept (BSC), only lineages that are (at least partly) reproductively isolated are regarded as species (Mayr, 1942; Coyne and Orr, 2004), ideally identified by an absence or strong limitation of introgressive hybridization in secondary contact zones (Dufresnes et al., 2020, 2023). This view is typically favored for the European herpetofauna, being followed by the taxonomic committee of the Societas Europaea Herpetologica (Speybroeck et al., 2020), and is thus particularly relevant here. In *Proteus*, only a single genomic sample showed signs of contemporary introgression (fig. 1), implying that, if lineages do come into contact, reproductive barriers effectively constrain gene flow, in support of species status under the BSC. In the northern part of the range, several of the youngest lineage pairs exhibit parapatric distributions across continuous, highly permeable karst aquifers (fig. 3). Direct contact is evident between the Kras/Carso and Ljubljanica lineages, whose mtDNA haplotypes co-occur in several localities near the Italo-Slovenian border along the Timavo underground river (figs. 1, 3). Potential contact may also occur between the Parkelj and Dolenjska lineages. Depigmented ("white") olms have been observed within the aquifer inhabited by Parkelj (Recknagel et al., 2022), and both lineages were

detected within the same spring by lineage-specific eDNA (Gorički et al., 2017) (fig. 3). Further north, the Dolenjska and Stična lineages are separated by only a few kilometers within the same hydrographic network (fig. 3) and seemingly hybridized recently: feeble ancestry from Stična (approx. 15%) was retrieved in a parapatric Dolenjska genomic sample from Poltarica Jama (see Figure 4a in Recknagel et al., 2024), while one Stična mitotype segregates within the Dolenjska range in Bobnova Jama (OQ296736; fig. 1; not mentioned by Recknagel et al., 2024). Reciprocally, the distribution of the same lineages in distinct river systems (e.g., Dolenjska, Paralittoral) suggests that their present isolation is evolutionary ephemeral, as the dynamic biohydrographic history potentially involves recurrent exchanges between populations.

Since assessing contact zones is often unfeasible – either because they do not exist or have not yet been located – an alternative approach in the spirit of the BSC is to interpret genetic divergence in light of the pace at which reproductive barriers evolve in respect to the "grey zone of speciation", i.e., the divergence window separating conspecific from reproductively isolated lineages (Roux et al., 2016; Dufresnes et al., 2021, 2023). In amphibians, when reproductive isolation primarily arises from hybrid genetic incompatibilities that accumulate gradually with genomic divergence, speciation can be approximated as clock-like. Consequently, divergence times and genetic distances correlate with reproductive isolation and can provide useful benchmarks (Dufresnes et al., 2021, 2023; Gippner et al., 2026) – as recently applied in other European salamandrids, such as the *Mesotriton alpestris* complex (e.g., Koster et al., 2026). Most candidate species of *Proteus*, dated at 4-16 Ma in nuclear timetrees and 3-17 Ma in mitochondrial timetrees, fall well above the grey zone observed for European anurans (2-6 Ma), where gene flow is consistently restricted above 6 Ma and pervasive below 2 Ma (Dufresnes et al., 2021); a similar window (2.6-7 Ma) was retrieved when extending comparisons to other amphibians, including Caudata (Gippner et al., 2026). This argument alone should, however, be treated with caution because (i) divergence estimates depend on calibration schemes and datasets, limiting direct comparisons across studies; (ii) it remains unknown whether speciation in *Proteus* follows a clock-like process; and (iii) if so, whether this process occurs at a comparable rate to other amphibians. It is, in fact, expected to be slower, given the species' long generation times that should lower the rate of molecular evolution, thus potentially delaying the accumulation of reproductive isolation for a given timeframe.

Complementary insights may be obtained from sequence divergence directly, notably at mitochondrial barcoding genes commonly used in amphibian taxonomy, such as 16S (Vences et al., 2005). At this marker, excluding comparisons affected by cyto-nuclear discordance, only the youngest (hybridizing) lineage pair (Stična/Dolenjska) shows less than 3% divergence ($n = 78$, 1367 bp aligned; fig. 8; sequences from Recknagel et al. (2024), analyzed with MEGA 11, Tamura et al., 2021). A threshold of 3% divergence in 16S is considered conservative (e.g., Vieites et al., 2009), above which amphibian lineages typically correspond to valid species under the BSC (Malone and Fontenot, 2008; Dufresnes et al., 2021). The lower divergence observed for Stična/Dolenjska (1.8%) falls within the grey zone but still corresponds to a higher probability of representing distinct species than subspecies; equal probability was estimated at 1.6% at this marker (Dufresnes et al., 2021). As above, whether such thresholds apply to *Proteus* depends on the comparability of substitution rates. To explore this, we examined the relationship between 16S pairwise distances and divergence times in *Proteus* and compared it with that of other European amphibians delimited under the BSC (data from Dufresnes et al., 2021). The relationships are remarkably similar, suggesting that 16S

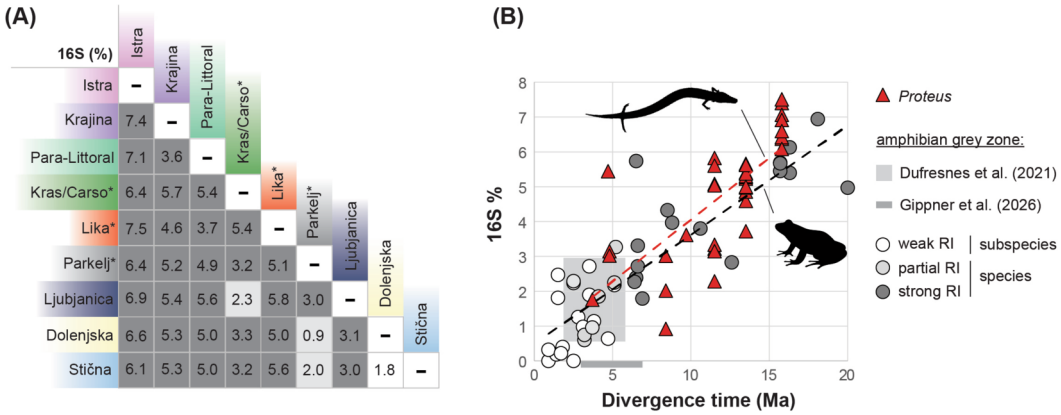

Figure 8. Pairwise 16S distances (% of sequence differentiation) among *Proteus* lineages in the context of species delimitation. (A) 16S distance matrix; values above and below the commonly used amphibian threshold of 3% are shown by dark and light grey respectively; lineages with historically introgressed mtDNA are indicated by asterisks – their 16S divergence reflects evolution since the introgression event, and thus underestimates true lineage divergence. (B) Relationship between 16S and divergence time in *Proteus* (red triangles) compared to other Western Palearctic anuran amphibian lineages delimited from evidence for reproductive isolation (RI), as inferred by analyses of their contact zone (circles); for the latter, circle darkness shows the degree of RI, allowing to define the grey zone of speciation (grey square) – the divergence window that contain both subspecies-level and species level lineages (data from Dufresnes et al., 2021). A refinement of the amphibian temporal grey zone inferred from a broader taxon set is also highlighted (Gippner et al., 2026).

evolves at a comparable rate in *Proteus* (fig. 8). By extension, and assuming similar patterns in the nuclear genome, the grey zone of speciation defined for other amphibians should thus be applicable to *Proteus* (fig. 8).

An older but historically important metric of divergence is allozyme distance, which was shown to correlate with DNA divergence and divergence times (Maxson and Maxson, 1979), and with Nei's $D > 0.15$ considered indicative of genetic isolation underlying distinct species in *Plethodon* salamanders (Highton, 2000). In *Proteus*, three lineages were surveyed using allozymes by Sket and Arntzen (1994) – Ljubljanica (as "Planina"), Parkelj (as "Jelševnik"), and Stična (as "Vir" and "Rupnica"). All three, while corresponding to the shallowest phylogenomic and mitochondrial divergences, exhibit $D \geqslant 0.25$ from their closest relatives, which is thus well above the proposed threshold.

In summary, there is unequivocal support for recognizing the nine *Proteus* lineages as distinct species under the GLC (Recknagel et al., 2024). Support under the BSC is more indirect but broadly consistent: (i) lineages in direct or potential contact (parapatry) show no or restricted evidence of ongoing hybridization; and (ii) their levels of divergence, based on commonly used metrics in amphibian systematics, are comparable to or exceed those observed between reproductively isolated species.

Moreover, the increase in morphological differentiation with phylogenetic divergence (fig. 6) indicates that stable phenotypic differences accumulate progressively during lineage divergence, even though they remain largely non-diagnostic and often imperceptible to the human eye. Such a pattern is common in European amphibians, where speciation frequently precedes conspicuous phenotypic diversification, particularly for conservative traits subject to strong stabilizing selection. As a result, recently diverged species often remain morphologically cryptic despite long histories of independent evolution (e.g. Ambu et al., 2025; Koster et al., 2026). Rather than arguing against species hypotheses, these subtle but progressively diverging morphotypes should therefore

be regarded as signatures of ongoing evolutionary divergence and the gradual emergence of independently evolving species.

Accordingly, we provisionally recognize all nine *Proteus* lineages as distinct species. Further confirmation should come from expanded genomic sampling in parapatric zones, which will help refine the grey zone of speciation in this genus.

Nomenclature review

The tumultuous history of early *Proteus* research was reviewed in detail by Aljančič (2019: see also Mattes, 2018). Olms had been known long before their taxonomic recognition, as illustrated by carving on 15th century medieval tombstones (stećci) in the Boljuni necropolis near Stolac, Bosnia and Herzegovina (Mulaomerović, 2012). In the literature, the olm was first mentioned by Valvasor (1689) as a lizard-like earthworm, based on local testimonies, and later by Steinberg (1758), who documented the capture of "white, four-legged fishes" by a fisherman in 1751 from the Malnj spring of the Planinsko polje, which is linked to Postojna Jama. The first reported hypogeous observation is a 1752 drawing of a cave identified as Črna Jama (Postojna-Planina cave system), with mentions of locals purportedly catching and exporting *Proteus* ("snakes") to Venice (Shaw and Čuk, 2015). In the following decade, Scopoli (1762), based on specimen(s) brought to him from a different area (Stična) by his associate, the botanist Wulfen, proposed to Linnaeus that the olm be included as a new *Lacerta* species in the next edition of *Systema Naturae*. Although convinced of the novelty of the animal, Linnaeus (1766), assuming Scopoli's specimen was a larva, refrained from naming it until an adult was found. Instead, it was Laurenti (1768), who recognized a category of amphibians with lungs and gills, who formally described the species as *Proteus anguinus* Laurenti, 1768.

Laurenti's description, accompanied by a drawing of an olm in swimming position (Laurenti, 1768: Pl. 4, Fig. 3), states "Habitat verno tempore in lacu Tschirnicensi Carnioliae [It lives in the springtime in Lake Cerknica, Carniola], and indicates that both the specimen and the drawing were provided by Father Hohenwart (Sigismund Ernst von Hohenwart 1745-1825) (Laurenti, 1768: p. 37). The diagnosis succinctly describes the animal's general characteristics, namely an elongated white body, coral-like external gills, a compressed tail, and the absence of eyes. The illustrated and examined specimen thus corresponds to the name-bearing type (holotype), and according to Laurenti's account, its origin was Lake Cerknica (star 0 in fig. 9).

The origin of Laurenti's specimen has nevertheless been questioned (Sket, 2007; Aljančič, 2019). Olms do not directly inhabit Lake Cerknica – an open karstic aquatic environment which partly dries every year – although washed-out individuals are occasionally found in the area after floods (Aljančič, 1966; Aljančič et al., 2016), notably at its source (Drole, 2017). When Scopoli (1772) eventually published his own description of the species, he explicitly corrected Laurenti's type locality, stating "non in *lacu Zirchizenfi*, sed prope *Sittich* e crypta subterranea, aeslivo tempore una cum aquis exit quandoque [not in Lake Cerknica, but in an underground cave near Stična, in summer it sometimes comes out with the waters]", suggesting he knew of the origin of the few *Proteus* specimens that circulated at the time (Mattes, 2018). Supporting this interpretation, Configliachi and Rusconi (1821) narrated that the first olms described were not from Cerknica but from near the mouth of caverns close to Stična, where peasants found them in small puddles, as they had been cast out after heavy rains. Likewise, Freyer (1847), in reviewing the history of research on the olm, recounted that Scopoli first learned of the species from the people of Stična, and that it was Scopoli who provided Hohenwart with the specimen from which Laurenti

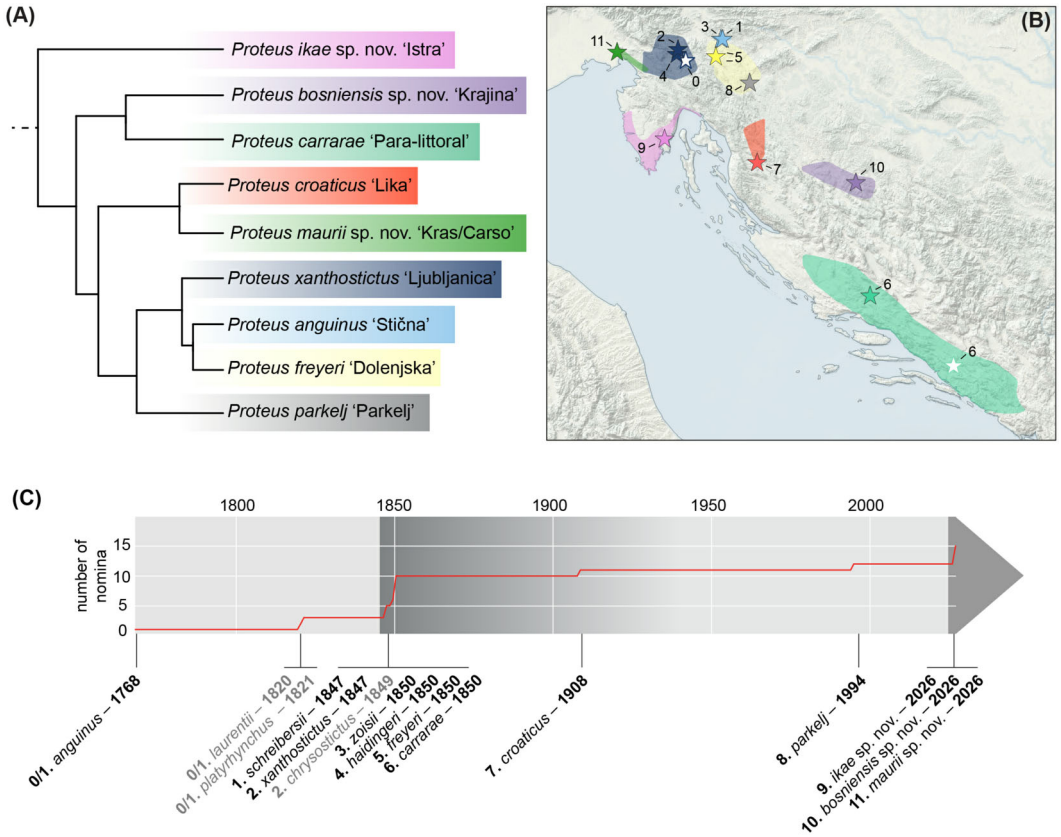

Figure 9. History of *Proteus* systematics and taxonomic revision. (A) Phylogeny of *Proteus* species and assignment of available names according to the Principle of Priority. (B) Identity of type localities based on species distributions (range adapted from fig. 3). (C) Timeline of name availability and delimitation history; for each nomen, numbers refer to type localities on the map; the red line shows the cumulated number of available names over time; names in grey emphasize objective synonyms; on the arrow, light and dark shading emphasizes whether the olm was considered as a single species or multiple species, respectively. For the nomen *anguinus*, two type localities are shown: the one given by Laurenti (1768; white star "0") and the one corresponding to the putative origin of the holotype (filled star "1") according to Aljančič (2019), which corresponds to the valid type locality. For the nomina *freyeri* and *carrarae*, restricted type localities through lectotype designation are shown in colored stars, while white stars show the alternative origin of some paralectotypes.

prepared his description, a statement with which other authors agreed (e.g., Duméril et al., 1854).

As investigated by Aljančič (2019), a shared origin of Laurenti's and Scopoli's material is also quite plausible given the relationships among the scholars involved. Specifically, the Carniolan-born Hohenwart was a student of Wulfen (Scopoli's associate and collector), accompanied him on natural history expeditions, and as Jesuits, both were likely aware of olms being kept captive by monks at Stična Abbey. Collected specimens were rare by then (Mattes, 2018), and the late 18th and early 19th century scientific literature suggests that Stična was the only area where olms could be easily observed. In contrast, the presence of *Proteus* in the Postojna-Planina cave system was not specifically reported before the mid-19th century (Hochenwart, 1838). Laurenti, who resided in Vienna, may have referred to Lake Cerknica as an approximation, as the lake was already a famous place and was considered the source of all smaller lakes and interconnected subterranean waters of the whole Carniolan karst (Schreibers, 1801).

Whether Laurenti's specimen came from Lake Cerknica or Stična has important nomenclatural consequences, as these regions are

inhabited by different candidate species of olms (Ljubljanica and Stična, respectively). After careful evaluation of the evidence, Aljančič (2019) concluded that it was more parsimonious to assume that Stična was the true area of origin, and suggested that Virski studenec, the only karst spring in the area of Stična where olms may be observed outside caves, should be regarded as the type locality of Laurenti's taxon (star 1 in fig. 9). Under this interpretation, which we follow here, the Stična lineage thus corresponds to *Proteus anguinus* sensu stricto.

Similarly acknowledging that surface waters are not the primary habitat of the olm, Fejérváry (1926) had proposed to amend the type locality of *P. anguinus* to "Magdalenen-Grotte [Magdalena Cave]", a confirmed place of occurrence conveniently chosen for its geographic proximity to Lake Cerknica (Fejérváry, 1926: p. 231). However, this action is not valid in the absence of neotype designation, and appears inappropriate if Laurenti's specimen is considered to have been collected from Stična.

After Laurenti's and Scopoli's descriptions, *Proteus* was eventually included in the 13th edition of *Systema Naturae* (Gmelin, 1789: p. 1056). The species was then studied in detail for the first time in the late 1790s by Schreibers (1801), who, with the support of Baron Sigmund Zois (a philanthropist nobleman and naturalist from Carniola), provided unprecedented details on its anatomy and demonstrated the paedomorphic nature of the species, thereby stimulating strong interest among early 19th-century zoologists. This prominence, in turn, gave rise to numerous alternative classifications. Shaw (1802) transferred *P. anguinus* to *Siren* Österdam, 1766, and several authors placed it in newly erected genera: *Larvarius* Rafinesque, 1815; *Platyrhynchus* Leuckart, 1816; *Hypochthon* Merrem, 1820; *Caledon* Goldfuss, 1820; *Phanerobranchus* Leuckart, 1821; and *Apneumona* Fleming, 1822. Another genus, *Hemitriton* Van der Hoeven, 1833, included *Hypochthon* as a subgenus and was later restricted to *Proteus* through designation of *P. anguinus* as the type species (Dubois and Raffaëlli, 2009). Several family-rank taxa were also proposed – see discussion on family-group nomenclature of Proteidae in Dubois and Ohler (2015), who demonstrated that the correct authorship of Proteidae is Bonaparte, 1831. In addition, several variant names arose through subsequent misspellings, such as *Protaeus* in Oppel (1811: 79), *Hypohton* in Cuvier (1829: p. 129), *Hydochton* in Gray (1831: p. 108), *Protheus* in Hochenwart (1838: p. 37), *Catedon* in Duméril et al. (1854: p. 185), and *Proteus anguineus* in Mertens and Müller (1940: p. 14) when citing Schreiber (1912), who had nevertheless spelled the name correctly.

As part of these generic reassignments, two additional specific nomina were introduced. The first, *Hypochthon laurentii* Merrem, 1820, has sometimes been interpreted as a distinct taxon and associated to a holotype specimen (Brame and Gorham, 1972). This interpretation is erroneous, however, as Merrem clearly referred to Laurenti's species: "Proteus anguinus. Laur. *rept. p*. 37. *t*. 4. *f*. 3" (Merrem, 1820: pp. 187-188). The second, *Phanerobranchus platyrhynchus* Leuckart, 1821, reused the author's previously proposed genus name *Platyrhynchus* (Leuckart, 1816) as a species epithet under the new genus *Phanerobranchus*, likewise with explicit reference to "Prot. anguinus Laur." (Leuckart, 1821: p. 260). Thus, both *Hypochthon laurentii* and *Phanerobranchus platyrhynchus* are replacement names (objective synonyms) and have the same name-bearing type and type locality as *Proteus anguinus* Laurenti, 1768.

By the mid-19th century, the genus name *Hypochthon* was preferred over *Proteus* (e.g. Bonaparte, 1831; von Tschudi, 1838), with *Hypochthon laurentii* in widespread use (e.g., Freyer, 1842). At the time, a major focus of olm research was on the understanding of its distribution (Hochenwart, 1838; Freyer, 1847), and as new populations were discovered, notable variation in morphology, coloration, and gill shape began to be recognized (Michahelles,

1830; Freyer, 1846). Synthesizing the accumulating knowledge, Fitzinger (1850) published an extensive taxonomic revision based on an impressive collection of 479 specimens (including 140 living individuals) from 11 localities. He distinguished seven species, and for each, provided names, localities, and detailed diagnoses, including morphological measurements, which we revisited and illustrated in fig. 7.

(1) *Hypochthon laurentii* from "Magdalena-Grotte [Magdalena Cave]", one of the largest and best-studied olm populations, part of the Postojna cave system. Fitzinger examined 312 specimens (90 living) from this population, 15 of which are catalogued in NHMW (19957/1-15). This population belongs to the Ljubljanica lineage.

(2) *Hypochthon schreibersii* from "Vir" [Vir pri Stični, Slovenia] (star 1 in fig. 9). Fitzinger examined 78 specimens (16 living), ten of which are catalogued in NHMW (19962/1, 19966/2-8, 19967/1-2). This population belongs to the Stična lineage.

(3) *Hypochthon zoisii* from "Rupa" [Rupe/Rupnica near Stična, Slovenia] (star 2 in fig. 9). Fitzinger examined 11 specimens (10 living), four of which are catalogued in NHMW (19959/2-5). This population belongs to the Stična lineage.

(4) *Hypochthon xanthostictus* from "Bedén [near Laze, Slovenia]" (star 3 in fig. 9). Fitzinger examined 12 living specimens from this population, one of which is catalogued in NHMW (19959/1). This population belongs to the Ljubljanica lineage.

(5) *Hypochthon haidingeri* from "Kleinhäusler-Grötte [Planinska jama, Slovenia]" (star 4 in fig. 9), which is directly connected to the Postojna cave system. Fitzinger examined 40 specimens (2 living), seven of which are catalogued in NHMW (19963/1-7). This population belongs to the Ljubljanica lineage.

(6) *Hypochthon freyeri* from "Kumpole [Kompoljska jama, Slovenia]" and "Potiskavz [Potiskavška jama, Slovenia]" (stars 5 in fig. 9). Fitzinger examined 16 specimens (9 living) from Kumpole, 12 of which are catalogued in NHMW (19969/1-12), and one specimen from Potiskavz (not present in NHMW). Both populations belong to the Dolenjska lineage.

(7) *Hypochthon carrarae* from "Sign [Sinj, Croatia]" and "der Narenta [Neretva River, Croatia and Bosnia-Herzegovina]". These correspond to the only two olm populations known in Dalmatia at the time. Fitzinger (1850: 296) provided additional details: "der Bach Gorizizza bei Sign [Gorizizza spring near Sinj]" and "eine Quelle an der Narenta . . . nahe an der Strasse die nach Mostar führt" [a spring on the Narenta near the road to Mostar] (stars 6 in fig. 9). He examined four specimens from Sinj (one in NHMW: 19980/1) and one from the Narenta (none identified in NHMW). Both populations belong to the Paralittoral lineage.

Fitzinger's *Historia Hypochthonum* having been in preparation for years, his findings were circulated prior to their publication. As a consequence, most of his names had already been introduced by Freyer (1847, 1849), raising the question of whether some were made available. In particular, Freyer (1846) reported an unnamed species sighted in 1836 and 1845 in underground caves at "Bedén near Lase [Bedenj ponor, northern slope of the Jakovški grič, about half a kilometer west of Laze]" following floods in the Planinsko polje, characterized by dark coloration, golden spots, distinctive head and gill morphology, for which he provided illustrations and a detailed diagnosis, also noting that live specimens had been sent to Schreibers for examination. In a subsequent review of known olm localities, Freyer (1847) applied Fitzinger's forthcoming taxonomy and

listed the Laze population as "*Hyp. xanthostictus* Fitzinger [*H. schreibersii* Freyer]" (Freyer, 1847: p. 39). By honoring Schreibers, and elsewhere recounting the 1845 discovery of the dark golden-spotted olm at Laze (Freyer, 1847: p. 38), Freyer clearly linked these names with his earlier diagnosis (Freyer, 1846). Accordingly, *xanthostictus* must be regarded as available from Freyer (1847). In contrast, *schreibersii*, proposed only in synonymy and not subsequently used for that taxon, was never made available for it. Instead, when commenting on the species' unusual coloration, Freyer (1849) introduced a replacement name, *chrysostictus*, writing "*Hypochthon xanthostictus Fitz*. besser *chrysostictus mihi*" and listed the Laze population as "*Hypochthon chrysostictus*". By explicitly favoring *chrysostictus* over *xanthostictus*, Freyer (1849) thereby made *chrysostictus* available, although it remains a junior (objective) synonym of *xanthostictus* under the Principle of Priority.

Another four names traditionally attributed to Fitzinger (1850) also appear in these earlier publications. Freyer (1847) associated them with localities as follows: (i) "Rupa bei Sittich [Rupa near Stična] (*Hyp Zoizii* FITZ.)"; (ii) "Vir, die Quelle bei Sittich [the spring near Stična] (*Hyp. Schreibersii* MICHACHELLES)"; (iii) "jenseits Potitkaviz bei Strug [beyond Potiskavec near Strugah] (*Hyp. Freyeri* FITZINGER); and (iv) "*Hyp. Carrarae* FITZ. bei Sign in Dalmatien [near Sinj in Dalmatia]". As no diagnoses were provided, the three names attributed to Fitzinger were not made available by Freyer (1847).

For the Vir species, however, Freyer (1847) attributed *schreibersii* to Michahelles (although he misspelled his name). Michahelles (1830) had reported that olms from the surroundings of Vir differed morphologically from those of the Magdalena cave, notably in having a shorter head, snout and tail, and concluded that they represented a distinct species; he also noted color differences in a subsequent publication (Michahelles, 1831). Michahelles praised Schreibers for his scientific achievement based on specimens from this population (Schreibers, 1801), which explains the intended tribute by Freyer (1847) and Fitzinger (1850). By explicitly referring to Michahelles's indications when listing *schreibersii* from Vir, Freyer (1847) thereby made this name available for that taxon.

Freyer (1849) again distinguished the same taxa, but in a slightly different manner. He listed "*Hypochthon Schreibersii Michahelles*", "*Hypochthon Freyeri Fitz*" and "*Hypochthon carrarae*", still without diagnosis – and thus without making the latter two available – and attributed *zoisii* to Michahelles as "*Hypochthon Zoisii Michahelles*". However, Michahelles (1830, 1831) had only discussed differences between olms from Vir and the Magdalena cave. Although Rupa (*zoisii*) and Vir (*schreibersii*) are geographically close ("one hour apart"), they were treated as separate localities by Fitzinger (1850), and Michahelles made no statement regarding the nature of specimens from Rupa, merely noting that such material had been sent to Baron Zois (Michahelles, 1831). Consequently, *zoisii* was not made available by Freyer (1849), as it was not explicitly linked to a diagnosis or a previously published indication.

In these publications, the mention of *Hypochthon laurentii*, particularly when attributed to Fitzinger as "*Hypochthon laurentii* Fitz" (e.g., Freyer, 1842, 1846), has sometimes been interpreted as the establishment of a new taxon and thus as a junior homonym of Merrem's *laurentii* (Frost, 2026). However, it appears that Freyer and Fitzinger used this name simply to designate or circumscribe the then-recognized species of olm. This is evident in Freyer (1846), who, when reporting his new species from Laze, compares it to "*Hypochthon Laurentii*" and refers to the populations of that "known species" ("den bekannten"). More generally, as noted above in relation to the credits to Michahelles and to himself, Freyer preferentially cited authors who first distinguished the delimited species (taxonomic status) rather than those who coined their names (nomenclatural status).

Accordingly, "*Hypochthon laurentii* Fitz" refers to Fitzinger's taxonomic framework – particularly his restriction of that species to Magdalena Cave – rather than to a new name.

From this point of view, the authorship and dates for the seven species listed by Fitzinger (1850) and mentioned by Freyer (1846, 1847, 1849) should be corrected as follows:

(1) *Hypochthon xanthostictus* Freyer, 1847, with objective synonym *Hypochthon chrysostictus* Freyer, 1849
(2) *Hypochthon schreibersii* Freyer, 1847
(3) *Hypochthon freyeri* Fitzinger, 1850
(4) *Hypochthon carrarae* Fitzinger, 1850
(5) *Hypochthon zoisii* Fitzinger, 1850
(6) *Hypochthon haidingeri* Fitzinger, 1850
(7) *Hypochthon laurentii* Merrem, 1820

Based on distributions and type localities, three taxa – *H. xanthostictus*, *H. chrysostictus* and *H. haidingeri* – belong to the Ljubljanica lineage. As *xanthostictus* is the oldest available name, that lineage should be referred to as *Proteus xanthostictus* (Freyer, 1847), with *H. chrysostictus* and *H. haidingeri* treated as junior synonyms. While Freyer's *xanthostictus* type specimen clearly seems atypical for Ljubljanica, it likely stems from riboflavin-induced yellow blotches (Istenič and Zigler, 1974) – as frequently observed in "white" *Proteus* specimens – that must particularly contrast against a pigmented skin following prolonged light exposure or alcohol preservation, as acknowledged by Freyer (1842) himself to explain the dark coloration of such specimens. Accordingly, Fitzinger (1850) applied this name on typical depigmented specimens, as represented by NHMW 19959/1 (fig. 7).

Hypochthon carrarae belongs to the Paralittoral lineage and represents the oldest (and only) available name for this lineage, as *Hypochton carrarae* Fitzinger, 1850. Because its syntypes originate from two distinct ranges (Sinj and the Neretva River), and that the species may be phylogeographically structured (Recknagel et al., 2024), we here restrain the type locality to Sinj, Dalmatia, Croatia by designating NHMW 19980/1 as the lectotype of *Hypochton carrarae* Fitzinger, 1850.

Hypochthon freyeri belongs to the Dolenjska lineage and likewise represents the oldest (and only) available name, as *Proteus freyeri* (Fitzinger, 1850). Although its syntypes originate from sites separated by only a few kilometers, we here anticipate on any future taxonomic subdivision of this genetically diverse species (Recknagel et al., 2024) by designating NHMW 19969/7 from Kompoljska jama, Dobrepolje, Slovenia as the lectotype of *Proteus freyeri* (Fitzinger, 1850).

Finally, *H. schreibersii* and *H. zoisii* belong to the Stična lineage and are therefore junior synonyms of *Proteus anguinus* (and of its objective synonym *H. laurentii*).

In his review of a decade of zoological progress in Croatia, Brusina (1880) acknowledged the recent discovery of the olm in northeastern Croatia – previously known only from Carniola and Dalmatia – and based on a single specimen from Otočac that he considered distinct from Slovenian and Dalmatian forms, proposed the name *Proteus croaticus*. Brusina (1908) later mentioned his taxa as a subspecies, *Proteus anguinus croaticus* and recounted the discovery by reproducing a 1899 letter from the donor Mihovil Jurković, a schoolteacher. In this letter, the origin of the specimen is more precisely given as "Gackoj vodi kod Otočca" [Gacka brook near Otočac], captured in the summer of 1879. The original find is attributed to a woman washing laundry in a branch of the Gacka River behind the old town, where water emerges among rocks and disappears underground; she reportedly retrieved the animal with her washing paddle, after which Jurković's pupils, bathing nearby, recognized its unusual nature and brought it to their teacher.

While this taxon has been acknowledged in some works (e.g., Sket, 1997), others have treated it as unavailable ("*Proteus croaticus* nom. nud." in Gottstein Matočec et al., 2002),

presumably because Brusina (1880) did not provide any diagnosis or indication (only mentioning that his taxon is "distinct" from other olms). Likewise, Jurković's letter featured in Brusina (1908: p. 250) includes little descriptive elements, but it does comment on the coloration of the specimen, specifying that the body had a beautiful fine flesh coloration ("lijepe putenaste boje") that became paler in alcohol. Before 1931, coloration details were considered as an "indication" that was sufficient for nomenclatural availability. We therefore consider *Proteus anguinus croaticus* as made available by Brusina (1908), with the 1879 Otočac specimen as the holotype (initially presumably curated at HPM, but subsequently lost; Karaman, 1921), and the Gacka river near Otočac as the type locality. This taxon belongs to the Lika lineage and represents the oldest (and only) available name for that lineage, as *Proteus croaticus* Brusina, 1908.

Since the second half of the 19th century, the olms' systematics was marked by a progressive taxonomic deflation and the re-instatement of *Proteus* and *anguinus* through application of the Principle of Priority. Based on skeleton examination, Cope (1866) concluded on the validity of *Proteus zoisii*, *P. carrarae*, *P. xanthostictus*, *P. schreibersii* and *P. anguinus*, but not of *P. freyeri* (synonymized with *P. xanthostictus*) and *P. haidingeri* (synonymized with *P. anguinus*); he nevertheless examined only a single specimen per taxon. In his catalog of BMNH amphibians, Boulenger (1882) considered *carrarae* and *zoisii* as varieties, *P. anguinus* var. *carrarae* and *P. anguinus* var. *zoisii*, and grouped all other Fitzinger's taxa under the nominal *P. anguinus*. Brusina (1908) followed this trend by downranking his *croaticus* as a subspecies. Fejérváry (1926), who examined specimens from two origins, recognized Fitzinger's *freyeri* as a distinct subspecies, *P. anguinus freyeri*. In their European list of amphibians and reptiles, Mertens and Müller (1928) considered *Proteus anguinus* without subspecific distinction, but recognized two subspecies in the second edition (Mertens and Müller, 1940), *P. a. anguinus* and *P. a. zoisii*; the latter was even still mentioned (although with expressed doubts) as a species in some work (e.g., McCrady, 1954). Throughout the second half of the 20th century, *Proteus* was once again universally considered as a monotypic genus and *P. anguinus* as a monotypic species, as notably emphasized by a morphological re-assessment that included Fitzinger's types, which concluded on clinal variation among proposed taxa to justify their synonymy (Grillitsch and Tiedemann, 1994).

Within this conservative framework, the "black olm" – so named for its melanistic pigmentation, expressed even in the absence of light – discovered in the 1980s, was described as a distinct subspecies, *Proteus anguinus parkelj* Sket and Arntzen, 1994, with holotype ULBF J8 and type locality "Na Trati, Jelševnik near Črnomelj, Slovenia". In addition to its non-troglomorphic behavior and pigmentation, the authors demonstrated proteic (allozyme) and phenotypic differentiation from the "white" populations, regrouped as *P. a. anguinus*, while also discussing the paraphyly of the latter (Sket and Arntzen, 1994). The status of *P. a. parkelj* subsequently prompted debate, due to conflicting interpretations of the morphological and genetic variation among *Proteus* populations (Grillitsch and Tiedemann, 1994; Goricki and Trontelj, 2006; but see Arntzen and Sket, 1996, 1997). As assigned by Recknagel et al. (2024), the type locality of *P. a. parkelj* corresponds to the Parkelj lineage, which should therefore be recognized as *Proteus parkelj* Sket and Arntzen, 1994.

Finally, *Proteus bavaricus* Brunner, 1956, described from an Upper Pleistocene fossil from southeastern Germany, may either designate a distinct extinct species or correspond to one of the extant *Proteus* lineages, in which case it would represent a northern population persisting outside the present range of the genus during the last glacial stage. Under the latter hypothesis, the most parsimonious interpretation is that this population belongs to

either the Stična, Ljubljanica, or Dolenjska lineages, which occupy the northernmost portions of the current *Proteus* distribution and are therefore geographically closest to southeastern Germany. In such a case, the nomen *bavaricus* would become a junior synonym of either *anguinus*, *xanthostictus*, or *freyeri*. Resolving this issue will require a reassessment of the evolutionary distinctiveness of *P. bavaricus*, notably through the discovery of additional fossils from older deposits – which would support an earlier origin and potential species-level distinction – and through detailed osteological comparisons with extant lineages. As the available evidence does not allow to settle on this case, we leave *P. bavaricus* unassigned, especially as this nomen does not threaten the nomenclatural stability of the three candidate extant species with which it may potentially prove conspecific.

Considering extant populations, the 12 available names identified here thus correspond to six species (Stična: *P. anguinus*; Ljubljanica: *P. xanthostictus*; Dolenjska: *P. freyeri*; Paralittoral: *P. carrarae*; Lika: *P. croaticus*; and Parkelj: *P. parkelj*), while the remaining three (Istra, Krajina, Kras/Carso) are newly described in the following section.

Taxonomic revision

Zoobank article LSID

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Based on the above, we provide a taxonomic revision of *Proteus*, by recognizing nine species, six with available names, and three newly described. To provide molecular diagnoses, SNPs fixed between species were identified in the 16S (1367 bp) and COI sequences (660 bp) with MolD (Fedosov et al., 2022), based on the sequences published on GenBank by Recknagel et al. (2024). To confirm their identity, newly-collected type specimens were barcoded at a short portion of 16S following Vences et al. (2005), with primers 16S-A/B, and sequences (517 bp aligned) were deposited on GenBank. For external diagnoses, we refer to the analyses of phenotypic morphological traits conducted in the above section, noting that no single character is fully diagnostic (i.e., without overlap), and that one species (Parkelj) could not be measured. Instead, we report the most important average differences (based on data scaled by total body length), notably with closely related species (table 2, fig. 5). Note that, apart from Istra, field identification is only possible through geographic and molecular information. Brief species-specific life-history information is provided.

Proteus anguinus **Laurenti, 1768** (fig. 10)

Identity

The Stična lineage.

Etymology

anguinus is a latin construct meaning “snake-like”, which refers to the elongated cylindrical body of the olm.

Vernacular names

Stična’s olm (English), Stički močeril (Slovenian).

Type series

Holotype, the specimen provided and pictured by Hohenwart, used for diagnosis and figured in Laurenti (1768). While given as “in lacu Tschirnicensi Carnioliae [in Lake Cerknica, Carniola]” by Laurenti (1768), the type locality is more likely Virski studenec near Stična, Slovenia (see Aljančič, 2019 and the previous section).

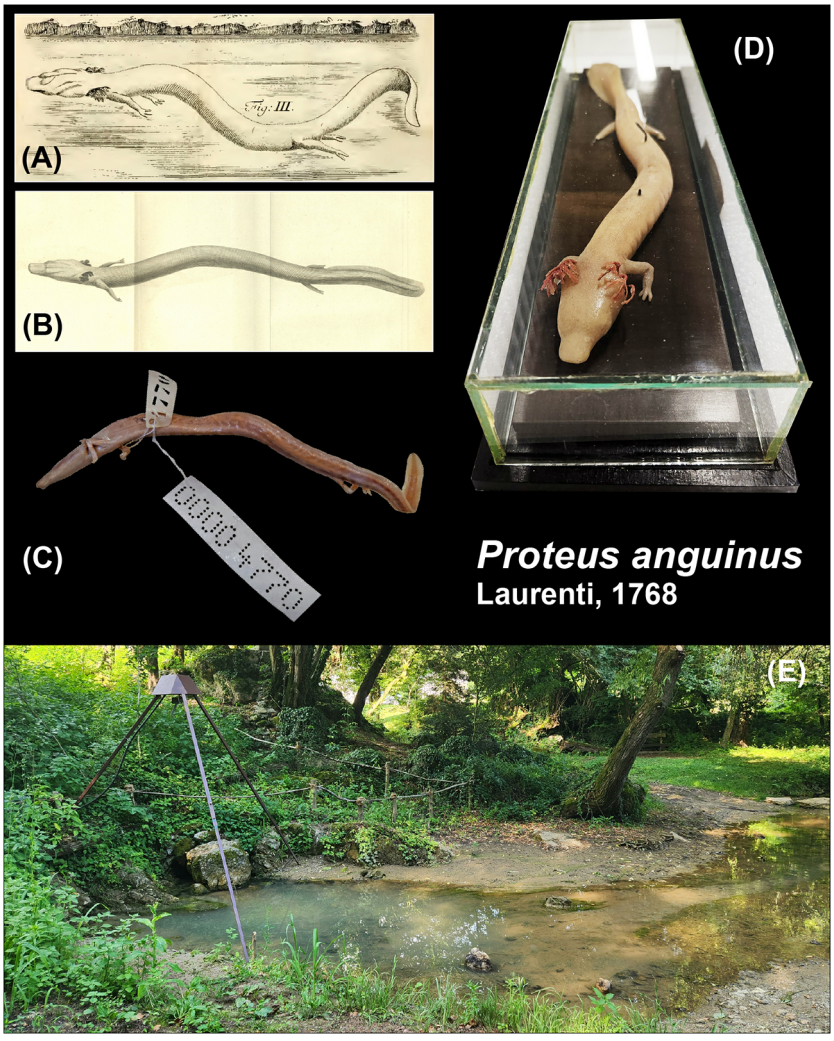

Figure 10. *Proteus anguinus* Laurenti, 1768 – the Stična species. (A) Laurenti (1768)'s drawing of the type specimen of *P. anguinus*, which most likely originated from Vir pri Stični. (B) Schreibers (1801)'s drawing of *P. anguinus*, examined for the first comprehensive work on the biology of the species, based on specimens from Stična area, which was the only population known by scholars at the time. (C) MNHN-RA 0000.4770, the specimen mentioned by Cloquet (1826: p. 394) as being donated by Baron Zoïs – and thus potentially among those used for Schreibers's research – reportedly when the French troops retreated from the Austrian provinces during the Napoleonic wars in 1813 (B Kryštufek pers. comm.), making it one of the oldest *Proteus* specimen still curated. (D) Wax specimen MNHN-RA 1986.0996, purportedly donated in the early 19th century – a common practice as biological specimens of olms were rare at the time. (E) Virski studenec in Vir pri Stični, the type locality of *P. anguinus* according to Aljančič (2019), the only place where olms could be easily observed in the area of Stična – from where the specimens studied by Scopoli and Laurenti supposedly originated; the site is monitored for olm activity by cameras. Type specimens of the junior synonyms *Hypochthon schreibersii* and *Hypochthon zoisii* are displayed in figs. S5 and S6 in the Supplementary material. Photo credits: C. Dufresnes (C-E).

Synonym(s)

Hypochthon laurentii Merrem, 1820 (objective); *Phanerobranchus platyrhynchus* Leuckart, 1821 (objective); *Hypochthon schreibersii* Freyer, 1847 (subjective; type locality: Vir pri Stični, Slovenia – potentially same as *P. anguinus*; type series: 78 syntypes examined by Fitzinger, including NHMW 19962/1, 19966/2-8, and 19967/1-2, illustrated in fig. S5); *Hypochthon zoisii* Fitzinger, 1850 (subjective; type

locality: Rupe/Rupnica near Stična, Slovenia; type series: 11 syntypes examined by Fitzinger, including NHMW 19959/2-5, two being illustrated in fig. S6 in the Supplementary material).

Molecular diagnosis

At 16S, *P. anguinus* can be distinguished from other members of the genus *Proteus* by: 'A' in the site 19, 'T' in the site 39, 'A' in the site 519. At COI, it can be distinguished by: 'T' in the site 102, 'T' in the site 156, 'A' in the site 255.

External diagnosis

According to our morphological analyses, *P. anguinus* most resembles the other two white olm species from Slovenia, *P. xanthostictus* and *P. freyeri*, to which it is phylogenetically close. It can be diagnosed from these species through a combination of characters including, on average, a higher and wider head, longer gills, as well as shorter hindlimbs (fig. 5).

Distribution, life-history and threats

Proteus anguinus is restricted to the low Dolenjska karst of central Slovenia, where it is known from a narrow west-east belt extending from the Višnjica valley through the surroundings of Stična and Vir pri Stični to Šentpavel and Mačji Dol (Sket, 1997; Hudoklin and Aljančič, 2017). Most records originate from karst springs, estavelles (karst openings that alternately discharge or absorb water) and intermittent overflow outlets connected to subterranean groundwater (Sket, 1997; Hudoklin and Aljančič, 2017). Although the known localities form a geographically coherent cluster, direct hydrological connections among them remain uncertain. Historically, *P. anguinus* was the first olm lineage to be studied, notably through the pioneer anatomical investigations of Schreibers (1801). With an extent of occurrence of only 15 km^2 and an area of occupancy of 36 km^2, *P. anguinus* is among the most range-restricted members of the genus, and we recommend that it be classified as Critically Endangered under IUCN Criterion B.

***Proteus xanthostictus* (Freyer, 1847)** (fig. 11)

Identity

The Ljubljanica lineage.

Vernacular names

Ljubljanica's olm (English), Ljubljaniški močeril (Slovenian).

Etymology

xanthostictus is a Greek construct, meaning "yellow-spotted", in reference to the first observation of this species by Freyer (1846), which probably results from high concentrations of riboflavin yielding yellow markings, especially on darker (e.g. light-altered) individuals.

Type series

Holotype, the specimen pictured by Freyer (1847), which originates from Bedén ponor, near Laze in the Planinsko polje, Slovenia. Its fate is unclear – it was potentially part of the specimen series mentioned to have been sent to Schreibers, which were subsequently lost in a fire during the Austrian Revolution of 1848 (Freyer, 1849).

Synonym(s)

Hypochthon chrysostictus Freyer, 1849 (objective) and *Hypochthon haidingeri* Fitzinger, 1850 (subjective; type locality: Planinska jama, Slovenia; type series: 40 syntypes examined by Fitzinger, including NHMW 19963/1-7, illustrated in fig. S7 in the Supplementary material). The specimens considered as "*Hypochton laurentii*" by Fitzinger (1850), which originate from Magdalena Cave, correspond to this species (312 specimens examined by Fitzinger, including NHMW 19957/1-15, eight being illustrated in fig. S8 in the Supplementary material).

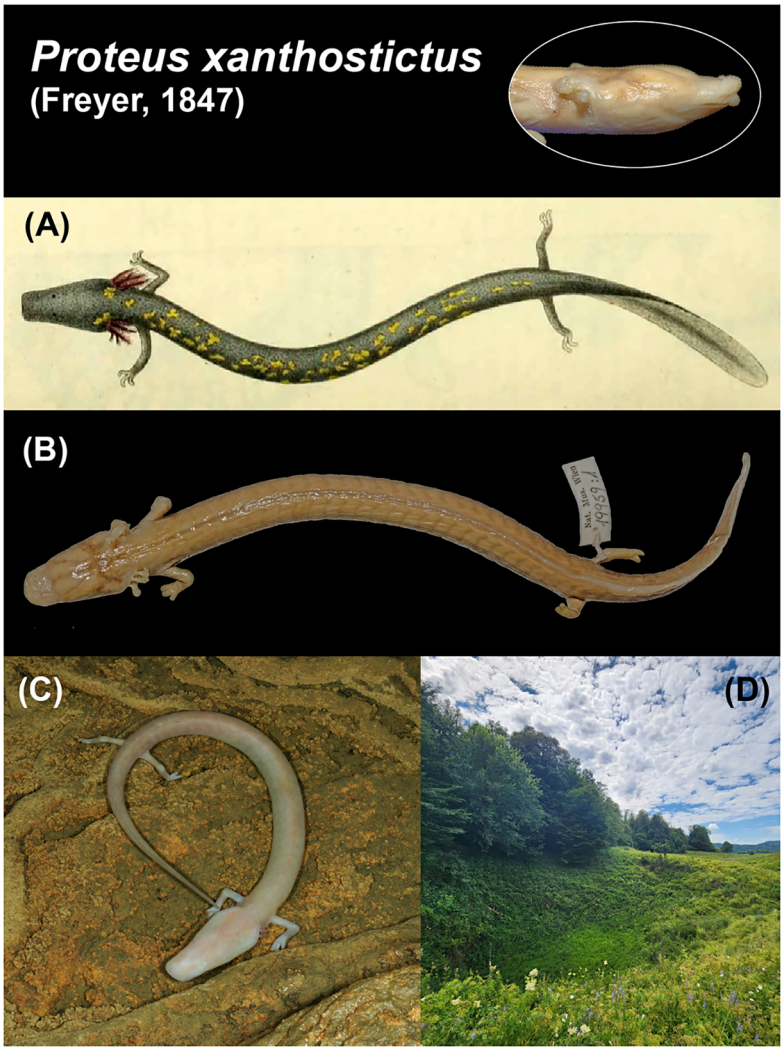

Figure 11. *Proteus xanthostictus* (Freyer, 1847) – the Ljubljanica species. (A) Drawing of the type specimen by Freyer (1846). (B) NHMW 19959/1, the only remaining specimen examined by Fitzinger (1850), while the original series included 12 specimens; remaining type specimens of the junior subjective synonym *Hypochthon haidingeri* are displayed in fig. S7 in the Supplementary material. (C) Live specimen from Planinska Jama, Slovenia. (D) The type locality, Bedén ponor near Laze, Slovenia. Photo credits: D. Jablonski (top right; B); S. Voitel (C); C. Dufresnes (D).

Molecular diagnosis

At 16S, *P. xanthostictus* can be distinguished from other members of the genus *Proteus* by: 'A' in the site 73, 'G' in the site 216, 'G' in the site 326. At COI, it can be distinguished by: 'T' in the site 21, 'T' in the site 30, 'A' in the site 207.

External diagnosis

According to our morphological analyses, *P. xanthostictus* generally resembles the other two white olm species from Slovenia, *P. anguinus* and *P. freyeri*, to which it is phylogenetically close. It can be diagnosed from these species through a combination of characters including,

on average, a longer head with a larger snout tip and shorter gills (fig. 5).

Distribution, life-history and threats

Proteus xanthostictus is distributed across the Ljubljanica karst of southwestern and south-central Slovenia, from the upper Pivka and Lož-Cerknica basins through the Postojna-Planina cave system and Planinsko polje to the Ljubljanica springs near Vrhnika (Sket, 1997). In the west of its range, *P. xanthostictus* meets the Kras/Carso species along the Timavo underground river system, and the presence of both mtDNA lineages suggest secondary contact (Recknagel et al., 2024). Like most members of the genus, *P. xanthostictus* is generally depigmented, although individuals with darker pigmentation and yellowish markings have occasionally been reported (Freyer, 1846). The species is considered threatened by groundwater pollution (Aljančič, 2019), and with an extent of occurrence of approx. 1300 km^2, an area of occupancy of approx. 200 km^2, we recommend its provisional assessment as Endangered under IUCN Criterion B.

***Proteus freyeri* (Fitzinger, 1850)** (fig. 12)

Identity

The Dolenjska lineage.

Vernacular names

Freyer's olm (English), Freyerjev močeril (Slovenian).

Etymology

freyeri is a tribute to Heinrich Freyer (1802-1866), a Carniolan naturalist and curator of natural history collections (in Ljubljana and Trieste), who made important contributions on olm distribution research (e.g., Freyer, 1846, 1847, 1849, 1850).

Type series

Lectotype 19969/7 from Kompoljska jama, near Kompolje, Slovenia, and 16 paralectotypes, including 15 from the type locality (including NHMW 19969/1-6 and 19969/8-12, illustrated in fig. S9 in the Supplementary material), and one from the nearby cave of Potiskavška jama, Slovenia.

Molecular diagnosis

At 16S, *P. freyeri* can be distinguished from other members of the genus *Proteus* by: 'A' in the site 85, 'C' in the site 96, 'T' in the site 238, 'C' in the site 1122. At COI, it can be distinguished by: 'G' in the site 78, 'A' in the site 87, 'C' in the site 165, 'T' in the site 321.

External diagnosis

According to our morphological analyses, *P. freyeri* generally resembles the other two white olm species from Slovenia, *P. anguinus* and *P. xanthostictus*, to which it is phylogenetically close. It can be diagnosed from these species through a combination of characters including, on average, a longer tail, a smaller interlimb distance, as well as a narrower head and snout (fig. 5).

Distribution, life-history and threats

Proteus freyeri is widely distributed throughout southeastern Slovenia, extending from the Radensko-Dobrepolje region and the upper Krka valley through Suha krajina, the Ribnica-Kočevje region and the surroundings of Dolenjske Toplice and Novo mesto to Bela krajina, with an isolated historical record from Ozaljska pećina in Croatia (Hudoklin and Aljančič, 2017). In Bela krajina, *P. freyeri* was also detected within two sites also inhabited by *P. parkelj* according to eDNA and visual observations (Gorički et al., 2017; Recknagel et al., 2022). In the north of its range, nuclear and mitochondrial introgression from *P. anguinus* suggest recent hybridization (Recknagel et al.,

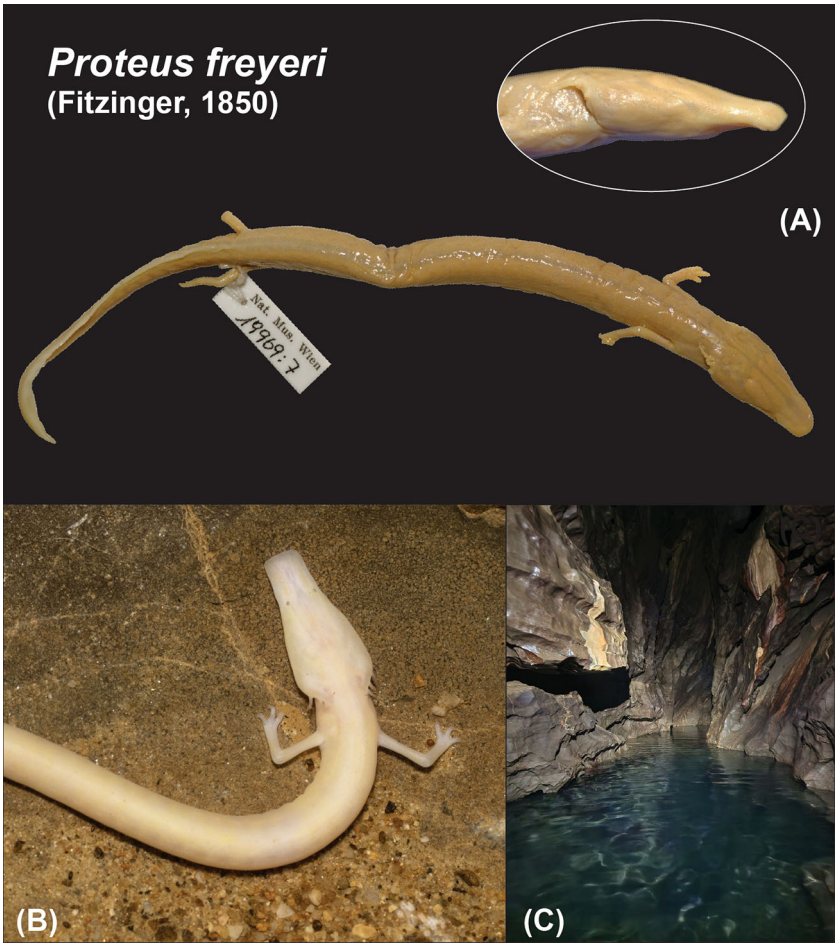

Figure 12. *Proteus freyeri* (Fitzinger, 1850) – the Dolenjska species. (A) Lectotype NHMW19969/7; remaining paralectotypes are displayed in fig. S9 in the Supplementary material. (B) Live topotypic specimen. (C) The type locality, Kompoljska Jama, Slovenia (approx. 50 m from the entrance). Photo credits: D. Jablonski (top right; A-B); C. Dufresnes (C).

2024). In a perennial karst spring, *P. freyeri* individuals were observed as emerging regularly into a shallow surface pool at nighttime (Premate et al., 2022), indicating that the species can exploit surface habitats while maintaining close association with the subterranean environment. With an extent of occurrence of approx. 1400 km^2 and an area of occupancy of approx. 250 km^2, *P. freyeri* should be provisionally considered as Endangered under IUCN Criterion B.

***Proteus carrarae* (Fitzinger, 1850)** (fig. 13)

Identity

The Para-littoral lineage.

Vernacular names

Dalmatian olm (English), Dalmatinska čovječja ribica (Croatian), Hercegovačka čovječija ribica (Bosnian).

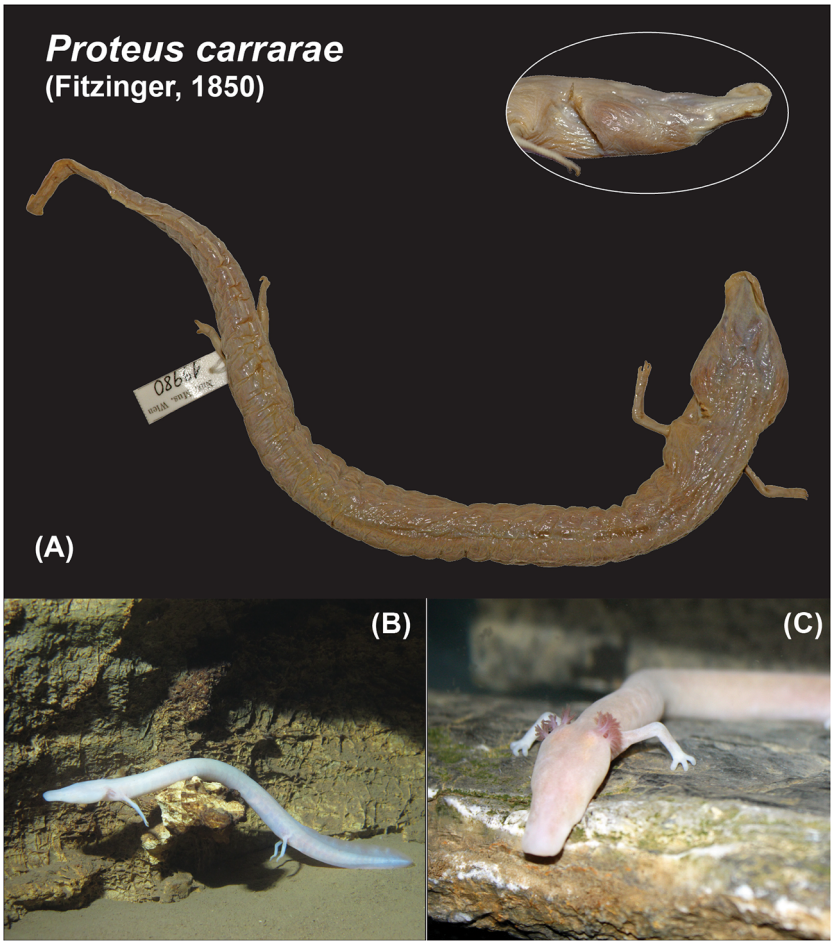

Figure 13. *Proteus carrarae* (Fitzinger, 1850) – the Para-littoral species. (A) Lectotype NHMW 19980/1 from Sinj, Croatia. (B) Live specimen from the Trebišnjica River Basin, Bosnia and Herzegovina. (C) Topotypic live specimen from Vedrine, Sinj, Croatia. Photo credits: D. Jablonski (top right; A); L. Balazs (Devon Karst Research Society – *Proteus* Project in BiH) (B); D. Jelić (C).

Etymology

carrarae is a tribute to Francesco Carrara, a Dalmatian Italian archaeologist from Split, who sent olm specimens from the Neretva River to Fitzinger (1850), on which he based the description.

Type series

Lectotype NHMW 19980/1 from Sinj, Croatia and four paralectotypes, including three from the type locality and one from the Narenta river.

Molecular diagnosis

At 16S, *P. carrarae* can be distinguished from other members of the genus *Proteus* by: 'G' in the site 51, 'T' in the site 138, 'A' in the site 179. At COI, it can be distinguished by: 'A' in the site 270, 'T' in the site 318, 'A' in the site 321.

External diagnosis

According to our morphological analyses, *P. carrarae* can be diagnosed from most other species through a combination of various characters including, on average, more spaced but

shorter limbs, which translates into the lowest Wolterstorff Index of the complex (fig. 5).

Distribution, life-history and threats

Proteus carrarae extends along the coastal Dinaric Karst from northern Dalmatia to southern Herzegovina and the Dubrovnik hinterland possibly extending as far south as the Bay of Kotor if an uncertain eDNA record from Sopot (Risan) is confirmed (Gorički et al., 2017). It has a broad elevational range from coastal springs at or near sea level, including the microsprings of the Neretva estuary (approx. 7 m a.s.l.) and the large Ombla spring near Dubrovnik, to the upper reaches of the Trebišnjica drainage near Bileća and the upper Trebižat drainage above 500 m a.s.l. Throughout much of its range, the species is occasionally recorded in syntopy with the semi-subterranean cyprinid fishes *Delminichthys ghetaldii* in caves of the Dubrovnik and Trebinje region, and *Delminichthys adspersus* in caves of the Trebižat-Vrljika drainage (Delić et al., 2023). Such associations appear to be uncommon despite overlapping distributions, possibly reflecting competition for limited subterranean food resources, particularly small aquatic cave invertebrates. Molecular datasets revealed some phylogeographic subdivision between the northwestern and southeastern parts of its range (Recknagel et al., 2024), suggesting allopatric isolation and possibly additional (subspecific) taxa to acknowledge in the future, notably with range-wide genomic sampling. A long-term capture-mark-recapture study in Vruljak 1 Cave revealed pronounced site fidelity, with most recaptured individuals moving less than 10 m between observations and some remaining at virtually the same location for several years (Balázs et al., 2020). As in other species, the main threats include groundwater pollution, hydrological alteration, excessive water abstraction, and degradation of karst spring habitats. With an extent of occurrence of approx. 8600 km^2 and an area of occupancy of approx. 250 km^2, *P. carrarae* is the most widespread species of the complex, but it remains eligible for the Endangered category under IUCN Criterion B2.

***Proteus croaticus* Brusina, 1908** (fig. 14)

Identity

The Lika lineage.

Vernacular names

Croatian olm (English), Hrvatska čovječja ribica (Croatian).

Etymology

croaticus is a latinized adjective referring to Croatia. When the name was proposed in the late 19th century (Brusina, 1880), "Croatia" corresponded to the kingdom of Croatia-Slavonia (within the Austria-Hungarian empire), which excluded Dalmatia; thus, this species was the first and only olm documented in the country boundaries of that time.

Type series

Holotype, the specimen mentioned by Brusina (1880, 1908), which originates from a spring of the Gacka behind the old town of Otočac, Croatia; it was initially curated at HPM, but was lost by the early 20th century (Karaman, 1921).

Molecular diagnosis

At 16S, *P. croaticus* can be distinguished from other members of the genus *Proteus* by: 'C' in the site 48, 'C' in the site 50, 'T' in the site 51. At COI, it can be distinguished by: 'T' in the site 3, 'G' in the site 75, 'T' in the site 195.

External diagnosis

According to our morphological analyses, *P. croaticus* can be diagnosed from most other species, notably those neighboring its range, through a combination of various characters

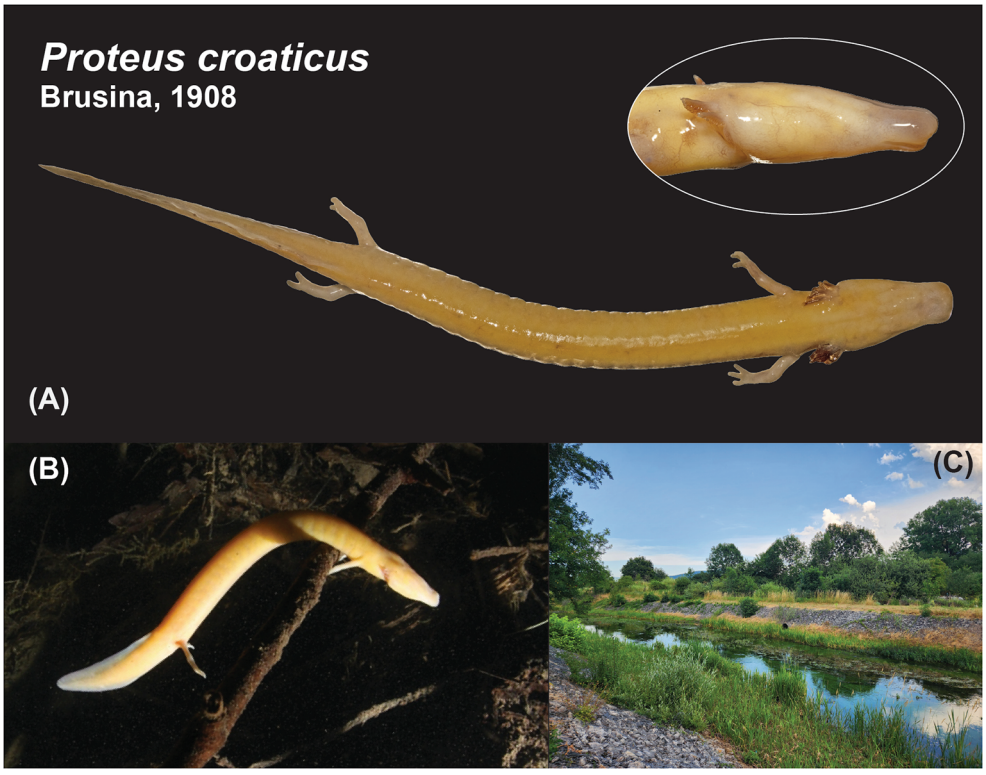

Figure 14. *Proteus croaticus* Brusina, 1908 – the Lika species. (A) Representative specimen (HDBI 2965/1) from Ponor Rupecice, Croatia. (B) Live specimen from Gorski Kotar, Croatia. (C) View on the Gacka river behind the old town of Otočac, Croatia, the type locality of *P. croaticus*; the description mentions a brook flowing into the river, many of such have been canalized underground, as the river underwent dramatic diking since the 19th century. Photo credits: D. Jablonski (top right; A); P. Kovač Konrad (B); C. Dufresnes (C).

including, on average, a longer tail and weakly spaced limbs (fig. 5). It also features, like its sister species Kras/Carso, the lowest number of myomeres on average (23.6; table 2).

Distribution, life-history and threats

Proteus croaticus is restricted to the hilly karst of central Croatia, where it is primarily associated with the aquifer systems of the Lika and Gorski Kotar regions, occurring across a series of high poljes situated between approximately 300 and 800 m a.s.l. Although these poljes are separated at the surface, they remain interconnected through extensive subterranean drainage networks, with many rivers disappearing into sinkholes and flowing beneath the surrounding massifs. Water temperatures may locally fall below 5°C, making this one of the coldest environments occupied by the genus (Sket, 1997). Within a small part of its distribution, *P. croaticus* occurs in syntopy with the semi-subterranean cyprinid fishes *Telestes polylepis* and *T. karsticus*. At several localities, particularly the Rupećica River sinkhole, individuals exhibit an unusually intense yellow pigmentation, which is further accentuated against the characteristic black bacterial biofilm covering the limestone walls of the cave system. In Zagorska peć near Ogulin, cave divers recorded adult olms throughout a submerged siphon as deep as 113 m, representing the deepest published in situ record for *Proteus* (Kovač Konrad and Koller, 2017). With an extent of occurrence of approx. 440 km^2 and an area of occupancy of approx. 60 km^2, we provisionally recommend

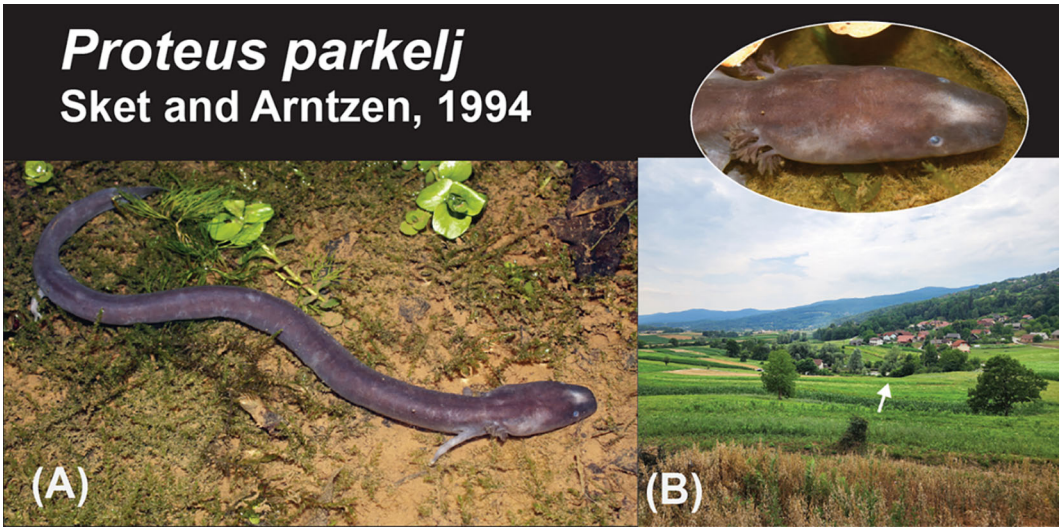

Figure 15. *Proteus parkelj* Sket and Arntzen, 1994 – the Parkelj species. (A) Live specimen from Jelševnik, Slovenia. (B) View on the Dobliška depression, which covers the distribution of *P. parkelj*, with the type locality (Na Trati, Jelševnik, Slovenia) in the foreground (arrow). Photo credits: K. Chouchane (top right; A); C. Dufresnes (B).

to list *P. croaticus* as Endangered under IUCN Criterion B.

Proteus parkelj **Sket and Arntzen, 1994**
(fig. 15)

Identity

The Parkelj lineage.

Vernacular names

Black olm (English), Črni močeril (Slovenian).

Etymology

"Parkelj" is the Slovene name for Krampus, a dark often black-furred, horned figure of the Saint Nicholas tradition, which is deeply rooted in Austria and neighboring countries like Slovenia; it is notably used to nickname a devil-looking cookie, parkeljn (plural parkeljni), traditionally sold in Ljubljana around St. Nicholas day, which the descriptors found to resemble black olms (Sket and Arntzen, 1994).

Type series

Holotype ULBF J8 and nine paratypes, including six adults (ULBF J1-J3, ULBF J6-J7 and ZMA Herp. 9239), one embryo (ULBF J10), one cleared/stained specimen (ULBF J5) and one skeleton (ULBF J4), all from Na Trati, Jelševnik near Črnomelj, Slovenia.

Molecular diagnosis

At 16S, *P. parkelj* can be distinguished from other members of the genus *Proteus* by: 'C' in the site 73, 'A' in the site 96, 'C' in the site 240. At COI, it can be distinguished by: 'G' in the site 24, 'G' in the site 450.

External diagnosis

This species could not be included in our morphological analyses, and the following refers to previously documented differences between the dark ecotype associated to the Parkelj lineage and other (depigmented) *Proteus* species. *Proteus parkelj* is externally distinguished by dark pigmentation due to abundant melanophores in both the epidermis and the dermis (synthetized even in the absence of light), while

other species are completely depigmented. Its skin is thicker and more complex, with more multicellular mucous glands in dermis and an increased number of layers of epidermal cells (Sket and Arntzen, 1994; Aljančič et al., 2021). Cranial morphology differs markedly, with *P. parkelj* exhibiting a shorter, broader snout, a more angular and robust skull, stronger cranial musculature, and as confirmed by geometric morphometric analyses, a wider skull with laterally positioned elements, in contrast to the elongated, narrow, "duck bill" rostrum typical of other *Proteus* species (Sket and Arntzen, 1994; Ivanović et al., 2013). Osteological differences include fewer vomerine teeth (16-17 vs. 22-30), larger premaxillae, shorter and more widely separated vomers, and a more posteriorly positioned jaw articulation point (Sket and Arntzen, 1994; Ivanović et al., 2013). Body proportions also differ: *P. parkelj* has a longer trunk with more trunk vertebrae (34-35 vs. 29-31), a shorter tail with fewer caudal vertebrae that decrease distally and end in 3-5 rudimentary elements, and shorter limbs (Sket and Arntzen, 1994; Ivanović et al., 2013). These comparisons are however restricted to only some of the other species, represented by the material examined (from Slovenia and Italy), and should be re-assessed. The species retains externally visible, functional eyes with cornea, lens, and a well-organized retina containing 3 photoreceptor types (versus only 2 in other species assessed), resulting in more developed visual capability, whereas other *Proteus* species have regressed, often skin-covered eyes with reduced or absent lenses and simplified retinas (Aljančič et al., 2021).

Distribution, life-history and threats

Proteus parkelj is restricted to a very small area of Bela krajina in southeastern Slovenia, west of Črnomelj, where it occupies the Dobličica-Jelševniščica spring system at the margin of the Kočevski Rog plateau (Sket and Arntzen, 1994; Gorički et al., 2017). Unlike the remaining species of the genus, which are typically associated with extensive cave systems, *P. parkelj* appears to inhabit relatively shallow karst aquifers composed of fissures, small submerged cavities and spring-connected groundwaters (Bizjak Mali and Sket, 2019; Koren et al., 2023). Most records originate from karst springs, intermittent resurgences, water-supply shafts and other groundwater outlets rather than accessible caves, and much of the species' distribution has been reconstructed through eDNA surveys (Gorički et al., 2017); direct hypogean observations have only been made within a large siphon at depths of approximately 15-20 m (Mihajlovski, 2012; Hudoklin and Aljančič, 2017). Hydrological monitoring indicates rapid responses of the aquifer to rainfall and suggests hydraulic connectivity among several springs, although some outlets appear to drain independent groundwater systems (Koren et al., 2023). The ecology of populations identified as *P. parkelj* differs markedly from that of other olms. Individuals frequently emerge into spring pools and other surface waters, particularly at night and following rainfall, but rapidly retreat underground when disturbed or exposed to light (Sket, 1993; Sket and Arntzen, 1994). The shallow nature of its habitat probably results in greater exchange with surface environments and consequently higher nutrient availability than in typical cave systems. The species has been observed sharing isolated water holes with the newt *Triturus carnifex* and in small spring resurgences, with the minnow *Phoxinus lumaireul*, whereas larger resurgences are inhabited by predatory fishes (e.g., *Perca* and *Esox*), whose presence may restrict surface activity and explain why *P. parkelj* is most frequently observed at the margins of these pools. Depigmented individuals inhabiting the same groundwater system (Gorički et al., 2017; Recknagel et al., 2022) supposedly correspond to sympatric *P. freyeri* individuals, although a hypogean ecotype for the species cannot be excluded. With a calculated extent of occurrence of only 3 km^2 and an area of occupancy of approx. 20 km^2

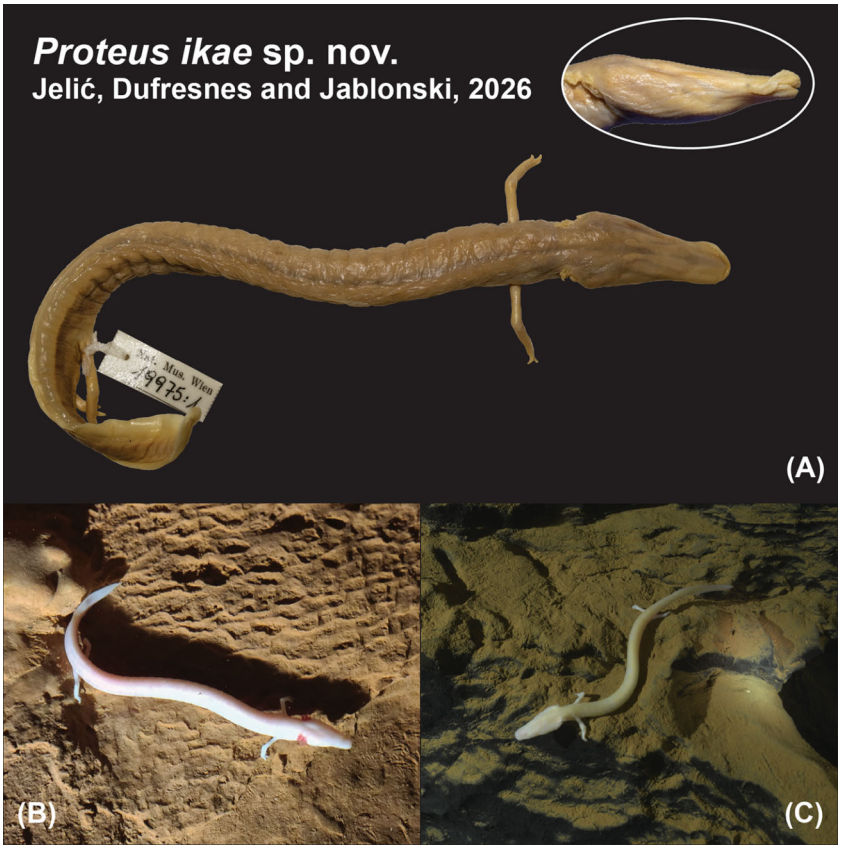

Figure 16. *Proteus ikae* sp. nov. – the Istra species. (A) Holotype NHMW 19975/1. (B) Live specimen from Baredine Cave, Croatia. (C) Live specimen from Pincinova jama, Croatia. Photo credits: D. Jablonski (top right; A); C. Dufresnes (B); D. Jelić (C).

(within the range of previous estimations; Sket and Arntzen, 1994; Gorički et al., 2017), *P. parkelj* is the most geographically restricted species of the genus. Its small range, occurrence in a single karst system, and the rapid infiltration of agricultural and wastewater pollution into its shallow aquifer make it exceptionally vulnerable to localized disturbances (Koren et al., 2023; Glavan and Cvejić, 2024). Additional threats include inappropriate handling and collection of individuals for the pet trade, which may facilitate pathogen transmission and contribute to population decline. We therefore recommend that *P. parkelj* be considered as Critically Endangered under IUCN Criterion B.

***Proteus ikae* sp. nov. Jelić, Dufresnes and Jablonski, 2026** (fig. 16)

Identity

The Istra lineage.

Vernacular names

Istrian olm (English), Istarska čovječja ribica (Croatian).

Etymology

ikae is a latinized noun dedicated to Ika (also rendered as Ica), an indigenous Histro-Liburnian female deity documented by Roman-era votive inscriptions from Plomin and Pula in Istria, whose cult has been associated primarily with springs and water.

Type series

Holotype NHMW 19975/1, adult collected in 1886 at the coal mine of Carpano near Labin, Istria, Croatia, and acquired by NHMW from A. Valle in 1892. Measurements are given in table 3.

Molecular diagnosis

At 16S, *P. ikae* sp. nov. can be distinguished from other members of the genus *Proteus* by: 'C' in the site 64, 'C' in the site 97, 'C' in the site 106, 'C' in the site 189. At COI, it can be distinguished by: 'C' in the site 18, 'C' in the site 78.

External diagnosis

According to our morphological analyses, *P. ikae* sp. nov. substantially differs from all other species of the genus and can be diagnosed by its elongated, narrow snout, limited gills, short tail as well as weakly spaced but longer limbs, which translates into the highest Wolterstorff Index of the complex (fig. 5).

Distribution, life-history and threats

Proteus ikae sp. nov. appears to be primarily associated with deep karst aquifer systems of the Istrian Peninsula and is only occasionally flushed to the surface through large karst springs. The species has been recorded from springs and wells at or near sea level, including the historic Nimfej spring and the main water source beneath the Pula Arena, situated between the Roman amphitheatre and the Adriatic coast. Most additional records originate from deep vertical caves and pits that provide access to the deeper karstic groundwater network (Polak et al., 2012). Accordingly, unlike several other *Proteus* species, *P. ikae* sp. nov. predominantly inhabits deep aquifer systems rather than shallow cave streams. Its habitat is typically characterized by conspicuous yellow to reddish clay and mud deposits coating the cave floor and walls, creating a striking contrast with the otherwise white limestone bedrock. The karst aquifers of Istria are subject to increasing anthropogenic pressures, particularly intensive groundwater abstraction for public water supply, tourism-related water demand and groundwater pollution – as observed in surface ponds throughout the peninsula (M. Denoël, pers. obs.). In addition, noticeable reductions in groundwater levels and cave water bodies have been observed at several localities during recent years (D. Jelić, pers. obs.), highlighting the potential vulnerability of this highly localized species to ongoing hydrological changes. With an extent of occurrence of approx. 1150 km^2 and a verified area of occupancy of only approx. 50 km^2, *P. ikae* sp. nov. should be provisionally considered as Endangered under IUCN Criterion B.

Proteus bosniensis **sp. nov. Šunje, Jelić, Zimić, Dufresnes and Jablonski, 2026**

(fig. 17)

Identity

The Krajina lineage.

Vernacular names

Bosnian olm (English), Bosanska čovječja ribica (Bosnian).

Etymology

bosniensis is a latinized adjective meaning "from Bosnia". The name itself supposedly roots back from the ancient hydronym Bosna, the primary river running through the country, which means "running water" or "flowing current" in Proto-Indo-European languages. *bosniensis* thus conveys both the endemic nature of the species to Bosnia and its association with freshwaters.

Type series

Holotype NMBH 11568, adult collected on 25th June 2026 by D. Jelić, E. Šunje, C. Dufresnes

Table 3. Morphometric measurements of the type series of the three new species described.

Holotype	Status	Species	Locality	TBL	HL	TL	MHW	HH	MSW	WST	MGL	HCD	SFD	DFH	FLL	HLL	NM
NHMW 19975/1	Holotype	*P. ikae* sp. nov.	coal mine of Carpano near Labin, Istra, HR	206	35	52	16	9.5	7.7	7.7	3	4.3	42	98	20	19.2	23
NMBH 11568	Holotype	*P. bosniensis* sp. nov.	Bobijaško Oko, Lušci Palanka, BiH	232	28.5	69	20.1	15.5	10.1	8.7	4.1	6.1	43.6	112	18.8	17.7	24
NMBH 11569	Paratype	*P. bosniensis* sp. nov.	Bobijaško Oko, Lušci Palanka, BiH	195	23.3	57	14.3	10.2	8.3	6.3	2.5	3.8	34.1	94	15.8	14.4	25
NMBH 11570	Paratype	*P. bosniensis* sp. nov.	Bobijaško Oko, Lušci Palanka, BiH	186	25.7	55	14.2	9.7	7.3	6.3	3.5	4.8	32.5	95	18.2	16.3	24
NMBH 11571	Paratype	*P. bosniensis* sp. nov.	Bobijaško Oko, Lušci Palanka, BiH	166	22.0	52	12.6	9.6	7.4	6.6	3.0	3.0	28.7	79	15.3	13.1	24
NMBH 11572	Paratype	*P. bosniensis* sp. nov.	Suvaja, Lušci Palanka, BiH	81	11.3	23	6.6	3.9	3.5	2.6	0.0	2.1	16.1	38	7.3	6.0	24
NMBH 11573	Paratype	*P. bosniensis* sp. nov.	Suvaja, Lušci Palanka, BiH	88	12.2	26	6.8	4.6	4.0	2.9	0.0	1.8	15.0	42	8.4	7.5	24
NMBH 11574	Paratype	*P. bosniensis* sp. nov.	Suvaja, Lušci Palanka, BiH	92	13.6	28	7.6	5.2	4.0	3.6	0.7	1.4	17.6	42	9.2	8.2	25
NMBH 11575	Paratype	*P. bosniensis* sp. nov.	Suvaja, Lušci Palanka, BiH	89	12.2	24	7.4	4.6	4.1	2.9	0.0	2.1	17.6	43	8.3	7.2	24
NMBH 11576	Paratype	*P. bosniensis* sp. nov.	Suvaja, Lušci Palanka, BiH	74	10.7	23	5.6	3.4	3.7	2.4	0.0	1.0	14.0	33	7.6	6.0	24
NMBH 7867	Paratype	*P. bosniensis* sp. nov.	Bobijaško Oko, Lušci Palanka, BiH	264	31.5	67	16.5	10.2	9.3	6.0	2.6	6.7	41.7	135	20.9	14.6	27
MSNM Am 1818	Holotype	*P. maurii* sp. nov.	Pozzo di Vermegliano, Ronchi dei Legionari, IT	167	27.7	39	12.8	8.5	7.9	6.4	5.5	3.9	34.3	88	15.7	13.1	24
NHMW 19974/1	Paratype	*P. maurii* sp. nov.	Tržič/Monfalcone, IT	167	24	44.5	13.9	8.6	6.9	5.0	7.0	2.0	30.0	83	15.5	13.7	23
NHMW 19974/2	Paratype	*P. maurii* sp. nov.	Tržič/Monfalcone, IT	202	33	56	12.5	6.5	7.4	7.1	7.0	3.9	40.5	99	16.5	13.0	24

All metric variables are given in mm. TBL, total body length; SFD, snout-forelimb distance; HL, head length; MHW, maximum head width; HH, head height; MSW, minimum snout width; WST, width of the snout tip; MGL, maximum gill length; HCD, hindlimb-cloaca distance; TL, tail length; DFH, interlimb distance; FLL, forelimb length; HLL, hindlimb length; NM, number of myomeres. HR, Croatia; BiH, Bosnia and Herzegovina; IT, Italy.

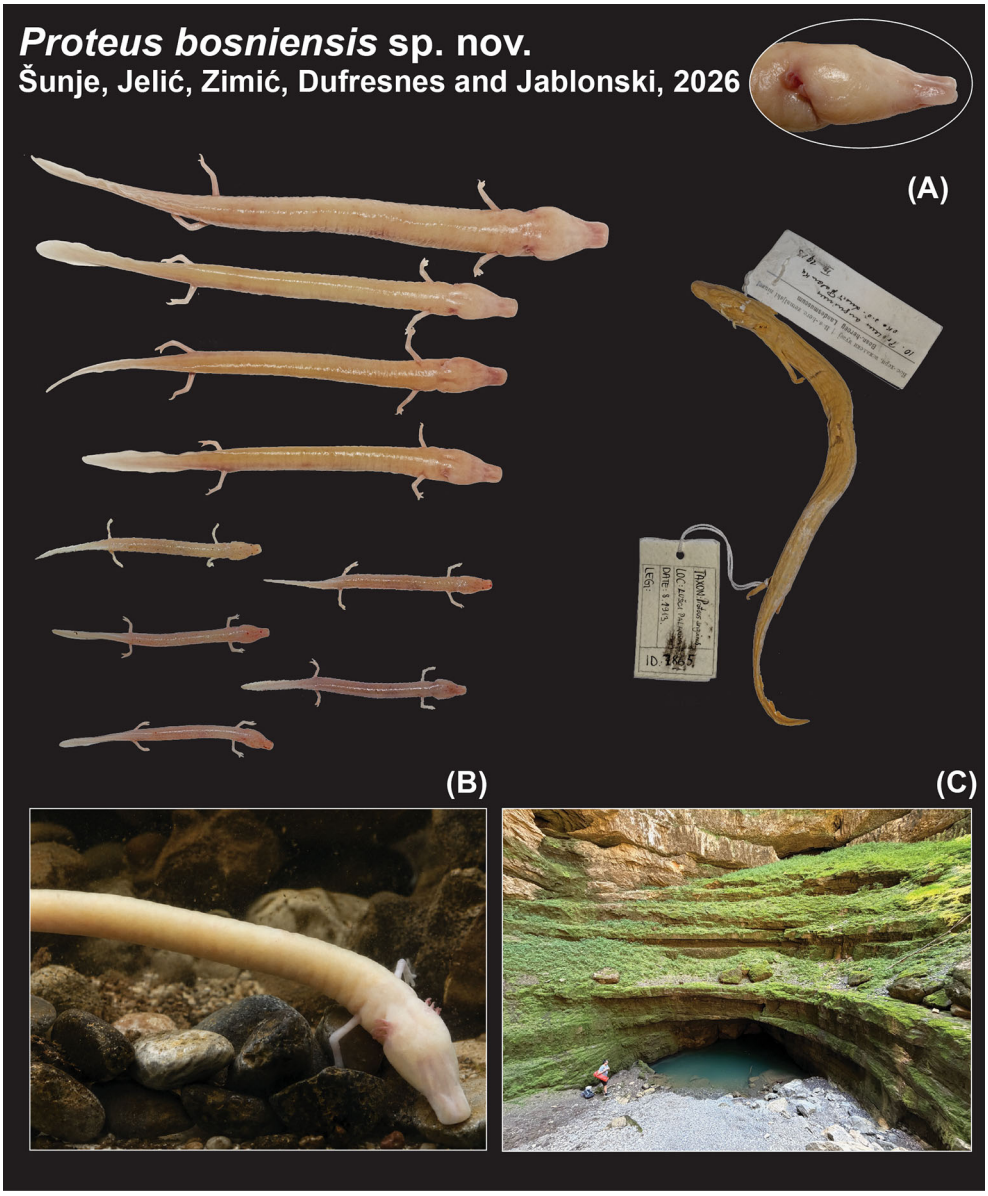

Figure 17. *Proteus bosniensis* sp. nov. – the Krajina species. (A) Type series, including the holotype (NMBH 11568; top) and three adult paratype specimens (NMBH 11569-11571) from Bobijaško Oko, Lušci Palanka, Bosnia and Herzegovina; five juvenile paratype specimens (NMBH 11572-11576) from Suvaja, Lušci Palanka, Bosnia and Herzegovina (bottom); one historical adult paratype specimen (NMBH 7867) from Bobijaško Oko (right). (B) Live adult specimen from Bobijaško Oko. (C) The type locality, Bobijaško Oko, Lušci Palanka, Bosnia and Herzegovina. Photo credits: D. Jablonski (top right; A-C).

and D. Jablonski in Bobijaško Oko, Lušci Palanka, Bosnia and Herzegovina (GenBank accession of 16S: PZ748789). Nine paratypes: NMBH 11569-11571, three adults collected at the type locality (same date and collectors as holotype); NMBH 11572-11576, five juveniles collected in Suvaja, Lušci Palanka, Bosnia and Herzegovina (same date and collectors as holotype; GenBank accessions of 16S: PZ748793-PZ748797); NMBH 7867, adult collected at the type locality in August 1913 by an unknown collector. Measurements are given in table 3.

Molecular diagnosis

At 16S, *P. bosniensis* sp. nov. can be distinguished from other members of the genus *Proteus* by: 'T' in the site 44, 'G' in the site 46, 'C' in the site 66. At COI, it can be distinguished by: 'G' in the site 9, 'A' in the site 15.

External diagnosis

According to our morphological analyses, *P. bosniensis* sp. nov. can be diagnosed from most other species, notably those neighboring its range, through a combination of various characters including, on average, a shorter but broader and higher head, giving the species a "piggy" appearance (fig. 5).

Distribution, life-history and threats

Proteus bosniensis sp. nov. is restricted to the upper reaches of the Una River and Sana River drainages within the Danube Basin of northwestern Bosnia and Herzegovina, primarily surrounding Grmeč. The species inhabits a complex karst landscape composed of a series of high karst poljes (approximately 600 m a.s.l.) that drain through extensive underground systems into lower poljes (around 300 m a.s.l.), emerging through large karst springs such as Klokot, Krušnica, Sanica and Dabar. Cave systems throughout its range are characterized by extensive black bacterial biofilms coating the limestone walls and support exceptionally rich subterranean communities, making this one of the biodiversity hotspots of the northwestern Dinaric karst. The distribution of this species is currently underestimated, but with a calculated extent of occurrence of approx. 700 km^2 and an area of occupancy of approx. 30 km^2, it has a restricted distribution, and we provisionally recommend its assessment as Endangered under IUCN Criterion B.

***Proteus maurii* sp. nov. Manenti, Barzaghi, Dufresnes and Jablonski, 2026** (fig. 18)

Identity

The Kras/Carso lineage.

Vernacular names

Classic Karst olm (English), Proteo del Carso Classico (Italian).

Etymology

maurii honors Edgardo Mauri, an Italian naturalist who has selflessly devoted countless time and effort to the study, monitoring and conservation of the Italian populations of *Proteus*. His exceptional knowledge of the species, its habitats and the history of its occurrence in the Classical Karst, has benefited numerous researchers of various origins, and much of the current understanding of the Italian populations has benefited, directly or indirectly, from his longstanding dedication.

Type series

Holotype MSNM Am 1818, adult collected on 19th June 2026 by R. Manenti and B. Barzaghi in Pozzo di Vermegliano, Ronchi dei Legionari, Italy (GenBank accession of 16S: PZ748798). Two paratypes: NHMW 19974/1, adult collected in Tržič/Monfalcone from "Cisternes des Hauses Primoschitz's [cistern of the Primoschitz's house]", acquired by NHMW in 1900 from Schreiber's collection; NHMW 19974/2, adult collected in Tržič/Monfalcone from "Fumagalli [Fumagalli's house]", acquired by NHMW in April 1930 from the Zoological institute of the University of Vienna. Measurements are given in table 3.

Molecular diagnosis

At 16S, *P. maurii* sp. nov. can be distinguished from other members of the genus *Proteus* by: 'T' in the site 27, 'A' in the site 154, 'G' in the site 276. At COI, it can be distinguished by: 'C'

Figure 18. *Proteus maurii* sp. nov. – the Kras/Carso species. (A) Type series, including the holotype (MSNM Am 1818; top) and two paratypes (NHMW 19974/1-2; middle and bottom). (B) Live spring-dwelling specimen from Mucille, Ronchi dei Legionari, Italy. (C) The type locality, Pozzo di Vermegliano, Ronchi dei Legionari, Italy. Photo credits: D. Jablonski (top right; A: paratypes); B. Barzaghi (A: holotype; B), C. Dufresnes (C).

in the site 54, 'C' in the site 114, 'C' in the site 123.

External diagnosis

According to our morphological analyses, *P. maurii* sp. nov. can be diagnosed from most other species through a combination of several characters, including a more elongated head, a shorter tail, and longer limbs – as seen in *P. ikae* sp. nov. – as well as a small myomere count (approx. 23.6) – as seen in its sister species *P. croaticus* (table 2, fig. 5).

Distribution, life-history and threats

Proteus maurii sp. nov. is distributed throughout the Classical Karst of northeastern Italy and

adjacent Slovenia, from the Gradisca d'Isonzo area southwards through the provinces of Gorizia and Trieste to the Timavo/Reka system, where it comes into contact with *P. xanthostictus* (Recknagel et al., 2024). The species is currently known from more than 40 localities, including caves, springs and estavelles (Lanza et al., 2007; Mauri et al., 2018; Barzaghi et al., 2026; this study). It occupies a wide variety of groundwater habitats, ranging from large subterranean rivers and cave lakes to water-filled fissures, deep pools, vertical shafts and groundwater-fed springs. Rather than depending exclusively on accessible cave systems, *P. maurii* sp. nov. appears to exploit the extensive network of fractures and conduits that characterizes the Classical Karst aquifer (Barzaghi et al., 2026). Recent observations indicate that the species regularly exploits groundwater-surface ecotones at night, particularly springs and estavelles characterized by periodic flooding, where the probability of exploitation by surface predatory fish (such as the pike *Esox cisalpinus*) is lower (Manenti et al., 2024, 2026). Some permanent estavelles are also used continuously, suggesting that ecotones may be stable components of the species' habitat, which it shares with other syntopic amphibians (e.g., *Rana latastei*, *Lissotriton vulgaris meridionalis*, *Pelophylax esculentus*; Brognoli et al., 2025). The diet of the species includes aquatic crustaceans (*Troglocaris*), annelids and other macroinvertebrates (e.g., *Asellus aquaticus*). Feeding grounds include pools below cave shafts that open directly to the surface (which are richer in organic matter and prey) but also periodically flooded cave areas and temporary springs, highlighting the importance of ecotones for energy transfer between terrestrial, surface freshwater and subterranean ecosystems (Barzaghi et al., 2026). Preliminary investigations also suggested morphological variation between groundwater and ecotone habitats (R. Manenti and B. Barzaghi pers. obs.). Seasonal activity peaks during summer and winter, whereas circadian rhythms seem absent, as in other *Proteus* species (Lo Parrino et al. in press). Only a single larva (3.5 cm) was recorded in the wild, namely a spring habitat, where it already exhibited the characteristic troglomorphic morphology of the genus, while retaining sparse dorsal melanophores and externally visible eyes (Manenti et al., 2024). The species is threatened by deterioration of groundwater quality, increasing drought frequency likely associated with climate change, groundwater abstraction, and infrastructure development affecting springs and estavelles. Continued monitoring of potentially invasive predatory species is warranted, such as the expanding red swamp crayfish (*Procambarus clarkii*), as well as introduced fishes – a recurrent threat to paedomorphic Balkan amphibians (Denoël et al., 2019). Increased scientific interest following the formal recognition of the species should also be accompanied by measures minimizing disturbance and illegal collection. With an extent of occurrence of only approx. 170 km^2 and an area of occupancy of approx. 120 km^2, *P. maurii* sp. nov. has one of the narrowest distributions in the genus despite being locally well documented, and we therefore provisionally recommend its assessment as Endangered under IUCN Criterion B.

Conclusions

By reviewing, compiling and re-assessing the phylogeography, distribution, morphological variation and nomenclatural history of *Proteus*, we recognize, name and characterize nine species, providing a formal taxonomic framework for future evolutionary and ecological research, biodiversity monitoring, and species-level conservation. This revision reveals the olm as one of the most remarkable examples of microendemism among European and Western Palearctic amphibians, with few equivalents, such as *Speleomantes* (Chiari et al., 2012) and *Lyciasalamandra* (Veith et al., 2016). In contrast to terrestrial newts, which are strongly

diversified at the scale of the Balkan Peninsula but show comparatively shallower phylogeographic structure within the Dinarides (e.g., *Mesotriton*, Koster et al., 2026; *Lissotriton*, Mars et al., 2025; *Triturus*, Wielstra et al., 2013), *Proteus* has evolved into a mosaic of narrowly endemic species, each restricted to one or a few groundwater systems, illustrating the exceptional role of subterranean environments in promoting biodiversity.

Although this revision resolves much of the historical taxonomic confusion surrounding the genus, which was exacerbated after molecular evidence challenged the traditional view of a single phenotypically conservative species, it should not be regarded as a final synthesis. The identity of numerous historical and peripheral populations remains to be established, several distributional gaps still require targeted surveys, and unexplored karst regions may yet harbor additional endemic species unknown to science. In this context, the first species distribution models developed for the genus provide a valuable framework for guiding future prospection, particularly when integrated with hydrogeological information and environmental DNA surveys, as well as for assessing the potential impacts of future climate change. Moreover, the phylogeographic structure recovered within some widespread species, such as *P. carrarae*, suggests that further taxonomic subdivision may ultimately prove warranted as genomic, morphological and ecological data continue to accumulate. More broadly, integrating cave-specific ecological variables, hydrogeological connectivity, functional morphology and whole-genome data will provide an increasingly refined understanding of the processes that generated this extraordinary complex. We hope that the present revision will serve as a robust foundation for these future studies and contribute to the long-term conservation of *Proteus*, which stands as one of Europe's most distinctive genera and features some of its most threatened species.

Supplementary materials. Data are available on https://doi.org/10.1163/15685381-bja10266 under Supplementary Materials.

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References

Aljančič, G. (2019): History of research on *Proteus anguinus* Laurenti 1768 in Slovenia. Folia Biol. Geol. **60**: 39-69.

Aljančič, G., Aljančič, M., Golob, Z. (2016): Salvaging the washed-out *Proteus*. Nat. Slov. **18**: 65-67.

Aljančič, G., Aljančič, M., Sket, B. (2021): History and biology of the black Proteus (*Proteus anguinus parkelj*). Acta Carsol. **50**: 205-232.

Aljančič, M. (1966): Dve novi nahajališči močerila v Sloveniji. Naše jame **8**: 64-65.

Ambu, J., Litvinchuk, S.N., Caballero-Díaz, C., Nicieza, A., Velo-Antón, G., Gonçalves, H., Martínez-Freiría, F., Martínez-Gil, H., Beltrán, J.F., Donaire-Barroso, D., Hernandez, A., Suchan, T., Crochet, P.A., Martínez-Solano, Ĺ., Dufresnes, C. (2025): Genomic, phenotypic and environmental correlates of speciation in the midwife toads (*Alytes*). Mol. Ecol. **34**: e17736.

Arntzen, J.W., Sket, B. (1996): Speak of the devil: the taxonomic status of *Proteus anguinus parkelj* revisited (Caudata: Proteidae). Herpetozoa **8**: 165-166.

Arntzen, J.W., Sket, B. (1997): Morphometric analysis of black and white European cave salamanders, *Proteus anguinus*. J. Zool. **241**: 699-707.

Badino, G. (2004): Cave temperatures and global climatic change. Int. J. Speleol. **33**: 103-113.

Badino, G. (2010): Underground meteorology-"What's the weather underground?". Acta Carsol. **39**: 427-448.

Bailon, S. (1995): Présence de *Mioproteus wezei* (Amphibia, Proteidae) dans le Pliocène supérieur (MN 16) d'Europe de l'Ouest. Neues Jb. Geol. Paläontol. Monatshefte **1995**: 1-8.

Balázs, G., Lewarne, B., Herczeg, G. (2020): Extreme site fidelity of the olm (*Proteus anguinus*) revealed by a long-term capture-mark-recapture study. J. Zool. **311**: 99-105.

Barzaghi, B., Grassi, G., Creanza, T., Gajdošová, M., Zampieri, V., Lapadula, S., Galbiati, M., Balázs, G., Borgatti, D., Balestra, V., Messina, V., Mauri, E., Ficetola, G.F., Manenti, R. (2026): Understanding benefits and risks of exploiting spring habitats by subterranean animals: insights from a mark-recapture study on the olm (*Proteus anguinus*). Hydrobiologia **853**: 1273-1288.

Bizjak, M.L., Sepčić, K., Bulog, B. (2013): Long-term starvation in cave salamander effects on liver ultrastructure and energy reserve mobilization. J. Morphol. **274**: 887-900.

Bizjak, M.L., Sket, B. (2019): History and biology of the "black proteus" (*Proteus anguinus* parkelj, Sket and Arntzen, 1994, Amphibia: Proteidae): a review. Folia Biol. Geol. **60**: 5-37.

Bonaparte, C.L. (1831): Saggio di una distribuzione metodica degli animali vertebrati. Gior. Arcad. Sci. Lett. Arti **49**: 3-77.

Bonett, R.M., Bierbaum, E.L., Hess, A.J., Trame, S.D., Eckhardt, C.W., Herrboldt, M.A., McGouran, C.N., Kolozsvary, A.D., Sowell, S., Flusche, A.M., McGlone, R. (2025): Compounding heterochrony shapes the salamander visual system across adaptive zones. Proc. Roy. Soc. Lond. B: Biol. Sci. **292**: 2055.

Bonett, R.M., Ledbetter, N.M., Hess, A.J., Herrboldt, M.A., Denoël, M. (2022): Repeated ecological and life cycle transitions make salamanders an ideal model for evolution and development. Dev. Dyn. **251**: 957-972.

Bonett, RM., Trujano-Alvarez, A.L., Williams, M.J., Timpe, E.K. (2013): Biogeography and body size shuffling of aquatic salamander communities on a shifting refuge. Proc. Roy. Soc. Lond. B Biol. Sci. **280**: 20130200.

Boulenger, G.A. (1882): Catalogue of the Batrachia, Gradientia s. Caudata and Batrachia Apoda in the Collection of the British Museum, 2nd Edition. Taylor and Francis, London.

Brame Jr., A.H., Gorham, S.W. (1972): A checklist of the living and fossil salamanders (Order Caudata) of the World. Pasadena, CA. Available at https://amphibiansoftheworld.amnh.org/Bibliography/B/Brame-and-Gorham-1972-Checklist-Living-Fossil-Salamand.-World-Unpubl.-MS.

Brikiatis, L. (2014): The De Geer, Thulean and Beringia routes: key concepts for understanding early Cenozoic biogeography. J. Biogeogr. **41**: 1036-1054.

Brognoli, D., Lo Parrino, E., Terraneo, G., Grassi, G., Zampieri, V., Galbiati, M., Balestra, V., Messina, V., Barzaghi, B., Lapadula, S., Manenti, R. (2025): Importance of spring habitats for amphibians: the case of estavelle ecotones in the classical karst region. Animals **15**: 3228.

Brunner, G. (1956): Nachtrag zur Kleinen Teufelshöhle bei Pottenstein (Oberfranken). Neues Jb. Geol. Paläontol. Monatshefte **1956**: 75-100.

Brusina, S. (1880): Jedan decenium naše zoologičke literature: (1867-1877). JAZU **52**: 190-272.

Brusina, S. (1908): Naravoslovne crtice sa sjevero-istočne obale Jadranskoga mora. JAZU **173**: 1-31.

Bulog, B., Mihajl, K., Jeran, Z., Toman, M.J. (2002): Trace element concentrations in the tissues of *Proteus anguinus* (Amphibia, Caudata) and the surrounding environment. Water Air Soil Pollut. **136**: 147-163.

Campillo, L.C., Barley, A.J., Thomson, R.C. (2020): Model-based species delimitation: are coalescent species reproductively isolated? Syst. Biol. **69**: 708-721.

Chan, K.O., Grismer, L.L. (2026): Friendly graphical user interface for statistical and visual support in species diagnosis. Syst. Biol. **75**: 814-823.

Chiari, Y., van der Meijden, A., Mucedda, M., Lourenço, J.M., Hochkirch, A., Veith, M. (2012): Phylogeography of Sardinian cave salamanders (genus *Hydromantes*) is mainly determined by geomorphology. PLoS ONE **7**: e32332.

Cloquet, H. (1826): Protée. In: Dictionnaire des sciences naturelles, t. 43, p. 392-396. F.G. Levrault, Strasbourg.

Configliachi, P., Rusconi, M. (1821): Observations on the natural history and structure of the *Proteus anguinus*. A. Constable, Edinburgh.

Cope, E.D. (1866): On the structures and distribution of the genera of the arciferous Anura. J. Acad. Nat. Sci. Philadelphia Ser. 2 **6**: 67-112.

Coyne, J.A., Orr, H.A. (2004): Speciation. Sinauer Associates, Sunderland, MA.

Crnobrnja-Isailović, J., Schmidt, B.R., Denoël, M., Ficetola, F.G., Cogălniceanu, D., Martínez-Solano, I., Corti, C., Crochet, P.-A., Ferri, B., Halpern, B., Jablonski, D., Krása, A., Litvinchuk, S., Maletzky, A., Manenti, R., Poboljšaj, K., Schulte, U., Sotiropoulos, K., Speybroeck, J., Strachinis, I., Romano, A., Üzüm, N., Wilkinson, J., Hobin, L., Bellotto, V., Clay, J., Allen, D., Trottet, A. (2025): Measuring the pulse of European biodiversity. In: European red list of amphibians. European Commission, Brussels.

Cuvier, G. (1829): Le règne animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Nouvelle édition revue et augmentée. Deterville, Paris.

de Leeuw, A., Bukowski, K., Krijgsman, W., Kuiper, K.F. (2010): Age of the Badenian salinity crisis: impact of Miocene climate variability on the circum-mediterranean region. Geology **38**: 715-718.

de Leeuw, A., Mandic, O., Krijgsman, W., Kuiper, K., Hrvatović, H. (2012): Paleomagnetic and geochronologic constraints on the geodynamic evolution of the Central Dinarides. Tectonophysics **530-531**: 286-298.

de Queiroz, K. (1998): The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. In: Endless forms: species and speciation, p. 57-75. Howard, D.J., Berlocher, S.H., Eds, Oxford University Press, Oxford.

de Queiroz, K. (2007): Species concepts and species delimitation. Syst. Biol. **56**: 879-886.

Delić, T., Pipan, T., Ozimec, R., Culver, D.C., Zagmajster, M. (2023): The subterranean species of the Vjetrenica Cave System in Bosnia and Herzegovina. Diversity **15**: 912.

Denoël, M., Joly, P., Whiteman, H.H. (2005): Evolutionary ecology of facultative paedomorphosis in newts and salamanders. Biol. Rev. **80**: 663-671.

Denoël, M., Ficetola, G.F., Sillero, N., Džukić, G., Kalezić, M., Vukov, T.D., Muhovic, I., Ikovic, V., Lejeune, B. (2019): Traditionally managed landscapes do not prevent amphibian decline and the extinction of paedomorphosis. Ecol. Monogr. **89**: e01347.

Drole, F. (2017): Izvir, Marija, Magdalena in zgodba o človeški ribici. Jamar **9**: 56-57.

Dubois, A., Raffaëlli, J. (2009): A new ergotaxonomy of the family Salamandridae Goldfuss, 1820 (Amphibia, Urodela). Alytes **26**: 1-85.

Dubois, A., Ohler, A. (2015): An often overlooked Rule of the Code, and its bearing on the authorship and date of the nomen Proteidae (Amphibia. Urodela). Bionomina **9**: 41-49.

Dufresnes, C., Pribille, M., Alard, B., Gonçalves, H., Amat, F., Crochet, P.A., Dubey, S., Perrin, N., Fumagalli, L., Vences, M., Martínez-Solano, I. (2020): Integrating hybrid zone analyses in species delimitation: lessons from two anuran radiations of the Western Mediterranean. Heredity **124**: 423-438.

Dufresnes, C., Brelsford, A., Jeffries, D.L., Mazepa, G., Suchan, T., Canestrelli, D., Nicieza, A., Fumagalli, L., Dubey, S., Martínez-Solano, I., Litvinchuk, S.N., Vences, M., Perrin, N., Crochet, P.A. (2021): Mass of genes rather than master genes underlie the genomic architecture of amphibian speciation. Proc. Natl. Acad. Sci. USA **118**: e2103963118.

Dufresnes, C., Poyarkov, N., Jablonski, D. (2023): Acknowledging more biodiversity without more species. Proc. Natl. Acad. Sci. USA **120**: e2302424120.

Duméril, A.M.C., Bibron, G., Duméril, A.H.A. (1854): Erpétologie Générale ou Histoire Naturelle Complète des Reptiles, Volume 9. Librairie Encyclopédique de Roret, Paris.

Estes, R. (1981): Handbuch der Paläoherpetologie, Part 2. Gymnophiona, Caudata. Gustav Fischer, Jena.

Estes, R., Darevsky, I. (1977): Fossil amphibians from the Miocene of the North Caucasus, U.S.S.R.. J. Palaeontol. Soc. India **20**: 164-169.

Fedosov, A., Achaz, G., Gontchar, A., Puillandre, N. (2022): MOLD, a novel software to compile accurate and reliable DNA diagnoses for taxonomic descriptions. Mol. Ecol. Resour. **22**: 2038-2053.

Fejérváry, G.J. (1926): Note sur la variation du protée et description d'individus provenants d'un nouvel habitat. Ann. Hist.-Nat. Mus. Natl. Hung. **24**: 228-236.

Fitzinger, L. (1850): Über den *Proteus anguinus*. Sitzungsber. Kaiserl. Akad. Wiss. Math.-Naturwissensch. Classe **5**: 291-303.

Fleming, J. (1822): The philosophy of zoology; or a general view of the structure, functions, and classification of animals, Volume 2. A. Constable, Edinburgh.

Freyer, H. (1842): Fauna der in Krain bekannten Säugethiere, Vögel, Reptilien und Fische. Laibach.

Freyer, H. (1846): Über eine neue Art von *Hypochthon* (*Proteus*). Arch. Naturgesch. **12**: 289-290.

Freyer, H. (1847): Zur Geschichte der Entdeckung des *Proteus*. Allg. Dt. Naturhist. Zt. **2**: 38-43.

Freyer, H. (1849): Ueber den Olm, *Proteus* oder *Hypochthon*. Ber. Mitt. Freunden Naturwissensch. Wien **5**: 56-58.

Freyer, H. (1850): Močarilec. In: Slovensko berilo za pervi gimnazijalni razred, p. 93-98. J. Blaznik, Ljubljana.

Frost, D.R. (2026): Amphibian species of the World: an online Reference. version 6.2. American Museum of Natural History, New York, NY. Available at https://amphibiansoftheworld.amnh.org/index.php.

Garnett, S.T., Christidis, L. (2017): Taxonomy anarchy hampers conservation. Nature **546**: 25-27.

Gippner, S., Ruthsatz, K., Dufresnes, C., Vences, M. (2026): Inferring time-to-speciation from hybrid zone analysis informs assessments of taxonomic inflation. Mol. Ecol. **35**: e70361.

Glavan, M., Cvejić, R. (2024): Evaluation of agricultural measures to safeguard the vulnerable karst groundwater habitat of the black olm (*Proteus anguinus parkelj*) from nitrate pollution. Sustainability **16**: 11309.

Gmelin, J.F. (1789): Caroli a Linné. Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tom. 1. Pars. 3.

Goldfuss, G.A. (1820): Handbuch der Zoologie. Zweite Abtheilung. J.L. Schrag, Nürnberg.

Gorički, Š. (2006): Filogeografska in morfološka analiza populacij močerila (*Proteus anguinus*). PhD Thesis, Ljubljana.

Gorički, Š., Trontelj, P. (2006): Structure and evolution of the mitochondrial control region and flanking sequences in the European cave salamander *Proteus anguinus*. Gene **378**: 31-41.

Gorički, Š., Stanković, D., Snoj, A., Kuntner, M., Jeffery, W.R., Trontelj, P., Pavićević, M., Grizelj, Z., Năpăruş-Aljančič, M., Aljančič, G. (2017): Environmental DNA in subterranean biology: range extension and taxonomic implications for *Proteus*. Sci. Rep. **7**: 45054.

Gottstein Matočec, S., Bakran-Petricioli, T., Bedek, J., Bukovec, D., Buzjak, S., Franičević, M., Jalžić, B., Kerovec, M., Kletečki, E., Kralj, J., Kružić, P., Kučinić, M., Kuhta, M., Matočec, N., Ozimec, R., Rađa, T., Štamol, V., Ternjej, I., Tvrtković, N. (2002): An overview of the cave and interstitial biota of Croatia. Nat. Croat. **11** (Suppl. 1): 1-112.

Gray, J.E. (1831): A synopsis of the species of the Class Reptilia. In: The animal kingdom arranged in conformity with its organization, by the Baron Cuvier, with additional descriptions of all the species hitherto named, and of many not before noticed. Volume 9. Griffith, E., Ed., Whittaker, Treacher and Co., London.

Grillitsch, H., Tiedemann, F. (1994): Die Grottenolm-Typen Leopold Fitzingers (Caudata: Proteidae: *Proteus*). Herpetozoa **7**: 139-148.

Han, H., Guo, X., Yu, H. (2016): Variable selection using mean decrease accuracy and mean decrease Gini based on Random Forest. In: 2016 7th IEEE international conference on software engineering and service science (ICSESS), p. 219-224. IEEE, Beijing.

Hawes, R.S. (1945): On the eyes and reactions to light of *Proteus anguinus*. Q. J. Microsc. Sci. **86**: 1-53.

Hervant, F., Mathieu, J., Durand, J.P. (2000): Metabolism and circadian rhythms of the European blind cave salamander *Proteus anguinus* and a facultative cave dweller, the Pyrenean newt (*Euproctus asper*). Can. J. Zool. **78**: 1427-1432.

Highton, R. (2000): Detecting cryptic species using allozyme data. In: The biology of plethodontid salamanders, p. 215-241. Bruce, R.C., Jaegger, R.G., Houck, L.D., Eds, Springer, Cham.

Hochenwart, F. (1838): Beiträge zur Naturgeschichte, Landwirtschaft und Topographie des Herzogthums Krain. J. Blasnik, Laidbach.

Hrvatin, M., Tičar, J., Zorn, M. (2020): Rocks and tectonic structure of Slovenia. In: The geography of Slovenia, small but diverse, p. 23-34. Perko, D., Ciglič, R., Zorn, M., Eds, Springer, Cham.

Hudoklin, A., Aljančič, G. (2017): Pregled razširjenosti človeške ribice ter njenega odkrivanja na nizkem dolenjskem krasu. Dolenjski kras **7**: 212-227.

Issartel, J., Hervant, F., de Fraipont, M., Clobert, J., Voituron, Y. (2009): High anoxia tolerance in the subterranean salamander *Proteus anguinus* without oxidative stress nor activation of antioxidant defenses during reoxygenation. J. Comp. Physiol. B **179**: 543-551.

Istenič, L., Zigler, I. (1974): Riboflavin as "pigment" in the skin of *Proteus anguinus* Laur. Naturwissenschaften **61**: 686-687.

IUCN (2012): IUCN Red List categories and criteria: Version 3.1, 2nd Edition. IUCN, Gland.

Ivanović, A., Aljančič, G., Arntzen, J.W. (2013): Skull shape differentiation of black and white olms (*Proteus anguinus anguinus* and *Proteus a. parkelj*): an exploratory analysis with micro-CT scanning. Contrib. Zool. **82**: 107-114.

Jelić, D., Kuljerić, M., Koren, T., Treer, D., Šalamon, D., Lončar, M., Podnar-Lešić, M., Janev-Hutinec, B., B.ogdanović, T., Mekinić, S. (2015): Crvena knjiga vodozemaca i gmazova Hrvatske. Ministry of, Environmental and Nature Protection, State Institute for Nature Protection, Croatian Herpetological Society HYLA, Zagreb.

Karaman, S. (1921): Beiträge zur Herpetologie von Jugoslavien. Glasnik Hrvatskoga Naravoslovnoga Društva **33**: 193-208.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M. (2017): Climatologies at high resolution for the earth's land surface areas. Sci. Data **4**: 1-20.

Koren, K., Brajkovič, R., Bajuk, M., Vraničar, Š., Fabjan, V. (2023): Hydrogeological characterization of karst springs of the white (*Proteus anguinus anguinus*) and black olm (*Proteus anguinus parkelj*) habitat in Bela krajina (SE Slovenia). Geologija **66**: 151-166.

Kos, M., Bulog, B., Szél, Á., Röhlich, P. (2001): Immunocytochemical demonstration of visual pigments in the degenerate retinal and pineal photoreceptors of the blind cave salamander (*Proteus anguinus*). Cell Tissue Res. **303**: 15-25.

Kostanjšek, R., Diderichsen, B., Recknagel, H., Gunde-Cimerman, N., Gostinčar, C., Fan, G., Kordiš, D., Trontelj, P., Jiang, H., Bolund, L., Luo, Y. (2022): Toward the massive genome of *Proteus anguinus*-illuminating longevity, regeneration, convergent evolution, and metabolic disorders. Ann. N.Y. Acad. Sci. **1507**: 5-11.

Kostanjšek, R., Zakšek, V., Bizjak-Mali, L., Trontelj, P. (2023): The olm (*Proteus anguinus*), a flagship groundwater species. In: Groundwater, Ecology and Evolution, 2nd Edition, p. 305-327. Malard, F., Griebler, C., Rétaux, S., Eds, Academic Press, San Diego, CA.

Koster, S., Theodoropoulos, A., Beukema, W., Ambu, J., Babik, W., Canestrelli, D., Chiocchio, A., Cogălniceanu, D., Cvijanović, M., de Visser, M.C., Dufresnes, C., France, J., Hyseni, A., Jablonski, D., Kranželić, D., Lukanov, S., Martínez-Solano, I., Naumov, B., Pabijan, M., Salvi, D., Schmidt, B., Sotiropoulos, K., Stănescu, F., Stanković, D., Šunje, E., Szabolcs, M., Vacheva, E., Vörös, J., Zimić, A., Wielstra, B. (2026): Five hidden species in a widespread, European vertebrate: disentangling the alpine newt cryptic species complex through genomic phylogeography. Mol. Ecol. **35**: e70300.

Kovač Konrad, P., Koller Šaric, K. (2017): The deepest finding of an olm (*Proteus anguinus*): Zagorska peć, Ogulin, Croatia. Acta Carsol. **46**: 347-351.

Kranjec, N. (1981): Razširjenost in variabilnost močerila (*Proteus anguinus* Laurenti). Diploma Thesis, Ljubljana.

Krstić, N., Savić, L., Jovanović, G., Bodor, E. (2005): Lower Miocene lakes of the Balkan Land. Acta Geol. Hung. **46**: 291-299.

Kuhn, M. (2008): Building predictive models in R using the caret package. J. Stat. Softw. **28**: 1-26.

Lanza, B., Andreone, F., Bologna, M.A., Corti, C., Razzetti, E. (2007): Fauna d'Italia. Amphibia, Vol. XLII. Calderini, Bologna.

Laurenti, J.N. (1768): Synopsin Reptilium. J.T. de Trattnern, Viennae.

Leuckart, F.S. (1816): Dissertatiuncula inauguralis de *Equo bisulco* Molinae. Göttingen.

Leuckart, F.S. (1821): Einiges über die Fischartigen Amphibien. Isis von Oken **9**: 257-265.

Liaw, A., Wiener, M. (2002): Classification and regression by randomForest. R news **2**: 18-22.

Linnaeus, C. (1766): Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Holmiae.

Liu, J., Slik, F., Zheng, S., Lindenmayer, D.B. (2022): Undescribed species have higher extinction risk than known species. Conserv. Lett. **15**: e12876.

Lo Parrino, E., Lapadula, S., Brognoli, D., Terraneo, G., Barzaghi, B., Boulamail, S., Balesstra, V., Galbiati, M., Gandini, J.L., Grassi, G., Falaschi, M., Ficetola, F.G., Inguscio, S., Messina, V., Mauri, E., Passoni, F.,

Zampieri, V., Cozzoli, F., Manenti, R. The rhythm of the night: assessing temporal variation of activity patterns in arhythmic environments from field data. Ecosphere: in press.

Macaluso, L., Villa, A., Mörs, T. (2022): A new proteid salamander (Urodela, Proteidae) from the middle Miocene of Hambach (Germany) and implications for the evolution of the family. Palaeontology **65**: e12585.

Malone, J.H., Fontenot, B.E. (2008): Patterns of reproductive isolation in toads. PLoS ONE **3**: e3900.

Mammola, S., Leroy, B. (2018): Applying species distribution models to caves and other subterranean habitats. Ecography **41**: 1194-1208.

Mandic, O., de Leeuw, A., Vuković, B., Krijgsman, W., Harzhauser, M., Kuiper, K.F. (2011): Palaeoenvironmental evolution of Lake Gacko (Southern, Bosnia and Herzegovina): impact of the middle Miocene climatic optimum on the Dinaride lake system. Palaeogeogr. Palaeoclimatol. Palaeoecol. **299**: 475-492.

Manenti, R., Di Nicola, M.R., Zampieri, V., Grassi, G., Creanza, T., Mauri, E., Ficetola, G.F., Barzaghi, B. (2024): Wandering outside of the Styx: surface activity of an iconic subterranean vertebrate, the olm (*Proteus anguinus*). Ecology **105**: e4252.

Manenti, R., Zampieri, V., Cassarino, F., Brognoli, D., Mauri, E., Terraneo, G., Lo Parrino, E., Bruschi, R., Balestra, V., Lapadula, S., Galbiati, M., Messina, V., Falaschi, M., Barzaghi, B., Ficetola, G.F., Melotto, A. (2026): Living at the interface: behavioral, evolutionary and ecological insights of spring use by highly mobile stygobiont crustaceans, *Troglocaris planinensis* (Decapoda: Atyidae). Ecol. Evol. **16**: e73338.

Mars, J., Koster, S., Babik, W., France, J., Kalaentzis, K., Kazilas, C., Martínez-Solano, I., de Visser, M.C., Wielstra, B. (2025): Phylogenomics yields new systematic and taxonomical insights for *Lissotriton* newts, a genus with a strong legacy of introgressive hybridization. Mol. Phylogenet. Evol. **204**: 108282.

Mattes, J. (2018): Traveling olms: Local and global Perspectives on the research on *Proteus anguinus* (1700-1930). In: The scientific dialogue linking America, Asia and Europe between the 12th and the 20th Century. Theories and techniques travelling in space and time, p. 186-203. D'Angelo, F., Ed., Associazione culturale Viaggiatori, Naples.

Mauri, E., Abbona, I., Papi, F. (2018): Storia delle ricerche del Proteo in Italia e attuali conoscenze a 250 anni dalla sua prima descrizione da parte di Laurenti. In: Atti del Convegno SPELEO2018, p. 121-125. Regione Autonoma Friuli Venezia Giulia.

Maxson, L.R., Maxson, R.D. (1979): Comparative albumin and biochemical evolution in plethodontid salamanders. Evolution **33**: 1057-1062.

Mayr, E. (1942): Systematics and the origin of species. Columbia University Press, New York, NY.

McCrady, E. (1954): A new species of *Gyrinophilus* (Plethodontidae) from Tennessee caves. Copeia **1954**: 200-206.

Merrem, B. (1820): Versuch eines Systems der Amphibien. J.C. Krieger, Marburg.

Mertens, R., Müller, L. (1928): Liste der Amphibien und Reptilien Europas. Abhandl. Senckenberg. Naturforsch. Gesell. **41**: 1-62.

Mertens, R., Müller, L. (1940): Die Amphibien und Reptilien Europas (Zweite Liste, nach dem Stand vom 1. Januar 1940). Abhandl. Senckenberg. Naturforsch. Gesell. **451**: 1-56.

Miaud, C., Corti, C., Andreone, F., Aljančič, G., Arntzen, J., Crnobrnja-Isailović, J., Poboljšaj, K., Denoël, M., Guillaume, O., Edgar, P., Trontelj, P., Jelić, D., Zakšek, V. (2024): *Proteus anguinus*. The IUCN Red List of Threatened Species 2024: e.T18377A227229041. IUCN, Gland.

Michahelles, K. (1830): Neue südeuropäische Amphibien. Isis von Oken **23**: 189-195.

Michahelles, K. (1831): Beiträge zur Naturgeschichte des *Proteus anguinus*. Isis von Oken **24**: 499-509.

Mihajlovski, M. (2012): Raziskovanje izvira reke Dobličice. Dolenjski kras **6**: 136-138.

Mihevc, A. (2007): The age of karst relief in west, Slovenia. Acta Carsol. **36**: 35-44.

Młynarski, M., Szyndlar, Z., Estes, R., Sanchiz, B. (1984): Amphibians and reptiles from the Pliocene locality of Węże II near Działoszyn (Poland). Acta Palaeontol. Polon. **29**: 209-226.

Mocochain, L., Clauzon, G., Bigot, J.-Y., Brunet, P. (2006): Geodynamic evolution of the peri-Mediterranean karst during the Messinian and the Pliocene: evidence from the Ardèche and Rhône Valley systems canyons, Southern France. Sediment. Geol. **188-189**: 219-233.

Năpăruş-Aljančič, M., Gorički, Š., Stanković, D., Kuntner, M., Aljančič, G. (2017): GIS analysis to assess the groundwater habitat pollution of black proteus. Nat. Slov. **19**: 47-49.

Oppel, M. (1811): Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. J. Lindauer, Münich.

Palcu, D.V., Krijgsman, W. (2023): The dire straits of Paratethys: gateways to the anoxic giant of Eurasia. Geol. Soc. Lond. Spec. Publ. **523**: 111-139.

Palcu, D.V., Golovina, L.A., Vernyhorova, Y.V., Popov, S.V., Krijgsman, W. (2017): Middle Miocene paleoenvironmental crises in Central Eurasia caused by changes in marine gateway configuration. Glob. Planet. Change **158**: 57-71.

Pavlek, M., Mammola, S. (2021): Niche-based processes explaining the distributions of closely related subterranean spiders. J. Biogeogr. **48**: 118-133.

Pezdirc, M., Heath, E., Bizjak-Mali, L., Bulog, B. (2011): PCB accumulation and tissue distribution in cave salamander (*Proteus anguinus anguinus*, Amphibia, Urodela) in the polluted karstic hinterland of the Krupa River, Slovenia. Chemosphere **84**: 987-993.

Polak, S., Bedek, J., Ozimec, R., Zakšek, V. (2012): Subterranean fauna of twelve Istrian caves. Ann. Ser. Hist. Nat. **22**: 7-24.

Pollock, L.J., O'Connor, L.M.J., Mokany, K., Rosauer, D.F., Talluto, L., Thuiller, W. (2020): Protecting biodiversity (in all its complexity): new models and methods. Trends Ecol. Evol. **35**: 1119-1128.

Premate, E., Fišer, Ž., Kuralt, Ž., Pekolj, A., Trajbarič, T., Milavc, E., Hanc, Ž., Kostanjšek, R. (2022): Behavioral observations of the olm (*Proteus anguinus*) in a karst spring via direct observations and camera trapping. Subterr. Biol. **44**: 69-83.

Rafinesque, C.S. (1815): Analyse de la nature, ou Tableau de l'Univers et des corps organisés. J. Barravecchia, Palermo.

Recknagel, H., Premate, E., Zakšek, V. (2022): First sighting of 'white' and 'black' olms (*Proteus anguinus*) in the same spring. Nat. Slov. **24**: 39-41.

Recknagel, H., Zakšek, V., Delić, T., Gorički, Š., Trontelj, P. (2024): Multiple transitions between realms shape relict lineages of *Proteus* cave salamanders. Mol. Ecol. **33**: e16868.

Roux, C., Fraïsse, C., Romiguier, J., Anciaux, Y., Galtier, N., Bierne, N. (2016): Shedding light on the grey zone of speciation along a continuum of genomic divergence. PLoS Biol. **14**: e2000234.

Schlegel, P.A. (2008): Magnetic and other non-visual orientation mechanisms in some cave and surface urodeles. J. Ethol. **26**: 347-359.

Schlegel, P.A., Steinfartz, S., Bulog, B. (2009): Non-visual sensory physiology and magnetic orientation in the Blind Cave Salamander, *Proteus anguinus* (and some other cave-dwelling urodele species). Review and new results on light-sensitivity and non-visual orientation in subterranean urodeles (Amphibia). Anim. Biol. **59**: 351-384.

Schreiber, E. (1912): Herpetologia europaea; eine systematische Bearbeitung der Amphibien und Reptilien welche bisher in Europa aufgefunden sind. G. Fischer, Jena.

Schreibers, K. (1801): A historical and anatomical description of a doubtful amphibious animal of Germany, called, by Laurenti, *Proteus anguinus*. Philos. Trans. Roy. Soc. **91**: 241-264.

Scopoli, J.A. (1762): Letter to Linnaeus, May 3, 1762. L3077.14.8. Collection of the Linnaeus Society, London.

Scopoli, J.A. (1772): Annus V. historico-naturalis. Ch. G. Hilscher, Lipsiae.

Sessions, S., Bulog, B., Mali, L.B. (2015): The phoenix rises: Reversal of cave adaptations in the blind cave salamander, *Proteus anguinus*? FASEB J. **29**: LB36.

Shaw, G. (1802): General zoology or systematic natural history. Volume III, Part 1, Amphibia. T. Davison, London.

Shaw, T.R., Čuk, A. (2015): Slovene Karst and caves in the past. ZRC Publishing, Ljubljana.

Sket, B. (1993): Nova rasa človeške ribice (Kako se "naredi" novo podvrsto ali članek o članku). Proteus **56**: 3-11.

Sket, B., Arntzen, J.W. (1994): A black, non-troglomorphic amphibian from the karst of Slovenia: *Proteus anguinus parkelj* n. ssp. (Urodela: Proteidae). Contrib. Zool. **64**: 33-53.

Sket, B. (1997): Distribution of *Proteus* (Amphibia: Urodela: Proteidae) and its possible explanation. J. Biogeogr. **24**: 263-280.

Sket, B. (2007): Kaj vemo in kaj si mislimo o človeški ribici. Utrinki iz zgodovine in nekaj novosti. Proteus **70**: 14-27.

Smithson, P.A. (1991): Inter-relationships between cave and outside air temperatures. Theor. Appl. Climatol. **44**: 65-73.

Špelić, M., Del Ben, A., Petrinjak, K. (2021): Structural setting and geodynamics of the Kvarner area (Northern Adriatic). Mar. Petrol. Geol. **125**: 104857.

Speybroeck, J., Beukema, W., Dufresnes, C., Fritz, U., Jablonski, D., Lymberakis, P., Martínez-Solano, Í., Razzetti, E., Vamberger, M., Vences, M., Vörös, J., Crochet, P.-A. (2020): Species list of the European herpetofauna – 2020 update by the Taxonomic Committee of the Societas Europaea Herpetologica. Amphib.-Reptil. **41**: 139-189.

Spielman, D., Brook, B.W., Frankham, R. (2004): Most species are not driven to extinction before genetic factors impact them. Proc. Natl. Acad. Sci. USA **101**: 15261-15264.

Steinberg, F.A. (1758): Gründliche Nachricht von dem in dem Inner-Crain gelegenen Czirknitzer-See. Reichbardtin, Laybach.

Sukumaran, J., Knowles, L.L. (2017): Multispecies coalescent delimits structure, not species. Proc. Natl. Acad. Sci. USA **114**: 1607-1612.

Syromyatnikova, E.V. (2022): Review of records of *Mioproteus* (Caudata: Proteidae) from Southeastern Europe. Paleontol. J. **56**: 1428-1436.

Tamura, K., Stecher, G., Kumar, S. (2021): MEGA11: Molecular Evolutionary Genetics Analysis Version 11. Mol. Biol. Evol. **38**: 3022-3027.

Valavi, R., Elith, J., Lahoz-Monfort, J.J., Guillera-Arroita, G. (2021): Modelling species presence-only data with random forests. Ecography **44**: 1731-1742.

Valavi, R., Elith, J., Lahoz-Monfort, J.J., Guillera-Arroita, G. (2023): Flexible species distribution modelling methods perform well on spatially separated testing data. Glob. Ecol. Biogeogr. **33**: 369-383.

Valvasor, J.V. (1689): Die Ehre des Herzogthums Crain. Volume 1. W.M. Endtner, Laybach-Nürnberg.

Van der Hoeven, J. (1833): Handboek der Dierkunde, of Grondbeginsels der Natuurlijke Geschiedenis van het Dierenrijk. Tweeden Deels. C.G. Sulpke, Amsterdam.

Veith, M., Göçmen, B., Sotiropoulos, K., Ehl, S., Godmann, O., Steinfartz, S. (2016): Seven at one blow: The origin of major lineages of the viviparous Lycian salamanders (*Lyciasalamandra* Veith and Steinfartz, 2004) was triggered by a single paleo-historic event. Amphib.-Reptil. **37**: 373-387.

Vences, M., Thomas, M., van der Meijden, A., Chiari, Y., Vieites, D.R. (2005): Comparative performance of the 16S rRNA gene in DNA barcoding of amphibians. Front. Zool. **2**: 5.

Vieites, D.R., Wollenberg, K.C., Andreone, F., Köhler, J., Glaw, F., Vences, M. (2009): Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. Proc. Natl. Acad. Sci. USA **106**: 8267-8272.

Voituron, Y., de Fraipont, M., Issartel, J., Guillaume, O., Clobert, J. (2010): Extreme lifespan of the human fish (*Proteus anguinus*): a challenge for ageing mechanisms. Biol. Lett. **7**: 105-107.

von Meyer, H. (1845): Zur Fauna der Vorwelt, Vol. 1: Fossile, Saeugethiere, Voegel und Reptilien aus dem Molasse-Mergel von Oeningen. H. Keller, Frankfurt am Main.

von Tschudi, J.J. (1838): Classification der Batrachier mit Berücksichtigung der fossilen Thiere dieser Abtheilung der Reptilien. Petitpierre, Neuchâtel.

Vörös, J., Márton, O., Schmidt, B.R., Gál, J.T., Jelić, D. (2017): Surveying Europe's only cave-dwelling chordate species (*Proteus anguinus*) using environmental DNA. PLoS ONE **12**: e0170945.

Vörös, J., Ursenbacher, S., Jelić, D. (2019): Population genetic analyses using 10 new polymorphic microsatellite loci confirms genetic subdivision within the Olm, *Proteus anguinus*. J. Hered. **110**: 211-218.

Wielstra, B., Crnobrnja-Isailović, J., Litvinchuk, S.N., Reijnen, B.T., Skidmore, A.K., Sotiropoulos, K., Toxopeus, A.G., Tzankov, N., Vukov, T., Arntzen, J.W. (2013): Tracing glacial refugia of *Triturus* newts based on mitochondrial DNA phylogeography and species distribution modeling. Front. Zool. **10**: 13.