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Taxonomic authority in endemic freshwater fishes of a Mediterranean biodiversity hotspot: From expeditionary natural history to systematics

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Abstract

Taxonomy has long been guided by natural scientists whose choices, methods, and values shape how biodiversity is named and used today. This study reconstructs the making of one regional fauna, the endemic freshwater fishes now recognized from the territory of the modern Greek state, focusing on the researchers who collected and described these species and how they shaped freshwater fish systematics. We review sources screened through 2025 and analyze the description record of endemic species, which extends from 1837 to 2017. Using a dataset of 91 valid endemic species and 47 scientists, we examine who named what, when, and under which institutional, linguistic, and political conditions. For each species, we traced nomenclatural history, type locality, publication type and language; for each author, we compiled demographics, nationality, affiliations, discipline, and fieldwork activity, cross-checking multiple sources and, where possible, verifying details directly with living authors. Species descriptions accumulated in uneven pulses. The slow early phase was dominated by non-domestic expeditions (1830s-1900s). A pronounced interwar peak (1920s-1930s) was led by Balkan and Greek scientists, followed by wartime contraction (1940s). Renewed momentum followed the post-war decades and especially after 2000 as analytical tools improved. Authorship was highly skewed, with four prolific contributors (Karaman, Stephanidis, Economidis and Kottelat) producing nearly two-thirds of the names. Publication practices shifted gradually from monographs to serials, and from German to English, while about three-quarters of original combinations changed at least once. Overall, this study offers a people-centred baseline for Greek freshwater ichthyology, honoring its pioneers and showing how methods, taxonomic concepts, and cultural influences co-evolved. Within this context, it aims also to inform broader discussions on how taxonomic knowledge is formed and sustained within specific historical settings.

Keywords: Taxonomy; Endemism; History; Nomenclature; Ichthyology; Freshwater Fish.

Introduction

Humans have depicted and described fishes for millennia, from Paleolithic engravings of salmonids, pikes and eels in southwestern France (Moyle & Moyle, 1991) to the earliest mentions of fish in ancient Greek literature (Voultsiadou & Tatolas, 2005). Systematic classification, however, took shape far later. Early taxonomic thinking in zoology traces to Plato's typological "dichotomies", a two-part system that arranged entities based on their relationship to ideas or forms (Vasil'ieva, 2003). Although he introduced the concepts of "species", "genus", and "essence", his integration of these into moral or aesthetic values was of limited benefit to biological practice (Vasil'ieva, 2003). Aristotle upgraded Plato's system and proposed a new classification system for animals based on their morphological and functional characteristics (Gangias *et al.*, 2017), laying empirical foundations that early modern naturalists would later transform.

"Modern" ichthyology has a history of around 470 years. Belon's *De aquatilibus* (1553) laid its foundations and Rondelet, Salviani and Gessner followed with major contributions during the 16th century (Kottelat & Freyhof, 2007). These works remained standard references in ichthyology well into the 17th century. During the following century, Artedi provided an important classification system of fishes, based largely on earlier naturalist explorers, which earned him the title of "Father of Ichthyology" (Moyle & Cech, 2004). His work was later adopted and systematized by Carl von Linné (Linnaeus) who wrote *Systema Naturae* (two volumes in 1758 and 1759) (Moyle & Moyle, 1991), marking the starting point for modern binomial and hierarchical zoological nomenclature. Subsequent syntheses by Bloch, Cuvier, Valenciennes and Lacepède produced volumes of reference works that shaped 18th-19th century ichthyology.

Despite these efforts, Europe's freshwater ichthyofauna remained undercounted well into the 20th century, as successive catalogues and checklists revised species totals upward (Kottelat & Freyhof, 2007). This pattern changed substantially in 2007 with Kottelat & Freyhof's legendary *Handbook of European Freshwater Fishes*, which listed 546 native and 33 introduced species, including at least 47 species new to science. This upward trend reflects both genuine discovery and shifting taxonomic concepts as morphological taxonomy was complemented - and sometimes overturned - by genetic evidence. Given ongoing taxonomic work, advances in genetic and "omics" tools, bioinformatic technology and the overall diversity and complexity of freshwater ecosystems, further new species are expected to be identified. This is particularly true for cryptic taxa or under-explored regions and remote areas, mostly in South and Central America, Tropical Asia and Africa (Closs *et al*., 2016).

In Greece, located at the crossroads of three continents, freshwater fish fauna has been shaped by dynamic geological and evolutionary history, with repeated basin isolation and reconnection promoting high speciation and endemism (Reyjol *et al*., 2007; Barbieri *et al*., 2015; Zogaris & Economou, 2017). This particular biodiversity necessitated the systematic recording, description and classification of species as early as the 19th century (e.g., Heckel, 1837; Steindachner, 1892). Yet, despite the fact that taxonomic research of freshwater fishes in Greece has a history of almost two centuries, its human and historical dimensions remain largely neglected and scattered. In an era defined by the collapse of Empires, nationalist and social movements, the emergence of new states, two world wars, and profound political transitions that decisively shaped Greece's territorial and sociopolitical landscape, taxonomic science in the country continued to progress. Within this broader context, the names assigned to endemic fishes are more than labels. They encode who identified, described, named and classified each taxon, when and where it was recorded, and on what diagnostic evidence. Interpreted historically, these names take on significance beyond their nominal role, revealing how ichthyology itself has evolved.

Reviewing these efforts is therefore essential both for understanding the evolution of freshwater fish taxonomic research in Greece and for recognizing the laborious scientific work of the researchers who, often under adverse conditions, advanced our knowledge of the freshwater fish fauna. Such a synthesis is timely, as "problematic" taxa are re-evaluated in the context of modern social and scientific debates related to the preservation of historical integrity and relevance of the taxonomic names (Guedes *et al*., 2023; Raposo *et al*., 2023; Thiele, 2023; Jiménez-Mejías *et al*., 2024). It also serves as a source of inspiration for prospective fish taxonomists against the observed trend of erosion in taxonomic skills in museums and academic institutions (Collares-Pereira *et al*., 2016).

This study traces the historical development of freshwater fish systematics in Greece from the 19th century to the present, focusing on the individuals, practices, and intellectual contexts that shaped knowledge of the country's endemic freshwater fishes. We restricted the core analyses to endemic and near-endemic taxa because they most clearly capture geographically-focused diversification and its associated naming history on river and lake-basin biogeography directly related to the country; moreover, these taxa are central to national conservation priorities. Widespread taxa with pan-European authorships remain an integral part of the fauna, but much of their nomenclatural and revisionary history was established beyond Greece and is therefore less informative for a Greece-centred synthesis of taxonomic practice. We also identified key milestones and examined naming patterns through the etymology of scientific names to indicate how methods, taxonomic concepts, and cultural influences co-evolved. Overall, we aim to clarify the scientific legacy of this body of work and pay tribute to the researchers involved, while contributing to broader discussions on how taxonomic knowledge is formed and sustained within specific historical settings.

Materials and Methods

Between December 2024 and March 2025, we assembled a dataset for all freshwater fish species considered endemic to Greece. The dataset includes strictly Greek endemics, southern Balkan endemics, near endemics (species occurring in Greece and in transboundary freshwater bodies), and Asia Minor endemics that form part of the same regional fauna (Barbieri *et al*., 2015). "Valid species" are those with an accepted authorship (taxonomic authority) under current usage. Unnamed or provisionally designated taxa with uncertain taxonomic status were recorded separately for reference (e.g., *Alburnus* sp. Volvi, *Eudontomyzon* sp. Almopaios, *Rutilus* sp. Sperchios, *Squalius* sp. Aoos, *Squalius* sp. Evia) but not pooled with valid species. Each valid species was assigned to its respective ichthyoregion(s) based on Barbieri *et al*. (2015): (1) Thrace, (2) Macedonia-Thessaly, (3) Southeast Adriatic, (4) Western Aegean, (5) Ionian and (7) Eastern Aegean (excluding (6) Crete which has no endemic freshwater fish species). Synonyms and previous nomenclature of the species were extracted from the IUCN Red List (IUCN, 2025). The etymology of each scientific name was retrieved from the ETYFish Project (Scharpf & Lazara, 2025). For each species, we recorded: (i) the first publication describing the taxon and its year; (ii) publication type (serial, standalone, or catalogue/record); (iii) publication language; and (iv) the earliest publication explicitly confirming taxonomic identity using genetic evidence.

For all authors involved in describing, documenting, or validating the endemic species, we compiled the following variables: a) full name as used in publications and standardized form; b) gender; c) year of birth and death (where applicable) and age at the first relevant publication related to an endemic fish species of Greece; d) country of origin; e) nationality/ethnicity; f) institutional affiliation at the time of publication; g) institution type and country; h) scientific background and discipline of the author; and i) whether the author collected samples in the region. To improve accuracy, we cross-checked author metadata against multiple sources including institutional profiles, obituaries, historical registers, and published biographies. We additionally used an AI-assisted tool to identify candidate sources and search terms. AI output was not treated as a primary source and was not entered into the dataset unless independently verified against primary documents or authoritative references. For living authors, we attempted direct verification by email or telephone to confirm key details (dates, affiliations, field activity). All correspondence was documented in the database.

To better understand patterns of collaboration, taxonomic focus, and spatial structure in our dataset, we visualized the author-species connections as a network using Gephi (version 0.10.1; Gephi Consortium, 2024). Data were organized in node-edge format, with nodes representing researchers and fish species. An edge was drawn between an author and a species whenever the author participated in a taxonomic publication on that species (original description, subsequent revision, or first genetic validation). Network structure was explored using the ForceAtlas2 layout algorithm for spatial organization and the Modularity method for cluster detection. The modularity value quantifies the strength of the network's cluster structure; with higher values (approaching 1) indicating denser within-group connections than expected by chance and lower or negative values reflecting weaker or absent modular organization. Node size was scaled according to degree centrality emphasizing the most highly connected researchers and taxa.

The analyses covered the historical continuum from soon after the establishment of the Greek state through the present, a period characterized by shifting scientific practices, evolving institutions, and major geopolitical transformations. The territorial formation of modern Greece reflects a sequence of conflicts, geopolitical shifts, and treaty-based adjustments between 1832 and 1947. To anchor this temporal and geopolitical landscape, Figure 1 illustrates the territorial formation and subsequent boundary changes of the Greek state through conflicts, treaties and political realignments. Examined within this framework, the data were treated in relation to the conditions and contexts in which they were produced.

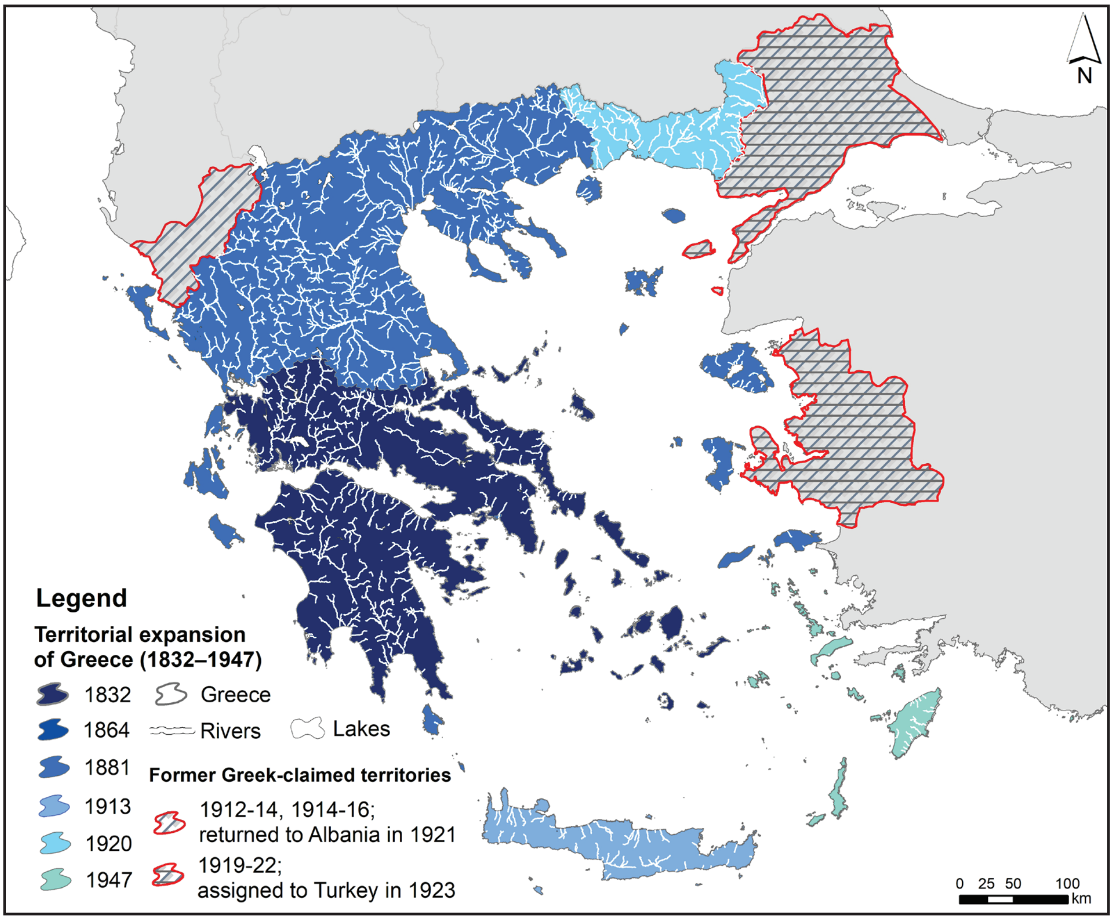

***Fig. 1*:** Territorial formation of the modern Greek state (1832-1947). The Greek state was established as a kingdom in 1832 (Treaty of London) and expanded through subsequent cessions in 1864 (Treaty of London), 1881 (Convention of Constantinople), and 1913 after the Balkan Wars (Treaties of London and Bucharest). Further boundary adjustments followed World War I in 1920 with territory ceded by Bulgaria (San Remo Conference), and after World War II in 1947 with the cession of the Dodecanese by Italy (Treaty of Paris). Former Greek-claimed territories, across these turbulent periods, include areas occupied in 1912-13 and administered in 1914-16, which were returned to Albania in 1921 (confirmation of the 1913 Protocol of Florence), as well as regions awarded under the post-World War I settlement in 1919-22 (Treaty of Sèvres, 1920) but ultimately assigned to Turkey in 1923 (Treaty of Lausanne), following the end of the Greco-Turkish War.

Results

From 1837 to 2017, 47 scientists described 91 taxonomically valid endemic freshwater fish species from Greece (Table 1 & 2; Fig. 2), including 43 endemics restricted to Greece, 29 endemics to the southern Balkans, 14 near endemics, and five Asia Minor endemics. No new endemic species descriptions were recorded after 2017. Species occur across six ichthyoregions with 80 species confined to a single ichthyoregion, 10 occurring in two, and one spanning three. Endemics are absent from Crete and the ichthyoregion of Southern Anatolia. Forty-one species (45.1%) are currently assessed as threatened (i.e. Critically Endangered, Endangered, or Vulnerable) and one species is listed as extinct. The remaining 49 species (53.8%) are assessed as Least Concern or Near Threatened.

Authors were predominantly male (87.2%). The mean age at first relevant description was 45.4 years (SD 12.6; range 26-84). The most prolific contributors (59 species; 64.8%) were Karaman (22 species), followed by Stephanidis (16 species), Economidis (13 species) and Kottelat (8 species) (Fig. 3a). Among the remaining 43 authors, 32 contributed to a single description (35.1% of the species), and eleven authors described two to four species (32 species in total; 35.1% of the species).

In terms of geographical origin, researchers originated mainly from Central Europe (31.9%), predominantly from Germany, Austria and Czech Republic. Greece is represented by nine researchers (19.1%), followed by Western Europe (10.6%), mainly France and Belgium. Italy, other Balkan countries, and North America (United States and Canada) each account for 8.5% of authors. Lastly, Northern Europe (6.4%) is represented by UK and Sweden and Eastern Europe (6.4%) by Russia and Ukraine.

Institutional affiliations of the 47 authors were quite diverse. Seventeen authors (36%) were affiliated with nine natural history museums, 13 (28%) with universities, and seven (15%) with research institutes (Fig. 3b).

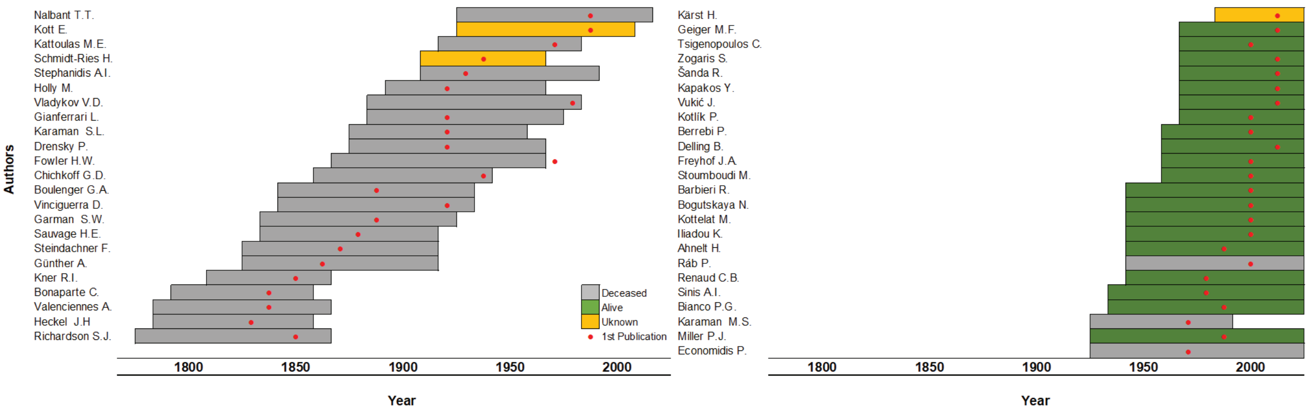

Fig. 2: Lifespans of the 47 authors and timing of their first publication related to descriptions of endemic Greek freshwater fishes (red dots). Grey bars indicate deceased authors; green bars, authors still living; yellow bars, authors for whom survival status or exact year of death is uncertain. Dots falling outside a bar indicate works published posthumously.

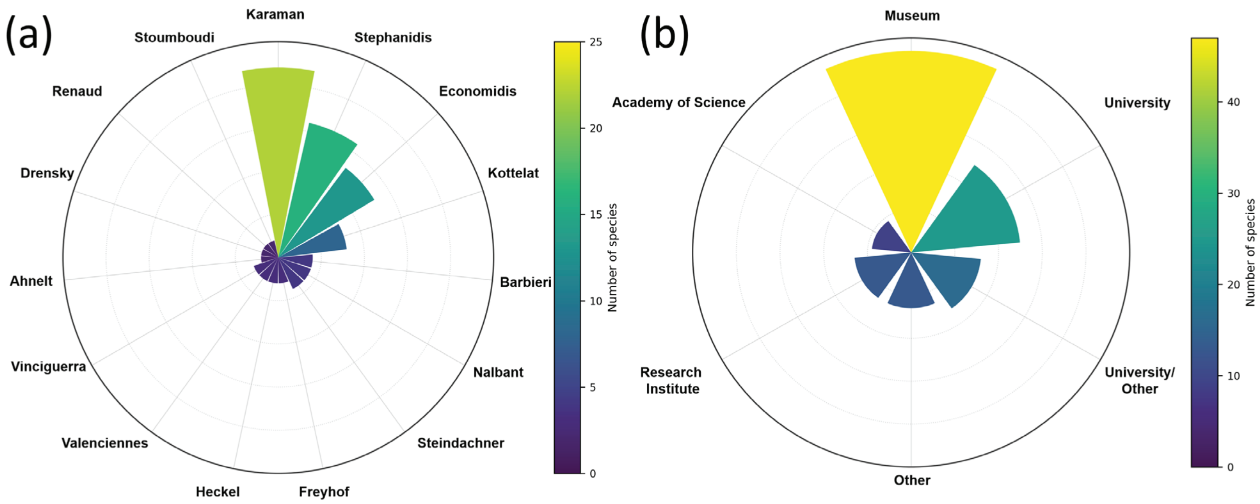

Fig. 3: Authors contribution to species descriptions (a) and institutional affiliations of authors at the time of their first relevant publication (b). Bar length indicates the number of species per category, and the color map encodes the same counts, with darker purple = fewer and yellow = more.

Table 1. List of endemic species of Greece: Scientific name, IUCN common name, current taxonomic authority, and previous nomenclature. Species listed in chronological order based on year of authorship.

Species	Common name	Authority	Year	Synonyms/Previous Nomenclature
Barbus cyclolepis	Maritsa barbel	Heckel	1837	*Barbus tauricus* ssp. *polylepis* Battalgil, 1941
Vimba melanops	Macedonian vimba	(Heckel)	1837	*Abramis melanops* Heckel, 1837
Barbus peloponnesius	Peloponnese barbel	Valenciennes	1842	*Pseudobarbus leonhardi* Bielz, 1853
Pelasgus stymphalicus	Stymphalia minnow	(Valenciennes)	1844	*Leuciscus stymphalicus* Valenciennes, 1844
Squalius peloponensis	Peloponnese chub	(Valenciennes)	1844	*Leuciscus peloponensis* Valenciennes, 1844
Alburnus scoranza	Skadar bleak	Bonaparte	1845	NA
Squalius cii	Marmara chub	(Richardson)	1856	*Leuciscus cii* Richardson, 1857
Pachychilon pictum	Albanian roach	(Heckel & Kner)	1858	*Squalius pictus* Heckel & Kner, 1858
Squalius fellowesii	Aegean chub	(Günther)	1868	*Leuciscus fellowesii* Günther, 1868
Luciobarbus albanicus	Albanian barbel	(Steindachner)	1870	*Barbus albanicus* Steindachner, 1870
Valencia letourneuxi	Corfu valencia	(Sauvage)	1880	*Fundulus letourneuxi* Sauvage 1880
Silurus aristotelis	Aristotle's catfish	Garman	1890	*Glanis aristotelis* Agassiz, 1857
Pachychilon macedonicum	Macedonian roach	(Steindachner)	1892	*Leuciscus (Leucos) macedonicus* Steindachner, 1892
Petroleuciscus smyrnaeus	Smyrna chub	(Boulenger)	1896	*Leuciscus smyrnaeus* Boulenger, 1894
Luciobarbus graecus	Greek barbel	(Steindachner)	1896	*Barbus graecus* Steindachner, 1896 *Luciobarbus kottelati* Turan, Ekmekçi, Ilhan & Engin, 2008 *Luciobarbus lydianus* Boulenger, 1896 *Messinobarbus carottae* Bianco, 1998
Pelasgus epiroticus	Epirus minnow	(Steindachner)	1896	*Paraphoxinus epiroticus* Steindachner, 1896
Knipowitschia thessala	Thessaly goby	(Vinciguerra)	1921	*Gobius thessalus* Vinciguerra, 1921
Pelasgus marathonicus	Marathon minnow	(Vinciguerra)	1921	*Leucaspius marathonicus* Vinciguerra, 1921
Alosa macedonica	Macedonian shad	(Vinciguerra)	1921	*Clupea macedonica* Vinciguerra, 1921
Sabanejewia balcanica	Balkan Golden loach	(Karaman)	1922	*Cobitis balcanica* Karaman, 1922 *Cobitis montana* Vladykov, 1925
Alburnoides prespensis	Prespa spirlin	(Karaman)	1924	*Alburnoides bipunctatus* var. *prespensis* Karaman, 1924
Alburnus belvica	Prespa bleak	Karaman	1924	*Chalcalburnus belvica-Alburnus alburnus* ssp. *belvica* Karaman, 1924
Barbus prespensis	Prespa barbel	Karaman	1924	*Barbus graecus* var. *prespensis* Karaman, 1924
Chondrostoma prespense	Prespa nase	Karaman	1924	*Chondrostoma nasus* ssp. *prespensis* Karaman, 1924

Continued

Table 1 continued

Species	Common name	Authority	Year	Synonyms/Previous Nomenclature
Cobitis meridionalis	Prespa spined loach	Karaman	1924	*Cobitis taenia* var. *meridionalis* Karaman, 1924
Pelasgus prespensis	Prespa minnow	(Karaman)	1924	*Paraphoxinus epiroticus* fma. *prespensis* Karaman, 1924
Rhodeus meridionalis	Vardar bitterling	Karaman	1924	*Rhodeus amarus* var. *meridionalis* Karaman, 1924
Rutilus prespensis	Dalmatian roach	(Karaman)	1924	*Leucos aula* var. *ohridana* Karaman, 1924 *Leucos aula* var. *prespensis* Karaman, 1924 *Rutilus basak* (Heckel, 1843) *Rutilus prespensis* ssp. *vukovici* Marić, 1988 *Rutilus prespensis* (Karaman, 1924) *Rutilus rubella* ssp. *karamani* Fowler, 1977
Salmo macedonicus	Macedonian trout	(Karaman)	1924	*Trutta fario* ssp. *macedonica* Karaman, 1924
Gobio bulgaricus	Aegean gudgeon	Drensky	1926	*Gobio gobio* ssp. *bulgarica* Drensky, 1926
Ladigesocypris ghigii	Rhodes minnow	(Gianferrari)	1927	*Leucaspius ghigii* Gianferrari, 1927 *Leucaspius prosperi* Gianferrari, 1927
Oxynoemacheilus bureschi	Struma stone loach	(Drensky)	1928	*Nemachilus bureschi* Drensky, 1928 *Orthrias brandti* ssp. *macedonicus* Sorić, 1999
Alburnus macedonicus	Doiran bleak	Karaman	1928	*Alburnus alburnus ssp. macedonicus* Karaman, 1928
Barbus macedonicus	Macedonian barbel	Karaman	1928	*Barbus barbus* ssp. *macedonicus* Karaman, 1928 *Barbus barbus* ssp. *thessalus* Stephanidis, 1971 *Barbus thessalus* Stephanidis, 1971
Chondrostoma vardarense	Vardar nase	Karaman	1928	*Chondrostoma nasus* ssp. *vardarensis* Karaman, 1928
Cobitis ohridana	Ohrid spined loach	Karaman	1928	*Cobitis taenia* ssp. *ohridana* Karaman, 1928
Cobitis vardarensis	Vardar spined loach	Karaman	1928	*Cobitis taenia* ssp. *vardarensis* Karaman, 1928
Squalius vardarensis	Vardar chub	Karaman	1928	*Squalius cephalus* ssp. *vardarensis* Karaman, 1928
Economidichthys pygmaeus	Western Greece goby	(Holly)	1929	*Gobius martensii* var. *previscus* Stephanidis, 1939 *Gobius pygmaeus* Holly, 1929
Gobio skadarensis	Skadar gudgeon	Karaman	1937	*Gobio gobio lepidolaemus* ssp. *skadarensis* Karaman, 1937
Scardinius graecus	Greek rudd	Stephanidis	1937	NA
Salmo farioides	West Balkan trout	Karaman	1938	NA
Salmo pelagonicus	Pelagonian trout	Karaman	1938	NA
Salmo peristericus	Prespa trout	Karaman	1938	*Salmo macedonicus* ssp. *peristericus* Karaman, 1938

Continued

Table 1 continued

Species	Common name	Authority	Year	Synonyms/Previous Nomenclature
Telestes beoticus	Boeotian riffle dace	(Stephanidis)	1939	*Rutilus beoticus* Stephanidis, 1939
Pelasgus thesproticus	Thesprotian minnow	(Stephanidis)	1939	*Leucaspius stymphalicus* var. *thesproticus* Stephanidis, 1939
Squalius pamvoticus	Pamvotida chub	(Stephanidis)	1939	*Leuciscus cabeda* var. *pamvoticus* Stephanidis, 1939
Telestes pleurobipunctatus	Epiros riffle dace	(Stephanidis)	1939	*Rutilus pleurobipunctatus* Stephanidis, 1939
Alburnoides strymonicus	Struma spirlin	(Chichkoff)	1940	*Alburnoides bipunctatus strymonicus* Chichkoff, 1940
Tropidophoxinellus spartiaticus	Spartian minnowroach	(Schmidt-Ries)	1943	*Rutilus spartiaticus* Schmidt-Ries, 1943
Alburnus thessalicus	Thessaly bleak	Stephanidis	1950	*Alburnus alburnus thessalicus* Stephanidis, 1950
Barbus euboicus	Evia barbel	Stephanidis	1950	NA
Barbus sperchiensis	Sperchios barbel	Stephanidis	1950	*Barbus cyclolepis cholorematicus* Stephanidis, 1971 *Barbus euboicus* ssp. *sperchiensis* Stephanidis, 1950
Alburnoides thessalicus	Thessalian spirlin	Stephanidis	1950	*Alburnoides bipunctatus* var. *thessalicus* Stephanidis, 1950
Barbus strumicae	Struma barbel	Karaman	1955	*Barbus cyclolepis* ssp. *strumicae* Karaman, 1955
Cobitis strumicae	Struma spined loach	Karaman	1955	*Cobitis (Bicanestrinia) rhodopensis* Vassilev, 1998 *Cobitis peschevi* Sivkov & Dobrovolov, 1984 *Cobitis taenia* ssp. *strumicae* Karaman, 1955
Barbus pergamonensis	Anatolian barbel	Karaman	1971	*Barbus plebejus* ssp. *pergamonensis* Karaman, 1971 *Luciobarbus pergamonensis* (Karaman, 1971)
Squalius keadicus	Evrotas chub	(Stephanidis)	1971	*Leuciscus (Telestes) souffia* ssp. *keadicus* Stephanidis, 1971
Squalius moreoticus	Stymphalia chub	(Stephanidis)	1971	*Leuciscus (Squalius) cephalus* ssp. *moreoticus* Stephanidis, 1971
Tropidophoxinellus hellenicus	Hellenic minnowroach	(Stephanidis)	1971	*Rutilus alburnoides* ssp. *hellenicus* Stephanidis, 1971
Pungitius hellenicus	Greek stickleback	Stephanidis	1971	NA
Romanogobio elimeius	Greek stone gudgeon	(Kattoulas, Stephanidis & Economidis)	1973	*Gobio albipinnatus* ssp. *elimeius* Kattoulas, Stephanidis & Economidis, 1973 *Gobio persus* ssp. *stankoi* Karaman, 1974
Gobio feraeensis	Thessaly gudgeon	Stephanidis	1973	*Gobio gobio* ssp. *feraeensis* Stephanidis, 1973
Cobitis trichonica	Trichonida spined loach	Stephanidis	1974	NA
Squalius prespensis	Prespa chub	(Fowler)	1977	*Leuciscus cephalus* ssp. *prespensis* Fowler, 1977
Caspiomyzon hellenicus	Greek brook lamprey	(Vladykov, Renaud, Kott & Economidis 1982)	1982	*Eudontomyzon hellenicus* Vladykov, Renaud, Kott & Economidis, 1982
Alosa vistonica	Thracian shad	Economidis & Sinis	1986	*Alosa caspia* ssp. *vistonica* Economidis & Sinis, 1986

Continued

Table 1 continued

Species	Common name	Authority	Year	Synonyms/Previous Nomenclature
Knipowitschia milleri	Acheron spring goby	(Ahnelt & Bianco)	1990	*Orsinigobius milleri* Ahnelt & Bianco, 1990
Economidichthys trichonis	Trichonida dwarf goby	Economidis & Miller	1990	NA
Knipowitschia goerneri	Corfu dwarf goby	Ahnelt	1991	NA
Rutilus ylikiensis	Yliki roach	Economidis	1991	NA
Scardinius acarnanicus	Trichonis rudd	Economidis	1991	NA
Cobitis stephanidisi	Velestino spined loach	Economidis & Nalbant	1996	NA
Cobitis arachthosensis	Arachthos spined loach	Economidis & Nalbant	1996	NA
Cobitis hellenica	Louros spined loach	Economidis & Nalbant	1996	NA
Cobitis punctilineata	Angitis spined loach	Economidis & Nalbant	1996	NA
Barbus balcanicus	Large-spot barbel	Kotlík, Tsigenopoulos, Ráb & Berrebi	2002	NA
Pelasgus laconicus	Evrotas minnow	(Kottelat & Barbieri)	2004	*Pseudophoxinus laconicus* Kottelat & Barbieri, 2004
Salariopsis economidisi	Trichonis blenny	Kottelat	2004	*Salaria economidisi* Kottelat, 2004
Oxynoemacheilus pindus	Pindus stone loach	(Economidis)	2005	*Barbatula pindus* Economidis, 2005
Rutilus panosi	Achelous roach	Bogutskaya & Iliadou	2006	*Leucos panosi* (Bogutskaya & Iliadou, 2006)
Squalius orpheus	Thracian chub	Kottelat & Economidis	2006	NA
Oxynoemacheilus theophilii	Aeolian stone loach	Stoumboudi, Kottelat & Barbieri	2006	*Barbatula bergamensis* Erk'akan, Nalbant & Özeren, 2007
Alburnus vistonicus	Vistonida shemaya	Freyhof & Kottelat	2007	NA *(Chalcalburnus chalcoides macedonicus)*
Alburnus volviticus	Volvi bleak	Freyhof & Kottelat	2007	*Chalcalburnus chalcoides* ssp. *macedonicus* Stephanidis, 1971
Phoxinus strymonicus	Aegean minnow	Kottelat	2007	NA
Aphanius almiriensis	Almiri killifish	Kottelat, Barbieri & Stoumboudi	2007	NA
Caspiomyzon graecus	Epirus brook lamprey	Renaud & Economidis	2010	*Eudontomyzon graecus* Renaud & Economidis, 2010
Salmo lourosensis	Louros trout	Delling	2011	NA
Valencia robertae	Peloponnese valencia	Freyhof, Kärst, & Geiger	2014	NA
Alburnoides economoui	Spercheios spirlin	Barbieri, Vukić, Šanda, Kapakos & Zogaris	2017	NA (formerly referred as *Alburnoides bipunctatus*)

Table 2. Researchers who have contributed to the taxonomy and study of the endemic freshwater fish species occurring in Greece. The table lists each researcher's full name, nationality/ethnicity, institutional affiliation, and primary/secondary scientific specialties. It also indicates whether the individual is known or presumed to have collected material in Greece or the surrounding region, and records the number of species for which the researcher is cited as describing author or co-author in the taxonomic authority.

Full Name (Name - Family Name)	Nationality/Ethnicity	Institution/Affiliation	Specialty 1	Specialty 2	Collected samples in the region	Number of species (involved in authority)
Harald Ahnelt	Austrian	Natural History Museum of Vienna	Ichthyology		Not	2
Roberta Barbieri	Italian	Hellenic Centre for Marine Research	Ichthyology	Systematics	Yes	4
Patrick Berrebi	French	Université Montpellier I	Biology	Genetics	Yes	1
Pier Giorgio Bianco	Italian	University of Naples Federico II	Zoology	Ichthyology	Yes	1
Nina Bogutskaya	Russian	Natural History Museum of Vienna	Ichthyology	Systematics	Not	1
Charles Lucien Bonaparte	French	National Museum of Natural History of Paris	Biology	Ornithology/ Ichthyology	Probably not	1
George Albert Boulenger	Belgian-British	British Museum	Zoology	Botany/Ichthyology	Probably not	1
Georges D Chichkoff	Bulgarian	University of Sofia	Zoology	Ichthyology	Not	1
Bo Delling	Swedish	Swedish Museum of Natural History	Zoology	Systematics	Yes	1
Pencho Drensky	Bulgarian	Bulgarian Academy of Sciences	Zoology	Entomology/ Ichthyology	Yes	2
Panos S Economidis	Greek	Aristotle University of Thessaloniki	Ichthyology	Systematics	Yes	13
Henry Weed Fowler	American	Academy of Natural Sciences of Philadelphia	Zoology	Ichthyology	Not	1
Jörg Arthur Freyhof	German	Leibniz Institute of Freshwater Ecology and Inland Fisheries	Ichthyology	Systematics	Yes	3
Samuel Walton Garman	American	Harvard's Museum of Comparative Zoology	Ichthyology	Herpetology	Probably not	1
Matthias F Geiger	German	Leibniz Institute for the Analysis of Biodiversity Change	Evolutionary Biology	Systematics	Yes	1

Continued

Table 2 continued

Full Name (Name - Family Name)	Nationality/Ethnicity	Institution/Affiliation	Specialty 1	Specialty 2	Collected samples in the region	Number of species (involved in authority)
Luisa Gianferrari	Italian	Museum of Natural History of Milan	Biology	Genetics	Probably not	1
Albert Charles Lewis Gotthilf Günther	German-British	British Museum	Zoology	Ichthyology/ Herpetology	Probably not	1
Johann Jakob Heckel	Austrian	Natural History Museum of Vienna	Zoology	Ichthyology	Not	3
Maximilian Holly	Austrian	Natural History Museum of Vienna	Ichthyology		Probably not	1
Konstantina Iliadou	Greek	University of Patras	Biology	Ichthyology	Yes	1
Yannis Kapakos	Greek	Hellenic Centre for Marine Research	Biology	Ichthyology	Yes	1
Mladen Stanko Karaman	Serbian	University of Pristina/ University of Kragujevac	Entomology	Ichthyology	Not	1
Stanko Luka Karaman	Bosnian Serbian	Macedonian Museum of Natural History	Biology	Ichthyology/ Carcinology	Probably not	22
Heiko Kärst	German	German Killifish Assoziation	Zoology	Ecology	Yes	1
Marios E Kattoulas	Greek	Aristotle University of Thessaloniki	Biology	Zoology	Yes	1
Rudolf Ignaz Kner	Austrian	Natural History Museum of Vienna	Zoology/Ichthyology	Geology/Paleontology	Not	1
Petr Kotlík	Czech	Academy of Sciences of the Czech Republic	Zoology	Genetics	Not	1
Maurice Kottelat	Swiss	Freelance taxonomist	Ichthyology	Systematics	Yes	8
Edward Kott	Canadian	Wilfrid Laurier University	Ichthyology		Not	1
Peter James Miller	British	University of Bristol	Ichthyology	Systematics	Probably not	1
Theodor T Nalbant	Romanian	Romanian Academy of Science	Ichthyology		Yes	4
Petr Ráb	Czech	Academy of Sciences of the Czech Republic	Molecular biology	Systematics	Not	1

Continued

Table 2 continued

Full Name (Name - Family Name)	Nationality/Ethnicity	Institution/Affiliation	Specialty 1	Specialty 2	Collected samples in the region	Number of species (involved in authority)
Claude B Renaud	Canadian	Canadian Museum of Nature	Zoology	Ichthyology	Not	2
Sir John Richardson	British	Naturalist/explorer	Medicine and Surgery	Ichthyology	Probably not	1
Henri Émile Sauvage	French	Museum of Natural History of Boulogne-sur-Mer	Paleontology	Ichthyology	Probably not	1
Radek Šanda	Czech	National Museum	Zoology	Systematics	Yes	1
Hans Schmidt-Ries	German	Koenigsberg University	Hydrobiology	Ichthyology	Probably yes	1
Apostolos I Sinis	Greek	Aristotle University of Thessaloniki	Biology	Ichthyology	Yes	1
Franz Steindachner	Austrian	Natural History Museum of Vienna	Zoology	Ichthyology/ Herpetology	Yes	4
Alexandros I Stephanidis	Greek	University of Athens/ independent researcher	Ichthyology	Systematics	Yes	16
Maria Stoumboudi	Greek	Hellenic Centre for Marine Research	Ichthyology	Biology	Yes	2
Costas Tsigenopoulos	Greek	Hellenic Centre for Marine Research	Evolutionary Biology	Ecology	Yes	1
Achille Valenciennes	French	National Museum of Natural History of Paris	Zoology	Parasitology	Probably not	3
Vadim Dimitrievitch Vladykov	Canadian	University of Ottawa	Zoology	Ichthyology	Yes	1
Diego Vinciguerra	Italian	Aquarium of Rome	Medicine and Surgery	Botany/Zoology/ Ichthyology	Yes	3
Jasna Vukić	Czech	Charles University	Evolutionary biology	Ichthyology/ Systematics	Probably yes	1
Stamatis Zogaris	Greek	Hellenic Centre for Marine Research	Ichthyology	Ecology/Biogeography	Yes	1

Academies of science contributed five authors (11%) and the rest were related to municipal aquariums, aquarium fish associations, independent researchers/freelancers or hybrid academic–independent roles (Fig. 3b). Overall, 62% of authors operated without being formally linked to university or academy settings.

Nearly half of the authors (23; 48.9%) conducted fieldwork and collected specimens in the region, with an additional 4.2% possibly involved in sampling. For the rest, either there is positive evidence that they did not participate in fieldwork (11; 23.4%) or information was unavailable (11; 23.4%). Their scientific background, based on their expertise, ranged from zoology/zoology-ichthyology (15/1), ichthyology (14), general biology (8), evolutionary biology (3), medicine and surgery (2) and hydrobiology, molecular biology, paleontology and entomology, each represented by a single author. Overall, 63.8% of the authors were/are zoologists/ichthyologists.

The network comprising all authors and freshwater fish species endemic to Greece visualizes the historical and contemporary links between authors' taxonomic work and ichthyofaunal diversity (Fig. 4). The modularity algorithm generated a high modularity value (0.8), indicating a strongly partitioned network in which most nodes are more densely connected within groups than between them. This pattern reflects well-defined clusters corresponding to distinct research lineages, geographical groups or periods of collaboration. Of the 25 modular-

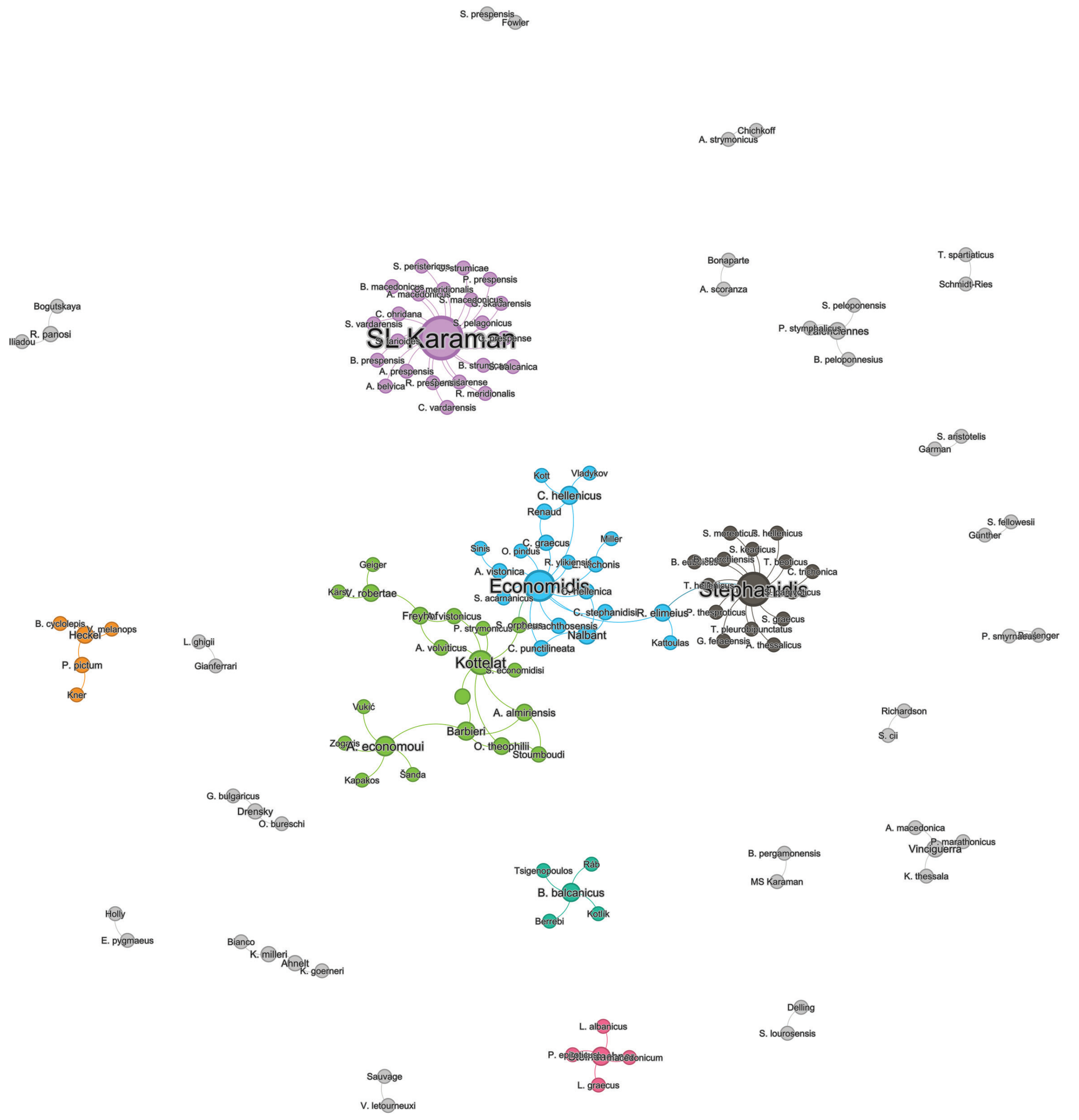

Fig. 4: Network of 47 authors and 91 endemic freshwater fish species of Greece. Distinct cluster colors display the 25 different groups derived from modularity test (modularity = 0.8). Grey color denotes the peripheral modularity groups with less than 3% of nodes.

ity groups detected, four major groups, each centered on a small core of highly connected authors, accounted for more than half of all nodes in the network. Degree centrality analyses confirmed that these key authors, including Karaman, Stephanidis, Economidis, and Kottelat occupied the most central positions within the network, representing the dominant structural units and the primary axes of taxonomic collaboration. Less central contributors (e.g., Heckel, Steindachner, Vinciguerra and Valenciennes) formed smaller peripheral clusters composed of few nodes and limited cross-cluster connections. Certain species (e.g., *Romanogobio elimeius, Squalius orpheus, Aphanius almiriensis*, and *Caspiomyzon graecus*) functioned as connective nodes among otherwise separate groups (Fig. 4). These species linked multiple prominent author-centered groups, and collectively formed the largest central cluster of the network.

Species descriptions were unevenly distributed across time with 16 species described during the 19th century, 59 during the 20th century, and 16 during the 21st century (Fig. 5). Up to 1937, all species were described by non-Greek scientists; Greek scientists became increasingly represented from the 1930s onward. The 1920s had the highest number of descriptions, followed by the 2000s. The 1930s, 1970s, and 1990s each contributed nine descriptions (Fig. 5). Across the periods shown in Fig. 5 (panels A-G), description activity, and genetic characterization works from the 1980s, varied markedly among decades.

Name ascribing issues were most commonly etymologically related to type localities (69 species; 75.8%), followed by honorifics for living or deceased scientists (14; 15.4%) and morphological characteristics typical of a taxon (8; 8.8%). Nomenclatural stability was limited as the original names changed for approximately three-quarters of species, while one-quarter remained unchanged. Changes include not only genus transfers, but also synonyms.

The majority of the species descriptions (69.2%) appeared in serial publications as journals (38), bulletins (14), annals (6), proceedings (3), an annal/magazine (1) and a magazine (1). Standalone publications (27.5%) included books (15), article collections (4), theses (3) and memoirs (3). The rest (3; 3.3%) were catalogues (2) or electronic catalogue (1). Standalone formats dominated in the 19th and early 20th centuries; serials became overwhelmingly prevalent from the late 20th century onward. Publication language also shifted markedly. German language predominated early (34 works; 37.3%), reflecting institutional affiliations and Austro-German influence in the Balkans. English language rose to prominence over time (31; 34.1%), followed by Greek (11; 12.1%), French (9; 9.9%), Italian (5; 5.5%), and Bulgarian (1; 1.1%).

Discussion

This review traced the evolution of freshwater-fish taxonomic research in Greece from the mid-19th century to the first quarter of the 21st century and highlights how successive waves of naturalists, zoologists, ichthyologists, taxonomists and geneticists jointly constructed today's taxonomic understanding of Greece's endemic freshwater fishes. Across regions and taxa, the tempo and direction of taxonomic discovery commonly covary with sociopolitical history, institutional capacity and

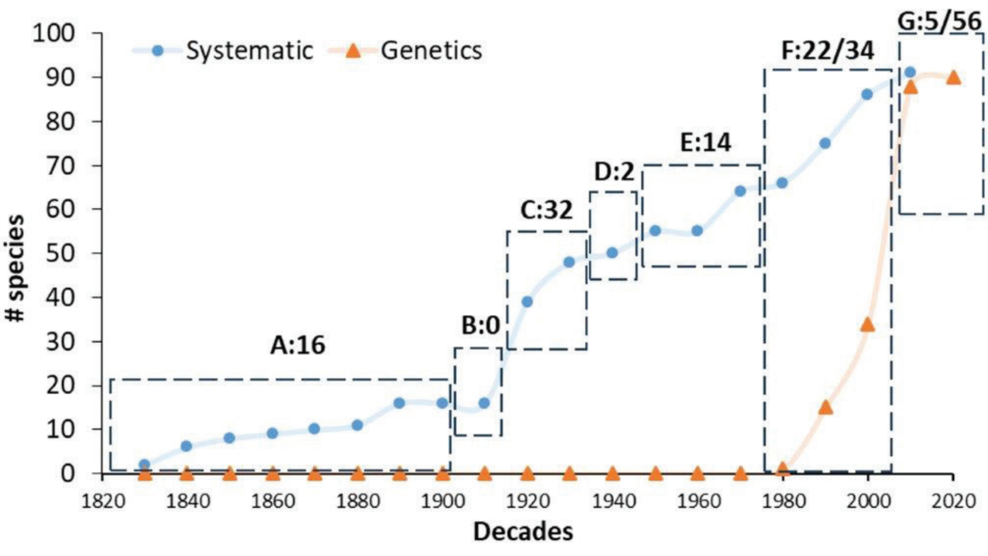

Fig. 5: Decadal time series of species descriptions using systematic and genetic tools; panels A-G delineate periods defined by major socio-historical events and methodological shifts: A. Naturalism, expeditions, museum collections; B. Balkan Wars, First World War; C. Greco-Turkish War, conventional ichthyology, museum collections; D. Second World War, Greek civil war; E. Domestic political turmoil, post-war reconstruction, last efforts by old pioneers; F. Collaboration with scientists abroad, establishment of Ichthyology Laboratory at the Aristotle University of Thessaloniki, Handbook by Kottelat & Freyhof (2007), Phylogenetic Species Concept; G. Intense international collaboration, advances in genetics including eDNA tools. Numbers above panels indicate the total number of species described using systematic tools for each period, including the number of species genetically characterized after the slashes.

methodological innovation, particularly where access to collections, mobility, and professional networks determines who can collect and who can publish (Fontaine *et al*., 2012; Joppa *et al*., 2011; Costello *et al*., 2013; Engel *et al*., 2021). Our dataset also indicates a historically gendered structure to participation. Women faced formal and informal barriers throughout much of the 20th century, including exclusion from networks and constrained access to fieldwork opportunities contributing to gendered imbalances in authorship and honorific naming (Maroske & May, 2018; Toogood *et al*., 2020). However, the increased participation of women after 2000 (10.6% of authors) reflects the expansion of higher education, evolving professional norms and policies promoting equal access (European Commission, 2025).

A key historical result is that all endemic freshwater species described up to 1937 were authored by non-Greek scientists. Similar early dominance by foreign researchers has been reported in other Greek taxa and in freshwater fishes of other regions (Pafilis, 2010; Skelton, 1996; Kaya *et al.*, 2025). This pattern mainly reflects the long research tradition in biology and ichthyology in Western and Central Europe and the United States during the 19th- early 20th centuries, together with the concentration of major collections and publishing centers. It also aligns with political geography, since large parts of present-day Greece lay outside the Greek state until 1947, and border formation constrained centrally organized faunistic research. However, most non-Greek researchers did not pursue comprehensive studies of Greek freshwater fish taxonomy or biogeography. With exceptions such as Karaman (Karaman, 1922, 1924, 1928) many practiced scientific "cherry-picking" (see Fig. 4), securing small numbers of specimens, from a few species, and limited their efforts to narrow geographic coverage. Even so, their efforts provided foundational descriptions and baselines that paved the way for successive advances in taxonomic work (e.g., Stephanidis, 1939), assisted in many cases by the textbooks produced by the early European taxonomists.

Roughly one-third of scientists in our dataset originated from Central Europe (e.g., Germany, Austria, Czech Republic) consistent with the geographic proximity to the Balkans and the long history of expeditions led by the two strongest empires (i.e. the German-Prussian and Austro-Hungarian) until the end of World War I. Domestic efforts expanded after mid-century, with Greek institutions increasingly leading the taxonomic work from the 1970s onward. However, participation and recognition still depended on access to collections, stable funding and mobility. Comparative studies across zoology show persistent geographic imbalances in authorship, affiliation, and even in who is honored in eponyms. Most first authors and honorees still come from the Global North even when species are from the Global South (DuBay *et al*., 2020; see also Maroske & May, 2018; Toogood *et al*., 2020). The Greek case fits this broader pattern, as early non-Greek dominance gave way to progressive nationalization of effort, but participation and recognition continued to be structured by access to museums, networks and funding. This is still the case at the global scale given the unequal distribution of taxonomists across regions and the insufficient taxonomic expertise in less scientifically advanced countries (Closs *et al*., 2016).

The historical pattern of discovery in Greece's freshwater ichthyofauna was not a smooth accumulation but a series of pulses (for wider ichthyological records, see also Nellen & Dulčić, 2008), whose timing aligns with shifting access, institutional capacity and major socio-historical disruptions. Descriptions were sparse and irregular in the 19th century, followed by a pronounced interwar peak (1920s-1930s), major wartime contraction (1940s), and renewed momentum from the late 20th century onwards. This pattern aligns with a broader transition from expeditionary natural history toward laboratory-anchored systematics and, later, widespread integration of molecular evidence (Kottelat & Freyhof, 2007; Kaya *et al*., 2025). In Greece, the 1910s coincide with a complete pause during the Balkan Wars (1912-1913) and World War I (1914-1918). A steep rise followed in the interwar period and was followed by a decline during World War II (1939-1945; war in Greece began in 1940) and the Greek Civil War (1946-1949). Post-war decades show uneven activity during reconstruction and the political turbulence of the 1960s to mid-1970s, while also capturing late contributions by interwar pioneers (notably Stephanidis and Karaman). From the late 1970s onward, activity increased and remained sustained into the 21st century, alongside increased collaboration, the establishment of domestic laboratories (notably at the Aristotle University of Thessaloniki and the Hellenic Centre for Marine Research in Athens) (Tsikliras, 2025).

Methodological and technological changes help explain both the tempo of discovery and the later nomenclatural instability. Technological innovations (e.g., lithography) and travel affected the evolution of ichthyology as early as the late 18th century (Kreklau, 2018). Field access in Greece through the 19th and early 20th centuries was constrained by underdeveloped infrastructure and wartime damage (Theodosis, 2016), which limited mobility. In addition, field sampling relied on low-precision printed maps, while field equipment was basic, often homemade, and difficult to acquire. Specimens were preserved in glass containers with formaldehyde, which were too heavy and fragile to travel, while live fish handling was minimal, with little control over dissolved oxygen, temperature, or water quality *in situ* or *ex situ*. Moreover, field photography was essentially absent; *ex-situ* imaging was rare, low-quality, and slow to process. Finally, access to bibliography even until the late 20th century (i.e. before the internet era) depended on libraries, postal reprints, and personal contacts, often hampered by language barriers.

By the mid-20th and early 21st centuries, this landscape changed drastically. Paved roads, regional flight links, and mobile and satellite mapping tools opened remote basins and enabled precise georeferencing and repeatable sampling, while equipment became standardized. The first documented freshwater electrofishing in Greece appears in the early 1970s (Economidis *et al*., 1981; I. Paschos pers. comm.), while it later became the standardized method under harmonized European guidance (Economou *et al*., 2016). Preservation shifted from formalin in glass to high-purity ethanol in plastic vials, facilitating genetics and robust re-examination. Live fish could be maintained in field aquaria or transported to laboratories with controlled recirculating systems (Kalogianni *et al*., 2023) and fin clipping became the standard non-destructive method required for genetic work (Tsoupas *et al*., 2022). Imaging and microscopy were transformed by digital cameras and high-resolution optics.

Meanwhile, a modern European trend in freshwater ichthyology was emerging from the late 20th century onward, characterized by the extensive integration of morphological approaches, while molecular tools (electrophoresis in the 1980s; PCR, mitochondrial (mtDNA) and nuclear markers from the mid-1990s; DNA barcoding and eDNA in the 2000s-2020s) reshaped diagnosis and identification. This modern trend marked a shift from descriptive taxonomy toward a molecularly informed and conservation-oriented discipline, reinforcing Greece's position within the broader European trend of freshwater systematics. Maurice Kottelat played a pivotal role in standardizing taxonomic concepts across Europe and redefining several Balkan and Greek endemics through comparative revisions and coordinated checklists. His work provided the taxonomic framework later consolidated by Greek researchers such as Economou *et al*. (2007), Koutsikos *et al*. (2012), Barbieri *et al*. (2015) and Vardakas *et al*. (2022), who incorporated genetic and biogeographic data into regional syntheses. In parallel, internet-based bibliographic access, specialized databases, and rapid communications accelerated collaboration and scientific publication. As basin-scale surveys became standardized and georeferenced, broader regional overviews expanded, consistent with the high rate of nomenclatural change in our dataset (approximately three-quarters of species) as characters were reinterpreted and taxa were re-circumscribed under new evidence.

Across 91 valid endemic species described by 47 scientists, output averages 1.9 species per scientist, but contribution was highly skewed. Network analysis confirmed that the four hyper-prolific scientists (i.e., Karaman, Stephanidis, Economidis and Kottelat) accounted together for more than half of all nodes (57%), occupying the most central positions and connected multiple taxa across distinct periods. Their positions bridged generations of researchers, while single yet distinctive figures formed peripheral micro-groups (<3% of nodes). This imbalance is not unique to Greece and mirrors regularities in scientific output where a small core of specialists account for most assigned names, while a long tail of occasional contributors adds the rest (Joppa *et al*., 2011; Costello *et al*., 2013; Engel *et al*., 2021). Comparable concentrations appear in European freshwater fishes, where a handful of museum taxonomists (e.g. Cuvier, Valenciennes, Steindachner, Günther) produced many early descriptions, a pattern that persisted into the late 20th century with a small group of systematists leading many revisions and new species proposals (Kottelat & Freyhof, 2007). Global overviews likewise report that a minority of highly active authors generate much of the annual "naming capacity", especially in vertebrates, where access to large museum series and collaborative networks amplifies output (Fontaine *et al*., 2012; Costello *et al*., 2013).

Conceptual shifts help explain both the uneven pace of descriptions and limited stability of original names. Through the late 20th century, morphology-based diagnoses predominated, whereas after 2007, wider adoption of the Phylogenetic Species Concept (PSC; see Economou *et al*., (2007) for explanations) together with routine molecular evidence exposed cryptic diversity, prompted numerous genus transfers and synonymies, and tightened distributional limits. In Greece this played out evidently as the national freshwater fish species checklist expanded by about 53% (i.e., 62 species have undergone taxonomic changes; Vavalidis *et al*., 2019) between the 1991 list (Economidis, 1991) and the 2007 basin-based update (Economou *et al*., 2007). This rise attributed chiefly to taxonomic re-evaluation and a shift in species concepts rather than to wholesale additions of truly novel taxa. These conceptual shifts reshape ichthyogeographical boundaries and the composition of regional units used in conservation planning. When Greek river basins are clustered under an "older" taxonomy versus a post-2007 taxonomy aligned with the phylogenetic species concept, the resulting regions differ significantly. This shift demonstrates how nomenclatural updates propagate into biogeographical inference and, by extension, into prioritization schemes (Vavalidis *et al*., 2019).

At the same time, the growing integration of genetics offers a route to greater long-term stability provided names are anchored to vouchered material and open reference libraries. A recent barcoding survey for Greece (COI, 406 specimens across 39 species) largely corroborated prevailing classifications while flagging a subset of lineages that merit revision (Tsoupas *et al*., 2022). Regionally, the backbone provided by Kottelat & Freyhof (2007) and the annotated checklist of Barbieri *et al*. (2015) continues to stabilize usage across borders, especially when paired with curated molecular datasets. Future taxonomic practice will also need to address emerging pressures and complications, including non-native species introductions (Koutsikos *et al*., 2019; Vardakas *et al*., 2022), aquarium-trade taxa with weak nomenclatural anchoring (Papavlasopoulou *et al*., 2014) and an increasing documentation of hybrids (natural and artificial) across genera and higher ranks (Kottelat, 1997; Collares-Pereira *et al*., 2013).

Nearly half of Greece's endemic freshwater fishes in our study are currently listed as threatened, with one species already extinct (the Thracian Shad, *Alosa vistonica*; Ford, 2024). Risk is concentrated in range-restricted endemics confined to springs, headwaters, or short river reaches. In such aquatic systems even slight disturbances (water abstraction, episodic pollution, channel and bank alterations), can cause rapid declines (Vardakas *et al*., 2017; Kalogianni *et al*., 2022). Early faunistic works therefore have ongoing value as baseline snapshots of assemblages and habitats under comparatively less altered conditions, complementing modern monitoring in a Mediterranean biodiversity hotspot.

Our etymology analysis indicates that toponymic epithets dominate over honorifics and morphology-based names. These locality-based epithets reflect a conventional practice in which early names recorded collection localities or presumed ranges (e.g., *Gobius thessalus* now *Knipowitschia thessala* from the region of Thessaly; *Rutilus beoticus* now *Telestes beoticus* from the region of Boeotia). Valenciennes followed this norm as he described *Leuciscus peloponensis* (now *Squalius peloponensis*) from material brought by the naturalists of the French Scientific Expedition in the Morea in 1829, with type locality "Morea" (= Peloponnese) (Cuvier & Valenciennes, 1844). Steindachner likewise favored locality-based epithets (e.g. *Paraphoxinus epiroticus* now *Pelasgus epiroticus*) including material from sites he visited such as the Lake Pamvotis in Epirus (Steindachner, 1896). However, some toponyms warrant re-examination. For instance, *Barbus albanicus* (now *Luciobarbus albanicus*) was initially linked to Lake Skadar although the type material originated from Lake Pamvotis and the species is restricted to Greece (Steindachner, 1896; Economidis & Herzig-Straschil, 2003). Another intriguing example is *Barbus graecus* (now *Luciobarbus graecus*) initially described by Steindachner (1896) from specimens erroneously thought to originate from River Acheloos (Western Greece). Most probably they were captured in Eastern Greece (in Lakes Yliki, Paralimni or in the River Sperchios) and sold afterwards in Western Greece (Economidis, 2012). However, its broader biogeography remains perplexing given its distribution in western Turkey (Zogaris *et al*., 2023) and introduction to Greece prior to description has been proposed (Freyhof *et al*., 2025). Vinciguerra and Karaman continued the prevalence of toponyms, but eponyms were present from the outset. For instance, Günther honored the British archaeologist Charles Fellowes (1799-1860) by giving his name to *Leuciscus fellowesii* (now *Squalius fellowesii*), who presented the holotype to the British Museum (Natural History). Overall, toponyms reflect practical convention, while eponyms mark specific debts and relationships.

Currently there is a large debate about eponyms. Some argue that personal honorifics should cease altogether (Guedes *et al*., 2023), while others propose a narrower reform that cancels only clearly harmful eponyms (e.g., those commemorating perpetrators of oppression) (Thiele, 2023). However, the International Commission on Zoological Nomenclature (ICZN) continues to emphasize nomenclatural stability and does not change established names on ethical grounds per se (Ceríaco *et al*., 2023); any alteration must proceed through Code-compliant mechanisms. Acknowledging that bulk revision processes should be avoided and any future nomenclatural changes should be based on universality, stability, neutrality, and transculturality (Jiménez-Mejías, 2024), for Greek ichthyology, we recommend thoroughly documenting etymologies and historical contexts (including problematic ones) and adopting inclusive practices for future names. This would be satisfied also by a fifth possible principle such as timelessness. Consistent with these considerations, and apart from *L. albanicus* (and pending further biogeographic data on *L. graecus*), we flag *Ladigesocypris ghigii* as a potentially problematic eponym. It honors Alessandro Ghigi, an Italian zoologist, with the epithet proposed by his student and colleague Luisa Gianferrari to honor Ghigi who collected the holotype. Ghigi joined the Fascist Party in 1924, publicly supported Italy's racial laws (1938) and advanced "race science" in 1939 (Ghigi, 1939). Gianferrari also supported similar ideas at the time. Moreover, it is related to the imperialistic era of Italy, when Dodecanese Archipelago was a territory of Italy (from 1912 to 1947). While we acknowledge the renaming risks (see Scharpf, 2023), we propose that future consideration be given to the epithet of *Ladigesocypris ghigii* not only on ethical grounds, but also on the need to preserve timelessness, which transcends arguments related to decontextualization of the moment in which the name was coined. We recommend a neutral, toponymic epithet derived from the species' type locality and distribution (Rhodes Island, Greece), ensuring clarity, cultural neutrality, and long-term stability.

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