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Vicariant patterns and dispersal in European freshwater fishes

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The vicariant relationships of numerous primary freshwater fishes of Europe are analysed; eight Euro-Siberian or Holarctic species have vicariant sisters in either North America or East Asia; eight European species have sisters in Siberia, East Asia or North America; there are three pairs of vicars, both members of which live in central Europe; four central European species have one or several vicariant sister(s) in various south European-western Asian areas, other pairs of vicars being exclusively south European-western Asian. Vicariism results, in freshwater animals, from range extension, by means of river captures, followed by interruption of the range. Several cases of sympatric occurrence of closely related species in Europe are mentioned, the sympatry resulting from recent range extension of one species in to the formerly exclusive range of its sister.

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Introduction

Modern Biogeography gives much attention to sister taxa having vicariant ranges; it is considered that the common range of the members of a pair or group of vicars is informative for the range of their immediate ancestor; proponents of the "Vicariance Biogeography" school consider also that sympatric occurrence of close relatives is the only fact which proves that dispersal has taken place.

The present paper analyses the vicariant relationships of the genuine freshwater fishes of Europe, the affinities of which are sufficiently well known, as well as the cases of sympatric occurrence of closely related species.

Vicariant relationships of the European freshwater fish species

Some fish species present in the inland waters of Europe have wide ranges also outside the continent.

Two of them are Euro-Siberian and eastern North American: *Esox lucius* and *Thymallus thymallus*. Their sisters, *E. reicherti* (Nelson 1972) and *Th. grubei* (Pivnica & Hensel 1975) live in northern East Asia* (Fig. 1).

* The term East Asia is used here in a strictly biogeographical sense, for the "East Asian subregion" of ichthyologists, the area between the water divide Amur River — rivers of the Arctic Ocean slope of Siberia and the divide between northern and central Vietnam on one hand and the Mekong River drainage on the other hand (Banarescu 1960, 1972); "northern East Asia" means the northern part of this subregion, while "northeastern Asia" may also include extreme eastern Siberia in the Arctic Ocean basin.

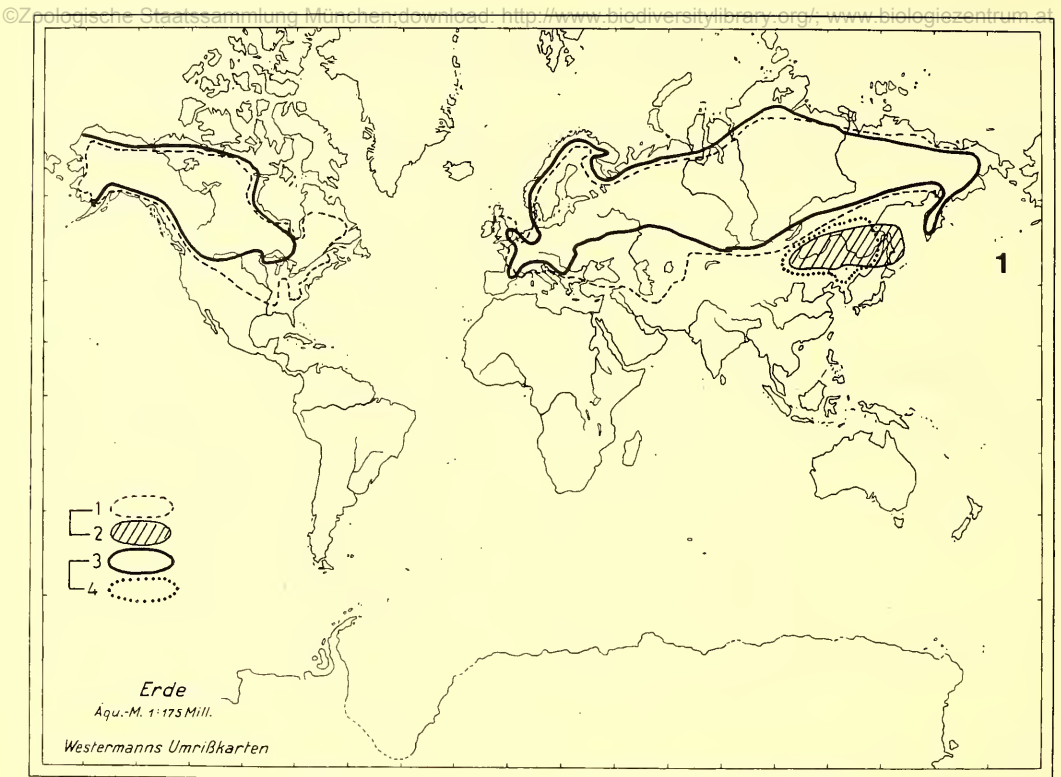


Fig. 1. Distribution of the Euro-Siberian and Eastern North American fish species and of their vicariant sisters. 1. *Esox lucius*; 2. *E. reicherti*; 3. *Thymallus thymallus*, 4. *Th. grubei*.

Five species are Palearctic, living in Europe, Siberia and East Asia (or only in Europe and East Asia); a single one of them, the cold-adapted *Phoxinus phoxinus*, has a vicariant sister: the eastern North American *Ph. neogaeus* (Howes 1985) (Fig. 2).

Eight species have Euro-Siberian ranges; one of them, *Tinca tinca*, has no sister in the recent fauna; the sisters of two others, *Rutilus rutilus* and *Gymnocephalus cernuus*, live sympatrically with these in a part of their ranges. Five Euro-Siberian species have vicariant sisters: that of *Perca fluviatilis* is the eastern North American *P. flavescens*, those of the salmonid *Hucho hucho* and of the cyprinids *Leuciscus idus* and *Carassius carassius* are East Asian (*L. walecki* and *C. auratus*, Fig. 3) while *Leuciscus leuciscus* has five vicariant sisters, each with a limited range: one in the western Balkan, the four others in various areas of western Asia (Berg 1932, 1948–1949; Banarescu 1964, Fig. 136).

Several European (or partially also western Asian) species, either widely distributed throughout the continent or confined to a part of it, have vicariant sisters in other continental areas: the sisters of *Cottus gobio* and *C. poecilopus* range in the Arctic Ocean basin of Siberia (*C. sibiricus* and *C. czanaga*: Berg 1948–1949; Holcik & Pirnicka 1968), that of *Umbra krameri* is the eastern North American pair *U. limi* – *U. pygmaea* (Nelson 1972), while those of the cobitid *Misgurnus fossilis* and of the silurids *Silurus glanis* and *Parasilurus aristotelis* are East Asian: a group of seven species of *Misgurnus*, which represent together the sister of *M. fossilis* and respectively *S. soldtivi* and *P. asotus* (Fig. 4).

Two other groups of vicars consist each in two European (or an European and an western Asian) and one East Asian species:



Fig. 2. Distribution of the Palearctic *Phoxinus phoxinus* and of its vicariant sisters. 1. *Phoxinus phoxinus*; 2. *Ph. neogaeus*.

Gobio uranoscopus (Danube, Vardar, rivers of Thessaly) – *G. ciscausicus* (northern slope of the Caucasus) – *G. rivuloides* (Hwangho River basin in China) (Banarescu & Nalbant 1973).

Cobitis elongata (Danube River basin) – *C. bilseli* (central Anatolia) – *C. macrostigma* (middle Yangtse basin) (Banarescu & Nalbant 1957) (Fig. 5).

Similar vicariant patterns are displayed by the percoid genus *Stizostedion*, with three European and two North American species (these may represent together the sister of the European group, or each of them may be the sister on an European species) and the cyprinid subgenus *Romanogobio*, with three European species (two of them largely sympatric) and four East Asian ones (three of these occurring sympatrically in the Hwangho basin) (Banarescu & Nalbant, 1973).

Vicariant patterns are displayed also by genera and groups of genera. Howes (1978, 1979, 1981) analyzes the relationships of several Eurasian genera of Cyprinidae; all European or Euro-Siberian ones have sisters in East Asia:

Aspius (Europe, the Near East, fossil also in Siberia) – *Elopichthys* (continental East Asia). The *Rutilus-Acanthobrama* group (Europe, Siberia, the Near East) – *Chondrostoma* (Europe, western Asia) and the *Abramis-Vimba* group (Europe, fossil in Siberia) – the *Xenocypris* group (East Asia). *Pelecus* (Europe) – possible sister *Hemiculterella* (East Asia).

These data demonstrate that the European fish fauna has closest affinities with the Siberian one: many species are shared by both areas (and most now exclusively European genera once lived in Siberia, too, being even represented by the same species in central Europe and in Siberia); only two pairs

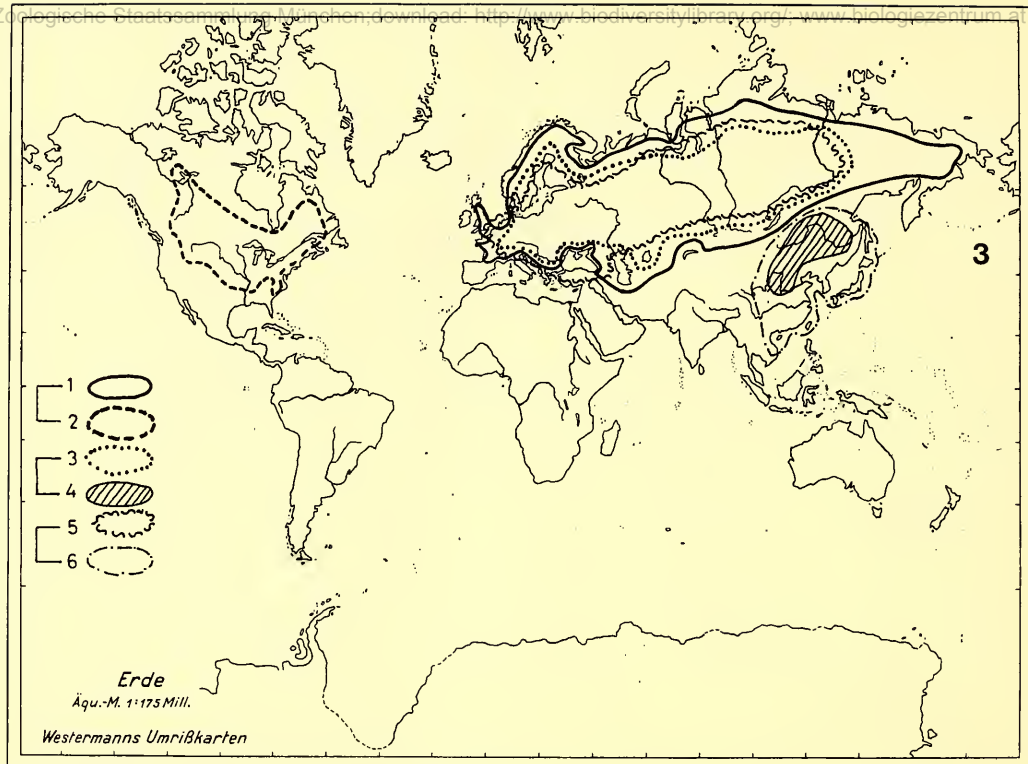


Fig. 3. Distribution of three Euro-Siberian fish species and of their vicariant sisters. 1. *Perca fluviatilis*; 2. *P. flavescens*; 3. *Leuciscus idus*; 4. *L. walecki*; 5. *Carassius carassius*; 6. *C. auratus* (autochthonous occurrence).

of European-Siberian vicars are known (both in *Cottus*). The European fish fauna has also close affinities with the western Asian one.

The affinities of the European or Euro-Siberian fish fauna are different if one considers non-Ostariophysi (Umbridae, Esocidae, Percidae) or Ostariophysi (Cyprinidae, Cobitidae, Siluridae).

The European (Euro-Siberian) taxa of Percidae (*Perca*, *Stizostedion*), Umbridae, Esocidae, partly of Salmonidae (*Thymallus*) have closer affinities with the eastern North American fauna: Percidae and Umbridae live in both areas, being represented by vicariant sisters in each of them, and are absent from East Asia, while the Euro-Siberian populations of *Esox lucius* and *Thymallus thymallus* are conspecific with the North American ones, each of these species being represented by a vicariant sister in East Asia.

The much more numerous European and Euro-Siberian Ostariophysi and the salmonid *Hucho hucho* have on the contrary vicariant sisters (at the specific, generical or supra-generical level) in East Asia and no close relatives in North America. A single Euro-Siberian genus of Ostariophysi is present in North America: *Phoxinus*. This ranges however also in northern East Asia, the East Asian populations being conspecific with the Euro-Siberian ones, while in North America lives a vicariant sister (Fig. 2).

More numerous than the groups containing one European and one or a few extra-European vicars, are those consisting in exclusively European or European and western Asian species. Three pairs of vicariant species are known, both members of which inhabit "central Europe" in a wide sense, i. e. the areas north of the Pyrenees, Alps, Dinarids and Balkans (Fig. 6): *Gymnocephalus schraetser* (Danube

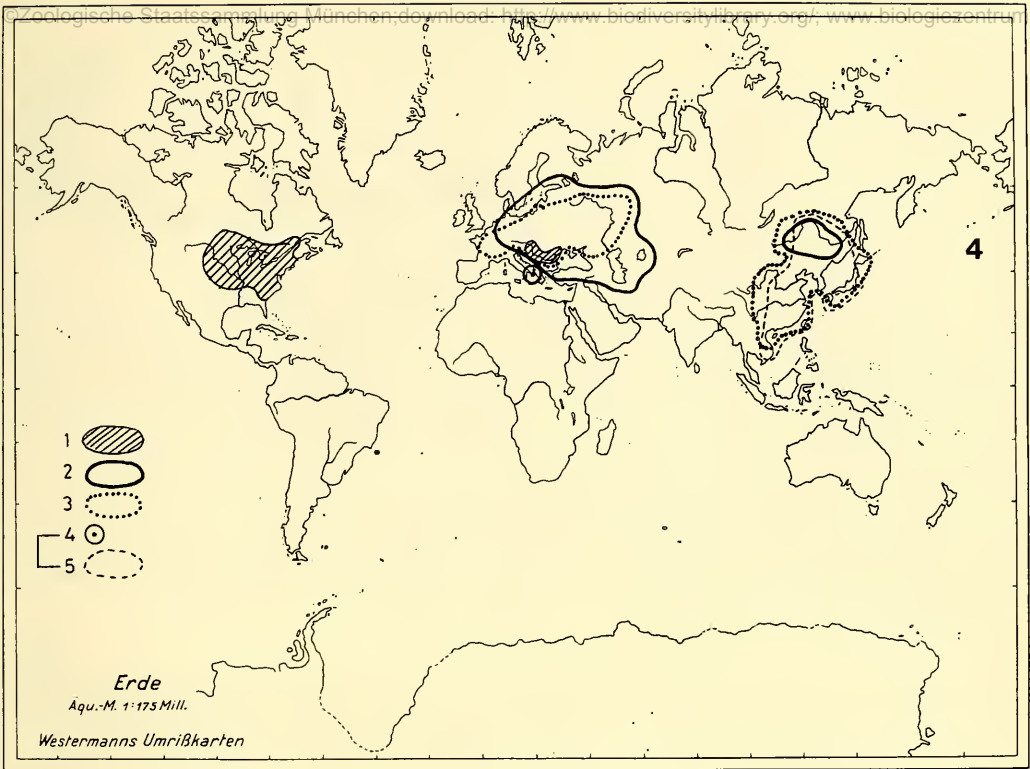


Fig. 4. Distribution of three European fish species and of their vicariant sisters in other continental areas. 1. *Umbra* (*U. krameri* in Europe, pair *U. pygmaea* – *U. limi* in eastern North America); 2. Pair *Silurus glanis* (Europe) – *S. soldatovi* (northern East Asia); 3. Genus *Misgurnus* (*M. fossilis* in Europe – seven species in East Asia); 4.–5. Pair *Parasilurus aristotelis* (4) – *P. asotus* (5).

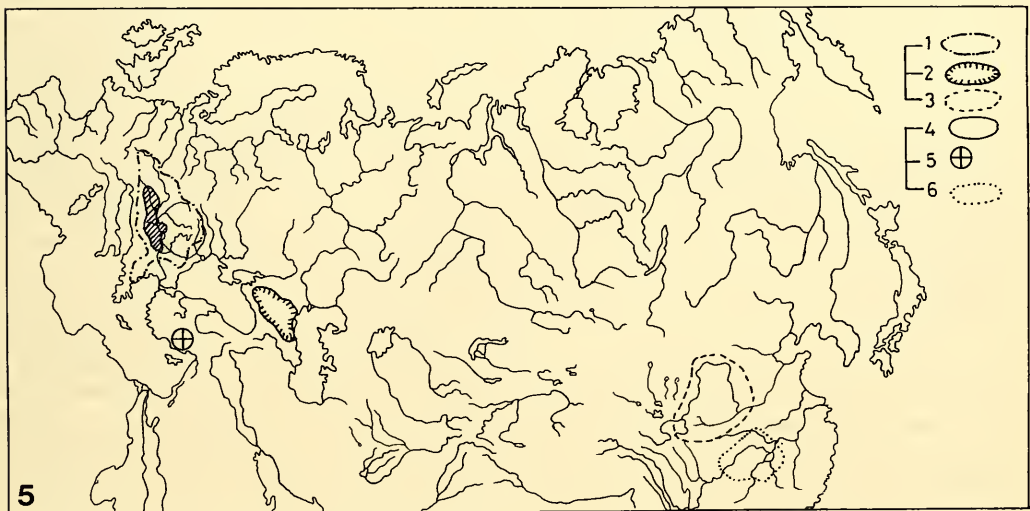


Fig. 5. Distribution of two groups of fishes, each including three vicariant sisters in Europe-west Asia and East Asia. 1. *Gobio uranoscopus*; 2. *G. ciscaucasicus*; 3. *G. rivuloides*; 4. *Cobitis elongata*; 5. *C. bilseli*; 6. *C. macrostigma*.

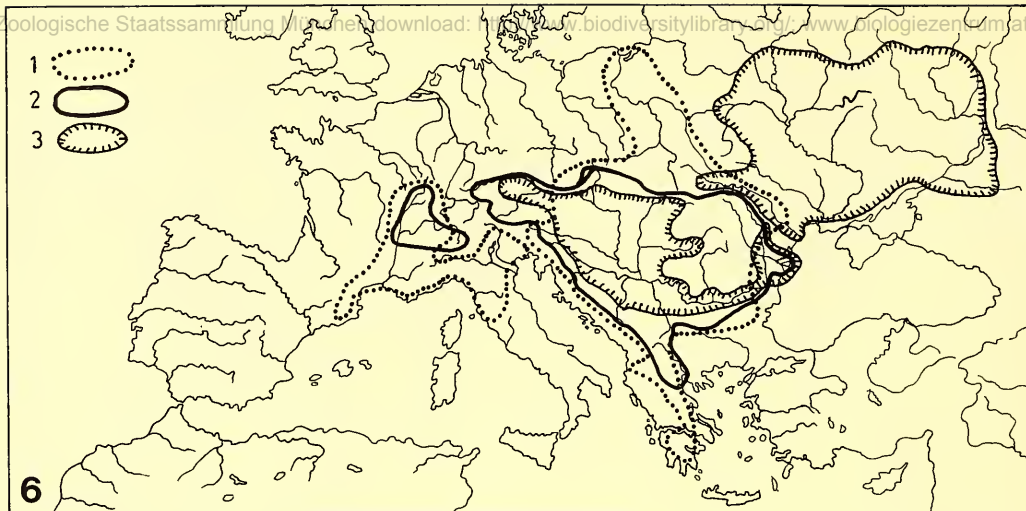


Fig. 6. Distribution of three pairs of vicariant Central European fishes. 1. *Barbus meridionalis* (western) – *B. peloponnesius* (eastern); 2. *Zingel asper* (western) – *Z. streber* (eastern); 3. *Gymnocephalus schraetser* (western) – *G. acerina* (eastern).

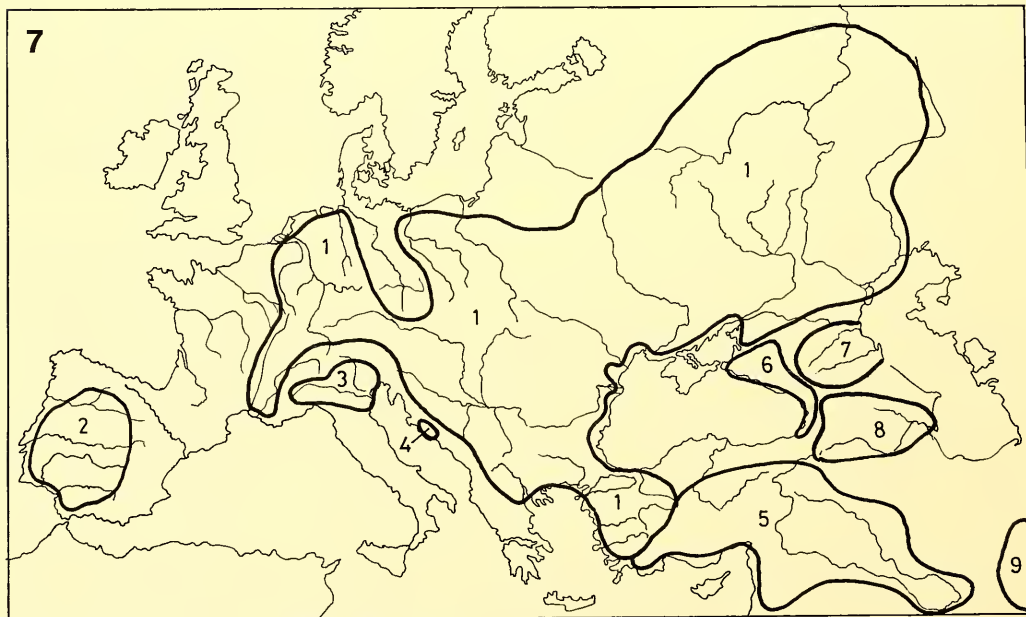


Fig. 7. Distribution of the *Chondrostoma nasus* species-group. 1. *Ch. nasus*; 2. *Ch. polylepis*; 3. *Ch. soetta*; 4. *Ch. kneri*; 5. *Ch. regium*; 6. *Ch. colchicum*; 7. *Ch. oxyrhynchum*; 8. *Ch. cyri*; 9. *Ch. orientalis* (after Banareescu 1960, modified).

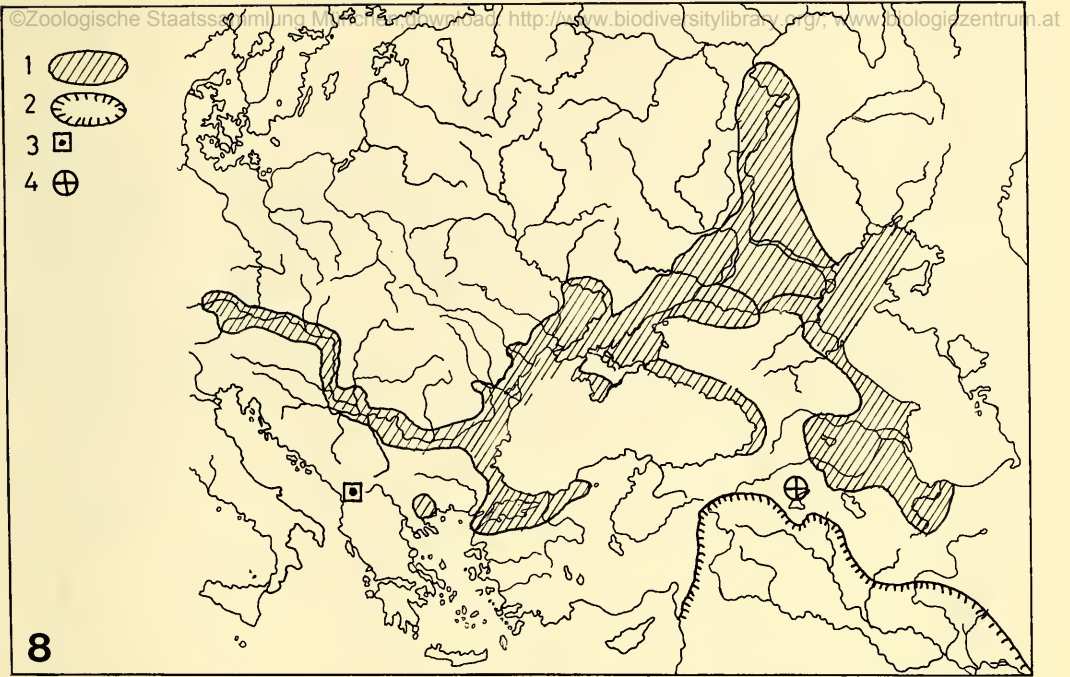


Fig. 8 Distribution of the species of *Chalcalburnus*. 1. *Ch. chalcoides*; 2. *Ch. mossulensis* (= sellal), northern limit of the range; 3. *Ch. belvica*, 4. *Ch. tarichi* (after Banareescu 1964 and Economidis 1986).

River basin) – *G. acerina* (east of the Danube: from the Dnjestr to the Don River basin); *Zingel asper* (Rhône River basin) – *Z. streber* (Danube and Vardar basins); *Barbus meridionalis* (southern France, Italy) – *B. peloponnesius* (Vistule, Dnjestr, Danube etc to southern Greece; according to unpublished data of Dr. P. S. Economidis, *meridionalis* and *peloponnesius* actually are distinct but closely related species, not conspecific subspecies as formerly believed).

These three pairs consists each of a western and an eastern species; in the first case the Danube species is the western, in the two others it is the eastern member of the pair.

A greater number of pairs or groups include each a central European rather widely distributed species and one or several southern European/western Asian species with more restricted ranges. The best example is furnished by the *Chondrostoma nasus* group: *Ch. nasus* in central Europe/eastern Balkan and one species in each of the following eight areas: the Atlantic slope of the Iberian peninsula; northern Italy; Neretva River in the western Balkan; central Anatolia to the Tigris/Euphrat; the Caspian Sea slope of the northern Caucasus; Kuban River and western Transcaucasia; eastern Transcaucasia; southwestern Iran (Fig. 7).

Other examples are: *Chalcalburnus chalcoides* (basins of the Black, Caspian, Aegean and Aral seas) – *Ch. belvica* (lake Prespa, western Balkan; according to Economidis (1986), this species is a *Chalcalburnus*, not an *Alburnus*) – *Ch. tarichi* (lake Van, eastern Anatolia) – *Ch. mossulensis* (western Syria and Tigris/Euphrat) (Fig. 8).

Scardinius erythrophthalmus (central Europe, eastern Balkan; well differentiated subspecies in Italy and the western Balkan). *S. graecus* (southern Greece) (Banareescu 1964, fig. 147).

Leuciscus, subgenus *Telestes*: *L. souffia* (basins of the Rhône, upper Rhine and Danube; well differentiated subspecies in Italy and lake Skadar, western Balkan) – *L. polylepis* (a tributary of the Da-

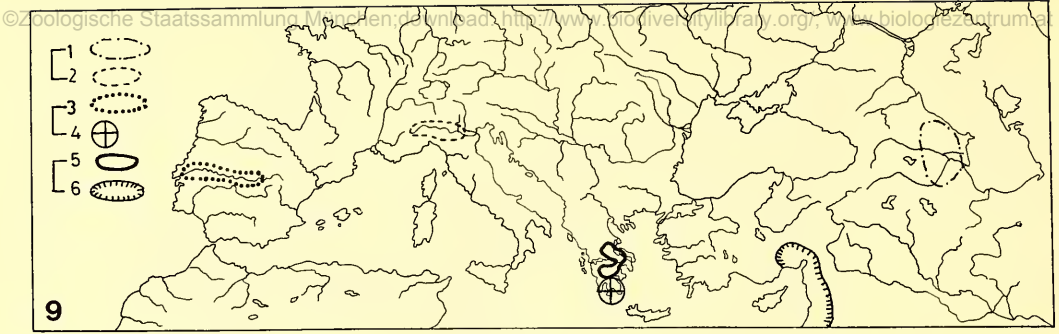


Fig. 9. Distribution of three pairs of southern European-western Asian vicariant fish species. 1. *Sabanejewia caspia*; 2. *S. larvata*; 3. *Cobitis paludieola*; 4. *Cobitis* sp.; 5. *Pseudophoxinus stymphalicus*; 6. *P. zeregi*.

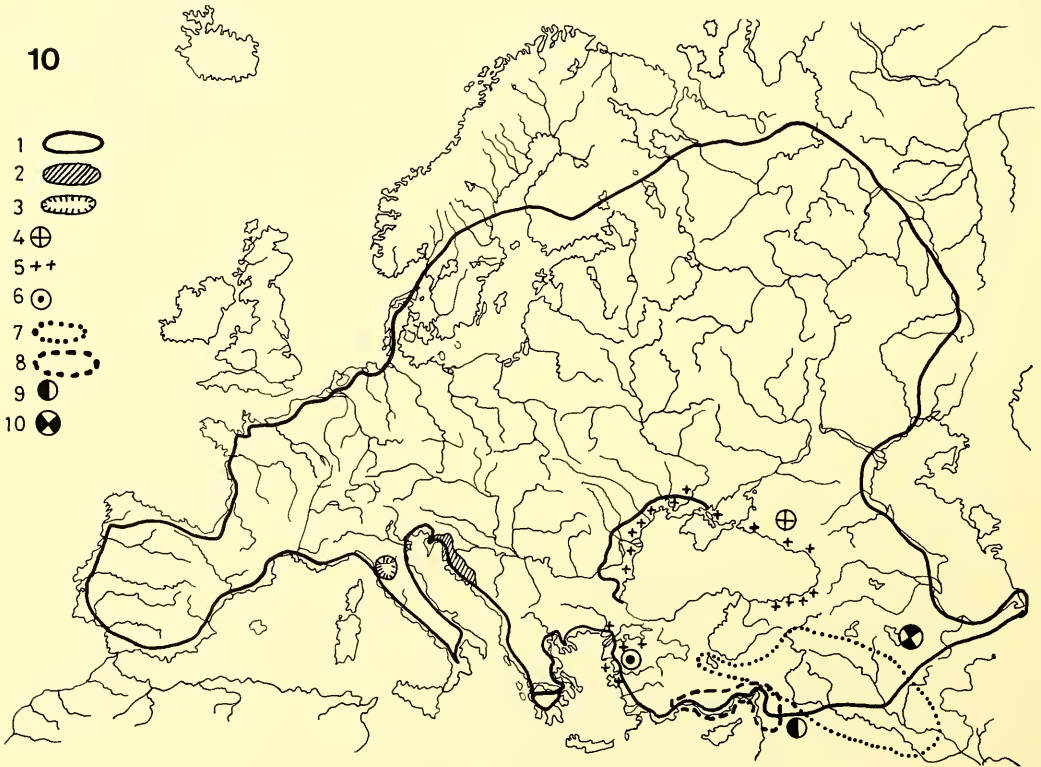
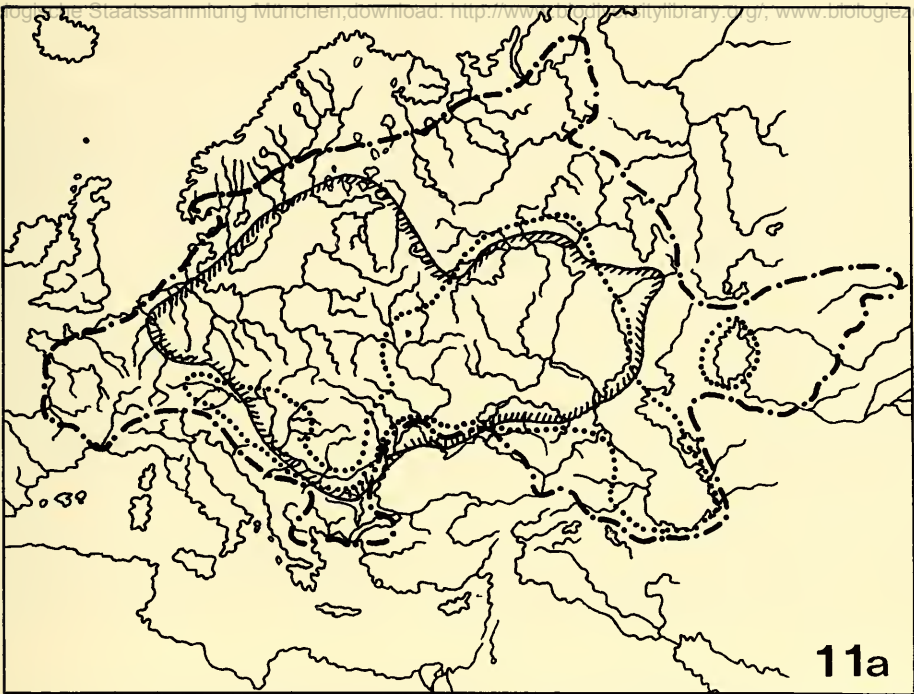


Fig. 10. Distribution of the species of the *Leuciscus cephalus* group. 1. *L. cephalus*; 2. *L. illyricus*; 3. *L. lacumonis*; 4. *L. aphipsi*; 5. *L. borysthenicus*; 6. *L. cephaloides*; 7. *L. lepidus*; 8. *L. berak*; 9. *L. spurius*; 10. *L. ulanus* (the range of *L. squaliusculus* from the Aral Sea basin not mapped) (after Banarescu 1964, modified).

nube in Croatia) – *L. ukliva* (Cetina River, western Balkan) – *L. turskyi* (several other rivers of the western Balkan) (Berg 1932; Banarescu 1964, fig. 131; Vuković & Ivanović, 1971).

Aspius aspius (Europe, northern Anatolia) – *A. vorax* (western Syria and the Tigris/Euphrat) (Banarescu 1964, fig. 152).



11a



11b

Fig. 11. Distribution of the species of the genera *Abramis* and *Blicca*. 1. *A. brama*; 2. *A. sapa*; 3. *A. ballerus*; 4. *Blicca bjoerkna* (after Banarescu 1964, modified).

©Zool Also the genera *Alburnus*, *Barbus* (species with spinified dorsal ray) and *Cobitis* s. str. include each a central European and several, partly sympatric, southern species, some of which are surely vicariant sisters of the central European one.

Other pairs or groups of vicars are confined to southern Europe/western Asia; examples are: *Sabanejewia caspia* (Caspian Sea slope on both sides of the Caucasus mountains) – *S. larvata* (northern Italy); *Cobitis paludicola* (Tajo River basin in Spain/Portugal) – an undescribed *Cobitis* species in Greece (T. Nalbant, personal information); *Pseudophoxinus stymphalicus* (central and southern Greece) – *P. zeregi* (from southern Turkey to the upper Jordan River) (Fig. 9).

Further lineages restricted to southern Europe/western Asia are: the genus *Phoxinellus* (formerly *Paraphoxinus*) in the western Balkan; the subgenus *Leucos* (= *Orthroleucus*) of *Rutilus*, distributed from the Iberian peninsula to eastern Transcaucasia and probably Iran; the *Chondrostoma* species with horse-shoe shaped mouth (apparently two groups) the *toxostoma* group consisting of three vicariant species or subspecies in northern Spain, southern France and northern/central Italy and the *phoxinus* group, including two largely sympatric species on the Atlantic slope of Portugal/Spain, another on the Mediterranean sea slope of Spain, the fourth one in the western Balkan; the *Barbus bocagei* – *B. capito* group, that has a disjunct range in the Iberian peninsula and western Asia (Karaman 1971; Almaca 1983); the subgenus *Bicanestrinia* of *Cobitis*, ranging from southern Greece to southwestern Iran.

Most species within these lineages have restricted ranges and they surely represent pairs or groups of vicars; a few species are however sympatric and the interrelations between species being not known, the vicariant relationships can not be established.

Interpretation of the vicariant relationships

Proponents of the Vicariance Biogeography school consider that the common range of the members of a group of vicars is informative for the range of the immediate ancestor: this could be obtained by adding the ranges of the descendants. According to the author's opinion, vicariant relationships can however also result from dispersal.

The manner in which a mother species splits into two or more daughter species is different in genuine freshwater fishes (and other freshwater animals) and in terrestrial organisms. Divides between river basins are uncrossable barriers for freshwater fishes. Were river basins permanent, each species would be confined to a single river basin. Actually, most species live in several basins; this is possible because river basins are continuously changing, as a consequence of the frequent occurrence of river captures. By mean of a river capture, a tributary of a certain river A becomes tributary of river B; its fauna, consisting of species characteristic to the fauna of river A basin enters the basin of river B, gets the possibility to disperse throughout this basin and later, as a result of the interruption of the gene flow between the populations of the two basins, the individuals from river B basin evolved in distinct species, which are vicariant sisters for the species inhabiting river B basin (Banareescu 1986).

Let us consider again the numerous examples of vicariant sisters mentioned above; could one accept that there were once, during the history of the earth, a single river basin encompassing what are now the Atlantic slope of the Iberian peninsula, western, central and eastern Europe etc. east to southwestern Iran, this river having been inhabited by the common ancestor of the nine species of the *Chondrostoma nasus* group (Fig. 7) ? Or that there were a single river basin extending from France and England throughout the entire eastern Europe and Siberia to the Atlantic slope of North America and which was inhabited by the ancestor of the pair *Perca fluviatilis* – *P. flavescens* (Fig. 3, 1 and 2) ? I think few people would accept this possibility.

Actually the common ancestors of these pairs or groups of vicars had initially much more restricted ranges, which encompassed only a part of the common range of the descendants. The initial ranges

gradually extended and split in the ranges of the recent daughter species, as a consequence of the numerous river captures which modified the riverine net.

It would be hardly possible to establish, in each peculiar case, which was the initial range of the common ancestor. This is however possible in some cases, for example in that of the two *Perca* species. The genus belongs to the tribe Percini, that is prevailing European, its sister being the North American Etheostomini; the splitting of the common ancestor of the two tribes was probably correlated with the breakup of the North Atlantic continent in Europe and North America; the tribe Percini evolved in Europe, the ancestral *Perca* having later extended its range to Siberia and farther to North America; the appearance of the Bering strait isolated subsequently the American populations which evolved in a distinct species.

One can on the contrary not know where did the ancestral *Umbra* species live: in North America, in Siberia or in Europe.

A general remark is necessary for the exclusively European groups of vicars, most of which include a central European and one or several southern species. All European fish taxa belong to lineages having Holarctic, Eurasian or Holarctic and East Asian ranges; all European genera or groups of species have relatives either in North America or in East Asia, none in Africa. Central Europe is geographically closer to North America and East Asia than is south Europe; one can therefore accept that the initial ranges of the ancestors of all pairs or groups of vicars present now in Europe (or also in western Asia) were in central Europe; river captures across the present Pyrenees, Alps etc. have favoured range extensions in the southern peninsulas, then the isolation of the southern populations which evolved later in distinct species.

Sympatric occurrence of relatives, resulting from dispersal

The fish fauna of Europe offers also examples of sympatric occurrence of two or more close relatives, this sympatry having resulted from range extension. In one lineage, the *Leuciscus cephalus* group (Fig. 10), most species have restricted vicariant ranges, but one species, *L. cephalus*, inhabits most of the continent, its wide range encompassing, at least partially, also the ranges of its sisters.

The distribution pattern of the *L. cephalus* group confirms the above assertion: that central Europe represented the initial range of the ancestors of the groups which now include several vicariant species in the continent. The ancestor of the *L. cephalus* group lived in central Europe (the area where now only the nominal species lives); it extended its range southwards; the southern populations evolved in distinct species. Subsequent river captures enabled the central European *L. cephalus* to re-invade the southern areas where it lives now sympatrically (but in a certain measure allotopically) with its sisters. The southern populations of *L. cephalus* began already to diverge from the central European ones, being assigned to distinct subspecies, which will later become full species. This is a typical example of double colonization (Mayr 1963).

A good example of total sympatry of the species of a lineage is that of the three species of *Abramis* and of its sister, the monotypic *Blicca* (Fig. 11); the main part of the ranges of the four species is the same, only the limits of distribution differing.

These species evidently evolved from a common ancestor through geographic isolation (like all biparental organisms), the sympatry being secondary. Arguments were advanced (Banarescu 1960) that the group originated in Siberia, the species having later extended their ranges to Europe, where they became sympatric, their later extinction from Siberia being determined by the Ice Age cooling.

Several pairs of sympatric sisters live in central Europe (in a wide sense), one species of each pair being confined to the Ponto-Caspian basin (a part of what is here considered "central Europe"), while the second is more widely distributed:

Stizostedion volgense – *S. lucioperca*; *Gymnocephalus baloni* – *G. cernuus*; *Abramis sapa* – *A. balerus*; *Rutilus pigus* (probably also including the "forms" *heckeli* and *caspius*) – *R. rutilus*.

It is remarkable that the Ponto-Caspian genuine freshwater fish fauna, and above all the Danube basin one, are the richest in the continent, double colonization (i. e. sympatric occurrence of former vicariant sisters, due to range extension of at least one of them) having contributed to their enriching.

Zusammenfassung

Mehrere in Europa vorkommende Süßwasserfischarten haben vikariierende Schwesterarten in anderen kontinentalen Gebieten: die Schwesterarten von zwei euro-sibirisch-nordamerikanischen, von drei eurosibirischen und von drei europäischen Arten leben in Ostasien, während die nächstverwandten Schwesterarten des paläarktischen *Phoxinus phoxinus*, der euro-sibirischen *Perca fluviatilis* und der mitteleuropäischen *Umbra krameri* das östliche Nordamerika bewohnen (Abb. 1–4) und die der zwei europäischen *Cottus*-Arten eine sibirische Verbreitung haben. Es gibt noch zwei Fälle von je drei Schwesterarten: eine mitteleuropäische, eine kaukasische oder anatolische und eine ostasiatische (Abb. 5).

Die Beziehungen der europäischen und eurosibirischen Fauna sind näher zu Nordamerika im Fall der Percidae und der Esocidae, zu Ostasien im Fall der Ostariophysi.

Es gibt drei Paare vikariierender mitteleuropäischer Schwesterarten (Abb. 6), während mindestens fünf ziemlich weit verbreitete mitteleuropäische Fische eine oder mehrere (bis acht) vikariante Schwesterarten mit beschränktem Bereich in südeuropäisch-westasiatischen Gebieten (Abb. 7, 8) besitzen; mindestens drei Paare von vikariierenden Schwesterarten sind ausschließlich südeuropäisch-westasiatisch (Abb. 9).

Die vikariierenden Beziehungen entstehen bei genuinen Süßwassertieren durch Flußanzapfungen. Sie erlauben gewissen Arten, ihren Bereich zu erweitern, und isolieren sofort die Populationen aus dem angezapften Fluß; diese beginnen divergent zu evolvieren und werden später neue Arten. Man soll nicht behaupten, daß die Urart einen sehr ausgedehnten Bereich besaß, der die Bereiche aller heutiger Tochterarten umfaßte.

Es gibt auch viele Fälle von sympatrischen Vorkommen nahverwandter Fischarten: *Leuciscus cephalus* kommt im südlichen Teil seines Verbreitungsgebietes zusammen mit seinen Verwandten vor (Abb. 10); die drei *Abramis*-Arten und *Blicca bjoerkna* sind fast vollständig sympatrisch (Abb. 11), während drei oder vier ponto-kaspische, genuine Süßwasserfische und drei Donauendemiten zusammen mit deren weiterverbreiteten Schwesterarten vorkommen. Das Zusammenvorkommen verwandter Arten ist ein sicherer Beweis für eine Ausbreitung bzw. doppelte Kolonisation; der Artenreichtum der ponto-kaspischen und der Donau-Fischfauna ist zum großen Teil eine Folge doppelter Kolonisation.

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