

A description of *Leuciscus lepidus* (HECKEL, 1843) with comments on *Leuciscus* and leuciscine - aspinine relationships

(Pisces: Cyprinidae)

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Abstract

The external morphology, sensory canals and osteology of *Leuciscus lepidus* (HECKEL, 1843), a species from the Tigris-Euphrates and adjacent basins are described based on the collections of the Zoologisches Museum und Zoologisches Institut, Universität Hamburg, Senckenberg Museum, Frankfurt a. Main and the Naturhistorisches Museum Wien. Wide anatomical in- and out-group comparisons are made to arrive at the phylogenetic relationships of *L. lepidus* (HECKEL, 1843) within the genus and the subfamily Leuciscinae. It is shown that several species of *Leuciscus* (*L. cephalus* (LINNAEUS, 1758), *L. pyrenaicus* GÜNTHER, 1868, *L. illyricus* (HECKEL & KNER, 1858), *L. svallize* (HECKEL & KNER, 1858), *L. spurius* (HECKEL, 1843) and *L. lepidus* (HECKEL, 1843), the latter being the most derived member of this lineage and the entire genus) form an assemblage characterized by a suite of common derived features some of which are specializations shared with genera of the tribe Aspinini sensu BOGUTSKAYA (1990a, 1991a) or, partly, the aspinine group sensu HOWES (1978, 1984). Morphological differences between the Aspinini and the Pseudaspinini are also discussed.

Key words: Cyprinidae, *Leuciscus*, Aspinini, Pseudaspinini, external morphology, sensory canals, osteology, systematic position.

Zusammenfassung

In der vorliegenden Arbeit werden die äußere Morphologie, die sensorischen Kanäle und osteologische Merkmale von *Leuciscus lepidus* (HECKEL, 1843), einer aus dem Tigris-Euphrat-Einzugsgebiet stammenden Art, beschrieben. Das untersuchte Material stammt aus den Sammlungen des Zoologischen Museums und des Zoologischen Institutes der Universität Hamburg, des Senckenberg Museums, Frankfurt a. Main und des Naturhistorischen Museums in Wien. Anhand ausführlicher anatomischer Vergleiche wird die Stellung von *L. lepidus* (HECKEL, 1843) innerhalb der Gattung *Leuciscus* und der Unterfamilie Leuciscinae diskutiert. Es wird gezeigt, daß einige Arten der Gattung *Leuciscus* (*L. cephalus* (LINNAEUS, 1758), *L. pyrenaicus* GÜNTHER, 1868, *L. illyricus* (HECKEL & KNER, 1858), *L. svallize* (HECKEL & KNER, 1858), *L. spurius* (HECKEL, 1843) und *L. lepidus* (HECKEL, 1843)) eine Reihe abgeleiteter Merkmale aufweisen, die zum Teil auch bei Vertretern der Gruppe Aspinini sensu BOGUTSKAYA (1990a, 1991a) bzw. Teilen der "aspinine group" sensu HOWES (1978, 1984) zu finden sind. In der Folge werden auch die morphologischen Unterschiede zwischen Aspinini und Pseudaspinini diskutiert.

Introduction

The subject of this study is *Leuciscus lepidus* (HECKEL, 1843) distributed in the Tigris-Euphrates basin, Quwaiq and Orontes systems and in south-eastern Anatolia from Beyşehir Lake in the west (KURU 1980, KRUPP 1985, COAD 1991, and others). This species has been described from external features or only cited in recent literature (KHALAF 1961, BECKMAN 1962, SAADATI 1977, KURU 1979, COAD 1980a, 1980b, 1982,

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1985, 1991, KRUPP 1985, MAHDI, no date). A wide comparative anatomical study of *L. lepidus* proved interesting in connection with the taxonomy and phylogeny of the genus *Leuciscus* and its supposed close relatives. The genus *Leuciscus* CUVIER, 1817, has not yet been revised although it is a central group for understanding the phylogeny and systematics of the subfamily Leuciscinae and is apparently ancestral for many phylogenetic lineages within the subfamily. The genus *Leuciscus* is widely distributed throughout Eurasia, from the Iberian Peninsula to the Amur River and from the Kolyma River to the Tigris-Euphrates basin. According to the critically analyzed data from the extensive literature both "classical" and recent (BERG 1932, 1949, 1962a, 1962b, BANARESCU 1964, VUCOVIC & IVANOVIC 1971, BIANCO 1983, ECONOMIDIS 1991, and many others), the genus includes 30 - 35 species, some of them being of doubtful taxonomic status: *Leuciscus ahipsi* ALEKSANDROV, 1927; *L. bergi* KASCHKAROV, 1925; *L. borysthenicus* (KESSLER, 1859); *L. carolitertii* DOADRIO, 1987; *L. cephaloides* BATTALGIL, 1942; *L. cephalus* (LINNAEUS, 1758); *L. danilewskii* (KESSLER, 1877); *L. gaderanus* GÜNTHER, 1899; *L. idus* (LINNAEUS, 1758); *L. illyricus* (HECKEL & KNER, 1858); *L. keadicus* STEPHANIDIS, 1971; *L. latus* (KEYSERLING, 1861); *L. lehmanni* BRANDT, 1852; *L. lepidus* (HECKEL, 1843); *L. leuciscus* (LINNAEUS, 1758); *L. lindbergi* ZANIN & EREMEEV, 1934; *L. lucumonis* BIANCO, 1983; *L. merzbacheri* (ZUGMAYER, 1912); *L. microlepis* (HECKEL, 1843); *L. mongolicus* (KESSLER, 1876); *L. polylepis* STEINDACHNER, 1866; *L. pyrenaicus* GÜNTHER, 1868; *L. schmidti* (HERZENSTEIN, 1896); *L. smyrnaeus* BOULENGER, 1896; *L. souffia* RISSO, 1826; *L. spurius* (HECKEL, 1843); *L. squaliusculus* (KESSLER, 1872); *L. svallize* (HECKEL & KNER, 1858); *L. turskyi* HECKEL, 1843; *L. ukliva* HECKEL, 1843; *L. ulanus* GÜNTHER, 1899; *L. waleckii* (DYBOWSKI, 1869).

Leuciscus berak (HECKEL, 1843), *L. cephalopsis* (HECKEL, 1843) and *L. agdamicus* (KAMENSKIY, 1901) are considered to be synonyms of *L. cephalus* (PELLEGRIN 1928, BERG 1949, ABDURAKHMANOV 1962, KÄHSBAUER 1966, COAD 1991). *Leuciscus cephaloides*, a poorly known species from a restricted locality in Western Anatolia is possibly one of the local forms of *L. cephalus*. *Leuciscus gaderanus* seems to be a synonym of *L. ulanus*¹, both are endemics of Urmia (Reza'iyeh) Lake. *Leuciscus pyrenaicus* was synonymized (BERG 1932, 1949, LADIGES & VOGT 1979, and others) with *L. cephalus* but has recently been regarded as a separate species by BIANCO (1990). *Leuciscus illyricus* from Dalmatia is considered by BIANCO & KNEZEVIC (1987) to be a doubtful species which possibly represents a subspecies or a cold-water ecophenotype of *L. cephalus*.

The taxonomic status of some daces from Middle Asia is also rather questionable. For example, KAFANOVA (1959) supposed *L. latus* and *L. lehmanni* to be subspecies of *L. leuciscus* and referred *L. lindbergi* and *L. bergi* as, respectively, a subspecies and an ecomorph of *L. schmidti*. *Leuciscus latus* is also assigned as a subspecies of *L. lehmanni* by some authors (NIKOLSKIY 1938, SVETOVIDOVA 1967). *Leuciscus danilewskii* from the Don River basin previously synonymized with *L. leuciscus* (SCHAPOSCHNIKOVA 1964, SHCHERBUKHA 1972, MOVTCAN & SMIRNOV 1981) has been reinstated as valid (BOGUTSKAYA 1991b). *Leuciscus keadicus* from the Evrotas River, Greece, was originally

¹ GÜNTHER (1899) mentioned that the propriety of distinguishing *L. gaderanus* from *L. ulanus* may be questioned: the main difference was the number of l.l. scales - 44 in *L. ulanus* and 40 in *L. gaderanus*. Three specimens from the Nazlu Chai (ZISP N 26869) have, however, 42, 42 and 45 l.l. scales and lack other principal differences.

described as *L. souffia keadicus* (STEPHANIDIS 1971) but is now regarded as a distinct species (ECONOMIDIS 1991).

There are several problems concerning the limits and content of the genus *Leuciscus*. Thus, *Pseudophoxinus pleurobipunctatus* (STEPHANIDIS, 1939) was recently transferred by BIANCO (1988, 1990) to *Leuciscus* because of its similarity in some external characters, except for the number of rows of pharyngeal teeth, to *L. souffia*. Two Chinese daces - *L. merzbacheri* and *L. mongolicus* - were excluded from *Leuciscus*. The former was described as *Aspiopsis merzbacheri* but considered by BERG (1949) and HOWES (1978) as belonging to *Leuciscus*; later HOWES (1984) re-established *Aspiopsis* ZUGMAYER, 1912, and showed that *L. mongolicus* should be allocated to a new genus, *Genghis* HOWES, 1984.

According to BERG (1949) and BANARESCU (1964) the genus *Leuciscus* should be grouped into four subgenera - *Leuciscus* CUVIER, 1817 s.str., *Squalius* BONAPARTE, 1841, *Idus* HECKEL, 1843, and *Telestes* BONAPARTE, 1837. Since their phylogenetic origin and relationships are not clearly known and morphological borders between these "subgenera" are uncertain, it was suggested (BIANCO 1983, 1986, BIANCO & RECCHIA 1983, BIANCO & KNEZEVIC 1987) that it is better to consider the four subdivisions (without special taxonomic status) as *L. leuciscus*, *L. cephalus*, *L. idus* and *L. souffia* species complexes. The *L. cephalus* complex, characterized by serrated pharyngeal teeth in two rows (2.5 - 5.2) and an anal fin margin distinctly convex or almost straight, is comparatively better investigated taxonomically. It includes, according to BIANCO (1983, 1986, 1990, and others), *L. illyricus*, *L. svallize*, *L. lucumonis*, *L. aphipsi*, *L. borysthenicus*, *L. agdamicus*, *L. squaliusculus*, *L. lepidus*, *L. cephaloides*, *L. ulanus*, *L. gaderanus*, *L. spurius*, *L. pyrenaicus*, *L. cephalus* and *Leuciscus* sp. from the Krka River in Dalmatia.

The data from the literature cited above (except for those of Howes) are mostly based on the examination of external characters. The analysis of numerous anatomical features and cephalic sensory canals of the *Leuciscus* species (HOWES 1984, BOGUTSKAYA 1988a, 1988b, 1990a, 1991a, 1991b) showed that there exists no distinct morphological borders between subgenera sensu BERG (1949) but there are some species or groups of species which differ from the nucleus of *Leuciscus*. The majority of *Leuciscus* species possess a wide suite of shared characters which can be considered as plesiomorphic for the Leuciscinae. This fact, according to HOWES (1984), suggests that *Leuciscus*, as presently recognized, can not be defined by a set of unique characters and is therefore a non-monophyletic assemblage. This problem, on the one hand, needs further, wide and comparative morphological studies and, on the other, arises from the systematic methodology practised (i.e. different emphasis in using anagenetic components of evolution and ancestral characters in systematic reconstructions).

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Materials and method

As in previous studies (BOGUTSKAYA 1988a, 1988b, 1990a, 1991a, 1991b and others) a wide range of species belonging to the Leuciscinae as well as to other cyprinid subfamilies has been examined. The material listed in those papers have been reexamined together with more recently prepared material including skeletal preparations, dissections and radiographs. The species² presently examined for this study are:

L. lepidus (ZMH 1134, 2 specs SI 194.0 and 219.4 mm; ZMH 2463, 8 specs SI 84.5 - 167.7 mm; ZMH 3554, 7 specs SI 102.5 - 211.9 mm; ZISP 25424, 1 spec SI 107.6 mm; SMF, 8 uncatalogued specs SI 37.2 - 77.5 mm; ZMH 1134, 3 heads of large specs; ZMH 1134, 2 skelet. prepar.; syntypes: NMW 49342, 2 specs SI 223.1 and 237.0 mm; NMW 49343, 2 specs SI 85.8 and 105.6 mm; NMW 49344, 1 spec SI 160.8 mm; SMF 847, 1 spec SI 102.9 mm³; *L. aphipsi* (61; 5)⁴, *L. bergi* (40; 9), *L. borysthenticus* (>200; 10), *L. carolitertii* (7; 4; 2 paratypes SMF 21214, 21215), *L. cephalus* (>200; 12; 6 syntypes of *L. berak* NMW 48915), *L. danilewskii* (67; 4; lectotype ZISP 2944, paralectotype ZISP 50162), *L. idus* (52; 5), *L. illyricus* (22; 17 syntypes NMW 49313, 49315, 49322, 49324, 49331, 49339 - 49341), *L. latus* (4; 1), *L. lehmanni* (7; holotype ZISP 2315), *L. leuciscus* (>100; 30), *L. lindbergi* (18; 3;" syntypes ZISP 25090), *L. lucumonis* (6 paratypes SMF 16967), *L. microlepis* (5; lectotype NMW 49415, 5 paralectotypes NMW 49414, 49416, 49421, 1 paralectotype SMF 3434; 5 syntypes of *L. tenellus* NMW 16001, 16002, 49613) *L. mongolicus* (holotype ZISP 2472; holotype of *Squalius huanchicus* ZISP 2483), *L. polylepis* (11; 6 syntypes NMW 49713 - 49715), *L. pyrenaicus* (13; 4), *L. schmidti* (15; 5; 12 syntypes ZISP 9692, 9693, 9706), *L. smyrnaeus* (20; 1), *L. souffia* (28; 5), *L. spurius* (2; 2 syntypes NMW 49572), *L. squaliusculus* (8; 2; 30 syntypes ZISP 2074, 2075, 2081), *L. svallize* (5; 7 syntypes NMW 49593 - 49595, 49596, 49597, 49612, SMF 3398), *L. turskyi* (10; 18 syntypes NMW 49629), *L. ukliva* (8; 7 syntypes (?) NMW 49635, 49636), *L. ulanus* (3), *L. waleckii* (50; 5), and also *Aspiolucius esocinus* (KESSLER, 1874) (8; 1), *Aspius aspius* (LINNAEUS, 1758) (40; 15), *A. vorax* (HECKEL, 1843) (7; 1; 1 syntype NMW 76776), *Elopichthys bambusa* (RICHARDSON, 1844) (4; 1), *Oreoleuciscus sp.n.* (32; 6), *O. humilis* WARPACHOWSKI, 1889 (200; 95; lectotype ZISP 6378; 6 paralectotypes ZISP 4211, 50027), *Pseudaspius leptoccephalus* (PALLAS, 1776) (20; 6), *Tribolodon brandti* (DYBOWSKI, 1872) (28; 5), *T. hakuensis* (GÜNTHER, 1880) (23; 4).

The last two dorsal rays in contact at the base are counted as two, not one ray. Total number of vertebrae includes 4 Weberian vertebrae and the fused preural centrum as the last one. Pore counts were made from both left and right sides of the head; number of canal openings on an individual bone includes entry and exit ones. Skeletal preparations are made after clearing and staining with alizarin red "S". The drawings are made by the author.

Abbreviations:

Institutions: NMW - Naturhistorisches Museum in Wien; SMF - Senckenberg Museum, Frankfurt a. Main; ZISP - Zoological Institute, Russian Academy of Sciences, St. Petersburg; ZMH - Zoologisches Museum und Zoologisches Institut, Universität Hamburg.

l.l. - lateral line, s.l. - standard length, D - dorsal fin, A - anal fin, sp.br. branchial spines, vert. - vertebrae.

Cephalic sensory canals: CIO - infraorbital canal, CPM - preopercular-mandibular canal, CSO - supraorbital canal, CST - supratemporal canal.

Skull measurements: L bas.n. - length of neurocranial base without pharyngeal process, H eth - depth of ethmoid region on the level of the posterior margin of supraethmoid, H soc - depth of neurocranium on the

² The author's study of the genus *Leuciscus* gave reasons for considering the following taxa as valid species though for most of them it is not discussed herein.

³ The specimens from ZMH 4400, 2521, 2522, and 15082 labelled as *L. lepidus* are actually *L. cephalus orientalis* NORDMANN.

⁴ In parentheses: the first number is the number of specimens (non-type material) externally examined, partially dissected and radiographed; the second number - if shown - indicates the number of skeletal preparations, followed by the data on type material examined.

vertical from the anterior border of the supraoccipital, Lt eth - width of neurocranium between lateral margins of lateral ethmoids, Lt spho - width of neurocranium between lateral margins of sphenotic lateral processes, Lt pto - width of neurocranium between lateral margins of pterotics on the level of the posterior pterotic process base.

Abbreviations used in the figures: aart - anguloarticular, boc - basioccipital, dn - dentary, ectpt - ectopterygoid, entpt - entopterygoid, eoc - exoccipital, epo - epiotic, eth.l. - lateral ethmoid, f - frontal, f.dil.op - dilatator fossa, f.st - subtemporal fossa, ic - intercalar, io - infraorbitals, iop - interoperculum, keth - kinethmoid, meth - mesethmoid, mtpt - metapterygoid, mx - maxilla, op - operculum, orbs - orbitosphenoid, orbs.sept. - interorbital septum of orbitosphenoid, p - parietal, p.m. - masticatory plate of pharyngeal process, pal - palatine, peth - preethmoid, pmx - premaxilla, pop - preoperculum, pr.asc.d. - ascending dorsal process of maxilla, pr.cor. - coronoid process, pr.ph. - pharyngeal process of basioccipital, pr.pto - pterotic process, pr.r.asc. - rostral ascending process of premaxilla, pr.spho - lateral process of sphenotic, pro - prootic, ps - parasphenoid, pts - pterosphenoid, rart - retroarticular, seth - supraethmoid, soc - supraoccipital, spo - supraorbital, v - vomer.

Comparative description of *Leuciscus lepidus* (HECKEL, 1843)

Lectotype: NMW 49342: 1, Tigris, Mosul, coll. Kotschy; Sl 237.0 mm; D III 9, A III 10, 1.1.47, sp.br. 11, vert. 44, number of pores: CSO 16/17 (number of pores on left/right side of a head), CIO 26/29, CPM 24/26, CST 9; for measurements see Table 1.

Paralectotypes: 5 specs NMW 49342: 2, 49343: 1 - 2, 49344: 1, SMF 847; Tigris, Mosul, coll. Kotschy; Sl 90.8 - 233.8 mm; D III 8, 9, A III 10, 11, 1.1. 46 - 49, sp.br. 9 - 11, vert. 44, 45; CSO 12 - 17, CIO 23 - 29, CPM 21 - 26, CST 9, 11; for measurements see Table 1.

Body is elongated, fusiform. Head is long (28 - 33% Sl), dorsally flattened and moderately broad (width at nape 13 - 16% Sl). Head width at nape is only slightly smaller than depth there. Infraorbital space is flat, broad (8 - 12% Sl or 29 - 39% lc). Eye, in particular in the larger fishes, is small, its horizontal diameter (7 - 9% Sl or 26 - 28% lc in fishes of 37 - 52 mm Sl and 4.5 - 6.5% Sl or 13 - 22% lc in longer ones) being shorter than snout length (8 - 10% Sl or 25 - 33% lc). Snout is long, pointed; lower jaw is projected forward relative to the upper jaw; triangularly expanded symphysis lies in a median notch of the upper jaw. Mouth is terminal, its tip is on or slightly above the level of the middle of the eye; posterior end of the upper jaw reaches the vertical from the middle of the nostril. Lower jaw is long (11 - 14% Sl or 35 - 46% lc); its joint with a quadrate is in line with the centre or (in larger specimens) the posterior part of the eye. As can be seen in Table 1 there are some differences in several measurements between fishes from the Tigris and from Anatolia, the latter having a larger head. However, there are too few specimens for statistic analysis.

Leuciscus lepidus differs from all other *Leuciscus* species in its elongated, long, rather pointed head with projecting lower jaw, which is a typical asp-like feature developed early in ontogeny and is not characteristic even for those *Leuciscus* species the adults of which feed partly or preferably on actively moving prey. The digestive tract of *L. lepidus* from about 100 mm Sl already contains, judging from the radiographs, the remnants of fishes.

Dorsal fin has (8) 9 (10) branched rays; its origin is on (in the small fishes) or somewhat posterior to the vertical from the posterior end of the ventral fin base. Dorsal fin margin is straight or slightly concave. Anal fin has 9 - 11, commonly 10, branched rays (9 - 12 given by COAD (1982, 1985) for *L. lepidus* from Iran). Anal fin margin is convex or wavy (convex-concave). All counts are usual for a *Leuciscus* species.

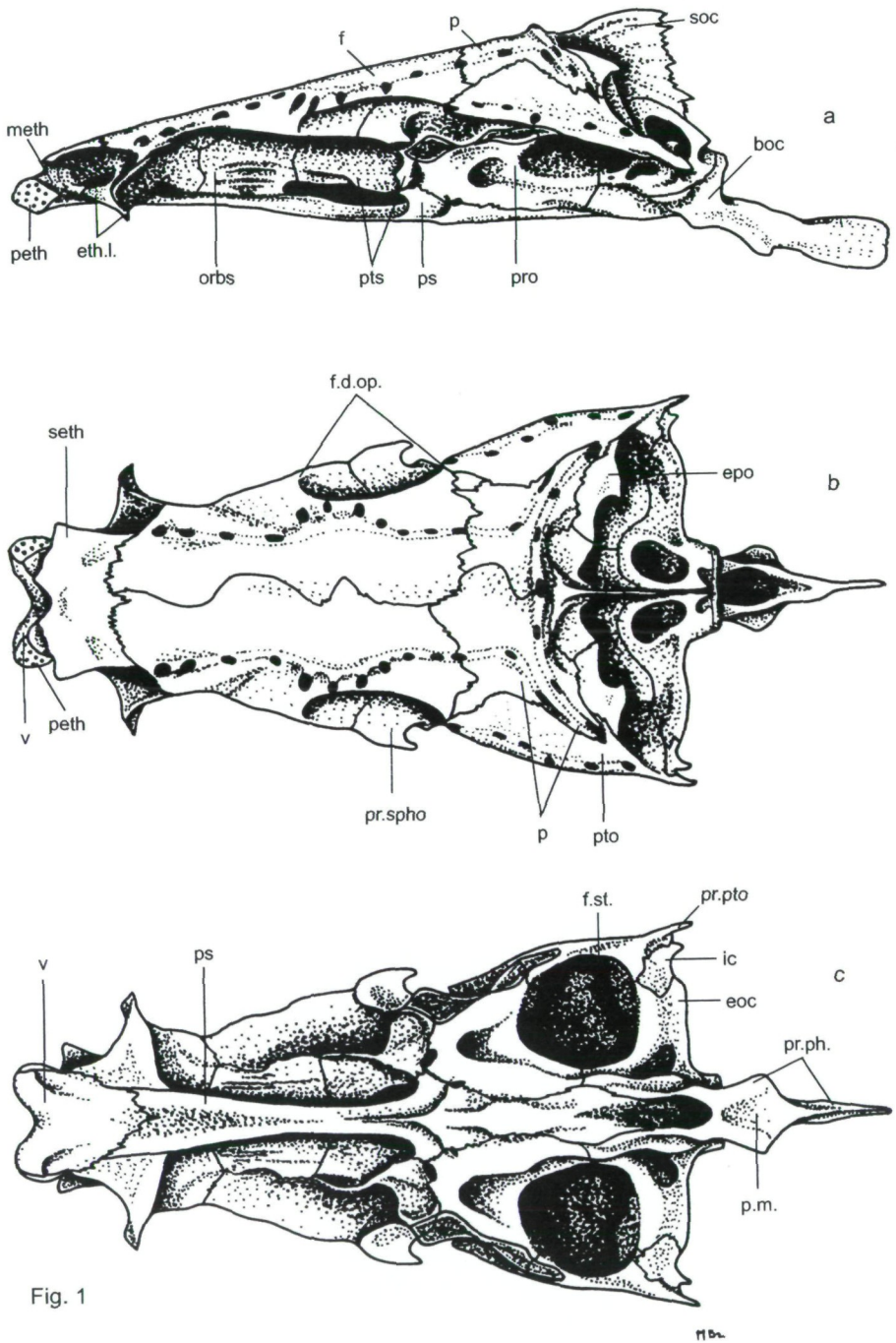


Fig. 1

Fig. 1. *Leuciscus lepidus*. Beyşehir Lake, SI unknown, neurocranium base length 53.1 mm, ZMH 1134. Neurocranium, lateral (a), dorsal (b) and ventral (c) views. Cartilage dotted.

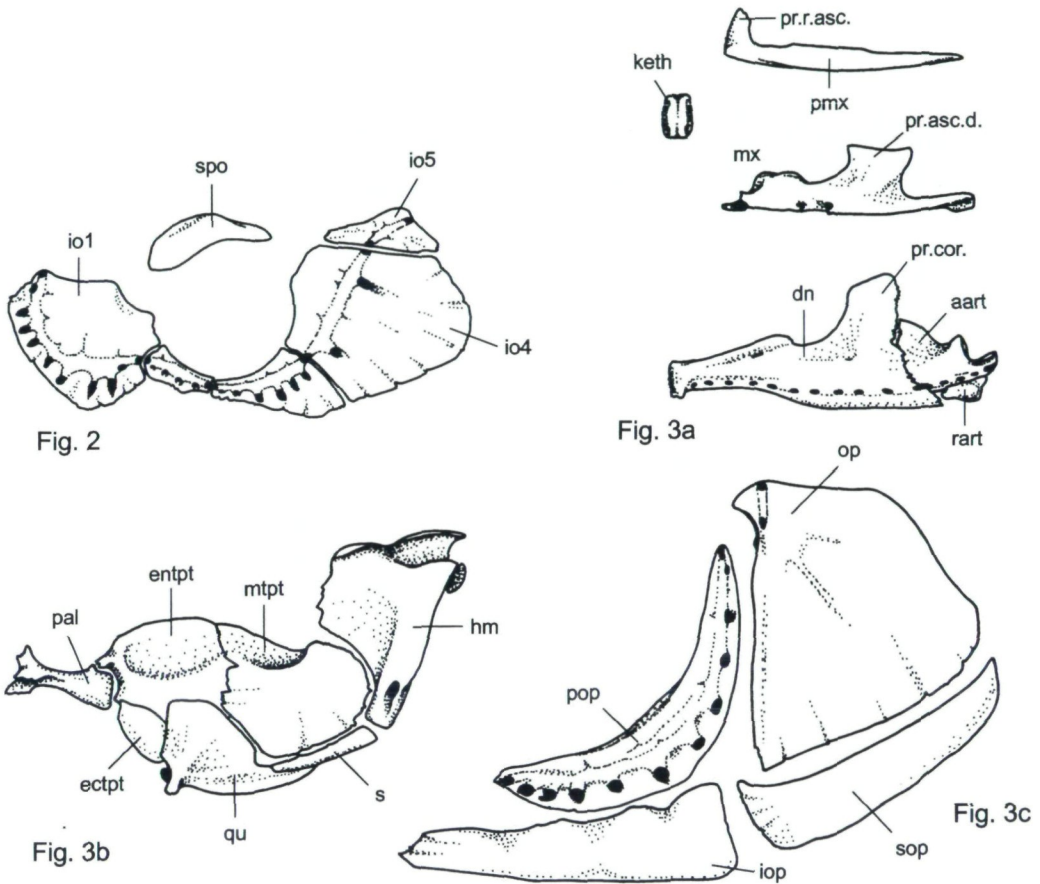


Fig. 2 - 3. *Leuciscus lepidus*, Beyşehir Lake, SI unknown, neurocranium base length 53.1 mm, ZMH 1134. (2) Circumorbitals, (3) Jaws (a), palato-quadrate complex and hyomandibular (b) and opercular bones (c).

Gill-rakers are short and widely spaced, (8) 9 - 11 in total (12 - 18 total given by COAD 1985). Pharyngeal teeth 2.5 - 5.2, 2.5 - 4.2, strongly hooked and serrated. Total number of vertebrae 42 - 45 (46) (abd. vert. 23 - 25 (26), caud. vert. 18 - 20) (total number of vertebrae given in COAD (1985) is 41 - 43). In the genus *Leuciscus*, the number of vertebrae varies between 35 and 46, commonly being 40 - 44; the smallest numbers occur in *L. squaliusculus*, *L. borysthenicus* and *L. smyrnaeus* - 35 - 40. In *Aspius* AGASSIZ, 1832, *Aspiolucius* BERG, 1907, *Elopichthys* BLEEKER, 1859, *Tribolodon* SAUVAGE, 1833, *Pseudaspius* DYBOWSKI, 1869, and *Luciobrama* BLEEKER, 1870, the vertebral number ranges from 47 to 55.

Scales are of moderate size, 45 - 50 in l.l. (up to 55 according to COAD 1982, 1985). Among *Leuciscus* the number of l.l. scales ranges from 30 to 60, 40 - 55 being the most

usual number; the lowest number, 36 - 40, occurs in *L. borysthenicus*, and in *L. smyrnaeus* which has s.l. 30 - 35, the lateral line often incomplete and interrupted; the greatest number, 65 - 78 and 71 - 80, are in, respectively, *L. microlepis* and *L. turskyi*. The increased number of l.l. scales is a widespread feature among the Leuciscinae and occurs, for example, in *Aspius*, *Aspiolucius*, *Elopichthys*, *Pseudaspius* and some species of *Pseudophoxinus* BLEEKER, 1859.

The lateral line is complete as in most *Leuciscus* species, and there is usually one, rarely two, terminal unpierced scales. It is slightly curved downward behind the pectorals. CSO is lengthened in its posterior section and downwardly bent passing close to CST: it reaches the lateral border of the parietal and often enters the pterotic in a groove or entirely enclosed in a bone canal. The elongation of CSO continues in ontogeny appearing in fishes of 50 - 80 mm SL; the other cephalic canals complete their formation earlier - the latter morphological events are: completion of lateral line in specimens from 43.0 mm SL and CIO-CPM intercommunication above the opercular antero-dorsal process in specimens of 41 - 43 mm SL and disappearance of CIO canal interruptions below the eye and anterior to the pterotic in fishes of 43 - 47 mm SL. The same configuration of CSO as in *L. lepidus* usually occurs among *Leuciscus* species in *L. latus*, *L. lehmanni*, *L. cephalus*, *L. pyrenaicus*, *L. svallize*, *L. illyricus* and *L. ulanus*, and also in *Aspius*, *Aspiolucius* and *Pseudaspius*. CIO, CPM and CST are complete. The overall topography of the cephalic sensory canals is a typical *Leuciscus* pattern (BOGUTSKAYA 1988a) but the number of canal pores is strongly increased: (12) 13 - 17 (18, 19) in CSO, 21 - 32 (33, 37) in CIO, 21 - 28 (30) in CPM and (9) 11, 13 (15) in CST, being as numerous as in *Aspius* (15 - 19, 22 - 28 (29), 23 - 29 and 7 - 9 in CSO, CIO, CPM and CST respectively in *A. aspius*). Increased number of pores can be also well illustrated by the number of canal openings on the individual bones: (4) 5 - 7 on the nasal, (7) 8 - 11 on the frontal, 7 - 11 on the 1st infraorbital, 7 - 12 on the dentary, 3 - 5 on the anguloarticular and (9) 10 - 14 (15) on the preoperculum. In most *Leuciscus* species CSO usually has 9 - 12, most often 10 or 11 pores with 3 or 4 and 6 or 7 openings in, respectively, the nasal and frontal; slightly increased number of CSO pores - up to 13, rarely 15 - occurs in *L. cephalus*, *L. idus*, *L. microlepis* and *L. svallize* with number of nasal and frontal openings up to 5 (6) and 7, 8 (9) respectively. CIO usually possesses fewer than 20 pores with (4) 5 (6) openings in the 1st infraorbital; 17 - 23 and 19 - 25 CIO pores occur in *L. cephalus* and *L. svallize* with (5) 6 - 8 (9) and 5 - 8 1st infraorbital openings respectively. CPM most commonly has 14 - 18 pores, 17 - 21 occurring only in *L. bergi*, *L. cephalus*, *L. idus* and *L. microlepis*; the most frequent number of openings is 2 or 3 in the anguloarticular, 9 - 11 in the preoperculum and 5 or 6 in the dentary; the later number is only increased to 5 - 7 (8) in *L. waleckii*, *L. idus*, *L. bergi*, *L. svallize* and (5) 6 - 8 (9) in *L. cephalus* and *L. microlepis*. An increased number of sensory pores is a derived character within the Leuciscinae as a whole, for example, in some species of *Pseudophoxinus*, in the tribes Elopichthyini, Aspinini and Pseudaspinini sensu BOGUTSKAYA (1990a, 1991b). In each of these groups, however, increase in sensory pore numbers occurs on a base of different canal patterns (types of canal arrangement and interconnections) (BOGUTSKAYA 1988a, 1990b, 1991c, 1992). Among the taxa mentioned, *Leuciscus*, the Aspinini (*Aspius* and *Aspiolucius*) and Elopichthyini (a monotypic tribe) have a similar cephalic canal pattern characterized specifically by a complete CPM communicating with CIO. The three latter genera have a comparatively high number of pores but the numbers differ in the individual canals: CSO 20 - 24, CIO 25 - 30, CPM

23 - 32, CST 11 - 15 (*Aspius vorax*); CSO 15 - 20, CIO 30 - 36, CPM 25 - 31, CST 7 - 9 (*Aspiolucius esocinus*); CSO 19 - 21, CIO (21) 23, 24 (26), CPM (24) 25 - 27, CST 9 - 11 (*Elopichthys bambusa*).

The neurocranium (Fig. 1) is comparatively broad and low, especially in its ethmoid region; proportions of the neurocranium (% L bas.n.) are as follows: H eth 9 - 11%, H soc 30 - 31%, Lt eth 38 - 40%, Lt spho 44 - 46%, Lt pto 51 - 53%. A similar depth of neurocranium in both ethmoid and occipital regions (less than 11% and less than 33% L bas.n. respectively) occurs among the examined *Leuciscus* species only in *L. cephalus* and *L. pyrenaicus*. In *Leuciscus*, the depth and width of the neurocranium vary; compared to other leuciscins, the neurocranium can be characterized as being moderately deep and broad: in most species H eth, H soc, Lt spho and Lt pto are between 12 - 15, 32 - 36, 35 - 40, 46 - 53 and 50 - 58% L bas.n. respectively (13 - 15, 32 - 36, 35 - 38, 47 - 52 and 50 - 55% L bas.n. respectively in *L. leuciscus*, fig. 4). In *L. borysthenticus*, *L. smyrnaeus* and *L. squaliusculus*, the skull is much broader in its posterior portion: Lt spho is 53 - 60% and Lt pto is 57 - 64% L bas.n.. *Aspius aspius* is characterized by somewhat shallower neurocranium (Fig. 7) (its width in all regions is as in most *Leuciscus*): H eth is 7 - 10 and H soc is 30 - 34% L bas.n. *Aspius vorax* and *Aspiolucius esocinus* have a narrower skull: Lt eth, Lt spho and Lt pto are about 32, 41, 43 and 32, 35, 42% L bas.n. respectively. Narrow (to different degrees) neurocrania also occur in the members of the Pseudaspinini - *Oreoleuciscus*, *Tribolodon*, *Pseudaspius*, *Luciobrama* (HOWES 1978, 1984, BOGUTSKAYA 1988b, 1991a, and others) but in contrast to the Aspinini (*Aspius*, *Aspiolucius*) and *Elopichthys* which have short and broadened bones of ethmoid region, it is accompanied in the Pseudaspinini by a marked elongation of the ethmoid region (HOWES 1978: fig. 3, BOGUTSKAYA 1990b: fig. 1, 3, 1991a: fig. 4, 5).

In order to estimate the degree of "wideness" or "narrowness" of crania in undissected fishes measurements were made of neurocranial width (Lt pto) in relation to cranial roof length (L.cr.r., length of the neurocranium from the anterior margin of the supraethmoid to the beginning of scales at nape which occurs just behind CST at supraoccipital crest base). In *L. lepidus* Lt pto is 68 - 82% L cr.r.; and in the closest species there was found almost the same width: 78 - 83% in *L. ulanus*, 82 and 72% in the holotypes of *L. mongolicus* and *L. huanchicus* respectively, 68 - 77% in *L. illyricus* and *L. svallize*, 76 - 82% in *L. pyrenaicus*. The species with narrow crania have Lt pto less than 65% L cr.r., commonly less than 60% (*Aspius vorax*, *Aspiolucius*, *Oreoleuciscus*, *Pseudaspius*, *Luciobrama*). It should be mentioned here that in the species with a broad skull and in the species with a narrow skull (as measured in large adult specimens) there is a difference in ontogenetic trends of skull development. In the species with a moderately broad skull (most *Leuciscus* spp.) the maximum cranial width changes only slightly in ontogeny, for example, in *L. lepidus* Lt pto in fishes of Sl less than 180 mm varies from 68 to 81% L cr.r. and from 72 to 82% in fishes longer than 180 mm. But in *L. cephalus* characterized by much broader skull, Lt pto (along with the supraethmoid and interorbital space width) markedly increases: 74 - 82% L cr.r. in specimens of 50 - 150 mm Sl (similar to *L. lepidus* of the same size) and from 79 (commonly 81) to 94% L cr.r. in larger specimens. The same tendency as in *L. cephalus* occurs in *A. aspius*. The contrary ontogenetic changes can be seen in the above mentioned narrow-skulled species of the tribe Pseudaspinini, for example, in *Oreoleuciscus humilis* Lt pto is 56 - 64 L cr.r. in fishes of 60 - 120 mm Sl and 40 - 45 in specimens of Sl more than 350 mm.

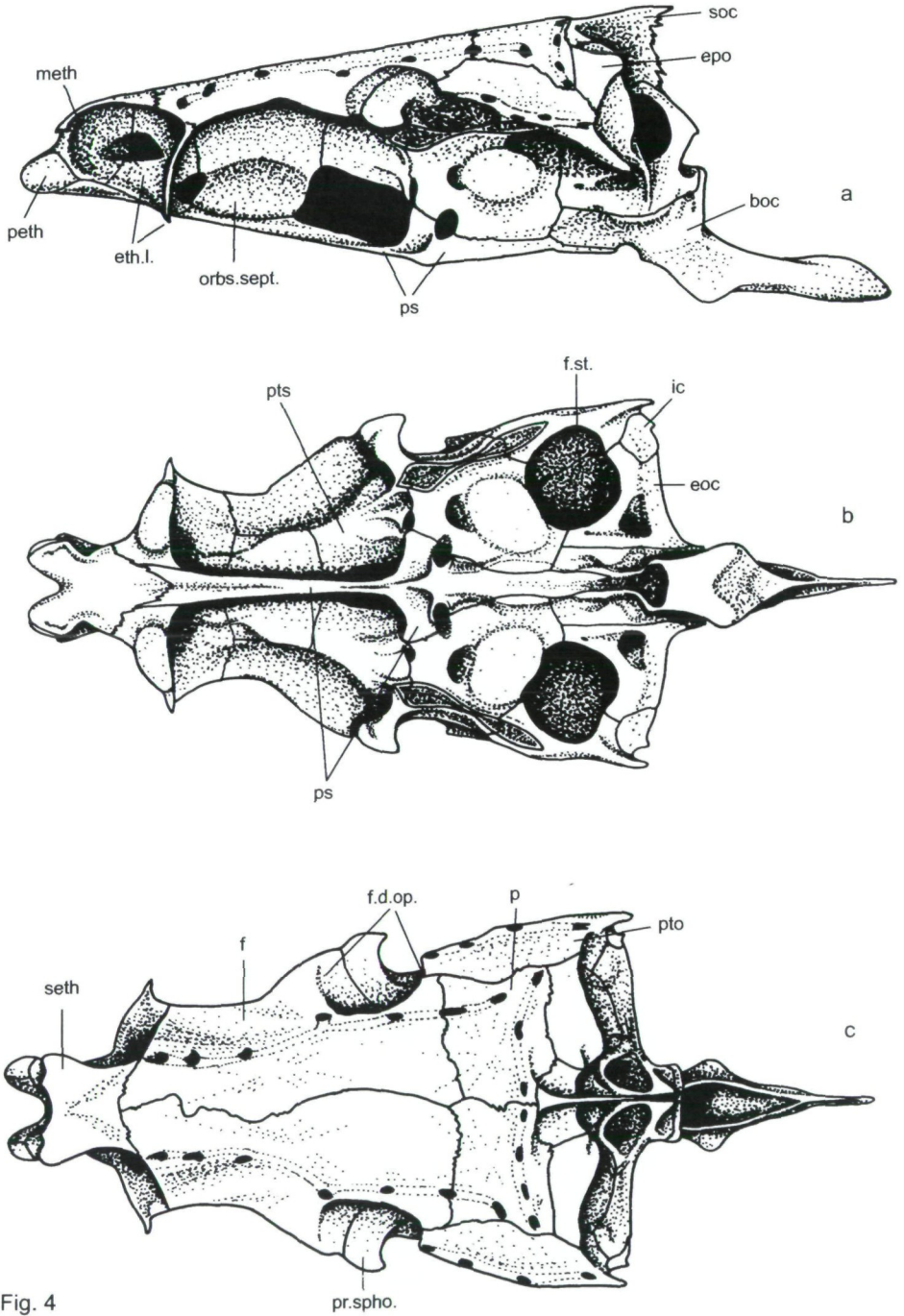


Fig. 4

Fig. 4. *Leuciscus leuciscus*, Dnieper River, Sl 176.2 mm. Neurocranium, lateral (a), ventral (c) and dorsal (c) views.

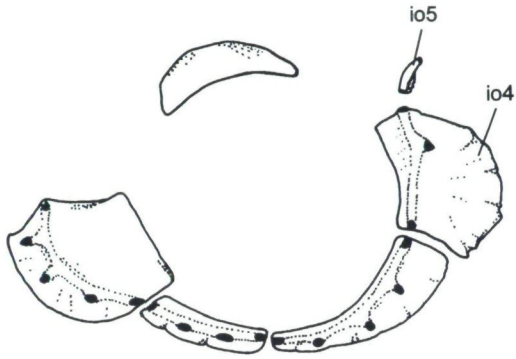


Fig. 5

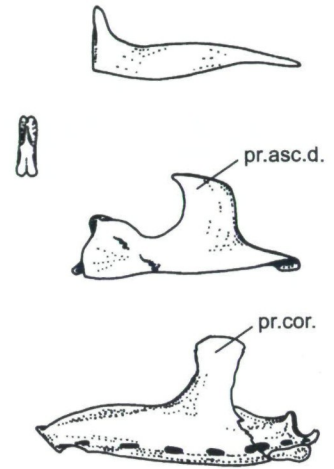


Fig. 6a

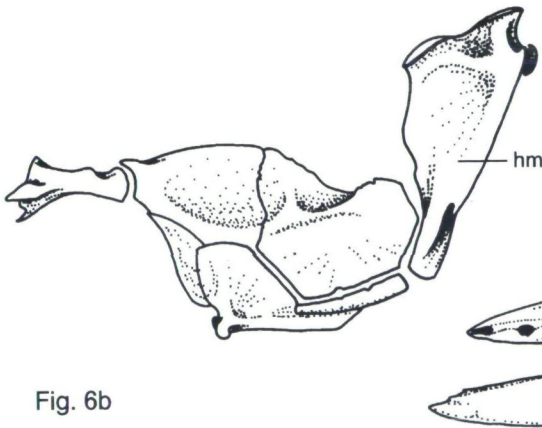


Fig. 6b

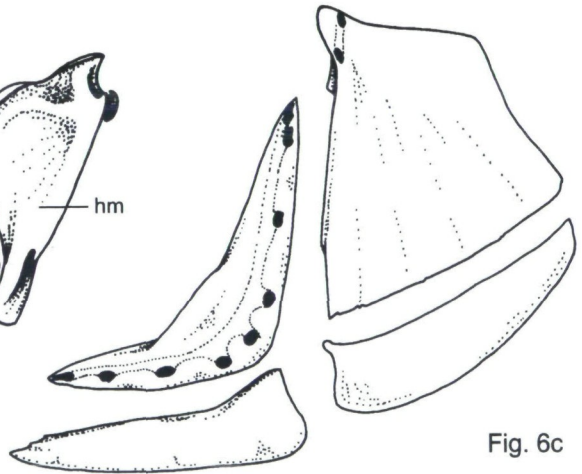


Fig. 6c

Fig. 5 - 6. *Leuciscus leuciscus*, Dnieper River, Sl 176.2 mm. (5) Circumorbitals, (6) Jaws (a), palato-quadrate complex and hyomandibular (b), opercular bones (c).

The supraethmoid is broad and short, its width is between 140 - 196% of its length in the midline. The antero-medial part of the supraethmoid is slightly produced rostrally, and the medial anterior notch and two lateral anterior notches are shallow. The mesethmoid is depressed. The preethmoid is entirely cartilaginous. The vomer is wide and shallowly indented on the anterior margin, without well-defined lateral notches separating the anterior processes of the vomerine head from its shaft as it occurs in most *Leuciscus* (Fig. 1c, 4b).

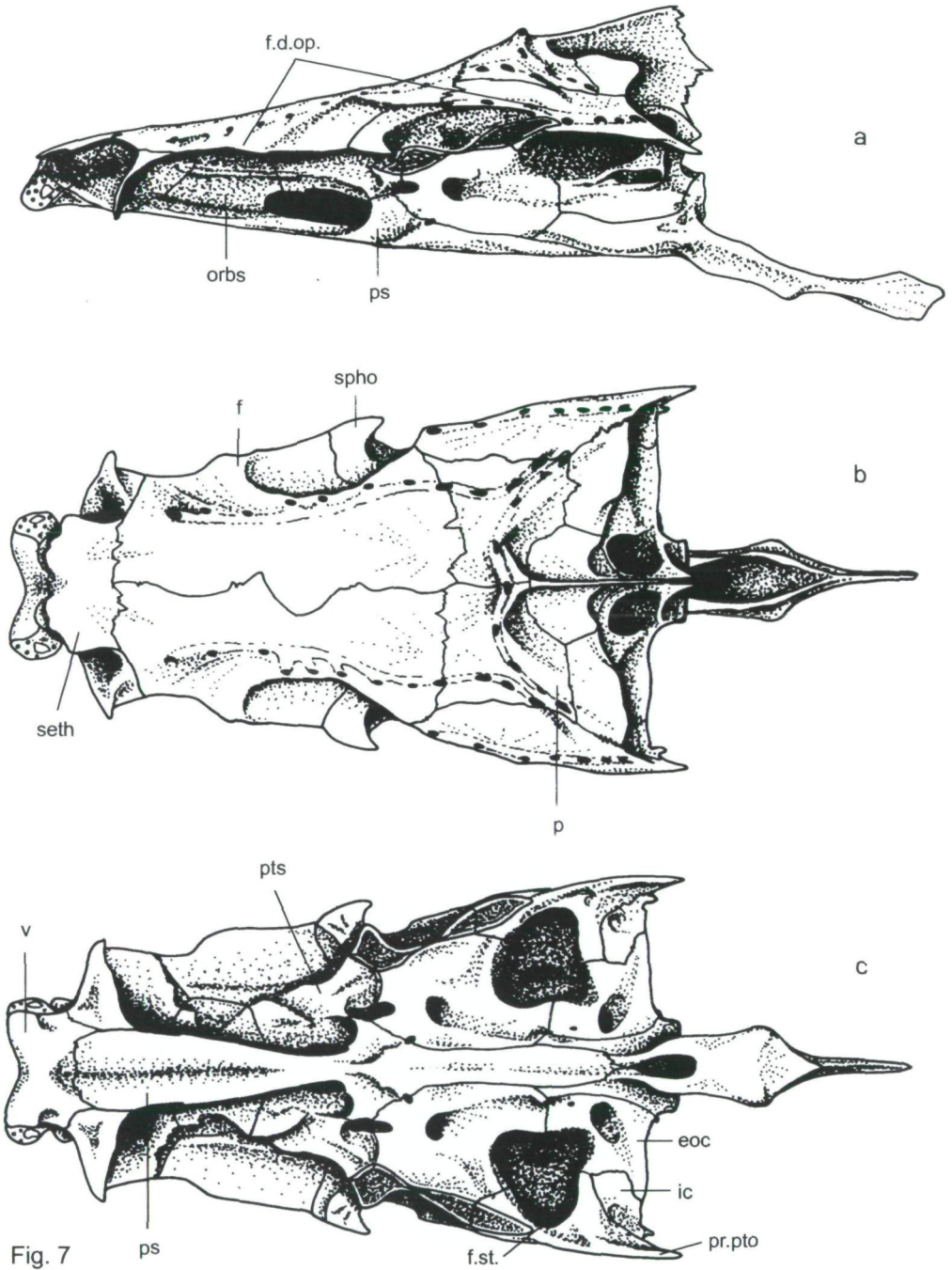


Fig. 7. *Aspius aspius*, Volga River mouth, SI 420.0 mm. Neurocranium, lateral (a), dorsal (b) and ventral (c) views. Cartilage dotted.

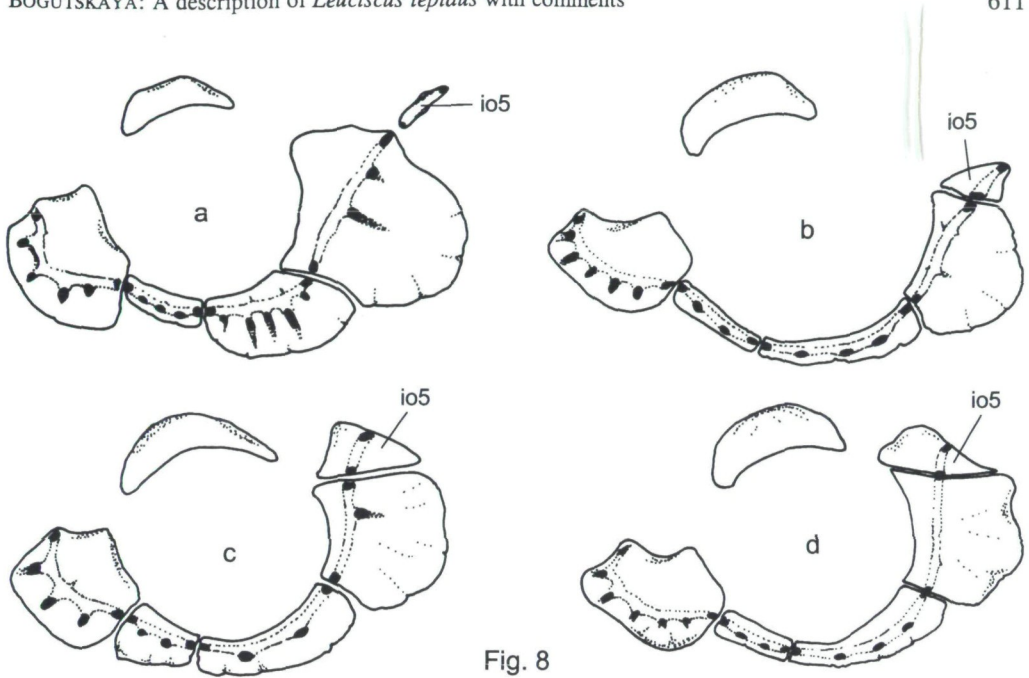


Fig. 8

Fig. 8. Circumorbitals of a) *Aspius aspius*, Volga River mouth, Sl 420.0 mm, b) *Leuciscus spurius*, Karasu River, south-eastern Turkey, Sl 80.6 mm, c) *Leuciscus pyrenaicus*, Guadiana River, Sl 147.5 mm, d) *Leuciscus cephalus orientalis*, Marmara Lake, Turkey, Sl 136.4 mm.

The supraethmoid in most *Leuciscus* species possesses shallow but prominent elements (medial and lateral notches and processes) of the anterior margin. Its width is about equal to its length in the midline or a little larger (in *L. borysthenticus* and *L. idus* up to 130% of its length) being 28 - 34% Lt pto. In contrast, the supraethmoid of *L. lepidus* has a smoothed anterior margin and can be considered as rather shortened and broad (its width is 32 - 39% Lt pto in specimens of 37 - 77 mm Sl and 35 - 42% in larger ones) being almost of the same shape and size as in *A. aspius*, the width of supraethmoid of which is 150 - 210% of its length and 36 - 44% Lt pto. In *A. vorax* and *Aspiolucius esocinus* the supraethmoid is generally smaller but also relatively shortened. Within the genus *Leuciscus* there are also a few species which are characterized by a slightly broadened supraethmoid (*L. ulanus*, *L. pyrenaicus*, *L. illyricus*) or a wide one (*L. cephalus*) along with a broad and shortened vomer. In the latter species the supraethmoid width varies from 120 to 200% of its length and increases in ontogeny: in fishes up to 180 mm Sl it is between 35 and 39% Lt pto and in longer specimens - between 38 and 43% Lt pto. In all cases the shortening of the supraethmoid coincides with the shortening and broadening of the vomer (Fig. 1b, 1c, 7b, 7c) In *L. lepidus*, *L. cephalus*, *L. mongolicus*, *L. ulanus*, *L. illyricus*, *L. svallize*, *L. pyrenaicus* and the Aspinini the supraethmoid is rectangular while in the Pseudaspinini it is elongated (its length being greater, often markedly, than its width), with rounded lateral margins of the anterior part of the bone and a narrower posterior part (see, for example, Fig. 3 in HOWES 1978 and Fig. 4, 5 in BOGUTSKAYA 1991a). The vomer of the latter is also elongated.

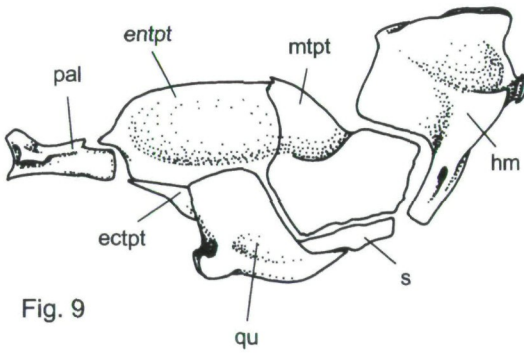


Fig. 9

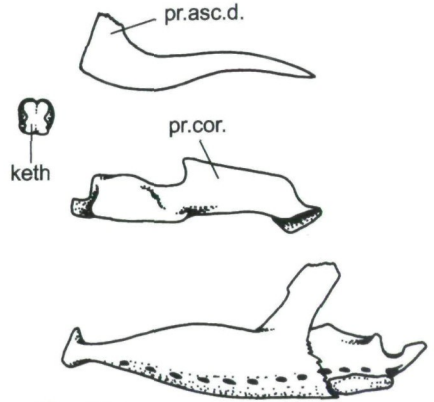


Fig. 10a

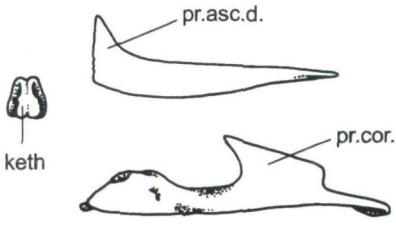


Fig. 10b

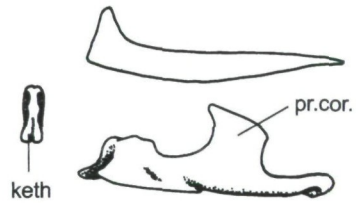


Fig. 10c

Fig. 9. *Aspius aspius*, Volga River mouth, Sl 420.0 mm. Palato-quadrates complex and hyomandibular.

Fig. 10. Jaws of a) *Aspius aspius*, the same specimen, b) *Leuciscus cephalus*, Oka River, Sl 151.0 mm, c) *L. pyrenaicus*, Guadiana River, Sl 147.5 mm.

The depth of the mesethmoid determines the entire depth of the ethmoid region which is, as already mentioned, comparatively low in *L. lepidus*, *L. cephalus*, *L. pyrenaicus*, *L. illyricus*, *L. svallize*, *L. ulanus*, *L. spurius* (the latter four spp. seen in radiographs), where the mesethmoid is depressed. This feature is widely spread in leuciscins with low neurocrania.

In *L. lepidus* the lateral ethmoid contains the entire olfactory foramen. This foramen in most *Leuciscus* species and generalized taxa of the subfamily lies between the mesethmoid and lateral ethmoid. In many morphologically derived leuciscins, including some of the Aspinini and Pseudaspinini, the olfactory foramen is bordered by the lateral ethmoids; among *Leuciscus* species studied by dissections this feature is also present in *L. cephalus* and the larger specimens of *L. pyrenaicus* and *L. idus*. As to the preethmoid ossification, the degree varies greatly from absence to complete development within *Leuciscus* and other genera under consideration.

The entire orbital region is markedly depressed. The interorbital septum of the orbitosphenoid is highly reduced being only a thickened base of the orbitosphenoid lateral wings. The pterosphenoid is elongate, being longer than the orbitosphenoid, and has a long contact (over about 1/2 of its length) with the paired bone in front of the orbital opening - the feature also found within *Leuciscus* in larger specimens of *L. cephalus* and *L. idus*. The pterosphenoid bears a prominent lateral shelf which serves as a site for the origin of the anterior part of the adductor arcus palatini muscle, the most part of which (all of the muscle in *Leuciscus* except for *L. cephalus* which resembles *L. lepidus*) has its origin from the pterotic and parasphenoid. The pterosphenoid contacts the ascending process of the parasphenoid by the comparatively extensive postero-lateral process; it is the only example within *Leuciscus* of such an extensive lateral contact between the pterosphenoid and parasphenoid. The parasphenoid is broadened anteriorly almost to the same degree as in *Aspius* (Fig. 1c, 7c); the interorbital part of the parasphenoid is also wide in *L. cephalus* and *L. pyrenaicus* compared to the typical *Leuciscus*-like condition (Fig. 4b). The parasphenoid is horizontally aligned, without a prominent angle (about 160° in most *Leuciscus*) between its interorbital and cerebral parts. The orbital opening between the pterosphenoid, orbitosphenoid and parasphenoid (from lateral view) is extremely shallow (Fig. 1a). The carotid foramen is very small. Most of these features, more or less pronounced, are characteristic of some other piscivorous cyprinids with depressed crania and distinguish *L. lepidus* from the majority of *Leuciscus* species, the typical representative of which is *L. leuciscus* (Fig. 4). Concerning the characters mentioned, *L. lepidus* closer resembles *Aspius*, especially *A. aspius*. Within the genus *Leuciscus* there are also those species representing the intermediate grades or stages of development of some structures in the orbital region between the typical *Leuciscus* state and those found in *L. lepidus* and the *Aspinini*. A more depressed, compared to typical *Leuciscus*, orbital region (shallow interorbital septum, slightly curved or almost straight parasphenoid, elongated pterosphenoid, shallow orbital opening, small carotid foramen) also occurs in *L. mongolicus*, *L. illyricus*, *L. svallize*, *L. ulanus*, *L. spurius*, *L. pyrenaicus* and, to the greatest degree, *L. cephalus*, where in the larger specimens the interorbital septum is entirely lacking. It has to be emphasized that the features described here, along with some other (elongation of occipital cranial region, shape of jaws, etc.), develop comparatively late in the ontogeny of these *Leuciscus* species from a more generalized type while in the more morphologically specialized *L. lepidus* and the *Aspinini* they can be found at much earlier ontogenetic stages (already present in fishes of SL about 50 - 80 mm).

The dilatator fossa in *L. lepidus* is comparatively long due to the rostral expansion onto the frontal; its length is about 33% L bas.n. while in the other *Leuciscus* species studied it is 20 - 27% L bas.n. The frontal, which bears a ridge, and the antero-lateral portion of the pterotic form a medial roof to the fossa. The lateral process of the sphenotic is hooked, with a deeply indented posterior border. The two latter characters are mosaically spread in *Leuciscus*, the *Aspinini* and some other taxa (i.e. *Alburnini*) so its phylogenetic significance is unclear.

The subtemporal fossa is forwardly deepened with the sphenotic contributing to the anterior apex; the fossa opening is slightly triangular. In *Leuciscus* it is usually ovate or round and the fossa is formed from the epiotic, exoccipital, prootic and pterotic; only in *L. idus*, *L. cephalus* and larger specimens of *L. waleckii* does the sphenotic also

contribute to the fossa. This feature is also found in the Aspinini and, among the taxa close to *Leuciscus*, in some ecomorphs of *Rutilus rutilus* (LINNAEUS, 1758), *Rutilus frisii* (NORDMANN, 1840), and *Leucalburnus satunini* (BERG, 1910).

The posterior part of the neurocranium (behind the vertical from the anterior border of supraoccipital) is lengthened due to the extension of the posterior portion of the epiotic and the exoccipital wing, and due to the markedly posteriorly lengthened lateral portion of the parietal and elongation of the pterotic. The cranial roof is relatively short being 72 - 74% L bas.n. (71 - 73% L bas.n. in *Aspius*) which differs from the state in other *Leuciscus* species (75 - 79% L bas.n.). The posterior pterotic process is long, pointed, and caudally directed. The supraoccipital crest is deep, highly pronounced, with a concave dorsal margin. The relative elongation of the posterior cranial portion (formation of a "postcranial platform" sensu HOWES 1978, 1984) is a common but variously developed feature in predatory leuciscins with a depressed, more or less attenuated neurocranium, and is discussed in the literature (HOWES 1978, 1984). The only problem is to estimate the degree of elongation since in different taxa one finds different states of its development. In the case under consideration the most prominent feature shared by *L. lepidus* and the Aspinini is a posteriorly expanded lateral portion of the parietal (Fig. 1b, 7b, cf. *L. leuciscus*, fig. 4c) though the postcranial platform is much narrower in *L. lepidus*.

Tab. 1: Measurements of *Leuciscus lepidus*. Lectotype from Tigris = NMW 49342: 1, Paralectotypes from Tigris (n = 5) = NMW 99342: 2, NMW 49343, NMW 49344 and SMF 847; Specimens from Anatolia (n = 17) = ZMH 1134, ZHM 2463 and ZHM 3554.

Character	Tigris (Lectotype)	Tigris (Paralectotypes)	Anatolia Beysehir L., Aksu R.
SL, mm	237,0	85,8 - 223,1	84,5 - 219,4
in % SL			
prO	7,8	7,6 - 8,8	8,3 - 9,8
Oh	4,8	4,8 - 6,5	4,5 - 6,5
poO	15,8	14,8 - 16,3	16,5 - 19,6
lc	28,0	27,8 - 30,0	30,5 - 33,3
hc	15,7	15,7 - 16,8	17,1 - 19,0
lac	14,4	13,5 - 14,3	13,3 - 16,0
io	10,6	9,9 - 10,6	8,4 - 9,9
lmd	11,9	11,8 - 12,5	12,0 - 14,3
H	23,6	22,3 - 24,4	21,7 - 26,3
h	11,7	10,6 - 12,2	10,3 - 12,0
pD	55,6	53,1 - 55,9	54,3 - 59,2
poD	34,9	33,7 - 36,5	31,5 - 35,6
lpc	18,6	16,7 - 20,0	16,2 - 20,0
lD	11,4	11,1 - 11,7	10,0 - 12,5
hD	18,8	17,1 - 20,8	16,2 - 19,9
lA	12,2	11,2 - 13,0	9,9 - 10,8
ha	14,0	14,5 - 16,3	12,6 - 15,1
lP	18,6	17,7 - 19,9	15,5 - 18,1
lV	15,9	15,5 - 17,2	12,8 - 14,9
P-V	26,9	26,2 - 29,1	22,1 - 28,2
V-A	23,2	20,3 - 24,1	17,9 - 23,0

The pharyngeal process has a deeply indented masticatory plate which is pentagonal. The masticatory plate, compared to *Leuciscus* species where it is located mostly under the basioccipital bone body, is shifted posteriorly in *L. lepidus* (its anterior margin lies almost on the level of the posterior articulating surface of the basioccipital) as it occurs in *Aspius* and *Aspiolucius* too.

The infraorbitals (Fig. 2) are large; the 3rd, 4th and 5th are expanded. The upper part of the 4th and triangular-shaped 5th infraorbital cover almost the entire surface of the dilatator operculi muscle over the dilatator fossa, though in smaller specimens the size of these elements varies and they are proportionally smaller. Sometimes the 4th and 5th infraorbitals are fused. The infraorbital sensory canal in these bones runs at a divergent angle to the orbit. Compared to the other *Leuciscus* species and even *Aspius* (Fig. 8a) and *Pseudaspius*, the 4th infraorbital in *L. lepidus* - in large specimens - is exclusively broad. In most *Leuciscus* species the 4th infraorbital is moderately broad (its depth on the level of sensory canal is about equal to its length) and does not reach with its posterior border the free margins of the preoperculum and the antero-dorsal opercular process; the 5th infraorbital is tube-like or with a small lamellar portion (Fig. 5). The same configuration of infraorbitals was also found in the type-specimens of *L. mongolicus* and *L. huanchicus* differing from the description given by HOWES (1984). In *L. ulanus* and *L. spurius* (Fig. 8b) the 4th and 5th infraorbitals are more extensive, the latter being well-defined and triangular-shaped. In *L. pyrenaicus* (Fig. 8c) and *L. cephalus* (Fig. 8d) occurs a more derived state - most commonly the 4th infraorbital is very broad (its length is up to 170% of its depth) and reaches the borders of the preoperculum and the antero-dorsal process of the operculum (in *L. cephalus* the latter process usually fits a notch on the posterior margin of the 4th bone), the 5th infraorbital is extensive and covers the entire outer surface of the dilatator fossa closely adjoining the borders of the fossa. This character state may be less prominent in smaller specimens. Like in some individuals of *L. lepidus* (in two specimens on one side of the head) and, more often, in *L. cephalus* and *L. pyrenaicus* the 4th and 5th infraorbitals are fused forming one complex bone. This feature is much more frequent in *L. illyricus* and *L. svallize* but their infraorbitals are narrower. The 5th infraorbital is extremely variable in *L. svallize*: i.e. it may be absent with only the dermal sensory canal segment present; be a tube-like bone; be a triangular-shaped bone of various configuration, or be fused with the 4th infraorbital sometimes showing a suture. The angle formed by CIO behind the eye varies in the *Leuciscus* species mentioned and seems to be correlated with postorbital space length. These species, including *L. lepidus*, differ from the Aspinini, the group which also possesses an expanded 4th infraorbital of similar configuration, in having a broad triangular 5th infraorbital which, in the Aspinini as well as in the Pseudaspinini and Elopichthyini, is tube-like or narrow.

The premaxilla and maxilla are elongate; the shape of the maxillary ascending dorsal process (Fig. 3a) is closer to that of *L. pyrenaicus* (Fig. 10c) than to the comparatively broad and low process of *L. cephalus* (Fig. 10b). The coronomeckelian bone is elongate and pointed at the ends. The lower jaw is long, 57 - 60% L bas.n. In most *Leuciscus* species the length of the lower jaw is between 40 and 48% L bas.n., being a little longer in *L. idus* and *L. waleckii* - up to 47 - 51 and 48 - 49% L bas.n. respectively. In larger specimens of *L. cephalus* and *L. pyrenaicus* it can attain 58% L bas.n. and 61 - 65% L bas.n. in species of the Aspinini. Long jaws (with the upper one being weakly protractile)

are a common feature of all active predatory cyprinids; more significant are the morphological differences in structure of the jaws in different phylogenetic assemblages of the leuciscins with long jaws. Thus, in *Elopichthys bambusa* the premaxilla has a large rostral ascending process and is non-protractile being entirely fused (in specimens longer than 330 - 400 mm) with the maxilla which has a very broad and shallow ascending dorsal process; the kinethmoid is short and wide; the coronoid process is high, placed on the very end of the lower jaw and formed from both the dentary and anguloarticular (the closest state occurs only in *Luciobrama*). In the other piscivorous leuciscins the premaxilla is protractile, though weakly, and the coronoid process is entirely formed by the dentary. In the Aspinini (Fig. 10a) the ascending dorsal process of the maxilla is also wide and shallow (almost entirely reduced in *Aspiolucius*) and the kinethmoid is broad. In contrast, the Pseudaspinini have the maxillary ascending dorsal process well-defined, comparatively narrow and high, and the kinethmoid rather long and rod-shaped.

The palato-quadrate complex and opercular bones in *L. lepidus* are without special peculiarities compared to the other *Leuciscus* species (Fig. 3b, 3c, 6b, 6c,). The hyomandibular (Fig. 3b) is shallow, its depth being 38 - 40% L bas.n. (cf. 40 - 54%, mostly more than 43% L bas.n. in other *Leuciscus* (Fig. 6b); 30 - 42 and 27% L bas.n. in *Aspius* (Fig. 9) and *Aspiolucius* respectively; the hyomandibular ventral limb is well-pronounced similar to the Aspinini in contrast to the most Pseudaspinini with a reduced hyomandibular ventral limb.

Tab. 2: The main morphological differences between the tribes Aspinini and Pseudaspinini.

Character	Character state	
	Aspinini	Pseudaspinini
CPM-CIO connection	always present	absent (except for <i>Tribolodon brandii</i> with secondarily elongated CPM); CPM terminates at the superior end of preoperculum
Supraethmoideum	broad, short, rectangular-shaped	elongated, often narrow, with rounded anterior part
Subtemporal fossa	with contribution from sphenotic	with contribution from supraoccipital (in <i>Tribolodon</i> and <i>Oreoleuciscus humilis</i> only in larger specimens)
Hyomandibula	with relatively long ventral limb	with short or reduced ventral limb (except for <i>Luciobrama</i>)
Dorsal ascending process of maxilla	broad and shallow	narrow, relatively deep
Cleithral anterior margin	convex or straight	from concave to markedly bifurcated
Postcleithrum	short	long

The anterior margin of the cleithrum is oblique. The coracoid is shallow, especially in its anterior part. The supracleithrum is ovate, without a pronounced dorsal process or a notch below it. The cleithral anterior border is straight, more or less oblique, or convex in *Leuciscus*, the Aspinini and the most other Leuciscinae. The only group possessing a concave or even markedly bifurcate anterior end of the cleithral horizontal limb among the Leuciscinae is the Pseudaspinini s.l. (including *Phoxinus* AGASSIZ, 1835, and most North American leuciscins).

The description given may be helpful for distinguishing *L. lepidus* by some externally visible characters from *L. cephalus* and *L. spurius* distributed in the same area since identifications of the specimens of these species are sometimes confused in the collections. The only characters usually used for their identification are number of l.l. scales and number of anal branched rays, both partly overlapped in *L. lepidus* with *L. cephalus* on the one hand and *L. spurius* on the other hand. *Leuciscus lepidus* differs from both other species by an elongated, pointed head with a projecting lower jaw, a markedly increased number of cephalic pores and posteriorly expanded lateral portions of the parietals.

To summarize all the data described, the comparison undertaken revealed that within the genus *Leuciscus* there can be distinguished a monophyletic assemblage ("*L. cephalus* s.l. - *L. lepidus*" group) which includes *L. cephalus*, *L. pyrenaicus*, *L. illyricus*, *L. svallize*, *L. ulanus*, *L. spurius* and *L. lepidus*, the latter species being the most derived member of this group and the entire genus. These species share such specialized characters as a shallow neurocranium with depressed ethmoid and orbital regions, a reduced parasphenoidal angle and a reduced interorbital septum, a broad supraethmoid and vomer, expanded 4th and 5th infraorbitals the latter being triangular-shaped, and a long lower jaw with a comparatively shallow maxillary ascending dorsal process. *L. pyrenaicus* and, in particular, *L. cephalus* display the closest morphological affinities to *L. lepidus* but the latter differs from them by such specializations as high number of cephalic pores (though increased a little in *L. cephalus*), elongated occipital region of the neurocranium with a posteriorly expanded lateral portion of the parietal, and a lengthened dilatator fossa.

Unfortunately, there is too little material of *L. merzbacheri* and *L. mongolicus* to judge their relationships with this group of species. *L. merzbacheri*, assigned to a separate genus *Aspiopsis*, is characterized by a rather elongate body, small scales (l.l. 70), and an elongate cranium; in the shape of its infraorbitals this species closely resembles the aspinins (HOWES 1984). *L. mongolicus*⁵ was also assigned to a monotypic genus *Genghis* close to the aspinine group due to the resemblance in a number of characters (HOWES 1984); however, judging by the description of HOWES (1984) and specimens examined, *L. lepidus* is comparatively much more derived (in particular, having strongly increased number of sensory cephalic pores) than *L. mongolicus*.

A lack of equivalent data on some *Leuciscus* species makes it impossible at present to revise the taxonomic structure of the genus. The "*L. cephalus* s.l. - *L. lepidus*" group, in

⁵ *Squalius huanchicus* is usually considered as a synonym of *Squalius mongolicus* (= *Leuciscus mongolicus*) but the holotypes of both nominal species differ in shape of mouth, length of lower jaw, cranial width, and some other features; the holotype of *Sq. huanchicus* is closer to the description of *L. mongolis* given by HOWES (1984).

case the entire genus is anatomically studied in detail, could receive subgeneric rank. This does not coincide with *L. cephalus* species complex sensu BIANCO (1983) and others. *Leuciscus squaliusculus*, *L. smyrnaeus* and *L. borysthenicus* stand apart by having a reduced number of vertebrae, a low number of l.l. scales, a broad and deep neurocranium, cephalic sensory canals with low numbers of pores, and the reduction of some canal portions. By this complex of characters they markedly differ from all of the other *Leuciscus* species.

The "*L. cephalus* s.l. - *L. lepidus*" group is related to *Aspius* and *Aspiolucius* recognized by BOGUTSKAYA (1990a) as the tribe Aspinini. *Leuciscus lepidus* is the species closest to this tribe. The most prominent derived characters shared by them are as follows: a highly increased number of sensory pores in cephalic canals along with a similar canal pattern (cephalic canals are complete, without an interruption between CPM and CIO which occurs in the tribe Pseudaspinini where CPM terminates on preoperculum), a depressed ethmoid region of the neurocranium with a broad and short supraethmoid and vomer, an anteriorly expanded intercalar with well-defined, pointed posterior process, a sphenotic contributing to the subtemporal fossa, and a shallow hyomandibular with a well-developed ventral limb. However, I still retain *L. lepidus* in the *Leuciscus* genus since it lacks some specializations defining the tribe Aspinini, namely a high vertebral number, numerous small scales, a short and broad kinethmoid, a shallow elongated ectopterygoid, an exceedingly broad and low dorsal ascending process of the maxilla, a short postcleithrum, and a tubular 5th infraorbital along with an expanded 4th one.

The tribe Aspinini represents, in my opinion, a distinct monophyletic group not immediately related to the Elopichthyini and the Pseudaspinini (BOGUTSKAYA 1988b, 1990a, 1991a). The members of these three tribes are considered to represent only one assemblage by HOWES (1978, 1984) who includes in it ("aspinine group") 10 genera of leuciscins (*Aspius*, *Aspiolucius*, *Aspiopsis*, *Genghis*, *Elopichthys*, *Tribolodon*, *Oreoleuciscus*, *Pseudaspius*, *Luciobrama*, *Pogonichthys* GIRARD, 1854) which are mostly active predators with an elongate body. Almost each of the characters distinguishing this "aspinine group" - elongation of the cranium, extent of the dilatator fossa, shallow orbitosphenoid septum, CIO divergent from the orbit in the 4th infraorbital, and some others already mentioned above - represents a similar general feature which has a completely different structural genesis in the individual groups of genera as in the case with a long lower jaw. Thus, these characters seem to be superficial similarities of a convergent nature related to active movement, general elongation of the head and body, and formation of strong jaws for capturing prey. Those specializations that distinguish the tribes Aspinini and Pseudaspinini are detailed in Table 2.

The origin and distribution of the "*L. cephalus* s.l. - *L. lepidus*" group and the Aspinini on the one hand and the Pseudaspinini on the other differ: the former are connected with the northern and eastern Mediterranean and Ponto-Aralo-Caspian region (*A. aspius* extends also to more northerly basins and *L. cephalus*, *A. vorax*, *L. spurius*, *L. lepidus* to the Tigris-Euphrates system and adjacent basins). The Pseudaspinini s.l. (including *Phoxinus* and, possibly, the North American leuciscins except for *Notemigonus* RAFINESQUE, 1819) have their origin in Eastern Asia.

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