FishTaxa (2016) 1(3): 118-126

ISSN: 2458-942X

Journal homepage: www.fishtaxa.com © 2016 FISHTAXA. All rights reserved



Article

Historical review on the taxonomy of Squalius berak Heckel, 1843 (Teleostei: Cyprinidae)

Hamid Reza ESMAEILI* Roozbehan KHAEFI, Rasol ZAMMANIAN NEJAD

Ichthyology and Molecular Systematics Lab., Department of Biology, College of Sciences, Shiraz University, Shiraz, Iran. Corresponding author: E-mail: hresmaeili@shirazu.ac.ir

Abstract

The Mesopotamian chub, *Squalius berak* was described from Kueik (Qweik) River in Aleppo Province in Syria by Heckel (1843) and appeared as name only and spelled Berag on p. 1041. It was considered as synonym of *Leuciscus cephalus* (Linnaeus, 1758) for the Euphrates and Tigris Rivers populations. The name of *S. berak* has sometimes been used for various populations of *Squalius* from south-western Anatolia and now as valid species distributed in the Euphrates and Tigris River drainages in Iran, Iraq, Syria and Turkey which drain into the Persian Gulf. *Squalius berak* is distinguished from other *Squalius* species found in the adjacent Caspian Sea, Namak Lake, Kavir and Persian Gulf basins by having a sub-terminal mouth, upper lip projecting beyond lower lip and absence of knob on lower jaw symphysis.

Keywords: Mesopotamian chub, Morphology, Re-description, Distribution, Persian Gulf, Middle East, Tigris River.

Zoobank: urn:lsid:zoobank.org:pub:91D6523E-E9BA-470C-8DAA-426AC8A696F5

Introduction

Chubs of the genus *Squalius* are widespread in Europe and the Middle East (Kottelat and Freyhof 2007; Turan et al. 2009, 2013; Özuluğ and Freyhof 2011; Khaefi et al. 2016). The genus has a high species diversity especially in the Mediterranean basin (Geiger et al. 2014), with only two species known from the Euphrates and Tigris drainages (*S. lepidus* and *S. berak*) (Turan et al. 2013) and 4 species from different basins of Iran: *S. berak* (Tigris River drainage), *S. lepidus* (Tigris River drainage), *S. namak* (Namak Lake basin), and S. *turcicus* (Urmia and southern Caspian Sea basin) (Khaefi et al. 2016).

The type locality of *S. berak* is Kueik River in Aleppo Province in Syria (Heckel, 1843). The name of *S. berak* has sometimes been used for various populations of Squalius from south-western Anatolia (e.g. Kosswig and Battalgil 1943), which are now recognised by Özuluğ and Freyhof (2011) as *S. kosswigi* (type locality: Gümüldür, approximately 40 km south of Izmir) and S. fellowesii (type locality: Eşen Stream [at Xanthos, approximately 55 km west of Fethiye]). In the same volume, Heckel (1843) also described *S. cephalopsis* from the same Kueik River in Aleppo. But, shortly thereafter (1848) he treated *S. cephalopsis* as a synonym of *S. orientalis* and listed both S. berak and S. orientalis as occurring in the Kueik (pp. 229, 252). He also commented that local fishermen did not distinguish S. berak from S. orientalis and that both were known under the single vernacular name, berak. Turan et al. (2013) examined some *Squalius* specimens from the upper part of the Kueik River and they identified them as S. berak using the data in Heckel (1843). They could not obtain any specimen identifiable as S. cephalopsis from the upper part of the Kueik. Turan et al. (2013) had no opportunity to sample the lower part of Kueik River (in Syria) because of the local political situation. They had also examined photographs of the syntypes of S. berak (NMW 48715) provided by J. Freyhof. Heckel (1843) reported that S. berak has 42-43 total lateral line scales and 7 branched dorsal-fin rays [7½ in our notation], and S. cephalopsis 40-41 total lateral line scales and 8 [8½] branched dorsal-fin rays. The diagnosis of S. cephalopsis was very short, in a footnote. In 1848 (p. 225) Heckel, listed *S. cephalopsis* as a synonym of *S. orientalis* and described *S. orientalis* in detail, apparently on the basis of the 1843 material. Heckel (1848) did not explain the synonymy between S. cephalopsis and S. orientalis, or how his S. orientalis is distinguished from S. berak. The collected specimens from the Kueik River have 41-42 + 1 lateral line scales and 8½ branched dorsal-fin rays; the mouth is large, its corner almost reaching the vertical through the anterior margin of the eye in both sexes, and the cleft is straight or slightly

curved near the angle. Moreover, the general body and mouth shape of our specimens is similar to the figure of *S. berak* in Heckel (1848: pl. 10 fig. 1). The figure of *S. cephalopsis* in Heckel (1843: pl. 16 fig. 2) shows a fish with a small mouth, with well-developed chin, the corner not reaching the vertical through the anterior margin of the eye, and the mouth cleft strongly curved near the angle. Without more material and a wider sampling in the Kueik we cannot comment further on the validity of *S. cephalopsis* and tentatively retain it as valid.

Squalius berak has been considered as synonym of Leuciscus cephalus (Linnaeus, 1758) (now Squalius cephalus) by Coad (1991, 1995), Bogutskaya (1997) and Fricke et al. (2007). However, later, it has been considered as valid species (Doadrio and Carmona 2006; Turan et al. 2009; Bogutskaya and Zupančič 2010; Özuluğ and Freyhof 2011; Turan et al. 2013; Khaefi et al. 2016). Here we got opportunity to examine photographs of type which are available in NMW and fresh specimens collected from Tigris River tributaries which drain to the Persian Gulf, to provide additional information on S. berak.

Material and Methods

After anesthesia, fishes were fixed in 5% formaldehyde. Measurements were made with a dial caliper and recorded to 0.1 mm. All measurements were made point to point, never by projections. Methods for counts and measurements follow Kottelat and Freyhof (2007). Standard length (SL) was measured from the tip of the snout to the end of the hypural complex. The caudal-fin base is situated behind the end of the hypural complex. The length of the caudal peduncle was measured from behind the base of the last anal-fin ray to the end of the hypural complex, at mid-height of the caudal-fin base. Lateral-line scales are counted from the anteriormost scale (the first one to touch the shoulder girdle) to the one at the end of the hypural complex; scales on the caudal-fin base are separated by '+'. Total lateral-line scale count was also used for comparisons. Gill rakers are counted on the first gill arch. The last two branched rays articulating on a single pterygiophore in the dorsal and anal fins are noted as '1½'.

Abbreviations used: SL, standard length; HL, ZM-CBSU, Zoological Museum of Shiraz University, Collection of Biology Department, Shiraz; NMW, Naturhistorisches Museum Wien, Vienna.

Results

Squalius berak Heckel, 1843

(Figs. 1-5)

Common name: Mesopotamian chub

Description: Squalius berak is distinguished from other Squalius species found in the adjacent Caspian Sea, Namak Lake, Kavir and Persian Gulf basins by having a sub-terminal mouth, upper lip projecting beyond lower lip and knob on lower jaw symphysis absent. Squalius berak can separated from S. lepidus by lower scale counts (40-43 vs. 45-50); blunt and shorter head (head depth 50-63 %HL) (vs. pointed and longer head, head depth 44-53 %HL).

Squalius berak can be diagnosed from S. namak by having no knob on lower jaw symphysis (a dominant, large size knob on lower jaw symphysis); posterior tip of each flank scale without any pigmentation (vs. bold grey or brown, roundish or crescent-shaped blotch on posterior tip of each flank scale in S. namak). Squalius berak is distinguished from S. turcicus by having sub-terminal mouth (vs. terminal mouth); having no knob on lower jaw symphysis (vs. small know on the lower lip symphysis).

Description: See Figures 1-5 for general appearance and Table 1 for morphometric data. Body elongated, compressed; dorsal and ventral body profile slightly convex; upper head profile concave or straight. Interorbital area straight. Belly between anus and posterior pelvic-fin base compressed. Snout pointed. Mouth subterminal, upper lip projecting beyond lower lip. Mouth cleft straight, oblique. Snout obtuse, markedly rounded. Head length



Figure 1. Syntype of Squalius berak, NMW-48915 (1).



Figure 2. Radiograph of syntype of Squalius berak, NMW-48915 (1).

greater than body depth at dorsal-fin origin (body depth at dorsal-fin origin 75-95 %HL). No symphysial knob on lower jaw. Upper lip thick. Largest recorded sample 144 mm in SL.

Dorsal fin with 3 unbranched and 8½ branched rays, distal margin straight or slightly convex. Dorsal-fin origin behind vertical through pelvic-fin origin. Tip of dorsal fin reaching vertical through anal-fin origin when pressed. Anal fin with 3 simple and 7½-8½ (mode 8½) branched rays; distal margin convex or straight. Posteriormost point of anal fin at tip of first or second branched ray. Pectoral fin with 15-17 (usually 16), pelvic fin with 9-10 (mode 9) rays. A large axillary pelvic lobe present. Caudal fin forked, with 9+8 branched rays. Lateral line complete, with 40-43 scales on body, 2 on caudal-fin base. Scale rows between dorsal-fin origin and lateral line 8½, scale rows between pelvic-fin origin and lateral line 4½; 15-17 (mode 16) circumpeduncular scales, 18-21 predorsal scales. Gill rakers on first gill arch 8-9 (mode 9). No external sexual dimorphism observed.

Coloration: In life: head and body silvery brown, darker on back. Belly white. Peritoneum black. Scale pocket well pigmented above lateral line, with a bold, brown or black, crescent-shaped, vertically elongated or roundish anterior scale mark on scales below lateral line. Free margins of scales above lateral line pale. Caudal-, anal-pelvic- and pectoral-fin rays orange, caudal-fin rays with black pigments. Dorsal-fin membranes hyaline with dark-grey rays. In preservation: Head and body pale brown, darker on back. Dorsal and caudal fins with blackish rays and hyaline membranes; rays whitish and membranes yellowish in pectoral, pelvic and anal fins.

Habitat: It is found in small to medium sized streams mostly in mountains and hilly areas. The Tigris River



Figure 3. Syntype of Squalius berak, NMW-48915 (2-6).

drainage in Iran, Iraq, Syria and Turkey (Fig. 6).

Conservation: While the species is believed to have declined due to many threats in the area (e.g., pollution, habitat destruction, habitat modification, drought), it is still widespread occurring in many more than 10 independent populations and its decline is not thought to be great enough to qualify it for NT or any of the threat categories. It is therefore assessed as LC (see Freyhof 2014).

Distribution: Squalius berak has been reported from: Iran: West Azerbaeijan prov.: Badin Abad River at Piranshahr, 36°28'36"N 45°19'54"E. — Iran: Kurdistan prov.: Boeen River at road between Baneh and Boeen, 35°56'35.5"N 45°19'36.8"E. — Turkey: Kilis prov.: stream Sünnep 10 km east of Kilis, 36°45'50"N 37°15'14"E. — Turkey: Sivas prov.: Kangal stream under railway bridge at Çetinkaya, 39°15'4.644"N 37°37'7.464"E. — Turkey: Erzurum prov.: Karasu stream at Kandilli, 39°91'24"N 40°85'40"E. — Turkey: Erzurum prov.: stream Arkaçayırlar at Paşayurdu close to the road from Ilıca to Aşkal, 39°58'59.952"N 40°59'31.308"E. — Iraq: Tabin River west of Zarbi, 35°48'06"N 44°58'47"E. — Iraq: stream Zalm at Khurmal, 35°18.38'N 45°58.26'E (Fig. 7).

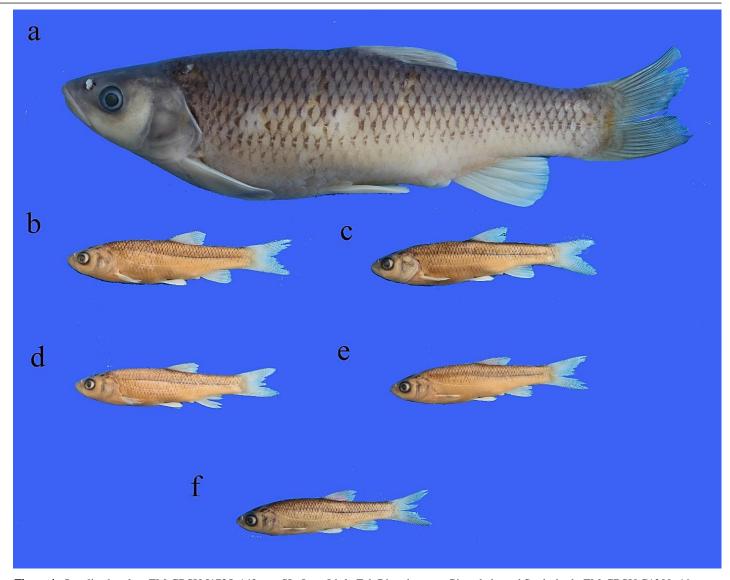


Figure 4. *Squalius berak.* a. ZM-CBSU J1725, 143 mm SL; Iran: Little Zab River between Piranshahr and Sardasht; b. ZM-CBSU G1300, 46 mm SL; c. ZM-CBSU G1301, 44 mm SL; d. ZM-CBSU G1302, 44 mm SL; ZM-CBSU G1303, 38 mm SL; ZM-CBSU G1304, 37 mm SL; Iran: Kurdestan Prov. Boein, Baneh.



Figure 5. 5. Live specimen of S. berak. ZM-CBSU J1740, 137 mm SL; Iran: Little Zab River between Piranshahr and Sardasht.

Table 1. Morphometric data of *Squalius berak*. ZM-CBSU G1300, 5, Iran: Kurdestan Prov. Boein, Baneh. ZM-CBSU J1740, 137 mm SL; ZM-CBSU J1725, 143 mm SL; Iran: Little Zab River between Piranshahr and Sardasht.

	Range	Mean	SD
Standard length (mm)	37.4-143.4	69.6	47.5
In percent of standard length			
Head length	26.9-30.6	28.1	1.2
Snout length	6.5-8.8	7.9	0.7
Postorbital distance	13.1-15.4	14.1	0.9
Interorbital distance	10.7-11.9	11.2	0.5
Predorsal length	51.4-55.0	53.3	1.2
Postdorsal length	49.8-55.0	52.7	2.0
Dorsal-fin base length	18.3-24.0	21.1	2.0
Dorsal-fin depth	9.7-11.6	10.6	0.7
Anal-fin base length	14.5-18.7	16.9	1.3
Anal-fin depth	8.6-9.9	9.3	0.4
Preanal length	68.7-74.6	71.2	1.9
Pectoral-fin length	16.3-19.1	17.6	0.9
Pelvic-fin length	13.9-15.9	14.8	0.9
Depth of caudal peduncle	9.8-12.0	10.7	0.7
Body depth at dorsal-fin origin	20.4-27.0	22.6	2.6
Distance between pectoral and anal-fin origins	42.5-52.2	46.0	3.6
Distance between pectoral and pelvic-fin origins	21.5-29.8	24.9	3.4
Distance between pelvic and anal-fin origins	19.5-22.6	21.4	1.1
Length of caudal fin	19.3-26.4	23.0	2.6
Length of caudal peduncle	20.5-23.3	21.6	0.9
In percent of head length			
Head depth	21.2-58.4	53.4	4.7
Snout length	46.1-31.0	28.1	3.2
Postorbital distance	37.4-55.8	50.2	3.5
Interorbital width	17.1-43.2	39.9	1.9
Eye diameter	70.0-30.0	24.6	4.6
Length of caudal fin	24.0-92.7	82.1	9.3
Mouth width	21.2-29.7	26.8	2.2

Material examined: NMW 48915, 6, syntypes, 64-304 mm SL; Syria: Aleppo. —ZM-CBSU J1725, J1740, J1741, 3, 133-137 mm SL; Iran: West Azerbaijan prov.: Little Zab River at road between Piranshahr and Sardasht, 36°28'36"N 45°19'54"E. —ZM-CBSU G1723, 2, 43-52 mm SL; Iran: Kordistan prov.: Boeen River at road between Baneh and Boeen, 35°56'35.5"N 45°56'36.5"E.

Comparative materials: See Khaefi et al. (2016).

Discussion

This paper is aimed to provide an exhaustive review of the systematics, taxonomy and morphology of a chub which is nested in the 'Euro-Asiatic' lineage and is called the Mesopotamian chub, *S. berak* described from Kueik River in Aleppo province in Syria (Heckel, 1843). Chubs of the genus *Squalius* Bonaparte, 1837 represent a large genus of cyprinids with about 49 species widespread in the Western Palearctic (Ozulug and Freyhof 2011; Turan et al. 2013; Khaefi et al. 2016). The species of *Squalius* were for long placed in *Leuciscus*, until morphological and molecular data showed that *Leuciscus* as earlier understood, was paraphyletic (e.g., Zardoya and Doadrio



Figure 6. Natural habitat of Squalius berak, Little Zab tributary, Tigris River drainage, Iran.



Figure 7. Distribution map of Squalius berak in Iran, Iraq and Turkey.

1999; Bogutskaya 1994; Turan et al. 2013). Molecular and morphological studies have identified two major groups within this genus: I) the 'Mediterranean' lineage, which is limited to the Iberian and Apennine Peninsulas

and the eastern Adriatic basin. II) the 'Euro-Asiatic' lineage, (*S. cephalus* group) which is distributed from the Ebro in Spain east to the Ural and south to Iran and Syria (see (Durand et al. 2000; Sanjur et al. 2003; Ozulug and Freyhof 2011). Within the 'Euro-Asiatic' lineage or *S. cephalus* group, traditionally, only two species were recognized, the long-snouted chub *S. lepidus* from the Middle East and the short-snouted chub *S. cephalus* from all the rest of the distribution area (Ozulug and Freyhof 2011). The short-snouted 'Euro-Asiatic' chubs were all identified as *S. cephalus* or subspecies of *S. cephalus* till 2006 (see Kottelat & Economidis 2006). Later, it was supposed that both groups, are comprised of several distinct taxa and therefore, several new species were described (see Kottelat and Economidis 2006; Stoumboudi et al. 2006; Doadrio et al. 2007; Bogutskaya and Zupancic 2010; Zupancic et al. 2010; Ozulug and Freyhof 2011; Turan et al. 2013, Khaefi et al. 2016) showing taxonomic challenges and tumultuous history of chubs including *S. berak* at the genus and species levels.

Based on the tree topologies (COI sequences) obtained from the different analytical approaches (ML, NJ and BI), Khaefi et al. (2016) showed that the relationships between the different species of the chubs cannot be resolved by the COI marker (e.g., several specimens of *S. lepidus* cluster within a clade composed of mainly S. berak and vice versa). The Bayesian analysis-based estimation of the relationships between the mitochondrial COI sequences placed the chub specimens into four to six groups, with lowest differentiation between S. orientalis and S. turcicus (0.8% K2P) and largest differentiation between S. lepidus and S. turcicus (5.4% K2P). The *Squalius* population from Lake Namak is closest to *S. lepidus* from the Euphrates drainage in Turkey (1.3% K2P). As stated by Khaefi et al. (2016), two chub species are found in the Euphrates and Tigris drainage of the Persian Gulf basin: Squalius lepidus which is very widespread and usually inhabits larger rivers and streams in lowland habitats and S. berak, which is found in headwater streams and rivers in mountainous habitats and was usually identified as S. cephalus (Esmaeili et al. 2010). It was described from the Kueik River in Syria, a small endorheic drainage west to the Euphrates (Khaefi et al. 2016). Squalius berak from the Sünnep, a headwater stream of the Kueik in Turkey, shares the COI barcode sequence with superficially similar, round-headed Squalius found in the Euphrates and Tigris drainage. However, the lineage sorting between S. lepidus and S. berak is not complete and both species seem occasionally to hybridize. This might lead to the false classifications of a few individuals and populations of both species based on their COI barcode sequence (see Khaefi et al. 2016).

It seems that the taxonomic challenges and tumultuous history of the Mesopotamian chub, *S. berak* is going to be continued in future.

Acknowledgements

We are pleased to thank S. Vatandoust, A. Gholamhosseini, M. Masoudi, H.R. Mehraban, M. Razbanian, R. Sadeghi and H. Darvishnia, for helping during field work in Iran. Many thanks to Environment Departments of Kurdistan and Urmia provinces for supporting field surveys in Iran. We would like to thank N. Bogutskaya and A. Naseka (Dolsko) for preparing the syntype photos of *S. berak* and A. Palandacic and E. Mikschi, (NMW) for sending the photos and giving permission to use them. The project was financially supported by Shiraz University and was approved by the Ethics Committee of Biology Department (ECBD-SU-909821).

Literature cited

Bogutskaya N.G. 1994. A description of *Leuciscus lepidus* (Heckel, 1843) with comments on Leuciscus and leuciscine - aspinine relationships (Pisces: Cyprinidae). Annalen des Naturhistorischen Museums in Wien 96B: 599-620.

Bogutskaya N.G. 1997. Contribution to the knowledge of Leuciscine fishes of Asia Minor: Part 2. An annotated checklist of Leuciscine fishes (Leuciscinae, Cyprinidae) of Turkey with descriptions of a new species and two new subspecies. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 94: 161-186.

Bogutskaya N.G., Zupančič P. 2010. Squalius janae, a new species of fish from the Adriatic Sea basin in Slovenia (Teleostei:

- Cyprinidae). Zootaxa 2536: 53-68.
- Coad B.W. 1991. Fishes of the Tigris-Euphrates Basin: a critical checklist. Syllogeus 68: 1-49.
- Coad B.W. 1995. Freshwater fishes of Iran. Acta Scientiarum Naturalium Academiae Scientiarum Bohemicae Brno 29(1): 1-64.
- Doadrio I., Carmona J.A. 2006. Phylogenetic overview of the genus *Squalius* (Actoynopterigii, Cyprinidae) in the Iberian Peninsula, with description of two new species. Cybium, International Journal of Ichthyology 30: 199-214.
- Durand J.D., Unlü E., Doadrio I., Pipoyan S., Templeton A.R. 2000. Origin, radiation, dispersion and allopatric hybridization in the chub Leuciscus cephalus. Proceedings of the Royal Society of London B, Biological Sciences 267: 1687-1697.
- Esmaeili H.R., Coad B.W., Gholamifard A., Nazari N., Teimori A. 2010. Annotated checklist of the freshwater fishes of Iran. Zoosystematica Rossica 19: 361-386.
- Fricke R., Bilecenoglu M., Sari H.M. 2007. Annotated checklist of fish and lamprey species (Gnathostomata and Petromyzontomorphi) of Turkey, including a Red List of threatened and declining species. Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie) 706: 1-169.
- Freyhof J. 2014. *Squalius berak*. The IUCN Red List of Threatened Species 2014: e.T19451142A19850085. http://dx.doi.org/10.2305/IUCN.UK.2014-1.RLTS.T19451142A19850085.en. Downloaded on 11 November 2016.
- Geiger M., Herder F., Monaghan M., Almada V., Barbieri R., Bariche M., Berrebi P., Bohlen J., Casal-Lopez M., Delmastro G., Denys G., Dettai A., Doadrio I., Kalogianni E., Kärst H., Kottelat M., Kovacic M., Laporte M., Lorenzoni M., Marcic Z., Özulug M., Perdices A., Perea S., Persat H., Porcellotti S., Puzzi C., Robalo J., Sanda R., Schneider M., Slechtova V., Stumboudi M., Walter S., Freyhof J. 2014. Spatial heterogeneity in the Mediterranean Biodiversity Hotspot affects barcoding accuracy of its freshwater fishes. Molecular Ecology Resources 14: 1210-1221.
- Heckel J.J. 1843. Ichthyologie. In: J. von Russegger. Reisen in Europa, Asien und Africa, mit besonderer Rücksicht aufdie naturwissenschaftlichen Verhältnisse der betreffenden Länder unternommen in den Jahren 1835 bis 1841. Erster Band. Reise in Griechhenland, Unteregypten, im nördlichen Syrien und südöstlichen Kleinasien. Schweizerbart, Stuttgart, pp: 991-1099.
- Heckel J.J., Kner R. 1858. Die Süsswasserfi sche der Österreichischen Monarchie, mit Rücksichtauf die angrenzenden Länder. Leipzig, 388 p.
- Khaefi R., Esmaeili H.R., Sayyadzadeh G., Geiger M.F., Freyhof G. 2016. *Squalius namak*, a new chub from Lake Namak basin in Iran (Teleostei: Cyprinidae). Zootaxa 4169(1): 145-159.
- Kosswig C., Battalgil F. 1943. Türkiye tatlı su balıklarının zoogeografik ehemmiyeti (Zoogeographic importance of Turkish freshwater fishes). Türk Fiziki Tabii İlimler Sosyetesi Yıllık Bildiriler Arsivi II, 8: 18-31.
- Kottelat M., Freyhof J. 2007. Handbook of European Freshwater Fishes. Kottelat, Cornol and Freyhof, Berlin. 646 p.
- Özuluğ M., Freyhof J. 2011. Revision of genus *Squalius* in Western and Central Anatolia, with description of four new species (Teleostei: Cyprinidae). Ichthyological Exploration of Freshwaters 22: 107-148.
- Sanjur O.I., Carmona J.A., Doadrio I. 2003. Evolutionary and biogeographical patterns within Iberian populations of the genus Squalius inferred from molecular data. Molecular Phylogenetics and Evolution 29: 20-30.
- Stoumboudi M.T., Kottelat M., Barbieri R. 2006. The fishes of the inland waters of Lesbos Island, Greece. Ichthyological Exploration of Freshwaters 17: 129-146.
- Turan D., Yilmaz B.T., Kaya C. 2009. *Squalius kottelati*, a new cyprinid species (Teleostei: Cyprinidae) from Orontes River Turkey. Zootaxa 2270: 53-62.
- Turan D., Kottelat M., Doğan E. 2013. Two new species of *Squalius*, *S. adanaensis* and *S. seyhanensis* (Teleostei: Cyprinidae), from the Seyhan River in Turkey. Zootaxa 3637(3): 308-324.
- Zardoya R., Doadrio I. 1999. Molecular evidence on the evolutionary and biogeographical patterns of European Cyprinids. Journal of Molecular Evolution 49: 227-237.