REVISION OF THE LAMPREY GENUS <u>EUDONTOMYZON</u> REGAN, 1911

by

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△ E. danfordi

○ E. mariae complex

⬭ E. morii

□ E. hellenicum 134b

ABSTRACT

The validity of the Palearctic lamprey genus Eudontomyzon is reasserted. This revision of the genus, at the specific level, recognizes four species: E. danfordi Regan, 1911; E. mariae (Berg, 1931) complex; E. morii (Berg, 1931) and a new species from Greece. E. mariae complex is believed to be made up of a number of subspecies, yet to be elucidated. E. danfordi vladykovi Oliva and Zanandrea, 1959, redescribed as Lampetra (E.) vladykovi, Holčík, 1963 are junior subjective synonyms of E. mariae complex, whereas E. gracilis (Kux, 1965) is referable to E. danfordi. A key to the ammocoetes and adults of the four species, except for ammocoetes of E. morii which have never been described, is provided.

RESUME

La validité du genre de lamproie Paléarctique Eudontomyzon est réaffirmée. Cette révision du genre, au niveau spécifique, reconnait quatre espèces: E. danfordi Regan, 1911; complexe E. mariae (Berg, 1931); E. morii (Berg, 1931) et une nouvelle espèce de Grèce. On croit que le complexe E. mariae est formé de sous-espèces qui restent à mettre à jour. E. danfordi vladykovi Oliva et Zanandrea, 1959, redécrite comme Lampetra (E.) vladykovi, Holčík, 1963 sont synonymes subjectifs juniors du complexe E. mariae, alors qu' E. gracilis (Kux, 1965) s'applique à E. danfordi. Une clé aux ammocètes et adultes des quatre espèces, sauf pour les ammocètes d' E. morii qui n'ont jamais été décrites, est fournie.

INTRODUCTION

Eudontomyzon is a genus of palearctic, freshwater lampreys. Regan (1911), based on the type-species *Eudontomyzon danfordi* (by monotypy), characterized his newly established genus as follows: a broad supraoral lamina bearing two cusps; disc covered with numerous teeth; transverse lingual lamina with single denticulated ridge and two dorsal fins. Since its establishment as a genus by Regan (1911), it has been varioulsy treated. Creaser and Hubbs (1922) suggested it be considered a subgenus of *Petromyzon* Linnaeus. In his review of lampreys of the northern hemisphere, Berg (1931) treated it as a subgenus of *Lampetra* Gray, although he cautiously added: "Perhaps, *Eudontomyzon* is a valid genus.". Following these pioneering studies, authors opted for either Regan's of Berg's interpretation. Some of them however, after first treating *Eudontomyzon* as a subgenus of *Lampetra*, (Oliva, 1953a; 1953b; 1960; 1962; 1966; Oliva and Hensel, 1962; Holčík, 1963; Balon and Holčík, 1964; Holčík et al., 1965), recognized its generic status in later articles (Oliva and Zanandrea, 1959; Balon, 1964a; 1964b; Holčík, 1970a; 1970b; 1970c; Holčík and Nalbant, 1974; Johal and Oliva, 1980). The converse, to my knowledge, has never occured.

The most recent treatment of *Eudontomyzon* as a subgenus of *Lampetra* is that of Bailey (1980). Within *Lampetra* (sensu lato), Bailey (1980) includes the following taxa: Entosphenus Gill, Eudontomyzon Regan, Lampetra (sensu stricto) Gray, Lethenteron Creaser and Hubbs, Okkelbergia Creaser and Hubbs and Tetrapleurodon Creaser and Hubbs. His reason for lumping all these taxa under the same genus is largely based on their possession of a similar supraoral lamina. He adds however, that relationships among the six suggested subgenera are not well understood. Pending more research that will elucidate these relationships, it is significant that in recent publications, Hubbs and Potter (1971), Hardisty and Potter (1971a; 1971b; 1971c), Vladykov and Kott (1979a; 1979b), Potter (1980), some of the most knowledgeable lamprey students, all consider Eudontomyzon as a valid genus, even though their classifications of certain other genera differ. It is equally significant that the first advocate (Berg, 1931) for the treatment of Eudontomyzon as a subgenus of Lampetra questionned the correctness of his interpretation.

A number of basic dentitional differences make the inclusion of Eudontomyzon within the genus Petromyzon, as proposed by Creaser and Hubbs (1922), untenable. Vladykov and Follett (1967) outlined those differences, as follows. The transverse lingual lamina in Petromyzon is bilobed, being strongly bent inward along a vertical median axis. In Eudontomyzon, it is not bilobed, being slightly convex. Moreover, in Eudontomyzon, there is typically an enlarged median cusp on the transverse lingual lamina and if, as I found in E. mariae complex, it is not always taller than the other cusps on the ridge, at least its base is always wider. This feature is never found in Petromyzon, no cusp being more prominent than the other. Lastly, in Petromyzon, unlike the condition in Eudontomyzon, there is no broad supraoral lamina with two large lateral teeth separated by a bridge, which may bear one to three cusps, but instead, a single supraoral tooth with one or more cusps.

Although Lampetra sensu stricto and Eudontomyzon share a number of dentitional characteristics, one such characteristic sets them apart; the presence of exolaterals in one or more rows, in the latter and their absence in the former (Vladykov and Follett, 1967). This single characteristic I feel, warrants a generic position for Eudontomyzon. Nevertheless, three lines of evidence suggest that Lampetra sensu stricto and Eudontomyzon are closely related. All refer to the E. mariae complex. Firstly, Holčík (1970a; 1970b; 1970c) suggested that north Slovakian populations of L. planeri (Bloch) have higher trunk myomere counts than more northern or southern populations of the same taxon, because of introgressive hybridization with E. mariae from the Vistula river basin, which also have high numbers of trunk myomeres. Holčík (1970a; 1970b; 1970c) found the number of trunk myomeres in 150 adults from the Poprad river basin (Poprad River per say and six tributary brooks) ranged from 61 to 68 with mean 64.5 and in 30 adults from the Hornád River, the range was identical but the mean was 65.0. The Poprad river basin belongs to the Vistula river basin but the Hornád River drains into the Tisa river basin. However, in the Tertiary period, part of the upper Hornád river basin did belong to the Poprad basin. As far as is known, E. mariae does not presently occur in the Poprad or Hornád river basins, although it does occur sympatrically with L. planeri in at least one part of the Vistula basin (Rembiszewski, 1968). Both species may therefore also have been sympatric in these river basins in the past. Secondly, the hypothesis of introgressive hybridization between E. mariae and L. planeri is sound, because Rembiszewski (1968) has reported hybrids between these two species in the Jeziorka River, Poland. In fact, the three adult hybrids had much higher numbers of trunk myomeres than L. planeri, but roughly the same as in E. mariae. The absence of posterials in at least one specimen of the E. mariae complex, as in all Eurasian members of Lampetra sensu stricto (L. fluviatilis (Linnaeus), L. planeri (Bloch), L. zanandreai Vladykov, 1955, L. lanceolata Kux and Steiner), is the final piece of evidence in support of the recent evolutionary divergence of the two genera.

To make matters more complex, specimens of four North American and one Asian species, belonging to genera which by definition do not possess exolaterals have been shown to exhibit, in the lateral fields, what Vladykov, Kott and Pharand-Coad (1975), Vladykov and Kott (1976a, 1978) call supplementary marginals. These authors however, do not offer any method for distinguishing between supplementary marginals and exolaterals. Although one may argue that teeth close to the marginal series can be considered supplementary marginals, the fact remains that "good" exolaterals, lying in the middle of the exolateral field, or close to the endolaterals have been found in all species referred to above and are documented below. In view of this, the relationships of the *Eudontomyzon* genus with these members of the genera *Lampetra* and *Lethenteron* require further investigation.

Creaser and Hubbs (1922) produced a figure of the disc of *Lampetra aepyptera* (Abbott), which appeared as *Lampetra* (*Okkelbergia*) *lamottenii* (Le Sueur), but was subsequently synonymized as the former in Hubbs and Trautman (1937) and Vladykov and Kott (1976a), where an exolateral row, next to the marginal series, is present on both sides of the disc, and near the endolaterals, there are two exolateral cusps on the right side and one on the left side. Berg (1931) alluded to the presence of exolaterals in the aforementionned figure. Vladykov, Kott and Pharand-Coad (1975) confirmed the presence of exolaterals in *Lampetra aepyptera*. In their figure 6 of a disc of this species, an exolateral cusp, on each side of the disc, close to the endolaterals is clearly apparent. More recently, Bailey (1980) also confirmed the occurrence of exolaterals, in what he calls *Lampetra* (*Okkelbergia*) *aepyptera*. Furthermore, *Lethenteron meridionale* Vladykov, Kott and Pharand-Coad, 1975, also possesses exolaterals. Their figure 3 of the holotype disc, clearly shows, on the left side, five cusps near the marginal row and two cusps in the middle of the exolateral field and on the right side, three cusps near the marginal row and two cusps in the middle of the exolateral field. Lethenteron alaskense Vladykov and Kott, 1978, also possesses exolaterals. Their figure 3 of the holotype disc, clearly exhibits, one cusp on each side, in the middle of the exolateral field. Lethenteron reissneri (Dybowski) is yet another lamprey with exolaterals. Vladykov and Kott (1978) say it possesses "supplementary marginals" along the lateral field. Their figure 7c) is that of a disc of L. reissneri bearing an exolateral row, on both sides, close to the marginal series and one cusp on the left, in the middle of the exolateral field. In Berg (1948) can be seen two figures of L. reissneri discs, of interest here. Figure 28 is identified by Berg (1948) as Lampetra reissneri (= Lethenteron reissneri) and has an exolateral cusp on the left side. Figure 30, simply identified as Lampetra sp., from the Tym' River, Sakhalin Island, is tentatively identified here as L. reissneri, as three adult specimens from the same locality were identified as such by Vladykov and Kott (1978) and the presence of exolaterals and posterials excludes the possibility of it being a Lampetra sensu stricto. It exhibits an exolateral cusp on each side. Kott (1974) reported the presence of one or two exolaterals, on either or both lateral fields, in 21.1% of the Lethenteron lamottenii (Le Sueur) he examined. These were usually found close to the endolaterals. He did not however, state the sample size.

The purpose of this study is to revise the genus Eudontomyzon, at the specific level. "The genus (Eudontomyzon) is in need of revision since the species are poorly defined."

Vladykov and Kott (1979b: 11). The addition of a new species to the genus, *E. hellenicum* Vladykov et al., in prep., further indicated the need for a revision. A key to larvae and adults of the *Eudontomyzon* species recognized in this work, is provided.

It is the intent of the author, in the future, to conduct infraspecific studies on *E. mariae* complex and *E. hellenicum*, to reveal possible subspecies. The species, herein referred to as *E. mariae* complex, has a very extensive range (Adriatic, Aegean, Baltic and Black sea basins) and presents wide variation in some taxonomic characters. A geographic study of those characters may turn up new subspecies. However, a larger sample of adults from various parts of the range is required before such a study is undertaken. Populations of *E. hellenicum* from the Louros river basin (Ionian sea basin), on the one hand and from the Struma river basin (Aegean sea basin), on the other, may be attributable to distinct subspecies, as both river basins are separated from each other by the Pindus mountain range.

MATERIAL

Collection data for the 958 lamprey specimens of the genus Eudontomyzon studied, appear in the following sequence: alphanumeric tags; number of specimens; developmental stage (a =ammocoete; ā = metamorphosing ammocoete; t = metamorphosed individual); sex (if t); total length, mm; locality; geographic coordinates (lat, long); collection date; collector(s); repository institution (ASL = Zoological Institute of the Academy of Sciences of the USSR, Leningrad; BM = British Museum (Natural History), London; LRHB=Laboratórium rybárstva a hydrobiológie SPA, Bratislava; MPW = Universytet Wrocławski, Muzeum Przyrodnicze, Wrocław; MSNV = Museo Civico di Storia Naturale, Verona; MV = Naturhistorische Museum, Vienna; NMC = National Museum of Natural Sciences, Ottawa; PC = personal collection; ROM = Royal Ontario Museum, Toronto; SNM = Slovenské Národné Múzeum, Zoologické Oddelenie, Bratislava; UO = University of Ottawa, Biology Dept ; ZMH = Zoologisches Institut und Museum, Universität Hamburg); catalog number (if applicable); remarks.

E. danfordi

(334a, 6ā, 79t)

Black Sea Basin

Tisa River Basin

Czechoslovakia

Celluloid 1-2; 1a, 149 mm; 1t (♀), 152.5 mm; Topl'a R, Lukov, Slovakia; 49°18'N; 21°5'E; 1949; T. Weisz; UO.

W(VDV) 5841-63; 23a, 74-175 mm; Topl'a R, Lukov, Slovakia; 49°18'N, 21°5'E; 14 March 1960; T. Weisz; UO.

W(VDV) 5806-14; 9a, 171-208 mm; Topl'a R, Lukov, Slovakia; 49°18'N, 21°5'E; 4 Sept 1960; Z. Kux, T. Weisz; UO.

Y421-4; 1a, 160.5 mm; 3t, 157.5 - 179 mm; Topl'a R, Lukov, Slovakia; 49°18'N, 21°5'E; MSNV217; see Zanandrea (1959a) Table 6, collections #1-2 (4 out of 23 specimens from these collections were studied).

W(VDV) 5817; 1t (♀), 158 mm; Ulička Brook, Ulič, Slovakia; 48°58'N, 22°26'E; 16 Oct 1962; T. Weisz; UO.

W(VDV) 5728; 1t (♀), 164 mm; Okna R, near Remetské Hámre, Vyhorlat mountain range, Slovakia; 48°51'N, 22°10'E; 11 Sept 1960; J. Holčík, V. Mišík; SNM LF 36553; see Holčík (1963) p. 52 and Table 1.

W(VDV) 5778-800; 23a, 70.5 - 177.5 mm; Okna R, above Jasenov, Vyhorlat mountain range, Slovakia; 48°43'N, 22°9'E; 13 Sept 1960; J. Holčík, V. Mišík; SNM 35622-44.

W(VDV) 5825, 5827; 2t (2♂), 210.5 - 241 mm; Okna R, Vyhorlat mountain range, Slovakia; 4 Sept 1964; Z. Kux, T. Weisz; UO.

W(VDV) 5819; 1t (♀), 176.5 mm; Rudava R, Vel'ké Leváre, Slovakia; 48°30'N, 17°0'E; 19 July 1964; UO; This specimen was kept alive in an aquarium until 17 May 1965. Its locality is most probably erroneous. see Results and Discussion p.53

Ukrainian SSR, USSR

W(VDV) 4085 -90; 6a, 36 - 110.5 mm; Tereshova R, near Ganichi and Podpleša, Subcarpathian Ukraine; 48°8'N, 23°49'E; 29 Aug 1924; V.D. Vladykov; UO; see Vladykov (1925) p. 248 and 252.

Untagged; 1a, 46 mm; Tereshova R, near Neresnitsa, Subcarpathian Ukraine; 48°7'N, 23°46' E; April - Aug 1924; V.D. Vladykov; ROM 23762; see Vladykov (1925) p. 248 and 252.

Untagged; 2a, 139 - 176 mm; Tereblya R, Bushtyna, Subcarpathian Ukraine; 48°3'N, 23°28'E; 20 June 1925; V.D. Vladykov; UO.

Untagged; 1a, 112 mm; 1ā, 167.5 mm; Tisa R, near Velikiy Bychkov?, Subcarpathian Ukraine; 47°58'N, 24°1'E; 1 Sept 1926; V.D. Vladykov; UO.

082-90, W(VDV)4084; 6a, 74 - 164 mm; 1ā, 142 mm; 3t (1♂:2?), 140-157 mm; Subcarpathian Ukraine; 1920-4; V.D. Vladykov; UO.

J(DPQ)704-7, 711; 4a, 90 - 112 mm; 1t (♀), 181 mm; Subcarpathian Ukraine; V.D. Vladykov; UO.

<u>Rumania</u>

Y508; 1t, 186 mm; Someşul Mare R, Rodna, Transylvania; 47°25'N, 24°49'E; Sept 1949; MSNV 391; see Zanandrea (1959a) Table 1, collection #7 (1 of 2 specimens in this collection was studied).

Y513-6; 2a, 77 - 182 mm; 1ā, 154 mm; 1t, 154mm; Sălăuta Brook, Transylvania; 47°18'N, 24°21'E; Oct 1958; MSNV256; see Zanandrea (1959a) Table 1, collections #15-6.

Y471-2; 2t (1♀:1?), 168.5 - 199 mm; Someşul Mare R, NE Transylvania; Aug 1949; MSNV412; see Zanandrea (1959a)

Table 1, collection #14.

Y501-6; 6a,101 - 145.5 mm; Gurghiu Brook, Transylvania; 46°47'N, 24°43'E; MSNV421.

Y428 - 35; 8t (1♀:7?), 150 - 214 mm; Someşul Mic R, Iara Brook, near Cluj, Transylvania; 46°46'N, 23°36'E; MSNV390; see Zanandrea (1959a) Table 1, collection #13 (8 out of 22 specimens in this collection were studied).

O 102-4; 3t (1♂:2♀), 205 - 240.5 mm; Răcătău Brook, near Cluj, Transylvania; 46°39'N, 23°12'E; 12 Aug 1961; P. Bănărescu; ZMH2222.

Untagged, W(VDV)6461 - 75, Y517 - 67; 117a, 38 - 126 mm; 7t (3♀:4?), 188 - 228 mm; Iara Brook, near Valea Ierii, Transylvania; 46°39'N, 23°21'E; 20 May, 23 July, 4 Nov 1937; MSNV 393.

p G318 - 27; 10a, 96 -160mm; Iara Brook, near Valea Ierii, Transylvania; 46°39'N, 23°21'E; 28 Sept 1937; P.A. Chappuis; UO.

p G315 - 7; V(DPQ)3367, W(VDV)4069 - 79, 4081, 4083; 16a, 21.5 - 79.5 mm; 1t, 176.5 mm; Iara Brook, near Valea Ierii, Transylvania; 46°39'N, 23°21'E; 23 March 1938; P.A. Chappuis; UO.

W(VDV)4681 - 93, 4695 - 700, 5580, 5582 - 92; 9a, 84.5 - 181.5 mm; 22t (4♀:18?), 182 - 216 mm; Someşul Mic R and/or Iara Brook, Transylvania; UO.

Y507; 1t, 214.5 mm; brook near Criş, Transylvania; 46°17'N, 22°54'E; 5 Sept 1950; MSNV392; see Zanandrea (1959a) Table 1, collection #10.

Y509; 1a, 146 mm; watercourse near Năsăud or Vasçău, Transylvania; Sept 1945; MSNV395; see Zanandrea (1959a) Table 1, collection #5 (1 of 2 specimens in this collection was studied).

W(VDV)4496 - 500, Y468; 6a, 61 - 95 mm; Mureşul R, NE Transylvania; 3 July 1953; Alopescu; MSNV411.

R(DPQ)4912; 1t ,150 mm; Transylvania; C.G. Danford, J.A. Harvie-Brown; BM; syntype of Eudontomyzon danfordi, see Regan (1911) p. 201.

W(VDV)4045; 1a, 164 mm; upper Bega R, Banat; June 1962; P. Bănărescu; UO.

W(VDV)4039 - 41; 3t, 175 - 179 mm; Bistra Mărului Brook, Banat; 45°32'N, 22°23'E; Autumn 1962; A. Toader; UO.

W(VDV)4031 - 3; 3t (3♂), 172.5 -182 mm; Bistra Mărului Brook, Banat; 45°32'N, 22°23'E; 15 June 1963; P. Bănărescu; UO.

W(VDV)4668 - 80, 5889 - 900; 18a, 133 - 180.5 mm; 7t (2♀:5?), 142 - 199 mm; Bistra Mărului Brook, Banat; 45°32'N, 22°23'E; 1964; A. Toader; UO.

W2317 - 78, W(VDV)4025 - 6, 5593 - 600; 72a, 58-190 mm; Bistra Mărului Brook, Banat; 45°32'N, 22°23'E; 4 July 1965; P. Bănărescu; UO.

Y469 - 70; 2t (2♀), 168.5 - 192 mm; Bistra Mărului Brook, near Poiana Mărului, Banat; 45°24'N, 22°33'E; June 1962; P. Bănărescu; MSNV 111.

Y425 - 7, 511 - 2; 2a, 169 - 175 mm; 3t, 201- 234 mm; Bistra Mărului Brook, near Poiana Mărului, Banat; 45°24'N, 22°33'E; Autumn 1962; MSNV 109, 112.

Untagged; 1t (♀), 184 mm; 8 Sept 1962; P. Bănărescu; NMC 71 - 322A.

E. mariae complex
(174a, 6â, 39t)

Baltic Sea Basin

Vistula River Basin

Poland

B(DPQ)2920, 2922; 2t (1♂:1♀), 160.5 - 168.5 mm; Jeziorka R, Piaseczno district, near Warsaw; 52°15'N, 21°0'E; 29 April 1965; J.M. Rembiszewski; UO.

Untagged; 6t (3♂:3♀), 141 - 159 mm; Jeziorka R, Piaseczno district, near Warsaw; 52°15'N, 21°0'E; 25 April 1968; J.M. Rembiszewski; MPW.

Y841, 847; 2t (1♂:1♀), 169.5 - 171 mm; Jeziorka R, about 20 km from Warsaw; 52°15'N, 21°0'E; J.M. Rembiszewski; UO.

Y828 - 9; 1a, 158 mm; 1â, 177.5 mm; Wilga R, about 60 km SE of Warsaw; 51°52'N, 21°18'E; 2 Sept 1968; J.M. Rembiszewski; UO.

Y830 - 1; 2a, 175 -177 mm; Wilga R, about 60 km SE of Warsaw; 51°52'N, 21°18'E; 18 Oct 1968; J.M. Rembiszewski; UO.

Y832; 1a; 165 mm; Wilga R, about 60 km SE of Warsaw; 31 Oct 1968; 51°52'N, 21°18'E; J.M. Rembiszewski; UO.

Black Sea Basin

Dnepr River Basin

Belorussian SSR, USSR

0168; 1a, 116.5 mm; Svisloch'R, Minskaya Oblast': 53°26'N, 28°59'E; 11 May 1959; UO.

Ukrainian SSR, USSR

0164 - 5; 2a, 135.5 - 151 mm; Sozh R, Chernigovskaya Oblast'; 51°57'N, 30°48'E; 29 May 1960; UO.

0149 - 57; 9a, 71 - 137.5 mm; Perga R, near Perga, Zhitomirskaya Oblast'; 51°24'N, 27°53'E; 22 April 1979; UO.

0169; 1a, 191 mm; Uzh R, near Rudnya-Veresnya, Kiyevskaya Oblast'; 51°11'N, 30°6'E; 11 Feb 1978, UO.

0166 - 7; 2a, 152.5 - 180 mm; Desna R, near Pirnovo, Kiyevskaya Oblast'; 50°26'N, 30°31'E; 1978; UO.

0148; 1a, 179 mm; Dnepr R, near Kozin, Kiyevskaya Oblast'; 24 July 1966; UO.

<u>Donets River Basin</u>

<u>Ukrainian SSR, USSR</u>

0112 - 7; 6t (5♂:1♀), 171 - 183.5 mm; Khar'kov R, near Khar'kov; 50°0'N, 36°15'E; 24 April - 5 May 1930; Khar'kov Institute of Scientific and Practical Veterinary Medecine; ASL23124; syntypes of <u>Lampetra</u> (<u>Eudontomyzon</u>) <u>mariae</u>, see Berg (1931) p. 95.

<u>Dnestr River Basin</u>

<u>Poland</u>

Y833 - 7; 5a, 159 - 181.5 mm; Strwiąż R; J. M. Rembiszewski; UO.

<u>Danube River Basin</u>

<u>Czechoslovakia</u>

W(VDV)5701 - 16; 15a, 34 - 191 mm; 1t (♂), 168 mm; Mutnianka Brook, Mutné, Slovakia; 49°30'N, 19°17'E; 17 Oct 1961; I. Bastl, J. Holčík, V. Mišík; SNMLF53005 - 21; see Holčík (1963) p. 53-4.

W(VDV)5801; 1t, 148.5 mm; Hraničný Kriváň Brook, Slovakia; 49°27'N, 19°36'E; 23 Aug 1960; E.K. Balon, J. Holčík, V. Mišík;

SNMLF32411/456; see Holčík (1963) p. 53.

068 - 77; 10a, 91 - 151.5 mm; Hraničný Kriváň Brook, Slovakia; 49°27'N, 19°36'E; 23 Sept 1960; J. Holčík, V. Mišík; UO.

W(VDV)5804; 1t (♀), 131 mm; Hraničný Kriváň Brook, Slovakia; 49°27'N, 19°36'E; 28 April 1961; J. Holčík, V. Mišík; SNMLF 41863/460; see Holčík (1963) p. 53, Table 3, p. 58.

W(VDV)5729 - 77; 49a, 42 - 212 mm; Biela Orava R, at the confluence of Mutnianka Brook, Slovakia; 49°21'N, 19°12'E; 24 April 1961; J. Holčík and V. Mišík; SNM42770 - 829.

Untagged; 20a, 88 - 182 mm; 2a, 152 - 165.5 mm; Turiec R, Slovakia; 49°7'N, 18°55'E; 9 Sept 1973; Laboratórium rybárstva a hydrobiológie SPA; LRHB.

W(VDV)5821 - 2; 2a, 150 - 153.5 mm; Hron R, Brezno, Slovakia; 48°49'N, 19°39'E; 9 Sept 1959; Z. Kux, T. Weisz; UO.

W(VDV)5816; 1t (♀), 182 mm; Rudava R, Vel'ké Leváre, Slovakia; 48°30'N, 17°0'E; 19 July 1964; UO; This specimen was kept alive in an aquarium until 15 April 1965.

W(VDV)5828 - 40; 13a, 84.5 - 191 mm; Ipel'R, Rovňany; 48°27'N, 19°45'E; 17 Aug 1962; Z. Kux, T. Weisz; UO.

W(VDV)5717; 1a, 186.5 mm; intermittent pond, near Medveďov, floodplain of Danube R, Slovakia; 47°46'N, 17°41'E; 8 April 1959; E.K. Balon; SNM26903.

Y456 - 63; 8a, 163-200 mm; MSNV265.

<u>Ukrainian SSR, USSR</u>

0158 - 63; 6a, 71-179.5 mm; Siret R, near Komarovcy, Chernovtsy Oblast'; 48°12'N, 25°34'E; 1-6 Aug 1971; UO.

Rumania

Y510; 1a, 185 mm; Suceava Brook, Moldavia; 47°32'N, 26°32'E; 1 Oct 1948; MSNV394; see Zanandrea (1959a) Table 1, collection #9.

W(VDV)4034 - 5; 2t (2♂), 159 - 168 mm; Argeş R, near Oeşti-Ungureni, Walachia; 45°16'N, 24°39'E; July 1963; G. Tomulescu; UO.

W(VDV)4042 - 4, 5160; 4a, 36 - 126 mm; Bratia R, Berevoeşti-Ungureni, Walachia; 45°14'N, 24°55'E; July 1960; P. Bănărescu; UO.

W(VDV)4036 - 8; 3t (3♀), 159 - 162 mm; Argeş R, near Albeşti-Ungureni, Walachia; 45°13'N, 24°40'E; June 1963; F. Scărlătescu; UO.

Austria

Y464, 467; 2t, 134-195 mm; Mur R, near Graz, Steiermark; 47°4'N, 15°27'E; 1956; MSNV120; see Zanandrea (1959a) Table 6, collections # 8-9 (4 out of 13 specimens in these collections were studied). Adults bearing tags Y465 - 6, 132.5 - 139 mm in TL, although included in these collections, were re-identified as *Lampetra* sp. . see Results and Discussion p.72 .

W(VDV)5418; 1t (♀), 123 mm; Drava R; 1867; F. Steindachner; MV50013; see Zanandrea (1959a) Table 6, collection # 10 and Holčík (1963) p. 53.

Yugoslavia

Y436 - 45; 10a, 128 - 168 mm; Sava R, Ljubljana; 46°2'N, 14°30'E; 1957; MSNV409; see Zanandrea (1959a) Table 6, collection # 17.

Y446 - 55; 8a, 110 - 173.5 mm; 2t (2♂), 144 - 147 mm; Sava R, Ljubljana; 46°2'N, 14°30'E; MSNV401.

Adriatic Sea Basin

Drin River Basin

Yugoslavia

W(VDV)5864 - 76; 5a, 189.5 - 207.5 mm; 8t (6♀:2?), 153.5 - 195 mm; Lake Ohrid; 41°0'N, 20°45'E; S. Hadžišče; UO.

Aegean Sea Basin

Vardar River Basin

Yugoslavia

Y772; 1t (♂), 152.5 mm; Vardar R; April or May 1949; A. Dimovsky; NMC77 - 1713.

E. morii
(4t)

Yellow Sea Basin

Yalu River Basin

People's Republic of China

J(DPQ)1577; 1t, 171 mm; upper Yalu R, Ko-sui-in, Manchuria; July 1926; T. Mori; ASL23145; syntype of Lampetra (Eudontomyzon) morii, see Berg (1931) p. 97.

-091 - 3; 3t (2♀:1?), 172.5 - 211.5 mm; upper Yalu R, near Changbai, Jilin Province; 41°26'N, 128°11'E; July 1975; NMC80-930.

E. hellenicum
(237a, 13â, 66t)

Aegean Sea Basin

Struma River Basin

Greece

W804 - 26, 2310 - 1; 25a, 86 - 126 mm; Milopótamos Brook, near Milopótamos and Dráma, Macedonia; 41°9'N, 24°4'E; 7 Sept 1973; P. S. Economidis; UO; paratypes of Eudontomyzon hellenicum, see Vladykov et al., in prep..

W(VDV)6476 - 83, Y757 - 63; 15a, 33 - 130 mm; Milopótamos Brook, near Milopótamos and Dráma, Macedonia; 41°9'N, 24°4'E; 19 May 1977; P. S. Economidis, A. I. Sinis, V. D. Vladykov; NMC77 - 1754; paratypes of Eudontomyzon hellenicum, see Vladykov et al., in prep..

Y785 - 800; 8a, 121 - 150 mm; 8t (6♂:2♀), 104.5 - 136.5 mm; Milopótamos Brook, near Milopótamos and Dráma, Macedonia; 41° 9'N, 24°4'E; 7 Oct 1977; G. Asmis, P. S. Economidis; UO; Specimens bearing tags Y785 - 8 were kept alive in an aquarium at the Laboratoire de Zoologie, Université de Thessaloníki, until 15 Dec 1977; paratypes of E. hellenicum, see Vladykov et al., in prep..

Y801 - 27; 11a, 79 - 152 mm; 16t (7♂:9♀), 111 - 151.5 mm; Milopótamos Brook, near Milopótamos and Dráma, Macedonia; 41°9'N, 24°4'E; 28 Dec 1977; G. Asmis, P. S. Economidis, A. I. Sinis; UO; paratypes of Eudontomyzon hellenicum, see Vladykov et al., in prep..

W766 - 70, 2312 - 3; 6a, 55 - 139.5 mm; 1t (♂), 130 mm; Ayannis Brook, near Sérrai, Macedonia; 41°5'N, 23°33'E; 7 Sept 1973; P. S. Economidis; UO; paratypes of Eudontomyzon hellenicum, see Vladykov et al., in prep..

W771 - 86, 788 - 98, W(VDV)4114; 22a, 91 - 128 mm; 6t (4♂:2♀), 103 - 137 mm; Kefalárion Brook, near Kefalárion, Macedonia; 41°4'N, 24°16'E; 7 Oct 1972; P. S. Economidis;

UO; paratypes of Eudontomyzon hellenicum, see Vladykov et al., in prep..

Y764 - 71; 4a, 93 - 100 mm; 1s, 113.5 mm; 3t (2♂:1♀), 99 - 139 mm; Kefalárion Brook, near Kefalárion, Macedonia; 41°4'N, 24°16'E; Oct 1972; E. Tsakalidis; NMC77 - 1740; paratypes of Eudontomyzon hellenicum, see Vladykov et al., in prep..

W2314 - 5; 2a, 49 - 90.5 mm; Kefalárion Brook, near Kefalárion, Macedonia; 41°4'N, 24°16'E; 7 Sept 1973; P. S. Economidis; UO; paratypes of Eudontomyzon hellenicum, see Vladykov et al., in prep..

W(VDV)4080, Y730 - 47; 15a, 54 - 128.5 mm; 4t (3♂:1♀), 95.5 - 110 mm; Kefalárion Brook, near Kefalárion, Macedonia; 41°4'N, 24°16'E; 17 May 1977; E. Tsakalidis; NMC77 - 1752; paratypes of Eudontomyzon hellenicum, Y744 is the holotype and bears NMC77 - 1773, see Vladykov et al., in prep..

Y580 - 99, 629 - 729; 119a, 60.5 - 133 mm; 2t (2♀), 103 - 105 mm; Kefalárion Brook, near Kefalárion, Macedonia; 41°4'N, 22°16'E; 19 May 1977; P. S. Economidis, A. I. Sinis, V. D. Vladykov; NMC77 - 1753; paratypes of Eudontomyzon hellenicum, see Vladykov et al., in prep..

Ionian Sea Basin

Loúros River Basin

Greece

0105 - 6; 2t (1♂:1♀), 135.5 - 149 mm; Loúros R, Ípiros; 1968; P. S. Economidis; ZMH4210.

W799 - 803; 4a, 92.5-152 mm; 1t (♀), 146 mm; Filippiás Brook, near Filippiás, Ípiros; 39°12'N, 20°53'E; 27 Nov 1969;

P. S. Economidis; UO; paratypes of Eudontomyzon hellenicum, see Vladykov et al., in prep..

Y748 - 56; 9a, 79 - 126.5 mm; Filippiás Brook, near Filippiás, Ípiros; 39°12'N, 20°53'E; 17 Oct 1973; F. Theocharis; NMC77 - 1741; paratypes of Eudontomyzon hellenicum, see Vladykov et al., in prep..

Y773 - 84; 2a, 124 - 138.5 mm; 10t (4♂:6♀), 124.5-151 mm; Filippiás Brook, near Filippiás, Ípiros; 39°12'N, 20°53'E; 20 Oct 1977; G. Asmis, P. S. Economidis; UO; paratypes of Eudontomyzon hellenicum, see Vladykov et al., in prep..

O176 - 95; 3a, 151 - 189 mm; 4ã, 135 - 156.5 mm; 13t (5♂:8♀), 129 - 158.5 mm; Filippiás Brook, near Filippiás, Ípiros; 39°12'N, 20°53'E; 13 Nov 1979; P. S. Economidis; PC; paratypes of Eudontomyzon hellenicum, see Vladykov et al., in prep..

METHODS

The lamprey life cycle, regardless of mode of life, is divided into three major stages. What follows is the terminology in use to designate these stages, along with their characteristics.

Ammocoete stage: The lamprey, from hatching to the onset of metamorphosis, is called an ammocoete. This larval period lasts several years. The ammocoete is characterized by an oral hood, triangular nostril, eyes covered with a more or less thick layer of skin and branchial openings connected by a groove.

Juvenile stage: Metamorphosis is the period of transition between the larval and adult stages. In this stage, the lamprey is either termed a metamorphosing or transforming ammocoete, a juvenile or a subadult. This period lasts a couple of months. A metamorphosing ammocoete is characterized by the possession of characters intermediate between those of an ammocoete and adult.

Adult stage: This is the stage of the post-metamorphosis lamprey. It extends up to the death of the spent individual at the end of the spawning period. At this stage, the lamprey is either termed a metamorphosed or transformed individual, or an adult. Adults live a few months or a couple of years depending on their mode of life. The adult lamprey is characterized by a suctorial disc, buccal funnel studded with, and tongue bearing keratinous teeth, circular nostril, eyes not covered by any layer and branchial openings not connected by a groove.

Throughout, I used the various synonyms pertaining to the three developmental stages described above, indiscriminately.

Specimens were preserved in 5% formalin. For easy and rapid recognition of individual specimens, small plastic alphanumeric tags were attached to them. For uniformity, geographic names appearing in this thesis were spelled according to gazetteers listing the official standard names approved by the US Board on Geographic Names. Unapproved variant spellings were not included, but can be found in the appropriate gazetteers, cross-referenced to the conventional spellings. Gazetteers are listed in the Literature Cited under the country name.

Meristic (i.e.: trunk myomeres), morphometric and pigmentation characters were typically taken on the left side. Trunk myomeres were counted under a desk magnifying glass, using insect pins as markers. Dentitional and pigmentary characters as well as sex were determined with the help of a dissection microscope. Morphometrics were measured with fine tip calipers to the nearest 0.5 mm, except the weight, which was measured using a top-loading balance to a precision of 0.01 g.

The methodology followed in this work was essentially taken from Vladykov (1950, 1955, 1960) and Zanandrea (1956a), for the study of ammocoetes, and from Hubbs and Trautman (1937), Vladykov (1949, 1955), Zanandrea (1956b), Vladykov and Follett (1958) and Holčík (1963), for the study of metamorphosed individuals. The teeth terminology follows Vladykov and Follett (1967). A few modifications and additions were made to the methodologies of the above authors, explanations of which follow.

Adult Characters

Meristic - Dentition: Number, type (uni-, bi- or tricuspid) and arrangement of teeth were considered (fig. 1).

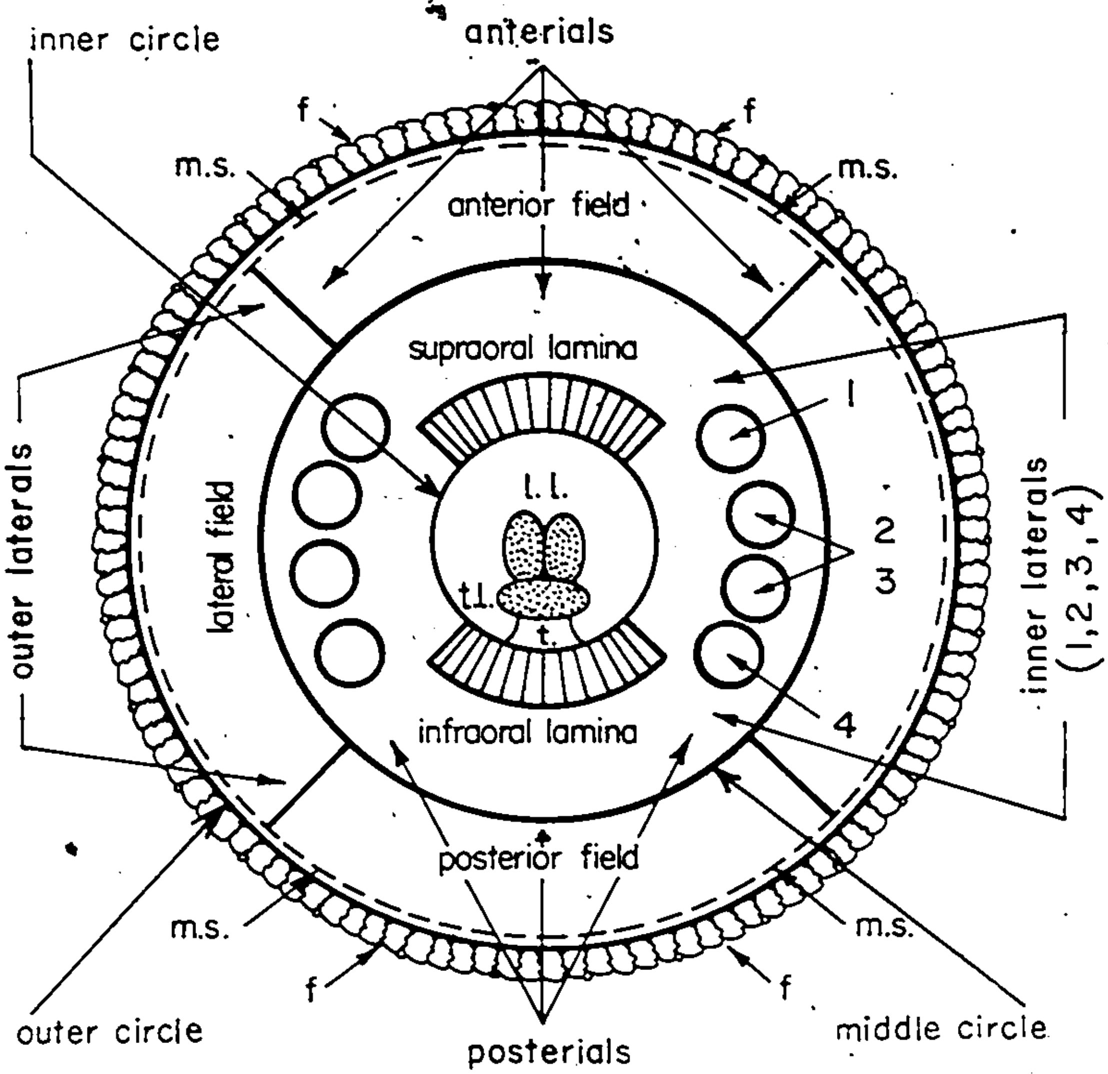
Lingual laminae: Transverse

Longitudinal: There are two placed side by side.

Supraoral lamina

Endolaterals: There are three or four, on each side of the disc. The first endolateral on a given side of the disc is next to the supraoral lamina and the last one (third or fourth) is

Fig. 1. Schematic drawing of the disc and dentition of a holarctic lamprey, after Vladykov and Follett (1967). The abbreviations are as follows: f.- oral fimbriae; l.l.- longitudinal laminae; m.s.-marginal series; t.- tongue bearing three lingual laminae; t.l.-transverse lamina.


inner circle
anterials
f
f
m.s.
m.s.
anterior field
supraoral lamina
outer laterals
lateral field
l. l.
t.l.
t.
1
2
3
4
inner laterals (1,2,3,4)
infraoral lamina
posterior field
m.s.
m.s.
f
f
outer circle
posterials
middle circle

next to the infraoral lamina.

Infraoral lamina

First anterial row: The one immediately above the supraoral lamina

First posterial row: The one immediately below the infraoral lamina

Rows: The number of anterial, exolateral (on each side of the disc) and posterial rows were counted along a median line. This median line is rectilinear in the case of the anterial and posterial fields and curvilinear in the exolateral fields. There is one exception to this methodology, concerning the posterial rows. In E. mariae complex, the number of teeth in the first posterial row is highly variable (Table 3) and even when only one posterial cusp was present in this row, whether in the median position or not, a posterial row was said to occur. The marginal row was excluded from these counts.

- Trunk myomeres: The first myomere is the one whose first myoseptum lies on or is posterior to the posterior edge of the seventh branchial opening and the last myomere is the one in which the lower angle of its second myoseptum falls on or is anterior to the anterior edge of the cloacal slit. In some specimens, the last myoseptum lies perpendicular to the cloacal slit instead of the usual acute angle position. In case of a discontinuity between the upper and lower parts of a trunk myomere (i.e.: partial myoseptum), the lower part has precedence and is the one counted.

Morphometric: In parentheses, next to each morphometric, is its abbreviation as it appears in the tables and in the text (figs. 2,3).

Total length (TL): The length from the anteriormost tip of the oral fimbriae to the extremity of the caudal fin. Even though there may be a fleshy overhang projecting anteriorly to the oral fimbriae, it is still the latter which take precedence. This remark also applies to the following measurements: $d\text{-}B_1$, d-n, d and d-O.

Head length ($d\text{-}B_1$): The length from the anteriormost tip of the oral fimbriae to the anterior edge of the first branchial opening

Prenostril length (d-n): The length from the anteriormost tip of the oral fimbriae to the anterior edge of the nostril

Disc length (d): The length of the closed disc taken longitudinally from the base of the posteriormost fimbria to the extremity of the anteriormost fimbria. The closing of the disc is achieved by compressing both sides, between

Fig. 2. Schematic drawing of the side-view of an adult male lamprey with two dorsal fins. Explanations for abbreviations are found in Methods, under adult morphometrics.

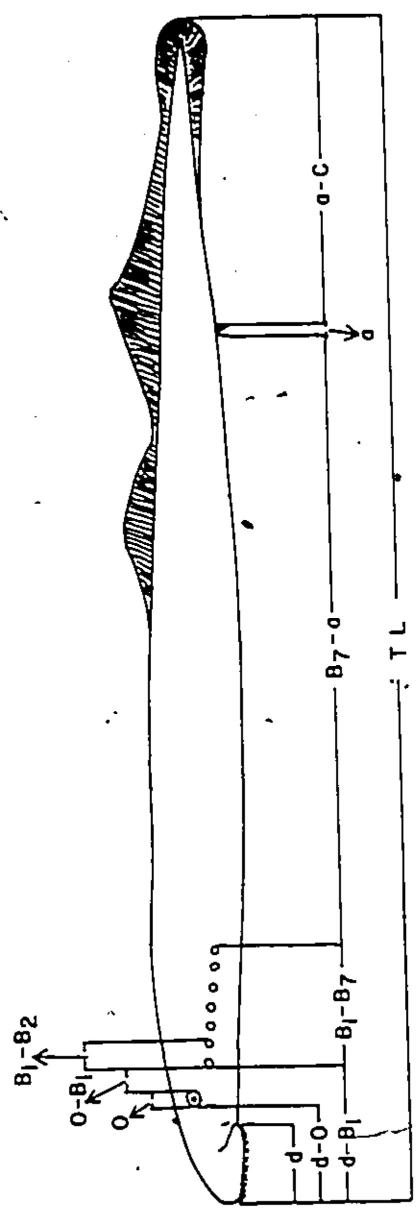
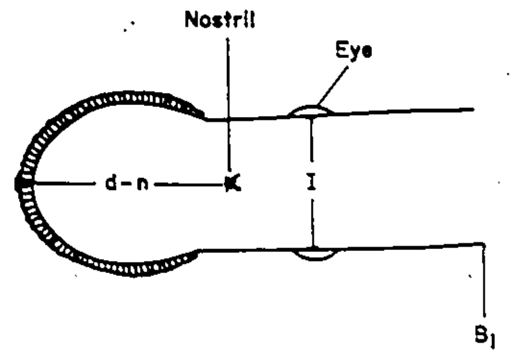
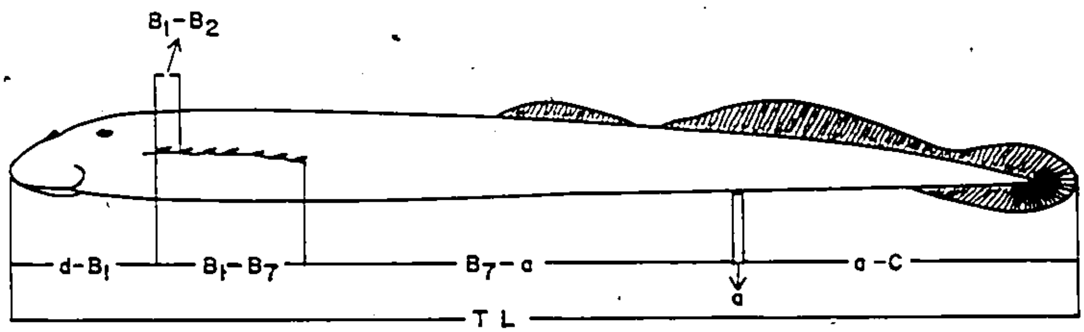

a-C
a
B7-a
TL
B1-B7
B1-B2
O-B1
O
d-O
d-B1
d

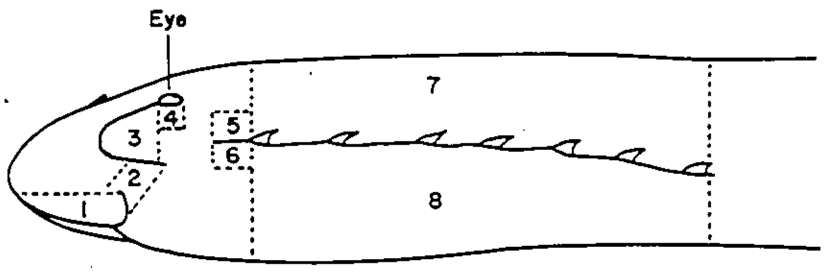
Fig. 3. Schematic drawing of the dorsal view of the head of an adult lamprey. Explanations for abbreviations are found in Methods, under adult morphometrics.

Fig. 4. Schematic drawing of the side-view of an ammocoete with two dorsal fins. Explanations for abbreviations are found in Methods, under Ammocoete Characters.

Fig. 5. Schematic drawing of the side-view of the head and branchial region of an ammocoete. Numbers refer to pigmentation areas, as follows: 1-Upper lip; 2-Between upper lip and cheek; 3-Cheek; 4-Subocular; 5-Upper prebranchial; 6-Lower prebranchial; 7-Upper branchial; 8-Lower branchial.


Nostril
Eye
d-n
I
B1


B1-B2
d-B1
B1-B7
B7-a
a-C
a
T L


Eye
1
2
3
4
5
6
7
8

the thumb and index, till they meet.

Snout length (d - O): The length from the anteriormost tip of the oral fimbriae to the anterior edge of the eye

Branchial region length ($B_1 - B_7$): The length from the anterior edge of the first branchial opening to the posterior edge of the seventh branchial opening

Trunk length (B_7 - a): The length from the posterior edge of the seventh branchial opening to the anterior edge of the cloacal slit

Cloacal slit length (a): The length of the cloacal slit from its anterior to its posterior edge

Tail length (a - C): The length from the posterior edge of the cloacal slit to the extremity of the caudal fin

Eye diameter ($\dot{O}$): It was taken horizontally.

Interocular distance (I): The distance separating the dorsal edges of both eyes

Postocular length (O - B_1): The length from the posterior edge of the eye to the anterior edge of the first branchial opening

Interbranchial opening distance (B_1 - B_2): The distance separating the posterior edge of the first branchial opening from the anterior edge of the second branchial opening

Urogenital papilla length: The length from its appearance out of the cloacal slit to its extremity

Precloacal intestine width: The external diameter of the intestine taken at the level where a vertical line drawn from the origin of the first dorsal fin intersects the intestine. In order to expose the intestine, a longitudinal incision slightly lateral to the ventral midline was made on the right side of the specimens.

Body wet weight: Specimens were left to rehydrate in tap water at least one hour, then blotted with an absorbent paper towel before being weighed.

Morphological - Caudal fin shape: Only two states occur in the *Eudontomyzon* genus: rounded and spade-like. The rounded condition is said to occur when a tangent to the edge of the fin does not intersect more than one point. The spade-like condition is when at least one straight edge is present.

Pigmentary: The following scheme was devised to estimate degree of pigment coverage in a given area.

-	:	absence of to trace coverage of area considered
+	:	1% to under 25% coverage
++	:	25% to under 75% coverage
+++	:	over 75% coverage

Note that it is not the intensity (i.e.: darkness) of pigment which is considered but the degree of pigment coverage.

- Caudal fin pigmentation

Sex: The same incision to expose the intestine was used for examination of the gonads.

Juvenile Characters

Only total length and body wet weight were taken.

Ammocoete Characters

Number of trunk myomeres and following morphometrics were taken as in adults: $B_1 - B_7$, B_7 - a, a, a - C, $B_1 - B_2$ and body wet weight (figs. 4, 7).

Morphometric: Total length (TL): The length from the anterior edge of the upper lip, also called oral hood, to the extremity of the caudal fin

Head length ($d - B_1$): The length from the anterior edge of the upper lip to that of the first branchial opening

Prenostril length (d - n): The length from the anterior edge of the upper lip to the anterior tip of the nostril

Morphological - Caudal fin shape: as in adults

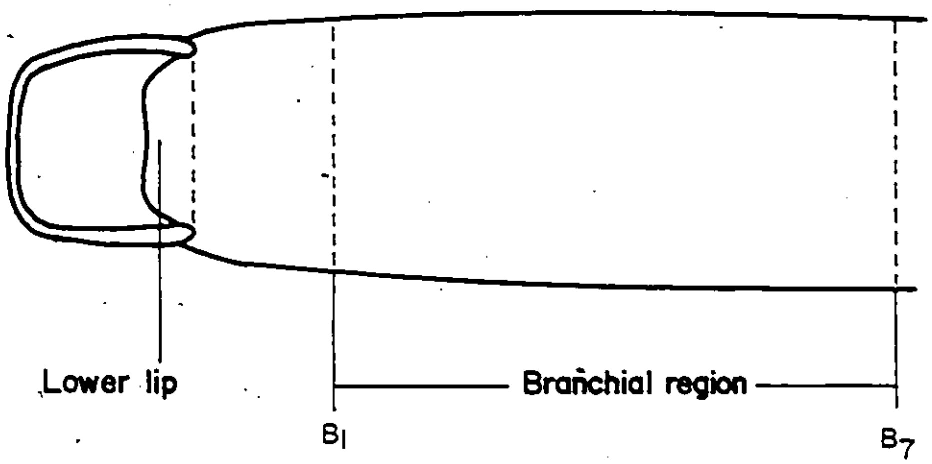
Pigmentary: The same scheme used in adults to estimate pigment coverage was used in the ammocoetes (figs. 5,6,8).

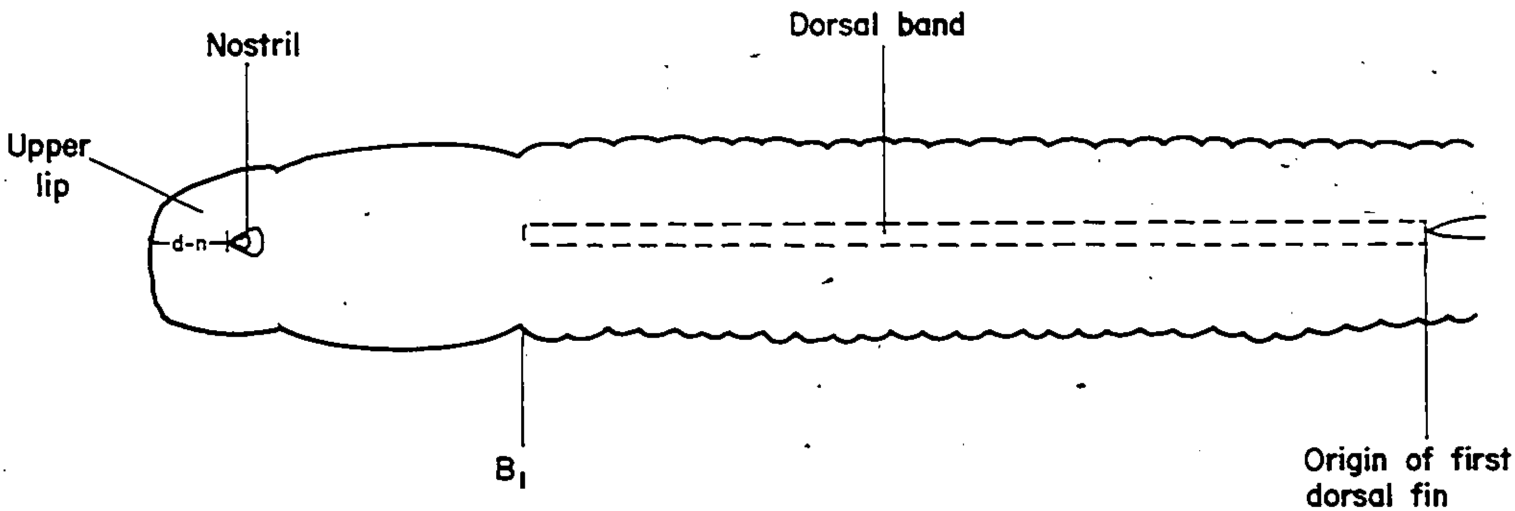
Upper lip: Only its lower lateral flap was considered.

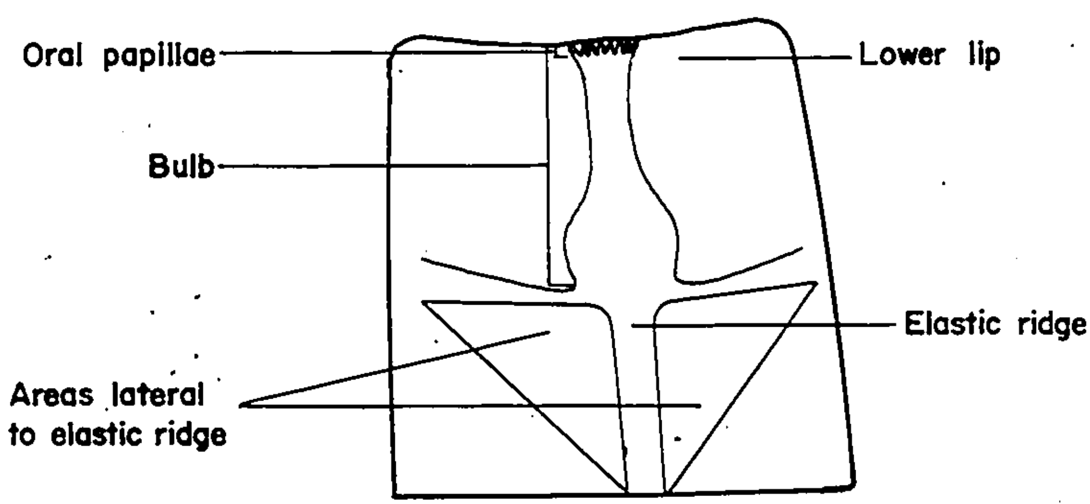
Fig. 6. Schematic drawing of the ventral view of the head and branchial region of an ammocoete.

Fig. 7. Schematic drawing of the dorsal view of the head and back (up to the first dorsal fin) of an ammocoete.

Fig. 8. Schematic drawing of the dorsal view of the tongue precursor. The two fleshy oral papilla-bearing appendages, lateral to the bulb, are omitted.


Lower lip
Branchial region
B_1
B_7


Nostril
Dorsal band
Upper lip
d-n
B_1
Origin of first dorsal fin


Oral papillae
Lower lip
Bulb
Elastic ridge
Areas lateral to elastic ridge

Area between upper lip and cheek

Cheek: Area ventral and anterior to the eye

Subocular area

Prebranchial area: It extends from the anteriormost tip of the branchial groove to the anterior edge of the first branchial opening.

Upper: Above branchial groove

Lower: Below branchial groove

Branchial region: Upper: Above branchial openings

Lower: Below branchial openings

Ventral: Underside of the body

Lower lip: Often, one must push aside both lateral flaps of the upper lip to study the pigmentation of the lower lip.

Caudal fin

Dorsal: Area along the back from the anterior edge of B_1 to the origin of the first dorsal fin

Tongue precursor: To expose the tongue precursor, a transverse incision was made across the ventral surface slightly anterior to B_1. From there, a longitudinal slit was made on the right side up to the lateral edge of the lower lip. The flap thus created was then lifted, thereby exposing the tongue precursor on the inner surface of the flap.

Bulb

Along elastic ridge: The areas lateral to the elastic ridge. These areas approximate the shape of two right-angle triangles placed side by side, one a mirror image of the other.

Morphometrics were standardized by expressing them as percentages of total length, branchial region length and interocular distance. In adults, the following morphometrics were expressed as a percentage of TL: d - B_1, B_1 - B_7, B_7 - a, a, a - C, d, d - n, d - O, O, O-B_1; as a percentage of B_1 - B_7: d, d - n, d - O, d - B_1, B_1 - B_2; and O as a percentage of I. In ammocoetes, the following morphometrics were expressed as a percentage of TL: d - B_1, B_1 - B_7, B_7 - a, a, a - C, d - n; as a percentage of B_1 - B_7: d - n, d - B_1, B_1 - B_2.

Two univariate statistical tests were used in the analysis of the data. The F-test, an anova (analysis of variance), was used for the statistical analysis of the total length and the standardized morphometrics, which are continuous variables (Tables 12, 13, 15). The Chi-square or more precisely the 2 X C contingency test, a goodness-to-fit test, was used for the statistical analysis of the meristic and pigmentary characters, which are discrete or discontinuous variables (Tables 14, 16). The chosen confidence level was $P \leq 0.002$ in the case of the F-test and $P \leq 0.05$ in the case of the Chi-square test. The F-test was two-sided, whereas the Chi-square test is invariably one-sided.

The raw data are deposited at the National Museum of Natural Sciences, Ottawa.

RESULTS AND DISCUSSION

The generally accepted thesis, among lamprey specialists, that parasitic and nonparasitic lampreys belong to distinct taxa is followed here.

The genus Eudontomyzon has a discontinuous Eurasian distribution (fig. 20). It is made up of exclusively freshwater, parasitic and nonparasitic species. There are two dorsal fins. The caudal fin may be rounded or spade-like in shape. The number of trunk myomeres varies from 53 to 74.

Adults range in total length between 95.5 and 300 mm.They are characterized by the presence of at least one and often numerous rows of teeth on all fields of the disc. Exceptionally however, rows of teeth may be absent from the posterial field. Teeth on the various fields may be villiform or non-villiform. The supraoral lamina is made up of two large lateral teeth and additional cusps (up to three) may be present along the bridge. There are usually three or four endolaterals on each side of the disc, all of which, when present, may be unicuspid, bicuspid or tricuspid. The infraoral lamina may bear 5 to 12 teeth. The transverse lingual lamina is slightly convex, with a single ridge, and bears an enlarged median cusp, not necessarily taller, but certainly wider than other cusps on the lamina. The number of cusps on the transverse lingual lamina may vary from 1 to 15. Teeth may be absent on the longitudinal lingual laminae, or number as many as 17. The velar apparatus may be winged or wingless. The number of velar tentacles ranges from 2 to 15.

Ammocoetes may reach 230 mm in total length, exceptionally 250 mm. Pigmentation coverage of various body areas exhibits wide variation.

Eudontomyzon danfordi Regan, 1911

(figs. 9a, 10a, 14a, 16a, 17a, 18a, 19a)

Etymology of specific epithet: Named after C.G. Danford, the principal collector of the syntypes

Common names: Hadyna, Iche, Ils, Jiche, Jige, Juge, Juzyk, Mangour, Naiang, Ouche, Ouge, Podkouv-hol, Pychkar, Pychkor, Pyskaryl, Pyškor, Pyskyr, Pytchkar, Pytchkarel, Rybarov, Rybarovka, Vangour, Vizitchik, Vouge (Ukrainian: Subcarpathian Ukraine, Vladykov (1927a))

Carpathian lamprey (Oliva, 1953a; 1953b; 1962; Holčík, 1966b)

Chişcar or Cícar (Rumanian: Transylvania, Grossu et al. (1962), Bănărescu et al. (1971))

Hungarian lamprey (Berg, 1931; Vladykov and Kott, 1976b; Zhukov, 1969; Potter, 1980)

Synonymy: Eudontomyzon danfordi Regan, 1911. Ann. Mag. Nat. Hist. 7(8): 200-1 (Rumania: Transylvania, in general and Sebés Brook, Transylvania, in particular; six syntypes in British Museum (Nat. Hist.); type-species by monotypy); Vladykov, 1931. Mém. Soc. Zool. France 29(4): 225, 228-30, 362 (Black sea basin: Danube (Tisa) basin-Tisa, Kusva, Chopourka (Sopurka), Apchicia (Apchica, Apsica), Tereshova, Tereblya, Rika, Borzhava, Latorica, Uh rivers, Subcarpathian Ukraine); Chappuis, 1939. Arch. Hydrobio. 34: 645-50, 654, 656-7, fig. 1 (Tisa river basin: Subcarpathian Ukraine; Someşul River and affluent Someşul Rece

River, Arieş River, Iara and Sebés brooks, Crişul Repede River and affluent Drăgan River, Rumania (Transylvania)); Balon, 1964a. Biol. (Čas. Slov. Akad. Vied) 19(5): 344, 347 (Tisa river basin, Slovakia); Bănărescu, 1968. Bul. Inst. Cerc. Proiec. Pisc. 27(3): 54 (fresh waters of Rumania); Holčík, 1970a. Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.) 34(1): 22 (Tisa river basin, eastern Slovakia); Holčík, 1970c. Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.) 34(4): 304, 306-7 (Danube (Tisa) river basin: Hornád River, Slovakia); Bănărescu et al., 1971. European inland water fish. A multilingual catalogue.: fig. 3 (Tisa river basin); Hardisty and Potter, 1971b. The biology of lampreys 1: 141, 149, 154, 156 (Danube basin); Vladykov and Kott, 1976c. Rev. Trav. Inst. Pêches Marit. 40(3-4): 787-9; Potter, 1980. Can. J. Fish. Aquat. Sci. 37: 1596-7, 1602, 1604, 1608, fig. 3 (Danube basin)

<u>Petromyzon</u> (<u>Eudontomyzon</u>) <u>danfordi</u> (in part); Creaser and Hubbs, 1922. Occ. Pap. Mus. Zool. Univ. Mich. 120: 5 (Rumania: Transylvania)

<u>Lampetra</u> <u>Bergi</u> Vladykov, 1925. Zool. Anz. 64(11): 251-2 (Subcarpathian Ukraine); Vladykov, 1926. Ryby Podkarpatské Rusi: 16 (Tisa river basin, Subcarpathian Ukraine)

<u>Lampetra</u> (<u>Eudontomyzon</u>) <u>danfordi</u>; Berg, 1931. Ann. Mus. Zool. Acad. Sci. URSS. 32(1): 92-4, 96, 116, Plate 3, figs. 2-3 (Tisa river basin: Tereblya and Tereshova rivers, Subcarpathian Ukraine; Transylvania, in general and Sebés Brook, Transylvania, in particular); Oliva, 1953a. Věst. Král. Čes. Spol. Nauk, Tř. Mat.-Přírodověd. 9:9, 12-3, 16-7, figs. 3a, b, 4 (Danube (Tisa)

river basin: Subcarpathian Ukraine; Topl'a River, Slovakia); Oliva, 1953b. Sbor. ČSAZV. 26(1-2): 41 (Czechoslovakia); Oliva, 1960. Przeg. Zool. 1959: 281 (Danube basin); Oliva, 1962. Nár. Muz. 1:3 (Czechoslovakia); Holčík, 1963. Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.) 27(1): 51-2, 56, 59-61, fig. 1 (Tisa river basin: Topl'a and Okna rivers, Czechoslovakia (Slovakia); Subcarpathian Ukraine, USSR; Someşul Rece River and Mureşul river basin, Rumania); Holčík, 1966b. Biol. Prá. (Slov. Akad. Vied) 12(1): 86, 95, 98, fig. 2 (Hornád River, Slovakia); Zhukov, 1969. Prob. Ich. 9(2): 181 (Danube basin)

Eudontomyzon danfordi vladykovi (in part): Oliva and Zanandrea, 1959. Doriana, Ann. Mus. Civ. Stor. Nat. "G. Doria" Suppl. 2(98): 4 (Danube basin: Lukov, Czechoslovakia); Zanandrea, 1959a. Arch. Zool. Ital. 44: 219, 225, 228, 230, 232-3, 246-9, Tables 4-8 (Danube (Tisa) river basin: Topl'a River, Czechoslovakia)

Eudontomyzon danfordi (in part): Zanandrea, 1959a. Arch. Zool. Ital. 44: 216-7, 219, 221-2, 224, 230-3, 246-8, 250, Tables 1-5, 8, figs. 1, 3, 5 (Danube (Tisa) river basin: Tereshova and Tereblya rivers, Ukrainian SSR (Subcarpathian Ukraine); Someşul Mare River and affluent Sălăuta Brook, Someşul Mic and Crişul Alb rivers, Mureşul River and tributaries Arieş and Strei rivers and Iara and Sebés brooks, Rumania (Transylvania); Bănărescu, 1969. Fau. Rep. Soc. Rom. 12(1): 9, 19, 22, 25-8, 35-38, 41, 44, 48-50, 53-4 (Black sea basin - Danube (Tisa) river basin: Czechoslovakia; Ukrainian SSR (Subcarpathian Ukraine); Vişeu

River, Someşul river basin (Someşul Rece River, Someşul Cald River and affluents Risca and Agirbici brooks, Transylvanian Bistriţa River, Anies, Capus, Cormaia, Sălăuta brooks), Körös river basin (Crişul Repede River and affluent Drăgan River, Crişul Negru River, Vida River and affluent Toplita Brook, Moneasa Brook), Mureşul river basin (Bistra, Gudea-Mare, Gudea-Unita, Iara, Lapusna, Rastolita, Sebés, Toplita, Zebrac brooks), Timişul river basin (Timişul River and affluent Birzava Brook, Bistra Mărului Brook and affluent Sucu Brook), Rumania); Vladykov and Kott, 1976b. Wilfrid Laurier Univ. Mus. Zool. Contrib. 1: 5 (Black sea basin)

Lampetra (Eudontomyzon) danfordi vladykovi (in part); Oliva, 1962. Nár. Muz. 1: 3 (Czechoslovakia)

Eudontomyzon vladykovi (in part); Bănărescu, 1969. Fau. Rep. Soc. Rom. 12(1): 26-7, 42, 44-5, figs. 18-20 (Tisa river basin: Bistra Mărului Brook, Banat, Rumania); Vladykov and Kott, 1976c. Rev. Trav. Inst. Pêches Marit. 40(3-4): 788; Potter, 1980. Can. J. Fish. Aquat. Sci. 37: 1604, 1608 (Danube basin)

Eudontomyzon gracilis; Bănărescu, 1969. Fau. Rep. Soc. Rom. 12(1): 25, 35 (Black sea basin: Danube basin); Holčík, 1970a. Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.) 34(1): 22 (Tisa river basin, eastern Slovakia); Bănărescu et al., 1971. European inland water fish. A multilingual catalogue: fig. 4 (Tisa river basin); Vladykov and Kott, 1976b. Wilfrid Laurier Univ. Mus. Zool. Contrib. 1: 6 (Topl'a River, Slovakia); Potter, 1980. Can. J. Fish. Aquat. Sci. 37: 1604 (Slovakia)

Type-locality: Transylvania, Rumania

Mode of life: Ectoparasitic (Vladykov, 1926; Chappuis, 1939; Zanandrea, 1959a; Oliva, 1960; Grossu et al., 1962; Holčík, 1963; Balon, 1964a; Kux, 1965; Bănărescu, 1969; Holčík, 1970c; Vladykov and Kott, 1976b: 1976c; Potter, 1980)
Scavenger (Grossu et al., 1962; Kux, 1965; Bănărescu, 1969)

Hosts: Zanandrea (1959a) found fish remnants in *E. danfordi* intestines. Grossu et al. (1962) listed *E. danfordi* hosts belonging to four fish families: Cyprinidae, Cobitidae, Cottidae and Salmonidae. The cyprinid hosts are *Barbus barbus* (Linnaeus), *B. meridionalis petenyi* Heckel and less frequently, *Leusciscus cephalus* (Linnaeus). The cobitid hosts are *Noemacheilus barbatulus* (Linnaeus) and *Cobitis* sp. . The sole representative from the cottid family is *Cottus gobio* Linnaeus. Salmonids, without being more specific, are said to be infrequently parasitized. Although Bănărescu (1969) admits trouts are seldom parasitized in natural streams, he says *E. danfordi* does inflict serious damages to them in hatcheries. Holčík (1963) confirmed *Barbus meridionalis petenyi*, as a host. According to Bănărescu (1969), *E. danfordi* seldom parasitizes *Barbus barbus* but, is often found parasitizing *Cottus gobio* and another cottid, not mentionned by Grossu et al. (1962), *C. poecilopus* Heckel.

Economic importance: In certain regions of Rumania, peasants consume *E. danfordi* (Bănărescu, 1969). Rumanian fishermen occasionally use it as live bait (Bănărescu, 1969), but it is not specified at which developmental stage.

E. danfordi inflicts serious damages to trouts in Rumanian hatcheries (Bănărescu, 1969).

Habitat: *E. danfordi* was found in submountainous areas in Slovakia, at altitudes ranging from roughly 465 to 550 m (Holčík, 1966b). In Subcarpathian Ukraine, it occurs almost exclusively above 250 m of altitude (Vladykov, 1931). In Rumania, it occurs in mountain watercourses and is seldom found at lower altitudes (Grossu et al., 1962; Bănărescu, 1969).

Spawning period: *E. danfordi* is a lithophylic spawner (Holčík, 1966b). In Subcarpathian Ukraine, spent individuals of *E. danfordi* have been ~~found~~ dead in April and May (Vladykov, 1927b). Chappuis (1939) says that spawning occurs from the end of May into June in Iara Brook, Transylvania (Rumania). Bănărescu (1969) believes spawning takes place between the end of June and the beginning of July in the Bistra Mărului Brook, Banat (Rumania).

Geographic distribution: *E. danfordi* is endemic to the Tisa river basin of the Danube basin in Czechoslovakia (Slovakia), Ukrainian SSR (Subcarpathian Ukraine) and Rumania (Transylvania and Banat). For more precise information on watercourses inhabited, consult the synonymy and the Material section. Note that Subcarpathian Russia, then also called Ruthenia and referred to in Vladykov (1925, 1926, 1927a, 1931), at that time belonged to Czechoslovakia. It is now the part of Ukrainian SSR called Subcarpathian Ukraine.

I studied one of the syntypes of E. danfordi (BM) designated by Regan (1911). It is an adult, of undetermined sex, measuring 150 mm in total length, with 62 trunk myomeres and weighing 4.05g. Its urogenital papilla does not protrude out of the cloaca and secondary sexual characters are absent, indicating a sexually immature specimen. The precloacal intestine width is two mm. Other morphometrics, in mm, are as follows: d-B_1 - 13.5; B_1-B_7 - 13.0; B_7-a - 74.5; a - 1.0; a-C - 48.0; d - 7.0; d-n - 7.5; d-O - 9.0; O - 2.0; O-B_1 - 4.0; B_1-B_2 - 2.0; I - 4.0. The supraoral lamina bears two and the infraoral nine cusps. The endolateral formula is 1-2-2 on both sides of the disc. There are six anterial and three posterial rows. The first anterial row consists of seven cusps and the first posterial row 16 cusps. There are three exolateral rows on each side of the disc. The caudal fin has a spade-like shape.

Regan (1911) designated six syntypes, all adults from the imprecise locality of Transylvania, measuring 120 to 220 mm in total length. Another adult specimen, 210 mm in total length, collected in the Sebés Brook, Transylvania, which Bănărescu (1969) considers as the type-locality, was never included in the type-series. Regan (1911) described the dentition of E. danfordi, as follows: teeth on all fields numerous, villiform; three endolaterals on each side of the disc, the first and third being uni- or bicuspid whereas the second is bi- or tricuspid; infraoral lamina with nine to 11 cusps; transverse lingual lamina usually with an enlarged median cusp. He also had at his disposal, six ammocoetes measuring 95 to 185 mm in total length.

In 64 adults, the total length ranged from 140 to 241 mm (Table 1), and wet weight, in 48 of these, having the same range in total length, varied between 2.66 and 21.65 g. Out of 37 adult specimens studied, Vladykov (1925, 1931) determined the range in total length to be 180 to 300 mm. Oliva (1953a) studied nine adults measuring 149 to 194 mm total length. Bănărescu (1969) reported adult total lengths of 156 to 260 mm. The overall range in total length for E. danfordi adults is thus 120 to 300 mm. In nine adults, from Subcarpathian Ukraine and Slovakia, Oliva (1953a) found trunk myomeres ranging from 62 to 66. The most frequent trunk myomere counts in adults (Table 5) were 63 (26.3%), 64 (21.1%) and 65 (24.6%). A urogenital papilla was evident in only eight adults out of 64 examined for this character, measuring between 0.5 and 3.0 mm in length. In 30 adults, intestine width ranged from 0.5 to 5.0 mm. Oliva (1953a) reported a $d\text{-}B_1/TL\%$ value of 16, in one adult. This exceeds by 2.5%, the range recorded in Table 1 for this ratio. However, Holčík (1963) studied the same specimens as Oliva (1953a), and the highest $d\text{-}B_1/TL\%$ value he recorded, was 12.2, which agrees with the values in this study (Table 1). I can think of two explanations for this discrepancy; either a typographical error in Oliva (1953a), or a differential shrinkage of the specimen during the decade between measurements, the $d\text{-}B_1$ having shrivelled more than the rest of the body. A total of 138 endolateral formulae counts were recorded for E. danfordi. The majority of counts were made up of three endolaterals (96.4%), with four endolaterals (2.9%) and two endolaterals (0.7%) making up the rest. The typical formulae are 1-2-2 (59.4%) and 2-2-2 (23.2%). Other variant formulae are: 1-2-1 (8.7%), 1-1-2, 2-2-1, 2-3-2, 1-2-2-1, 2-2-2-1 (all 1.4%), 1-2, 1-3-2 (each 0.7%). Holčík (1963) recorded 39 endolateral formulae counts as follows: 1-2-2 (41.0%), 2-2-2 (20.5%), 1-2-1

(15.4%), 2-2-1 (7.7%), 1-3-1, 1-3-2, 1-2-2-1 (all 5.1%). Bănărescu (1969) reported that the lateralmost teeth of the infraoral lamina were sometimes bicuspid. All 39 adult specimens, whose transverse lingual lamina dentition was studied, possessed an enlarged median cusp. Of those, 30 specimens were examined in greater detail and their median enlarged cusp was found to be flanked on the left side by four to eight and on the right side four to seven cusps. The total number of cusps ranged from 9 to 15, with a mean of 12.7 and standard deviation 1.6. The two longitudinal lingual laminae of only one specimen were studied and they bore 10 and 11 cusps. Zanandrea (1959a) found 10 to 12 cusps on these lingual laminae. Figure 9a, in Vladykov et al. (1982, MS), shows the tongue of an E. danfordi adult bearing 13 teeth (one is bicuspid) on the right longitudinal lamina and 17 cusps on the left one (not all cusps are visible on the figure). The teeth on the longitudinal lingual laminae may thus vary from 10 to 17. All 63 adults in which the caudal fin shape was studied had a spade-like caudal fin. The range in the number of velar tentacles of 26 adult E. danfordi was determined by Vladykov et al. (1982, MS) to be 9 - 15, with mean 12.3 and standard deviation 1.4. The length of the median tentacle, in a subsample of 13 specimens, ranged from 2 to 3.5 mm, with mean 2.6 and standard deviation 0.5. The lateralmost tentacles on both sides are arranged into two short wings folded onto the dorsal surface of the velar apparatus (Vladykov and Kott, 1976c; Vladykov et al., 1982 MS). Each wing, in a subsample of 15 specimens, was made up of two to four tentacles (Vladykov et al., 1982 MS), with mean 2.9 and standard deviation 0.7. Vladykov and Kott (1976c) and Vladykov et al. (1982, MS) mistook two E. danfordi adults for E. vladykovi (= E. mariae complex). Both specimens had previously been identified by Holčík (1963) as E. danfordi from Okna

River (see Holčík (1963) p. 52-3, part of SNM LF36545-52). One of the specimens had 11, the other 9 velar tentacles. They were re-identified as nominal E. vladykovi, because neither possessed wings on their velar apparatus. However, I suggest that in recently metamorphosed E. danfordi which have not begun their adult trophic phase, as is the case with these two specimens, the wings are not yet formed. This seems to be a plausible hypothesis, because although their function is unknown, the presence of wings is positively correlated with a parasitic mode of life, having been detected by Vladykov and Kott (1976c) in only three parasitic species up till now: Eudontomyzon danfordi, Entosphenus tridentatus (Gairdner), Tetrapleurodon spadiceus (Bean). Hardisty (1971) reported a range of 7500 to 10300 and mean 9000 eggs / female. According to Chappuis (1939), adults live two years, feeding only during the first. They die in June or the beginning of July, after spawning (Chappuis, 1939). Zanandrea (1959a) reported an adult life of 17 to 19 months. The total length, in the ammocoetes at my disposal, ranged from 21.5 to 208 mm (Table 9), and wet weight, in 321 of these, having the same range in total length, varied between 0.02 and 14.29 g. Chappuis (1939) reported a maximum total length of 200 mm for ammocoetes. The most frequent trunk myomere counts in ammocoetes (Table 10) were 62 (24.2%) and 63 (23.7%). The tongue precursor pigmentation was determined in only four ammocoetes. The pigment coverage of the bulb was either absent to trace (i.e.: -) in 75% of the specimens or slight (i.e.: +) in the remaining 25%. The pigment coverage along the elastic-ridge exhibited extreme variation: absent to trace (i.e.: -) in 25%, slight (i.e.: +) in 50 %, strong (i.e.: +++) in 25%. Of the 178 ammocoetes looked at for caudal fin shape, only two exhibited a rounded condition; the rest had spade-like caudal fins. According to Chappuis (1939), larvae may live 4 + years. Six metamorphosing ammocoetes measured 142 to 175 mm in total length and 2.62 to 7.93 g in wet weight. Zanandrea (1959a) studied two metamorphosing specimens, one of which I studied. They were collected in September and measured 134 and 152 mm in total length. According to the material at my disposal, E. danfordi undergoes metamorphosis between the 1st of September and some undetermined date in October.

Bănărescu (1969) mistook spawning individuals of E. danfordi from the Bistra Mărului Brook, Tisa river basin, Banat, for E. vladykovi (= E. mariae complex). This conclusion was reached on the basis of two lines of evidence. Firstly, Bănărescu (1969) gave as a distinguishing characteristic between E. danfordi and the nominal E. vladykovi, the fact that the two dorsal fins were at a distance from each other in the former and close together in the latter. The distance separating the dorsal fins is dependant on sexual maturity (Vladykov, 1931) and thus, does not constitute a specific difference. Secondly, his figure 19, supposedly depicting the buccal and lingual dentitions of a specimen of the nominal E. vladykovi, in fact, represents those of E. danfordi. The well exposed, strongly developed transverse lingual lamina, with a sharp, enlarged median cusp, flanked on each side by five equally sharp cusps, does not belong to a nonparasitic species.

Holčík (1970a) put forth the idea that E. gracilis had questionable taxonomic status and was probably based on the starving forms of E. danfordi, which occur during a short period just following metamorphosis and during spawning. Bănărescu (1969) also questioned the validity of E. gracilis. I submit that Lampetra (Eudontomyzon) gracilis Kux, 1965 is a junior synonym of E. danfordi Regan, 1911, for the following reasons. Most of the views put forth by Kux (1965) were derived from aquarium experiments. I have evidence to suggest that Kux (1965) mixed up samples in his experiments. A specimen bearing tag W(VDV) 5819 (Material, p.9), said to come from Rudava River (outside Tisa basin), Slovakia and which was part of the aquarium experiments by Kux (1965), was identified by him as nonparasitic nominal Lampetra (Eudontomyzon) vladykovi. It turns out to be a spent E. danfordi female, which according to Kux (1965) are only found in the Tisa basin. It seems that Kux's erroneous identification was based on the very narrow intestinal width (i.e.: 0.5 mm). At spawning however, both parasitic and nonparasitic species have narrow intestines. Vladykov (1927b) reported intestinal diameters ranging from 0.3 to 1.0 mm in spawning E. danfordi. My identification of the above specimen as a E. danfordi is based upon the study of its velar apparatus. It has 14 tentacles and wings are present, one made up of two, the other three tentacles. As mentionned above, the presence of wings is positively correlated with a parasitic mode of life and therefore cannot apply to nominal E. vladykovi. Another specimen, this one bearing tag W(VDV)5817 (Material, p.9), from Ulička Brook, was identified by Kux as nominal E. gracilis, which Kux (1965) described as the nonparasitic derivative of E. danfordi. However, it has 13 velar tentacles and wings are present, each with three tentacles. Again, within the genus, this characteristic is exclusive to E. danfordi. It seems remarkable that nominal E. gracilis would have the same larval life span (i.e.: 4+ - 5+ years) (Kux, 1965) as E. danfordi, even though they differ in mode of life. Indeed, Potter (1980) provides evidence that nonparasitic members of a paired species have a longer larval life than their parasitic counterpart. Kux (1965) says that E. danfordi and nominal E. gracilis are sympatric, undergo metamorphosis in synchrony (end of July well into August) and are indistinguishable as ammocoetes. In the first eight to nine months of adult life, _E. danfordi_ and nominal _E. gracilis_ can only be segregated on the basis of intestinal and gonadal development (Kux, 1965). These statements lead me to believe that Kux (1965) was comparing _E. danfordi_ adults in their first year of adult life, which he took as true _E. danfordi_, with some in their second year of adult life, which he took as nominal _E. gracilis_. The specimen, which appeared in Vladykov and Kott (1976c) as _E. gracilis_ with six velar tentacles and no wings, had no accompanying collection data other than collection date (April 1964), and was not examined by the present author, so no judgment could be borne concerning its taxonomic status.

Eudontomyzon mariae (Berg, 1931) complex

(figs. 9b, 10b-d, 11a, 13a, 14b-c, 16b-c, 17b, 18b, 19b-d)

Etymology of specific epithet: Named after Maria M. Ivanova-Berg, the Russian ichthyologist

Common names: South russian lamprey (Berg, 1931; Oliva and Hensel, 1962; Oliva, 1966)

Ukrainian lamprey (Kokotshashwili, 1942; Balon, 1964a; 1964b; Abakumov, 1966; Oliva, 1966; Zhukov, 1969; Holčík, 1970a; 1970b; Vladykov and Kott, 1976b; Potter, 1980)

Danube lamprey (Balon, 1964a; 1964b)

Danube brook lamprey (Karaman, 1974)

Chişcar or Cicar (Rumanian: Moldavia, Grossu et al. (1962), Bănărescu et al. (1971))

Ţipari (Rumanian: Walachia, Grossu et al. (1962))

Synonymy: Petromyzon planeri (not Bloch); Wajgel, 1884. Verh. Zool. Bot. Ges. 33(1883): 311, Plate 17, fig. 3 (Danube basin: upper Prut River, Ukrainian SSR); Hankó, 1922. Magyar Tudom. Akad. Balk. -Kutat. Tudom. Ered.: 1, 4, 6, fig. 4 (Beli Drim river basin: Bistrica Brook, Yugoslavia)

Lampetra planeri (not Bloch) (in part); Berg, 1906. Izv. Akad. Nauk St. Petersburg Series 5, 24(3): 181 (Dnepr river basin: Irpen River; Don (not Volga) river basin, USSR); Oliva, 1953a. Věst. Král. Čes. Spol. Nauk; Tř. Mat.-Přírodověd. 9: 18 (Danube River, Slovakia); Bănărescu, 1969. Fau. Rep. Soc. Rom.

12(1): 26, 53 (Moldova River, Rumania); Holčík, 1970a. Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.) 34(1): 25, fig. 3 (Siret river basin, Rumania); Holčík, 1970c. Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.) 34(4): 304 (Siret river basin: Moldova River, east Rumania)

Petromyzon (Eudontomyzon) danfordi (not Regan) (in part): Creaser and Hubbs, 1922. Occ. Pap. Mus. Zool. Univ. Mich. 120: 2 (Prut River, Ukrainian SSR)

Petromyzon fluviatilis (not Linnaeus): Karaman, 1928. Skop. Nauc. Drust. Glas. 6(2): 148, 170 (Vardar River, Macedonia, Yugoslavia)

Lampetra (Eudontomyzon) mariae Berg, 1931. Ann. Mus. Zool. Acad. Sci. URSS. 32(1): 92, 94-6, 115-6, Plate 1, fig. 3, Plate 4, figs. 1-4, Plate 8, fig. 1 (Black sea basin: Prut and Dnestr rivers, Dnepr river basin (Dnepr, Goryn, Irpen, Teterev, Uzh, Volma rivers), Don river basin (Don, Donets, Kazanka, Khar'kov, Lopanj rivers), Kuban' river basin (Il' River), western Transcaucasian rivers, USSR; Adriatic sea basin: Drin river basin, Yugoslavia; 36 syntypes in Zoological Institute of the Academy of Sciences of the USSR, Leningrad (cat. #23124)); Kokotshashwili, 1942. Trav. Univ. Staline Tbilissi 22: 91 (Prut, Dnestr, Dnepr, Don, Donets, Kuban' river basins and west Georgian SSR river basin, near Batumi); Oliva and Hensel, 1962. Acta Univ. Carol.-Biol. 1: 99-103 (Vistula river basin: Skawa River and Rudawa Brook, Poland; Prut river basin: Lipa Zlota Brook, Ukrainian SSR); Holčík, 1963. Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.) 27(1):

51, 59, 61 (Vistula river basin: Skawa River and Rudawa Brook, Poland; Danube basin: Rumania); Bely, 1966. Zool. Zh. 45(4): 590 (Dnepr River, Ukrainian SSR); Oliva, 1966. Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.) 30(2): 142-4 (Baltic sea basin: Neman river basin - Berezyna, Isloch and Peretut' rivers, Belorussian SSR and upper Vistula river basin - Skawa River and Rudawa Brook, Poland; Black sea basin: Prut to Kuban' river basins inclusively, USSR); Zhukov, 1968. Zool. Zhur. 47(9): 1419 (Baltic and Black sea basins); Zhukov, 1969. Prob. Ich. 9(2): 181-5 (Baltic sea basin: upper Neman river basin-Berezyna, Isloch and Peretut' rivers, Belorussian SSR and upper Vistula river basin, Poland; Black sea basin: Dnepr river basin - Iput, Ratomka and Svisloch' rivers, Belorussian SSR); Elanidze et al., 1970. [Atlas of the freshwater fish of Georgia.]: 45, fig. 1 (Prut, Dnestr, Dnepr, Don, Donets, Kuban' river basins and Georgian SSR)

Eudontomyzon danfordi vladykovi (in part) Oliva and Zanandrea, 1959. Doriana, Ann. Mus. Civ. Stor. Nat. "G. Doria" Suppl. 2(98): 2, 4, fig. (Danube basin: Danube River, Čiiistovo, near Bratislava, Czechoslovakia (south Slovakia), poorly preserved holotype deposited at Charles University, Prague (Holčík (1963) p. 53 and Dr. Ota Oliva, in litt. 15 Oct. 1979); region of Graz and Drava River, Austria); Zanandrea, 1959a. Arch. Zool. Ital. 44: 216, 218-9, 225, 230-3, 246-50, Tables 3-8, figs. 2, 4, 6-7 (Danube basin: Danube, Drava, Mur and Raab rivers, Grünau Brook, Austria; Danube River, Czechoslovakia; Bednja Brook (Drava river basin) and Sava River and tributaries Lonja Brook and Maksimir Lake, Yugoslavia)

Eudontomyzon danfordi (not Regan) (in part); Zanandrea, 1959a. Arch. Zool. Ital. 44: 234, Tables 1, 4-5 (Danube basin: Siret river basin - Suceava Brook, Rumania); Bănărescu, 1969. Fau. Rep. Soc. Rom. 12(1): 26 (Moldavian Bistriţa River, Rumania); Vladykov and Kott, 1976b. Wilfrid Laurier Univ. Mus. Zool. Contrib. 1: 5 (Baltic and Black sea basins)

Eudontomyzon mariae; Zanandrea, 1959a. Arch. Zool. Ital. 44: 217-21, 228, 232-3, 246-9 (Khar'kov River, USSR; Sava river basin, Yugoslavia); Balon, 1964b. Pol. Arch. Hydr. 12(2): 234, 241 (Vistula river basin: Skawa River and Rudawa Brook, Poland); Bănărescu, 1968. Bul. Inst. Cerc. Proiec. Pisc. 27(3): 54 (fresh waters of Rumania); Bănărescu, 1969. Fau. Rep. Soc. Rom. 12(1): 9, 19, 22, 25-7, 36, 38, 42, 44-5, 49-50, 53-4, figs. 21-5 (Black sea basin - Danube (Prut River), Bug, Dnestr, Dnepr, Don, Kuban' river basins, USSR; Danube basin: Galbenu Brook, Argeş River and its affluents Rîul Tîrgului and Dîmboviţa and Rîul Doamnei and Bratia rivers and Vîlsan and Ilfov brooks, Rumania; Danube basin: Bosna River, tributary of Sava River, Yugoslavia); Holčík, 1970a. Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.) 34(1): 22, 25, 27-8, 30-1, Table 3 (Baltic sea basin: Neman river basin, Belorussian SSR and Vistula river basin - Jeziorka and Skawa rivers and Rudawa Brook, Poland; Black sea basin: Belorussian watercourses and Kuban' river basin, RSFSR); Holčík, 1970b. Bio. (Čas. Slov. Akad. Vied) 25(2): 123, 126, 128 (Vistula river basin, Poland); Holčík, 1970c. Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.) 34(4): 304, 307 (upper Neman and lower Danube river basins); Bănărescu et al., 1971.

European inland water fish. A multilingual catalogue.: fig. 5 (Europe); Hardisty and Potter, 1971b. The biology of lampreys. 1: 135, 168, Table 2; Holčík and Nalbant, 1974. Věst. Čs. Spol. Zool. 38(2): 95-6 (Danube basin: Siret river basin - Moldova River, eastern Rumania); Vladykov and Kott, 1976b. Wilfrid Laurier Univ. Mus. Zool. Contrib. 1: 6 (Baltic and Black sea basins); Vladykov and Kott, 1976c. Rev. Trav. Inst. Pêches Marit. 40(3-4): 788; Potter, 1980. Can. J. Fish. Aquat. Sci. 37: 1604.

Lampetra (_Eudontomyzon_) _danfordi_ _vladykóvi_ (in part); Oliva, 1962. Nár. Muz. 1: 3 (Czechoslovakia)

Lampetra (_Eudontomyzon_) _vladykovi_; Holčík, 1963. Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.) 27(1): 56-7, 59-61, figs. 2-8 (Danube basin: Danube and Drava rivers, Austria; Danube River, Hraničný Kriváň and Mutnianka brooks, Czechoslovakia (Slovakia); Oltenia and Muntenia, Rumania; Drava and Sava river basins, Yugoslavia); Balon and Holčík, 1964. Frag. Faun. 11(13): 189, 191-3, 202, 204, 206 (Danube basin: Austria; Czechoslovakia; Yugoslavia; Danube River and Olt, Jiu and Argeş river basins, Rumania; Orava valley reservoir basin - Czarna Orawa River, Bukowiński Brook, Poland; Biela Orava River, Hraničný Kriváň, Jelešná and Mutnianka brooks, Czechoslovakia (Slovakia)); Holčík et al., 1965. Ac. Rer. Natur. Mus. Nat. Slov. 11: 105 (Orava valley reservoir basin: Czarna Orawa River, Bukowiński Brook, Poland; Biela Orava River, Hraničný Kriváň, Jelešná and Mutnianka brooks, Czechoslovakia (Slovakia)); Holčík, 1966a. Biol. Prá. (Slov. Akad. Vied) 12(1): 8, 25-7, figs. 1, 3, 6, 8, (Orava valley reservoir basin: Czarna Orawa River, Poland;

Biela Orava River, Jelešná and Mutnianka brooks, Czechoslovakia (Slovakia))

Eudontomyzon vladykovi; Balon, 1964a. Bio. (Čas. Slov. Akad. Vied) 19(5): 344, 347 (Danube basin, Slovakia); Balon, 1964b. Pol. Arch. Hydr. 12(2): 234, 241 (Danube basin: Czarna Orawa River, Poland); Holčík, 1970a. Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.) 34(1): 22, 25 (Danube basin, Slovakia); Holčík, 1970c. Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.) 34(4): 304, 307 (upper and middle Danube basin); Bănărescu et al., 1971. European inland water fish. A multilingual catalogue.: fig. 6 (Europe: Danube basin); Vladykov and Kott, 1976b. Wilfrid Laurier Univ. Mus. Zool. Contrib. 1: 6 (Baltic and Black sea basins)

Lampetra (Eudontomyzon) danfordi (not Regan) (in part); Balon and Holčík, 1964. Frag. Faun. 11(13): 192 (Siret river basin, Rumania)

Eudontomyzon vladykovi (in part); Bănărescu, 1969. Fau. Rep. Soc. Rom. 12(1): 9, 19, 22, 25-7, 35-6, 42, 44-5, 49-50, 53-4 (Black sea basin - Danube basin: Austria; Czechoslovakia; Cibin River, Rumania; Drava and Sava river basins, Yugoslavia); Vladykov and Kott, 1976c. Rev. Trav. Inst. Pêches Marit. 40(3-4): 788; Potter, 1980. Can. J. Fish. Aquat. Sci. 37: 1604, 1608 (Danube basin)

Eudontomyzon vladykovi vladykovi; Karaman, 1974. Fol. Balc. 3(5): 2, 4, 12, fig. 1 (Danube basin)

Eudontomyzon vladykovi stankokaramani Karaman, 1974. Fol. Balc. 3(5): 2-4, 6, 12, fig. 2 (Beli Drim river basin: Bistrica Brook, Istočka River, Rastavički Brook, Yugoslavia)

Type-locality: Khar'kov River, near Khar'kov, Donets river basin, Ukrainian SSR, USSR

Mode of life: Nonparasitic (Zanandrea, 1959a; Oliva, 1960; Holčík, 1963; Balon, 1964a; Kux, 1965; Bănărescu, 1969; Zhukov, 1969; Holčík, 1970c; Hardisty and Potter, 1971b; Vladykov and Kott, 1976b; 1976c) Members of the *E. mariae* complex may be facultative ectoparasites. This would explain both Wajgel's (1884) report of *Petromyzon planeri* (= *E. mariae* complex) sucking blood of fishes in the Prut River, Ukrainian SSR, and Balon and Holčík's (1964) observation of a lamprey wound on the side of the body of a *Leuciscus cephalus* from Jelešná Brook, Slovakia, where a specimen of *Lampetra* (*Eudontomyzon*) *vladykovi* (= *E. mariae* complex) was collected (Holčík et al., 1965). I consider the above, to be very isolated and rare cases that indicate the rather recent departure from a parasitic mode of life of the derivative of *E. danfordi*, and that for all intents and purposes, *E. mariae* complex may be considered a nonparasitic species. Indeed, Abakumov (1966) found that *E. mariae* complex adults, from Kuban' river basin, RSFSR, never develop a completely patent foregut, a condition which precludes efficient parasitic feeding, to say the least.

Habitat: This lamprey was found in submountainous and mountainous areas of Slovakia (Holčík et al., 1965), at altitudes ranging from 600 to ≈750 m (Holčík, 1966a). In the Orava valley reservoir basin of Poland and Czechoslovakia, *E. mariae* complex is found in brooks which at least partially flow through peat bogs (Holčík, 1963; Balon and Holčík, 1964), indicating a tolerance to low pH. In Walachia, Rumania, it is reported from clear, fast-flowing mountain watercourses, with gravelly and stony beds (Grossu et al., 1962; Bănărescu, 1969).

Spawning period: According to Balon (1964b) and Holčík (1966a), members of the Eudontomyzon mariae complex are lithophylic spawners. According to Abakumov (1966), spawning occurs at water temperatures of 11 to 12°C. The males construct circular nests five to ten cm of diameter, in areas with current (Holčík et al., 1965). According to Zhukov (1969), spawning takes place from 13 April to 11 May in the Berezyna River and from 28 April to 14 May in the Peretut' River, both of the upper Neman river basin in Belorussian SSR. Spawning occured between 24 April and 5 May in the Khar'kov River, Donets river basin, Ukrainian SSR (Berg, 1931). Spawning took place on the 28th of April in the Hraničný Kriváň Brook, Orava valley reservoir basin, Slovakia, at a water temperature of 15.9°C (Holčík, 1963; Holčík et al., 1965). This brook is shallow (20 cm), its bottom is gravelly and there are no aquatic plants (Holčík, 1963). Bănărescu (1969) believes that in the Argeş River, Danube basin, Rumania, reproduction occurs in July, since the dorsal fins grow taller and are drawn closer together between the end of June and the beginning of July. Spawning took place on the 4th of March, at Makhindjauri, near Batumi, Georgian SSR (Berg, 1948).

Geographic distribution: *E. mariae* complex is the most widespread species of the genus. It is found in the Adriatic, Aegean, Baltic and Black sea basins. Although *E. mariae* complex is almost exclusively distributed in Europe, it is also found in a couple of Asian localities belonging to the Black sea basin. Indeed, it was reported from west Transcaucasia, namely in the vicinity of Novorossiysk, RSFSR (Berg, 1931) and near Batumi, Georgian SSR (Berg, 1931; Kokotshashwili, 1942). In the Danube basin, it is excluded from the Tisa basin. *E. mariae* complex is found in the following countries: Austria, Yugoslavia, Czechoslovakia (Slovakia), Poland, Rumania (Walachia, Moldavia), USSR (Belorussian SSR, Ukrainian SSR, RSFSR, Georgian SSR). For more precise information on watercourses inhabited, consult the synonymy and the Material section.

I studied six of the syntypes of E. mariae (ASL 23124) designated by Berg (1931). They are adults, five males and one female, collected between 24 April and 5 May 1930 and measuring 171 to 183.5 mm in total length, with 64 to 73 trunk myomeres and weights 6.78 to 12.69 g. In the males, the urogenital papilla measures 5.5 to 8.5 mm in length and in the female it does not protrude out of the cloaca. Also, secondary sexual characters are well developed in all specimens, indicating sexually mature individuals. Precloacal intestine widths were not determined. The range of other morphometrics, in mm, are as follows: d-B_1 - 17.5 to 21.5; B_1-B_7 - 18.5 to 22.0; B_7-a - 83.5 to 92.5; a - 1.5 to 4.0; a-C - 42.5 to 49.5; d - 7.0 to 10.0; d-n - 8.0 to 11.0; d-O - 10.5 to 13.5; O - 3.0 to 3.5; O-B_1 - 5.5 to 6.0; B_1-B_2 - 2.0 to 3.0; I - 4.5 to 6.5. The supraoral lamina always bears two cusps. However, in one specimen, an additional small cusp is found near the base of the large right cusp, not along the bridge, as is reported in a number of specimens (Berg, 1931). The infraoral lamina bears from six to ten teeth, all cusps, except in one case, where a bicuspid tooth is found on the extreme right of the lamina. The number, type and arrangement of endolaterals is extremely variable. Out of 12 counts, three endolaterals occur 75% of the time and four, 25% of the time. The endolateral formula on the left side, could not be ascertained in one of the individuals. What follows are the endolateral formulae with their respective frequency in parentheses: 1-1-2-2 (3); 1-2-1 (2); 1-2-2 (2); 2-2-1 (2); 2-2-2 (1); 1-2-2-2 (1). Four anterial rows were found in five cases and three rows was found in a single specimen. Posterials, in one or two rows occur with equal frequency. The first anterial row consists of five to nine cusps. The first posterial row was found to be either continuous (inthree cases) or discontinuous (in three cases). When it was continuous, there were 13 to 19 cusps. When it was discontinuous, there were only four to six teeth. Exolaterals occured in one (16.7% of the counts) or two rows (83.3% of the counts). In the three specimens examined for this character, the transverse lingual lamina bore an enlarged median cusp which was wider but no higher than the other cusps in two of the cases. A single specimen had its tongue dentition studied in detail, as it required excision. The median enlarged cusp on the transverse lingual lamina, significantly higher than the other cusps, was flanked by one cusp on the left and two on the right. The longitudinal lingual laminae have respectively 11 (left) and 10 (right) cusps. The caudal fin is of spade-like shape in all cases and is either moderately (i.e.: ++) or strongly (i.e.: +++) pigmented.

In adults, the total length ranges from 123 to 195 mm (Table 1). In 37 adults, measuring 131 to 195 mm in total length, wet weight varied between 3.61 and 12.69 g. Berg (1931) found the total length ranged from 120 to 206 mm in 60 adults. The 13 adults studied by Oliva and Hensel (1962) ranged in total length from 130 to 182 mm. The 72 adults, studied by Abakumov (1966), measured 130 to 200 mm in total length. In 247 adults, Zhukov (1969) recorded total lengths of 135 to 222 mm, with wet weights, in 243 of these, ranging from 3.8 to 18.0 g. The overall range in total length for *E. mariae* complex adults is thus 120 to 222 mm. The most frequent trunk myomere count in adults (Table 5) was 65 (17.9%). A urogenital papilla was evident in 24 adults out of 39 examined for this character, measuring between 0.5 and 8.5 mm in length. In 16 adults, intestine width ranged from < 0.5 (i.e.: thread-like) to 1.0 mm. Berg (1931) reported that counts of four endolaterals were more prevalent than three in *E. mariae*. However, as stated before, out of six syntypes studied, only 25% of the counts were four instead of three. Furthermore, out of eight discs of *E. mariae* figured in Oliva and Hensel (1962), there were only four counts (i.e.: 25% of counts) with four endolaterals. The rest of the specimens had three endolaterals. The fact that Oliva and Hensel (1962) and this study show the same low ratio for four against three endolaterals, albeit from small sample sizes, and that my counts were made on a subsample of the type-series, I consider three endolaterals to be the more typical state. A total of 54 endolateral formulae counts were recorded for *E. mariae* complex. The majority of counts were made up of three endolaterals (83.4%), with four endolaterals (11.2%), one endolateral (3.7%) and two endolaterals (1.9%) making up the rest. The typical formulae are 1-2-2 (25.9%), 1-2-1 (22.2%), 2-2-1 (13.0%) and

2-2-2 (11.1%). Other variant formulae are: 1-1-1, 2-2-3, 1-1-2-2 (each 5.6%), 2, 1-1-2-1 (each 3.7%), 1-2, 1-2-2-2 (each 1.9%). Oliva and Hensel (1962) reported two additional endolateral formulae, namely, 1-2-1-2 and 1-2-2-1. Holčík (1963) recorded 46 endolateral formulae counts as follows: 1-2-1 (71.7%), 1-1-1 (19.6%), 1-2 (4.3%), 1-2-2, 1-3-1 (each 2.2%). E. mariae complex is the only species of the genus, where more than two teeth may be found on the supraoral lamina (Table 3). Out of 35 adults studied for this character, two specimens (5.7%) had three and one specimen (2.9%) had four teeth on their supraoral lamina. The majority of specimens (91.4%) had only two supraoral teeth. Berg (1931) described the teeth as villiform in E. mariae. On Plate 4, fig. 1, in Berg (1931), five anterial rows can be discerned on the disc of one of the syntypes. This is one count higher than that found in this study (Table 3). The posterial field was examined in 31 specimens (Table 3). Twenty eight of those (90.3%) had posterial rows and three specimens (9.7%) were without them, although they did possess a few sparsely distributed posterials. Of the ones with posterial rows, 16 had the number of teeth in the first row determined. Ten of them had a continuous first posterial row and the remainder, a discontinuous one. The continuous first posterial row possessed 12 to 20 teeth, with mean 16.2 and standard deviation 2.6. The discontinuous one possessed 1 to 12 teeth, with mean 5.0 and standard deviation 3.9. The overall mean and standard deviation for the number of teeth in the first posterial row is given in Table 3. Figure 22, in Bănărescu (1969), depicts the disc of a E. mariae specimen from the Argeş river basin, Rumania, without any posterials. All 14 adults, whose transverse lingual lamina dentition was studied, possessed an enlarged median cusp, which in three specimens (21.4%) was wider, but not noticeably higher than other cusps on the lamina. Three specimens, including a syntype were examined in greater detail, and their median enlarged cusp was found to be flanked, on the left, by one to four and on the right, two or three cusps. The range for total number of cusps, from two specimens was determined as four to seven. Kokotshashwili (1942) reported the aberrant case of an E. mariae adult with a depression in place of a median enlarged cusp, on its transverse lingual lamina. This depression was flanked on each side by three cusps. The longitudinal lingual laminae were studied in another specimen, aside from one of the syntypes mentionned above, and a count of five cusps was determined on both laminae. Thus, the number of cusps on these laminae ranges from 5 to 11, with mean 7.8 and standard deviation 3.2. Only one out of 29 adult specimens in which the caudal fin shape was studied had a rounded caudal fin, the others had spade-like shapes. The range in the number of velar tentacles of ten adult E. mariae was determined by Vladykov et al. (1982, MS) to be 8-12, with mean 9.8 and standard deviation 1.2. The range in the number of velar tentacles of eight adult nominal E. vladykovi (discounting the two misidentified E. danfordi, see Results and Discussion, p.50)wasdetermined by Vladykov et al. (1982, MS) to be 7-10, with mean 8.5 and standard deviation 1.1. There is a 72.2% overlap between the above counts of E. mariae and nominal E. vladykovi. The overall range in the number of velar tentacles of 18 adult E. mariae complex is therefore 7-12, with mean 9.2 and standard deviation 1.3. The velar apparatus of E. mariae complex is wingless (Vladykov and Kott, 1976c; Vladykov et al., 1982 MS). Zhukov (1969) found a range of 1950 to 3270 and mean 2380 eggs / female. Of 20 females examined, Bely (1966) obtained a mean fecundity of 5122 eggs / specimen. In 24 females examined, Abakumov (1966) found 2274 to 7106 eggs / specimen, with mean 4899. The d ur ation of the adult life is approximately eight months (Holčík et al., 1965). The total length, in the ammocoetes at my disposal, ranged from 34 to 212 mm (Table 9), with corresponding wet weights from 0.07 to 15.17 g. According to Grossu et al. (1962) and Bănărescu (1969), ammocoetes of <u>E. mariae</u> complex may reach 230 mm in total length. That they may considerably exceed this figure is indicated by the report of a <u>E. mariae</u> complex metamorphosing ammocoete, 250 mm in total length (Grossu et al., 1962). The most frequent trunk myomere counts in ammocoetes (Table 10) were 62 (20.8%), 63 (16.1%) and 64 (16.7%). The tongue precursor pigmentation was determined in nine ammocoetes. The pigment coverage of the bulb was usually absent to trace (i.e.: -) (88.9%), with one case in which it was moderate (i.e.: ++) (11.1%). The pigment coverage along the elastic ridge exhibited extreme variation: absent to trace (i.e.: -) in 44.4%, slight (i.e.: +) in 11.1%, moderate (i.e.: ++) and strong (i.e.: +++) in 22.2% each. Of the 166 ammocoetes looked at for caudal fin shape, only two exhibited a rounded condition; the rest had spade-like caudal fins. Six metamorphosing ammocoetes measured 150 to 179 mm in total length and 6.51 to 9.57 g in wet weight. Zanandrea (1959a) studied three metamorphosing specimens, measuring 167 to 194 mm in total length. Metamorphosis takes place between the end of August and the beginning of September in the Orava valley reservoir basin (Holčík et al., 1965). According to the material at my disposal, members of the <u>E. mariae</u> complex undergo metamorphosis between the 24th of July and the 9th of September.

The dentitional counts reported by Zanandrea (1959a) for the nominal _E. danfordi vladykovi_ are biased by the inclusion of misidentified adults. It should be noted that Zanandrea (1959a) provisionally considered the nonparasitic nominal _E. danfordi vladykovi_, as a subspecies of _E. danfordi_, because, he did not want to elevate it to the specific level, until he knew more about the extent of dentitional variation in _E. mariae_ throughout its range. Zanandrea (1959a) observed that the ranges in counts of various dentitional characters (anterial and exolateral rows, first posterial row, supraoral lamina, transverse and longitudinal lingual laminae) in _E. danfordi_, were contained inside the ones of its nominal subspecies. Some of the ranges (anterial and exolateral rows and first posterial row) in the latter taxon were extended on the lower side compared to the former taxon. The observation that nominal _E. danfordi vladykovi_ had counts as high as those in _E. danfordi_, I feel, was due to the inclusion of nine immature adults of _E. danfordi_, from the Topl'a River, Tisa basin, Slovakia, within the counts of the nominal taxon. I studied four adult specimens from the Topl'a River, three of which were part of the material examined and identified by Zanandrea (1959a) as _E. danfordi vladykovi_. I also studied five adult specimens outside the Tisa basin (Austria: two from Mur and one from Drava rivers; Yugoslavia: two from Sava River), all studied and identified in Zanandrea (1959a) as the nominal subspecies. The dentitional character counts mentionned above, except supraoral laminae, in the four specimens from the Tisa basin are higher on the average than those of the five specimens outside the Tisa basin. Although there is some overlap in the various dentitional character counts, some of them can be used to segregate the taxa. One of the specimens from the Tisa basin has 14 (6-I-7) cusps on its transverse lingual lamina, compared to 7 (3-I-3) in one of the specimens outside the Tisa basin. Another one of the Tisa specimens has five anterial rows, compared to three or four in the specimens outside the Tisa basin. Another piece of evidence, in support of a misidentification, is taken from morphometrics. Zanandrea (1959a), in his Table 5, gives the mean $\frac{d}{B_1 - B_7}$ % for the nine specimens (6♂:3♀) from Topl'a River, as 57.7, which falls within the E. danfordi range (Table 1), but is much higher (7.7%), than the upper limit for E. mariae complex (Table 1), within which are included the five specimens, mentionned above, from outside the Tisa basin. Furthermore, in the same table, Zanandrea (1959a) gives the mean $\frac{O - B_1}{TL}$ % for the three females from Topl'a River, as 2.2, which is lower (0.2%), than the lower limit found in E. mariae complex (Table 1), but within the range for E. danfordi (Table 1). Zanandrea (1959a) also noted that two immature adults from the Topl'a River, identified by him as nominal E. danfordi vladykovi, had poorly developed gonads, as one would expect in immature E. danfordi. Zanandrea (1959a) presumably mistook the nine recently metamorphosed E. danfordi for nonparasitic lampreys, because they all had small intestinal diameters (1.0 - 2.0 mm; $\overline{X}$ = 1.3 mm). However, small intestinal diameters are expected in parasitic lampreys at the beginning of their adult trophic phase. These last two points are supported by Holčík (1963) who studied six recently transformed adults from Topl'a River, and found them to be conspecific with parasitic E. danfordi. He added that E. danfordi collected in autumn, just after metamorphosis, have thin intestines and apparently ressemble nominal E. vladykovi, which seems to be the reason for Zanandrea's (1959a) misidentification (Holčík, 1963). In view of the above evidence, I submit that the lampreys from the Topl'a River (Tisa river basin) are referable to the parasitic species, E. danfordi.

Two of four adult specimens, bearing tags Y465-6 (Material, p.16), from the Mur River, tributary of the Drava River in Austria and identified in Zanandrea (1959a) as the nominal E. danfordi vladykovi are re-identified here as Lampetra sensu stricto. The caudal fin was rounded and bore no pigment in both cases. Only in one specimen could the dentition be studied. The supraoral lamina had two cusps. The endolateral formula was 2-2-2 on both sides of the disc. The infraoral lamina bore five teeth, the two lateralmost bicuspid. There were neither exolaterals, nor posterials and only two anterial rows.

Zanandrea (1959a) says E. danfordi is endemic to the Tisa river basin and yet, he includes in his Table 1, listing the material of E. danfordi he studied, an ammocoete, 190 mm in total length, from Suceava Brook, which is in the Siret river basin, Rumania, outside the Tisa basin. This seems to have been an oversight on his part, because E. mariae, not E. danfordi, was recently shown to inhabit the Siret basin. Indeed, Holčík and Nalbant (1974) found an E. mariae adult, 138 mm in total length, from the Moldova River. This specimen had been previously identified by Bănărescu (1969) as Lampetra planeri. Grossu et al. (1962) also reported E. danfordi from the Siret basin, namely, the Moldavian Bistriţa River. They supported their claim with the fact that the common name for lampreys in Moldavia, as in Transylvania, is "Chişcar" or "Cicar", meaning "one who is always hungry", which they felt alluded to E. danfordi's parasitic feeding. However, the presence in Moldavia of the nonparasitic species E. mariae, as stated above, implies that ethnozoological data alone is not sufficient to make an accurate identification. The reason why the same common name is used in Moldavia for a nonparasitic species and in Transylvania for a parasitic species may be because of the proximity of the two regions, the former lying to the East of the Carpathian mountains, and the latter, to the West.

I believe Eudontomyzon danfordi vladykovi (in part) Oliva and Zanandrea, 1959, redescribed by Holčík (1963) as Lampetra (Eudontomyzon) vladykovi, to be junior synonyms of E. mariae (Berg, 1931), for the following reasons. Berg (1931) gave as a distinct characteristic of E. mariae, the fact that its first posterial row was discontinuous, a condition, he added, not found in E. danfordi, where the first posterial row is always continuous. However, a number of E. mariae specimens with a continuous first posterial row have been found. Berg (1931), in the article of description of E. mariae, reproduced the figure (Plate 17, fig. 3) from Wajgel (1884), depicting the disc of a lamprey from Prut River, Ukrainian SSR. Berg (1931) identified this specimen as E. mariae, against his own diagnostic character since, a continuous first posterial row made up of 14 cusps is clearly discernible on the figure. Bănărescu (1969), in studying 28 of the 36 E. mariae syntypes, found one specimen with a continuous posterial row and I have found three specimens with this characteristic, out of only six syntypes examined. Bănărescu (1969) added that the number of specimens with a continuous posterial row was greater in samples of E. mariae from the Argeş river basin, Rumania, than in the type-series. I studied five specimens from the Argeş River, and of the two specimens in which the first posterial row could be studied, both had a continuous row made up of 17 cusps. As the number of specimens possessing a continuous posterial row increased as one moved closer to the area where nominal E. vladykovi exists, Bănărescu (1969) suggested that E. vladykovi may be a subspecies of E. mariae. Indeed, E. vladykovi Oliva and Zanandrea, 1959, was described as different from E. mariae, by the possession of a continuous first posterial row. However, Oliva and Zanandrea (1959) admitted to having few specimens of E. mariae as comparative material. Holčík (1963), in redescribing nominal E. vladykovi, found two specimens that did not possess a continuous posterial row, out of 13 discs figured (neotype plus sample from new topotypic locality). Furthermore, Balon and Holčík (1964) suggested E. vladykovi may be a subspecies of E. mariae, on the basis of an adult specimen of nominal E. vladykovi from Bukowiński Brook, Danube basin, Poland, which did not possess a continuous posterial row. Both E. mariae and nominal E. vladykovi are said to be nonparasitic, although, as discussed above, an isolated case of parasitism is suspected in each case. In his description of E. mariae, Berg (1931) also reported the occasional presence of one or more additional cusps on the bridge of the supraoral lamina. Indeed, Berg (1931) produced three figures of the disc (Plate 4, figs. 1, 3-4), showing an additional supraoral cusp on one of the syntypes, and one and three additional respectively on two specimens from the Kazanka River, Don river basin. Likewise, the holotype of nominal E. danfordi vladykovi and a specimen of the same nominal taxon from Drava River, Austria, both have an additional supraoral cusp (Oliva and Zanandrea, 1959). Holčík (1963) also found an additional supraoral cusp in nominal E. vladykovi, as follows: In Czechoslovakia, two specimens from Hraničný Kriváň Brook (new topotypic locality) and one from Mutnianka Brook; in Austria, one specimen from Danube River. Berg (1931) reported a fecundity of 2429 eggs for a nearly ripe E. mariae specimen from the Dnepr River, its eggs measuring from 0.76 to 0.90 mm in length. Holčík et al. (1965), studying six females of the nominal E. vladykovi from Hraničný Kriváň Brook, found the number of eggs ranged from 2247 to 3485, with an average length of 0.92 mm. The number of eggs in the E. mariae female falls in the fecundity range for the nominal E. vladykovi and their egg lengths match considering the E. mariae was not completely ripe and the nominal E. vladykovi were spawning. This last statement is confirmed by Berg (1931) who points out that the eggs in E. mariae when ripe, reach more than a mm in length. The spawning periods are also strikingly similar in E. mariae and nominal E. vladykovi, at similar latitudes. In the former case, Berg (1931) reported that spawning of the type-series occured between 24 April and 5 May at 50°N, whereas Holčík (1963) and Holčík et al. (1965) reported that spawning occured on the 28 April at 49°27'N in the nominal E. vladykovi sample from which the neotype was selected.

A lot of ink has flowed, concerning the identity of lampreys from the upper Prut River, Danube basin, near Kolomyya, Ukrainian SSR and considered by Wajgel (1884) as Petromyzon planeri. Creaser and Hubbs (1922) stated that they were E. danfordi, based on the report by Wajgel (1884) that the lampreys sucked the blood of fishes. Berg (1931), on the basis of Wajgel's (1884) figure (Plate 17, fig. 3) of one of the specimens' disc, believed them to be E. mariae. Bănărescu (1969) accepted the judgment of Berg (1931). Oliva (1953a) could not decide whether they were E. danfordi or E. mariae. Finally, in the face of conflicting evidence, Grossu et al. (1962) submitted that both species were present in the Prut River. A study of the disc figure (Plate 17, fig. 3) revealed the reason for the confusion over the years. Some dentitional characters purported to E. danfordi, others to E. mariae, still others were common to both species. The transverse lingual lamina bears one enlarged median cusp flanked on the left by four and on the right five cusps. A total of ten cusps on the transverse lingual lamina is more reminiscent of the condition in E. danfordi (9-15 cusps), than that in E. mariae complex (4-9 cusps), although, it is only one cusp above the upper limit reported in this latter species. Berg (1931) emphatically stated that E. mariae, to which he assigned the specimens from the Prut River, does not possess a continuous first posterial row and yet, a continuous first posterial row made up of 14 cusps is clearly discernible on the figure. This second character would apply to E. mariae complex rather than E. danfordi, although its numeric value is but one cusp removed from the lower limit found in E. danfordi (Table 3). There are two exolateral rows on the right side and apparently none on the left side. There are however, a few exolateral cusps on the left exolateral field, but these do not form a continuous row. This third character would be closer to the condition of reduced teeth numbers found in E. mariae complex (Table 3). There is only one posterial row, which could only be attributed to E. mariae complex (Table 3). There are two supraoral and seven infraoral cusps and four anterial rows, the first being made up of seven cusps. These four characters apply equally well to both species (Table 3). The endolateral formula, on both sides of the disc, is 2-2-1-1. This last dentitional character is hard to judge, because it has not been recorded in either of the two species. Wajgel (1884) said that the 17 adults he collected in the Prut River ranged between 143 and 190 mm in total length and that ammocoetes attained 197 mm in total length. These characters could apply to either species (Tables 1 and 9). The presence of lampreys belonging to the Eudontomyzon genus in the Prut River, fits the wide-ranging geographic distribution of E. mariae complex much better than that of E. danfordi, which as far as is known is endemic to the Tisa basin. Oliva and Hensel (1962) found a specimen from the Lipa Zlota Brook, a tributary of the Prut River, which although in poor condition and without being specific, they maintain, possesses all the characters of

E. mariae. On the basis of what has been said above, concerning dentition and geographic distribution, I too consider the lampreys from the Prut River as members of the *E. mariae* complex.

Karaman (1974) described a nominal subspecies, Eudontomyzon vladykovi stankokaramani, from the Drin river basin, Adriatic sea basin, Yugoslavia. Based upon his description of the dentition, and the present study of eight adults, referable to the E. mariae complex, from Lake Ohrid, in the same river basin, I feel that Karaman's (1974) lamprey, belongs to the E. mariae complex. Karaman (1974) studied 12 adult specimens, ranging in total length from 125 to 181 mm, compared to 153.5 to 195 mm for the ones from Lake Ohrid. This shift in range is most probably due to the difference in maturity between the two samples. Karaman's (1974) specimens were mature adults, whereas the ones from this study are immature. An exolateral row on both sides of the disc and three posterial rows, confirming the identification as E. mariae complex (Table 3), can be clearly seen on Figure 2 (Karaman, 1974), depicting the dentition of the nominal E. vladykovi stankokaramani. The first anterial row, on this same figure, is made up of 11 cusps, which is one count over the upper limit of variation in this character, for E. mariae complex (Table 3). Unfortunately, the extent of variation in this character, in the nominal form, is not known because no mention of it was made in the text. All other dentitional characters extracted from Figure 2 and mentionned in the text fall within the ranges found in E. mariae complex (Table 3). Still based on Figure 2, the first posterial row is continuous and has 15 cusps, but again Karaman (1974) did not discuss this character in his article. In the two specimens from Lake Ohrid in which the first posterial row could be studied, it was continuous and had 15 cusps in one case and was discontinuous with 12 cusps in the other. One out of twelve adults, the holotype, has a larger d-B_1/TL% (12.7) than the maximum one recorded for E. mariae complex (Table 1). Other morphometrics recorded by Karaman (1974) fall within the ranges found in this study for E. mariae complex (Table 1) except for a single specimen with 38.3 as B_7-a/TL%, which is significantly lower (6.6%) than the ones recorded here. The morphometrics of 65 ammocoetes measuring 46 to 203 mm in total length and studied by Karaman (1974) fall within the ranges found in this study (Table 9), except again the B_7-a/TL% is significantly smaller than the ones here. Karaman's (1974) results for B_7-a/TL% are: range = 46.3 - 54.3, $\bar{X}$ = 50.8, s = 1.8. Nine transforming ammocoetes of the nominal E. vladykovi stankokaramani were reported by Karaman (1974) to have been collected between February and April. This is very interesting as all the metamorphosing ammocoetes in this study, belonging to three species, undergo metamorphosis between 24 July and 13 November. Trunk myomeres range between 58 and 62 in the ammocoetes and adults of the nominal subspecies (Karaman, 1974), which falls into the lower range of 58 to 73 found in ammocoetes and adults of the E. mariae complex (Tables 5 and 10). I suggest that the lampreys discussed above are nonparasitic as the longest ammocoetes substantially exceed the longest adults. As stated above, the longest adult measures 195 mm in total length and ammocoetes 195 to 218 mm in total length occur in Lake Ohrid and have been found in the following tributaries of the Beli Drim River: Bistrica Brook (Hankó, 1922), Istočka River and Rastavički Brook (Karaman, 1974). Berg (1931) suggested, as I do, that the ammocoetes reported by Hankó (1922) belong to E. mariae.

Karaman (1928) mentionned two recently metamorphosed adults, 190 mm in total length, from the Vardar River, Aegean sea basin, Yugoslavian Macedonia. He identified them as Lampetra fluviatilis (Linnaeus), but Berg (1931) believes they are either L. planeri (Bloch), or rather

Eudontomyzon mariae. Myagreement with Berg's latter interpretation is based upon the study of an adult male, from the same locality, measuring 152.5 mm in total length and possessing a single posterial row, a condition incompatible with either *Lampetra fluviatilis* or *L. planeri*. The four cusps on the left of the transverse lingual lamina's median enlarged cusp, exclude *E. hellenicum*, the only other possibility.

<u>Eudontomyzon</u> <u>morii</u> (Berg, 1931)
(figs. 9c,11b-d, 13b, 15a-b)

Etymology of specific epithet: Named after Prof. Tamezo Mori, a famous Japanese ichthyologist

Common names: There is a Manchurian common name (Chung, 1961), but no translator could be found to transliterate the Chinese characters. The following common names were taken from Mori (1952) and Chung (1961): Chil-seong-baem, Chil-seong-ga-mool-chi, Chil-seong-go-gi, Chi-seong-jang-eo (Korean: upper Yalu River); Chil-seong-mal-bae-ggob (Korean: Ja-Sung River, Pyung-An-Book-Do Province); Arinare-sunayatsume, Arinare-yatsume, Kokawa-yatsume (Japanese).

Manchurian lamprey (Berg, 1931; Zhukov, 1969; Vladykov and Kott, 1976b; Potter, 1980)

Korean lamprey (Vladykov and Kott, 1976b; Potter, 1980)

Synonymy: <u>Lampetra</u> (<u>Eudontomyzon</u>) <u>morii</u> Berg, 1931. Ann. Mus. Zool. Acad. Sci. URSS. 32(1): 87, 92, 97, 116, Plate 5, fig. 1 (upper Yalu River, Manchuria; four syntypes in Zoological Institute of the Academy of Sciences of the USSR, Leningrad (cat. #23145); Mori, 1952. Mem. Hyogo Univ. Agri. 1(3) Bio. Ser. 1: 14 (upper Yalu River, North Korea); Ma and Yu, 1959. Chin. J. Zool. 3(3): 115 (Huan River, People's Republic of China); Oliva and Hensel, 1962. Acta Univ. Carol. - Biol. 1: 101-3 (upper Yalu River, Manchuria); Zhukov, 1969. Prob. Ich. 9(2): 181 (Yalu River)

Eudontomyzon morii; Zanandrea, 1959a. Arch. Zool. Ital. 44: 217 (East Asia); Matsubara, 1963. [Fish morphology and hierarchy. Part 1: 95 (upper Yalu River); Bănărescu, 1969. Fau. Rep. Soc. Rom. 12(1): 25, 35 (Yalu River, People's Republic of China); Hardisty and Potter, 1971b. The biology of lampreys. 1: 128; Vladykov and Kott, 1976b. Wilfrid Laurier Univ. Mus. Zool. Contrib. 1: 6 (Yellow sea basin: upper Yalu River); Potter, 1980. Can. J. Fish. Aquat. Sci. 37: 1604 (Yellow sea basin)

Type-locality: upper Yalu River, Ko-sui-in, Manchuria, People's Republic of China

Mode of life: Ectoparasitic (Ma and Yu, 1959; Vladykov and Kott, 1976b; Potter, 1980)

Hosts: Ma and Yu (1959) listed E. morii hosts belonging to two fish families: Cyprinidae (76%) and Cobitidae (24%). The cyprinid hosts are Sarcocheilichthys nigripinnis czerskii (Berg) (called Chilogobio nigripinnis soldatovi Berg by Ma and Yu) 41.7%, Phoxinus percnurus mantschuricus Berg 20%, Pseudogobio esocinus (Temminck and Schlegel) 10.3% and Carassius auratus (Linnaeus) 4%, while the cobitid hosts were Noemacheilus barbatulus toni (Dybowski) (called Barbatula toni (Dybowski) by Ma and Yu) 20% and Cobitis taenia Linnaeus 4%.

Geographic distribution: E. morii is endemic to the upper Yalu river basin, which drains into the Yellow Sea. In Manchuria, People's Republic of China, it is found in the

Yalu and Huan rivers. In North Korea, it is reported from the Yalu and Ja-Sung rivers.

No statistical tests were used to compare E. morii with the other members of the genus because too few specimens of E. morii (N=4) were available for study. I studied one of the syntypes of E. morii (ASL 23145) designated by Berg (1931). It is an adult, of undetermined sex, collected in July 1926 and measuring 171 mm in total length, with 68 trunk myomeres and weight 3.37 g. The weight is an underestimate, the specimen being extremely dehydrated. Its urogenital papilla does not protrude out of the cloaca and secondary sexual characters are absent, indicating a sexually immature specimen. The precloacal intestine width could not be determined. Other morphometrics, im mm, are as follows: d-B_1 - 20.0; B_1-B_7 - 17.5; B_7-a - 80.5; a - 2.0; a-C - 51.5; d - 10.5; d-n - 11.5; d-O - 13.0; O - 2.0; O-B_1 - 5.0; B_1-B_2 - 2.0; I - 4.5. The supraoral lamina bears two and the infraoral ten cusps. The endolateral formula is 1-1-1 on both sides of the disc. There are three anterial rows and a single posterial one. The first anterial row consists of three cusps. The number and type of teeth could not be determined in the first and only posterial row. There is a single exolateral row on each side of the disc. The transverse lingual lamina possesses an enlarged median cusp, flanked on the left by nine and on the right by seven cusps. The longitudinal lingual laminae have respectively 14 (left) and 15 (right) cusps. The caudal fin has a spade-like shape and is moderately (i.e.: ++) pigmented.

Berg (1931) designated four syntypes, all adults from upper Yalu River, Ko-sui-in, Manchuria, measuring 153 to 165 mm in total length. I cannot explain the rather substantial difference in total length between the syntype I studied and the type-series.

The total length, in the adults at my disposal, ranged from 171 to 211.5 mm (Table 1). In three of those, measuring 172.5 to 211.5 mm in total length, wet weight varied between 6.30 and 10.32 g. Berg (1931) studied eight adults, measuring 153 to 212 mm in total length. Ma and Yu (1959) recorded adult total lengths ranging from 180 to 290 mm. The overall range in total length for E. morii adults is thus 153 to 290 mm. A urogenital papilla was not apparent in any of the material at my disposal. In the same three adults as above, intestine width ranged from 3.0 to 4.0 mm. The teeth on all fields are villiform. The two lateralmost teeth of the infraoral lamina are usually bicuspid (Berg, 1931; Ma and Yu, 1959). Eight endolateral formulae counts were recorded for E. morii. All counts were made up of three endolaterals, with 2-2-2 being the typical formula (75%) and 1-1-1 being the only other variant formula (25%). Ma and Yu (1959) stated that posterials are always in two rows, but my observations indicate a single row (Table 3) and are in agreement with Berg (1931). Figure 2 (Ma and Yu, 1959) shows only one row of posterials and one of marginals. Ma and Yu (1959) thus include the row of marginals with the posterials, which I do not (Methods, p.26), therefore, there is no conflict between our respective observations. Ma and Yu (1959) simply say that exolaterals are numerous, and according to their figure 2, they are present in at least one row on each side of the disc. My findings are that they occur equally frequently in one or two rows (Table 3). Aside from the syntype, whose tongue dentition was described above, another specimen of E. morii had its transverse lingual lamina studied. It also bore an enlarged median cusp, flanked by nine cusps on the left and eight on the right. Berg (1931) reported a transverse lingual lamina with an enlarged median cusp flanked by nine cusps on both sides. According to Ma and Yu (1959), the transverse lingual lamina has six to nine cusps on each side of its median enlarged cusp. The range for the number of cusps on the transverse lingual lamina is thus 13 to 19. As mentionned above, a longitudinal lingual lamina may have 14 or 15 cusps. All four adult specimens had spade-like caudal fins. Ma and Yu (1959) also reported a spade-like caudal fin for this species. Egg numbers vary between 14000 and 20000/female (Ma and Yu, 1959). Neither ammocoetes nor metamorphosing individuals were available. Both these developmental stages in E. morii have never been described.

Eudontomyzon hellenicum Vladykov et al., 1982 MS
(figs. 9d-e, 12, 15c-d, 16d-e, 17c-d, 18c, 19e)

Etymology of specific epithet: The specific epithet is the latinized derivation of the Greek word "Hellēn", which means Greek.

Common name: Greek brook lamprey (Vladykov et al., 1982 MS)

Synonymy: Eudontomyzon mariae (not Berg): Economidis, 1972. Hell. Oc. Limn. (Inst. Oc. Fish. Res.) 11: 560 (Struma river basin: Ayannis, Kefalárion and Milopótamos brooks, Macedonia, Greece); Economidis, 1974. [Morphological, systematic and zoogeographical study of the freshwater fishes of east Macedonia and west Thrace, Greece]: 8-9, 113-4, 116-7, 122, 125, 128, 130, fig. 1 (Struma river basin: Ayannis, Kefalárion and Milopótamos brooks, east Macedonia, Greece)

Type-locality: Kefalárión Brook, near Kefalárion, Struma river basin, Macedonia, Greece

Mode of life: Nonparasitic (Vladykov et al, 1982 MS)

Habitat: E. hellenicum lives in shallow (25-75 cm deep), clear, fairly fast-flowing brooks. The substrate of these is gravelly, with some rocks and aquatic plants. Economidis (1974) says that it also lives in mud, especially between the roots of aquatic plants. He does not specify whether this behavior is restricted to ammocoetes.

Spawning period: An interesting phenomenon, unique in the genus, exists in E. hellenicum. Although its spawning has never been witnessed, in all likelihood, there are two distinct spawning periods during the year, within a locality. In Kefalárion Brook, Struma river basin, Greek Macedónia, sexually mature specimens with well developed secondary sexual characters were collected in October 1972. Dr. P. S. Economidis (in litt., 15 March 1980) collected some E. hellenicum, in spawning condition, from the same locality, on 18 January 1980. On the other hand, specimens in spawning condition were collected from the same locality, on 17 and 19 May 1977. The above data would seem to indicate that there are two distinct populations in Kefalárion Brook, spawning at a roughly four month interval, one at the end of January, the other at the end of May.

Geographic distribution: E. hellenicum is endemic to Greece. It is found in two river basins, the Struma (Aegean sea basin) and Loúros (Ionian sea basin). In the Struma basin, this species is known from three brooks: Milopótamos, Ayannis, and Kefalárion (Economidis, 1974). In the Loúros basin, this lamprey occurs in the Loúros River per say and in one of its tributaries, Filippiás Brook.

I studied the holotype of E. hellenicum (NMC 77-1773) designated by Vladykov et al. (1982, MS). It is an adult male, collected on 17 May 1977 and measuring 95.5 mm in total length, with 58 trunk myomeres and weight 2.38 g. Its urogenital papilla measures one mm in length and secondary sexual characters are well developed, indicating a sexually mature specimen. The precloacal intestine width is thread-like (<0.5 mm). Other morphometrics, in mm, are as follows: d-B_1 - 12.5; B_1-B_7 - 11.5; B_7-a - 44.5; a - 1.0; a-C - 28.0; d - 7.0; d-n - 7.0; d-O - 8.5; O - 2.0; O-B_1 - 3.5; B_1-B_2 - 2.0; I - 4.5. The supraoral lamina bears two and the infraoral eight cusps. The endolateral formulae are 2-2-1 on the left and 2-2-2 on the right side of the disc. There are four anterial and three posterial rows. The first anterial row consists of six cusps and the first posterial row ten cusps. There are five exolateral rows on each side of the disc. Apart from the enlarged median cusp, no other teeth can be discerned on the transverse lingual lamina. The longitudinal lingual laminae are likewise so undeveloped, that no cusps are apparent on them. The caudal fin is rounded and strongly (i.e.: +++) pigmented.

In addition to the holotype and all paratypes (Vladykov et al., 1982 MS), two other specimens from the Louros River were studied. The total length, in the adults at my disposal, ranged from 95.5 to 158.5 mm (Table 1), with corresponding wet weights from 1.90 to 7.41 g. Economidis (1974) recorded total lengths of 99 to 141 mm in 12 adults. According to Economidis (1974), the number of trunk myomeres ranges from 55 to 63 in adults, which is comparatively similar to the findings of this study (Table 5). The most frequent trunk myomere counts in adults (Table 5) were 56 (20.0%) and 57 (26.2%). A urogenital papilla was evident in only 12 adults out of 66 examined for this character, measuring either 0.5 or 1.0 mm in length. In 56 adults, intestine width ranged from <0.5 (i.e.: thread-like) to 1.0 mm. A total of 102 endolateral formulae counts were recorded for E. hellenicum. The majority of counts were made up of three endolaterals (92.2%), with four endolaterals (7.9%) making up the rest. The typical endolateral formula is 2-2-2 (74.5%). Other variant formulae are: 1-2-2 (8.8%), 2-2-2-2 (4.9%), 2-2-3 (2.9%), 1-2-1, 2-2-2-1 (each 2.0%), 1-1-1, 2-2-1, 2-3-2, 3-2-2, 2-2-2-3 (all 1.0%). Dr. Panos S. Economidis (in litt. 12 Aug. 1979), contrary to his statement in Economidis (1974), said that he agreed with my observations that uniform posterial rows are always present in E. hellenicum. He explained that his observations had been based on badly preserved specimens, with only Berg's figures as comparative material. This is why he wrote in Economidis (1974: 8): "Denticules labials postérieurs absents ou présents, chez quelques exemplaires, mais ne forment pas de séries;" (translation by Economidis of an excerpt from his original Greek paper). All 24 adult specimens, whose transverse lingual lamina dentition was studied, possessed only an enlarged median cusp without any cusps on either side of it. The two longitudinal lingual laminae of the holotype were examined and no cusps could be discerned on them. An interesting situation exists in and is restricted to E. hellenicum adults. Nine out of 66 (13.6%) specimens possess additional cusps inside, but close to, the ring formed by linking the supraoral lamina, endolaterals and infraoral lamina. These one or two teeth per specimen occur in various positions, as follows: one cusp below each lateral supraoral tooth (one case); one cusp next to each first endolateral (three cases); one cusp next to the first left (two cases) and right (one case) endolateral; one cusp next to the third left (one case) and right (one case) endolateral. All 58 adults in which caudal fin shape was examined had rounded caudal fins. The range in the number of velar tentacles, in ten adult E. hellenicum was determined by Vladykov et al. (1982, MS) to be 2-5, with mean 3.7 and standard deviation 1.2. All the tentacles are stub-like (<1 mm long) and no wings are present (Vladykov et al., 1982 MS). The total length, in the ammocoetes at my disposal, ranged from 33 to 189 (Table 9), and wet weight, in 232 of these, having the same range in total length, varied between 0.10 and 12.34 g. Economidis (1974) recorded total lengths of 25 to 144 mm in 71 ammocoetes. According to Economidis (1974), the number of trunk myomeres ranges from 56 to 63 in ammocoetes, which is comparatively similar to the findings of this study (Table 10). The most frequent trunk myomere counts in ammocoetes (Table 10) were 56 (21.6%), 57 (24.7%) and 58 (19.8%). The tongue precursor pigmentation was determined in 11 ammocoetes. The pigment coverage of the bulb was either absent to trace (i.e.: -) in 54.5% of the specimens or slight (i.e.: +) in the remaining 45.5%. The pigment coverage along the elastic ridge exhibited extreme variation: absent to trace (i.e.: -) in 36.4%, slight (i.e.: +) and moderate (i.e.: ++) in 18.2% each, strong (i.e.: +++) in 27.3%. Of the 218 ammocoetes looked at for caudal fin shape, only two exhibited a spade-like condition; the rest had rounded caudal fins. Thirteen metamorphosing ammocoetes measured 113.5 to 156.5 mm in total length and 2.99 to 7.94 g in weight. Economidis (1974) recorded total lengths of 114 to 142 mm in three metamorphosing ammocoetes. According to the material at my disposal, <u>E. hellenicum</u> undergoes metamorphosis between the 7th of October and the 13th of November.

TABLE 1. Morphometrics (in percentage of total and branchial lengths and interocular width) of adults (sexes combined) of four *Eudontomyzon* species. Data refer to mean, standard deviation (in parentheses) and range.

Species	River basin	N	TL, mm	$\frac{d-B_1}{TL}$	$\frac{B_1-B_7}{TL}$	$\frac{B_7-A}{TL}$	$\frac{a}{TL}$	$\frac{a-C}{TL}$	$\frac{d}{TL}$	$\frac{d-n}{TL}$	$\frac{d-O}{TL}$	$\frac{O}{TL}$	$\frac{O-B_1}{TL}$	$\frac{d}{B_1-B_7}$	$\frac{d-n}{B_1-B_7}$	$\frac{d-O}{B_1-B_7}$	$\frac{d-B_1}{B_1-B_7}$	$\frac{O_1-B_7}{B_1-B_7}$	$\frac{O}{I}$
E. danfordi	Tisa (Czechoslovakia, Ukrainian SSR, Romania)	68*	181.1(21.4) 140-241	11.4(1.4) 7.8-13.5	9.9(0.7) 8.6-11.4	49.4(2.1) 42.9-52.5	1.0(0.2) 0.6-1.7	29.6(1.?) 25.6-32.?	5.7(1.0) 2.8-7.5	6.4(1.1) 4.1-8.3	7.5(1.2) 4.8-9.3	1.5(0.2) 1.0-2.1	3.0(0.3) 2.2-3.5	57.7(8.5) 37.3-74.4	64.5(9.9) 43.8-86.7	75.1(10.1) 50.0-93.3	115.2(10.7) 90.3-140.0	13.6(1.7) 9.8-16.7	45.8(8.1) 33.3-75.0
E. mariae complex	Vistula (Poland), Donets (Ukrainian SSR), Danube (Czechoslovakia, Austria, Yugoslavia, [illegible]), Drin and Vardar ([illegible])	33†	162.3(16.8) 123-195	10.0(1.5) 6.9-12.1	10.8(1.0) 8.5-12.3	50.5(2.4) 44.9-54.4	1.1(0.4) 0.4-2.2	28.3(1.9) 24.1-31.3	4.4(1.1) 2.2-5.8	4.7(1.1) 2.5-6.5	5.9(1.2) 2.7-7.6	1.5(0.4) 0.7-2.1	3.0(0.3) 2.4-3.7	40.2(7.8) 23.5-50.9	43.3(9.2) 26.5-63.3	55.6(8.7) 33.4-66.7	92.6(9.8) 70.3-110.0	13.7(1.5) 10.0-16.2	49.0(10.3) 25.0-66.7
E. morii	Yalu (People's Republic of China)	4	187.8(19.5) 171-211.5	12.4(0.5) 11.7-13.0	9.6(0.8) 8.7-10.2	47.3(0.2) 47.0-47.5	1.4(0.2) 1.2-1.7	30.1(0.2) 29.8-30.4	6.7(0.5) 6.1-7.2	7.2(0.4) 6.7-7.5	8.1(0.5) 7.6-8.7	1.5(0.2) 1.2-1.7	2.9(0.1) 2.8-3.1	70.7(9.8) 60.0-81.3	75.7(9.7) 65.7-86.7	85.5(11.7) 74.3-96.7	133.3(14.6) 116.3-143.3	12.6(1.2) 11.4-13.9	49.6(1.2) 48.4-51.8
E. hellenicus	Struma and Loúros (Greece)	66	123.2(15.9) 95.5-158.5	10.7(1.0) 8.4-13.1	10.5(0.7) 9.5-12.4	49.4(1.8) 46.4-54.7	1.0(0.3) 0.6-2.0	29.8(1.7) 26.2-33.0	5.3(0.8) 2.9-7.3	5.4(0.7) 3.6-7.3	6.7(0.9) 4.4-8.9	1.6(0.2) 1.1-2.1	3.0(0.3) 2.1-3.8	50.0(6.3) 30.8-66.7	51.1(5.4) 33.5-69.2	64.0(6.8) 46.2-79.2	101.9(6.9) 87.5-116.7	14.7(1.6) 9.7-18.5	42.9(5.7) 33.3-57.1

*This value is the sample size mode. The data for TL and ratios were calculated from samples ranging in size from 69 to 66 except for the O ratio in which it was 73.

†The sample size was 33 for the O ratio.

TABLE 2. Morphometrics (in percentage of total and branchial lengths and interocular width) of adults (sexes separate) of four *Eudontomyzon* species. Data refer to mean, standard deviation (in parentheses) and range.

Species	River basin	Sex	N	TL, mm	$\frac{d-B_1}{TL}$	$\frac{B_1-B_7}{TL}$	$\frac{B_7-a}{TL}$	$\frac{a}{TL}$	$\frac{a-C}{TL}$	$\frac{d}{TL}$	$\frac{d-n}{TL}$	$\frac{d-O}{TL}$	$\frac{O}{TL}$	$\frac{O-B_1}{TL}$	$\frac{d}{B_1-B_7}$	$\frac{d-n}{B_1-B_7}$	$\frac{d-O}{B_1-B_7}$	$\frac{d-B_1}{B_1-B_7}$	$\frac{O}{B_1-B_7}$	$\frac{O}{I}$
E. danfordi	Tisa (Czechoslovakia, Ukrainian SSR, Rumania)	♂	7	133.8(37.3) 100-241	12.6(0.5) 12.0-13.3	10.5(0.5) 9.8-11.0	46.8(2.9) 42.9-51.4	1.1(0.3) 0.7-1.7	29.4(2.0) 26.8-31.3	6.6(0.7) 5.7-7.5	7.2(0.6) 6.2-7.8	8.4(0.4) 7.9-9.0	1.6(0.2) 1.4-1.8	3.1(0.2) 2.9-3.3	67.2(6.4) 53.8-72.0	63.7(6.0) 56.4-74.0	79.9(3.8) 74.4-84.0	119.4(6.1) 110.0-125.0	12.9(1.4) 10.8-15.0	44.4(9.6) 33.3-62.5
		♀	21*	192.1(22.1) 152.5-210.5	11.5(1.1) 9.1-13.1	10.2(0.7) 9.0-11.4	48.1(2.1) 43.7-51.5	1.0(0.2) 0.6-1.6	29.2(1.5) 25.6-31.8	5.9(0.7) 4.3-7.1	6.5(1.0) 4.3-8.2	7.6(1.0) 4.9-9.2	1.5(0.3) 1.0-2.1	3.0(0.2) 2.5-3.3	59.0(6.8) 43.8-66.7	63.5(9.3) 43.8-77.8	73.8(9.3) 50.0-84.4	117.6(9.0) 93.8-128.4	13.5(1.6) 9.8-16.7	45.7(7.4) 33.3-63.6
E. mariae complex	Vistula (Poland), Dniester (Ukrainian SSR), Danube (Czechoslovakia, Austria, Yugoslavia, Rumania), Drin and Vardar (Yugoslavia)	♂	16†	163.8(12.9) 141-181.5	11.1(0.5) 10.1-12.1	11.1(0.7) 9.7-12.2	49.6(2.0) 44.9-53.8	1.1(0.5) 0.6-2.2	28.5(1.6) 25.9-31.3	5.2(0.4) 4.4-5.8	5.5(0.[illegible]) 4.8-[illegible].5	6.7(0.4) 6.2-7.6	1.7(0.3) 1.2-2.1	3.1(0.2) 2.4-3.6	46.3(2.5) 41.7-50.0	49.7(5.8) 41.1-63.1	60.5(4.3) 52.9-66.7	99.8(5.2) 90.7-110.0	13.2(1.5) 10.0-14.6	52.6(7.5) 36.4-63.6
		♀	18	160.6(18.1) 121-195	9.4(1.5) 6.9-11.5	10.7(1.1) 9.1-12.1	51.7(2.0) 47.7-54.4	1.0(0.2) 0.4-1.4	27.9(2.3) 21.3-30.6	3.9(1.1) 2.2-5.3	4.2(1.1) 2.5-5.7	5.5(1.3) 2.7-7.6	1.5(0.4) 0.7-2.0	3.0(0.2) 2.8-3.5	36.4(7.9) 23.5-45.5	39.9(8.8) 26.5-52.6	50.9(9.1) 27.4-61.5	87.7(9.1) 73.0-103.2	14.0(1.5) 11.4-16.7	43.1(11.7) 25.0-66.7
E. morii	Yalu (People's Republic of China)	♀	2	201.8(11.0) 193-211.5	12.7(0.5) 12.3-13.0	9.7(0.7) 9.2-10.2	47.5(0.1) 47.4-47.5	1.5(0.3) 1.3-1.7	30.0(0.2) 29.8-30.1	6.8(0.2) 6.6-6.9	7.3(0.2) 7.1-7.4	8.1(0.6) 7.8-8.7	1.6(0.1) 1.5-1.7	3.0(0.2) 2.8-3.1	69.8(3.4) 67.4-72.2	75.2(7.5) 69.8-80.6	85.6(12.5) 76.7-94.4	131.3(14.7) 120.9-141.7	12.8(1.6) 11.6-13.9	50.0(5.1) 46.2-53.8
E. hellenicum	Struma and Louros (Greece)	♂	11	124.6(13.9) 95.5-145.5	11.2(1.0) 9.4-13.1	10.6(0.6) 9.6-12.4	49.0(1.6) 46.4-53.2	1.1(0.3) 0.7-2.0	29.7(1.5) 27.8-33.0	5.5(0.9) 3.4-7.3	5.7(0.7) 4.3-7.3	7.1(0.9) 5.3-8.9	1.7(0.2) 1.4-2.1	3.1(0.3) 2.5-3.7	51.8(6.9) 33.3-66.7	53.3(5.5) 41.7-63.7	67.0(6.3) 54.2-79.2	105.1(6.4) 89.3-116.7	15.0(1.6) 10.7-18.2	47.6(4.4) 33.3-50.0
		♀	33	133.8(16.6) 93-159.5	10.3(0.8) 8.4-11.7	10.4(0.7) 9.5-12.1	49.9(1.9) 47.3-54.7	1.0(0.2) 0.6-1.5	29.9(1.8) 26.2-32.7	5.0(0.6) 2.9-6.7	5.1(0.5) 3.6-5.8	6.3(0.6) 4.4-7.8	1.6(0.2) 1.3-2.0	2.9(0.3) 2.3-3.8	49.2(5.1) 30.8-56.0	49.9(4.5) 33.5-57.1	61.0(6.0) 45.2-75.0	93.8(5.9) 87.5-111.1	11.4(1.7) 9.7-18.5	43.3(5.9) 33.3-57.1

*This value is the sample size mode. The data for TL and ratios were calculated from samples ranging in size from 19 to 21.

†The sample size was 15 for the $\frac{O}{I}$ ratio.

TABLE 3. Dentition of adults (sexes combined) of four Eudontomyzon species. Data refer to mean, standard deviation (in parentheses), range and number of counts made (in square brackets).

Species		E. danfordi*	E. mariae complex**	E. morii†	E. hellenicum††
No. of teeth					
Supraoral lamina		2.0(0.0) 2[77]	2.1(0.4) 2-4[35]	2.0(0.0) 2[4]	2.0(0.0) 2[62]
Infraoral lamina		9.8(0.9) 7-12[70]	7.1(1.7) 5-10[32]	7.8(1.7) 6-10[4]	8.9(1.1) 7-11[55]
First anterial row		8.0(1.5) 6-13[71]	6.8(1.3) 5-10[32]	3.8(1.0) 3-5[4]	6.2(0.8) 4-8[64]
First posterial row		20.7(2.5) 15-28[63]	10.1(7.3) 0-20[19]	21.3(2.5) 19-24[3]	11.5(1.5) 10-15[55]
No. of cusps					
Endolaterals	First	1.3(0.4) 1-2[144]	1.3(0.5) 0-2[63]	1.8(0.5) 1-2[8]	1.9(0.3) 1-3[118]
	Second	2.0(0.2) 1-3[142]	1.9(0.3) 1-2[62]	1.8(0.5) 1-2[8]	2.0(0.1) 1-3[111]
	Third	1.9(0.3) 0-2[142]	1.5(0.7) 0-3[58]	1.8(0.5) 1-2[8]	2.0(0.3) 1-3[106]
	Fourth	0.03(0.2) 0-1[148]	0.1(0.5) 0-2[72]	0.0(0.0) 0[8]	0.1(0.5) 0-3[128]
No. of rows					
Anterials		5.4(0.7) 4-7[70]	3.1(0.6) 2-4[34]	3.0(0.0) 3[4]	3.6(0.5) 3-4[64]
Exolaterals		3.5(0.7) 2-5[140]	1.9(0.5) 1-4[59]	1.5(0.5) 1-2[8]	4.1(0.7) 2-6[125]
Posterials		3.0(0.5) 2-4[72]	1.5(0.8) 0-3[31]	1.0(0.0) 1[4]	2.3(0.7) 1-4[61]

River basin: *Tisa (Czechoslovakia, Ukrainian SSR, Rumania)

**Vistula (Poland), Donets (Ukrainian SSR), Danube (Czechoslovakia, Austria, Yugoslavia, Rumania), Drin and Vardar (Yugoslavia)

†Yalu (People's Republic of China)

††Struma and Loûros (Greece)

TABLE 4. Dentition of adults (sexes separate) of four Eudontomyzon species. Data refer to mean, standard deviation (in parentheses), range and number of counts made (in square brackets).

Species		E. danfordi*		E. mariae complex**		E. morii+	E. hellenicum++	
Sex		♂	♀	♂	♀	♀	♂	♀
No. of teeth								
Supraoral lamina		2.0(0.0) 2[7]	2.0(0.0) 2[21]	2.1(0.3) 2-3[16]	2.2(0.6) 2-4[15]	2.0(0.0) 2[2]	2.0(0.0) 2[31]	2.0(0.0) 2[31]
Infraoral lamina		10.0(0.9) 9-11[6]	9.9(0.9) 8-11[21]	7.3(1.7) 5-10[15]	7.1(1.9) 5-10[14]	7.5(0.7) 7-8[2]	9.0(1.0) 7-11[28]	8.7(1.2) 7-11[27]
First anterial row		7.3(1.1) 6-9[7]	8.7(1.8) 6-12[21]	6.5(1.1) 5-9[15]	7.1(1.3) 5-9[15]	4.0(1.4) 3-5[2]	6.2(0.8) 4-8[32]	6.2(0.9) 4-8[32]
First posterial row		20.3(1.6) 18-23[7]	20.5(2.5) 15-23[19]	10.3(7.4) 0-19[9]	9.9(7.7) 0-20[10]	22.5(2.1) 21-24[2]	11.8(1.6) 10-15[26]	11.3(1.3) 10-15[29]
No. of cusps								
Endolaterals	First	1.4(0.5) 1-2[14]	1.3(0.5) 1-2[42]	1.3(0.5) 1-2[31]	1.4(0.6) 0-2[25]	2.0(0.0) 2[4]	1.9(0.3) 1-2[57]	1.9(0.3) 1-3[61]
	Second	2.0(0.0) 2[14]	2.0(0.2) 1-2[42]	1.8(0.4) 1-2[31]	2.0(0.2) 1-2[24]	2.0(0.0) 2[4]	2.0(0.1) 2-3[51]	2.0(0.1) 1-2[60]
	Third	1.9(0.4) 1-2[14]	1.9(0.3) 1-2[41]	1.5(0.6) 0-2[32]	1.6(0.9) 0-3[20]	2.0(0.0) 2[4]	2.0(0.2) 1-3[51]	2.0(0.3) 1-3[55]
	Fourth	0.0(0.0) 0[14]	0.0(0.0) 0[42]	0.3(0.6) 0-2[32]	0.1(0.3) 0-2[33]	0.0(0.0) 0[4]	0.1(0.5) 0-3[64]	0.1(0.4) 0-2[64]
No. of rows								
Anterials		5.1(1.1) 4-7[7]	5.5(0.7) 4-7[21]	3.3(0.5) 3-4[15]	3.0(0.6) 2-4[16]	3.0(0.0) 3[2]	3.6(0.5) 3-4[31]	3.6(0.5) 3-4[33]
Exolaterals		3.1(0.6) 2-4[14]	3.3(0.8) 2-5[41]	1.9(0.3) 1-2[28]	2.0(0.7) 1-4[27]	1.8(0.5) 1-2[4]	4.2(0.7) 2-5[61]	4.0(0.7) 3-6[64]
Posterials		2.7(0.8) 2-4[7]	3.0(0.5) 2-4[21]	1.5(0.9) 0-3[15]	1.5(0.7) 0-2[15]	1.0(0.0) 1[2]	2.4(0.6) 1-3[29]	2.3(0.7) 1-4[32]

River basin: *Tisa (Czechoslovakia, Ukrainian SSR, Rumania)

**Vistula (Poland), Donets (Ukrainian SSR), Danube (Czechoslovakia, Austria, Yugoslavia, Rumania), Drin and Vardar (Yugoslavia)

+Yalu (People's Republic of China)

++Struma and Loúros (Greece)

TABLE 5. Number of trunk myomeres in adults (sexes combined) of four *Eudontomyzon* species.

Species	River basin	N	No. trunk myomeres		
			Range	$\bar{X}$	s
E. danfordi	Tisa (Czechoslovakia, Ukrainian SSR, Rumania)	57	59-68	63.7	1.6
E. mariae complex	Vistula (Poland), Donets (Ukrainian SSR), Danube (Czechoslovakia, Austria, Yugoslavia, Rumania), Drin and Vardar (Yugoslavia)	39	60-73	66.2	3.3
E. morii	Yalu (People's Republic of China)	4	68-74	70.5	2.6
E. hellenicum	Struma and Loúros (Greece)	65	53-62	57.4	2.0

TABLE 6. Number of trunk myomeres in adults (sexes separate) of four *Eudontomyzon* species.

Species	River basin	Sex	N	No. trunk myomeres Range	$\bar{X}$	s
E. danfordi	Tisa (Czechoslovakia, Ukrainian SSR, Rumania)	♂	7	63-65	64.1	0.9
		♀	17	59-68	63.6	2.1
E. mariae complex	Vistula (Poland), Donets (Ukrainian SSR), Danube (Czechoslovakia, Austria, Yugoslavia, Rumania), Drin and Vardar (Yugoslavia)	♂	16	65-73	67.8	2.4
		♀	18	60-72	65.4	3.7
E. morii	Yalu (People's Republic of China)	♀	2	69-74	71.5	3.5
E. hellenicum	Struma and Loúros (Greece)	♂	33	53-62	57.2	2.3
		♀	32	55-62	57.2	2.0

TABLE 7. Caudal fin pigmentation (in percentage) in adults (sexes combined) of four *Eudontomyzon* species. In parentheses is the number of specimens.

Species	River basin	N	Degree of pigmentation			
			−	+	++	+++
E. danfordi	Tisa (Czechoslovakia, Ukrainian SSR, Rumania)	56	19.6(11)	3.6(2)	12.5(7)	64.3(36)
E. mariae complex	Vistula (Poland), Donets (Ukrainian SSR), Danube (Czechoslovakia, Austria, Yugoslavia, Rumania), Drin (Yugoslavia)	30	6.7(2)	3.3(1)	13.3(4)	76.7(23)
E. morii	Yalu (People's Republic of China)	4	-	-	50.0(2)	50.0(2)
E. hellenicum	Struma and Loúros (Greece)	62	-	1.6(1)	19.3(12)	79.0(49)

TABLE 8. Caudal fin pigmentation (in percentage) in adults (sexes separate) of four Eudontomyzon species. In parentheses is the number of specimens.

Species	River basin	Sex	N	Degree of pigmentation			
				—	+	++	+++
E. danfordi	Tisa (Czechoslovakia, Ukrainian SSR, Rumania)	♂	7	14.3(1)	-	14.3(1)	71.4(5)
		♀	19	10.5(2)	-	15.8(3)	73.7(14)
E. mariae complex	Vistula (Poland), Donets (Ukrainian SSR), Danube (Czechoslovakia, Austria, Yugoslavia, Rumania), Drin (Yugoslavia)	♂	11	18.2(2)	-	18.2(2)	63.6(7)
		♀	15	-	-	-	100.0(15)
E. morii	Yalu (People's Republic of China)	♀	2	-	-	-	100.0(2)
E. hellenicum	Struma and Loúros (Greece)	♂	31	-	-	16.1(5)	83.9(26)
		♀	31	-	3.2(1)	29.0(9)	67.7(21)

TABLE 9. Morphometrics (in percentage of total and branchial lengths) of ammocoetes of three *Eudontomyzon* species. Data refer to mean, standard deviation (in parentheses) and range.

Species	River basin	N	TL, mm	$\frac{d-B_1}{TL}$	$\frac{B_1-B_7}{TL}$	$\frac{B_7-a}{TL}$	$\frac{a}{TL}$	$\frac{a-C}{TL}$	$\frac{B-n}{TL}$	$\frac{d-n}{B_1-B_7}$	$\frac{d-B_1}{B_1-B_7}$	$\frac{B_1-B_2}{B_1-B_7}$
E. danfordi	Tisa (Czechoslovakia, Ukrainian SSR, Rumania)	191*	105.8(43.3) 21.5-208	7.5(0.8) 5.8-10.3	12.2(1.0) 10.2-14.7	50.9(2.8) 48.1-58.9	1.0(0.3) 0.5-2.4	29.4(1.5) 22.2-32.7	2.6(0.4) 1.8-4.0	21.6(2.4) 15.0-28.6	61.3(4.3) 50.0-75.0	14.5(2.4) 8.8-21.7
E. mariae complex	Vistula (Poland), Dnepr (Belorussian and Ukrainian SSR), Dnestr (Poland), Danube (Czechoslovakia, Ukrainian SSR, Rumania, Yugoslavia), Drin (Yugoslavia)	174	136.8(44.0) 34-212	7.4(1.2) 5.3-11.8	12.7(1.5) 9.4-20.5	53.5(1.4) 50.0-58.0	0.9(0.3) 0.0†-1.6	26.8(2.2) 17.6-30.8	2.4(0.5) 1.8-4.5	19.0(2.6) 12.5-28.6	58.3(5.1) 45.7-75.0	15.0(2.5) 10.0-25.0
E. hellenicum	Struma and Louros (Greece)	237	105.0(21.5) 33-189	8.3(1.0) 6.6-13.6	12.7(0.8) 10.9-16.2	51.3(1.3) 46.8-55.4	1.1(0.2) 0.7-1.8	28.0(1.4) 21.2-31.7	3.1(0.4) 1.9-4.6	24.5(2.6) 14.3-33.3	66.0(5.5) 53.3-90.0	13.7(1.9) 7.4-20.0

*This value is the sample size mode. For TL, the sample was 330. For the ratios $\frac{d-B_1}{TL}$, $\frac{B_1-B_7}{TL}$ and $\frac{B_7-a}{TL}$, it was 190.

†Morphometrics, being taken with an accuracy of 0.5mm, any measurement smaller than this was recorded as 0.

TABLE 10. Number of trunk myomeres in ammocoetes of three *Eudontomyzon* species.

Species	River basin	N	No. trunk myomeres		
			Range	$\bar{X}$	s
E. danfordi	Tisa (Czechoslovakia, Ukrainian SSR, Rumania)	190	58-70	62.8	1.7
E. mariae complex	Vistula (Poland), Dnepr (Belorussian and Ukrainian SSR), Dnestr (Poland), Danube (Czechoslovakia, Ukrainian SSR, Rumania, Yugoslavia), Drin (Yugoslavia)	168	58-70	63.5	2.2
E. hellenicum	Struma and Louros (Greece)	227	53-62	57.4	1.7

TABLE 11. Pigmentation patterns (in percentage) in ammocoetes of three *Eudontomyzon* species. In parentheses is the number of specimens.

Species		*E. danfordi**				*E. mariae* complex**				*E. hellenicum*†			
Degree of pigmentation		-	+	++	+++	-	+	++	+++	-	+	++	+++
Pigmentation area													
Upper lip		36.4(64)	44.9(79)	18.2(32)	0.6(1)	61.3(106)	35.3(61)	3.5(6)	-	0.4(1)	11.6(27)	78.4(183)	9.1(21)
Between upper lip and cheek		-	-	4.0(7)	96.0(169)	-	1.1(2)	7.5(13)	91.4(159)	4.0(9)	20.7(48)	39.7(92)	35.8(83)
Cheek		1.7(3)	1.7(3)	26.1(46)	70.5(124)	-	5.2(9)	58.4(101)	36.4(63)	-	4.2(10)	24.1(57)	71.7(170)
Subocular		78.4(138)	11.9(21)	4.5(8)	5.1(9)	90.8(158)	2.3(4)	2.9(5)	4.0(7)	33.8(80)	26.6(63)	10.5(25)	29.1(69)
Prebranchial	Upper	22.2(39)	26.7(47)	21.6(38)	29.5(52)	34.5(60)	23.6(41)	25.3(44)	16.7(29)	62.6(147)	32.8(77)	3.8(9)	0.9(2)
	Lower	27.8(49)	40.9(72)	23.3(41)	8.0(14)	52.6(91)	28.3(49)	14.5(25)	4.6(8)	82.8(193)	15.5(36)	1.7(4)	-
Branchial	Upper	0.6(1)	0.6(1)	71.0(125)	27.8(49)	-	2.3(4)	79.2(137)	18.5(32)	-	3.0(7)	94.5(224)	2.5(6)
	Lower	93.2(164)	6.8(12)	-	-	91.4(159)	5.7(10)	1.7(3)	1.1(2)	48.5(114)	50.6(119)	0.9(2)	-
	Ventral	77.3(133)	21.5(37)	1.2(2)	-	92.5(136)	5.4(8)	2.0(3)	-	28.0(66)	71.6(169)	0.4(1)	-
Lower lip		35.2(62)	40.3(71)	19.9(35)	4.5(8)	69.4(120)	22.0(38)	8.7(15)	-	0.4(1)	7.6(18)	45.3(107)	46.6(110)
Caudal fin		1.2(2)	67.6(117)	28.3(49)	2.9(5)	2.3(4)	11.1(19)	40.4(69)	46.2(79)	-	1.3(3)	85.8(193)	12.9(29)
Dorsal		33.7(56)	41.0(68)	19.9(33)	5.4(9)	16.6(24)	37.9(55)	20.7(30)	24.8(36)	3.8(9)	16.5(39)	31.8(75)	47.9(113)

River basin: *Tisa (Czechoslovakia, Ukrainian SSR, Rumania)

**Vistula (Poland), Dnepr (Belorussian and Ukrainian SSR), Dnestr (Poland), Danube (Czechoslovakia, Rumania, Yugoslavia), Drin (Yugoslavia)

†Struma and Loúros (Greece)

TABLE 12. Adult (sexes combined) morphometric characters found to be statistically different between different pairs of *Eudontomyzon* species at the 99.998% confidence level using the F-test. Data taken from Table 1. All $P \leq 0.002$.

Specific pairs		
E. danfordi - *E. mariae* complex	*E. danfordi* - *E. hellenicum*	*E. mariae* complex - *E. hellenicum*
TL	TL	TL
d-B_1/TL	B_1-B_7/TL	a-C/TL
B_1-B_7/TL	d-n/TL	d/TL
B_7-a/TL	d-O/TL	d-n/TL
a-C/TL	d/B_1-B_7	d-O/TL
d/TL	d-n/B_1-B_7	d/B_1-B_7
d-n/TL	d-O/B_1-B_7	d-n/B_1-B_7
d-O/TL	d-B_1/B_1-B_7	d-O/B_1-B_7
d/B_1-B_7	B_1-B_2/B_1-B_7	d-B_1/B_1-B_7
d-n/B_1-B_7		O/I
d-O/B_1-B_7		
d-B_1/B_1-B_7		

TABLE 13. Adult morphometric characters exhibiting sexual dimorphism in *Eudontomyzon* species, as derived from the F-test at the 99.998% confidence level. Data taken from Table 2. All $P < 0.002$.

E. danfordi	*E. mariae* complex	*E. hellenicum*
	$d-B_1/TL$	$d-B_1/TL$
	B_7-a/TL	$d-n/TL$
	d/TL	$d-O/TL$
	$d-n/TL$	$d-n/B_1-B_7$
	d/B_1-B_7	$d-O/B_1-B_7$
	$d-n/B_1-B_7$	$d-B_1/B_1-B_7$
	$d-O/B_1-B_7$	
	$d-B_1/B_1-B_7$	

TABLE 14. Probabilities for adult (sexes combined) characters found to be statistically different between different pairs of Eudontomyzon species at the 95% confidence level using the Chi-square test. Data taken from Tables 3, 5 and 7.

Specific pairs		
E. danfordi - E. mariae complex	E. danfordi - E. hellenicum	E. mariae complex - E. hellenicum
Dentition	Dentition	Dentition
Infraoral lamina, P<0.005	Infraoral lamina, P<0.005	Infradral lamina, P<0.005
First anterial row, P<0.005	First anterial row, P<0.005	First anterial row, P=0.01-0.025
First posterial row, P<0.005	First posterial row, P<0.005	First posterial row, P<0.005
Endolaterals: Second, P<0.005	Endolaterals: First, P<0.005	Endolaterals: First, P<0.005
Endolaterals: Third, P<0.005	Endolaterals: Third, P=0.025-0.05	Endolaterals: Second, P<0.005
	Endolaterals: Fourth, P=0.01-0.025	Endolaterals: Third, P<0.005
Rows: Anterials, P<0.005	Rows: Anterials, P<0.005	Rows: Anterials, P<0.005
Rows: Exolaterals, P<0.005	Rows: Exolaterals, P<0.005	Rows: Exolaterals, P<0.005
Rows: Posterials, P<0.005	Rows: Posterials, P<0.005	Rows: Posterials, P<0.005
Trunk myomeres, P<0.005	Trunk myomeres, P<0.005	Trunk myomeres, P<0.005
	Pigmentation area	
	Caudal fin, P<0.005	

TABLE 15. Ammocoete morphometric characters found to be statistically different between different pairs of *Eudontomyzon* species at the 99.998% confidence level using the F-test. Data taken from Table 9. All $P \leq 0.002$.

Specific pairs		
E. danfordi - *E. mariae* complex	*E. danfordi* - *E. hellenicum*	*E. mariae* complex - *E. hellenicum*
TL	$d-B_1/TL$	TL
B_1-B_7/TL	B_1-B_7/TL	$d-B_1/TL$
B_7-a/TL	a/TL	B_7-a/TL
a-C/TL	a-C/TL	a/TL
d-n/TL	d-n/TL	a-C/TL
$d-n/B_1-B_7$	$d-n/B_1-B_7$	d-n/TL
$d-B_1/B_1-B_7$	$d-B_1/B_1-B_7$	$d-n/B_1-B_7$
		$d-B_1/B_1-B_7$
		B_1-B_2/B_1-B_7

TABLE 16. Probabilities for ammocoete characters found to be statistically different between different pairs of _Eudontomyzon_ species at the 95% confidence level using the Chi-square test. Data taken from Tables 10 and 11.

Specific pairs		
E. danfordi - _E. mariae_ complex	_E. danfordi_ - _E. hellenicum_	_E. mariae_ complex - _E. hellenicum_
Trunk myomeres, P=0.005-0.01	Trunk myomeres, P<0.005	Trunk myomeres, P<0.005
Pigmentation area	_Pigmentation area_	_Pigmentation area_
Upper lip, P<0.005	Upper lip, P<0.005	Upper lip, P<0.005
Cheek, P<0.005	Between upper lip and cheek, P<0.005	Between upper lip and cheek, P<0.005
Subocular, P<0.005	Subocular, P<0.005	Cheek, P<0.005
Prebranchial: Upper, P=0.005-0.01	Prebranchial: Upper, P<0.005	Subocular, P<0.005
Prebranchial: Lower, P<0.005	Prebranchial: Lower, P<0.005	Prebranchial: Upper, P<0.005
Branchial: Ventral, P<0.005	Branchial: Upper, P<0.005	Prebranchial: Lower, P<0.005
Lower lip, P<0.005	Branchial: Lower, P<0.005	Branchial: Upper, P<0.005
Caudal fin, P<0.005	Branchial: Ventral, P<0.005	Branchial: Lower, P<0.005
Dorsal, P<0.005	Lower lip, P<0.005	Branchial: Ventral, P<0.005
	Caudal fin, P<0.005	Lower lip, P<0.005
	Dorsal, P<0.005	Caudal fin, P<0.005
		Dorsal, P<0.005

Key to species of the genus Eudontomyzon (larvae and adults)
(Numbers in parentheses represent percentage occurrence for a given character)

1- One dorsal fin; exclusively freshwater; North America......Ichthyomyzon

Two dorsal fins (In spawning adults, the two dorsal fins may be so close together, as to appear a single continuous fin.); exclusively freshwater; Eurasia..2

2- Oral hood instead of suctorial disc; no buccal funnel, tongue or teeth; triangular nostril; eyes covered with a more or less thick layer of skin; branchial openings connected by a groove....................ammocoete 3

Suctorial disc instead of oral hood; buccal funnel studded with, and tongue bearing keratinous teeth; circular nostril; eyes not covered by any layer; branchial openings not connected by a groove.........adult 4

3- Rounded caudal fin (99.1%); pigment coverage of upper (87.5%) and lower (91.9%) lip moderate (i.e.: ++) or strong (i.e.: +++); 53-62 trunk myomeres; max. TL 189 mm...E. hellenicum Vladykov, Renaud, Kott and Economidis, 1982 MS

Spade-like caudal fin (98.9% in E. danfordi and 98.8% in E. mariae complex); pigment coverage of upper (81.3% in E. danfordi and 96.6% in E. mariae complex) and lower (75.5% in E. danfordi and 91.4% in E. mariae complex) lip absent to trace (i.e.: -) or slight (i.e.: +); 58-70 trunk myomeres; max. TL211 (E. danfordi) and at least 250 mm (E. mariae complex)....E. danfordi and E. mariae complex

4- Parasitic mode of life; intestine width 0.5 to 5.0 mm (Extreme care must be taken, to avoid confusion between parasitic and nonparasitic lampreys, during two periods of the adult life; shortly after metamorphosis and during the spawning season. At these times, adults belonging to the two divergent modes of life are difficult to tell apart, because both groups possess narrow (max. diameter: 1 mm) intestinal tracts, even to the point of being thread-like (i.e.: <0.5 mm) in diameter.) 5

Nonparasitic mode of life; intestine width <0.5 to 1.0 mm.....6

5- First anterial row with 6 - 13 teeth; 4 - 7 anterial rows; 2 - 4 posterial rows; 59 - 67 (98.2%) trunk myomeres; Tisa river basin, Europe .... E. danfordi

First anterial row with 3 - 5 teeth; 3 anterial rows; 1 posterial row; 68 - 74 trunk myomeres; Yalu river basin, Asia .... E. morii

6- Villiform cusps on anterial, exolateral and posterial fields; posterial rows may (90.3%) or may not (9.7%) be present and if present, the first posterial row may (62.5%) or may not (37.5%) be continuous; 1 - 2 exolateral rows (93.2%); the three lingual laminae bear teeth (dissection may be required to expose some of them);

spade-like caudal fin (96.6%); 7 - 12 velar tentacles; 60 - 73 trunk myomeres; TL 123 - 222 mm; Adriatic, Aegean, Baltic and Black sea basins .... E. mariae complex

Cusps on anterial, exolateral and posterial fields not villiform, but larger; posterial rows always present and first posterial row always continuous; 3 - 6 exolateral rows (99.2%); apart from median enlarged cusp of the transverse lingual lamina, no teeth are present on the tongue; rounded caudal fin; 2 - 5 velar tentacles; 53 - 59 (86.2%) trunk myomeres; TL 95.5 - 158.5 mm; Aegean and Ionian sea basins .... E. hellenicum

Sexual Dimorphism

Differences between males and females of adult *E. danfordi*, *E. mariae* complex and *E. hellenicum* were looked for in the dentitional characters (Table 4), as well as in the number of trunk myomeres (Table 6) and caudal fin pigmentation (Table 8), using the Chi-square test at the 95% confidence level. No differences between sexes were found except in the number of trunk myomeres ($P = 0.005-0.01$) and caudal fin pigmentation ($P < 0.005$) of *E. mariae* complex adults and in the number of exolateral rows ($P = 0.025-0.05$) of *E. hellenicum* adults. The statistically significant difference in the number of trunk myomeres between males and females of *E. mariae* complex may be attributable to a latitudinal cline. Indeed, 93.8% of the males compared to 66.7% of the females were collected above 45°N latitude. Furthermore, since no statistically significant differences in the number of trunk myomeres were found in the other species of the genus, one can infer that the differences observed in *E. mariae* complex are not of sexual nature. Although the above data suggests a cline in the number of trunk myomeres in *E. mariae* complex, larger samples from numerous localities are required to ascertain its presence. The statistically significant difference in the number of exolateral rows between males and females of *E. hellenicum* is too close to the acceptable confidence level to be considered important. Differences between males and females of adult *E. danfordi*, *E. mariae* complex and *E. hellenicum* were looked for in the morphometric characters (Table 2), using the F-test at the 99.998% confidence level. The list of morphometric characters exhibiting sexual dimorphism is presented in Table 13. Because morphometrics were found to be widely overlapping, and since specimens were not divided according to their sexual maturity in order to maintain adequate sample sizes, a more realistic level of confidence (P= 0.002) was taken in place of the conventional P= 0.05. Even this highly stringent level of significance did not substantially lower the number of characters retained had the latter level been used. Indeed, one character each was dropped from E. danfordi and E. mariae complex and four characters were dropped from E. hellenicum. The absence of sexual dimorphism in the E. danfordi adults (Table 13) is due to the fact that very few (4♂:4♀), in the sample, were sexually mature. On the other hand, sexually mature individuals were very well represented in the E. mariae complex sample (15♂:12♀) and less so in E. hellenicum (15♂:15♀). In fact, of the 27 sexually mature E. mariae complex specimens ten males and seven females were collected during spawning. The long list of characters exhibiting sexual dimorphism (Table 13) in E. mariae complex and E. hellenicum, in sharp contrast to the condition in E. danfordi, indicates that sexual dimorphism, at least in morphometrics, appears only close to the spawning season, before this period (i.e.: prespawning stage), both sexes in the adult, being morphometrically indistinct.

Fig. 9. Photograph of side-view of adults.

a- *Eudontomyzon danfordi*; W(VDV)5825; ♂; 210.5 mm TL; Okna River, Vyhorlat mountain range, Slovakia. (Notice the large, well vascularized intestine; precloacal intestine width, 4.5 mm; dorsal fins far apart; urogenital papilla, not yet apparent.)

b- *E. mariae* complex; Y841; ♀; 169.5 mm TL; Jeziorka River, near Warsaw, Poland.

c- *E. morii*; 092; ♀; 196 mm TL; upper Yalu River, near Changbai, People's Republic of China.

d- *E. hellenicum*; holotype; Y744; ♂; 95.5 mm TL; Kefalárion Brook, near Kefalárion, Greek Macedonia.

e- *E. hellenicum*; paratype; Y586; ♀; 105 mm TL; Kefalárion Brook, near Kefalárion, Greek Macedonia.

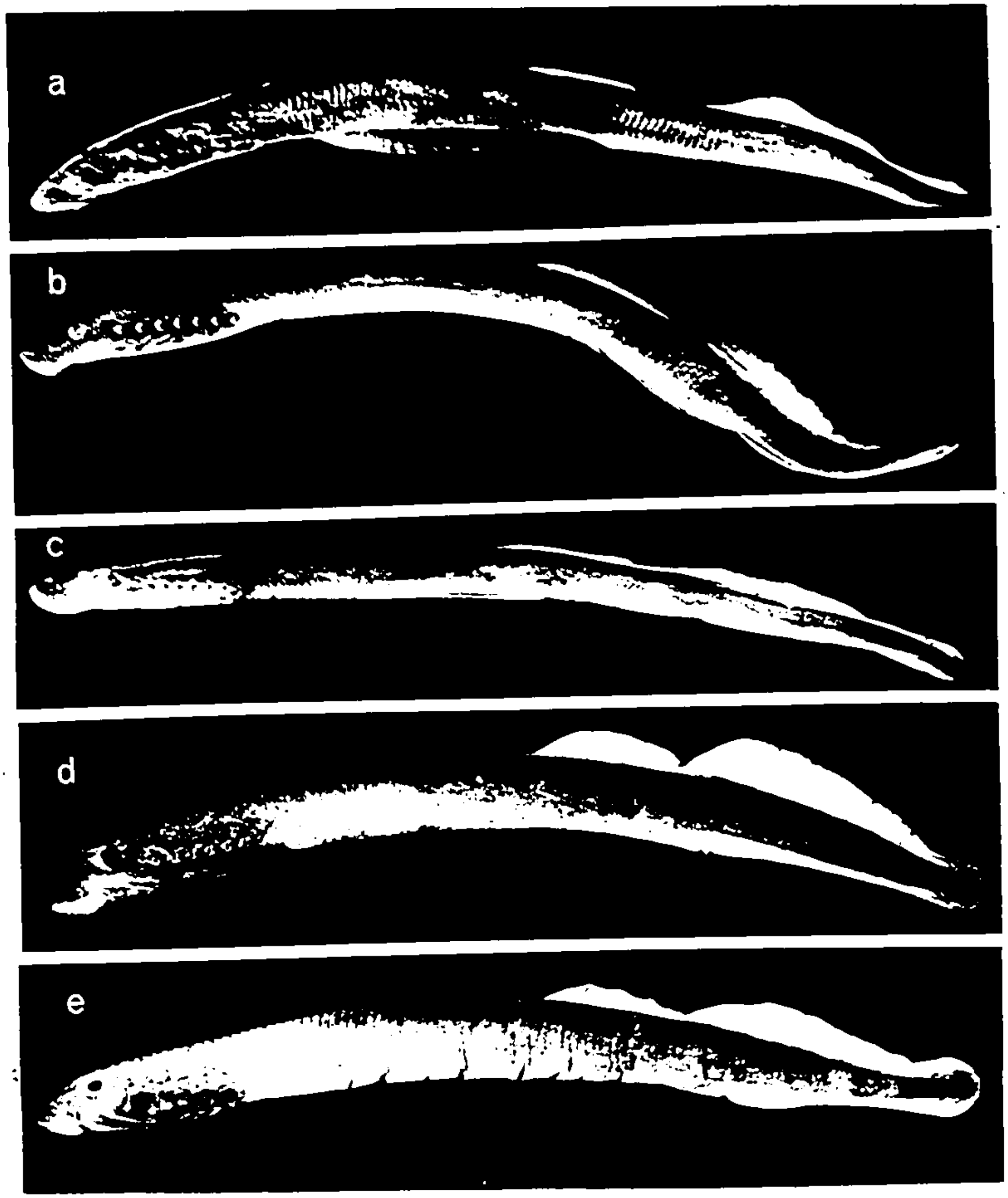

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Fig. 10. Photograph of oral discs.

a- Eudontomyzon danfordi; W(VDV)5825; ♂; 210.5 mm TL; 15.5 mm d; Okna River, Vyhorlat mountain range, Slovakia.

b- E. mariae complex; syntype; 0112; ♂; 171 mm TL; 9 mm d; Khar'kov River, near Khar'kov, Ukrainian SSR. (Notice the continuous first posterial row made up of 13 cusps.)

c- E. mariae complex; syntype; 0114; ♂; 180 mm TL; 10 mm d; Khar'kov River, near Khar'kov, Ukrainian SSR. (The first posterial row is continuous, and made up of 19 cusps, 18 of which are discernible. There are four endolaterals (1-1-2-2) on the left side and three (1-2-2) on the right side.)

d- E. mariae complex; syntype; 0116; ♀; 175 mm TL; 7 mm d; Khar'kov River, near Khar'kov, Ukrainian SSR. (Notice the discontinuous first posterial row made up of four cusps, three on the left side and one on the right side. Two of the three cusps on the left side are hard to discern. There are three endolaterals (2-2-2) on the left side and four (1-1-2-2) on the right side.)

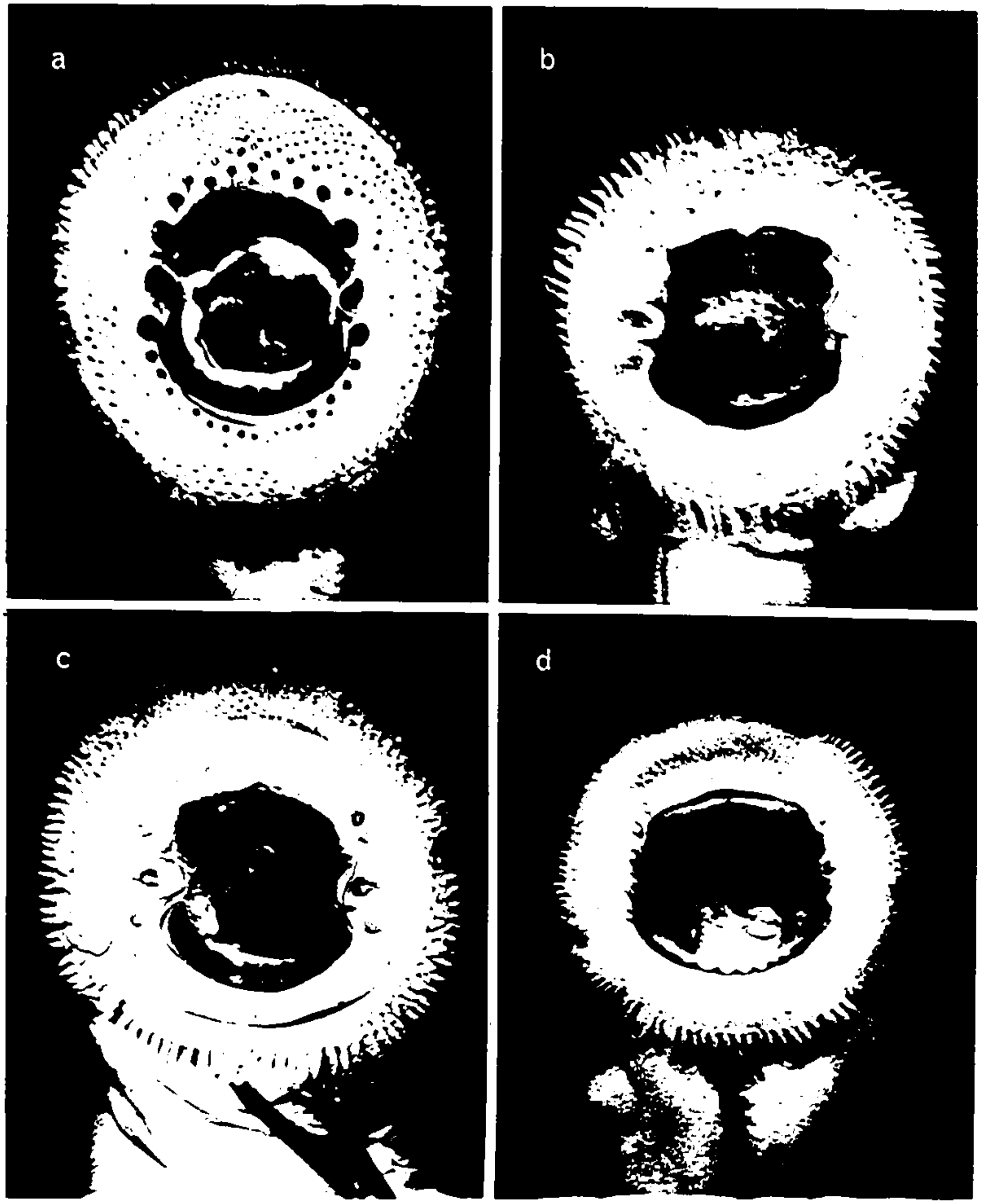
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Fig. 11. Photograph of oral discs.

a- Eudontomyzon mariae complex; Y841; ♀; 169.5 mm TL; 8 mm d; Jeziorka River, near Warsaw, Poland. (Notice the discontinuous first posterial row made up of two cusps, one on each side.)

b- E. morii; syntype; J(DPQ)1577; undetermined sex; 171 mm TL; 10.5 mm d; upper Yalu River, Ko-sui-in, People's Republic of China.

c- E. morii; 092; ♀; 196 mm TL; 13 mm d; upper Yalu River, near Changbai, People's Republic of China.

d- E. morii; 093; ♀; 211.5 mm TL; 14.5 mm d; upper Yalu River, near Changbai, People's Republic of China.

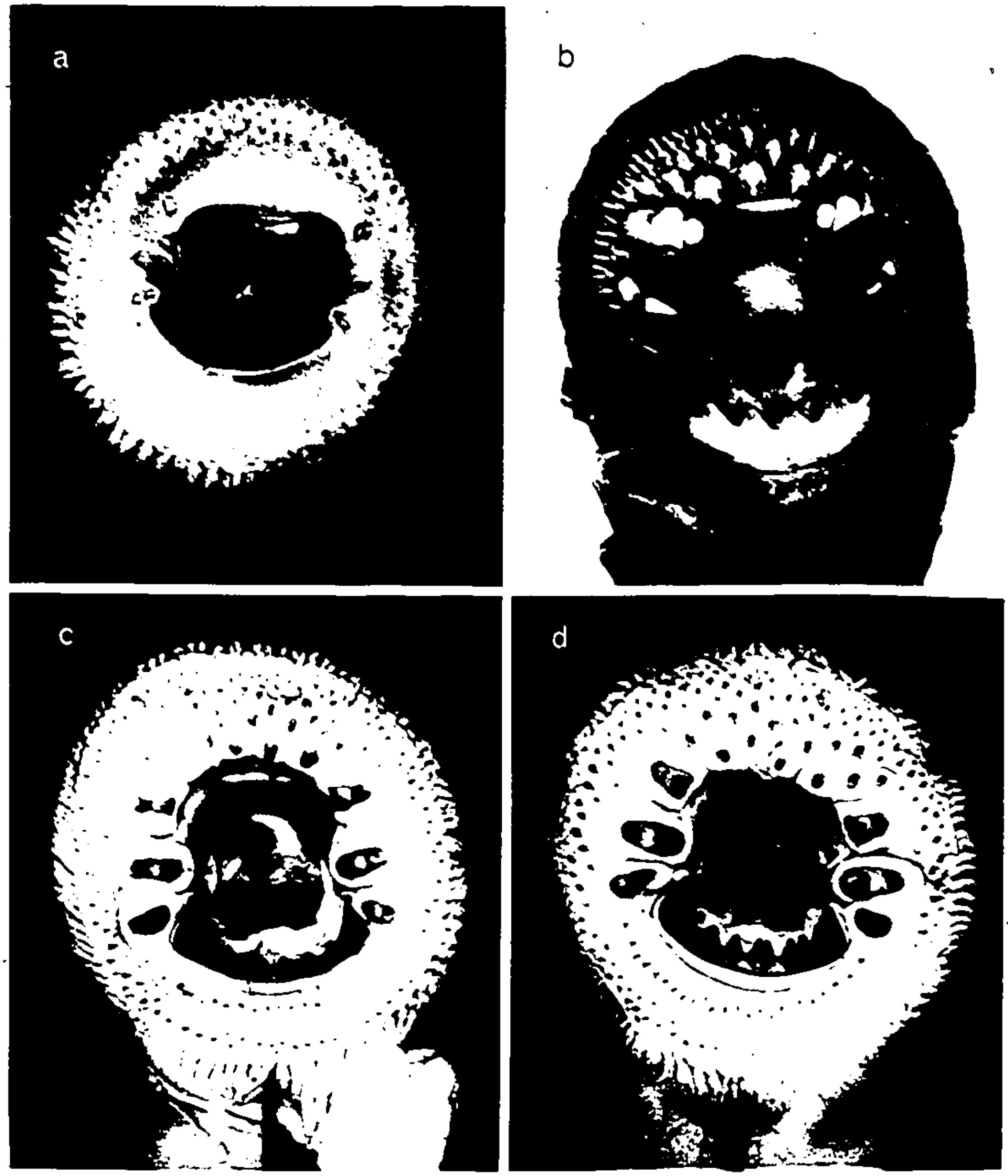
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Fig. 12. Photograph of oral discs.

a- Eudontomyzon hellenicum; holotype; Y744; ♂; 95.5 mm TL; 7 mm d; Kefalárion Brook, near Kefalárion, Greek Macedonia.

b- E. hellenicum; paratype; Y745; ♂; 100 mm TL; 5.5 mm d; Kefalárion Brook, near Kefalárion, Greek Macedonia.

c- E. hellenicum; paratype; Y747; ♂; 110 mm TL; 8 mm d; Kefalárion Brook, near Kefalárion, Greek Macedonia.

d- E. hellenicum; paratype; Y817; ♂; 130 mm TL; 7.5 mm d; Milopótamos Brook, near Dráma, Greek Macedonia.

e- E. hellenicum; paratype; Y779; ♀; 141 mm TL; 7.5 mm d; Filippiás Brook, near Filippiás, Ípiros, Greece.

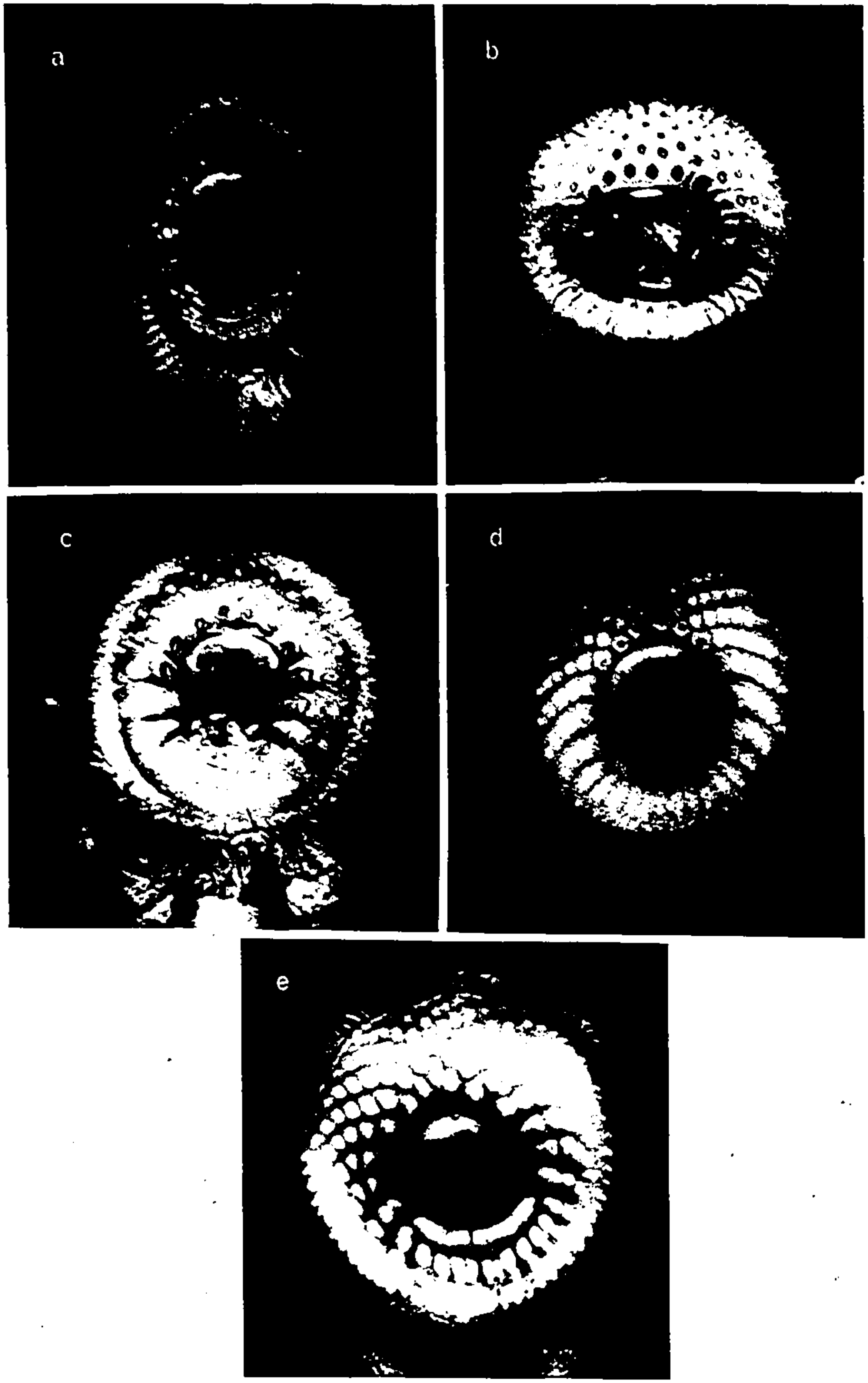
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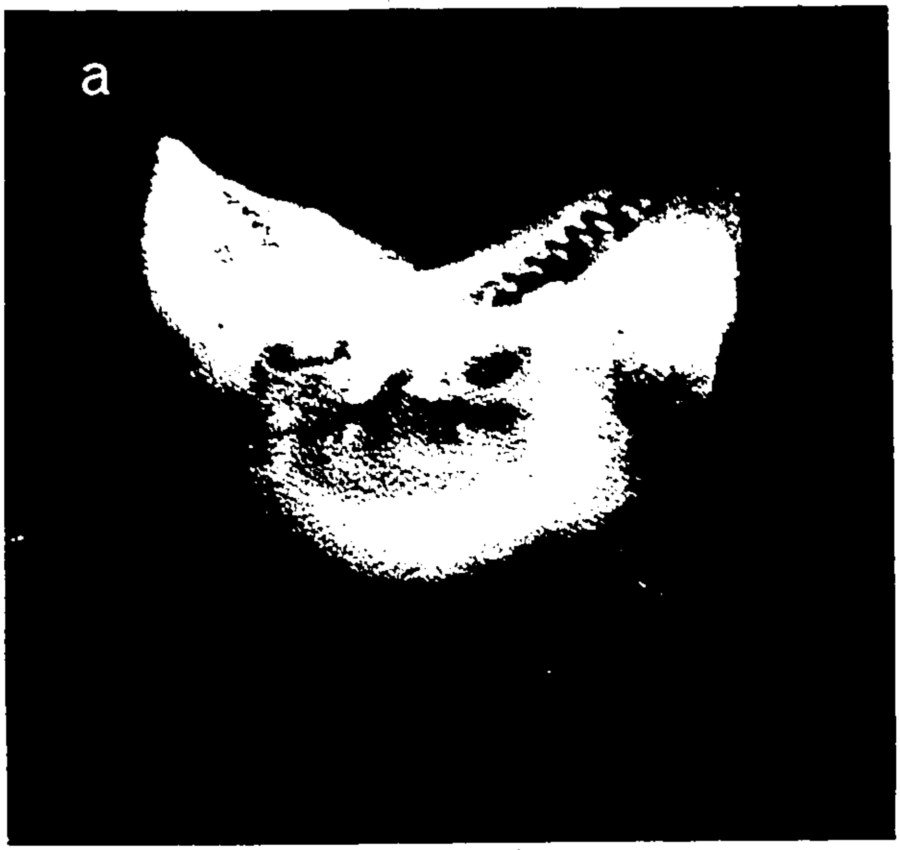
Fig. 13. Photograph of lingual laminae.

a- Eudontomyzon mariae complex; syntype; 0112; ♂; 171 mm TL; Khar'kov River, near Khar'kov, Ukrainian SSR.

b- E. morii; syntype; J(DPQ)1577; undetermined sex; 171 mm TL; upper Yalu River, Ko-sui-in, People's Republic of China.

a



b

Fig. 14. Photograph of side-view of the posterior part of adults.

a- Eudontomyzon danfordi; W(VDV)5817; ♀; 158 mm TL; Ulička Brook, Ulič, Slovakia. (Notice the spade-like caudal fin shape; dorsal fins far apart; urogenital papilla, not yet apparent. The precloacal intestine width is one mm. Although it is not apparent in this photograph, the caudal fin pigmentation is ++.)

b- E. mariae complex; B(DPQ)2922; ♂; 168.5 mm TL; Jeziorka River, near Warsaw, Poland. (Notice the spade-like caudal fin shape; +++ caudal fin pigmentation; downturned tail; contiguous dorsal fins; 5 mm urogenital papilla length. The precloacal intestine width is undetermined.)

c- E. mariae complex; Y841; ♀; 169.5 mm TL; Jeziorka River, near Warsaw, Poland. (Notice the spade-like caudal fin shape; +++ caudal fin pigmentation; upturned tail; contiguous dorsal fins; 2 mm urogenital papilla length; well developed anal fin-like fold. The precloacal intestine width is 0.5 mm.)

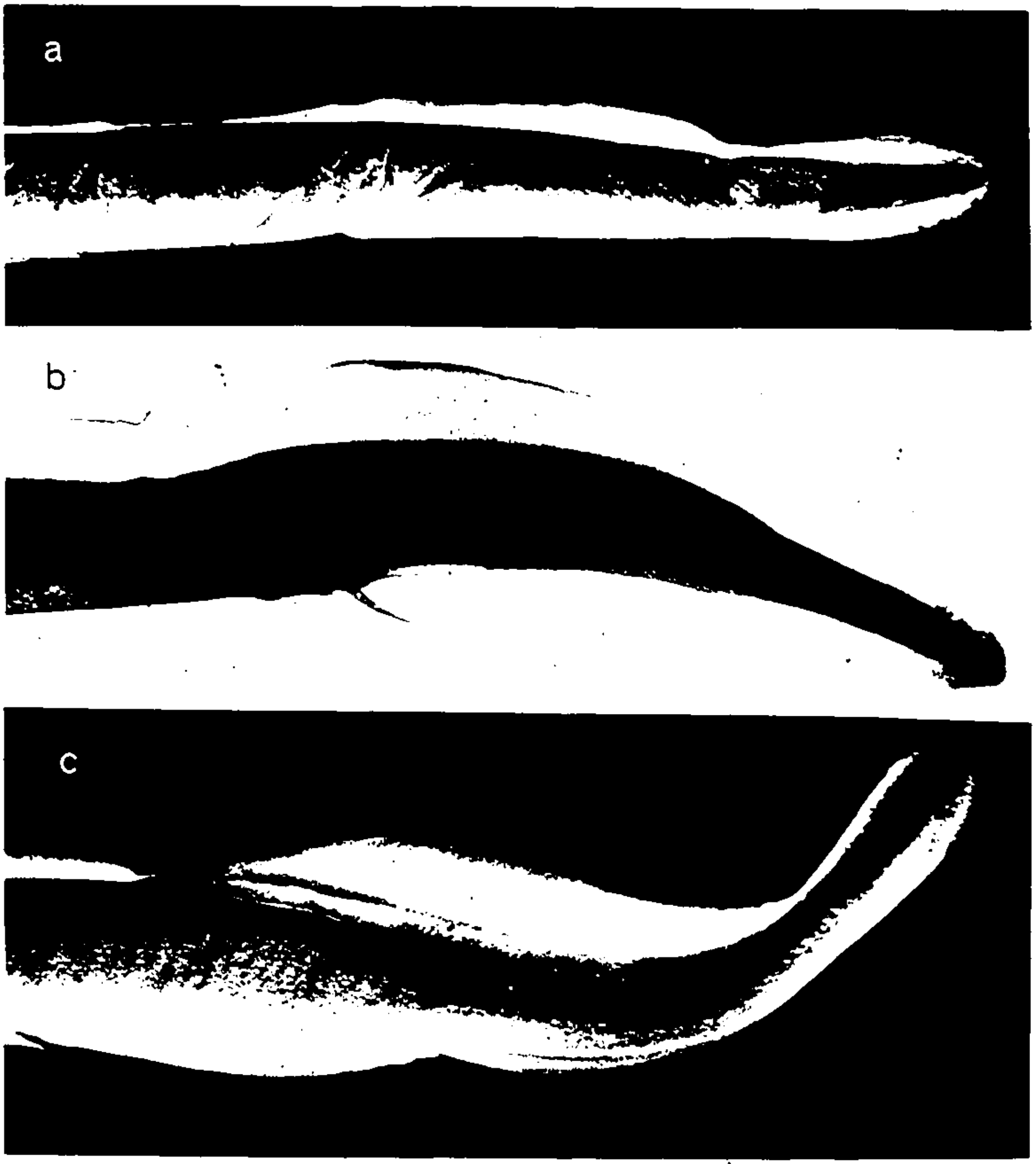

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Fig. 15. Photograph of side-view of the posterior part of adults.

a- Eudontomyzon morii; syntype; J(DPO)1577; undetermined sex; 171 mm TL; upper Yalu River, Ko-sui-in, People's Republic of China. (Notice the spade-like caudal fin shape; ++ caudal fin pigmentation; dorsal fins far apart; urogenital papilla, not yet apparent. The precloacal intestine width is undetermined.)

b- E. morii; 092; ♀; 196 mm TL; upper Yalu River, near Changbai, People's Republic of China. (The caudal fin is spade-like in shape, although, the slight folding upon themselves of the caudal fin edges make them appear sharper. The caudal fin pigmentation is +++. The dorsal fins are far apart, but, the interspace is further left, outside the range of this photograph. The urogenital papilla is not yet apparent and the precloacal intestine width is 3.5 mm.)

c- E. hellenicum; holotype; Y744; ♂; 95.5 mm TL; Kefalárion Brook, near Kefalárion, Greek Macedonia. (Notice the rounded caudal fin shape; +++ caudal fin pigmentation; contiguous dorsal fins; one mm urogenital papilla length. The precloacal intestine width is thread-like (<0.5 mm).)

d- E. hellenicum; paratype; Y586; ♀; 105 mm TL; Kefalárion Brook, near Kefalárion, Greek Macedonia. (Notice the rounded caudal fin shape; ++ caudal fin pigmentation; contiguous dorsal fins; one mm urogenital papilla length; well developed anal fin-like fold. The precloacal intestine width is thread-like (<0.5 mm).)

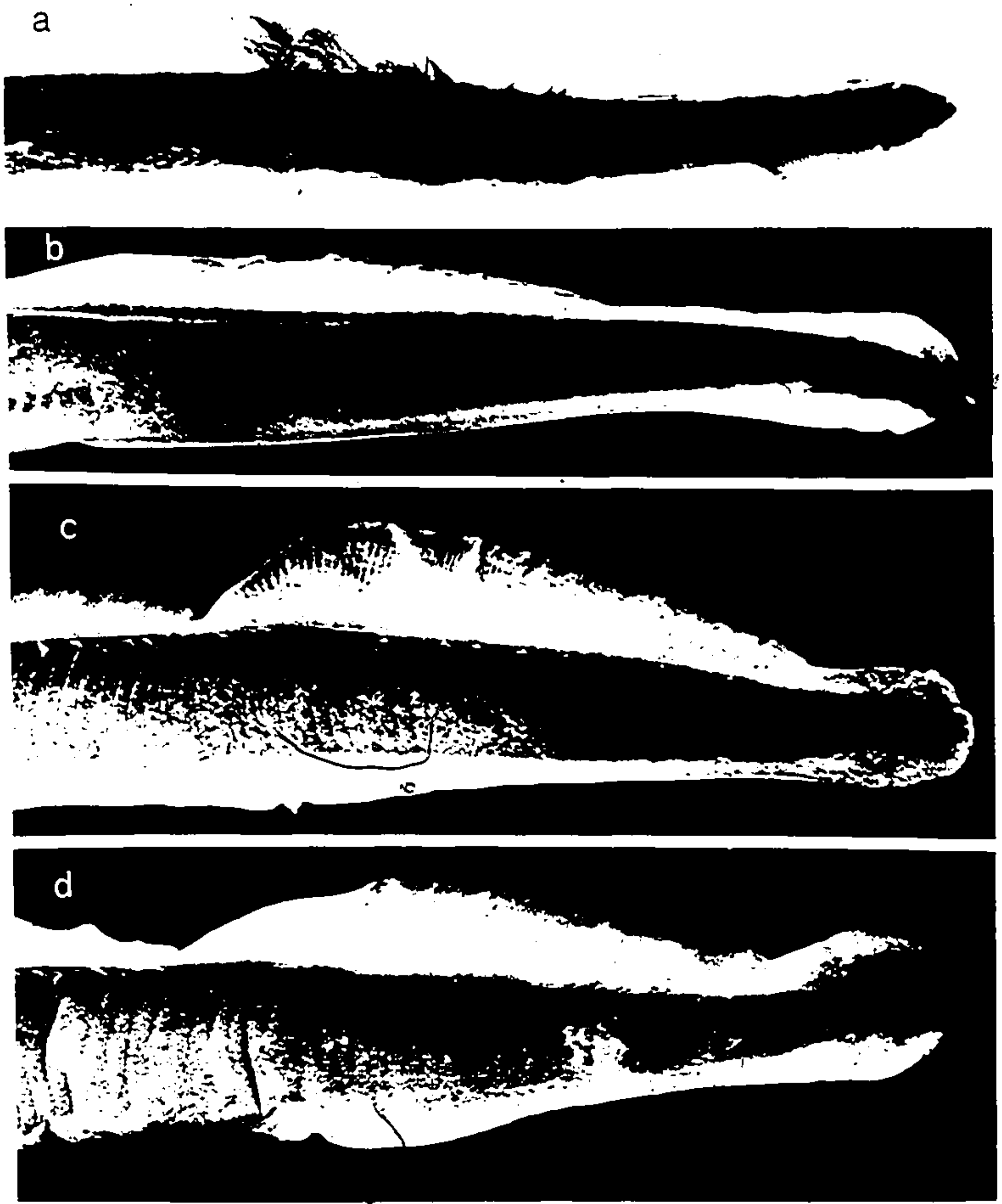
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Fig. 16. Photograph of side-view of the anterior part of ammocoetes.

a- *Eudontomyzon danfordi*; W(VDV)5812; 208 mm TL; Topl'a River, Lukov, Slovakia. (Notice the – upper lip pigmentation.)

b- *E. mariae* complex; Y830; 177 mm TL; Wilga River, Poland. (Notice the + upper lip pigmentation.)

c- *E. mariae* complex; W(VDV)5738; 205 mm TL; Biela Orava River, Slovakia. (Notice the – upper lip pigmentation.)

d- *E. hellenicum*; paratype; Y584; 131 mm TL; Kefalárion Brook, near Kefalárion, Greek Macadonia. (Notice the ++ upper lip pigmentation.)

e- *E. hellenicum*; paratype; Y582; 132.5 mm TL; Kefalárion Brook, near Kefalárion, Greek Macedonia. (Notice the ++ upper lip pigmentation.)

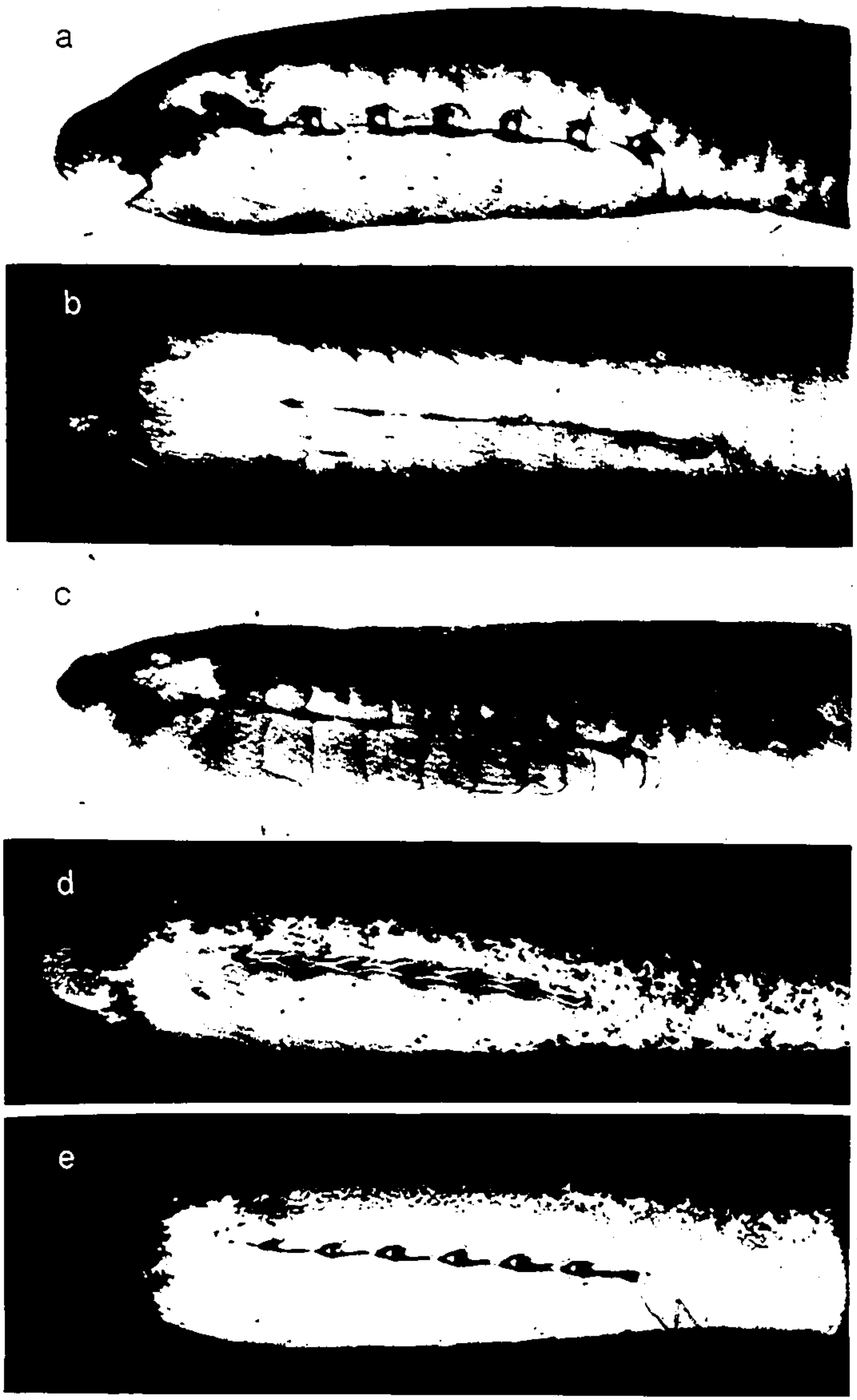
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Fig. 17. Photograph of side-view of the posterior part of ammocoetes.

a- Eudontomyzon danfordi; W(VDV)5812; 208 mm TL; Topl'a River, Lukov, Slovakia. (Notice the spade-like caudal fin shape and ++ caudal fin pigmentation.)

b- E. mariae complex; W(VDV)5751; 210 mm TL; Biela Orava River, Slovakia. (Notice the spade-like caudal fin shape and +++ caudal fin pigmentation.)

c- E. hellenicum; paratype; Y584; 131 mm TL; Kefalárion Brook, near Kefalárion, Greek Macedonia. (Notice the rounded caudal fin shape and ++ caudal fin pigmentation.)

d- E. hellenicum; paratype; W2311; 126 mm TL; Milopótamos Brook, near Dráma, Greek Macedonia. (Notice the rounded caudal fin shape and +++ caudal fin pigmentation.)

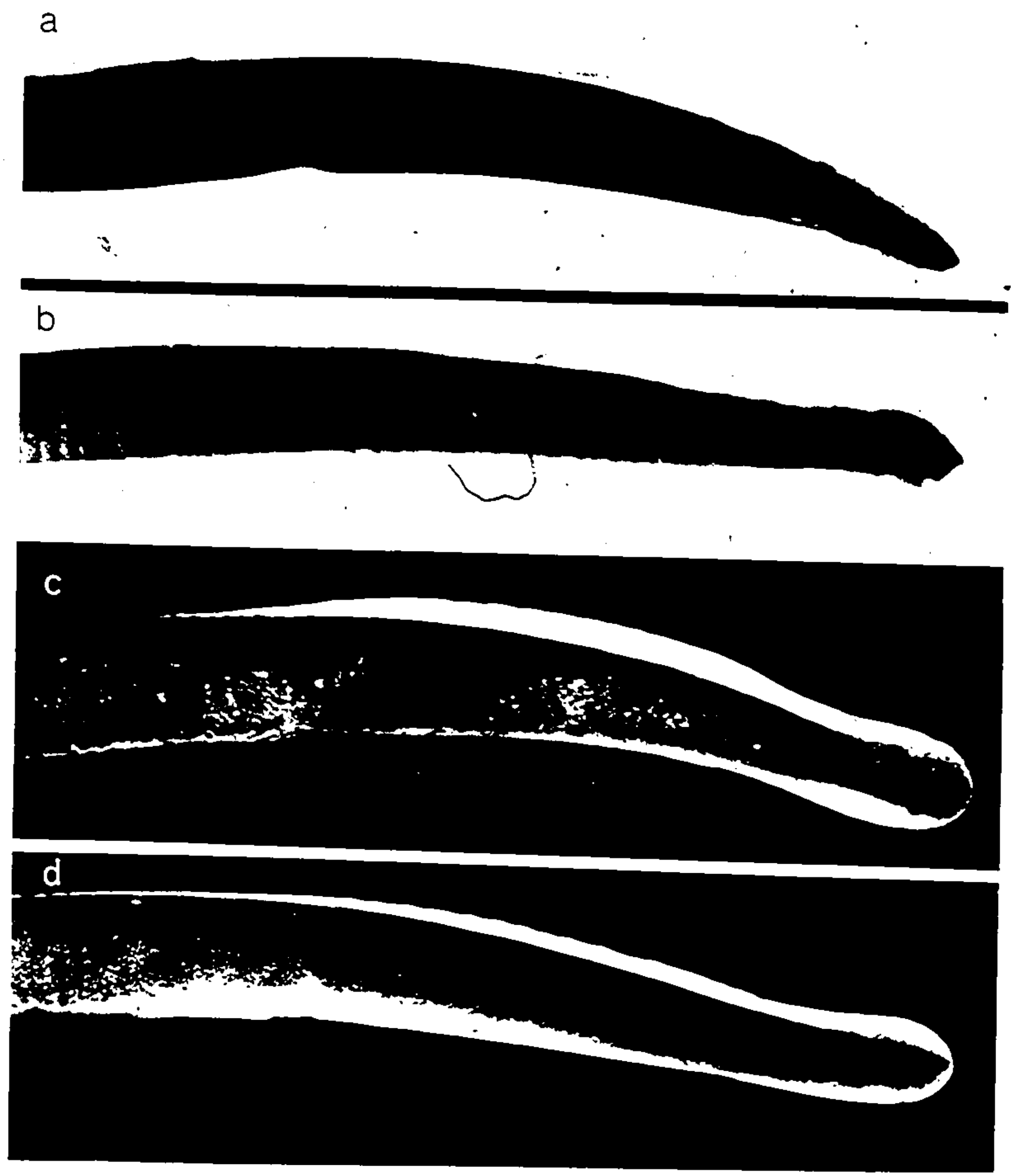
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Fig. 18. Photograph of ventral view of the head and branchial region of ammocoetes.

a- Eudontomyzon danfordi; W(VDV)5811; 204 mm TL; Topl'a River, Lukov, Slovakia. (Notice the + lower lip pigmentation and — ventral branchial region pigmentation.)

b- E. mariae complex; Y830; 177 mm TL; Wilga River, Poland. (Notice the + lower lip pigmentation and — ventral branchial region pigmentation.)

c- E. hellenicum; paratype; Y584; 131 mm TL; Kefalárion Brook, near Kefalárion, Greek Macedonia. (Notice the ++ lower lip pigmentation and + ventral branchial region pigmentation.)

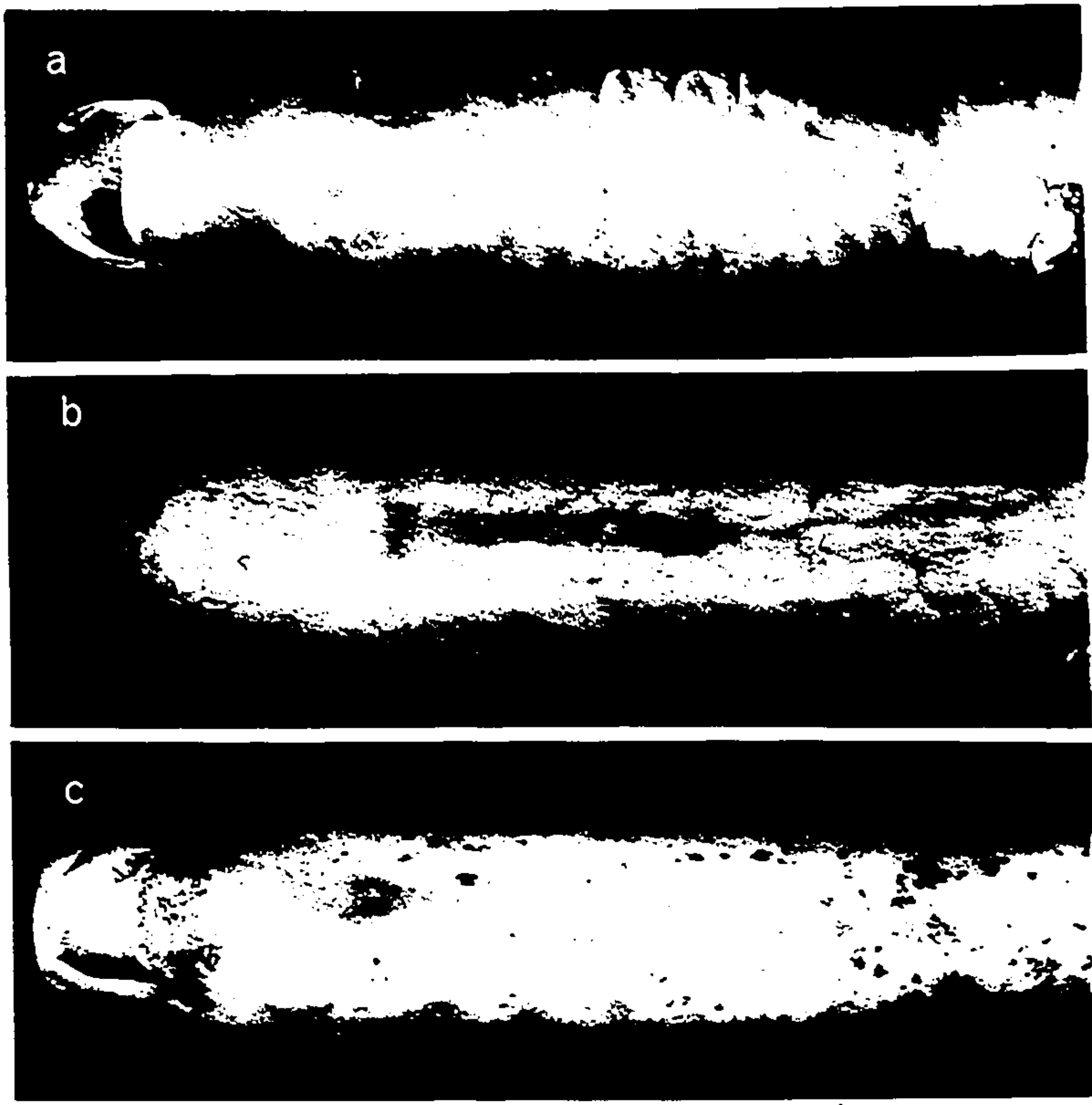
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Fig. 19. Photograph of dorsal view of tongue precursors (most of the lower lip and the two fleshy oral papilla-bearing appendages, lateral to the bulb, were removed).

a- Eudontomyzon danfordi; untagged; 139 mm TL; Tereblya River, Bushtyna, Subcarpathian Ukraine. (Notice the – bulb pigmentation and + pigmentation in the areas lateral to the elastic ridge.)

b- E. mariae complex; Y831; 175 mm TL; Wilga River, Poland. (Notice the – bulb pigmentation and + pigmentation in the areas lateral to the elastic ridge.)

c- E. mariae complex; W(VDV)5751; 210 mm TL; Biela Orava River, Slovakia. (Notice the – bulb pigmentation and – pigmentation in the areas lateral to the elastic ridge.)

d- E. mariae complex; W(VDV)5876; 207.5 mm TL; Lake Ohrid, Yugoslavia. (Notice the ++ bulb pigmentation and +++ pigmentation in the areas lateral to the elastic ridge.)

e- E. hellenicum; paratype; W825; 121.5 mm TL; Milopótamos Brook, near Dráma, Greek Macedonia. (Notice the + bulb pigmentation and +++ pigmentation in the areas lateral to the elastic ridge.)


a
b
c
d
e

Zoogeographical Considerations

The east-west palearctic discontinuity in the distribution of Eudontomyzon is also found in some fish species (Cyprinus carpio Linnaeus, Rhodeus sericeus (Pallas) and Misgurnus fossilis (Linnaeus)). This distribution is interpreted by Bănărescu (1969) to mean that Eudontomyzon originated in the intervening zone, namely Siberia, from where it dispersed to Europe and east Asia. It subsequently became extinct in Siberia due to glaciation, finding no refugium in that region. Bănărescu's interpretation gives credence to one of the hypotheses put forth by Berg (1931), that Eudontomyzon species are relicts. I suggest that only E. morii and E. hellenicum fit Berg's hypothesis, E. danfordi and E. mariae complex being too widespread to be called relict species.

According to this study, all Eudontomyzon species are allopatric. Oliva (1966) believes Lampetra (Eudontomyzon) mariae (= E. mariae complex) penetrated into the upper Vistula river basin (Baltic sea basin) from the Dnestr River (Black sea basin) in the post-glacial period when temporary connections were present. Zhukov (1968) believes Lampetra (E.) mariae (= E. mariae complex) penetrated into the upper Neman river basin (Baltic sea basin) from the Dnepr basin (Black sea basin) during a post-glacial period when a temporary connection was present. Karaman (1974) believes the nominal E. vladykovi stankokaramani (= E. mariae complex) immigrated to the Drin basin from the Danube basin when these two were temporarily connected. In the above three cases (Oliva, 1966; Zhukov, 1968; Karaman, 1974), a Black sea origin is hypothesized for E. mariae complex.

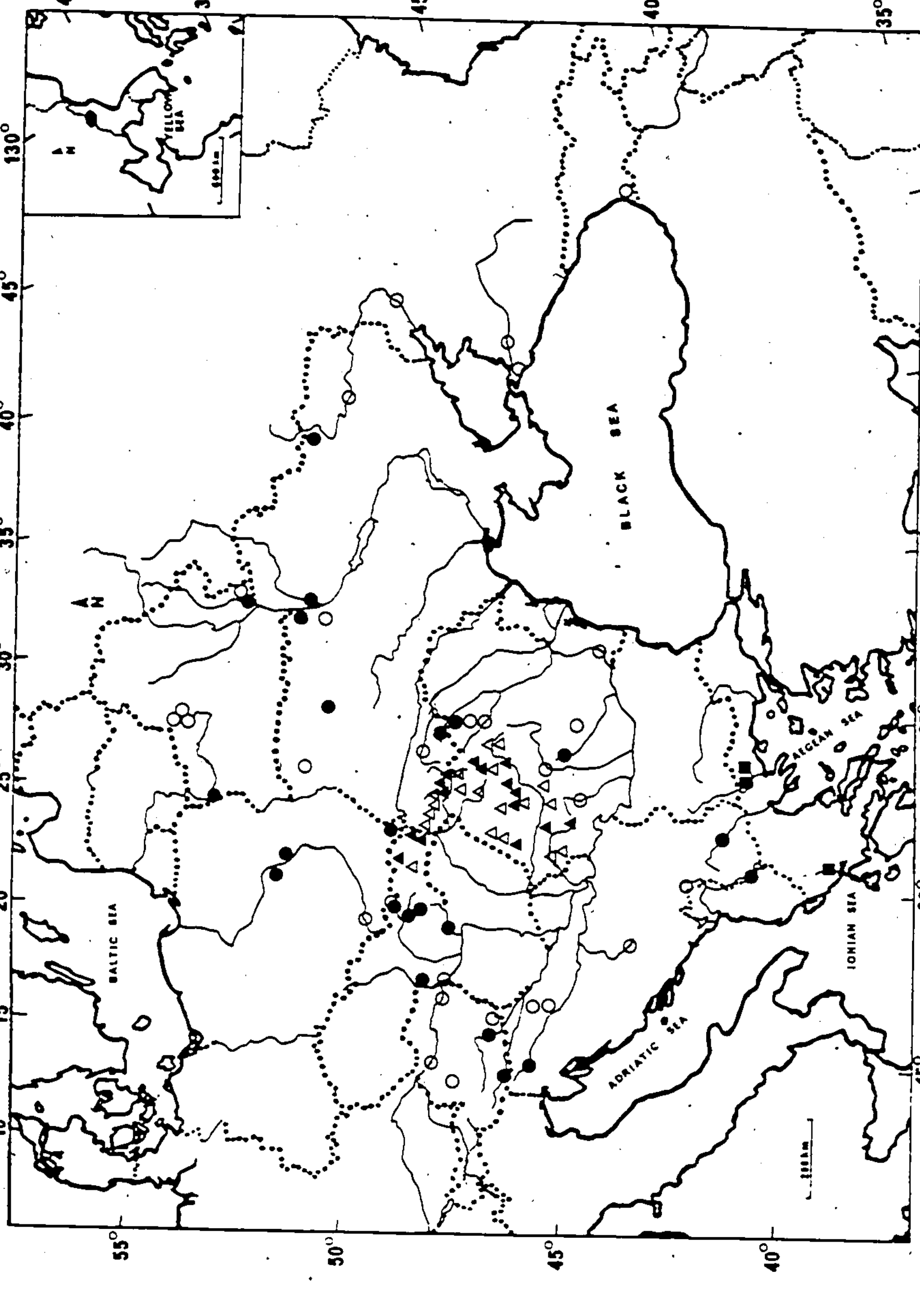
Fig. 20. Geographic distribution of the genus Eudontomyzon. Solid symbols represent material examined in this study and open symbols are literature records.

△ *E. danfordi*

● *E. mariae* complex

○ *E. morii*

□ *E. hellenicum*


BLACK SEA
BALTIC SEA
ADRIATIC SEA
AEGEAN SEA
IONIAN SEA
YELLOW SEA

A lamprey, *Petromyzon ftuviatis* (sic), was reported by Kovačev (1921) from the Maritsa River, Bulgaria, which drains into the Aegean Sea. It is difficult to make a statement regarding the identity of this lamprey, as no description accompanied its mention. However, it is not improbable (Berg, 1948), it may belong to the *Eudontomyzon* genus. This probability is reinforced by the presence of two *Eudontomyzon* species (*E. mariae* complex and *E. hellenicum*) in the Balkan Peninsula.

Aberrations

Out of 788 specimens looked at, on both sides of the body, for deviations from the normal branchial opening count (*E. danfordi*: 191a, 6ā, 64t; *E. mariae* complex: 174a, 5ā, 39t; *E. morii*: 4t; *E. hellenicum*: 235a, 4ā, 66t), only two of them, both *E. danfordi* adults (W(VDV)4031, Y425) had an aberrant six branchial openings on the left and the normal count of seven on the right side. Both specimens came from two collections made in the Bistra Mărului Brook, Banat, Rumania. This makes for an overall 0.25% incidence abnormality per specimen.

LITERATURE CITED

Abakumov, V.A. 1966. [Systematics and ecology of the Ukrainian lamprey, Lampetra mariae Berg.] Vop. Ikh. 6(4): 609-18. (in Russian).

Austria 1962. US Board on Geographic Names Gazetteer. Department of Interior, Washington. 391 p.

Bailey, R.M. 1980. Comments on the classification and nomenclature of lampreys - an alternative view. Can. J. Aquat. Sci. 37: 1626-9.

Balon, E.K. 1964a. Predbežný zoznam kruhoústych a rýb Slovenska (Petromyzones et Teleostomi). Bio. (Čas. Slov. Akad. Vied). 19(5): 343-58.

——— 1964b. Spis i ekologiczna charakterystyka słodkowodnych krągłoustych i ryb Polski. Pol. Arch. Hydr. 12(2): 233-51.

Balon, E.K. and J. Holčík 1964. [New for Poland lampreys and fishes from the Danube basin (Black Orava).] Frag. Faun. 11(13): 189-206. (in Polish).

Bănărescu, P. 1968. Lista revizuită a peştilor din România. Bul. Inst. Cerc. Proiec. Pisc. 27(3): 53-61.

——— 1969. Cyclostomata şi Chondrichthyes (ciclostomi şi selacieni). Fau. Rep. Soc. Rom. 12(1): 5-54.

Bănărescu, P., M. Blanc, J.-L. Gaudet and J.-C. Hureau 1971. European inland water fish. A multilingual catalogue.

Fishing News (Books) Ltd., London. 24 pages, 393 figs., XIX pages.

Bely, N. D. 1966. [Morphological and some biological peculiarities of Lampetra mariae Berg from the Dnepr River.] Zool. Zh. 45(4): 585-90. (in Russian).

Berg, L. S. 1906. Ubersicht der Marsipobranchii des russischen reiches. Izv. Akad. Nauk St. Petersburg. Series 5, 24(3): 169-83.

——— 1931. A review of the lampreys of the northern hemisphere. Ann. Mus. Zool. Acad. Sci. URSS. 32(1): 87-116 + 8 plates.

——— 1948. Freshwater fishes of the USSR and adjacent countries. Acad. Sci. USSR Zool. Inst., Guide to the Fauna of the USSR No. 27, Vol. 1, Leningrad. 504p. (transl. from Russian by Israel Program for Scientific Translations, Jerusalem, 1962).

Chappuis, P. A. 1939. Über die lebensweise von Eudontomyzon danfordi Regan. Arch. Hydrobio. 34: 645-58 + 1 plate.

Chung, M.-K. (ed.) 1961. [Illustrated encyclopedia, The fauna of Korea (2), Fishes.] Ministry of Education, Seoul. 861p. (in Korean).

Creaser, C.W. and C. L. Hubbs 1922. A revision of the holarctic lampreys. Occ. Pap. Mus. Zool. Univ. Mich. 120: 1-14 + 1 plate.

Czechoslovakia 1955. US Board on Geographic Names Gazetteer. Department of Interior, Washington. 879p.

Economidis, P.S. 1972. [Catalog of the fishes of Greece.] Hell. Oc. Limn. (Inst. Oc. Fish. Res.). 11: 421-599. (in Greek).

——— 1974. [Morphological, systematic and zoogeographical study of the freshwater fishes of east Macedonia and west Thrace, Greece.] Thessaloníki. 179p. + 1 folded map. (in Greek).

Elanidze, R., M. Demetrashvili, O. Burchuladze and B. Kurashvili 1970. [Atlas of the freshwater fish of Georgia.] "Metsniereba" Publ. House, Tbilisi. 115p. (in Georgian and Russian).

Greece 1960. US Board on Geographic Names Gazetteer. Department of Interior, Washington. 454p.

Grossu, A., V. Homei, P. Barbu and A. Popescu 1962. Contribution à l'étude des pétromyzonides de la République Populaire Roumaine. Trav. Mus. Hist. Nat. "G. Antipa". 3: 253-79.

Hankó, B. 1922. [Ernö Csiki állattani kutatasai Albániában. I. Halak.] Magyar Tudom. Akad. Balk. - Kutat. Tudom. Ered.: 1-6 + 1 plate. (in Hungarian).

Hardisty, M.W. 1971. Gonadogenesis, sex differentiation and gametogenesis. In The biology of lampreys. 1: 295-359. M.W. Hardisty and I. C. Potter (eds.). Acad. Press, New York.

Hardisty, M.W. and I.C. Potter 1971a. The behaviour, ecology and growth of larval lampreys. In The biology of lampreys. 1: 85-125. M. W. Hardisty and I. C. Potter (eds.). Acad. Press, New York.

——— 1971b. The general biology of adult lampreys. In The biology of lampreys. 1: 127-206. M. W. Hardisty and I. C. Potter (eds.). Acad. Press, New York.

——— 1971c. Paired species. In The biology of lampreys. 1: 249-77. M. W. Hardisty and I. C. Potter (eds.). Acad. Press, New york.

Holčík, J. 1963. Notes on the Czechoslovakian lampreys with redescription of Lampetra (Eudontomyzon) vladykovi (Oliva and Zanandrea, 1959). Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.). 27(1): 51-63.

——— 1966a. [The development and forming of the fishfauna in the Orava Valley Reservoir.] Biol. Prá. (Slov. Akad. Vied). 12(1): 1-75. (in Slovak).

——— 1966b. [Ichthyological investigation of the Carpathian mountains 4. The fishes of the River Hornád (east Slovakia) with regard to the valley reservoir building.] Biol. Prá. (Slov. Akad. Vied). 12(1): 76-116. (in Slovak).

——— 1970a. On the occurence of Lampetra planeri (Bloch, 1784) in the Poprad River (northern Slovakia) and notes to its taxonomy and ecology. Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.). 34(1): 22-32.

——— 1970b. A note on the number and variation of trunk myomeres in Lampetra planeri (Bloch, 1784) with regard to populations from the Poprad and Hornád river basins. Bio. (Čas. Slov. Akad. Vied). 25(2): 123-8.

——— 1970c. Discovery of the Brook lamprey, Lampetra planeri (Bloch, 1784), in the Hornád River (Danube basin, Czechoslovakia). Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.). 34(4): 304-8.

Holčík, J., V. Mišík, I. Bastl and A. Kirka 1965. [Ichthyological investigation of the Carpathian mountains. 3. Fishes of the Orava Valley Reservoir and its tributaries.] Ac. Rer. Natur. Mus. Nat. Slov. 11: 93-139. (in Slovak).

Holčík, J. and T. Nalbant 1974. Note on the occurrence of the Brook lamprey, Lampetra planeri (Bloch, 1784) (Cyclostomata) in Roumania. Věst. Čs. Spol. Zool. 38(2): 95-7.

Hubbs, C. L. and I. C. Potter 1971. Distribution, phylogeny and taxonomy. In The biology of lampreys. 1: 1-65. M. W. Hardisty and I. C. Potter (eds.). Acad. Press, New York.

Hubbs, C. L. and M. B. Trautman 1937. A revision of the lamprey genus Ichthyomyzon. Univ. Mich. Mus. Zool. Misc. Publ. 35: 7-109.

Johal, M. S. and O. Oliva 1980. Key characters of larvae of two European lamprey species (Cyclostomata). Věst. Čs. Spol. Zool. 44: 197-212.

Karaman, S. 1928. [A contribution to the ichthyology of Yugoslavia I.] Skop. Nauc. Drust. Glas. 6(2): 147-76. (in Serbo-Croat).

Karaman, M. S. 1974. Eudontomyzon vladykovi stankokaramani n. ssp., a new subspecies of lamprey from tributaries of the Ohrid-Drim-Skadar System in west Balkan peninsula. Fol. Balc. 3(5): 1-12.

Kokotshashwili, G. V. 1942. [To the question about the presence of the Ukraine lamprey, Lampetra mariae Berg, in the rivers of Georgia.] Trav. Univ. Staline Tbilissi 22: 85-9, 91. (in Russian).

Kott, E. 1974. A morphometric and meristic study of a population of the American brook lamprey, Lethenteron lamottei (LeSueur), from Ontario. Can. J. Zool. 52(8): 1047-55.

Kovačev, V.T. 1921. Opit za izučvane ikhtiologichnata fauna na Maritsa i neynite pritotsi. Bulg. Prirod. Driz. Trud. 9: 90-4.

Kux, Z. 1965. Lampetra gracilis, nový neparasitický druh mihule z východního Slovenska. Čas. Mor. Mus. (Acta Mus. Mor.)50: 293-302.

Ma, C.F. and C.L. Yu 1959. [Preliminary observations on L. morii.] Chin. J. Zool. 3(3): 115-7. (in Chinese).

Matsubara, K. 1963. [Fish morphology and hierarchy.] Part 1, Ishizaki-Shoten, Tokyo. 789p. (in Japanese).

Mori, T. 1952. Checklist of the fishes of Korea. Mem. Hyogo Univ. Agri. 1(3) Bio. Ser. 1: 1-228.

Oliva, O. 1953a. Příspěvek k přehledu našich mihulí (Petromyzones Berg, 1940). Věst. Král. Čes. Spol. Nauk, Tř. Mat.-Přírodověd. 9: 1-19 + 2 plates.

——— 1953b. Seznam kruhoústých a ryb v Československu. Sbor. ČSAZV. 26(1-2): 41-6.

——— 1960. [Some remarks on the geographical distribution and systematic position of cyclostomes and fishes of central Europe.] Przeg. Zool. 1959: 272-84. (in Polish).

——— 1962. Druhý seznam kruhoústých a ryb Československa. Nár. Muz. 1: 3-7.

——— 1966. Further note on Polish lampreys (Petromyzonidae). Věst Čs. Spol. Zool. (Acta Soc. Zool. Bohem.). 30(2): 142-5.

Oliva, O. and K. Hensel 1962. On the occurrence of the South russian lamprey, _Lampetra_ (_Eudontomyzon_) _mariae_ Berg, 1931, in the Vistula basin. Acta Univ. Carol. -Biol. 1: 99-104.

Oliva, O. and G. Zanandrea 1959. Posizione sistematica di una lampreda di Cilistovo (Cecoslovacchia). Doriana, Ann. Mus. Civ. Stor. Nat. "G. Doria" Suppl. 2(98): 1-5.

People's Republic of China 1979. US Board on Geographic Names Gazetteer. Department of Interior, Washington. 919p.

Poland 1955. US Board on Geographic Names Gazetteers. Department of Interior, Washington. Vol. 1, 613p.; Vol. 2, p. 615-1267.

Potter, I.C. 1980. The Petromyzoniformes with particular reference to paired species. Can. J. Fish. Aquat. Sci. 37: 1595-615.

Regan, C.T. 1911. A synopsis of the marsipobranchs of the order Hyperoartii. Ann. Mag. Nat. Hist. 7(8): 193-204.

Rembiszewski, J.M. 1967. [Contribution to the knowledge of the lampreys (Petromyzonidae) of the genus _Lampetra_ Gray in Poland. I. _Lampetra_ (_Eudontomyzon_) _mariae_

Berg.] Frag. Faun. 13(14): 249-59. (in Polish).

——— 1968. Observations on hybrids of Lampetra (Lampetra) planeri (Bloch, 1784) x Lampetra (Eudontomyzon) mariae Berg, 1931. Věst. Čs. Spol. Zool. (Acta Soc. Zool. Bohem.). 32(4): 390-3.

——— 1971. Minogi dorzecza Sanu i Strwiąża. Frag. Faun. 17(20): 545-57.

Rumania 1960. US Board on Geographic Names Gazetteer. Department of Interior, Washington. 450p.

Sterba, G. 1962. Die neunaugen (Petromyzonidae). In Handbuch der binnenfischerei Mitteleuropas 3 B: 263-352. R. Demoll and H.N. Maier (eds.). E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

USSR 1970. US Board on Geographic Names Gazetteers. Department of Interior, Washington. Vol.1 (A-B), 715p.; Vol. 2 (C-J), 797p.; Vol. 3 (K), 878p.; Vol. 4 (L-N), 897p.; Vol. 6 (S-T), 934p.; Vol. 7 (U-Z), 783p.

Vladykov, V.D. 1925. Über einige neue fische aus der Tschechoslowakei (Karpathorussland). Zool. Anz. 64(11): 248-52.

——— 1926. Ryby Podkarpatské Rusi. Uzhorod. 147p.

——— 1927a. [Common names of the fishes of Subcarpathian Russia.] Pros. 5: 205-32. (in Russian).

——— 1927b. Zur frage über das asterben unserer lampreten (Petromyzonidae) nach der laichzeit. Zool. Anz. 74(10): 237-9.

——— 1931. Poissons de la Russie sous-carpathique

(Tchécoslovaquie). Mém. Soc. Zool. France 29(4): 217-374.

——— 1949. Québec lampreys (Petromyzonidae) I. List of species and their economical importance. Dept. Fish. Prov. Qué. 26: 7-67.

——— 1950. Larvae of eastern American lampreys (Petromyzonidae) I. - Species with two dorsal fins. Nat. Can. 77(3-4): 73-95.

——— 1955. Lampetra zanandreai, a new species of lamprey from northern Italy. Copeia (3): 215-23.

——— 1960. Description of young ammocoetes belonging to two species of lampreys: Petromyzon marinus and Entosphenus lamottenii. J. Fish. Res. Bd. Can. 17(2): 267-88.

Vladykov, V.D. and W.I. Follett 1958. Redescription of Lampetra ayresii (Günther) of western North America, a species of lamprey (Petromyzontidae) distinct from Lampetra fluviatilis (Linnaeus) of Europe. J. Fish. Res. Bd. Can. 15(1): 47-77.

——— 1967. The teeth of lampreys (Petromyzonidae): Their terminology and use in a key to the holarctic genera. J. Fish. Res. Bd. Can. 24(5): 1067-75.

Vladykov, V.D. and E. Kott 1976a. Is Okkelbergia Creaser and Hubbs, 1922 (Petromyzonidae) a distinct taxon? Can. J. Zool. 54(3): 421-5.

——— 1976b. Tentative list of holarctic lampreys (Petromyzonidae) and their broad distribution. Wilfrid

Laurier Univ. Mus. Zool. Contrib. 1: 1-6.

——— 1976c. The taxonomic significance of velar tentacles in holarctic lampreys (Petromyzonidae). Rev. Trav. Inst. Pêches Marit. 40(3-4): 787-9.

——— 1978. A new nonparasitic species of the holarctic lamprey genus Lethenteron Creaser and Hubbs, 1922, (Petromyzonidae) from northwestern North America with notes of other species of the same genus. Biol. Pap. Univ. Alaska. 19: 1-74.

——— 1979a. Satellite species among the holarctic lampreys (Petromyzonidae). Can. J. Zool. 57(4): 860-7.

——— 1979b. List of northern hemisphere lampreys (Petromyzonidae) and their distribution. Dept. Fish. Oc., Misc. Spec. Publ. 42: 1-30.

Vladykov, V.D., E. Kott and S. Pharand-Coad 1975. A new nonparasitc species of lamprey, genus Lethenteron (Petromyzonidae), from eastern tributaries of the Gulf of Mexico, USA. Nat. Mus. Nat. Sci. (Ottawa) Publ. Zool. 12: 4-36.

Vladykov, V.D., C.B. Renaud, E. Kott and P.S. Economidis 1982. MS. A new nonparasitic species of holarctic lamprey, genus Eudontomyzon Regan, 1911 (Petromyzontidae) from Greece.

Wajgel, L. 1884. Die zusammenziehung der zwei arten von Petromyzon (P. planeri und P. fluviatilis) in eine. Verh. Zool. Bot. Ges. 33(1883): 311-20.

Yugoslavia 1961. US Board on Geographic Names Gazetteer Department of Interior, Washington, 495p.

Zanandrea, G. 1956a. Appunti sulle lamprede dell'Austria. Boll. Zool. 23(2): 439-47.

——— 1956b. Le lamprede del Danubio: Considerazioni e confronti. Boll. Pes. Pisc. Idro. 11(2): 264-80.

——— 1959a. Lamprede parassite e non parassite nel bacino del Danubio e la nuova entità sistematica Eudontomyzon danfordi vladykovi. Arch. Zool. Ital. 44: 215-50 + 2 plates.

——— 1959b. Speciation among lampreys. Nature 184: 380.

——— 1961. Studies on European lampreys. Evol. 15: 523-34.

——— 1962. Lamprede in Europa. Ric. Sci. 2(8): 710-23.

Zhukov, P.I. 1968. [The routes of penetration of ponto-caspian ichthyofauna into the rivers of the Baltic sea basin.] Zool. Zhur. 47(9): 1417-9. (in Russian)

——— 1969. New data on the biology of freshwater lampreys in White Russia. Prob. Ich. 9(2): 181-6. (translation of Vop. Ikh. 9(2): 240-6. (in Russian)).