Journal of Natural History
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713192031

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To cite this Article: K. Iliadou, J. Sourdis, P. S. Economidis and A. Wheeler , 'Morphological differentiation among species of the genus Scardinius (Pisces: Cyprinidae) in Greece', Journal of Natural History, 30:3, 459 - 473
To link to this article: DOI: 10.1080/00222939600770241
URL: http://dx.doi.org/10.1080/00222939600770241

JOURNAL OF NATURAL HISTORY, 1996, **30**, 459–473

Morphological differentiation among species of the genus *Scardinius* (Pisces: Cyprinidae) in Greece

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(*Accepted 7 December 1994*)

The systematics of the species *Scardinius erythrophthalmus*, *Scardinius graecus* and *Scardinius acarnanicus* in Greece has been studied. Descriptive statistics were computed and Phylogenetic, Principal Component and Gabriel graph analyses were applied in order to establish the differentiation of these three taxa. The geographical distribution of these taxa in Greece, their derivation and their development in particular areas as well as their relations are discussed.

KEYWORDS: *Scardinius*, freshwater, Pisces, differentiation, morphometric analysis, Greece.

Introduction

The cyprinid genus *Scardinius* Bonaparte, 1837 is widely distributed in western, central and eastern Europe as well as in western Asia from Asia Minor to the Aral Sea (Berg, 1949; Ladiges and Vogt, 1965). Members of the genus are found in the north and central regions of Greece but not in the south (Peloponnesus).

We consider that the genus *Scardinius* in Greece is represented by three species: the European species *Scardinius erythrophthalmus* (Linnaeus, 1758) and two endemic species: *Scardinius graecus* Stephanidis, 1937 and *Scardinius acarnanicus* Stephanidis, 1939 (Economidis, 1991). There are only a few studies dealing with the systematics of these three taxa but these are based on characters derived from samples of only a few individuals (Koller, 1927; Stephanidis, 1937, 1939a, b; Schmidt-Ries, 1943; Economidis, 1974). There are no recent works on the issue except for the check-list of Economidis (1991) and a review of the taxa referred to as *Scardinius* which is in preparation by three of the present authors.

The populations of these species are distributed in three biogeographical areas and are genetically isolated by land barriers. The populations of *Scardinius erythrophthalmus* occur in Thrace, Macedonia and Thessaly. The populations of *Scardinius graceus* exist only in Boeotia in the eastern–central part of Greece, whereas the populations of *Scardinius acarnanicus* live in Etoloacarnania in the western–central part of Greece (Fig. 1).

The main goal of the present work is to confirm the existence of three species of the genus *Scardinius* in Greece, and to elucidate their morphological differentiation within the genus.

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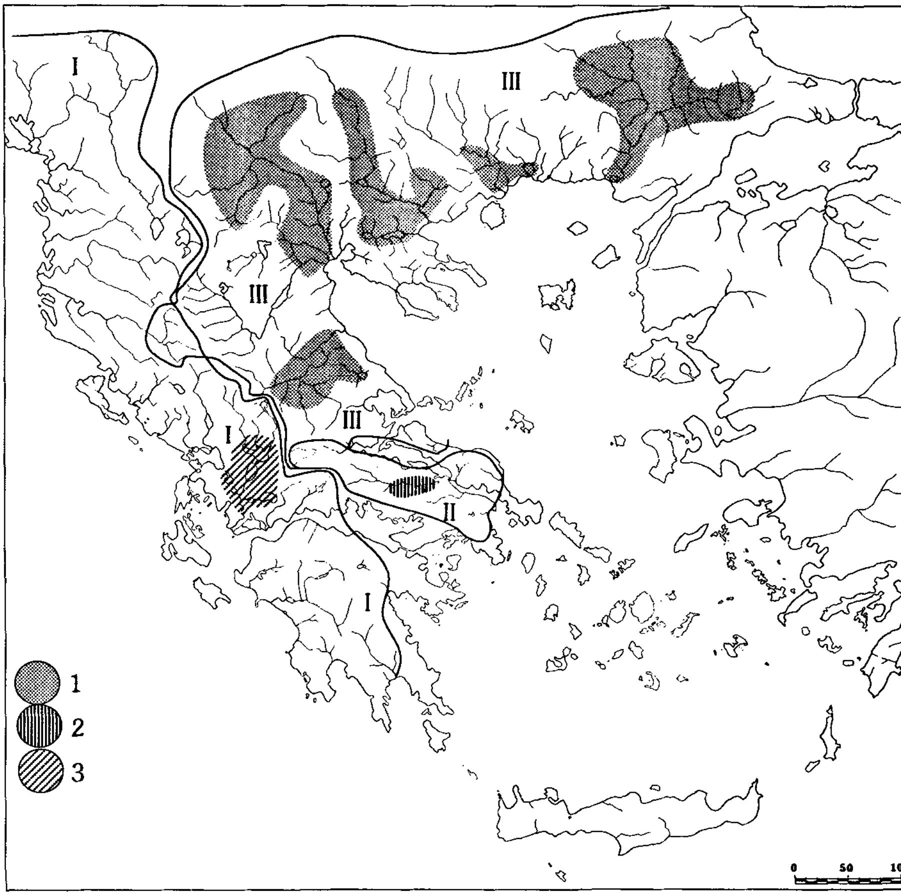

1, *Scardinius erythrophthalmus*; 2, *Sc.* graecus; 3, *Sc. acarnanicus*.
I, South Adriatic–Ionian Division; II, Attico–Boeotia Division; III, Ponto–Aegean Division
(after Economidis and Banarescu, 1991)

FIG. 1. Distribution of the species of the genus *Scardinius* in Greece.

Taxonomic note

The species *S. erythrophthalmus* is widely distributed in Europe ranging from England to the Aral Sea (Berg, 1949; Economidis, 1974). The endemic species *S. graecus* was originally described in 1937 by Stephanidis from the lakes Yliki and Paralimni and there has been no further discussion of its taxonomy. The first report of the presence of a third taxon (later to be recognized as *Scardinius acarnanicus*) in the waters of western-central Greece, was made by Koller (1927) on the basis of four specimens from the River Aspropotamos (= Acheloos) and five specimens from Lake Angelocastro (= Lysimachia), deposited in the collections of the Natural History Museum of Vienna. These specimens were classified by Koller (1927) as *Scardinius scardafa* Bon. *plotizza* Heck. Some years later Berg (1932) changed the nomenclature of this population to *Scardinius erythrophthalmus scardafa* (Bonaparte, 1832). Meanwhile, Stephanidis (1939a) looking at new material collected in the same drainage, noted some characteristic differences in the body proportions and in the colour of fins, which are not red but dark grey. Based on these features, Stephanidis named the population as *Scardinius scardafa plotizza* forma acarnanicus nov. forma. Due in part to the fact that the paper by Stephanidis (1939a) was written in Greek, little attention was given to it by taxonomists. This is the main reason for the broad acceptance of the nomenclature given by Berg and its wide use (Ladiges and Vogt, 1965, 1979; Ondrias, 1971; Economidis, 1973; Iliadou and Ondrias, 1980).

However, the comparison of recently collected material with preserved specimens from natural history museums, mainly those of London, Vienna and Paris has shown that the forma acarnanicus described by Stephanidis (1939a) must be elevated to full species rank, as a second endemic species *Scardinius acarnanicus* Stephanidis, 1939 (Economidis, 1991).

Materials and methods

Sampling

Three samples were collected by means of seine, trammel and set gill nets from three different sites of Greece from 1986 to 1989. The first sample consisted of 81 individuals of *S. erythrophthalmus* and came from Lake Koronia in northern Greece (Macedonia). The second sample of 191 fishes of *S. graecus* was from Lake Yliki in eastern–central Greece (Boeotia) and the third sample of 89 specimens of *S. acarnanicus* was collected from Lakes Lysimachia and Trichonis in western–central Greece (Etoloacarnania).

Study areas

Lake Koronia is located in the Lagada basin in north Greece and is connected to the adjacent Lake Volvi by a canal. Water flows from Lake Koronia into Lake Volvi which has a lower water level, and then flows into Strymonikos Gulf through a small river (Fig. 2).

Lake Yliki is in the Kopais basin and with adjacent Lake Paralimni form the remains of a much larger lake which has partly dried out. Recently its water has been directed to supply the artificial Lake Marathon which is part of the water supply system of Athens (Fig. 2).

Lakes Lysimachia and Trichonis are in the western–central part of Greece in the region called Etoloacarnania. These natural lakes belong to the Acheloos River system. Water exits from lake Trichonis at the western end through an artificial canal that connects the lakes. The water of lake Lysimachia reaches the Acheloos River through another artificial canal at the western end of the lake (Fig. 2).

Laboratory work

Measurements. All fish, except juveniles, were measured and weighed. A detailed morphological study of each individual including a set of 42 morphometric and meristic characters was made. Vertebral counts included the four vertebrae of the Weberian complex but excluded the urostyle. The last branched (soft) ray of the dorsal and anal fins was counted as two. Morphometric characters of each individual were measured to 0·1 mm with calipers and were expressed as a percentage of standard length, head length or other body measurement.

Data analysis. Simple descriptive statistics, e.g. the mean ($\bar{x}$), standard error ($S\bar{x}$), standard deviation (S) and coefficient of variation (C.V.) were computed for each of the three samples.

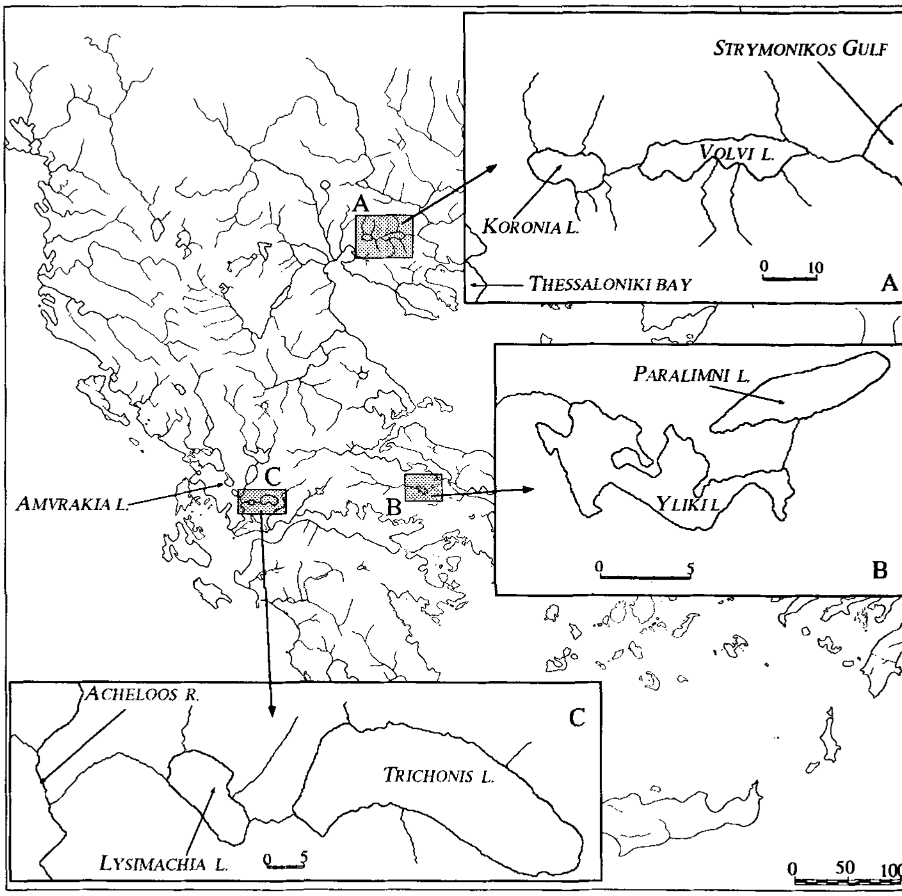

FIG. 2. Sampling areas in Greece.

In order to elucidate the differentiation of the species, the three following methods were applied:

(a) Phylogenetic Analysis. The UPGMA method using the Mahalanobis distance (Mahalanobis, 1936; Balakrishnan and Sanghvi, 1968) was applied. The Mahalanobis distance was estimated by means of 21 characters for which no missing values occurred in all individuals among the three samples.

Furthermore the differentiation of the three species were studied including a sample of *S. erythrophthalmus* from Poland (Klimczyk-Janikowska, 1975). Only the mean values of 16 characters for this sample were available, so the use of Mahalanobis distance was not possible. For this reason, another distance, suitable for mean values of characters, was applied. This distance is a modification of the D_2 distance (Krimbas and Sourdis, 1987) and is defined as:

$$D_2(a, b) = (1/n) \sum_{i=1}^{n} (|a(i) - b(i)|/\Delta(i))$$

where $a(i)$ and $b(i)$ are the mean values of the i character in samples a and b, $\Delta(i)$ is the difference between the maximum and minimum values of the character i among all samples, and n is the number of characters.

(b) Principal Component Analysis. By this analysis the *n* original character values are transformed into a set of *n* variables (principal components). The dispersion or differentiation of species is supposed to be depicted in the space of two or three transformed variables (Piazza *et al.*, 1981).

(c) Gabriel Graphs. By this method the samples are represented in a two dimensional space and are connected according to their distance interrelations: two samples A and B are connected if the following inequality holds for every third sample C

$$d^2_{AB} < d^2_{AC} + d^2_{CB}$$

(Matula and Sokal, 1980). As distance the D_2 was used.

Results

The descriptive statistics of all characters studied are presented in Tables 1 and 2, whereas Tables 3 and 4 illustrate the morphological differences between the species on the base of *t*-test.

As is obvious from Tables 3 and 4, 40 of 51 morphological features (78%) from comparison (I) of populations of *S. acarnanicus* and *S. erythrophthalmus*, 35 of 51 morphological features (69%) from comparison (II) of populations of *S. acarnanicus* and *S. graecus* and 41 of 51 morphological features (80%) from comparison (III) of populations of *S. graecus* and *S. erythrophthalmus* show that the species differ significantly.

In Tables 1–4 it appears that:

(a) for comparison (I), 13 of 40 (33%) features are as body proportions greater in *S. acarnanicus* than in *S. erythrophthalmus*. These features are the preorbital distance, post-orbital distance, head length, preventral distance, preanal distance, distance P-V, distance V-A, diameter of eye, branched rays of pectoral fin, scales of lateral line and gill rakers.

(b) for comparison (II), 18 of 35 (51%) features are as body proportions greater in *S. acarnanicus* than in *S. graecus*. These features are the interorbital width, head depth, max. body depth, minimum body depth, predorsal distance, preventral distance, distance P-V, distance V-A, length of dorsal fin base, length of pectoral fin, length of ventral fin, preorbital distance, diameter of eye, post-orbital distance, interorbital width and head depth.

(c) for comparison (III), 14 of 41 (34%) features are as body proportions greater in *S. graecus* than in *S. erythrophthalmus*. These features are the preorbital distance, post-orbital distance, head length, post-dorsal distance, caudal peduncle length, preventral distance, minimum body depth, diameter of eye, branched rays of pectoral fin, scales of lateral line and gill rakers.

In Fig. 3 (*a*) the differentiation of the three samples is depicted by a UPGMA dendrogram using the Mahalanobis distance on 21 morphometric and meristic characters with no missing values. A second dendrogram of the three samples is shown in Fig. 3 (*b*). This dendrogram was inferred by means of D_2 distance on the mean values of the total set of characters studied (excluding some of them, such as sex and weight). A third dendrogram is depicted in Fig. 3 (*c*). In this case only 16 morphometric characters were used. This dendrogram was evaluated as a test of the reliability of the dendrogram of Fig. 3 (*d*) where only these 16 characters for the Polish sample were available.

Table 1. Morphometric characters of the three species of the genus *Scardinius* in Greece.

Characters	*S. acarnanicus* Lakes Lysimachia and Trichonis				
	n	x̄ ± Sx̄	s	C.V.	Range
1. Total length	89	229·01 ± 3·12	29·42	12·85	193·00–328·00
2. Standard length	89	189·88 ± 2·73	25·78	13·58	157·00–277·00
% of standard length					
3. Preorbital distance	89	7·71 ± 0·04	0·36	4·63	6·79–8·76
4. Diameter of eye	89	6·57 ± 0·06	0·59	8·91	4·98–7·53
5. Post-orbital distance	89	12·96 ± 0·05	0·44	3·39	12·02–14·03
6. Interorbital width	89	7·59 ± 0·03	0·32	4·25	6·78–8·30
7. Head depth	89	19·10 ± 0·07	0·69	3·64	17·73–21·35
8. Head length	89	25·76 ± 0·08	0·78	3·03	23·77–28·41
9. Max. body depth	89	29·84 ± 0·16	1·47	4·94	26·65–33·32
10. Min. body depth	89	10·32 ± 0·04	0·37	3·57	9·59–11·27
11. Predorsal distance	89	56·42 ± 0·12	1·13	1·99	54·00–59·60
12. Post-dorsal distance	89	32·98 ± 0·09	0·82	2·48	30·60–34·60
13. Caudal peduncle length	89	18·92 ± 0·10	0·94	4·95	16·42–22·73
14. Preventral distance	89	52·84 ± 0·11	1·06	2·00	50·17–55·18
15. Preanal distance	89	75·62 ± 0·15	1·44	1·90	72·29–78·60
16. Distance P-V	89	28·55 ± 0·12	1·17	4·08	25·71–31·65
17. Distance V-A	89	27·70 ± 0·19	1·77	6·38	23·03–31·46
18. Height of dorsal fin	89	16·37 ± 0·11	1·00	6·09	13·74–18·90
19. Length of dorsal fin base	88	10·84 ± 0·05	0·49	4·48	8·91–12·00
20. Height of anal fin	89	13·54 ± 0·08	0·72	5·32	11·23–15·00
21. Length of anal fin base	89	10·11 ± 0·06	0·59	5·88	8·70–11·53
22. Length of pectoral fin	88	20·53 ± 0·11	1·06	5·18	16·58–22·99
23. Length of ventral fin	89	16·78 ± 0·10	0·93	5·55	13·82–21·12
% of head length					
24. Preorbital distance	89	29·95 ± 0·13	1·19	3·96	27·27–33·73
25. Diameter of eye	89	25·52 ± 0·22	2·12	8·32	20·56–29·40
26. Post-orbital distance	89	50·33 ± 0·16	1·47	2·91	47·62–54·44
27. Interorbital width	89	29·50 ± 0·16	1·54	5·22	26·00–34·92
28. Head depth	89	74·20 ± 0·34	3·20	4·31	67·96–86·31
% of max. body depth					
29. Min. body depth	89	34·66 ± 0·20	1·86	5·38	30·91–40·18
% of caudal peduncle length					
30. Min. body depth	89	54·71 ± 0·37	3·50	6·39	44·80–65·71
% of preorbital distance					
31. Diameter of eye	89	85·44 ± 0·93	8·79	10·29	64·21–107·14
% of post-orbital distance					
32. Diameter of eye	89	50·80 ± 0·54	5·07	9·98	38·33–60·10
% of interorbital width					
33. Diameter of eye	89	86·89 ± 1·04	9·85	11·34	61·88–108·33
% of distance P-V					
34. Length of pectoral fin	88	72·06 ± 0·56	5·24	7·27	59·28–85·27
% of distance V-A					
35. Length of ventral fin	89	60·88 ± 0·61	5·71	9·39	45·32–80·12
% of preanal distance					
36. Predorsal distance	89	74·62 ± 0·19	1·75	2·34	70·80–79·84
37. Preventral distance	89	69·88 ± 0·14	1·29	1·84	67·10–72·96
% of post-dorsal distance					
38. Caudal peduncle length	89	57·37 ± 0·27	2·53	4·41	50·91–68·18

Table 1. (*Continued*).

		S. graecus Lake Yliki			
Characters	*n*	x̄ ± Sx̄	s	C.V.	Range
1. Total length	189	176·59 ± 1·90	26·08	14·77	153·00–422·00
2. Standard length	189	144·61 ± 1·64	22·60	15·63	125·00–363·00
% of standard length					
3. Preorbital distance	165	7·74 ± 0·03	0·41	5·24	6·77–8·67
4. Diameter of eye	165	6·53 ± 0·03	0·43	6·58	4·35–7·54
5. Post-orbital distance	165	13·20 ± 0·04	0·52	3·93	12·03–14·63
6. Interorbital width	165	6·88 ± 0·03	0·33	4·80	5·87–7·92
7. Head depth	165	16·49 ± 0·06	0·79	4·77	14·06–18·27
8. Head length	165	26·52 ± 0·07	0·86	3·25	24·59–29·26
9. Max. body depth	165	24·04 ± 0·12	1·52	6·31	20·46–29·75
10. Min. body depth	165	9·38 ± 0·03	0·41	4·41	8·09–10·53
11. Predorsal distance	165	55·69 ± 0·09	1·16	2·08	52·71–59·23
12. Post-dorsal distance	165	35·27 ± 0·08	1·04	2·95	32·09–40·29
13. Caudal peduncle length	165	21·33 ± 0·07	0·90	4·20	18·47–23·46
14. Preventral distance	165	50·94 ± 0·09	1·19	2·33	47·08–53·86
15. Preanal distance	165	70·97 ± 0·12	1·52	2·15	66·92–79·89
16. Distance P-V	165	25·93 ± 0·09	1·21	4·66	19·64–29·64
17. Distance V-A	165	21·89 ± 0·09	1·20	5·46	15·54–25·62
18. Height of dorsal fin	164	16·24 ± 0·07	0·87	5·37	13·02–18·00
19. Length of dorsal fin base	164	9·76 ± 0·04	0·57	5·85	8·03–11·62
20. Height of anal fin	165	13·71 ± 0·05	0·70	5·13	10·95–15·19
21. Length of anal fin base	165	11·20 ± 0·05	0·66	5·85	9·23–12·78
22. Length of pectoral fin	164	19·41 ± 0·07	0·85	4·38	16·52–21·15
23. Length of ventral fin	165	14·80 ± 0·05	0·68	4·62	12·87–16·28
% of head length					
24. Preorbital distance	165	29·20 ± 0·10	1·28	4·39	25·69–33·09
25. Diameter of eye	165	24·63 ± 0·13	1·67	6·78	16·70–27·14
26. Post-orbital distance	165	49·80 ± 0·11	1·35	2·71	46·18–55·29
27. Interorbital width	165	25·96 ± 0·09	1·17	4·53	22·43–29·84
28. Head depth	165	62·25 ± 0·26	3·38	5·42	52·58–70·30
% of max. body depth					
29. Min. body depth	165	39·13 ± 0·19	2·40	6·13	32·13–46·51
% of caudal peduncle length					
30. Min. body depth	165	44·03 ± 0·20	2·56	5·82	38·10–53·57
% of preorbital distance					
31. Diameter of eye	165	84·49 ± 0·52	6·68	7·91	51·80–97·78
% of post-orbital distance					
32. Diameter of eye	165	49·49 ± 0·28	3·58	7·24	30·21–56·65
% of interorbital width					
33. Diameter of eye	165	95·00 ± 0·53	6·78	7·14	58·52–114·29
% of distance P-V					
34. Length of pectoral fin	164	75·11 ± 0·43	5·53	7·36	55·76–95·64
% of distance V-A					
35. Length of ventral fin	165	67·87 ± 0·43	5·51	8·12	50·22–96·53
% of preanal distance					
36. Predorsal distance	165	78·50 ± 0·16	2·11	2·68	71·38–83·50
37. Preventral distance	165	71·79 ± 0·11	1·39	1·93	66·06–75·86
% of post-dorsal distance					
38. Caudal peduncle length	165	60·51 ± 0·19	2·46	4·06	51·79–66·00

Table 1. (*Continued*).

Characters	*S. erythrophthalmus* Lake Koronia				
	n	x̄ ± Sx̄	s	C.V.	Range
1. Total length	79	179·87 ± 1·61	14·29	7·95	158·00–244·00
2. Standard length	79	145·66 ± 1·34	11·92	8·18	128·00–200·00
% of standard length					
3. Preorbital distance	79	7·12 ± 0·03	0·30	4·20	6·55–7·86
4. Diameter of eye	79	7·10 ± 0·04	0·37	5·15	6·00–7·86
5. Post-orbital distance	79	11·83 ± 0·04	0·38	3·20	10·72–13·02
6. Interorbital width	79	9·27 ± 0·04	0·34	3·66	8·55–10·24
7. Head depth	79	19·76 ± 0·06	0·55	2·77	18·29–21·09
8. Head length	79	24·14 ± 0·07	0·61	2·55	22·97–25·38
9. Max. body depth	79	32·77 ± 0·16	1·42	4·32	30·30–36·70
10. Min. body depth	79	11·18 ± 0·05	0·42	3·78	10·07–12·32
11. Predorsal distance	79	56·24 ± 0·12	1·04	1·84	53·93–58·60
12. Post-dorsal distance	79	33·63 ± 0·12	1·05	3·12	30·77–36·45
13. Caudal peduncle length	79	19·42 ± 0·11	1·00	5·16	16·57–22·10
14. Preventral distance	79	50·42 ± 0·10	0·87	1·72	48·31–52·50
15. Preanal distance	79	72·00 ± 0·14	1·24	1·73	69·29–75·16
16. Distance P-V	79	27·72 ± 0·10	0·89	3·23	25·35–30·33
17. Distance V-A	79	25·22 ± 0·14	1·26	4·99	22·50–28·66
18. Height of dorsal fin	79	19·62 ± 0·09	0·83	4·22	17·82–21·69
19. Length of dorsal fin base	79	12·60 ± 0·06	0·57	4·55	11·03–13·77
20. Height of anal fin	79	16·29 ± 0·09	0·79	4·84	14·48–18·38
21. Length of anal fin base	79	14·42 ± 0·09	0·83	5·76	12·50–15·98
22. Length of pectoral fin	79	22·09 ± 0·09	0·80	3·60	20·32–24·00
23. Length of ventral fin	79	18·27 ± 0·08	0·67	3·67	16·76–20·00
% of head length					
24. Preorbital distance	79	29·48 ± 0·12	1·10	3·73	27·03–31·94
25. Diameter of eye	79	29·43 ± 0·15	1·34	4·56	24·84–32·70
26. Post-orbital distance	79	49·01 ± 0·14	1·25	2·54	45·82–52·63
27. Interorbital width	79	38·41 ± 0·16	1·40	3·65	35·21–41·57
28. Head depth	79	81·90 ± 0·30	2·63	3·21	74·58–88·24
% of max. body depth					
29. Min. body depth	79	34·14 ± 0·18	1·57	4·58	30·00–37·95
% of caudal peduncle length					
30. Min. body depth	79	57·69 ± 0·42	3·74	6·49	49·18–71·43
% of preorbital distance					
31. Diameter of eye	79	99·96 ± 0·66·	5·85	5·86	78·95–115·56
% of post-orbital distance					
32. Diameter of eye	79	60·11 ± 0·39	3·49	5·80	50·00–67·10
% of interorbital width					
33. Diameter of eye	79	76·74 ± 0·54	4·77	6·22	62·50–88·00
% of distance P-V					
34. Length of pectoral fin	79	79·75 ± 0·39	3·50	4·39	71·43–87·22
% of distance V-A					
35. Length of ventral fin	79	72·63 ± 0·50	4·40	6·06	63·27–82·68
% of preanal distance					
36. Predorsal distance	79	78·14 ± 0·18	1·63	2·08	74·34–81·52
37. Preventral distance	79	70·04 ± 0·15	1·37	1·96	68·20–74·50
% of post-dorsal distance					
38. Caudal peduncle length	79	57·76 ± 0·28	2·46	4·25	50·29–63·13

Table 2. Meristic characters of the three species of the genus *Scardinus* in Greece.

Characters	*S. acarnanicus* Lakes Lysimachia and Trichonis				
	n	x̄ ± Sx̄	s	C.V.	Range
1. Rays of dorsal fin D					
(a) simple	88	3·00 ± 0·00	0·00	0·00	3–3
(b) branched	88	7·94 ± 0·03	0·28	3·48	7–9
2. Rays of anal fin A					
(a) simple	89	3·00 ± 0·00	0·00	0·00	3–3
(b) branched	89	9·37 ± 0·06	0·53	5·63	8–10
3. Rays of pectoral fin P					
(a) simple	85	1·00 ± 0·00	0·00	0·00	1–1
(b) branched	85	14·26 ± 0·08	0·71	4·95	13–16
(c) simple	81	1·57 ± 0·06	0·57	36·05	1–3
4. Rays of ventral fin V					
(a) simple	89	1·98 ± 0·02	0·15	7·49	1–2
(b) branched	89	7·96 ± 0·02	0·21	2·60	7–8
(c) simple	2	1·00 ± 0·00	0·00	0·00	1–1
5. Rays of caudal fin C					
(a) branched	89	16·97 ± 0·02	0·23	1·38	16–18
6. Scales of lateral line L.1.	80	41·09 ± 0·09	0·76	1·85	40–43
7. Scales rows above L.1.	86	7·01 ± 0·01	0·11	1·53	7–8
8. Scales rows below L.1.	84	3·01 ± 0·03	0·24	8·09	2–4
9. Gill rakers	86	14·43 ± 0·10	0·90	6·21	12–17
10. Vertebrae	79	38·03 ± 0·06	0·53	1·39	36–39

Characters	*S. graecus* Lake Yliki				
	n	x̄ ± Sx̄	s	C.V.	Range
1. Rays of dorsal fin D					
(a) simple	164	2·99 ± 0·01	0·08	2·60	2–3
(b) branched	164	7·94 ± 0·02	0·26	3·32	7–9
2. Rays of anal fin A					
(a) simple	164	3·00 ± 0·00	0·00	0·00	3–3
(b) branched	164	10·70 ± 0·05	0·59	5·50	10–12
3. Rays of pectoral fin P					
(a) simple	165	1·00 ± 0·00	0·00	0·00	1–1
(b) branched	165	14·96 ± 0·06	0·74	4·96	13–17
(c) simple	159	1·51 ± 0·04	0·56	37·05	1–3
4. Rays of ventral fin V					
(a) simple	165	1·97 ± 0·01	0·17	8·70	1–2
(b) branched	165	7·95 ± 0·02	0·30	3·73	7–9
(c) simple	13	1·00 ± 0·00	0·00	0·00	1–1
5. Rays of caudal fin C					
(a) branched	164	16·97 ± 0·03	0·34	2·00	15–19
6. Scales of lateral line L.1.	119	42·31 ± 0·11	1·18	2·79	38–44
7. Scales rows above L.1.	100	7·68 ± 0·07	0·69	9·00	5–9
8. Scales rows below L.1.	90	3·09 ± 0·05	0·44	14·19	2–4
9. Gill rakers	161	21·37 ± 0·09	1·16	5·44	17–24
10. Vertebrae	163	39·86 ± 0·04	0·53	1·33	38–41

Table 2. (*Continued*).

Characters	*n*	$\bar{x} \pm S\bar{x}$	s	C.V.	Range
	S. erythrophthalmus Lake Koronia				
1. Rays of dorsal fin D					
(a) simple	79	2·99 ± 0·01	0·11	3·74	2–3
(b) branched	79	8·05 ± 0·02	0·22	2·72	8–9
2. Rays of anal fin A					
(a) simple	79	3·00 ± 0·00	0·00	0·00	3–3
(b) branched	79	10·96 ± 0·05	0·46	4·22	10–12
3. Rays of pectoral fin P					
(a) simple	77	1·03 ± 0·03	0·23	22·07	1–3
(b) branched	77	13·03 ± 0·08	0·68	5·25	11–14
(c) simple	77	2·01 ± 0·07	0·63	31·51	1–4
4. Rays of ventral fin V					
(a) simple	79	1·94 ± 0·03	0·24	12·57	1–2
(b) branched	79	7·90 ± 0·03	0·30	3·82	7–8
(c) simple	7	1·00 ± 0·00	0·00	0·00	1–1
5. Rays of caudal fin C					
(a) branched	78	16·95 ± 0·04	0·39	2·29	15–18
6. Scales of lateral line L.1.	54	40·80 ± 0·12	0·87	2·13	39–43
7. Scales rows above L.1.	47	7·64 ± 0·07	0·48	6·29	7–8
8. Scales rows below L.1.	48	3·38 ± 0·07	0·48	14·34	3–4
9. Gill rakers	77	11·58 ± 0·09	0·78	6·72	9–14
10. Vertebrae	78	37·97 ± 0·08	0·72	1·88	36–39

Principal Component Analysis of the three samples was performed using the same data set of the dendrogram 3 (*b*). The positions of the three samples are shown in the space of the two principal components in Fig. 4 (*b*).

The evaluation of the Gabriel graph, usually, is an attempt to reach the unknown mode of speciation or dispersion of samples, populations or species. The Gabriel graph of the three samples is presented in Fig. 5 (*a*).

Adding the Polish sample the dendrogram of Fig. 3 (*d*) was derived using 16 morphometric characters. Fig. 4 (*a*) shows the position of the four samples in the space of the two principal components when these 16 morphometric characters were analysed. Finally, the Gabriel graph of the four samples is presented in Fig. 5 (*b*).

Discussion

It is notable that in all types of analysis we performed on the three samples, the two samples of *S. acarnanicus* and *S. graecus* form a separate group.

This is the case in Phylogenetic analysis despite the two distance estimators used, Mahalanobis and D_2 being entirely different. The Principal Component Analysis provides further confirmation of this mode of differentiation of the three taxa. In Gabriel graphs, the two taxa *S. acarnanicus* and *S. graecus* with the pair of the Greek and Polish samples of *S. erythrophthalmus* show a remarkable interrelation.

Speciation of freshwater fishes in Greece is a particularly complicated problem. It is generally accepted (Economidis and Banarescu, 1991) that species have been isolated in different periods in the water systems of the region and therefore an extensive divergence of speciation patterns exists. Obviously this is the main reason for the apparent variation of the origin and the constitution of the species in every particular

Table 3. Differences of morphometric characters of the three species of the genus *Scardinius* in Greece.

Characters	I	II	III
% of standard length			
1. Preorbital distance	***	—	***
2. Diameter of eye	***	—	***
3. Post-orbital distance	***	***	***
4. Interorbital width	***	***	***
5. Head depth	***	***	***
6. Head length	***	***	***
7. Max. body depth	***	***	***
8. Min. body depth	***	***	***
9. Predorsal distance	—	***	***
10. Post-dorsal distance	***	***	***
11. Caudal peduncle length	***	***	***
12. Preventral distance	***	***	***
13. Preanal distance	***	***	***
14. Distance P-V	***	***	***
15. Distance V-A	***	***	***
16. Height of dorsal fin	***	—	***
17. Length of dorsal fin base	***	***	***
18. Height of anal fin	***	—	***
19. Length of anal fin base	***	***	***
20. Length of pectoral fin	***	***	***
21. Length of ventral fin	***	***	***
% of head length			
22. Preorbital distance	**	***	—
23. Diameter of eye	***	***	***
24. Post-orbital distance	***	**	***
25. Interorbital width	***	***	***
26. Head depth	***	***	***
% of max. body depth			
27. Min. body depth	—	***	***
% of caudal peduncle length			
28. Min. body depth	***	***	***
% of preorbital distance			
29. Diameter of eye	***	—	***
% of post-orbital distance			
30. Diameter of eye	***	—	***
% of interorbital width			
31. Diameter of eye	***	***	***
% of distance P-V			
32. Length of pectoral fin	***	***	***
% of distance V-A			
33. Length of ventral fin	***	***	***
% of preanal distance			
34. Predorsal distance	***	***	—
35. Preventral distance	—	***	***
% of post-dorsal distance			
36. Caudal peduncle length	—	***	***

I: *S. acarnanicus* and *S. erythrophthalmus*. II: *S. acarnanicus* and *S. graecus*. III: *S. graecus* and *S. erythrophthalmus*.

$*p < 0{\cdot}05$; $**p < 0{\cdot}01$; $***p < 0{\cdot}001$.

Table 4. Differences of meristic characters of the three species of the genus *Scardinius* in Greece.

Characters	I	II	III
1. Rays of dorsal fin D			
(a) simple	—	—	—
(b) branched	**	—	***
2. Rays of anal fin A			
(a) simple	—	—	—
(b) branched	***	***	***
3. Rays of pectoral fin P			
(a) simple	—	—	—
(b) branched	***	***	***
(c) simple	***	—	***
4. Rays of ventral fin V			
(a) simple	—	—	—
(b) branched	—	—	—
(c) simple	—	—	—
5. Rays of caudal fin C			
(a) branched	—	—	—
6. Scales of lateral line L.1.	*	***	***
7. Scales rows above L.1.	***	***	—
8. Scales rows below L.1.	***	—	***
9. Gill rakers	***	***	***

I: *S. acarnanicus* and *S. erythrophthalmus*. II: *S. acarnanicus* and *S. graecus*. III: *S. graecus* and *S. erythrophthalmus*.
$*p<0{\cdot}05$; $**p<0{\cdot}01$; $***p<0{\cdot}001$.

geographical area of the country. According to Economidis and Banarescu (1991) there are three main ichthyogeographical zones: the Ponto-Aegean Division, the Attico-Boeotia Division and the South Adriatic-Ionian Division (Fig. 1).

The Ponto-Aegean area includes all rivers and lakes from north-eastern Bulgaria to the Sperchios River in central Greece, which run into the Black and Aegean Seas. The fish fauna of this area has a strong affinity with the central European fauna, as well as those of the Ponto-Caspian and the Danubian regions.

In the Attico-Boeotia area, all rivers of the eastern slope of mainland Greece (Attica and Boeotia), Euboea Island and the Lakes Yliki and Paralimni are inhabited by a distinctive poor fish fauna which consists almost entirely of endemic species (Vinciguerra, 1921; Stephanidis, 1937, 1939a; Economidis and Banarescu, 1991).

In the third area, the Adriatic and Ionian sea slope of the Balkan Peninsula, from Lake Skadar and Drin River in the north to Eurotas River at the southeast end of Peloponnesus, are included. In this area the fish fauna is richer with more endemic species and shows a wider distribution than that of the two other areas.

In all the above areas the genus *Scardinius* is present. However, the particular *Scardinius* species in these areas are quite distinct (Fig. 1). The species *Scardinius erythrophthalmus* demonstrates a more or less continuous distribution in Greece from Thrace to Thessaly. This species is concentrated in the Ponto-Aegean Division and is closely related to its ancestral populations of central Europe. It seems that the populations of this species may have been recently dispersed with other limnophile species from the Danube River during the last glaciation (Banarescu, 1960; Economidis, 1974; Economidis and Banarescu, 1991). In the present study, the analysis of the

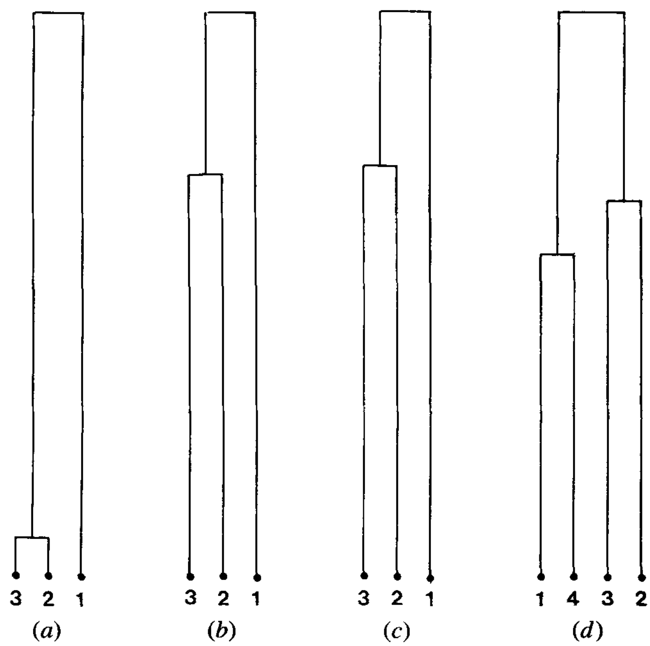

FIG. 3. Dendrograms of the four species: (1) *S. erythrophthalmus*; (2) *S. graecus*; (3) *S. acarnanicus*; (4) *S. erythrophthalmus* from Poland. See text for details.

differentiation data between the populations of Greece and Poland has showed that these populations are related. This is in accordance with the fact that the species *Scardinius erythrophthalmus* is continuously and widely distributed from central Europe to central Greece (Thessaly) without any particular differentiation in isolated populations.

On the contrary, the range of the species *Scardinius graecus* is limited to a narrow zone consisting of the Yliki and Paralimni lake system (Fig. 2). It is worth pointing out that until recently there was a huge shallow lake, Lake Kopais in the same system. Lake Kopais, well known since historical times, dried in the first decades of this century (Dimitrakos, 1970).

The whole system remained isolated since at least the upper Tertiary. It is accepted from the species composition of its primary fish fauna that this system was not affected by glaciation. Because of the existence of Lake Kopais, a limnophile species, *Scardinius graecus*, has been present for a long period of time.

The species *Scardinius acarnanicus* belongs to the faunistic complex of South Adriatic-Ionian Division. This region includes a rich ichthyofauna with many endemic and intruder taxa. It is possible that the ichthyofauna of the South Adriatic-Ionian Division is formed by the invasion of intruders, into the existing ichthyofauna of the upper Tertiary during the Quaternary. The species *Scardinius acarnanicus* is an endemic limnophile species which is found only in the Acheloos River system with some other endemic limnophile species. It is considered that all these species belong to an old faunistic stock which developed in the water of this system.

Based on the time of isolation of each of the three species and the area of their distribution, *Scardinius graecus* seems to be older than *Scardinius acarnanicus*. Perhaps, these two taxa are derived from a common stock and their morphological differences are proportional to the time and the conditions of their isolation. Finally,

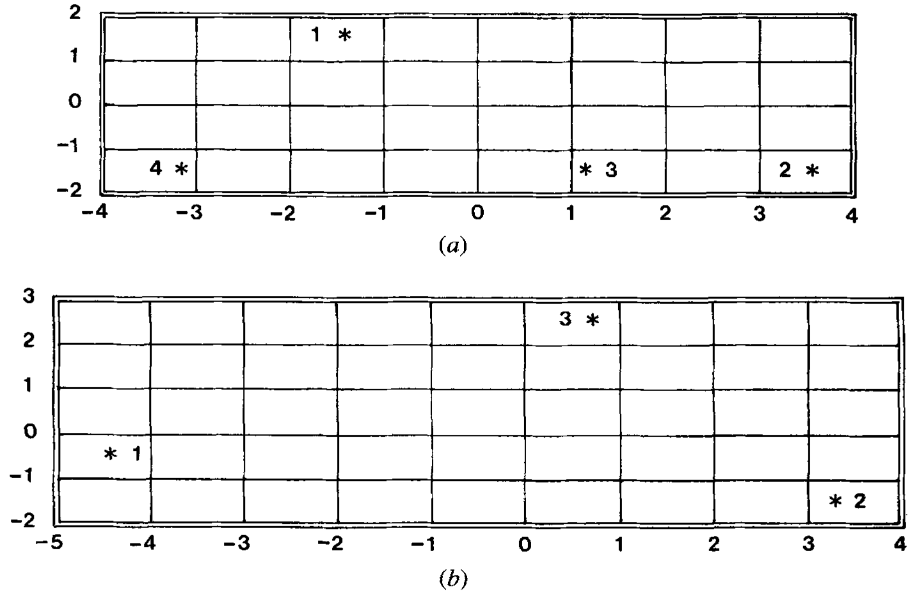

FIG. 4. The position of the four species in the space of the two Principal Components: (1) *S. erythrophthalmus*; (2) *S. graecus*; (3) *S. acarnanicus*; (4) *S. erythrophthalmus* from Poland. See text for details.

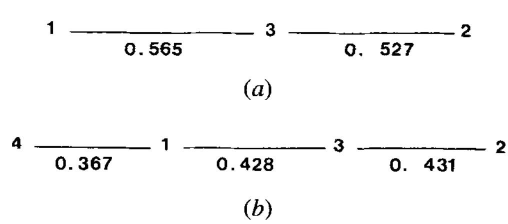

Fig. 5. Gabriel graphs of the four species.

the continuously distributed species *Scardinius erythrophthalmus* obviously is the most recent one.

References

BALAKRISHNAN, V. and SANGHVI, L. D., 1968, Distance between populations on the basis of attribute data, *Biometrics*, **24,** 859–865.

BANARESCU, P. M., 1960, Einige Fragen zur Herkunft und Verbreitung der Süsswasserfischfauna der europäischmediterranean Unterregion, *Archiv für Hydrobiologie*, **55,** 16–134.

BERG, L. S., 1932, Übersicht der Verbreitung der Süsswasserfische Europas, *Zoogeographica*, **1,** 107–208.

BERG, L. S., 1949, *Freshwater fishes of the U.S.S.R. and adjacent countries*, Volume 2, Israel Program for Scientific Translations, Jerusalem, 496 pp. (translated from Russian in 1964).

DIMITRAKOS, S. D., 1970, *Geography, World Atlas, Greece*. Athens, 896 pp. [in Greek].

ECONOMIDIS, P. S., 1973, A list of the fishes of Greece, *Hellenic Oceanology and Limnology*, **11,** 421–599 [in Greek].

ECONOMIDIS, P. S., 1974, *Morphological, systematical and zoogeographical study of the freshwater fishes of eastern Macedonia and western Thrace*, Ph.D. Thesis, University of Thessaloniki, Greece, 179 pp. [in Greek].

ECONOMIDIS, P. S., 1991, Checklist of freshwater fishes of Greece, *Recent status of threats and protection, Hellenic Society for the Protection of Nature, Athens*, 47 pp.

ECONOMIDIS, P. S. and BANARESCU, P. M., 1991, The distribution and origins of freshwater fishes in the Balkan Peninsula, especially in Greece, *Internationale Revue der gesamten Hydrobiologie*, **76**, 257–283.

ILIADOU, K. and ONDRIAS, J., 1980, The biology of *Scardinius erythrophthalmus* of the Lysimachia and Trichonis Lakes, Greece, *Biologia Gallo-Hellenica*, **9**, 195–206.

KLIMCZYK-JANIKOWSKA, M., 1975, Biometric characteristic and food of the rudd (*Scardinius erythrophthalmus L.*) from the reservoir at Goczalkowice, *Acta Hydrobiologica*, **17**, 71–80.

KOLLER, O., 1927, Süsswasserfische aus Griechenland (Ichthyologische Mitteilung No. VI), *Zoologischer Anzeiger*, **LXX**, 267–270.

KRIMBAS, C. B. and SOURDIS, J., 1987, Recent improvements on handling allelic isozyme data for tree construction, *Isozymes*, **15**, 49–62.

LADIGES, W. and VOGT, D., 1965, *Die Süsswasserfische Europas* (Hamburg & Berlin: Verlag Paul Parey), 250 pp.

LADIGES, W. and VOGT, D., 1979, *Die Süsswasserfische Europas*, Zweite Auflage (Hamburg & Berlin: Verlag Paul Parey). 299 pp.

MAHALANOBIS, P. C., 1936, On the generalized distance in statistics, *Proceedings of the National Institute of Science of India*, **2**, 49–55.

MATULA, W. D. and SOKAL, R., 1980, Properties of Gabriel Graphs relevant to geographic variation research and clustering of points in the plane, *Geographical Analysis*, **12**, 205–222.

ONDRIAS, J. C., 1971, A list of the fresh and sea water fishes of Greece, *The Practica of the Institute of Oceanographic and Fishing Research, Athens*, **Xa**, **3** (23)–**77** (96).

PIAZZA, A., MENOZZI, P. and CAVALLI-SFORZA, L. L., 1981, The making and testing of geographic gene-frequency maps, *Biometrics*, **37**, 637–659.

SCHMIDT-RIES, H., 1943, Die Fische Griechenlands. I. Die Süsswasserfische, *Zeitschrift für Fischerei und Deren Hilfswissenschaften* (Berlin), **41**, 319–344.

STEPHANIDIS, A., 1937, Poissons d'eau douce, Nouveaux pour l'ichthyofaune de la Grece (Note ichthyologique No 1), *Acta Institutis Musei Zoologiae Universitatis Atheniensis*, **1**, 263–268.

STEPHANIDIS, A., 1939a, *The freshwater fishes of western Greece and of the island of Corfu*, Ph.D. Thesis, University of Athens, Greece, 44 pp. [in Greek].

STEPHANIDIS, A., 1939b, The freshwater fishes of Attikoboeotia, *Deltion Physikon Epistimon*, **5**, 49–60 (in Greek).

VINCIGUERRA, D., 1921, Descrizione di tre nuove specie di pesci delle acque dolci di Grecia, *Annali Musei Civico Storia Naturali, Genova*, **9**, 322–331.