

HABERMEHL

# Die Altersbestimmung bei Versuchstieren

Von Professor Dr. Karl-Heinz Habermehl, Gießen. 1980. 131 Seiten mit 82 Abbildungen und 26 Tabellen. Balacron brotschiert DM 46,—

Es ist Aufgabe dieses Buches, dem experimentell tätigen Wissenschaftler die Altersbestimmung, zumindest aber eine Altersschätzung oder -beurteilung bei den von ihm verwendeten Versuchstieren anhand anatomischer, morphologischer und entwicklungsphysiologischer Merkmale zu ermöglichen. Das wird immer dann erforderlich sein, wenn solche Daten aus verschiedenen Gründen, so z. B. bei Tieren aus fremder Zucht, nicht zur Verfügung stehen.

In gleicher, bewährter Art der Darstellung wie in seinem zuvor erschienenen Buch, das sich mit der Altersbestimmung überwiegend bei den landwirtschaftlichen Haus- und Nutztieren beschäftigt, widmet sich hier Professor Habermehl ausführlich den Versuchstieren, bei denen sich die Altersbestimmung nach ganz anderen Kriterien richtet. Von der Maus über Katze, Hund und Miniaturschwein bis zu den Primaten werden die als Versuchstiere verwendeten Säuger berücksichtigt, wobei für jede Tierart die physiologischen Daten,

die Methoden zur prä- und postnatalen Altersbestimmung sowie Merkmale am Gebiß und am Skelett beschrieben werden. Dabei wird deutlich, daß die Altersfeststellung beim größten Teil der als Versuchstiere verwendeten kleinen Nagearten weitaus schwieriger ist, als etwa bei den Haus- und Nutztieren oder bei größeren Tieren überhaupt, weil bestimmte Veränderungen, z. B. am Gebiß, bei diesen nur eine untergeordnete Rolle spielen. Den Angaben über die Möglichkeit der Altersbestimmung bei Embryonen und Feten kommt daher besondere Bedeutung zu, auch im Hinblick auf teratologische Untersuchungen.

Zahlreiche Abbildungen und Tabellen sowie ein Literatur- und ein Sachverzeichnis ergänzen das Buch zu einem übersichtlichen und unentbehrlichen Hilfsmittel für die experimentelle Arbeit mit Versuchstieren.

**PAUL PAREY** Berlin und Hamburg

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## Zeitschrift für zoologische Systematik und Evolutionsforschung

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- e. Die Seitenplatten sind als lokale Verdickungen der Pharynxcuticula Spezialbildungen der Chaetodermatidae. Sie sind der eigentlichen Radula ebenfalls nicht homolog.
- f. Der Radulaapparat der Chaetodermatidae hat sich direkt, wie schon von SALVINI-PLAWEN (1969, 1972, 1975) angenommen, aus dem bei Limifossoridae plesiomorph erhaltenen Typus entwickelt und liegt bei den Chaetodermatidae in einer hochspezialisierten (apomorphen) Form mit nur einer einzigen, distichen Zahnreihe vor. Die entsprechend homologen Muskeln bestätigen, daß es sich bei der Zängentasche (mit Basalplatte) um die Radulascheide handelt: sie hat jedoch eine ihrer ursprünglichen Funktionen, nämlich die, kontinuierlich neue Zähne zu bilden, verloren, wogegen die der Basalmembran-Abscheidung in unveränderter Form erhalten blieb (vgl. SALVINI-PLAWEN und NOPP 1974).

#### Summary

##### *On the derivation of the radula-apparatus in Chaetodermatidae (Caudofoveata, Mollusca)*

1. There are three different opinions about the derivation of the radula-apparatus in Chaetodermatidae:
  - a. The Chaetodermatidae possess one row of five teeth (KOWALEVSKY 1901; NIERSTRASZ 1902), or one row of three teeth (IVANOV 1979).
  - b. The radula is a highly specialized product consisting of one row of two teeth (BOETTIGER 1955, SCHWABL 1961, SALVINI-PLAWEN 1969, 1972, 1975); the basal-plate is a highly thickened radula-membrane (ribbon). The radula in Chaetodermatidae has derived from that in Limifossoridae.
  - c. The basal-plate is a fused radula (SCHELTEMA 1972, 1981).
2. New anatomical investigations (DEIMEL 1981) demonstrated that the radula-apparatus in Limifossoridae is operated by 6-7 (mostly paired) muscles. The cone-shaped organ in Chaetodermatidae possesses 13 (mostly paired) muscles.
3. The comparison of the musculature of the radula-apparatus showed that six muscles (Nr. 1-6) in Limifossoridae are homologous to six muscles (Nr. 1-6) in Chaetodermatidae.
4. The inclusion of other characters of the radula-apparatus demonstrates that they are likewise in concurrence.
5. The basal-plate represents a highly thickened radula-membrane (ribbon) which is not homologous to a true radula.
6. The lateral-plates as special structures in Chaetodermatidae are local thickenings of the pharyngeal cuticle; they are also not homologous to a true radula.
7. The Chaetodermatidae are closely related to the Limifossoridae. Their radula-apparatus has differentiated from the same type as that of the Limifossoridae. It represents a highly specialized product consisting of one row of two teeth. The six homologous muscles confirm that the pouch of the basal-plate in Chaetodermatidae corresponds to the radula-sheath in Limifossoridae.

#### Literatur

- BOETTIGER, C., 1955: Beiträge zur Systematik der Urmollusken (Amphineura). Zool. Anz. Suppl. 19, 223-256.
- DEIMEL, K., 1981: Die Muskulatur des Radulaapparates bei Caudofoveata (Limifossoridae, Chaetodermatidae). Diss. 592, Inst. Zool. Univ. Wien.
- IVANOV, D. I., 1979: Aufbau und funktionelle Morphologie des Radulaapparates von *Chaetoderma* (Mollusca, Caudofoveata). Zool. Schurn 58, 1302-1306 (In Russ.).
- KOWALEVSKY, A., 1901: Sur le genre *Chaetoderma*. Arch. zool. exper. (3), 9, 262-283.
- NIERSTRASZ, H., 1902: The Solenogastres of the Siboga-Expedition. Siboga-Exp. Monogr. 47, 1-46.
- SALVINI-PLAWEN, I. V., 1969: Faunistische Studien am Roten Meer im Winter 1961/62: V. Caudofoveata und Solenogastres (Mollusca, Aculifera). Zool. Jahrb. Syst., 96, 52-68.
- 1972: Zur Morphologie und Phylogenie der Mollusken: Die Beziehungen der Caudofoveata und der Solenogastres als Aculifera, als Mollusca und als Spiralia. Zool. Anz. 200, 205-394.
- 1975: Mollusca - Caudofoveata. Marine Invertebrates of Scandinavia (Oslo) 4, 1-55.
- 1977: Caudofoveata (Mollusca) des Forschungsprojektes Polymède. Bull. Mus. nat. Hist. nat. Paris, sér. 3, (447), Zool. 310, 413-421.
- 1977: Caudofoveata (Mollusca), Priapulida und apode Holothurien (*Labidoplax*, *Myriotrochus*) bei Banyuls und im Mittelmeer allgemein. Vie Milieu, Vol. XXVII, fasc. 1, sér. A, 55-81.
- 1978: The Species-Problem in Caudofoveata (Mollusca). Zool. Anz. 200, 18-26.
- 1981: The molluscan digestive system in Evolution. Malacologia 21, 371-401.
- SALVINI-PLAWEN, I. V.; NOPP, H., 1974: Chitin bei Caudofoveata (Mollusca) und die Ableitung ihres Radulaapparates. Z. Morph. Tiere 77, 77-86.
- SALVINI-PLAWEN, I. V.; WARÉN, A., 1972: Skandinavische Caudofoveata (Mollusca): Nachtrag. Sarsia 51, 3-6.

- SCHELTEMA, A., 1972: The radula of Chaetodermatidae (Mollusca, Aplacophora). Z. Morph. Tiere 72, 361-370.
- 1976: Two new species of *Chaetoderma* from off West Africa (Aplacophora, Chaetodermatidae). J. moll. Stud. 42, 223-234.
- 1981: Comparative morphology of the radula and alimentary tracts in the Aplacophora. Malacologia 20, 361-383.
- SCHWABL, M., 1961: *Crystallophrisson* (= *Chaetoderma*) *hartmani* nov. spec., eine neue Aplacophore aus dem Ostpazifik. Zool. Anz. 166, 257-278.
- SPENGLER, J. W., 1881: Die Geruchsorgane und das Nervensystem der Mollusken. Z. wiss. Zool. Vol. 35, 333-383.
- WARÉN, A., 1891: Studien über die Solenogastres I. Kongl. Svenska Vetensk. Akad. Hand. 24, 1-66.
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## Aphanius (Nardo, 1827) and Cyprinodon (Lac., 1803) (Pisces: Cyprinodontidae), an attempt for a genetic interpretation of speciation<sup>1</sup>

By W. VILLWOCK

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Most of the Old World cyprinodonts of the genus *Aphanius* and nearly all of the New World representatives of the genus *Cyprinodon* inhabit corresponding remains of ancient inland-waters with different, yet comparable ecological conditions (i. e. of composition and degree of salinity, temperature) produced through arid climate which evolved during the course of earth-history.

Old World species of *Aphanius* are widely distributed along ancient, as well as recent coastlines of the Mediterranean Sea, the Arabian Peninsula, as far as Iran and Karachi/Pakistan (Fig. 1). Within these areas of distribution they are not only common in bodies of water with marine conditions (though rarely in actual shallow marine waters near to the coast, as for instance on the Island of Sardinia) but are also found in salt pans or other closed coastal lagoons with hypersalinity. On the other hand they even exist in fresh-water (i. e. Central Asia Minor).

*Cyprinodon* with its different species is found today in the area of the West Indies and the Atlantic as well as the Caribbean Gulf Coast, throughout the desert drainages of the southern United States and northern Mexico, to the ancient and recent coastline of the Gulf of California in the west (e. g. Salton Sea) (Fig. 2).

The regions mentioned, both in the Old and in the New World, derived their present characters through comparable geomorphological changes since the Miocene. The more or less continuous distribution along the ancient Tethys Sea slowly disintegrated into in-

<sup>1</sup> Extended paper given during the "2nd Intern. Congress of Systematic and Evolutionary Biology, Vancouver/Canada, July 17-24, 1980". Supported by Deutsche Forschungsgemeinschaft, Bonn-Bad Godesberg/FRG.

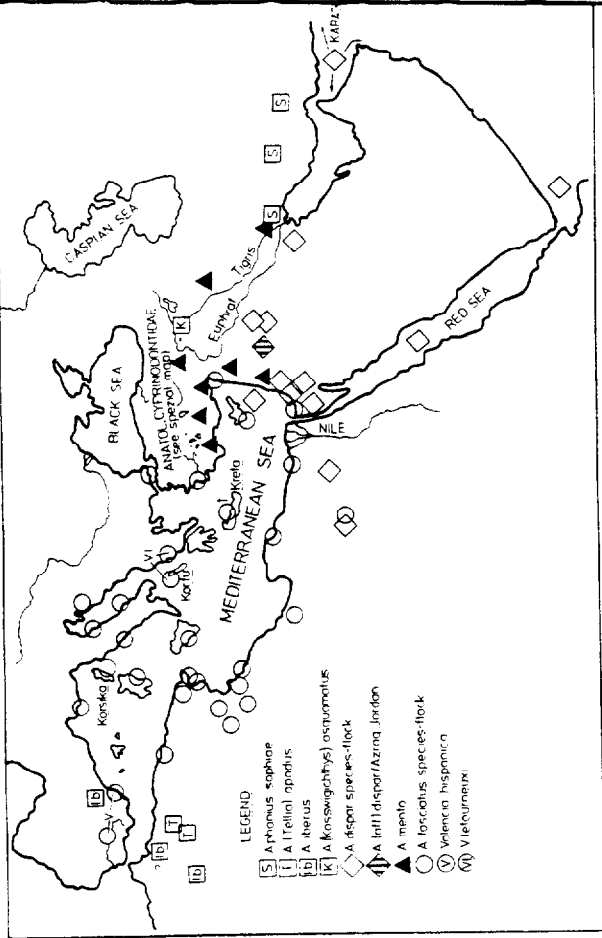


Fig. 1. Distribution map of Old World cyprinodontids (see legend and text)

dependent larger or smaller areas until the present situation was reached within postglacial times (LIKMAN 1953; DE BEAUFORT 1951; VILLWOCK 1964; BLACKWELDER et al. 1948; MILLER 1981). Through this, the old panmictic macropopulations of the ancestors of the recent *Aphanius* or *Cyprinodon* fell into smaller and smaller ones as well.

In the course of their phylogenetic separation into partly very small populations, existing at least on a few hundreds specimens each, both genera, *Aphanius* as well as *Cyprinodon*, developed a series of so-called regressive characters (KOSHWIG 1956; AKSIRAY and VILLWOCK 1962; VILLWOCK 1981; MILLER 1948, 1950; IUNGS et al. 1974; CONSTANTZ 1981) which are astonishingly similar in the two genera (i. e. scale-reductions, reductions of ventral fins). Remarkable are not only the phenomena themselves, but also the corresponding feed-back to predominant biotop factors of their habitats, especially to bittersalt conditions (mainly SO<sub>4</sub><sup>2-</sup>). The reason for mentioning these reductions, not discussed here in detail, is to point out the near relations between the representatives of both genera which show in their individuals similar reactions when confronted with similar evolutionary situations. It is interesting to note that all these briefly commented reduction phenomena were proved to be of polygenic heritability following the Mendelian rules (KOSHWIG l. c.; KOSHWIG and AKSIRAY 1949; AKSIRAY and VILLWOCK l. c.; VILLWOCK 1963).

The Old World oviparous toothcarps are today – apart from the xiphophorine life-bearing ones – the best investigated lower vertebrates as far as mechanisms of microevolution, i. e. speciation, are concerned. Because of the more detailed knowledge of the speciation mechanisms for *Aphanius* compared with those known for *Cyprinodon* the presentation of the former will be discussed at the beginning of this paper.

The results of numerous inter- and intraspecific crossbreeding experiments show that the circum-Mediterranean and Near East species of *Aphanius* have to be distinguished from those endemic to Anatolia (= Asia Minor). In almost all interspecific hybridizations between two non-Anatolian species on the one hand and non-Anatolian with endemic

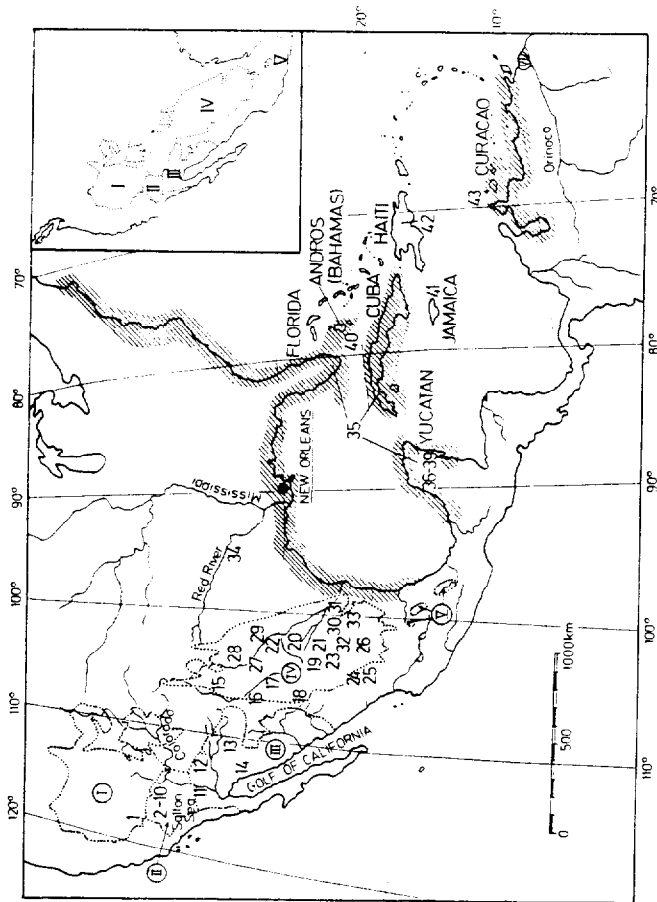


Fig. 2. Distribution map of the genus *Cyprinodon*. 1 = *C. radiosus*; 2-10 = *C. diabolis*; *C. salinus*, *C. nevadensis* and sp.; 11-12, 14 = *C. maculatus* and sp.; 13 = *C. n. sp.* (extinct); 15 = *C. tularosii*; 16 = *C. n. sp.*; 17 = *C. fontinalis*; 18 = *C. n. sp.*; 19 = *C. n. sp.*; 20 = *C. n. sp.*; 21 = *C. macrolepis*; 22 = *C. eximius*; 23-24, 26 = *C. nazas*; 25 = *C. meeki*; 27 = *C. elegans*; 28 = *C. pecosensis*; 29 = *C. bovinus*; 30-31 = *C. atrovirus* and *bifasciatus*; 32 = *C. latifasciatus* (extinct); 33 = *C. albaverezi*; 34 = *C. rubroflaviventris*; 35 = *C. variegatus*; 36-39 = *C. beltrami*, *C. labiosus*, *C. mayra*, *C. simius*; 40 = *C. laciniatus*; 41 = *C. jamaicensis*; 42 = *C. bonidi*; 43 = *C. dearborni* (systematic names after MILLER 1981, according to whom "the status of named West Indian forms and the distinct mainland population of *C. variegatus* around the Yucatan Peninsula is uncertain", MILLER l. c., legend to Fig. 2). - Small section in the map: I = Great Basin; II = Mohave; III = Sonoran; IV = Chihuahuan; V = Hidalgo Province (roman numerals correspond with the main map). No. II is often considered further discussed in the presented paper. According to the author's opinion the populations I-III (partim)/I-14 belong to the "*C. maculatus* Group", the populations 35-43 to the "*C. variegatus* Group" (see text). (Drawings after MILLER [1981], modified)

Anatolian ones on the other, the hybrids are sterile in both sexes (VILLWOCK 1964). However, crossbreeding between the endemic Anatolian species themselves shows a much more differentiated situation concerning hybrid sterility or fertility, respectively, than those of the two groups mentioned before (non-An. × non-An. and non-An. × endemic An. species). The results show that there are at least three more or less well definable taxonomic units: *Aphanius anatoliae* (LEIDENFROST 1912, Figs. 3 a-d) of the south-western and western part of central Anatolia (Fig. 4), *A. chantrei* (GAILLARD 1895, Fig. 3 c) which inhabits different bodies of fresh water in northern central Anatolia along the river Kizilirmak (Fig. 4) and lastly the monotypic *A. (Kosswigibys) osquamatus* (SÖZER 1942, Fig. 3 f) with its restricted distribution far away from the former two Anatolian species at Hazer-Gözü in East Anatolia (see also Fig. 4).

The intra- and interspecific relationship between the numerous, mostly well isolated populations of *A. anatoliae* and *A. chantrei* are at the center of the following discussion.

Fig. 4. Distribution map of endemic Anatolian species of the genus *Aphanius*: 1 a/c, 2-5: *Aphanius (Aphanius) chantrei*, - 7-24: *A. anatoliae anatoliae*, 25: *A. an. burdurensis*, 26: *A. an. transgrediens*, 27-28: *A. an. splendens* (see Figs. 3 a-c, compare text). - The term "Formenkreis" means different populations belonging to different interterritory-groups within the same species, or, in other words, reflecting different stages of *speces in statu nascenti*. - Small section of the map: Historic development of Anatolian water-systems during the Pliocene/Pleistocene. I = Kizilirmak Basin; II = Tuz Golu- and Gumra (1)-Eregli (2) Basin, the latter surrounded by pointed line. III = Burdur- (1)-Acti Gol (2) Province (3 and 4: not discussed), IV: "link" between II and III; V: Egirdir (1) and Beysehir (2, extinct). (Roman numerals correspond with the main map)

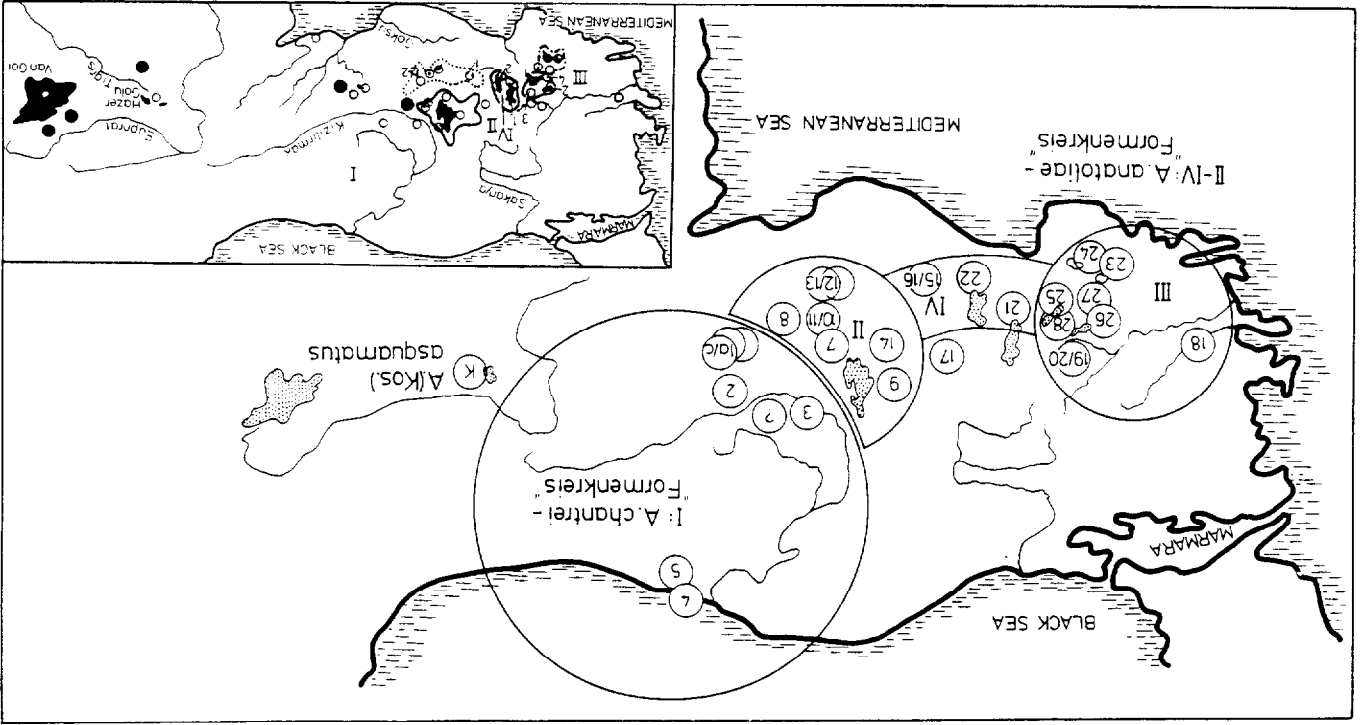
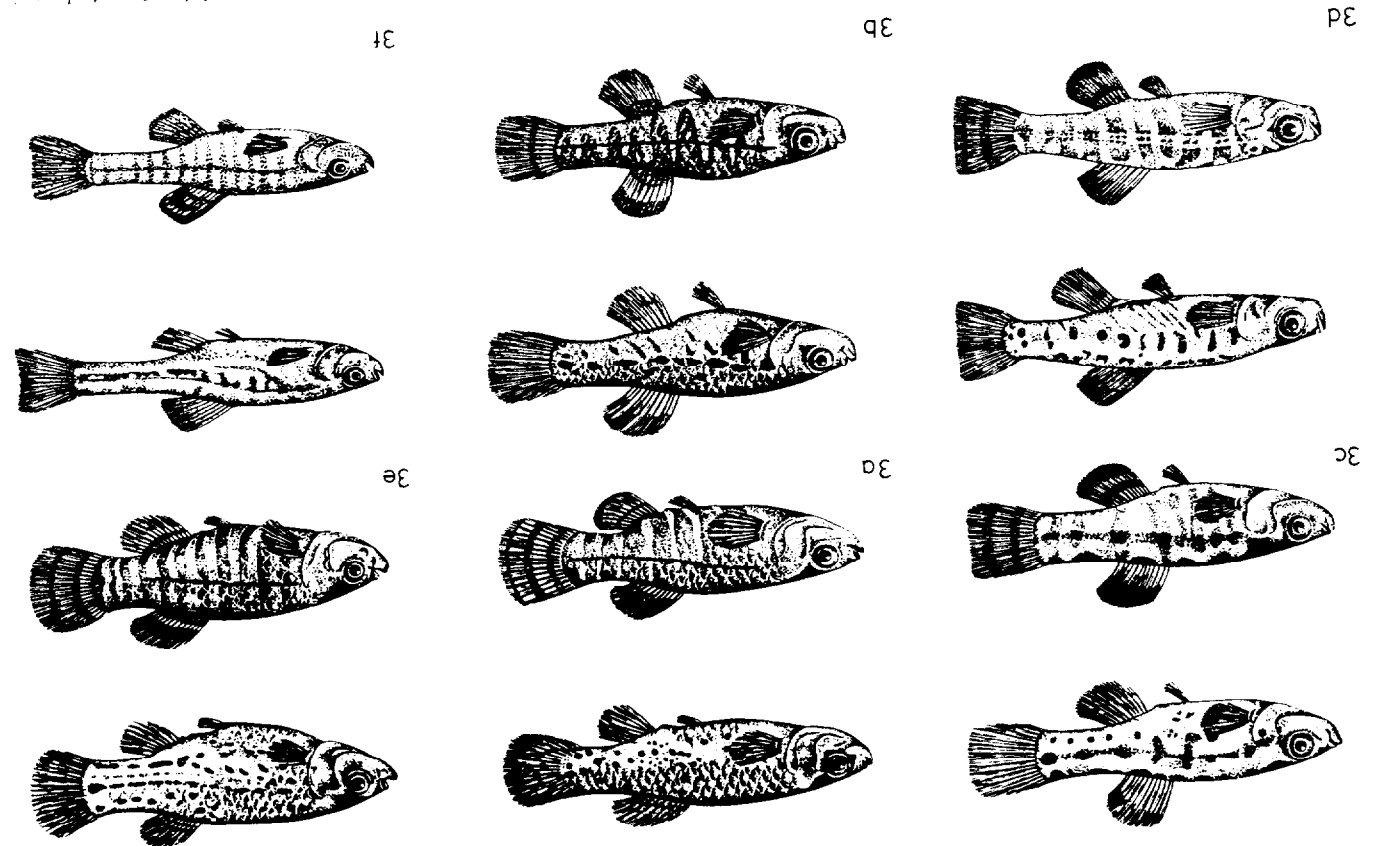


Fig. 3. *Aphanius (Aphanius)* from Asia Minor. 3a = *A. anatoliae anatoliae*, 3b: *A. an. burdurensis*; 3c = *A. an. transgrediens*; 3d = *A. an. splendens*, 3e = *A. chantrei*; 3f = *Aphanius (Koswigichthys) asquamatus*. (Systematic names sensu VILLWOCK 1964)



The results of intraspecific crossbreeding proved *A. anatoliae* to exist in at least two population groups represented by the south-western populations on the one hand (Fig. 4: nos. 18–28) and the western central-Anatolian ones on the other (Fig. 4: nos. 7–14). The most interesting populations are those, which today live between the above mentioned two and which demonstrate at a first glance a surprising interrelationship to each of them (Fig. 4, nos. 15/16 and 21–22). One of these populations, called Çumra (15/16), produces all-fertile hybrids with the members of the western central-Anatolian group (i. e. 7–14), but only a few fertile  $F_1$ - $\delta$  apart from sterile ones<sup>2</sup> with the south-western populations (i. e. 18–28). The same was noticed with another special population, called Eğridir (21). This one is the easiest to combine with all the south-western toothcarp but shows a similar reaction in crosses with all western central-Anatolian populations, as does Çumra with the south-western ones – while the reciprocal crosses between Çumra and Eğridir give an all-fertile offspring. The fact of two species in statu nascendi with an overlapping remain of hybrid-fertility at their common distribution center (Çumra/Eğridir: 15/16 and 21) has therefore to be recognized.

Most interesting are the sterility-phenomena of the hybridmales (females see<sup>2</sup>), because they are different from one another, i. e. they show a gradient of sterility which ranges from histologically fertile gonad structures (but which are in reality unable to segregate usable/movable fertile sperm), to those which completely lack even early germcells. In between these extremes there are numerous hybrids with gonads which ceased sperm-formation at different meiotic stages (VILLWOCK 1958; KARBE 1961). The gradient of this male-sterility can clearly be correlated with distance of geographic separation or, in other terms, the nearer the tested populations are located to each other the less are the sterility characters shown by their hybrid- $\delta$ , which characters were developed during times of separation. A very similar situation has been found with the results of crossbreeding experiments between any of the *A. chantrei*-populations (Fig. 4: nos. 1a/c–5) and those of *A. anatoliae* (Fig. 4: 7–28), whereas the intraspecific crosses of *A. chantrei* resulted in all-fertile hybrids.

The hybrid- $\varphi$  may be neglected in the course of an attempted genetic interpretation, because all are fertile<sup>2</sup>. This fact is important with regard to the possibility of using them for backcrosses, at the end of which an all-hybrid-male fertility can again be noticed.

The different sterility phenomena discussed here may at best be explained on the basis of the assumption of substitution genes and transfer of gene-function, an interpretation which was introduced to lower vertebrate-genetic first by KOSWIG (1947). The supposed geomorphological history of Anatolia (LAHN 1948; LÜTTIG et al. 1976) suggests that the ancestors of *A. anatoliae* and *A. chantrei* formed a more or less continuous, i. e. panmictic macropopulation which became divided into two separated ones (VILLWOCK 1958), both of these carrying the same complex of genes controlling all-over fertility at the beginning (VILLWOCK 1964, see Fig. 5). In simplifying the attempted genetic basis situation the whole complex of fertility-genes may be identified by the capital A / Fig. 5. According to the hypothesis of substitution genes it may be supposed that A became with further evolution of the ancestors of *A. anatoliae* substituted by another complex B, so that interbreeding males have had at least the formal constitution A and B (AB) with regard to the interfertility controlling genes. In the course of separation into different groups one of the isolated population-group may have lost A so that only B remained, or, in other words, male-fertility was transformed in the latter one to B. This process should not have had any consequences regarding hybrid-fertility because A and B were substitutes of the same control-mechanism. However, the situation would change dramatically if the gene-complex B became substituted again, for instance by C. In the course of potential crossbreeding between populations either bearing AB or BC fertile as well as sterile hybrid- $\delta$  can be expected within the same offspring, since  $AB \times BC$  results in the following combinations:

<sup>2</sup> The corresponding hybrid- $\varphi$  are without exception fertile.

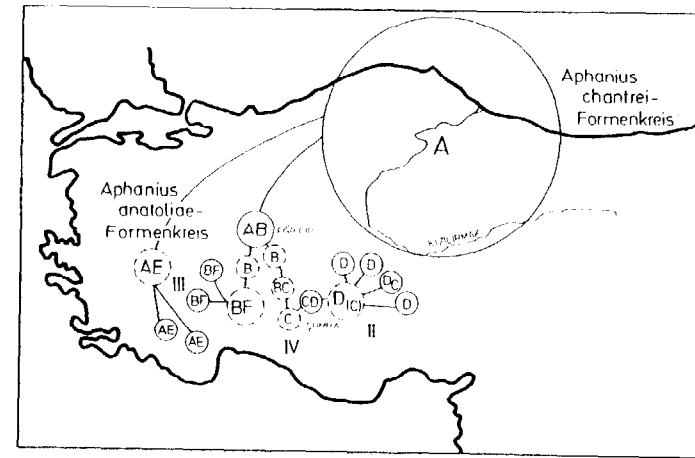


Fig. 5. Graph of genetic interpretation model. Capital letters represent different stages of gene substitution and transfer of the gene function (see text)

AB, AC, BB and BC. Among these four AB, BB and BC are compatible recombinations resulting in fertile males, whereas the combination AC is an incompatible one giving hybrid- $\delta$  sterility. The same process might have occurred repeatedly, due to the degree of separation actually found between the populations of today and the time that has passed since they formed an ancient macropopulation. For instance, B (from BC) might have been lost and C might again have been substituted by another D etc. The gradual differences of the male-sterility phenomena might be easily explained through the assumption that the fertility controlling gene-complexes (A, B, C etc.) represent a polygenic system existing on a series of non-additive, but complementary genes which are able to form numerous different combinations. These might result in the various types of hybrid- $\delta$  sterility actually found in the hybrid-offspring discussed above.

The above briefly explained hypothesis works well even when applied to the different backcross phenomena, especially to the reoccurring fertile hybrid- $\delta$  which are found in the course of repeated backcrosses towards one of the parental forms. According to the genetic distance, as indicated by the degree of separation in distance and time, backcrosses have to be repeated the more times the longer the separation lasted, in order to get back at least some compatible combinations. The latter ones result in some again fertile  $F_2R$ -,  $F_3R$ -,  $F_4R$ - ...  $F_nR$ - backcross- $\delta$ , while others show sterility phenomena decreasing with the counts of repeated backcrosses, according to the recombinations being expected from the high number of polygenes involved in hybrid-fertility control.

If this hypothesis is applied to New World cyprinodonts and their inter- and intraspecific relationships, as indicated by the results of crossbreeding series of *Cyprinodon* (CORZILLIUS 1979), an astonishing parallelism to the Old World *Aphanius* is noticeable in that again all-fertile interbreeding populations (some still given species status) are found as well as others which, in being sterile in the hybrid- $\delta$ , produce a resemblance to the situation exemplified by the endemic Anatolian toothcarp. There are on the one hand species such as *Cyprinodon macularius* (Fig. 6a) and its relatives (i. e. *C. salinus*, *C. nevadensis*; see also Fig. 2) which were proved to give progenies that are more or less fertile in both sexes of their hybrids (CORZILLIUS l. c.). The *C. variegatus* group on the other hand (Fig. 6c, c. f. Fig. 2) in appearing to represent at least more than one single species, bears a great resemblance to *Aphanius anatoliae*. In between both is found *C. rubrofluvialilis* (Fig. 6b, compare Fig. 2).

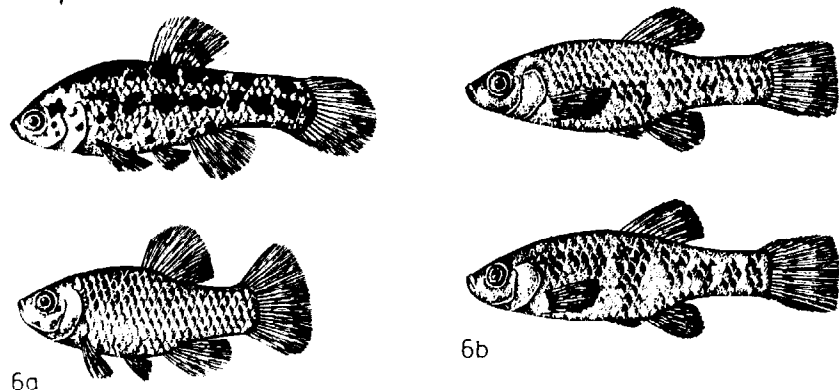


Fig. 6. *Cyprinodon* species, representing some main groups. 6a = *C. macularius* ("C. macularius-Group"); 6b = *C. rubrofluviatilis*; 6c = *C. variegatus* ("C. variegatus-Group"). - (see text)

The hybridization between representatives of the eastern and the western *Cyprinodon* species-flocks which produces all-male sterility while the females are fertile, resembles (as far as has been tested up to now) the situation between *A. anatoliae* and *A. chantrei*. Crosses between test-species of the western species-group, i. e. west of *C. rubrofluviatilis* (see Fig. 2) and the latter, results in an all-F<sub>1</sub>-hybrid fertility: The few F<sub>2</sub>-offsprings, however, which hatched did not survive for long ("hybrid break-down" sensu STEBBINS 1958). Crosses between *C. rubrofluviatilis* and representatives of *C. variegatus* are more successful than the former ones (number of F<sub>2</sub>-survivals), indicating that *C. rubrofluviatilis* is genetically nearer to *C. variegatus* than to any of the so-called western species<sup>1</sup> (CORZILLIUS 1979: 78ff, see also STEVENSON and BUCHANAN 1973). In other words, *C. rubrofluviatilis* acts as a certain "link" between the eastern and western species of *Cyprinodon* (with some more affinities to the former than to the latter), in the same way that the populations of Çumra and Eğirdir do in the population-chain of *Aphanius anatoliae* (see p. 189). Apart from the greater complexity of the phenomena in discussion within *Cyprinodon* compared with *Aphanius* (differing geographic dimensions, numbers of isolated populations etc.), the situation as a whole, which is found within the genus *Cyprinodon* is rather comparable to an infraspecies-flock ("Formenkreis") undergoing different degrees of speciation than to a group of valid species. In this respect *Cyprinodon* resembles the situation of the endemic Anatolian toothcarp and

<sup>1</sup> Sufficient knowledge is not available on the genetic background of the southern population groups of *Cyprinodon* which follow the outlines of the ancient basins IV and V shown in Fig. 2 (according to MILLER 1981; informations on the systematic status see: MILLER 1968, 1976; CORZILLIUS 1979). Moreover, it has to be taken into account, that most likely hetero- and homogametic ♂♂ as well as homo- and heterogametic ♀♀ evolved in certain *Cyprinodon* units, through which the situation within the genus *Cyprinodon* is additionally made more complicated than within the Anatolian *Aphanius*.

so the genetic interpretation of speciation which works for *Aphanius* should also be a working model for *Cyprinodon*. Further evidence for the explanation given for the relationships within the genera *Aphanius* and *Cyprinodon* can be drawn from enzyme-electrophoresis (SCHOLL et al. 1978; TURNER 1972, 1974; TURNER et al. 1977; CORZILLIUS 1979; SOLTZ and HIRSHFIELD 1981).

The taxonomic consequences of the experimental results here discussed have to be explained separately. However, the discussion should not follow that of PARENTI (1981).

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#### Summary

Old World cyprinodontids (Pisces: Cyprinodontidae) of the genus *Aphanius* and New World representatives of the genus *Cyprinodon* inhabit corresponding remains of different abiotic factors (i. e. composition and degree of salinity, temperature), produced by arid climates, for instance in barren plains or similar regions. Old World species of *Aphanius* are widely distributed around ancient as well as recent outlines of the Mediterranean Sea, along the Arabian Peninsula as far as Iran and Karachi/Pakistan. Within these distribution patterns they are not only common to marine waters but are also found in salt-pans or other closed coastal lagoons with hypersaline conditions. *Cyprinodon* with its different species is found today from the West-Indies and the eastern Atlantic and Gulf Coast throughout the desert drainage of the southern United States and northern Mexico to the very ancient and the recent coasts of the Gulf of California in the west (i. e. Salton Sea). The regions mentioned, both in the Old and in the New World, derived their present characters from comparable geomorphologic changes since the Miocene. The more or less continuous distribution along the ancient Thetys slowly disintegrated into independent larger and smaller areas, until the present situation was reached within post-glacial times. Through this, old panmictic populations of the ancestors of recent *Cyprinodon* or *Aphanius*, respectively, fell into smaller ones as well. By means of crossbreeding experiments it can be shown that speciation took place in both cyprinodont units by way of microevolution which corresponds to the course of the historic development of their habitats, - an interdependency which is to be shown by the presented paper. The idea of substitution-genes and transfer of gene function, put forward by KOSSWIG (1947) et al. is discussed as an interpretation of the different degrees in species formation which is detectable in both groups of cyprinodont fishes in question.

#### Résumé

Le genre *Aphanius* (Nardo, 1827) et le genre *Cyprinodon* (Lac., 1803) (Pisces: Cyprinodontidae), un modèle d'interprétation génétique pour la spéciation

Parmi les Cyprinodontidés de l'ancien monde et du nouveau monde il y a des espèces du genre *Aphanius* et du genre *Cyprinodon*, qui, respectivement, chacun dans sa zone de développement, colonisent des endroits semblables. La ressemblance des lieux de colonisation comprend la géologie (géomorphologie; formation géologique) ainsi que la diversification climatique des eaux et la condition écologique. Ces poissons ont colonisés également des eaux marines, saumâtres (jusqu'à hypersalées) et douces; plus ou moins isolées: *Aphanius* dans le région Méditerranéenne au Moyen et au Proche Orient, *Cyprinodon* dans le sud des Etats-Unis et au Mexique du Nord et du centre (avoisinant les côtes et les îles de l'Atlantique et de la mer des Caraïbes). Dans l'ère postglaciale, particulièrement dans les savannes arides des deux zones, les populations, à l'origine homogènes, ont commencé à se diversifier, mettant en scène des procédés de spéciation d'importances diverses. Des expériences d'hybridation (ainsi que des résultats expérimentaux ultérieurs) permettent de reconnaître un système gradué des phénomènes de fertilité et de stérilité chez l'espèce *Aphanius* de l'ancien monde, reflétant les facteurs d'isolation (l'espace et le temps).

Avec l'aide de l'hypothèse sur l'existence des gènes de substitution et du transfert de la fonction des gènes (KOSSWIG 1947) on y trouve l'application de l'interprétation génétique.

En effet, ce modèle d'interprétation peut également être appliqué aux espèces *Cyprinodon* du nouveau monde, comme on a pu le démontrer par les croisements actuels en particulier par les expé-

riences (par ex. enzyme-electrophorèse). Pareillement on y trouve une parenté graduelle comprenant un groupe d'espèces de l'ouest (*C. macularius*-groupe) et de l'est (groupe *C. variegatus*). Entre eux il existe un intermédiaire géographique et génétique, ici représenté par *C. rubrofluvialis* (actuellement le classement de parenté des espèces *Cyprinodon* du Nord et du Centre du Mexique n'est pas possible.) La grandeur de l'ensemble de la zone de développement des *Cyprinodons* ainsi que le plus grand nombre d'espèces et des populations (comparé aux espèces *Aphanius*) qui en résultent, ont engendré une plus grande complexité à l'égard des nuances des phénomènes de fertilité et de stérilité parmi les hybrides. Cependant ce phénomène ne contredit pas l'interprétation génétique du modèle ci-présenté.

### Zusammenfassung

*Aphanius* (Nardo, 1827) und *Cyprinodon* (Lac., 1803) (Pisces: Cyprinodontidae), ein Versuch für eine genetische Interpretation der Speziation

Altweltliche Vertreter des Cyprinodontiden-Genus *Aphanius* und neuweltliche Angehörige der Gattung *Cyprinodon* (Pisces: Cyprinodontidae) besiedeln in ihren jeweiligen Verbreitungsgebieten vergleichbare Habitate. Die Vergleichbarkeit reicht von der geomorphologischen Entwicklung und der klimatisch bedingten (postglazialen) Aufgliederung ihrer Wohngewässer bis hin zu deren ökologischer Beschaffenheit: Im Mittelmeerraum, dem Vorderen und Mittleren Orient (*Aphanius*) respektive in den Südstaaten der USA, dem nördlichen und zentralen Mexiko (mit den angrenzenden atlantischen und karibischen Küsten- und Inselgebieten: *Cyprinodon*) besiedeln diese Fische mehr oder weniger isolierte marine, brackige (bis hypersaline) und Süßgewässer. Besonders in den ariden Steppengebieten beider Verbreitungsareale ist es postglazial zur Aufsplitterung ursprünglich „einheitlicher“ (panmiktischer) Großpopulationen gekommen. Dadurch sind Speziationsprozesse unterschiedlichen Ausmaßes in Gang gesetzt worden.

Kreuzungsexperimente (u. a. experimentelle Befunde) lassen an den besonders gut untersuchten altweltlichen, endemisch-anatolischen (= kleinasiatischen) *Aphanius*-Arten (*A. anatolicus*, *A. chantrei*) ein abgestuftes System von Bastard-Fertilitäts-/Sterilitätsphänomenen erkennen, das die wirksamen Isolationsfaktoren (Raum und Zeit) gut widerspiegelt. Mit Hilfe der Annahme von Substitutionsgenen und Transfer der Genfunktion sensu KOSWIG (1947) läßt sich hierfür eine genetische Erklärung finden und in Anwendung bringen. Dieses Interpretationsmodell läßt sich auf Grund vorliegender Kreuzungs- u. a. Experimente (z. B. Enzym-Elektrophorese) auch auf die neuweltlichen *Cyprinodon*-Arten übertragen. Auch sie zeigen ein entsprechend abgestuftes Verwandtschaftsgefüge, bestehend aus einer westlichen (*Cyprinodon macularius*-Gruppe) und einer östlichen Artengruppe (*C. variegatus*-Gruppe), sowie einem geographischen und genetischen „Bindeglied“ in der Populationskette, im Experiment repräsentiert durch *C. rubrofluvialis* (die verwandtschaftliche Einordnung der *Cyprinodon*-Arten aus Nord- und Zentralmexiko ist z. Z. noch nicht möglich).

Die Größe des Gesamtverbreitungsgebietes von *Cyprinodon* und die daraus resultierende größere Zahl von Populationen und Arten gegenüber den entsprechenden Verhältnissen bei den kleinasiatischen *Aphanius*-Arten hat naturgemäß auch eine größere Komplexität in der graduellen Abstufung der Fertilitäts-/Sterilitätsphänomene bei *Cyprinodon* hervorgebracht, die jedoch nicht dem Modellcharakter der vorgetragenen genetischen Interpretation widerspricht.

### Literature

- AKSIRAY, F.; VILLWOCK, W., 1962: Populationsdynamische Betrachtungen an Zahnkarpfen des südwest-anatolischen Aci- (Tuz-) Gölü. Zool. Anz. 168, 87–101.
- BLACKWELDER, E.; HUBBS, C. L.; MILLER, R. R., 1948: The Great Basin, with Emphasis on Glacial and Postglacial Times. Bull. Univ. Utah 38, 1–166.
- BEAUFORT, L. F. DE, 1951: Zoogeography of the Land and Inlandwaters. London: Sidgwick & Jackson. 1–208.
- CONSTANTZ, G. D., 1981: Life History Patterns of Desert Fishes, in: Fishes in North American Deserts. New York: John Wiley & Sons. 237–290.
- CORZILLIUS, B., 1979: Weitere Untersuchungen über Speziationsphänomene in der neuweltlichen Zahnkarpfengattung *Cyprinodon* (Pisces: Cyprinodontidae). Diss., Fachbereich Biologie, Universität Hamburg. 1–106.
- ERMAN, S., 1953: Zoogeography of the Sea. London: Sidgwick & Jackson. 1–417.
- GAILLARD, C., 1895: Notes sur quelques espèces de *Cyprinodons* de l'Asie Mineure et de la Syrie. Arch. Mus. Hist. nat., Lyon, 6, 3–15.
- HUBBS, C.; DREWRY, G. E., 1959: Survival of  $F_1$ -hybrids between *Cyprinodont* fishes, with a discussion of the correlation between hybridization and phylogenetic relationship. Publ. Inst. Mar. Sci. 6, 81–91.

- KARBE, L., 1961: Cytologische Untersuchungen der Sterilitätserscheinungen bei anatolischen Zahnkarpfen, ein Beitrag zum Speziationsproblem. Mitt. Hamburg. Zool. Mus. Inst. 59, 73–104.
- KOSWIG, C., 1947: Über Substitutionsgene und den Transfer der Genfunktion. Experimentia 3, 401–410.
- 1953: Über die Verwandtschaftsbeziehungen anatolischer Zahnkarpfen. Hydrobiologi. Istanbul Univ. Fen Fak. B 1, 186–198.
- 1956: Über Makro- und Mikropopulationen des Zahnkarpfens *Anatolichthys*. Zool. Anz. 156 (5/6), 75–90.
- KOSWIG, C.; AKSIRAY, F., 1949: Die Schuppenreduktion natürlicher Zahnkarpfenpopulationen genetisch betrachtet. Portugaliae Acta Biol. A, 88–105.
- LAHN, E., 1948: Contribution à l'étude géologique et géomorphologique des lacs de la Turquie. Publ. Inst. Etud. Rech. Minières en Turquie, B 12, 89–178.
- LEIDENFROST, G., 1912: Fishes from Asia Minor. Allattani Közlemenyek. Organ. Kgl. ungar. nat. wiss. Ges. 11 (3), 125–132.
- LÜTTIG, G.; STEFFENS, P., 1976: Explanatory Notes for the Paleogeographic Atlas of Turkey from the Oligocene to the Pleistocene. Bundesanst. f. Geowiss. und Rohstoffe, Hannover, 2–64.
- MILLER, R. R., 1948: The cyprinodont fishes from the Death Valley system of eastern California and southwestern Nevada. Misc. Publ. Mus. Zool. Univ. Michigan 68, 1–155.
- 1950: Speciation in fishes of the genera *Cyprinodon* and *Empetrichthys*, inhabiting the Death Valley Region. Evolution 4, 155–163.
- 1981: Coevolution of Deserts and Pufffishes (Genus *Cyprinodon*) in the American Southwest. In: Fishes in North American Deserts. New York: John Wiley & Sons. 39–94.
- PARENTI, L. R., 1981: A Phylogenetic and Biogeographic Analysis of Cyprinodontiform Fishes (Teleostei, Atherinomorpha). Bull. Amer. Mus. Nat. Hist., New York, 168, 335–557.
- SCHOLL, A.; CORZILLIUS, B.; VILLWOCK, W.: Beitrag zur Verwandtschaftsanalyse altweltlicher Zahnkarpfen der Tribus Aphaniini (Pisces, Cyprinodontidae) mit Hilfe elektrophoretischer Untersuchungsmethoden. Z. zool. Syst. Evolut.-forsch. 16, 116–132.
- SÖZER, F., 1942: Contributions à la connaissance des Cyprinodontides de la Turquie. Rev. Fac. Sci. Univ. d'Istanbul 7, 307–316.
- SOLTZ, D. L.; HIRSCHFELD, M. F., 1981: Genetic Differentiation of Pufffishes (Genus *Cyprinodon*) in the American Southwest. In: Fishes in North American Deserts. New York: John Wiley & Sons. 291–334.
- STEBBINS, G. L., 1958: The Inviability, Weakness and Sterility of interspecific Hybrids. Adv. in Genetics 9, 147–215.
- STEVENSON, M. H.; BUCHANAN, T. M., 1973: An analysis of hybridization between the cyprinodont fishes *Cyprinodon variegatus* and *C. elegans*. Copeia 1973 (4), 682–692.
- TURNER, B. J., 1972: Genetic divergence and variation of Death Valley pupfish population. Ph. D. diss., Univ. of Calif., Los Angeles. pp. 144.
- 1974: Genetic divergence of Death Valley pupfish species: Biochemical versus morphological evidence. Evolution 28, 281–294.
- TURNER, B. J.; LIU, R. K., 1977: Extensive Interspecific Genetic Compatibility in the New World Killifish Genus *Cyprinodon*. Copeia 1977 (1), 259–269.
- VILLWOCK, W., 1958: Weitere genetische Untersuchungen zur Frage der Verwandtschaftsbeziehungen anatolischer Zahnkarpfen. Mitt. Hamburg. Zool. Mus. Inst. 56, 81–152.
- 1963: Genetische Analyse des Merkmals „Beschuppung“ bei anatolischen Zahnkarpfen (Pisces, Cyprinodontidae) im Auflösungversuch. Zool. Anz. 170, 23–45.
- 1964: Genetische Untersuchungen an altweltlichen Zahnkarpfen der Tribus Aphaniini (Pisces, Cyprinodontidae) nach Gesichtspunkten der Neuen Systematik. Z. zool. Syst. Evolut.-forsch. 2, 267–382.
- 1981: Distribution, Ecology and Intraspecific Variability of some external Characters in *Aphanius* (Pisces: Cyprinodontidae). A Contribution to regressive Evolution in Fish. Rapp. Comm. int. Mer Médit. 27 (5), 119–125.

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