DISTRIBUTION, ECOLOGY AND INTRASPECIFIC VARIABILITY OF SOME EXTERNAL CHARACTERS IN APHANIUS (PISCES: CYPRINODONTIDAE). A CONTRIBUTION TO REGRESSIVE EVOLUTION IN FISH.

by

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Abstract: Intensive studies, especially on South-west Anatolian aphaniine species as well as on Western Mediterranean ones, leave no doubt that certain characters in regression (i.e. scales, teeth and ventral fins) are under genetic control, which follows Mendelian inheritance. Crossbreeding analyses gave rise to the assumption that the reductions which can be seen in the characters mentioned, do not show a distribution by chance. All the characters on the one hand which undergo reductions are very often combined with one another in the same specimen (or population) and on the other hand, seem to be nearly related to some special biotop factors (i.e. waterchemistry). The mode of reductions in discussion is very similar to that which can be shown to occur in certain characters of cavernicolous animals (i.e. eye- and pigment reduction) and which is called the phenomenon of regressive evolution.

Résumé: Depuis presque 40 ans on a fait des recherches sur les Cyprinodontes ovipares de la région de la méditerranée et de l'Orient adjoint, pour préciser les mécanismes de la micro-évolution. Les recherches se basent sur les différences du développement des écailles, des nageoirs et des dents chez les neuf espèces de genre Aphanius. Les expériments surtout avec les espèces provenent de l'Ouest de Turquie tont confirmé que la réalisation des differences suit les règles de Mendel. Les hybridations démontrent que certains characteristiques sont combinés et montrent des relations avec la composition de l'eau (surtout le chemisme). La façon de réduction rappelle les phénomènes de l'évolution regressive chez les animales cavernicoles.

Within the last 40 years oviparous toothcarps (Pisces: Cyprinodontidae) of the Mediterranean region and the adjoining Near and Middle East have been repeatedly at the center of scientific investigations for answering questions on the mechanisms of (micro-) evolution (Villwock, 1964). In the course of these efforts differences in the development of scales, teeth and ventral fins were mainly used as indicators.

Reductions of scales and/or fins are not regressive processes restricted to Old World toothcarps (or toothcarps at all), but are phenomena occuring in numerous other taxa as well (e.g. Blenniiformes, Apodes). It is remarkable that these reductions came into existence independently from each other, or, in other words, that they appeared under very different ecological conditions during the course of evolution. The particularity of scale- and fin-reductions in toothcarps, Old World Aphanius as well as New World Cyprinodon, is given by the fact that there is a correlation between the existence and degree of these regressive characters on the one hand and some special ecological conditions of the habitats of these fishes on the other. It is an outstanding fact that scale- and fin-reduction do not exist either under freshwater conditions (with one single exception) or marine ones, not even in hypersaline waters of marine composition. The reductions concerned are, as a rule, restricted to specimen (or populations) living in bodies of water which are or were subjected to arid climatic conditions and, as a result, became and become enriched in bitter- (SO_4''-) salts. Frequently, reductions of scales and ventral fins are also combined with alterations in the shape and arrangement of teeth.

Reduced scales are not only smaller in size (they may even be macroscopically invisible) but are also simpler in substructures than normal ones. The diminution obviously takes place through the division of scale-germs at a very early stage of their ontogenetic development with an early stop of growth and final differentiation (figs.1a-c) (Akşiray 1952, Ermin 1946). The reduction of fins among these toothcarps is normally restricted to the ventral ones and effects the number of fin-rays and, as a result, not only the size of the external parts of the fins, but also the structure of their interior skeleton (figs. 2a-c) (Nalbandoglu 1959). The teeth, most often arranged in one single row along the jaws and of tricuspid shape, may all or in part be reduced to conical ones, i.e. both types may occur in the same specimen (fig. 3) (Özarslan 1958), eventually together with intermediate stages.

As highly instructive at an attempted interpretation of this briefly explained situation may be mentioned the Southwest Anatolian Lake Aci-Göl which is surrounded by a series of fountains that differ slightly from each other in their water-chemistry. It can be shown that the toothcarp-populations which exist in fountains with predominantly freshwater conditions hardly ever show reductions, whereas in other populations which are forced to live in fountains influenced by sulfate-brackish lakewater, reductions are very common. The third group of fountains, defined by changes in their water-composition from fresh- to highly brackish water, is inhabited by so-called 'mixed' populations as far as the degree of scale-reductions is concerned (Akşiray 1952, Akşiray & Villwock 1962). Cross-breeding experiments between specimen of differently scaled populations proved these reduction phenomena to be based on a complex polygenic heriditary which is also true for other types of reductions. As the results of further experimental investigations show, i.e. F_1-progeny between Aphanius (Tellia) apodus x A. iberus (Villwock 1981: in press), it is very probably that the variability in the hybrid characters depends not only on the degree of heterozygosity but also on biogenic influences, such as the left-right asymmetries in the counts of ventral fin-rays, for instance, show. As far as the alterations in structure and formation of teeth from normally developed ones are concerned there is, up to the present, no definite answer. Investigations of different Aphanius species have shown that there are continously formed generations of teeth, the first of which are merely conical ones. These teeth are then replaced during the course of further development of the embryos by a second and even a third generation which form at least that single row of tricuspid teeth regularily found in Aphanius s.str. (Franz & Villwock 1972). In the monotypic Aphanius (Kosswigichthys) asquamatus all the teeth along the jaws are conical. They are more numerous than in all other Aphanius and, strangely, form more or less 2-3 irregular rows, instead of the single common in Aphanius itself. The question which is still unanswered, is, in how far the more numerous and irregularily arranged teeth of A. (K.) asquamatus are the result of ontogenetic processes similar to those which lead to the phenomena of scale-reductions. In other words, it might be possible that the special tooth arrangement of A. (K.) asquamatus has to be seen as the result of an ontogenetic early division of tooth-germs into at least two separate ones, with growth and structures restricted to those of the primary dentition, as is the case for scales and their reduction phenomena (see figs. 1a-c).

With reference to the phylogenetic history of these regressive characters it has to be pointed out, that there is no evidence of a merely fortuitous development of these because then the same coincidances should have taken place repeatedly and independently from one another in different species of Aphanius (and in a corresponding way in New World Cyprinodon). That the different reduction phenomena which occur in recent toothcarps may have been derived from hybrid origin, i.e. very interbreeding of 'normally' developed Aphanius s.str.-like and A. (K.) asquamatus-like ancestors is an assumption that might explain the situation found among the Anatolian toothcarps (see Kosswig 1953). This hypothesis, however, would not explain where the 'reduced' ancestor and representatives of non-Anatolian species would have derived their reductions from. An instantaneous (which means a direct) influence from the bit-

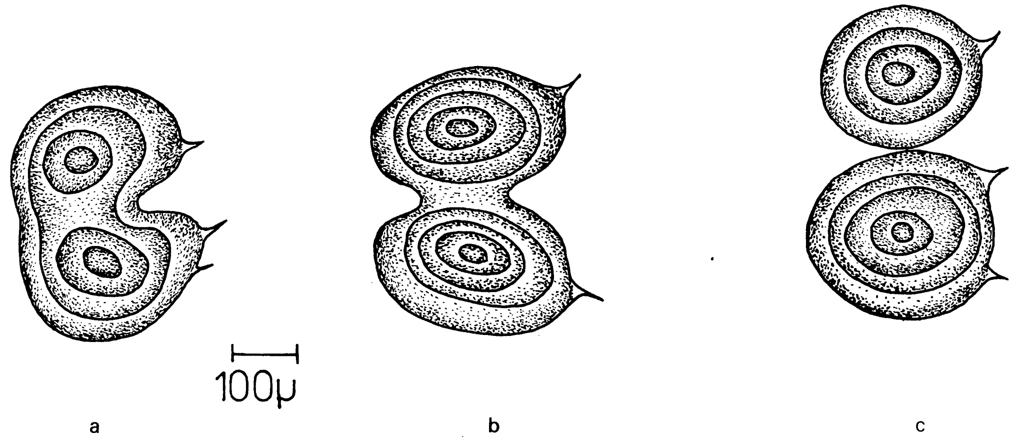

Fig. 1

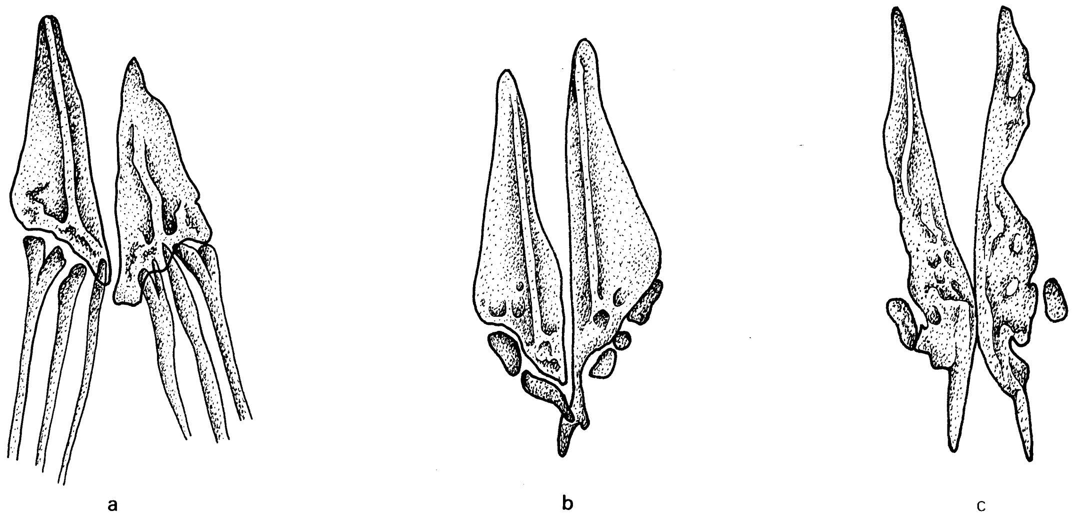

Fig. 2

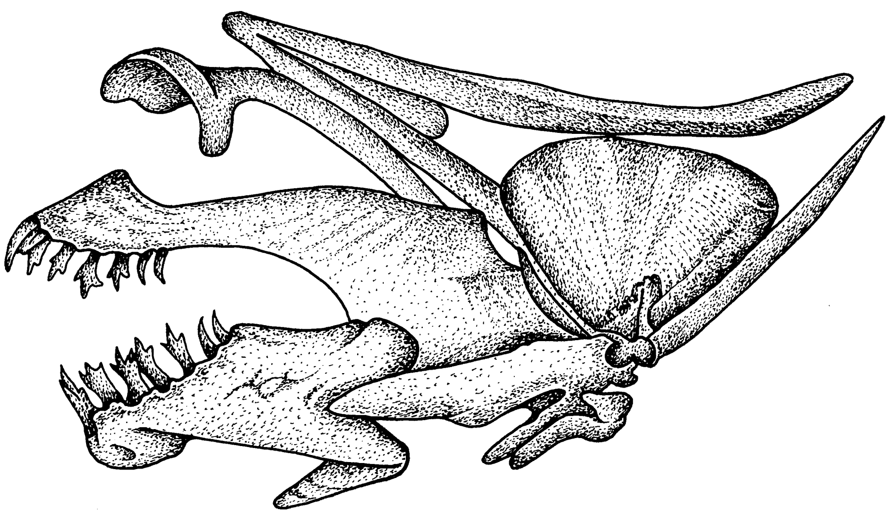

Fig. 3

tersalt conditions on certain ontogenetic developmental stages could not be proved (Grimm 1976). Most probably, we have to consider that, corresponding to the situation in cavernicolous animals (i.e. loss of eyes and body pigment), the stabilizing selection which normally acts upon the continuance of biologically worthwhile characters dropped its efficiency (Kosswig 1976). Because of the fact that quite different fish living under quite different environmental conditions lost scales, fins and even teeth, we may be allowed to suggest that these characters may be dispensable if life circumstances change during the course of evolution, especially to extreme ones as in the toothcarps in question.

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text (figs.): all drawings Monika HÄNEL/Hamburg

figs. 1a-c: Different stages of division of scale-germs (after AKŞIRAY 1952, altered).

figs. 2a-c: Rudimentation of ventral-fins (after NALBANDOGLU 1959, altered).

fig. 3: Jaw skeleton (after ÖZARSLAN 1958, altered).