EVOLUTION OF BLENNIOIDEI IN THE MEDITERRANEAN SEA

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Résumé.

L'évolution du peuplement de quelques Blennioidei (Pisces, Perciformes) au cours du tertiaire et du quaternaire est brièvement discutée.

Deux espèces du genre *Tripterygion*, *T. tripteronotus* et *T. xanthosoma*, très similaires dans leurs caractères morphologiques, habitent des biotopes bien distincts. On peut supposer qu'il s'est produit deux immigrations successives en Méditerranée à deux époques différentes après la fin des périodes glaciaires. Les premiers arrivants n'auraient pas colonisé la zone nouvellement immergée par suite du dégel progressif des masses glaciales polaires ; par contre, la deuxième vague d'immigrants se serait installée près de la surface (niche laissée inoccupée par les premiers immigrants). Après établissement des barrières sexuelles, ces deux populations auraient évolué en deux espèces différentes.

Contrairement au genre *Tripterygion*, l'évolution des espèces du genre *Blennius* qui étaient endémiques en Méditerranée, se serait déroulée sur place après la fin des périodes glaciaires. Durant ce laps de temps (environ 10 000 années), une différenciation multiple serait à l'origine d'espèces jumelles (sibling species) à caractères morphologiques comparables, mais à exigences écologiques différentes (tabl. 1).

Blennius fluviatilis montre une distribution périméditerranéenne dans les eaux douces. Cette espèce pourrait dériver d'un ancêtre qui vivait en Méditerranée pendant le miocène, période pendant laquelle cette zone s'est progressivement dessalée. Ce descendant, indifférent aux variations de salinité et de température, aurait conquis de la sorte, pendant le pliocène, toute la Méditerranée et aurait immigré dans divers biotopes de l'eau douce. Grâce à leur tolérance aux températures froides, ces poissons auraient pu survivre pendant les périodes glaciaires. Une espèce proche de *B. fluviatilis*, *B. pavo*, vit en eau de mer et en eau saumâtre dans la région de l'Atlantique Est et de la Méditerranée. Elle dériverait probablement du même ancêtre que la première et n'aurait immigré qu'après la fin des périodes glaciaires.

Ces trois exemples illustrent le cours de la phylogenèse des éléments faunistiques méditerranéens

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The suborder Blennioidei (Perciformes, Pisces) is known to have existed since the Eocene period (BERG, 1958). The species of this taxon are today found in oceans all over the world and have also gone over to living in fresh water. In the European Mediterranean Sea the Blennioidei are represented by the Blenniidae with 19, Clinidae with 1, and Tripterygiidae with 3 species. When, about 60

species-group	species *Blennius*	morphology	ecology		
			light demands	water movement	salinity
Sphinx	*sphinx*		photophil	euryklyd (1)	stenohaline
	rouxi		»	klydophob	»
	zvonimiri	very similar	photophob	klydophob ?	»
	incognitus	very similar	euryphot	klydophob	»
Canevae	*canevae*	very similar	euryphot	euryklyd	stenohaline
	nigriceps	very similar	photophob	?	»
	adriaticus	very similar	photophil	klydophob ?	»
	dalmatinus	very similar	»	klydophob	euryhaline

TABLE 1. — *Morphological and ecological comparison of* 8 Blennius *species* (after EGGERT, 1931 ; ABEL, 1962 ; ZANDER, 1972 b) (1) This new term proposed is derivated from the Greek word κλγδων = surf.

million years ago, the first representatives of these fishes appeared, the present-day Mediterranean Sea formed part of the Tethys, the great tropical ocean, reaching from India to America. Only one

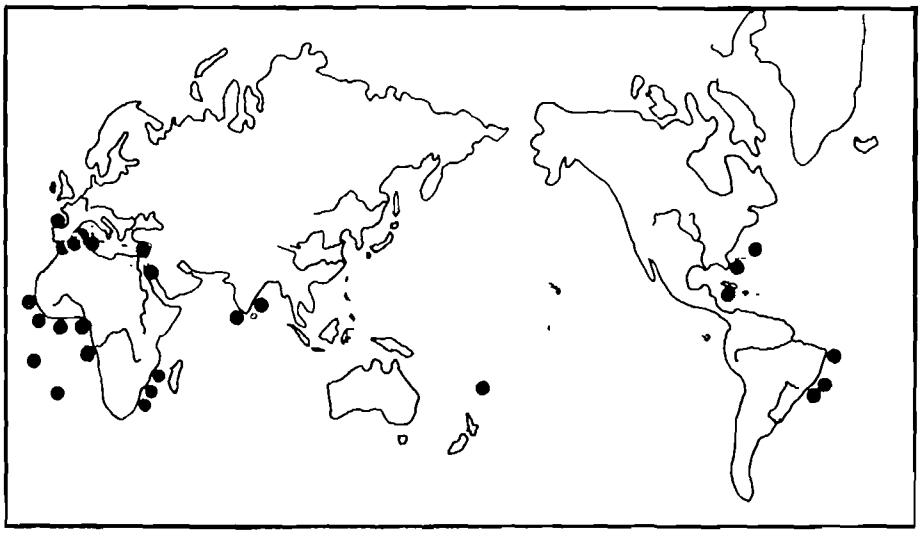

FIG. 1. — *Places of discovery of* Blennius cristatus. After : ZANDER, 1972 a.

of the blennioidean species, *Blennius cristatus*, can be considered as a true tethyan relict, as this occurs in morphologically identical populations throughout the whole world (fig. 1).

Diverse paleohistorical events have influenced the distribution and further evolution of the Blennioidei decisively (EKMAN, 1953 ; MARS, 1963 ; RUGGIERI, 1967).

a) In the lower Miocene, the connection ceased between the Indian Ocean and the Mediterranean Sea.

b) In the upper Miocene, the Mediterranean Sea was cut off from the Atlantic Ocean, too ; it turned to a great extent to fresh water conditions or even dried out completely in places.

c) At the beginning of the Pliocene period the Straits of Gibraltar were opened, so that marine conditions were reestablished.

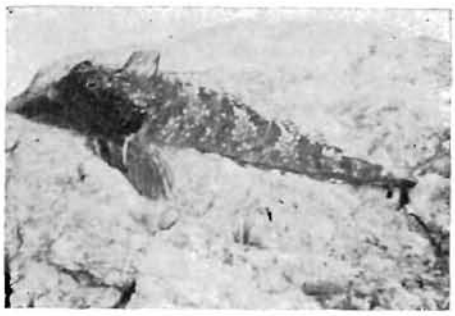

FIG. 2. — *Tripterygion tripteronotus*, male.

FIG. 3. — *Tripterygion xanthosoma*, male and female (right).

d) The first lowerings of temperature occured in the Eocene period, and caused a replacement of the old tropical fauna by a subtropical one.

e) Drastic climatic changes happened in the Quaternary, resulting in the extinction of subtropical species and the colonization by boreal faunal elements in the Mediterranean Sea. A reimmigration of warm-water species was possible in the interglacial periods from the coast of West Africa, which had served as a refuge for the Mediterranean species.

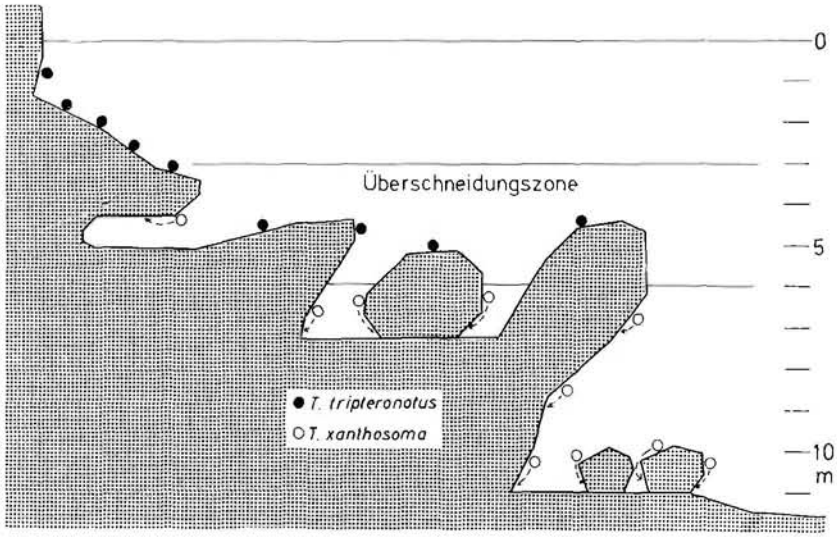

FIG. 4. — *Vertical distribution of* Tripterygion tripteronotus *and* T. xanthosoma *in the Banyuls area* (France). After : ZANDER and HEYMER, 1970.

f) The direction of currents in the Straits of Gibraltar has depended on the climatic changes. During the interglacial periods warm, near-surface water flowed into the Mediterranean Sea, and the deeper water (from below 200 m) flowed out of it into the Atlantic Ocean ; during the glacial periods the current directions had been the reverse. Therefore, the reimmigration of species from the West-African refuge was facilitated by the postglacial in flux of surface-water.

Subsequently the phylogeny of some blennioidean species should be discussed with regard to paleohistorical events. These little demersal fishes live at the upper rocky littoral level, which extends vertically up to the water surface in most cases. As adult individuals remain in close neighborhood of their habitats, the only chance for further distribution lie in the larvae having a planctonic way of life.

Blennius cristatus mentioned above may have existed since the Eocene period. According to distinct morphological characteristics (e.g. well developed lateral organs, absence of canine teeth) it seems to be an ancient species and can be considered as the ancestor form in the evolution of the other *Blennius* species (ZANDER, 1972 a). The origin of the genus *Tripterygion,* which will also be treated in this paper, must have occured before the Miocene period, for it is distributed in the Indian and Atlanto-Mediterrannean region, but in each of them with different species.

There are 3 *Tripterygion* species in the Mediterranean Sea (*T. tripteronotus* (RISSO) in the Atlantic Ocean, too). *T. tripteronotus* and *T. xanthosoma* ZANDER and HEYMER hardly differ in morphological characteristics but distinctly in the preference for different ecotopes (ZANDER and HEYMER, 1970) (fig. 2 and 3). While one mostly finds *T. tripteronotus* in bright biotopes between 0 and 2 m below water surface and at most up to a depth of 6 m, *T. xanthosoma* chiefly lives between 6 and 8 m in places below overhanging rocks (fig. 4) where less than 10 % light reception can be measured (« Reflexlichtzone » ; RIEDL, 1966) ; it has been found up to 25 m depth. For the most part, both species inhabit sympatrically the whole of the Mediterranean Sea. It is supposed that they have differentiated after the end of the glacial periods from a common ancestor living in the refuge area of West

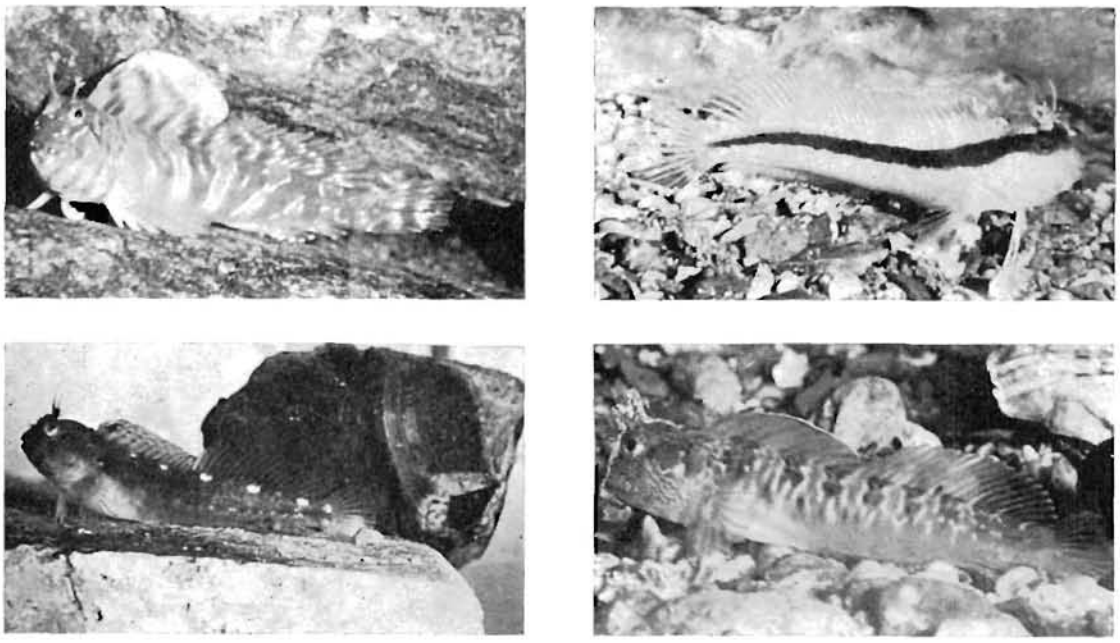

FIG. 5 à 8. — *Above, left :* Blennius sphinx, *male, right :* B. rouxi, *male ; below, left :* B. zvonimiri, *male, right :* B. incognitus, *male.*

Africa. Thereafter a twofold immigration in the Mediterranean Sea is conceivable : the first immigration is that of the northern margin populations, being less sensitive to cold than the central populations. These latter followed in a second wave as temperature and water level almost reached present conditions. It is presumed (ZANDER and HEYMER, l.c.) that the first immigrators (= *T. xanthosoma*) stayed in their chosen ecotopes and did not follow the ascending water surface, caused by the melting of the polar ice. The result was an adaptation to the changed situations (depth, light) of their habitats and the establishment of sexuel barriers to the later immigrating populations (= *T. tripteronotus*) colonizing the upper light zone.

Where as the speciation of the *Tripterygion*-species can be explained by multiple immigrations in the Mediterranean Sea, the phylogeny of the *Blennius*-species, being endemic in this area, is more difficult to judge. We have to consider *Blennius sphinx* CUVIER and VALENCIENNES, *B. rouxi* COCCO, *B. zvonimiri* KOLOMBATOVIC, *B. incognitus* BATH (subgenus *Salaria*, Sphinx-species-group) (fig. 5 to 8), and *B. canevae* VINCIGUERRA, *B. nigriceps* VINCIGUERRA, *B. adriaticus* STEINDACHNER and KOLOMBATOVIC, *B. dalmatinus* STEINDACHNER and KOLOMBATOVIC (*subgenus Lipophrys*, Canevae-species-group) (fig. 9 to 12). Beside these species, *B. basiliscus* CUV. and VAL. and *B. fluviatilis* ASSO which will be dealt below are recorded exclusively in the Mediterranean Sea. The Sphinx and the Cane-

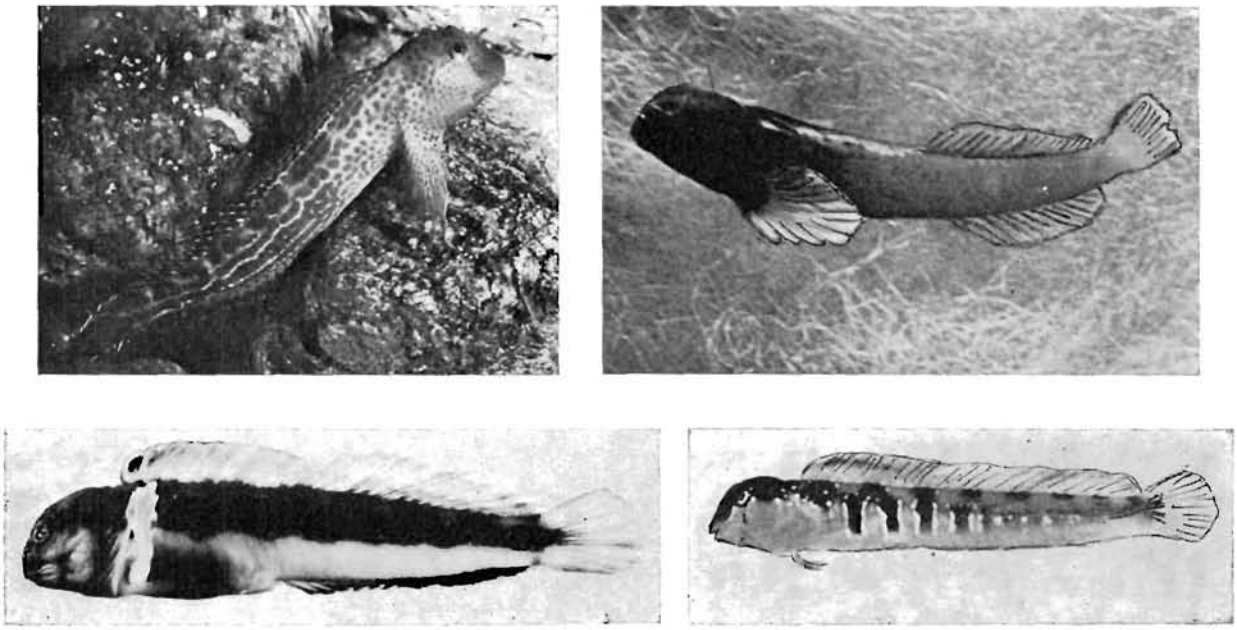

FIG. 9 à 12. — *Above, left :* Blennius canevae, *male subdominance colouring, right :* B. nigriceps, *male ; below, left :* B. adriaticus, *male* (photo H. BATH), *right :* B. dalmatinus, *male nuptial colouring.*

vae-species-groups are completely endemic there. Representatives of both of these groups are considered to be highly evolved in respect of morphological, ecological, and ethological characteristics (e.g. by possession of clublike glands at dorsal and anal fins in the males, by the colonization of hapting holes, and by the attraction of females, by pronounced optic signs of the males ; ZANDER, 1972 a). It is assumed that their speciation took place very late and in the Mediterranean Sea itself after their ancestors had immigrated from the West African refuge in postglacial times. This interval of only 10 000 years appears realistic if we suppose an ancestor which had been tolerant to changes in light, water movement, and eventually in salinity and temperature. The speciation took place after this ancestor had colonizated different biotopes, and each of its descendants had adapted themselves to them. This assumption is supported by the existence of sibling species just in the Sphinx - and Canevae-species-groups, which are hardly to be distinguished in morphological characteristics, but clearly differ in their ecology (table 1).

Relations of the Sphinx and Canevae-species-groups to another *Blennius* species only can be estimated. While *B. sphinx* and its relatives show similarities in morphology to *B. gattorugine* of the world-wide Gattorugine-species-group, the Canevae-species-group seems to have more similarity with *B. sanguinolentus* (also Gattorugine-species-group) ; both of the species mentioned are distributed in the Eastern Atlantic and in the Mediterranean Sea.

Though in the cases discussed above a differentiation of the species after an ancestor had immigrated from a west African refuge is possible, this assumption breaks down in the following case. *Blennius fluviatilis* Asso today lives in fresh and sometimes brackish waters of the Mediterranean area (Steinitz, 1954 ; Kosswig, 1967 ; Sasse, 1972) (fig. 13). Kosswig distinguishes, by their geological age 3 types of waters inhabited by this species :

a) « recent alluvial regions near sea level », (e.g. little rivers with direct connection to the Marmaris) ;

b) « lakes of postglacial age at higher altitudes (Lake Garda, Le Bourget) » ;

c) « lakes that have lost their contact with the Mediterranean since the Pliocene (Lake Tiberias, Lake Gölbasi) ».

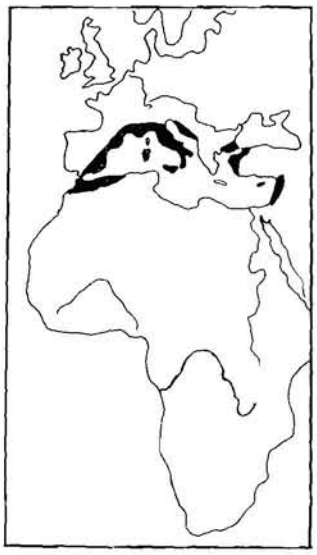

Fig. 13. — *Distribution of* Blennius fluviatilis.

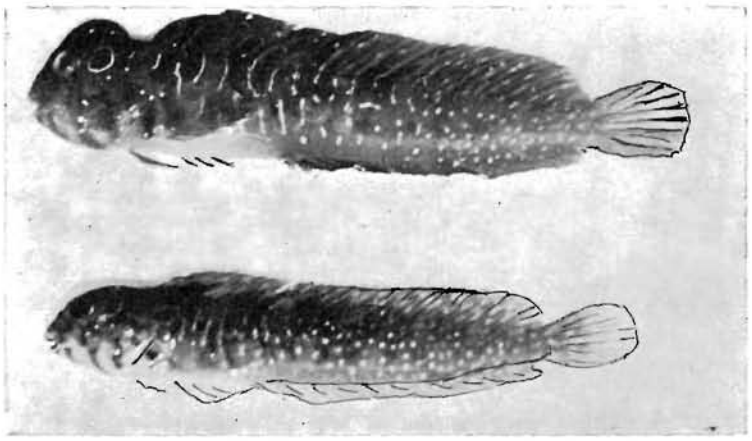

Fig. 14. — Blennius pavo, *male above, female below.*

B. fluviatilis is related very closely with *B. pavo* Risso living in marine and brackish waters of the Mediterranean Sea and the European Atlantic coast (fig. 14). Both species are euryhaline, so that, e.g., they could be caught together in the harbour of Cagliari/Sardinia. *B. pavo* tolerates brackish waters of 5 ‰, while even populations of *B. fluviatilis* which are sensitive to higher salt concentrations (Le Bourget) can tolerate up to 15 ‰ salinity (N. Peters, unpubl.). On the basis of the paleohistorical events mentioned above, it is not necessary to consider *B. fluviatilis* as a polytopic derivate of *B. pavo*, as Kosswig (1967) suggested without knowledge of the paper of Ruggieri (1967). It suffices to assume an eurytherm and euryhaline ancestor of both species which tolerated not only the desalination of the Mediterranean Sea in the upper Pliocene period, but also adapted itself to the changing conditions. After the marine influx in the upper Miocene this fish began partly to invade in rivers and lakes, and partly, according to their ecological eurypotency, to distribute over the whole of the Mediterranean Sea. From that area it was possible to immigrate in fresh waters at any time ; so on the one hand the populations of the Jordan Valley graben, which had been seperated since Pliocene, appeared ; on the other hand those populations came into existence, which inhabit waters resulting from the time after the glacial periods. Therefore it was possible that each isolated population could develop morphological characteristics which differ from those of other populations (Sasse, 1972). Because of its eurythermy *B. fluviatilis* could survive the glacial periods in the Mediterranean area, eventually in waters with an influx of warm springs (Kosswig, 1967). The speciation of *B. pavo* on the other hand probably took place in the West African refuge : this species extended after the glacial periods into marine and brackish waters of the Mediterranean Sea.

The examples discussed above show what different patterns in the evolution of blennioids has followed. At the same time they indicate the modes of phylogeny of other Mediterranean faunal elements.

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