Predator-driven macroevolution in flyingfishes inferred from behavioural studies: historical controversies and a hypothesis

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Abstract

Flyingfishes (Exocoetidae) are unique oceanic animals that use their tail and their large, wing-like pectoral fins to launch themselves out of the water and glide through the air. Independent observations document that flyingfishes use their gliding ability to escape from aquatic predators such as dolphins (marine mammals). The fossil record of flyingfishes is very poor. Nevertheless, the evolution of gliding among flyingfishes and their allies (Beloniformes) was analysed and reconstructed by the ethologist Konrad Lorenz (1903 – 1989) and other zoologists. In this article I review the comparative method in evolutionary biology, describe historical controversies concerning the biology and systematics of flyingfishes and present a hypothesis on the phylogenetic development of gliding among these marine vertebrates. This integrative model is based on behavioural studies and has been corroborated by molecular data (evolutionary trees derived from DNA sequences).

Introduction

Since the publication of Darwin´s classical book (1872, 1st ed. 1859), evolutionary biology has relied primarily upon comparative studies of extant organisms (animals, plants), supplemented whenever possible by information obtained from the fossil record. This interaction between neontological and palaeontological research has greatly enriched our knowledge of the evolutionary history (phylogeny) of a variety of macro-organisms, notably hard-shelled marine invertebrates (molluscs etc.) and vertebrates, for which thousands of well-preserved fossils have been described. Such comparative studies have become considerably more significant with the development of molecular methods for reconstructing DNA-sequence-based phylogenies and with the increased rigour with which the comparative method has been applied. Charles Darwin used a strictly comparative approach when he remarked that "in searching for the gradations through which an organ in any species has been perfected, we ought to look exclusively to its lineal progenitors; but this is scarcely ever possible, and we are forced to look to other species and genera of the same group, that is to the collateral descendants from the same parent-form" (Darwin 1872, p. 182).

Since Darwin's time, the comparative method has been improved and refined so considerably that evolutionary patterns (phylogenies) and adaptations by natural selection have been studied and elucidated in many groups of organisms.

In this review of the phylogenetic development of certain marine vertebrates (Beloniform fishes) I first summarize the power of the comparative method and outline the history of a branch of ichthyological research with reference to the work of the pioneers in this field of evolutionary inquiry. In the second part I develop a hypothesis that explains the evolution of gliding in flyingfishes (Fig. 1) that is based on comparative behavioural studies carried out in the field and on recent molecular data.
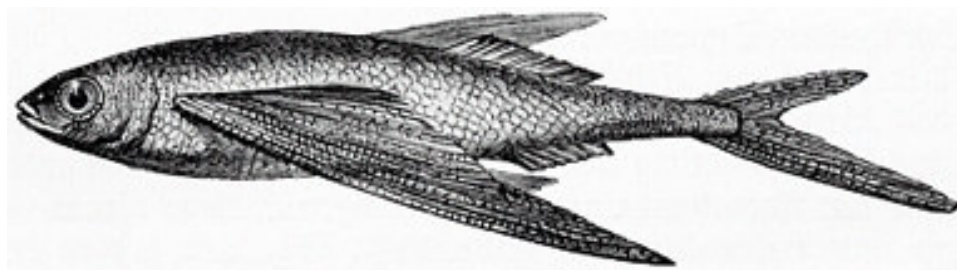
Fig. 1: Lateral view of a gliding flyingfish (Exocoetus volitans). The enlarged pectoral fins and the asymmetrical tail lobes, with the lower larger than the upper, are apparent. Since exocoetids feed mainly on plankton, their mouth is very small (Adapted from Matzdorff 1910).

Historical science and the comparative method

It has long been known that not all scientific hypotheses and theories can be tested in the laboratory using experimental methods. Historical hypotheses are common in fields such as astronomy, astrophysics, planetary science, geology, archaeology, and evolutionary biology. Nevertheless, many experimentalists regard historical sciences as inferior on the grounds that its hypotheses can not be verified unequivocally. The considerable number of chemists and physicists who have repeatedly attacked the scientific status of the Synthetic Theory of Biological Evolution provides proof for this conclusion (Cleland 2001, Kutschera and Niklas 2004). The most severe recent attack on the significance of the historical sciences comes from Henry Gee, one of the former Editors of the journal *Nature*. This prominent person expressed his attitude in a popular book in the following words: "(Historical hypotheses) can never be tested by experiment, and so they are unscientific...No science can ever be historical" (Gee 2000, p. 5 – 8). In two essays, the philosopher C. R. Cleland (2001, 2002) concluded that, although there are fundamental methodological differences between historical and experimental research, there is no evidence for the contention that historical science is epistemically inferior to laboratory tests.

Evolutionary biology shares with geology and other classical historical sciences the task of interpreting properties of extant systems that can not be understood today without understanding their past. In contrast to the phenomena analysed by the geologist (for instance, the hypothesis of continental drift), living organisms such as the famous

finches in the Galapagos Islands are distinct from the inorganic world: they have become adapted to their environment via the process of natural selection (Endler 1986, Futuyma 1998, Junker and Hoßfeld 2001, Kutschera 2001, 2003, Mayr 1963, 2001, Bell 1997, Niklas 1997). Comparisons among groups of extant organisms (species) are the most commonly used technique for examining how living systems are adapted to their specific environments. These uses of what is today called "the comparative method" provided the empirical basis for many arguments in Darwin´s *The Origin of Species* (1872) and thousands of related publications that followed.

Harvey and Pagel (1991) have pointed out that it is the second nature of biologists to think comparatively because comparisons establish the generality of evolutionary phenomena. For example, we cannot physically re-run the evolutionary sequences that resulted in the phylogenetic development of brooding behaviour in leeches and other phenomena (Kutschera and Wirtz, 2001). However, it is possible to reconstruct the origin and development of this behaviour through strict use of the classical comparative method, combined with an analysis of DNA-sequences and the resulting molecular phylogenies (Borda and Siddall 2004, Kutschera 2004). Because leeches are soft-bodied worms (annelids), the fossil record of this group of invertebrates is very poor. Likewise, the number of fish-like vertebrates that display a morphology similar to that of extant members of the flyingfi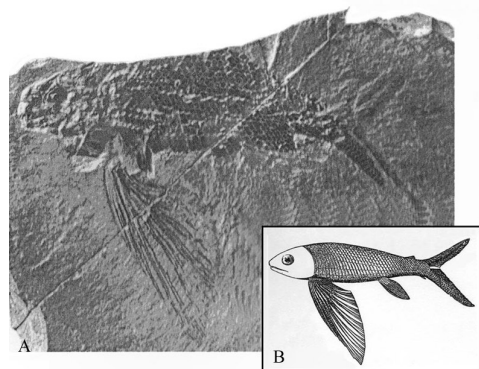shes (Exocoetidae) (Fig. 1) is rather limited. The geologist Othenio Abel (1875 – 1946), founder of a branch of the natural sciences that he called Palaeobiology (a term that is still in use today), published a monograph on fossil flyingfishes (Abel 1906). One representative specimen, the flyingfish *Thoracopterus niederristi* from the Triassic, is depicted in Fig. 2 A. The reconstruction of this vertebrate (Fig. 2 B) clearly shows all the basic features of extant exocoetids: exceptionally large, winglike pectoral fins, enlarged pelvic fins, a small mouth and an elongated lower lobe of the tail (Abel 1926). However, to my knowledge, no intermediate fossil species have ever been found so that a historical reconstruction of the evolution of gliding can only be achieved through the comparative method (Harvey and Pagel 1991).

Fig. 2: The fossil flyingfish Thoracopterus niederristi (Triassic) from the Raibler Schichten (Austria). Original specimen (A) and reconstruction of the animal (B) (Adapted from Abel 1906).

Flyingfish flight and the aeroplane theory: a historical controversy

The ability of aquatic vertebrates to glide above the surface of the water has evolved in several groups of the bony fishes (Osteichthyes). However, we shall discuss here only the most successful of these, the oceanic flyingfishes comprising the family Exocoetidae (Fig. 1) and related taxa. In one of the first scientific publications on this subject, Möbius (1878) summarized his observations, which have formed the groundwork for many subsequent articles on gliding fishes, as follows: "They are more frequently observed in rough weather, and in a disturbed sea than during calms; they dart out of the water…. and they rise without regard to the direction of the wind or waves. The fins are kept quietly distended without any motion, except an occasional vibration caused by the air, whenever the surface of the wing is parallel with the current of the wind. Their flight is rapid, but gradually decreasing in velocity, greatly exceeding that of a ship going ten miles an hour, and a distance of 500 feet. Generally it is longer when the fishes fly against, rather than with, or at an angle to, the wind. Any vertical or horizontal deviation from the straight course, when flying with or against the wind, is not caused at the will of the fish, but by currents of air…. in a rough sea, when flying against the course of the waves; they then frequently overtop each wave, being carried over it by the pressure of the disturbed air. They….fall on board vessels. This never happens from the lee side, but during a breeze only, and from the weather side. During the night they frequently fly against the weatherboard, where they are caught by the current of air and carried upwards to the height of 20 feet above the surface of the water, whilst under ordinary circumstances they keep close to it" (Möbius 1878, p. 344 – 346, translated by the author). The above description is fairly representative of the so-called "aeroplane theory". There are, however, several variants to it, the most notable being the addition of the use of the tail by later writers, both as a propeller in water, and also as an explanation of the loud buzzing sound always heard when the fish fly near or over a boat.

Despite this early exact description of gliding in flyingfishes, a controversy emerged among naturalists as to whether or not these animals flap their wings during flight. Dunford (1906) summarized both concepts as follows: "1. Flying-fish do fly, moving their wings with extreme rapidity. I have carefully and frequently watched them and there can be no doubt whatsoever about it. 2. Flying-fish do not flap their wings, but use them as aeroplanes, like swallows when in skimming or sailing flight. I have carefully and frequently watched them, and there can be no doubt whatsoever about it".

Somewhat similar remarks will be heard in any ordinary group of ship passengers watching the fish. Some will insist that they see the wings flapping, and some will say that they are quite still. It should be noted that Darwin (1872) obviously referred to hypothesis (1.) when he remarked that: "… it is conceivable that flying-fish, which glide far through the air, slightly rising and turning by the aid of their fluttering fins, might have been modified into perfectly winged animals" (Darwin 1872, p. 177).

Among the majority of scientists, the "wing-flapping-hypothesis" (1.) was abandoned around the year 1920, due to careful observations by independent investigators (Hankin 1920, Abel 1911, 1926). Hence, the aeroplane theory (2.) was accepted by most of the workers in this field and the competing concept 1 was no longer discussed. However,

about sixty years ago, a field naturalist re-vitalized the wing-flapping hypothesis based on observations during a trip taken on Pacific waters. In his report, Troxell (1937) presented a list of seven points in apparent support of a flapping flight in exocoetids. Breder (1937) discounted these claims and summarized the evidence in support of the aeroplane theory. The pectoral muscles of these motorless gliders are small and in no way adequate to the demands of wing-flapping exertion. There is nothing like a sternum-like structure for the necessary attachment of a corresponding (non-existent) muscle mass, as in bats, birds or pterodactyls. Moreover, the fins are not articulated, and the apparent movement of the "fish-wings" are probably a reaction to forces from the beating tail (Rayner 1986).

In a classical paper, Breder (1930) pointed out that power is applied by flyingfishes only as long as they are in contact with water: "After the forepart of the body has been thrust out of the water by rapid swimming and the pectoral fins are spread, very effective power is supplied by the long lower caudal lobe, the only part submerged, combining the advantages of the slight resistance to motion in air with the strong reactive effect of motion in water. As soon as the tail leaves the water it immediately stops oscillating, and the fish becomes a glider. Up to this time they (the animals) may be considered as a pusher type of plane" (Breder 1930, p. 115 – 116).

This careful description of the flight among flyingfishes of the family Exocoetidae (Fig. 1) has been corroborated by many biologists and can be considered a brief summary of the tenets of the aeroplane theory of gliding. Breder (1930) used the distribution of wing area to classify flyingfishes into two distinct aerodynamic designs. The monoplane type (*Exocoetus* and related taxa, Fig. 1) has a single set of long narrow main wings (pectoral fins) and the biplane type (*Cypselurus* etc.) has under wings (pelvic fins) staggered far back from the main wings. These aerodynamic designs have implications for the maximum distance travelled in gliding and the evolution of flight performance in these aquatic vertebrates (see Fig. 8).

The gliding of members of the family Exocoetidae was studied extensively during the period around 1900 to ca. 1930, as possible analogues to airplanes (Adams 1906, Hoernes 1913, Abel 1926). Descriptions of flights by these animals were considered living model systems for airplanes, because the design of *Exocoetus* was regarded as perfectly in accord with the aerodynamics of gliders. As Breder (1930) pointed out, through modification of paired fins, members of the Exocoetidae have evolved aerodynamic lifting surfaces that enable them to glide one metre above the water for a distance of more than 100 m. The design of the out-stretched pectoral fins was likened by several naturalists to the swept-back wings of hirundine birds such as swallows.

Flyingfishes: why do they leave the water?

It has long been known that there are fishes that can move about on land, sometimes far away from the water. The best-known of these amphibious fishes are the mudskippers (*Periophthalmus* sp.), which dig burrows in the soft, muddy substrate of mangrove swamps of tropical Africa (Keenleyside 1979). Nevertheless, the popular expression "like a fish out of the water" conveys the general inability of fish to survive in the absence of their

aquatic environment. This is to a large extent due to the fact that the majority of fishes are unable to exchange gases effectively in air. Sayer and Davenport (1991) have summarized the selective forces that may have caused this step in the evolution of certain members of the bony fishes (Osteichthyes). Extant amphibious fishes leave the water for a number of reasons associated with the degradation of their aquatic habitat, or certain biotic factors. In open aquatic systems, such as large freshwater bodies or coastal waters, the dominant selective forces are possibly the interaction between predation, competition and food availability (Sayer and Davenport 1991).

The question of why flyingfishes glide for 200 m and more through the air, using their tail and the large, wing-like pectoral fins to keep them above the water, has long been a matter of debate. Do they fly to escape large predators, like dolphinfishes and dolphins (marine mammals), or is it an energy-saving mechanism? Adams (1906) was one of the first naturalists to provide evidence for the hypothesis that members of the Exocoetidae fly to evade attacks from predators below. Based on numerous opportunities to watch flyingfishes in various parts of the world, he summarized his observations as follows: "One theory is that they keep up the flight by going against the wind, soaring like sea-birds; but as a fact, the fish will start off in all directions from the bows of a vessel, or when chased out of the water by enemies – as often in a calm as in rough weather, against, across, or before the wind, and, …, will often change the direction of their flight, which is done by touching the water with the lower tip of the vibrating tail. I once spent the greater part of a distinctly warm afternoon, in a dead calm in the Gulf of Aden, watching schools of the Sailors´ Dolphins bounding out of the water, chasing the flyingfishes as greyhound course hares" (Adams 1906, p. 147).

In numerous subsequent reports it has been documented that sometimes a tuna, dolphin or shark can be seen as a fleeting shadow just below the surface following the flight path of flyingfishes. The lateral line is placed along the ventral surface allowing the flyingfish to detect a predator striking from below, and especially adapted eyes enable them to see in both air and water. In addition, it is well known that flyingfishes, which feed mainly on plankton, serve as food for many aquatic predators, including other (larger) fishes, especially tunas, marlin and dolphinfish as well as dolphins, birds, squids and porpoises. This is in accordance with the observation that flyingfishes are a dominant food source found in the stomachs of dolphins (Collette and Parin 1998).

Rayner (1986) pointed out that the periodic flights of exocoetids could be part of an energy-saving strategy similar to that used by penguins and some marine mammals which repeatedly jump out of the water when travelling over long distances. Moreover, Rayner (1986) proposed that an analysis of the biochemical properties of the caudal musculature would be useful in order to verify this hypothesis. Davenport (1992) provided evidence indicating that it is improbable that exocoetids use their flights as part of an energy-saving strategy. This conclusion is based on a comparative analysis of red versus white muscle tissue in exocoetids compared with other marine vertebrates. Davenport (1992) suggested that acceleration to take-off speed in the Exocoetidae requires use of anaerobic white muscles via the inefficient biochemical pathway of glycolysis.

Today, humans are the top-predators in the biosphere. It is not surprising that there are commercial fisheries for flyingfishes in many tropical countries. Adams (1906)

commented on this issue as follows: "It is truly amazing to contemplate the countless millions of these fish in tropical waters. Often for weeks together one may every few minutes see startled shoals scatter from the ship´s bows. I have watched for hours the sea thick with myriads of juveniles from a couple of inches in length. These do not fly, but flap on the surface; the flight begins when the fish are about three or four inches long, and increases in length as their size increases. The adults come on board chiefly at night, and mostly in rough weather. … They are often collected and fried for breakfast. The flesh is very white and firm, but somewhat dry, and the bones are particularly hard. Fishermen bring them for sale to ships in the Japanese Ports" (Adams 1906, p. 148).

Since that time several sophisticated techniques have been developed to catch large numbers of flyingfishes, including gill-netting (Japan, Vietnam, Barbados), dip-netting of spawning swarms (Indonesia, India) and attraction to artificial light and dip-netting at night (Pacific islands) (Collette and Parin 1998). During the period from 1983 to 1989, annual global catches of flyingfishes were around 36 000 to 49 000 tonnes (FAO 1991). These data documented that members of the Exocoetidae are an important resource in some tropical areas of the world that support a major commercial food industry.

Systematics of flyingfishes: a matter of debate

The best known gliding fishes are the oceanic Exocoetidae, surface-dwelling (epipelagic) animals which are common throughout tropical and sub-tropical seas. However, in European marine coastal waters a taxonomically unrelated species is known, the flying gurnard (*Dactylopterus volitans*) (Fig. 3 A, B). Chen et al. (2003) have recently shown that the Dactylopteridae can be added to the Smegmamorpha, but no close relationship to the needlefishes (Beloniformes, relatives of the exocoetids) was apparent in these molecular phylogenies. The question whether or not *Dactylopterus* is capable of gliding short distances above the surface of the water is still unanswered. According to Klausewitz (1960), Nelson (1976) and Müller (1983) the flying gurnard can glide, but Lorenz (1965) and Rayner (1986) concluded that is now believed that these reports of flight in *Dactylopterus* are mistaken. In a recent monograph on marine fishes this controversial point is summarized as follows:

"Although these benthic fishes (the Dactylopteridae) are often called 'flying gurnards', they cannot fly or glide out of the water" (Smith and Heemstra 1986, p. 490). A number of tropical freshwater fishes perform short flapping flight, at least in captivity (aquaria). For instance, the freshwater hatchet fishes of South America (Gasteropelecidae), small animals up to 7 cm in length, make brief jumps out of the water (members of the genera *Thoracocharax*, *Gasteropelecus*, *Carnegiella* and others). According to Rayner (1986) these vertebrates are the only fish which actively flap their "wings" (i.e. the extended pectoral fins) in air to obtain thrust (Fig. 4 A).
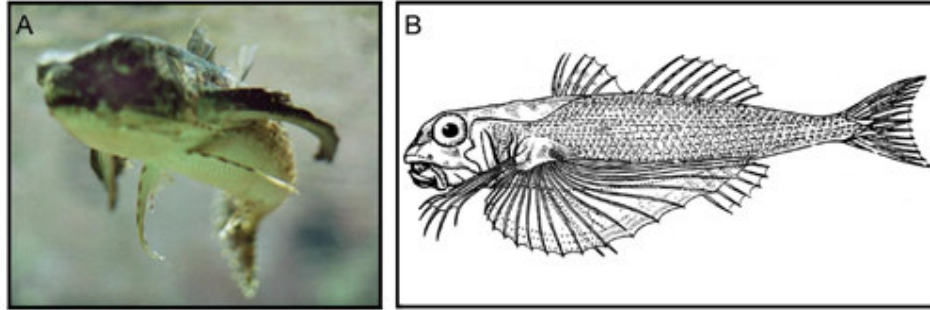
Fig. 3: Adult individual of the European marine species "flying gurnard" (Dactylopterus volitans). This fish can glide under water using the enlarged pectoral fins, but appears to be unable to leave the water for true flights. Original photograph (A), schematic view of the animal (B).

Wing beat rates of up to 80 Hz have been recorded, which results in a buzzing sound during the jump of the fish. Since the large pectoral fin muscles (that are absent in members of the Exocoetidae) are "white" and contain almost no mitochondria (Fig. 4 B) the flapping jumps must be sustained via anaerobic metabolism (glycolysis) and can only be of short duration (Rayner 1986). According to Klausewitz (1960) there are reports indicating that under natural conditions *Thoracocharax* jumps out of the water in response to predatory attacks, but more field observations are necessary to corroborate this hypothesis (Keenleyside 1979, Rayner 1986).

The taxonomy of the marine flyingfishes, which are easily recognized by their huge pectoral fins (Fig. 1), is confusing and still a matter of debate. In his classical monograph on the "Fishes of the World", Nelson (1976) grouped the Flyingfishes and Halfbeaks together (one family, Exocoetidae), which comprised the subfamilies Exocoetinae and Hemirhamphinae. The families Belonidae (Needlefishes) and Scomberesocidae (Sauries) were regarded as close relatives of the exocoetids (see Fig. 8). Ten years later, the halfbeaks were elevated to the rank of a family (Hemiramphidae), so that the Exocoetidae (flyingfishes) no longer included the subfamily Hemirhamphinae sensu Nelson (1976). It is interesting to note that on one page of this monograph the halfbeak Oxyporhamphus micropterus is described as a "shortwing flyingfish", but this species is not regarded as a member of the Exocoetidae (flyingfishes) (Smith and Heemstra 1986, p. 391). In a careful analysis, Dasilao et al. (1997) concluded that *Oxyporhamphus* is a member of Exocoetidae, with which it shares a total of 10 derived osteological/myological conditions.
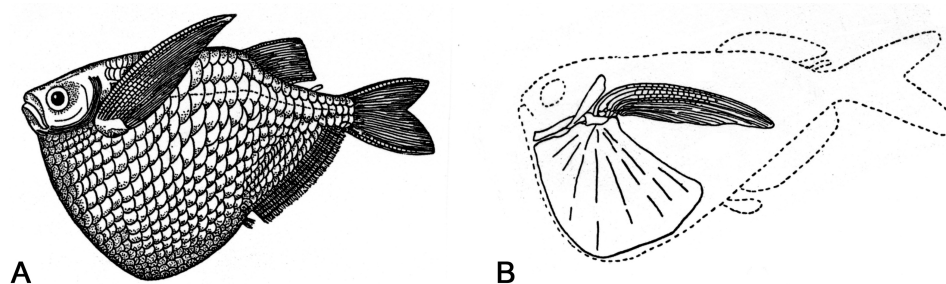
Fig. 4: A South American hatchet fish (Thoracocharax) that is able to perform flapping flight by rapidly beating its enlarged pectoral fins (A). The fish has a highly compressed body with large pectoral fin muscles (B) (Adapted from Klausewitz 1960).

Since that time, a consensus emerged among ichthyologists that can be summarized as follows. The order Beloniformes (also called "flyingfishes and their allies") comprises five closely related families: the needlefishes (Belonidae), easily identified by their elongated upper/lower jaws and a long body; the halfbeaks (Hemiramphidae), fishes that are characterized by a long lower jaw in juveniles of all genera (and adults of most species) and short or moderately long pectoral fins; flyingfishes (Exocoetidae), unique aquatic vertebrates that use their tail and their large, wing-like pectoral fins to launch themselves out of surface waters and glide through the air; sauries (Scomberesocidae), oceanic fishes that live near the surface of the water, and ricefishes (Adrianichthyidae), a group that is not discussed in this article (Collette et al. 1984, Smith and Heemstra 1986, Collette and Parin 1998, Lovejoy 2004). The phylogenetic development of gliding in the Beloniformes has been investigated by numerous biologists. This topic is discussed in the next section.

Evolutionary ethology: the observations of Konrad Lorenz

Generations of naturalists have observed and described the flight among members of the family Exocoetidae (see Fish 1990 and references cited therein). The zoologist Konrad Lorenz (1903 – 1989) was one of the first to speculate on the phylogenetic development of gliding in the Beloniformes. His key publication, published in an obscure journal in German (Lorenz 1963), has never been cited in any of the reviews and original papers dealing with this subject (see, for instance, Fish 1990, Davenport 1992, Dasilao and Sasaki 1998, Lovejoy 2000, Lovejoy et al. 2004). It is likely that these authors were unaware of Lorenz´ work, therefore making it worthwhile to briefly recapitulate the basic observations and conclusions of this eminent scientist.
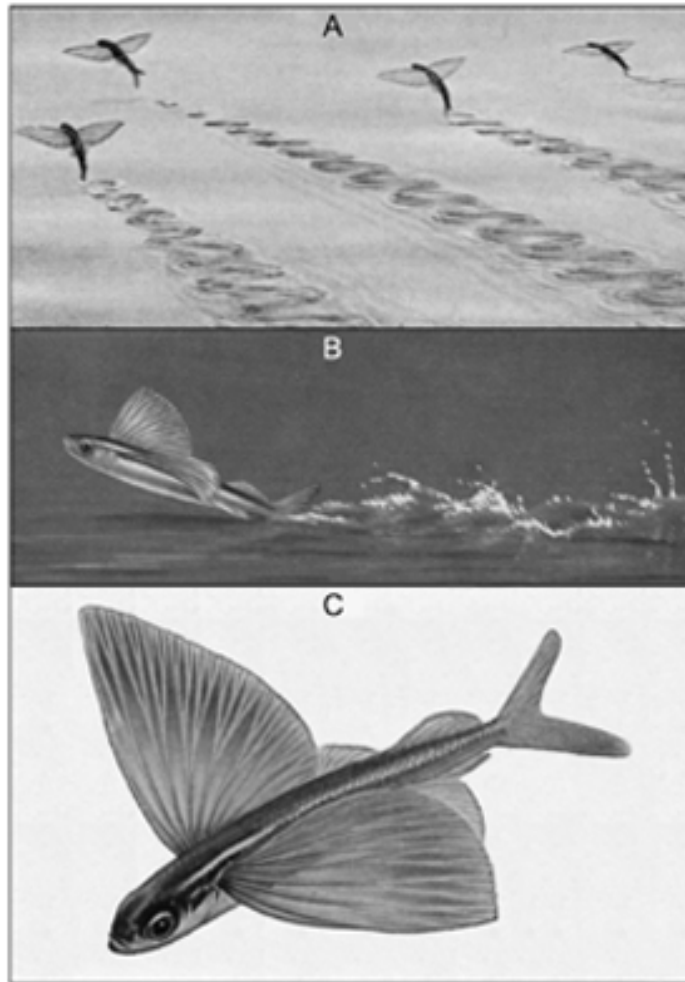
Fig. 5: Tracks of oceanic flyingfishes. The animals are using their tail to accelerate before leaping (A). Functioning like an outboard motor, the enlarged lower caudal lobe vibrates in a rapid side-to-side motion, generating a forward momentum (B). The California Flyingfish (Cypselurus californicus), an example of the four-winged group within the Exocoetidae, in flight (C) (Adapted from Lorenz 1963).

The Austrian biologist Konrad Lorenz is regarded as the founder of modern ethology, the systematic study of animal behaviour by means of the comparative method. His insights, concepts and hypotheses contributed to our understanding of how behavioural patterns evolved. Lorenz is also known for his work on the roots of

aggression in animals and humans (Jahn 1998). The popular essay discussed here (Lorenz 1963) is to a large extent based on the work of earlier naturalists and on an article published three years earlier on the systematics and biology of flyingfishes (Klausewitz 1960). It should be noted that Lorenz (1963) did not include any references or the source of his figures. However, his illustration on the title page, reproduced here in modified form (Fig. 5), is a copy from earlier work on the Exocoetidae, as reviewed in Fish (1990).

In his review article, Lorenz (1963) described his own observations of flyingfishes and their allies as follows. Flyingfishes carry out a form of powered gliding. The caudal muscles beat the tail at a rate of 50 – 70 beats/s, which propels the fish out of the water (Fig. 5 A, B, 6 B, 7 A). As soon as the body is free of the water surface, the broad pectoral fins open at a maximal angle and an airborne glide begins (Fig. 5 C, 6 B, 7 B). Additional power can be derived during the glide by sculling the water with the enlarged lower lobe of the tail, which results in speeds of up to 70 km/h. Exocoetids do not flap their wing-like fins, but these organs can be used to steer and turn away from surface obstacles such as large rocks or boats.
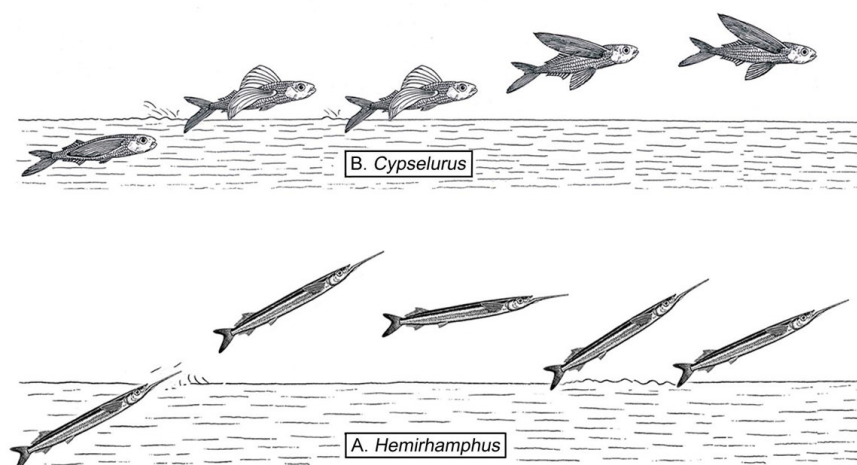

Fig. 6: Behaviour of the halfbeak Hemirhamphus (A) and the four-winged flyingfish Cypselurus (B) in response to attacks from aquatic predators. The halfbeak simply leaps from the water. The three successive stages in a flight by a cypselurine gliding fish can be summarized as follows (B). The fish approaches the water surface with paired fins folded (1.), pectoral fins spread as the animal breaks through the surface and the tail continues to oscillate in the water as the fish taxis along the surface (2.), pelvic and pectoral fins spread as the fish becomes fully airborne (3.) (Adapted from Klausewitz 1960).

Lorenz (1963) argued that the evolution of flight in Beloniform fishes can be reconstructed based on behavioural studies of extant species. He observed in aquaria that some fish species that inhabit the upper ten cm of the water (region just below the surface) have a forked caudal fin with a significantly enlarged lower lobe. These fish species (members of the genera *Pelecus* and *Alburnus*) occasionally "walk on the surface of the water" in response to attacks from predators. Halfbeaks (*Hemirhamphus*, *Oxyporhamphus*) are intermediate forms that display predator-driven jumps out of the water that are reminiscent of the flights of the exocoetids (Fig. 6 A, B). Hence, the evolution of flight in the Beloniformes originated with now extinct species that temporarily "walked out of the water" to escape predators. Lorenz (1963) did not distinguish between exocoetids that have two versus four "wings" (Fig. 8) However, he pointed out that the surface of the water, viewed from below, looks like a mirror: the aquatic prey organism, driven out of the liquid medium, becomes invisible to the predator.

Fig. 7: Oscillatory side-to-side movement of the tail of a flyingfish, viewed from above (A). A four-winged (biplane-type) cypselurid fish, front view in flight (B) (Adapted from Breder 1930).

The evolution of gliding in Beloniform fishes: a synthesis

Darwin (1872) proposed that the phylogenetic development of novel body plans is driven by the same mechanisms that cause the origin of new varieties and species. This classical concept of "phylogenetic gradualism" (Gould 2002) has developed into a basic tenet of the modern theory of biological evolution: large phenotypic changes (origin of higher taxa) are brought about by successive microevolutionary processes. Although exceptions to this rule exist, there is consensus among the majority of biologists that macroevolution (phylogenetic development above the species level) is the product of numerous microevolutionary steps (Mayr 1963, 2001; Futuyma 1998; Zimmer 1998, Carroll 2000, 2001; Simons 2002, Kutschera and Niklas 2004, 2005).

The predator-driven development of gliding in Beloniform fishes discussed here is an example of a macroevolutionary trend. It is obvious that the beating tail of the exocoetids, which propels the fish clear of the water, and the enlarged pectoral fins are

organs that have undergone an "intensification and/or change in function" (Mayr 1963): the tail acts as a "motor", the fins are "wings", the flyingfish displays the aerodynamic properties of an aeroplane or a hirundine bird (swallow).
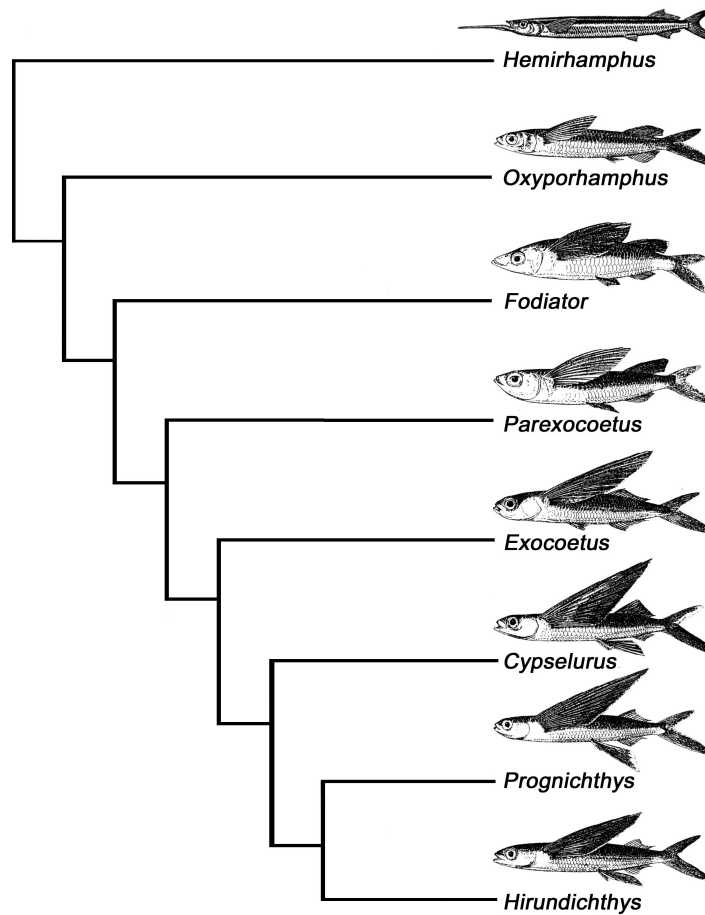

Fig. 8: Cladogram of halfbeaks (Hemirhamphidae) and flyingfishes (Exocoetidae). According to this scheme, the shortwing flyingfish Oxyporhamphus is a member of the Exocoetidae. Three four-winged (biplane-type) exocoetids are depicted in the lower part of the cladogram (Cypselurus, Prognichtys, Hirundichthys) (Adapted from Dasilao and Sasaki, 1998).

A hypothesis for this macroevolutionary trend in the Beloniformes, based on observations of extant "model organisms" that represent various stages in phylogeny, is depicted in Figure 9. This scheme is an expanded and modified version of the "historical reconstruction" presented by Lorenz (1963), with reference to Klausewitz (1960). The data of Dasilao and Sasaki (1998) (Fig. 8) are largely in accordance with the phylogenetic hypothesis discussed here.

Members of the fish family Cyprinidae (minnows or carps) that inhabit the upper region of the waters (*Pelecus*, *Alburnus* and others), are able to "walk on the surface" to escape predatory attacks (Fig. 9 A). These "walking fish" may represent the ancestral stage in this evolutionary trend. Halfbeaks, represented by members of the genus *Hemirhamphus*, are prone to leap out of the water; they usually perform a short "walk on the surface" before they temporarily leave the liquid medium (Fig. 9 B). According to Lorenz (1963), the hemirhamphid *Oxyporhamphus* represents an intermediate form between a typical halfbeak and a true flyingfish. This "shortwing flyingfish" (Smith and Heemstra 1986) has an elongated lower jaw only as a juvenile (i.e., it recapitulates the halfbeak stage during ontogeny), a deeply forked caudal fin (lower lobe longer than upper), and longer wing-like pectoral fins than other typical halfbeaks (Fig. 9 C). Dasilao et al. (1997) have provided evidence that, based on morphological data, the halfbeak Oxyporhamphus should be considered a basal flyingfish, as suggested by Lorenz (1963). However, molecular data presented by Lovejoy et al. (2004) place *Oxyporhamphus* within the *Hemirhamphus* clade. These contradictory results indicate that the "shortwing-halfbeak" *Oxyporhamphus* is an extant intermediate form between the Hemiramphidae and the Exocoetidae.

Breder (1930) was the first to distinguish between two categories of flyingfishes (Exocoetidae), "two-wingers" (*Fodiator*, *Parexocoetus*, *Exocoetus* etc.) in which the enlarged pectoral fins make up most of the lifting surfaces, and "four-wingers" (*Cypselurus*, *Prognichthys*, *Hirundichthys* etc.) in which both pectoral and pelvic fins are hypertrophied (Fig. 8). According to Collette and Parin (1998) two-winged exocoetids may glide for a distance of 25 m, whereas four-winged species may achieve 200 m or more with the extra lift generated by the enlarged pelvic fins. However, both types of exocoetids use their hypertrophied lower portion of the asymmetrical tail fin to provide the impetus for the free flight (Fig. 7 A). A number of studies have shown that "two-wingers" like *Parexocoetus* (Fig. 9 D), along with *Exocoetus* and *Fodiator*, are the least sophisticated gliders. These "primitive" flyingfishes are at the base of the exocoetid tree, as studied by cladistic methods (Fig. 8; Dasilao and Sasaki 1998).

It is obvious that the more sophisticated "biplane gliders" (*Cypselurus* and related taxa) (Fig. 9 E) evolved from more basal "two-wingers"; these "living airplanes" represent the extant peak in Exocoetid evolution. They build up speed by taxiing like aircraft and resemble herring-like swallows. The subtropical flyingfish *Hirundichthys* depicted in Fig. 8 is a bird-like vertebrate, with black fins that look like the wings of some Aves that glide over large distances (Smith and Heemstra 1986).

Lovejoy et al. (2004) reconstructed the phylogeny of 54 species of Beloniform fishes, using fragments of two mitochondrial and two nuclear genes. These molecular data generally confirm the concept depicted here (Fig. 9), with the exception that the intermediate form *Oxyporhamphus* occurs deeply within the *Hemirhamphus* clade.
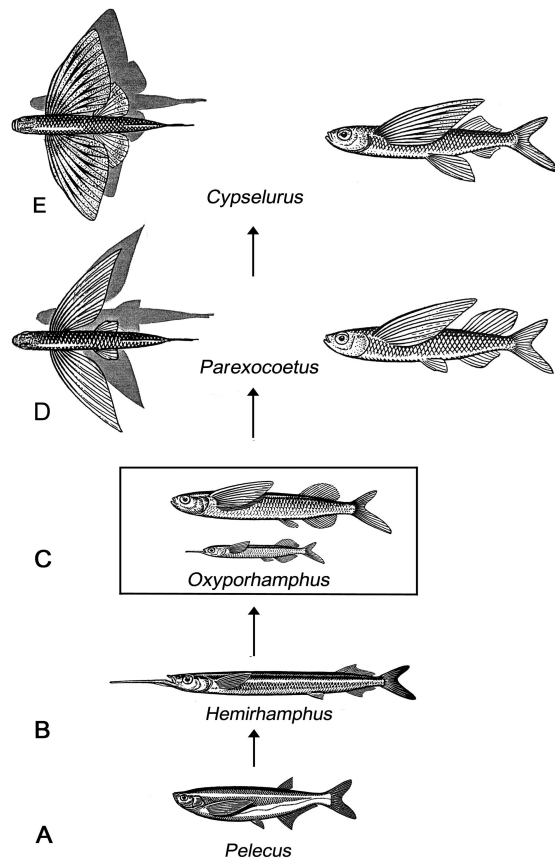

Fig. 9: Predator-driven evolution of gliding in Beloniform fishes, based on behavioural studies of extant species. Cyprinid (Pelecus) that occasionally leaps at the surface (A), halfbeak (Hemirhamphus) that jumps out of the water (B). The short-wing flyingfish (Oxyporhamphus), depicted as adult and juvenile individuum, represents an intermediate form that recapitulates the halfbeak-stage during ontogenesis (C). Monoplane-type flyingfish (Parexocoetus) that has a single set of long pectoral fins (wings) (D) and biplane-type (Cypselurus) that has under wings (pelvic fins) staggered far back from the main wings (E) (Adapted from Lorenz 1963).

In addition, the phylogenetic trees reconstructed on the basis of DNA-sequence data shed light on the ontogenetic recapitulation of the "halfbeak stage" in the "shortwing flyingfish" *Oxyporhamphus* and related taxa (Lovejoy 2000, Lovejoy et al. 2004; for historical accounts, see Gould 1977 and Levit et al. 2004). This topic is beyond the scope of the present article.

In conclusion, the results summarized here show that the evolutionary history of Beloniform fishes can be reconstructed without fossil data. Based on behavioural studies, molecular data and the strict use of the comparative method, the phylogenetic development of gliding in the exocoetids has now been elucidated: the macroevolutionary trend depicted here (Fig. 9) was driven by predatory attacks from below. In marine exocoetids, this selection pressure must have been severe, so that novel bird-like body plans evolved in this unique group of epipelagic fishes.

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