Trends of avian locomotion in water – an overview of swimming styles

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Abstract Adaptation to an aquatic lifestyle occurred in the evolution of several primarily terrestrial clades of tetrapods. Among these lineages, aquatic birds' adaptations differ in many ways from other secondarily aquatic vertebrates. As a consequence of the evolution of flight, birds with swimming and diving abilities represent unique locomotion skills and complex anatomical solutions. Here we attempt to overview some of the main aspects of avian locomotion in water and highlight the diversity of their aquatic habits and locomotion types, with the best-known extinct and extant examples. The main features that can distinguish the different groups among these swimmers and divers are their different techniques to overcome buoyancy, the transformation of wings or hind limbs into aquatic propulsive organs, and their swimming techniques besides the presence or absence of the flying and/or terrestrial abilities. Understanding how the musculoskeletal system of aquatic birds evolved to face the requirements of moving in various environments with different physical characteristics provides a good opportunity to get a better view of convergent and divergent evolution.

Keywords: locomotion, swimming, diving, aquatic birds, ecomorphology, evolution

Összefoglalás A vízi életmódhoz való alkalmazkodás többször kialakult az elsődlegesen szárazföldi tetrapodák evolúciója során. Ezen leszármazási vonalak között a vízimadarak alkalmazkodása sok tekintetben különbözik a többi másodlagosan vízi életmódra áttért gerincesétől. A repülés evolúciójának következményeként az úszási és merülési képességekkel rendelkező madarak mozgásformái és komplex anatómiai adaptációi egyedülállóak. Jelen tanulmányban kísérletet teszünk a madarak főbb vízi mozgásformáinak áttekintésére, különös tekintettel mozgástípusaik sokféleségére, példaként említve a legismertebb kihalt és recens képviselőiket. A főbb jellemzők, amelyek megkülönböztethetik egymástól a különböző úszó és merülő csoportokat, azok a víz felhajtóerejének leküzdésére kialakult technikák, a szárnyak vagy a hátsó végtagok vízi meghajtószervekké való átalakulása, valamint az egyes úszásmódok mellett a repülés és/vagy a szárazföldön való mozgás képességének megléte vagy hiánya. Annak megértése, hogy a vízi életmódhoz alkalmazkodott madarak izom- és csontszerkezete hogyan fejlődött úgy, hogy az megfeleljen az eltérő fizikai jellemzőkkel rendelkező közegben való mozgáshoz, kiváló lehetőséget nyújt arra, hogy átfogóbb képet alkothassunk a konvergens és divergens evolúcióról.

Kulcsszavak: mozgás, úszás, merülés, vízimadarak, ökomorfológia, evolúció

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Introduction

During the history of Earth, several primarily terrestrial lineage of tetrapods have returned to the water and adapted on different levels to live in an aquatic environment (Kelley & Pyenson 2015, Motani & Vermeij 2021). Some of these transitions could be connected to the colonisation of aquatic environments during the recovery after devastating mass extinctions, however, most of these events are scattered through geological time and probably were driven by the available food sources and high productivity of aquatic habitats (Vermeij & Motani 2018). The aquatic adaptation of different clades to similar physical parameters and challenges has resulted in similar anatomical solutions and thus, convergent forms in many cases (Lindgren *et al.* 2010, Motani & Vermeij 2021, Gutarra & Rahman 2022). The waters of the Mesozoic were ruled by several clades of marine reptiles (such as sauropterygians, ichthyopterygians, mosasaurs, etc.), several of which survived to this day (like crocodiles, sea turtles, etc.) (Bardet 1994, Bardet *et al.* 2014). From the beginning of the Cenozoic, the radiation of aquatic mammals (such as pinnipeds, cetaceans, sirenians, etc.) has begun (Uhen 2007, Kelley & Pyenson 2015, Motani & Vermeij 2021). Nowadays, aquatic birds represent important components of both marine and freshwater ecosystems. The first avialans obviously adapted to specialised (foot-propelled) swimming and diving (Hesperornithiformes) evolved and colonised the marine and freshwater ecosystems back in the Cretaceous (Marsh 1880, Chiappe & Witmer 2002, Galton & Martin 2002, Bell & Chiappe 2015). Although most of the main groups of modern birds evolved in the Middle to Late Cretaceous, after the Cretaceous-Paleogene extinction birds diversified drastically and conquered the empty ecological space and environments (Moen & Morlon 2014, Brusatte *et al.* 2015). Through the following era numerous species appeared, including early anatids (Zelenkov 2020), grebes (Kurochkin 1976, Zelenkov 2015), loons (Storer 1956, Mayr 2004), rails (García-R *et al.* 2014), alcids (Konyukhov 2002, Smith & Clarke 2015) and penguins (Jadwiszczak 2009, Ksepka & Ando 2011).

Waterfowl show different levels of specialisation ranging from shorebirds to highly aquatic forms (Ashmole 1971). Due to the evolution of powered flight, the rigidity of their body enhanced, and their fore- and hind limbs became suitable for the variant types of movements, and this dual (initially aerial and terrestrial) locomotor system led to different ecomorphological innovations (Gatesy & Dial 1996, Kristoffersen 2001). Their morphologies and locomotion types are exceedingly diverse: they can use their wings or legs (or rarely both) as the main source of thrust production in different ways (Storer 1945). The best swimmers have lost their ability to fly due to the transformation of their wings into flippers (e.g. penguins) (Schreiweis 1982, Louw 1992, Watanabe *et al.* 2021), or sometimes even their ability to effectively move on land because of their highly modified hind limbs (e.g. grebes and loons) (Shufeldt 1898, Clifton *et al.* 2018). However, besides the highly specialised swimmers, many examples of 'amphibious flyers' (e.g. alcids) with the ability to swim and dive, fly, and sometimes also to walk effectively are known (Storer 1945, Raikow *et al.* 1988, Bribiesca-Contreras *et al.* 2021). Because air and water represent highly different physical characteristics (density, viscosity, etc.) and because of the presence of distinct mechanical loads during movements in different environments, the musculoskeletal

system of birds with aquatic habits must deal with various constraints, which required trade-offs and novel solutions in their morpho-functional adaptations (Raikow *et al*. 1988, Habib 2010, Fish 2016, Bribiesca-Contreras *et al.* 2021).

Among the secondarily aquatic vertebrate taxa, birds' adaptation is unique and in certain aspects deviates from the usual tendencies seen in other tetrapods, since they represent not just a transition between land and water, but a shift from an aerial life to an aquatic (Fish 2016, Fernández *et al*. 2020, Motani & Vermeij 2021). Given the special body plan and evolutionary path of birds among secondarily aquatic vertebrates, explaining their adaptation and functional trade-offs requires understanding their behaviour and locomotor techniques.

Here we intend to sum up and discuss the diverse locomotor and foraging techniques of birds adapted to swimming and diving, in order to form a basis for further comparative works. To highlight and introduce the different trends of avian locomotion in water, we provide summary illustrations based on the available literature.

Aquatic bird locomotor groups

With the intention of highlighting the different trends in avian aquatic locomotion and to describe the most distinguishable locomotor groups, with certain ecological and/or anatomical characteristics, previous authors proposed classifications. These concepts mostly followed the same (and most unambiguous) separation of groups with different propulsive organs (e.g. foot and/or wing) (Townsend 1909, Storer 1945), however, the approach was slightly different. While the concept of Ashmole (1971) emphasised the ecological connections and behaviour besides swimming style, Fish (2016) linked the locomotor groups to evolutionary stages to outline the possible steps of the transition from an aerial to a predominantly aquatic type of movement. From a third perspective, Clifton *et al*. (2018) introduced the terms 'lesser diving' and 'highly diving' for foot-propelled swimming birds based on anatomical and consequent behavioural traits. An additional important viewpoint would be for categorising swimming birds is to take into account their propulsive efficiency, which could also be in connection with their anatomical adaptations (Johansson & Norberg 2001, Johansson & Norberg 2003).

In this work, we attempt to summarize these notions to establish a background for further comparative studies. However, knowing the complexity of the behaviour of birds, we must keep in mind, that every kind of approach could contain outliers and examples which are difficult to classify, moreover the borders and distinctions between different locomotor groups in some cases can be blurry. Another difficulty worth mentioning is that while widespread taxa, and those that are easily accessible in zoos and collections, are frequently studied (such as grebes or cormorants) (Schmid *et al*. 1995, Johansson & Norberg 2001, White *et al*. 2008, Clifton *et al*. 2018), relatively little is known about other rare birds' aquatic behaviour (like finfoots) (Olson 2003, Shepherd 2006, Nurza *et al*. 2017). Following Ashmole (1971), the term 'diving' herein refers to the movement which starts with a resting state on the water-air interface, while 'plunging' is an action that begins from the air. We do not separate taxa from marine environments from those of freshwater ecosystems.
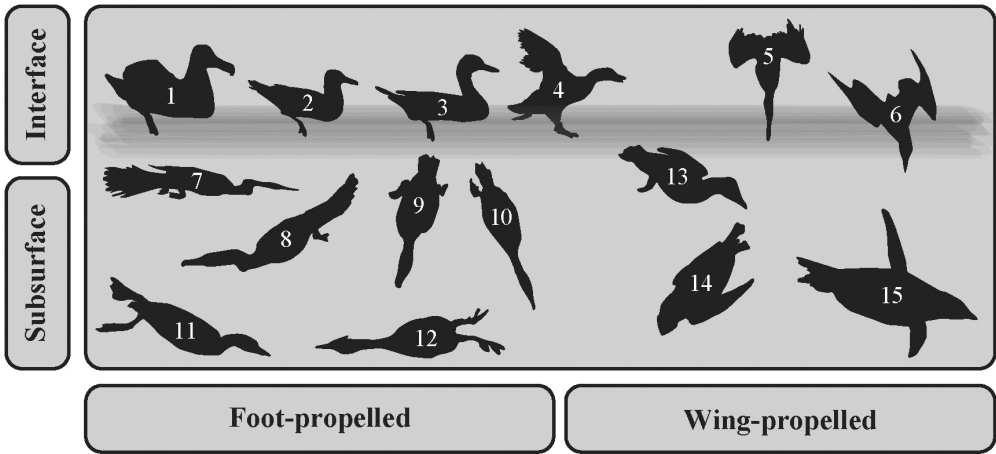
Figure 1. Aquatic bird locomotor groups based on Ashmole (1971), Kristoffersen (2001), Gough *et al*. (2015), Fish (2016), and Clifton *et al*. (2018): (**1–3**) surface swimmers; (**4**) 'skittering'; (**5–6**) plunge-divers; (**7–10**) lesser diving foot-propelled birds; (**11–12**) highly diving foot-propelled birds; (**13–14**) asymmetrical subaqueous flyers; (**15**) symmetrical subaqueous flyers. Examples: (**1**) Wandering Albatross *(Diomedea exulans)*; (**2**) European Herring Gull *(Larus argentatus)*; (**3**) Mallard *(Anas platyrhynchos)*; (**4**) Common Eider *(Somateria mollissima)*; (**5**) Great White Pelican *(Pelecanus onocrotalus)*; (**6**) Northern Gannet (*Morus bassanus*); (**7**) American Darter *(Anhinga anhinga)*; (**8**) Great Cormorant *(Phalacrocorax carbo)*; (**9**) Magellanic Flightless Steamer Duck *(Tachyeres pteneres)*; (**10**) Common Merganser *(Mergus merganser)*; (**11**) Common Loon *(Gavia immer)*; (**12**) Great Crested Grebe *(Podiceps cristatus)*; (**13**) Long-Tailed Duck *(Clangula hyemalis)*; (**14**) Atlantic Puffin *(Fratercula arctica)*; (**15**) King Penguin *(Aptenodytes patagonicus)*

1. ábra Vízimadár mozgási csoportok Ashmole (1971), Kristoffersen (2001), Gough *et al*. (2015), Fish (2016) és Clifton *et al*. (2018) nyomán: (**1–3**) felszíni úszók; (**4**)'skittering'; (**5–6**) becsapódó-merülők; (**7–10**) kevéssé specializált lábbal merülő madarak; (**11–12**) erősen specializált lábbal merülő madarak; (**13–14**) aszimmetrikus víz alatti repülést végzők; (**15**) szimmetrikus víz alatti repülést végzők. Példák: (**1**) vándoralbatrosz *(Diomedea exulans)*; (**2**) ezüstsirály *(Larus argentatus)*; (**3**) tőkés réce *(Anas platyrhynchos)*; (**4**) pehelyréce *(Somateria mollissima)*; (**5**) rózsás gödény *(Pelecanus onocrotalus)*; (**6**) szula *(Morus bassanus)*; (**7**) amerikai kígyónyakúmadár *(Anhinga anhinga)*; (**8**) nagy kárókatona *(Phalacrocorax carbo)*; (**9**) óriás gőzhajóréce *(Tachyeres pteneres)*; (**10**) nagy bukó *(Mergus merganser)*; (**11**) jeges búvár *(Gavia immer)*; (**12**) búbos vöcsök *(Podiceps cristatus)*; (**13**) jegesréce *(Clangula hyemalis)*; (**14**) lunda *(Fratercula arctica)*; (**15**) királypingvin *(Aptenodytes patagonicus)*

The distinction of different locomotor groups *(Figure 1)* is based on exclusive behaviours and anatomical characteristics that are missing from other clusters. For example, even though cormorants use paddling while swimming on the surface, such as non-diver surface swimmers (Johnsgard 1987), the diving performance divides them from the latter group (Zeffer & Norberg 2003). Similarly, although some of the volant advanced wing-propelled birds occasionally plunge from the air (Ashmole 1971), their ability to dive into considerable depth directly from the surface using only their limbs (Ryan & Nel 1999, Low *et al*. 2015) differentiates them from plunge-divers, that are less adapted and most of all utilise momentum to dive and overcome buoyancy (Ashmole 1971).

Physical problematics of diving

The ecological shift from a terrestrial (and aerial) mode of life to an aquatic, requires changes in morphology, physiology, and behaviour. Regarding locomotion, among others, drag reduction, buoyancy control, the increase of stability, and locomotor performance are the main trajectories of evolution (Fish 2016, Houssaye & Fish 2016, Gutarra & Rahman 2022). Aquatic movements mostly depend on the foraging style but include other territorial, escape, or comfort behaviours (Livezey & Humphrey 1982, Johnsgard 1987), and the extent of adaptation varies in accordance with these. Waterbirds are known to utilise aquatic resources at a wide range, depending on their ecology, from surface swimming and dabbling to reaching extreme depths, while consuming planktonic food sources, employing benthic foraging, or performing pursuit diving (Ashmole 1971). Swimming and diving ability could also contribute to the vertical and horizontal distribution of habitats between different taxa (Pöysä 1983a, 1983b, Hustler 1991, Pecsics *et al*. 2017). However, since all of the known aquatic bird taxa (both extant and extinct) continued laying eggs, the reproduction requires some sort of terrestrial abilities even from the most capable divers and swimmers that depend solely on seafood (Shufeldt 1898, Willener *et al*. 2016).

As a result of the different constraints that affect the body in water, significant changes could undergo in morphology, as well as in the inner structure of semi-aquatic and aquatic taxa's bones (Zeffer *et al*. 2003, Habib & Ruff 2008, Hinić-Frlog & Motani 2010). The structural changes could be related either in connection with the adaptation to a buoyant environment (Mendoza & Tambussi 2015, Houssaye *et al*. 2016), but also can be connected to the increased bone strength in elements that are exposed to the strains of swimming (Habib & Ruff 2008, Habib 2010). Besides the anatomical changes caused by the physical constraints of the aquatic mode of life, the heritage of the flying ancestry also had left its mark even on the body plan of most aquatic waterfowl. Among others, the streamlined body shape, developed sternal keel, and powerful pectoral and pelvic musculature (Ostrom 1976, Heers & Dial 2012) provided optimal 'starting point' to develop aquatic abilities and due to the rigid body, the production of thrust relies on the limbs (appendicular locomotion) (Gatesy & Dial 1996). However, in order to provide the proper amount of thrust, to propel the body in a denser environment, and to overcome drag forces both submerged and on the water surface, the structure of fore- and hind limbs shows certain adaptations: such as smaller wings (Raikow *et al*. 1988) or flatter and rigid hydrofoil-like flippers (Louw 1992), webbed or lobbed feet (Johansson & Norberg 2003, Tokita *et al*. 2020). In order to support the streamlined body shape, some of the most aquatic forms, such as loons, grebes, and penguins incorporated to some extent, the hind limbs into the abdominal skin (Kaiser 2011, Clifton *et al*. 2018). The best pursuit divers must be able not just to dive effectively, but also to take sudden turns and use a locomotor technique that provides them enough propulsive force (Clifton & Biewener 2018).

During wing-propelled diving, thrust (the forward component of force) is generated by the lift forces – which are the sum of forces that act perpendicular to the motion direction – of wing strokes (Clark & Bemis 1979). According to Lovvorn and Liggins (2002), this type of

thrust production is energetically much more beneficial, than foot-propulsion. Ducks during dives use drag-based (forces that oppose the relative motion of the object in fluid) propulsion to hold their position close to the bottom (Ribak *et al*. 2010). And while previously it was known that paddling is clearly drag-based, according to Johansson and Norberg (2003), at least the later phases of power strokes of the (delta-shaped) webbed feet of cormorants and ducks provide hydrodynamic lift forces. The feet of grebes and loons continuously generate hydrodynamic lift due to the direction of movement and position (Johansson & Norberg 2001, Clifton & Biewener 2018).

Semi-aquatic and aquatic taxa must face buoyancy, the force that is produced by the displaced mass of water and acts opposite to the body weight. Buoyancy is neutral when these two forces are equal (the body is floating), and negative when it causes the animal to sink. Positive buoyancy moves the body upwards in the water column. Penetrating under the surface is problematic for the highly buoyant volant taxa, which must exert force, or gain extra momentum in order to counteract the upward-directed force of water, dive, and reach their foraging depth (Hustler 1991, Eliason *et al*. 2020). The most common way for aquatic vertebrates to decrease the effect of the buoyant force is to increase the density of the body. One solution can be to increase the mass of the skeletal elements with changes in bone microanatomical features (Chinsamy *et al*. 1998, Wilson & Chin 2014, Cerda *et al*. 2015, Houssaye *et al*. 2016). A partially, or fully vettable feather coat could also provide a solution (such as in the case of cormorants and anhingas), however, in this case, the birds could be exposed to the negative effects of weather while they dry their feathers (Grémillet *et al*. 2005, Ryan 2007). The buoyant force decreases with increasing depth and hydrostatic pressure, and since the effect of buoyancy during shallow dives is maximal, shallow diving requires more energy compared to the dives of those species that descend deeper (Kato *et al*. 2006). For example, in shallow water, both penguins and cormorants are positively buoyant, but in addition, this can help in ascending and supports the bird to reach the water surface (Ribak *et al*. 2005, Kato *et al*. 2006). Deep divers descend beyond the depth where buoyancy is minimal or neutral and can spend most of their energy searching and capturing prey (Lovvorn *et al*. 2001), while shallow divers remain in the zone of maximal buoyancy, and must work against it during the entire dive sequence (Kato *et al*. 2006).

Surface swimmers

Birds with aquatic habits (both surface swimmers and divers) typically use their feet to propel themselves on the air-water interface *(Figure 2)* (Ashmole 1971, Ancel *et al*. 2000), between plunges and dive sequences, except for penguins that mainly move with the rowing motion of their flipper-like wings *(Figure 3)* (Butler 2000). Aquatic taxa generally represent a broad, boat-shaped body that provides them stability while floating (Stolpe 1932, Bovy 2002).

The category 'surface swimmer' stands for those buoyant birds that are mostly restricted to the surface and do not necessarily show such drastic anatomical adaptations in connection with their aquatic lifestyle that would affect their terrestrial or aerial abilities, like in more derived foot-propelled aquatic groups (Clifton *et al*. 2018b). On occasion, they are able to partially or fully submerge, however they are not capable of performing deep or long-time

diving (for example, albatrosses, gulls, dabbling ducks) (Ashmole 1971, Raikow 1973, Butler & Jones 1982). Dabbling birds for example mostly submerge only with the front part of their body (Johnsgard 2010), and their oily waterproof feather coat helps them to forage upside down. Some of them have good terrestrial (e.g. walking or even running) capabilities (Provini *et al.* 2012). The propulsion is provided by the alternate strokes of the feet (Gough *et al.* 2015, Fish 2016), and the paddling movements are supported by lobed or webbed feet, which evolved convergently in several taxa with different phylogenetic background (Tokita *et al.* 2020). Besides progress and resting, eating from the surface could be the advantage of this low-speed movement: such as grasping organisms, or even filtering plankton (Ashmole 1971).

Skittering (special locomotor technique)

Some of the birds that propel themselves by alternate paddling on the water surface apply special temporary locomotor techniques (in short: 'skittering') in order to avoid wave drag and excel the speed-limiting effect of waves generated by the surface swimming (hull speed) without flying (Gough *et al.* 2015). A peculiar way of locomotion is the so-called 'steaming', which is sometimes also mentioned as 'wing-paddling' (Fish 2016). Steaming, as a regular behaviour is mostly cited in connection with large, heavy anatids, especially the steamer ducks (*Tachyeres* spp.) and eider ducks (*Somateria* spp.), however other birds, like alcids, also apply this movement occasionally to a lesser extent (Livezey & Humphrey 1986, Gough *et al.* 2015). During steaming, these waterfowl increase their body angle and gain extra acceleration from the power strokes of the slightly flexed wings combined with foot-paddling. However, this rapid oaring is restricted to just a limited time interval and used only in those cases when the birds have to escape insecure situations or need acceleration for other temporary reasons (Livezey & Humphrey 1986, Gough *et al.* 2015). Steaming is particularly interesting in the case of the Magellanic Flightless Steamer Duck *(Tachyeres pteneres)*, which birds' wing size does not allow the take-off, however, the strong and otherwise functional wings are regularly used as paddlers on the surface (Livezey & Humphrey 1986, Fulton *et al.* 2012).

Besides steaming, another temporary water-surface related speed accelerator behaviour is the so-called 'paddle-assisted flying', which was studied in more depth by the observation of the Common Eider *(Somateria mollissima)* by Gough *et al*. (2015): unlike steaming, in this case, the body stands out completely from the water, the bird paddles against the surface while flapping the wings, to overcome wave drag. A similar series of movements is used by other aquatic avian taxa as well, in order to gain acceleration prior to the take-off (Norberg & Norberg 1971).

Plunge-divers

Plunge-divers are those volant birds that are generally more buoyant and less adapted for aquatic locomotion than other, more derived avian divers. In order to penetrate below the surface and reach the underwater prey, they use the momentum gained from the controlled

fall *(Figure 3)* (Weiss *et al.* 2014, Chang *et al.* 2016). The anatomy of the neck, the structure of the beak, and the cranial shape help plunge-divers to strike and dive into the water with the minimal chance of damage and injuries (Sharker *et al.* 2019). Some of them, such as kingfishers, terns, gulls, pelicans, and tropicbirds dive only to a very small depth, not considerably deeper than their own length (surface-plungers), however, others, like gannets and boobies are able to penetrate for several meters below the surface (deep-plungers) (Ashmole 1971). After the end of the descent, these deep-plungers use foot-propulsion and mainly asymmetrical subaqueous flight (wing-propulsion) for a short period, prior they ascend back to the surface, where they employ paddling with their (mostly) webbed hind feet (Lee & Reddish 1981, Corre 1997).

Foot-propelled divers

Among avian groups, foot-propelled diving occurred in different lineages, such as in ducks, snakebirds (anhingas) and cormorants, and in the highly specialised grebes and loons *(Figure 2)*. The more advanced foot-propelled divers are characterised by an elongated body, caudally positioned hind limbs, with powerful pelvic and leg musculature (Kristoffersen 2001, Clifton *et al.* 2018). The majority of them are still capable to fly. Flightlessness is known among foot-propelled divers – with no claim of being exhaustive – in the case of the Cretaceous Hesperornithiformes birds with highly reduced wing bones (Marsh 1880, Martin & Tate 1976), and for several anatids, such as the Magellanic Flightless Steamer Duck (Livezey & Humphrey 1986), moreover for the Galapagos Cormorant *(Phalacrocorax harrisi)* (Shufeldt 1915), and several flightless grebes, like the Titicaca Grebe *(Rollandia microptera)*, the Junin Grebe *(Podiceps taczanowskii)*, and the recently extinct Atitlán Grebe *(Podilymbus gigas)* (Livezey 1989). However, it must be noted that the loss of flight and the shrinking of wing sizes (at least in the better known Cenozoic taxa) were not primarily related to the modification of their wings to propulsive organs (Livezey & Humphrey 1986, Livezey 1989). Those taxa, that have lost their flying capabilities only recently (e.g. some thousand years ago) are sometimes mentioned as 'neoflightless' (Habib & Ruff 2008).

Among foot-propelled divers, following Clifton *et al*. (2018) a distinction can be made between those taxa that retained much of their terrestrial abilities and able to move effectively on a substrate (like diving, and sea ducks, cormorants), and also sometimes to climb (anhingas) (lesser diving foot-propelled birds), and those that have lost much of their walking skills due to their anatomical adaptations – especially in their abdominal region, pelvic girdle and on the legs – (loons, grebes) and are rather clumsy on land (highly diving foot-propelled birds).

On the water surface, both groups apply alternate paddling (Ancel *et al*. 2000) and during the descent and horizontal underwater swimming, much of the propulsion is provided by the strong hind feet (Johnsgard 1987). Usually, both the lesser and highly diving taxa hold their wings close to the body, and strike with them only rarely, for example during sudden turns (Townsend 1909, Owre 1967), or the phase of submergence from the surface (Kelso 1922), or in the case of some anatids, the wings are held partly extended and used as a diving plane (Townsend 1909, Brooks 1945).

Among ducks, several different techniques are known. For example, Lesser Scaups *(Aythya affinis)*, Ruddy Ducks *(Oxyura jamaicensis)* and Mergansers (*Mergus* spp.) dive with simultaneous (symmetrical) leg strokes (White 1957, Tome & Wrubleski 1988). Besides simultaneous symmetrical strokes, Canvasbacks *(Aythya valisineria)* occasionally dive with alternate (asymmetrical) strokes (Tome & Wrubleski 1988), and their wings are always folded such as in *Mergus* spp. (Townsend 1909, Brooks 1945), and in the case of all the above mentioned ducks (Tome & Wrubleski 1988). Steamer Ducks (*Tachyeres* spp.) also dive with alternate strokes of their feet (Livezey & Humphrey 1982b).

The diving phenomenon was deeply studied in the case of cormorants (Schmid *et al.* 1995, Ancel *et al.* 2000, Ribak *et al.* 2005) however, information related to the slower swimmer anhingas are more controversial (Owre 1967), but according to Audubon (1838), anhingas can dive both with alternate and symmetrical paddling. Cormorants are pursuit hunters, diving in greater depths, while anhingas dive only in shallow waters, and as ambush fish-eaters lurking slowly under the surface (Hustler 1991). The feather coat of cormorants is more water and cold resistant therefore these birds are able to forage in colder waters (Grémiller *et al.* 2005). The feather coat of anhingas is getting completely wet during dives, and cannot hold back air bubbles under the feathers (Ryan 2007). The density of their skeletal elements are somewhat higher, compared to cormorant species (Owre 1967), while the pneumatization of the body and the size of the air sacks are not well developed, therefore, combined with their fully wettable feather coat, they need less energy to act against buoyancy during their shallow dives (Owre 1967, Hustler 1991). In addition, this type of feather coat is a limiting factor for their distribution since they prefer only warm waters (Ryan 2007). Despite that anhingas' attributes do not make them fast underwater hunters, they present efficient climbing abilities (Owre 1967, Diederle 2016). Cormorants use their feet paddling backwards, then every power stroke is followed by a gliding phase when their hind limbs are held in an extended position (Ribak *et al.* 2005). During paddling, the feet are positioned ventrally (Ribak *et al.* 2005). This simultaneous symmetrical striking is an energetically more optimal swimming method, which produces greater levels of (in this case lift-based) thrust than the asymmetrical paddling (Johansson & Norberg 2001, Ribak *et al.* 2005).

Grebes and loons almost never leave the water, and just rarely show erect posture standing on hind limbs (Shufeldt 1898). They are rather clumsy on land, since the proximal hind limbs are integrated into the abdominal skin (Clifton *et al.* 2018). These birds during their underwater pursuit dives employ simultaneous (symmetrical) strokes with their laterally positioned feet – without the use of the wings (Townsend 1909) – which provides them powerful lift-based thrust (Johansson & Norberg 2001, 2003, Ribak *et al.* 2005, Clifton & Biewener 2018). Under the surface, both grebes and loons synchronously move their feet laterally backwards and extend the intertarsal ankle joint, then in the following phase the feet are moving forward with closed digits. The movement of the feet are more lateral and not ventral like in cormorants (Johansson & Norberg 2001, Clifton & Biewener 2018). Their swim includes periodic power and recovery strokes, without a gliding phase following the power stroke (Ribak *et al.* 2005, Clifton *et al.* 2018). Rotation is limited at the hip joint, and is present only at the knee to some extent, supported by the high cnemial crest, which
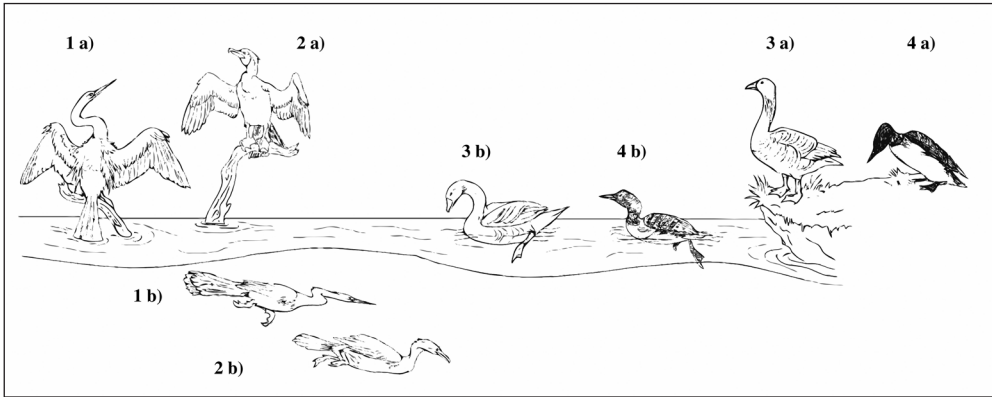
Figure 2. Foot-propelled birds with examples for swimming and terrestrial locomotion abilities
(**1**) American darter *(Anhinga anhinga)* (**a**: drying its wings, **b**: underwater swimming);
(**2**) Great Cormorant *(Phalacrocorax carbo)* (**a**: drying its wings, **b**: underwater swimming);
(**3**) Greylag Goose *(Anser anser)* (**a**: standing, **b**: dabbling);
(**4**) Common Loon *(Gavia immer)* (**a**: unable to stand, **b**: swimming on surface)

2. ábra Úszás közben lábukat használó madarak példákkal az úszási és szárazföldi mozgási képességeik tekintetében
(**1**) amerikai kígyónyakúmadár *(Anhinga anhinga)* (**a**: szárnyait szárítja, **b**: felszín alatt úszik);
(**2**) nagy kárókatona *(Phalacrocorax carbo)* (**a**: szárnyait szárítja, **b**: felszín alatt úszik);
(**3**) nyári lúd *(Anser anser)* (**a**: áll, **b**: vízfelszínről táplálkozik);
(**4**) jeges búvár *(Gavia immer)* (**a**: nem képes állni, **b**: a vízfelszínen úszik)

limits the flexion and extension of the knee, but permits long-axis rotation of the *tibiotarsus* (Clifton & Biewener 2018, Clifton *et al.* 2018).

The reconstructed anatomy and appearance of the extinct Hesperornithiformes are similar to grebes and loons (Zinoviev 2011), however, in some features they also resemble to cormorants and probably these similarities make them an example for mosaic evolution (Bell *et al.* 2017).

Wing-propelled divers

Among diving birds, a wide spectrum of uses of wings exists, and in contrast to foot-propulsion, wing-propelled techniques are known only from the Cenozoic fossil record (Kristoffersen 2001). One of the most extreme morphological and structural responses among birds for locomotion-related mechanical loadings is present in the forelimbs of wing-propelled divers (Habib & Ruff 2008, Serrano *et al.* 2020), thus this behavior *(Figure 3)* represents a strong selective pressure (Smith *et al.* 2021).

Several anatids – such as the White-winged Scoter *(Melanitta deglandi)* and Surf Scoter *(Melanitta perspicillata)* – extend the wings partially during and following the submergence but do not use them for propulsion (Brooks 1945). In contrast, some authors mentioned that Long-tailed Ducks (or Oldsquaw) *(Clangula hyemalis)* apply wing-propulsion for diving and horizontal progression (Townsend 1909, Snell 1985), however, understanding this phenomenon probably needs further observations. The only group of songbirds, that
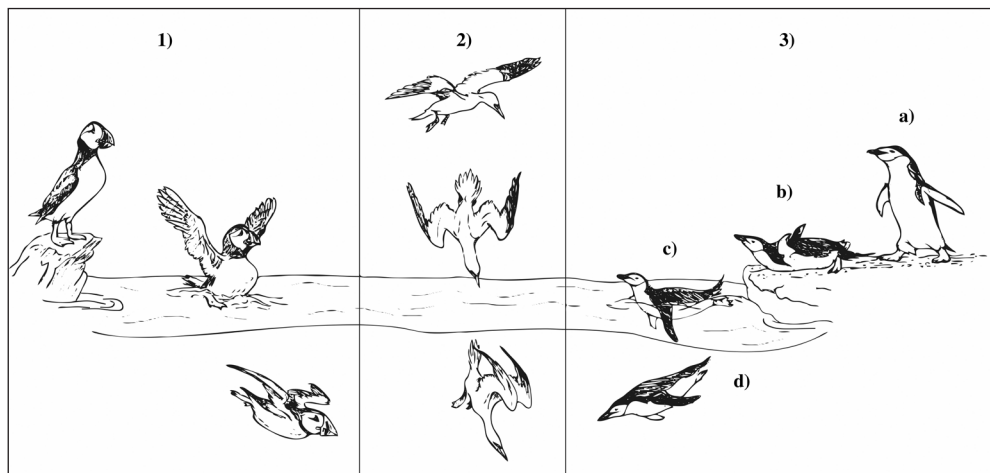
Figure 3. Wing-propelled birds with examples for flying, aquatic and terrestrial locomotion abilities (**1**) Atlantic Puffin *(Fratercula arctica)*; (**2**) Northern Gannet *(Morus bassanus)*; (**3**) Chinstrap Penguin *(Pygoscelis antarcticus)* (**a**: walking, **b**: tobogganing, **c**: swimming on surface, **d**: diving)

3. ábra Úszás közben szárnyukkal evező madarak példákkal a repülési, vízi és szárazföldi mozgási képességeik tekintetében (**1**) lunda *(Fratercula arctica)*; (**2**) szula *(Morus bassanus)*; (**3**) kantáros pingvin *(Pygoscelis antarcticus)* (**a**: sétál, **b**: hason csúszik, **c**: a felszínen úszik, **d**: merül)

are adapted to wing-propulsion are the dippers (Cinclinidae), which progress underwater and search for prey with the thrust produced by the partially opened wings (Goodge 1959). While dippers do share some convergent features (e.g. related to musculature and the feathers) with other wing-propelled divers, the osteological modifications are subordinate (Smith *et al.* 2021).

Following Fish (2016) those taxa that perform underwater flight using wing-propulsion can be grouped regarding their aerial skills. During wing-propulsion, thrust is based on the lift forces produced by the wing strokes (Clark & Bemis 1979). The wings of active flyers (such as Cinclinidae, Alcidae, and genus *Pelecanoides*) must be functional not just in the air but in the water, they employ asymmetrical subaqueous flight (Fish 2016). In their case, the production of thrust is larger during downstrokes, while the upstrokes provide a smaller amount of thrust, however, this movement could counteract buoyancy (Spring 1971, Johnsgard 1987, Johansson & Aldrin 2002). Contrary, in the case of the symmetrical subaqueous flight of flightless wing-propelled birds (such as Sphenisciformes), an important amount of thrust is being produced during both the down- and upstrokes of wings (Clark & Bemis 1979, Lovvorn & Liggins 2002). In addition to wings, certain groups, like alcids use leg strokes to some extent (see the video footage in Enstipp *et al.* 2018), probably to counteract buoyancy (Townsend 1909, Johnsgard 1987).

The wing anatomy of flightless taxa shows flattened bones, with more prominent epiphyses, a drastically decreased mobility of the distal wing joints, together with the wing elevator/retractor muscles becoming more emphasized (Schreiweis 1982, Louw 1992,

Watanabe *et al.* 2021). While the changes in pectoral and wing-elevator musculature can be already experienced in volant wing-propelled taxa (Bribiesca-Contreras *et al.* 2021), the most drastic anatomical alterations probably happen after the loss of flight. According to Raikow *et al.* (1988), the stiffening of joints and reduction of wing elements' mobility cannot be observed among those wing-propelled birds that are still active flyers. Despite that birds that perform asymmetrical subaqueous flight exemplify an adaptation to move both in the water and air (Kovacs *et al.* 2000).

Besides penguins, other (now-extinct) flightless wing-propelled taxa are known, such as the Plotopteridae from the North Pacific Ocean (Eocene to early Miocene), that group highly resembles penguins in many aspects of their adaptations (Dyke *et al.* 2011, Mayr 2020). Flightlessness appeared at least two times among auks (Pan-Alcidae): flightless stem-group alcids (Mancallinae) are known from the Miocene to Pleistocene of the Pacific coasts of North America and Japan (Smith 2011, Watanabe *et al.* 2021), while among crown-group alcids Great Auks represented this evolution in the North Atlantic, at least from the Pliocene until the 19th century when their last species *Pinguinus impennis* became extinct due to human activity (Fuller 1999, Watanabe *et al.* 2021).

Future perspectives

In an attempt to deeper understand the complexity of aquatic birds' swimming habits, we must take into account not just the comparative anatomical descriptions (Schreiweis 1982, Louw 1992, Clifton *et al.* 2018, Watanabe *et al.* 2021), but the newer advanced methods and modeling techniques. However, besides the significance of the latter sources, the importance of traditional field observations must not be forgotten (Brooks 1945, Shepherd 2006).

While numerous studies discussed the locomotion skills of some of the best foot- or wing-propelled swimmer and diver taxa – like grebes (Johansson & Norberg 2001), auks (Johansson & Aldrin 2002), and penguins (Clark & Bemis 1979) – relatively little attention has been paid to reliably record (with photo documentation or video recording) and to publish the various swimming habits of less adapted aquatic birds. It would be particularly remarkable to gain more data about the different uses of wings of diving ducks, not only in nature, but also in an observation tank. A possible direction for future works could be the application of three-dimensional methods or tomographic tools in order to better understand the biomechanics of how the skeleton adapts to the movements in different habitat with different physical characteristics (Habib & Ruff 2008, Habib 2010, Eliason *et al.* 2020). These studies would be interesting not just for the comparison of extant taxa with fossil remains, but also to find novel concepts for bioinspired materials and design or even robotics.

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