

Aspects of cranial adaptation in foot-propelled diving birds – foraging and visual fields of some piscivorous species

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Abstract The adaptation to an aquatic lifestyle has occurred several times during the evolution of birds. The transition from a terrestrial to an aquatic lifestyle requires enormous changes in morphology, physiology, and behaviour. In addition to many physical parameters, aquatic foraging is also a limiting factor, despite the fact that aquatic habitats are often rich in food and prey. Despite many previous studies (foraging, physiology, anatomy, ecology, etc.) and a large amount of data regarding piscivore foot-propelled diving birds, our knowledge on the possible relationships between cranial morphology, feeding mechanism, visual abilities and binocularity is still very limited. In this study, we attempt to achieve a deeper understanding of the visual abilities and foraging related attributes of 5 recent and 1 extinct species of foot-propelled diving birds. We attempted to measure the horizontal visual fields of these species using 3D visualization techniques. According to our model, the narrowest horizontal binocular field was measured in Anhinga (*Anhinga anhinga*), and the widest was measured in the cases of Great Cormorant (*Phalacrocorax carbo*) and Goosander (*Mergus merganser*). Our results support the prediction that binocular field variation among aquatic birds is primarily associated with foraging methods and activities.

Keywords: evolution, skull shape, cranial morphology, ecomorphology, morphometrics, anatomy, binocular vision, visual field, aquatic birds, piscivorous birds

Összefoglalás A vízi életmódhoz való alkalmazkodás több alkalommal kialakult a madarak evolúciója során. A szárazföldi életmódról a vízi életmódra való áttérés óriási változásokat követel meg morfológiai, élettani és viselkedésszerű vonatkozásban is. Számos fizikai paraméter mellett a vízben való táplálékkeresés is korlátozó tényező, annak ellenére, hogy a vízi élőhelyek általában gazdagok táplálékban és zsákmányállatokban. Az elsősorban lábukat használó halebő búvármadarakkal kapcsolatban számos korábbi tanulmány (táplálkozás, fiziológia, anatómia, ökológia stb.) és a rengeteg adatmennyiség ellenére a koponyamorfológia, a táplálkozási mechanizmus, a látási képességek és a binokularitás közötti lehetséges összefüggésekről szóló ismeretek erősen korlátozottak. Jelen tanulmányban 5 recens és 1 kihalt faj vizuális képességeinek és táplálkozáshoz köthető tulajdonságainak kapcsolatát vizsgáltuk látótereik mérésével, 3D vizualizációs technológiák segítségével. A modell szerint a vizsgált fajok közül a legkeskenyebb binokuláris látómezővel a kígyónyakú madár (*Anhinga anhinga*), a legszélesebbel pedig a nagy kárókatona (*Phalacrocorax carbo*) és a nagy bukó (*Mergus merganser*) rendelkeznek. Eredményeink erősítik azt az észrevételt, miszerint a vízimadarak binokuláris látómezejében való eltérések elsősorban az életmódbeli és a táplálék megszerzésében való különbségeknek köszönhetők.

Kulcsszavak: evolúció, koponyaalak, koponyasajátosságok, ökomorfológia, morfometria, anatómia, binokuláris látás, látómező, vízimadarak, halebő madarak

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Introduction

The transition from a terrestrial lifestyle to an aquatic requires tremendous changes in morphology, physiology and behaviour. Buoyancy is a major determinant of the locomotory cost in diving animals, especially in aquatic birds due their highly pneumatic skeletal system (Kato *et al.* 2006). For the success of living and feeding in aquatic environment, several bird clades chose different evolutionary traits to increase their locomotor performance, buoyancy control, and reduce drag forces at the same time (Fish 2016, Houssaye & Fish 2016, Gutarra & Rahman 2022). In addition to many physical parameters, foraging in water is also a limiting factor, despite the fact that aquatic habitats are often rich in food and prey (Dethier *et al.* 2003). Different foraging behaviours, swimming and diving abilities highly contribute to the coexistence of sympatric species in the same environment and in the vertical and horizontal partitioning of the habitat (Livezey & Humphrey 1982, Pöysä 1983a, 1983b, Johnsgard 1987, Hustler 1992). A central tenet of optimal foraging theory is that natural selection has produced predators that employ behavioural strategies which maximize foraging efficiency (MacArthur & Pianka 1966, Pyke *et al.* 1977). This assumes that predators have evolved phenotypes that maximize fitness in particular environments. Sensory systems play a key role in finding prey; vision is particularly the most important. The specific capacities of sensory organs are dictated by their adaptive significance and physiological trade-offs. For instance, the amphibious behaviour presents major sensory problems to seabirds since optical requirements in air are fundamentally different from those in water (Lythgoe 1979).

During the history of Earth, several primarily terrestrial clades of birds have returned to the water and adapted, on different levels, to live in an aquatic environment (Kelley & Pyenson 2015, Motani & Vermeij 2021) (*Figure 1*). The aquatic adaptation of different lineages to similar physical parameters and challenges has resulted in similar external morphology (Lindgren *et al.* 2010, Motani & Vermeij 2021, Gutarra & Rahman 2022). The first known avialans adapted to foot-propelled swimming and diving are the members of the order Hesperornithiformes which includes a small and restricted group of marine toothed, foot-propelled diving birds (Panteleyev *et al.* 2004). These birds evolved and colonised the marine and freshwater ecosystems in the Cretaceous (Marsh 1880, Chiappe & Witmer 2002, Bell & Chiappe 2016). One of the most well-preserved species are known from numerous fossil remains, *Hesperornis regalis* (Bell & Chiappe 2022). There are many anatomical similarities with today's diving species, this bird also had a long flexible neck with long and narrow jaws but armed with sharp recurved teeth formed together a perfect tool to catch fast fishes (Cracraft 1982, Houde 1987, Witmer & Martin 1987, Padian & Chiappe 1998). Since the discovery of *Hesperornis* (Marsh 1880) several specimens have been found, therefore, the elements of the

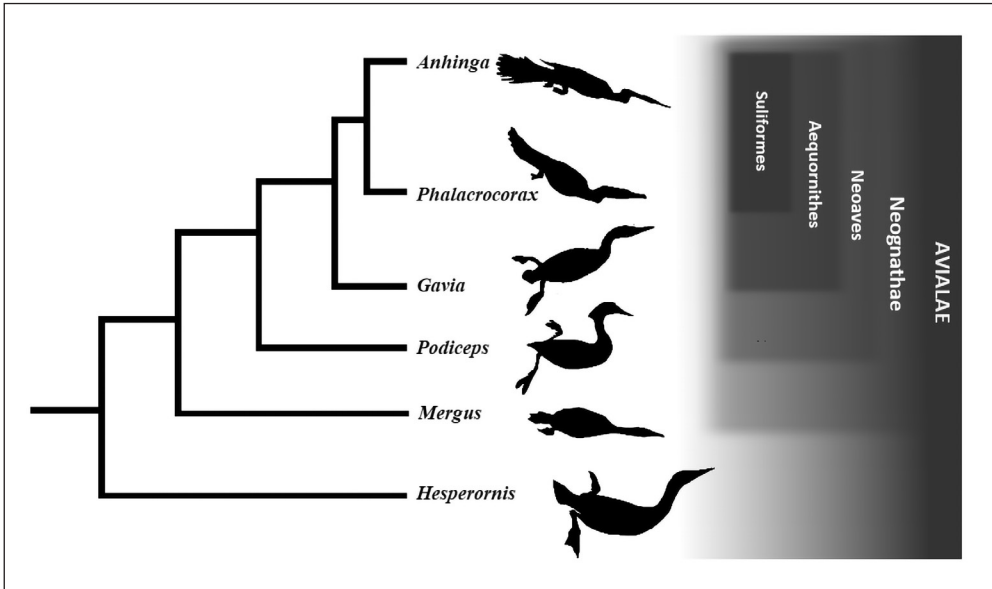


Figure 1. Foot-propelled diving bird lineages in Earth history (Braun & Kimball 2021)

1. ábra Lábbal úszó, víz alá bukó madárcsoportok a földtörténet során (Braun & Kimball 2021)

cranium are better known and paint a more accurate picture of the whole skull (Gregory 1952, Gingerich 1973, Bühler *et al.* 1988).

According to our current knowledge, the most of the main clades of modern birds evolved in the Middle to Late Cretaceous (Moen & Morlon 2014). Some species of modern clades already adapted to aquatic life, as the loon-like *Polarornis*, but its taxonomic position is still disputed (Mayr *et al.* 2018). After the Cretaceous-Paleogene mass extinction, birds diversified dramatically and conquered numerous empty ecological spaces (Brusatte *et al.* 2015). Through the following era, numerous foot-propelled piscivorous species appeared, including grebes (Kurochkin 1976, Zelenkov 2015), loons (Storer 1956, Mayr 2004), anhingas (Mayr *et al.* 2020), cormorants (Mayr 2015) and early anatids (Alvarez & Olson 1978, Zelenkov 2020).

The more advanced foot-propelled divers are characterised by an elongated body, caudally positioned hind limbs, with powerful pelvic and leg musculature to make them enable to pursuit hunt their underwater prey (Kristoffersen 2001, Clifton & Biewener 2018, Segesdi & Pecsics 2022).

Several studies discussed the various anatomical adaptations of these groups previously, but our understanding of the adaptation of cranial features and visual abilities are still limited (Martin 2007, 2012, 2014).

The study of the visual abilities of birds, as related to their ecology and evolution, has a long history, and over the past several years, huge amount of data has been collected, mainly quantified as visual fields (Martin 2014, Cerio & Witmer 2020). “In vivo” observations on field are difficult, time and access to living specimens of rare species is extremely limited. Studies with endangered species raise additional problems and difficulties, furthermore, comparison to extinct species is impossible. Performing ophthalmological studies and measures on living

or dead specimens requires expensive infrastructure, technologies, specific training and experience. Modelling in a virtual area is a well-established practice. Some authors have even predicted static visual fields in extinct species using inverse perimetry (Stevens 2006) or used simple ray tracing method (Rinehart & Breton 2009).

Binocular field topography varies among species associated with controlling bill and legs, position changes during hunting, foraging activities (Martin & Wanless 2015), and feeding their offspring (Martin *et al.* 2005). In diving birds, binocularity enables accurate control of the bill, and their time to reach the prey items (Martin 2014). Binocular field topography represents an important trait for further understanding the evolution of avian vision and creates a broader picture of convergent evolution of distinct lineages.

Unfortunately, despite numerous studies and the enormous amount of data with regards to the feeding ecology of foot-propelled diving birds, our knowledge about the potential relationships between cranial morphology, feeding mechanism, visual abilities and binocularity is still limited.

In this preliminary study, our aim was to increase our understanding regarding the role of binocularity in foot-propelled fish-eating birds, and observe the differences in skull morphology that reflect on feeding habits. The virtual models allow us to predict and measure static visual fields in two dimensions within a virtual environment, and to give a rough estimation of binocularity in diving piscivorous birds.

Materials and Methods

Species and specimens

This study is based on skulls from 5 extant and 1 extinct species. All skulls are from adult specimens in the collection of the Eötvös Loránd University, Budapest, Hungary, Great Cormorant (*Phalacrocorax carbo*), the collection of the Hungarian Natural History Museum Budapest, Hungary, Great Crested Grebe (*Podiceps cristatus*), Goosander (*Mergus merganser*), the digital archives of University of Wyoming, Laramie, USA, Common Loon (*Gavia immer*), and the Natural History Museum of London, London, United Kingdom, Anhinga (*Anhinga anhinga*). For the extinct bird *Hesperornis regalis*, a virtual model was created in Blender free 3D modelling software (Community 2018), following the previous studies as references (Gingerich 1973, Bühler *et al.* 1988) (Figure 2).

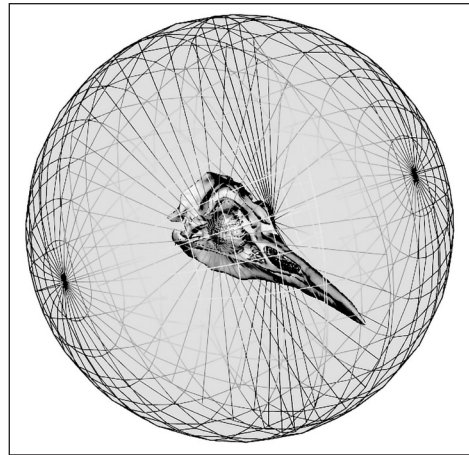


Figure 2. The 3D digital model of *Hesperornis regalis* that we used in our study. The parameters of the skull was based on previous studies as references (Gingerich 1973, Bühler *et al.* 1988)

2. ábra A *Hesperornis regalis* koponyájának 3D modellje, amelyet jelen tanulmányunkban használtunk. A koponya paramétereikhez korábbi tanulmányokat használtunk referenciaként (Gingerich 1973, Bühler *et al.* 1988)

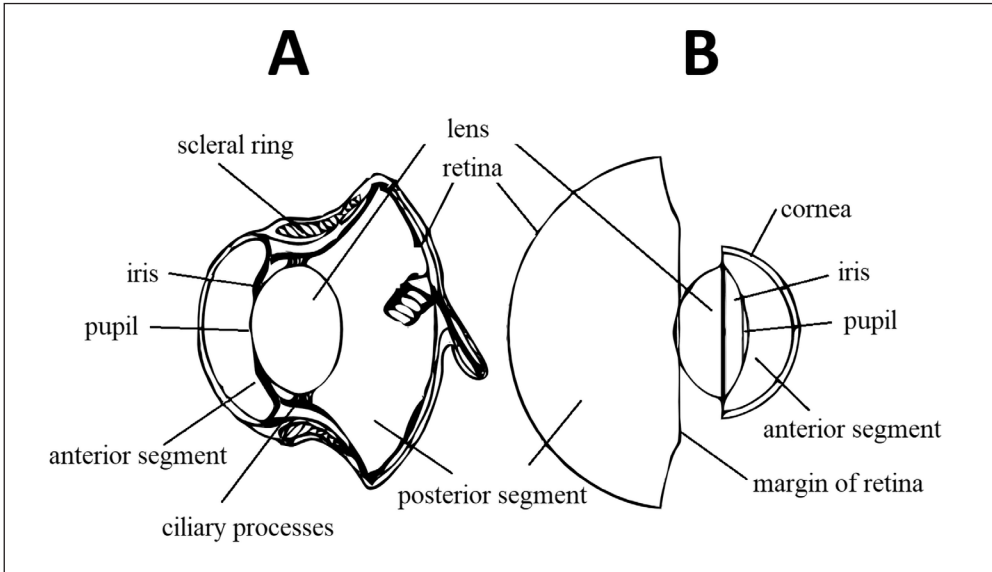


Figure 3. A) Simplified cross section of an avian eyeball with anatomical dimensions in *caudal* view (Schmitz 2009). B) Schematic eyeball used for the model (Cerio & Witmer 2020)

3. ábra A) A madárszem egyszerűsített keresztmetszeti ábrája az anatómiai dimenziókkal *alsó* nézetben (Schmitz 2009). B) Sematikus szem, amely modellként szolgált (Cerio & Witmer 2020)

For the study, larger extant species from different clades were deliberately chosen that feed almost exclusively on fish in their adult age. Information of foraging behaviour was gathered from primary literature (Cramp 1978, del Hoyo *et al.* 1992).

No birds were killed in order to obtain their skull; all either died of natural causes or whilst in captivity.

Models and procedures

We attempted to depict horizontal sections through the visual fields. For our measures, we captured the skulls in dorsal view at the plane of optic axes and used schematic eyeballs to calculate the visual fields, and to estimate the binocular sections. Schematic eyeballs utilize several simplifying assumptions to estimate the optical performance of the visual apparatus (Cerio & Witmer 2020). Some of these assumptions are known to be slightly inaccurate but are nonetheless useful approximations for assessing optical performance, and can provide theoretical estimates of the peripheral limits of visual fields (Martin 2007). Despite the aspects of inaccuracy, these schematic eyeballs are good enough to estimate the size of the visual areas that are mathematically consistent with behavioural measurements. Gross morphology of the eyeball was based on previous studies (Ritland 1982, Schmitz 2009, Cerio & Witmer 2020) (Figure 3). Due to the aim of this recent study, we were counting in every situation with slightly converged eyes in a relaxed position without the scientific data of eye movements. The skulls were standardised and fixed at the tip of the bill (90°) and at the cross section of optic axis of left eye and the right eye (0°).

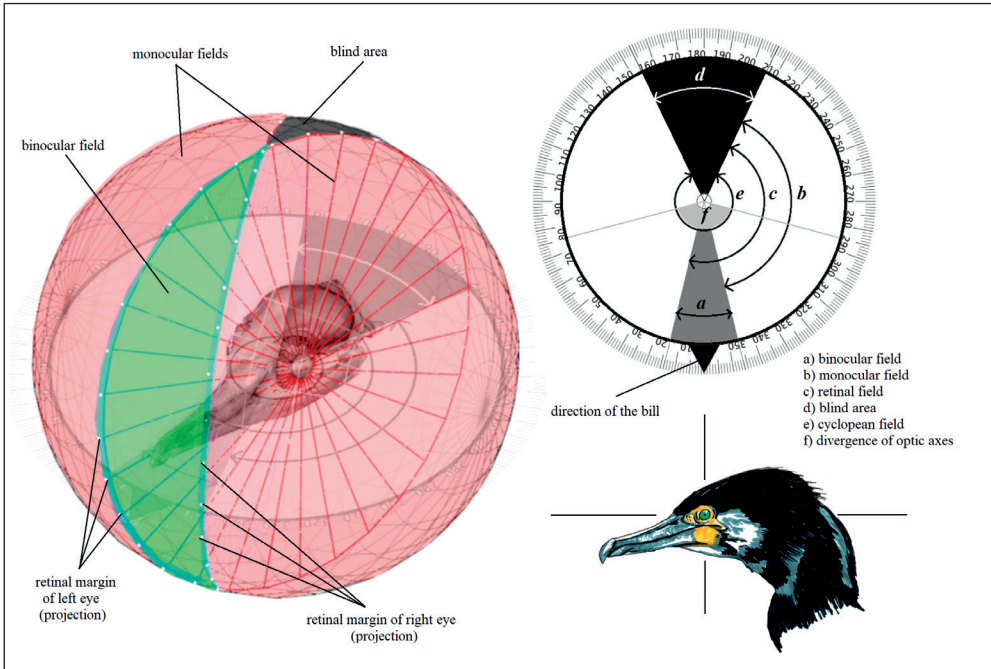


Figure 4. Visual fields in Great Cormorant. Perspective views of orthographic projection of the retinal margin boundaries of the two eyes in slightly converged, relaxed position. In the diagram the bird's head is positioned at the centre of a transparent sphere with the bill tips and field boundaries projected onto the surface of the sphere (without the positions of *pecten* and optical axes)

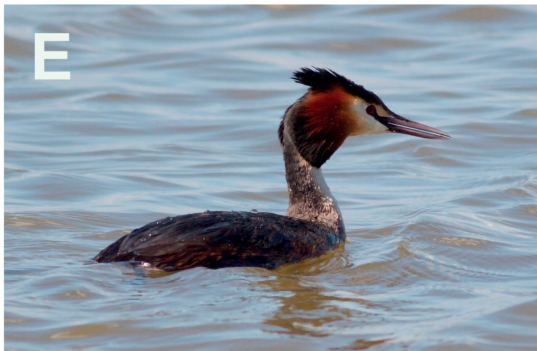
4. ábra A nagy kárókatona látómezeje. Perspektivikus nézet a retina széleinek ortografikus kivetítésével, ahol a szemek kissé konvergáltak, nyugalmi állapotban vannak. Az ábrán a madár feje egy átlátszó gömb közepén helyezkedik el, a csőr végével és a látómező hatáiraival a gömb felületére vetítve (a *pecten* és az optikai tengelyek megjelölése nélkül)

Visual fields of foot-propelled diving birds were measured in a horizontal plane when the eyes are in a standard relaxed position and slightly converged (*Figure 4*).

Results

According to our model, the narrowest horizontal binocular field was measured in Anhinga, and the widest was measured in the cases of Great Cormorant and Goosander. The results of Common Loon, Great Crested Grebe and *Hesperornis* were ranged between the previously mentioned species. Obviously, the species with wider binocular fields have narrower monocular fields and greater blind areas (*Table 1, Figure 5*).

The visual field scores showed that foraging behaviour and environmental conditions were important predictors. In poor visibility conditions, swamps and lakes with dense vegetation, a wide binocular field is less important for the Anhinga. Even slower prey items do not require better depth perception either.



▼ : direction of the bill
■ : binocular field
■ : blind area

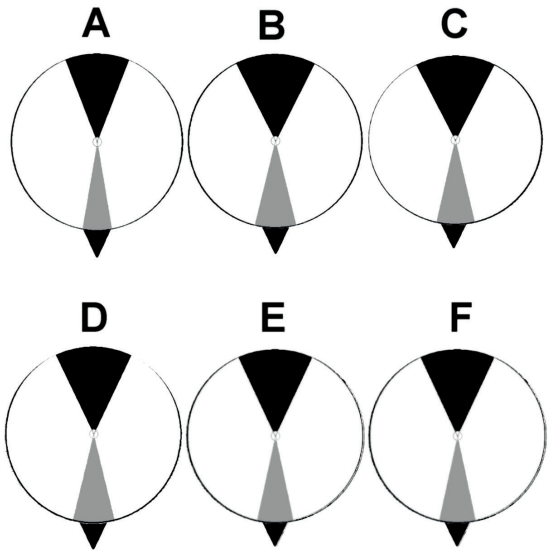


Figure 5. Horizontal sections through the visual fields of birds with slightly converged eyes in a relaxed position: *Anhinga* (A), *Phalacrocorax* (B), *Mergus* (C), *Gavia* (D), *Podiceps* (E), *Hesperornis* (F) (Photos: *Anhinga*: Tibor Csörgő; *Phalacrocorax*: Dániel Baráth; *Mergus*, *Gavia*, *Podiceps*: József Mészáros; *Hesperornis*: 3D digital image modelled and rendered in Blender by the authors)

5. ábra A madarak látómezejének vízszintes metszete, ahol a szemek kissé konvergáltak, nyugalmi állapotban vannak: *Anhinga* (A), *Phalacrocorax* (B), nagy bukó *Mergus* (C), *Gavia* (D), *Podiceps* (E), *Hesperornis* (F) (Fényképek: *Anhinga*: Csörgő Tibor; *Phalacrocorax*: Baráth Dániel; *Mergus*, *Gavia*, *Podiceps*: Mészáros József; *Hesperornis*: 3D digitális kép Blenderben modellezve és renderelve a szerzők által)

Moreover, in better visual conditions, binocularity plays a more important role in the pursuit of relatively small and fast prey items (Common Loon, Great Crested Grebe, Goosander). Furthermore, it has a greater role in feeding from the bottom during pecking and fishing from the upper layer of the water column (Great Cormorant, Goosander) (Figure 5).

In our model, the scores of Great Crested Grebe and the extinct *Hesperornis* were the same on each level (Table 1).

Table 1. Comparison of visual field parameters in horizontal section

1. táblázat A látómező paramétereinek összehasonlítása vízszintes metszetben

	<i>Anhinga</i>	Great Cormorant	Goosander	Common Loon	Great Crested Grebe	<i>Hesperornis</i>
binocular field	20°	28°	28°	26°	24°	24°
monocular field	148°	140°	139°	140°	143°	143°
retinal field	168°	168°	167°	166°	167°	167°
blind area	44°	52°	54°	54°	50°	50°
cyclopean field	316°	308°	306°	306°	310°	310°
divergence of optic axes	140°	124°	126°	126°	130°	130°

Discussion

In our study, the binocular field of *Anhinga* was the smallest. Despite the evidence of obvious similarities with cormorants, in other respects than orbital region, the shape of the bill and certain muscles associated with these regions, features of the skull are very different due to the extreme elongated skull (Marugán-Lobón *et al.* 2022). These are consequences of different lifestyle and hunting methods. Their adaptation to obtain fish evolved on different directions, while ecological ranges of the species may overlap, both appear to be most proficient in quite different habitats. The cormorant exhibits a far greater degree of specialization for active pursuit of fish and the skull is adapted for precise and powerful prehension. The *Anhinga* has achieved proficiency in an aquatic environment through adaptations, which emphasize slow, prowling progression under water (Owre 1967). Prey is usually approached by stealth and pierced with a thrust of the mandibles. Far less buoyant, an adaptation which facilitates its remaining submerged while moving slowly, it does

not remain long in the water after prey is secured (Owre 1967, Dostine & Morton 1989). Although these birds are not fast swimmers, they are very effective ambush aquatic hunters, relying on their quick necks and sharp bills to catch prey. They target slower-moving species of fish and stalk them underwater, finally striking out with their long neck and spearing the prey with the beak (Hustler 1992), then bring the prey above water and manipulate it in order to swallow the fish head first in ideal direction (Owre 1967). The binocular field is long and narrow, and the central placement of the bill suggests that vision is used to guide the bill position during visual foraging (Hayes *et al.* 1991).

The binocular field of Great Cormorant is wider than in the case of Anhinga. The visual fields of cormorants are associated with visually guided pecking or lunging at prey. The bill tip projection falls centrally or within the lower half of the binocular area. The binocular field is relatively long and narrow, the maximum binocularity occurs at or above the projection of the tip of the bill (Martin *et al.* 2008, White *et al.* 2008). Great cormorants eat almost exclusively fish less than 20 cm in length and occasionally eat larger fishes and crustaceans and molluscs (Jepsen *et al.* 2018, Lyach *et al.* 2018). Fish are taken mostly in shallow water less than 20 m deep, but they hunt throughout the whole water column, from the surface to the bottom, depending on the attributes of their prey. They dive in and pursue fish under the water using their vision, eating small fish underwater and bringing larger fish to the surface to swallow (Lehikoinen *et al.* 2017). Great cormorants may forage alone or in flocks, varying regionally and possibly with subspecies. Great cormorants eat a wide variety of fish species, but may rely primarily on only a few species that are abundant locally, often bottom-dwelling ones. In those areas where Great Cormorants are sharing habitat with the swifter pursuit hunter Double-crested Cormorants (*Nannopterum auritum*), they eat more bottom-dwelling fish species (Ross 1977).

In our study, the Goosander showed similar attributes to cormorants. Foraging behaviour, rather than diet, is the primary driver of binocular field size and binocular shape associated with the horizontal plane among the Anatidae (Cantlay *et al.* 2023). Goosanders are skilled diving predators, eating mainly slower and smaller fish species. Their serrated bills are well suited for capturing small and slippery preys. Similarly to cormorants, a hooked *rostrum* is ideal for fishing in upper water column. Clear water is preferred for feeding because these birds hunt primarily by sight (Wood & Hand 1985, Brewer *et al.* 1991). Mergansers are usually foraging in shallow water, but they will hunt wherever prey is abundant. Other merganser species forage in several different ways as they float at the surface and looking underwater column as they go, they dive in deep or shallow water to search for prey (Munro & Clemens 1939). Mergansers diving to obtain fish, therefore, had lesser mean angular separation sizes (the bill tip is furthest from the maximum binocular field width) compared to their relatives, as they are dependent upon visual discrimination of food items in the bill (Lisney *et al.* 2013, Cantlay *et al.* 2023).

Common Loons are visual predators, locating fish by sight and diving deep to catch them. The binocular field is similar to the Great Cormorant and Goosander but a bit narrower. These swift-swimmer birds' binocular field is projecting to tip of the bill as they are targeting schooling fishes with higher speed. They generally hunt in water 2 to 4 m deep. Because they rely on sight, clear water is critical to Common Loons (Barr

1996, McIntyre & Barr 1997), and they do not fish at night. The prey consists of small or medium sized fish, including cod, herring, sprat, sculpins, and occasionally, other small vertebrates and invertebrates. Food is usually swallowed underwater, their oesophagus is relatively elastic. When they find a suitable prey species in abundance, they will fully exploit it (del Hoyo *et al.* 1992).

The diet of Great Crested Grebe consists mainly of large fish, but also includes insects and other invertebrates. Larger prey item does not requires broad binocular field. These birds catch their prey by diving under the surface of the water, similarly to loons, but they forage the most during dawn and dusk, probably because this is when their prey are closest to the surface (Newbrey *et al.* 2012). This makes the fish easier to detect visually and also reduces diving distance (Ulenaers *et al.* 1992, Gwiazda 1997). Large sized grebes are fast and aggressive hunters. At higher speed, these birds spear larger fishes with their long bill (Cramp 1978).

In our model, the results were exactly same in the case of *Hesperornis* and Great Crested Grebe. The skull is elongated with a long rostrum similar to that seen in large grebe and loon species (Figure 6). These similarities make them an example for mosaic

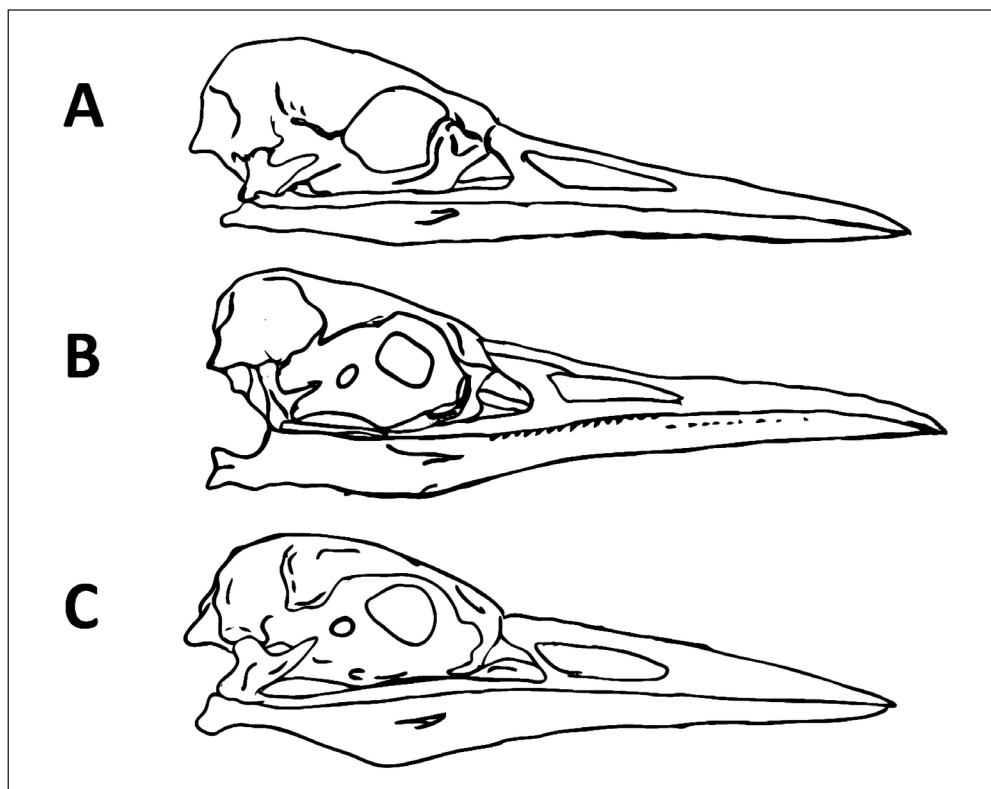


Figure 6. Convergent attributes on the skulls of Common Loon (*Gavia immer*) (A), Great Crested Grebe (*Podiceps cristatus*) (B) and *Hesperornis regalis* (C) (lateral view)

6. ábra Konvergens tulajdonságok a jeges búvár (*Gavia immer*) (A), búbos vöcsök (*Podiceps cristatus*) (B) és a *Hesperornis regalis* (C) koponyáin (oldalnézet)

evolution (Bell & Chiappe 2016). This elongation is due primarily to the length of the premaxilla (Bell & Chiappe 2022). The dentary and maxillae of hesperornithiforms bear small recurved teeth set in a groove (O'Connor 2019). The retention of teeth in birds is a conserved character with similar molecular and developmental mechanisms inherited from their non-avian reptilian ancestors. The number, shape, and arrangement of teeth in the jaws of *Hesperornis* have trophic implications, with the increased number of teeth in the dentary having been related to a piscivorous diet (Wu *et al.* 2021). The distinct and delicately hooked cranial terminus of the premaxilla, which may have been emphasized by the shape of the keratinous beak, may have also been useful for the retention or capture of larger fish. In addition to many other similar characteristics that they share with grebes, the absence of teeth in *premaxilla* suggests that these fast swimming underwater hunters may spear occasionally larger fishes with their long bill. Several other features of the skull of *Hesperornis* have been used to support interpretations of a diving lifestyle. The large size of the auricular *fossae*, the reduced dorsal pneumatic recess, and the flattened cerebellar *fossa* as traits shared with modern diving birds. The latter two of these features was noted as possibly associated with the expansion of the dural sinuses (Elzanowski & Galton 1991), a convergent feature found in modern diving birds (Jessen 2001). Unless the few exceptions, it is interesting to note that among modern diving birds, foot-propelled species are generally found in shallow, primarily freshwater environments, while pelagic marine divers are primarily wing-propelled birds (Houde 1987). This represents a dichotomy between shallow and deep-water diving, with wing-propelled divers typically engaging in much deeper dives than foot-propelled divers (Bell *et al.* 2019).

A number of species of waterfowl are active and feed at night, while others, such as the pursuit-diving mergansers, appear to be limited to foraging under brighter conditions (del Hoyo *et al.* 1992, Lisney *et al.* 2013).

The maximum width of the binocular field is in a range of bird species equal only 20–30 degrees. Thus, it has been proposed (Martin & Katzir 1999) that the essential function of binocularity in birds may lie in the provision in each eye of an optic flow-field, which expands symmetrically about a target point in front of the head.

It can be suggested that this width represents an optimal trade-off that provides sufficient optic flow-field information to ensure accurately controlled rapid approaches towards objects during foraging, while at the same time, maximising the width of the peripheral, and hence cyclopean, visual field within constraints imposed by each eye's optical design (Martin 2007). In the case of aquatic piscivore birds, not only the food but the hydrodynamic demands and the drag forces affect the cranial morphology (Harrison 1957, Pecsics *et al.* 2017).

In an attempt to deeper understand the complexity of aquatic birds' foraging behaviour and visual fields, we must take into account not just the comparative anatomical descriptions but the newer advanced methods and modelling techniques. However, besides the significance of the latter sources, the importance of traditional field observations must not be forgotten.

Our results support the prediction that binocular field variation among aquatic birds is primarily associated with foraging methods and activities rather than phylogeny. The

variation in binocular field characteristics probably reflect the different perceptual challenges experienced by different species when foraging in aquatic environments. In future studies should rather examine the differences of closely related species that may have effect on the cranial morphology of these birds. With a larger sample size (including more species) and using parameters of soft tissues of the eye will create a more complex vision regarding the evolution of those features which are supporting underwater foraging.

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