

Water bird fauna in the Carpathian Basin from the beginnings through historical times

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Abstract This study aims to summarize the knowledge about the evolution and fossil remains of avian fauna near waterbodies, since ornithologists, who rarely come across or research the paleontology of birds, do not possess significantly detailed knowledge about the evolution and evidence of the current avian fauna.

Keywords: birds, waterfowls, evolution, aquatic environments, Carpathian Basin

Összefoglalás „A Kárpát-medencei vizek madárvilága a kezdetektől a történelmi időkig” tanulmányban a szerző összefoglalja mindazt, amit a vízi élőhelyek madárvilágának evolúciójáról, fosszilis leleteiről jelenleg tudunk. Azért tartottuk szükségesnek mindezt megírni, mivel a madarak őslénytanával nemigen foglalkozó, és vele ritkán találkozó ornitológusok nem rendelkeznek túl gazdag ismeretekkel a mai madárvilág kialakulásáról és annak bizonyítékairól.

Kulcsszavak: madarak, vízi madárvilág, evolúció, vízi környezet, Kárpát-medence

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Introduction

Aquatic and wet environments have always provided ample living conditions for birds, even when the surface merely consisted of snow and ice fields (like Antarctica), steep cliffs, or bare beaches or sandbanks. This is due to the fact that birds can acquire their food supply from water, while the relatively dry area necessary for reproduction is provided by the environments listed. Some aquatic bird species downright build their nests onto the water. Due to their constant body temperature and usually waterproof feathers, the climate of the environment only influences their abundance through the amount of nutrition they and their offspring require. In case of low nutrient supply, the birds are forced to migrate. It concludes from the above that they mostly consume other animals, however, exclusively herbivores are also included (such as geese).

They usually live in pairs which can last for their entire lifetime, but there are also polygamous species. Nests can be absent altogether (as with the penguins of Antarctica), or can be quite simple (consisting of a few pebbles and sticks), but can even be carefully prepared and expanded for years (as with storks) or formed out of mud (as with flamingos). The number of nestlings can vary from one to a dozen, and can either be nidifugous or incessors.

Based on their way of lives they can be swimmers, leaping into water from heights, waders, and species living at the shore or in wet environments:

- swimmers can propel themselves either with their wings (penguins, razorbills, petrels) and can usually dive more easily and can spend more time underwater, or with their legs (*Hesperornis*, divers, grebes, pelicans, cormorants, geese, Anatidae etc.);
- seabirds usually leap into the water from great heights to catch their prey (gannets, petrels, razorbills etc.);
- waders stand and walk shallow waters to collect aquatic animals with their long beaks;
- species living on the shore are usually smaller in size, rarely venture to open waters, and collect their nutrition from the flora or coastal sand;
- species living in wet environments are tied more to the wildlife of where they live, nest and feed, but they don't actually require large surface of water.

From the Jurassic-Cretaceous boundary, the findings of the above-mentioned types emerge fairly early among recent birds. In fact, they make up the majority of fossilized remains of avian fauna of the Cretaceous period (Ornithure – Neornithes). Whether this has taphonomic reasons or they in fact constituted the majority of this early phase of avian fauna could not be proven at that time, but all signs point to this.

Those belonging to taxons outside of the species of orders featured in the part describing taxonomy can also be tied to near-water environments (osprey, kingfisher, dipper etc.), but they are not the subject of this paper.

According to their relation to aquatic environments, we can distinguish between swimmers (dabblers, divers), waders, those living on the shore and those living in wet environments. The fluffy or naked skin of nestlings, and their incessorous or nidifugous nature also indicates their primary or secondary connections with water. Their body covered in down feathers, the early leaving of their nests and their ability to feed on their own all indicate their ancient characteristics still present from the reptilian origins.

Since in case of extinct taxons, we cannot know the exact environments in which they lived, we are also going to discuss groups or species that probably were not that partial to aquatic environments, but their place in taxonomy classifies them as belonging to this category.

The paper, of course, is not all-encompassing, thus, we are only going to mention the most representative taxons. We found it necessary, however, to also include data of recent avian fauna of the Carpathian Basin to present the formation and relations of recent fauna in the Quarter from the past few hundreds of thousands of years.

Taxonomy

Since the genome of extinct species was lost during fossilization, their inclusion in more recent, DNA-based systems is not possible (Sybley & Ahlquist 1990, Sybley & Monroe 1990, Jarvis *et al.* 2014) neither from a practical, nor from a theoretical point of view. From the practical standpoint, there is no definitive DNA to compare, and from the theoretical standpoint, there is no way to distinguish between analogous features formed by convergence and

homologous features passed on from their ancestors. Due to these shortcomings, we are going to use the old system of classification (Wetmore 1960), which includes extinct groups (orders, families). In the past decades, a number of revisions synonymized or reclassified rather many previously classified species into different taxons. We took these changes into account by necessity, but did not agree with them in all cases, aiming at a classification as transparent as possible.

Data was extracted primarily from the works of Brodkorb (1963, 1964, 1967), Olson (1977, 1985), Kurochkin (1995, 2006), Mourer-Chauviré (1995), Mlikovský (1996, 2002), Tyrberg (1998), Feduccia (1999) and Mayr (2009), complemented with other sources (see bibliography) and with data from other works of this paper's author. References are thus kept to those absolutely necessary.

It is worth noting that families that have no known ancestors from prehistoric times are not featured in the listing.

Abbreviations: Q1-Q2 – lower Pleistocene; Q3 (Q3/I-Q3/II) – middle Pleistocene; Q4/I – upper Pleistocene; Q4/II – Holocene; + – Quaternary extinct/fossil species. Cl. – Class; Scl. – Subclass; Ord. – Order; Subord. – Suborder; Fam. – Family; Subfam. – Subfamily.

Cl. Aves (Linnaeus, 1758)

Scl. Ornithurae (Haeckel, 1866)

Ord. Hesperornithiformes (Sharpe, 1899)

These birds were present from the beginning of the Cretaceous and typical to the era. Their vestigial wings suggest that even their earliest known representatives (145 million years ago) were already highly specialized, thus, they had to be formed much earlier than that. However, they match with recent birds in almost all known skeletal characteristics (Ornithurae – Neornithes), differing from Sauriurae birds, which are also contemporaries.

Fam. Hesperornithidae (Sharpe, 1899)

Aquatic birds with vestigial wings, toothed beaks, with a similar constitution to that of *Gavia* (loons), but of a much bigger size. Dyke and his colleagues reported *Hesperornis* remains not identified to the species level (*Hesperornithidae* indet.) in 2010 from the lower Cretaceous of Cornet in Transylvania (Romania) (Dyke *et al.* 2010).

Hesperornithidae are typical aquatic birds – propelling themselves with their legs – of the Cretaceous period that already have vestigial wings (only the humerus remained, albeit in a deformed form). They lived from the lowermost to the uppermost Cretaceous in several parts of the globe. Their largest representatives were on par, and even bigger than nowadays pelicans. Since their legs were located in the rear, their movement on solid ground was most likely poor. They probably ate fish in waters near shores similarly to recent foot-propelled birds, and this must have resulted in the degradation of their vestigial wings. At the end of the Cretaceous, they went extinct along with *Archaeornithae*, *Enantiornithae* and dinosaurs.

Ord. Sphenisciformes (Sharpe, 1891)

They constitute the most special group within the present avian fauna both in terms of morphology and lifestyle. Most of their characteristics have rather ancient features, which suggest the early development of the order, even though their earliest remains come from the beginning of the Tertiary.

Fam. Spheniscidae (Bonaparte, 1831)

The origin and biological relatives are matters of debate. Genetically – debatably – they are tied to seabirds. Nowadays, they are only present on the Southern Hemisphere on shores along cold streams. They feed on fish and pelagic crabs (krill). Due to their typical morphological characteristics (the nature of feathers, lack of cervical apteria, the lack of pneumatization in bones, the existence of the paleopulmo), they differ from every other group of birds. Their earliest – although contested – representative is *Palaeocursornis biharicus* Kessler *et* Jurcsák, 1986 from the Lower Cretaceous of Transylvania (Cornet, Romania) [new combination: *Protospheniscus biharicus* (Kessler *et* Jurcsák, 1986), (Kessler, J. 2013)].

Ord. Gaviiformes Wetmore *et* Miller, 1926

Loons are typically aquatic birds, with well-developed swimming legs in the rear.

Fam. Gaviidae Allen, 1897

Fish-eating birds tied to water, they paddle with their legs after diving underwater. They only live on seashores of northern parts of the Northern Hemisphere, only visiting non-freezing freshwater bodies inland in winter. In the Carpathian basin, we knew a questionable *Gavia* sp. remain from the late Oligocene of Máriahalom, Hungary (Kessler & Rabi manuscript), as well as an extinct species from the middle Miocene: *Gavia schulzii* Mlikovský, 1998 from Austria (Mlikovský 1998). Recent species from the Carpathian Basin and Europe are known since the Quaternary:

– *Gavia stellata* Pontoppidan, 1753

Known from the Carpathian Basin: **Q4/II:** Kazánszoros-Töröklik (Cuina Turcului Cave-Cazanele), Romania (Kessler 1974a).

– *Gavia arctica* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/II:** Kőtelek-Huszársarok, Hungary (Jánossy 1979b).

Ord. Podicipediformes (Fürbringer, 1888)

Grebes are similar in appearance, swimming and lifestyle to loons.

Fam. Podicipedidae Bonaparte, 1831

They are present on every continent except Antarctica, mostly near freshwater, but certain species also live on the seashore. Their fossil species are known – except the debated *Eurolimnornis corneti* Kessler and Jurcsák, 1986 (Lower Cretaceous, Transylvania – Cornet, Romania) (Kessler & Jurcsák 1986) – from the late Oligocene to the Pliocene.

Extinct genera and species of the family are represented by *Podiceps csarnotanus* Kessler, 2009 from the middle Pliocene of Csarnóta 2, Hungary (Kessler, E. 2009a).

Recent *Podiceps* species are known since the Quaternary.

– *Podiceps nigricollis* Brehm, 1831

Known from the Carpathian Basin: **Q2:** Nagyharsány-hegy 1-4, Hungary (Jánossy 1979a, 1979b).

– *Podiceps griseigena* (Boddaert, 1783)

Known from the Carpathian Basin: **Q4/II:** Ludas-Budzsák, Hungary; Remetelórév-Bólyi-kő Cave (Piatra Boiului-Lorău); Kazánszoros-Töröklik (Cuina Turcului Cave-Cazanele); Vargyasi-szoros Caves (Vârghiș Defile) (all in Romania) (Bökönyi 1974, Gál 2004, Kessler 1974, 1982, 1985).

– *Podiceps auritus* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/I**: Endröd 119; Pilisszántó (all in Hungary) (Jánossy 1979a, 1979c, 1985, Gál 2004, 2007b).

– *Podiceps ruficollis* (Pallas, 1764)

Known from the Carpathian Basin: **Q4/II**: Maroslele-Pana, Hungary (Jánossy 1979c).

– *Podiceps cristatus* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/II**: Ecsegfalva 23, Endröd 3/6, Gyula-Castle, Maroslele-Pana, Ludas-Budzsák, Nagykörú-Tsz, Tiszalúc-Sarkad, Tiszavasvári-Deákhalmi-dűlő (all in Hungary) (Bökönyi 1974, Jánossy 1979c, 1985, Gál 2004, 2007b, Pike-Tay *et al.* 2004).

Ord. Procellariiformes Fürbringer, 1888

Seabirds typically spending their whole – usually long – lives above the open sea and are only on ground when nesting or raising the nestlings.

Fam. Diomedoididae (Fischer, 1985)

Apart from the four recent families of seabirds, we also know of an extinct family, described also from the Upper Oligocene of Hungary, based on a femur wing imprint that surfaced from the late clay mines of Szépvölgy, Buda, from deep sea sediments and named *Diomedeoides harmathi* Kessler, 2009 (Kessler, E. 2009).

Ord. Pelicaniformes Sharpe, 1891

Pelecaniformes are typically aquatic birds, they even gather their food from the water. Their incessorous, bare nestlings, however, show that this attachment to water may be a secondary characteristic in their case.

Fam. Elopterygidae Andrews, 1913

Remains with debatable affiliation from Upper Cretaceous of the Hátszegi Basin (Transylvania, Romania) was discovered by Ferenc Nopcsa, who then sold it to the British Museum, where C. A. Andrews classified and described it as *Elopteryx nopcsai* Andrews, 1913 (Andrews 1913). Two, once again British, paleornithologists in the seventies of the last century thought to have discovered two large owls in them based on the bones (*Heptasteornis andrewsi* and *Bradycneme draculae* Harrison *et* Walker, 1975) (Harrison & Walker 1975). The remains of a distal humerus discovered in 2005 in the presence of the author also in Szentpéterfalva (Sânpetru, Romania, Hațeg Basin) decided that it actually belongs to the ancient Pelicans described by Andrews, which thus should be a valid species, despite it being viewed as Troodontidae Alvarezsauridae, or theropod dinosaur (Kessler *et al.* 2005).

Fam. Pelicanidae Vigors, 1825

The largest species of the order belong to the family of Pelicans. Except the polar regions, they can be found on every continent, on larger bodies of freshwater, as well as the sea. They eat fish. They nest in reed beds and on the coastal sand of flat islands, forming large groups. Recent species from the Carpathian Basin are known since the Quaternary. Extinct species are not known hence.

– *Pelecanus onocrotalus* Linnaeus, 1768

Known from the Carpathian Basin: **Q4/II**: Ács-Vaspuszta, Bajcsa-Castle, Békés-Város-erdő, Maroslele-Pana, Zalaszentistván (all in Hungary); Peterd-Tordai-hasadék (Cheile Turzii-Defile, Petrești), Romania; Padina, Serbia (Jánossy 1979c, Classon 1980, Bartosiewicz 1991, Kessler & Gál 1998, Gál 2002, 2004).

– *Pelecanus* sp.

Known from the Carpathian Basin: **Q4/II**: Szegvár-Tűzköves, Hungary; Kazán-szoros-Töröklik (Cuina Turcului Cave-Cazanele), Parác (Parța) (all in Romania) (Kessler 1974, 2009a, Jánossy 1985, Kessler & Gál 1997, Gál 2004, 2007b).

Fam. Phalacrocoracidae (Bonaparte, 1854)

Cormorants can be found on most continents except Antarctica, Middle and Northern Asia, on larger bodies of freshwater, as well as seashores. Cormorants have dark – but not waterproof – feathers, and characteristic beaks. They mostly eat fish, and even though they paddle with their feet, they are also exceptional divers, diving into the water from even great heights. They live in large groups and nest on branches of trees, cliffs or the coastal sand. Their earliest extinct finds are also from the late Cretaceous and Eocene, but their classification is uncertain and debatable. Recent species from the Carpathian Basin are known since the Quaternary. Extinct species are not known hence.

– *Phalacrocorax carbo* Shaw et Nodder, 1801

Known from the Carpathian Basin: **Q4/II**: Endrőd 3/6, Röszke-Lúdvár, Tiszaluc-Dankadomb (all in Hungary); Parác (Parța), Püspökfürdő Lake (Băile Episcopopești) (all in Romania) (Kessler 1974, Jánossy 1979c, 1985, Kessler & Gál 1997, Gál 2004, 2007b).

Fam. Sulidae (Reichenbach, 1849)

Boobies and gannets are large to middle-sized fish-eating seabirds, catching their prey by diving from heights. They form large groups on the cliffs and coastal sand of sea shores, and their guano may accumulate into thick layers. Their earliest finds are known from the middle Eocene (*Eostega lebedinskyi* Lambrecht, 1927 from Transylvania, Romania) and *Microsula pygmaea* (Milne-Edwards, 1874) from middle Miocene of Austria (Göhlich 2003). The fossil species from Transylvania was described by Lambrecht (Lambrecht 1929) based on a jawbone, and according to the revision, this was indeed correct (Mlikovský 2007).

Fam. Anhingidae Reichenbach, 1849

Snakebirds today are tropical, freshwater birds, harpooning fish with their long, sharp beaks. They nest on trees along the coast. Fossil remains are rather rare in Europe, they are only known from the Carpathian Basin (named *Anhinga pannonica* Lambrecht, 1916 and *Anhinga* sp.) from the late Miocene of Tataros in Transylvania (Tătăruș), Romania (Lambrecht 1916b), Götzendorf, Austria (Mlikovský 1992), and from the middle Miocene of Mátraszőlös, Hungary (Gál et al. 1998-1999).

Fam. Phaethontidae (Bonaparte, 1853)

Tropicbirds, as their name suggests, live at tropical seas, with a medium-sized and typical tail feathers. Their diet consists of fish. They prepare their nests inside cavities of cliffs on rocky shores. Two extinct species are known in the Carpathian Basin: *Heliadornis paratethydicus* Mlikovský, 1997 from late Miocene of Austria (Mlikovský 1997), while *H. minor* Kessler, 2009 is known from the late Pliocene of Ajnácskő (Hajnáčka), Slovakia (Kessler, J. 2009a).

Ord. Ardeiformes (Wagler, 1930)

Waders (herons, storks, ibises, flamingos) form a group with a rather distinctive form and lifestyle. They have long beaks, necks and legs. They live in wet environments all across

the globe except the polar regions, feeding on invertebrates living in water or on dry land, fish, and other smaller vertebrates. They live in groups and prepare their nests on trees and reed beds, except for flamingos, who build their tower-like nests out of mud on lake shores with shallow waters.

Subord. Phoenicopteri Fürbringer, 1888

Fam. Palaelodidae (Stejneger, 1885)

Representatives of the order still alive today are the flamingos, well-known from the typical shape of beaks and pink feathers. They feed on tiny krill or single-celled algae in highly alkaline still waters. They inhabit tropical and subtropical areas. The extinct species *Palaelodus goliath* Milne-Edwards, 1863 was reported from the middle Miocene of Hungary (Mátraszőlös) (Gál *et al.* 2000).

Subord. Plataleae Newton, 1884

Fam. Threskiornithidae Richmond, 1917

This family contains ibises and spoonbills. Recent species from the Carpathian Basin are known since the Quaternary. Extinct species are not known hence.

– *Plegadis falcinellus* (Linnaeus, 1766)

Known from the Carpathian Basin: **Q4/I:** Ohábaponor Cave (Bordu Mare-Ohaba Ponor), Romania (Kessler 1985).

– *Platalea leucorodia* Linnaeus, 1758

Known from the Carpathian Basin: **Q4/II:** Ecsegfalva 23, Endrőd 39, 119, Szolnok-Szanda, Tiszalúc-Sarkad, Tiszavasvári-Keresztfal (all in Hungary); Parác (Parța), Romania (Jánossy 1985, Kessler & Gál 1997, Gál 2004, 2007b, Pike-Tay *et al.* 2004).

Subord. Ardeae (Wagler, 1831)

Fam. Ardeidae (Vigors, 1825)

This family includes herons, egrets, night ravens, the earliest fossil representatives of which are known from the Miocene of the Carpathian Basin (*Proardeola walkeri* Harrison, 1979) from the middle Miocene of Mátraszőlös, Hungary and Kőalja (Subpiatra), Romania (Gál *et al.* 2000, Kessler & Venczel 2009), *Egretta polgardiensis* Kessler, 2009 from the late Miocene of Polgárdi, Hungary (Kessler 2009a, Ardeidae gen. *et sp.* indet. from the middle Miocene of Felsőtárkány-Felnémet 2/3, Mátraszőlös 2 (Kessler & Hír 2012a). Recent species from the Carpathian Basin are known since the Quaternary.

– *Egretta alba* Linnaeus, 1758

Known from the Carpathian Basin: **Q4/II:** Ecsegfalva 23, Endrőd 3/6, 119, Esztergom-Alsósziget, Maroslele-Pana, Nagykörű-Tsz, Ószentiván-Tisza-sziget, Tiszaszőlös-Domaháza-puszta (all in Hungary) (Bökönyi 1964, Jánossy 1979c, 1985, Gál 2004, 2007b Pike-Tay *et al.* 2004).

– *Egretta garzetta* (Linnaeus, 1766)

Known from the Carpathian Basin: **Q4/II:** Endrőd 3/6; 119, Hungary (Jánossy 1985, Gál 2004, 2007b).

– *Ardea cinerea* Linnaeus, 1758

Known from the Carpathian Basin: **Q4/I:** Vindija, Croatia; Puszkaporos, Hungary (Lambrecht 1912, 1916, 1933, M. Malez 1961, V. Malez 1973, 1988, 1991, Jánossy 1979c, 1986) **Q4/II:** Balatonkeresztúr-Réti-dűlő, Balatonszemes-Bagódomb, Ecsegfalva 23,

Endröd 3/6, 39, 119, Kőtelek-Huszársarok, Maroslele-Pana, Nagykörű-Tsz, Rösztke-Lúdvár, Tiszaszőlős-Domaháza-pusztá (all in Hungary) (Bökönyi 1964, Jánossy 1979c, 1985, Gál 2004, 2007a, 2007b, Pike-Tay *et al.* 2004).

– *Ardea purpurea* Linnaeus, 1766

Known from the Carpathian Basin: **Q4/II**: Bajcsa Castle, Debrecen-Nyulas, Ecsegfalva 23, Endröd 39, Mezőfény, Tiszapolgár-Csőszhalom, Polgár-Csőszhalom, Rösztke-Lúdvár (all in Hungary) (Jánossy 1979c, 1985, Gál 2002b, 2004, 2007b, Pike-Tay *et al.* 2004).

– *Ardeola* sp.

Known from the Carpathian Basin: **Q4/I**: Vindija, Croatia (M. Malez 1961, V. Malez 1973, 1988, 1991); Puskaporos, Hungary (Kessler, J. 2009b).

– *Ixobrychus minutus* (Linnaeus, 1866)

Known from the Carpathian Basin: **Q1**: Betfia 9, Romania (Gál 2002a).

– *Botaurus stellaris* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/II**: Ecsegfalva 23, Endröd 3/6 (all in Hungary) (Gál 2004, 2007b, Pike-Tay *et al.* 2004).

– *Botaurus* sp.

Known from the Carpathian Basin: **Q1**: Beremend 17, Hungary (Kessler 2009a).

– *Nycticorax nycticorax* Linnaeus, 1758

Known from the Carpathian Basin: **Q4/II**: Ecsegfalva 23, Tiszaszőlős-Domaháza-pusztá (all in Hungary) (Gál 2007b, Pike-Tay *et al.* 2004).

– *Nycticorax* sp.

Known from the Carpathian Basin: **Q1**: Beremend 17, Hungary (Kessler, J. 2009a).

Fam. Ciconiidae (Gray, 1840)

It contains actual storks (*Ciconia* genus) and tropical storks (*Mycteria* and *Anastomus* genera). Their earliest finds in the Carpathian Basin are *Ciconia stehlini* Jánossy, 1992, from the late Pliocene of Hungarian site Beremend 15 (Jánossy 1996), while *Pelargosteon tothi* Kretzoi, 1941, was found in the early Pleistocene of Betfia, Transylvania (Romania) (Kretzoi 1962, Gál 2002). Recent species from the Carpathian Basin are known since the Quaternary.

– *Ciconia ciconia* Linnaeus, 1758

Known from the Carpathian Basin: **Q4/II**: E

ndröd 39, Lambrecht Cave, Rösztke-Lúdvár, Tác-Fövénypusztá, Tác-Gorsium, Túrkeve-Móricz (all in Hungary); Püspökfürdő-Lake (Băile Episcopesti), Romania (Kessler 1974b, Jánossy 1979c, 1985, Bökönyi 1984, Gál 2004, 2007c).

– *Ciconia nigra* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/II**: Endröd 39, 119, Szajol-Felsőföld, Tiszalúc-Danka-domb, Kisköre-Szingegát, Rösztke-Lúdvár (all in Hungary) (Jánossy 1979c, 1985, Gál 2004, 2007b, 2007c).

– *Ciconia* sp.

Known from the Carpathian Basin: **Q4/II**: Endröd 3/6, Nagykörű-Tsz, Tiszaszőlős-Domaháza-pusztá (all in Hungary) (Gál 2004, 2007b).

– + *Ciconia stehlini* Jánossy, 1992

Known from the Carpathian Basin: **MN 16**: Beremend 15, Hungary (Jánossy 1992) **Q1**: Betfia 9, Romania (Gál 2002) **Q2**: Beremend 16, 17, Hungary (Jánossy 1996).

– + *Pelargosteon tothi* Kretzoi, 1962

Known from the Carpathian Basin: **Q1:** Kőröshegy, Hungary (Kretzoi & Krolopp 1975) **Q2:** of Betfia 7 “Aven”, Romania (Kretzoi 1962, Kessler 1975, Gál 2002) **Q3/I:** of Budapest-Várhegy, Hungary (Jánossy 1980, 1986).

Ord. Anseriformes Wagler, 1831

Out of the four families of geese, only the Anseridae form a significant group both in terms of the extinct and the recent fauna.

Fam. Anatidae Leach, 1820

Geese is a species-rich family (with more than 50 recent genera and more than 160 recent species), representatives of which are present on every dry land except Antarctica. Several subfamilies are distinguished within the family.

Subfam. Cygninae (Vigors, 1825)

Swans are the largest species of the order, living in freshwater areas and seashores. They are herbivores and nest in large groups among aquatic plants. Species living in frigid and temperate zones are migrants. Their extinct species are known from the late Oligocene (*Cygnopterus neogradensis* Kessler *et* Hír, 2009 and *Cygnanser csakvarensis* Lambrecht, 1933 and from the middle Miocene of Hungary (Mátraszőlös and Csákvár) (Kessler & Hír 2009, respectively Lambrecht 1933). Recent species from the Carpathian Basin are known since the Quaternary from the Carpathian Basin.

– *Cygnus olor* (Gmelin, 1789)

Known from the Carpathian Basin: **Q4/I:** Nándori Cave (Curata-Nandru, Romania) (Téglás 1896) **Q4/II:** Endröd 3/6, 119, Ludas-Budzsák, Mezökomárom (all in Hungary); Kazán-szoros-Töröklik (Cuina Turcului Cave-Cazanele), Parác (Parța) (all in Romania); Starcevo, Serbia (Bökönyi 1974, Kessler 1974, 2009a, Jánossy 1979b, Classon 1980, Kessler & Gál 1997, Gál 2004, 2007b).

– *Cygnus cygnus* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/II:** Szilágyzovány (Zăuan), Romania; Starcevo, Serbia (Classon 1980, Gál 2004, Bindea 2008).

– *Cygnus* sp.

Known from the Carpathian Basin: **Q4/II:** Dunaújváros-Intrecisa, Hungary; Kazánszoros-Töröklik (Cuina Turcului Cave-Cazanele), Romania (Jánossy 1985, Kessler 1974a).

Subfam. Anserinae Vigors, 1825

Geese are moderately large herbivores living, nesting, and migrating in large groups. They live near freshwater and seashores, and hatch their eggs in nests on the ground. *Bran-ta* species of black geese live on wet, grassy areas of the seashore, while *Anser* species of grey geese live near freshwaters. *Tadorna* species of shelducks also live on seashores, but rarely near freshwater, and nest in cavities they create. The earliest sign of shelducks comes from the middle Miocene of Hungary (*Tadorna minor* Kessler *et* Hír, 2011, from Mátraszőlös) (Kessler & Hír 2012a). Extinct geese species from the Quaternary of Carpathian Basin are:

– + *Anser subanser* Jánossy, 1982

Known from the Carpathian Basin: **Q3:** Somssich-hegy 2, Várhegy, Hungary; Brassó-Fortyogó Hill, (Gensperger Cave-Braşov), Romania (Jánossy 1983).

Branta species are only known with recent forms since the Pleistocene from the Carpathian Basin. Recent species from the Carpathian Basin are known since the Quaternary.

– *Anser anser* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/I**: Teufelslucken, Austria; Velika Pecina, Croatia; Lambrecht Cave, Mérk (all in Hungary) (Lambrecht 1912, Soergel 1966, Jánossy 1979a, 1979b, V. Malez 1975, 1984, 1988) **Q4/II**: Teufelslucken, Austria; Balatonkeresztúr-Réti-dűlő, Balatonszemes-Bagódomb, Debrecen-Nyulas, Ecsegfalva 23, Endrőd 3/6, 39, 119, Jászó, Kőtelek, Kőtelek-Huszársarok, Ludas-Budzsák, Mezőfény, Mezőzombor-Községi Cemetery, Nagykörű-Tsz, Szajol-Felsőföld, Szolnok-Szanda, Szerencs-Taktaföldvár, Tatabánya-alsó-Törekvés Cave, Tiszaszőlős-Domaháza-szőlős (all in Hungary); Bólyikő Cave (Piatra Boiului Cave-Loräu), Gyulafehérvár (Alba Iulia), Szegyestel-völgy Caves (Sighiștel Defile), Parác (Parța) (all in Romania); Starcevo, Serbia (Soergel 1966, Bökönyi 1974, Jánossy 1979b, 1985, Classon 1980, Kessler 1982, 1985, 2009a, Kessler & Gál 1997, Gál 2004, 2005, 2007a, Pike-Tay *et al.* 2004).

– *Anser fabalis* Latham, 1790

Known from the Carpathian Basin: **Q4/I**: Bivak Cave, Hungary; Detrekösztmiklós-Pálffy Cave (Dzereva Skála), Slovakia (Lambrecht 1913, 1933, Mottl 1938, 1941, Jánossy 1979a, 1979b) **Q4/II**: Teufelslucken, Austria; Endrőd 39, Maroslele-Pana, Szolnok-Szanda (all in Hungary); Starcevo, Serbia (Bökönyi 1964, Soergel 1966, Jánossy 1979b, 1985, Classon 1980, Gál 2004, 2007b).

– *Anser albifrons* (Scopoli, 1769)

Known from the Carpathian Basin: **Q4/I**: Merkenstein, Austria; Remetehegy Niche, Hungary, (Lambrecht 1933, Wettstein & Mühlhofer 1938) **Q4/II**: Teufelslucken, Austria; Endrőd 119, Maroslele-Pana, Mezőfény, Ószentiván-Tiszasziget, Pilismarót-Malompaták, Szajol-Felsőföld (all in Hungary); Vársonkolyos Caves (Șuncuiuș Defile), Romania (Soergel 1966, Bökönyi 1964, Jánossy 1979b, 1985, Kessler 1985, Gál 2004, 2007b, 2007c).

– *Anser erythropus* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/II**: Teufelslucken, Austria; Dunaújváros-Intrecisa, Hungary (Soergel 1966, Jánossy 1985).

– *Anser* sp.

Known from the Carpathian Basin: **Q4/I**: Pilisszántó, Hungary; Detrekösztmiklós-Pálffy Cave (Dzereva Skála), Slovakia (Lambrecht 1913, 1933, Mottl 1938, 1941) **Q4/II**: Ludas-Budzsák, Nagykörű-Tsz, Neszmély-Tekeres Creek, Szegvár-Tűzköves, Esterházy Cave (all in Hungary); Érmihályfalva (Valea lui Mihai), Kisbács-Bácsatorok (Baciu), Körösrév Caves (Vadu Crisului), Vár-Sonkolyos Caves (Șuncuiuș Defile) (all in Romania) (Bökönyi 1974, Jánossy 1985, Kessler 1985, 1995, Jurcsák & Kessler 1986, Gál 2004, 2007b).

– *Branta ruficollis* (Pallas, 1769)

Known from the Carpathian Basin: **Q3**: Hundsheim, Austria (Jánossy 1974) **Q4/I**: Balla Cave, Hungary; Detrekösztmiklós-Pálffy Cave (Dzereva Skála), Slovakia (Lambrecht 1913, 1933, Mottl 1938, 1941).

– *Branta leucopsis* (Bechstein, 1803)

Known from the Carpathian Basin: **Q4/II**: Nagykörű-Tsz, Hungary (Gál 2007b).

– *Branta* sp.

Known from the Carpathian Basin: **Q4/II**: Parác (Parța), Romania (Kessler & Gál 1997, Gál 2004).

– *Tadorna tadorna* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q2**: Betfia 5, 7, Romania (Kessler 1975, Gál 2002) **Q4/II**: Parác (Parța), Romania; Padina, Serbia (Classon 1980, Kessler & Gál 1997, Gál 2004).

– *Tadorna ferruginea* (Pallas, 1764)

Known from the Carpathian Basin: **Q4/I**: Teufelslucken, Austria; Körösmart (Râpa), Romania (Soergel 1966, Hamar & Csák 1969, Kessler 1974).

– *Tadorna* sp.

Known from the Carpathian Basin: **Q2**: Nagyarsány-hegy 1-4, Hungary (Jánossy 1979a, 1979b).

Subfam. Anatinae (Vigors, 1825)

Ducks form the group with the largest number of species, both in terms of recent and fossilized ones. They are the smallest in size of the order, and show wide diversity in their colors and shapes. They are much more attached to water than geese, they feed mostly from waters on invertebrates, but also plants. They usually nest in reed beds, but several species nest in tree burrows. Nestlings are – just like in case of the other families – nidifugous.

Based on their swimming abilities we distinguish between ducks, diving ducks and seaducks, but they undergo numerous methods of classification (Eider Ducks, Stiff-tailed Ducks etc.). Fossil species of their different recent genera are known since the late Oligocene as *Mionetta robusta* (Milne-Edwards 1868) from Máriahalom, Hungary (Kessler & Rabi manuscript), and the late Miocene, like *Dendronessa* sp. from Götzendorf, Austria (Mlíkovský 1991), *Mionetta consobrina* (Milne-Edwards 1867) from the middle and late Miocene of Hungary (Mátraszőlös) (Kessler & Hír 2012a), *Anas velox* (Milne-Edwards 1868) from Hungary (Mátraszőlös and Rudabánya) (Kessler & Hír 2012a), *A. sansanensis* (Milne-Edwards 1868) from Austria (Atzelsdorf) (Göhlich 2009), *A. denesi* Kessler, 2013 from Hungary (Polgárdi) (Kessler, J. 2013), *A. albae* Jánossy, 1979 from the late Miocene and Pliocene of Hungary (Polgárdi and Csarnóta 2, Villány 3) (Jánossy 1979b, 1991) and from the middle Miocene of Romania (Kőalja-Subpiatra) (Kessler & Venczel 2009), *Clangula matraensis* and *Mergus minor* Kessler, 2009 from the middle Miocene of Mátraszőlös, Hungary (Kessler, J. 2009a), *Bucephala cereti* Boeuf et Mourer-Chauviré, 1992 from Mátraszőlös, Hungary (Gál *et al.* 1998-1999), *Mergus minor* Kessler, 2009 from Mátraszőlös, Hungary (Kessler, J. 2009a) and *Mergus connectens* Jánossy, 1972 from the early Pleistocene of Betfia, Romania (Jánossy 1979b).

Recent species from the Carpathian Basin are known since the Quaternary.

– *Anas platyrhynchos* Linnaeus, 1758

Known from the Carpathian Basin: **Q3**: Vértesszőlös 2, Hungary (Jánossy, 1969) **Q4/I**: Merkenstein, Teufelslucken (all in Austria); Vindija, Croatia; Bajót-Jankovich Cave, Budapest-Remetehegy Niche, Cserépfalu-Subalyuk Cave, Csákvár-Eszterházy Cave, Herman Ottó Cave, Pilisszántó Niche, Puskaaporos Niche, Répáshuta-Balla Cave, Szilvásváradszállókői Cave, Tokod-Nagyberek, Varbó-Lambrecht Kálmán Cave (all in Hungary); Körösmart (Râpa), Nándori Cave (Curata-Nandru), Oháaponor (Bordu Mare Cave-Ohaba Ponor), Körösrév-Kecske Cave, Pince Cave (Caprei and Pivnițe Caves-Vadu Crișului),

(all in Romania); Detrekőszentmiklós-Pálffy Cave (Dzereva Skála), Slovakia (Lambrecht 1912, 1913, 1915, 1916, 1933, Mottl 1938, 1941, Wettstein & Mühlhofer 1938, M. Malez 1961, Jánossy 1965, 1979a, 1979b, 1986, Soergel 1966, V. Malez 1973, 1988, 1991, Kessler 1974a, 1985, Fischer & Stephan 1977, Jurcsák & Kessler 1988, Gál 2002a, 2003) **Q4/II**: Grosse Offenbergerhöhle, Teufelslucken (all in Austria); Bodajk-Rigólyuk, Csákvár-Esterházy Cave, Dunaújváros-Intrecisa, Ecsegfalva 23, Endrőd 3/6, 39, 119, Legény Cave, Maroslele-Pana, Paks-Dunakömlőd, Röszeke-Ludvár, Szajol-Felsőföld, Szolnok-Szanda, Tác-Fövénypusztá, Tác-Gorsium, Tiszaszőlős-Domaháza-pusztá (all in Hungary); Kiszersida (Đeršida Mică), Kőrösbánlak Cave (Bălnaca), Kőrösrévi Caves (Vadu Crișului Defile), Ompolmező (Poiana Ampoiului), Parác (Parța), Peterd-Tordai-hasadék-Magyar Cave (Cheile Turzii Defile-Ungureasca Cave-Petrești), Püspökfürdő Lake (Băile Episcopesci), Remetelórév-Bólyikó Cave (Piatra Boiului-Lorău) (all in Romania) (Lambrecht 1914, Bökönyi 1964, 1984, Soergel 1966, Kessler 1974b, 1982, 1985, Jánossy 1979a, 1979b, 1985, Kordos 1984, Kőrösi 1991, Bocheński & Tomek 1994, Kessler & Gál 1997, 1998, Bindea 2008, Gál 2004, 2007b, 2007c, Pike-Tay *et al.* 2004).

– *Anas penelope* Linnaeus, 1758

Known from the Carpathian Basin: **Q2**: Nagyarsány-hegy 1-4, Hungary (Lambrecht 1916, 1933, Jánossy 1979a) **Q4/I**: of Budapest-Remetehegy Niche, Puszkaporos Niche, Répáshuta-Balla Cave (all in Hungary); Kőrösmart (Râpa), Nándori Cave (Curata-Nandru), Ohábaponor (Bordu Mare Cave-Ohaba Ponor) (all in Romania); Detrekőszentmiklós-Pálffy Cave (Dzereva Skála-Pálffy Cave), Slovakia (Lambrecht 1912, 1913, 1916, 1933, Mottl 1938, 1941, Kessler 1974, 1985, Fischer & Stephan 1977, Jánossy 1979a, 1986, Musil 1980, Jurcsák & Kessler 1988, Gál 2002a, 2003) **Q4/II**: Teufelslucken, Austria; Dunaújváros-Intrecisa, Endrőd 39, Tiszaszőlős-Domaháza-pusztá (all in Hungary); Püspökfürdő Lake (Băile Episcopesci), Romania (Jánossy 1965, 1985, Soergel 1966, Kessler 1974, 1985, Gál 2004, 2007b).

– *Anas strepera* Linnaeus, 1758

Known from the Carpathian Basin: **Q1**: Beremend 17, Hungary; Betfia 2, Kőrösmart (Râpa), (all in Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kretzoi 1941, Kessler 1974a, 1975, Jánossy 1977, 1979b, 1992, 1996, Gál 2002a) **Q4/I**: Pilisszántói Niche, Hungary; Detrekőszentmiklós-Pálffy Cave (Dzereva Skála), Slovakia (Lambrecht 1913, 1915, 1933, Mottl 1938, 1941, Jánossy 1979a, 1979b 1986) **Q4/II**: Ecsegfalva 23, Hungary (Pike-Tay *et al.* 2004, Gál 2007b).

– *Anas crecca* Linnaeus, 1758

Known from the Carpathian Basin: **Q3/II**: Vindija, Croatia (M. Malez 1961, V. Malez 1973, 1988, 1991) **Q4/I**: Velika Pecina, Vindija (all in Croatia); Bajót-Hóman Cave, Budapest-Remetehegy Niche, Puszkaporos Niche, Tatabánya-Szelim Cave (all in Hungary); Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas), Novi III (Novi Caves) (all in Slovakia) (Nehring 1880, Lambrecht 1912, 1913, 1916, 1933, Mottl 1938, 1941, M. Malez 1961, V. Malez 1973, 1975, 1984, 1988, 1991, Jánossy 1979a, 1979b, 1986) **Q4/II**: Teufelslucken, Austria; Bodajk-Rigólyuk, Csákvár-Esterházy Cave, Ecsegfalva 23, Endrőd 3/6, Tác-Fövénypusztá, Tác-Gorsium (all in Hungary); Diószeg (Diosig), Gura Chindiei (all in Romania) (Soergel 1966, Kessler 1977, 1985, Jánossy 1979b, 1985, Bökönyi 1984, Kordos 1984, Gál 2004, 2007b, Pike-Tay *et al.* 2004).

– *Anas acuta* Linnaeus, 1758

Known from the Carpathian Basin: **Q1:** Beremend 17, Hungary; Betfia 2, Romania (Kormos 1913, Čapek 1917, Lambrecht 1933, Kretzoi 1941, Kessler 1975, Jánossy 1977, 1979b, 1992, 1996, Gál 2002) **Q2:** Nagyharsány-hegy 1-4, Hungary (Lambrecht 1916, 1933, Jánossy 1979a, 1979b) **Q3:** Vértesszőlős, Hungary (Jánossy 1979a, 1979b, 1990) **Q4/I:** Vindija, Croatia; Detreköszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulás), Slovakia (Lambrecht 1913, 1933, Mottl 1938, 1941, M. Malez 1961, V. Malez 1973, 1988, 1991) **Q4/II:** Teufelslucken, Austria; Ecsegfalva 23, Hungary; Peterd-Tordai-hasadék-Magyar Cave (Cheile Turzii Defile-Petrestii), Püspökfürdő Lake (Băile Episcopopești) (all in Romania) (Soergel 1966, Kessler 1974, 1985, Kessler & Gál 1998, Gál 2004, 2007b, Pike-Tay *et al.* 2004).

– *Anas querquedula* Linnaeus, 1758

Known from the Carpathian Basin: **Q1-2:** Nagyharsány-hegy 1-4, Hungary; Betfia 2, 9, Betfia “Aven” (all in Romania) (Kormos 1913, Lambrecht 1916, 1933, Čapek 1917, Kretzoi 1941, Kessler 1975, Jánossy 1977, 1979b, Gál 2002a) **Q4/I:** Vindija, Croatia; Cserépfalu-Subalyuk Cave, Pilisszántó Niche, Tokod-Nagyberek (all in Hungary); Körösmart (Râpa), Romania (Lambrecht 1915, 1933, M. Malez 1961, V. Malez 1973, 1988, 1991, Kessler 1974, Jánossy 1979a, 1979b, Gál 2002) **Q4/II:** Teufelslucken, Austria; Ecsegfalva 23, Endröd 3/6, Legény Cave (all in Hungary); Gálospetri (Galoșpetru), Körösbánlak Cave (Bălnaca), Püspökfürdő Lake (Băile Episcopopești) (all in Romania) (Lambrecht 1914, Soergel 1966, Kessler 1974, 1982, 1985, Jánossy 1985, Gál 2002a, 2004, 2007b, Pike-Tay *et al.* 2004).

– *Anas chrypeata* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q1-2:** Beremend 16, 17, Nagyharsány-hegy 1-4 (all in Hungary); Betfia 2, 9, Betfia “Aven” (all in Romania) (Lambrecht 1916, 1933, Kessler 1975, Jánossy 1979a, 1979b, 1992, 1996, Gál 2002a) **Q3:** Süttő, Hungary (Jánossy 1979a) **Q4/I:** Körösmart (Râpa), Nándori Cave (Curata-Nandru) (all in Romania) (Jánossy 1965, 1979a, 1979b, Kessler 1974a, Fischer & Stephan 1977, Jurcsák & Kessler 1988, 1985, Gál 2002a, 2003) **Q4/II:** Gálospetri (Galoșpetreu), Körösrévi Caves (Vadu Crișului Defile), Püspökfürdő Lake (Băile Episcopopești), Vársonkolyosi Caves (Șuncuius Defile) (all in Romania); Starcevo, Serbia; Endröd 3/6, 119, Hungary (Jurcsák 1969, Kessler 1974b, 1980-1981, 1982, 1985, Classon 1980, Jánossy 1985, Gál 2002a, 2004, 2007b).

– *Anas* sp.

Known from the Carpathian Basin: **Q1:** Beremend 17, Hungary; Betfia 2, Romania (Kormos 1913, Čapek 1917, Lambrecht 1933, Kretzoi 1941, Kessler 1975, 2009a, Jánossy 1977, 1979b, Gál 2002a) **Q3/I:** Vindija, Croatia; Budapest-Vár-Hill, Hungary (M. Malez 1961, V. Malez 1973, 1988, 1991, Jánossy 1979a, 1979b) **Q4/I:** Krapina, Croatia; Tata, Hungary; Nándori Cave (Curata-Nandru), Romania; Lándzsásótfalu (Hörka-Ondrej), Liszkófalva-Baráthegy Cave (Lisková), Novi III, (Novi Caves) (all in Slovakia) (Lóczy 1877, Nehring 1880, Téglás 1880, Róth 1881, Lambrecht 1912, 1915, 1933, V. Malez 1973, 1984, V. Malez-Bačić 1975, Jánossy 1979b, 1986, M. Malez & V. Malez 1988, Mlíkovský 2000c) **Q4/II:** Berettyószentmárton, Endröd 3/6, Maroslele-Pana, Mezőfény, Pomáz-Zravlyák, Szajol-Felsőföld, Szolnok-Szanda, Tiszalúc-Sarkad (all in Hungary); Radnót (Iernuț), Romania (Bökonyi 1964, Jánossy 1977, 1979b, 1985, Gál 2004, 2007b, 2007c, Bindea 2008).

– *Aythya nyroca* (Güldenstadt, 1769)

Known from the Carpathian Basin: **Q1**: Betfia 2, 9, Romania (Kormos 1913, Čapek 1917, Lambrecht 1933, Kretzoi 1941, Kessler 1975, Jánossy 1977, 1979b, Gál 2002a) **Q3/I**: Tarkó 3, Hungary (Jánossy 1962, 1976, 1979a, 1979b) **Q4/I**: Vindija, Croatia; Bajót-Jankovich Cave, Budapest-Remetehegy Niche, Csákvár-Eszterházy Cave, Pilisszántói I. Niche, Puszkaporos Niche (all in Hungary); Nándori Cave (Curata-Nandru), Romania (Lambrecht 1912, 1915, 1916, 1933, Mottl 1941, M. Malez 1961, Jánossy 1965, 1979a, 1979b, 1986, V. Malez 1973, 1988, 1991, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002a, 2003) **Q4/II**: Teufelslucken, Austria; Ecsegfalva 23, Endrőd 119, Legény Cave, Ludas-Budzsák, Mezőfény, Nagykörű-Tsz, Röske-Ludvár, Tizzaszőlős-Domaháza-pusztá (all in Hungary) (Lambrecht 1914, Soergel 1966, Bökönyi 1974, Jánossy 1985, Gál 2004, 2007b, Pike-Tay *et al.* 2004).

– *Aythya fuligula* Linnaeus, 1758

Known from the Carpathian Basin: **Q4/I**: Krapina, Vindija (all in Croatia); Detreköszentmiklós-Pálffy Cave (Dzeráv a Skála-Plavecky Mikulas), Slovakia (Lambrecht 1913, 1915, 1933, Mottl 1938, 1941, M. Malez 1973, 1984, 1988, 1991, Malez-Bačić 1975, M. Malez & V. Malez 1988) **Q4/II**: Ecsegfalva 23, Felsőtárkány-Petényi Cave, Ludas-Budzsák, Röske-Ludvár, Tác-Gorsium, Tápiószele-Tüzköves (all in Hungary); Gálospetri (Galošpetreu), Romania (Bökönyi 1974, 1984, Jánossy 1977, 1979a, 1979b, 1985, Kessler 1980-1981, Gál 2002a, 2004, 2007b, Pike-Tay *et al.* 2004).

– *Aythya ferina* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/I**: Teufelslucken, Austria; Vindija, Croatia; Hámor-Puszkaporos Niche, Hungary (Lambrecht 1912, 1916, 1933, Mottl 1941, M. Malez 1961, Soergel 1966, V. Malez 1973, 1988, 1991, Jánossy 1979a, 1979b, 1986) **Q4/II**: Ecsegfalva 23, Endrőd 3/6, 119, Maroslele-Pana, Nagykörű-Tsz, Tác-Gorsium, Tápiószele-Tüzköves (all in Hungary) (Bökönyi 1964, 1984, Jánossy 1977, 1979b, 1985, Gál 2004, 2007b, Pike-Tay *et al.* 2004).

– *Aythya marila* (Linnaeus, 1761)

Known from the Carpathian Basin: **Q4/II**: Tizzaszőlős-Domaháza-pusztá, Hungary (Gál 2007b).

– *Aythya* sp.

Known from the Carpathian Basin: **Q1**: Beremend 17, Hungary (Kessler 2009a) **Q2**: Nagyharsány-hegy, Somssich-hegy 2 (all in Hungary) (Jánossy 1981a, 1982b, 1983, 1986, Kessler 2009a).

– *Bucephala clangula* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/I**: Bajót-Hóman Cave, Hungary (Jánossy 1979a, 1979b) **Q4/II**: Gura Chindiei, Romania (Kessler 1985).

– *Melanitta nigra* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/I**: Detreköszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas), Slovakia (Lambrecht 1913, 1933).

– *Mergus albellus* Linnaeus, 1758

Known from the Carpathian Basin: **Q4/I**: Jankovits Cave, Puszkaporos (all in Hungary); Detreköszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas), Slovakia (Lambrecht 1913, 1933, Jánossy 1986).

– *Mergus serrator* Linnaeus, 1758

Known from the Carpathian Basin: **Q4/II**: Kazán-szoros-Töröklik (Cuina Turcului Cave-Cazanele), Vársonkolyos-Kismagyar Cave (Napișteleu Cave, Șuncuiuș) (all in Romania); Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas), Slovakia (Lambrecht 1913, 1933, Kessler 1974c, 1977a, 1983, 2009a).

– *Mergus merganser* Linnaeus, 1758

Known from the Carpathian Basin: **Q4/I**: Vindija, Croatia (M. Malez 1961, V. Malez 1973, 1988, 1991); Balla Cave, Hungary (Lambrecht 1912) **Q4/II**: Teufelslucken, Austria; Kazán-szoros-Töröklik (Cuina Turcului Cave-Cazanele), Ohábaponor (Bordu Mare Cave, Ohaba Ponor) (all in Romania) (Soergel 1966, Kessler 1981, 1985, 2009a).

– Anatidae indet.

Known from the Carpathian Basin: **Q1**: Betfia 9, Romania (Gál 2002); **Q2**: Somssich-hegy 2, Hungary (Jánossy 1981a, 1982b, 1983, 1986).

Subord. Ralli (Reichenbach, 1852)

This suborder is containing rails, finfoots and members of an extinct family.

Fam. Rallidae Vigors, 1825

Rails are small to medium-sized birds which prefer hiding, and live in wet environments with tall grass. There are also flightless and barely flying species, especially on islands of Oceania. Most well-known are coots, rails, corncrakes and crakes. From the Upper Oligocene of Kolozsvár (Cetățuie, Cluj, Romania), we know *Rallicrex kolozsvarensis* Lambrecht, 1933 (Lambrecht 1933), from the early, middle and late Miocene of Hungary (Litke, Felsőtárkány, Mátraszőlős, Polgárdi) *R. litkensis* Kessler *et* Hír, 2012 and *R. polgardiensis* Jánossy, 1991 (Jánossy 1991, Kessler 2009b, Kessler & Hír 2012b). Several species are known from the Miocene of Europe, including Hungary, such as *Paleoaramides beaumontii* (Milne-Edwards 1869) from early Pleistocene of Beremend 17, *Miorallus major* (Milne-Edwards 1869) from late Miocene of Rudabánya, *Porzana matraensis* Kessler, 2009 from middle Miocene of Mátraszőlős, *P. estramosi* Jánossy, 1979 and *P. kretzoi* Kessler, 2009 from middle and late Miocene of Mátraszőlős and Polgárdi (Jánossy 1979 a, 1979b, 1991, Gál *et al.* 1998-1999, Kessler, J. 2009b), Rallidae indet. from middle Miocene of Kőalja (Subpiatra, Romania) (Kessler & Venczel 2009).

Recent species from the Carpathian Basin are known since the Quaternary.

– *Porzana porzana* (Linnaeus, 1766)

Known from the Carpathian Basin: **Q1**: Beremend 16, 17, Hungary; Betfia 9, Romania (Jánossy 1992, 1996, Gál 2002) **Q4/I**: Budapest-Remetehegyi Niche, Hámor-Puskaporos Niche, Pilisszántói I. Niche, Szilvásvárad-Istállóskői Cave, Tatabánya-Szelim Cave (all in Hungary); Barcarozsnyó (Rîșnov), Romania; Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas), Slovakia (Lambrecht 1912, 1915, 1916, 1933, Jánossy 1952, 1955, 1979a, 1979b, Gál 1998, 2002) **Q4/II**: Bodajk-Rigólyuk, Ecsegfalva 23 (all in Hungary) (Kordos 1984, Pike-Tay *et al.* 2004, Gál 2007b).

– *Porzana parva* (Scopoli, 1769)

Known from the Carpathian Basin: **Q1**: Beremend 17, Hungary; Betfia 9, Romania (Jánossy 1992, 1996, Gál 2002).

– *Porzana pusilla* Pallas, 1776

Known from the Carpathian Basin: **Q1**: Betfia 9, Romania (Gál 2002).

– *Crex crex* Linnaeus, 1758

Known from the Carpathian Basin: **Q1**: Betfia 2, 9, Romania (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979b, Gál 2002a) **Q4/I**: Teufelslucken, Austria; Bajót-Hóman Cave, Budapest-Remetehegyi Niche, Felsőtárkány-Peskő Cave, Gencsapáti, Hámor-Puskaporos Niche, Kőszeg, Pilisszántói I. Niche, Répáshuta-Balla Cave, Szilvászvárad-Istállóskői Cave, Tatabánya-Kálvária Hill No. 4. Cave, Tatabánya-Szelim Cave, Varbó-Lambrecht Kálmán Cave (all in Hungary); Barcarozsnyó (Rîșnov), Körösmart (Râpa), Nándori Cave (Curata-Nandru) (all in Romania); Detreköszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas), Slovakia (Lambrecht 1912, 1915, 1916, 1933, Jánossy 1952, 1955, 1979a, 1979b, Soergel 1966, Hamar & Csák 1969, Kessler 1974, Jurcsák & Kessler 1988, 2003, Gál 1998, 2002a, 2004, 2005) **Q4/II**: Knochenhöhle, Austria; Felsőtárkány-Petényi Cave, Legény Cave (all in Hungary); Vársonkolyosi Caves (Șuncuiuș Defile), Romania (Lambrecht 1914, Jánossy 1979a,c, Kessler 1982, Bocheński & Tomek 1994).

– *Crex* sp.

Known from the Carpathian Basin: **Q1**: Beremend 16, 17, Hungary (Jánossy 1992, 1996).

– *Rallus aquaticus* Linnaeus, 1758

Known from the Carpathian Basin: **Q1**: Betfia 2, 9, Romania (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979b, Gál 2002) **Q4/I**: Merkenstein, Austria; Vindija, Croatia; Bajót-Jankovich Cave, Budapest-Remetehegyi Niche, Cserépfalu-Subalyuk Cave, Felsőtárkány-Peskő Cave, Gencsapáti, Hámor-Puskaporos Niche, Pilisszántói I. Niche, Tatabánya-Szelim Cave, Tokod-Nagyberek, Varbó-Lambrecht Kálmán Cave (all in Hungary); Körösmart (Râpa), Romania; Detreköszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas), Slovakia (Lambrecht 1912, 1915, 1916, 1933, Wettstein & Mühlhofer 1938, M. Malez 1961, Hamar & Csák 1969, V. Malez 1973, 1988, 1991, Kessler 1974a, Jánossy 1979a, 1979b, Gál 2002a) **Q4/II**: Bodajk-Rigólyuk, Cserépfalu-Subalyuk (all in Hungary) (Kordos 1984, Kessler 2009b).

– *Gallinula chloropus* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q1**: Beremend 17, Hungary (Jánossy 1992, 1996) **Q4/I**: Vindija, Croatia (M. Malez 1961, V. Malez 1973, 1988, 1991) **Q4/II**: Grosse Offenbergerhöhle, Austria; Ecsegfalva 23, Mezőlak-Szélmező Puszta, Tiszaszőlős-Domaháza puszta (all in Hungary); Vársonkolyos-Kismagyar Cave (Napișteleu-Șuncuiuș), Romania (Kessler 1977, Krolopp & Vörös 1982, Bocheński & Tomek 1994, Gál 2002a, 2007b, Pike-Tay *et al.* 2004).

– *Fulica atra* Linnaeus, 1758

Known from the Carpathian Basin: **Q2**: Betfia 5, Romania (Kessler 1975, Jánossy 1979b, Gál 2002) **Q4/II**: Teufelslucken, Austria; Bajcsa-Vár, Ecsegfalva 23, Endrőd 3/6, 39,119, Maroslele-Pana, Mezőfény, Mezőlak-Szélmező-Puszta, Mezőzombor-községi cemetery, Nagykörű-Tsz, Ordacsehi-Kistöltés, Ószentiván-Tiszasziget, Tiszaszőlős-Domaháza-puszta, Tiszavalk-Négyesi határ, Visegrád Castle (all in Hungary); Gálospetri (Galoșpetreu), Püspökfürdő Lake (Băile Episcopescu) (all in Romania) (Bökönyi 1964, Bökönyi & Jánossy

1965, Soergel 1966, Kessler 1974b, 1980-1981, 1985, Jánossy 1979b, 1985, Krolopp & Vörös 1982, Gál 2002a, 2004, 2005, 2007b, Pike-Tay *et al.* 2004).

Fam. Heliornithidae (Gray, 1849)

Finfoots resemble smaller grebes in appearance and lifestyle quite closely. They live in South America and Africa (only 5 recent species in total). Only one fossil find is known, namely *Heliornis sumegensis* Kessler, 2009 from the late Miocene of Hungary (Sümege) (Kessler, J. 2009b).

Subord. Grues Bonaparte, 1854

Similarly to the previous suborder, they are fairly large birds (with long necks and legs) not tied too much to wet and aquatic environments. They are excellent flyers, with numerous extinct and recent taxons. They nest on the ground and their nestlings are nidifugous. They are usually herbivores, but there are also omnivorous and carnivorous types.

Fam. Gruidae (Vigors, 1825)

Cranes represent larger species of the order due to their excessively long necks and legs. They are present on all continents except Antarctica and Australia. They live on tundras, forest-grass areas and high plateaus. They feed on plants, smaller vertebrates and insects. They build their nests on the ground, their nestlings are nidifugous. They are migratorious. Extinct species *Balearica excelsa* Milne-Edwards, 1868 is known from the late Oligocene of Hungary (Máriaahalom) (Kessler & Rabi manuscript), while extinct species of the genus *Grus* (*G. pentelici* Gaudry, 1862) are known from the late Miocene of Hungary (Csákvár) (Kretzoi 1957).

Recent species from the Carpathian Basin are known since the Quaternary.

– *Grus grus* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/I:** Teufelslucken, Austria; Lovas, Hungary; Körösmart (Râpa), Romania (Soergel 1966, Hamar & Csák 1969, Kessler 1974a, Jánossy 1979b, 1987, Gál 2002a) **Q4/II:** Alattyán-Tulát, Balatonkeresztúr-Réti-dűlő, Békés-Városerdő, Dunaújváros-Koszider, Ecsegfalva 23, Endrőd 39,119, Folyás-Szilmege, Füzesabony, Gyula-Castle, Jánoshida, Kőtelek-Huszársarok, Ludas-Budzsák, Maroslele-Pana, Polgár-Folyás, Röske-Ludvár, Székesfehérvár, Szolnok-Szanda, Tác-Fövénypuszta, Tác-Gorsium, Tiszalúc-Dankadomb, Tiszalúc-Sarkad (all in Hungary); Aranyosmeggyes (Medieșu Auriu), Kisbács-Bácsatorok (Baciu), Parác (Parța), Peterd-Tordai-hasadék-Magyar Cave (Cheile Turzii Defile Caves-Petrești), Szalacs (Sălacea), Szilágyzovány (Zăuan) (all in Romania); Starcevo, Serbia; Tokod-Erzsébetakna, Hungary (Bökönyi 1964, 1974, 1984, Bökönyi & Jánossy 1965, Jánossy 1979a, 1979b, 1985, Jurasák & Kessler 1988, Kessler 1995, Kessler & Gál 1997, 1998, Bartosiewicz 1997, Classon 1980, Gál 2004, 2005, 2007b, 2007c, Bindea 2008, Pike-Tay *et al.* 2004).

Subord. Otides Wagler, 1830

Fam. Otididae (Gray, 1840)

Bustards are large birds, yet they fly well. They live in Eurasia, Africa and Australia. They live in areas with tall grass. They feed on plants and invertebrates. Sexual dimorphism is significant; the males keep a harem, they nest on the ground, their nestlings are nidifugous. Certain species migrate. Extinct species known from the Quaternary of the Carpathian Basin are the following:

– + *Otis khozatzkii* Bochenski et Kurchkin, 1987

Known from the Carpathian Basin: **MN 13:** Polgárdi 4, 5, Hungary (Jánossy 1991).

– + *Otis kalmani* Jánossy, 1972

Known from the Carpathian Basin: **MN 13:** Polgárdi 4,5, Hungary (Kessler 2009b) **MN 15:** Beremend 26, Csarnóta 2 (all in Hungary) (Kessler 2009b) **MN 16:** Beremend 38, Hungary (Kessler 2009b) **Q1:** Beremend 16, 17, Hungary; Betfia 2, 9, Romania (Kessler 1975, Jánossy 1979c, 1992, 1996, Gál 2002a) **Q2:** Nagyharsány-hegy 1-4, Villány 5 (all in Hungary); Betfia 5, 7, Romania (Jánossy 1979c, Gál 2002a, Kessler 2009b).

– + *Otis lambrechtii* Kretzoi, 1941

Known from the Carpathian Basin: **MN 15:** Beremend 26, Hungary (Kessler 2009b) **MN 16:** Beremend 38, Hungary (Kessler 2009b) **Q1:** Beremend 17, Hungary; Betfia 2, 9 Romania (Kretzoi 1941, 1962, Kessler 1975, Jánossy 1979c, 1992, 1996, Gál 2002a) **Q2:** Nagyharsányhegy 1-4, Hungary; Betfia 5, 7, Romania (Kretzoi 1941, 1962, Kessler 1975, Jánossy 1979a,c, Gál 2002a) **Q3:** Hundsheim, Austria; Beremend 23, Hungary; Betfia 7, Romania (Jánossy 1974, 1979c, Kessler 1975, 2009b, Gál 2002a).

Recent species from the Carpathian Basin are known since the Quaternary.

– *Otis tarda* Linnaeus, 1758

Known from the Carpathian Basin: **Q3/I:** Budapest-Várhegy (Jánossy 1979c) **Q4/I:** Varbó-Lambrecht Kálmán Cave (Jánossy 1979a,c, 1986) **Q4/II:** Teufelslucken, Austria; Ecsegfalva 23, Endröd 39, 119, Ludas-Budzsák, Nosza-Gyöngypart, Szajol-Felsőföld, Tószeg-Laposhalom, Turkeve-Móricz (all in Hungary); Nagyvárad-Szálka Hill (Salca-Oradea), Parác (Parța), Peterd-Tordai-hasadék-Magyar Cave (Cheile Turzii Defile, Ungureasca Cave-Petrești), Vizakna (Ocna Sibiului) (all in Romania); Starcevo, Szabadka-Palics (Palič-Subotica) (all in Serbia); Érsekújvár (Nové Zámsky) Kisvárad (Nitriansky Hrádok) (all in Slovakia) (Soergel 1966, Jurcsák & Kessler 1973, Bökönyi 1974, Jánossy 1979c, 1985, Kessler & Gál 1997, 1998, Classon 1980, Gál 2004, 2007b, 2007c, Pike-Tay et al. 2004, Bindea 2008).

– *Otis tetrax* Linnaeus, 1758

Known from the Carpathian Basin: **Q3/I:** Budapest-Várhegy, Hungary (Jánossy 1979a,c) **Q4/I:** Subalyuk, Hungary (Jánossy 1979a,c) **Q4/II:** Tác-Fövény-Pusztá, Tác-Gorsium (all in Hungary) (Jánossy 1979c, 1985, Bökönyi 1984).

– *Otis* sp.

Known from the Carpathian Basin: **Q2:** Somssich-hegy 2, Hungary (Jánossy 1981a, 1982b, 1983, 1986) **Q3/I:** Betfia 7/4, Romania (Kessler 1975, Jánossy 1979c, Gál 2002a).

Ord. Charadriiformes (Huxley, 1867)

Charadriiformes is an order rich in species which are small to middle in size, and prefer aquatic environments. They feed on invertebrates and smaller vertebrates, or can even be necrophages (like seagulls, for example). They live in pairs and hatch their eggs on the ground or ledges of cliffs. Their nestlings are nidifugous. They might migrate in frigid and temperate zones. They occur worldwide. Current-day avian fauna is represented by stone curlews, avocets, oystercatchers, plovers, redshanks, sandpipers, jacanas, quails, pranticoles, razorbills, skuas, gulls, arctic terns, marsh terns etc. Their earliest find in Europe is *Kievornis rogovitshi* Averianov, Potapova et Nesson, 1990 from the Eocene of Ukraine.

Subord. Charadrii (Huxley, 1867)**Fam. Scolopacidae (Vigors, 1825)**

Sandpipers are the species-rich family of woodcocks, snipes, curlews, godwits, redshanks, phalaropes, etc. They live in wet environments and feed on invertebrates. They nest on the ground and are excellent flyers. They are migrants. Extinct species have already been reported from the Miocene and Pliocene of Carpathian Basin sites. (For example *Gallinago veterior* Jánossy, 1979 from the middle and late Miocene and Pliocene of Hungary (Mátraszőlős, Polgárdi, Csarnóta). Other extinct species is *Scolopax baranensis* Jánossy, 1979, is known from the middle and late Pliocene of Hungary (Csarnóta, Beremend) (Jánossy 1979b, Gál *et al.* 1998-1999, Kessler, J. 2009b).

Recent species from the Carpathian Basin are known since the Quaternary.

– *Gallinago media* (Latham, 1787)

Known from the Carpathian Basin: **Q1:** Betfia 2, Romania (Kormos 1913, Čapek 1917, Lambrecht 1933, Kretzoi 1941, Kessler 1975, Jánossy 1979b, Gál 2002) **Q3/I:** Tarkő 11, Hungary (Jánossy 1979a, 1979b) **Q4/I:** Grosse Offenbergerhöhle, Austria; Körösmart (Râpa), Szegvestel-Tibocoia Cave (Sighiștel Defile-Tibocoia Cave) (all in Romania); Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas), Slovakia; Hámor-Puskaporos Niche, Pilisszántói I. Niche (all in Hungary) (Lambrecht 1912, 1913, 1916, 1933, Hamar & Csák 1969, Kessler 1974, 1982, 1985, Jánossy 1979a, 1979b, 1986, Bocheński & Tomek 1994, Gál 2002a).

– *Gallinago gallinago* Linnaeus, 1758

Known from the Carpathian Basin: **Q1:** Betfia 2, Romania (Kormos 1913, Čapek 1917, Lambrecht 1933, Kretzoi 1941, Kessler 1975, Jánossy 1977, 1979a, 1979b, Gál 2002a) **Q4/I:** Vindija, Croatia; Bajót-Hóman Cave, Hámor-Puskaporos Niche, Pilisszántói I. Niche (all in Hungary); Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas), Slovakia (Lambrecht 1912, 1913, 1915, 1916, 1933, M. Malez 1961, V. Malez 1973, 1988, 1991, Jánossy 1979a, 1979b, 1986) **Q4/II:** Gálospetri (Galospetreu), Romania (Kessler 1980-1981, Gál 2002a).

– *Lymnocyptes minimus* (Brünnich, 1764)

Known from the Carpathian Basin: **Q4/II:** Grosse Offenbergerhöhle, Austria (Bocheński & Tomek 1994).

– *Limosa limosa* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q1:** Betfia 2, 9, Romania; Beremend 17, Hungary (Kormos 1913, Čapek 1917, Lambrecht 1933, Kretzoi 1941, Kessler 1975, Jánossy 1977, 1979a, 1979b, 1992, 1996; Gál 2002a) **Q1-2:** Betfia “Aven”, Romania (Kessler 1975, Jánossy 1979b, Gál 2002a) **Q4/I:** Vindija, Croatia; Hámor-Puskaporos Niche, Hungary; Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas), Slovakia (Lambrecht 1912, 1913, 1916, 1933, M. Malez 1961, V. Malez 1973, 1988, 1991, Jánossy 1979a, 1979b, 1986) **Q4/II:** Ecsegfalva 23, Hungary (Pike-Tay *et al.* 2004, Gál 2007b).

– *Numenius arquata* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/I:** Cserépfalu-Subalyuk Cave, Gencsapáti, Tata, Tatabánya-Szelim Cave (all in Hungary); Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas), Slovakia (Lambrecht 1913, 1915, 1933, Jánossy 1979a, 1979b, 1986)

Q4/II: Starcevo, Serbia (Classon 1980, Gál 2004).

– *Numenius phaeopus* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/I:** Teufelslucken, Austria; Varbó-Lambrech Kálmán Cave, Hungary; Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas), Slovakia (Lambrech 1913, 1933, Soergel 1966, Jánossy 1979a, 1979b).

– *Numenius* sp.

Known from the Carpathian Basin: **Q4/I:** Hámor-Puskaaporos Niche, Pilisszántói I. Niche (all in Hungary) (Lambrech 1912, 1915, 1916, 1933, Jánossy 1979a, 1979b, 1986).

– *Tringa totanus* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q1-2:** Betfia 5, Romania (Kessler 1975) **Q4/I:** Hámor-Herman Ottó Cave, Hungary; Ohábaponor-Bordu Mare Cave (Ohaba Ponor), Romania; Óruzsín-Antal Cave (Oruzer), Slovakia (Nehring 1880, Róth 1881, Lambrecht 1912, 1915, 1933, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003).

– *Tringa glareola* Linnaeus, 1758

Known from the Carpathian Basin: **Q1:** Betfia “Aven”, Romania (Kessler 1975, Jánossy 1979b, Gál 2002a) **Q4/I:** Gura Cheii Cave (Braşov), Romania (Jurcsák & Kessler 1988).

– *Tringa erythropus* (Pallas, 1764)

Known from the Carpathian Basin: **Q1:** Betfia 9, Romania (Gál 2002a) **Q4/I:** Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas), Slovakia (Lambrech 1913, 1933).

– *Tringa nebularia* (Gunnerus, 1767)

Known from the Carpathian Basin: **Q1:** Betfia 9, Romania (Gál 2002a).

– *Tringa ochropus* Linnaeus, 1758

Known from the Carpathian Basin: **Q1:** Betfia 9, Romania (Gál 2002a) **Q3/I:** Betfia 7/4, Romania (Gál 2002a, Jánossy 1979b, Kessler 1975).

– *Tringa hypoleucos* Linnaeus, 1758

Known from the Carpathian Basin: **Q1:** Teufelslucken, Austria; Betfia 2, 9, Romania (Kormos 1913, Čapek 1917, Lambrecht 1933, Kretzoi 1941, Soergel 1966, Kessler 1975, Jánossy 1979b, Gál 2002a) **Q4/II:** Körösbánlaci Cave, Romania (Kessler 1982).

– *Tringa* sp.

Known from the Carpathian Basin: **Q1:** Betfia 5, Romania (Kessler 1975) **Q4/I:** Budapest-Remetehegyi Niche, Hungary (Lambrech 1933, Jánossy 1979a, 1979b) **Q4/II:** Grosse Offenbergerhöhle, Austria; Herkulesfürdő-Rablók Cave (Hoţilor Cave-Băile Herculane), Romania (Bocheński & Tomek 1994, Gál 2002a).

– *Scolopax rusticola* Linnaeus, 1758

Known from the Carpathian Basin: **Q3/I:** Hundsheim, Austria (Jánossy 1971, 1974, 1979b) **Q4/I:** Velika Pecina; Vindija (all in Croatia); Budapest-Remetehegyi Niche, Hámor-Puskaaporos Niche, Pilisszántói I. Niche (all in Hungary); Ohábaponor-Bordu Mare Cave (Ohaba Ponor), Romania; Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas), Slovakia (Lambrech 1912, 1913, 1914, 1915, 1933, M. Malez 1961, V. Malez 1973, 1975, 1984, 1988, 1991, Jánossy 1979a, 1979b, 1986, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002a, 2003) **Q4/II:** Grosse Offenbergerhöhle, Teufelslucken (all in Austria); Csákvár-Esterházy Cave, Ecsegfalva 23, Felsőtárkány-Petényi Cave, Hillebrand Cave (Kölyuk II), Legény Cave (all in Hungary); Kisbács-Bácsitorok (Baciu), Körösrévi Caves (Vadu Crişului

Defile), Remetelórév-Bólyikői Cave (Piatra Boiului, Lorău), Vársonkolyos-Kis Magyar Cave (Șuncuiuș, Ungureasca Cave), Vársonkolyosi Caves (Șuncuiuș Defile) (all in Romania) (Lambrecht 1914, Kretzoi 1954, Soergel 1966, Kessler 1977, 1982, Jánossy 1979a, 1979b, Bocheński & Tomek 1994, Kessler in Lazarovici & Maxim 1995, Gál 2002a, 2007b, Pike-Tay *et al.* 2004).

– *Scolopax* sp.

Known from the Carpathian Basin: **Q4/I**: Teufelslucken, Austria; Novi I, III (Novi Caves), Slovakia (Nehring 1880, Róth 1881, Lambrecht 1912, 1933, Soergel 1966).

Fam. Charadriidae Leach, 1820

Plowers form the richest family of the order regarding to the number of species. They live near water, but they also have representatives preferring dry areas. Compared to the present number of species, we know of exceptionally few extinct ones. Only examples of extinct species from the Carpathian Basin were reported from the late Miocene of Hungary (Polgárdi) (*Charadrius lambrechtii* Kessler, 2009 and *Calidris janossyi* Kessler, 2009) (Kessler, J. 2009b).

Recent species from the Carpathian Basin are known since the Quaternary.

– *Arenaria interpres* Linnaeus, 1758

Known from the Carpathian Basin: **Q4/I**: Petényi Cave, Hungary (Jánossy 1979a, 1979b).

– *Philomachus pugnax* Linnaeus, 1758

Known from the Carpathian Basin: **Q1**: Betfia 9, Romania (Gál 2002) **Q4/I**: Pilisszántói I. Niche, Tatabánya-Szelim Cave (all in Hungary) (Lambrecht 1915, 1933, Jánossy 1979a, 1979b, 1986).

– *Charadrius hiaticula* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/I**: Teufelslucken, Austria (Soergel 1966).

– *Charadrius* sp.

Known from the Carpathian Basin: **Q4/I**: Szilvásváradszőlőskői Cave, Hungary (Jánossy 1952, 1955).

– *Calidris alpina* C. L. Brehm, 1822

Known from the Carpathian Basin: **Q4/I**: Pilisszántói I. Niche, Hungary; Detreköszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas), Slovakia (Lambrecht 1913, 1915, 1933, Jánossy 1979a, 1979b, 1986).

– *Calidris ferruginea* Merem, 1804

Known from the Carpathian Basin: **Q4/I**: Merkenstein, Austria (Wettstein & Mühlhofer 1938).

– *Vanellus vanellus* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q1**: Beremend 16, Hungary; Betfia 5, Romania (Lambrecht 1933, Kessler 1975, Jánossy 1992, 1996) **Q4/I**: Vindija, Croatia; Hámor-Puskaporos Niche, Pilisszántói I. Niche (all in Hungary) (Lambrecht 1912, 1915, 1933, M. Malez 1961, V. Malez 1973, 1988, 1991, Jánossy 1979a, 1979b, 1986) **Q4/II**: Teufelslucken, Austria; Legény Cave, Ordascsehi-Kistöltés (all in Hungary); Kőrösrévi Caves (Vadu Crișului Defile), Romania (Lambrecht 1914, Soergel 1966, Kessler 1982, Gál 2005, 2007a).

– *Pluvialis squatarola* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/I**: Merkenstein, Austria; Esküllő-Igric Cave (Igreț-Aștileu), Romania (Wettstein & Mühlhofer 1938, Kessler 1985).

Fam. Recurvirostridae Bonaparte, 1854

Avocets search for small invertebrates in shallow waters, with long legs and beaks. They nest on the coastal sand. Only one supposedly extinct species from Carpathian Basin is known from the early Pleistocene of Betfia, Transylvania (Romania) (Gál 2002).

Recent species from the Carpathian Basin are known since the Quaternary

– *Recurvirostra avosetta* Linnaeus, 1758

Known from the Carpathian Basin: **Q4/I**: Vindija, Croatia (M. Malez 1961, V. Malez 1973, 1988, 1991, V. Malez & Rukavina 1979).

– *Himantopus himantopus* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q4/I**: Pilisszántói I. Niche, Hungary (Lambrecht 1915, 1933, Jánossy 1979a, 1979b, 1986).

Subord. Lari Sharpe, 1891**Fam. Lariidae Vigors, 1825**

Gulls and terns are spread out all across the globe, with a great number of species. They live on the shores of open waters. They feed on invertebrates, small vertebrates, carcasses, and some species near human settlements look for food on garbage heaps. They nest on coastal sand or walls of cliffs. Their nestlings are fluffy, but their parents feed them. Many species migrate, their young roam. Fossil species are not known from the Carpathian Basin.

Recent species from the Carpathian Basin are known since the Quaternary.

– *Larus minutus* Pallas, 1766

Known from the Carpathian Basin: **Q3**: Vindija, Croatia (M. Malez 1961, V. Malez 1973, 1988, 1991, V. Malez & Rukavina 1979).

– *Larus ridibundus* Linnaeus, 1758

Known from the Carpathian Basin: **Q1**: Beremend 17, Hungary (Jánossy 1992, 1996) **Q4/I**: Merkenstein, Austria; Vindija, Croatia; Hámor Puskaporos Niche, Pilisszántói I. Niche, Répáshuta-Balla Cave (all in Hungary) (Lambrecht 1912, 1915, 1916, 1933, Wettstein & Mühlhofer 1938, M. Malez 1961, V. Malez 1973, 1988, 1991, Jánossy 1979a, 1979b, 1986).

– *Larus argentatus* Pontoppidan, 1763

Known from the Carpathian Basin: **Q4/II**: Maroslele-Pana, Hungary (Bökönyi 1964, Jánossy 1979b, 1985, Gál 2004, 2007b).

– *Larus canus* Linnaeus, 1758

Known from the Carpathian Basin: **Q4/I**: Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas), Slovakia (Lambrecht 1913, 1933).

– *Larus* sp.

Known from the Carpathian Basin: **Q4/I**: Vindija, Croatia (M. Malez 1961, V. Malez 1973, 1988, 1991, M. Malez & Rukavina 1979).

– *Sterna Hirundo* Linnaeus, 1758

Known from the Carpathian Basin: **Q4/I**: Pilisszántói I. Niche, Hungary (Lambrecht 1915, 1933, Jánossy 1979a, 1979b, 1986).

– *Sterna* sp.

Known from the Carpathian Basin: **Q1-2**: Betfia 5, Romania (Kessler 1975).

– *Chlidonias niger* (Linnaeus, 1758)

Known from the Carpathian Basin: **Q1**: Betfia 9, Romania (Gál 2002a).

– *Chlidonias* sp.

Known from the Carpathian Basin: **Q4/I**: Varbó-Lambrecht Kálmán Cave, Hungary (Jánossy 1979a).

Conclusions

The presented rich database grants the possibility to become familiar with the evolution and understanding of aquatic birds. They are well-presented, and even dominant, in avian fauna since the beginning of the Cretaceous, contrary to Sauriurae birds, where we do not know of species specifically living in wet environments neither from the Jurassic, nor from the Cretaceous. In the Paleogene, among recent birds (Ornithurae – Neornithes), they also constitute a majority compared to birds living in other environments, although this might also have taphonomic reasons, as shown by the avian fauna of Grube Messel.

In the case of most aquatic birds, the nestlings leave their nests early and start feeding autonomously. This is also a sign of maintaining old characteristics. Staying in their nests and being fed by their parents are either supposedly signs of typical nesting characteristics (for example with auks, penguins, where the fluffy nestlings cannot follow their parents to open waters due to various reasons), or the fact that the switch to living in aquatic environments is a secondary characteristic in their case. In contrary, a large number of the members of the listed group were or are not living in wet environments anymore (terrorbirds, Otidae, stone curlews etc.).

Another peculiarity while studying the database is that in the case of numerous groups (orders, families), the earliest representatives lived in entirely different – and rather distant – environments than their current representatives. This is especially conspicuous in the case of flightless or barely flying types. This can have a number of possible reasons:

- the common ancestor could have formed before the dry “bridges” between the continents disappeared;
- becoming flightless is a subsequently formed characteristic;
- signs of being related were formed in an analogue way during evolution and their ancestral connection is only apparent.

The study of the database also makes it possible to mark the location where certain groups and types formed, and the direction in which they spread. The primer nature of Otidae in the Carpathian Basin is a typical example of this.

Data can, of course, be misleading, since finds of species that the fly well and roam large areas while immature can surface from rather unexpected places (as with the remains of seabirds).

The author is hoping to aid ornithologists and paleontologists in gaining knowledge on the geological history of the presence of taxons tied more or less to aquatic environments, trace the formation of certain units of taxonomy, and, especially, familiarize themselves with the ancient avian fauna of the Carpathian Basin.

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