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Growth duration, life history and ecological traits of bony-toothed birds (Odontopterygiformes): implications from bone histology

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abstract

Bony-toothed birds (Odontopterygiformes), an order of seabirds that existed throughout most of the Cenozoic, had unusually fragile, thin-walled bones. This complicates their study and draws attention to microscopic methods, which are applicable even to fragmentary remains. The histological structure of long bones of the limbs of two species from the lower Lutetian locality Ikove (Luhansk Oblast, Ukraine) was studied: *Lutetodontopteryx tethyensis* and cf. *Dasornis* sp., representing the two main clades of the order. The well-preserved microstructure of the bones sheds light on the growth pattern of these birds, which turned out to be similar to that of recent Neognathae: with rapid and typically sharply terminated bone growth. This resulted in the apposition of azonal woven-parallel tissue, covered with outer and inner circumferential layers (OCL and ICL), usually sharply delimited from it. Like in other birds, osteohistological features allow to distinguish gross developmental stages of the animals (juveniles, young adults, and older adults) and provide hints about events of their life history, such as egg-laying or moulting, which enhance the development of resorption cavities and, probably, secondary osteons. The humeri of *L. tethyensis* show a structure of the outer cortex unusual for birds, which indicates a less abrupt than usual growth cessation. Age determination from the sublayers in the inner circumferential layer (a method which works in some species of recent birds but not in other) proved impossible for *L. tethyensis*; for cf. *Dasornis* sp. the question remains open. The duration of the growth in the studied species cannot currently be determined precisely, but can be estimated at 10^2 days, probably (in contrast to previous inferences) less than one year. A relatively short development supports the hypothesis about Odontopterygiformes being specialised consumers of squid, based on the morphology of the pseudoteeth. Eating squid can be an explanation of the observed osteohistological features, which could be caused by calcium deficiency.

Тривалість росту, онтогенетичні події та екологічні особливості псевдозубих птахів (Odontopterygiformes): дані гістології кісток

Станіслав Добровольський, Леонід Горобець

Резюме. Псевдозубі птахи (Odontopterygiformes) — ряд морських птахів, що існували впродовж більшої частини кайнозою – вирізнялися крихкими тонкостінними кістками, що ускладнює їхнє дослідження і привертає увагу до мікроскопічних методів, застосовних навіть до фрагментарних решток. Було досліджено гістологічну будову довгих кісток кінцівок двох видів із нижньолютетського місцезнаходження Ікове (Луганська область): *Lutetodontopteryx tethyensis* та cf. *Dasornis* sp., що представляють обидві основні клади ряду. Добре збережена мікроструктура кісток проливає світло на характер росту цих птахів, який виявився подібним до такого у сучасних Neognathae: із швидким наростанням кісток та, як правило, досить різким його припиненням. Це призводило до відкладення багатої на судини грубоволокнисто-паралельної тканини без ростових шарів, вкритої зовнішнім та внутрішнім окружними шарами (OCL та ICL), зазвичай чітко від неї відмежованими. Як і в інших птахів, остеогістологічні ознаки дозволяють розрізнити основні вікові стадії (ювенільні, молоді дорослі, старші дорослі особини) і зберігають сліди онтогенетичних подій, таких як відкладання яєць або линяння, які призводять до посиленого розвитку резорбційних порожнин та, ймовірно, вторинних остеонів. У плечових кістках *L. tethyensis* спостерігається нетипова для птахів гістологічна будова зовнішнього кортексу, яка свідчить про менш різке, ніж зазвичай, припинення росту. Визначення віку за прошарками у внутрішньому окружному шарі (метод, що у сучасних птахів придатний для одних видів і непридатний для інших) для *L. tethyensis* виявилося неможливим; для cf. *Dasornis* sp. питання залишається відкритим. Тривалість розвитку в досліджених видів зараз неможливо визначити точно, але можна оцінити в 10^2 днів, ймовірно (на відміну від попередніх припущень) менше одного року. Відносно короткий період розвитку дає підстави розглядати гіпотезу про спеціалізацію Odontopterygiformes на споживанні кальмарів, що узгоджується з попередніми припущеннями, заснованими на морфології псевдозубів. Живлення кальмарами може бути поясненням виявлених у кістках гістологічних структур, що могли бути спричинені дефіцитом кальцію.

Ключові слова: Псевдозубі, остеогістологія, ріст, живлення.

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Introduction

Bony-toothed birds (Odontopterygiformes) are known from most of the Cenozoic (from the early Paleocene to late Pliocene or early Pleistocene) and from all continents [Mayr *et al.* 2019; Kloess *et al.* 2020]. Their phylogenetic affinities are unclear. In the latest analysis, they make up a polytomy with Galloanseres and Neoaves [Mayr *et al.* 2019]. Some morphological features suggest that Odontopterygiformes can be a sister group or subgroup of Galloanseres [Mayr 2009; Mayr 2011; Zelenkov & Kurochkin 2015; Mayr 2017].

In the early Eocene, Odontopterygiformes were one of the most widespread and abundant groups of seabirds [Mlíkovský 2009; Zelenkov & Kurochkin 2015]. Being specialised for soaring lifestyle and having large body size [Mayr 2017; Mayr *et al.* 2019], they are considered as morphological and ecological analogues of extant albatrosses [Bourdon 2011; Louchart *et al.* 2018], but, at the same time, they possessed unique features, the most prominent of which are bony pseudoteeth. The way of life, feeding, and individual development of Odontopterygiformes are known insufficiently, partly because of the fragility of their thin-walled bones. It draws attention to histological methods, which are applicable even to fragmentary material and can substantially improve our understanding of the biology of extinct vertebrates.

Bone histology is considered the best instrument to elucidate growth rates of extinct vertebrates [Bailleul *et al.* 2019; Prondvai *et al.* 2019]. In addition, bone microstructure preserves traces of many life history events, such as egg-laying, environmental influences, diseases, and others [Chinsamy 1997; Padian 2013], although these traces are often difficult to disentangle and decipher [Pratt *et al.* 2018].

In many animals, including early and some recent birds, bones contain annual marks, sometimes enabling quite precise age determination, albeit this method has certain difficulties [Schucht *et al.* 2021]. If such marks are absent, only tentative age estimates are possible [Erickson 2005; D'Emic & Benson 2013]. They are based mainly on the relationship between the apposition rate of primary periosteal bone tissue and its microstructure, known as Amprino's rule: broad categories of bone tissue types (woven-parallel, parallel-fibered, and lamellar tissue) correspond to certain, notably different (although partly overlapping) ranges of apposition rate [de Buffrénil *et al.* 2021].

This rule allows only for rough conclusions about the apposition rate: for any given type of bone tissue, this rate strongly varies between skeletal elements and between taxa, sometimes by an order of magnitude. It is generally higher in larger animals [Cubo *et al.* 2012; Padian & Woodward 2021] and larger bones [Castanet *et al.* 2000]. Its dependence on individual age and environmental conditions (e.g. food availability) also exists [Starck & Chinsamy 2002; Cubo *et al.* 2012]. In recent birds, bone apposition rate depends mostly on body size and developmental mode: precocial or altricial [Cubo *et al.* 2012]. Intraspecific variation also can be considerable [de Margerie *et al.* 2004]. Nevertheless, Amprino's rule holds true [Castanet *et al.* 2000; de Margerie *et al.* 2002; Curry Rogers & Erickson 2005] and can help reduce uncertainty in estimates of developmental and metabolic rates of extinct vertebrates [de Ricqlès *et al.* 2003; Curry Rogers & Erickson 2005; de Buffrénil *et al.* 2021].

Growth rates of extinct birds were remarkably diverse, although recent ones, with a few exceptions, grow extremely fast [Prondvai *et al.* 2019; Atterholt & Woodward 2021]. This ability probably evolved several times among Aves and possibly even within Ornithuromorpha during the Cretaceous [Atterholt *et al.* 2021]. The studied Mesozoic crown-group birds (*Vegavis* Clarke *et al.*, 2005) and their close relatives (*Ichthyornis* Marsh, 1872, *Hesperornis* Marsh, 1872 and *Iteravis* Zhou *et al.*, 2014), based on bone microstructure, had similarly rapid and uninterrupted growth [Chinsamy *et al.* 1998; Wilson & Chin 2014; O'Connor *et al.* 2015; Marsà *et al.* 2017], whereas more basal *Patagopteryx* Alvarenga & Bonaparte, 1992, *Vorona* Forster *et al.*, 1996*, Archaeorhynchus* Zhou & Zhang, 2006 and Enantiornithes grew substantially slower: during several years in the case of most Enantiornithes [Chinsamy *et al.* 1995; Starck & Chinsamy 2002; Wang *et al.* 2017; Atterholt *et al.* 2021]. The more basal *Confuciusornis* Hou *et al.*, 1995 was fast-growing again [de Ricqlès *et al.* 2003], and the even more basal *Jeholornis* Zhou & Zhang, 2002 and *Archaeopteryx* Meyer, 1861 were still slow-growing [Padian & Woodward 2021]. Non-avian theropods had a fast-growing bone tissue, but, due to larger body size, their growth typically lasted several years and was interrupted annually [Atterholt *et al.* 2021; Padian & Woodward 2021].

Most of crown-group birds reach adult size within one year, usually within a few weeks or months [Padian & Woodward 2021]. The exceptions are some non-flying, insular (i.e. lacking predation pressure), and/or large birds, such as *Genyornis* Stirling & Zietz, 1896 (Gastornithiformes), *Pezophaps* Strickland, 1848 (Columbiformes), *Apteryx* Shaw, 1813 (Apterygiformes), Aepyornithidae (Aepyornithiformes), and Dinornithiformes. Their bones contain lines of arrested growth (LAGs), which are interpreted as annual marks and indicate growth during several years [Bourdon *et al.* 2009; Chinsamy *et al.* 2020a; Chinsamy & Worthy 2021; Canoville *et al.* 2022]. However, flightlessness, insularity, and large size do not necessarily result in slow growth, as shown by *Raphus* Brisson, 1760 (Columbiformes) [Angst *et al.* 2017]. When did the ancestors of recent birds gain their modern growth pattern, it remains unclear. It could happen after [Canoville *et al.* 2022] or before [Padian & Woodward 2021] the appearance of Neornithes, possibly near the base of Ornithurae [Chinsamy 2002; Starck & Chinsamy 2002]. In any case, later some taxa lost this pattern again. Therefore, the growth pattern of extinct birds with no close recent relatives cannot be trivially inferred from their phylogenetic affinities (which are often uncertain themselves), flying ability, or any other features.

Bone growth rate is one of the factors limiting developmental rate of birds. This factor is expected to be especially strong in birds with relatively long wing bones, and this is supported by the example of albatrosses [Carrier & Auriemma 1992]. Therefore, the clarification of bone growth rates of

Odontopterygiformes is of great interest to shed light on their overall developmental rate. This can, in turn, imply consequences for other aspects of their biology, including ecology.

Materials and Methods

The examined bones (Table 1) were collected in 2013 by L. V. Gorobets and E. O. Zvonok in the lower Lutetian locality Ikove (Luhansk Oblast, Ukraine; described by Udovichenko [2009], Zvonok *et al.* [2012], and Dernov & Udovychenko [2023]) and identified by L. V. Gorobets.

Table 1. **The list of examined bones**
Таблиця 1. **Список досліджених кісток**

Taxon	Skeletal element		Collection number
Pelagornithidae cf. *Dasornis* sp.	femur	right	NMNHU-p Av-34
	humerus	right (?)	NMNHU-p Av-42
Lutetodontopteryx tethyensis Mayr & Zvonok, 2012	humerus	right	NMNHU-p Av-11
	femur	right	NMNHU-p Av-18
	tibiotarsus	left	NMNHU-p Av-19
?*Lutetodontopteryx tethyensis* Mayr & Zvonok, 2012	humerus	?	NMNHU-p Av-8
	femur	left	NMNHU-p Av-26

The species considered represent different clades with nearly family-level morphological differences (Zelenkov & Kurochkin 2015), although all Odontopterygiformes are now grouped into a single family Pelagornithidae [Mayr *et al.* 2019].

A general description of the histology of these bones, except for the specimen Av-8, is provided in [Dobrovolsky 2023*b*]. A complete set of micro- and macrophotographs of the bones is available on Figshare (https://doi.org/10.6084/m9.figshare.c.6415514), whereas the 3D models of the well-preserved bones on Sketchfab (https://sketchfab.com/scotoplanes/models). The present paper discusses the features that have immediate or potential implications for growth rate and life history.

The samples were taken from the bones near the broken end (approximately at the mid-diaphysis in most cases, except for Av-18 and Av-34, where it was located more proximally and distally respectively). Thin sections were prepared and photographed according to the technique described in [Dobrovolsky 2023*a*]. Their thickness is approximately 70 µm.

The diameter of primary osteons was measured in bones that have retained them. Usually, taking measurements of primary osteons is complicated by their poorly distinguishable borders. In the majority of bones they were measured on thin sections imaged in transmitted light equivalently to imaging between circular polarisers. In Av-42, primary osteons were poorly visible in these conditions and they were examined on a thick section in reflected light (Fig. 1*a*). The osteons and osteocyte lacunae were measured by simple self-made scripts on the basis of manual markings on the images.

Abbreviations. ICL, inner circumferential layer; OCL, outer circumferential layer; NMNHU, National Museum of Natural History, National Academy of Sciences of Ukraine.

Results

Woven-parallel tissue

The primary tissue (except OCL) in all the bones, where it has been preserved, is densely vascularised (with primary osteons formed around vascular canals) and contains numerous osteocyte lacunae. In the humeri of both species and in the tibiotarsus of *L. tethyensis* (Av-19), this tissue is represented by typical woven-parallel (also known as fibrolamellar [de Buffrénil & Quilhac 2021]) complex, although strongly different in the direction of vascular canals and bone fibres (Fig. 1). In one femur of *L. tethyensis* (Av-26), this direction is mostly circumferential, giving the impression of parallel-fibered bone (for instance, a very similar tissue of the mallard was interpreted in this way by de Margerie and colleagues [de Margerie *et al.* 2002: Fig. 1*c*], but the numerous primary osteons suggest the attribution to the woven-parallel complex. This is supported by the structure of the bone on the mediocaudal side, where the direction of the canals changes to longitudinal (Fig. 1*d*).

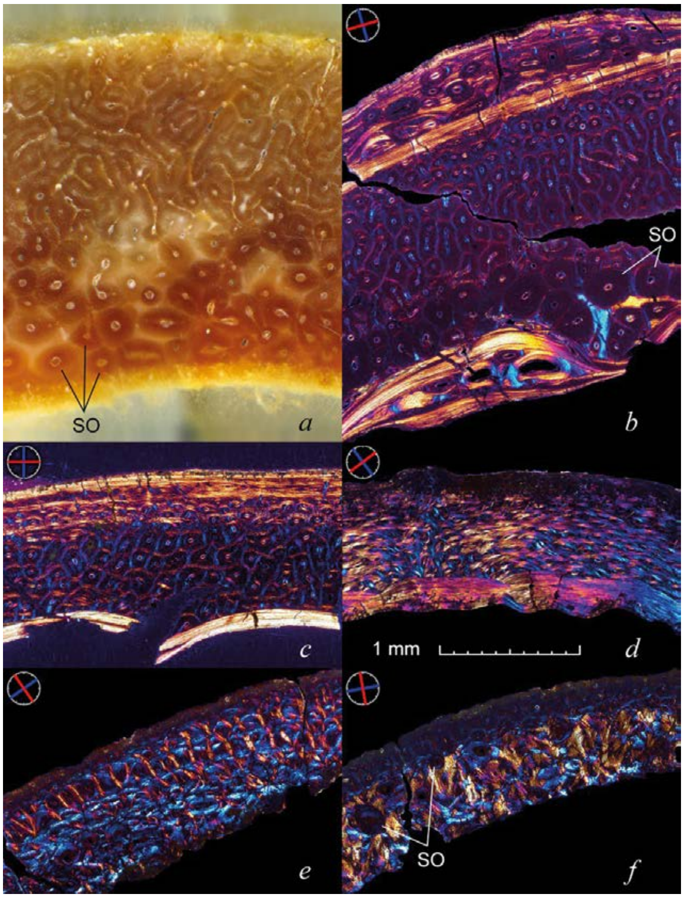

Fig. 1. The bones that have retained the woven-parallel (fibrolamellar) tissue. Transverse sections. Cf. *Dasornis*: (*a*) Av 42 (humerus), craniodorsal side. *L. tethyensis*: (*b*) Av 11 (humerus), cranial side; (*c*) Av 8 (humerus); cranial or caudal side; (*d*) Av 26 (femur), mediocaudal side; (*e*) Av 19 (tibiotarsus), cranial side; (*f*) Av 19 (tibiotarsus), caudal side. The periosteal surface of all bones is at the top; (*a*) polished (thick) section in reflected light; (*b–f*) thin sections in transmitted light, polarised light microscopy (the brightness is taken from an analogue of image between circular polarisers, and the colour from an image between crossed linear polarisers with full-wave plate). Red and blue lines in the circle indicate directions of bone fibres, highlighted in these colours. The scale bar is the same for each image. SO, secondary osteons.

Рис. 1. Кістки, що зберегли грубоволокнисто-паралельну (фіброламелярну) тканину. Поперечні зрізи. Cf. *Dasornis*: (*a*) Av 42 (плечова), краніодорсальний бік. *L. tethyensis:* (*b*) Av 11 (плечова), краніальний бік; (*c*) Av 8 (плечова), краніальний або каудальний бік; (*d*) Av 26 (стегнова), медіокаудальний бік; (*e*) Av 19 (тибіотарсус), краніальний бік; (*f*) Av 19 (тибіотарсус), каудальний бік. Періостальна поверхня всіх кісток — угорі; (*a*) аншліф у відбитому світлі; (*b–f*) шліфи у прохідному світлі, поляризаційна мікроскопія (яскравість взято з аналогів знімків між круговими поляризаторами, а колір — зі знімків між лінійними поляризаторами з повнохвильовою пластинкою). Червона та синя лінії в колі показують напрямок кісткових волокон, підсвічених у ці кольори. Масштаб скрізь однаковий. SO — вторинні остеони.

In the humeri (Av-8 and Av-11) and tibiotarsus (Av-19) of *L. tethyensis*, primary osteons become progressively smaller from inner to outer compacta. In Av-26, this is true for osteocyte lacunae, but not for the osteons or vascular canals.

The diameter of primary osteons is known to correlate with bone apposition rate and may potentially be of interest to skeletochronology [de Margerie *et al.* 2002; Lee *et al.* 2013]. So, it was measured in those bones where primary osteons are preserved. In the bones where they noticeably diminish towards the outer surface, the inner and outer regions of the compacta were examined separately (Table 2).

Table 2. Mean diameter of primary osteons in the examined bones

Таблиця 2. Середній діаметр первинних остеонів у досліджених кістках

Specimen	Number of measured osteons	Mean diameter of osteons, μm	Standard deviation, μm
Av-8 (0.0–0.4 mm under the outer surface)	83	70	16
Av-8 (0.4–1.0 mm under the outer surface)	137	112	19
Av-11 (0.0–0.3 mm under OCL)	30	80	18
Av-11 (0.3–1.0 mm under OCL)	45	120	23
Av-19 (0.0–0.2 mm under the outer surface)	45	87	15
Av-19 (0.2–1.0 mm under the outer surface	210	100	22
Av-26	50	54	13
Av-42	50	130	20

In the woven-parallel tissue of Av-26 (the only examined femur that retained this tissue), several additional parameters, which can be related to growth rate, were measured in the way described by [Cubo *et al*. 2012]. These parameters are as follows: vascular density (105 canals/mm^2), the fractions of differently oriented vascular canals (circular: 0.66; oblique: 0.25; radial: 0.09), and the parameters of osteocyte lacunae, which turned out to be distinctly different in the inner and outer half of the primary cortex: density in a single plane (inner cortex: 0.0030 cells/µm^2; outer cortex: 0.0023 cells/µm^2), mean area of the projection onto the image plane (inner: 48 µm^2, SD = 15 µm^2; outer: 36 µm^2, SD = 11 µm^2), and mean ratio of the minor and the major axes (inner: 0.50, SD = 0.16; outer: 0.48, SD = 0.15).

In one femur of *L. tethyensis* (Av-18) and the femur of cf. *Dasornis* sp. (Av-34), no distinct woven-parallel tissue is observed due to Haversian remodelling (Fig. 2).

Circumferential layers

The majority of the bones possess inner and outer circumferential layers (ICL and OCL), also known as internal and external fundamental systems. The exceptions are Av-19, which has only minor remains of ICL and no OCL, and Av-26, which has a thick ICL and no or almost no OCL. When present, these layers are sharply delimited from the adjacent tissue, with a usually less than ~10 µm thick transition. The exception is Av-8 with smooth transition and intermingling of the woven-parallel tissue and OCL in some places (Fig. 1*c*). Another humerus of *L. tethyensis* (Av-11) bears an unusual deposition of bone tissue ('bulge') outwards of OCL (Fig. 1*b*). It is delimited by a LAG and differs from OCL in less ordered fibres and numerous secondary osteons.

ICL of Av-26 contains several regions with sharp change of direction of bone fibres, indicating alternating resorption and apposition (no less than 3 cycles; Fig. 1*d*). One similar feature is present in ICL of Av-34 (implying one cycle).

Secondary remodelling

The extent of Haversian remodelling in the bones varies greatly. It is absent in Av-8, only two small secondary osteons are seen in Av-26 in almost complete cross-section of the bone, the osteons in Av-19 are more numerous yet still rare, but they form dense Haversian bone in the inner layer of the compacta in Av-11 and Av-42 (Fig. 1 *a*, *b*; Fig. 4), whereas they replaced all the woven-parallel tissue in Av-18 and Av-34 (Fig. 2). In Av-19 and Av-34, most of the secondary osteons are immature (with wide vascular canals and without the characteristic inner lining that brightly shines under polarising

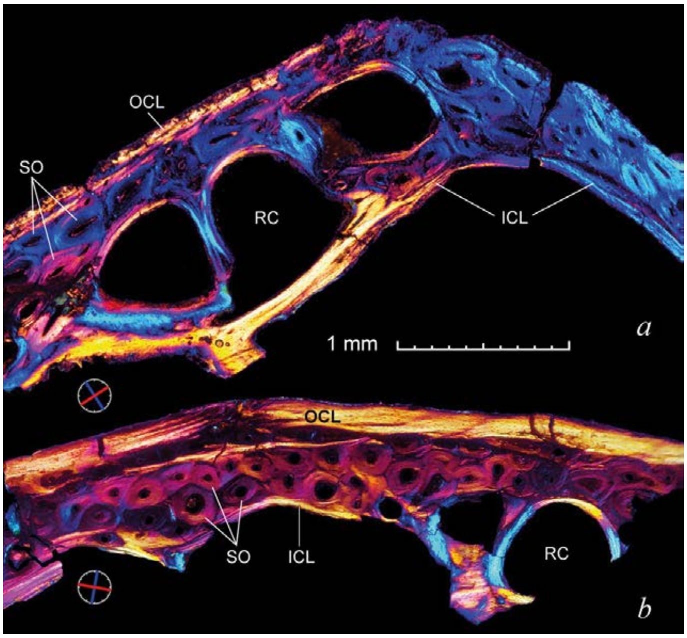

Fig. 2. Heavily remodelled specimens. Femora, transverse sections of cranial side; periosteal surface is at the top. (*a*) Av-18 (*L. tethyensis*); (*b*) Av-34 (cf. *Dasornis*). Polarised light microscopy (see the caption of Fig. 1). Large resorption cavities (RC) are seen. The tissue between the inner (ICL) and outer (OCL) circumferential layers is replaced by secondary osteons (SO).

Рис. 2. Сильно ремодельовані зразки. Стегнові кістки, поперечні зрізи краніального боку; періостальна поверхня — вгорі. (*a*) Av-18 (*L. tethyensis*); (*b*) Av-34 (cf. *Dasornis*). Поляризаційна мікроскопія (див. підпис до рис. 1). Видно великі резорбційні порожнини (RC). Тканина між внутрішнім (ICL) та зовнішнім (OCL) окружними шарами заміщена вторинними остеонами (SO).

microscope). The specimen Av-34 shows no less than two generations of secondary osteons. Some of them contain reversal lines, implying their resorption and refilling.

The most heavily remodelled bones (Av-18 and Av-34) show, in addition to secondary osteons, large erosion cavities, partially refilled with lamellar tissue (Fig. 2), sometimes referred to as 'endosteal osteons' [de Ricqlès *et al.* 2016]. The cavities visible in Av-18 are up to 0.7 mm wide (while the bone wall is 0.5–1.3 mm thick), and in Av-34, up to 0.2 mm wide (in 0.9 mm thick bone wall). In both bones, walls of the cavities are lined with ~0.06 mm thick parallel-fibered or lamellar tissue. In Av-34, the cavities partially destroy ICL, implying remodelling in adulthood. In Av-11, such cavities (up to 0.4 mm wide) are observed only inside ICL (Fig. 1*b*).

Growth marks

No growth marks clearly useful for skeletochronology are seen in the woven-parallel complex of the examined bones. Prominent dark and light lines, evidently isochrons, are present in the primary tissue of Av-8 (Fig. 3) and inside primary and secondary osteons of Av-11, but the circumstances and period of their formation are unknown, so they cannot be utilised. However, some layering is present in other bone structures. In particular, Av-11 contains several probable LAGs in the aforementioned 'bulge' outwards of OCL.

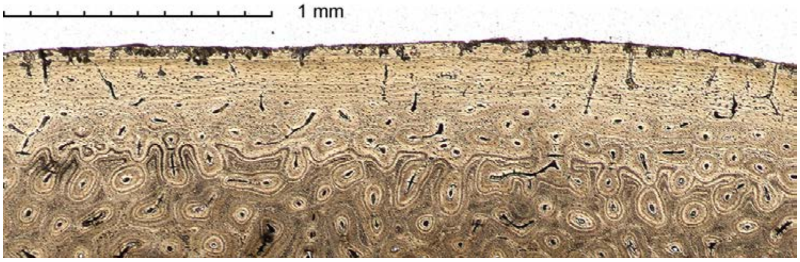

Fig. 3. Humerus of cf. *L. tethyensis* (Av-8), transverse section; periosteal surface is at the top. The meandering layers in the woven-parallel tissue mark former positions of the bone surface, including borders of the primary osteons.

Рис. 3. Плечова кістка cf. *L. tethyensis* (Av-8), поперечний зріз; періостеальна поверхня вгорі. Хвилясті прошарки у грубоволокнисто-паралельній тканині відмічають колишні положення поверхні кістки, зокрема межі первинних остеонів.

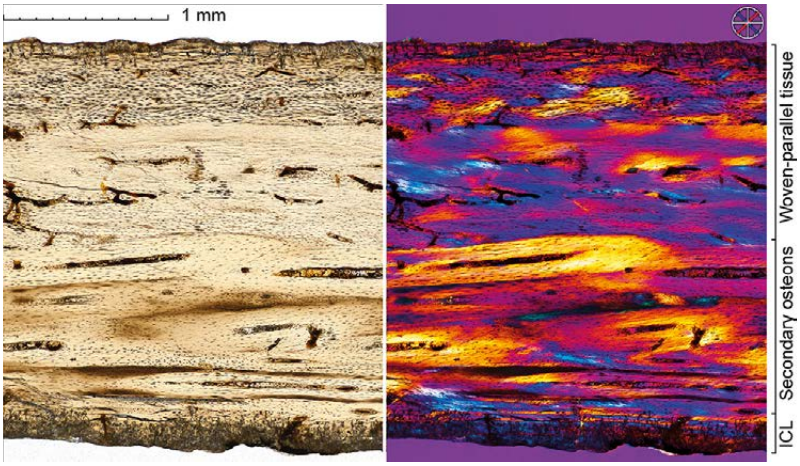

Fig. 4. Humerus of cf. *Dasornis* (Av-42), longitudinal section; the periosteal surface is at the top. Views in normal light and between crossed polarisers with full-wave plate. ICL (in the bottom) shows layers that differ in fibre direction and, consequently, in colour in the right image.

Рис. 4. Плечова кістка cf. *Dasornis* (Av-42), поздовжній зріз; періостеальна поверхня вгорі. Вигляд у звичайному світлі та між схрещеними поляризаторами з фазовою пластинкою. В ICL (унизу) видно прошарки, що відрізняються напрямком волокон і, як наслідок, кольором на правому знімку.

Fine layering is observed also in OCL and especially ICL, when they are present. The number of the layers depends on the way of counting: the pairs of adjacent bright and dark lines seen under polarising microscope are more numerous than the rows of osteocyte lacunae (used by Klomp & Furness [1992] and a number of subsequent authors, e.g. Broughton *et al.* [2002] and Drozdowska & Meissner [2014]). Additionally, the number of the layers in ICL (regardless of the way of counting) strongly varies along the circumference of the bone, at least partially due to endosteal resorption. In Av-8, about 5–10 rows of lacunae can be traced in ICL and 15–20 in OCL. Av-11 shows 7–10 rows of lacunae in OCL and a much higher and variable number (up to several dozen) in ICL. In Av-18, the counting is difficult, but these numbers can be estimated at 5–10 in each layer. Av-26 has no or almost no OCL and a thick ICL with several dozen fine layers (in some places, no less than 30 and possibly even 40 rows of lacunae). Av-42 has poorly preserved ICL and OCL, which precludes counting of lacunae rows, but its ICL contains no less than 10 layers with different direction of bone fibres, judging from different colours between crossed polarisers with wave plate (best seen on the longitudinal section, Fig. 4).

Discussion

Ontogenetic stages

Bones of birds that have reached adult body size can be identified based on the presence of OCL [Wilson & Chin 2014]. Usually, its appearance approximately coincides with fledging, but can occur somewhat earlier [Atterholt & Woodward 2021]. In addition, the bones of skeletally mature birds have well-mineralised epiphyses. Less reliable indicators of skeletal maturity are well-developed ICL and extensive Haversian remodelling [de Ricqlès *et al.* 2003].

All of the described bones come from skeletally mature animals (according to the well-developed OCL), except for Av-26 and Av-19. Both of them have poorly mineralised epiphyses and neither have OCL. However, these bones also have reached an approximately adult size, according to their comparison with the type specimens [Mayr & Zvonok 2012] and the presence of well-developed ICL in Av-26 and incipient ICL plus pronounced diminishing of the primary osteons towards the periosteum in Av-19.

General growth pattern

The basic histological features of *Lutetodontopteryx tethyensis* and cf. *Dasornis* sp. are similar to those of recent Neognathae and imply a similar growth pattern. The woven-parallel (fibrolamellar) complex, observed in all of the examined bones except for heavily remodelled ones, is typically formed in juvenile tetrapods with high metabolic rates and medium or large body size [de Buffrénil & Quilhac 2021]. The humeri and tibiotarsus of *L. tethyensis* show the diminishing of primary osteons towards the outer surface, suggesting some decrease of apposition rate towards the end of rapid growth (the size of primary osteons is known to increase with apposition rate [de Margerie *et al.* 2002]). ICL and OCL of both species, consisting of lamellar or parallel-fibered tissue and sharply delimited from the underlying bone, imply abrupt termination of fast apposition and beginning of slow apposition (an exception is shown by the humeri of *L. tethyensis*, see 'Particular ontogenetic events' below). OCL and ICL are deposited an order of magnitude slower than the woven-parallel complex [de Margerie *et al.* 2002]. So, Odontopterygiformes share the bone growth pattern with recent and the majority of extinct Neognathae (as well as a number of Mesozoic taxa): until reaching adult size, the bone undergoes rapid periosteal growth and endosteal resorption, then these processes stop and are succeeded by much slower apposition on the outer and inner surfaces of the bone.

Growth marks

The absence of annual growth marks in the woven-parallel tissue of all the examined bones cannot completely rule out their presence in Odontopterygiformes, because most of this tissue in all the bones has been resorbed. However, the birds, which are known to grow for >1 year, retain growth marks (often numerous) even in adult bones because of the slowdown of apposition rate at the end of growth and, consequently, close spacing of these marks: hundreds or even tens of micrometres [Chinsamy 2002; Turvey *et al.* 2005; Bourdon *et al.* 2009; Chinsamy & Worthy 2021; Canoville *et al.* 2022]. Therefore, uninterrupted growth and reaching adult size within one year is more probable for Odontopterygiformes, especially given that it is observed in the majority of crown-group birds (almost all Neognathae and some Palaeognathae), including large albatrosses and (at least in the first approximation) ostrich and emu [Carrier & Auriemma 1992; Bourdon *et al.* 2009; Chinsamy & Worthy 2021; Padian & Woodward 2021; Canoville *et al.* 2022]. The same is probably true for a number of extinct taxa closely related to Neornithes, whose woven-parallel complex also shows no growth marks [Chinsamy *et al.* 1998; Chinsamy 2002; Wilson & Chin 2014].

Layering in OCL and ICL and its potential value for skeletochronology have been studied in many bird species, because the possibilities to determine the age of birds are very limited in comparison with other vertebrates. The results turned out to be vastly different. Some authors reported that the lines in ICL [Klomp & Furness 1992] or OCL [Van Soest & Van Utrecht 1971] do correspond to years, at least in the majority of examined species. In other cases, ICL, OCL, or both were completely non-informative [Broughton *et al.* 2002; Drozdowska & Meissner 2014]. Some researchers report in OCL non-annual, but very similar lines accompanying annual ones [Klevezal 1972; Broughton *et al.* 2002]. In addition, the number of the lines can vary across the same bone [Lewis 1979]. Therefore, the number of the lines in ICL and OCL is not a reliable indicator of age, unless already tested on the same taxon [de Ricqlès *et al.* 2003; Drozdowska & Meissner 2014; Klevezal & Smirina 2016]. Sometimes annual layers in the bones can be discerned with the help of stable isotope studies [Woodward *et al.* 2013; Klevezal & Smirina 2016] and it is a promising direction for further research.

There is evidence that at least layers in ICL of the femur of *L. tethyensis* (Av-26) do not reflect annual cycles. There are no less than 30 (and possibly more) rows of lacunae in some places, and fine lamellations seen under a polarising microscope (counted as pairs of bright and dark lines) are even more numerous. If the bird really was ≥ 30 years old, it would have developed OCL (and probably more extensive secondary remodelling). Whether the other found types of layering (layers with different directions of bone fibres in ICL of Av-42 or LAGs in the 'bulge' outwards of OCL in Av-11) reflect annual cycles, remains unknown. If they do, these individuals of cf. *Dasornis* sp. and *L. tethyensis* are at least ~10 and at least ~5 years old, respectively.

Prominent growth marks in the primary tissue of Av-8 and in osteons of Av-11 reveal the course of bone apposition, but do not seem to carry usable skeletochronological information.

In regard to growth marks, it should be noted that the Eocene climate of modern eastern Ukraine had well-defined seasonality, as shown by annual rings in fossil wood recovered from Ikove. The fauna and flora of the locality suggest subtropical climate with an alternation of dry and wet seasons [Dernov & Udovichenko 2020]. It excludes the possibility that the bones did not form growth marks due to constant environmental conditions.

Bone apposition rate

In the absence of reliable growth marks, only rough estimates of the bone apposition rate are possible [Erickson 2005; D'Emic *et al.* 2013], but nevertheless they can reduce uncertainty on this issue [De Ricqlès *et al.* 2003; Curry Rogers & Erickson 2005; de Buffrénil *et al.* 2021].

The apposition rate in long bones has been studied in many bird species from all three major clades: Palaeognathae (*Dromaius novaehollandiae* [Castanet *et al.* 2000; Cubo *et al.* 2012; Kuehn *et al.* 2019], *Struthio camelus* [Castanet *et al.* 2000; Cubo *et al.* 2012]), Galloanseres (*Anas platyrhynchos* [de Margerie *et al.* 2002; Montes *et al.* 2007; Montes *et al.* 2010; Cubo *et al.* 2012], *Gallus gallus* [Montes *et al.* 2007; Montes *et al.* 2010], *Coturnix japonica* [Starck & Chinsamy 2002]), and Neoaves (*Streptopelia decaocto*, *Turdus merula* [Cubo *et al.* 2012], *Aptenodytes patagonicus* [de Margerie *et al.* 2004]). According to all these studies, the woven-parallel complex, which forms the bulk of the primary bone tissue in the majority of recent birds (as well as in Odontopterygiformes), is usually deposited with a rate of several dozen μm/day, but in some bones of some species this rate can exceed 100 μm/day (in the case of large birds, such as *S. camelus*, *D. novaehollandiae*, and *A. patagonicus*, but also in *S. decaocto*, *T. merula* and, very rarely, in *A. platyrhynchos*). The highest values were reported for the femur of *A. patagonicus* (171 μm/day, a climate adaptation [de Margerie *et al.* 2004]) and the humerus of *T. merula* (195±63 μm/day, possibly related to altriciality [Cubo *et al.* 2012]). However, even in species that occasionally show an apposition rate of >100 μm/day in some bones, the majority of long bones, in most cases, grow 2–3 times slower [de Buffrénil *et al.* 2021]. The rates <10 μm/day are also rare and mostly restricted to small bones (e.g. phalanges) and wing bones if they are not used for locomotion.

Subtypes of the woven-parallel tissue, differentiated by vascular orientation, have largely overlapping ranges of apposition rates and, accordingly, are not important for skeletochronology. The exception may be the tissue with radial canals, which is associated with the fastest apposition [de Margerie *et al.* 2004; Werning 2013; de Buffrénil *et al.* 2021], but it was not observed in substantial amounts in the Odontopterygiformes bones considered herein.

De Margerie *et al.* [2002] found a relatively close and roughly linear relationship between bone apposition rate and the diameter of primary osteons in the mallard (*Anas platyrhynchos*). If these parameters were similarly related in Odontopterygiformes, the bone apposition rate could be estimated at 20–60 μm/day for the femur of *L. tethyensis* Av-26 (see Table 2). The other examined bones have much larger primary osteons (falling outside the range of diameters observed by de Margerie *et al.* [2002], suggesting uncertain, but probably much higher apposition rate. This is consistent with the larger size of these bones. But it must be stressed that such inferences currently cannot be regarded as more or less reliable estimates: the relationship of the primary osteons diameter and bone apposition rate remains insufficiently studied to draw conclusions on fossil taxa [Lee *et al.* 2013], although this is a promising line of research [de Buffrénil *et al.* 2021].

Noteworthy is that the primary tissue of Av-26 is nearly identical in fibre pattern to the tissue of mallard with the apposition rate of 2–30 (in half of the cases, about 7–14) μm/day [de Margerie *et al.* 2002: Fig. 1*c*]. However, the apposition rate of the tissue with any given vascular or fibre pattern varies greatly depending on the taxon and other factors.

Cubo *et al.* [2012] in a study of 16 recent amniote species (including 5 birds) derived an equation to estimate the bone apposition rate for the femur based on the concentration of vascular canals and osteocyte lacunae, size and shape of the lacunae, and orientation of the canals. This equation explains 85% of the variance of bone apposition rate in the sample from which it was derived. The root-mean-square deviation of its predictions for this sample is 17 μm/day. Application of this equation to Av-26 (the only examined femur that preserved primary tissue) gives a rate of 91 μm/day for the inner half of the primary cortex and 55 μm/day for the outer half. These figures should not be considered even as approximate, but only as indicative. The equation itself contradicts some observations: positive correlation of the growth rate with vascular density [Klein & Sander 2008], with the proportion of radial canals [Werning 2013; de Buffrénil *et al.* 2021], and weak negative correlation with osteocyte volume [D'Emic & Benson 2013]. These contradictions are probably caused by the derivation of the equation from a small sample. Although this equation describes the sample on which it was obtained relatively well, it can be expected to perform worse on other samples. Moreover, tibiae and humeri from the same sample could not be described by well-performing equations [Cubo *et al.* 2012]. Nevertheless, such approach, if improved by a larger amount and a more precise quantification of the source data, is regarded as having considerable perspectives for palaeobiology [de Buffrénil *et al.* 2021].

In the femur of recent birds, the woven-parallel tissue is deposited with a rate of ~20–100 μm/day in most cases, sometimes over 100 μm/day, especially in species with large body size. For the tibiotarsus and humerus (excluding birds not using wings for locomotion), this rate has the same order of magnitude, although can be up to 2–3 times higher or lower than in the femur [de Margerie *et al.* 2002; Starck & Chinsamy 2002; de Ricqlès *et al.* 2003; Cubo *et al.* 2012; de Buffrénil *et al.* 2021; and others].

If the apposition rate in Av-26 constituted several dozen μm/day, the bone should have grown to its present radius (4 mm) in ~10^2 days, probably less than a year. Growth during one year would require an apposition rate of $\lesssim$ 11 μm/day, which is unusually low for bird femora (although close to the apposition rate of a histologically similar tissue in the tibiotarsus of the mallard [de Margerie *et al.* 2002]). The other examined bones show even less clues to their apposition rate, apart from being composed of woven-parallel tissue. However, apposition rates of different skeletal elements of the same species must be related by a certain ratio to produce certain proportions of the adult skeleton. Therefore, the humeri had to grow several times faster than the femora (under the assumption of simultaneous maturation, as in most birds [Yan & Zhang 2020]). In any case, even the largest of the studied bones, the humerus Av-42 (with a radius of ~15 mm), growing with a rate of several dozen μm/day, did not necessarily requires >1 year to reach the adult radius.

It should be noted that all the described bones of Odontopterygiformes are fully or almost fully grown and, due to resorption, can contain information only about the last stages of growth, when it is usually somewhat slower. In addition, the bone apposition begins not from zero radius, but from the radius of the embryonic bone. All this can cause overestimation of the growth duration. However, this inaccuracy is non-essential in comparison with the aforementioned uncertainties.

Some inferences regarding growth of Odontopterygiformes were made by Louchart *et al.* [2013, 2018] based on X-ray microtomography and thin sections of the pseudoteeth of *Pelagornis mauretanicus* (late Pliocene/early Pleistocene species with a wingspan of 4–5, possibly 6 metres). They concluded that the pseudoteeth probably began to grow only after the termination of jaw bone growth. The speed of the pseudoteeth growth was estimated to be moderate: primary bone tissue preserved near their tips is intermediate between parallel-fibered and woven-fibered tissues and, based on the measurements in *Anas platyrhynchos* by de Margerie *et al.* [2002], could grow with a rate of 10–30 μm/day, at least in the end of pseudoteeth development [Louchart *et al.* 2013]. In addition, if the pseudoteeth grew on their tips, the rhamphotheca that covered them could harden only after the termination of their growth, making the development of the bird quite long. However, Louchart *et al.* [2018] noted that structures similar to pseudoteeth can also develop in another (and faster) way, as evidenced by the spurs of recent birds, which are initially separated from the leg bone and develop hard keratinous sheaths even before bony cores. The growth history of pseudoteeth, like other avian bones, is obscured by extensive resorption and Haversian remodelling, reported by Louchart *et al.* [2013]. The issue might be clarified by X-ray microtomography of the pseudoteeth of juvenile birds.

The estimation of the development duration of *Pelagornis mauretanicus* based on comparison with recent albatrosses also gives a very long time span. If this species had the same ratio of fledging time and body size as the largest albatross *Diomedea exulans*, it could have fledged about 18 months after hatching [Louchart *et al.* 2018]. This implies high altriciality, which is not known in basal Neornithes [Louchart *et al.* 2013; Louchart *et al.* 2018], although prevails among seabirds [Masden *et al.* 2010].

Long growth time is expected even in smaller insular seabirds due to their protection from predators (which weakens the selection for fast development) and the possibility of long periods without food. This is strongly expressed in recent albatrosses. In addition, the rate of their development can be limited by bone growth rate: for instance, *Diomedea epomophora* with a 42 cm long humerus has an extremely long fledging period of 236 days [Carrier & Auriemma 1992]. Longer development time is a known tendency in insular birds in general. In addition to predation pressure, nutrition, and adult body size, growth rates of birds can be related to clutch size and several other factors [Sandvig *et al.* 2019; Sandvig *et al.* 2022].

Particular ontogenetic events

Heavy Haversian remodelling and large erosion cavities of Av-18 and Av-34 (femora of *L. tethyensis* and cf. *Dasornis* sp. respectively; Fig. 2) imply extensive resorption with subsequent reconstruction. The same, but to a lesser extent, applies to Av-11 (humerus of *L. tethyensis*; Fig. 1*b*). At least in Av-11 and Av-34, the resorption continued after the onset of skeletal maturity. At least in Av-34, it occurred in more than one episode.

Extensive and repeated bone resorption in birds can be caused by egg-laying. It is known to damage not only medullary, but also structural bone (at least in domestic hen), inducing dilation of the Haversian canals, development of larger resorption cavities, and destruction of cancellous bone [Wilson & Thorp 1998; Whitehead 2004; Alfonso-Carrillo *et al.* 2021; Benavides-Reyes *et al.* 2021; Yamada *et al.* 2021], especially under calcium or general food shortage [Newman & Leeson 1999; Zhao *et al.* 2020]. In mammals, erosion cavities are most commonly found in pregnant females [Chinsamy 1990]. So, reproduction has been employed for explanation of erosion cavities and other manifestations of extensive resorption in bird bones [de Ricqlès *et al.* 2016].

Another possible explanation is moulting, despite the near-absence of calcium in feathers. In many recent bird species, moulting induces temporary widening of vascular canals, sometimes to such extent that compact bone looks like cancellous one [Meister 1951]. Therefore, moulting has also been employed for the explanation of the cavities [Dabee 2013; Angst *et al.* 2017], porosity [Cerda *et al.* 2014], and Haversian remodelling [Chinsamy *et al.* 2020b; Monfroy & Kundrát 2021] in fossil and recent bird bones.

On the other hand, both erosion cavities and Haversian remodelling are present not only in birds and, consequently, can have other causes than egg-laying and moulting. In mammals, the cavities are observed not only in pregnant females, but also in other individuals [Chinsamy 1990].

Whatever causes these cavities, they accumulate with age in both birds [Sukhanova 2021] and mammals [Chinsamy 1990]. The extent of Haversian remodelling also increases with individual age. In addition, it strongly varies between taxa [Chinsamy *et al.* 1998; Louchart *et al.* 2013; Padian *et al.* 2016].

Av-26 (femur of cf. *L. tethyensis*, Fig. 1*d*) is remarkable for the absence of resorption cavities and much less extensive Haversian remodelling compared to Av-18 (the same skeletal element of probably the same species, Fig. 2*a*). It is obviously a consequence of lower individual age, as evidenced by the absence of developed OCL.

Nevertheless, ICL of Av-26 has undergone several episodes of resorption followed by apposition. Thus, resorption in the medullary cavity several times resumed after it had generally ceased and was replaced by ICL apposition. Traces of one such event are also seen in Av-34. This phenomenon is known in birds [Drozdowska & Meissner 2014; de Ricqlès *et al.* 2016] and mammals [Tomassini *et al.* 2021], but its causes remain unclear. It has been hypothesised to reflect extraction of calcium for the needs of migration or reproduction, remodelling caused by increased loading or growth under conditions of malnutrition [Drozdowska & Meissner 2014]. In the case of Av-26, reproduction and migration are unlikely because of the absence or near-absence of OCL, which suggests that the bird died at the stage of pre-fledgling or, possibly, fledgling [Atterholt & Woodward 2021] and did not finish growth, while birds typically begin reproduction well after the end of growth [Erickson *et al.* 2007; Zheng *et al.* 2013].

Regarding reproduction, it should be noted that no medullary tissue (which could testify to egg-laying) was observed in the described bones.

The 'bulge' observed outwards of OCL of Av-11 (humerus of *L. tethyensis*; Fig. 1*b*) resembles a number of pathologies. Comparable formations in humans are known to be caused by various diseases. Most of them, unlike this 'bulge', consist of porous bone tissue with poorly ordered fibres, but, for instance, chronic treponemal diseases can cause slow-growing deposits of parallel lamellae [Schultz 2001]. Comparable outgrowths, but very porous again, were observed on bones of adult turkeys [Lanyon & Rubin 1984] and roosters [Rubin & Lanyon 1984] after cutting off the epiphyses and especially after application of a cyclic artificial loading. In addition, similar structures (but, apparently, with a rather chaotic vascular pattern) were described by Canoville *et al.* [2022] in cassowary, emu, and ostrich, and interpreted as likely pathologies. However, the 'bulge' in Av-11 can probably be explained without involving pathologies. Av-8 (the same skeletal element of presumably the same species) also shows unusual structure of the outer cortex: an ill-defined OCL, intermingled somewhere with the woven-parallel complex (Fig. 1*c*). Therefore, the lack of typical avian cortex structure may be normal for the humeri of *L. tethyensis*. Alternation of the OCL layers with underlying bone tissue is also locally seen in the femur of cf. *Dasornis* (Av-34, Fig. 2*b*). This suggests an unusually gradual, as for birds, termination of bone apposition, locally alternating with its minor resumption. A similar structure was described in the tibiotarsus of *Genyornis newtoni* (Gastornithiformes) and interpreted as a result of alternation of more and less favourable environmental conditions [Chinsamy & Worthy 2021]. The absence of a sharp border between OCL and the woven-parallel complex is reported for some recent birds, especially large ones: *Aquila*, *Buteo*, *Corvus*, and *Gyps* [Ponton *et al.* 2004]. In the kangaroo

Macropus fuliginosus, alternating layers of the woven-parallel and parallel-fibered tissue form annually [Chinsamy & Warburton 2020].

Thus, all the described bones come from skeletally mature individuals, except for Av-26 and Av-19, which were approaching skeletal maturity (more and less closely, respectively). Av-26 shows unexpected in such a young bird resorption, caused by unknown factors (possibly malnutrition). Av-18 and Av-34, on the contrary, were relatively old individuals, which have probably undergone a number of moulting and, possibly, egg-laying cycles. Av-34 died during or shortly after an episode of bone resorption. Av-8 and Av-11 (humeri of *L. tethyensis*) suggest unusually slow and intermittent, as for birds, termination of bone apposition.

Ecological implications

The trophic niche of pelagornithids is currently known only in general terms. It is hypothesised that they captured their prey near the water surface [Mayr 2009]. Their prey was likely fish or squid [Mayr 2017]. This grouping is very broad. It includes both main groups of animals inhabiting surface layers of the seas and having considerable, although not too large, body size. But feeding on fish and on squid needs different predation strategies. In some regions, squid constitutes >50% of diet of seabirds, but it is observed mostly in small parts of the oceans: waters of Hawaii and California. In the north-east of the North Atlantic, squid constitutes approximately 1% (by mass) of the diet of seabirds, while in the south-east of the North Atlantic it constitutes 16%. Why seabirds prefer feeding on fish is not completely clear [Furness 1994].

Pelagornithids were a highly specialised group [Mayr 2017]. This specialisation likely manifested itself also in feeding. Since many recent birds prefer either fish or squid, pelagornithids probably also preferred a particular type of prey.

Research into the diet of fossil birds should employ various methods, each of which can exclude some types of diet, narrowing the dietary possibilities [Miller & Pittman 2021]. This study presents results of osteohistological examination and, similarly to other methods, it does not give an exact answer though provides arguments in favour of one of the hypotheses.

The non-ossified mandibular symphysis and the presence of intraramal hinge in Odontopterygiformes imply their ability to swallow large prey. At the same time, these features weaken the jaws, diminishing grasping strength, which was probably compensated by the pseudoteeth [Louchart *et al.* 2013]. It is also notable that the jaw of *L. tethyensis* is hollow and thin-walled (Fig. 5), which further weakened it. The pseudoteeth are hollow as well [Howard 1957; Howard & White 1962; Louchart *et al.* 2013].

A remarkable feature of the pseudoteeth is alternation of shorter and longer ones (Fig. 5). It can be another compensation of the weak bite: the prey initially came in contact only with the longest 'teeth', so the bite force was distributed on a small number of 'teeth' creating a high pressure on their tips. Larger animals with stronger jaws do not need such adaptation. However, a possible relationship between teeth morphology and diet should also be taken into account. Olson [1985] suggested that uneven 'teeth' imply soft-bodied prey (probably squid), otherwise the short 'teeth' would not work at all. This was supported by Mayr *et al.* [2019], who also noted the probable fragility of these long 'teeth' and hypothesised that the large body size of Odontopterygiformes, which enabled good soaring efficiency [Ksepka 2014], could be caused by the need of search for shoals of these molluscs. On the other hand, recent mammals that specialise in feeding on squid (e.g. sperm whales) have not very sharp teeth, unlike piscivorous mammals (dolphins) and reptiles (gharials), which have mostly non-differentiated, elongated teeth with acute tips. This can imply that squid eaters tend to kill their prey by squashing between the jaws instead of piercing by the teeth. However, animals with sharp cutting teeth can eat squid as well [Massare 1987].

Another unusual feature of the pseudoteeth of some Odontopterygiformes is their inclination forward (Fig. 5). It also can be an adaptation for handling soft food items (using the dentition as a fork), as proposed by Westerberg [1990] for leptocephali, although this is disputed [Tsukamoto & Miller

Fig. 5. Lower jaw of *Lutetodontopteryx tethyensis* from Ikove (NMNHU-p Av-12).

Рис. 5. Нижня щелепа *Lutetodontopteryx tethyensis* з Ікового (NMNHU-p Av-12).

2021]. Forward-inclined teeth are also observed in some pterosaurs (e.g. *Rhamphorhynchus*) that are known to consume both fish and cephalopods [Hoffmann *et al.* 2020]. Some authors argue that Odontopterygiformes and *Rhamphorhynchus* captured their prey by skimming similarly to recent *Rynchops* (Laridae) using the teeth as prey trap [Mayr 2011; Mayr *et al.* 2019; Kloess *et al.* 2020], but for pterosaurs skimming was shown to be unlikely [Humphries *et al.* 2007]. Other authors supposed aerial surface capture of prey for both Odontopterygiformes and pterosaurs [Milner & Walsh 2009].

Fledging time of large pelagornithids was previously estimated at about 18 months [Louchart *et al.* 2018]. It could be an argument against their specialisation on feeding on squids. The abundance of most squids varies during the year [Luckhurst 2018], and specialisation in such food is risky for long-growing birds. According to our results, the development of pelagornithids was not too long (less than one year), so the hypothesis about their specialisation on squid consumption is not improbable.

The unusual resorption in ICL of Av-26 and Av-34, which could be caused by shortage of calcium, is in line with the idea of feeding on squids. They contain less calcium than the majority of marine animals (fishes, crustaceans, gastropods, bivalves, other cephalopods such as octopuses) [Özden & Erkan 2011]. Our results support the hypothesis about pelagornithids being specialised feeders on squids.

Conclusions

Bone histology suggests that the studied species of Odontopterygiformes were similar in growth rate and metabolic rate to extant Neognathae. Bone growth duration of *L. tethyensis* is estimated at 10^2 days. The layering of its ICL do not reflect years, making age determination using this feature impossible for this species. The results show that feeding on squids was possible for large pelagornithids. Refinement of the data on their trophic niche requires further studies using additional methods.

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