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Birds in the Pavlovian culture: Dolni Vestonice II, Pavlov I and Pavlov II

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ABSTRACT

New research affords new data on bird usage in the Pavlovian culture. This is the first article to report on bird remains excavated at Dolní Věstonice II and Pavlov II, and to discuss a small group of bones from Pavlov I. Although the two sites share a number of striking similarities, including the high frequency of Raven (*Corvus corax*), there are also some differences, e.g., in the ratio of the bird taxa. The former may be common for the whole Pavlovian culture; the latter may depend from specific usages of the sites by the Gravettian people.

1. Introduction

The Mid Upper Palaeolithic toolmaking culture known as the Pavlovian, interpreted as a local unit of the Early Gravettian, is documented in Moravia around 29–25 ka BP (Klíma, 1959; Svoboda, 2007; Verpoorte, 2009). The process which led to the emergence of this culture unit in Europe remains unclear and controversial (Conard, 2000; Svoboda, 2007; Kozłowski, 2013). Pavlovian settlement is documented by the presence of open-air camps, occupied over a longer period. Some, including Dolní Věstonice I and II and Předmostí I, include great deposits of mammoth bone (Klíma, 1963; Absolon and Klíma, 1977; Svoboda, 1991). Lithic inventories of this culture unit are characterised by long-distance transport of the lithic raw materials and the presence of backed forms. Furthermore, the lithic inventories are accompanied by rich and varied assemblages of organic material: bone, antler and ivory (Svoboda, 2007). Pavlovian sites include very rich and diverse faunal assemblages, mostly dominated by reindeer, wolf, mammoth, fox (two species), and hare (Musil, 2003). Predators are important components: wolf, fox, wolverine, bear, and lion which, in the best studied assemblage from Pavlov I make up approximately half of the faunal assemblage (Wojtal et al., 2012).

Bird remains are known from a few Pavlovian culture sites, i.e., Pavlov I, Dolní Věstonice I, Milovice IV, Předmostí (Skutil and Stehlik, 1939; Tyrberg, 1998; Musil, 2005a; Svoboda et al., 2011). As a rule they are mentioned in more general zooarchaeological articles in lists of species and are not analysed extensively either zoologically or taphonomically. A different situation is observed at Pavlov I. Most of the material from this site was analysed and thoroughly discussed by Bochenski et al. (2009), but a small part of this faunal assemblage was later found to have been left out of this study. The present work analyses this missing part.

Finally, some Pavlovian sites have known faunal assemblages but with no publication of bird bones. This was the case for Pavlov II and Dolní Věstonice II (Klíma, 1976; West, 2001). The bird remains from these two sites are also a subject of our study.

2. Material and methods

The present paper discusses bird bone assemblages excavated by B. Klíma and J. Svoboda at Dolní Věstonice II, Pavlov I and Pavlov II in the period 1952–1986 (Svoboda, 1991; Klíma, 1976, 1995, 2005). Different recovery procedures were used at these three sites: at Pavlov I, almost all cultural layers were wet-sieved, whereas at Dolní Věstonice II sediments were wet-sieved only partially (i.e., selected parts), and in the case of Pavlov II animal remains were collected only during a standard exploration (without sieving). The full faunal assemblage from this fieldwork was analysed and is now stored at Budišov Castle and at Dolní Věstonice. Bones were identified with the help of an osteological bird collection of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, using available identification keys (Bacher, 1967; Kraft, 1972; Tomek and Bocheński, 2000). Every bone was examined under direct light for possible surface modification such as traces of abrasion, weathering, and for damage made by birds of prey (beak and/or claw marks) or humans (cut-marks, burning, trampling, polishing). The observed modifications were recorded and the more exceptional were photographed.

The results of our analyses are presented in terms of NISP and MNI for the three sites. For Dolní Věstonice II, the MNE measure

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was used. To calculate NISP and MNI we used a standard procedure, but unfortunately no such procedure is available where MNE is concerned (Lyman, 1994). In the present study, we used a combined method to obtain an MNE value for every element. This was done by comparing two values: (1) the value obtained from the sum of fragments of an individual bone from two sides of the body; and (2) the value derived from a number of complete bones, combined with the more numerous terminals (proximal or distal) from both sides as well. Finally, (3) we selected the higher value of the two.

3. Results

3.1. Dolní Věstonice II

As well as 24,353 remains of mammals (7285 identified more closely) this assemblage included 165 avian bones (Table 1). They make up 1.9% of an assemblage which was identified taxonomically more closely than as to the class. The bird bones were poorly preserved, and their surfaces were heavily damaged, probably by root etching and humic acids (Fig. 1).

Table 1
Bird species from Dolní Věstonice II.

Taxon	NISP		MNI
	N	%	N
Lagopus lagopus	8	4.8	2
Lagopus sp. (*L. lagopus*/*L. muta*)	7	4.2	1
Tetraonidae indet. (*Tetrao tetrix*/*Lagopus* sp.)	1	0.6	–
Corvus corax	128	77.6	9
Aves indet.	21	12.7	–
Total	165	100	12

Fig. 1. Selected bones from Dolní Věstonice II with typically damaged surfaces. A, B – Raven ulna shaft; C – Raven carpometacarpus; D – Willow Ptarmigan/Grouse (*Lagopus lagopus*) or Rock Ptarmigan (*Lagopus muta*) humerus distal part; E – humerus shaft of an unidentified bird species. Photo P. Wojtal.

The remains of Raven (*Corvus corax*) are evidently the most abundant (77.6% of the total NISP). They belong to at least 9 individuals. The bones of the Willow Ptarmigan/Grouse (*Lagopus lagopus*) and other only generally identified Tetraonids were found in much lower quantities (cumulatively 16 NISP and 3 MNI). Almost 13% of the material could not be identified closer than to the class Aves. However, every bone came either from a Raven/Tetraonid sized bird or from a specimen of undetermined size.

The raven skeleton is represented mainly by the long bones of limbs (108 NISP, 67 MNE), and, to a lesser extent, by bones of the pectoral girdle (14 NISP, 11 MNE) and tail vertebrae (5 units) (Table 2). Among the long bones, the ulna is the most numerous (both NISP and MNE over 20%). Less common are leg bones (femur, tibiotarsus, tarsometatarsus) and carpometacarpus (each at nearly 10%). There was only a single humerus and no fragments of sternum, pelvis, mandible, or cranium.

Table 2
Skeletal fragments from Dolní Věstonice II.

Element	Raven		Tetraonids		Aves indet.	
	NISP	MNE	NISP	MNE	NISP	MNE
Quadratum	1	1	–	–	–	–
Coracoid	9	6	2	1	–	–
Scapula	4	4	–	–	–	–
Furcula	1	1	–	–	–	–
Humerus	1	1	1	1	2	1
Ulna	31	17	3	2	–	–
Radius	10	5	–	–	–	–
Carpometacarpus	13	8	2	2	–	–
Wing phalanx	1	1	–	–	–	–
Pelvis	–	–	1	1	–	–
Caudal vertebrae	5	5	–	–	–	–
Femur	16	11	1	1	–	–
Tibiotarsus	15	8	4	4	1	1
Fibula	1	1	–	–	–	–
Tarsometatarsus	16	11	2	1	–	–
Pedal phalanx	4	4	–	–	–	–
Element indet.	–	–	–	–	18	–
Total	128	84	16	13	21	2

Tetraonids are represented by 16 elements only, from different parts of the body. They are too few to be of any use in subsequent quantitative analyses. A considerable number of fragments displaying distinctive bird features were also identified, although more specific identification was not possible.

Bones of the raven are considerably fragmented (Table 3). Approximately 5% are complete. Most of the fragments, more than 60%, do not retain any of the articular facets. In the case of the most abundant bone, the ulna, this value is close to 90%.

Table 3
The fragmentation of the long bones of Raven from the Dolní Věstonice II assemblage. The values are presented as percentages (100% = N).

Element	N	Whole bone (%)	Proximal part (%)	Distal part (%)	Shaft (%)
Coracoid	9	11.1	11.1	–	77.8
Scapula	4	–	100	–	–
Humerus	1	–	–	–	100
Ulna	31	–	3.2	9.7	87.1
Radius	10	–	30.0	10.0	60.0
Carpometacarpus	13	15.4	23.1	7.7	53.8
Femur	16	6.3	43.8	12.5	37.5
Tibiotarsus	15	–	6.7	20.0	73.3
Tarsometatarsus	16	12.5	12.5	25.0	50.0
Total	115	5.2	19.1	12.2	63.5

One Raven ulna is with evident traces of human activity (Fig. 2). Its surface appears to have been smoothed, and edges polished.

3.2. Pavlov I

This is a group of 50 bones of 6 taxa (Table 4) omitted from the analysis of Bochenski et al. (2009). More than half are from raven (*Corvus corax*). There were also a few bones of swans and birds of prey, as well as either Willow Ptarmigan/Grouse (*L. lagopus*) or Rock Ptarmigan (*Lagopus muta*). This list of taxa from the site is

Fig. 2. Fragment of Raven ulna with polished edge (indicated by an arrow) and smoothed surface. Photo P. Wojtal.

completed by Snowy Owl (*Nyctea scandiaca*). The material increases the MNI of the birds of prey and swans at the site.

Table 4
Birds from Pavlov I not included by Bochenski et al. (2009).

Taxon	NISP	Increased MNI	Bone (quantity, if > 1)
Cygnus cygnus/ *Cygnus olor*	3	1	Femur, Tibiotarsus, Phalanx digiti pedis
Cygnus sp.	3	–	Tarsometatarsus (3)
Nyctea scandiaca	1	1	Phalanx digiti pedis
Gyps sp./*Aepygius* sp./*Gypaetus* sp.	2	1	Ulna, Phalanx digiti pedis
Accipiter sp./*Buteo* sp.	1	1	Humerus
Lagopus sp.	4	–	Coracoid, Carpometacarpus, Tibiotarsus, Tarsometatarsus
Corvus corax	29	–	Coracoid (2), Scapula, Humerus (3), Radius (2), Carpometacarpus (5), Phalanx digiti manus, Femur (2), Tarsometatarsus, Phalanx digiti pedis (7)
Aves indet.	7	–	Vertebra (3), Phalanx digiti pedis (4)
Total	50	4	

As the assemblage examined here accounts for less than 5% of the whole bird assemblage and the preliminary analyses did not show it to be substantially different from the material described before, we concluded there is no point in re-analysing the whole assemblage. We believe the analyses made by Bochenski et al. (2009) to be still valid, and consequently the present study should be regarded only as a supplement, rather than a revision. The combined material is presented in the Appendix. Collectively, the assemblage from Pavlov I includes 1095 bones of birds from 20 taxa (Appendix), compared to 83,362 bones of mammals, of which 51,735 have been identified. The bird bones from Pavlov I make up 2.0% of the remains assignable to a closer taxonomical rank (i.e., more specific than class).

3.3. *Pavlov II*

As well as 968 mammal remains (484 identified more closely), the assemblage from this site includes two bones of birds. Both fragments (scapular part of coracoid and a radius proximal) belong to raven (*Corvus corax*). The bird bones constitute 0.4% of material from Pavlov II which could be identified taxonomically in detail (i.e., more precisely than to class).

4. Discussion

The different recovery procedures used at the investigated sites could have had an impact on the faunal compositions. However, the number of bird bones compared to that of mammal bones is exceedingly small everywhere, making up a mere 2% of the more closely identified material. This supports the notion that for Gravettian people birds played very minor roles as food, while mammals were of paramount importance (Absolon, 1938; Musil, 1997, 2005a). Nevertheless, this ratio need not reflect the actual deposition, especially because bird bone is more fragile and more likely to be damaged.

In the case of Pavlov I, the supplementary material examined by us here does not alter the general conclusions reached by Bochenski et al. (2009). The Corvids and Tetraonids evidently prevail. The handful of bones belonging to large birds of prey and to swans support the notion that Palaeolithic people preferred catching larger birds to smaller ones (Laroulandie, 2003; Guminski, 2005; Bochenski et al., 2009).

The one additional taxon from Pavlov I (Snowy Owl) was reported by Tyrberg (1998), but the presence of this taxon at the site was dubious. Tyrberg cited the work of Skutil and Stehlik (1939) who referred to the site as “Pavlovské kopce” (“Pavlovian hills”). Because at this time Pavlov I was unknown, this information may actually refer to Dolní Věstonice I, excavated starting from 1924 (Absolon, 1945). However, the confirmed presence of the Snowy Owl is not surprising. This bird was fairly common in the Moravian Pleistocene, as noted by Skutil and Stehlik (1939).

There is another taxon, the Pintail (*Anas acuta*), listed at Pavlov I by Musil (1997, 2005a). However, in the examined material no bone unequivocally belonging to this species was found. As it is unclear whether the bone of this species subsequently went missing or was identified incorrectly, we decided to regard this taxon as not present at Pavlov I, and therefore we did not include it in our final list (Appendix).

Similarly as at Pavlov I (Bochenski et al., 2009), the number of taxa recorded at Dolní Věstonice II does not reflect the natural biodiversity of the area. This suggests that a special factor, most likely, predator presence, was responsible for the accumulation of bone. Acknowledging the archaeological character of the open-air site, we believe that this factor was the presence of humans. This is supported by the presence of numerous flint artifacts, several hearths, and storage pits interpreted as an agglomeration of activity areas. Further lithic finds are accompanied by numerous remains of Pleistocene fauna bearing traces of human activity (West, 2001; Wojtal et al., 2012).

As a unique characteristic of Pavlov I, Bochenski et al. (2009) cited the frequency of bones of raven. At Dolní Věstonice II the percentage is even higher, whereas the values obtained for Pavlov II may be misleading given its limited, and as such, probably unrepresentative, material. As there are no other Upper Palaeolithic open-air sites with a comparable number of raven remains (Stewart, 2007) it is possible that the observed interest in raven may have been specific for the Pavlovian culture. At other Central European Upper Palaeolithic open-air sites, bird remains are very poorly represented and are recorded only in a limited number of sites as solitary finds or, at best, a handful of specimens (Bratlund, 2002; Fladerer and Salcher, 2004; Musil, 2005b; Vlačiky, 2009). At these sites, no remains of raven were discovered.

The ubiquitous presence of raven in the Moravian Stone Age was noted by Musil (1955). Čapek (1911) and Skutil and Stehlik (1939) mentioned the presence of raven in Předmostí, although they did not provide a detailed quantitative analysis. Admittedly, at one Gravettian site in Moravia, Milovice IV, raven was not present (Svoboda et al., 2011). Nevertheless, given the rescue nature of the fieldwork carried out at this site and the limited quantity of excavated bones, the material from Milovice IV may be regarded as unrepresentative.

The methods of catching ravens, and the motivation for this activity remain uncertain. V. Čapek suggested that Paleolithic people may have caught Ravens while scavenging mammoth bones (cited by Skutil, 1946, p. 50). Bochenski et al. (2009) proposed that Ravens could have been snared with nets and their flight feathers were used for fletching arrows. Musil (2005a) made a few suggestions concerning the animals documented at Pavlov I, some of which may be applied to Ravens as well, i.e.,: i) some animals may have been hunted as pests, ii) some animals were snared with nets, iii) animal skulls could have been used for ritual purposes. Unfortunately, all these hypotheses are highly speculative. We are inclined to think that the limited number of more fragile elements, such as skulls, is more likely to be the result of taphonomical factors than of cultural ones (see Wojtal et al., 2012). However, since Gravettian people not only ate animals but also used their body parts for raw materials (Musil, 1997), there may have been more than one reason for catching ravens. Various ways of using birds are mentioned by Serjeantson (2009), including ritual, aesthetic, pecuniary, ludic, and, obviously, culinary. All of them may have had their places in the Gravettian, but with the data now at hand it is hard to find a solid basis for any of them.

We expected Tetraonids to be present in the assemblages. This group, traditionally hunted by humans, is well represented at numerous Pleistocene sites (Serjeantson, 2009). What is more perplexing is the presence in the assemblage from Dolní Věstonice II of a small percentage of bone of Willow Ptarmigan/Grouse, especially as compared to the nearby site of Pavlov I where the percentage of this species is substantially higher. This difference is not easy to interpret. Nevertheless, the different percentages may be tentatively assumed to result from dissimilar uses of these two sites. Although both represent typical multi-seasonal Pavlovian mega-sites, burials were discovered only at Dolní Věstonice II, in contrast to Pavlov I, a site with only a very small number of human remains (Klíma, 1987; Trinkaus et al., 2010).

The bird bones from Dolní Věstonice II originate from almost all parts of the body. The absence of a few elements, such as the skull, sternum or pelvis, may be explained by their fragility and, consequently, perishability in the ground. Therefore, it is reasonable to assume that whole birds were brought to the site. This is one more similarity with the assemblage from Pavlov I.

The poor preservation of the bone may be the main cause of the underrepresentation of humeri and the overrepresentation of ulnae at Dolní Věstonice II. In the ulnae of raven, unlike in the humeri, the shaft is robust, and thus, less likely to perish. Moreover, even when heavily damaged the ulnae could be still suitable for identification. However, it is still tempting to claim that this overrepresentation of ulnae was due to a special interest of Gravettian people in the flight feathers of the raven or in the ulnae themselves, as raw material.

We cannot offer a satisfactory explanation for the high degree of bone fragmentation and overrepresentation of shafts. Although these could be due to the eating habits of the people (Steadman et al., 2002; Laroulandie, 2005) we do not think this is the case for Dolní Věstonice II. Here, the most frequent bone (raven ulna), mostly represented by shafts, comes from the wing, not a particularly meaty part of the body.

The decay of the assemblage from Dolní Věstonice II is a likely reason for the discovery of only a single obvious direct trace of human modification. This very small number of similar traces (e.g., burning or cut marks) is extremely unfortunate, as they could be very helpful in establishing the ways the bones were treated (Wojtal, 2007; Serjeantson, 2009), and, consequently, the reasons why they were treated at all.

The number of bird bones excavated at Pavlov II is too small to permit any more definitive conclusions. Nevertheless the presence of raven at this site and the low bird-mammal ratio are remarkable.

It is possible that analyses of bird assemblages from other Pavlovian sites will help in understanding the role played by birds for the people of the Gravettian in Moravia. We have already seen that birds did not rank first as a food source; nevertheless it is likely that they were used for various other purposes. What these purposes were exactly, and whether they were widespread or confined to individual sites, remains unclear. We suspect the raven had a special significance, but without more detailed data, not the least, taphonomical, secured from other Pavlovian sites, it is hard to be more specific.

5. Conclusions

1. A peculiar feature of bird assemblages from Pavlov I and Dolní Věstonice II is the dominance of two taxa: Tetraonids and Raven. The presence of nearly complete skeletons suggests that whole carcasses were brought to the site.
2. This interest in raven could be a characteristic feature of the Pavlovian people, yet their reason for catching these birds remains unclear.
3. There are a few noticeable differences between the assemblages from Pavlov I and Dolní Věstonice II. The former included bones of larger birds (i.e., swans, birds of prey) and a significant percentage of Tetraonids, traditionally,\ a game bird. In the assemblage from Dolní Věstonice II, the people were less interested in Tetraonids than in raven, and no trace of other bird species was found. These differences could be the result of differences in the way these two sites were used.
4. Similar analysis made for other Gravettian sites in Moravia may be expected to assist our study of the role of birds for the people of the Pavlovian culture.

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Appendix

List of bird taxa present at Pavlov I (Bochenski et al., 2009; this paper).

Taxon	NISP				MNI	
	2009	2014	Total		Total	
	N		N	%	N	%
Cygnus cygnus	2	–	2	0.2	1	1.2
Cygnus cygnus/Cygnus olor	5	3	8	0.7	2	2.5
Cygnus columbianus	6	–	6	0.5	2	2.5
Cygnus sp.	–	3	3	0.3	–	–
Anas querquedula	1	–	1	0.1	1	1.2
Asio flammeus	1	–	1	0.1	1	1.2
Nyctea scandiaca	–	1	1	0.1	1	1.2
Haliaetus albicilla	2	–	2	0.2	1	1.2
Gyps fulvus	2	–	2	0.2	1	1.2
Gyps sp./*Aepygius* sp./*Gypaetus* sp.	–	2	2	0.2	1	1.2
Accipiter sp./*Buteo* sp.	–	1	1	0.1	1	1.2
Accipitridae indet.	1	–	1	0.1	–	–
Falco cf. *tinnunculus*	1	–	1	0.1	1	1.2
Falco cf. *peregrinus*	2	–	2	0.2	1	1.2
Lagopus lagopus	312	–	312	28.5	31	38.6
Lagopus muta	21	–	21	1.9	4	4.9
Lagopus sp. (*L. lagopus/L. muta*)	58	4	62	5.7	–	–
Tetrao tetrix	62	–	62	5.7	5	6.2
Tetraonidae indet. (*Tetrao tetrix/Lagopus* sp.)	56	–	56	5.1	–	–
Perdix perdix	1	–	1	0.1	1	1.2
Charadriiformes indet. (size *Larus*)	1	–	1	0.1	1	1.2
Turdus sp.	1	–	1	0.1	1	1.2
Passeriformes indet. (size *Emberiza*)	1	–	1	0.1	1	1.2
cf. *Pica pica*	1	–	1	0.1	–	–
Pica pica/Garrulus glandarius	1	–	1	0.1	1	1.2
Pyrrhocorax pyrrhocorax	7	–	7	0.6	1	1.2
Pyrrhocorax/Corvus monedula	9	–	9	0.8	1	1.2
Corvus monedula	12	–	12	1.1	2	2.5
Corvidae indet. (small size)	3	–	3	0.3	–	–
Corvus corax	445	29	474	43.3	18	22.4
Aves indet.	31	7	38	3.5	–	–
Total	1045	50	1095	100	81	100

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Bird remains from Dolni Vestonice I and Predmosti I (Pavlovian, the Czech Republic)

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ABSTRACT

Dolní Věstonice I and Předmostí I, two large and important Pavlovian sites in Moravia (Czech Republic), have yielded extraordinary assemblages of lithic artefacts as well as animal remains. In this paper, the bird remains from both these sites are analysed in terms of their species, anatomical representation and bone fragmentation. The large share of tetraonid and raven (*Corvus corax*) remains, and the over-representation of ulnas among the raven bones, are similarities shared by both sites included in the study, and by the other sites from Pavlovian times.

1. Introduction

The early phase of the Gravettian (Pavlovian) settlement is known from territories in Central Europe, especially southern Moravia. Several unique, large and multi-seasonal settlements situated at lower altitudes and along rivers are known from that period. These have provided numerous and well preserved animal remains, mammoths in particular, as well as reindeer, horses, numerous carnivores (especially wolves and foxes) and birds, which give a unique record and a possibility for the reconstruction of human behaviour and the subsistence strategies of Pavlovian hunter–gatherers (Musil, 2005, 2010; Wojtal et al., 2011, 2012; Wojtal and Wilczyński, 2013; Wilczyński et al., 2015b).

Interesting results, although they are not entirely unambiguous, have been presented from complex studies of the avifauna from Pavlov I and Dolní Věstonice II (Bochenski et al., 2009b; Wertz et al., 2015), two sites located on the slopes of the Pavlov Hills. Both assemblages are relatively rich and show essential similarities, as in the presence of the dominant taxa (ravens and tetraonids) and the frequencies of particular bones. On the other hand, they seem to differ in other aspects, such as the presence of large bird taxa, e.g., swans or vultures. However, an interpretation of the observed similarities and differences must remain more or less speculative, due to the lack of a wider frame within which such qualities can be analysed.

Bird usage by Gravettian people, including the Pavlovian area, has not yet been holistically studied, and the available data does not suggest a rapid adjustment. This is because the available data is not only scarce but is also rather patchy. In most studies, the information on birds seems to have only a supplementary character to different kinds of data, e.g., data on mammals. For example, some papers inform us of the presence of bird bones, but provide more specific data only about a chosen bird bone, while the quantities of the others remain unknown (e.g., Münzel et al., 2002; Antl and Fladerer, 2004; Antl-Weiser et al., 2010). Other papers provide information about the quantities but not identifications of the bones (e.g., Salcher-Jedrasiak, 2012), and one may also find papers where only the size of the discovered birds is indicated (e.g., Manne et al., 2012). In rarer cases, a statement has been made about the lack of birds (e.g., Wiśniewski et al., 2009; Wilczyński et al., 2015a) but more often their presence is just passed over in silence.

This state of affairs, although perhaps unsatisfactory, is understandable. Bird bones are particularly tricky to identify, and interpretations are liable to biased. The bones of many birds are so alike that, without a good comparative collection, their differentiation is not feasible (see also Serjeantson, 2009). A hurried identification may result in a bias toward either a particular bird species, or particular bone types (Livingston, 1989; Bovy, 2002).

Moreover, due to their relatively small size, bird bones are generally prone to be overlooked and not collected if sieving is not

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conducted at the archaeological site. Thus, various methods of excavation may give different fauna reports (Ericson, 1987; Livingston, 1989; Laroulandie, 2005). Furthermore, the deposition of the bones may not be homogenous, for there are many predators that feed on birds: humans, carnivores, or other birds (owls, eagles). Those predators may leave distinctive traces: either characteristic marks on the bone surfaces; or specific patterns of the bone deposits (e.g., owls tend to leave more distal bones than eagles or humans Bramwell et al., 1987). Recognition of these patterns may be troublesome, as some marks, such as the evidence of cultural modifications, are often left only in small quantities (Dirrigl, 2001). Furthermore, more than one predator species can deposit the bones, which makes the patterns unreadable. What makes the situation even worse is the fact that bird bones are generally found in not very large numbers, and as these numbers are unfriendly to statistical analysis, this increases the possibility of biased interpretations.

All of these difficulties should not obscure the fact that birds are a perpetual element of the human environment. Without knowledge about the character of the human–bird relationship within a given culture, the picture of that culture must remain incomplete. To acquire this knowledge, it is essential to study the available materials methodically, and to look for similarities and differences within them. The best course perhaps is to start with large archaeological open sites, to reduce the biases caused by small bone quantities and assemblages that were deposited by various raptor species.

This is why the analyses of the big Pavlovian assemblages may be a good starting point in understanding the human–bird relationship during the Gravettian. For now, it may be useful to check whether the observed similarities in the Pavlov I and Dolní Věstonice II sites are not coincidental, i.e., whether they can be supported by information from other sites, preferably ones in the close vicinity and ones from more distant regions. Dolní Věstonice I and Předmostí I are the sites which most closely fit these criteria (Fig. 1).

Both of these sites, arguably two of the most important Pavlovian assemblages, have provided numerous and varied anthropological, archaeological and paleontological materials. At both, assemblages of bird remains are known to be present, but these were only studied in the first half of the last century (Tyrberg, 1998), and the published results may be now regarded as too fragmentary. In the case of Dolní Věstonice I, the published paper (Skutil, 1946) encompasses only a part of the whole assemblage; whereas papers about Předmostí I provide only fragmentary data, i.e., the names of the bird taxa without the types and numbers of the collected bones (Čapek, 1911; Skutil and Stehlík, 1939). The main goals of this paper are to provide more comprehensive data on the avifauna of these two sites, and to find a common pattern of all the known Pavlovian bird assemblages.

2. Characteristics of the assemblages

At Dolní Věstonice I, archaeological and paleontological material began to be collected at the beginning of the 20th century. The first regular excavation was begun in 1923, while the most recent fieldwork was done in the 1990s (Absolon, 1938; Klíma, 1963, 2001; Svoboda et al., 2002; Oliva, 2009, 2014). During this fieldwork, different areas of the site were investigated, and numerous lithic artefacts, bone products, human remains, and objects of art including the famous 'Dark Venus' were discovered. In different parts of the site, some structures accompanied by hearths were recorded, as well as very large mammoth bone accumulations (Klíma, 1963, 2001; Oliva, 2014, pp. 61–71). Human artefacts were generally accompanied by vast assemblages of animal bones, which were collected over the entire surface area of the site. The uncalibrated radiocarbon dates for the Pavlovian occupation of this site overlap in a range between 29 and 25 ka BP (Damblon et al., 1996).

The fieldwork at Předmostí commenced at the end of the 19th century, and the largest part of the currently known archaeological and paleontological collection comes from this period. The material was obtained during regular fieldwork, as well as from clay mining in several loess deposits in a different part of the site. Excavations also continued in the 20th century, to 2006 (Klíma, 1963; Svoboda et al., 1994, 2002, 2013; Oliva, 2009). Among the very large collection of mammoth bones at Předmostí, settlement structures and a unique mass burial site were discovered (Svoboda, 2005; Oliva, 2009). From the animal remains, the vast majority were mammoth bones, with other taxa appearing much less frequently (Pokorný, 1951; Musil, 1959). The radiocarbon dates obtained from this site overlap in the period of around 26 ka BP (Jöris and Weninger, 2004).

Finds from both sites were collected directly during the course of fieldwork, and sometimes, as was the case in Předmostí, during work related with loess exploitation. Only during recent excavations led by B. Klíma and J. Svoboda were more accurate recordings undertaken, including the sieving of sediment.

Fig. 1. Location of the sites of Dolní Věstonice I and Předmostí I within the borders of the modern Czech Republic (black line), and within the range of the Gravettian culture (yellowish area, after Kaczanowski and Kozłowski, 1998). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Material and methods

In this paper, the bird assemblages from Dolní Věstonice I and Předmostí I are analysed. Bones from Dolní Věstonice I were collected during standard excavations, as well as during the sieving of a small part of the excavated sediment. A part of the material, i.e., bones excavated in 1924–1926, were identified by Skutil (1946), but his paper does not include all the data needed for our research (e.g. how much the bones were fragmented, or if there were any human modifications). Therefore, it was necessary to re-examine these bones, along with the bones excavated after Skutil's study.

The bones from Předmostí were collected mainly during standard excavations (Oliva, 2009). There were no bird bones discovered during more recent excavations (Wojtal and Wilczyński, 2013).

The studied material is stored at the Anthropos Institute of the Moravian Museum, in Budišov (all of the bones from Předmostí I and the majority of the bones from Dolní Věstonice I), and partly in Brno (the bones analysed by Skutil, 1946). The deposits of artefacts, now separated from the 'common' bone assemblages, were not checked by us to ascertain whether they contained any modified bird bones. However, Zelinková's (2007) study suggests that those deposits do not contain avian remains.

For the identification, the comparative skeleton collection of ISEA PAS was used, as well as the available identification keys (Bacher, 1967; Woelfle, 1967; Erbersdobler, 1968; Kraft, 1972; Tomek and Bochenski, 2000; Bochenski and Tomek, 2009). A direct light and a low power microscope were used to recognize possible modifications on the bone surfaces, made either by environmental conditions (e.g., abrasion, weathering), animals in general (e.g., gnaw marks, marks of beak and claws, signs of trampling or joints' overextension) or humans in particular (e.g., cut marks, polished surfaces, burning).

Fig. 2. Preservation of the bird bones in Dolní Věstonice I (A–D) and Předmostí I (E–H). The bones look rather battered (A–H); they are etched by roots (B); coated with calcium (E–F); and some have undergone preservative treatments (H). The found modifications are either ambiguous (C) or might have been made during the exploration (D). A. *Tadorna* sp., right coracoid; B. *Corvus corax*, shaft of right ulna; C. *Bucephala clangula*, proximal part of left ulna; D. *Corvus corax*, distal part of left femur; E. *Circus aeruginosus*, distal part of left femur; F. Accipitridae middle size, proximal part of left tibiotarsus; G. *Anser albifrons*, proximal part of right humerus; H. Accipitridae middle size, right carpometacarpus. Photos P. Wojtal, K. Wertz.

The results are presented in terms of the NISP (Number of Identified Specimens), MNE (Minimum Number of Elements), and the MNI (Minimum Number of Individuals). The method for the MNE calculation is after Wertz et al. (2015).

The ratio of wing-to-leg elements was obtained from the number of wing bones (the sum of humeri, ulnas and carpometacarpi) divided by the sum of the wing and leg bones (the mentioned wing bones + femurs + tibiotarsi + tarsometatarsi), and then expressed as a percentage (Ericson, 1987; Livingston, 1989). The ratios were separately calculated for the NISP and MNE values. Obtained deviations from the baseline 1:1 proportion were evaluated by a Chi-square test.

For a possible hint as to the significance of the birds for Pavlovian people, the number of bird bones from each site was compared with part of the related mammal assemblage. From Dolní Věstonice I, the mammal bones collected during the 1924–1928 and 1948–1952 excavations were roughly counted, and from Předmostí I an approximate number of all of the mammal bones stored in Budišov was obtained.

4. Results

The bones from both sites are not currently in very good shape. They are weathered, etched by roots, sometimes covered by a calcium layer, portioned, and generally look rather battered. Some bones have been glued or protectively coated with varnish (Fig. 2).

4.1. Dolní Věstonice I

At least 12 species from six bird families, with 138 identifiable bones, were present at the site (Table 1). The raven (*Corvus corax*), with 61 bones, is the best represented species, although another member of the Corvidae family, the jackdaw (*Corvus monedula*), is represented by only three bones. This family constitutes 46% of all the bird remains found on the site. The Tetraonidae family, yielding more than 35% of the assemblage, is the second largest bird family. Every other family yields less than 10% of the remains found in the assemblage, and every bird bone has been identified to at least the taxonomic family.

Table 1
Bird taxa from Dolní Věstonice I.

Order, family	Taxon	NISP		MNE		MNI
		N	%	N	%	N
Anseriformes, Anatidae	*Melanitta nigra*	1	6.5	1	8.0	1
	Bucephala clangula	4		4		2
	Tadorna sp.	2		2		1
	Anatidae middle size	2		2		–
Galliformes, Tetraonidae	*Lagopus lagopus*	33	37.7	29	39.3	4
	Lagopus muta	11		10		2
	Lagopus sp.	5		2		–
	Lyrurus (*Tetrao*) *tetrix*	3		3		1
Charadriiformes, Scolopacidae	*Scolopax rusticola*	1	0.7	1	0.9	1
Accipitriformes, Accipitridae	Accipitridae middle size	1	0.7	1	0.9	1
Strigiformes, Strigidae	*Strix aluco*	1	8.0	1	9.8	1
	Bubo (*Nyctea*) *scandiacus*	10		10		2
Passeriformes, Corvidae	*Corvus monedula*	3	46.4	3	41.4	1
	Corvus corax	61		43		5
Total		138	100.0	112	100.0	22

The recovered remains are mainly bones of limbs and coracoids (Table 2). Both the raven and the tetraonids are strongly represented by ulnas and femurs, whereas almost all of the recorded humeri belong to the tetraonids. Coracoids, carpometacarpi and tarsometatarsi are averagely represented. Three of the six pedal phalanges belong to the Snowy Owl (*Bubo scandiacus*); while one belongs to a middle-sized member of the Accipitridae family, and could not be identified more closely.

Table 2
Bird bones found at Dolní Věstonice I.

Element	Total			*Corvus corax*			Tetraonidae			Others	
	NISP		MNE	NISP		MNE	NISP		MNE	NISP	MNE
	N	%		N	%		N	%			
Coracoid	16	11.6	14	9	14.8	7	5	9.6	5	2	2
Scapula	3	2.2	3	1	1.6	1	1	1.9	1	1	1
Humerus	12	8.7	9	2	3.3	1	9	17.3	7	1	1
Ulna	32	23.2	22	15	24.6	9	11	21.2	7	6	6
Radius	6	4.3	5	4	6.6	3	2	3.8	2	–	–
Carpometacarpus	15	10.9	13	6	9.8	4	7	13.5	7	2	2
Wing phalanges	1	0.7	1	–	–	–	1	1.9	1	–	–
Pelvis	1	0.7	1	1	1.6	1	–	–	–	–	–
Femur	18	13.0	16	9	14.8	7	6	11.5	6	3	3
Tibiotarsus	13	9.4	9	4	6.6	2	6	11.5	4	3	3
Tarsometatarsus	15	10.9	13	8	13.1	6	4	7.7	4	3	3
Pedal phalanges	6	4.3	6	2	3.3	2	–	–	–	4	4
Total	138	100.0	112	61	100.0	43	52	100.0	44	25	25

No statistically significant variation in the wing-to-leg ratio is observed. For the record: the raven ratio is 52.3% for the NISP ($\chi^2 = 0.09$; $P > 0.05$) and 48.2% for the MNE value ($\chi^2 = 0.03$; $P > 0.05$). For the tetraoid family, the ratio is 62.8% for the NISP ($\chi^2 = 2.81$; $P > 0.05$) and 60% for the MNE value ($\chi^2 = 1.40$; $P > 0.05$).

The long bones are rather fragmented (Table 3), with less than 15% of them having both epiphyses. However, the shafts (i.e., the parts with all their epiphyses broken) are not that numerous, as their number does not constitute 20% of the entire assemblage.

Table 3
The fragmentation of birds' long bones at Dolní Věstonice I.

Long bone	Total					*Corvus corax*					Tetraonidae				
	N	Whole	Prox	Dist	Shaft	N	Whole	Prox	Dist	Shaft	N	Whole	Prox	Dist	Shaft
	100%	(%)	(%)	(%)	(%)	100%	(%)	(%)	(%)	(%)	100%	(%)	(%)	(%)	(%)
Coracoid	16	25.0	37.5	12.5	25.0	9	22.2	44.4	–	33.3	5	40.0	40.0	20.0	–
Scapula	3	–	100	–	–	1	–	100	–	–	1	–	100	–	–
Humerus	12	16.7	25.0	41.7	16.7	2	–	–	–	100	9	11.1	33.3	55.6	–
Ulna	32	–	21.9	50.0	28.1	15	–	–	46.7	53.3	11	–	36.4	63.6	–
Radius	6	16.7	50.0	33.3	–	4	–	75.0	25.0	–	2	50.0	–	50.0	–
Carpometacarpus	15	20.0	46.7	13.3	20.0	6	–	50.0	–	50.0	7	42.9	28.6	28.6	–
Femur	18	16.7	66.7	11.1	5.6	9	22.2	55.6	22.2	–	6	–	100	–	–
Tibiotarsus	13	–	23.1	46.2	30.8	4	–	–	50.0	50.0	6	–	16.7	50.0	33.3
Tarsometatarsus	15	26.7	26.7	40.0	6.7	8	12.5	37.5	50.0	–	4	50.0	25.0	–	25.0
Long bone NISP	130	13.1	36.9	31.5	18.5	58	8.6	32.8	27.6	31.0	51	17.6	39.2	37.3	5.9

In the assemblage, no evident trace of human modification is found. Only the papillae of one raven's ulna are missing, as if the bone has been polished, but the polishing itself cannot be confirmed with magnification, perhapse due to a coat of varnish (Fig. 3).

The number of all identified bird remains at the site is significantly lower than that of the mammals. The combined number of mammal remains collected during the 1924–28 and 1948–52 excavations is higher than 14,500. Thus, the number of bird bones is less than 1% of the total bone assemblage.

Table 4
Bird taxa found at Předmostí I.

Order, family	Taxon	NISP		MNE		MNI
		N	%	N	%	
Anseriformes, Anatidae	*Cygnus cygnus*	4	8.1	3	9.2	1
	Cygnus sp.	3		0		–
	Anser anser	3		3		1
	Anser fabalis	1		1		1
	Anser albifrons	8		7		1
	Anser sp.	4		2		–
	Mareca (*Anas*) *penelope*	1		1		1
	Anatidae middle size	3		3		–
Galliformes, Tetraonidae	*Lagopus lagopus*	54	23.5	42	24.9	8
	Lagopus muta	3		3		1
	Lagopus sp.	18		6		–
	Lyrurus (*Tetrao*) *tetrix*	3		3		2
Gruiformes, Gruidae	*Grus grus*	1	0.3	1	0.5	1
Charadriiformes, Laridae	*Chroicocephalus* (*Larus*) *ridibundus*	1	1.5	1	1.8	1
	Larus argentatus	2		1		1
	Larus hyperboreus	1		1		1
	Larus marinus	1		1		1
Accipitriformes, Accipitridae	*Gyps fulvus*	6	3.6	6	5.5	1
	Aquila chrysaetos	1		1		1
	Circus aeruginosus	2		2		1
	Accipitridae middle size	3		3		–
Strigiformes, Strigidae	*Bubo* (*Nyctea*) *scandiacus*	9	2.7	9	4.1	1
Passeriformes, Corvidae	*Corvus corax*	200	60.2	117	53.9	13
Total identifiable		332	100.0	217	100.0	38
Aves indet.		7		3		–
Total		339		220		38

4.2. Předmostí I

At this site, 339 bird remains were found, of which 332 have been identified to seven families with 18 species (Table 4). Over 60% of these bones are of the Corvidae family, with only one species present, the raven (*Corvus corax*). The second largest representation is the Tetraonidae family of the Galliformes order, from which three species represent nearly 25% of the assemblage. Every other family is represented by no more than a tenth of the whole assemblage. Only seven bird bones proved impossible to identify further (i.e. to their taxonomic order).

Almost all parts of the bird skeleton are represented in the assemblage (Table 5). Most common are ulnas and femurs, in the case of the raven, and humeri and ulnas, in the case of the tetraonids. Also moderately well represented are tibiotarsi, coracoids, carpometacarpi and tarsometatarsi; with each of these bones yielding ~10% of the assemblage. Among nine pedal phalanges, at least six belong to the Snowy Owl (*Bubo scandiacus*), while two have been identified only to the taxonomic class Aves.

Table 5
Bird bones found at Předmostí I.

Element	Total			*Corvus corax*			Tetraonidae			Others	
	NISP		MNE	NISP		MNE	NISP		MNE	NISP	MNE
	N	%		N	%		N	%			
Vertebra	1	0.3	1	–	–	–	–	–	–	1	1
Coracoid	28	8.3	22	15	7.5	11	3	3.8	2	10	9
Scapula	8	2.4	8	6	3.0	6	1	1.3	1	1	1
Humerus	55	16.2	33	26	13.0	13	22	28.2	14	7	6
Ulna	80	23.6	41	51	25.5	23	15	19.2	10	14	8
Radius	9	2.7	6	5	2.5	3	4	5.1	3	–	–
Carpometacarpus	29	8.6	22	23	11.5	16	3	3.8	3	3	3
Wing phalanges	5	1.5	5	3	1.5	3	–	–	–	2	2
Pelvis	1	0.3	1	1	0.5	1	–	–	–	–	–
Femur	49	14.5	33	35	17.5	23	12	15.4	8	2	2
Tibiotarsus	36	10.6	18	19	9.5	9	8	10.3	4	9	5
Fibula	1	0.3	1	–	–	–	–	–	–	1	1
Tarsometatarsus	28	8.3	20	15	7.5	8	10	12.8	9	3	3
Pedal phalanges	9	2.7	9	1	0.5	1	–	–	–	8	8
Total	339	100.0	220	200	100.0	117	78	100.0	54	61	49

The observed variation in the ratio of wing-to-leg elements is statistically significant only in the case of the raven, if counted for the NISP value, which is 59.2% ($\chi^2 = 5.69$; $P < 0.02$). The variation for the MNE value remains statistically insignificant (56.5%; $\chi^2 = 1.56$; $P > 0.05$). No statistically significant variation is encountered within the tetraonid group (for the NISP: 57.1%; $\chi^2 = 1.43$; for the MNE: 56.2%; $\chi^2 = 0.72$; and for both: $P > 0.05$).

The remains are fragmented (Table 6), with less than 10% of the long bones having both epiphyses present, while one third of them are shafts (i.e., with all the epiphyses broken). The presence of these shafts is absolutely prominent in the case of the ravens' ulnas, the most numerous bones in the assemblage. As much as 90% of these bones are found without any epiphysis. Among the tetraonids, less than 15% of the long bones are shafts. No clear trace of a human modification is found in the assemblage.

Table 6
The fragmentation of birds' long bones at Předmostí I.

Long bone	Total					*Corvus corax*					Tetraonidae				
	N	Whole	Prox	Dist	Shaft	N	Whole	Prox	Dist	Shaft	N	Whole	Prox	Dist	Shaft
	100%	(%)	(%)	(%)	(%)	100%	(%)	(%)	(%)	(%)	100%	(%)	(%)	(%)	(%)
Coracoid	28	14.3	25.0	42.9	17.9	15	13.3	20.0	53.3	13.3	3	33.3	33.3	33.3	–
Scapula	8	–	100	–	–	6	–	100	–	–	1	–	100	–	–
Humerus	55	5.5	43.6	27.3	23.6	26	3.8	42.3	30.8	23.1	22	9.1	50.0	22.7	18.2
Ulna	80	3.8	8.8	16.3	71.3	51	5.9	2.0	2.0	90.2	15	–	33.3	53.3	13.3
Radius	9	11.1	44.4	33.3	11.1	5	–	60.0	20.0	20.0	4	25.0	25.0	50.0	–
Carpometacarpus	29	20.7	44.8	27.6	6.9	23	13.0	56.5	21.7	8.7	3	33.3	–	66.7	–
Femur	49	12.2	34.7	28.6	24.5	35	17.1	37.1	14.3	31.4	12	–	33.3	58.3	8.3
Tibiotarsus	36	2.8	22.2	27.8	47.2	19	5.3	5.3	31.6	57.9	8	–	37.5	12.5	50.0
Tarsometatarsus	28	25.0	32.1	25.0	17.9	15	6.7	26.7	40.0	26.7	10	40.0	50.0	10.0	–
Long bone NISP	322	9.6	30.1	25.5	34.8	195	8.7	28.2	20.5	42.6	78	11.5	39.7	34.6	14.1

The number of bird bones, in comparison with ones from mammals, is very small. Roughly, the number of mammal bones from the site that are stored in Budišov is between 30,000 and 35,000. Thus, the share of bird bones does not exceed 1.2% of the total bone assemblage.

5. Discussion

To make this chapter less cumbersome, we shall abbreviate ‘Předmostí I’ to ‘P·I’ and ‘Dolní Věstonice I’ to ‘DV·I’, with the exception of the figures and tables. The names of the other sites (like Dolní Věstonice II or Pavlov I) will not be abbreviated.

Čapek (1911) noted the bones of ‘*Anser* (*Bernicla*?)’ and *Anas* (average size) at P·I; while Skutil and Stehlík (1939) listed *Branta bernicla* and *Anas platyrhynchos*; and Tyrberg (1998) reported ‘*Branta* sp.?’ and ‘*Anas* sp.’ at the same site. We did not find the remains of *Branta bernicla* or *Anas platyrhynchos* in the assemblage, and we believe all of these names may actually refer to the same two bones, which have been identified by us as ‘*Anser* sp.’ and either ‘*Mareca* (*Anas*) *penelope*’ or ‘Anatidae, middle size’.

In addition, in the two studied assemblages, no smaller birds (for example, small passerines, typically most numerous in the natural habitat, and smaller owls or falcons) were noted. Although Skutil and Stehlík (1939), and afterward Tyrberg (1998) listed the fieldfare (*Turdus pilaris*) at P·I, we did not find its bones in the material. Nevertheless, it is clear that these smaller birds must have been present in the Moravian landscape, since in Pavlov I some of their bones were found. Their absence in DV·I and P·I is probably caused by the deficient method of excavation.

Nine Pavlovian open sites have yielded known numbers of bird bones (Fig. 4). Those with identified taxa are clearly dominated by ravens and/or the Tetraonidae family. These two groups of birds

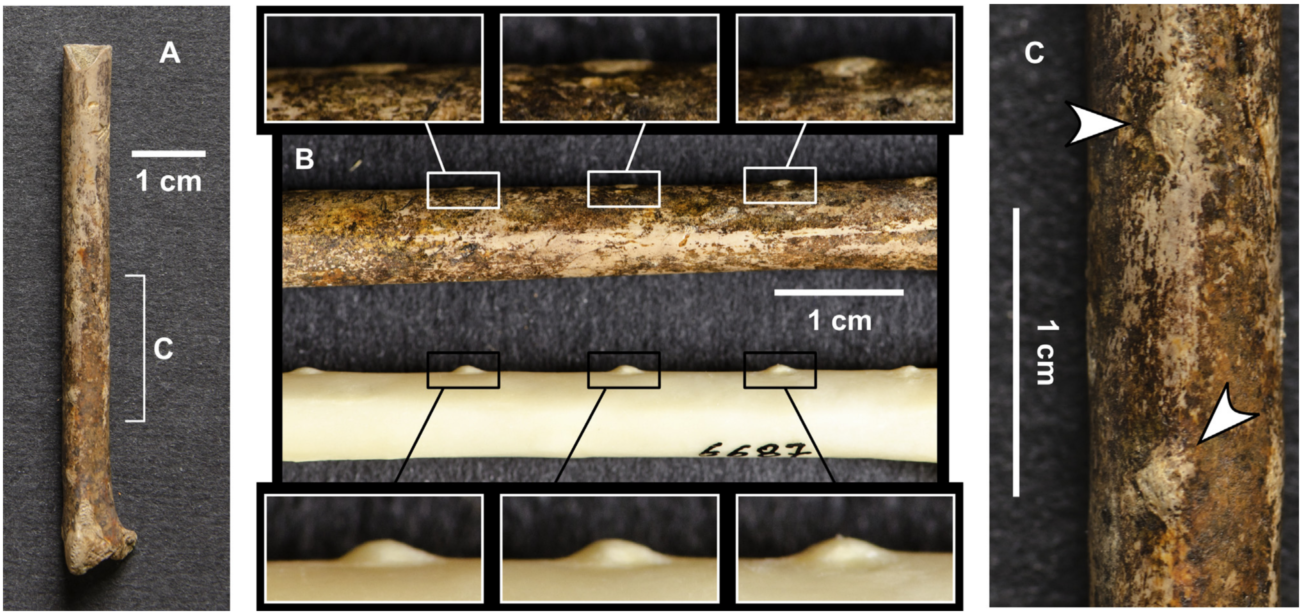

Fig. 3. Raven's ulna from Dolní Věstonice I with supposedly polished papillae (A–C). The papillae do not protrude from the ulna's surface, in contrast to a typical raven's ulna like one from the ISEA PAS comparative collection (B). However, no clear trace of polishing was found on the bone's surface (C, the arrows indicate papillae).

combined reach more than 80% of the identified bones in every richer assemblage in terms of the NISP (and no less than 65% in the poorer accumulations), and no less than 50% in terms of the MNI. It is clear that these proportions do not mirror the natural biodiversity in the sites' vicinities, and this suggests a special role played by these two groups of birds. Raven bones are abundant not only in the sites from the Pavlov Hills, but also in the remoter P·I.

As the bird bones were recovered in an obvious cultural context, the base assumption is that the main agent for their deposition was human. Unfortunately, this assumption cannot be fortified with clear records of human-made bone modifications, as no such traces have been found (the polishing of the ulna at DV·I is not that evident). Such a lack is probably, at least partly, caused by the mediocre state of the bone preservation, along with the obfuscating layer of varnish, but other factors are also possible. Firstly, bird meat might have been processed without the use of tools, as birds do not require butchering but may be disarticulated and eaten with bare hands and teeth (Steadman et al., 2002). Secondly, the birds might have been primarily used for something else than for their meat, e.g., for their feathers. Plucking them would not have left any traces on the bones. However, typical animal-made modifications, such as traces of gnawing or the marks of birds' beaks or claws (Bochenski et al., 2009a) were also not observed.

As for the (assumingly) human deposits, the abundance of tetraonid remains in P·I and DV·I is obvious. These birds, being mediocre flyers with a fair amount of (arguably) tasty meat, are a

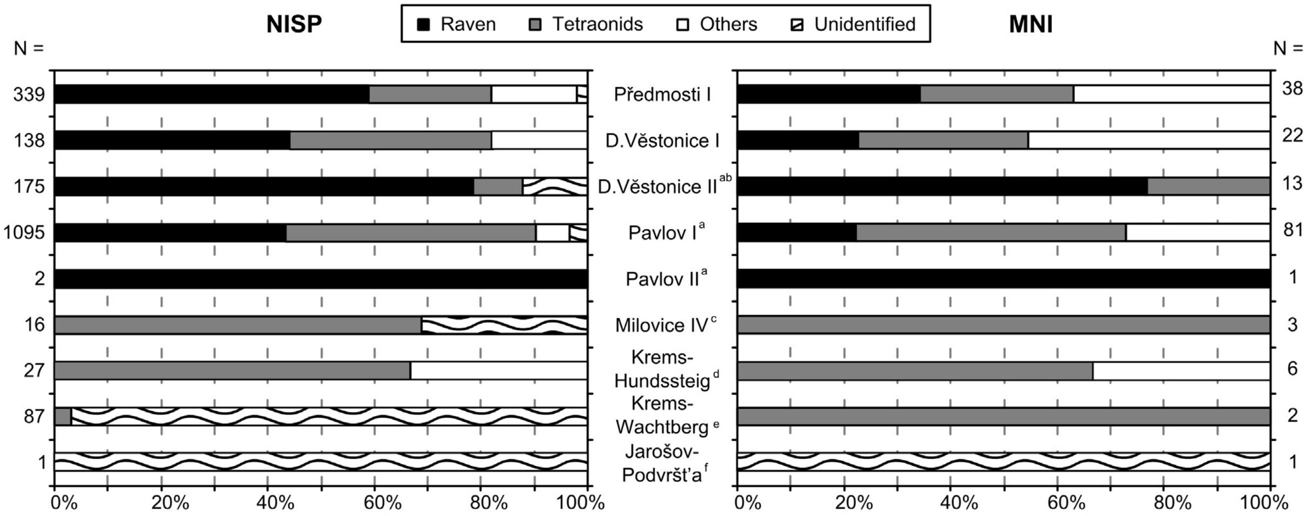

Fig. 4. Comparison of the Pavlovian birds' assemblages with known numbers of bird bones: a – Wertz et al. (2015); b – Wojtal et al., in prep.; c – Svoboda et al. (2011); d – Bauernfeind (2008), where besides the bones, some fragments of *Tetrao urogallus*'s eggshells were found; e – Händel et al. (2015); f – Musil (2005).

decent source of food. Also, as they are widely approved as game birds at present, it is difficult to imagine that they were used differently by Pavlovian people. Moreover, this assumption is supported by the relatively big number of tetraonid humeri and femora — bones whose predominance in an assemblage is recognized as an indicator of an anthropogenic deposition (Mourer-Chauviré, 1983; Baales, 1992; Bochenski, 2005). The numerous presences of willow ptarmigan/grouse in Pavlovian sites confirm the existence of a cold steppe environment (a so-called 'mammoth steppe') during the Gravettian period.

More troublesome for interpretation is the large share of raven bones in the Pavlovian assemblages. Such abundant depositions most probably resulted from the widespread hunting of ravens during the Pavlovian, although the reasons for catching these birds remain unclear (see the discussion in Wertz et al., 2015). The overrepresentation of wing bones at P·I, shown by the wing-to-leg ratio, may indicate that ravens were not mainly used as food, for in that kind of assemblage leg bones usually prevail (Ericson, 1987). On the other hand, the wing-to-leg ratio as an indicator may mirror, not the cultural selection or the body parts disposal, but the density-mediated attrition (Higgins, 1999; Dirrigl, 2001). The idea here is: the more robust bones are, the better they tend to be preserved. The bone density varies in different taxa depending on their feeding behaviour and their ways of locomotion (e.g., capable flyers, like geese or teal, would have a different wing-leg bone proportion than weaker flyers, like diving ducks or grebes) (Livingston, 1989; Bovy, 2002). From this, the P·I case would therefore suggest that ravens are better flyers than pedestrians, and so their wing bones are denser than the bones of their legs. Raven ulnas appear to be distinctly robust, although such appearances may be misleading along with the whole density-mediated attrition theory. Bovy (2002) observed, that since the theory implies a different survivorship of the various bones over time, such changes should be recognizable in the bone abundances in well-stratified sites. However, her research did not confirm the theory-based predictions. She also noted that bone density, being a complex attribute which should be measured and defined precisely, is not always predictable from bones' appearance only. Unfortunately, precise measurements of bone densities are rare, with the remarkable exception of Dirrigl's (2001) study on turkeys. Nevertheless, such a study has never been conducted with ravens. Therefore, explanations based only on their bone density must remain hypothetical, also because there is one assemblage where different raven bones (i.e., the coracoid and scapula) prevail (Bramwell et al., 1987).

In our view, the bone assemblages from DV·1 and P·1 strengthen the hypothesis that ravens' ulnas were used as a raw material for technology, or as disposable parts of flight feathers' packages. It is well recognized that the wings of bigger birds, like diurnal raptors, swans or cranes, were widely used in prehistory for making tools (e.g., flutes, whistles, needles, awls, and containers for ochre) (Wijngaarden-Bakker, 1997; Münzel et al., 2002; Laroulandie, 2004; Gál, 2005; Conard et al., 2009; Antl-Weiser et al., 2010) as well as obtaining feathers (for fans, brooms, arrow fletching, or perhaps symbolic purposes) (Bovy, 2002; Peresani et al., 2011; Finlayson et al., 2012). A similar usage of the raven bones during the Pavlovian is indicated mainly by the presence of a few human-modified raven ulnas found at Pavlov I and at Dolní Věstonice II (Bochenski et al., 2009b; Wertz et al., 2015; Wojtal et al., in prep.), and the one possibly-modified ulna at DV·I. The overrepresentation of this bone at the sites is rather unusual. Typically, bird ulnas tend to be preserved in relatively small numbers at archaeological sites, whether or not they are anthropogenic or non-anthropogenic (see e.g., Bramwell et al., 1987; Livingston, 1989; Baales, 1992; Cassoli and Tagliacozzo, 1997; Tagliacozzo and Gala, 2002; Laroulandie, 2005). Also noteworthy may be the high degrees of fragmentation of this bone, and especially the high share of shafts. Perhaps this may suggest some bone processing. The lower number of shafts at DV·I may also be deceptive, since it may simply result from a deficient exploration of the site.

The present state of research does not allow us to say whether an interest in ravens during the Gravettian was confined to Pavlovian Moravia, or was more widespread. In the Upper Palaeolithic open-air sites, either in Central Europe or in the Central Russian Plain, raven bones are rarely ever noted (but see Soffer, 1985; Musil, 2005), so the former case is possible. However, the study of Finlayson et al. (2012) shows that Neanderthals extensively hunted all the various members of the Corvidae family, so perhaps the mentioned scarcity may be just due to the specific spatial distribution of ravens at the time. Nevertheless, ravens were certainly present in the vicinity of Milovice IV, another site from the Pavlov Hills, but their bones have not been excavated there (Svoboda et al., 2011). Perhaps this absence may result from the diversified usage of birds at the Pavlovian sites, or may result from the unrepresentative number of bones at the site (see Fig. 4).

The bones of large birds such as swans, geese, vultures, eagles and snowy owls were probably also deposited in P·I due to their usage as a raw material. Bones of these birds have already been found at Pavlov I, and some of them bear cut marks (Bochenski et al., 2009b). A curious thing at P·I is the relatively large number of feet bones among the remains of snowy owls. This may suggest some usage of owls' feet by the Pavlovian people, particularly as an eagle owl's claw has been known to be used as a pendant in the Palaeolithic (Gál, 2005).

As Pavlov I is near DV·I, the complete absence of the large birds in the latter site is a little perplexing. This absence cannot be explained by deficient methods of exploration, for bones such as swans' humeri or ulnas would surely have been noticed and retrieved. Therefore, we think that their absence at DV·1 and Dolní Věstonice II (Wertz et al., 2015), may indicate a diverse usage of the birds at Pavlovian sites.

However, the differences in the presence of gulls at the Pavlovian site may be plausibly explained by the diversification of the paleoenvironment. Although water reservoirs must have been close to P·I, similarly to the sites from the Pavlov Hills (for this is where all the amphibious birds from DV·I and Pavlov I must have been caught), gulls were probably abundant only at the former place. As for their usage, they might have been hunted opportunistically for bones or feathers.

Both sites in the study share a similarity regarding long bone fragmentation with Pavlov I and Dolní Věstonice II. At all four assemblages, the share of whole bones (i.e., with two epiphyses) never exceeds 15% of the related assemblage, while the share of the shafts (i.e., parts with both epiphyses broken) always does. Other similarities in these four sites are the fair shares of carpometacarpi and tarsometatarsi (Bochenski et al., 2009b; Wertz et al., 2015). If those bones were scarce, it would indicate that the birds' dismemberment took place outside the settlement, or the utilisation of those parts somewhere else (Laroulandie, 2005).

Although the presented numbers of mammal bones in the assemblages cannot be exact, their predominance over the bird bones is doubtless. This is another similarity with the other Pavlovian open sites (see Table 7), and supports the theory that, for Pavlovian people, birds were not a real dietary alternative to larger-sized mammals (Absolon, 1938; see also; Soffer, 1985), although they could have been used as a complement to the diet.

Table 7
A comparison of the quantities of bird and mammal bones at the Main Upper Palaeolithic Central European open-air localities. Superscript letters: a – to avoid a possible overestimations of the bones, the numbers do not contain the indeterminate mammal remains along with the indeterminate fragments of large, medium and small mammal bones (categories in which the numerous broken fragments of the bones already identified may be contained); b – hare/fox size; c – reindeer/wolf size and bigger; d – no data beside the presence of 'parts of bird wings' and 'a tubular bone from a grouse sized bird'; e – the number includes bones fitted to the 'big size mammals' category; f – from South-East area only; g – only the bones excavated between 1948 and 1952; h – additionally, after 2012 *c.*, about 2000 bones of arctic foxes were discovered during the wet sieving (unpublished data).

Epoch	Open-air site	Excavated bones			References
		Birds	Mammals[a]		
			Small[b]	Medium and large[c]	
Aurignacian	No data	No data	No data	No data	
Pavlovian	Grub-Kranawetberg	a few?[d]	1	434	Antl and Fladerer, 2004; Antl-Weiser et al., 2010; Bosch et al., 2012
	Krems-Wachtberg (2005–12)	87	657	13 512[e]	Händel et al., 2015
	Krems-Hundssteig	27	19	1 055	Bauernfeind, 2008; Fladerer et al., 2008
	Pavlov I	1 095	12 260[f]	14 004[f]	Bochenski et al., 2009b; Wojtal et al., 2012; Wertz et al., 2015
	Pavlov II	2	45	439	Wojtal and Wilczyński, 2013
	Pavlov VI	–	6	357	Wojtal et al., 2011
	Dolní Věstonice I	138	1 054[g]	5 787[g]	Wilczyński et al., 2015a
	Dolní Věstonice II	175	2 784	4 185	Wertz et al., 2015; Wojtal et al., in prep.
	Předmostí	339	Unknown	Mammoth MNI >1 000	Musil, 2010
	Jarošov-Podvršt'a	1	164	101	Musil, 2005
	Spytihněv-Duchonce	–	6	623	Škrdla et al., 2008
	Milovice IV	16	81	322	Svoboda et al., 2011
Late Gravettian	Kraków-Spadzista	–	91[h]	7 063	Wilczyński et al., 2012
	Jaksice II	–	2	781	Wilczyński et al., 2015b; unpublished data
	Petřkovice	–	–	6	Nývltová Fišaková, 2008
	Milovice I	–	2	62 586[e]	Brugère and Fontana, 2009
	Trencianskie Bohuslavice	–	58	1 186	Vlačiky, 2012
	Moravany nad Váhom Lopata II	2	52	1 841	Vlačiky, 2012
	Bodrogkeresztúr-Henye	–	1	167	Vörös, 2000

Whatever the role of birds was for the Pavlovian people, it must have changed over time. At the Central European sites from the subsequent period, the Late Gravettian, bird bones are practically absent (Table 7), even at the sites where wet sieving was conducted and huge numbers of bones were excavated. For example, at a Late Gravettian site from the Pavlov Hills (Milovice I), the remains of all small-game are practically absent, both smaller mammals and birds. Interestingly, at the contemporaneous site Kraków Spadzista, located 350 km further north than Milovice I, the bones of small mammals (especially arctic foxes) were numerously excavated, but not a single bird bone. Because this absence of birds cannot be explained by an analytical bias or by low numbers of bones, they indicate a switch in the people's bird hunting behaviour.

Unfortunately, we do not know what kind of disposition humans had toward birds just before the Pavlovian. From the available Early Upper Palaeolithic records in Central Europe, we have no well-documented open-air localities containing animal remains (Table 7). The prevalent sites are types of workshops, and Aurignacian paleontological record is known only from a few cave sites, like the Mladeč and Mamutowa Cave, where the relationship between hunting and the discovered animal remains is not entirely clear (Teschler-Nicola, 2006; Wojtal, 2007).

6. Conclusions

1. Both sites were located in a similar cold tundra-steppe ('*mammoth steppe*') environment, and both were close to water reservoirs. However, different fauna was present in their vicinities.
2. The Tetraonidae family and the raven clearly predominate in the bird assemblages at Dolní Věstonice I and Předmostí I. Ravens were no less willingly hunted than tetraonids, and such an interest in ravens, also observed at the other Pavlovian sites, may be a unique feature of the Pavlovian culture.
3. Birds might have been hunted intentionally either for their meat (tetraonids) or for their bones and feathers. The bones of bigger birds (swans, geese, birds of prey, ravens) might have been used as a raw material for tool making. Furthermore, the different taxa compositions at the nearby sites (Dolní Věstonice I and II, Pavlov I) may indicate a diverse use of birds at Pavlovian settlements.
4. It is possible that people hunted ravens to use their ulnas as a raw material, or for their flight feathers.
5. Birds probably played only a subsidiary role as a food for Pavlovian people, while mammals were of the greatest importance for subsistence. Interestingly, during the subsequent time period, the Late Gravettian, people seemed to cease hunting birds completely.

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RESEARCH ARTICLE

The taphonomy of medium-sized grouse in food remains of the northern goshawk *Accipiter gentilis*, compared with damage done by man and other predators

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Abstract

This study describes bone damage of medium-sized grouse (*Lyrurus tetrix* and *Lagopus* spp.) in food remains of the northern goshawk *Accipiter gentilis* and compares it to damage done by other birds of prey and humans. In general, the 'signature' left on the bones by the goshawk is similar to those of other diurnal birds of prey, but it differs from human-derived damage and from owl pellets. These differences are visible in bone preservation, fragmentation and perforation. This study is the first to describe the characteristic damage to the sternum and coracoid that is probably typical of other raptors as well. Reliable analysis of zooarchaeological materials requires not only correct identification to the species but also determining where the bones came from at a given site. Bird bones from open-air archaeological sites may contain food remains of the goshawk, whose habitat is forests in the vicinity of open areas. This study will assist in determining the factor(s) responsible for the accumulation of zooarchaeological materials.

KEYWORDS

bird bones, food remains, goshawk, grouse, taphonomy, zooarchaeology

1 | INTRODUCTION

The *Lagopus* species often dominate in fossil materials (Tyrberg, 1995), and they were often hunted by humans (Baales, 1992; Serjeantson, 2009). It is known, however, that grouse are also food for various predators. Therefore, the correct determination of the factor depositing the archaeological material is very important. Although birds, especially medium-sized grouse (*Lyrurus tetrix* and *Lagopus* spp.), are the staple food of the northern goshawk (Brüll, 1977; Tornberg, Korpimaki, & Byholm, 2006), its food remains have not yet been studied taphonomically. The northern goshawk occurs and nests in forests, often near openings, where it also hunts. The remains of its victims are abandoned in the vicinity of the nest and under roosts and may get mixed with traces of human occupation at some open-air archaeological sites that were temporarily or alternately occupied by man. This article describes the typical damage to bird bones in the food of the northern goshawk, thereby filling the gap in our understanding of the taphonomy of predators that hunt similar prey as humans do.

2 | MATERIAL AND METHODS

Food remains of the northern goshawk *Accipiter gentilis* have been collected from under roosts and eyries in northern Finland since the 1970s. They were the basis for several scientific studies on the diet composition and food preferences of this species (Tornberg, 1997, 2001; Tornberg et al., 2006; Tornberg, Reif, & Korpimäki, 2012). A huge collection of these remains (several cubic meters) was kept by the University of Oulu, and now, after the space reduction of its natural history museum, it is in the possession of one of its collectors and co-author of this paper, Risto Tornberg. For luck of time, it was not possible to study all the material for this paper. We limited ourselves to examining randomly selected 26 large complete samples from

9 years (1975, 1979, 1981, 1991–1992, 2000 and 2013–2015), which together constituted a representative amount of goshawk food remains. A significant portion of the food remains examined contained body parts that were still in articulation, partly covered with skin, feathers or fur. All samples have been combined and analysed as one material. This procedure eliminates possible differences between individual northern goshawks and makes the results representative of the entire *A. gentilis* species.

To save time, the bones were identified only to higher taxa levels (genera, families and orders) using the ISEA PAS osteological collection and identification keys (Bochenski & Tomek, 2009; Cohen & Serjeantson, 1996; France, 2009, 2011; Schmid, 1972; Tomek & Bochenski, 2009). During the research, and in accordance with literature data (Tornberg, 1997, 2001), it quickly became apparent that medium-sized grouse (*L. tetrix* and *Lagopus* spp.) definitely dominated in the assemblage, whereas the remaining prey belonged to many different taxonomic groups. Therefore, we decided to analyse only medium-sized grouse thoroughly and provide only basic data for the remaining prey of the northern goshawk.

Bird bone fragmentation was analysed according to the methodology proposed by Bochenski, Tomek, Boev, and Mitev (1993) and consistently used in later papers (Bochenski et al., 1998; Bochenski, Huhtala, Sulkava, & Tornberg, 1999; Bochenski, Korovin, Nekrasov, & Tomek, 1997; Bochenski & Nekrasov, 2001; Bochenski & Tomek, 1994; Bochenski, Tomek, Tornberg, & Wertz, 2009; Bochenski & Tornberg, 2003; Lloveras, Nadal, et al., 2014; Lloveras, Thomas, Lourenço, Caro, & Dias, 2014).

The ratio of the wing to the leg bones was calculated as the number of wing fragments (humerus, ulna and carpometacarpus) divided by the sum of wing and leg fragments (femur, tibia and tarsometatarsus), expressed as a percentage (Ericson, 1987). The ratio of the proximal to distal elements was calculated as the number of proximal fragments (scapula, coracoid, humerus, femur and tibiotarsus) divided by the sum of proximal and distal fragments (ulna, radius, carpometacarpus and tarsometatarsus), expressed as a percentage (Bochenski & Nekrasov, 2001). The ratio of the core to the limb elements was calculated as the number of core fragments (sternum, pelvis, scapula and coracoid) divided by the sum of core and limb fragments (humerus, ulna, radius, carpometacarpus, femur, tibiotarsus and tarsometatarsus), expressed as a percentage (Bochenski, 2005; Bramwell, Yalden, & Yalden, 1987). The chi-square test was used to assess the statistical significance of the obtained deviations from the hypothesized natural proportions: 6:6 for wing-to-leg ratio, 10:8 for proximal-to-distal ratio and 6:14 for core-to-limb ratio (paired bones count for 2 and single bones for 1 in these proportions).

For each skeletal element, the number of identified specimens (NISP) was established and the minimum number of individuals (MNI) was calculated for the medium-sized grouse species together. The results are presented both as absolute numbers (MNI Element) and as the percentage of the number of fragments of the element that produced the highest MNI value (i.e., Total MNI%). The MNI values are certainly underestimated as they have been calculated from all combined material (i.e., not for each year or sample separately), bones have not been identified to species and proximal and distal parts have not been fitted together. The minimum number of elements (MNE) was calculated in a similar way to the MNI, that is, for all medium-sized grouse bones of a specific skeletal element. It is the sum of the complete bones (left and right) and the proximal (left and right) or distal (left and right) fragments, whichever is more numerous (for characteristic of NISP, MNE and MNI values, see Lyman, 1994 and Serjeantson, 2009). The results are presented as percentages of the total number of all skeletal elements included in the analysis (MNE%).

The bone surface was examined for holes and perforations made by the northern goshawk's claws and beak when handling the prey. The number and position of the perforations on the bone were noted.

3 | RESULTS

3.1 | Preservation and fragmentation of bones

Medium-sized grouse (*L. tetrix* and *Lagopus* spp.) were by far the most numerous victims of *A. gentilis*; their remains accounted for more than half of all the bones (981 out of 1818) (Table 1). Ducks, corvids, pigeons, large and small grouse (capercaillie and hazel grouse) and hares and squirrels were also relatively numerous. Among the other

TABLE 1 Number of identified specimens (NISP), minimum number of elements (MNE) and minimum number of individuals (MNI) by taxon recovered from non-ingested food remains of the northern goshawk

	NISP	MNE	MNI
Lepus sp.	47	47	7
Sciurus sp.	28	26	8
cf. *Arvicola* sp.	1	1	1
Anser sp.	1	1	1
Anatinae	157	155	24
Bonasa bonasia	42	42	7
Grouse (medium sized)	**981**	**954**	**109**
Tetrao urogallus	60	60	7
Galliformes indet.	124		
Columba sp.	48	48	7
Charadriiformes	7	7	2
Accipiter nisus	3	3	1
Accipiter gentilis	3	3	1
Accipitridae indet.	1		
Asio flammeus	8	8	1
Strigiformes indet.	8		
Corvidae	222	219	19
Passeriformes (up to *Turdus* size)	23	22	4
Aves indet.	54		
Total	1818	1596	199

Note: Medium-size grouse (*Lyrurus tetrix* and *Lagopus* spp.), which is the main topic of this study, is marked in bold.

victims there were owls, diurnal birds of prey, charadriids and some passerines up to the size of a thrush.

In terms of the NISP and MNE, the most frequent bones of medium-sized grouse are the coracoid, humerus and scapula (Figure 1). The sternum and femur are half as numerous; the remaining bones are much rarer in the material. Remains of the skull and mandible are scarce. By far the best skeletal elements for the MNI calculation are coracoid, sternum, scapula and humerus—the MNI% values obtained on their basis range from 90% to 100% (Tables 2 and 3).

The elements of the axial skeleton are largely fragmented (Table 2). The sternum is usually damaged, but its front part is preserved with the rostrum sterni and the corpus sterni of different sizes, with jagged fracture edges (Figure 2a). In contrast, long bones are mostly complete; in most cases, the percentage of whole long bones exceeds 90%, (Table 3). The scapula, which is not a typical long bone, often survives as the epiphysis with a part of corpus scapulae of varying length.

3.2 | Bone ratios based on the MNE

The wing bones were more numerous than the leg bones; proximal skeletal elements were more numerous than distal elements, whereas core elements were more numerous than limb elements (Table 4). The deviation from the expected proportions (6:6, 10:8 and 6:14, respectively) is statistically significant ($p < 0.05$) for each of the three ratios mentioned above ($\chi^2 = 29.776$, $\chi^2 = 300.550$ and $\chi^2 = 280.541$, respectively). The differences between the data obtained on the basis of NISP and MNE were marginal (Table 4).

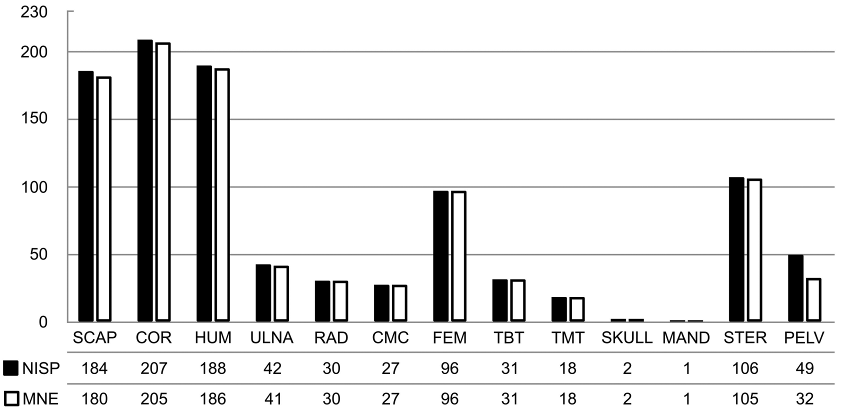

FIGURE 1 Skeletal elements of medium-sized grouse (*Lyrurus tetrix* and *Lagopus* spp.) recovered from non-ingested food remains of the northern goshawk. cmc, carpometacarpus; cor, coracoid; fem, femur; hum, humerus; mand, mandibula; pelv; pelvis; rad, radius; scap, scapula; ster, sternum; tbt, tibiotarsus; tmt, tarsometatarsus

TABLE 2 Fragmentation of the skull, mandible, sternum and pelvis of medium-sized grouse (*Lyrurus tetrix* and *Lagopus* spp.) recovered from non-ingested food remains of the northern goshawk

Skull

Number of fragments	Whole skull (%)	Skull with beak and brain case without back part (%)	Brain case (%)	Whole beak (%)	End of beak (%)	Other fragments (%)	MNE (%)	Element MNI (*N*)	Total MNI (%)
2	50	-	50	-	-	-	0.2	2	2

Mandible

Number of fragments	Whole mandible (%)	One branch (%)	Articular part (%)	Tip of mandibula (%)	Middle part of branch (%)	MNE (%)	Element MNI (*N*)	Total MNI (%)
1	100	-	-	-	-	0.1	1	1

Sternum

Number of fragments	More than half with rostrum (%)	Less than half with rostrum (%)	Fragments without rostum (%)	MNE (%)	Element MNI (*N*)	Total MNI (%)
106	73	26	1	11	105	96

Pelvis

Number of fragments	Synsacrum with 1 or 2 ilium-ischii-pubis bones (%)	Ilium-ischii-pubis bone (%)	Synsacrum whole or partial (%)	Acetabulum region (%)	MNE (%)	Element MNI (*N*)	Total MNI (%)
49	49	2	16	33	3	32	29

Abbreviations: MNE, minimum number of elements; MNI, minimum number of individuals.

TABLE 3 Fragmentation of long bones of medium-sized grouse (*Lyrurus tetrix* and *Lagopus* spp.) recovered from non-ingested food remains of the northern goshawk, expressed as percentages of the total number of fragments for the element found

Bone	Element NISP (*N*)	Whole bone (%)	Proximal part (%)	Distal part (%)	Shaft (%)	MNE (%)	Element MNI (*N*)	Total MNI (%)
Scapula	184	45	55	-	-	19	99	91
Coracoid	207	95	4	1	-	21	109	100
Humerus	188	93	4	3	-	19	98	90
Ulna	42	86	12	2	-	4	23	21
Radius	30	90	10	-	-	3	16	15
cmc	27	96	-	-	4	3	15	14
Femur	96	97	3	-	-	10	49	45
tbt	31	94	6	-	-	3	19	17
tmt	18	100	-	-	-	2	12	11

Abbreviations: cmc, carpometacarpus; MNE, minimum number of elements; MNI, minimum number of individuals; NISP, number of identified specimens; tbt, tibiotarsus; tmt, tarsometatarsus.

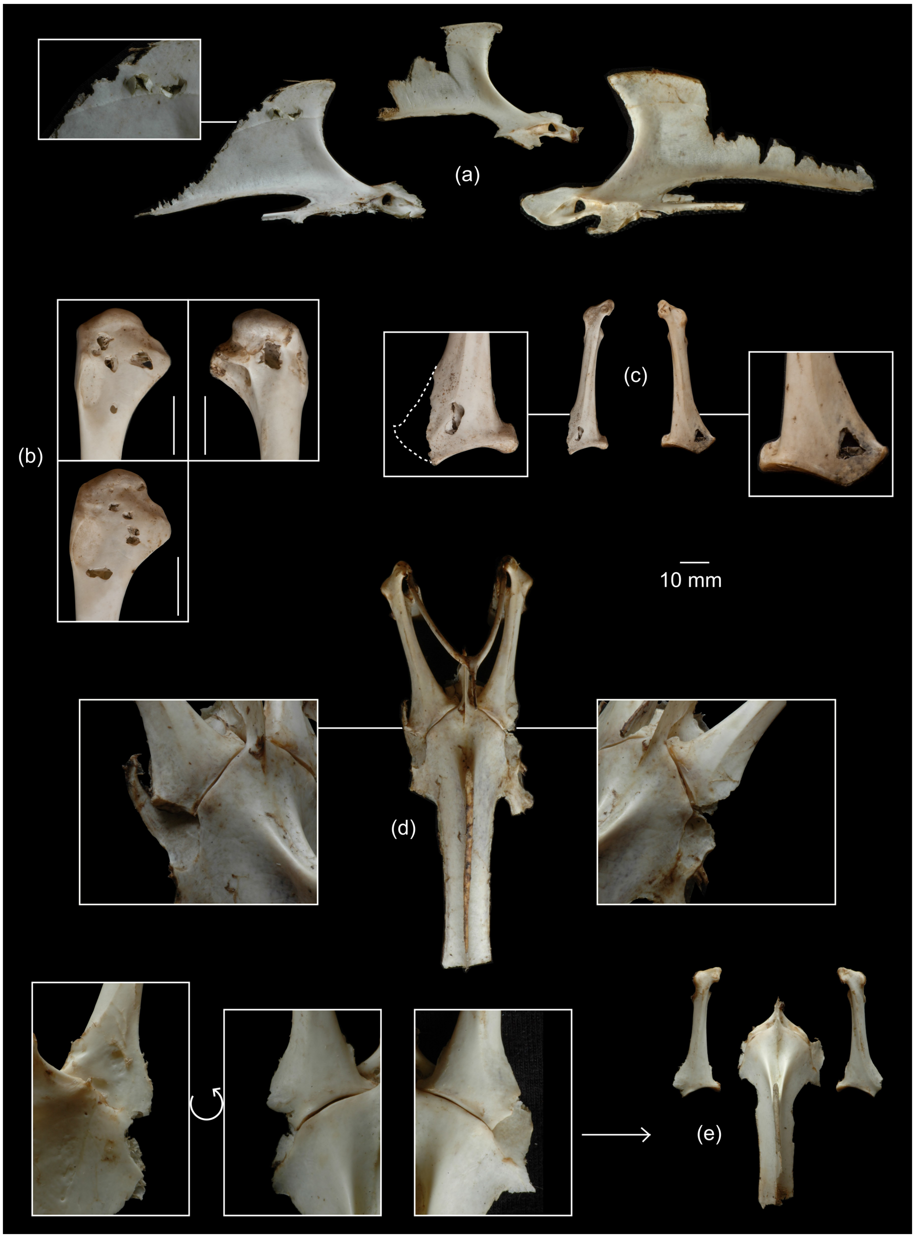

FIGURE 2 Damage to medium-sized grouse (*Lyrurus tetrix* and *Lagopus* spp.) bones recovered from non-ingested food remains of the northern goshawk: (a) perforated sternum with jagged fracture edges; (b) proximal humerus with multiple perforations; (c) perforated sternal part of the coracoid; (d) articulated sternum and coracoid: on the right-hand side, processus craniolateralis (sternum) and processus lateralis (coracoid) are damaged, whereas on the left-hand side, they are not damaged; (e) damage to processus craniolateralis (sternum) and processus lateralis (coracoid) are visible on the left- and right-hand sides; they can also be seen when the bones are disarticulated [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 4 Medium-sized grouse (*Lyrurus tetrix* and *Lagopus* spp.) recovered from non-ingested food remains of the northern goshawk: ratios of wing to leg elements, proximal to distal elements and core to limb elements, calculated from NISP and MNE

Value	Wing–leg	Prox–dist	Core–limb
NISP	63.9	85.8	55.8
MNE	63.7	85.7	54.9

Abbreviations: MNE, minimum number of elements; NISP, number of identified specimens.

3.3 | Perforations

Perforations attributable to the beak and/or claws were observed on approximately 10% of bones (Table 5). Individual skeletal elements were affected to a varying degree by punctures. The most frequently punctured element was the sternum (about 40% of all sterna were perforated), followed by the pelvis (about 25%), humerus and coracoid (about 10% each).

Almost half of the perforated humeri (9 out of 20) and every fifth sternum (9 out of 43) have two or more perforations (Figure 2a,b); multiple perforations were less frequently observed on other bones.

The coracoid was most often perforated in the sternal part (14 out of 16 perforated coracoids, Figure 2c); on the humerus, sternum and pelvis no higher frequency of perforation was found in any particular region.

A significant number of sterna were preserved in articulation with coracoids. Some of these combined elements show characteristic damage, which indicates that *A. gentilis* tends to hit specific body parts of its victims, in this case, the breast region (sternum-coracoid connection). This results in frequent damage to the processus craniolateralis of the sternum and the processus lateralis of the coracoid (Figure 2d,e). Altogether, about 77% of sterna (82 out of 106) have their processus craniolateralis damaged and about 48% coracoids (99 out of 207) have their processus lateralis damaged.

TABLE 5 Perforated bones of medium-sized grouse (*Lyrurus tetrix* and *Lagopus* spp.) recovered from non-ingested food remains of the northern goshawk

Punctured bones	Quantity (*N*)	Punctured element frequency (%)
Scapula	4	2
Coracoid	16	8
Humerus	20	11
Ulna	1	2
Femur	1	1
Tibiotarsus	3	10
Skull & beak	1	50
Sternum	43	41
Pelvis	13	27
Total	102	10

The share of immature specimens was about 8% (80 out of 981 bones).

4 | DISCUSSION AND CONCLUSIONS

Reliable ways to distinguish bones anthropogenic in origin from those accumulated by avian predators include cut marks, burn marks, damage to the humerus and ulna during the disarticulation of the elbow by overextension and worked bone (Laroulandie, 2005; Serjeantson, 2009). However, such traces are usually sparse, even if from the archaeological context it appears that it was man who deposited the material. Therefore, various types of analyses of bone composition and fragmentation play an important role in taphonomic research.

4.1 | Taxa composition

The composition of the fauna found in a given archaeological material can be a valuable clue about its origin (Bochenski, 2005; Lloveras, Cosso, Solé, Claramunt-López, & Nadal, 2018). What matters here is not only the species composition, which may vary depending on the geographic region and season, but also the size of the preferred prey, which is more constant for a given predator. In Fennoscandia, the main food of the goshawk is grouse, especially *L. tetrix* and *L. lagopus*, whereas corvids, thrushes, pigeons and hares and squirrels are important prey under certain circumstances (Tornberg et al., 2006). Thus, the food remains researched by us reflect well the actual goshawk diet in this region. The list of bird species in the northern goshawk's diet is very long, and today, grouse does not constitute its main food everywhere. Currently, the main food of the goshawk in Central Europe are partridges and doves (Brüll, 1977), but in historical times, grouse could also play a role similar to that in Fennoscandia.

4.2 | Skeletal composition

The frequency of individual skeletal elements in archaeological materials may be an indication of its origin. In food remains deposited by man, usually, the humerus and femur dominate (Mourer-Chauviré, 1983). However, in food remains from birds of prey and owls, the situation is more complicated because it depends on several factors, including the size of the victim (Baales, 1992; Mourer-Chauviré, 1983) and whether the bones were swallowed and spit out as pellets or the meat was stripped of them and the bones themselves were not ingested (Bochenski, 2005). The coracoid and humerus predominate in the material currently studied, which matches the uneaten food remains of other large diurnal raptors including the imperial eagle, golden eagle, white-tailed eagle and gyrfalcon (Bochenski, 2005; Bochenski et al., 1999; Bochenski et al., 1997; Bochenski & Tornberg, 2003; Bramwell et al., 1987; Lloveras et al., 2018). These raptors, including the goshawk currently under study, also have a very low percentage of skulls and mandibles in uneaten food remains, and their prey's sterna, coracoids and humeri give very high MNI values. In addition to these species, also a few others, including the crested caracara and Egyptian vulture, have a large amount of sterna in their uneaten food remains (Lloveras, Nadal, et al., 2014; Montalvo et al., 2011).

4.3 | Fragmentation

In terms of the degree of fragmentation of long bones, the studied food remains of the goshawk fit well with the Category 3 distinguished by Bochenski (2005), which includes non-ingested food remains of diurnal birds of prey. This category is characterized by a very low degree of fracture, with more than 60% of the bones intact. Most species of diurnal birds of prey are included in it, which is confirmed by various independent studies (Bochenski et al., 2009; Bochenski & Tornberg, 2003; Laroulandie, 2002; Lloveras et al., 2018; Lloveras, Nadal, et al., 2014). The large fragments of the sternum with the preserved rostrum sterni and the jagged edges of the corpus sterni are also typical of the non-ingested food remains of various diurnal birds of prey (Bochenski et al., 2009; Lloveras et al., 2018; Lloveras, Nadal, et al., 2014), gulls (Serjeantson, Irving, & Hamilton-Dyer, 1993) and possibly other avian predators.

4.4 | Ratios

The results obtained from all three bone ratios (wing/leg, proximal/distal and core/limb) fully agree with the bone damage found in non-ingested food remains of diurnal birds of prey (Bochenski, 2005). The wing/leg ratio: in most species of diurnal birds of prey, uneaten food remains are dominated by wing bones (Bochenski et al., 1997; Laroulandie, 2002; Lloveras, Nadal, et al., 2014; Lloveras, Thomas, et al., 2014; Montalvo et al., 2011) although there are also exceptions, such as for example, the Golden Eagle, where a slight predominance of leg bones was observed (Lloveras et al., 2018). In pellet materials, the wing/leg ratio is usually close to 1:1 (Bochenski, 2005) whereas assemblages accumulated by man can have very different wing/leg ratios, depending on for instance the purpose for which the birds were collected, hunting method, differential transport of carcases or the properties of the bones themselves (Bovy, 2002, 2012; Ericson, 1987; Laroulandie, 2010; Lefèvre & Laroulandie, 2014). The proximal/distal element ratio: high preponderance of proximal elements in food remains of the northern goshawk corresponds to Category 3 predators, which include the golden eagle (Bochenski, 2005). It is noteworthy that a similarly high dominance of proximal elements was also found independently in studies on food remains of the golden eagle (Lloveras et al., 2018). Pellets of diurnal birds of prey and owls show either an equal share of proximal and distal elements (Category 1 predators) or a slight dominance of proximal elements (Category 2 predators), which in turn allows to distinguish between these three groups of predators (Bochenski, 2005). The core/limb ratio distinguishes between pellet materials of owls and diurnal raptors (limb elements prevail) and non-ingested food remains of diurnal raptors (core elements prevail) (Bochenski, 2005). The currently studied northern goshawk material fits this pattern very well, because core elements prevail to a similar degree as in several independent studies on golden eagles (Bochenski et al., 1999; Bramwell et al., 1987; Lloveras et al., 2018).

4.5 | Perforations

The perforations found on the bones of the northern goshawk victims are similar to those left by other species of raptors. Possible differences may be in the percentage of damaged bones. Current results indicate that the northern goshawk perforates the bones of its victims to a rather moderate degree (about 10%). A similarly low percentage of perforated bones was found in Bonelli's eagle victims (approximately 6%; Lloveras, Thomas, et al., 2014), slightly higher in golden eagle victims (approximately 14%; Lloveras et al., 2018) and the highest in Egyptian vulture (approximately 28%; Lloveras, Nadal, et al., 2014). A common feature of all species of birds of prey that have so far been examined for bone perforation of their victims is the high frequency of perforations on the sternum, pelvis, humerus and coracoid (Bochenski et al., 2009; Laroulandie, 2000, 2002; Lloveras et al., 2018). The northern goshawk, currently under study, is no exception. For two reasons, it can be expected that the sternum will be most prone to perforation. First, there is a lot of meat on the sternum, and second, it is an element of the skeleton with a relatively large surface area. Bochenski et al. (2009) have already suggested that the shape and surface of the prey sternum may play a significant role in the amount of perforations. They found that the wide sternum of ducks was more often perforated than the narrow sternum of galliforms.

The simultaneous damage to the sternum by breaking the processus craniolaterales and the coracoid by breaking the processus lateralis was noticed due to the fact that many food remains in the studied material, including the sternum-coracoid complex, were still in articulation. Such damage has also been found on many isolated sterna and corcaoids. This damage has not been described anywhere before. It seems that it may also be characteristic of other species of birds of prey. Due to the high frequency of sterna and coracoids damaged in this way, it can be expected that they will also be visible on bones from archaeological excavations.

Current studies, including skeletal composition, fragmentation and perforations, indicate that the goshawk damages the bones of its prey in a manner typical of diurnal raptors. Bird bones from open-air archaeological sites that were temporarily or alternately occupied by man may contain food remains of the goshawk, whose habitat is forests in the vicinity of open areas. This study will assist in determining the factors responsible for the accumulation of zooarchaeological materials.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

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RESEARCH ARTICLE

How to distinguish duck and wader remains eaten by the peregrine falcon *Falco peregrinus* from those eaten by other birds of prey and humans: A taphonomic analysis

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Abstract

Bird bones from archeological sites near cliffs and at the entrance to caves may have been accumulated by the peregrine falcon and not by humans. To find out who deposited these remains—humans, peregrine falcons, or some other predators—taphonomic studies must be carried out. This study shows the characteristic damage to the bones of modern birds done by peregrine falcons. These include greater than expected abundance of humeri and coracoids, relatively little fragmentation of long bones, perforations mainly seen in the sternum and humerus, and characteristic proportions of the preserved skeleton elements. The described features make it possible to clearly distinguish food remains deposited by diurnal birds of prey from those accumulated by humans or owls. To identify the most likely species of bird of prey that has accumulated a given assemblage, it is important not only to establish the taxonomic composition of the assemblage but also to take into account the prey size preferred by the various raptors. The present research shows that the differences between bone damage of different victims of peregrine falcons are relatively small, which indicates that the results of our research are quite universal and can be applied to different geographic areas inhabited by different species of birds.

KEYWORDS
actualistic studies, bird bones, ducks, food remains, peregrine falcon, taphonomy, waders, zooarcheology

1 | INTRODUCTION

The peregrine falcon (*Falco peregrinus*) and humans have more in common in a zooarcheological context than one might think. The main food of the peregrine falcon is medium-sized birds such as pigeons, ducks, waders, gulls, ptarmigans, or corvids, depending on the geographic area and availability of prey (Cramp & Simmons, 1980). Medium-sized birds were also hunted and eaten frequently by humans (Blasco et al., 2014; Blasco et al., 2016; Serjeantson, 2009). The peregrine falcon usually nests on cliff edges under an overhang (Cramp & Simmons, 1980), that is, in places potentially used by humans in prehistoric times. All this means that the food remains of the peregrine falcon could mix with the food remains of people who lived or camped in caves and similar shelters. Indeed, in at least two cases (Sibudu Cave, South Africa, and Marmot Cave, Russia), it was found that some bird remains came from the food debris of a large falcon, whereas other bird remains were left by humans (Val, 2016; Val et al., 2016; Volkova & Zelenkov, 2014).

So far, only one study was published analyzing pigeon bone damage in food remains of the peregrine falcon (Laroulandie, 2002). However, the bones of pigeons may differ in physical properties and size from bones of other taxonomic groups and thus may be damaged somewhat differently. In this paper, we present a taphonomic analysis of two other prey categories, ducks and waders, each represented by very rich bone material. In conjunction with the Laroulandie (2002) study, we obtain a significantly improved picture of modern bone damage in birds eaten by the peregrine falcon. This will make it possible to distinguish even more reliably the remains accumulated by the peregrine falcon from those accumulated by humans at archeological sites.

2 | MATERIAL AND METHODS

Food remains of the peregrine falcon *F. peregrinus* have been collected from under roosts and nests in Finland to study the diet composition of this species for several dozen years (Sulkava, 1968; Tornberg et al., 2016). The nests were situated in three different types of places, which is characteristic of peregrine falcons in Finland (Sulkava, 1968): on a terrace of a steep cliff, on the ground on peatland, and on a tree in an old nest of a bird of prey. Feeding places were located 50–200 m from the nest. Bird remains often consisted of skeletal elements still held together by tendons; sometimes, wings remained attached to the gnawed skeleton (Sulkava, 1968). The remains were collected not for a taphonomic study but only for taxonomic identification. Thus, there was a risk that not all less diagnostic skeletal elements such as ribs, vertebrae, or phalanges have been collected. In this situation, we decided to limit the research to the main elements of the skeleton (long bones, crania, mandibles, sterna, and pelves). Pellets were also collected but were easily separated from uneaten bird remnants; they were not taken into account in this study because they were not numerous and they contained small, difficult to identify remains. From this huge collection of noningested food remains, we randomly selected 22 large samples from 7 years (1976, 1994, 2003–2006, and 2009) for this study. For analyses, all samples were combined and treated as one sample, which eliminated possible differences between individual peregrine falcons.

Most of the remains have only been identified generally to higher taxonomic units (genera, families, and orders) which allowed for a great time saving but should not affect taphonomic research. The ISEA PAS comparative collection and bone identification manuals (Bochenski & Tomek, 2009; Cohen & Serjeantson, 1996; Tomek & Bochenski, 2000, 2009; Woelfle, 1967) were used for identification. Detailed taphonomic research was carried out on the two most numerous groups of prey: ducks and waders. The ducks were dominated by teals *Anas crecca* and mallards *Anas platyrhynchos*, whereas the waders included representatives of various genera such as *Scolopax*, *Vanellus*, *Pluvialis*, *Numenius*, *Gallinago*, *Tringa*, and others (Tornberg et al., 2016).

Bone fragmentation was studied using the method proposed by Bochenski et al. (1993): Six fragmentation categories were distinguished for the skull (whole skull, skull with beak and brain case without back part, brain case, whole beak, end of beak, and other fragments); for mandibula, five categories were distinguished (whole mandibula, one branch, articular part, tip of mandibula, and middle part of branch); three categories for sternum (more than half with rostrum, less than half with rostrum, and fragments without rostrum); four categories for pelvis (synsacrum with one or two ilium-ischii-pubis bones, ilium-ischii-pubis bone, synsacrum whole or partial, and acetabulum region); and four categories for long bones (whole bone, proximal part, distal part, and shaft). The same fragmentation categories were used in many later papers by various authors (Bochenski et al., 1997; Bochenski et al., 1998; Bochenski et al., 1999; Bochenski et al., 2009; Bochenski & Nekrasov, 2001; Bochenski & Tomek, 1994; Bochenski & Tornberg, 2003; Lloveras, Nadal, et al., 2014; Lloveras, Thomas, et al., 2014; Wertz et al., 2021).

For each skeletal element of a given taxon, the number of identified specimens (NISP) and the minimum number of individuals (MNI) were calculated. The results are presented both as absolute numbers (element MNI) and as a percentage of the number of fragments of the element that produced the highest MNI value (i.e., total MNI %). Element MNI is the sum of whole bones (left or right) and proximal (left or right) or distal (left or right) fragments, whichever combination is the most numerous (Lyman, 1994). The MNI values were calculated from all materials combined (i.e., not separately for each year or sample), bones were not identified to species, and proximal and distal parts were not matched. The minimum number of elements (MNE) was calculated in a similar way to the MNI, that is, for all combined specimens of a given taxon. The MNE is the sum of whole bones (left

TABLE 1 Number of identified specimens (NISP), minimum number of elements (MNE), and minimum number of individuals (MNI) by taxon recovered from noningested food remains of the peregrine falcon

	NISP	MNE	MNI
Anser sp.	3	2	1
Mergus merganser	1	1	1
Anseriformes (size of a seaduck/goose)	1	1	1
Ducks	**705**	**686**	**138**
Lagopus sp.	8	8	2
Lyrurus tetrix	4	4	2
Galliformes indet.	3	3	
Columba sp.	62	62	16
Cuculus canorus	16	16	1
Fulica atra	1	1	1
Cf. Lariidae	3	3	1
Waders	**687**	**653**	**113**
Falconiformes/Strigiformes	7	7	2
Corvidae.	24	24	8
Passeriformes (up to *Turdus* size)	18	18	4
Aves indet.	140	79	
Total	1683	1568	291

Note: Ducks and waders, which are the main topic of the study, are marked in bold.

and right) and proximal (left and right) or distal (left and right) fragments, whichever is the most numerous (details of NISP, MNE, and MNI are provided by Lyman, 1994, and Serjeantson, 2009). The results are presented as percentages of the total number of all skeletal elements included in the analysis (MNE %).

The wing-to-leg ratio was calculated as the MNE of wing bones (humerus, ulna, and carpometacarpus) divided by combined MNE of the wing and leg bones (femur, tibiotarsus, and tarsometatarsus), expressed as a percentage (Ericson, 1987). The ratio of proximal to distal skeletal elements was calculated as the MNE of proximal bones (scapula, coracoid, humerus, femur, and tibiotarsus) divided by the MNE of proximal and distal bones (ulna, radius, carpometacarpus, and tarsometatarsus), expressed as a percentage (Bochenski & Nekrasov, 2001). The chi-square test was used to determine the statistical significance of the obtained deviations from the natural proportions.

The surfaces of all skeletal elements were checked for possible perforations made by the peregrine falcon when killing and eating the prey. The traces of digestion were not checked because the analyzed material consisted only of noningested food remains.

3 | RESULTS

A total of 1683 bone remains of the victims of the peregrine falcon were examined (Table 1). The most numerous victims were ducks (NISP = 705) and waders (NISP = 687), which together accounted for 83% of all the bones. Pigeons, corvids, and small passerines were much less numerous. The largest victims were the occasional goose, merganser, and black grouse.

In terms of NISP, MNE, and MNI, the humerus of both ducks and waders was by far the most abundant element of the skeleton (Figure 1 and Tables 2 and 3). The second most numerous element was the coracoid, closely followed by the scapula and ulna. Each of the three bones of the leg and the axial skeleton was much less numerous.

Both in ducks and waders, the elements of the axial skeleton (head, sternum, and pelvis) are sparse (Table 2). In the case of the skull, the most frequently preserved fragment is the beak, whereas in the case of the sternum, its front part with the rostrum sterni, regardless of the size of the corpus sterni fragment; the fracture edges are jagged (Figure 2e). Long bones are much less fragmented in both

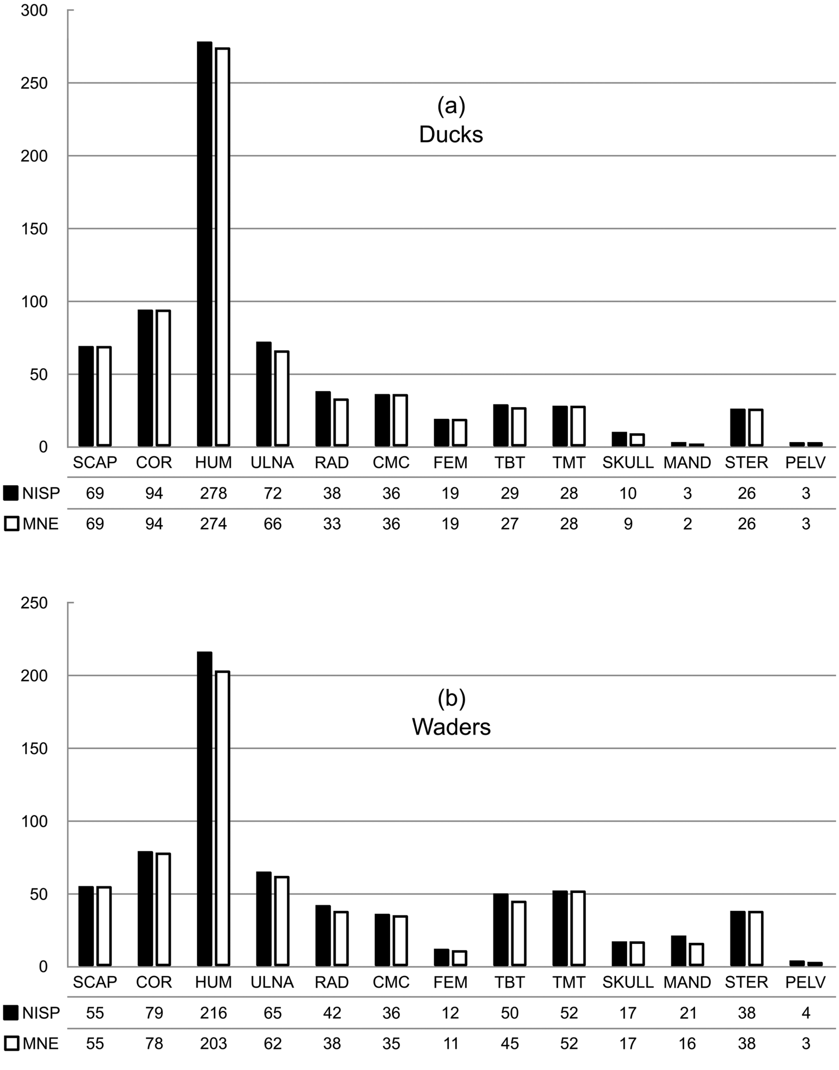

FIGURE 1 Skeletal elements of ducks and waders recovered from noningested food remains of the peregrine falcon. Abbreviations: cmc, carpometacarpus; cor, coracoid; fem, femur; hum, humerus; mand, mandibula; pelv, pelvis; rad, radius; scap, scapula; ster, sternum; tbt, tibiotarsus; tmt, tarsometatarsus

TABLE 2 Fragmentation of the skull, mandible, sternum, and pelvis of ducks and waders recovered from noningested food remains of the peregrine falcon

Skull	Number of fragments	Whole skull (%)	Skull with beak and brain case without back part (%)	Brain case (%)	Whole beak (%)	End of beak (%)	Other fragments (%)	MNE (%)	Element MNI (*N*)	Total MNI (%)
Ducks	10	40	-	10	10	40	-	1	9	7
Waders	17	29	6	-	59	6	-	3	17	15
Mandible	**Number of fragments**	**Whole mandible (%)**	**One branch (%)**	**Articular part (%)**	**Tip of mandibula (%)**	**Middle part of branch (%)**	**MNE (%)**	**Element MNI (*N*)**	**Total MNI (%)**	
Ducks	3	33	-	33	33	-	0.3	2	1	
Waders	21	38	24	-	38	-	2	16	14	
Sternum	**Number of fragments**	**More than half with rostrum (%)**	**Less than half with rostrum (%)**	**Fragments without rostrum (%)**	**MNE (%)**	**Element MNI (*N*)**	**Total MNI (%)**			
Ducks	26	46	54	-	4	26	19			
Waders	38	16	84	-	6	38	34			
Pelvis	**Number of fragments**	**Synsacrum with 1 or 2 ilium-ischii-pubis bones (%)**	**Ilium-ischii-pubis bone (%)**	**Synsacrum whole or partial (%)**	**Acetabulum region (%)**	**MNE (%)**	**Element MNI (*N*)**	**Total MNI (%)**		
Ducks	3	100	-	-	-	0.4	3	2		
Waders	4	75	-	-	25	0.5	3	3		

Abbreviations: MNE, minimum number of elements; MNI, minimum number of individuals.

TABLE 3 Fragmentation of long bones of ducks and waders recovered from noningested food remains of the peregrine falcon, expressed as percentages of the total number of fragments for the element found

	Bone	Element NISP (*N*)	Whole bone (%)	Proximal part (%)	Distal part (%)	Shaft (%)	MNE (%)	Element MNI (*N*)	Total MNI (%)
Ducks	Scapula	69	4	96	-	-	10	38	28
	Coracoid	94	79	21	-	-	14	51	37
	Humerus	278	85	13	1	-	40	138	100
	Ulna	72	76	15	8	-	10	40	29
	Radius	38	68	16	16	-	5	17	12
	cmc	36	94	6	-	-	5	19	14
	Femur	19	79	16	5	-	3	12	9
	tbt	29	52	7	41	-	4	14	10
	tmt	28	100	-	-	-	4	16	12
Waders	Scapula	55	5	95	-	-	8	29	26
	Coracoid	79	95	4	1	-	12	43	38
	Humerus	216	82	12	4	2	31	113	100
	Ulna	65	80	11	8	2	9	32	28
	Radius	42	76	17	7	-	6	19	17
	cmc	36	86	11	3	-	5	19	17
	Femur	12	75	17	8	-	2	6	5
	tbt	50	30	8	60	2	7	24	21
	tmt	52	92	-	8	-	8	27	24

Abbreviations: cmc, carpometacarpus; MNE, minimum number of elements; MNI, minimum number of individuals; NISP, number of identified specimens; tbt, tibiotarsus; tmt, tarsometatarsus.

studied groups of birds (Table 3). In most cases, the percentage of whole bones exceeds 75%, with the tarsometatarsus and carpometacarpus showing the highest percentage of whole bones, followed by the humerus. In waders, the coracoid is also overwhelmingly intact. Of all the long bones, the tibiotarsus and scapula are the most fragmented, the latter with only one articular end being an atypical long bone.

In both ducks and waders, wing bones were statistically more numerous than leg bones ($p < 0.05$; $\chi^2 = 202.676$ for ducks and $p < 0.05$; $\chi^2 = 90.352$ for waders); in ducks, the preponderance of the wing bones was larger than in waders (Table 4). Also, in both ducks and waders, the proximal skeletal elements were statistically more numerous than the distal skeletal elements ($p < 0.05$; $\chi^2 = 96.570$ for ducks and $p < 0.05$; $\chi^2 = 34.602$ for waders), and the values for both taxonomic groups were very similar.

Perforations attributable to beak and/or claws of the peregrine falcon were observed on about 10% of duck bones and about 11% of waders (Table 5). Individual skeletal elements differed in the frequency of punctures. The most frequently perforated element was the sternum (50% of the sterna was perforated in both ducks and waders), followed by the humerus (19% in ducks and 25% in waders). The remaining bones were affected to a much lesser extent or not at all. More than a quarter of the perforated humeri of ducks (15 out of 53) and more than a third of the perforated humeri of waders (19 of 54) have two or more perforations (Figure 2). The greatest number of perforations was in the vicinity of both articular parts (proximal and distal); on shafts, perforations were observed sporadically.

A considerable number of sterna have been preserved in articulation with the coracoids. Some of these connected skeletal elements were damaged near where they connect, which shows that *F. peregrinus* tends to damage the breast area of its victims when ripping meat from this muscle-rich area of the body. This often results in damage to the processus craniolateralis of the sternum and the processus lateralis of the coracoid (Figure 2). Overall, in ducks, about 38% of sterna (10 out of 26) had at least one processus craniolateralis broken off, and about 46% of coracoids (43 out of 94) had broken off processus lateralis. In waders, only 8% of the sterna were damaged this way (3 out of 38) but the percentage of coracoids damaged in this way (40%, or 32 out of 79) was as high as in ducks.

4 | DISCUSSION AND CONCLUSIONS

Humans rarely leave marks on the bones of the birds they eat (Laroulandie, 2005a; Serjeantson, 2009). Cut marks, burn marks, tooth marks, and other distinctive damage are usually rare even at archeological sites known to contain human food remains. There are, however, notable exceptions describing numerous traces of human activity on bird bones (e.g., Cassoli & Tagliacozzo, 1997; Goffette et al., 2020; Laroulandie, 2005b, 2014; Tagliacozzo & Gala, 2002). In view of the

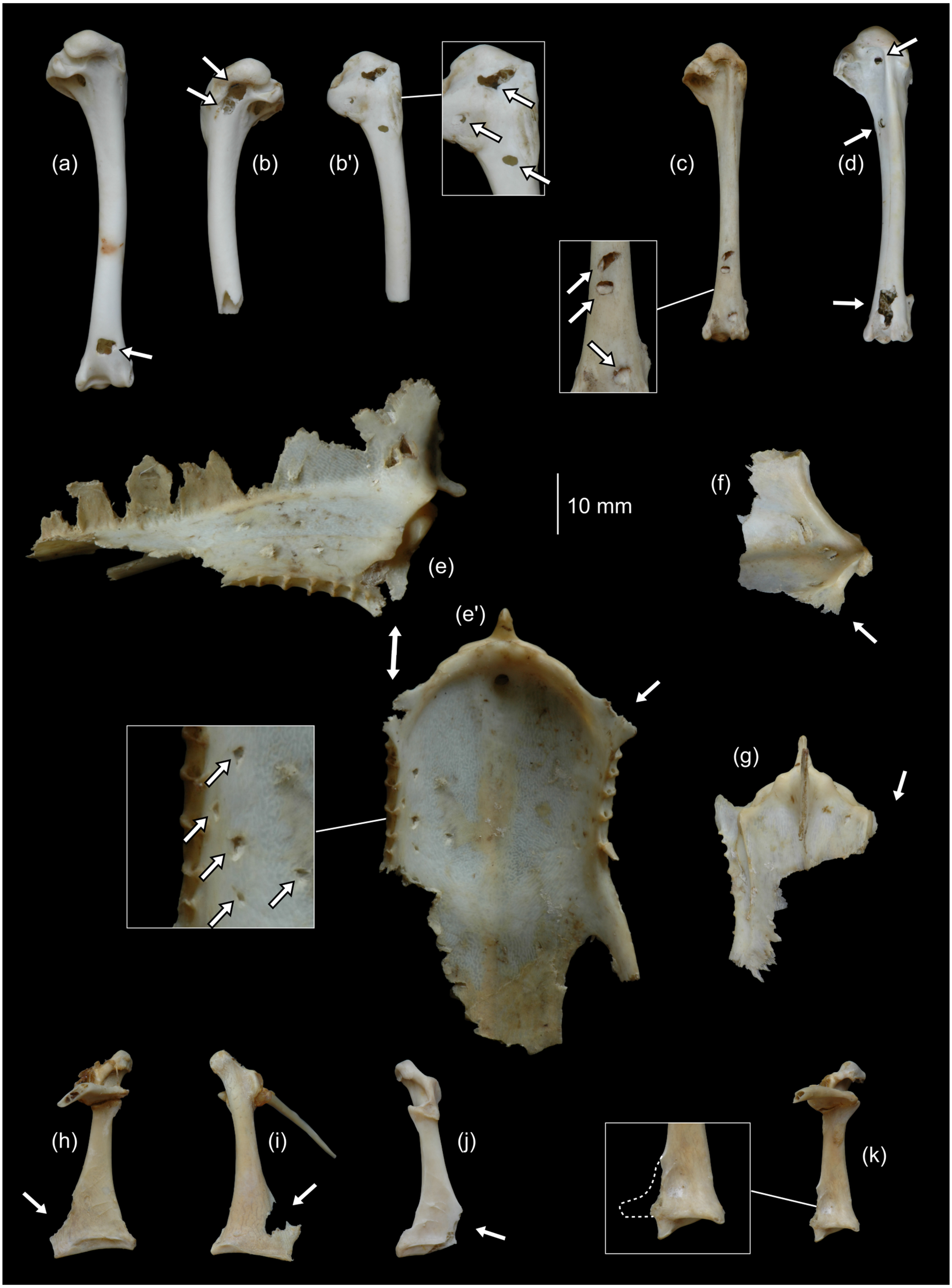

FIGURE 2 Legend on next page.

FIGURE 2 Damage to duck (a, b, b′, e, e′, h–j) and wader (c, d, f, g, k) bones recovered from noningested food remains of the peregrine falcon: (a) humerus with perforation in distal end; (b, b′) proximal humerus with multiple perforations; (c, d) humeri with multiple perforations; and (e, e′) sternum in lateral and dorsal view, respectively, with multiple perforations and both processus craniolaterales broken off. Note the jagged edges of the fracture; (f) anterior part of sternum with damaged processus craniolateralis; (g) sternum with damaged processus craniolateralis; and (h–k) coracoids with damaged processus lateralis [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 4 Ducks and waders recovered from noningested food remains of the peregrine falcon: Ratios of wing to leg elements, and proximal to distal elements, calculated from minimum number of elements (MNE)

Taxon	Wing–leg	Prox–dist
Ducks	83.6	74.8
Waders	73.5	67.7

TABLE 5 Perforated bones of ducks and waders recovered from noningested food remains of the peregrine falcon

	Ducks		Waders	
Punctured bones	Quantity (*N*)	Punctured element frequency (%)	Quantity (*N*)	Punctured element frequency (%)
Coracoid	1	1	1	1
Humerus	53	19	54	25
Ulna	3	4	2	3
Femur	1	5	1	8
tbt	-	-	1	2
Skull and beak	-	-	1	6
Sternum	13	50	19	50
Pelvis	1	33	-	-
Total	72	10	79	11

Abbreviation: tbt, tibiotarsus.

frequent lack of direct evidence of human activity, one has to resort to various taphonomic analyses.

The predominance of the humerus in food remains is typical for both human-derived assemblages and those accumulated by different species of birds of prey (Bochenski, 2005). The difference is that in the materials accumulated by humans, apart from humeri, there is usually also a lot of femora (Baales, 1992; Mourer-Chauviré, 1983) whereas in food remains of diurnal birds of prey, apart from humeri, there are usually also many coracoids (Bochenski, 2005). The predominance of these two skeletal elements (humerus and coracoid) has been observed, for example, in food remains of the imperial eagle, golden eagle, gyrfalcon, and goshawk (Bochenski et al., 1997; Bochenski et al., 1999; Bochenski & Tornberg, 2003; Wertz et al., 2021). In pellets of large owls such as eagle owl and snowy owl, apart from traces of digestion, the predominance of tarsometatarsi is characteristic (Baales, 1992; Bochenski, 2005; Bochenski et al., 1993; Bochenski & Nekrasov, 2001; Laroulandie, 2002), although the size of the prey can also influence the anatomical representation (Rufà & Laroulandie, 2019). The currently studied material is dominated by humeri and, to a lesser extent, coracoids, whereas leg bones are rare. As shown above, it corresponds to the traits typical of many diurnal birds of prey. This is also in line with the data obtained for the pigeon victims of the peregrine falcon (Laroulandie, 2002).

Low fragmentation of most long bones in food remains of the peregrine falcon matches Category 3 predators, where over 60% of the bones are unbroken (Bochenski, 2005). This category includes most species of diurnal birds of prey including pigeon victims of the peregrine falcon (Bochenski et al., 2009; Bochenski & Tornberg, 2003; Laroulandie, 2002; Lloveras, Nadal, et al., 2014; Wertz et al., 2021). Another characteristic of diurnal birds of prey, also present in the currently studied food remains of the peregrine falcon, is the very low degree of breakage of the coracoids, which distinguishes their food remains from the owls, and the relatively high degree of fragmentation of the scapulae and tibiotarsi (Bochenski, 2005). The sternum with the preserved rostrum sterni and the jagged edges of the fractures is also typical of the noningested food remains of other diurnal birds of prey (Bochenski et al., 2009; Lloveras et al., 2018; Lloveras, Nadal, et al., 2014; Wertz et al., 2021) and gulls (Serjeantson et al., 1993).

In most cases, the proportions of wing to leg bones clearly differentiate pellets of owls and diurnal birds of prey, where the wing-to-leg ratio is close to 1:1 from uneaten food remains of diurnal birds of prey, where wing elements clearly predominate (Bochenski, 2005). In the present research, the pronounced predominance of the wing bones in both ducks and waders fits very well with the pattern typical of uneaten food remains of most diurnal birds of prey, including pigeon victims of the peregrine falcon (Bochenski et al., 1997; Laroulandie, 2002; Lloveras, Nadal, et al., 2014; Lloveras, Thomas, et al., 2014; Montalvo et al., 2011; Wertz et al., 2021). Assemblages collected by humans are more difficult to characterize unambiguously in terms of the wing-to-leg ratio, because these proportions depend on many different factors, including the purpose for which the birds were hunted, the manner of hunting, and the transport of the carcasses (Bovy, 2012; Ericson, 1987; Laroulandie, 2010; Lefèvre & Laroulandie, 2014).

The proximal to distal element ratio distinguishes food remains of three groups of predators (Bochenski, 2005; Bochenski & Nekrasov, 2001). Category 1 consists of pellets of durinal birds of prey (ratio 1:1), Category 2 includes pellets of all owls and uneaten food remains of the gyrfalcon and imperial eagle (proximal elements account for approximately 60%), and Category 3 consists of uneaten food remains of the golden eagle and goshawk (proximal elements account for 80% or more) (Bochenski, 2005; Wertz et al., 2021). The values for uneaten food remains in the present study fall between Category 2 and Category 3 predators. In this respect, both ducks and waders differ slightly from pigeon victims of the peregrine falcon, which fall under Category 2 (Bochenski, 2005; Laroulandie, 2002). This may be due to the relatively small sample of pigeons in the Laroulandie (2002) study or some other factors that are currently difficult to explain.

Current research indicates that the peregrine falcon perforates the bones of its victims to a moderate extent (about 10% to 11%), which is similar to the degree of bone perforation by Bonelli's eagle (6%), goshawk (10%), and golden eagle (14%) (Lloveras, Thomas, et al., 2014; Wertz et al., 2021; Lloveras et al., 2018, respectively). A greater degree of bone perforation was reported for the Egyptian vulture (28%) and pigeon victims of the peregrine falcon (37%) (Lloveras, Nadal, et al., 2014; Laroulandie, 2002, respectively). However, all these data should be treated with caution as they may be affected by various factors including small sample size, specific bone anatomy, age of prey, and others. The elements of the skeleton most frequently perforated in the present research (sternum and humerus) were also often perforated by other species of diurnal birds of prey, which is probably due to the relatively large surface of these bones and their location close to large muscles. On distal humerus, the location of perforations made by peregrine falcons differs from the location of perforations made by humans. During the dismemberment of the bird by humans, perforation may occur within the fossa olecrani, which is the result of overextension of the elbow joint (Laroulandie, 2005a, 2005b). Peregrine falcons seem to puncture bones elsewhere with their beak and/or claws, and the perforations vary in their shape, quantity, and placement (Figure 2a,c–d).

The simultaneous damage to the sternum by fracture of the processus craniolateralis and damage to the coracoid by fracture of the processus lateralis has already been described for victims of the northern goshawk (Wertz et al., 2021). It can be expected that other species of diurnal raptors also damage the bones of their prey in this way. This type of damage has never been observed in human food debris. The area of the bird's breast is attractive due to the large amount of meat that predators tear off the prey before swallowing.

The composition of the fauna identified in a given assemblage is one of the basic clues as to the origin of the accumulated remains (Andrews, 1990; Bochenski, 2005; Lloveras et al., 2018). However, the size of the prey and their abundance in the habitat where the predator likes to hunt are even more important than the list of species itself. It is known that the peregrine falcon most often hunts for medium-sized birds, whose taxonomic composition depends on the habitat and geographic region (Cramp & Simmons, 1980). This is also reflected in our material, where ducks and waders clearly dominate and all the much smaller and much larger birds are rarer.

All factors analyzed in this paper have recently been included in multitaxa taphonomic approaches intended to provide a more complete picture of a given bone assemblage (e.g., Denys et al., 2018; Lebreton et al., 2020).

As shown in the present study, damage to bird bones in food remains of the peregrine falcon is largely typical of damage caused by other species of diurnal birds of prey. Also, the differences between bone damage in ducks, waders (both current research), and pigeons (Laroulandie, 2002) are relatively small, which bodes well for identifying the damage in different geographic regions where the peregrine falcon hunts for different prey. Minor differences in the frequency of a given type of damage may result from a small sample size in different studies or from the relative difference between the size of the prey and the predator. However, the overall pattern of damage is clearly visible and should be discernable at archeological sites.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SHORT REPORT

Where the snags are: Looking into bird bones

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Abstract

A study of bird remains from the Koziarnia Cave (Poland) revealed the presence of nearly a dozen bony shreds (*snags*) projecting from the natural canals in bones; the snags were made of a material that accumulated during the Late Pleistocene. This paper describes this phenomenon and determines the most probable agent responsible for its occurrence by utilizing observations of snag microstructure, taphonomic analysis of bird assemblages from Koziarnia Cave, and surveys of collected bird remains (modern and fossilized). The presence of snag may be a good qualitative indicator of an agent responsible for the accumulation of bird bones at archeological sites and could be useful in future taphonomic studies.

KEYWORDS

bird bones, cave archeology, intratendinous ossification, scientific inquiry, taphonomy, zooarcheology

1 | INTRODUCTION

During a re-examination of bird bones from the Koziarnia Cave for a different project (Kot et al., 2019), we noticed needle-like structures projecting from bone canals of birds, mainly from tendinous canals (details in Section 3; Figures 1–3). To the best of our knowledge, this phenomenon (hereafter referred to as *snags*) has not yet been described. From visual analysis alone, the snags appear to be bony shreds jammed into the bone canals; to some scholars, this may suggest intentional human activity.

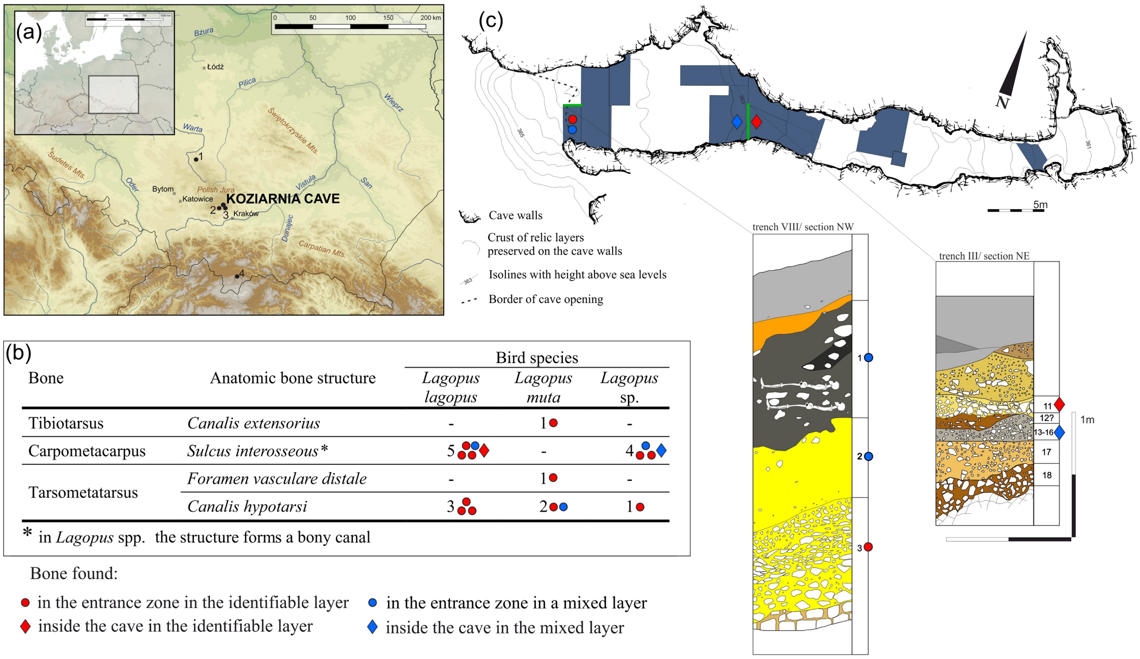
Humans worldwide have used animal bones for millennia—including producing needles (e.g., d'Errico et al., 2018) and splinters from bird remains (Laroulandie, 2014; Serjeantson, 2009).

Such needles and splinters could have had varied uses, including making clothes. Shreds of bone jammed in the tendinous canals of other bones could suggest the use for either ornamental intentions or for extracting tendons. The tendons could have been used as substitutes for fibrous plants for making threads, considering that plants do not thrive in harsh cold climates. However, because tendons are poorly preserved at archeological sites, it is difficult to confirm their presence and thus evaluate their significance.

Other hypotheses concerning the presence of snags include sheer coincidence, recurring activity of an animal predator, and humans processing birds with their bare hands. In these cases, the snags would be intratendinous ossifications (IOs), which are a distinct structural feature of the musculoskeletal systems of various birds such as galliforms, owls, passerines, hummingbirds, or penguins (Berge & Storer, 1995). Validating the hypotheses regarding the involvement of animal or human agents for the presence of snags could provide a qualitative indicator useful in future taphonomic studies of bone assemblages from archeological sites.

2 | MATERIAL AND METHODS

The main material of our study consists of 17 bird bones with bony shreds (snags) jammed into their canals such that they project from natural openings in the bones (details in Section 3; Figures 1–3). The bones were found at the Koziarnia Cave (Poland) during archeological fieldwork conducted from 1958 to 1963 (Chmielewski et al., 1967) and were analyzed along with the other bird remains found there (Bocheński, 1974).



Bone	Anatomic bone structure	Bird species *Lagopus lagopus*	 *Lagopus muta*	 *Lagopus* sp.
Tibiotarsus	*Canalis extensorius*	-	1 🔴	-
Carpometacarpus	*Sulcus interosseous**	5 🔴🔴🔴🔵♦	-	4 🔴🔴🔵🔷
Tarsometatarsus	*Foramen vasculare distale*	-	1 🔴	-
	Canalis hypotarsi	3 🔴🔴🔴	2 🔴🔵	1 🔴

* in *Lagopus* spp. the structure forms a bony canal

Bone found:

- 🔴 in the entrance zone in the identifiable layer
- ♦ inside the cave in the identifiable layer
- 🔵 in the entrance zone in a mixed layer
- 🔷 inside the cave in the mixed layer

FIGURE 1 (a) Locations of Koziarnia Cave and other sites mentioned in the text: 1, Rockshelter in Krucza Skała; 2, Rockshelter in Żytnia Skała; 3, Mamutowa Cave; 4, Obłazowa Cave. (b,c) The number and placement of the *snags* found within bones and cave trenches (steel-blue polygons) and layers in Koziarnia Cave. The map template is courtesy of Claudio Berto [Colour figure can be viewed at wileyonlinelibrary.com]

The snags were noticed only recently during a re-examination of the collection of bird remains for a new project that aimed to determine and re-evaluate the stratigraphy and chronology of the cave and track human and animal activity therein (Kot et al., 2019, 2020).

Twelve bones with snags were found in the entrance zone of the cave in a loess Layer VIII-3 (Figure 1b,c), dating from the Late Pleistocene (MIS 3/2) (Berto et al., 2021; Kot et al., 2020). Single flint artifacts found in this layer, which can be attributed to the Gravettian technocomplex, indicated human occupation in the Upper Paleolithic (Kot et al., 2020). One bone with a snag came from Layer 2 in Trench IV inside the cave; a cave bear's bone from the same layer was radiocarbon dated to 31–29 ky cal (Kot et al., 2020). Both Layers VIII-3 and IV-2 were regarded as a single chronostratigraphic unit (Layer 11) by Chmielewski et al. (1967), but new results did not confirm the previous correlation of the layers from the inner and outer part of the cave (Kot et al., 2020). For this reason, in the paper, we use a unified layer numbering for the inner part of the cave, whereas the layers found in the entrance zone (Trench VIII) are enumerated separately. The remaining four bones with snags were recovered from sediments with mixed or undeterminable stratigraphy.

Anatomical terminology used to describe the bones and their structures follows Baumel and Witmer (1993). The osteological collection at the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, was used. All bird bones from the Koziarnia Cave were subjected to taphonomic analysis to establish the most probable depositor of bird bones in the cave. Bones covered with cave sediments were cleaned with a brush and water. The surfaces of the bones were observed under a low-power microscope (Leica MZ-6, 6.3—400× magnification) and several optical-stereoscopic microscopes (Olympus SZX9, metallographic Nikon Eclipse LV 100, and digital Nikon Shuttlepix microscopes; each with a 6.3—200× magnification). Possible traces of human activity, such as cut marks, burn marks, peeling, joint overextension (Fernández-Jalvo & Andrews, 2016; Laroulandie, 2005); animal activity such as marks showing gnawing, trampling, or traces of digestion; and postdepositional environmental modifications such as root etchings, weathering, and abrasions (Fernández-Jalvo & Andrews, 2016), were recorded. Bone frequencies were presented in terms of minimum number of elements (MNE) values (Lyman, 1994; Serjeantson, 2009). Select bones were observed using field emission scanning electron microscopy (SEM-FE), which enabled the use of energy dispersive X-ray spectroscopy (SEM-EDS) for quantitative elemental analysis. A standard acceleration voltage of 20 kV was used for the latter. Two EDS spectrometers placed on opposite sides of the SEM specimen chamber enabled the acquisition of sufficient SEM-EDS spectra, regardless of the orientation and morphology of the sample.

To determine the contribution of animal activity to the features observed in the bird bones from the Koziarnia Cave, the bones discarded by birds of prey were examined. The criteria for choosing the samples were (i) the availability of the material, (ii) their origin being in a region where the relevant birds (*Lagopus* spp.) occur, and (iii) their inclusion in material discarded by a raptor that preys on *Lagopus* spp. As a result, the bones studied were those discarded by *Accipiter gentilis* and those from *Bubo bubo* pellets collected in northern Finland in the second half of the 20th century; the majority of the material

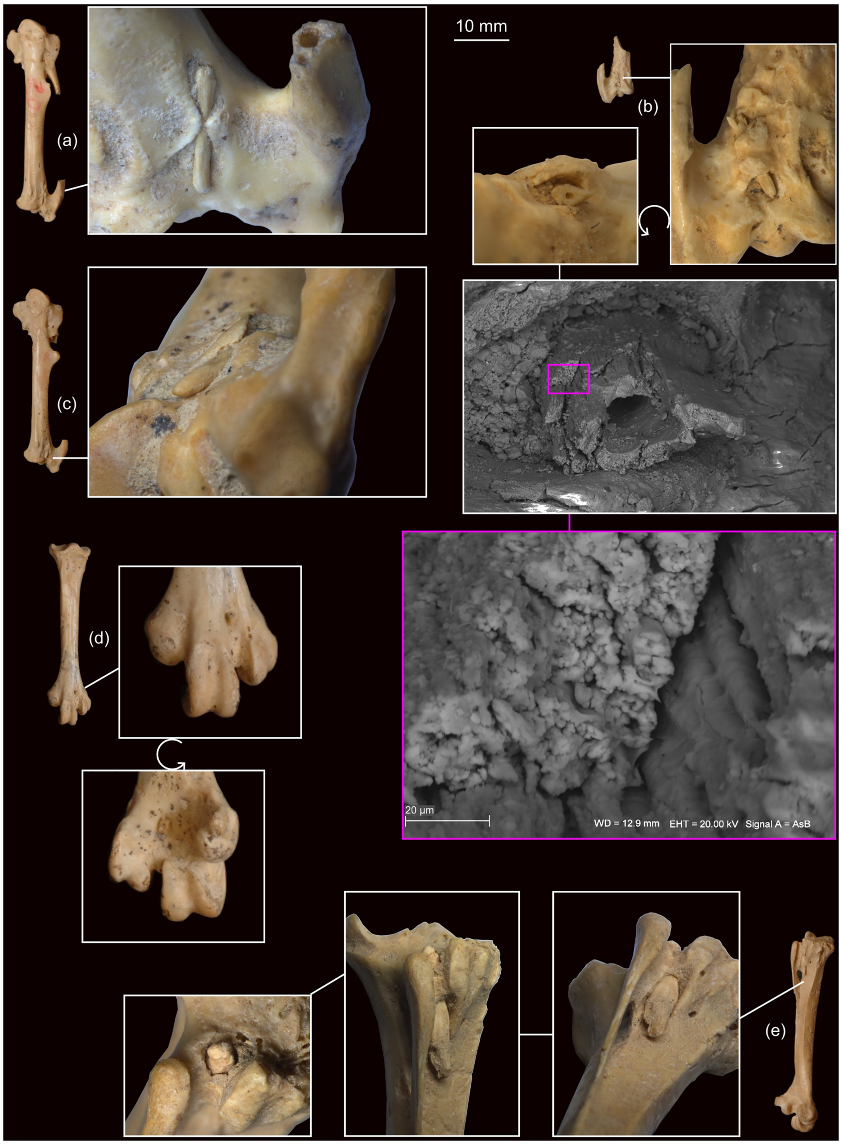


FIGURE 2 *Snags* stuck in *Lagopus* bones recovered from Koziarnia Cave; snags projecting from (a–c) tendinous canals in carpometacarpus samples, (d) vascular foramen in tarsometatarsus sample, and (e) a tendinous canal in tarsometatarsus sample [Colour figure can be viewed at wileyonlinelibrary.com]

had already been analyzed as part of other studies (Tornberg, 1997, 2001; Tornberg et al., 2006, 2012; Wertz et al., 2020). The collected remains had previously been stored at the Natural History Museum of the University of Oulu; however, since the closure of its collection, they had been stored by one of the authors (R. Tornberg).

As the aim of the survey was purely qualitative (answering the question "Is there any?"), the samples were chosen to increase the chance of a positive outcome rather to obtain a reliable frequency of occurrence. Rough estimates suggest that approximately 170 bones with natural bone canals (i.e., carpometacarpus [CMC], tibiotarsus [TBT], and tarsometatarsus [TMT]), which were discarded by *A. gentilis*, were examined. The number of bones regurgitated by *B. bubo* and analyzed was impossible to establish due to high fragmentation of the material.

Another qualitative survey of the presence of snags was conducted on bird bones from archeological sites in Poland such as the Obłazowa Cave, Mamutowa Cave, Rockshelter in Żytnia Skała, and Rockshelter in Krucza Skała (Figure 1a). The material is stored at the ISEA PAS and has been studied previously (Bocheński, 1974; Bocheński & Tomek, 2004; Lemanik et al., 2020).

3 | RESULTS AND DISCUSSION

3.1 | Description of the snags

Snags were found in three types of *Lagopus* spp. bones: CMC, TBT, and TMT (Figures 1–3). All snags, with one exception, were projected from tendinous canals; the exception was a snag projecting from a vascular foramen in the TMT (Figure 2d). The snags had a bone-like color and the general appearance of bony shreds. At least one snag was hollow in the middle; under a low-powered microscope, this may have resembled a medullary cavity, but SEM observations revealed the fibrous structure of the snag, implying that it may have been an IO

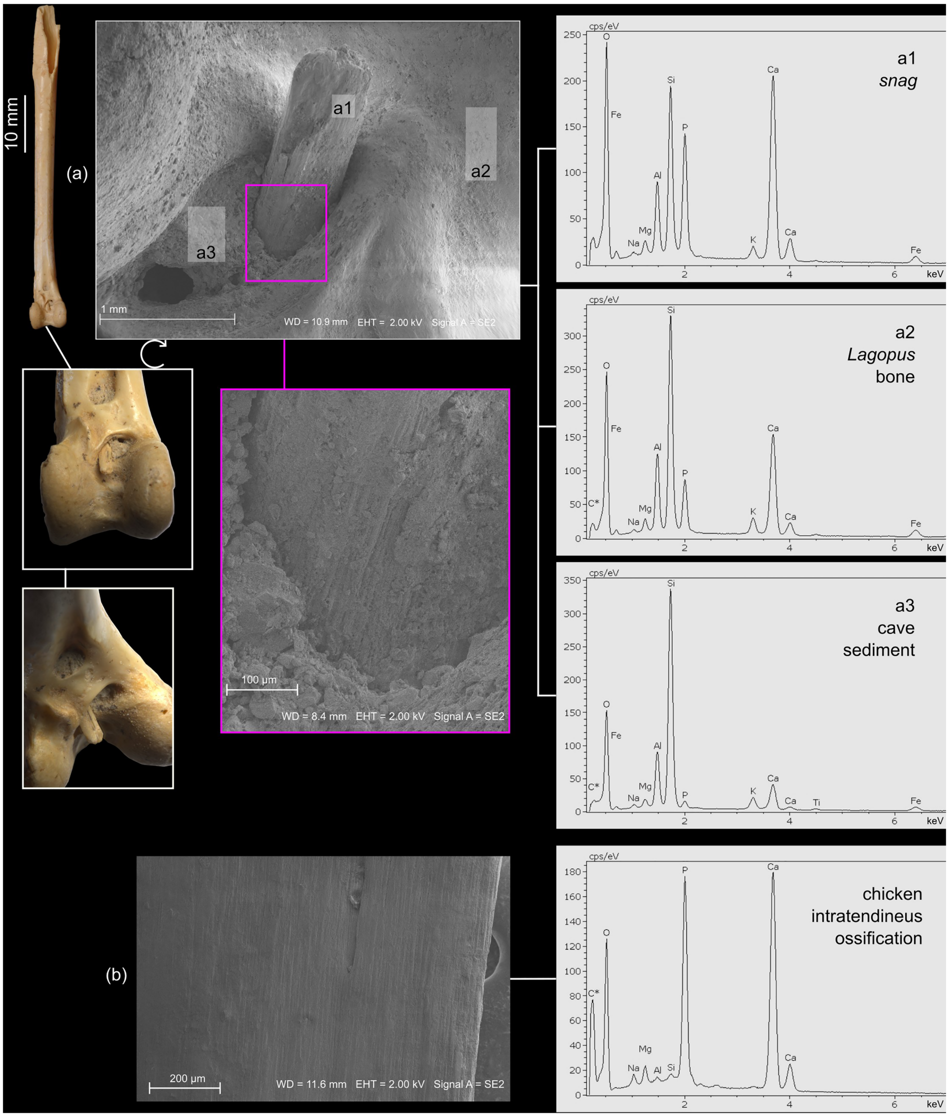


FIGURE 3 Microstructure and energy dispersive X-ray spectroscopy (EDS) spectra of (a) a *snag* projecting from a tendinous canal in a tibiotarsus sample and (b) an intra-tendinous ossification in a modern chicken. The white rectangles numbered a1–a3 show areas subjected to EDS analysis; the charts on the right present the corresponding EDS results [Colour figure can be viewed at wileyonlinelibrary.com]

(Figures 2b and 3b). The other snags appeared to have the same structure (Figure 3a). EDS revealed that a snag consisted of a bony substance, calcium phosphate (most likely hydroxylapatite), soiled with various aluminum phyllosilicates (i.e., clay minerals) from cave sediments (Figure 2). As Berge and Storer (1995) noted, the ossifications within tendons develop in "bare" or unsheathed segments of tendons at some distance from the skeletal attachment. The possible hypotheses to explain the formation of ossified tendons that get stuck in canals as snags are (1) natural postdepositional processes, such as fluvial transport or soil movement, that occur in caves; (2) pathological physiological processes; (3) predator/scavenger activity; or (4) human activity.

Hypotheses (1) and (2) imply sheer coincidence and are confuted by the nontrivial number of snags found. Bone pathologies are rare among remains of wild-living birds (Waldron, 2009). In addition, no bone with a snag is affected by a pathognomonic sign such as an eburnation (see Waldron, 2009). Hypothesis (2) also fails to explain the presence of *snags* in the vascular foramen.

The more plausible hypothesis is Hypothesis (3), according to which a snag may be a tendinous ossification that was stuck in the bone canal after a raptor/scavenger tugged or severed the tendon. The most likely raptor would be an animal that preys on *Lagopus* spp., such as a carnivorous mammal, an owl, or a diurnal bird of prey. Hypothesis (4), which suggests human activity implies, as mentioned in the introduction, the purposeful use of bird bones (e.g., for ornamentation or to extract tendons) or processing of the bird body with bare hands and teeth (Laroulandie, 2005; Steadman et al., 2002).

3.2 | Tracking bone depositors (deposited taxa, bone modifications, skeletal composition) at the site

No clear traces of human or animal activity were observed on bones with snags. Analysis of whole bird bone assemblage from the Koziarnia Cave may reveal the main depositor of the birds in the cave;

however, such an analysis can only reveal a probable reason for the snags. Grouse, including *Lagopus* spp., do not inhabit caves (Voous, 1960); therefore, it is clear that those birds were deposited therein by a raptor or scavenger. The animal depositor of the *Lagopus* can also have preyed on the rodents that were abundant at the site but not on small passerines (Berto et al., 2021). Although the remains of a few potential depositors like *Falco columbarius*, *Haliaeetus albicilla*, *Canis lupus*, and *Vulpes lagopus* have been identified at the site (Berto et al., 2021); this alone does not make them the probable depositors. As Andrews (1990) concluded, the remains of a given raptor in an assemblage suggests that it itself was also preyed upon; paradoxically, this makes this raptor the least likely depositor.

Overall, the bird bone assemblage at the Koziarnia Cave was heavily affected by postdepositional processes such as root etching and abrasion (Table S1). These may have obscured subtle traces of animal activity and may be why so few firm animal traces have been detected (Table S2). Singular tooth marks observed on *Lagopus* bones from the relevant layers (Layers VIII-3 and 11) demonstrate that at least some of the birds had been discarded by carnivorous mammals. Nevertheless, this proportion was probably rather small because bones accumulated by carnivorous mammals tend to be heavily modified either by gnawing or gastric juices (Andrews, 1990; Krajcarz & Krajcarz, 2014; Lloveras et al., 2012), and these modifications are difficult to conceal. For this reason, owls or diurnal birds of prey seem to be the more probable culprits (e.g., Andrews, 1990).

No clear traces of human activity have been discovered on bird bones from the relevant layers, although there are five cut marks on bones identified as chicken bones or galliform bones that come from mixed or uncorrelated layers; however, as mentioned before, humans can process a bird without leaving such traces. The evidence against human-created deposition is the frequency of the *Lagopus* bones deposited in the relevant layers (Figure 4). A large share of TMTs and CMCs corresponds well to bones discarded by owls, particularly snowy owls (*Bubo scandiacus*) and eagle owls (*Bubo bubo*) (Baales, 1992; Bochenski, 2005; Laroulandie, 2002); human-created assemblages usually contain a much larger share of humeri and femora (Bochenski, 2005; Mourer-Chauviré, 1983). Notably, both snowy owls and eagle owls leave the bones of their prey digested to a less-than-moderate degree (Andrews, 1990).

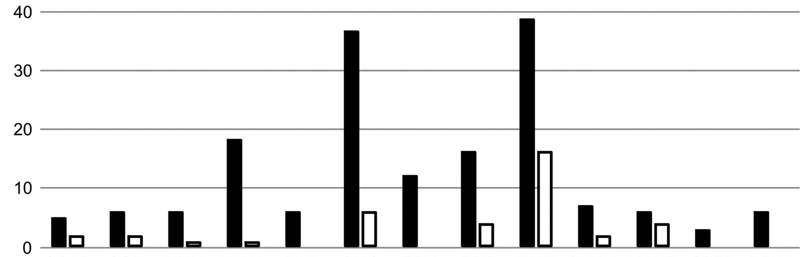
3.3 | Surveys on collections of (1) noningested bones discarded by *Accipiter gentilis*, (2) *Bubo bubo* pellets, and (3) fossil bones of *Lagopus*-sized tetraonids from various cave sites

Among the bones that were discarded by both *A. gentilis* and *B. bubo*, we discovered some with confined IOs (Figure 5a–c). Six were in the canals of *Lagopus* bones discarded by *A. gentilis* (three in CMCs and three in TBTs; Figure 5a,b) and one was in the TBT of a *Tetrao urogallus* regurgitated by *B. bubo* (Figure 5c). Both assemblages could not be compared in terms of their "IO-holding" potential, as reflected by the composition of taxa, anatomical representation, and bone fragmentation. Many bones discarded by *A. gentilis* can still be articulated and are often surrounded by entanglement of dried or ossified tendons projecting in various directions. The occurrence of such may arguably enhance the probability that an ossified tendon could reach the vascular foramen in the TMT and become stuck therein. The TBT extracted from the *B. bubo* pellet showed obvious traces of digestion (Figure 4c).

If raptors, particularly owls, are indeed responsible for the presence of snags, the occurrence of snags should not be limited to the Koziarnia Cave. A survey conducted of bird bones from available cave sites has proven this correct, and similar assemblages were found at other sites (Table S3; Figure 5d). Notably, the four assemblages in which snags were discovered are believed to have been deposited mainly by owls (Table S3). No bone with a jammed snag showed distinctive indications of predation such as tooth marks or digestion traces.

4 | SUMMARY AND CONCLUDING REMARKS

This paper described the phenomenon of snags: bony shreds jammed in the remains of birds recovered at some cave sites, including the Koziarnia Cave. The snags are built of threads that resemble the structure of bird IOs. The taphonomic study of bird bones from the Koziarnia Cave suggested that an owl was the most likely depositor of the *Lagopus* bones; they were also indicated as the most likely depositors of bones with snags at other sites where these were found.



	SCAP	COR	HUM	ULNA	RAD	CMC	FEM	TBT	TMT	SKULL	MAND	STER	PELV
3-VIII ■	5	6	6	18	6	36	12	16	38	7	6	3	6
11 □	2	2	1	1	0	6	0	4	16	2	4	0	0

FIGURE 4 Frequency of the *Lagopus* bones in Koziarnia Cave from the layers in which the *snags* were discovered (Layer VIII-3 and Layer 11), presented in minimum number of element (MNE) values. cmc, carpometacarpus; cor, coracoid; fem, femur; hum, humerus; mand, mandibula; pelv; pelvis; rad, radius; scap, scapula; ster, sternum; tbt, tibiotarsus; tmt, tarsometatarsus

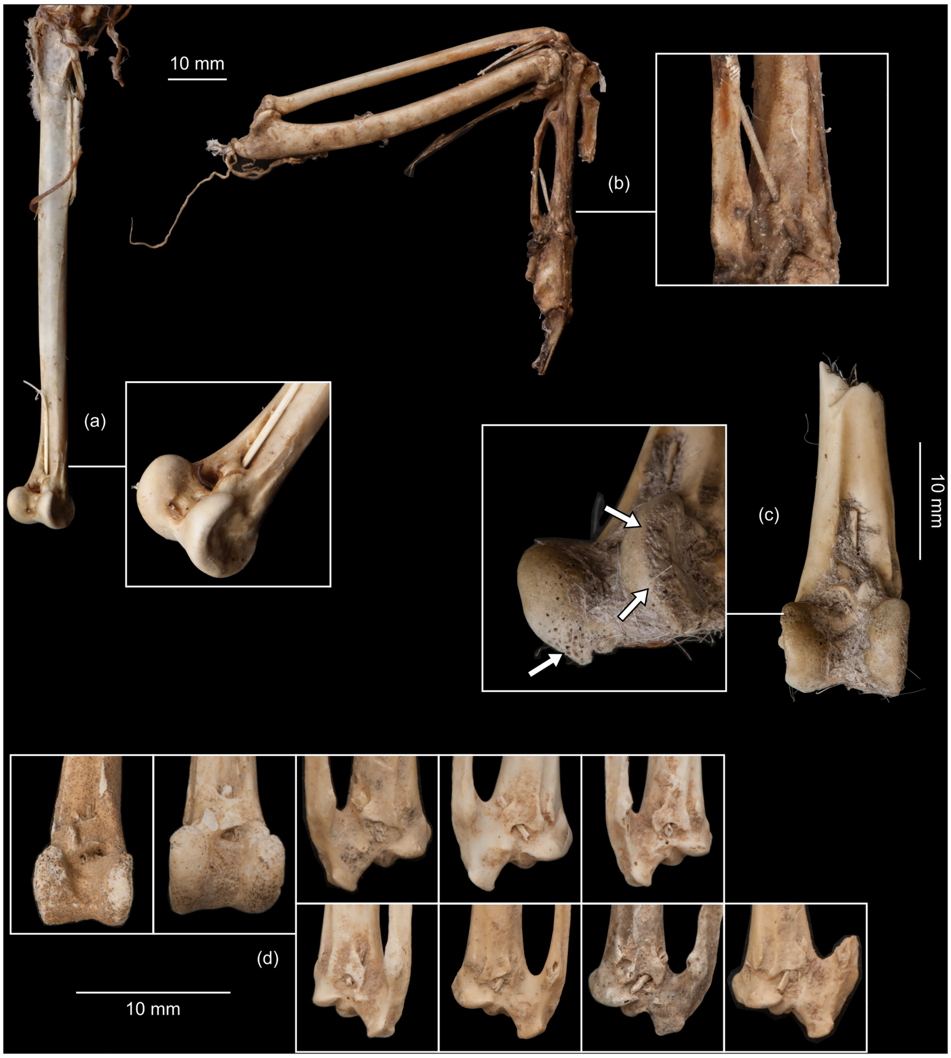


FIGURE 5 Bones with *snags* discovered during the surveys conducted as part of this study. (a,b) *Lagopus* bones discarded by *Accipiter gentilis*, (c) *Tetrao urogallus* bone regurgitated by *Bubo bubo*; the arrows show the clear traces of digestion, (d) *Lagopus* spp. or *Lagopus*-sized galliform bones recovered from various cave sites [Colour figure can be viewed at wileyonlinelibrary.com]

Surveys of modern material discarded by a large diurnal bird of prey (*A. gentilis*) and a large owl (*B. bubo*) revealed the presence of IOs stuck in the natural canals of the bones of their prey. Large diurnal birds of prey and owls consume their prey in different ways; the former tend to strip the flesh off them and eat only part of the bones, whereas the latter are more prone to swallow the prey whole or in large pieces (Andrews, 1990; Serjeantson, 2009). It is obvious that the *T. urogallus* eaten by the *B. bubo* was consumed in pieces. We can only hypothesize how the snags became jammed in the canals; it seems clear that this might have occurred due to tugging on a tendon while the flesh was being stripped off the carcass, or as the carcass was being divided, although this could also have happened as the bones were squeezed during pellet formation. We do not know whether snags may occur in assemblages accumulated by carnivorous mammals, although their different methods of processing food (crushing and shredding) may result in a negative outcome. It is even less probable, that a snag could be found among bones discarded by humans. Humans can obtain meat without tugging the tendons in bird carcasses; they may use sharp tools to divide these, and/or they may cook them—thereby reducing firmness and cohesion of the flesh—before portioning the food.

The presence of snags may therefore be a good qualitative indicator of bird of prey depositions at archeological sites.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on reasonable request from the corresponding author. Pertinent additional data can be found in the Supporting Information of this article.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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Supporting information

Filename	Description
oa2976-sup-001-Data S1.docxWord 2007 document , 15.9 KB	Table S1. Post-depositional modifications observed on the bird bone assemblage. Table S2. Raptor/scavenger modifications on the *Lagopus* bones. Table S3. *Snags* discovered in the fossil material stored at ISEA PAS

Table S1. Post-depositional modifications observed on bird bone assemblage at Koziarnia Cave (stratigraphy follows Berto et al. in prep.)

	Reliable layers									Unreliable and mixed layers	
	Cave entrance	Cave interior									
Layer	3-VIII	9	10	11	12	13	15	17	18	Cave entrance	Cave interior
Bones (N)	241	1	30	116	25	6	1	2	4	90	294
abrasion (%)	27	100	60	44	64	33		50		29	32
root etching (%)	83									44	1.4
weathering (%)	5				8			100	75	6	3
rodent gnawing (%)				0.9						1.1	0.7
manganese (%)	55		17	23	52	50	100	50		24	31

Table S2. Raptor/scavenger modifications on *Lagopus* bones from Koziarnia Cave (stratigraphy follows Berto et al. in prep.)

	Reliable layers									Unreliable and mixed layers	
	Cave entrance	Cave interior									
Layer	3-VIII	9	10	11	12	13	15	17	18	Cave entrance	Cave interior
All *Lagopus* bones	229	1	24	96	24	6	1	2	4	59	215
gnawed bones	3			1	2					2	0
digested bones	11			1				1		3	5

Table S3. *Snags* discovered in the fossil material stored at ISEA PAS

Found bones with *snags*	Site	Layer/chronology	Implied depositor of the bones
7 bones (CMC) of the galliform bird of *Lagopus* size.	Obłazowa Cave, Western Entrance (WE)	IIA (Magdalenian)	*Stix nebulosa*: based on traces of digestion on rodents incisors and molars. (Lemanik et al. 2020)
1 bone (CMC) of *L. lagopus*.	Rockshelter in Żytnia Skała	Layer corresponding to Würm glaciation	Most probably owls, although human or other raptor might also have contributed (remark in the introduction that concerns multiple sites; Bocheński 1974)
3 bones (CMC) of *L. lagopus* and 2 bones (CMC) of *Lagopus* sp.	Mamutowa Cave	Layer 2 (Würm)	
5 bones (3 CMC, 2 TBT) of *L. lagopus.*	Rockshelter in Krucza Skała	Layer: 3/2, II/I, 4, 3, “?”; The oldest layer (I) dated to 12520 BP.	Most probably an owl, with a suggestion of *Bubo bubo*. Human regarded as improbable. (Bocheński and Tomek 2004)

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SPECIAL ISSUE PAPER

Whose talon is this? A manual for the identification of ungual phalanges of European birds of prey: Falcons and owls

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Abstract

This paper is the first of two scheduled publications for this project. It contains a dichotomous key to the identification of the ungual phalanges of European owls and falcons; the second part will contain accipitrids. The manual(s) will facilitate the work of zooarchaeologists and palaeontologists, especially since comparative specimens in osteological collections are often difficult to access and/or incomplete. This, in turn, will indirectly contribute to a more in-depth interpretation of zooarcheological materials, because bird talons were used to produce symbolic objects and decorations in different archeological periods and in various geographical areas.

KEYWORDS
claws, dichotomous key, falcons, owls, talons, ungual phalanges, zooarcheology

1 | INTRODUCTION

Avian talons are composed of two components: the bony core and the keratinous sheath that envelops it. The keratin sheath decomposes and is not preserved in archeological materials. The bony core of the last phalanx or talon is called ungual. This work is about ungual phalanges.

Few elements of the skeleton have a cognitive potential in archeology as big as the ungual phalanges of birds of prey. The use of talons for decoration or as symbolic objects was widespread throughout the world and across various epochs and archeological cultures; invariably the talons used by humans were always from raptors (Serjeantson, 2009). People perforated talons for suspension in as faraway places as Romania (e.g., Gál, 2005), Estonia (Konsa et al., 2003; Luik, 2012), and Sweden (Clark, 1948; Forssander, 1931). A peregrine falcon ungual phalanx is known from pre-Viking Age ship burial in Estonia (Peets et al., 2013). The talons of large owls such as Eagle Owl (*Bubo bubo*) and Snowy Owl (*Bubo scandiacus*) may also have had similar symbolic importance because they were saved deliberately by people at various prehistoric sites (Altuna et al., 1991; Eastham, 1998; Gourichon, 1994; Harrison, 1986; Laroulandie, 2016; Mourer Chauviré, 1975, 1983; Mourer-Chauviré, 2019). Already Neanderthals are known to deliberately remove talons from birds of prey as it can be inferred from cut-marks on multiple specimens from various localities in France, Italy, and Croatia (Laroulandie et al., 2016; Morin & Laroulandie, 2012; Radovčić et al., 2015; Romandini et al., 2014). Hunters must have associated talons of birds of prey with power and with hunting skill, and they might wear or carry them to ensure the virtues for themselves (Serjeantson, 2009).

The identification of pedal phalanges including ungual phalanges is always a challenge because unlike typical elements that count two (left and right), there are eight ungual phalanges (four toes on each leg) on every bird of prey. Ungual phalanges from each toe differ in size and morphology (e.g., Kessler, 2017), which must be included when assessing the individual variation within a species. Also, there is big sexual size dimorphism in many diurnal and nocturnal raptors, with females being larger than males. The matter is further complicated by the fact that there are several dozen species of diurnal birds of prey and owls in Europe, and comparative specimens in osteological collections are often incomplete.

So far, no proper manuals have been developed to help identify the ungual phalanges of diurnal birds of prey and owls. A step in the right direction is descriptions of morphological differences between various species of falcons (Solti, 1980, 1981a, 1981b, 1996), but the papers contain very few illustrations, and they do not include a proper dichotomous key. Another interesting approach is that described by Mosto and Tambussi (2014), who showed that an isolated talon of North American raptors can be correlated with the corresponding digit (I, II, III or IV) based on a series of ratios, calculations and morphological features.

The present study is meant to fill the gap by creating a manual for the identification of ungual phalanges of all European and Levantine falcons (Falconidae) and owls (Strigiformes). The second part of the publication, which is planned in the near future, will contain the key to the ungual phalanges of all European accipitrids (Accipitridae).

2 | MATERIAL AND METHODS

2.1 | Species and collections

The manual covers all species of owls and falcons found in Europe, except for the Eurasian pygmy owl *Glaucidium passerinum* and the lanner falcon *Falco biarmicus* which were not available in the collections studied. *G. passerinum* is the smallest owl in Europe, even smaller than *Otus scops* (Cramp, 1985). *F. biarmicus* is the size of *Falco peregrinus*, occurs in southern Europe and Africa, and is a falconry bird (Cramp & Simmons, 1980). The manual does not cover any extinct species, nor does it take into account extant species that have changed their range and are currently not present in Europe. The number of specimens of each species studied varied considerably, reflecting the situation in osteological collections in Europe. We examined a total of 594 specimens from eight collections (Table S1): ISEA – Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland; NMNHS – National Museum of Natural History, Bulgarian Academy of Sciences, Sofia, Bulgaria; NHMUT – Natural History Museum, University of Tartu, Estonia; ABo - ArchaeoBone, Haren, the Netherlands; HNHM - Hungarian Natural History Museum, Budapest, Hungary; PACEA – De la Préhistoire à l'Actuel: Culture, Environnement et Anthropologie, Université de Bordeaux, France; UMB – University Museum of Bergen, Department of Natural History, Bergen, Norway; NMNHU - National Museum of Natural History at the National Academy of Sciences of Ukraine, Kyiv, Ukraine.

The introductory part of the manual is designed to separate all falcons, owls, and accipitrids, that is, birds belonging to three different orders (Falconiformes, Strigiformes and Accipitriformes) and representing five different families (Falconidae, Strigidae, Tytonidae, Accipitridae, and Pandionidae) (Dickinson & Remsen, 2013). This turned out to be a difficult task. Therefore, we decided to identify "atypical" species already in the introductory part of the manual (e.g. *Tyto alba* or *O. scops*). The manual for the genus *Falco* also includes two non-falcon species (*T. alba* and *Pernis apivorus*), because due to their superficial similarity, it may happen that someone could pre-classify them there. *T. alba* is also independently identified in the introductory part of the manual, and *P. apivorus* is also included in the Accipitridae.

2.2 | Measurements

Measurements were taken using digital calipers accurate to 0.01 mm and captured directly to computer. The measurements are illustrated in Figures 1 and S1 and summarized in Data S1. We used metric features in many places in the manual. The boundaries of the division are of course arbitrary; they correctly define the lower and/or upper limits for the specimens we have examined from some species, but the side effect is that some species are unintentionally split into two groups (Appendix S1). In such cases, we try to include such a split species in both branches of the manual. Another danger of arbitrary splitting is that the ranges of some species are very close to the border of the split. In such cases, special caution is recommended, because individuals that fall outside the given size range can always be found. The probability of such an event is the greater the fewer specimens of a given species have been measured. Due to the relatively small number of measured individuals from many species, we recommend that the size ranges should be treated as indicative and not final values. It should also be remembered that specimens from modern populations may differ in size from individuals of the same species from (pre) historical times (e.g., Mourer Chauviré, 1975).

2.3 | Osteological features and manual layout

Osteological terminology follows Baumel and Witmer (1993) and is illustrated in Figure 1. As for the morphological features, we have chosen to rely only on the more obvious ones, which will be visible in the photographs and which can be clearly described. As is the case with other elements of the skeleton, it is difficult to find an obvious feature that can be applied to all European species; there are always species that are ambiguous or nonspecific in terms of a certain feature. Also, there are very few, if any, features that would apply to all specimens of a given species. This is a well-known but rarely admitted fact in

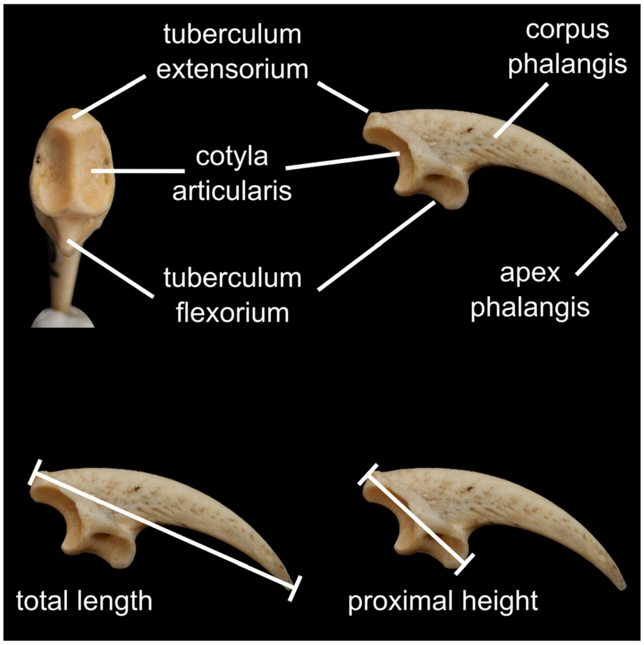

FIGURE 1 Osteological terminology and selected measurements of ungual phalanges of owls and falcons used in the printed part of the manual. All measurements are illustrated in Figure S1. [Colour figure can be viewed at wileyonlinelibrary.com]

morphological studies. In this manual, we have applied a similar principle to our earlier keys (Bochenski, 1994; Tomek & Bochenski, 2000): At least two thirds of the specimens of a given species must exhibit a given condition to be considered typical of that species. This means, however, that almost always less typical specimens may occur.

Some features were used several times in various places in the manual, sometimes slightly modified. While this may appear to be an editorial error, it was a deliberate act; the same feature can distinguish between different taxa.

Some anatomical structures are very small and confirmation of their presence requires the use of up to 10X magnification, depending on personal eyesight.

In the subsequent sections of the manual, taxa that pass through a given point are listed in square brackets, and digit numbers are given in round brackets. This is to facilitate comparisons with modern specimens, and in doubtful cases (e.g., a damaged specimen) end the determination at an earlier stage.

Some branches of our manual end up with two or more undifferentiated taxa. This is especially true of smaller species, which are less frequently found in archeological deposits. We preferred to refrain from distinguishing some taxa because we had too few individuals to take such a risk. We leave any possible expansion of the unfinished legs of the key to experienced researchers who have access to other rich comparative collections.

The illustrations relating to specific features described in the manual (Figures 2–8) are not to scale. They show the individual states of each feature and are intended to complement the description and facilitate the location of a given structure on bone.

Ungual phalanges of all owl species and large falcons are illustrated in the photos in several predefined views: lateral, medial, articular, flexorial, and flexorio-articular views. These specimens are shown both at life size and enlarged and are available as supporting information (Appendix S2). With the exception of *Falco tinnunculus*, the small falcons are not included there because they are so small and similar to each other that it would not make much sense.

Like any other, this manual is intended to help identify bird bones; it cannot replace comparisons with real bones from comparative collections.

3 | MANUAL FOR THE IDENTIFICATION

3.1 | Whose talon is this? (Figure 2)

Features typical of ungual phalanges of diurnal birds of prey and owls: (i) The cotyla articularis is divided by a dorso-plantar ridge into lateral and medial parts. In most cases the ridge is distinct, but sometimes, it is only a slight longitudinal bulge in the plantar part of the cotyla articularis. This feature distinguishes nearly all birds (except the great bustard) from mammals; (ii) the corpus phalangis of diurnal birds of prey and owls bear no visible neurovascular sulci along the lateral and medial surfaces of the bone, contrary to most other birds that have such sulci; (iii) the tuberculum flexorium of diurnal birds of prey and owls can be of various shapes but is always large, prominent, and well pronounced. Of the non-predatory birds, only the ungual phalanges of the swifts (Apodiformes) are superficially similar to the phalanges of the falcons in that the tuberculum flexorium is situated almost parallel to the dorsal edge of the phalanx. However, in swifts, the tuberculum is closer to the center of the phalanx length. Common Swift *Apus apus* is clearly smaller than the smallest falcons, and only the ungual phalanges of the Alpine swift *Tachymarptis melba* are of a similar size to the phalanges of the smallest falcons.

3.2 | Distinguishing owls, falcons, accipitrids, and identification of odd taxa including *Pandion*

1 (Figure 2)

a - In lateral and/or medial view, the tuberculum flexorium protrudes extremely far plantarly and is narrow proximo-distally……***Pandion haliaetus*** **(1–4)**

b - In lateral and/or medial view, the tuberculum flexorium protrudes much less plantarly and is elongated proximo-distally………………..2

2 (Figure 2)

a - (i) Proximal height less than 12.0 mm; AND (ii) There are no foramina on either the lateral or medial edges (or just below them) of the cotyla articularis. (Foramina clearly below the edge of the cotyla articularis, often situated in a shallow groove, are regarded as "no foramina"); AND (iii) There is no bony collar or crest around the cotyla articularis; the collar is only on both sides of the tuberculum flexorium. [all *Falco* spp. (1–4) and possibly some specimens of *P. apivorus* and *T. alba*]……………………………35

b - (i) Proximal height of any size; (ii) There are small foramina on the lateral and medial edges (or just below them) of the cotyla articularis, but sometimes there is a foramen on one side only; (iii) Bony collar or crest around the cotyla articularis is present (most Strigiformes) or absent (Accipitridae). [Strigiformes and Accipitridae]……………………………………………………………………3

Note: The foramina described in (ii) are small, and to make sure that they are really missing, it is advisable to use a higher magnification, that is, 10X.

3 (Figure 3)

a - (i) The tuberculum flexorium is broad latero-medially but short dorso-plantarly; (ii) the foramina lateral and medial of the tuberculum flexorium are better visible in the strictly plantar view than in the lateral/latero-plantar or medial/medialo-plantar views, respectively. [most Strigiformes (2–4) and possibly a few specimens of Accipitridae]……………………………………………………………..5

b - (i) The tuberculum flexorium is narrow latero-medially but elongated dorso-plantarly; (ii) the foramina lateral and medial of the tuberculum flexorium are better visible from the sides than in the

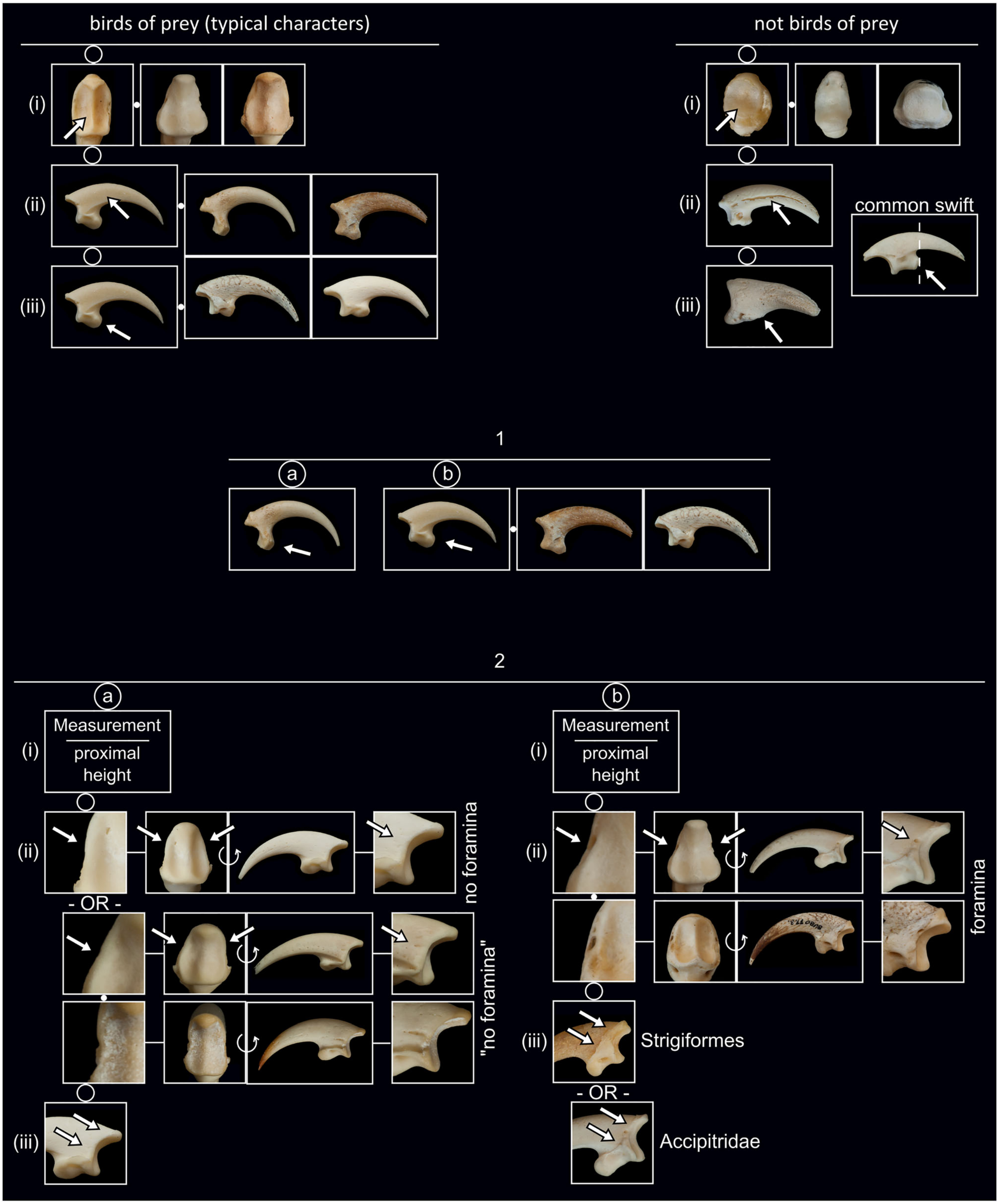

FIGURE 2 Illustrations of features 1 and 2 described in the text [Colour figure can be viewed at wileyonlinelibrary.com]

strictly plantar view (i.e., in lateral/latero-plantar or medial/medialo-plantar view, respectively). [many Accipitridae (1–4) and some Strigidae (1)]..9

c - One of the above two conditions is in contradiction to the other (e.g. tuberculum flexorium is elongated dorso-plantarly but the foramina are very well visible in plantar view, or the tuberculum is relatively broad latero-medially but the foramina are not so well visible in plantar view) or it is difficult to unambiguously classify the shape of the tuberculum and/or the visibility of the foramina..4

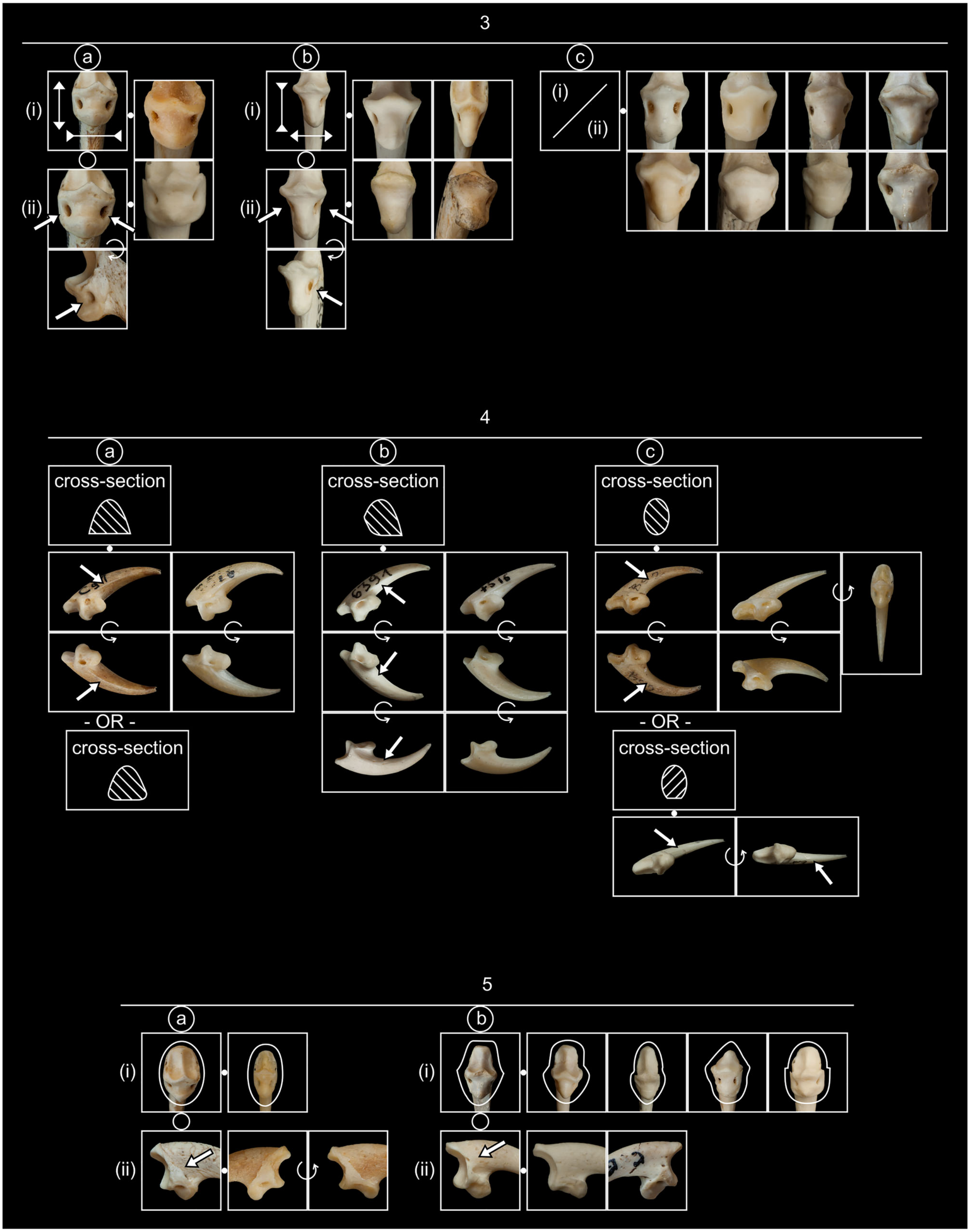

FIGURE 3 Illustrations of features 3–5 described in the text [Colour figure can be viewed at wileyonlinelibrary.com]

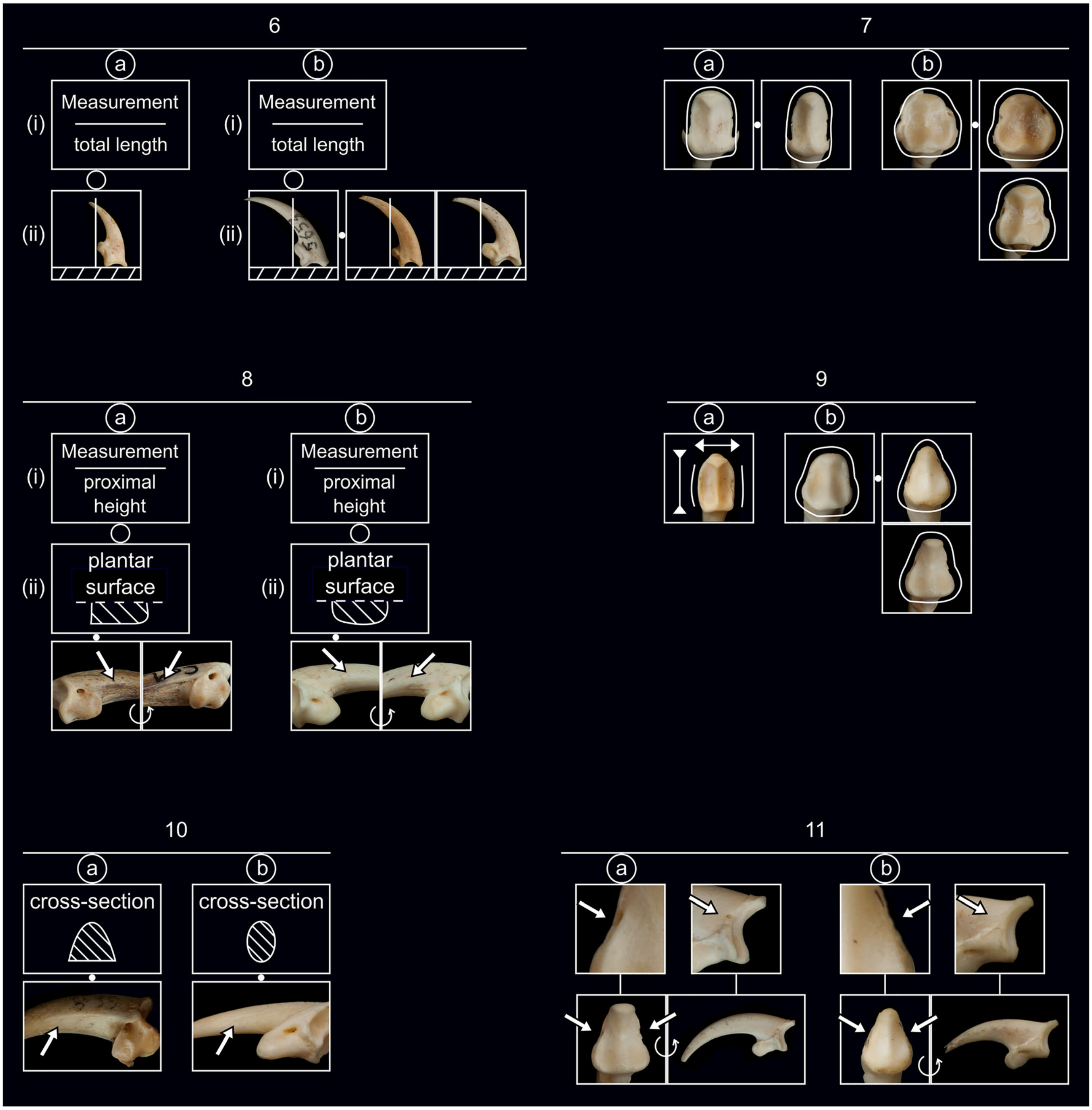

FIGURE 4 Illustrations of features 6–11 described in the text [Colour figure can be viewed at wileyonlinelibrary.com]

Note: The appearance of the tuberculum flexorium and the foramina on its both sides distinguish most owls well from diurnal raptors. However, there are exceptions in both groups and ambiguous cases.

4 (Figure 3)

a - The plantar surface of the corpus phalangis is flattened and delimited by two edges: the lateral and medial, which results in the cross-section of the corpus phalangis having the shape of an arc with a flat base as wide as the corpus phalangis...**Accipitridae**

b - The plantar surface of the corpus phalangis on the lateral side is delimited by an edge, and on the medial side it gradually turns into the medial surface (in the middle of which the edge runs)...**Accipitridae**

c - (i) The plantar surface of the corpus phalangis gradually turns into the lateral and medial surface, resulting in either an oval cross-section of the corpus phalangis or a nearly-oval cross-section, with a narrow strap of flat base which is narrower than the width of the corpus phalangis and any edges delimiting the plantar surface are not sharp. [some Strigiformes (1) and possibly *E. caeruleus* (1)]...5

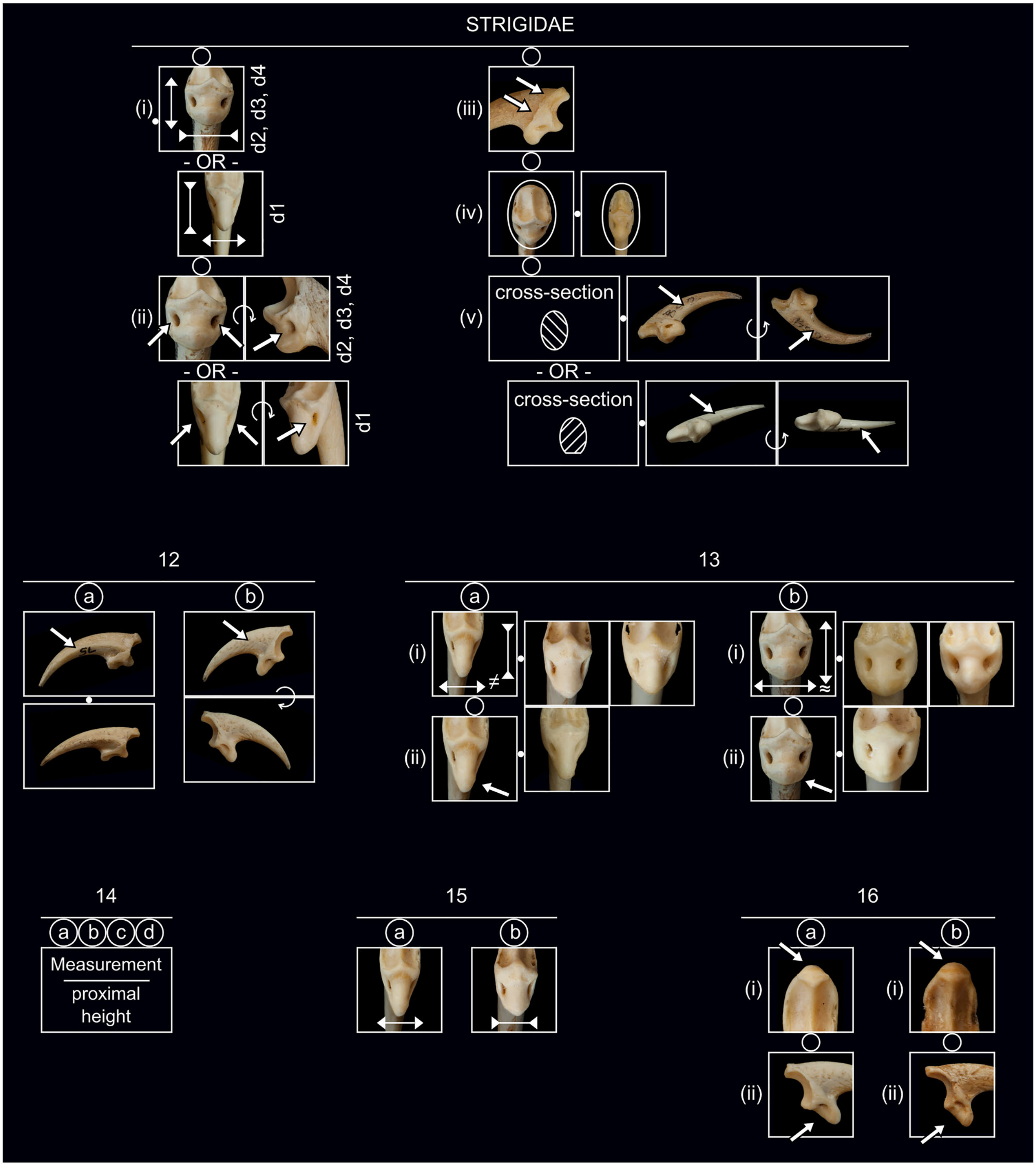

FIGURE 5 Illustrations of features 12–16 described in the text [Colour figure can be viewed at wileyonlinelibrary.com]

Note: The edges are not always very sharp; sometimes, they are slightly rounded, and therefore, it is best to compare the ungual phalanges that represent these two groups (owls and diurnal birds of prey).

5 (Figure 3)

a - (i) The cotyla articularis and tuberculum flexorium roughly fit into one common oval or circle; (ii) There is a wide bony collar around the tuberculum flexorium and cotyla articularis. [Strigidae]......... 12

b - The cotyla articularis and tuberculum flexorium cannot be fitted in one oval or circle (the contour line is disturbed at the border of the cotyla and tuberculum); (ii) The wide bony collar is only around the tuberculum flexorium. [*T. alba* (1–4); *O. scops* (2–4); possibly *C. gallicus* (3) and *E. caeruleus* (1–4)]...................................6

Note: Occasionally, the bony collar can be broken off and not visible around (the whole) cotyla articularis. In such cases, the common

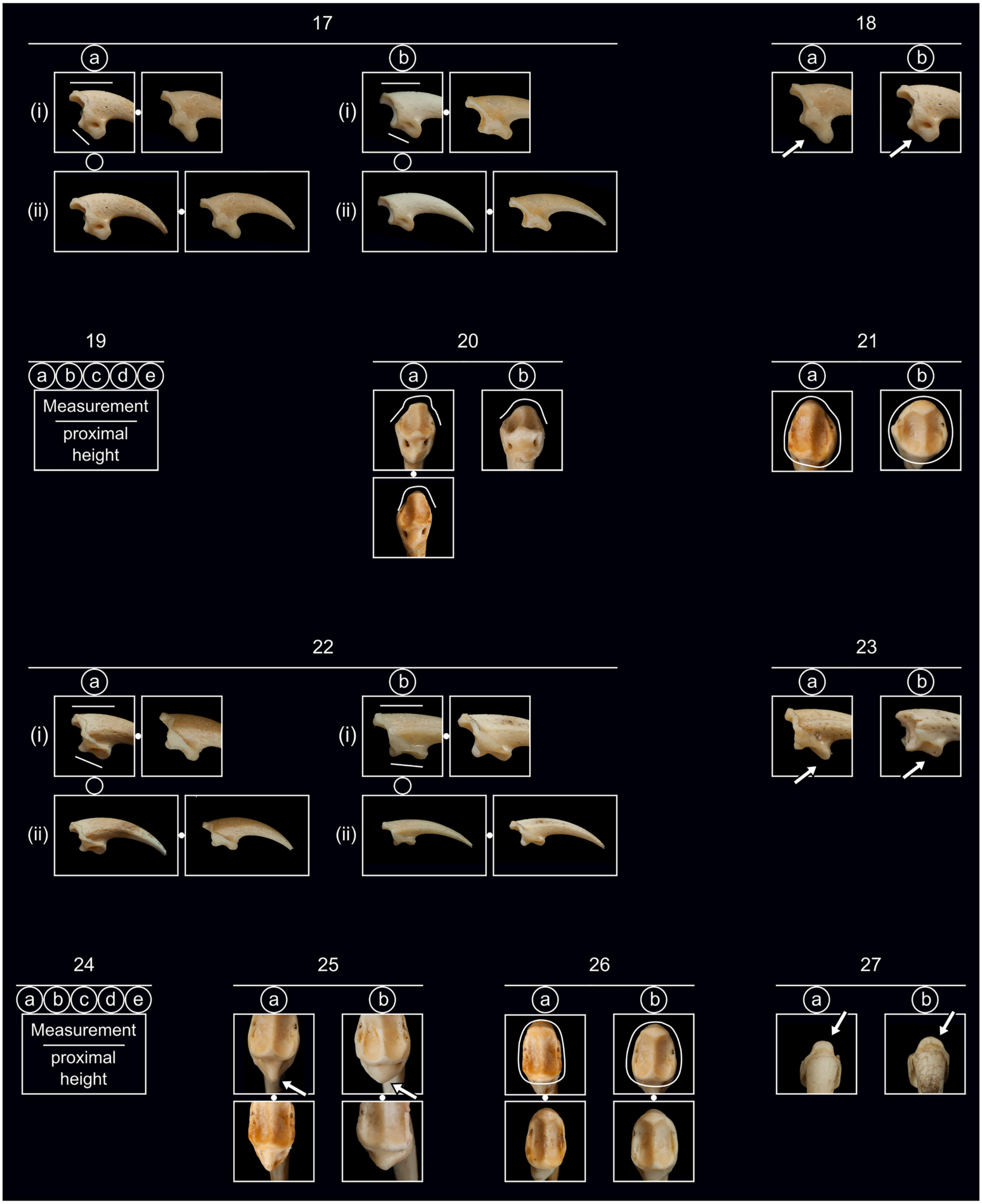

FIGURE 6 Illustrations of features 17–27 described in the text [Colour figure can be viewed at wileyonlinelibrary.com]

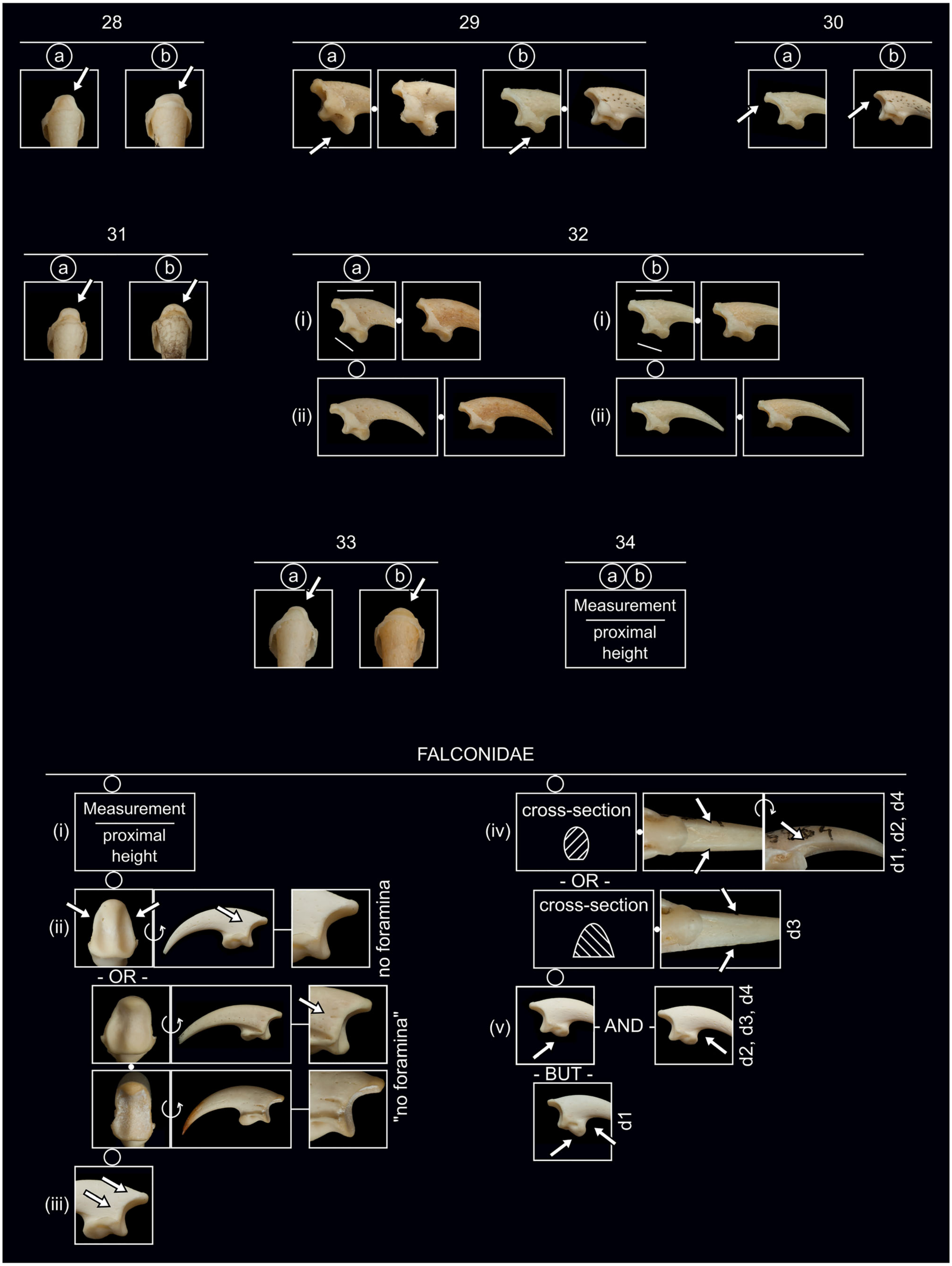

FIGURE 7 Illustrations of features 28–34 described in the text [Colour figure can be viewed at wileyonlinelibrary.com]

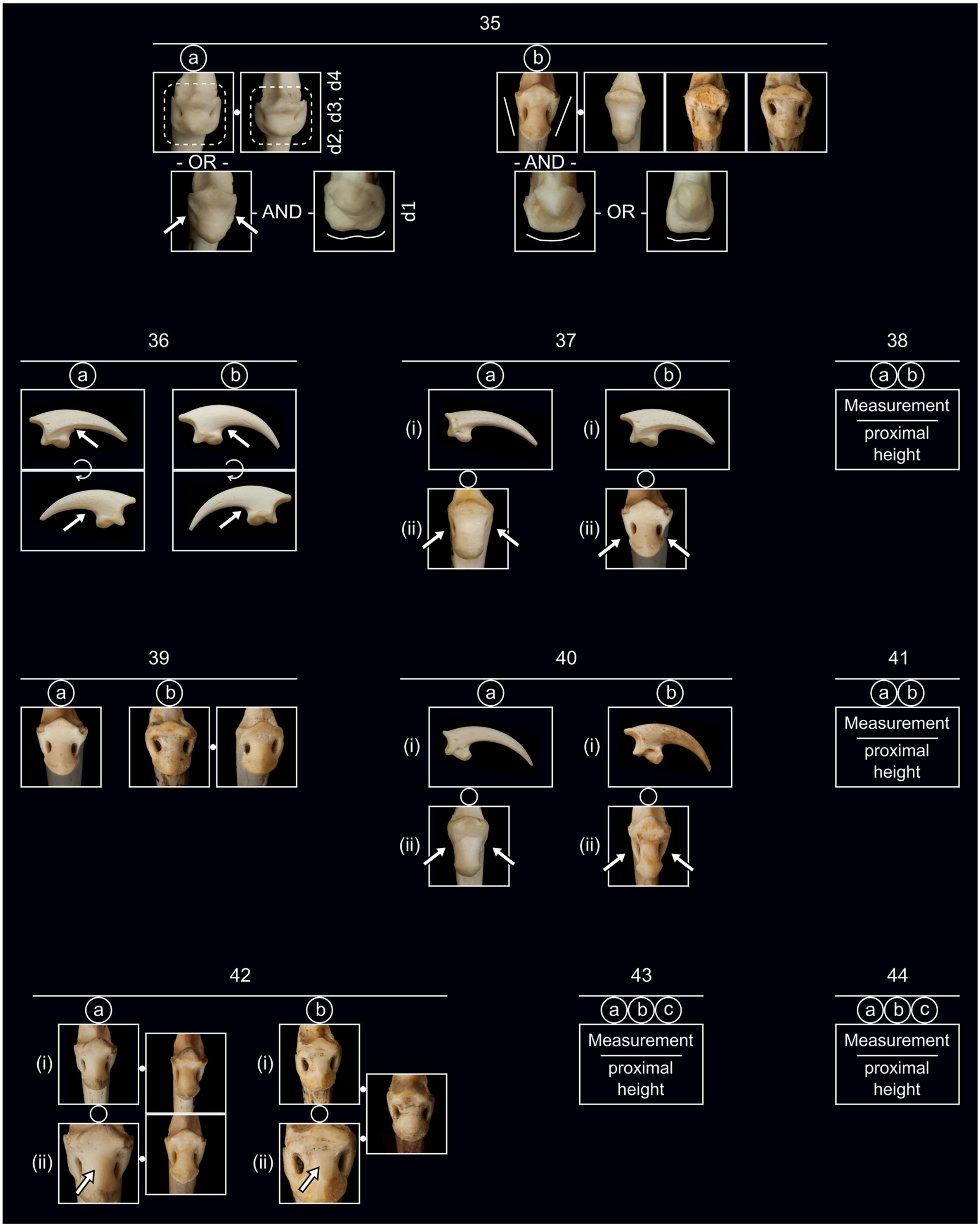

FIGURE 8 Illustrations of features 35–44 described in the text [Colour figure can be viewed at wileyonlinelibrary.com]

oval or circle may be disturbed; check for collar remnants in the dorsal part of the cotyla articularis.

6 (Figure 4)

a - (i) Total length less than 8 mm, AND (ii) The tip of the corpus phalangis (apex phalangis) protrudes very little farther plantarly than the tuberculum flexorium or as far as the tuberculum. The easiest way to check this is to place the ungual phalanx vertically with the articular surface down so that the tuberculum extensorium and medial prominence touch the flat horizontal surface……………………………………………………………… ***Otus scops* (2–4)**

b - (i) Total length greater than 8 mm; AND (ii) The tip of the corpus phalangis (apex phalangis) protrudes distinctly further plantarly than the tuberculum flexorium. [*T. alba* (1–4); *C. gallicus* (3); *E. caeruleus* (1–4)]………………………………………………………………………7

7 (Figure 4)

a - The cotyla articularis is elongated……………………… ***Tyto alba* (1–4)**

b - The cotyla articularis is pear-shaped. [*C. gallicus* (3); *E. caeruleus* (1–4)]…………………………………………………………………8

8 (Figure 4)

a - (i) Proximal height greater than 7 mm; (ii) The plantar surface of the corpus phalangis is flattened and delimited by two edges: the lateral edge is sharp whereas the medial edge is rounded……………………………………………………… ***Circaetus gallicus* (3)**

b - (i) Proximal height less than 7 mm; (ii) The plantar surface of the corpus phalangis is rounded or very slightly flattened, lateral and medial edges, if at all visible, are rounded….. ***Elanus caeruleus* (1–4)**

9 (Figure 4)

a - The cotyla articularis is narrow, elongated dorso-plantarly and its lateral and medial edges are roughly parallel to each other. [Strigidae (1) and possibly some Accipitridae]…………………………. 10

b - The cotyla articularis is pear-shaped. [Accipitridae; *O. scops* (1)]…………………………………………………………………………… 11

10 (Figure 4)

a - The plantar surface of the corpus phalangis is flattened and delimited by two edges: the lateral and medial, which results in the cross-section of the corpus phalangis having the shape of an arc with a flat base……………………………………………………… **Accipitridae**

b - The plantar surface of the corpus phalangis gradually turns into the lateral and medial surface, resulting in an oval cross-section of the corpus phalangis. [Strigidae (1)]………………………………………. 12

11 (Figure 4)

a - There are small foramina on the lateral and medial edges (or just below them) of the cotyla articularis, but sometimes there is a foramen on one side only. The position of the foramina can be different: they can be on the edge of the cotyla or more to the side of the bone……………………………………………………………… **Accipitridae**

b - There are no foramina either on the lateral or on the medial sides of the cotyla articularis……………………………………………… ***Otus scops* (1)**

Note: The foramina are small, and, especially in small species, they are only visible under higher magnification, that is, 10X.

3.3 | Strigidae (Figure 5)

The family Strigidae is characterized by the following features: (i) In digits 2–4, the tuberculum flexorium is broad latero-medially but short dorso-plantarly. In digit 1, the tuberculum flexorium is narrow latero-medially but elongated dorso-plantarly; (ii) in digits 2–4, the foramina lateral and medial of the tuberculum flexorium are better visible in the strictly plantar view than in the lateral/latero-plantar or medial/medialo-plantar views, respectively. In digit 1, the foramina lateral and medial of the tuberculum are better visible from the sides than in the strictly plantar view; (iii) there is a bony collar or crest around the tuberculum flexorium and cotyla articularis; (iv) the cotyla articularis and tuberculum flexorium roughly fit into one common oval or circle; (v) the plantar surface of the corpus phalangis gradually turns into the lateral and medial surface, resulting in an oval cross-section of the corpus phalangis. However, sometimes, the plantar surface of the corpus phalangis is slightly flattened. This flattening is narrower than the width of the corpus phalangis, and any edges delimiting the plantar surface are not sharp.

Note: *T. alba* and *O. scops* clearly differ from other owls and are already identified in the introductory part of the manual. To save space, these two species of owls are no longer included in the owl manual. Thus, to ensure that no species are omitted, the identification of the owls should be started with the introductory part of the manual.

12 (Figure 5)

a - There is an edge along the medial side of the corpus phalangis. [Strigiformes (3)]…………………………………………………………………… 19

b - The medial and lateral sides of the corpus phalangis look the same (no edge). [Strigiformes (1–2, 4)]…………………………………………… .. 13

13 (Figure 5)

a - (i) The tuberculum flexorium is usually noticeably longer than it is wide; (ii) The tuberculum flexorium tapers more or less evenly over its entire length. [Strigiformes (1)]………………………………… 14

b - (i) The tuberculum flexorium is similarly long as it is wide; (ii) The tuberculum flexorium tapers more strongly at the very distal end. [Strigiformes (2, 4)]…………………………………………………………… 24

14 (Figure 5, Appendix S1)

a - Proximal height greater than 12 mm……………………… ***Bubo bubo* (1)**

b - Proximal height: 8–12 mm. [*B. bubo* (1), *B. scandiacus* (1), *S. nebulosa* (1), *S. uralensis* (1)]……………………………………………… . 15

c - Proximal height: 5–8 mm. [*S. ulula* (1), *S. aluco* (1), *A. otus* (1), *A. flammeus* (1)].. 17

d - Proximal height less than 5 mm....................***Aegolius funereus* (1), *Athene noctua* (1)**

15 (Figure 5)

a - The tuberculum flexorium is narrow lateromedially. [*S. uralensis* (1), *S. nebulosa* (1)]... 16

b - The tuberculum flexorium is relatively wider lateromedially…***Bubo scandiacus* (1), *Bubo bubo* (1)**

16 (Figure 5)

a - (i) In articular view, the tuberculum extensorium protrudes above the dorsal rim of the cotyla articularis, taking the shape of a narrow cone; (ii) In lateral and/or medial view, the plantar edge of the cotyla articularis overhangs the tuberculum flexorium…***Strix uralensis* (1)**

b - (i) In articular view, the tuberculum extensorium protrudes slightly above the dorsal rim of the cotyla articularis, taking the shape of a wider arch; (ii) In lateral and/or medial view, the plantar edge of the cotyla articularis blends smoothly into the tuberculum flexorium... ***Strix nebulosa* (1)**

17 (Figure 6)

a - In lateral and/or medial view, (i) the plantar edge of the tuberculum flexorium deviates much from the dorsal edge of the corpus phalangis; and (ii) the corpus phalangis is more stocky, especially in the proximal part. [*S. ulula* (1), *S. aluco* (1)]................................ 18

b - In lateral and/or medial view, (i) the plantar edge of the tuberculum flexorium only little deviates from the dorsal edge of the corpus phalangis; and (ii) the corpus phalangis is more slender, also in the proximal part............................. ***Asio otus* (1), *Asio flammeus* (1)**

18 (Figure 6)

a - In lateral and/or medial view, the tuberculum flexorium is relatively long relative to the cotyla articularis..................***Strix aluco* (1)**

b - In lateral and/or medial view, the tuberculum flexorium is relatively short relative to the cotyla articularis.............***Surnia ulula* (1)**

19 (Figure 6, Appendix S1)

a - Proximal height greater than 11.5 mm.......................***Bubo bubo* (3)**

b - Proximal height: 10–11.5 mm…***Bubo bubo* (3), *Bubo scandiacus* (3)**

c - Proximal height: 7.5–10 mm. [*B. scandiacus* (3), *S. nebulosa* (3), *S. uralensis* (3)].. 20

d - Proximal height: 4.5–7.5 mm. [*S. ulula* (3), *S. aluco* (3), *A. otus* (3), *A. flammeus* (3)]... 22

e - Proximal height less than 4.5 mm. [*A. funereus* (3), *A. noctua* (3)].. 23

20 (Figure 6)

a - In flexorial view, the dorsal half of the cotyla articularis resembles a rectangular "chimney". [*S. uralensis* (3), *S. nebulosa* (3)]............ 21

b - In flexorial view, the dorsal half of the cotyla articularis tapers gradually to form a more uniform arch..............***Bubo scandiacus* (3)**

21 (Figure 6)

a - The cotyla articularis is relatively more elongated… ....***Strix nebulosa* (3)**

b - The cotyla articularis is relatively rounder..............***Strix uralensis* (3)**

22 (Figure 6)

a - In lateral and/or medial view, (i) the plantar edge of the tuberculum flexorium deviates much from the dorsal edge of the corpus phalangis; and (ii) the corpus phalangis is more stocky, especially in the proximal part.............................***Surnia ulula* (3), *Strix aluco* (3)**

b - In lateral and/or medial view, (i) the plantar edge of the tuberculum flexorium only little deviates from the dorsal edge of the corpus phalangis; and (ii) the corpus phalangis is more slender, also in the proximal part.............................. .***Asio otus* (3), *Asio flammeus* (3)**

23 (Figure 6)

a - The tuberculum flexorium is more extended distalo-plantarly… ***Aegolius funereus* (3)**

b - The tuberculum flexorium is less extended distalo-plantarly… ***Athene noctua* (3)**

24 (Figure 6, Appendix S1)

a - Proximal height greater than 13 mm.......................... ***Bubo bubo* (2)**

b - Proximal height: 10.5–13.0 mm. [*B. bubo* (2, 4), *B. scandiacus* (2, 4)]...31

c - Proximal height: 8.0–10.5 mm. [*B. bubo* (4), *B. scandiacus* (2, 4), *S. uralensis* (2, 4), *S. nebulosa* (2, 4)]... 25

d - Proximal height: 5.0–8.0 mm. [*S. uralensis* (4), *S. nebulosa* (4), *S. aluco* (2, 4), *S. ulula* (2, 4), *A. otus* (2, 4), *A. flammeus* (2, 4)]......32

e - Proximal height less than 5.0 mm. [*A. otus* (4), *A. flammeus* (4), *A. funereus* (2, 4), *A. noctua* (2, 4)].. 29

25 (Figure 6)

a - The distal end of the tuberculum flexorium is thin and elongated (best seen in articular view). [*S. uralensis* (2, 4), *S. nebulosa* (2, 4)]…26

b - The distal end of the tuberculum flexorium is relatively wide (best seen in articular view). [*B. bubo* (4), *B. scandiacus* (2, 4)]............... 27

26 (Figure 6)

a - The cotyla articularis is relatively more elongated…***Strix nebulosa* (2, 4)**

b - The cotyla articularis is relatively rounder. [*S. uralensis* (2, 4)]......28

27 (Figure 6)

a - In dorsal view, the proximal end of the phalanx is relatively narrow...***Bubo bubo* (4), *Bubo scandiacus* (4)**

b - In dorsal view, the proximal end of the phalanx tapers gradually to form a wide more uniform arch..........................***Bubo scandiacus* (2)**

28 (Figure 7)

a - In dorsal view, the proximal end of the phalanx is relatively narrow..***Strix uralensis* (4)**

b - In dorsal view, the proximal end of the phalanx tapers gradually to form a wide more uniform arch.............................. .***Strix uralensis* (2)**

29 (Figure 7)

a - The tuberculum flexorium is more extended distalo-plantarly… ***Aegolius funereus* (2, 4)**

b - The tuberculum flexorium is less extended distalo-plantarly. [*A. otus* (4), *A. flammeus* (4), *A. noctua* (2, 4)]................................ 30

30 (Figure 7)

a - In lateral and/or medial view, the dorsal part of the cotyla articularis is relatively more proximally elongated...........***Asio otus* (4), *Asio flammeus* (4)**

b - In lateral and/or medial view, the dorsal part of the cotyla articularis is relatively less proximally elongated...... .***Athene noctua* (2, 4)**

31 (Figure 7)

a - In dorsal view, the proximal end of the phalanx is relatively narrow…***Bubo bubo* (4), *Bubo scandiacus* (4)**

b - In dorsal view, the proximal end of the phalanx tapers gradually to form a wide more uniform arch… ***Bubo bubo* (2), *Bubo scandiacus* (2)**

32 (Figure 7)

a - In lateral and/or medial view, (i) the plantar edge of the tuberculum flexorium deviates much from the dorsal edge of the corpus phalangis; and (ii) the corpus phalangis is more stocky, especially in the proximal part. [*S. uralensis* (4), *S. nebulosa* (4), *S. aluco* (2, 4), *S. ulula* (2, 4)]..33

b - In lateral and/or medial view, (i) the plantar edge of the tuberculum flexorium only little deviates from the dorsal edge of the corpus phalangis; and (ii) the corpus phalangis is more slender, also in the proximal part..................... . ***Asio otus* (2, 4), *Asio flammeus* (2, 4)**

33 (Figure 7)

a - In dorsal view, the proximal end of the phalanx is relatively narrow. [*S. uralensis* (4), *S. nebulosa* (4), *S. aluco* (4), *S. ulula* (4)]......... 34

b - In dorsal view, the proximal end of the phalanx tapers gradually to form a wide more uniform arch......... ***Strix aluco* (2), *Surnia ulula* (2)**

34 (Figure 7)

a - Proximal height greater than 7 mm…***Strix uralensis* (4), *Strix nebulosa* (4)**

b - Proximal height less than or equall to 7 mm…***Strix aluco* (4), *Surnia ulula* (4)**

3.4 | Falconidae with superficially similar species (Figure 7)

It is difficult to identify a feature that would clearly distinguish all ungual phalanges of the genus *Falco* from the phalanges of owls and diurnal birds of prey. Therefore, it is better to rely on a set of the following features:

(i) Proximal height less than 12.0 mm; AND (ii)There are no foramina on either the lateral or medial edges (or just below them) of the cotyla articularis (foramina clearly below the edge of the cotyla articularis, often situated in a shallow groove, are regarded as "no foramina"); AND (iii) There is no bony collar or crest around the cotyla articularis; the collar is only on both sides of the tuberculum flexorium; AND (iv) The plantar surface of the corpus phalangis is somewhat flattened and delimited by two edges: the lateral and medial. The flattening is narrower than the width of the corpus phalangis and the edges delimiting the plantar surface are often not sharp (only in the case of one phalanx, that of digit 3, the flattening is wide); (v) Phalanges 2–4: in lateral and/or medial view, the plantar edge of the tuberculum flexorium usually only slightly deviates from the dorsal edge of the corpus phalangis, and the semicircular indentation between tuberculum flexorium and corpus phalangis is usually shallow (for phalanx 1, this feature does not work).

35 (Figure 8)

a - In digits 2–4, the tuberculum flexorium is roughly square in shape. In digit 1, the foramina lateral and medial of the tuberculum flexorium are poorly visible in flexorial view, and there are two bulges in the plantar edge of the cotyla articularis in the distal view..***Tyto alba* (1–4)**

b - The tuberculum flexorium narrows distally in flexorial view, and the plantar edge of the cotyla articularis is flat, rounded or has only one bulge in distal view. [*Falco* spp. (1–4), *P. apivorus* (1–4)]..36

36 (Figure 8)

a - One of the two edges delimiting the plantar surface of the corpus phalangis extends only to the distal end of the tuberculum flexorium (lateral edge), and the other edge extends further to the cotyla articularis (medial edge). The difference in the course and length of these two edges makes the whole ungual phalanx asymetrical. [*Falco* spp. (3), *P. apivorus* (3)]... 37

b - The two edges (lateral and medial) delimiting the plantar surface of the corpus phalangis extend to the distal end of the tuberculum flexorium, making the entire ungual phalanx symetrical. [*Falco* spp. (1–2, 4), *P. apivorus* (1–2, 4)].. 40

37 (Figure 8)

a - (i) The corpus phalangis is relatively slender and lightly built; (ii) The foramina lateral and medial of the tuberculum flexorium are barely (or not) visible in the flexorial and/or flexorio-articular view because they are (partially) obscured by the tuberculum, which is shaped like a broad cylinder............... ... ***Pernis apivorus* (3)**

b - (i) The corpus phalangis is relatively more robust and stocky; (ii) The foramina lateral and medial of the tuberculum flexorium are clearly visible in the flexorial and/or flexorio-articular view, because the plantar ridge of the tuberculum is narrower. [*Falco* spp. (3)]... . 38

38 (Figure 8, Appendix S1)

a - Proximal height greater than 5.5 mm. [*F. cherrug* (3), *F. rusticolus* (3), *F. peregrinus* (3)]... 39

b - Proximal height less than 5.5 mm................ ...**smaller *Falco* spp. (3)**

39 (Figure 8)

a - In flexorial view, the tuberculum flexorium is relatively longer and latero-medially compressed................................ ***Falco peregrinus* (3)**

b - In flexorial view, the tuberculum flexorium is relatively shorter but wider latero-medially............... ***Falco cherrug* (3), *Falco rusticolus* (3)**

Note: We did not have the opportunity to study *F. biarmicus*, which is similar in size to *F. peregrinus*.

40 (Figure 8)

a - (i) The corpus phalangis is relatively slender and lightly built; (ii) The foramina lateral and medial of the tuberculum flexorium are barely (or not) visible in the flexorial and/or flexorio-articular view because they are (partially) obscured by the tuberculum, which is shaped like a broad cylinder..........***Pernis apivorus* (1–2, 4)**

b - (i) The corpus phalangis is relatively more robust and stocky; (ii) The foramina lateral and medial of the tuberculum flexorium are clearly visible in the flexorial and/or flexorio-articular view, because the plantar ridge of the tuberculum is narrower. [*Falco* spp. (1–2, 4)]...41

41 (Figure 8, Appendix S1)

a - Proximal height greater than 6.0 mm. [*F. cherrug* (1–2, 4), *F. rusticolus* (1–2, 4), *F. peregrinus* (1–2, 4)]...................................42

b - Proximal height less than 6.0 mm...........**smaller *Falco* spp. (1–2, 4)**

42 (Figure 8)

a - In flexorial view, (i) the tuberculum flexorium is relatively longer and latero-medially compressed; (ii) The ridge between the foramina situated on either side of the tuberculum is clearly convex. [*F. peregrinus* (1–2, 4)]...43

b - In flexorial view, (i) the tuberculum flexorium is relatively shorter but wider latero-medially; (ii) The ridge between the foramina situated on either side of the tuberculum is flattened. [*F. cherrug* (1–2, 4), *F. rusticolus* (1–2, 4)]... . 44

43 (Figure 8, Appendix S1)

a - Proximal height greater than 8.5 mm............. ***Falco peregrinus* (1–2)**

b - Proximal height: 6.5–8.5 mm..................... .***Falco peregrinus* (1–2, 4)**

c - Proximal height less than 6.5 mm........................***Falco peregrinus* (4)**

Note: We did not have the opportunity to study *F. biarmicus*, which is similar in size to *F. peregrinus*.

44 (Figure 8, Appendix S1)

a - Proximal height greater than 8.5 mm...***Falco cherrug* (1–2), *Falco rusticolus* (1–2)**

b - Proximal height between 7.0 and 8.5 mm...***Falco cherrug* (1–2, 4), *Falco rusticolus* (1–2, 4)**

c - Proximal height less than 7.0 mm...***Falco cherrug* (4), *Falco rusticolus* (4)**

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supporting information.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Wertz, K., Tomek, T., & Bochenski, Z. M. (2023). Whose talon is this? A manual for the identification of ungual phalanges of European birds of prey: Falcons and owls. *International Journal of Osteoarchaeology*, *33*(4), 562–576. https://doi.org/10.1002/oa.3144

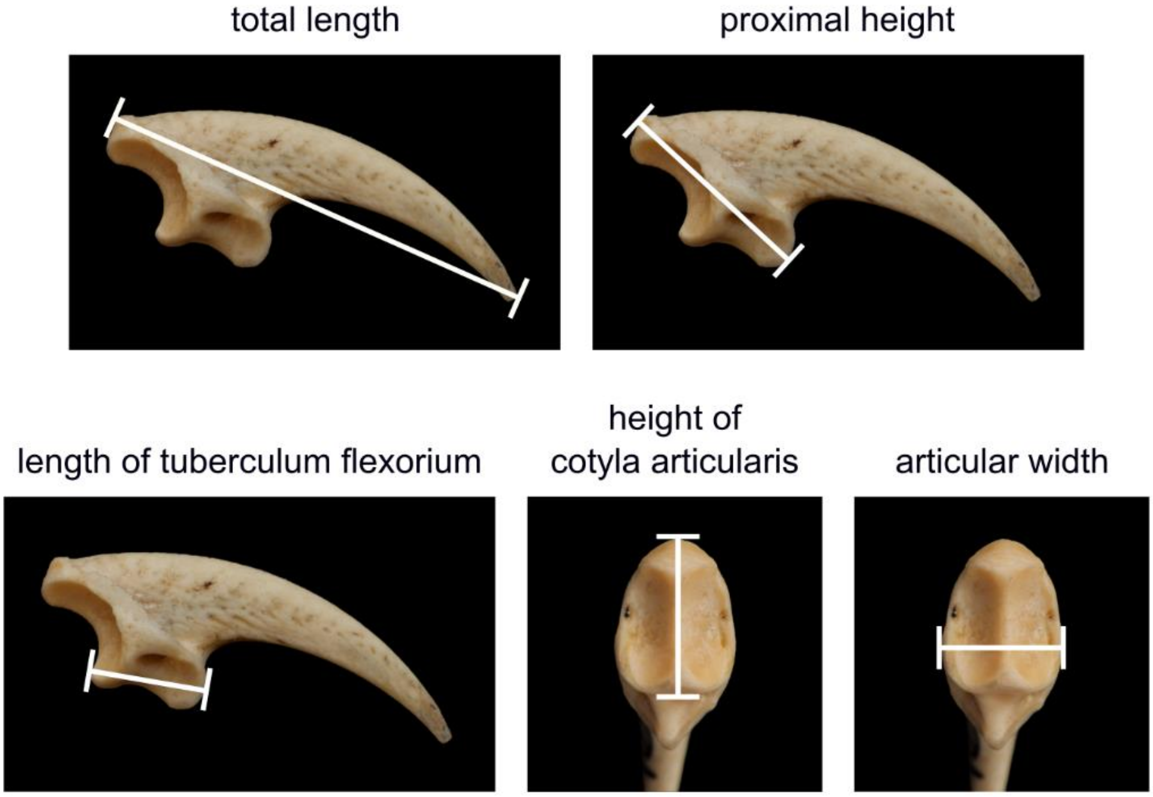
(6) Wertz, K., Tomek, T., Bochenski, Z.M. (2023) Whose talon is this? A manual for the identification of ungual phalanges of European birds of prey: falcons and owls. International Journal of Osteoarchaeology, 33: 562-576.

Supporting information

Filename	Description
oa3144-sup-0001-Figure S1.pdfPDF document, 143.4 KB	**Figure S1.** PDF file with illustrations of measurements
oa3144-sup-0002-Table S1_corrected.pdfPDF document, 122.7 KB	**Table S1.** PDF file with modern comparative specimens
oa3144-sup-0003-Data S1_corrected.xlsxExcel 2007 spreadsheet , 46.6 KB	**Data S1.** Excel spreadsheet of measurements of ungual phalanges of owls and falcons
oa3144-sup-0004-Appendix S1_corrected.pdfPDF document, 174.7 KB	**Appendix S1.** PDF file with division of species into groups of different sizes
oa3144-sup-0005-Appendix S2_corrected.pdfPDF document, 2.2 MB	**Appendix S2.** PDF file with photographs of ungual phalanges of owls and falcons in predefined views

Supporting Figure 1 (Fig S1)

for: Wertz K., Tomek T., Bochenski Z.M. Whose talon is this? A manual for the identification of ungual phalanges of European birds of prey: falcons and owls. *International Journal of Osteoarchaeology*.



Measurements of ungual phalanges of owls and falcons (refer to Data S1).

Supporting Table 1 (Tab S1)
for: Wertz K., Tomek T., Bochenski Z.M. Whose talon is this? A manual for the identification of ungual phalanges of European birds of prey: falcons and owls. *International Journal of Osteoarchaeology.*

Taxon: \\ Collection:	ISEA	NMNHS	NHMUT	ABo	HNHM	PACEA	UMB	NMNHU	Total
Pandion haliaetus	4	-	-	-	3	-	-	1	8
Elanus caeruleus	1	-	-	-	-	-	-	-	1
Pernis apivorus	8	-	-	-	1	-	-	5	14
Gypaetus barbatus	2	-	-	-	3	1	-	-	6
Neophron percnopterus	1	5	-	-	1	-	-	-	7
Circaetus gallicus	-	1	-	-	4	-	-	-	5
Gyps fulvus	2	5	-	-	4	1	-	-	12
Aegypius monachus	2	4	-	-	1	-	-	2	9
Clanga pomarina	5	1	-	-	2	-	-	2	10
Clanga clanga	-	-	-	-	3	-	-	-	3
Aquila rapax	1	-	-	-	2	-	-	1	4
Aquila heliaca	1	2	-	-	15	1	-	1	20
Aquila chrysaetos	4	3	1	-	5	-	5	-	18
Aquila fasciata	-	-	-	-	1	-	-	-	1
Hieraaetus pennatus	2	3	-	-	2	-	-	-	7
Circus aeruginosus	9	-	-	-	11	-	-	-	20
Circus cyaneus	1	-	-	-	6	-	-	-	7
Circus macrourus	1	-	-	-	2	-	-	-	3
Circus pygargus	2	-	-	-	4	-	-	-	6
Accipiter nisus	17	-	-	-	8	-	-	-	25
Accipiter gentilis	14	-	-	-	18	-	-	-	32
Haliaeetus albicilla	14	-	-	-	5	-	-	-	19
Milvus milvus	3	-	-	-	2	1	-	-	6
Milvus migrans	3	1	-	-	2	-	-	3	9
Buteo lagopus	4	-	-	-	5	-	5	-	14
Buteo buteo	38	-	-	-	14	-	-	-	52
Buteo rufinus	1	-	-	-	2	-	-	-	3
Tyto alba	21	-	-	1	1	1	-	-	24
Surnia ulula	3	-	-	-	2	-	-	-	5
Athene noctua	8	-	-	-	4	-	-	-	12
Aegolius funereus	3	-	-	-	1	-	-	-	4
Otus scops	3	-	-	-	1	-	-	-	4
Asio otus	44	-	-	-	4	-	-	-	48
Asio flammeus	6	-	-	-	4	-	-	-	10
Strix aluco	32	-	-	-	7	-	-	-	39
Strix uralensis	7	-	-	-	3	-	-	-	10
Strix nebulosa	3	-	-	-	1	1	-	-	5
Bubo scandiacus	2	2	-	-	2	-	-	-	6
Bubo bubo	6	3	-	-	5	1	5	-	20
Falco naumanni	2	-	-	-	-	-	-	-	2
Falco tinnunculus	41	-	-	-	-	-	-	-	41

Taxon: \\ Collection:	ISEA	NMNHS	NHMUT	ABo	HNHM	PACEA	UMB	NMNHU	Total
Falco vespertinus	4	-	-	-	-	-	-	-	4
Falco eleonorae	1	-	-	-	-	-	-	-	1
Falco columbarius	2	-	-	-	-	-	-	-	2
Falco subbuteo	7	-	-	-	1	-	-	-	8
Falco cherrug	-	-	-	-	6	1	-	-	7
Falco rusticolus	1	-	-	-	1	-	5	-	7
Falco peregrinus	6	-	-	-	5	-	3	-	14
Total	342	30	1	1	174	8	23	15	594

ISEA - Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland
NMNHS – National Museum of Natural History, Bulgarian Academy of Sciences, Sofia, Bulgaria
NHMUT – Natural History Museum, University of Tartu, Estonia
ABo - ArchaeoBone, Haren, the Netherlands
HNHM - Hungarian Natural History Museum, Budapest, Hungary
PACEA – De la Préhistoire à l’Actuel: Culture, Environnement et Anthropologie, Université de Bordeaux, France
UMB – University Museum of Bergen, Department of Natural History, Bergen, Norway
NMNHU - National Museum of Natural History at the National Academy of Sciences of Ukraine, Kyiv, Ukraine

Supporting Data 1 (Data S1) for: Wertz K., Tomek T., Bochenski Z.M. Whose talon i

Measurement ranges for all species of owls and falcons included in the manual. The arithmetic mean and standard dev known) and jointly for all specimens of known and unknown sex. The measurements are illustrated in Figure S1. N stan two different digits (i.e., digits 1 and 2) are shown together in the same cell.

				Total length						Pr	
Taxon	sex	digit		Min	Max	MEAN	SD	N		Min	Max
Tyto alba	♀	1		12,44	15,5	-	-	3		5,57	7,25
Tyto alba	♀	2		13,76	17,32	-	-	3		5,14	6,56
Tyto alba	♀	3		12,21	15,4	-	-	3		4,72	6,09
Tyto alba	♀	4		11,85	14,61	-	-	3		4,76	6,11
Tyto alba	♂	1		11,72	15	13,195	1,064	6		5,15	6,97
Tyto alba	♂	2		12,99	17,23	14,527	1,479	6		4,99	6,33
Tyto alba	♂	3		12,01	15,02	12,935	1,080	6		5,13	5,96
Tyto alba	♂	4		10,53	13,83	12,246	1,181	5		4,19	5,87
Tyto alba	?+♀+♂	1		11,16	15,5	13,331	0,923	23		5,15	7,25
Tyto alba	?+♀+♂	2		12,96	17,32	14,969	1,198	22		4,99	6,56
Tyto alba	?+♀+♂	3		11,91	15,4	13,207	0,943	23		4,72	6,21
Tyto alba	?+♀+♂	4		10,53	14,61	12,485	0,973	22		4,19	6,11
Surnia ulula	?+♀+♂	1		11,13	11,72	-	-	4		5,86	6,34
Surnia ulula	?+♀+♂	2		12,47	13,82	13,018	0,506	5		6,02	6,55
Surnia ulula	?+♀+♂	3		12,17	12,89	-	-	4		5,66	6,04
Surnia ulula	?+♀+♂	1 or 3		12,16	12,16	-	-	1		6,24	6,24
Surnia ulula	?+♀+♂	4		10,22	11,25	10,772	0,384	5		5,23	5,77
Athene noctua	?+♀+♂	1		6,36	8,07	7,236	0,617	8		3,73	4,48
Athene noctua	?+♀+♂	2		8,37	10,21	9,217	0,775	7		3,85	4,53
Athene noctua	?+♀+♂	3		7,55	9,43	8,626	0,588	7		3,45	4,24
Athene noctua	?+♀+♂	4		6,56	8,05	7,533	0,519	7		3,25	4
Aegolius funereus	♂	1		-	-	-	-	-		4,1	4,1
Aegolius funereus	♂	2		-	-	-	-	-		4,22	4,22
Aegolius funereus	♂	3		-	-	-	-	-		4,35	4,35
Aegolius funereus	♂	4		-	-	-	-	-		3,53	3,53
Aegolius funereus	?+♀+♂	1		5,99	6,69	-	-	2		3,92	4,1
Aegolius funereus	?+♀+♂	2		7,52	8,67	-	-	2		3,97	4,45
Aegolius funereus	?+♀+♂	3		7,6	8,8	-	-	2		3,82	4,35
Aegolius funereus	?+♀+♂	4		5,64	6,08	-	-	2		3,42	3,53
Otus scops	?+♀+♂	1		5,15	5,62	-	-	2		3,2	3,21
Otus scops	?+♀+♂	2		6,51	7,28	-	-	3		3,01	3,32
Otus scops	?+♀+♂	3		6,19	6,67	-	-	3		2,92	3,24
Otus scops	?+♀+♂	4		5,25	5,96	-	-	3		2,7	3,07
Asio otus	♀	1		10,22	12,48	11,091	0,880	8		5,19	6,1
Asio otus	♀	2		12,06	14,78	13,095	0,977	8		5,15	5,98
Asio otus	♀	3		12,21	15,19	13,218	1,106	8		5,02	5,75
Asio otus	♀	4		9,45	11,93	10,707	0,885	7		4,6	5,27
Asio otus	♂	1		9,78	12,4	11,219	0,843	12		4,93	6,12
Asio otus	♂	2		11,64	14,58	12,955	0,899	14		5,14	6,04
Asio otus	♂	3		11,71	14,1	13,028	0,784	13		4,86	5,81
Asio otus	♂	4		9,62	11,58	10,618	0,757	13		4,37	5,39
Asio otus	?+♀+♂	1		9,31	12,48	11,090	0,710	46		4,93	6,23
Asio otus	?+♀+♂	2		11,64	14,78	12,938	0,767	46		5,05	6,16
Asio otus	?+♀+♂	3		11,71	15,19	12,979	0,745	47		4,86	5,81
Asio otus	?+♀+♂	4		9,35	11,93	10,497	0,702	43		4,37	5,43
Asio flammeus	♀	1		11,93	11,98	-	-	2		5,78	6,43
Asio flammeus	♀	2		13,66	13,75	-	-	2		5,89	6,36
Asio flammeus	♀	3		13,48	13,81	-	-	2		5,55	5,98
Asio flammeus	♀	4		11,51	11,72	-	-	2		5,09	5,61
Asio flammeus	♂	1		11,89	11,89	-	-	1		5,79	5,79
Asio flammeus	♂	2		13,16	13,16	-	-	1		5,82	5,82
Asio flammeus	♂	3		13,14	13,14	-	-	1		5,56	5,56
Asio flammeus	♂	4		10,86	10,86	-	-	1		4,97	4,97
Asio flammeus	?+♀+♂	1		11,22	12,31	11,796	0,307	10		5,12	6,43
Asio flammeus	?+♀+♂	2		12,95	13,95	13,354	0,340	10		5,38	6,36

Asio flammeus	?+♀+♂	3		12,98	14,11	13,340	0,410	10	5,07	5,98
Asio flammeus	?+♀+♂	4		10,54	11,88	11,125	0,441	10	4,87	5,61
Strix aluco	♀	1		12,18	14,51	13,358	0,856	16	6,77	7,87
Strix aluco	♀	2		14,43	17,55	16,208	0,938	16	6,8	7,83
Strix aluco	♀	3		13,68	16,03	14,833	0,862	15	6,09	6,98
Strix aluco	♀	4		11,62	13,88	12,674	0,708	16	6,04	6,93
Strix aluco	♂	1		11,42	13,74	12,659	0,716	9	6,32	7,88
Strix aluco	♂	2		14,18	16,56	15,411	0,758	9	6,41	7,65
Strix aluco	♂	3		13,24	15,62	14,247	0,721	9	6,05	7,32
Strix aluco	♂	4		11,06	13,04	11,958	0,699	9	5,64	6,77
Strix aluco	?+♀+♂	1		11,42	14,51	12,922	0,840	39	6,32	7,88
Strix aluco	?+♀+♂	2		14,18	17,55	15,738	0,921	39	6,27	7,83
Strix aluco	?+♀+♂	3		13,24	16,03	14,454	0,795	38	5,88	7,32
Strix aluco	?+♀+♂	4		11,06	13,88	12,264	0,750	38	5,52	6,93
Strix uralensis	♀	1		15,96	17,53	-	-	2	8,73	9,88
Strix uralensis	♀	2		19,11	20,87	-	-	2	8,82	10,11
Strix uralensis	♀	3		17,48	20,23	-	-	2	8,05	9,19
Strix uralensis	♀	4		15,69	16,65	-	-	2	7,9	8,71
Strix uralensis	?+♀+♂	1		14,3	17,74	16,772	1,057	9	8,49	10,08
Strix uralensis	?+♀+♂	2		17,67	20,99	20,320	1,159	9	8,37	10,17
Strix uralensis	?+♀+♂	3		16,76	20,23	18,929	1,126	9	7,73	9,19
Strix uralensis	?+♀+♂	4		13,97	17,15	16,346	0,975	9	7,45	8,71
Strix nebulosa	?+♀+♂	1		19,93	21,03	-	-	4	8,97	10,38
Strix nebulosa	?+♀+♂	2		20,79	23,1	-	-	4	8,87	9,99
Strix nebulosa	?+♀+♂	3		20,62	21,5	-	-	3	8,83	9,19
Strix nebulosa	?+♀+♂	4		12,51	19,05	16,654	2,753	5	6,24	9,1
Bubo scandiacus	♀	2		26,94	26,94	-	-	1	11,66	11,66
Bubo scandiacus	♀	3		25,62	25,62	-	-	1	10,92	10,92
Bubo scandiacus	♀	4		22,44	22,44	-	-	1	10,97	10,97
Bubo scandiacus	?+♀+♂	1		18,72	22,8	21,258	1,580	5	9,88	11,39
Bubo scandiacus	?+♀+♂	2		22,3	27,12	24,968	1,827	6	9,72	11,66
Bubo scandiacus	?+♀+♂	3		20,56	25,62	23,508	1,830	5	8,9	10,92
Bubo scandiacus	?+♀+♂	4		19,31	22,99	21,288	1,440	6	8,97	10,97
Bubo bubo	♀	1		26,14	28,62	-	-	3	11,77	15,07
Bubo bubo	♀	2		27,11	33,56	-	-	4	11,34	13,81
Bubo bubo	♀	3		29,69	31,33	-	-	2	10,17	12,73
Bubo bubo	♀	4		22,51	29,41	-	-	4	9,81	12,71
Bubo bubo	♂	1		22,89	24,16	-	-	3	11,65	12,58
Bubo bubo	♂	2		26,87	28,81	-	-	3	11,19	11,84
Bubo bubo	♂	3		25,52	28,02	-	-	3	10,29	10,86
Bubo bubo	♂	4		22,2	24,11	-	-	3	9,62	10,15
Bubo bubo	?+♀+♂	1		22,89	29,02	26,222	1,976	19	11,65	15,92
Bubo bubo	?+♀+♂	2		26,87	34,33	30,745	2,586	20	11,19	14,53
Bubo bubo	?+♀+♂	3		25,52	33,08	29,709	2,394	18	10,17	12,86
Bubo bubo	?+♀+♂	4		22,2	29,41	26,076	2,231	20	9,62	12,71
Falco naumanni	?+♀+♂		1-2	7,68	8,11	-	-	4	3,49	4,26
Falco naumanni	?+♀+♂	3		7,64	7,84	-	-	2	3,28	3,52
Falco naumanni	?+♀+♂	4		6,85	6,89	-	-	2	3,19	3,43
Falco tinnunculus	♀		1-2	9,01	11,54	10,179	0,561	33	4,22	5,35
Falco tinnunculus	♀	3		7,79	9,7	8,795	0,494	17	3,61	4,26
Falco tinnunculus	♀	4		6,97	9,01	8,046	0,519	17	3,48	4,23
Falco tinnunculus	♂		1-2	8,62	10,84	9,859	0,649	14	4,04	5,07
Falco tinnunculus	♂	3		7,33	9,93	8,534	0,838	7	3,63	4,08
Falco tinnunculus	♂	4		6,85	8,31	7,636	0,509	7	3,34	3,97
Falco tinnunculus	?+♀+♂		1-2	8,62	12,09	10,135	0,671	80	4,04	5,66
Falco tinnunculus	?+♀+♂	3		7,33	10,22	8,740	0,614	41	3,43	4,66
Falco tinnunculus	?+♀+♂	4		6,85	9,38	8,033	0,581	41	3,34	4,65
Falco vespertinus	♀		1-2	7,72	8,13	-	-	4	3,51	4,01
Falco vespertinus	♀	3		7,53	8,02	-	-	2	3,26	3,3
Falco vespertinus	♀	4		6,73	6,82	-	-	2	2,93	3,1
Falco vespertinus	♂		1-2	7,71	7,94	-	-	2	3,73	4,12
Falco vespertinus	♂	3		7,45	7,45	-	-	1	3,36	3,45
Falco vespertinus	♂	4		6,54	6,54	-	-	1	3,19	3,32
Falco vespertinus	?+♀+♂		1-2	7,71	8,13	7,865	0,170	6	3,51	4,12

Falco vespertinus	?+♀+♂	3			7,45	8,02	-	-	3		3,26	3,45
Falco vespertinus	?+♀+♂	4			6,54	6,82	-	-	3		2,93	3,32
Falco eleonorae	♀		1-2		11,3	11,61	-	-	2		5,42	5,85
Falco eleonorae	♀	3			11,05	11,05	-	-	1		4,69	4,69
Falco eleonorae	♀	4			10,02	10,02	-	-	1		4,78	4,78
Falco eleonorae	?+♀+♂		1-2		11,3	11,61	-	-	2		5,42	5,85
Falco eleonorae	?+♀+♂	3			11,05	11,05	-	-	1		4,69	4,69
Falco eleonorae	?+♀+♂	4			10,02	10,02	-	-	1		4,78	4,78
Falco columbarius	♂		1-2		9,03	9,23	-	-	4		4,08	4,54
Falco columbarius	♂	3			8,49	8,55	-	-	2		3,79	3,8
Falco columbarius	♂	4			7,51	7,74	-	-	2		3,6	3,7
Falco columbarius	?+♀+♂		1-2		9,03	9,23	-	-	4		4,08	4,54
Falco columbarius	?+♀+♂	3			8,49	8,55	-	-	2		3,79	3,8
Falco columbarius	?+♀+♂	4			7,51	7,74	-	-	2		3,6	3,7
Falco subbuteo	♀		1-2		8,81	10,54	9,803	0,789	6		4,67	5,12
Falco subbuteo	♀	3			8,84	9,64	-	-	3		4,12	4,5
Falco subbuteo	♀	4			7,68	8,72	-	-	3		3,94	4,45
Falco subbuteo	♂		1-2		8,46	10,04	9,166	0,507	7		4,33	5,43
Falco subbuteo	♂	3			8,48	9,68	-	-	4		3,73	4,54
Falco subbuteo	♂	4			7,37	8,69	-	-	4		3,76	4,56
Falco subbuteo	?+♀+♂		1-2		8,21	10,54	9,293	0,750	16		3,94	5,43
Falco subbuteo	?+♀+♂	3			7,94	9,68	9,045	0,638	8		3,64	4,54
Falco subbuteo	?+♀+♂	4			7,14	8,72	7,955	0,613	8		3,47	4,56
Falco cherrug	♀		1-2		18,57	20,77	-	-	4		8,77	9,89
Falco cherrug	♀	4			16	16	-	-	1		7,81	7,81
Falco cherrug	♂		1-2		16,9	17,97	-	-	2		7,66	8,71
Falco cherrug	♂	3			14,55	14,55	-	-	1		6,55	6,55
Falco cherrug	♂	4			13,39	13,39	-	-	1		6,44	6,44
Falco cherrug	?+♀+♂		1-2		16,9	21,5	19,451	1,307	14		7,66	9,89
Falco cherrug	?+♀+♂	3			14,55	17,05	15,872	1,088	5		6,55	7,76
Falco cherrug	?+♀+♂	4			13,39	16	15,257	0,970	6		6,44	7,81
Falco rusticolus	♂		1-2		18,93	23,45	20,822	1,609	6		8,22	10,42
Falco rusticolus	♂	3			16,21	18,09	-	-	3		6,94	7,52
Falco rusticolus	♂	4			14,44	16,22	-	-	3		6,75	7,48
Falco rusticolus	?+♀+♂		1-2		18,93	25,28	22,025	1,786	14		8,22	11,13
Falco rusticolus	?+♀+♂	3			16,21	19,2	17,880	1,188	7		6,94	8,25
Falco rusticolus	?+♀+♂	4			14,44	17,41	16,193	1,022	7		6,75	8,01
Falco peregrinus	♀		1-2		18,99	21,16	20,096	0,740	9		8,74	10,62
Falco peregrinus	♀	3			14,99	17,9	17,004	1,150	5		7,32	8,19
Falco peregrinus	♀	4			15,95	16,86	16,364	0,366	5		7,34	8,08
Falco peregrinus	♂		1-2		16,59	17,02	-	-	2		7,55	8,33
Falco peregrinus	♂	3			14,85	14,85	-	-	1		6,72	6,72
Falco peregrinus	♂	4			13,85	13,85	-	-	1		6,54	6,54
Falco peregrinus	?+♀+♂		1-2		14,55	21,39	18,842	1,947	25		7,22	10,62
Falco peregrinus	?+♀+♂	3			13,64	18,02	16,266	1,623	13		6,31	8,19
Falco peregrinus	?+♀+♂	4			12,17	17,09	15,336	1,603	13		6,15	8,14

s this? A manual for the identification of ungual phalanges of European birds of prey: falcons and owls.

iation are only calculated when the number of specimens is greater than or equal to five. Measurements for each sp
ds for the number of ungual phalanges measured which in the case of phalanges only from one digit (1, 2, 3 or 4) is

ximal height				Length of tuberculum flexorium						Height of cotyla ar		
MEAN	SD	N		Min	Max	MEAN	SD	N		Min	Max	MEAN
-	-	3		3,25	4,35	-	-	3		4,19	5,21	-
-	-	3		3,26	4,06	-	-	3		3,96	4,98	-
-	-	3		2,75	3,75	-	-	3		3,7	4,63	-
-	-	3		2,54	3,51	-	-	3		3,75	4,66	-
6,192	0,613	6		3,1	4,07	3,732	0,358	6		3,76	4,92	4,305
5,677	0,470	6		2,68	4,07	3,277	0,519	6		3,91	4,81	4,295
5,452	0,284	6		2,76	3,39	3,047	0,212	6		3,09	4,5	3,882
5,272	0,662	5		2,46	3,45	3,020	0,423	5		3,45	4,17	3,812
6,213	0,465	24		3,1	4,35	3,615	0,308	24		3,76	5,21	4,458
5,817	0,400	24		2,68	4,07	3,339	0,327	24		3,91	4,98	4,351
5,460	0,336	24		2,75	3,77	3,098	0,260	24		3,09	4,63	3,937
5,348	0,423	23		2,46	3,51	2,890	0,273	23		3,45	4,66	3,998
-	-	4		3,26	3,87	-	-	4		4,5	5,04	-
6,268	0,214	5		3,44	3,91	3,636	0,184	5		4,47	4,94	4,690
-	-	4		3,39	3,96	-	-	4		4,03	4,37	-
-	-	1		3,23	3,23	-	-	1		4,67	4,67	-
5,526	0,215	5		2,98	3,41	3,154	0,163	5		3,92	4,15	4,014
4,060	0,295	8		2	2,82	2,360	0,326	8		2,67	3,1	2,863
4,191	0,291	8		2,26	2,93	2,603	0,272	8		2,74	3,72	3,239
3,811	0,272	7		2,19	2,83	2,436	0,256	7		2,23	3,37	2,763
3,694	0,309	8		1,78	2,42	2,111	0,257	8		2,64	3,13	2,821
-	-	1		2,39	2,39	-	-	1		3,14	3,14	-
-	-	1		2,1	2,1	-	-	1		2,69	2,69	-
-	-	1		2,64	2,64	-	-	1		3,17	3,17	-
-	-	1		1,58	1,58	-	-	1		2,6	2,6	-
-	-	3		2,3	2,39	-	-	2		3,14	3,16	-
-	-	3		2,1	2,57	-	-	2		2,69	3,06	-
-	-	3		2,64	2,7	-	-	2		2,66	3,17	-
-	-	3		1,58	1,94	-	-	2		2,57	2,6	-
-	-	2		2,15	2,18	-	-	2		1,85	1,92	-
-	-	3		2,16	2,46	-	-	3		1,98	2,24	-
-	-	3		2,11	2,41	-	-	3		1,81	1,99	-
-	-	3		1,87	2,19	-	-	3		1,66	1,92	-
5,634	0,332	8		2,75	3,49	3,243	0,258	8		3,48	4,16	3,820
5,641	0,320	8		3,09	3,67	3,326	0,230	8		3,74	4,41	4,041
5,385	0,271	8		2,89	3,43	3,155	0,208	8		3,62	4,13	3,814
4,994	0,244	7		2,19	2,86	2,614	0,241	7		3,32	3,94	3,654
5,628	0,381	12		2,81	3,68	3,359	0,259	12		3,16	4,28	3,895
5,671	0,294	14		2,87	3,76	3,396	0,244	14		3,69	4,42	4,100
5,438	0,276	13		3,02	3,69	3,309	0,195	13		3,47	4,14	3,907
4,940	0,348	13		2,33	3,1	2,788	0,236	13		3,24	3,86	3,651
5,640	0,328	47		2,75	3,68	3,330	0,225	47		3,16	4,98	3,976
5,672	0,279	48		2,87	3,87	3,398	0,238	48		3,69	4,52	4,125
5,427	0,252	48		2,89	3,78	3,276	0,195	48		3,47	4,4	3,887
4,970	0,294	45		2,19	3,26	2,792	0,240	45		3,24	4,16	3,673
-	-	2		3,4	4	-	-	2		4,09	4,29	-
-	-	2		3,73	4	-	-	2		4,41	4,62	-
-	-	2		3,45	3,84	-	-	2		4,1	4,11	-
-	-	2		2,95	3,33	-	-	2		3,93	4,31	-
-	-	1		3,39	3,39	-	-	1		4,21	4,21	-
-	-	1		3,49	3,49	-	-	1		4,52	4,52	-
-	-	1		3,39	3,39	-	-	1		4,02	4,02	-
-	-	1		2,58	2,58	-	-	1		3,72	3,72	-
5,646	0,373	10		3,06	4	3,363	0,259	10		3,52	4,29	3,962
5,838	0,267	10		3,08	4	3,494	0,293	10		4,01	4,73	4,354

5,522	0,229	10		3,15	3,84	3,443	0,241	10		3,68	4,11	3,977
5,077	0,216	10		2,58	3,33	2,864	0,270	10		3,5	4,31	3,827
7,242	0,346	16		3,8	4,75	4,216	0,308	16		4,05	5,16	4,691
7,203	0,315	16		3,87	4,89	4,404	0,264	16		4,69	5,58	5,095
6,569	0,262	16		3,62	4,52	4,151	0,271	16		4,13	4,85	4,423
6,334	0,267	16		3,13	3,98	3,596	0,238	16		3,97	4,69	4,319
6,862	0,507	9		3,47	4,76	3,908	0,402	9		3,93	5,71	4,579
6,917	0,475	9		3,93	4,76	4,224	0,297	9		4,59	5,43	5,011
6,473	0,429	9		3,75	4,47	4,040	0,279	9		3,9	4,71	4,312
6,080	0,431	9		2,96	4,48	3,619	0,570	9		3,16	4,93	4,158
7,040	0,419	39		3,47	4,76	4,048	0,359	39		3,93	5,71	4,676
7,001	0,433	39		3,7	4,89	4,287	0,298	39		4,59	5,58	5,013
6,454	0,346	39		3,57	4,52	4,039	0,276	39		3,9	4,85	4,343
6,140	0,364	38		2,96	4,48	3,503	0,363	38		3,16	4,93	4,246
-	-	2		5,4	5,58	-	-	2		5,76	6,2	-
-	-	2		5,07	5,84	-	-	2		6,46	7,21	-
-	-	2		4,82	5,92	-	-	2		5,69	6,5	-
-	-	2		4,34	5,15	-	-	2		5,47	6,14	-
9,448	0,507	10		4,77	5,97	5,258	0,349	10		5,69	6,5	6,095
9,483	0,539	10		4,65	5,84	5,322	0,342	10		6,13	7,21	6,856
8,606	0,441	10		4,63	5,92	5,144	0,437	10		5,49	6,53	6,049
8,321	0,384	10		3,97	5,15	4,464	0,334	10		5,32	6,32	5,880
-	-	4		4,17	4,83	-	-	4		6,14	6,7	-
-	-	4		4,2	6,82	-	-	4		6,44	7,51	-
-	-	3		4,12	4,86	-	-	3		6,38	7,1	-
7,896	1,213	5		3,72	4,72	4,200	0,376	5		3,85	7,06	5,584
-	-	1		6,44	6,44	-	-	1		9,02	9,02	-
-	-	1		6,17	6,17	-	-	1		8,4	8,4	-
-	-	1		5,49	5,49	-	-	1		8,56	8,56	-
10,506	0,578	5		5,43	5,84	5,632	0,189	5		7,44	8,14	7,758
10,527	0,780	6		5,63	6,52	6,168	0,334	6		7,97	9,02	8,288
9,720	0,736	5		5,54	6,17	5,798	0,265	5		6,84	8,4	7,388
9,630	0,703	6		4,85	5,63	5,258	0,275	6		7,2	8,56	7,650
-	-	4		6,51	8,83	-	-	4		7,82	9,75	-
-	-	4		6,65	8,68	-	-	4		8,55	10,19	-
-	-	4		6,08	8,09	-	-	4		7,82	9,54	-
-	-	4		5,25	6,91	-	-	4		7,56	9,34	-
-	-	3		6,73	6,78	-	-	3		7,48	8,84	-
-	-	3		6,54	7,14	-	-	3		8,43	8,75	-
-	-	3		6,14	6,84	-	-	3		7,62	8,17	-
-	-	3		5,45	5,61	-	-	3		7,57	8,13	-
13,276	1,138	20		6,51	9,76	7,566	0,840	20		7,48	10,59	8,999
12,848	0,990	20		6,54	9,31	7,788	0,774	20		8,43	10,45	9,404
11,700	0,853	20		6,08	8,47	7,277	0,643	20		7,62	9,54	8,730
11,108	0,914	20		5,25	7,13	6,176	0,618	20		7,56	9,34	8,513
-	-	4		2,09	2,66	-	-	4		2,46	2,64	-
-	-	2		1,93	2,14	-	-	2		2,31	2,35	-
-	-	2		2,06	2,06	-	-	2		2,19	2,26	-
4,756	0,306	33		2,55	3,41	2,928	0,277	33		2,8	3,8	3,182
3,952	0,190	17		2,15	2,59	2,364	0,125	17		2,44	2,93	2,736
3,854	0,192	17		1,95	2,56	2,329	0,152	17		2,22	2,8	2,652
4,688	0,323	14		2,39	3,38	2,919	0,324	14		2,71	3,36	3,105
3,886	0,168	7		2,06	2,49	2,303	0,160	7		2,45	2,86	2,709
3,756	0,226	7		2	2,77	2,319	0,247	7		2,43	2,69	2,570
4,771	0,336	80		2,34	3,71	2,950	0,306	80		2,59	3,8	3,162
3,950	0,215	41		2,04	2,76	2,381	0,176	41		2,42	3,15	2,728
3,890	0,225	41		1,95	2,8	2,368	0,175	41		2,22	3,09	2,654
-	-	4		2,13	2,63	-	-	4		2,42	2,54	-
-	-	2		1,94	2,21	-	-	2		2,22	2,22	-
-	-	2		1,78	1,86	-	-	2		2,01	2,09	-
-	-	4		2,28	2,91	-	-	4		2,22	2,51	-
-	-	2		2,06	2,25	-	-	2		2,16	2,19	-
-	-	2		1,96	2,21	-	-	2		2,03	2,11	-
3,843	0,219	8		2,13	2,91	2,494	0,273	8		2,22	2,54	2,426

-	-	4		1,94	2,25	-	-	4		2,16	2,22	-
-	-	4		1,78	2,21	-	-	4		2,01	2,11	-
-	-	2		3,21	4,35	-	-	2		3,51	3,69	-
-	-	1		3,18	3,18	-	-	1		3,17	3,17	-
-	-	1		3,24	3,24	-	-	1		3,14	3,14	-
-	-	2		3,21	4,35	-	-	2		3,51	3,69	-
-	-	1		3,18	3,18	-	-	1		3,17	3,17	-
-	-	1		3,24	3,24	-	-	1		3,14	3,14	-
-	-	4		2,5	3,01	-	-	4		2,62	2,93	-
-	-	2		2,25	2,31	-	-	2		2,45	2,58	-
-	-	2		2,21	2,24	-	-	2		2,32	2,45	-
-	-	4		2,5	3,01	-	-	4		2,62	2,93	-
-	-	2		2,25	2,31	-	-	2		2,45	2,58	-
-	-	2		2,21	2,24	-	-	2		2,32	2,45	-
4,955	0,158	6		3,05	3,49	3,258	0,172	6		3,02	3,34	3,237
-	-	3		2,69	2,89	-	-	3		2,71	2,91	-
-	-	3		2,55	2,8	-	-	3		2,54	2,92	-
4,691	0,425	7		2,58	3,55	3,071	0,315	7		2,71	3,41	3,024
-	-	4		2,43	2,91	-	-	4		2,58	2,97	-
-	-	4		2,41	2,85	-	-	4		2,51	2,95	-
4,702	0,426	16		2,58	3,55	3,144	0,260	16		2,5	3,41	3,047
4,101	0,353	8		2,19	2,91	2,626	0,245	8		2,5	2,97	2,741
3,995	0,371	8		2,1	2,85	2,544	0,259	8		2,24	2,95	2,620
-	-	4		5,34	6,14	-	-	4		6,06	6,96	-
-	-	1		5,19	5,19	-	-	1		5,29	5,29	-
-	-	2		4,54	5,26	-	-	2		5,22	5,65	-
-	-	1		3,99	3,99	-	-	1		4,42	4,42	-
-	-	1		3,85	3,85	-	-	1		4,45	4,45	-
9,094	0,616	14		4,54	6,5	5,516	0,527	14		5,22	6,96	6,278
7,266	0,445	5		3,99	4,83	4,456	0,300	5		4,42	5,15	4,904
7,213	0,513	6		3,85	5,19	4,497	0,522	6		4,45	5,29	4,908
9,128	0,776	6		4,74	6,23	5,452	0,510	6		5,89	7,08	6,310
-	-	3		4,1	4,71	-	-	3		4,88	5,38	-
-	-	3		4,14	4,7	-	-	3		4,56	5,27	-
9,742	0,910	14		4,74	6,94	5,926	0,658	14		5,89	7,71	6,748
7,703	0,539	7		4,1	5,56	4,779	0,463	7		4,88	5,76	5,384
7,481	0,466	7		4,14	5,12	4,609	0,353	7		4,56	5,78	5,253
9,597	0,578	9		5,2	6,62	5,909	0,576	9		5,92	6,65	6,273
7,756	0,311	5		4,38	4,9	4,722	0,220	5		5,02	5,56	5,280
7,728	0,283	5		4,49	5,21	4,804	0,259	5		4,93	5,39	5,200
-	-	2		4,6	5,24	-	-	2		4,8	5,31	-
-	-	1		4,26	4,26	-	-	1		4,28	4,28	-
-	-	1		4,23	4,23	-	-	1		4,23	4,23	-
9,022	0,942	27		4,52	6,64	5,586	0,650	27		4,8	6,65	5,943
7,371	0,622	14		3,93	4,9	4,523	0,334	14		4,28	5,56	5,024
7,357	0,667	14		3,95	5,21	4,554	0,379	14		4,19	5,39	4,941

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ecies and for each ungual phalanx are given separately for each sex (if
equal to the number of bird specimens; it differs when the phalanges of

ticularis			Articular width					
SD	N		Min	Max	MEAN	SD	N	
-	3		2,29	3,52	-	-	3	
-	3		2,81	4,07	-	-	3	
-	3		2,67	3,9	-	-	3	
-	3		2,39	4,03	-	-	3	
0,392	6		2,11	3,27	2,677	0,381	6	
0,336	6		2,36	4	3,265	0,528	6	
0,453	6		2,07	3,86	3,043	0,571	6	
0,290	5		2,06	3,79	3,018	0,624	5	
0,359	24		2,1	3,52	2,776	0,337	24	
0,264	24		2,36	4,07	3,271	0,387	24	
0,378	24		2,07	3,9	3,191	0,381	24	
0,275	23		2	4,03	3,125	0,469	23	
-	4		2,91	3,04	-	-	4	
0,172	5		3,67	4	3,818	0,154	5	
-	4		4,03	4,2	-	-	4	
-	1		3,23	3,23	-	-	1	
0,111	5		2,97	3,28	3,124	0,145	5	
0,161	8		1,53	2,43	1,954	0,342	8	
0,326	8		2,05	3,18	2,704	0,428	8	
0,404	7		2,15	3,25	2,719	0,427	7	
0,170	8		1,53	2,54	2,091	0,401	8	
-	1		2,09	2,09	-	-	1	
-	1		2,91	2,91	-	-	1	
-	1		2,67	2,67	-	-	1	
-	1		2,18	2,18	-	-	1	
-	2		1,96	2,26	-	-	3	
-	2		2,46	2,91	-	-	3	
-	2		2,67	3,15	-	-	3	
-	2		2,18	2,35	-	-	3	
-	2		1,45	1,55	-	-	2	
-	3		1,79	2,11	-	-	3	
-	3		1,71	1,97	-	-	3	
-	3		1,35	1,73	-	-	3	
0,236	8		2,15	2,89	2,456	0,216	8	
0,278	8		2,84	3,67	3,208	0,256	8	
0,196	8		2,99	3,91	3,413	0,352	8	
0,244	7		2,6	3,18	2,861	0,232	7	
0,347	12		2,21	2,83	2,538	0,181	12	
0,205	14		2,94	3,76	3,295	0,229	14	
0,203	13		3,24	3,92	3,495	0,236	13	
0,180	13		2,53	3,22	2,891	0,228	13	
0,306	47		2,15	2,89	2,545	0,186	46	
0,228	48		2,84	3,76	3,304	0,210	46	
0,186	48		2,99	3,94	3,482	0,247	47	
0,202	45		2,53	3,22	2,897	0,204	43	
-	2		2,91	3,11	-	-	2	
-	2		3,74	3,8	-	-	2	
-	2		4,02	4,19	-	-	2	
-	2		3,37	3,42	-	-	2	
-	1		2,79	2,79	-	-	1	
-	1		3,51	3,51	-	-	1	
-	1		3,65	3,65	-	-	1	
-	1		2,85	2,85	-	-	1	
0,296	10		2,25	3,11	2,712	0,288	10	
0,220	10		3,09	3,89	3,561	0,280	10	

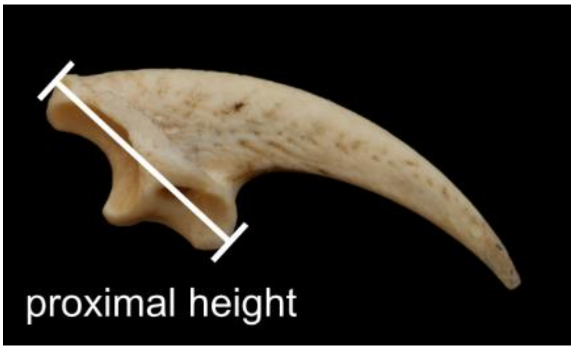
0,152	10		3,32	4,27	3,767	0,342	10	
0,223	10		2,49	3,42	3,081	0,311	10	
0,293	16		2,86	3,64	3,291	0,215	16	
0,262	16		4,03	4,67	4,387	0,188	16	
0,204	16		3,92	5,6	4,648	0,356	16	
0,226	16		3,26	4,9	3,721	0,357	16	
0,529	9		2,64	3,41	3,077	0,298	9	
0,281	9		3,7	4,66	4,124	0,367	9	
0,331	9		3,72	4,64	4,258	0,327	9	
0,509	9		2,98	3,76	3,429	0,296	9	
0,367	39		2,64	3,71	3,175	0,270	39	
0,262	39		3,7	4,73	4,243	0,295	39	
0,258	39		3,72	5,6	4,375	0,402	39	
0,312	38		2,98	4,9	3,550	0,324	38	
-	2		3,57	4,21	-	-	2	
-	2		4,86	5,99	-	-	2	
-	2		5,27	6,1	-	-	2	
-	2		4,1	4,82	-	-	2	
0,262	10		3,57	4,43	3,947	0,260	10	
0,348	10		4,76	6,34	5,473	0,467	10	
0,347	10		4,95	6,1	5,512	0,312	10	
0,353	10		4,1	4,82	4,520	0,262	10	
-	4		3,44	4,09	-	-	4	
-	4		4,3	5,03	-	-	4	
-	3		4,31	5,15	-	-	3	
1,424	5		3,28	4,54	4,060	0,473	5	
-	1		7,31	7,31	-	-	1	
-	1		7,35	7,35	-	-	1	
-	1		5,92	5,92	-	-	1	
0,304	5		4,2	5,64	4,872	0,513	5	
0,490	6		5,66	7,56	6,610	0,701	6	
0,596	5		5,8	7,35	6,556	0,549	5	
0,513	6		4,65	6,18	5,453	0,540	6	
-	4		5,25	6,85	-	-	4	
-	4		7,13	9,1	-	-	4	
-	4		7,49	9,32	-	-	4	
-	4		6,06	7,86	-	-	4	
-	3		5,04	5,7	-	-	3	
-	3		7,46	7,72	-	-	3	
-	3		7,3	8,31	-	-	3	
-	3		6,22	6,7	-	-	3	
0,869	20		4,91	6,89	6,099	0,621	20	
0,713	20		6,75	9,34	8,371	0,748	20	
0,662	20		6,61	9,59	8,596	0,862	20	
0,566	20		5,51	7,86	7,003	0,672	20	
-	4		1,92	2,1	-	-	4	
-	2		2,02	2,12	-	-	2	
-	2		1,66	1,76	-	-	2	
0,174	33		1,86	2,63	2,352	0,195	33	
0,125	17		1,99	2,53	2,219	0,187	17	
0,138	17		1,55	2,54	1,919	0,230	17	
0,200	14		1,76	2,86	2,333	0,316	14	
0,158	7		1,96	2,52	2,261	0,223	7	
0,101	7		1,45	2,24	1,883	0,314	7	
0,186	80		1,76	2,92	2,372	0,252	80	
0,151	41		1,68	2,68	2,235	0,221	41	
0,142	41		1,45	2,54	1,933	0,232	41	
-	4		1,65	1,85	-	-	4	
-	2		1,84	2,03	-	-	2	
-	2		1,27	1,42	-	-	2	
-	4		1,81	2	-	-	4	
-	2		1,73	1,92	-	-	2	
-	2		1,58	1,63	-	-	2	
0,106	8		1,65	2	1,826	0,095	8	

-	4		1,73	2,03	-	-	4	
-	4		1,27	1,63	-	-	4	
-	2		2,62	2,79	-	-	2	
-	1		2,77	2,77	-	-	1	
-	1		2,38	2,38	-	-	1	
-	2		2,62	2,79	-	-	2	
-	1		2,77	2,77	-	-	1	
-	1		2,38	2,38	-	-	1	
-	4		1,85	2,21	-	-	4	
-	2		1,98	2,2	-	-	2	
-	2		1,71	1,94	-	-	2	
-	4		1,85	2,21	-	-	4	
-	2		1,98	2,2	-	-	2	
-	2		1,71	1,94	-	-	2	
0,129	6		2,14	2,4	2,267	0,105	6	
-	3		2,19	2,5	-	-	3	
-	3		1,81	2,07	-	-	3	
0,277	7		1,9	2,34	2,127	0,154	7	
-	4		1,93	2,31	-	-	4	
-	4		1,64	2,02	-	-	4	
0,285	16		1,73	2,4	2,136	0,196	16	
0,163	8		1,87	2,5	2,164	0,200	8	
0,232	8		1,45	2,07	1,820	0,208	8	
-	4		4,72	5,33	-	-	4	
-	1		4,41	4,41	-	-	1	
-	2		3,74	3,93	-	-	2	
-	1		3,59	3,59	-	-	1	
-	1		3,14	3,14	-	-	1	
0,499	14		3,74	5,33	4,595	0,474	14	
0,293	5		3,59	4,22	4,018	0,258	5	
0,276	6		3,14	4,41	3,707	0,464	6	
0,489	6		4,45	5,28	4,780	0,361	6	
-	3		4,27	4,85	-	-	3	
-	3		3,84	4,23	-	-	3	
0,547	14		4,45	5,7	5,194	0,444	14	
0,367	7		4,27	5,23	4,839	0,343	7	
0,453	7		3,84	4,55	4,209	0,265	7	
0,246	9		4,14	4,67	4,396	0,160	9	
0,208	5		3,79	4,37	4,194	0,231	5	
0,178	5		3,32	3,85	3,642	0,196	5	
-	2		3,27	3,35	-	-	2	
-	1		3,17	3,17	-	-	1	
-	1		2,83	2,83	-	-	1	
0,593	27		3,27	4,67	4,103	0,410	27	
0,465	14		3,17	4,55	3,968	0,415	14	
0,469	14		2,83	3,85	3,464	0,337	14	

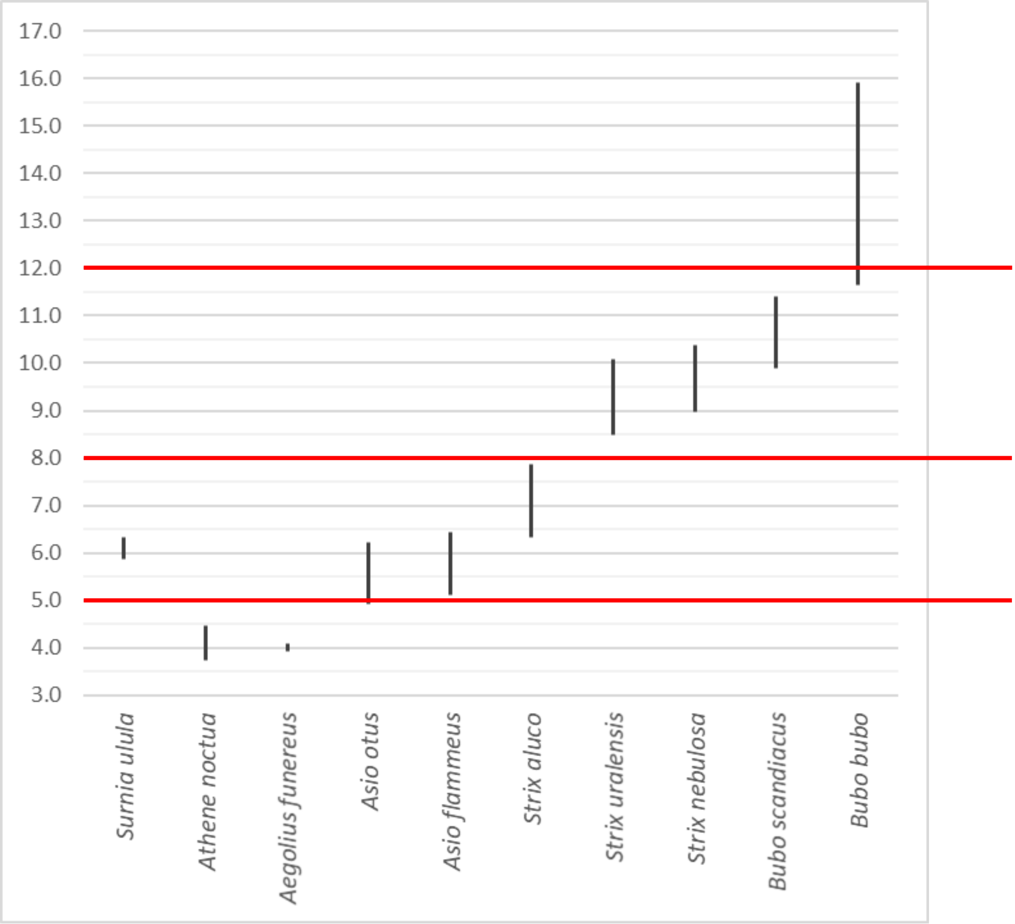
Supporting Appendix S1

for: Wertz K., Tomek T., Bochenski Z.M. Whose talon is this? A manual for the identification of ungual phalanges of European birds of prey: falcons and owls. *International Journal of Osteoarchaeology*.

1. Measurement used



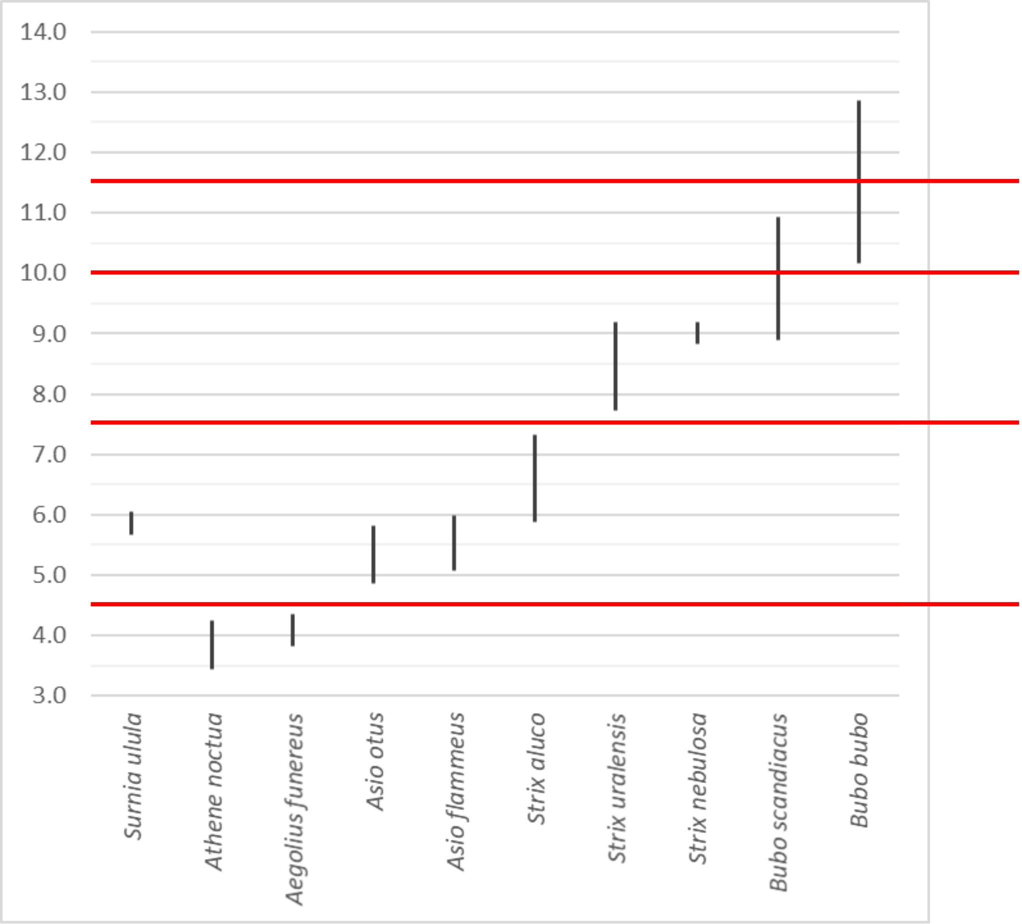
2. Information for manual, step #14:



Strigidae, digit 1, proximal height. The range of measurements and the number of measured bird specimens are presented in the table below. The red lines indicate the values used to divide the taxa by size.

Taxon	Min	Max	N
Surnia ulula	5.9	6.3	4
Athene noctua	3.7	4.5	8
Aegolius funereus	3.9	4.1	3
Asio otus	4.9	6.2	47
Asio flammeus	5.1	6.4	10
Strix aluco	6.3	7.9	39
Strix uralensis	8.5	10.1	10
Strix nebulosa	9.0	10.4	4
Bubo scandiacus	9.9	11.4	5
Bubo bubo	11.7	15.9	20

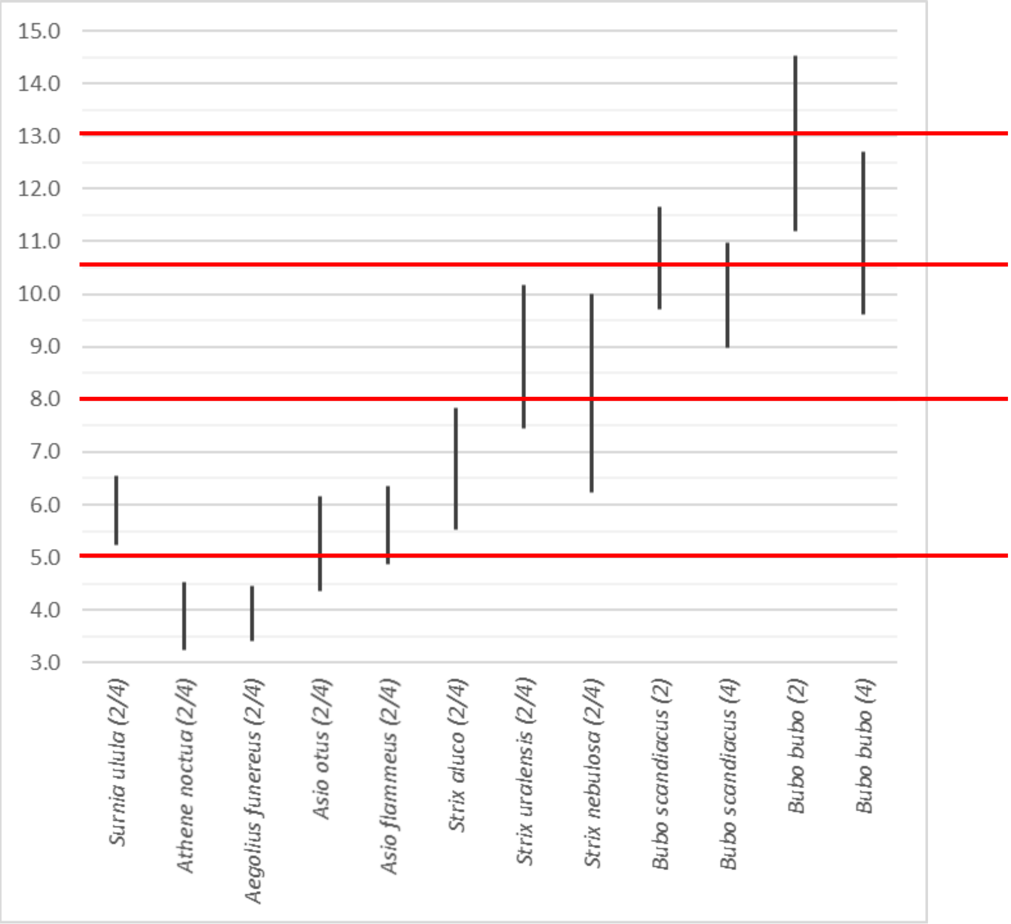
3. Information for manual, step #19:



Strigidae, digit 3, proximal height. The range of measurements and the number of measured bird specimens are presented in the table below. The red lines indicate the values used to divide the taxa by size.

Taxon	Min	Max	N
Surnia ulula	5.7	6.0	4
Athene noctua	3.5	4.2	7
Aegolius funereus	3.8	4.4	3
Asio otus	4.9	5.8	48
Asio flammeus	5.1	6.0	10
Strix aluco	5.9	7.3	39
Strix uralensis	7.7	9.2	10
Strix nebulosa	8.8	9.2	3
Bubo scandiacus	8.9	10.9	5
Bubo bubo	10.2	12.9	20

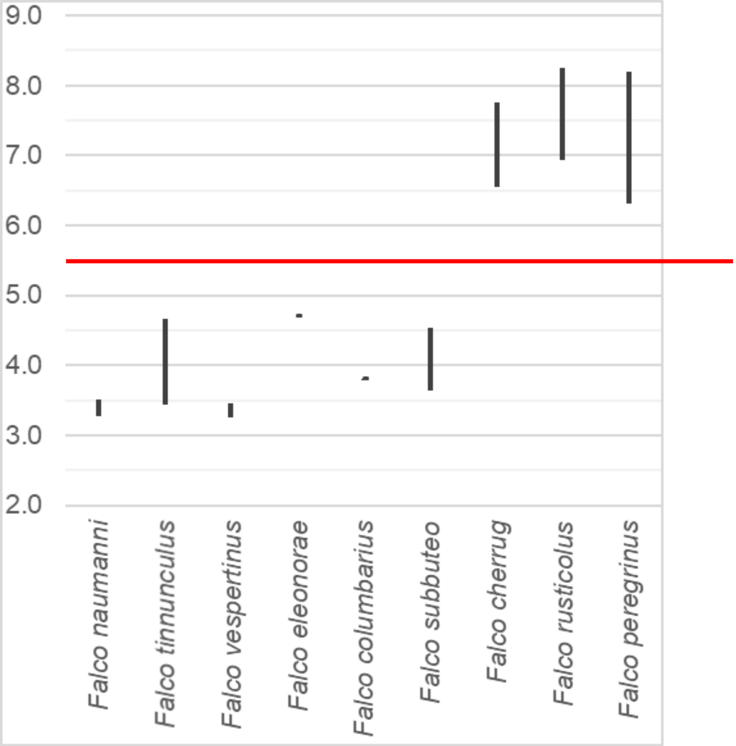
4. Information for manual, step #24:



Strigidae, digits 2 and 4, proximal height. The range of measurements and the number of measured bird specimens are presented in the table below. The red lines indicate the values used to divide the taxa by size.

Taxon	Min	Max	N
Surnia ulula (2/4)	5.2	6.6	5
Athene noctua (2/4)	3.3	4.5	8
Aegolius funereus (2/4)	3.4	4.5	3
Asio otus (2/4)	4.4	6.2	48
Asio flammeus (2/4)	4.9	6.4	10
Strix aluco (2/4)	5.5	7.8	39
Strix uralensis (2/4)	7.5	10.2	10
Strix nebulosa (2/4)	6.2	10.0	5
Bubo scandiacus (2)	9.7	11.7	6
Bubo scandiacus (4)	9.0	11.0	6
Bubo bubo (2)	11.2	14.5	20
Bubo bubo (4)	9.6	12.7	20

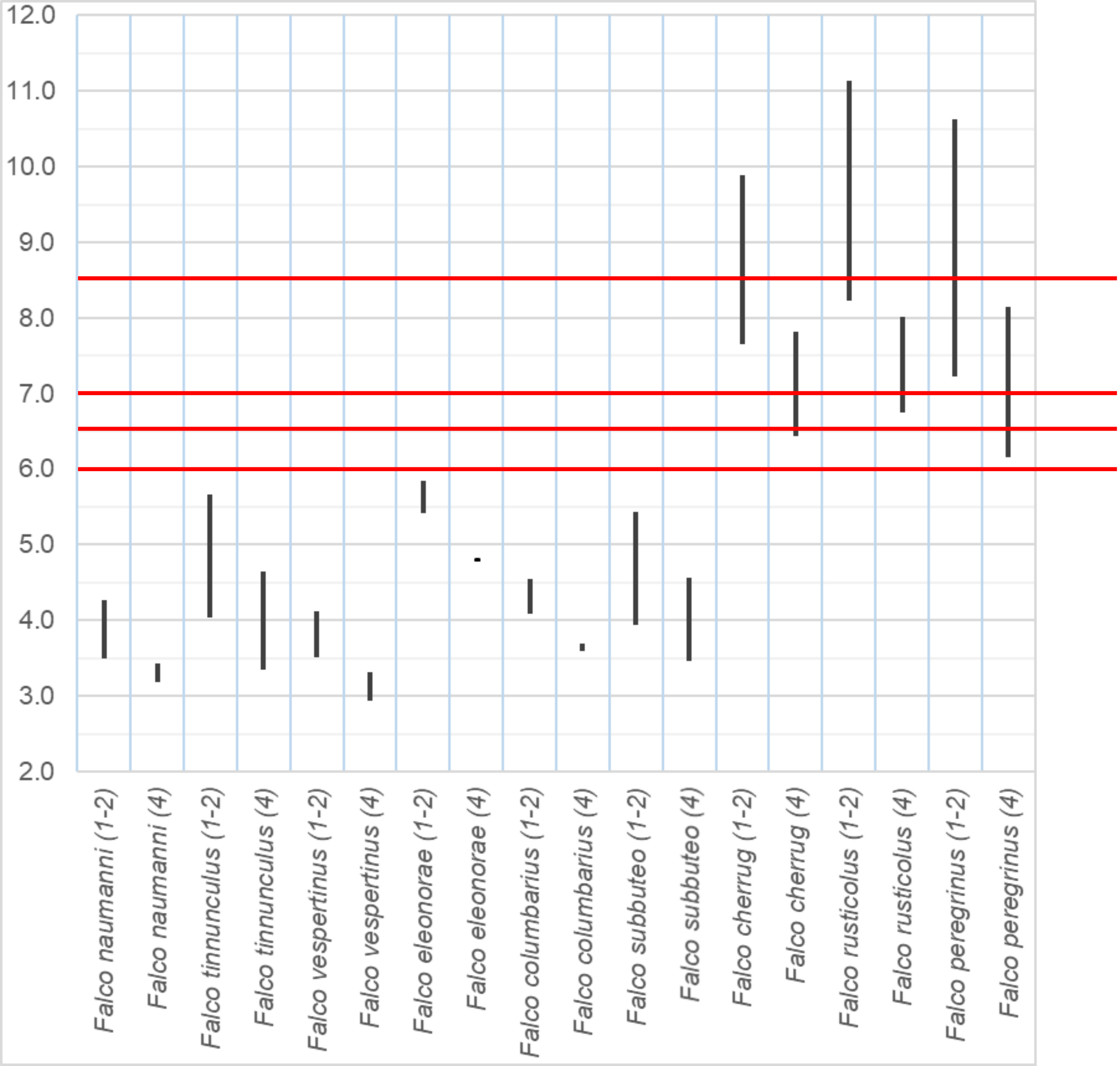
5. Information for manual, step #38:



Falconidae, digit 3, proximal height. The range of measurements and the number of measured bird specimens are presented in the table below. The red line indicates the value used to divide the taxa by size.

Taxon	Min	Max	N
Falco naumanni	3.3	3.5	2
Falco tinnunculus	3.4	4.7	41
Falco vespertinus	3.3	3.5	4
Falco eleonorae	4.7	4.7	1
Falco columbarius	3.8	3.8	2
Falco subbuteo	3.6	4.5	8
Falco cherrug	6.6	7.8	5
Falco rusticolus	6.9	8.3	7
Falco peregrinus	6.3	8.2	14

5. Information for manual, steps #41, #43, #44:



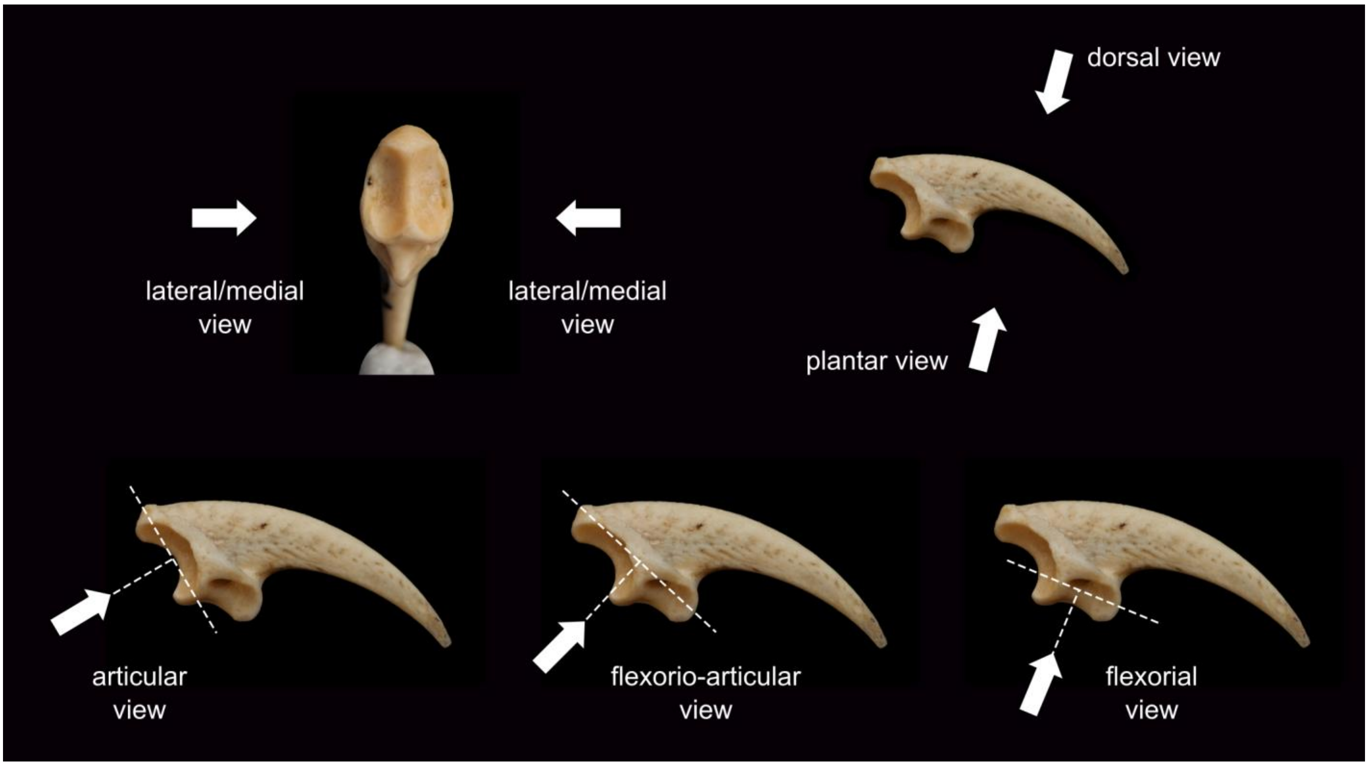
Falconidae, digits 1, 2, and 4, proximal height. The range of measurements and the number of measured bird specimens are presented in the table below. The red lines indicate the values used to divide the taxa by size.

Taxon	Min	Max	N
Falco naumanni (1-2)	3.5	4.3	2
Falco naumanni (4)	3.2	3.4	2
Falco tinnunculus (1-2)	4.0	5.7	41
Falco tinnunculus (4)	3.3	4.7	41
Falco vespertinus (1-2)	3.5	4.1	4
Falco vespertinus (4)	2.9	3.3	4
Falco eleonorae (1-2)	5.4	5.9	1
Falco eleonorae (4)	4.8	4.8	1
Falco columbarius (1-2)	4.1	4.5	2
Falco columbarius (4)	3.6	3.7	2

Taxon	Min	Max	N
Falco subbuteo (1-2)	3.9	5.4	8
Falco subbuteo (4)	3.5	4.6	8
Falco cherrug (1-2)	7.7	9.9	7
Falco cherrug (4)	6.4	7.8	6
Falco rusticolus (1-2)	8.2	11.1	7
Falco rusticolus (4)	6.8	8.0	7
Falco peregrinus (1-2)	7.2	10.6	14
Falco peregrinus (4)	6.2	8.1	14

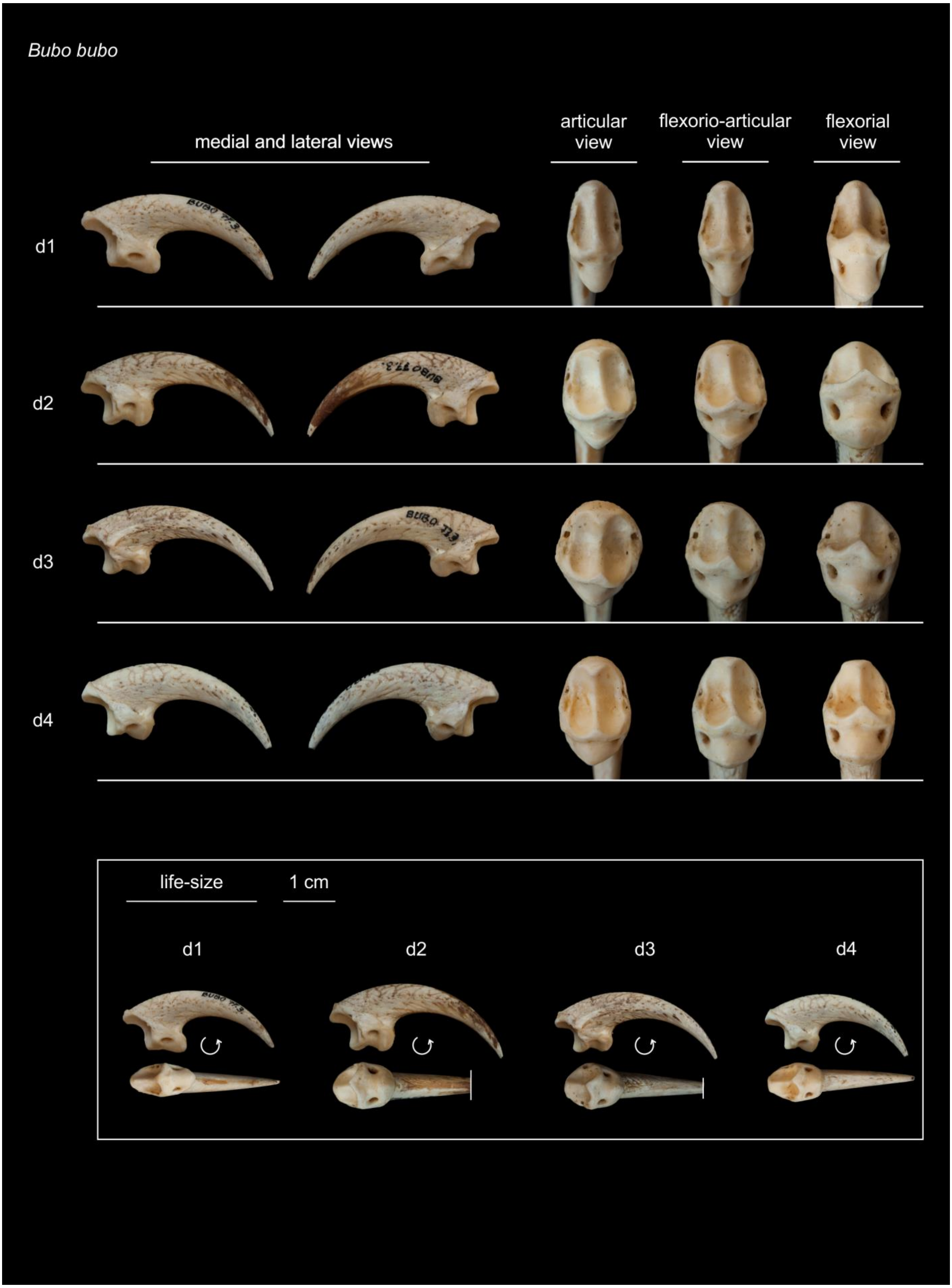
Supporting Appendix S2

for: Wertz K., Tomek T., Bochenski Z.M. Whose talon is this? A manual for the identification of ungual phalanges of European birds of prey: falcons and owls. *International Journal of Osteoarchaeology*.

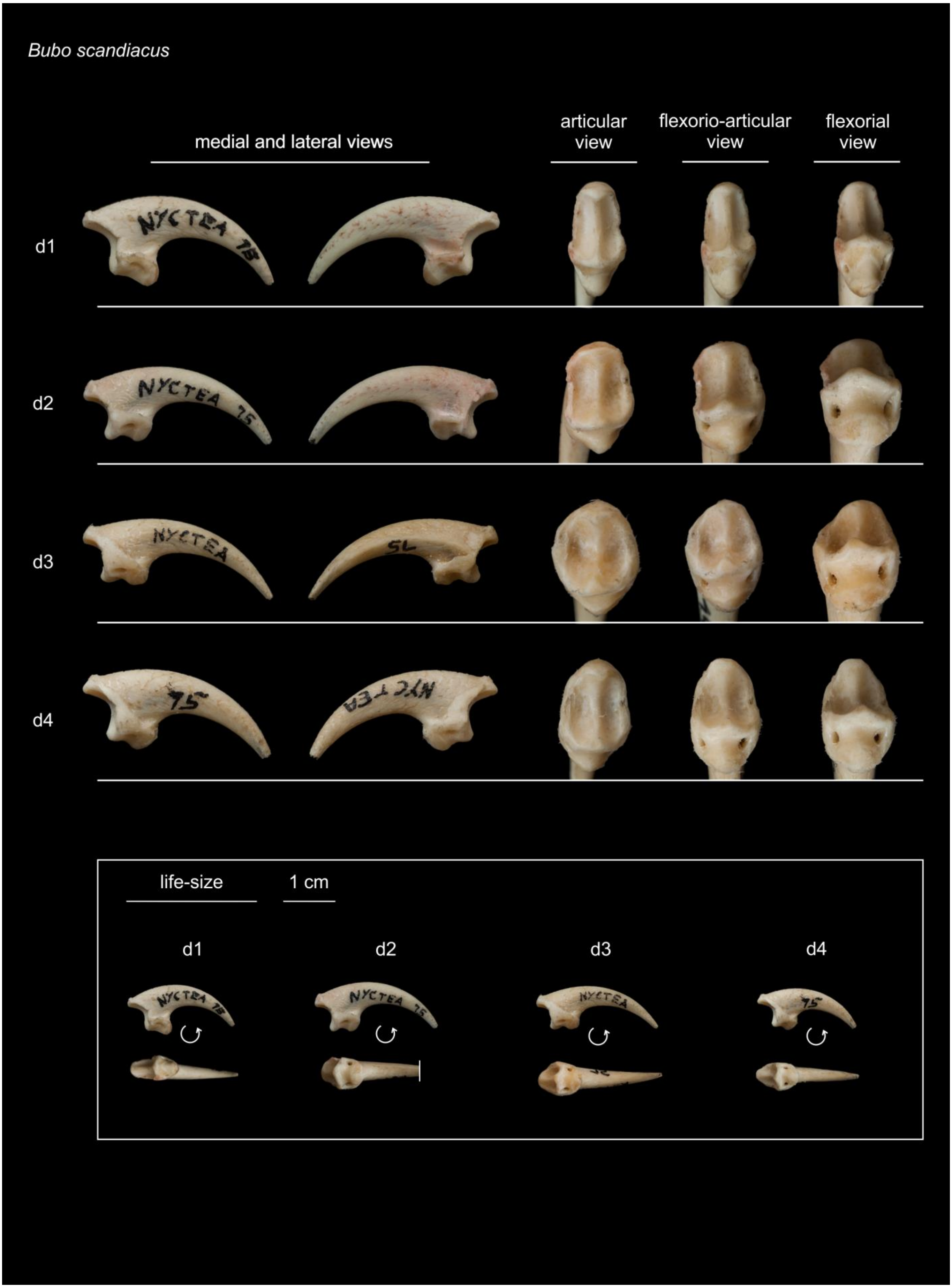


Predefined views in which ungual phalanges were photographed: lateral, medial, articular, flexorial and flexorio-articular views. The plantar and dorsal views are terms used to describe features in the manual.

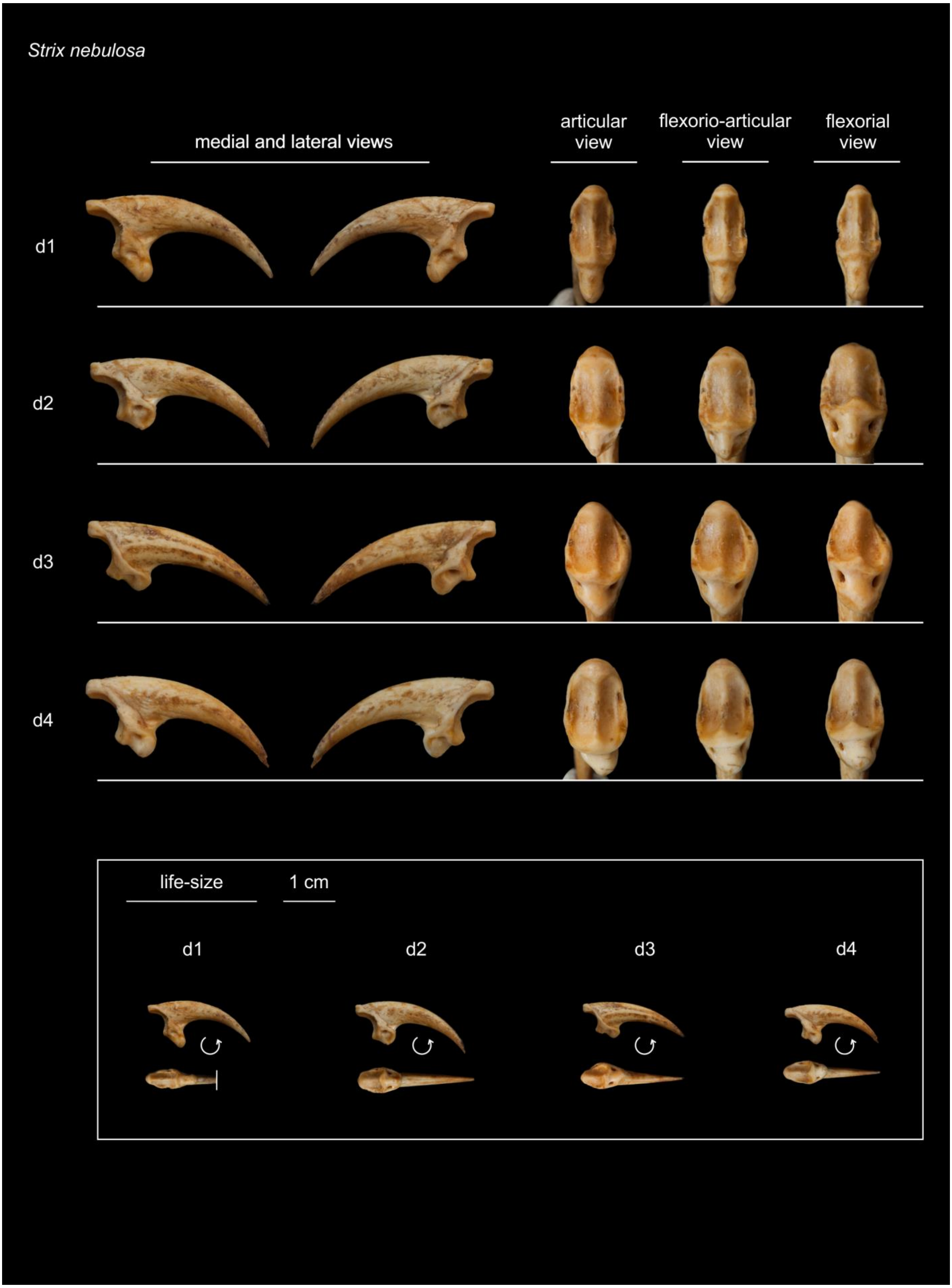
On the following pages are ungular phalanges of all species of owls and four species of falcons identified in the present manual. With the exception of *Falco tinnunculus*, the small falcons are not included because they are so small and similar to each other that it would not make much sense The order of the species presented is as follows: *Bubo bubo, Bubo scandiacus, Strix nebulosa, Strix uralensis, Strix aluco, Surnia ulula, Asio otus, Asio flammeus, Athene noctua, Aegolius funereus, Otus scops, Tyto alba, Falco rusticolus, Falco peregrinus, Falco cherrug, Falco tinnunculus.* The framed photos at the bottom of each plate are life-size and the remaining photographs are enlarged.



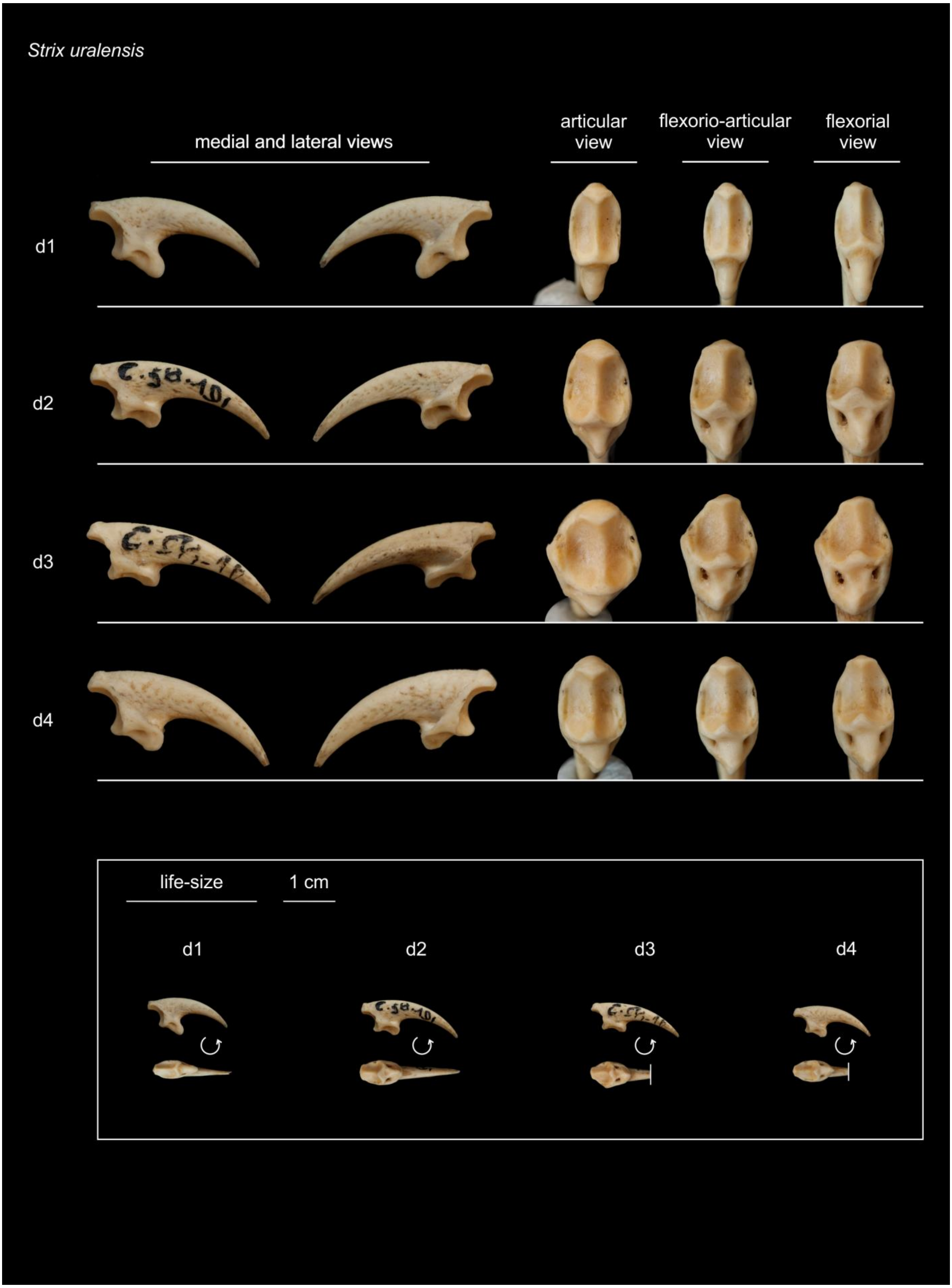
Bubo bubo; #2010.511.1; Hungarian Natural History Museum, Budapest, Hungary.



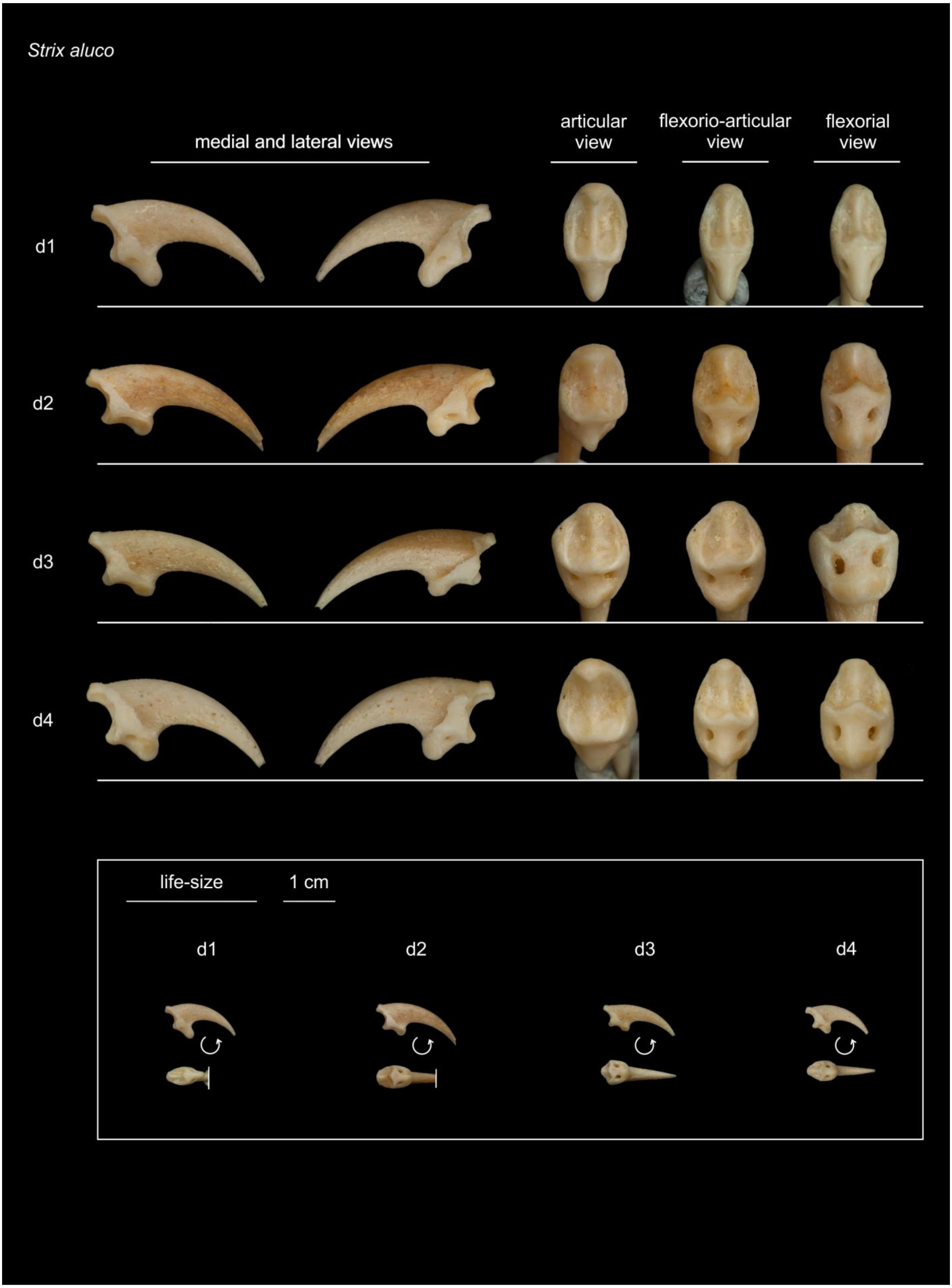
Bubo scandiacus; #2010.1755.1; Hungarian Natural History Museum, Budapest, Hungary.



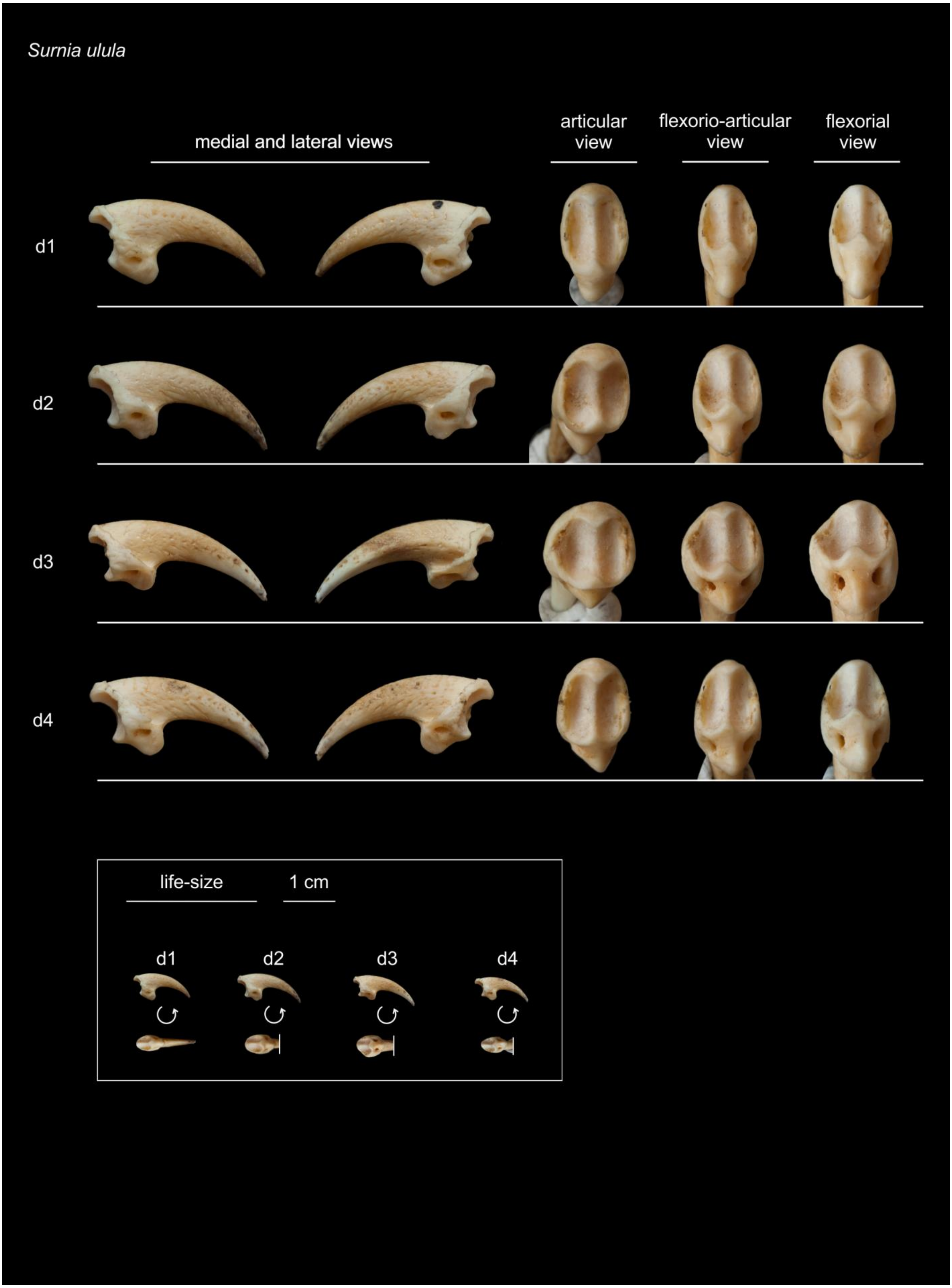
Strix nebulosa; #2010.1637.1; Hungarian Natural History Museum, Budapest, Hungary.



Strix uralensis; #58.10.1; Hungarian Natural History Museum, Budapest, Hungary.



Strix aluco; #ISEA 5776; Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.



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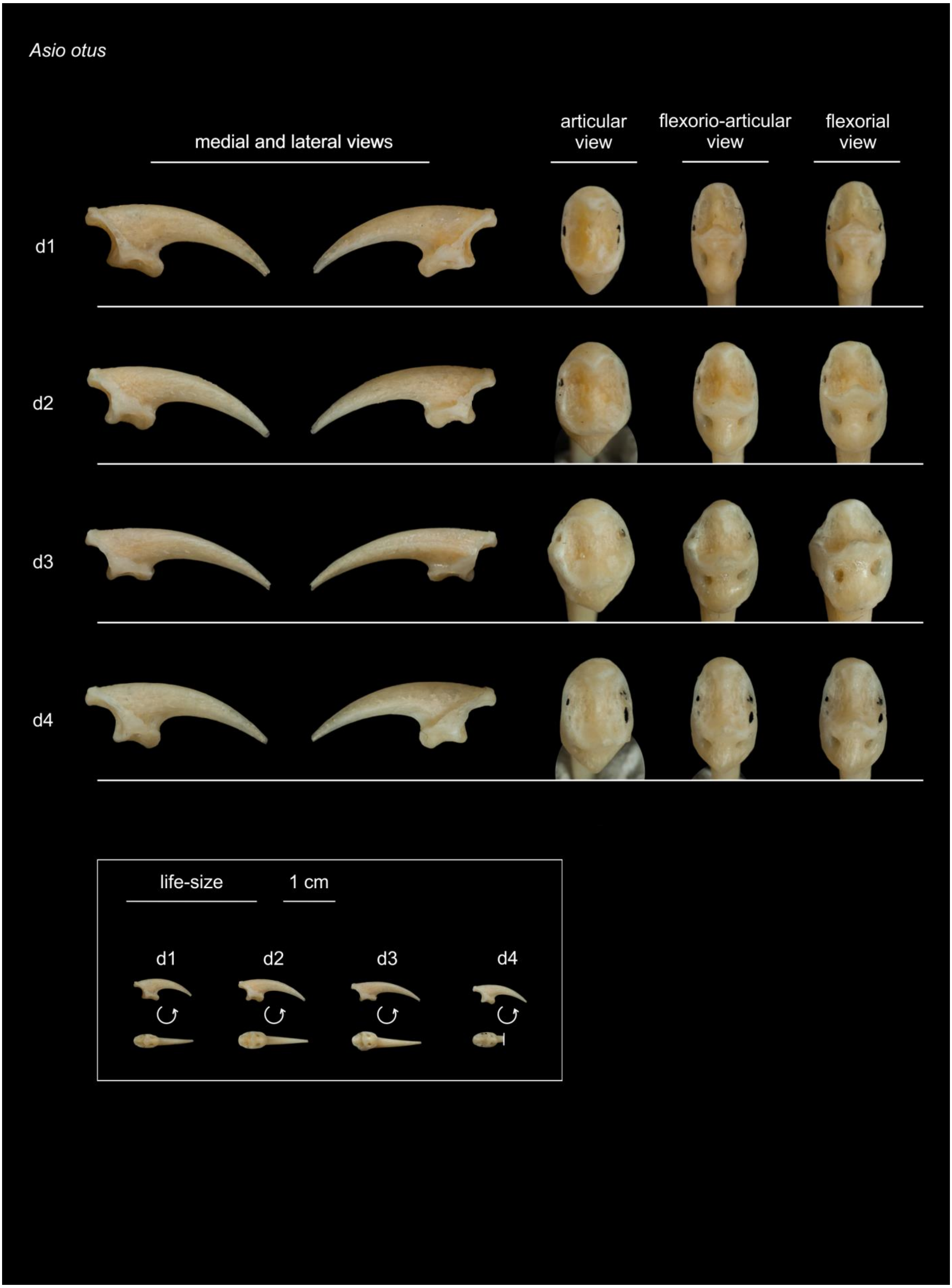
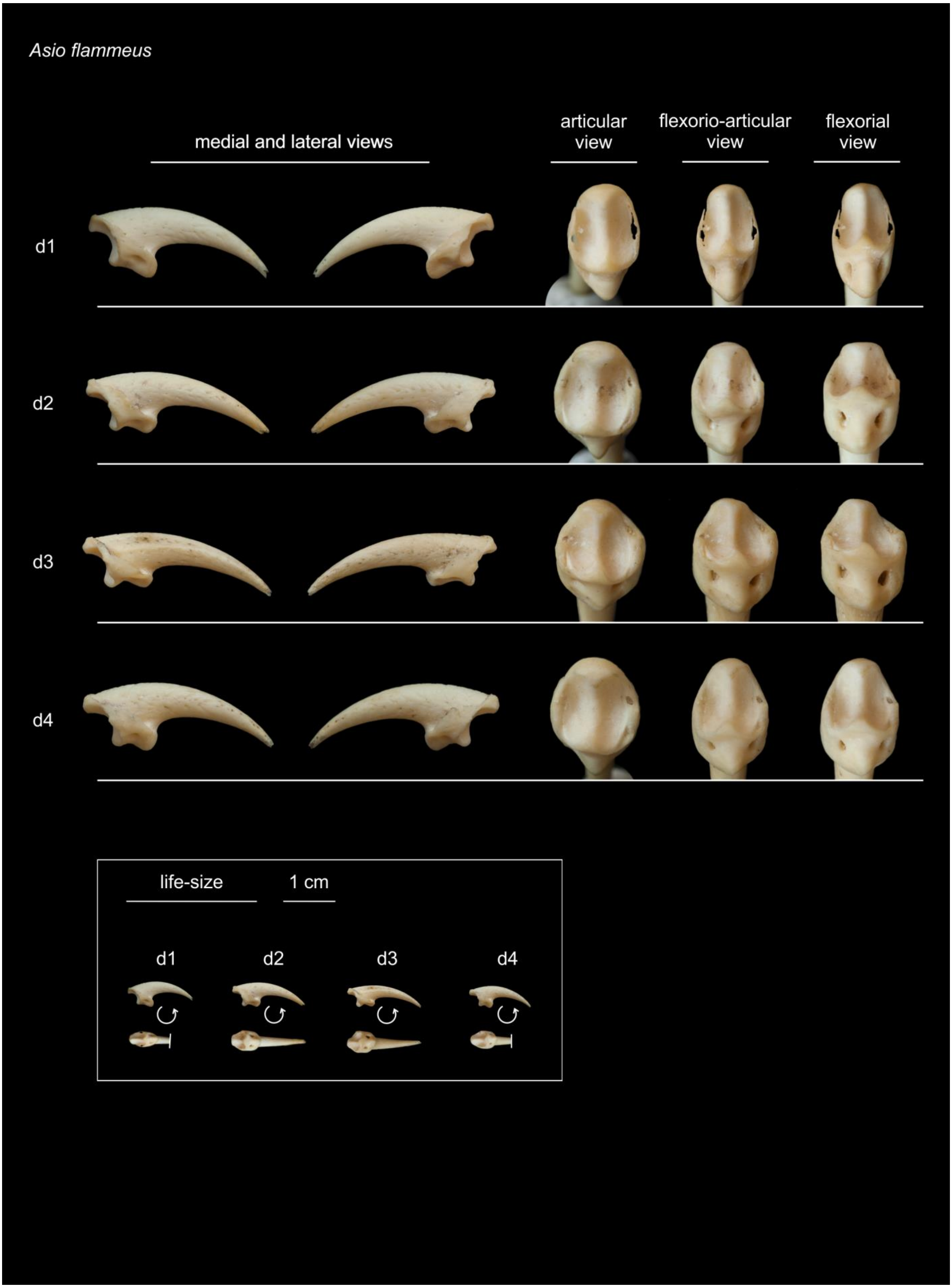
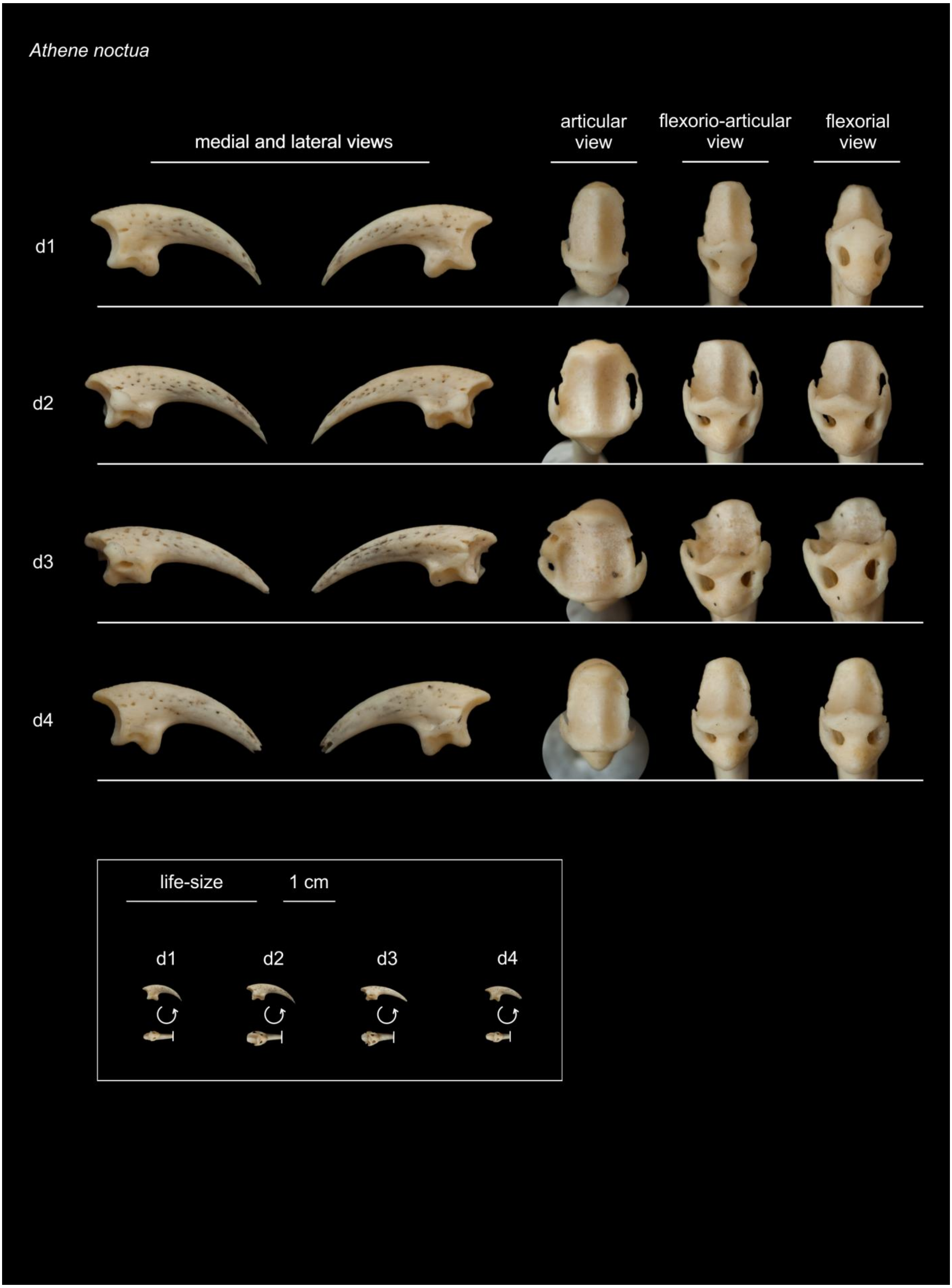


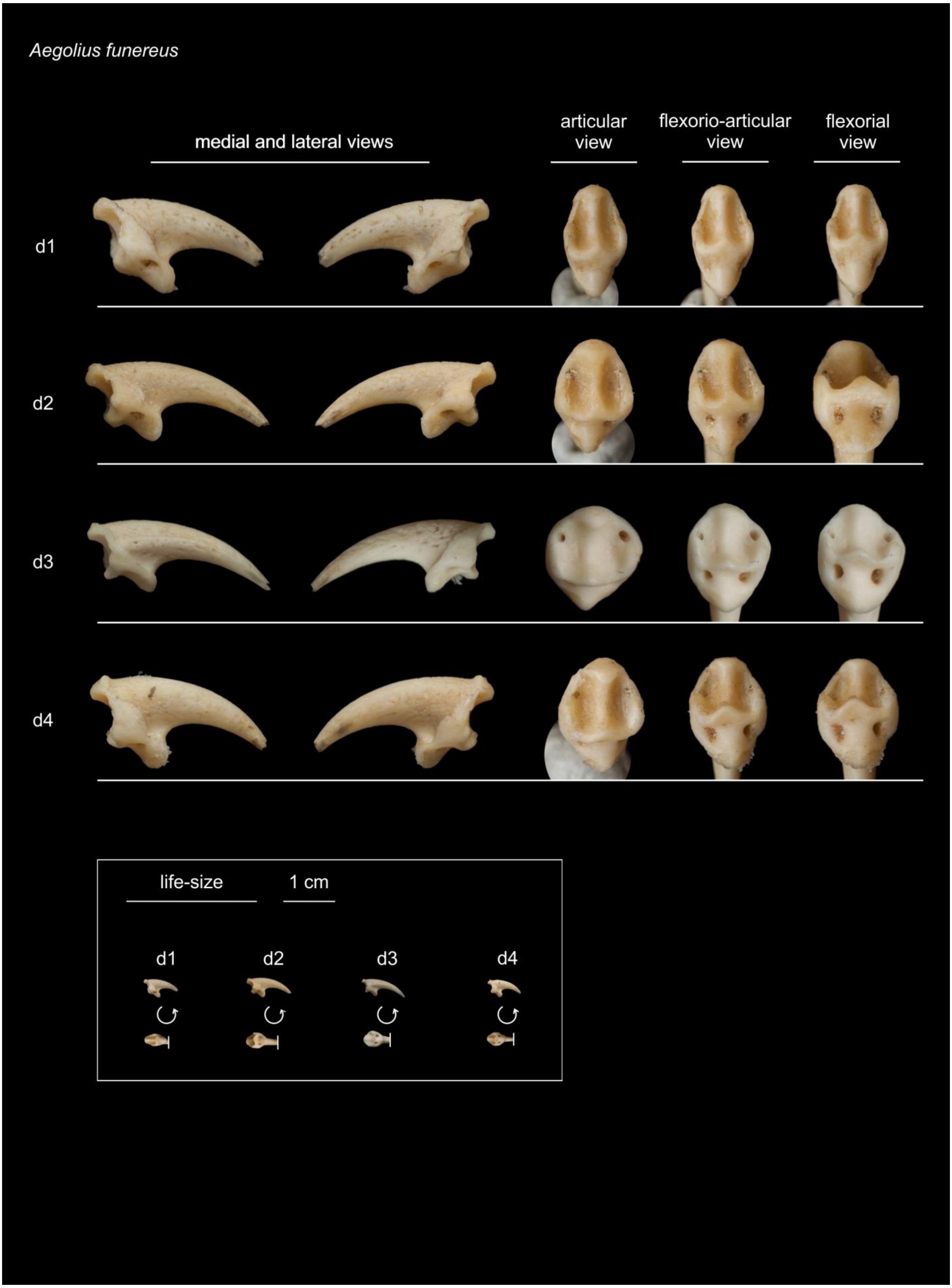
Asio otus; #ISEA 7423; Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.



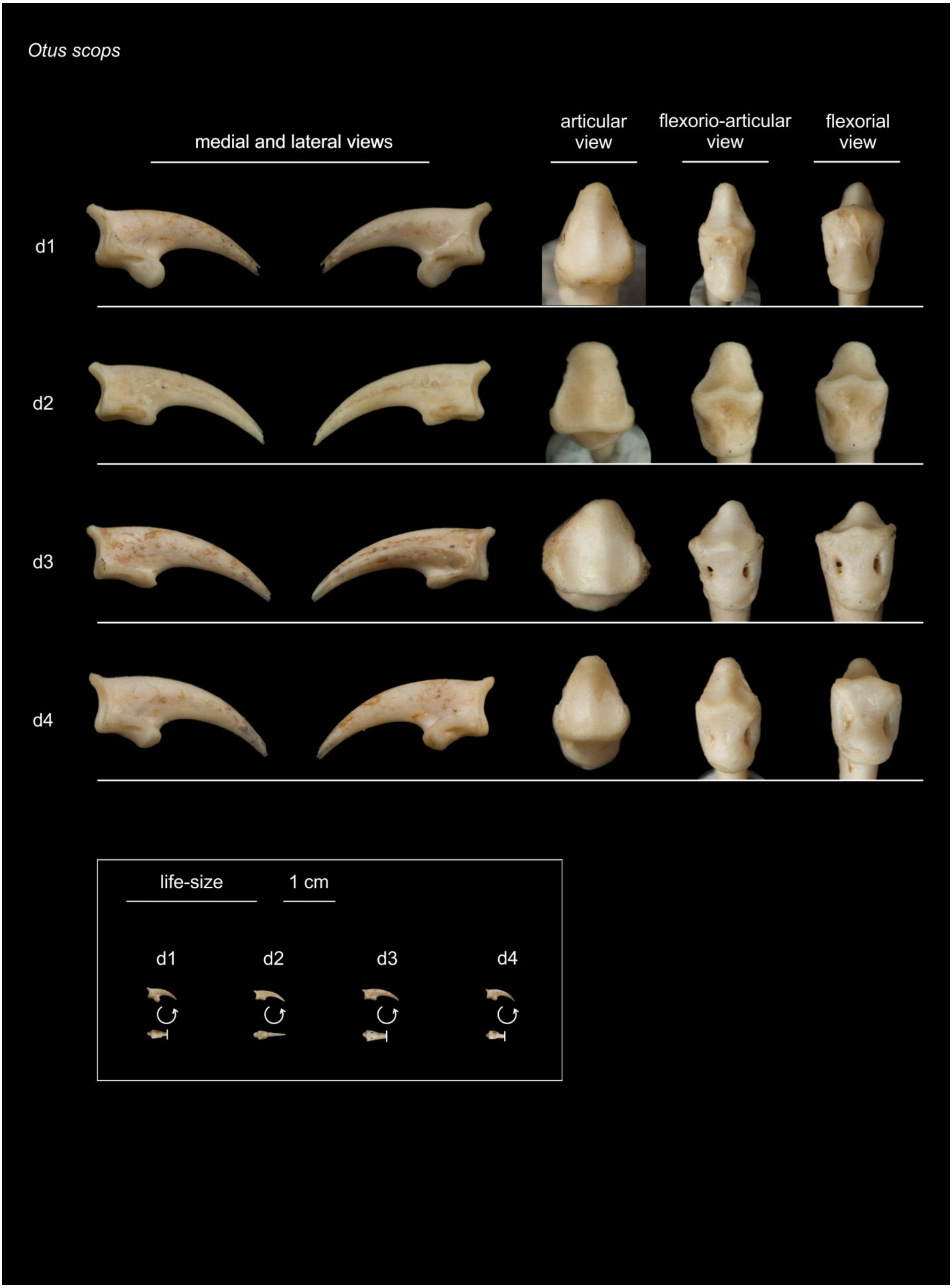
Asio flammeus; #58.24.1; Hungarian Natural History Museum, Budapest, Hungary.



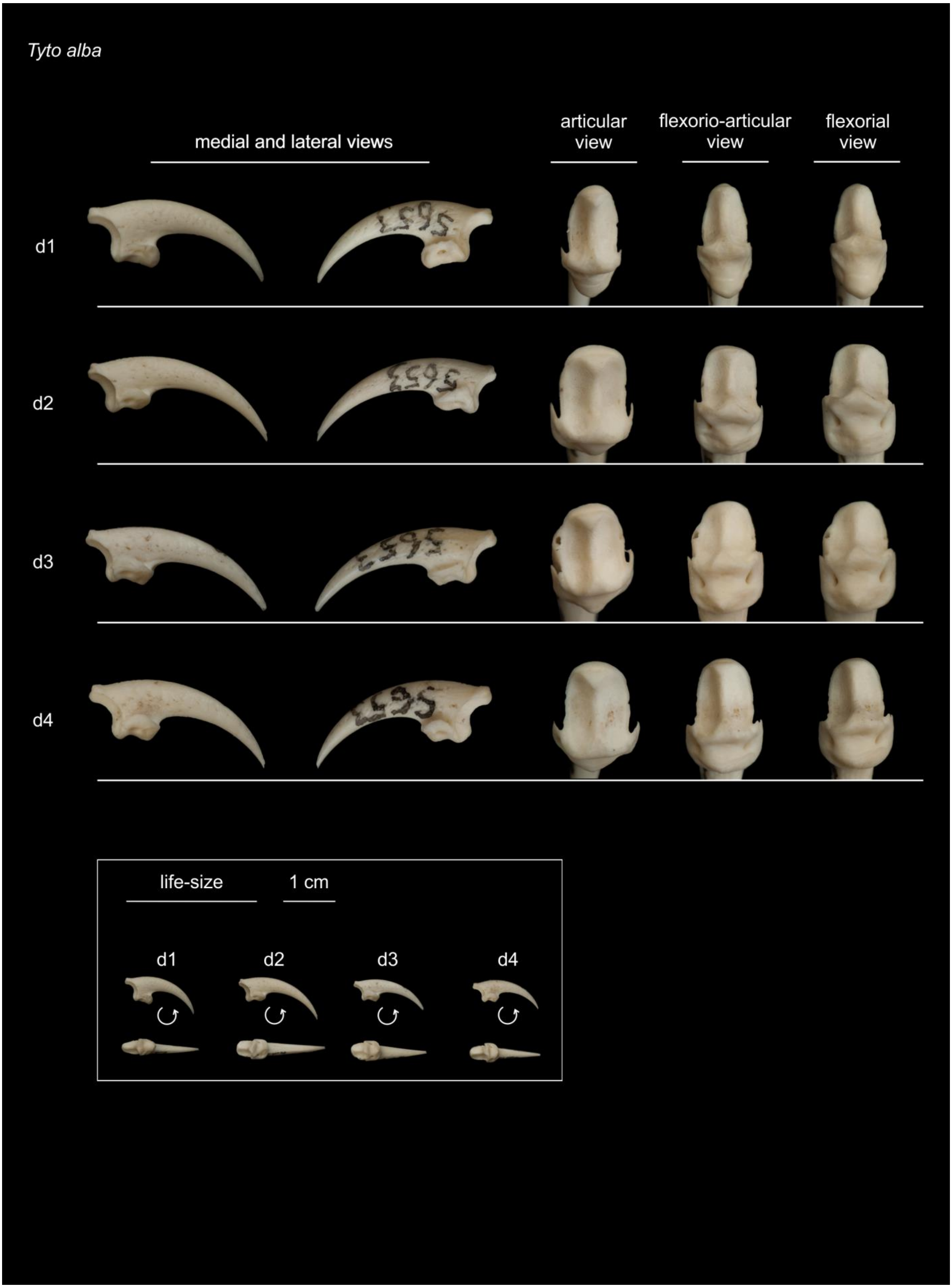
Athene noctua; #59.21.1; Hungarian Natural History Museum, Budapest, Hungary.



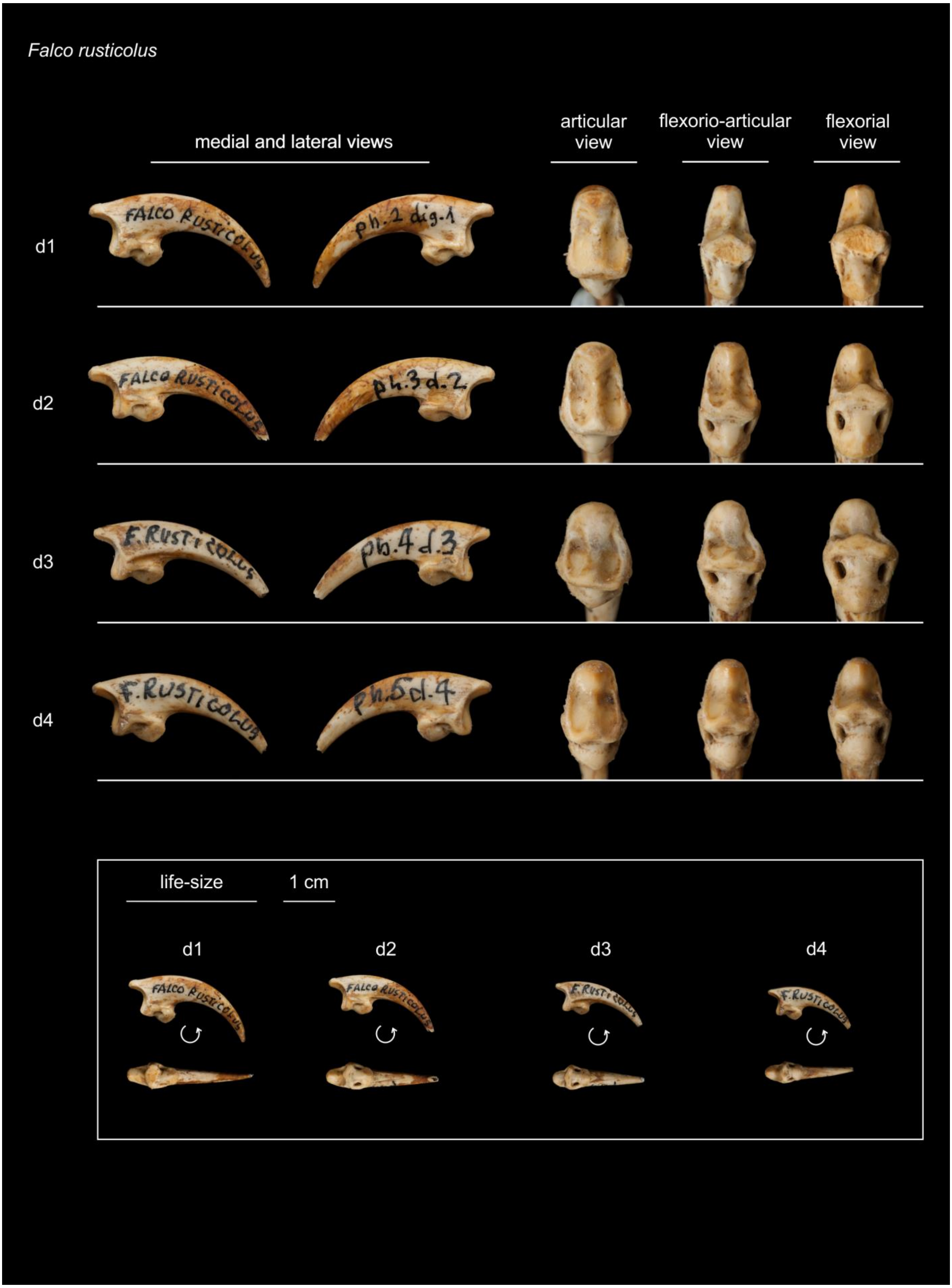
Aegolius funereus; digits 1-2,4: #2010.1626.1; Hungarian Natural History Museum, Budapest, Hungary; digit 3: #ISEA 5823; Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.



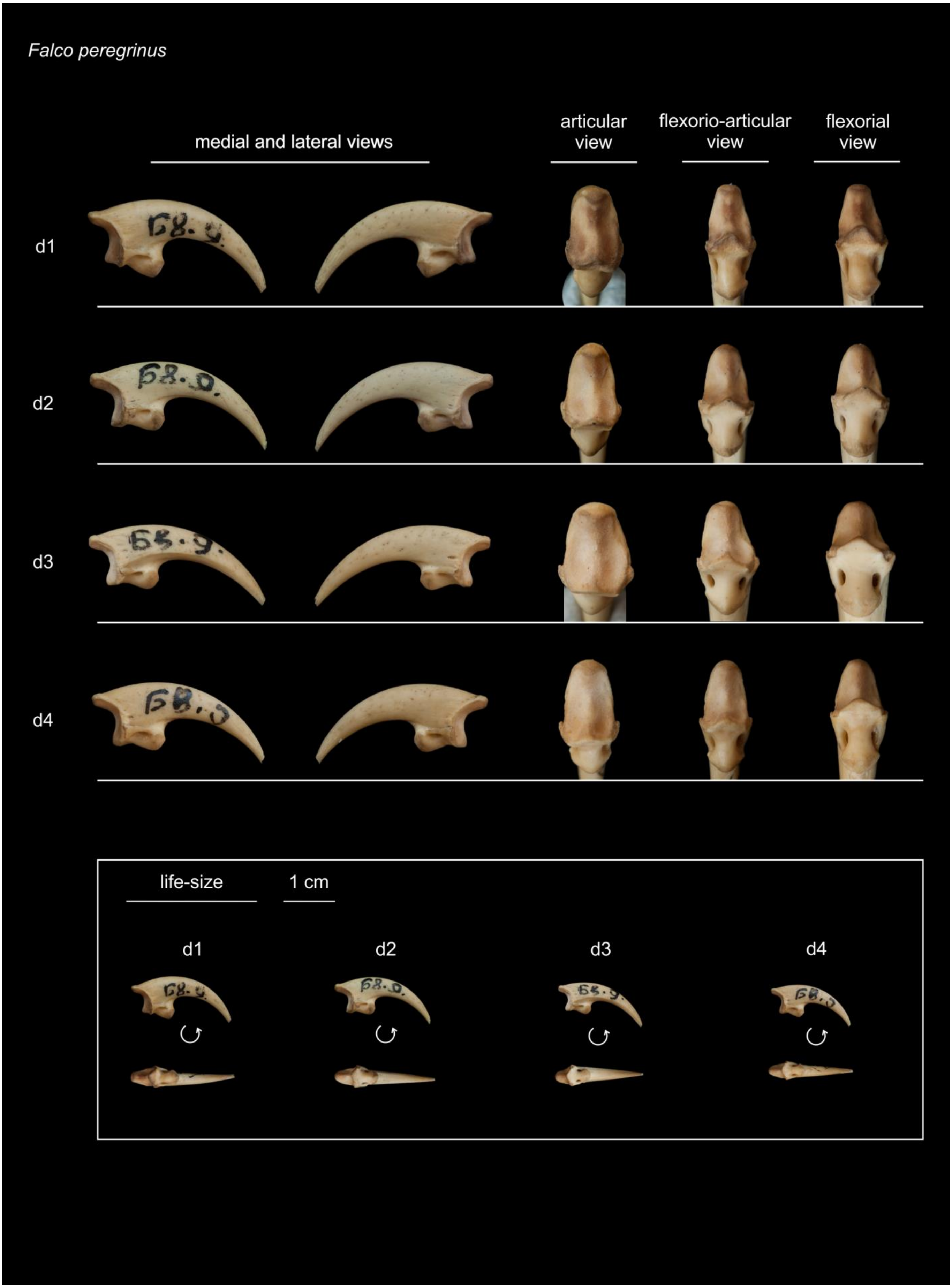
Otus scops; digits 1,3-4: #59.58.1; Hungarian Natural History Museum, Budapest, Hungary; digit 2: #ISEA 6240; Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.



Tyto alba; #ISEA 5653; Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.



Falco rusticolus; #2010.294.1; Hungarian Natural History Museum, Budapest, Hungary.



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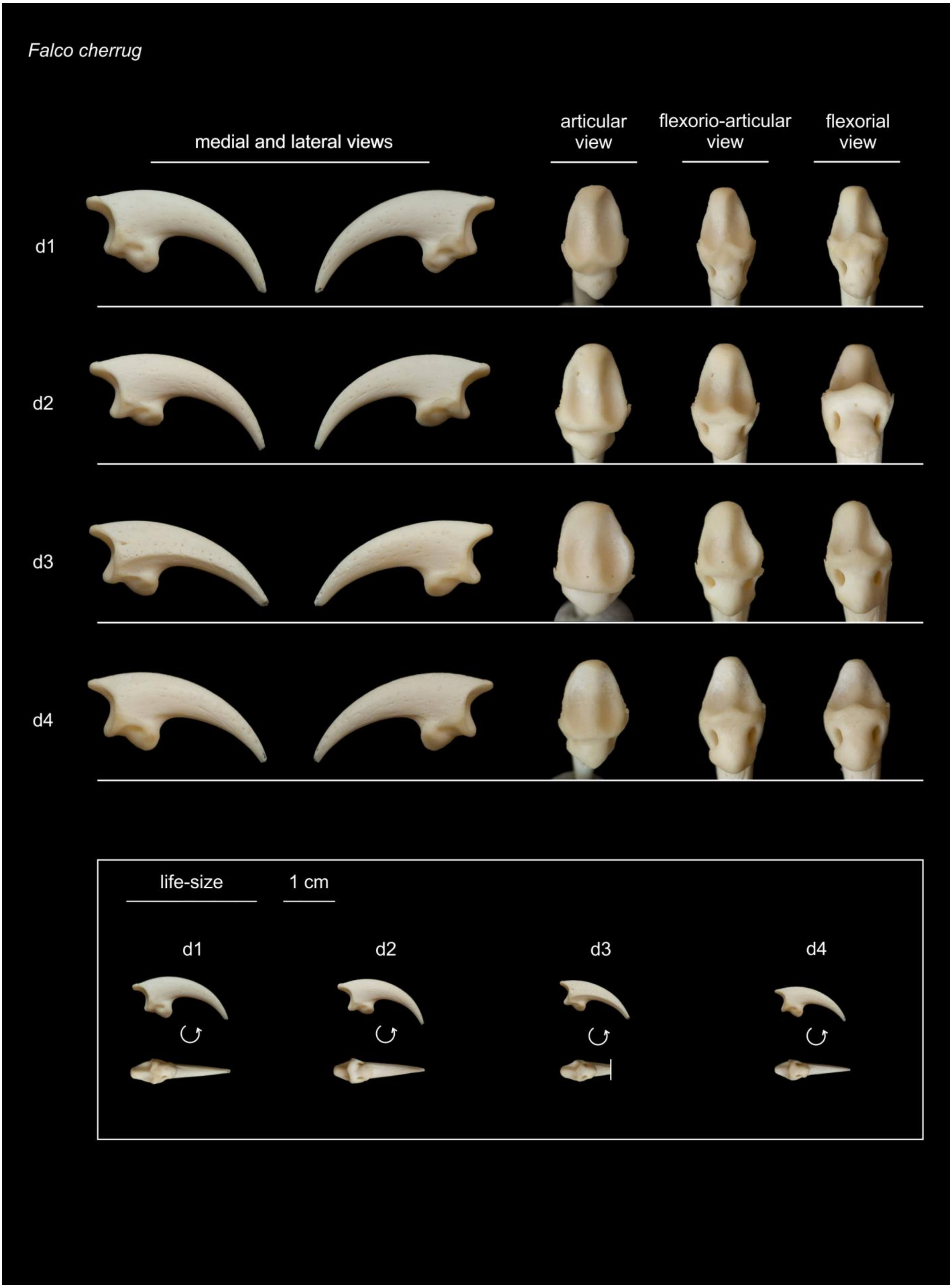
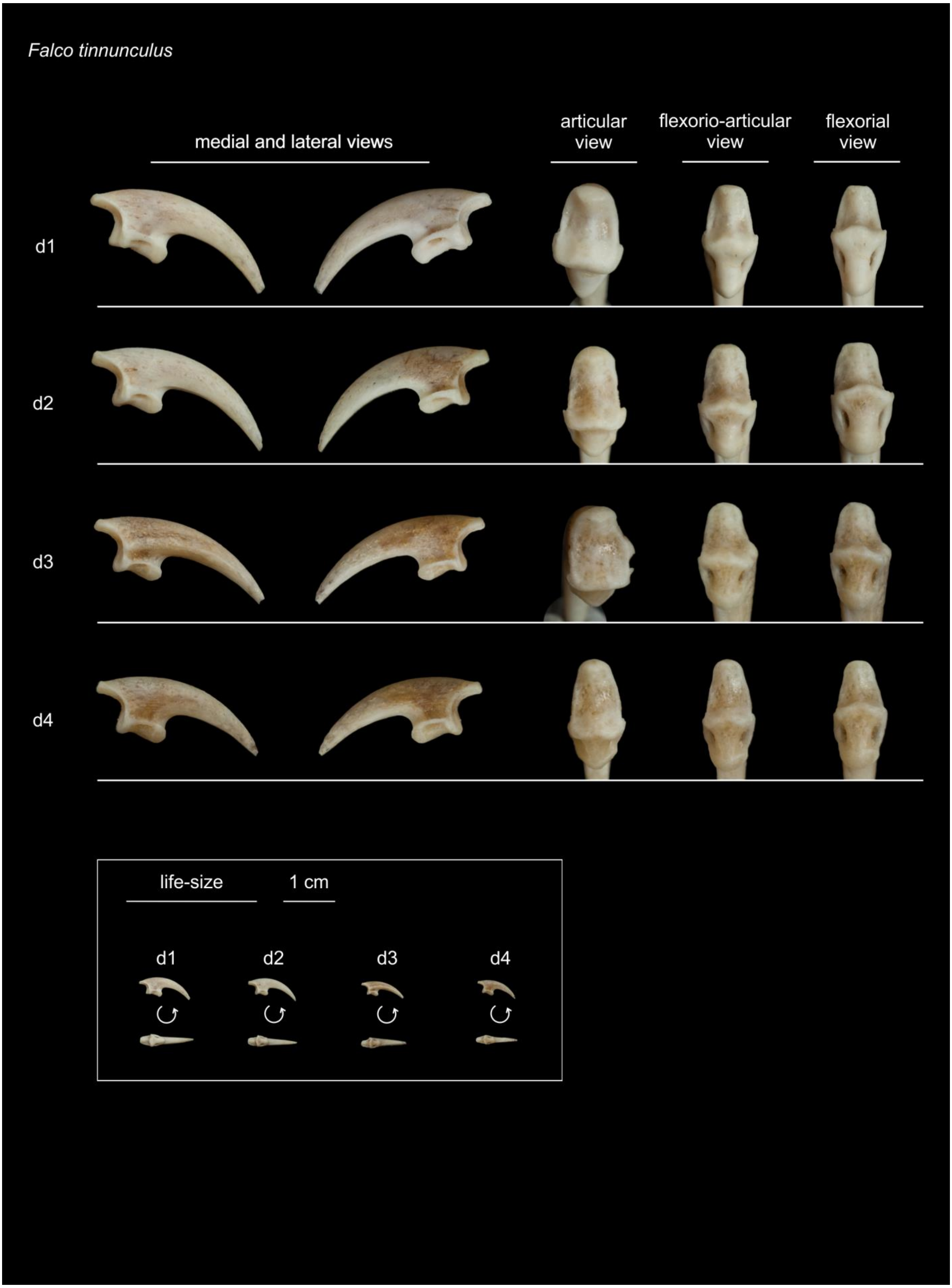


Falco cherrug; #2021.34.1; Hungarian Natural History Museum, Budapest, Hungary.



Falco tinnunculus; #ISEA 4734; Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.

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RESEARCH ARTICLE

Whose talon is this? A manual for the identification of ungual phalanges of European accipitrid birds of prey

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Abstract

Claws of avian raptors have been used to make symbolic objects and decorations in many geographic regions and cultures; thus, their species identification increases our ability to draw more in-depth conclusions from zooarcheological materials. It is the first ever manual for identification of ungual phalanges of European Accipitridae. It can be used in conjunction with a previously published manual for owls and falcons as well as independently.

KEYWORDS
accipitrid birds of prey, claws, dichotomous key, talons, ungual phalanges, zooarcheology

1 | INTRODUCTION

Although avian ungual phalanges are not very numerous in archeological contexts, they are often interpreted as ornamental elements or having some kind of symbolic meaning (Fiore et al., 2004; Serjeantson, 2009). Peculiar accumulations of leg phalanges including ungual phalanges were reported from many Neolithic sites in Israel, Lebanon, and Syria (e.g., Gourichon, 2002; Hooijer, 1961; Pichon, 1984, 1985; Recchi & Gopher, 2002; Simmons & Nadel, 1998; Tchernov, 1993). Ungual phalanges were made into pendants in many places in Europe, from Croatia (Radovčić et al., 2015) and Romania (Gál, 2005) to Estonia (Konsa et al., 2003; Luik, 2012) and Sweden (Clark, 1948; Forssander, 1931). Cut marks, nicks, and polished facets observed on some ungual phalanges could be interpreted as evidence that several ungual phalanges were used together as decoration (Laroulandie et al., 2016). Shooting an eagle or other raptor would have certainly added to the status of the hunter and in a way placed his skill on par with that of his prey, which in the case of birds of prey was characterized by its keen eye, superior speed, or agility (Amkreutz & Corbey, 2008).

Identification of avian ungual phalanges found within an archeological context is of vital importance for the interpretation of a particular site and in-depth analyses of the ways of living, activities, habits, or beliefs of people in the past. Only by knowing the species from which an ungual phalanx was procured can we see whether the specimen was obtained from a bird living locally or perhaps brought from far away. We may draw possible conclusions on the seasonality (did the bird breed locally or was it only a winter migrant?). Did the people choose certain species or one of the sexes for their amulets and decoration or were they more opportunistic? What features did the species have in common? Did they hunt actively (e.g., eagles) or scavenged (e.g., vultures)? Are there any species-specific differences between ungual phalanges used for different purposes or worn/used by different groups of people? Many similar questions can be put forward, and an experienced archeologist will certainly be able to draw profound conclusions provided that he or she is able to identify the ungual phalanx with the sufficient precision. Additionally, correctly identified ungual phalanges may be useful for paleoecological reconstructions of archeological sites.

There are no keys or manuals to help identify ungual phalanges of European accipitrid birds of prey. Researchers must rely on hard-to-reach comparative collections and their own experience. The situation is only slightly better in North America, where there is one publication facilitating the identification of local species (Mosto & Tambussi, 2014). There are some studies on talons of European birds of prey but they focus on morphological adaptations to various habitats and predator–prey relations, and they analyze entire digits with horny sheats (e.g., Appleton et al., 2016; Csermely & Rossi, 2006; Musindo, 2006), which do not preserve in archeological deposits. The only other papers that include bony cores of talons are those that describe fossil birds, often as old as the Paleogene (e.g., Mayr, 2006a, 2006b).

The goal of this study is to present the first manual for the identification of ungual phalanges of European accipitrid birds of prey. This

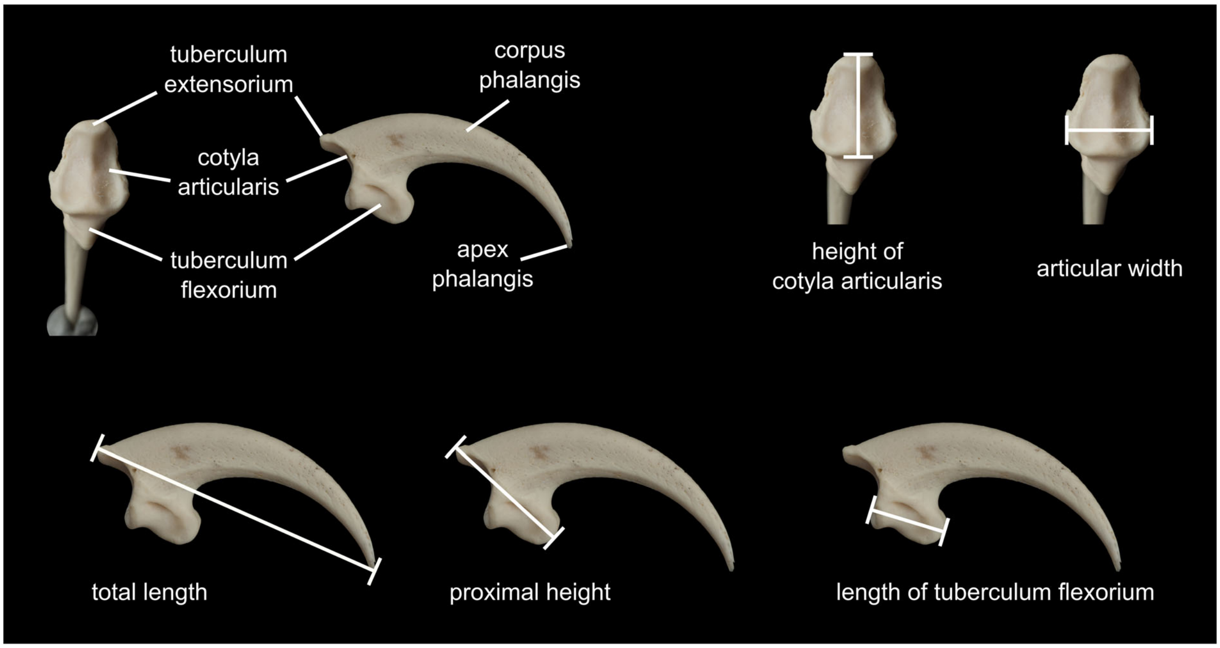

FIGURE 1 Osteological terminology and measurements of ungual phalanges [Colour figure can be viewed at wileyonlinelibrary.com]

is a continuation of our first paper that includes a manual for European owls and falcons (Wertz et al., In press).

2 | MATERIALS AND METHODS

The manual covers all common accipitrid birds of prey found nowadays in Europe; vagrant and extinct species are excluded. Taxonomy and systematics are according to Dickinson and Remsen (2013), with minor changes. The number of specimens of each species varies depending on their availability in osteological collections. A total of 321 specimens from 27 species were studied; they came from the following seven collections (Table S1): ISEA—Institute of Systematics and Evolution of Animals PAS; NMNHS—National Museum of Natural History, Bulgarian Academy of Sciences, Sofia, Bulgaria; NHMUT—Natural History Museum, University of Tartu, Estonia; HNHM—Hungarian Natural History Museum, Budapest, Hungary; PACEA—De la Préhistoire à l'Actuel: Culture, Environment et Anthropologie, Université de Bordeaux, France; UMB—University Museum of Bergen, Department of Natural History, Bergen, Norway; and NMNHU—National Museum of Natural History at the National Academy of Sciences of Ukraine, Kyiv, Ukraine.

This study is intended as an independent entity. Being sure that an ungual phalanx belongs to the accipitrid bird, one can start with this manual. In case of doubt, the identification can be started from the preliminary part of the manual (Wertz et al., In press), which includes the division into owls, falcons, *Pandion*, and accipitrid birds of prey.

Measurements were taken with digital calipers with an accuracy of 0.01 mm, captured directly on a computer (Figure 1, Data S1). Metric features are used in many places in the manual. The boundaries of the division into taxa of different sizes are arbitrary. They correctly define the lower and/or upper limits for the specimens of some taxa, but a side effect is that some species are inadvertently divided into two groups (Appendix S1). In such cases, we try to include such a split species in both sections of the manual. Another danger of an arbitrary division is that the ranges of some species come very close to the dividing line. In such cases, extreme caution is advised as you can always find specimens outside the size range given. It should also be taken into account that specimens from modern populations may differ in size from specimens of the same species from (pre-) historic times (e.g., Pleistocene). Due to the relatively small number of measured specimens from certain species, it is recommend that the size ranges be used as indicative and not final values.

Osteological terminology follows Baumel and Witmer (1993) and is illustrated in Figure 1. It is difficult to find an obvious morphological feature that could be applied to all European species; there are always species that are ambiguous or nonspecific for a certain feature. Moreover, there are very few, if any, features that would apply to all specimens of a given species. This is a well-known, but rarely recognized, fact in osteological research. In this manual, we applied a similar principle to our earlier keys (Bochenski, 1994; Tomek & Bochenski, 2000): At least two thirds of the specimens of a species must exhibit a specific condition for a feature to be considered typical of that species. However, this means that almost always less typical specimens can happen.

Some features have been used several times in different places in the manual, sometimes only slightly modified. This is a deliberate action because the same feature can distinguish between different taxa and/or between ungual phalanges of different digits.

Many branches of our manual, especially those involving smaller species, end in two or more undifferentiated taxa. This does not mean that they are indistinguishable; we preferred to refrain from

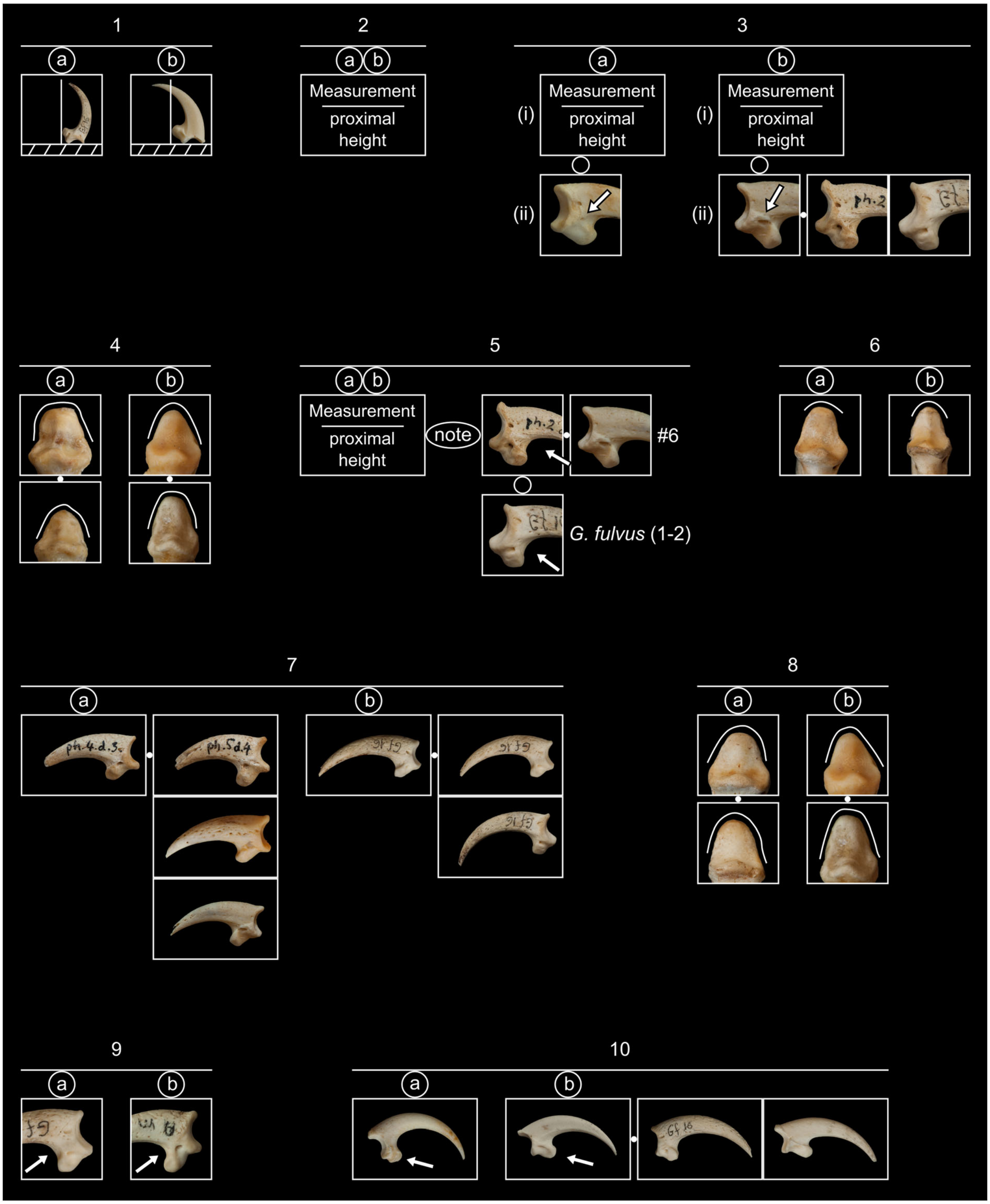

FIGURE 2 Illustrations of Features 1–10 described in the text [Colour figure can be viewed at wileyonlinelibrary.com]

identifying some taxa as we had too few specimens to do so reliably. We leave the possible development of the unfinished branches of the key to experienced researchers who have access to other rich comparative collections.

To facilitate comparisons with modern specimens at all stages of the manual, taxa passing through a given stage are listed in square brackets and digit numbers in parentheses. In case of doubt (e.g., when trying to identify a damaged specimen), such presentation of partial data will also facilitate a meaningful completion of the identification at an earlier stage of the manual.

The illustrations relating to specific features described in the manual (Figures 2–8) are not to scale; both large and small taxa are shown

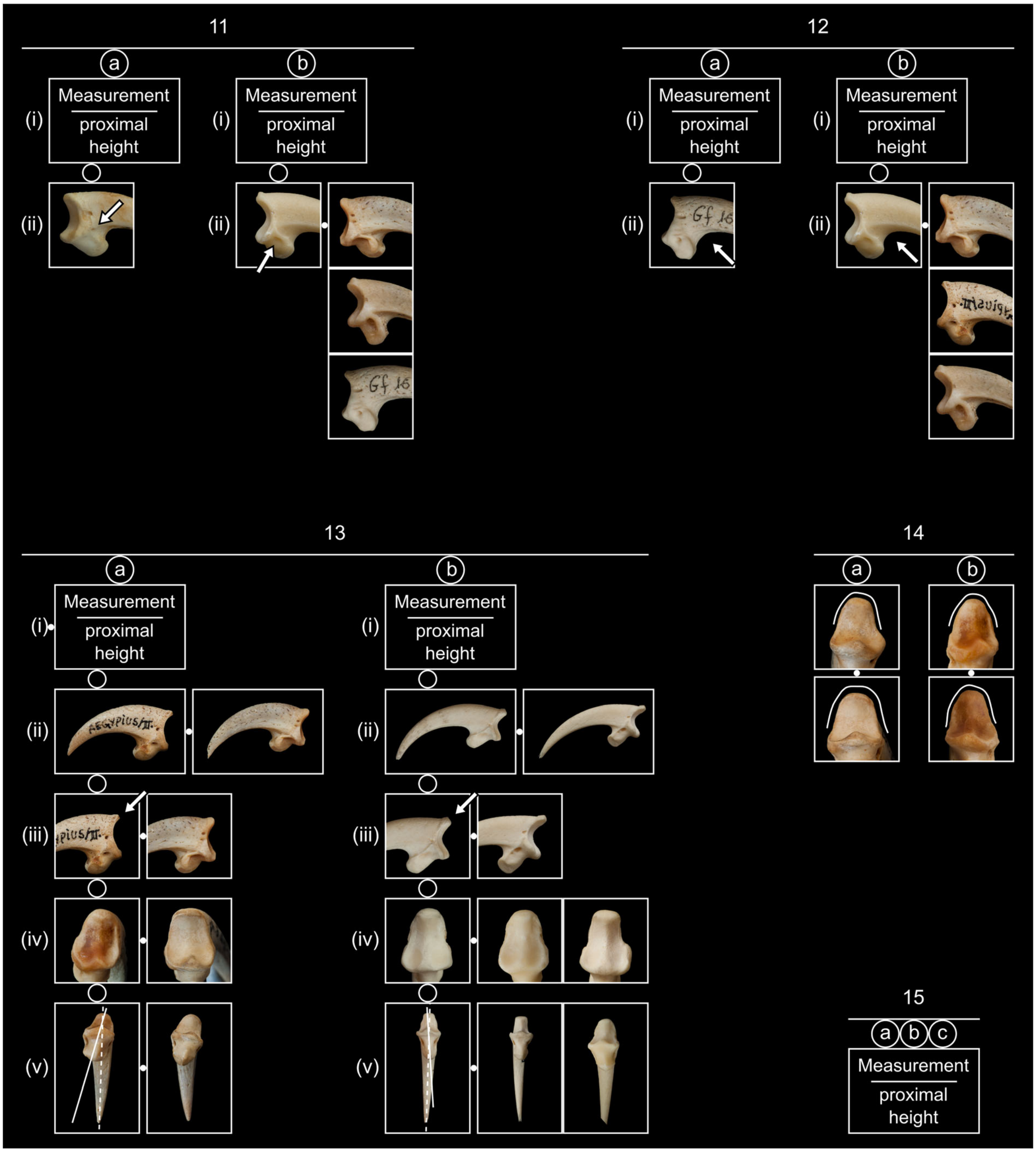

FIGURE 3 Illustrations of Features 11–15 described in the text [Colour figure can be viewed at wileyonlinelibrary.com]

there in the same size. These illustrations only show the states of individual features and are intended to supplement the description and indicate the location of a given structure on the bone.

In addition, the ungual phalanges of all accipitrid birds of prey are illustrated in the photos in several predefined views: lateral, medial, articular, flexorial, and flexorio-articular. These specimens are shown both in life-size and in magnification (Appendix S2). These illustrations can be used to roughly verify the correctness of identification, especially in the absence of comparative specimens in the collection.

It must be emphasized that no manual can replace comparisons with real bones; it is only a help, not a substitute for the comparative collection.

3 | MANUAL FOR THE IDENTIFICATION

Notes: In square brackets [], taxa passing through a given step of the manual are listed, and in parentheses () are their digit numbers. Taxa at the final stages of identification are marked in bold.

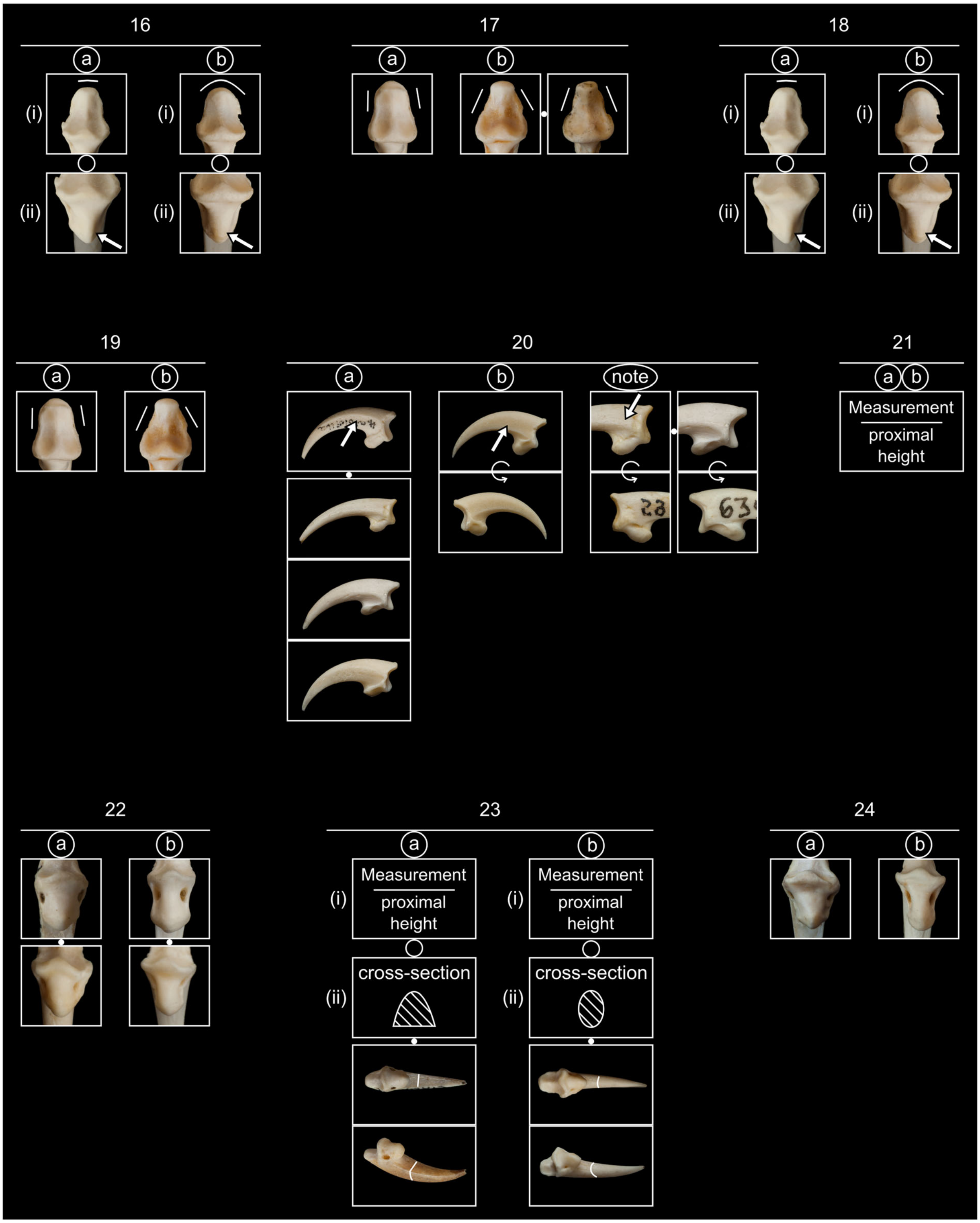

FIGURE 4 Illustrations of Features 16–24 described in the text [Colour figure can be viewed at wileyonlinelibrary.com]

1 (Figure 2)

a — The tip of the corpus phalangis (apex phalangis) protrudes plantarly less or as far as the tuberculum flexorium. The easiest way to check this is to place the ungual phalanx vertically with the cotyla articularis down (tuberculum extensorium and medial prominence touch the flat horizontal surface) [most vultures (1–4)].

....2

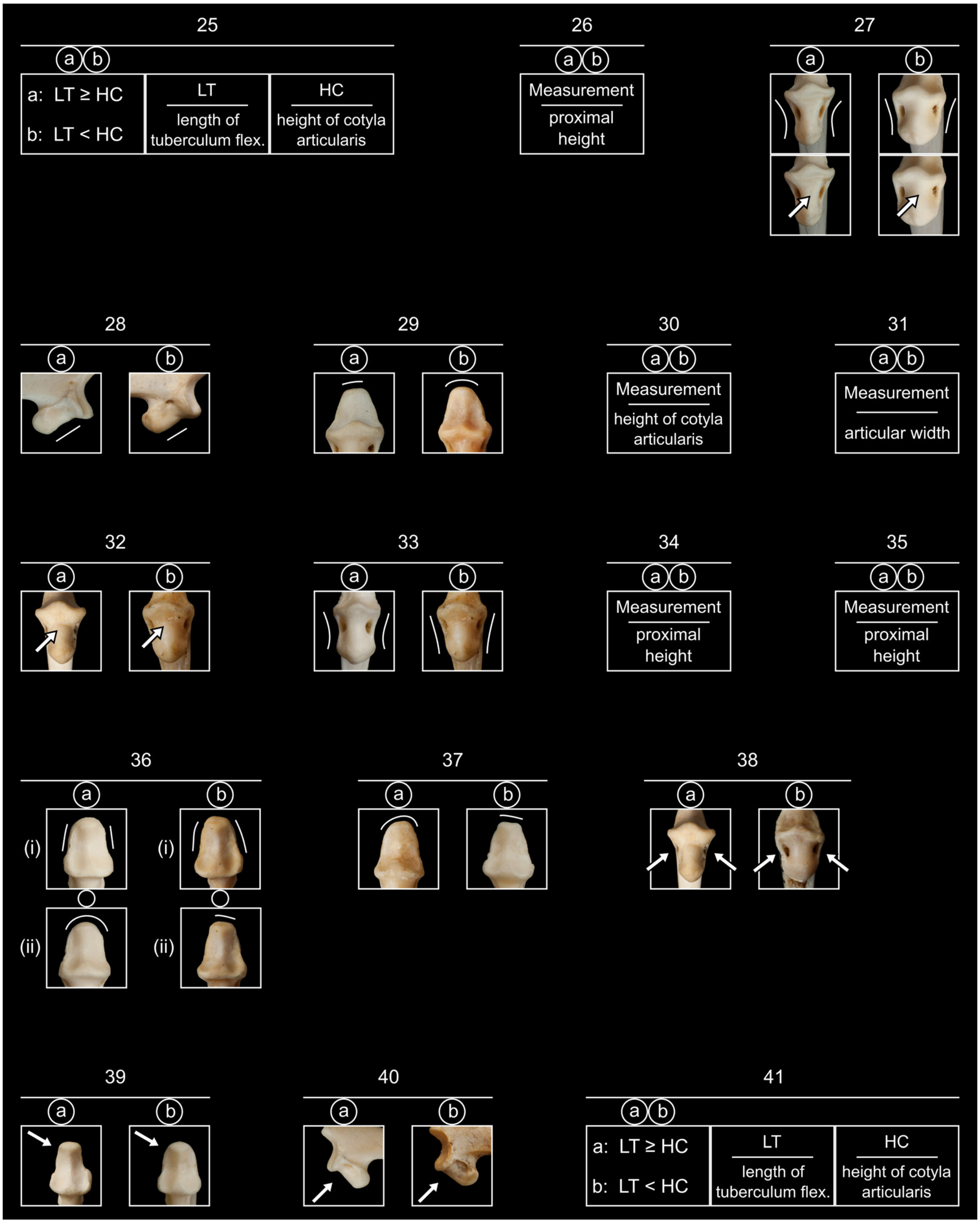

FIGURE 5 Illustrations of Features 25–41 described in the text [Colour figure can be viewed at wileyonlinelibrary.com]

b — The tip of the corpus phalangis (apex phalangis) protrudes distinctly further plantarly than the tuberculum flexorium [other Accipitridae (1–4), including some vultures (1–2)].

....10

2 (Figure 2, Appendix S1)

a — Proximal height less than 9.0 mm.

....***Neophron percnopterus* (3–4)**

b — Proximal height greater than 9.0 mm [*N. percnopterus* (1–3),-*G. barbatus* (1–4), *A. monachus* (1–4), *G. fulvus* (1–4)].

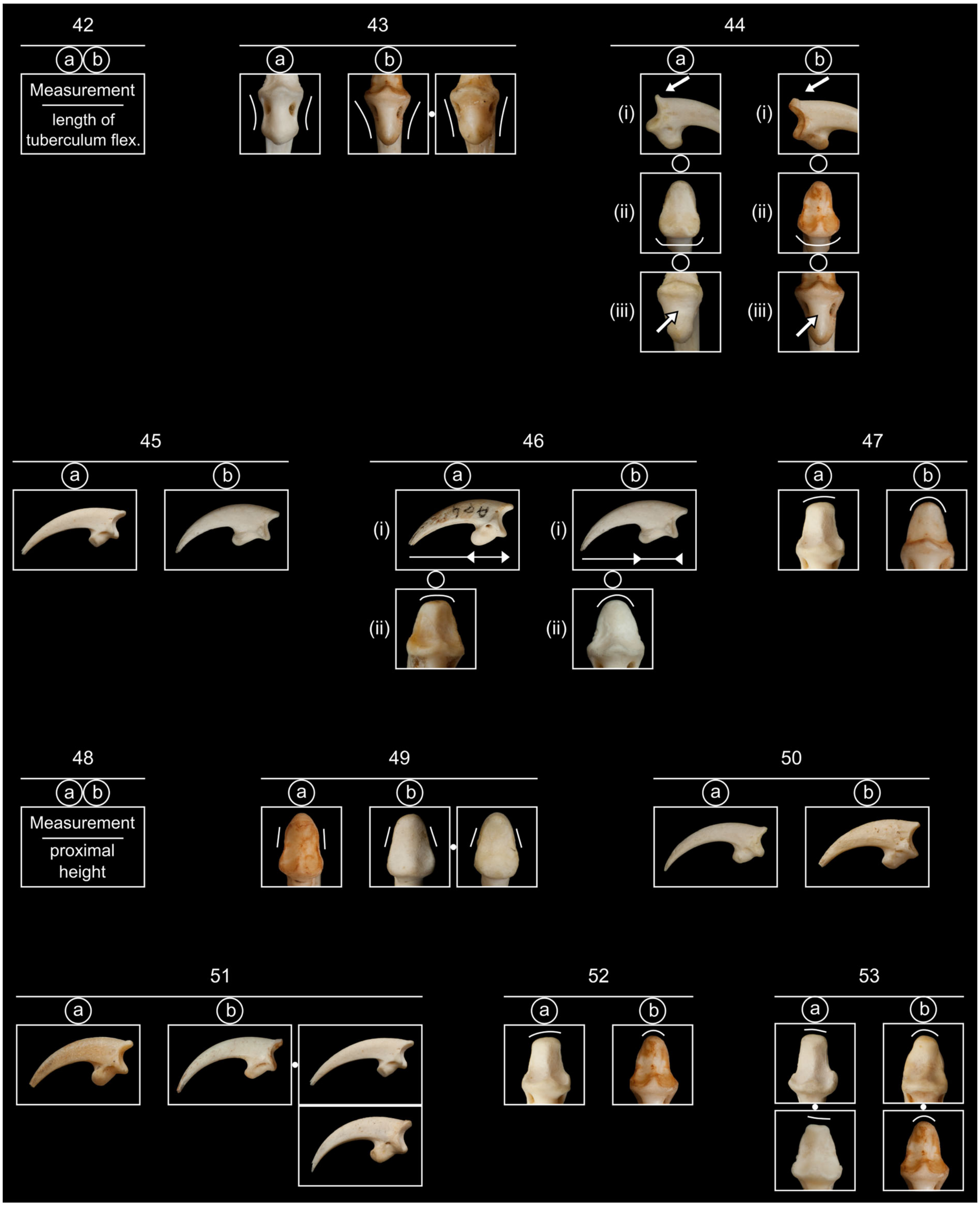

FIGURE 6 Illustrations of Features 42–53 described in the text [Colour figure can be viewed at wileyonlinelibrary.com]

....3

3 (Figure 2)

a — (i) Proximal height: 9.0–12.0 mm; AND (ii) the foramina lateral and medial of the tuberculum flexorium are located at the base of the tuberculum (in the corner between the tuberculum and the corpus phalangis) and are usually small [*N. percnopterus* (1–3) and some *G. barbatus* (3–4)].

....4

b — (i) Proximal height in any size range; (ii) the foramina lateral and medial of the tuberculum flexorium are located within the

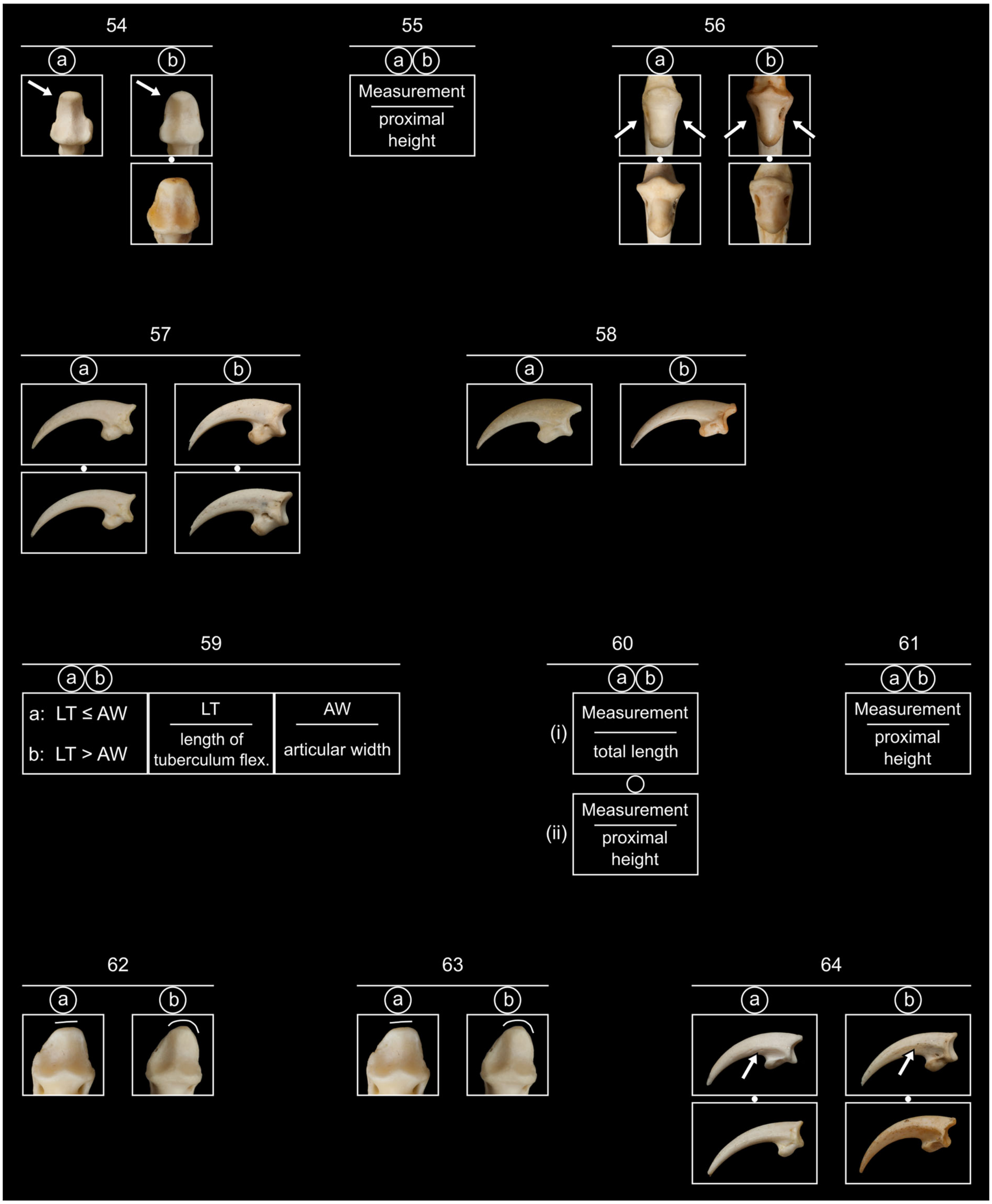

FIGURE 7 Illustrations of Features 54–64 described in the text [Colour figure can be viewed at wileyonlinelibrary.com]

tuberculum (they are separated from the corpus phalangis by a bony crest) and are usually relatively large [*G. barbatus* (1–4), *A. monachus* (1–4), *G. fulvus* (1–4)].

....5

4 (Figure 2)

a — The proximal part of the cotyla articularis is relatively stockier.

....***Neophron percnopterus*** **(1–3)**

b — The proximal part of the cotyla articularis is comparatively more slender.

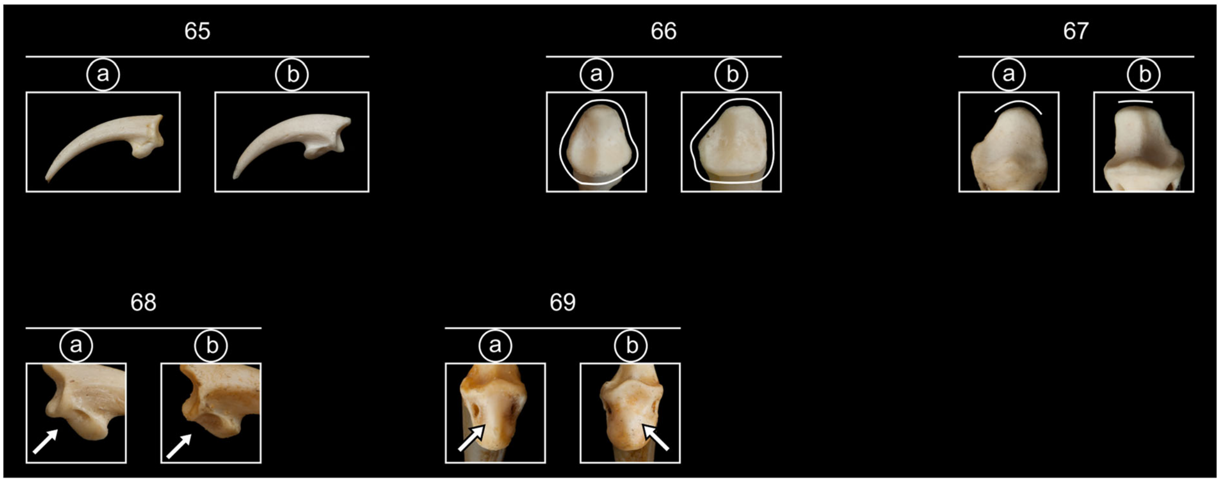

FIGURE 8 Illustrations of Features 65–69 described in the text [Colour figure can be viewed at wileyonlinelibrary.com]

.... ***Gypaetus barbatus* (3–4)**

5 (Figure 2, Appendix S1)

a — Proximal height greater than 15.0 mm [*G. barbatus* (1–2), *A. monachus* (1–2)].

....6

b — Proximal height less than 15.0 mm [*G. barbatus* (3–4), *A. monachus* (3–4), *G. fulvus* (1–4)].

....7

Note: Due to the small number of measured specimens, it cannot be ruled out that there will be specimens outside the given limit of 15 mm. If the proximal height is 14.0–15.0 mm but the tuberculum flexorium is undercut, the identified specimen belongs to *A. monachus* or *G. barbatus* and one should proceed to Step 6 (Phalanges 1–2). And if the proximal height is 15.0–16.0 mm but the tuberculum flexorium is not undercut, the identified specimen belongs to *G. fulvus* (1–2) (as in Features 9 and 12).

6 (Figure 2)

a — The proximal part of the cotyla articularis is relatively stockier.

.... ***Aegypius monachus* (1–2)**

b — The proximal part of the cotyla articularis is comparatively more slender.

.... ***Gypaetus barbatus* (1–2)**

7 (Figure 2)

a — Corpus phalangis is wide, stocky, and "inflated" all along its length [*G. barbatus* (3–4), *A. monachus* (3–4)].

....8

b — Corpus phalangis is relatively narrow and slender [*G. fulvus* (1–4), some *A. monachus* (3–4)].

....9

8 (Figure 2)

a — The proximal part of the cotyla articularis is relatively stockier.

.... ***Aegypius monachus* (3–4)**

b — The proximal part of the cotyla articularis is comparatively more slender.

.... ***Gypaetus barbatus* (3–4)**

9 (Figure 2)

a — The tuberculum flexorium is not undercut (i.e., the transition between the tuberculum and corpus phalangis is almost straight).

.... ***Gyps fulvus* (1–4)**

b — The tuberculum flexorium is undercut (i.e., in the transition between the tuberculum flexorium and corpus phalangis, there is a semicircular indentation of varying depth).

.... ***Aegypius monachus* (3–4)**

Note: To avoid ambiguity, this is best seen by arranging the proximal part of the phalanx so that its dorsal edge is horizontal.

10 (Figure 2)

a — In lateral and/or medial view, the tuberculum flexorium protrudes extremely far plantarly and is narrow proximo-distally.

.... ***Pandion haliaetus* (1–4)**

b — In lateral and/or medial view, the tuberculum flexorium protrudes much less plantarly and is elongated proximo-distally [Accipitridae (1–4), including some vultures (1–2)].

....11

11 (Figure 3)

a — (i) Proximal height: 9.0–12.0 mm; AND (ii) the foramina lateral and medial of the tuberculum flexorium are located at the base of the tuberculum (in the corner between the tuberculum and the corpus phalangis) and are usually small.

....***Neophron percnopterus* (1–2)**

b — (i) Proximal height in any size range; (ii) the foramina lateral and medial of the tuberculum flexorium are located within the tuberculum (they are separated from the corpus phalangis by a bony crest) and are usually relatively large [other Accipitridae (1–4), including some larger vultures: *G. fulvus* (1–2), *A. monachus* (1–2), *G. barbatus* (1–2)].

....12

12 (Figure 3)

a — (i) Proximal height: 11.0–16.0 mm; AND (ii) the tuberculum flexorium is not undercut (i.e., the transition between the tuberculum and corpus phalangis is almost straight).

....***Gyps fulvus* (1–2)**

b — (i) Proximal height in any size range; (ii) the tuberculum flexorium is undercut (i.e., in the transition between the tuberculum flexorium and corpus phalangis, there is a semicircular indentation of varying depth [other Accipitridae (1–4), including some larger vultures: *A. monachus* (1–2), *G. barbatus* (1–2)].

....13

Note: To avoid ambiguity, this is best seen by arranging the proximal part of the phalanx so that its dorsal edge is horizontal.

13 (Figure 3)

a — (i) Proximal height: 14.0–18.5 mm; (ii) the corpus phalangis is wide, stocky, and "inflated" all along its length; (iii) in a lateral and/or medial view, the dorsal part of the cotyla articularis is only slightly extended proximally; (iv) the cotyla articularis is shaped like a relatively wide but short pear; (v) the tuberculum flexorium is strongly oblique to the long axis of the bone, so that part of it often protrudes beyond the corpus phalangis [*A. monachus* (1–2), *G. barbatus* (1–2)].

....14

b — (i) Proximal height in any size range; (ii) the corpus phalangis is relatively narrow and slender; (iii) in a lateral and/or medial view, the dorsal part of the cotyla articularis is usually more proximally extended; (iv) the cotyla articularis is shaped like a relatively narrow and long pear; (v) the tuberculum flexorium is less oblique to the long axis of the bone [other Accipitridae (1–4)].

....15

Notes: (i) It may happen that a specimen from point "a" does not meet one of the four morphological features, but most of the features must be met in order to identify a specimen as a vulture; (ii) some of the features listed in point "a" are also observed in non-vultures, but never all four features in one specimen.

14 (Figure 3)

a — The proximal part of the cotyla articularis is relatively stockier.

....***Aegypius monachus* (1–2)**

b — The proximal part of the cotyla articularis is comparatively more slender.

....***Gypaetus barbatus* (1–2)**

15 (Figure 3, Appendix S1)

a — Proximal height at least 18 mm [*H. albicilla* (1–2), *A. chrysaetos* (1–2), *A. heliaca* (1–2)].

....18

b — Proximal height: 14.5–18 mm [*H. albicilla* (1–2), *A. chrysaetos* (1–2), *A. heliaca* (1–2), *A. fasciata* (1–2), *A. rapax* (1–2)].

....16

c — Proximal height less than 14.5 mm [other Accipitridae (1–4)].

....20

16 (Figure 4)

a — (i) The dorsal edge of the cotyla articularis is flattened; (ii) the ridge between the foramina on both sides of the tuberculum flexorium is narrow lateromedially, giving the impression of a "squeezed nose."

....***Aquila chrysaetos* (1–2), *Aquila heliaca* (1–2), *Aquila fasciata* (1–2)**

b — (i) The dorsal edge of the cotyla articularis is rounded (forms an arch); (ii) the ridge between the foramina on both sides of the tuberculum flexorium is wider lateromedially and more flattened [*H. albicilla* (1–2), *A.heliaca* (1–2), *A. fasciata* (1–2), *A. rapax* (1–2)].

....17

Notes: (i) These features separate *A. chrysaetos* very well from *H. albicilla*. However, *A. heliaca* and *A. fasciata* show variability in this respect; (ii) we only checked one *A. rapax*, so we do not know the variability of this species.

17 (Figure 4)

a — The cotyla articularis is relatively wide, also in its dorsal half, where its edges are roughly parallel to each other.

....***Haliaeetus albicilla* (1–2)**

b — The cotyla articularis tapers in the dorsal part (its edges in the dorsal part are oblique to each other).

....***Aquila heliaca* (1–2), *Aquila fasciata* (1–2), *Aquila rapax* (1–2)**

18 (Figure 4)

a — (i) The dorsal edge of the cotyla articularis is flattened; (ii) the ridge between the foramina on both sides of the tuberculum flexorium is narrow lateromedially, giving the impression of a "squeezed nose."

....***Aquila chrysaetos* (1–2), *Aquila heliaca* (1–2)**

b — (i) The dorsal edge of the cotyla articularis is rounded (forms an arch); (ii) the ridge between the foramina on both sides of the tuberculum flexorium is wider lateromedially and more flattened [*H. albicilla* (1–2), *A. heliaca* (1–2)].

....19

Note: These features separate *A. chrysaetos* very well from *H. albicilla* but *A. heliaca* shows variability in this respect.

19 (Figure 4)

a — The cotyla articularis is relatively wide, also in its dorsal half, where its edges are roughly parallel to each other.

....

***Haliaeetus albicilla* (1–2)**

b — The cotyla articularis tapers in the dorsal part (its edges in the dorsal part are oblique to each other)

....

***Aquila heliaca* (1–2)**

20 (Figure 4)

a — There is an edge along the medial side of the corpus phalangis [Accipitridae (3)].

....59

b — The medial and lateral sides of the corpus phalangis look the same (no edge) [Accipitridae (1–2, 4)].

....21

Note: In some species, the edge along the medial side of the corpus phalangis is close to the plantar side of the phalanx but extends all the way to the cotyla articularis, making the entire ungual phalanx asymmetrical.

21 (Figure 4, Appendix S1)

a — Proximal height less than or equal to 8 mm [*P. apivorus* (1–2, 4), *C. gallicus* (4), *E. caeruleus* (1–2, 4), *H. pennatus* (4), *C. pomarina* (4), *A. gentilis* (4), *A. nisus* (1–2, 4), *B. buteo* (1–2, 4), *B. lagopus* (4), *B. rufinus* (4), *C. aeruginosus* (1–2, 4), *C. cyaneus* (1–2, 4), *C. macrourus* (1–2, 4), *C. pygargus* (1–2, 4), *M. migrans* (1–2, 4), *M. milvus* (4)].

....22

b — Proximal height: 8–14.5 mm [*C. gallicus* (1–2, 4), *H. albicilla* (4), *A. chrysaetos* (4), *A. fasciata* (4), *A. heliaca* (1–2, 4), *A. rapax* (1–2, 4), *H. pennatus* (1–2), *C. clanga* (1–2, 4), *C. pomarina* (1–2, 4), *A. gentilis* (1–2, 4), *B. buteo* (1–2), *B. lagopus* (1–2), *B. rufinus* (1–2, 4), *C. aeruginosus* (1–2), *M. migrans* (1–2), *M. milvus* (1–2)].

....24

Note: Some ungual phalanges of the same species are listed in both size categories because this is their range of variation.

22 (Figure 4)

a — The tuberculum flexorium is broad lateromedially also at half its length but very short dorso-plantarly [*Circaetus gallicus* (4), *Elanus caeruleus* (1–2, 4)].

....23

b — The tuberculum flexorium is narrow lateromedially but elongated dorso-plantarly [*P. apivorus* (1–2, 4), *H. pennatus* (4), *C. pomarina* (4), *A. gentilis* (4), *A. nisus* (1–2, 4), *B. buteo* (1–2, 4), *B. lagopus* (4), *B. rufinus* (4), *C. aeruginosus* (1–2, 4), *C. cyaneus* (1–2, 4), *C. macrourus* (1–2, 4), *C. pygargus* (1–2, 4), *M. migrans* (1–2, 4), *M. milvus* (4)].

....41

23 (Figure 4, Appendix S1)

a — (i) Proximal height greater than 7.0 mm; (ii) the plantar surface of the corpus phalangis is flattened and delimited by two edges: the lateral and medial, which results in the cross-section of the corpus phalangis having the shape of an arc with a flat base as wide as the corpus phalangis.

....***Circaetus gallicus* (4)**

b — (i) Proximal height less than 7.0 mm; (ii) the plantar surface of the corpus phalangis gradually turns into the lateral and medial surface, resulting in an oval cross-section of the corpus phalangis.

....***Elanus caeruleus* (1–2, 4)**

Note: Ungual phalanges of *Elanus caeruleus* can be confused with those of owls because they have a short tuberculum flexorium and an oval cross-section of the corpus phalangis.

24 (Figure 4)

a — The tuberculum flexorium is broad lateromedially also at half its length but very short dorso-plantarly.

....***Circaetus gallicus* (1–2, 4)**

b — The tuberculum flexorium is narrow lateromedially but elongated dorso-plantarly [*H. albicilla* (4), *A. chrysaetos* (4), *A. fasciata* (4), *A. heliaca* (1–2, 4), *A. rapax* (1–2, 4), *H. pennatus* (1–2), *C. clanga* (1–2, 4), *C. pomarina* (1–2, 4), *A. gentilis* (1–2, 4), *B. buteo* (1–2), *B. lagopus* (1–2), *B. rufinus* (1–2, 4), *C. aeruginosus* (1–2), *M. migrans* (1–2), *M. milvus* (1–2)].

....25

25 (Figure 5)

a — Length of tuberculum flexorium greater than or equal to the height of cotyla articularis [*A. chrysaetos* (4), *A. fasciata* (4), *A. heliaca* (4), *A. rapax* (4), *C. clanga* (4), *C. pomarina* (4), *A. gentilis* (1–2, 4), *M. migrans* (1–2)].

....26

b — Length of tuberculum flexorium smaller than the height of cotyla articularis [*H. albicilla* (4), *A. heliaca* (1–2), *A. rapax* (1–2), *H. pennatus* (1–2), *C. clanga* (1–2), *C. pomarina* (1–2), *B. buteo* (1–2), *B. lagopus* (1–2), *B. rufinus* (1–2, 4), *C. aeruginosus* (1–2), *M. migrans* (1–2), *M. milvus* (1–2)].

....34

Note: Due to the small number of examined *A. fasciata* and *A. rapax* specimens, we are not sure if all the specimens will go to point “a” only.

26 (Figure 5, Appendix S1)

a — Proximal height less than 9.3 mm [*A. heliaca* (4), *C. clanga* (4), *C. pomarina* (4), *A. gentilis* (4), *M. migrans* (1–2)].

....30

b — Proximal height greater than 9.3 mm [*A. chrysaetos* (4), *A. fasciata* (4), *A. heliaca* (4), *A. rapax* (4), *A. gentilis* (1–2), *M. migrans* (1–2)].

....27

27 (Figure 5)

a — The tuberculum flexorium is slender because its lateral and medial edges are concave in the central part, and the ridge between the foramina situated on both sides of the tuberculum is relatively narrow [*A. gentilis* (1–2), *M. migrans* (1–2)].

....28

b — The tuberculum flexorium is stout: Its lateral and medial edges are not concave in the central part but are more or less straight, and the ridge between the foramina on both sides of the tuberculum is wide [*A. chrysaetos* (4), *A. fasciata* (4), *A. heliaca* (4), *A. rapax* (4)].

....29

28 (Figure 5)

a — The plantar edge of the tuberculum flexorium is straight and relatively long, in lateral and/or medial view.

....***Accipiter gentilis* (1–2)**

b — The plantar edge of the tuberculum flexorium is comparatively short, in lateral and/or medial view.

....***Milvus migrans* (1–2)**

29 (Figure 5)

a — The dorsal edge of the cotyla articularis is flattened.

....***Aquila chrysaetos* (4)**

b — The dorsal edge of the cotyla articularis is rounded (forms an arch).

....***Aquila fasciata* (4), *Aquila heliaca* (4), *Aquila rapax* (4)**

30 (Figure 5, Appendix S1)

a — Height of cotyla articularis less than 5 mm [*A. gentilis* (4), *C. pomarina* (4)].

....31

b — Height of cotyla articularis greater than 5 mm [*A. heliaca* (4), *C. clanga* (4), *C. pomarina* (4), *M. migrans* (1–2)].

....32

31 (Figure 5, Appendix S1)

a — Articular width less than 3.5 mm.

....***Accipiter gentilis* (4)**

b — Articular width greater than 3.5 mm [*A. gentilis* (4), *C. pomarina* (4)].

....33

32 (Figure 5)

a — The ridge between the foramina situated on both sides of the tuberculum flexorium is relatively narrow but widens sharply just before joining the cotyla articularis.

....***Milvus migrans* (1–2)**

b — The ridge between the foramina on both sides of the tuberculum is comparatively wide and only widens slightly just before joining the cotyla articularis.

....***Aquila heliaca* (4), *Clanga clanga* (4), *Clanga pomarina* (4)**

33 (Figure 5)

a — The lateral and medial edges of the tuberculum flexorium are concave in the central part of the tuberculum.

....***Accipiter gentilis* (4)**

b — The lateral and medial edges of the tuberculum flexorium are not concave in the central part of the tuberculum, but are more or less straight.

....***Clanga pomarina* (4)**

34 (Figure 5, Appendix S1)

a — Proximal height greater than or equal to 13.5 mm.

....***Aquila heliaca* (1–2), *Aquila rapax* (1–2), *Clanga clanga* (1–2)**

b — Proximal height less than 13.5 mm [*H. albicilla* (4), *H. pennatus* (1–2), *C. clanga* (1–2), *C. pomarina* (1–2), *B. buteo* (1–2), *B. lagopus* (1–2), *B. rufinus* (1–2, 4), *C. aeruginosus* (1–2), *M. migrans* (1–2), *M. milvus* (1–2)].

....35

35 (Figure 5, Appendix S1)

a — Proximal height less than or equal to 10 mm [*H. pennatus* (1–2), *B. buteo* (1–2), *B. lagopus* (1–2), *B. rufinus* (4), *C. aeruginosus* (1–2), *M. migrans* (1–2), *M. milvus* (1–2)].

....37

b — Proximal height greater than 10 mm [*H. albicilla* (4), *H. pennatus* (1–2), *C. clanga* (1–2), *C. pomarina* (1–2), *B. buteo* (1–2), *B. lagopus* (1–2), *B. rufinus* (1–2)].

....36

36 (Figure 5)

a — (i) The cotyla articularis is relatively wide in its dorsal part where its edges are roughly parallel to each other; (ii) the dorsal edge of the cotyla articularis is rounded (forms a wide arch).

....***Haliaeetus albicilla* (4)**

b — (i) The cotyla articularis is comparatively narrow in the dorsal part where its edges are usually oblique to each other); (ii) the dorsal edge of the cotyla articularis is usually flattened

……………………………***Hieraaetus pennatus* (1–2), *Clanga clanga* (1–2), *Clanga pomarina* (1–2), *Buteo buteo* (1–2), *Buteo lagopus* (1–2), *Buteo rufinus* (1–2)**

37 (Figure 5)

a — The dorsal edge of the cotyla articularis is rounded (forms an arch) [*B. rufinus* (4), *M. migrans* (1–2), *M. milvus* (1–2)].

………38

b — The dorsal edge of the cotyla articularis is flattened [*H. pennatus* (1–2), *B. buteo* (1–2), *B. lagopus* (1–2), *C. aeruginosus* (1–2)].

………39

38 (Figure 5)

a — The foramina lateral and medial of the tuberculum flexorium are barely (or not) visible in the plantaro-proximal and/or plantar view because they are (partially) obscured by the tuberculum, which is shaped like a broad cylinder.

…………………………………………………………………………………***Milvus migrans* (1–2), *Milvus milvus* (1–2)**

b — The foramina lateral and medial of the tuberculum flexorium are clearly visible in the plantaro-proximal and/or plantar view because the plantar ridge of the tuberculum is narrow.

………***Buteo rufinus* (4)**

39 (Figure 5)

a — The dorsal part of the cotyla articularis is very narrow, long, and slender.

……***Circus aeruginosus* (1–2)**

b — The dorsal part of the cotyla articularis is relatively wider and stockier [*H. pennatus* (1–2), *B. buteo* (1–2), *B. lagopus* (1–2)].

………40

40 (Figure 5)

a — There is a distinct, relatively deep, often sharp indentation between tuberculum flexorium and cotyla articularis, best visible in lateral and/or medial view.

…………………………***Buteo buteo* (1–2), *Buteo lagopus* (1–2), and some *Hieraaetus pennatus* (1–2)**

b — There is a relatively shallow indentation between tuberculum flexorium and cotyla articularis, best seen in lateral and/or medial view.

……***Hieraaetus pennatus* (1–2)**

41 (Figure 5)

a — Length of tuberculum flexorium greater than or equal to the height of cotyla articularis [*P. apivorus* (1–2, 4), *H. pennatus* (4), *C. pomarina* (4), *A. gentilis* (4), *A. nisus* (1–2, 4), *C. aeruginosus* (4), *C. cyaneus* (4), *C. macrourus* (4), *C. pygargus* (4), *M. migrans* (1–2, 4), *M. milvus* (4)].

………42

b — Length of tuberculum flexorium smaller than the height of cotyla articularis [*P. apivorus* (1–2, 4), *H. pennatus* (4), *A. nisus* (1–2), *B. buteo* (1–2, 4), *B. lagopus* (4), *B. rufinus* (4), *C. aeruginosus* (1–2), *C. cyaneus* (1–2), *C. macrourus* (1–2), *C. pygargus* (1–2, 4), *M. migrans* (1–2), *M. milvus* (4)].

………53

42 (Figure 6, Appendix S1)

a — Length of tuberculum flexorium less than 4.0 mm [*P. apivorus* (4), *A. nisus* (1–2, 4), *C. aeruginosus* (4), *C. cyaneus* (4), *C. macrourus* (4), *C. pygargus* (4), *M. migrans* (4), *M. milvus* (4)].

………47

b — Length of tuberculum flexorium greater than 4.0 mm [*P. apivorus* (1–2, 4), *H. pennatus* (4), *C. pomarina* (4), *A. gentilis* (4), *A. nisus* (1–2), *C. aeruginosus* (4), *M. migrans* (1–2, 4), *M. milvus* (4)].

………43

43 (Figure 6)

a — The lateral and medial edges of the tuberculum flexorium are concave in the middle, and the distal end of the tuberculum widens considerably [*H. pennatus* (4), *A. gentilis* (4), *C. aeruginosus* (4)].

………45

b — The lateral and medial edges of the tuberculum flexorium are parallel to each other or converging, any concavity is shallow and the distal end of the tuberculum is much narrower than the proximal end [*P. apivorus* (1–2, 4), *C. pomarina* (4), *A. nisus* (1–2), *C. aeruginosus* (4), *M. migrans* (1–2, 4), *M. milvus* (4)].

………44

44 (Figure 6)

a — (i) The processus extensorius clearly protrudes dorsally in relation to the dorsal edge of the corpus phalangis; AND (ii) the plantar edge of the cotyla articularis is flattened, and the flat, straight section is long; AND (iii) the ridge between the foramina on both sides of the tuberculum flexorium is very wide.

……***Pernis apivorus* (1–2, 4)**

b — (i) The processus extensorius protrudes slightly or not at all dorsally; (ii) the plantar edge of the cotyla articularis is rounded, and the flattening, if there is any, is short; (iii) the ridge between the foramina situated on both sides of the tuberculum flexorium is clearly narrower [*C. pomarina* (4), *A. nisus* (1–2), *C. aeruginosus* (4), *M. migrans* (1–2, 4), *M. milvus* (4)].

………51

45 (Figure 6)

a — The corpus phalangis is slender, thin in lateral and/or medial view.

....***Circus aeruginosus* (4)**

b — The corpus phalangis is stout, thick in lateral and/or medial view [*H. pennatus* (4), *A. gentilis* (4)].

....46

46 (Figure 6)

a — (i) The tuberculum flexorium is relatively short, in lateral and/or medial view; (ii) the dorsal edge of the cotyla articularis is flattened.

....***Hieraaetus pennatus* (4)**

b — (i) The tuberculum flexorium is relatively long, in lateral and/or medial view; (ii) the dorsal edge of the cotyla articularis is rounded (forms an arch).

....***Accipiter gentilis* (4)**

47 (Figure 6)

a — The dorsal edge of the cotyla articularis is flattened.

.................***Circus aeruginosus* (4), *Circus cyaneus* (4), *Circus macrourus* (4), *Circus pygargus* (4)**

b — The dorsal edge of the cotyla articularis is rounded (forms an arch) [*P. apivorus* (4), *A. nisus* (1–2, 4), *M. migrans* (4), *M. milvus* (4)].

....48

48 (Figure 6, Appendix S1)

a — Proximal height less than or equal to 5 mm.

....***Accipiter nisus* (1–2, 4)**

b — Proximal height greater than 5 mm [*P. apivorus* (4), *A. nisus* (1–2), *M. migrans* (4), *M. milvus* (4)].

....49

49 (Figure 6)

a — The lateral and medial edges of the dorsal part of the cotyla articularis are roughly parallel to each other.

....***Accipiter nisus* (1–2)**

b — The dorsal part of the cotyla articularis narrows dorsally because its lateral and medial edges are oblique [*P. apivorus* (4), *M. migrans* (4), *M. milvus* (4)].

....50

50 (Figure 6)

a — The corpus phalangis is relatively slender and lightly built.

....***Pernis apivorus* (4)**

b — The corpus phalangis is comparatively more robust and stocky.

....***Milvus migrans* (4), *Milvus milvus* (4)**

51 (Figure 6)

a — The corpus phalangis is comparatively more robust and stocky.

....***Clanga pomarina* (4)**

b — The corpus phalangis is relatively slender and lightly built [*A. nisus* (1–2), *C. aeruginosus* (4), *M. migrans* (1–2, 4), *M. milvus* (4)].

....52

52 (Figure 6)

a — The dorsal edge of the cotyla articularis is flattened.

....***Circus aeruginosus* (4)**

b — The dorsal edge of the cotyla articularis is rounded (forms an arch).

....***Accipiter nisus* (1–2), *Milvus migrans* (1–2, 4), *Milvus milvus* (4)**

53 (Figure 6)

a — The dorsal edge of the cotyla articularis is flattened [*H. pennatus* (4), *B. buteo* (1–2), *C. aeruginosus* (1–2), *C. cyaneus* (1–2), *C. macrourus* (1–2), *C. pygargus* (1–2, 4)].

....54

b — The dorsal edge of the cotyla articularis is rounded (forms an arch) [*P. apivorus* (1–2, 4), *A. nisus* (1–2), *B. buteo* (4), *B. lagopus* (4), *B. rufinus* (4), *M. migrans* (1–2), *M. milvus* (4)].

....56

54 (Figure 7)

a — The dorsal part of the cotyla articularis is very narrow, long, and slender.

......***Circus aeruginosus* (1–2), *Circus cyaneus* (1–2), *Circus macrourus* (1–2), *Circus pygargus* (1–2, 4)**

b — The dorsal part of the cotyla articularis is comparatively wider and stockier [*H. pennatus* (4), *B. buteo* (1–2)].

....55

55 (Figure 7, Appendix S1)

a — Proximal height greater than or equal to 8 mm.

....***Buteo buteo* (1–2)**

b — Proximal height less than 8 mm.

....***Hieraaetus pennatus* (4)**

56 (Figure 7)

a — The foramina lateral and medial of the tuberculum flexorium are barely (or not) visible in the plantaro-proximal and/or plantar view because they are (partially) obscured by the tuberculum, which is shaped like a broad cylinder [*P. apivorus* (1–2, 4), *M. migrans* (1–2), *M. milvus* (4)].

....57

b — The foramina lateral and medial of the tuberculum flexorium are clearly visible in the plantaro-proximal and/or plantar view because the plantar ridge of the tuberculum is narrow [*A. nisus* (1–2), *B. buteo* (4), *B. lagopus* (4), *B. rufinus* (4)].

....58

57 (Figure 7)

a — The corpus phalangis is relatively slender and lightly built.

....***Pernis apivorus* (1–2, 4)**

b — The corpus phalangis is comparatively more robust and stocky

....***Milvus migrans* (1–2, 4), *Milvus milvus* (4)**

58 (Figure 7)

a — The corpus phalangis is comparatively more robust and stocky

....***Buteo buteo* (4), *Buteo lagopus* (4), *Buteo rufinus* (4)**

b — The corpus phalangis is relatively slender and lightly built.

....***Accipiter nisus* (1–2)**

59 (Figure 7)

a — The length of tuberculum flexorium is less than or equal to the articular width [*E. caeruleus* (3), *C. gallicus* (3)].

....60

b — The length of tuberculum flexorium is greater than the articular width [other Accipitridae (3)].

....61

60 (Figure 7)

a — (i) Total length about 20 mm; (ii) proximal height about 9 mm.

....***Circaetus gallicus* (3)**

b — (i) Total length about 12 mm; (ii) proximal height about 5 mm.

....***Elanus caeruleus* (3)**

Note: Due to the small number of specimens studied, a reliable range of measurements cannot be given.

61 (Figure 7, Appendix S1)

a — Proximal height greater than 12 mm [*H. albicilla* (3), *A. chrysaetos* (3)].

....62

b — Proximal height: 9–12 mm [*H. albicilla* (3), *A. chrysaetos* (3), *A. fasciata* (3), *A. heliaca* (3), *A. rapax* (3), *C. pomarina* (3), *C. clanga* (3)].

....63

c — Proximal height: 6–9 mm [medium size Accipitridae (3)].

....64

d — Proximal height less than 6 mm.

..........***Accipiter nissus* (3), *Circus cyaneus* (3), *Circus macrourus* (3), *Circus pygargus* (3), some *Milvus migrans* (3)**

62 (Figure 7)

a — The dorsal edge of the cotyla articularis is flattened.

....***Aquila chrysaetos* (3)**

b — The dorsal edge of the cotyla articularis is rounded (forms an arch).

....***Haliaeetus albicilla* (3)**

63 (Figure 7)

a — The dorsal edge of the cotyla articularis is flattened.

....***Aquila chrysaetos* (3), *Aquila fasciata* (3), *Clanga pomarina* (3); and some: *Aquila heliaca* (3), *Clanga clanga* (3)**

b — The dorsal edge of the cotyla articularis is rounded (forms an arch).

........***Haliaeetus albicilla* (3), *Aquila rapax* (3), and some: *Aquila heliaca* (3), *Clanga clanga* (3)**

64 (Figure 7)

a — The edge along the medial side of the corpus phalangis is situated close to the plantar side of the phalanx [*P. apivorus* (3), *A. gentilis* (3), *B. buteo* (3), *B. lagopus* (3), *B. rufinus* (3)].

....65

b — The edge along the medial side of the corpus phalangis is approximately on the centerline of the phalanx [*H. pennatus* (3), *C. pomarina* (3), *Caeruginosus* (3), *M. milvus* (3), *M. migrans* (3)].

....67

65 (Figure 8)

a — The corpus phalangis is relatively slender and lightly built.

....***Pernis apivorus* (3)**

b — The corpus phalangis is comparatively more robust and stocky [*A. gentilis* (3), *B. buteo* (3), *B. lagopus* (3), *B. rufinus* (3)].

....66

66 (Figure 8)

a — The cotyla articularis is pear-shaped, almost symmetrical.

....***Accipiter gentilis* (3)**

b — The cotyla articularis is almost vertical on the lateral side and oblique or bulging on the medial side.

....***Buteo buteo* (3), *Buteo lagopus* (3), *Buteo rufinus* (3)**

67 (Figure 8)

a — The dorsal edge of the cotyla articularis is rounded (forms an arch).

....***Milvus migrans* (3), *Milvus milvus* (3)**

b — The dorsal edge of the cotyla articularis is flattened [*H. pennatus* (3), *C. pomarina* (3), *C. aeruginosus* (3)].

....68

68 (Figure 8)

a — There is a deep indentation between the plantar part of the cotyla articularis and the tuberculum flexorium.

....***Circus aeruginosus* (3)**

b — There is a shallow depression between the plantar part of the cotyla articularis and the tuberculum flexorium [*H. pennatus* (3), *C. pomarina* (3)].

....69

69 (Figure 8)

a — The ridge between the foramina on both sides of the tuberculum flexorium is narrow lateromedially, giving the impression of a "squeezed nose."

....***Hieraaetus pennatus* (3)**

b — The ridge between the foramina on both sides of the tuberculum flexorium is wide lateromedially.

....

***Clanga pomarina* (3)**

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Supporting information

Filename	Description
oa3165-sup-0001-Table_S1.pdfPDF document, 135.2 KB	**Table S1.** Modern comparative specimens.
oa3165-sup-0002-Data_S1.xlsxExcel 2007 spreadsheet , 49.6 KB	**Data S1.** Measurements of ungual phalanges.
oa3165-sup-0003-Appendix_S1_corrected.pdfPDF document, 568.9 KB	**Appendix S1.** Illustrations referring to key steps that use species division into groups of varying size.
oa3165-sup-0004-Appendix_S2.pdfPDF document, 4.1 MB	**Appendix S2.** Photographs of ungual phalanges in predefined views.

Supporting Table S1

for: Bochenski Z.M., Tomek T., Wertz K., Whose talon is this? A manual for the identification of ungual phalanges of European accipitrid birds of prey. *International Journal of Osteoarchaeology.*

Modern comparative specimens and their provenance.

Taxon: \\ Collection:	ISEA	NMNHS	NHMUT	HNHM	PACEA	UMB	NMNHU	Total
Pandion haliaetus	4	-	-	3	-	-	1	8
Elanus caeruleus	1	-	-	-	-	-	-	1
Pernis apivorus	8	-	-	1	-	-	5	14
Gypaetus barbatus	2	-	-	3	1	-	-	6
Neophron percnopterus	1	5	-	1	-	-	-	7
Circaetus gallicus	-	1	-	4	-	-	-	5
Gyps fulvus	2	5	-	4	1	-	-	12
Aegypius monachus	2	4	-	1	-	-	2	9
Clanga pomarina	5	1	-	2	-	-	2	10
Clanga clanga	-	-	-	3	-	-	-	3
Aquila rapax	1	-	-	2	-	-	1	4
Aquila heliaca	1	2	-	15	1	-	1	20
Aquila chrysaetos	4	3	1	5	-	5	-	18
Aquila fasciata	-	-	-	1	-	-	-	1
Hieraaetus pennatus	2	3	-	2	-	-	-	7
Circus aeruginosus	9	-	-	11	-	-	-	20
Circus cyaneus	1	-	-	6	-	-	-	7
Circus macrourus	1	-	-	2	-	-	-	3
Circus pygargus	2	-	-	4	-	-	-	6
Accipiter nisus	17	-	-	8	-	-	-	25
Accipiter gentilis	14	-	-	18	-	-	-	32
Haliaeetus albicilla	14	-	-	5	-	-	-	19
Milvus milvus	3	-	-	2	1	-	-	6
Milvus migrans	3	1	-	2	-	-	3	9
Buteo lagopus	4	-	-	5	-	5	-	14
Buteo buteo	38	-	-	14	-	-	-	52
Buteo rufinus	1	-	-	2	-	-	-	3
Total	140	25	1	126	4	10	15	321

ISEA - Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland

NMNHS – National Museum of Natural History, Bulgarian Academy of Sciences, Sofia, Bulgaria

NHMUT – Natural History Museum, University of Tartu, Estonia

HNHM - Hungarian Natural History Museum, Budapest, Hungary

PACEA – De la Préhistoire à l’Actuel: Culture, Environnement et Anthropologie, Université de Bordeaux, France

UMB – University Museum of Bergen, Department of Natural History, Bergen, Norway

NMNHU - National Museum of Natural History at the National Academy of Sciences of Ukraine, Kyiv, Ukraine

Supporting Data 1 (Data S1) for: Bochenski Z.M., Tomek T., Wertz K. W

Measurement ranges for all species included in the manual. The arithmetic mean and standard deviation are only
specimens of known and unknown sex. The measurements are illustrated in Figure 1. N stands for the number of
2, 1-3 or 1-4) are shown together in the same cell.

			Total length					
Taxon	sex	digit	Min	Max	MEAN	SD	N	Min
Pandion haliaetus	♀	1-4	26,44	28,09	-	-	3	11,59
Pandion haliaetus	?+♀+♂	1-4	23,61	28,09	25,493	1,171	27	9,38
Elanus caeruleus	?+♀+♂	1-2	13,84	14,69	-	-	2	5,56
Elanus caeruleus	?+♀+♂	3	12,23	12,23	-	-	1	5,09
Elanus caeruleus	?+♀+♂	4	10,92	10,92	-	-	1	5,08
Pernis apivorus	♀	1-2	19,51	19,51	-	-	1	7,83
Pernis apivorus	♀	3	18,43	18,43	-	-	1	6,86
Pernis apivorus	?+♀+♂	1-2	14,8	19,83	17,863	1,366	17	5,76
Pernis apivorus	?+♀+♂	3	16,56	20,14	18,430	1,041	9	5,91
Pernis apivorus	?+♀+♂	4	12,07	15,79	14,425	1,253	8	5,31
Gypaetus barbatus	?+♀+♂	1-2	28,79	35,59	32,073	2,025	12	15,05
Gypaetus barbatus	?+♀+♂	3	21,1	26,24	24,180	2,028	5	11,31
Gypaetus barbatus	?+♀+♂	4	17,59	21,52	19,445	1,336	6	10,11
Neophron percnopterus	?+♀+♂	1-2	20,4	23,19	21,896	0,879	10	9,74
Neophron percnopterus	?+♀+♂	3	18,54	20,92	-	-	4	7,45
Neophron percnopterus	?+♀+♂	4	13,94	14,91	-	-	4	6,67
Circaetus gallicus	♂	1-2	24,2	24,25	-	-	2	10,53
Circaetus gallicus	♂	3	23,14	23,14	-	-	1	8,7
Circaetus gallicus	♂	4	18,58	18,58	-	-	1	8
Circaetus gallicus	?+♀+♂	1-2	21,99	24,25	23,365	0,680	10	10,44
Circaetus gallicus	?+♀+♂	3	20,32	23,15	22,144	1,193	5	8,7
Circaetus gallicus	?+♀+♂	4	16,58	18,66	17,972	0,924	5	7,77
Gyps fulvus	?+♀+♂	1-2	26,35	34,18	31,104	2,347	16	12,35
Gyps fulvus	?+♀+♂	3	26,71	32,28	30,341	1,628	10	12,16
Gyps fulvus	?+♀+♂	1-3	-	-	-	-	-	11,94
Gyps fulvus	?+♀+♂	4	21,37	26,07	24,853	1,612	7	9,96
Aegypius monachus	?+♀+♂	1-2	27,46	34,43	32,407	1,867	13	15,72
Aegypius monachus	?+♀+♂	3	24,26	28,09	26,920	1,582	5	12,7
Aegypius monachus	?+♀+♂	4	18,01	21,94	20,283	1,781	6	10,34
Clanga pomarina	?+♀+♂	1-2	21,34	25,51	23,441	1,169	15	10,34
Clanga pomarina	?+♀+♂	3	17,36	19,96	19,233	0,832	8	8,04
Clanga pomarina	?+♀+♂	4	14,52	16,49	15,308	0,612	8	7,23
Clanga clanga	♀	1-2	25,43	27,19	-	-	3	12,13
Clanga clanga	♀	3	20,76	22,18	-	-	2	9,69
Clanga clanga	♀	4	17,4	17,72	-	-	2	8,46
Clanga clanga	?+♀+♂	1-2	25,43	29,2	27,342	1,666	5	12,13
Clanga clanga	?+♀+♂	3	20,76	24,54	-	-	3	9,66
Clanga clanga	?+♀+♂	4	17,4	19,6	-	-	3	8,46
Aquila rapax	♀	1-2	30,37	30,37	-	-	1	14,5
Aquila rapax	♀	3	-	-	-	-	-	10,31
Aquila rapax	?+♀+♂	1-2	29,85	34,22	-	-	4	14,5
Aquila rapax	?+♀+♂	3	21,84	25,24	-	-	2	10,31
Aquila rapax	?+♀+♂	4	18,6	18,6	-	-	1	9,72
Aquila heliaca	♀	1-2	29,12	37,79	33,067	2,645	10	13,86
Aquila heliaca	♀	3	24,22	25,98	-	-	2	11,05
Aquila heliaca	♀	4	17,89	22,14	20,350	1,602	5	8,69
Aquila heliaca	♂	1-2	28,66	33,33	30,333	1,669	8	13,55
Aquila heliaca	♂	3	22,83	24,58	-	-	4	10,03
Aquila heliaca	♂	4	18,19	20,32	-	-	4	8,99
Aquila heliaca	?+♀+♂	1-2	28,66	41,46	32,713	2,779	38	13,52
Aquila heliaca	?+♀+♂	3	22,83	28,05	24,578	1,486	14	9,78
Aquila heliaca	?+♀+♂	4	17,89	22,4	20,310	1,360	16	8,69

Aquila chrysaetos	♀	1-2		37,06	46,03	41,733	3,247	6		16
Aquila chrysaetos	♀	3		27,8	30,31	-	-	3		11,41
Aquila chrysaetos	♀	4		21,44	25,22	-	-	3		10,55
Aquila chrysaetos	♂	1-2		36,54	43,88	39,571	2,470	9		16,27
Aquila chrysaetos	♂	3		26,21	28,77	27,982	1,032	5		11,32
Aquila chrysaetos	♂	4		20,8	22,61	21,730	0,695	5		10,42
Aquila chrysaetos	?+♀+♂	1-2		30,54	50,61	40,903	4,252	31		14,55
Aquila chrysaetos	?+♀+♂	3		25,32	33,54	28,967	2,152	15		10,22
Aquila chrysaetos	?+♀+♂	4		19,85	27,13	22,704	2,026	14		9,97
Aquila fasciata	♂	1-2		33,43	38,41	-	-	2		15,46
Aquila fasciata	♂	3		27,19	27,19	-	-	1		11,44
Aquila fasciata	♂	4		23,11	23,11	-	-	1		10,41
Aquila fasciata	?+♀+♂	1-2		33,43	38,41	-	-	2		15,46
Aquila fasciata	?+♀+♂	3		27,19	27,19	-	-	1		11,44
Aquila fasciata	?+♀+♂	4		23,11	23,11	-	-	1		10,41
Hieraaetus pennatus	♀	1-2		24,45	26,56	-	-	2		10,8
Hieraaetus pennatus	♀	3		19,81	19,81	-	-	1		8,13
Hieraaetus pennatus	♀	4		17,17	17,17	-	-	1		7,41
Hieraaetus pennatus	♂	3		18,15	18,15	-	-	1		8,32
Hieraaetus pennatus	♂	4		16,28	16,28	-	-	1		7,73
Hieraaetus pennatus	?+♀+♂	1-2		20,81	27,04	23,798	2,166	11		9,27
Hieraaetus pennatus	?+♀+♂	3		16,9	19,94	18,529	1,137	7		7
Hieraaetus pennatus	?+♀+♂	4		13,42	17,17	15,400	1,436	5		6,59
Circus aeruginosus	♀	1-2		18,51	21,71	20,325	1,019	16		7,74
Circus aeruginosus	♀	3		16,69	18,74	17,841	0,699	8		6,49
Circus aeruginosus	♀	4		13,37	15,79	15,153	0,834	8		5,98
Circus aeruginosus	♂	1-2		17,49	20,3	19,180	1,057	6		7,29
Circus aeruginosus	♂	3		15,52	17,83	-	-	3		6,15
Circus aeruginosus	♂	4		13,1	15,06	-	-	3		5,68
Circus aeruginosus	?+♀+♂	1-2		17,14	21,71	19,379	1,455	40		6,61
Circus aeruginosus	?+♀+♂	3		13,61	18,74	16,851	1,409	20		5,93
Circus aeruginosus	?+♀+♂	4		12,92	15,92	14,473	1,076	19		5,59
Circus cyaneus	♀	1-2		16,31	17,19	-	-	3		7,05
Circus cyaneus	♀	3		13,27	13,27	-	-	1		5,48
Circus cyaneus	♀	4		10,95	11,89	-	-	2		5,07
Circus cyaneus	♂	1-2		13,11	13,59	13,327	0,174	6		5,88
Circus cyaneus	♂	3		10,79	10,94	-	-	3		4,67
Circus cyaneus	♂	4		8,66	9,02	-	-	3		4,25
Circus cyaneus	?+♀+♂	1-2		12,65	17,19	14,525	1,688	13		5,79
Circus cyaneus	?+♀+♂	3		10,76	13,86	11,748	1,421	6		4,42
Circus cyaneus	?+♀+♂	4		8,66	11,89	9,854	1,308	7		4,04
Circus macrourus	♀	1-2		17,07	17,59	-	-	2		7,52
Circus macrourus	♀	3		14,18	14,18	-	-	1		5,94
Circus macrourus	♀	4		12,1	12,1	-	-	1		5,51
Circus macrourus	♂	1-2		14,18	15,21	-	-	4		6,29
Circus macrourus	♂	3		12,04	12,04	-	-	1		5,01
Circus macrourus	♂	4		10,05	10,1	-	-	2		4,81
Circus macrourus	?+♀+♂	1-2		14,18	17,59	15,552	1,425	6		6,29
Circus macrourus	?+♀+♂	3		12,04	14,18	-	-	2		5,01
Circus macrourus	?+♀+♂	4		10,05	12,1	-	-	3		4,81
Circus pygargus	♀	1-2		12,32	12,5	-	-	2		5,35
Circus pygargus	♀	3		10,49	10,49	-	-	1		4,35
Circus pygargus	♀	4		9,15	9,15	-	-	1		4,08
Circus pygargus	♂	1-2		10,84	11,53	11,202	0,275	6		4,91
Circus pygargus	♂	3		9,66	10,1	-	-	3		3,76
Circus pygargus	♂	4		7,84	8,04	-	-	3		3,51
Circus pygargus	?+♀+♂	1-2		10,59	12,5	11,333	0,571	12		4,91
Circus pygargus	?+♀+♂	3		9,29	10,49	9,795	0,453	6		3,76
Circus pygargus	?+♀+♂	4		7,48	9,15	8,020	0,583	6		3,51
Accipiter nisus	♀	1-2		10,69	15,16	13,604	0,928	27		5,43
Accipiter nisus	♀	3		9,29	10,73	9,845	0,509	13		3,79

Accipiter nisus	♀	4		7,66	10,5	8,441	0,755	12		3,55
Accipiter nisus	♂	1-2		9,86	13,06	10,933	1,020	12		4,24
Accipiter nisus	♂	3		7,37	9,4	8,125	0,691	6		2,98
Accipiter nisus	♂	4		6,2	8,3	6,958	0,813	6		2,67
Accipiter nisus	?+♀+♂	1-2		9,53	15,16	12,646	1,644	48		4,24
Accipiter nisus	?+♀+♂	3		6,87	10,73	9,188	1,065	24		2,92
Accipiter nisus	?+♀+♂	4		5,8	10,5	7,829	1,053	23		2,59
Accipiter gentilis	♀	1-2		24,49	30,49	27,702	1,628	35		11,46
Accipiter gentilis	♀	3		16,37	18,76	17,871	0,669	17		7,92
Accipiter gentilis	♀	4		13,54	17	15,207	0,746	18		7,5
Accipiter gentilis	♂	1-2		20,37	24,91	22,744	1,151	28		9,27
Accipiter gentilis	♂	3		13,71	15,51	14,933	0,549	12		6,42
Accipiter gentilis	♂	4		11,42	13,37	12,247	0,600	12		5,74
Accipiter gentilis	?+♀+♂	1-2		20,37	30,49	25,498	2,864	63		9,27
Accipiter gentilis	?+♀+♂	3		13,71	18,76	16,656	1,595	29		6,42
Accipiter gentilis	?+♀+♂	4		11,42	17	14,023	1,625	30		5,74
Haliaeetus albicilla	♀	1-2		38,31	38,8	-	-	2		18,77
Haliaeetus albicilla	♀	3		31,62	31,62	-	-	1		13,91
Haliaeetus albicilla	♀	4		27,32	27,32	-	-	1		13,05
Haliaeetus albicilla	?+♀+♂	1-2		31,66	40,82	36,604	2,248	36		14,81
Haliaeetus albicilla	?+♀+♂	3		25,27	31,62	28,989	1,832	17		10,89
Haliaeetus albicilla	?+♀+♂	4		22,22	29,19	25,677	1,543	18		10,58
Milvus milvus	♀	1-2		19,55	19,99	-	-	3		9,21
Milvus milvus	♀	3		15,24	15,24	-	-	1		7,04
Milvus milvus	♀	4		13,76	13,76	-	-	1		6,71
Milvus milvus	?+♀+♂	1-2		18,22	21,63	19,604	1,080	11		8,38
Milvus milvus	?+♀+♂	3		15,24	16,59	15,856	0,548	5		6,32
Milvus milvus	?+♀+♂	4		12,4	14,39	13,538	0,862	5		5,76
Milvus migrans	♀	1-2		18,16	18,43	-	-	2		9,2
Milvus migrans	♀	3		15,2	15,2	-	-	1		7,15
Milvus migrans	♀	4		12,53	12,53	-	-	1		6,42
Milvus migrans	?+♀+♂	1-2		17,02	18,9	17,797	0,619	12		7,66
Milvus migrans	?+♀+♂	3		13,63	15,2	14,518	0,709	5		5,89
Milvus migrans	?+♀+♂	4		11,48	12,74	12,060	0,558	5		5,52
Buteo lagopus	♀	1-2		18,19	23,52	20,608	2,143	6		8,43
Buteo lagopus	♀	3		14,12	17,42	-	-	3		6,41
Buteo lagopus	♀	4		11,91	14,88	-	-	3		6,03
Buteo lagopus	♂	1-2		18,65	21,82	19,857	0,906	12		8,49
Buteo lagopus	♂	3		15,06	16,24	15,435	0,416	6		6,69
Buteo lagopus	♂	4		11,57	13,46	12,548	0,704	5		5,82
Buteo lagopus	?+♀+♂	1-2		18,19	23,81	20,458	1,558	28		8,43
Buteo lagopus	?+♀+♂	3		14,12	17,42	15,451	0,860	14		6,41
Buteo lagopus	?+♀+♂	4		11,57	14,88	12,940	0,883	13		5,82
Buteo buteo	♀	1-2		18,63	21,43	20,166	0,879	11		9,12
Buteo buteo	♀	3		15,52	16,51	15,922	0,339	6		6,94
Buteo buteo	♀	4		12,82	13,72	13,202	0,293	6		6,15
Buteo buteo	♂	1-2		18,41	22,03	19,782	0,948	12		8,64
Buteo buteo	♂	3		14,89	16,62	15,737	0,650	6		6,55
Buteo buteo	♂	4		12,27	14,08	13,102	0,804	6		6,04
Buteo buteo	?+♀+♂	1-2		15,26	22,99	19,924	1,529	103		7,9
Buteo buteo	?+♀+♂	3		12,31	16,92	15,634	0,945	52		5,9
Buteo buteo	?+♀+♂	4		9,8	14,38	12,948	0,948	52		5,39
Buteo rufinus	♀	1-2		24,36	26,19	-	-	2		11,87
Buteo rufinus	♀	3		17,07	17,07	-	-	1		8,56
Buteo rufinus	♀	4		16,42	16,42	-	-	1		8,09
Buteo rufinus	?+♀+♂	1-2		21,83	26,19	23,898	1,542	6		10,6
Buteo rufinus	?+♀+♂	3		17,07	17,94	-	-	3		8,18
Buteo rufinus	?+♀+♂	4		14,12	16,42	-	-	3		7,23

hose talon is this? A manual for the identification of ungual phalanges of European accipitrid birds of pr

calculated when the number of specimens is greater than or equal to five. Measurements for each species and for e
ungual phalanges measured which in the case of phalanges only from one digit (3 or 4) is equal to the number of bir

Proximal height					Length of tuberculum flexorium						Height c	
Max	MEAN	SD	N		Min	Max	MEAN	SD	N		Min	Max
12,74	-	-	3		5,17	5,66	-	-	3		10,26	10,6
12,74	11,044	0,748	27		4,27	6,66	5,076	0,609	27		7,54	10,6
6,72	-	-	2		3,5	4,05	-	-	2		4,31	4,76
5,09	-	-	1		3,28	3,28	-	-	1		3,59	3,59
5,08	-	-	1		3,13	3,13	-	-	1		3,85	3,85
7,83	-	-	1		5,38	5,38	-	-	1		5,12	5,12
6,86	-	-	1		4,35	4,35	-	-	1		4,58	4,58
7,96	6,940	0,617	17		4	5,53	4,696	0,452	17		4,49	5,27
7,15	6,577	0,411	9		3,83	4,99	4,228	0,448	9		4,01	4,84
6,53	5,803	0,388	8		3,51	4,56	3,843	0,366	8		3,65	4,34
17,08	16,108	0,633	12		9,61	11,85	10,637	0,618	12		10,84	12,13
13,02	12,268	0,663	5		7,48	8,81	8,184	0,586	5		7,54	9,05
12,08	10,753	0,698	6		6,13	7,23	6,715	0,421	6		7,14	7,78
11,12	10,504	0,463	14		6,46	7,59	7,068	0,327	14		6,75	7,89
9,24	8,110	0,695	6		5,46	7,2	6,075	0,619	6		5,1	5,68
7,66	-	-	4		4,93	5,4	-	-	4		4,7	4,9
11,04	-	-	2		6,21	6,35	-	-	2		7,63	7,87
8,7	-	-	1		5,75	5,75	-	-	1		5,87	5,87
8	-	-	1		5,02	5,02	-	-	1		5,51	5,51
11,75	10,955	0,414	10		6,21	7,22	6,673	0,331	10		7,11	8,59
8,88	8,808	0,076	5		5,48	5,91	5,632	0,190	5		5,63	5,94
8,15	7,990	0,156	5		4,93	5,23	5,040	0,113	5		5,21	5,51
14,38	13,121	0,562	21		7,52	9,51	8,398	0,504	21		9	10,79
13,75	12,992	0,595	10		7,94	9,24	8,494	0,484	10		8,58	10,73
12,93	-	-	3		7,75	8,15	-	-	3		9,04	10,18
11,47	11,022	0,498	9		6,52	7,76	7,190	0,415	9		7,29	8,58
17,43	16,759	0,550	14		9,63	11,68	10,481	0,531	14		10,87	12,7
13,47	12,949	0,293	7		8,37	9,32	8,881	0,363	7		8,37	9,12
11,5	10,804	0,478	7		6,47	7,88	7,186	0,438	7		6,72	7,82
12,26	11,316	0,567	16		6,2	7,44	6,820	0,380	16		7	8,3
9,04	8,489	0,339	8		5,18	6,06	5,580	0,314	8		5,17	5,78
8,28	7,593	0,375	8		4,55	5,49	4,918	0,336	8		4,46	5,08
13,05	-	-	3		7,39	7,84	-	-	3		8,13	8,46
9,75	-	-	2		6,49	6,67	-	-	2		5,73	6
8,55	-	-	2		5,74	5,78	-	-	2		5,16	5,38
13,54	12,884	0,631	5		7,39	8,27	7,888	0,373	5		8,13	8,95
9,75	-	-	3		6,31	6,67	-	-	3		5,73	6
8,79	-	-	3		5,74	5,97	-	-	3		5,16	5,48
15,44	-	-	2		8,61	9,19	-	-	2		10,05	10,5
10,31	-	-	1		7,07	7,07	-	-	1		6,95	6,95
16,14	15,558	0,673	5		8,61	10,04	9,396	0,533	5		10,05	11
11,29	-	-	3		7,07	7,55	-	-	3		6,95	7,46
10,48	-	-	2		6,65	6,65	-	-	2		6,48	6,6
19,11	16,170	1,624	10		8,02	12,02	9,746	1,148	10		9,45	12,77
11,68	-	-	3		7,41	8,15	-	-	3		7,11	7,21
10,71	9,946	0,810	5		5,39	7,12	6,536	0,702	5		5,59	6,49
15,12	14,256	0,556	8		8,13	9,57	8,778	0,564	8		8,83	9,94
10,32	-	-	4		6,61	7,35	-	-	4		6,34	6,86
9,62	-	-	4		6,1	6,48	-	-	4		5,38	5,93
19,11	15,532	1,341	38		8,02	12,02	9,427	0,901	38		8,83	12,77
11,68	10,769	0,605	16		6,44	8,15	7,339	0,531	16		6,27	7,45
10,88	9,945	0,651	17		5,39	7,76	6,555	0,542	17		5,38	6,92

20,42	18,445	1,580	6	9,66	11,75	10,763	0,726	6	10,93	14,02
13,14	-	-	3	7,59	8,42	-	-	3	7,46	8,76
12,65	-	-	3	6,78	8,31	-	-	3	6,8	7,8
20,73	17,854	1,345	10	9,75	12,31	10,836	0,723	10	10,68	13,7
13,46	11,898	0,894	5	7,37	11,41	8,582	1,698	5	7,43	8,47
12,13	10,996	0,656	5	6,43	7,76	7,142	0,492	5	6,82	7,46
20,93	18,342	1,725	34	9,2	12,47	10,969	0,868	34	10,14	15,56
13,68	12,122	1,060	16	6,8	11,41	8,211	1,091	16	6,85	8,9
12,65	11,336	0,917	14	6,43	8,35	7,451	0,678	14	6,24	7,8
16,76	-	-	2	10,29	10,95	-	-	2	10,04	10,49
11,44	-	-	1	7,94	7,94	-	-	1	7,22	7,22
10,41	-	-	1	7,18	7,18	-	-	1	6,16	6,16
16,76	-	-	2	10,29	10,95	-	-	2	10,04	10,49
11,44	-	-	1	7,94	7,94	-	-	1	7,22	7,22
10,41	-	-	1	7,18	7,18	-	-	1	6,16	6,16
11,68	-	-	2	6,76	7,52	-	-	2	7,16	7,6
8,13	-	-	1	5,41	5,41	-	-	1	5,38	5,38
7,41	-	-	1	4,83	4,83	-	-	1	4,82	4,82
8,32	-	-	1	5,44	5,44	-	-	1	5,25	5,25
7,73	-	-	1	4,85	4,85	-	-	1	4,93	4,93
11,94	10,602	0,848	11	5,5	7,52	6,427	0,653	11	6,07	8,07
8,32	7,663	0,540	7	4,32	5,44	4,959	0,470	7	4,47	5,74
7,73	7,022	0,518	5	4,15	4,85	4,468	0,343	5	4,16	4,93
9,49	8,761	0,546	16	4,8	5,92	5,329	0,357	16	4,79	6,44
7,47	6,936	0,341	8	4,12	5,06	4,494	0,345	8	3,75	4,87
6,79	6,403	0,298	8	3,4	4,3	3,999	0,313	8	3,67	4,46
8,43	7,868	0,407	6	4,53	5,69	5,017	0,422	6	4,83	5,35
6,83	-	-	3	4,05	4,31	-	-	3	3,83	4,04
6,28	-	-	3	3,6	3,96	-	-	3	3,56	3,88
9,77	8,282	0,710	40	4,33	6,14	5,142	0,420	40	4,08	6,44
7,47	6,617	0,457	20	3,9	5,06	4,374	0,325	20	3,62	4,87
6,79	6,162	0,386	19	3,4	4,44	3,932	0,297	19	3,47	4,46
7,45	-	-	4	4,31	4,58	-	-	4	4,59	5,26
5,76	-	-	2	3,69	3,74	-	-	2	3,34	3,41
5,62	-	-	2	3,36	3,46	-	-	2	3,18	3,63
6,26	6,023	0,153	6	3,48	3,82	3,637	0,136	6	3,94	4,25
4,77	-	-	3	3,11	3,23	-	-	3	2,92	2,97
4,31	-	-	3	2,77	2,95	-	-	3	2,62	2,67
7,45	6,500	0,655	14	3,27	4,58	3,900	0,459	14	3,8	5,26
5,76	5,051	0,531	7	2,86	3,82	3,374	0,372	7	2,79	3,74
5,62	4,661	0,585	7	2,64	3,46	3,044	0,332	7	2,62	3,63
7,69	-	-	2	4,38	4,71	-	-	2	5,13	5,18
5,94	-	-	1	3,72	3,72	-	-	1	3,69	3,69
5,51	-	-	1	3,54	3,54	-	-	1	3,39	3,39
6,72	-	-	4	3,63	4,19	-	-	4	4,11	4,31
5,01	-	-	1	3,05	3,05	-	-	1	3,01	3,01
4,86	-	-	2	2,92	3,33	-	-	2	2,91	3
7,69	6,827	0,623	6	3,63	4,71	4,088	0,425	6	4,11	5,18
5,94	-	-	2	3,05	3,72	-	-	2	3,01	3,69
5,51	-	-	3	2,92	3,54	-	-	3	2,91	3,39
5,67	-	-	2	3,37	3,64	-	-	2	3,61	3,68
4,35	-	-	1	3,05	3,05	-	-	1	2,72	2,72
4,08	-	-	1	2,68	2,68	-	-	1	2,54	2,54
5,23	5,085	0,110	6	2,9	3,11	3,013	0,073	6	3,36	4,01
3,95	-	-	3	2,44	2,62	-	-	3	2,43	2,57
3,68	-	-	3	2,15	2,31	-	-	3	2,33	2,46
5,67	5,169	0,220	12	2,9	3,64	3,148	0,215	12	3,18	4,01
4,35	3,983	0,202	6	2,44	3,05	2,680	0,206	6	2,33	2,72
4,08	3,680	0,206	6	2,15	2,68	2,340	0,185	6	2,18	2,54
6,21	5,878	0,210	28	3,48	4,14	3,804	0,181	28	3,64	4,12
4,38	4,043	0,140	13	2,33	2,93	2,695	0,180	13	2,45	2,84

4,34	3,841	0,197	13		2,38	2,82	2,579	0,120	13		2,1	2,92
5,96	4,817	0,644	12		2,71	3,95	3,042	0,394	12		2,67	3,83
4,85	3,605	0,740	6		1,96	2,64	2,192	0,237	6		2,01	2,6
3,88	3,090	0,420	6		1,84	2,61	2,030	0,296	6		1,76	2,25
6,21	5,502	0,653	49		2,69	4,14	3,541	0,451	49		2,67	4,12
4,85	3,849	0,479	24		1,96	2,93	2,510	0,319	24		1,78	2,84
4,34	3,555	0,471	24		1,84	2,82	2,373	0,324	24		1,76	2,92
13,29	12,301	0,463	35		7,39	9,14	8,040	0,416	35		7,34	8,4
8,9	8,390	0,277	18		5,2	6,08	5,648	0,276	18		4,72	5,35
8,43	7,875	0,260	18		5,04	6,05	5,418	0,235	18		4,23	4,93
10,46	9,889	0,283	28		6,11	7,05	6,555	0,263	28		5,53	6,9
7,19	6,872	0,205	13		4,27	6,16	4,796	0,446	13		3,89	4,55
6,58	6,278	0,238	12		4,07	4,66	4,393	0,183	12		3,37	4,61
13,29	11,229	1,270	63		6,11	9,14	7,380	0,823	63		5,53	8,4
8,9	7,753	0,800	31		4,27	6,16	5,291	0,553	31		3,89	5,35
8,43	7,236	0,833	30		4,07	6,05	5,008	0,553	30		3,37	4,93
18,81	-	-	2		10,77	10,78	-	-	2		13,82	13,96
13,91	-	-	1		8,6	8,6	-	-	1		9,82	9,82
13,05	-	-	1		8,09	8,09	-	-	1		8,99	8,99
18,98	17,257	1,296	36		8,26	12,22	10,547	0,929	36		10,92	13,96
14,15	12,878	0,910	18		6,91	9,68	8,252	0,698	18		8	9,82
13,35	12,290	0,803	18		6,71	8,87	7,914	0,573	18		7,05	8,99
9,83	-	-	3		5,9	6,54	-	-	3		6,11	6,8
7,04	-	-	1		4,79	4,79	-	-	1		4,54	4,54
6,71	-	-	1		4,55	4,55	-	-	1		4,39	4,39
9,83	9,180	0,535	11		5,38	6,54	6,000	0,341	11		5,76	6,8
7,34	6,826	0,422	5		4,19	4,79	4,544	0,249	5		4,54	5,06
6,73	6,382	0,426	5		3,83	4,55	4,250	0,277	5		4,07	4,53
9,27	-	-	2		6,06	6,16	-	-	2		5,92	6,07
7,15	-	-	1		4,94	4,94	-	-	1		4,67	4,67
6,42	-	-	1		4,19	4,19	-	-	1		4,09	4,09
9,27	8,401	0,496	12		4,84	6,16	5,619	0,388	12		5,24	6,07
7,15	6,358	0,479	5		3,92	4,94	4,396	0,436	5		3,82	4,67
6,42	5,856	0,343	5		3,65	4,19	3,948	0,215	5		3,5	4,09
10,84	9,792	0,964	6		4,76	6,34	5,737	0,599	6		5,69	7,42
7,71	-	-	3		4,13	4,9	-	-	3		4,23	5,17
7,4	-	-	3		3,68	4,31	-	-	3		3,97	4,77
10,72	9,319	0,601	12		5,14	6,02	5,526	0,268	12		5,8	7,32
7,53	6,955	0,303	6		4,24	4,96	4,465	0,272	6		4,31	5,18
6,49	-	-	4		3,54	3,97	-	-	4		3,87	4,8
10,84	9,616	0,747	28		4,76	6,72	5,663	0,451	28		5,69	7,42
7,71	7,115	0,436	14		4,05	4,96	4,520	0,314	14		4,23	5,18
7,4	6,584	0,523	12		3,54	4,55	4,012	0,328	12		3,87	4,96
10,44	9,688	0,463	11		5,36	6,65	5,980	0,399	11		6,09	6,86
7,55	7,217	0,282	6		4,48	5,42	4,855	0,335	6		4,43	5
6,84	6,525	0,278	6		3,99	4,36	4,130	0,148	6		3,93	4,39
10,8	9,298	0,664	12		5,32	6,63	5,748	0,375	12		5,8	7,03
7,93	6,925	0,514	6		4,12	5,3	4,525	0,415	6		4,22	4,84
7,25	6,343	0,478	6		3,75	4,66	4,013	0,345	6		3,88	4,47
11,06	9,555	0,654	103		4,6	6,87	5,874	0,460	103		4,75	7,1
7,93	7,067	0,424	52		3,73	5,42	4,598	0,352	52		3,81	5,9
7,28	6,393	0,404	52		3,32	4,66	4,058	0,301	52		3,53	4,58
12,74	-	-	2		6,93	7,38	-	-	2		8	8,38
8,56	-	-	1		5,28	5,28	-	-	1		5,73	5,73
8,09	-	-	1		5,1	5,1	-	-	1		5,36	5,36
12,74	11,638	0,719	6		6,13	7,38	6,853	0,442	6		7,42	8,38
8,56	-	-	3		4,91	5,47	-	-	3		5,34	5,73
8,09	-	-	3		4,45	5,1	-	-	3		4,8	5,36

ey. *International Journal of Osteoarchaeology.*

ach ungual phalanx are given separately for each sex (if known) and jointly for all
d specimens; it differs when the phalanges of two or more different digits (i.e., digits 1-

f cotyla articularis				Articular width					
MEAN	SD	N		Min	Max	MEAN	SD	N	
-	-	3		5,11	5,94	-	-	3	
9,164	0,908	27		4,59	5,94	5,033	0,317	27	
-	-	2		3,74	3,97	-	-	2	
-	-	1		3,53	3,53	-	-	1	
-	-	1		3,3	3,3	-	-	1	
-	-	1		4,42	4,42	-	-	1	
-	-	1		3,91	3,91	-	-	1	
4,782	0,241	17		3,14	4,42	3,577	0,357	17	
4,449	0,283	9		3,41	3,91	3,687	0,163	9	
3,951	0,238	8		2,44	3,36	2,744	0,302	8	
11,443	0,456	12		8,08	10,38	9,287	0,635	12	
8,324	0,666	5		6,32	7,59	6,926	0,504	5	
7,445	0,221	6		5,22	6,45	5,715	0,430	6	
7,355	0,310	14		5,92	6,72	6,340	0,258	14	
5,400	0,236	6		4,77	5,29	5,052	0,221	6	
-	-	4		3,33	3,61	-	-	4	
-	-	2		6,34	6,64	-	-	2	
-	-	1		5,99	5,99	-	-	1	
-	-	1		4,65	4,65	-	-	1	
7,699	0,404	10		6,2	6,68	6,473	0,153	10	
5,804	0,132	5		5,6	5,99	5,768	0,154	5	
5,398	0,121	5		4,32	4,69	4,550	0,172	5	
9,914	0,541	21		7,4	8,31	7,899	0,261	21	
9,606	0,639	10		7,15	8,32	7,865	0,358	10	
-	-	3		7,21	7,53	-	-	3	
8,037	0,426	9		5,42	6,46	6,060	0,339	9	
11,849	0,523	14		9,07	10,88	10,122	0,556	14	
8,683	0,246	7		8,24	9,51	8,997	0,467	7	
7,129	0,421	7		5,74	6,91	6,380	0,462	7	
7,585	0,372	16		5,26	6,36	5,836	0,345	16	
5,373	0,203	8		4,56	5,23	5,004	0,249	8	
4,691	0,189	8		3,68	4,24	4,010	0,187	8	
-	-	3		6,15	6,26	-	-	3	
-	-	2		5,31	6,04	-	-	2	
-	-	2		4,32	4,68	-	-	2	
8,576	0,345	5		6,15	7,1	6,550	0,486	5	
-	-	3		5,31	6,04	-	-	3	
-	-	3		4,32	5	-	-	3	
-	-	2		8,41	8,73	-	-	2	
-	-	1		6,87	6,87	-	-	1	
10,550	0,379	5		7,57	8,95	8,352	0,543	5	
-	-	3		6,53	7,15	-	-	3	
-	-	2		4,73	5,68	-	-	2	
10,540	0,964	10		7,43	10,25	8,560	0,868	10	
-	-	3		6,75	7,29	-	-	3	
6,104	0,384	5		4,95	5,94	5,512	0,398	5	
9,249	0,339	8		7,04	8	7,623	0,312	8	
-	-	4		6,01	6,57	-	-	4	
-	-	4		4,69	5,22	-	-	4	
10,264	0,853	38		7,04	10,25	8,310	0,709	37	
6,946	0,399	16		6,01	7,4	6,706	0,418	16	
6,162	0,416	17		4,69	5,97	5,398	0,395	17	

12,722	1,101	6		8,5	11,43	10,130	1,073	6	
-	-	3		6,85	8,18	-	-	3	
-	-	3		5,77	6,93	-	-	3	
11,933	0,828	10		9,07	10,67	9,742	0,554	10	
7,850	0,407	5		6,62	7,77	7,202	0,425	5	
7,030	0,272	5		5,71	6,73	6,148	0,375	5	
12,436	1,273	34		8,09	11,93	10,009	0,996	34	
8,068	0,636	16		6,54	8,18	7,399	0,610	16	
7,195	0,471	14		5,6	6,98	6,327	0,524	14	
-	-	2		8,04	8,45	-	-	2	
-	-	1		6,24	6,24	-	-	1	
-	-	1		5,28	5,28	-	-	1	
-	-	2		8,04	8,45	-	-	2	
-	-	1		6,24	6,24	-	-	1	
-	-	1		5,28	5,28	-	-	1	
-	-	2		5,76	6,36	-	-	2	
-	-	1		4,91	4,91	-	-	1	
-	-	1		4,43	4,43	-	-	1	
-	-	1		4,59	4,59	-	-	1	
-	-	1		4,08	4,08	-	-	1	
7,065	0,604	11		4,83	6,36	5,461	0,542	11	
5,149	0,411	7		3,98	4,91	4,401	0,330	7	
4,596	0,302	5		3,44	4,43	3,894	0,379	5	
5,818	0,436	16		3,81	5,01	4,375	0,360	16	
4,365	0,321	8		3,41	4,12	3,841	0,244	8	
4,080	0,270	8		2,93	3,56	3,278	0,176	8	
5,175	0,189	6		3,72	4,28	4,018	0,194	6	
-	-	3		3,36	3,71	-	-	3	
-	-	3		2,93	3,2	-	-	3	
5,441	0,508	40		3,65	5,01	4,206	0,348	40	
4,082	0,346	20		3,26	4,12	3,674	0,275	20	
3,862	0,293	19		2,93	3,56	3,179	0,186	19	
-	-	4		3,63	4	-	-	4	
-	-	2		3,26	3,38	-	-	2	
-	-	2		2,72	2,85	-	-	2	
4,102	0,115	6		2,89	3,35	3,097	0,171	6	
-	-	3		2,56	2,69	-	-	3	
-	-	3		2,26	2,31	-	-	3	
4,400	0,469	14		2,89	4	3,353	0,391	14	
3,159	0,344	7		2,53	3,38	2,880	0,354	7	
2,947	0,398	7		2,16	2,85	2,464	0,276	7	
-	-	2		3,72	4	-	-	2	
-	-	1		3,33	3,33	-	-	1	
-	-	1		2,95	2,95	-	-	1	
-	-	4		3	3,4	-	-	4	
-	-	1		2,65	2,65	-	-	1	
-	-	2		2,3	2,48	-	-	2	
4,525	0,492	6		3	4	3,408	0,383	6	
-	-	2		2,65	3,33	-	-	2	
-	-	3		2,3	2,95	-	-	3	
-	-	2		2,94	3,32	-	-	2	
-	-	1		2,75	2,75	-	-	1	
-	-	1		2,33	2,33	-	-	1	
3,510	0,248	6		2,51	2,59	2,560	0,028	6	
-	-	3		2,33	2,41	-	-	3	
-	-	3		1,85	2,02	-	-	3	
3,497	0,212	12		2,26	3,32	2,632	0,276	12	
2,515	0,132	6		2,14	2,75	2,392	0,199	6	
2,358	0,130	6		1,79	2,33	1,997	0,188	6	
3,839	0,143	28		2,55	3,02	2,795	0,132	28	
2,625	0,122	13		1,97	2,34	2,169	0,118	13	

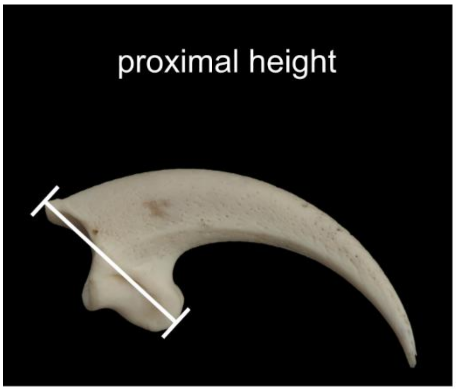
2,419	0,214	13	1,63	2,25	1,813	0,155	13
3,126	0,354	12	1,9	2,85	2,219	0,324	12
2,223	0,208	6	1,5	2,19	1,795	0,283	6
2,015	0,190	6	1,25	1,76	1,427	0,195	6
3,581	0,427	49	1,9	3,02	2,588	0,357	49
2,460	0,293	24	1,46	2,34	2,026	0,272	24
2,260	0,290	24	1,23	2,25	1,668	0,253	24
7,818	0,293	35	5,63	7,18	6,453	0,389	35
5,064	0,185	18	4,5	5,23	4,848	0,178	18
4,508	0,204	18	3,63	4,26	3,953	0,175	18
6,265	0,328	28	4,6	5,63	5,066	0,299	28
4,170	0,179	13	3,61	4,08	3,842	0,130	13
3,798	0,336	12	3	3,42	3,163	0,134	12
7,128	0,836	63	4,6	7,18	5,837	0,777	63
4,689	0,483	31	3,61	5,23	4,426	0,529	31
4,224	0,439	30	3	4,26	3,637	0,424	30
-	-	2	9,81	9,97	-	-	2
-	-	1	7,7	7,7	-	-	1
-	-	1	6,51	6,51	-	-	1
12,639	0,889	36	8,25	10,21	9,430	0,590	36
8,967	0,572	18	6,5	7,95	7,352	0,405	18
8,371	0,554	18	5,66	6,63	6,259	0,311	18
-	-	3	4,96	5,55	-	-	3
-	-	1	3,64	3,64	-	-	1
-	-	1	2,99	2,99	-	-	1
6,314	0,316	11	4,36	5,55	4,927	0,348	11
4,714	0,221	5	3,43	3,99	3,740	0,227	5
4,296	0,205	5	2,94	3,26	3,088	0,147	5
-	-	2	4,54	4,54	-	-	2
-	-	1	3,71	3,71	-	-	1
-	-	1	3,06	3,06	-	-	1
5,667	0,296	12	3,87	5,05	4,475	0,306	12
4,216	0,309	5	3,23	3,71	3,464	0,172	5
3,830	0,237	5	2,72	3,06	2,880	0,133	5
6,723	0,712	6	4,28	5,52	5,033	0,467	6
-	-	3	3,44	4,33	-	-	3
-	-	3	2,86	3,43	-	-	3
6,332	0,441	12	4,69	5,61	5,051	0,270	12
4,618	0,296	6	3,8	4,56	4,015	0,290	6
4,290	0,349	5	2,84	3,62	3,162	0,288	5
6,548	0,523	28	4,28	5,78	5,117	0,364	28
4,716	0,315	14	3,44	4,62	4,060	0,346	14
4,452	0,341	13	2,84	3,62	3,227	0,252	13
6,441	0,259	11	4,7	5,54	5,130	0,283	11
4,710	0,241	6	3,97	4,56	4,178	0,220	6
4,188	0,186	6	3,19	3,55	3,320	0,124	6
6,208	0,356	12	4,52	5,84	4,983	0,349	12
4,432	0,218	6	3,72	4,26	3,937	0,229	6
4,135	0,266	6	2,95	3,56	3,183	0,221	6
6,387	0,418	103	3,75	6	5,130	0,455	103
4,622	0,333	52	3,15	4,64	4,033	0,310	52
4,203	0,239	52	2,36	3,58	3,227	0,264	52
-	-	2	6,26	6,93	-	-	2
-	-	1	5,08	5,08	-	-	1
-	-	1	4,2	4,2	-	-	1
7,905	0,333	6	5,28	6,93	6,277	0,642	6
-	-	3	4,41	5,11	-	-	3
-	-	3	3,55	4,26	-	-	3

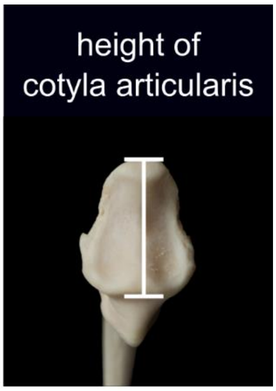
Appendix S1

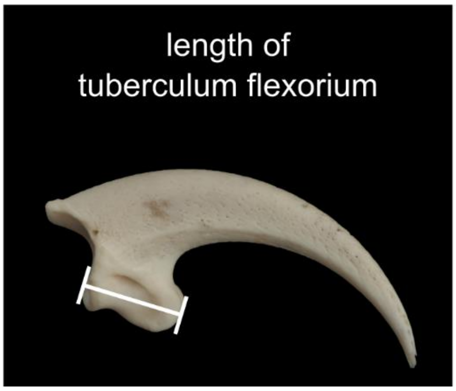
for: Bochenski Z.M., Tomek T., Wertz K. Whose talon is this? A manual for the identification of ungual phalanges of European accipitrid birds of prey. *International Journal of Osteoarchaeology*.

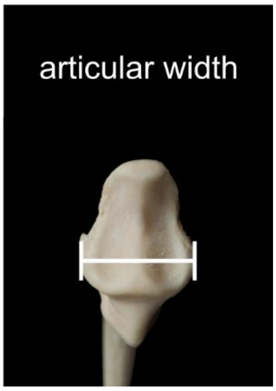
Illustrations refer to key steps that use species division into groups of varying size.

1. Measurements used in Appendix S1

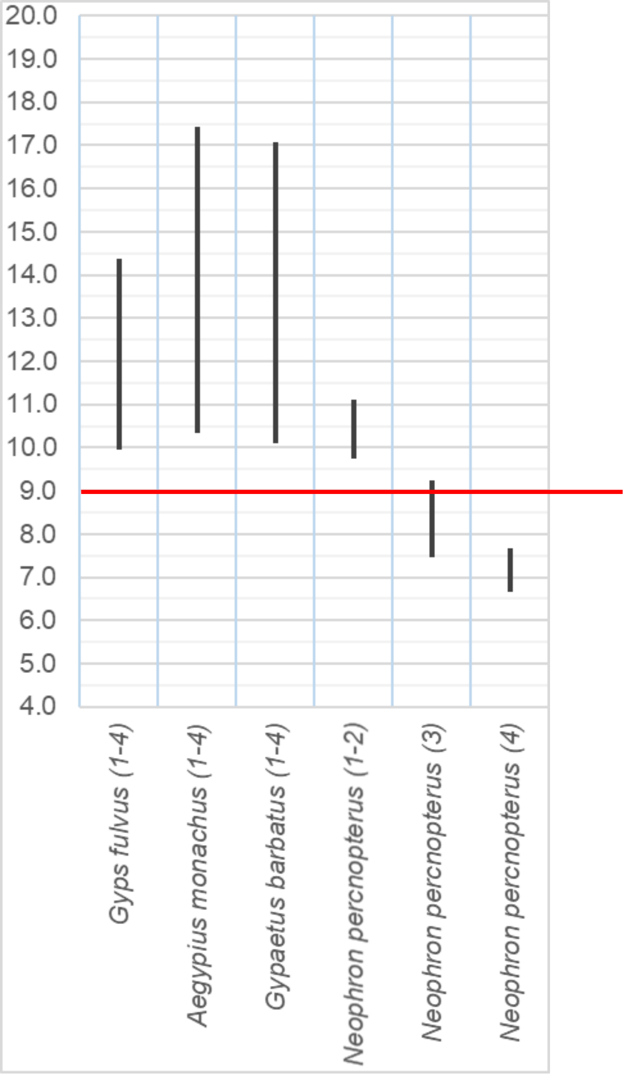








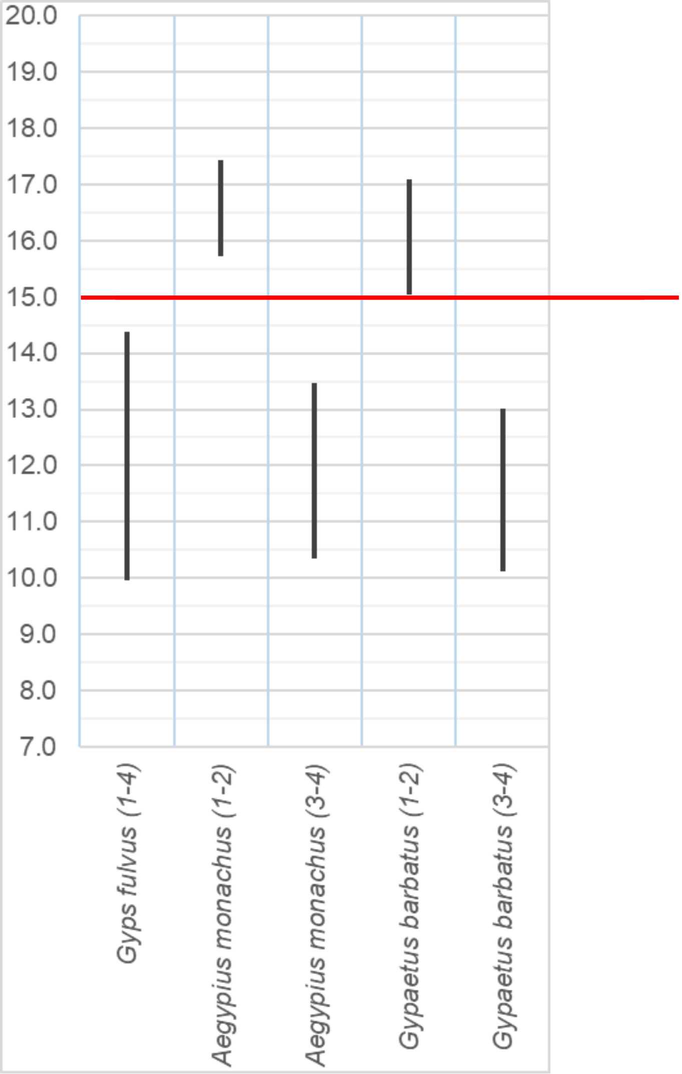
2. Information for manual, step #2



Vultures (digit numbers in parentheses), proximal height. The range of measurements and the number of measured bird specimens are presented in the table below. The red line indicates the value used to divide the taxa by size.

Taxon	Min	Max	N
Gyps fulvus (1-4)	10.0	14.4	12
Aegypius monachus (1-4)	10.3	17.4	7
Gypaetus barbatus (1-4)	10.1	17.1	6
Neophron percnopterus (1-2)	9.7	11.1	7
Neophron percnopterus (3)	7.5	9.2	6
Neophron percnopterus (4)	6.7	7.7	4

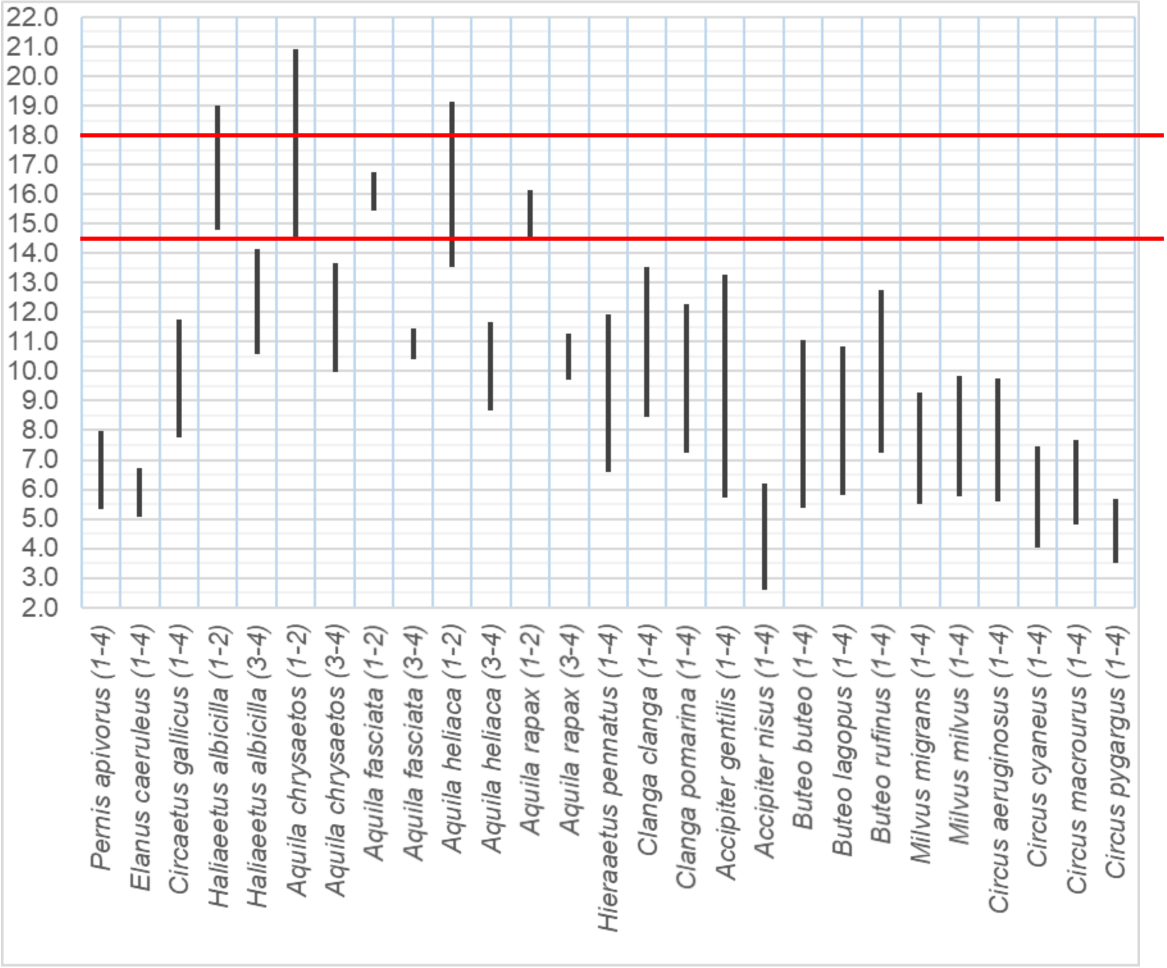
3. Information for manual, step #5



Vultures (digit numbers in parentheses), proximal height. The range of measurements and the number of measured bird specimens are presented in the table below. The red line indicates the value used to divide the taxa by size.

Taxon	Min	Max	N
Gyps fulvus (1-4)	10.0	14.4	12
Aegypius monachus (1-2)	15.7	17.4	7
Aegypius monachus (3-4)	10.3	13.5	7
Gypaetus barbatus (1-2)	15.1	17.1	6
Gypaetus barbatus (3-4)	10.1	13.0	6

4. Information for manual, step #15

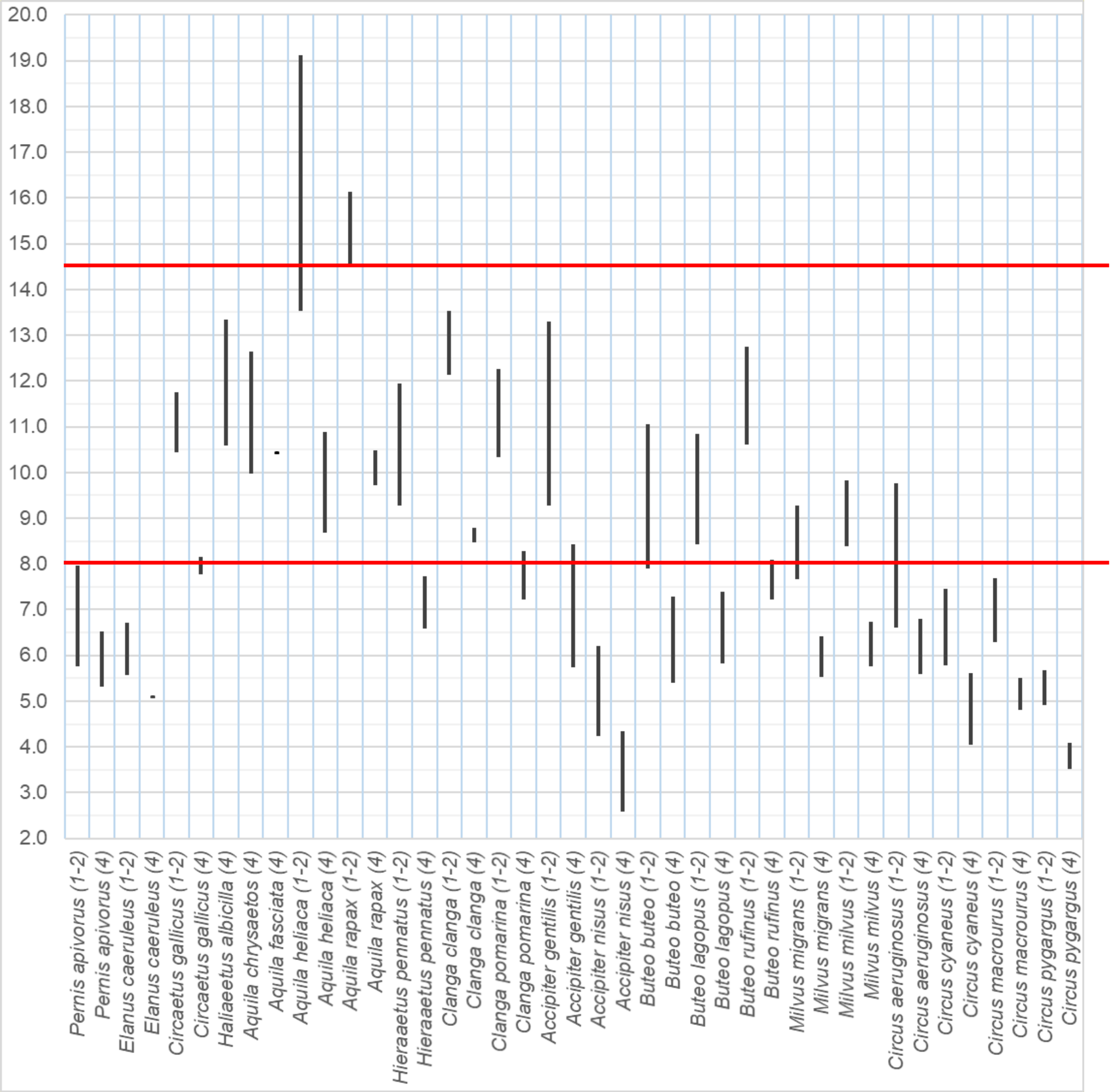


Accipitridae (digit numbers in parentheses), proximal height. The range of measurements and the number of measured bird specimens are presented in the table below. The red lines indicate the values used to divide the taxa by size.

Taxon	Min	Max	N
Pernis apivorus (1-4)	5.3	8.0	9
Elanus caeruleus (1-4)	5.1	6.7	1
Circaetus gallicus (1-4)	7.8	11.8	5
Haliaeetus albicilla (1-2)	14.8	19.0	18
Haliaeetus albicilla (3-4)	10.6	14.2	19
Aquila chrysaetos (1-2)	14.6	20.9	18
Aquila chrysaetos (3-4)	10.0	13.7	16
Aquila fasciata (1-2)	15.5	16.8	1
Aquila fasciata (3-4)	10.4	11.4	1
Aquila heliaca (1-2)	13.5	19.1	19
Aquila heliaca (3-4)	8.7	11.7	19
Aquila rapax (1-2)	14.5	16.1	3
Aquila rapax (3-4)	9.7	11.3	3

Taxon	Min	Max	N
Hieraaetus pennatus (1-4)	6.6	11.9	7
Clanga clanga (1-4)	8.5	13.5	3
Clanga pomarina (1-4)	7.2	12.3	8
Accipiter gentilis (1-4)	5.7	13.3	32
Accipiter nisus (1-4)	2.6	6.2	25
Buteo buteo (1-4)	5.4	11.1	52
Buteo lagopus (1-4)	5.8	10.8	14
Buteo rufinus (1-4)	7.2	12.7	3
Milvus migrans (1-4)	5.5	9.3	6
Milvus milvus (1-4)	5.8	9.8	6
Circus aeruginosus (1-4)	5.6	9.8	20
Circus cyaneus (1-4)	4.0	7.5	7
Circus macrourus (1-4)	4.8	7.7	3
Circus pygargus (1-4)	3.5	5.7	6

5. Information for manual, step #21

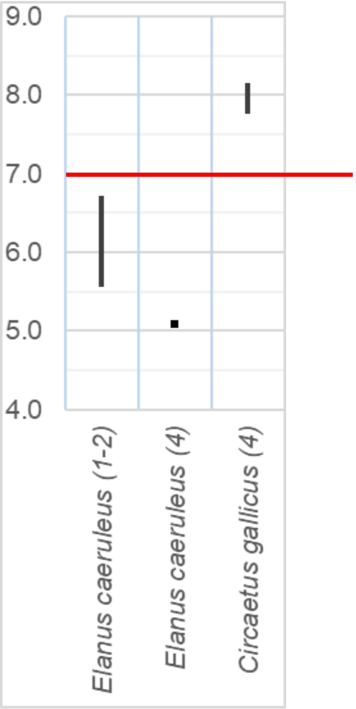


Accipitridae (digit numbers in parentheses), proximal height. The range of measurements and the number of measured bird specimens are presented in the table below. The red lines indicate the values used to divide the taxa by size.

Taxon	Min	Max	N
Pernis apivorus (1-2)	5.8	8.0	9
Pernis apivorus (4)	5.3	6.5	8
Elanus caeruleus (1-2)	5.6	6.7	1
Elanus caeruleus (4)	5.1	5.1	1
Circaetus gallicus (1-2)	10.4	11.8	5
Circaetus gallicus (4)	7.8	8.2	5
Haliaeetus albicilla (4)	10.6	13.4	18
Aquila chrysaetos (4)	10.0	12.7	14

Taxon	Min	Max	N
Aquila fasciata (4)	10.4	10.4	1
Aquila heliaca (1-2)	13.5	19.1	19
Aquila heliaca (4)	8.7	10.9	17
Aquila rapax (1-2)	14.5	16.1	3
Aquila rapax (4)	9.7	10.5	2
Hieraaetus pennatus (1-2)	9.3	11.9	6
Hieraaetus pennatus (4)	6.6	7.7	5
Clanga clanga (1-2)	12.1	13.5	3
Clanga clanga (4)	8.5	8.8	3
Clanga pomarina (1-2)	10.3	12.3	8
Clanga pomarina (4)	7.2	8.3	8
Accipiter gentilis (1-2)	9.3	13.3	32
Accipiter gentilis (4)	5.7	8.4	30
Accipiter nisus (1-2)	4.2	6.2	25
Accipiter nisus (4)	2.6	4.3	24
Buteo buteo (1-2)	7.9	11.1	52
Buteo buteo (4)	5.4	7.3	52
Buteo lagopus (1-2)	8.4	10.8	14
Buteo lagopus (4)	5.8	7.4	13
Buteo rufinus (1-2)	10.6	12.7	3
Buteo rufinus (4)	7.2	8.1	3
Milvus migrans (1-2)	7.7	9.3	6
Milvus migrans (4)	5.5	6.4	5
Milvus milvus (1-2)	8.4	9.8	6
Milvus milvus (4)	5.8	6.7	5
Circus aeruginosus (1-2)	6.6	9.8	20
Circus aeruginosus (4)	5.6	6.8	19
Circus cyaneus (1-2)	5.8	7.5	7
Circus cyaneus (4)	4.0	5.6	7
Circus macrourus (1-2)	6.3	7.7	3
Circus macrourus (4)	4.8	5.5	3
Circus pygargus (1-2)	4.9	5.7	6
Circus pygargus (4)	3.5	4.1	6

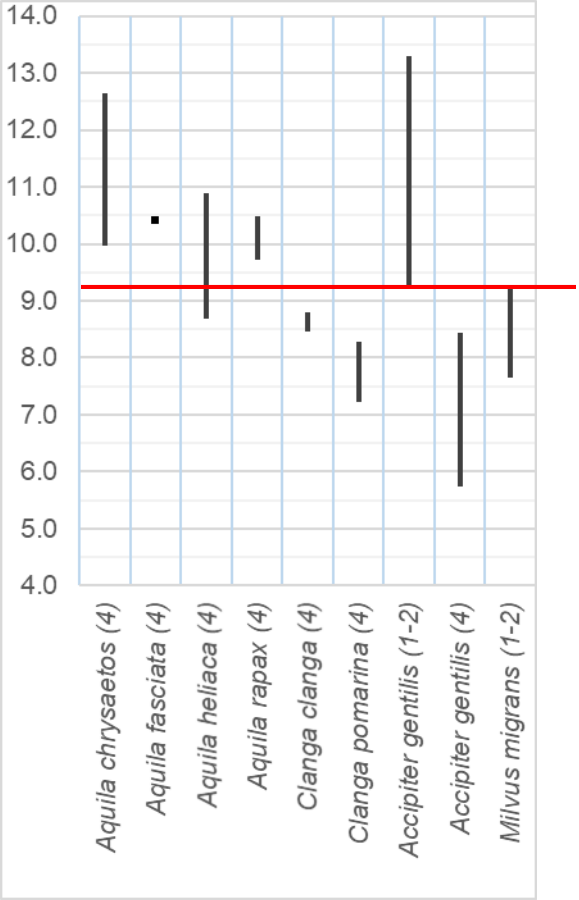
6. Information for manual, step #23



Accipitridae (digit numbers in parentheses), proximal height. The range of measurements and the number of measured bird specimens are presented in the table below. The red line indicates the values used to divide the taxa by size.

Taxon	Min	Max	N
Elanus caeruleus (1-2)	5.6	6.7	1
Elanus caeruleus (4)	5.1	5.1	1
Circaetus gallicus (4)	7.8	8.2	5

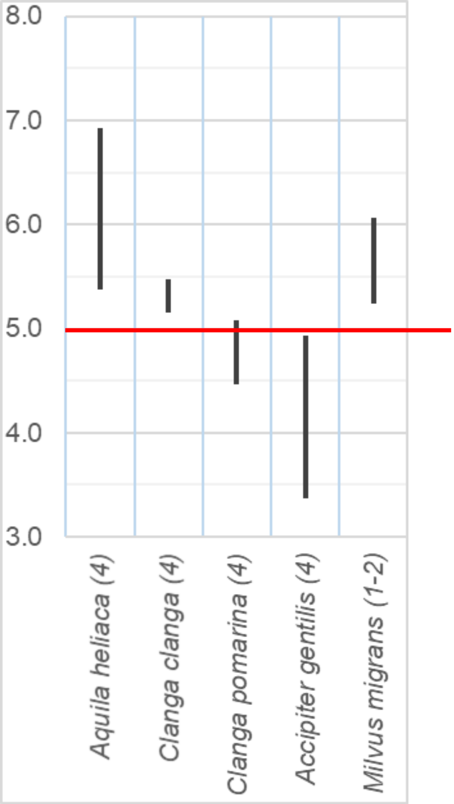
7. Information for manual, step #26



Accipitridae (digit numbers in parentheses), proximal height. The range of measurements and the number of measured bird specimens are presented in the table below. The red line indicates the values used to divide the taxa by size.

Taxon	Min	Max	N
Aquila chrysaetos (4)	10.0	12.7	14
Aquila fasciata (4)	10.4	10.4	1
Aquila heliaca (4)	8.7	10.9	17
Aquila rapax (4)	9.7	10.5	2
Clanga clanga (4)	8.5	8.8	3
Clanga pomarina (4)	7.2	8.3	8
Accipiter gentilis (1-2)	9.3	13.3	32
Accipiter gentilis (4)	5.7	8.4	30
Milvus migrans (1-2)	7.7	9.3	6

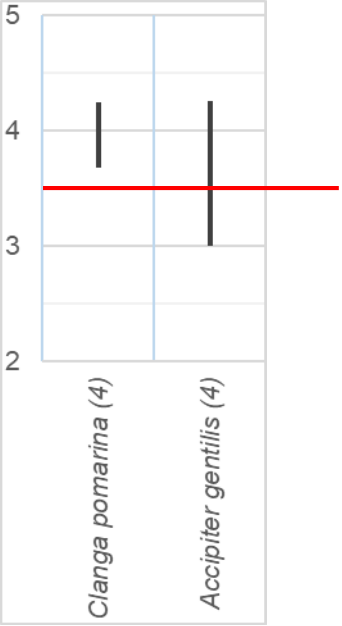
8. Information for manual, step #30



Accipitridae (digit numbers in parentheses), height of cotyla articularis. The range of measurements and the number of measured bird specimens are presented in the table below. The red line indicates the values used to divide the taxa by size.

Taxon	Min	Max	N
Aquila heliaca (4)	5.4	6.9	17
Clanga clanga (4)	5.2	5.5	3
Clanga pomarina (4)	4.5	5.1	8
Accipiter gentilis (4)	3.4	4.9	30
Milvus migrans (1-2)	5.2	6.1	6

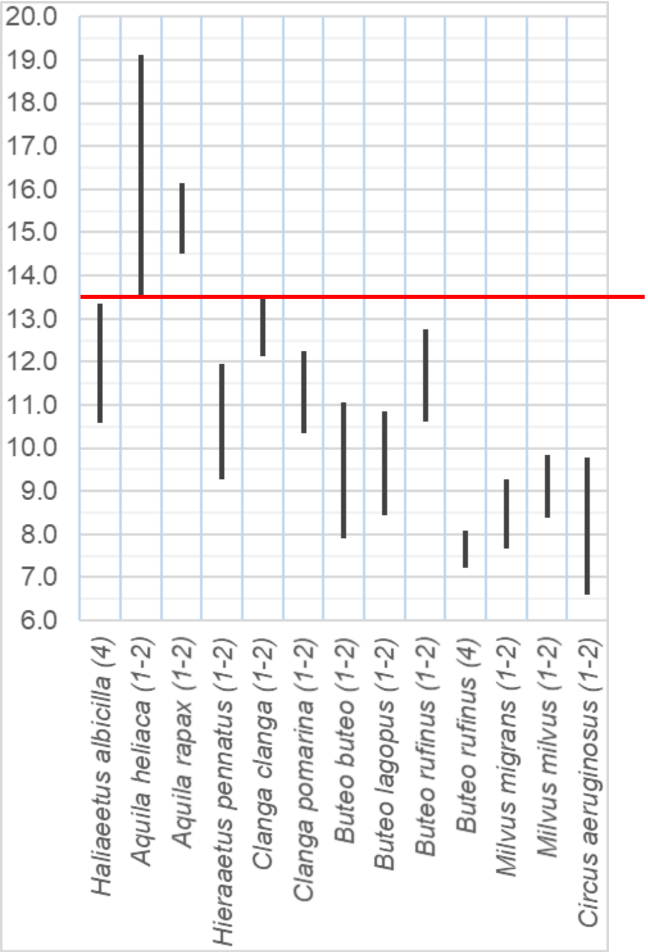
9. Information for manual, step #31



Accipitridae (digit numbers in parentheses), articular width. The range of measurements and the number of measured bird specimens are presented in the table below. The red line indicates the values used to divide the taxa by size.

Taxon	Min	Max	N
Clanga pomarina (4)	3.7	4.2	8
Accipiter gentilis (4)	3.0	4.3	30

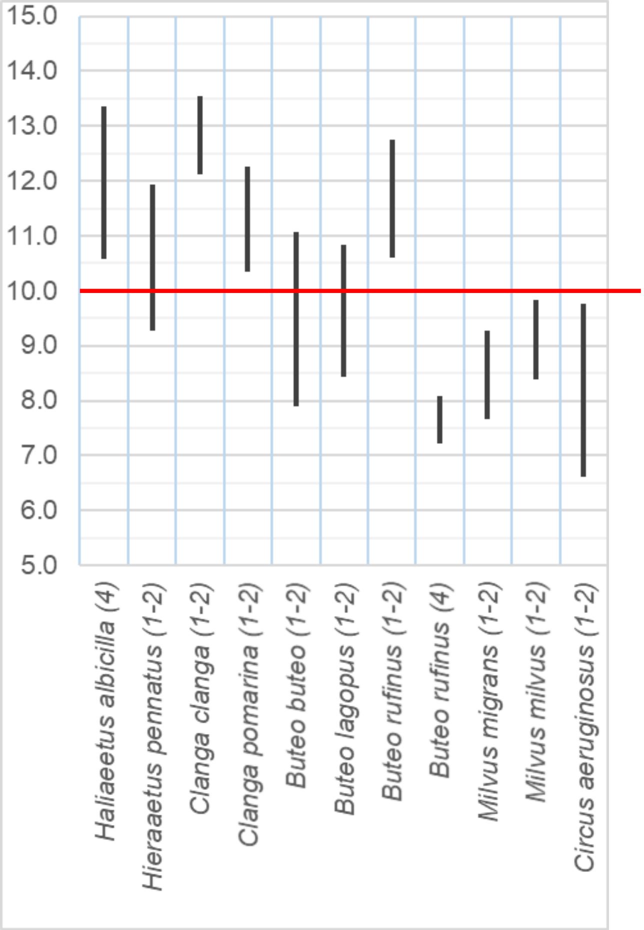
10. Information for manual, step #34



Accipitridae (digit numbers in parentheses), proximal height. The range of measurements and the number of measured bird specimens are presented in the table below. The red line indicates the values used to divide the taxa by size.

Taxon	Min	Max	N
Haliaeetus albicilla (4)	10.6	13.4	18
Aquila heliaca (1-2)	13.5	19.1	19
Aquila rapax (1-2)	14.5	16.1	3
Hieraaetus pennatus (1-2)	9.3	11.9	6
Clanga clanga (1-2)	12.1	13.5	3
Clanga pomarina (1-2)	10.3	12.3	8
Buteo buteo (1-2)	7.9	11.1	52
Buteo lagopus (1-2)	8.4	10.8	14
Buteo rufinus (1-2)	10.6	12.7	3
Buteo rufinus (4)	7.2	8.1	3
Milvus migrans (1-2)	7.7	9.3	6
Milvus milvus (1-2)	8.4	9.8	6
Circus aeruginosus (1-2)	6.6	9.8	20

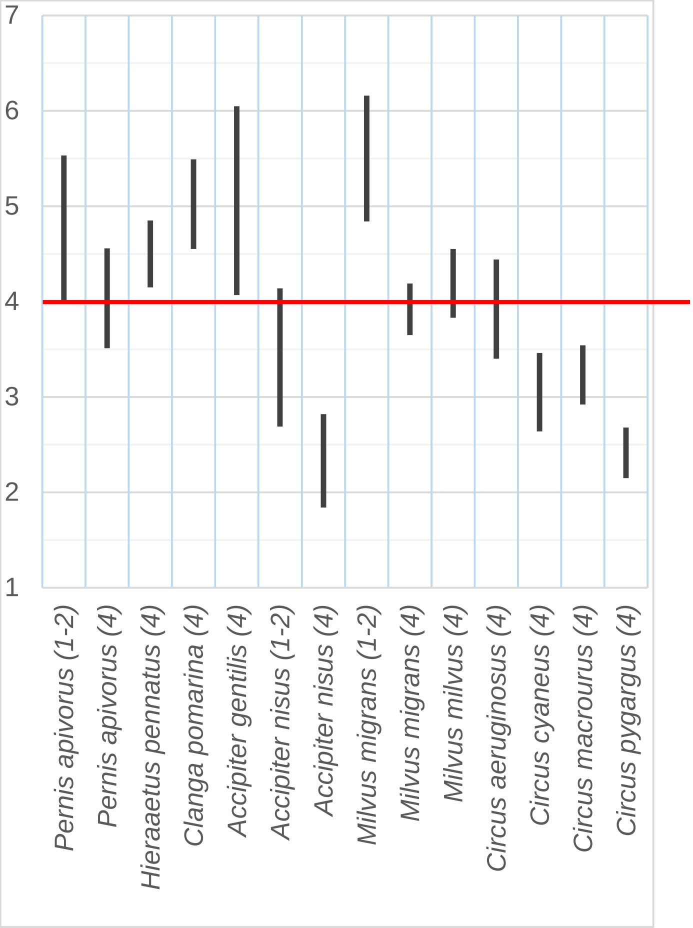
11. Information for manual, step #35



Accipitridae (digit numbers in parentheses), proximal height. The range of measurements and the number of measured bird specimens are presented in the table below. The red line indicates the values used to divide the taxa by size.

Taxon	Min	Max	N
Haliaeetus albicilla (4)	10.6	13.4	18
Hieraaetus pennatus (1-2)	9.3	11.9	6
Clanga clanga (1-2)	12.1	13.5	3
Clanga pomarina (1-2)	10.3	12.3	8
Buteo buteo (1-2)	7.9	11.1	52
Buteo lagopus (1-2)	8.4	10.8	14
Buteo rufinus (1-2)	10.6	12.7	3
Buteo rufinus (4)	7.2	8.1	3
Milvus migrans (1-2)	7.7	9.3	6
Milvus milvus (1-2)	8.4	9.8	6
Circus aeruginosus (1-2)	6.6	9.8	20

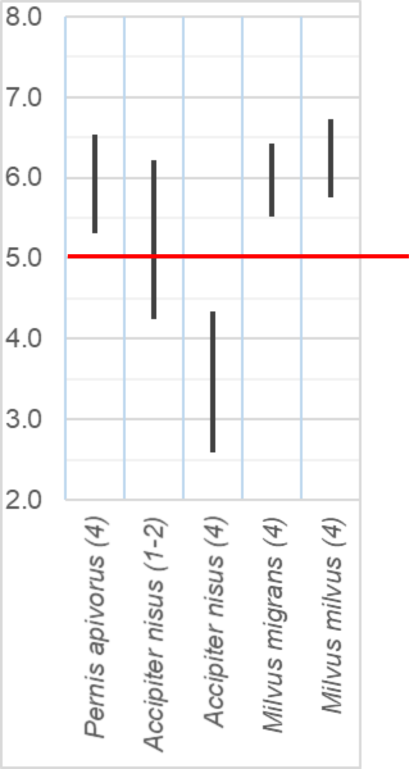
12. Information for manual, step #42



Accipitridae (digit numbers in parentheses), length of tuberculum flexorium. The range of measurements and the number of measured bird specimens are presented in the table below. The red line indicates the value used to divide the taxa by size.

Taxon	Min	Max	N
Pernis apivorus (1-2)	4.0	5.5	9
Pernis apivorus (4)	3.5	4.6	8
Hieraaetus pennatus (4)	4.2	4.9	5
Clanga pomarina (4)	4.6	5.5	8
Accipiter gentilis (4)	4.1	6.1	30
Accipiter nisus (1-2)	2.7	4.1	25
Accipiter nisus (4)	1.8	2.8	24
Milvus migrans (1-2)	4.8	6.2	6
Milvus migrans (4)	3.7	4.2	5
Milvus milvus (4)	3.8	4.6	5
Circus aeruginosus (4)	3.4	4.4	19
Circus cyaneus (4)	2.6	3.5	7
Circus macrourus (4)	2.9	3.5	3
Circus pygargus (4)	2.2	2.7	6

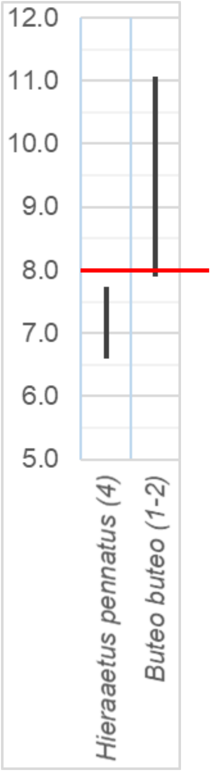
13. Information for manual, step #48



Accipitridae (digit numbers in parentheses), proximal height. The range of measurements and the number of measured bird specimens are presented in the table below. The red line indicates the value used to divide the taxa by size.

Taxon	Min	Max	N
Pernis apivorus (4)	5.3	6.5	8
Accipiter nisus (1-2)	4.2	6.2	25
Accipiter nisus (4)	2.6	4.3	24
Milvus migrans (4)	5.5	6.4	5
Milvus milvus (4)	5.8	6.7	5

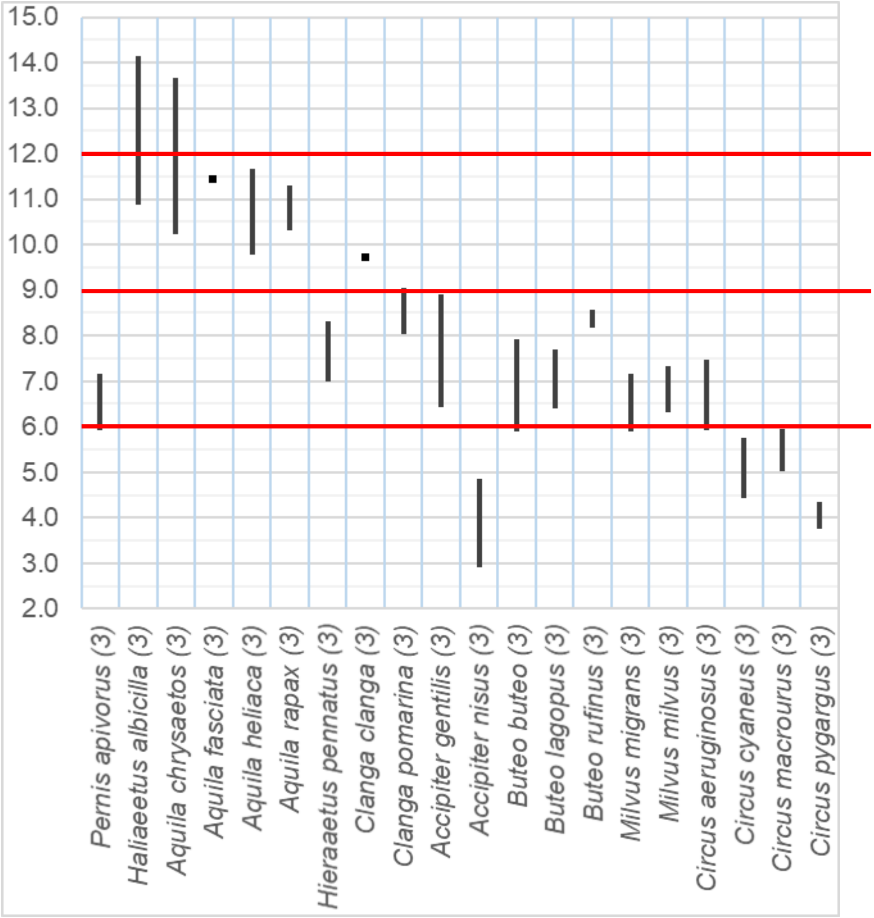
14. Information for manual, step #55



Accipitridae (digit numbers in parentheses), proximal height. The range of measurements and the number of measured bird specimens are presented in the table below. The red line indicates the value used to divide the taxa by size.

Taxon	Min	Max	N
Hieraaetus pennatus (4)	6.6	7.7	5
Buteo buteo (1-2)	7.9	11.1	52

15. Information for manual, step #61



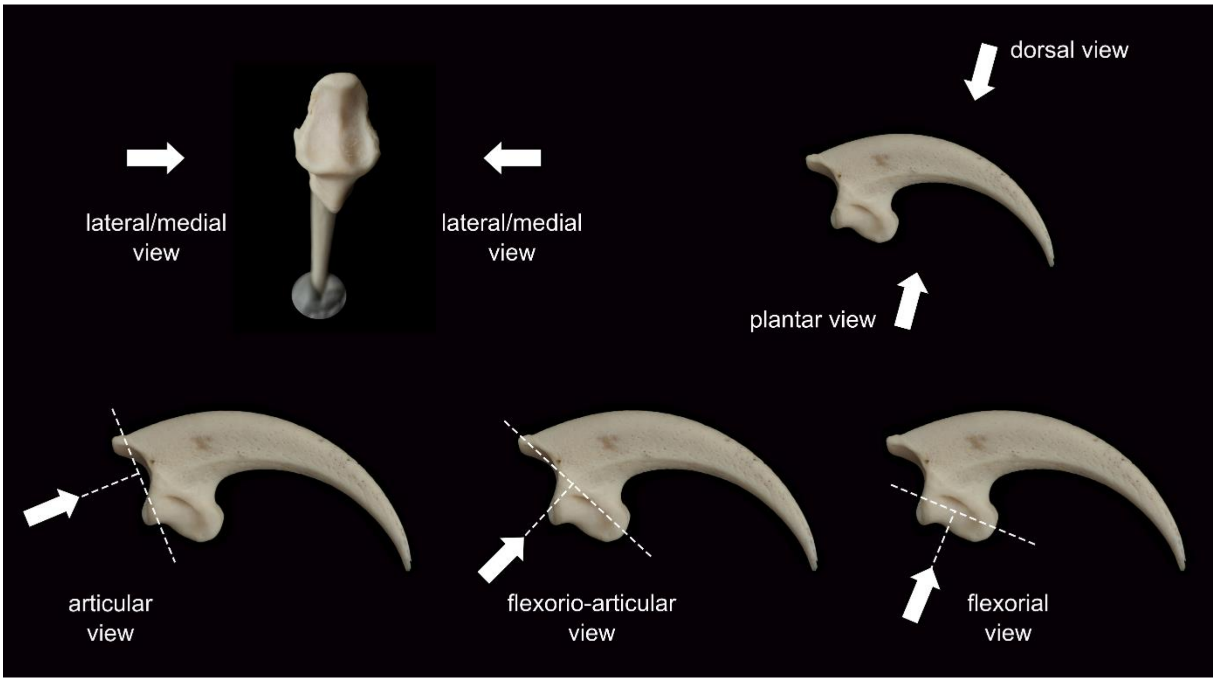
Accipitridae (digit numbers in parentheses), proximal height. The range of measurements and the number of measured bird specimens are presented in the table below. The red lines indicate the values used to divide the taxa by size.

Taxon	Min	Max	N)
Pernis apivorus (3)	5.9	7.2	9
Haliaeetus albicilla (3)	10.9	14.2	18
Aquila chrysaetos (3)	10.2	13.7	16
Aquila fasciata (3)	11.4	11.4	1
Aquila heliaca (3)	9.8	11.7	16
Aquila rapax (3)	10.3	11.3	3
Hieraaetus pennatus (3)	7.0	8.3	7
Clanga clanga (3)	9.7	9.8	3
Clanga pomarina (3)	8.0	9.0	8
Accipiter gentilis (3)	6.4	8.9	31
Accipiter nisus (3)	2.9	4.9	24
Buteo buteo (3)	5.9	7.9	52
Buteo lagopus (3)	6.4	7.7	14
Buteo rufinus (3)	8.2	8.6	3
Milvus migrans (3)	5.9	7.2	5

Taxon	Min	Max	N)
Milvus milvus (3)	6.3	7.3	5
Circus aeruginosus (3)	5.9	7.5	20
Circus cyaneus (3)	4.4	5.8	7
Circus macrourus (3)	5.0	5.9	2
Circus pygargus (3)	3.8	4.4	6

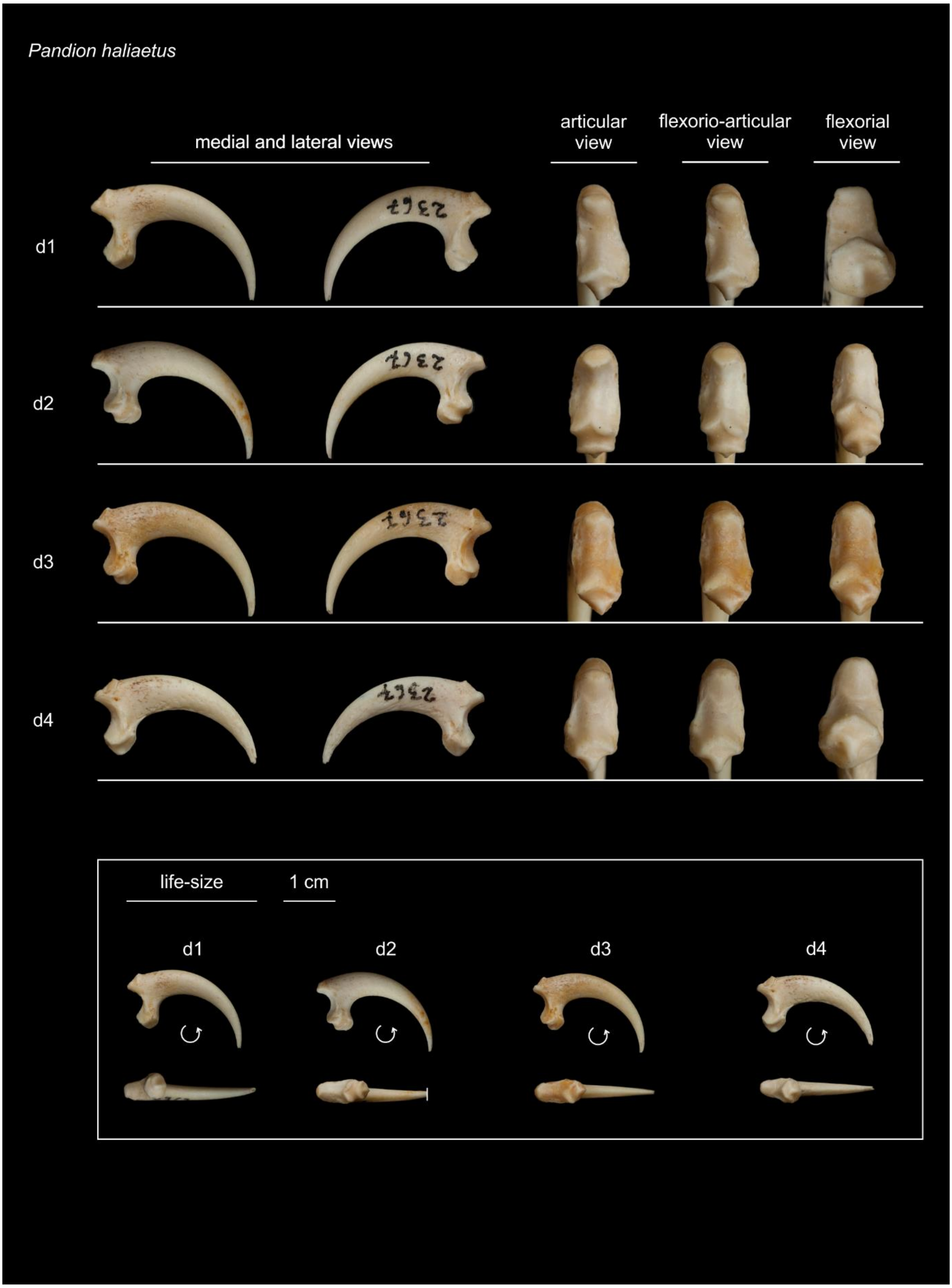
Appendix S2

for: Bochenski Z.M., Tomek T., Wertz K., Whose talon is this? A manual for the identification of ungual phalanges of European accipitrid birds of prey. *International Journal of Osteoarchaeology*

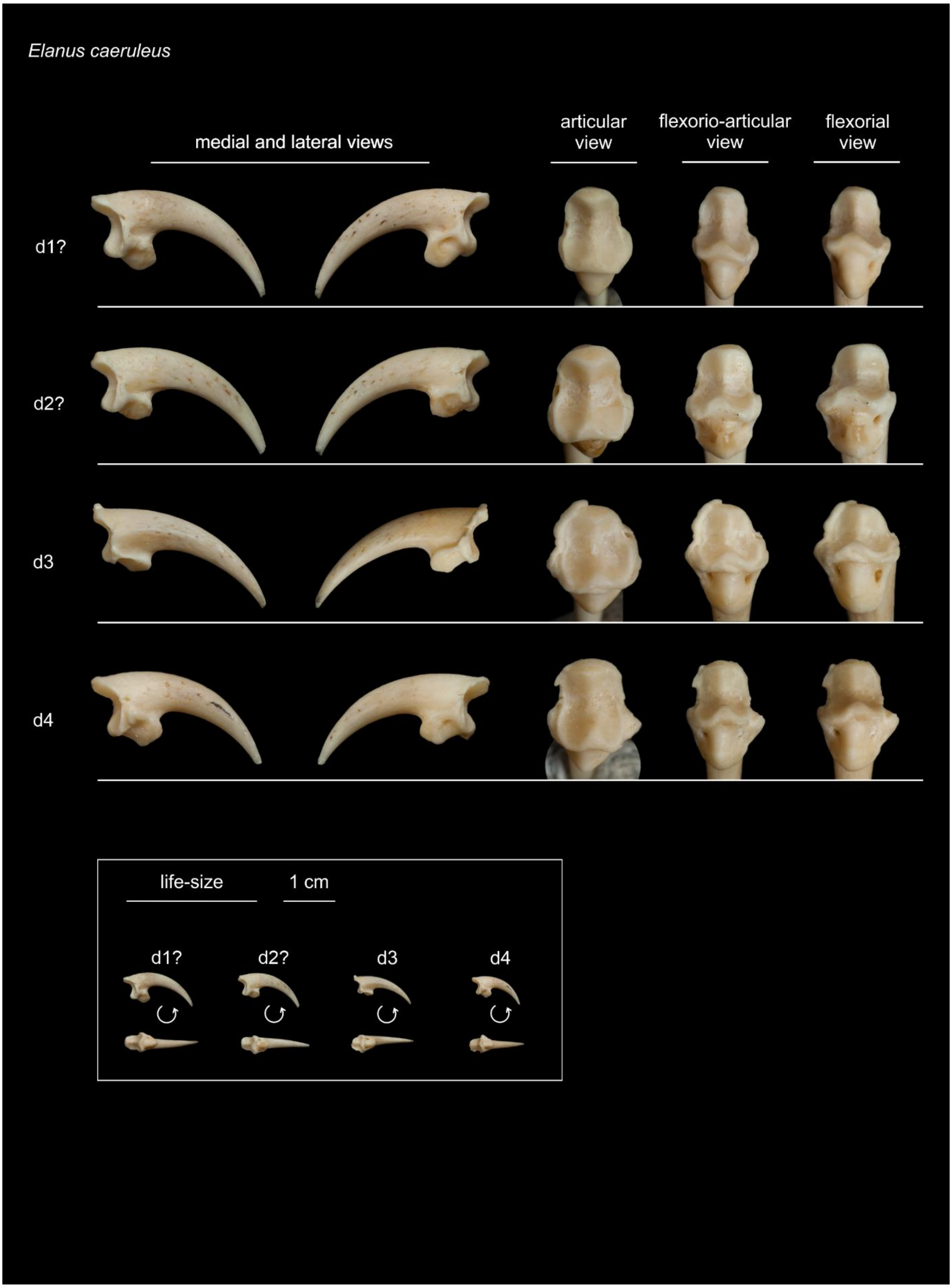


Predefined views in which ungual phalanges were photographed: lateral, medial, articular, flexorial, and flexorio-articular views. The plantar and dorsal views are terms used to describe features in the text.

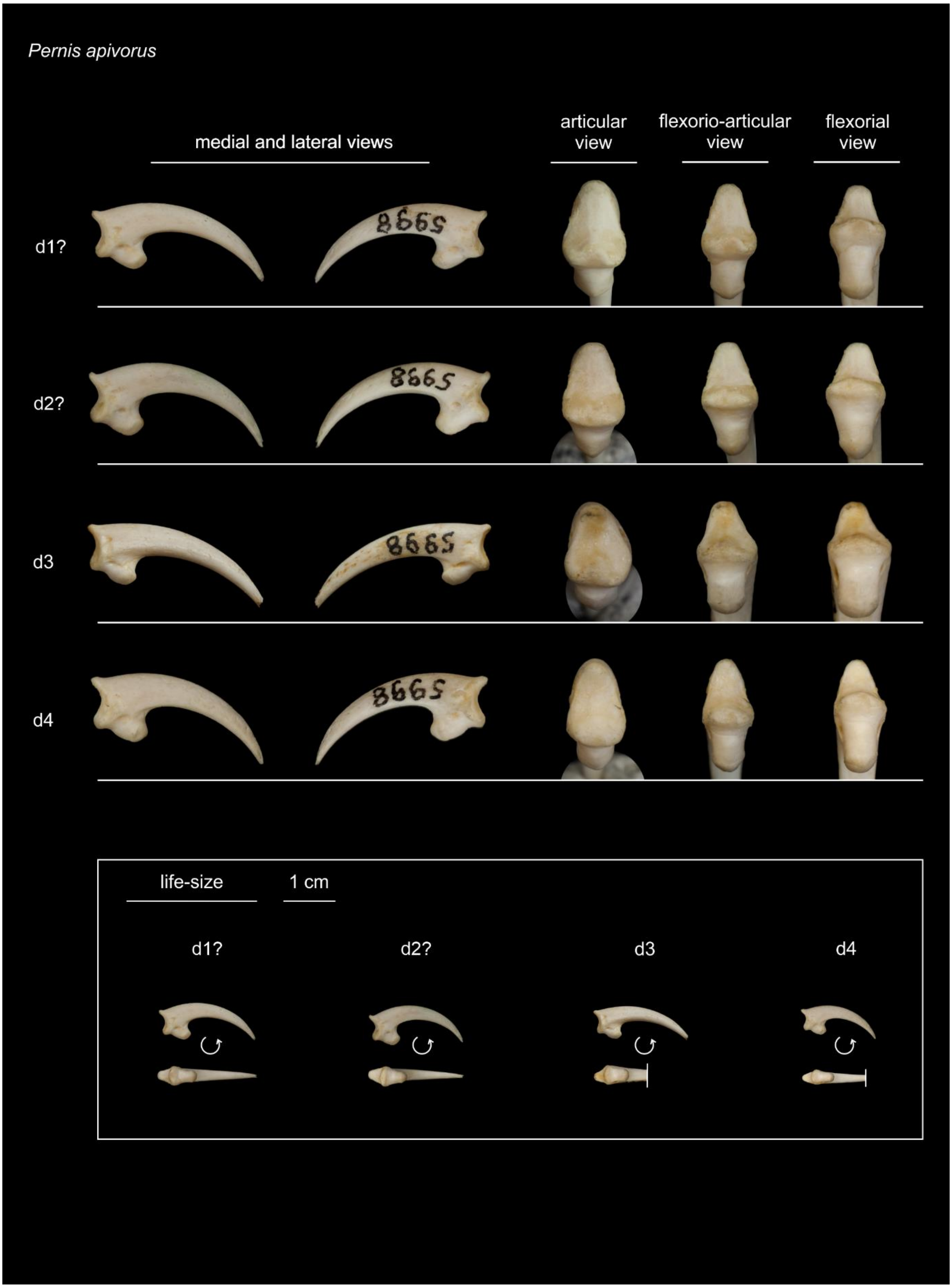
On the following pages are ungular phalanges of all species of accipitrid birds identified in the present manual. The framed photos at the bottom of each plate are life-size and the remaining photographs are enlarged. Right and left bones are not distinguished. In some specimens, the claws from digit 1 and digit 2 can be swapped, which is marked with a question mark (?). However, it does not affect their identification because they are practically the same size. The order of the species presented is as follows: *Pandion haliaetus, Elanus caeruleus, Pernis apivorus, Gypaetus barbatus, Neophron percnopterus, Gyps fulvus, Aegypius monachus, Circaetus gallicus, Clanga clanga, Clanga pomarina, Aquila chrysaetos, Aquila fasciata, Aquila heliaca, Aquila rapax, Hieraaetus pennatus, Circus aeruginosus, Circus cyaneus, Circus macrourus, Circus pygargus, Accipiter gentilis, Accipiter nisus, Haliaeetus albicilla, Milvus migrans, Milvus milvus, Buteo buteo, Buteo lagopus, Buteo rufinus.*



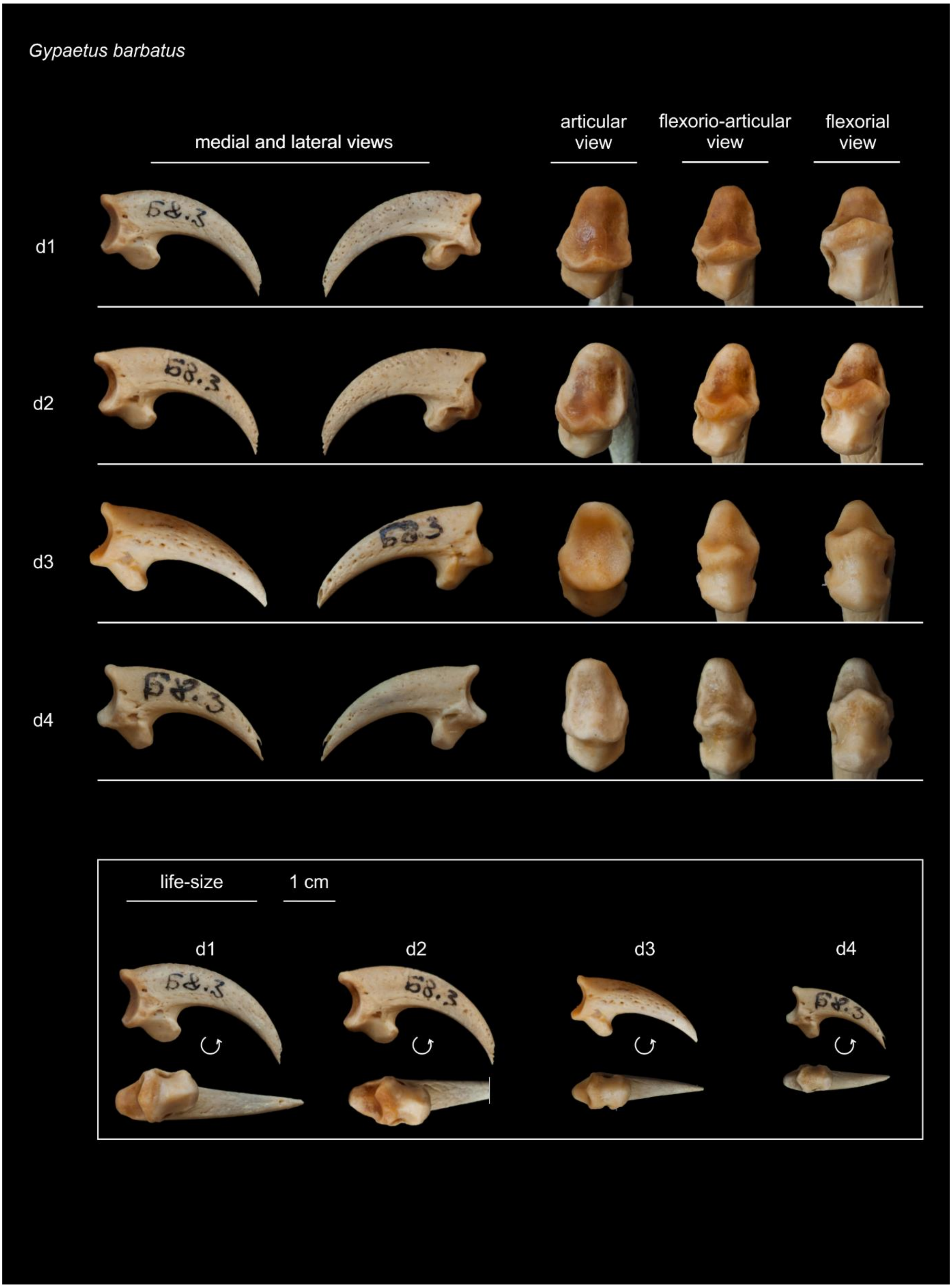
Pandion haliaetus; #ISEA 2367; Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.



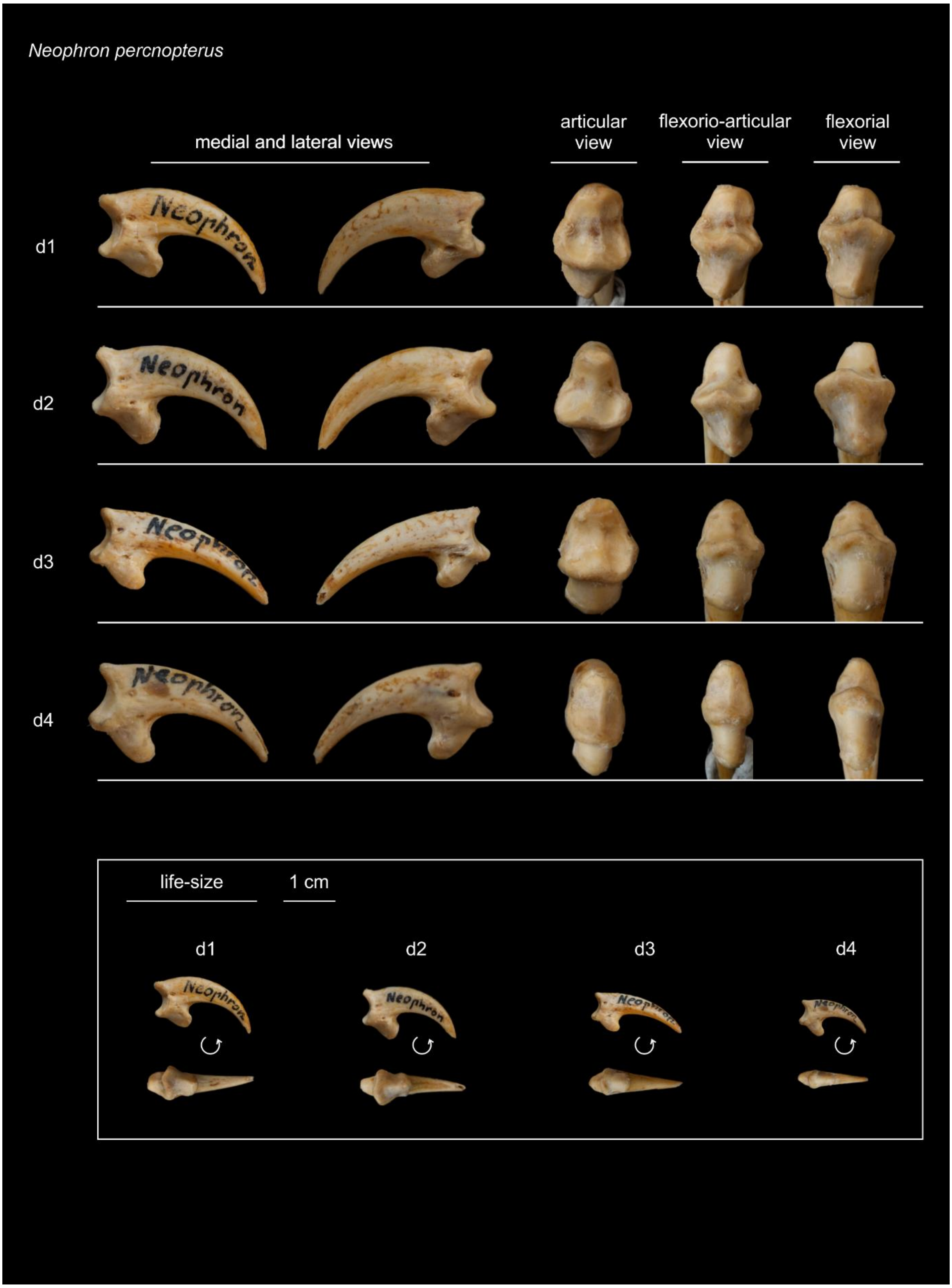
Elanus caeruleus; #ISEA 3278; Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.



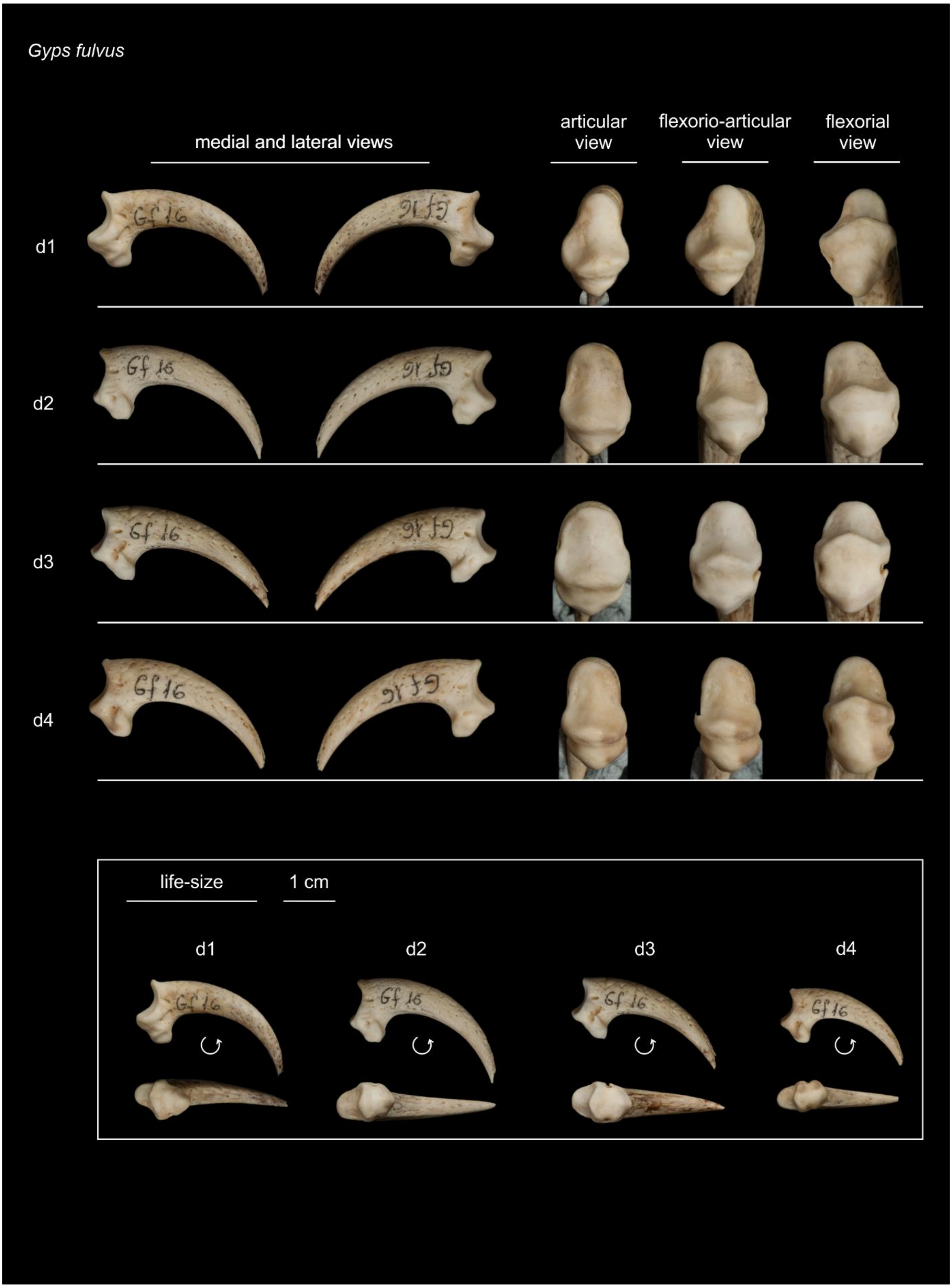
Pernis apivorus; #ISEA 5998; Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.



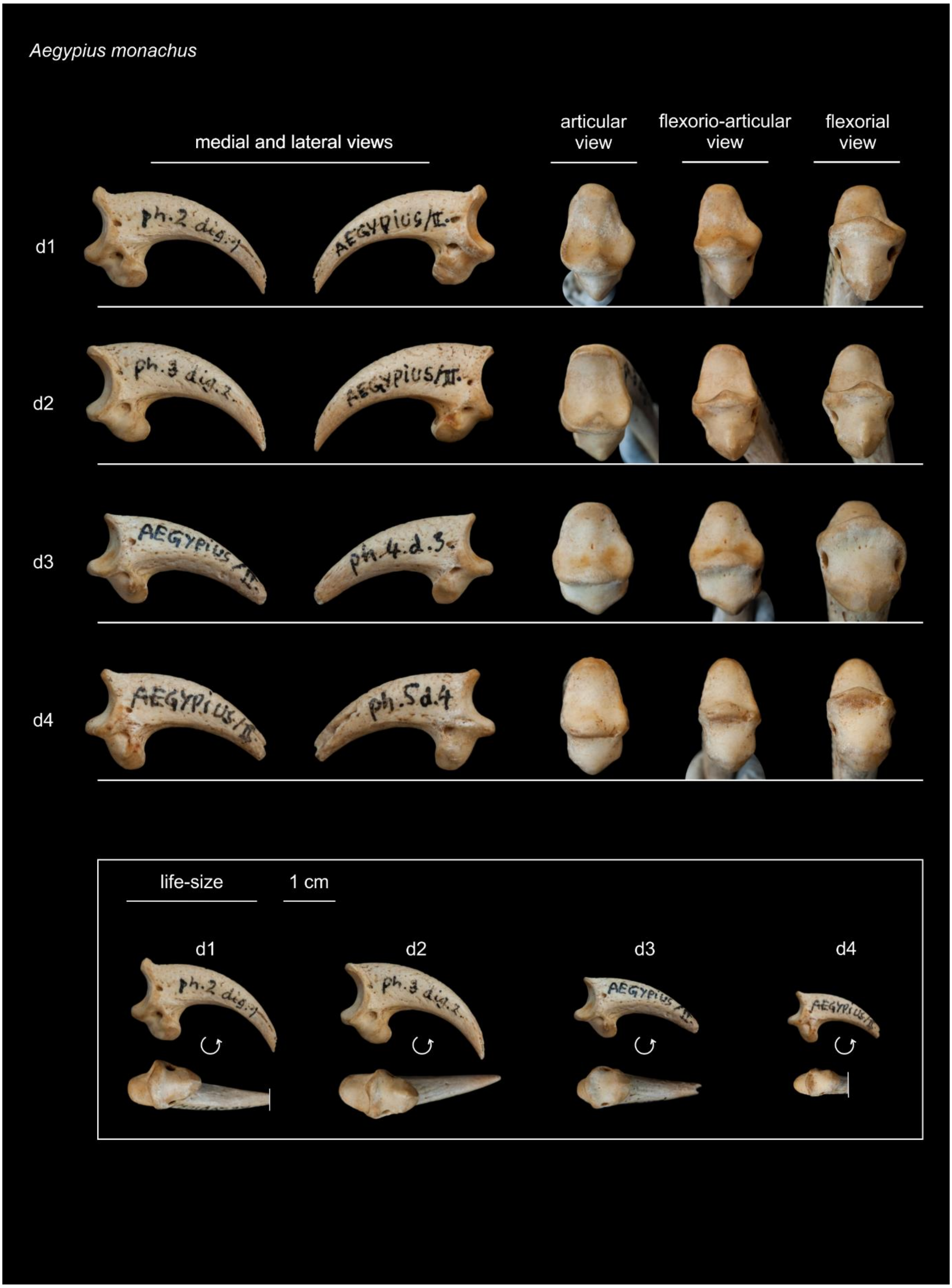
Gypaetus barbatus; #68.3.1; Hungarian Natural History Museum, Budapest, Hungary.



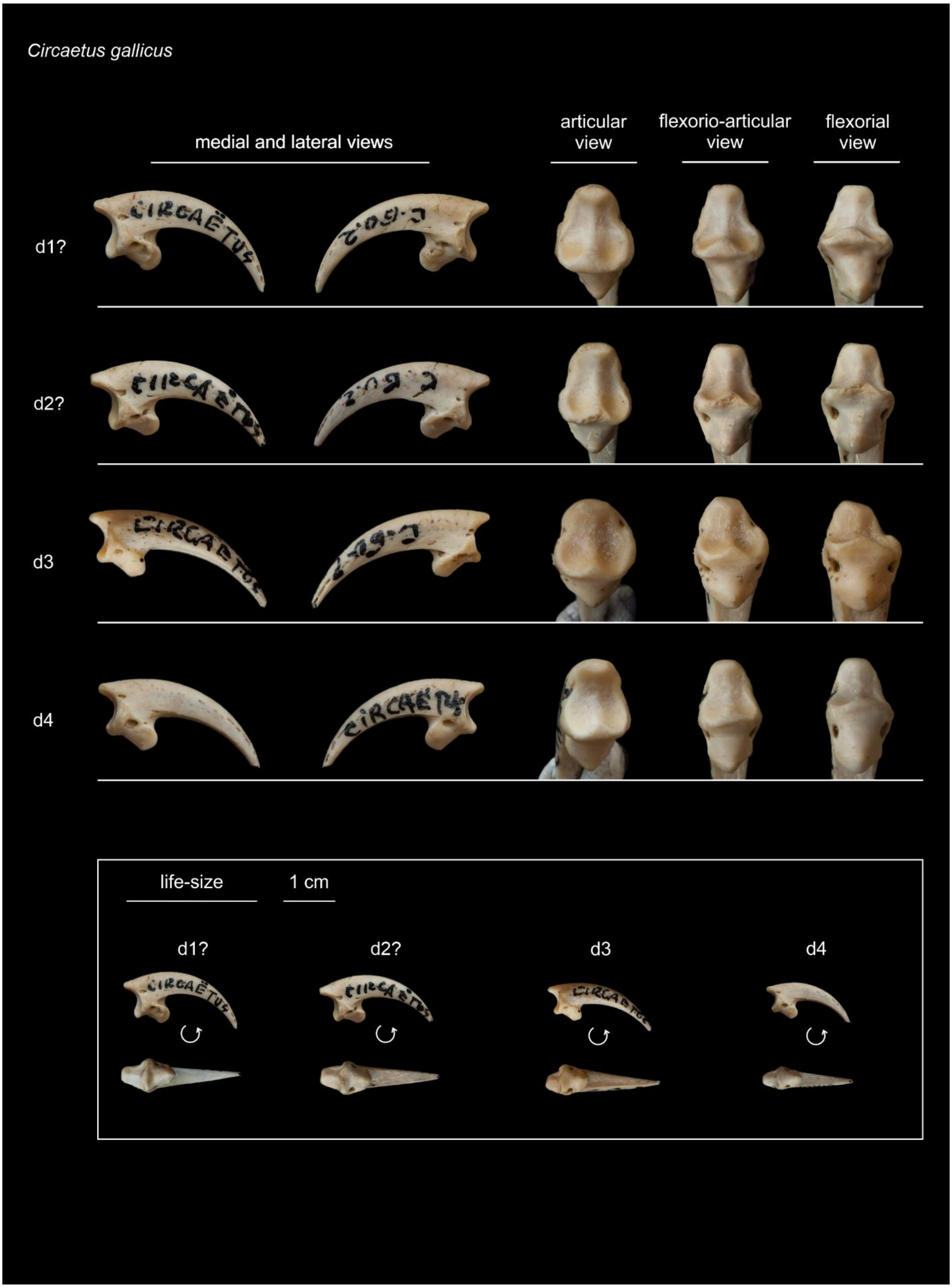
Neophron percnopterus; #2010.1206; Hungarian Natural History Museum, Budapest, Hungary.



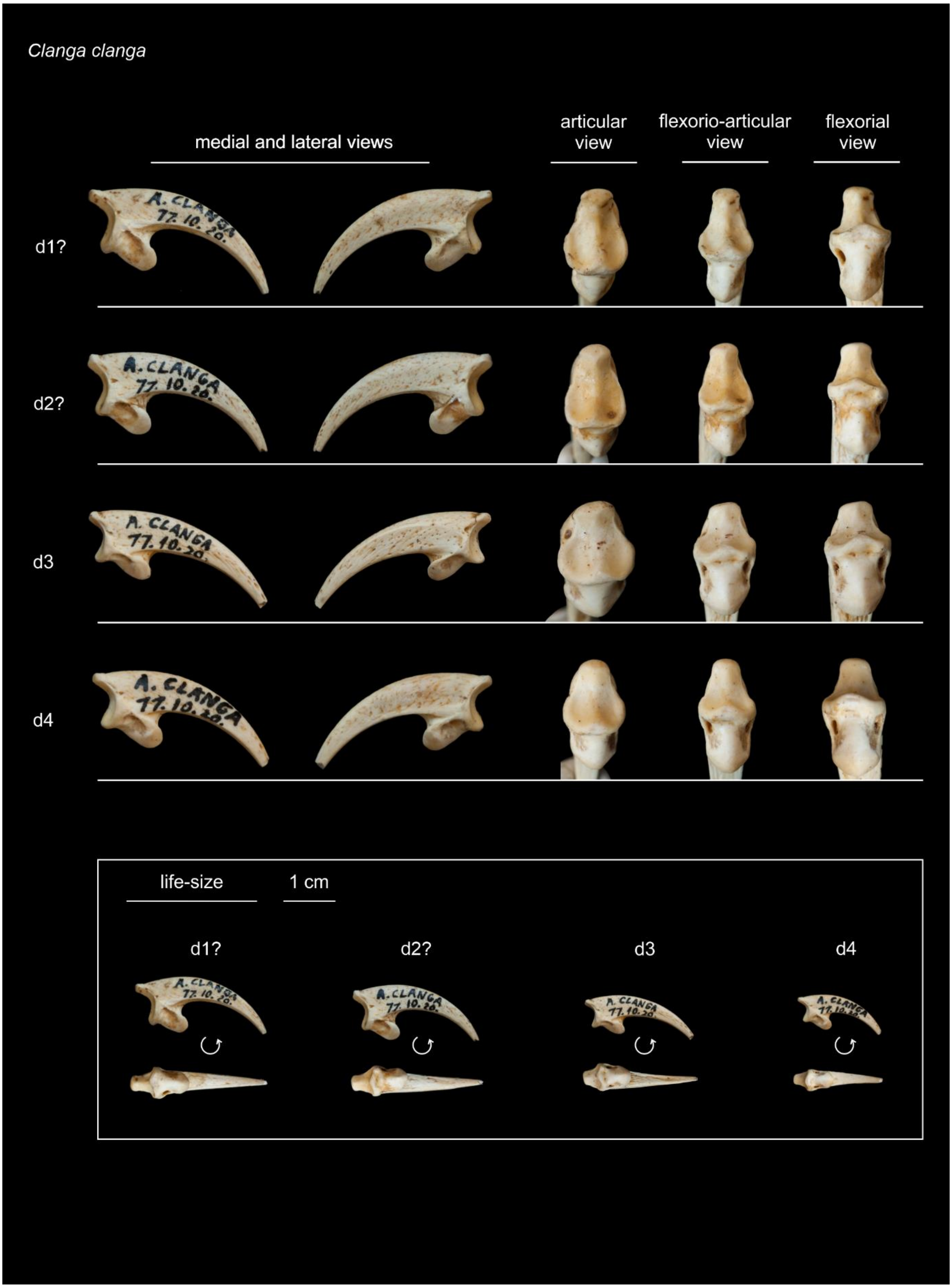
Gyps fulvus; #16/2016; National Museum of Natural History, Bulgarian Academy of Sciences, Sofia, Bulgaria.



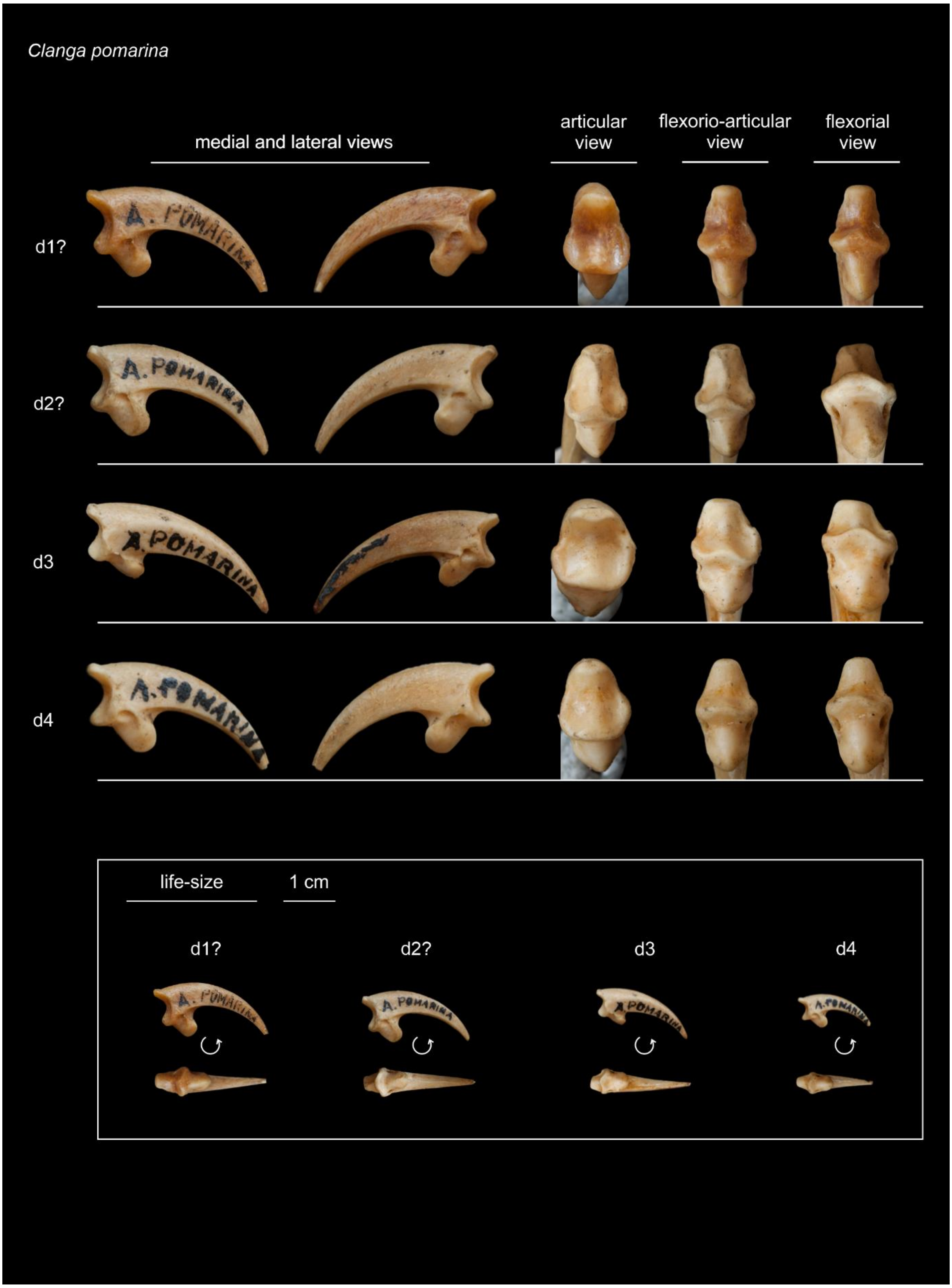
Aegypius monachus; Specimen from the reference key collection; Hungarian Natural History Museum, Budapest, Hungary.



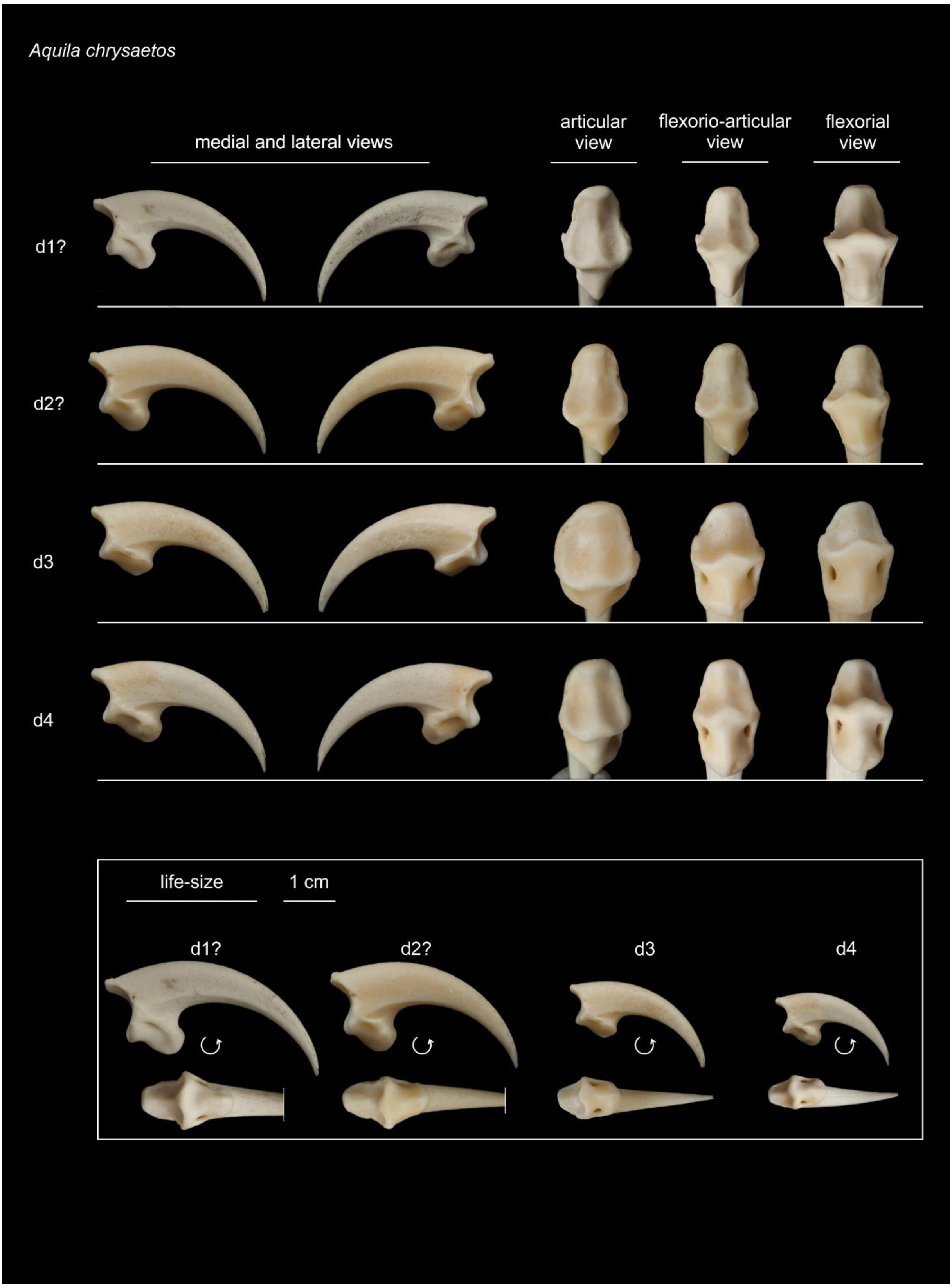
Circaetus gallicus; #60.2.1; Hungarian Natural History Museum, Budapest, Hungary.



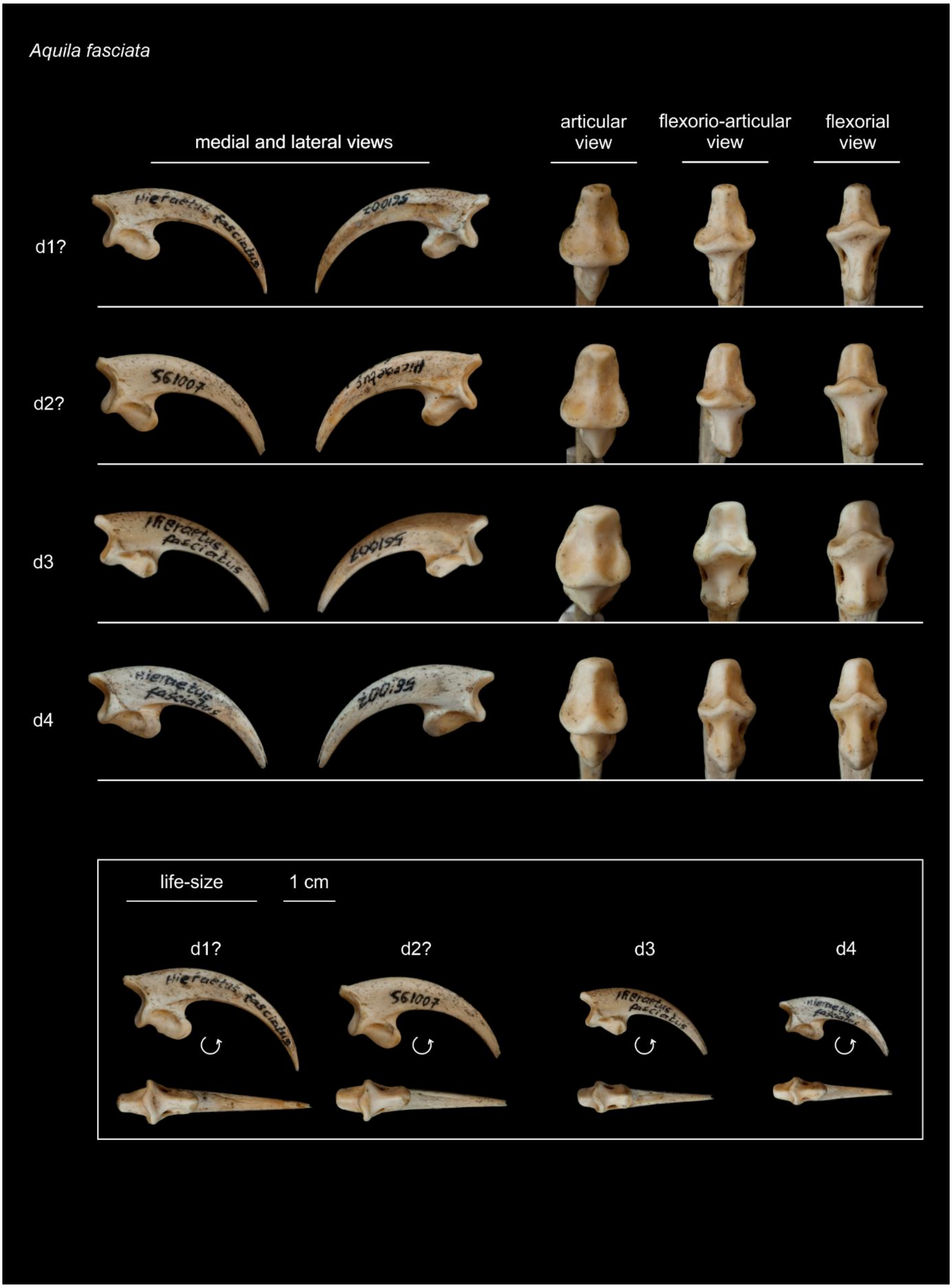
Clanga clanga; #2010.229.1; Hungarian Natural History Museum, Budapest, Hungary.



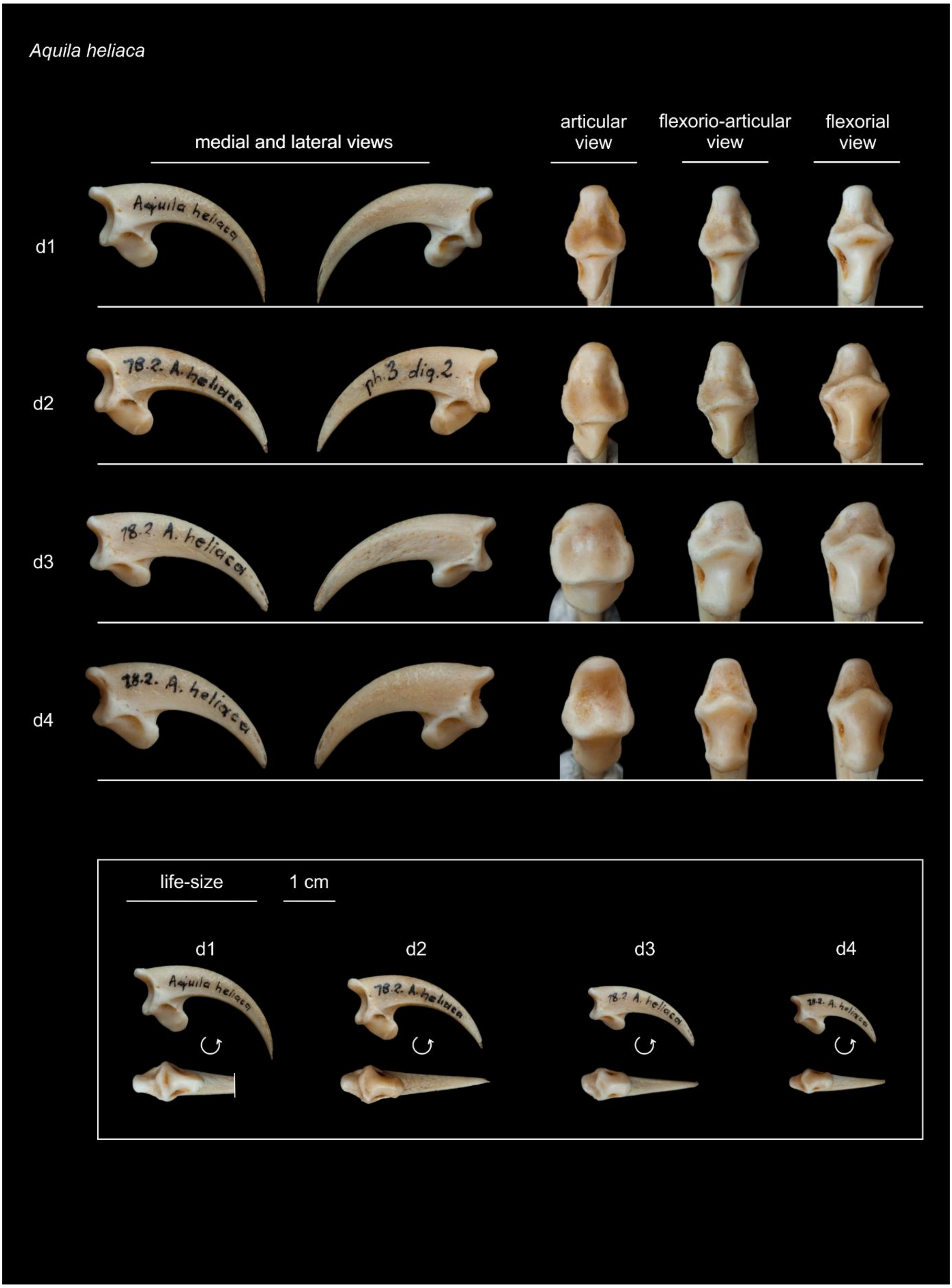
Clanga pomarina; #2010.1279.1; Hungarian Natural History Museum, Budapest, Hungary.



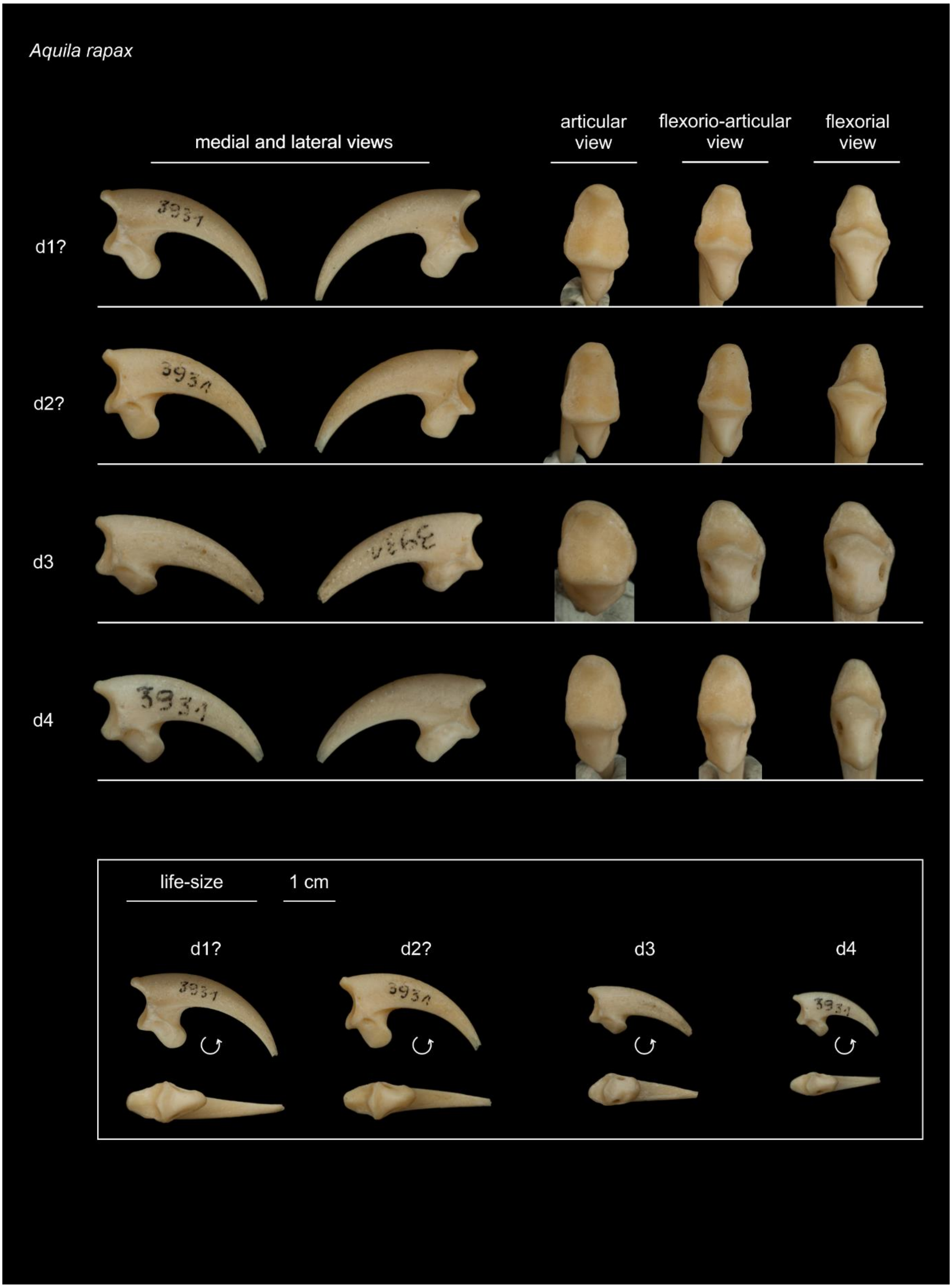
Aquila chrysaetos; #2012.2108.1; Hungarian Natural History Museum, Budapest, Hungary.



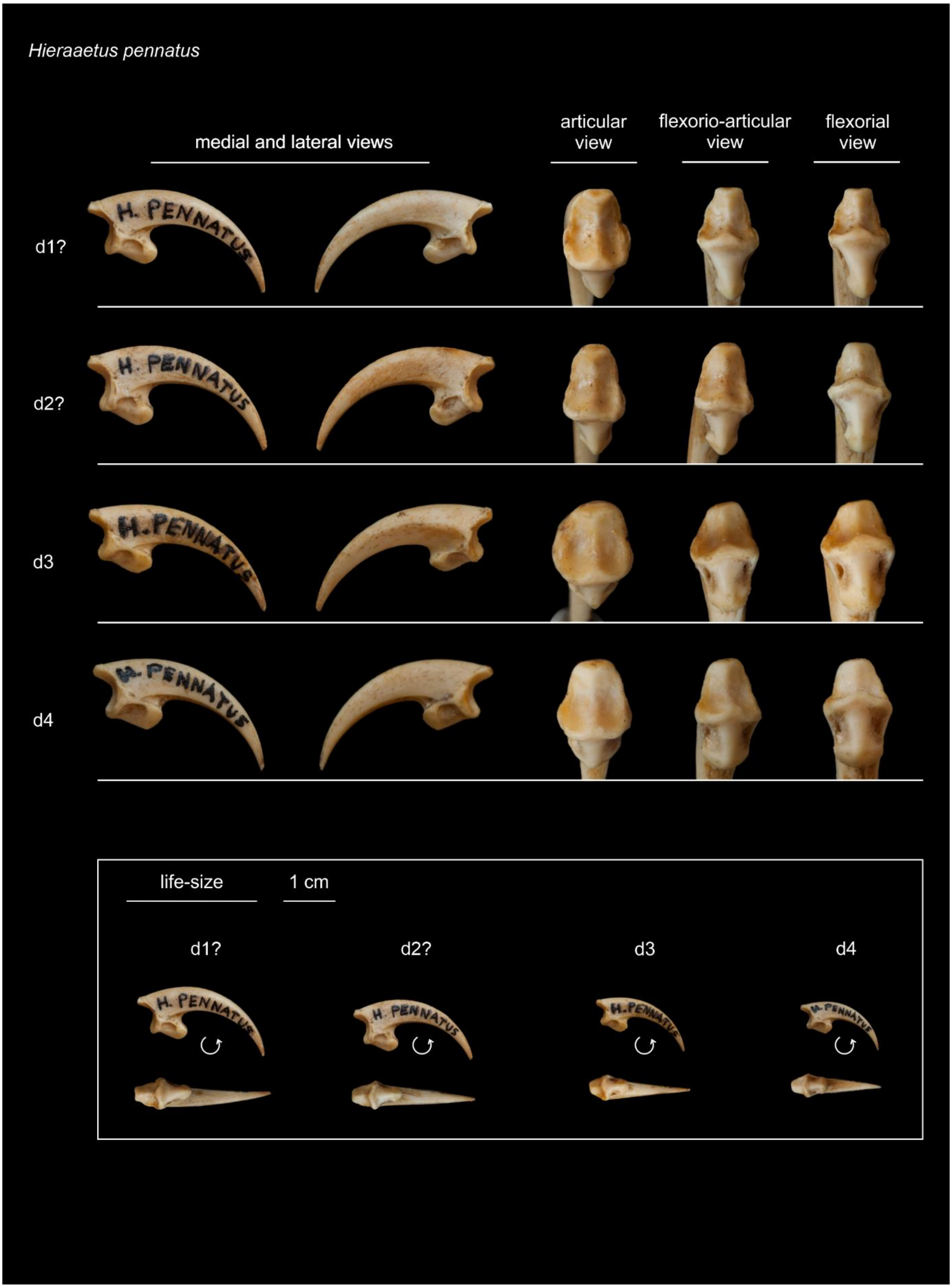
Aquila fasciata; #2010.295.1; Hungarian Natural History Museum, Budapest, Hungary.



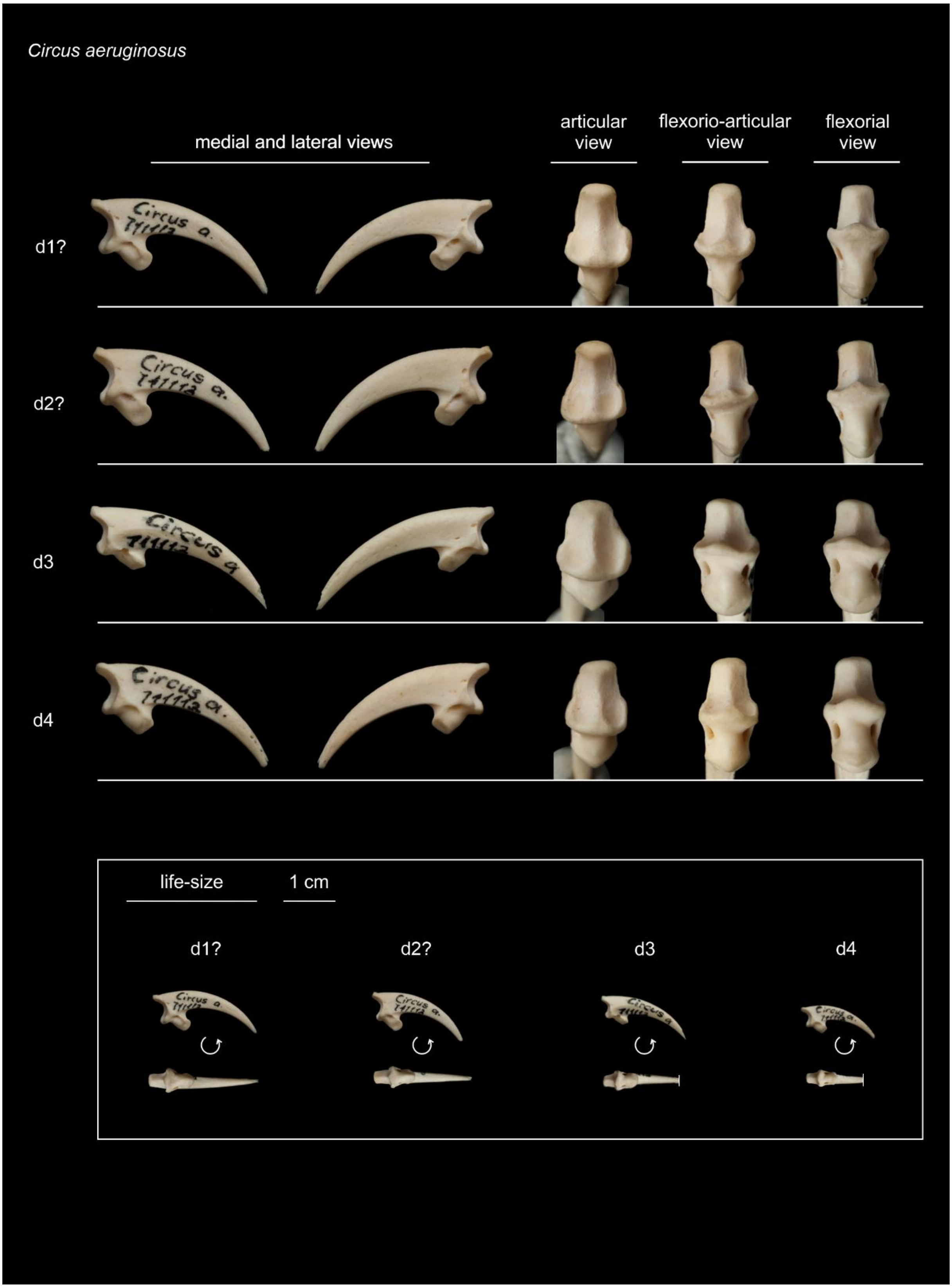
Aquila heliaca; #2010.267.1; Hungarian Natural History Museum, Budapest, Hungary.



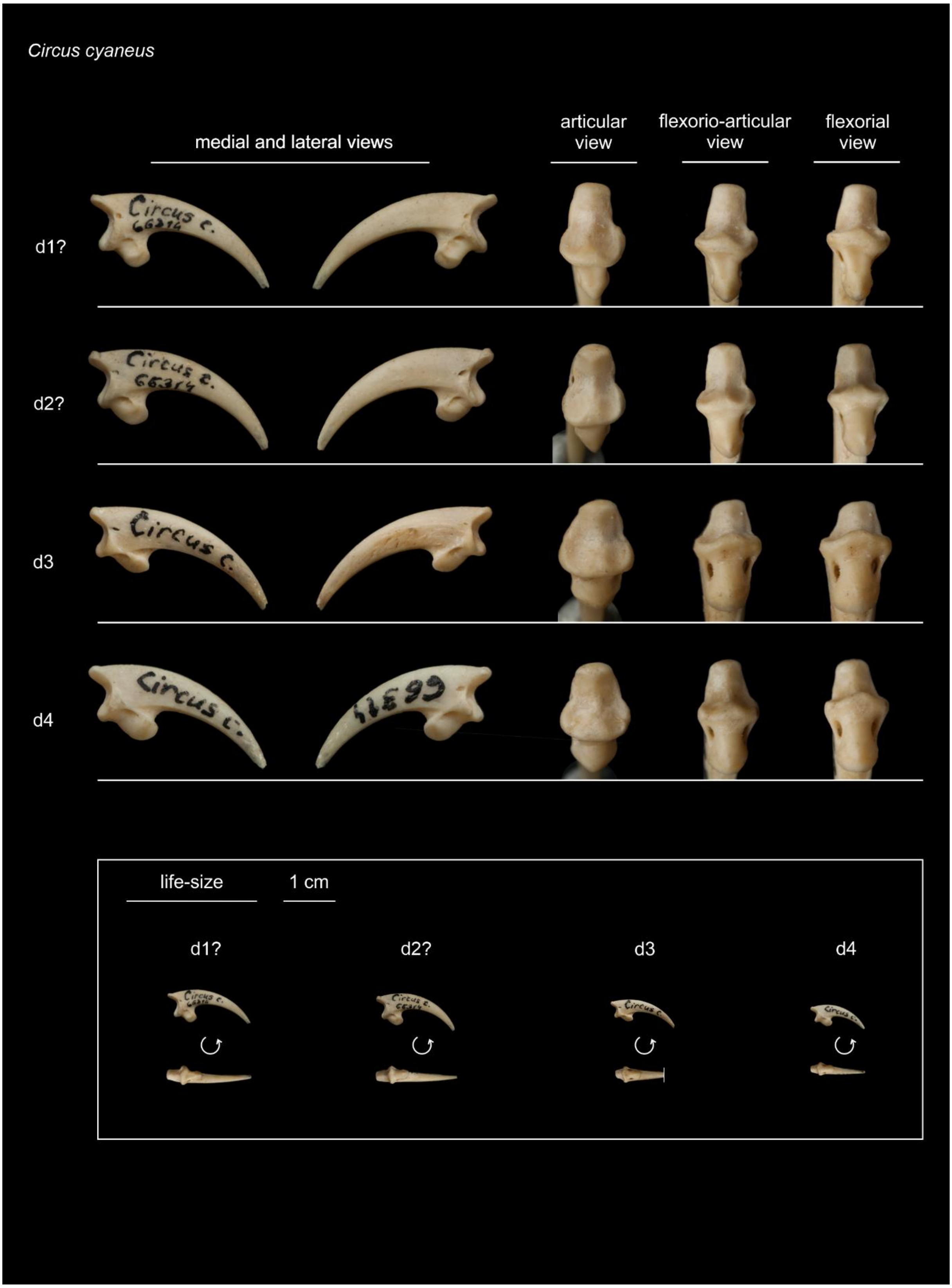
Aquila rapax; #ISEA 3931; Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.



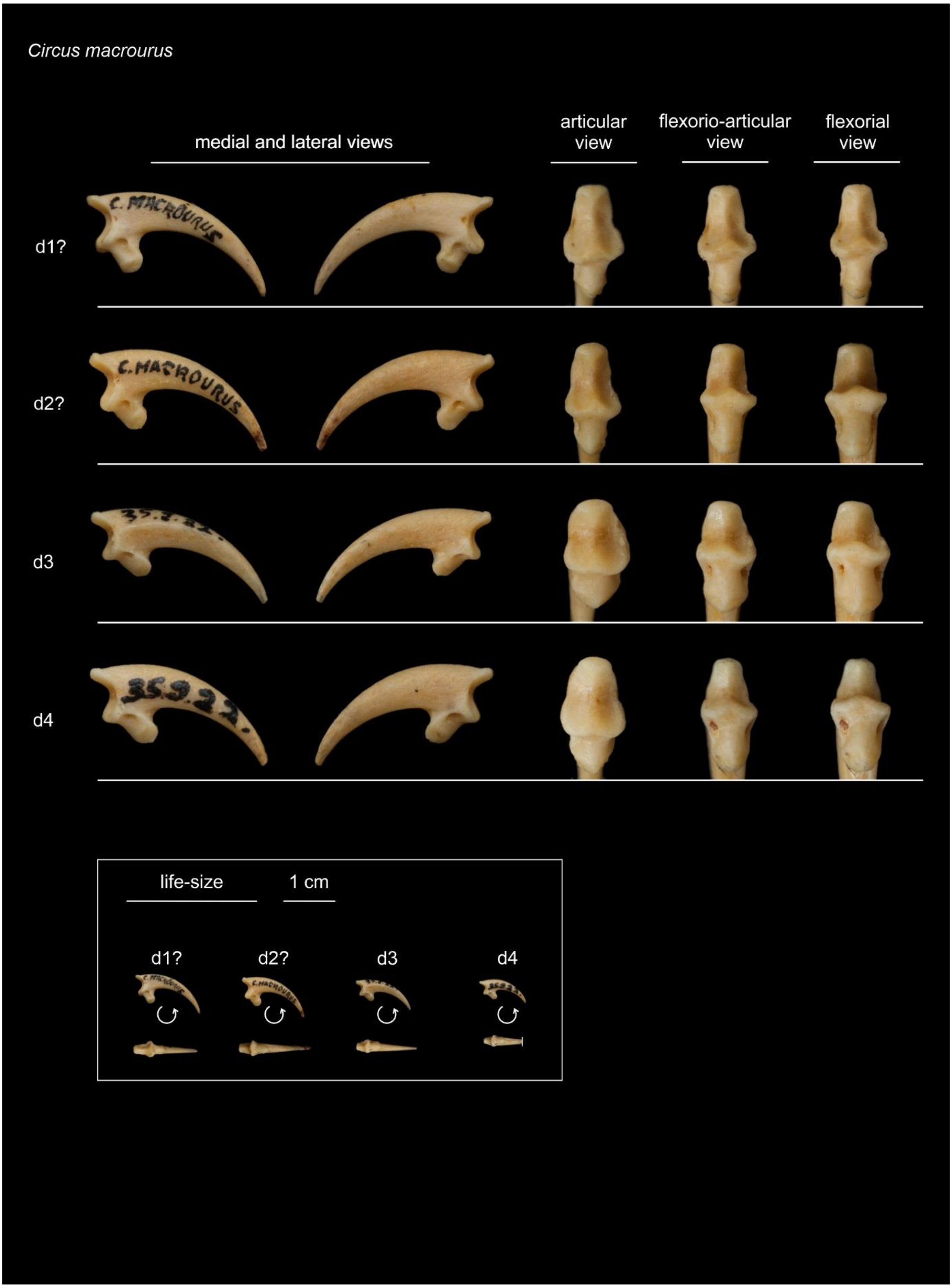
Hieraaetus pennatus; #2010.296.1; Hungarian Natural History Museum, Budapest, Hungary.



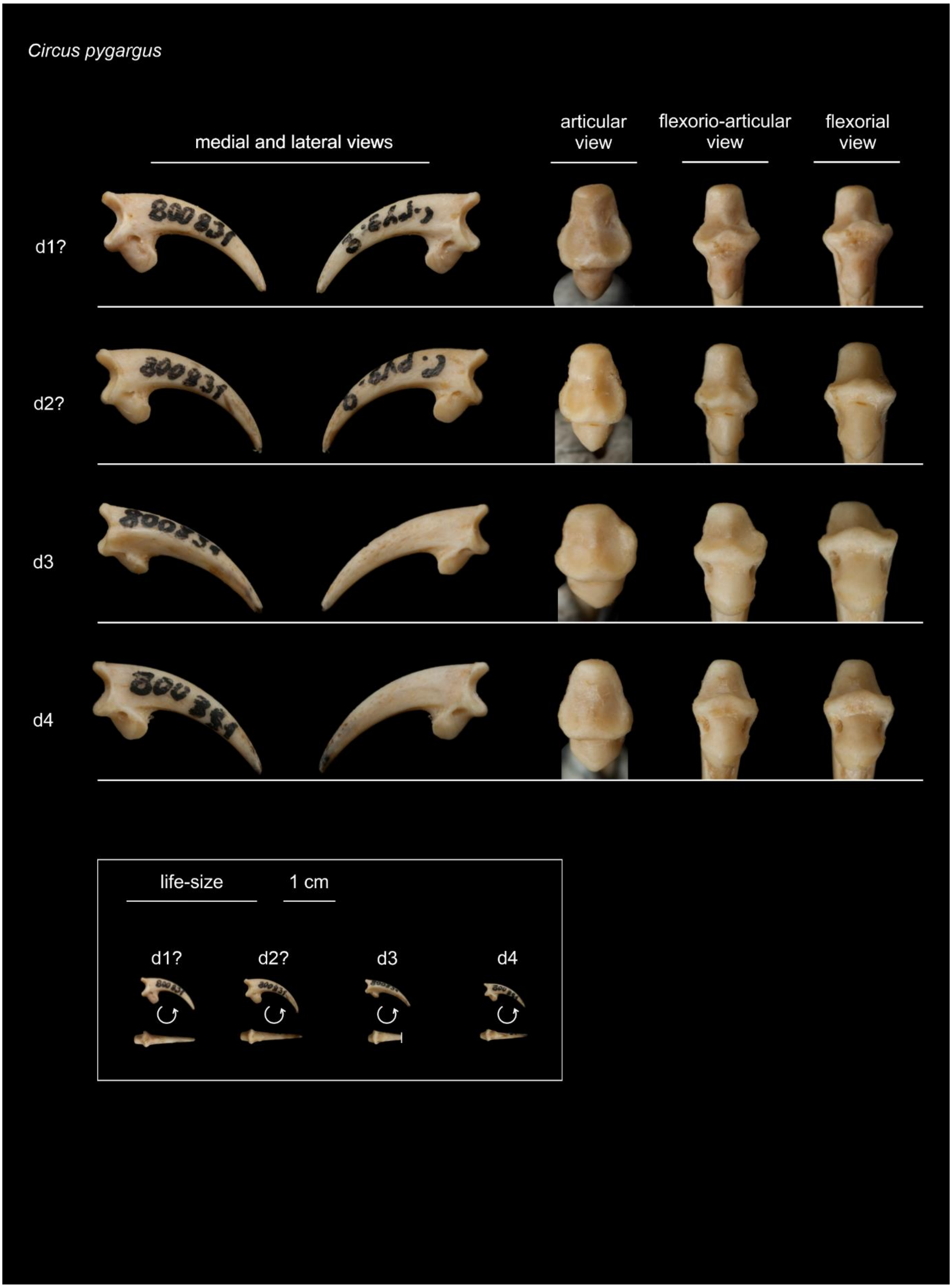
Circus aeruginosus; #2010.216.1; Hungarian Natural History Museum, Budapest, Hungary.



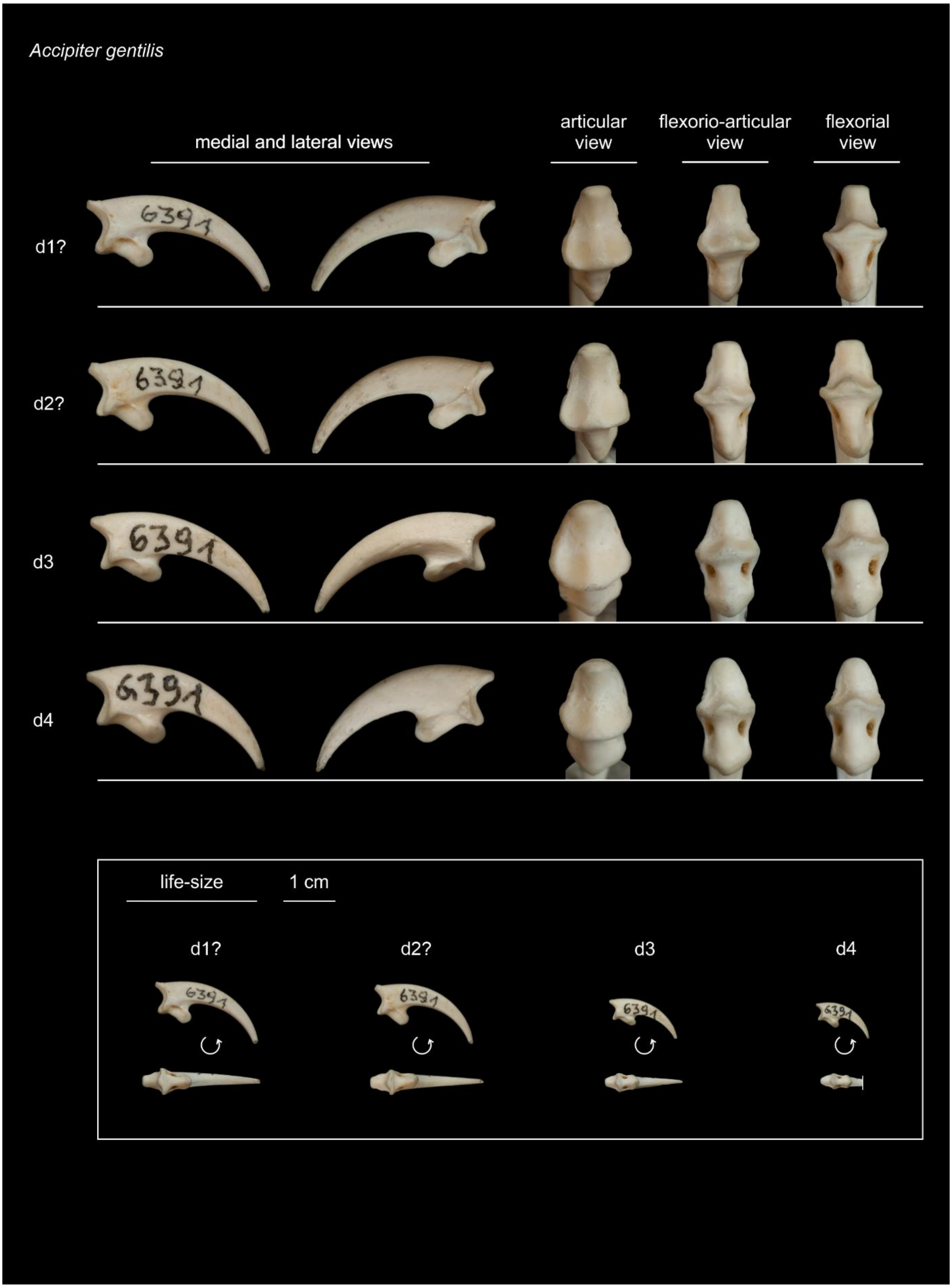
Circus cyaneus; #66.48.1; Hungarian Natural History Museum, Budapest, Hungary.



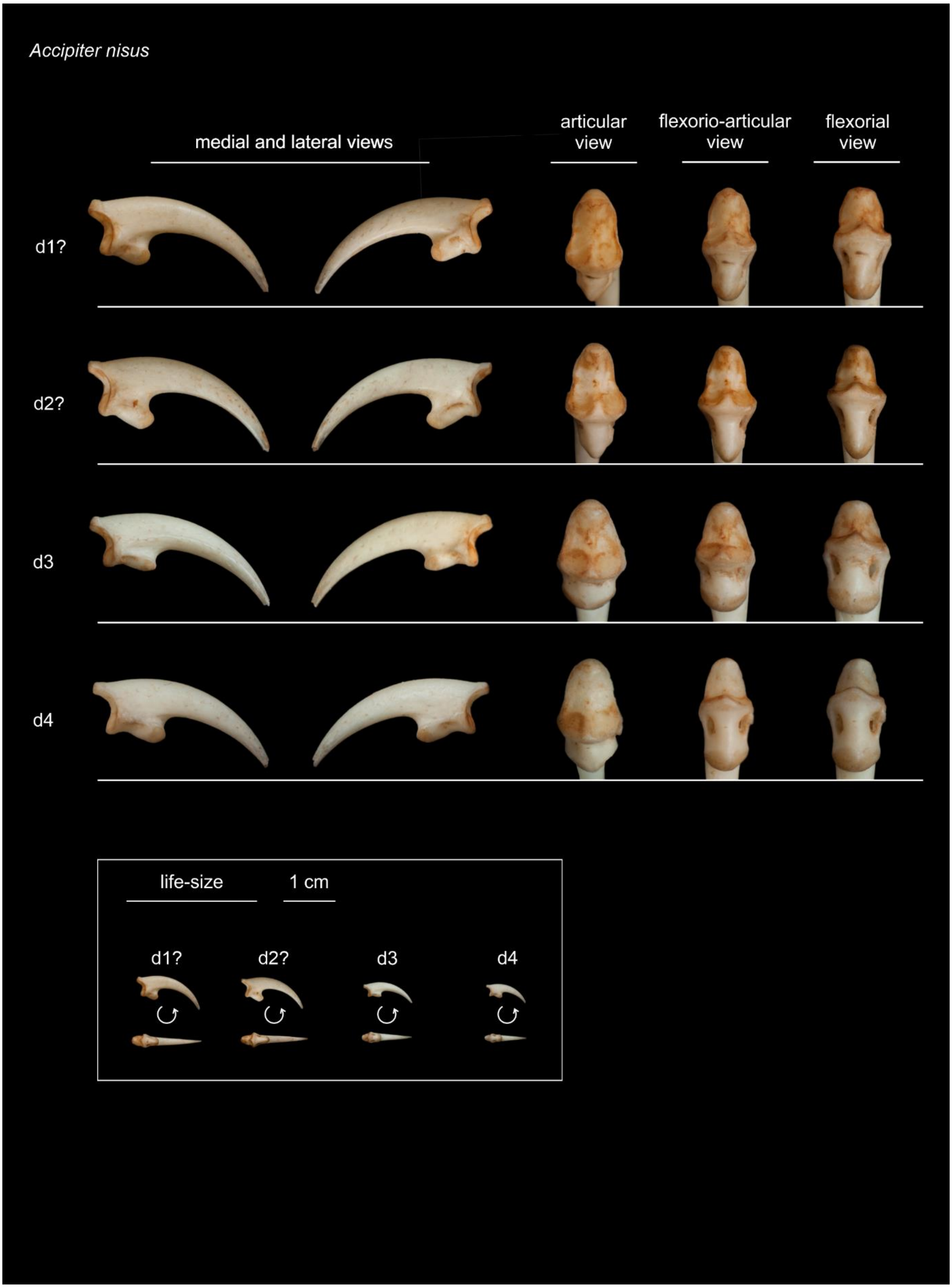
Cirus macrourus; #60.7.1; Hungarian Natural History Museum, Budapest, Hungary.



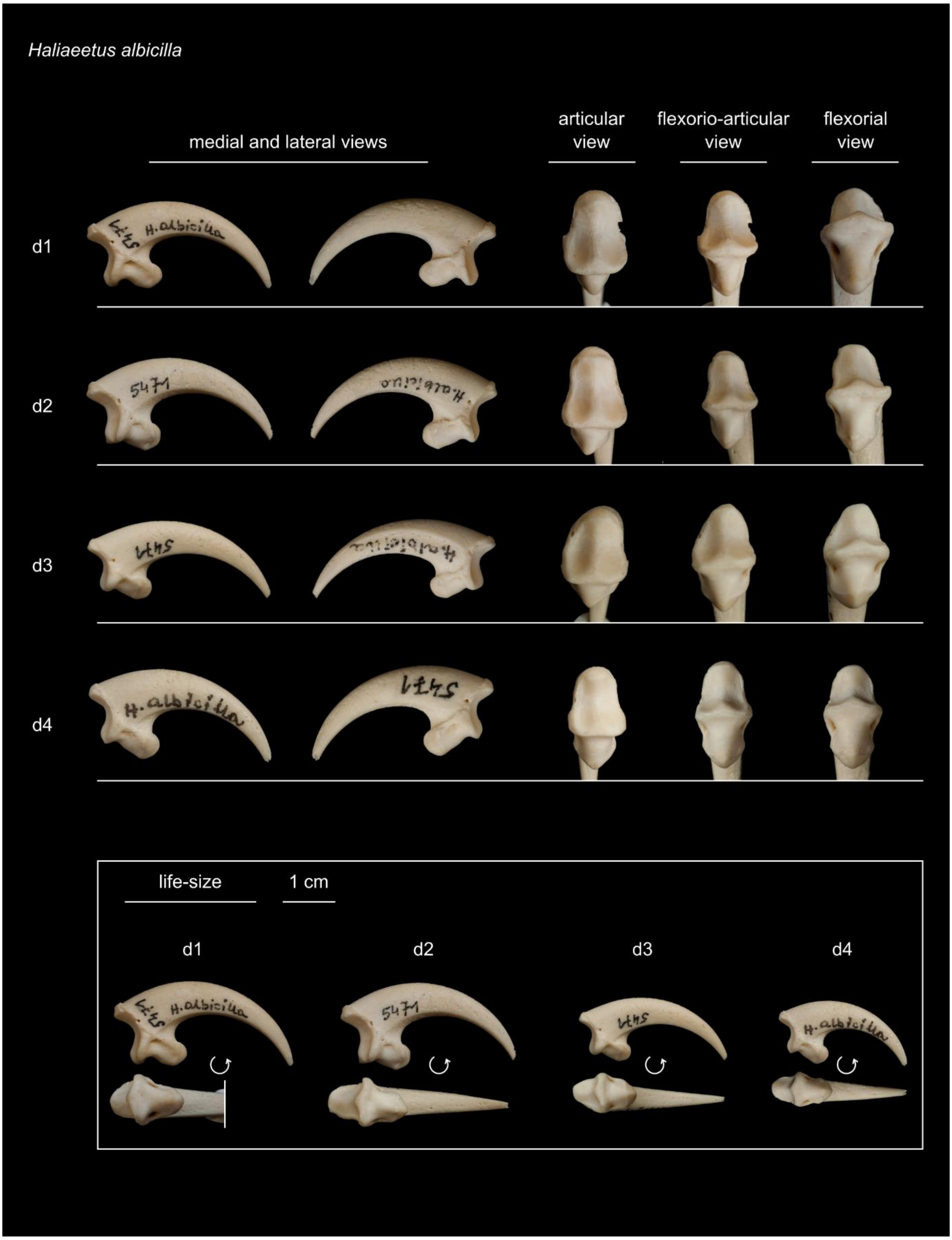
Circus pygargus; #2010.1204.1; Hungarian Natural History Museum, Budapest, Hungary.



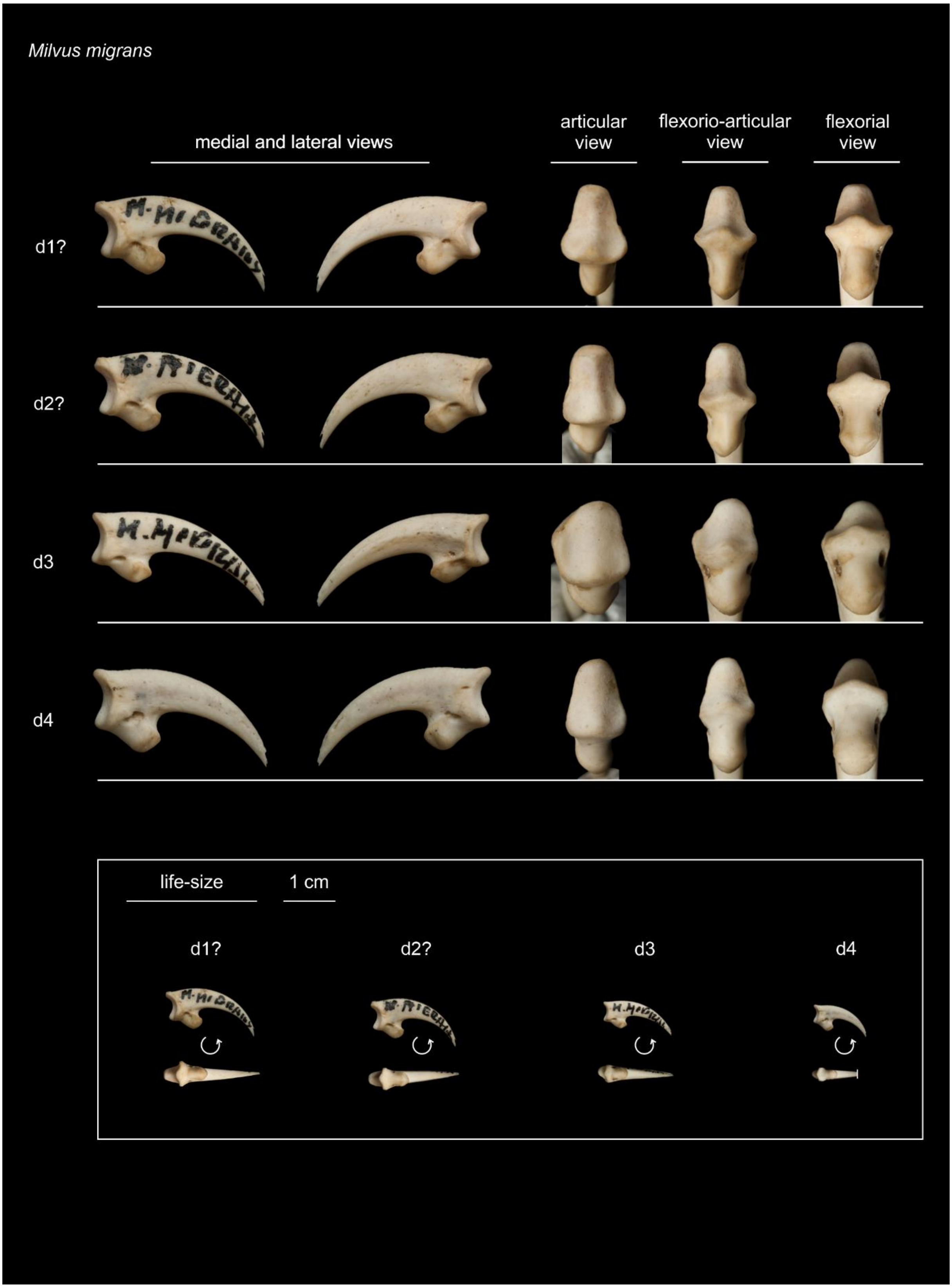
Accipiter gentilis; #ISEA 6391; Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.



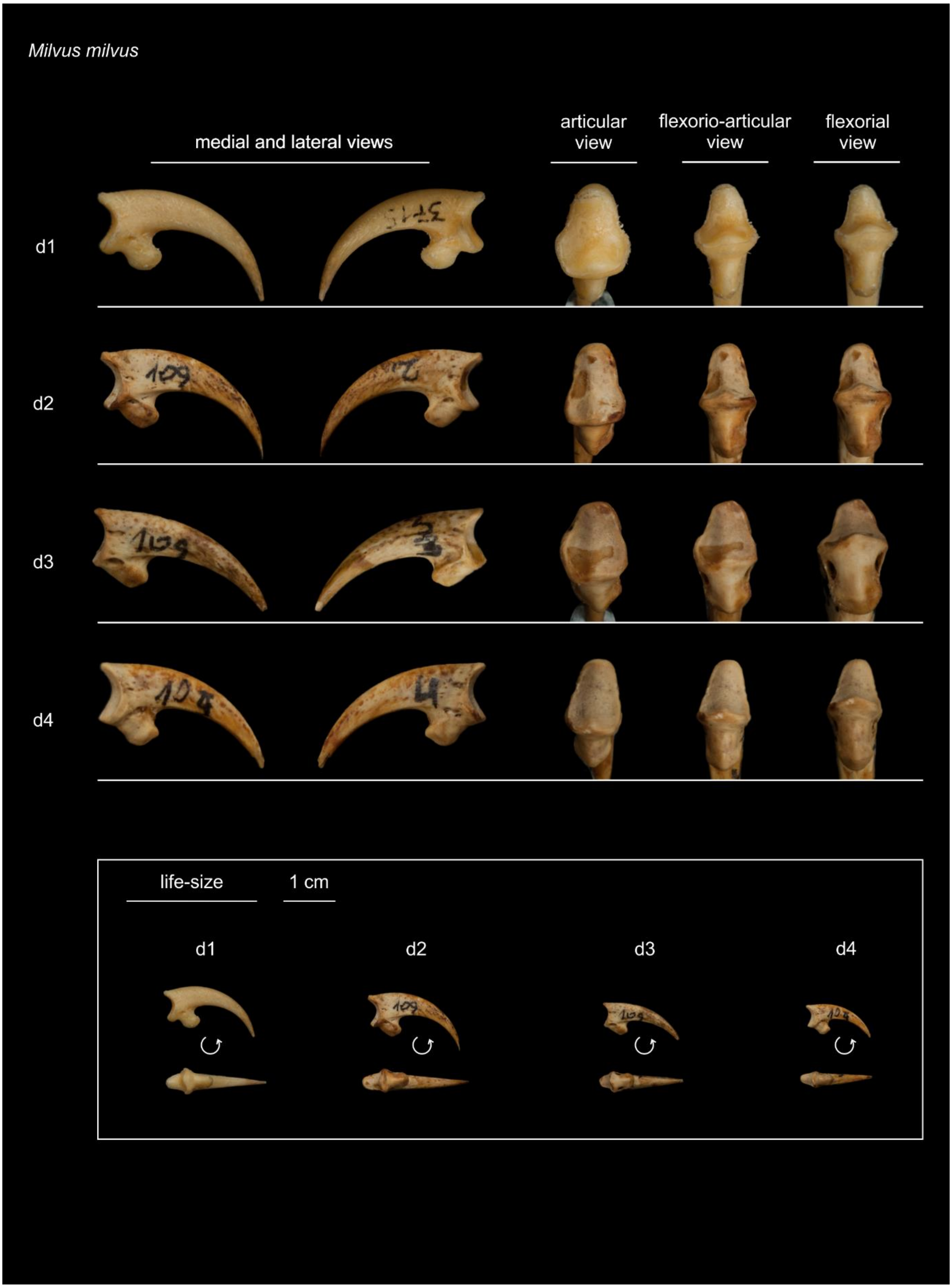
Accipiter nisus; #ISEA 8495; Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.



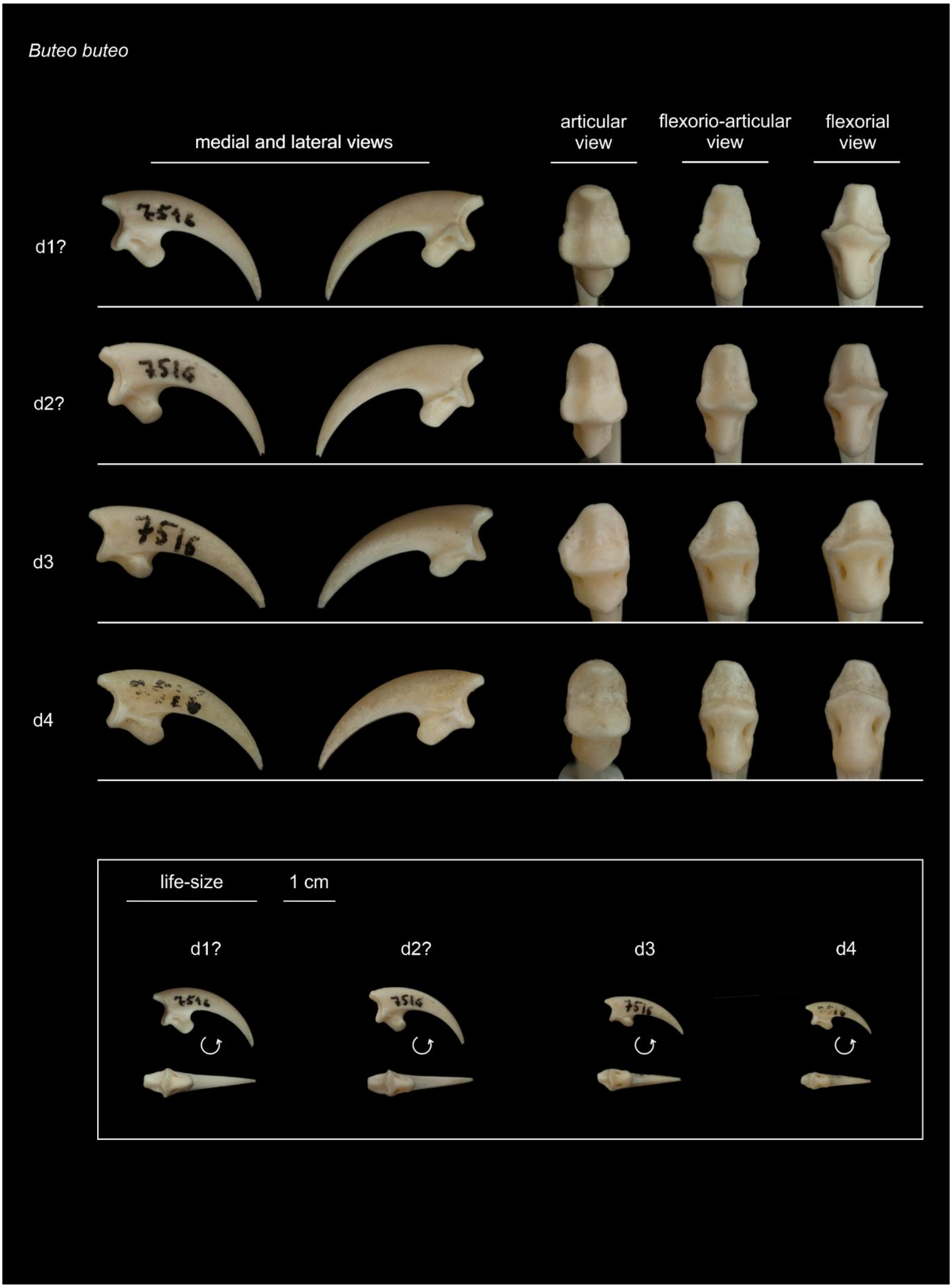
Haliaeetus albicilla; #ISEA 5471; Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.



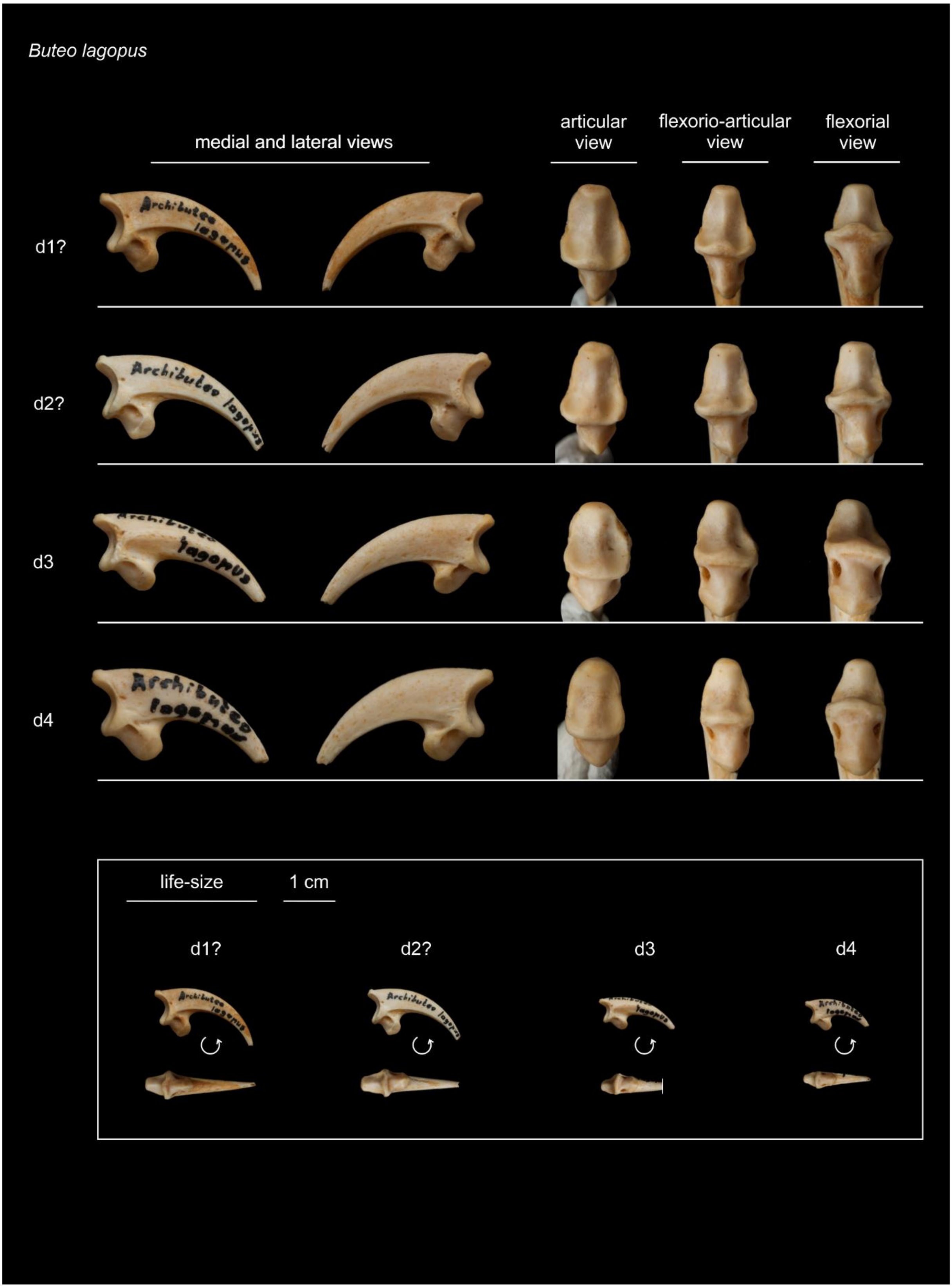
Milvus migrans; #58.47.1; Hungarian Natural History Museum, Budapest, Hungary.



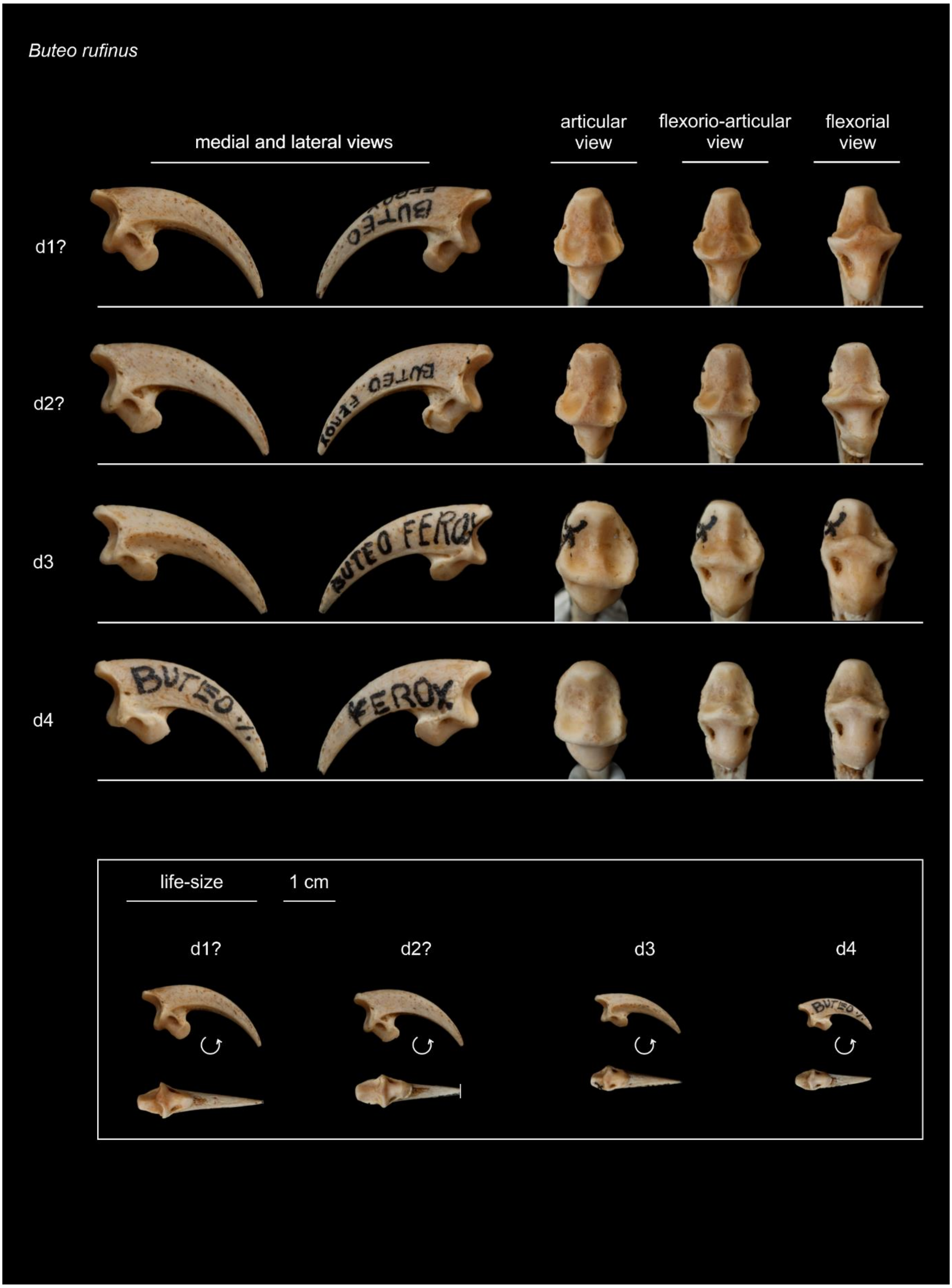
Milvus milvus; digit 1: #ISEA 3715; Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland; digits 2-4: #109; De la Préhistoire à l'Actuel: Culture, Environment et Anthropologie, Université de Bordeaux, France.



Buteo buteo; #ISEA 7516; Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.



Buteo lagopus; #2010.1167.1; Hungarian Natural History Museum, Budapest, Hungary.



Buteo rufinus; #2010.202.1; Hungarian Natural History Museum, Budapest, Hungary.