RESEARCH PAPER

First substantial evidence for Old World vultures (Aegypiinae, Accipitridae) from the early Palaeolithic and Iberomaurusian of Morocco

Albrecht Manegold[1] · Rainer Hutterer[2]

Abstract

Remains of at least three species of large aegypiine vultures from early Palaeolithic and Iberomaurusian of Ifri n'Ammar, Morocco are the first substantial fossil record of these taxa in the Maghreb. They can be tentatively referred to the two extant species *Aegypius monachus* (Cinereous Vulture) and *Gyps fulvus* (Griffon Vulture), and to the extinct *Gyps melitensis*. Few fragments of remarkably large bones may belong to especially large specimens of *A. monachus*, but it cannot be ruled out that they are indeed remains of the so far only insufficiently known palaeospecies *A. prepyrenaicus* Hérnandez, 2001, originally described from the Upper Pleistocene of Spain. Two vulture species definitely occurred contemporarily; *Gyps fulvus* was found in the entire sequence, while *A. monachus* occurred only between 13,800 and 17,000 calBP. *G. melitensis* was found only once in an unknown stratigraphic context. All remains were found along with human artefacts in a cave deposit. Few bones show longitudinal scratches, which probably are cut marks, indicating that humans made use of the flesh, feathers and/or bones of these vultures. None of these species were previously recorded for the Upper Pleistocene of the Maghreb, and the fossil specimens provide important evidence for the former distribution of Old-World vultures in this area, which is insufficiently known and which changed dramatically during the twentieth century.

Keywords Aegypiinae · *Aegypius monachus* · *Aegypius prepyrenaicus* · *Gyps fulvus* · *Gyps melitensis* · Iberomaurusian · Maghreb · Ifri n' Ammar

Introduction

The Pleistocene record of aegypiine vultures in the Mediterranean region is quite extensive, but virtually restricted to its northwest and northeast parts as well as to several Mediterranean islands (Sánchez Marco 2007). Remains of extant Cinereous (*Aegypius monachus*) and Griffon Vultures

✉ Albrecht Manegold
  albrecht.manegold@smnk.de

  Rainer Hutterer
  r.hutterer@leibniz-zfmk.de

1   Abteilung Biowissenschaften/Zoologie, Staatliches
    Museum Für Naturkunde Karlsruhe, Erbprinzenstraße 13,
    D-76133 Karlsruhe, Baden-Württemberg, Germany

2   Stiftung Zoologisches Forschungsmuseum Alexander
    Koenig, Adenauerallee 160, D-53113 Bonn,
    Nordrhein-Westfalen, Germany

(*Gyps fulvus*) are frequently recorded (Jánossy 1989; Mlíkovský 1998; Sánchez Marco 2004, 2007). The extinct *Gyps melitensis* is distinguished from *G. fulvus* by its larger size and was originally described from cave deposits of Malta (Lydekker 1890). It was also reported from several other Mediterranean islands as well as mainland Spain, Monaco, France, and even Austria and Germany (Mourer-Chauviré 1975; Jánossy 1989; Louchart 2002; Sánchez Marco 2004, 2007, and references therein), though some of these records might have been based on misidentified bones of either *A. monachus* or *G. fulvus* (Mlíkovský 1998, 2002). Another palaeospecies, *Aegypius prepyrenaicus* Hernández, 2001 was described on the basis of a large proximal ulna (approx. 8% larger than the corresponding bone of *A. monachus*) from the Upper Pleistocene of Spain, but Sánchez Marco (2007) regarded it a *nomen dubium*.

In the Eastern Mediterranean, fossil evidence for *G. fulvus* and *A. monachus* is only reported for cave deposits of Israel (Tchernov 1962; Sánchez Marco 2004) and the Lebanon (Hooijer 1961; Kersten 1991), where both species are

often found in the same horizons (Kersten 1991). Unfortunately, none of these specimens were described or illustrated, which makes more detailed comparisons with other vulture remains impossible.

In northern Africa, a single, fragmentary bone from the Pleistocene of Egypt was referred to *G. africanus* (Bocheński 1991). The avifauna of the cave site Haua Fteah, Libya, comprises more the 60 species of birds, but surprisingly no vulture remains are reported so far (MacDonald 1997). Bird remains are also well represented in the Pleistocene of the Maghreb, though most of them remain to be identified (Steele 2012). Remains of a large raptor, probably a vulture, are mentioned for the Middle Pleistocene hominid site of Jebel Irhoud, Morocco (Thomas 1981; Steele 2012: 119), but no further information is available.

Here we describe remains of aegypiine vultures from Ifri n'Ammar, a cave with rich Iberomaurusian and Middle Palaeolithic deposits in the Eastern Rif Mountains of Northern Morocco, which is already well known for a diverse Middle Palaeolithic mammal fauna (Mikdad et al. 2000; Hutterer 2010; Richter et al. 2010). The vulture material from the Middle Palaeolithic sections was preliminarily referred to *A. monachus* (Hutterer 2010), but actually represents both *A. monachus* and *Gyps fulvus*. Fossil evidence for *A. monachus* and *G. fulvus* is also relevant for reconstructing former areas of distribution for both species, which changed dramatically in the first half of the twentieth century.

Material and methods

The fossil specimens described herein were excavated during archaeological excavations of the rock shelter Ifri n'Ammar in N Morocco. Excavations were conducted between 1997 and 2015 by members of the Institut National des Sciences de l'Archéologie et du Patrimoine, Rabat (INSAP) and the Commission for the Archaeology of non-European Cultures (KAAK, Bonn) of the German Archaeological Institute DAI. The rock shelter is situated at 150 m in the eastern hills of the Plaine du Guerrouaou (34°47′03.68″N, 03°05′32.42″E), a large depression at 375 m surrounded by hills up to 1022 m elevation. The 6.3 m deep sediment filling covers a time range of 11,000–180,000 calBP. Principal publications on the archaeology of the site are by Mikdad et al. (2000), Moser (2003), and Nami and Moser (2010). All bones form part of the INSAP collections.

We follow Amadon (1977), who suggested to merge the monotypic taxa *Agypius monachus*, *Sarcogyps calvus*, *Torgos tracheliotos*, and *Trigonoceps occipitalis* into the genus *Aegypius*, and we follow Seibold and Helbig (1995) who applied the name Aegypiinae for a clade comprising the genera *Aegypius*, *Gyps*, and *Necrosyrtes*. For a more detailed

discussion on the nomenclature of aegypiine vultures, see Manegold et al. (2014).

We compared the fossils with osteological specimens of extant Gypaetinae and Aegypiinae, i.e., *Aegypius calvus* NHMUK 1858.1.10.1, ZFMK 22.11.54, ZFMK 83 SK 134, ZFMK 85 SK 29, ZMB 2000/4629; *Aegypius monachus* NHMUK 1848.3.8.2, SAPM 9, SMF 6379, ZMB 1900/14, ZMB 2000/1425, ZMB 2000/1426, ZMB 2000/1427; *Aegypius occipitalis* NHMUK 1867.10.5.11, NHMUK S/1954.30.54; *Aegypius tracheliotos* NHMUK 1930.3.24.248, SMF 1845, ZMB 2000/1432; *Gypaetus barbatus* SMF 11,790; *Gyps africanus* NHMUK S/1983.19.7, SMF 7977; *Gyps bengalensis* NHMUK S/1004.2.19, NHMUK S/1004.2.28; *Gyps coprotheres* NHMUK S/1983.19.3, NHMUK S/1983.19.4, SMF 8754; *Gyps fulvus* NHMUK 1861.3.24.6, SMF 7202, SMF 7203; *Gyps himalayensis* NHMUK S/2005.18.1 (partial skeleton), ZMB 2012/75; *Gyps tenuirostris* NHMUK 1885.8.18.36 (partial skeleton); *Gyps rueppelli* NHMUK S/1952.1.171; *Necrosyrtes monachus* NHMUK 1860.1.19.8, SMF 6440.

The anatomical terminology follows Baumel and Witmer (1993) as far as not stated otherwise.

Measurements were taken in accordance to the guidelines of von den Driesch (1976) and Louchart (2002). The height of the os quadratum was measured from the dorsal margin of the capitulum squamosum to the ventral margin of the condylus lateralis. Measurements of bones of the fossil *A. prepyrenaicus* and *G. melitensis* as well as additional measurements of extant aegypiine vultures were taken from the literature (Louchart 2002; Sánchez Marco 2007).

Institutional abbreviations

Institutional abbreviations. INSAP, Institut National des Sciences de l'Archéologie et du Patrimoine, Rabat, Morocco; NHMUK, Natural History Museum London/Tring, UK; SNSB-SAPM Staatssammlung für Anthropologie und Paläoanatomie Munich, Germany; SMF, Senckenberg Forschungsinstitut und Naturmuseum Frankfurt/Main, Germany; ZFMK, Zoologisches Forschungsmuseum Alexander Koenig Bonn, Germany; ZMB, Museum für Naturkunde Berlin, Germany.

Other abbreviations

Other abbreviations. ale, area lig. elastici; cd, condylus dorsalis; cde, caudal depression; cdj, cotyla quadratojugalis; cf, caput femoris; ch, caput humeri; cm, condylus medialis; cto, crista transversalis obliqua; ecd, epicondylius dorsalis; ecv, epicondylus ventralis; fmb, fossa m. brachialis; fp, fossa poplitea; fu, furrow; iit, impressio iliotrochantericus; liz, lacuna interzygapophysialis; pal, attachment site

for proximal articular ligament; pex, proc. extensorius; pf, pneumatic foramina; pfl, proc. flexorius; po, proc. orbitalis; ps, pons supratendinosus; psp, proc. spinosus; suh, sulcus humerotricipitalis; sus, sulcus scapulotricipitalis; tub, tubercle; I–III, trochlea metatarsi I–III.

Systematic palaeontology

Class **Aves** Linnaeus, 1758
Order **Accipitriformes** Vieillot, 1816
Family **Accipitridae** Vigors, 1824
Subfamily **Aegypiinae** W. P. Sclater, 1924

Genus *Aegypius* Savigny, 1809

Aegypius monachus Linnaeus, 1766
Figures 1a; 2c–d, s; 3 m, t, v–x

Referred material. Left quadratum lacking proc. orbitalis (INSAP/IA01/I14/19); left distal humerus (INSAP/IA/K15/24B); proximal right carpometacarpus (INSAP/IA/H13/21); distal left tarsometatarsus (INSAP/IA02/no number), terminal phalanges (INSAP/IA/no number; INSAP/IA01/K12/16; INSAP/IA02/I16/21).

Description and comparisons. Quadratum—With a total height of 31.0 mm, specimen INSAP/IA01/I14/19 is comparable in size to the quadratum of *A. monachus* ($\bar{x}$ = 30.4 mm (30.1–30.7 mm); n = 2). The dorsal margin of its cotyla quadratojugalis is strongly pronounced and laterally protruding, and the condylus medialis protrudes far ventrally (Fig. 1a). These characters are shared with *Aegypius*, but not with *Gyps*, in which the dorsal margin of the cotyla quadratojugalis is indistinct and which condylus medialis is not as elongated (Fig. 1a–d).

Humerus—The fragmentary distal end of a huge left humerus (INSAP/IA/K15/24B; Fig. 2c–d) strongly resembles that of *Aegypius*, i.e., both epicondylus dorsalis and epicondylus ventralis are very robust, and sulcus humerotricipitalis as well as sulcus scapulotricipitalis are deep and marked (Fig. 2c–f; Sánchez Marco 2007; Manegold et al. 2014). In *Gyps*, the epicondyli are less strongly developed and the sulcus humerotricipitalis is much shallower (Fig. 2k). The distal width of the specimen is 50.7 mm and thus larger than corresponding measurements of extant *A. monachus* and of the extinct *G. melitensis* (Table 1).

Carpometacarpus—The highly fragmentary proximal right carpometacarpus (INSAP/IA/H13/21; Fig. 2s) bears a large pneumatic foramen in its fovea carpalis cranialis, which is characteristic for *Aegypius*, although quite variable in respect of size and shape (Sánchez Marco 2007; Manegold et al. 2014). In *Gyps*, the fovea carpalis cranialis is generally not pneumatised, but few specimens show a longitudinal furrow pierced by minute foramina. Due to its fragmentary preservation, no meaningful measurements can be taken from the specimen, but it is comparable in size to *A. monachus* (Fig. 2s–t).

Tarsometatarsus—The fragment of a distal left tarsometatarsus (INSAP/IA02/no number) lacks trochlea metatarsi II, but its huge size and the short wing-like process of the trochlea metatarsi IV clearly indicate that it belongs to an aegypiine vulture (Fig. 3m). The width of its trochlea metatarsi III (10.7 mm) is larger than the corresponding measurements for *A. monachus* ($\bar{x}$ = 9.7 mm (8.9–10.3 mm); n = 9) and *G. fulvus* ($\bar{x}$ = 9.9 mm (9.3–10.5 mm); n = 10) (measurements taken from Sánchez Marco 2007). As in *Aegypius*, the trochlea metatarsi II extends further distal than trochlea metatarsi III (Fig. 3m), which is also the case in several species of *Gyps*, such as *G. africanus, G. bengalensis, G. tenuirostris* and *Gyps rueppelli.* In others such as *G. coprotheres, G. fulvus,* and *G. himalayensis* as well as *G. melitensis,*
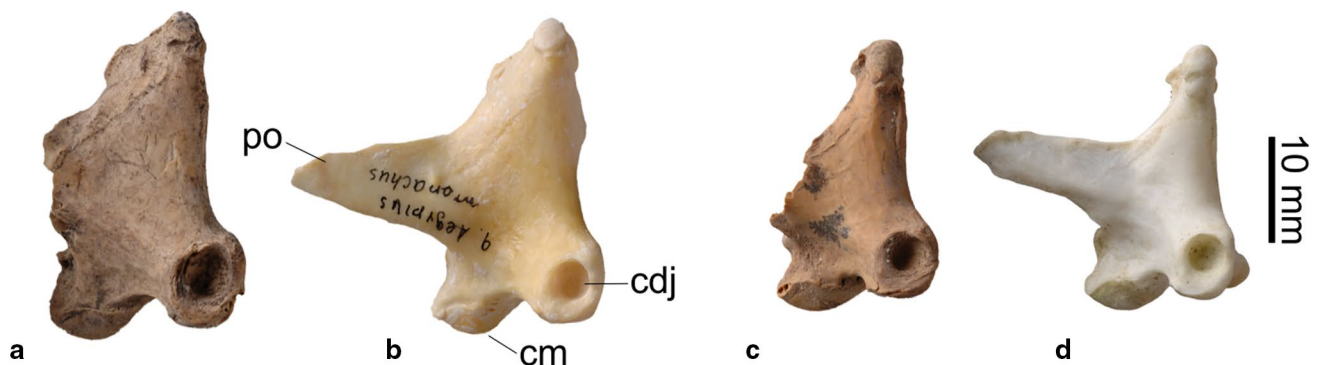

Fig. 1 Left ossa quadrata of fossil aegypiine vultures from Ifri n'Ammar (**a, c**) in comparison with corresponding bones of modern relatives (**b, d**): (**a**) *Aegypius* cf. *monachus* INSAP/IA01/I14/19, (**b**) *A. monachus* SAPM 9, (**c**) *Gyps* cf. *fulvus* INSAP/IA97/M13/25, and (**d**) *G. fulvus* SMF 7202

◄**Fig. 2** Humeri (**a, c–d, g–j**), coracoid (**n**), radius (**o**), os carpi ulnare (**q–r**), and carpometacarpus (**s**) of fossil aegypiine vultures from Ifri n'Ammar in comparison with corresponding bones of modern relatives (**b, e–f, k–l, m, p, t**): (**a–b**) proximal left humerus of (**a**) Aegypiinae gen. et sp. indet. INSAP/IA97/L16/15 and (**b**) *A. monachus* SAPM 9; (**c–f**) distal left humerus of (**c–d**) *Aegypius* cf. *monachus* INSAP/IA/K15/24B and (**e–f**) *A. monachus* SAPM 9 in cranial (**c, e**) and caudal view (**d, f**); (**g–h**) shaft of left humerus of *Gyps* cf. *fulvus* INSAP/IA02/H15/23B in cranial (**g**) and caudal view (**h**); (**i–j**) distal right humerus of *Gyps* cf. *fulvus* (**i**) INSAP/IA10/N14/25A and (**j**) INSAP/IA97/M14/18; (**k–l**) distal left humerus of *G. fulvus* SMF 7202 in cranial (**k**) and caudal view (**l**); left coracoid of (**m**) *G. fulvus* SMF 7202 and (**n**) *Gyps* cf. *fulvus* INSAP/IA10/P14/27A; distal right radius of (**o**) *Gyps* cf. *fulvus* INSAP/IA97/M13/Enl.22 and (**p**) *G. fulvus* SMF 7202; (**q–r**) left os carpi ulnare of *Gyps* cf. *fulvus* INSAP/IA/H11/5; (**s**) right proximal carpometacarpus of *Aegypius* cf. *monachus* INSAP/IA/H13/21 and (**t**) left mirrored carpometacarpus of *A. monachus* SAPM 9. Arrows indicate cut marks

trochlea metatarsi II and III are more or less on the same level (Fig. 3o; Mourer-Chauviré 1975; Louchart 2002).

Terminal phalanges—Three right terminal pedal phalanges (Fig. 3t, v–x) can be referred to Aegypiinae, because the proc. flexorius of all terminal phalanges does not project far distally as in other Accipitridae (Ballmann 1973). One of them (Fig. 3t) probably is pedal phalanx I/2 as it bears a shallow but distinct proc. extensorius. The remaining terminal phalanges exhibit a dorsoplantarly deep proc. extensorius, a prominent longitudinal crest and broad articular facets, which is also characteristic for *Aegypius*. The terminal phalanges of *Gyps* are much weaker with proc. flexorius and proc. extensorius being less developed (Fig. 3s). Remarkably, all ungual phalanges are larger than those measured for *A. monachus* and *G. fulvus* (Table 2).

Remarks. In respect of the postcranial skeleton, *A. monachus* is very similar to the slightly smaller and less robust *A. tracheliotos*. The latter is clearly distinguished from the former by its proportionally more elongated tarsometatarsi (Manegold et al. 2014; Manegold and Zelenkov 2014), but this character is not discernible in the present material. It seems nevertheless reasonable to refer the above listed specimens from Ifri n' Ammar to *A. monachus*, because of their large size and robustness.

Genus *Gyps* Savigny, 1809

Gyps cf. *fulvus* Hablizl, 1783
Figures 1c; 2 g–j, n, o, q–r; 3a, e–j, p, r; 4a, b, d–e, g–j, l–m, o–q, s

Referred material. Left quadratum lacking proc. orbitalis (INSAP/IA97/M13/25); cervical vertebrae (CV) (no number [CV #]; INSAP/IA/I4/18 [CV10]; INSAP/IA/I14-15/K14-15/23-24 [CV10]; INSAP/IA/I16/25; INSAP/IA/I16/26; INSAP/IA/K16/22; INSAP/IA97/M12/21 [CV10]; INSAP/

IA97/M12/23; INSAP/IA97/M14/23 [CV11–13; number refers to three associated cervical vertebrae]; INSAP/IA97/M14/24; INSAP/IA97/M20/13); thoracic vertebrae (TV) (INSAP/IA02/I14/21 [TV1]; INSAP/IA99/L19/24B [TV5]); extremitas omalis of left coracoid (INSAP/IA10/P14/27A); shaft of left humerus (INSAP/IA02/H15/23B); distal right humerus (INSAP/IA10/N14/25A; INSAP/IA97/M14/18); distal right radius (INSAP/IA97/M13/22); right (INSAP/no number) and left os carpi ulnare (INSAP/IA/H11/5; INSAP/IA/H13/9); right (INSAP/IA/G13/17), fragments of proximal right femur (INSAP/IA/K15/24B); left distal tibiotarsus (INSAP/IA/K13/23A; INSAP/IA97/M14/23), Pedal phalanges (INSAP/IA97/M14/23; INSAP/IA97/M14/24; INSAP/IA97/L11/18; INSAP/IA10/P14/27B; INSAP/IA/G17/19; INSAP/IA/I12/18).

Description and comparisons. Quadratum—Specimen INSAP/IA97/M13/25 differs from the quadratum of *Aegypius*, but resembles that of *Gyps* in having the dorsal margin of the cotyla quadratojugalis reduced and by its dorsoventrally short condylus medialis (Fig. 1c–d). With a total height of 25.3 mm, it is comparable in size to the quadratum of *G. fulvus* ($\bar{x} = 25.0$ mm (24.8–25.1 mm); $n = 2$).

Cervical vertebra—All large vertebrae from Ifri n'Ammar are comparable in size to those of *G. fulvus*, which are craniocaudally elongated and thus distinct from those of *Aegypius* (Lydekker 1890) (Fig. 4). Cervical vertebra (CV) INSAP/IA97/M14/24 resembles CV5, an uncatalogued specimen resembles CV 7, and specimens INSAP/IA/K16/22 and INSAP/IA97/M20/13 resemble CV8 of *G. fulvus*. The last-mentioned specimens are distinguished from CV8 of *Aegypius* by the lack of lateral prongs and a deeply furrowed area lig. elastici. Specimen INSAP/IA/M12/23 resembles CV9, and specimens INSAP/IA/I14-15/K14-15/23-24 and INSAP/IA/I4/18 show strong resemblance to CV10 of *G. fulvus*, i.e., they all have a rectangular, shallow lacuna interzygapophysialis, a craniocaudally short proc. spinosus, and prominent cristae transversales obliquae (only discernible in INSAP/IA/I4/18). Three associated cervical vertebrae (INSAP/IA97/M14/23) are comparable to CV11, 12, and 13 of *G. fulvus*. Two additional cervical vertebrae (INSAP/IA/I16/25; IA/I16/26) are similar to CV15 and 16 of *G. fulvus*, because in these vertebrae the proc. spinosus reaches the cranial margin of arcus vetrebrae and is flanked by two lateral pits; the basis of the proc. transversus is broad, concave and pierced with pneumatic foramina, and the facies articularis caudalis is rectangular. In INSAP/IA/I16/25, only the ventral part of the corpus vertebrae is preserved, but it strongly resembles INSAP/IA/I16/26 in respect of size and shape of the facies articularis caudalis.

Thoracic vertebra—The trapezoid facies articularis caudalis, the shallow, crest-like proc. ventralis and the large lateral pneumatic foramen indicate that specimen INSAP/IA02/I14/21 (Fig. 4s) is one of the cranialmost thoracic vertebrae

Fig. 3 Femora (**a, c**), tibiotarsi (**e–k**), tarsometatarsi (**m–n**), and pedal phalanges (**p, t, v–x**) of fossil aegypiine vultures from Ifri n'Ammar in comparison with corresponding bones of modern relatives (**b, d, l, o, q, s, u, y**): (**a–b**) proximal right femur of (**a**) *Gyps* cf. *fulvus* INSAP/IA/K15/24B, and (**b**) *A. monachus* SAPM 9. (**c–d**) Distal left femur of (**c**) *?Gyps melitensis* (no number), and (**d**) *A. monachus* SAPM 9. (**e–l**) Distal left tibiotarsus of (**e–h**) *Gyps* cf. *fulvus* INSAP/IA97/M14/23 in (**e**) cranial, (**f, h**) caudal, and (**g**) distal view; (**h**) detail of INSAP/IA97/M14/23 showing cut marks at its caudomedial margin. (**i–j**) Distal left (**i**) and (**j**) right tibiotarsus of *Gyps* cf. *fulvus* (**i**) INSAP/IA/K13/23A, and (**j**) INSAP/IA/G13/17. (**k–l**) Distal right tibiotarsus of (**k**) Aegypiinae gen. et sp. indet. INSAP/IA10/N13/25B, and (**l**) *G. fulvus* SMF 7202. (**m–o**) Distal left tarsometatarsus of (**m**) *Aegypius* cf. *monachus* INSAP/IA02/no number, (**n**) Aegypiinae gen. et sp. indet. INSAP/IA02/K13/22, and (**o**) *G. fulvus* SMF 4321. (**p–y**) Pedal phalanges of *Gyps* cf. *fulvus* (**p, r**), *G. fulvus* SMF 7202 (**q, s**), *Aegypius* cf. *monachus* (**t, v–x**), and *A. monachus* SAPM 9 (**u, y**). (**p, q**) Pedal phalanx II/1 of (**p**) *Gyps* cf. *fulvus* INSAP/IA97/M14/23, and (**q**) *G. fulvus* SMF 7202. (**r–s**) Pedal phalanx II/3 of (**r**) *Gyps* cf. *fulvus* INSAP/IA10/P14/27B, and (**s**) *G. fulvus* SMF 7202. (**t–x**) Terminal pedal phalanges of (**t–u**) *Aegypius* cf. *monachus* (**t**) no number, (**u**) INSAP/IA/K12/16, (**v**) INSAP/IA02/I16/21 and (**x**) *A. monachus* SAPM 9. Arrows indicate cut marks
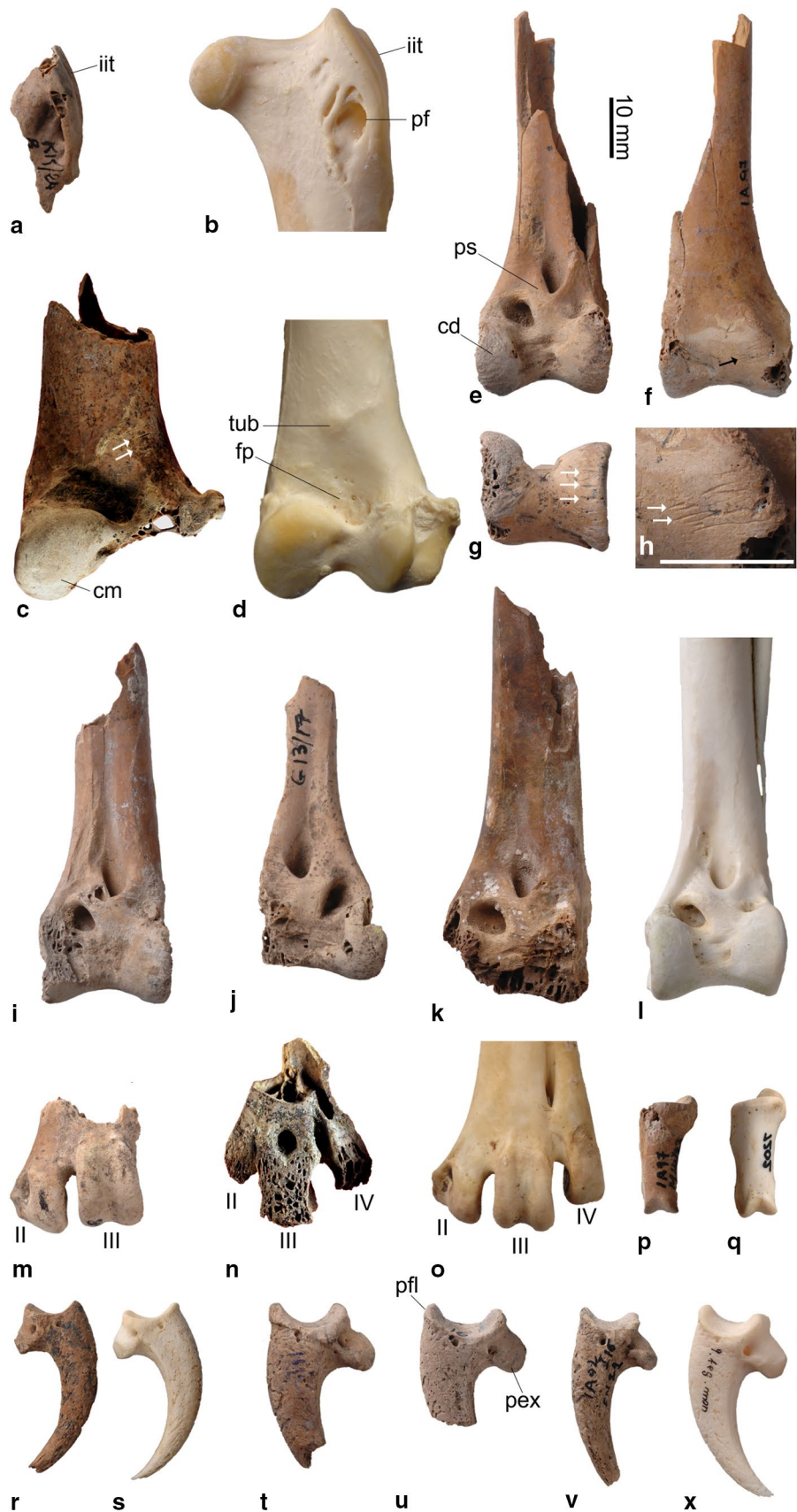
Table 1 Measurements of humeri of fossil Aegypiinae from Ifri n'Ammar in comparison with those of extant and extinct Aegypiinae (all measurements in mm)

	Proximal width	Caput width	Caput depth	Distal width
Aegypiinae gen. et sp. indet. (IA97/L16/15)	60.8	32.9	17.3	–
Aegypius monachus (IA/K15/24B)	–	–	–	50.7
Aegypiinae gen. et sp. indet. (IA01/I13/6)	–	–	–	46.1
Aegypiinae gen. et sp. indet. (IA01/K13/13)				45.7
A. monachus	58.0 (53.8–60.4) n=7	30.2; 33.0	15.5; 15.7	45.0–47.2
A. tracheliotos	53.7 (52.0–55.3) n=3	29.6	13.7	45.3 (43.5–47.3) n=3
G. fulvus	55.3 (54.0–56.8) n=6	29.9 (27.7–31.7) n=6	15.3 (14.6–16.3) n=6	45.1 (43.6–46.0) n=5
G. melitensis[a]	–	–	–	47.9; 48.4

[a]Measurements after Sánchez Marco ([2007])

Table 2 Measurements of pedal phalanges of fossil Aegypiinae from Ifri n'Ammar in comparison with those of extant and extinct Aegypiinae (all measurements in mm)

	I/2		II/3		III/4	
	(1)	(2)	(1)	(2)	(1)	(2)
Aegypius monachus (IA/no number)	14.0	20.0	–	–	–	–
Aegypius monachus (IA/K12/16)	–	–	14.0	19.2	–	–
Gyps cf. *fulvus* (IA97/L11/18)	–	–	10.0	13.7	–	–
Gyps cf. *fulvus* (IA10/P14/27B)	–	–	9.8	13.0	–	–
Aegypius monachus (IA/I16/21)	–	–	–	–	9.9	15.6
Gyps cf. *fulvus* (IA/G17/19)	–	–	–	–	9.3	13.0
Gyps cf. *fulvus* (IA/I12/18)	–	–	–	–	9.0	13.1
A. monachus	12.2 n=1	17.0 n=1	12.2; 12.7 n=2	17.7; 17.8 n=2	8.1; 8.3 n=2	13.2; 13.4 n=2
G. fulvus	9.7; 10.4 n=2	12.5; 13.3 n=2	10.6 n=2	13.3; 14.0 n=2	9.0; 9.1 n=2	13.1; 13.6 n=2

Measurements are taken in accordance to Louchart ([2002]; Fig. 9) with (1) being the dorsoventral height of articular facet, and (2) being the proximal height from distal tip of proc. flexorius to dorsal margin of articular facet (all measurements in mm)

(TV), probably the TV1, whereas the fragmentary INSAP/IA99/L19/24B resembles TV5 of *G. fulvus* in size and shape.

Coracoid—The extremitas omalis of a left coracoid (INSAP/IA10/P14/27A; Fig. 2n) resembles extant *G. fulvus* in its distinct longitudinal ligamental attachment site and the deep concave area just proximal to the facies articularis humeralis. The proximodistal length and lateromedial width of the facies articularis humeralis is 28.6 mm and 17.0 mm, respectively, which is comparable to the dimensions of *G. fulvus* (Fig. 2m–n).

Humerus—Although only fragmentarily preserved, the shaft of a left humerus (INSAP/IA02/H15/23B; Fig. 2g–h) can be referred to *G. fulvus*, because both sulcus humerotricipitalis and sulcus scapulotricipitalis are shallow and indistinct. In contrast to *Aegypius*, both sulci do not reach towards the level of the proximal margin of the fossa m. brachialis (Fig. 2h, l). The width of the fragmentary shaft just proximal of fossa m. brachialis is 23.5 mm, which is comparable to the size of *G. fulvus*. The epicondylus ventralis and the attachment site for the proximal articular ligament of the distal right humerus (INSAP/IA10/N14/25A) (Fig. 2i) and the epicondylus dorsalis of another specimen (INSAP/IA97/M14/18) (Fig. 2j) are as indistinct as in *Gyps* (Fig. 2k), and the specimen is thus clearly distinguishable from the corresponding bone of *Aegypius* (Fig. 2e–f; Manegold et al. 2014).

Radius—As in all Aegypiinae, the facies articularis ulnae of the fragmentary distal right radius (INSAP/IA97/M13/22; Fig. 2o) shows a pair of deep depressions with the cranial one being highly pneumatic. It shows several
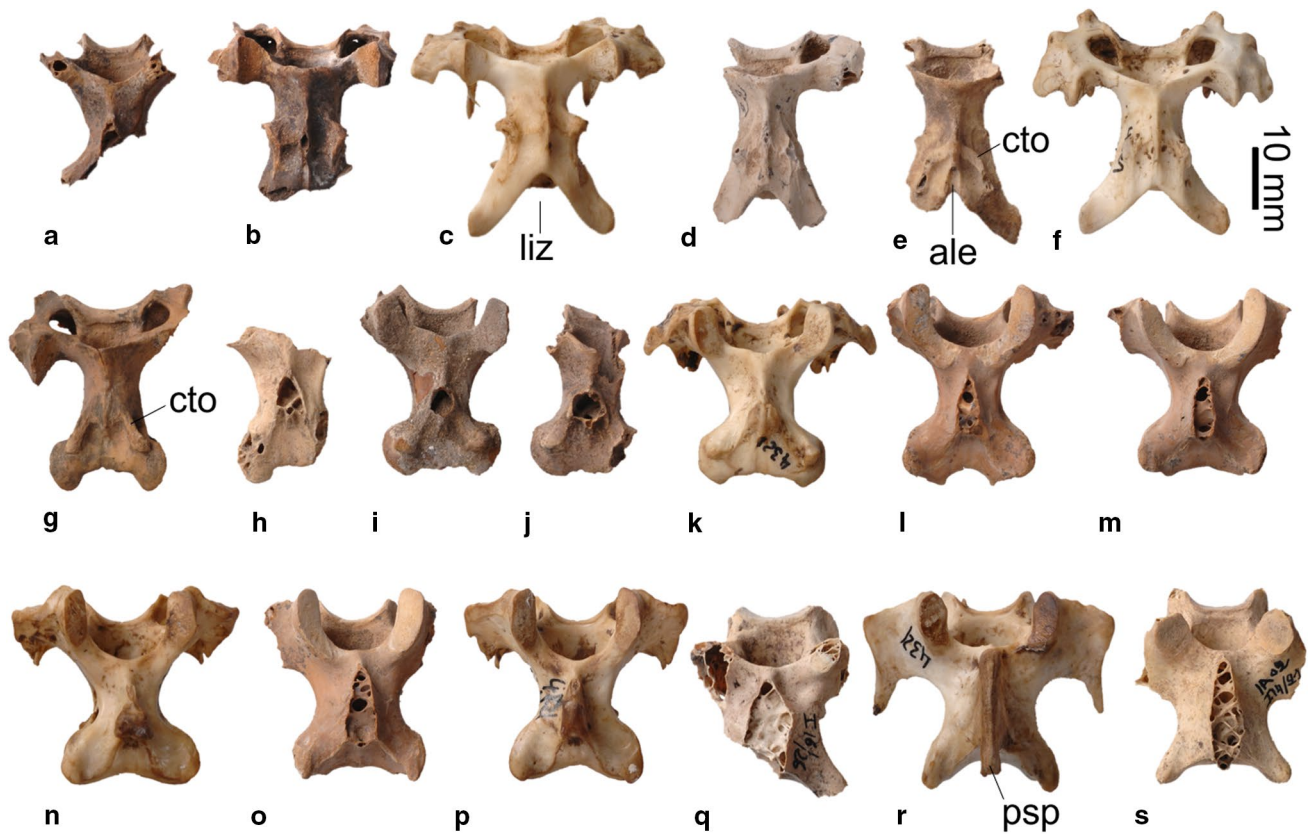
Fig. 4 Cervical (CV) and thoracal vertebrae (TV) referable to *Gyps* cf. *fulvus* (**a, b, d, e, g, h, i, j, l, m, o, q, s**) in comparison with corresponding bones of extant *G. fulvus* SMF 4321 (**c, f, k, n, p, r**): (**a**) CV 5, INSAP/IA97/M14/24, (**b**) CV 7, INSAP/IA/no number, (**c**) CV 7, (**d**) CV8, INSAP/IA/K16/22, (**e**) CV 8, INSAP/IA97/M20/13, (**f**) CV 8, (**g**) CV 9, INSAP/IA97/M12/23, (**h**) CV 10, INSAP/IA/I14-15/ K14-15/23–24/, (**i**) CV 10, INSAP/IA97/M12/21, (**j**) CV 10, INSAP/IA/I4/18, (**k**) CV 10, (**l**) CV 11, INSAP/IA97/M14/23, (**m**) CV 12, INSAP/IA97/M14/23, (**n**) CV 12, (**o**) CV 13, INSAP/IA97/M14/23 (**p**) CV 13 (**q**) CV 15/16, INSAP/IA/I16/26 14, (**r**) CV 15, (**s**) CT 1, INSAP/IA/I14/21

features characteristic for *Gyps*, such as a more distinct caudal depression (but see Sánchez Marco 2007), a distinct furrow cranial of the facies articularis radiocarpalis, and a more distal ligamental attachment site on its caudal surface (Fig. 2o–p). With a distal width of 19.7 mm, specimen INSAP/IA97/M13/22 falls within the size range of *G. fulvus* ($\bar{x} = 19.2$ mm (18.5–19.9 mm); $n = 5$).

Os carpi ulnare—All three ossa carporum ulnaria from Ifri n'Ammar show characteristic features of Aegypiinae, such as a pneumatised facies articularis ulnocarpalis (Fig. 2q). Compared to *A. monachus*, the incisura metacarpalis is rostrocaudally broader as it is the case with *G. fulvus* (Sánchez Marco 2007). All specimens fall well within the size range of *G. fulvus* and are smaller than the average os carpi ulnare of *A. monachus* (Fig. 2q–r; Table 3).

Femur—Two small fragments of a proximal right femur probably belong to the same individual (INSAP/IA/K15/24B). One of them (Fig. 3a) shows several pneumatic foramina craniomedially of the crista iliotrochantericus, which is characteristic for Accipitridae (Holdaway 1994), as well as a crescent-shaped impressio iliotrochantericus, which is found in *Aegypius* and *Gyps* (Fig. 3b). Based on its proximal width, this femur appears to be slightly smaller than that of *G. fulvus*, but distinctly smaller than *A. monachus* (Table 3).

Tibiotarsus—In contrast to *Aegypius* and virtual all the remaining Accipitridae (Ballmann 1973), the distal end of tibiotarsus of *Gyps* is craniocaudally deep and in distal view it appears to be square rather than oblong (Fig. 3g; Lydekker 1890). This feature is discernible in all three distal tibiotarsi from Ifri n'Ammar (Fig. 3e–j). The margins of the condyli are more or less abraded in all specimens, so that meaningful measurements are hardly possible, but they all seem to fall in the size range of *G. fulvus* (Table 3).

Pedal phalanges—Pedal phalanx II/1 (INSAP/IA97/M14/23; Fig. 3p) is not abbreviated as in most Accipitridae

Table 3 Measurements of ossa carporum ulnaria, femora and tibiotarsi of fossil Aegypiinae from Ifri n'Ammar in comparison with those of extant and extinct Aegypiinae (all measurements in mm)

	Os carpi ulnare	Femur			Tibiotarsus	
	Maximal width	Proximal width	cf width	Distal width	Distal width	Distal depth
Gyps cf. *fulvus* (IA/H11/5)	21.1	–	–	–	–	–
Gyps cf. *fulvus* (IA/H13/9)	21.3	–	–	–	–	–
Gyps cf. *fulvus* (IA/no number)	20.1	–	–	–	–	–
Gyps cf. *fulvus* (IA/K15/24B)	–	29.7	–	–	–	–
Gyps cf. *fulvus* (IA/no number left)	–	–	14.0	–	–	–
Gyps cf. *fulvus* (IA/no number right)	–	–	15.6	–	–	–
Gyps cf. *fulvus* (IA/I13/18 left)	–	–	[12.8]	–	–	–
Gyps cf. *fulvus* (IA/I13/18 right)	–	–	14.6	–	–	–
Aegypiinae gen. et sp. indet. (IA/I14/20)	–	–	13.1	–	–	–
Aegypiinae gen. et sp. indet. (IA/K14/24B)	–	–	13.2	–	–	–
Aegypiinae gen. et sp. indet. (IA/M14/23)	–	–	14.4	–	–	–
Aegypiinae gen. et sp. indet. (IA/no number)	–	–	–	38.0	–	–
Gyps cf. *fulvus* (IA/G13/17)	–	–	–	–	–	[19.7]
Gyps cf. *fulvus* (IA/K13/23A)	–	–	–	–	[23.0]	–
Gyps cf. *fulvus* (IA97/M14/23)	–	–	–	–	26.0	20.0
A. monachus	24.1; 24.2	38.3[a] (36.5–42.4) $n=10$	14.5	36.8[a] (35.1–39.0) $n=10$	–	–
A. tracheliotos	22.2	33.2	14.0	33.9	26.2	20.2
Gyps fulvus	22.1 (21.2–23.0) $n=4$	35.7[a] (31.8–38.4) $n=14$	14.0	33.6[a] (31.0–35.3) $n=14$	24.5[b] (23.0–26.5) $n=9$	20.7[b] (19.6–22.5) $n=9$
G. melitensis	20.5; 21.6[a]	39.2[a] (38.9–39.4) $n=3$	–	35.7[a]	26.5[b] (26.3–28.0) $n=4$	22.7; 24.8[b]

[a]Measurements after Sánchez Marco (2007)

[b]After Louchart (2002)

including *Aegypius*, but elongated as in all species of *Gyps* (Fig. 3q). INSAP/IA97/M14/24 is indistinguishable from pedal phalanx III/3 of *G. fulvus*, and specimens INSAP/IA97/L11/18, INSAP/IA10/P14/27B (Fig. 3r), INSAP/IA/G17/19 and INSAP/IA/I12/18 are of the same size as phalanx II/3 and III/4 of *G. fulvus*, respectively.

Remarks. All species of *Gyps* are very similar osteologically, but *G. fulvus* is larger than white-backed (*G. africanus*) and slightly larger than Rüppell's Vulture (*G. rueppelli*). The last mentioned species are today restricted to Africa south of the Sahara, though *G. rueppelli* has been regularly reported in small numbers in North Africa and on the Iberian Peninsula in recent years (Ramírez et al. 2011). Thus, it seems most likely that the fossil specimens described above are remains of G. *fulvus*, but because of the fragmentary nature of the material this identification remains tentative. Three specimens (extremitas sternalis of coracoid INSAP/IA10/P14/27A, distal humerus INSAP/IA10/N14/25A, and distal

tibiotarsus INSAP/IA10/N13/25B) show cut marks (Fig. 2i; 3f–h).

?***Gyps melitensis*** Lydekker, 1890
Figure 3c

Referred material. Distal left femur (INSAP/IA/no number).

Description and comparisons. Femur—The distal femur is only imperfectly preserved, lacking most of its condylus lateralis and sulcus intercondylaris. In contrast to *Aegypius* but as in *Gyps*, the femur lacks a distinct tubercle proximal to fossa poplitea (Manegold et al. 2014), only a narrow and shallow, more distally situated crest is discernible (Fig. 3c). The distal width of the femur measures 38.0 mm, which is wider than any distal femur measured for *G. fulvus* (Table 3). According to Lydekker (1890) the width of one distal femur of *G. melitensis* from Malta is 44.0 mm, but Sánchez Marco (2007) gives only 35.7 mm for the same specimen (Table 3).

Remarks. Because it lacks a distinct tubercle proximal to the fossa poplitea and because of its large size, this specimen is tentatively referred to *G. melitensis*, which was not reported previously for the Maghreb. This femur shows several cut marks at its caudomedial margin.

Aegypiinae gen. et sp. indet.
Figures 2a; 3 k, n

Referred material. Dorsal fragment of a costa vertebralis (INSAP/IA/K16/26); proximal left humerus (INSAP/IA97/L16/15); fragments of further two humeri (INSAP/IA01/I13/6; IA01/K13/13); caput femoris of right femur (INSAP/IA/no number; INSAP/IA/I13/18; INSAP/IA/I14/20; INSAP/IA97/M14/23); caput femoris of left femur (INSAP/IA/no number; INSAP/IA/I13/18); right distal tibiotarsus (INSAP/IA97/L19/12); left distal tibiotarsus (INSAP/IA10/N13/25B); proximal right fibula (no number); fragment of proximal right tarsometatarsus (INSAP/IA/K16/24); distal left tarsometatarsus (INSAP/IA02/K13/22).

Description and comparisons. Costa vertebralis—The dorsal fragment of a sternal rib is comparable in size with that of *A. monachus* and *G. fulvus*, and shows a similar pattern of pneumatic foramina on its cranial and caudal surface. The fragmentary nature of the specimen does not allow identification beyond the subfamily level, and because the sternal ribs of the Bearded Vulture (*Gypaetus barbatus*) are also pneumatic, referral this fragment to Aegypiinae is only tentative.

Humerus—Fragments of a huge proximal left humerus (INSAP/IA97/L16/15; Fig. 2a) can be referred to Aegypiinae, because it shows numerous minute foramina along the caudodistal margin of caput humeri, which is characteristic for this taxon (Fig. 2b). However, *Aegypius* and *Gyps* apparently are indistinguishable on the basis of the proximal end of their humeri by means of discrete characters. The fossil specimen is clearly larger than *G. fulvus* and its proximal width even exceeds that measured for the largest specimen of our restricted sample of comparative skeletons of *A. monachus* (Table 1), though it might belong to *G. melitensis* or a large fossil species of *Aegypius* (see below). Fragments of two further humeri (INSAP/IA01/I13/6 and IA01/K13/13) are smaller (Table 1) and may belong to *G. fulvus*.

Femur—Six femoral heads are tentatively assigned to Aegypiinae due to their large size. Two of them (INSAP/IA/I14/20; INSAP/IA/K14/24B) are, however, narrower than the caput femoris of *G. fulvus*. One specimen (INSAP/no number) is similar in size to the caput femoris of *G. fulvus* and *A. tracheliotos*, and two others (INSAP/IA/I13/18; INSAP/IA97/M14/23) are comparable in size to *A. monachus* (Table 3). One fossil specimen (INSAP/no number) is distinctly wider than the caput femoris of the latter species

(Table 3). All these specimens are much too fragmentary for any identification beyond the subfamily level.

Tibiotarsus—The huge size and overall similarity allow the assignment of a distal right tibiotarsus (INSAP/IA/K16/24) to Aegypiinae. Only its cranial surface is preserved and its condyli are heavily abraded, so that no meaningful measurements are possible. The intercondylar tubercle on the pons supratendinosus is quite indistinct, and the position of the tuberositas retinaculi medialis seems to be more similar to the situation in *G. fulvus*, but the lack of more diagnostic characters makes a more detailed identification impossible. The same applies for a distal left tibiotarsus (INSAP/IA10/N13/25B; Fig. 3k), which lacks both condyli and the area of the incisura intercondylaris, so that differentiating characters of *Aegypius* and *Gyps* are no longer discernible.

Fibula—The proximal fragment of a right fibula (INSAP/no number) is comparable in size and morphology to the corresponding bone of the larger aegypiine vultures, but its poor preservation does not allow more meaningful measurements and comparisons.

Tarsometatarsus—The lateral fragment of a proximal tarsometatarsus (INSAP/IA/K16/24) can be referred to Aegypiinae, because of its large size and the lack of a tuberculum m. fibularis brevis. A large, but heavily abraded distal left tarsometatarsus (INSAP/IA02/K13/22; Fig. 3n) probably is also referable to an aegypiine vulture, but the poor preservation prevents any further identification.

Remarks. Most of the specimens listed above are fragments of rather indistinctive bones. Others are insufficiently preserved so that the identification beyond the subfamily level is not possible.

Discussion

It is evident that at least three different vulture species are represented in the bird material collected at Ifri n'Ammar. Seven remains are referable to *A. monachus*, 30 specimens can be tentatively referred to *G. fulvus*. A distal femur with features characteristic for *Gyps* clearly exceeds the corresponding bone of *G. fulvus* in size, and is most likely referable to *G. melitensis*.

Four bones, a distal humerus (INSAP/IA/K15/24B) and three pedal phalanges (INSAP/no number; INSAP/IA/K12/16; INSAP/IA02/I16/21) show diagnostic characters of *Aegypius*, but are larger than the corresponding bones of *A. monachus*. However, our comparisons are based on a small sample of comparative skeletons of *A. monachus* that might not reflect the actual size range within this species. All fossil specimens mentioned above might belong to large individuals of *A. monachus*. Alternatively, they might indicate the presence of a separate, now extinct *Aegypius* species, such

as *A. prepyrenaicus*. This palaeospecies was described from the Upper Pleistocene of Spain on the basis of a particular large proximal ulna (Hérnandez 2001), but Sánchez Marco (2007) regarded it as *nomen dubium*. A fragmentary proximal humerus (INSAP/IA/L16/15) and a left caput femoris (INSAP/no number) fall within the same size category as the aforementioned bones, but cannot be positively referred to either *Aegypius* or *Gyps* due to the lack of diagnostic characters. They might either belong to large specimens of *A. monachus*, or to *G. melitensis* or even to the enigmatic *A. prepyrenaicus*. Given the fragmentary nature of the material and the insufficient data on the size range of *A. monachus*, however, we abstain from further speculations on the presence of a fourth species of vulture at Ifri n'Ammar.

Palaeoecological implications

Bones of *Aegypius monachus* and *Gyps fulvus* co-occurred in the Ifri n'Ammar for more than 2.000 years, from level 16 to 24. This is equivalent to a calibrated age of about 14,735–14,378 calBP (level 17) to 16,411–16,159 calBP (level 24). Bones of *G. fulvus* were found in almost all levels, from the top (level 5) to level 27, the beginning of the Palaeolithic (Hutterer 2010). In a diagram in Mikdad et al. (2000: fig. 38), records of *Gyps* in the upper levels 12–15 were misidentified as *Aegypius*. The period of overlap of *Aegypius monachus* and *Gyps fulvus* found here coincides with a high concentration of eggshells of *Struthio camelus* in the cave (Hutterer 2010), and therefore probably with a sufficient supply of food for two species of vultures.

Evidence for the manipulation of bird bones

Extremitas omalis of left coracoid (INSAP/IA10/P14/27A), distal humerus INSAP/IA10/N14/25A and distal tibiotarsi INSAP/IA97/M14/23 und INSAP/IA10/N13/25B show cut marks. This is not surprising as all the larger bones found in the Ifri n'Ammar were left by humans and had been manipulated while preparing animals as food, or in the course of other unknown practices.

Implications on distributional changes

The modern distribution of aegypiine vultures in the Maghreb changed dramatically during the first half of the twentieth century. *G. fulvus* was a common breeding bird in Morocco, Algeria and Tunisia, but witnessed a dramatic decline and local extinction since 1900 (Thomsen and Jacobsen 1979; Cramp and Simmons 1980; Isenmann and Moali 2000; Isenmann 2005). Evidence of *A. monachus* for the Upper Pleistocene is especially noteworthy, because this species does no longer breed in the Maghreb region (Thiollay 1994). Its former status in North Africa is uncertain, because

it was frequently confused with the Lappet-faced Vulture (*A. tracheliotos*) (Cramp and Simmons 1980). It formerly bred in Morocco, but apparently was restricted to few colonies in the Tangier Peninsula (Heim de Balsac and Mayaud 1962; Thévenot et al. 2003). Reports on vulture colonies in the north of Algeria from the late 19th and early twentieth century might pertain to this species (Sharpe 1878), although they are generally regarded as former breeding evidence for *A. tracheliotos* (Heim de Balsac and Mayaud 1962; Isenmann and Moali 2000).

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