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

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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 (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 Haoua Fteha, Libya, comprises more than 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 *G. 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 (KAARK, Bonn) of the German Archaeological Institute DAI. The rock shelter is situated at 150 m in the eastern hills of the Plaine du Guerroua (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 *Aegypius monachus*, *Sarcogyps calvus*, *Torgos tracheliotus*, 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 tracheliotus* NHMUK 1930.3.24.248, SMF 1845, ZMB 2000/1432; *Gypae tus 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. preprenaicus 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 media lis; cto, cristra transversalis obliqua; ecc, epycondylus dorsalis; ecv, epycondylus ventralis; fmb, fossa m. brachialis; fp, fossa poplitea; fu, furrow; iht, impressio ili trochantericus; lis, lacuna interzygapophysialis; pal, attachment site

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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; 3m, 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* (\(\bar{x} = 30.4 \text{ mm} (30.1–30.7 \text{ mm}; n = 2)\). 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 pneumatized, 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* (\(\bar{x} = 9.7 \text{ mm} (8.9–10.3 \text{ mm}; n = 9)\) and *G. fulvus* (\(\bar{x} = 9.9 \text{ mm} (9.3–10.5 \text{ mm}; n = 10)\) (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. tenurostris* and *Gyps rueppelli*. In others such as *G. coprotheres*, *G. fulvus*, and *G. himalayensis* as well as *G. melitensis*,

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![Fig 1](https://via.placeholder.com/150)

**Fig. 1** Left ossa quadrata of fossil aegypiine vultures from Iffr 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

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trociloid 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 dorsoplanarly 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. tracheliotus. 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/I14/18 [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 dorsally 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 (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 craniodiagonally 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/I12/23 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 craniodiagonally short proc. spinosus, and prominent cristae transversales oblique (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 vertebrae 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 (e) ?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–u) 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
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Coracoid—The extremitas omalis of a left coracoid (INSAP/IA10/P14/27A; Fig. 2 n) 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. 2 m–n).

Humerus—Although only fragmentarily preserved, the shaft of a left humerus (INSAP/IA02/H15/23B; Fig. 2 g–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. 2 h, 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. 2 i) and the epicondylus dorsalis of another specimen (INSAP/IA97/M14/18) (Fig. 2 j) are as indistinct as in Gyps (Fig. 2 k), and the specimen is thus clearly distinguishable from the corresponding bone of Aegypius (Fig. 2 e–f; Manegold et al. 2014).

Radius—As in all Aegypiinae, the facies articularis ulnae of the fragmentary distal right radius (INSAP/IA97/M14/18; Fig. 2 o) shows a pair of deep depressions with the cranial one being highly pneumatic. It shows several

| 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 | 30.2; 33.0 | 15.5; 15.7 | 45.0–47.2 |
| A. tracheliotos | 53.7 | 29.6 | 13.7 | 45.3 |
| G. fulvus | 55.3 | 29.9 | 15.3 | 45.1 |
| G. melitensis | – | – | – | 47.9; 48.4 |

*Measurements after Sánchez Marco (2007)
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 osa carporum ulnaria from Ifri n’Ammar show characteristic features of Aegypini, 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

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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, p, r): (a) CV 5, INSAP/IA97/M14/24, (b) CV 7, INSAP/IA/no number, (c) CV 7, (d) CV 8, INSAP/IA/K16/22, (e) CV 8, INSAP/IA97/M20/13, (f) CV 9, INSAP/IA97/M12/23, (g) 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

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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; INSAP/IA/I14/20; INSAP/IA/K16/24); proximal right fibula (no number); fragment of proximal right tarsometatarsus (INSAP/IA02/K13/22).

Description and comparisons. Costa vertebralis—The dorsal fragment of a costo vertebralis (INSAP/IA/K16/26) is comparable in size to 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 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/K13/24B) 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 Aegipiinae, 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 Aegypiinae, 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 (Hernández 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.

**Palaeoeological 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 and Moali 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. tracheliotus*) (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. tracheliotus* (Heim de Balsac and Mayaud 1962; Isenmann and Moali 2000).

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