Paläontologische Zeitschrift
2007, Vol. **81/4**, p. 457–462, 31-12-2007

Synonymy and actual affinities of the putative Middle Eocene "New World vulture" *Eocathartes* LAMBRECHT, 1935 and "hornbill" *Geiseloceros* LAMBRECHT, 1935 (Aves, Ameghinornithidae)

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with 2 figures and 1 table

MAYR, G. 2007. Synonymy and actual affinities of the putative Middle Eocene "New World vulture" *Eocathartes* LAMBRECHT, 1935 and "hornbill" *Geiseloceros* LAMBRECHT, 1935 (Aves, Ameghinornithidae). – Paläontologische Zeitschrift **81** (4): 457–462, 2 figs., 1 tab., Stuttgart, 31. 12. 2007.

Kurzfassung: Die Taxonomie und Verwandtschaftsbeziehungen des mutmaßlichen "Neuweltgeiers" *Eocathartes robustus* LAMBRECHT, 1935 und des "Nashornvogels" *Geiseloceros robustus* LAMBRECHT, 1935 aus dem mittleren Eozän des Geiseltals werden revidiert. Es wird dargelegt, dass die Holotypus-Exemplare zu einem einzigen Individuum gehören, dessen Osteologie sehr derjenigen von *Strigogyps sapea* (PETERS, 1987) aus dem mittleren Eozän von Messel ähnelt. Die Art wird *Strigogyps robustus* (LAMBRECHT, 1935), n. comb. zugeordnet und ist ein weiterer Beleg für die große Ähnlichkeit zwischen den eozänen Avifaunen des Geiseltals und der Grube Messel. *Strigogyps* ist ein Vertreter der Ameghinornithidae, deren Verwandtschaftsbeziehungen ungeklärt sind; Cathartidae (Neuweltgeier) und Bucerotidae (Nashornvögel) sind aus dem Geiseltal nicht nachgewiesen.

Schlüsselwörter: fossile Vöge • Geiseltal • Messel • *Strigogyps robustus* n. comb. • Taxonomie

Abstract: The taxonomy and phylogenetic affinities of the putative "New World vulture" *Eocathartes robustus*, LAMBRECHT, 1935 and the "hornbill" *Geiseloceros robustus* LAMBRECHT, 1935 from the Middle Eocene of the Geisel Valley in Germany are revised. It is shown that the holotype specimens belong to a single individual, whose osteology closely resembles that of *Strigogyps sapea* (PETERS, 1987) from the Middle Eocene of Messel (Germany). The species is classified into *Strigogyps robustus* (LAMBRECHT, 1935), n. comb., and provides further evidence for the great similarity between the Eocene avifaunas of the Geisel Valley and Messel. *Strigogyps* is a representative of the Ameghinornithidae whose phylogenetic affinities are uncertain; there is no fossil record of either Cathartidae (New World vultures) or Bucerotidae (hornbills) from the Geisel Valley.

Keywords: fossil birds • Geisel Valley • Messel • *Strigogyps robustus* n. comb. • taxonomy

Introduction

In 1935, the Hungarian palaeornithologist Kálmán Lambrecht described two avian species from the Middle Eocene of the Geisel Valley (Geiseltal) in Germany as *Eocathartes robustus* and *Geiseloceros robustus*. *E. robustus* was based on a pelvis and associated hindlimb bones and considered to be the earliest fossil representative of the New World vultures (Cathartidae; LAMBRECHT 1935; CRACRAFT & RICH 1974). The holotype of *G. robustus* consists of elements of the wing skeleton and the pectoral girdle and, according to LAMBRECHT (1935: 362), was found only two meters away from the bones of *E. robustus*. LAMBRECHT (1935: 365) noted that "these remains are the most difficult problem in the newer collection of bird specimens. The preserved bones, which besides the forelimbs also constitute parts of the shoulder girdle, exhibit such a peculiar morphology that it was not even possible to determine their family-level affiliation on the basis of the comparative osteological collection at my disposal" [my translation]. Although LAMBRECHT (1935) refrained from an explicit phylogenetic assignment of *Geiseloceros*, he made only comparisons with extant hornbills (Bucerotidae), for

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0031–0220/07/0081–457 $ 2.70
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Tab 1. Length measurements (maximum length in mm) of major limb elements of different species of *Strigogyps* in comparison; measurements of *Strigogyps robustus* after LAMBRECHT (1935) in brackets.

	humerus	ulna	carpometacarpus	tibiotarsus	tarsometatarsus
Strigogyps robustus (GMH 5883 and 5884)	~104 [117]	~90 [90]	~49 [51]	~196 [215]	~105 [116[1]/110[2]]
Strigogyps sapea (holotype)	~87	~75	~38	~150	~83
Strigogyps sp. (SMF-ME 11094)	71.8	56.6	37.7	—	—
Strigogyps dubius (holotype of "*Ameghinornis minor*")	120.3[3]	—	—	—	—

[1] LAMBRECHT (1935: 363)
[2] LAMBRECHT (1935: 365)
[3] after MOURER-CHAUVIRÉ (1981)

which reason BRODKORB (1971) classified the fossil into the Bucerotidae.

It was first assumed by P. Houde (in OLSON 1985: 136) that the remains of *Eocathartes robustus* and *Geiseloceros robustus* are from a single individual, and OLSON (1985) questioned their correct identification. Because of similar proportions of the wing bones, I tentatively assigned *Geiseloceros robustus* to the Idiornithidae in an earlier revision of part of the avian material from the Geisel Valley (MAYR 2002, see also MAYR 2005a). Idiornithids are extinct representatives of the Cariamae, the clade including extant Cariamidae (seriemas). These birds have a more elongate and proportionally longer tarsometatarsus than *Eocathartes robustus*, and I thus regarded the phylogenetic affinities of the latter uncertain (MAYR 2002).

However, here I present evidence that the two partial skeletons assigned to *Eocathartes* and *Geiseloceros* are indeed from a single individual, which does not belong to the Idiornithidae. Instead, and except for its larger size (Tab. 1), it perfectly matches *Strigogyps* ("*Aenigmavis*") *sapea* (PETERS, 1987) from the Middle Eocene German fossil site Messel. *S. sapea* has originally been considered an Old World representative of the Phorusrhacidae, a further taxon of the Cariamae (PETERS 1987), but this classification has meanwhile been disproved (ALVARENGA & HÖFLING 2003; MAYR 2005b). The Geisel Valley specimens provide new information on the poorly known osteology of *Strigogyps*, and further corroborate the great similarity between the avifauna of the Geisel Valley and the more comprehensive and better studied one of Messel (MAYR 2002).

Material and methods

Osteological terminology follows BAUMEL & WITMER (1993), measurements are in millimeters.

Institutional abbreviations: GMH – Geiseltalmuseum Halle, Halle/Saale, Germany; SMF – Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

Systematic paleontology

Aves LINNAEUS, 1758
Ameghinornithidae MOURER-CHAUVIRÉ, 1981

Strigogyps GAILLARD, 1908

1935 *Eocathartes* LAMBRECHT: 362, pl. 1.
1935 *Geiseloceros* LAMBRECHT: 365, pl. 2.
1981 *Ameghinornis* MOURER-CHAUVIRÉ: 638, pl. 1.
1983 *Ameghinornis* MOURER-CHAUVIRÉ: 127, pl. 5.
1987 *Aenigmavis* PETERS: 72, figs. 1–11.
2007 *Ameghinornis* PETERS: 25.
2007 *Aenigmavis* PETERS: 25, figs. 1, 2.

Strigogyps robustus (LAMBRECHT, 1935) n. comb.

* 1935 *Geiseloceros robustus* LAMBRECHT: 362, pl. 1.
1935 *Eocathartes robustus* LAMBRECHT: 365, pl. 2.

Holotype: GMH 5884 (holotype of "*Geiseloceros robustus*", Fig. 1A)

Referred specimen: GMH 5883 (holotype of "*Eocathartes robustus*", Fig. 1B); although I consider this specimen to be from the same individual as the holotype GMH 5884, it is listed as a "referred specimen" to avoid future taxonomic confusion.

Type locality and horizon: "Grube Cecilie" opencast brown coal pit of the Geisel Valley (Geiseltal) near Halle, Sachsen-Anhalt, Germany; Middle Eocene (MP 13, i.e., about 44 ma; MLÍKOVSKÝ & HESSE 1996; LEGENDRE & LÉVÊQUE 1997).

Description and comparison: The right coracoid is visible in ventral view, of the left one only the extremitas sternalis is preserved (Fig. 2D). In its proportions the bone resembles the coracoid of a specimen of *Strigogyps* sp. from Messel (SMF-ME 11094; compare Figs. 2A and 2D). It is much stouter than the corresponding bone of the Idiornithidae, Phorusrhacidae, and Cariamidae, and more closely matches the coracoid of the Cathartidae in proportions. The large extremitas omalis measures more than one third of the entire length of the bone. The processus lateralis is well developed, whereas this process is very short in the Phorusrhacidae and Cariamidae (no complete coracoid of the Idiornithidae has been figured by MOURER-CHAUVIRÉ 1983 who, how-

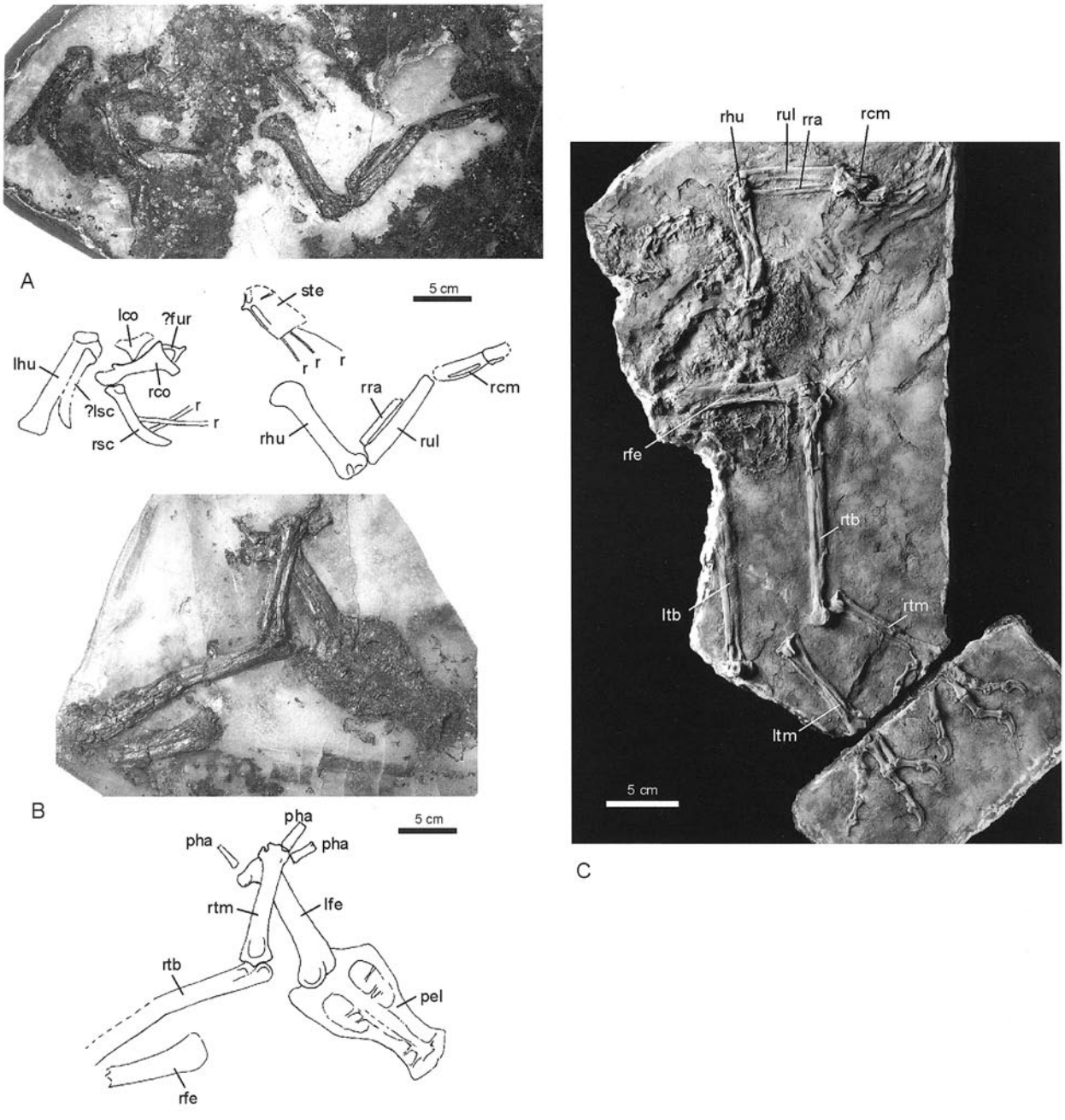


Fig. 1. Specimens of *Strigogyps robustus* (LAMBRECHT, 1935) from the Middle Eocene of the Geisel Valley and *Strigogyps* ("*Aenigmavis*") *sapea* (PETERS, 1987) from the Middle Eocene of Messel in comparison. **A**: *Strigogyps robustus*, wing and pectoral girdle elements (holotype of "*Geiseloceros robustus*"; GMH 5884) with interpretative drawing. **B**: *Strigogyps robustus*, pelvis and hindlimb elements (holotype of "*Eocathartes robustus*"; GMH 5883) with interpretative drawing. **C**: *Strigogyps sapea* (holotype, SMF-ME 1818), specimen coated with ammonium chloride. – Abbreviations: fur – furcula, lco – left coracoid, lfe – left femur, lhu – left humerus, lsc – left scapula, ltb – left tibiotarsus, ltm – left tarsometatarsus, pel – pelvis, pha – pedal phalanx, r – rib, rcm – right carpometacarpus, rco – right coracoid, rfe – right femur, rhu – right humerus, rra – right radius, rsc – right scapula, rtb – right tibiotarsus, rtm – right tarsometatarsus, rul – right ulna, ste – sternum.

ever, considered this bone to be very similar to the coracoid of the Cariamidae). A foramen nervi supracoracoidei cannot be discerned; this foramen is absent in the Cariamae but present in the Cathartidae.

The scapula of *Strigogyps*, which has not been described so far, is unusually short and stout, with a very short acromion (Fig. 2E). Compared to extant birds, it resembles the scapula of the Cathartidae, whereas in the Cariamidae the acromion is much longer.

A U-shaped bone next to the extremitas sternalis of the right coracoid may represent the extremitas sternalis of the furcula. If this interpretation is correct, the furcula of *Strigogyps* is characterized by the presence of a well-developed apophysis furculae.

It has not been mentioned by LAMBRECHT (1935), that the slab with the wing elements also preserves the cranial portion of the sternum, which is visible in ventral view. The bone exhibits a well-developed spina externa and shallow sulci articulares coracoidei, the processus craniolaterales seem to have been very small.

The right humerus is visible in cranial, the left one in caudal view. The bone appears to be more robust than the humerus of *Strigogyps dubius* ("*Ameghinornis minor*"), but owing to considerable crushing it may appear stouter than it originally was. As far as comparable, the proximal and distal ends of the bone resemble those of *S. dubius*. As in the latter, the crista deltopectoralis is very short.

As in *S. sapea*, the ulna is unusually stout and much shorter than the humerus (Fig. 2).

The pelvis, which is not preserved in any of the previously described specimens of *Strigogyps*, is visible in ventral view in GMH 5883 (Fig. 2F). It resembles the pelvis of the American Black Vulture *Coragyps atratus* (Cathartidae) in proportions, contrary to LAMBRECHT (1935) who considered it more similar to the wider pelvis of the Turkey Vulture *Cathartes aura*. It also resembles the pelvis of the Red-legged Seriema, *Cariama cristata* (Cariamidae), but is clearly distinguished from the mediolaterally narrow pelvis of the Phorusrhacidae (e.g., ANDREWS 1899; ALVARENGA & HÖFLING 2003). The caudal margins of the fossae renales are well-delimited, tubercula praeacetabularia cannot be discerned. Caudal closure of the foramina ilioischiadica supports a position of *Strigogyps* within neognathous birds.

The femur is a stout and robust bone and of similar proportions to that of extant Cathartidae, but much stouter than the femur of the Idiornithidae (the femur of the Cariamidae is intermediate in its proportions). The sulcus patellaris is well developed. It cannot be discerned whether there was a pneumatic foramen on the cranio-lateral side of the proximal end (such a foramen is present in the Cathartidae, but absent in the Cariamae).

The distal end of the tibiotarsus is poorly preserved. LAMBRECHT (1935) assumed that the pons supratendineus has been destroyed. However, absence of this osseous bridge is a presumably autapomorphic feature of *Strigogyps* (MAYR 2005b). As in *S. sapea* (PETERS 2007), the condylus lateralis has a circular outline. The proximal end of the bone is too poorly preserved to allow the recognition of morphological details.

The poorly preserved tarsometatarsus resembles that of *S. sapea* in its proportions (Figs. 2G, H).

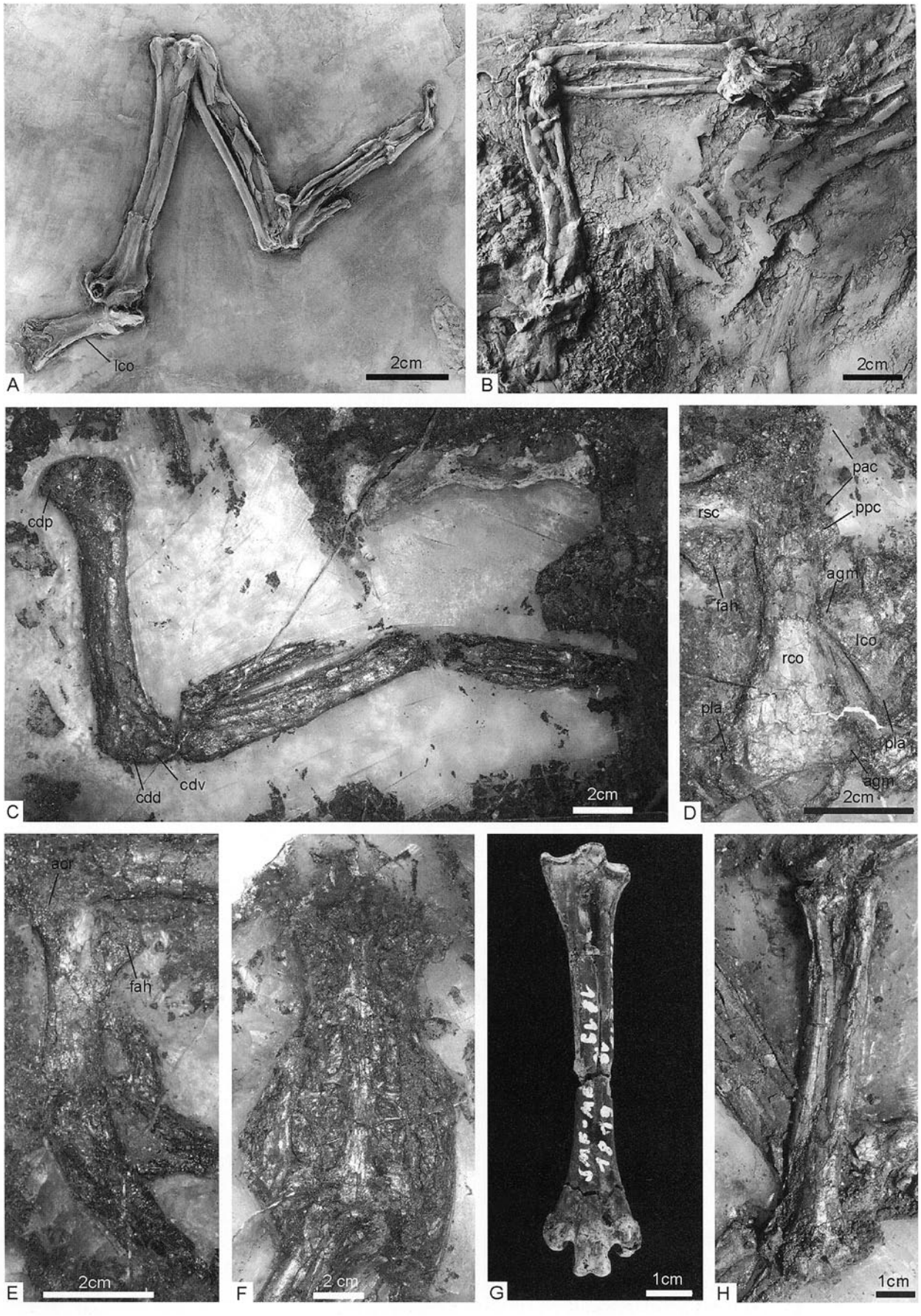
Discussion

As noted above, *Strigogyps sapea* from the Middle Eocene of Messel was originally classified into the taxon "*Aenigmavis*" and considered an Old World representative of the Phorusrhacidae (PETERS 1987). The taxonomy of the species was revised by MAYR (2005b), who noted that its distal tibiotarsus closely resembles that of *Strigogyps dubius* GAILLARD, 1908 from the Upper Eocene of the Quercy fissure fillings in France. Based on comparisons with *S. sapea*, MAYR (2005b) further detailed that another putative Old World phorusrhacid, "*Ameghinornis minor*" MOURER-CHAUVIRÉ, 1981 from the Quercy fissure fillings, is a junior synonym of *S. dubius*.

MOURER-CHAUVIRÉ (2006) followed this taxonomic revision of the Quercy species. PETERS (2007) also concurred with classification of *Strigogyps*, "*Ameghinornis*", and "*Aenigmavis*" into the Ameghinornithidae, but considered it "more appropriate to keep these genera taxonomically separate" (PETERS 2007: 25). In the case of the Quercy taxa this was justified with the fact that the remains of *Strigogyps dubius* and "*Ameghinornis minor*" were based on non-comparable skeletal elements. However, if different bones of putatively closely related birds from the same locality are classified into different taxa just because conspecifity cannot be definitely proven, the result will be taxonomic chaos. I thus maintain allocation of the Quercy remains to a single species, *Strigogyps dubius*. Because the binomial nomenclature was introduced to reflect relationships, I also prefer assignment of the Messel species to *Strigogyps* against its classification into "*Aenigmavis*". Even if one considers its separation on the "genus"-level justified, *Aenigmavis* PETERS, 1987 would be a junior synonym of *Eocathartes* LAMBRECHT, 1935 (as first revisor, I designate *Geiseloceros* as a synonym of *Eocathartes*).

The phylogenetic affinities of *Strigogyps* have not yet been convincingly established (MAYR 2005b). Clearly, however, this taxon is not a member of the Phorusrhacidae (ALVARENGA & HÖFLING 2003; MAYR 2005b). Some differences, such as the morphology of the coracoid and the plesiomorphic presence of a well-developed hallux, were noted previously (MAYR 2005b), and the referred specimen of *Strigogyps robus-*

Fig. 2. Skeletal elements of *Strigogyps* in comparison. **A**: left wing of *Strigogyps* sp. from the Middle Eocene of Messel (SMF-ME 11094). **B**: right wing of *Strigogyps sapea* from the Middle Eocene of Messel (SMF-ME 1818). **C**: right wing of *Strigogyps robustus* from the Middle Eocene of the Geisel Valley (GMH 5884). **D**: right coracoid of *Strigogyps robustus* in ventral view (GMH 5884). **E**: right scapula of *Strigogyps robustus* in lateral view (GMH 5884). **F**: pelvis of *Strigogyps robustus* in ventral view (GMH 5883). **G**: left tarsometatarsus of *Strigogyps sapea* from the Middle Eocene of Messel in dorsal view (SMF-ME 1819). **H**: right tarsometatarsus of *Strigogyps robustus* in dorsal view (GMH 5883). – Specimens in A and B coated with ammonium chloride. – Abbreviations: acr – acromion, agm – angulus medialis of coracoid, cdd – condylus dorsalis, cdp – crista deltopectoralis, cdv – condylus ventralis, fah – facies articularis humeralis, lco – left coracoid, pac – processus acrocoracoideus, pla – processus lateralis of coracoid, ppc – processus procoracoideus, rco – right coracoid, rsc – right scapula.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tus further documents that *Strigogyps* lacks the derived, very narrow pelvis of phorusrhacid birds. *Strigogyps* can even be shown to be outside a clade including Idiornithidae, Phorusrhacidae, and Cariamidae because the hypotarsus does not exhibit the presumably derived morphology found in the latter taxa, in which it is block-like and without any distinct sulci and crests (by contrast, the hypotarsus of *Strigogyps* exhibits well-developed cristae hypotarsi; see PETERS 1987: fig. 6).

The reduced crista deltopectoralis of the humerus and very short ulna suggest that *Strigogyps* was incapable of sustained flapping flight. However, LAMBRECHT (1935) noted that the holotype of *S. robustus* originally showed the remains of primaries, of which especially the distal ones were well preserved. These feather remains are no longer discernible, but may indicate some capability for at least gliding flight. The species of *Strigogyps* most likely were terrestrial birds, although, judging from the rather short tarsometatarsus and the well-developed hallux, they probably were not cursorial.

Acknowledgements

I thank M. Hellmund and C. Koehn (GMH) for making the fossil specimens available for study, and D. Ksepka and H. Alvarenga for reviewing the manuscript.

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Manuskripteingang / manuscript received 31. 7. 2007;
Manuskriptannahme / manuscript accepted 22. 10. 2007.