THE SYSTEMATICS AND EVOLUTION OF THE CATHARTIDAE IN THE OLD WORLD TERTIARY

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One of the more intriguing problems in avian paleontology and zoogeography is the supposed occurrence of New World vultures (Cathartidae) in the Tertiary of Europe. Despite the fact that paleontologists have generally accepted these European records (Lambrecht 1933; Brodkorb 1964), avian zoogeographers have either discounted or ignored the fossil evidence in their discussions of the family (e.g., Lönnberg 1927; Mayr 1946). Clearly, if the species recorded in Europe are not cathartids, then the hypothesis of a New World origin for the family is strengthened. If, on the other hand, the specimens are cathartids, then previous conclusions about the origin and evolution of the family must be re-examined. The stratigraphic ranges of the fossil genera of cathartids and neocathartids are shown in figure 1.

In this paper we will present evidence, based upon an examination of nearly all the relevant fossil material, that cathartid vultures did indeed once live in the Old World. Furthermore, our studies reveal that several specimens previously allocated to different family-rank taxa are more properly placed in the Cathartidae. In one case these changes necessitate the proposal of a new generic name within the Sagittariidae, and we include this here even though it is unrelated to the main theme of the paper. The systematic and morphological section of this paper will discuss only those taxa which we accept as valid European records of the Cathartidae. In the discussion section, we will treat other taxa which have been considered cathartids but for which there is insufficient supporting evidence. We will not discuss the late Tertiary history of the Cathartidae as it offers little information regarding the origin and dispersal of the family; the North American history of the family has been discussed by Loye Miller (1960).

MATERIALS EXAMINED

In addition to those fossil specimens mentioned in the text, we examined skeletons of all recent cathartid species. We also made numerous examinations of skeletons of all the nonpasseriform families.

The following abbreviations are used throughout the text: Ba. M., Naturhistorisches Museum, Basel; B. M. (N. H.), British Museum (Natural History); L. G. L., Laboratoire de Géologie de la Faculté des Sciences, Lyon; M. H. N. L., Muséum d'Histoire naturelle, Lyon; M. U., Bayerischen Staatssammlung für Paläontologie und historische Geologie, Munich; and P. M., Muséum National d'Histoire naturelle, Paris.

DIAGNOSIS OF THE CATHARTIDAE

The Cathartidae have long been known as a very distinct family osteologically (e.g., Ligon 1967). Because the fossil species discussed in this paper are known only from tarsometatarsi and/or tibiotarsi, only these elements will be characterized here.

The tibiotarsi of the Cathartidae have the distal end compressed somewhat lateromedially; the condyles of unequal size; the external condyle rounded distally (sometimes slightly flattened) and not elongated anteroposteriorly; the anterior intercondylar fossa typically narrow and deep; the posterior intercondylar sulcus narrow; the internal condyle projecting further anterior relative to the external condyle; the supratendinal bridge broad and oriented nearly perpendicular to the long axis of the shaft; low internal ligamental prominence; and the distal opening of the supratendinal bridge located close to the base of the internal condyle. The tarsometatarsi of the cathartids have a low to moderately developed intercotylar prominence; a hypotarsus that is rectangular in shape (in both proximal and posterior views) and without a bony canal; a deep and long anterior metatarsal groove; and a distal end that is compressed somewhat anteroposteriorly, with the trochleae having only a slight curvature when seen from the distal end.

When taken in combination, the above characters can be used to recognize these elements as being cathartid. It is our experience that recognition of the tarsometatarsus is somewhat easier than the tibiotarsus.

SYSTEMATICS AND MORPHOLOGY

Family **CATHARTIDAE**

Genus *EOCATHARTES* Lambrecht

Eocathartes Lambrecht 1935, p. 362.

The Condor 74:272–283, 1972

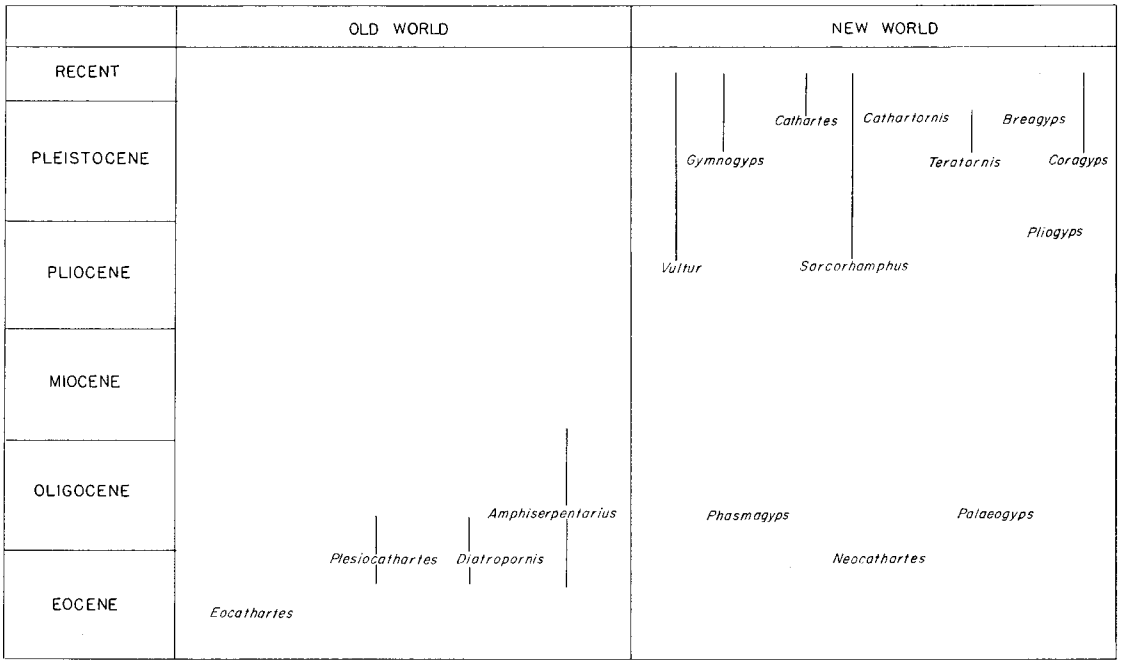

FIGURE 1. Stratigraphic ranges of the genera of Cathartidae and Neocathartidae as constructed from present information. Ranges of *Plesiocathartes, Diatropornis,* and *Amphiserpentarius* are estimated because of uncertainty in the age of the phosphorites du Quercy.

TYPE SPECIES: *Eocathartes robustus* Lambrecht.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Middle Eocene (Lutetian) of Germany.

DIAGNOSIS: Generic diagnosis not possible on information given.

REMARKS: Lambrecht (1935:362–363) was of the opinion that the tarsometatarsus definitely has a morphology characteristic of the cathartids. The deep anterior metatarsal groove, the relative positions of the trochleae, and the proportions of the hindlimb strongly suggest that *Eocathartes* is a cathartid vulture. Unfortunately, neither Lambrecht's discussion nor his figure is sufficiently detailed to construct a generic diagnosis.

Eocathartes robustus Lambrecht

Eocathartes robustus Lambrecht 1935, p. 362.

HOLOTYPE: Geiseltal Museum, no number; flattened skeleton including pelvis, femora, tibiotarsus, tarsometatarsus, phalanges.

HORIZON AND LOCALITY: Middle Eocene deposits (Braunkohle), Geiseltales, Grube Cecilie near Halle/Saale, Saxony, Germany.

HYPODIGM: Holotype only.

DIAGNOSIS: Not possible (see above); only species in genus.

REMARKS: The holotype of *E. robustus* is preserved as a flattened skeleton in which most of the bones are crushed or greatly damaged. We have not examined the holotype.

Genus *DIATROPORNIS* Oberholser

Tapinopus Milne-Edwards 1892, p. 79.
Diatropornis Oberholser 1899, p. 203.

TYPE SPECIES: *Diatropornis ellioti* (Milne-Edwards).

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Late Eocene to possibly Middle Oligocene of France.

DIAGNOSIS: Small sized vultures. Tibiotarsus with external condyle rounded and not especially elongated anteroposteriorly. Internal condyle elongated anteroposteriorly, with slight notch in distal margin. Distal end compressed lateromedially. Supratendinal bridge not steeply inclined, its axis nearly perpendicular to long axis of shaft. Tendinal groove located slightly internal to middle of shaft.

Tarsometatarsus with trochleae compressed lateromedially. Trochleae with sides nearly parallel, not robust. Anterior surface of middle trochlea meets shaft gradually, not abruptly. Middle trochlea projects further distally than internal trochlea. Distal foramen (in posterior view) very close to external intertrochlear notch. Intercotylar prominence low and blunt. Anterior metatarsal groove moderately deep.

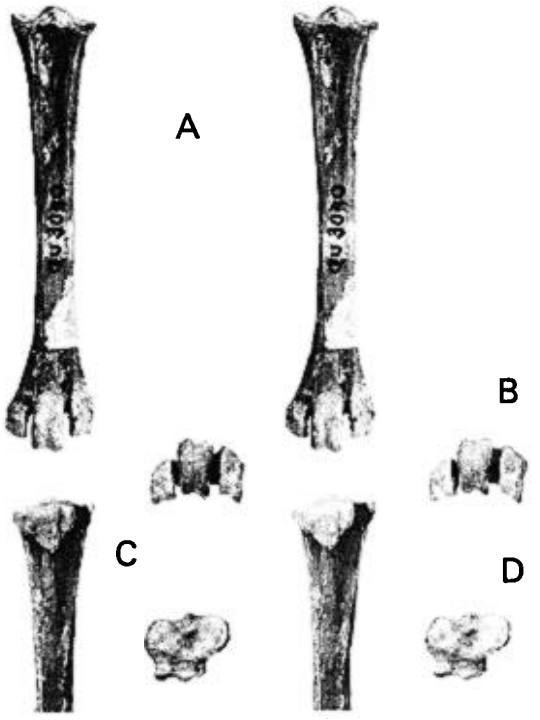

FIGURE 2. Tarsometatarsus of *Diatropornis ellioti* (holotype; P. M. No. Qu3040). A, stereos of anterior view; B, stereos of distal end; C, stereos of posterior view of proximal end; D, stereos of proximal end. All about × 1.1.

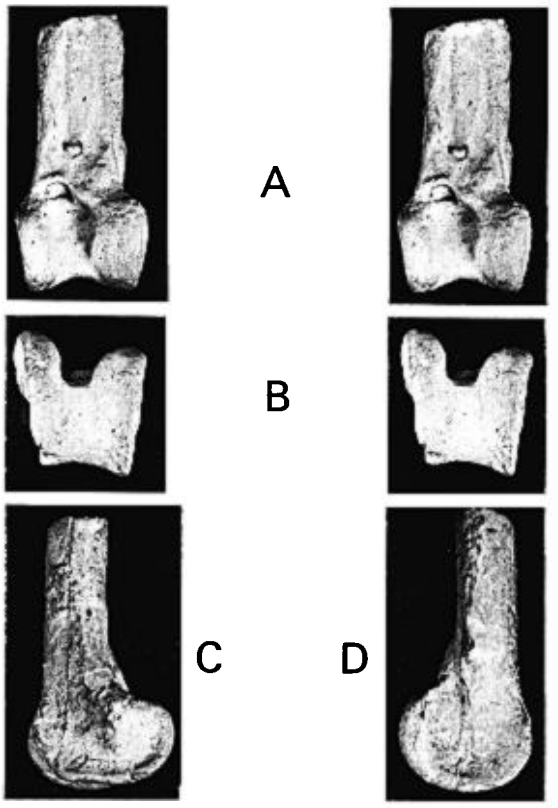

FIGURE 3. Tibiotarsus of *Diatropornis ellioti* (cast of P.M. No. Qu3102). A, stereos of anterior view of distal end; B, stereos of distal end; C, internal condyle; D, external condyle. All about × 1.6.

REMARKS: The configurations of the anterior metatarsal groove and the hypotarsus and the relative positions of the trochleae indicate that *D. ellioti* is indeed a cathartid. *Diatropornis* differs from most other cathartids in having the shaft more slender; the trochleae compressed more lateromedially; and in having the distal foramen very close to the external intertrochlear notch. Morphological comparisons with other genera are presented below.

Diatropornis ellioti (Milne-Edwards)

Figures 2–3

Tapinopus ellioti Milne-Edwards 1892, p. 79.
Diatropornis ellioti (Milne-Edwards): Oberholser 1899, p. 203.

HOLOTYPE: P.M. No. Qu3040, complete right tarsometatarsus.

HORIZON AND LOCALITY: Upper Eocene to middle Oligocene deposits (phosphorites du Quercy), Boussac near Caylux (probably other localities also; precise locality data not available on all specimens), France.

HYPODIGM: Holotype; P.M. No. Qu3041, complete left tarsometatarsus; P.M. No. Qu3042, distal end of right tarsometatarsus; P.M. No. Qu3043, complete right tarsometatarsus; P.M. No. Qu3044, broken complete right tarsometatarsus; Ba.M. No. QW523, distal end of right tarsometatarsus; M.H.N.L. No. PQ5, complete left tarsometatarsus; P.M. Nos. Qu3102, Qu3105, and Qu3122, distal ends of left tibiotarsi.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: See tables 1 and 2.

REMARKS: All of the tarsometatarsi assigned to this species conform very closely to the holotype in size and morphology. The tarsometatarsus of *D. ellioti* was about three-quarters the length of that of *Cathartes aura*.

The three tibiotarsi are assigned to *D. ellioti* principally as a matter of convenience. They differ generically from the presumably contemporaneous *Amphiserpentarius* and are from a cathartid of approximately the same size as *D. ellioti*. Rather than erecting a new species name at this time, we consider them *D. ellioti* until associated material is found. Although the tibiotarsi are slightly larger than the holotype tarsometatarsus, intrapopulation variability (and perhaps also some variation due to possible stratigraphic differences) could account for the differences. There are slight differences in the morphology of the

TABLE 1. Measurements (in mm) of tarsometatarsi of *Diatropornis ellioti*.

	P.M. No. Qu3040 (holotype)	P.M. No. Qu3041	P.M. No. Qu3043	P.M. No. Qu3042	P.M. No. Qu3044	Ba. M. No. QW523	M.H.N.L. No. PQ5
Total length	53.0	56.6+	60.0	–	–	–	59.0
Breadth across trochleae	11.2	12.0	13.0	11.6	12.2	12.4	12.3
Breadth of external trochlea	2.6	3.1	3.2	3.4	3.3	3.2	3.3
Breadth of middle trochlea	4.0	4.4	–	4.3	4.2	4.7	4.3
Breadth of internal trochlea	2.8	–	3.3	3.0	3.3	3.1	3.3
Depth of middle trochlea	6.6	–	7.7	7.3	7.3	7.8	7.2
Breadth of middle of shaft	4.5	4.8	4.9	–	–	–	4.7
Depth of middle of shaft	3.9	4.4	4.4	–	–	–	4.7
Breadth of proximal end	10.5	–	11.6	–	11.2	–	11.3
Depth of proximal end	8.6	–	–	–	8.4	–	9.4

three tibiotarsi in that P.M. Nos. Qu3102 and Qu3122 have the tubercle on the supratendinal bridge less well developed; the supratendinal bridge itself slightly narrower proximodistally; and the bone somewhat smaller (table 2). Again, the differences between Qu3105 and the other two tibiotarsi probably reflect individual variation and certainly do not justify specific recognition based on present evidence.

Genus *PLESIOCATHARTES* Gaillard

Plesiocathartes Gaillard 1908, p. 41.

TYPE SPECIES: *Plesiocathartes europaeus* Gaillard.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Late Eocene to possibly medial Oligocene of France.

DIAGNOSIS: Very small sized vultures. Tarsometatarsus with internal trochlea reduced in size. Middle trochlea projecting distally well beyond internal trochlea. Posterior metatarsal groove well developed distally.

REMARKS: *Plesiocathartes* can be included in the Cathartidae on the basis of the deep anterior metatarsal groove and the relative positions of the trochleae. Gaillard (1908:41) stated that the internal trochlea is large and the external trochlea is small, but the trochleae are very nearly the same size and the internal may be somewhat smaller (the internal trochlea is slightly damaged).

Plesiocathartes is quite distinct morphologically from *Diatropornis* which is also found in the phosphorites du Quercy. In *Plesiocathartes*, the internal trochlea is smaller and projects less distally relative to the external trochlea; the middle trochlea is less elongated anteroposteriorly relative to the other trochleae; the distal foramen is located more proximally; and the posterior metatarsal groove is much deeper distally.

TABLE 2. Measurements (in mm) of the tibiotarsi of *Diatropornis ellioti*.

	P.M. No. Qu3102	P.M. No. Qu3105	P.M. No. Qu3122
Depth of internal condyle	11.8	13.1	11.9
Depth of external condyle	11.1	12.4	11.1
Breadth across posterior end of condyles	8.2	8.2	8.3
Breadth across anterior end of condyles	11.2	11.5	11.2
Breadth of shaft	6.7	6.4	–
Depth of shaft	6.3	5.6	–

Plesiocathartes europaeus Gaillard

Figure 4

Plesiocathartes europaeus Gaillard 1908, p. 41.

HOLOTYPE: M.H.N.L. No. PQ1058, distal end of left tarsometatarsus.

HORIZON AND LOCALITY: Upper Eocene to middle Oligocene deposits (phosphorites du Quercy); plateau du Quercy, France.

HYPODIGM: Holotype only.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: Lateromedial breadth across trochleae, 7.7 mm; breadth of external trochlea, 2.2 mm; breadth of middle trochlea, 2.7 mm; breadth of internal trochlea, 2.1 mm; anteroposterior depth of middle trochlea, 4.0 mm.

REMARKS: *Plesiocathartes europaeus* is the smallest known cathartid, its tarsometatarsus being only 40–50% as long as that of *Cathartes aura*. *Diatropornis ellioti* was approximately 30–40% larger than *P. europaeus*.

Genus *AMPHISERPENTARIUS* Gaillard

Amphiserpentarius Gaillard 1908, p. 44.

TYPE SPECIES: *Amphiserpentarius schlosseri* Gaillard.

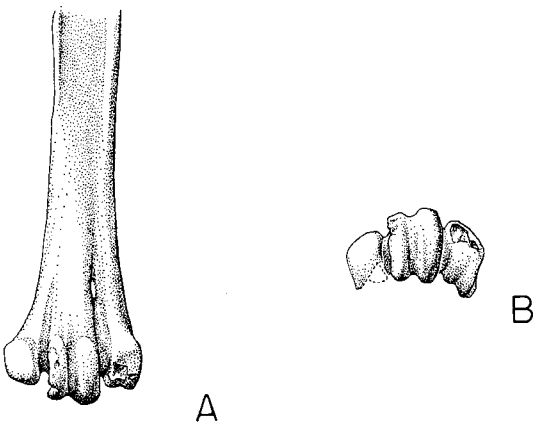

FIGURE 4. Tarsometatarsus of *Plesiocathartes europeaus* (drawn from cast of holotype; M.H.N.L. No. PQ1058). A, anterior view of distal end; B, distal end. Both about × 2.3.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Late Eocene to late Oligocene or early Miocene of France.

DIAGNOSIS: Medium sized vultures. Tibiotarsus with distal end compressed lateromedially. Distal opening of supratendinal bridge large and located very near internal condyle. Tendinal groove located slightly external to midline of shaft. Supratendinal bridge moderate to steeply inclined, its axis sometimes approaching long axis of shaft. Anterior intercondylar fossa deep and narrow. Internal condyle elongated anteroposteriorly and in internal view gently curving posteriorly, without notch in distal border. External condyle rounded distally.

REMARKS: It is evident after a comparison with skeletons of the living *Sagittarius serpentarius* that *A. schlosseri* is not a secretary-bird (see Brodkorb 1964:259). The tibiotarsus of *A. schlosseri* differs from that of *S. serpentarius* in the following features: (1) the internal and external condyles are not flattened distally and not greatly elongated anteroposteriorly; (2) in distal view, the posterior margins of the condyles converge toward each other and are not more or less parallel; (3) in distal view, the posterior intercondylar sulcus is decidedly shallower; and (4) the tendinal groove is larger and deeper.

In the shapes and positions of the condyles, the shape of the anterior intercondylar fossa and posterior intercondylar sulcus, and in the features of the supratendinal bridge and tendinal groove, *A. schlosseri* resembles the Cathartidae more than any other family we have examined.

Gaillard (1908) thought that *Amphiserpentarius* was somewhat intermediate between *Sagittarius* and the cathartid genera *Sarcoramphus* and *Cathartes*, and on the basis of a superficial morphological comparison, his conclusion is true to a certain extent. However, when *Amphiserpentarius* is compared with early Tertiary cathartids rather than with recent genera, the affinities of *Amphiserpentarius* to the New World vultures become clearer. The tibiotarsus of *Amphiserpentarius* resembles those of *Diatropornis*, *Phasmagyps*, and *Palaeogyps*, the latter two genera from the early Oligocene of Colorado (Wetmore 1927), in the following characters: (1) a deep anterior intercondylar fossa; (2) the external condyle projects noticeably anteriorly (compared to *Cathartes*); (3) the tendinal groove is well marked compared to modern cathartids; and (4) in distal view, the condyles are more compressed lateromedially.

Amphiserpentarius resembles *Palaeogyps* more than it does *Phasmagyps*, and the former two genera are similar to each other and differ from *Phasmagyps*, as follows: (1) the anterior intercondylar fossa is slightly broader and the condyles therefore are spread more anteriorly; and (2) in side view, the anterior end of the external condyle is raised more distally so that the distal margin of the condyle appears flatter. *Amphiserpentarius* does differ from *Palaeogyps* in that the internal condyle curves posteriorly (not raised) and is less flattened distally; the posterior margin of the external condyle projects more posteriorly; and the outer margin of the external condyle is straighter (in distal view).

As noted above, *Amphiserpentarius* shares several morphological similarities with *Diatropornis*. On the other hand, *Amphiserpentarius* differs from *Diatropornis* as follows: (1) the internal condyle gently slopes posteriorly and is not raised; (2) the supratendinal bridge is arched rather than depressed; and (3) the tendinal groove is located more externally.

Amphiserpentarius schlosseri Gaillard

Figures 5–7

Amphiserpentarius schlosseri Gaillard 1908, p. 45.

HOLOTYPE: M.U. No. 1, distal end of left tibiotarsus (holotype apparently destroyed).

HORIZON AND LOCALITY: Holotype and P.M. No. Qu3225, upper Eocene to middle Oligocene deposits (phosphorites du Quercy), plateau du Quercy, France; P.M. No. Av.8734, upper Oligocene or lower Miocene deposits (Aquitanian in age), San Gerand-le-Puy, Allier, France.

HYPODIGM: Holotype, cast M.H.N.L. No. PQ1045; P.M. No. Qu3225, distal end of right

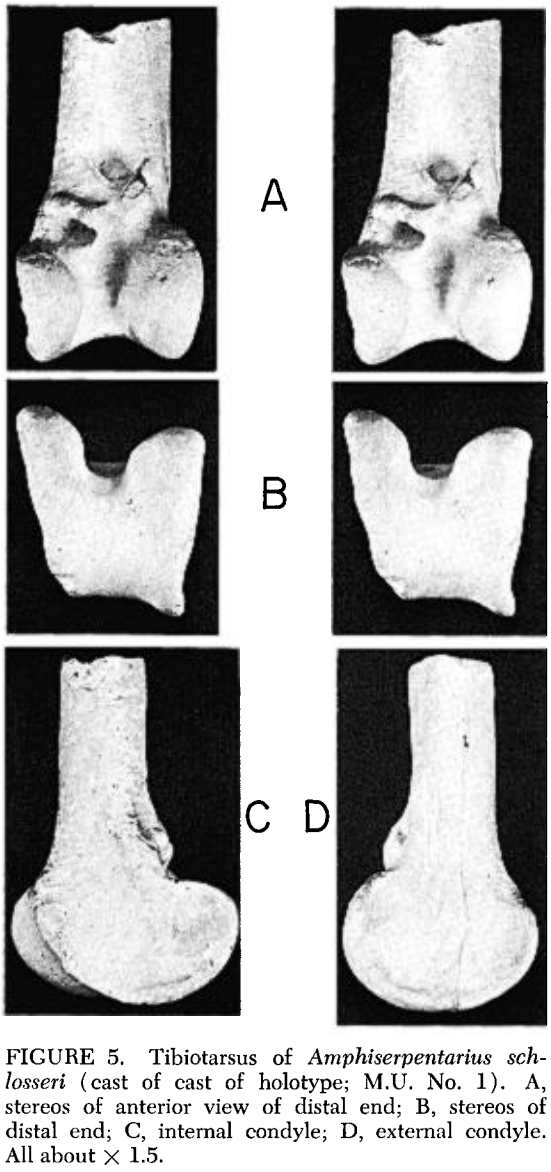

FIGURE 5. Tibiotarsus of *Amphiserpentarius schlosseri* (cast of cast of holotype; M.U. No. 1). A, stereos of anterior view of distal end; B, stereos of distal end; C, internal condyle; D, external condyle. All about × 1.5.

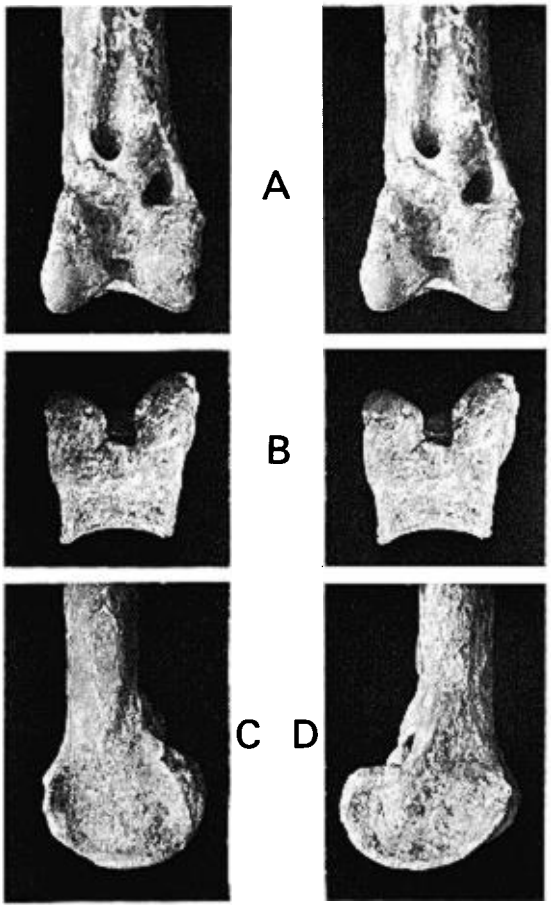

FIGURE 6. Tibiotarsus of *Amphiserpentarius schlosseri* (referred specimen; P.M. No. Qu3225). A, stereos of anterior view of distal end; B, stereos of distal end; C, external condyle; D, internal condyle. All slightly greater than × 1.4.

tibiotarsus; P.M. No. Av.8734, distal end of left tibiotarsus.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: See table 3.

REMARKS: Gaillard (1908) described *A. schlosseri* on the basis of a distal tibiotarsus in the collections of the Munich Museum. This specimen was lost and apparently destroyed during World War II. One of the referred specimens, P.M. No. Qu3225, is very similar to a cast of the holotype that is housed in the Muséum d'Histoire naturelle, Lyon (M.H.N.L. No. PQ1045), and we suggest that this Paris Museum specimen be designated the neotype.

We believe designation of a neotype is justified because the species limits of the material referred to *A. schlosseri* are not certain and may be modified with the discovery of additional material. All of the criteria of the International Code of Zoological Nomenclature are met.

Compared to the cast of the holotype, P.M. No. Qu3225 (fig. 6) is somewhat smaller (see table 3), with the external condyle slightly less elongated anteroposteriorly, the supratendinal bridge oriented more nearly parallel to the long axis of the shaft (i.e., less horizontal), and the tendinal canal displaced slightly more externally. The cast of the holotype is probably slightly larger than the original, but in any case the measurements of these two specimens are easily within the range of a single species. The morphological differences may be important but could also represent intraspecific variability. Until further evidence is found to the contrary, we prefer to assign P.M. No. Qu3225 to *A. schlosseri*.

Another specimen that can be referred to

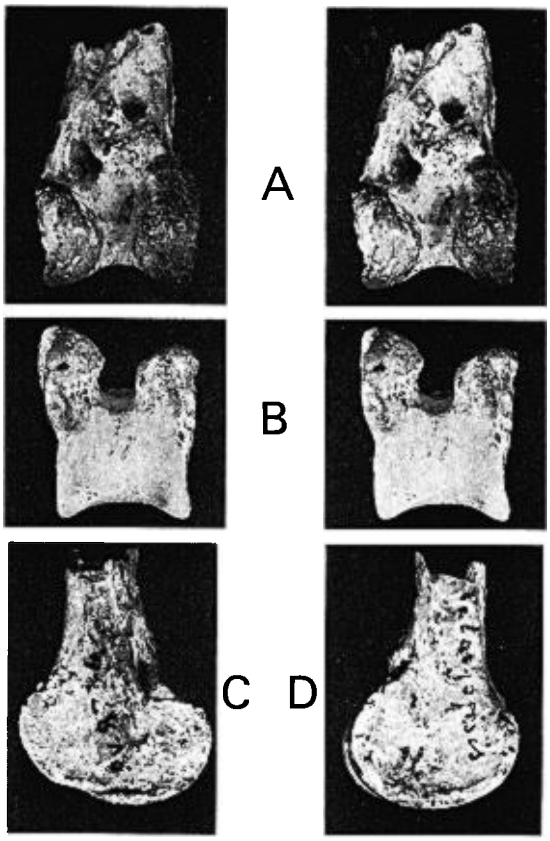

FIGURE 7. Tibiotarsus of *Amphiserpentarius schlosseri* (referred specimen; P.M. No. Av.8734). A, stereos of anterior view of distal end; B, stereos of distal end; C, internal condyle; D, external condyle. All about × 1.4.

A. schlosseri is a distal left tibiotarsus, P.M. No. Av.8734, from deposits at San Gerand-le-Puy (Aquitanian in age). This tibiotarsus (fig. 7) was originally part of the type material of a ciconiid *Pelargopappus magnus* (Milne-Edwards 1868, plate 72, figs. 1–19). Direct comparison with specimens of *A. schlosseri* and recent genera reveals that P.M. No. Av. 8734 is a cathartid vulture. The other specimen in the type series of *P. magnus*, a distal right tarsometatarsus (P.M. No. Av.8735), is a ciconiid and becomes the lectotype of the species.

TABLE 3. Measurements (in mm) of tibiotarsi of *Amphisepentarius schlosseri.*

	M.H.N.L. No. PQ1045 (holotype)[a]	P.M. No. Av.8734	P.M. No. Qu3225 (neotype)
Depth of external condyle	17.4	16.3	15.5
Depth of internal condyle	18.4	18.2	17.2
Breadth across posterior end of condyles	12.6	12.6	11.7
Breadth across anterior end of condyles	17.1	15.1	15.0
Breadth of middle of shaft	10.4	–	10.1
Depth of middle of shaft	8.0	–	8.1

[a] Holotype destroyed; measurements from cast.

P.M. No. Av.8734 is intermediate in size between the cast of the holotype and the neotype. In terms of morphology, P.M. No. Av. 8734 tends to resemble P.M. No. Qu3225 rather than the cast of the holotype, for example, in the orientation of the supratendinal bridge and in having the external condyle slightly less elongated anteroposteriorly. The San Gerand-le-Puy tibiotarsus differs from both the cast of the holotype and the neotype in not having the posterior margin of the internal condyle gently sloping; instead it is raised. The differences between the phosphorites de Quercy and San Gerand-le-Puy tibiotarsi in the shape of the internal condyle may be taxonomically important, but we hesitate in naming a new species for the latter until more evidence is forthcoming.

Family SAGITTARIIDAE

With the removal of *Amphiserpentarius schlosseri* from the *Sagittariidae*, it becomes necessary to place *A. robustus* in a new genus, to be called

AMYNOPTILON, new genus

TYPE SPECIES: *Amynoptilon robustum* (Milne-Edwards).

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Late Oligocene or early Miocene of France.

DIAGNOSIS: In characters of the tarsometatarsus differs from *Sagittarius* (only other genus in family), as follows: (1) in proximal view, the cotylar portion of bone less compressed anteroposteriorly (less elongated lateromedially) and more nearly square-shaped; (2) in posterior view, internal ridge of hypotarsus longer proximodistally and projects proximally much more; (3) in side view, area of intercotylar prominence protrudes much less proximally but instead is flatter and more nearly level; (4) posterior metatarsal groove more distinct and extends to internal side where it is deeper internal to hypotarsus; (5) in internal view, shaft much thicker anteroposteriorly; (6) in lateral view, side of shaft without well-marked tendinal groove; (7) external trochlea extends less distally relative to middle trochlea; (8) in anterior view, middle trochlea more compressed latero-

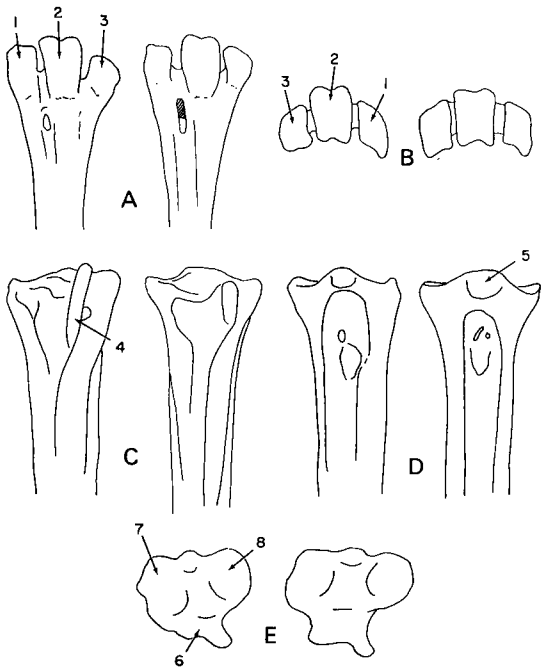

FIGURE 8. Tarsometatarsi of *Amynoptilon robustum* (left) and *Sagittarius serpentarius* (right). A, anterior view of distal end; B, distal end; C, posterior view of proximal end; D, anterior view of proximal end; E, proximal end. 1, outer trochlea; 2, middle trochlea; 3, inner trochlea; 4, internal ridge of hypotarsus; 5, intercotylar prominence; 6, hypotarsus; 7, external cotyla; 8, internal cotyla.

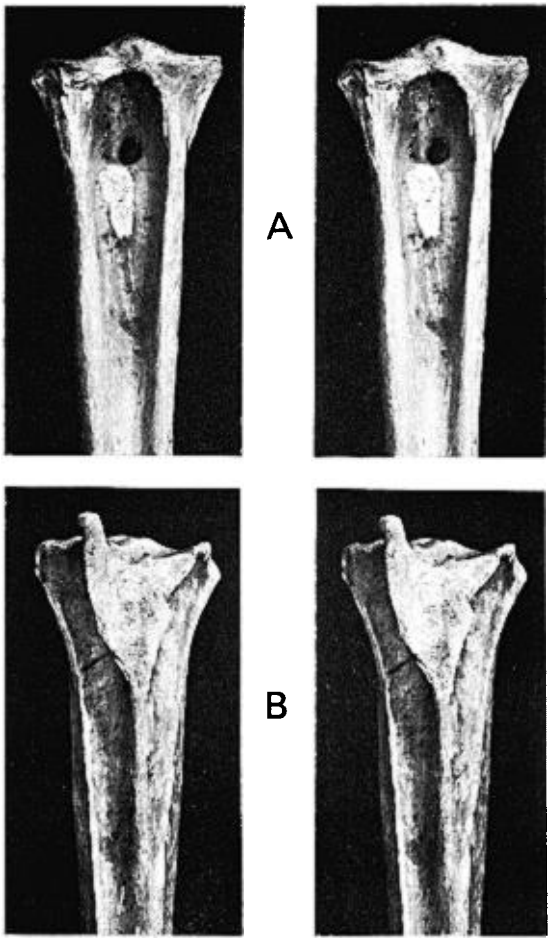

FIGURE 9. *Amynoptilon robustum* (holotype; P.M. No. Av.2816). A, stereos of anterior view of proximal end; B, stereos of posterior view of proximal end. All about × 1.1.

medially and elongated proximodistally; (9) middle trochlea extends further distally relative to internal trochlea; (10) base of external trochlea deeper anteroposteriorly; and (11) anterior metatarsal groove deeper proximally, undercutting intercotylar prominence much more, and is less well marked distally.

REMARKS: A comparison of the type of *A. robustum* with *Sagittarius* and other nonpasseriform families convinces us that *Amynoptilon* is a sagittariid. The configurations and positions of the trochleae, the configurations of the shafts, and the specific features of the proximal end are very similar in *Amynoptilon* and *Sagittarius* (fig. 8) and separate them from other families. The tarsometatarsus of *A. robustum* is shorter and heavier than that of *S. serpentarius* but is approximately the same size proximally and distally. This suggests that *A. robustum* may not have reached the same level of cursorial adaptation as seen in the living Secretary-bird.

The major morphological differences between *Amynoptilon* and *Sagittarius* are in the characters of the proximal end of the bone; the distal ends are much more similar. Thus, it might be suggested that the opposite ends of the tarsometatarsus have undergone different evolutionary rates from the early Miocene to the present. This makes possible the realistic assumption that *Amynoptilon* was morphologically similar to the ancestor of *Sagittarius*.

ETYMOLOGY: *amynon*, Greek, defending; *ptilon*, Greek, wing; in reference to the behavioral trait of the recent Secretary-bird of receiving snake strikes on the wing feathers where the bites will be harmless.

Amynoptilon robustum (Milne-Edwards)

Figures 8–10

Serpentarius robustus Milne-Edwards 1871, vol. 2, p. 465.

Amphiserpentarius robustus (Milne-Edwards): Lambrecht 1933, p. 400.

HOLOTYPE: P.M. No. Av. 2816, complete left tarsometatarsus.

HORIZON AND LOCALITY: Lower Miocene deposits (Aquitanian in age); Dept. Allier, Langy, France.

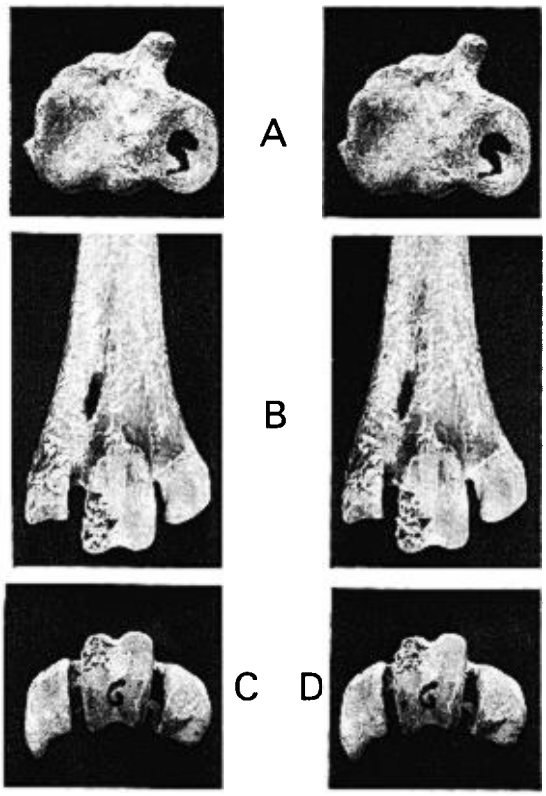

FIGURE 10. *Amynoptilon robustum* (holotype; P.M. No. Av.2816). A, stereos of proximal end; B, stereos of anterior view of distal end; C, stereos of distal end. All about × 1.2.

HYPODIGM: Holotype; M.H.N.L. No. St. G. 57, proximal end of right tarsometatarsus; L.G.L. No. 91.733, distal end of left tarsometatarsus; L.G.L. No. 91.735, distal end of left tarsometatarsus.

DIAGNOSIS: Same as for genus; only included species.

MEASUREMENTS: See table 4.

REMARKS: The holotype of *A. robustum* is in a near perfect state of preservation (figs. 9–10). The referred specimens assigned to this species are morphologically very similar to the holotype although they differ somewhat in size. Two specimens, L.G.L. No. 91. 733 and L.G.L. No. 91.735, are noticeably larger than the holotype and their conspecificity can be questioned. In our opinion, it is probably best to ascribe these size differences to sexual variation or to slight differences within a chronocline (there is no evidence that the deposits of all the specimens are strictly contemporaneous). The third referred specimen, M.H.N.L. No. St. G. 57, is only slightly smaller than the holotype and is well within the range of variability of a single species.

TABLE 4. Measurements (in mm) of tarsometatarsi of *Amynoptilon robustum*.

	P.M. No. Av.2816 (holotype)	M.H.N.L. No. St.G.57	L.G.L. No. 91.733	L.G.L. No. 91.735
Total length	213.0	–	–	–
Breadth across trochleae	20.5	–	–	27.0
Breadth of inner trochlea	5.8	–	7.2	7.2
Breadth of middle trochlea	8.0	–	9.9	9.9
Breadth of outer trochlea	4.9	–	–	6.7
Depth of middle trochlea	11.0	–	12.7	12.3
Breadth of middle of shaft	8.8	–	–	–
Depth of middle of shaft	9.4	–	–	–
Breadth of proximal end	21.4	19.6	–	–
Depth of proximal end	19.3	18.3[a]	–	–

[a] Measurement approximate, bone slightly damaged.

DISCUSSION

ADDITIONAL EUROPEAN GENERA ASSIGNED TO THE CARTHARTIDAE

Prior to the inclusion of *Amphiserpentarius* in the Cathartidae, five monotypic genera of the family were known from Tertiary deposits of Europe (Brodkorb 1964). In the systematic section, we have discussed three of these genera which we accept as valid records for the Cathartidae. The possible relationships of the other two genera remain to be examined.

The first of these presumed cathartids, *Lithornis vulturinus*, was described by Owen (1842) for a nearly complete sternum, a dorsal vertebra, the distal end of a left femur, the proximal end of a left tibiotarsus, and a few ribs, all from lower Eocene deposits (London Clay) of Sheppey, England. The elements are cemented together by matrix, and it is impossible to discern any characters in Owen's figures that enable concrete statements regarding the relationships of this bird. From his discussion (p. 208), it seems clear that Owen was also including the Old World vultures (Accipitridae: Gypaetinae) as possible relatives of *L. vulturinus*. Owen placed *Lithornis* in the "Vulturidae," but it is uncertain what falconiform taxa he included in this family. We can find no evidence for synonymizing Owen's "Vulturidae" with the Cathartidae as currently recognized. He concluded that the genus will probably be "referable to a member of the group of Accipitrine Scavengers

which are so abundant in the warmer latitudes of the present world." Lydekker (1891: 34–35) believed that *Lithornis* was very accipitrid-like and that the proportions of the coracoid and femur were not those of a cathartid. Lambrecht (1933:403–405) placed *Lithornis* as *incertae sedis* in the Accipitridae near the Gypaetinae.

Unfortunately, the type specimen of *L. vulturinus* was destroyed during the bombardment of London in World War II (A. J. Charig, C. A. Walker, pers. comm.) and thus its status probably never will be known. Several other specimens have been referred to *L. vulturinus* (Lydekker 1891:35). One of these, B.M. (N.H.) No. 33138, consists of a rock fragment containing a sternum, several ribs, coracoids, and the proximal half of a left humerus; a second specimen, B.M. (N.H.) No. A56, includes a pelvis and sacrum. Although Lydekker did not state his reasons for referring these specimens to *L. vulturinus*, we assume he did so because they resembled falconiform birds and were from the London Clay of Sheppey. Lydekker thought that both specimens were similar to accipitrids, but he did not mention that he had compared them to the type, which perhaps he did.

Lambrecht (1933:404, figs. 134D-134E) illustrated a distal end of a right humerus in the collections of the British Museum (Natural History) which he referred to *L. vulturinus*. This humerus is apparently not part of any of the previously mentioned material, and we have not located the source of this specimen. One of us (J. C.) has examined this humerus and can confirm that it is not cathartid; details about this specimen will be published at a future date (C. A. Walker, pers. comm.).

At the present time we believe that it would be best to place *Lithornis* as *incertae sedis* near (or within) the Accipitridae. No evidence exists for recognizing any of the specimens that have been assigned to *L. vulturinus* as belonging to the Cathartidae. The referred specimens need further preparation and study before they can be allocated properly. Because the holotype is destroyed, it may be necessary to designate one of the referred specimens as the neotype.

Another European species assigned to the Cathartidae is *Teracus littoralis*, which is based on a femur and coracoid from the early Oligocene (Tongrian in age) of France (Milne-Edwards 1867–71). This species was first named "*ieracus littoralis*" by Aymard (1856: 233). Milne-Edwards (1867–71, Vol. 2:453) apparently transcribed this spelling erroneously as "*Teracus*," which has been followed by subsequent authorities (Lydekker 1891:28; Lambrecht 1933:405; Brodkorb 1964:252). Lydekker incorrectly cited the journal and year of Aymard's name, and Lambrecht and Brodkorb incorrectly cited the page number. Because Aymard failed to present a description or illustrations of the type specimen, the name *Ieracus littoralis* must be considered a *nomen nudum*. Milne-Edwards (1867–71, pl. 185, figs. 20–23) illustrated a femur and coracoid and named these two elements *Teracus littoralis*, which therefore becomes the valid name.

Aymard (1856:233) considered *Teracus* to be a member of the "tribu des faucons," but it is impossible to say what taxa were meant to be included within this group. From the illustrations published by Milne-Edwards (pl. 185, figs 20–23), we are able to say that *Teracus* is definitely not a falconid as evidenced by the shape of the proximal end of the femur. Furthermore, if the coracoid is accurately depicted and not damaged, then *Teracus* is also not a cathartid. We know of no evidence that the femur and coracoid came from the same animal, and until both specimens are re-examined and evidence provided to the contrary, we cannot accept *Teracus* as a valid record for the Cathartidae. One of us (J. C.) was unable to locate this specimen in the museums of Paris or Lyon.

INTRAFAMILIAL RELATIONSHIPS

Each of the early Tertiary genera of cathartids possesses certain features that were probably derived within their own separate lineages. Few, if any, of these features appear to be shared, thus it is difficult to make strong assertions regarding intergeneric affinities. In contrast to the late Tertiary cathartids, the early genera, *Diatropornis*, *Amphiserpentarius*, *Phasmagyps*, and *Palaeogyps*, all have the distal end of the tibiotarsus compressed lateromedially, but this character is quite possibly primitive within the family and therefore of no value in recognizing relationships. Despite the fact that we noted similarities between the various genera (see above), we are unable to recognize primitive-derived sequences among these characters and therefore are unable to evaluate them in terms of the information they provide about relationships.

ORIGIN AND DISPERSAL OF THE CATHARTIDAE

Most, if not all, avian zoogeographers have considered the Cathartidae to be New World

in origin. Lönnberg (1927:22) believed the family arose in the neotropics, and Mayr (1946:6, 27) considered North America as the most likely place of origin, citing Wetmore's descriptions (1927, 1944) of North American cathartids from the early Tertiary as evidence. Both Lönnberg and Mayr were apparently either unfamiliar with, and unconvinced by, the European fossil record.

The earliest cathartids in the New World are *Palaeogyps prodromus* and *Phasmagyps patritus* from lower Oligocene sediments of Colorado (Wetmore 1927). *Neocathartes grallator*, a peculiar terrestrial vulture with reduced wings and elongated hindlimbs, from upper Eocene deposits of Wyoming is placed in its own family (Wetmore 1944). *Neocathartes* is clearly very closely related to the Cathartidae, and in our opinion the recognition of a separate superfamily (Wetmore 1944, 1960) obscures this fact.

Obviously, the present fossil record of the Cathartidae does not permit us to point with certainty to the place of origin of the family. It does, however, provide some evidence in support of an alternative hypothesis and at least extends the possibilities recognized until this time.

The presence of Eocene-Oligocene cathartids in Europe offers, we believe, evidence just as convincing for considering the Cathartidae as having arisen in the Old World as do the modern distribution patterns of the family in supporting a New World origin (Lönnberg 1927; Mayr 1946). The four European genera appear more likely to encompass those morphological characters which could be postulated for an ancestral group than do the New World genera. For example, it seems most reasonable to derive the cathartids from some group of small raptorial birds (whether these were falconiform or not is open to question and is outside the content of this paper) that became more "specialized" for carrion feeding. *Plesiocathartes* and *Diatropornis* were small, whereas all known early North American cathartids were large. Moreover, the North American Oligocene genera, *Phasmagyps* and *Palaeogyps*, were fairly uniform morphologically and show some similarity to the late Tertiary and recent genera. No known genus of North American cathartids could have given rise to the terrestrial *Neocathartes*, whereas the slender tarsometatarsus of *Diatropornis* suggests, although not strongly, that the ancestors of *Neocathartes* possibly existed in the Old World in the early Eocene.

We propose the hypothesis that the cathartids originated and radiated in the tropical-subtropical environments of Europe (or Eurasia) during the late Cretaceous, Paleocene, and/or early Eocene. Emigration to the Western Hemipshere could have occurred during the early Eocene when faunal interchange between Europe and North America across the North Atlantic landbridge, as supported by geological and faunal evidence (Simpson 1947; Kurten 1967; Szaley and McKenna 1971), reached a peak for the Teritary. Simpson (1947) did not support faunal interchange across the North Atlantic principally because geological evidence was lacking or at least negative. However, geological evidence now exists and Simpson's data support this conclusion. Considerable additional faunal evidence has also been accumulated since Simpson's paper (D. E. Russell, pers. comm.).

Either a separate invasion or the one which gave rise to *Neocathartes* could have given rise to the Oligocene cathartids *Phasmagyps* and *Palaeogyps*. We do not reject the possibility of a Bering Landbridge route of dispersal of the cathartids, but there is no evidence one way or the other for this hypothesis.

It is difficult to suggest an explanation for the extinction of the European cathartids. Possibly this extinction resulted from the deterioration of the climate through the Tertiary and a subsequent effect on their food supply, or perhaps to competition with Old World vultures, or to a combination of both. The tibiotarsus from San Gerand-le-Puy assigned to *Amphiserpentarius schlosseri* at least shows that cathartids persisted in Europe as late as the early Miocene.

COMMENTS ON THE SAGITTARIIDAE

The presence of a Secretary-bird, *Amynoptilon robustum*, in the European Tertiary is confirmed in this paper. Thus, the possibility that the Sagittariidae originated in Europe (or Eurasia) cannot be rejected. It is reasonably certain that many of the modern mammal families of Africa are descended from groups that emigrated into Africa from Europe during the early Tertiary (Cooke 1968) and perhaps the Secretary-birds did likewise.

SUMMARY

Amphiserpentarius schlosseri Gaillard of the late Eocene or early Oligocene of France is found not to be a Secretary-bird (Sagittariidae) but is instead a member of the Cathartidae. Other European fossils accepted as valid cathartids are: *Eocathartes robustus* (medial

Eocene), *Diatropornis ellioti* (late Eocene or early Oligocene), and *Plesiocathartes europaeus* (late Eocene or early Oligocene). The morphological and stratigraphic evidence suggests that an Old World origin of the cathartids is just as plausible as a New World origin.

Amphiserpentarius robustus of the early Miocene of France is a valid sagittariid but is generically distinct from the recent *Sagittarius*. Since the type-species of *Amphiserpentarius* is now assigned to the Cathartidae, a new genus, *Amynoptilon*, is erected for *A. robustus*.

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DEDICATION

This paper is dedicated to the memory of Loye Miller, who devoted much of his scientific career to the study of the fossil Cathartidae.

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