

**PALAEOTIS WEIGELTI RESTUDIED : A SMALL MIDDLE EOCENE  
OSTRICH (AVES : STRUTHIONIFORMES)**

by

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SOMMAIRE

	Page
Abstract, Kurzfassung, Résumé .....	28
Introduction .....	28
Abbreviations .....	31
Systematic paleontology .....	31
Family Struthionidae VIGORS, 1825 .....	31
<i>Palaeotis</i> LAMBRECHT, 1928 .....	34
Acknowledgements .....	38
Literature cited .....	39
Captions to figures .....	41

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## ABSTRACT

*Palaeotis weigelti*, from the Middle Eocene of central Europe, is a flightless, paleognathous bird. It appears to be a member of the ostrich lineage on the basis of trivial derived characters. It is a very primitive ratite, however, and does not possess any of the highly specialized cursorial adaptations that characterize the modern steppe- and savanna- dwelling ostriches.

## KURZFASSUNG

*Palaeotis weigelti* aus dem Miozän Europas (Vorkommen Geiseltal und Messel) ist ein flugunfähiger, palaeognather Vogel. Nach einfachen abgeleiteten Merkmalen gehört *Palaeotis* offenbar zur Entwicklungslinie der Strausse. Dabei ist es ein sehr primitiver Ratite ohne die hochspezialisierten Adaptationen moderner Steppen- und Savannenstrausse.

## RESUME

*Palaeotis weigelti*, de l'Eocène moyen d'Europe centrale est un oiseau paléognathe incapable de voler. Il semblerait qu'il appartienne à la lignée de l'autruche d'après quelques caractères dérivés triviaux. Cependant, c'est un ratite très primitif qui ne possède aucune des adaptations à la course hautement spécialisées qui caractérisent les autruches actuelles que l'on trouve dans les steppes et les savanes.

## INTRODUCTION

*Palaeotis weigelti* LAMBRECHT, 1928, from the middle Eocene of Geiseltal, has long been regarded as the only known Paleogene member of the bustard family, Otididae, the next oldest record of a bustard being *Otis affinis* from the Miocene of Bavaria. We have restudied all the known material of *Palaeotis*, including two nearly complete skeletons that were not available to Lambrecht when he described *Palaeotis*, and discovered that it is a flightless, paleognathous bird having close affinities with the ostriches (Struthionidae).

Ratites (Ratitae *sensu* Merrem 1813, Struthioniformes *sensu* Sibley and Ahlquist 1981) are a group of mostly very large, flightless, and shaggy-looking birds that are united by possession of the paleognathous palate (Pycraft 1900, Bock 1963), bill with rhamphothecal grooves (Parkes and Clark 1966), and pelvis with a large ilioischadic foramen (Cracraft 1974).

The early Tertiary record of ratite birds is very poor, particularly in light of their large size which might be expected to improve their chances of being preserved. Olson (1985) provides the most complete and up to date summary of the fossil record of ratite birds, but his treatment of them is spread about among his discussions of unrelated paleognathous and neognathous birds.

The earliest certain ratite yet known is a late Paleocene rheiform from Brazil, *Diogenornis fragilis* ALVARENGA, 1983. The French fossil *Remiornis minor* (LEMOINE, 1878), which rivals *Diogenornis* in age, is a ratite, not a gastornithid, according to Martin (1983). Martin did not refer *Remiornis* to any specific family or order of ratites, however.

Many other incomplete fossils of large flightless birds have been referred to the ratite group. Like *Palaeotis*, some of these specimens were discovered in Europe and many were described as being most closely related to ostriches. All the Tertiary fossils

described as, and still believed to be ratites by at least some authors, are listed in Table 1, exclusive of eggshells, regardless of whether we concur with their identification. The supposed eleutherornithid *Saurornis* FISCHER, 1967 is not included here because it was discovered to be based on an incorrectly described bone of a mammal (Haubold and Krumbiegel 1984). Excluding *Diogenornis* and *Palaeotis*, the most ancient Tertiary specimens in which the parts of the skeleton that are diagnostic of ratites (*sensu* Cracraft 1974) are preserved do not appear until the Miocene and none of these differ significantly from neospecies of ratites. While paleospecies of emus and rheas are known only from much the same geographical ranges as are now inhabited by their extant kin, the early fossil record of ostriches is richest in Eurasia, not Africa. Kurochkin and Lungu (1970) suggested that the three Pliocene ostriches, *Struthio asiaticus*, *S. chersonensis*, and *S. wimani* may actually represent only one biological species.

While reviewing and revising incorrectly described fossils of paleognathous birds from the Northern Hemisphere, one of us (P.H.) became suspicious about the Lambrecht's allocation of *Palaeotis* to the bustard family. Lambrecht's description of *Palaeotis* was based exclusively on a partial tarsometatarsus and phalanx (figured by Lambrecht 1928, 1933). Another nearly complete specimen of *Palaeotis* (GM 4362) was discovered in 1933, shortly after Lambrecht published his description of *Palaeotis*. This newer specimen was informally referred to *P. weigelti* in the 1930's, probably by Lambrecht. We corroborate the identification of GM 4362 as *P. weigelti* on the basis of its tarsometatarsus, which agrees with the published figures of the holotype in the configuration of its trochleae, large interosseous foramen, and deep groove along its anterior surface. The holotype phalanx (proximal phalanx of pedal digit IV) also agrees with GM 4362, both phalanges being short and robust and possessing a large proximally protruding insertion of the tendon of the extensor digitorum IV brevis muscle.

GM 4362 is essentially complete, although it is somewhat crushed and deformed. It is remarkable that its correct identity as a ratite bird was not recognized earlier because the skeleton includes such diagnostic parts as the skull, scapulocoracoid (fusion of the scapula and coracoid occurs only in flightless birds), and the pelvis.

We found three additional specimens of *P. weigelti* in the collections of the Geiseltalmuseum. One of the three is the holotype specimen of *Paleogrus geiseltalensis* (= *Ornitocnemus geiseltalensis*) (Lambrecht 1935). This specimen is in very poor condition and includes only a severely crushed distal tibiotarsus and a less severely damaged tarsometatarsus with some associated phalanges. Its preservation is so poor that its identification would be impossible were it not for the availability of other, better specimens (i.e. GM 4362) of its kind with which to compare it. Cracraft (1973) observed that the diaphysis of its tarsometatarsus is more robust than in cranes so he questioned the validity of its allocation to the Gruidae. We consider *Paleogrus geiseltalensis* to be a junior synonym of *Palaeotis weigelti*. The holotype tarsometatarsus of *Paleogrus geiseltalensis* is indistinguishable from *Palaeotis weigelti* and both have the same type locality. Distinguishing details of the proximal tarsometatarsi match perfectly in both holotypes. The tarsometatarsus of *Paleogrus geiseltalensis* agree with *Palaeotis weigelti* and is inconsistent with the Gruidae in its : simple, unperforated hypotarsus ; relatively small intercotylar eminence ; large, shallow medial cotyla ; and robust diaphysis.

Another very important specimen of *Palaeotis weigelti* (HLMD Me 7530) was collected in the Messel Shale but remained unprepared at the Hessisches

Table 1. - The Tertiary record of ratite and putatively ratite birds. Taxonomic allocations follow the original authors (except for *Palaeotis* and *Remiornis*) and do not necessarily reflect our own opinion. See text for comments.

Pliocene :

Struthionidae :

- Struthio asiaticus* MILNE-EDWARDS, 1871, India  
*S. chersonensis* (BRANDT, 1873), Greece, Ukraine, Kazastan  
*S. wimani* LOWE, 1931, China, Mongolia  
*S. bradydactylus* BURCHAK-ABRAMOVICH, 1939, Odessa

Rheidae :

- Heterorhea dabbenei* ROVERETO, 1914, Argentina

Dromaiidae :

- Dromiceius ocypus* MILLER, 1963, Australia

Dromornithidae :

- Dromornis australis* OWEN, 1872, Australia

Miocene :

Struthionidae :

- Struthio orlovi* KUROCHKIN and LUNGU, 1970, Moldavia

Opisthodactylidae :

- Opisthodactylus patagonicus* AMEGHINO, 1891, Argentina

Dromornithidae :

- Barawertornis tedfordi* RICH, 1979, Australia  
*Bullockornis planei* RICH, 1979, Australia  
*Dromornis stirtoni* RICH, 1979, Australia  
*Ibandornis lawsoni* RICH, 1979, Australia  
*I. woodburnei* RICH, 1979, Australia

Oligocene :

Aepyornithidae :

- Stromeria fajumensis* LAMBRECHT, 1929, Egypt  
*Eremopezus eocaenus* ANDREWS, 1904, Egypt

Eleutherornithidae :

- Proceriavis martini* HARRISON and WALKER, 1979, England

Eocene :

Eleutherornithidae :

- Eleutherornis helveticus* SCHAUB, 1940, Switzerland

Struthionidae :

- Palaeotis weigelti* LAMBRECHT, 1928, Germany

Paleocene :

Opisthodactylidae :

- Diogenornis fragilis* ALVARENGA, 1983, Brazil

family uncertain :

- Remiornis minor* (LEMOINE, 1878), France

Landesmuseum. This specimen was informally referred to the Gruidae. In its unprepared state, the specimen provided little information as to its correct taxonomic position. It did, however, show a clear impression of the right wing, which was obviously diminutive, vestigial, and incapable of supporting the bird in flight. We realized that this specimen could well be another specimen of *Palaeotis* because we strongly suspected that *Palaeotis* was a true ratite (i.e. flightless as well as paleognathous). We therefore obtained permission to completely prepare this skeleton. Our suspicions were corroborated when we discovered that several key parts of the skeleton were preserved in the Messel specimen, including the palate, sternum, scapulocoracoid, wing, and pelvis. We also made a transverse lapidary thin section through the tibiotarsus of HLMD Me 7530 and found its pattern of microscopic vascularization to be completely consistent with what is known for ratite birds and unlike that of neognathous birds. It is worth noting that X-ray photographs taken of the skull before preparation did not reveal to us that the palate was preserved in this specimen. Only superficial features that were readily visible to the naked eye appeared in the radiograph. The palate of HLMD Me 7530 proved to be intact and remarkably undeformed, providing unambiguous and incontrovertible evidence for the relationship of *Palaeotis* and paleognathous birds.

#### ABBREVIATIONS

GM : Geiseltalmuseum, Martin-Luther University, Halle/S., German Democratic Republic.

HLMD : Hessisches Landesmuseum, Darmstadt, Federal Republic of Germany.

USNM : National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

#### SYSTEMATIC PALEONTOLOGY

Class AVES LINNAEUS, 1758

Subclass NEORNITHES GADOW, 1893

Superorder PALAEOGNATHAE PYCRAFT, 1900

Order STRUTHIONIFORMES (LATHAM 1790)

*Expanded osteological diagnosis* : Distinguished from all known families of birds by : rynchokinetic skull : paleognathous palate : rhamphothecal grooves ; splenial unfused, extending to or near to the mandibular symphysis ; fused scapulocoracoid ; unkeeled sternum ; vestigial wing ; ilioischadic foramen large ; and tarso-metatarsus with simple, unperforated hypotarsus.

*Included families* : Struthionidae, Rheidae, Casuariidae (includes emus), Apterygidae, Dinornithidae and Aepyornithidae.

Family STRUTHIONIDAE VIGORS, 1825

*Type genus* : *Struthio* LINNAEUS, 1758, by monotypy

*Included genera* : *Struthio* LINNAEUS, 1758 and *Palaeotis* LAMBRECHT, 1928

**Expanded osteological diagnosis** : Distinguished from all other sufficiently known families of ratite birds by combination of : humerus long, spindley and lacking a pneumatic foramen ; radius and ulna short ; carpometacarpus with accessory foramina between each of the metacarpal bones (not the intermetacarpal space) ; scapulocoracoid with large acrocoracoid and glenoid fossa ; and ilioischadic foramen not circumscribed caudally by fusion of the ilium and ischium.

#### Subfamily STRUTHIONINAE

**Included genera** : *Struthio* LINNAEUS 1758, by monotypy

**Diagnosis** (all of the following characters are *derived* within the Struthioninae) : bill flat and broad ; osseous palate without caudal process of palatine and pterygoid fossa ; cervical vertebrae elongate ; presumed clavicle fused to scapulocoracoid ; preacetabular ilium shorter than postacetabular ilium ; pubes fused to form symphysis ; femur with large condyles ; tibiotarsus with pronounced anterior cnemial crest, reduced lateral cnemial crest, without tendinal groove, and with distal condyles extensively coalesced ; tarsometatarsus without spherical intercotylar eminence and without deep groove on anterior surface ; and pes didactylous.

#### Subfamily PALAEOTIDINAE, new subfamily

**Included genera** : *Palaeotis* LAMBRECHT, 1928

**Diagnosis** (all the following characters are *primitive* within the Struthionidae) : bill narrow ; palate with caudal process of palatine and pterygoid fossa ; cervical vertebrae stout ; preacetabular ilium equal in length to postacetabular ilium ; femur gracile ; tibiotarsus with large lateral cnemial crest, tendinal groove, and differentiated medial and lateral condyles ; tarsometatarsus with spherical intercotylar eminence, deep groove along anterior surface, conspicuously sculpted origin of the extensor digit IV brevis muscle, and large interosseous foramen ; and pes tridactylous.

#### DESCRIPTION

The only known species of this genus is smaller than all extant ratites except kiwis (Apterygidae).

**Skull** : Palate paleognathous (*sensu* Bock 1963) ; pterygoid-quadrangle articulation complex, saddle-shaped, and includes orbital process of the quadrangle ; basipterygoid processes large (deduced from presence of large articular surface on medial aspect of pterygoids) ; pterygoids continuous with palatines and vomer ; vomer very large and probably articulates with premaxillae ; orbital septum probably continuous with nasal septum ; zygomatic process large and closely applied to quadrangle. Similar to Tinamidae and Lithornithidae with respect to : bill moderately long and narrow ; palatines with caudal process ; supraorbital region narrow ; and coronal suture unfused. Pterygoid fossa present as in the Apterygidae and Lithornithidae (Houde 1986). Prefrontals long and narrow ; groove for nasal gland present along supraorbital margin ; and postorbital process large.

**Quadrangle** : Otic process lacks distinct prootic and squamosal condyles.

**Mandible** : Foveae for nervous corpuscles of mandibular nerve large and conspicuous ; splenial large and unfused, forming part of mandibular symphysis ; rhamphothecal

grooves form "w" shaped pattern as in Apterygidae and Lithornithidae.

*Cervical vertebrae* : Stout.

*Thoracic vertebrae* : Spinous processes very tall.

*Caudal vertebrae* : Lateral processes absent.

*Sternum* : Unkeeled ; posterior margin probably single-notched bilaterally.

*Scapulocoracoid* : Diminutive ; coracoid portion narrow ; acrocoracoid process and glenoid fossa large as in Rheidae.

*Humerus* : Long and spindley ; no pneumatic foramen ; and pectoral crest present. See "Discussion" below.

*Antebrachium* : Short.

*Carpometacarpus* : Carpals and metacarpals fused together but visibly distinct from each other ; all articular surfaces suggest restricted movement of joints ; and accessory foramina present between each of the metacarpals. Accessory foramen between major and minor metacarpals (not the intermetacarpal space) is formed by a thin connection between the metacarpals that differs from the intermetacarpal process in that it fuses to the minor metacarpal, is more localized on the ventral surface, and does not seem to be a muscular insertion. Accessory foramina of the carpometacarpus occur occasionally in rheas (Rheidae) and penguins (Spheniscidae).

*Pelvis* : Bilaterally compressed as in most ratites exclusive of the Dinornithidae and Aepyornithidae ; preacetabular ilium approximately equal in length to postacetabular ilium as in Casuariidae ; iliac crest forms pronounced process dorsal to acetabulum as in the Rheidae ; bones of postacetabular pelvis and ilioischadic foramen long, straight, and narrow ; and ilioischadic foramen not circumscribed caudally by fusion of the ilium and ischium.

*Femur* : Short relative to lengths of tibiotarsus and tarsometatarsus but gracile with small condyles ; centrally located insertion of ilirotrochanteris caudalis muscle.

*Tibiotarsus* : Similar to Casuariidae as follows : anterior cnemial crest well developed but not so much as in *Struthio* and the Rheidae ; lateral cnemial crest large ; tendinal groove present ; medial and lateral condyles distinct from one another as in "primitive" ratites (sensu Cracraft 1974) and Lithornithidae.

*Tarsometatarsus* : Similar to Casuariidae as follows : hypotarsus narrow and streamlined ; deep groove present along anterior surface ; and overall configuration of trochleae. Different from Casuariidae and similar to Lithornithidae as follows : intercotylar eminence distinct and spherical in anterior view ; origin of extensor digiti brevis muscle conspicuous ; and interosseous foramen large. Plantar tendons alongside tarsometatarsus heavily ossified.

*Digits* : Relatively longer than in other ratites but more robust than in Tinamidae and Lithornithidae ; terminal phalanges cylindrical, not narrow or hooked.

## PALAEOOTIS LAMBRECHT, 1928

**Type species** : *Palaeotis weigelti* LAMBRECHT, 1928, by monotypy.

**Diagnosis** : As for the subfamily.

*Palaeotis weigelti* LAMBRECHT, 1928

(Figures 1-6)

- *Palaeotis weigelti* LAMBRECHT, 1928, pp. 1-11, pl. 1 ; Lambrecht 1933, pp. 527, 889, figs. 157a, 199c, d ; Brodkorb 1967, p. 173 ; Olson 1985, p. 179.

- *Paleogrus geiseltalensis* LAMBRECHT, 1935, p. 361, fig. 1 ; Brodkorb 1967, p. 148 ; Cracraft 1973, p. 80 ; new synonymy.

- *Ornitocnemus geiseltalensis* (LAMBRECHT) Brodkorb, 1967, p. 148 ; Cracraft 1973, p. 80.

**Holotype** : GM 4415 : right tarsometatarsus (lost, except a proximal fragment) and GM 4418 : a pedal phalanx ; collected by J. Weigelt in 1926 or 1927 ; figured by Lambrecht (1928, 1933).

**Type locality** : Site I of Cecile Mine, Geiseltal, near Halle/S., German Democratic Republic. Paleontological work in this mine was limited to the short period of time after the mine was abandoned by miners and before it became flooded and collapsed. It is now impossible to revisit this locality.

**Horizon** : Layer between Middle and Upper Coal, Geiseltal Brown Coal, upper Middle Eocene.

**Referred specimens** :

GM 5882 : holotype of *Paleogrus geiseltalensis* ; distal right tibiotarsus, right tarsometatarsus and one pedal phalanx ; collected from Site II of Cecile Mine (Leichenfeld I) in 1930 ; figured by Lambrecht (1935).

GM 4361 : distal right tibiotarsus and proximal right tarsometatarsus ; collected from Site IV of Cecile Mine in 1933.

GM 4362 : incomplete skeleton consisting of a skull and mandible, cervical and part of thoracic vertebral column, some ribs, right scapulocoracoid, and entire pelvic appendages ; collected from Site III of Leonhard Mine in 1933 ; all from the Geiseltal Brown Coal ; upper Middle Coal Horizon (Zone III), upper Middle Eocene.

HLMD Me 7530 : incomplete skeleton consisting of a skull with the palate, cervical and caudal vertebral column, sternum, ventral fragment of right scapulocoracoid and left scapulocoracoid lacking dorso-caudal portion of scapula, left humerus lacking distal extremity, left radius, ulna, and carpometacarpus, impression of distal right pectoral appendage, ribs, pelvis, left and head of right femora, left tibiotarsus lacking distal extremity, and impression of shaft of right tibiotarsus ; collected from the Messel Quarry ; Messel Oil Shale ; equivalent to Lower Coal of Geiseltal, lower Middle Eocene (Franzen and Haubold 1986).

**Diagnosis** : As for the subfamily and genus.

**Distribution** : Known only from the middle Eocene of the Messel Oil Shale in the Federal Republic of Germany and the contemporaneous Geiseltal Brown Coal in the German Democratic Republic.

**Measurements** (to the nearest millimeter) :

**Skull** : GM 4362 : greatest width 50 ; length of cranium to nasofrontal region 63 ; total length of skull (measured in two pieces) 135 ; HLMD Me 7530 : greatest width 46.



*Mandible* : GM 4362 : length > 100 ; width at level of mandibular symphysis 12.  
*Scapulocoracoid* : GM 4362 (r) : length 89 ; sternal extremity to procoracoid process 43 ; sternal extremity to acromion 58 ; length of scapula from acromion 64 ; width scapula 7 ; HLMD Me 7530 (l) : sternal extremity to procoracoid process 33.  
*Humerus* : HLMD Me 7530 (l) : length (lacking distal end) 81 ; estimated length (assuming the missing distal piece was actually articulated with the radius and ulna) 117 ; shaft diameter 4.  
*Ulna* : HLMD Me 7530 (r) : length 74 ; anterior-posterior width distal condyle 7.  
*Radius* : HLMD Me 7530 : length 72 (r) ; diameter of shaft 3 (l).  
*Carpometacarpus* : HLMD Me 7530 (l) : length 34 ; proximal articular width 6 ; proximal anterior-posterior height 14 ; proximo-distal length of alular metacarpal 9 ; anterior-posterior diameter major metacarpal 4 ; dorsal-ventral diameter major metacarpal 3.  
*Pelvis* : GM 4362 : length 170 ; preacetabular length 78 ; postacetabular length 78 ; HLMD Me 7530 : length 120 ; preacetabular length 58 ; postacetabular length 57.  
*Femur* : GM 4362 ; length 136 (l), 145 (r) ; anterior-posterior diameter of head 14 (r) ; HLMD Me 7530 : length 117 (l) ; anterior posterior width of lateral condyle with tibiofibular crest 28 (l) ; anterior-posterior diameter of head 12 (r).  
*Tibiotarsus* : GM 4362 (r) : length 268 ; anterior-posterior width of lateral condyle 19 ; HLMD Me 7530 (l) : antero-posterior diameter of mid-shaft 10.  
*Tarsometatarsus* : GM 4362 : length 207 (l), 200 (r) ; proximal width 23 (l) ; proximal depth 26 (r) ; distal width 27 (r) ; width middle trochlea 11 (r) ; anterior-posterior diameter of mid-shaft 11 (l) ; length of inner minus middle trochlea 12 (l) ; length of outer minus middle trochlea 6 (r).  
*Digit II* : GM 4418 : proximal phalanx 23 ; GM 4362 : total length 51 (r) ; proximal phalanx 27 (l), 26 (r) ; middle phalanx 14 (r) ; distal phalanx 15 (r).  
*Digit III* : GM 4362 : total length 94 (l) ; proximal phalanx 33 (l), 32 (r) ; proximal middle phalanx 31 (l), 26 (r) ; distal middle phalanx 17 (l) ; distal phalanx 17 (l).  
*Digit IV* : GM 4362 (r) : total length (assuming that distal phalanges were preserved in articulation and still lie in their correct positions) 55 ; proximal phalanx 27 ; proximal middle phalanx 16 ; distal phalanx 13.

## DISCUSSION

Lambrecht wrote at length about a pathological alar phalanx of *Palaeotis*, going so far as to speculate that this bone was broken as the result of intraspecific battle during courtship, a common behavior of male bustards. This bone is, however, neither pathological nor a phalanx. It is, instead, the medial half of the proximal end of the holotype tarsometatarsus. The distal portion of the holotype tarsometatarsus, figured by Lambrecht (1928, 1933), has been lost for many years, to the best of our knowledge.

*Palaeotis weigelti* may have been a sexually dimorphic species, like many neospecies of paleognathous birds. The holotype phalanx (GM 4418) and the Messel skeleton (HLMD Me 7530) are smaller than specimens GM 5882 and GM 4362.

We are describing the humerus of *Palaeotis* as long and spindley but the only known humerus of *Palaeotis* (HLMD Me 7530) lacks the distal end. The total length of the humerus can be estimated because the missing end was apparently articulated correctly with the radius and ulna before it was broken off the slab. The fractured shaft of the humerus is not expanded and, so, was not near the distal end of the bone.

*Palaeotis* represents a primitive grade in the evolution of ratites. It shares a number of characters with cassowaries (Casuariidae) but these traits are demonstrably symplesiomorphous because of their occurrence in more primitive paleognathous birds, such as the Lithornithidae and Tinamidae. Clearly primitive characters of *Palaeotis* include its : small size ; narrow bill ; large foveae for corpuscles of the mandibular nerve ; caudal process of the palatine ; pterygoid fossa ; large zygomatic process ; persistent coronal suture ; large unfused splenial that contributes to the mandibular symphysis ; open-ended ilioischadic foramen ; gracile femur with centrally placed insertion of the ilioprochialis caudalis muscle ; tibiotarsus with large lateral cnemial crest, tendinal groove, and well differentiated medial and lateral condyle ; tarsometatarsus with spherical intercotylar eminence, deep groove along anterior surface, conspicuously concave origin of the extensor digiti IV brevis muscle, and large interosseous foramen ; and relatively long toes.

An inhabitant of the forest, *Palaeotis* was ecologically primitive. The Messel Oil Shale and Geiseltal Brown Coal are both recognized as representing forest environments (Mai 1981). According to Kurochkin and Lungu (1970), ancestors of ostriches "would not have occurred in eastern Europe in the Early Tertiary, as this area was forested ; an open steppe environment did not prevail here until the late Miocene". We believe, instead, that members of the ostrich lineage were present in eastern Europe in the early Tertiary but acquired their characteristic and widely recognized cursorial specializations only when the environment of Europe became more open. The observation that primitive ostriches were forest dwellers is consistent with the fact that the most primitive of the modern paleognaths (i.e. tinamous, cassowaries, kiwis, and moas) are forest dwellers (Cracraft 1974).

*Palaeotis* is the oldest fossil yet known to exhibit some characters that are derived for the ratites as a group, compared with the primitive outgroups Tinamidae and Lithornithidae. These characters include : the long and narrow prefrontals ; large postorbital process ; unkeeled sternum ; fused scapulocoracoid ; bilaterally compressed pelvis ; short femur relative to the tibiotarsus and tarsometatarsus ; and loss of the hallux. Geologically older birds, such as *Diogenornis* however, presumably possessed these traits already.

*Palaeotis* exhibits no derived characters, such as closure of the ilioischadic foramen (a derived character in the Rheidae, Casuariidae, and Dromaiidae), that would preclude it from being a candidate as an actual ancestor of modern ostriches. This is why all of the characters that distinguish the subfamily Palaeotidinae are primitive characters and all of the characters that define the Struthioninae are derived.

Derived characters that establish *Palaeotis*' relationship with ostriches are its : large acrocoracoid and glenoid fossa of the scapulocoracoid ; long humerus together with short distal wing ; lack of pneumatization of the humerus ; and accessory foramina of the carpometacarpus. Accessory foramina of the carpometacarpus are also found occasionally in rheas but their occurrence is more consistent in ostriches. The osseous bridge that circumscribes the posterior accessory foramen is, furthermore, better ossified in ostriches than in rheas, and it thus more closely resembles that of *Palaeotis*. The supracetabular iliac crest and scapulocoracoid of *Palaeotis* are also rhea-like and lend credence to the hypothesis of monophyly of ostriches and rheas (Cracraft 1974, Sibley and Ahlquist 1985) relative to other ratite birds. Some characters common to both extant ostriches and rheas are nevertheless convergent in these modern birds (Olson 1985). For example, the wide bill of ostriches and rheas must be convergent since both *Diogenornis* and *Palaeotis* primitively retain narrow bills.

The derived characters that we use to unite *Palaeotis* with the ostriches are trivial characters ; they do not include any characters as impressive as the didactylous foot. Among extant ratites, though, the long, non-pneumatic humerus and short distal wing is both distinctive and functionally specialized in ostriches. And although accessory foramina of the carpometacarpus do appear in some rheas and penguins, their occurrence in the ratite group is almost exclusively limited to ostriches. In the distant evolutionary history of all taxa, there are ancestors that had not yet evolved the specific specializations that we use to characterize the modern forms so familiar to us. But if these ancestors were actually members of lineages leading to extant species, then taxonomy should reflect the monophyly of the extant species. Such is the case with the famous fossil horse *Hyracotherium*. The monophyly of *Hyracotherium* and modern horses is widely accepted as correct despite the much greater primitive similarity of *Hyracotherium* to other early Eocene ungulates. We believe that the relationship of *Palaeotis* and ostriches is analagous to the case of *Hyracotherium* and horses.

There are two conflicting hypotheses in the recent literature that attempt to explain the evolution of ostriches. One hypothesis assumes that all ratite birds are strictly monophyletic, although the specific order of divergence of the various lineages of ratites is disputed by its advocates (Cracraft 1974, Prager *et al.*, 1976, Sibley and Ahlquist 1981). The other hypothesis holds that ratites are polyphyletic, ostriches having evolved from the gruiform family Ergilornithidae in Asia (Olson 1985). This second hypothesis assumes that the didactylous foot in ostriches and ergilornithids is synapomorphic and that the paleognathous palate, rhamphothecal grooves, and open ilioischadic foramen are homoplastic.

We do not concur with the idea that the paleognathous palate is homoplastic because paleognathous birds are generally alike each other and differ from neognathous birds in a plethora of non-osteological characters : myology (Hofer 1950, McGowan 1982), rhamphothecal grooves (Parkes and Clark 1966), plumage as chicks (Pycraft 1900, Jehl 1971), pterylography (Parker 1864, Chandler 1916), spermatozoa (McFarlane 1971), gonads (Meier 1979), Bursa of Fabricius (Berens von Rautenfeld and Budras 1982), ocular pecten (Semba and Mathers MS), cardiovascular system (Glenny 1965, Baumel 1968), osseous microvascularization (Amprino and Godina 1944, Zavattari and Cellini 1956), cortical neuroanatomy (Craigie 1935a, b, 1940a, b, Pearson 1972), eustachian tubes (Hopkins 1906), coelomic cavities (Duncker 1979), proteins (Sibley 1960, Wilson *et al.* 1964, Miller and Feeney 1964, Kaplan 1965, Fitch and Margoliash 1967, Osuga and Feeney 1968, Feeney and Alison 1969, Gysels 1970, Sibley and Ahlquist 1972, Sibley and Frelin 1972, Krampitz *et al.* 1974, Ho *et al.* 1976, Prager *et al.* 1976, Stapel *et al.* 1984), DNA (Takagi *et al.* 1972, Takagi and Sasaki 1974, de Boer 1980, Sibley and Ahlquist 1981, 1985), behavior (Meise 1963), and parasites (Kellogg 1913).

Our study of *Palaeotis* is consistent with the idea that ratites are each others' closest relatives : *Palaeotis* is, in many ways, intermediate between the disparate extant ratites and completely consistent with the paleognath "bauplan". In contrast, the existence of *Palaeotis*, a paleognathous, tridactylous, primitive ostrich, clearly conflicts with the notion that ostriches evolved from non-paleognathous ancestors that were already didactylous and that bear little resemblance to other paleognathous birds. Reduction in the number of digits is a widespread cursorial adaptation in non-avian tetrapods that could have also evolved convergently in ergilornithids and ostriches.

Our allocation of *Palaeotis* to the Struthionidae is biogeographically plausible in light of the relatively large number of Eurasian Tertiary fossil remains that have been

attributed to ostriches. The Eurasian origin of ostriches that we advocate does not differ greatly from the biogeographic implications implied by the hypothesis of ostrich origins from ergilornithid ancestors. Ostriches may have evolved exclusively in Eurasia and subsequently dispersed to Africa sometime during the middle Tertiary. It is equally possible that dispersal between Africa and Eurasia was more frequent and continuous, such that representatives of all grades of primitive and derived ostriches were present in both continents, but there is as yet no empirical evidence for this.

Very little can be learned by comparing the remains of *Palaeotis* with those of the other putative ratites from the Paleogene of Europe, *Remiornis minor*, *Eleutherornis helveticus*, and *Proceriavis martini*. *Remiornis minor*, which is known from a pelvis, tibiotarsus, and tarsometatarsus, and *Eleutherornis helveticus*, which is only known from a partial pelvis, are both much larger than *Palaeotis weigelti*. Like *Palaeotis* and other primitive paleognathous birds, the tarsometatarsus of *Remiornis* has a deep groove along its anterior surface and a large interosseous foramen, and the tibiotarsus exhibits a tendinal groove. The tibiotarsus of *Remiornis* appears to be more advanced as a ratite (i.e., like ostriches) than *Palaeotis*, though, because the medial and lateral condyles are more coalesced with each other than in *Palaeotis*. The pelvis of *Remiornis* is dorsoventrally crushed, still largely unprepared, and still undescribed. In its present condition it presents no characters that either ally *Remiornis* with, or distinguish it from, other ratites.

The incomplete pelvis of *Eleutherornis* appears to be bilaterally compressed, as in most ratites and *Palaeotis*. However, *Eleutherornis* is represented almost exclusively by the antero-ventral synsacrum, which is not visible in any of the known specimens of *Palaeotis*. The only vestige of the ilium that is preserved in *Eleutherornis* is too small to be useful for comparison.

Similarly, the only known remains of *Proceriavis martini* are too fragmentary to permit significant comparison to *Palaeotis*. *Proceriavis* is known only from a fragment of a cervical vertebra so small that Harrison and Walker (1979) could not even identify its position in the vertebral column, and a single phalanx which they misidentified as belonging to digit IV. The vertebra is probably the fourth or fifth cervical vertebra, because of its dorsally rectangular shape. The phalanx is probably the proximal phalanx of digit III. It could not be the proximal phalanx of digit IV, as claimed, because it would therefore have to possess a proximally projecting process on the medial side of the proximal articular surface, which it does not. Both the vertebra and the phalanx of *Proceriavis* resemble those of cassowaries, as claimed by Harrison and Walker (1979). The phalanx of *Proceriavis* is indistinguishable from that of *Palaeotis*. The vertebrae of *Palaeotis* are also similar to those of cassowaries, but the rostral cervical vertebrae of *Palaeotis* are unfortunately too crushed to be compared with *Proceriavis*. These few similarities between *Palaeotis* and *Proceriavis* are sufficient to suggest that *Palaeotis* may eventually be proven to be a senior synonym of *Proceriavis*.

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Storrs L. Olson was the first to suggest to us that *Palaeotis* was not a bustard. We thank Wighart von Koenigswald for loaning us the Messel specimen of *Palaeotis* and for granting us permission to prepare it. This work was supported by an NSF Dissertation Grant (BSR 8313209) and Smithsonian Predoctoral Fellowship to P. Houde.

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#### CAPTIONS TO FIGURES

- Figure 1. - *Palaeotis weigelti* (GM 4362), photograph of part of referred skeleton. Abbreviations : Cr - cervical cranium, Cv - cervical vertebrae, Fe - femur, Ma - mandible, Ot - ossified tendons, Pf - prefrontal, Pl - pelvis, Pm - premaxilla, Ps - pes, Sc - scapulocoracoid, Sp - splenial, Tm - Tarsometatarsus, Tt - tibiotarsus.
- Figure 2. - *Palaeotis weigelti* (HLMD Me 7530), referred skeleton. Abbreviations : Cm - carpometacarpus, Cv - Cervical vertebrae, Fe - femur, Hu - humerus, If - ilioischadic "foramen", Pl - pelvis, Sc - scapulocoracoid, Sm - skull and mandible, Tm - tarsometatarsus, Tt - tibiotarsus, Ul - ulna.

Figure 3. - Stereophotographs of the skull and palate of *Palaeotis weigelti* (HLMD Me 7530), ventral aspect. Abbreviations : Is - interorbital septum, Ma - mandible, Mx - maxilla, Oc - occipital condyle, Pa - palatine, Pr - ventral part of prefrontal, Pt - pterygoid, Qu - quadrate, Qj - quadratojugal, Tc - tympanic cavity, Zp - zygomatic process.

Figure 4. - Ventral aspect of the palate of *Palaeotis weigelti*. Abbreviations : Cp - caudal process of palatine, Fb - facet for articulation with basipterygoid, Fq - facet for articulation with quadrate, Mx - maxilla, Pa - palatine, Pf - pterygoid fossa, Pm - premaxilla, Pt - pterygoid, Vo - vomer.

Figure 5. - Scapulocoracoid of *Palaeotis weigelti*. Abbreviations : Ac - acromion, Ap - acrocoracoid process, Gl - glenoid process.

Figure 6. - Carpometacarpi of *Palaeotis weigelti* (HLMD Me 7530) and ostrich (USNM 346697), showing accessory foramina. Cross-hatching indicates parts of bone that were preserved in this specimen, but which were not fully prepared until after the photograph was taken.



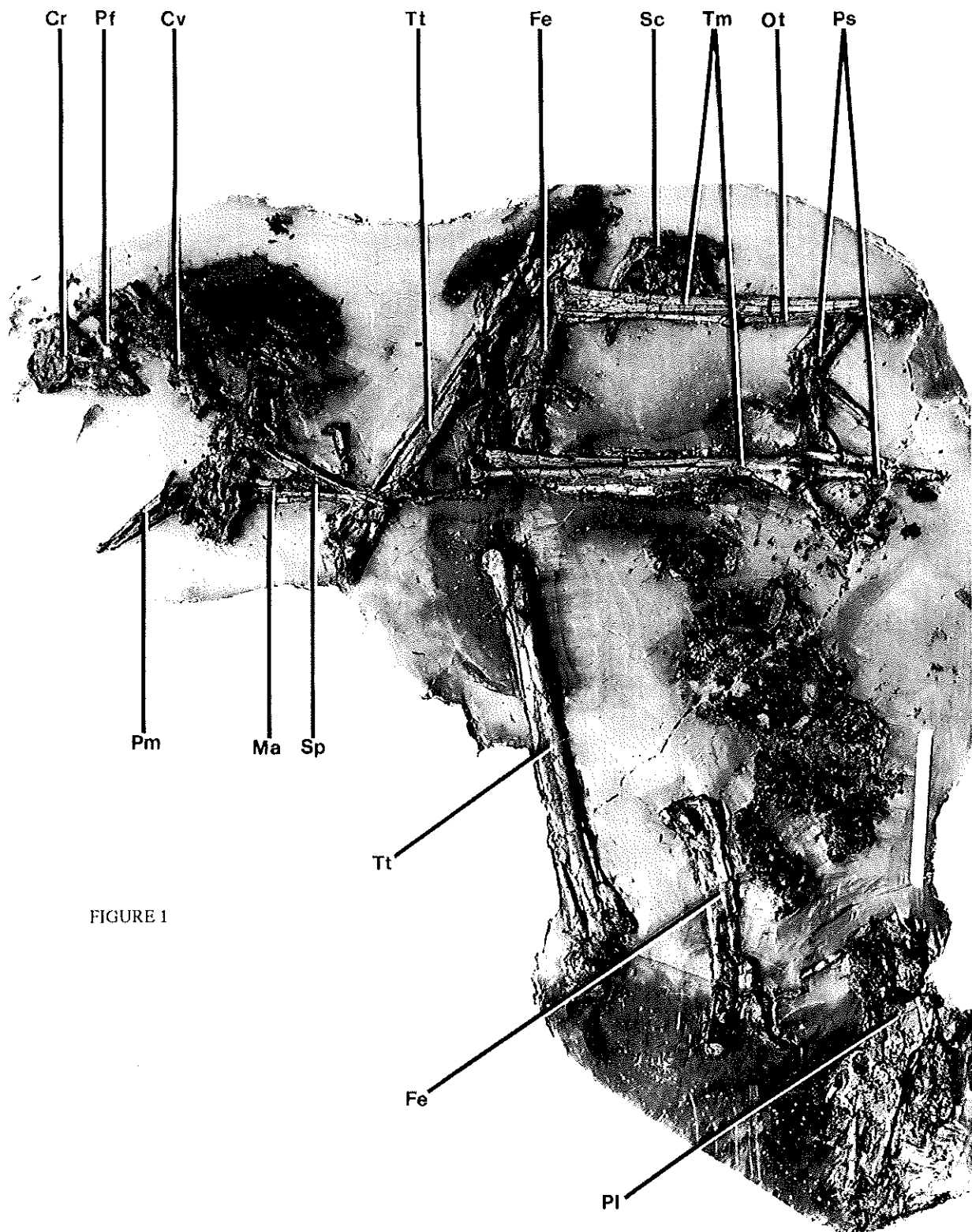


FIGURE 1

FIGURE 2

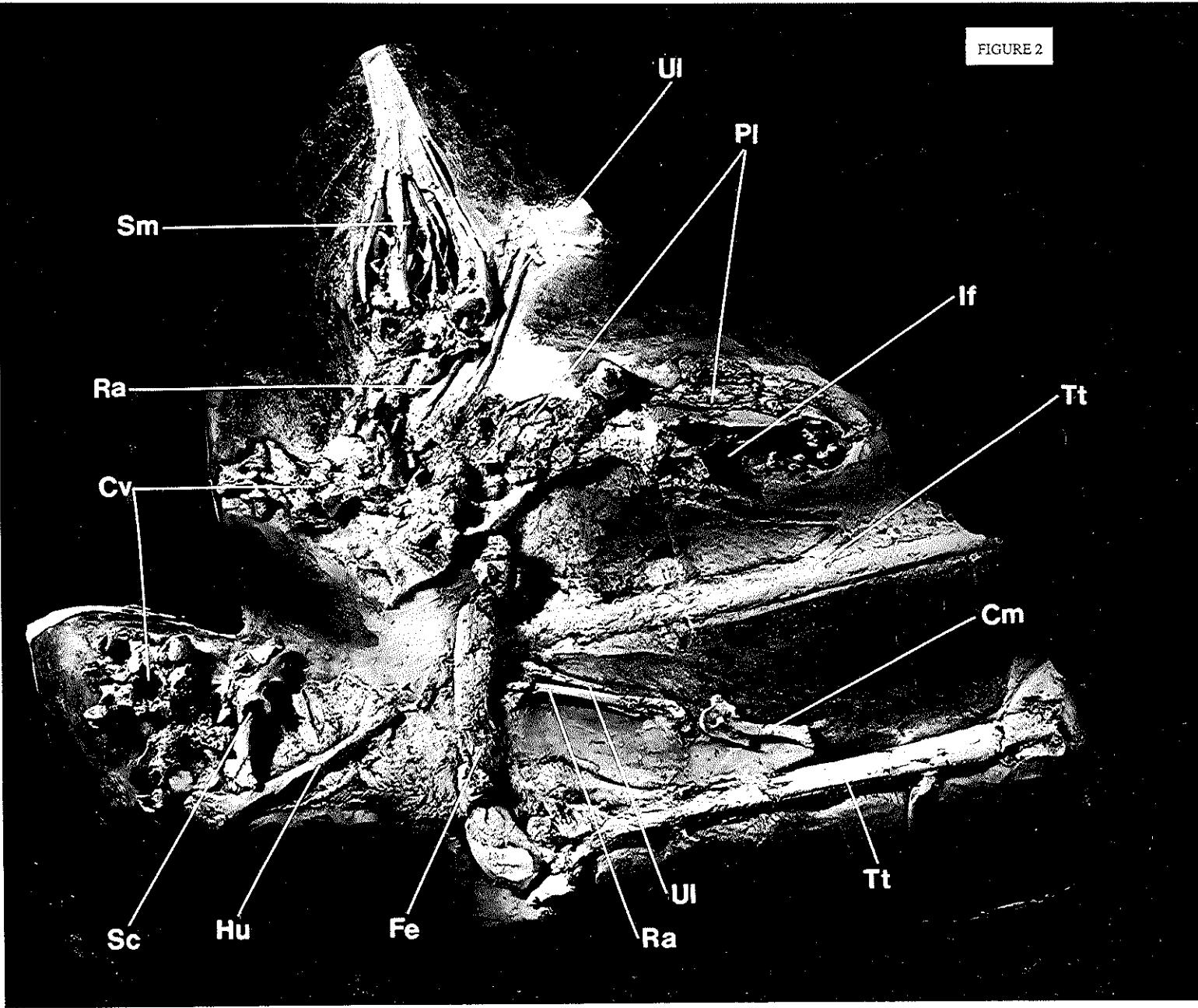
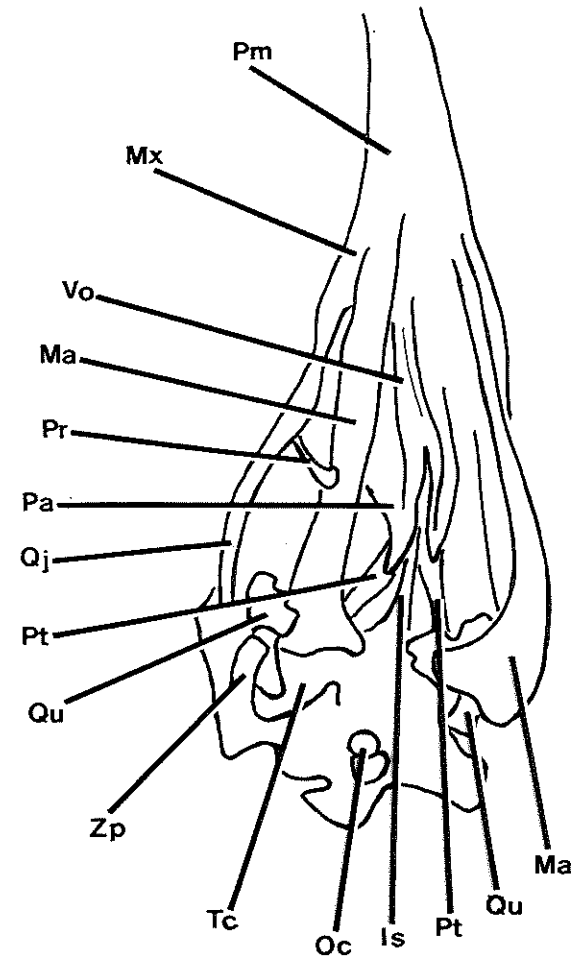
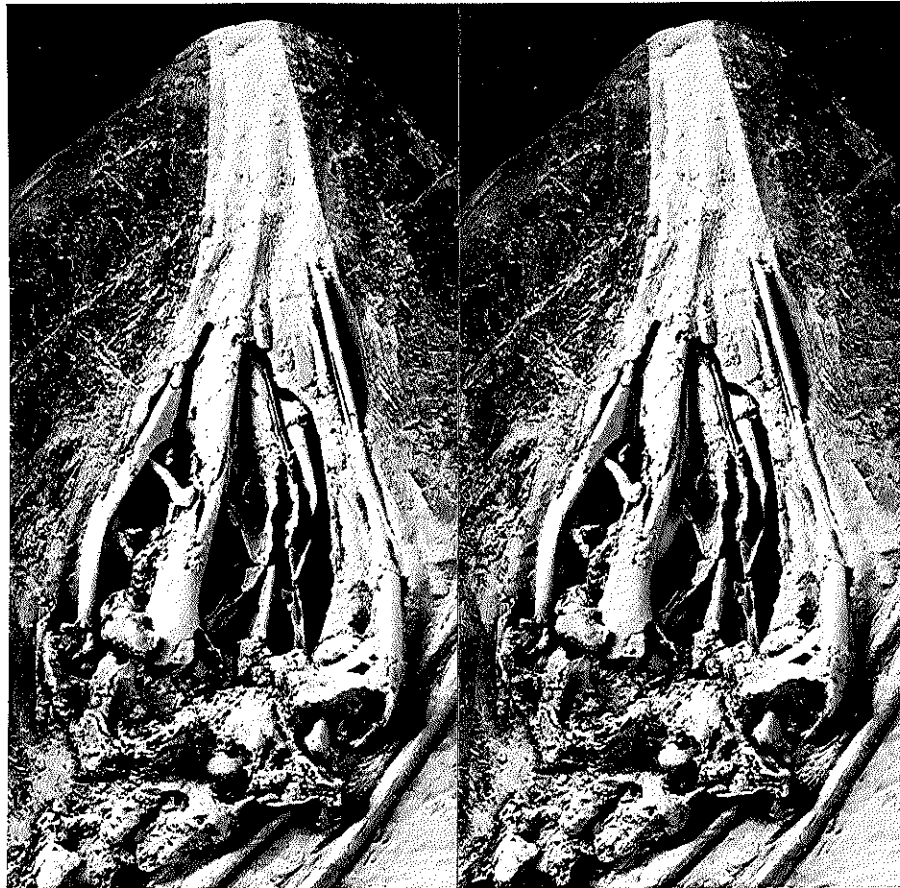


FIGURE 3



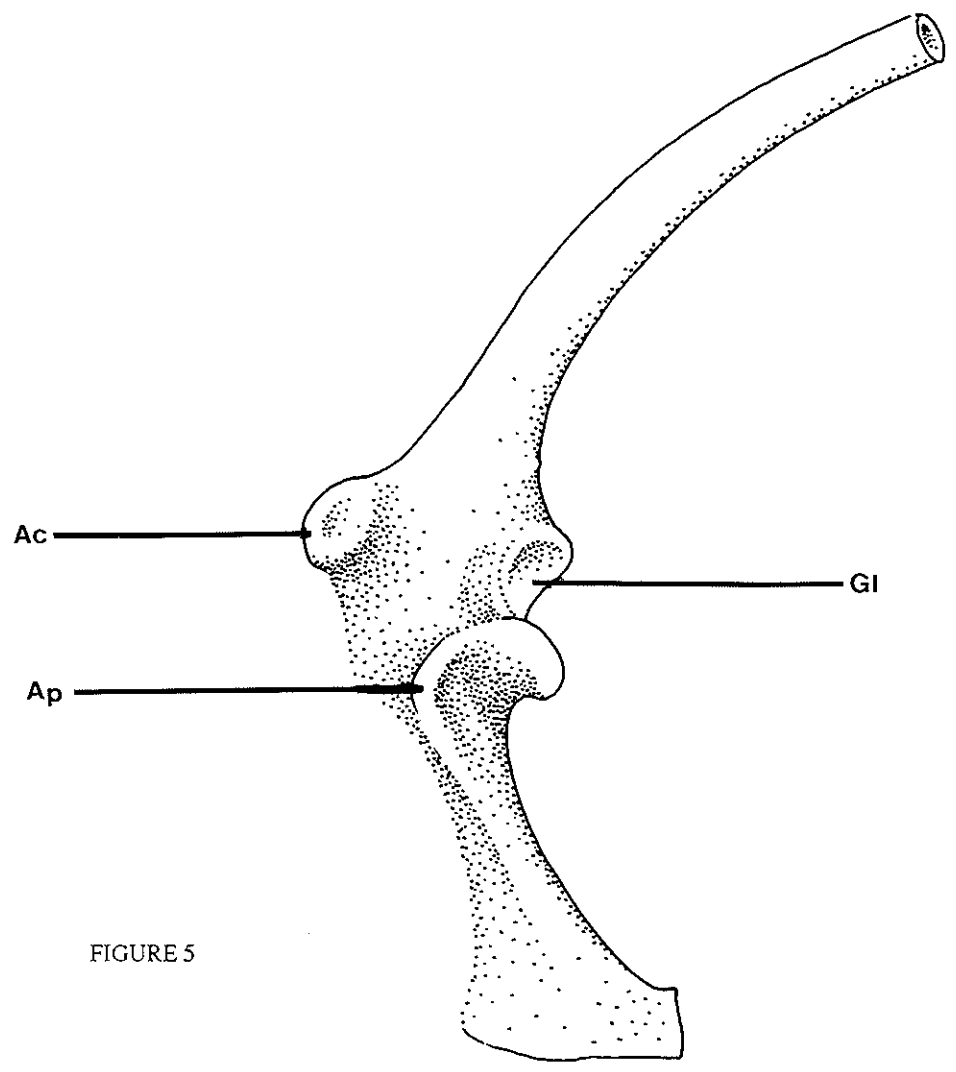
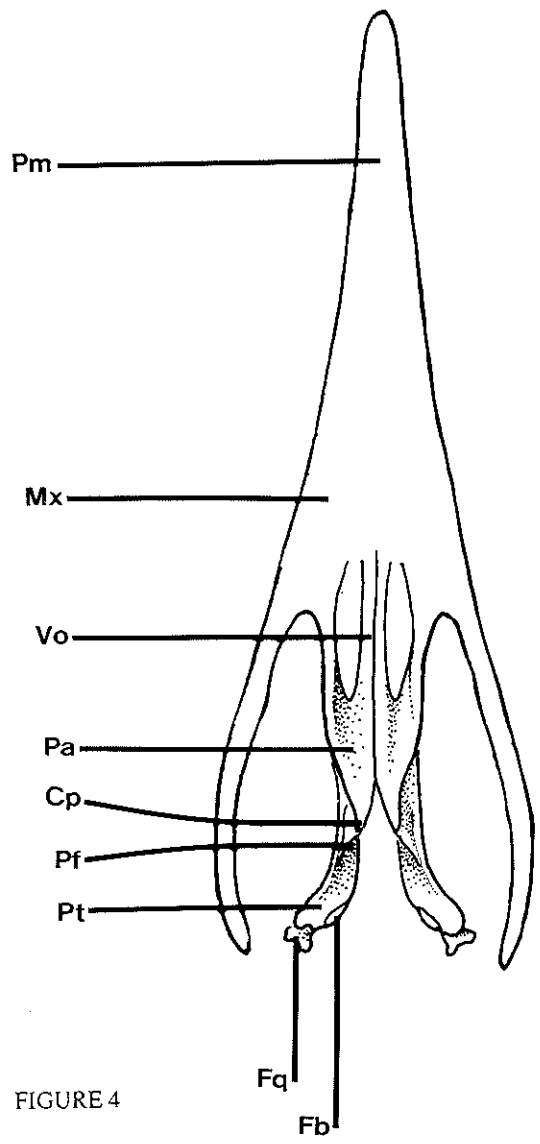
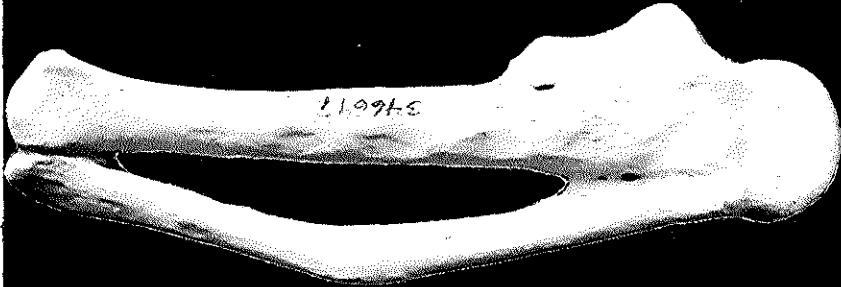
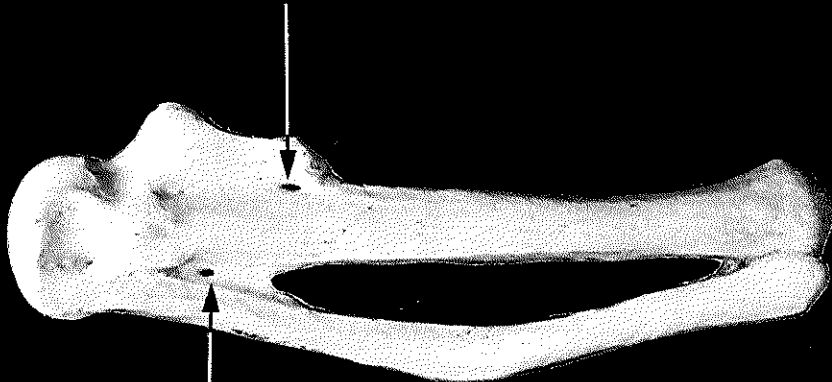


FIGURE 6



Struthio



Palaeotis

