19

DESCRIPTION OF THE SKULL OF THE GENUS *SYLVIORNIS* POPLIN, 1980 (AVES, GALLIFORMES, SYLVIORNITHIDAE NEW FAMILY), A GIANT EXTINCT BIRD FROM THE HOLOCENE OF NEW CALEDONIA

Cécile MOURER-CHAUVIRÉ & Jean Christophe BALOUET

MOURER-CHAUVIRÉ, C. & BALOUET, J.C. 2005. Description of the skull of the genus *Sylviornis* Poplin, 1980 (Aves, Galliformes, Sylviornithidae new family), a giant extinct bird from the Holocene of New Caledonia. *In* ALCOVER, J.A. & BOVER, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 205-118.

Resum

El crani de *Sylviornis* mostra una articulació craniorostral completament mòbil, amb dos còndils articulars situats sobre el rostrum, el qual s'insereix al crani en dues superfícies articulars allargades. La presència de dos procesos rostropterigoideus sobre el basisfenoide del rostrum i la forma dels palatins permet confirmar que aquest gènere pertany als Galliformes, però les característiques altament derivades del crani justifiquen el seu emplaçament a una nova família, extingida, Sylviornithidae. El crani de *Sylviornis* està extremadament eixamplat i dorsoventralment aplanat, mentre que el rostrum és massís, lateralment comprimit, dorsoventralment aixecat i mostra unes cristae tomiales molt fondes. El rostrum exhibeix un ornament ossi gran. La mandíbula mostra una símfisi molt allargada, les branques laterals també presenten unes cristae tomiales fondes, i la part posterior de la mandíbula és molt gruixada. Es discuteix el possible origen i l'alimentació de *Sylviornis*.

Paraules clau: Aves, Galliformes, Extinció, Holocè, Nova Caledònia.

Abstract

The skull of *Sylviornis* shows a completely mobile craniorostral articulation, with two articular condyles situated on the rostrum, which insert into two elongated articular surfaces on the cranium. The presence of two rostropterygoid processes on the basisphenoid rostrum and the shape of the palatines make it possible to confirm that this genus belongs to the Galliformes, but the highly derived characteristics of the skull justify its placement in a new, extinct family Sylviornithidae. The cranium of *Sylviornis* is extremely widened and dorsoventrally flattened, while the rostrum is massive, laterally compressed, dorsoventrally raised and displays very sharp cristae tomiales. The rostrum bears a large bony ornament. The mandible shows a very elongated symphysis, the lateral branches also show sharp cristae tomiales, and the posterior part of the mandible is very thick. The possible diet of *Sylviornis* is discussed.

Key words: Aves, Galliformes, Extinction, Holocene, New Caledonia.

INTRODUCTION

The genus *Sylviornis* was described by F. Poplin (1980) from some very fragmentary postcranial remains, gathered by J. M. Dubois in a fossiliferous well situated at Ure, in the Kanumera bay, on Isle of Pines, to the south-east of the main island of New Caledonia. These remains were attributed to a ratite. More complete material was collected by F. Poplin and J. C. Balouet in 1980 and made it possible to show that this bird was in fact a galliform, which was attributed to the recent family Megapodiidae (Poplin *et al.*, 1983; Poplin & Mourer-Chauviré, 1985). Later, J. C. Balouet discovered several other fossiliferous localities on the main island and found very numerous remains of *Sylviornis* in one of the Pindai caves, in particular a cranium and a rostrum.

These elements of the skull of *Sylviornis* were described by Balouet in his doctoral dissertation, which has remained unpublished (Balouet, 1984), and were illustrated with a short description in two later papers (Balouet, 1986; 1991). We think that it is necessary to publish on this material in more details. Our paper will be limited to the description of the cranial material. The species *Sylviornis neocaledoniae* Poplin, 1980 was described from the material of Isle of Pines. The material from the main island differs from that of Isle of Pines by the absence of a pygostyle, whereas the pygostyle is present in the type-population. It is likely that the form from the main island represents a second species, but it will not be described here.

The Pindai caves are situated on the Nepoui peninsula, on the western coast of the main island. The *Sylviornis* remains described here come from the main Pindai cave, the description of which is given by Balouet and Olson (1989). Charcoal associated with *Sylviornis* or other extinct bird bones have given a radiocarbon age of 1750 ± 50 BP (Gif 6341). *Sylviornis* is the most abundant bird in this locality.

The 23 other bird species, studied by Balouet and Olson (1989) include 7 extinct species. The rest of the fauna includes very numerous Chiroptera (at least 4 species), a new family, genus and species of primitive crocodile, Mekosuchidae (Balouet & Buffetaut, 1987), the horned tortoise *Meiolania* (Gaffney *et al.*, 1984) and a monitor lizard, *Varanus* (Balouet, 1984; 1991).

Systematic study

Order Galliformes

Family **Sylviornithidae** nov. fam.

Type-genus: *Sylviornis* Poplin, 1980, the only included genus.

Remark: The genus *Sylviornis* was placed in the recent family Megapodiidae based mainly on characteristics of the postcranial skeleton. The study of the skull shows that this genus is highly derived. The characters that bring together *Sylviornis* and the Megapodiidae can be considered as plesiomorphic.

Family diagnosis: True mobile articulation between the cranium and the rostrum, with two articular condyles on the rostrum, formed by the anterior part of the embryonic nasal bones, which are inserted into two articular surfaces borne by the posterior parts of embryonic nasal bones, later fused to frontals. Lacrimals fused to frontals and forming a ventrally oriented lobe; this lobe bears a small articular surface which comes into contact with a tubercle situated on the rostrum. Cranium very flattened and widened posteriorly, with a very strong development of exoccipitals and squamosals. On the ventral surface, flexure of the posterior part of the cranium just posteriorly to the basipterygoid processes; the basitemporal plate makes an angle of ca. 135 ° relative to the plane of the basisphenoid rostrum. Occipital condyle situated almost in the center of the posterior surface of the cranium; its axis is parallel to the surface of the basisphenoid rostrum; occipital foramen situated just ventral to the dorsal surface. Rostrum very elevated and narrow and bearing a bony dorsal ornament; naris situated close to the posterior part in the adult; rostrum ending anteriorly in a pointed hook, with cutting tomial crests on the ventral surface. Quadratojugal with a sigmoid shape in the adult; its anterior part articulates with a surface situated at mid-length of the posterior border of the rostrum; posterior portion wide and paddle-shaped. Left and right palatines fused posteriorly in the adult. Vomer absent. Mandible with anterior part narrow and laterally compressed; mandibular symphysis very long and thick; posterior part very widened, with thick bone; long and thick retroarticular processes, not pointed posteriorly and dorsally but rather with a rounded profile. These characteristics are considered autapomorphic.

Distribution: Holocene of New Caledonia.

Genus *Sylviornis* Poplin, 1980

Sylviornis cf. *neocaledoniae* Poplin, 1980

Description of the cranial material from the main Pindai cave (the anatomical terminology generally follows Weber, 1996).

List of the material examined (this material is preserved in the collection of the Paris Muséum national d'Histoire naturelle):

Cranium, adult, NCP 241; Cranium, juv., NCP 260 + 262; Nasal, posterior part, juv., right, NCP 261; Frontals, juv., left, NCP 264-265; Squamosal, juv., left, NCP 262; Ethmoids, juv., NCP 316-319; Quadrates, left, NCP 41-45, 222-240; Quadrates, right, NCP 46-64, 244, 268-270; Quadrates, juv., NCP 272-276; Pterygoids, left, NCP 65-77, 245, 320-322, 325; Pterygoids, right, NCP 78-99; Pterygoids, juv., NCP 323-324; Palatines, right and left fused, NCP 121-136, 250, 277; Palatines, left, NCP 137-153; Palatines, right, NCP 154-168, 251, 278-279; Quadratojugals, left, complete, NCP 114-120; Quadratojugals, left, incomplete, NCP 169-177, 192-195, 281-283; Quadratojugals, right, complete, NCP 106-113, 246, 253-259; Quadratojugals, right, incomplete, NCP 178-191; Quadratojugals, left, juv., NCP 203-210, 284; Quadratojugals, right, juv., NCP 198-202, 247-249, 285-286; Jugals, juv., NCP 211, 287-289; Quadrate + pterygoid + quadratojugal, left, NCP 252, right, NCP 271; Rostrum, adult, NCP 242; Rostrum, juv., NCP 220, 263; Nasal, anterior part, juv., NCP 221, 290-293; Mandible, symphyses and fragments of symphyses, NCP 213, 215, 243, 294-295, 299, 310-312; Mandible, fragments of branches, NCP 216, 313;

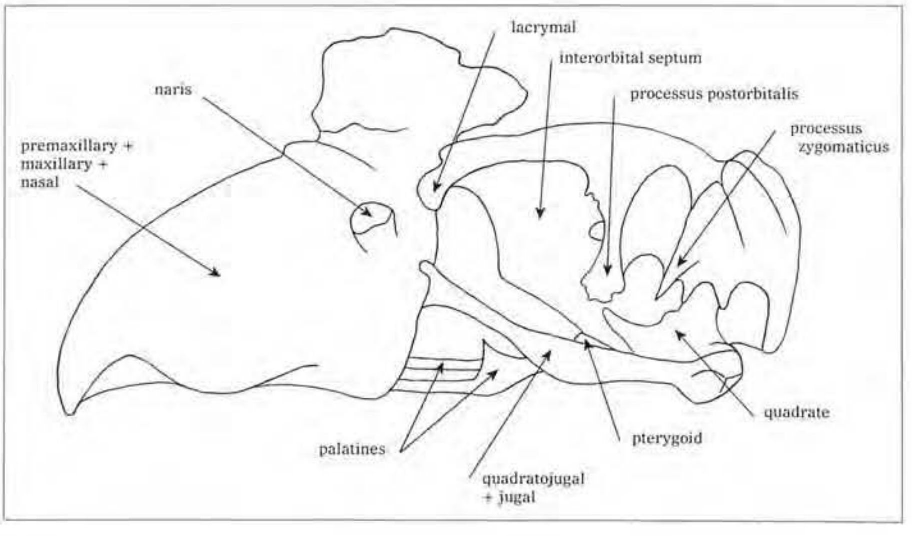

Fig. 1. *Sylviornis* cf. *neocaledoniae*. Reconstruction of the skull, showing the position of the different elements, left lateral view.

Fig. 1. Sylviornis *cf.* neocaledoniae. *Reconstrucció del crani, mostrant la posició dels diferents elements, norma lateral esquerra.*

Mandible, framents of articular parts, NCP 214, 217, 296-297; Articular, juv., NCP 219, 315; Angular, juv., NCP 212; Supraangular, juv., NCP 218, 314; Articular + supraangular + angular, right, juv., NCP 298.

In addition, several fragments of mandible collected in July 2003 by T. H. Worthy, A. Anderson, C. Sand, J. Jones, and F. Pechey in the same cave, have been examined on photographs. This material is at present deposited in the Museum of New Zealand Te Papa Tongarewa, Wellington, but has not been catalogued.

A restoration of the different cranial elements is given in figures 1 and 2.

Adult cranium (NCP 241, fig. 3)

The skull of *Sylviornis* is prokinetic and characterized by the presence of a true craniorostral hinge, with two parts completely separated. According to Bock (1964, p. 4): "the prokinetic skull is characterized by a hinge or region of bending at the junction of the nasal and frontal bones; hence the entire jaw moves as a unit". However Bock indicates that this articulation does not necessarily correspond to the suture between the embryonic nasal and frontal bones. The juvenile cranium (NCP 260 + 262) shows that the frontals are contiguous in the sagittal plane, but that their junction leaves a wide triangular space between them at their anterior end (fig. 4). This can also be seen on the juvenile cranium of other Galliformes, for example in the chicken (Jollie, 1957, fig. 2), or in a juvenile of the megapode *Alectura lathami* (Weber, 1996, fig. 3). The posterior part of the nasal (NCP 261) inserts in this triangular space. The juvenile material shows that the nasals consist of two different parts that articulated along a rectilinear hinge. The anterior part of the nasal is made up of two branches that later fuse with the premaxillary and the maxillary. The posterior part of the nasal later fuses with the frontal. In the juvenile the two parts of the nasal must have been held together by fibrous ligaments. From the juvenile elements it is possible to state that the hinge between the cranium and the rostrum was embryologically intranasal and not frontonasal. The features of the juvenile cranium also shows that a true craniorostral articulation was already present in the early stages of development of *Sylviornis.*

The adult cranium is extremely widened and flattened. This is largely due to the development of the exoccipitals in dorsal and lateral directions. The crista nuchalis transversa is rectilinear on the dorsal surface of the skull, then it continues laterally, forming two wide, projecting occipital crests at the level of the junction between the parietals and the squamosals with the supraoccipital and the exoccipitals, and then continues on ventrally along the paroccipital processes.

On the dorsal surface, the lacrimals are fused with the anterior part of the frontals. The fusion is still discernable by the presence of a large foramen on the left side. In some Galliformes, particularly in the Cracidae, the lacrimals are extended by a long process that penetrates inside the orbital cavity. In the Megapodiidae the lacrimals are very small, sometimes barely visible, and fused with the frontals and the nasals at the level of the craniofacial flexion zone. They do not have an orbital process. In *Sylviornis* the orbital process is also absent. The anterior part of the cranium, dorsal to the craniorostral hinge, is formed by the junction of the posterior part of the nasals with the ethmoid. This part

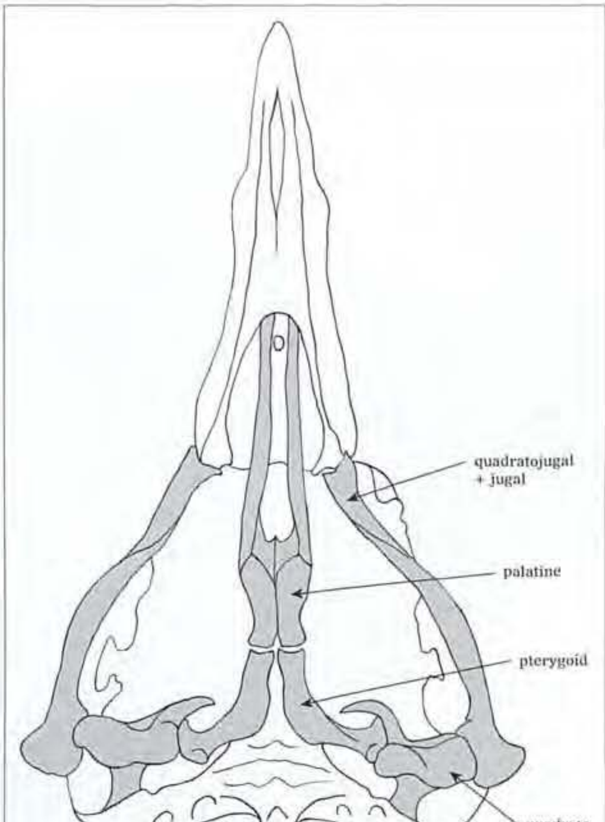

Fig. 2. *Sylviornis* cf. *neocaledoniae.* Reconstruction of the skull showing the position of the different elements, ventral view.
Fig. 2. Sylviornis *cf.* neocaledoniae. *Reconstrucció del crani, mostrant la posició dels diferents elements, norma ventral.*

shows, in the sagittal plane, a median tubercle flanked by two depressions, indicating the presence of a synovial joint. On the posterior part of the supraorbital ridge, there is a series of small foramina.

The posterior surface is characterized by the very great enlargment of the exoccipitals, which is continued by the strongly ventrally projecting paroccipital processes. The supraoccipital bears a smooth median ridge. The occipital foramen is higher than wide and is situated just ventral to the dorsal surface. The occipital condyle is situated almost at the center of the posterior surface, its dorsal surface is slightly concave. On each side of the occipital condyle there are two well-marked depressions containing foramina for blood-vessels and nerves.

The ventral surface is characterized by the presence of two processus rostropterygoideus (Weber, 1996). They are oval in shape, slightly elevated relative to the surface of the basisphenoid rostrum, oriented in parallel in an anteroposterior direction, and separated by a wide space, ca. 140 % wider than the adjacent width of the rostropterygoid processes. These processes are situated at the base of the basisphenoid rostrum, which is triangular in shape, relatively short anteroposteriorly, and wide at its base. At the anterior end of the basisphenoid rostrum the interorbital septum widens and fuses with the ethmoid. Usually in birds the ventral part of the cranium is a relatively flat surface and the basitemporal plate (or basiparasphenoid plate in Ericson, 1996) is a horizontal plane in the prolongation of

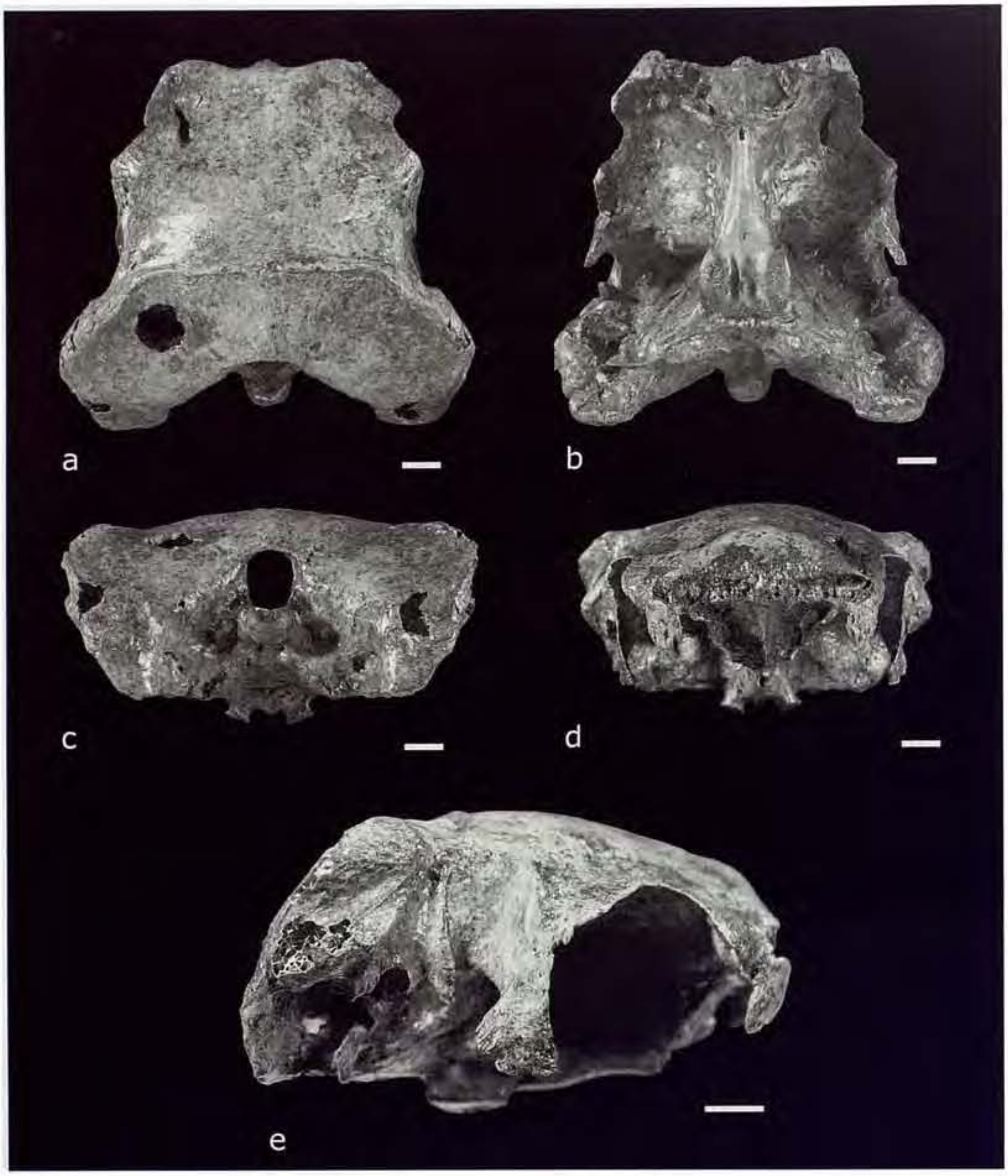

Fig. 3. *Sylviornis* cf. *neocaledoniae*. Adult cranium, NCP 241; a) dorsal view; b) ventral view; c) posterior view; d) anterior view; e) right lateral view. The scale bar represents 10 mm.

Fig. 3. Sylviornis *cf.* neocaledoniae. *Crani adult, NCP 241; a) norma dorsal; b) norma ventral; c) norma posterior; d) norma anterior; e) norma lateral dreta. L'escala representa 10 mm.*

the palate. In the posterior part of the cranium, there is a flexure between the ventral and the posterior surfaces, and this flexure is situated either at the level of the occipital condyle, or slightly ventrally relative to the condyle. In *Sylviornis* the flexure is situated between the basisphenoid rostrum and the basitemporal plate, just posterior to the basipterygoid processes. The basitemporal plate, rather than being near coplanar with the basisphenoid, makes an angle of ca. 135 ° with the ventral surface of the rostrum. In the recent megapodes, the flexure occurs at the posterior part of the basitemporal plate, which, unlike in *Sylviornis*, is slightly inflated.

On the lateral surface, the postorbital process is strongly developed and directed ventrally. It widens ventrally in the shape of a spatula, with an indented edge. This ventral part of the postorbital process probably corresponds to an aponeurosis ossificans (Zusi & Livezey, 2000). Posteriorly, there is a zygomatic process that is pointed, directed ventrally and slightly anteriorly, and is smaller than the postorbital process. This zygomatic process is very similar to that of some adult megapodes (genera *Alectura, Leipoa, Aepypodius, Macrocephalon*) but it is different in the genus *Megapodius*. Its ventral part is named by Zusi and Livezey (2000) aponeurosis zygomatica ossificans. Between the two processes is a temporal fossa corresponding to the insertion of M. adductor mandibulae externus (AME), pars coronoidea. This fossa is wide and deep, with a well-defined outline. Posterior to the zygomatic process is a second temporal fossa, or fossa temporalis secundaria (Weber 1996), for the insertion of M. add. mand. ext., pars articularis (Zusi & Livezey, 2000). This triangular-shaped fossa is delimited anteriorly by a ridge that is situated in the prolongation of the zygomatic process, and posteriorly by the thick and inflated crista nuchalis. Ventral to this fossa is the quadrate articulation, and posteriorly to the quadrate articulation is a very large tympanic cavity. Anterior to the postorbital process, the orbital fossa is closed medially by the interorbital septum, pierced on each side by a wide foramen opticum.

The anterior surface shows the craniorostral hinge with a median tubercle in the sagittal plane and, on each side, two medio-laterally oriented articular surfaces. On each side the lacrimals form anteriorly a lobe situated ventrally relative to the hinge and ventrally oriented. On the medial side of the lacrimals there is a small, rounded, articular facet, which comes into contact with a process of the rostrum, situated ventrally relative to the articular condyles of the hinge. Then, more ventrally, and medially situated there is the ethmoid, with a median ridge, and the two alae ethmoidales. On each side of the ethmoid there is a wide orbitonasal foramen, and ventral to the foramen a large articular surface, oval in shape and slightly concave. On a cast of the cranium it is possible to see that the right ala ethmoidale was extended in lateroventral direction by a thin, sharp process. This process was subsequently broken on the specimen NCP 241.

Juvenile cranium (NCP 260, 261, 262, fig. 4)

This juvenile cranium has been reconstructed from isolated unfused bones, based on matching sizes and shapes. As for the adult, its general shape is very wide and flat. The supraorbital region is much narrower than in the adult because the lacrimals are not yet fused with the frontals. The crista nuchalis transversa is much less developed and the cristae occipitales are less projecting in lateral and dorsal directions. The squamosal is anteroposteriorly elongated and does not show the enormous swelling of its posterior part that is seen in the adult.

Several juvenile ethmoids have been identified. They show a wide, flat part at their anterior side, and a ventral keel. On each side of the keel is the sulcus olfactorius. Dorsally the anterior part shows articular surfaces which in the adult are fused with the ventral surface of the nasals (fig. 5, g).

Rostrum (NCP 242, fig. 5, a-c))

The adult rostrum NCP 242 does not fit with the cranium NCP 241 and comes from a slightly larger individual. This rostrum is formed by the fusion of the anterior parts of the nasals, the premaxillaries, the maxillaries and the maxillo-palatines. It shows a true hinge, with two large articular condyles, which project ca. 1 cm from the lateral facies immediately in front of them and which insert into the articular surfaces of the posterior parts of the nasals. Its dorsal part bears in the adult a bony ornament, made of very thin cancellated bone, and is incompletely preserved. At the anterior part and at the base of this ornament, there is a groove and a flattened surface. Ventral to the articular condyle, there is a small process [3 mm by 3 mm] that articulates with the small articular surface situated on the ventral process of the lacrimal.

The beak is extremely high and narrow. Its surface has a shagreened aspect that indicates the presence, in adults, of a thick ramphotheca. On the juvenile specimens the surface of the beak is rather smooth. The nostril is rounded and situated almost at the posterior part of the rostrum. The anteriormost part of the beak is a narrow point, ventrally directed. The external tomial crest forms a dorsally oriented sinus, then a ventrally oriented lobe. In ventral view one can see two external tomial crests, two internal ones that continue onto the posteroventral angle of the beak, and one median crest. Anteriorly the adoral surface is formed by the ventral fusion of the premaxillaries. Posteriorly there is a secondary palate formed by the ventral fusion of the maxillaries.

In posterior view, ventral to the craniorostral hinge, there are the two processes that articulate with the lacrimal processes, then two large openings of the internal nares. On

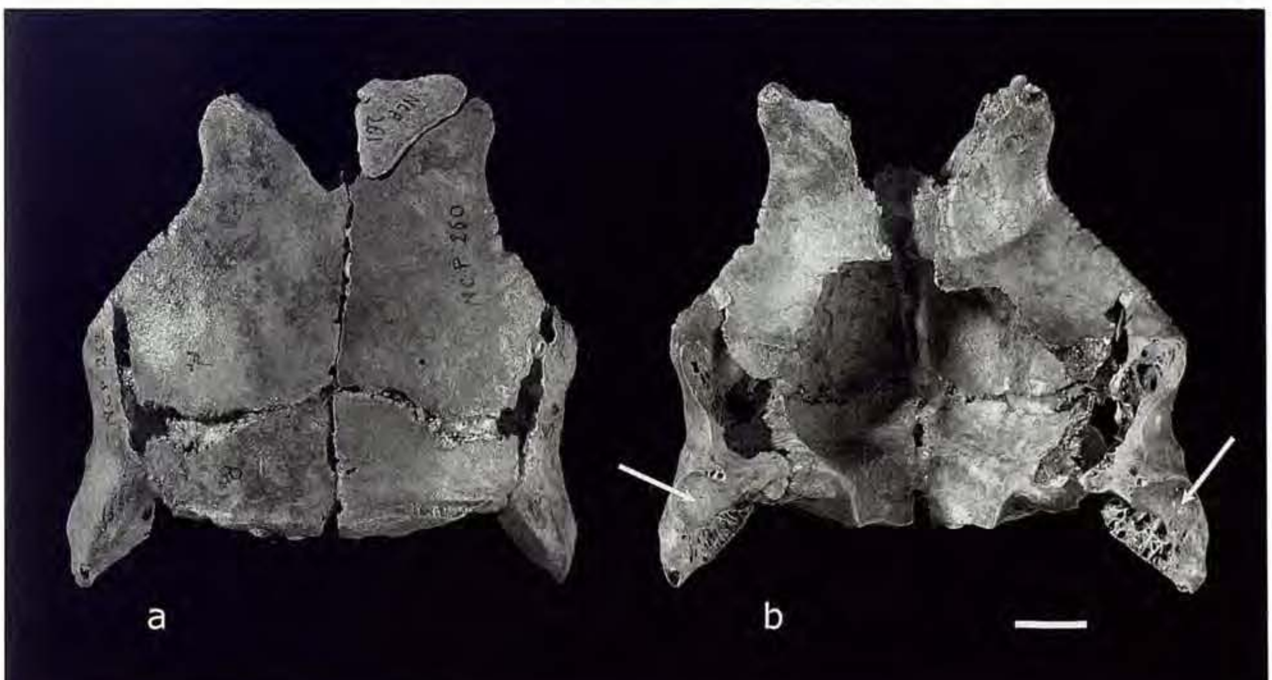

Fig. 4. *Sylviornis* cf. *neocaledoniae*. Reassembled juvenile cranium, NCP 260 + 262; a) dorsal view (the posterior part of the right nasal NCP 261 has been placed in the anterior opening of the frontals); b) ventral view without the nasal NCP 261. The arrows indicate the articular surfaces for the quadrates. The scale bar represents 10 mm.

Fig. 4. Sylviornis *cf.* neocaledoniae. *Crani juvenil remuntat, NCP 260 + 262; a) norma dorsal (la part posterior del nasal dret NCP 261 s'ha situat a l'obertura anterior dels frontals); b) norma ventral sense el nasal NCP 261. Les fletxes indiquen les superfícies articulars per als quadrats. L'escala representa 10 mm.*

Fig. 5. *Sylviornis* cf. *neocaledoniae*. Adult rostrum, NCP 242; a) right lateral view; b) posterior view (for a and b the thick arrow indicates the tubercle which corresponds to the articular surface found on the ventral process of the lacrimal, and the thin arrow indicates the indentation for the articulation with the anterior part of the quadratojugal); c) ventral view. Juvenile rostrum and left nasal, NCP 263, and right nasal, NCP 290; d) right lateral view (the thick arrow indicates the tubercle which later becomes the articular condyle of the adult and the thin arrow indicates the tubercle which corresponds to the articular surface found on the ventral process of the lacrimal); e) dorsal view. Right juvenile nasal, anteriorpart, NCP 221; f) medial view. Juvenile ethmoid, NCP 316; g) right lateral view (one can see the sulcus olfactorius). The scale bar represents 10 mm.

Fig. 5. Sylviornis *cf.* neocaledoniae. *Rostre adult, NCP 242; a) norma lateral dreta; b) norma posterior (per a a i b la flexta gruixada indica el tubercle que correspon a la superfície articular que es troba sobre el procés ventral del lacrimal, i la fletxa prima indica la indentació per a l'articulació amb la part anterior del quadratojugal); c) norma ventral. Rostre juvenil i nasal esquerre, NCP 263, i nasal dret, NCP 290; d) norma lateral dreta (la fletxa gruixada indica el tubercle que posteriorment es transforma en el còndil articular de l'adult i la fletxa prima indica el tubercle que correspon a la superfície articular que es troba sobre el procés ventral del lacrimal); e) norma dorsal. Nasal juvenil dret, part anterior, NCP 221; f) norma medial. Etmoide juvenil, NCP 316; g) norma lateral dreta (es pot veure el sulcus olfactorius). L'escala representa 10 mm.*

each side there is a small indentation that corresponds to the articulation of the anterior part of the quadratojugal.

In the juvenile specimens, the anterior part of the nasal is not yet fused with the premaxillary (NCP 263 + 290, fig. 5, d-e). Anteriorly it shows two branches, a dorsal one, which inserts into a groove situated on the posterior part of the premaxillary (NCP 263), and a maxillary one, which probably rested against the maxillary (fig. 5, f). Posteriorly it presents, on each lateral side, a large tubercle that, in the adult, becomes the articular condyle, and ventrally a very small point that bears the articular surface for the lacrimal (fig. 5, d).

Quadrate (fig. 6, c-f)

The processus oticus ends dorsally in two articular condyles, the squamosal and the prootic ones, which are contiguous but distinct in the adults. The squamosal condyle is about twice as large as the prootic one. On the anterior surface of the processus oticus, the eminentia articularis is a poorly delimited tubercle, projecting dorsally. The processus orbitalis, triangular in shape, is very elongated, slightly incurved medially, and ends in a rounded lobe. The articular surface for the quadratojugal is a deep socket, surrounded by a thick rim. The mandibular articulation is made up of two obliquely elongated condyles,

Fig. 6. *Sylviornis* cf. *neocaledoniae.* Right and left fused palatines, NCP 250; a) dorsal view; b) ventral view. Right quadrate, NCP 244; c) medial view; d) lateral view; e) dorsal view; f) ventral view. Right quadratojugal, fused with the jugal, NCP 246; g) lateral view; h) dorsal view; i) medial view. Juvenile right palatine, unfused, NCP 251; j) ventral view. Adult left pterygoid, NCP 245; k) dorsal view; l) ventral view. Juvenile left pterygoid, NCP 323; m) ventral view. Three juvenile stages of right quadratojugals, still unfused with the jugals, medial views; n) NCP 247, juvenile; o) NCP 248, more juvenile; p) NCP 249, still more juvenile. The scale bar represents 10 mm.

Fig. 6. Sylviornis *cf.* neocaledoniae. *Palatins dret i esquerre fusionats, NCP 250; a) norma dorsal; b) norma ventral. Quadrat dret, NCP 244; c) norma medial; d) norma lateral; e) norma dorsal; f) norma ventral. Quadratojugal dret fusionat amb el jugal, NCP 246; g) norma lateral; h) norma dorsal; i) norma medial. Palatí dret juvenil, no fusionat, NCP 251; j) norma ventral. Pterigoide adult esquerre, NCP 245; k) norma dorsal; l) norma ventral. Pterigoide juvenil esquerre, NCP 323; m) norma ventral. Tres estadis juvenils de quadratojugals drets, encara no fusionats amb els jugals, normes medials; n) NCP 247, juvenil; o) NCP 248, més juvenil; p) NCP 249, encara més juvenil. L'escala representa 10 mm.*

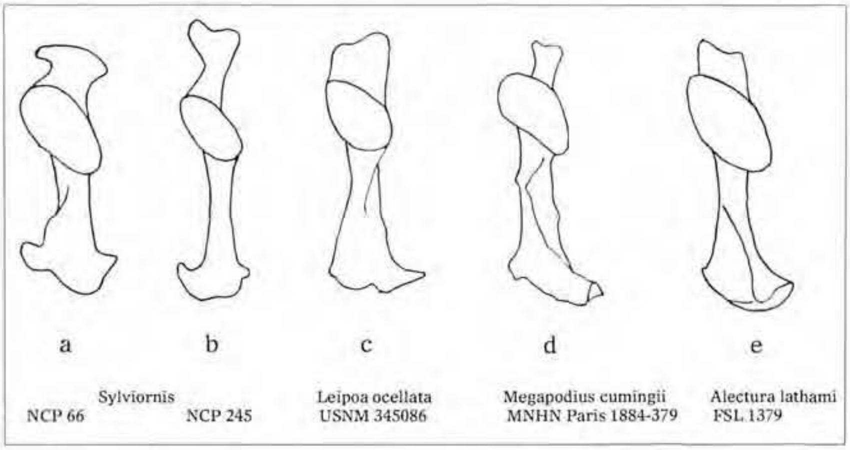

Fig. 7. Drawings of left pterygoids, dorsal view, in two different individuals of *Sylviornis* cf. *neocaledoniae* (a, b) and in three recent genera of megapodes (c, d, e). Not to scale.

Fig. 7. Dibuixos de pterigoides esquerres, norma dorsal, a dos diferents individus de Sylviornis *cf.* neocaledoniae *(a, b) i a tres gèneres recents de megàpodes (c, d, e). No a escala.*

medialis and lateralis, separated by a shallow groove. The lateral condyle is much larger than the medial one. At the anterior part of the medial condyle there is an almost hemispheric, convex, articular surface for the pterygoid (in recent megapodes this surface is more dorsally situated and clearly separated from the medial condyle). The articular surface for the pterygoid continues dorsally along the ventral border of the orbital process, on its medial side. On the medial surface, at the posterior end, dorsally relative to the condylus lateralis, there is a flattened surface for the retroarticular process of the mandible. A pneumatic foramen is present, in the middle of the medial surface of the bone, at the base of the otic process.

Pterygoid (fig. 6, k-m)

This bone shows a large, oval, articular surface for the processus rostropterygoideus, a surface that is oriented at about 45 ° in relation to the long axis of the bone. The ratio between the length of the articular surface and the length of the bone is highly variable. Some pterygoids are long with a small articular surface (NCP 245), others are short with a large articular surface (NCP 66; see fig. 7). At the anterior end of the pterygoid is the articular surface for the palatine, which is made up of an elongated surface on the ventral side, and a point on the dorsal side. The posterior end, widened and crescent-shaped, bears a rounded articular surface for the quadrate on the medial side, and a hook-shaped extension on the lateral side.

The articulation with the processus rostropterygoideus is not situated at the anterior end of the bone, but rather at its anterior third and this characteristic is also found in the recent megapodes that we have been able to study (see fig. 7), whereas in the Cracidae and Phasianidae, as well as the Anatidae, the articulation is situated at the anterior end. This characteristic cannot be considered as a synapomorphy of *Sylviornis* and the megapodes, however, because it is also present in the primitive Anseriformes Anhimidae and Anseranatidae (Dzerzhinsky, 1995), as well as in the Eocene Anseranatidae *Anatalavis* (Olson, 1999). This characteristic is therefore considered as plesiomorphic.

Palatine (fig. 6, a-b, j)

The palatine shows the charateristic shape of the Galliformes, with a narrow posterior part and a very elongated anterior branch. It is different form the anseriformes palatine, which has a wide, wing-like posterior part and a short anterior branch. On some specimens the right and left palatines are fused posteriorly, but this fusion probably occurred relatively late in development because in the available material, the number of individuals with fused vs. unfused palatines is about equal. Most unfused palatines come from small, juvenile, individuals, but there are also large-sized, unfused palatines. When the palatines are unfused, the medial surface is rough, indicating the presence of a fibrous joint.

The fused palatines show two branches that end cranially by a flattened paddle, with a rough and fibrous surface. These branches probably fit into the cavity between the primary and secondary palates, and were probably attached in this cavity by ligaments. The symphyseal part of the palatines shows, on its dorsal side, a point oriented dorsally and a median ridge. At its posterior part there are the two, clearly separated, rounded articular surfaces for the pterygoids. On its ventral side there are two elongate, slightly concave, muscle impressions. There is no contact for a possible vomer and no piece that could be interpreted as a vomer has ever been found.

Quadratojugal (fig. 6, g-i, n-p)

It is formed by the fusion of the quadratojugal sensu stricto with the jugal. Here also the fusion occurs late, as in some adult-sized individuals the jugal is still unfused. The adult quadratojugal has a very sinuous shape. It is dorsoventrally flattened on its anterior part, then latero-medially flattened on its posterior part, and it ends posteriorly in an oval paddle, with a strong dorsal tubercle on its medial side for the quadrate articulation. This shape changes according to age. Young individuals do not have a posterior paddle but only a tubercle for the quadrate (NCP 249, fig. 6, p), after which the paddle develops progressively (NCP 248, 247, fig. 6, o-n). Likewise young individuals have a much more rectilinear quadratojugal, and it becomes more sinuous as it grows. The anterior part of the quadratojugal is made up of a rough articular surface on the medial side, and a point on the lateral side. This articular surface and point rest against an indentation on the posterior side of the rostrum, where they must have been tied by ligaments, in such a way that the rostrum could move around the craniorostral hinge.

Mandible (fig. 8)

No complete mandible is known. The fragments indicate that the mandibular symphysis was very long (NCP

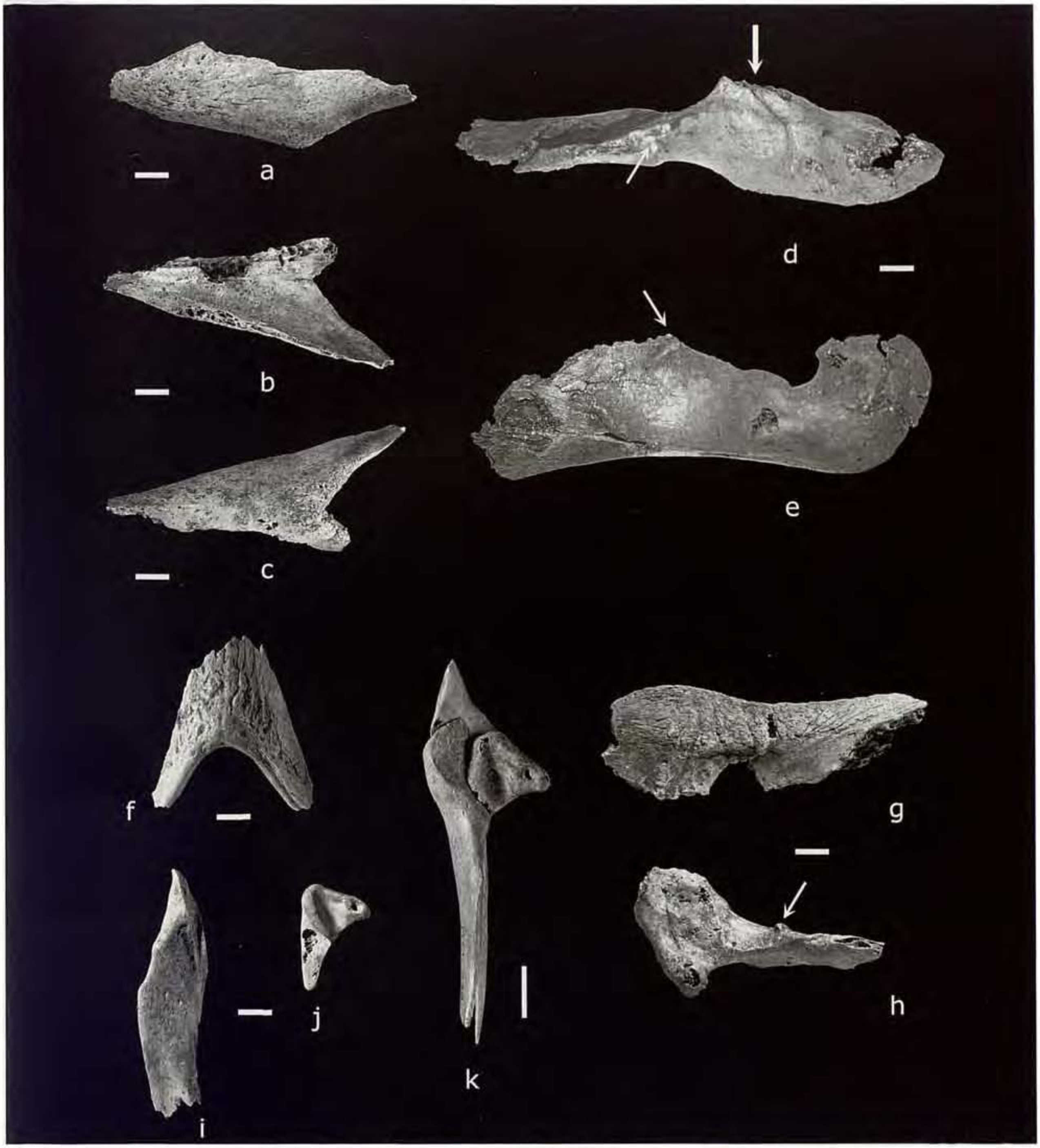

Fig. 8. *Sylviornis* cf. *neocaledoniae*. Symphysial part of juvenile mandible, NCP 243; a) left lateral view; b) dorsal view; c) ventral view. Part of a mandible, left ramus collected by T. H. Worthy *et al.*; d) dorsal view; e) lateral view (in d the thick arrow indicates the position of the processus mandibularis medialis which is broken on this specimen; in d and e the thin arrow indicates the processus coronoideus; the crista paracoronoidea caudalis is not visible on this mandible). Symphysial part of adult mandible, NCP 215, with a corrugated surface; f) ventral view. Intermediate part of left ramus of mandible, NCP 216; g) medial view (the broken part on the right corresponds to the symphysis; this specimen shows the sigmoid outline of the tomial crest, which corresponds to the shape of the rostral tomial crests). Posterior part of left ramus of mandible, NCP 217; h) dorsal view (this part shows the two articular surfaces for the quadrate, separated by a very smooth ridge; the retroarticular process and the tip of the medial mandibular process are broken; the arrow indicates the dorsal end of the crista paracoronoidea caudalis). Juvenile right surangular, NCP 218; i) medial view. Juvenile right articular, NCP 219; j) dorsal view. Juvenile right angular, surangular and articular joined, NCP 298; k) dorsal view. The scale bar represents 10 mm.

Fig. 8. Sylviornis *cf.* neocaledoniae. *Part simfisària de mandíbula juvenil, NCP 243; a) norma lateral esquerra; b) norma dorsal; c) norma ventral. Part d'una mandíbula, branca esquerra, recollit per T. H. Worthy* et al.*; d) norma dorsal; e) norma lateral (a d la fletxa gruixada indica la posició del processus mandibularis medialis que a aquest exemplar està romput; a d i e la fletxa prima indica el processus coronoideus; la crista paracoronoidea caudalis no és visible a aquesta mandíbula). Part simfisària de mandíbula adulta, NCP 215, amb una superfície ondulada; f) norma ventral. Part intermitja de branca de mandíbula esquerra, NCP 216; g) norma medial (la part rompuda de la dreta correspon a la símfisi; aquest espècimen mostra el perfil sigmoideu de la cresta tomial, que correspon a la forma de les crestes tomials rostrals). Part posterior de branca de mandíbula esquerra, NCP 217; h) norma dorsal (aquesta part mostra les dues superfícies articulars per al quadrat, separades per una aresta molt suau; el procés retroarticular i la punta del procés mandibular medial estan romputs; la fletxa indica el final dorsal de la crista paracoronoidea caudalis). Surangular juvenil dret, NCP 218; i) norma medial. Articular juvenil dret, NCP 219; j) norma dorsal. Angular juvenil dret, surangular i barra articular junts, NCP 298; k) norma dorsal. L'escala representa 10 mm.*

243, minimal length 64.5 mm, fig. 8, a-c), and that the bone was very thick at the level of the symphysis (NCP 213, minimal depth of the symphysis 18.3 mm). The fragments of mandibular symphysis from adults, particularly NCP 215 (fig. 8, f), show a strongly corrugated ventral surface, with anteroposteriorly oriented ridges. On the fragment of mandibular ramus NCP 216 (fig. 8, g), the dorsal part forms a sharp edge, with a sinuous line that articulates with the external tomial crest of the rostrum. Both internal and external surfaces of this mandibular ramus show a shagreened ornamentation.

The articular part of the mandible (NCP 217, fig. 8, h) shows two articular cotylae for the two mandibular condyles of the quadrate, separated by a smooth ridge. This articulation is not situated in a depression. The medial mandibular process is short and wide, with a pneumatic foramen on its lateral side, ventral to its tip. On the dorsal side of the mandibular ramus, close to the articulation, there is a processus coronoideus and, on the lateral side, a dorsoventrally oriented crista paracoronoidea caudalis (Weber, 1996). This crista has a tubercle at its dorsal part, and is not incurved but quite straight.

The posterior part of a left mandible collected by T. H. Worthy *et al.* (fig. 8, d-e) shows that, in the adult, this area is extremely thick in a mediolateral direction. The retroarticular process of this mandible is very wide, both mediolaterally and anteroposteriorly. The dorsalmost part of this retroarticular process is incompletely preserved but it seems to have a rounded outline, while in the recent megapodes it ends by a dorsally, or dorsoposteriorly oriented point.

In most birds in which both are present, the medial process and the retroarticular process of the mandible are approximately the same size, but in *Sylviornis*, the retroarticular process is much more developed than the medial mandibular one.

The development of the posterior part of the mandible can be correlated with the strong development, both in lateral and posterior directions, of the posterior part of the cranium. There is a strong contrast between the anterior part of the mandible, which forms two cutting blades, and the posterior part which is very thick and massive.

Among the juvenile material there are numerous unfused mandibular bones, such as angulars, articulars, and supraangulars (fig. 8, i-k). This indicates that fusion of the mandibular bones probably occurred late during the development of the animal.

Measurements (in mm)

Adult cranium (NCP 241)

Total length from the lacrimal process to the posteriormost part of the paroccipital process: 100; maximum width at the level of the exoccipitals: 108; maximum dorsoventral height from the top of the cranial vault to the sphenoid, between the rostropterygoid processes: 56.0; minimum width of the frontals at the level of the orbits: 65.6; minimum width of the parietals and squamosals at the level of the temporal fossa: 73.4; width at the level of the craniorostral hinge: 57.0; anteroposterior length from the tubercle situated in the middle of the craniorostral hinge to the occipital condyle: 93.4; anteroposterior length from the same point to the posteriormost part of the paroccipital process: 106.6; anteroposterior length from the same point to the crista nuchalis transversa, in the sagittal plane: 67.0; anteroposterior length of the supraoccipital, from the crista nuchalis transversa to the top of the occipital foramen, in the sagittal plane: 25.0; dorsoventral height of the posterior and lateral part of the cranium, from the top of the crista occipitalis to the base of the paroccipital process: 53.0; internal width of the occipital foramen: 12.0; internal height of the occipital foramen: 16.0; width of the occipital condyle: 12.0; height of the occipital condyle: 9.0; anteroposterior length of the rostropterygoid processes: 16.2 and 16.2; width of the rostropterygoid processes: 7.5 and 7.2

Adult rostrum (NCP 242)

Maximum length from the anterior point of the beak to the articular condyle of the craniorostral hinge: 148.0; dorsoventral height of the rostrum from the top of the articular condyle of the hinge to the posterior angle: ca. 69.0; length from the point of the beak to the posterior angle: ca. 102.0; maximum width between the tips of the two articular condyles: 60.0; length of the bony ornament at its base: 52.0; width of the bony ornament at its base: 41.2; width of the premaxillaries at the level of the external tomial crests: 26.6; width of the rostrum at the level of the posterior angle: 22.2 ; at the level of the articular surfaces for the quadratojugals: 30.0; dorsoventral height from the flattened surface situated at the base of the bony ornament, to the internal tomial crest: 64.0; dorsoventral and anteroposterior diameter of the external naris: 12.5 and 12.0

Mandibles

Anterior parts: see table 1

Cranial parts of mandibles	NCP 213 adult	NCP 243 juvenile	NCP 295 juvenile	NCP 294 juvenile
Length of the almost complete mandibular symphysis	-	-	-	47.8
Length of the mandibular symphysis as preserved	57.0	64.5	54.0	-
Maximum dorsoventral heigth of the complete symphysis	-	16.2	13.6	12.0
Maximum dorsoventral heigth of the symphysis as preserved	18.0	-	-	-

Table 1. *Sylviornis* cf. *neocaledoniae*, Pindai Cave, New Caledonia. Measurements (mm) of the anterior parts of mandible.

Taula 1. Sylviornis *cf.* neocaledoniae, *Pindai Cave, New Caledonia. Mesures (en mm) de les parts anteriors de la mandíbula.*

Posterior part (specimen collected by T. H. Worthy *et al.*): dorsoventral height at the level of the articular surface for the quadrate: 23.0; height from the top of the retroarticular process to the ventralmost part of the mandible: estim. 42.5; anteroposterior length of the retroarticular process at the level of the articular surface for the quadrate: 33.6; mediolateral width of the mandible at the level of the articular surface for the quadrate: estim. 46.0 (based on the specimen collected by T. H. Worthy *et al.* and on NCP 217)

Quadrates, pterygoids, palatines, and quadratojugals
See tables 2 to 5.

JUSTIFICATION FOR THE CREATION OF A NEW FAMILY

The presence of two well-developed basipterygoid processes makes it possible to state that *Sylviornis* belongs to Galliformes or to Anseriformes (Weber, 1993; Dzerzhinsky, 1995; Ericson, 1996; Livezey, 1997), and the presence of palatines with very elongated anterior branches and posterior parts (partes laterales) that are narrow and not wing-like shows that it belongs to Galliformes.

Among the Galliformes, the postcranial skeleton shows more similarities with Megapodiidae than with other families (Poplin *et al.*, 1983; Poplin & Mourer-Chauviré, 1985), but these similarities seem to be symplesiomorphic. The cranial characteristics also present some similarities with Megapodiidae, as for example the slightly developed lacrimal, devoid of orbital process ; the position of the articular surface for the rostropterygoid process at the first third of the pterygoid and not at its anterior end; the presence of well developed alae ethmoidales. The first two characteristics are symplesiomorphies and the third one is variable within the Galliformes (Ericson, 1996).

The creation of a new family is justified by the presence of numerous autapomorphic characteristics in the skull and mandible, characteristics that are indicated in the diagnosis. To our knowledge *Sylviornis* is the only bird to show a true diarthrosis, of ginglymus type, between the skull and the beak, and to show a cranial flexure situated just posterior to the basiperygoid processes.

COMPARISON WITH OTHER EXTINCT GALLIFORM FAMILIES

Three extinct families have been described within the Galliformes, the Gallinuloididae Lucas, 1900, the Quercymegapodiidae Mourer-Chauviré, 1992, and the Paraortygidae Mourer-Chauviré, 1992. These three families display primitive characteristics compared with the recent families of Galliformes (Mourer-Chauviré, 1992; Mayr, 2000; Dyke & Gulas, 2002; Mayr & Weidig, 2004). These characteristics are mainly the presence of a hollow, cup-like, scapular facet on the coracoid, and the absence of a transverse ridge at the beginning of the incisura capitis on the humerus. These characteristics are absent in *Sylviornis* which on the contrary displays the derived character states.

DISCUSSION

It is possible to think that the the ancestor of *Sylviornis* was a galliform comparable in its osteological features to the recent megapodes, which would have reached New Caledonia at an unknown date, and would have evolved there in insular isolation, where it became flightless and acquired its highly derived cranial features. This ancestral form could have reached New Caledonia when it was still

Quadrates	Extremes	Mean	sd	n	V
Dorsoventral heigth from the tip of processus oticus to the ventralmost part of condylus medialis	34.0-38.8	36.15	1.25	35	3.45
Craniocaudal length from the cranial tip of processus orbitalis to the caudal part of processus mandibularis	46.0-51.3	47.90	1.89	9	3.95
Mediolateral width of the top of processus oticus	16.7-20.2	18.35	0.84	35	4.58
Craniocaudal length of the mandibular articular surface	28.0-35.8	30.59	1.71	33	5.59

Table 2. *Sylviornis* cf. *neocaledoniae*, Pindai Cave, New Caledonia. Measurements (mm) of the quadrates.

Taula 2. Sylviornis *cf.* neocaledoniae, *Pindai Cave, New Caledonia. Mesures (en mm) dels quadrats.*

Pterygoids	Extremes	Mean	sd	n	V
Maximum craniocaudal length	31.4-40.8	36.77	2.12	35	5.77
Maximum length of the articular facet for the processus rostropterygoideus	12.4-17.4	14.66	1.28	34	8.73
Width of this articular facet	6.6-8.6	7.66	0.49	34	6.40

Table 3. *Sylviornis* cf. *neocaledoniae*, Pindai Cave, New Caledonia. Measurements (mm) of the pterygoids.

Taula 3. Sylviornis *cf.* neocaledoniae, *Pindai Cave, New Caledonia. Mesures (en mm) dels pterigoides.*

able to fly. Alternatively it may have colonized New Caledonia during the Eocene, via the now submerged Rennell ridge (Balouet, 1984). Olson (1980) has demonstrated that megapodes are able to cross large expanses of seawater and to colonize islands. The recent discoveries of many extinct megapodes in South Pacific islands (Jones *et al.*, 1995; Steadman, 1999) clearly indicates that megapodes were much more widespread in the past, and that their recent distribution is relictual. A large, extinct, form of the genus *Megapodius*, *M. molistructor*, was also present in the Holocene of New Caledonia (Balouet & Olson, 1989).

The oldest representative of the family Megapodiidae, the genus *Ngawupodius*, has been described from the late Oligocene of South Australia (Boles & Ivison, 1999), and it is therefore possible to suppose that a comparable form may have reached New Caledonia at an indeterminate period, between the late Oligocene and the Holocene.

An instance of convergent evolution possibly occurred in the Fiji Islands where Worthy (2000) has described a giant flightless megapode, *Megavitiornis*, from Viti Levu island. In the dimensions of its postcranial skeleton the Pindai *Sylviornis* is on average 25 % larger than *Megavitiornis*, but the head of *Sylviornis* is proportionately much larger, being about twice as large as the estimated length for *Megavitiornis*. In *Megavitiornis* the rostrum is very high, and relatively narrow, but not so narrow as in *Sylviornis*. The associated cranial fragments show that in *Megavitiornis* the craniorostral hinge was unfused, but there was not a true diarthrosis, with two articular condyles and two concave articular surfaces. The nasal shows a robust maxillary process, indicating that it was not completely fused with the maxillary and the premaxillary to form a massive rostrum as in *Sylviornis*. The anterior part of the mandible of *Megavitiornis* also shows convergence with that of *Sylviornis*. It is very high dorsoventrally and very robust, and its symphysis occupies ca. 45 % of the mandibular length. But its posterior part is different. In *Megavitiornis* the processus mandibulare lateralis is a very robust, rounded prominence, and the retroarticular process is prominent, narrow and deep, whereas in *Sylviornis* the mandibular ramus is so thick at its posterior part that the processus mandibulare lateralis is not visible, and the retroarticular process is very long anteroposteriorly, wide at its base, and seems to have a rounded outline at its top. In the postcranial skeleton the main differences between *Megavitiornis* and *Sylviornis* are the shape of the tarsometatarsus, which is proportionally more robust in *Megavitiornis*, and the presence, on one of the two tarsometatarsi described, of a sulcus extensorius connected by a groove to the distal foramen (Worthy, 2000).

In conclusion, *Megavitiornis* shows some convergent evolution with *Sylviornis*, but is less advanced. It is possible to think that several different forms of megapodes, or megapode-like galliforms, colonized the South Pacific islands at different periods of time, and have given rise to somewhat convergent but unrelated forms.

Fused palatines	Extremes	Mean	sd	n	V
Craniocaudal length of the fused part from the cranial point to the pterygoid articulations measured on the dorsal face	24.7-31.8	28.81	2.12	13	7.36
Maximum craniocaudal length from the tip of the branch to the pterygoid articulation	90.5-ca. 98.0	-	-	3	-
Maximum width	17.4-21.9	19.37	1.47	10	7.59
Width of the caudal part (two articular surfaces for the pterygoids measured together)	13.1-21.3	17.00	2.49	13	14.65
Dorsoventral heigth of the articular surfaces for the pterygoids	8.6-11.6	10.25	0.80	13	7.80

Table 4. *Sylviornis* cf. *neocaledoniae*, Pindai Cave, New Caledonia. Measurements (mm) of the fused palatines.

Taula 4. Sylviornis *cf.* neocaledoniae, *Pindai Cave, New Caledonia. Mesures (en mm) dels palatins fusionats.*

Quadratojugals	Extremes	Mean	sd	n	V
Maximum craniocaudal length	84.5-99.4	91.22	3.25	21	3.56
Width of the cranial part	13.0-18.1	14.99	1.42	19	9.47
Heigth of the cranial part (dorsoventral)	5.4-8.0	6.29	0.75	19	11.92
Maximum dorsoventral heigth of the branch	9.6-12.7	11.02	0.83	21	7.53
Width of the branch at the same level	3.9-6.7	5.17	0.66	21	12.77
Maximum craniocaudal length of the articular palette for the quadrate	16.0-19.0	17.76	0.71	21	4.00

Table 5. *Sylviornis* cf. *neocaledoniae*, Pindai Cave, New Caledonia. Measurements (mm) of the quadratojugals.

Taula 5. Sylviornis *cf.* neocaledoniae, *Pindai Cave, New Caledonia. Mesures (en mm) dels quadratojugals.*

Diet of *Sylviornis*

There is some similarity between the skull of *Sylviornis* and that of the early Tertiary bird *Diatryma* which also shows a narrow, cutting beak, a mobile craniorostral articulation, and a very complex articulation between the quadratojugal and the posterior part of the rostrum (Andors, 1988). Witmer and Rose (1991) have put forward the hypothesis that *Diatryma* was a carnivorous predator but Andors (1988; 1992), using other arguments, has shown that it was vegetarian.

The Australian Dromornithidae, previously considered as ratites, have been studied again by Murray & Megirian (1998) who have shown that, according to their cranial characteristics, they must be classified within the Anseriformes. Some of these Dromornithidae have a very high, narrow beak, ending anteriorly in a hook, and a completely mobile craniorostral articulation, as in *Sylviornis* (Murray & Vickers-Rich, 2004). The mandible was very high dorsoventrally. However, according to Murray & Megirian (1998, p. 78), the rostrum was round-tipped rather than pointed, and the hooked tip differed markedly from the slender, sharply pointed hook in raptors and carrion-eating birds. Their conclusion is that the Dromornithidae were specialized herbivores, able to shear tough plant material. In *Sylviornis* the shape of the rostrum is very pointed and the hooked tip resembles that of raptors, or of birds widely recognized as carnivorous such as the Phorusrhacidae. In posterior view the shape of the cranium, in the Dromornithidae, is very different in its dorsoventral elongation from that of *Sylviornis*.

The Mauritian Dodo, *Raphus cucullatus*, also had a beak ending in a powerful hook. But this hook was mainly formed by the ramphotheca and the bony beak shows a much less pronounced point (Strickland & Melville, 1848). In the Dodo the anterior part of the rostrum is wide and becomes narrower in its middle part. In the Rodrigues Solitaire, *Pezophaps solitaria*, the rostrum is elongated and narrow (Newton & Newton, 1870), but in these two forms, unlike *Sylviornis*, the rostrum is not massive. Its dorsal part consists of a rather thin bony blade formed by the fusion of the processus frontalis of the premaxillary with the processus premaxillaris of the nasal. Ventrally there is a slot-like external naris that is very elongated anteroposteriorly. There is no articulation between the cranium and the rostrum, just a flexion zone. The ventral surface of the rostrum does not show cutting tomial crests. The mandible has narrow and elongated branches and a very short symphysis. It is clear that the diet of *Sylviornis* was different from that of the Raphidae, which were primarily vegetarian.

In the islands devoid of terrestrial mammals, the ecological niche of large herbivores is often filled by large land-tortoises. This is the case for example, in the recent giant tortoises of Aldabra and the Galapagos, and of the recently extinct tortoises of Madagascar and the Mascarenes. In all these forms the masticatory apparatus is not a single cutting blade but a wide triturating surface. The most extreme case is that of the Mascarenian tortoises, which have several ridges, each of them bearing a row of small bony tubercles (Bour, 1979-80).

In the Hawaiian Islands there were no giant land-tortoises and their ecological niche was probably occupied by the flightless ducks called moa-nalos (Olson & James, 1991). In these forms the premaxillaries and the dentaries were very short, massive, and generally presented blunt tooth-like projections.

Most of the cranial characteristics of *Sylviornis* are different from those of the typically vegetarian forms such as the weird anseriforms, the Australian Dromornithidae, the Hawaiian moa-nalos, pigeons in the Raphidae, or the Mascarenian tortoises.

Balouet (1986) proposed the hypothesis that *Sylviornis* was vegetarian and fed on roots and tubercles. This hypothesis was significantly supported by the very high numbers of *Sylviornis* in the fossil sample, which implies that it could not have been a carnivorous predator, hunting and feeding on other large vertebrates. However it is also possible to propose that *Sylviornis* fed on invertebrates. In this case, the available alimentary resources, such as marine organisms or terrestrial gastropods, for example, could have been abundant and varied enough to sustain a large population of this species. We think that the skull of *Sylviornis* has evolved as an adaptation to a particular and highly specialized diet, but it is not possible at this stage to be more precise.

Sylviornis and the oral tradition

Sylviornis was contemporaneous with the first arrival of man in New Caledonia and its disappearance is certainly due to overhunting (Balouet, 1986; 1987). The oral tradition has retained the memory of a vanished bird, called Du (Griscelli, 1976). According to tradition this bird was giant and flightless. It laid a single egg and did not incubate it. This egg took four months to hatch (from November to April). The Du moved along on the ground very rapidly, with its wings spread out. It had a red feathering and a bony ornament on the head. P. Griscelli writes: "It seems that the Du had on its head a kind of bony, solid, casque, in the shape of a star" (1976, p 5, our translation). But the word "Ghi" which designates this ornament should rather be translated as helmet. According to the inhabitants of Houaïlou the Du laid an egg on the top of a lizard sheltered in the hollow of a banyan, then went away, leaving the lizard to incubate it for four months and to break the shell with its jaw. Lastly P. Griscelli states that "tradition attributes great aggressiveness to this bird, in connection with totemic rites and cannibalism" (1976, p. 5, our translation).

Acknowledgements

The authors want to express their thanks to the Paris National Museum of Natural History, L. Ginsburg, P. Janvier, F. Poplin, S. Tillier, and A. Tillier; to the National Museum of Natural History, Smithsonian Institution, Washington, S. Olson, H. James, A. Ross, J. Dean and B. Schmidt; to the Office de la Recherche Scientifique et Technique d'Outre Mer, D. Frimigacci and B. Vienne; to the Service des Eaux et Forêts, Nouméa, F. Boulet and Y. Letocart; to the Musée Néocalédonien, P. Gaudin and E. Kasarherou; to the tribes of Isle of Pines and Nepoui, and their authorities, as well as to F. Hannecart, and to P. Millener from New Zealand. We thank an anonymous reviewer for his improvements and useful comments, and T. Worthy for sharing his information with us. Photographs are by N. Podevigne (Université Claude Bernard - Lyon 1).

References

Andors, A.V. 1988. *Giant groundbirds of North America (Aves, Diatrymidae)*. Ph. D. dissertation, Columbia University, New York, xvi + 577 pp. (unpublished).

Andors, A.V. 1992. Reappraisal of the eocene groundbird *Diatryma* (Aves: Anseromorphae). *Natural History Museum of Los Angeles County, Science Series*, 36: 109-125.

Balouet, J.C. 1984. *Paléontologie des Vertébrés de Nouvelle Calédonie et Paléobiogéographie du Pacifique Sud Ouest*. Thèse de 3ème cycle, Université Pierre et Marie Curie - Paris 6, n° 84-39, 84 pp. (unpublished).

Balouet, J.C. 1986. Une actualité millénaire. Premiers colons de Nouvelle-Calédonie. *L'Univers du Vivant*, Paris, 7: 35-47.

Balouet, J.C. 1987. Extinctions des vertébrés terrestres de Nouvelle Calédonie, *in* Les Extinctions dans l'histoire des Vertébrés. *Mémoires de la Société géologique de France*, 150: 177-183.

Balouet, J.C. 1991. The fossil vertebrate record of New Caledonia. *In* Vickers-Rich, P.; Monaghan, J.M.; Baird, R.F. & Rich, T.H. (eds.), *Vertebrate Palaeontology of Australasia*: 1383-1409. Pioneer Design Studio and Monash University Publications Committee, Melbourne.

Balouet, J.C. & Buffetaut, E. 1987. *Mekosuchus inexpectatus*, n. g., n. sp., Crocodilien nouveau de l'Holocène de Nouvelle Calédonie. *Comptes Rendus de l'Académie des Sciences de Paris*, t. 304, Sér. II, 14: 853-856.

Balouet, J. C. & Olson, S.L. 1989. Fossil Birds from Late Quaternary deposits in New Caledonia. *Smithsonian Contributions to Zoology*, 469: iv + 38 pp.

Bock, W.J., 1964. Kinetics of the Avian Skull. *Journal of Morphology*, 114: 1-42.

Boles, W.E. & Ivison, T.J. 1999. A New Genus of Dwarf Megapode (Galliformes: Megapodiidae) from the Late Oligocene of Central Australia. *In* Olson, S.L. (ed.), *Avian Paleontology at the close of the 20th Century: Proceedings of the 4th International Meeting of the Society for Avian Paleontolgy and Evolution, Washington, D.C., 4-7 June 1996. Smithsonian Contributions to Paleobiology*, 89: 199-206.

Bour, R. 1979-80. Histoire de la tortue terrestre de Bourbon. *Bulletin de l'Académie de l'Ile de la Réunion*, 25: 97-147.

Dyke, G.J. & Gulas, B.E.. 2002. The Fossil Galliform Bird *Paraortygoides* from the Lower Eocene of the United Kingdom. *American Museum Novitates*, 3360: 14 pp.

Dzerzhinsky, F.Y. 1995. Evidence for common ancestry of the Galliformes and Anseriformes. *Courier Forschungsinstitut Senckenberg*, 181: 325-336.

Ericson, P.G.P. 1996. The skeletal evidence for a sister-group relationship of anseriform and galliform birds - a critical evaluation. *Journal of Avian Biology*, 27: 195-202.

Gaffney, E.S.; Balouet, J.C. & Broin, F. de. 1984. New occurrences of Extinct Meiolaniid Turtles in New Caledonia. *American Museum Novitates*, 2800: 6 pp.

Griscelli, P. 1976. Deux oiseaux fossiles de Nouvelle-Calédonie. *Bulletin de la Société d'Etudes historiques de la Nouvelle Calédonie*, 29: 3-6.

Jollie, M.T. 1957. The head skeleton of the chicken and remarks on the anatomy of this region in other birds. *Journal of Morphology*, 100 (3): 389-436.

Jones, D.N.; Dekker, R.W.J & Roselaar, C.S. 1995. *Bird Families of the World. The Megapodes (Megapodiidae)*. Oxford University Press, Oxford. New York and Tokyo. 262 pp.

Livezey, B.C. 1997. A phylogenetic analysis of basal Anseriformes, the fossil *Presbyornis*, and the interordinal relationships of waterfowl. *Zoological Journal of the Linnean Society*, 121: 361-428.

Mayr, G. 2000. A new basal galliform bird from the Middle Eocene of Messel (Hessen, Germany). *Senckenbergiana Lethaea*, 80 (1): 45-57.

Mayr, G. & Weidig, I. 2004. The Early Eocene bird *Gallinuloides wyomingensis* - a stem group representative of Galliformes. *Acta Palaeontologica Polonica*, 49(2): 211-217.

Mourer-Chauviré, C. 1992. The Galliformes (Aves) from the Phosphorites du Quercy (France): Systematics and Biostratigraphy. *Natural History Museum of Los Angeles County, Science Series*, 36: 67-95.

Murray, P.F. & Megirian, D. 1998. The skull of Dromornithid birds: Anatomical evidence for their relationship to Anseriformes. *Records of the South Australian Museum*, 31: 51-97.

Murray, P.F. & Vickers-Rich, P. (2004). *Magnificent Mihirungs. The Colossal Flightless Birds of the Australian Dreamtime*. Indiana University Press. Bloomington. 416 pp.

Newton, A. & Newton, E. 1870. On the osteology of the Solitaire or Didine Bird of the Island of Rodriguez, *Pezophaps solitaria* (Gmel.). *Philosophical Transactions of the Royal Society, London*, 159: 327-362.

Olson, S.L. 1980. The significance of the distribution of the Megapodiidae. *Emu*, 80: 21-24.

Olson, S.L. 1999. The Anseriform Relationships of *Anatalavis* Olson and Parris (Anseranatidae), with a new species from the Lower Eocene London Clay. *In* Olson, S.L. (ed.), *Avian Paleontology at the close of the 20th Century: Proceedings of the 4th International Meeting of the Society for Avian Paleontolgy and Evolution, Washington, D.C., 4-7 June 1996. Smithsonian Contributions to Paleobiology*, 89: 231-243.

Olson, S.L. & James, H.F. 1991. Description of Thirty-two New Species of Birds from the Hawaiian Islands: Part I. Non-Passeriformes. *Ornithological Monographs*, 45: 1-88.

Poplin, F. 1980. *Sylviornis neocaledoniae*, n. g., n. sp. (Aves), Ratite éteint de la Nouvelle Calédonie. *Comptes Rendus de l'Académie des Sciences de Paris*, t. 290, Sér. D: 691-694.

Poplin, F. & Mourer-Chauviré, C. 1985. *Sylviornis neocaledoniae* (Aves, Galliformes, Megapodiidae), oiseau éteint de l'Ile des Pins (Nouvelle Calédonie). *Geobios*, 18 (1): 73-97.

Poplin, F.; Mourer-Chauviré, C. & Evin, J. 1983. Position systématique et datation de *Sylviornis neocaledoniae*, Mégapode géant (*Aves, Galliformes, Megapodiidae*) éteint de la Nouvelle Calédonie. *Comptes Rendus de l'Académie des Sciences de Paris*, t. 297, Sér. II: 301-304.

Steadman, D.W. 1999. The biogeography and extinction of megapodes in Oceania. *In* Dekker *et al.*, Proceedings of the Third International Megapode Symposium. *Zoologische Verhandelingen*, 327: 7-21.

Strickland, H.E. & Melville, A.G. 1848. *The Dodo and its Kindred, or the history, affinities and osteology of the Dodo, Solitaire, and other extinct birds of the islands Mauritius, Rodriguez, and Bourbon*. Reeve, Benham, and Reeve. London. 141 pp.

Weber, E. 1993. Zur Evolution basicranialer Gelenke bei Vögeln, insbesondere bei Hühner- und Entenvögeln (Galloanseres). *Zeitschrift für zoologische Systematik und Evolutionsforschung*, 31: 300-317.

Weber, E. 1996. Das Skelet-Muskel-System des Kieferapparatus von *Aepypodius arfakianus* (Salvadori, 1877) (Aves, Megapodiidae). *Courier Forschungsinstitut Senckenberg*, 189: 132 pp.

Witmer, L.M. & Rose, K.D. 1991. Biomechanics and the jaw apparatus of the gigantic Eocene bird *Diatryma*: implications for diet and mode of life. *Paleobiology*, 17(2): 95-120.

Worthy, T.H. 2000. The fossil megapodes (Aves: Megapodiidae) of Fiji with description of a new genus and two new species. *Journal of The Royal Society of New Zealand*, 30 (4): 337-364.

Zusi, R.L. & Livezey, B.C. 2000. Homology and phylogenetic implications of some enigmatic cranial features in Galliform and Anseriform birds. *Annals of Carnegie Museum*, 69 (3): 157-193.