PIPID FROGS FROM THE UPPER CRETACEOUS OF IN BECETEN, NIGER

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ABSTRACT. A vertebrate assemblage from the Coniacian–Santonian Ibeceten Formation of southern Niger includes pipid frogs, which are described herein. The fossils occur within fluviatile-lacustrine strata and consist of disarticulated elements. Two pipid taxa are present: the hyperossified *Pachybatrachus taqueti* gen. et sp. nov., and another unidentified taxon. The phylogenetic relationships of both are discussed in the context of recent hypotheses of pipid evolution. *Pachybatrachus* exhibits some derived features unknown in other pipids. These include supplementary accretion of bone on the atlantal centrum, which is involved in an additional articulation with the skull, as well as on the ventral surface of other vertebral centra. Following cladistic analysis, it is proposed that *Pachybatrachus* is a pipine closely related to the living African forms *Hymenochirus* and *Pseudhymenochirus*. The presence of the primitive state for some hymenochirine synapomorphies suggests that *Pachybatrachus* is their sister taxon. The relationships of the unidentified taxon remain equivocal owing to the fragmentary condition of available remains.

THE aquatic freshwater pipids have one of the most extensive fossil record of all frogs, with the oldest remains attributed to this group being early Cretaceous (Nevo 1968; Estes *et al.* 1978). Apart from their putative occurrence in the Lower Cretaceous of Israel, all known fossil pipids are from Africa and South America (Báez 1996). To date, the earliest known pipids from South America are from the middle Cretaceous of Patagonia (Báez and Calvo 1990), whereas recent finds in Africa extend their record back to the Albian–Cenomanian in this continent (Evans *et al.* 1996). Living representatives of this family are restricted to the latter two continents: they inhabit sub-Saharan Africa and tropical South America east of the Andes, extending as far north as Panama. However, the fossil record shows that pipids had a wider geographical range on those continents in the past, reaching further north and south than they do today (Báez 1981, 1996, and references cited therein). It should be noted here that the name Pipidae is used in the traditional broad sense, i.e. applied to those pipoid taxa that are closer to the living *Xenopus*, *Silurana*, *Pipa*, *Hymenochirus* and *Pseudhymenochirus* than to Rhinophrynidae and the extinct Palaeobatrachidae. Pipidae was defined by Ford and Cannatella (1993) as the node-based name for the most recent common ancestor of living pipids and all of its descendants. However, the uncertain position of several fossil taxa still needs to be clarified; hence we use Pipidae in the traditional sense.

The material described here is from the Upper Cretaceous (Coniacian–Santonian) of In Beceten, Niger. This site (about 15° 3′ N, 6° 2′ E) is located in the Iullemmeden Basin (or Iullmeden Basin; Hartley and Allen 1994), a vast interior tectonic depression that extends south-west of the Air Massif (Text-fig. 1). The fossils occur in the Ibeceten Formation, a sequence of shales and sandstones deposited in a fluvial-lacustrine environment (Moody and Sutcliffe 1991). This formation overlies marine limestones, containing ammonites, including vascoceratids of the genus *Nigericeras* Schneegans and is thus early Turonian. A succession of siltstones and shales overlies the sequence that includes the In Beceten frog-bearing beds. These overlying strata have been dated as Campanian–Maastrichtian on the basis of the presence of the ammonite genus *Lybicoceras* and by correlation with the *Mosasaurus* shales of Nigeria. All these data suggest an early 'Senonian' (Broin *et al.* 1974; Taquet 1976), or, more precisely, a late Coniacian–Santonian (Mateer *et al.* 1992), age for the frog-bearing beds.

The fossil material was collected during several field trips led by Drs D. E. Russell and P. Taquet.

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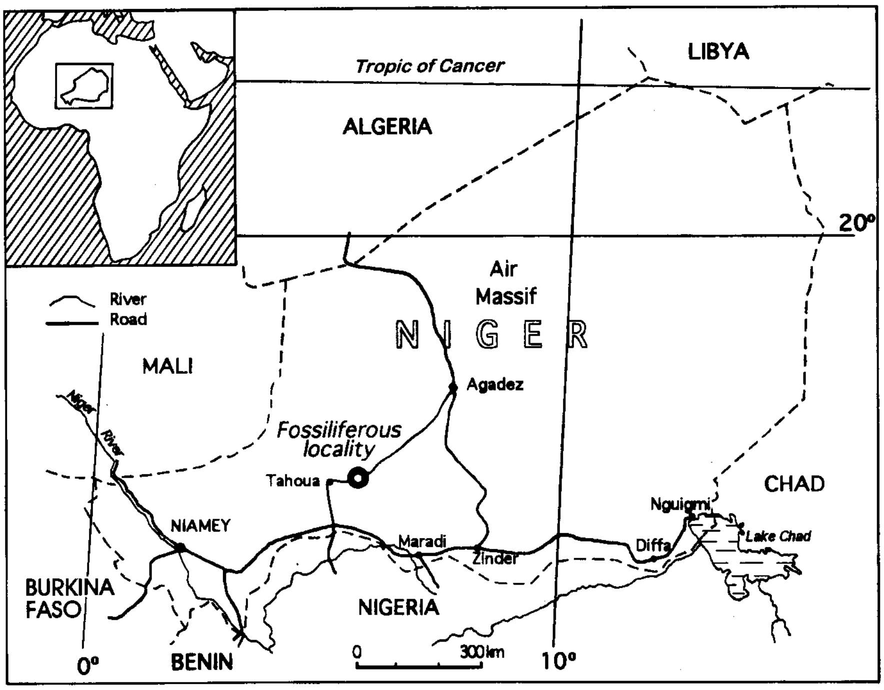


TEXT-FIG. 1. Map of Niger showing the location of the fossil site.

Most fossils lie exposed on the ground surface, the matrix having been removed during the rainy seasons. This may explain traces of erosion visible on several bones, although post-mortem transportation might also have caused some of this erosion. A large number of the specimens collected came from screen-washing operations.

The In Beceten fauna includes dipnoan and actinopterygian fishes, anuran and caudate amphibians, lizards, snakes, turtles, crocodilians, and sauropod and theropod dinosaurs (de Broin *et al.* 1974; Buffetaut 1976; Rage 1984; Rage *et al.* 1993). The material is housed in the Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris (MNHN), France.

In an earlier and preliminary paper on the In Beceten fauna (Broin *et al.* 1974), Vergnaud-Grazzini mentioned the presence of pipid and ranid frogs. Subsequently, assignment of some of the remains to Ranidae was questioned by Rage (1984). In this contribution we present the results of the study of the material representing a species 'très proche des *Xenopus*', and a new form, of which some skeletal elements 'évoqueraient *Hymenochirus* ou *Pipa*', according to Vergnaud-Grazzini (Broin *et al.* 1974, p. 470). The non-pipid remains are not discussed herein.

Recently, Cannatella and Trueb (1988*a*, 1988*b*) presented a hypothesis of relationships based on shared derived character states for extant pipid genera including *Xenopus*, *Silurana*, *Hymenochirus* and *Pseudhymenochirus* from Africa, and *Pipa* from South America. These authors proposed *Xenopus* as the sister taxon to all other extant pipids, and *Silurana* (a generic name resurrected for *X. tropicalis* and *X. epitropicalis* by Cannatella and Trueb 1988*a*) as the sister taxon of the pipines, that is [*Pipa*+[*Hymenochirus*+*Pseudhymenochirus*]]. This placement of *Silurana*, however, was discussed in a subsequent paper by Cannatella and de Sá (1993). Data from DNA sequences and reappraisal of morphology suggest, instead, that *Silurana* and *Xenopus* are sister groups (de Sá and Hillis 1990), which comprise the clade Xenopodinae (Cannatella and de Sá 1993). The evolutionary relationships of the taxa represented by the remains from In Beceten are discussed in the context of such hypotheses, although the non-congruence of character states in several fossil taxa suggests that a reanalysis including extant and extinct pipids is necessary (see Báez 1996).

Institutional abbreviations. CPBA-V, Paleontología Vertebrados, Facultad de Ciencias Exactas, Universidad de Buenos Aires; DGM: Divisão de Geologia e Mineralogia, Departamento Nacional da Producão Mineral, Rio de Janeiro; KU, Natural History Museum, The University of Kansas; MCZ, Museum of Comparative Zoology, Harvard University; MNHN, Muséum National d'Histoire Naturelle, Paris; UMMZ, Museum of Zoology, University of Michigan.

SYSTEMATIC PALAEONTOLOGY

Class AMPHIBIA Linnaeus, 1758
Order ANURA Rafinesque, 1815
Family PIPIDAE Gray, 1825

Genus PACHYBATRACHUS gen. nov.

Derivation of name. From the Greek *pachus*, meaning thick, and *batrachos*, meaning frog.

Type and only known species. Pachybatrachus taqueti sp. nov.

Diagnosis. As for the only known species.

Pachybatrachus taqueti sp. nov.

Plate 1, figures 1–6; Text-figures 2A–K, 3A–G

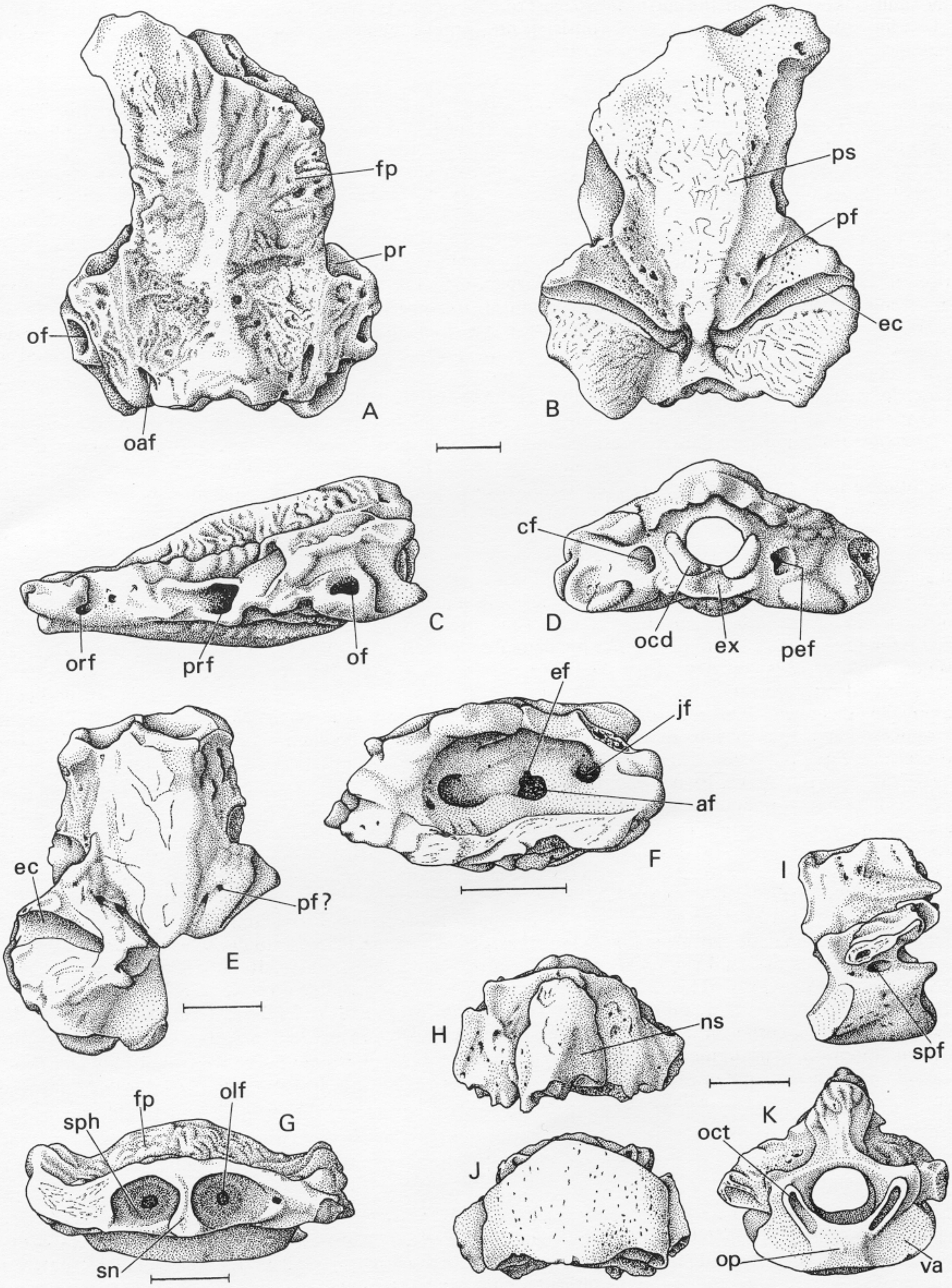
Derivation of specific name. After Dr Philippe Taquet, palaeontologist of the Muséum National d'Histoire Naturelle, Paris, France, who conducted several expeditions to In Beceten.

Holotype. MNHN-IBC 1404 (braincase and otic capsules); Ibeceten Formation (Coniacian–Santonian) (Moody and Sutcliffe 1991); In Beceten (or Ibeceten), approximately 90 km east-north-east of Tahoua, Republic of Niger (Text-fig. 1).

Referred material. MNHN-IBC 1605 (braincase and otic capsules); 1606 (right otoccipital); 1607 (incomplete right otoccipital); 1608 (left otoccipital); 1609 (braincase and otic capsules); 1610 (anterior portion of braincase); 1611–1612 (atlantal complexes); 1613–1615 (presacral vertebrae, III); 1614 (presacral vertebra, V?); 1616–1618 (presacral vertebrae); 1619–1623 (sacrococcyx).

Diagnosis. Hyperossified pipine (*sensu* Cannatella and Trueb 1988*a*); frontoparietal heavily exostosed with vermicular ornamentation; deep and narrow Eustachian canals cross otic capsules obliquely; sphenethmoid fused to frontoparietal and parasphenoid; nerve foramina between fused vertebra I and II small, but not minute; bony accretion on atlantal centrum forming an odontoid process that articulates with an excavation on ventral surface of the braincase, articular surface of prezygapophyses of presacral vertebrae simple; articular surface of postzygapophyses curved ventromedially to form a groove; accretions of bone present on ventral surface of presacral vertebral centra and sacrococcyx.

Description. The skull as well as the postcranial skeletal elements are hyperossified. The dorsal surface of the cranium bears a peculiar, and presumably dermal, vermicular sculpturing that is coarse and compact. Maxillae, premaxillae, nasals, squamosals and mandibles are not preserved. Despite the absence of the anterior parts of



TEXT-FIG. 2. For caption see opposite.

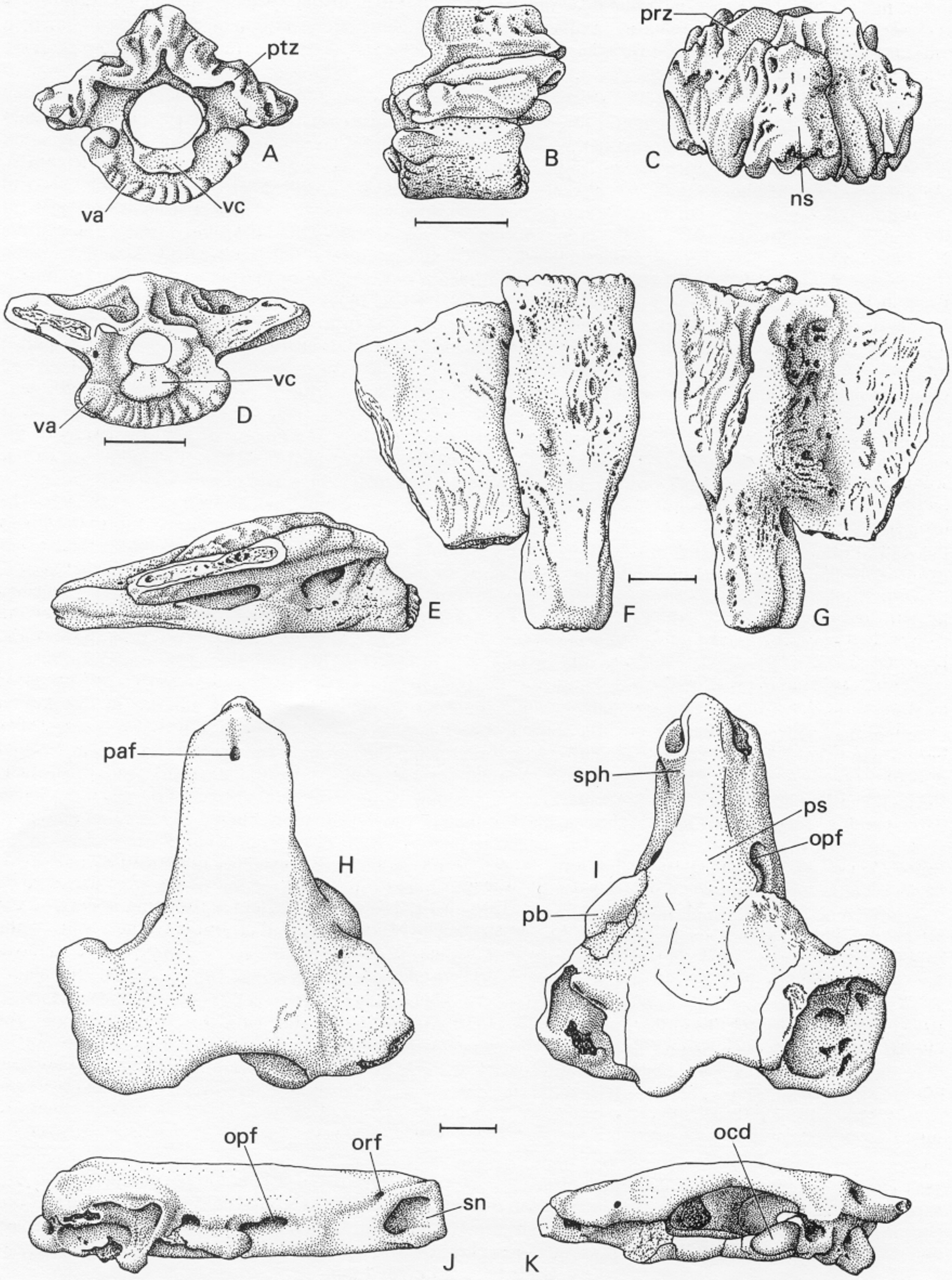
the skull, it is evident from the parts that do exist that the cranium was distinctly wedge-shaped in lateral profile (Text-fig. 2C). The postcranial remains consist of presacral vertebrae, along with the sacrococcyx, all of which bear accretions of bone on their ventral surfaces.

Cranial skeleton. The frontoparietal is azygous, extraordinarily robust and heavily exostosed, and lacks any indication of a medial suture or parietal foramen (Text-fig. 2A). Anteriorly, this element is fused completely with the sphenethmoid. Owing to this fact and the breakage in most specimens, it is difficult to reconstruct precisely the shape of the anterior margin of the frontoparietal. However, in one specimen (MNHN-IBC 1610), the configuration of the anterior border seems to be biconcave, consisting of an anteromedial, rostral projection and, on each side, an anterolateral process associated with the well-ossified post-nasal wall (planum antorbitale *sensu* Paterson 1945). In the largest specimens (e.g. MNHN-IBC 1604), the dorsal surface of the frontoparietal is not flat: there is a dorsolaterally oriented supraorbital flange on each side and a medial frontoparietal dome that extends from the midorbital region to the posterior margin of the bone. In another much smaller, but nonetheless well-ossified specimen (MNHN-IBC 1609), the frontoparietal is flat. The ventral margin of the lamina perpendicularis cannot be discerned owing to fusion between the frontoparietal and the side wall of the neurocranium. Although the dermal ornamentation of the frontoparietal is united synostotically to that of the prootics and exoccipitals, it is possible to discern the rounded posterolateral and posterior margin of the frontoparietal by the orientation of the sculpturing.

The prootics and the exoccipital are indistinguishably fused to form a single bone – the otoccipital of some authors. Furthermore, the paired exoccipitals are fused dorsomedially and dorsoventrally; the nature of the medial association of the prootics is unknown. The roof of the otic capsule bears the same kind of vermicular sculpturing as the frontoparietal; presumably, this exostosis is dermal in origin despite the endochondral origin of the bone beneath. By contrast, the dorsal surface of the pars cranialis of the prootic is smooth. The posterolateral margin of the frontoparietal is united to the dermal sculpturing of the otic capsule, and forms the roof of a bony canal that probably housed the occipital artery. Anteriorly, this canal ends at the level of the anterior limit of the dermal sculpturing on the otic capsule. Near the anteromedial margin of the prootic, where it articulates with the frontoparietal, there is a foramen from which the ramus ophthalmicus superficialis of the facial nerve probably exited the cranium. The small prootic foramen lies between the side wall of the neurocranium, medially, and the anterior portion of the prootic, laterally. Owing to this position, the foramen is not visible in the lateral view of the skull (Text-fig. 2C). In MNHN-IBC 1605, there is a second foramen of uncertain identity lateral to the prootic foramen. On the lateral wall of the neurocranium, in all specimens examined, there is at least one foramen, possibly the optic foramen, immediately anterior to the prootic foramen. The ventral surface of the otic capsule bears a deep excavation for the Eustachian tube. The Eustachian canal is narrow, deep and almost straight, crossing the capsule in an anterolateral-posteromedial direction (Text-fig. 2B, D). By contrast to the irregular surface of most of the otic capsule, the walls of the Eustachian canal are smooth. A distinct mark, running along the posterolateral margin of the canal, probably corresponds to the posterior limit of the otic plate of the pterygoid. A shallow, curved channel that may have accommodated the carotid artery lies at the medial terminus of each Eustachian canal. Posterolateral to the Eustachian canal, the otic capsule is flat in the larger specimens, but inflated slightly in the smaller one (Text-fig. 2E). Ventrolateral to the condyloid fossa there is a distinct posterior projection of the otic capsule.

A large fenestra ovalis and an anterodorsal opening for the ramus hyomandibularis of cranial nerve VII are evident when the otic capsule is seen in lateral aspect. The ramus hyomandibularis passes from the prootic ganglion and exits the skull via a wide passage that represents the cranioquadrate passage (Paterson 1945). Because of breakage in NMHN-IBC 1606, it is possible to observe a large acoustic foramen and, above it, a small endolymphatic opening on the medial wall of the otic capsule (Text-fig. 2F). In one specimen (MNHN-IBC 1609), two acoustic foramina are present, separated from one another by a thin bridge of bone. The jugular foramen lies posterior to the acoustic foramen. Posterior to the former lie one or two perilymphatic foramina, but these do not open into the cranial cavity. It seems likely that two foramina were actually present, but in some specimens (e.g. MNHN-IBC 1605), the delicate bony partition separating the foramina has been destroyed.

TEXT-FIG. 2. *Pachybatrachus taqueti* gen. et sp. nov. A–D, MNHN-IBC 1604, holotype; braincase and otic capsules in A, dorsal; B, ventral; C, left lateral; and D, posterior views. E, MNHN-IBC 1609; braincase and otic capsules, ventral view. F, MNHN-IBC 1606; right otic capsule, medial view. G, MNHN-IBC 1610; braincase, anterior view. H–K, MNHN-IBC 1611; atlantal complex in H, dorsal; I, left lateral; J, ventral; and K, anterior views. Scale bars represent 2 mm.



TEXT-FIG. 3. For caption see opposite.

The margin of the foramen magnum is completely ossified. Slightly anterior to the foramen magnum, the ventral surface of the fused prootics and exoccipitals is excavated to accommodate the hypertrophied 'odontoid' process of the atlas (Text-fig. 2D). The occipital condyles are reniform and posteromedially oriented; the articular facets are well separated. Large condyloid fossae housing the perilymphatic and jugular foramina flank the condyles, bounded medially and posteriorly by heavy deposits of bone adjacent to the condyles themselves. A sheet of bone bridging the medial end of the right Eustachian canal, which might correspond to a poorly preserved pterygoid, is evident in only one specimen (MNHN-IBC 1609). Examination of this specimen suggests that each pterygoid formed an extensive otic plate that invested the otic capsule ventrally. The exoccipitals lack ventral ridges associated with the posteromedial margins of the Eustachian canals; thus, it seems unlikely that the pterygoids were expanded medially to form a single, medial opening for the canals. Therefore, it is assumed that paired, bony openings were present. The boundaries of the pterygoid otic plates may be inferred from the relief on the ventral surface of the otic capsules. Thus, they could have extended from the posterolateral margin of the parasphenoid, anteriorly, to a point just to the rear of the Eustachian canal, posteriorly. No significant synostotic fusion of the pterygoid to the otic capsule is evident.

The sphenethmoid is united synostotically to adjacent elements. Thus, it is fused to the overlying frontoparietal and to the parasphenoid ventrally. Anterolaterally, the sphenethmoid is united synostotically to the planum antorbitale; thus, the orbitonasal foramen is enclosed in bone. Sphenethmoidal ossification also forms the boundaries of the large foramina for the olfactory nerves. Lateral to each olfactory foramen, there is a small foramen (MNHN-IBC 1609–1610) which may have housed the medial branch of the ramus ophthalmicus profundus of the trigeminal nerve. Although the most frontal portion of the sphenethmoid (i.e. the anterior part of the septum nasi) is not preserved, the anterior neurocranium can be observed. In transverse section, the latter is thick-walled and composed of two adjacent compartments probably corresponding to the paired olfactory canals. Each compartment extends posteriorly from the region of the anterior margin of the orbit to a point level with the anterior margin of the frontoparietal dome, which is located approximately in the midorbital region. The wide, bony medial septum that separates the compartments becomes narrower toward the anterior end and projects beyond the level of the planum antorbitale, but it is not possible to assess its total length owing to breakage. In a small specimen (MNHN-IBC 1609), the bony septum terminates posteriorly at the level of the orbitonasal foramina, and does not reach the orbital region. Two small foramina (probably for the optic and trochlear nerves), completely enclosed in bone, are located in the side walls of the braincase in the posterior region of the orbit.

The parasphenoid is wide and fused completely to the neurocranial bones; thus, its anterior and posterior ends are difficult to determine. However, it does not seem to extend much beyond the level of the planum antorbitale, nor does it extend in an anterolateral direction ventral to the planum antorbitale. The posterior terminus of the parasphenoid lies between the otic capsules and seemingly lacks a well-developed posteromedial process. The ventral surface of the parasphenoid is slightly convex. Two foramina are present on each side, near the union of the parasphenoid with the otic capsules. The anterior, and more lateral, opening may represent the palatine foramen, whereas the posterior one probably corresponds to a foramen for the carotid artery.

Postcranial skeleton. The postcranium is represented by several incomplete vertebrae and portions of the fused sacrum and coccyx. The vertebral centra are opisthocoelous. The atlas and the second vertebra are fused to form an atlantal complex (MNHN-IBC 1611–1612) and the bilateral spinal nerve foramina between these vertebrae although small, are not minute. In one specimen (MNHN-IBC 1612), traces of the fusion of the neural arches of the first two vertebrae are evident, whereas the fusion of the centra is complete. The anterior margin of the lamina of the atlas (*sensu* Cannatella and Trueb 1988*a*) is slightly convex (Text-fig. 2H); hence, the spinal cord was not exposed dorsally between this vertebra and the occiput. The atlantal complex (vertebrae I+II) bears a thick and rather high neural spine (Text-fig. 2I). On each side, slightly below the level of the postzygapophyses, a thick horizontal lamina runs from the posterior border of the second vertebral neural arch to an area located between the spinal nerve foramen and the corresponding articular cotyle. These laminae do not project strongly laterally, but, as they are partly broken off, their true lateral extension remains unknown. On the anterior face, the articular cotyles appear as narrow furrows on MNHN-IBC 1611, whereas they are slightly wider on 1612. The centrum of the atlantal complex is thickened by accretion of bone on the ventral

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TEXT-FIG. 3. A–G, *Pachybatrachus taqueti* gen. et sp. nov. A–C, MNHN-IBC 1614; presacral vertebra (5° ?) in A, posterior; B, left lateral; and C, dorsal views. D, MNHN-IBC 1619; sacrococcyx, anterior view. E–G, MNHN-IBC 1620; sacrococcyx in E, right lateral; F, ventral; and G, dorsal views. H–K, pipid, unidentified genus and species, MNHN-IBC 1602; braincase and otic capsules in H, dorsal; I, ventral; J, right lateral; and K, posterior views. Scale bars represent 2 mm.

surface (see below). This accretion extends anteriorly where it forms a short sagittal projection that mimics an 'odontoid' process. On either side of this process, the bone growth forms a surface that resembles the articular cotyles of the atlas of most anurans. The latter surfaces could be considered as the articular cotyles; however, from their shape and orientation the rather narrow furrows cited above appear to be the true cotyles. The additional surfaces apparently articulated with the swellings that are located ventral to the occipital condyles of the skull.

The vertebrae are imbricate with thick neural arches, each of which bears a well-developed spinous process that terminates posteriorly in short parasagittal processes. Anterior to the neural spine, between the prezygapophyses, the neural arch is elevated and bears a delicate medial ridge that articulates with a groove located on the ventral surface of the spinous process of the neural arch of the preceding vertebra. There is some variation in the anterior–posterior length of the neural arches of the vertebrae, possibly reflecting regional variation in the vertebral lengths, with the more anterior vertebrae having relatively shorter neural arches. The articular surface of each prezygapophysis is simple, whereas the articular surface of each postzygapophysis is curved ventromedially to form a distinct tongue-and-groove articulation with the prezygapophysis of the preceding vertebra; this is especially evident in specimens MNHN-IBC 1614 and 1616 (Text-fig. 3A). Transverse processes are not preserved on any of the available vertebrae, but, as in the atlantal complex, a horizontal expansion of variable thickness runs along each side of the vertebrae. This expansion may be either a modified transverse process or the base of a broken transverse process.

All vertebrae referred to this species, including the atlantal complex, are characterized by a thick accretion of bone on the ventral surface of each centrum. The anterior and posterior margins of this bony accumulation bear several furrows and ridges that may have articulated with similar structures on adjacent vertebrae. The articular condyle, anteriorly, and the articular cotyle, posteriorly, occupy only a reduced part of the anterior and posterior faces of the centrum.

The sacrum is fused to the coccyx (Text-fig. 3E–G). Dorsally, the sacral portion of the bone bears a thick spinous process, only the anterior part of which is distinguishable; posteriorly, the process widens markedly then vanishes, merging with the dorsal surface of the sacral diapophyses. As in the presacral vertebrae, a thin medial ridge anterior to the neural spine is present on the neural arch of the sacrum, but in general it is more reduced than in the other vertebrae. The sacral diapophyses are broadly expanded. Two large spinal nerve foramina and, occasionally, a third small foramen, are present on each side of the sacrococcyx, indicating that more than one vertebra participates in the formation of the sacral portion of the sacrococcyx. There is a ventral accretion of bone on the sacrococcyx similar to that on the presacral vertebrae (Text-fig. 3D). Posterior to the level at which the posterior margin of the sacral diapophyses unites with the coccygeal part (= urostyle), the bony deposition decreases in width and is fused indistinguishably to the wide, well-ossified hypochord. Dorsally, the coccygeal part of the sacrococcyx lacks a distinct ridge.

Remarks. In this hyperossified species, the fused prootics and exoccipitals bear a groove to accommodate the Eustachian tube, the optic foramina are enclosed in bone, the sacrum is fused with the coccyx, the vertebral centra are opisthocoelous and dorsoventrally flattened, and thus presumably epichordal, and it seems likely that the otic plate, formed by the medial and posterior branches of the pterygoid, at least partially floored the Eustachian canal. These character states are some of the diagnostic characters of extant pipids (Cannatella and Trueb 1988*a*), although consideration of some fossil pipoid taxa, such as palaeobatrachids, indicates that some of these synapomorphies diagnose more inclusive groups of pipoids (Cannatella and de Sá 1993; Báez 1996).

The monophyly of Pipinae [*Pipa* + [*Hymenochirus* + *Pseudhymenochirus*]] was supported by 18 osteological derived character states in the analysis performed by Cannatella and Trueb (1988*a*), but only a few of those characters could be assessed in *Pachybatrachus* because of the lack of preservation of appropriate structures. *Pachybatrachus* shares with pipines the wedge-shape of the skull in lateral profile, a posteriorly acuminate parasphenoid, and presacral vertebrae bearing parasagittal spinous processes. 'Anterior margin of the atlas not indented and concealing the spinal cord' was listed as a synapomorphy of Pipinae by Cannatella and Trueb (1988*b*), but this condition occurs in some fossil pipid taxa lacking several derived character states shared by pipines and thus either diagnoses a more inclusive group or is homoplastic. The presence of a crest on the dorsal surface of the otic capsule for the insertion of the external portion of the depressor mandibulae muscle, another pipine synapomorphy (Cannatella and Trueb 1988*a*, 1988*b*), might not be evident in *Pachybatrachus* owing to intense accumulation of dermal bone in this region. In *Pachybatrachus*, the dermal sculpturing extends anteriorly up to the level of the passage for the ramus hyomandibularis of the facial nerve, whereas the anterior portion of the prootic lacks this secondary deposition of bone, thus forming a 'ridge' that might have provided an attachment site for that muscle. There is some variation, however, in the development of that crest among pipines: for example, it is not well developed in *Pseudhymenochirus* (Cannatella and Trueb 1988*b*). As in pipines, the spinal nerve foramina between the atlas and the second vertebra are small in *Pachybatrachus*, but they are not minute; thus, in this feature, *Pachybatrachus* appears less derived than extant pipines. In addition, the frontoparietal bears supraorbital flanges and the neural arches are completely imbricated, as in pipines, but not as in *Xenopus* and *Silurana*.

A few, presumably derived, character states are shared by *Pachybatrachus*, pipines and *Silurana*. These characters are: the presence of anterolateral alae on the frontoparietal; fusion of the first and second vertebrae; and, apparently, absence of discrete vomers. However, the hypothesis that *Silurana* is the sister taxon of *Xenopus*, as discussed by Cannatalla and de Sá (1993), implies that these characters might be homoplastic in *Silurana* and the pipines.

The evidence discussed above indicates that *Pachybatrachus* is either a stem pipine (i.e. a sister group of the clade that includes the most recent common ancestor of *Pipa*, *Pseudhymenochirus* and *Hymenochirus* and all of its descendants), or should be placed within the node-based Pipinae (*sensu* Cannatella and de Sá 1993). In general, this is in agreement with the opinion of Vergnaud-Grazzini (*in* Broin *et al.* 1974), who cited the presence of a new species resembling *Hymenochirus* or *Pipa* in the Cretaceous of In Beceten.

Within Pipinae, the species of *Pipa* form a well-corroborated clade (Trueb and Cannatella 1986), whereas the Hymenochirini, including *Pseudhymenochirus* and *Hymenochirus*, constitute another monophyletic subgroup (Cannatella and Trueb 1988*b*; Cannatella and de Sá 1993). The remarkable degree of ossification and coalescence of dermal and endochondral elements in the species from Niger, as well as its incomplete preservation, limit comparison and assessment of the osteological synapomorphies diagnostic of these two groups in *Pachybatrachus*.

Cannatella and Trueb (1988*b*) listed several characters that are present in their derived state in Hymenochirini, but none of these characters can be examined in the available material, except for the fusion of the cultriform process of the parasphenoid to the sphenethmoid and prootics, and of the medial and lateral rami of the pterygoid to the otic capsules. The cultriform process of the parasphenoid is not evident owing to its fusion to the sphenethmoid and prootics, a derived condition, whereas in the probable absence of fusion of both rami of pterygoid to the otic capsules, *Pachybatrachus* exhibits the plesiomorphic conditions.

The nearly straight and narrow, but deep, Eustachian canals, which cross the ventral surface of the otic capsules obliquely, presumably represent a derived character state that supports closer relationships with the Hymenochirini, because canals with these characteristics occur in members of this group among the pipids examined. By contrast, in *Xenopus* and *Pipa* (except for the highly derived *P. pipa* and *P. snethlageae*), the Eustachian canal curves anteromedially, circumscribing the inner ear region. Although the quadrate complex of *Pachybatrachus* seems to occupy a more posterior position than in living hymenochirines, the morphology of this region resembles that found in this group. As in the Hymenochirini, however, the detailed configuration and relationships of the individual elements of this region are difficult to determine, owing to the extensive ossification. If the ridge posterior to the margin of the Eustachian canal marks the posterior terminus of the otic plate of the pterygoid, the broad and approximately triangular shape of this plate resembles the condition seen in *Hymenochirus* and *Pseudhymenochirus*.

Only one large acoustic foramen is present on the medial wall of the otic capsule in the larger specimens of *Pachybatrachus*. Possibly this is a consequence of post-mortem breakage, because in one of the specimens (MNHN-IBC 1605) it is evident that a delicate bony partition lying slightly lateral to the medial wall of the otic capsule was present. Anterior and posterior acoustic foramina occur in extant *Xenopus*, *Silurana* and *Hymenochirus*, as well as in many pipoids (Trueb and Cannatella 1982; Henrici 1991). Thus, the presence of a single wide acoustic foramen in *Pipa* (*P.*

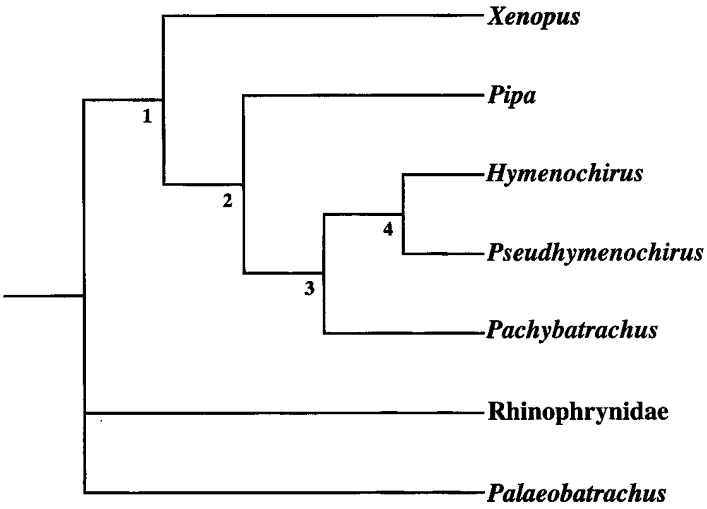
carvalhoi, *P. pipa*, Paterson 1955, 1960; *P. snethlageae*, *P. parva*, pers. obs.) seems to be a derived character state.

Pachybatrachus has two perilymphatic foramina, as in *Hymenochirus* and *Pseudhymenochirus*, but unlike *Xenopus*, *Silurana* and *Pipa*, in which only one foramen is present. However, in *Xenopus* and *Silurana* this single opening occurs on the posterior wall of the otic capsule and corresponds to the inferior perilymphatic foramen, whereas in *Pipa* it is located on the medial wall of the otic capsule and corresponds to the superior perilymphatic foramen (Paterson 1960; AMB, pers. obs.). In *Hymenochirus*, the superior perilymphatic foramen opens into the cranial cavity, whereas a second foramen, the foramen accessorius, occurs near the jugular foramen (Paterson 1960). In *Pseudhymenochirus* (KU 206875) two perilymphatic foramina appear at the level of the jugular foramen, but their identity remains unknown. In *Pachybatrachus*, the two closely spaced foramina are located slightly posterior to the jugular foramen, and thus lead into an extracranial space. A similar superficial arrangement occurs in rhinophrynids, in which superior and inferior foramina are present; thus this might represent the plesiomorphic condition for pipoids.

Cannatella and Trueb (1988*a*) listed six uniquely derived osteological character states that support the clade *Pipa*, but only two of those synapomorphies could be assessed in *Pachybatrachus* owing to incomplete preservation or the high degree of ossification. *Pachybatrachus* is more plesiomorphic than *Pipa* in having, as in other pipids, occipital condyles with elongated articular facets, and condyles oriented posteromedially in ventral view. Cannatella and Trueb (1988*a*) interpreted the orbitonasal foramen enclosed in bone in *Pipa* as a reversal to the plesiomorphic state found in the outgroups, but this condition occurs in other fossil and living pipid taxa lacking other autopomorphies of *Pipa* or many pipine synapomorphies (e.g. *Silurana epitropicalis*, KU 195661; '*Xenopus*' *romeri* Estes, 1975*b*; see also below); thus the phylogenetic meaning of this trait is unclear. *Pachybatrachus* resembles the most derived of the living species of *Pipa*, *P. pipa*, in having an extremely flat neurocranium, a dorsal dome on the frontoparietal which is coupled with a midorbital transverse depression, and dorsally oriented supraorbital flanges. This last feature also occurs in *Hymenochirus*.

Several features of the vertebrae warrant comment. The marked anterior protrusion of the neural arches between the prezygapophyses occurs in Hymenochirini, as well as in the more derived species of *Pipa*, *P. pipa* and *P. snethlageae*. In all these taxa, this part of the neural arch has an elaborate surface that may provide additional areas of articulation between successive vertebrae, as it does in *Pachybatrachus*. However, in both *Pipa pipa* and *P. snethlageae*, the anterior part of the arch forms a structure separated from the prezygapophyses by a notch. Each side of this structure bears slanting articular surfaces, and resembles the zygosphene of many squamates. In these two species, as in other members of the genus *Pipa*, the articular surfaces of the pre- and postzygapophyses of the presacral vertebrae are relatively flat. By contrast, the Hymenochirini lack the zygosphene-like structure and the ventrally curved lateral part of the postzygapophyses wraps around the lateral margin of the prezygapophyses, as in *Pachybatrachus*. It is noteworthy that in extant *Xenopus* and *Silurana*, the zygapophyses develop a system of interlocking ridges and grooves (Vergnaud-Grazzini 1966), but this character state has not been reported in any Cretaceous–Miocene pipid taxon hitherto described. The presence of 'normal' zygapophyses lacking complex articular surfaces is clearly evident in disarticulated vertebrae referred to *Xenopus* (including *S. tropicalis*) from the Paleocene of Brazil (Estes 1975*a*, 1975*b*) and the Miocene of Morocco (Vergnaud-Grazzini 1966), and in the Eocene *Shelania* from Patagonia (AMB, pers. obs.). The vertebrae of *Pachybatrachus* resemble those of some species of *Hymenochirus* (e.g. *H. boettgeri*, *H. curtipes*) in having extremely thick neural spines.

The relationship of *Pachybatrachus* to the pipines was explored using PAUP 3.1 for Macintosh (Swofford 1993). Only the 13 characters that could be assessed in the fossil taxon were included in the analysis (Appendix 2). *Palaeobatrachus* and Rhynophrynidae were employed as outgroups, according to the hypothesis of pipoid relationships proposed by Cannatella and de Sá (1993). Data on *Palaeobatrachus* and Rhynophrynidae were obtained from the literature (Špinar 1978; Trueb and Cannatella 1982; Henrici 1991). Character states used in the analysis for *Silurana* were identical



TEXT-FIG. 4. Cladogram depicting the hypothetized relationships of *Pachybatrachus* and selected pipids. Node 1. (Pipidae): sphenethmoid enclosing optic foramina; parasphenoid fused to the braincase; sacrum and coccyx fused. Node 2 (Pipinae): skull wedge-shaped in lateral profile; frontoparietal bearing supraorbital flanges; posterior terminus of parasphenoid acuminate; presacral vertebrae with parasagittal spinous processes. Node 3 (unnamed): Eustachian canals straight and cross the otic capsules diagonally; extensive contact between pterygoid and parasphenoid; articular surface of postzygapophyses of presacral vertebrae curved ventrally. Node 4 (Hymenochirini): medial and lateral rami of pterygoid synostotically fused to prootic.

to those for *Xenopus*; hence the former was not included as a separate taxon. All character transformations were unordered and the character-state optimization used the ACCTRAN setting. An exhaustive search yielded one minimal tree of 15 steps, and a CI, excluding uninformative characters, of 0·92 (Text-fig. 4). *Pachybatrachus* appears to be a pipine and is more closely related to the Hymenochirini than to *Pipa*. This is supported by a few, presumably derived, character states, including the straight Eustachian canal crossing the otic capsules diagonally, a (probable) broad contact between the parasphenoid and the otic plate formed by the pterygoid, and the elaborate articular surfaces of the postzygapophyses (node 3, Text-fig. 4). This relationship implies that the spinal foramen between vertebrae I and II may have been minute in the ancestor of pipines, but that reversal to an intermediate condition occurred in *Pachybatrachus*, or that reduction of the foramen occurred convergently in the two pipine lineages. The lack of fusion of the otic plate of the pterygoid to the otic capsules and of the squamosal to the prootic in adults are primitive traits of *Pachybatrachus*, unlike the derived condition of these characters in extant hymenochirines. No derived character states supporting a closer relationship to either *Hymenochirus* or *Pseuhymenochirus* was found. This suggests that *Pachybatrachus* might be the sister group of the Hymenochirini; however, it differs from them in having a broader braincase and a relatively more posterior position of the quadrate. Judging by the size of some of the bones referred to *Pachybatrachus*, we estimate that the largest individuals could have reached snout–vent lengths of up to 70 mm, thus falling outside the size range of living hymenochirine species (24–46 mm). In addition, this taxon possesses some uniquely derived character states, such as the coarse vermicular sculpturing of the skull, the additional accumulation of bone on the vertebral centra and sacrococcyx, and the supplementary areas of articulation between atlas and skull.

Whereas no autapomorphies of *Pipa* were found in *Pachybatrachus*, the plesiomorphic state of two unambiguous derived features of this extant genus are present. Thus, the overall resemblance of the skull of *Pachybatrachus* to that of *Pipa pipa* is parsimoniously interpreted as the result of convergent evolution. In this regard, it is interesting to note that a flattened snout and shovel-like skull are some of the cranial modifications for burrowing among vertebrates (Wake 1993). However, comparison is difficult because little is known of the mode of life of this bizarre living pipid species.

Family PIPIDAE Gray, 1825

Unidentified genus and species

Plate 1, figures 7–11; Text-figure 3H–K

Referred material. MNHN-IBC 1602 (braincase and otic capsules).

Horizon and locality. Ibeceten Formation (Coniacian–Santonian) (Moody and Sutcliffe 1991); In Beceten (or Ibeceten), approximately 90 km east-north-east of Tahoua, Niger (Text-fig. 1).

Description. This species is represented by a well-ossified braincase (Text-figs. 3H–K; Pl. 1, figs 8–11). Nasals, pterygoids, squamosals, palatoquadrates, maxillary arches and mandibles are not preserved.

The frontoparietal is azygous, and fused anteriorly to the underlying sphenethmoid and posteriorly to the fused prootics and exoccipitals. The bone has a flat, relatively wide dorsal table bounded by weak parasagittal crests. A narrow depression located at about the level of the orbitonasal foramina possibly corresponds to the pineal opening. The frontoparietal lacks both anterolateral processes and a conspicuous rostral projection and the anterior margin of the bone is smoothly convex. Although the limits of the frontoparietal are not obvious, owing to its fusion with neighbouring elements, its posterior margin seems to lie near the dorsal margin of the foramen magnum.

The prootic and exoccipital are completely fused. Similarly, the exoccipitals are fused to one another dorsally and ventromedially. The nature of the medial association of the prootics is unknown. The dorsal surface of each prootic is smooth and lacks crests. Anteriorly, weak sutures mark the border of the overlying frontoparietal. A ventrally deflected flange lies along the posterior margin of the dorsal surface of the prootic. One unidentified foramen occurs on this margin, and pierces the prootic flange, dorsally and laterally to the foramen magnum (Text-fig. 3K). Anteroventrally, a prominent process abuts the neurocranium slightly posterior and ventral to the wide optic foramen; thus, the prootic foramen is not visible in the ventral view of the skull. Although most of the floor of each otic capsule is not preserved, the medial portion of the wide furrow that, in life, accommodated the Eustachian tube is visible on the right side of the skull, anterior to the inner ear region. The margins of the wide foramen magnum are completely ossified, and the occipital condyles are located on its ventral margin. A condyloid fossa is visible lateral to the right condyle (Text-fig. 3K), but as a result of breakage and poor preservation no foramen is evident.

The sphenethmoid is well ossified and extends from the nasal region, anteriorly, to the prootic foramen region, posteriorly. Its anterior portion forms the thick-walled housing for the posterior end of the nasal organs. A bony septum, presumably derived from the sphenethmoid cartilage and representing the septum nasi, separates the nasal capsules medially (Text-fig. 3J). The anterior terminus of the septum is broken whereas the posterior end lies at the level of the orbitonasal foramina; the latter are completely enclosed in bone. In the orbital region, the sphenethmoid continues the floor and sides of the braincase; ventrally, it is encrusted by the cultriform process of the parasphenoid (Text-fig. 3I). The sides of the sphenethmoid diverge dorsolaterally to meet the overlying frontoparietal. The dorsal extent of the sphenethmoid in the orbital region is difficult to assess owing to fusion of this bone with the frontoparietal. The large optic foramina are enclosed by the sphenethmoid (Text-fig. 3J). Posterior to these foramina, a wide, ventrally directed pillar of bone meets

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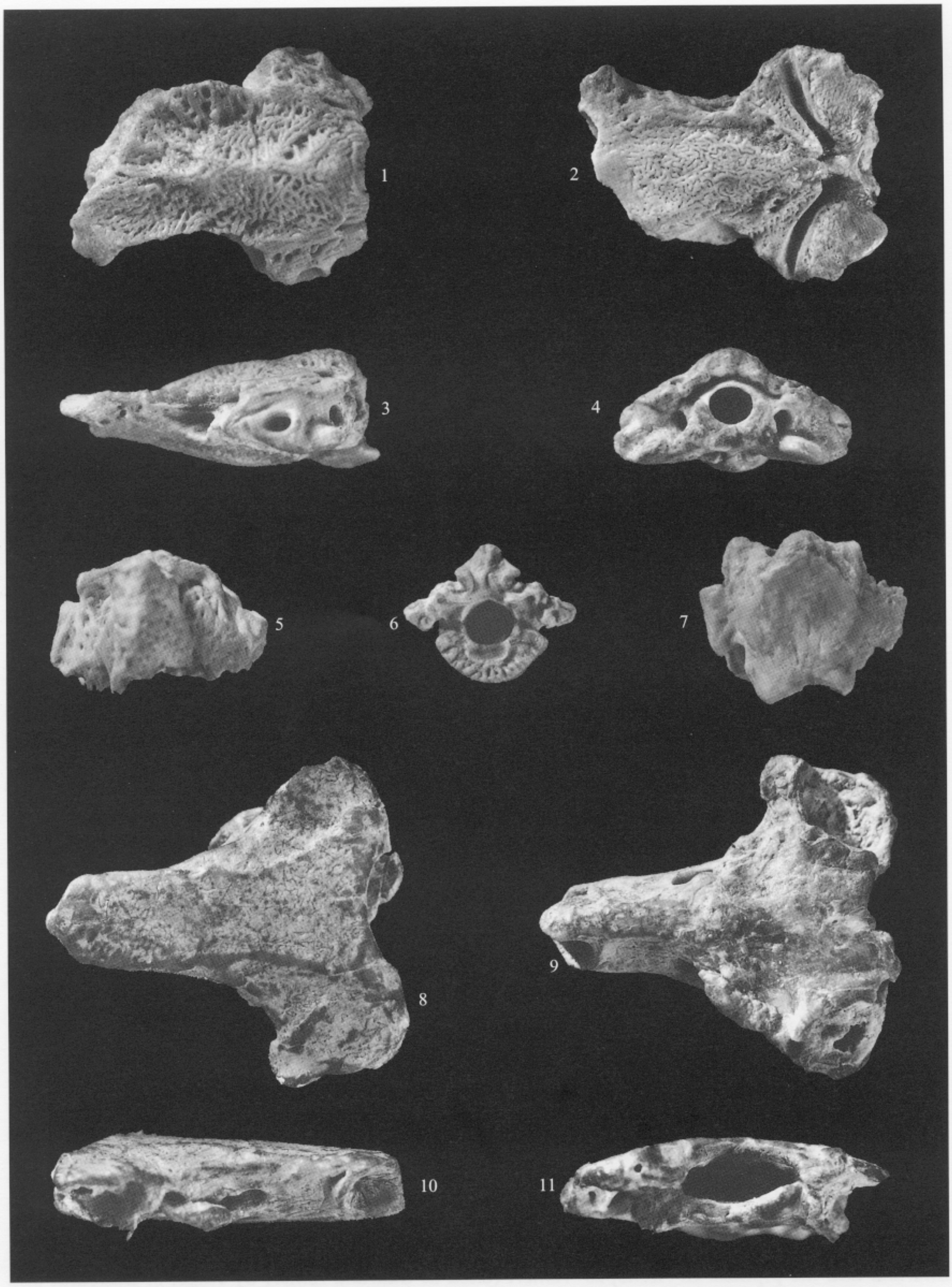
EXPLANATION OF PLATE 1

Figs 1–6. *Pachybatrachus taqueti* gen. et sp. nov. 1–4, MNHN-IBC 1604, holotype; braincase and otic capsules in 1, dorsal; 2, ventral; 3, left lateral; and 4, posterior views; all × 4. 5, MNHN-IBC 1611; atlantal complex, dorsal view; × 6. 6, MNHN-IBC 1614; presacral vertebra, posterior view; × 5.

Figs 7–11, unidentified pipids. 7, MNHN-IBC 1650; posterior presacral vertebra, ventral view; × 5. 8–11, MNHN-IBC 1602; braincase and otic capsules in 8, dorsal; 9, ventral; 10, right lateral; and 11, posterior views; all × 4.

PLATE 1



BÁEZ and RAGE, *Pachybatrachus*, unidentified pipids the anteroventral portion of the otic capsule, separating two foramina. The anterior foramen lies between the side wall of the neurocranium, medially, and the prootic, laterally. The posterior foramen is relatively more lateral than the anterior foramen, and its posterior margin is formed by the prootic at the anteromedial corner of the otic capsule. One of these two openings corresponds to the prootic foramen.

The parasphenoid is partially fused to the sphenethmoid and only the margins of the posteromedial portion lying between the otic capsules are clearly visible (Text-fig. 3I). The anteriormost end of the bone is not preserved. The cultriform process is relatively narrow anteriorly, but widens slightly at a point immediately anterior to the level of the orbitonasal foramina. There is no evidence that discrete vomers were attached to the ventral surface of the parasphenoid. The lateral margins of the parasphenoid are difficult to trace posterior to the level of the orbitonasal foramina owing to its fusion to the overlying sphenethmoid. Each side of the parasphenoid bears a laterally directed expansion at the level of the posterior margin of the optic foramen and adjacent to the union of the pseudobasal process and the sphenethmoid (Text-fig. 3I). The posterior portion of the parasphenoid terminates between the otic capsules, reaching a point corresponding only to the midlength of the latter.

Remarks. The azygous frontoparietal and the lanceolate shape of the parasphenoid, which lacks alae and has a long cultriform process extending forwards beyond the level of the orbitonasal foramina, leave no doubts as to the pipoid affinities of this specimen. Moreover, the presence on the ventral surface of the otic capsules of excavations for the Eustachian tubes and the enclosure of the optic foramina in bone suggest that it represents a pipid taxon. The skull is not wedge-shaped in lateral aspect, and the dorsal surface of the otic capsules lacks crests, thus indicating that the depressor mandibulae muscle originated from connective tissue fascia overlying the crista parotica, as in *Xenopus* and *Silurana*, but unlike the derived condition in most pipines (Cannatella and Trueb 1988*a*, 1988*b*).

Overall, there is a superficial resemblance to *Xenopus*, but species of this taxon have departed little from the most recent common ancestor of the pipid lineages alive today. Only a few diagnostic synapomorphies have been recognized in the osteology of *Xenopus*: fused and shallow nasals, azygous vomers, and strongly posteriorly curved transverse processes of the fourth vertebra (Cannatella and Trueb 1988*a*). A single median vomer has been considered a synapomorphy of *Xenopus sensu stricto* (i.e. not including *X. tropicalis* and *X. epitropicalis*) by Cannatella and Trueb (1988*a*). This condition was also commented on by Paterson (1939), who mentioned that no indications of a paired origin of the vomer is found in *X. laevis*, even during metamorphosis. However, this evidence is contradicted by the recent work of Trueb and Hanken (1992) on this species. It is of interest to point out, therefore, that paired vomers occur in several postmetamorphic specimens of *Xenopus* including *X. fraseri* (MNHN 4402), *X. borealis* (UMMZ 152330) and *X. largeni* (KU 206863).

Nasals and the fourth presacral vertebra are not preserved in the fossil species from Niger; thus, it is not possible to assess the presence of the proposed diagnostic synapomorphies of *Xenopus* that involve these elements.

The two living species of *Silurana* are united by two unambiguous derived characters (Cannatella and Trueb 1988*a*), but neither of these can be assessed in the species from Niger because the appropriate soft structures are not preserved. Diagnostic derived character states of *Silurana* also include three osteological features (absence of discrete vomers, frontoparietals with anterolateral processes and fusion of the first and second vertebrae), which have been used to support the monophyly of a clade including *Silurana* + the pipines (Cannatella and Trueb 1988*a*). However, the morphological evidence for this hypothesis of relationships remains equivocal (Cannatella and de Sá 1993) and thus these characters may be homoplastic within Pipidae, as commented on above. In this regard, it is interesting to consider the evidence provided by fossil species. In the specimen from Niger there is no evidence that a discrete vomer (or vomers) was present: a slight expansion of the parasphenoid at the level of the orbitonasal foramina might be an indication that the vomers were fused to this bone, but no conclusive statement can be made based on the available evidence. The possible absence of discrete vomers is important because the absence of vomers characterizes *Silurana* and the pipines. In '*Xenopus*' *romeri* (cited as *Silurana romeri* by Rage, *in* Buffetaut and

Rage 1993, but still of uncertain phylogenetic position) from the middle Paleocene of Brazil (Estes 1975*a*, 1975*b*), a large azygous vomer is present and is attached or fused to the overlying bones in the anterior region of the braincase. In this taxon, this condition is associated with the presence of anterolateral processes on the frontoparietal and fusion of the atlas and second presacral vertebra.

The fossil species from Niger has a more heavily and extensively ossified braincase than in any living species of *Xenopus* and *Silurana* examined, especially in the ethmoidal region. The anterior end of the nasal capsules was probably roofed by the nasals, whereas the posterior part was completely surrounded by the ethmoidal ossifications. Moreover, ventrally, these ossifications support (or are continuous with) the septum nasi, at least throughout the preserved portion. No distinct anterolateral processes on the sphenethmoid are evident, unlike the condition in *Silurana* and the pipines. Enclosure of the orbitonasal foramen in bone is interpreted as a consequence of this intense ossification, a condition which occurs convergently in the genus *Pipa*.

The parasphenoid resembles that of *Xenopus* and *Silurana* in being of lanceolate shape, with a well-developed posteromedial process between the otic capsules which is lacking in the pipines. This shape is probably primitive for pipids, because it also occurs in other pipoids (e.g. palaeobatrachids; Špinar 1972). However, in the species from Niger, the posterior terminus of this bone lies far anterior to the ventral margin of the foramen magnum, unlike the condition in *Xenopus* and *Silurana*. Even in metamorphosing larvae of *Xenopus laevis*, the parasphenoid extends well posteriorly (Trueb and Hanken 1992), although data for other species of this genus are not available. Conversely, in the pipines it does not extend so far posteriorly, a condition that appears to occur not only in adults, but also in larvae and juveniles (e.g. in *Pipa carvalhoi*; Sokol 1977, pl. 7; and *Hymenochirus curtipes*, KU 204134, snout–vent length 16·5 mm, AMB pers. obs). In *Pipa*, remnants of cartilage, probably representing the solum synoticum, are visible between the otic capsules and posterior to this bone, but this does not occur in the species from Niger, this region being completely ossified and lacking any evidence of a suture.

The otic capsules extend far forward, which, despite the intense ossification of the skull, is a juvenile feature. Another potentially juvenile feature is the presence of a narrow pila metoptica separating the large optic foramen from the prootic foramen, on each side of the braincase. The absence of a dorsal table defined by well-developed parasagittal crests might also be the consequence of immaturity. This evidence suggests that the fossil specimen represents a young individual.

To summarize, this taxon exhibits the plesiomorphic condition for three pipine synapomorphies (skull wedge-shaped, parasphenoid posteriorly acuminate, otic capsule bearing hypertrophied crests): this suggests that it is not a member of that clade. In addition, it lacks one of the two apomorphic features of the cranium (presence of anterolateral alae on the frontoparietal) present in *Silurana* and Pipinae. If discrete vomers are truly absent, this is a resemblance to the condition in Pipinae and *Silurana*. However, we note that information on the osteogenesis of the skull is critical for evaluation of this character. These bones appear at a late stage in the development of *Xenopus laevis* (Trueb and Hanken 1992); thus, it is possible that loss of the centre of ossification may have occurred as a result of heterochronic changes. Discrete vomers are absent in developmental material of *Hymenochirus curtipes*, but data on other pipids are not available. Synostotic fusion of the vomers to overlying bones might also result in their apparent absence in adults, as occurs in '*Xenopus*' *romeri*.

The available material is fragmentary and non-diagnostic; until additional material is found we prefer not to establish a formal name on the basis of these remains. Some similarity between the Paleocene '*Xenopus*' *romeri* and the species from Niger was noted by Vergnaud-Grazzini (*in* Broin *et al.* 1974). These species resemble each other in the extent to which the skull bones are fused, the high degree of ossification in the ethmoidal region, and, consequently, the enclosure of orbitonasal foramina in bone, and the rather extensive bony septum nasi, which in '*X.*' *romeri* extends forward or almost the entire length of the nasals (AMB, pers. obs). It is noteworthy that this latter feature was considered a pipine synapomorphy by Cannatella and Trueb (1988*a*). The two fossil taxa differ significantly in the proportions of the braincase (broader in '*X.*' *romeri*), the shape of the frontoparietal which bears anterolateral processes in '*X.*' *romeri*, and the shape of the parasphenoid which in '*X.*' *romeri* has a narrower anterior region of the cultriform process, and a posterior terminus that almost reaches the ventral margin of the foramen magnum.

OTHER DISARTICULATED BONES OF PIPID FROGS

Other isolated skeletal elements of anurans recovered from the Ibeceten Formation may also represent pipid taxa. However, it is difficult to determine the proper association of bones with each other or with the material described above; thus, they are described and discussed separately below.

Angulosplenial

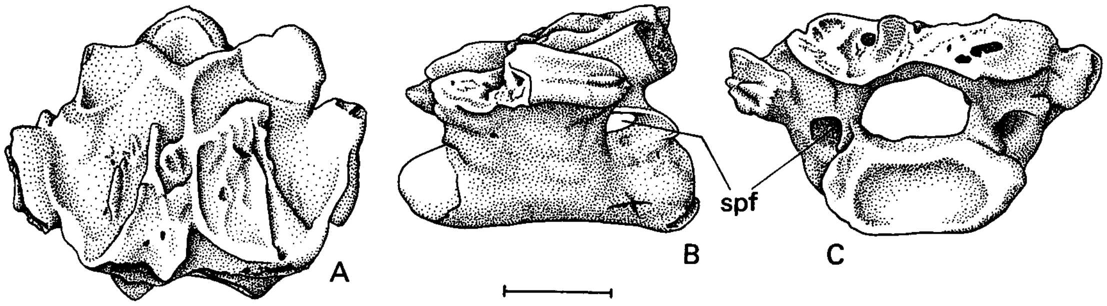
The posterior portion of a lower jaw (MNHN-IBC 1631), which bears a well-developed coronoid process expanded into a flange (a pipid synapomorphy; Cannatella and Trueb 1988*a*), undoubtedly represents a member of the Pipidae. Moreover, as in pipids, the Meckelian canal is closed. The coronoid flange is secondarily reduced in *Pipa pipa* and *P. snethlageae*; furthermore, in these living taxa the posterior end of the angulosplenial has a distinct medially directed curve (Trueb and Cannatella 1986) that is not evident in the fossil specimen. The preserved portion is 12 mm long, indicating an individual of large size.

Presacral vertebra

One opisthocoelous vertebra (MNHN-IBC 1650; Text-fig. 5A–C; Pl. 1, fig. 7), lacking the thick accretion of bone present in the vertebrae referred to *Pachybatrachus*, is tentatively assigned to the Pipidae. It is larger and in general more elongate than the vertebrae referred to *Pschybatrachus*. The anterior third of the neural arch is smooth and extends laterally into the rectangular and flat-surfaced prezygapophyses. This part of the vertebra lies in a more ventral plane than the posterior two-thirds, which bears irregular longitudinal wrinkles on both sides of the fine and rib-like neural spine. This morphology indicates that the neural arch of the preceding vertebra overlapped the anterior portion of the succeeding vertebra (i.e. the neural arches were completely imbricated). The posterior part of the neural arch is somewhat damaged and the postzygapophyses are not preserved, but it is clear that a posteriorly projecting spinous process was not present. The anterior condyle and posterior cotyle are large and depressed. Although the distal portions of the transverse processes are broken off, the pronounced anterior orientation of the dorso-ventrally flattened basal parts of these processes indicates that this vertebra is a posterior presacral. A large spinal foramen opens at the base of the neural arch on each side of the central cotyle. The presence of an intravertebral spinal foramen is uncommon in anurans: for example, it is present in Tertiary pelobatid material, as yet undescribed, from Europe. The opisthocoelous condition and the anterior orientation of the transverse processes are consistent with referral to the Pipidae, despite the presence of bilateral intravertebral spinal foramina. This vertebra differs from those of extant *Xenopus* and *Silurana* and resembles those of pipines in having fully imbricated neural arches and prezygapophyses lacking complex articular surfaces.

Ilia

Sixteen incomplete basal portions of ilia (MNHN-IBC 1630, 1635–1649), all with the same general morphology, can be referred to the Pipidae. This is based on the presence of a conspicuous dorsal prominence, an elongate or dumbbell-shaped (Trueb 1996) acetabulum and the absence of a preacetabular expansion in the lateral plane. The dorsal prominence is relatively wide-based and low, unlike the high and knobbed prominence of *Hymenochirus* which represents the derived condition. The shaft has an oval cross section and a fine ridge runs diagonally from the acetabulum on to the ventral margin of the preserved portion of the shaft. No ridge is present in specimens of extant *Xenopus* and *Silurana* examined for this feature, but does occur in some specimens of '*Xenopus*' *romeri* (DGM 577 and 578), and the pipines. The presence or absence of a prominent



TEXT-FIG. 5. Unidentified pipid, MNHN-IBC 1650; posterior presacral vertebra in A, dorsal; B, left lateral; and C, posterior views. Scale bar represents 2 mm.

crest on the dorsolateral aspect of the iliac shaft could not be assessed because only the most posterior part of the shaft is preserved.

Scapula

One scapula (MNHN-IBC 1632) is clearly referable to the Pipidae because of its relative shortness and configuration. It bears a small articular surface for the clavicle on the anterior margin, thus indicating that scapula and clavicle were separate elements and that the former was slightly overlain anteriorly by the latter. The scapula has a straight anterior margin and its posterolateral angle has a distinct projection. Although the pars acromialis is broken off in this specimen, it is evident that a small notch separated it from the pars glenoidalis. The anterior margin of the preserved portion is 5 mm wide and its lateral margin is 4·5 mm long.

A fused scapula and clavicle is a derived condition, present in *Xenopus*, *Silurana* and *Hymenochirus*, and, although reversed in *Pipa*, has been considered a synapomorphy of extant pipids (Cannatella and Trueb 1988*a*). The presence of a medial notch is a primitive character state for pipids; this notch is lacking in the living species of *Pipa*. The scapula MNHN-IBC 1632 has a well-developed body, thus contrasting with the extreme reduction of the portion lateral to the glenoid region in extant *Xenopus* and *Silurana*, as well as in some fossil taxa (e.g. '*Xenopus*' *romeri*; Estes 1975*b*). In all these taxa, and unlike the Hymenochirini, the area of fusion between the clavicle and scapula is marked by a distinct bump on the anterior edge of the combined element. The articular surface of the pars glenoidalis has a transverse orientation in the fossil scapula, whereas in extant pipines it is usually posteriorly directed.

Humeri

Five fragments representing the distal end of humeri (MNHN-IBC 1651–1655) are referred to the Pipidae. In all cases the eminentia capitata is spherical, well-ossified, and relatively small with respect to the well-developed epicondyles. The medial epicondyle is particularly large, producing an asymmetrical shape to the distal end of the bone. In ventral view, a fine longitudinal crest extending almost to the humeral ball is visible. There is some variation in the definition of fine crests on the medial and lateral sides of the bone, and of the ventral fossa in the sample, but the taxonomic significance of this variation is unknown as there have been no studies of these features. In specimens MNHN-IBC 1651–1654, the olecranon scar is relatively short and the fossa cubitalis is triangular, deep and clearly demarcated anterior to the eminentia capitata. By contrast, in MNHN-IBC 1655, the ventral fossa is not well demarcated and forms a long triangular depressed area between the epicondyles. Furthermore, in this specimen, the crests along the sides are barely discernible. The small size of the humeral ball relative to the distal width of all these bones resembles the general condition in pipines. In *Xenopus* and *Silurana*, the epicondyles are relatively narrower, and equally developed. The distal end of the humerus has a symmetrical appearance. The wide medial epicondyle and crests on the epicondyles (particularly in specimens 1651–1654), resembles hymenochirine humeri (at least in *H. boettgeri*, the only species available for comparison), although in the latter, the crests are more strongly developed. Referral to *Pachybatrachus* would be in agreement with the proposed hymenochirine affinities of this taxon.

Discussion

The ilia and the humeri may belong to *Pachybatrachus* because these elements show some resemblance to pipines and this agrees with the pipine relationships of this taxon. The portion of the lower jaw might represent either of the two taxa described above, but because of its large size, we suppose that it does not represent *Pachybatrachus*. It seems possible that individuals of the unidentified taxon, represented by a braincase exhibiting juvenile features, might have attained a large body size. The presacral vertebra that is distinct from those referred to *Pachybatrachus*, and the scapula MNHN-IBC 1632 might belong to this same taxon.

DISCUSSION

At least two pipid taxa are present in the Coniacian–Santonian Ibeceten Formation: the hyperossified hymenochirini *Pachybatrachus* and an unidentified taxon the relationships of which remain equivocal. The suggested phylogenetic relationships of *Pachybatrachus*, coupled with the relationships of the living pipid genera as currently understood, indicate that the divergence of the lineages represented today by *Pipa* and Hymenochirini had already occurred by the late Coniacian, and, consequently, that of xenopodines (*Xenopus* + *Silurana*) from pipines.

The main phase of Mesozoic sedimentation in the Iullemmeden Basin, as in other basins in the western and central part of Africa, developed in relation to the opening of the South Atlantic (Moody and Sutcliffe 1991; Janssen *et al.* 1995). Throughout the Aptian (121–113 Ma; Gradstein *et al.* 1994), Africa and South America were still connected north of the Niger Delta, but became completely separated from each other in the Albian–Cenomanian (Szatmari *et al.* 1987), *c.* 99 Ma (Gradstein *et al.* 1994). The divergence of pipines from their common ancestor may have been coincident with the final break-up of Western Gondwanaland. Furthermore, at this time, marine incursions and subsidence periodically isolated the north-western part of Africa from the rest of the continent (Reyment and Dingle 1987; Genik 1993) and this might have acted as an important vicariant factor, resulting in the isolation of pipid populations and enabling divergence.

The area in which the pipids, described herein, lived in the late Cretaceous was probably well within the wet-tropical belt, because the locality was close to the position of the equator, which ran diagonally through the Saharan region at that time (Scotese and Golonka 1993). A diverse fauna, including fish, salamanders, anurans, pelomedusid turtles, crocodiles, squamates and sauropod and theropod dinosaurs, was established in a fluvial-lacustrine environmental setting. The presence of lungfishes, particularly *Protopterus* (de Broin *et al.* 1974; Werner 1993), suggests seasonal climatic conditions. In general, anurans that live in arid or seasonally arid environments tend to have hyperossified skulls (Trueb 1993). Perhaps, the intense ossification of *Pachybatrachus* was related to the acquisition of a degree of burrowing ability to avoid periods of desiccation. Some features of pipids, such as the expanded sacral diapophyses and sliding ilia, have been interpreted as advantageous for burrowing either in bottom muds or on land (Whiting 1961); moreover, it has been reported that extant pipids occasionally burrow underwater in mud, and are considered to be facultative burrowers (Emerson 1976). Several features of *Pachybatrachus*, including the strongly ossified ethmoidal region, the additional articulation between the skull and the fused first and second presacral vertebrae, and the ventrally reinforced vertebral centra, might be specializations in this respect.

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APPENDIX 1

Abbreviations used in figures

af	acoustic foramen	orf	orbitonasal foramen
cf	condyloid fossa	paf	parietal foramen
ec	Eustachian canal	pb	pseudobasal articulation
ef	endolymphatic foramen	pef	perilymphatic foramen
ex	excavation for the odontoid process	pf	palatine foramen
fp	frontoparietal	pr	prootic
jf	jugular foramen	prf	prootic foramen
ns	neural spine	prz	prezygapophysis
oaf	occipital artery foramen	ps	parasphenoid
ocd	occipital condyle	ptz	postzygapophysis
oct	occipital cotyle	sn	nasal septum
of	oval fenestra	spf	spinal nerve foramen
olf	olfactory foramen	sph	sphenethmoid
op	odontoid process	va	ventral accretion of bone
opf	optic foramen	vc	vertebral centrum

APPENDIX 2

List of specimens of extant species examined (cleared-and-stained, and dry skeletons)

Rhinophrynus dorsalis Duméril and Bibron, 1841, Tehuantepec, Oaxaca, Mexico. KU 69084–085
Xenopus fraseri Boulenger, 1905, no locality data. MNHN 4402
Xenopus gilli Rose and Hewitt, 1927, South Africa. UMMZ 152290
Xenopus laevis Daudin, 1802, no locality data. KU 129701
Xanopus laevis Daudin, 1802, no locality data. MCZ 26585
Xenopus largeni Tinsley, 1995, Ethiopia. KU 206863
Xenopus muelleri (Peters, 1844), Kenya. KU 129699
Xenopus muelleri (Peters, 1844), Dodoma, Tanzania. MCZ 14799
Xenopus muelleri (Peters, 1844), near Ft Johnston. MCZ 85213
Xenopus muelleri (Peters, 1844), Morogoro, Tanzania. MCZ 51689
Xenopus wittei Tinsley, Kobel and Fischberg, 1979, Kigezi, Uganda. CPBA-V-42
Silurana epitropicalis (Fischberg, Colombelli and Picard, 1982), Kinshasa F.D., Zaire. KU 195661
Silurana tropicalis Gray, 1864, Paiata, Liberia. MCZ 11866
Silurana tropicalis Gray, 1864, no locality data. MNHN GR 30–32
Silurana tropicalis Gray, 1864, Sierra Leone. KU 195667
Silurana tropicalis Gray, 1864, no locality data. CPBA-V-36
Pseudhymenochirus merlini Chabanaud, 1920, Sierra Leone. KU 206875
Hymenochirus boettgeri (Tornier, 1896), Ngiti, Kivu, East Congo. MCZ 46080
Hymenochirus boettgeri (Tornier, 1896), Zaire. UMMZ 132927
Hymenochirus boettgeri (Tornier, 1896), Zaire. CPBA-V-51
Hymenochirus boulengeri Witte, 1930, Kpteli, near Buta, Zaire. MCZ21615
Hymenochirus sp., no locality data. UMMZ 154773
Hymenochirus curtipes Noble, 1924, Kinshasha, Zaire. KU 204130, 31, 34, 37
Hymenochirus curtipes Noble, 1924, no locality data. KU 204126
Pipa carvalhoi (Miranda-Ribeiro, 1937), Espirito Santo, Brazil. CPBA-V-9
Pipa carvalhoi (Miranda-Ribeiro, 1937), Santa Tereza, Espirito Santo, Brazil. CPBA-V-30
Pipa parva Ruthven and Gaige, 1923, El Vigia, Mérida, Venezuela. CPBA-V-24
Pipa pipa (Linnaeus, 1758), Leticia, Colombia. UMMZ 152284
Pipa pipa (Linnaeus, 1758), Santa Cecilia, Ecuador. UMMZ 168408
Pipa pipa (Linnaeus, 1758), Belem, Para, Brazil. CPBA-V-7
Pipa snethlageae Müller, 1914, Belem, Para, Brazil. CPBA-V-20
Pipa snethlageae Müller, 1914, River Ampyacu, Estirén, Peru. MCZ 85571

APPENDIX 3

Characters and character states used in the analysis of *Pachybatrachus* relationships. For each character (0) denotes the primitive condition.

1. skull shape in lateral profile: rounded and domed (0); wedge-shaped (1).
2. frontoparietal: supraorbital flanges present (0); supraorbital flanges absent (1).
3. sphenethmoid: not enclosing the optic foramina (0); enclosing the optic foramina (1).
4. parasphenoid: not fused to the braincase (0); at least partially synostotically fused to the braincase (1).
5. parasphenoid posterior terminus: expanded between the otic capsules (0); acuminate (1).
6. pterygoid medial ramus–parasphenoid contact: limited or no contact (0); extensive contact (1).
7. medial and lateral rami of pterygoid: not fused to the otic capsule (0); fused to the otic capsule (1).
8. Eustachian canal: curved, circumventing the inner ear region, or horizontal (0); crosses the otic capsule diagonally (1).
9. shape of articular surface of the occipital condyles: elongate, reniform (0); circular (1).
10. orientation of the articular surface of the occipital condyles: posteromedial in ventral view (0); posterolateral in ventral view (1).
11. postzygapophyses of presacral vertebrae: articular surface simple (0); articular surface ventrally curved forming a groove (1); articular surface bears grooves and ridges (2).
12. spinous processes of presacral vertebrae: single (0); paired, parasagittal (1).
13. sacrum–coccyx relationship: articulated (0); fused (1).

APPENDIX 4

Distribution of character states among the seven taxa examined in the analysis. Numbers in the top row refer to characters described in Appendix 3. ?: the character does not apply owing to a logical conflict.

	Characters												
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13
Rhinophrynidae	0	1	0	0	0	?	0	?	0	0	0	0	0
Palaeobatrachus	0	0	0	0	0	0	0	?	0	0	0	0	0
Xenopus	0	0	0	1	0	0	0	0	0	0	2	0	1
Pipa	1	1	1	1	1	0	0	0	1	1	0	1	1
Hymenochirus	1	1	1	1	1	1	1	1	0	0	1	1	1
Pseudhymenochirus	1	1	1	1	1	1	1	1	0	0	1	1	1
Pachybatrachus	1	1	1	1	1	1	0	1	0	0	1	1	1