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Microvertebrate fauna from Gadoufaoua (Niger, Aptian, Early Cretaceous)

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ABSTRACT
In the palaeogeographical context of the opening of the South Atlantic Ocean at the end of the Early Cretaceous, we document here the first microvertebrate fauna recorded from the Aptian deposits of Gadoufaoua, Niger. A systematic study of the fauna has resulted in a significant expansion of the existing faunal list and increase our knowledge of the palaeobiodiversity of the Gadoufaoua fossil site. Some taxa were previously recorded (lungfishes, crocodilians, chelonians, etc.), but several new taxa are described here for the first time, including the first occurrence of a stem-boreosphenidan mammal in Africa for this time-interval. In addition, chondrichthyans, pterosaurs and lissamphibians are documented. The analysis of taxonomic diversity and preservation of the fossils confirms a floodplain depositional environment (more precisely channel-type), in a higher velocity flow regime than previously thought based on studies of the macrofauna. To confirm the depositional environment inferred by the state of preservation of the fossils, a preliminary comparison with the fauna of similar age from the Santana Formation (Brazil) has been undertaken. The hypothesis of a communication between Africa and South America during the Aptian, as had already been demonstrated based on studies of the macrofauna, is strengthened.

KEY WORDS
Microvertebrates, Cretaceous, Niger, Gadoufaoua, Africa, palaeobiogeography.

RÉSUMÉ

La faune de microvertébrés de Gadoufaoua (Niger, Aptien, Crétacé inférieur).

Dans le contexte paléogéographique de l'ouverture de l'Atlantique Sud à la fin du Crétacé inférieur, nous documentons ici la première faune de microvertébrés des gisements de Gadoufaoua (Niger, Aptien). L'étude systématique des taxons les plus représentatifs permet d'actualiser la liste faunique et d'accroître significativement nos connaissances sur la paléobiodiversité de Gadoufaoua. Certains taxons étaient déjà connus (dipneustes, crocodiliens, chéloniens, etc.), mais de nouveaux sont également décrits ici pour la première fois, notamment le premier mammifère boréosphénidé souche en Afrique à cette époque, ainsi que des chondrichtyens, des ptérosaures et des amphibiens. L'analyse de la diversité taxonomique et de l'état de conservation des fossiles confirme un environnement de dépôt en plaine inondable (plus précisément de type canal), soumis à un hydrodynamisme plus élevé que ce qui avait été établi précédemment dans les études de la macrofaune. Une comparaison préliminaire avec la faune d'âge similaire de la Formation Santana (Brésil) est effectuée. L'hypothèse d'une communication entre l'Afrique et l'Amérique du Sud pendant l'Aptien, comme cela avait déjà été démontré par l'étude de la macrofaune, est renforcée.

MOTS CLÉS
Microvertébrés,
Crétacé,
Niger,
Gadoufaoua,
Afrique,
paléogéographie.

INTRODUCTION

Continental microvertebrate faunas are important because they provide abundant data concerning the biodiversity of a fossil site, as well as providing information concerning possible continental faunal interchange. In addition, fossils of some taxa (for example, lissamphibians, some sauropsids and mammals) are only represented by microremains, because of the minute size of many of these taxa during the Mesozoic. Thus, to be complete, the study of a fossil site must include consideration of the "microremains" component. Furthermore, microvertebrate studies make it possible to test palaeobiographical scenarios based mostly on macrofaunas (Grigorescu *et al.* 1999; van den Berg *et al.* 2012; Haddoumi *et al.* 2016; Lasseron 2019; Lasseron *et al.* 2020).

To date, only a few African Mesozoic continental microvertebrate faunas have been described: these are known from the Middle Jurassic of the Mahajanga Basin, Madagascar (Flynn *et al.* 2006), Middle and Late Jurassic to Early Cretaceous of Anoual, Morocco (Knoll 2000; Evans & Sigogneau-Russell 2001; Haddoumi *et al.* 2016; Lasseron 2019; Lasseron *et al.* 2020), Early Cretaceous of the Douiret Formation, Tunisia (Cuny *et al.* 2010a; Fanti *et al.* 2012) and from the Late Cretaceous of Wadi Milk, northern Sudan (Rauhut & Werner 1995).

Gadoufaoua in the remote Ténéré Desert of Niger is one of the most famous palaeontological sites of Africa. Known since the 1960s, this locality has yielded numerous Lower Cretaceous (Aptian-Albian) vertebrate remains (see paragraph History of exploration). However, until this study, there were no data available concerning the microfauna associated with these remains.

We describe here, for the first time, microvertebrate remains from this locality. The objective of this study is to update the faunal list of the Gadoufaoua deposits by considering data provided by the microfauna in order to compare this fauna with those of other localities of similar ages. The purpose is then to highlight the existence of potential palaeobiogeographical affinities between these localities, in a global context preceding the opening of the South Atlantic Ocean, as has previously been done using some groups, such as the crocodilian (Buffetaut & Taquet 1977; Buffetaut 1981) and actinopterygian faunas (Maisey 2000).

GEOGRAPHIC, GEOLOGICAL AND HISTORICAL SETTINGS

Geographical and geological context

The Gadoufaoua deposits are located southeast of the Aïr massif in the South-central Sahara Desert. The outcrop of fossiliferous strata is about 2 km wide over a length of approximately 180 km with an area of 360 km^2 (Fig. 1; Taquet 1976).

Gadoufaoua is located in the Iullemmeden Basin, which extends from Algeria in the north over Mali and Benin in the west, Chad to the east, and northern Nigeria to the south (Taquet 1976). The continental Mesozoic deposits of the Iullemmeden Basin are currently divided into the Agadez, Irhazer, and Tegama groups (Moody & Sutcliffe 1991; Fig. 1). The fossiliferous beds in the region of Gadoufaoua are part of the Tegama Group. They were subdivided into eight units, numbered from 1 to 8 and bearing the abbreviation GAD by the French geologists of the Commissariat à l'Énergie Atomique (CEA 1965; Fig. 1). The studied material comes from unit GAD 5, which also yielded numerous macroremains of vertebrates (see below) and corresponds to the top of the Elrhaz Formation (Faure 1966; Taquet 1976). This stratigraphic unit comprises an alternation of clay and sandstone banks, often channalized, with a thickness of up to *c.* 60 m. The site of Gadoufaoua was dated by geological correlation with other Saharan localities and utilising its vertebrate associations (Taquet 1976). Currently, it is dated as Aptian (*c.* 125 to 113 Ma). Evidence for a more precise range within the Aptian is lacking.

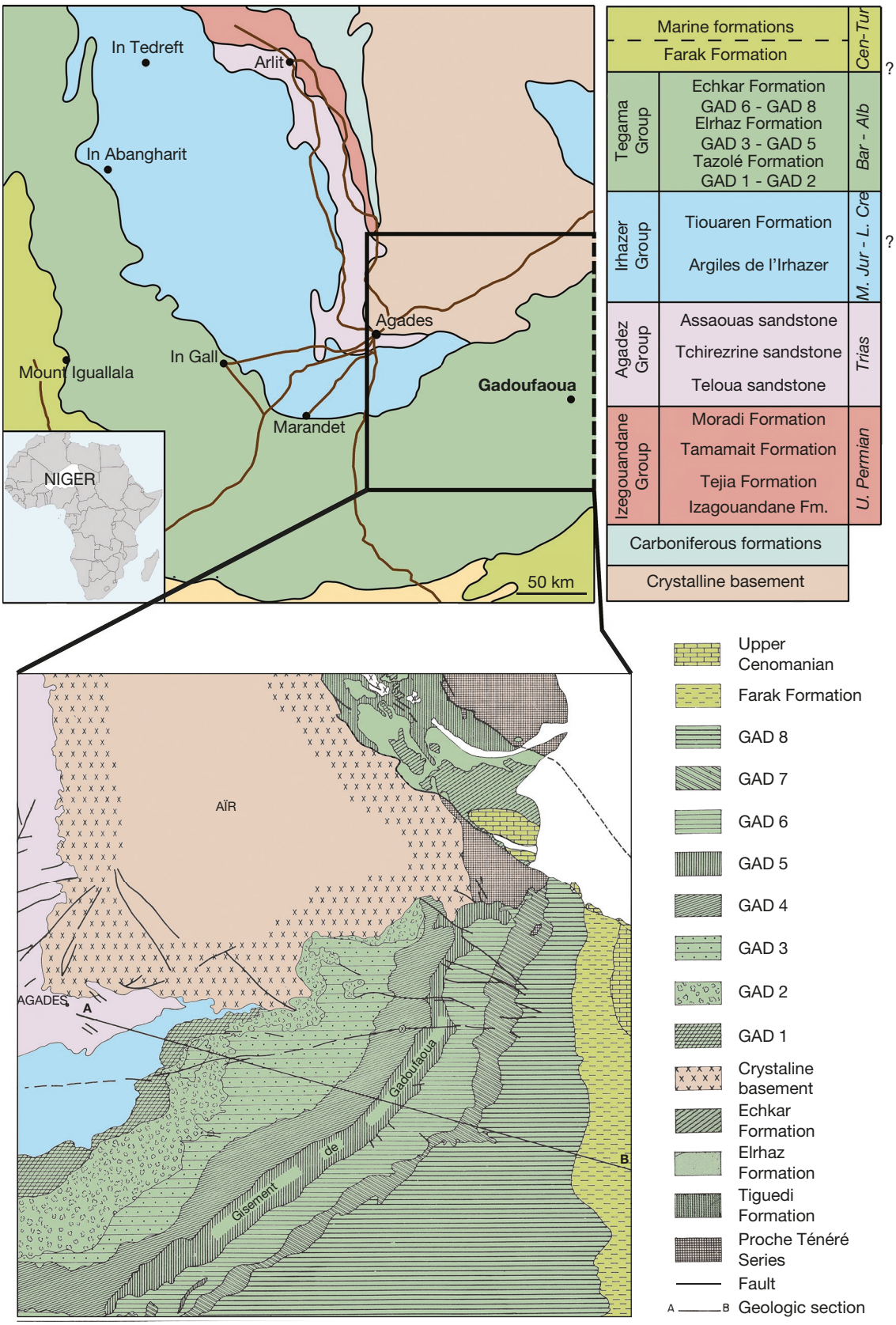

Fig. 1. — Geological map of Gadoufaoua, Niger (modified after CEA 1965; Faure 1966; Taquet 1976; Moody & Sutcliffe 1991; Rauhut & Lopez-Arbarello 2009; Young *et al.* 2017).

Fig. 2. — Picture of the actinopterygian scales treated before counting.

History of exploration

In 1965, Professor Philippe Taquet of the Muséum national d'Histoire naturelle (MNHN) made his first trip to the Ténéré Desert, in Niger. Although fossils had previously been reported in the region (Chudeau 1907; Arambourg & Joleaud 1943; Faure 1966), this was the first serious scientific investigation. Following the invitation of the CEA., he conducted a survey of the promising site of Gadoufaoua. Taquet discovered the skeletons of several large vertebrates, including crocodilians (de Broin & Taquet 1966; Buffetaut 1981; Taquet 2015), dinosaurs (Taquet 1976; Galton & Taquet 1982; Taquet & Russell 1998, 1999; Galton 2009), chelonians, actinopterygians and chondrichthyans (Taquet 1976; de Broin 1980; Wenz 1999; Pérez-García 2019a, b). Since then, in recent decades, other expeditions have been organized, leading to the discovery of new dinosaurs (Sereno *et al.* 1998, 2007; Sereno & Wilson 2005; Brusatte & Sereno 2007; Sereno & Brusatte 2008; Sereno 2017), as well as crocodilian (Larsson & Gado 2000; Sereno *et al.* 2001, 2003; Sereno & Larsson 2009) and chelonian material (Sereno & ElShafie 2013).

In 1970, as part of Taquet's fifth expedition to the Gadoufaoua region, in addition to the macroscopic material, residues from six tons of matrix obtained using bulk screening techniques by Donald Russell were sent to the MNHN (Taquet 1976). This material remained unstudied for almost 50 years. The results of a recent analysis of some of this material are presented below.

MATERIAL AND METHODS

The study of microvertebrate faunas

Microvertebrate sites are defined as those where the majority of the collected fossil remains are millimetric to centimetric in size (Rogers & Brady 2010). Such assemblages are frequently the result of strong hydrodynamic sorting (Sankey & Baszio 2006). The benefits of studying such assemblages are numerous. Given the large sample size, the probability of obtaining "rare" taxa (otherwise not often present in the macrofauna) is much higher. By analyzing the data produced, it is possible therefore to focus on many topics, including taphonomy, the reconstruction of palaeoenvironments and palaeobiogeography (Sankey & Baszio 2006). Although microremains are often highly abraded and fragmented, rendering their identification problematic, their number compensates for this and it has been proven that they can be considered reliably representative of local palaeobiodiversity (Rogers & Brady 2010).

Identification of the material

The material studied here comes from processing a small fraction (less than 100 kg) of the six tons of sedimentary material obtained from the GAD 5 unit in 1970 by Taquet and his team and now housed at the MNHN. Only this small sample was studied for reasons detailed in the discussion (Comparison of the GAD and GADb sites).

After being separated from the lithoclasts by acid digestion and sieving, as well as visual inspection, the fossils from this sample were sorted and identified with a binocular microscope, and then counted and catalogued.

The fossils were examined using a Leica MEB115 binocular stereomicroscope, equipped with auxiliary fiber-optic lighting (Fiber-Lite MI-150) and a Zeiss Discovery V8 stereomicroscope, equipped with Leica LED1000 ring light. The observations and image acquisitions were made using an optical platform (Nikon SMZ1270 and Photonic Optics auxiliary lighting) under Archimed, then processed using Photofiltre 7. Drawings were made through a camera lucida associated with the binocular microscope. Diversity calculations and statistical analyses were performed using Past (version 3.25, Hammer *et al.* 2001) and RStudio (version 1.1.463, R Core Team 2014).

Counting methods

All specimens were counted. When the number of specimens was relatively small (n < 100), counting was done manually, but in the case of larger batches, it was performed using the Python script "Count Image Elements", developed by Auréliane Gailliègue (PhD student, Institut des Sciences du Calcul et des Données). The principle is quite simple and based on image segmentation. The material is spread on a uniform black or white background and photographed (Fig. 2), after ensuring that none of the fossils were in contact with each other. This image is then imported into the Python environment, where the script counts the number of elements based on the differences in contrast between the fossils and the background. This script has already been tested and used several times (Lasseron *et al.* 2020; Allain *et al.* 2022) and has always given statistically acceptable results (at a 95% threshold). It was therefore considered sufficiently reliable to allow exhaustive counting with a relatively small and acceptable margin of error. Some 3703 microvertebrate specimens were obtained from the Gadoufaoua sample forming the basis of this study and were counted using the above methods. The specimens were then identified (whenever possible). At least 20 species are present in the assemblage.

Separation of sites

We do not have information concerning the exact position of sites from which the material was collected. However, some of this material was stored at the MNHN in a separate box. During sorting and identification of samples, we found this material to have a lighter color and a better quality of fossil preservation than other seen in other samples. This suggested a different depositional environment to that of other samples so, as a result, this sample was separated from the rest. It is referred to below as "site GADb". Fossils from this sample were then compared to those obtained from the other lithology in order to determine whether the potential difference in environment of deposition is reflected in faunal compositions. This permitted a determination as to whether or not a distinction has to be made between the two samples.

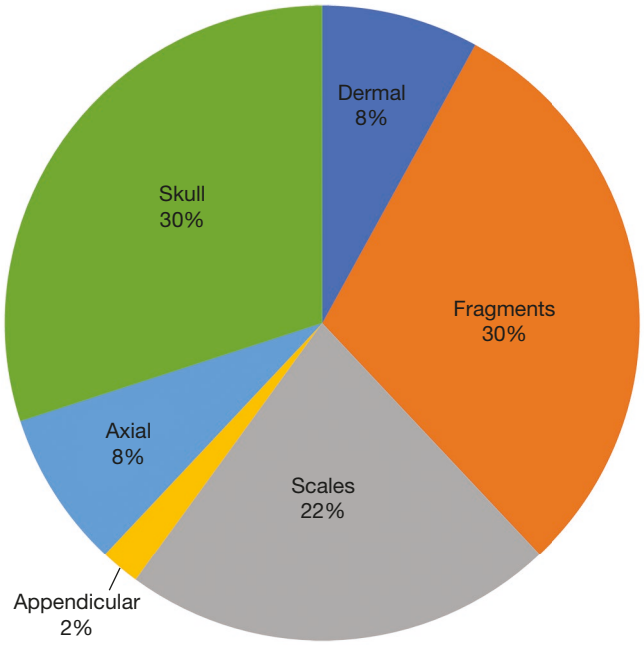

Fig. 3. — Anatomical distribution of the fossil remains of the Gadoufaoua's microfauna.

Abbreviations

CEA	Commissariat à l'énergie atomique;
GAD	Gadoufaoua;
MNE	minimal number of elements;
MNHN	Muséum national d'Histoire naturelle.

SYSTEMATIC PALAEONTOLOGY

30% of isolated microvertebrate remains are unidentifiable bone fragments. 30% represent cranial bones and teeth, 10% belong to the appendicular or to the axial skeleton and 8% consist of dermal skeletal elements (osteoderms, turtle plates). The remainder of the assemblage, 22%, comprises actinopterygian scales (Fig. 3).

Described below are taxa not previously described in the literature and which are important from a stratigraphic or biogeographic point of view together with other particularly well-preserved specimens. From the total number of fossils examined (n = 3703), at least 20 taxa can be recognised. A complete catalogue of specimens is available in Appendix 1.

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Infraclass EUSELACHII Hay, 1902

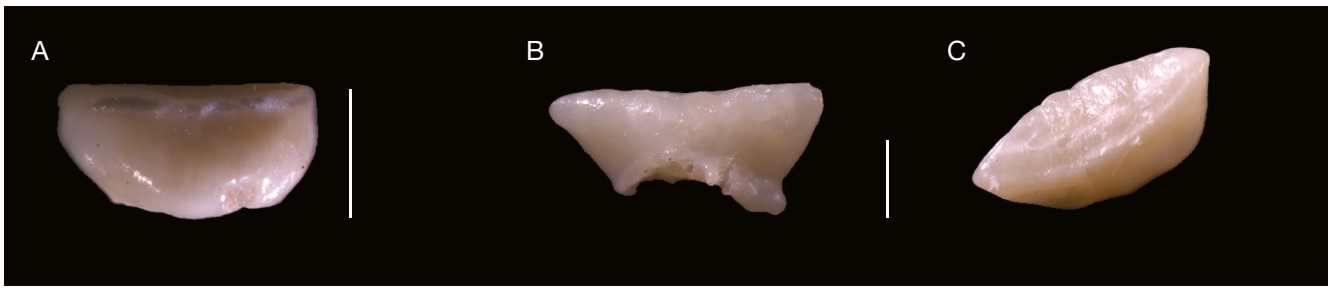

Fig. 4. — MNHN.F.GDF-M39, ?*Tribodus* Brito & Ferreira, 1989 tooth: **A**, labial view; **B**, lingual view; **C**, occlusal view. Scale bars: 0.5 mm.

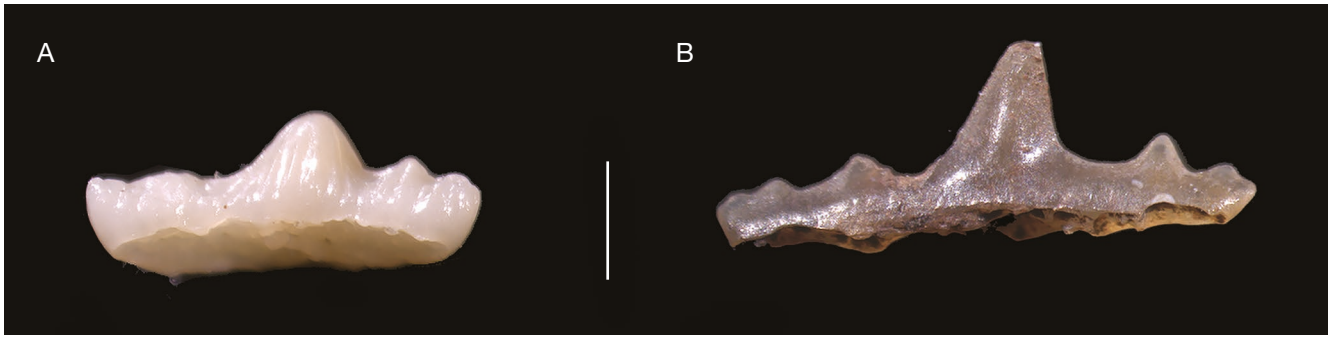

Fig. 5. — Chondrichthyans, Hybodontidae Agassiz, 1843 teeth: **A**, MNHN.F.GDF-M83, morphotype I (lingual view); **B**, MNHN.F.GDF-M73, morphotype II (lingual view). Scale bar: 1 mm.

Order †HYBODONTIFORMES Owen, 1846
Family †Distobatidae Werner, 1989

?† *Tribodus* Brito & Ferreira, 1989 sp. indet.

Material. — MNHN.F.GDF-M39, 40 teeth (Fig. 4).

Description
Forty tooth crowns are tentatively referred to this taxon, but all lack roots. The crowns are between 2 and 4 mm long. Crowns are 0.5 to 1 millimeter in height. They are about one millimeter thick, longer than wide and have a flat diamond or hexagon outline in occlusal view (Fig. 4C). This is a diagnostic character for the genus *Tribodus*. The occlusal surface is almost flat but bears a slight mesiodistal depression. All specimens are probably anterolateral teeth (Brito 1992; Vullo 2007; Vullo & Néraudeau 2008; Cappetta 2012). However, the absence of root makes it difficult to confidently attribute them to *Tribodus*, hence we use open nomenclature.

Family †Hybodontidae Agassiz, 1843
Hybodontidae gen. et sp. indet.

Morphotype I

Material. — MNHN.F.GDF-M83, 5 teeth (Fig. 5A).

Description
The teeth are between 2 and 5 mm high. They are convex labially. Roots are not preserved. The main cusp is not very high but wide and slightly inclined lingually and the accessory cusps are also wider than those of *Egertonodus* Maisey, 1987 and *Polyacrodus* Jaekel, 1889 (Duffin & Sigogneau-Russell 1993; Rees 1996; Underwood & Rees 2002; Vullo 2007; Rees & Underwood 2008; Cappetta 2012). Wrinkles on the labial and lingual surfaces are very marked and rise high along the cusps. This morphology is reminiscent of that of the family Hybodontidae (Cappetta 2012).

Morphotype II

Material. — MNHN.F.GDF-M73, 2 teeth (Fig. 5B).

Description
The teeth are about 2 mm in mesiodistal length. Roots are not preserved. The following characteristics distinguish them from *Hybodus* Agassiz, 1837 (Duffin & Sweetman 2011; Cappetta 2012): there is a tall and well-developed main cusp which is triangular in lingual and labial views. It is aligned with two pairs of high and thin accessory cusps in the mesio-distal plane. They are well separated by wide, deep and rounded notches. The labial surface of the main cusp is slightly convex and has a vertical wrinkle that does not reach the apex. The lingual surface is more strongly

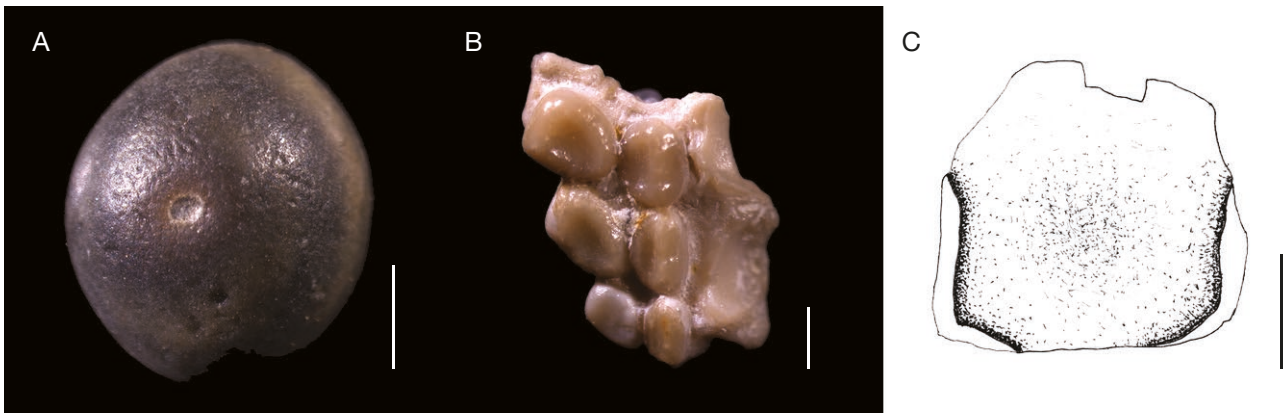

Fig. 6. — **A**, MNHN.F.GDF-M36 Ginglymodi Cope, 1872 tooth (lingual view); **B**, MNHN.F.GDF-M19, Pycnodontiformes Berg, 1937 prearticular/vomer (lingual view); **C**, MNHN.F.GDF-M85, Pycnodontiformes incisiform tooth (lateral view). Scale bars: A, 2 mm; B, C, 1 mm.

convex than the labial one. These teeth lack the more numerous wrinkles occuring on the teeth of *Egertonodus* and *Polyacrodus* (Duffin & Sigogneau-Russell 1993; Rees 1996; Underwood & Rees 2002; Vullo 2007; Rees & Underwood 2008; Cappetta 2012).

Class ACTINOPTERYGII Cope, 1887
Subclass NEOPTERYGII Regan, 1923
Infraclass HOLOSTEI Müller, 1846
Clade GINGLYMODI Cope, 1872

Ginglymodi
gen. et sp. indet.

Material. — MNHN.F.GDF-M07, 58 teeth (GADb); MNHN.F.GDF-M36, 473 teeth (Fig. 6A); MNHN.F.GDF-M97, 260 scales (GADb).

Description

The teeth are about 5 mm in diameter with a crown height of 1 to 3 mm. Roots are not present or poorly preserved. Some teeth have a circular acrodine cap in occlusal view, others have a horizontal wear facet. The crown is low and rounded. Neither ornamentation nor carinae are present. This morphology is reminiscent of some Ginglymodi (Cavin 2010; Grande 2010). Such teeth are very common in Jurassic and Cretaceous deposits and are often referred to as oral teeth of *Lepidotes* Agassiz, 1832 (Pouech *et al.* 2015). Gadoufaoua is the type-locality of another ginglymodian, *Pliodetes nigeriensis* Wenz, 1999 (Wenz 1999; Lopez-Arbarello 2012), but this taxon is edentulous so it is unlikely that these teeth belong to this genus. The ganoid scales are thin and diamond-shaped, with "peg and socket" joints as is the case in *P. nigeriensis* specimen MNHN-GDF-1275. However, as for the teeth, they do not bear enough diagnostic characters to attribute them with confidence to this taxon. As a result, both the teeth and scales are attributed to Ginglymodi gen. sp. indet.

Fig. 7. — MNHN.F.GDF-M63, Teleostei Müller, 1844 vertebra (anterior/posterior view). Scale bar: 1 mm.

Order †PYCNODONTIFORMES Berg, 1937

Pycnodontiformes gen. et sp. indet.

Material. — MNHN.F.GDF-M13, 3 teeth (GADb); MNHN.F.GDF-M19, 1 prearticular/vomer (GADb; Fig. 6B); MNHN.F.GDF-M82, 3 vomers; MNHN.F.GDF-M85, 6 incisiform teeth (Fig. 6C).

Description

MHNH-GDF-m 19 is a prearticular or vomer fragment with a surface area of 6 mm^2. Exact determination is problematic due to the fragmentary nature of the specimen. It bears two rows of three teeth all of which are 1 mm in diameter. They are circular in occlusal view and all have a central depression.

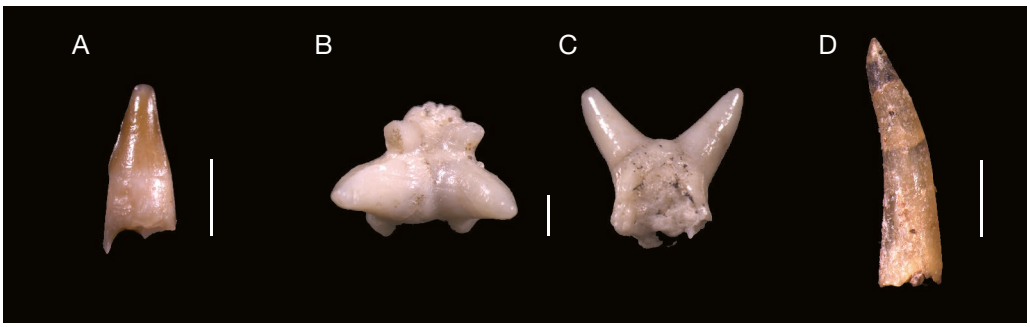

Fig. 8. — **A**, MNHN.F.GDF-M04, Amiiformes Hay, 1929 tooth (labial/lingual view); **B**, **C**, MNHN.F.GDF-M29, Amiiformes premaxillary: **B**, anterior view; **C**, dorsal/ventral view **D**, MNHN.F.GDF-M53, Ichthyodectiformes Bardack & Sprinkle, 1969 tooth (mesial/distal view). Scale bars: A, 2 mm, B, C, 0.5 mm; D, 1 mm.

Fig. 9. — MNHN.F.GDF-M18, dental plate of ?*Ptychoceratodus* Jaekel, 1926 (occlusal view). Scale bar: 2 mm.

The vomer fragments have molariform teeth symmetrically distributed along the antero-posterior axis of the bone. Vomerine teeth are ovoid in occlusal view and about 2 mm long. They are low in labial view. The occlusal surface is flat and has a marked mesiodistal edge, from which about twenty vertically oriented wrinkles terminate.

Incisiform teeth have unadorned surfaces and are flattened labiolingually. In labial view, they are wider than high (2 to 3 mm high) and slightly convex in lateral view. There is a clearly noticeable edge in occlusal view. This edge is almost horizontal in labial view.

The molariform teeth are rounded or ovoid in shape in occlusal view and the crest and wrinkles that are present on some in occlusal view are strongly reminiscent of pycnodontiforms (Kriwet 2002; Pouech *et al.* 2015; Szabó *et al.* 2016; Cooper & Martill 2020). Pycnodontiform teeth show significant morphological variations (Cuny *et al.* 1991; Kriwet 2005; Buscalioni *et al.* 2008; Pouech *et al.* 2015) and few diagnostic characters (Poyato-Ariza & Wenz 2002), which renders identification to a lower taxonomic rank problematic. Thus, we assign them to Pycnodontiformes gen. et sp. indet.

Infraclass TELEOSTEI Müller, 1844

Teleostei gen. et sp. indet.

Material. — MNHN.F.GDF-M06, 79 vertebrae (GADb); MNHN.F.GDF-M63, 148 vertebrae (Fig. 7).

Description

These vertebrae are between 0.5 and 5 mm in diameter. Only the strongly amphicoelous centra remain. Both their anterior and posterior articular surfaces are strongly concave. Some have a central perforation probably representing the notochordal canal. Laterally, ridges are observed aligned in parallel to the antero-posterior axis, which delimit deep depressions. This morphology is typical of teleosts (Brinkman & Neuman 2002; Forey & Sweetman 2011).

Order AMIIFORMES Hay, 1929

Amiiformes gen. et sp. indet.

Material. — MNHN.F.GDF-M04, 128 teeth (GADb) (Fig. 8A); MNHN.F.GDF-M65, 139 teeth.

Description

The tooth crowns are between 4 and 6 mm high, labiolingually compressed with a spearhead-like shape. The mesial and distal edges are overdeveloped and fused with the apical cap. The labial side is more convex than the lingual side. When the root is preserved, it is circular with an ornamentation of vertical wrinkles. There is a strong constriction between the root and the crown. This morphotype is often referred to Caturidae Owen, 1860 (Lambers 1994; Forey & Sweetman 2011). However, other halecomorph actinopterygians have quite a similar morphology, such as *Calamopleurus* Agassiz, 1843 from the Cretaceous of the Brazilian Santana Formation and of North Africa (Grande & Bemis 1998). An assignation to Amiiformes has, therefore, been made.

Order ICHTHYODECTIFORMES Bardack & Sprinkle, 1969

Ichthyodectiformes gen. et sp. indet.

Material. — MNHN.F.GDF-M53, 10 teeth (Fig. 8D).

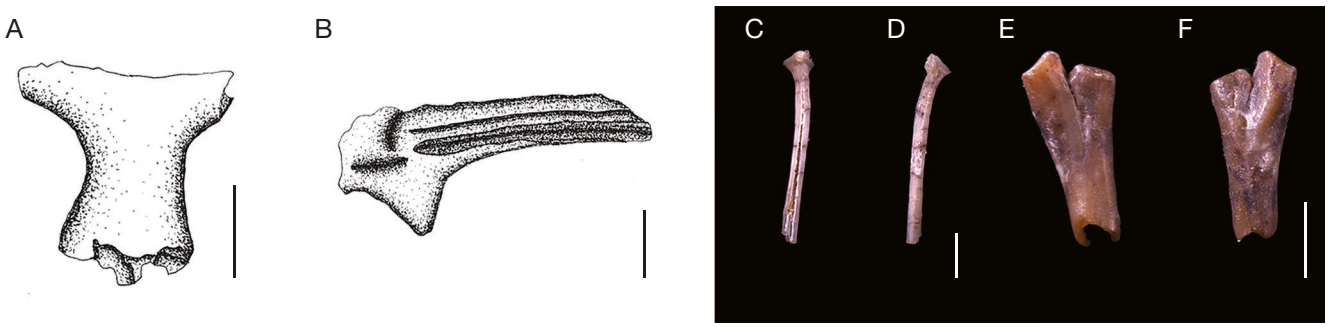

Fig. 10. — Anura Von Waldheim, 1813: **A**, MNHN.F.GDF-M60, scapula (anterior/posterior view); **B**, MNHN.F.GDF-M61, ilium (anterior/posterior view); **C**, **D**, MNHN.F.GDF-M75, urostyle: **C**, dorsal view; **D**, ventral view; **E**, **F**, MNHN.F.GDF-M81, zeugopod: **E**, anterior view; **F**, posterior view. Scale bars: A, B, 2 mm; C, D, 3 mm; E, F, 1 mm.

Description

Tooth crowns are smooth, high, tapered apically and very lingually recurved. They are about 3 mm high and compressed labiolingually, forming mesial and distal carinae, which extend over the entire height of the crown. The apex bears a small acrodine cap. They are oval in cross-section. The enamel is thin and smooth. This suite of characters is specific to this order (Vullo 2007; Pouech 2008; Berrell *et al.* 2014) and resemble those of the ichthyodectiform *Aidachar pankowskii* Forey & Cavin, 2007 from the Cenomanian Kem Kem beds of Morocco. However, the Gadoufaoua specimens lack diagnostic characters (Forey & Cavin 2007; Cavin *et al.* 2015; Ibrahim *et al.* 2020).

Class SARCOPTERYGII Romer, 1955
Subclass DIPNOI Müller, 1844
Order CERATODONTIFORMES Berg, 1940
Family Ptychoceratodontidae Martin, 1982

?Ptychoceratodus Jaekel, 1926

Material. — MNHN.F.GDF-M18, 1 left dental plate (GADb) (Fig. 9).

Description

A small tooth plate (3 mm in length) was found among the Gadoufaoua microremains. It is unclear if this plate belongs to the upper or lower dentition. Five distinct straight crests, bearing dentin bumps and radiating from the mesiolingual angle, are preserved. The most mesial crest is oriented almost at right angles to the internal margin of the tooth plate, while the most distal crest is subparallel to it. The size of the crests decreases along the mesiodistal axis. The distance between the ridges increases from the distal side to the mesial side. The plate is ornamented: it has multiple small perforations that are randomly distributed but which are limited to inter-ridges spaces. The right angle of the tooth plate, its length about twice longer than its width, and the radiating straight ridges oriented posteriorly except for the first one are reminiscent of *Arganodus tiguidiensis* Tabaste, 1963 and permit distinction from species of *Ceratodus* Agassiz, 1838, in particular *C. africanus* Haug, 1905 (Goodwin *et al.* 1999; Soto & Perea 2010; Alves *et al.* 2013). However, in *A. tiguidiensis*, tooth plates generally have seven crests for lower plates and eight for upper plates (Cavin *et al.* 2015), and the genus *Arganodus* Martin, 1979 is usually characterized by seven crests on the tooth plates (Skrzycki *et al.* 2018). Tabaste (1963) described one tooth plate with six crests for *A. tiguidiensis*, as did Cavin *et al.* (2015), but no specimen with five crests is known for this species. This crest count is known for *Neoceratodus africanus* Haug, 1905 (Tabaste 1963), but the general morphology of the Gadoufaoua specimen does not permit assignment to this species (see Cavin *et al.* 2015: fig. 2C). Ptychoceratodontidae are characterized by tooth plates bearing four to six radiating crests (Martin 1982; Skrzycki 2015), but no definitive diagnosis of this family has yet been provided (Skrzycki 2015). The genus *Ptychoceratodus*, in particular, is characterized by the presence of occlusal pits in the inter-ridge furrows, tooth plates of triangular shape and with five to six ridges and slender ridges as well as deep inter-ridge furrows. These characters are reminiscent of the Gadoufaoua specimen (Skrzycki 2015; Bhat & Ray 2020) which is thus assigned to Ptychoceratodontidae, and with less certainty to *Ptychoceratodus*.

Class AMPHIBIA Linnaeus, 1758
Subclass LISSAMPHIBIA Haeckel, 1866
Order ANURA Von Waldheim, 1813

Anura fam. et gen. et sp. indet.

Material. — MNHN.F.GDF-M60, 6 scapulae (Fig. 10A); MNHN.F.GDF-M61, 10 ilia (Fig. 10B); MNHN.F.GDF-M75, 2 urostyles (Fig. 10C, D); MNHN.F.GDF-M81, 11 zeugopods (Fig. 10E, F); MNHN.F.GDF-M27, 1 zeugopod (GADb).

Description

The scapulae measure about 5 mm long by 3 mm wide. Although they are fragmented, a flat lateral face and a concave internal face (ventral/dorsal view) can be distinguished. The dorsal part is slightly bifid and more developed than the ventral part. The glenoid cavity, when preserved, is subcircular. The acromial process, noticeable in some specimens, is

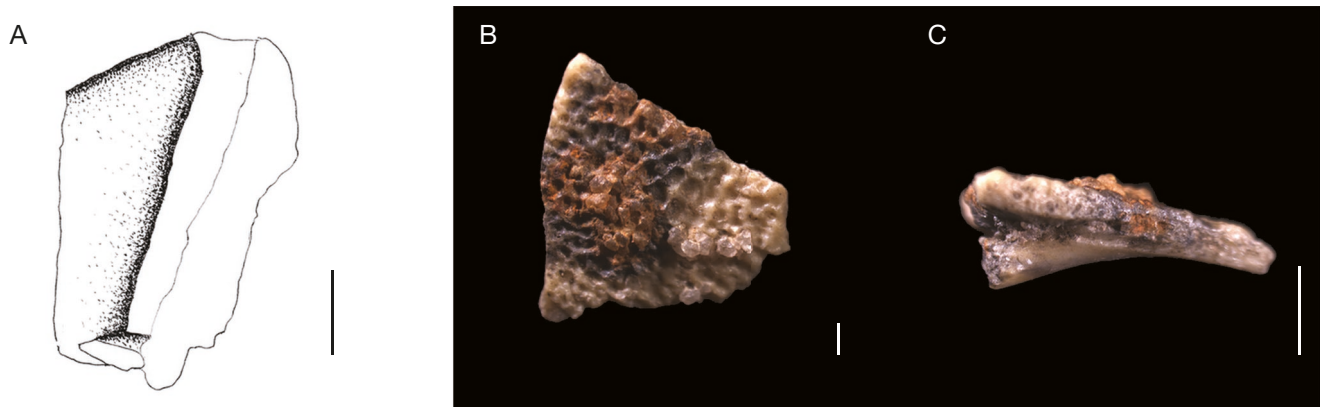

Fig. 11. — Testudines Batsch, 1788: **A**, MNHN.F.GDF-M08, peripheral plate of *Teneremys lapparenti* de Broin, 1980 (dorsolateral view); **B**, **C**, MNHN.F.GDF-M38, pleural plate of Araripemydidae: **B**, ventral view; **C**, lateral view. Scale bars: A, 2 mm; B, C, 1 mm.

well developed ventrally. The scapular notch between these two parts is not noticeable. This morphotype is diagnostic of anurans (Vullo 2007).

The ilia measure between a few millimeters and 10 mm in length depending on their state of preservation. Specimens bear a rounded acetabulum, but the ridge defining it is not well defined. The ilium blade has a dorsal ridge (iliac ridge). It appears slightly curved. This elongated ilial morphotype is characteristic of anurans (Sweetman & Evans 2011).

The two urostyles characteristic of this taxon (Rocek & Nessov 1993; Blanco *et al.* 2016), measure 5 and 10 mm. They are straight and thin. The proximal end is preserved on one specimen, but it is severely damaged and deformed. The articulation is bicondylar and there are no transverse processes. The condyloid pit is ellipsoidal and filled with sediment. On the dorsal surface, a central depression of varying depth between the two specimens is present along the entire length of the bones.

Zeugopods, often fragmented, comprise two fused bones, characteristic of anurans (Rocek 2000). They measure between 5 and 7 mm. Their cross-section is figure of eight-shaped. They are too incomplete to bear diagnostic characteristics that would permit a more accurate anatomical (radioulna, tibiofibula) or taxonomic assignment.

Class SAUROPSIDA Huxley, 1864
Order TESTUDINES Batsch, 1788
Family Pelomedusidae Cope, 1868
Genus *Teneremys* de Broin, 1980

† *Teneremys lapparenti* de Broin, 1980

Material. — MNHN.F.GDF-M08, 1 peripheral plate (GADb) (Fig. 11A); MNHN.F.GDF-M09, 18 plate fragments; MNHN.F.GDF-M54, 55 plate fragments; MNHN.F.GDF-M84, 2 pleural plates.

Description

Among the remains collected, plate fragments of this taxon range from 25 to 50 mm². They are wide in lateral view. The fused ribs clearly noticeable on the pleural plates allow them to be identified as chelonian plates. Folding of the shell boundary of the peripheral plate is also characteristic of chelonians.

There is practically no ornamentation on the plates, which, among the chelonians previously observed at Gadoufaoua, is characteristic of *Teneremys lapparenti* (de Broin 1980).

Family Araripemydidae Price, 1973

Araripemydidae gen. et sp. indet.

Material. — MNHN.F.GDF-M14, 26 plate fragments (GADb); MNHN.F.GDF-M38, 4 pleural plates (Fig. 11B, C); MNHN.F.GDF-M50, 56 plate fragments.

Description

The plate fragments have similar dimensions to those of *Teneremys lapparenti*. However, they are thinner in lateral view. Ornamentation is clearly visible, consisting of small granules and tight bulges, a diagnostic feature of this Gadoufaoua taxon (de Broin 1980), and which also distinguish it from *Francemys gadoufaouaensis* Pérez-García, 2019 (Pérez-García 2019b). There are variations between specimens in the regularity of the ornamentation (depending on the position of the plate on the animal). The pleural plates were determined by the presence of fused ribs that are clearly visible. Their low convexity indicates a very low shell (de Broin 1980).

Note

There is an ongoing debate concerning the generic and specific attribution of the Araripemydidae taxon present in Gadoufaoua, between *Taquetochelys decorata* de Broin, 1980 (de Broin 1980; Pérez-Garcia 2019a) and *Laganemys tenerensis* Sereno & ElShafie, 2013 (Sereno & ElShafie 2013, Ibrahim *et al.* 2020). Given the very fragmentary nature of the microvertebrate remains studied, a precise assignment is difficult beyond family rank. These plates are therefore assigned to Ararypemydidae gen. et sp. indet.

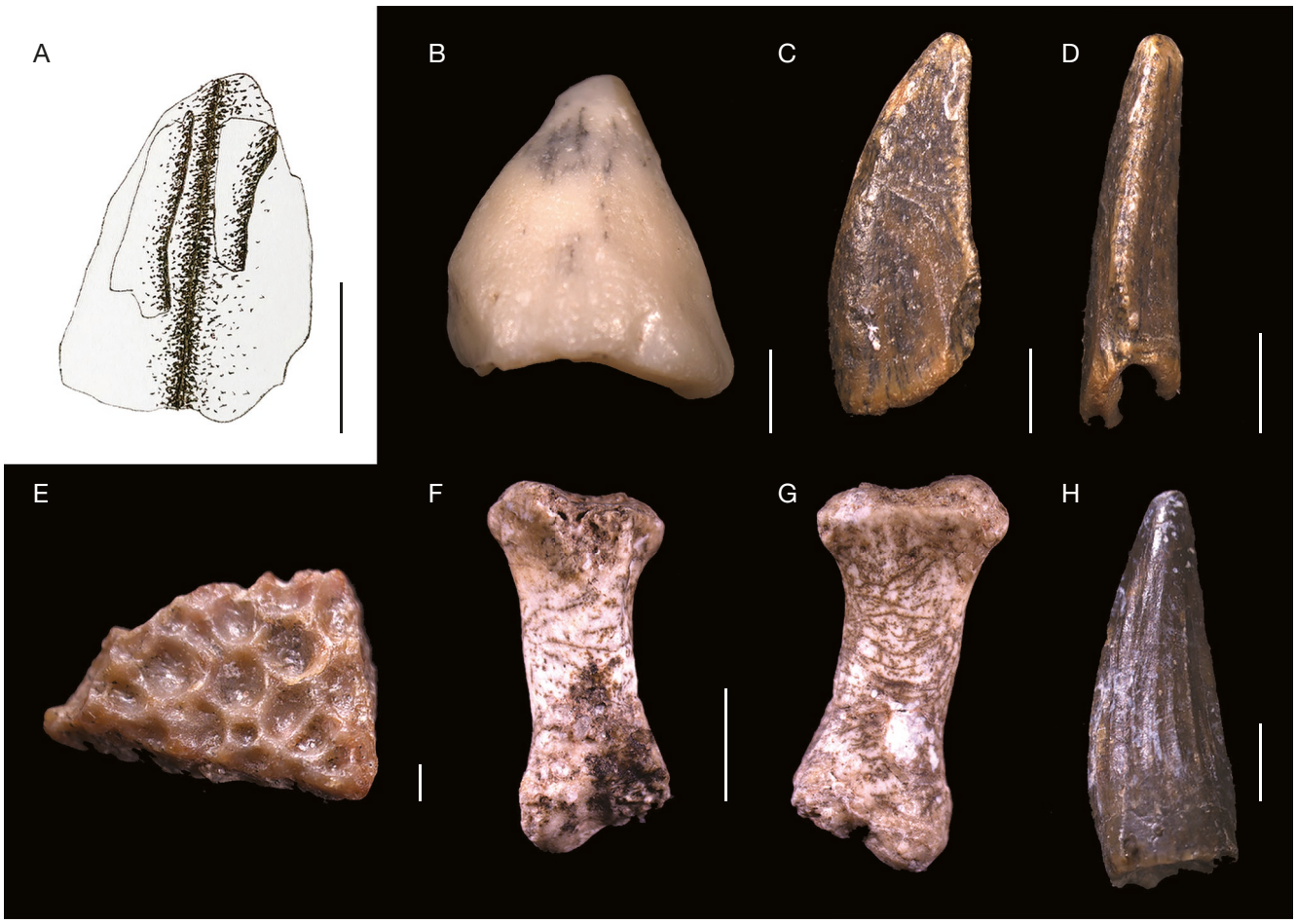

Fig. 12. — Crocodyliformes Hay, 1929: **A**, MNHN.F.GDF-M40, tooth morphotype I (mesial/distal view); **B**, MNHN.F.GDF-M41, tooth morphotype II (labial view); MNHN.F.GDF-M42, tooth morphotype III; **C**, labial/lingual view; **D**, mesial/distal view; **E**, MNHN.F.GDF-M59, osteoderm (dorsal/ventral view); **F**, **G**, MNHN.F.GDF-M72, Uruguaysuchidae Rusconi, 1933 metacarpus; **F**, anterior view; **G**, posterior view; **H**, MNHN.F.GDF-M24, *Stolokrosuchus lapparenti* Larsson & Gado, 2000 tooth (lingual view). Scale bars: 2 mm.

Subclass DIAPSIDA Osborn, 1903
Order CROCODYLIFORMES Hay, 1929
Crocodyliformes gen. et sp. indet.

Morphotype I

Material. — MNHN.F.GDF-M40, 21 teeth (Fig. 12A).

Description
Tooth crowns measure about 5 mm high. They are rather fragmented and subcircular in cross-section, with a basal diameter that varies from 2 to 4 mm. Mesial and distal carinae are clearly visible. When the enamel is preserved, it is unornamented. After comparison with many specimens from the MNHN collections (material not inventoried), they could belong to juvenile individuals of *Sarcosuchus imperator* de Broin & Taquet, 1966.

Morphotype II

Material. — MNHN.F.GDF-M41, 35 teeth (Fig. 12B).

Description
These teeth are 3 to 4 mm high and are triangular in labial and lingual views. They are flattened labio-lingually. Carinae, lacking ornamentation, are clearly discernible. The base of the crown tends to split in two. Apically, there is a pronounced lingual curvature.

Morphotype III

Material. — MNHN.F.GDF-M42, 22 teeth (Fig. 12C, D).

Description
These teeth are very elongated and rather slender. They measure between 5 and 7 mm in height and are highly compressed labio-lingually with unornamented carinae. They are lingually curved from base to apex.

Note
The identification of the last two morphotypes remains uncertain. They could represent two of the known Gadoufaoua crocodyliform taxa previously described but could also belong

to the same taxon (perhaps one of the two Uruguaysuchidae Rusconi, 1933; Sereno & Larsson 2009). They might also pertain to a small, yet unidentified taxon.

Crocodyliformes indet. (osteoderms)

MATERIAL. — MNHN.F.GDF-M15, 10 osteoderms (GADb); MNHN.F.GDF-M59, 26 osteoderms (Fig. 12E).

DESCRIPTION
These osteoderm fragments have an average surface area of 10 mm² (but vary in shape). They are thin and flat and are ornamented with subcircular depressions of a few square millimeters on the outer surface and are smooth on the inner surface. Depressions of the outer surface are delimited by high wrinkles.

Family ?†URUGUAYSUCHIDAE Rusconi, 1933

Uruguaysuchidae gen. et sp. indet.

MATERIAL. — MNHN.F.GDF-M72, 1 metacarpal (Fig. 12F, G).

DESCRIPTION
This straight, trapezoidal metacarpal is much longer than wide (6 mm by 2 mm). It is reminiscent of the two Uruguaysuchidae taxa present in Gadoufaoua (*Anatosuchus minor* Sereno, Sidor, Larsson & Gado, 2003 and *Araripesuchus wegeneri* Buffetaut, 1981), by its distal condyles marked by pits in dorsal extension (Sereno & Larsson 2009). The proximal end is flattened and expanded lateromedially.

Family †PEIROSAURIDAE Gasparini, 1982

†*Stolokrosuchus lapparenti* Larsson & Gado, 2000

MATERIAL. — MNHN.F.GDF-M24, 3 teeth (GADb); MNHN.F.GDF-M43, 46 teeth (Fig. 12H).

DESCRIPTION
These fragmented teeth measure between 8 and 10 mm in height. They are conical, massive and elongated. They have fine, clearly visible apicobasal striations, covering the entire surface of the crown and converging towards the apex in some specimens. There are no carinae or they are not clearly noticeable. After comparison with a specimen from the MNHN collections, (material not inventoried), the relatively small size of the teeth could indicate a juvenile individual.

Order †PTEROSAURIA Kaup, 1834
Clade†ORNITHOCHEIROIDEA Seeley, 1870
sensu Unwin, 2003

Family ?†ORNITHOCHEIRIDAE Seeley, 1870
Ornithocheiridae gen. et sp. indet.

Morphotype I

MATERIAL. — MNHN.F.GDF-M48, 13 teeth (Fig. 13A, B).

DESCRIPTION
The teeth are between 8 and 12 mm high. They are slender and lingually curved. The root is not preserved. There is a very strong labiolingual compression, which distinguishes them from the teeth of crocodiles. The state of conservation of the teeth does not permit determination of ornamentation, if present. The cross section is oval.

Morphotype II

MATERIAL. — MNHN.F.GDF-M49, 9 teeth (Fig. 13C, D).

DESCRIPTION
These thin teeth are not well preserved, most of the apical parts are missing. They have a height between 0.8 and 1.3 mm. There is also very strong labiolingual compression, but they are not curved and there is no ornamentation. The cross-section is ellipsoidal.

NOTE
These two morphotypes are characteristic of Ornithocheiroidea *sensu* Unwin, 2003 (Pentland *et al.* 2019). No evidence of such morphotypes has been observed in Lonchodectidae Hooley, 1914: *Lonchodectes compressirostris* Owen, 1851 has "spike-shaped teeth" but "with wide, subcircular bases" (Rodrigues & Kellner 2013). The teeth of *Lonchodectes giganteus* Bowerbank, 1846 "are conical and elongated" also with a subcircular base (Rodrigues & Kellner 2013). Rigal *et al.* (2018), describe "short, conical teeth" and "straight, conical crowns" that they attribute to *Lonchodraco* Rodrigues & Kellner, 2013, in contrast to teeth described here. Lonchodectidae is diagnosed as having "teeth with constricted bases" (Unwin 2003), which is not the case here. Although they could belong to Ornithocheiridae (Vullo & Néraudeau 2009; Martill *et al.* 2011; Martill *et al.* 2018), this attribution remains problematic, so they have been left in open nomenclature. Finally, these morphotypes could belong to the same taxon, but there is no evidence to support this hypothesis (Wellnhofer & Buffetaut 1999).

Clade SAURISCHIA Seeley, 1888
Suborder THEROPODA Marsh, 1881
Theropoda gen. et sp. indet.

Family ?†ABELISAURIDAE Bonaparte & Novas, 1985

MATERIAL. — MNHN.F.GDF-M30, 2 carinae (GADb) (Fig. 13E, F); MNHN.F.GDF-M37, 2 teeth.

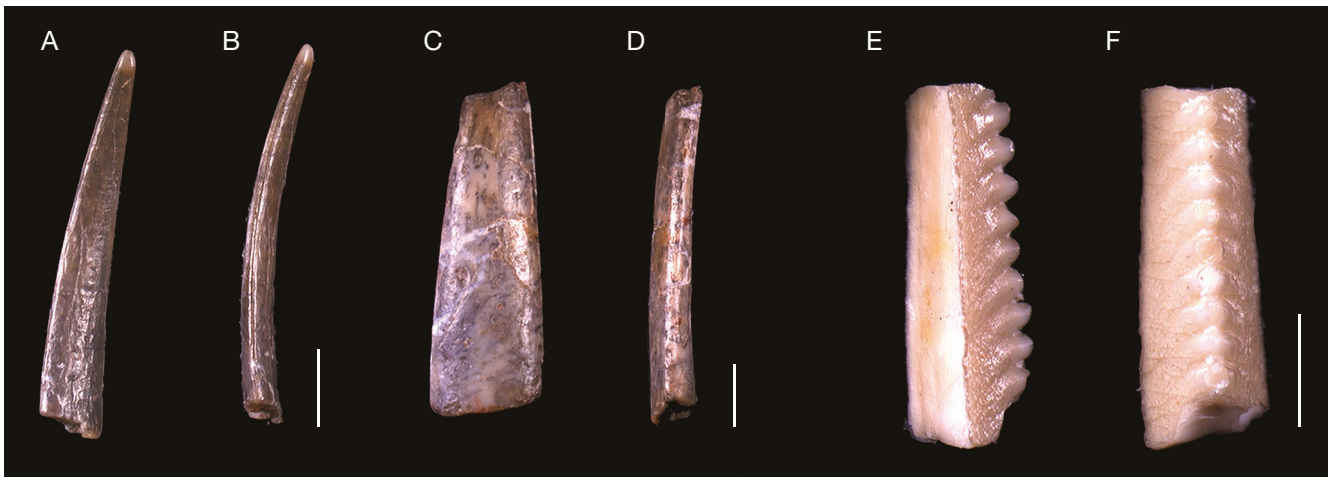

Fig. 13. — ?Ornithocheiridae Seeley, 1870 teeth: **A**, **B**, MNHN.F.GDF-M48, morphotype I: **A**, lingual view; **B**, mesial/distal view; **C**, **D**, MNHN.F.GDF-M49, morphotype II: **C**, lingual view; **D**, mesial/distal view; **E**, **F**, MNHN.F.GDF-M30, theropod carina: **E**, lingual/labial view; **F**, mesial/distal view. Scale bars: A-D, 3 mm; E, F, 1 mm.

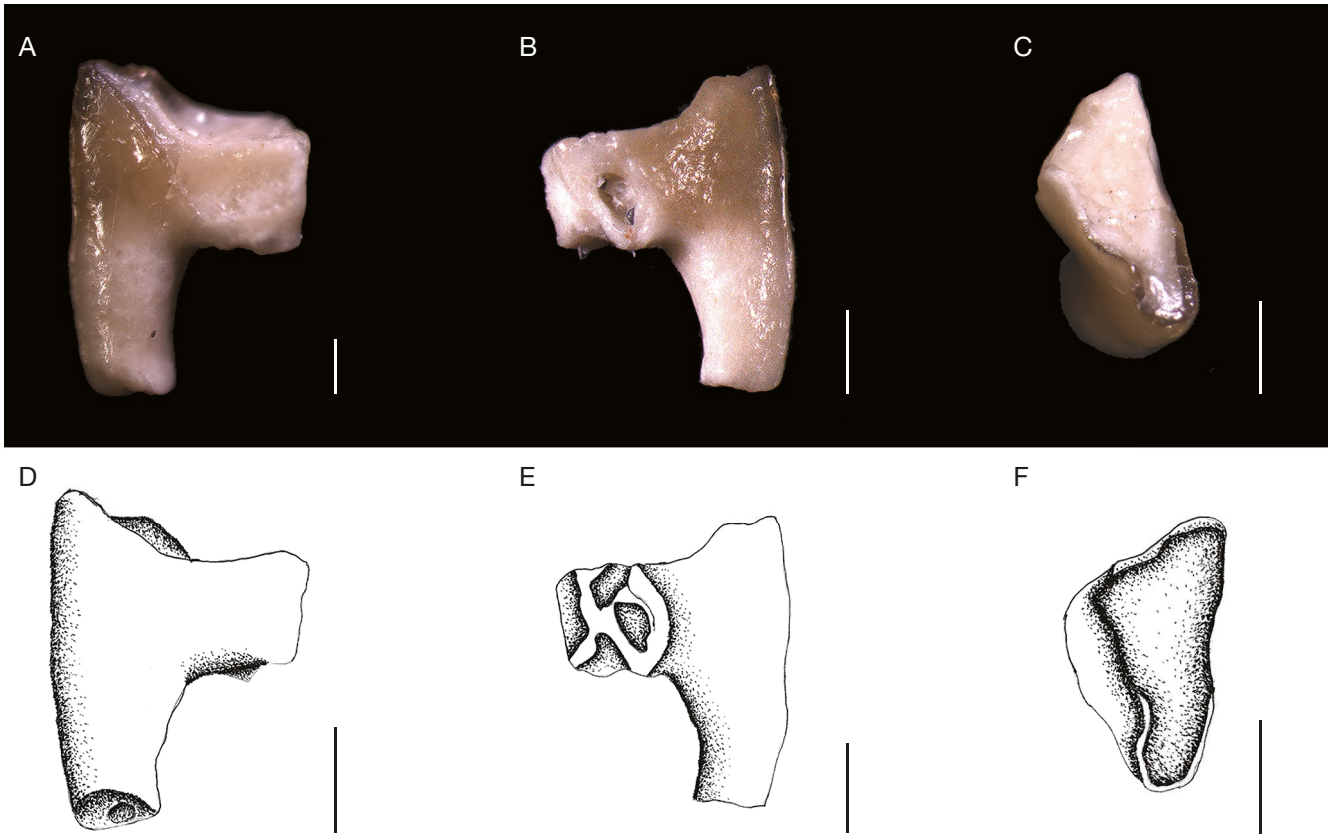

Fig. 14. — MNHN.F.GDF-M96, Stem-Boreosphenida Luo, Cifelli & Kielan-Jaworowska, 2001 tooth: **A**, **B**, **D**, **E**, mesial/distal view; **C**, **F**, occlusal view. Scale bars: A, 0.3 mm; B, C, 0.5 mm; D-F, 1 mm.

Description

No complete teeth are known. Fragmentary carinae are about 3 mm long. The numerous denticles characteristic of the teeth of theropods are clearly visible. There are three denticles per mm.

Other fragments represent only the basal part of the crown. These are highly compressed labiolingually and therefore have an oval cross-section. The carinae are poorly marked but extend along the entire length of both sides of the base. The denticles are poorly preserved and number 4 per mm.

For all specimens, the denticles are weakly apically hooked.

For both the teeth and the carinae, the shape of the denticles and their number are typical of theropod teeth and could be assignable to Abelisauridae (Sereno & Brusatte 2008; Hendrickx *et al.* 2015).

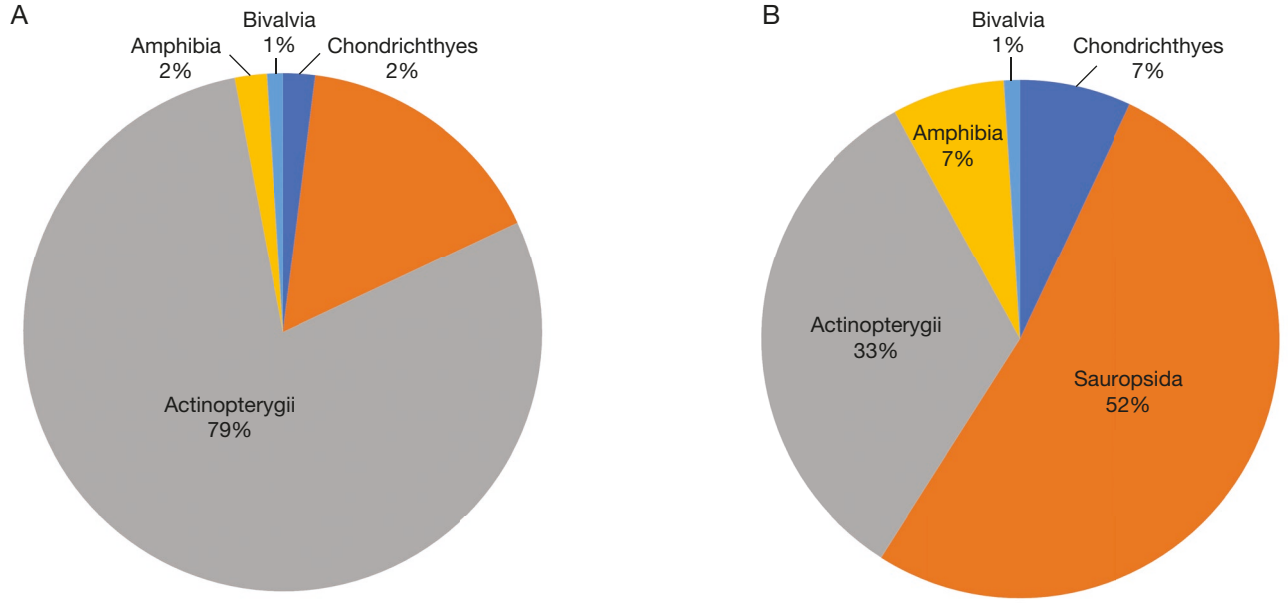

Fig. 15. — Relative abundance of classes in Gadoufaoua: **A**, all the remains; **B**, removing the teeth and scales of actinopterygians.

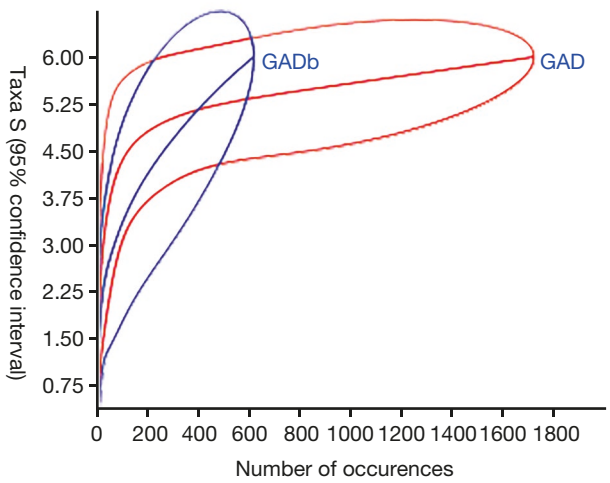

Fig. 16. — Rarefaction curves for Gadoufaoua and the GADb level.

Class MAMMALIA Linnaeus, 1758
Order THERIIFORMES McKenna & Bell, 1997
Clade HOLOTHERIA Wible *et al.*, 1995
Clade CLADOTHERIA McKenna, 1975
Clade ZATHERIA McKenna, 1975
Infraclass ?STEM-BOREOSPHENIDA Luo, Cifelli & Kielan-Jaworowska, 2001

?Stem-Boreosphenida gen. et sp. indet.

Material. — MNHN.F.GDF-M96, 1 upper left molar (Fig. 14).

Description

This tooth is very fragmented and poorly preserved. A small part of the crown can be seen together with one root. The molar is 1.5 mm long, 0.25 mm wide and 2 mm high. Only the protocone, very pinched, is visible, but based on the shape of the crown in occlusal view, it can be assumed that it would be a tribosphenic molar. The trigon basin is well marked. This tooth is highly compressed mesio-distally (clearly visible at the level of the protocone). The crown is higher on the labial side than on the lingual side. All these characteristics combined (especially the pinched protocone) suggest that this tooth belongs to the stem-Boreosphenida (Kielan-Jaworowska *et al.* 2004) but it has been left in open nomenclature in view of its fragmentary state of preservation.

RESULTS

Taxonomic list

New taxa are described for the first time in Gadoufaoua: *Tribodus*, Ornithocheiridae, Amiiformes, Anura and a stem-boreosphenidan. With regard to *Tribodus*, during the Aptian in Africa, this genus was previously known only in Tunisia (Cuny *et al.* 2004). The boreosphenidan represents the only Aptian African occurrence of this taxon but boreosphenidans have an older record occurring in the Late Jurassic of Morocco (Haddoumi *et al.* 2016; Lasseron 2019; Lasseron *et al.* 2020). An updated taxonomic list is available in Appendix 2, including these new taxa together with those identified in previous studies (de Broin & Taquet 1966; Taquet 1976; de Broin 1980; Sereno *et al.* 1998, 2001, 2003, 2007; Wenz 1999; Taquet & Russell 1999; Larsson & Gado 2000; Sereno & Wilson 2005; Brusatte & Sereno 2007; Sereno & Brusatte 2008; Sereno & Larsson 2009; Sereno & ElShafie 2013; Sereno 2017; Pérez-García 2019a, b).

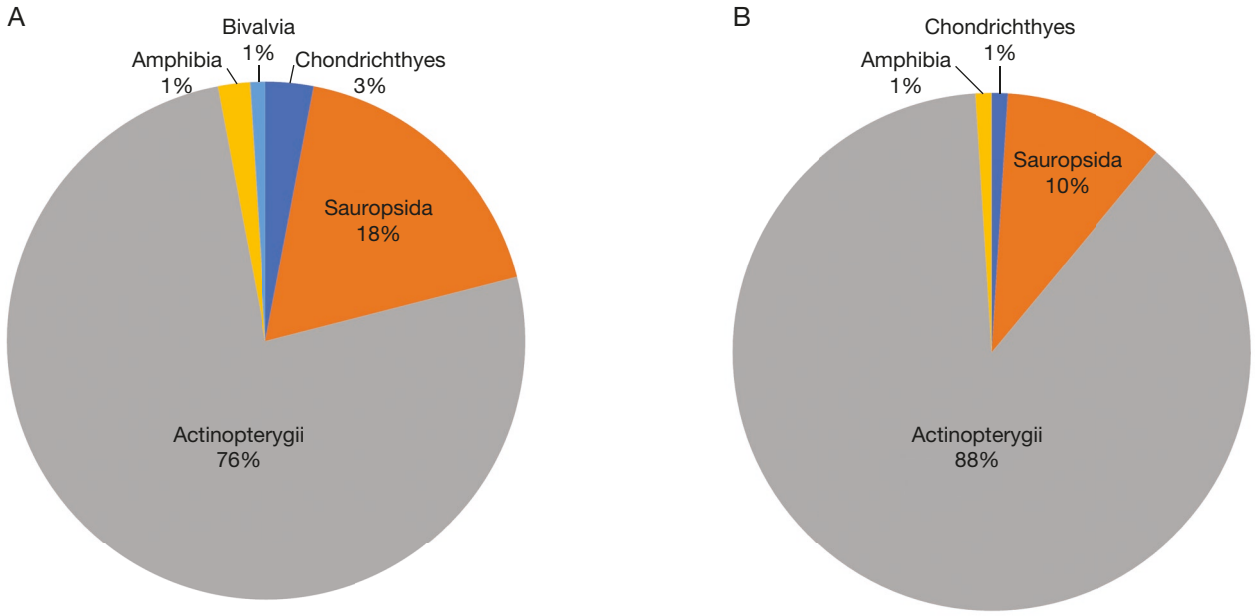

Fig. 17. — Relatives abundance of classes in: **A**, all the sedimentary material except GADb; **B**, GADb.

Diversity

The relative abundance of taxa (Fig. 15A) was determined using MNE (Minimal Number of Elements). The number of individuals cannot be estimated due to limited and biased representation of paired elements (e.g. limbs).

Initially, the Gadoufaoua microfauna appears to be dominated by actinopterygians (79%). One might think that there is an over-representation of the latter because of the large number of teeth and scales found (22% and 21% of the sample respectively). A second analysis was therefore carried out excluding them (Fig. 15B) in order to reduce the over-representation bias as much as possible. Only teeth and vertebrae are counted in the second analysis. Here, actinopterygians represent only 33% of the fauna, which is now dominated by sauropsids. These analyses are made without considering unidentified material which represents 36% of the assemblage (percentages are therefore recalculated). Unidentified material consists of 972 fragments of skeletal elements and 25 osteoderms (belonging to two different morphotypes). Other diversity graphs are provided in Appendices 3; 4.

DISCUSSION

Comparison of the GAD and GADb sites

As mentioned above (paragraph Separation of sites), some lighter-colored material containing better-preserved specimens was found in the original collection. It was not known whether or not this came from the same horizon as the other bulk samples.

As illustrated in Figure 16, the GADb level rarefaction curve does not show a plateau. The sampling effort is therefore insufficient to perform α (within a sample) and β (between samples) diversity analyses, which would have been useful to interpret the diversity (Sankey & Baszio 2006).

However, the relative abundance of taxa from the two sites of collection can be compared and appear to be approximately identical (Fig. 17), except for the teeth of ichthyodectiforms and pterosaurs which have not been found at GADb. A Wilcoxon test was performed for matched samples with the following assumptions: H0, the two levels can be considered identical; H1, the two levels cannot be considered identical. The p-value is 0.059, so at a 95% confidence interval, H0 cannot be rejected. In other words, the palaeontological content of the two sites is similar, and the material from GADb has been integrated with the rest of the material.

Although it is acknowledged that more data could be gathered by studying the rest of the sediments and agreed that an extensive study of the 6 tons of sediments would be ideal, several issues prevent it. First, the rarefaction curve in Figure 16 shows a plateau for the "GAD" sediments (which can now be associated with GADb) meaning that the locality was sampled sufficiently to account for the paleodiversity of the ecosystem, so more extensive studies would bring much less data and few new occurrences (if any). Second, because the preparation and sorting of sediment is very time-consuming, only one sample of the material was processed and studied. Third, the collection was interesting because it was associated with the GADb sample, which in view of its sedimentological and preservational differences to the bulk of the collection, warranted further study. Finally, although the remaining 5900 kg are accessible, unfortunately they are not as well preserved or conserved throughout the years, especially from humidity, which may have resulted in a loss of identifiable fossils affecting perceived abundance and diversity.

Depositional environment

The microvertebrates found at Gadoufaoua are mainly aquatic and some exclusively fresh water (exclusively terrestrial taxa

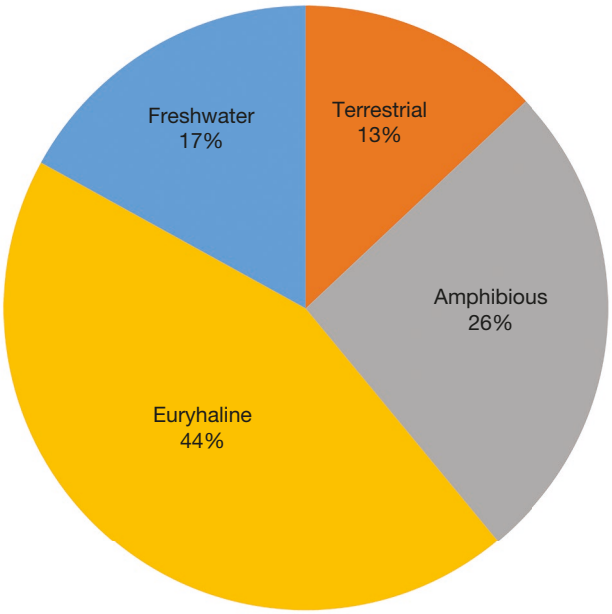

FIG. 18. — Relative abundance of taxa following their living environments in Gadoufaoua (based on identified taxa).

TABLE 1. — Worldwide distribution of some relevant taxa from Gadoufaoua, during the Early Cretaceous: **0**, absent; **1**, present.

Taxa	Africa	America	Europe	Asia	Oceania
Tribodus	1	1	1	0	0
Amiiformes	1	1	1	1	0
Mawsonia	1	1	0	0	0
Ptychoceratodus	1	1	0	0	0
Sarcosuchus	1	1	0	0	0
Araripesuchus	1	1	0	0	0
Carcharodontosaurus	1	1	0	0	0
Stem-Boreosphenida	1	1	1	0	0

represent 13% of the microfauna; Fig. 18). Considering only the macrofauna provides a somewhat different interpretation of the palaeoenvironment and sedimentological context. Whereas it suggests a typical floodplain environment (Taquet 1976), in the microfauna a high fragmentation of the fossils was observed, without predation marks, indicating a higher hydrodynamism than suggested by the macrofauna. This would be more in line with channel-type depositional environment (Silcox & Rose 2001). Given the large scale of the Gadoufaoua deposit, it is not surprising to observe several different deposition environments within it. It seems likely, therefore, that the microvertebrate remains studied here are derived from horizons different to those yielding macroremains.

COMPARISON WITH THE FAUNA OF SANTANA (BRAZIL)

Among vertebrate faunas of similar age to that of Gadoufaoua, the Santana Group, in the Araripe basin of Brazil, is particularly well-known. Although no studies focusing on microremains have been carried out at this time, it can be noted that many of the taxa described at this locality are also present at Gadoufaoua, in both the microfauna and the macrofauna. This is notable in the case of hybodontiforms (*Tribodus*; Brito & Ferreira 1989), semionotiforms (Brito & Gallo 2003), pycnodontiforms (Poyato-Ariza & Wenz 2002), ichthyodectiforms (Maisey 1991), amiiforms (Grande & Bemis 1998), actinistians (*Mawsonia* Mawson & Woodward, 1907; Maisey 1991), turtles (Pelomedusidae; Price 1973), crocodilians (*Araripesuchus* Price, 1959; Price 1959, *Sarcosuchus* de Broin & Taquet, 1966; Souza *et al.* 2019), pterosaurs (Ornithocheiridae; Frey *et al.* 2003), saurischians (Martill *et al.* 1996), and anurans (Leal & Brito 2006). Nevertheless, the faunal assemblage of the Santana Formation contains a greater diversity of actinopterygians, due to the marine influences that are clearly established (Veiga *et al.* 2019). However, actinopterygian diversity at Gadoufaoua is probably underestimated because they are represented only by isolated elements that are difficult to assign with precision.

The two faunas are linked, but they are not identical representing different palaeoenvironmental influences. The Santana Formation was deposited in a lagoonal environment with stenohaline taxa (*Araripichthys* Silva Santos, 1985, *Tharrias* Jordan & Branner, 1908, *Axelrodichthys* Maisey, 1986; Maisey 1991) while Gadoufaoua sometimes represents a much quieter continental environment, where the preservation of typically terrestrial taxa is possible (dinosaurs, mammals, etc.) but where a strong aquatic influence is still felt.

PALAEOBIOGEOGRAPHIC IMPLICATIONS

The similarity between the fauna of the Santana Formation and that of Gadoufaoua (although based on preliminary data) is consistent with palaeogeography. At this time (Aptian-Albian), Gondwana had already broken-up and the South Atlantic Ocean was opening. South America and Africa were separated but this separation was quite recent having taken place during the Barremian to Middle Albian (Pletsch *et al.* 2001).

Thus, some taxa present in Gadoufaoua show affinities with South America. Examples are *Sarcosuchus* (Buffetaut & Taquet 1977) and *Araripesuchus* (Ortega *et al.* 2000). *Tribodus* is observed in Africa during the Aptian-Albian (Cuny *et al.* 2004) while its presence has been confirmed in Europe in the Cenomanian (Vullo 2007) and in Brazil in the Albian (Brito 1992). The presence of the genus *Tribodus* in Gadoufaoua therefore suggests, like *Sarcosuchus* and *Araripesuchus*, that there are still very close links between the continental faunas of South America and Africa and shows that the fauna of Gadoufaoua dates to the opening of the South Atlantic.

Finally, the Gadoufaoua deposits have yielded the only known stem-boreosphenidan tooth from the Early Cretaceous of Africa (the only mammal-linked fossils previously known from the Aptian-Albian were ichnofossils; Mateus *et al.* 2017). The presence of this stem-boreosphenidan at Gadoufaoua is congruent with the occurrence of this taxon in Ksar Metlili around the Jurassic-Cretaceous transition (Morocco; *Hypomylos* Sigogneau-Russell, 1992 and *Tribotherium* Sigogneau-Russell, 1991, Sigogneau-Russell *et al.* 1988; Lasseron 2019; Lasseron *et al.* 2020) and demonstrated extension of its geographical distribution at a time when it is only otherwise observed in North America (Kielan-Jaworowska & Cifelli 2001).

The taxonomic distribution of these taxa and others from Gadoufaoua is also shown in Table 1.

CONCLUSION

The study of the microvertebrate fauna from Gadoufaoua has resulted in the identification of new taxa previously not reported from the region (see Appendix 2). Among these new forms, the presence of a tribosphenic mammalian molar is noteworthy as the first occurrence of a stem-boreosphenidan in Africa in the Early Cretaceous. This demonstrates a more global distribution of this taxon than previously thought at this time. The presence of the genus *Tribodus* in Gadoufaoua also suggests, like *Sarcosuchus* and *Araripesuchus* that there were still very close links between the continental faunas of South America and Africa and would indicate that the fauna of Gadoufaoua dates back to the opening of the South Atlantic.

The presence of numerous amphibious or euryhaline taxa together with those of terrestrial affinity supports a channel-type environment with strong hydrodynamism, as evidenced by the many unidentifiable fragments recovered, which were not produced as the result of predation. This is at odds with conclusions drawn from a study of the macrofauna (Taquet 1976) but can be explained by the large size of the deposit and differences in environments of deposition within it.

Study of the Gadoufaoua microvertebrate fauna has permitted an important revision of the faunal list to include new taxa. It has also highlighted the need to reconsider some of the macro material. It appears that some taxa have been identified without full consideration. For example, *Platycheloides* Haughton, 1928 (de Broin 1980) has recently been revised to *Francemys gadoufaouaensis* (Pérez-García 2019b) and the debate remains open on the taxonomic placement of Spinosauridae Stromer, 1915 (Taquet & Russell 1999; Sereno *et al.* 1998; Sues *et al.* 2002; Allain 2002; Carrano *et al.* 2012) and Araripemydidae (de Broin 1980; Sereno & ElShafie 2013; Pérez-García 2019a; Ibrahim *et al.* 2020).

The study of microremains deposits associated with macroremains needs to be further developed. Data obtained from them are complementary to a "classical" macroscopic palaeontological study and provides insights concerning community structure, palaeoenvironment, palaeogeography, etc., that cannot be obtained from study of the macrofauna in isolation.

A similar study with the same protocol involving the Santana Formation of Brazil would permit collection of data allowing for a more robust comparison on the microfauna. This could also be extended to other known deposits of Late Jurassic and Early Cretaceous age, such as those of the Douiret Formation (Tunisia, Aptian-Albian; Cuny *et al.* 2010a; Fanti *et al.* 2012), Red Sandstone Group (Tanzania, Cretaceous; Roberts *et al.* 2004; O'Connor *et al.* 2006), Cabao Formation (Libya, Lower Cretaceous; Le Loeuff *et al.* 2010); Angeac-Charente (France, Berriasian-early Valanginian; Allain *et al.* 2022), Ksar Metlili (Morocco, Tithonian-Berriasian; Lasseron *et al.* 2020) and Kut Island (Thailand; Cuny *et al.* 2010b) dated at the Jurassic-Cretaceous boundary (Tithonian-Berriasian).

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APPENDICES

Appendix 1. — Catalogue of all specimens studied.

ID	Description	Origin	Remarks
MNHN.F.GDF-M01	Bone fragments indet.	GADb	–
MNHN.F.GDF-M02	Metapode indet.	GADb	Fragment
MNHN.F.GDF-M03	Actinopterygian scales	GADb	–
MNHN.F.GDF-M04	Amiiformes teeth	GADb	–
MNHN.F.GDF-M05	Vertebrae indet.	GADb	Fragments
MNHN.F.GDF-M06	Vertebrae teleosteens	GADb	–
MNHN.F.GDF-M07	Ginglymodi teeth	GADb	–
MNHN.F.GDF-M08	Peipheral Teneremys lapparenti	GADb	–
MNHN.F.GDF-M09	Plates Teneremys lapparenti	GADb	–
MNHN.F.GDF-M10	Phalanges indet.	GADb	Fragment
MNHN.F.GDF-M11	Osteoderms indet. Morphotype I	GADb	–
MNHN.F.GDF-M12	Osteoderms indet. Morphotype II	GADb	–
MNHN.F.GDF-M13	Pycnodontiformes teeth	GADb	1 incisiform, 2 vomerine
MNHN.F.GDF-M14	Plates Ararypemyidae	GADb	–
MNHN.F.GDF-M15	Crocodyliformes osteoderms	GADb	–
MNHN.F.GDF-M16	Branchial arc osteichthyan	GADb	Broken in two
MNHN.F.GDF-M17	Teeth indet.	GADb	Fragments
MNHN.F.GDF-M18	Left dental plate ?Ptychoceratodus	GADb	–
MNHN.F.GDF-M19	Pycnodontiformes prearticular/vomer	GADb	–
MNHN.F.GDF-M20	Lissamphibia vertebra	GADb	–
MNHN.F.GDF-M21	Long bones indet.	GADb	Fragments
MNHN.F.GDF-M22	Lissamphibia tooth	GADb	–
MNHN.F.GDF-M23	Hybodontidae teeth	GADb	–
MNHN.F.GDF-M24	Stolokrosuchus lapparenti teeth	GADb	–
MNHN.F.GDF-M25	Actinopterygian lepidotrich ray	GADb	–
MNHN.F.GDF-M26	Proximal humerus indet.	GADb	–
MNHN.F.GDF-M27	Zeugopoda Anura	GADb	–
MNHN.F.GDF-M28	Crocodyliformes teeth indet.	GADb	–
MNHN.F.GDF-M29	Premaxillary Amiiformes	GADb	In connexion
MNHN.F.GDF-M30	Theropoda carinae	GADb	–
MNHN.F.GDF-M31	Osteichthyes dentaries	GADb	–
MNHN.F.GDF-M32	Dentary indet.	GADb	–
MNHN.F.GDF-M33	Bone fragments indet.	–	–
MNHN.F.GDF-M34	Osteichthyes premaxillaries	–	–
MNHN.F.GDF-M35	Actinopterygians scales	–	–
MNHN.F.GDF-M36	Ginglymodi teeth	–	–
MNHN.F.GDF-M37	Theropoda teeth	–	–
MNHN.F.GDF-M38	Ararypemyidae plates	–	–
MNHN.F.GDF-M39	? Tribodus teeth	–	–
MNHN.F.GDF-M40	Crocodyliformes teeth morphotype I	–	–
MNHN.F.GDF-M41	Crocodyliformes teeth morphotype II	–	–
MNHN.F.GDF-M42	Crocodyliformes teeth morphotype III	–	–
MNHN.F.GDF-M43	Stolokrosuchus lapparenti teeth	–	–
MNHN.F.GDF-M44	Osteoderms indet. Morphotype I	–	–
MNHN.F.GDF-M45	Osteoderms indet. Morphotype II	–	–
MNHN.F.GDF-M46	Testudines indet. Plates	–	–
MNHN.F.GDF-M47	Coproliths	–	–
MNHN.F.GDF-M48	Ornitocheiridae teeth morphotype I	–	–
MNHN.F.GDF-M49	Ornitocheiridae teeth morphotype II	–	–
MNHN.F.GDF-M50	Ararypemyidae plates	–	–
MNHN.F.GDF-M51	Long bones indet.	–	Fragments
MNHN.F.GDF-M52	Teeth fragments Ornithocheiridae	–	–
MNHN.F.GDF-M53	Ichthyodectiformes teeth	–	–
MNHN.F.GDF-M54	Teneremys lapparenti plates	–	–
MNHN.F.GDF-M55	Teeth fragments indet.	–	–
MNHN.F.GDF-M56	Vertebrae fragments indet.	–	–
MNHN.F.GDF-M57	Phalanges indet.	–	–
MNHN.F.GDF-M58	Vertebrae osteichthyans	–	–
MNHN.F.GDF-M59	Crocodyliformes osteoderms	–	–
MNHN.F.GDF-M60	Anura scapula	–	–
MNHN.F.GDF-M61	Anura ilia	–	–
MNHN.F.GDF-M62	Actinopterygians lepidotrich rays	–	–
MNHN.F.GDF-M63	Teleostei vertebrae	–	–
MNHN.F.GDF-M64	Distal femur indet.	–	–
MNHN.F.GDF-M65	Amiiformes teeth	–	–
MNHN.F.GDF-M66	Proximal femurs indet.	–	–

Appendix 1. — Continuation.

ID	Description	Origin	Remarks
MNHN.F.GDF-M67	Dentary indet.	–	–
MNHN.F.GDF-M68	Pinctada shells	–	–
MNHN.F.GDF-M69	Hybodontidae teeth	–	–
MNHN.F.GDF-M70	Metapod indet.	–	–
MNHN.F.GDF-M71	Anura radio-ulna	–	–
MNHN.F.GDF-M72	Uruguaysuchidae metacarpal	–	–
MNHN.F.GDF-M73	Hybodontidae teeth	–	–
MNHN.F.GDF-M74	Lissamphibia tooth	–	–
MNHN.F.GDF-M75	Anura urostyles	–	–
MNHN.F.GDF-M76	Frontal Lissamphibia	–	–
MNHN.F.GDF-M77	Batrachians long bones	–	–
MNHN.F.GDF-M78	Ceratodontidae tooth	–	Fragment
MNHN.F.GDF-M79	Proximal tibia indet.	–	–
MNHN.F.GDF-M80	Proximal humerus indet.	–	–
MNHN.F.GDF-M81	Anura zeugopods	–	–
MNHN.F.GDF-M82	Pycnodontiformes vomers	–	–
MNHN.F.GDF-M83	Hybodontidae teeth	–	–
MNHN.F.GDF-M84	Teneremys lapparenti pleurals	–	–
MNHN.F.GDF-M85	Pycnodontiformes incisiform teeth	–	–
MNHN.F.GDF-M86	Vertebrae Mesoeucrocodylia	–	–
MNHN.F.GDF-M87	Diapsida humerus indet.	–	–
MNHN.F.GDF-M88	Vertebrae Lissamphibia	–	–
MNHN.F.GDF-M89	Proximal ulnae indet.	–	–
MNHN.F.GDF-M90	Ilia indet.	–	–
MNHN.F.GDF-M91	Proximal radii indet.	–	–
MNHN.F.GDF-M92	Vertebrae indet.	–	–
MNHN.F.GDF-M93	Proximal humeri indet.	–	–
MNHN.F.GDF-M94	Actinopterygians skull fragments	–	–
MNHN.F.GDF-M95	Osteichthyes skull fragments	–	–
MNHN.F.GDF-M96	Boreosphenida tooth	GAD bis	–
MNHN.F.GDF-M97	Actinopterygians scales	GAD bis	–

Appendix 2. — Updated taxonomic list of Gadoufaoua. The following is the updated taxonomic list of Gadoufaoua (**in bold**, previously unidentified taxa observed in the study; de Broin & Taquet 1966; Taquet 1976; de Broin 1980; Taquet & Russell 1999; Wenz 1999; Larsson & Gado 2000; Sereno *et al.* 1998, 2001, 2003, 2007; Sereno & Wilson 2005; Brusatte & Sereno 2007; Sereno & Brusatte 2008; Sereno & Larsson 2009; Sereno & ElShafie 2013; Sereno 2017; Pérez-Garcia 2019a, b). The hierarchy, names and dates are based on informations from FossilWorks (fossilworks.org).

Bivalvia Linnaeus, 1758
Pteriomorphia Beurlen, 1944
Pteroidea Newell, 1965
Pteriidae Gray, 1847
Pinctada Röding, 1798
Pinctada indet.

Vertebrata Lamarck, 1801
Chondrichthyes Huxley, 1880
Elasmobranchii Bonaparte, 1838
†Hybodontiformes Owen, 1846
†Hybodontidae Agassiz, 1843 indet.
†Distobatidae Werner, 1989
†*Tribodus* Brito & Ferreira, 1989
†*Tribodus* Brito & Ferreira, 1989 indet.

Osteichthyes Huxley, 1880
Actinopterygii Cope, 1887
Neopterygii Regan, 1923
Ginglymodi Cope, 1871
†Pycnodontiformes Berg, 1937
†Pycnodontiformes indet.
Amiiformes Hay, 1929
Ichthyodectiformes Bardack & Sprinkle, 1969
Ichthyodectiformes indet.

Sarcopterygii Romer, 1955
Actinistia Cope, 1870
Coelacanthiformes Berg, 1937
†Mawsoniidae Schultze, 1993
†*Mawsonia* Mawson & Woodward, 1907
†*Mawsonia* Mawson & Woodward, 1907 indet.

Dipnoi Müller, 1844
Ceratodontiformes Berg, 1940
Ptychoceratodontidae Martin, 1982
†*Ptychoceratodus* Jaekel, 1926

Tetrapoda Goodrich, 1930
Amphibia Linnaeus, 1758
Lissamphibia Haeckel, 1866
Anura Von Waldheim, 1813
Anura indet.

Sauropsida Huxley, 1864
Testudines Batsch, 1788
Pelomedusoides Cope, 1868
†*Francemys* Pérez-Garcia, 2019
†*F. gadoufaouaensis* Pérez-Garcia, 2019
†*Teneremys* Broin, 1980
†*T. lapparenti* Broin 1980
Araripemyidae Price, 1973
†*Taquetochelys* Broin, 1980
†*T. decorata* Broin, 1980
†*Laganemys* Sereno & ElShafie, 2013
†*L. tenerensis* Sereno & ElShafie, 2013

Diapsida Osborn, 1903
Archosauria Cope, 1868
Crocodyliformes Hay, 1929
†Pholidosauridae Eastman, 1902
†*Sarcosuchus* Broin & Taquet, 1966
†*S. imperator* Broin & Taquet, 1966
†Uruguaysuchidae Rusconi, 1933
†*Anatosuchus* Sereno, 2003
†*A. minor* Sereno, 2003
†*Araripesuchus* Price, 1959
†*A. wegeneri* Buffetaut, 1981
†Peirosauridae Gasparini, 1982
†*Stolokrosuchus* Larsson & Gado, 2000
†*S. lapparenti* Larsson & Gado, 2000

†Pterosauria Kaup, 1834
†Ornithocheiridae Seeley, 1870
†Ornithocheiridae indet.

Dinosauria Owen, 1842
Saurischia Seeley, 1888
Sauropoda Marsh, 1878
†Rebbachisauridae Bonaparte, 1997
†*Nigersaurus* Sereno, 1999
†*N. taqueti* Sereno, 1999

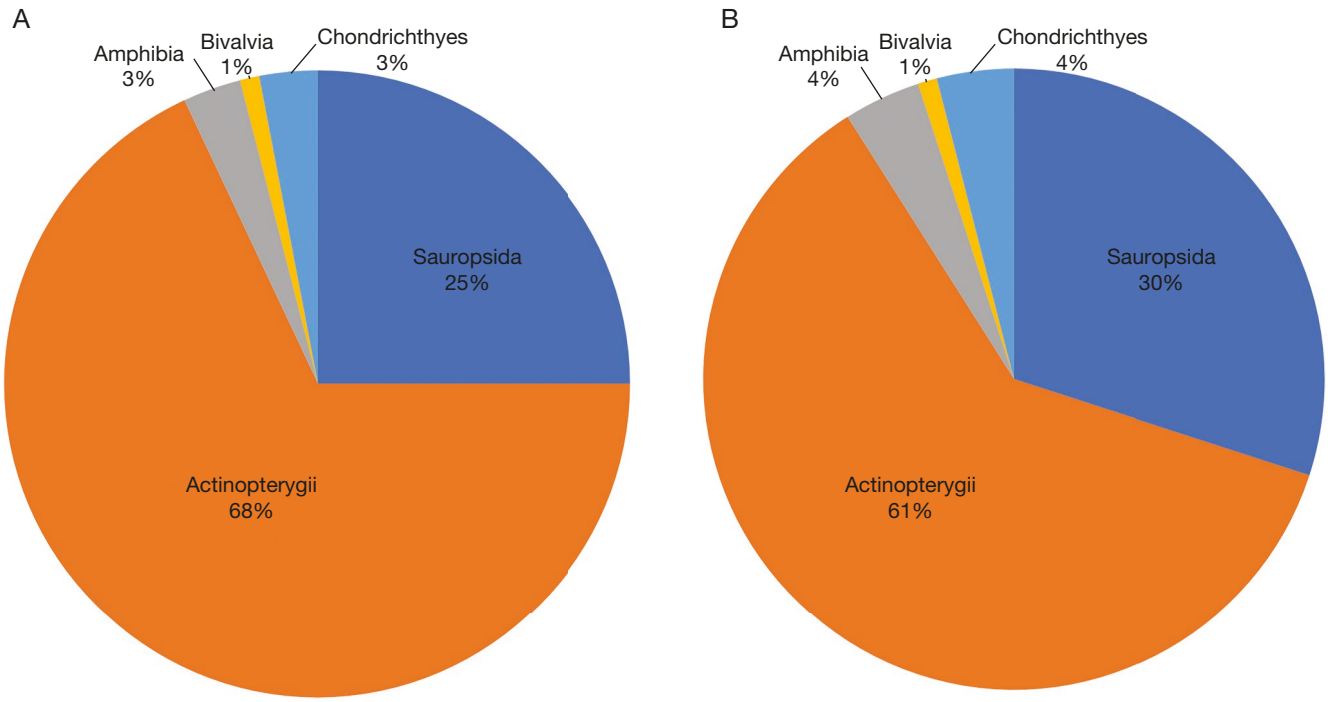
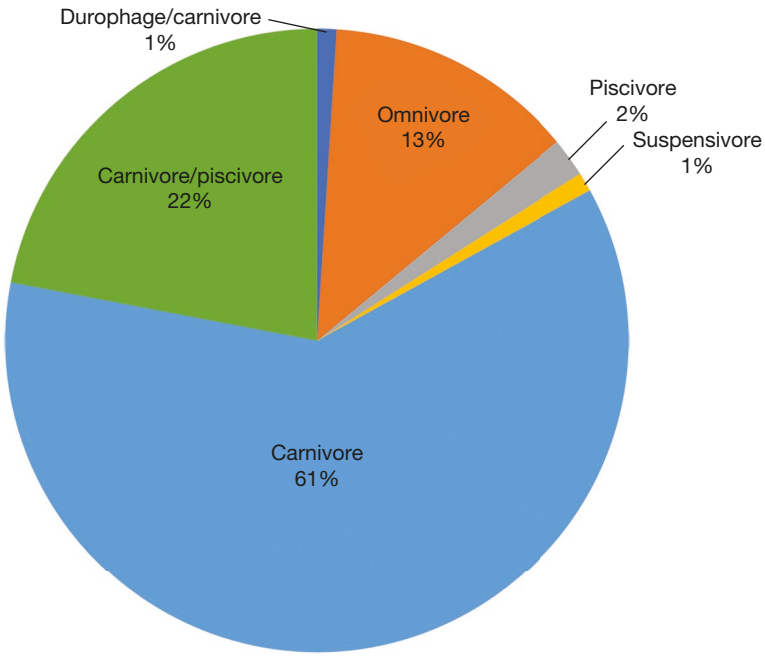
Theropoda Marsh, 1881
†Spinosauridae Stromer, 1915
†*Cristatusaurus* Taquet & Russell, 1998
†*C. lapparenti* Taquet & Russell, 1998
†*Suchomimus* Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sidor, Varricchio, Wilson & Wilson, 1998
†*S. tenerensis* Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sidor, Varricchio, Wilson & Wilson, 1998
†Abelisauridae Bonaparte & Novas, 1985
†*Kryptops* Sereno & Brusatte, 2008
†*K. palaios* Sereno & Brusatte, 2008
†Noasauridae Bonaparte & Powell, 1980
†*Afromimus* Sereno, 2017
†*A. tenerensis* Sereno, 2017
†Carcharodontosauridae Stromer, 1931
†*Carcharodontosaurus* Stromer, 1931
†*C. saharicus* Depéret & Savornin, 1925

†*C. iguidensis* Brusatte & Sereno, 2007
†*Eocarcharia* Sereno & Brusatte, 2008
†*E. dinops* Sereno & Brusatte, 2008

†Ornithischia Seeley, 1888
†Dryosauridae Stefano, 1903
†*Elrhazosaurus* Galton, 2009
†*E. nigeriensis* Galton & Taquet, 1982
† Iguanodontidae Bonaparte, 1850
†*Ouranosaurus* Taquet, 1976
†*O. nigeriensis* Taquet, 1976
†*Lurdusaurus* Taquet & Russell, 1999
†*L. arenatus* Taquet & Russell, 1999

Mammalia Linnaeus, 1758
Theriiformes McKenna & Bell, 1997
Holotheria Wible, Rougier, Novacek, McKenna & Dashzeveg, 1995
Cladotheria McKenna, 1975
Zatheria McKenna, 1975
?Stem-Boreosphenida Luo, Cifelli & Kielan-Jaworowska, 2001

Appendix 3. — Relative abundance of the Gadoufaoua taxa: **A**, excluding only actinopterygian scales; **B**, excluding only actinopterygian teeth; mammalian taxon represented only by a tooth.



Appendix 4. — Distribution of diets among the Gadoufaoua fauna (data from Fossil Works, insectivore diet is observed once).