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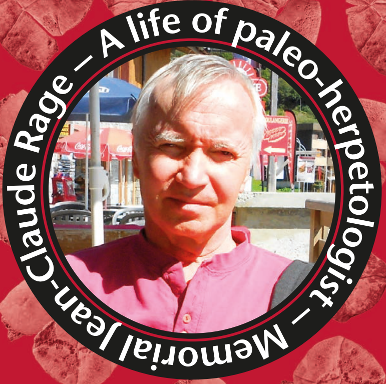

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Laurent CHIRIO &
Roger BOUR†

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The oldest erymnochelyine turtle skull, *Ragechelus sahelica* n. gen., n. sp., from the Iullemmeden basin, Upper Cretaceous of Africa, and the associated fauna in its geographical and geological context

France de LAPPARENT de BROIN
Centre de Recherches sur la Paléobiodiversité et les Paléoenvironnements,
CR2P (CNRS, MNHN, UPMC, Sorbonne Université),
Département Origines et Évolution, Muséum national d'Histoire naturelle,
case postale 38, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
france.delapparent123@orange.fr

Laurent CHIRIO
Lycée Saint-Exupéry, B.P. 31 – Brazzaville (Congo)

Roger BOUR†
35 rue des Cottages, F-91230 Montgeron (France)

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ABSTRACT

We describe the skull of *Ragechelus sahelica*, n. gen., n. sp., a pleurodiran Pelomedusoides turtle, the oldest skull known of the Erymnochelyinae. The specimen comes from the surroundings of Indamane village, from a littoral late Maastrichtian level of the Iullemeden sedimentary basin (southwestern Niger, Africa). It is compared on the one hand to the members of the subfamily including remains from the neighboring Ibeceten locality, but from an underlying continental Senonian, and, on the other hand, particularly to the bothremydid *Nigeremys gigantea* (Bergounioux & Crouzel, 1968), from a littoral Maastrichtian level close to that of Indamane, and from a closer to Indamane locality than Ibeceten. The associated fauna is reviewed in its stratigraphic context. Palaeogeographic considerations and systematic relationships indicate Erymnochelyinae widely diversified, in Africa from that time onwards, up to these days in Madagascar and notably with incursions in Western Europe during the Eocene times.

KEY WORDS
Niger,
Indamane,
Ibeceten,
Nigeremys,
Pelomedusoides,
Palaeobiogeography,
new genus,
new species.

RÉSUMÉ

Le plus ancien crâne de tortue érymnochélyinée, Ragechelus sahelica n. gen., n. sp.*, du bassin des Iullemmeden, Crétacé supérieur d'Afrique, et la faune associée dans son contexte géologique et géographique.* Nous décrivons ici le crâne de *Ragechelus sahelica*, n. gen., n. sp., tortue pleurodire Pelomedusoides, le plus ancien crâne connu des Erymnochelyinae. Il a été trouvé près du village d'Indamane, dans le Maastrichtien supérieur littoral du bassin sédimentaire des Iullemmeden (sud-ouest du Niger, Afrique). Il est comparé d'une part aux membres de cette sous-famille et notamment à des restes provenant du niveau sénonien continental d'une localité voisine, Ibeceten, et d'autre part particulièrement au bothremydidé *Nigeremys gigantea* (Bergounioux & Crouzel, 1968), provenant d'un niveau littoral maastrichtien proche de celui d'Indamane et d'une localité plus proche d'Indamane que d'Ibeceten. La faune associée est inventoriée dans son contexte stratigraphique. Les considérations paléogéographiques et les relations systématiques montrent que les Erymnochelyinae auxquels appartient le nouveau taxon se sont largement diversifiés à partir de cette période en Afrique jusqu'à l'heure actuelle à Madagascar, avec notamment des incursions en Europe occidentale à l'Éocène.

MOTS CLÉS
Niger,
Indamane,
Ibeceten,
Pelomedusoides,
Nigeremys,
Paléobiogéographie,
genre nouveau,
espèce nouvelle.

INTRODUCTION

This work is written in honour to Jean-Claude Rage who participated to the first study of the continental fauna and flora of the Iullemmeden (or Iullemeden) basin, from the Upper Cretaceous of Ibeceten (Niger), Senonian. The fauna of Ibeceten includes plants and various vertebrates (Broin *et al.* 1974), among which squamata (studied by J.-Cl. Rage), dinosaurs and turtles.

The littoral new turtle MNHN.RA.2018.0078 skull is particularly compared to the continental Pelomedusoides turtles from this neighboring Ibeceten locality (Fig. 2, at "puits d'Ibeceten"; Greigert 1966: pl. 1; Fig. 3, "Ibécéten"), It is shown the new taxon may be related to one of the Ibeceten turtles, of the podocnemidid subfamily Erymnochelyinae. In this work, subfamily Erymnochelyinae is considered sensu Broin (1988a, b) (and Lapparent de Broin & Werner 1998: fig. 5) and not sensu "Magnatribe Erymnochelydand Broin, 1988, new rank of Gaffney *et al.* 2011", and not according to other modifications of the first meaning of this subfamily which have been introduced in more recent works, such as Cadena (2015) or Ferreira *et al.* (2018b) after others (see Discussion).

The new skull is also particularly compared to another littoral turtle, *Nigeremys gigantea* (Bergounioux & Crouzel, 1968) from a close locality, member of the Nigeremydini (new rank *sensu* Lapparent de Broin & Guntupalli Prasad in press, including Nigeremydina and a part of Taphrosphyini sensu Gaffney *et al.* 2006) (see below in Discussion); we add *Ilatardia cetiotesta* Pérez-García, 2019 in the tribe. This recently named taxon is close together in age, in locality (Ilatarda) and in morphology to *Nigeremys*. They are both much different from the new described eymnochelyine we think closely related to a Ibeceten form of the same Iullemmeden area.

The currently known Niger turtles are examined into the context of the different layers of the Upper Cretaceous, through the successive stratigraphic interpretations (Greigert 1966; Greigert *et al.* 1954; Dikouma 1990, 1994; Dikouma *et al.* 1993, 1994; Lingham-Soliar 1991, 1998; Moody & Sutcliffe 1991) and in relation to the recorded associated fauna. This allows to show the taxonomic and environmental diversity.

In the Iullemmeden basin, the Niger strata follow southern by equivalent layers, such as "Mosasaurus Shales" of the Maastrichtian Dukamaje Formation (Halstead 1979c), in the neighboring northern Nigeria, Sokoto area (Sokoto on the Fig. 1), and notably with already described turtles. Thus, the Mosasaurus shales yielded *Sokotochelys umarumohammedi* Halstead, 1979 (syn. junior: *S. lawanbungudui* Halstead, 1979) (Halstead 1979a-c; Walker 1979; Soliar 1988) a bothremydid turtle that we have shown as related to *Nigeremys* Broin, 1977 (Swinton 1930; Walker 1979; Broin 1988a, b; Lapparent de Broin & Werner 1998; Lapparent de Broin 2000a; Pérez-García 2019a; Lapparent de Broin & Guntupalli Prasad in press).

Palaeogeographic considerations are made here, as well from previous knowledge and publications (notably Greigert (1966); and see references in Lapparent de Broin 2001 and below) as from new data of this study. We propose here to show the diversity in turtles of the considered part of the Iullemmeden basin of Niger: we show that, from the Senonian to the Palaeocene times of the Iullemmeden basin, there were several turtle specimens of different taxa, which have been collected in various layers (five to six), in different close localities (at least four) of the basin.

MATERIAL AND METHODS

The new skull and only collected specimen (LC), was prepared (FLB) by water and manual chisel, the phosphatic gypsum crust making inefficient any acid attack, not making known all sutures. For comparison of fossils and living species, notable complete skeletons and stuffed specimens were observed by us (among which are type and historical specimens) of the collections of AMNH (H), DNPM, MNB, MNHN (Bour 2006), MNRJ, NHM (Hoogmoed & Gruber 1983; Spix 1824), NMW, SMNS and ZSM (Strauch 1890). Lists of observed material are available (FLB, RB). From the observed material of living species and from the figures given by the zoologists, a great anatomical homogeneity is

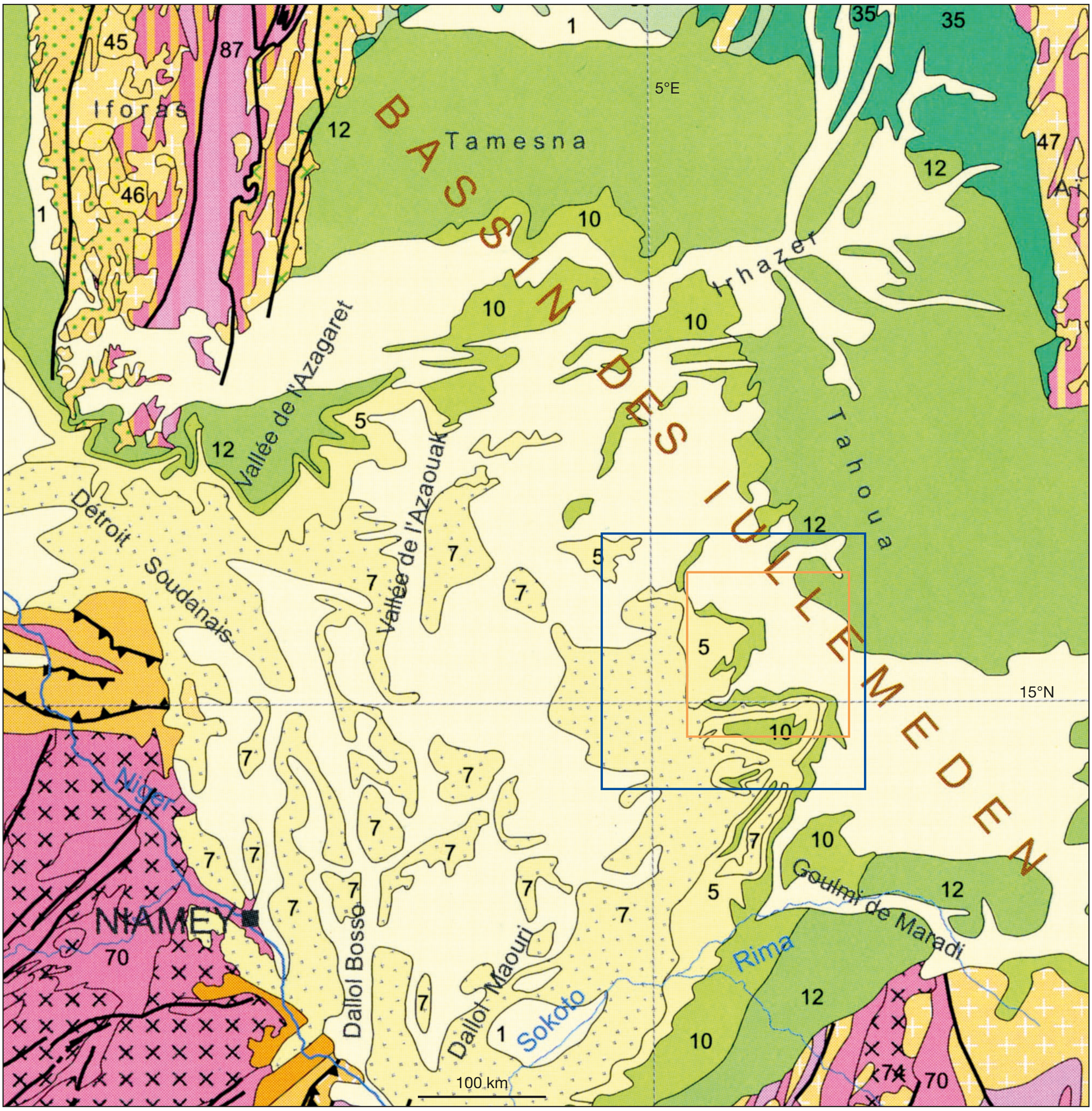

FIG. 1. — Geological map of the Iullemeden basin, extract from the Geological map of Africa, 1:10 millionth (Thiéblemont & Chêne 2016). Numbers: **1**, Quaternary, 2.6-0 Ma, sedimentary; **5**, Paleogene to Pleistocene, 66-0.012 Ma, sedimentary; **7**, Tertiary, 66-2.6 Ma, sedimentary; **10**, Upper Cretaceous, 100.5-66 Ma. Sedimentary; **12**, Lower Cretaceous, 145-100.5 Ma, sedimentary; **39**, Paleozoic; **45**, **46**, Proterozoic; **70**, **86**, **87**, Archean. **Blue square**, area represented Fig. 2 (geographical map). **Orange square**, area represented in Fig. 3 (Greigert's geological map).

noted concerning the skull diagnostic features, as for the fossils; eventual variability (including sexual) is taken here into account when necessary and any essential variability is given in the text.

ABBREVIATIONS

Institutions

AMNH	American Museum of Natural History, Paleontology, Zoology, New York;
MCZH	Museum of Comparative Zoologie, Harvard;
MNB	Museum für Naturkunde in Berlin;
MNHN	Muséum national d'Histoire naturelle, Paris;
MNHN.F.	MNHN, collection de Paléontologie;
MNHN.RA	MNHN, collections d'Anatomie comparée (AC) et de Zoologie des Amphibiens et Reptiles (Z);
MNRJ	Museu Nacional da Universidade Federal do Rio de Janeiro;
MPEG	Museu Paraense Emilio Goeldi, Belem;
MZIZ	Zoological Museum of the Zoological Institute of the Academy of Sciences of Russia (Зоологический музей Зоологического института РАН);
NHM	Natural History Museum, London;
ZSM	Zoologische Staatssammlung München;
SMNS	Staatliches Museum für Naturkunde, Stuttgart;
WNM	Wiener Naturhistorische Museum, Wien.

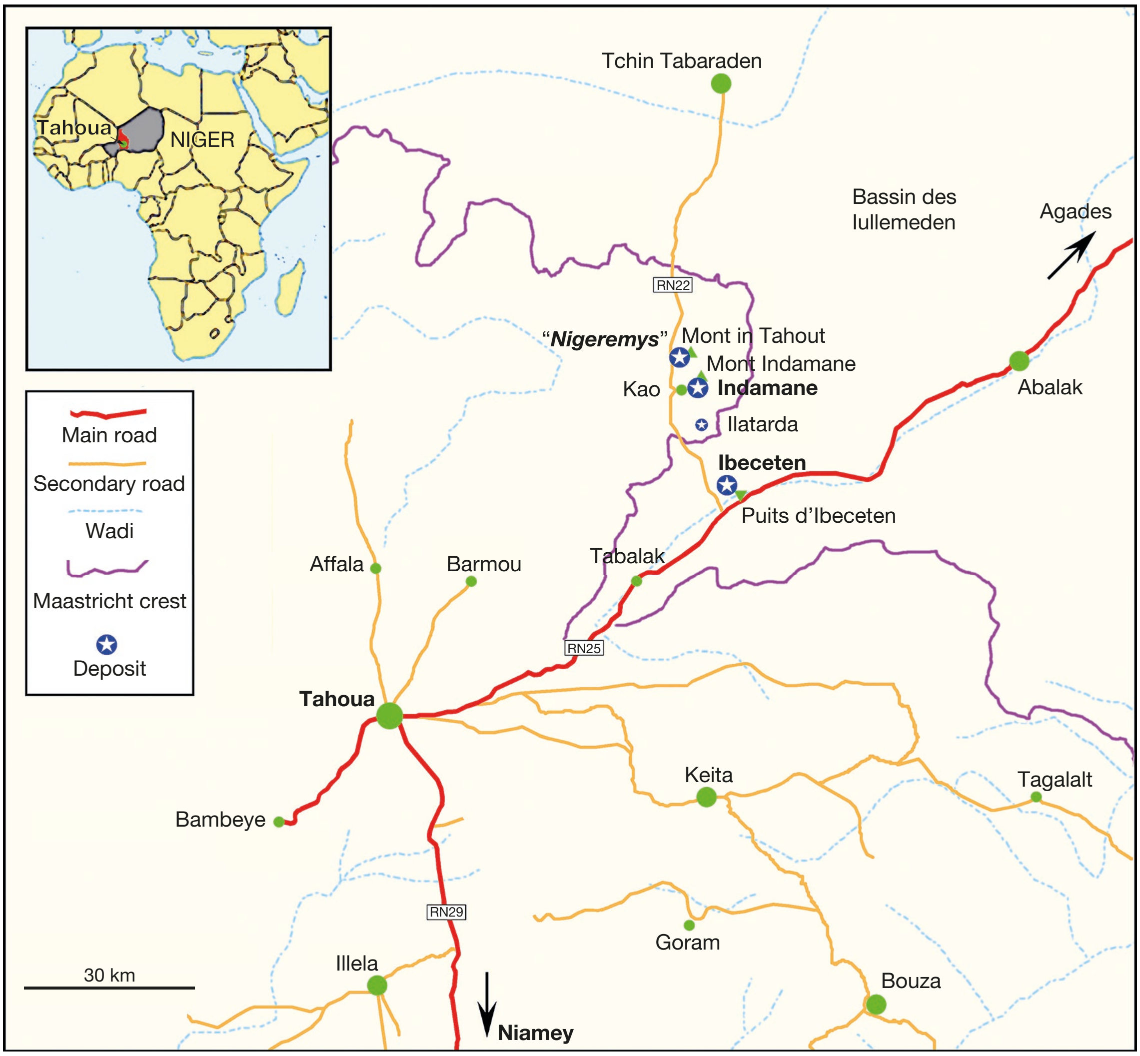

FIG. 2. — Geographical location, northern to southern, of: Mont In Tahout area (*Nigeremys* locality), Indamane (*Ragechelus saherica* n. gen., n. sp. locality), Ibeceten (Erymnochelyine locality) and Ilatarda, fossil localities with turtles (stars), in southwestern Niger, Tahoua district between Niamey and Agades, Iullemeden basin, Upper Cretaceous. Purple line, raised edge of the Upper Cretaceous outcropping (symbols: "10" in Fig. 1, "Cr 9-8" in Fig. 3), overhanging the reg with dunes including the Ibeceten Senonian outcropping (Cr7 in Fig. 3).

GEOLOGICAL CONTEXT OF STUDIED IULLEMMEDEN LOCALITIES, HISTORICAL BACKGROUND AND ASSOCIATED FOSSILS

MONT INDAMANE – GEOLOGY AND STRATIGRAPHY

The skull of *Ragechelus sahelica* n. gen., n. sp. was collected in a locality situated on the littoral of the eastern part of the marine Iullemmeden basin (Figs 1, 2, 3). The Iullemmeden basin is a geological Saharan site (Fig. 1) which is limited toward the northeast by a discontinuous crest, representing the border of a Massif, forming a line of cuestas and domes (green symbol 10 on Fig. 1, squares Figs 2 and 3, violet line on Fig. 2), among which Mont Indamane (Mt Indamane), the new skull locality. This border surrounds and overhangs a reg (this being in northeastern position on the Figs 2 and 3), where is situated the Ibeceten locality on the Tahoua-Agades road (Figs 1, 2, 3).

The Mt Indamane site (or Mont Igdaman or Mont In Daman or Mont In Dama, Mt Igdaman in previous publications [Figs 2, 3]; Idama, IDA in Dikouma [1990: fig. 17]; Igdaman in Greigert [1966: 115, pl. 37]) is positioned in southeastern Niger, in the Tahoua district, near the Indamane village, 7 km east of Kao. This site is already known by the presence of defined late Maastrichtian vertebrate taxa, attributed to continental and marine forms; they notably include mosasaurs, in the Mosasaurus shales beds, and also dinosaurs in Senonian beds. Mosasaurus shales are identified by reference to the Dukamaje Formation of Nigeria (see Halstead 1979a, c).

Greigert (1966: 85, 116, pl. 37) was the first to give a simplified synthetic stratigraphic section of the "Mt Igdaman" we reproduce here (Fig. 4), in comparison to more recent data (Dikouma 1990, 1994; Dikouma *et al.* 1993, 1994; Lingham-Soliar 1991; Moody & Sutcliffe 1991). Greigert described the Mont as constituted of 4 to 5 domes on a same basement. He distinguished several Terms (after Radier (1957) for Gao basin), among which, notably, Terms I and II at Indamane

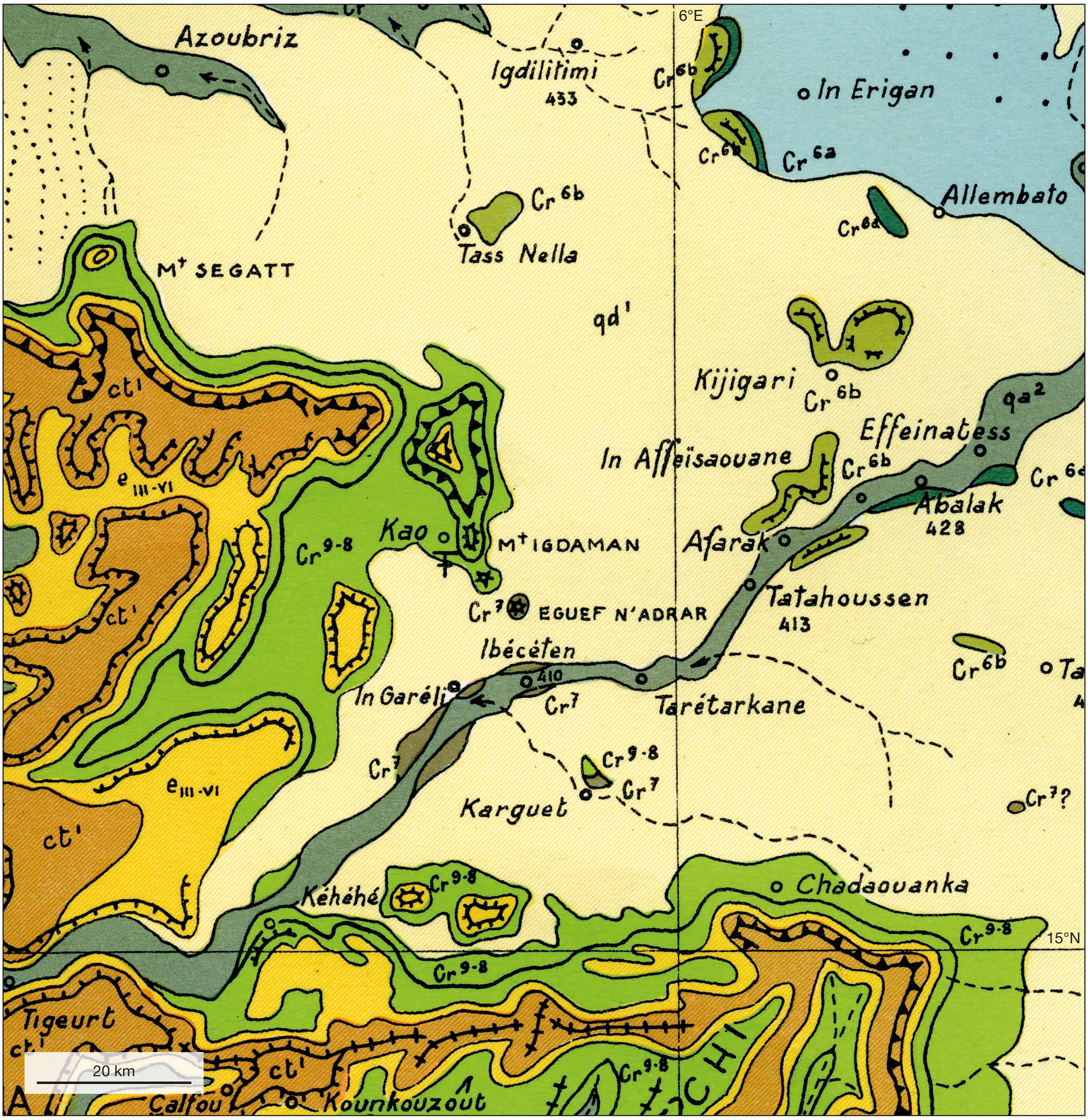

Fig. 3. — Geological map of Iullemmeden basin. Extract from Greigert (1961), focused on the northeastern basin part, area of Kao to Ibeceten with Mont Indamane (Mt Igdaman). Legend, from Greigert (1961): Cr 9-8, including (from top to bottom, [Mt Indamane Maastrichtian outcropping]: **1**, Upper sandstones; **2**, Mosasaurus shales; 3, Lower sandstones. **Cr7**, lower and middle Senonian, with gypsum [including Ibéceten outcropping]; **Cr6**, Turonian; **Cr6b**, Turonian (white limestones); **Cr6a**, lower Turonian (*Nigericeras* zone); **CR6a-b**, lower Turonian and Upper Cenomanian (*Neolobites vibrayeani* zone, Tegama group sandstones); **e III-VI**, lower Eocene; **ct**, terminal continental (simplified); **qa2**, filled fossil valleys; **qd1**, fixed oriented recent dunes (barchans); **F**, fossils at Mont Indamane and Ilatarda.

for the lower Senonian-late Maastrichtian part, and up to Palaeocene (Term VII) and upwards. In the Iullemmeden basin, these layers, littoral with alternative more continental and transgresssive intercalations, overlay the "late Turonian" White limestones sequence of the Lower sandstones & mudstones ("Calcaires blancs") (Greigert 1966; Moody & Sutcliffe 1991). At Mt Indamane, Term I is composed of "Lower sandstones and mudstones" (extending from lower Senonian to late Maastrichtian) outcropping in terraces, the highest one constituting a dome basement (Fig. 4), and including the phosphatic bone bed of *Ragechelus sahelica* n. gen., n. sp., below and close to the base of the dome. The layers of the upper terrace of Term I pass to the Term II, "Mosasaurus shales" sensu Greigert (1966). The Indamane upper part of the Lower sandstones and mudstones beds and the "Mosasaurus shales" are indicated as dating from late Maastrichtian, and the sequence follows upward in the area by Terms III and upper layers, which are not delimited in Greigert (1966)'s section (Fig. 4). Mosasaurus shales present littoral fluctuations, passing to Tertiary layers, including Palaeocene and Eocene parts, and up to the ground surface which may, besides, include Quaternary fossil elements.

At Mt Indamane, Greigert (1966) mentioned plant remains and invertebrate marine fossils, among which the bivalve *Veniella* [i.e. *Roudaireia*] *auressensis* (Coquand, 1862) and the ammonite *Libycoceras ismaeli* Zittel, 1884 (Fig. 4). This ammonite is represented in two successive Maastrichtian transgressive fluctuations in the basin, which are mentioned in Dikouma (1990: fig. 103) and Dikouma *et al.* (1993), forming successively part of the Farin Doutchi (Mosasaurus shales) and In Wagar Formations of Hanon (1984). They correspond to the "first and second *Libycoceras* transgressions" of the inedited synthetic section established by the discoverers of *Nigeremys gigantea* (Bergounioux & Crouzel, 1968) (see below); its holotype (MNHN.F.1964-27.840) comes from a similar level to that of Indamane new skull in a close area at Mt In Tahout (Mt In Touhount). The foraminifer *Laffiteina bibensis* Marie, 1945 is mentioned by Greigert (1966) in the Mosasaurus shales of other Iullemmeden localities, and by Dikouma (1990), Dikouma *et al.* (1993) in both *Libycoceras* levels of the basin, above the layer corresponding to the bed of *Ragechelus sahelica* n. gen., n. sp. (Bardet 2012; Cappetta 1972; Dikouma 1990; Dikouma 1994; Dikouma *et al.* 1993, 1994; Greigert 1966; Greigert *et al.* 1954; Lingham-Soliar 1991).

The new skull was found by one of us (LC) on March 11, 2005, on the outcropping ground, on a terrace at the foot of one of the domes constituting the Mt Indamane. The skull was near a damaged carapace of *c.* 30 cm, possibly belonging to the same specimen, and another much fragmented carapace; both were not collected.

Inlaid of a gypsum crust, the skull was lying in a rich phosphatic bone bed (Fig. 4) where various dissociated bones were recognized: a large much eroded bone (a dinosaur humerus?), crocodile bones, many fish vertebrae, shark teeth, batoid jaw parts and teeth, irregular sea urchins and molluscs (bivalves, gastropods), revealing a mixed fauna of continental, coastal and lagoon areas. Dinosaur presence is possible being present with mosasaur in the equivalent bone bed which yielded *Nigeremys* skull (see below). Mosasaurs were not observed by us (LC) in the immediate proximity of *Ragechelus sahelica* n. gen., n. sp. skull. They were not mentioned in this bone bed by Greigert (1966), taken over by Dikouma (1990, 1994) and Dikouma *et al.* (1993, 1994). However, an English expedition collected in the "Mt Igdaman", Ilartada and other sites of the Tahoua area, various mosasaur bones which were described by Lingham-Soliar (1991, 1998) including *Igdamanosaurus* Lingham-Soliar, 1991. The Mt Indamane bone bed is presented by Lingham-Soliar (1991) in a synthetic section (from D. Ward): "Grey silts with phosphorite bands packed with coprolites, fish and reptile bones" (Lingham-Soliar 1991: fig. 2). It is just mentioned: "Outcropping all the way around the hill [Mt Indamane] are a sequence of bone beds from which the reptile and fish remains were obtained". The presence of mosasaur and turtle with the skull in the bone bed is not indicated. However, in their Indamane section, Moody & Sutcliffe (1991) situate mosasaurs in their bed 25, higher than the bone bed.

Fishes (Selachia, Osteichthya) from Iullemmeden basin were collected by a French expedition (1966) and studied by Cappetta (1972). They lied in several beds including the "Mt Igdaman" bone bed and the marls situated at the base of the Mentess cliff. Mentess ("M" in Greigert [1966: 98, pl. 1]) is situated more northwestern to Mt In Tahout (Fig. 2), in the same surrounding line of cuestas and domes as Mt In Tahout and Mt Indamane. The Mentess sequence begins by marls of the Term II, i. e. above the bone bed of Greigert's Term I of Mt Indamane, this layer not outcropping in the locality. This marly bed was considered by Greigert (1966) as representing "Mosasaurus shales", stratigraphically situated above the bone bed of Indamane. Greigert (1966) did not included the bone bed in the Mosasaurus shales contrary to other authors (Dikouma 1990, 1994; Dikouma *et al.* 1993, 1994; Moody & Sutcliffe 1991) (Fig. 4).

Forming the highest terrace of the Term I, among other terraces which are superposed, Greigert (1966) described the phosphatic bone bed of the Lower sandstones and mudstones as a layer of 0.10 to 0.80 m, situated at the foot of a dome. The bone bed is described as full of fish vertebrae, crocodile remains, batoids and sawfish teeth (and not mentioning mosasaur and turtle). He indicates fossils from this bone bed show the presence of gypsum crystallization. This phosphatic and gypsum bone bed corresponds to the layer of *Ragechelus sahelica* n. gen., n. sp. according to the skull lying in such a bone bed with gypsum crystallization, and because of the associated fossils and the finding point by us (LC) in the Mont at the foot of a dome. Greigert (1966: pl. 37) described this Indamane bone bed as overlaid by white silt sandstones with turtles and selachians; in his text (Greigert 1966: 115, 116) he specifies the silt sandstones as being themselves separated from marls with carapaces of large turtles and selachian teeth: these marls seem to be those where the English expedition collected large turtle carapaces (now housed in the NHM) and they seem to constitute the bed 19 of Moody & Sutcliffe (1991) (Fig. 4).

Overlying his Term I, over white sandstones/marls with turtles, Greigert (1966) situated black marls with salt (gypsum symbol being figured on the pl. 38) and (above) yellow marls. These layers of his Term II include the Maastrichtian bivalve *Veniella* [i.e. *Roudaireia*] *auressensis* (and other fossils), and are attributed at Indamane to Mosasaurus shales by comparison with other neighboring localities of the basin such as Mentess (Greigert 1966: 98), Ilatan (Greigert 1966: 103, pl. 3), and Chinchinanan (Greigert 1966: 115). For him, Mosasaurus shales do not include the basal bone bed but Dikouma (1990, 1994) and Dikouma *et al.* (1993, 1994) taking over the Iullemmeden basin and particularly the Mt Indamane (after Greigert 1966; Moody & Sutcliffe 1991), included the bone bed of the Lower sandstones and mudstones of Term I of Greigert (1966) in the Mosasaurus shales with the Greigert's Term II. But Dikouma (1990, 1994) specified the passage between Terms I and II is progressive, the sequences

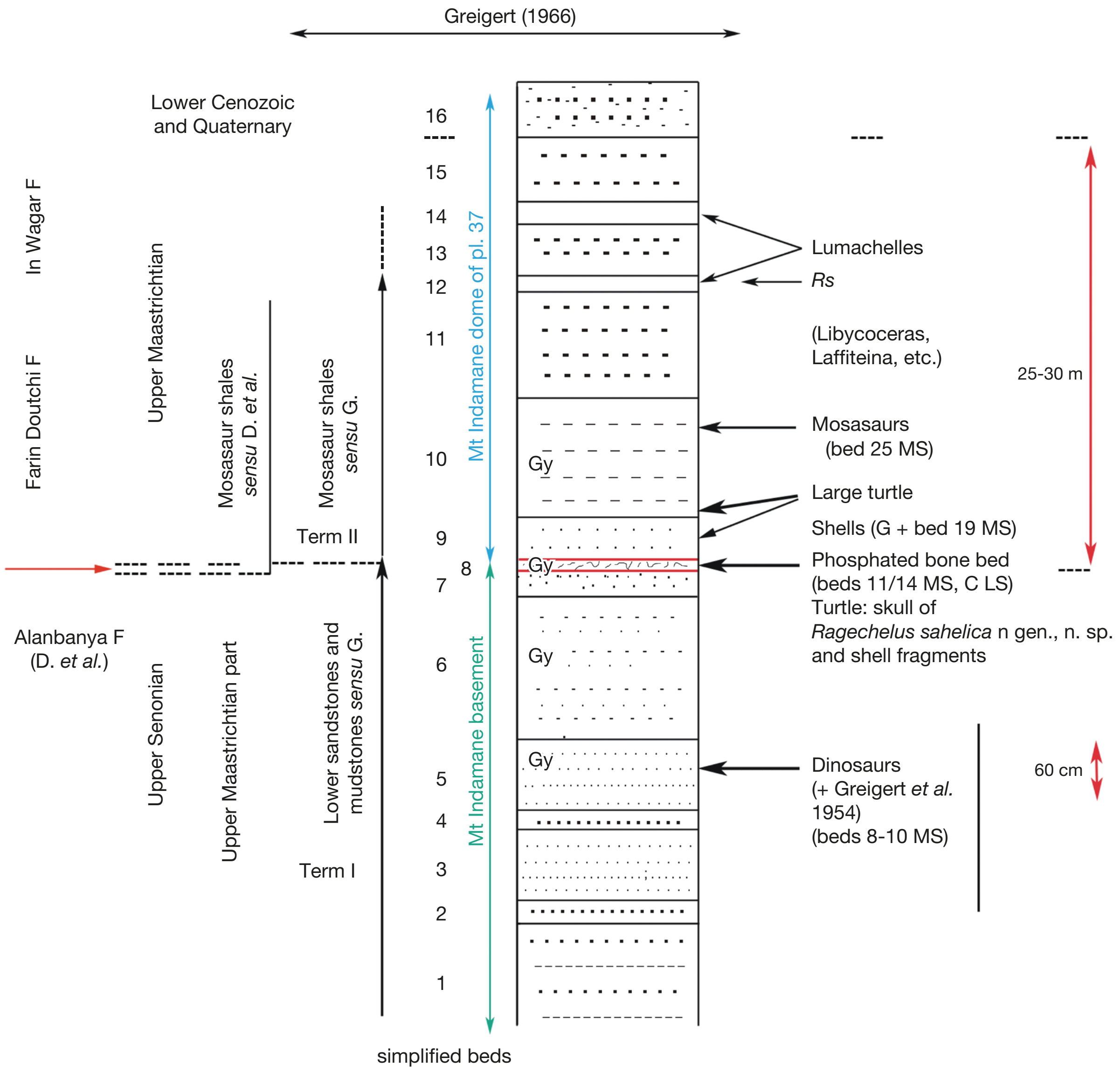

Fig. 4. — Log, simplified stratigraphic section, from Greigert (1966: pl. 37)'s Mont Indamane, presenting 16 banks, from bottom to top: alternately, **1**, **3**, **5**, gypsiferous sandy marls and **2**, **4**, fine and silty sandstones; at top of **5**, large dinosaur site (of Greigert *et al.* [1954]); **6**, grey and black gypsiferous marls; **7**, gypsiferous marls; **8**, phosphatic breccia: fish, crocodile, batoids, sawfish (bone bed of the new turtle skull); **9**, white sandstones: turtles, selachians; **10**, black marls, salt; **11**, **13**, **15**, yellow marls [with *Libycoceras* and Laffiteines]; **12**, lumachella, with Rs (*Veniella* [*Roudaireia*] *ouressensis*); **14**, lumachella; **16**, ferrugineous sandstones (overlying crust). C LS, bank C in Lingham-Soliar (1991 [after David Ward]); **D** *et al.*, Dikouma *et al.* (1993, 1994); **F**, Formation; **G**, Greigert (1966); **MS**, banks 8-10, 11/14, 19 and 25 in Moody & Sutcliffe (1991). Not to scale.

being alternatively more or less littoral (littoral plains with mangroves), up to the top: Dikouma specified it is difficult to separate the Mosasaurus shales beds and the immediately underlying Lower sandstones and mudstones layers part including the bone bed. It is noted gypsum is widely present in the Mt Indamane sequence; being mostly of secondary origin (Dikouma (1990), it may be present in marls, although not inlaying the bones, as well as in the silty phosphatic and ferruginous bone bed layers where it incrusts the bones (Fig. 4). Anyway, several bone beds with gypsy mosasaurs are mentioned toward the base of the Mosasaurus shales sequence, at Ilatarda, Mentess and In Tahout (Lingham-Soliar 1991, 1998; Moody & Sutcliffe 1991; Soliar 1988).

As far as the bone bed is concerned, Dikouma (1990: 37) defined it (as BB, at "Indama"): "a bed of 3 to 10 cm with vertebrate remains [not detailed taxa] in a pyrite, gypsum and ferruginous binder". BB is positioned in the middle (Dikouma *et al.* 1993: fig. 5) or slightly above the middle (Dikouma *et al.* 1994) of the first member F1 of three members (F1 to F3) of the Farin Doutchi Formation. Thus, a relatively important top part of the Lower sandstones and mudstones of Greigert (1966) is included in the F1 member. In their figures and in their texts (Dikouma (1990, 1994) and Dikouma *et al.* (1994)) only mentioned fishes and reptiles by places and crocodiles (dyrosaurids are sometimes specified) in the basal bone bed of the Formation (i.e. BB). Dikouma (1990: fig. 21) and Dikouma *et al.* (1993: fig. 5) also presented a detailed section of Mt Indamane area, with detailed invertebrate fauna, plants and vertebrates (fish and crocodile), in comparisons with sections of Ilatarda dome and of several domes of the Mt In Touhount (Dikouma 1990: 46, 47, figs 21, 23, 24, 27, 28).

In Greigert (1966), Dikouma (1990, 1994) and Dikouma *et al.* (1993, 1994) the overlying Upper sandstones and mudstones of Terms III and IV represent the terminal Maastrichtian, the In Wagar Formation, then followed by the Palaeocene Garadoua Formation and post-Palaeocene Formations. No turtle has been mentioned there from the In Wagar Formation which includes several siltites and sandstones layers with plants (such as *Ficus*, wood, roots). All these Formations are not delimited in the log of Greigert (1966) (Fig. 4) although they are included. As the transition between the underlying Alanbanya and Farin Doutchi Formations, that with the In Wagar Formation is progressive (Dikouma 1990). The Palaeocene mention has here its importance, having furnished turtle fragments at Indamane (see below) and in the close In Tahout area (In Touhount, see below). Toward the middle and upper part of the Palaeocene Garadoua Formation (Term VII), Dikouma (1990, 1994), Dikouma *et al.* (1993, 1994) situate the successive *Ranikothia* and *Lockhartia* transgressions.

Below the Farin Doutchi Formation, Dikouma (1990, 1994) and Dikouma *et al.* (1993, 1994) consider the Alanbanya Formation, as constituted by the Lower sandstones and mudstones of Greigert (1966) less the part including the phosphatic bone bed (BB) of *Ragechelus sahelica* n. gen., n. sp., which is included in Farin Doutchi Formation, first member F1. Alanbanya Formation is given as late Maastrichtian in Dikouma *et al.* (1993) and equivalent to the Taloka Formation of Nigeria. The Taloka Formation is included in the Maastrichtian beds in Nigeria (Soliar 1988). The base of the Alanbanya Formation is not delimited in relation to the Lower sandstones and mudstones of Greigert (1966) (Fig. 4).

Presence of several Maastrichtian Indamane levels with turtle, and associated fauna

As soon as 1954, Greigert *et al.* (1954) indicated the presence of turtles in several levels of gypsiferous marls above the bone bed: “Dans ces marnes, on trouve d’ailleurs, à plusieurs niveaux des plaques de grande Tortue”. Lingham-Soliar (1991) cited the fossils of the English expedition collected with mosasaurs: [The layers of the Mt Indamane] “yielded the remains of a number of vertebrates, some similar to those found in the Mosasaurus Shales of Nigeria: the sea snake *Palaeophis,* pelomedusid turtles, sharks (including sawfish sharks and rays), cat fish, and the remains of the marine teleost *Stratodus* (David Ward pers. comm.)”. It is not said which precise layer yielded each fossil category, in which bed were the mosasaurs and turtles in relation to which of the different beds described by Greigert (1966) and Cappetta (1972). Moody & Sutcliffe (1991: fig. 8) situated the large complete turtles (English expedition) at the top of bed 19 of their Indamane sequence: “Numerous complete shells of large to very large pelomedusid turtles (1-1.5 m-long)” while mosasaurs are situated in the marls of the bed 25 (Fig. 4). This size includes that possible for the shell of the bothremydid *Nigeremys* holotype, coming from the area of Mont In Tahout (Fig. 1) (see below), this being estimated to *c.* 120 cm. They are larger than those possible for the shell of the erymnochelyine *Ragechelus sahelica* n. gen., n. sp. skull, estimated to *c.* 30-50 cm, thus better coinciding with the size of the damaged carapace found in the bone bed with the skull. This overlying marl bed 19 is not the mentioned bone bed of *R. sahelica* n. gen., n. sp., this being a phosphatic bank where the bones are dissociated and incrusted of gypsum: that is perhaps represented by the bed 14 of Moody & Sutcliffe (1991), obviously in their interval of beds 11-14 (Fig. 4). Bed 19 corresponds to that, seen above, of the marl bed “with shells of large turtles” cited by Greigert *et al.* (1954) and Greigert (1966), therefore above the bone bed. Thus, the turtle *R. sahelica* n. gen., n. sp. is not yielded by the same bank as these large marl “pelomedusids”, also cited by Moody & Sutcliffe (1991) as “*Podocnemis* sp. and Pelomedusids” (Moody & Sutcliffe 1991: table 2, in the Faunal list from Mosasaurus Shales at Kehehe and Mt Indamane).

This presence of several fossiliferous beds (bone beds and marls) with turtles is strengthened by D. Ward in Lingham-Soliar (1991) and Moody & Sutcliffe (1991), after Greigert *et al.* (1954) and Greigert (1966). It agrees with the multiplicity of Maastrichtian turtle taxa here recorded in the Iullemmeden area, belonging to the family Bothremydidae: *Nigeremys*, *Ilatardia*, others of In Tahout area (see below) and another new one from Indamane (Pérez-García pers. comm.); beside the erymnochelyine *Ragechelus sahelica* n. gen., n. sp. (Figs 5-9) and other erymnochelines and Pelomedusoides of the Ibeceten level (Fig. 10) and at In Tahout (see below). *R. sahelica* n. gen., n. sp. appears as coming from a similarly textured bone bed bank as *Nigeremys* and *Ilatardia* but not obligatory of the same exact geological bank. The broken bones, the inlaying gypsum in a phosphatic not marly bed correspond to a similar littoral environment for the fossils, less continental than the underlying Lower sandstones and mudstones with dinosaurs of Indamane (Greigert *et al.* 1954; Greigert 1966) and those of the Ibeceten beds (Broin *et al.* 1974) and In Tahout area (see below). The bone bed represents a more perturbed fossilization in a littoral deposit than in the overlying littoral marl beds with complete turtle shells.

Summarizing the associated vertebrate fauna collected in the Iullemmeden basin with the new skull, first studied vertebrates were fishes. Osteichtya and Selachii (Cappetta 1972) were found in Palaeocene (Sessao) and Maastrichtian (Mentess, Igdaman) localities. At Mt Indamane, the fishes were collected *c.* 30 meters below the top, in the bone bed of Greigert (1966) (upper part of Term I) and considered here as the layer of *Ragechelus sahelica* n. gen., n. sp. Cited Maastrichtian fishes include *Igdabatis sigmodon*, *Coelodus* sp. 2 (a different species from *Coelodus* sp. 1 from Mentess) and *Stratodus apicalis*, beside an indetermined genus (not shared with Mentess) and beside three Maastrichtian species shared with Mentess. The list was retaken in Dikouma (1990) and Dikouma *et al.* (1994). The mosasaurs, which were collected in the Mosasaurus shales of the Iullemmeden basin include at least six taxa (Bardet 2012; Polcyn *et al.* 2012; list needing to be revised: N. Bardet pers. comm.). Among which at "Mt Igdaman" are: *Igdamanosaurus aegyptiacus* Zdansky, 1935, cf. ?*Angolasaurus* Antunes, 1964, *Halisaurus* sp., *Plioplatecarpus* sp., cf. *Mosasaurus hoffmanni* Mantell, 1829, and *Goronyosaurus* sp. *Pluridens walkeri* Lingham-Soliar, 1998 was described from the neighbor Ilatarda locality (southern to Indamane, Fig. 2), in a layer possibly showing less signs of gypsum crystallization on the mosasaur than at Indamane: Ilatarda is the locality of the turtle *Ilatardia*.

To resume, the other Mt Indamane vertebrates which are associated with turtle and which are already studied are only fishes and mosasaurs. Of crocodiles, there is only their simple mention and few figures of dyrosaurs (Dikouma 1990: pl. 10): this attribution agrees with the amphicoelous vertebrae collected with *Nigeremys* (MNHN.F.1964-27 coll.) at In Tahout (see below). Of *Palaeophis*, there is only the mention of Lingham-Soliar (1991); it is not mentioned by Moody & Sutcliffe (1991) and it seems not yet studied.

Mt Indamane and Ibeceten lower "Upper sandstones and mudstones, Senonian level"

Below the Maastrichtian bone bed terrace, Greigert (1966) described another more basal terrace in the Mont, below gypsiferous marls, on the roof of silt sandstones, as a site of large sauropod dinosaur bones (Greigert *et al.* 1954). This constitutes (as agreed by Dikouma 1990) an underlying Senonian layer corresponding, on the whole, to the continental Senonian of Ibeceten (Figs 1; 3) (Broin *et al.* 1974). This locality is close to the well of Ibeceten or Ibéssetène (puits d'Ibeceten; Figs 2, 3). This site ("Ibeceten 1" in Lapparent de Broin 2000a) is positioned on the side of the road to Agades, at narrow proximity of the well, on two very few elevated hills, far and well southern to Mt Indamane" (Ph. Taquet pers. comm.). Ibeceten site yielded many remains of fossil angiosperm plants, dipnoid fishes and others, and reptiles (pleurodiran turtles, squamates, crocodiles, dinosaurs) (Broin *et al.* 1974; Buffetaut 1974). The madtsoid snake of Ibeceten was studied by Jean-Claude Rage in Broin *et al.* (1974) and retaken as Madtsoia aff. *madagascariensis* Hoffstetter, 1961 in Rage (1981). Ibeceten turtle set includes numerous dissociated Pelomedusoides shell plates (including three different Pelomedusoides nuchal morphotypes, among which that of *Erymnochelys*), upper and lower jaw parts of one taxon and one corresponding basisphenoid, of similar size, girdles and appendicular limbs, with a dominant form defined by one of us (Broin *et al.* 1974) as "possibly near the origin of the erymnochelydian lineage": it is effectively potentially affinis of *Ragechelus sahelica* n. gen., n. sp., being identified as erymnochelyine notably by one of the two present morphological plastral patterns (Fig. 10A-G) and conform other elements; preserved cervicals centra have a cordiform cotyle and a corresponding condyle similar (although less low) to those of *Erymnochelys* sp. from the Mio-Pliocene of Zaïre (République démocratique du Congo) (Hirayama 1992), *E. madagascariensis* and *Turkanemys pattersoni* Wood, 2003 (Miocene from Kenya) (Broin *et al.* 1974; Lapparent de Broin 2000a; Lapparent de Broin & Guntupalli Prasad in press) (see below). The Ibeceten site was also taken over in the Moody & Sutcliffe (1991)'s study, considering it in a nonmarine, fluvial-lacustrine environmental setting and being part of the Santonian Senonian. Within the Senonian, the age of this level is debatable, varying from "lower Senonian" or "lower and middle Senonian", or Coniacian to Campanian, Campanian or "Late Senonian" but not including the Maastrichtian part, according to authors (Broin *et al.* 1974; Dikouma (1990), Dikouma *et al.* 1994; Greigert 1966; Moody & Sutcliffe 1991).

Mont in Tahout area – "Nigeremys site" – in relation to Ibeceten: turtle and associated fauna

Two localities with defined turtles were known in the Tahoua district, one Senonian (not Maastrichtian) more continental: Ibeceten, with continental erymnochelyine turtles (Broin *et al.* 1974), and one more littoral with the bothremydid turtle *Nigeremys gigantea*. This taxon has been collected by geologists of the Dutch Bataafse International Petroleum Maaetschappij Company (Netherlands) (MNHN.F.1964-27 coll.). It comes from the same late Maastrichtian Farin Doutchi Formation as the new *Ragechelus sahelica* n. gen., n. sp. of Mt Indamane. Stratigraphically, the erymnochelyine *R. sahelica* n. gen., n. sp. bone bed might be correlated with the layer of "*Nigeremys* site" (Fig. 2). The locality of *Nigeremys* was previously geographically associated to Ibeceten (Broin 1977; Lapparent de Broin & Werner 1998; Lapparent de Broin 2000a): it was presented as situated as east to Ibeceten, at its vicinity, in Lapparent de Broin & Werner (1998), under the name of "Ibeceten 2" in Lapparent de Broin (2000a). *Nigeremys* comes from one of the domes of the Mont In Tahout area, a close but northern area to Mt Indamane domes, and thus northern and less close to Ibeceten ("*Nigeremys*" site in Fig. 2) (ITT, In Touhount in Dikouma 1990: fig. 17; In Tahout in Lingham-Soliar 1998: fig. 1). The "*Nigeremys* site" geographic longitude and latitude coordinates have been given as 15°14'N and 5°21'E (measured around 1963). *Ragechelus sahelica* n. gen., n. sp. coodinates are 15°26'N and 5°48'E (measured in 2005 by one of us [LC]). The name of locality of *Nigeremys* ("*Nigeremys* site") needed to be separated from Ibeceten. Actually, *R. sahelica* n. gen., n. sp. of Indamane and *N. gigantea* of Mt In Tahout area are located on the same eastern line of monts and crest system including the outcropping Maastrichtian beds and dominating the "reg" (a fixed erg) with the road of Ibeceten to Agades (where the Ibeceten well is situated). The locality Ilatarda of the *Ilatardia* Pérez-García, 2019 turtle, was already known for mosasaurs (Lingham-Soliar 1998): it is also on the same line of monts, very close and just southern in relation to Mt Indamane, (Fig. 2; ILA in Dikouma 1990: fig. 17; Lingham-Soliar 1998: fig. 1) and northern to Ibeceten.

Mt In Tahout (or In Touhount, Dikouma 1990: fig. 21; Lingham-Soliar 1998: fig. 1) yielded mosasaurs (Lingham-Soliar 1991). In this area, "*Nigeremys* site" (Fig. 2) geographical coordinates do not exactly correspond to those given at Mt In Tahout for mosasaurs: 15°22'N and 5°52'E. This is because Mt In Tahout is a wide and complex area including "*Nigeremys* site", similarly to Mt Indamane where several domes were mentioned. As far as the locality of *Nigeremys* is concerned, its layer produced a phosphatic matrix with gypsum crystallization, as the bone bed of *Ragechelus sahelica* n. gen., n. sp. Indeed, inedited work-data included the synthetic section of the area in the basin, which was established in La Haye (1963) and given to MNHN by geologists of the Netherlands Company, discoverers of *Nigeremys* MNHN.F.1964-27.840 holotype and of other associated fossils (MNHN.F.1964-27 coll.). They show *Nigeremys* has been collected in a Cretaceous-early Cenozoic sequence, with locally the addition by places of some surface Quaternary – recognized as mammals and crocodiles – specimens. The synthetic section dates from the most inferior Cretaceous sequence (Continental intercalaire), including in the upper part the present Senonian-Maastrichtian fauna and passing by Palaeocene and Eocene layers, up to Quaternary ground, as at Indamane.

As in the inferior lower Cretaceous part of the section, the upper part of the synthetic section, from "Senonian" to "middle Eocene", yielded vertebrate fossil remains. Among them, are recognized mosasaur, dinosaur, crocodile, turtle and fish bones (MNHN.F.1964-27 coll.). This upper part includes from base to top:

1) basally (overlying the inferior part of the "Lower Sandstones", which includes the White limestones ["Calcaires blancs"]), the upper part of the "Lower Sandstones" (Lower sandstones and mudstones); that is represented by the Gypsiferous clays ("Argiles à gypse"), and that may globally correspond to the continental layer of Ibeceten (Broin *et al.* 1974) and to the "large dinosaur site" ("gisement à grands dinosaures") of Indamane (Greigert *et al.* 1954; Greigert 1966).

2) the overlying "Mosasaurus shales", that include (in the section figure) the two levels of the first and second *Libycoceras* transgressions (both included in the extended Mosasaur shales contrary to Dikouma 1990), and the Upper Sandstones. The bone bed of *Nigeremys* and associated other vertebrates is positioned in the first *Libycoceras* transgression level; another bone bed is situated in the second *Libycoceras* transgression level with collected fish, mosasaur and dinosaur but without turtle.

And 3) a late Palaeocene layer (lower papyraceous shales).

These layers are followed by early Eocene and middle Eocene beds ("upper" papyraceous shales) (without mentioned vertebrates).

In the sequence sheet, the fossil work numbers of the collected specimens are juxtaposed to the named levels. It allowed identifying *Nigeremys* skull (MNHN.F.1964-27.840) position (N.840 in the sheet) as: "Mosasaurus shales, late Maastrichtian *Libycoceras* first transgression". Bergounioux & Crouzel (1968) listed the presence with the skull of *Mosasaurus* [i.e. *Goronyosaurus* Lingham-Soliar, 1991] *nigeriensis* (Swinton, 1930), *Stratodus apicalis* Cope and *Onchosaurus pharao* Dames". From the incrusted gypsum in the bones, the matrix and the fragmentation of the fossils, it corresponds to one of the late Maastrichtian bone beds (above seen), that of *Ragechelus sahelica* n. gen., n. sp. being included. After their gift, the collected MNHN.F.1964-27 taxa were not revised after a first determination of Pr. C. Arambourg and J. Signeux. The global content of the collection has just been identified (FLB, Nathalie Bardet) with the aim of the present work. In the associated "Mosasaurus shales" list, it is checked they include several (listed) selachians and teleost fish and crocodiles (mainly amphicoelous vertebrae: crocodiles often given in the list as "dyrosaurids"), dinosaurs and mosasaurs (being checked as such and now recognized in the drawers, separated from crocodiles and dinosaurs with which they may have been confused in the joined list), and coprolithes. Among the fishes are checked *Stratodus* (species not verified) and *Onchosaurus pharao*: this is not included in the Cappetta (1972) list at Mt Indamane but it was indicated in the Damergou (Cappetta, 1972) (Zinder district, east to Tahoua district) and *Enchodus lamberti* is included in the list of fishes of the Farin Doutchi Formation in Dikouma (1990) and Dikouma *et al.* (1994).

In this MNHN.F.1964-27 coll., we recognize the presence of few turtle elements:

1) Turtle elements associated with the *Nigeremys* skull: Pelomedusoides fragments are preserved from the level of the first *Libycoceras* transgression of the "Mosasaurus shales": there are an undeterminable plate fragment and a slender gypsiferous fragmentary and moderate in size ilium MNHN.F.1964-27.657 (small for the *Nigeremys* size, being of a shell of *c.* 50 cm long, against *c.* 120 cm for *Nigeremys* skull: conform in size to the shell of *Ragechelus sahelica* n. gen., n. sp.) and slender as in living *Erymnochelys madagascariensis*. The presence of gypsum on the *Nigeremys* skull as on the ilium and other fossils (turtle, mosasaurs, crocodile and dinosaur included) indicates their origin in gypsiferous layers, which laterally agrees with the gypsiferous bone beds with vertebrates as known at Mentess, Ilatan, Indamane and Ilatarda: as gypsum (with similar gypsum crystallization pattern on the bones) is mentioned on bones of several layers in the Kao sequence (Greigert 1966), it was asked if the precise stratigraphical correlation of *Nigeremys* layer with *R. sahelica* n. gen., n. sp. bone bed was possible: noting the absence of collected mosasaurs with *Ragechelus* n. gen. in its Indamane bone bed, such a correlation is possible although not certain. However, the presence of *Nigeremys* in the level of the first *Libycoceras* transgression attests its belonging to the Farin Doutchi Formation, as the skull of *R. sahelica* n. gen., n. sp., and this lower position agrees with the Indamane bone bed in the Greigert's (1966) sequence. Anyway, *Ragechelus* n. gen. and *Nigeremys*, both late Maastrichtian in age, do not come from the underlain continental Senonian bone bed, outcropping at Indamane (Greigert 1966; Greigert *et al.* 1954) and Ibeceten (Broin *et al.* 1974) in layers situated Paragraph 2a (below). They really come from one of the upper bone beds including the upper bone bed of Greigert (1966) and the BB of Dikouma (1990, 1994), Dikouma *et al.* (1994). They do not come either from the overlying Mosasaurus shales marls with large turtles and from Palaeocene beds (Paragraph 2b, below).

2) Few large indeterminant Pelomedusoides turtle plates (shells *c.* at least 50 to 80 cm long) are present in several other layers than in the first *Libycoceras* transgression level:

a) In Lower sandstones, continental inferior Senonian levels of the section, "Gypsiferous clays" (Argiles à gypse). With *Ceratodus* elements and Dinosaur remains, some undetermined Pelomedusoides turtle elements assembled in lots MNHN.F.1964-27.955, MNHN.F.1964-27.956 and MNHN.F.1964-27.317 and 317A to E of a moderate size (perhaps shells of 50 cm); they include several shell plates, and a Pelomedusoides ilium MNHN.F.1964-27.1964-27.317. They are bright brown and smooth; the plates have only marks of scute sulci, the fragmentary hypoplastron MNHN.F.1964-27.955A has a stout beginning of inguinal process and a narrow dorsal femoral overlap. A costals 7-8 part shows the iliac pleurodiran scar. The ilium (317) is conform to that of *E. madagascariensis* except the shaft is a little relatively wider. Their layer is named "*Pseudoceratodes* bank". Greigert (1966: 75) mentions also the *Pseudoceratodes* presence in Elleba area: "EL" in Greigert (1966: pl. 1), east to Mentess on the approximate same northern latitude, but in the same "Aureole Crétacé moyen" as that of Ibeceten "I", externally to the figured line (Fig. 2) of crests where Maastrichtian is outcropping, northern to Indamane. There, *Pseudoceratodes* is mentioned by Greigert as coming from the Lower sandstones and mudstones, just above a dinosaur bank. The "*Pseudoceratodes*" dinosaur bank of the present section is not attested as exactly corresponding to the Lower sandstones and mudstones bank of Indamane with dinosaurs ("large dinosaur site" of Greigert (1966)) and with that of Ibeceten although it is possible. The turtle fragments features are not enough determinant to be attributed to any turtle of Ibeceten, but we notice the similarity by the bright brown colour of some pieces. This, knowing dinosaurs are present in several successive underlying Senonian banks of Lower sandstones and mudstones: indeed, there are other dinosaur remains in the MNHN.F.1964-27 collection. There are present in another bank, situated below, at the base of the Gypsiferous clays of the section, just overlaying the "Lower Sandstones White limestones" sequence ("Calcaires blancs") (see Greigert 1966: 55). This lower bank may be too much basal to be correlated with the Indamane "large dinosaur site" of Greigert (1966). A turtle plate MNHN.F.1964-27.655A is associated to dinosaur remains ("*Carcharodontosaurus*" is listed) in this bank; it is a bridge stout peripheral of 5 cm long, from a carapace of *c.* 40 cm long, i.e. a rather large form, as in the upper bank, and possibly as large as *Ragechelus sahelica* n. gen., n. sp.; but it was not from a shell as large as the English shells from the much overlying Mt Indamane Mosasaur shales. It comes from a moderately decorated turtle as found in bothremydids; it is not incrusted of gypsum; it is not strongly decorated as in Taphrosphyini (emend., *sensu* Lapparent de Broin & Guntupalli Pradad in press, *Taphrosphys* group of Broin [1988b], Taphrosphyini Gaffney *et al.* 2006 without Nigeremydini), having simply weekly marked polygons and dichotomic sulci as often in the marine bothremydid forms, such as in some Bothremydini of Ammonite Hills (Egypt, Maastrichtian); the surface is not bright as some plates of the upper gypsiferous clays level.

b) In upper levels of the sequence, late Palaeocene: from the lower Papyraceous shales, Term VI of Greigert (1966) (Garadoua Formation above the In Wagar Formation; Dikouma 1990, 1994), the set of samples number MNHN.F.1964-27.663 includes two bothremydid turtle distinct taxa: the first is represented by two smooth indeterminable large plates, the second by two strongly decorated plates. The decorated plates of the second taxon have protruding relatively large irregular polygons: each polygon is proportioned about equilaterally in length on width, contrary to the also protruding but shorter for their width and smaller polygons of *Taphrosphys* group. These decorated elements indicate a new undetermined Palaeocene form (shell of at least *c.* 74 cm long). By its strong decoration, this second taxon differs from the first one. It differs also from the plates with some smooth or marine basic decoration which have been seen above in the continental and littoral gypsiferous clays of the Lower sandstones and mudstones, and from the continental Ibeceten Pelomedusoides. Such protruding decorations are not the case of the shells associated with the known *Nigeremys* group members and with erymnochelyines.

STRATIGRAPHIC POSITION OF *RAGECHELUS SAHELICA* N. GEN., N. SP. IN RELATION TO IBECETEN AND *NIGEREMYS* SITE

To conclude on that point, Dikouma (1990, 1994) and Dikouma *et al.* (1993, 1994) considered the Farin-Doutchi Formation beginning shortly below the *R. sahelica* n. gen., n. sp. Indamane bone bed (BB of Dikouma 1990), this being included in the middle of the inferior term FD1 (on three terms) of the Formation. *R. sahelica* n. gen., n. sp. being in the Indamane Maastrichtian bone bed, close to Greigert's Term I top, is then intercalated between: - on the one hand the "Senonian" (not differentiated) sites of Lower sandstones and mudstones with less littoral beds, those seen in the Indamane Term I, at Ibeceten and at the "*Nigeremys* site" (see above); these layers correspond to the Alanbanya Formation of Dikouma (1990, 1994) and Dikouma *et al.* (1993: 113, figs 2, 3; Dikouma *et al.* 1994); - and, on the other hand, the marls with carapaces of large turtles of Indamane and the superposed marls of the Mosasaurus shales. In other words, the new skull is positioned at late Maastrichtian, below the "Mosasaurus shales" part including the "*Roudaireia*" (*Veniella*) levels (Term II) of Greigert (1966) (Fig. 4), while *Nigeremys* is recorded from the *Libycoceras* first transgression level including the bone bed in the joined section (i.e. moasaurs shales *sensu lato* of Dikouma *et al.* 1994).

The littoral sites with mosasaurs indicate their place of life, while when dinosaurs accompany them, those are carried post-mortem from near shore; the turtle presence in a locality does not indicate its place of life, both places of life being possible: littoral or freshwater continental; a marked decoration is indicative of its euryhaline living environment.

"*KAOSAURUS SPINIFERUS*" OF MT INDAMANE AND ASSOCIATED TURTLE

Beside mosasaurs, in various open papers, Michaut (2002, 2007, 2013, 2015) and Kané & Michaut (2007) presented an enigmatic "vertebrate" of the Mosasaurus shales of "In Daman", below the name of "*Kaosaurus spiniferus*" as being the "sister taxon of Testudines". Poorly preserved & amazingly reconstructed, it seems a chimera of several animals, by association of turtle (large fragmentary jointed costals?), not recognized by us bones, possibly of various fishes (possibly

Table 1. — Skull mensurations (in mm). Abbreviations: **H**, height; **L**, length; **pmx**, premaxillary; **ptp**, processus trochlearis pterygoideus; **Pter**, pterygoid; **Q**, quadrate; **Sq**, squamosal; **W**, width.

Skull mensurations in mm	
L from anterior pmx extremity to basioccipital extremity	109
L up to squamosal extremity	127
W left triturating surface at posterior palatine medial extremity	21
W palate at processus trochlearis pterygoideus root	49
W at posteroventral jaw maxillary extremity	70
W at processus trochlearis pterygoideus	61
W at suture between Pter, posterior to ptp, at root pter wings	34
W at meatus quadrati	99
Anterior angle snout	55.5°
H from highest preserved supraoccipital point to area articularis quadrati	62
L snout from pmx tip to posterior maxillary jaw border:	55
L between anterior and posterior pmx suture extremities, ventral	29
Preserved left postorbital space, parasagitally	33
Inter-pmx vertical anterior suture	9
Space between external naris and orbit: best preserved, left side	15
Maxillary space below left orbit / and right orbit	15
L palate from pmx tip to basicranium at medial border of the fossa	71
L basicranium, ventral between pter at angle fossa, and posterior suture exoccipital - basioccipital	33
External naris W	22
External naris H	15
Orbit: right, longest diameter	24
Orbit: right, H	14
Orbit: left, longest diameter	21
Orbit: left, H	12
Interorbital space W at its posterior end	31
Full H, at meatus Q from Sq to area articularis quadrati	39
Meatus quadrati, left, W	19
Meatus quadrati, left, H	32
Area articularis quadrati, W	17
Area articularis quadrati, L	6

including some cat fish, and crocodile (?) fragments, according to the decoration), and of other animals (?), from Maastrichtian and Palaeocene layers up to possibly Quaternary surface layers (cat fish, crocodile): the name is not valid as far as the ICZN rules are concerned, missing a definition of a holotype, specimen(s) to be deposited in a named public collection with institutional numbers, formal diagnosis, and a kind of publication with a review process. It might be interesting to observe the "costals", if really turtle pieces (associated too much numerous "costals" are figured).

However, a Mt Indamane, true "Testudines indet." are mentioned by Michaut, by numerous remains of shells from 50 cm long or more, of at least two taxa (?). One peripheral plate is figured in one of these open publications (Michaut 2002) beside a figured posterior carapace border. The peripheral is decorated rather similarly to the two decorated peripherals from the Palaeocene lower Papyraceous shales of *Nigeremys* site area (MNHN.F.1964-27.663), which are mentioned above. It represents an undetermined new bothremydid turtle, decorated in a different pattern from that of *Taphrosphys* group and unknown elsewhere, except perhaps by that from the *Nigeremys* site we identified in the Palaeocene papyraceous shales.

SYSTEMATIC PALAEONTOLOGY.

Order TESTUDINES Linnaeus, 1758
Suborder PLEURODIRA Cope, 1864
Hyperfamily Pelomedusoides Cope, 1868
Superfamily Podocnemidoidea Cope, 1868
Family Podocnemididae Cope, 1868
Subfamily Erymmnochelyinae Broin, 1988

Genus *Ragechelus* n. gen.

urn:lsid:zoobank.org:act:A7E9333B-FD76-4C4B-AE63-1A68CED1407E

Type species. — *Ragechelus sahelica* n. gen., n. sp.

Diagnosis. — As for type and only species (type by monotypy).

Etymology. — In honour to our missing Jean-Claude Rage friend, who studied fossils from the neighbouring Ibeceten area, and χελύζ, turtle (fem.) in greek.

Ragechelus sahelica n. sp.
(Figs 5-9)

urn:lsid:zoobank.org:act:B201BDDE-1F71-49D9-8904-0D68D9595834

Holotype. — One skull, MNHN.RA.2018.0078.

Etymology. — From Sahel, geographical area of discovery.

Type locality and horizon. — Near Indamane village (or In Daman), at Mont Indamane (Mont Igdaman), 15°26'N, 5°48'E, at altitude 478 m, Tahoua district, southwestern Niger, Iullemmeden basin. Upper Cretaceous, late Maastrichtian. Gypsiferous phosphatic bone bed in the upper part of Lower Sandstones and Mudstones of "Term I" of Greigert (1966), and in the base of the Mosasaurus shales or Farin-Doutchi Formation, FD1 member (see Dikouma [1990] and Dikouma *et al.* [1994]).

Diagnosis. — A podocnemidid taxon diversified in the continental lineage of Erymnochelyinae posteriorly to the Gondwana break which separated Africa and South America. It is not a member of Stereogenyina because without their smooth, long and medially widened "secondary palate". Diagnosed as unique: by the meatus quadrati shape, "narrow hot air balloon" shaped, i.e. notable for its great height for its width and inferiorly pointed, closer to *Erymnochelys madagascariensis* and to some of the *Neochelys arenarum* specimens, instead of wider and rounded in other Erymnochelyinae; by the flat and narrow anterior meatus wall without precolumellar fossa and with an incurved incisura columellae auris; developed triturating maxillary-palatine surfaces moderately widened, even barely posteriorly, with two strong crests, unique in erymnochelyines because the intermedial one is much less developed than the medial one, contrary to *Turkanemys*, *Dacquemys* and *Mogharemys*. Oblique inclined anterolateral border of the processus trochlearis pterygoideus as in *Dacquemys*. Long skull (phenotypic category), being longer for its width than in *Neochelys*, "*N. fajumensis*" and *Mogharemys*; moderately wide for its full length (79.20%), with a triangular snout but notably transversally wide anteriorly at the not pointed external naris, long palate and short basicranium (46% of the palate length up to this basicranium); as preserved (and possible when living) moderate postorbital roof cover joining approximately the mid

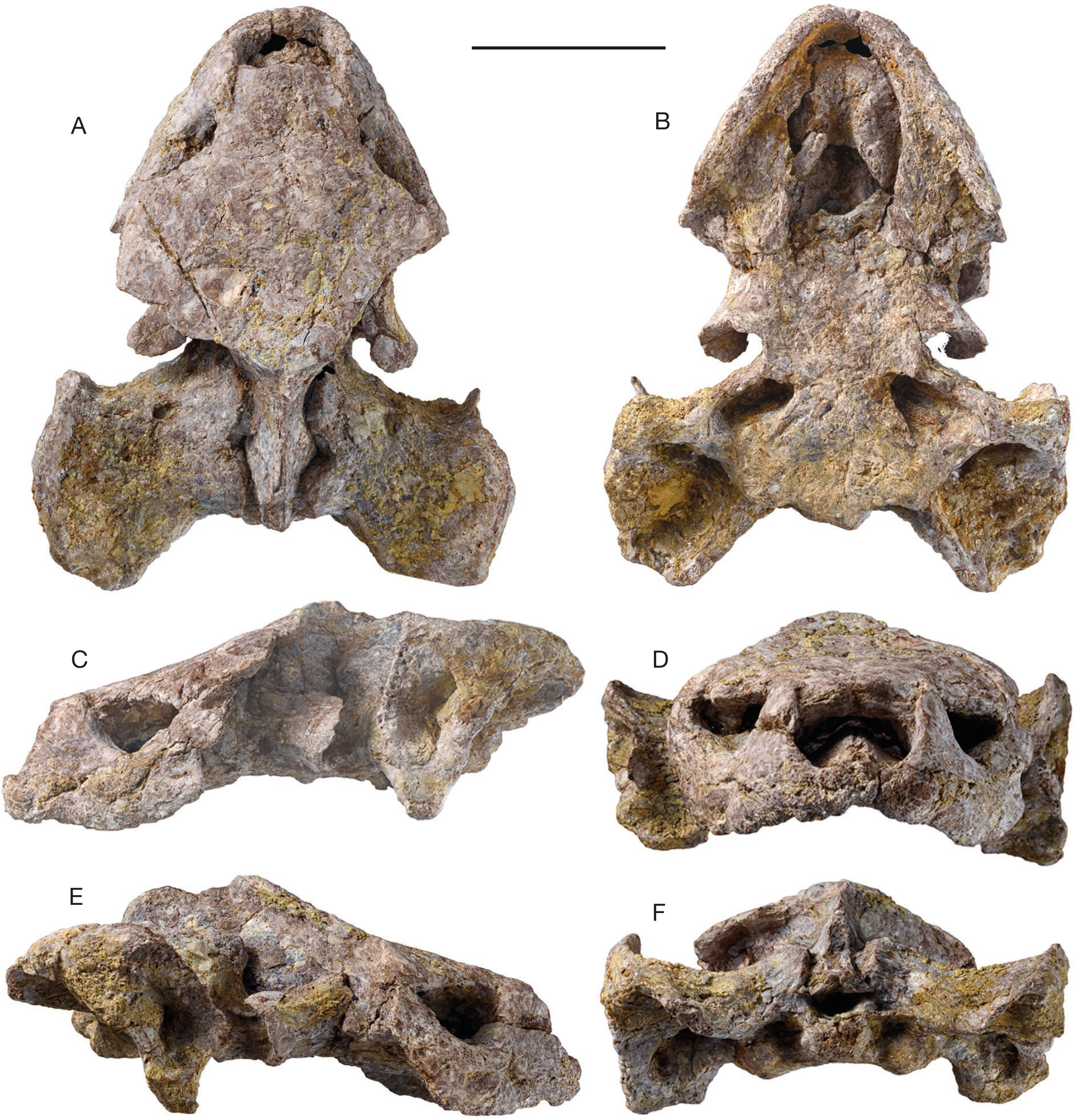

FIG. 5. — *Ragechelus sahelica* n. gen., n. sp., Indamane, southwestern Niger, late Maastrichtian; photographs of the skull, holotype MNHN-RA-2018.0031: **A**-**F**, dorsal, ventral, left lateral, anterior, right lateral and posterior views. Scale bar: 4 cm.

length of the meatus quadrati superior border, with an incurved dorsal posterior notch; not much elevated skull, with a primitive straight oblique roof cover in lateral view, the more similarly with *Turkanemys* among the longer skulls category where the full roof cover is known, not being posteriorly elevated and rounded as the more globose *Erymnochelys* skull, and not being anteroposteriorly convex in lateral view and much roofed as *Dacquemys*. Similarly or not, according to a distribution in mosaic in other erymnochelyines: consistent interorbital width with orbits nearly laterally positioned, and with relatively moderate proportions: orbit height being less great than the interorbital space, maxillae relatively high below the orbits (height less great than the interorbital space) and antorbital space still less great, and shortest inter-premaxillae suture; external naris less wide than the interorbital space but its width greater than the orbit long transversal diameter. Relatively moderately widened carotid foramen, no ventral prootic.

DESCRIPTION AND COMPARISONS

Preservation state

The skull is covered by a phosphatic gypsiferous crust that has been partly cleaned but the scute sulci are not visible and the sutures are more or less apparent by places (sometimes more visible under water). Parts of the lateral cheeks and roof (mainly quadratojugal, part of both postorbitary and jugal) are missing, as well as the supraoccipital crest, and a very small part of the right exoccipital at the occipital condyle. The medioanterior palatal part is pushed into the skull by longitudinal breaks in the maxillae while the roof is also moderately pushed into the skull by longitudinal breaks at the maxillary-prefrontal suture and at the parietal suture with the prootic and opisthotic (making the skull a little less high

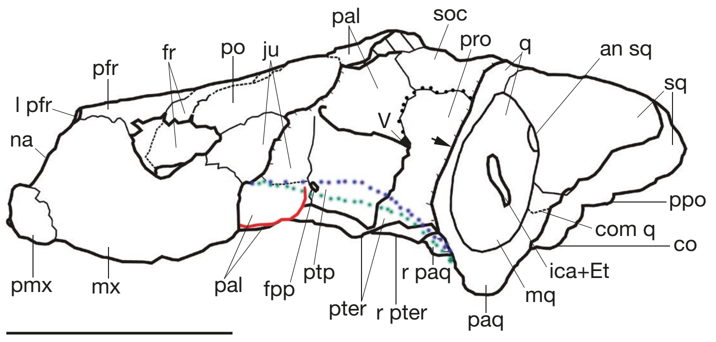

Fig. 6. — *Ragechelus sahelica* n. gen., n. sp., Indamane, southwestern Niger, late Maastrichtian. Lateral view of the skull, holotype MNHN-RA-2018.0031. Abbreviations: **an sq**, antrum squamosum; **co**, condylus occipitalis; **com q**, commissura quadrati; **fpp**; foramen palatinum posterius; **fr**, frontal; **ica+Et**, incisura columellae auris with the Eustachian tube; **ju**, jugal; **l pfr**, left prefrontal; **mq**, meatus quadrati; **mx**, maxilla; **na**, external nare; **pal**, palatine; **pfr**, prefrontal; **pmx**, premaxilla; **paq**, processus articularis quadrati; **pmx**, premaxilla; **po**, postorbital; **ppo**, processus paroccipitalis opisthotici; **pro**, prootic; **pter**, pterygoid; **ptp**, processus trochlearis pterygoideus; **q**, quadrate; **r paq**, right processus articularis quadrati; **r pter**, right pterygoid; **soc**, supraoccipital; **sq**, squamosal; **V**, foramen trigemini; **black arrow**, position of the foramen stapediotemporale; **blue and green dotted lines**, hypothetic positions for the skull lateral notch border; **red line**, border of the palatal medial crest. Scale bar: 4 cm.

than in life but preserving its oblique straight line of elevation toward the back). However, considering the potential height (from the crushing degree), the skull roof was not much dorso-ventrally elevated. The remaining crust covers the bones by places, making them thicker than in living animal; only a small part of the dorsal roof sutures and a part of the ventral sutures are visible or suspected; at least the dorsal sutures extremities appear at their free border (Figs 5, 6).

Skull measurements (Table 1)

The skull belonged to a relatively narrow turtle. Compared to a living adult *Erymnochelys madagascariensis* (Grandidier, 1867) specimen MNHN-RA-0.9544, with a skull of 8 cm up to squamosal extremity and a carapace of 31 cm long, *Ragechelus sahelica* n. gen., n. sp. skull of 13 cm ought to have a dorsal shell of *c.* 45-50 cm long.

Views

In overview (Fig. 5A), the skull is relatively long for its width compared to some other erymnochelyines (*Neochelys* Bergounioux, 1954, *Mogharemys blanckenhorni* Dacqué (1912) (Gaffney *et al.* 2011), "*N.*" *fajumensis* (Andrews, 1903)), belonging as *Eocenochelus eremberti* (Broin, 1977), *Erymnochelys madagascariensis*, *Turkanemys pattersoni* Wood, 2003 and *Dacquemys paleomorpha* Williams, 1954, to the morphotype of longer skulls in relation to the formers; that knowing skulls may be laterally posteriorly more rounded and slightly wider for their full length, presumably according to the sex, as observed in *Erymnochelys* and the South American living *Peltocephalus dumerilianus* (Schweigger, 1812). The skull is moderately wide, for the ratio of its full length up to the condyle, in relation to its width at meatus of quadrate (79.20%). The skull is triangular on the whole, progressively widened up to each meatus quadrati, with a trapezoidal snout that is not anteriorly pointed, the external naris being relatively wide with a straight transversal border. Ventrally, the palate is long up to the pterygoid processes extremities where begins the basicranium; this represents 46% of the palate length. In dorsal view, the external naris is less wide than the interorbital space and visible in dorsal view but a small anterior border of prefrontals is missing. The interorbital space is wide and it much hides the orbits that are much more lateral than dorsal. The antorbital space is shorter than the width of the external naris and the orbit length. Behind the orbits (on the better preserved left side) the postorbital is long, beside and above a preserved jugal part, and the roof is broken just at its extremity, the missing quadratojugals not letting see its lateral union with the quadrate and the squamosal on the right; but the junction part of the quadratojugal and the squamosal above the quadrate is preserved on the left. A moderate postorbital roof cover is likely (as partly preserved at the medial parietal borders, and possible when alive), approximately joining the mid length of the meatus quadrati superior border to the quadratojugal union with the squamosal: the posterior notch had to follow a curve possibly barely longer than the preserved roof part, by consideration of the unbroken limits; it might just reach the anterior otic chamber external part. The interorbital space has its two lateral borders that are parallel along a good part of their anterior length, up to the suture prefrontal-frontal, longer than in the more covered *E. madagascariensis* skull and overall the fully covered *Dacquemys*. The posterior incompletely covered dorsal skull and otic part show the great foramen stapediotemporale, at the transversal prootic-opisthotic suture, medially to the longitudinal quadrate suture, in a moderately anterior position (when this position is variable in known podocnemidids): the foramen is more anterior on the right side. The foramens might be possibly just visible in dorsal view when the roof was complete. The depression postmortem of the roof is shown by the breaks between the cranial box and the otic part (parietal and supraoccipital being pushed inside downward). The skull had a relatively straight contour, seen in dorsal (Fig. 5A) and ventral view (see Fig. 5B; 7), in relation to the globous *E. madagascariensis* skull which is anteriorly more narrowly snouted and posteriorly rounded, and perhaps its dorsal contour was closer to that of *E. eremberti*; but this is flattened and slightly distorted (Pérez-García *et al.* 2017;

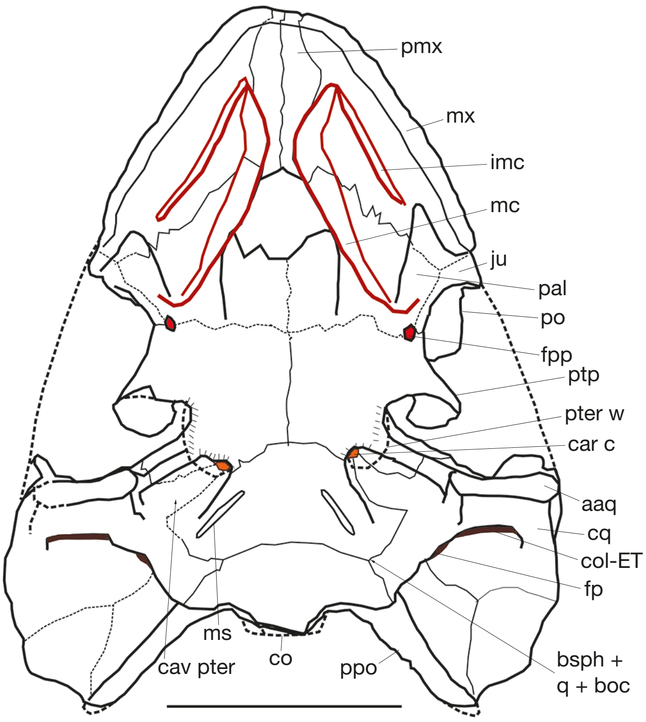

Fig. 7. — *Ragechelus sahelica* n. gen., n. sp., Indamane, southwestern Niger, late Maastrichtian; interpretative drawing of the skull, holotype MNHN-RA-2018.0031. Abbreviations: **aaq**, area articularis quadrati; **boc**, basioccipital; **bsph**, basiphenoid; **car c**, carotid canal; **cav pter**, cavum pterygoideum; **co**, condylus occipitalis; **col-Et**, columella auris with the Eustachian tube passage; **cq**, commissura quadrati; **fpp**, foramen palatinum posterius; **fp**, fenestra postotica; **imc**, intermediate maxillo-palatine crest; **ju**, jugal; **mc**, medial maxillo-palatine crest; **ms**, muscle insertion zone; **mx**, maxilla; **pal**, palatine; **pmx**, premaxilla; **po**, postorbital; **ppo**, processus paroccipitalis opisthotici; **pter w**, pterygoid wing; **ptp**, processus trochlearis pterygoideus; **q**, quadrate. Ventral view. Scale bar: 4 cm.

Broin *in* Merle 2008), not allowing to measure the length/width ratio. Anyway, considering the variability in living forms and by comparison with fossils, as seen in dorsal view, the skull contour of *Ragechelus sahelica* n. gen., n. sp. is less rounded in dorsal view than in *Erymnochelys*, *Dacquemys* and *Turkanemys* and less wide than in *Erymnochelys* (and *Peltocephalus* in South American podocnemididnes, where a slight difference of width and roundness is observed in several skulls, being probably due to sex); it is as narrow but less rounded than *Dacquemys* (in Gaffney *et al.* 2002), and, except by a wider naris part and a less rounded lateral border, its dorsal shape was the closest to that of *Turkanemys* or possibly the closest to *E. eremberti*.

The ventral face (Fig. 5B) shows the long premaxillae are anteriorly incurved (with a break), showing the probable presence of an anterodorsally pointed beak of the lower jaw implying a long lower jaw, possibly as that of *Erymnochelys* and *Turkanemys* and more than that of aff. *Erymnochelys* sp. of Madagascar (cf. *Erymnochelys* sp. in Gaffney & Forster 2003). The foramina premaxillae are not visible. There is a strong maxillary-palatine triturating surface covered by two longitudinal strong crests and palatines are poorly widened posteriorly. The intermediary crest is less prominent than the medial one, which makes the border of the sulcus palatinus, and both crests are ventrally rounded, being incrusted. The shape of the sulcus palatinus at the choanae opening is trapezoidal as that of *Erymnochelys* and there is no remain of vomer. The palate is wide posteriorly to this area and shows the prominence of the processus trochlearis pterygoidei on each side, which is characteristic of Pleurodira, in the subtemporal fosses. The two processes are inclined (as in *Dacquemys* and *Peltocephalus*) doing a well oblique anterolateral face, obviously visible as fully inclined in ventral view. The basicranium (Fig. 8) morphology has incidence on the identification. The quadrate, the basioccipital and the basisphenoid are united, hiding the fenestra postotica which is separated from the foramen jugulare posterius: this is a podocnemidoid feature (Podocnemididae and Bothremydidae). Posteriorly to the palate, the pterygoids are moderately wide, and they show the root of broken pterygoid wings (their presence being a pleurodiran character); the wing presence is attested by the visible break of the bones (the pterygoid laterally and ventrally) in the place they were positioned, but what is podocnemidine is that they were posteriorly prolonged, partly covering posteriorly a fossa on each side, the cavum pterygoideum (Gaffney *et al.* 2011) where strong lower jaw pterygoid muscles were inserted and where caratoid enters the basicranium. The fossae are oval and deep, and in their back, a rounded foramen is present and well visible (Fig. 7[car c]), the foramen posterius canalis carotici interni for the entrance in the skull of the carotid. The surface of each fossa presents the sutures of the basisphenoid, the quadrate and the pterygoid, converging toward the foramen, which is well anteromedial in the fossa corner, and no ventral prootic is present. With the part of the fossa which was covered in ventral view by pterygoid wings, all that configuration is podocnemidid. The carotid foramen

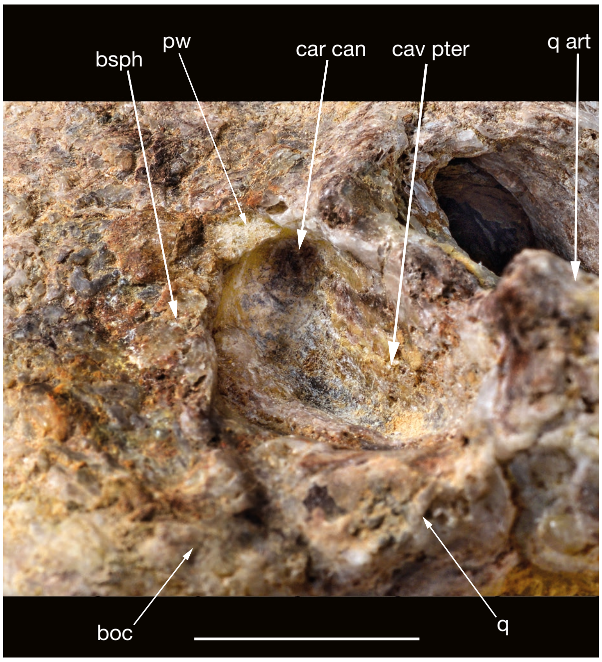

Fig. 8. — *Ragechelus sahelica* n. gen., n. sp., Indamane, southwestern Niger, late Maastrichtian; detail of the skull, holotype MNHN-RA-2018.0031, showing the rounded carotid foramen for entrance in te besicranium, at the back of the deep cavum pterygoideum, below the (broken here) podocnemidid pterygoid wing; Abbreviations: **boc**, basioccipital; **bsph**, basisphenoid; **car can**, enlarged carotid foramen; **cav pter**, cavum pterygoideum; **pw**, break of the pterygoid wing at its posterior base; **q**, quadrate; **q art**, area articularis quadrati. Ventral view. Scale bar: 2 cm.

is rather large, and this is compatible with erymnochelyines (see Broin 1991: 513) although it is moderate in relation to those where it is visible in the fossa, i.e. *Erymnochelys* and *Neochelys* (being generally hidden by the pterygoid wings or in the shadow of the photograph in other erymnochelyine taxa) (see Discussion). The quadrate facets for the lower jaw (area articularis quadrati) are short for their width as shown on the left side where it is complete, as in *Erymnochelys* notably, as in *Peltocepehalus*, being mostly longer for its width in podocnemidids. The basisphenoid shows the oblique, narrow and elongate scars for muscular insertions. Their oblique position on each side, parallel to the medial border of the fossa but well moved apart from this border is podocnemidid and not bothremydid. Lateral to the basicranium, on each side, is the ventral face of the quadrate that is united to the squamosal and with the paroccipital process of the opisthotic; this is shaped in a rounded posteriorly protruding stick (as in podocnemidids which are known for that skull part). Medially to the process and below the basicranium border, the opisthotico-squamosal surface is concave and anteromedially it opens toward the inner skull (cavum acustico-jugulare) through the fenestra postotica; this in theory gives principally passage to the lateral head vein (vena capitis lateralis), the stapedial artery, and a hyomandibular branch of the facial nerve VII. Just in the corner of the fenestra postotica, at the top of the processus articularis quadrati, ends the groove for the passage of the columella auris and the Eustachian tube, which both laterally enter in the incisura columellae auris of the meatus quadrati, in front of the commissura quadrati which exteriorly closes the quadrate on itself in podocnemidids. The ventral convex surface posterior to the groove and the commissura is that of the antrum squamosum (or antrum postoticum), made by the quadrate and the squamosal (Broin 1988a, b, 1991; Antunes & Broin 1988; Gaffney 1979; Gaffney *et al.* 2006, 2011; Lapparent de Broin *et al.* 2007).

The posterior face (Fig. 5F) shows medially the supraoccipital crest, broken at its root, pushed into the foramen magnum (appearing as relatively small here). On each side, the foramen magnum is closed medially by the supraoccipital and on each side by the exoccipitals; below the latter, the condylus occipitalis shows the union of the exoccipitals (the right one slightly incomplete Fig. 5F), with the basioccipital ventrally; the posteroinferior face of the basicranium is a thick incrusted structure made of the exoccipital, basioccipital, opisthotic and quadrate. The crust is too much strong to allow detailing each foramen and suture, and it just shows a protruding surface (in relation to the fenestra postotica area) with a depression in which had to be the foramen jugulare posterius (for the vena posterior cerebralis, the vagus nerve X, and the accessory nerves XI), the whole being therefore separated from the lateral and more anterior fenestra postotica, as in other Podocnemidoidea.

In lateral view (Figs 5C, E; 6; 8; 9), the unique external naris opens dorsoanteriorly (obliquely), missing above a little part of the prefrontal borders, the latter being slightly pushed into the naris, and this is longer than the orbits. These are slightly depressed post-mortem but anyway they were longer than high and not large in the skull, as high as the naris, slightly less high than the length of the antorbital space and of the suborbital space, and the orbit length is as great as the naris width. The suborbital space shows that the maxillae are relatively high below the orbits (height less great than the interorbital space width). The shortest measurement is that of the anterior premaxillae suture. This is well seen on the anterior view (Fig. 5D), showing the external naris is wider than high although the dorsal roof depression (roof pushed in the naris at the prefrontal-maxillary sutures). Behind the external naris, the skull (even if depressed post-mortem and taking into account the possible importance of the depression) was not much elevated, with a primitive straight oblique roof cover (Figs 5C, E; 6). Among the erymnochelyines, the roof of *R. sahelica* n. gen., n. sp. was not as much elevated posteriorly as it is in *Turkanemys* and in the globose *Erymnochelys* skull (which is a little more posteriorly elevated with a rounding of all the surface). However, the rather straight direction of the lateral profil is the more comparable to that of *Turkanemys* and probably of *Eocenochelus eremberti*, as for the dorsal contour view. In *Dacquemys* the roof is different, being anteroposteriorly longly curved with a rounded contour in lateral view. Behind the orbit, on the left side (Figs 5C; 6), the better preserved maxilla ends complete on the ventral border of a lateral notch, also preserved by a part of the ventral border of the jugal; but a part of the posterior part of this bone and the whole quadratojugal suturing anteriorly to the quadrate are missing: help to the preserved left jugal part and because of its horizontal free ventral border, the lateral notch had not to develop higher than this border; from there, the dorsal notch dorsal border joined the quadrate-quadratojugal area (missing) above a free protruding processsus articularis quadrati, making for this reason: either a much inclined dorsal border as in *Erymnochelys* (being often very small in this as in *Peltocephalus*) and as in some *Neochelys arenarum* Broin, 1977 individuals; or a less inclined border, the notch being more rectangular, similarly to other individuals of *N. arenarum.* Anyway, only a less long than high notch was possible as in *N. arenarum* examples (Broin 1977; Pérez-García & Lapparent de Broin 2015). Pelomedusoides taxa are not all known by their lateral notch (in particular erymnochelyines where it is very variable) (Gaffney *et al.* 2006, 2011) but their morphology indicates sometimes a tendency to the regression of the lateral notch. That is indicated by the way the bones participate to the notch border and to its secondary filling. This configuration is shown with figures given for some bothremydids, *Erymnochelys* and *Peltocephalus* in Lapparent de Broin & Werner (1998), as it is known by *E. eremberti* in Lapparent de Broin *et al.* (2018). Here, the presence of strong maxillo-palatine crests and of a symphyseal beak is indicative of this possibility of link with a week lateral notch presence; but this is not strengthened by the high lateral notch in *Dacquemys* and *Turkanemys* and as well as known in some stereogenyines which present long palate and long lower jaw symphysis. Anyway, the free maxillary posterior border, below the more posterior free jugal posterior border, shows the notch was not fully regressed as it is in *E. eremberti*. Posterodorsally to the processus trochlearis pterygoidei, on each side, the breaking of the skull does a slit in the place of the foramen trigemini (nerve V), at the junction of the prootic and the parietal, on the medial border of the external otic surface. This foramen is visible as an oval mark full of matrix. The slit is visible on both sides (Figs 5C, E; 6) and the foramen superior part is visible on the left side above the posterosuperior border of the rolled processus trochlearis pterygoidei (Figs 5C; 6). The slit posterodorslly extends, bordering the cranial braincase. The ventral part of the cerebral wall (constituted by the parietal and the supraoccipital) is ventrally pushed in, medial to the prootico-opisthotic suture. The lateroposterior external otic face is preserved by nearly exclusively the quadrate and the squamosal. The left side (Fig. 9) only shows a very small quadratojugal lateroposterior part at its junction with the squamosal, above the meatus quadrati. In the latter, the closed quadrate behind together the columella and the Eustachian tube is podocnemidid contrary to bothremydids were the Eustachian tube passage is posterior to the commissural quadrati (not being included in the incisura). The meatus quadrati is here unique by together its shape and its absence of precolumellar fossa: it is high and relatively narrow, post-mortem slightly more on the left side; the quadratojugal on the right side (Fig. 5E) and also a part of inferior quadrate border on the left (Figs 5C, D; 6) are missing. Although a small deformation, the meatus is enough preserved to show a “hot air balloon” shape, i.e. it is superiorly rounded (but with a great height for its relative narrow width) being inferiorly pointed, rather as in *N. arenarum* (see Pérez-García & Lapparent de Broin 2015) and also in *Erymnochelys madagascariensis* individuals (small variations of width and rounded shape in specimens of both) but, contrary to them, there is no precolumellar fossa on the flat and narrower anterior surface. This precolumellar fossa absence is also given for *Mogharemys* (*fide* Gaffney *et al.* 2006), but in this, the meatus is rounded and very wide and the walls are concave, the incisura columellae auris is wider, the processus articularis quadrati is not protrudent and the area articularis quadrati is short and wide, all that as in *Turkanemys* (this area is generally longer for its width in podocnemidids). The precolumellar fossa is variable in size (depth, width or length) in living *Podocnemis* species (Williams 1954a) and in *Erymnochelys* specimens. Here, the elongate meatus inferiorly ends in a protruding processus articularis quadrati, a little longer than in *E. madagascariensis* and *N. arenarum*. It is protruding as in the living South-American podocnemidine *Peltocephalus* (podocnemidine *sensu* Broin 1988a, b, 1991) and as in *Bairdemys* in stereogenyines. But in both latter, the meatus is rounded and much wider as in *Mogharemys* and as in the other podocnemidids including the other erymnochelyines; however, the articular process is mostly not protruding

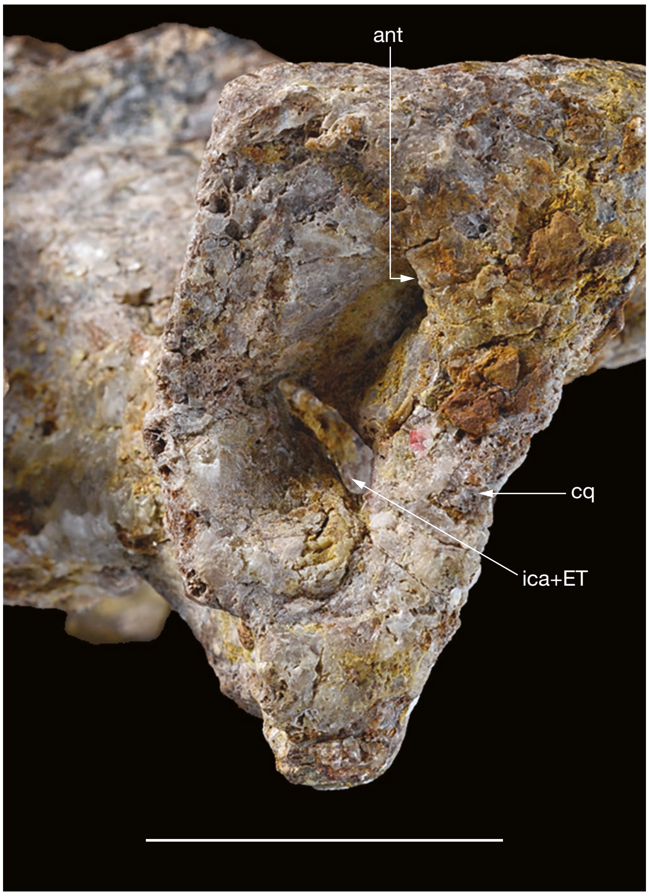

Fig. 9. — *Ragechelus sahelica* n. gen., n. sp., Indamane, southwestern Niger, late Maastrichtian; detail of the skull, cavum tympani area, holotype MNHN-RA-2018.0031. Abbreviations: **ant**, antrum squamosum; **cq**, commissura quadrati; **ica+Et**, incisura columellae auris with Eustachian tube. Left lateral view. Scale bar: 2 cm.

in podocnemidids. Endly, *Turkanemys* and *Ragechelus* n. gen. share a rather similar lateral profile, but the lateral notch and meatus quadrati areas are fully different; *Ragechelus* n. gen. appears as closer to *Neochelys* and *Erymnochelys* for these areas.

In *Ragechelus*, above about the mid part of the meatus quadrati is the squamosal, anteriorly beginning at mid meatus length (where the quadratojugal laterally ends, after covering the roof). In the inferior-middle part of the meatus, the incisura columellae auris is united to the Eustachian tube in a long, inclined and slightly curved and moderately wide slit (which widens inferiorly). Anteriorly, the inclined meatus wall is flat, being without precolumellar fossa, and the inclined posterior wall is transversal so that, nearly alone, its wide thickened external border is visible in Figures 5C, E and 6, with the suture of the rolled on itself quadrate, making the commissura quadrati (Figs 1C, E; 6). Posteriorly above this commissura is the antrum squamosum (or postoticum), opening in the meatus by a flattened entrance, the antrum being less swollen than in the living freshwater pelomedusids, approximately as in living podocnemidids and less flattened than in bothremydids. The antrum is more developed in terrestrial or half-terrestrial forms.

Summary of ratios
Palatino-pterygoid suture > roof cover length > pterygoid width behind the processus trochlearis oticus > basicranium length > interorbital space > external naris width *c.* = orbit length > suborbital space > or = to external naris height > antorbital space > inter-premaxillae suture.

DISCUSSION

RAGECHELUS SAHELICA N. GEN., N. SP. AND *NIGEREMYS*: RELATIONSHIPS AND DISTINCTION

They are both Podocnemidoidea principally by the quadrate union with the basisphenoid and basioccipital. Because their presence in close Maastrichtian layers of Iullemmeden basin (Niger), the comparison of *Ragechelus sahelica* n. gen., n. sp. with the bothremydid *Nigeremys gigantea* (see above) was necessary. The holotype skull of *N. gigantea* is longer than that of *R. sahelica* n. gen., n. sp., being 24 cm long up to squamosals and it corresponded to a carapace of *c.* 110-120 cm long, as the large shells of NHM coll. mentioned in marls of Indamane (see above). Both skulls were incrusted of gypsiferous phosphate and found with the same late Maastrichtian "Mosasaurus shales fauna" as a whole. It is easy to differentiate the two forms because, being a Bothremydidae, *Nigeremys* has a small rounded incisura columellae auris only integrating the columella, and the commissura quadrati separates it from the posterior quadrate notch of the groove for the Eustachian tube (knowing that the commissura quadrati May be not fully close, remaining a long and thin not closed slit in some other bothremydids (Gaffney *et al.* 2006)). While *R. sahelica* n. gen., n. sp. is a podocnemidid by features such as the incisura columellae auris which is inferiorly closed including both the columella and the Eustachian tube and by the presence of prolonged pterygoid wings which partly hided the cavum pterygoideum. *Nigeremys* has also a deep cavum pterygoideum ("podocnemidoid fossa"of Lapparent de Broin & Werner 1998) in a basicranial ventral surface that is as short as in all the Nigeremydini and not in Taphrophyini (restricted to *Taphrosphys* group of Broin 1988b), Bothremydini and primitive forms: it is a fossa for the insertion of lower jaw pterygoid muscles. However, being present in bothremydids only in some forms, it is parallelized with the cavum pterygoideum or "enlarged carotid canal" of Podocnemididae, and it is not partly covered by pterygoid wings as it is in all the Podocnemididae. For the insertion of their jaw muscles, bothremydid groups have either a primitively flat basicranial pterygoid surface, without these deep muscular fossae (such as *Zolhafha bella* Lapparent de Broin & Werner, 1998, *Taphrosphys* in Gaffney *et al.* 2011 and *Sankuchemys sethnai* Gaffney, Sahni, Schleich, Singh & Srivastava, 2003) or a weakly concave pterygoid surface: These and similar other bothremydids have a primitive Pelomedusoides long basicranial ventral surface as in podocnemidids, *Ragechelus sahelica* n. gen., n. sp. included. Other bothremydids, the Nigeremydini, including *Nigeremys gigantea*, present a deeper fossa in a derived characteristic short basicranial surface. Because all the bothremydids do not present the deep fossae (cavum pterygoideum) these are realized by parallelism in Erymnochelyinae and Bothremydidae. So that it was a mistake (Lapparent de Broin & Werner 1998) to have talked, without doing the distinction, about a podocnemidoid fossa together for the occasional bothremydid cavum pterygoideum and for the determinant podocnemidid "enlarged carotid canal", as seen by Gaffney *et al.* (2006). The podocnemidid cavum of *R. sahelica* n. gen., n. sp. is a deep depression which was half hidden below the pterygoid wings (broken here), these not being developed in bothremydids, *Nigeremys* included. The prootic (its ventral face being pushed inside by the quadrate-basicranium union) is not apparent in podocnemidids. It is still ventrally present in many bothremydids, others than *Nigeremys* where it is absent, as in *R. sahelica* n. gen., n. sp. and all other podocnemidids. A widened carotid canal foramen is not present in *Nigeremys* as in any other bothremydid, contrary to *R. sahelica* n. gen., n. sp. and various podocnemidids (see below). *Nigeremys* skull is massive, wide and thick with a large triangular snout, with strong and medially crested maxillary triturating surfaces: there is a certain analogy of having developed triturating surfaces, traducing an analogue feeding pattern of strong and hard preys (such as hard molluscs, echinids, hardly scuted fishes and others). The other members of the *Nigeremys* group variously develop the triturating surfaces, each in its way but always in a same general shape. For example, *Ilatardia* triaturating surfaces are less wide and less strongly crested than in *Nigeremys*; those of *Azzabaremys moragjonesi* Gaffney, Moody & Walker, 2001 have a double crest transversally developed. And *Acleistochelys maliensis* Gaffney, Roberts, Sissoko, Bouaré, Tapanila & O'Leary, 2007 has on each side a long intermediate crest in its more elongated snout than in the others. But as Nigeremydini, all of them share: - the wide and large snout in the skull, triangular in shape, - with skull parallel lateral borders posterior to the snout ending in protruding squamosal points, - the wide palate anterior to small few protruding and much inclined processus trochlearis pterygoidei, - anterior to a short basicranium surface, - the occipital condyle resulting in an anterior position. In all these nigeremydines, the cavum pterygoideum, without developed pterygoid wings, is more or less deep and delimited medioposterioly, but well delimited lateroanteriorly by the much overlying quadratopterygoid wall on the short basicranial surface.

R. sahelica n. gen., n. sp. shares a basal common ancestor with South American podocnemidids. However, in our opinion, *R. sahelica* n. gen., n. sp. branch developed in Africa after the break of the Gondwana (which occurred toward the early Cretaceous), in a subfamily constituted by the successive derivation of subgroups known at least as soon as late Cretaceous episods (effective at Senonian of Ibeceten level and at Maastrichtian of Indamane and Berivotra in Madagascar) and then by successive steps at early Eocene, Oligocene, Miocene-Holocene (Pérez-García *et al.* 2017: fig. 1). It includes *Erymnochelys s. l.* (*sensu* Gaffney *et al.* 2011) which is present as soon as early Miocene in Africa (Egypt, Kenya, République démocratique du Congo, Namibia) (Gaffney *et al.* 2011; Hirayama 1992; Lapparent de Broin 2000a, 2003) up to the living *E. madagascariensis*. While, as soon as late Cretaceous in South America the podocnemidid branch also saw derivations of various species, up to the Miocene-extant *Podocnemis* and (only in present times) *Peltocephalus dumerilianus*. This shares with podocnemidine Maastrichtian-to-extant forms at least a part of the typical podocnemidine cervical pattern (saddle joints) and differently developed pectorals (few anteriorly developed), in relation to erymnochelyines. As it presents some similarities with erymnochelyines, among some of the latest phylogenetic propositions this living Amazonian *P. dumerilianus* is proposed as sister taxon of various African (or of African origin) species, the derivations of which have occurred between Eocene and Miocene times, a long time after the Gondwanan landmasses breakup: *Peltocephalus* is presented as sister taxon of the living Madagascan *Erymnochelys* (firstly in Gaffney *et al.* 2011). This is acceptable in a molecular analysis (such as Vargas-Ramírez *et al.* 2008) where no fossils are introduced and because *Peltocephalus* (and *Podocnemis*) (South America) and *Erymnochelys madagascariensis* (Madagascar) are the only remaining living podocnemidids. But it cannot be admitted in a work integrating fossils, without taking into account the Gondwana breakup age and the possible age of the starting point of the clades. In such cladistic analyses, the introduction of this South American living *Peltocephalus* as sister taxon of the Madagascan form is done after the derivation of the Kenyan *Turkanemys* (effective at Miocene and obviously related to *Erymnochelys,* that as even been seen by Gaffney *et al.* (2011) in their text, contrary to their cladogram). The introduction of the living South American form is done after the derivation in the old world of other taxa of the erymnochelyine lineage, being of the *Erymnochelys* group or not such as early to late Eocene *Neochelys* and Eocene to Plio-Pleistocene sterogenyines (see their distribution in Pérez-García 1917: fig. 1).Similarly, the introduction of *Peltocephalus* is done after the derivation of the Oligocene Egyptian erymnochelyine *Dacquemys*. This taxon is not associated to a shell, so that, as *Mogharemys*, it cannot theorically figure in the *Erymnochelys* group. However dissociated shells, which are conform to the *Erymnochelys* group, are present in their localities. Thus, in these phylogenies, extant Amazonian forms are then introduced in an old lineage, late in the late Paleogene-Neogene of Africa, which is not possible because of the palaeogeogaphy. And that is strengthened by the knowledge of *Ragechelus sahelica* n. gen., n. sp. As said above, the Ibeceten form and the Madagascan aff. *Erymnochelys* sp. lower jaw were not introduced in Gaffney *et al.* (2011) and in other recent phylogenies, an introduction which ought to have alerted the authors. In cladistic analyses works, variants to *Peltocephalus* introduction within the African erymnochelyine clade are those of other South American Amazonian recent taxa. Such is as the late Miocene, *Caninemys* Meylan, Gaffney & Campos, 2009) (Cadena 2015), a form appeared after the continental Gondwana breakup. In another analysis (Ferreira *et al.* 2018b) extant *Peltocephalus* is proposed as sister taxon of a clade uniting the Miocene African *Mogharemys* (known by a partial skull broken in two parts) with stereogenyines (the first species of which dating from the African middle-late Eocene). The presentation of *Mogharemys* in (Gaffney *et al.* 2011) or close to (Ferreira *et al.* 2018b) the stereogenyines is contrary to its crested palate, pterygoid and interparietal scute morphology, that are closer, notably, to those of *Dacquemys*. This latter analysis also presents the rupture of the *Erymnochelys* lineage *sensu nostro,* as well as *sensu* Gaffney *et al.* (2011) and Cadena (2015). In particular it breaks the genus *Neochelys*, notably contrary to Broin (1977), Cadena (2015), Pérez-García & Lapparent de Broin (2013, 2015) and Pérez-García *et al.* (2017).

By the absence of a smooth "secondary palate", *R. sahelica* n. gen., n. sp. is not a representative of the erymnochelyine Stereogenyina (Ferreira *et al.* 2015, 2018a; Gaffney *et al.* 2011; Pérez-García *et al.* 2017; Weems & Knight 2013; Zouhri *et al.* 2017). The presence of the two maxillo-palatine crests is rare in podocnemidids but the presence of one crest is frequent. In podocnemidines (*sensu* Broin 1988a, 1991): two maxillo-palatine crests are always present in *Podocnemis unifilis* group (*sensu* Williams 1954a). There are always three crests in *P. expansa* group, one only in *Caninemys* (one specimen); and in *Peltocephalus* there is rarely one, which is week, either on one side (one specimen) or on both sides (two specimens on 15 observed skulls). In Erymnochelyinae *sensu nostro*, the stereogenyine forms with their apomorphic flat surfaces being set apart, one crest may be present: it is barely or not visible in *Neochelys* and "*N*". *fajumensis* (the intermediate crest being represented by a line of dots and the medial crest by a striated border). These both features are a little accentuated in *Erymnochelys*. More developed crests are present in others: *Turknanemys*, *Dacquemys* and *Mogharemys*. These taxa share both crests of similar importance contrary to *R. sahelica* n. gen., n. sp. where the medial crest is much stronger than the other one. Both equal crests are stronger than in *R. sahelica* n. gen., n. sp. in the long *Dacquemys* skull and still much stronger in the short *Mogharemys* skull. So that, this erymnochelyine tendency of developing crests is realized in relation to the diet, in their own way in each species, as in other podocnemidoid members, including podocnemidines and bothremydids of the *Nigeremys* group (Nigeremydini). In *R. sahelica* n. gen., n. sp., the carotid canal foramen (Figs 7, 8) is enlarged (an erymnochelyine feature) and rounded; it is much wider than in South American forms (*Peltocephalus* excepted); but it is not as wide as in the living *Erymnochelys*, the Eocene *N. arenarum* and (as drawn in Gaffney *et al.* 2011) the Oligocene *Dacquemys*. It is unknown in the Miocene *Mogharemys*, its skull being incompletely preserved. The carotid foramen is not apparent in *Turkanemys* figures, but what appears of the cavum pterygoideum is great. In the Stereogenyina of the *Shweboemys* group of Zouhri *et al.* 2017, the cavum pterygoideum is large; the foramen is figured as minute (Gaffney *et al.* 2011: fig. 55) in the Eocene basal stereogenyine *Cordichelys antiqua* (Andrews, 1903) (but not being fully visible on the photographs). The cavum is complete, but the foramen is a little wider, seeming as large as in *R. sahelica* n. gen., n. sp., in *Latentemys* (Gaffney *et al.* 2011: fig. 58). The cavum is not completely preserved and the carotid foramen is not preserved in *Brontochelys gaffneyi* (Wood, 1970). However, as in *Shweboemys pilgrimi* Swinton, 1939, the preserved sulcus cavernosus entrance and/or the sulcus itself are very wide (seen on MNHN.F casts of the three species). The cavum is large, but the foramen is unknown in stereogenyine *Stereogenys* and *Bairdemys*. Thus, in all these erymochelyines, the cavum pterygoideum is deep, doing "the enlarged carotid canal", as convenient to have a wide muscular insertion surface. But in fine, the carotid foramen at the entrance in the basicranium is variable: it is often in the shadow in the figures, and it is hidden below the pterygoid wing when preserved. As shown in Broin (1991) and Lapparent de Broin & Werner (1998: fig. 5) the inner entrance of the carotid canal in the braincase is different according to extant podocnemidid groups. The carotid foramen varies from minute to wide and the prootic is inside, eroded in various ways (*Podocnemis expansa*, other *P.* spp., against *Peltocephalus*, *Erymnochelys*, *Neochelys*) to which we add Gaffney *et al.* (2011)'s data, with the record of the modification due to the pterygoid which developed in the sulcus cavernosus on the basisphenoid, beside the prootic place, in *Peltocephalus* alone. The inner basicranium structure (prootic erosion, sulcus cavernosus width, trabeculae shape and rostrum basisphenoidale length) is unknown in most species, including *R. sahelica* n. gen., n. sp. The moderate size of the foramen of *R. sahelica* n. gen., n. sp. in relation to *Erymnochelys* and *Neochelys* may correspond to a weaker inner prootic erosion. Anyway, as in them both, the prootic is missing ventrally and the carotid foramen is enlarged. If *R. sahelica* n. gen., n. sp. is attributed to the subfamily by the enlarged carotid foramen, it is also due to the combination of the whole shape and proportions of the skull and morphological similarities particularly with living *Erymnochelys, Eocenochelus*, *Turkanemys* and also *Dacquemys* and *Mogharemys* (in the way they are known) at times occurring after the Gondwana breakup. These five genera are members or potential members of the *Erymnochelys* group; the two last are only potentially members, being defined on a skull, but according to the preserved shells in their locality: what is not known for *Ragechelus*, missing a shell. But *Ragechelus* n. gen. has also affinities with other erymnochelyines such as *Neochelys* (primitively) by some similarity for the meatus quadrati shape (as with *Erymnochelys*), and (by derivation) possibly by a lateral notch tendency to filling as in *Erymnochelys* and *Eocenochelus*, and anyway by a not high lateral notch and a not much rounded meatus quadrati. It shares characters with taxa as well with short skulls as with long skulls. For example, it shares with the two latter and *Turkanemys* the long triturating surfaces implying a longer and stronger upper jaw than in the Ibeceten Senonian form. But as the latter, *Erymnochelys* has no strong palatal crests, contrary to *Ragechelus* n. gen. and *Turkanemys*, as well as contrary to *Mogharemys* and *Dacquemys.* All that shows an adaptative feeding diversity from the Senonian to Present, evidenced in this mosaic of alternatively shared characters.

INDAMANE AND IBECETEN ERYMNOCHELYINES REPRESENT AN OLD-WORLD LINEAGE.

The postcranial of *Ragechelus sahelica* n. gen., n. sp. is unknown. With few skeletal elements and without shell together with a skull, satisfying relationships will be difficult to establish. The skull is considered as erymnochelyine: its presence at Indamane, at the same times as the aff. *Erymnochelys* sp. of Madagascar (Gaffney & Forster 2003) and close to the time of the Ibeceten erymnochelyine of the continental Senonian (Fig. 10A-G), allow showing in Cretaceous of Niger the old attestation of the African erymnochelyine lineage

This erymnochelyine Ibeceten form was closely related to the *Erymnochelys* group. A great lot of dislocated elements of several turtle species (at least three) have been collected in this Senonian locality (Broin *et al.* 1974) which is well separated from the Maastrichtian level of the locality of the bothremydid *Nigeremys* (see above). Ibeceten turtle elements are of several unknown podocnemidids, including one smaller form notably represented by an entoplastron. This is not pelomedusid. In this smaller form (Fig. 10G), the humeropectoral sulcus position crosses the entoplastron as in podocnemidids, not being posterior to it as in this Pelomedusidae family (as also in primitive Bothremydidae). Further, the sulcus is not medially as posterior to the epihyoplastral suture as in most *Peltocephalus* specimens (Fretey 1987; MNHN coll., E. Cadena pers. comm.). But as in *Peltocephalus*, this Ibeceten specimen is not of the *Erymnochelys* group due to the intergular which primitively separates the gulars, up to the entoplastron, that it overlaps (Fig. 10G) in front of the junction of the humerals, as also as in other erymnochelyines (Pérez-García *et al.* 2017: fig. 1) and podocnemidines. In Ibeceten most other material and only in what we consider as this *Erymnochelys* group-branch of the subfamily (Pérez-García *et al.* 2017), the long gulars meet behind the short intergular on the entoplastron (Fig. 10A-C, E, F). The humeropectoral sulcus of this unique Ibeceten smaller

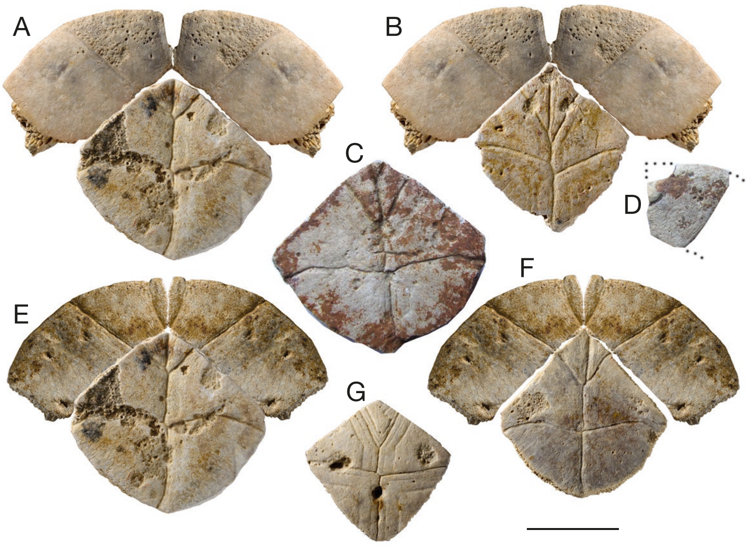

Fig. 10. — Podocnemididae from Ibeceten, south-western Niger, Senonian, Gularo-Intergular pattern, MNHN.F.IBC coll. **A**-**F**, Erymnochelyine Erymnochelys group, variability in shape of plates and scutes: alternative epiplastral and entoplastral combinations: **A**, epiplastron IBC560 and entoplatron IBC1898; **B**, epiplastron IBC560 and entoplastron IBC1903; **C**, entoplastron IBCx1; **D**, IBCx2, fragmentary epiplastron; **E**, epiplastron IBC1893 and entoplastron IBC1898; **F**, epiplastron IBC1893 and entoplastton IBC542. Podocnemididae indet., primitive intergular pattern; **G**, IBC1899, entoplastron. Ventral views. Scale bar: 2 cm.

form has not two convex sinuosities which are present on the other Ibeceten entoplastra of the *Erymnochelys* group (Fig. 10A-C, E, F); it is less derived than in these and in the Cenozoic erymnochelyines. Then, the great majority of anterior plastral Ibeceten plates agree with the *Erymnochelys* group by the typical anterior lobe scutes configuration. Ibeceten erymnochelyine humeropectoral sulcus covers nearly all the posterior mid-part of the entoplastron, its course doing a convex sinuosity on each side of the medial sagittal line; however, from the preserved epiplastra, the sulcus does not cover them, or it just reaches the lateral angle of the entoplastron, when it overlaps the epiplastral corner in Cenozoic erymnochelyines. In South American forms, as a whole, the humerals are more posteriorly extended on the anterior lobe than in erymnochelyine Afro-European forms, even if laterally the humeropectoral sulcus may run a little anteriorly on a part of epiplastra. In *Podocnemis* group, the humeropectoral sulcus is rather straight and it is situated at the transversal level of the epihyoplastral suture. However, at Palaeocene of Bolivia, the humeropectoral sinuosities of the Ibeceten form are seen in some of the adults of the podocnemidine *Lapparentemys vilavilensis* (Broin, 1971) (Broin 1991) but in a anteriorly advanced position; however, it is not the case in the young and other specimens where the sulcus runs straightly or in a wide V line, as in adults of extant *Podocnemis* and *Peltocephalus.* In *Bauruemys elegans* (Martin Suarez, 1969) (Late Cretaceous of Brazil) there are also some sinuosities of the sulcus humeropectoral. But as a whole, in erymnochelyines the humerals are less posteriorly extended. The important fact is the *Erymnochelys* group (*sensu* Pérez-García *et al.* 2017) gular-intergular pattern never happens in South America.

The majority of the skeletal Ibeceten bones agree with the Erymnochelyinae as compared notably with *E. madagascariensis* and *Eocenochelus*: carapace plates shape (many of them being costulated as in *Erymnochelys*); iliac suture scar by its shape and position on costals 7 and 8; xiphiplastral pelvis scars, but being present two morphotypes for the ichiatic insertion: one primitively more posteriorly extended in the anal extremity as in several *Eocenochelus* species, and one less extended, more derived as in other *Eocenochelus* species and in *Erymnochelys* (Pérez-García 2017; Pérez-García *et al.* 2017; Pérez-García & Smith 2017); anterior and posterior limb and girdle bones robust as in *Eocenochelus* (being slender in *Erymnochelys*), beside few Ibeceten smaller and relatively lower for their width pelvis elements; and there are many identical fragmentary dentaries and maxillae (Lapparent de Broin & Guntupalli Prasad in press: fig. 7.3). The dentaries are of a form agreeing with the lower jaw of aff. *Erymnochelys* sp. from the Berivotra area, Maastrichtian of Madagascar (Gaffney & Forster 2003) (cf. *Erymnochelys* sp. in this work), but they present a slightly shorter symphysis. It is also shorter than in *E. eremberti* and the Miocene to living erymnochelyine forms (see Wood 2003) and shorter than that we can establish for *Ragechelus sahelica* n. gen., n. sp., from the snout shape and its ventral palate length. Found together with the "erymnochelyine" plastral plates, dentaries and maxillae, there is a single Ibeceten preserved podocnemidid basisphenoid and there are podocnemidid vertebrae. These are not podocnemidine centra, i.e. they lack saddle joints, reduced ventral central crest, eventually linked posterior postzygapophyses; all that in a variable number of neck vertebrae (see Broin 1991) (Lapparent de Broin & Guntupalli Prasad in press: figs 7.5, 7.6). They have not the low condyles (wide for their short height) seen in some cervicals of *Turkanemys* and *Erymnochelys* (Hirayama 1992; Wood 2003), but they have similarly other cordiform joints. The basisphenoid had ventral muscle scars conform to those of

R. sahelica n. gen., n. sp., i. e. the scars are separated from the border of the bone at the difference with the Bothremydidae where they border the bone; and the basisphenoid must have had contact with pterygoid wings to partly cover a concave cavum pterygoideum (of which the slope below the lateral border is preserved); the place of entrance of the carotid in the anteromedial corner of the bone is also in conformity with podocnemidids but the basisphenoid alone does not give the external size of the carotid foramen (Lapparent de Broin & Guntupalli Prasad in press: fig. 7.3).

There are skeletal features showing *Peltocephalus* is not related to the *Erymnochelys* group. Thus, *Peltocephalus* differs by the primitive intergular-gular pattern (closer to Fig. 10G). Never found in the Americas, known in Africa as soon as in the Senonian Ibeceten plates, the *Erymnochelys* group pattern (Fig. 10A-F) is well known during the Cenozoic times. It is seen in Europe as soon as the early Eocene and up to the late Eocene by *Eocenochelus* Pérez-García, Lapparent de Broin & Murelaga, 2017 (Broin 1977; Broin *in* Merle 2008; Pérez-García & Chapman 2017; Pérez-García *et al.* 2017, 2019; Pérez-García & Smith 2017) and in Africa (Pérez-García *et al.* 2017: fig. 1) as soon as continental deposits are preserved: first by the early Oligocene "*Podocnemis*" *fajumensis sensu* Andrews (1903) ("*P.*" *blanckenhorni* Reinach, 1903), and then in the Neogene of Africa by "*Podocnemis*" *aegyptiaca* Andrews, 1900 (possible shell for the *Mogharemys blanckenhorni* Dacqué, 1912 skull), *Kenyemys williamsi* Wood, 1983, *Turkanemys pattersoni* Wood, 2003 of Kenya (Pérez-García *et al.* 2017: fig. 1), and *Erymnochelys* sp. of Zaïre (République démocratique du Congo) (Hirayama 1992) up to *Erymnochelys madagascariensis*. Some erymnochelyines (including *Neochelys* and the Stereogenyini) do not present the *Erymnochelys* group derived intergular scute pattern. However, they have the anteriorly positioned humeropectoral sulcus on the entoplastron and epiplastra and some have a reduced intergular at the length of the gulars (in various species).

Thus, within the frame of anteriorly advanced pectorals on the anterior lobe, there is a variability of the intergular length and width in relation to the humeropectoral sulcus position, that functions in a structural complex, within a species-specific framework. In some forms, the first variability is for the intergular: contrary to the *Erymnochelys* group, it is primitively never shortest than the gulars. The variability may consist in the gulars (which extend posteriorly on the entoplastron), being nearly linked or linked by a dot or by a small width to the pectorals; intergular and gulars may be as long, in a triradiate conjunction with the pectorals. But in other species, the intergular length and width is variable even in one species (*Neochelys arenarum* Broin, 1977), the scute being linked or not to the pectorals and, when linked, by a variable width (from a dot up to a wide proportion of contact with pectorals) (Broin 1977; Pérez-García & Lapparent de Broin 2013, 2015). An extreme intergular variability is the norm of *Andrewsemys libyca* (Andrews, 1903) (*Stereogenys libyca-cromeri* in Andrews (1906)) where the long intergular much posteriorly separates the humerals in a unique way (Pérez-García 2017).

A second variability is of the sulcus overlap on the epiplastra as seen above: the sulcus is at the epi-hyoplastral suture level except just laterally (among which some *Neochelys* spp., *Eocenochelus, Turkanemys, Kenyemys* and other African members of the *Erymnochelys* group). However, in other species and groups of species ("*Podocnemis*" *fajumensis*, *Neochelys*, *Shweboemys* group, "*Stereogenys*" *podocnemoides* Reinach, 1903), it is completely anterior, together on the entoplastron and epiplastra (Andrews 1906; Broin 1977; Broin *in* Merle 2008; Cadena 2015; Dacqué 1912; Pérez-García & Chapman 2017; Pérez-García & Lapparent de Broin 2013, 2015; Pérez-García *et al.* 2013, 2019; Pérez-García *et al.* 2017; Pérez-García & Smith 2017; Reinach 1903; Weems & Knight 2013; Wood 1983, 2003). Thus in Cenozoic African and African in origin erymnochelyines, the sulcus is always more anterior (laterally or both medially and laterally) with respect to the situation in extant podocnemidines, *Peltocephalus* included (as seen by Gaffney *et al.* 2011) and Ibeceten forms, making shorter humerals and longer pectorals: to define a Pelomedusoides taxon, it is then necessary to always consider a plastral complex of structures, integrating together the humeropectoral sulcus position on the epiplastra in relation to the epihyoplastral suture, its anterior, middle or posterior level on the entoplastron, added to the intergular-gulars pattern and the sinuosity of the course of the sulci. And all that must be in harmony with the conjunction of the palaeogeographical and stratigraphical data. *Peltocephalus* has rarely one of these specific variabilities: its humeropectoral sulcus is posterior to the epihyoplastral suture on the entoplastron as in primitive podocnemidid forms, even if, laterally, it overlaps the epiplastra on a small part of its course, which most often forms a wide open V on the lobe (Fretey 1987; Institutional referred coll. in material and methods; E. Cadena figs. by pers. comm.); as a whole the sulcus is more posterior than in *Podocnemis* and in the small Ibeceten form. *Peltocephalus* intergular length is variable in length, rarely contacting the pectorals (Fretey 1987) but it is never shortest than the gulars which are not united. For us, *Peltochephalus* is not the sister taxon of *Erymnochelys* and not a member of the *Erymnochelys* group, no more than of any other erymnochelyine. That is even if some *Peltocephalus* characters are somehow similar or really similar to those of some Afro-European erymnochelyines and particularly *Erymnochelys*: enlarged carotid foramen, lateral notch filling, long jaw, skull cover, domed shell with short nuchal. By contrast, *Peltocephalus* has shared features with *Podocnemis* and other South American forms such as *Lapparentemys* and *Bauruemys* (saddle joints known only in South America), and with some Maastrichtian poorly known podocnemidines: "*Podocnemis*" *brasiliensis* Staesche, 1944 has the closer humeropectoral position to *Peltocephalus*, and *Pricemys caiera* Gaffney, Meylan, Wood, Simons & Almeida Campos, 2011 has a parietal scute with diverging lateral borders as in *Peltocephalus* (and as also in the extant *Podocnemis sextuberculata*, although this is of the *P. unifilis* global morphotype). Thus, *Peltocephalus* may be seen as closer to *Podocnemis* lineage than to Afro-European forms.

That shows the possibility of a reserve of South American characters not found in the old world, which might be extended by comparisons of postcranial bones from Cretaceous Brazilian forms (França & Langer 2005; Ferreira 2011; Martin Suarez 1969) (MNRJ and MNHN.F coll.) with living forms (MNHN.RA coll.).

In fine, as, among erymnochelyines, *R. sahelica* n. gen., n. sp. shares skull characters mostly with *Erymnochelys*, *Eocenochelus* and *Turkanemys*, and according to the intergular-gular typical pattern presence in the close underlying layer of Ibeceten in the Niger Tahoua district, it is possible that the plastron of *R. sahelica* n. gen., n. sp. had this pattern: new expeditions on Mont Indamane to collect shells in its bone bed would be welcome. However, as several other African species and *Neochelys* do not present this short intergular pattern in erymnochelyines (Pérez-García & Lapparent de Broin 2013, 2015) and because the presence of the other Inbeceten undetermined podocnemidid entoplastron without this pattern (Fig. 10G), nothing is certain. However, in size the *Ragechelus* n. gen. skull agrees with the largest Ibeceten erymnochelyine elements.

Contrary to which is deduced from Gaffney *et al.* (2006, 2011), Cadena (2015), Cadena *et al.* (2012) and Ferreira *et al.* (2018b) analyses (notably), we think no erymnochelyine presence is attested in continental South America before and after the Gondwana breakup, while this subfamily is attested in Africa (Broin *et al.* 1974) and Madagascar (Gaffney & Forster 2003) as soon as Senonian and up to now in Madagascar. Around the Gondwana breakup, the first pre-podocnemidid presence is attested early and close to the break in the Aptian-Albien boundary of Brazil (*Brasilemys* Lapparent de Broin, 2000b) and another one is attested from Albian-Cenomanian boundary of Kem Kem (*Hamadachelys* Tong & Buffetaut, 1996) (Gaffney *et al.* 2006; Lapparent de Broin 2000a). The first attested podocnemidines are recorded at late Cretaceous times after the break in South America (Gaffney *et al.* 2011), as well erymnochelyines are recorded in Africa at those times; both might have derived independently from related forms such as *Brasilemys* (Brazil) and *Hamadachelys* (Morocco) or from their earlier Cretaceous common ancestor. Some analogies of skull and shell shape between living *Erymnochelys* and *Peltocephalus* are here considered as the possible expression of vicariance, and of similar life and feeding patterns, in the two separated continents. It is seen in *Peltocephalus* by the (not known in all compared taxa): global well covered shape of the skull (as *Erymnochelys, Turkanemys* and *Dacquemys*) and more inclined trochlear processes (as in *Dacquemys* and *Ragechelus* n. gen., but also in primitive pleurodiran forms and some bothremydids, which shows it is an adaptative and potentially reversive feature), reduced lateral notch (as *Erymnochelys* and the most in *Eocenochelus*; but not in *Turkanemys* and *Dacquemys*; but also in bothremydids), analogous upper and lower strong beaked jaws (as *Ragechelus*, *Eocenochelus, Turkanemys*, also but different in *Mogharemys* and *Dacquemys*; and also in some bothremydids) moved by powerful pterygoid muscles that insert in the cavum pterygoideum (all erymnochelyine forms, *Ragechelus* n. gen. included, as in all other podocnemidids and some bothremydids). Living *Peltocephalus* and *Erymnochelys* share a more "terrestrial" pattern of a more domed shell than in *Podocnemis* species. However, their plastral pattern differs and that is significant of their distant relation. According to the long temporal distance between the Gondwana breakup and the extant existence of *Peltocephalus* and *Erymnochelys*, their similarities appear as an independent issue of a followed evolution in each continent. That in Africa, since the Senonian to now, has been acquired step by step, while a podocnemidid evolution also occurs in South America, on the other side. Because the analyses forgot to introduce all the necessary characters and the testimony of the previous existence of the Erymnochelyinae in Africa and Madagascar at Senonian-late Cretaceous (see above) and to correlate the starting point of the clades with the age of the Gondwana breakup, close relationship of *Peltocephalus* and *Erymnochelys* as sister taxa is not credible. Molecular data (Vargas-Ramírez *et al.* 2008) situate living *Erymnochelys* as diverging fom living *Peltocephalus*, and living *Podocnemis* is given as diverging from *Erymnochelys*. It can be admitted because among living Pleurodira, they are the only remaining extant taxa of Podocnemididae and we agree morphologically living *Podocnemis* shares podocnemidid characters with *Peltocephalus* and has some more derived features. As molecular analyses cannot integrate molecular data for fossils, the given tree between the podocnemidid origin (at the early Cretaceous times) and the present time is very incomplete and, over all, the analyses cannot ingregrate the Gondwana break. No more is admitted the clade *Peltocephalus* / *Mogharemys* + Stereogenyinae (Ferreira *et al.* 2018b).

Although the absence of postcranial, the data given in the diagnosis and the description and comparisons allow situating the *Ragechelus sahelica* n. gen., n. sp. rather basally in the Erymnochelyinae. *R. sahelica* n. gen., n. sp. has characters of its own among the taxa, beside differentiating features which are distributed in mosaic among the subfamily. In particular, there are those which may result from the variability according to the feeding habits and habitat. Found in a littoral Maastrichtian area with marine faunas as well as continental ones (dinosaurs), *R. sahelica* n. gen., n. sp. might come as well from a freshwater stream or pond of the adjacent terrestrial part of the continent as from the brackish to salted waters of the bay. *Erymnochelys madagascariensis* is only known recently in Madagascar but its origin is in the Mio-Pliocene continental forms of Africa, a long time after the Maastrichtian lower jaw of aff. *Erymnochelys* sp. As the erymnochelyines are known as tolerant (*Eocenochelus* being littoral in Eocene of Europe) and as *Erymnochelys* might have joined Madagascar crossing the sea no before the Plio-Pleistocene (if supported by a suitable stream), it is possible that, similarly, *R. sahelica* n. gen., n. sp. really lived in the littoral brackish area where it fossilized rather than in an adjacent continental freshwater pond or river. Nowadays *E. madagascariensis* feeds of aquatic continental plants (Kuchling 1988, 1993) but *Eocenochelus eremberti* and *Ragechelus* n. gen. diet is unknown.

CONCLUSION: RELATIONSHIPS AND PALAEOGEOGRAPHICAL CONSIDERATIONS

Relationships of *Ragechelus sahelica* n. gen., n. sp. with erymnochelyine Ibeceten forms, and *Nigeremys gigantea*

All the Iullemmeden basin turtles are Pelomedusoides, i.e. northern Gondwanan elements (Broin 1988a). On the systematics point of view, instead of being related to the new skull form, *N. gigantea* is part of Nigeremydini, a group unique to the Trans Saharan sea way (Cretaceous-Eocene) while *R. sahelica* n. gen., n. sp. is related with Afro-European Cenozic erymnochelyines. *Ragechelus sahelica* n. gen., n. sp. is defined as an Erymnochelyinae at late Maastrichtian times when the Gondwanan landmasses were already separated. Identically, the Ibeceten erymnochelyine is differentiated from podocnemidines at Senonian, also when the Gondwanan landmasses were already separated, and no known South American form presents its anterior lobe pattern. Among Erymnochelyinae, *R. sahelica* n. gen., n. sp. appears as primitive by some features. It is the testimony of an erymnochelyine presence at the same times as that of the lower jaw of aff. *Erymnochelys* sp. of Madagascar (Gaffney & Forster 2003).

We recognize two families in the Iullemmeden basin: the Bothremydidae and the Podocnemididae Erymnochelyinae.

1) The Bothremydidae Nigeremydini of the Trans Saharan sea way. This sea arm longitudinally divided the northern half of Africa, from the northern African platform of Tethys to the Guinea Gulf in Atlantic, from Late Cretaceous to Early Eocene; it is variable in extension (full dividing sea arm or a gulf only) and was effective during the Maastrichtian of the Iullemmeden basin of Niger (Greigert 1966; Dikouma *et al.* 1994: fig. 1; Moody & Sutcliffe 1991: fig. 12; Lingham-Soliar 1998: fig. 1; Scotese 2001). In the sea way, beside *Nigeremys* the tribe includes the Maastrichtian *Ilatardia* and *Sokotochelys* (of the same geological area) and the Egyptian *Arenila* from the mouth of the sea way on the Tethys platform and, after, the Malian Palaeocene *Azabbaremys* and *Acleistochelys maliensis*. We detect the presence of several other undefined Iullemmeden basin Pelomedusoides, but without knowing to which group they can belong. We do not recognize any Taphrosphyini *sensu nostro* in the Maastrictian Iullemmeden basin, contrary to the northern sea way part, in the Maastrichtian Ammonite Hills member of the Dakhla Formation (Egypt), open on the Tethys, where *Arenila* is present with *Taphrosphys* and bothremydine forms (*s.l.*) (Lapparent de Broin & Werner 1998).

And 2) The Podocnemididae Erymnochelyinae, including the skull of *Ragechelus sahelica* n. gen., n. sp. This subfamily, already present in the continental Senonian of Ibeceten, was already known by its large repartition in the world (Pérez-García 2017: fig. 1). *Ragechelus sahelica* n. gen., n. sp. is not recorded as formally associated to *Nigeremys* but they are both present in similar bone beds of the Iullemmeden basin. The presence of *Ragechelus* n. gen. in the Indamane bone bed can represent a continental freshwater form, that has been carried along from the continent, as well as a brackish form, an inhabitant of the littoral sea.

No marine cryptodire turtles (Chelonioids or Dermochelyoids) are preserved in the Iullemmeden basin, although they are present in other Late Cretaceous and Paleogene basins such as those of the Moroccan Maastrichtian and Palaogene phosphates and the Egyptian Maastrichtian Ammonite Hills. However, these formations are possibly not exactly stratigraphically correlated during the Maastrichtian times, and anyway they were more open on the high sea than the late Maastrichtian Trans Saharan seaway of the Iullemmeden basin (Dikouma 1990; Dikouma *et al.* 1993, 1994; Lapparent de Broin & Werner 1998; Zouhri 2017; Zouhri *et al.* 2018).

Palaeogeographical considerations and taxa distribution

Ragechelus sahelica n. gen., n. sp. participates to the knowledge of the turtle fauna of Africa during the Upper Cretaceous. The alternating marine and continental levels of fluctuation of the Iullemmeden basin of Niger yielded a variable littoral to continental fauna occupying the Tahoua district in the studied Kao-Ibeceten area. That produced, between Turonian and Cenozoic times, several layers of gypsiferous marls and bone beds, including several lots of turtle taxa: 1) at Ibeceten in the continental Senonian layer with an undefined erymnochelyine form among two or three other Pelomedusoides; 2) at In Tahout and 3) Indamane area, both very poorly preserved Senonian forms might have or not belonged to these erymnochelyines or to bothremydids; 4) the new *R. sahelica* n. gen., n. sp. erymnochelyine, and 5) the bothremydid *Nigeremys*, and 6) *Ilatardia*, both lied in one or in two distinct but close gypsiferous late Maastrichtian bone beds; 7) several other different undetermined turtle remains were mentioned in other superposed Maastrichtian Mosasaurus shales marl layers; and 8) endly during the late Palaeocene, a Thanetian layer (lower papyraceous shales) yielded several undetermined turtle taxa, much poorly preserved, but just enough to indicate the presence of at least a new undetermined bothremydid, a decorated form. Therefore, the two families (at least), Bothremydidae and Podocnemididae, which existed in the Indamane area, were both represented by several genera of several groups. Both families result from a long evolution in the northern Gondwana, as shown by the various Podocnemidoid presences since the early Cretaceous of northern Africa and South America (Broin 1980; Lapparent de Broin 2000a; Pérez-García 2019b) just before or just after the beginning of the continental drift.

The pre-Podocnemididae are continental in the early-middle Cretaceous of Gondwana, and, from Senonian, podocnemidid freshwater forms are known by the *Erymnochelys* branch in Africa (Ibeceten) as then by the Eocene *Neochelys* branch in Europe. Basally continental at Ibeceten, the attestation of littoral Erymnochelyinae (*Eocenochelus* on the one hand and the Stereogenyina on the other hand, and perhaps *R. sahelica* n. gen., n. sp. and aff. *Erymnocelys* in Madagascar) show family members have probably been able to come out of Africa by littoral ways. The unity of the subfamily is the more in its African geographical origin. Erymnochelyinae much disperse in the world by several branches which are not yet phylogenetically inter-related. One branch, on the one hand, possibly includes *R. sahelica* n. gen., n. sp., that of *Erymnochelys s. l.* Miocene forms. This continental branch gradually diversified during the Tertiary (with *Turkanemys* as a Miocene landmark) up to the Pliocene and led to the living Madagascan species (recent in Madagascar). On the other hand, the subfamily had to early develop other forms (not yet identified, missing Palaeocene forms) leading to the western European *Neochelys* (known as soon as earliest Eocene), possibly come in Europe from northern Africa, following the Tethys margins and crossing short sea arms. Stereogenyina branch also developed from an unknown origin in the subfamily and spread by littoral way outside Africa: *Bairdemys* is the only erymnochelyine known as having reached Americas by a littoral way, towards a last at the Oligocene time, remaining in northern South-America up to y Pliocene (Weems & Knight 2013); the branch also spread by littoral way eastern, up to Pakistan and Burma (Ferreira *et al.* 2015; Gaffney *et al.* 2011; Pérez-García *et al.* 2017; Weems & Knight 2013; Zouhri *et al.* 2017). Ibeceten forms are too poorly preserved to be positioned but they indicate possible origins of the three branches and of the other not situated taxa we enumerated in Pérez-García *et al.* (2017).

It is assumed *Erymnochelys madagascariensis* is of a recent introduction from Africa.

Before Holocene to Present times, Erymnochelyinae were present in Madagascar at least at Maastrichtian by the Gaffney & Forster (2003)'s form: member or not of the *Erymnochelys* group as in Ibeceten, this is not proved because its material, a lower jaw, is not joined to any plastral element. But this jaw is however related at the subfamilial level to *Erymnochelys*. The question is if the subfamily was present in Madagascar notably toward the Senonian time of Ibeceten or earlier, before the separation of Africa: no correlated Madagascan continental beds attests this possibility up to now.

The Bothremydidae developed in Africa and surrounding areas before the Maastrichtian times, as soon as the late Albian-early Cenomanian upper part of the "Continental intercalaire saharien", before the large marine Cenomano-Turonian transgression (Lapparent 1960; Bergounioux & Crouzel 1968; Gmira 1995; Lapparent de Broin 2000a). They are attested during the Cenomanian, from the margins of the Tethys to Europe and up to North America (Haas 1978a, b; Joyce *et al.* 2016; Pérez-García 2018).

In Africa they are notably known in the Trans Saharan sea way that was already initiated during the Turonian (Moody & Sutcliffe 1991) by Senonian to Palaeocene indetermined and nigeremydine forms described above, from the Iullemmeden basin.

During the Mastrichtian, the Nigerian bothremydid *Nigeremys* and *Ilatardia* testify to the development of the littoral Nigeremydini in the Kao area of the Trans Saharan sea. This tribe is up to now unknown elsewhere, while other African bothremydid groups are present in northern African part and disperse farther in the world (Europe, Americas). Thus, the Taphrosphyini *sensu nostro* and Bothremydini (both present elsewhere) dispersed much widely along western Tethys margins: during the Maastrichtian, in Ammonite Hills, beside Nigeremydini, Bothremydini and Taphrosphyini (*sensu nostro*) were present, as well as at the same age Taphrosphyini are present in Syria (Bardet *et al.* 2000) and in Morocco (Phosphate coll., OCP DEK/GE 113, DEK/GE 441, Sidi Daoui area, FLB pers. obs.). The tribe Taphrosphyini was also known as soon as the Maastrichtian in Europe (Mont-Aimé, France) (Broin 1977; Montenat & Merle 2018; Pérez-García 2018) showing an earlier than late Maastichtian origin, while Bothremydini also diversified from Africa to North America as soon as at Campanian times (Gaffney *et al.* 2006). On the other side of the Atlantic, the *Taphrosphys* group was known during the earliest Cenozoic by the type species *Taphrosphys sulcatus* (Leidy, 1856) from the lower Danian boundary of New Jersey. The Taphrosphyini are known as diversified in the early Cenozoic of Tunisia and Morocco, while they widely spread in Americas at least up to Peru (Bardet *et al.* 2017; Gaffney *et al.* 2006; Lapparent de Broin 2000a; Lapparent de Broin & Werner 1998). Contrary to the geographically restricted Nigeremydini, and as the other Bothremydidae, the erymnochelyine *Ragechelus* n. gen. participated to its wider world subfamilial dispersion, including in Madagascar. It has been shown than other undetermined bothremydid turtles were present in the Iullemmeden basin which could participate to a wide geographical expansion including toward Madagascar. (Lapparent de Broin & Werner 1998: tables 3 and 4, to be updated).

In Madagascar Bothremydidae are known by Cenomanian and Maastrichtian forms (Lapparent de Broin 2000a; Gaffney & Forster 2003; Lapparent de Broin & Werner 1998). The *Sokatra* Gaffney & Krause, 2011 skull, from the Maastrichtian Berivotra area (as the aff. *Erymnochelys* sp. lower jaw of Gaffney & Forster (2003)), is enough primitive to result of this early bothremydid dispersion before the separation of Madagascar and Africa. However, it might result from a bothremydid invasion by a sea way, if helped by a suitable stream when the landmasses were not too much separated. In India, Bothremydidae are possibly known as soon as early Albian-middle Turonian (Ayyasami & Das 1990), before the complete separation of the landmasses: Africa, Madagascar and India. In these lands, their known Maastrichtian genera are different showing their diversification is different in each of these continents. However, some closer relationships have been proposed between Madagascan and Indian forms (Gaffney & Krause 2011; Gaffney & Forster 2003; Gaffney *et al.* 2006, 2011; Lapparent de Broin & Guntupalli Prasad in press): they might partly result from a common Gondawanan ancestral origin, dating from before the landmasses searation. *Carteremys pisdurensis* Jain, 1977 from the infratrappean Lameta Formation has been attributed to *Shweboemys pisdurensis* (Jain, 1977) by Jain (1986) and thus considering it as a podocnemidid (a stereogenyine): it is now reconsidered as a bothremydid (Lapparent de Broin & Guntupalli Prasad in press) of unknown origin.

The question of a former Gondwanan common origin of the Podocnemidoidea of Africa, Madagascar and India before the Gondwanan break may be compared to the question raised by some large aquatic snakes. Rage (1981) redefined the Senonian Ibeceten snake *Madtsoia* (Rage *in* Broin *et al.* 1974) as *Madtsoia* aff. *madagascariensis* Hoffstetter, 1961, by comparison with a Maastrichtian form of Madagascar; this attribution is in favour of a contact between Madagascar and Africa before the breaking or at least when the separation was not too much important for littoral reptiles. This latter condition implies a suitable stream helped, because the Maastrichtian Indian-Madagascan landmass was already far from Africa. A similar condition could be necessary for the entrance in Madagascar of an erymnochelyine at Maastrichtian, after the separation of the landmasses. This is possible, Erymnochelyinae being known as tolerant to the salt when necessary, as seen above. Either their presence at the Maastrichtian of Madagascar is the result of such a littoral/sea way passage, or it is the result of a diversification of the subfamily before the break, as it may be testified by the subfamily presence in the Senonian of Ibeceten. Here the diagnosis of the Maastrichtian Madagascan turtle of Gaffney & Forster (2003) as an erymnochelyine is not in doubt; but it is the only witness of the presence of the family before the Holocene-extant presence of *Erymnochelys madagascariensis.*

As far as *Madtsoia* is concerned, *M.* aff. *madagascariensis* Ibeceten material is relatively poor (Rage 1981) and it is then part of the genus taken with a comprehensive sense (Hussam Zaher, pers. comm.). It would be possible that the Niger and Madagascan snake forms were formerly closely related, also with the Indian form (Mohabey *et al.* 2011) before the landmasses break. And they may be more closely related than with the typical Argentina *Madtsoia* form. This, in the best case, might have shared with the Afro-Madagascan-Indian group of forms a much more ancient Gondwanan origin than thought, and then they might testify of a less close relationship (Garberoglio *et al.* 2019; Laduke *et al.* 2010; Rage *et al.* 2014).

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