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Identification of the Lower Cretaceous pleurodiran turtle *Taquetochelys decorata* as the only African araripemydid species

Taquetochelysdecorata, *tortue pleurodire du Crétacé Inférieur: seule espèce d'Araripemydidé d'Afrique*

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ABSTRACT

Araripemydidae is a clade of freshwater pleurodiran turtles originally described in South America, where it is represented by the Brasilian Aptian–Albian *Araripemys barretoi*. Two potential members of this lineage were defined in an Aptian level of Africa, in Gadoufaoua (Niger): *Taquetochelys decorata*, described from several isolated plates, and *Lagaremys tenerensis*, known from an almost complete skeleton. The review of the Araripemydidae record, and the analysis of the intraspecific variability present in that and in other clades of Pleurodira, allow me to refute their attribution to two different forms. '*L. tenerensis*' is here recognized as a junior synonym of *T. decorata*. Therefore, the priority of *T. decorata* is demonstrated, as well as its attribution to Araripemydidae. The almost complete skeletal anatomy of the two currently recognized members of this Aptian–Albian clade (i.e. the African *T. decorata* and the South American *A. barretoi*) is well known, which is uncommon for the Cretaceous pleurodiran turtles.

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RÉSUMÉ

Les Araripemydidae sont un clade de tortues pleurodires d'eau douce originellement décrits en Amérique du Sud, où ils sont représentés au Brésil, à l'Aptien–Albien, par *Araripemys barretoi*. Deux membres potentiels de cette lignée ont été décrits dans un niveau aptien d'Afrique à Gadoufaoua (Niger) : *Taquetochelys decorata*, décrit à partir de plusieurs plaques isolées, et *Lagaremys tenerensis*, connu par un squelette presque complet. L'étud des spécimens d'Araripemydidae de ces deux continents actuels

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et l'analyse de la variabilité intraspécifique présente dans ce clade et dans d'autres groupes de Pleurodira permettent de réfuter leur attribution à deux formes différentes. « *L. tenerensis* » est reconnu ici comme un synonyme junior de *T. decorata*. Par conséquent, la priorité de *T. decorata* est démontrée, ainsi que son attribution aux Araripemydidae. L'anatomie squelettique presque complète des deux membres actuellement reconnus dans ce clade aptien-albien (*T. decorata* en Afrique et *A. barretoi* en Amérique du Sud) est bien connue, ce qui est rare pour les tortues pleurodires du Crétacé.

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1. Introduction

Gadoufaoua is the oldest African fossiliferous locality where the synchronic and sympatric presence of several taxa of Pleurodira has been recorded. It is located in the Illumeden Basin of the Ténéré Desert, in central Niger (Lapparent de Broin, 2000). Broin (1980) identified several Aptian (Lower Cretaceous) freshwater forms, two of them being defined as representatives of new genera and species, *Teneremys lapparenti* Broin, 1980 and *Taquetochelys decorata* Broin, 1980. The latter was recognized as a member of Araripemydidae, corresponding to the first representative of this clade defined in Africa.

The type series of *T. decorata* was composed of its holotype, a partial hypoplastron and ten disarticulated plates, nine of them corresponding to carapace elements and the last one to a partial xiphiplastron. Those elements were figured by Broin (1980, pl. 2–3). In addition, she indicated the presence of about thirty additional elements attributable to this form, which remained unpublished until now.

The presence of a mesoplastron in this taxon, recognized in the holotype, allowed Broin (1980) to characterize this form as different from the other araripemydid member known at that time, i.e. the Brasilian Aptian–Albian *Araripemys barretoi* Price, 1973, from the Santana Formation of the Araripe Basin, in the State of Ceará. In fact, the ornamental pattern present on that plate was radically different from that of the South American form. The presence of this pattern in other isolated plates of Gadoufaoua allowed Broin (1980) to attribute all of them to *T. decorata*.

A second member of Araripemydidae was subsequently described in the Brasilian state of Ceará, *Araripemys arturi* (Fielding et al., 2005). This species was synonymized with *A. barretoi* by Gaffney et al. (2006), who considered that the limited information available on *T. decorata* (i.e. only that published by Broin (1980)) was not enough to confirm its attribution to Araripemydidae. They pointed out that if new articulated specimens from Gadoufaoua became available, this taxon might become diagnosable. Fortunately, one of the most complete Lower Cretaceous skeletons of a pleurodiran turtle found worldwide was discovered in that region a few years later (Sereno and ElShafie, 2013). This specimen was an unquestionable member of Araripemydidae, confirming the identification of this group in Africa by Broin (1980). In addition, this specimen possessed mesoplastra, a character shared with the holotype of *T. decorata*, from the same level and region (i.e. the GAD 5 level of the Elrhaz Formation, in Gadoufaoua), but not with the South American taxon *A. barretoi*. However, Sereno and ElShafie (2013) found several putative differences between the previously figured material of *T. decorata* and the new specimen. So, they attributed it to a new form, '*Lagaremys tenerensis*'.

The type series of *T. decorata* has been revised, and each of these elements is represented here in both dorsal and ventral views. In addition, the other elements cited by Broin (1980) as attributable to the shell of this species, but hitherto unpublished, are also analyzed and figured here. The almost complete skeleton of '*L. tenerensis*' allows me to confirm that all these isolated elements are compatible with a single form. Thus, '*L. tenerensis*' is identified as a junior synonym of *T. decorata*.

Institutional abbreviations: ALG, Algora collection, deposited in the "Museo de Paleontología de Castilla-La Mancha", Cuenca, Spain; AMNH, American Museum of Natural History, New York; GDF, Gadoufaoua collection, deposited in the MNHN.F; MCNA, "Museo de Ciencias Naturales de Alava", Vitoria-Gasteiz, Spain; MNHN.F, Paleontology Collection of the "Muséum national d'histoire naturelle", Paris, France; MNN, "Museum national du Niger", Niamey, République du Niger.

2. Systematic palaeontology

TESTUDINES Batsch, 1788
PLEURODIRA Cope, 1864
PELOMEDUSOIDES Cope, 1868
ARARIPEMYDIDAE Price, 1973
TAQUETOCHELYS Broin, 1980

T. decorata Broin, 1980
Figs. 1–3

Synonymy. *L. tenerensis* Sereno and ElShafie, 2013.

Type series. The holotype, MNHN.F GDF 847, hypoplastron (Fig. 1P); and ten paratypes: GDF 838, first costal (Fig. 1F); GDF 839, costal (Fig. 2C and D); GDF 840, costal (Fig. 1L); GDF 841, costal (Fig. 2W–X); GDF 842, costal (Fig. 2AG–AH); GDF 843, costal (Fig. 3S and T); GDF 844, peripheral (Fig. 1D); GDF 845, peripheral (Fig. 1E); GDF 846, peripheral (Fig. 1A); GDF 848, xiphiplastron (Fig. 1R).

Other specimens here identified as attributable to this taxon. The peripherals MNHN.F GDF 853 (Fig. 1B), and GDF 854 (Fig. 1C). Several costals corresponding to the first pair: GDF 905 (Fig. 2A and B), GDF 858 (Fig. 2E and F), GDF 859 (Fig. 2 G and H), GDF 851 (Fig. 2I and J), GDF 906 (Fig. 2K and L). Several second to eighth costals: GDF 855 (Fig. 1K),

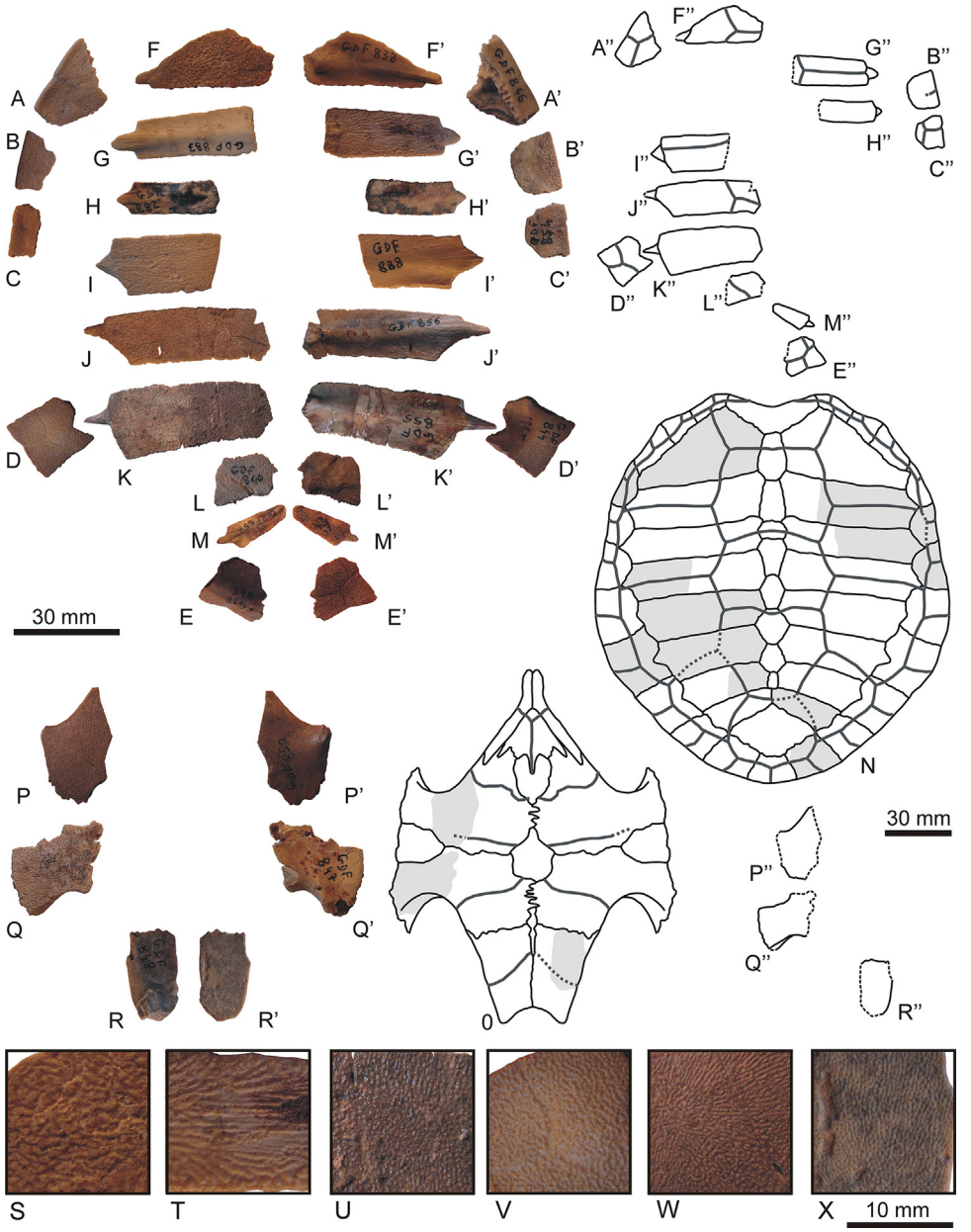

Fig. 1. Specimens of *Taquetochelys decorata*, from the Aptian (Early Cretaceous) of Gadoufaoua (Illumeden Basin, Niger). A–M, Selection of several plates corresponding to the carapace, including peripherals (A–E) and costals (F–M). All of them are figured in dorsal and ventral views. The drawings represent the dorsal view. A, MNHN.F GDF 846. B, GDF 853. C, GDF 854. D, GDF 844. E, GDF 845. F, GDF 838. G, GDF 883. H, GDF 882. I, GDF 888. J, GDF 856. K, GDF 855. L, GDF 840. M, GDF 857. N–O, Location of the plates of the carapace (N) and the plastron (O) of *T. decorata* included in this figure, on a modified reconstruction of that proposed by Sereno and ElShafie (2013) based the only known articulated shell of this taxon. P–R, Plastral plates, corresponding to the right partial hyoplastron GDF 850 (P), right partial hypoplastron GDF 847 (Q) and left partial xiphiplastron GDF 848 (R). All of them are in dorsal and ventral views. The drawings represent the ventral view. S–X, Decoration of the outer surface of several plates. S, Costal GDF 838. T, Costal GDF 883. U, Costal GDF 855. V, Peripheral GDF 844. W, Hyoplastron GDF 850. X, Xiphiplastron GDF 848.

Fig. 1. Spécimens de *Taquetochelys decorata*, de l'Aptien (Crétacé inférieur) de Gadoufaoua (bassin d'Illumeden, Niger). A–M, Sélection de plusieurs plaques de la carapace, correspondant aux périphériques (A–E) et aux costales (F–M). Tous ces éléments sont représentés en vues dorsale et ventrale. Les dessins représentent la vue dorsale. A, MNHN.F GDF 846. B, GDF 853. C, GDF 854. D, GDF 844. E, GDF 845. F, GDF 838. G, GDF 883. H, GDF 882. I, GDF 888. J, GDF 856. K, GDF 855. L, GDF 840. M, GDF 857. N–O, Localisation des plaques de la carapace (N) et du plastron (O) de *T. decorata* inclues dans cette figure, sur une reconstitution modifiée d'après celle proposée par Sereno et ElShafie (2013), à partir de la seule carapace articulée connue de ce taxon. P–R, Plaques plastrales, correspondant à l'hyoplastron droit partiel GDF 850 (P), à l'hypoplastron droit partiel GDF 847 (Q) et au xiphiplastron gauche partiel GDF 848 (R). Toutes les plaques sont représentées en vues dorsale et ventrale. Les dessins représentent la vue ventrale. S–X, Décoration de la surface extérieure de plusieurs plaques. S, Costale GDF 838. T, Costale GDF 883. U, Costale GDF 855. V, Périphérale GDF 844. W, Hyoplastron GDF 850. X, Xiphiplastron GDF 848.

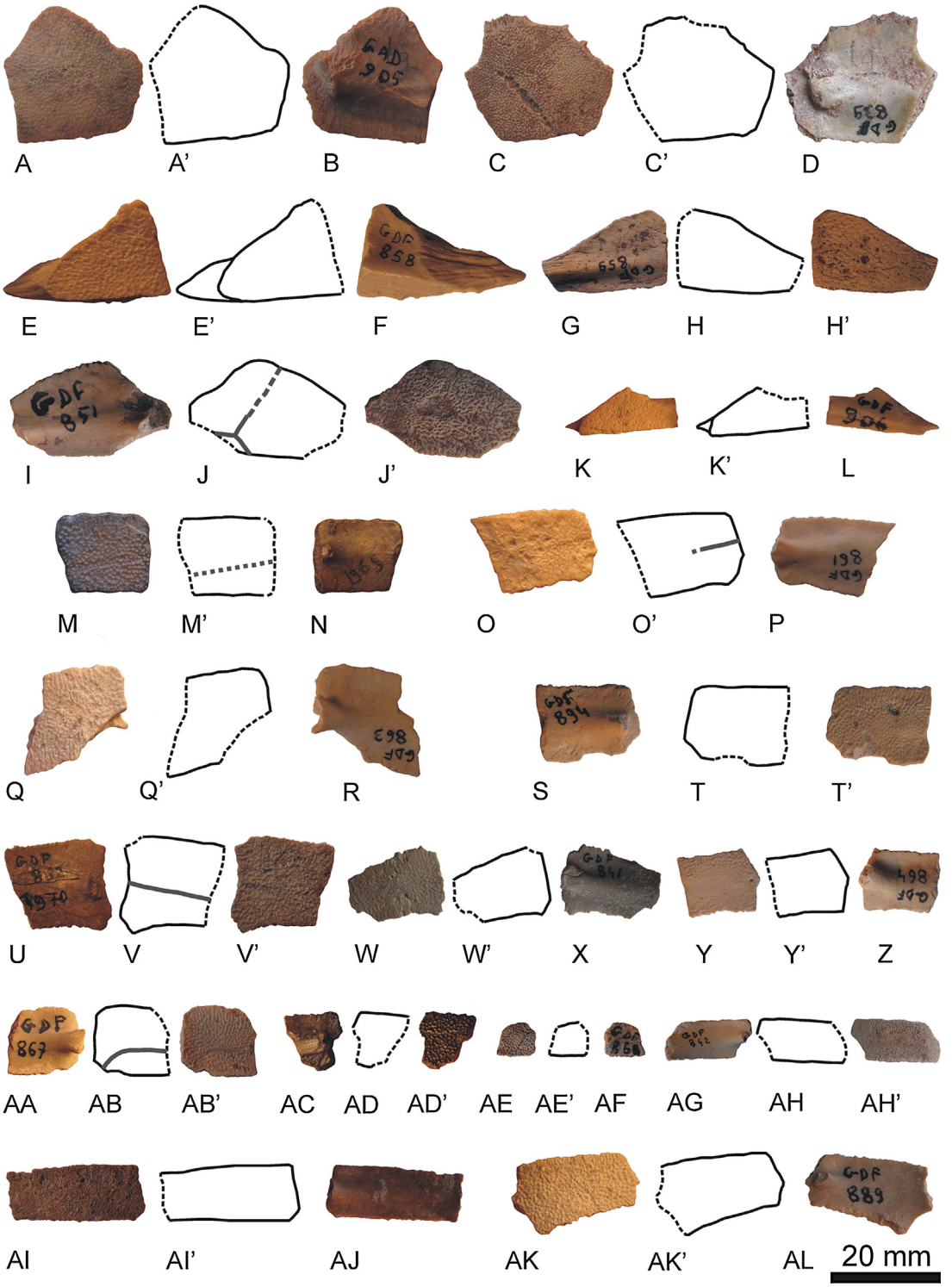

Fig. 2. Partial costal plates of *Taquetochelys decorata*, from the Aptian (Early Cretaceous) of Gadoufaoua (Illumeden Basin, Niger). A–B, MNHN.F GDF 905. C–D, GDF 839. E–F, GDF 858. G–H, GDF 859. I–J, GDF 851. K–L, GDF 906. M–N, GDF 873. O–P, GDF 861. Q–R, GDF 863. S–T, GDF 894. U–V, GDF 862. W–X, GDF 841. Y–Z, GDF 864. AA–AB, GDF 867. AC–AD, GDF 869. AE–AF, GDF 868. AG–AH, GDF 842. AI–AJ, GDF 1701. AK–AL, GDF 889.

Fig. 2. Plaques costales partielles de *Taquetochelys decorata*, de l'Aptien (Crétacé inférieur) de Gadoufaoua (bassin d'Illumeden, Niger). A–B, MNHN.F GDF 905. C–D, GDF 839. E–F, GDF 858. G–H, GDF 859. I–J, GDF 851. K–L, GDF 906. M–N, GDF 873. O–P, GDF 861. Q–R, GDF 863. S–T, GDF 894. U–V, GDF 862. W–X, GDF 841. Y–Z, GDF 864. AA–AB, GDF 867. AC–AD, GDF 869. AE–AF, GDF 868. AG–AH, GDF 842. AI–AJ, GDF 1701. AK–AL, GDF 889.

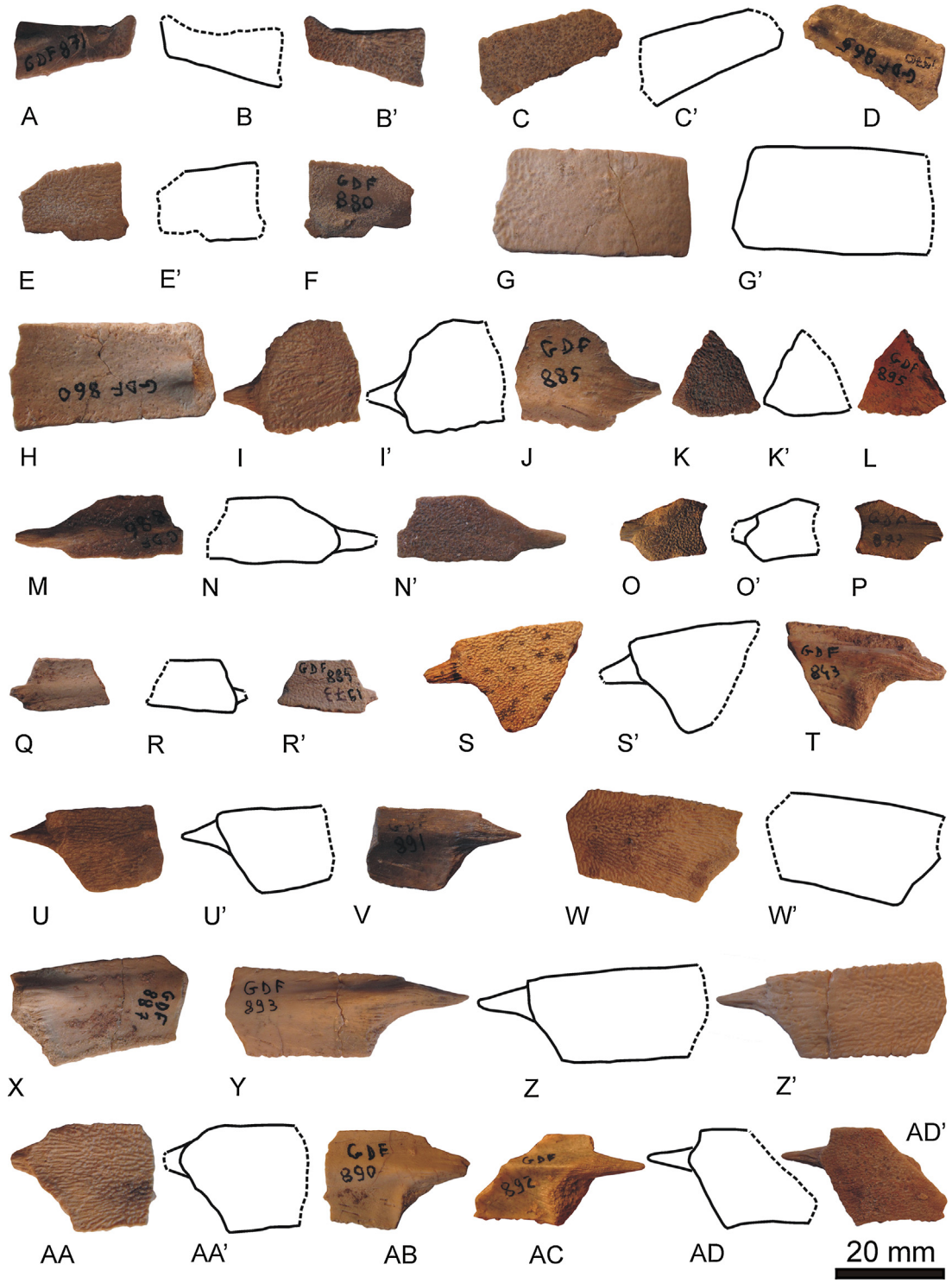

Fig. 3. Partial costal plates of *Taquetochelys decorata*, from the Aptian (Early Cretaceous) of Gadoufaoua (Illumeden Basin, Niger). A–B, MNHN.F GDF 871. C–D, GDF 865. E–F, GDF880. G–H, GDF 860. I–J, GDF 885. K–L, GDF 895. M–N, GDF 886. O–P, GDF 877. Q–R, GDF 884. S–T, GDF 843. Y–V, GDF 891. W–X, GDF 887. Y–Z, GDF 893. AA–AB, GDF 890. AC–AD, GDF 892. All of them are in dorsal and ventral views. The drawings represent the dorsal view.
Fig. 3. Plaques costales partielles de *Taquetochelys decorata*, de l'Aptien (Crétacé inférieur) de Gadoufaoua (bassin d'Illumeden, Niger). A–B, MNHN.F GDF 871. C–D, GDF865. E–F, GDF 880. G–H, GDF 860. I–J, GDF 885. K–L, GDF 895. M–N, GDF 886. O–P, GDF 877. Q–R, GDF 884. S–T, GDF 843. U–V, GDF 891. W–X, GDF 887. Y–Z, GDF 893. AA–AB, GDF 890. AC–AD, GDF 892. Tous ces éléments sont représentés en vues dorsale et ventrale. Les dessins représentent la vue dorsale.

GDF 857 (Fig. 1M), GDF 856 (Fig. 1J), GDF 860 (Fig. 3G and H), GDF 861 (Fig. 2O and P), GDF 862 (Fig. 2U and V), GDF 863 (Fig. 2Q and R), GDF 864 (Fig. 2Y and Z), GDF 865 (Fig. 3E and F), GDF 867 (Fig. 2AA and AB), GDF 868 (Fig. 2AE and AF), GDF 869 (Fig. 2AC and AD), GDF 871 (Fig. 3A and B), GDF 873 (Fig. 2M and N), GDF 877 (Fig. 3O and P), GDF 880 (Fig. 3C and D), GDF 882 (Fig. 1H), GDF 883 (Fig. 1G), GDF 884 (Fig. 3Q and R), GDF 885 (Fig. 3I and J), GDF 886 (Fig. 3M and N), GDF 887 (Fig. 3W and X), GDF 888 (Fig. 1I), GDF 889 (Fig. 2AK and AL), GDF 890 (Fig. 3AA and AB), GDF 891 (Fig. 3U and V), GDF 892 (Fig. 3AC and AD), GDF 893 (Fig. 3Y and Z), GDF 894 (Fig. 2S and T), GDF 895 (Fig. 3I and J), and GDF 1701 (Fig. 2AI and AJ). The hyoplastron GDF 850 (Fig. 1P). The almost complete skeleton MNN GAD28 (see figs. 14.4–14.18 in Sereno and ElShafie, 2013).

Locality and horizon. Late Aptian, Early Cretaceous. GAD 5 level, Elrhaz Formation, Gadoufaoua, Illumeden Basin, Ténéré Desert, central Niger (Broin, 1980; Lapparent de Broin, 2000; Sereno and ElShafie, 2013).

3. Discussion

As indicated (see introduction), the first defined araripemydid was a South American taxon: the Brasilian Aptian–Albian *A. barretoi* (Price, 1973). This form is known by numerous specimens, including several relatively complete skeletons (Gaffney et al., 2006; Meylan, 1996; Price, 1973). The description of the Aptian *T. decorata* from a few disarticulated plates allowed us to recognize the presence of the clade Araripemydidae in Africa (Broin, 1980). The subsequent finding of an almost complete skeleton of an araripemydid in the type area where *T. decorata* was defined (i.e. the Aptian GAD 5 level of the Elrhaz Formation, in Gadoufaoua, central Niger) allowed me to confirm the presence of this clade on that continent (Sereno and ElShafie, 2013). However, this skeleton was attributed to a new form, '*L. tenerensis*' (Sereno and ElShafie, 2013). Sereno and ElShafie (2013) justified the designation of a new taxon because the range of differences between the hypoplastra of '*L. tenerensis*' and the holotype of *T. decorata* did not allow the attribution of both specimens to the same form. The review of previously published material from Gadoufaoua and the study of unpublished specimens from this locality, as well as the comparative analysis with other members of Pleurodira (including the only other araripemydid currently recognized, *A. barretoi*), allows me to recognize several shared characters among the holotypes of *T. decorata* and '*L. tenerensis*' as exclusive within araripemydidae (e.g., the presence of mesoplastra and of an ornamental pattern composed of tubercles instead of pits). However, all the putative differences recognized by Sereno and ElShafie (2013) between both synchronic and sympatric forms are here identified as part of the intraspecific variability usually recognized in pleurodiran taxa known from several specimens (including, among others, *A. barretoi*).

Sereno and ElShafie (2013) reported four characters as different between *T. decorata* and '*L. tenerensis*'. The first one was the morphology of the lateral margin of the hypoplastra. They indicated that the sutural margin of the hypoplastra of '*L. tenerensis*' with the fifth and sixth peripherals (probably referring to the sixth and seventh ones) is divided discretely into two parts, the suture with the most posterior of these peripherals angling posteromedially at approximately 30° (see fig. 14.14a in Sereno and ElShafie, 2013). They characterized the margin of the holotype of *T. decorata* as gently convex (see Fig. 1Q). Intraspecific variability is recognized in the araripemydid *A. barretoi*, specimens with an angulate margin as that present in the holotype of '*L. tenerensis*' (e.g., Fig. 4D), but also others with a convex margin (e.g., Fig. 4E), being identified here. Intermediate states are also recognized for this taxon (e.g., Fig. 4G). In fact, intraspecific variability for this character is identified in numerous pleurodiran taxa. For example, specimens with well-developed angulate (e.g., Fig. 4O), slightly angulated (e.g., Fig. 4P) or rounded margins (e.g., Fig. 4N and Q), are recognized for the Cenomanian bothremydid *Algorachelus peregrinus* Pérez-García, 2016.

The second character recognized by Sereno and ElShafie (2013) as different between *T. decorata* and '*L. tenerensis*' referred to the contact area of the hypoplastra with the mesoplastra. These authors indicated that the suture between these elements has a discrete angle of approximately 50° in '*L. tenerensis*', giving the mesoplastra a distinctive pentagonal shape (see fig. 14.14a in Sereno and ElShafie, 2013). They characterized this margin as more irregular in *T. decorata* (see Fig. 1Q). As a consequence, the ramus of each hypoplastron between the mesoplastron and the posterior embayment was identified as proportionately shorter in '*L. tenerensis*'. The first-hand review of the holotype of *T. decorata* allows me to recognize that the anterior margin of the hypoplastron was broken, so the ratio between the length of the area in contact with the mesoplastron and that of the region located behind this plate is unknown (Fig. 1Q). Since *A. barretoi* lacks mesoplastra, the intraspecific variability for that character cannot be evaluated in that taxon. The difference in morphology between the mesoplastron-hypoplastron suture of the holotypes of *T. decorata* and '*L. tenerensis*' is much less than that recognized in other species of Pleurodira, as is the case of the aforementioned *Algorachelus peregrinus*, which shows clearly concave margins in some specimens (e.g., Fig. 4P), being angulated in others (e.g., Fig. 4Q), intermediate states also being recognized (e.g., Fig. 4N and O). The ratio between the length of the area of contact of the hypoplastron with the mesoplastron and that of the region located behind it is recognized as markedly variable in *Algorachelus peregrinus*, the contact of the mesoplastron with this plate being much shorter in some specimens (e.g., Fig. 4N and Q) that in others (e.g., Fig. 4O and P).

The third difference between both taxa indicated by Sereno and ElShafie (2013) concerned the embayment for the hind limb. They recognized the outline as more deeply arched in '*L. tenerensis*', with a smooth margin approximately twice the width of that in *T. decorata*. The study of the holotype of *T. decorata* allows me to recognize that the postero-lateral development of the embayment is not preserved, because this plate is broken (Fig. 1Q). In addition, the morphology of the embayment of this hypoplastron cannot be well defined, because a significant portion of its medial region is not preserved (see Fig. 1O). Variability in the contour of this structure is identified in other forms of

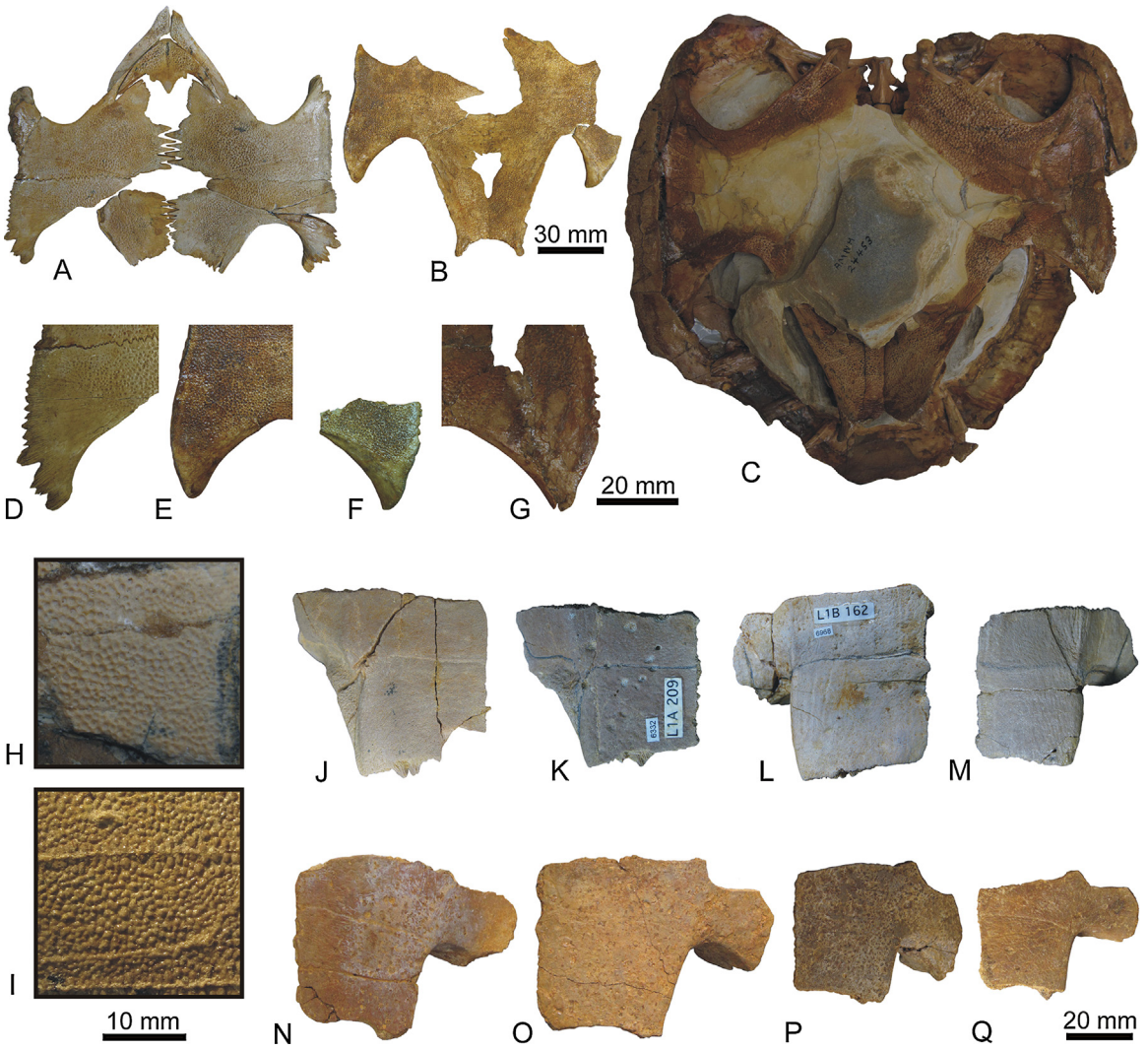

Fig. 4. Specimens corresponding to three species of three families of Pleurodira (Araripemydidae, Dortokidae and Bothremydidae), in which intraspecific variability affecting the hypoplastron can be recognized. All of them are represented in ventral view. A-I, Three individuals of the araripemydid *Araripemys barretoi*, from the Aptian–Albian of Ceará (Brasil). A, Partial plastron of AMNH 22550. B, Partial plastron of AMNH 22556. C, Ventral view of the shell of AMNH 24453. D, Detail of the lateral region of the right hypoplastron of AMNH 22550. E, Detail of the lateral region of the right hypoplastron of AMNH 22556. F, Detail of the latero-posterior region of the left hypoplastron of AMNH 22556. G, Detail of the lateral region of the left hypoplastron of AMNH 24453. H, Decoration of the outer surface of the costal plates of AMNH 24460. I, Detail of the external cast of the costal plates of AMNH 24457. J-M, Four hypoplastra of the dortokid *Dortoka vasconica*, from the Campanian of Laño (Burgos, Spain). J, MCNA L1A95-99. K, MCNA 6332. L, MCNA 6968. M, MCNA 6696. N–Q, Four hypoplastra of the bothremydid *Algorachelus peregrinus*, from the Cenomanian of Algora (Guadalajara, Spain). N, ALG 153. O, ALG 154. P, ALG 155. Q, ALG 156.

Fig. 4. Spécimens correspondant à trois espèces de trois familles de Pleurodira (Araripemydidae, Dortokidae et Bothremydidae), dans lesquelles une variabilité intraspécifique affectant l'hypoplastron peut être reconnue la variabilité intraspécifique affectant l'hypoplastron. Tous sont représentés en vue ventrale. A-I, Trois individus de l'Araripémydidé *Araripemys barretoi*, de l'Aptien–Albien de Ceará (Brésil). A, Plastron partiel de AMNH 22550. B, Plastron partiel de AMNH 22556. C, Vue ventrale de la carapace de AMNH 24453. D, Détail de la région latérale de l'hypoplastron droit de AMNH 22550. E, Détail de la région latérale de l'hypoplastron droit de AMNH 22556. F, Détail de la région latéro-postérieure de l'hypoplastron gauche de AMNH 22556. G, Détail de la région latérale de l'hypoplastron gauche de AMNH 24453. H, Décoration de la surface extérieure des plaques costales de AMNH 24460. I, Détail du moule externe des plaques costales de AMNH 24457. J-M, Quatre hypoplastrons du dortokidé *Dortoka vasconica*, du Campanien de Laño (Burgos, Espagne). J, MCNA L1A95-99. K, MCNA 6332. L, MCNA 6968. M, MCNA 6696. N–Q, Quatre hypoplastrons du bothrémydidé *Algorachelus peregrinus*, du Cénomanien d'Algora (Guadalajara, Espagne). N, ALG 153. O, ALG 154. P, ALG 155. Q, ALG 156.

Pleurodira, including the araripemydid *A. barretoi* (see the specimens of *Araripemys* in fig. 7 of Fielding et al. (2005), now identified as belonging to the same form sensu Gaffney et al., 2006; and Fig. 4A–C). Sereno and ElShafie (2013) indicated that a weakly developed or absent smooth margin is present in *A. barretoi*. This condition is recognized in some specimens (e.g., Fig. 4G), but this margin is identified here as well-developed in others (e.g., Fig. 4F), being similar to that of the holotype of '*L. tenerensis*' (see fig. 14.14a in Sereno and ElShafie, 2013). In fact,

the development of this margin is generally subject to intraspecific variability in Pleurodira. Thus, the development of a region equivalent to the area recognized as a smooth margin for the araripemydids, but also developed in a more medial region, is identified as highly variable in the Campanian dortokid *Dortoka vasconica* (Lapparent de Broin and Murelaga, 1996), being well-developed in some specimens (e.g., Fig. 4J and K), but poorly developed or absent in others (e.g., Fig. 4L and M).

The last character that allowed Sereno and ElShafie (2013) the definition of a new taxon is the identification of differences in the ornamental pattern of the holotype of *T. decorata* and in that of the hypoplastra of '*L. tenerensis*'. The ornamental pattern of both specimens, as well as that of the other specimens here attributed to *T. decorata*, is composed of low tubercles, which, in some regions, are grouped to form radiating ridges (Fig. 1S–X). In contrast, the ornamental pattern of *A. barretoi* is composed of pits (see the outer surface of a costal plate in Fig. 4H, and the detail of an external cast of another costal in Fig. 4I). Sereno and ElShafie (2013) noted differences in the size and prominence of the pattern of tubercles in the hypoplastra of the holotypes of *T. decorata* and '*L. tenerensis*', and also in their organization into radiating ridges and sulci, and in its development in the posteromedial portion of these plates. As Broin (1980) indicated, variations in different regions of a single plate, in several zones of the shell of the same individual, and in the same region of the shell of several individuals are present (see Figs. 1–3, particularly Fig. 1S–X). In fact, these variations can be markedly greater than those observed when those hypoplastra are compared. In addition, relevant variations in all aspects relative to the ornamental pattern considered by Sereno and ElShafie (2013) are here recognized for *A. barretoi*. Thus, the ornamental pattern is relatively well-developed in the posteromedial portion of the hypoplastra of some specimens (Fig. 4E–G), being absent in this area in others (Fig. 4D). The pits are smaller and more numerous in some specimens (Fig. 4E) than in others (Fig. 4D), a more anastomosed pattern being recognized in some individuals (Fig. 4G).

Therefore, none of the characters recognized by Sereno and ElShafie (2013) as different between the holotypes of *T. decorata* and '*L. tenerensis*' allows me to support the identification of both putative synchronous and sympatric species as different forms. In fact, although the intraspecific variability of one species may differ from that of others, the comparative study of several specimens of the other currently recognized araripemydid (i.e. *A. barretoi*), as well as those of other members of Pleurodira, shows that all characters used by Sereno and ElShafie (2013) for the definition of the second African araripemydid are usually recognized as subject to intraspecific variability, both in closely related taxa and in others belonging to different lineages of Pleurodira. No other character can be established to support the attribution of the holotypes of *T. decorata* and '*L. tenerensis*' to two different species. As indicated, the holotype of *T. decorata* shows characters different from those of the other known member of Arapemydidae, all of them being shared with the holotype of '*L. tenerensis*' (i.e. the presence of mesoplastra, and an ornamental pattern composed of tubercles instead of pits). Considering all this, the priority of *T. decorata* is demonstrated, and '*L. tenerensis*' is recognized as a junior synonym of this form. Consequently, the attribution of *T. decorata* to Araripemydidae, carried out by Broin (1980), but questioned by Gaffney et al. (2006) awaiting the finding of a more complete specimen, can be confirmed here. Thus, the hypothesis proposed by Broin (1980) regarding the African *T. decorata* as a form closely related to the synchronic South American *A. barretoi* is supported.

A description of the complete shell of *T. decorata* is available in Sereno and ElShafie (2013), based on the holotype of '*L. tenerensis*'. Some additional characters were provided by Broin (1980) from the study of isolated plates. In addition, Broin (1980) recognized intraspecific variability in a character of the carapace, which is supported here: the presence of a continuous neural series from the nuchal to the suprapygal in some specimens, this series being shorter in others, allowing a short to large medial contact of the last pair of costals. This range of variability is also recognized here for *A. barretoi*. Several shell characters of the differential diagnosis between the South American species and that from Gadoufaoua (based on the holotype of '*L. tenerensis*', MNN GAD28, now attributed to *T. decorata*) proposed by Sereno and ElShafie (2013) are here refuted. Thus, these authors characterized the carapace length of the African form (i.e. approximately 15 cm), as smaller than that of *A. barretoi* (20–30 cm). Several plates of *T. decorata* corresponding to individuals of larger size than MNN GAD28, compatible with the size recognized for *A. barretoi*, are identified (e.g., Figs. 1A, I and Q; 3G, H and S–AD). A deeply interdigitating suture between the hypoplastron and the xiphiplastron is not present in all specimens of *A. barretoi*. Thus, the deeply interdigitating area is limited to the lateral half in some specimens (e.g., Fig. 4B), but absent in others, an arrangement similar to that identified for *T. decorata* (see fig. 14.13 in Sereno and ElShafie, 2013) being recognized in these last specimens (e.g., Fig. 4A). No evidence of a different arrangement of the contact between the first dorsal vertebra and the nuchal plate can be established between both taxa, because that region is unknown in *T. decorata*.

Fragmentary remains attributable to araripemydids have been identified in Lower Cretaceous and basal Upper Cretaceous levels (from the Barremian, or possibly before, to the lower Cenomanian) of other African countries, including Morocco, Algeria, Tunisia, and Ethiopia (see Lapparent de Broin, 2000, and references therein). The poor information provided by these remains is insufficient to propose a precise systematic allocation. However, the presence of at least two different ornamental patterns is supported here, one corresponding to that of *Taquetochelys* and the other being compatible with *Araripemys*. In fact, the absence of mesoplastra in a hyoplastron with an ornamental pattern similar to that of *Araripemys*, from the Kem beds of Morocco (see plate XVII I-J in Gmira, 1995), supports the presence of an African form probably closely related to *A. barretoi*. The confirmation of the presence of Araripemydidae in Gadoufaoua was recognized by Sereno and ElShafie (2013) as clear evidence of the active faunal exchange between South America and Africa immediately prior to the Late Cretaceous. However, the identification of this clade in Africa at least from the Barremian, and in South

America at least from the lower Aptian, demonstrates that this lineage was already present in both continental masses before the isolation (see Lapparent de Broin, 2000; Scotese, 2014).

4. Conclusions

The recent finding of an almost complete turtle skeleton from the Aptian (Early Cretaceous) of Gadoufaoua (Ténéré Desert, central Niger) confirmed the presence of Araripemydidae in Africa. This clade of pleurodiran turtles had been originally described by a South American species, *A. barretoi*. The skeleton from Gadoufaoua was attributed to a new taxon, '*L. tenerensis*'. Although a potential araripemydid had been previously described at the same level and area (i.e. *T. decorata*), its attribution to this clade had been questioned by subsequent authors, and was proposed as a *nomen dubium*.

The previously recognized putative differences between the holotype of *T. decorata* and that of '*L. tenerensis*', which allowed the diagnosis of the latter taxon, are here identified as forming part of the intraspecific variability of the same form. This variability is recognized as compatible with that present in *A. barretoi* by the personal observation of specimens of this South American taxon, as well as with that of other members of Pleurodira known from several specimens belonging to other lineages. In this way, the African *T. decorata* is identified as a senior synonym of '*L. tenerensis*'. Thus, *T. decorata* is the only species of Araripemydidae currently identified in Africa, the Brazilian *A. barretoi* being the only currently recognized representative of this clade defined outside this continent. The cranial and the postcranial anatomy of both members of this Aptian–Albian clade are well known, which is uncommon for the Cretaceous pleurodiran turtles.

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