A NEW PACHYOSTOTIC SQUAMATE REPTILE FROM THE CENOMANIAN OF FRANCE

by JEAN-CLAUDE RAGE *and* DIDIER NÉRAUDEAU

ABSTRACT. Cenomanian beds from western France have yielded a new pythonomorph squamate (Reptilia) that is described here as *Carentonosaurus mineaui* gen. et sp. nov. This fossil is referred to non-mosasaurid mosasauroid lizards, i.e. to 'aigialosaurs'. It has been found in sediments of marine origin and its anatomy confirms that it was an aquatic lizard. It is characterized by a combination of characters that has not been reported, thus far, for squamates. Moreover, its vertebral column includes non-pachyostotic cervical vertebrae and highly pachyostotic dorsal vertebrae as in several other 'aigialosaurs'. This new taxon is perhaps restricted to the upper Cenomanian. It lived in shallow and rather warm water of the inner shelf. It is worth mentioning that nearly all pachyostotic squamates are concentrated in the Cenomanian and/or lower Turonian deposits of the present European-North African-Middle East portion of the Tethys. A parallel is drawn between the high percentage of pachyostotic squamates and the fact that this period corresponds to both the largest transgression of the Phanerozoic and the warmest period in the whole of the Mesozoic and Caenozoic.

KEY WORDS: Cenomanian, Cretaceous, new taxon, pachyostosis, Pythonomorpha, Reptilia, Squamata.

CRETACEOUS beds of marine origin have produced lizards adapted to aquatic life. These fossils make up the mosasauroid assemblage that belongs to the pythonomorph squamates. They have been generally referred to three or four families: the Aigialosauridae, Dolichosauridae, Mosasauridae, and sometimes Coniasauridae. However, the phylogenetic relationships of the aigialosaurids, dolichosaurids, and coniasaurids, as well as the composition of these families, appear to be debatable (Calligaris 1988; Carroll and DeBraga 1992; Benton 1993; Dal Sasso and Pinna 1997; Caldwell 2000). Following Lee (1997), these three families are hereafter referred to as 'aigialosaurs'. The latter assemblage might form the paraphyletic stem group of the more derived Mosasauridae. In contrast to the general view, Caldwell (1999) suggested that mosasauroids are not closely related to extant varanoid lizards, an opinion previously put forward by Cope (1869). However, given uncertainty about relationships of the group, we follow the traditional opinion in retaining the mosasauroids as varanoid lizards. The latter assemblage is paraphyletic and represents the stem group of snakes (Lee 1997). Note that the term 'lizard' is used here as a short-hand for the paraphyletic assemblage composed of non-serpentian squamates.

Apart from *Pachyvaranus*, a varanoid *incertae sedis* from the Maastrichtian of Morocco (Arambourg 1952), and an indeterminate dolichosaur from the Turonian of France (Rage 1989), all 'aigialosaurs' are represented by articulated skeletons.

The Cenomanian of western France has yielded disarticulated elements, mainly vertebrae, of a new varanoid lizard that is described herein. It is assigned to the 'aigialosaur' assemblage *sensu* Lee (1997). Most fossils were found in one locality, Madame Island. A few other specimens that belong, or may belong, to this taxon come from other localities. The specimens from Madame Island are housed in the Laboratoire de paléontologie of the Muséum national d'Histoire naturelle (MNHN), Paris, France.

THE LOCALITY

The specimens from Madame Island were collected by one of us (DN) in the echinoid-rich Cenomanian beds (Néraudeau 1991) that crop out on the tidal flat and cliffs of Madame Island on the western coast of France (Text-fig. 1A). This vertebrate material comes from two stratigraphical units of the Upper
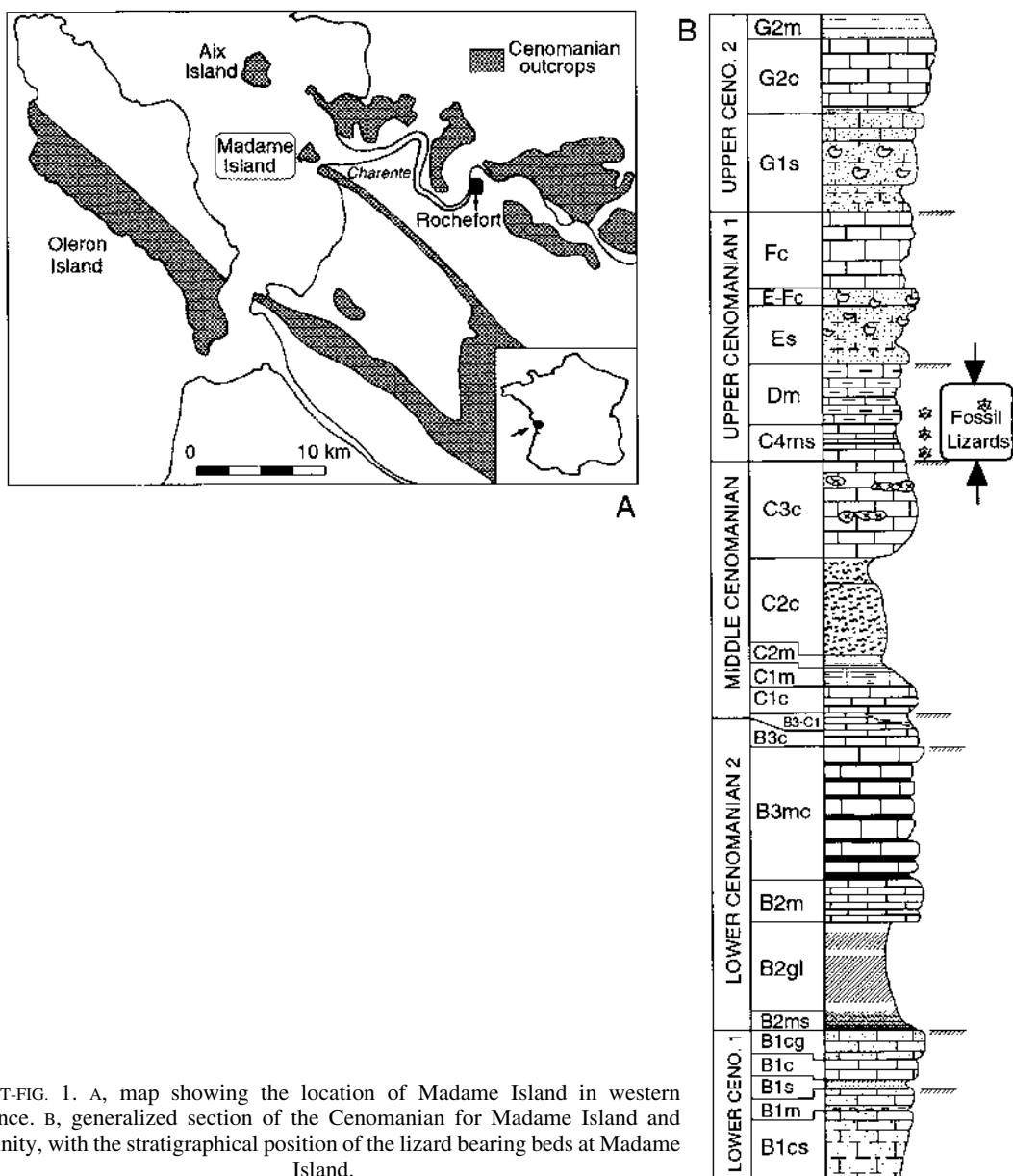
TEXT-FIG. 1. A, map showing the location of Madame Island in western France. B, generalized section of the Cenomanian for Madame Island and vicinity, with the stratigraphical position of the lizard bearing beds at Madame Island.

Cenomanian beds (Néraudeau *et al.* 1997) (Text-fig. 1B): (1) some vertebrae were collected from C4ms, the lower unit of the Upper Cenomanian 1; (2) the largest part of the material (vertebrae, one rib, and one fragmentary pectoral girdle) has been collected from the overlying Dm unit. The Dm unit belongs to the Upper Cenomanian Guerangeri Zone, dated by *Thomelites* cf. *lattense* and *Pseudocalycoceras* sp. (Néraudeau *et al.* 1997).

The oldest vertebra, from C4ms, comes from a level located about 0·20 m above the boundary between C4ms and C3c, i.e. the boundary between the Middle and Upper Cenomanian. This boundary corresponds to a regional discontinuity and probably to the 'Ce 4' sequence boundary of de Graciansky *et al.* (1998).

The youngest vertebra comes from a level located about 0·05–0·15 m above the base of Dm and approximately 1–1·20 m below the top of Dm, i.e. the boundary with the younger sandy unit Es (Néraudeau *et al.* 1997). Therefore, the lizard material as a whole was distributed through a stratigraphical thickness of about 0·50 m.

DEPOSITIONAL ENVIRONMENTS

The C4ms silty unit is interpreted as representing the beginning of a trangressive episode (not really as a 'lowstand systems tract'; Néraudeau *et al.* 1997); it corresponds to a very shallow environment. The invertebrate remains associated with the vertebrates are mainly fragmented rudists and stromatoporids derived from the previous reefal environments of the C3c unit. Some oysters and more rarely some spatangoid echinoids (*Mecaster*) comprise the other part of the invertebrate fauna. Apart from the lizard, vertebrates are represented only by fish (elasmobranchs: indeterminate cretoxyrhinids and neoselachians; actinopterygians: indeterminate pycnodontiforms) (D. Dutheil, pers. comm. 2000). The energy level was relatively high at the time of deposition, in a palaeoenvironmental context close to the coast under wave action.

The vertebrate-rich Dm unit corresponds to a highstand systems tract and a shallow environment open to outer shelf influences. Lithologically, Dm is a silty limestone, generally yellow but locally grey, with local concentrations of organic matter (Néraudeau 1991) and sometimes identifiable remains of land plants, such as *Frenelopsis* and *Araucarioxylon* (J. Dejax, pers. comm. 1999). The invertebrate fauna associated with the vertebrate remains is very abundant and well preserved, combining organisms fossilized *in situ*, such as echinoids, and shells transported and brought in by currents, such as those of cephalopods. The allochthonous fauna of cephalopods comprises mainly *Nautilus triangularis* showing remains of the shell covered by epizoans. The *in situ* fauna of echinoids comprises mainly juvenile *Mecaster grossouvrei*, sometimes preserved with some of their spines (Area A in Néraudeau 1991). These spatangoids with large ambulacra characterize silty and sandy substrates in shallow, temperate water (Néraudeau 1995). The Dm unit has yielded the same fish fauna as the C4ms unit, plus the elasmobranch *Squalicorax* (Anacoracidae).

Finally, in the deposits from which the lizard has been collected (in both C4ms and Dm), organisms of various ecological affinities are preserved together: land plants, echinoids of the shallow inner shelf, cephalopods of the deeper shelf. This association of different environmental components could be evidence of a depositional environment at the crossroads of marine and continental influences, such as a lagoon (protected by a rudist reef?) or more likely a temporary reservoir of water ('baïne' in French), isolated from the open sea during low tide by a sand bank but inundated during high tide.

SYSTEMATIC PALAEONTOLOGY

REPTILIA Laurenti, 1768
SQUAMATA Oppel, 1811
VARANOIDEA Gray, 1827
PYTHONOMORPHA Cope, 1869
'AIGIALOSAURS'

CARENTONOSAURUS gen. nov.

Derivation of name. Latin, *Carentonia*, 'Charente', a river close to Madame Island.

Type species. Carentonosaurus mineaui sp. nov.

Diagnosis. As for the type and only known species.

Carentonosaurus mineaui sp. nov.

Text-figures 2–4

Derivation of name. Dedicated to Mr Mineau and his family for their kind assistance during field work.

Holotype. A mid- or posterior dorsal vertebra (MNHN, IMD 21).

Type locality and horizon. Madame Island ('Département' of Charente Maritime, western France); Dm unit, lower upper Cenomanian.

Referred material. 49 vertebrae [14 from C4ms unit (MNHN, IMD 1–14); 35 from Dm unit (MNHN, IMD 15–20 and IMD 22–50)], one rib (MNHN, IMD 51) from Dm unit, and a fragmentary pectoral girdle (MNHN, IMD 52) from Dm unit; all specimens from Madame Island. Three vertebrae from La Couronne (private collections of D. Pouit and R. Vullo). Perhaps two vertebrae from Les Renardières (MNHN, RND 8, and private collection of D. Pouit), two vertebrae from Roullet-Saint-Estèphe (private collection of L. Villier), and two vertebrae from Douce Amie ('Guéranger collection', Musée Vert of Le Mans, uncatalogued).

Geographic and stratigraphic ranges. Lower upper Cenomanian of Madame Island ('Département' of Charente Maritime) and upper Cenomanian of La Couronne ('Département' of Charente). Perhaps lower Cenomanian of Les Renardières ('Département' of Charente Maritime), basal upper Cenomanian of Roullet-Saint-Estèphe ('Département' of Charente) and upper Cenomanian of Douce Amie ('Département' of Sarthe). All localities are in western France.

Diagnosis. Varanoid lizard characterized by the association of pachyostotic mid- and posterior dorsal vertebrae and non-pachyostotic cervical, sacral, and caudal vertebrae. Each vertebra is characterized by a combination of the following characters: (1) presence of a zygosphene with well-shaped articular facets, but zygantrum without articular facets; (2) anterior border of zygosphene concave but not deeply notched; (3) frequent presence of paracotylar, parazygosphenal, and zygantral foramina, but absence of lateral and subcentral foramina; (4) prezygapophyseal facets somewhat larger than postzygapophyseal facets; consequently, vertebrae wider across prezygapophyses (paradiapophyses excluded) than across postzygapophyses; (5) precondylar constriction absent. Moreover, posterior cervical and dorsal vertebrae are very depressed. The axis of the cotyle-condyle system is weakly oblique, except in anterior cervical, sacral, and caudal vertebrae. Moreover, except in anterior cervical vertebrae, the paradiapophyses and epidiapophyseal ridges project strongly laterally; interzygapophyseal ridges are approximately parallel to the vertebral axis. Rib weakly curved with a reduced pseudotuberculum. Scapula short dorsoventrally, glenoid area well-defined.

Remarks. Among pachyostotic Varanoidea, *Carentonosaurus* differs from *Pachyvaranus* in having a zygosphene-zygantrum system and parazygosphenal foramina. It is distinguished from *Simoliophis*, *Eupodophis*, *Pachyophis*, *Pachyrhachis*, and *Haasiophis* by its paradiapophyses projecting laterally beyond the prezygapophyseal facets, by the presence of epidiapophyseal ridges, and in having vertebrae wider across prezygapophyses than across postzygapophyses. It further differs from *Simoliophis* and *Eupodophis* in lacking zygantral facets and in having parazygosphenal foramina. It differs from *Eidolosaurus* by its more strongly protruding paradiapophyses and the subtriangular ventral surface of its centra; from *Adriosaurus* and '*Acteosaurus*' *crassicostatus* by its non-pachyostotic neural spine; from *Adriosaurus* in having paradiapophyses protruding as much in dorsal as in cervical vertebrae; from *Acteosaurus tommasinii* by its clearly pachyostotic and wider vertebrae; and from *Mesoleptos* at least by its shorter ribs.

Description

Carentonosaurus mineaui gen. et sp. nov. is mostly represented by vertebrae. Some are affected by pachyostosis whereas others are non-pachyostotic.

   In 'aigialosaurs' that have pachyostotic vertebrae, pachyostosis occurs in the mid- and posterior dorsal region, but it is difficult to determine whether the most anterior dorsal vertebrae are pachyostotic. Most cervical vertebrae, i.e. those that are clearly anterior to the pectoral girdle, are unequivocally non-pachyostotic; but it is not impossible that
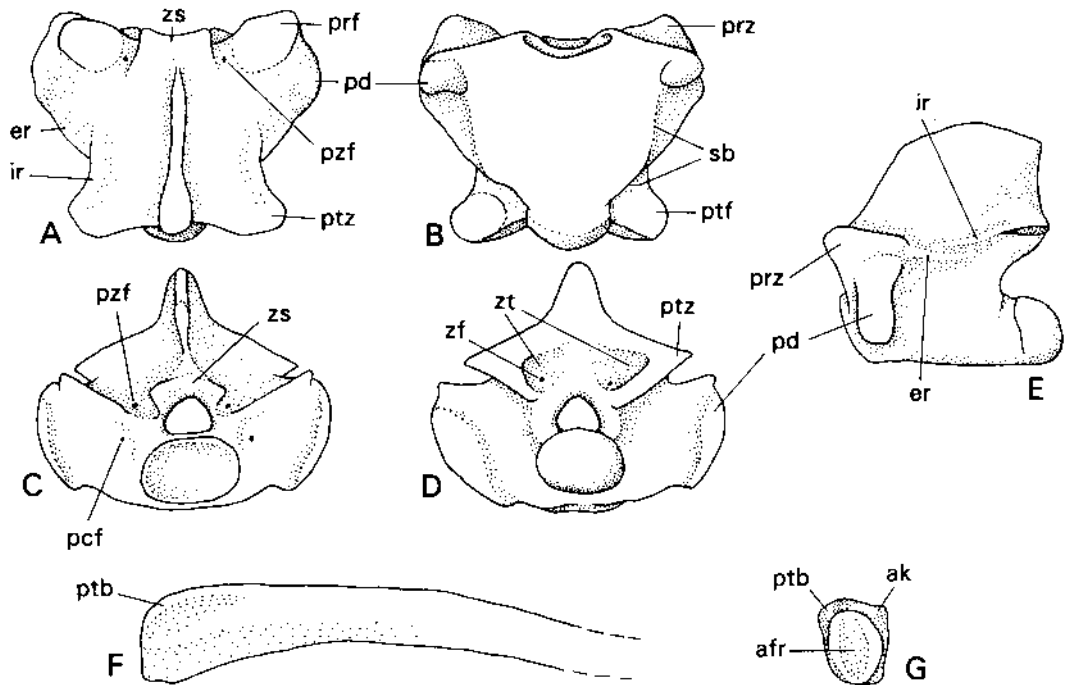
TEXT-FIG. 2. Drawings identifying morphological features described in the text. A–E, dorsal vertebra in A, dorsal, B, ventral, C, anterior, D, posterior, and E, left lateral views. F–G, rib in F, anterodorsal and G, proximal views. Abbreviations: ak, anterodorsal keel; afr, articular facet of the rib; er, epidiapophyseal ridge; ir, interzygapophyseal ridge; pcf, paracotylar foramen; pd, paradiapophysis; prf, prezygapophyseal facet; prz, prezygapophysis; ptb, pseudotuberculum; ptf, postzygapophyseal facet; ptz, postzygapophysis; pzf, parazygosphenal foramen; sb, subcentral border; zf, zygantral foramen; zs, zygosphene; zt, zygantrum.

pachyostosis affects posteriormost vertebrae of the cervical region. In *Carentonosaurus*, the identification of vertebral regions is difficult because all vertebrae are disarticulated. Pachyostotic vertebrae certainly come from the dorsal region. Moreover, several vertebrae are weakly thickened, and show a morphology that is intermediate between that of pachyostotic and non-pachyostotic ones. They probably come from the level of the pectoral girdle, i.e. they might be posterior cervical and/or anterior dorsal vertebrae. To sum up, we assume that in *C. mineaui*: (1) mid- and posterior dorsal vertebrae are pachyostotic; (2) anterior dorsal vertebrae are either pachyostic or 'intermediate'; (3) posterior cervical vertebrae are either 'intermediate' or non-pachyostotic; and (4) more anterior cervical vertebrae are non-pachyostotic.

   The available vertebral material includes 20 vertebrae that are pachyostotic, 15 non-pachyostotic specimens, and 12 vertebrae that show an intermediate condition. Moreover, the condition in one vertebra (MNHN, IMD 48) cannot be determined. In addition, there is one sacral and one caudal vertebra; neither is pachyostotic.

Holotype. The holotype is a nearly complete vertebra (Text-fig. 3A–E). It belongs to the middle or posterior part of the dorsal region. The vertebra is very heavily built, pachyostotic, strikingly depressed, and wide. Its measurements are as follows: width across articular facets of prezygapophyses, 11·7 mm; width across paradiapophyses, 14·1 mm; length from cotylar rim to tip of condyle, 9·3 mm; horizontal diameter of condyle, 4·3 mm.

   In dorsal view, the anterior part of the vertebra is markedly wider than the posterior one. This results mainly from the marked lateral projection of the paradiapophyses. However, even the width across the prezygapophyseal facets exceeds that across the postzygapophyses. None of the zygapophyseal articular facets is entirely preserved; however, the facets of the prezygapophyses are somewhat larger than those of the postzygapophyses (this is confirmed by the other vertebrae). The neural arch appears to be affected by pachyostosis; it is more or less swollen laterally and it forms a step behind each prezygapophyseal facet. Each paradiapophysis is prolonged posteriorly by a blunt ridge that
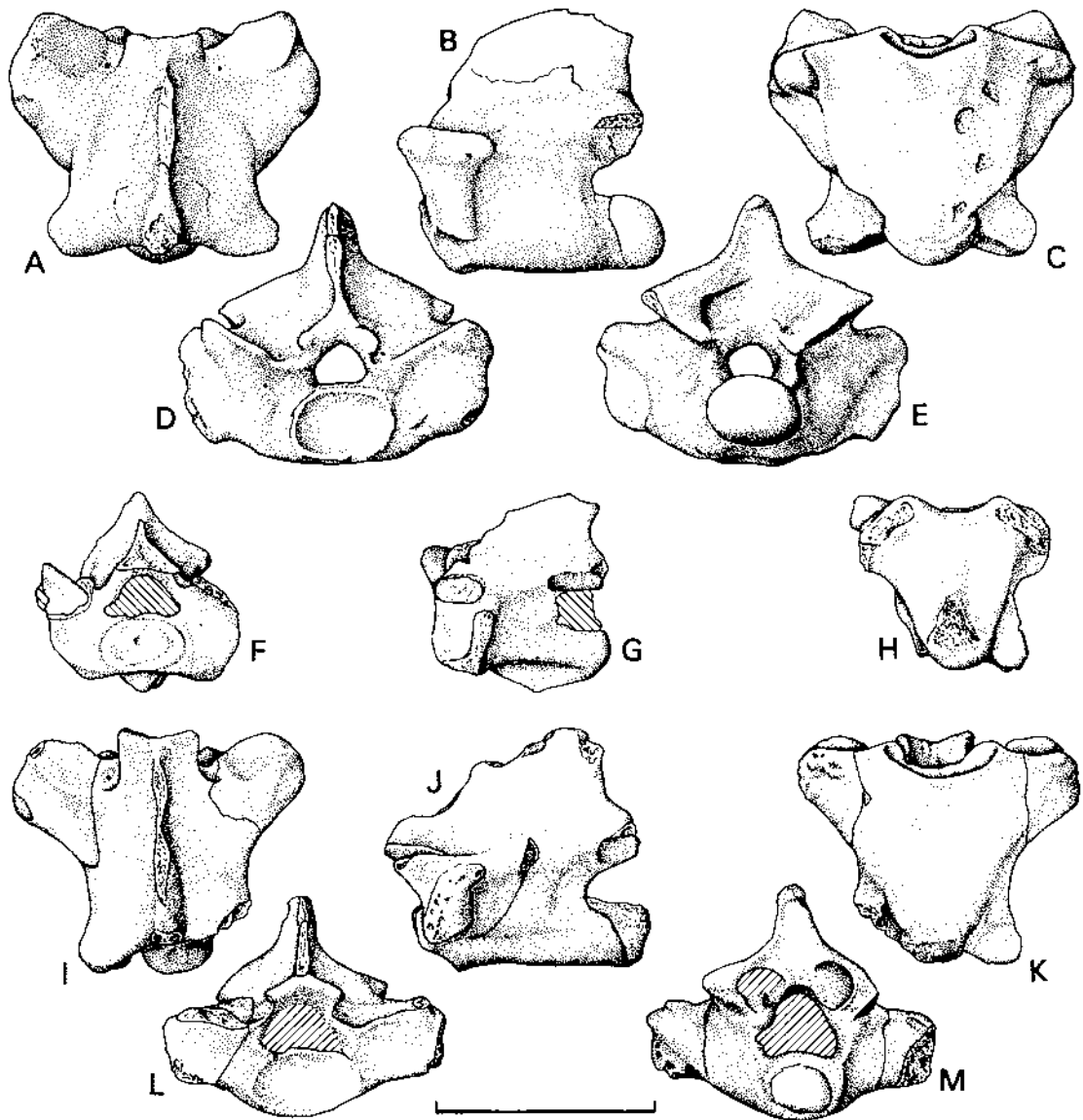
TEXT-FIG. 3. *Carentonosaurus mineaui* gen. et sp. nov., Madame Island, upper Cenomanian. A–E, mid- or posterior dorsal vertebra, holotype, MNHN IMD 21, in A, dorsal, B, left lateral, C, ventral, D, anterior, and E, posterior views. F–H, anterior cervical vertebra, MNHN IMD 35, in F, anterior, G, left lateral, and H, ventral views. I–M, posterior cervical vertebra, MNHN IMD 40, in I, dorsal, J, left lateral, K, ventral, L, anterior, and M, posterior views. Scale bar represents 1 cm.

originates from the paradiapophyseal tip, runs posteromedially, and clearly projects laterally; here, we name it as an 'epidiapophyseal ridge'. Only the posterior half of each interzygapophyseal ridge appears, running subparallel to the vertebral axis. Anteriorly, the ridge passes above the epidiapophyseal ridge before grading into the neural arch without reaching the prezygapophysis. The postzygapophyses do not project strongly laterally. The prezygapophyses stand out weakly against the bulk of the paradiapophyses; their articular facets are ovoid. A zygosphene is present; its anterior border is barely concave. A parazygosphenal foramen opens on either side between the zygosphene and each

prezygapophyseal facet. The neural spine protrudes slightly posteriorly; anteriorly it reaches the zygosphenal roof. It is not thickened by pachyostosis. The posterior border of the neural arch forms a very shallow concavity.

In anterior view, the strongly depressed condition of the vertebra is striking. No clear limit appears between the neural spine and the roof of the zygosphene. The latter is poorly preserved and its morphology cannot be described, but it is well preserved in some other vertebrae (see below). In cross section, the neural canal is small and subtriangular. The cotyle is slightly depressed and it is as wide as the zygosphene. The prezygapophyseal facets are markedly inclined. A small paracotylar foramen opens on the right side. The paradiapophyses project laterally beyond the prezygapophyseal tips.

In lateral aspect, the neural spine is rather high; the anterior border forms a curve the convexity of which is directed anterodorsally, whereas the incomplete posterior border was apparently vertical or perhaps slightly inclined posteriorly. The neural arch clearly slopes anteriorly. The prezygapophysis lacks any trace of a prezygapophyseal process. The paradiapophyses are narrow and dorso-ventrally elongate; they form a single articular facet. The blunt epidiapophyseal ridge fades out in the lateral wall at a point anterior to the level of the postzygapophysis. The posterior part of the lateral wall swells. The axis of the condyle is weakly inclined: the condyle faces slightly dorsoposteriorly. The vertebra lacks lateral foramina.

In ventral view, the surface of the centrum is broad and well delimited by subcentral borders. As a result of the swelling of the posterior parts of the lateral walls, the subcentral borders arch strongly posterolaterally. The ventral surface of the centrum is barely convex and its sagittal part is flat. Because of the obliquity of the cotyle-condyle system, the cotyle is partly exposed in ventral aspect. There is no precondylar constriction. Subcentral foramina are absent.

In posterior view, the border of the neural spine is rather thick and hollowed by a shallow vertical groove. Above the zygantrum, the dorsal borders of the neural arch are nearly straight. The zygantrum appears as two symmetrical fossae which lack articular facets. The absence of facets is astonishing since the zygosphene has well-shaped articular facets. A zygantral foramen opens in the bottom of the right depression.

Intracolumnar variation. As stated above, cervical, dorsal, sacral, and caudal (non-anterior caudal) vertebrae are available. Cervical and dorsal vertebrae show the peculiar association of a well-shaped zygosphene and absence of articular facets in the zygantrum, as well as the presence of paracotylar, parazygosphenal, and zygantral foramina, which appears to be unique in lizards. However, the foramina are not constant (see below). In addition, all vertebrae are slightly wider across the prezygapophyses (paradiapophyses excluded) than across the postzygapophyses, whatever their position in the vertebral column (this character is not observable in post-dorsal vertebrae). In all cervicals and dorsals, the thickness of the neural spine is similar to that of the holotype.

Cervical vertebrae. Three vertebrae come from the anterior part of the cervical region; two of these are represented only by their centrum, but one is nearly complete (Text-fig. 3F–H). They are small, not depressed, and not pachyostotic. The zygosphene is not preserved. The centrum is triangular, narrow, and not obviously elongate. It bears the base of a hypapophysis that is broken away. The paradiapophyses are markedly elongate dorsoventrally, very narrow anteroposteriorly, and they bend posteriorly. The paradiapophyses and epidiapophyseal ridges do not project strongly laterally. The cotyle is depressed; the axis of the cotyle and condyle is approximately horizontal. The long axis of the prezygapophyseal facet is oblique in dorsal view.

More posterior (but perhaps not posteriormost) cervical vertebrae are represented by 12 specimens that are also not affected by pachyostosis (Text-fig. 3I–M). They differ from anterior cervicals in being larger and more markedly depressed, and in having cotyles and condyles with slightly oblique axes. In addition, their centrum clearly widens anteriorly, and there is neither a hypapophysis nor a haemal keel. The paradiapophyses are not curved and are less elongate dorsoventrally than those of the anterior cervical vertebrae. These cervicals differ from the holotype in being more depressed and in having a triangular centrum that is convex ventrally in transverse section. In some vertebrae, the midline of the ventral surface is flat. The subcentral borders are nearly straight, i.e. different from those of the holotype. In some vertebrae the paradiapophyses and epidiapophyseal ridges are less protruding than in the holotype, but in the others they protrude laterally as much as in the holotype. These vertebrae certainly occupied a more posterior position in the cervical region. In dorsal view, the epidiapophyseal ridge of each cervical forms a concavity that is posterolaterally directed, whereas the ridge is clearly convex posterolaterally in the holotype. In lateral aspect, the paradiapophyses are often damaged; they do not differ significantly from those of the holotype. In several vertebrae, the epidiapophyseal and interzygapophyseal ridges merge and form a single, blunt interzygapophyseal ridge. When they do not merge, the two ridges are less clearly distinct from one another than in the holotype, while the cotyle and condyle appear to be more depressed. The neural spine is rectangular, about twice as long as high, as in the holotype. It differs in having a straight anterior border. Both the anterior and posterior borders are nearly vertical.

'Intermediate' vertebrae (posterior cervical and/or anterior dorsal vertebrae). Twelve specimens are regarded as
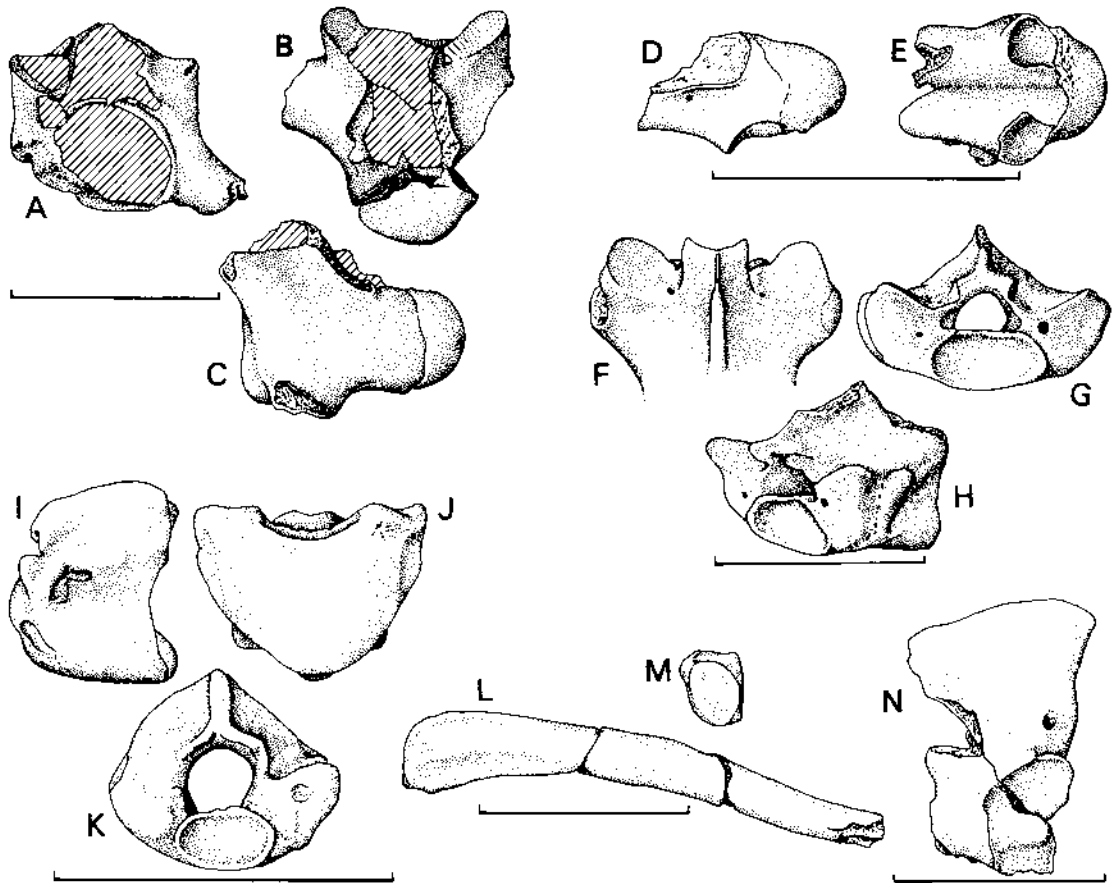
TEXT-FIG. 4. *Carentonosaurus mineaui* gen. et sp. nov., Madame Island, upper Cenomanian. A–C, sacral vertebra, MNHN IMD 49, in A, anterior, B, dorsal, and C, left lateral views. D–E, centrum of caudal vertebra, MNHN IMD 50, in D, left lateral and E, ventral views. F–H, well-preserved zygosphene (of a cervical vertebra), MNHN IMD 39, in F, dorsal, G, anterior, and H, oblique anterolateral views. I–K, dorsal vertebra of a juvenile individual showing pachyostosis, MNHN IMD 6, in I, left lateral, J, ventral, and K, anterior views. L–M, rib, MNHN IMD 51, in L, anterodorsal and M, proximal views. N, pectoral girdle, left scapulocoracoid, MNHN IMD 52, lateral view. Scale bars represent 1 cm.

'intermediate' vertebrae, although there is no clear limit between confirmed cervical, 'intermediate', and confirmed dorsal (i.e. pachyostotic) regions. In the 'intermediate' vertebrae, pachyostosis becomes perceptible. It appears as a slight swelling of the posterolateral walls of the vertebrae; as a result, the subcentral borders tend to form a posterolaterally directed convexity. However, the centrum remains approximately triangular; it clearly widens anteriorly. The ventral surface is nearly flat. On the whole, the vertebrae are less depressed than the cervicals. The paradiapophyses and epidiapophyseal ridges project laterally as in the holotype. In dorsal aspect, the epidiapophyseal ridge can be slightly concave, straight, or slightly convex posterolaterally. The paradiapophyses resemble those of the holotype. As in confirmed cervicals, the epidiapophyseal and interzygapophyseal ridges can remain distinct or merge. None of these vertebrae preserves an entire neural spine.

Mid- and posterior dorsal vertebrae. Vertebrae from these regions are exemplified by the holotype. Within pachyostotic vertebrae, it is not possible to distinguish mid-dorsal from posterior dorsal vertebrae. The only noticeable variation is that, as in more anterior regions, the epidiapophyseal and interzygapophyseal ridges unite as a single ridge in various vertebrae.

Sacral vertebra. One incomplete vertebra is available (Text-fig. 4A–C). It is not pachyostotic and it is characterized mainly by its shortness and by the presence of sacral processes (sacral 'ribs'). Only the base of the left process is preserved; it is very robust, somewhat flattened dorsoventrally, and directed lateroventrally. The vertebra is much shorter than the cervicals and dorsals. The neural arch is broken away but, based on the lateral walls, it was comparatively reduced, narrower than the centrum. The prezygapophyseal facets are smaller than in cervical and dorsal vertebrae. The presence or absence of a zygosphene cannot be confirmed. The cotyle is relatively larger than in more anterior vertebrae and faces anteriorly. The condyle is damaged, but its axis is horizontal. Apparently, the ventral surface of the centrum did not bear pedicels, articular facets, or processes.

Caudal vertebra. Caudal vertebrae are represented by a single posterior half centrum (Text-fig. 4D–E) that does not show pachyostosis. The ventral surface forms a sagittal groove limited laterally by blunt ridges. The depth of the ridges increases posteriorly where each of them bears a damaged process close to the condyle. The cross-sections are more or less circular, which suggests that these processes were probably short pedicels for the articulation of a chevron bone. When chevrons are fused to the centrum (haemapophyses), each branch is compressed laterally. As in the sacral vertebra, the axis of the condyle appears to be horizontal.

Other variation. The zygosphene, which is poorly preserved in the holotype, may be observed in other vertebrae (Text-fig. 4F–H). It is well shaped, narrow, and its anterior border is more or less concave. Unlike the zygosphene of other lizards, the anterior border is never deeply notched (although, in one juvenile vertebra it is rather deeply concave). The articular facets face ventrolaterally; they are clearly limited and oval, but they are truncated posteriorly. The larger the vertebra, the narrower is the zygosphene. As in the holotype, the zygosphenes always bear articular facets but these are always absent in zygantra.

Some juvenile vertebrae are known. They are characterized by their small size and a cotyle that is markedly wider than high. It is worth noting that the dorsal vertebral centrum of juveniles is already heavily affected by pachyostosis (Text-fig. 4I–K).

The presence of vertebral foramina is not constant. When foramina are not visible, this generally results from the type of fossilization. However, in those specimens where foramina are preserved, some of them can be absent. Parazygosphenal foramina are the most constant. This variation is not correlated with the position of the vertebrae within the vertebral column.

Rib. One incomplete holocephalous rib is referred to *Carentonosaurus* because its articular facet fits the vertebral paradiapophyses and because this genus is the only tetrapod in the locality. On the whole, the curvature of the rib is not well marked; in fact, it is sinuous rather than regularly curved (Text-fig. 4L). The rib has a rounded cross-section but the proximal portion is modified by the presence of low longitudinal ridges. The diameter decreases smoothly proximodistally. The articular facet is oval with a dorsoventrally elongate depression (Text-fig. 4M). This depression matches the paradiapophysis of the vertebrae. A low posterodorsal keel occurs on the proximal portion; it represents the reduced pseudotuberculum. A very low anterodorsal keel runs along the proximal portion, an apparently unique condition amongst squamates. Between the two keels, the surface is flat. On the anteroventral border of the proximal part, a low tubercle might represent the anteroventral 'pinching' known in various squamates (Hoffstetter and Gasc 1969). This rib does not show any trace of pachyostosis.

Pectoral girdle. A fragmentary pectoral girdle is represented by an incomplete left scapula and a fused fragment of coracoid (Text-fig. 4N). The scapula shows a typical hatchet-like shape. Unusually, a rather large foramen opens near the posterior border and glenoid rim. As in other aquatic varanoids, the scapula is relatively short dorsoventrally (Caldwell *et al.* 1995). However, among living lizards such a short scapula is also present in helodermatids (Lecuru 1968), which demonstrates that shortening of this bone is not necessarily an adaptation to aquatic life. The part of the coracoid that is preserved is very small. A break separates the scapula from the coracoid, but it is uncertain whether this follows a suture line or is a break in a co-ossified scapulocoracoid. Since the lower part of the scapulocoracoid fenestra is damaged, its depth cannot be evaluated. It is also not possible to determine whether coracoid fenestrae were present. The glenoid articular area is well defined, and the glenoid fossa is directed mainly laterally (and slightly posteriorly).

Other possible occurrences of Carentonosaurus

Outside the type locality, *Carentonosaurus mineaui* may be confidently reported from only one site: La Couronne ('Département' of Charente); upper Cenomanian. This locality has produced three well-preserved dorsal vertebrae. Further specimens from three localities apparently represent this species, but this cannot be confirmed. They include: two very worn vertebrae from the lower Cenomanian of Les Renardières ('Département' of Charente Maritime;

Néraudeau and Moreau 1989); two incomplete vertebrae from the basal upper Cenomanian of Roullet-Saint-Estèphe ('Département' of Charente); and two incomplete and worn vertebrae from the upper Cenomanian (*Calycoceras naviculare* Zone; 'Sables du Perche') of Douce Amie, near Le Mans ('Département' of Sarthe).

DISCUSSION

A phylogenetic analysis cannot be performed because the available material provides too few characters. Moreover, in the presumably closely related forms (see below), only one aspect of the vertebrae is visible, restricting the number of characters available in these taxa. Therefore, our objective is only to show that the fossil from Madame Island is a distinct taxon.

The most striking feature of the vertebrae is the association of an overall lizard-like morphology with the presence of a well-developed zygosphene and of foramina so far known only in snakes. The lizard-like morphology mainly results from the combination of the following characters: (1) very narrow (= anteroposteriorly very short) and dorsoventrally elongate paradiapophyses; (2) articular facets of zygapophyses strongly inclined above horizontal; (3) absence of prezygapophyseal processes; (4) nearly straight borders of the neural arch in posterior aspect; (5) posterior border of the neural arch in dorsal view not deeply concave; (6) lack of articular facets in the zygantrum; (7) absence of lateral foramina; (8) absence of subcentral foramina. Characters 2, 3, and 5 are also encountered in most primitive snakes.

Within Squamata, a zygosphene-zygantrum system occurs in all snakes and in various extant families of lizards (Lacertidae, Teiidae, Gymnophthalmidae, Iguanidae, Cordylidae), although it is not present in all species of these families but chiefly in the largest ones (Estes *et al*. 1988). In addition, it is present in the mosasauroid lizards (Hoffstetter 1955; Lee 1997; Caldwell and Cooper 1999). However, in lizards the roof of the zygosphene is nearly always incomplete and deeply embayed. In *Carentonosaurus* the anterior border of the zygosphene is only slightly concave, as also appears to be the case in at least some 'aigialosaurs'.

Paracotylar foramina have not been reported previously in lizards; however, they are present in *Pachyvaranus* (this feature was not described in Arambourg 1952) and in vertebrae that belong to a primitive mosasaur (N. Bardet, pers. comm. 1999). Moreover, zygantral foramina are very rare in lizards. Up to now, parazygosphenal foramina have also never been reported in lizards but they are known in a few snakes: *Pouitella pervetus*, a snake of lapparentophiid grade from the Cenomanian (Rage 1988); *Palaeophis colossaeus*, a palaeophiid from the Eocene (Rage 1983); and the Acrochordidae, an advanced extant family (Hoffstetter and Gayrard 1964).

Despite these 'snake-like' foramina, *Carentonosaurus* cannot be considered a snake because of the lizard features listed above. Moreover, the overall morphology of the non-pachyostotic vertebrae is characteristically lizard-like and very different from that of snakes.

The oblique axis of the condyle-cotyle system is a derived feature that occurs only in the Varanoidea *sensu* Lee (1997) (Estes *et al*. 1988). Since *Carentonosaurus* cannot be referred to the snakes, then it has to belong to the lizards of the paraphyletic varanoid assemblage. The comparative narrowness of the neural arch at the level of the postzygapophyses, the marked anterior slope of the neural arch, the dorsoventral elongation of the paradiapophyses (three features that occur only in various varanoid lizards, and are therefore derived?), and the presence of articulated chevrons (a plesiomorphic character; Pregill *et al*. 1986) are consistent with this referral.

Within varanoid lizards, the presence of a zygosphene, the weak obliquity of the condyle-cotyle system, and the lack of a precondylar constriction of the centrum point to the mosasauroids (Caldwell 1999). In addition, the sacral vertebra is clearly procoelous (the cotyle is deep and the condyle is strongly prominent); this shows that *Carentonosaurus* cannot be attributed to the Mosasauridae. In the latter group, vertebrae of the sacral and caudal regions are not markedly procoelous. This is corroborated by the fact that the glenoid articular area of the pectoral girdle is well defined in *Carentonosaurus*, whereas it is poorly shaped in mosasaurids (Caldwell *et al*. 1995).

Consequently, *Carentonosaurus* is referred to non-mosasaurid Mosasauroidea, i.e. to the 'aigialosaurs' *sensu* Lee (1997). Comparisons should be made within the latter assemblage and non-pachyostotic

'aigialosaurs' can be ruled out from comparisons. Therefore, the following taxa are excluded from the discussion: *Aigialosaurus* Gorjanovic-Kramberger, 1892; *Aphanizocnemus* Dal Sasso and Pinna, 1997; *Carsosaurus* Kornhuber, 1893; *Coniasaurus* Owen, 1850; *Dolichosaurus* Owen, 1850; *Haasia* Polcyn, Tchernov and Jacobs, 1999; *Opetiosaurus* Kornhuber, 1901; and *Pontosaurus* Gorjanovic-Kramberger, 1892.

Pachyostosis results in thickening of bone, but it is not always easy to distinguish massive non-pachyostotic vertebrae from true pachyostotic vertebrae. For example, Lee *et al.* (1999) stated that the only pachyostotic squamates are the snakes *Simoliophis*, *Mesophis*, *Pachyrhachis* and *Pachyophis*, to which *Haasiophis* and *Eupodophis* should now be added (*Eupodophis* is a replacement name for *Podophis* Rage and Escuillié, 2000; Rage and Escuillié 2002). It should be noted that *Mesophis* Bolkay, 1925, is represented by a single specimen that is poorly known. It cannot be located and is not considered here. However, several extinct varanoid lizards have thickened vertebrae. They are considered here to be pachyostotic.

Among 'aigialosaurs', pachyostosis occurs in *Adriosaurus suessi* Seeley, 1881, *Eidolosaurus trauthi* Nopcsa, 1923, *Mesoleptos zendrini* Cornalia and Chiozza, 1852, *Acteosaurus crassicostatus* Calligaris, 1993, and perhaps *Acteosaurus tommasinii* von Meyer, 1860. Moreover, *Pachyvaranus crassispondylus* Arambourg, 1952, is a pachyostotic varanoid that probably does not belong to the mosasauroids because it lacks a zygosphene-zygantrum system. However, apart from this feature, its vertebrae look like those of mosasauroids, more specifically those of 'aigialosaurs', and it should be compared to *Carentonosaurus*. In addition, several snakes have pachyostotic vertebrae; since they have all been recovered from the Cenomanian, they are included in the present comparison. These snakes are *Simoliophis* Sauvage, 1880 (two species), *Pachyophis woodwardi* Nopcsa, 1923, *Pachyrhachis problematicus* Haas, 1979, *Haasiophis terrasanctus* Tchernov *et al.*, 2000, and *Eupodophis descouensi* (Rage and Escuillié, 2000).

Among these taxa, only *Pachyvaranus, Simoliophis* and to a lesser degree *Eupodophis* are known by disarticulated vertebrae. *Pachyvaranus*, from the Maastrichtian of Morocco (Arambourg 1952), is reminiscent of *Carentonosaurus* because its vertebrae are pachyostotic and markedly depressed, its paradiapophyses project laterally beyond the prezygapophyseal tips, the prezygapophyseal width surpasses the postzygapophyseal width and paracotylar foramina are present. However, the vertebrae of *Pachyvaranus* clearly differ from those of *Carentonosaurus* in lacking a zygosphene and parazygosphenal foramina; moreover, the subcentral ridges were probably less arched laterally in all vertebrae of the Moroccan fossil. Arambourg (1952) allocated osteoderms to *Pachyvaranus*, but they probably do not belong to a lizard.

Simoliophis is restricted to the Cenomanian of south-western Europe and North Africa (Rage and Cappetta 2002). Its vertebrae are strongly pachyostotic but they differ markedly from those of *Carentonosaurus*. They are high and rather narrow. The subcentral borders are parallel; as a result the ventral face of the centrum is approximately rectangular. Zygantral facets are present and they are well shaped. The width of vertebrae across the prezygapophyses is similar to that across the postzygapophyses. Laterally, the paradiapophyses do not reach the level of the tip of the prezygapophyses. The vertebrae lack epidiapophyseal ridges, while the neural spine is affected by pachyostosis. The vertebrae lack parazygosphenal foramina. The only disarticulated vertebra of *Eupodophis* (Cenomanian, Middle East) is approximately similar to those of *Simoliophis*.

Pachyophis (Cenomanian, Bosnia-Herzegovina; Lee *et al.* 1999), *Pachyrhachis* and *Haasiophis* (Cenomanian, Middle East; Caldwell and Lee 1997; Lee and Caldwell 1998; Tchernov *et al.* 2000) are snakes represented only by articulated skeletons preserved on limestone slabs; therefore, comparisons with *Carentonosaurus* cannot be thorough. However, in these three genera, as in *Simoliophis* and *Eupodophis*, the vertebrae are as wide across the prezygapophyses as across the postzygapophyses; the paradiapophyses do not project laterally beyond the prezygapophyseal facets; there is no epidiapophyseal ridge; and the neural spine is affected by pachyostosis.

Eidolosaurus trauthi from the Cenomanian or lower Turonian (Langer 1961) of the Komen area (Slovenia) is known from a single specimen, the ventral face of which is exposed. The ribs are clearly pachyostotic but pachyostosis does not alter the morphology of vertebrae much. The centrum is approximately cylindrical with nearly parallel subcentral borders, and the paradiapophyses do not project laterally. Therefore, the vertebrae of *Eidolosaurus* clearly differ from those of *Carentonosaurus*.

Adriosaurus suessi is known from the Cenomanian or lower Turonian of Komen (Slovenia) and from the lower Turonian of Hvar, Croatia (Lee and Caldwell 2000). The type specimen of *Adriosaurus suessi* shows poorly preserved vertebrae in ventral aspect; as far as comparison is possible, their ventral surfaces are similar to those of *Carentonosaurus*. Another specimen shows the dorsal surface of dorsal vertebrae (Lee and Caldwell 2000). The neural spines of pachyostotic vertebrae are strongly affected by pachyostosis; therefore, they differ from those of *Carentonosaurus*, which are not thickened. This difference does not result from ontogenetic variation because the obviously smaller taxon (*Adriosaurus*) has the clearly thicker neural spines. Moreover, in *Adriosaurus*, the paradiapophyses are more laterally protruding in cervicals than in dorsal vertebrae (Lee and Caldwell 2000); in *Carentonosaurus*, they protrude as much in dorsal as in cervical vertebrae, or even less in cervicals. In addition, there is apparently no distinct epidiapophyseal ridge in *Adriosaurus*.

Mesoleptos zendrini is based on a poorly preserved specimen from the Cenomanian or lower Turonian of the Komen area. It comprises crushed and fragmentary vertebrae of the dorsal region, ribs and fragments of the pelvic girdle and one hindlimb. Some anterior dorsal vertebrae appear to be anteriorly widened. This is the only observable feature of the vertebrae and it cannot be confirmed. The specimen is so badly preserved that Gorjanovic-Kramberger (1892) regarded the length of the ribs as the only available feature. *Mesoleptos zendrini* should be best considered a *nomen dubium*. Two fragmentary specimens from this area and from the lower Turonian of Hvar (Croatia) were referred to this taxon by Calligaris (1988), but this referral is not confirmed and, in any case, the specimens are uninformative.

Acteosaurus tommasinii is represented by an incomplete articulated specimen from the Cenomanian or lower Turonian of Komen (von Meyer 1860). It is exposed in dorsal view and is missing the skull, anterior cervical vertebrae, pectoral girdle (but anterior limbs are present), and posterior caudal vertebrae. It is markedly smaller than *Carentonosaurus*. Cervical vertebrae are not pachyostotic. From the dorsal surface only, it is difficult to determine whether dorsal vertebrae are pachyostic; they are clearly narrower and more elongate than those of *Carentonosaurus*. In the smaller dorsal vertebrae of *Carentonosaurus*, the length of the neural arch is similar to that in *A. tommasinii*, but the vertebrae of *Carentonosaurus* are markedly wider (up to 1·5 times). Larger dorsal vertebrae of *Carentonosaurus* are even wider. In cervical vertebrae, these differences in proportions are somewhat less pronounced. Further comparisons are not possible.

Acteosaurus crassicostatus was erected by Calligaris (1993). The species is based on a specimen from the Cenomanian or lower Turonian of Komen that is exposed in dorsal aspect. It is composed of dorsal vertebrae, ribs and the anterior limbs. Vertebrae anterior to the pectoral area are not preserved. All vertebrae and ribs are strongly pachyostotic. The neural spine is thick and the neural arch is swollen. The ribs are exceedingly thick and resemble those of the snake *Pachyophis*. *Acteosaurus crassicostatus* is only slightly larger than the small *A. tommasinii*. However, while pachyostosis is either barely apparent or lacking in the latter species, it is very pronounced in *A. crassicostatus*. Moreover, the vertebrae of *A. crassicostatus* are clearly wider than those of *A. tommasinii*. Consequently, the referral of *A. crassicostatus* to the genus *Acteosaurus* is questionable. Although markedly larger than *A. crassicostatus*, *Carentonosaurus* has less thickened neural arches and its neural spines are not affected by pachyostosis. These two taxa are clearly distinct.

Carentonosaurus thus differs from all other 'aigialosaurs' that have pachyostotic vertebrae, except perhaps *Mesoleptos*, which is badly preserved rendering comparisons impossible. The fossil from Madame Island represents a new genus and species. Its relationships within mosasauroids cannot be established on the basis of the available material.

COMMENTS ON PACHYOSTOSIS

Pachyostotic bone occurs in various living and extinct fish and tetrapods. In tetrapods, pachyostosis affects animals readapted to life in water; it should not be confused with pathological hyperostosis (Schlüter *et al.* 1992). Pachyostotic swelling of bone is a stable feature that may be regarded as a character of systematic significance (de Buffrénil and Rage 1993; Lee *et al.* 1999; Meunier *et al.* 1999).

As stated above, we regard ten, perhaps 11, squamate genera (all extinct) as pachyostotic: '*Acteosaurus' crassicostatus*, *Adriosaurus*, *Eidolosaurus*, *Eupodophis*, *Haasiophis*, *Mesoleptos*, *Pachyophis*, *Pachyrhachis*, *Pachyvaranus*, *Simoliophis*, and perhaps *Acteosaurus tommasinii*. Apart from *Pachyvaranus*, which is Maastrichtian in age, all have been recovered from the Cenomanian.

The cause(s) of pachyostosis is (are) unknown. It appears to be unquestionably connected to aquatic life and, at least in fish, may result from peculiar hydrochemistry (Gaudant and Meunier 1996). According to von Nopcsa (1923) and de Ricqlès (1989), pachyostosis in tetrapods would be characteristic of animals incompletely adapted to marine life. Functionally, pachyostosis might have acted to provide a ballast that improves hydrostasis (de Buffrénil *et al*. 1990; Hoffstetter 1955) in approaching neutral buoyancy (Scanlon *et al*. 1999) or might correspond to an increase of erythrocyte-forming tissues (Hoffstetter 1955).

In squamates, pachyostotic vertebrae and ribs are known only in basal snakes and in various close relatives of snakes, i.e. 'aigialosaurs' (Lee 1997; Caldwell 1999). Therefore, although this cannot be demonstrated, it is hard to deny that pachyostosis has a phylogenetic significance within squamates.

In conclusion, irrespective of the hypothetical cause(s), function(s), and significance of pachyostosis, it is clear that with the exception of the Maastrichtian *Pachyvaranus*, all pachyostotic genera of squamates have been recovered from Cenomanian and/or lower Turonian deposits. This period corresponds to the largest transgression of Phanerozoic times. Former landmasses were turned into marine platforms on which water was rich in nutrients and carbonates. Moreover, the early late Cretaceous (including the Cenomanian and early Turonian) was also the warmest period of the whole of the Mesozoic and Cainozoic, following early Cretaceous cooling and preceding a cooling trend during the latest Cretaceous (Maastrichtian) (Frakes *et al*. 1994). Although we cannot assert that these peculiar conditions caused pachyostosis in most squamates from that time, it is hard to regard this as only a coincidence.

In addition, these pachyostotic taxa have all been recovered in a rather restricted palaeogeographical area, i.e. from westernmost Europe and westernmost North Africa to the Middle East, under Mediterranean-Tethyan influences. We cannot explain this geographic concentration.

CONCLUSIONS

Carentonosaurus is a very distinctive 'aigialosaurid' lizard characterized mainly by the presence of a non-notched zygosphene and of parazygosphenal foramina; the presence of zygosphenal articular facets but absence of zygantral articular facets; the frequent presence of paracotylar and zygantral foramina; and the association of pachyostotic dorsal vertebrae (presumably mid- and posterior dorsal vertebrae) with non-pachyostotic cervicals. Moreover, the vertebrae are exceedingly dorso-ventrally depressed.

It differs clearly from other 'aigialosaurs', except perhaps *Mesoleptos zendrini*. *Mesoleptos* is represented by a single poorly preserved specimen with which no comparison can be made; *M. zendrini* should be regarded a *nomen dubium*. The fossil from Madame Island is regarded as a new genus and species. Unfortunately, the available material precludes the detailed analysis needed to establish its relationships within Mosasauroidea.

The localities that yielded *Carentonosaurus* are all distributed in western France, near the boundary of the Paris and Aquitaine basins (the outcrops are in the northern part of the Aquitaine Basin and in the south-western part of the Paris Basin). From a stratigraphical point of view, it may be stated confidently that *Carentonosaurus* occurs in the upper Cenomanian, perhaps only in the lower upper Cenomanian; its presence in the lower Cenomanian (Les Renardières) is doubtful.

Carentonosaurus was an aquatic animal, as were the other 'aigialosaurid' lizards from the mid-Cretaceous. The slight curvature of the rib suggests that at least a part of the trunk was laterally compressed. This morphology and the reduction of the pseudotuberculum of the rib (Hoffstetter and Gasc 1969) characterize squamates highly adapted to aquatic life. Moreover, irrespective of its phylogenetic significance, pachyostosis is probably another consequence of this mode of life (see above). According to the fauna associated with *Carentonosaurus* and to the sediments at Madame Island, this lizard lived in the shallow and rather warm water of the inner shelf, between a few metres and a few tens of metres in depth.

REFERENCES

ARAMBOURG, C. 1952. Les Vertébrés fossiles des gisements de phosphates (Maroc, Algérie, Tunisie). *Service Géologique du Maroc, Notes et Mémoires*, **92**, 1–372.

BENTON, M. J. 1993. Reptilia. 681–715. *In* BENTON, M. J. (ed.). *The fossil record 2.* Chapman and Hall, London, xvii + 845 pp.

BOLKAY, S. J. 1925. *Mesophis nopcsai* n. g., n. sp. eine neues, schlangenähnliches Reptil aus der unteren Kreide (Neocom) von Bilek-Selista (Ost-Hercegovina). *Glasnik Zemaljskog Muzeja u Bosni i Hercegovini*, **37**, 125–135.

BUFFRÉNIL, V. de and RAGE, J.-C. 1993. La 'pachyostose' vertébrale de *Simoliophis* (Reptilia, Squamata): données comparatives et considérations fonctionnelles. *Annales de Paléontologie*, **79**, 315–335.

—— RICQLÈS, A. de, RAY, C. E. and DOMNING, D. 1990. Bone histology of the ribs of the archaeocetes (Mammalia, Cetacea). *Journal of Vertebrate Paleontology*, **10**, 455–466.

CALDWELL, M. W. 1999. Squamate phylogeny and the relationships of snakes and mosasauroids. *Zoological Journal of the Linnean Society*, **125**, 115–147.

—— 2000. On the aquatic squamate *Dolichosaurus longicollis* Owen, 1850 (Cenomanian, Upper Cretaceous) and the evolution of elongate necks in squamates. *Journal of Vertebrate Paleontology*, **20**, 720–735.

—— CARROLL, R. L. and KAISER, H. 1995. The pectoral girdle and forelimb of *Carsosaurus marchesetti* (Aigialosauridae), with a preliminary phylogenetic analysis of mosasauroids and varanoids. *Journal of Vertebrate Paleontology*, **15**, 516–531.

—— and COOPER, J. A. 1999. Redescription, palaeobiogeography and palaeoecology of *Coniasaurus crassidens* Owen, 1850 (Squamata) from the Lower Chalk (Cretaceous; Cenomanian) of SE England. *Zoological Journal of the Linnean Society*, **127**, 423–452.

—— and LEE, M. S. Y. 1997. A snake with legs from the marine Cretaceous of the Middle East. *Nature*, **386**, 705–709.

CALLIGARIS, R. 1988. I Rettili fossili degli 'strati calcarei ittiolitici di Comeno' e dell'isola di Lesina. *Atti del Museo Civico di Storia Naturale di Trieste*, **41**, 85–125.

—— 1993. *Acteosaurus crassicostatus* nuova species di Dolichosauridae negli 'strati calcarei ittiolitici' di Comeno. *Atti del Museo Civico di Storia Naturale di Trieste*, **45**, 29–34.

CARROLL, R. L. and DEBRAGA, M. 1992. Aigialosaurs: mid-Cretaceous varanoid lizards. *Journal of Vertebrate Paleontology*, **12**, 66–86.

COPE, E. D. 1869. On the reptilian orders Pythonomorpha and Streptosauria. *Proceedings of the Boston Society of Natural History*, **12**, 250–261.

CORNALIA, E. and CHIOZZA, L. 1852. Cenni geologici sull'Istria. *Giornale dell R. Istituto Lombardo di Scienze e Lettere*, **3**, 18–30.

DAL SASSO, C. and PINNA, G. 1997. *Aphanizocnemus libanensis* n. gen. n. sp., a new dolichosaur (Reptilia, Varanoidea) from the Upper Cretaceous of Lebanon. *Paleontologia Lombarda*, **7**, 3–31.

ESTES, R., DE QUEIROZ, K. and GAUTHIER, J. 1988. Phylogenetic relationships within Squamata. 117–281. *In* ESTES, R. and PREGILL, K. (eds). *Phylogenetic relationships of the lizard families*. Stanford University Press, Stanford, CA, xii + 631 pp.

FRAKES, L. A., PROBST, J. L. and LUDWIG, W. 1994. Latitudinal distribution of paleotemperature on land and sea from early Cretaceous to middle Miocene. *Comptes Rendus de l'Académie des Sciences*, II, **318**, 1209–1218.

GAUDANT, J. and MEUNIER, F. 1996. Observation d'un cas de pachyostose chez un Clupeidae fossile du Miocène terminal de l'Ouest algérien, *Sardina ?crassa* (Sauvage, 1873). *Cybium*, **20**, 169–183.

GORJANOVIC-KRAMBERGER, C. 1892. *Aigialosaurus*: ein neue Eidechse a.d. Kreideschiefern der Insel Lesina mit Rücksicht auf die bereits beschriebenen Lacertiden von Comen und Lesina. *Glasnika Hrvatskoga Prirodoslovno Drustvo u Zagrebu*, **7**, 74–106.

GRACIANSKY, P. C. de, HARDENBOL, J., JACQUIN, T. and VAIL, P. R. (eds). 1998. Mesozoic and Cenozoic sequence stratigraphy of European basins. *SEPM (Society for Sedimentary Geology), Special Publication*, **60**, 1–786.

GRAY, J. E. 1827. Reptilia. 424–434. *In* KING, P. P. (ed.). *Narrative of a survey of the intertropical and western coasts of*

Australia. Performed between the years 1818 and 1822, with an appendix containing various subjects. Vol. 2, Appendix B. John Murray, London, 464 pp.

HAAS, G. 1979. On a new snakelike reptile from the Lower Cenomanian of Ein Jabrud, near Jerusalem. *Bulletin du Muséum National d'Histoire Naturelle*, C, **1**, 51–64.

HOFFSTETTER, R. 1955. Squamates de type moderne. 606–662. *In* PIVETEAU, J. (ed.). *Traité de Paléontologie*, **5**. Masson, Paris, 1113 pp.

—— and GASC, J.-P. 1969. Vertebrae and ribs of modern reptiles. 201–310. *In* GANS, C., BELLAIRS, A. D'A. and PARSONS, T. S. (eds). *Biology of the Reptilia 1, Morphology A*. Academic Press, London and New York, xv + 373 pp.

—— and GAYRARD, Y. 1964. Observations sur l'ostéologie et la classification des Acrochordidae (Serpentes). *Bulletin du Muséum National d'Histoire Naturelle*, **36**, 677–696.

KORNHUBER, A. G. 1893. *Carsosaurus Marchesettii*, ein neuer fossiler Lacertilier aus den Kreideschichten des Karstes bei Komen. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt*, **17** (3), 1–15.

—— 1901. *Opetiosaurus bucchichi*, eine neue fossile Eidechse aus der unteren Kreide von Lesina in Dalmatien. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt*, **17** (5), 1–24.

LANGER, W. 1961. Über das Alter der Fischschiefer von Hvar-Lesina (Dalmatien). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1961**, 329–331.

LAURENTI, J. N. 1768. *Specimen medicum, exhibens synopsin Reptilium*. Trattnern, Vienna, 214 pp.

LÉCURU, S. 1968. Remarques sur le scapulo-coracoïde des Lacertiliens. *Annales des Sciences Naturelles, Zoologie et Biologie Animale*, **10**, 475–510.

LEE, M. S. Y. 1997. The phylogeny of varanoid lizards and the affinities of snakes. *Philosophical Transactions of the Royal Society of London*, B, **352**, 53–91.

—— and CALDWELL, M. W. 1998. Anatomy and relationships of *Pachyrhachis problematicus*, a primitive snake with hindlimbs. *Philosophical Transactions of the Royal Society of London*, B, **353**, 1521–1552.

—— —— 2000. *Adriosaurus* and the affinities of mosasaurs, dolichosaurs, and snakes. *Journal of Paleontology*, **74**, 915–937.

—— —— and SCANLON, J. D. 1999. A second primitive marine snake: *Pachyophis woodwardi* from the Cretaceous of Bosnia-Herzegovina. *Journal of Zoology*, **248**, 509–520.

MEUNIER, F., BEAREZ, P. and FRANCILLON-VIEILLOT, H. 1999. Some morphological and histological aspects of hyperostosis in the eastern Pacific marine fish *Prionotus stephanophrys* Lockington, 1880 (Triglidae). 125–133. *In* SERET, B. and SIRE, J. Y. (eds). *Proceedings of the 5th Indo-Pacific Fish Conference*. Société Française d'Ichtyologie, Paris, 244 pp.

MEYER, H. von 1860. *Acteosaurus tommasinii* aus dem schwarzen Kreide-Schiefer von Comen am Karste. *Palaeontographica*, **7**, 223–231.

NÉRAUDEAU, D. 1991. Lateral variations of size-frequency distribution in a fossil echinoid community and their palaeoecological significance. *Lethaia*, **24**, 299–309.

—— 1995. Diversité des échinides fossiles et reconstitutions paléoenvironnementales. 337–345. *In* GAYET, M. and COURTINAT, B. (eds). *First European Palaeontological Congress*. Geobios, Mémoire Spécial, **18**, 431 pp.

—— and MOREAU, P. 1989. Paléoécologie et paléobiogéographie des faunes d'échinides du Cénomanien nord-aquitain. *Geobios*, **22**, 293–324.

—— THIERRY, J. and MOREAU, P. 1997. Variation in echinoid biodiversity during the Cenomanian–early Turonian transgressive episode in Charentes (France). *Bulletin de la Société Géologique de France*, **168**, 51–61.

NOPCSA, F. von 1923. Vorläufige Notiz über die Pachyostose und Osteosklerose einiger mariner Wirbeltiere. *Anatomischer Anzeiger*, **56**, 353–359.

OPPEL, M. 1811. *Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben*. Lindauer, Munich, 87 pp.

OWEN, R. 1850. Description of the fossil reptiles of the Chalk Formation. 378–404. *In* DIXON, F. (ed.). *The geology and fossils of the Tertiary and Cretaceous formations of Sussex*. Longman, Brown, Green and Longman, London, xvi + 422 pp.

POLCYN, M. J., TCHERNOV, E. and JACOBS, L. 1999. The Cretaceous biogeography of the eastern Mediterranean with a description of a new basal mosasauroid from 'Ein Yabrud, Israel. 259–290. *In* TOMIDA, Y., RICH, T. H. and VICKERS-RICH, P. (eds). *Proceedings of the Second Gondwanan Dinosaur Symposium*. National Science Museum Monographs, **15**, 385 pp.

PREGILL, G. K., GAUTHIER, J. A. and GREENE, H. W. 1986. The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea. *Transactions of the San Diego Society of Natural History*, **21**, 167–202.

RAGE, J.-C. 1983. *Palaeophis colossaeus* nov. sp. (le plus grand serpent connu?) de l'Eocène du Mali et le problème du genre chez les Palaeopheidae. *Comptes Rendus de l'Académie des Sciences*, II, **296**, 1741–1744.

—— 1988. Un serpent primitif (Reptilia, Serpentes) dans le Cénomanien (base du Crétacé supérieur). *Comptes Rendus de l'Académie des Sciences*, II, **307**, 1027–1032.

—— 1989. Le plus ancien lézard varanoïde de France. *Bulletin de la Société d'Etudes Scientifiques de l'Anjou*, **13**, 19–26.

—— and CAPPETTA, H. 2002. Vertebrates from the Cenomanian, and the geological age of the Draa Ubari fauna (Libya). *Annales de Paléontologie*, **88**, 79–84.

—— and ESCUILLIÉ, F. 2000. Un nouveau serpent bipède du Cénomanien (Crétacé). Implications phylétiques. *Comptes Rendus de l'Académie des Sciences*, *IIa*, **330**, 513–520.

—— —— 2002. *Eupodophis*, new name for the genus *Podophis* Rage and Escuillié, 2000, an extinct bipedal snake, preoccupied by *Podophis* Wiegmann, 1843 (Lacertilia, Scincidae). *Amphibia-Reptilia*, **23**, 232–233.

RICQLÈS, A. de, 1989. Les mécanismes hétérochroniques dans le retour des tétrapodes au milieu aquatique. 337–348. *In* DAVID, B., DOMMERGUES, J. L., CHALINE, J. and LAURIN, B. (eds). *Ontogenèse et évolution*. Geobios, Mémoire Spécial, **12**, 380 pp.

SAUVAGE, H. E. 1880. Sur l'existence d'un Reptile du type ophidien dans les couches à *Ostrea columba* des Charentes. *Comptes Rendus de l'Académie des Sciences*, **91**, 671–672.

SCANLON, J. D., LEE, M. S. Y., CALDWELL, M. W. and SHINE, R. 1999. The palaeoecology of the primitive snake *Pachyrhachis*. *Historical Biology*, **13**, 127–152.

SCHLÜTER, T., KOHRING, R. and MEHL, J. 1992. Hyperostotic fish bones ('Tilly bones') from presumably Pliocene phosphorites of the Lake Manyara area, northern Tanzania. *Paläontologische Zeitschrift*, **66**, 129–136.

SEELEY, H. G. 1881. On remains of a small lizard from the Neocomian rocks of Comen, near Trieste, preserved in the geological museum of the university of Vienna. *Quarterly Journal of the Geological Society of London*, **37**, 52–56.

TCHERNOV, E., RIEPPEL, O., ZAHER, H., POLCYN, M. J. and JACOBS, L. L. 2000. A fossil snake with limbs. *Science*, **287**, 2010–2012.

JEAN-CLAUDE RAGE

Laboratoire de Paléontologie
Paléontologie, UMR CNRS 5143
Muséum national d'Histoire naturelle
8 rue Buffon
75005 Paris, France
e-mail jcrage@mnhn.fr

DIDIER NERAUDEAU

Laboratoire de Paléontologie
Géosciences, UMR 6118
Université de Rennes 1
Campus de Beaulieu
35042 Rennes cedex, France
e-mail Didier.Neraudeau@univ-rennes1.fr