POEKILOPLEURON BUCKLANDII, THE THEROPOD DINOSAUR FROM THE MIDDLE JURASSIC (BATHONIAN) OF NORMANDY

by RONAN ALLAIN *and* DANIEL J. CHURE

ABSTRACT. *Poekilopleuron bucklandii*, described by Eudes-Deslongchamps in 1838, is one of the earliest discovered dinosaurs. Although incomplete, it is one of the best preserved Middle Jurassic theropods known from Europe. Unfortunately, the only specimen of *P. bucklandii*, housed in the Musée de la Faculté des Sciences de Caen, was destroyed during World War II. However, casts of some parts of the type skeleton have been found in the collections of the Museum National d'Histoire Naturelle, Paris. These casts and Eudes-Deslongchamps' monograph are used to redescribe the specimen. *Poekilopleuron* shares one synapomorphy with the Spinosauroidea and we tentatively assign it to that clade. The possible synonymy between *Poekilopleuron* and *Megalosaurus* is examined and we conclude that *Megalosaurus* is a *nomen dubium* and that the name should be restricted to the type dentary.

KEY WORDS: France, Middle Jurassic, Dinosauria, Theropoda, Megalosauridae.

THE theropod *Poekilopleuron bucklandii* from the Middle Bathonian of Normandy was described by Eudes-Deslongchamps in 1838, 13 years after *Megalosaurus bucklandii* from the Middle Bathonian of Stonesfield in Oxfordshire (Buckland 1824; Mantell 1827). Eudes-Deslongchamps attached the specific name of *bucklandii* to his new genus, so that in case of synonymy of the two genera, the synonymy would involve the suppression of only the generic name (Hulke 1879). Since that time, there have been several discussions about the synonymy of *Poekilopleuron* with *Megalosaurus bucklandii* (Hulke 1879; Huene 1908, 1926; Steel 1970). The issue is difficult to resolve because of the absence of comparable material between the genera. Moreover, the only specimen of *Poekilopleuron bucklandii*, housed in the Musée de la Faculté des Sciences de Caen, was destroyed during World War II (Bigot 1945). Fortunately, the casts of the gastral basket, the phalanges and the left forelimb of *Poekilopleuron* were given by A. Bigot to the Muséum National d'Histoire Naturelle in 1897 and are still preserved in Paris. This cast material and the best preserved bones (caudal vertebrae, tibia and astragalus) figured by Eudes-Deslongchamps are redescribed here.

Institutional abbreviations. BMNH, The Natural History Museum, London; MNHN, Muséum National d'Histoire Naturelle, Paris; OUMJ, Oxford University Museum; YPM, Yale Peabody Museum, New Haven.

SYSTEMATIC PALAEONTOLOGY

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1888
THEROPODA Marsh, 1881
TETANURAE Gauthier, 1986
?SPINOSAUROIDEA Stromer, 1915
FAMILY *incertae sedis*

Genus POEKILOPLEURON Eudes-Deslongchamps, 1838

[Palaeontology, Vol. 45, Part 6, 2002, pp. 1107–1121, 1 pl.]

Types species. P. bucklandii Eudes-Deslongchamps, 1838.

Poekilopleuron bucklandii Eudes-Deslongchamps, 1838

Plate 1; Text-figures 1–5

Synonymy. Numerous emendations and spelling variants of *Poekilopleuron bucklandii*, which are unjustified (ICZN Art. 33), have been introduced in the literature. These are:

1837	*Poecilopleuron* Bronn, p. 519, *nomen nudum.*
1842	*Poikilopleuron bucklandi* Eudes-Deslongchamps; Owen, p. 84.
1849	*Poecilopleurum bucklandi* Eudes-Deslongchamps; Bronn, p.686.
1870	*Poicilopleuron bucklandi* Eudes-Deslongchamps; Leidy, p. 5.
1879	*Megalosaurus bucklandi* Buckland; Hulke, p. 233.
1926	*Megalosaurus poikilopleuron* Eudes-Deslongchamps; Huene, p. 66.
1973	*Poekilopleuron bucklandi* Eudes-Deslongchamps; White, p.146.
1974	*Poecilopleuron bucklandi* Eudes-Deslongchamps; Welles and Long, p. 203.

Holotype. Uncatalogued partial skeleton housed in the Musée de la Faculté des Sciences de Caen and destroyed during World War II (Bigot 1945). It included 21 caudal vertebrae, several chevrons, gastralia, ribs, humerus, radius, ulna, first metacarpal, manual phalanges, femur, tibia, fibula, astragalus, third metatarsal and pedal phalanges

Plastotype. Casts of the holotype housed in the Muséum National d'Histoire Naturelle (MNHN 1897-2), including gastralia, humerus, radius, ulna, first metacarpal, third metatarsal and pedal phalanges (Eudes-Deslongchamps 1838, pls 4, 7–8). Casts of the humerus, radius, ulna, and pedal phalanges are also in the Yale Peabody Museum (YPM 4938).

Locality. Carrière de la Maladrerie, Caen, Normandie, France.

Horizon and age. Banc Royal of the Calcaire de Caen Formation, *Procerites progracilis* Zone, Middle Jurassic (Middle Bathonian) (Dugué *et al.* 1998).

Diagnosis. Large theropod with elongate mid-caudal neural spines as long as their corresponding centrum length; deltopectoral crest extending down to mid-length of humerus; ulna lacking olecranon process; distal end of radius as wide as proximal end; strong ulnar process at mid-length of the posteromedial edge of the radius; convex lateral margin of the ascending process of the astragalus.

Description

We describe here the elements represented by casts and the most important of the destroyed bones (caudal vertebrae, tibia, fibula, astragalus) figured by Eudes-Deslongchamps.

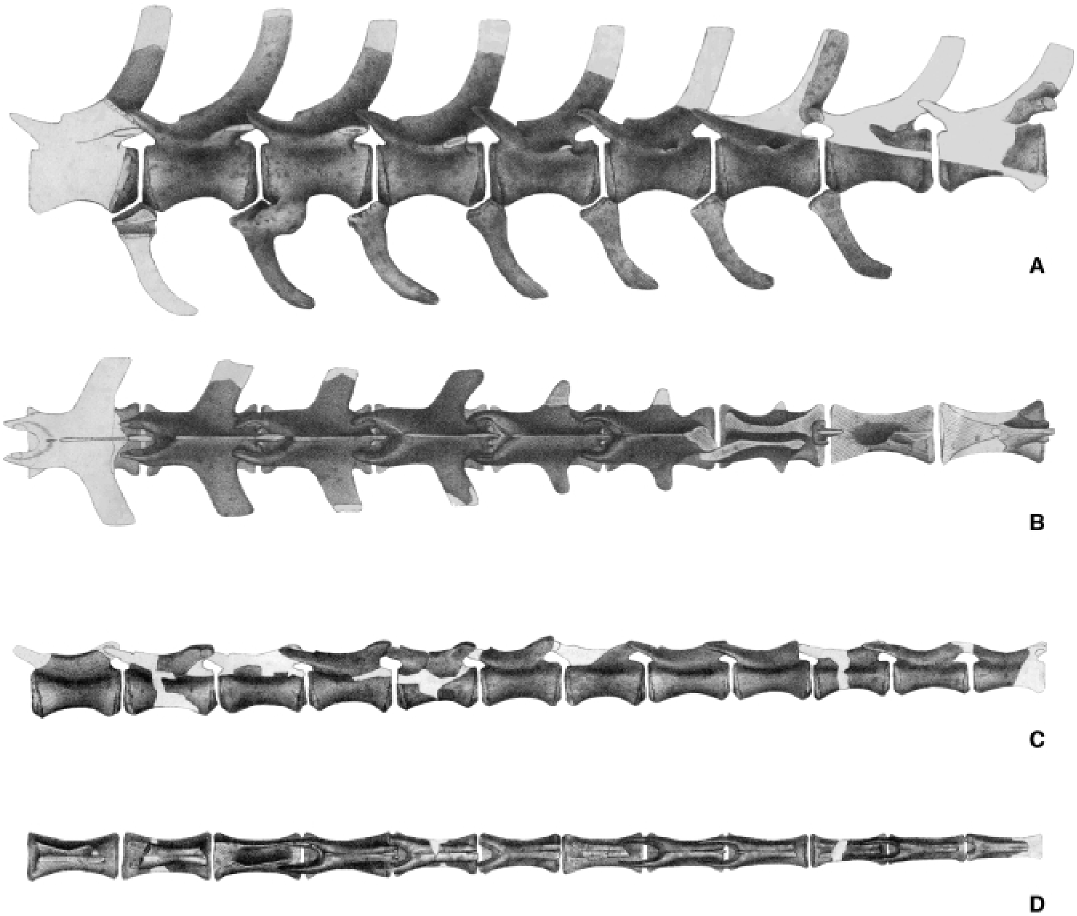
Caudal vertebrae and chevrons. The axial skeleton was represented only by two series of caudals with associated chevrons (Eudes-Deslongchamps 1838, pl. 2, figs 1–6). Because of the differences between the series Eudes-Deslongchamps (1838) concluded that they were separated by a dozen missing vertebrae. Huene (1908) at first identified the anterior series as caudals 17–25 (Text-fig. 1A–B), but later (1926) placed the first well-preserved vertebra of this series as caudal 10–15, while the more posterior series (Text-fig. 1C–D) was identified as caudals 30–41 (Huene 1908, 1926). Comparison with *Allosaurus fragilis* (Madsen 1976) allows more precise placement. The transition point (Russell 1972), where the caudal vertebrae lose their transverse processes, occurs in caudal 27 in *Allosaurus fragilis* and in caudal 34 in *Ceratosaurus nasicornis* (Gilmore 1920). Assuming that the total number of caudal vertebrae in

---

EXPLANATION OF PLATE 1

Dorsal view of the plaster cast of the reconstructed gastral basket of *Poekilopleuron bucklandii* (Eudes-Deslongchamps, 1838) from the Middle Bathonian of the Carrière de la Maladrerie; MNHN 1897-2; ×0·25.

ALLAIN and CHURE, *Poekilopleuron*



TEXT-FIG. 1. Caudal vertebrae of *Poekilopleuron bucklandii* (based on Eudes-Deslongchamps 1838, pl. 2, figs 1–2, 4–5). A, first series of caudal vertebrae in lateral view; × 0·14. B, first series of caudal vertebrae in dorsal view; ×0·14. C, second series of caudal vertebrae in lateral view; ×0·1. D, second series of caudal vertebrae in dorsal view; × 0·1.

Poekilopleuron is roughly the same as in *Allosaurus* and *Ceratosaurus* (*c.* 50 caudal vertebrae), the first series described by Eude-Deslongchamps would correspond to caudal vertebrae 21–29. Similarly in the second series, the neural spines tend to become smaller posteriorly and are finally lost at the ninth vertebra of this series. According to Eudes-Deslongchamps, the length of the centrum of the last vertebra of the first series is nearly equal to that of the first centrum of the second series, but centra length can be quite similar over a number of caudal vertebrae (Gilmore 1920, p. 100). Using the total number of caudal vertebrae in *Allosaurus* and *Ceratosaurus*, and the development of the neural spines between both series, it seems that there were no more than five or six missing vertebrae between the first and second series (35–46).

The centra are constricted medially, and concave with a longitudinal ridge ventrally. These ends are slightly concave, circular anteriorly and more oval posteriorly along the series, with a bevelled ventral margin for chevron articulation. The transverse processes are dorsoventrally flat and slope posteriorly and slightly dorsally. In contrast to *Allosaurus* and *Neovenator* (Hutt *et al.* 1996), the distal caudal prezygapophyses extend anteriorly less than one-half the centrum length. The postzygapophyses are directed downward and weakly developed. They become laterally compressed posteriorly in the series. The neural spines are anteroposteriorly narrow and extremely tall in comparison with those of *Allosaurus* and most large theropods. The height from the base of the transverse process of the spine of the second vertebra of the series (the twenty-second of the tail) is as long as the length of its centrum. A small additional spur is located anterior to the neural spines on the neural arches (Text-fig. 1A–B), but is not as well developed as in *Allosaurus*, *Acrocanthosaurus* (Stovall and Langston 1950), *Lourinhanosaurus* (Mateus 1998) and *Siamotyrannus* (Buffetaut *et al.* 1996).

The six chevrons figured by Eudes-Deslongchamps (1838, pl. 2, fig. 1) are about as long as the neural spines and curve posteroventrally. This curvature increases posteriorly in *Poekilopleuron* but does not reach the dramatic bend observed in the L-shaped middle chevrons of *Allosaurus*, *Acrocanthosaurus* and *Neovenator*. The chevron of the second centrum of the series is fused to the third centrum, a pathology due to injury or disease.

Gastral basket. The gastral cuirass is one of the most poorly understood parts of the theropod skeleton. Few even moderately complete baskets are known; most of those are in coelurosaurs and very few have been described in any detail (Lambe 1917; Matthew and Brown 1923; Sternberg 1933; Ostrom 1978; Russell and Dong 1993; Norell and Makovicky 1997). Among non-coelurosaurian theropods, only *Allosaurus* (Chure 2000*a*) and *Poekilopleuron bucklandii* (Eudes-Deslongchamps 1838) have reasonably complete baskets. No broad comparative studies have been done on cuirass morphology and its phylogenetic significance remains unevaluated.

Taquet (1998, pp. 184–189) described the confused conditions surrounding the collection of the bones of *P. bucklandii* over a period of several weeks. The gastralia all came from one large block, but the elements were somewhat jumbled (Eudes-Deslongchamps 1838) and did not come out as a single unit. Eudes-Deslongchamps first removed the isolated pathological seventh gastralia, then the rest of the gastralia which were in two series (elements 1–6 and 8–14 in Eudes-Deslongchamps 1838, pl. 4, figs 1–2). The relative position of these three separate groups of gastralia is unknown. Eudes-Deslongchamps then reconstructed the gastral basket (1838, pl. 4, fig. 1) and made a cast of that reconstruction. The cast is figured here (Pl. 1). It is not identical to the reconstructed cuirass as figured in Eudes-Deslongchamps (1838, pl. 4, figs 1–2) and should be used with caution. Differences noted include the following:

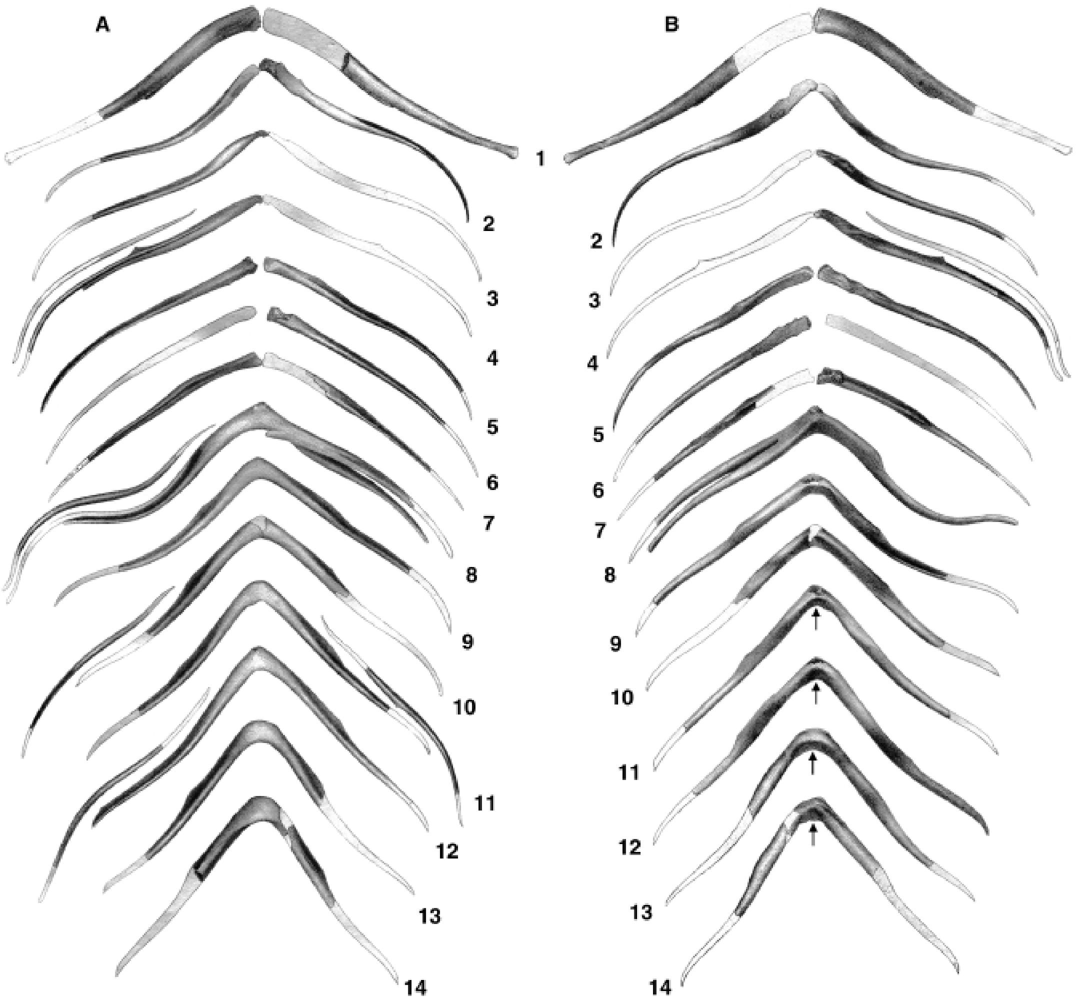
1. There are 12 rows of gastralia in the cast versus 14 in the figures. Rows 1–7 have fused medial elements in both the figures and the cast, but comparison between the figures and cast breaks down in rows 8–14 and it is from this part of the basket that the discrepancy arises.
2. Missing parts of the medial gastralia are restored in the cast.
3. Lateral gastralia are restored in the cast and their placement in a particular row is largely conjectural.
4. Some elements occupying the same position in the cast and Eudes-Deslongchamps' figures do not compare well morphologically.

Recent work on a complete and well-preserved gastral cuirass of *Allosaurus* (Chure 2000*a*) has helped in interpreting the gastralia of *P. bucklandii*. It appears that Eudes-Deslongchamps was in error in identifying ventral and dorsal views. The excavations (Eudes-Deslongchamps 1838, pl. 4, fig. 1b) at the junction of the cornua, and sometimes extending onto the cornuae, occur on the inner (dorsal) rather than outer (ventral) surface of gastralia (DJC, pers. obs.). Thus, we identify Eudes-Deslongchamps' plate 4, figure 1 as a dorsal view, plate 4, figure 2 as a ventral view, and the cast is of the dorsal surface.

In *Allosaurus*, the angle of divarication of the medial gastralia is greater in the cranial end of the basket than in the caudal end. This reflects the narrowing of the basket as it nears the pelvis and hindlimbs. This also seems to be the condition in *Acrocanthosaurus atokensis* (Harris 1998). As reconstructed by Eudes-Deslongchamps, this angle of divarication is greater caudally than cranially in *Poekilopleuron bucklandii*. Interpreting the French specimen in light of what is known in these other two taxa, we identify the sequence of gastralia in *P. bucklandii* as follows (with the identification given in the published plates of Eudes-Deslongchamps following in parentheses): 1(14), 2(8), 3(9), 4(10), 5(11), 6(12), 7(13), 8(7), 9(6), 10(5), 11(4), 12(3), 13(2), 14(1) (Text-fig. 2).

In a complete *Allosaurus* cuirass described by Chure (2000*a*) the cranial pair of medial gastral elements do not overlap, but instead abut and form a cranially facing notch of 90 degrees. In addition, this gastral row consists only of medial elements. In *Poekilopleuron bucklandii*, the morphology of the medial end of Eudes-Deslongchamps' fourteenth gastral element appears to be truncate and unlike that of overlapping medial elements. Furthermore, Eudes-Deslongchamps (1838, p. 71) reported that this gastralia lacked a groove on its cranial margin. This suggests that there was no element lateral to this one. On the basis of shape and the lack of a groove we interpret this bone as coming from the first row of the basket (Text-fig. 2).

In rows 2–6 (14 and 8–12 of Eudes-Deslongchamps) the medial elements are unfused. Most the of the median ends of medial elements in these rows are incomplete and the contacts between right and left gastralium are unknown or poorly defined, but are figured as abutting. However, in row 7(13) the median end of the right medial element is expanded and overlaps the dorsal surface of the median end of left medial element. This overlapping, rather than abutting, contact is typical for theropods (Lambe 1917; Norell and Makovicky 1997; Chure 2000*a*). Unfortunately, it is not possible to identify the medial elements of row 10 of the cast with any of the elements in Eudes-Deslongchamps' figures. With the exception of the first, each cornua has a groove along its cranial margin for a sliding articulation with its lateral element. This is typical of theropods (Norell and Makovicky 1997; Chure 2000*a*).



TEXT-FIG. 2. New reconstruction of the gastral basket of *Poekilopleuron bucklandii* (based on Eudes-Deslongchamps 1838, pl. 4, fig.1); × 0·25. A, ventral view; B, dorsal view. Arrows indicate concavity on caudal surface of fused medial elements indicating that this is a dorsal view.

The median element in row 8(7) is pathological, with a bifurcated left ramus. It is possible that this bifurcation is the result of fusion of the left cornuae of two gastral rows (7 and 8). In the cast of *Poekilopleuron bucklandii* there is what appears to be an unfused right medial element for row eight (Pl. 1), which might be the mate for one of the rami on the left side. Unfortunately, this separate medial element was not figured by Eudes-Deslongchamps and the discrepancy cannot be resolved. In light of this uncertainty, we interpret the bifurcation as a developmental pathology, but not the result of fusion between gastral rows. Norell and Makovicky (1997) described a pathologically bifurcated medial gastral element in an unidentified dromaeosaur from Mongolia. However, in that specimen the bifurcation is more distally located and the two rami of the bifurcation are more divergent. All preserved lateral elements are incomplete. Only lateral elements for rows 4(10) and 8(7) were found in place. The placement of others in the cast or Eudes-Deslongchamps' figures is conjectural.

The right and left medial elements in rows 9–14 (6–1) fuse to form a single V-shaped gastralium. At their point of fusion the cranial margin is sometimes smoothly rounded and sometimes bears a cranially directed nipple.

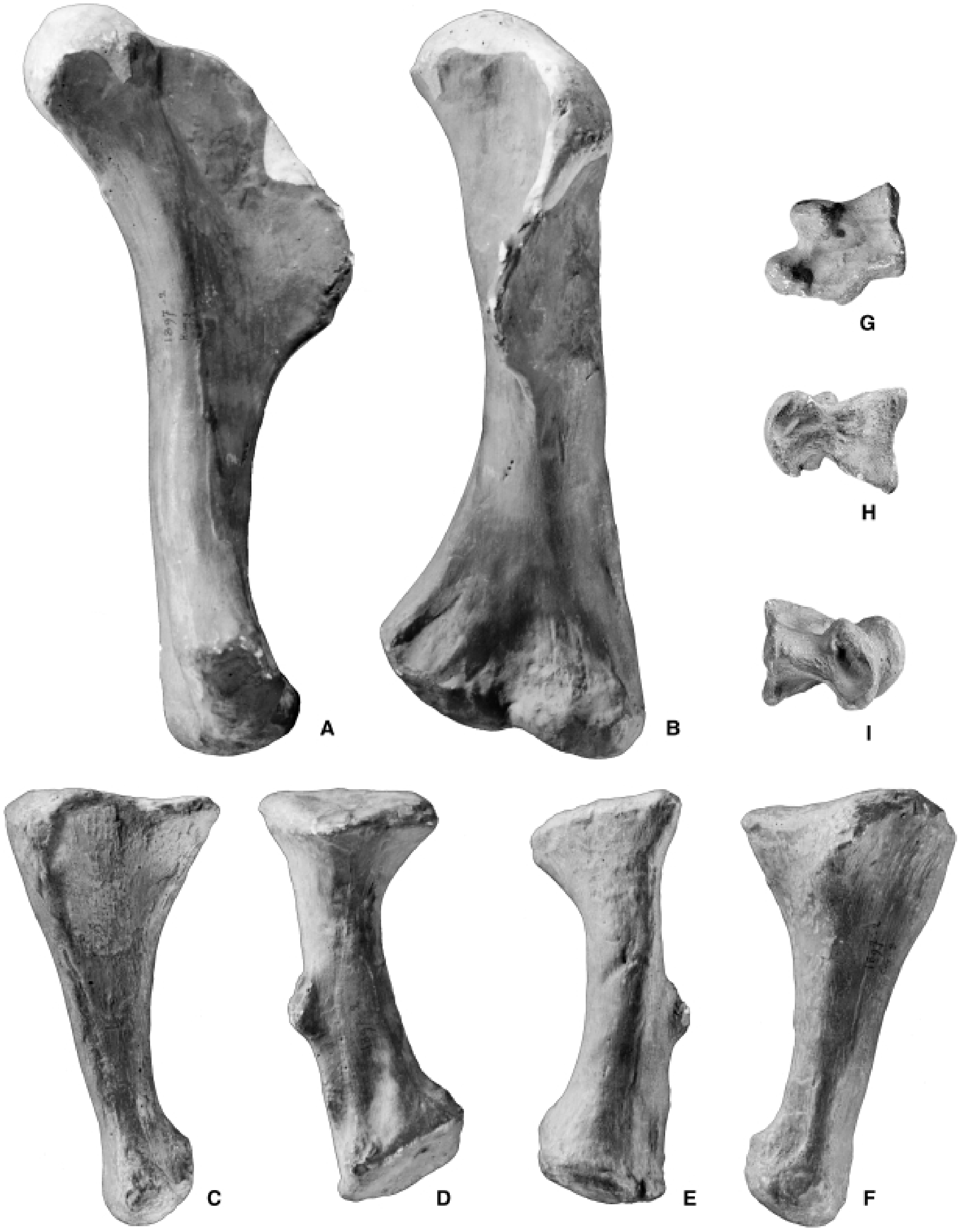
The cuirass of *Poekilopleuron bucklandii* is one of the most complete known for any theropod and is certainly one of the best illustrated, thanks to Eudes-Deslongchamps. As noted above, however, comparison with other theropods is hampered by the lack of equally complete and preserved baskets and a lack of adequate descriptions where such baskets do exist. Gastral baskets have been reported in the primitive theropods *Syntarsus rhodesiensis* (Raath 1977) and *S. kayentakayae* (Tykoski 1998) but these accounts are cursory. In neither taxon are the medial elements fused. *Allosaurus* is the only other basal tetanurine for which a good gastral basket is available. *Poekilopleuron bucklandii* differs from *Allosaurus* in having fused medial elements (Chure 2000*a*). The single V-shaped medial element reported by Gilmore (1920) in *Allosaurus fragilis* is now recognized as a furcula (Chure and Madsen 1996). *Acrocanthosaurus atokensis* (Harris 1998) resembles *Poekilopleuron bucklandii* in having fused V-shaped medial elements in the caudal portion of the basket and unfused medial elements in the cranial half. The angle between the cornuae in the fused medial elements is more acute in *Acrocanthosaurus* than in *Poekilopleuron* and the cornuae are much longer.

The cuirass of coelurosaurs retains the features seen in primitive theropods, with two medial and two lateral elements per row and no fused medial elements (Matthew and Brown 1923; Sternberg 1933; Ostrom 1978; Russell and Dong 1993; Norell and Makovicky 1997). Lambe (1917) identified a displaced, incomplete element in an *Albertosaurus* specimen as the part of a fused medial element. Thulborn (1984) suggested that this might be part of a furcula, but the bone has been lost and is not available for examination. However, the discovery of furculae in several genera of tyrannosaurids (Makovicky and Currie 1998) raises serious questions about assuming that a displaced V-shaped element should be identified *a priori* as a medial gastral element. Osborn (1906) reported fused medial gastral elements in the cranial portion of the cuirass of the type of *Tyrannosaurus rex* (CM 9380). These elements are currently in a mounted skeleton and thus difficult to examine. However, they do not appear to be furculae and they are much too large to fit in the narrow pectoral girdle region of tyrannosaurs as restored by Makovicky and Currie (1998). If these median V-shaped elements are not pathological, they are so large that they must be from the mid-region of the cuirass. However, we remain uncertain as to the nature of these elements.

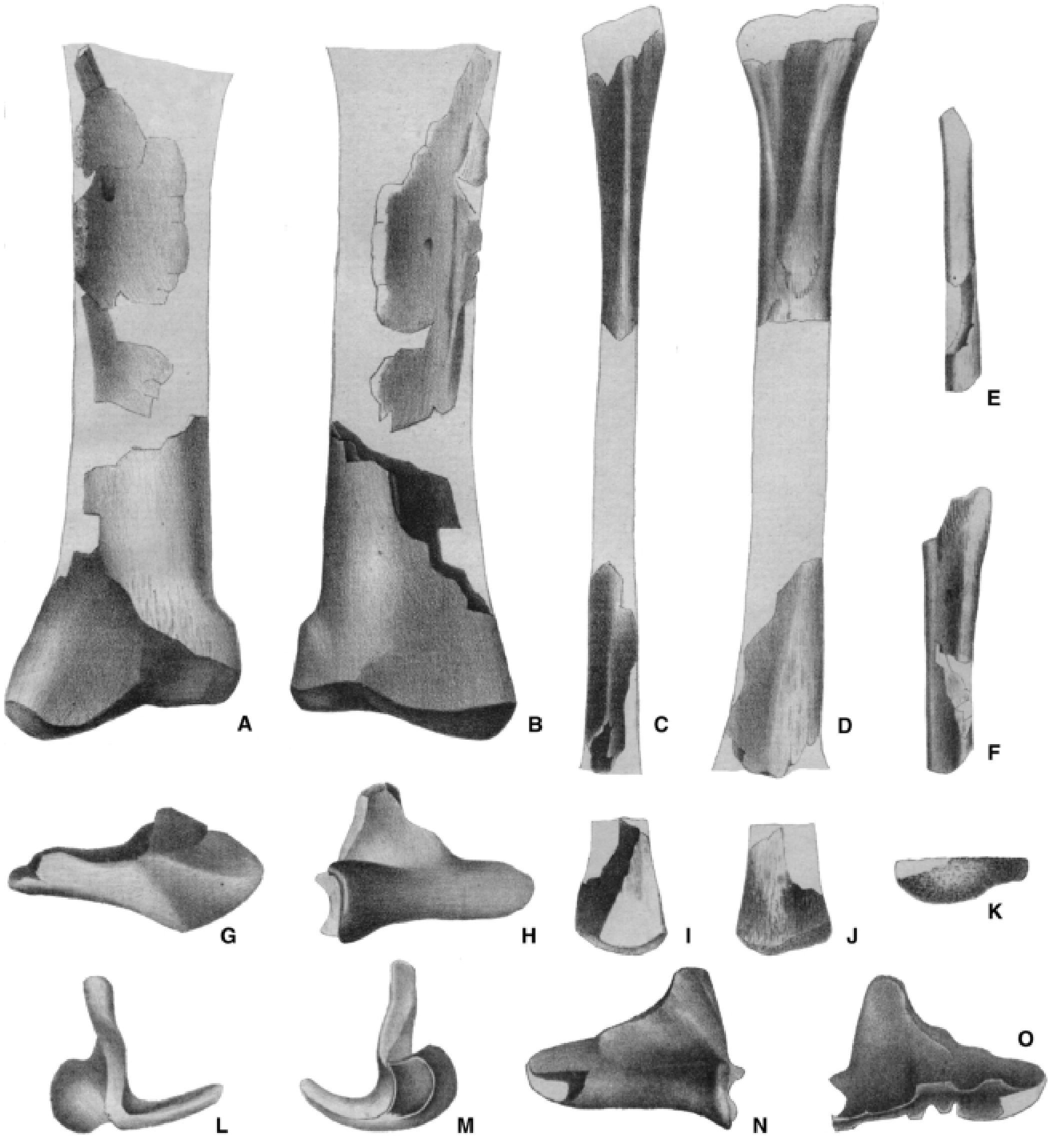
Humerus. The humerus is 31 cm long and rather slender compared to that of *Baryonyx* (Charig and Milner 1997), *Megalosaurus*? (Huene 1926, OUM-J13575), *Torvosaurus* (Galton and Jensen 1979) or *Acrocanthosaurus* (Currie and Carpenter 2000). Although its proximal end is incomplete (Eudes-Deslongchamps 1838, pl. 7, figs 1–4), the head was restored on the cast given by Bigot to the MNHN in 1897 (Text-fig. 3A–B) and was thereafter figured as complete by Nopsca (1906). The proximal end has a maximum width estimated at 11 cm, whereas the anteroposteriorly flattened distal end is 12 cm wide. In lateral view, the distal third of the bone is slightly projected forwards, contrasting with the straight posterior margin of the shaft of *Torvosaurus* and *Eustreptospondylus* (Huene 1926; Walker 1964). The inner curvature of the shaft of the humerus is less marked than in *Allosaurus* (Madsen 1976), *Baryonyx*, *Eustreptospondylus*, *Megalosaurus*? and *Torvosaurus*, and the humeral head is in a higher position than in these latter taxa. In anterior view, the shaft of the humerus is not sigmoid as in *Allosaurus*, *Acrocanthosaurus* and *Afrovenator* (Sereno *et al.* 1994). The deltopectoral crest is confluent with the head, high, and extends down to mid-length of the shaft as in *Eustreptospondylus* and *Megalosaurus*? (OUM-J13575). It projects anteriorly and, in contrast to *Allosaurus* and *Acrocanthosaurus*, is oriented nearly at right angles to the proximal end. Its distal part is not recurved medially as in *Torvosaurus*. The distal end is rotated outward from the plane of the proximal end, so that the humeral torsion is well marked. In contrast to *Eustreptospondylus*, the rounded radial condyle is well below the ulnar condyle and is anteroposteriorly thicker (5 vs. 3·5 cm).

Ulna and radius. The ulna (18 cm) is slightly longer than the radius (17 cm), yet is relatively short and stout (Text-fig. 3C, F). The proximal end is triangular and is slightly depressed anteriorly where it forms the articulating surface for the humerus. In contrast to most theropods such as *Allosaurus, Baryonyx*, *Megalosaurus*? (BMNH 36585) and *Torvosaurus*, there is no olecranon process. The proximal end is thus flat in lateral view. The shaft of the ulna is not bowed caudally as in *Baryonyx* and most of the coelurosaurs. The radius is slightly curved anteriorly (Text-fig. 3D–E). The proximal end is triangular and as large as the distal end, whereas it is flattened transversally in *Torvosaurus* and *Baryonyx*. The shaft is unique in the development of a posteromedial ulnar process at its mid-length that contacts the anterior edge of the ulna. The massive distal end is rounded and its articular surface has a shallow concavity at its centre.

Metacarpal I. The first left metacarpal is the only manual element preserved (Text-fig. 3G–I). Eudes-Deslongchamps (1838) misidentified this element at a pedal phalanx. It is 6 cm long, 3·9 cm wide proximally and 4·1 cm wide distally. The first metacarpal closely resembles that of *Allosaurus*. Its proximal end is divided into two articular surfaces. The proximomedial face is triangular and concave where it contacts the first distal carpal. The proximolateral face slopes strongly laterally where it articulates with the second metacarpal, whereas it is continuous with the proximomedial face in *Torvosaurus*. This second articular surface extends as far as the mid-length of the bone. The distal condyles are



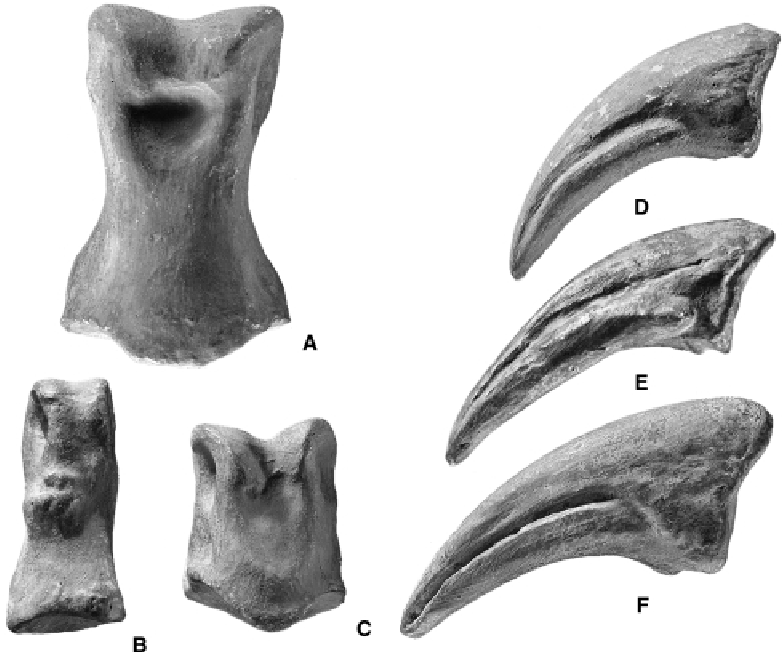
TEXT-FIG. 3. *Poekilopleuron bucklandii*, MNHN 1897-2, from the Middle Bathonian of the Carrière de la Maladrerie; ×0·33. A, medial, and B, anterior views of the plaster cast of the left humerus. C, medial, and F, lateral views of the plaster cast of the left ulna. D, medial, and E, lateral views of the plaster cast of the left radius. G, dorsal, H, lateral, and I, medial views of the plaster cast of the first left metacarpal.



TEXT-FIG. 4. Hindlimbs of *Poekilopleuron bucklandii* (based on Eudes-Deslongchamps 1838, pl. 6, figs 3–4, 7, 10–14; pl. 7, figs 19–20; pl. 8, figs 3–4); × 0·18. A, anterior, and B, posterior views of the right tibia. C, anterior, and D, medial views of the right fibula. E, anterior?, and F, medial views of the left fibula. G, distal view of the right tibia. H, anterior view of the right astragalus. I, medial, J, lateral, and K, distal views of the right fibula. L, medial, and M, lateral views of the right astragalus. N, anterior, and O, posterior views of the left astragalus.

separated by a deep sulcus and are strongly asymmetrical, the lateral one being larger. In contrast to *Acrocanthosaurus*, there are deep medial and lateral ligament pits.

Tibia. The distal end of the tibia of *Poekilopleuron* is 16·5 cm wide and 8 cm long anteroposteriorly (Text-fig. 4A–B, G) as against 16·2 cm by 9·4 cm in *Megalosaurus*? (OUM-J13568). The anterior surface is depressed where it contacts the astragalus, the fibula and the calcaneum. The astragalar overhang which accommodates the dorsal process of astragalus, has a lateral expansion that is more pronounced than in *Allosaurus* (Madsen 1976), *Megalosaurus*? (BMNH



TEXT-FIG. 5. *Poekilopleuron bucklandii*, MNHN 1897-2, from the Middle Bathonian of the Carrière de la Maladrerie; × 0·5. A, plaster cast of the second phalanx of the third right pedal digit in dorsal view. B, plaster cast of the first phalanx of the first left pedal digit in dorsal view. C, plaster cast of the third phalanx of the fourth left pedal digit in dorsal view. D, ungual phalanx of the fourth left? digit. E, ungual phalanx of the third right? digit. F, ungual phalanx of the second left digit.

31809) and *Streptospondylus* (Meyer 1832; Allain 2001; MNHN 8607). It slopes continuously at about 45 degrees medially, whereas the astragalar overhang of *Megalosaurus*? becomes nearly parallel lateral to the shaft of the tibia. There is a distinct, nearly vertical shoulder on the shaft of the bone 6 cm above the base of the medial condyle.

Fibula. Little can be said about the fibula. The piece of bone figured by Eudes-Deslongchamps (Text-fig. 4C–D) as the distal end of the fibula shows an unusual distal expansion. Its general morphology and comparisons with the fibula of a newly discovered megalosaur from the Middle Bathonian of Normandy (Allain in press), suggest that it is the proximal end of the right fibula. The pieces previously identified as metatarsals (Text-fig. 4E–F, I–K; Eudes-Deslongchamps, 1838, pl. 8, fig. 5), are probably parts of the shaft and distal ends of the fibulae.

Astragalus. The right astragalus is 10 cm high and 14·5 cm broad, giving a height to breadth (H/B) index (Welles and Long 1974) of 0·69, comparable to the 0·69 H/B indices of *Torvosaurus* (Galton and Jensen 1979; Britt 1991). The H/B indices of *Allosaurus fragilis* (ranging from 0·85 to 1) and *Streptospondylus altdorfensis* (0·81) are higher than in *Poekilopleuron*. As in *Streptospondylus* and in contrast with *Allosaurus* and *Sinraptor*, there is no process on the posterior margin of the articulating surface close to the medial edge of the astragalus (Text-fig. 4L–M). The ascending process is 6·7 cm high (Text-fig. 4H, N–O). Its lateral margin is slightly convex whereas it is concave in *Streptospondylus* (Allain 2001). The medial edge of the dorsal process begins rather far laterally. The triangular ascending process is reminiscent of that of *Torvosaurus* (Britt 1991), its shape being more rectangular and symmetrical in *Acrocanthosaurus* and *Streptospondylus*. It is also higher and less tapered than in *Sinraptor* (Currie and Zhao 1993) and *Eustreptospondylus*. The shallow fibular articulation (Text-fig. 4M), anterolateral to the ascending process, is not as wide as in *Sinraptor*. According to Eudes-Deslongchamps' illustrations (Text-fig. 4H, N), there is no horizontal groove running across the anterior face of the astragalar condyles in contrast to *Allosaurus*, *Eustreptospondylus, Sinraptor* and *Streptospondylus*.

Phalanges. Casts of 16 of the 20 left or right pedal elements figured by Eudes-Deslongchamps exist (Text-fig. 5A–F). The reconstructed pes of the original publication (Eudes-Deslongchamps 1838, pl. 7, fig. 27) is erroneous, the phalanx I-1 being the first left metacarpal. Following *Allosaurus* and other large tetanurans, *Poekilopleuron* should have five metatarsals and a phalangeal formula of 2-3-4-5-0. We have tentatively identified the third metatarsal (Eudes-Deslongchamps 1838, pl. 8, fig. 6) and the phalanges I-1 (pl. 8, fig. 8), I-2 (pl. 8, fig. 26), II-1 (pl. 8, fig. 12), II-2 (pl. 8, fig. 17), II-3 (pl. 8, figs 22, 24), III-1 (pl. 8, fig. 9), III-2 (pl. 8, figs 11-12), III-3 (pl. 8, figs 13-14), III-4 (pl. 8, fig. 25), IV-2 (pl. 8, fig. 15), IV-3 (pl. 8, fig. 16) and IV-5 (pl. 8, fig. 23). Digit III is complete and nearly 40 cm long. The phalanges are not significantly different from those of other large theropods: each phalanx is excavated on the extensor surface proximal to the distal articulation; the collateral ligament fossae are equally developed on phalanges of the third digit, whereas they are more strongly developed on the lateral side of the phalanges of the first and second digits and on the medial side of the phalanges of the fourth digit. The pedal ungual of the second digit is the longest, followed by that of the third, fourth, second and first digit. The claws are roughly triangular in cross-section.

DISCUSSION

The phylogenetic affinities of Poekilopleuron bucklandii

The limited and fragmentary nature of the only known specimen of *Poekilopleuron bucklandii* and its subsequent destruction which prevents re-examination makes phylogenetic analysis difficult. Using the phylogeny of carnivorous dinosaurs of Holtz (2000), it seems that *Poekilopleuron* is a tetanuran theropod, as shown by the well-expanded humeral ends, the humeral torsion, the distal end of the tibia expanded to back the calcaneum, the fibular distal end less than twice anteroposterior width at midshaft, the mediolaterally reduced and craniocaudally wide astragalar ascending process, the extensive contact between the first and the second metacarpals, and the metacarpal I that is approximately as broad as long. On the other hand, *Poekilopleuron* does not exhibit several derived features known in more advanced Neotetanurae. These include: the sigmoid humeral shaft as in Allosauridae, such as *Allosaurus* and *Acrocanthosaurus*; the medial process on the posterior margin of the articulating surface of the astragalus, which is present in all Allosauroidea of which the astragalus is known (i.e. *Acrocanthosaurus, Allosaurus* and *Sinraptor*); the dramatic bend observed in the L-shaped middle chevrons of *Acrocanthosaurus*, *Allosaurus* and *Neovenator*.

Molnar *et al.* (1996) examined the morphology of the distal end of the tibia in theropods in detail. They observed that *Poekilopleuron bucklandii* shares two features with the basal tetanurines *Acrocanthosaurus atokensis*, *Allosaurus fragilis*, *Erectopus superbus*, *Megalosaurus bucklandii* and *Piatnitzkysaurus floresi*. These are the presence of a medial buttress and a truncate medial malleolus. With the exception of *Piatnitzkysaurus*, the genera concerned, as well as spinosauroids, have a distal projection of the fibular flange which forms the distalmost part of the tibia.

Overall, the evidence suggests that *Poekilopleuron* is a basal tetanurine more primitive than the Allosauroidea. However, *Poekilopleuron bucklandii* exhibits one synapomorphy of Spinosauroidea (*sensu* Sereno *et al.* 1998): a humeral deltopectoral crest more than 45 per cent of humeral length. Even if the assignment of *Poekilopleuron* to the Spinosauroidea is weakly supported, we tentatively refer it to this latter clade, pending a more detailed phylogenetic analysis of the European Megalosauridae (or any other permutation of this name) currently in progress (Allain 2002).

Comments on the status of Megalosaurus *and* Poekilopleuron

The theropod *Megalosaurus* was the first Mesozoic genus of dinosaur to be formally named and as such it holds an important historical and emotional place in dinosaur palaeontology. It has been a magnet for the association of other taxa, such as *Poekilopleuron* (Paul 1988; Padian 1997). The problem preventing synonymy of *Poekilopleuron* with *Megalosaurus* is not the quality of the French and English material preserved, but the taxonomic and nomenclatural status of the latter genus. A thorough revision of *Megalosaurus* is needed but is beyond the scope of the present paper. However, some comments on the generic holotype specimen are appropriate.

The lectotype specimen of *Megalosaurus bucklandii* (Molnar *et al.* 1990; Benton and Spencer 1995; Rauhut 2000) is the rostral portion of a right dentary with teeth (OUM-J13505). As specified by Buckland

(1824) and pointed out by Cuvier (1824) and Owen (1856), the bones discovered at Stonesfield were neither found together in one spot nor associated. At present, no convincing case has been made that all the Stonesfield theropod material referred to *Megalosaurus* actually belongs to that taxon, and we view with some skepticism the assignment of other non-associated material to the species represented by the dentary (see Buckland 1824 and Glut 1997, pp. 587–592 for details of this material). There are least seven genera of mid-sized to gigantic theropods in the Upper Jurassic Morrison Formation (i.e. *Allosaurus*, *Ceratosaurus*, *Elaphrosaurus*, *Marshosaurus*, *Saurophaganax*, *Stokesosaurus*, *Torvosaurus*). These genera are sympatric and can occur in the same quarry (Forster 1998; Turner and Peterson 1999; Chure 2000*b*). At least four large theropods (*Allosaurus*, *Ceratosaurus*, *Lourinhanosaurus* and *Torvosaurus*) are now known from the Upper Jurassic of Portugal (Mateus 1998; Perez-Moreno *et al.* 1999; Mateus and Antunes 2000*a*, *b*). Thus, it is not out of the question that several large theropods may have co-existed in Europe during the Mid Jurassic. We see the referral of much of the large theropod material to the genus *Megalosaurus* as problematic and presenting two serious potential problems. First, any phylogenetic analysis of *Megalosaurus* using the referred material may actually be analyzing a chimaera. Secondly, the practice of referring material to *Megalosaurus* may be obscuring the diversity of the Middle Jurassic theropod fauna of Europe. Contrary to what was previously reported (Molnar *et al.* 1990), three theropods, two of which are large, have been recovered in Stonesfield, as shown by the three different ilia housed in the collections of The Natural History Museum and Oxford University Museum. The smallest one (BMNHR83) was referred by Huene (1932, pl. 3, fig. 2) to *Iliosuchus incognitus*. The other two described by Buckland (1824, pl. 43, fig. 3; OUM-J13560) and Owen (1856, p. 15, not figured; BMNH31811) were both referred to *Megalosaurus bucklandii*, but they are quite different from one another in shape and proportions. Similarly, a femur from Stonesfield referred to *Megalosaurus bucklandii* by Owen (1856, tables 7–8; BMNH31806) is straight in medial view with a medially directed femoral head, while that described originally by Buckland (1824, pl. 44, figs 1–2; OUMJ13561) is strongly sigmoid with an anteromedially directed femoral head, similar to that of *Ceratosaurus nasicornis* (Gilmore 1920, p. 109). Finally, Phillips (1871, p. 208) reported 'there are in reality two forms of scapulae in the Oxford collection placed in the megalosaurian series, one of which is anchylosed to the coracoid, the other not so. They differ enough to be certainly referable to different species of animals, the second mentioned being of larger size.'

Although numerous other skeletal parts have been referred to *Megalosaurus bucklandii* (Owen 1856; Huxley 1869; Phillips 1871; Walker 1964; Molnar *et al*. 1990; Britt 1991; Padian 1997), these elements are of uncertain relationship to the type dentary and the status of the genus must hinge on the dentary alone. Our examination of the dentary does not reveal any diagnostic features as noted by Molnar (1990). We consider the genoholotypic specimen of *Megalosaurus bucklandii* a *nomen dubium* and recommend that the name *Megalosaurus* be restricted to the dentary (OUMJ13506), pending thorough taxonomic revision in progress by L. Canning, P. M. Barrett and P. Powell. Since there is no dentary material of *Poekilopleuron bucklandii*, the synonymy between *P. bucklandii* and *Megalosaurus bucklandii* cannot be determined.

Acknowledgments. This work was partly supported by research grants from the EC TMR Programme and from the Jurassic Foundation (RA) and the US National Park Service (DJC). RA thanks D. Serrette and P. Loubry for the photographs. We both thank A. Milner, S. Chapman, and P. Powell for access to material in their care in The Natural History Museum, London and Oxford University Museum.

REFERENCES

ALLAIN, R. 2001. Redescription de *Streptospondylus altdorfensis*, le dinosaure théropode de Cuvier, du Jurassique de Normandie. *Geodiversitas*, **23**, 349–367.

—— 2002. Les Megalosauridae (Dinosauria, Theropoda). Nouvelle découverte et révision systématique: implications phylogénètiques et paléobiogéographiques. Unpublished PhD thesis, Muséum National d'Histoire Naturelle, Paris, 322 pp.

—— in press. Discovery of megalosaur (Dinosauria, Theropoda) remains in the middle Bathonian of Normandy (France) and its implications for the phylogeny of basal Tetanurae. *Journal of Vertebrate Paleontology.*

BENTON, M. J. and SPENCER, P. S. 1995. *Fossil reptiles of Great Britain*. Chapman & Hall, London, 386 pp.

BIGOT, A. 1945. La destruction des collections et des bibliothèques scientifiques de Caen. *Bulletin de la Société Linnéenne de Normandie*, *Volume Supplémentaire*, 1–75.

BRITT, B. B. 1991. Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. *Brigham Young University Geology Studies*, **37**, 1–72.

BRONN, H. G. 1838. *Lethaea geognostica, oder Abbildungen und Beschreibungen der für die Gebirgs-Formationen bezeichnendsten Versteinerungen*. Stuttgart, 544 pp.

—— 1849. *Indexus palaeontologicus oder Uebersicht der bis jetzt bekannten fossilen Organismen. B. Enumerator palaeontologicus: Systematische Zusammenstellung und geologische Entwickellungs-Gesetze der organischen Reiche*. Stuttgart, 1106 pp.

BUCKLAND, W. 1824. Notice on the *Megalosaurus* or great fossil lizard of Stonesfield. *Transactions of the Geological Society of London*, **2**, 390–396.

BUFFETAUT, E., SUTEETHORN, V. and TONG, H. 1996. The earliest known tyrannosaurid from the Lower Cretaceous of Thailand. *Nature*, **381**, 689–691.

CHARIG, A. J. and MILNER, A. C. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum*, *Geology Series*, **53**, 11–70.

CHURE, D. J. 2000*a*. Observations on the morphology and pathology of the gastral basket of *Allosaurus*, based on a new specimen from Dinosaur National Monument. *Oryctos*, **3**, 29–37.

—— 2000*b*. New records of *Ceratosaurus*, *Torvosaurus*, *Coelurus*, and *Stokeosaurus* and their implications for theropod community structure and biozonation in the Late Jurassic of the Western Interior, U.S.A. *Journal of Vertebrate Paleontology*, **20** (Supplement to No. 3), 35A.

—— and MADSEN, J. H. 1996. On the presence of furculae in some non-maniraptoran theropods. *Journal of Vertebrate Paleontology*, **16**, 573–577.

CURRIE, P. J. and CARPENTER, K. 2000. A new specimen of *Acrocanthosaurs atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. *Geodiversitas*, **22**, 207–246.

—— and ZHAO, X.-J. 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences*, **30**, 2037–2081.

CUVIER, G. 1824. *Recherches sur les ossemens fossiles, où l'on rétablit les caractères de plusieurs animaux dont les révolutions du globe ont détruit les espèces*. Dufour et d'Ocagne, Paris, **5** (2), 547 pp.

DUGUÉ, O., FILY, G. and RIOULT, M. 1998. Le Jurassique des Côtes du Calvados. *Bulletin Trimestriel de la Société Géologique de Normandie et des Amis du Muséum du Havre*, **85** (2), 1–132.

EUDES-DESLONGCHAMPS, J. A. 1838. Mémoire sur le *Poekilopleuron bucklandii*, grand saurien fossile, intermédiaire entre les crocodiles et les lézards. *Mémoire de la Société Linnéenne de Normandie*, **6**, 37–146.

FOSTER, J. R. 1998. Aspects of vertebrate paleoecology, taphonomy, and biostratigraphy of the Morrison Formation (Upper Jurassic), Rocky Mountain region, Western United States. PhD dissertation, University of Colorado, Boulder, 405 pp.

GALTON, P. M. and JENSEN, J. A. 1979. A new large theropod dinosaur from the Upper Jurassic of Colorado. *Brigham Young University Geology Studies*, **26**, 1–12.

GAUTHIER, J. 1986. Saurischian monophyly and the origin of birds. 1–55. *In* PADIAN, K. (ed.). *The origin of birds and the evolution of flight*. Memoirs of the California Academy of Sciences, **8**, 98 pp.

GILMORE, C. W. 1920. Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *Bulletin of the United Sates National Museum*, **110**, 1–154.

GLUT, D. F. 1997. *Dinosaurs: the encyclopedia*. McFarland and Co., Jefferson and London, 1076 pp.

HARRIS, J. D. 1998. A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. *Bulletin of the New Mexico Museum of Natural History and Science*, **13**, 1–75.

HOLTZ, T. R. 2000. A new phylogeny of the carnivorous dinosaurs. *Gaia*, **15**, 5–61.

HUENE, F. VON 1908. Die Dinosaurier der europäischen Triasformation mit Berücksichtigung der aussereuropäischen Vorkommnisse. *Geologische und Palaeontologische Abhandlungen*, **1**, 1–419.

—— 1926. The carnivorous Saurischia in the Jura and Cretaceous formations, principally in Europe. *Revista del Museo de la Plata*, **29**, 35–167.

—— 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geologie und Palaeontologie*, **4**, 1–361.

HULKE, J. W. 1879. Note on *Poikilopleuron bucklandi* of Eudes Deslongchamps (père), identifying it with *Megalosaurus bucklandi*. *Quarterly Journal of the Geological Society of London*, **35**, 233–238.

HUTT, S., MARTILL, D. M. and BARKER, M. J. 1996. The first European allosaurid dinosaur (Lower Cretaceous, Wealden Group, England). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1996**, 635–644.

HUXLEY, T. H. 1869. On the upper jaw of *Megalosaurus*. *Quarterly Journal of the Geological Society of London*, **26**, 12–31.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE 1999. *International Code of Zoological Nomenclature, 4th edition*. International Trust for Zoological Nomenclature, London, 306 pp.

LAMBE, L. M. 1917. The Cretaceous theropod dinosaur *Gorgosaurus*. *Geological Survey Canada, Department of Mines, Memoir*, **100**, 1–84.

LEIDY, J. 1870. Remarks on *Poecilopleuron valens*, *Clidastes intermedius*, *Leiodon proriger*, *Baptemys wyomingensis*, and *Emys stevensonianus*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **1870**, 3–5.

MADSEN, J. H. 1976. *Allosaurus fragilis*: a revised osteology. *Bulletin of the Utah Geological and Mineralogical Survey*, **109**, 1–163.

MAKOVICKY, P. J. and CURRIE, P. J. 1998. The presence of a furcula in tyrannosaurid theropods, and its phylogenetic and functional implications. *Journal of Vertebrate Paleontology*, **18**, 143–149.

MANTELL, G. 1827. *Illustrations of the geology of Sussex: containing a general view of the geological relations of the south-eastern part of England; with figures and descriptions of the fossil of Tilgate Forest*. L. Relfe, London, 92 pp.

MARSH, O. C. 1881. Principal characters of American Jurassic dinosaurs. Pt. V. *American Journal of Science* (*Series 3*), **21**, 417–423.

MATEUS, O. 1998. *Lourinhanosaurus antunesi*, a new Upper Jurassic allosauroid (Dinosauria: Theropoda) from Lourinha, Portugal. *Memorias da Academia das Ciencias de Lisboa*, **37**, 111–124.

—— and ANTUNES, M. T. 2000*a*. *Ceratosaurus* (Dinosauria: Theropoda) in the Late Jurassic of Portugal. *Abstracts, 31st International Geological Congress, Rio de Janeiro, Brazil.*

—— 2000*b*. *Torvosaurus* sp. (Dinosauria: Theropoda) in the Late Jurassic of Portugal. *Livro de Resumos do I Congresso Iberico de Paleontologia*, Evora, Portugal, 115–117.

MATTHEW, W. D. and BROWN, B. 1922. The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. *Bulletin of the American Museum of Natural History*, **46**, 367–385.

MEYER, H. V. 1832. *Paleologica zur Geschichte der Erde*. Frankfurt am Main, 560 pp.

MOLNAR, R. E., ANGRIMAN, A. L. and GASPARINI, Z. 1996. An Antarctic Cretaceous theropod. *Memoirs of the Queensland Museum*, **39**, 669–674.

—— KURZANOV, S. M. and DONG, Z.-M. 1990. Carnosauria. 169–209. *In* WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria.* University of California Press, Berkeley, 733 pp.

NOPCSA, F. V. 1906. Zur Kenntnis des Genus *Streptospondylus*. *Beiträge zur Paläontologie und Geologie*, **19**, 59–83.

NORELL, M. A. and MAKOVICKY, P. J. 1997. Important features of the dromaeosaur skeleton: information from a new specimen. *American Museum Novitates*, **3215**, 1–28.

OSBORN, H. F. 1906. *Tyrannosaurus*, Upper Cretaceous carnivorous dinosaur (second communication). *Bulletin of the American Museum of Natural History*, **22**, 281–296.

OSTROM, J. H. 1978. The osteology of *Compsognathus longipes*. *Zitteliana*, **4**, 73–118.

OWEN, R. 1842. Report on British fossil reptiles. *Report of the British Association for the Advancement of Science*, **11**, 60–204.

—— 1856. Monograph on the fossil reptilia of the Wealden formations Part III : *Megalosaurus bucklandi*. *Palaeontographical Society Monographs*, **1856**, 1–26.

PADIAN, K. 1997. *Megalosaurus*. 415–417. *In* CURRIE, P. J. and PADIAN, K. (eds). *Encyclopedia of dinosaurs*. Academic Press, San Diego, 869 pp.

PAUL, G. S. 1988. *Predatory dinosaurs of the world*. Simon and Schuster, New York, 464 pp.

PEREZ-MORENO, B. P., CHURE D. J., PIRES, C., MARQUES DA SILVA, C., DOS SANTOS, V., DANTAS, P., POVOAS, L., CACHAO, M., SANZ, J. L. and CARVALHO, A. M. 1999. On the presence of *Allosaurus fragilis* (Theropoda: Carnosauria) in the Upper Jurassic of Portugal: first evidence of an intercontinental dinosaur species. *Journal of the Geological Society, London*, **156**, 449–452.

PHILIPS, J. 1871. *Geology of Oxford and the Valley of the Thames*. Clarendon Press, Oxford, 529 pp.

RAATH, M. A. 1977. The anatomy of the Triassic theropod *Syntarsus rhodesiensis* (Saurischia: Podokesauridae) and a consideration of its biology. Unpublished PhD thesis, Rhodes University, Rhodesia, 233 pp.

RAUHUT, O. 2000. The interrelationships and evolution of basal theropods (Dinosauria, Saurischia). Unpublished PhD thesis, University of Bristol, 440 pp.

RUSSELL, D. A. 1972. Ostrich dinosaurs from Late Cretaceous of Western Canada. *Canadian Journal of Earth Sciences*, **9**, 375–402.

—— and DONG, Z.-M. 1993. A nearly complete skeleton of a new troodontid dinosaur from the Early Cretaceous of the Ordos Basin, Inner Mongolia, Peoples' Republic of China. *Canadian Journal of Earth Sciences*, **30**, 2163–2173.

SEELEY, H. G. 1888. The classification of the Dinosauria. *Report of the British Association for the Advancement of Science*, **1887**, 698–699.

SERENO, P. C., BECK, A. L., DUTHEIL, D. B., GADO, B., LARSSON, H. C. E., LYON, G. H., MARCOT, J. D., RAUHUT, O. W. M., SADLEIR, R. W., SIDOR, C. A., VARRICCHIO, D. D., WILSON, G. P. and WILSON, J. A. 1998. A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. *Science*, **282**, 1298–1302.

—— WILSON, J. A., LARSSON, H. C. E., DUTHEIL, D. B. and SUES, H. D. 1994. Early Cretaceous dinosaurs from the Sahara. *Science*, **265**, 267–271.

STEEL, R. 1970. Teil 14. Saurischia. *In* KUHN, O. (ed.). *Handbuch der Paläoherpetologie*. Gustav Fischer, Stuttgart, 87 pp.

STERNBERG, C. M. 1933. A new *Ornithomimus* with complete abdominal cuirass. *The Canadian Field Naturalist*, **47** (5), 79–83.

STOVALL, J. W. and LANGSTON, W. 1950. *Acrocanthosaurus atokensis*, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. *American Midland Naturalist*, **43**, 696–728.

TAQUET, P. 1998. *Dinosaur impressions. Postcard from a paleontologist.* Cambridge University Press, Cambridge, 244 pp.

TURNER, C. E. and PETERSON, F. 1999. Biostratigraphy of dinosaurs in the Upper Jurassic Morrison Formation of the Western Interior, USA. 77–114. *In* GILLETTE, D. D. (ed.). *Vertebrate paleontology in Utah*. Utah Geological Survey, Miscellaneous Publication, **99** (1), 554 pp.

TYKOSKI, R. S. 1998. The osteology of *Syntarsus kayentakayae* and its implications for ceratosaurid phylogeny. Unpublished MS thesis, University of Texas at Austin, 217 pp.

WALDMAN, M. 1974. Megalosaurids from the Bajocian (Middle Jurassic) of Dorset. *Palaeontology*, **17**, 325–339.

WALKER, A. D. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Philosophical Transactions of the Royal Society of London*, **248**, 53–134.

WELLES, S. P. and LONG, R. A. 1974. The tarsus of theropod dinosaurs. *Annals of the South African Museum*, **64**, 191–218.

WHITE, J. E. 1973. Catalogue of the genera of dinosaurs. *Annals of the Carnegie Museum*, **44**, 117–155.

RONAN ALLAIN

Laboratoire de Paléontologie
Muséum National d'Histoire Naturelle
UMR 8569 du CNRS
8 rue Buffon
75005 Paris, France
e-mail rallain@mnhn.fr

DANIEL J. CHURE

Dinosaur National Monument
PO Box 128
Jensen UT 84035, USA
e-mail Dan_Chure@nps.gov

Typescript received 16 July 2001
Revised typescript received 2 November 2001