



THE POSTCRANIAL ANATOMY OF THE MEGALOSAUR *DUBREUILLOSAURUS VALESDUNENSIS* (DINOSAURIA THEROPODA) FROM THE MIDDLE JURASSIC OF NORMANDY, FRANCE

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ABSTRACT—The osteology of the postcranial skeleton of the holotype of *Dubreuillosaurus valesdunensis* (Allain, 2002) from the Middle Jurassic Calcaires de Caen Formation (Bathonian) is described here. In addition to previous phylogenetic analyses, characters of the caudal vertebrae show that *Dubreuillosaurus*, gen. nov., is distinct from *Poekilopleuron*. Some features of *Dubreuillosaurus* are unique among Spinosauroida, including the medioventrally directed femoral head and the convex anterior surface of the distal end of the femur. A re-examination of the observations made by Eudes-Deslongchamps on *Poekilopleuron* suggests that megalosaurids were piscivorous to a certain extent.

INTRODUCTION

Knowledge of the diversity and phylogeny of European megalosaurs has increased through the recent redescription of *Poekilopleuron bucklandii* by Allain and Chure (2002) and *Streptospondylus altdorfensis* by Allain (2001), and by the discovery and description of the skull of a new specimen from the Middle Jurassic of Normandy (Allain, 2002a, b, c). The latter specimen, being sympatric with *Poekilopleuron bucklandii*, was questionably referred to the same genus as *Poekilopleuron? valesdunensis*, pending detailed description of its postcranial material and a phylogenetic revision of the European theropods closely related to Megalosauridae.

The holotype of *Poekilopleuron? valesdunensis* (MNHN 1998-13) was discovered in an abandoned quarry, previously exploited for the Pierre de Caen (Calcaires de Caen Formation, Middle Bathonian; Allain 2002a, b). Unfortunately, the quarry of Conteville in which the material was collected was redeveloped before the first field season in 1998, and only the cranial skeleton and a few ribs were collected directly from the in-situ fossiliferous calcareous bed. The following four field seasons, between 1999 and 2001, were devoted to sorting through several cubic meters of sediment previously scattered throughout the quarry by a mechanical digger. Thus, more than two thousand fragments of the postcranial skeleton of *Poekilopleuron? valesdunensis*, ranging in size from about one to ten centimetres, were collected. The preparation and reconstruction of the collected fragments took more than two years prior to this study. These restored postcranial remains of the Conteville megalosaur are described here.

Recent phylogenetic analyses of basal tetanuran theropods (Allain, 2002b, c, in prep.; Holtz et al., 2004), including the postcranial material described here, suggests that *Poekilopleuron bucklandii* is the most basal spinosauroid known to date and does not support the monophyly of a *P. bucklandii* + *P? valesdunensis* clade. Therefore, a new generic name is proposed for the theropod of Conteville.

Institutional Abbreviations

ML, Museu da Lourinha, Portugal; **MNHN**, Muséum National d'Histoire Naturelle, France; **OUM**, Oxford University Museum, England.

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1888
THEROPODA Marsh, 1881
TETANURAE Gauthier, 1986
SPINOSAUROIDEA Stromer, 1915
MEGALOSAURIDAE Huxley, 1869
DUBREUILLOSAURUS, gen. nov.

DUBREUILLOSAURUS VALESDUNENSIS (Allain, 2002)
Poekilopleuron? valesdunensis Allain, 2002:549.

Holotype—MNHN 1998-13, nearly complete skull and associated postcranial material including cervical, dorsal, sacral, and caudal vertebrae, ribs, chevron bones, scapula, coracoid, femur, fibula, and fifth metatarsal.

Etymology—The generic name is in honor of the Dubreuil family, who discovered the specimen in 1994.

Type Locality—Conteville, Calvados, France.

Horizon and Age—*Progracilis* zone of the 'Calcaire de Caen' formation, Middle Jurassic (Middle Bathonian).

Revised Diagnosis—Tetanurine characterized by very low skull, at least three times longer than high; parietals not visible in lateral view; straight medial margin of upper temporal fenestra; well-developed ventral process on jugal ramus of ectopterygoid; deeply grooved posterior margin of ectopterygoid ahead of subtemporal fenestra; double curvature of anterodorsal margin of maxillary nasal ramus; absence of quadrate–quadratojugal fenestra; large external mandibular fenestra; mylohyoid foramen largely opened anteroventrally; femoral head medioventrally directed; convex anterior surface of distal end of femur.

DESCRIPTION

Cervical Vertebrae

Two fragments of cervical vertebrae have been identified (Fig. 1). One is a centrum broken at the level of the anterior margin of the deep pleurocoels (Fig. 1A). The centrum was not fused to the neural arch. It is 45 mm (excluding the ball-like anterior articulation, which is not preserved) long and its posterior articular surface is 36 mm wide and 39 mm high. The concave posterior articular surface indicates that the cervical vertebrae are opisthocoelous. There is a faint ventral keel along the midline of the centrum.

The impression of the left lateral side of a posterior cervical

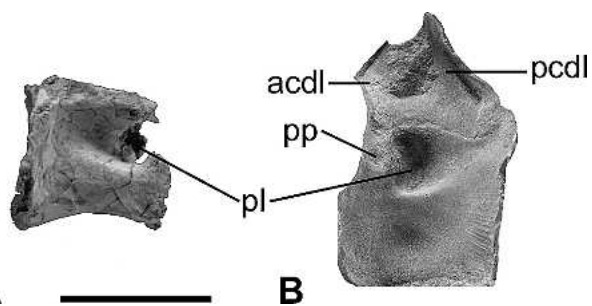


FIGURE 1. Cervical vertebrae of *Dubreuillosaurus valesdunensis* (MNHN 1998–13). **A**, centrum in right lateral view. **B**, posterior cervical in left lateral view. **Abbreviations:** **acdl**, anterior centrodiapophyseal lamina; **pcdl**, posterior centrodiapophyseal lamina; **pl**, pleurocoel; **pp**, parapophysis. Scale bar equals 2 cm.

vertebra has been recovered and a cast of this impression has been made (Fig. 1B). The centrum is 50 mm long (excluding the ball-like anterior articulation). A deep pleurocoel invades the centrum anterolaterally, posterior to the parapophysis. The lower part of the neural arch contacts the centrum but the neurocentral suture is clearly visible. Though incomplete, the neural arch is high above the centrum as in *Streptospondylus* (Allain, 2001). Only the anterior and posterior centrodiapophyseal laminae are visible.

Dorsal Vertebrae

The dorsal axial skeleton of *Dubreuillosaurus* is represented by at least seven incomplete vertebrae (Fig. 2). Two fragments, assumed here to be the anterior part of two anterior dorsal (pectoral) centra, are morphologically similar (Fig. 2A–D). As in other basal Tetanurae, these centra are opisthocoelous. They are broken at the level of the pleurocoels, which invade each centrum anterolaterally. The pleurocoels open into a pair of internal chambers separated by a midline lamina of bone (Fig. 2B, D).

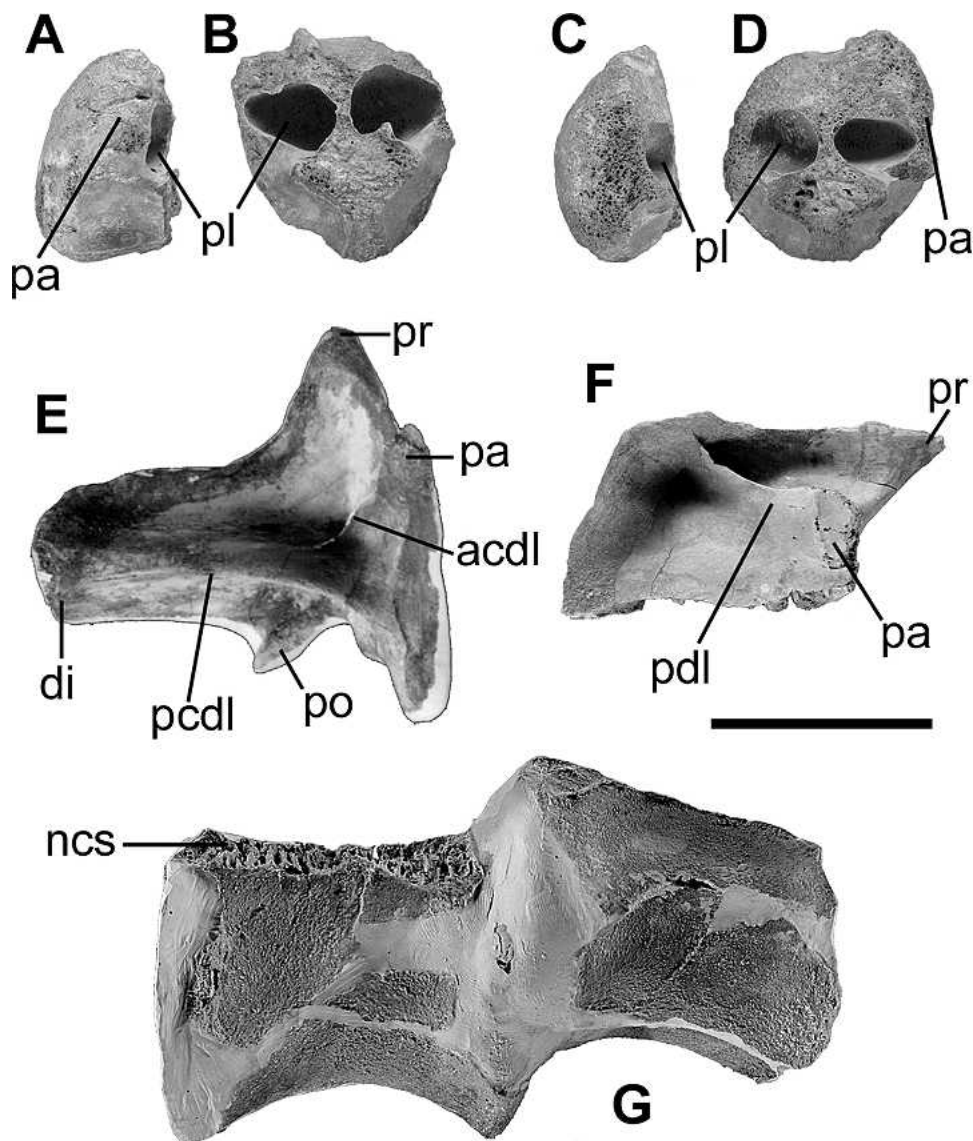


FIGURE 2. Dorsal vertebrae of *Dubreuillosaurus valesdunensis* (MNHN 1998–13). Centra of anterior dorsals in left lateral (**A**, **C**) and posterior (**B**, **D**) views. **E**, neural arch of a middle dorsal in ventral view. **F**, neural arch of a posterior dorsal in right lateral view. **G**, centra of middle dorsals in lateral view. **Abbreviations:** **acdl**, anterior centrodiapophyseal lamina; **di**, diapophysis; **ncs**, neurocentral suture; **pcdl**, posterior centrodiapophyseal lamina; **pdl**, paradiapophyseal lamina; **pl**, pleurocoel; **po**, postzygapophysis; **pp**, parapophysis; **pr**, prezygapophysis. Scale bar equals 2 cm

Small protuberances situated anterior to the pleurocoels indicate the parapophysis, which extends up to the neural arch. The ventral surfaces of the centra are strongly keeled. The keel of each centrum extended anteriorly probably to form the hypapophysis. This latter is not bifurcated as in *Streptospondylus* (MNHN 8787), *Eustreptospondylus* (OUM-J13558), and *Lourinhanosaurus* (ML370).

A cast of two articulated posterior dorsal centra has been made (Fig. 2G). The first of the two is complete. As in *Streptospondylus*, it is significantly longer (70 mm) than high (55 mm). Unlike anterior dorsal vertebrae, the middle dorsal centra are amphiplatyan. The neurocentral suture is open. There is neither pleurocoel nor depression on the anterodorsal corner of the lateral surface of the centrum of the mid-dorsal vertebrae. The ventral surface of the centrum is concave but is not as wide as those of *Streptospondylus*.

Different pieces of dorsal neural arches and neural spines have been collected. One is the neural spine and the base of diapophyses of an anterior dorsal vertebra. The neural spine is spine-like and anteroposteriorly very short, as in *Sinraptor* (Currie et Zhao, 1993a:figs. 14D–F, 15A–C) and *Streptospondylus* (Allain, 2001:fig. 1). It is inclined posterodorsally, and its anterior and posterior margins bear large scars for attachment of the inter-spinous ligaments.

The prezygapophysis, postzygapophysis, parapophysis, and diapophysis have been observed on the cast of the base of the right lateral side of a neural arch (Fig. 2E). This neural arch must be located in the anterior dorsal series because only the dorsal half of the parapophysis is visible at the ventral edge of the neural arch. The diapophysis is 65 mm long and is directed laterally. The pneumatization of dorsal vertebrae of *Dubreuillosaurus* is less complex than in *Sinraptor* and other carnosaurs. There are only two laminae in the middorsal region: the anterior centrodiapophyseal lamina, which joins the parapophysis and the base of the diapophysis, and the posterior centrodiapophyseal lamina, which joins the centrum and the diapophysis. While the anterior

centrodiapophyseal lamina is short and thin, the posterior one is strongly developed and runs ventrally all along the length of the diapophysis. The pneumatic infradiapophyseal, infrapostzygapophyseal, and infraprezygapophyseal fossae delimited by these laminae are very shallow, possibly relating to the immaturity of the animal.

On a fragmentary second neural arch, the parapophyses are well above the ventral margin of the neural arch pointing to a mid-dorsal vertebra (Fig. 2F). The area of the neural arch that contacts the centrum is intricately sculptured, but was not fused to the centrum. The prezygapophyses are anteriorly directed. The thin anterior paradiapophyseal lamina is nearly horizontal in such a way that the infraprezygapophyseal fossa is underneath the infradiapophyseal fossa. The neural spine of the middle dorsal vertebrae is tall, plate-like, and slightly inclined posteriorly.

Sacral Vertebrae

There were at least four sacral vertebrae in *Dubreuillosaurus*. The first fragment of the sacrum corresponds to the right lateral side of two partially fused sacral vertebrae, probably the second and the third sacrals according to their corresponding ribs (Fig. 3). The centrum of the third sacral vertebra is 85 mm long and has an anterior intervertebral articulation that is approximately 45 mm tall. Its lateral side is concave. An intervertebral foramen opens into a canal within the anterior half of the third sacral. The extensive distal articular facet of the third sacral rib, which contacts the ilium laterally, is longer (43 mm) than tall (17 mm), while it is more square in *Allosaurus* (Madsen, 1976), and taller than long in the sacrum of the type series of *Megalosaurus bucklandii* (OUM-J13576, Buckland, 1824:pl. 42, fig. 1). The sutural surface for the second sacral rib is shared by the second and third sacrals and that for the third rib has a small contact with the fourth sacral. The posterior face of the third sacral is slightly concave and was not fused with the fourth sacral. The neural canal is larger than in dorsal and caudal vertebrae (Fig. 3B).

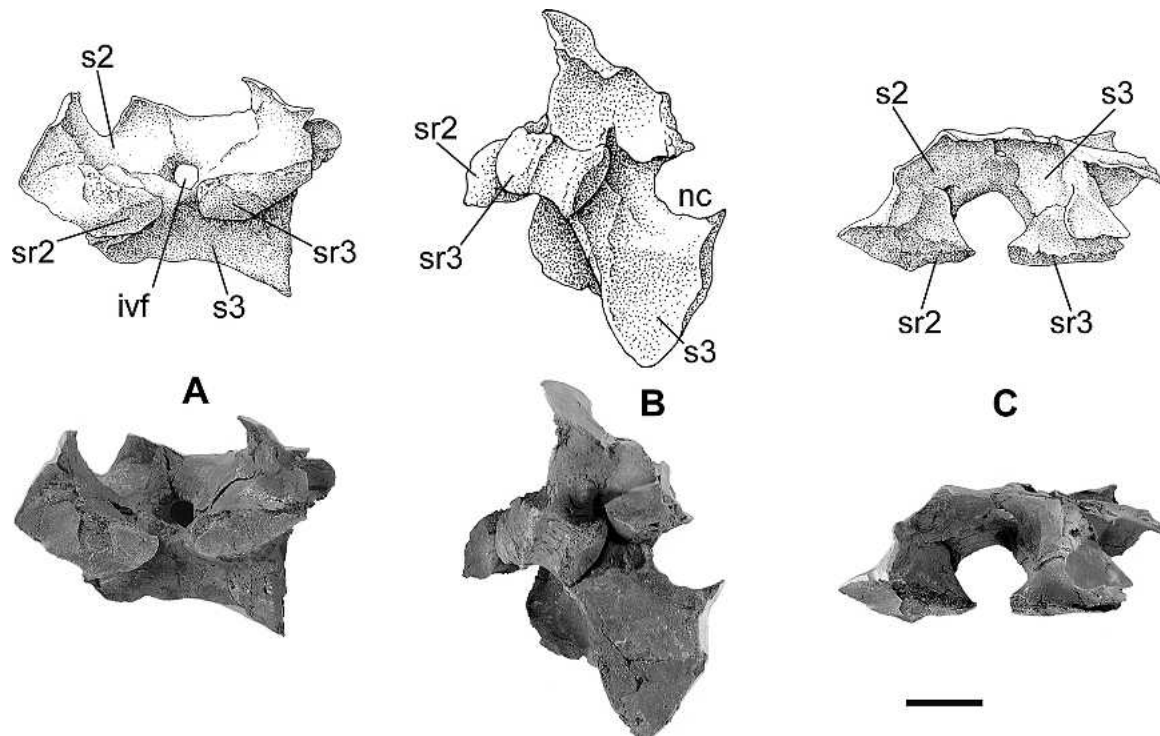


FIGURE 3. Sacral vertebrae of *Dubreuillosaurus valesdunensis* (MNHN 1998-13). Second and third sacral in left lateral (A), posterior (B), and dorsal views (C). **Abbreviations:** ivf, intervertebral foramen; nc, neural canal; s, sacral vertebra; sr, sacral rib. Scale bar equals 2 cm.

The last sacral vertebra is broken anteriorly (Fig. 4A). Its posterior articular face is slightly concave and circular with a diameter of 65 mm. The postzygapophysis and hyposphene are sunk into a pit at the base of the neural arch. The rectangular articular facet for the last sacral rib is intricately sculptured, allowing no movement between the rib and the centrum. The last sacral rib of the right side was recovered (Fig. 4B–C). It was not fused with the last sacral vertebra. It is 90 mm long and 27 mm high in lateral view. It is made up of a wide and sculptured articular surface that contacts the sacral vertebra medially, and a laterally curved posterior process and a dorsolaterally extended bony blade that contact the ilium (Fig. 4B).

Caudal Vertebrae

The caudal skeleton is represented by numerous caudal vertebrae and a few chevron bones (Figs 5, 6). Both are of particular interest because they are among the few elements of *Dubreuillosaurus* that can be compared with similar elements of *Poekilopleuron bucklandii* (Allain and Chure, 2002).

The neural arch of an anterior caudal vertebra has been removed from the same calcareous block that yielded the last sacral vertebra (Fig. 5A–D). The prezygapophyses, the left transverse process and a large part of the neural spine are broken. The 62 mm-long neurocentral suture is open. The neural arch is transversely constricted at midlength, above the suture (Fig. 5A). The right transverse process is 75 mm long and expanded distally. It is directed slightly dorsally and posteriorly with a 25° angle. The postzygapophyseal facets are oriented lateroventrally, diverging at an angle of 65° (Fig. 5D). The neural spine is broken anteriorly and dorsally. It is 45 mm long anteroposteriorly at the base. It is strongly inclined backward at an angle of 50° and extends farther away from the postzygapophyses than in other theropods (Fig. 5C).

The mid-caudal skeleton is represented by at least seven vertebrae (Fig. 5E–I). All of them have transverse processes and are thus located anterior to the transition point defined by Russell (1972). The lengths of the four preserved centra vary between 60 mm and 65 mm. The intervertebral articulations are concave, the anterior concavity being more pronounced than the posterior one. The anterior articular surface is rounded, while the posterior one is vertically ovate. The ventral surfaces of the centra are narrow and bear a shallow longitudinal groove. In contrast to *Poekilopleuron* (Allain and Chure 2002), the transverse pro-

cesses of *Dubreuillosaurus* are spatulate distally. The prezygapophyses extend anteriorly but are not very elongated and barely overhang the preceding vertebra. The articular facets of the prezygapophyses are not in a distal position, but located posterior to a small triangular process, unknown in other theropods (Fig. 5I). The neural spine is positioned posteriorly on the neural arch and less inclined posteriorly than in the anterior caudal neural spine. A small accessory neural spine is found anterior to the main neural spine (Fig. 5F–G). This spur has been described in various taxa. In *Allosaurus* (Madsen, 1976), *Poekilopleuron* (Eudes-Deslongchamps, 1838; Allain and Chure, 2002) and *Siamotyrannus* (Buffetaut et al., 1996), it is directed anteriorly and the large concavity formed between the spur and the neural spine opens anteriorly. In *Acrocanthosaurus* (Stovall and Langston, 1950), *Afrovenator* (Sereni et al. 1994), *Lourinhanosaurus* (Mateus, 1998), and *Dubreuillosaurus* the spur is directed more dorsally and the concavity formed with the neural spine opens dorsally only.

The two most distal caudal vertebrae found (Fig. 5J–M) have 40 mm and 38 mm-long centra, with a concave posterior articular surface that is 10 mm high and 12 mm wide. The anterior intervertebral articulation is flat. Each centrum is keeled ventrally. The neural arch is completely fused with the centrum and extends over the total length of the centrum. Transverse processes and neural spine are absent. In contrast to those of *Allosaurus*, the zygapophyses are short and jut out beyond the anterior and posterior faces of the centrum.

Chevrons

Two chevron bones have been recovered. One was associated with the last sacral, the anterior caudal vertebrae, and the proximal end of the left femur. The shaft of this anterior chevron is straight and 110 mm long. The proximal articular facets are linked together by a bar across the top of the haemal canal. Unlike the condition in *Baryonyx* (Charig and Milner, 1997), there is a 7 mm-long process anterior to the anterior articulation facet.

The second chevron bone is only 90 mm long (Fig. 6A–C). It bears an anterior process, but also a posterior process, which is unknown in *Poekilopleuron*. The distal end of the chevron is slightly curved posteriorly.

Ribs

Many cervical dorsal and sacral rib fragments have been collected. None of the cervical ribs is complete distally (Fig 7). The cervical ribs are not fused to the vertebrae which is a further indication of immaturity. The smaller cervical rib is probably the axial rib (Fig. 7A). The capitulum and tuberculum are bridged by a thin lamina of bone. Two other laminae join the anterodorsal process to the tuberculum and the capitulum. The three laminae delimit a deep pneumatic opening at the base of the shaft of the cervical ribs. Another excavation enters the anterior cervical ribs posteromedially, below the tuberculum. In the more posterior cervical vertebrae, the anterodorsal process of the cervical rib is reduced and more distally positioned (Fig. 7D–E). There is no posteromedial excavation.

The dorsal ribs do not seem to differ significantly from the ribs of other large theropods (Madsen 1976; Currie and Zhao, 1993; Fig. 8). The angle between the proximal end and the shaft of the dorsal ribs is wider in the posterior dorsal ribs. There is a shallow depression on the posteromedial surface of the proximal end, below the tuberculum. The tubercular articulation is reduced in the posterior dorsal ribs. The shaft is rectangular proximally and rounded distally in cross section.

Gastralia

Two V-shaped elements have been recovered and identified as posterior medial gastral elements that have fused to form a single

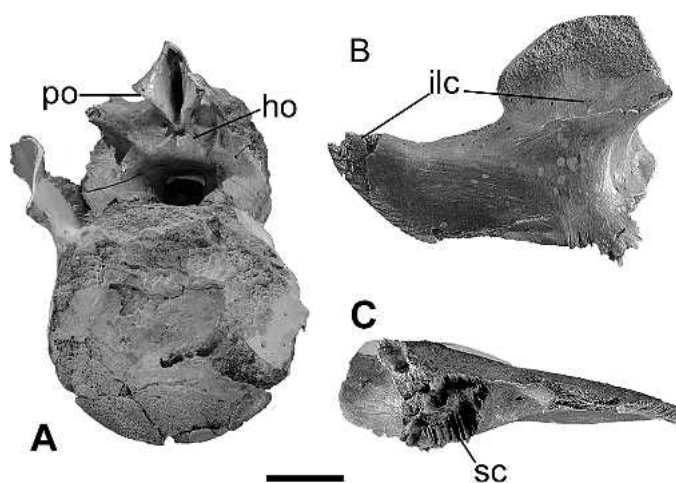


FIGURE 4. Fifth sacral vertebra and rib of *Dubreuillosaurus valesdunensis* (MNHN 1998-13). **A**, Fifth sacral vertebra in posterior view. **B–C**, fifth right sacral rib in ventrolateral (**B**) and ventromedial (**C**) views. **Abbreviations:** ho, hyposphene; ilc, contact with ilium; po, postzygapophyses; sc, contact with sacral. Scale bar equal 2 cm.

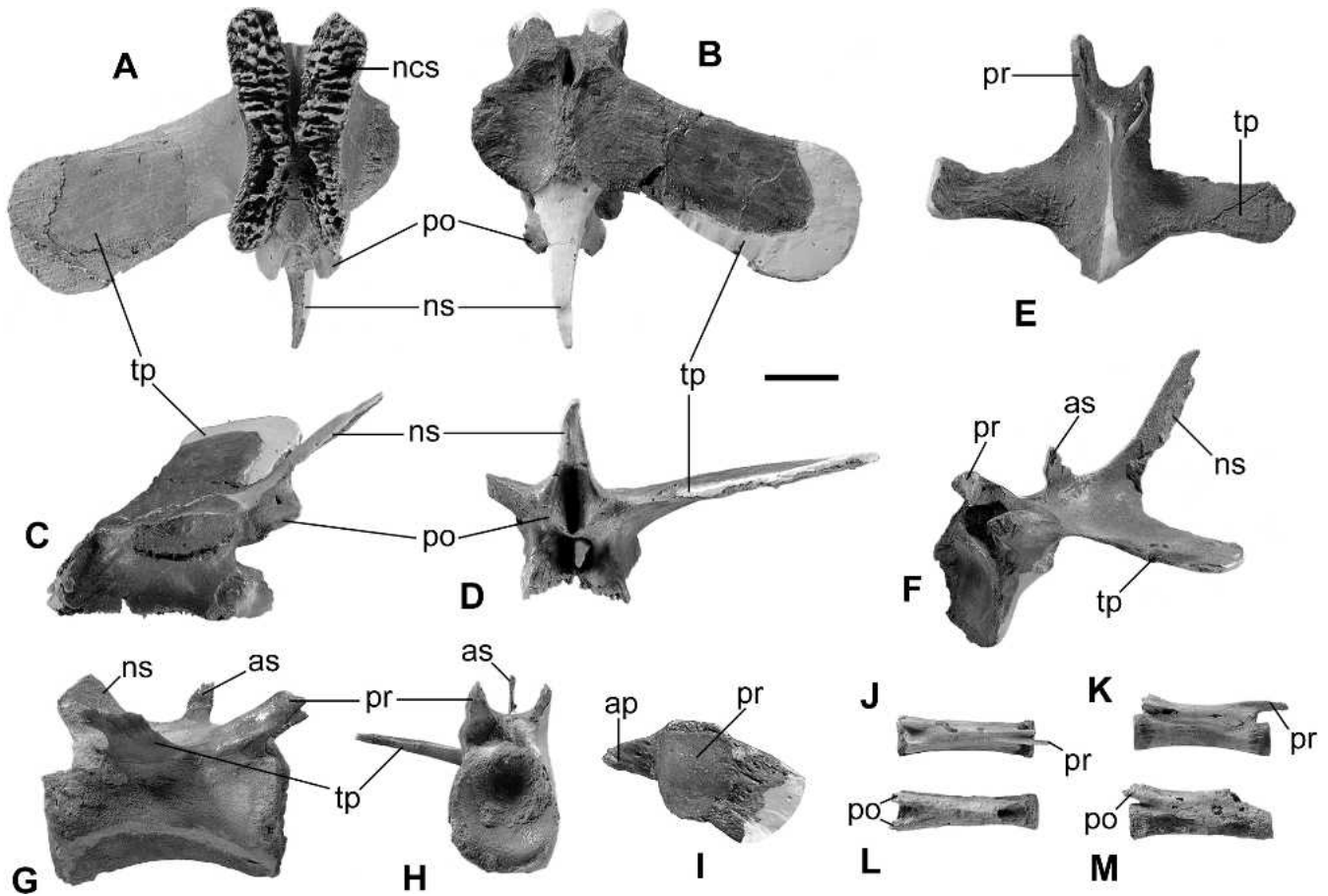


FIGURE 5. Caudal vertebrae of *Dubreuillosaurus valesdunensis* (MNHN 1998-13). Anterior neural arch in ventral (A), dorsal (B), left lateral (C), and posterior (D) views. Middle neural arch in dorsal (E), anterolateral (F), lateral (G), and anterior views (H). I, detailed view of the articular surface of the right prezygapophysis of a middle caudal, in left lateral view. J–M, distal caudal in dorsal (J, L) and lateral (K, M) views. **Abbreviations:** ap, anterior process; as, anterior spur; ncs, neurocentral suture; ns, neural spine; po, postzygapophysis; pr, prezygapophysis; tp, transverse process. Scale bars equal 2 cm except for I (0.67 cm).

gastralium (Fig. 6D–E). The rami are rounded in cross section. Indeed, fused, acutely angled, medial gastral elements are also known (Allain and Chure, 2002) in *Poekilopleuron bucklandii*, in *Acrocanthosaurus* (Harris, 1998), and in tyrannosaurids (Claessens, 2004), and are restricted to the caudal portion of the gastral basket. In *Poekilopleuron bucklandii*, the angle of divarication

decreases posteriorly and reaches 70° in the last gastral pair (Allain and Chure, 2002). The 100° and 110° angles of divarication of the V-shaped elements of *Dubreuillosaurus* suggest they are cranially placed in the distal series. One of the two gastralia is pathological, having been fractured and subsequently healed (Fig. 6E).

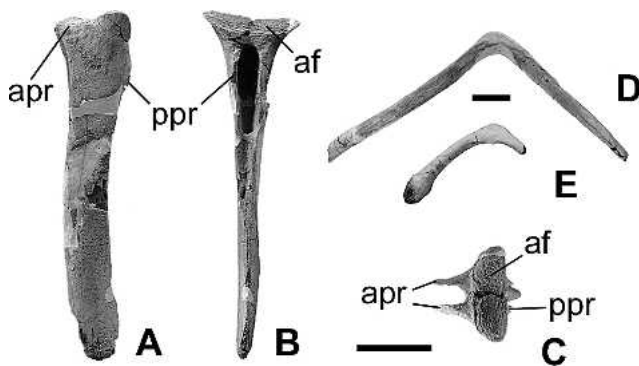


FIGURE 6. *Dubreuillosaurus valesdunensis* (MNHN 1998-13). Chevron in lateral (A), posterior (B) and proximal (C) views. D, posterior gastralium in ventral view. E, pathological gastralium in ventral view. **Abbreviations:** af, proximal articular facet; apr, anterior process; ppr, posterior process. Scale bars equal 2 cm.

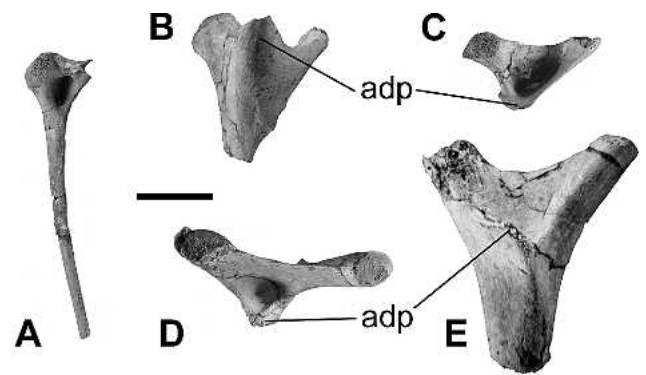


FIGURE 7. Cervical ribs of *Dubreuillosaurus valesdunensis* (MNHN 1998-13). A, axial rib in posterior view. B–C, anterior cervical rib in posterior (B) and proximal (C) views. D–E, posterior cervical rib in posterior (E) and proximal view (D). **Abbreviations:** adp, anterodorsal process. Scale bar equals 2 cm.

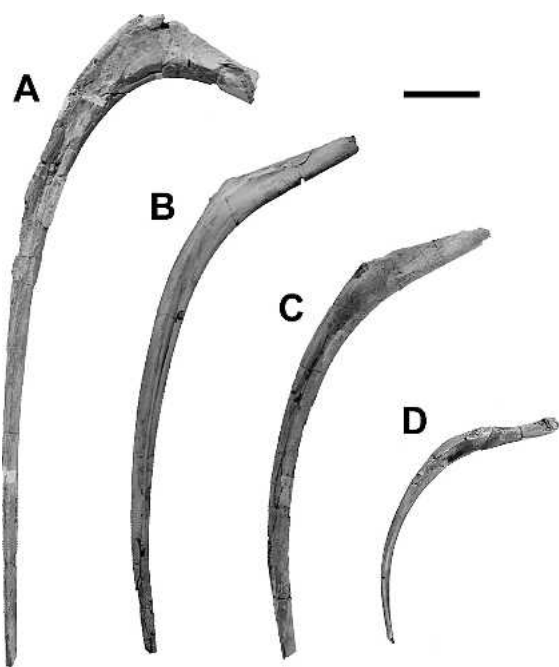


FIGURE 8. Dorsal ribs of *Dubreuillosaurus valesdunensis* (MNHN 1998-13). **A**, anterior dorsal rib in posterior view. **B**, middle dorsal rib in posterior view. **C**, middle dorsal rib in posterior view. **D**, posterior dorsal rib in posterior view. Scale bar equals 4 cm.

Pectoral Girdle

The pectoral girdle of *Dubreuillosaurus* is known by the proximal end of the left scapula, and the distal blade of the left or right scapula (Fig. 9). The maximum height of the proximal end is approximately 90 mm. The suture with the coracoid is sigmoid (Fig. 9A–B). The glenoid facet is slightly concave and faces more ventrally than laterally. Although partially broken, the acromial process was not so sharply offset from the anterodorsal margin of

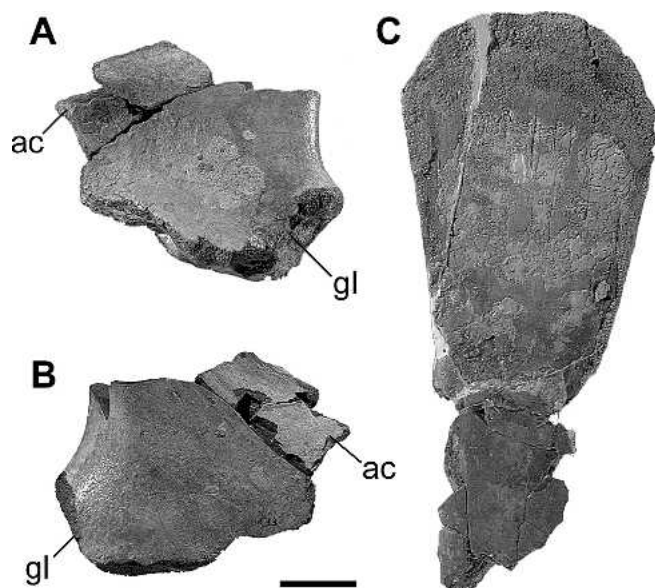


FIGURE 9. Scapula of *Dubreuillosaurus valesdunensis* (MNHN 1998-13). **A–B**, proximal end of the left scapula in lateral (**A**) and medial (**B**) views. **C**, distal end of the scapular blade. **Abbreviations:** **ac**, acromial process; **gl**, glenoid. Scale bar equals 4 cm.

the scapular blade as in *Allosaurus* (Gilmore, 1920), *Sinraptor* (Currie et Zhao, 1993), *Acrocanthosaurus* (Currie and Carpenter 2000), or tyrannosaurids (Maleev, 1974). The distal end of the scapula is strongly expanded distally (Fig. 9C). Its maximum distal height is 69 mm, while its minimum measurable height is 35 mm.

Manual Phalanx

The single manual element recovered is the ungual phalanx of the first or second left digit (Fig. 10A). It is 83 mm long when measured along the outside curve. Its outside curvature is comparable to that on the unguals of *Baryonyx* (Charig et Milner, 1997).

Hind Limb

The medial part of the proximal end, the distal end, and a natural cast of the shaft of the left femur are known for *Dubreuillosaurus* (Fig. 11A–D). The estimated length of the left femur is 450 mm. The femoral head is directed ventromedially at an angle of less than 90 degrees to the shaft as in more primitive theropods such as *Ceratosaurus* (Gilmore, 1920; Madsen et Welles, 2000), *Dilophosaurus* (UCMP 37302), and *Herrerasaurus* (Novas, 1993). Only the base of the lesser trochanter is preserved (Fig. 11A). It clearly differs from the trochanteric shelf in coelophysoids and *Dilophosaurus* in being wing-like like those of other basal Tetanurae. The lateral distal condyle is incompletely preserved (Fig. 11C–D). The floor of the deep intercondylar groove has a low longitudinal ridge. There is no extensor groove on the anterior surface of the distal end but a convexity as in the basal saurischian *Herrerasaurus* (Novas, 1993).

The right tibia is badly damaged and only the proximal end is preserved. The proximal condyles are separated by a deep posterior groove as in many theropods, and the medial condyle is higher than the lateral condyle.

The left fibula of *Dubreuillosaurus* has a 75 mm, anteroposteriorly expanded, proximal end (Fig. 11E). The medial side of the proximal end is only slightly concave as in *Eustreptospondylus* (OUM-J13558) and *Baryonyx* (Charig and Milner, 1997), while it is deeply grooved in allosauroids. The fibular shaft gradually narrows from the proximal end to the mid-shaft (Fig. 11F). The distal end is not preserved.

Pes

There is little available information on the *Dubreuillosaurus* pes since the pedal elements are only represented by the fifth left

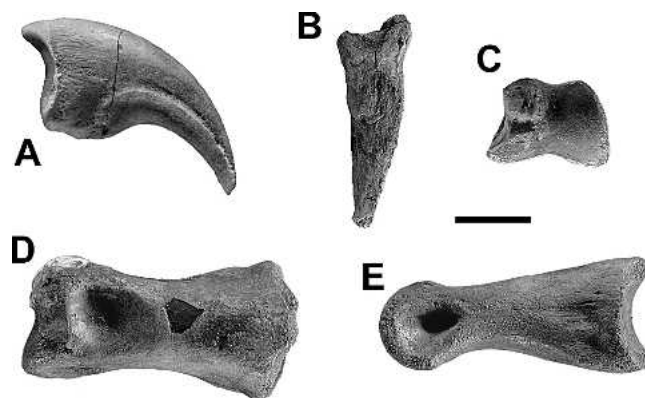


FIGURE 10. Pedal and manual elements of *Dubreuillosaurus valesdunensis* (MNHN 1998-13). **A**, Ungual phalanx of the left manus. **B**, fifth left metatarsal in medial view. **C–E**, phalanx III-1 of the left pedal digit in distal (**C**), dorsal (**D**), and lateral (**E**) views. Scale bar equals 2 cm.

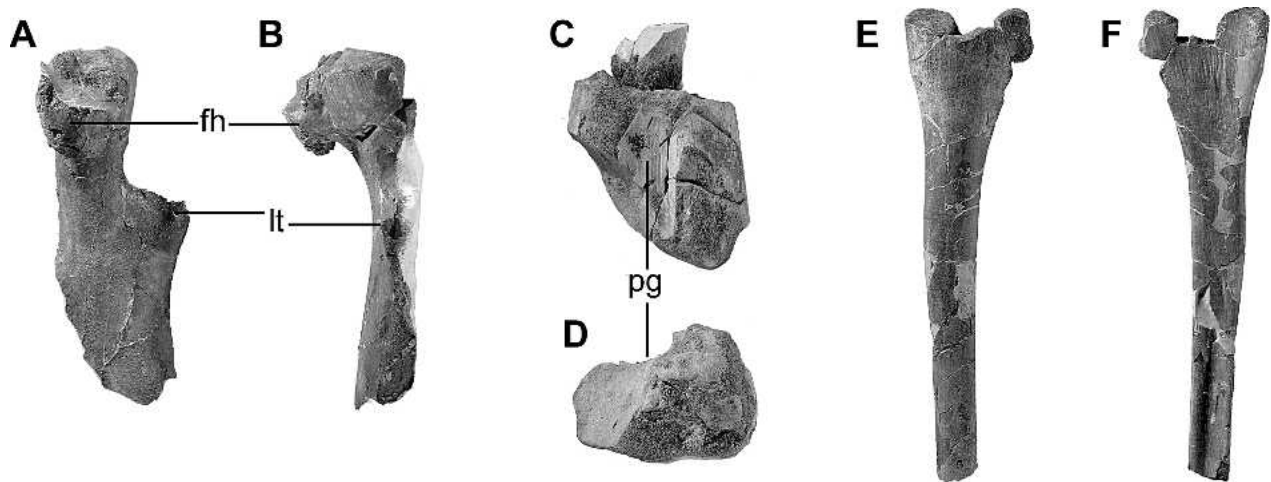


FIGURE 11. Hindlimb of *Dubreuillosaurus valesdunensis* (MNHN 1998-13). Proximal end of left femur in medial (A) and anterior (B) views. Distal end of left femur in posterior (C) and distal (D) views. Left fibula in lateral (E) and medial (F) views. **Abbreviations:** fh, femoral head; lt, lesser trochanter; pg, posterior groove. Scale bar equals 4 cm.

metatarsal and the first phalanx of the third left digit. The fifth metatarsal is 58 mm long and tapers distally (Fig. 10B). It lacks a distal articular facet and is not bowed anteriorly as in *Allosaurus* or *Sinraptor*. The proximal end is triangular in cross section. The anteromedial surface is rough over all its length, where it contacts the fourth metatarsal.

The left pedal phalanx III-1 is 65 mm long, with a proximal width of 35 mm and a distal width of 31 mm (Fig. 10C–E). The proximal and distal articular facets are symmetrical. The collateral ligament fossae are equally developed and the dorsal surface is excavated on the extensor surface proximal to distal articular surface.

DISCUSSION

Considering *Megalosaurus bucklandii* as a nomen dubium (Allain and Chure, 2002), *Dubreuillosaurus valesdunensis* together with *Eustreptospondylus oxoniensis* (Walker, 1964) are the only Middle to Late Jurassic European megalosaurids known by both cranial and postcranial material. *Dubreuillosaurus* differs from *Poekilopleuron bucklandii* from the same area and age, in having spatulate caudal transverse processes, anterior caudal neural spines that are more strongly posteriorly inclined; shorter prezygapophyses on distal caudals, and an anterodorsally directed accessory spur, anterior to the neural spine. The femur of *Dubreuillosaurus* is unique among spinosauroids. Indeed, its femoral head is medioventrally directed while it is inclined at an angle of 90° in other spinosauroids such as *Baryonyx*, *Afrovenator*, *Eustreptospondylus*, and *Lourinhanosaurus* (Allain, 2002b). Unlike the condition in the latter taxa, there is no extensor groove on the anterior surface of the distal end of the femur in *Dubreuillosaurus*. Among Megalosauridae (sensu Allain, 2002a, b, c, in prep.), *Dubreuillosaurus* differs from *Eustreptospondylus*, *Streptospondylus*, and *Lourinhanosaurus* in that the hypapophyses on anterior dorsal vertebrae are simple, unbifurcated anteriorly.

Diet of Megalosaurids

The dietary habit of spinosauroids has long been debated (Taquet, 1984; Charig and Milner 1986, 1997; Kitchener, 1987; Sereno et al., 1998; Sues et al., 2002; Holtz, 2003). Inferring from the gastric contents of *Baryonyx* (Charig and Milner, 1997), both fish and terrestrial vertebrates were part of the diet of spinosau-

roids. It is, however, unclear if spinosauroids were predominantly piscivorous (Sues et al., 2002). Moreover, the recent description of a pterosaur as part of the spinosauroid diet shows that spinosauroids were more probably opportunistic carnivores (Buffetaut et al., 2004).

In recent decades, piscivory has not been reported in any other group of carnivorous dinosaur with the possible exception of the noasaurid *Masiakasaurus* from the Late Cretaceous of Madagascar (Carrano et al., 2002). However, in the less inclusive clade of Spinosaurioidea, another case of piscivory had been reported long ago by Eudes-Deslongchamps (1838), who gave a detailed description of the gastric contents of *Poekilopleuron bucklandii*. The stomach contents were associated with the ribs of *Poekilopleuron* embedded in the so-called Mouen block. The contents included ten small, rounded pebbles interpreted as gastroliths, a tooth of the hybodont shark *Polyacrodus* sp. (Eudes-Deslongchamps, 1838:pl. 1, fig. 6), and several dark yellow fragments. The latter fragments resemble skeletal fragments of cartilaginous fishes (Eudes-Deslongchamps, 1838:33–37). This thorough examination of the stomach contents of *Poekilopleuron* proves that this theropod used gastroliths, and fed, at least partially, on fishes.

Paleontologists have long dismissed gastrolith-like stones found near theropod dinosaurs (e.g. Currie, 1997). Nevertheless, gastroliths have already been reported in various theropods including *Lourinhanosaurus* (Mateus, 1998), *Baryonyx* (Charig and Milner, 1997), and *Sinornithomimus* (Kobayashi and Lu, 2003). Only a single gastrolith was collected near the skeleton of *Baryonyx* (Charig and Milner, 1997) and it might well be that it was swallowed accidentally. But this is not the case for *Lourinhanosaurus* and *Poekilopleuron*, for which 32 and 10 gastroliths have been found respectively. The use of gastroliths to aid digestion in some theropod dinosaurs is thus likely.

Inclusion of fishes as part of the megalosaurid diet is consistent with both taphonomic and phylogenetic data. *Poekilopleuron* and *Dubreuillosaurus* were discovered in the same coastal, low-energy deposits, rich in plant fossils, fishes, and invertebrates (Eudes-Deslongchamps, 1838; Allain, 2002a, b). In-situ mangrove roots, which intersect the bone layer, indicate limited water depth (Dangeard and Rioult, 1961; Dugué et al., 1998). The close association of the different remains of both *Dubreuillosaurus* and *Poekilopleuron* and the preservation of fragile bones such as gastralia and skull elements, indicate that the skeletons of

these theropods were not transported prior to burial. *Poekilopleuron* and *Dubreuillosaurus*, therefore, were used to walking in such a mangrove environment probably for predation or scavenging. The hybodont shark *Polyacrodus* is common in European Mesozoic paralic and shallow environments (Landemaine, 1991), and thus could also have been part of the diet of megalosaurids. Obviously, the inferred piscivory of megalosaurids does not rule out other sources of food such as scavenging or predation on terrestrial animals. Megalosaurids are now considered as the sister-group of spinosaurids within a monophyletic spinosauroid clade (Serenó et al., 1994; Allain 2002a, b c; Carrano and Sampson, 2003). In a phylogenetic sense, the habit of feeding on fish would thus appear to be primitive for spinosauroids (i.e., Megalosauridae) and not a prerogative of the unique spinosaurids.

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