Journal of Vertebrate Paleontology 23(1):156–165, March 2003

A NEW SPECIES OF *STRUTHIOSAURUS* (DINOSAURIA: ANKYLOSAURIA) FROM THE UPPER CRETACEOUS OF VILLEVEYRAC (SOUTHERN FRANCE)

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ABSTRACT—A new species of the ankylosaur *Struthiosaurus* from the Upper Cretaceous (lower Campanian) of the Villeveyrac-Mèze Basin, southern France, is described from a partial skeleton that includes distal dorsal vertebrae, synsacrum and pelvic girdle. *Struthiosaurus languedocensis*, sp. nov. is a small-sized nodosaurid (less than 3 m length) characterised by distal dorsal centra that are very compressed laterally and hourglass in shape in ventral view; ischium directed immediately caudal from the acetabulum, with a robust shaft that does not taper distally and that is weakly curved in a caudoventral orientation. The synsacrum of *S. languedocensis* consists of ten co-ossified vertebrae, including five dorsals, four sacrals and a caudal. Among ankylosaurs, only *Polacanthus foxii* has a similar synsacral count, but there are significant differences in the pelvic structure between *Struthiosaurus* and *Polacanthus*. The presence of an ischium lacking a distinct nodosaurid-like ventral flexion appears to be diagnostic for the genus *Struthiosaurus*, as suggested by additional remains recovered from the upper Campanian of Laño (Iberian Peninsula). Current data suggests that *Struthiosaurus* is represented by different species in southwestern and central Europe.

INTRODUCTION

Our knowledge of ankylosaurian dinosaurs from the Late Cretaceous (Campanian–Maastrichtian) of Europe is based mainly on fossil material from Austria and Transylvania, with some fragmentary remains from southern France. Nopcsa (1929) recognized three taxa: *Struthiosaurus austriacus* from Muthmannsdorf, Austria; *S. transylvanicus* from Sânpetru, Transylvania (now Romania); and *Rhodanosaurus ludgunensis* from Quarante, southern France. Since then, new ankylosaurian remains have been found in a few other European localities, but most of the specimens are isolated or fragmentary (Pereda Suberbiola, 1992). The nodosaurid *Struthiosaurus* is the only well known genus. *S. austriacus* Bunzel, 1871 from the Lower Campanian of Austria is the type species (see Pereda Suberbiola and Galton, 1994, 2001). *S. transylvanicus* Nopcsa, 1915 from the Maastrichtian of Romania may represent a valid species but the type material is probably inadequate to distinguish it from *S. austriacus* (Pereda Suberbiola and Galton, 1997). *Rhodanosaurus ludgunensis* Nopcsa, 1929 from the upper Campanian–Lower Maastrichtian of Languedoc is based on non-diagnostic material and is regarded as a nomen dubium (Coombs and Maryanska, 1990; Pereda Suberbiola, 1993a).

In 1998, a partially complete, articulated skeleton of an ankylosaur, consisting of the pelvic girdle, synsacrum and distal dorsal vertebrae, was found in the Campanian deposits of the Villeveyrac-Mèze Basin near Montpellier in southern France. The specimen collected represents a new species of *Struthiosaurus*.

Abbreviations—**MCNA**, Museo de Ciencias Naturales de Alava/Arabako Natur Zientzien Museoa, Vitoria-Gasteiz, Spain; **PIUW**, Paläontologisches Institut, Universitat Wien, Vienna, Austria; **UM2**, Université des Sciences et Techniques du Languedoc, Montpellier, France.

GEOLOGICAL SETTING

The Upper Cretaceous Villeveyrac-Mèze Basin is located between the towns of Pézenas and Mèze, in the Department of Hérault, southern France (Fig. 1). The ankylosaur material was collected from the L'Olivet site of the Villeveyrac quarry, located about 30 km east of Montpellier, by the Laboratoire de Paléontologie of the Université de Montpellier II and the field museum La Plaine des Dinosaures (Mèze, Hérault). The remains come from the continental deposits in the basal part of the basin. The deposits consist of lignite-bearing, grey clays situated above an Albian–Cenomanian aged bauxite (Berger et al., 1981). The lower-most part of the beds is composed of clays, marls and intercalated sandstones (Fig. 1). Equivalent beds elsewhere in the basin have yielded gastropods, charophytes, and palynomorphs that indicate a Fuvelian age (see Feist and Freytet, 1983). The Fuvelian is a regional stratigraphic unit (formerly considered a stage) established in southern France. Magnetostratigraphy suggests that the Fuvelian is correlated with the lower part of the Campanian (Westphal and Durand, 1990). The ankylosaurian remains of the L'Olivet Quarry were found in association with plant remains and other vertebrate bones (see faunal list in Table 1). Buffetaut et al. (1996) presented a historical account of the discoveries and gave a faunal list. This list, however, is a composite of the vertebrates found at different levels in the Villeveyrac quarry, which probably ranges from the lower to upper Campanian.

Sedimentary features (fine grained, presence of organic matter and ferruginous sulfur crusts) suggest a quiet and brackish environment where bones and plant remains carried by waters accumulated. The ankylosaurian partial skeleton was found lying with the dorsal side up, in contrast to the more common upside down (Sternberg, 1970; Carpenter, 1984).

SYSTEMATIC PALEONTOLOGY

THYREOPHORA Nopcsa, 1915
ANKYLOSAURIA Osborn, 1923
NODOSAURIDAE Marsh, 1890
STRUTHIOSAURUS Bunzel, 1870

Type Species—*Struthiosaurus austriacus* Bunzel, 1871

Range—Campanian to Maastrichtian.

Generic Diagnosis—See Pereda Suberbiola and Galton (1994, 2001).

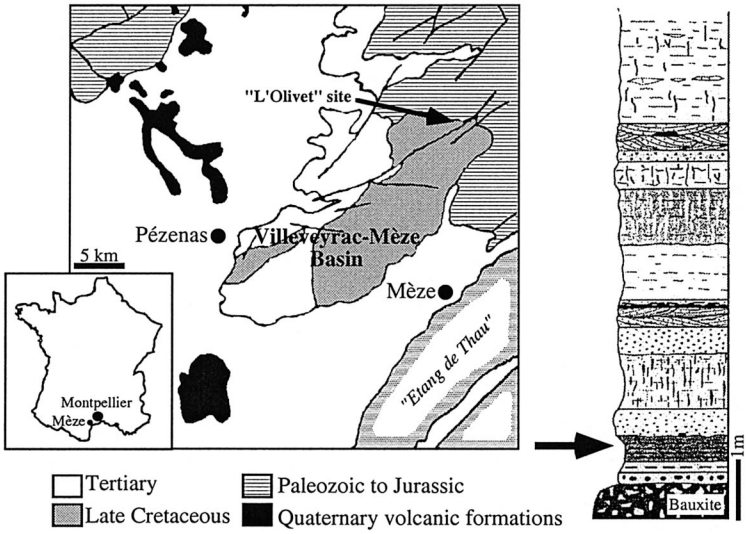

FIGURE 1. Location map of the Villeveyrac-Mèze Basin (southern France) showing the field area from which the remains of *Struthiosaurus languedocensis*, sp. nov. were recovered; and stratigraphical column of L'Olivet Quarry. Arrow indicates the ankylosaur horizon.

STRUTHIOSAURUS LANGUEDOCENSIS, sp. nov (Figs. 2–4)

Holotype—UM2 OLV-D50 A–G CV, complete synsacrum and pelvic girdle, and the four caudal-most dorsal vertebrae.

Etymology—Refers to Languedoc, the region from which the fossil came.

Type Locality—L'Olivet Quarry, Villeveyrac; Department of Hérault, southern France.

Type Horizon—Lignite-bearing grey clays from the Villeveyrac-Mèze Basin, Upper Cretaceous, lower Campanian (''Fuvelian'' continental local stage).

Referred Material from the Same Horizon—UM2 OLV-D18–20 CV, three isolated teeth; OLV-D29 CV, a distal caudal vertebra with fused chevon; OLV-D27 CV, a cervical spine; and OLV-D21–22 CV, two dermal scutes.

Diagnosis—Small-sized nodosaurid (length 2.5 to 3.0 m), with ischium directed immediately caudal to the acetabulum; distal dorsal centra very compressed laterally, hourglass shaped. Shares with *S. austriacus* nearly straight to slightly curved ischium. Differs from *S. austriacus* in robust, parallel-sized ischium that ends distally in a blunt knob.

TABLE 1. Faunal list from the lignite bearing-beds of the lower part of the ''Fuvelian'' series (Lower Campanian) of the Villeveyrac-Mèze Basin, L'Olivet Quarry, southern France (see Buffetaut et al., 1996; Lapparent de Broin and Murelaga, 1999; this paper).

- Bony fish
  - Ginglymodi
    - Lepisosteidae indet.
  - Teleostei
    - Sparidae indet.
- Amphibians
  - Anura indet.
- Squamates
  - Squamata indet.
- Turtles
  - Cryptodira
    - Solemydidae
      - *Solemys* aff. *vermiculata*
  - Pleurodira
    - Bothremydidae
      - *Polysternon provinciale*
- Crocodilians
  - Eusuchia
- Dinosaurs
  - Ankylosauria
    - Nodosauridae
      - *Struthiosaurus languedocensis* sp. nov.

DESCRIPTION

Measurements for the holotype are presented in Table 2.

Dorsal Vertebrae and Ribs

Four vertebrae (Fig. 2) representing the caudalmost dorsals in advance of the synsacrum (UM2 OLV-D50 D–G CV) are preserved, each bearing a pair of co-ossified ribs (Fig. 2A). All the vertebrae demonstrate some degree of damage due to crushing. The intervertebral articular face of each vertebra is platycoelous to slightly amphicoelous and has an ovoid to heart-shaped morphology, with the greatest dimension in the transverse plane. At midlength, the centra are compressed laterally, such that the minimum width is less than half the diameter of the articular faces (Fig. 2C). As a result, the centra appear hourglass-shaped in ventral view. The ventral surface of each vertebra bears a weak, longitudinally oriented keel.

The articular surfaces of the best preserved vertebra (the first one in the series) are offset in lateral view, with the cranial face more ventrally positioned than the caudal face. The neural canal is oval with the long axis oriented vertically. The ventral margin of the neural canal has a deep fossa along the dorsal surface of the centrum. The prezygapophyses are prominent, forming a single, U-shaped structure, whereas the postzygapophyses are reduced and separated. Both the prezygapophyses and postzygapophyses extend slightly beyond the articular faces of the centra. The diapophyses are moderately inclined upward, and are positioned 90° to each other. Only one vertebra preserves the neural spine, which is a laterally compressed blade. The top of the neural spine is slightly higher than the transverse processes and fused ribs.

The ribs are firmly co-ossified to the dorsal vertebrae at both the transverse process (i.e., at the diapophysis) and at the cen-

TABLE 2. Measurements (in mm) of the holotype of *Struthiosaurus languedocensis* sp. nov. (UM2 OLV-D50 A-G CV) from the Lower Campanian of Villeveyrac, southern France.

Dorsal vertebrae:	Dorsal a	Dorsal b	Penultimate dorsal	Caudalmost dorsal
Centrum length	40	41	36	40
Centrum height	48	42	47	47
Centrum width	57	57	54	54
Vertebral height (including neural spine)	+130	+94	—	+90

Synsacrum:	Maximum width	Maximum craniocaudal length
Synsacrum	—	420
Sacral ribs S2-S3	—	23
Sacral foramina 1	80	15
Sacral foramina 2	62	34
Sacral foramina 3	72	33
Sacral foramina 4	65	15
Pelvic girdle:		
Maximum width between preacetabular processes	665	
Maximum width at acetabulum	530	
Minimum width between postacetabular processes	170	
Maximum diameter of acetabulum	110	
Ilium (right):		
Total length	490	
Width at acetabulum	150	
Length of preacetabular process	270	
Maximum width of preacetabular process	125	
Minimum width of preacetabular process	105	
Length of postacetabular process	110	
Width of postacetabular process	70	
Ischium (left):		
Length	165	
Height at midlength	35	
Pubis (left):		
Length	105	

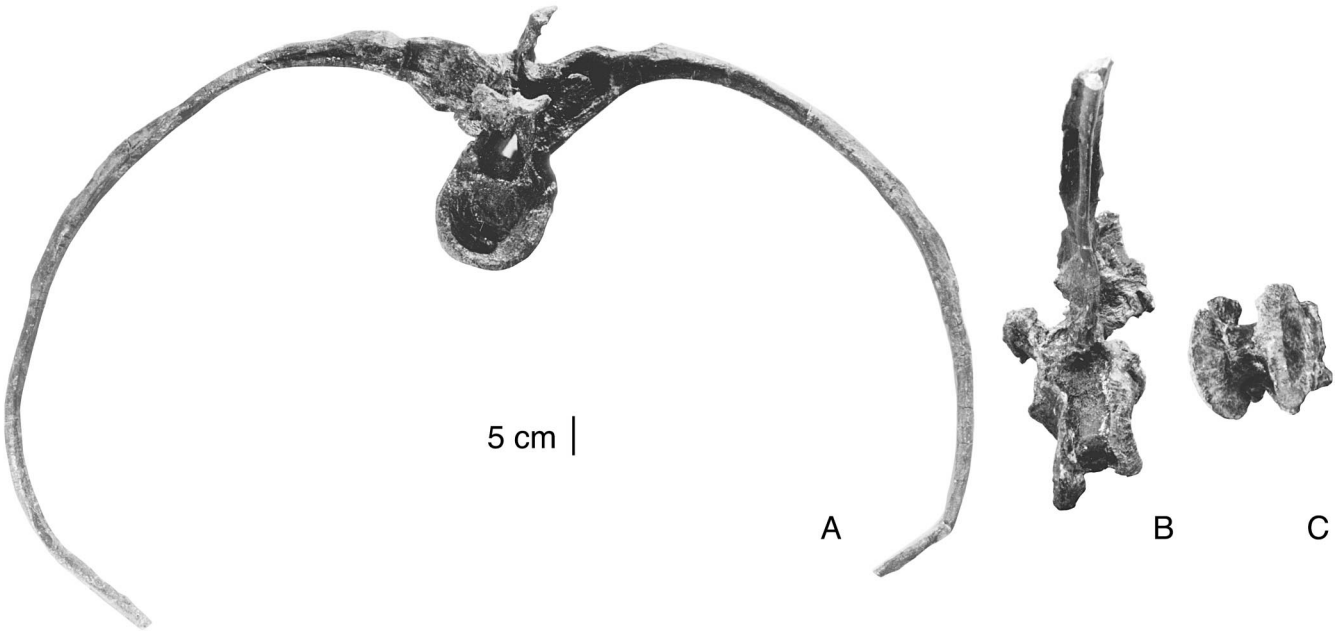

FIGURE 2. **A**, cranial; **B**, left lateral; and **C**, ventral views of a distal dorsal vertebra of *Struthiosaurus languedocensis*, sp. nov. (holotype, UM2 OLV-D50 D CV) from the Lower Campanian of Villeveyrac, southern France. Scale bar equals 5 cm.

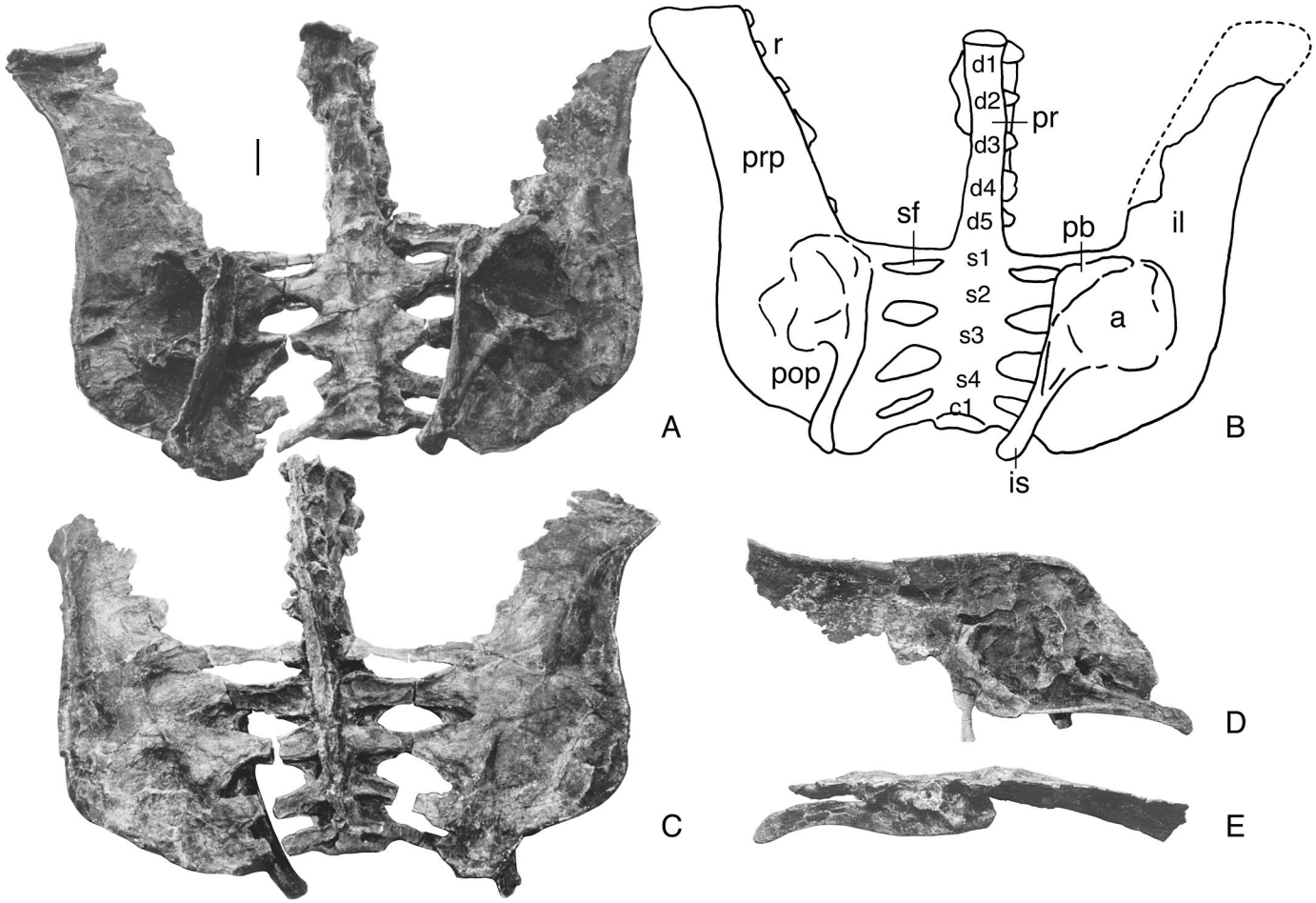

FIGURE 3. **A**, ventral and **C**, dorsal views of the pelvic girdle and synsacrum of *Struthiosaurus languedocensis*, sp. nov. (holotype, UM2 OLV-D50 A–C CV); **B**, schematic illustration of the pelvic girdle and synsacrum in ventral view; **D**, right pelvic girdle in ventral view; **E**, left pelvic girdle in medial view. **Abbreviations: a**, acetabulum; **d1–5**, presacral rod dorsal vertebrae; **il**, ilium; **is**, ischium; **pb**, pubis; **pop**, postacetabular process of ilium; **pr**, presacral rod; **prp**, preacetabular process of ilium; **r**, rib; **sf**, sacral foramen; **s1–4**, sacral vertebrae; **c1**, synsacrum caudal vertebra. Scale bar equals 10 cm.

trum. The ribs are T-shaped in cross-section. The maximum width between adjacent ribs is 65 cm. The last dorsal rib contacts the cranioventral surface of the preacetabular process of the ilium.

Synsacrum

The synsacrum (Fig. 3; UM2 OLV-D50 C CV) consists of ten fused vertebrae, including five dorsals, four sacrals and one caudal. It is crushed ventrolaterally and, consequently, it is somewhat distorted. The vertebrae are firmly co-ossified, such that the sutures between adjacent centra are almost completely obliterated and the entire structure is slightly bowed (convex dorsally) in lateral view. The neural spines are low and narrow. Ossified tendons occur as rod-like structures along both sides of the neural spines and are arranged in two series of three tendons. On the ventral surface of the synsacrum, there is a very shallow groove on the second and third sacral centra. The five cranial-most centra, forming the presacral rod, are more slender than their caudal counterparts. The ribs of the presacral rod are broken, but they remain fused proximally to vertebrae and distally to the preacetabular process of the ilia. The first centrum of the presacral rod is similar in size and shape to those of the caudal-most free dorsal vertebrae. The first sacral centra is wider than those of the presacral rod, but not as wide as the caudal-most centra. The ribs of the first sacral vertebra are thin and contact the ilia just in front of the acetabulum. The second and third sacral centra are the widest of the synsacrum (and probably represent the ''primitive reptilian sacrum''; Galton, 1999). These vertebrae bear robust horizontal processes composed of coalesced between the sacral ribs and adjacent transverse processes. Distal expansion of the sacral ribs contributes to the medial wall of the acetabulum. Ribs of the ninth and tenth synsacral vertebrae fuse to the postacetabular process of the ilium. In dorsal view, these ribs are obliquely oriented with the penultimate rib being the most robust. In lateral view, the ribs of the presacral rod are aligned in the same horizontal plane, and are situated slightly more dorsally than the rest of the synsacral ribs. The rib height of the first sacral vertebra is intermediate between that of the presacral ribs and those of the other sacral ribs. On both sides, from the first sacral to the tenth synsacral vertebrae, there are four sacral foramina between the sacral ribs; the second and third are the largest, whereas the first is the widest.

Pelvic Girdle

The pelvis (Fig. 3) is virtually complete, consisting of paired ilia, ischia and pubes (UM2 OLV-D50 A–B CV). There is no

evidence of dermal armour directly associated with the dorsal surface of the ilia.

Ilium—The right ilium is more complete than the left one, the latter lacking the cranial-most portion of the preacetabular process. The ilia are oriented in a horizontal position overhanging the hindlimbs. Near the acetabulum, the iliac blade is slightly convex dorsally. The shaft of the ilium is roughly S-shaped in dorsal view and the lateral border of the preacetabular blade diverges cranially. The preacetabular process is long (about 55 per cent of total ilium length) and gently tapers cranially. It diverges laterally from the midline at about 30°. The postacetabular segment is relatively short (about 22 per cent of ilium length); it projects caudally to form a blunt knob. The acetabulum is closed medially forming a shallow subcircular cup receiving contributions from both the ilium and the ischium, and is situated opposite the first three sacral ribs.

Ischium—Both ischia are complete. The right ischium is slightly distorted, whereas the left ischium is well preserved and oriented almost parallel to the longitudinal axis of the synsacrum. The proximal end of each ischium is widely expanded and laterally concave, forming the medial wall of the acetabulum. Each ischium is directed immediately caudal from the acetabulum, almost oriented in the horizontal plane. The shaft is rod-like with a slight ventral flexion. Distally, the ischium forms a blunt, knob-like structure.

Pubis—Although the right pubis is somewhat damaged, the left pubis remains well preserved. It is fused firmly to both the ilium and the ischium on the craniomedial wall of the acetabulum. The pubis is relatively small and crescentic in shape, with a short, blunt prepubic process and a blade-like postpubic process.

Referred Material

Material from the same quarry and horizon as the holotype consists of three teeth, a caudal vertebra, and three armour elements (Fig. 4). These remains could belong to the same or to another individual.

Each tooth (UM2 OLV-D18–20 CV) is relatively small (mesio-distal length approximately 5.5 mm), laterally compressed and has an asymmetrical, leaf-shaped crow (Fig. 4A, B). The crown is longer than high. Separated by a large apical cusp, there are 2 to 4 denticles on each margin of the crown. On one side, the marginal denticles exhibit wear facets. A rimmed cingulum is present basally on each side of the crown, higher on one side than the other. The crown lacks any vertically oriented grooves, but small ridges are visible, just above the cingulum. The root is broken, but seems to be constricted below the crown.

The caudal vertebra (UM2 OLV-D29 CV) is small and, as suggested by the craniocaudally long centrum and the absence of transverse processes, it comes from the distal part of the tail (Fig. 4F). The centrum is laterally compressed and bears a longitudinal ridge. The zygapophyses, while present, are small. A chevron is fused caudally to the vertebra.

The dermal armour (Fig. 4C–E) includes two low-keeled scutes and a fragmentary spine from the cervical region (UM2 OLV-D21, 22, and 27 CV). The scutes are oval, longer than wide (about 10 cm long and 7 cm wide). The ventral-most surface is not excavated. These scutes probably come from the dorsal region of the body. The cervical spine (greatest length: 11.1 cm; basal length: 9.4 cm) is asymmetrical, blunted distally, and dorsoventrally compressed. The specimen closely resembles the lateral spines of the cervical half-rings of the genus *Struthiosaurus* (Pereda Suberbiola et al., 1995).

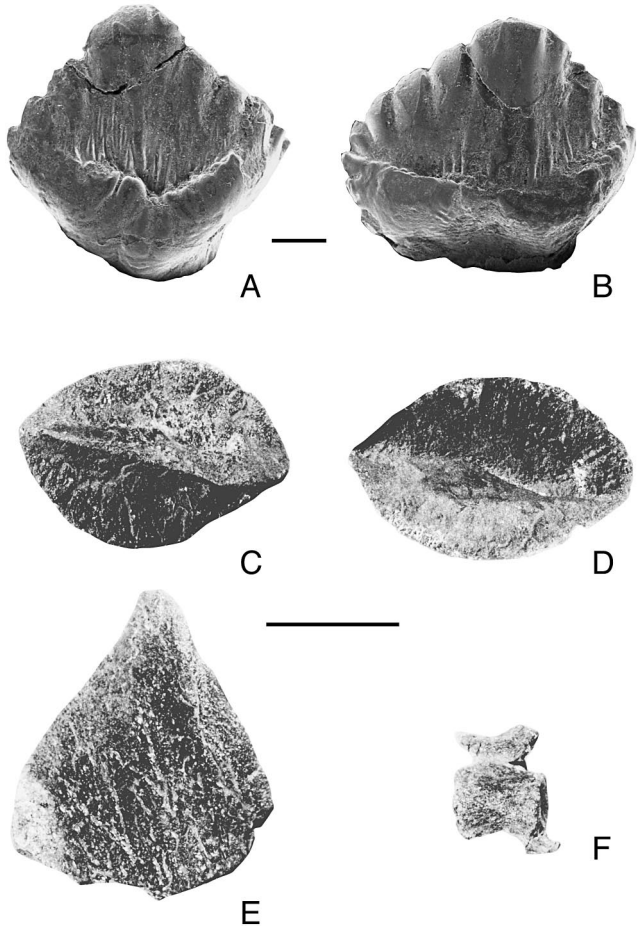

FIGURE 4. Referred specimens of *Struthiosaurus languedocensis*, sp. nov. from the Lower Campanian of Villeveyrac, southern France. **A**, **B**, UM2 OLV-D18 CV, opposite crown faces of one tooth; **C**, **D**, UM2 OLV-D21 and 22 CV, two low-keeled scutes in dorsal view; **E**, UM2 OLV-D21 CV, cervical spine in dorsal view; F, UM2 OLV-D29, distal caudal vertebra and chevron in left lateral view. Scale bars equals 2 mm (**A**, **B**) and 50 mm (**C**–**F**).

COMPARISONS

The Villeveyrac ankylosaur appears to represent a relatively small individual, with an estimated body length of 2.6 to 2.8 m. This compares well with a number of other ankylosaur taxa, including *Struthiosaurus austriacus* (Pereda Suberbiola and Galton, 2001), *Mymoorapelta maysi* (Kirkland and Carpenter, 1994), *Gargoyleosaurus parkpinorum* (Carpenter et al., 2000) and *Minmi paravertebra* (Molnar, 1996).

Fusion between the centra and the neural arches, and between the sacral ribs and the vertebrae and ilium, as well as co-ossification between adjacent sacral centra, suggests that the Villeveyrac specimen represents an adult individual (see Galton, 1982; Coombs, 1986).

The caudal-most dorsal vertebrae of *Struthiosaurus languedocensis* differ from those of other ankylosaurs, including *S. transylvanicus* (unknown in *S. austriacus*), in demonstrating prominently compressed centra of the dorsal series. Although somewhat distorted, the dorsal vertebrae do not appear to have undergone extensive post-mortem deformation, and consequently the lateral compression is not considered to represent a taphonomic artifact. The transverse processes demonstrate a moderate vertical inclination (about 40–45° from the horizontal), as in *Edmontonia* (Gilmore, 1930) and *Ankylosaurus*

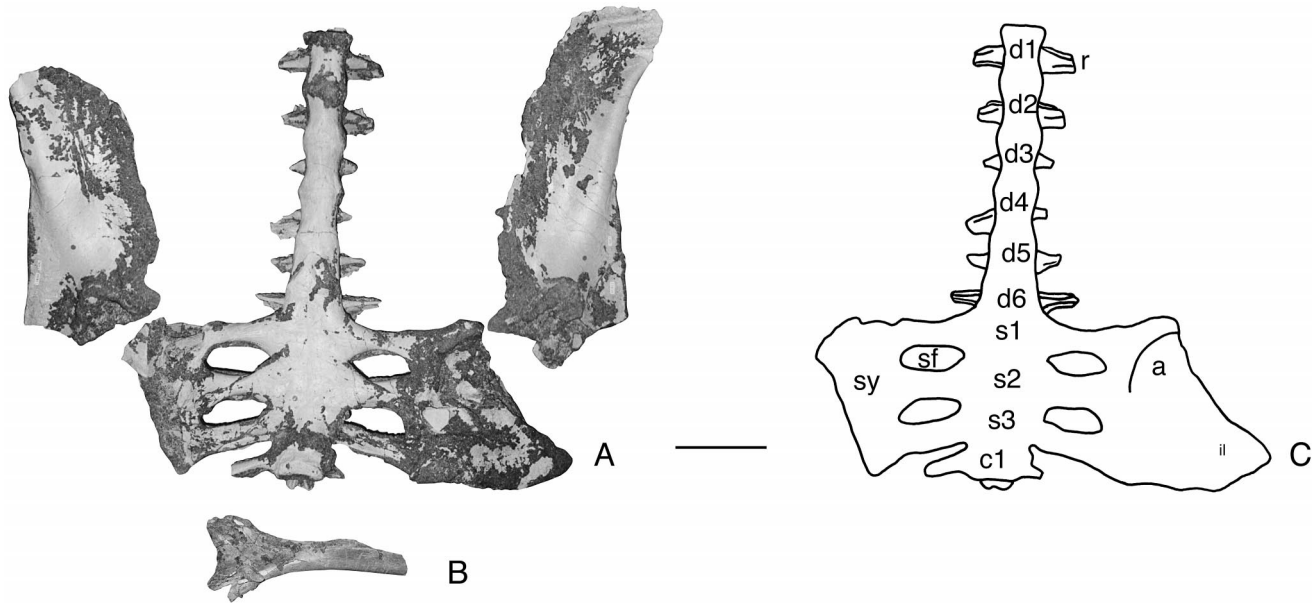

FIGURE 5. Pelvic girdle and synsacrum of *Struthiosaurus* sp. from the upper Campanian of Laño, Iberian Peninsula. **A**, MCNA 7420.1–3, synsacrum and fragmentary left and right ilia in ventral view. The bones are partially covered with iron oxides; **B**, MCNA 7420.4, left ischium in medial view; **C**, schematic illustration of the synsacrum in ventral view. Abbreviations as in Figure 3 caption plus: **d1–6**, presacral rod dorsal vertebrae; **s1–3**, sacral vertebrae; **sy**, sacricostal yoke. Scale bar equals 10 cm.

(Brown, 1908), but in contrast to *Animantarx* (60°; Carpenter et al., 1999) and *Talarurus* (50°; Maleev, 1956). The neural canal is excavated into the dorsal surface of the centrum, as in other ankylosaurs, including *Polacanthus*. The cranial articular face of the centra is lower than the caudal one, similar to *Edmontonia* and *Talarurus*. This feature suggests dorsal flexion of the vertebral column just in advance of the presacral rod.

Similar to most ankylosaurs, including material attributed to *Struthiosaurus* sp. (Pereda Suberbiola, 1999), the ribs of *S. languedocensis* are fused to the caudal-most dorsal vertebrae both at the centrum and along the transverse process (Coombs and Maryanska, 1990; Coombs, 1995). Although unknown for both *S. austriacus* and *S. transylvanicus*, it is likely due to the fragmentary state of the material.

The synsacrum of *Struthiosaurus languedocensis* consists of ten fused vertebrae, as in *Polacanthus foxii* (Hulke, 1888; Pereda Suberbiola, 1994) and *Struthiosaurus* sp. (Fig. 5; Pereda Suberbiola, 1999). Among most ankylosaur taxa, the number of synsacral vertebrae is generally fewer; nine are known in *Nodosaurus textilis* (Lull, 1921), *Edmontonia longiceps* and *E. rugosidens* (Gilmore, 1930; Carpenter, 1990), and *Talarurus plicatospineus* (Maleev, 1956); eight in *Niobrarasaurus colei* (Carpenter et al., 1995), and probably *Euoplocephalus tutus* (Carpenter, 1982); and a minimum of seven in the synsacrum of *Sauropelta edwardsorum* (Carpenter and Kirkland, 1998).

The presacral rod of *Struthiosaurus languedocensis* is composed of five vertebrae (Fig. 3B). This number varies from three to six within the Nodosauridae; three are known in *Sauropelta* (Carpenter and Kirkland, 1998), four in *Nodosaurus* and *Edmontonia* (Lull, 1921; Carpenter, 1990), five in *Polacanthus* (Pereda Suberbiola, 1994), and six in a synsacrum referred to *Struthiosaurus* sp. (Fig. 5; Pereda Suberbiola, 1999). In ankylosaurids, the number of presacral rod vertebrae is unclear—Maryanska (1977) reported four to five vertebrae for *Pinacosaurus* and *Talarurus*; *Euoplocephalus* has three (Coombs, 1986; four according to Carpenter, 1982). Finally, Dong (1993) described two dorsosacrals in *Tianchisaurus*, although the cranial-most portion of the synsacrum appears to be broken.

As interpreted, *Struthiosaurus languedocensis* has four sacral vertebrae, similar to *Sauropelta* (Ostrom, 1970), *Panoplosaurus* (Sternberg, 1921; Carpenter, 1990), *Polacanthus* (Pereda Suberbiola, 1994), *Talarurus* (Maleev, 1956), *Pinacosaurus* (Maryanska, 1977; Godefroit et al., 1999), and *Tianchisaurus* (Dong, 1993). In contrast, *Nodosaurus* (Lull, 1921), *Edmontonia* (Gilmore, 1930; Carpenter, 1990), *Niobrarasaurus* (Carpenter et al., 1995), *Gastonia* (Kirkland, 1998), *Silvisaurus* (Carpenter and Kirkland, 1998), *Euoplocephalus* (Carpenter, 1982; Coombs, 1986), and *Struthiosaurus* sp. (Pereda Suberbiola, 1999) reportedly have three sacral vertebrae. The number of true sacrals is three or four in *Mymoorapelta* (Kirkland et al., 1998). The significance of the sacral count in ankylosaurs is unclear, and may not be a reliable taxonomic character (Coombs and Deméré, 1996). Similar to *Nodosaurus*, *Edmontonia*, *Niobrarasaurus*, *Gastonia*, *Texasetes* and *Tianchisaurus*, the ventral surface of the sacral centra of *Struthiosaurus languedocensis* has a shallow sagitally oriented groove.

Among ankylosaurs, the first or second caudal vertebra is frequently incorporated into the synsacrum. In *Struthiosaurus languedocensis*, *Polacanthus* (PeredraSuberbiola, 1994), *Niobrarasaurus* (Carpenter et al., 1995), *Tianchisaurus* (Dong 1003), and *Euoplocephalus* (Carpenter 1982), only the first caudal vertebra contributes to the synsacrum. In contrast, there are two caudals fused to the sacral complex in *Edmontonia* (Gilmore, 1930; Carpenter, 1990), *Nodosaurus* (Lull, 1921), and *Silvisaurus* (Carpenter and Kirkland, 1998).

The preacetabular process of the ilium of *Struthiosaurus languedocensis* is folded ventrally, a feature common to most ankylosaurs (Coombs, 1979). In *Mymoorapelta* (Kirkland and Carpenter, 1994) and *Animantarx* (Carpenter et al., 1999), the cranial part of the preacetabular process is folded ventrolaterally. In *S. languedocensis*, the ratio of the length of the preacetabular process to the total length of the ilium is comparable with that of *Sauropelta* (0.55), somewhat intermediate to those of both *Polacanthus* (0.48) and *Euoplocephalus* (0.67) (see Pereda Suberbiola, 1994). The preacetabular process of *S. languedocensis* is transversely broader than that of *Sauropelta*

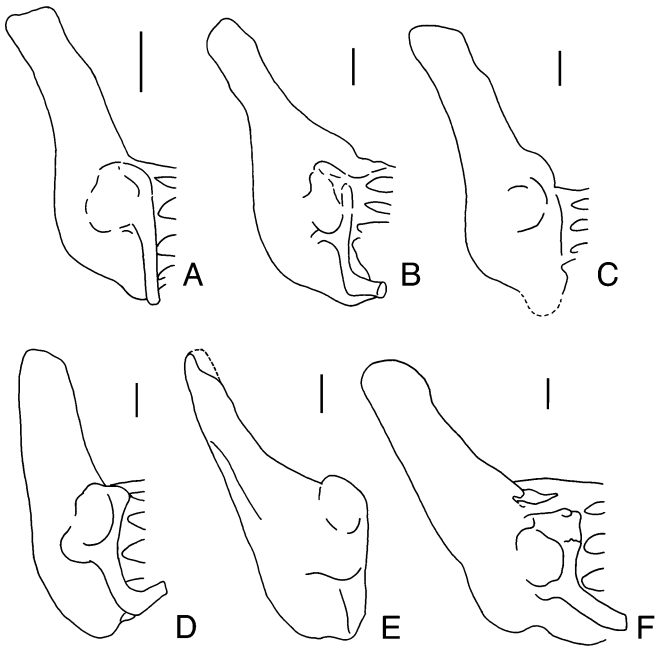

FIGURE 6. Schematic illustrations of ankylosaurian right pelvic girdle and sacral ribs in ventral view. **A**, *Struthiosaurus languedocensis* (UM2 OLV-D50 B CV; lower Campanian, Villeveyrac, France). **B**, *Sauropelta edwardsorum* (Aptian–Albian, Montana, USA), modified after Coombs (1978:fig. 14). **C**, *Edmontonia longiceps* (Campanian–Maastrichtian; Alberta, Canada), after Carpenter (1990:fig. 21.15E). **D**, *Polacanthus foxii* (Barremian, Isle of Wight, England) after Pereda Suberbiola (1994:pl. 2, figs. 1, 2). **E**, *Gastonia burgei* (Barremian, Utah, USA), after Kirkland (1998:fig. 5F). **F**, *Euoplocephalus tutus* (Campanian, Alberta, Canada), from Coombs (1978:fig. 13; 1979:fig. 2). A and F are partially reconstructed, C and E lack the ischium and pubis, and the latter also lacks the sacral ribs. Scale bars equals 10 cm.

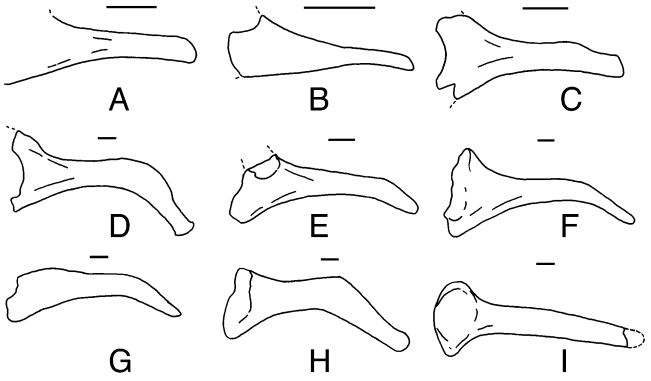

FIGURE 7. Schematic illustrations of ankylosaurian ischia in lateral view. **A**, *Struthiosaurus languedocensis* (UM2 OLV-D50 A CV in part; lower Campanian; Villeveyrac, France). **B**, *S. austriacus* (PIUW 2349/41; lower Campanian; Muthmmansdorf, Austria). **C**, *Struthiosaurus* sp. (MCNA 7420.4; upper Campanian; Laño, Spain). **D**, **E**, *Sauropelta edwardsorum* (Aptian–Albian, Montana, USA), modified after Ostrom (1970:pl. 25, fig. B and G). **F**, *Edmontonia rugosidens* (Campanian; Montana, USA), after Gilmore (1930:fig. 17). **G**, *Edmontonia longiceps* (Campanian–Maastrichtian; Alberta, Canada), after Carpenter (1990:fig. 21.15F). **H**, *Gastonia burgei* (Barremian; Utah, USA), after Kirkland (1998:fig. 5A). **I**, *Ankylosaurus magniventris* (Maastrichtian; Alberta, Canada), after Coombs (1979:fig. 3). All left ischia (but E and H reversed drawings). Scale bars equals 5 cm.

(Coombs, 1978, 1979) and *Gastonia* (Kirkland, 1998), but narrower that the condition noted in *Euoplocephalus* (Coombs, 1979). Similar to most ankylosaurs, with the exception of *Polacanthus* (Pereda Suberbiola, 1994) and *Mymoorapelta* (Kirkland and Carpenter, 1994), the preacetabular process of *S. languedocensis* diverges craniolaterally. The lateral border of the ilium of *S. languedocensis* is comparable with that of both *Sauropelta* and *Edmontonia* (Carpenter, 1990), a structural intermediate between the rectilinear morphology of *Euoplocephalus* (Coombs, 1979) and *Gastonia* (Kirkland, 1998), and the convex contour of *Pinacosaurus* (Buffetaut, 1995) (see Fig. 6). The postacetabular process of *S. languedocensis* is similar in relative length to that of *Sauropelta*, *Edmontonia*, and *Polacanthus*. It is considerably longer that that reported for the ankylosaurids *Euoplocephalus* and *Pinacosaurus*, although shorter than that of *Minmi* (Molnar, 1996). The distal knob-like terminus of the postacetabular process is situated medially similar to *Sauropelta* (Coombs, 1979), *Edmontonia* (Carpenter, 1990) and *Nodosaurus* (Lull, 1921), and contrary to *Polacanthus*. There is no evidence of a ridge extending caudally from the acetabulum as in *Sauropelta* (Coombs, 1979) and *Gastonia* (Kirkland, 1998). The ilium of *S. languedocensis* looks most like that of *Edmontonia longiceps* (Carpenter, 1990) (Fig. 6).

The ischium of *Struthiosaurus languedocensis* is unique among ankylosaurs in being oriented immediately caudal to the acetabulum (Fig. 3E). In contrast, the ischium of most ankylosaurids is near vertical while those of most nodosaurids are directed caudoventrally (Coombs, 1979). The significance of this character is unclear, but it could be related to hindlimb biomechanical. The ischial shaft of *S. languedocensis* is relatively robust along its entire length, similar to the ankylosaurids *Euoplocephalus* and *Ankylosaurus* and in contrast to most nodosaurids (e.g., *Sauropelta*, *Edmontonia*; see Fig. 7), where it becomes distinctly tapered.

The pubis of *Struthiosaurus languedocensis*, unlike that of ankylosaurids such as *Euoplocephalus* (Coombs, 1979), is not a nubbin, but is crescentic-like as in the nodosaurids *Sauropelta* (Ostrom, 1970) and *Edmontonia* (Gilmore, 1930).

The chevrons are fused intervertebrally to the centra of the distal caudal vertebrae, as in *S. austriacus* (Pereda Suberbiola and Galton, 2001), *Mymoorapelta* (Kirkland and Carpenter, 1994), *Edmontonia* (Gilmore, 1930), and the ankylosaurids *Ankylosaurus* (Brown, 1908), *Euoplocephalus* (Parks, 1924), *Talarurus* (Maleev, 1956), and *Pinacosaurus* (Maryanska, 1977; Godefroit et al., 1999). In contrast, chevrons do not appear to fuse to the distal caudals in *Hylaeosaurus* (Pereda Suberbiola, 1993b) and *Niobrarasaurus* (Carpenter et al., 1995). In *Sauropelta*, chevrons may be occasionally fused to caudals (Ostrom, 1970).

Struthiosaurus austriacus (PIUW 2349/41 and uncatalogued; Bunzel, 1871; Seeley, 1881; Nopcsa, 1929; Pereda Suberbiola and Galton, 1994, 2001) and *S. languedocensis* share an ischium without a sharp flexion. However, the ischium of *S. austriacus* clearly differs from that of *S. languedocensis* in having a more slender shaft, tapering distally (Fig. 7A, B). Furthermore, *S. languedocensis* can be distinguished from *S. transylvanicus* (BMNH R4966, R3848) on the basis of a more pronounced lateral compression of the dorsal centra.

Additional comparisons of *Struthiosaurus languedocensis* should be made with referred remains of *Struthiosaurus* sp. from the upper Campanian of Laño, Iberian Peninsula (Pereda Suberbiola, 1999). Of particular relevance is a partial skeleton, consisting of the synsacrum, a fragmentary pelvis and hindlimb elements (MCNA 7420; see Fig. 5). The Laño material is referred to *Struthiosaurus* on the basis of overall size and similarities of the ilia (preacetabular process diverges cranially from the parasagittal axis, concave lateral border) and femora (ridge-like anterior trochanter, fourth trochanter located proximally

near the midlength) of *S. austriacus*. Pereda Suberbiola (1999) listed some minor (specific?) differences compared to *S. austriacus* and, after discussing the great osteological variability observed in this ankylosaur, he referred the Laño remains to as *Struthiosaurus* sp. indet. The synsacrum of the Laño specimen consists of ten fused vertebrae, and is similar in size (length 42.5 cm) to that of *S. languedocensis*. Based on field data, Pereda Suberbiola (1999) described the MCNA 7420 synsacrum as including six dorsals, three sacrals and one caudal. In fact, the sixth vertebra of the synsacrum may be either the last element of the presacral rod or the cranial-most sacral. The ribs of this vertebra are broken proximally, so it is not possible to know if they contact the sacricostal yoke. The centra of the caudal-most free dorsal vertebrae and presacral rod do not demonstrate the pronounced lateral compression of *S. languedocensis* and more closely resemble the condition noted in *S. transylvanicus*. Moreover, the transverse processes of the last dorsal vertebra are oriented dorsolaterally at approximately 65° from the horizonal (versus 45° in *S. languedocensis*). Common to both *Struthiosaurus* sp. from Laño and *S. languedocensis*, the centra with the broadest articular faces are located at the seventh and eigth positions along the synsacrum. However, these specimens can be readily distinguished from one-another by the morphology of the sacral ribs (in *Struthiosaurus* sp. the caudal-most sacral ribs have similar dimensions to the preceding ribs, while in *S. languedocensis* the caudal-most sacral ribs are considerably more slender than their cranial counterparts). The ischium of *Struthiosaurus* sp. is slightly curved and superficially resembles that of *S. languedocensis*. However, it exhibits a prominent bulge along the dorsal surface that is absent in *S. languedocensis* (compare Fig. 7A, C). Moreover, the dorsal and ventral borders of the shaft in *S. languedocensis* are nearly parallel with each other. The proximal end of the ischium in *Struthiosaurus* sp. is concave when viewed laterally, similar to the condition noted in *Edmontonia* (Gilmore, 1930) and *Sauropelta* (Ostrom, 1970), unlike the fan-shape ankylosaurids *Talarurus* (Maleev, 1956), *Ankylosaurus* (Coombs, 1979) and *Euoplocephalus* (Coombs, 1986). Owing to the fragmentary nature of the ischium of *Struthiosaurus* sp., it remains unclear if, similar to *S. languedocensis*, the distal process was bulbous. In contrast to both *Struthiosaurus* sp. and *S. languedocensis*, the referred ischium of *S. austriacus* is relatively thinner and tapers distally (Fig. 7B).

DISCUSSION

Within the Ankylosauria, two families are recognised: the Nodosauridae and Ankylosauridae (Coombs, 1978; Sereno, 1986, 1999; Coombs and Maryanska, 1990; Lee, 1996; Hill, 1999; but see Carpenter, 2001 for a different interpretation). Nodosaurids and ankylosaurids can be distinguished from each other by a number of features (Coombs, 1978; Sereno, 1986, 1999; Coombs and Maryanska, 1990). *Struthiosaurus* is considered as a member of the family Nodosauridae (Coombs, 1978; Pereda Suberbiola and Galton, 1994, 2001; Carpenter, 2001).

According to Coombs (1979), the ischium of nodosaurids is characterised by a distinct midshaft flexion whereas the ischium of ankylosaurids is rectilinear or very slightly curved. The ischium of *Struthiosaurus languedocensis* more closely resembles the ankylosaurid condition, with a gentle curvature of the shaft (see Fig. 7). An ischium referable to *S. austriacus* (Pereda Suberbiola and Galton, 2001) also demonstrates a slight ventral curvature, and suggests that such a form is probably autapomorphic for *Struthiosaurus*. However, *S. languedocensis* shares a number of pelvic features typically characterised as representing the nodosaurid condition (see Coombs, 1978, 1979); e.g., the preacetabular process of the ilium is relatively narrow (versus the transversely broad morphology of most ankylosaurids), the postacetabular segment of the ilium is relatively long (versus abbreviated in ankylosaurids), and the body of the pubis is crescentic-shaped (versus a nubbin in ankylosaurids).

Referable material from the same stratigraphic horizon also appears to demonstrate features generally considered characteristic for members of the Nodosauridae (e.g., isolated teeth with distinct cingula, osteoderms lacking an excavation along the ventral surface; see Coombs and Maryanska, 1990). Furthermore, an isolated dermal spine closely resembles that previously described for the cervical half-rings of *Struthiosaurus* (Pereda Suberbiola et al., 1995).

The material of *Struthiosaurus austriacus* from Muthmannsdorf (Austria) contains only very fragmentary pelvic remains and no synsacrum, so the assignment of the Villeveyrac ankylosaur to the genus *Struthiosaurus* is mainly based on comparisons with more complete *Struthiosaurus* specimens from Laño. This material is assigned with centainty to the genus *Struthiosaurus* on the basis of lower jaw, femoral and dermal armour features (Pereda Suberbiola et al., 1995; Pereda Suberbiola, 1999).

All remains of ankylosaurs from the Upper Cretaceous (Campanian–Maastrichtian) of Europe appear to belong to the nodosaurid *Struthiosaurus*. Buffetaut et al. (1997) suggested that members of the Ankylosauridae may also be present in southern France but they did not provide any evidence. Sigé (*in* Garcia et al., 2000) tentatively identified several isolated teeth from the Aix-en-Provence Basin to the Ankylosauridae, but a review of this material shows them to be indistinguishable from those previously described as nodosaurid from other contemporary localities of southern France (Sigé et al., 1997) and the Iberian Peninsula (Pereda Suberbiola, 1999). At present, ankylosaurids remain unknown from the Late Cretaceous of southern Europe.

CONCLUSION

Struthiosaurus languedocensis, sp. nov. from the lower Campanian of Villeveyrac is the first well-known ankylosaur from the Upper Cretaceous of southern France. This species is characterized by an ischium oriented immediately caudal to the acetabulum, almost horizontally in lateral or medial view. *S. languedocensis* can readily distinguished from *S. austriacus* on the basis of ischium morphology, and from *S. transylvanicus* in having laterally compressed distal dorsal centra. *S. languedocensis* shares with *Struthiosaurus* sp. (Laño) a synsacrum composed of ten fused vertebrae, and a relatively wide preacetabular process of the ilium that diverges cranially from the midline. However, both taxa may be discretely identified on the basis of sacral count (four sacrals in *S. languedocensis* versus probably 3 in the Laño synsacrum) and ischium shape (shaft with nearly parallel borders in *S. languedocensis* versus a dorsal bulge in the Laño specimen). These differences could either have a taxonomic significance or be due to individual variation (e.g., sexual dimorphism). *Struthiosaurus* is a member of the Nodosauridae. There is no current evidence of the presence of ankylosaurids in the Late Cretaceous of Europe.

ACKNOWLEDGMENTS

We are grateful for field assistance to various colleagues: Dr J. Sudre, Dr B. Marandat, Dr J. Michaux, Dr N. Bardet, Dr S. Ducrocq, Dr F. Senegas, Dr E. Paradis, Mrs P. Sourouille, also the students of the DEA 1998 promotion's, the SODICAPEI Society, the Villeveyrac Municipality and Mr A. Cabot from the field Museum ''La Plaine des Dinosaures.'' We thank to Prof M. Vianey-Liaud, who initiated this project and who found the specimen, and Mr X. Valentin who has identified the fossiliferous level and prepared the material. The junior author wishes to thank the following people and institutions for access

to specimens in their care: Messrs J. C. Corral and J. Alonso (MCNA, Vitoria-Gasteiz), Miss S. Chapman and Dr A. C. Milner (BMNH, London), and Prof Dr G. Rabeder and Mag Dr K. L. Rauscher (PIUW, Vienna). We are also grateful to Dr N. Bardet and Dr P. Godefroit for useful suggestions and Dr K. Carpenter, Dr P.M. Galton and Dr M.K. Vickaryous for providing critical reviews and improvements of the manuscript. Photographs are by Mr G. Vignard, Mrs I. Mommens (Aix-en-Provence Museum) and the junior author. Infography of the figures is by M. H. Lavina (UMR 8569 du CNRS, MNHN, Paris). This work was supported by funds from the Conseil Régional Languedoc-Roussillon and the Laboratoire de Paléontologie of the Université de Montpellier.

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Received 9 August 2001; accepted 16 January 2002.