

A NEW ELASMOSAURID PLESIOSAUR FROM THE LOWER JURASSIC OF SOUTHERN FRANCE

by NATHALIE BARDET, PASCAL GODEFROIT *and* JACQUES SCIAU

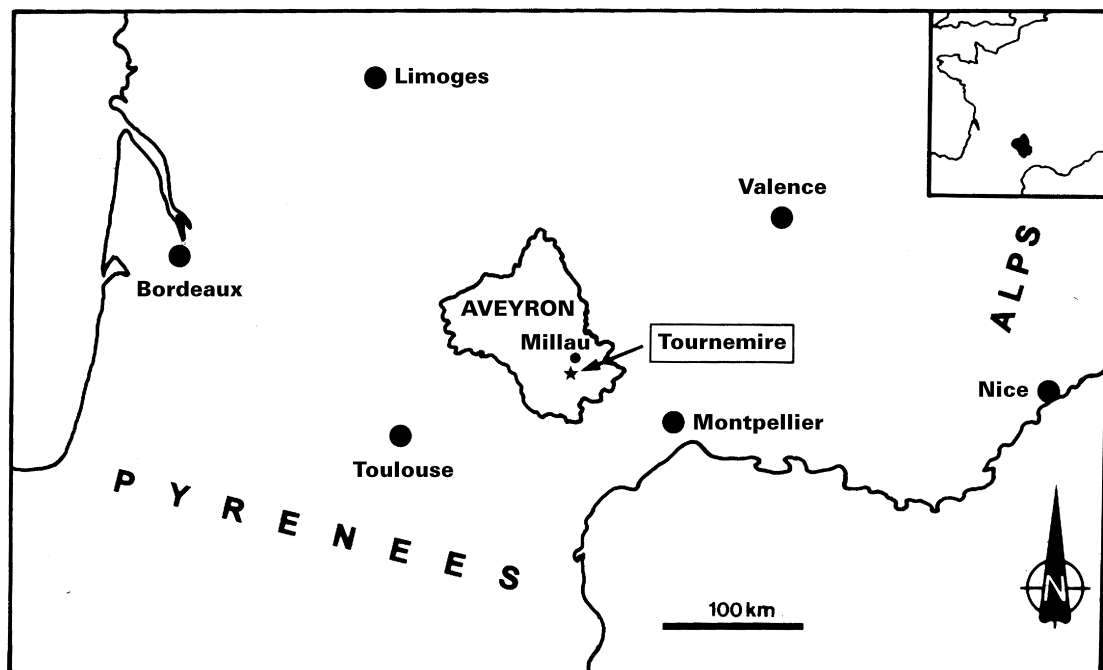
ABSTRACT. *Plesiosaurus tournemirensis* Sciau, Crochet and Mattei, based on a nearly complete skeleton with skull from the Upper Toarcian (Lower Jurassic) of Tournemire (Aveyron Department, southern France), is here redescribed and reinterpreted. Comparisons with other plesiosaurs indicate that it belongs to a new genus, *Occitanosaurus*. *O. tournemirensis* is characterized mainly by its spatulate premaxillae with short facial process, very high postorbital broadly contacting posterior ramus of the maxilla, trapezoidal jugal excluded from orbital margin, orbit diagonally oriented, temporal fenestra with a sigmoidal anterior margin, 43 cervical vertebrae, powerful interclavicle-clavicle complex and coracoids with a pointed protuberance on lateral border and expanded posterolateral cornua. Cranial and cervical vertebra features show that this new genus is undoubtedly a representative of the Elasmosauridae. A preliminary cladistic analysis of long-necked plesiosaurs reveals that, within Elasmosauridae, *Occitanosaurus* is a close relative of *Microcleidus* and *Muraenosaurus*.

THE plesiosaurs form a monophyletic group of large predatory marine reptiles whose stratigraphical range is uppermost Triassic to uppermost Cretaceous (Brown 1981). They vary mainly in the proportions of their head and neck, such that two superfamilies can be distinguished within the Plesiosauria: Plesiosauroidae, with usually small heads and long necks; and Pliosauroidae, with larger heads and shorter necks (Welles 1943; Brown 1981). This dichotomy is clear in Late Jurassic and Cretaceous forms, but mosaic evolution seems to characterize the early radiation of the group during the Early Jurassic.

Complete skeletons of plesiosaurs are abundant in the Hettangian–Sinemurian of Dorset, England. Some exceptionally well preserved specimens have also been discovered in the Toarcian of the Baden-Württemberg district, Germany. Most of the specimens were unearthed during the last century and at the beginning of this century. The bulk of the descriptions also dates from this time. Recent studies on Liassic plesiosaurs include revisions of the pliosauroids *Rhomaleosaurus zetlandicus* (Phillips, 1854) by Taylor (1992), *Rhomaleosaurus megacephalus* (Stutchbury, 1846) by Cruickshank (1994) and *Rhomaleosaurus thorntoni* (Andrews, 1922) by Cruickshank (1996) as well as of the plesiosauroids *Thalassiodracon hawkinsi* (Owen, 1838) by Storrs and Taylor (1996) and *Plesiosaurus dolichodeirus* Conybeare, 1824 by Storrs (1997).

In 1986, the nearly complete skeleton of a plesiosaur was discovered in the vicinity of Tournemire (Aveyron Department, southern France) (Text-fig. 1) and was subsequently excavated by the palaeontological team of the Musée Municipal de Millau. The skeleton was found in a marly layer belonging to the lower part of the *Aalensis* Zone (Upper Toarcian, Lower Jurassic). A preliminary description was published by Sciau *et al.* (1990) and the fossil was named *Plesiosaurus tournemirensis* Sciau, Crochet and Mattei, 1990. Recently, Storrs (1997) concluded that this species was probably another example of the German taxon, *P. guilelmiimperatoris* Dames, 1895. A more careful examination of the specimen leads to a different interpretation of its taxonomic status, as discussed in the present paper.

Institutional abbreviations. CMNH, Colorado Museum of Natural History, Denver; GPIT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen; MMM, Musée Municipal de Millau; NHM, The Natural History Museum, London; SMNS, Staatliches Museum für Naturkunde, Stuttgart; UCMP, University of California Museum of Paleontology, Berkeley.



TEXT-FIG. 1. Geographical location of site yielding MMM J. T. 86-100.

SYSTEMATIC PALAEOLOGY

Superorder SAUROPTERYGIA Owen, 1860

Order PLESIOSAURIA de Blainville, 1835

Superfamily PLESIOSAUROIDEA Gray, 1825

Family ELASMOSAURIDAE Cope, 1869

Type genus. *Elasmosaurus* Cope, 1868.

Emended diagnosis. Weakly excavated ventral cheek margin; palate without anterior pterygoid vacuities; platycoelous vertebral articular surfaces; more than 40 cervical vertebrae; cervical centra longer than high; lateral keel in mid-anterior cervical vertebrae. For a characterization of elasmosaurids see Brown (1993).

Genus OCCITANOSAURUS gen. nov.

Derivation of name. From *Occitania*, the area where the Occitan language is spoken (currently includes most of southern France, Val d'Aran of Spain and several Piedmont valleys of Italy) and *Sauros* (Greek): lizard.

Type species. *Plesiosaurus tournemirensis* Sciau, Crochet and Mattei, 1990

Diagnosis. As for type and only species of the genus, *Occitanosaurus tournemirensis* (Sciau, Crochet and Mattei, 1990).

Occitanosaurus tournemirensis (Sciau, Crochet and Mattei, 1990)

(Plates 1–4; Text-figures 1–5)

- 1990 *Plesiosaurus tournemirensis* Sciau, Crochet and Mattei, p. 115.
 1997 cf. *Plesiosaurus guilelmiimperatoris* Dames, 1895; Storrs, p. 146.

Holotype. MMM J. T. 86-100, Musée Municipal de Millau, Aveyron, an almost complete, partially disarticulated skeleton (193 bones) including the skull, vertebral series from the atlas-axis to the sacrum (43 cervical, three pectoral, 16 dorsal and four sacral vertebrae), associated ribs, some gastralia, complete pectoral girdle (interclavicle-clavicle complex, scapulae, coracoids), pelvic girdle (ilia, ischia and pubes), right forelimb (humerus, radius, ulna, carpal and metacarpal elements, phalanges) and both hindlimbs (femora, tibiae, fibulae, tarsal and metatarsal elements, phalanges).

Type locality. Tournemire (43°56'25''N, 3°1'14''E), Aveyron Department, southern France (Text-fig. 1), Marnes feuilletées, *Aalensis* Zone, *Pleydellia celtica* Subzone, Upper Toarcian, Lower Jurassic (Fauré and Cubaynes 1983; Mennessier *et al.* 1984).

Emended diagnosis. Small elasmosaurid *c.* 4 m long; dorso-cephalic index = 25.6; spatulate premaxillae, separated from maxillae by a well-marked constriction and with a short facial process ending just behind the external nares; maxillae constricted under the middle of the orbits and excluded from internal nares by palatine-vomer contact; small teeth around the premaxilla-maxilla suture; well-developed triangular prefrontals excluding frontals from external nares; frontals with narrow anterior premaxillary process separating the prefrontals; postorbitals very high, broadly contacting the posterior ramus of the maxillae; trapezoidal jugals excluded from the orbital margin by postorbital-maxilla contact; orbits diagonally directed; parietals without pineal foramen; temporal fenestrae with a sigmoidal anterior margin; vertebral formula: 43 cervical, three pectoral, 16 dorsal and four sacral vertebrae; cervico-dorsal index = 191; powerful interclavicle-clavicle complex with a notched wide transverse anterior plate and a narrow longitudinal posterior peg contacting coracoids; coracoids with lateral border bearing a pointed protuberance and expanded posterolateral cornua.

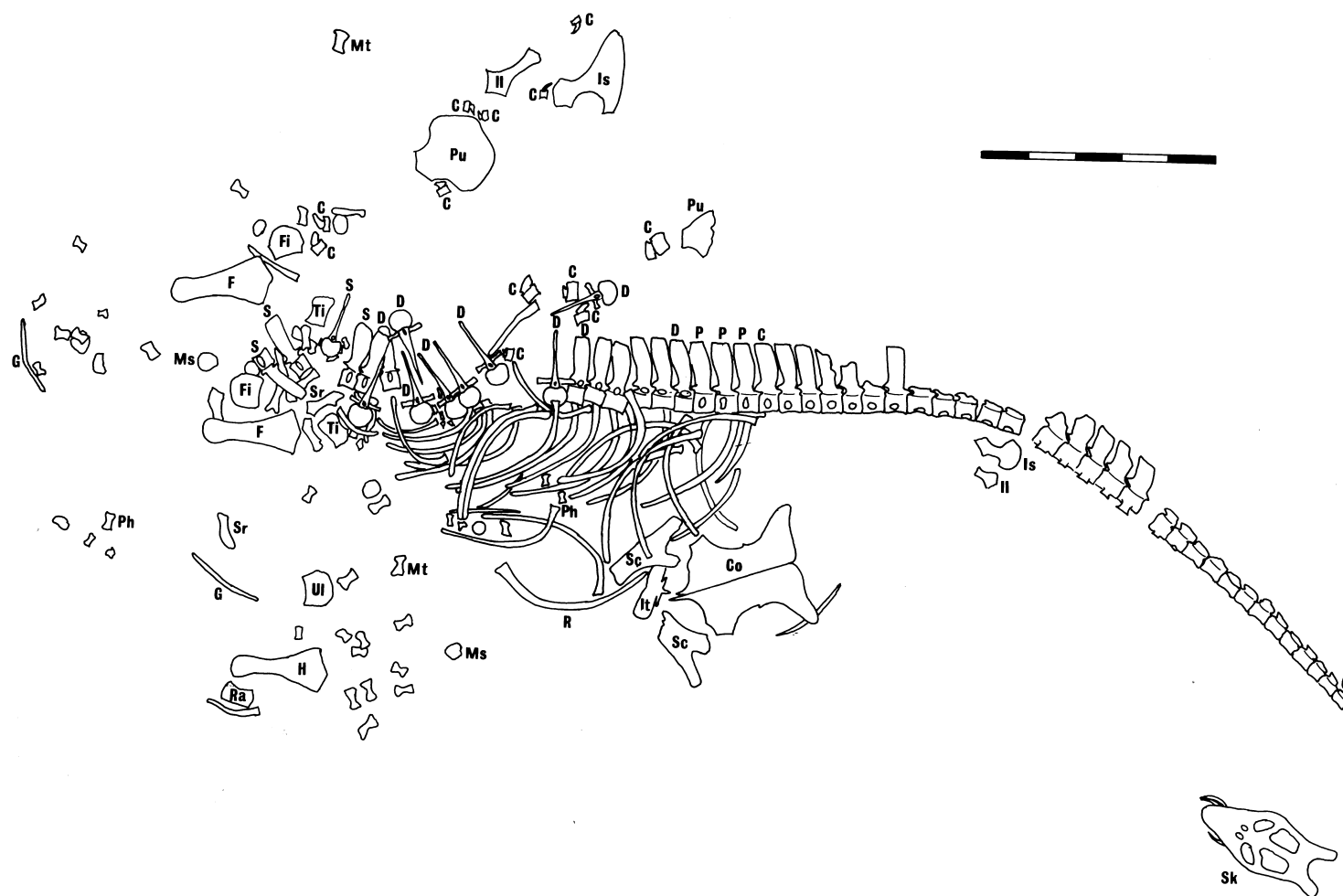
Remarks. *Occitanosaurus* shows many plesiomorphic characters when compared with more derived elasmosaurids. For example, the basicranium is not completely covered by the pterygoids, the cervical centra are not 'dumb-bell'-shaped, the cervical ribs are dicranopleurous, the humerus is not markedly enlarged distally, the epipodials remain proportionally long, the *spatium interosseum* is developed, the ulna is crescentic, the scapulae do not meet in the midline and are excluded from the pectoral bar by the interclavicle-clavicle complex, the intercoracoid foramen is absent and the femur is as long as the humerus.

DESCRIPTION

MMM J. T. 86-100 is a partially disarticulated and nearly complete skeleton (Text-fig. 2). One-hundred-and-ninety-three bones were discovered, but the mandible, most of the gastralia, the caudal vertebrae and some paddle elements are missing. Most of the cervical vertebrae and the anterior dorsals are articulated. The skull, the posterior dorsals and sacrals, the ribs, the pectoral girdle and the hindlimbs lie close to their original position. In contrast, the most anterior cervicals, the forelimb and the pelvic girdle are displaced. The paddles are completely disarticulated.

Size. The size of the animal can be estimated by summing the lengths of the skull and vertebrae. The missing tail was probably composed of 25 vertebrae (average number in plesiosaurs) and was comparable in length to the trunk (estimation based on *Cryptoclidus eurymerus* (Phillips, 1871), *Muraenosaurus leedsii* Seeley, 1874a and *Hydrotherosaurus alexandrae* Welles, 1943). *Occitanosaurus* was thus *c.* 3.90 m long, the same value obtained by Sciau *et al.* (1990).

Ontogenetic stage. The presence of neural arches fused to the vertebral centra, cervical centra with well-marked longitudinal crests and posterolateral cornua on the coracoids indicates that this specimen was an adult (*sensu* Brown



TEXT-FIG. 2. Plan view of the Tournemire outcrop showing partially disarticulated specimen of *Occitanosaurus tournemirensis* (MMM J. T. 86-100). Abbreviations: C, cervical vertebra; Co, coracoid; D, dorsal vertebra; F, femur; Fi, fibula; G, gastralia; H, humerus; Il, ilium; Is, ischium; It, interclavicle-clavicle complex; Ms, mesopodial; Mt, metapodial; Pu, pubis; R, rib; Ra, radius; S, sacral vertebra; Sc, scapula; Sk, skull; Sr, sacral rib; Ti, tibia; Ul, ulna. Scale bar represents 0.5 m.

TABLE 1. Skeletal measurements (except axial skeleton – see Table 2) of *Occitanosaurus tournemirensis* (Sciau, Crochet and Mattei, 1990) (MMM J. T. 86-100).

Length of the skull	250 mm
Length of the orbit (r)	56 mm
Length of the temporal fenestra (r)	69 mm
Length of the snout	100 mm
Length of the humerus (l)	208 mm
Antero-posterior diameter of the humeral head (l)	51 mm
Dorso-ventral diameter of the humeral head (l)	47 mm
Antero-posterior diameter of the humeral diaphysis (l)	46 mm
Antero-posterior diameter of the distal epiphysis of the humerus (l)	91 mm
Dorso-ventral diameter of the distal epiphysis of the humerus (l)	24 mm
Length of the femur (l)	208 mm
Antero-posterior diameter of the femoral head (l)	56 mm
Dorso-ventral diameter of the femoral head (l)	57 mm
Antero-posterior diameter of the femoral diaphysis (l)	39 mm
Antero-posterior diameter of the distal epiphysis of the femur (l)	98.5 mm
Dorso-ventral diameter of the distal epiphysis of the femur (l)	28.5 mm
Length of the coracoid (r)	285 mm
Length of the post glenoid region of the coracoid (r)	188 mm
Interglenoid width of the joined coracoids	450 mm
Width across the cornua of the joined coracoids	490 mm
Length of the scapula (r)	190 mm
Width of the scapula (r)	105 mm
Width of the interclavicle	132 mm
Length of the ilium (r)	140 mm
Antero-posterior width of the proximal head of the ilium (r)	65 mm
Antero-posterior width of the distal head of the ilium (r)	49 mm
Antero-posterior diameter of the pubis (r)	170 mm
Medio-lateral diameter of the pubis (r)	176 mm
Length of the ischium (r)	158 mm
Width of the ischium	137 mm
Diameter of the pelvic fenestra	55 mm

1981). On the other hand, some characters remain typically juvenile (*sensu* Brown 1981), i.e. most of the cervical ribs are not fused to the lateral apophysis of the centra, the articular surfaces of the centra are not rough and, except for the interclavicle and clavicles, none of the girdle elements is fused together. It can therefore be concluded that this specimen was probably a 'subadult'.

Skull and dentition (Text-fig. 3; Pl. 1; Table 1)

The skull is nearly complete, but somewhat dorso-ventrally crushed. It is 295 mm long and 130 mm wide. Because of the post-mortem crushing, the presumed length of the skull before deformation is c. 250 mm and the width c. 110 mm. The dorso-cephalic index (ratio of skull length / trunk length $\times 100$; Sollas 1881) is 25.6.

Premaxillae. The premaxillae form a short spatulate muzzle. In dorsal view, they unite in a closed medial suture along their whole length. They are ornamented by numerous vascular foramina and by radiated striations relating to the deep sockets for the implantation of the enlarged premaxillary teeth. Posteriorly, the premaxillae form a short and very narrow median bar extending between the external nares and meeting the anterior process of the frontals. The contact with the maxillae is marked by a constriction of the muzzle. The premaxillae bear five dental alveoli of which the first is the smallest and is positioned close to the midline; the third and fourth teeth are by far the largest and the fifth is distinctly smaller than the preceding three. Medial to these functional alveoli, five smaller ones are present for replacement teeth. The palatal plates of the premaxillae are joined in a closed suture along their anterior third; posteriorly, they are separated by the anterior portion of the vomers.

Maxillae. The maxillae are very long and narrow in ventral view. They take part in the anterior margin of the temporal fenestrae but do not participate in the lateral margin of the internal nares. They are pierced by about 12 dental alveoli: the first two are distinctly smaller than the following three; the posterior alveoli progressively decrease in size and are set in a more medial position. Alveoli for replacement teeth can be observed in the anterior portion of the maxillae. The dorsal surfaces of the maxillae are broad and convex with a constriction under the median part of the orbit. They form the anterolateral margin of the external nares and the lateral margin of the orbits. The posterior contact with the postorbitals is very extensive. The anterior suture with the premaxillae is straight and bends anteroventrally, whereas the suture with jugal is very short and vertical.

External nares. The external nares are small and have the outline of an apple pip. They are close to each other and are only separated by the narrow facial processes of the premaxillae. They are bordered by premaxillae, maxillae and prefrontals.

Prefrontals. The prefrontals are well-developed and distinct from the maxillae. They are sub-triangular and separated from each other by the narrow anterior processes of the frontals. They participate in the posterolateral margin of the external nares and in the anterior margin of the orbits. They articulate with maxillae (straight suture) and with the frontals ('V'-shaped suture).

Frontals. The frontals form the medial margin of the orbits. They form a very narrow medial anterior process, separating the prefrontals and contacting the facial processes of the premaxillae at the level of the posterior corner of the external nares. In dorsal view, they do not participate in the posterior margin of these apertures, but are excluded from them by the medial expansion of the prefrontals. Posteriorly, they contact the parietals in an interdigitating suture.

Postfrontals. The postfrontals are short and robust quadrangular bones. They participate in the posteromedial margin of the orbits and in the anteromedial margin of the temporal fenestrae. They contact the frontals and the parietals medially and the postorbitals laterally. The suture with the frontal is wavy and that with the parietal and postorbital is straight.

Orbits. The orbits are not very large, are ovoid in shape and dorsolaterally oriented. There is no evidence of a sclerotic ring.

Postorbitals. The postorbitals are roughly triangular. Dorsally, they contact the postfrontals and participate in the anterolateral margin of the temporal fenestrae and in the posterolateral margins of the orbits. They articulate posteriorly with the squamosals and anteriorly with the maxillae in very reduced sutures. Ventrally, they unite with the jugal in a long and straight suture. The postorbitals are excluded from the parietals by the postfrontals.

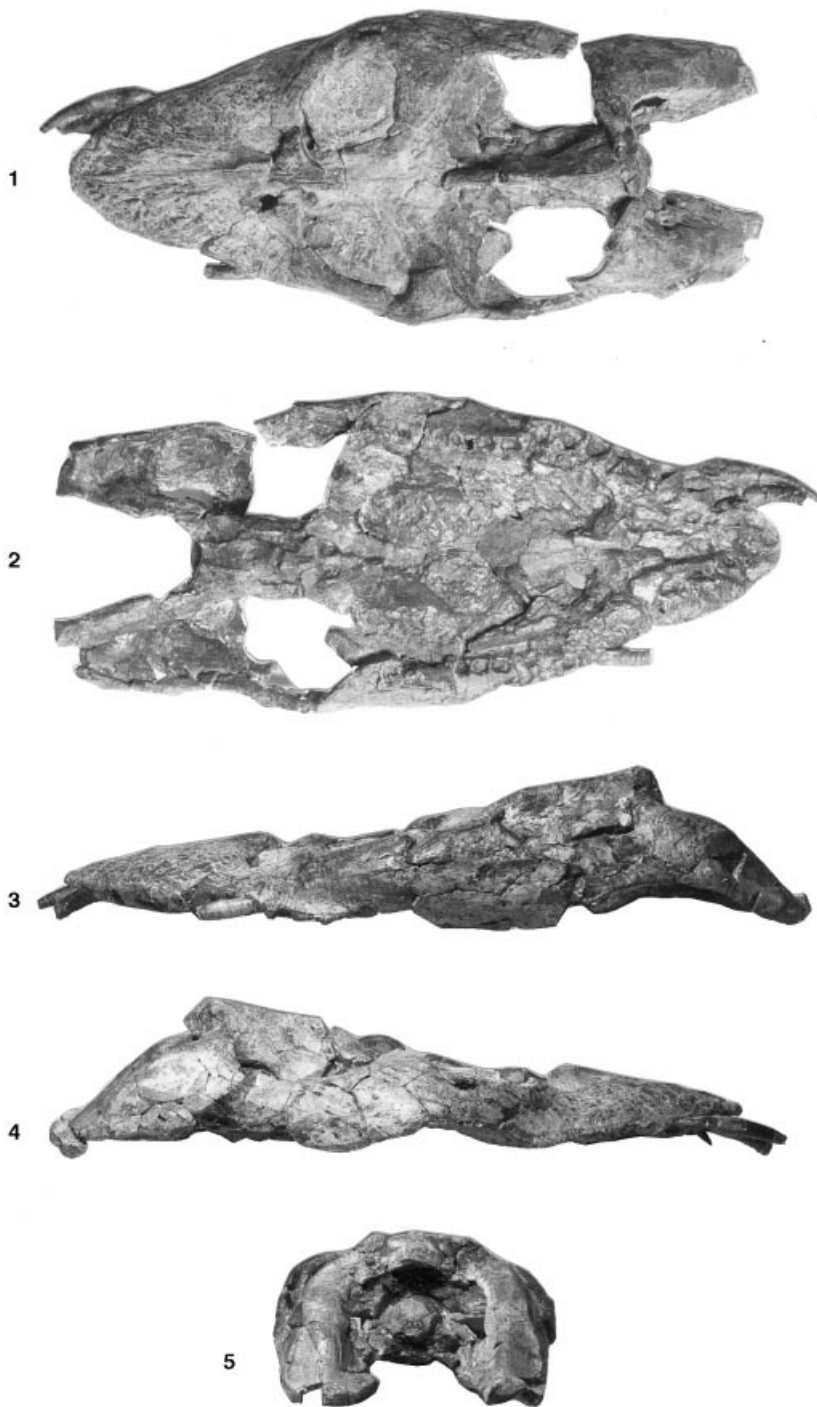
Jugals. The jugals are trapezoidal with a horizontal long axis. Their dorsal border contacts the postorbital in a straight suture, their anterior border contacts the maxilla and their posterior border the squamosal. They are excluded both from the orbit by the postorbital-maxilla contact and from the supratemporal fenestra by postorbital-squamosal contact. The ventral margin does not contact the maxilla but takes part in the anterior margin of the infratemporal fossa.

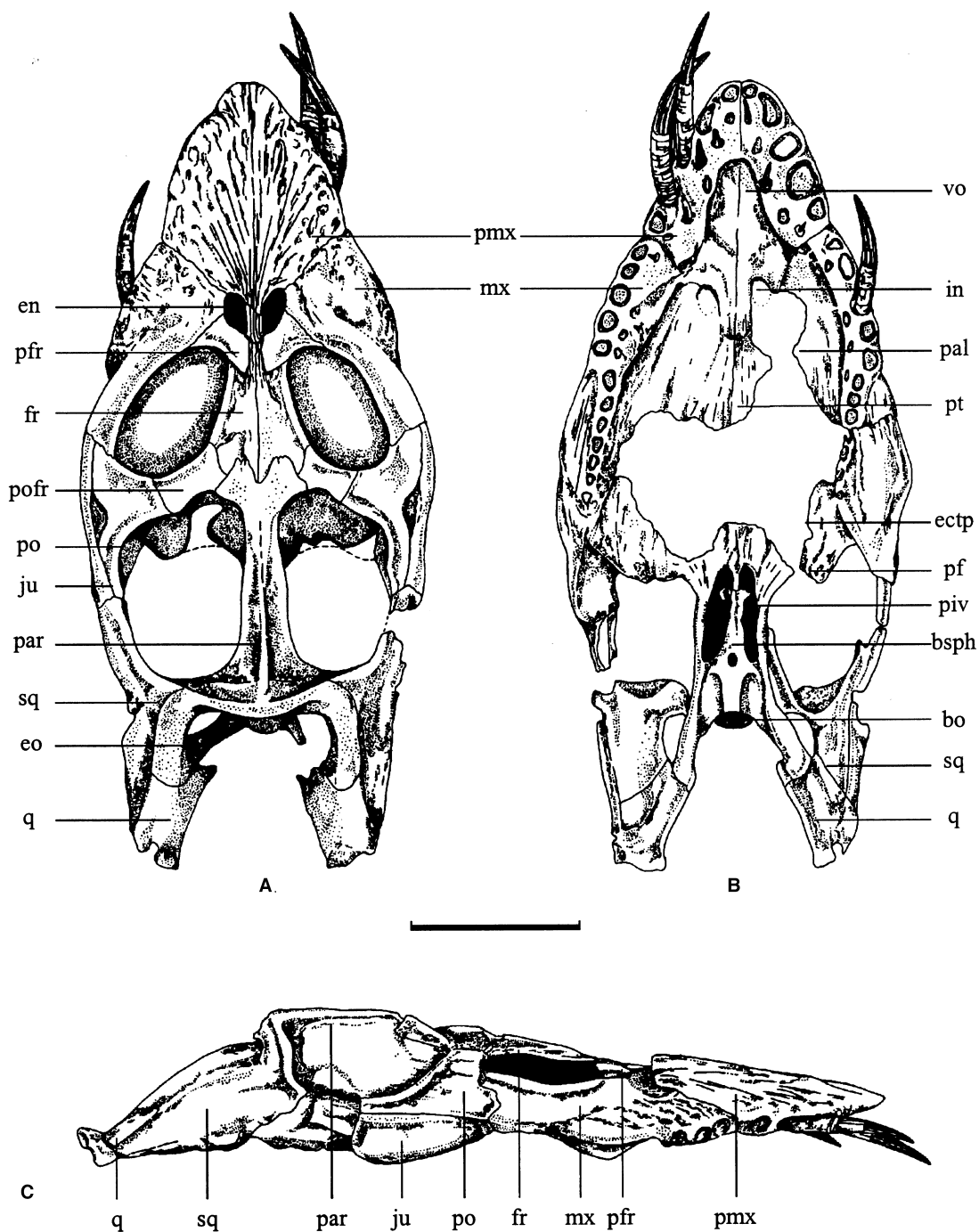
Parietals. The parietals are completely fused, forming a narrow intertemporal bar. In the midline of the skull, they form a salient sagittal crest, flanked by deep excavations for the temporal musculature. There is no trace of a pineal foramen. The parietals broaden in front of the temporal fenestrae, contacting the frontals and the postfrontals. Posteriorly, the parietals appear to expand into two lateral branches which are completely fused with the squamosals. They form the whole mesial margin of the upper temporal fenestrae.

Squamosals. The squamosals are typical triradiate bones composed of a medial, an anterior and a posteroventral ramus. The medial bar made by the fusion of the squamosals and the parietals forms the posterior margin of the supratemporal

EXPLANATION OF PLATE 1

Figs 1–5. *Occitanosaurus tournemirensis* (Sciau, Crochet and Mattei, 1990); holotype (MMM J. T. 86-100); Upper Toarcian, Tournemire, France; skull and dentition. 1, dorsal view. 2, ventral view. 3, left lateral view. 4, right lateral view. 5, occipital view. All $\times 0.33$.





TEXT-FIG. 3. Interpretative drawing of the skull of *Occitanosaurus tournemirensis* (MMM J. T. 86-100). A, dorsal view; B, ventral view; C, right lateral view. Abbreviations: bo, basioccipital; bsph, basisphenoid; ectp, ectopterygoid; en, external nares; eo, exoccipital-opisthotic; fr, frontal; in, internal nares; ju, jugal; mx, maxilla; pal, palatine; par, parietal; pf, pterygoid flange; pfr, prefrontal; piv, posterior interpterygoid vacuity; pmx, premaxilla; po, postorbital; pofr, postfrontal; pt, pterygoid; q, quadrate; sq, squamosal; vo, vomer. Scale bar represents 50 mm.

fenestrae. This posterior bar bears a salient occipital crest, perpendicular to the sagittal crest of the parietals. The anterior ramus of the squamosal forms the posterolateral margin of the supratemporal fenestra, contacting the postorbital and the jugal anteriorly. The posteroventral ramus is wide and slopes steeply posteroventrally. Its ventral border is concave, forming the dorsal margin of a well-developed infratemporal fossa. The occipital crest of the posterior bar of the supratemporal fenestra continues posterolaterally on the dorsal border of the posteroventral ramus. Ventrally, the squamosal contacts the quadrate and pterygoid.

Supratemporal fenestrae. The supratemporal fenestrae are proportionally large compared with the orbits, subtrapezoidal and about 1.5 times as long as wide. In dorsal view, they bear a characteristic anterior sigmoidal margin.

Quadrates. The quadrates are joined to the ventral ramus of the squamosals, forming a pair of broad posterior pillars on the back of the skull. The squamosal-quadrate suture forms an inverted 'V'. The articular facets are posteriorly and somewhat laterally situated; they are strongly convex anteroposteriorly as the lateral condyle is located in front of the medial one. Medially, the quadrates contact the posterior lamina of the pterygoids.

Basioccipital, basisphenoid and parasphenoid. The basioccipital and the basisphenoid are completely fused together and antero-posteriorly elongated. The occipital condyle is prominent and well-rounded so that, in spite of the absence of the exoccipitals, it can nevertheless be deduced that the condyle was solely formed by the basioccipital. The pterygoid processes are large and posterolaterally oblique. They contact the posterior lamina of the pterygoids along their full length. Two longitudinal ridges run along the ventral surface of the basioccipital, from the occipital condyle to the presumed junction of the basioccipital and the basisphenoid. A median foramen, on the anterior part of the bone, can be interpreted as the ventral opening of the carotid foramen. The parasphenoid is very narrow, short and completely fused with the basisphenoid; it is keeled between the two posterior interpterygoid vacuities.

Exoccipital and opisthotic. The fused exoccipital-opisthotic is represented only by a narrow but robust pillar between the basioccipital and the quadrate, on the right side of the skull.

Supraoccipital. The supraoccipital is too fragmentary to be described.

Pterygoids. The pterygoids are formed by an anterior, a posterior and a lateral ramus. The anterior ramus is thin, triangular and very damaged; anteriorly it contacts the vomer, laterally the palatine and medially the other pterygoid without an anterior interpterygoid vacuity. The posterior ramus is very narrow and forms anteriorly the lateral margin of the posterior interpterygoid vacuity, then contacts the pterygoid process of the basioccipital; it seems to fold under the basicranium but does not cover it completely in ventral view. Backwards, it curves outwards and its posterior margin unites with the medial edge of the quadrate. The lateral ramus is not very expanded and contacts the ectopterygoid.

Ectopterygoids. The ectopterygoids are small bones uniting the lateral rami of the pterygoids with the posteromedial borders of the maxilla. They bear very weak pterygoid flanges.

Palatines. The partially preserved palatines form thin and flat plates of bone. They contact the maxillae laterally, the pterygoids medially, the ectopterygoids posteriorly and the vomers anteriorly.

Vomers. The vomers form the anterior part of the palate. They are formed by a sub-triangular anterior portion, which is thrust between the premaxillae and which contacts the maxillae, and a narrow posterior ramus, which enters between the anterior part of the palatines and meets the anterior angle of the pterygoids.

Internal nares. The internal nares open medially between vomers and palatines at the same level as the external ones, i.e. in front of the third maxillary tooth.

Teeth. Three teeth are preserved *in situ*, two on the right premaxilla and one on the left maxilla. They are long (31–54 mm) and rounded in cross section (maximum diameter between 6.7 mm and 9.4 mm). The crowns are ornamented by numerous fine longitudinal striations. The apex is worn so that the ornament tends to be erased distally. The crown represents almost one-third of the total height of each tooth. The teeth are irregular in size and the alveoli around the premaxilla-maxilla suture are notably smaller than the others.

TABLE 2. Axial skeleton measurements of *Occitanosaurus tournemirensis* (Sciau, Crochet and Mattei, 1990) (MMM J. T. 86-100), in millimetres.

No.	Length	Width	Height	No.	Length	Width	Height
Atlas-axis	26	23.5	17	P1	47	61	44
C1	22	25	17	P2	44.5	61	45
C2	24.5	28	18	P3	47	57	44.5
C3	27.5	29	19	D1	46	55.5	44.5
C4	28.5	29	18.5	D2	48	52.5	46.5
C5	30	30	20.5	D3	45	49	48
C6	32	31	21.5	D4	47.5	47.5	45
C7	32	32.5	21	D5	46.5	48	46
C8	35	34	21	D6	45	47	51
C9	38	33	22	D7	45.5	49	46
C10	38	34	23	D8	42	50	47
C11	38.5	37	10	D9	42	51	46
C12	41	34.5	23	D10	42	54	44.5
C13	44	36	25.5	D11	42.5	52.5	44
C14	44	37	26	D12	39.5	54	42
C15	45	38	29.5	D13	38	52	40
C16	45	38	27	D14	41	46	37
C17	48.5	39.5	30	D15	38.5	49.5	41
C18	48.5	42	30	D16	37.5	45	38
C19	50	43	30.5	S1	39	46	39.5
C20	53	43	33.5	S2	37.5	45	36.5
C21	50	48	35	S3	38.5	44	34
C22	54	44	36	S4	35	46.5	35
C23	55	46	35				
C24	54	47	37				
C25	54	47	38.5				
C26	54.5	50.5	35.5				
C27	56.5	52	36.5				
C28	56	53.5	38.5				
C29	56.5	52.5	39				
C30	56	55.5	39				
C31	55	55	40				
C32	52	55	40				
C33	54.5	55	40				
C34	52	54.5	42				
C35	50	55	42.5				
C36	49	55	42				
C37	50.5	55.5	40.5				
C38	49	58	40.5				
C39	49	57	42				
C40	45.5	57	42				
C41	44	60	41				

Others elements. Sciau *et al.* (1990) mentioned the absence of nasal and lachrymal bones as characteristic for the new species *Plesiosaurus tournemirensis*. However, the absence of a nasal bone is a diagnostic feature of the Plesiosauria (Brown 1981).

Axial skeleton (Pl. 2; Table 2)

The vertebral column appears to be complete from the atlas-axis to the last sacral vertebra. It includes 66 vertebrae, i.e. 43 cervicals, three pectorals (*sensu* Seeley 1874a and Brown 1981), 16 dorsals and four sacrals. Most of the cervical

and dorsal vertebrae were found in articulation. The entire caudal series is missing. Sciau *et al.* (1990) previously described 12 caudal vertebrae in *O. tournemirensis*. These are here considered to be the anteriormost cervical vertebrae, displaced and disarticulated during burial from their natural position relative to the trunk region. These vertebrae fit very well with the rest of the cervical series so that it can reasonably be assumed that the neck is complete. The articular surfaces of all the vertebrae are of platycoelous type. The neural arches are always fused to the centra. The cervico-dorsal index (ratio of neck length / trunk length $\times 100$; Sollas 1881) is 191.

Cervical vertebrae. The atlas-axis complex (Pl. 2, fig. 1) is closely similar to that of a specimen of *Muraenosaurus leedsii* Seeley, 1874a from the Callovian of England described in detail by Andrews (1910, fig. 49). The length of the neck (1.86 m) has been estimated by summing the length of each cervical vertebra. The size of the cervical vertebrae increases regularly towards the back of the neck. The centra are relatively elongated with their length always exceeding their height and, from the sixth to the 19th vertebra, their width (see Table 2). The articular surfaces are elliptical (Pl. 2, figs 4, 6) and not grooved ventrally as in Late Cretaceous advanced elasmosaurs ('dumb-bell'-shaped, see Welles 1943). The margins form an abrupt angle with the centrum sides. From the seventh to the 24th cervical vertebra, a longitudinal crest, or lateral keel, is developed on the sides of the centrum (Pl. 2, fig. 3) and is probably linked to the insertion of an aponeurosis (Brown 1981). This longitudinal crest is split into two from the 14th to the 18th cervical vertebra and the lower keel is longer than the upper one. The ventral nutritive paired foramina are very close together on the anteriormost vertebrae and progressively migrate laterally on most posterior vertebrae. The ventral surface is always convex. The lateral apophyses, set very low on the anteriormost centra, progressively migrate dorsally. The diapophysis and the parapophysis are clearly differentiated from the 35th to the 39th cervical vertebra. The neural arches form a posteriorly inclined thin plate of bone which is low and triangular in the anterior cervicals (Pl. 2, fig. 2), but becomes higher and rectangular in the posterior ones (Pl. 2, fig. 5). The pre- and postzygapophyses are small and oriented in the same horizontal plane.

Pectoral vertebrae. The pectoral vertebrae (Pl. 2, figs 7–8) are large and characterized by lateral apophyses articulating with both the centrum and the neural arch. Their articular surfaces are more rounded than those of the cervical vertebrae. The neural arch forms a high, rectangular and almost vertical plate of bone in the pectoral, dorsal and sacral vertebrae.

Dorsal vertebrae. The dorsal vertebrae (Pl. 2, figs 9–10) are characterized by lateral apophyses located on the neural arch. Their articular faces are well-rounded and the nutritive foramina are well-spaced, located up on the lateral surfaces of the centra.

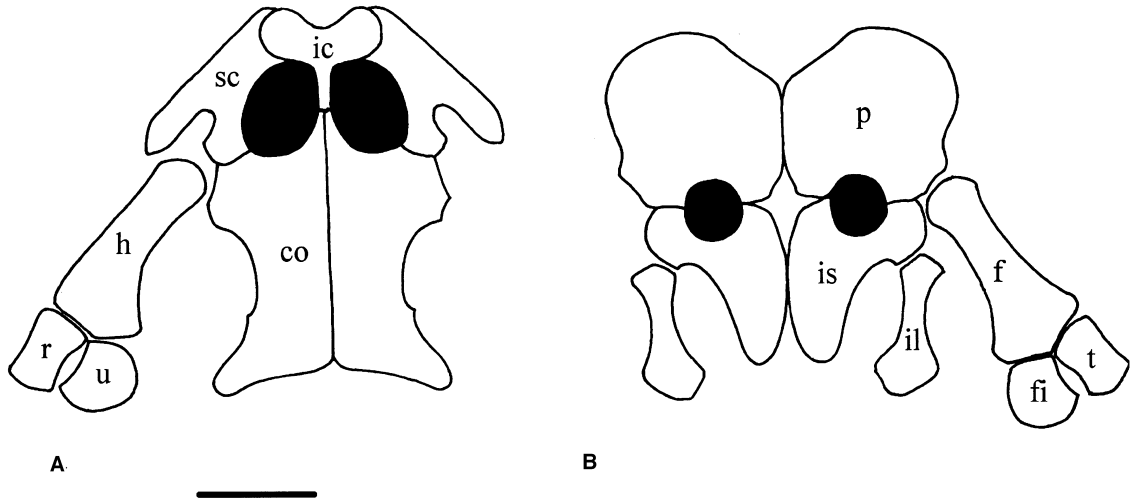
Sacral vertebrae. There are four sacral vertebrae (Pl. 2, figs 11–12), as is typical for plesiosaurs (Brown 1981). Their centra bear large, kidney-shaped insertion zones which occupy most of the lateral surfaces for the modified sacral ribs. The articular facets are rounded.

Ribs and gastralia. The ribs of plesiosaurs were described in detail by Andrews (1910). Only few cervical ribs are preserved in *Occitanosaurus tournemirensis*. The anteriormost ones are typically hatchet-shaped, with a prominent anterior flange. As the diapophysis and the parapophysis are separated on the posterior cervical centra, the ribs are double-headed, with a distinct tuberculum and capitulum. The dorsal ribs (Pl. 2, fig. 13) are single-headed, long, robust and curved, with a flat and enlarged articular head. The sacral ribs (Pl. 2, fig. 16) are short, massive and bear, on their anterior and posterior sides, well-developed facets for contact with the adjacent sacral ribs. The distal end forms a continuous articular surface for the ilium. Very few gastralia are preserved (Pl. 2, fig. 14). Their central part has a typical boomerang shape with a wide angle between the two branches.

Girdles (Text-fig. 4; Pls 3–4; Table 1)

The complete pectoral girdle is preserved close to its natural position. Apart from the clavicles and interclavicle which are apparently fused together, the other elements remain separated. The pelvic girdle is incomplete, displaced and its elements are disarticulated. Only one ischium and one ilium were found. Both pubes are preserved but one is incomplete.

Interclavicle-clavicle complex. The interclavicle and clavicles are apparently fused together without any visible suture, as in *Muraenosaurus leedsii* (Brown 1981, fig. 21). The complex (Text-fig. 4A; Pl. 3, figs 1–2) is strongly developed and is probably composed of a median thick elongated interclavicle flanked with two lateral thin ala corresponding to the clavicles. The anterior portion of the supposed interclavicle is thick and forms a ventral promontorium. Its anterior



TEXT-FIG. 4. Interpretative drawings in dorsal view of the pectoral girdle and forelimb (A) and of the pelvic girdle and hindlimb (B) of *Occitanosaurus tournemirensis* (MMM J. T. 86-100). Abbreviations: co, coracoid; f, femur; fi, fibula; h, humerus; ic, interclavicle-clavicles; il, ilium; is, ischium; p, pubis; r, radius; sc, scapula; t, tibia; u, ulna. Scale bar represents 100 mm.

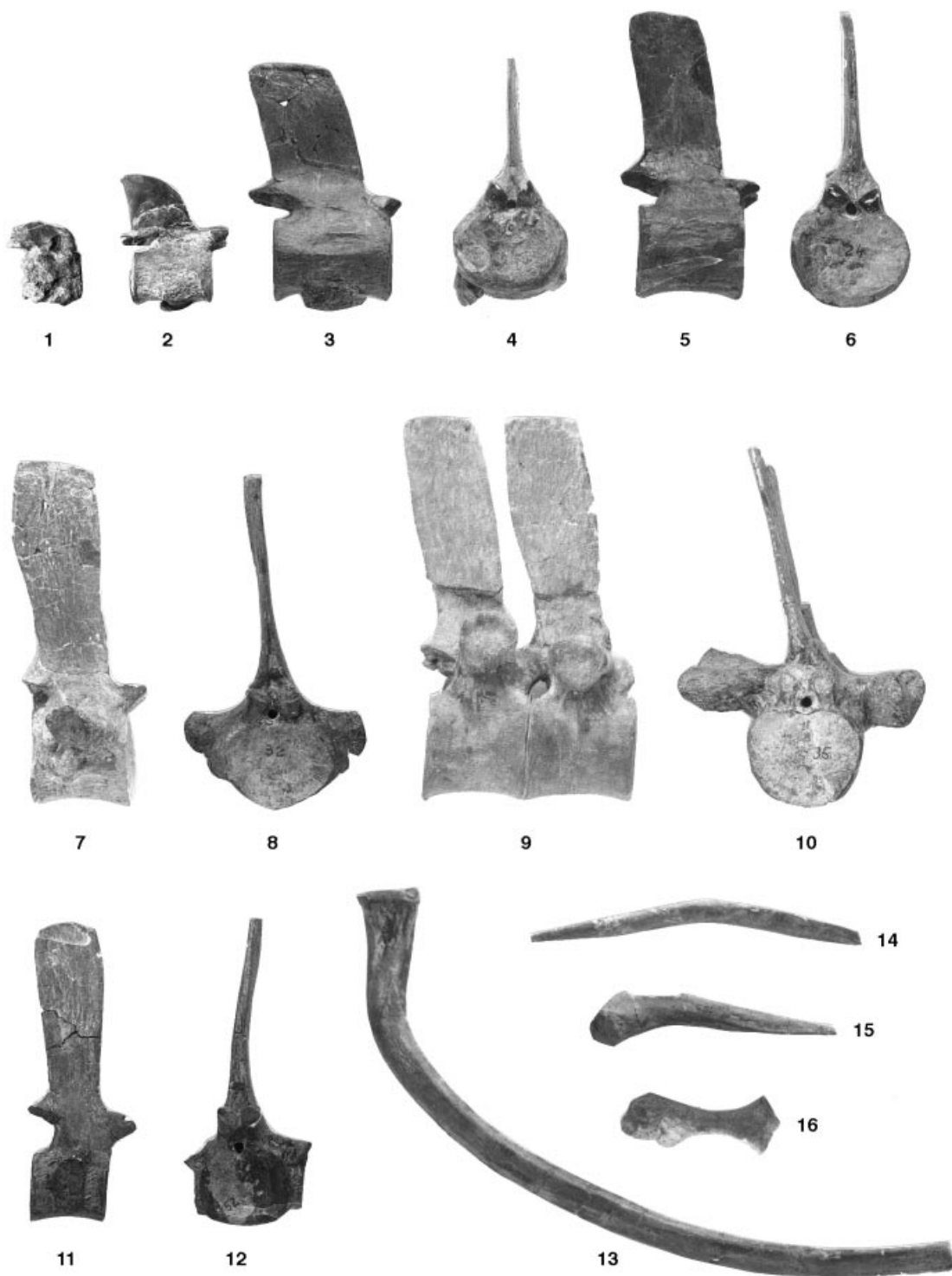
margin is deeply notched anteriorly and the bone is particularly smooth at this level. The posterior part of the interclavicle is peg-shaped. It is triangular in cross section and bears along its full length a thin ventral crest asymmetrically curved towards the right side, forming a gutter. The supposed clavicles form thin alae with ragged margins. Ventrally, their posterior halves exhibit large elliptical contact areas for the ventral ramus of the scapulae. Posteriorly, the ala terminate in small and triangular wings.

Scapula. The scapula (Text-fig. 4A; Pl. 3, figs 3–4) is, as usual in plesiosaurs, a triradiate bone. The posterior ramus is short, thick and expanded at its extremity, where it bears two facets which together form an angle of about 90°. The anterolateral one (glenoid facet) is distinctly smaller than the posterior one (coracoid facet). The shaft of the posterior ramus is triangular in cross section and bears two well-developed medial crests, one ventral and one dorsal, delimiting a large and flat medial surface which forms the anterolateral margin of the pectoral fenestration. The dorsal ramus is thin, but relatively long and broad. Its anterior and posterior borders are parallel and its upper suprascapular border is very rough, indicating the presence of a cartilaginous cap. A rough gutter runs along the anterior border of its dorsal side, indicating a muscle insertion area. The ventral ramus is thin, broad, relatively short and rectangular in shape. The ventral rami of the scapulae do not meet in the midline of the girdle and do not contact the anterior processes of the coracoids to form a pectoral bar; they were apparently separated from each other by the broad interclavicle.

Coracoid. The coracoid (Text-fig. 4A; Pl. 3, figs 5–6) is a large and broad plate of bone. It is very thin posteriorly and laterally. The medial border is nearly straight, indicating that the coracoids were united along their entire length, and rough, indicating the presence of cartilage. Its anterior half is thickened. The posterolateral cornua are well-developed,

EXPLANATION OF PLATE 2

Figs 1–16. *Occitanosaurus tournemirensis* (Sciau, Crochet and Mattei, 1990); holotype (MMM J. T. 86-100); Upper Toarcian, Tournemire, France; parts of axial skeleton. 1, atlas-axis in right lateral view. 2, anterior cervical in right lateral view. 3–4 median cervical in right lateral and anterior views. 5–6, posterior cervical in right lateral and anterior views. 7–8, pectoral vertebra in right lateral and anterior views. 9–10, two dorsal vertebrae in right lateral and anterior views. 11–12, sacral vertebra in right lateral and anterior views. 13, dorsal rib. 14, gastrarium. 15, pectoral rib. 16; sacral rib. All $\times 0.33$.



so that the lateral border of the bone is deeply concave. The width across the cornuae is up to 10 per cent. greater than the interglenoid one. Anterior to the cornua, the lateral border of the coracoid bears a pointed protuberance, probably marking the presence of a ligament insertion. The glenoid surface is deeply concave and anterolaterally directed. It forms an angle of about 140° with the contact surface for the scapula. Anteriorly, the coracoid terminates in a long and narrow medial process which forms the posteromedial margin of the pectoral foramen. This anterior process probably contacted the posterior process of the interclavicle. The posterior border of the coracoid is sigmoidal because its posteromedial angle is more anteriorly set than the lateral angle of the cornua.

Pectoral fenestration. This is elliptical and laterally delimited by the scapula, posteromedially by the coracoid and anteromedially by the interclavicle (Text-fig. 4A).

Pubis. The pubis (Text-fig. 4B; Pl. 4, figs 1–2) is large and nearly pentagonal. The posterior border is emarginated by a deep semicircular notch, forming the anterior margin of the pelvic foramen. The acetabular surface is posterolaterally directed and forms an angle of about 130° with the lateral articular facet for the ischium. The anterolateral angle of the pubis is rounded. The anterior border is convex, which may be related to a possibly incomplete ossification of the gastralia. The anteromedian border is straight and transversally directed. The posteromedial border of the pubis is developed posteriorly to contact the ischium.

Ilium. The ilium (Text-fig. 4B; Pl. 4, figs 3–4) is long and expanded at both extremities. The dorsal end (sacral) is more expanded anteroposteriorly and more laterally compressed than the ventral one (acetabular). The dorsal margin is formed by two rough facets, making together an angle of *c.* 90° : the *crista ilii* forms a gutter along the anterior facet. An elliptical knob located on the posteromedial angle of the medial face of the dorsal head, can be interpreted as an articular facet for the sacrum. The shaft of the ilium is nearly straight and oval in cross section. It bears a well-marked ridge on its ventral portion, which is continuous with the acetabular facet. The ventral end, capped by cartilage, bears two facets. The posterior one (ischial facet) is the largest and is mainly medially oriented. The acetabular facet is continuous with the previous one, also directed medially but forming a lip on the anterolateral face of the bone.

Ischium. As is typical in plesiosaurs, the ischium (Text-fig. 4B; Pl. 4, figs 5–6) is hatchet-shaped. It is a short bone, slightly longer than wide and nearly as long as the pubis. Its anterior border is deeply notched and forms the large semicircular margin of the pelvic fenestration. The articular head of the ischium is massive and bears three facets. The anterior one (pubic facet) faces anteriorly. The acetabular facet is laterally oriented and encloses an angle of *c.* 130° with the pubic facet. The posterior one (iliac facet) is posterolaterally directed, forming a very obtuse angle with the acetabular facet. The body of the ischium is separated from the articular head by a constriction and is posteriorly expanded in a thin blade of bone. Its medial border is rough, indicating the presence of cartilage in the symphyseal region. When the pubis and the ischium are articulated, the anteromedial corner of the ischium contacts the corresponding posteromedial process of the pubis to form a complete pelvic bar.

Pelvic fenestration. This is round and delimited anteriorly by the pubis and posteriorly by the ischium (Text-fig. 4B).

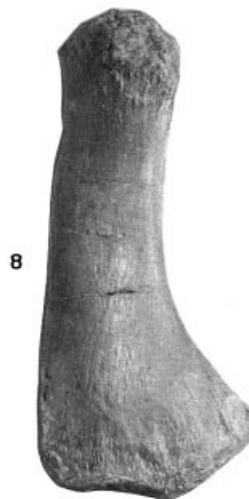
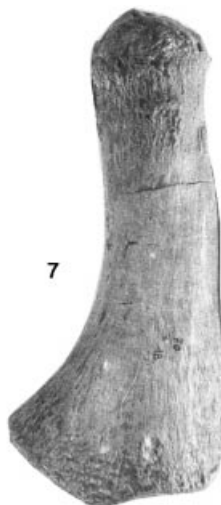
Paddles (Text-fig. 4; Pls 3–4; Table 1)

The right forelimb and both hindlimbs are preserved disarticulated on the posterior part of the carcass of *O. tournemirensis*. It can be assumed that the epipodials located near the humerus are the radius and the ulna and those near the femur are the tibia and the fibula.

Humerus. The humerus (Text-fig. 4A; Pl. 3, figs 7–8) is gracile and markedly asymmetrical in lateral view with a curved shaft. Its anterior border is nearly straight so that the radial facet lies in the axis of the humerus shaft. Its posterior border is very concave because of the distinctive enlargement of its posterodistal part. As a result, the ulnar

EXPLANATION OF PLATE 3

Figs 1–9. *Occitanosaurus tournemirensis* (Sciau, Crochet and Mattei, 1990); holotype (MMM J. T. 86-100); Upper Toarcian, Tournemire, France; pectoral girdle and forelimb. 1–2, interclavicle-clavicle complex in dorsal and ventral views. 3–4, left scapula in dorsal and ventral views. 5–6, left coracoid in dorsal and ventral views. 7–8, right humerus in dorsal and ventral views. 9, right carpus and metacarpus in ventral view. All $\times 0.33$.



facet faces backwards. The distal portion of the shaft bears a dorsal and a ventral crest which are rugose, slightly anteriorly displaced and continuous with the proximal head of the humerus. The ventral crest (deltopectoral crest), marking the insertion of the *M. coracobrachialis*, is somewhat more strongly developed than the dorsal one (tricipital crest), marking the insertion of the *M. subcoracoscapularis*, *M. subscapularis* and *M. subcoracoideus*. The humeral head is very convex and rugose and was probably covered in life by a thick cartilage cap.

Radius and ulna. The radius (Text-fig. 4A; Pl. 3, fig. 9) is a rather long and narrow hourglass-shaped bone. Its posterior border is thinner and slightly more convex than its anterior border. Both proximal and distal faces are convex and rugose. The crescentic ulna (Text-fig. 4A; Pl. 3, fig. 9) is wider and slightly shorter than the radius. Its posterior border is very convex, thick and rugose, while its anterior border is thinner and concave. The *spatium interosseum* between ulna and radius is well-developed.

Femur. The femur (Text-fig. 4B; Pl. 4, figs 7–8) is nearly the same size as the humerus, but differs in being almost symmetrical in lateral view. Its anterodistal and posterodistal parts are equally expanded so that the tibial facet faces forwards and the fibular one backwards. Consequently, the anterior and posterior borders of the shaft are symmetrically concave. On the proximal portion of the shaft, the ventral crest (trochanteric crest), which marks the insertion of the *M. puboischiofemoralis externus*, is more prominent than the dorsal one, for the insertion of the *M. puboischiofemoralis internus*.

Tibia and fibula. The tibia and fibula (Text-fig. 4B; Pl. 4, fig. 9) closely resemble the radius and ulna. The tibia is somewhat wider than the radius and its proximal border is more inclined backwards.

Carpus, tarsus, metapodials and phalanges. The carpal elements are small, circular, flattened and slightly depressed in the middle. Their borders are very rough. The intermedium is distinctly pentagonal. The anteroproximal border articulates with the radius, the posterodistal one with the ulna, the anterior one with the radiale, the posterior one with the ulnare and the distal one with elements of the distal carpal series. The radiale is distinctly shorter than the ulnare. The phalanges can not be rearranged with precision since the paddles have suffered post-mortem scattering. All are cylindrical, rather elongated, constricted in the middle and slightly flattened dorso-ventrally, with proximal heads somewhat wider than the distal ends. Tarsals, metatarsals and hindlimb phalanges are undistinguishable from, respectively, the carpals, metacarpals and forelimb phalanges.

PHYLOGENETIC RELATIONSHIPS OF *OCCITANOSAURUS*

In recent years, extensive revisions of the 'nothosaurs' (e.g. Rieppel 1989; Storrs 1991) have significantly improved our knowledge of the phylogeny of the Sauropterygia. Concerning the plesiosaurs, Brown (1993) pointed out that '...their classification is based upon current theory of phylogeny as perceived from a knowledge of the more advanced members of each lineage, in the relative absence of an understanding of their chronologically earlier interrelationships'. Recent efforts have focused on the revision of Early Jurassic pliosauroids and plesiosauroids (Taylor 1992; Cruickshank 1994, 1996; Storrs and Taylor 1996; Storrs 1997), as well as on the description of new Middle Jurassic taxa or specimens (Taylor and Cruickshank 1993; Brown and Cruickshank 1994; Godefroit 1994; Gasparini 1997), improving our knowledge of both plesiosaur phylogeny and diversity.

Within the Plesiosauroidea Gray, 1825, the Early Jurassic Plesiosauridae Gray, 1825 remain poorly known. The family includes the single basal genus *Plesiosaurus* Conybeare, 1821, currently comprising three species, *P. dolichodeirus* Conybeare, 1824 from the Lower Lias of England, *P. brachypterygius* von Huene, 1923 and *P. guilelmiimperatoris* Dames, 1895, both from the Upper Lias of Germany (Brown

EXPLANATION OF PLATE 4

Figs 1–9. *Occitanosaurus tournemirensis* (Sciau, Crochet and Mattei, 1990); holotype (MMM J. T. 86-100); Upper Toarcian, Tournemire, France; pelvic girdle and hindlimb. 1–2, left pubis in dorsal and ventral views. 3–4, left ilium in dorsal and ventral views. 5–6, left ischium in dorsal and ventral views. 7–8, right femur in dorsal and ventral views. 9, tarsus and metatarsus in dorsal view. All $\times 0.33$.

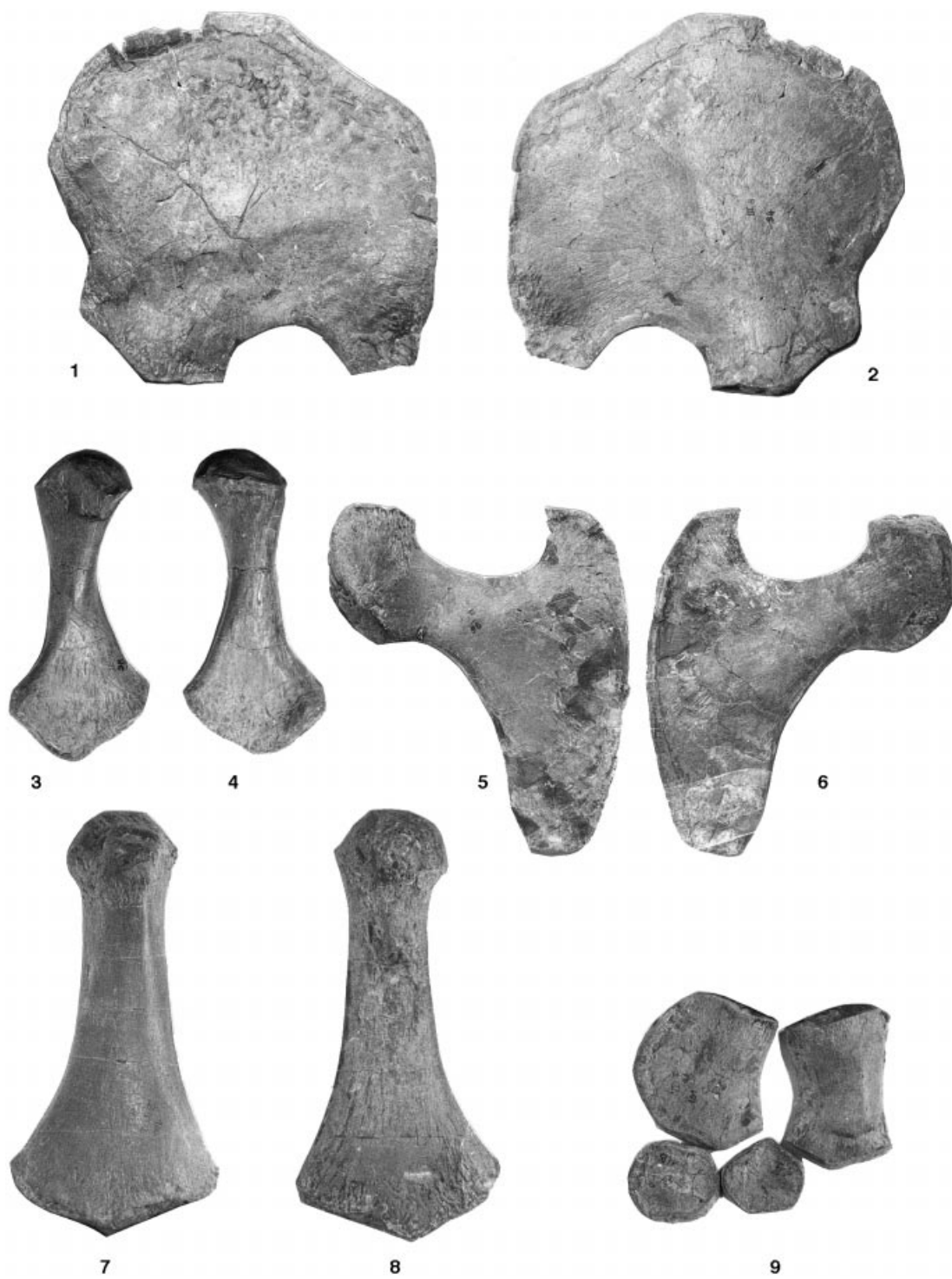


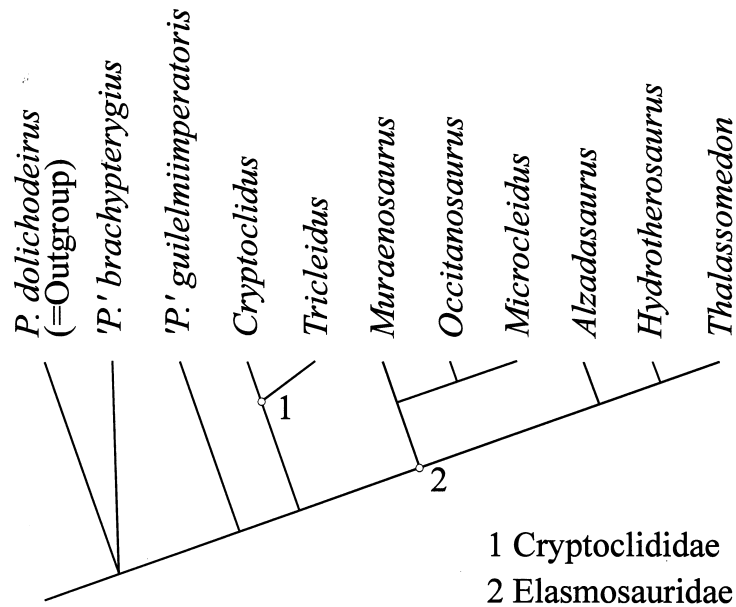
TABLE 3. Material used for comparisons. Asterisks refer to taxa personally inspected. When several specimens of the same taxon have been checked, respective collection numbers are mentioned. The main references used are indicated for each taxon.

* <i>Plesiosaurus dolichodeirus</i> Conybeare, 1824	NHM 22656, 41101 Sinemurian of Dorset	Storrs (1997)
*‘ <i>Plesiosaurus</i> ’ <i>brachypterygius</i> von Huene, 1923	GPIT Toarcian of Baden-Württemberg	von Huene (1923)
*‘ <i>Plesiosaurus</i> ’ <i>guilelmiimperatoris</i> Dames, 1895	SMNS 12039 Toarcian of Baden-Württemberg	Dames (1895) Fraas (1910)
* <i>Cryptoclidus eurymerus</i> (Phillips, 1871)	NHM R. 2860 Callovian of Cambridgeshire and Normandy	Andrews (1910) Brown (1981, 1993) Bardet (1993) Brown and Cruickshank (1994)
* <i>Tricleidus seeleyi</i> Andrews, 1909	NHM R.3539 Callovian of Cambridgeshire and Normandy	Andrews (1910) Brown (1981, 1993) Bardet (1993)
* <i>Microcleidus homalospondylus</i> (Owen, 1865)	NHM 36184 Toarcian of Yorkshire	Owen (1865) Watson (1909) Brown (1993)
* <i>Muraenosaurus leedsii</i> Seeley, 1874a	NHM R.2421, R.2422, R.2678, R.2861 Callovian of Cambridgeshire and Normandy	Andrews (1910) Brown (1981, 1993) Bardet (1993)
<i>Alzadasaurus colombiensis</i> Welles, 1962	UCMP 38349 Aptian of Colombia	Welles (1962)
<i>Thalassomedon haningtoni</i> Welles, 1943	CMNH 1588 Cenomanian of Colorado	Welles (1943)
<i>Hydrotherosaurus alexandrae</i> Welles, 1943	UCMP 33912 Maastrichtian of California	Welles (1943)

1981, 1993; Storrs 1997). The diagnosis of this family proposed by Brown (1981) is based on plesiomorphic characters only and is therefore subject to revision. On the other hand, our knowledge of the Cryptoclididae Williston, 1925 and Elasmosauridae Cope, 1869 has been significantly improved in recent years and their monophyly is better supported (Brown 1981, 1993; Brown and Cruickshank 1994). Finally, the validity of the Polycotylidae Cope, 1869 has long been questioned (see for example Welles 1962) and their phylogenetic position among Plesiosauria is still debated as they are considered either as related to the Pliosauridae (Persson 1963; Adams 1997) or as sister-group to the long-necked Elasmosauridae (Carpenter 1996, 1997).

To understand the phylogenetic affinities of *Occitanosaurus tournemirensis* among Plesiosauria, a preliminary cladistic analysis, including 11 species and 29 cranial, dental and postcranial characters, has been performed. Because missing data may influence cladistic analysis in rather unpredictable ways (see Platnick *et al.* 1991), the phylogenetic reconstruction has been based on a selection of plesiosaurian taxa of which the skeletal morphology is sufficiently known (see Table 3). Moreover, the analysis has been restricted and focused on long-necked plesiosaurs. The characters have been selected using the literature, mainly Brown (1981, 1993) and Storrs (1997) and our own observations (see specimens personally inspected in Table 3). Autapomorphies as well as ontogenetic and grade characters (time-dependent characters acquired independently by the entire order Plesiosauria and largely linked to aquatic adaptation improvements, *sensu* Brown 1981) have been excluded from the analysis. *Plesiosaurus dolichodeirus* Conybeare, 1824, a basal plesiosauroid from the Lower Lias of England recently revised by Storrs (1997), has been chosen as outgroup.

An exhaustive search for the most parsimonious trees was performed using the Hennig86 software (Farris 1988). All characters were equally weighted. Multistate characters have been treated as ordered



TEXT-FIG. 5. Cladogram showing phylogenetic relationships of *Occitanosaurus tournemirensis* among plesiosauroids.

(19, 29) or unordered (5, 15, 16, 17) depending on each case (see discussion of characters and matrix in Appendix 1 and 2). One single tree was generated, with a length of 57 steps, a consistency index (CI) of 61 and a retention index (RI) of 62 (Text-fig. 5).

Occitanosaurus belongs to the family Elasmosauridae, characterized by more than 40 cervical vertebrae, whose centra are elongated and bear both platycoelous articular surfaces and lateral keels. Within the Elasmosauridae, *Microcleidus homalospondylus* Watson, 1909, from the Toarcian of England, is the closest relative of *Occitanosaurus tournemirensis*. In both genera, the jugal is excluded from the orbital margin by the extended contact between the maxilla and the postorbital, a character also present in the advanced *Hydrotherosaurus alexandrae* Welles, 1943 from the Upper Cretaceous of California. Nevertheless, numerous characters justify the generic distinction between the taxa: the skull of *Occitanosaurus* (dorso-cephalic index = 25.6) is proportionally longer than that of *Microcleidus* (dorso-cephalic index = 20), with a more spatulate snout, higher postorbital, shorter facial process of the premaxilla and trapezoidal jugal (in *Microcleidus*, it is rectangular in lateral view); the neck of *Occitanosaurus* (cervico-dorsal index = 191) is proportionally longer than in *Microcleidus* (cervico-dorsal index = 170; 38 or 39 cervical vertebrae); the pectoral girdle is completely different in *Microcleidus*, the scapula participating in the pectoral bar, the coracoid lacking posterior cornua and the interclavicle being absent.

Muraenosaurus leedsii Seeley, 1874a from the Middle Jurassic of Europe apparently forms the sister-group of *Occitanosaurus* and *Microcleidus*. These three genera share the reduction of the tooth size around the premaxilla-maxilla suture. However, this latter character is ambiguous, as it is also present in the cryptocleidid *Tricleidus seeleyi* Andrews, 1909 from the Middle Jurassic of Europe and in '*P.* brachypterygius'.

The Cretaceous elasmosaurs considered in the present analysis (*Hydrotherosaurus alexandrae* Welles, 1943; *Thalassomedon haningtoni* Welles, 1943 from the lower Upper Cretaceous of Colorado; *Alzadasaurus colombiensis* Welles, 1962 from the Lower Cretaceous of Colombia) form a monophyletic group. They share several synapomorphies, such as the pterygoid completely extending beneath the basicranium into large plates, the development of large fangs around the premaxilla-maxilla suture, more than 50 cervical vertebrae, 'dumb-bell'-shaped cervical articular surfaces and an intercoracoid foramen. *Thalassomedon* and *Hydrotherosaurus* show a reduction of the number of dentary teeth.

Cryptoclididae form the sister-group of Elasmosauridae. The monophyly of the clade Cryptoclididae + Elasmosauridae is based, in the present cladogram, on frontals not separated by premaxillae, coracoids posteriorly expanded, enlargement of the distal end of the humerus and ventral processes of the scapulae meeting superficial to clavicles and interclavicle. Nevertheless, it should be noted that these latter two characters are not present in *Occitanosaurus*, a situation which probably reflects reversions. Brown (1993) discussed in detail the monophyly of cryptoclidids, a concept confirmed in the present paper. Cryptoclididae are characterized by their small vertical jugal, the relatively small size of their upper temporal fenestra correlated with the enlargement of their orbits, the deep emargination of their cheek margin, the absence of prefrontal, the reduction of tooth ornamentation and the increase of premaxillary and dentary tooth number (the latter two characters remain primitive in *Tricleidus*).

Finally, it appears that the genus *Plesiosaurus* is not monophyletic, as previously envisaged by Storrs (1997), who moreover considered that '*P. brachypterygius*' may be a junior synonym of '*P. guilelmiimperatoris*'. According to Brown (1993), '*P. guilelmiimperatoris*' and '*P. brachypterygius*' share a similar cheek morphology but differ in relative length of neck, the former resembling *P. dolichodeirus* whilst the latter resembles *Microcleidus*. In our analysis '*P. guilelmiimperatoris*' is the sister group of Elasmosauridae, whilst the phylogenetic position of '*P. brachypterygius*' remains unresolved. Only a revision of the German material would clarify the phylogenetic position of these two taxa. Whatever the results of such a study, these forms share the development of coracoid cornuae with Cryptoclididae and most Elasmosauridae. They also share with the elasmosaurids a large and straight jugal-postorbital suture, a temporal fenestra larger than the orbit, the lack of anterior pterygoid vacuity, an irregular dentition around the premaxilla-maxilla suture (these latter two characters at least for '*P. brachypterygius*') and lateral keel on the cervical vertebrae, a condition probably convergent and linked with an elongated neck. In *Plesiosaurus dolichodeirus*, the number of cervical vertebrae (38–40) is similar to that observed in basal elasmosaurids (convergence) but they remain plesiomorphic in all other cervical characters (moderate length, concave articular surface and lack of lateral keel).

PALAEOGEOGRAPHICAL DISTRIBUTION OF ELASMOSAURIDS

Elasmosaurids emerged by the Early Liassic, during the great early evolutionary radiation of Plesiosauria. *Eretmosaurus rugosus* Seeley, 1874b from the Sinemurian of England is known from two incomplete specimens. The neotype (NHM 14435, Brown and Bardet 1994) lacks the skull and the pectoral girdle is largely obscured in the matrix. Although the cervical vertebrae are of typical elasmosaurid morphology, they seem proportionally less elongated and less numerous than those of *Occitanosaurus*, and the coracoids are apparently devoid of posterolateral cornuae. Godefroit (1995) described also an indeterminate elasmosaurid from the Sinemurian of Belgium which resembles *Occitanosaurus* in the presence of double keels along some cervical centra, but its humerus is distinctly more symmetrical in lateral view. Unfortunately, neither the skull nor the girdles are preserved in this specimen. '*Plesiosaurus conybearei*' Sollas, 1881 from the Sinemurian of England seems typically elasmosaurid in the length and structure of its neck. On the other hand, its skull resembles that of contemporaneous early pliosaurs in its general proportions, the morphology of its teeth and the spatulate shape of its mandibular symphysis. Lydekker (1889, p. 269) remarked that the skull of '*P. conybearei*' closely resembles that of '*P. rostratus*' Owen, 1865 from the same locality, and that perhaps the skull of the holotype was not found with the postcranial skeleton. The holotype of this species was unfortunately destroyed in November 1940 (Persson 1963). By the Toarcian, two elasmosaurids lived in western Europe, *Microcleidus* (two species described) in the English basins, and *Occitanosaurus* (monospecific) in the Aquitanian Basin. Callovian elasmosaurs are represented by the genus *Muraenosaurus*, from the Oxford Clay of England (Andrews 1910; Brown 1981) and France (Bardet 1993). During the Mid and Late Jurassic, elasmosaurs apparently began to spread all over the world, as they have been reported from Argentina (Gasparini and Spalletti 1993), Wyoming (Mehl 1912) and India (Bardet *et al.* 1991). During the Early Cretaceous, elasmosaurs remain relatively discrete and known by *Brancasaurus* Wegner, 1914 from the Berriasian of Germany (Wegner 1914) and *Alzadasaurus* Welles, 1943 from the Aptian of Colombia (Welles 1943; Goñi and Gasparini 1983). During the Late Cretaceous, elasmosaurs achieved a world-wide distribution as they have been found in both the

northern and the southern hemisphere. They are especially abundant in North America, where most of the genera have been described (see Welles 1962) but they also occur in western Europe (see Bardet and Godefroit 1995), Russia (Rozhdestvensky 1973), Japan (Nakaya 1989), Africa and the Middle-East (see Werner and Bardet 1996), Madagascar (Bardet and Termier 1990), South America (Goñi and Gasparini 1983; Gasparini and Goñi 1985), New Zealand (Welles and Gregg 1971; Wiffen and Moislely 1986) and Antarctica (Gasparini *et al.* 1984; Chatterjee and Small 1989). Finally, *Aristonectes parvidens* Cabrera, 1941 from South America and *Morturneria seymourensis* (Chatterjee and Small, 1989) from Antarctica have been classified as cryptoclidids (Brown 1981; Chatterjee and Small 1989) but detailed study has revealed that they belong rather to elasmosaurids (Bardet *et al.* 1991). The Elasmosauridae disappeared at the end of the Maastrichtian, during the K/T biological crisis.

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NATHALIE BARDET

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

PASCAL GODEFROIT

Institut Royal des Sciences Naturelles de Belgique
 Département de Paléontologie
 rue Vautier 29
 1000 Bruxelles, Belgium
 e-mail pcodefr@kbinirnsb.be

JACQUES SCIAU

Musée Municipal de Millau
 Hôtel de Pegayrolles
 12100 Millau, France

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APPENDIX 1

Cranial characters

1. *Jugal configuration (large quadrilateral horizontal bar = 0; small narrow vertical bar = 1)*. Primitively in Plesiosauria, the jugal is a large, horizontally oriented quadrilateral element. This morphology results from the break of the infratemporal bar. Elasmosaurids, including *Occitanosaurus*, all retain this primitive pattern. In cryptoclidids, the increase of the orbit size remodels the jugal morphology, which becomes a small and narrow vertically orientated bar, separating the enlarged orbits from the cheek emargination (Brown 1993; Brown and Cruickshank 1994).
2. *Jugal - postorbital suture (short and/or sigmoidal = 0; long and/or straight = 1)*. In *Plesiosaurus dolichodeirus*, the jugal is a horizontal quadrilateral element; its dorsal contact with the postorbital is sigmoidal and not very extensive. This contact remains short in cryptoclidids. On the other hand, the jugal-postorbital contact is very extensive, forming a long and straight suture in elasmosaurids as well as in '*P*'. *brachypterygius* and '*P*'. *guilelmiimperatoris*.
3. *Jugal - orbit contact (yes = 0; no = 1)*. In most Sauropterygia, the jugal remains in contact with the orbital margin (Storrs 1991). In 'plesiosaurids' and elasmosaurids, it takes part in the ventral margin of the orbit whereas in cryptoclidids, it forms its posteroventral corner. In *Occitanosaurus*, *Microcleidus* and *Hydrotherosaurus* (cf. Welles 1943), the jugal is excluded from the orbital margin through an extended contact between the maxilla and the postorbital. The shape of both jugal and postorbital are nevertheless distinct in these taxa: in *Occitanosaurus*, the jugal is trapezoidal and the postorbital very high; in *Microcleidus*, the jugal is quadrangular and the postorbital distinctly lower; finally, in *Hydrotherosaurus*, the jugal is elongated and displaced posteriorly from the orbital area, whereas the postorbital is short.
4. *Cheek emargination (weakly emarginated = 0; strongly emarginated = 1)*. In *P. dolichodeirus*, the cheek is weakly emarginated and the jugal-squamosal ventral surface is almost flat, a plesiomorphic character retained by elasmosaurids. On the other hand, cryptoclidids exhibit a deep ventral excavation of cheek margin resulting from the enlargement of the orbit (Brown 1993; Brown and Cruickshank 1994). It should be noted that the cheek region of '*P*'. *brachypterygius* and '*P*'. *guilelmiimperatoris* were originally reconstructed as being deeply emarginated.
5. *Orbit - supratemporal fenestra relative sizes (orbit as large as fenestra = 0; orbit larger than fenestra = 1; orbit smaller than fenestra = 2)*. This character is coded as unordered. In *P. dolichodeirus*, the orbit and supratemporal fenestra are of equal size, which is here considered as the plesiomorphic condition. Two evolutionary trends can be recognized among Plesiosauroida: in '*P*'. *brachypterygius*, '*P*'. *guilelmiimperatoris* and elasmosaurids, the orbit is notably smaller than the supratemporal fenestra, whereas the orbit is distinctly larger than the supratemporal fenestra in cryptoclidids.
6. *Prefrontal (present = 0; absent = 1)*. The prefrontal is present in all Plesiosauria, with the exception of the cryptoclidids (cf. Brown 1981).
7. *Postfrontal shape (triangular = 0; quadrangular = 1)*. In *P. dolichodeirus*, the postfrontal is triangular, a primitive condition retained in '*P*'. *guilelmiimperatoris*, *Alzadasaurus* and *Thalassomedon*. In other plesiosauroids, the postfrontal is quadrangular. In cryptoclidids, the shape of this bone is uncertain.
8. *Frontals partly separated medially by premaxillae (yes = 0; no = 1)*. In *P. dolichodeirus* and '*P*'. *brachypterygius*, the frontals are partly separated medially by a dorsal extension of the premaxillae, as in pliosaurs, which is considered as the plesiomorphic condition. In all other studied plesiosaurs, the frontals are not separated medially by the premaxillae.
9. *Frontals excluded from external nares (yes = 0; no = 1)*. Primitively in numerous plesiosaurs, including *P. dolichodeirus*, '*P*'. *brachypterygius*, *Occitanosaurus* and *Microcleidus*, the frontals remain excluded from the external nares by developed prefrontals. In cryptoclidids, which apparently lost their prefrontals, and in elasmosaurids such as *Muraenosaurus* (Andrews 1910) and *Hydrotherosaurus* (Welles 1943), the frontals take part in the margin of the external nares.

10. *Pineal foramen* (present = 0; absent = 1). In most plesiosaurs, the pineal foramen is present and set in front of the supratemporal fenestra. In *Occitanosaurus* and in advanced elasmosaurs, such as *Hydrotherosaurus*, the pineal foramen is absent.

11. *Maxillae - internal nares contact* (yes = 0; no = 1). In *P. dolichodeirus* and in most plesiosaurs, the maxillae take part in the lateral margin of the internal nares. In *Cryptoclidus* and *Occitanosaurus*, the maxillae are excluded from the margin of the internal nares by an anterior extension of the lateral part of the palatines.

12. *Basicranium - pterygoid relationships* (pterygoids incompletely extended beneath basicranium = 0; completely extended into large plates = 1). In *P. dolichodeirus*, the pterygoids are incompletely extended beneath the basicranium, a plesiomorphic condition retained by the elasmosaurids *Occitanosaurus*, *Microcleidus* and *Muraenosaurus* as well as by '*P. brachypterygius*', '*P. guilelmiimperatoris*' and cryptoclidids. The pterygoids extend completely beneath the basicranium into large plates only in Cretaceous elasmosaurs and in polycotyliids (Carpenter 1996, 1997).

13. *Anterior pterygoid vacuities* (present = 0; absent = 1). In most plesiosaurs, except elasmosaurids and '*P. brachypterygius*', anterior pterygoid vacuities are present. In all elasmosaurids, including *Occitanosaurus*, the palate is closed anteriorly. This could be linked to cranial kinesis in relation with food habits. In *Muraenosaurus*, anterior pterygoid vacuities were mentioned by Andrews (1910, fig. 47), but the poor preservation of this area does not allow confirmation of this observation.

14. *Occipital condyle* (formed by basioccipital only = 0; formed by basioccipital and exoccipitals = 1). Primitively, the occipital condyle is formed solely by the basioccipital (Rieppel 1994). Only advanced cryptoclidids exhibit a participation of exoccipitals into the occipital condyle.

Dental characters

15. *Number of premaxillary teeth* (five = 0; more than five = 1; less than five = 2). This character is coded as unordered. The primitive number of premaxillary teeth in Plesiosauria is five (Brown 1981). In Cryptoclididae, there is a tendency to increase this number (*Cryptoclidus* possesses six teeth and *Kimmerosaurus* eight). The inverse trend can be observed in elasmosaurids: the premaxillae bear only four teeth in some Cretaceous forms such as *Thalassomedon*.

16. *Number of dentary teeth* (between 17 and 24 = 0; more than 24 = 1; less than 17 = 2). This character is coded as unordered. As for the number of premaxillary teeth, the number of dentary teeth tends to increase or decrease according to the taxa (Brown 1981). Primitively there are 17 to 24 teeth in *P. dolichodeirus*. The number of dentary teeth increases in advanced cryptoclidids (*Cryptoclidus* has about 25 teeth and *Kimmerosaurus* 36) and decreases in Cretaceous elasmosaurids (about 15 in *Hydrotherosaurus* and *Thalassomedon*). This number is unknown in *Occitanosaurus*.

17. *Dentition around the premaxilla-maxilla suture* (regular = 0; small teeth = 1; large fangs = 2). This character is coded as unordered. *P. dolichodeirus* presents a regular tooth row, a character found also in cryptoclidids except *Tricleidus* (Brown 1981, 1993). Among Plesiosauroidea, reduced or enlarged teeth around the premaxilla-maxilla suture are observed in several taxa. Smaller teeth are found in *Tricleidus*, *Microcleidus*, *Occitanosaurus*, *Muraenosaurus* and possibly '*P. brachypterygius*'. In *Alzadasaurus*, *Hydrotherosaurus* and *Thalassomedon* large fangs are developed around this suture.

18. *Teeth ornament* (present = 0; reduced or absent = 1). In *P. dolichodeirus* and most plesiosauroids, the teeth are slender and ornamented by fine and numerous longitudinal enamel ridges. In cryptoclidids, there is a trend to reduce the ornament of the teeth, ranging from the presence of only few ridges (*Cryptoclidus*) to a complete lack of ornament (*Kimmerosaurus*) (Brown 1981).

Postcranial characters

19. *Number of cervical vertebrae* (less than or equal to 40 = 0; between 41 and 50 = 1; more than 50 = 2). This character is coded as ordered. Brown (1981) considered the primitive number of cervical vertebrae in Plesiosauria to be probably around 28 to 32, as observed in Early Liassic genera. The primitive number of cervicals is here reconsidered as being less than or equal to 40. The primitive pattern is found in most basal plesiosauroids (38–40 in *P. dolichodeirus*, 36 or 37 in '*P. brachypterygius*' and '*P. guilelmiimperatoris*') and in cryptoclidids (about 26 in *Tricleidus* and 29–32 in *Cryptoclidus*). Elasmosaurids, with the exception of *Microcleidus* (38–39), all possess more than 40 cervicals, which is here considered as an apomorphy for the family. The number of cervicals regularly increases from 38 or 39 in *Microcleidus*, 43 in *Occitanosaurus*, 44 in *Muraenosaurus* to exceed 60 in latest Cretaceous forms like *Hydrotherosaurus* and *Thalassomedon*. The maximum is obtained in *Elasmosaurus*, which has 71 cervical vertebrae. The dorso-cephalic index is 191 in *Occitanosaurus*, reflecting the very great development of the neck in this species, and is by far the highest observed in Liassic plesiosaurs.

20. *Length of cervical centra* (length < height = 0; length > height = 1). Primitively in plesiosauroids, the length of the cervical vertebrae is less than their height (Brown 1981), as observed in basal 'plesiosauroids' and in cryptoclidids. In

elasmosaurids, the length of the cervical vertebrae always exceeds their height, which is considered as a synapomorphy for the elasmosaurid clade.

21. *Articular surfaces of cervical vertebrae (amphicoelous = 0; platycoelous = 1)*. Most sauropterygians, including 'plesiosauroids' and cryptoclidids are rather conservative in the form of the articular surface of their centra, which are plesiomorphically amphicoelous (Brown 1981). Possession of derived platycoelous articular surfaces is a synapomorphy for the elasmosaurid clade.

22. *Lateral keels on cervical vertebrae (no = 0; yes = 1)*. Lateral keels are longitudinal crests which divide the lateral surface of the centrum into subequal upper and lower concave areas (Brown 1981). Among elasmosaurs, this lateral keel is always present but is rarely divided into two as in *Occitanosaurus*. This character is absent in all short-necked forms, as well as in *P. dolichodeirus* and *Colymbosaurus trochanterius* (Owen, 1840), a long-necked cryptoclidid. It is thus regarded as a synapomorphy for the elasmosaurid clade, shared with 'P'. *brachypterygius* and 'P'. *guilelmiimperatoris*.

23. *Dumb-bell-shaped articular surfaces of the cervical vertebrae (no = 0; yes = 1)*. The articular surfaces of cervical centra are usually rounded or transversely oval in Plesiosauroidea, as observed in *P. dolichodeirus*. In Late Cretaceous elasmosaurids, the surface is typically dumb-bell-shaped because of the development of a strongly concave ventral surface. In more basal elasmosaurids such as *Occitanosaurus*, the articular surface remains oval.

24. *Median contact between ventral processes of scapulae (no = 0; yes = 1)*. The primitive condition in which there is no median contact between the ventral processes of the scapulae occurs in most Liassic plesiosauroids. The derived condition, in which the ventral processes of the scapulae in adult specimens meet in the ventral midline superficial to the clavicles and interclavicle, is always observed in cryptoclidids. Among elasmosaurids, only *Occitanosaurus* and *Alzadasaurus* retain the primitive condition.

25. *Posterior cornua on coracoids (absent = 0; present = 1)*. Brown (1981) showed that there is a variation between an almost complete absence of cornua (plesiomorphic condition) to a strong projecting development of the posterolateral angles of the coracoids (apomorphic condition) in adults. Cornuae are developed among numerous plesiosauroids but are lacking in *P. dolichodeirus*, *Microcleidus* and *Hydrotherosaurus*.

26. *Proportion of coracoids (postglenoid part/preglenoid part < 1.5 = 0; > 1.5 = 1)*. If A is the length between the anteriormost point of the coracoid and the posterior angle of the glenoid facet and B the length between the posterior angle of the glenoid facet and the posteriormost point of the coracoid, the ratio B/A is an estimation of the development of the posterior blade of the coracoid. In most advanced plesiosauroids, this plate is very well-developed (B/A > 1.5), but in numerous Liassic species, this plate remains relatively short (B/A < 1.5).

27. *Intercoracoid foramen (no = 0; yes = 1)*. In all Jurassic Plesiosauroidea, the coracoids unite along their entire length. They are separated posteriorly by a wide intercoracoid foramen only in Cretaceous elasmosaurids (Brown 1981).

28. *Humerus - femur relative lengths (humerus as large as femur = 0; humerus larger than femur = 1)*. In *P. dolichodeirus*, the humerus and femur are of the same size, a primitive condition retained by many plesiosauroids. In *Occitanosaurus*, the humerus and femur are nearly of the same length, as in all 'plesiosauroids', *Tricleidus* and Jurassic elasmosaurids. In *Cryptoclidus* and Cretaceous elasmosaurids except *Thalassomedon*, the humerus is distinctly longer than the femur.

29. *Distal extension of humerus (distal width / length less than 0.5 = 0; between 0.5 and 0.65 = 1; more than 0.65 = 2)*. This character is coded as ordered. The distal width / length ratio of the humerus is less than 0.5 in *P. dolichodeirus*, 'P'. *brachypterygius* and *Occitanosaurus*. Within the plesiosauroids, there is a trend to enlarge the distal part of the humerus relative to its length by an anterior expansion of the articular surface for the radius. The derived condition is observed in 'P'. *guilelmiimperatoris*, all elasmosaurids except *Occitanosaurus*, and cryptoclidids. Among elasmosaurids and cryptoclidids, the humerus becomes greatly enlarged distally (ratio more than 0.65) in *Cryptoclidus* and in advanced Cretaceous elasmosaurids.

APPENDIX 2

<i>P. dolichodeirus</i> (= outgroup)	00000	00000	00000	00000	00000	0000
'P'. <i>brachypterygius</i>	01012	01000	00100	0100?	?1?01	0000
'P'. <i>guilelmiimperatoris</i>	01012	00?20	???20	0?00?	?1?01	1001
<i>Tricleidus</i>	10011	1?110	?0000	01000	00011	1001
<i>Cryptoclidus</i>	10011	1?110	1?011	10100	00011	1012
<i>Occitanosaurus</i>	01102	01101	10100	?1011	11001	1000
<i>Microcleidus</i>	01102	01100	?0100	01001	11010	1001
<i>Muraenosaurus</i>	01002	01110	00?00	01011	11011	1001
<i>Alzadasaurus</i>	01002	00100	01100	02021	11101	1112
<i>Hydrotherosaurus</i>	01102	01111	?1?00	22021	111?0	1112
<i>Thalassomedon</i>	01002	00?20	???11	10110	00011	1011