CRANIAL OSTEOLOGY OF THE SAUROPTERYGIAN *PLESIOSAURUS BRACHYPTERYGIUS* FROM THE LOWER TOARCIAN OF GERMANY

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ABSTRACT. An osteological re-study of the holotype skull of *Plesiosaurus brachypterygius* leads to a correction of several inaccuracies and misidentifications of the original description by von Huene and reveals additional facts on the cranial anatomy of this plesiosaur. Comparison with the type species, *Plesiosaurus dolichodeirus*, from the Lower Lias of England shows considerable differences in many parts of the cranial skeleton, even though the two species are generally so similar that their inclusion in the same genus proposed by von Huene, and agreed with by all subsequent authors, can be supported. *Plesiosaurus brachypterygius* is provisionally considered as a valid species distinguishable from the contemporaneous *Plesiosaurus guilelmiimperatoris* by its much shorter limbs, a difference that cannot be explained by ontogenetic variation as proposed by Storrs. *Plesiosaurus brachypterygius* was probably an ichthyophagous form that occurred rarely in the Posidonienschiefer fauna.

THE Posidonienschiefer of south-western Germany has been known for more than 200 years for its exquisitely preserved marine vertebrates from the Lower Toarcian (Lower Jurassic), which have been the focus of numerous studies. Best known of the fossil vertebrates of this formation are the ichthyosaurs, which are both most numerous and best preserved. Rhamphorhynchoid pterosaurs, and teleosaurid and metriorhynchid crocodiles are less common. Sphenodontians and dinosaurs are rarities that have received considerable interest. In contrast to this, one group of tetrapods in the Posidonienschiefer has been almost completely neglected in past decades: the plesiosaurs. These are not as common as the ichthyosaurs nor as spectacular as the pterosaurs, but there is a considerable number of almost perfectly preserved and excellently prepared skeletons. Most of these are still undescribed and form a scientific treasure that might aid considerably in understanding the origins, phylogeny, morphology and ecology of the group as a whole.

The present paper is concerned exclusively with a re-description of the holotype skull of *Plesiosaurus brachypterygius* von Huene, 1923, a taxon based on a complete and very well-preserved skeleton in the Institut und Museum für Geologie und Paläontologie der Universität Tübingen (GPIT). We studied this skull about two years ago and recognized several inaccuracies in the original description. The recent thorough re-evaluation of the type-species of *Plesiosaurus*, *P. dolichodeirus* Conybeare, 1824 by Storrs (1997) led to the decision to publish the results of our investigations to provide an improved basis of knowledge on this important Upper Liassic plesiosaur species.

SYSTEMATIC PALAEONTOLOGY

Order SAUROPTERYGIA Owen, 1860
Suborder PLESIOSAURIA de Blainville, 1835
Family PLESIOSAURIDAE Gray, 1825

Genus PLESIOSAURUS De La Beche and Conybeare, 1821

Type species. Plesiosaurus dolichodeirus Conybeare, 1824.

Distribution. Lower Jurassic (Hettangian–Toarcian) of Western Europe.

[Palaeontology, Vol. 43, Part 1, 2000, pp. 29–40] **© The Palaeontological Association**

Plesiosaurus brachypterygius von Huene, 1923

Text-figures 1–5

Holotype. The holotype and only described specimen is a complete skeleton kept in the Institut und Museum für Geologie und Paläontologie der Universität Tübingen (catalogued as GPIT von Huene 1923, pls 1–2).

Locality and horizon. Steinbruch 29, Ohmden near Holzmaden, Baden-Württemberg. Posidonienschiefer, Lias epsilon II, 4 (Unterer Schiefer), *Harpoceras falcifer* Zone, Lower Toarcian.

Specific diagnosis. A definite diagnosis can only be given after an osteological re-examination of *Plesiosaurus guilelmiimperatoris*. At present the two species are clearly distinguishable by the length of the fore- and hindpaddles, which are only about half as long in *Plesiosaurus brachypterygius* than in *P. guilelmiimperatoris* of comparable size. According to Dames (1895), *P. guilelmiimperatoris* only possesses 14 maxillary teeth as compared to 16 in *P. brachypterygius* and about 18 in *Plesiosaurus dolichodeirus* (Storrs 1997). From Dames' figures it appears, however, possible that there were originally two or three more maxillary teeth. Otherwise the skulls of the two Upper Liassic species are apparently quite similar. *P. brachypterygius* differs from *P. dolichodeirus* mainly by the following features of the skull: there are only 16 teeth in the maxilla; the orbit is smaller and more anteriorly situated; the processus ascendentes of the premaxillaries are shorter and separated posteriorly by the frontals; the jugal is excluded from the orbital margin; the foramen parietale is smaller; the frontals are excluded from the orbital margin but reach the foramen parietale posteriorly; the prefrontals are narrower and more elongate, and meet the postfrontals posteriorly; the occipital rami of the squamosals do not meet in the midline and are restricted to the occipital surface of the skull; the pterygoids meet in a midline suture below the basis cranii; there is no anterior interpterygoid fenestra; and there are clear foramina incisiva.

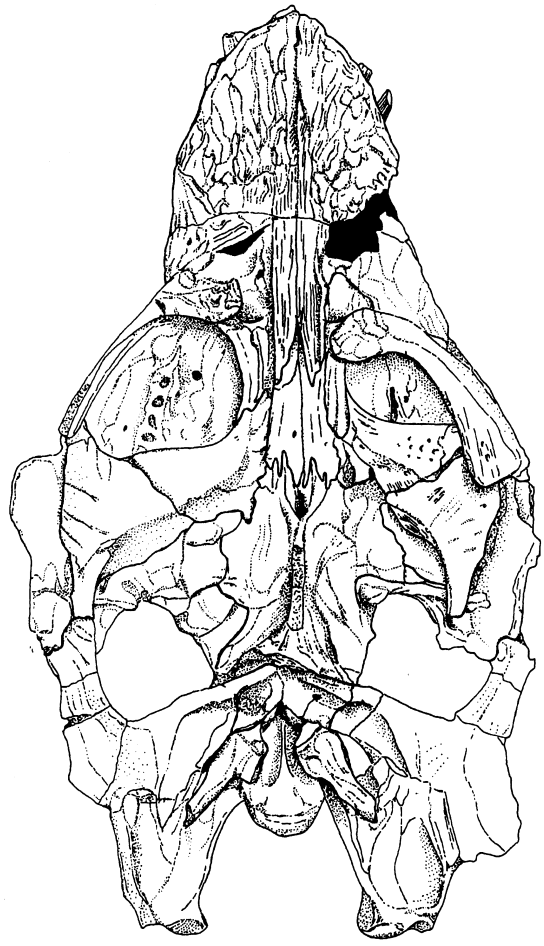
Description

Preservation. The skull is very much crushed dorsoventrally and many cracks run through the bones both on the dorsal and ventral surfaces of the skull (Text-figs 1–2). The bone substance itself is, however, well preserved and shows considerable detail. In some crucial areas sutures are difficult to trace. Where this is the case it has been clearly indicated in the following osteological description. All important measurements have been given by von Huene (1923) and need not be repeated here.

General outline and skull openings. In general outline the skull is relatively narrow. It appears wider than it was originally because of dorsoventral crushing. It probably was of quite constant width for most of its length except for the snout, which is moderately elongated and considerably pointed. It shows no constriction at the level of the maxillary-premaxillary contact. The external nares are small openings situated very close to the anterior orbital border (Text-figs 1, 3, 5). They are bordered by the premaxilla medially and anteriorly, maxilla laterally, and prefrontal posteriorly. The choanae are situated somewhat further posterior than the external nares, but almost on the same level (Text-figs 2, 4). They are very narrow and slit-like, and oriented exactly parallel to the long axis of the skull. The orbit is only well preserved on the left side. It is rounded with a slightly projecting posteroventral corner, and situated almost entirely in the anterior half of the skull (Text-fig. 1). The temporal fenestra is large and almost quadrangular in shape. It is considerably larger than the orbit (Text-figs 1, 3, 5).

Premaxilla. The border between premaxilla and maxilla is not clearly recognizable. This is mainly owing to the fact that a very prominent crack runs through the entire snout region at the position where the suture between these two bones should be expected (Text-figs 1–2), as compared to the type species, *Plesiosaurus dolichodeirus* (Storrs 1997). It is assumed here that the premaxilla ends behind the fifth alveolus of the upper dentition as in the type species (Text-figs 3–5). Apparently the snout is set off from the main portion of the skull, but this impression is caused by the incomplete preservation of the right alveolar margin at the level of the premaxillary-maxillary suture. On the left side it is clearly visible that the alveolar border of the snout was continuous without any constriction (Text-figs 1–2).

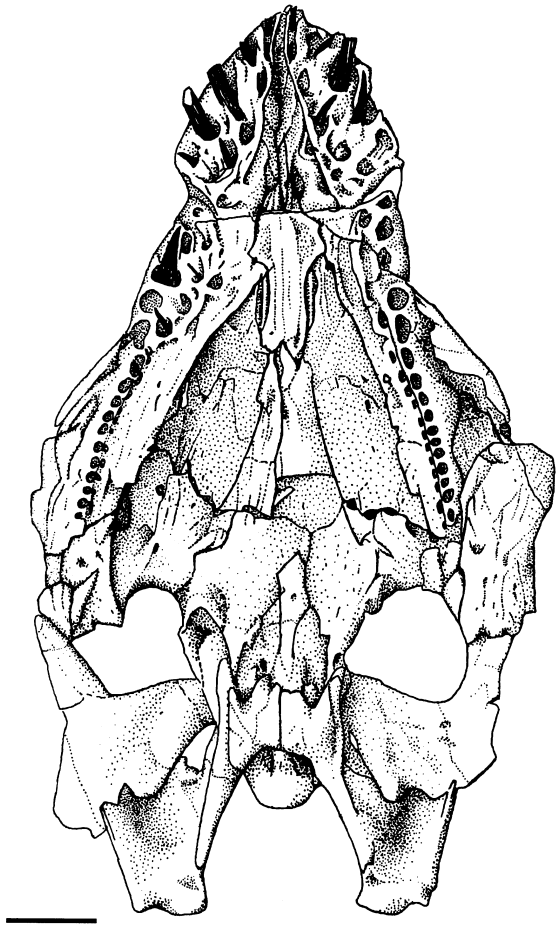
The premaxilla most probably bears five teeth. The anteriormost of these are oriented almost totally anteriorly, as is the case in most plesiosaurs, and judging from the size of the alveoli and the preserved basal parts of the tooth-crowns,



TEXT-FIG. 1. *Plesiosaurus brachypterygius* von Huene, 1923; skull of the holotype skeleton (GPIT von Huene 1923, pls 1–2) in dorsal view. Scale bar represents 20 mm.

the anteriormost pair of teeth was considerably smaller than the following. The second, third and fourth tooth-pairs are considerably larger than the first, as indicated by the remains of the teeth preserved in the specimen, particularly on the right side (Text-fig. 2). The fifth pair of premaxillary teeth was, apparently, at least somewhat smaller. The complete tooth crown preserved on the right side in the primary labial alveolus is extremely small as compared to the more anteriorly situated teeth (Text-fig. 2).

The dorsal surface of the premaxilla exhibits a very distinctive sculpture of anteriorly and anterolaterally-oriented ridges and furrows in the snout region proper (Text-figs 1, 3, 5). A similar sculpture was noted by Storrs (1997) in several specimens of *P. dolichodeirus* but considered as possibly artificial. In *P. brachypterygius* the surface sculpture of the bone is both so regular and prominently developed that there can be little doubt that it is a genuine feature. Each premaxilla forms a long and slender, strongly developed processus ascendens that extends posteriorly well beyond the anterior margin of the orbital aperture. The two processus ascendentes are divided posteriorly and thus expose the underlying frontals that form a triangular projection separating the two ascending processes for some distance (Text-figs 1, 3). The median premaxillary suture is very clear on the dorsal side for the entire length of the bone. The processus ascendens and the posterior half of the central strip of the snout region proper do not exhibit the sculpture otherwise ubiquitously present on the dorsal premaxillary surface. Posteriorly, the premaxilla contacts the frontal, and posterolaterally the prefrontal on the dorsal side of the skull. Ventrally the premaxilla is posteriorly sutured to the vomer.



TEXT-FIG. 2. *Plesiosaurus brachypterygius* von Huene, 1923; skull of the holotype in ventral view. Scale bar represents 20 mm.

Vomer. The vomers, which apparently are fused, or at least not showing a clear sagittal suture in ventral view, are deeply intruding as an anteriorly-narrowing, triangular process between the premaxillaries, ending anteriorly at about the level of the fourth premaxillary alveolus (Text-figs 2, 4). The ventral surface of the vomer does not bear any prominent surface sculpture. Posteriorly, the vomer contacts the anterior tips of the anterior pterygoid rami shortly behind the posterior margins of the choanae. The vomer forms the entire medial choanal margin. Anterior to the choanae it is slightly expanded, just to become narrower and narrower further towards the anterior. Between the vomer and the premaxillaries there are small elongated foramina incisiva situated at the level of the fourth to fifth premaxillary alveoli (Text-figs 2, 4).

Palatine. The palatines are large elements, the palatal surfaces of which are very well preserved and completely exposed. The palatine sends a long subtriangular process forwards along the lateral choanal margin, which it borders almost entirely. The maxilla is thus almost excluded from the choanal margin, only possibly contributing a tiny portion of the anterolateral margin of this aperture (Text-figs 2, 4). The ventral surface of the palatine is almost flat. Laterally the bone is sutured to the maxilla. As it is best seen on the left side, the maxillary-palatine suture, which is almost straight, is situated a considerable distance medial to the accessory alveolar row. Posteriorly, the palatine contacts the ectopterygoid. The suture is wide open on both sides of the skull (Text-fig. 2). Medially, the palatine contacts the pterygoid for most of its length in an almost straight suture paralleling the maxillary-palatine contact. A sutural

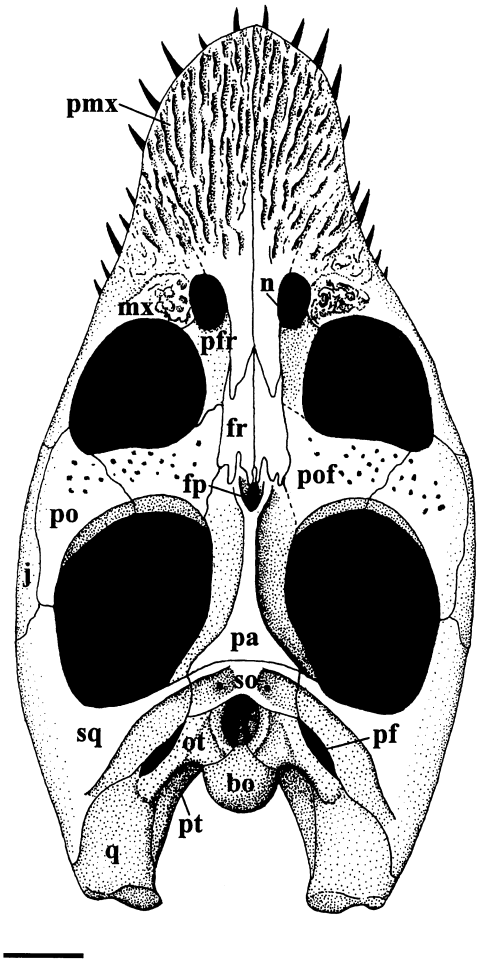
connection to the vomer is only established for a short distance immediately posterior to the choanal opening. As clearly shown on the left side, there is no real suborbital fenestra; the elements on the right side are just somewhat dislocated (Text-fig. 2).

Ectopterygoid. The ectopterygoid is a bone of considerable size. It contacts the pterygoid medially, palatine anteriorly, and maxilla and jugal laterally. The ventral surface of the bone is almost flat. Its posterior edge, forming the anterior margin of the fenestra subtemporalis, is sharpened. The medialmost portion of the posterior ectopterygoid margin is thickened into a bony knob in ventral view, which is also visible on the dorsal surface of the palate. The bone is also thickened where it establishes contact with the jugal (Text-figs 2, 4). A large foramen is present somewhat lateral to the centre of the right ectopterygoid, which is not present in its left counterpart (Text-fig. 2).

Pterygoid. The pterygoid is the largest palatal bone. It is a biramous element with a long, flattened anterior ramus and a slender posterior quadrate ramus, whereas a lateral ramus is almost entirely absent. There is no evidence for the original presence of an anterior interpterygoid fenestra; instead the two pterygoids anterior to the parashenoid are, as far as it can be observed, tightly joined by a clear sagittal suture (Text-figs 2, 4). The anterior rami only increase slowly in width from their anterior ends, where they contact the vomeral plate, backwards. At the level of contact with the ectopterygoid they reach their greatest width, being already separated, however, by the anteriormost extension of the processus cultriformis parasphenoidei. Further towards the posterior, the pterygoids form the lateral borders of the posterior interpterygoid fenestrae, and are considerably crushed so that it is hard to reconstruct their original outline. They were probably rather thin and delicate, originally almost vertically oriented plates (Text-fig. 4). The situation posterior to the interpterygoid vacuities is difficult to interpret. From the general structure of the basis cranii it is highly probable that the pterygoids were joined in the midline in this area, entirely covering the basioccipital and basisphenoid (Text-fig. 4). Evidence for this is provided by the fact that the basioccipital tubera are entirely covered in ventral view, and that there is a very marked step between the basioccipital condyle and the more anteriorly situated portion of the basis cranii (Text-fig. 2), as it is usually found in pliosaurs where the pterygoids are in contact sagittally. In plesiosaurs where this is not the case, as in, for example, *Muraenosaurus leedsii* (Andrews 1910; von Koken and Linder 1913; Maisch 1998), the ventral surfaces of basioccipital and basisphenoid are generally on the same level, whereas the distinct step seen in *Plesiosaurus brachypterygius* is found in taxa where the basis cranii is covered by the pterygoids, such as in *Leptocleidus* (Andrews 1922; Cruickshank 1997; pers. obs.), *Rhomaleosaurus* (Fraas 1910; Taylor 1992; Cruickshank 1994; pers. obs.) or *Liopleurodon* (Linder 1913; Andrews 1913; pers. obs.). A similar type of palate is found in Cretaceous elasmosaurids, although different in detail from that of pliosaurs (Carpenter 1997). It is, however, not known in *Plesiosaurus dolichodeirus* where the pterygoids are separated in the midline (Andrews 1896; Storrs 1997), and in some other Liassic plesiosauroid taxa, such as '*Plesiosaurus*' *macrocephalus* (Andrews 1896). The situation in *Plesiosaurus brachypterygius* is not totally unequivocal, sutures being practically impossible to identify in the crucial area because of considerable crushing. Nevertheless, a comparison of the specimen with, for example, *Muraenosaurus* on the one hand and *Rhomaleosaurus* on the other clearly indicates that the basis cranii must be entirely covered by the pterygoids directly anterior to the basioccipital condyle. This is in contrast to the interpretation of von Huene (1923) and, if correctly interpreted, would constitute a very significant difference from *Plesiosaurus dolichodeirus* as described and figured by Andrews (1896) and Storrs (1997). The quadrate rami of the pterygoids are long and slender. They extend back from the portion of the bone covering the basis cranii almost three quarters of the distance to the articulatory condyle of the quadrate (Text-figs 2, 4). They are inclined lateroventrally and continue anteriorly into prominent ridges lateral to the basis cranii.

Parasphenoid and basisphenoid. Most of the processus cultriformis of the parasphenoid is preserved. It is, however, somewhat dislocated towards the left side of the skull (Text-fig. 2). The parasphenoid forms the bony bridge between the posterior interpterygoid fenestrae. Anterior to these it expands somewhat, and apparently tapers out anteriorly into a rather narrow, pointed tip. There is not the least indication of a ventral sagittal crest on the parasphenoid as is found in, for example, many Cretaceous elasmosaurs. Instead, the ventral surface of the bone is practically flat. The basisphenoid, anterior to the portion covered by the pterygoids, is incompletely prepared. The foramina arteria carotici cerebralis posterius are, however, well visible on both sides just anterior to the pterygoid extensions (Text-figs 2, 4).

Basioccipital. The basioccipital is, as interpreted here, largely covered by the pterygoids in ventral view. Only the occipital condyle and a small posterior zone of the extracondylar part of the bone are visible (Text-fig. 2). The condyle itself is almost semi-hemispherical. The ventral surface of the extracondylar area bears a marked sagittal, ridge-like elevation, lateral to which it is slightly concave transversely (Text-figs 2, 4). The dorsal surface of the condyle is flattened and the dorsal margin slightly concave where it forms the ventral margin of the foramen occipitale magnum.



TEXT-FIG. 3. *Plesiosaurus brachypterygius* von Huene, 1923; skull of the holotype; reconstruction in dorsal view. Scale bar represents 20 mm.

Anterior to the condyle the dorsal surface of the basioccipital is partially exposed. It shows a low sagittal ridge lateral to which the long, anteroposteriorly elongated exoccipital facets, which are only slightly concave, are visible (Text-figs 1, 3).

Otoccipital. Both otoccipitals (exoccipito-opisthotics) are preserved. As noted by von Huene (1923), and as is usual in adult plesiosaurs, there is no indication of a suture subdividing these two elements on either side. The bones are not well preserved, and somewhat displaced anteriorly and laterally in almost symmetrical fashion (Text-fig. 1). The paroccipital processes are, as usual in plesiosaurs, long and slender, directed laterally as well as somewhat posteriorly and ventrally. The main parts of the otoccipitals are stout pillars of bone with considerably sharpened posterior edges (Text-figs 1, 3). The supraoccipital facets are largely exposed because of anterior displacement of the supraoccipital plate, but they show no detail. No nervous and vascular foramina are visible.

Supraoccipital. The supraoccipital is a wide, delicate plate of bone sutured to the occipital rami of the squamosals laterally, the parietals dorsally and the otoccipitals ventrally. The two latter sutures have opened so that the supraoccipital is now strongly displaced anteriorly (Text-fig. 1). It forms the dorsal margin of the foramen occipitale magnum, and does not contribute much to the lateral margins of this opening. The sagittal third of the bone is elevated;

laterally, deep pits are found which apparently lead into a pair of small foramina, which might be either for the ductus endolymphaticus or blood vessels (Text-figs 1, 3).

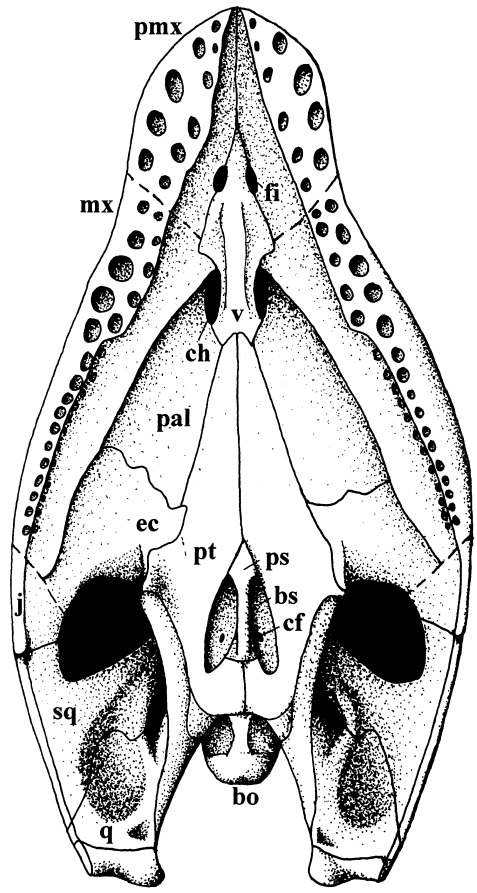
Maxilla. The anterior border of the maxilla cannot be satisfactorily determined because of the severe damage to the snout region. The maxilla is a large element that forms most of the anterior, and apparently also the entire ventral border of the orbit. There is no indication of a separate lacrimal, as described by von Huene (1923). The sutures he figured are obviously cracks (Text-fig. 1). The most dorsomedial extremity of the maxilla at the anteromedial corner of the orbit is considerably more sculptured than most of the rest of the bone and, because of crushing, has been markedly elevated on both sides of the skull, on superficial examination, giving the appearance of a separate element of the cranium (Text-figs 1, 3, 5). Under the binocular microscope there is, however, no suture visible between this portion of the maxilla and the rest of the bone. The maxillary-jugal suture is best seen on the left side of the skull in ventral view (Text-fig. 2). The jugal is largely as drawn and reconstructed by von Huene, except that it possesses a thin anterior extension that partially overlaps the posterior suborbital part of the maxilla, but does not reach the margin of the orbit. Posterodorsally the maxilla most probably established a short sutural contact with the postorbital (Text-figs 1, 3, 5). If this interpretation is correct, the anterior cheek region of *Plesiosaurus brachypterygius* would exhibit a rather 'nothosaurian' structure but be considerably different from the reconstruction of *Plesiosaurus dolichodeirus* presented by Storrs (1997, fig. 7). There is only evidence of 16 primary alveoli in the left maxilla (which is completely preserved; Text-fig. 2); von Huene (1923) recorded 17. He probably assumed that an additional tooth position was present at the level where the prominent crack referred to above runs through the snout. There is, however, no indication of either a primary or an accessory alveolus in this area. The second to fourth alveoli are considerably larger than the following, the third and fifth being the largest. As can be expected, there is a complete series of smaller accessory alveoli, the secondary tooth-row medial to the row of primary teeth. Medial again to this secondary tooth row, the maxilla extends considerably onto the palatal surface. It contacts the palatine and ectopterygoid medially. In contrast to elasmosaurids, but in accordance with Storrs' (1997) reconstruction of *Plesiosaurus dolichodeirus*, the maxilla is almost completely exluded from the choana (Text-figs 2, 4).

Jugal. The jugal is a large flat bony plate that is dorsally connected to the very broad postorbital and intervenes between the maxilla and squamosal. As noted above, there is little indication that the jugal entered the orbital margin at all. It was apparently excluded by a short contact between maxilla and postorbital. Anteriorly the jugal is drawn out into a thin rectangular projection that covers most of the lateral maxillary surface up to the level of the twelfth maxillary alveolus. The suture is well seen on the left side of the skull (Text-fig. 2). Posteriorly the contact with the squamosal was apparently relatively simple, but this cannot be totally clarified because both jugals, particularly the right one, have been considerably crushed and displaced (Text-figs 1–2). Posteroventrally the jugal ends freely in a small pointed process, as described and figured by von Huene (1923) and Brown & Cruickshank (1994), which can only be interpreted as a remnant of the lower zygomatic arch (Text-fig. 5).

Prefrontal. There is no evidence of a separately ossified nasal in the specimen, *contra* von Huene (1923). The prefrontal, however, is well ossified and clearly identifiable as an individual skull element. It borders the external narial opening posteriorly, as in *Plesiosaurus dolichodeirus*. In contrast to the latter species, it extends very far posteriorly and forms the entire dorsal orbital margin, as is clearly evident on the left side of the skull where the orbit and its margins are almost totally intact (Text-figs 1, 3, 5). It meets the postfrontal posteriorly, thereby completely excluding the frontal from the orbital border. This is a clear and important difference from *Plesiosaurus dolichodeirus*. Because of dorsoventral crushing, the supraorbital portion of the prefrontal is markedly elevated above the posteronarial part (Text-fig. 1). This probably prompted von Huene to assume the presence of two elements instead of one.

Frontal. The frontal is a small, subrectangular, elongated element. Its dorsal surface is almost flat. Anteriorly it contacts the processus ascendens of the premaxilla; laterally it is excluded by the prefrontal and postfrontal from the orbital margin, and forms a much longer suture with the latter. Posteriorly, the frontal contacts the parietal in a complex and deeply interdigitating suture well behind the posterior margin of the orbit (Text-figs 1, 3). The frontals enter the anterior margin of the foramen parietale.

Parietal. The large parietals, which are practically fused along their midline, are very squashed. Together they form a highly elevated sagittal crest, much of which is unfortunately broken off in this specimen (Text-fig. 1). This crest starts immediately behind the foramen parietale and continues up to the posterior margin where it merges into a transverse crest forming the posterior parietal margin. The parietal is not overlapped by the squamosal; instead, the ramus occipitalis of the latter is entirely restricted to the occipital surface of the skull (Text-figs 1, 3). Anterolaterally the

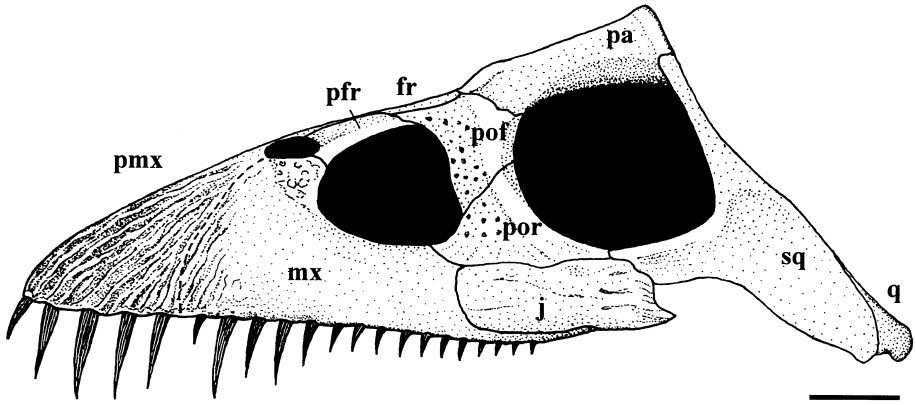


TEXT-FIG. 4. *Plesiosaurus brachypterygius* von Huene, 1923; skull of the holotype; reconstruction of the palate in ventral view. Scale bar represents 20 mm.

parietal contacts the large postfrontal, and there was possibly also a short parietal-postorbital contact. Unfortunately the lateral portions of the parietals are so squashed onto the palatal bones and so inadequately prepared that it is a challenge to delimit the bones (Text-fig. 1). The parietals form the lateral and posterior margins of the foramen parietale. The lateral margins of the foramen are raised. The foramen itself is rather small and elongated elliptical in shape with a pointed posterior projection (Text-figs 1, 3).

Postfrontal. Both postfrontals are well preserved, particularly the left one which is still perfectly articulated with the surrounding bones. It forms approximately the dorsal half of the very long and wide postorbital bar. It is of roughly rectangular shape with anteromedial and anterolateral projections. The zone where the original lateral surface of the bone merges into the original posterior surface is marked by a prominent ridge-like elevation, which also extends in similar fashion onto the postorbital. Part of the dorsal surface of the postfrontal is covered by numerous tiny foramina, as is the postorbital (Text-figs 1, 3, 5).

Postorbital. The postorbital forms the ventral half of the postorbital bar. Ventrally it is much expanded both anteriorly and posteriorly, forming a long, almost straight, sutural contact with the jugal and probably contacting the maxilla with its anterior extremity. Posteriorly it also establishes contact with the squamosal by means of a long and narrow process. Whether a posteromedial postorbital-parietal contact was also present is not clear but appears unlikely (Text-figs 1, 3, 5).



TEXT-FIG. 5. *Plesiosaurus brachypterygius* von Huene, 1923; skull of the holotype; reconstruction in left lateral view. Scale bar represents 20 mm.

Squamosal. The squamosal is a large triradiate element forming most of the lateral and posterior margins of the fenestra supratemporalis. The anterior zygomatic ramus is a narrow, flat plate, much distorted on both sides of the skull that anteriorly abuts against the jugal and postorbital. This bar widens posteriorly and ventrally into a short quadrate ramus that has been detached from the quadrate on the right side and squashed into almost the same plane as the zygomatic ramus (Text-fig. 1). The occipital ramus extends medially from the large, almost quadrangular, central part of the squamosal. It is entirely restricted, as noted above, to the occipital surface of the skull and the two squamosals do not meet in the midline (Text-figs 1, 3, 5). This is a further marked difference from *Plesiosaurus dolichodeirus*.

Epipterygoid. Both epipterygoids are partially exposed in dorsal view but they are much too deformed to be of any value (Text-fig. 1).

Quadrate. The quadrate is a high bone almost rectangular in posterior view. Ventrally it bears the articulatory trochlea which clearly consists of two parts; a strongly convex medial and equally strongly convex lateral portion (Text-figs 1–4). The posterior surface bears a marked ridge extending from the medial convex portion of the trochlea in laterodorsal direction up to the dorsolateral corner of the bone. Medially and laterally to this ridge the posterior surface is markedly concave (Text-fig. 1). The lateral surface of the quadrate is almost flat and meets the posterior surface approximately at right angles. The anterior surface of the bone is deeply excavated above the articulatory trochlea (Text-figs 2, 4). On the anterior surface a well-marked depression is found immediately dorsal to the medial portion of the articulatory trochlea (Text-figs 2, 4).

Dentition. Of the maxillary dentition, only the third-right primary maxillary tooth is well preserved and complete (Text-fig. 2). It is slender, conical and lingually curved, bearing very fine ridges both lingually and labially. The same general shape of the teeth is also found in the remaining portions of the premaxillary fangs. The shape and ornamentation of these teeth are typically plesiosaurid.

Comparison

Plesiosaurus dolichodeirus, the type-species of the genus known only from the Lower Liassic of Great Britain, has been described by Conybeare (1824), Owen (1865), Andrews (1896) and, most recently, by Storrs (1997) who provided a modern diagnosis of both the genus *Plesiosaurus* and its type species.

In comparing *Plesiosaurus brachypterygius* with *P. dolichodeirus*, a large number of differences in cranial morphology can be noted. Storrs (1997) noted the more robust skull and much larger pineal foramen of *Plesiosaurus dolichodeirus* as potentially distinguishing characters between the Lower Liassic species and the Upper Liassic *Plesiosaurus* specimens.

To this can be now added: the smaller and more anteriorly situated orbits; the more posteriorly situated

external nares; the presence of only 16 maxillary teeth; the more slender and anteroposteriorly oriented choanae; the clear presence of foramina incisiva; the exclusion of the jugal from the orbital margin; the contact of the pterygoids below the basis cranii; the lack of an anterior interpterygoid fenestra; the much larger size and posterior extent of the prefrontal; the exclusion of the frontal from the orbital margin, and its larger posterior extent; the contribution to the border of the foramen parietale and serrated suture with the parietal; and the lack of contact between the occipital rami of the squamosals and their restriction to the occipital surface of the skull in *Plesiosaurus brachypterygius*.

Even though these differences are numerous and (if all are correctly recorded, which is not beyond doubt in some cases) quite considerable, the general similarities between *Plesiosaurus dolichodeirus* and *P. brachypterygius*, both in the cranial and postcranial skeleton, strongly indicate a close relationship between the two species. Unfortunately, at present there are no clear cranial synapomorphies for the two species. These may only be identifiable after a complete revision of the Lower Jurassic plesiosaurs is available and a proper phylogenetic analysis can be carried out.

DISCUSSION

Storrs (1997) expressed the opinion that, apart from the type species, *Plesiosaurus guilelmiimperatoris* Dames, 1895, *Plesiosaurus brachypterygius* von Huene, 1923 and *Plesiosaurus tournemirensis* Sciau, Crochet and Mattei, 1990 were probably the only species correctly referred to that genus. He regarded the latter two species as synonyms of *P. gulelmiimperatoris*. Even though this is not improbable, because all the three referred species are from approximately the same stratigraphic level (Lower Toarcian) and the same sedimentary basin, it is here considered unwise to prematurely discard these taxa, which are both based on excellently preserved and complete material. Considerable proportional differences between *P. brachypterygius* and *P. guilelmiimperatoris* were noted by von Huene (1923), and these are considered here as probably of specific value. They are not as minor as Storrs (1997) assumed. The holotype of *P. guilelmiimperatoris* in Berlin lacks much of the fins, but those of the Stuttgart specimen (the holotype of *Seeleyosaurus holzmadensis* White, 1940) described by E. Fraas in 1910 but largely destroyed in World War II, are as completely and perfectly preserved as the Tübingen skeleton. Even though the Tübingen skull is larger than that of the Stuttgart skeleton and the animals are of approximately the same size, both the fore- and hindfins of the latter are almost twice as long as in *P. brachypterygius* (von Huene 1923; pers. obs.). This is certainly a difference that cannot be considered as ontogenetic variation, nor is it very likely to be within the range of individual variation within one species. *P. brachypterygius* should therefore remain a valid taxon until a complete and thorough revision of the Holzmaden plesiosaurs has been carried out.

Plesiosaurus brachypterygius was evidently a formidable aquatic predator. Its dentition suggests that it probably fed mainly on fish, belonging to the 'piercing guild' of Massare (1987). This would be consistent with the ecological picture for the marine reptiles of the Holzmaden area. The two groups of marine offshore reptiles represented are ichthyosaurs and plesiosaurs. The crocodiles probably inhabited the coastal waters (Westphal 1962). The ichthyosaurs are represented by medium-sized and large forms. The medium-sized forms, all of which belong to the genus *Stenopterygius*, probably fed largely on dibranchiate cephalopods with fish only constituting a minor part of their diet, as indicated by numerous finds with fossilized stomach contents (pers. obs.). The plesiosaurs, which are represented by at least four species (Robin O'Keefe, pers. comm. 1997; pers. obs.), therefore probably filled the ecological niche of medium-sized ichthyophagous predators in the fauna of the Posidonienschiefer. Their rare occurrence by comparison with ichthyosaurs and marine crocodiles, which is in strong contrast to both the Upper Liassic and the Middle (Oxford Clay) and Upper (Kimmeridge Clay) Jurassic deposits of Great Britain that yield reasonable numbers of marine reptiles, remains something of a mystery. Only about a dozen articulated plesiosaurs are known from the Posidonienschiefer, and just two of these belong to the Pliosauridae, whereas there are hundreds, and probably thousands, of articulated or partially articulated ichthyosaurs. More information on palaeoenvironment, and the aut- and synecology of these marine reptiles must be available before the reasons for this discrepancy can be tackled adequately.

Acknowledgements. Our sincere thanks go to Frank Westphal and Wolf-Ernst Reif, Tübingen, for constant scientific support, encouragement and constructive criticism. Rupert Wild (Stuttgart) provided access to specimens in his care. The members of the Tübingen Vertebrate Research Group, particularly Rainer Schoch and Andreas T. Matzke, as well as Leslie Noè (Derby) and Robin O'Keefe (Chicago) are thanked for extensive discussion. The paper benefited very much from the constructive criticism of A. R. I. Cruickshank (Leicester) and an anonymous reviewer.

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Typescript received 16 November 1998
Revised typescript received 16 September 1999

APPENDIX

Abbreviations used in text-figures

bo, basioccipital
bs, basisphenoid
cf, foramen arteria carotis interna
ch, choana
ec, ectopterygoid
fi, foramen incisivum
fp, foramen parietale
fr, frontal
j, jugal
mx, maxilla
n, naris
ot, otoccipital
pa, parietal
pal, palatine
pf, fenestra posttemporalis
pfr, prefrontal
pmx, premaxilla
po, postorbital
pof, postfrontal
ps, parasphenoid
pt, pterygoid
q, quadrate
so, supraoccipital
sq, squamosal
v, vomer