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THE CROCODILIAN *GONIOPHOLIS SIMUS* FROM THE LOWER CRETACEOUS OF NORTH-WESTERN GERMANY

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ABSTRACT. A re-evaluation of crocodilian material referred to *Goniopholis* from the Berriasian (Lower Cretaceous) of north-western Germany is presented, based on the description of a natural mould of a skull and mandible in the collections of the Institut für Paläontologie, Bonn. Along with other material from the Obernkirchen Sandstone of the Bückeburg Member of the German 'Wealden', the Bonn specimen is referred to *G. simus* Owen. Two previously recognized species of *Goniopholis* from Germany, '*G. pugnax*' Koken and '*G. minor*' Koken, are considered to be *nomina dubia*, because they are based on undiagnostic material, much of which can no longer be located. Two complete skeletons from the Hauterivian–Barremian of Bernissart, Belgium, previously assigned to *G. simus*, are considered to be representative of distinct species and should be redescribed and renamed. *G. simus* is restricted to the Berriasian of the Wessex-Weald Basin of southern England and the Niedersachsen Basin of north-western Germany. This is the first clear evidence of interchange between the non-marine vertebrate faunas of these two regions.

SPECIES of *Goniopholis* represent some of the northern hemisphere's most common and distinctive crocodilians during the Late Jurassic and Early Cretaceous. They are among the earliest crocodilians to resemble superficially the majority of living forms, with a broad, dorso-ventrally flattened rostrum, long tail and stout limbs; some species are estimated to have attained lengths in excess of 3 m (Hooley 1907). Unlike eusuchians, species of *Goniopholis* possess choanae secundare not completely contained within the pterygoids, amphicoelous vertebrae, a biserial paravertebral shield and a rigid gastral shield composed of interlocking, polygonal osteoderms. The type species, *Goniopholis crassidens*, was erected by Owen (1841) based on a partial, disarticulated skeleton from the Lower Cretaceous of Swanage, Dorset, southern England. The osteoderms from the paravertebral shield of this species are rectangular, with a well-developed processus articularis. Although now known to occur in many Mesozoic taxa, at the time of the specimen's discovery osteoderms such as these were not known for any other fossil crocodilian, and it was on the distinctiveness of this feature that Owen based the name *Goniopholis*, literally meaning 'angle scale' (Owen 1841, p. 72).

During the Late Jurassic and Cretaceous goniopholidids were widespread throughout the northern hemisphere, with abundant material being known from Europe, Asia and North America (Buffetaut 1982; Steel 1989). In Europe, the majority of *Goniopholis* species are known from the Wealden and Purbeck groups of southern England, where as many as five distinct species have been recognized (Owen 1841, 1849–84, 1878, 1879; Hulke 1878; Hooley 1907). With the exception of two nearly complete skeletons referred to *G. simus* from Bernissart, Belgium (Dollo 1883), the presence of *Goniopholis* in the Upper Jurassic and Lower Cretaceous of continental Europe, particularly in late Tithonian and Berriasian strata, has been uncertain. This is due primarily to the fragmentary nature of the material, which consists of isolated teeth, vertebrae, osteoderms, limb elements and, very rarely, skull fragments (Koken 1883, 1886, 1887, 1896; Edinger 1938; Jonet 1981; Huckriede 1982; von Oekentorp 1984; Buffetaut 1986*b*; Buscalioni and Sanz 1987*a*, 1987*b*; Norman 1987; Buffetaut *et al.* 1989; Cuny *et al.* 1991; Ortega *et al.* 1996).

In north-western Germany, material referred to *Goniopholis* was first discovered during the latter

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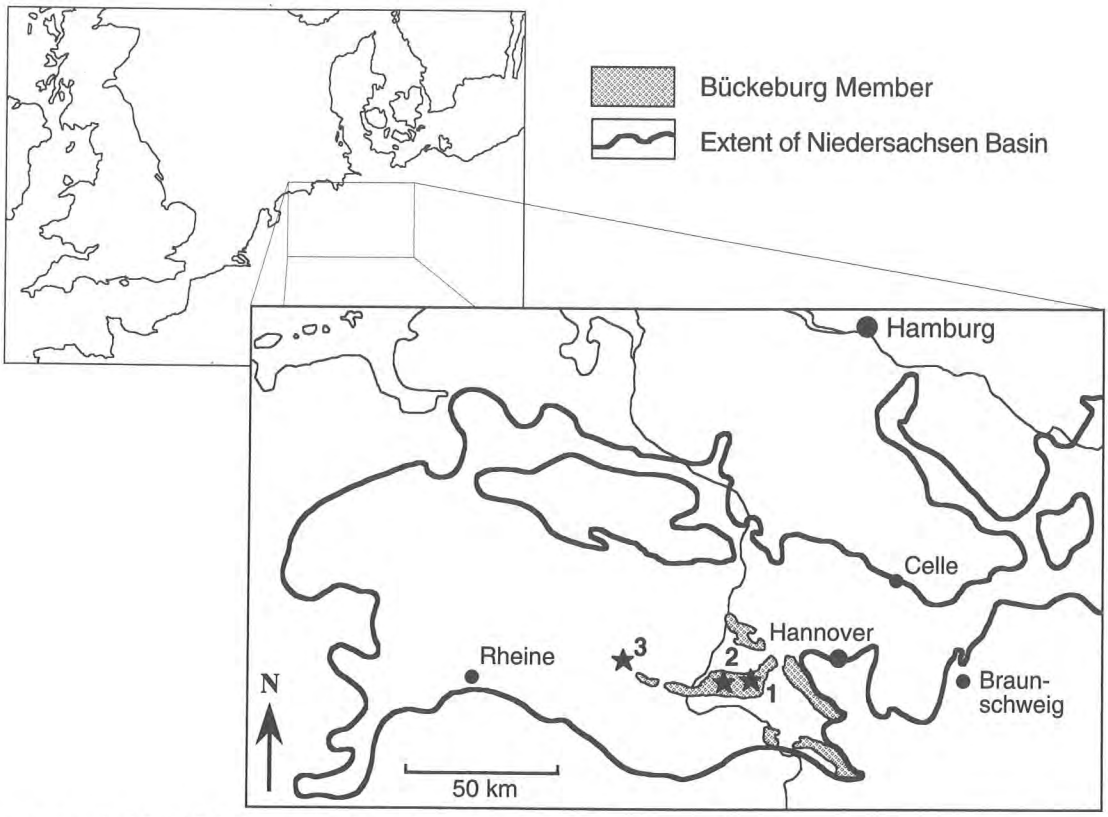
half of the nineteenth century. These specimens were collected from calcareous claystone units associated with coal seams in the Lower Obernkirchen Sandstone of the Bückeburg Member (Lower Cretaceous), at sites near Osnabrück, Wackerfield, Wendthagen and Obernkirchen (Text-fig. 1),



TEXT-FIG. 1. The Bückeburg Member of the 'Wealden' Formation of north-western Germany (after Pelzer 1988), and localities that have produced remains referable to *Goniopholis*. 1, Bückeburg; 2, Obernkirchen; 3, Osnabrück.

and were first described by Ernst Koken in 1887. Koken (1887) erected two species: '*G. pugnax*', based on a partial otoccipital, isolated teeth, vertebrae, rib fragments, a humerus, an ulna and several osteoderms from the gastral shield; and '*G. minor*', based only on cervical vertebrae and a partial osteoderm from the paravertebral shield.

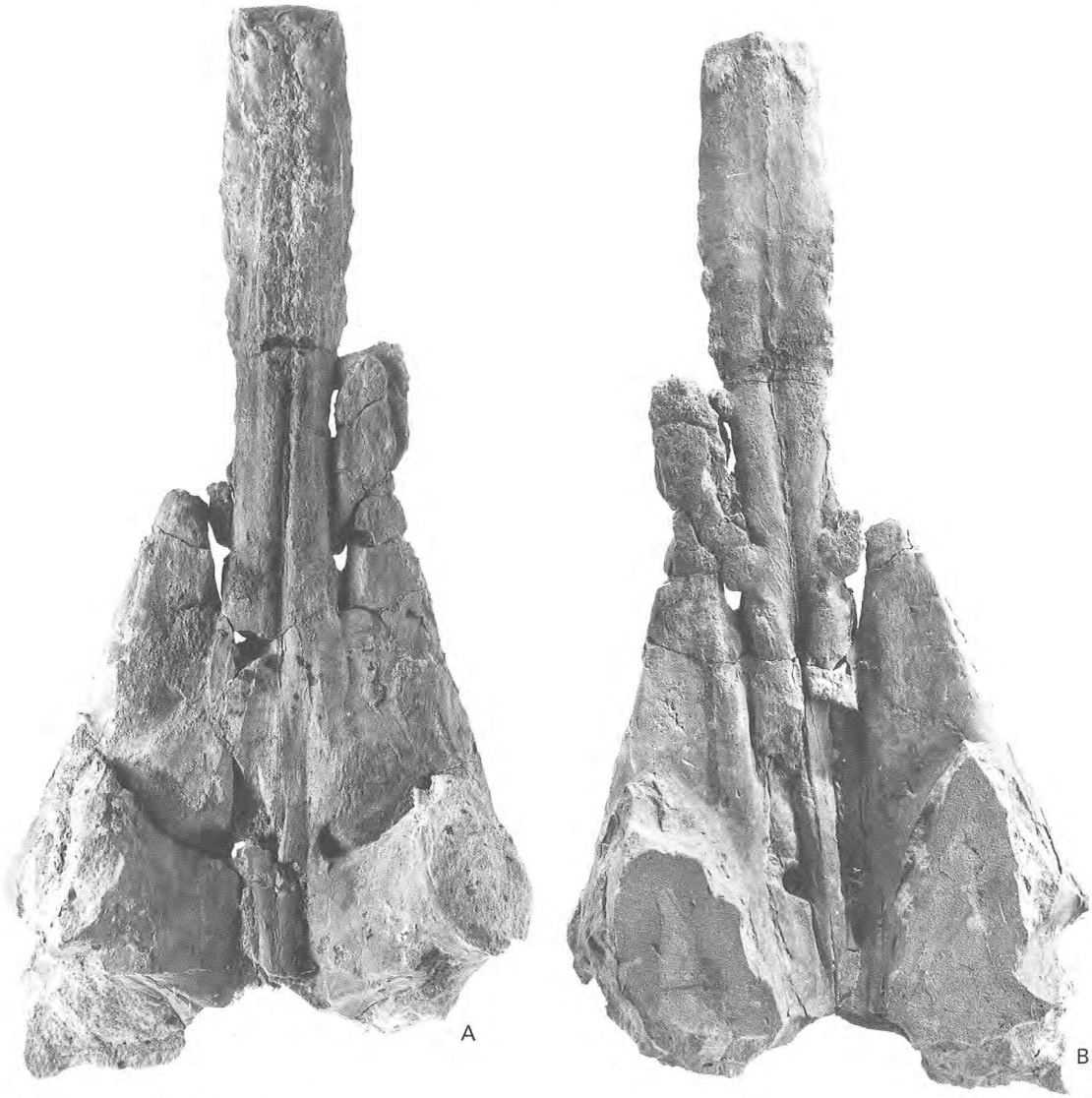
In 1896, Koken supplemented his original description of '*G. pugnax*' by referring a relatively complete rostrum maxillae and partial dentary, presented to him for study by the Bückeburg Natural History and Archaeology Society, to this species (Koken 1896). These specimens had been collected by the society from an exposure of 'Wealden Sandstone' in the vicinity of Bückeburg, and were apparently found in association, leading Koken to assume that they were from the same animal. Koken's reason for referring this material to '*G. pugnax*' was based on the stratigraphy of the site and the similarity of the teeth to those described in his original paper. Unfortunately, apart from the ulna (MB R2032), the corpus of a cervical vertebra (IGPMbg 1854) and three isolated teeth (MB R2077.1–3) referred to '*G. pugnax*', and the portion of an osteoderm from the paravertebral shield (IGPMbg V-Re-1-8) referred to '*G. minor*', all the material described by Koken (1887) can no longer be located and was presumably lost or destroyed during World War II.

TEXT-FIG. 2. *Goniopholis simus* (Owen, 1878); IPB R359 in dorsal aspect; ×0·2.

Between 1900 and 1930 additional crocodilian specimens, including natural moulds of as many as eight skulls, a right ramus mandibulae and isolated postcranial elements, were collected from an exposure of Obernkirchen Sandstone at a quarry near Obernkirchen by Max Ballerstedt of the Gymnasium Adolfinum, Bückeburg. Five of these specimens are missing, and are now represented only by photographs, held in the Georg-August-Universität, Göttingen, and four casts: BMNH R5262, a small (< 300 mm long) skull; GPIMü Pr. 280, another small skull; and BMNH R5260 and BMNH R5261, the two halves of a right ramus mandibulae. The three remaining specimens include natural moulds of the following material: the dorsal and ventral surfaces of a skull (IMGPGö 741-6); the ventral surface of a skull, minus the rostral half of the maxillae and premaxillae (GAB Sch. 1); and the dorsal surface of a skull (DFMMh Sch. 1a). Although the Ballerstedt skulls have never been studied, endocasts of the braincase and tympanic cavities obtained from two of these specimens were described by Edinger (1938) and referred to '*G. pugnax*' and '*G. minor*' respectively. Specimen numbers for these specimens were not cited by Edinger, and we have been unable to locate this material.

Crocodilian fragments from an Early Cretaceous (Aptian) site near Nehden, western Germany, originally noted by Huckriede (1982) and von Oekentorp (1984), were tentatively identified as *Goniopholis* sp. by Norman (1987). This material included two well preserved thoracic vertebrae, a number of osteoderms from the paravertebral shield, a partial left humerus and what may be the distal end of a left femur. Identification was based on direct comparison of the vertebrae with the specimens of *G. simus* from Bernissart (Norman 1987).

In 1992, during the re-organization and cataloguing of fossil collections in the Institut für Paläontologie, Universität Bonn, a large sawn block preserving the natural mould of the skull and mandible, and the endocast of the rostrum maxillae and orbital region of a species of *Goniopholis* was discovered (IPB R359; Text-figs 2–3). No information was associated with the specimen, so the



TEXT-FIG. 3. *Goniopholis simus* (Owen, 1878); IPB R359; endocast of the rostrum maxillae and orbital region in (A) dorsal aspect and (B) ventral aspect; ×0·35.

location from which it was collected along with the history of its discovery and acquisition by the Institut für Paläontologie are unknown. Nevertheless, the lithology of the matrix of the specimen suggests that it is derived from one of the calcareous claystones of the Upper Obernkirchen Sandstone of the Bückeburg Member of the north-western German 'Wealden' Formation. Only two specimens of the crocodilian *Pholidosaurus schauburgensis* and an isolated tooth, tentatively referred to *Goniophilis*, are recorded by Koken (1887) as coming from this unit.

The purpose of this paper is to review the taxonomic status of *Goniopholis* in north-western Germany based on the description of the Bonn specimen. This work forms part of a larger study on the taxonomy and evolutionary position of *Goniopholis* currently being undertaken by the first author.

Anatomical nomenclature

We have followed the anatomical terminology codified in *Nomina Anatomica Avium* (Baumel and Witmer 1993), and that outlined in Frey (1988), Rauhe (1993), Witmer (1995) and Rossman (1996). This terminology is used purely in a topographic sense and we do not imply any homology in the sense that it relates to common ancestry. Following Clark (1986), the fused exoccipital and opisthotic of crocodilians are referred to as the otoccipital. Cranial and caudal are used throughout in preference to anterior and posterior, except in the skull where rostral replaces cranial.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; BMNH, The Natural History Museum, London (formally the British Museum (Natural History)); CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; CMNH, Cleveland Museum of Natural History, Cleveland, Ohio, USA; DFMMh, Dinosaurier-Freilichtmuseum, Münchehagen, Germany; GAB, Gymnasium Adolfinum, Bückeburg, Germany; GPIMü, Geologisch-Paläontologisches Institut der Universität Münster, Germany; IMGPGö, Institute und Museum für Geologie und Paläontologie der Georg-August-Universität, Göttingen, Germany; IGPMbg, Institut für Geologie und Paläontologie der Philipps-Universität, Marburg, Germany; IPB, Institut für Paläontologie der Universität Bonn, Germany; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MB, Museum für Naturkunde der Humbolt-Universität, Berlin, Germany; MHNBP, Natural History Museum, Boulogne-Sur-Mer, France; OMNH, Oklahoma Museum of Natural History, Oklahoma, USA; TMM, Texas Memorial Museum, University of Texas at Austin, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

Abbreviations used in the figures are listed in the appendix.

SYSTEMATIC PALAEONTOLOGY

Order CROCODILIA Gmelin, 1788
Family GONIOPHOLIDIDAE Cope, 1875

Genus GONIOPHOLIS Owen, 1841

Goniopholis simus Owen, 1878

Text-figures 2–12

Holotype. BMNH 41098 and 41098a (the counter slab); a skull minus the mandible, along with two osteoderms from the paravertebral shield (Text-fig. 4).

Type locality. Collected some time during the late 1870s from the 'Middle' Purbeck of either the Lulworth or Durlston Formation, Swanage, Dorset, southern England (Owen 1878). The precise locality is unknown.

Stratigraphical range. Berriasian (Lower Cretaceous).

Distribution. Wessex-Weald Basin of southern England and Niedersachsen Basin of north-western Germany.

TEXT-FIG. 4. *Goniopholis simus* (Owen, 1878); BMNH 41098; holotype skull in dorsal aspect; × 0·35.

Revised diagnosis. Differing from all other crocodilian taxa in the possession of the following features: prefrontal contacts postorbital, excluding the frontal from the dorsal margin of the orbit; processus paroccipitalis and lamina ventrolateralis of the squamosal do not contact the quadrate; canalis quadratosquamosootoccipitalis exposed laterally, continuing caudally on the quadrate as a shallow sulcus; fenestra premaxillaris absent; diamond-shaped fossa premaxillaris on the rostral floor of the vestibulum nasi; transversely elongate foramen squamosootoccipitale.

G. simus also differs from other species of *Goniopholis* in the reduction of external sculpture on the nasal and maxilla.

DESCRIPTION OF THE BONN SPECIMEN

Preservation

The Bonn specimen is typical of the Obernkirchen Sandstone in being a natural mould. Impressions of the dorsal surface of the skull and portions of mandible are preserved (Text-fig. 2). Furthermore, the internal cavities of the rostrum maxillae and orbital region are preserved as a solid endocast (Text-fig. 3). No counter slab to the specimen has been found, so the nature of the ventral surface of the skull, lateral extent of the maxilla, jugal and quadratojugal, and caudomedial surfaces of each ramus mandibula cannot be commented on. Nevertheless, some aspects of the structure of the palate can be described from the impressions of the dorsal (internal) surfaces of the palatal elements preserved on the ventral surface of the endocast of the rostrum maxillae (Text-fig. 3B). The impressions of the mandible comprise a portion of left ramus rostral to the supraangular, and the lateral surface of the right ramus caudal to the end of the tooth row. Owing to the manner in which the slab was sawn, an impression of the articular region of the left ramus is missing. This permits a complete reconstruction of the mandible except for the portion of the rostrum rostral to a point level with the fourth dentary alveolus, the medial surface of the ramus caudal to the rostral limit of the fenestra mandibularis externa, and the dorsal surfaces of the supraangular and articular, including the fossa articularis quadratica and fossa retroarticularis. It is assumed, but cannot be demonstrated, that the impression of the lateral surface of the processus retroarticularis is preserved in entirety. No teeth were preserved in the mandible; however, a cut edge on the slab revealed a cross section through an isolated tooth. An endocast of the braincase was not present with the specimen when it was rediscovered. The broken surfaces along the caudal margin of the preserved endocast indicate that this part of the specimen may have been lost during collection. There is no evidence of any soft tissue elements on the endocast, and most of the sutures, foramina and fenestrae have close to what would be considered perfect definition had a cast of the skull been made without skin or tissue.

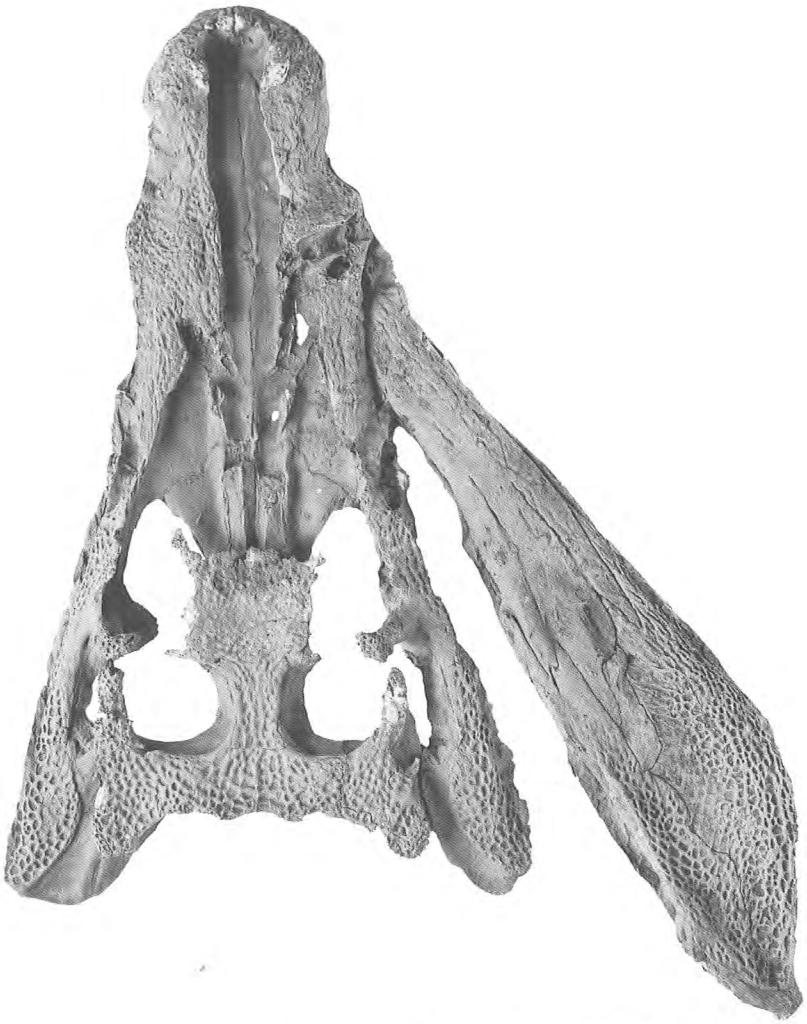
The mandible was not preserved in occlusion with the skull, nor were its rami in articulation. Assuming that the face on which the specimen is preserved (that shown in Text-fig. 2) represents the upper surface of the slab, the ramus mandibulae was preserved medial side up, sub-parallel to the right side of the skull. Hence, the portion of this ramus rostral to the end of the tooth row originally lay on top of the palate. The left ramus mandibulae was preserved lateral side up, on the same side as the right ramus mandibulae, but oriented perpendicular to it with the symphysial portion of the rostrum mandibulae alongside the right maxilla.

So that both the external and internal morphology of the bones could be examined, a series of silicon rubber casts were made using the specimen as a mould. These yielded a 'positive' copy of the skull and mandible. The first cast (Text-fig. 5) covered the entire skull and the caudal portion of the right ramus mandibulae. Before this cast was made the specimen received only basic cleaning, and the endocast of the rostrum maxillae and orbital region was left in place, preventing any replication of surfaces directly dorsal to these cavities. Due to the complexity of the caudal part of the skull, the portion of the cast that included the skull table could not be retrieved without damaging the specimen.

Prior to the making of the second cast, the endocast of the rostrum maxillae and orbital region was removed. As a result, the second cast duplicated the entire dorsal surface of the skull. Further silicon rubber casts were made of the left ramus mandibulae and the isolated tooth. During the removal of the former cast, the impression of the medial surface of the splenial was mostly destroyed.

Skull (Text-figs 6–9)

Form and proportions. The rostrum maxillae forms *c.* 60 per cent. of the total length of the skull, with the premaxillary portion being only slightly narrower than the maxillary portion, which, at its widest point, is still 20 per cent. narrower than the skull table. In dorsal aspect, the lateral margins of the rostrum maxillae are strongly concave for the reception of the mandibular pseudocanines at the suture between the premaxillae and maxillae. The rostrum maxillae is remarkably flat dorsoventrally, its maximum median depth being only 20 per cent. of its maximum width. The same is also true for the basicranium, where the height from the bottom of the foramen magnum to the horizontal plane of the skull table is less than 25 per cent. of the width of the latter. The skull table is 1·45 times broader than it is long, and in dorsal aspect the lateral margins are gently convex lateral to the foramina supratemporalia externa, but become concave caudally. In lateral aspect the skull table is only slightly elevated from the rostrum maxillae, the two regions being separated by a transverse, rostrally concave, crescent-shaped crista interobitalis. The medial margin of the orbit is almost level with the lateral margin of the foramen supratemporale externum, such that the interorbital plate is extremely broad. Sculpture on the skull consists of distinct, predominantly round, 2–4 mm wide pits, which are best developed on the skull



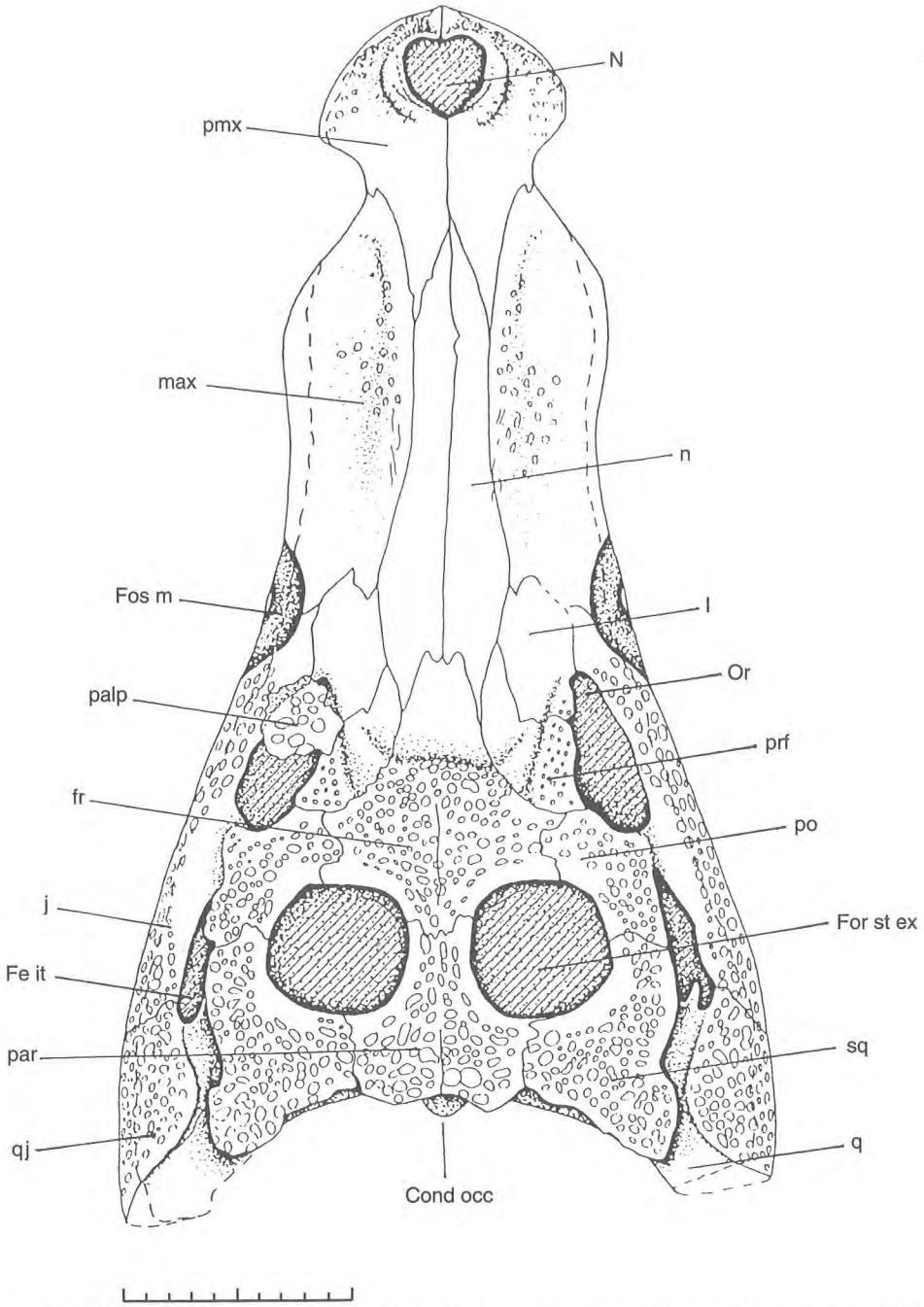
TEXT-FIG. 5. Silicon rubber cast of *Goniopholis simus* (Owen, 1878); IPB R359; cast made with the endocast of the rostrum maxillae and orbital region (Text-fig. 3) still in place; ×0·25.

table, quadratojugals and jugals. Similar sculpture on the rostrum maxillae is almost absent. Important cranial measurements are given in Table 1.

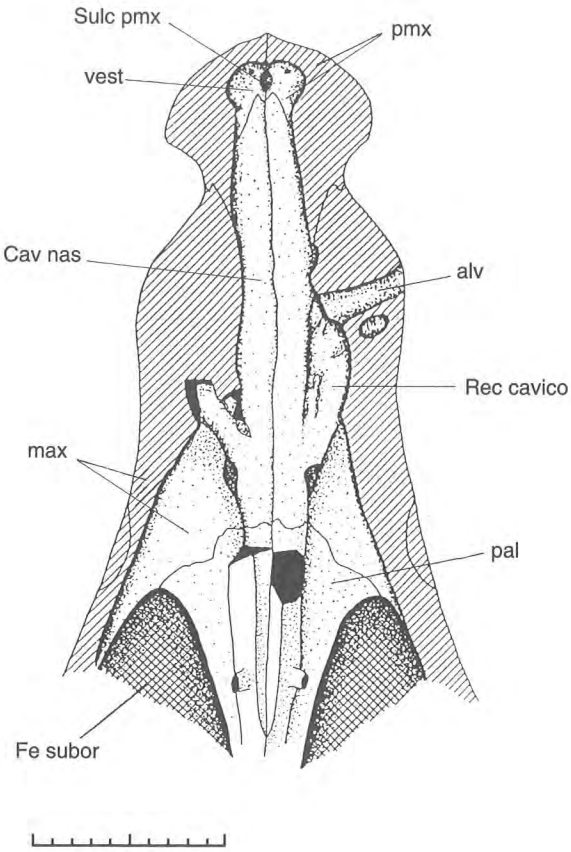
Foramen naris externum (Text-fig. 6). In dorsal aspect, this foramen is heart-shaped, with its axis aligned parallel to the median plane. It is directed dorsally and contained solely within the premaxillae. The rostral and lateral margins, the naris vallatus, are elevated above the level of the rostrum maxillae by a height of 10–15 mm.

Fenestra suborbitalis (Text-fig. 7). Only the rostral portions of each fenestra orbitalis are preserved. Each is broad and ovate, extending rostrally to a point beneath the caudal limit of the fossa maxillaris, and is bounded by the maxilla rostrally and the palatine medially.

Orbit (Text-figs 6, 8). In dorsal aspect, the orbit forms an ellipse that is elongated rostrocaudally with a slightly pointed rostral margin, being one-and-a-half times as long as it is wide. It is bounded by the lacrimal and prefrontal medially, the postorbital caudally and the jugal laterally.



TEXT-FIG. 6. *Goniopholis simus* (Owen, 1878); IPB R359; reconstruction of the skull in dorsal aspect. This view has been restored using details from two silicon rubber casts and the original natural mould (Text-fig. 2). The border of the second silicon rubber cast is shown as a dashed line. Scale bar represents 100 mm.



TEXT-FIG. 7. *Goniopholis simus* (Owen, 1878); IPB R359; reconstruction of the internal sinuses and cavities of the skull in dorsal aspect, based on the endocast of the rostrum maxillae and orbital region (Text-fig. 3) and first silicon rubber cast (Text-fig. 5), with the nasals, lacrimals, prefrontals and frontals removed. Single hatched areas indicate areas of external detail as seen in Text-figure 6. Scale bar represents 100 mm.

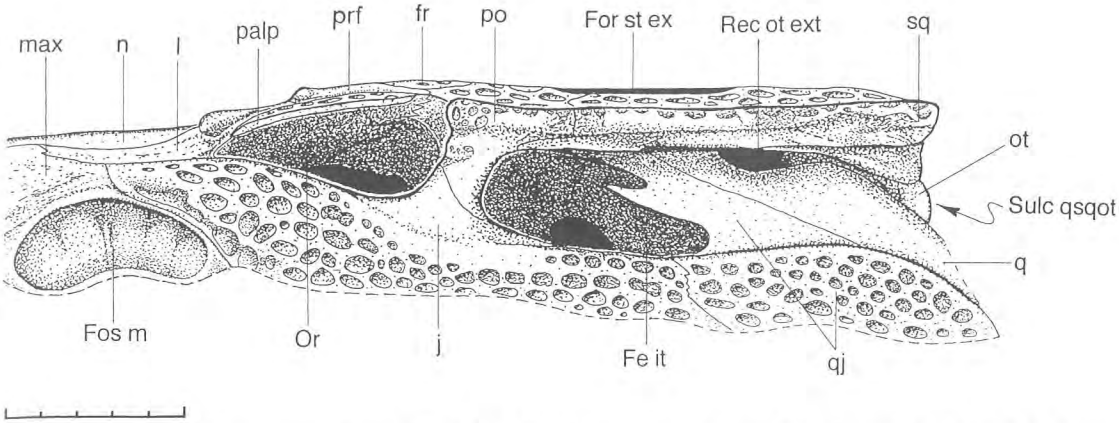
Foramen supratemporale externum (Text-fig. 6). This foramen is almost circular in outline, and is bounded by the squamosal caudolaterally, the parietal caudomedially, the postorbital rostrolaterally and the frontal rostromedially. The margins of the foramina are not elevated above the level of the rest of the skull table, and overhang only slightly the dorsal walls of the recessus supratemporales.

Fenestra infratemporalis (Text-figs 6, 8). This fenestra is slightly less than twice as long as it is high, and is bounded by the quadratojugal caudodorsally, the jugal laterally, the postorbital rostrally and a minor participation of the squamosal rostrodorsally. The processus infratemporalis of the quadratojugal enters the fenestra half way along its dorso-ventral margin.

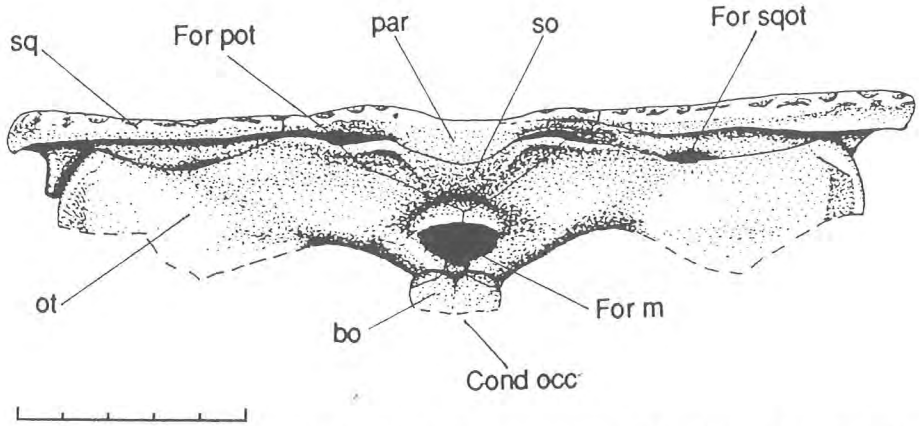
Foramen posttemporale (Text-fig. 9). This foramen is a wide, slit-like structure, eight times as long as it is high. It is bounded by the supraoccipital medioventrally, the parietal dorsally and a minor participation of the otoccipital lateroventrally. It is not visible in dorsal aspect.

Foramen squamosootoccipitale (Text-fig. 9). This foramen is approximately half the size of the foramen posttemporale, and is located mid way between the midline of the skull and the lateral margin of the skull table. It is bounded by the squamosal dorsally and the otoccipital ventrally.

Foramen magnum (Text-fig. 9). This foramen is transversely ovoid in shape, being two-and-a-half times wider than it is high. Apart from a small contribution the basioccipital ventrally, its margin is formed by the otoccipitals.



TEXT-FIG. 8. *Goniopholis simus* (Owen, 1878); IPB R359; reconstruction of the left rear of the skull in lateral aspect, based on the left and right sides of the first (Text-fig. 5) and second silicon rubber casts. The border of the first silicon rubber case is shown as a dashed line. Scale bar represents 50 mm.



TEXT-FIG. 9. *Goniopholis simus* (Owen, 1878); IPB R359; reconstruction of the occiput, based on the first (Text-fig. 5) and second silicon rubber casts, along with details from the original natural mould (Text-fig. 2). The border of the first silicon rubber cast is shown as a dashed line. Scale bar represents 50 mm.

Premaxilla (Text-figs 6–7). In dorsal aspect, the premaxillae are almost as broad as the maxillae and nasals, and, rostral to the suture with the maxillae, they have concave caudolateral margins. The foramen naris externum is located towards the rostral end of the premaxillae, 18·7 mm from the front of the skull. Rostral to this foramen, the premaxillae unite to form a rugose vertical crest. The premaxilla excludes the nasal from the foramen naris externum, and caudally, a long, broad process, which extends to a point level with the lateral swellings of the maxilla over the maxillary pseudocanines, also separates the nasal from the maxilla. External sculpturing is restricted to indistinct pits and rugosities on the medial and rostral surfaces.

The palatal surfaces of the premaxillae are not preserved; however, internally they form the dorsolateral walls of the cavitas nasalis. The internal rostral apex of the serrated, M-shaped suture between the premaxillae and maxillae is located just rostral to the caudal margin of the foramen naris externum. Two small pits, located rostrally within the vestibulum nasi, and 18·0 mm apart, are interpreted as the internal expression of tooth reception pits for the first dentary teeth. A fenestra premaxillaris is absent on this specimen, although on the rostral floor of the vestibulum nasi there is a small, median, diamond-shaped fossa, one-and-a-half times as long as it is wide, here termed the fossa premaxillaris.

TABLE 1. List of measurements for the Bonn specimen of *Goniopholis simus* (Owen, 1878); IPB R359.

Variable measured	Measurement (mm)
Skull	
1. Skull length, from tip of rostrum maxillae to condylus occipitalis	485·5
2. Skull width at lateral border of quadratojugals	290·5
3. Length of rostrum maxillae, from tip of premaxillae to rostral extent of orbits	301
4. Minimum width of rostrum maxillae	81
5. Maximum width of rostrum maxillae	161
6. Maximum width of premaxillae	116·7
7. Skull table width	197·6
8. Skull table length, from caudal limit of squamosals to caudal limit of orbit	137·6
9. Interorbital distance	106·1
10. Minimum distance between foramina supratemporalia externa	28·1
11. Foramen naris externum length	35·8
12. Foramen naris externum width	39·1
13. Fossa premaxillaris length	13
14. Fossa premaxillaris width	8·6
15. Fossa maxillaris length	57·0
16. Fossa maxillaris height	22·8
17. Fenestra infratemporalis length	73·8
18. Fenestra infratemporalis width/height	31·8
19. Foramen supratemporale externum length	59·1
20. Foramen supratemporale externum width	61·8
21. Orbit length	73·1
22. Orbit width	50
23. Fenestra suborbitalis maximum width	62·7
24. Foramen magnum height	10·1
25. Foramen magnum width	25·2
26. Foramen posttemporale height	2·4
27. Foramen posttemporale width	19·6
28. Foramen squamosootoccipitale height	1·8
29. Foramen squamosootoccipitale width	9·8
Mandible	
30. Mandible length (reconstructed)	540
31. Tooth row length (reconstructed)	300
31. Fenestra mandibularis externa length	70·6
32. Fenestra mandibularis externa height	18·7

Maxilla (Text-figs 6–8). The lateral margin of the maxilla is convex in the region that accommodated the maxillary pseudocanines, but becomes gently concave caudally. Caudomedially, a short, triangular caudal process separates the nasal from the rostral limit of the lacrimal. Apart from a slight dorsal swelling over the alveoli for the maxillary pseudocanines, external sculpture on the maxilla consists of indistinct scarring and small pits rostrally, which grade into rostrocaudal lineations caudally.

The fossa on the caudolateral margin of the maxilla is a deep, well-defined concavity, three times as long as it is high in lateral aspect, with a dorsally inflected ventral margin (Text-figs 6, 8). It is subdivided into five hemispherical concavities, positioned side by side in lateral aspect. There is a slight ridge between the second and third rostral-most of these concavities. The second concavity is slightly larger than the others, whilst the caudal-most (fifth) concavity is the smallest. The bone separating the fossa from the cavitas antorbitalis appears to have been extremely thin (< 2–3 mm). There is no evidence of a fenestra antorbitalis in this region.

Internally, the maxilla forms the lateral and ventral enclosure of the rostral portion of the cavitas nasalis. Rostrally, this cavity is ovoid in section, being three times as wide as it is high, with slightly sinuous lateral margins, becoming higher and narrower with parallel sides caudally.

Only the right recessus caviconchalis is preserved (Text-fig. 7). It is contained wholly within the maxilla and is ovoid in outline, being three times as long as it is wide, with a rounded rostral margin that is level with the broadest lateral expansion of the maxilla. Caudally, this recess communicates with the cavitas antorbitalis through a nearly circular apertura caudalis, whilst medially it is connected to the cavitas nasalis by two apertures: a small, rostrocaudally ovate apertura rostromedialis, and a larger, near circular apertura caudomedialis.

The maxilla forms the ventral and dorsolateral walls of the rostrally pointed cavitas antorbitalis, which is 25·4 mm deep at its broadest point. The nature of the ventral suture between the maxilla and lacrimal, along with the position of the foramen caudal n. maxillaris cannot be determined.

The internal suture between the maxillae and palatines originates at the rostral apex of each fenestra suborbitalis, and is smooth and convex rostrally. Rostral to this suture, the maxillae enclose the ventral margins of the choanae primae, which appears to have been ovoid in transverse section.

Although the internal portions of two alveoli are preserved on the right maxilla (Text-fig. 7), these provide no information on the morphology of the alveolus or tooth.

Nasal (Text-fig. 6). In dorsal aspect, the nasals have subparallel sides between the maxillae, but widen caudally along their contact with the lacrimals. The rostral process of the nasals wedges out between the premaxillae, ending just caudal to a point level with the rostral-most extent of the maxilla. A wide, triangular, caudal process separates the rostral extent of the prefrontal from the rostral process of the frontals, and a second, much shorter process enters the rostral process of frontals. The nasals are devoid of external sculpture.

The nasals form the roofing bones of the cavitas nasalis. Rostral to the recessus caviconchalis, the suture between the two nasal bones is flat, but caudally it forms a deep (up to 10 mm), medial septum. The ventral contact with the frontal lies *c.* 18 mm rostral to a point level with the suture between the palatine and maxilla. From this point, the nasal extends caudolaterally before petering out just rostral to the orbits.

Lacrimal (Text-figs 6, 8). The lacrimal is twice as long as it is wide in dorsal aspect. The border with the jugal is lateral to the rostral angle of the orbit. Medially, a small wedge of the maxilla separates the rostral process of the lacrimal from the nasal; this wedge is slightly larger on the right hand side of the skull than it is on the left. A rostrolaterally aligned crest, beginning at the caudal end of the dorsal suture with the jugal, extends caudally over the lacrimal and continues onto the prefrontal. Although heavily sculptured laterally with well-defined, small pits (up to 2 mm in diameter), medial to this crest the lacrimal is unsculptured.

Prefrontal (Text-figs 6, 8). In dorsal aspect the prefrontal is crescent-shaped with a prominent lateral flexure, wedging out acutely between the lacrimal and nasal. Caudolaterally, the prefrontal contacts the postorbital approximately 20 mm from the caudal curvature of the orbit, excluding the frontal from participating in the orbital margin. The crest originating on the lacrimal continues for the full length of the prefrontal, and medial to it the prefrontal is devoid of sculpture. This crest is partly contiguous with the crista interorbitalis that extends across the rostral process of the frontals.

Ventrally, the processus ventralis ('prefrontal pillar' *sensu* Iordansky 1973) is round in section (up to 11 mm in diameter), and is located just caudal to the rostral extent of the fenestra suborbitalis. A bulbous, ventrally directed, medial process of this process forms a hood over the caudomedial corner of the recessus pneumaticus caudolateralis. Just caudal to the base of the processus ventralis, the prefrontal contacts the palatine. The caudal margin of the prefrontal extends ventrally for 10·4 mm within the orbit, before running diagonally towards the uppermost portion of the processus ventralis.

Palpebral (Text-figs 6, 8). A single bony element, polygonal in outline, is preserved over the rostral margin of the left orbit. This element is flat and heavily sculptured with large (2–3 mm diameter), well-defined pits. Although its caudal margin is irregular and probably broken, there is no indication of sutured margins or any other marks where this element could have been attached to the skull. This element is interpreted as a palpebral, since no other portion of the skull that could account for its presence appears to be missing. A second small bony element is present on top of the right quadratojugal (Text-fig. 2). Unlike the *in situ* palpebral, however, this bone has a 3–4 mm high spine or crest. There is no indication of any sutural contact on this bone and no other portion of the skull corresponds with it in any way. This element can be interpreted as: (1) a second, caudal, left palpebral; (2) the caudal portion of the single, *in situ* left palpebral; or (3) part of the right palpebral. Because of the close proximity of this element to the right orbit, the third possibility seems the most likely.

Frontal (Text-fig. 6). A smooth, median suture, extending from a point just caudal to the rostral limit of the foramina supratemporalia to the level of the junction between the frontal, prefrontal and postorbital, indicates that the frontals are only partially fused. Rostral to a distinct, transverse, crescent-shaped crista interorbitalis, the wedge-like rostral process of the frontals extends to a point level with the rostral margin of the orbits, but is squared off due to the presence of two small, caudal processes of the nasals. The contact with the prefrontal and nasal is a continuous, rostrolaterally concave, gentle curve. Laterally, the frontal flares slightly around a square, medial process of the postorbital. Caudally, the serrated contact with the parietals consists of a short, square, caudal process; two short, blunt processes of the parietals extend rostrally on either side. The frontal forms the rostromedial border of the foramen supratemporale externum, this border being sharp, but not elevated. Within the recessus supratemporalis, the frontal broadly separates the postorbital from the parietal.

The crista interorbitalis forms a distinct step-up on the frontals, sharply demarcating the almost smooth rostral region from the heavily sculptured skull table. The sculpturing on the caudal portion of the frontals consists of well-defined, 2–3 mm wide, circular or nearly circular pits, distributed in a reticulate pattern. Caudal to the orbits, there is a slight medial concavity.

Ventrally, the frontals underlap the nasals to a considerable degree, extending 52·3 mm rostral to their maximum dorsal extent. Caudally, each frontal flares a little laterally; the junction between the frontal, postorbital and laterosphenoid is 10·4 mm ventral to the dorsolateral contact between the prefrontal and postorbital on the skull table. From this point, the serrated suture between the frontal and prefrontal runs rostroventrally to the lateral wall of the dorsum sellae.

The cristae ventrales of the frontals are low, parallel structures, a maximum of 20 mm apart, that run close to the midline of the skull. They extend from the caudal border of the processus ventralis of the prefrontal to the rostromedial extent of the laterosphenoid. Caudal to this point, the ventral surface of the frontals is not preserved.

Postorbital (Text-figs 6, 8). In dorsal aspect, a small, rounded rostrolateral process of the postorbital forms the dorsocaudolateral border of the orbit, such that the rostrolateral angle of the skull table is almost square. Medially, it forms the rostrolateral corner of the foramen supratemporale externum, the edges along this margin being sharp, but not elevated. Although this area is poorly preserved, there does not appear to have been a vascular foramen on the lateral edge of the dorsal section of this postorbital. Sculpture on the dorsal surface of the postorbital continues down the columna postorbitales, which is circular in cross section, and terminates at a large, rounded, rostrolateral process. There is no caudal process of the postorbital extending beneath the squamosal at the rostrodorsal angle of the fenestra infratemporalis. Ventromedial and slightly caudal to the orbit, a blunt process of the postorbital extends between the frontal and the laterosphenoid.

Parietal (Text figs 6, 9). As is the case with the frontals, a smooth, median suture, extending from the caudal margin of the skull table to a point level with the caudal limit of the foramina supratemporalia externa, indicates that the parietals are only partially fused. Between the foramina supratemporalia externa, the dorsal surface of the parietals is slightly concave. The lateral margins, which are sharp, but not elevated, form the caudomedial third of the foramina supratemporalia externa. No foramen orbitotemporale is preserved along the caudal wall of the recessus supratemporalis. The suture with the squamosal is straight caudally, but flares laterally, just caudal to the foramen supratemporale externum. The parietals form approximately one-third of the caudal margin of the skull table, and two blunt, caudal projections overhang the foramina posttemporalia. Sculpture on the dorsal surface of the parietals is similar to that on the frontals, but with larger pits (up to 3–4 mm in diameter).

Squamosal (Text-figs 6, 8–9). The medial margin of the squamosal is concave, and forms the caudolateral border of the foramen supratemporale externum. Dorsal to the recessus oticus externus, the lateral margin is concave, whilst the border with the postorbital is transversely oriented. In lateral aspect, a thin rostral process of the squamosal underlaps the postorbital, extending almost to the columna postorbitalis. Dorsal to the recessus oticus externus, there is a shallow, rostrocaudally aligned sulcus that becomes deeper caudally and continues around the caudolateral corner of the squamosal onto the occiput, finally ending at the foramen posttemporale. Caudal to the recessus oticus externus, the lamina ventrolateralis of the squamosal does not contact the quadrate laterally, such that the canalis quadratosquamosootoccipitalis ('cranioquadrate canal' *sensu* Iordansky 1973) is exposed; the squamosal forming the roof of the resulting sulcus (Text-fig. 9). In occipital aspect, the squamosal overhangs the lateral extent of the otoccipital by 14·2 mm. Sculpture on the dorsal surface of the squamosal is similar to that on the parietal and frontal.

Supraoccipital (Text-fig. 9). The supraoccipital is a wide, but shallow, triangular bone that is inclined caudoventrally, and excluded from the skull table by the parietals. Two slight, lateral processes form the ventral margins of the posttemporal foramina. Ventrally, the supraoccipital forms a deep invagination dorsal to the contact with the otoccipital.

Otoccipital (Text-figs 8–9). Although wide, the otoccipital does not extend beyond the lateral margin of the squamosal in occipital aspect, and the processus paroccipitalis forms a laterally projecting, rounded flange that does not contact the dorsal surface of the quadrate. As a result, the foramen quadratosquamosootoccipitale is not enclosed laterally, and the otoccipital forms the medial wall of the sulcus quadratosquamosootoccipitalis. The positions of the foramina hypoglossali, foramen vagi and foramen caroticum caudale are not evident.

The dorsal contact with the squamosal forms a deep fold, and situated mid-way along this contact is the foramen squamosootoccipitale. Dorsomedially, the otoccipital forms only one-third of the ventrolateral border of the foramen posttemporale. Medially, the otoccipitals unite dorsal to the foramen magnum to form a small caudal projection or hood.

Basioccipital (Text-fig. 9). The only portion of the basioccipital preserved on the specimen is that which forms the dorsal surfaces of the condylus occipitalis. This is a hemispherical structure with a shallow median sulcus, which forms the ventral margin of the foramen magnum.

Laterosphenoid. Only the rostral half of the lateral surface of the laterosphenoid, preserved as an impression, is evident on the endocast of the rostrum maxillae. A shallow facet mid-way along the caudal suture between the postorbital and frontal, and medioventral to the orbit, indicates that the processus dorsalis was not firmly sutured to the base of the skull table. It is unclear whether this process contacted the quadrate.

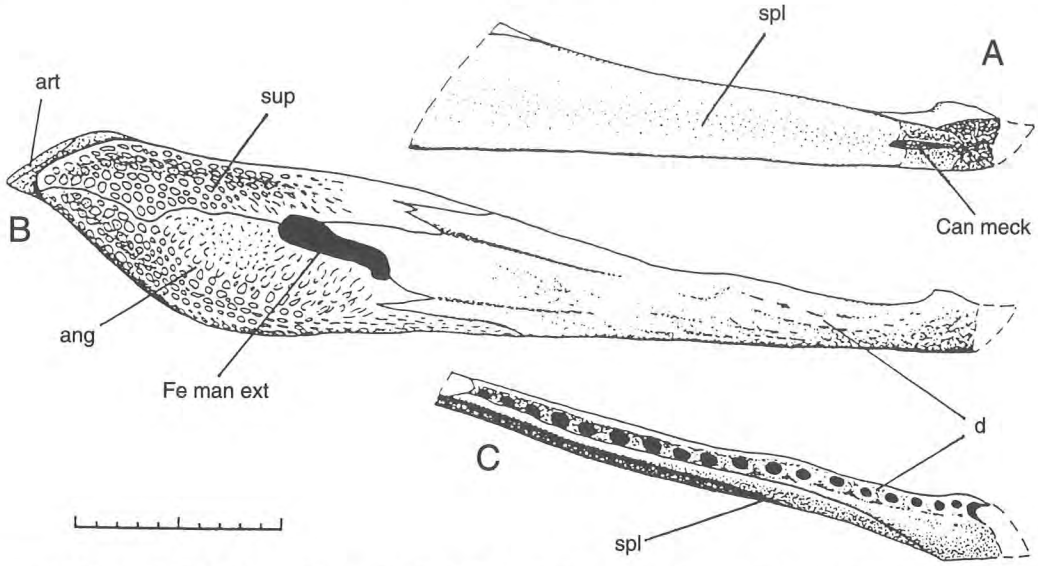
Jugal (Text-figs 6, 8). The jugal forms most of the ventral margin of the fenestra infratemporalis. Rostrally, it overlaps the maxilla, forming a shallow scarf joint, whilst dorsally it forms *c.* two-thirds of the rostral face of the columna postorbitalis, which is slightly inset medially from the lateral margin of the jugal. Lateral to this medial lip, the jugal is heavily sculptured to its rostral margin, with large, longitudinally ovoid, well-defined pits, aligned rostrocaudally into roughly linear patterns. The foramen ductus is located caudolateral to the columna postorbitalis, and is large and rostrocaudally elongate in outline. Caudally, the jugal contacts the quadratojugal in a straight, simple suture, which is located rostral to the caudolateral corner of the fenestra infratemporalis.

Quadratojugal (Text-figs 6, 8). The dorsal surface of the quadratojugal is clearly divided into two parts: a heavily sculptured lateral portion and a non-sculptured medial portion. These two regions are separated by a distinct, curved step that originates at the caudolateral corner of the fenestra infratemporalis, extending initially in a caudomedial direction and then curving caudolaterally, before ending lateral to the condylus mandibularis. Rostrally, the quadratojugal contacts the jugal 9·6 mm from the caudolateral corner of the fenestra infratemporalis. The triangular processus infratemporalis is situated midway along the caudodorsal margin of the fenestra infratemporalis. Rostrodorsal to the processus infratemporalis, the quadratojugal contacts the squamosal, broadly separating the quadrate from the fenestra infratemporalis.

Quadrate (Text-figs 6, 8). Unfortunately, only the dorsal surface of the left condylus mandibularis is preserved. Just medial to its midline, the caudal margin of the condyle is slightly inflected rostrally. The quadrate forms the ventral portion of the recessus oticus externus, and caudal to this region it does not contact the lamina ventrolateralis of the squamosal and processus paroccipitalis, such that the canalis quadratosquamoso-otoccipitalis is exposed laterally. The latter structure continues caudally on the quadrate as a shallow sulcus, terminating at a point level with the caudal margin of the squamosal in dorsal aspect. A foramen commune aerooticus is not evident on this specimen.

Vomer. Impressions of the vomer are preserved on the ventral surface of the endocast of the rostrum maxillae, medial to the choanae primae. The vomer is approximately five times as long as it is wide, and is 3–4 mm high. It does not appear to have been exposed ventrally on the palate.

Palatine (Text-fig. 7). Beyond a point level with the caudal extent of the orbits, the palatines are not preserved, so that their caudal contact with the pterygoids and the position of the choanae secundare cannot be



TEXT-FIG. 10. *Goniopholis simus* (Owen, 1878); IPB R359. Reconstruction of the mandible, in A, medial aspect; B, lateral aspect; C, dorsal aspect. Based on the first silicon rubber cast (Text-fig. 5), which included the caudal portion of the right ramus mandibulae, and the cast of the rostral portion of the left ramus mandibulae. Scale bar represents 100 mm.

determined. Internally, the processus rostralis flares laterally from a minimum width of 37·3 mm to a maximum of 113·3 mm, and has a broad, convex border with the maxillae. The palatines form the rostrodorsal and ventral walls of the ductus nasopharyngei.

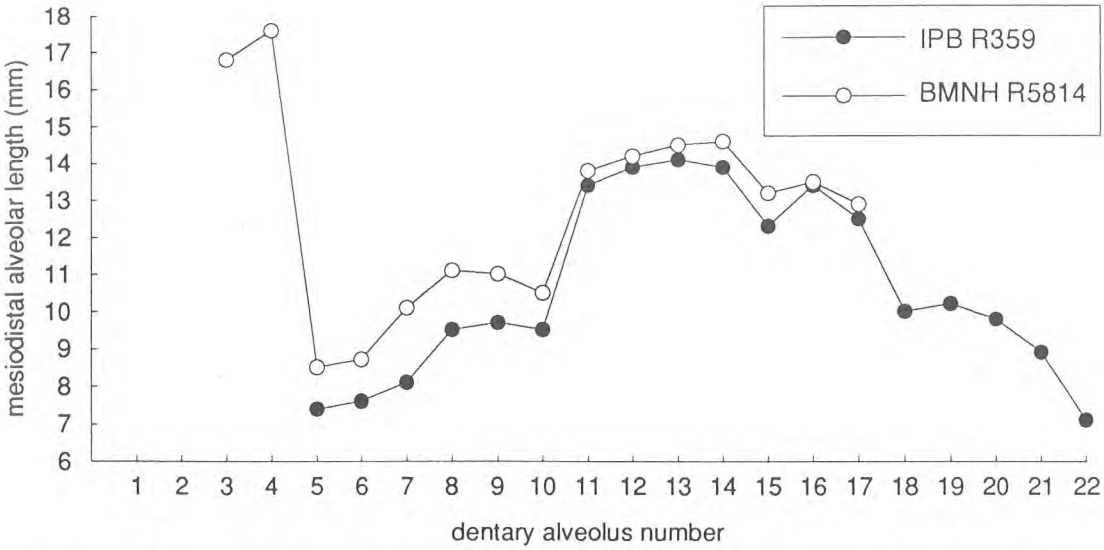
Pterygoid. Portions of the pterygoids forming the roof of the ductus nasopharyngei, caudal to the base of the processus ventralis of the prefrontal, are preserved as impressions on the ventral surface of the endocast of the rostrum maxillae. Dorsally they unite to form a narrow sulcus, which broadens rostrally to a maximum width of 2–3 mm at a point level with the processus ventralis of the prefrontals.

Mandible (Text-fig. 10)

Form and proportions. In lateral aspect, the ramus mandibulae is approximately four times deeper caudally than it is rostrally, with a short, caudoventrally directed processus retroarticularis. The caudodorsal margin of this process is slightly inflected dorsally. The tooth row forms approximately 55 per cent. of the reconstructed length of the ramus. In lateral aspect, the fourth and fifth dentary alveoli are raised above the rest of the tooth row, but the remainder of the dorsal margin of the dentary is only slightly festooned vertically, with a second, smaller peak between the 11th and 13th alveoli (see the following section on the dentary for the determination of alveolar numbers). If the missing portion of the dentary was reconstructed, in dorsal aspect the rostrum mandibulae would have been spatulate in outline, perhaps only slightly longer than it was wide. In dorsal aspect, the symphysial portion of the rostrum extends caudally to a point level with the sixth dentary alveolus. The lateral surface of each ramus mandibulae is heavily sculptured caudally and lightly sculptured or smooth rostrally and ventrally.

Fenestra mandibulae externa (Text-fig. 10). Contrary to previous descriptions of species of *Goniopholis*, for example those of Dollo (1883) and Hooley (1907), this specimen has a distinct external fenestra on the mandible. It is oblong, with its long axis aligned rostroventrally, being 3·7 times longer than it is high. The bottom rostroventral corner is slightly deflected ventrally. It is bounded rostrodorsally by the dentary, caudodorsally by the supraangular, and ventrally by the angular.

Dentary (Text-fig. 10). The exact number of dentary alveoli cannot be determined because the rostral-most portion of this bone is not preserved, nor can it be determined whether the third and fourth dentary alveoli were confluent. Nevertheless, if the sequence of dentary alveolar enlargement is similar to that seen in other platyrostral ('broad-snouted'), heterodont crocodilians (i.e. $1 = 4 \geqslant 3 \geqslant 2 = 5$), then it is likely that, as preserved, the rostral-most alveolus is the fourth in the series. If this is correct, there would have been 22 alveoli in the dentary. Mesiodistal alveolar lengths are shown in Text-figure 11. The caudal-most nine alveoli are set



TEXT-FIG. 11. Graph of mesiodistal alveolar lengths for the dentary of two specimens of *Goniopholis simus* (Owen, 1878); IPB R359 and BMNH R5814.

within a shallow alveolar groove. The dentary portion of the symphysis mandibulae extends caudally to a point level with the sixth alveolus. With the splenial *in situ*, the caudal limit of the sulcus associated with the canalis meckeli is level with the seventh dentary alveolus.

The dorsolateral contact between the dentary and the supraangular is 8·1 mm rostral to the caudal extent of the tooth row. Ventral to this contact, a thin, bipartite caudal process of the dentary underlaps the supraangular caudally to a point level with the rostral margin of the fenestra mandibulae externa. A triangular caudal process of the dentary wedges out between the two rostral processes of the angular, ventrorostral to the fenestra. Two converging sulci on the lateral surface of the dentary originate from a rostral process of the supraangular and a rostral process of the angular respectively, and extend rostrally to a point level with the 18th dentary alveolus. The external surface of the dentary is sculptured with small (1–2 mm diameter) pits and rostrocaudally aligned, 10–20 mm long lineations that are developed best on the ventral and ventrolateral surfaces.

Splenial (Text-fig. 10). The medial surface of the splenial is slightly concave, whilst caudal to the symphysial portion of the rostrum mandibulae, the dorsal surface forms approximately 50 per cent. of the width of the ramus along its length and the medial border of the tooth row from the 14th through to the 21st alveoli. In ventral aspect, it forms approximately 40 per cent. of the width of the ramus, but the extent of its caudal margin is not evident. Although the rostral extent of the splenial is not preserved, it does not appear to taper rostrally in medial aspect, and it is not clear whether it entered the symphysial portion of the rostrum mandibulae. Regardless, its rostral end appears to have been divided into two processes, one dorsal and one ventral to the sulcus associated with the canalis meckeli. There are no foramina on the preserved portions of the splenial.

Supraangular (Text-fig. 10). In lateral aspect, the supraangular bears a broad ridge parallel to its dorsal margin that extends from its caudal margin to a point above the fenestra mandibulae externa, of which the supraangular forms only a small portion (*c.* 13 per cent.) of the caudodorsal margin. Rostrally, a dorsal process overlaps the dorsal margin of the dentary. Ventral to this process, a second rostral process meets the dorsal sulcus on the external surface of the dentary. The supraangular does not contact the margin of the tooth row. Caudally, its lateral surface is covered in a reticulate pattern of well-defined, ovoid pits, 3–4 mm long, which degenerate into longitudinal lineations rostrally. Ventrally, these lineations are more vertically aligned. Caudally, the sculptured surface ends abruptly at a curved, caudoventrally aligned step.

Angular (Text-fig. 10). The angular has a broad ridge parallel to its ventral and caudoventral margins that fades out ventral to the fenestra mandibulae externa. Rostroventrally, a long, thin, rostral process overlaps the ventral margin of the dentary to a point level with the 20th dentary alveolus. Dorsal to this process, a second, shorter rostral process extends to the caudal end of the ventral sulcus on the external surface of the dentary. The angular alone forms the ventral and caudoventral margins of the fenestra mandibulae externa. Like the supraangular, it has a reticulate pattern of sculpturing on its external surfaces, consisting of well-defined, ovoid pits that degenerate rostrally into rostrocaudally aligned lineations. Rostrodorsally, these lineations are more vertically aligned. There is some rostrocaudal alignment of the caudal ovoid sculpturing on the ventral and caudoventral margins into chain-like lineations.

Articular (Text-fig. 10). Only a small impression of the lateral surface of the articular is preserved. It is unsculptured and forms the dorsocaudal surface of the processus retroarticularis.

Teeth

The single isolated tooth associated with the specimen is compressed buccolingually, with well-developed, closely spaced vertical striae that fade out at the base, and prominent, smooth, distal and mesial carinae.

DISCUSSION

Assignment of the Bonn specimen to Goniopholis

The anatomical construction of the skull and mandible of the Bonn specimen compares best to that of goniopholidid crocodilians, in particular those referable to *Goniopholis*. The characteristics of this genus are discussed in the works of Owen (1841, 1849–84, 1878, 1879), Hulke (1878), Lydekker (1890), Hooley (1907), von Nopsca (1928), Wiman (1931), Buffetaut (1982), Clark (1986) and Ortega *et al.* (1996), and in relation to the Bonn specimen include the following: at the suture between the premaxilla and maxilla, the lateral margin of the rostrum maxillae is strongly concave for the reception of the mandibular pseudocanines; short, broad premaxillae, with rostrally positioned, dorsally oriented, undivided foramen naris externum; exclusion of the nasals from the foramen naris externum by the premaxillae; broad interorbital plate, with the frontal forming only a small portion of the orbital margin; foramen supratemporale externum slightly larger than or of a similar size to the orbit, and nearly circular in outline; a flat skull table.

Another characteristic of the genus, not seen on the Bonn specimen, is the nature and position of the choanae secundare, which is situated mid-way between the palatines and pterygoid at a point level with the caudal margin of the fenestrae suborbitales, and is approximately three times longer than it is wide, and bipartite, with sharp palatal margins (see Buffetaut 1982, p. 31, fig. 7). An increase in the length of these choanae, combined with the presence of two smaller fenestrae between the palatines and maxillae, which are also connected to the ductus nasopharyngei, appears to be the main grounds upon which the American goniopholidid, *Eutretauranosuchus delfsi*, can be distinguished from *Goniopholis* (Mook 1967). A similar palatal construction in all the American species of *Goniopholis* (*G. stovalli*, *G. lucassi*, *G. gilmori* and *G.* (*Diplosaurus*) *felix*) may result in the referral of these taxa to *Eutretauranosuchus* (W. Langston Jr, pers. comm. 1996), but this possibility will not be discussed here.

In light of these similarities, in addition to the remaining natural moulds and casts of *Goniopholis* skulls and the ramus mandibulae from the Ballerstedt Collection (IMGPGö 741-6; GAB Sch. 1; DFMMh Sch. 1a; BMNH R5262; GPIMü Pr. 280; BMNH R5260; BMNH R5261), the Bonn specimen was compared with material of *G. crassidens* (BMNH 3798 and BMNH R3876), *G. simus* (BMNH 41098 and 41098a) and *Nannosuchus gracilidens* (BMNH 48217) from the Berriasian and lower Aptian of the Wessex-Weald Basin of southern England, and the skull and mandible of a relatively complete skeleton referred to *G. simus* (IRSNB R1537) from the Hauterivian–Barremian of Bernissart, Belgium. Further comparisons were made with specimens of *G. lucasii* (AMNH 5782) and *G. felix* (YPM 517 and YPM 986), *G. gilmorei* (CM 1339) and *G. stovalli* (OMNH 2392 and OMNH 2322) from the Tithonian Morrison Formation of Colorado, Wyoming and Oklahoma respectively, and an undescribed goniopholidid (TMM 4188-1) from the Lower Cretaceous of Arkansas. Skull fragments from the Lower Cretaceous of Galve, Spain, referred to *Goniopholis* cf. *G. crassidens* by Buscalioni and Sanz (1987*a*, 1987*b*) and two un-numbered specimens from the collections of the National Museum of Natural History, Washington and the American Museum of Natural History, New York were also examined. Comparisons with other taxa were made using illustrations and descriptions provided in the literature.

Comparison of the Bonn specimen with other Goniopholis *skulls from Germany*

The construction of the skull of the Bonn specimen agrees closely with that of the other *Goniopholis* specimens from the Ballerstedt Collection. Some variation in the overall size and proportions of the rostrum maxillae is evident: for example, the total cranial length of IMGPGö 741-6 is almost twice that of GPIMü Pr. 280, but this is by no means outside the range of variation exhibited by extant crocodilian species, and most probably relates to differences in ontogenetic stage or relative growth (Webb and Messel 1978; Hall and Portier 1994; Salisbury and Willis 1996; Monteiro *et al.* 1997). Although only two of the Ballerstedt *Goniopholis* specimens (IMGPGö 741-6 and GPIMü Pr. 280) show evidence of a palpebral, we do not consider this overtly significant in a taxonomic sense, since among living taxa these ossifications are free-floating elements, held in place only by thin integuments of tissue associated with the eye-lid (Wettstein 1937–54). As such, they could easily be lost during fossilization following the collapse of the eyeball. In the absence of any systematically variable characteristics, we therefore consider the Bonn specimen and other *Goniopholis* material from the Ballerstedt Collection to be representative of a single species.

Assignment of the German Goniopholis *material to* G. simus *Owen, 1878*

In all the crocodilians that we have examined, the prefrontal is excluded from contact with the postorbital by the frontal, which forms most of the dorsomedial margin of the orbit in those taxa lacking palpebrals. In species of *Goniopholis* and *Pholidosaurus*, the interorbital plate is extremely broad due to a more caudal position of the prefrontals. In both *G. simus* and the German *Goniopholis*, the condition is so extreme that the frontal is completely excluded from the orbital margin (or the medial edge of the palpebral) by a broad contact between the prefrontal and postorbital. This feature is particularly clear on the German specimens, but may have been overlooked on the holotype of *G. simus* since on both the left and right sides of the skull the rostrolateral portions of the skull table are broken. Examination of the counter slab associated with the holotype (BMNH 41098a) reveals an impression of the unbroken dorsal surface of the skull table. As in the German specimens, the suture between the frontal and prefrontal can be traced caudally to a contact with the postorbital, 3–4 mm medial to the orbital margin. This feature is also apparent on the dorsal surface of the right endocast of the orbit on the main slab (Text-fig. 12), and to our knowledge, is unique among crocodilians.

Clark (1986, p. 401) stated that the enclosure of the canalis quadratosquamosootoccipitalis was '...unique to mesoeucrocodylians [inclusive of thalattosuchians] among archosaurs.' However, a

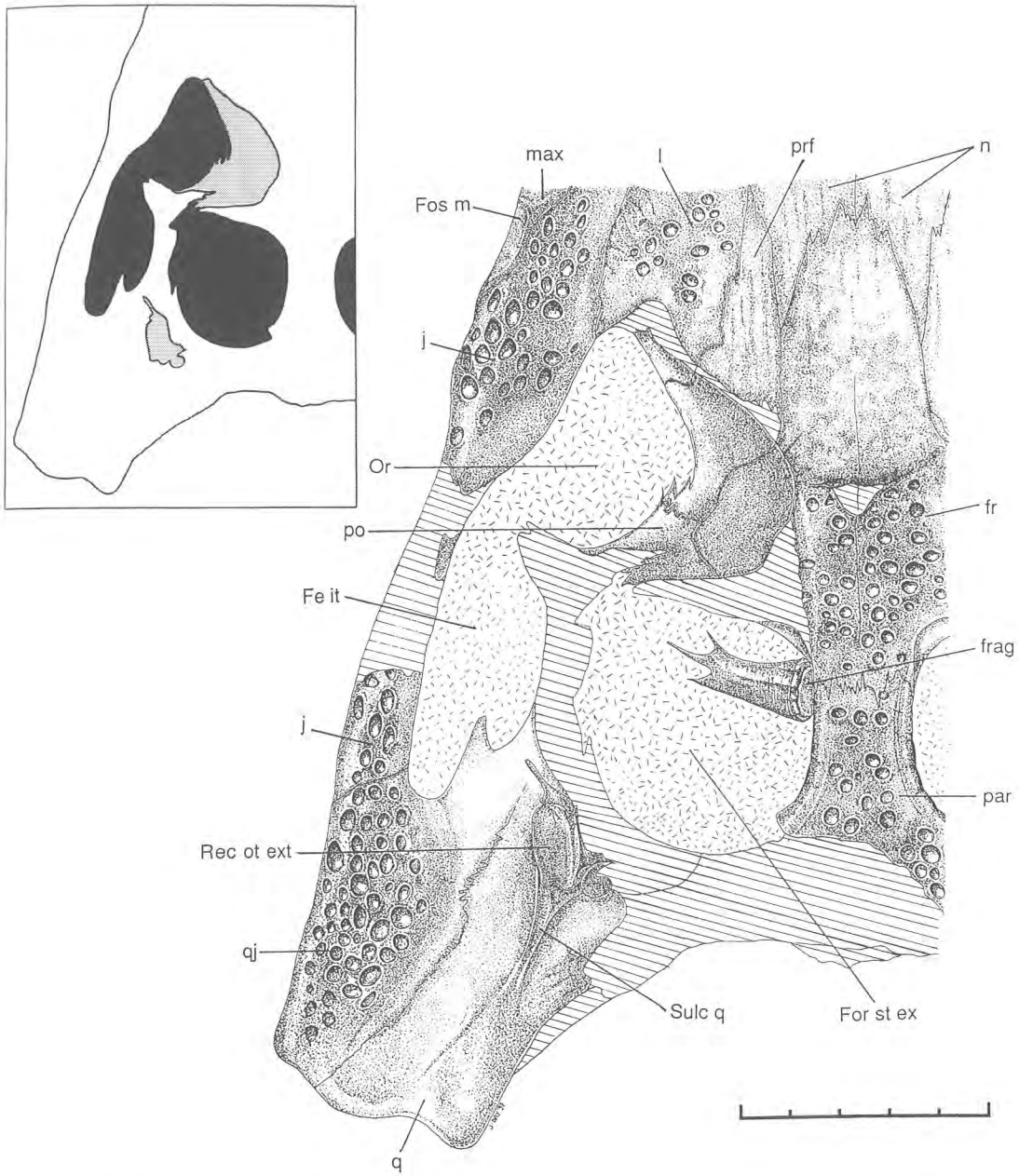
laterally exposed canalis quadratosquamosootoccipitalis is seen on the Bonn specimen and the cast of one of the missing Ballerstedt specimens (BMNH R5259). An examination of the holotype of *G. simus* reveals that, on the left side of the skull table, the slab and counter slab have been split along a horizontal plane that dissects the canalis quadratosquamosootoccipitalis. As a result, on the counter slab, as in the German specimens, it is possible to see that neither the lamina ventrolateralis of the squamosal nor the processus paroccipitalis contacted the dorsal surface of the quadrate caudal to the recessus oticus, and that the resulting sulcus is partially filled by sediment (Text-fig. 12). A longitudinal sulcus on the quadrate, which forms a causal continuation of the sulcus quadratosquamosootoccipitalis, is also apparent. A less laterally extensive processus paroccipitalis is also seen in *Hylaeochampsa vectiania* (Clark and Norell 1992) and many thallatosuchians, for example *Pelagosaurus typus* (illustrated by Koken 1887, p. 409, fig. 30a). However, in none of these forms is the canalis exposed laterally: in *P. typus* it is enclosed by a dorsal process of the otoccipital, and in *H. vectiania* by the lamina ventrolateralis of the squamosal. Unfortunately, the occipital and otic regions of many other Mesozoic crocodilians are poorly understood.

All crocodilians that we have examined thus far possess a fenestra premaxillaris. Koken (1896), illustrated and commented on the absence of this feature on the fragment of rostrum maxillae that he referred to '*G. pugnax*'. This is also clearly visible on IMGPGö 741-6 and the Bonn specimen. Although not commented upon before, the holotype of *G. simus* also lacks a fenestra premaxillaris (Text-fig. 4). Furthermore, as in the German specimens, in its place there is a small, diamond-shaped fossa premaxillaris, located just rostral to the ventral suture between the premaxillae and maxillae within the vestibulum nasi. Buscalioni and Sanz (1990) noted the extreme rostral position of the ventral suture between the premaxillae and maxillae in some American species of *Goniopholis*. This feature is apparent in *G. lucasii* (AMNH 5782), *G. stovalli* (OMNH 2392 and OMNH 2322) and *G. gilmorei* (CM 1339), and also appears to account for a correlated reduction in the size of the fenestra premaxillaris in these taxa (in *G. stovalli* there are two fenestrae, separated by a 3–4 mm broad septum), although in none of these taxa is the fenestra premaxillaris absent.

In comparison with other species of *Goniopholis*, in *G. simus* and the German *Goniopholis* material external sculpture is noticeably reduced on the nasal and maxilla, whilst the majority of other cranial bones are heavily sculptured with deep, circular pits, reticulations and ridges. Although differences in the size of sculpture pits can occur in living crocodilian taxa as a result of dietary deficiencies (C. A. Brochu, pers. comm. 1994), we are not aware of any cases where the actual pattern of pitting shows much variation.

Gomani (1997) illustrated, but did not comment upon, a foramen squamosootoccipitale on a specimen of *Malawisuchus mwakasyungutiensis* from the Lower Cretaceous of Malawi. Although this foramen is in the same position as that seen on the Bonn specimen and two of the Ballerstedt skulls (IMGPGö 741-6 and GPIMü Pr. 280), the absence of a foramen between the supraoccipital, otoccipital and squamosal in *M. mwakasyungutiensis* suggests that this is the foramen posttemporale, but in a more lateral position. Unfortunately, due to the poor preservation of the occiput, it cannot be determined whether such a foramen was present on the holotype of *G. simus*. In any case, the presence of a foramen squamosootoccipitale in addition to a foramen posttemporale in the German *Goniopholis* would appear to be unique among crocodilians. Considering its position and the lateral exposure of the canalis quadratosquamosootoccipitalis, it seems likely that this foramen represents the caudal opening of a subsidiary canal, which may have housed those structures that normally passed through the enclosed canalis quadratosquamosootoccipitalis in other species of *Goniopholis*.

Among the taxa referred to Goniopholididae, a fenestra mandibulae externa has only been described in *Eutretauranosuchus delfsi* (Mook 1967) and species of *Sunosuchus* (Young 1948; Buffetaut and Ingavat 1980; Buffetaut 1986*a*). This feature is clearly visible on both the Bonn specimen and a cast of one of the missing Ballerstedt specimens (BMNH R5260). Unfortunately, no mandibular material was associated with the holotype of *G. simus*. Nevertheless, another specimen, BMNH R5814, a partial skull from a quarry at Herston, near Swanage, Dorset, which can be referred to *G. simus* on the morphology of the interorbital plate (discussed above), does show



TEXT-FIG. 12. *Goniopholis simus* (Owen, 1878); BMNH 41098; drawing of the left rear corner of skull. Hatched areas represent broken bone and speckled areas matrix. Areas in grey shown on the inset diagram in the upper lefthand corner represent those surfaces of matrix endocasts that preserve bony impressions (illustrated on the main drawing). Scale bar represents 50 mm.

evidence of this fenestra, as does the holotype of *G. crassidens* (BMNH 3798) from Swanage; both specimens coming from either the 'Middle' or 'Upper' Purbeck Group. As to whether *G. crassidens* is distinct from *G. simus* cannot be determined until further examination and preparation of the

former holotype is completed. At present, comparisons between this specimen and material that can be referred to *G. simus* are limited to a second smaller slab that preserves an impression of skull table (Hooley 1907). However, the direct association of this slab with the main slab is still uncertain. Furthermore, we fail to see how Hooley (1907) was able to refer material from the Lower Aptian of the Isle of Wight (BMNH R3876) to this species based only on comparison with this specimen, which, in its current state of preparation, appears undiagnostic.

Although palpebral ossifications have never been described for any species of *Goniopholis*, our comparisons reveal that a single palpebral is present in *G. lucasii* (AMNH 5782), a specimen referred to *G. simus* from Bernissart (IRSNB R1537) and an undescribed goniopholidid from the Lower Cretaceous of Arkansas (TMM 41881-1). According to the figure published by Hulke (1878), the skull of a goniopholidid from the private collection of Mr Willett, may also have possessed a single palpebral. This bone is around the same size as the palpebral on the Bonn specimen. Unfortunately, the Willet specimen has thus far not been located, so further verification of the presence/absence of a palpebral is not possible. As first noted by Clark (1986), the type specimen of *Nannosuchus gracilidens* has what appears to be two palpebral ossifications in the orbit (Owen 1879, p. 10, pl. 3, fig. 1): a large bone, slightly smaller than the rostral palpebral of protosuchians, on the dorsomedial edge of the orbit, and possibly a second, smaller bone caudal to this in contact with the postorbital. In light of these observations, it would appear that palpebral ossifications are ubiquitous among goniopholidids, and that the taxonomic significance of this feature that has been stressed by previous authors, for example Clark (1986), may be unfounded.

Based on the peculiar morphology of the interorbital plate and otic region, the absence of a fenestra premaxillaris and the reduction of external sculpture on the maxillae and nasals, we refer the Bonn specimen and the skulls from the Ballerstedt Collection to *G. simus* Owen. Due to the outstanding preservation of the German specimens, we do not consider the fact that palpebral ossifications and a foramen squamosootoccipitale are unknown for the holotype of *G. simus* to be sufficiently significant to warrant non-referral of the German material to this species. The future collection of well-preserved material may verify this assumption.

The status of 'Goniopholis pugnax' *and* 'Goniopholis minor'

Koken (1887) used some characteristics of the dentition to distinguish '*G. pugnax*' from the other species of *Goniopholis* known at that time. According to Koken (1887), the teeth of '*G. pugnax*' are generally more robust than those of *G. simus* (the holotype) and in particular those of *G. tenuidens*. As a result, he noted that the vertical striations, often considered characteristic of the teeth of *Goniopholis* (following Owen 1841, 1878), are less closely spaced in '*G. pugnax*'. Koken also noted that on the lingual side of the teeth of '*G. pugnax*' there are approximately 22 vertical striations, whereas in *G. tenuidens* there are only 12. Koken (1887) used only size to differentiate between '*G. minor*' and '*G. pugnax*', specimens of the former being much smaller than those the latter.

Referring to Koken's original diagnosis for '*G. pugnax*', we have found that, as in living crocodilian taxa, dental characters such as the number of vertical striations are extremely variable for *Goniopholis*, and we agree with Hooley (1907, p. 53) that such features are insufficient to differentiate between species. Furthermore, we can find no additional characters in the description or illustrations provided by Koken (1887) that would allow '*G. pugnax*' to be differentiated from other species of *Goniopholis*. For taxonomic purposes Koken's (1887) definition is inadequate, and we propose that '*G. pugnax*' be considered a *nomen dubium*. Later referral of material to this taxon, for example, the fragments of rostrum maxillae and dentary described by Koken (1896), based purely on the characteristics of the dentition, should be considered invalid.

'*Goniopholis minor*' is even more poorly defined, and we can find no discrete characters in the definition of Koken (1887) that would allow this species to be differentiated from other Mesozoic crocodilians, let alone other species of *Goniopholis*. We therefore propose that this species should also be considered a *nomen dubium*.

The status of some other European goniopholidids

The two skeletons from Bernissart, Belgium, referred to *G. simus* by Dollo (1883), have never been described in detail, as Dollo's paper was intended only as a preliminary work. Although beyond the scope of the present paper, a preliminary examination of the skull and mandible of one of these skeletons (IRSNB R1537) – the other (IRSNB R1539) consisting of the postcranium only – indicates that several differences exist when compared with the English and German material of *G. simus*. For example, a fenestra mandibularis externa is absent, and the prefrontal does not contact the postorbital, such that the frontal contributes to the orbital margin. The outline of the skull table is also markedly different, due to the presence of a spine-like processus rostralis of the postorbital, forming the laterodorsal margin of the orbit, and a smooth, tuber caudolaterale of the squamosal. The fossa maxillaris is almost round in outline and does not have any internal divisions. A crista interorbitalis is also absent and the entire dorsal surface of the rostrum maxillae is uniformly sculptured with small, 2–3 mm wide pits (Hooley 1907). Thus, we consider that Dollo's (1883) assignment of this material to *G. simus* was incorrect, and that it most probably represents a distinct species of *Goniopholis*.

The material from Nehden, western Germany, tentatively identified as *Goniopholis* sp. by Norman (1987), is of approximately the same geological age as the Bernissart material (Norman and Weishampel 1990), although it is too fragmentary for detailed comparison with other European *Goniopholis*. Based on the form of the osteoderms from the paravertebral shield and vertebrae, we accept Norman's (1987) placement of this material in *Goniopholis*, but the species is indeterminate.

Buffetaut (1986*b*) described a left maxilla and premaxilla from the upper Tithonian of the Boulonnais, northern France (MHNBP 5.205), and based on comparison with drawings of the fragment of rostrum maxillae described by Koken (1896), assigned this specimen to '*G.* cf. *pugnax*'. We have not been able to examine this specimen, and although it is too incomplete to be referred confidently to *G. simus*, we agree with Buffetaut (1986*b*) that its overall proportions and the sequence of alveolar enlargement indicate that it is very similar to *Goniopholis* material from Germany, referred here to *G. simus*. Amending Buffetaut's (1986*b*) assignment of this specimen to *G.* cf. *pugnax*, in light of the present study we place it in *G.* cf. *simus*.

A small collection of postcranial material from the Isle of Wight and Ecclesbourne, Sussex, was assigned to *G. minor* by Lydekker (1890). The Isle of Wight material (BMNH R214) consists of osteoderms from the paravertebral shield, vertebrae, a coracoid, an articular and some fragmentary limb elements. A partial femur that also shares this number may belong to a small theropod dinosaur. The Ecclesbourne material (BMNH R608) consists of vertebrae and a femur. Excluding the osteoderms and a cervical vertebra, all of this material represents individuals probably no more than 1 m long, and it is likely that it was referred to *G. minor* only on the basis of its size. Pending further comparisons, we place this material in Crocodilia *incertae sedis*.

Biogeographical implications

Reference to some German Early Cretaceous strata as 'Wealden', for example by Dunker (1843–44), Koken (1883, 1886, 1887, 1896) and Edinger (1938), is misleading, since the majority of sediments are derived neither from the same basin, nor are they of an equivalent age to those of the English type sequence (Allen 1955, 1967; Kemper 1973*a*; Pelzer and Wilde 1987). During the Early Cretaceous two major depositional basins existed in what are now the Netherlands and north-western Germany: the West Netherlands Basin and the Niedersachsen [Lower Saxony] Basin (Allen 1967; Kemper 1973*a*; Ziegler 1990; Allen and Wimbledon 1991) (Text-fig. 1). Although the Niedersachsen Basin is dominated by muddy basin facies, the uppermost units contain some marginal limestones and fluvial-alluvial sandstones, accounting for the close resemblance to the Wealden of the English Weald (Allen 1962, 1967; Kemper 1973*a*, 1973*b*; Pelzer and Wilde 1987). However, unlike the type sequence of the Wealden, development of the Niedersachsen Basin largely

occurred during the Berriasian, and only the uppermost units (those of the Osterwald Member) are Valanginian (Allen 1955, 1967; Wolberg 1959; Kemper *et al.* 1981; Hoedemaeker 1987). Following the terminology of Clements (1993), sediments from the Bückeburg Member are now equated with those of the 'Middle' and 'Upper' Purbeck of the Lulworth and Durlston formations of the Purbeck Group (Martin 1940; Anderson 1962; Burger 1966; Kemper 1973*a*; Davey 1979; Herngreen *et al.* 1980; Allen and Wimbledon 1991).

The recognition of *G. simus* in the Niedersachsen Basin of north-western Germany during the Berriasian provides the first clear evidence of interchange between the non-marine vertebrate faunas of this region and those of the Wessex-Weald Basin of southern England. Up until now there has been little evidence of this, although this may have been due largely to a much less extensive knowledge of the German fauna, possibly as a result of the unusual preservation of much of the fossil material as natural moulds. Among the dinosaur taxa, material referred to the theropod *Altispinax* (*Megalosaurus*) *dunkeri* from both regions has recently been considered indeterminate by Molnar (1990). An isolated tooth (Dunker 1843–44), which was, unfortunately, lost, and a humerus, were assigned to *Iguanodon* by Koken (1887), but further comparisons with *I. mantelli* and *I. bernissartensis*, both known from the Wessex-Weald Basin, have proven inconclusive (Probst and Windolf 1993). Nevertheless, numerous three-toed footprints of the type usually attributed to *Iguanodon* in England (Benton and Spencer 1995 and references therein) have been found in the Obernkirchen Sandstone near Bückeburg (Probst and Windolf 1993). Other trackways also point to the existence of similar sized sauropods in each region: *Rotundichnus muenchehagensis*, from the upper Berriasian of Münchehagen (Hendricks 1981), and an as yet un-named ichnite from the Isle of Purbeck (Ensom 1987). Further track-ways in the Obernkirchen Sandstone, including those of a large carnosaur, *Bückeburgichnus maximus* (Kuhn 1958), and a nodosaur, *Metatetrapous valdensis* (Kuhn 1958), do not appear to be attributable to any ichnites or taxa based on skeletal material from the Berriasian Wessex-Weald Basin (Probst and Windolf 1993). The enigmatic ornithischian *Stenopelix valdenis* (Schmidt 1969; Sues and Galton 1982) and material referable to the pleurodire turtle *Plesiochelys*, both from the Obernkirchen Sandstone, are also not known from England.

The two other crocodilians from the Obernkirchen Sandstone, *Pholidosaurus meyeri* and *P. schauburgensis*, also appear remarkably similar to their counterparts in the Wessex-Weald basin, *P. decipiens* and *P. laevis*. Contrary to Andrews (1913), the only difference between the latter three forms relates to the size and density of sculpture pits on the skull table, a trait that often shows a high degree of intra-specific variation among extant crocodilian taxa (C. A. Brochu, pers. comm. 1994). It is likely that future work may show that this material can be referred to a single species. On the other hand, *Pholidosaurus meyeri*, originally based on a natural mould of a skull from Bückeburg, and described in detail by Dunker (1843–44), has been recorded from the lower Barremian of the Wessex Formation of Brook Bay, Isle of Wight (Lydekker 1887). However, Lydekker's assignment of this material (a partial skull; BMNH 28966) to *P. meyeri* is questionable, being based only on a comparison with Dunker's drawing (Dunker 1844, pl. 20, p. 74), which is not particularly informative. Our examination of Isle of Wight *Pholidosaurus* suggests that it may be distinct at the genus level, but, as with the other material, it needs to be re-examined and described in detail.

The presence of at least one, and perhaps even two, non-marine crocodilians in both the Wessex-Weald and Niedersachsen basins affords evidence of faunal continuity between these two regions during the Berriasian, and suggests that large-scale oceanic or orogenic separation was unlikely. The palaeogeographical reconstructions of Allen (1981) and Ziegler (1990) indicate that the basins were separated by a coastal expanse of approximately 500–700 km, and a shorter distance overland by the peneplained remains of the Variscan orogenic belt, which rose only a few hundred metres at most above sea level. Thus, for a crocodilian, dispersal could easily have occurred either along the coast or through inland fluvial systems.

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APPENDIX: ABBREVIATIONS USED IN THE TEXT-FIGURES

alv	alveolus maxillaris
ang	os angulare
art	os articulare
bo	os basioccipitale
Can meck	canalis meckeli
Cav nas	cavitus nasalis
Cond occ	condylus occipitalis
d	os dentale
Fe it	fenestra infratemporalis
Fe man ext	fenestra mandibulae externa
Fe subor	fenestra suborbitalis
For m	foramen magnum
For pot	foramen posttemporale
For sqot	foramen squamosootoccipitale
For st ex	foramen supratemporale externum
Fos m	fossa maxillaris
fr	os frontale
frag	indeterminate fragment of bone
j	os jugale
l	os lacrimale
max	os maxillare
n	os nasale
N	foramen naris externum
Or	aditus orbitae
ot	os otoccipitale
pal	os palatinum
palp	os palpebrale
par	os parietale
pmx	os premaxillare
po	os postorbitale
prf	os prefrontale
q	os quadratum
qj	os quadratojugale
Rec cavico	recessus caviconchalis
Rec ot ext	recessus oticus externus
so	os supraoccipitale
spl	os spleniale
sq	os squamosum
Sulc pmx	sulcus premaxillaris
Sulc q	sulcus quadratus
Sulc qsqot	sulcus quadratosquamosootoccipitalis
sup	os supraangulare
vest	vestibulum nasi