

A NEW SPECIES OF *GONIOPHOLIS* FROM THE UPPER JURASSIC OF PORTUGAL

by DANIELA SCHWARZ

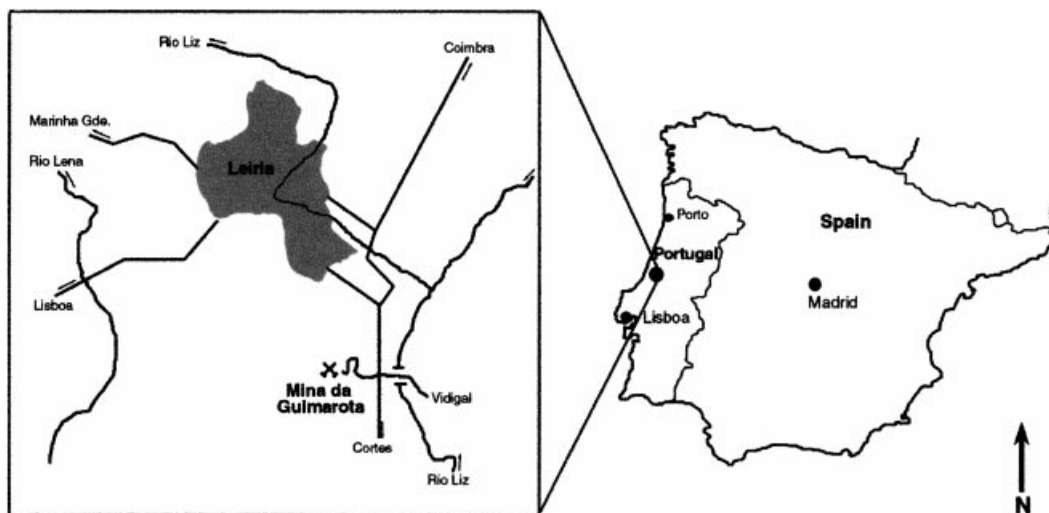
ABSTRACT. The new goniopholidid crocodile *Goniopholis baryglyphaeus* sp. nov. from the Kimmeridgian of Guimarota/Leiria, Portugal is based on the oldest known relatively complete skeleton of *Goniopholis* from Europe and consists of a nearly complete skull together with a mandible and various postcranial remains. *G. baryglyphaeus* shows characters that hitherto have only been described for *Goniopholis simus*: a caudal expansion of the prefrontal that excludes the frontal from the medial margin of the orbit; and the loss of contact between the paroccipital process and the lateral surface of the squamosal and the quadrate, which exposes the cranioquadrate canal laterally. This new species can be distinguished from other European *Goniopholis* species by an articular facet placed ventral to the retroarticular process, and directed slightly medioventrally; a caudal margin of the mandible forming almost a right angle at its caudoventral corner; an almost square rostralateral corner of the cranial table; a straight transverse suture between the parietal and the frontal with a median rostral process; a rostrally tapering wedge-like lacrimal, and a regular heavy skull-sculpturing. The new find of *Goniopholis* in Portugal shows that this genus was distributed in a larger area, and was present much earlier, than hitherto reported in south-western Europe.

KEY WORDS: European *Goniopholis*, partial skeleton, Kimmeridgian, Portugal.

A NEARLY complete skeleton of *Goniopholis*, consisting of a well-preserved skull together with an incomplete mandible, various vertebrae, osteoderms and parts of the girdles and limbs, was collected from the Kimmeridgian locality of Guimarota near Leiria in Portugal (Text-fig. 1).

The coal mine of Guimarota is situated on the margin of the Lusitanian Basin, a north–south-running sedimentary basin that was formed as a rift system in an initial phase of the opening of the North Atlantic. After deposition of continental and clastic strata with local evaporites, there was a transgression that interfingered with brackish-lacustrine conditions, and marine facies were deposited. Additionally, halokinetic movements led to fracture tectonics which divided the basin into small subbasins (Schmidt 1986). The vertebrate-bearing lignite coal layers ('Guimarota Strata') belong to the Alcobaça Formation, which can be correlated with the Kimmeridgian Abadia Formation (Schudack 2000a). The 'Guimarota Strata' (Schudack 1993) are divided into a lower ('Fundflöz' Schudack 1993) and an upper ('Ruafolge' Schudack 1993) layer, separated from each other by marly limestones (Schudack 2000a). Both layers consist of marls, shaly marls and lignite-coal marls. The stratigraphical age is controversial at present. It was determined on the basis of charophytes and ostracods to be Early Kimmeridgian (Helmdach 1971) and on palynomorphs as Oxfordian (Van Erve and Mohr 1988). Recent studies by Schudack (2000a, b) demonstrated that only the ostracods provide conclusive evidence and indicate, in contrast with earlier ideas (Schudack 1993), a Kimmeridgian age, without permitting a more precise dating of the layers. The environment was interpreted to be lagoonal, with freshwater influx, that was periodically flooded by salt water (Helmdach 1971; Schudack 2000a). Palynological investigations (Van Erve and Mohr 1988) indicate a wooded swamp region, comparable with recent tropical mangrove forests (Gloy 2000; Martin 2000).

The locality of Guimarota is ranked among the most important Upper Jurassic microvertebrate fossil deposits (Clemens *et al.* 1979; Martin 2000). General interest is based mainly on the rich fauna of early mammals. The most spectacular discovery was a complete skeleton of the small mammal *Henkelotherium guimarotae* (Krebs 1991). Long term screen-washing activities at the Free University, Berlin, also yielded a non-mammalian microvertebrate fauna consisting of the remains of fishes (Kriwet 2000), amphibians



TEXT-FIG. 1. Geographical position of the coal mine of Guimarota/Leiria, Portugal.

(Wiechmann 2000), turtles (Gaßner 2000), lizards (Broschinski 2000), crocodylians (Krebs and Schwarz 2000), pterosaurs and archaeopterygiformes (Gloy and Wiechmann 2000) and dinosaurs (Rauhut 2000). In contrast to the abundance of isolated remains, articulated skeletons are very rare. A nearly complete crocodylian skeleton of a teleosaur, *Machimosaurus hugii*, represents an erratic element in the ecosystem of Guimarota (Krebs and Schwarz 2000).

A second, partially complete skeleton of a crocodylian (IPFUB Gui Croc 1) is described in this paper. In a preliminary description of the crocodylian fauna of Guimarota and Uña (Spain) this individual was mentioned by Brinkmann (1989), who identified it as '*Goniopholis* sp.' As the detailed description in this article will show, this specimen is a new species of *Goniopholis*. Fossil remains of the genus *Goniopholis* are an important faunal element of the Guimarota ecosystem and are mostly represented by isolated teeth, scutes and cranial and postcranial elements (Brinkmann 1989).

The genus *Goniopholis* consists of amphibious, medium-sized, platyrostral and slightly brevirostrine neosuchians that are presumed to have been very similar in their habit to the recent brevi- and mesorostrine crocodylians (Buffetaut 1982). Neosuchians are diagnosed by several skull features: a rostral section that is wider than deep, the absence of a foramen at the premaxillo-maxillary suture in lateral view, a lateral descending process of the lacrimal that is laminar, a straight jugal whose lateral surface is not visible in ventral view, and a cranial projection of the surangular that is forked in lateral view (Ortega *et al.* 2000). Recently, *Goniopholis* has been considered as the sister group of a clade consisting of *Bernissartia*, Las Hoyas Neosuchia and Eusuchia (Ortega *et al.* 2000). *Goniopholis* has been reported in abundance from the middle and late Mesozoic of the Laurasian continent, mainly from eastern North America (Mook 1925), Europe (Table 1) and South East Asia (Buffetaut 1983). Its fossil remains are very common in deposits that accumulated in freshwater environments with periodic brackish influences in the Upper Jurassic and the Cretaceous (Table 1).

The assignment of all Laurasian *Goniopholis* remains to the genus have been questioned (see Salisbury *et al.* 1999 for a recent revision). Moreover, the North American *Goniopholis* remains require revision; their taxonomic status within the Goniopholididae is not well defined. The South East Asian material is very fragmentary. Thus I prefer to restrict the diagnosis here to the European *Goniopholis* species. Looking at the previously known, more complete specimens of *Goniopholis* this find is very important in being the oldest nearly complete skull and skeleton of the genus in Europe. The good preservation of the Guimarota material allows a detailed description of the specimen, and its identification as a new species.

The specimen (IPFUB Gui Croc 1; individual bones have separate numbers 1/1–1/49) is presently housed in the Institut für Paläontologie at the Freie Universität Berlin, Germany.

The institutional abbreviations used in this study are as follows: BMNH, The Natural History Museum, London; IPFUB, Institut für Paläontologie der Freien Universität Berlin.

SYSTEMATIC PALAEOONTOLOGY

CROCODYLIFORMES Walker, 1968

CROCODYLIFORMES Hay, 1930

MESOEUROCODYLIA Whetstone and Whybrow, 1983

NEOSUCHIA Benton and Clark, 1988

Family GONIOPHOLIDIDAE Cope, 1975

Genus GONIOPHOLIS Owen, 1841

Type species. *Goniopholis crassidens* Owen, 1841, from the Berriasian of Dorset, southern England

Goniopholis baryglyphaeus sp. nov.

Text-figures 2–6

Derivation of name. Greek βαρπς, heavy, and χλφη, sculpturing; in reference to the heavily sculptured dorsal surface of the skull.

Holotype. IPFUB Gui Croc 1, an articulated partial skeleton, including a nearly complete dorso-ventrally flattened skull with major portions of the lower jaw; four cervical vertebrae, six thoracic vertebrae, one sacral vertebra and three caudal vertebrae; the right and left coracoids, the left ischium and portions of the right femur, tibia and fibula, a metacarpal, and several dorsal and ventral osteoderms.

Type locality. The coal mine of Guimarota in Leiria/Portugal.

Stratigraphical range. Lower lignite coal layer ('Fundsichten') of the 'Guimarota Strata' within the Alcobaça Formation, Upper Jurassic (Kimmeridgian).

Diagnosis. *Goniopholis baryglyphaeus* is distinguished from all other European *Goniopholis* taxa by: a retroarticular process oriented caudodorsally; an articular with a facet placed ventral to the retroarticular process, and directed slightly medioventrally; a caudal margin of the mandible vertical and forming nearly a right angle at its caudoventral corner; nearly square rostralateral corners of the cranial table; a straight parieto-frontal suture with a small rostral process, and a rostrally tapering wedge-shaped lacrimal. *G. baryglyphaeus* is further characterized by heavy sculpturing all over the dorsal surface of the skull, including nasals, maxillae and premaxillae.

DESCRIPTION

Preservation

The skull is very well preserved although dorsoventrally compressed and laterally slightly distorted. The separated rostralmost parts of the rostrum can be added to the rest of the skull, so that it can be reconstructed to its full length. The ventral surface of the skull is destroyed, and the position of the choanae cannot be reconstructed. The mandible is preserved in several parts, but can be used to reconstruct almost the entire lower jaw. An isolated tooth was associated with the skull, but not in its original position. The postcranial skeleton is represented by isolated vertebrae, girdle and rib fragments and some osteoderms.

The fossil remains in Guimarota were collected in blocks of lignite. Although mostly disarticulated, occasionally remains which belong to one individual could be restored from adjacent blocks preserving the edges of sutures. All

TABLE 1. Compilation of European *Goniopholis* localities; numbers of different localities correspond to numbers on Text-figure 7.

Region and localities		Formation and age	Sedimentology	Material	Previous taxonomic assignment	Current taxonomic assignment
1. Isle of Skye/Scotland		Great Estuarine Group (Ostracod Limestone), Late Bathonian	nonmarine and lagoonal mudstones	isolated teeth and osteoscutes	<i>Goniopholis</i> sp. (Savage 1984)	cf. <i>Goniopholis</i> (Evans and Milner 1994)
Southern England	2a. Horns-leasow Quarry	Chipping Norton Formation, Early Bathonian	laminated shales, freshwater marls and clays, estuarine and shallow offshore marine to freshwater conditions	osteoderms and teeth	no former description	cf. <i>Goniopholis</i> (Evans and Milner 1994; Metcalf and Walker 1994)
	2b. Sharp's Hill	Sharp's Hill Formation, Early Bathonian				
	2c. Kirtlington Cement Quarry	Forest Marble Formation, Late Bathonian				
	2d. Watton Cliff and Swyre					
	2e. Leigh Delamere					
3. Dorset (different localities)		Purbeck Limestone Group, Berriasian	freshwater shales, limestones (oolitic), gypsum and anhydrite	parts of a mandible with teeth, ilium, pubis, osteoderms, vertebrae	<i>G. crassidens</i> (Owen 1841, 1878), holotype	<i>G. crassidens</i> (Salisbury 1999; Salisbury <i>et al.</i> 1999)
				complete skull minus mandible ('Mr. Willett's Crocodilian Skull', lost material)	<i>G. crassidens</i> (Hulke 1878)	<i>Goniopholis</i> sp. (Salisbury <i>et al.</i> 1999)
				partial skull with associated mandible, vertebrae, radius, ulna, ilium, ischium, femur, osteoderms	<i>G. crassidens</i> (Hooley 1907)	<i>Goniopholis</i> ?sp. (assignment to <i>G. crassidens</i> questioned by Salisbury 1999)
				complete skull, associated osteoderms	<i>G. simus</i> (Owen 1878; Hulke 1878; Hooley 1907), holotype	<i>G. simus</i> (Salisbury 1999; Salisbury <i>et al.</i> 1999)
				partial skull and mandible (BMNH R5814)	no formal description	<i>G. simus</i> (Salisbury <i>et al.</i> 1999)

TABLE 1. *Continued*

Region and localities		Formation and age	Sedimentology	Material	Previous taxonomic assignment	Current taxonomic assignment
4. Guimarota/Leiria, Portugal		'Guimarota Strata', Alcoaça Formation, Kimmeridgian	lignite-coal marls with marly limestones, lagoonal environment, fresh- and saltwater influx	partial mandible with teeth	<i>G. tenuidens</i> (Owen 1879)	<i>nomen dubium</i> (Salisbury 1999)
				left mandibular ramus	<i>Brachydectes major</i> (Owen 1879)	as fragmentary as <i>G. tenuidens</i> , <i>nomen dubium</i> (Salisbury 1999)
				complete skull, partial mandible, osteoderms, vertebra, humerus	<i>Nannosuchus gracilidens</i> (Owen 1879), juvenile of <i>G. simus</i> (Joffe 1967)	<i>Goniopholis</i> sp. (Salisbury 1999)
				left mandibular ramus	<i>Petrosuchus laevidens</i> Owen 1878	<i>G. simus</i> (Salisbury 1999; Salisbury <i>et al.</i> 1999)
			partial skeleton, skull and mandible	<i>Goniopholis</i> sp. (Brinkmann 1989)	<i>G. baryglyphaeus</i> sp. nov.	
5. Wimille/Boulogne-sur-mer, northern France	Formations gréseuses, Late Portlandian	grey limestones from shallow offshore marine environment	isolated tooth (lost material)	<i>G. undidens</i> (de la Moussaye 1885a, b)	<i>nomen dubium</i> (Buffetaut 1986)	
			isolated teeth, vertebrae, fragments of a skull	<i>G. undidens</i> (Sauvage 1885, 1888, 1909)	<i>nomen dubium</i> (Buffetaut 1986)	
			left premaxilla and maxilla	<i>G. cf. pugnax</i> (Buffetaut 1986)	<i>G. cf. simus</i> (Salisbury <i>et al.</i> 1999)	
North-western and western Germany	6a. Bückeberg, Obernkirchen, Osnabrück/	north-western Germany Obernkirchen Sandstone of the Bückeberg Member, Berriasian	units of calcareous clays associated with coal layers, nonmarine	isolated teeth, vertebrae, ribs, humerus, osteoderms, skull fragments (lost material) and ulna, cervical vertebra and three isolated teeth	<i>G. pugnax</i> (Koken 1887)	<i>nomen dubium</i> (Salisbury <i>et al.</i> 1999)

TABLE 1. *Continued*

Region and localities	Formation and age	Sedimentology	Material	Previous taxonomic assignment	Current taxonomic assignment	
			cervical vertebrae (lost material) and partial osteoderm	<i>G. minor</i> (Koken 1887)	<i>nomen dubium</i> (Salisbury <i>et al.</i> 1999)	
			'Ballerstedt collection': moulds of five skulls (lost material), moulds of three skulls, right mandible, isolated postcranial elements	endocasts of braincase and tympanic cavities of two specimens referred to <i>G. pugnax</i> and <i>G. minor</i> (Edinger 1938)	<i>G. simus</i> (Salisbury <i>et al.</i> 1999)	
			natural mould of skull and mandible, endocast of rostrum maxillae and orbital region	<i>Goniopholis</i> sp. (no formal description)	<i>G. simus</i> (Salisbury <i>et al.</i> 1999)	
7. Bernissart, Belgium	6b. Nehden/Sauerland, western Germany	Aptian	clays as limnic karst-cave fillings in Devonian limestones	cervical neural arch, first sacral vertebra, left humerus, distal end of left femur, osteoderms	<i>Goniopholis</i> sp. (Huckriede 1982; Norman 1987)	<i>Goniopholis</i> sp. (Salisbury <i>et al.</i> 1999)
			clays and lignite layers	skeleton with associated skull, single postcranial skeleton	<i>G. simus</i> (Dollo 1883)	<i>Goniopholis</i> sp. (Salisbury <i>et al.</i> 1999)
Spain	8a. Galve/Teruel	Castellar and Camarillas formations, Early Barremian	marls and bioturbated limestones, fluviolacustrine clays, continental environment	isolated teeth, cranial (maxilla) fragment	no formal description	<i>Goniopholis</i> sp., <i>G. cf. crassidens</i> (Buscalioni and Sanz 1987; Cuenca-Béscos <i>et al.</i> 1999)
	8b. Uña/Cuenca	Uña Formation, Late Barremian	limestones and lignite layers with marl layers, continental environment	isolated teeth, parts of mandible	no formal description	<i>Goniopholis</i> sp. (Brinkmann 1989)
	8c. Vadillos-San Román de Cameros, La Rioja	imprecisely dated as Berriasian–Aptian	fluviatile sandstones, continental environments	isolated skull	no formal description	<i>Goniopholis</i> sp. (Ortega <i>et al.</i> 1996)
	8d. Forcall/Castellón	Aptian	marls	fragment of rostrum (lacrimal, prefrontal, frontal)	no formal description	<i>G. cf. simus</i> (Buscalioni 1986)

cranial and postcranial material of the holotype of *Goniopholis baryglyphaeus* (IPFUB Gui Croc 1/1–1/49) was collected from a single block of lignite, and is of the appropriate proportions to be assigned to one individual. The dorsoventral compression of the skull results from loading by the overlying strata. The lignitic matrix was completely removed from the bone surfaces but all openings and fractures are filled with lignite and mostly could not be cleaned. Individual bones are often broken. The articular surfaces of the bones have been attacked by humic acids from the coal and are often rough and destroyed.

Skull

Form and proportions. The reconstructed skull length is 281 mm, of which the rostral part forms 66 per cent. The lateral margins of the maxillae are both vertically and laterally undulating. The anterior tip of the rostrum is rounded. A strongly developed notch at the suture between the premaxilla and the maxilla at the lateral margins provides space for the mandibular pseudocanine. The premaxillary portion of the rostrum is almost as broad as the maxillary portion, which at its widest point reaches the breadth of the cranial table. The rostrum is remarkably flattened dorsoventrally.

The skull widens in a posterior direction and reaches maximum width at the caudal margin of the cranial table. The cranial table is nearly rectangular and terminates caudolaterally in a rounded process of the squamosal. The cranial table is about 20 per cent broader than it is long and increases slightly in width from anterior to posterior by about 10 per cent. The lateral margins of the cranial table are indented anterior to the caudolateral process of the squamosal. The margins are convex at the level of the supratemporal fenestrae. The cranial table is visibly elevated from the rostrum. A broadly marked U-shaped interorbital crest separates the caudal part of the skull from the rostral part. The interorbital crest includes the lacrimal, prefrontal and frontal bones (Text-fig. 2A). The interorbital region is 41.1 mm wide. The medial margin of the orbit is situated anteroposteriorly to the lateral margin of the supratemporal fenestra. The bone bar between the orbit and the supratemporal fenestra is 13.4 mm wide.

The dorsal surface of the skull is covered by a regular pattern of heavy sculpturing. On the rostral part of the skull it consists of rounded pits 2–4 mm wide and about 2 mm deep that decrease slightly in size at the lateral margins of the rostrum. On the rostral portion of the maxilla they are rather longitudinally directed and occasionally blend into one another, but become regular and rounded again on the premaxilla. On the cranial table the pits become slightly larger and the widest pits are positioned on the quadratojugal, where they reach up to 5–6 mm in diameter and 3 mm in depth. The quadrate is unsculptured (Text-fig. 2A). The cranial measurements are given in Table 2.

External naris. The lateral margins of the external naris are preserved on the premaxillae (Text-fig. 2A). The external naris was separated from the anterior rostral contour by a premaxillary bar. The lateral margins indicate an undivided, nearly heart-shaped foramen (Text-fig. 3A). Internally the preserved parts of the fossa are covered by a weak sculpturing. The lateral margins of the naris are simple and not elevated above the level of the rostrum, and the step from the surrounding premaxillary bone is very low. As indicated by the preserved median contacts between the nasals and premaxillae, the nasals do not reach the external naris. A foramen incisivum is not preserved.

Orbit. The orbits are only partly preserved. The medial margin is largely formed by the prefrontal. The lacrimal with the visible lacrimal duct forms the rostromedial, and the prefrontal the caudomedial margin. The orbit is bounded by the jugal laterally, and the postorbital caudally (Text-figs 2A–B, 3A). The outline of the orbit can be reconstructed as elliptical with a subrounded tip rostrally. The opening is clearly smaller than the supratemporal fenestra.

Supratemporal fenestra. These paired openings are not elevated from the cranial table surface. Each is nearly square in outline, with subrounded corners (Text-fig. 2A). They are bounded rostromedially by the postorbital, rostromedially by the frontal, caudomedially by the parietal and caudolaterally by the squamosal. The main portion of the inner medial wall of these openings is formed by the parietal. Rostrally the frontal, and caudally the quadrate, also participate in this margin. At the suture between the quadrate and the parietal the opening into the rudimentary posttemporal passage is preserved as a slit-like foramen.

Infratemporal fenestra. The infratemporal fenestra faces dorsolaterally. The opening is probably about twice as long as it is wide. It is bounded laterally by the jugal and caudally and caudodorsally by the quadratojugal (Text-figs 2A, 3A). The dorsal margin of the infratemporal fenestra is formed by a rostral extension of the squamosal.

Palatal fenestra. The rostral portion of the left palatal fenestra is preserved (Text-fig. 2B). The opening has a semicircular rostral margin. It is bounded rostrally by the maxilla, by the tooth row laterally and by the palatine

TABLE 2. Measurements of skull and mandible of *Goniopholis baryglyphaeus* sp. nov.

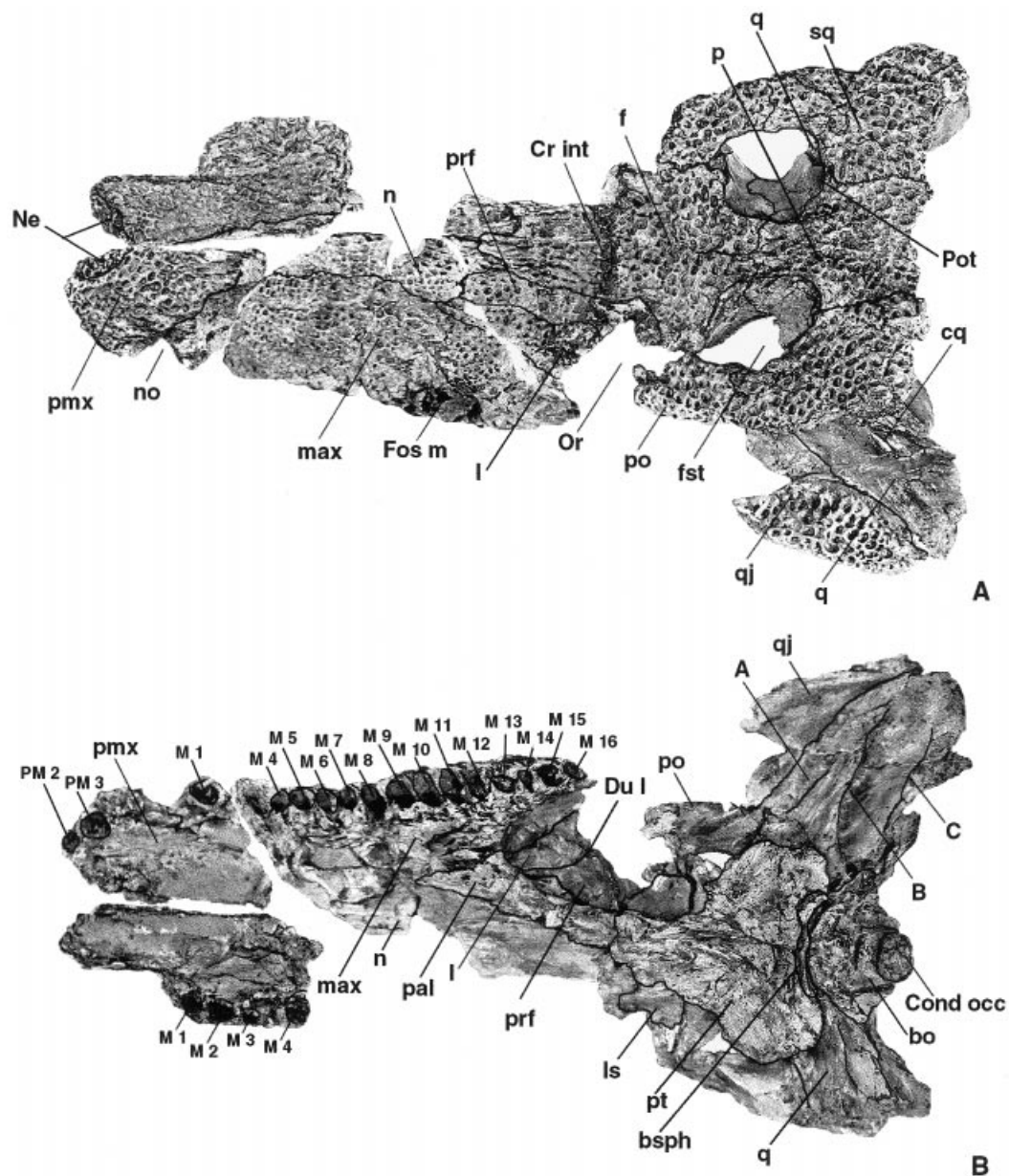
Skull	Measurement (mm)
1. Length	239.0
2. Reconstructed maximum skull length, from tip of premaxillae to occipital condyle	281.0
3. Length of rostral part of skull, from tip of premaxillae to rostral tip of the orbits	151.8
4. Maximum width of rostral part of skull, at rostral tip of orbits	56.5
5. Minimum width of interorbital bone	41.1
6. Length of cranial table, from interorbital crest to caudal end of squamosal	86.3
7. Maximum width of cranial table, at caudal end of squamosals	100.9
8. Length of external naris	12.2
9. Width of external naris	16.8
10. Width of premaxilla at external naris	25.9
11. Length of maxillar fossa	21.0
12. Width of maxillar fossa	16.0
13. Length of supratemporal fenestra	27.3
14. Width of supratemporal fenestra	24.1
15. Width of skull between supratemporal fenestrae	13.4
16. Length of preserved tooth row on maxilla	122.4
17. Width of palatal fenestra	35.8
18. Height of occipital surface, as preserved	49.9
19. Width of occipital surface at paroccipital process	103.3
20. Height of occipital condyle from ventral surface of skull	32.0
21. Height of occipital condyle	10.0
22. Width of occipital condyle	14.0
23. Height of foramen magnum	31.1
24. Width of foramen magnum	17.1
Mandible	
1. Height of mandible (dentary) at mandibular symphysis	17.0
2. Height of mandible (surangular) rostral to retroarticular process	56.2
3. Height of mandible (surangular) at retroarticular process	61.6
4. Width of retroarticular process	14.3
5. Length (craniocaudal) of articular facet	27.7
6. Width of articular facet of articular	33.0
7. Tooth crown height	10.1
8. Basal width of tooth crown	6.0

medially. The fenestra extends rostrally up to the thirteenth maxillary tooth. The roof of the fenestra is composed of the prefrontal and the lacrimal.

Choanae. The choanae are not preserved; as the nasopharyngeal duct reaches the pterygoid, participation of the pterygoid in the choanae is expected (Text-fig. 2B).

Posttemporal fenestra. The posttemporal fenestra is located in the occipital part of the skull at the boundary of the sutures between the supraoccipital ventromedially, the parietal dorsomedially and the squamosal dorsolaterally (Text-fig. 4A). As a result of the dorsoventral compression of the skull the posttemporal fenestra is preserved as a small and slit-like opening. The foramen is obscured in dorsal view by the caudally overhanging squamosal.

Foramen magnum. The foramen magnum is dorsally and laterally surrounded by the otoccipitals, which exclude the supraoccipital from the dorsal margin of the opening (Text-fig. 4A). The occipital condyle, formed by the basioccipital, bounds the foramen magnum ventrally.



TEXT-FIG. 2. Skull of *Goniopholis baryglyphaeus* sp. nov. A, dorsal, and B, ventral view; IPFUB Gui Croc 1, holotype. Visible sutures are lightly traced. Abbreviations: A, quadrate crest A; B, quadrate crest B; bo, basioccipital; bsph, basiphosphoid; C, quadrate crest C; Cond occ, occipital condyle; cq, cranioquadrate canal; Cr int, interorbital crest; Du l, lacrimal duct; f, frontal; Fos m, maxillary fossa; fst, supratemporal fenestra; l, lacrimal; ls, laterosphenoid; M 1–M 16, maxillary alveoli; max, maxilla; n, nasal; Ne, external naris; no, notch at the suture between premaxilla and maxilla; Or, Orbit; p, parietal; pal, palatine; pmx, premaxilla; PM 2–PM 3, premaxillary alveoli; po, postorbital; Pot, opening of the posttemporal canal; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratejugal; sq, squamosal. Both $\times 0.42$.

Premaxilla. The isolated premaxillae are about twice as long as they are wide. The lateral margins are convex in a lateral direction and are caudally indented by a wide notch (Text-fig. 2A). At the notch the oblique suture between the premaxilla and the maxilla runs caudomedially, ending at the fourth maxillary tooth. The suture is visible ventrally and is caudomedially directed (Text-fig. 2B). In its caudal portion, the premaxilla forms a wedge-shaped process, isolating the nasals from the external naris and the anterior portion of the maxilla. The contact between nasal and premaxilla extends along the caudal third of the latter, and ends rostrally at a level with the lateral notch (Text-fig. 3A).

Maxilla. The maxilla forms the largest part of the snout and the secondary palate. It is about three times longer than it is wide. Its lateral margin is 'festooned': it forms in lateral and in vertical direction two convex waves, with their maximum curvature at the level of the fourth and fifth and the tenth and eleventh maxillary teeth. A gentle dorsal expansion in the rostralateral portion of the bone marks the position of the maxillary pseudocanine. A semi-circular maxillar fossa with neat margins is preserved on the lateral margin of the left maxilla, 24.1 mm rostral from the orbit (Text-figs 2A, 3A). The fossa is not smooth inside, but the internal structure is destroyed. There is no antorbital fenestra. Rostromedially the maxilla is bounded by the nasal, caudomedially by the lacrimal, and caudally it meets the jugal behind the maxillar fossa. The maxilla extends caudally in a short projection beneath the jugal and ends at the first third of the orbit. On the ventral surface the secondary palate is partly preserved. The suture between the maxilla and the palatine is medio-rostrally directed. The ventral suture between the maxilla and the lacrimal in the roof of the palatal fenestra runs from the posterior margin of the palatal fenestra anteromedially (Text-fig. 2B).

Nasal. The nasals widen gradually in a caudal direction with their maximum width along their short lateral contact with the lacrimals. The internasal suture is a smooth line. The rostral process of each element wedges between the premaxillae, but ends about 15 mm behind the external naris. At their caudal contact with the frontal, both nasals form a W-shaped structure: laterally from the frontal they bear a caudal wedge-shaped process that separates a rostral portion of the prefrontal from the frontal (Text-fig. 2A).

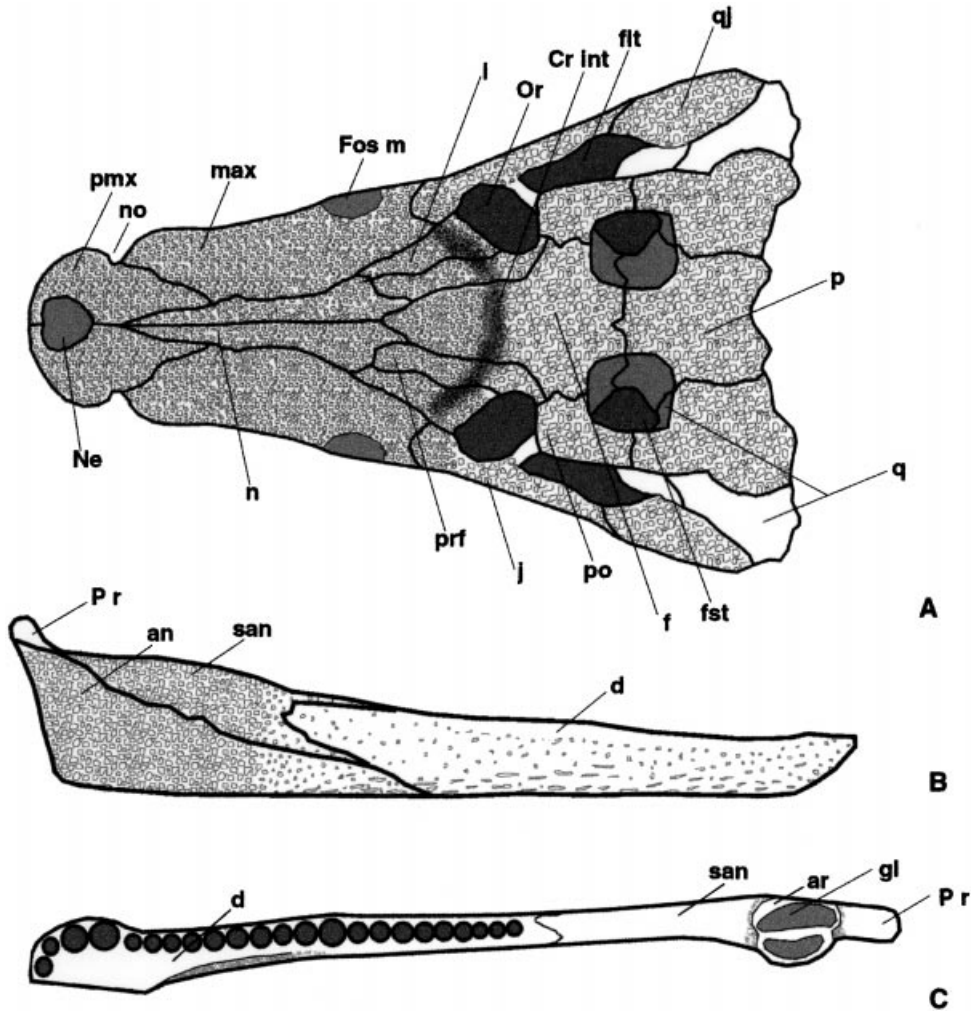
Prefrontal. The prefrontal is narrow and elongated. Rostrally it ends with a rounded margin between the lacrimal and the nasal. Laterally it is bounded by the lacrimal and medially by the frontal. Caudolaterally it takes part in the medial margin of the orbit and is in contact, at its caudal end, with the postorbital along 7.9 mm from the caudal curvature of the orbit (Text-fig. 2A). In ventral view, the prefrontal pillar is positioned medially at the anterior margin of the orbit and reaches the palate. The prefrontal pillar is transversely expanded in its dorsal half and columnar ventrally. The dorsal extent of the pillar laterally forms a small, curved, sharp crest that continues with a thin lamina underlying the medial part of the lacrimal (Text-fig. 2B).

Lacrimal. In dorsal view, the lacrimal is about half as wide as it is long in its caudal portion and tapers rostrally. Between the maxilla laterally and the nasal medially it terminates level with the maxillar fossa (Text-figs 2A, 3A). On the rostral margin of the orbit, the lacrimal contacts the jugal. Ventrally, the caudal opening of the lacrimal duct is located in the middle of the rostral margin of the orbit (Text-fig. 2B). From this opening the suture between the prefrontal and lacrimal runs anteriorly. The lacrimo-prefrontal suture is covered in its caudal half by the lateral lamina of the prefrontal.

Frontal. In dorsal aspect, the frontals are not fully fused into a single bone, as is indicated by a smooth median suture in the caudal third of the bone. The frontal is a relatively large bone integrated into the cranial table and the rostral part of the skull. The rostralmost portion of the bone widens caudally. The frontal is isolated from the medial margins of the orbits by the prefrontals. On the cranial table it contacts the postorbitals laterally (Text-fig. 2A). In its caudolateral portion, the frontal forms the anteromedial corners and the anterior third of the medial margin of the suratemporal fenestrae. It is also integrated into the inner medial wall of the supratemporal fossa avoiding the contact between the postorbital and parietal. Caudally, it contacts the parietal in a straight transverse suture with a small median rostral tip.

In ventral view, a small portion of the frontal is visible caudally to the orbits. The ventral portion of the frontal extends more rostrally than the dorsal portion. The ventral caudal margin of the element is obscured by the laterosphenoids that are pressed onto the ventral portion of the cranial table (Text-fig. 2B).

Postorbital. The rounded rostralateral corner of the postorbital gives the cranial table its characteristic rectangular shape. The jagged suture with the prefrontal and the frontal is positioned in the middle of the rostral margin of the suratemporal fenestra. The squamosal is contacted caudally by a jagged suture in the middle of the lateral margin of



TEXT-FIG. 3. Reconstruction of skull and mandible of *Goniopholis baryglyphaeus* sp. nov. A, skull in dorsal view. B, right mandibular ramus in lateral and C, in dorsal view. Abbreviations: an, angular; Cr int, interorbital crest; d, dentary; f, frontal; fit, infratemporal fenestra; Fos m, maxillary fossa; fst, supratemporal fenestra; gl, glenoid fossa; j, jugal; l, lacrimal; max, maxilla; n, nasal; Ne, external naris; no, notch at the suture between premaxilla and maxilla; Or, Orbit; p, parietal; pmx, premaxilla; P r, retroarticular process; po, postorbital; prf, prefrontal; q, quadrate; qj, quadratojugal; san, surangular; sq, squamosal.

the supratemporal fenestra (Text-fig. 2A). The smooth and robust postorbital bar is displaced medially. On the ventral surface of the postorbital two longitudinal crests with a median depression on the base of the postorbital bar mark the contact with the laterosphenoid (Text-fig. 2B).

Parietal. The parietal forms the caudomedial part of the cranial table and comprises one-third of the width of the cranial table. The dorsal surface of the parietal is slightly concave. Rostrally, the bone is contacted by the frontal and forms the caudal two-thirds of the medial margin of the supratemporal fenestra, as well as the largest portion of its medial wall. On the medial wall of the supratemporal fossa the parietal contacts the quadrate. The posttemporal canal opens between the parietal and the quadrate beneath the straight parieto-squamosal suture in the middle of the caudal margin of the supratemporal fenestra (Text-fig. 2A). Thus, contact

between the parietal and the squamosal in the supratemporal fossa is prevented by the quadrate. Caudally, the margin of the parietal is concave. No dorsoventral suture between the parietal and the supraoccipital is visible.

Squamosal. The caudal margin of the squamosal is slightly convex at the contact with the parietal but becomes concave laterally. A differentiated subrounded caudolateral process overlaps the occipital surface caudally. Caudolaterally, the squamosal forms the roof of the cranioquadrate canal which is exposed on the quadrate as a shallow sulcus (Text-fig. 2A). The squamosal is not integrated into the paroccipital process but ends more dorsally, where it overlaps the otoccipital. It can be clearly distinguished from the otoccipital by a slightly dorsally curved suture, which contains the posttemporal foramen (Text-fig. 4A). A squamosotoccipital foramen, as identified by Salisbury *et al.* (1999) is not visible. Laterally, the dorsal margin of the quadrate is visible, but the aural region is destroyed. A thin rostral process of the squamosal underlaps the postorbital laterally with a smooth suture and extends to the postorbital bar.

Jugal. The very robust and heavily sculptured jugal is about twice as long as it is wide and narrows from rostral to caudal. Its rostral process overlaps the maxilla. The ventral portion of the postorbital bar is formed by the jugal and is preserved as an unsculptured dorsal process which is inset medially from the lateral margin of the jugal (Text-fig. 4B). The diameter of this process is 8.8 mm, but the suture with the postorbital is not preserved. Caudally it contacts the quadratojugal via a transverse suture rostral to the caudal margin of the infratemporal fenestra. Rostrally, a heavy, serrated suture marks the contact to the maxilla. Medially the contact with the ectopterygoid is preserved as a rounded roughened area comprising one-third of the medial surface of the jugal. The contact area reaches cranially the suture of the maxilla and ends caudally ventral to the postorbital bar. A foramen is preserved as a small elongated opening at the caudal end of the dorsal process.

Quadratojugal. The quadratojugal can be subdivided into a caudolateral, heavily sculptured, robust part and a rostromedial, thinner smooth portion (Text-fig. 2A). With its medial part it contacts the quadrate in a simple suture that runs from caudolateral to rostromedial. Rostrally, the medial part ends in a convex outline and extends in a dorsal direction until it contacts the squamosal, but it does not reach the postorbital. The lateral part has a convex medial margin dorsally, and forms a rostral tip. Thus, the infratemporal fenestra is bounded caudally by both parts of the quadratojugal. The quadratojugal spine is not preserved. In ventral view, the lateral margin of the quadratojugal is slightly downturned, forming a depression that continues on the ventral side of the quadrate. The suture with the quadrate forms a smooth line (Text-fig. 2B).

Quadrate. The unsculptured quadrate is somewhat flexed ventrally at its caudal end and expanded laterally. It is overlapped rostr dorsally by the squamosal. As a result of the absence of lateral extension of the squamosal, the cranioquadrate canal is exposed as a shallow, laterally opened, sulcus. This sulcus runs transversely from the medially roofing squamosal in a caudolateral direction (Text-fig. 2A). In the caudal part of the medial wall of the supratemporal fossa the quadrate contacts the parietal.

On the occipital surface the quadrate is bounded medially by the otoccipital (Text-fig. 4A). The suture between the otoccipital and the quadrate is visible as a weak line beyond the paroccipital process. In ventral aspect three well-developed crests for the attachment of the mandibular adductor are preserved. The crests can be distinguished as A, B and C (Iordansky 1973), with crest B showing the greatest development. In the caudal depression behind crest B a reticular structure is developed (Text-fig. 2B). Medially, the quadrate contacts the pterygoid and the basisphenoid. The mandibular condyle is situated on the ventral flexure of the caudal end of the quadrate. It forms a broad articular surface subdivided into two portions by a medial incision. The lateral portion is dorsoventrally expanded and higher than the medial portion. A foramen aereum is not preserved.

Otoccipital. The otoccipitals form large paroccipital processes that are slightly flexed caudomedially. The lateral margins of the processes are rounded and both the quadrate and the ventral portion of the otoccipital are overhung (Text-fig. 4A). Laterally, they do not reach the lateral end of the squamosal on the cranial table. The suture between the otoccipital and the supraoccipital runs from the dorsal posttemporal fenestra ventromedially. Both otoccipitals contact each other with a smooth suture dorsal to the foramen magnum. The lateral walls of the foramen magnum are formed by two peg-like processes that meet the occipital condyle. Starting from these pegs the suture with the basioccipital runs in a ventral direction. In the ventrolateral portion of the bone a foramen is positioned ventral to the medial suture with the quadrate. A further, slit-like foramen is visible near the ventrolateral margin of the otoccipital and can be interpreted as the carotid foramen.

Supraoccipital. In occipital aspect the supraoccipital is slightly inclined. It is bounded dorsally by the parietal, which excludes the bone from the cranial table. Its lateral and ventral margins are formed by the otoccipitals (Text-fig. 4A). The supraoccipital is nearly subtrapezoidal in outline, transversely wider, and with a subrounded ventral angle. At its caudal surface the supraoccipital bears a median crest with slight lateral depressions.

Basioccipital and basisphenoid. The basioccipital forms the occipital condyle and is bounded dorsolaterally by the otoccipitals. The condyle has a well-developed subcircular articular facet. On its dorsal surface a shallow sulcus runs into the foramen magnum (Text-fig. 4A). The basioccipital is oriented ventrocranially and the lateral contact between the basioccipital and the otoccipital takes the form of a ridge. Ventral to the occipital condyle the basioccipital is expanded with a medial furrow and two lateral depressions.

On its ventral surface the inner wall of the basioccipital bears a median crest and laterally diverging tubera. Rostrally, it is bounded by the basisphenoid. The basisphenoid itself is exposed only in a narrow triangular area between the anterior pterygoid and the posterior basioccipital (Text-fig. 2B). A median inclination on the ventral margin of the basioccipital indicates the median Eustachian foramen. The lateral Eustachian foramina are visible 2 mm laterally from the mid foramen at the ventral margin of the basioccipital.

Palatine. As a result of the compression of the skull the palatines are badly damaged. Only portions of the ventral part of the left palatine are preserved at the level of the palatal fenestra. The palatal surface is flat. Rostrally, contact with the maxilla is marked by a suture, extending rostromedially from the rostralateral margin of the palatal fenestra (Text-fig. 2B). Caudally, the ventral part of both palatines is broken away, exposing the caudal portion of the nasopharyngeal canal. At this level, contact with the pterygoids is visible.

Pterygoid. The ventral surface of the pterygoid is broken away exposing the caudal end of the nasopharyngeal canal (Text-fig. 2B). This canal extends for about the first third of the pterygoid. The stout wings of both pterygoids are broken at their lateral ends and, owing to the dorsoventral compression of the skull, the degree of their inclination cannot be determined. At the caudal end of the pterygoid wings the basisphenoid is closely attached. The contact with the cranium is not preserved.

Ectopterygoid. The ectopterygoid is a massive bone that contacts the maxilla and the jugal rostrally. This attachment with the maxilla and jugal is visible as a subrounded roughened area at the jugal. The caudal tip of the ectopterygoid ends ventrally from the caudal end of the postorbital bar and does not participate in the postorbital bar. The anterior tip of the ectopterygoid reaches the caudal end of the posteriormost maxillary tooth. The ventral process of the bone has a diameter of 10.6 mm. The caudal contact with the pterygoid is not preserved.

Laterosphenoid. In ventral view, the laterosphenoid is slightly displaced rostrally and pressed onto the ventral portion of the cranial table (Text-fig. 2B). Its true position in the cranium cannot be determined. The bone is nearly triangular in shape but no morphological details are visible. The lateral end is broken away.

Mandible

Form and proportions. The mandible is preserved as separate portions that can be reconstructed into a stout mandibular ramus with a total length of approximately 320 mm (Text-fig. 3B–C). The lower jaw extends beyond the skull caudally by about 40 mm.

From rostral to caudal, the mandibular ramus deepens rapidly, its caudal end reaching at least two and a half times the depth of the rostral end. The ventral surface is flat at the level of the mandibular symphysis. The sculpturing on the lateral surface changes from small pits rostralmost to weak longitudinally aligned ridges at the dentary to a strongly developed pattern of regular pits on the caudal angular and surangular. The tooth row occupies about 50 per cent of the mandible length. The dorsal margin of the dentary is vertically slightly undulating. The articular contacts the surangular about 60 mm rostral from the caudal end of the mandible. The articular facet is positioned ventral to the retroarticular process and slightly medioventral to the lateral margin of the surangular. The long retroarticular process is directed caudodorsally and the caudal margin of the mandible is somewhat ventrally inclined, but very straight, forming nearly a right angle at its ventral end (Text-fig. 3B–C). An external mandibular fenestra is not preserved.

Dentary. The rostral symphysis between both dentaries reaches the level of the fifth or the sixth dentary tooth (Text-figs 3C, 4D). In the symphyseal region the dentary is laterally broadened and relatively low, but narrows and deepens

continuously in a caudal direction (Text-fig. 4E). The splenial itself is not preserved, but the attachment sutures on the dentary suggest that the splenial reached the symphysis.

The upper third of the lateral surface of the dentary is set off from the sculptured bone surface as a smooth area that begins at the level of the seventh dentary tooth and widens caudally. Between the sculptured and unsculptured areas a longitudinal row of small pits extends in the caudal direction. A vertical festooning of the dorsal margin of the dentary is present, with maximum curvature of the lateral dentary margin at the level of the fourth and fourteenth dentary alveoli. Starting at the mandibular symphysis, the Meckelian canal extends as far as the nineteenth dentary tooth where it is broadened. The dentary terminates 27.3 mm caudal to the tooth row and forms a dorsal process that extends 61.2 mm posterior to the caudoventral margin of the bone (Text-fig. 3C). The suture with the posterior surangular is forked. The smooth ventral margin of the process could be interpreted as the dorsal margin of the lateral mandibular fenestra, but since there is no corresponding structure on the rostral margin of the angular and the surangular, the existence of this fenestra remains uncertain.

Angular. On the rostral margin of the angular, the lateral contact with the dentary is marked by a roughened wedge-shaped area. The rostradorsal margin bears a small groove where the caudal margin of the dentary was contacted. The ventral portion of the angular is broken off and separately preserved. Ventrally the angular forms a trough that enclosed the Meckelian cartilage. In the caudal third of the trough a small foramen is visible. The angular forms the caudal end of the mandible. In lateral view, the contact with the surangular is a simple suture, running from the ventral part of the caudodorsal retroarticular process transversely to rostroventral (Text-fig. 4I).

Surangular. The lateral surface of the surangular is uneven ventrally. At its caudodorsal end the bone is unsculptured and laterally broadened, reaching 18.2 mm in width. The dorsal margin inclines slightly in caudodorsal direction.

The inner surface is smooth. A rounded crest runs from caudodorsal rostrally and seems to be broken away at its end, 61.4 mm from the caudal margin of the mandible (Text-fig. 4H). The attachment area for the articular is presumed to have been located here. The surangular participates with a thin lamina in the articular facet. The ventral contact with the angular is not visible medially.

Articular. The articular is preserved separately, but the retroarticular process is broken away. The articular facet is divided into lateral and medial portions, separated from each other by a rounded crest (Text-figs 3C, 4G). The lateral surface is positioned a little more caudally and widens from rostral to caudolateral. The medial surface is nearly kidney-shaped in lateral direction and is oriented parallel to the median crest. Ventrally, the bone continues as a thin elongate process, serving as an attachment surface for the surangular. The articular facet is placed ventral to the caudodorsally directed retroarticular process. The articulation surface is slightly medioventrally directed.

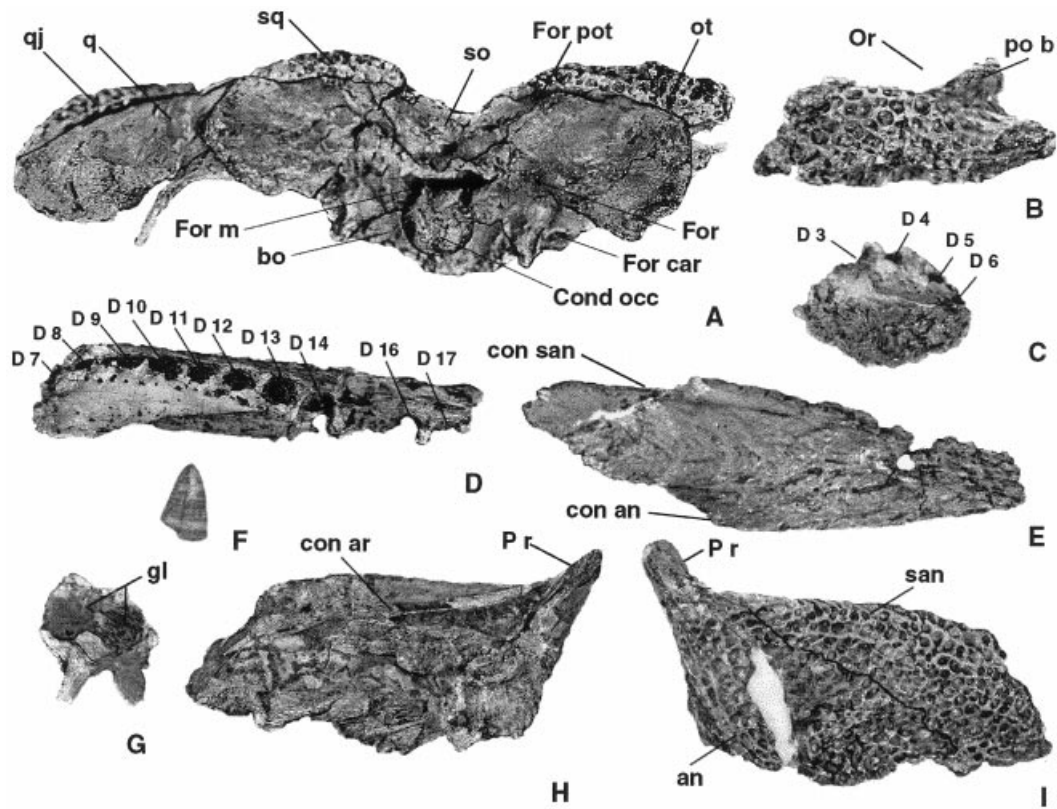
Dentition

Teeth. A single isolated tooth crown associated with the specimen is preserved. The base of the tooth is broken away. The stout, conical tooth has a rounded tip. It bears two well-developed smooth carinae on opposite sides that continue from the base to the apex of the crown. Additionally, several closely spaced wrinkled striae run from the base of the crown to the apex, thinning in this direction (Text-fig. 4F).

Pattern of dentition. Though no teeth are preserved *in situ*, the dentition patterns can be reconstructed from the alveoli (Text-figs 2B, 4C–D, 5). The rostrum contains 20–21 alveoli. The premaxilla has two alveoli preserved but there is room for at least two additional alveoli, so that the existence of 4–5 premaxillary alveoli is probable. In the maxilla, 16 alveoli are preserved. The mandibular rostrum contains 23 alveoli.

The different sizes of the alveoli indicate variation in tooth size (Text-fig. 5). The largest alveoli in the rostrum are the fourth and fifth and the tenth and eleventh maxillary alveoli. Alveolus size falls into three sine waves that agree with the lateral and vertical festooning of the maxillary rostrum. The first wave reaches its maximum at the second and third premaxillary alveolus. The second wave starts at the notch between premaxilla and maxilla and reaches a maximum at the level of the fourth maxillary alveolus. The third wave is more weakly developed than the other two and reaches a maximum at the tenth and eleventh maxillary alveoli.

In the dentary, the fourth alveolus is the largest and fits into the incision between the premaxilla and maxilla, indicating the pseudocanine. The third and fourth dentary alveolus are nearly the same size, contiguous and separated from each other by only a thin portion of interalveolar bone. Two sine waves in alveolus size are evident but are not so



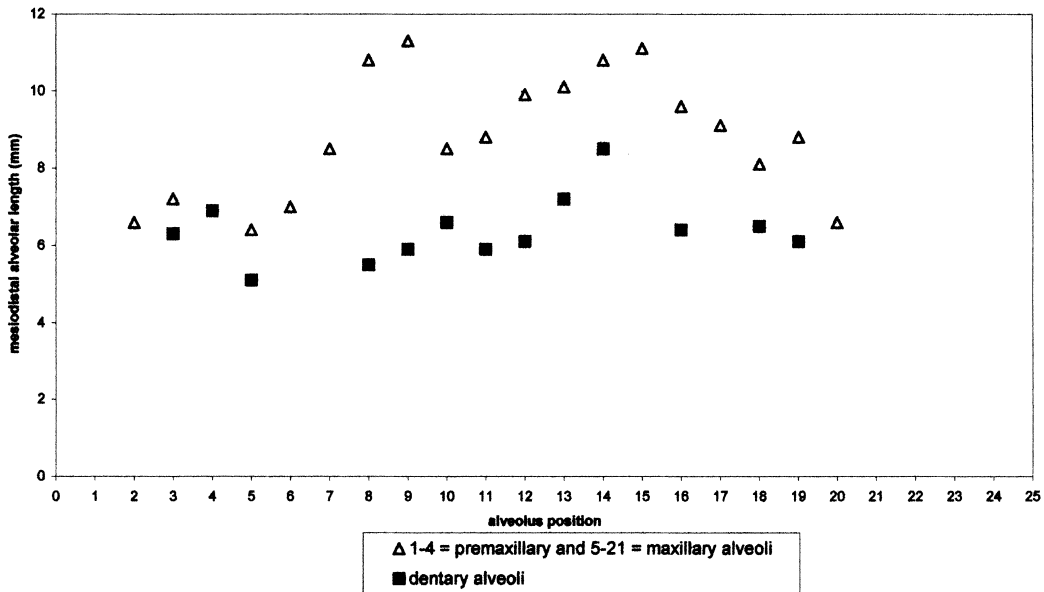
TEXT-FIG. 4. Elements of skull and mandible of *Goniopholis baryglyphaeus* sp. nov.; IPFUB Gui Croc 1, holotype. A, skull in occipital view. B, left jugal in lateral view. C, right dentary fragment in medial view. D, right dentary fragment in dorsal view. E, right dentary fragment in lateral view. F, tooth in lateral view. G, right articular in rostromedial view. H, caudal portion of right mandible in medial view. I, caudal portion of right mandible in lateral view. Visible sutures are lightly traced. Abbreviations: an, angular; bo, basioccipital; con an, dentary-angular contact; con ar, facet for articular-surangular contact; con san, dentary-surangular contact; Cond occ, occipital condyle; D 3–D 17, dentary alveoli; For, foramen; For car, carotid foramen; For m, foramen magnum; For pot, posttemporal foramen; gl, glenoid fossa; Or, Orbit; ot, otoccipital; P r, retroarticular process; po b, postorbital bar; po p, postorbital pillar; q, quadrate; qj, quadratojugal, san, surangular; so, supraoccipital; sq, squamosal. All $\times 0.6$.

clearly developed as in the maxillae. The first maximum is reached at the fourth dentary alveolus, the second in the fourteenth dentary alveolus. The slight festooning of the mandibular ramus corresponds to these maxima. There is no evidence of different morphotypes in the dentition of the animal, but with regard to the different sizes of the alveoli the possession of different sized and morphologically variable teeth is possible.

The pattern of dentition corresponds to that of recent crocodylians with interlocking premaxillary/maxillary and dentary teeth, and a clearly visible dentary pseudocanine that fits into an incision in the lateral margin of the rostrum (Kälin 1955).

Postcranial elements

Osteoderms. Several parts of the dorsal paravertebral shield are preserved as broken parts, but only two scutes are nearly complete. The rectangular scutes are about twice as wide as they are long. The dorsal surface is covered by heavy sculpture, consisting of regular rounded pits with diameters of 3–5 mm and a depth of about 3 mm. On the



TEXT-FIG. 5. Alveolar sizes of *Goniopholis baryglyphaeus* sp. nov., indicating the pattern of dentition in premaxilla and maxilla, and in dentary.

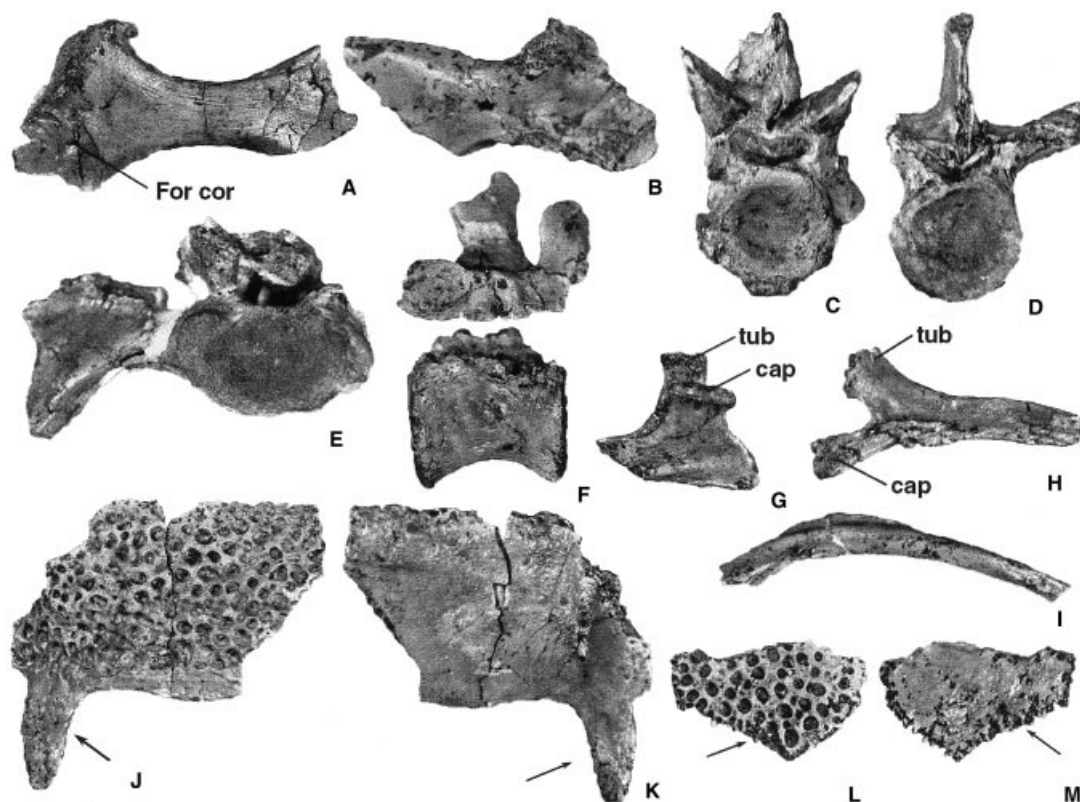
cranial margin a smooth area 4 mm long represents the point upon which each scute was imbricated with the preceding osteoderm. A smooth conical process, about 24 mm in length, is located on the cranio-lateral corner of each osteoderm and fitted into a longitudinal depression on the ventral side of the preceding osteoderm (Text-fig. 6J-K). A rounded expansion on the dorsal surface continues from the process in a caudal direction. These expansions are more strongly developed on the caudal osteoderms, from which also parts are preserved. Ventrally, the smooth surface of the osteoderms is covered by a reticular pattern of fine striae.

Some damaged ventral scutes are also preserved. The ventral osteoderms are rather hexagonal (Text-fig. 6L-M). Like the dorsal scutes they are heavily sculptured on the external surface and have a smooth internal surface bearing fine striae. The lateral margins bear serrated sutures.

Vertebrae. Different segments of the vertebral column are represented by 14 isolated amphicoelous vertebrae. The stout centra are concave ventrally. In the presacral vertebrae the centra are about as high as they are broad and have a length of between 25 and 30 mm. The neurocentral suture is still visible, but nearly closed.

In ventral aspect, the cervical vertebrae exhibit a small (6-7 mm high) rounded hypapophysis that develops into a rounded crest caudally (Text-fig. 6C). In the caudalmost cervical vertebra this crest has disappeared. The parapophyses have a nearly elliptical articular surface that increases in size caudally. In the cranial region they are slightly inclined ventrally, but caudally they become more laterally directed and approach the neurocentral suture. The diapophyses have a similar elliptical articular surface. They are directed ventrally, but also become laterally directed in more caudal cervical vertebrae. The neural arch is not preserved to its full height. As a result of dorsoventral compression the neural canal is more or less kidney-shaped in outline (Text-fig. 6C). The angle between the right and the left prezygapophysis is estimated to be about 90 degrees.

The thoracic vertebrae do not have hypapophyses. The articular surfaces of the transverse processes are not preserved. The neural arch is about 50 per cent taller than the centrum. The spinal process is very slender and extends about two-thirds of the length of the neural arch (Text-fig. 6D). The angle between the right and the left prezygapophysis is estimated to be about 90 degrees. The first sacral vertebra is preserved in articulation with the left sacral rib (Text-fig. 6E). The centrum is shorter and more elongated craniocaudally than the presacral vertebrae. The cranial articular surface of the centrum is subrounded and smaller than the caudal articular surface, which is nearly concave and laterally broadened. The short and stout rib is rotated dorsally, to a small degree. Its lateral articulation surface is lost.



TEXT-FIG. 6. A–N, elements of postcranial skeleton of *Goniopholis baryglyphaeus* sp. nov.: IPFUB Gui Croc 1, holotype. A, right coracoid in medial view. B, left ischium in lateral view. C, cervical vertebra in cranial view. D, thoracic vertebra in caudal view. E, first sacral vertebra in caudal view. F, caudal vertebra in lateral view. G, right cervical rib in lateral view. H, right thoracic rib in ventral view. I, left thoracic rib in lateral view. J, dorsal osteoderm in dorsal and K, in ventral view; arrows show articular process. L, ventral osteoderm in ventral and M, in dorsal view; arrows show marginal sutures. Abbreviations: For cor, foramen coracoideum; cap, capitulum; tub, tuberculum. All $\times 0.6$.

The caudal vertebrae decrease in size caudally. A single proximal caudal (Text-fig. 6F) is preserved together with its neural arch and was about the same size as the dorsal vertebrae. The neural arch is shortened craniocaudally and is slightly smaller than the dorsal vertebrae. The angle between the articular surfaces of the right and the left prezygapophysis is estimated to be about 100 degrees. A chevron is not preserved. An isolated portion of a caudal vertebra from the more cranial region consists only of the postzygapophyses that are the same size as the complete caudal vertebra and exhibit an angle of 105 degrees between their articular surfaces. Two further caudal vertebrae are only represented by centra. They are much smaller than the other vertebrae and have a centrum that is longitudinally slightly elongated.

Ribs. A right cervical rib is preserved (Text-fig. 6G). The cranial and caudal processes of the rib corpus are broken away. Medially the rib corpus bears a blunt crest, but the lateral surface is smooth. Two dorsal processes, the shorter capitulum and the 4-mm-longer and more slender tuberculum are preserved. The articular surface of the capitulum is rounded and larger than the more ellipsoid articular surface of the tuberculum.

A right and a left thoracic rib are also partly preserved. The corpus is laterally flattened and bears a cranial process. On the right thoracic rib the capitulum and the tuberculum are divided, and the capitulum is 3 mm longer and has a smaller articular surface than the tuberculum (Text-fig. 6H). On the left thoracic rib the processes are not preserved. They seem to have already fused into a single structure; thus a more caudal position is likely for this rib (Text-fig. 6I).

Pectoral girdle. The dorsal portions of the right and left coracoid are preserved (Text-fig. 6A). The middle portion of the robust coracoid is slightly curved. Its dorsal and ventral ends are broadened and the bone narrows in the middle. On the medial surface, the bone is slightly striated. The dorsal articular surface with the scapula is rounded and bears a round process oriented ventrolaterally for articulation with the humerus. The ovate foramen coracoideum is visible in lateral view, medial to the articulation area.

Pelvic girdle. From the elements of the pelvis only the dorsal portion of the left ischium is preserved (Text-fig. 6B). This stout bone broadens dorsally and ventrally, but its ventral portion is lost. On the dorsal end an incomplete articular surface for the ilium is more or less kidney-shaped. The bone widens caudally beyond the articulation surface. Cranially, at the level of the caudal expansion, a small deep depression is developed.

Limbs. Only fragments of the fore- and hindlimbs are preserved. These include a distal articulation surface of the right femur and portions of the tibia and fibula and a phalanx, but the fragmentary character of these elements prevents any detailed description.

DISCUSSION

Comparison with other Goniopholis specimens

There are as many as nine skulls of European *Goniopholis* (Table 1) that permit comparison between the different species: a complete skull of *G. crassidens* ('Mr. Willett's Crocodilian skull'; Hulke 1878), a partial skull of ?*G. crassidens* (Hooley 1907), the type specimen of *G. simus* (Owen 1878; Hulke 1878), all from southern England; four skulls of *G. simus* from north-western Germany (Salisbury *et al.* 1999) and two skulls of ?*G. simus* from Bernissart/Belgium (Dollo 1883). Described mandibular material that can be used for comparison with *G. baryglyphaeus* is known only for *G. simus* of southern England (BMNH R5814, Salisbury *et al.* 1999).

With the exception of *G. simus*, the European *Goniopholis* material listed in Table 1 is mostly of uncertain taxonomic status. Salisbury (1999) considered the skulls assigned to *G. crassidens* Owen, 1841 to belong to the same taxon as *G. simus* Owen, 1878 and *G. crassidens* is, therefore, only based on features of the postcranial skeleton. *G. tenuidens* Owen, 1879 is, owing to its very fragmentary material, a *nomen dubium* (Salisbury 1999). *G. simus* is confirmed as a valid taxon but *G. pugnax* (Koken, 1887) and *G. minor* (Koken, 1887) were considered to be *nomina dubia* by Salisbury *et al.* (1999). The two skeletons from Bernissart/Belgium referred to *G. simus* by Dollo (1883) were considered to belong to a different taxon instead (Salisbury *et al.* 1999). There remain only two valid European *Goniopholis* species, *G. simus* and *G. crassidens*, and the yet undescribed taxon from Bernissart to be compared with the Guimarota *Goniopholis*.

G. baryglyphaeus shows a combination of characters that is consistent with the descriptions of *Goniopholis* as given by Owen (1841, 1849–1884, 1878, 1879), Hulke (1978), Hooley (1907), Wiman (1931), Buffetaut (1982), Clark (1994), Ortega *et al.* (1996) and Salisbury *et al.* (1999). These characters include: a slightly brevirostrine skull with the lateral margins of the rostrum festooned both vertically and laterally; a notch at the suture between premaxilla and maxilla; an undivided external naris positioned near the rostral tip of the snout; nasals excluded from the external naris by the premaxillae and ending slightly caudal to the naris; orbits smaller than the supratemporal fenestrae; a short lacrimo-nasal suture, and a ventral surface of the mandible that is flat and sculptured at the level of the mandibular symphysis.

The maxillar fossa is typical of not only *Goniopholis* but also the entire family Goniopholididae (Buffetaut 1982). It is well developed in *G. baryglyphaeus*, but cannot be considered a character of the genus. The single preserved tooth shows all the characters described by Owen (1841, 1878) for *Goniopholis*, but because it is difficult to identify a crocodilian genus from isolated teeth, it cannot be used for assignment to it. The same problem pertains to isolated osteoderms. Although the name *Goniopholis* refers to the rectangular shape of the dorsal scutes (Owen 1841), this feature is not diagnostic of the genus because it is also found in other goniopholidids (Buffetaut and Hutt 1980). The vertebrae of *G. baryglyphaeus* fit well with the description of vertebrae of *G. crassidens* given by Owen (1841, 1878) and exhibit a similar neurocentral suture and a ventrally curved vertebral body.

The exposed interorbital crest of *G. baryglyphaeus* is also found in *G. simus* (Hooley 1907; Salisbury *et al.* 1999). *Nannosuchus gracilidens*, supposedly a juvenile *Goniopholis* (Joffe 1967; Salisbury 1999), also has this crista. It is absent in *G. crassidens* and the Bernissart *Goniopholis*.

Additionally, *G. baryglyphaeus* shows a combination of characters that hitherto have only been described for *G. simus* (Salisbury *et al.* 1999). These include: caudal expansion of the prefrontal, which excludes the frontal from the medial margin of the orbit, and the loss of contact between the paroccipital process and the lateral surface of the squamosal and the quadrate, which exposes the cranioquadrate canal laterally.

G. baryglyphaeus can be distinguished from individuals of all other European *Goniopholis* mostly on the basis of the caudal part of the mandible. In *G. simus*, the caudal margin of the mandible is much more transversely inclined, giving it a more rounded posterior margin, and the angular is restricted to the ventral half of the caudal part of the mandible. The retroarticular process of *G. simus* is dorsally oriented, and the articular surface of the articular is positioned dorsal to the retroarticular process and faces in a more dorsal direction. For *G. crassidens* and the Bernissart *Goniopholis* no descriptions of the posterior part of the mandible are available.

In *G. simus*, *G. crassidens* and the Bernissart *Goniopholis* the postorbital has, in contrast to the almost square angle of the rostralateral corner in *G. baryglyphaeus*, a rostralateral process (Salisbury *et al.* 1999). A description of the frontoparietal suture is only available for *G. simus* (Salisbury *et al.* 1999), but here the suture forms a caudal process, which is square in outline. The lacrimal in *G. simus* is much broader rostrally and bears a thin rostral process. Additionally, in contrast to *G. baryglyphaeus*, in *G. simus* the eleventh to fourteenth dentary alveoli are enlarged and nearly the same size, and the tenth dentary alveolus is much smaller than the eleventh.

Remarkable in *G. baryglyphaeus* is the regular heavy sculpture that covers the dorsal surface of the skull. Unlike *G. crassidens* (Hulke 1978) and *G. simus* (Salisbury *et al.* 1999), heavy sculpturing of the dorsal rostral surface was also reported by Dollo (1883) for the skull of ?*G. simus* from Bernissart/Belgium, and it is not a unique character of *G. baryglyphaeus* among the European representatives of the genus. As stated by Mook (1921), the density of skull-sculpturing depends to a large degree on ontogenetic status; it is weak in young, heavy in adults, and uniformly rough in old individuals. Considering the size difference between the skulls of *G. simus* (485.5 mm; Salisbury *et al.* 1999) and *G. baryglyphaeus* (239 mm), ontogenetic variability can be excluded. Additionally, the degree of skull-sculpturing within a species can vary geographically (Mook 1921), but *G. simus* from north-western Germany and the Bernissart *Goniopholis* are from a similar latitude. The Bernissart *Goniopholis* can be distinguished from *G. baryglyphaeus* by a prefrontal that does not contact the postorbital, a spine-like rostral process of the postorbital, and the lack of an interorbital crest (Salisbury *et al.* 1999), and must be considered to belong to a different taxon. The sculpturing character is, therefore, combined with other characters to distinguish between *G. baryglyphaeus* and other European *Goniopholis* material.

Palaeobiogeographical implications

During the Late Jurassic major parts of North America and Asia were emergent landmasses, whereas Europe and the eastern region of North America were covered by shallow epicontinental seas (Ziegler 1988). The Northern Hemisphere (Laurasia) was divided from the southern continent (Gondwana) by the Tethys Ocean. As the breaking up of these mega-continent proceeded, North America and Eurasia began to separate from each other and, as a result of the extensional tectonics, lagoonal environments with continental islands, including the Iberian Meseta, were formed on the continental margins (Ziegler 1988). The lagoons were mostly freshwater, but owing to periodic eustatic sea-level changes in the Late Jurassic and earliest Cretaceous (early Berriasian) the environment changed episodically to brackish water (e.g. Purbeck facies). Subsequently, during an extensive regression in the Early Cretaceous the brackish-limnic Wealden succession was deposited (Allen 1975). These environments seem to have been preferred by *Goniopholis*, since its fossil remains have most often been found on the margins of the epicontinental seas (Buffetaut 1982; Text-fig. 7).



TEXT-FIG. 7. Map of European *Goniopholis* localities as explained in Table 1. 1, Isle of Skye; 2a, Hornsleasow Quarry; 2b, Sharp's Hill; 2c, Kirtlington Cement Quarry; 2d, Watton Cliff and Swyre; 2e, Leigh Delamere; 3, Dorset; 4, Guimarota/Leiria; 5, Wimille/Boulogne-sur-mer; 6a, Bückerburg; 6b, Nehden; 7, Bernissart; 8a, Galve; 8b, Uña; 8c, Vadillos-San Román de Cameros; 8d, Forcall.

The only mention of *Goniopholis* in Portugal consists of a preliminary report of the crocodylian fauna of the Guimarota pit (Brinkmann 1989). In fact, Guimarota provides the oldest almost complete skeleton of *Goniopholis* in Europe. Other European Jurassic localities (Table 1) have yielded only fragmentary remains of teeth, osteoderms and bones. The fossil record does not improve until higher in the succession, in 'Purbeckian' and 'Wealden' facies (Berriasian).

Other Jurassic *Goniopholis* localities are exclusively in northerly locations (Table 1; Text-fig. 7), but the genus is very widespread in Lower Cretaceous deposits in Western Europe (Text-fig. 7). The new find of *Goniopholis* in Portugal shows that it was distributed in a larger area than previously assumed. In south-western Europe *Goniopholis* remains have been described from the lower Barremian (Lower Cretaceous) of Galve, Teruel Province, Spain (Buscalioni and Sanz 1987),

the upper Barremian of Uña, Cuenca Province, Spain (Brinkmann 1989), the Aptian (Lower Cretaceous) of Forcall, Castellón province (Buscalioni 1986) and the Lower Cretaceous of Vadillos-San Román de Cameros, La Rioja (Ortega *et al.* 1996). The lack of fossil material in Portugal and Spain between the Tithonian and the Barremian could be the product of a stratigraphical gap in the fossil record or imprecise dating of the Iberian stratigraphical record of crocodiles (Buscalioni 1986), mainly quoted as 'Wealden'. *Goniopholis baryglyphaeus* is about 9 myr older than other *Goniopholis* material.

Goniopholis baryglyphaeus and the crocodylian assemblage of Guimarota

The brackish-limnic conditions of the Guimarota locality correspond to those of other European deposits that have yielded *Goniopholis* (Table 1). Normally, the high degree of humic acids in coaly sediments dissolves organic material. However, fossils are preserved in calcareous deposits within coaly successions at Guimarota (Helmdach 1971). In fact, with the exception of Uña, Guimarota is the only coal deposit that contains *Goniopholis*.

From the beginning of palaeontological activities in Guimarota, remains of *Goniopholis* have been found: mainly single isolated teeth, osteoderms and rare bone fragments. The discovery of goniopholidid crocodile material was, therefore, not unexpected. But considering that most fossil material from Guimarota consists of microvertebrate remains, and is often fragmentary, the find of a nearly complete skeleton was surprising (Gloy 2000).

Crocodylian remains are abundant in the vertebrate fauna of the Guimarota locality. Until now, three crocodylian genera have been reported: *Machimosaurus hugii* (Krebs 1967), *Lisboasaurus estesii* (Buscalioni *et al.* 1996) and *Goniopholis baryglyphaeus*. Many tiny crocodylian remains from the locality were determined as *Theriosuchus*- and *Bernissartia*-like forms in a preliminary description (Brinkmann 1989), but this interpretation awaits further investigation. The new species of *Goniopholis* shows that the crocodylian fauna of Guimarota was relatively diverse. Other bone fragments that are too fragmentary to determine at species level correspond in size to *G. baryglyphaeus*. The relative frequency of *Goniopholis* in the Guimarota region, therefore, cannot be calculated.

The Guimarota ecosystem was probably the natural environment of *G. baryglyphaeus*. Like recent crocodylids and gharials, the species was able to tolerate salt water as well as freshwater influences. Correlations between skull length and total body size (Wermuth 1964) make it possible to estimate from the skull length of *G. baryglyphaeus* of 281 mm a total length for the specimen of about 2.1 m. The existence of a different species of *Goniopholis* in the locality shows that the Guimarota ecosystem had not only a distinctive mammal fauna (Martin 2000), but also a distinctive crocodylian fauna with unique species. In this ecosystem, *G. baryglyphaeus* was a top predator, feeding on the different vertebrates and invertebrates present.

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