

# ***Gobiosuchus kielanae* (Protosuchia) from the Late Cretaceous of Mongolia: anatomy and relationships**

HALSZKA OSMÓLSKA, STEPHANE HUA and ERIC BUFFETAUT



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The original description (Osmólska 1972) of the skull, postcranial skeleton, and armour of a protosuchian, *Gobiosuchus kielanae* (Gobiosuchidae Osmólska), is supplemented and revised on the basis of additional specimens from the type locality and horizon (Bayn Dzak, ?early Campanian Djadokhta Formation). It is suggested that *Gobiosuchus kielanae* was an entirely terrestrial and probably insectivorous animal. Assignment of *Gobiosuchus* to Protosuchia is supported by the following characters: basisphenoid larger than basioccipital; extensive ventral contact between quadrate and basisphenoid; pneumatic pterygoid; quadrate condyles only slightly protruding beyond posterior margin of braincase, and lack of retroarticular process. *Gobiosuchus* differs from other protosuchians in the following features: snout wider than high; palatal processes of premaxillae contacting along their entire length; closed supratemporal and mandibular fenestrae; basioccipital extending dorsally onto occiput and separating on each side ventromedial part of quadrate from contact with otoccipital; posterolateral process of squamosal extended far behind mandibular articulation; presence of cranioquadrate passage; descending process of prefrontal contacting palate; armour of sutured osteoderms encasing at least some of long limb bones; presence of peculiar accessory osteoderms in regions of articulation of limbs with girdles, and more than two longitudinal rows of dorsal osteoderms.

**Key words:** Crocodyliformes, Protosuchia, Gobiosuchidae, *Gobiosuchus*, osteology, habits, Late Cretaceous, Mongolia.

Halszka Osmólska [osm@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

Eric Buffetaut [buffetaut@ccr.jussieu.fr] and Stephane Hua [hua@ccr.jussieu.fr], Laboratoire de Paléontologie des Vertébrés et de Paléontologie Humaine, Université Pierre et Marie Curie, Tour 15, 4, place Jussieu, 75252 Paris Cedex 05, France.

## **Introduction**

*Gobiosuchus kielanae* Osmólska, 1972 was a small (about 60 cm long), long-necked and long-limbed, fully armoured crocodile (Fig. 1), which lived approximately 80 million years ago on the territory of today's Gobi Desert. It represents a member of the

Protosuchia Brown, 1934, the primitive group of the Crocodylia Gmelin, 1788, lately renamed as Crocodyliformes by Clark in Benton & Clark (1988), and including 'protosuchians', 'mesosuchians' and 'eusuchians'. The Protosuchia appeared in the Late Triassic and became extinct in the Late Cretaceous, *Gobiosuchus* being, as far as known, their geologically youngest member. As presently understood (Wu *et al.* 1994; Wu *et al.* 1997), protosuchians form the sister-group to all other crocodyliforms (grouped as Mesoeucrocodylia by Whetstone & Whybrow 1983). Protosuchia are characterized by several unique characters, among others (Wu *et al.* 1997): the structure of the ventral surface of the braincase where the basisphenoid occupies much more space than the basioccipital and the quadrates have long contacts with the basisphenoid, the distal, condyle-bearing ends of quadrates protruding only slightly beyond the posterior margin of the braincase, and the mandible lacking a retroarticular process.

When *G. kielanae* was first found in the sandstones of the ?early Campanian Djadokhta Formation (Gradziński *et al.* 1977; Jerzykiewicz & Russell 1991) at Bayn Dzak locality (Pre-Altai Gobi, Mongolia) by the Polish-Mongolian Palaeontological Expeditions (Kielan-Jaworowska & Dovchin 1969; Kielan-Jaworowska & Barsbold 1972), it appeared isolated in time, other primitive crocodyliforms then known, mostly with a protosuchian-grade palate, were few and either of the Late Triassic (one species) or Jurassic (four species) age (Table 1). Since then, the situation has changed and eleven new protosuchian species have been reported from the Jurassic and Cretaceous. The majority of the protosuchians – ten species – are now known from Asia (mainly from China), four are reported from North America, two from southern Africa and one, the oldest, from South America (Table 1).

*Gobiosuchus kielanae* was assigned by Osmólska (1972) to the family Gobiosuchidae, provisionally within the Protosuchia, among others because of the anterior position of the internal nares, located between the maxillae and palatines. Efimov (1983) considered the Gobiosuchidae as a member of the Notosuchia and erected two monotypic subfamilies, the Gobiosuchinae and the Artzosuchinae, within this family. He changed his opinion later (Efimov 1988a) re-assigning the Gobiosuchidae to the Protosuchia.

The protosuchian nature of *Gobiosuchus* was supported among others by Hecht & Tarsitano (1983), while Clark (in Benton & Clark 1988) considered that Protosuchia did not form a clade, and that *Gobiosuchus* occupied a more derived position within the Crocodyliformes Clark (in Benton & Clark 1988), constituting a sister taxon to the Mesoeucrocodylia.

According to the more recent phylogenetic analyses by Wu *et al.* (1994), Wu & Sues (1995), and Wu *et al.* (1997), the Protosuchia are monophyletic and *Gobiosuchus* is a member of this clade, as was earlier suggested by Osmólska (1972).

A second species of *Gobiosuchus*, *G. parvus* was described by Efimov (1983) from the deposits of the 'Barungoyotskaya Svita' (a possible equivalent of the Barun Goyot Formation: Gradziński *et al.* 1977) at Udan Sair (= Uden Khovol), based on a single specimen (housed in the Palaeontological Museum, Russian Academy of Sciences, Moscow). In our opinion, the validity of *G. parvus* is at the moment uncertain, because of the poor illustrations and the inadequate diagnosis of this species (see p. 283). *Gobiosuchus* sp. was mentioned by Efimov (1988a) from the Djadokhta Formation at Tugrikin Shire (= Toogreeg of Gradziński *et al.* 1977). This specimen, which is housed

Table 1. Distribution of protosuchian species (Fm – Formation, Sv – Svita).

| Species   | Age                              | Occurrence                            |
|---|----------------------------------|---------------------------------------|
| <i>Hemiprotosuchus leali</i><br>Bonaparte, 1971               | Los Colorados Fm, Late Triassic  | Ischigualasto, Argentina              |
| <i>Protosuchus haughtoni</i><br>(Bubsey & Gow, 1984)          | Elliot Fm, Early Jurassic        | Orange Free State,<br>southern Africa |
| <i>Protosuchus micmac</i><br>Sues <i>et al.</i> , 1996        | McCoy Brook Fm, Early Jurassic   | Nova Scotia, Canada                   |
| <i>Orthosuchus stormbergi</i><br>Nash, 1975                   | Elliot Fm, Early Jurassic        | Lesotho, southern Africa              |
| <i>Eopneumatosuchus colberti</i><br>Crompton & Smith, 1980    | Kayenta Fm, Early Jurassic       | Arizona, United States                |
| <i>Platyognathus hsui</i><br>Young, 1944                      | Lower Lufeng Fm, Early Jurassic  | Yunnan, China                         |
| <i>Dianosuchus changchiwaensis</i><br>Young, 1982             | Lower Lufeng Fm, Early Jurassic  | Yunnan, China                         |
| <i>Protosuchus richardsoni</i><br>(Brown, 1933)               | Moenave Fm, ?Early Jurassic      | Arizona, United States                |
| <i>Sichuanosuchus huidongensis</i><br>Peng, 1995              | Shangshaximiao Fm, Late Jurassic | Sichuan, China                        |
| <i>Shantungosuchus chuhsienensis</i><br>Young, 1961           | Mengyin Fm, ?Late Jurassic       | Shandong, China                       |
| <i>Shantungosuchus brachycephalus</i><br>Young, 1982          | Early Cretaceous                 | ?Ordos, China                         |
| <i>Shantungosuchus hangjiensis</i><br>Wu <i>et al.</i> , 1994 | Luohandong Fm, Early Cretaceous  | Ordos, China                          |
| <i>Edentosuchus tianshanensis</i><br>Young, 1973              | Tugulu Group, Early Cretaceous   | Xinjiang, China                       |
| <i>Sichuanosuchus shuhanensis</i><br>Wu <i>et al.</i> , 1997  | ?Early Cretaceous                | Sichuan, China                        |
| <i>Gobiosuchus kielanae</i><br>Osmólska, 1972                 | Djadokhta Fm, Late Cretaceous    | Pre-Altai Gobi, Mongolia              |
| <i>Gobiosuchus(?) parvus</i><br>Efimov, 1983                  | Barun Goyot Sv, Late Cretaceous  | Pre-Altai Gobi, Mongolia              |
| ? <i>Hoplosuchus kayi</i><br>Gilmore, 1926                    | Morrison Fm, Late Jurassic       | Utah, United States                   |

in the regional museum at Dalan Dzadgad – the administrative centre of the Mongolian southern Gobi province (Omnogov) – consists of the almost complete postcranium entirely encased in the osteodermal armour. It has been briefly studied by H. Osmólska, who concluded that the ornamentation of osteoderms very closely resembles that in *G. kielanae*. Some osteoderms from the Turonian–Coniacian deposits at Dzhar Khuduk (Kyzylkum Desert, Uzbekistan), were also quoted by Efimov (1988b) as probably assignable to *Gobiosuchus*, but neither a description nor illustration were given.

The description below is based upon five specimens of *G. kielanae*, including fragmentary skulls, some postcranial bones, and armour. This additional material allowed us to correct some mistakes made in the previous description (Osmólska 1972), which was based mainly on the holotype specimen.

## Material

The collection described is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw, for which the abbreviation ZPAL is used. All specimens come from the fine-grained sandstones of the Djadokhta Formation (Campanian) at sites called the 'Ruins' and 'Volcano' in Bayn Dzak.

ZPAL MgR-II/67 – holotype: almost complete skull, somewhat flattened dorsoventrally, with damaged cranial roof; mandible lacking; disarticulated postcranial skeleton including distal dorsal vertebrae, left humerus, proximal portions of the left ulna and radius, damaged left and right femora and tibiae, left fibula, fragmentary left carpus and metacarpus, fragmentary dorsal ribs, disarticulated armour (Figs 4, 5, 11A, 13C–F); site: Volcano.

ZPAL MgR-II/68 – posterior half of the skull, neck, thorax and proximal two thirds of the tail encased in armour, fragments of the proximal elements of the fore- and hind limbs (Figs 2, 3); site: Volcano.

ZPAL MgR-II/69 – skull with articulated mandible, lacking end of the snout, occiput, brain case and palate; three most proximal pairs of the dorsal cervical osteoderms articulated with the skull (Fig. 6); site: Ruins.

ZPAL MgR-II/70 – snout with articulated anterior part of mandible (Fig. 7); site: Ruins.

ZPAL MgR-II/71 – dorsal part of armour from ?posterior part of the neck and most of the thorax (Figs 11B, 13A, B); site: Ruins.

## Taxonomy and description

Crocodyliformes Clark in Benton & Clark 1988

Protosuchia Brown, 1934

Gobiosuchidae Osmólska, 1972

*Gobiosuchus* Osmólska, 1972

Type species: *Gobiosuchus kielanae* Osmólska, 1972.

**Generic diagnosis.** — *Gobiosuchus* differs from all crocodyliforms by its long, slender neck; it may be distinguished from other protosuchian genera by: closed supratemporal fenestrae; posterolateral process of squamosal very long, extending posteriorly far beyond quadrate condyle; incisive foramen absent and palatal wings of premaxilla in contact along their entire length; basisphenoid with posterolateral process on each side, which invades lateral portion of occiput, separating otoccipital from quadrate; very small, sharp, nearly conical maxillary teeth, not constricted at the base; external mandibular fenestra closed; mandibular symphysis fused without trace of suture in adults (dentaries are also fused in *Dianosuchus* Young, 1982, but this genus differs from *Gobiosuchus* by its large supratemporal fenestra); trunk covered by at least four longitudinal rows of dorsal osteoderms and up to six rows of ventral osteoderms; neck and tail covered by four dorsal and four ventral longitudinal rows of osteoderms; straplike, smooth accessory articular osteoderms present in regions between limbs and girdles; suturally joined osteoderms surround limbs.

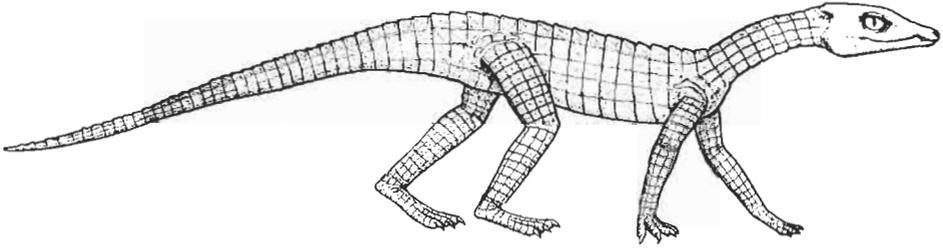


Fig. 1. Reconstruction of *Gobiosuchus kielanae* Osmólska, 1972 from the Djadokhta Formation of Bayn Dzak. About 1/5 natural size.

**Remarks.** — The above generic diagnosis is based mainly on the type species, because, except for the closure of the supraorbital and mandibular fenestrae and the number of maxillary teeth (18), conditions of other diagnostic features are unknown in *G. parvus*.

### *Gobiosuchus kielanae* Osmólska, 1972

Figs 1–13.

**Specific diagnosis.** — Species of *Gobiosuchus* with 16 maxillary teeth: estimated forelimb (humerus + radius) length and hind limb (femur + tibia) length respectively 86% and 117% of trunk length.

### Skull

**Skull as a whole.** The skull is brevirostrine (the rostrum is approximately 42% of the total skull length) and moderately deep, the rostrum being somewhat wider than deep (forenostral shape sensu Busbey, 1995). A very shallow notch is present on the premaxilla-maxilla contact. The skull is widened at the level of the orbits, but the snout is not clearly set off from the rest of the skull. The postorbital portion of the skull is parallel-sided. The cranial table is very wide. In the dorsal view hiding the lateral walls of the skull. The distinct posterior margin is deeply embayed due to an unusual posterolateral elongation of the squamosals, which extend far beyond the mandibular articulation. The supratemporal fenestrae are entirely closed by surrounding bones, but there are very shallow, slightly oblique depressions on the skull roof, probably marking their former position. The bottom of each depression is formed mostly of the parietal and squamosal, but with a narrow participation of the frontal anteriorly. The infratemporal fenestrae are strongly reduced due to the large quadratojugal. The paroccipital processes are weakly delimited, laterally narrow and sutured to the squamosals. The orbits are large, subrectangular, anteroposteriorly elongated and face anterolaterally. The external nares face laterodorsally. The postorbital bars are thin anterolaterally-posteromedially extending plates. The antorbital fossae are small, deep and subtriangular. The pterygoid flanges are relatively weakly deflected ventrally and placed at the posterior third of the ventral length of the skull. The quadrates are inclined and their dorsal surface is extensively fenestrated. The ventral surface of the braincase is very long, formed mostly of the basisphenoid.

The premaxilla is relatively long, somewhat less than half the length of the maxilla. It is almost subrectangular and gently convex laterodorsally. The premaxilla surrounds the nares, except posterodorsally and it forms the ventral half of the internarial bar. Along the anterolateral border of the nostril the premaxilla is flattened, forming a horizontal platform. The suture with the nasal is parallel to the longitudinal axis of the skull. The suture with the maxilla is almost perpendicular and ends in the middle of a shallow embayment on the ventral margin of the jaw.

In ventral view, the premaxilla is sutured to its fellow along its entire medial border. The premaxilla-maxilla suture is posterolaterally directed, extending laterally to the large pit adjacent to the shallow embayment in the ventral margin of the jaw. This pit receives the enlarged fourth dentary

Table 2. Measurements (mm) of skull and mandible in *G. kielanae*

|  | ZPAL MgR II/ |     |           |     |
|--|--------------|-----|-----------|-----|
|  | 67           | 68  | 69        | 70  |
| Length: (snout tip–occipital condyle)                        | 64           | –   | 63+ (68e) | –   |
| (snout tip–end of posterior process of squamosal)            | 73           | –   | 80e       | –   |
| Length of orbit  | 15e          | –   | 17        | –   |
| Height of orbit  | 11e          | 10  | 11        | –   |
| Postorbital length   | 31           | 28  | 23+       | –   |
| Preorbital length  | 27           | –   | 25+       | 25  |
| Medial parietal length                                       | –            | 15  | 17        | –   |
| Length of posterolateral process of squamosal                | 10           | 10  | –         | –   |
| Length of premaxilla   | 12           | –   | –         | 11  |
| Length of antorbital fossa                                   | 8            | –   | 8         | –   |
| Height of antorbital fossa                                   | 4            | –   | 6         | 3.5 |
| Length of basisphenoid                                       | 10           | –   | –         | –   |
| Posterior width of basicranium (between mandibular condyles) | 19           | 18  | –         | –   |
| Max. width across jugals                                     | 33e          | 31e | 32        | –   |
| Width of cranial table                                       | 33           | 31  | 32        | –   |
| Width of snout (between pmx/mx contacts)                     | 15           | –   | 15        | 13  |
| Height of snout (at pmx/mx contact)                          | 5            | –   | 7         | 4   |
| Length of mandible   | –            | –   | 64+ (73e) | –   |
| Posterior depth of mandible                                  | –            | 9   | 11        | –   |
| Depth of dentary   | –            | –   | 5         | 3.5 |
| Length of mandibular symphysis                               | –            | –   | 10e       | 7.5 |
| Length (tr.) of medial process of articular                  | –            | 6   | –         | –   |

tooth and is marked on the dorsal side of the snout by a low, rounded elevation. There are three very small, conical and sharp premaxillary teeth, separated by two smaller pits, so that the premaxillary teeth are more widely spaced than the maxillary teeth. Externally, the premaxilla is covered by fine, anterodorsally–posteromedially directed ridges, even around the naris.

The maxilla forms somewhat more than half of the length of the rostrum. It is slightly inclined dorsoventrally, weakly and uniformly convex. The antorbital fossa is distinctly triangular and occupies about the posterior half of the lateral wing of the maxilla. The floor of the fossa is horizontal in specimens ZPAL MgR-II/67 and 69 but rather inclined in ZPAL MgR-II/70. The margin delimiting the anterodorsal border of the fossa is sharp. The internal antorbital fenestra is placed almost vertically facing the narial passageway. The alveolar portion is very shallow and the alveolar margin is straight, except anteriorly, where it ascends slightly close to the contact with the premaxilla, forming the posterior portion of the marginal embayment of the jaw.

The posterior third of the maxilla is overlapped laterally by the jugal. The nasomaxillary suture is straight, parallel to the longitudinal axis of the skull. The contact with the prefrontal is extremely limited.

The palatal process of the maxilla is not sculptured. It is sutured to its fellow in the midline and, opposite the third maxillary tooth, its margin forms a broadly rounded anterior boundary of the exchoanal fenestra. Posterolateral to the choana, the maxilla gradually narrows backward, its



Fig. 2. *Gobiosuchus kielanae* Osmólska, 1972 from the Djadokhta Formation of Bayn Dzak. A. Stereophotograph of largely complete specimen (ZPAL Mg R-II/68) encased in armour, dorsal view. B. Stereophotograph of a fragment of the same specimen, dorsal view; visible proximal part of left humerus. Scale bars – 1 cm.

posterior tip forming a short medial contact with the ectopterygoid. The maxilla forms the entire lateral boundary of the large suborbital fenestra, the posterior boundary being formed in about equal shares by the ectopterygoid and pterygoid and the medial one, by the palatine. There are 16 homodont, closely spaced teeth, which are marginally placed. The tooth crowns are small, conical, and pointed. Teeth are not constricted at bases and do not bear any serrations. The external surface of the maxilla is sculptured, except for the ventral boundary of the antorbital fossa.

The nasals are joined by a very faintly marked suture, which e.g., in specimen ZPAL MgD-RII/70, is invisible. In ZPAL MgR-II/67, there is a distinct groove running along most of the internasal contact. The nasals are only very slightly vaulted transversely between the antorbital fenestrae and become flat anteriorly. They form about a half of the short internarial bar, overlapping the nasal processes of the premaxillae. Posteriorly, the nasal overlaps the prefrontal for a short distance. The nasomaxillary suture extends from the dorsal apex of the triangular antorbital fossa to the contact between the premaxilla and maxilla and is continued anteriorly by the nasopremaxillary suture. The surface, especially close to the bone margins, is covered by a fine ornamentation consisting of dense, thin grooves and ridges.

The frontals are firmly joined, and the interfrontal suture, in form of a fine line, is visible in specimens ZPAL MgR-II/67 and 68. The external surface is covered by low, thin ridges. In ZPAL MgR-II/69, there is a thin, relatively sharp crest extending along the interfrontal junction, continuous with the crest on parietals (Fig. 6B). The frontal is widest at its contact with the parietal and it gradually narrows forwards. At the level of the anterior orbital margin, the frontal meets the nasal in an interdigitating suture. Laterally, the frontal contacts the postorbital for a very short distance. More posteriorly, it has a long, firm contact with two palpebrals; thus, the frontal does not participate in formation of the orbital rim (Figs 3E, 8B). In the region of the nasofrontal contact, the frontal contacts the prefrontal. In ZPAL MgR-II/67, the dorsal margins of both orbits are damaged; this damage occurred along the lateral margins of the frontals, and the palpebrals have been here broken off.

Each frontal sends a descending process ventromedially, which bounds the olfactory tract laterally (Figs 3B, 9C). It seems that the opposing processes were in contact along the mid-line ventrally, enclosing the tract. There is also a possibility that there was an additional ossification in the mid-line, which was fused with these processes and enclosed the tract ventrally. Posteroventrally, the frontal contacts the laterosphenoid in a serrated suture almost perpendicular to the long axis of the skull. In ZPAL MgR II/68, on the ventral surface of the skull roof, the posterior section of the suture between the frontal and palpebral is visible on both sides. This suture is almost straight and extends posterolaterally-antromedially.

On the ventral surface of the skull roof, at the junction of the frontal, laterosphenoid, postorbital, and most probably also the quadratojugal and quadrate, a relatively deep, small depression is present (Figs 3B, 9C). It may represent a remnant of the supratemporal fossa.

The parietals are fused (contrary to Osmólska 1972: pl. 4A) forming a trapezium, widening towards the interdigitating suture with frontals. The line of the parietal fusion is marked by a thin, low crest that ends some distance in front of the posterior margin of the skull table. The parietals do not participate in the formation of the occipital plate. The external surface is covered by ridges; some of them are thicker than others, especially close to the posterior margin of the skull.

The postparietal, if present, cannot be distinguished from the parietals.

The lacrimal is small, flattened, and obliquely oriented, its posterior margin being more laterally positioned than the anterior. It bounds the antorbital fossa posteriorly. Within the dorsal corner of the antorbital fossa, there is a short lacrimal-maxilla contact. The suture with the prefrontal is not clearly defined, but it seems that there is no dorsal component of the lacrimal, and only the vertical, preorbital portion is developed (Fig. 8C). The ventral extremity of the lacrimal is expanded anteromedially-posterolaterally. Its most lateral portion contacts the anterior process of the jugal and the posterior end of the maxilla, while more medially it abuts the dorsal surface of the palatine, just in front of the antorbital fenestra. The external surface of the jugal is smooth.

The prefrontal is relatively long and contacts the frontal medially along an arched suture. It comes close to the dorsal corner of the antorbital fossa, and its pointed anterior tip seems to be wedged between the nasal and maxilla. Posteriorly, the prefrontal contacts the palpebral, and the suture has a roughly transverse course. At its posteromedial corner, the prefrontal sends a transversely flattened process ventrally, which abuts on the dorsally extended margins of the pterygoids or palatines (Fig. 8C), somewhat below the mid-height of the skull. A sharp, longitudinal ridge runs along the lateral margin of the prefrontal and overhangs the small vertical component of this bone

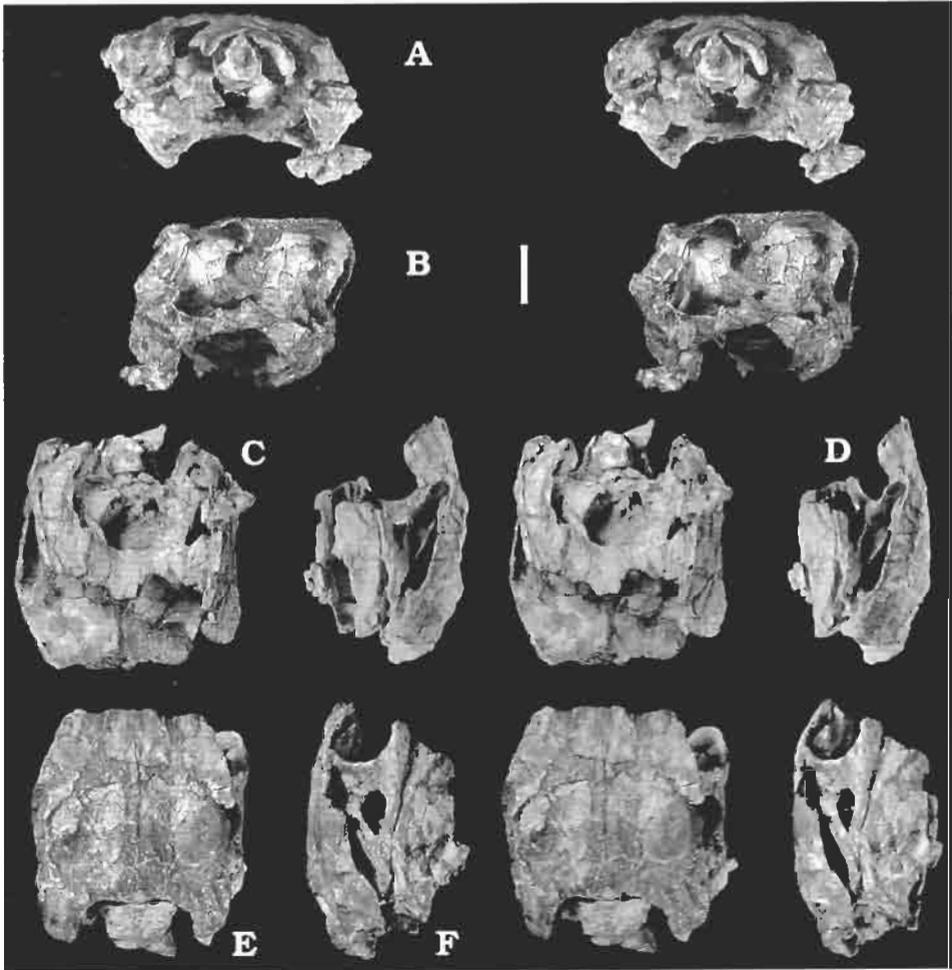


Fig. 3. *Gobiosuchus kielanae* Osmólska, 1972 from the Djadokhta Formation of Bayn Dzak. A–F. Stereophotographs of posterior portion of skull (ZPAL MgR-II/68), posterior, anterior, ventral, left lateral, dorsal, right lateral, views. Scale bar – 1 cm.

and the lacrimal. Below this ridge, there is a conspicuous tubercle on the prefrontal, which probably marks the contact with the lacrimal below.

The palpebrals are broken off in ZPAL MgR-II/67, whereas in ZPAL MgR-II/69 their limits are indistinct. However, in ZPAL MgR-II/68, on the ventral surface of the skull roof, a suture is visible between two wide palpebrals and the frontal. The anterior of the two palpebrals is also sutured to the prefrontal, while the posterior contacts the postorbital. In contrast to other protosuchians, there is no fenestra separating the palpebrals from the frontal. Thus, the contact between the palpebrals and frontal was firm, and these bones were virtually incorporated in the skull roof.

The postorbital has a wide and short dorsal, horizontal portion, and its contact with the frontal is short. As a result of the anteromedial expansion of the squamosal, the postorbital has only a very small contact with the parietal (Fig. 8B). Anteriorly, the dorsal portion of the postorbital contacts the palpebral, and its participation in the formation on the dorsal orbital rim is limited to the very posterior corner of the orbit. The descending process of the postorbital is placed medially to the

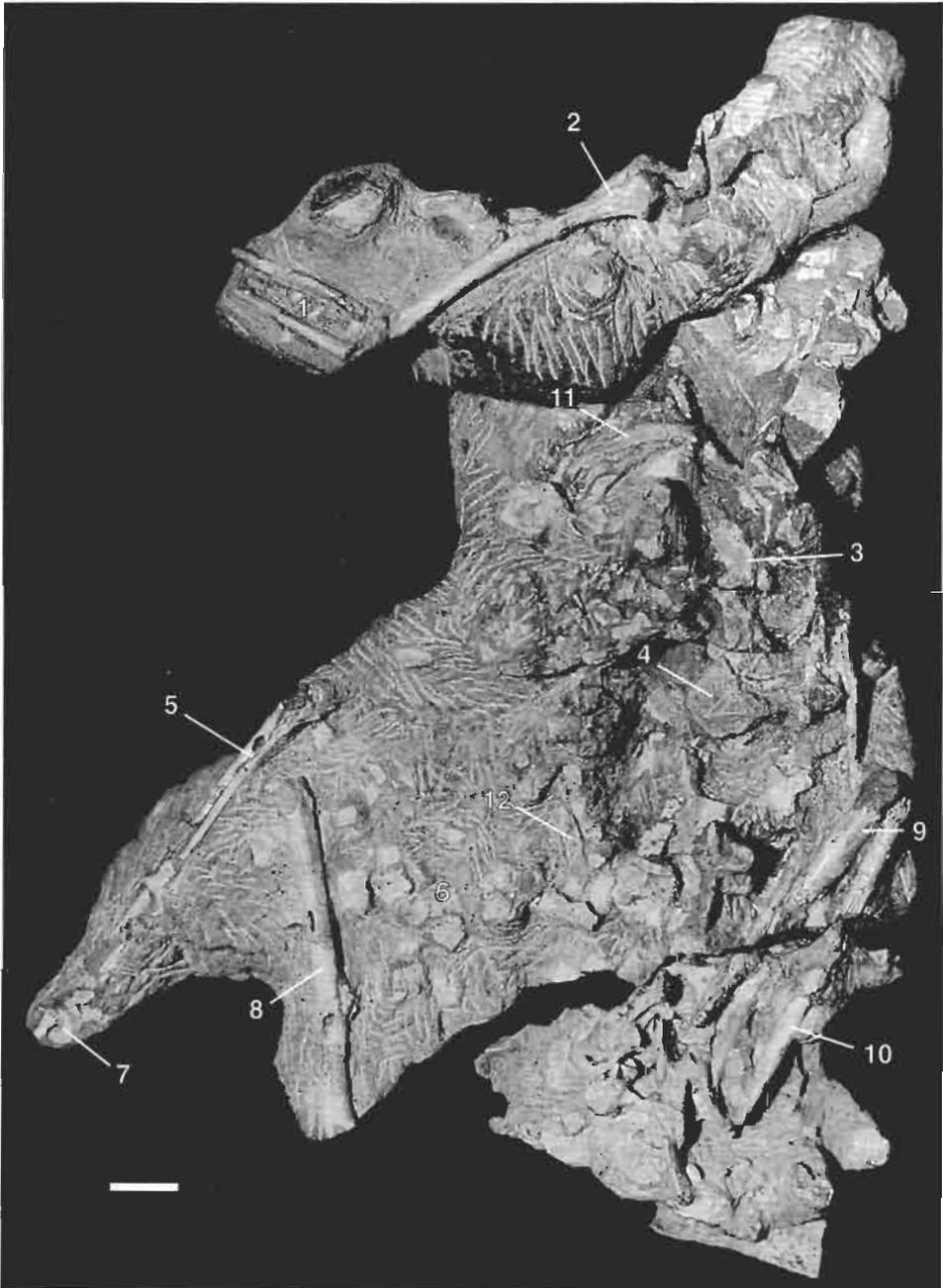
ascending process of the jugal. In lateral view (Figs 3F, 5C, 6C, 8C), the descending process seems to form about a dorsal half of the postorbital bar, but medially it extends along most of the length of the bar. The postorbital bar is flat, thin, and greatly expanded in an oblique plane, so that its anterior edge is superficial, while the posterior one is placed more medially. The long postorbital-quadratojugal contact continues posteroventrally to the greatly reduced infratemporal fenestra. There is almost no participation of the postorbital in the fenestra. There is no contact with the quadrate, and only a very short one with the laterosphenoid, due to the extensive anterodorsal development of the quadratojugal. The surface of the horizontal portion of the postorbital is roughly sculptured, but the jugal process seems smooth except for its anterolateral margin.

The squamosal is very wide. Its lateral margin is thick, whereas the bone is thin medially. Posterolaterally, the squamosal protrudes into a long process, which extends far beyond the mandibular condyle of the quadrate (Figs 3E, 5A, B, 8). In the skull of the specimen ZPAL MgR-II/68, which is preserved with the mandible adducted, the posterior extremity of this process is placed approximately at the level of the posterior limit of the mandible (Fig. 3D, F). This process is broken off in ZPAL MgR-II/69 (Fig. 6). The posterior process constitutes about one third of the total length of the squamosal. The lateral portion of the squamosal bends ventrally, partly concealing the otic region from the outside. This bend is especially strong along the posterior process. As a result of the aforementioned bend, the lower surface of the posterior process faces medioventrally. This surface is longitudinally divided by a thin septum into two parts, which are set at an angle to each other (Figs 5A, 9B). The medial part faces more medially than ventrally; it might locate the origin of the *m. depressor mandibulae* [following the muscle nomenclature of Iordansky (1973)]. The lateral half is concave but it faces more ventrally than medially. Anteriorly, close to the occiput, the septum ventrally produces a thin lamina, which bounds the otic region posteromedially, and abuts either the posterolateral process of the basisphenoid, or the contact between this process and the quadrate, close to the quadrate condyle (Figs 5E, 9A). This lamina corresponds to the occipital part of the squamosal in other protosuchians, although, as a result of the extreme elongation of the posterolateral process of the squamosal, it faces more posteromedially. The lamina bounds an opening posterolaterally, the dorsomedial and ventromedial margins of which are formed by the otoccipital (Figs 3A, 5D, E, 9A, B). On the occipital plate, this opening is ventral to the extremity of the paroccipital process. It does not open into the braincase cavity, but rather within the external otic recess, outside the braincase wall. It may have traversed the middle ear, but the middle ear region is not sufficiently well displayed in any of the ZPAL specimens. This opening occupies an approximately similar position as the cranioquadrate passage in the 'mesosuchians', which provides passage for one of the branches of the VII cranial nerve, the orbitotemporal artery, and the lateral cephalic vein (Iordansky 1973). It is probable that this opening played the same role in *Gobiosuchus*, although it may not be homologous with the cranioquadrate passage of the 'mesosuchians'.

The anterolateral contact of the squamosal with the postorbital is oblique and rather short. Due to the closing of the supratemporal fenestra, the parietosquamosal contact is very long (Figs 3E, 6B, 8B). The suture is almost straight and oblique, directed posteromedially-anterolaterally, and it ends anteriorly at the frontopostorbital suture. As far as preserved, the external surface of the squamosal is sculptured by thick ridges and grooves. Because of this rough ornamentation it is difficult to state whether there was a groove for the ear flap.

The jugal bounds the orbit and the infratemporal fenestra ventrally and posteroventrally. Anteriorly, it reaches the posteroventral corner of the antorbital fossa (Figs 5C, 6C, D, 8C). Below the orbit, the jugal is moderately deep and ventromedially inclined, so that the internal surface of the jugal faces dorsomedially (Figs 5C, 6C, D, 8B). The posterior process of the jugal is long, shallower than the anterior one and is externally marked by a sharp, longitudinal keel (Figs 3F, 5C, 8C). It becomes distinctly shallow posteriorly where its end underlies the quadratojugal ventrally, and approaches the mandibular articulation (contrary to Osmólska 1972: pl. 6c). The ascending process of the jugal is wide

Fig. 4. *Gobiosuchus kielanae* Osmólska, 1972 from the Djadokhta Formation of Bayn Dzak. Block of sandstone with disarticulated postcranium and armour (ZPAL MgR-II/67). 1 – left radius and ulna, 2 – left



humerus, posterolateral view, 3 – thoracic vertebra in dorsal view, 4 – thoracic osteoderm, outer side, 5 – left tibia and fibula, lateral view, 6 – appendicular osteoderms, inner sides, 7 – fragments of tarsals and metatarsals, 8 – left femur, posterior view, 9 – right femur, posterolateral view, 10 – right tibia, 11 – ‘articular’ osteoderm supposedly from pectoral region. 12 – ‘articular’ osteoderm supposedly from pelvic region. Scale bar – 1 cm.



Fig. 5. *Gobiosuchus kielanae* Osmólska, 1972 from the Djadokhta Formation of Bayn Dzak. (ZPAL MgR-II/67). A, C, D. Stereophotographs of skull, ventral, lateral and posterior views. B. Same skull, dorsal view. E. Posterior part of the same skull, posteroventral view. F. Outer side of a thoracic osteoderm. G. Left humerus, posterior view. Scale bars – 1 cm.



Fig. 6. *Gobiosuchus kielanae* Osmólska, 1972 from the Djadokhta Formation of Bayn Dzak. A–D. Stereophotographs of skull with articulated mandible (ZPAL MgR-II/69), ventral, dorsal, left and right lateral views; in B, paired nuchal osteoderms and two paired anterior cervical osteoderms visible. Scale bar – 1 cm.

and flattened in an oblique plane; it seems to form about half of the postorbital bar. The external surface of the jugal is covered by relatively rough, but poorly preserved ornamentation.

The quadratojugal is a wide sheet of bone, which is strongly inclined posteroventrally-anterodorsally. It forms the posterodorsal margin of the reduced infratemporal fenestra. The suture with the descending process of the postorbital is long. Medially and slightly dorsally, the quadratojugal contacts the quadrate for a very long distance, reaching the mandibular condyle, and its posterior end is thickened in this region and overlies the quadrate laterodorsally (Figs 3F, 5A, C, E, 6D, 9B). Although the quadratojugal extends to the quadrate condyle, it apparently does not participate in the craniomandibular articulation. Dorsally, along the contact with the quadrate, the dorsomedial edge of the quadratojugal bears a sharp ridge. Most of the quadratojugal surface is smooth.

The quadrate is a wide, strongly inclined bone, which is well exposed in the ventral and lateral views. Its posterior part has long contacts with the basisphenoid medially and with the quadratojugal laterally. There is no otic notch. A low crest extends along the basisphenoid-quadrate contact (Figs 5A, 8A). The contact with the basisphenoid continues onto the occipital plate (Figs 5E, 8A, 9A, B), separating the quadrate from the otoccipital (see below). The quadrate-laterosphenoid suture is well visible (Figs 3B, 9C) and extends some distance above the trigeminal foramen to a small

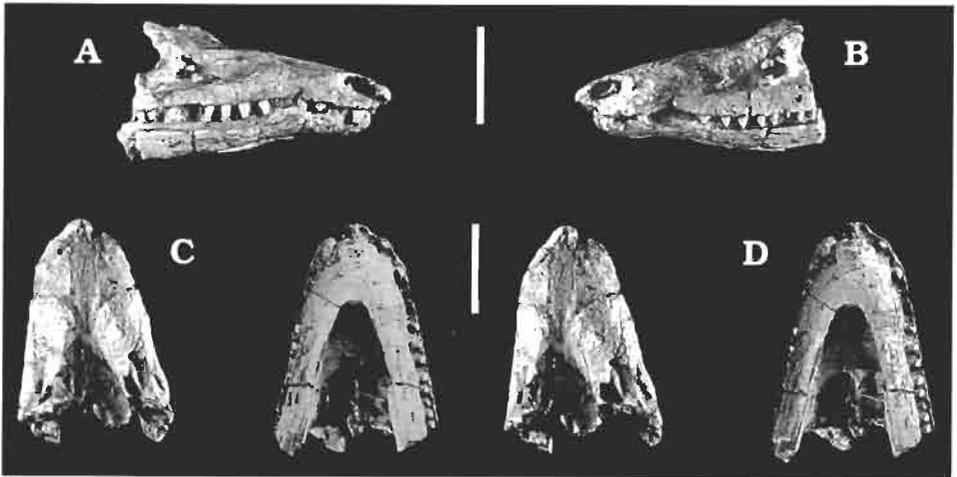


Fig. 7. *Gobiosuchus kielanae* Osmólska, 1972 from the Djadokhta Formation of Bayn Dzak. Anterior fragment of skull (ZPAL MgR-II/70). A, B. Right and left lateral views. C, D. Stereophotographs, dorsal and ventral views. Scale bars 1 cm.

depression on the ventral side of the skull roof (= the remnant of the supratemporal fossa; see above). As visible on the right side of the skull of ZPAL MgR-II/68, in the region of the trigeminal foramen, a small wedge of bone, probably representing the prootic, separates the quadrate from the laterosphenoid and most probably excludes the quadrate from the margin of the trigeminal foramen (this region is not sufficiently well preserved in any skull at our disposal). The anterodorsal end of the quadrate (probably representing the primary head of that bone) reaches with its lateral tip the aforementioned small depression on the ventral surface of the skull roof, and probably contacts the ventral surface of the squamosal there close to the contact of the latter with the postorbital. The medial portion of the anterodorsal end contacts medially the laterosphenoid and probably also the prootic.

The posterodorsal surface of the quadrate bears a large, sharply delimited depression, the bottom of which is subdivided by bony struts into several small fenestrae (Fig. 8D). It resembles the fenestration present on the surface of the quadrate in other protosuchians (Hecht & Tarsitano 1983).

The pterygoid ramus of the quadrate is steeply oriented and faces laterally. Hence, the quadrate-ptyergoid contact is mostly on the lateral surface of the braincase (Fig. 8A; see description of the pterygoid below). The condylar portion of the quadrate is differentiated from the main body of the bone. When seen ventrally, it protrudes slightly beyond the occiput, so that the mandibular and occipital articulations are placed almost in the same vertical plane, as in the primitive Crocodyliformes (probably except *Shantungosuchus hangjinensis*, see Wu *et al.* 1994: fig. 4b), but different from that in mesoeucrocodylians. In the occipital view, the quadrate condyle is placed slightly ventrally to the occipital condyle (Figs 5D, 9A), which resembles most other crocodyliforms. However, among the primitive crocodyliforms which have this region preserved and exposed, *Protosuchus haughtoni* (Busbey & Gow 1984: fig. 6) and *Sh. hangjinensis* (Wu *et al.* 1994: fig. 6b) display a mandibular articulation placed well below the articulation between the skull and vertebral column. The quadrate condyle is undivided. Its articular surface faces posteroventrally rather than ventrally. As visible in ZPAL MgR-II/67, there is a very weak depression on the anteroventral surface of the quadrate, which is located just in front of the medial part of the quadrate condyle, at the quadratebasisphenoid suture. In ZPAL MgR-II/68, in which the posterior half of the mandible is in natural articulation with the skull, the medial process of the articular attaches here the base of the braincase. Hence this depression most probably represents the articular surface for the medial process of the articular.

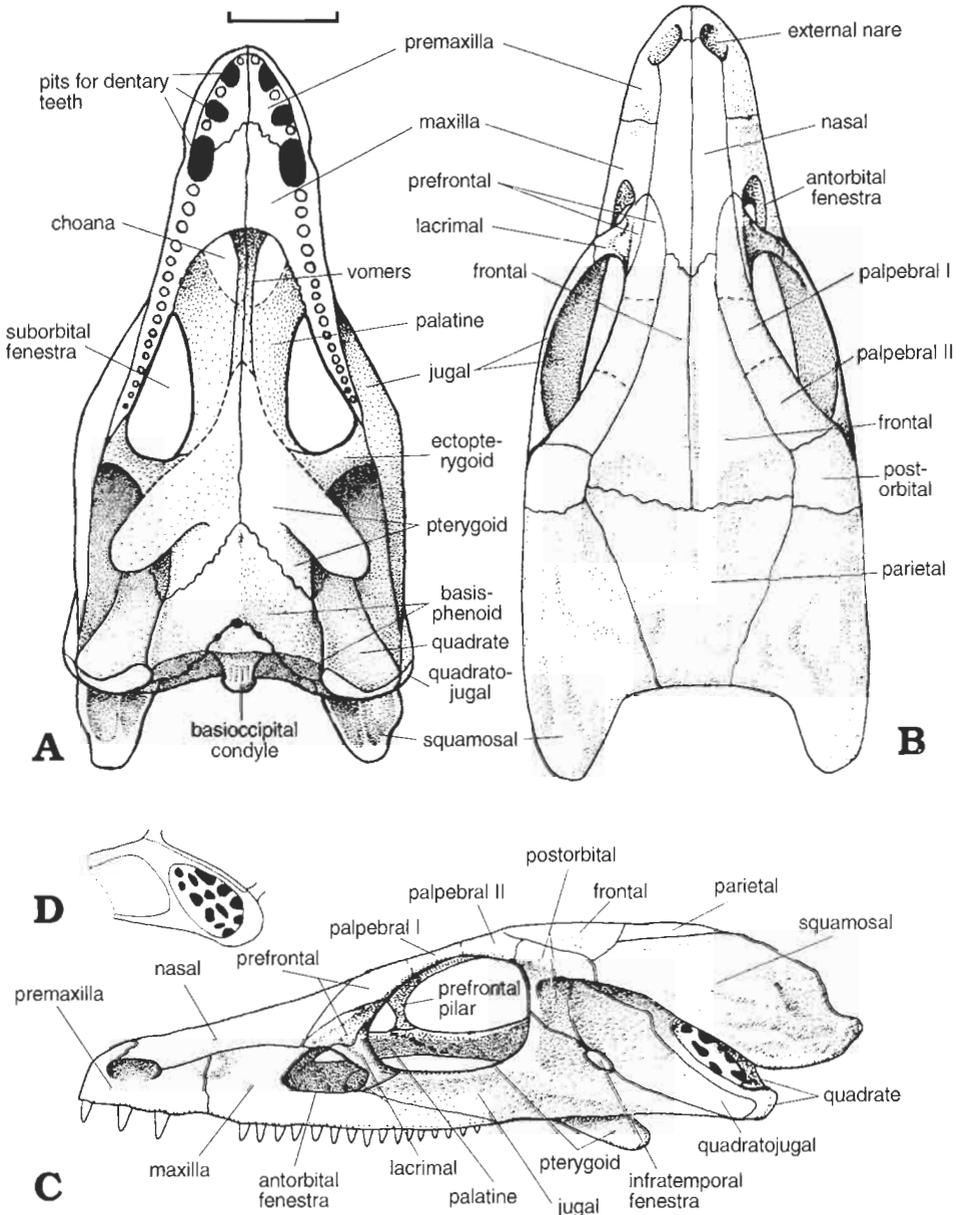


Fig. 8. *Gobiosuchus kielanae* Osmólska, 1972 from the Djadokhta Formation of Bayn Dzak. A–C. Reconstruction of skull, ventral, dorsal, left lateral view; based upon ZPAL MgR-II specimens 67, 68, 69, 70. D. Schematic drawing of dorsal surface of quadrate. Scale bar – 1 cm.

The occiput, basicranium, and palate are preserved in ZPAL MgR-II/67. In ZPAL MgR-II/68, in which only the posterior half of the skull is preserved, the braincase is well displayed, and part of its lateral wall (which is lacking in the holotype) is visible (Fig. 3B). The pre-choanal portion of the palate is also preserved in ZPAL MgR-II/70 (Fig. 7D).

The occipital plate lacks its dorsal portion in the holotype, whereas it is damaged in ZPAL MgR-II/68, and its medial portion is obscured by the articulated atlas, anterior part of the axis, and osteoderms. Exits of cranial nerves or vessels are not visible.

The basioccipital seems to form most of the occipital condyle. The condyle is very small and shallow, and it is separated from the occipital plate by a distinct, short neck. Anterior to the neck and close to its ventral limit, the basioccipital (Figs 5E, 9A) bears a rugose ridge, which corresponds to the reduced basioccipital tubera. The lateral extent of the basioccipital within the occipital plate seems narrow. Posteriorly, a small, horizontal, triangular portion of the basioccipital is deflected and invades the basicranium. Here, it is concave medially and, on both sides, sutured to the basisphenoid. Its ventral exposure is less than half as long as the basisphenoid. Within the basioccipital-basisphenoid suture there are three eustachian foramina, the medial of which is larger than lateral ones.

The exoccipital and opisthotic seem to be fused into an otoccipital. Sutures are not visible in this region. If the exoccipital portions of the condyle were present, they are not preserved. The paroccipital process is horizontal, shallow, and sutured laterally to the squamosal. The otoccipital bounds medially, mediadorsally, and medioventrally the cranioquadrate opening (see p. 266). Below the paroccipital process, there is a lateroventral extension of the otoccipital complex. It is ventrally sutured to the basisphenoid, the posterolateral process of which invades the occiput laterally. Thus, there is no otoccipital-quadrate contact, both bones being separated ventrolaterally by the process of the basisphenoid (see below).

The basisphenoid is greatly extended longitudinally and seems to be pneumatized. In ventral view, it is raised along its medial axis and somewhat concave on sides (Figs 5A, 8A, 9B). The basisphenoid has the shape of an arrow head and its lateral, oblique contacts are with the pterygoids anteriorly and quadrates posteriorly. A short contact occurs also dorsally with the ventral lamina of the posterolateral process of the squamosal (see above). The basisphenoid-quadrate contact is emphasized by a low crest, which separates the horizontal basisphenoid from the dorsolaterally inclined surface of the quadrate. On each side, the posterolateral processes of the basisphenoid turn dorsally at a right angle, invading the lateral portions of the occipital plate (Figs 3A, 5D, E, 8A, 9A, B). There, the basisphenoid laterally contacts the quadrate at the mandibular condyle and dorsomedially the exoccipital. Participation of the basisphenoid in formation of the occipital plate observed in *G. kielanae* (ZPAL MgR-II/67 and 68) is difficult to explain in terms of the ontogenetic development of the skull. To our knowledge, the basisphenoid never intervenes between the quadrate and otoccipital in any crocodyliform.

The parasphenoid rostrum is dorsoventrally expanded and sutured ventrally to pterygoids. Its connection with the basisphenoid body is not preserved in any skull at our disposal.

The lateral wall of the braincase is not complete in any of the ZPAL specimens. As far as could be observed in the specimen that best preserved this region (ZPAL MgR-II/68), the trigeminal foramen seems to be bordered by the laterosphenoid dorsally and the pterygoid ventrally or at least ventroanteriorly. On the right side of the skull, a very small fragment of a bone seems to be present at the foramen, between the laterosphenoid anteromedially and quadrate posterolaterally, which probably represents an anterior termination of the prootic and separates the quadrate from the trigeminal foramen (Figs 3B, 9C).

The laterosphenoid has a winglike shape. It joins in serrated sutures the frontal and its descending process anteromedially and the quadrate posterolaterally. The dorsal end of the laterosphenoid reaches the aforementioned small depression (= remnant of the supratemporal fossa) on the ventral surface of the skull roof. A posteroventral contact of the laterosphenoid with the pterygoid is probable but not preserved.

The pterygoid is weakly pneumatized. It is firmly sutured with its fellow along its entire length. The anterior processes of the pterygoids roof a longitudinal trough. This trough is the deepest at its posterior end, some distance anterior to the posterior margin of the suborbital fenestra, and it gradually becomes shallow anteriorly. The rostral portion of the anterior pterygoid process is poorly preserved and the contacts with the vomer and palatine are unclear. The anterior processes of the pterygoids extend dorsally, forming a shallow septum, which separates the palatines.

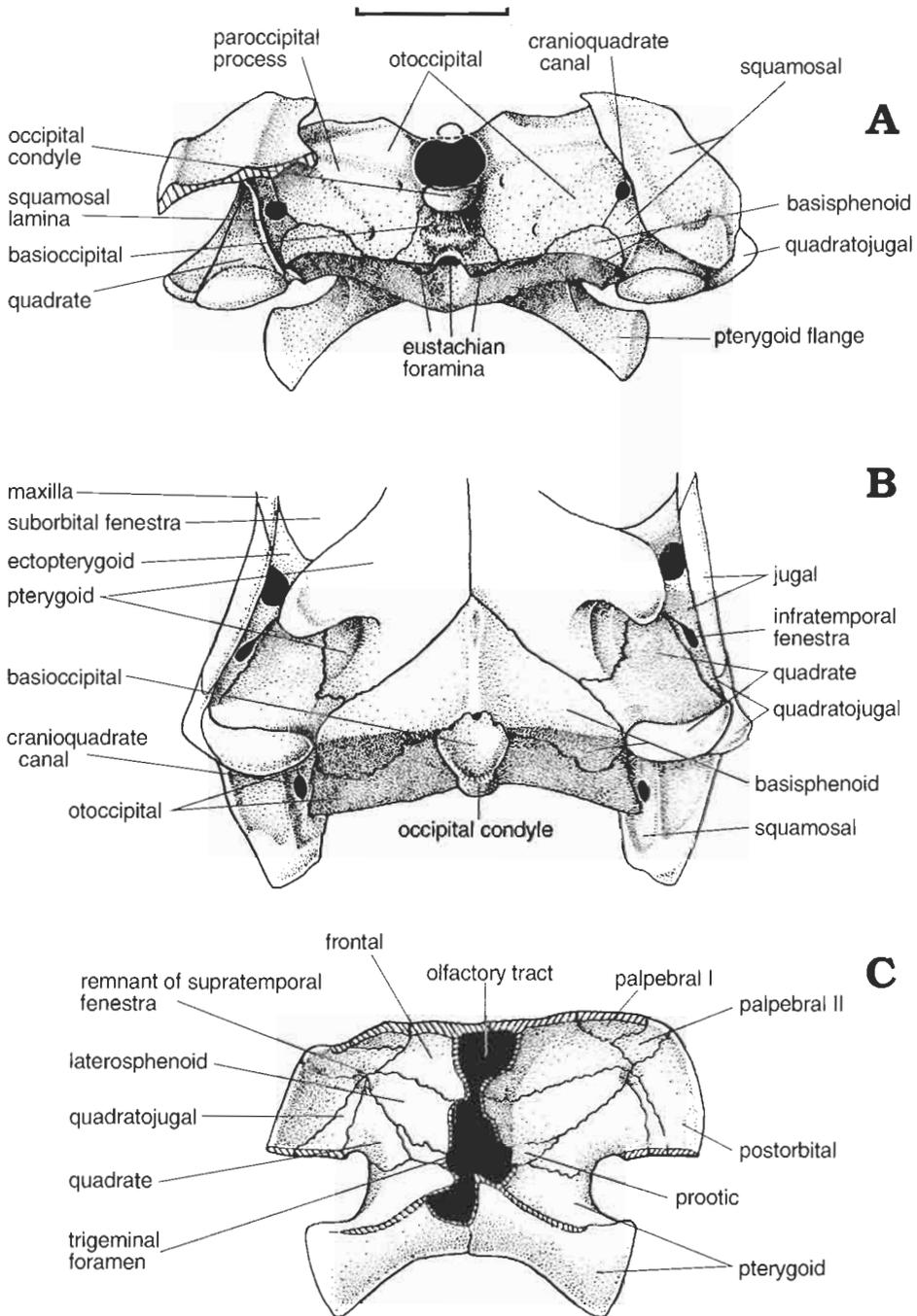


Fig. 9. *Gobiosuchus kielanae* Osmólska, 1972 from the Djadokhta Formation of Bayn Dzak. **A.** Reconstruction of occiput, posteroventral view. **B.** Reconstruction of posterior part of skull, ventroposterior view; based upon ZPAL MgR-II specimens 67, 68. **C.** Schematic drawing of anterior view of braincase, as preserved in ZPAL MgR-II/68 (compare Fig. 3B). Scale bar – 1 cm.

The pterygoid flange is stout and placed far anteriorly, due to a significant longitudinal extension of the cranial base. On its lateral surface, each flange bears a deep, thickened surface for contact with the mandible. Behind the base of the pterygoid flange, the pterygoid is extended into a long quadrate ramus. Two surfaces can be distinguished within the quadrate ramus, which are at about a right angle to each other. The horizontal (ventral) surface is triangular and medially contacts the basisphenoid along an oblique suture. The vertical (lateral) surface extends anterodorsally, and has an oblique sutural contact with the quadrate posterodorsally (Figs 8A, 9B).

The ectopterygoid is relatively short, contacting the maxilla and the jugal laterally. Its contact with the pterygoid is short and limited to the anterolateral portion of the pterygoid flange base.

The palatine is small and leaf-shaped. It forms the entire medial boundary of the suborbital fenestra. The palatines do not contact each other medially. An anterior process of the palatine bounds the exochoanal fenestra laterally. It contacts the palatal wing of the maxilla opposite the fourth (?third) through ninth maxillary tooth. The posterior contact with the pterygoid is unclear. The palatines are obliquely inclined towards their dorsomedial contact with the anterior processes of the pterygoids (see above), resulting in a distinct, narrow dorsal vaulting of the palate posterior to the exochoanal fenestra, along most of the suborbital fenestrae region.

The vomers are incompletely preserved and visible only in ZPAL MgR-II/67 and 70. They are firmly joined along the midline, forming a strong crest. As visible in ZPAL MgR-II/70 (Fig. 7D), each vomer slightly expands laterally above the crest. At the anterior borders of the exochoanal fenestrae the crest thickens and contacts the maxillae dorsal to the intermaxillary suture. It is not visible whether there was a contact with the pterygoids posteriorly.

All bones of the palate are smooth.

## Mandible

The mandible (Figs 3, 6, 7, 10) is preserved in ZPAL MgR-II/68, 69 and 70 but it is not complete in any of these specimens; its lingual side is not well exposed in any of them. As is best seen in ZPAL MgR-II/69, the mandible is shallow along its anterior half and twice as deep posteriorly, with weakly arched surangular region. The external mandibular fenestra is lacking and the retroarticular process is absent. The mandibular rami diverge only moderately posteriorly. The ornamentation on the mandibular bones is visible only in ZPAL MgR-II/70, in which the dentaries bear the shallow, longitudinal grooves, except in the symphyseal region, where the grooves curve and become parallel to the anterior margin of the mandible.

The dentaries are preserved in ZPAL MgR-II/69 and 70. They are completely fused with each other anteriorly without any trace of the suture. The symphyseal region is flat, horizontal and reaches to the level anterior of the fourth dentary tooth. Contacts with the angular and surangular are obliterated. There are only 14 teeth visible in ZPAL MgR-II/69, but posteriorly a few more seem to be present. The fourth tooth is enlarged, being about twice as tall as other dentary teeth, and the alveolar margin is elevated in this region. The teeth posterior to the fourth are set from the margin, and laterally a sharply demarcated, narrow shelf accommodates the maxillary teeth when the jaws are adducted. Other dentary teeth are of about the same size as the maxillary ones and do not differ in shape from the latter.

The splenial is incompletely preserved in ZPAL MgR-II/69 and 70. It is very narrow, at least anteriorly, and tapers to a sharp end at the level of the sixth or seventh dentary tooth, not reaching the symphysis.

Coronoid. In ZPAL MgR-II/70, a small piece of bone above the right splenial may represent the coronoid, but it is too poorly preserved to be sure.

The surangular bears a prominent ridge along its dorsal edge posterolaterally. Posteriorly, the bone curves ventrally and medially and covers the articular laterally. The contact with the angular is invisible, and it is not clear whether the latter bone was present on the lateral surface of the mandibular ramus.

The prearticular is absent.

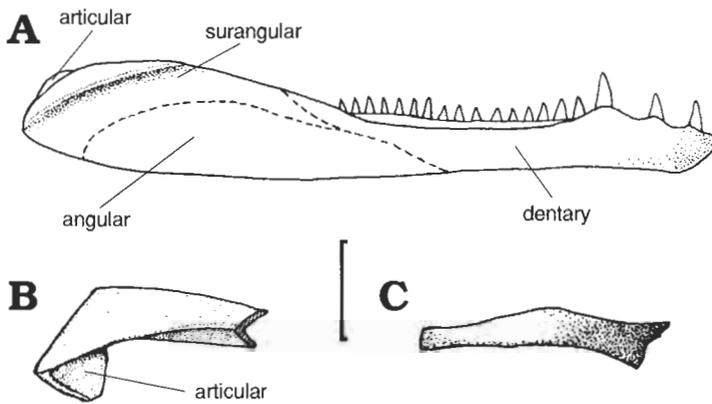


Fig. 10. *Gobiosuchus kielanae* Osmólska, 1972 from the Late Cretaceous Djadokhta Formation of Bayn Dzak. **A.** Reconstruction of left mandible, lateral view; based upon ZPAL MgR-II specimens 68, 69, 70. **B.** Schematic drawing of left articular region in ventral view; based upon ZPAL MgR-II/68. **C.** 'Articular' osteoderm supposedly from left pectoral region; same as Fig. 4: 11; ZPAL MgR-II/67. Scale bar – 1 cm.

The articular is visible only in ZPAL MgR-II/68 but it is not displayed dorsally, being hidden by the condyle of quadrate. There is a short medial process, the dorsal surface of which is continuous with the cotylus for the quadrate. The ventral surface of the medial process is slightly concave (Fig. 10B) and oblique, rising dorsally in a medial direction. With the mandible adducted, the dorsomedial tip of this process contacts the base of the braincase, at the quadrate-basisphenoid contact. This is in contrast with the more pronounced medial process in *Protosuchus richardsoni* (Brown, 1933), which contacts the basisphenoid and otoccipital (Clark 1986). The posterior surface of the articular is triangular and slopes ventroposteriorly, providing space for the insertion of the *m. depressor mandibulae*. The posteroventral tip of the articular is placed at the same level as the extremity of the posterior process of the squamosal.

### Postcranial skeleton

A large portion of the postcranium is preserved in ZPAL MgR-II/68 and includes the neck and the anterior half of the thoracic region, as well as part of the tail. The forelimbs are broken off at the base of the humeral head. Of the hind limbs, only the proximal part of the left femur is preserved. This specimen is almost completely freed from matrix and shows the osteodermal armour, which completely covers the animal's body. Although the body suffered a slight *post mortem* twist, the armour is preserved more or less in its original position. This provides satisfactory information about the external appearance of the body, whereas bones of the skeleton, including the vertebral column and girdles, are mostly concealed.

Specimen ZPAL MgR-II/71 consists of two fragments. One represents the dorsal armour covering the neck and anterior portion of the thorax; the ventral armour is not preserved and the skeletal bones are not exposed. This specimen is comparable to ZPAL MgR-II/68 in its proportions and ornamentation.

Specimen ZPAL MgR-II/67, the holotype of *Gobiosuchus kielanae*, shows mostly the internal skeleton, while the dermal armour is preserved mostly as isolated osteoderms scattered in the proximity of corresponding bones. The postcranial bones rest on a sandstone slab and are exposed in dorsal view. The skeleton lacks the tail and its bones are partly disarticulated. The left forelimb, part of the thoracic region of the vertebral column, the hindlimbs and the medially exposed right half of the pelvis are present.

**Vertebral column.** — All vertebrae are amphicoelous, with deeply concave anterior and posterior faces of the centra. The dorsal vertebrae have large neural canal – its diameter is only somewhat

smaller than that of the centrum. Specimens ZPAL MgR-II/67 and 68 are clearly adult animals, since the neural arches are firmly fused to the centra.

The atlas-axis complex is well preserved in ZPAL MgR-II/68, where it is still articulated with the occipital condyle (Fig. 3A). However, its dorsal side is concealed by large nuchal osteoderms (see below). In ventral view, the intercentrum of the atlas is clearly visible, and it is broader than long. The intercentrum is flanked on both sides by the lateral neural arches in typical crocodylian fashion. Only the anterior part of the centrum of the axis is preserved. It articulates tightly with the intercentrum of the atlas but is not fused to it. The parapophyses are clearly visible on the anterior edge of the ventral surface of the axis. A fragment of a cervical rib is still attached to the right parapophysis. In posterior view, the low neural arch of the axis is visible beneath the arched nuchal osteoderms.

**Postaxial cervical vertebrae.** The cervical part of the vertebral column is preserved in its entirety only in ZPAL MgR-II/68 (Fig. 2), but the vertebrae are completely hidden by the osteoderms. If one assumes that each transverse scute row covers one vertebra, there must be seven postaxial cervicals. Because the scutes of the ventral half of the armour have been more compressed laterally than those of the dorsal half, three cervical ribs are visible on the left side. The neck is very slender and its great length, which is only slightly shorter than the median length of the skull, is remarkable.

**Dorsal vertebrae.** In ZPAL MgR-II/67, besides various vertebral fragments, four dorsals from the middle part and three from the posterior part of the trunk are preserved. A centrum of one of the most anterior dorsals is also visible. It is spool-shaped, keeled, and bears strong parapophyses. Three of these medial dorsals (two of them articulated) are preserved on the main block of the rock and only the dorsal surfaces of their wide, flat arches are exposed. The maximum length of the arches is about 10 mm. The neural spines are broken off or incomplete, but their bases indicate that they were anteroposteriorly elongate. The transverse processes are relatively large, wide anteroposteriorly, and flat (Figs 4, 12A); the capitular and tubercular facets are separated. The pre- and postzygapophyses are very short anteroposteriorly, and their articular surfaces are nearly horizontal, which must have restricted vertical flexion of that part of the trunk. The anterior margin of the arch is deeply incised. On another block belonging to ZPAL MgR-II/67, three articulated posterior dorsals are joined with a sacral (see below). The centrum of the last dorsal is 6.5 mm long and 4 mm deep; it has a much narrower transverse process than the medial dorsals and elongate, relatively closely spaced postzygapophyses. Of the most anterior of these posterior dorsals, only the neural arch with postzygapophyses is preserved. In ZPAL MgR-II/68, most of the dorsal vertebrae are hidden inside the dermal armour (Fig. 2) and cannot be seen, except for a single dorsal at the posterior end of the preserved portion of the trunk. The centrum of this vertebra is amphicoelous, elongate, 8 mm long, 3 mm deep, and 4 mm wide; it does not bear any keel. There is a shallow, long neural spine; the features of the arch are as in ZPAL MgR-II/67.

The total number of the dorsal vertebrae present on that specimen, which includes the pectoral girdle but is broken anterior to the pelvis, can only be estimated on the basis of the number of the transverse rows of the osteoderms. If each osteodermal row is associated with one vertebra, there must have been at least nine dorsal vertebrae in *Gobiosuchus kielanae*. Comparison with other crocodylians (which have about fifteen dorsals) suggests that the actual number was probably much higher than nine.

On a small block belonging to ZPAL MgR-II/71, the position of which relative to the rest of the specimen is uncertain, there are three-and-a-half poorly exposed vertebrae, which are associated with rows of dorsal thoracic osteoderms.

**Sacrum.** A single sacral vertebra is preserved (see above) in ZPAL MgR-II/67, on the block bearing the pelvis, and it is located close to the pelvis. As this vertebra is articulated with the last dorsal, it can be identified as the first sacral. Its centrum is 6 mm long and the sacral rib is 3 mm long. Although somewhat shorter than those of the dorsal vertebrae, the centrum differs little from them, and does not exhibit the usual robustness of crocodylian sacral vertebrae.

**Caudal vertebrae.** In ZPAL MgR-II/68, the caudal vertebrae of the curved tail fragment are completely concealed by the bony armour that encircles them. Assuming that each osteodermal

row covers a single vertebra, this 75 mm long portion of the tail would contain thirteen caudals. The thickness of that tail segment varies little from front (14 mm) to back (11 mm) and it seems that the tail was relatively long, and may have accounted for half the total length of the animal's body. On a separate block, three vertebrae are preserved, which probably come from the proximal part of the tail. They are associated with two median dorsal rows of osteoderms. Their centra are damaged; the length of the centrum of the most posterior of these vertebrae, which is best preserved, may be estimated at 7 mm, its depth being 3.5 mm and the anterior width 4 mm. The transverse processes are horizontal and about 2 mm wide anteroposteriorly. The prezygapophyses are short, vertically oriented; the postzygapophyses are long, lateromedially flattened and directed posterodorsally.

**Ribs.** — Three cervical ribs, articulated with the vertebral column and with each other, are visible in specimen ZPAL MgR-II/68. They exhibit the usual crocodylian T-shaped condition. The diapophysial and parapophysial processes are very slender and 2 mm long. The lateral rod is 14 mm long, which more or less equals the length of two cervical vertebrae. In ZPAL MgR-II/67, two parallel, rod-shaped, compact bone fragments, about 25 mm long and 2 mm in diameter, may represent incomplete thoracic ribs. In ZPAL MgR-II/68, the proximal end of one of the anterior left thoracic ribs protrudes from under the dermal armour.

**Shoulder girdle.** — The left half of the shoulder girdle is visible in ZPAL MgR-II/68, but it is incomplete and only its external surface is exposed.

**Coracoid.** The total length of the coracoid is 10 mm, its distal width is 6 mm, and the diameter of the glenoid cavity is 4 mm. Contrary to Osmólska (1972: fig. 1), the coracoid is damaged at the level of the coracoid foramen. The anterior edge is straight and the distal edge is slightly convex. The posterior edge is markedly concave; close to the contact with the scapula it forms a bony ridge delimiting the ventral part of the glenoid cavity.

**Scapula.** This bone is straplike except for its proximal end, where its width increases from 3 to 4.5 mm to form the dorsal part of the glenoid cavity. The length as preserved is 12 mm. The anterior edge is straight while the posterior is indistinctly concave due to the widening of the scapula at the glenoid.

**Forelimb.** — The long bones of the fore- and hind limbs are thin-walled and hollow. A forelimb lacking carpus and manus is preserved in ZAL MgR-II/76 (Fig. 4), and the proximal parts of both humeri articulated with shoulder girdles are present in ZPAL MgR-II/68.

**Humerus.** In ZPAL MgR-II/67, the left humerus (Fig. 5G) is almost complete and exposed in posterior aspect. As preserved, it is 47 mm long. The distal end is severely damaged. However, the proximal end is sufficiently preserved to show that the articular surface is lateromedially elongate, strongly curved medially, and narrow anteroposteriorly. The deltopectoral crest is largely hidden and incompletely preserved. The medial edge is damaged proximally. The shaft is long and slender (diameter at midlength: 3 mm), with a slight sigmoidal curvature. A slight distal expansion is discernible, but distal condyles have been destroyed and nothing can be said about their shape and proportions.

In ZPAL MgR-II/68, the proximal articular heads of both humeri are joined with the shoulder girdle. The left humeral head can be seen in posterior view. The slender shaft with a nearly circular cross-section expands rapidly proximally to form a posteriorly convex end. As the distal end of the humeral head has been displaced inward and is now partly hidden by the pectoral girdle, little can be said about it. On the right humerus (Fig. 12B, C), the articular region is damaged, but one can see that it is strongly curved medially. The deltopectoral crest, on the lateral edge of the bone, is a well-marked triangular process that protrudes forward.

**Radius and ulna.** The left radius and ulna are partly preserved in ZPAL MgR-II/67. However, the region of the elbow articulation is destroyed; distal ends of both bones, represented partly by impressions in matrix, are separated from the proximal parts, being preserved on a small block of matrix detached from the main block. What is preserved are mainly the slender, rather straight shafts of the bones, which expand slightly proximally toward articular ends. No detailed description is possible. Both bones are of the same thickness. The ulna is approximately 40 mm long. It is 3 mm wide proximally and the diameter of its shaft is 2 mm. The radius is approximately 38 mm

long; the shaft diameter is 2 mm and the distal width (basing on the impression) equals 3 mm. Neither the carpus nor manus are known.

**Pelvis.** — The right half of the pelvis is present in ZPAL MgR-II/67, but only its medial surface is exposed (Figs 11A, 12 D–F). The acetabulum is perforate and circular in the outline. As preserved, the position of the pubis is close to horizontal (Fig. 12D), almost certainly due to displacement of the pubis after breakage.

**Ilium.** Only fragments of the ilium are preserved, and they do not allow any detailed description. Nevertheless, it can be seen that the ilium formed about the dorsal half of the acetabulum, and articulated with the ischium posteroventrally and with the pubis anteroventrally (Fig. 12E, F). Whether there was also a contact with the ischium anteriorly is uncertain, the proximal end of pubis being (?as preserved) wedged between both these bones.

The **ischium** is nearly complete. It is 12 mm long as measured from the acetabulum to the posteroventral edge. It forms the entire ventral margin of the acetabulum. The anterior process and the posterodorsal process, which reaches the ilium, are of roughly the same size. Close to the contact with the pubis, the anterior part of the anterior process is expanded lateromedially, triangular in cross-section. The posteroventral process of the ischium is relatively narrow at its inception, but widens rapidly to form a wide, thin, medially concave blade (Fig. 12E, F). The symphyseal edge of the blade, which met the left ischium, is 12 mm long, equaling the length of the entire ischium. The anterior margin of this process is deeply concave, while its posterior margin is straight distally, becoming concave proximally, where it borders the peduncle which reaches the ilium. The angle between the posterior edge of the blade and its ventral edge is about 45 degrees. The ilio-ischiadic contact is somewhat shorter than the articular facet for the contact with the pubis.

The **pubis** has a hollow shaft and is 15 mm long as preserved. About a third of its proximal part has only its lateral wall preserved, and distally, there is a break below which the rest of the pubis has undergone a rotation of about 90 degrees. The pubis expands distally from a proximal width of 1.5 mm to a distal width of 4 mm, which gives it the shape of a spatula. Because of a possible displacement of its proximal end, the relation of the pubis to the acetabulum is uncertain. However, as preserved, it inserts as a wedge between the ischium and the ilium close to the margin of the acetabulum.

**Hind limb.** — The hind limb is known in ZPAL MgR-II/67 (Fig. 4), but the pes is very fragmentary; in ZPAL MgR-II/68 only a proximal third of the femur is present.

**Femur.** The right femur is nearly complete in ZPAL MgR-II/67 and is 64 mm long, whereas only the distal two-thirds of the left one are preserved, measuring 51 mm. The femoral head is deflected medially and anteriorly. It is wider (6 mm) than the shaft and rectangular rather than rounded in cross-section. Two depressions, one anterior and one posterior, are visible on the articular head. The shaft is slender, 4 mm wide at midlength, and smooth. No trochanter is visible in the proximal region of the shaft. The distal condyles are visible only in ZPAL MgR-II/67. Although they are partly embedded in matrix, they appear to be deep and well-marked, the lateral one being larger than the medial.

**Tibia.** Both tibiae are preserved in ZPAL MgR-II/67, but their articular ends are crushed and distorted. Their exact shapes and relations to surrounding bones are uncertain. The proximal end of the right tibia articulates with the distal condyles of the femur and seems to conceal the fibula. The distal ends of tibiae are too incomplete to warrant description. The length of the right tibia is 56 mm and its diameter at midlength is 4 mm. The left tibia is 55 mm long with a proximal width of 5 mm.

**Fibula.** The right fibula is incomplete – 49 mm long as preserved, and only a 34 mm long proximal fragment of the shaft of the left one is reasonably well preserved. The proximal end is 4 mm wide, whereas the very slender shaft is 1.5 mm in diameter.

The **tarsus** and **pes** are fragmentary. A group of poorly preserved bony elements at the distal end of the left hindlimb in ZPAL MgR-II/67 apparently corresponds to part of the tarsus and metatarsus. A broken bone articulating with a remnant of the distal end of the fibula shows the outline of a normal crocodylian calcaneum, with a marked tuber. The preservation state does not allow to determine in which direction the tuber pointed. Further distally, three tubelike bone fragments with slightly enlarged proximal ends are probably the proximal extremities of three metatarsals.

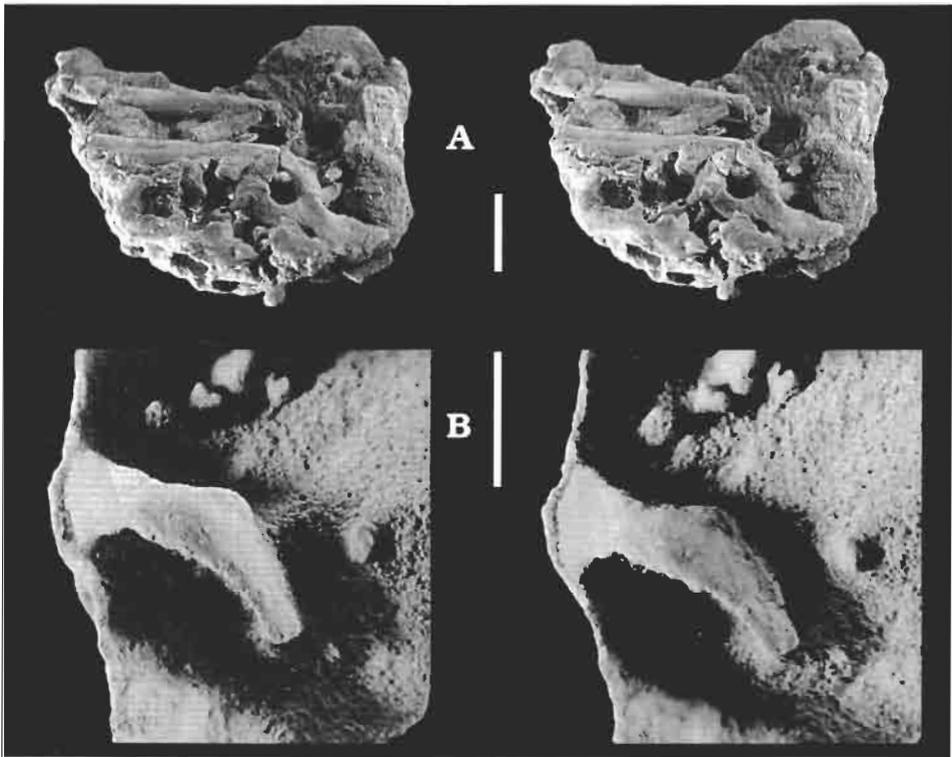


Fig. 11. *Gobiosuchus kielanae* Osmólska, 1972 from the Djadokhta Formation of Bayn Dzak. **A.** Stereophotograph of right half of pubis (ZPAL MgR-II/67), medial view. Proximal part of right femur and distal part of right tibia visible above. **B.** Stereophotograph of 'articular' osteoderm in right pelvic region (ZPAL MgR-II/71), outer (ventral) side. Scale bars – 1 cm.

**Dermal armour.** — The extensively developed bony armour in *Gobiosuchus kielanae* is one of the most striking features of this crocodylian, and it can be described in some detail on the basis of the well preserved articulated specimens available, especially ZPAL MgR-II/68 and 71, ZPAL MgR-II/678 providing also few complete osteoderms.

The body of *Gobiosuchus kielanae* was enclosed in bony scutes from the neck through the trunk to the tail (Figs 2, 13A, B), and the limbs, too, were armoured (Fig. 13C–F). As may be reconstructed on the basis of the well preserved armour in ZPAL MgR-II/68 and 71, the neck and tail were almost round in cross-section, while the thorax was oval, with a dorsoventral compression. The osteoderms in each dorsal and ventral row are joined by firm, zig-zag sutures. The dorsal osteoderms are easily distinguished from the smooth ventral ones by their distinctive ornamentation forming a triradiate, backward converging *fleur de lys* pattern, and their thickened posterior edge (Fig. 5F). Each transverse row of the dorsal osteoderms seems to meet the corresponding ventral row to form a bony ring around the body, but the true nature of this connection, whether sutural or not, is not clear. However, almost certainly in the cervical series these two portions were not firmly joined laterally (see below). Each transverse row of the dorsal and ventral osteoderms overlaps the anterior edge of the succeeding row. At the level of articulations of the limbs with the trunk, the curved, straplike osteoderms provide a transition between the thoracic armour and that which covers the limbs. The appendicular armour consists of osteoderms which are sutured with each other and bear a radial ornamentation pattern.

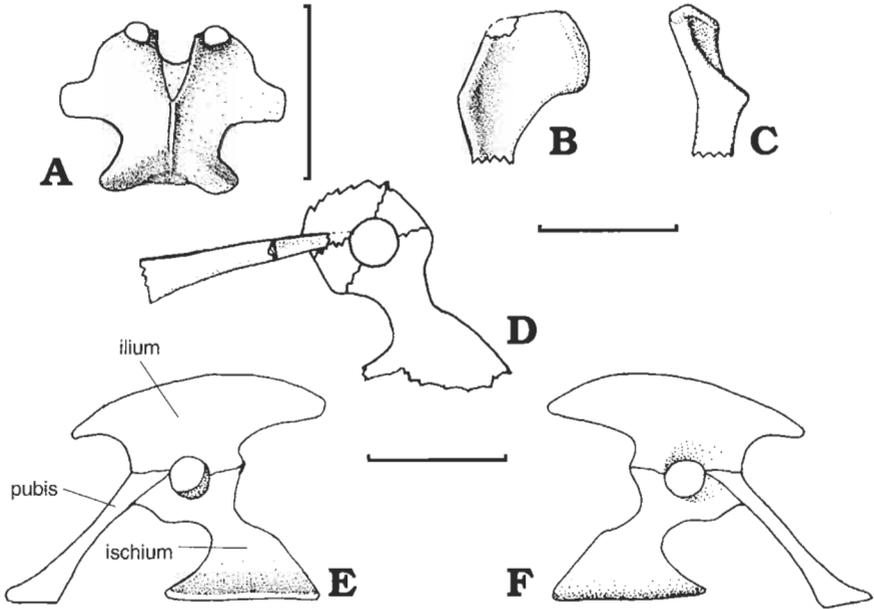


Fig. 12. *Gobiosuchus kielanae* Osmólska, 1972 from the Djadokhta Formation of Bayn Dzak. **A**. Reconstruction of a thoracic vertebra, dorsal view; based upon ZPAL MgR-II/67. **B**, **C**. Proximal end of right humerus (ZPAL MgR-II/68), anterior and lateral views. **D**. Schematic drawing of right half of pelvis with pubis position as found (ZPAL MgR-II/67). **E**, **F**. Reconstruction of pelvis, medial and lateral views. Scale bars – 1 cm.

**Nuchal osteoderms.** We describe as the nuchal osteoderms a pair of peculiar scutes that cover the atlas-axis complex and occupies a large part of the space between the posterolateral processes of the squamosals. These paired osteoderms are visible in ZPAL MgR-II/68 and 69 (Figs 3A, C, E, 6B). They are large (8 by 9 mm each in ZPAL MgR-II/69), quadrangular, and slightly broader than long. The anterior margin of these scutes is slightly upturned and bears a well-marked lateral spur, which is not found on other scutes. The lateral side of each of these osteoderms is angularly bent ventrally. Posteriorly, the nuchal osteoderms overlap the first transverse row of 'normal' cervical osteoderms.

**Cervical osteoderms.** There are eight transverse rows of cervical osteoderms in ZPAL MgR-II/68, plus the aforementioned pair of nuchal osteoderms above the atlas-axis complex. In ZPAL MgR-II/71, four posterior rows of dorsal cervical osteoderms are also preserved. Each row of the dorsal cervical region consists of four osteoderms, which are sutured to each other. These scutes are square to rectangular (the posterior ones), with a pronounced triradiate ornamentation and a raised ridge roughly parallel to the posterior margin. The posterior part of the dorsal osteoderm overlaps the anterior margin of the next osteoderm. The highest point on the external surface of the scute is where the base of the triradiate pattern intersects the ridge close to the posterior margin. It gives the sides of the neck a 'spiny' appearance in dorsal view (Fig. 13A). The thickness of the osteoderm increases from front to back, which gives it a triangular sagittal section.

The ventral osteoderms of the cervical region are visible only in ZPAL MgR-II/68. There are also four osteoderms in each transverse row.

Although it cannot be determined whether each ventral row was sutured to its dorsal counterpart in the cervical series, this seems unlikely on the basis of the preservation of the specimen ZPAL MgR-II/68, in which the ventral osteoderms have been displaced as a group relative to the dorsal ones.

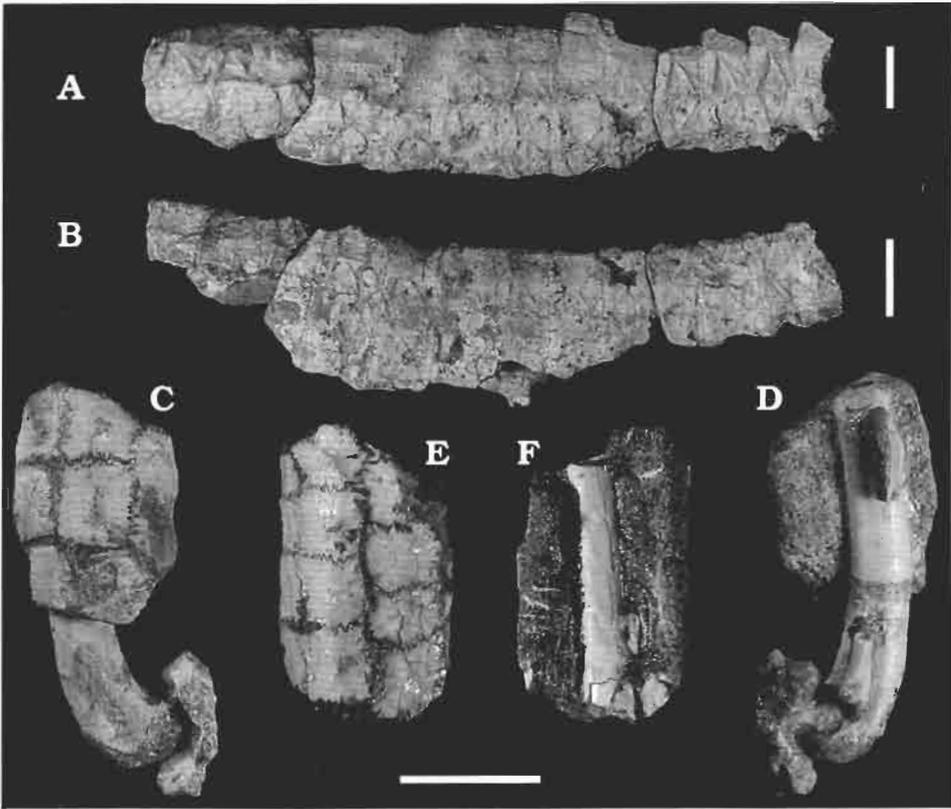


Fig. 13. *Gobiosuchus kielanae* Osmólska, 1972 from the Djadokhta Formation of Bayn Dzak. A, B. Fragment of armour from thoracic and posterior cervical region (ZPAL MgR-II/71), dorsal and right lateral views. C, D. Fragment of femur with appendicular osteoderms attached (ZPAL MgR-II/68), outer and inner sides. E, F. Another fragment of a limb bone with appendicular osteoderms attached (ZPAL MgR-II/68), outer and inner sides. Scale bars – 1 cm.

These ventral osteoderms are quadrangular (their exact shape cannot be determined because of the state of preservation) and rather smooth, but bear a faint longitudinal ridge and tiny pits which make the surface somewhat irregular.

**Thoracic osteoderms.** Dorsal osteoderms of the thoracic region are still articulated in ZPAL MgR-II/68 and 71, whereas they are disarticulated in ZPAL MgR-II/67. They are quadrangular, usually somewhat wider than long. Their ornamentation is similar to that of the cervical osteoderms. The anterior articular surface, overlapped by a more anterior osteoderm, is depressed relative to the rest of the scute. In each transverse row osteoderms are joined by sutures. It is not easy to determine the exact number of osteoderms in each dorsal row of the thoracic region. However, there were apparently six osteoderms in the middle region of the trunk, and at least four more anteriorly.

The ventral osteoderms of the thoracic region are visible only in ZPAL MgR-II/68. There are six sutured osteoderms in each transverse row in the middle part of the trunk. These osteoderms are rectangular, with a granular surface.

Each row meets its dorsal counterpart laterally to form a bony ring. Whether these two half-rings were suturally joined is not visible in any of our specimens. However, differently than in the cervical series (left side), there is no longitudinally continuous line of displacement between the ventral and

dorsal halves of the rings in the thoracic series, and, in the zone of junction, the lateral osteoderms of the half-rings are rather crushed than displaced.

**Caudal osteoderms.** The dorsal osteoderms of the caudal region are visible only in ZPAL MgR-II/68 above the most anterior caudals and on the more posterior tail fragment. Their ornamentation is fainter than that of the cervical and dorsal osteoderms, but shows the same triradiate pattern. At the level of the anterior caudals, they do not differ in shape from the thoracic osteoderms. Farther backward along the caudal series, they become anteroposteriorly elongated rectangles. There are four dorsal osteoderms per transverse row.

The ventral osteoderms are preserved in this specimen only in the more posterior section of the tail. They have a rectangular (longer than wide), rooflike shape and a smooth external surface. There are six such osteoderms in each transverse row.

**'Articular' osteoderms.** In ZPAL MgR-II/68, a smooth, strongly bent, narrow bony strip, 22 mm in length and of varying width 2 to 4 mm, is visible at the level of the articulation of the forelimb with the trunk (Figs 2, 10C). Two other fragments, respectively 11 and 17 mm in length, are visible in the pelvic region. Elements of the same type occur in ZPAL MgR-II/71, at the level of the shoulder and the pelvis (Fig. 11B), being respectively 6 and 13 mm long. These strips of bones cannot be referred to any element of the skull, mandible or postcranial skeleton. Their position and their semicircular shape suggest that they could provide an 'articular transition' between the thoracic armour and the rigid appendicular armour of osteoderms described below.

**Appendicular osteoderms.** A large part of the lateral surface of the left femur in ZPAL MgR-II/68 is covered by a mosaic of eight contiguous, square osteoderms, that are slightly curved in cross section and peculiarly ornamented (Fig. 13C, D). There is also another fragment of a limb bone which is covered by the same type of sutured scutes (Fig. 13E, F). The ornamentation consists of a weak central ridge surrounded by short radial grooves. Similar, disarticulated osteoderms, notably in the tarsal region, are visible along several limb elements in ZPAL MgR-II/67. They have a smooth, concave internal surface, and all four edges are denticulated. These peculiar osteoderms cannot be from the armour covering the axial skeleton because:

- their ornamentation is completely different from that of the axial osteoderms;
- they are firmly joined together along all four margins by interdigitating sutures, forming a mosaic and unmovable articulation, whereas all the transverse rows of osteoderms of the axial armour are articulated with one another by means of overlapping contacts, which allowed some flexion;
- the osteoderms with identical features are found in the close association with the fragments of the limb bones in ZPAL MgR-II/68 (Fig. 13C–F).

Therefore, it seems that these 'appendicular' scutes covered at least some sections of limbs, as suggested by their position in ZPAL MgR-II/67 and 68.

## Comparisons

At first glance, one may notice certain differences in the snout depth relative to its width (both measured at the lateral premaxilla-maxilla contact) among the three skulls of *G. kielanae*, which preserve this region. The depth to width ratio is 0.6 in ZPAL MgR-II/69, while slightly less than 0.4 in ZPAL MgR-II/67, both skulls being similar in size, the median length of the latter being 64 mm and that of the former estimated as 68 mm. In the smallest specimen ZPAL MgR-70 (only the snout is preserved) this ratio is slightly above 0.5. These differences may be caused by some insignificant deformations of the respective skulls, but may also indicate that, to a certain degree, this character was subject to individual or ontogenetic variation. As all these skulls come from the same strata and locality and the breadth-to-width ratio is only slightly different for each of them, we consider that they belong to the same species, *G. kielanae*.

*Gobiosuchus parvus* described by Efimov (1983, 1988b) was found in Udan Sair, a locality about 100 km distant from Bayn Dzak, from where all ZPAL *G. kielanae* specimens came. According to Efimov (1983, 1988b), both species come from the same strata [Djadokhta Formation (= Djadokhta 'Age' of Jerzykiewicz & Russell 1991)]; however, according to Jerzykiewicz & Russell, deposits in Udan Sair represent a younger, Barungoyotian 'Age'. According to Efimov (1988b: p. 45), *G. parvus* differs from *G. kielanae* in the shape of the orbit ('internal margins of orbits slightly elevated' [?]), the oblique position of the depressions on the skull table, a shorter posterior process of the squamosal, the pitted ornamentation on parietals, and the smaller size. In our opinion, these attributes do not appear a safe basis for a specific distinction of the Udan Sair form: the difference in size may be due to the individual age; ornamentation on the skull bones is not well preserved in any specimen of *G. kielanae* and does not allow comparisons; the supratemporal fenestrae in some crocodiles are often obliquely oriented in the juveniles (Dr. H.-D. Sues' personal information); the present inspection of the material of *G. kielanae* has shown that, depending on the preservation, the depressions on the skull roof may also look slightly oblique in some specimens of the latter species; the orbital margins in the less distorted skull (ZPAL MgR-II/69) of *G. kielanae* do not seem different from those in Efimov's form. Additionally, Efimov's conclusion about the shorter posterolateral process of squamosal in the Udan Sair specimen may be erroneous. Judging by his drawing of the holotype skull (Efimov 1983: fig. 9), on which the posterior margin of the skull is drawn with a broken line, the posteriormost part of the skull is not well preserved. Thus, it is also possible that the processes have been broken off. However, according to Efimov's description, the number of maxillary teeth (18) is greater by two than that in *G. kielanae* (16), and, according to his drawing (Efimov 1983: fig. 9), both dentaries are joined by a suture in the symphysis, whereas they are fused without any trace of a suture in all specimens of *G. kielanae*. Only these two differences might eventually be of a taxonomic value (although the latter character may also be due to a younger individual age of the Udan Sair specimen). Taking into account the possibility that Efimov's specimen comes from the younger deposits than ours, as well as the two differences just mentioned, we consider that the final judgement about the possible conspecificity of *G. parvus* with *G. kielanae* should be postponed until more and better material of the first form is found in Udan Sair.

Complete postcrania are so far unknown in most protosuchian taxa, except in *P. richardsoni* and *Orthosuchus stormbergi* Nash, 1975. The neck and limbs in these species are much shorter and stouter than they are in *G. kielanae*. Fragmentary postcranial remains of *Sichuanosuchus shuhanensis* Wu *et al.*, 1997 include some limb bones, which are also very slender and long in this species. Most of the left forelimb is preserved in *S. shuhanensis* (Wu *et al.* 1997). It shows that the combined humerus + radius length constitutes somewhat more than 127% of the skull length. This is close to proportion of these elements in *G. kielanae*, which equals 132%.

## Phylogenetic relationships

Although the crocodyliform nature of *Gobiosuchus* has never been questioned, there was no consensus as to its relationships within the Crocodylia. Originally, *Gobiosuchus*

was tentatively assigned to the Protosuchia (Osmólska 1972). Clark (in Benton & Clark 1988: figs 8.7, 8.8), who considered Protosuchia a paraphyletic group, suggested that *Gobiosuchus* was the sister taxon to the Mesoeucrocodylia. More recently, Clark (1994) published a detailed analysis of the phylogenetic relationships within the Crocodyliformes (= Crocodylia), which essentially confirmed his earlier (1988) hypothesis, except that, in the resulting cladogram (Clark 1995: fig. 5.2), *Gobiosuchus* was considered (together with *Eopneumatosuchus* Crompton & Smith, 1980) as the first offshoot of the Crocodyliformes.

Recent discoveries of new primitive crocodyliforms in China, as well as revisions of the earlier described but poorly known ones, provided new anatomical data, which allowed a re-examination of the problem of the monophyly of the Protosuchia and relationships of the alleged protosuchian taxa (Lü & Wu 1996; Sues *et al.* 1996; Wu *et al.* 1994; Wu & Li 1994; Wu & Sues 1995; Wu & Sues 1996; Wu *et al.* 1997). In the preliminary phylogenetic hypothesis of Wu & Sues (1995: fig. 4), the monophyly of the Protosuchia was confirmed and *Gobiosuchus* was considered as the sister taxon to the Protosuchidae plus *Shantungosuchus* Young, 1961 and *Sichuanosuchus* Peng, 1995. This arrangement has been recently modified in a more detailed cladogram presented by Wu *et al.* (1997: fig. 6, node D), in which *Gobiosuchus*, *Shantungosuchus*, and *Sichuanosuchus* constitute a sister-group to other Protosuchidae (*sensu* Wu *et al.* 1994). According to Wu *et al.* (1997, appendix 4) this clade is supported by four unequivocal synapomorphies: the frontal does not extend into the supratemporal fossa; the prearticular is absent; the anterior process of jugal is transversely broad below the orbits; the cranial table is nearly as wide as the ventral portion of the skull. We regard only the last three of these character states as valid, because the supratemporal fenestra is entirely closed in *Gobiosuchus* by an overgrowth of the frontal, parietal and squamosal; a remnant of the supratemporal fossa, in the form of a small concavity on the ventral surface of the skull table, has the frontal in its medial margin (Fig. 9C).

Re-investigation of *Gobiosuchus kielanae* allowed us to diagnose *Gobiosuchus* by several autapomorphies, the unequivocal ones being: (1) the long, slender neck; (2) the ventrolateral processes of the basisphenoid encroaches onto the occiput, separating the otoccipital and quadrate; (3) the incisive foramen is absent, resulting in contact of the palatal wings of the premaxillae along their entire length; (4) the supratemporal fenestra is closed; (5) the external mandibular fenestra is closed; (6) the limb bones are covered by armour of sutured osteoderms. The states of characters 1–3 and 6 are unknown in *G. parvus*. The very long posterolateral process of the squamosal present in *G. kielanae* should be at the moment considered as an equivocal autapomorphy for *Gobiosuchus* because, according to Efimov (1983, 1988b), this character state is absent in *G. parvus* (but see p. 283).

The protosuchian affinities of *Gobiosuchus*, as recently proposed by Wu *et al.* (1997), are supported by the following unequivocal synapomorphies (we follow here their opinion with only some minor changes): (1) the snout is shorter than the rest of the skull; (2) the snout abruptly broadens at the orbits; (3) the distal portion of the quadrate is weakly differentiated from the posteroventral surface of the braincase; (4) the quadrate has more than two fenestrae on its dorsal surface; (5) the pterygoid is pneumatized; (6) the basisphenoid is much longer than the basioccipital; (7) the quadrate is in broad contact with the basisphenoid on the ventral surface of the

braincase; (8) the retroarticular process is absent; (9) the articular has a medial process. The extreme reduction of the infratemporal fenestra, with an almost complete exclusion from its margin of the postorbital, which characterize *Gobiosuchus*, is in our opinion an equivocal protosuchian synapomorphy.

It should be noticed, however, that *Gobiosuchus* also exhibits a few derived characters, which are synapomorphic for the Mesoeucrocodylia, and these are: (1) the prefrontal pillar abutting on the palate; (2) the loss of the prearticular, and (3) more than two longitudinal rows of dorsal osteoderms. But, obviously, the number of protosuchian synapomorphies in *Gobiosuchus* outnumbers the mesoeucrocodylian ones. Because a detailed cladistic analysis of the Protosuchia was beyond the scope of this paper, we have here refrained from suggesting any closer relationships of *Gobiosuchus* within that taxon.

## Mode of life

Many of the unusual features of the skull, postcranium and armour of *Gobiosuchus* may suggest a mode of life different from that of most crocodylians and they deserve a functional interpretation. Small, sharp, closely set teeth suggest a small, relatively soft kind of prey, e.g. invertebrates or small vertebrates. The entrance to the throat was obviously very narrow: the widest posterior distance between the mandibular rami equals 15 mm. This suggests that any larger prey, e. g. adults of small vertebrates – lizards and mammals – known from the same strata, should be first dismembered.

In spite of the fact that the posterior processes of the squamosals are very long and overhang the craniomandibular articulation, a relatively wide gape of the jaws was possible (which, however, contradicts the suggested small prey), because the retroarticular process is absent.

Because of the mandibular articulation, placed almost at the level of the occiput, and the reduced retroarticular process, the *m. depressor mandibulae* was short and almost vertically directed; this may suggest quick action. The closure of the supratemporal fenestrae, remnants of which are present in the form of pits on the ventral surface of the skull roof, evidences that the *m. pseudotemporalis* was reduced. That corresponds to the situation in some extant short-snouted crocodylians (Iordansky 1964; Schumacher 1973), in which this feature is correlated with the enlargement of the *m. pterygoideus anterior*. According to Iordansky (1964), it suggests a quicker or stronger muscle contraction. Whether this was the case in *Gobiosuchus* we cannot be sure.

Unlike other crocodylians, no torsion between the mandibular rami was possible, because of the complete fusion of the mandibular symphysis.

The proportions of different segments of the body used for the reconstruction (Fig. 1) have been either directly measured on the specimens (skull and neck) or estimated (trunk and tail) on the basis of the length of the individual vertebrae preserved and assuming that the number of presacral vertebrae was the same as in other crocodylians (24 according to Hoffstetter & Gasc 1969). The length of the neck equals that of the skull, which is unusual among crocodylians. The trunk length, as estimated, is slightly more than 150% of the skull length. We have arbitrarily assumed that the tail was as long as the rest of the body, as it is in *Protosuchus* (Colbert & Mook

1951) and more primitive crocodylomorph reptiles. The hind limb length (femur + tibia) is estimated as 117% of the trunk length and 180% of the skull length. The forelimb length (humerus + radius) is estimated as 86% of the trunk length and 132% of the skull length. The forelimb length is 75% of the hind limb length. Compared with *Protosuchus richardsoni*, which is considered a long-limbed crocodyliform, *G. kielanae* has even longer limbs in relation to its trunk length. Somewhat similar limb proportions are found among sphenosuchians.

In spite of the great length of the neck in *Gobiosuchus*, its flexibility was restricted laterally and dorsoventrally by a limited mobility between the successive transverse rows of dorsal and ventral osteoderms and by the elongated cervical ribs. Additionally, there was almost no mobility between the skull and neck, because of the lateral expansion of the nuchal osteoderms, which seem to contact tightly the posterior edge of the skull roof and fill most of the space between the long posterior processes of the squamosals. It is evident, that the skull could only be moved laterally, together with the neck. Most probably elevation of the head alone could not be achieved. At the maximum flexion between particular neck segments, the lateral movement of the neck plus the skull, acting as a single unit, followed a broad arc. Most of the mobility of the neck region occurred in the area between the neck and trunk, just anterior to the pectoral girdle. The long neck enabled the animal to inspect an extensive area, e.g., when searching for food.

The articulation between the zygapophyses of the thoracic vertebrae was in a nearly horizontal plane, which allowed only a lateral flexion of the trunk. However, the extent of the lateral bending of the trunk was restricted by a limited mobility between elements of the armour.

The tail was round in cross-section, rather long, but its length cannot be ascertained. It was almost stiff, being completely encased by the armour and only a slight flexing was possible in lateral and dorsal directions.

The medially deflected proximal articular heads of the humerus and femur, as well as the rather straight shafts of these bones, indicate that the limbs could be held in an erect position (Parish 1987), and the body was held off the ground during locomotion, provided that the glenoid faced posteroventrally and the acetabulum laterally, which is probable but cannot be ascertained in our specimens.

There are very few ridges and processes on limb bones for muscle insertions, with the exception of the deltopectoral crest on the humerus. The high proximal position of the crest would speak in favour of a quick, but weak muscle action of the forelimb. There is no fourth trochanter on the femur and this may be linked with a weak development of *m. caudifemoralis*, which in amphibious crocodylians is used to move the tail for swimming. The functional meaning of the stiff bony armour around the limbs is unclear. Maybe, it conferred greater rigidity and strength to the long, slender limbs. Although the regions of the elbow and knee joints are not preserved, we presume that some flexibility had to be possible there. Either these regions were completely devoid of armour, or there were some specially modified scutes, similar to the articular scutes found in the region of the shoulder and hip joints.

As other (all?) protosuchians, *Gobiosuchus* was a long-legged, terrestrial animal, which is furthermore indicated by the round cross-section of its tail, unsuitable for efficient locomotion in water, and the limited mobility of its neck preventing the backward tossing of the head and speaking against the aquatic feeding (Ross & Meyer 1984).

There is an apparent contradiction between the elongation of the limbs, which would suggest a rapid terrestrial progression and the great development of the bony armour, which, although probably not too heavy, must have influenced locomotion by increasing inertia and then the metabolic cost. It cannot be excluded that the purpose of the long limbs was to keep the body high above the ground, and, to a lesser extent, to ensure a fast locomotion. The role of the armour may not have been purely defensive, it may as well have played a physiological role, e.g. reducing water loss in a dry environment. This extensive development of osteoderms may have also intervened in the support of the axial skeleton as mentioned for *Protosuchus* by Frey (1988).

According to Lefeld (1971), Sochava (1975) and Jerzykiewicz & Russell (1991), the environment of *Gobiosuchus* was semiarid, with dunes and ephemeral ponds and streams in the interdune areas. The accompanying vertebrate fauna includes terrestrial vertebrates: small mammals, lizards, turtles and a small mesoeucrocodylian *Shamosuchus* Mook, 1924; dinosaurs are represented by medium-sized herbivores, *Protoceratops*, *Pinacosaurus*, *Oviraptor* and the carnivores, *Velociraptor* and *Sauromithoides*. Although tall trees were probably not common components of the flora, low-growing plants must have been abundant enough to sustain the large populations of *Protoceratops*.

To sum up, *Gobiosuchus* was probably a small terrestrial predator, which fed mainly on insects and other small invertebrates, caught among a low vegetation, which covered the more humid parts of an otherwise arid environment.

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## Anatomia i pokrewieństwa późnokredowego krokodyla z Mongolii *Gobiosuchus kielanae* (Protosuchia)

HALSZKA OSMÓLSKA, STEPHANE HUA i ERIC BUFFETAUT

### Streszczenie

Praca zawiera opis czaszki i szkieletu pozaczaszkowego prymitywnego krokodyla, *Gobiosuchus kielanae* Osmólska, 1972, żyjącego pod koniec okresu kredowego, w kampanie, na terenie dzisiejszej pustyni Gobi w Mongolii. Był to bardzo mały (ok. 60 cm długi), długonogi krokodyl, o długiej, smukłej szyi, całkowicie okryty pancerzem z połączonych ze sobą skostnień skórnych. Małe rozmiary oraz małe, ostre zęby wskazują, że jego pożywieniem mogły być owady i inne drobne bezkręgowce, a także małe kręgowce – jaszczurki i ssaki. Szczegółowa analiza anatomiczna wykazała obecność u *G. kielanae* cech synapomorficznych Protosuchia, co potwierdza wcześniejsze, tymczasowe zaliczenie rodzaju *Gobiosuchus* (Osmólska 1972) do tej najprymitywniejszej grupy krokodyli. W budowie czaszki *Gobiosuchus* są też bardzo liczne cechy autapomorficzne, różniące go od wszystkich innych krokodyli, a także kilka cech charakteryzujących bardziej zaawansowane krokodyle z grupy Mesoeucrocodylia. Wobec przeważającej ilości cech charakterystycznych dla Protosuchia, cechy te uznano za konwergencje. *G. kielanae* jest najkompletniej zachowanym z dotychczas poznanych przedstawicieli Protosuchia. Jest również stratygraficznie najmłodszym znanym przedstawicielem tej słabo poznanej i nielicznej grupy prymitywnych krokodyli, gdyż większość jej przedstawicieli żyła podczas okresu jurajskiego, tylko nieliczne gatunki znane są z osadów wczesnej części okresu kredowego.