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## **A giant crocodile in the Dubois Collection from the Pleistocene of Kali Gedeh (Java)**

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## **Abstract**

The fauna of the Pleistocene *Homo*-bearing sites of Java has been well known for more than a century. A recent revision of the crocodylian remains confirmed both the validity of *Gavialis bengawanicus* Dubois 1908 and the synonymization of *Crocodylus ossifragus* Dubois 1908 with *Crocodylus siamensis* Schneider 1801. Here we report on a still unpublished crocodylian specimen collected by Dubois in the latest early Pleistocene of Kali Gedeh that can be tentatively referred to the genus *Crocodylus*. The size of the specimen, the approximately 1 m long lower jaw in particular, indicated that this crocodile attained a total length of about 6 or 7 meters. Along with specimens from the Plio-Pleistocene of Africa, this material provides evidence for gigantism in *Crocodylus*. It is not clear if the “temperature-size rule” applies to fossil crocodylians or not, but due to the growing interest in predicting future temperature-related size changes of the extant organisms, it would be interesting to study in detail the past reaction to temperature changes of crocodylians and other terrestrial ectothermic animals.

**Key words:** *Crocodylus*, fossil, *Homo erectus* fauna, Pleistocene gigantism, temperature-size rule

## **ABBREVIATIONS**

### **Institutional abbreviations**

**CD**, ‘Collectie Dubois’, Naturalis, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands;

**KNM**, The National Museums of Kenya, Nairobi, Kenya; **MB**, Museum für Naturkunde der

Humboldt Universität, Berlin, Germany; **RMNH**, Naturalis, Nationaal

Natuurhistorisch Museum, Leiden, The Netherlands.

### **Other abbreviations**

**HL**, head (skull) length measured sagittally from the tip of the premaxillae to the back of the skull

table; **ML**, mandible length measured from the anterior tip of the dentaries to the intersection of the

sagittal plane with a line drawn between the posterior tips of the retroarticular processes; **TL**, maximum total length of the body (from the tip of snout to the tip of the tail).

## **INTRODUCTION**

Because scientific data are often mixed with anecdotal reports, the maximum size of living crocodylians is problematic. Many accounts of very large crocodylians exist (e.g. Trutnau and Sommerlad, 2006, mention specimens over 7 m), but the data do not come from peer-reviewed literature and should be considered with caution. Whitaker & Whitaker (2008) recently summarized and discussed the available evidence. Curiously enough, the evaluation of “who is the biggest?” is not related to the TL of living specimens, but mostly to the HL of skeletons preserved in museum collections. This means that TL has to be estimated from HL. The same authors questioned the “1:7 hypothesis” according to which TL can be estimated as being 7 times HL. It seems that such ratio approximates well TL of specimens smaller than 4 m (TL) but that a different ratio (possibly 1:9) should be applied to larger specimens because of allometric growth. Moreover, it is likely that these ratios can be applied only to brevirostrine taxa and not to longirostrine forms (as *Gavialis* and *Tomistoma*), for which a ratio of about 1:6 seems more appropriate.

Among the extant crocodylian species, the largest skulls are those of *Tomistoma schlegelii* (Müller 1846) (HL 84.0 cm), *Gavialis gangeticus* (Gmelin 1789) (HL 77.3 cm) and *Crocodylus porosus* Schneider 1801 (HL 76.0 cm). Due to the different ratios to be applied to brevirostrine and longirostrine taxa (Whitaker & Whitaker 2008; see also Sereno et al. 2001) such ranking based on HL does not necessarily reflect the one based on TL. Apparently, *C. Crocodylus* (Brochu & Storrs 2012). Based on regression analyses available for the extant *Crocodylus niloticus* Laurenti 1768 and *C. porosus* (involving again HL; for details see Brochu & Storrs 2012) the TL of *Crocodylus thorbjarnarsoni* is estimated to be up to 7.5 m (HL 85 cm).

Here we report additional evidence of a giant Pleistocene crocodile, this time from the Indonesian island of Java. Fossil crocodylians from Java were originally described by Dubois (1908) who

erected the new species *Crocodylus ossifragus* Dubois 1908 and *Gavialis bengawanicus* Dubois 1908. *Crocodylus ossifragus* was later synonymized by Müller (1923) with the extant *Crocodylus siamensis* Schneider 1801. Delfino and de Vos (2010) recently revised the two species by studying the collections at Naturalis (Leiden, The Netherlands) and the Museum für Naturkunde der Humboldt–Universität (Berlin, Germany) and confirmed the validity of *G. bengawanicus* as well as the synonymization of *C. ossifragus* with *C. siamensis*. However, in the Dubois Collection at Naturalis there is a still-unpublished crocodylian partial skull and lower jaw from Kali Gedeh that, although currently labeled as *C. ossifragus*, are significantly larger than *C. siamensis* known from the same horizon. This paper aims at describing the cranial material from Kali Gedeh, discussing its taxonomic allocation, and providing evidence for a second case of gigantism among fossil *Crocodylus*. The large size of the Pleistocene representatives of some extant taxa (or taxa closely related to them) is discussed.

## **SYSTEMATIC SECTION**

Crocodylidae Cuvier 1807

*Crocodylus* Laurenti 1768

*Crocodylus* sp.

(Figs 1, 2)

### **Referred Material**

CD 14a and 14b, an incomplete skull and mandible.

### **Occurrence**

Kali Gedeh, Java, Indonesia. Trinil Haupt Knochenschicht Faunal

Unit, latest Early Pleistocene (van den Bergh 1999; de Vos & Long 2002).

### **Description**

The external surface of both the skull and the mandible is heavily damaged. They are irregularly and deeply exfoliated, as well as encrusted by a hard whitish concretion. Despite this, a very strong

ornamentation, represented mainly by crests up to several millimeters thick, is clearly present.

Sutures between bones, as well as foramina and other fine anatomical details, are not visible. Only the symphysis suture is partly visible.

CD 14a includes three large skull fragments joined together, as well as 10 poorly preserved fragments, all of which probably belong to the same specimen. The three main fragments represent the incomplete snout of a large crocodylian (Fig. 1A). Premaxillae, maxillae, and possibly the tip of the lacrimals and prefrontal (or even the frontal process) are preserved. The anterior portion of the palatines could be present, although the palate seems to be broken off posterior to the presumed fifth maxillary alveolus. Premaxillae are particularly wide respect to the rest of the snout. They show four alveoli (it is likely that second alveolus was crowded out during ontogeny) and a large pocket for the first dentary tooth (partly filled by matrix) located between the first and second alveolus (Fig. 2B). A fragment of first dentary tooth is stuck in the pocket of the right premaxilla. It is not clear whether these pockets completely pierced the premaxillae because a concretion on the external surface of the premaxillae hinders any firm conclusion, though this concretion could indicate a hole filled with matrix. The alveoli do not bear complete teeth (a partial tooth is preserved in the third right alveolus). The third alveolus is the largest having the right one a mesiodistal length of about 4 cm. The foramen incisivum does not preserve natural edges, but its position is quite far from the premaxillary tooth row and placed at the level of the largest alveolus. The external naris is drop-shaped and large in absolute size (9 cm long and 6.5 cm wide), but proportionally much smaller than in the *C. siamensis* specimens from Trinil (see Delfino & de Vos 2010). The narial rim is not elevated into a ridge but quite rounded. In dorsal view, a deep constriction is present at the premaxillo-maxilla suture. On the left side, a part of the fourth dentary tooth still lies in its occlusal position in the lateral notch between the premaxilla and the maxilla (Fig. 2C). On the right, a small tooth fragment (circular in section and without a central hole) is preserved in the same position, but surrounded by matrix. The poor preservation of the maxillae does not allow a precise count of the alveoli because teeth are not present. It seems that at least four alveoli are preserved on the right

side, whereas at least 10 alveoli should be represented on the left one. The largest alveolus appears to be the fourth and not the fifth, but this is probably an effect of the poor preservation of the area. Two extremely prominent preorbital ridges are developed on the dorsal surface corresponding with the last preserved tooth position: they are distinctly raised above the surrounding surface, vaguely symmetrical, slightly converging medially and approximately 10 cm long. The posterior end of the left ridge could coincide with the anterior edge of the corresponding orbit, but the matrix hides the morphology of the area. CD 14a (when the three fragments are juxtaposed) has approximately a maximum length of 62 cm and maximum width of 35 cm. Among the other isolated fragments, one has a maximum length of 23.7 cm and maximum width of 15.3 cm and is identifiable as the paired and partly preserved palatines (to which could be attached a small portion of the pterygoids). The lateral edges of this fragment show a smooth surface that probably constituted the border of palatal fenestrae. Fine anatomical details are not preserved. The allocation of the remaining unidentified fragments to a single skull is here accepted on the basis that they were presumably found together in the field (the size is nevertheless congruent).

CD 14b includes a few large mandible fragments (Fig. 1B-D). The right ramus is nearly complete (except the retroarticular process), whereas the left one is represented by part of the dentary, the angular, the surangular, and a rather complete articular. The left splenial is not preserved. The left dentary is preserved up to the eleventh alveolar space. Two maxillary teeth are laterally attached to the right dentary. Fragments of the quadrate condyles are attached to both articular surfaces of the mandible. The edges of the first alveoli are not detectable with precision, but it is possible to state that the symphysis reaches approximately the anterior edge of the fifth alveolus. The first, fourth, and eleventh alveoli are the largest; the first or the fourth are larger than the eleventh. The ninth interalveolar space corresponds to a large diastema. The right dentary seems to host fifteen tooth positions (but the preservation hinders a precise count and teeth positions between the fifth and the presumed tenth alveolus are doubtful). Most of the retroarticular process is broken off. The area between the foramen intermandibularis caudalis and the mandibular adductor fossa is mostly



missing. The external mandibular fenestra is relatively small. In dorsal view, the mandible is particularly narrow and long. The preserved portion of the right mandibular ramus has a ML of about 100 cm, but taking into consideration the posterior fragment of the left jaw that preserves a nearly complete retroarticular process, the ML should have reached about 105 cm at least.

### **Taxonomic Remarks**

CD 14a and 14b are clearly part of a single skull because fragments of the mandible are preserved along with the maxilla and vice-versa. The poor preservation of the specimen hinders any precise comparison and, despite a general crocodylid appearance (the lower jaw is clearly not that of gavialid or of a tomistomine), there are no characters allowing a sound generic identification. The current label identification as *Crocodylus ossifragus*, that is to say *Crocodylus siamensis* (according to Müller 1923; Delfino and De Vos 2010), or the previous identification as *Crocodylus porosus*, reported by a old label associated to the specimen, are not clearly supported by the morphological characters shown by the specimen. An exception could be the extremely prominent preorbital ridges which characterize both the species and that are also clearly present in the much smaller fossils of *C. siamensis* from several localities in Java (Delfino & de Vos 2010). Prominent preorbital ridges are present, but not exclusively, in most of the *Crocodylus* species (for a synthesis of the distribution of this character among extant and fossil species see for example the character matrix of Brochu 1999). The absence of any autoapomorphy of *Crocodylus* (Brochu 2000) hinders a confident identification of CD 14, but taking into consideration the presence of well developed preorbital ridges, the age of material, its provenience and its associated fauna it is tentatively referred to *Crocodylus* sp.

Notably, the acute angle delimited by the mandibular branches of CD 14b is comparable to that of fossil *C. siamensis* from other Javan localities (e.g. CD 18, MB R 1958; Delfino & de Vos 2010:fig. 27S and 28S) and to extant *C. siamensis* (e.g. RMNH 21695). Moreover, the five isolated teeth

from Kali Gedeh (CD 33 and CD 8), previously referred to *C. siamesi* (Delfino & de Vos 2010), are much smaller in size than those of CD 14 and it is not clear if they belonged to same taxon.

## DISCUSSION

### The size of the giant from Kali Gedeh

The skull and lower jaw CD 14a and 14b testify for the presence of a very large crocodile. How large is difficult to tell. The estimated ML of at least 105 cm indicates the presence of a specimen larger than the largest extant *Crocodylus*, a specimen of *C. porosus*, whose ML has been reported to be 98.3 cm (Whitaker & Whitaker 2008). The ML of *C. thorbjarnarsoni* KNM-ER 1683 (Brochu & Storrs 2012, fig. 1D), a little smaller than the largest available specimen (KNM-ER 1682) of this species, appears to be of about 100 cm. Assuming that the HL/ML ratio of 0.77 reported by Whitaker and Whitaker (2008) for *C. porosus* could be applicable to *C. thorbjarnarsoni*, the HL of 85 cm recorded for KNM-ER 1682 should correspond to a ML of 110 cm, therefore slightly higher than that of the lower jaw from Java. Nevertheless, the size of CD 14 is in the range of that of the largest fossil and extant *Crocodylus* specimens. Applying the above mentioned ratio to the fossil material from Java, a ML of about 105 should correspond to a HL of about 80 cm which is a considerable size even if smaller than that of largest specimen of *C. thorbjarnarsoni*.

On the basis of the regression analyses applied by Brochu and Storrs (2012), the Java remains could correspond to a crocodile with TL of about 6 m, but taking into consideration that such regressions can underestimate TL of very large specimens up to 20%, its size could reach about 7 meters. If the skull and lower jaw CD 14a and 14b would belong to *C. siamensis*, this would imply that this species attained in the past a size much larger than at present, because it is now a medium size crocodylian with males reaching a TL of up to 4 m (Simpson & Bezuijen 2010). Even if CD 14 pertains to *C. porosus*, it would be a remarkably large animal and larger than any known modern specimen (Whitaker & Whitaker 2008).

Crocodile specimens of the size of CD 14 were probably the largest predators on Java and, in analogy to what has been suggested for Africa (Brochu & Storrs 2012), they posed serious threats to our ancestors that inhabited the island.

### **Pleistocene giants**

The fact that very large size arose both in Africa (Plio-Pleistocene; Brochu and Storrs 2012) and Asia (early Pleistocene, this paper) is interesting. The large size of Pleistocene representatives of extant taxa (at specific or generic level) is a remarkable phenomenon that has been reported several times for mammals (among others, Davis 1981; Klein 1986; Klein & Scott 1989; Smith *et al.* 1995; Guthrie 2003; Raia *et al.* 2012) but much less frequently for ectothermic terrestrial vertebrates such as reptiles and amphibians, although paleoherpetologists working with Pleistocene faunas have sometimes expressed the suspicion that extant taxa were larger in the past. Holman (1998:205) wrote that “it is well known that Pleistocene amphibian and reptile species are sometimes larger than their modern equivalents”. An example includes large specimens of *Rana temporaria* Linnaeus 1758 from the Pleistocene of Europe that were previously referred to an extinct species, *Rana mehelyi* Bolkay 1911, and later synonymized with *R. temporaria* despite the current smaller size of the latter (Rage 1972). Pleistocene turtles are often larger and their shell thicker than their Recent representatives. As reported by Das (1991, 1997), the relatively large *Geoclemys sivalensis* Tewari and Badam 1969 from the Pleistocene of India is a synonym of the extant *Geoclemys hamiltonii* (Gray 1831) and *Hardella isoclina* Dubois 1908 from the Pleistocene of Java (from the same localities where *C. siamensis* occurred, but not at Kali Gedeh) is actually a large sized *Mauremys*. The same author (Das 1997), stated that also *Melanochelys tricarinata* (Blyth 1856) from the Pleistocene of India (see Lydekker 1889) is significantly larger than its living representatives. The tortoise *Testudo hermanni* was much more robustly-built and large in the Pleistocene of Italy than nowadays (Delfino & Bailon 2000; Delfino 2006). As far as congeneric species are considered, worth mentioning is the case of the monitor lizard *Varanus prisca* (Owen 1859) that inhabited

Australia during the Pleistocene: its TL significantly exceeded that of the largest living members of the genus and it represents the largest known terrestrial lizard (Molnar 2004; Hocknull *et al.* 2009).

Holman (1998) mentioned the large size of Pleistocene anguid lizards (genera *Anguis* and *Pseudopus*) from Europe.

As for crocodylians, it has to be mentioned that the selective killing of the largest specimens operated by humans could have severely reduced the frequency of the genes favouring gigantism (Whitaker & Whitaker 2008) and that therefore extant populations do not express the largest sizes that characterized them in former times. Nevertheless, there is a growing concern about the fact that climate change influences the body size of organisms and several lines of evidence indicate that an increase of temperature leads to a decrease in body size, the well known “temperature-size rule” (for a perspective on the topic see Sheridan & Bickford 2011). For endothermic animals, this temperature-mediated size decline agrees with the Bergmann’s rule which predicts an inverse correlation between temperature and mean body size (Teplitsky *et al.* 2008), but most ectothermic animals show the same effect, especially the aquatic species but also the terrestrial ones, because they mature at smaller body size (Forster *et al.* 2012).

To put this another way: because of the “temperature-size rule” we can expect to find large size representatives of extant species during the cold phases of the Pleistocene. As for the herpetofauna, there are controversial evidences. The above mentioned cases of Pleistocene amphibians and reptiles apparently support this hypothesis but the precise climatic parameters of the layers that yielded the fossil material should be checked. Experimental analyses on living amphibians (Bizer 1978; Morrison & Hero 2003; Measey & Van Dongen 2006; Reading 2007) and reptiles (Angilletta *et al.* 2004; Cruz *et al.* 2005) support the applicability of the Bergmann’s rule to some members of the herpetofauna but at this stage it is not possible to draw general conclusions because of several exceptions (Olalla-Tárraga *et al.* 2006; Olalla-Tárraga & Rodríguez 2007; Terribile *et al.* 2009).

Holman (1998) proposed that the large size of some Pleistocene amphibians and reptiles could be

explained by the fact that they responded to the reverse of the Bergmann's rule (and therefore he assumed that they were all coming from warm interglacials).

It is not known how crocodylian size reacts to temperature changes. Erickson and Brochu (1999) demonstrated that the extinct *Deinosuchus* attained its gigantic size (8-9 m) through prolonged growth, but this was not studied in relation to temperature. The works by Markwick (1994, 1998a,b) concerning crocodylians and temperature are focused on palaeoclimate and palaeobiogeography, but do not consider size variations in relation to temperature. In any case, as far as the large sized crocodylians from Kenya and Java are concerned, it should be tested if they really lived in climatic conditions significantly different from the extant ones.

In conclusion, the past reaction of crocodylians and other terrestrial ectothermic animals to the temperature changes has not been studied in detail, but when done this would provide relevant information because, as pointed out by Sheridan and Bickford (2011:401), the analysis of the fossil record "could help quantify the expected change in size of organisms as a result of current climate change".

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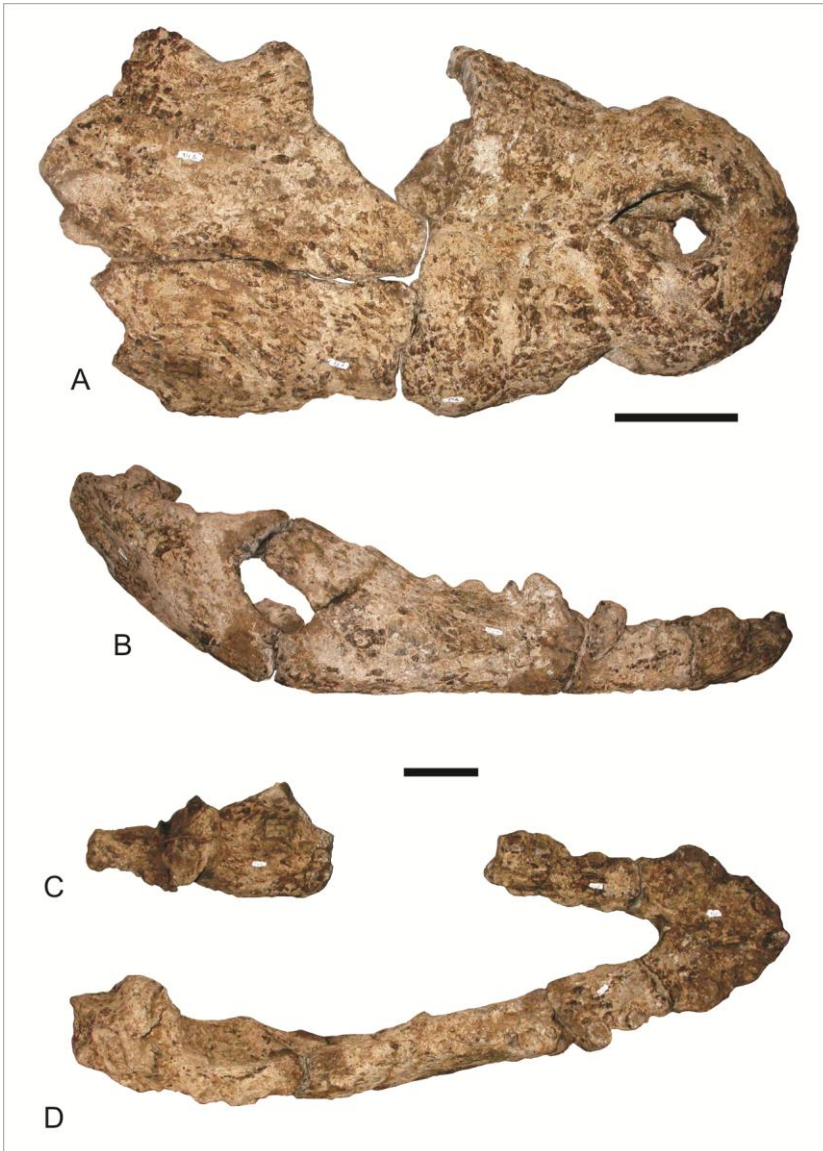
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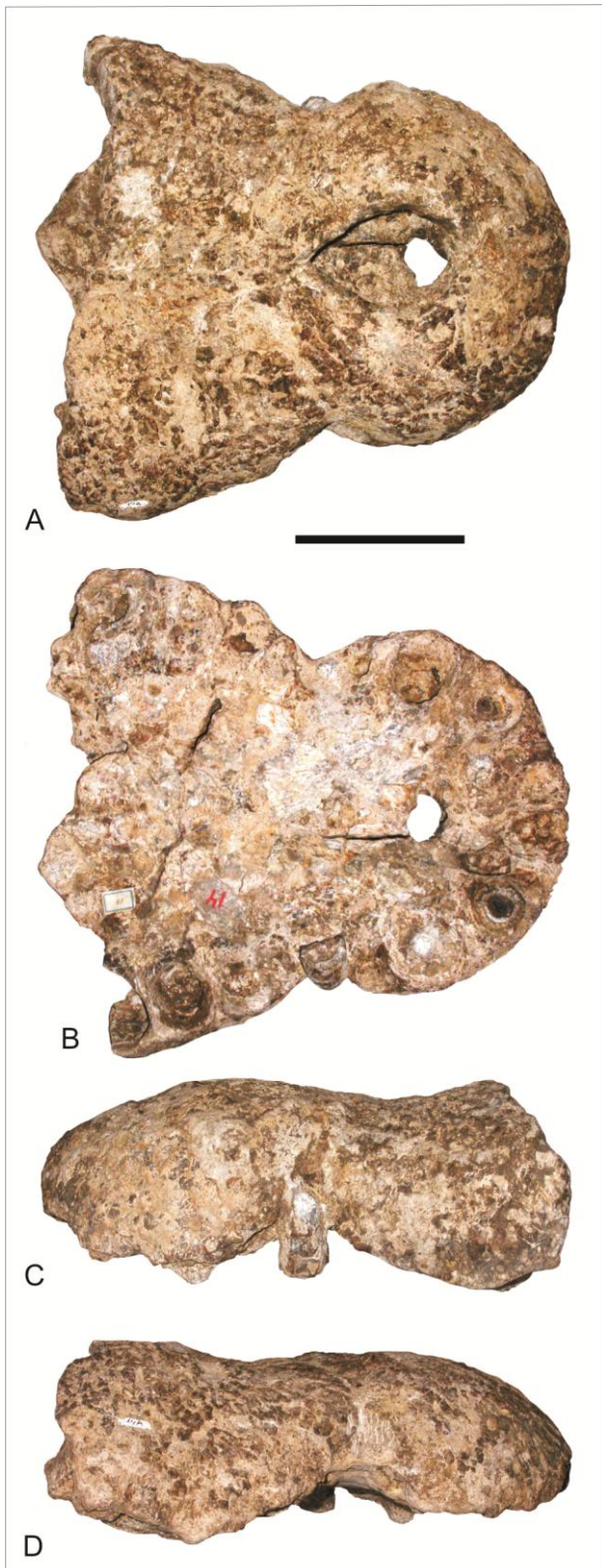
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## Figure Captions



**Figure 1** *Crocodylus* sp. from Kali Gedeh (Java). A, preserved portion of the skull in dorsal view (CD 14a). B, lower jaw in left lateral view (CD 14b). C posterior region of the left mandibular ramus in dorsomedial view (CD 14b). D, portion of the lower jaw preserved in anatomical connection, dorsal view (CD 14b). Scale bars equal 10 cm.



**Figure 2** *Crocodylus* sp. from Kali Gedeh (Java). A–D, anterior region of the rostrum in dorsal, ventral, left lateral, and right lateral views (CD 14a). Scale bar equals 10 cm.