

## THE 'DWARF' CROCODILES OF THE PURBECK FORMATION, DORSET: A REAPPRAISAL

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**ABSTRACT.** *Nannosuchus gracilidens* and *Theriosuchus pusillus* were described by Owen, who believed that they were dwarf goniopholid crocodiles, adapted for preying on the contemporary small mammals. Several skull characters, which are now known to alter during life in modern crocodiles, were investigated in these 'dwarfs'. A number of these characters in *Nannosuchus* indicate that it is merely a juvenile form. Furthermore, since a larger form from the same beds, *Goniopholis simus*, exhibits several specific features found also in *Nannosuchus*, it is concluded that the latter is the juvenile of *G. simus*. Both the skull morphology of *Theriosuchus* and the presence of similar, larger remains in the same bed, indicate that it, too, is a juvenile. Reappraisal of its characters shows that it belongs to the family Atoposauridae and not to the Goniopholidae. The goniopholids have been suggested as possible ancestors of the later, eusuchian crocodiles. However, signs of progression towards eusuchian characters are unknown in the goniopholids, but are found in such atoposaurids as *Theriosuchus* and a recently discovered form from Texas. The Atoposauridae therefore appear to merit investigation as possible ancestors of the Eusuchia. The meaning and usage of the term 'dwarf' are briefly discussed.

THE Mesosuchia, predecessors of modern crocodiles which inhabited the oceans and river complexes of late Jurassic times, are not uncommon as fossils. By this period they were already differentiated into long-snouted and short-snouted varieties, and all forms variously possessed most of the typical crocodilian characters such as:

1. A false palate formed by the premaxillae, maxillae, and palatines.
2. A pes modified to allow movement between the tarsals.
3. An armour of dermal osteoscutes.
4. A 'cranial table'.
5. A pubis totally excluded from the acetabulum.
6. Amphicoelous or amphiplatyan vertebrae.

They were distinguished from their Tertiary descendants, the Eusuchia, in that these more advanced forms had incorporated the pterygoids into their false palate, and had evolved procoelous vertebrae.

Members of one particularly widespread family of mesosuchians, the Goniopholidae, are the subject of this paper. In particular, the species *Nannosuchus gracilidens* and *Theriosuchus pusillus* will be discussed. These were originally discovered and collected from the freshwater limestones of the Purbeck Series of Dorsetshire (south-west England) by William Husband Beckles Esq., and later described and figured by Sir Richard Owen (1879a).

The outstanding feature of these two crocodiles is their extremely small size, which Owen interpreted as 'dwarfism'; the evidence for this view will be examined critically. This examination leads to a reappraisal of Owen's assignment of both the genera to the Goniopholidae; an attempt has also been made to reconstruct something of the environment and habits of these crocodiles, and to discuss them in the context of the evolution of the Eusuchia as a whole.

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## STRATIGRAPHY AND PALAEOECOLOGY

In late Jurassic times the 'Purbeck Basin' lay just to the west of the 'Wealden Basin' and the two formations represent a continuous depositional series in a slowly changing environment. Nevertheless, detailed study has been almost confined to the succeeding Wealden formation.

It is clear from the work of Taylor (1963), Casey (1963), and Allen (1959) that the area had been covered for some time by a sea which extended over southern England and most of France, and analysis of the ostracod fauna shows that by Purbeck times this sea had receded, leaving behind brackish and, finally, freshwater conditions. Casey shows that a large land mass was present to the north, spanning an area roughly from London to Belgium. Rivers draining this land mass formed a low-lying deltaic swamp (probably similar to present-day mangrove swamps) with alternating euryhaline and freshwater faunas. The sea made only a few temporary incursions into this lagoonal complex. One of these, however, was very widespread and caused the breakdown of the northern land barrier. This marine invasion is represented by an oyster bank, the so-called 'Cinder Bed', so extensive and so easily traceable that Casey has suggested using it as a marker horizon for the boundary of the Jurassic and Lower Cretaceous. His suggestion has been adopted by the British Mesozoic Committee, and the Lower Cretaceous is now regarded as beginning immediately above the Cinder Bed.

About 10 ft. below the Cinder Bed, still well within the freshwater limestones and lacustrine shales of the typical Middle Purbeck sequence, lies the horizon in which the 'dwarf' crocodiles are found. The original locality is now within private grounds, and correlation of the sections worked out by early geologists in the area (Austen 1852, Damon 1884) with the present exposure on Durlston Head is very difficult as the actual bed is mentioned by name (the 'Feather Bed') only in these sections. Comments on the lithology of this bed will therefore be confined to the blocks containing the fossil material.

The 'Feather Bed' is a fine-grained, pale grey, bioclastic limestone composed of débris (largely of gastropods) and an almost pure calcareous matrix. The argillaceous content is small and there are a few fragmentary plant remains. It is fairly finely bedded and there are traces of lamination within each bed. This type of bed appears to fall into Taylor's (1963) category of 'on delta' deposits, in which sedimentation is said to be extremely slow.

On the upper bedding planes the vertebrate material is undistorted and only slightly crushed, but between these planes is a 'bone soup' of crushed and distorted remains, disarticulated and, for the most part, unrecognizable. There is practically no interstitial matrix. Between bone layers the limestone is a calcareous ooze, and it seems likely that the 'Feather Bed' may represent an area where material dropped out of suspension and accumulated slowly on the delta floor, having been brought there by one or many rivers.

*Materials.* The two crocodilian species with which this paper is concerned are *Nannosuchus gracilidens* Owen and *Theriosuchus pusillus* Owen. All the material is in the Department of Palaeontology, British Museum (Natural History).

The remains of *Nannosuchus* consist of one fairly complete skull showing dorsal view only (the holotype—No. 48217), several incomplete lower jaws with teeth (Nos. 48244, 48329, 48217, and 48328), some isolated dermal scutes and other post-cranial remains in rather poor condition.

The remains of *Theriosuchus* include one well-preserved, fairly complete skull (the holotype—No. 48330), somewhat crushed but still three-dimensional with a partly exposed palate and a firmly attached lower jaw; a partially articulated skeleton (No. 48216); several blocks containing fragmentary or crushed material (Nos. 48273 and 48260); several incomplete lower jaws (Nos. 48240 *a* and *b*, 48302 and 48260); and an isolated femur (No. 48333). Material from the British Museum (Natural History) collection of Recent *Crocodylus* spp. was used for comparison.

*Methods.* Preparation in acetic acid was attempted and found to be unsuitable for two reasons. First, the material below the bedding plane, when exposed by this method, was found to be too crushed to be of value. Second, even the exposed material was found to be riddled with minute fractures and microcracks which were not apparent until the block was developed and the material isolated. It was not possible to prepare the material mechanically as the skulls and skeletons are important typespecimens which have been figured.

#### THE 'DWARF' CROCODILES

The new small crocodiles from the Purbeck beds were discussed by Owen in two papers published in 1879. In one (1879*a*) the morphology of both genera is given in some detail, and this is followed by a section in which their ecological relationships to the contemporary small mammals are discussed. In the other paper *Theriosuchus* alone is described; this is followed by an almost identical discussion of its ecology.

In these papers, Owen's main reason for regarding these genera as dwarf forms is that, in both genera, the specimens are all of uniformly small size, suggesting that this was the final, adult size. He then points out that these small crocodiles were contemporary with the small Mesozoic mammals, and suggests that the crocodiles may be dwarf forms which have become reduced in size, or dwarfed, in order to adapt to the size of this prey.

It is convenient to discuss first this ecological aspect of Owen's argument. It is certainly true that mammals do occur as an element in the varied vertebrate and invertebrate faunas of this horizon (Damon 1884). But, while Owen's suggestion may be correct, it is important to realize that, owing to the nature of the delta deposits, the fauna could well be a death assemblage, its members never being associated during life. Added to this, the work by Cott (1961) on *Crocodylus niloticus* indicates that young crocodiles feed upon invertebrates and fish, and prey upon mammals only later in life. This fact may be relevant to the possible feeding habits of the small fossil forms, whether or not these were dwarfs.

One of Owen's original reasons for believing that the two genera were dwarf forms was, as noted above, his assumption that the genera were of constant, small size. The validity of this assumption was first checked by taking measurements of a number of lower jaws (see Table 1). Where these were incomplete, the estimated original length is inserted in brackets.

From these series it may be seen that the sizes range from 4 cm. to 17 cm. in *Nannosuchus* and from 3.5 to 10.4 cm. in *Theriosuchus*. It is clear that Owen's belief that the specimens were of constant size is unfounded; there appear instead to be two growth series.

However, although the specimens are not of uniform size, even the largest is quite small and the genera may still be dwarf forms. It is therefore now necessary to attempt to establish whether these specimens show any specifically juvenile, or any specifically adult, features. Various characters of this kind may be found in Mook's (1921) work on

TABLE 1

<i>Nannosuchus</i>		
<i>Specimen No.</i>	<i>Incomplete jaw length (cm.)</i>	<i>Estimated complete length (cm.)</i>
48328	2.5	(4.0)
48244	8.0	(9.5)
48329	8.5	(9.5)
48217 (type)	12.0	
48217 (different individual)	12.0	(17.0)
<i>Theriosuchus</i>		
48240 (a, b)	2.8	(3.5)
48260	6.5	(7.5)
48330 (holotype)	7.2	(8.4)
48302	10.4	

individual and age variations in Recent crocodiles. A study of both Recent and fossil material in the British Museum (Natural History) both verified and amplified Mook's work. Six main characters were investigated, as follows:

1. *Skull ossification and rugosity.* Mook's growth series of Recent crocodiles showed, not surprisingly, that the degree of ossification and rugosity increased with age. In particular, the margins of the cranial table and orbits became overgrown in the older specimens.

2. *Development of the cranial table.* This second criterion taken from Mook's work was found to be of limited use, as the cranial table develops so soon after hatching that it is helpful in identifying only extremely young individuals.

3. *Closure of the sutures.* From examination of the growth series from the British Museum's collection, it was apparent that the sutures on the dorsal surface of the skulls became increasingly obscured in older specimens. In contrast, the palatal sutures remained clearly visible, and these therefore provided a less useful guide than the dorsal sutures.

4. *Size and shape of the supratemporal fenestrae.* The supratemporal fenestrae in crocodiles were found, as Mook discusses, to be slit-like in very young animals; they tended to widen out during ontogeny until at maturity they were roughly circular in shape. Young individuals also tended to have large orbits, and the size of the fenestrae relative to the size of the orbits changed throughout youth. In caimans, however, the supratemporal fenestrae were found to have a tendency to become smaller and sometimes to close up completely in old age.

5. *Ratio of pre-orbital to post-orbital length of the skull.* The changes in this ratio for *Crocodylus americanus* are shown in Table 2, taken from Mook's paper. Other comparative material studied gave similar results, though the growth series was not adequate for as complete a table of measurements as that below. It is clear that the snout tended to become relatively longer (compared with the post-orbital region) during life.

6. *Robustness of the teeth.* In all growth series observed, both by Mook and the

author, the teeth increased in girth with age and provided a general clue to the age of an individual.

TABLE 2

	(a) Length of post-orbital region (cm.)	(b) Length of pre-orbital region (cm.)	Ratio a/b
<i>Crocodylus americanus</i>			
Mus. Comp. Zool. No. 5002	3.0	3.3	0.909
Mus. Comp. Zool. No. 5008	3.7	5.2	0.711
Mus. Comp. Zool. No. 5007	4.5	7.0	0.642
Amer. Mus. No. 15182	6.5	12.6	0.515
Mus. Comp. Zool. No. 5032	7.2	14.8	0.486
Amer. Mus. No. 15175	9.7	20.8	0.466
Amer. Mus. No. 7120	11.8	26.0	0.453
Amer. Mus. No. 7132	12.0	27.8	0.431
Amer. Mus. No. 7121	12.2	28.1	0.433
Mus. Comp. Zool. No. 5391	12.5 (est.)	33.0	0.378
Mus. Comp. Zool. No. 10921	16.5	33.0	0.500
Mus. Comp. Zool. No. 13904	15.5	41.5 (est.)	0.373
Amer. Mus. No. 7139	17.0	53.0	0.320

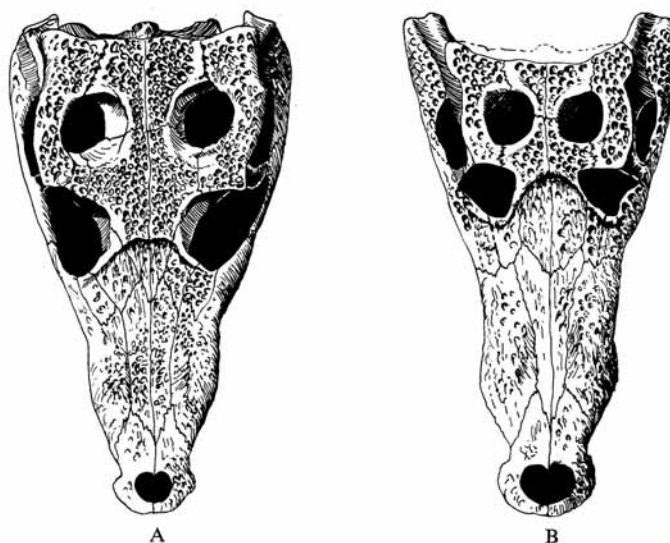
The condition of *Nannosuchus gracilidens* (text fig. 1a) with respect to the above criteria is as follows:

1. The skull is lightly ossified.
2. The cranial table is present but unthickened.
3. The sutures on the dorsal surface are relatively unobscured.
4. The supratemporal fenestrae do not possess that degree of rounding noted in mature Recent forms, and the orbits are relatively large.
5. Since only a single skull is known, its relatively short snout could be interpreted either as the juvenile stage of a long-snouted form, or as the adult of a short-snouted form. This character is therefore inconclusive.
6. The teeth of *Nannosuchus*, which are unfortunately disarticulated from the skull, are extremely slender and sharply recurved.

This evidence, which suggests that the skull of *Nannosuchus* is of a juvenile form, is not conclusive. Conclusive identification of *Nannosuchus* as a juvenile would require the discovery of a form whose morphology was in general similar to that of *Nannosuchus*, but which had such adult features as an increased degree of ossification, especially in the cranial table, less clear sutures on the dorsal surface, a more circular supratemporal fenestra, relatively smaller orbits and longer snout, and larger, more robust, teeth. Search for such a specimen revealed, among the larger Purbeckian goniopholids, the skull of *Goniopholis simus* (text fig. 1b) from the same horizon as *Nannosuchus*, and which was also originally described by Owen (1878). Owen's reasons for separating *Nannosuchus* from *Goniopholis* were its smaller size and more slender teeth—features which, on the basis of the above survey, cannot be regarded as taxonomically reliable. Furthermore, *Goniopholis* is extremely similar to *Nannosuchus* in details of the skull dermal bone-pattern, in the shape of the external naris and in the shape of the cranial table. Also, both genera possess an identical shallow curved ridge on the frontals,

continuous with the anterior margin of the orbit; this feature was noted by Owen and termed the 'semi-lunar ridge'. Finally, the differences between the two forms are, both in nature and in degree, readily explicable as being due to growth changes, as follows:

1. The supratemporal fenestrae of *Goniopholis simus* have the typical circular outline of a mature individual.
2. The orbits are relatively smaller in *Goniopholis simus*.
3. *Nannosuchus* has a ratio of pre-orbital to post-orbital length of 1:1. This ratio in *Goniopholis simus* is 2:1. This greater proportional snout length in the larger specimen shows clearly in text fig. 1 (*a* and *b*).



TEXT-FIG. 1. Dorsal views of the skulls of A, *Nannosuchus gracilidens* (type specimen, BM(NH) No. 48217)  $\times \frac{2}{3}$ ; B, *Goniopholis simus* (type specimen, BM(NH) No.41098)  $\times \frac{1}{3}$ .

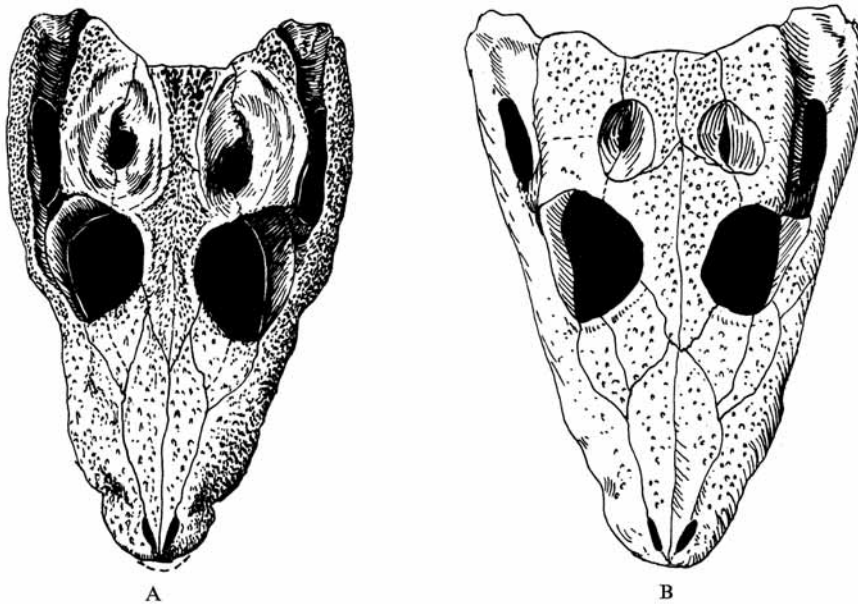
These characters strongly suggest that *Nannosuchus* is merely a juvenile *Goniopholis*. The great similarity between *Goniopholis simus* and *Nannosuchus gracilidens* indicates that the two species are closely related. There are, however, certain differences. First, the teeth of *Nannosuchus gracilidens* are so much more slender than those of the type skull of *Goniopholis simus* that the differences might conceivably be adaptive and not merely due to an age difference. Second, the pitting and ornament on the skull roof of *Nannosuchus* appears to be denser than in *G. simus*. This could represent a specific difference between them, but might also be due to weathering and a difference in preservation.

It is clear that there is just enough difference between these two forms for it to be possible to separate them into two species; this is the 'knife-edge' of taxonomy. However, as the two forms are known from the same series and locality it is preferable to regard them as conspecific, in the absence of any compelling reason for doing otherwise. *Nannosuchus*

*gracilidens* Owen may therefore be regarded as a junior synonym of *Goniopholis simus* Owen.

*Theriosuchus pusillus* (Fig. 2a) may now be examined similarly to establish its condition with respect to the criteria of age which were listed above:

1. The ossification of the skull is very slight.
2. The cranial table is unthickened.
3. The sutures are visible (though somewhat obscured by crushing).
4. The supratemporal fenestrae are not rounded, but are small and slit-like, and the relative size of the orbits is extremely large.



TEXT-FIG. 2. Dorsal views of the skulls of A, *Theriosuchus pusillus* (type specimen, BM(NH) No. 48330), natural size; B, the atosaur *Alligatorium meyeri*, natural size (after Lortet).

These criteria suggest that the type of *Theriosuchus* is an immature individual, and the presence of a femur assigned to the same genus (and indeed very similar to other femora of *Theriosuchus*), but almost twice the size of those on the block containing post-cranial remains (No. 48216), reinforces this view.

The affinities of this crocodile present greater problems than those of *Nannosuchus*. *Theriosuchus* is quite unlike typical goniopholids in the following characters:

1. The skull is extremely short-snouted, shorter even than that of a young goniopholid.
2. The orbits are far larger than the supratemporal fenestrae. Their size exceeds the estimated proportion in a young goniopholid of the same size.



3. The nasals bisect the external naris leaving paired apertures, a feature otherwise unknown in the Goniopholidae.
4. The areas occupied in *Theriosuchus* by the supratemporal fenestrae are covered with smooth thin bone, lappets of which close the fenestrae almost entirely, leaving only small slits. This overgrowth is not observed in any other goniopholid.
5. Very large palpebral bones are present, the ornament and pitting of which are similar to that of the skull. Palpebrals have not been described from any of the other known specimens of goniopholid, though this could be an accident of preservation.
6. The teeth are blunt, rounded, and spatulate, not conical or sharp as in other goniopholids.
7. The scutes are small and square, and show no sign of the characteristic goniopholid peg-and-socket articulation.

This last feature was one of the chief criteria used by Owen in assigning *Theriosuchus* to the family Goniopholidae. He figures one scute in his monograph, and shows the supposed peg, but this scute cannot be found among any of the material in the *Theriosuchus* collection. Since none of the scutes so far examined shows any sign of either peg or socket, it must be assumed that the feature noted by Owen was an artefact of preservation.

While the small size of the skull, plus many of the features outlined above suggest that the type specimen is that of a juvenile, like *Nannosuchus*, there is no similar but larger form known from any British horizon. However, crocodiles are also known from the Kimmeridgian of the Rhône area (i.e. from beds slightly older than those containing *Theriosuchus*). These forms have been described briefly by von Meyer (1851) and more thoroughly by Lortet (1892), and have been placed in a distinct family, the Atoposauridae. *Theriosuchus* and the atoposaurids are closely similar in many respects, as follows (see Fig. 2):

1. They are all small forms, the largest known being less than 90 cm. long.
2. They are all very short-snouted.
3. The orbits of all are proportionally large compared with the supra-temporal fenestrae.
4. The naris is paired in some genera of atoposaurids, as in *Theriosuchus*.
5. In all genera the supratemporal fenestrae are more or less overgrown—in one genus (*Alligatorellus*) they are entirely imperforate.
6. In all atoposaurids figured, the teeth appear blunt and rounded, as in *Theriosuchus*.
7. The osteoscutes are also similar in the two groups, being square and small with median longitudinal ridges on the dorsal scutes and shallow 'pinhole' pitting.

Even though the other post-cranial elements are not available for comparison, there can be little doubt that *Theriosuchus* is an atoposaurid. The appearance of an atoposaurid in England is not surprising, since both south-east England and the Rhône area were part of the same fluctuating basin. It is therefore proposed to transfer *Theriosuchus pusillus* Owen from the family Goniopholidae to the family Atoposauridae.



NOTE ON THE PROBLEMS OF EUSUCHIAN ANCESTRY

Cainozoic crocodylians, including the extant and almost all the extinct forms, are grouped together in the sub-order Eusuchia, the chief characters of which are as follows:

1. The vertebrae are procoelous, not amphicoelous or amphiplatyan as in the mesosuchians.
2. The pterygoids have entered into the formation of the secondary palate, whereas in the mesosuchians this is composed only of premaxillae, maxillae, and palatines.
3. The internal openings of the eustachian canal are enclosed in bone.
4. The external naris is undivided.
5. The supratemporal fenestrae tend to be small.
6. The post-orbital bars have become subdermal.
7. The frontals do not usually enter into the margins of the supratemporal fenestrae.

Characters 1, 2, and 3 are critical and definitive for the sub-order, while 4-7 are variable and are also possessed in 'mosaic fashion' by many mesosuchians.

Since all the Cainozoic Eusuchia are fully eusuchian in their characteristics, the group must have evolved from some progressive mesosuchian group (or groups) in the late Mesozoic. Romer (1956) has suggested that they may have evolved from the goniopholid mesosuchians. This family was common and widespread in the Cretaceous and possessed several generalized features (e.g. dermal bone pattern on the skull, sunken postorbital bar, undivided external naris) which would not debar them from ancestry of the Eusuchia. However, as far as is known, they all have amphicoelous vertebrae, and even the latest members have a typically mesosuchian palatal structure.

The goniopholids do not appear, in these two features at least, to be progressing towards the eusuchian conditions. It is therefore interesting to find that two genera of another mesosuchian family, the Atoposauridae, were more progressive in these features. The two genera are *Theriosuchus* and a small crocodylian recently found in the Wealden of Texas (i.e. slightly later in time than the Purbeckian) by Dr. Langston of the University Museum of Texas. The features of this new crocodile, as described by Dr. Langston (*personal communication*) seem clearly to ally it with *Theriosuchus* in the Atoposauridae. It has a similar short snout and very large orbits, a similar naris, similar blunt rounded teeth, and similar palpebral bones, while the pattern of dermal bones, and their ornament, are also similar to those of *Theriosuchus*. Dr. Langston has also found procoelous vertebrae in his specimen, and it is interesting to note that, in the specimen of *Theriosuchus* which shows the post-cranial skeleton (No. 48216), a single vertebra which is probably an anterior caudal has been displaced so that the face of the centrum can be seen. This is clearly procoelous, but has a central depression which is also found in the Texas specimen. It is quite unlike the typical amphicoelous centra of other mesosuchians, though its degree of convexity is not as great as in later eusuchians. *Theriosuchus* is therefore the earliest known procoelous crocodile.

Significantly, the condition of the palate is different in the Purbeck and Texas forms. In *Theriosuchus* the internal nares continue posteriorly into a median depression, extending beneath the pterygoid region. This depression (which may have been covered below by a soft palate in life) is walled laterally by outgrowths of the pterygoids, and roofed by the palatines. This condition is more advanced towards the eusuchian palatal

structure than is that of the typical mesosuchians. The American specimen is further advanced: the internal naris has migrated posteriorly and the pterygoid flanges are more extensive than those of *Theriosuchus*, though they do not meet in the midline, nor do they extend beneath the median depression ventrally, as in eusuchians, to form a posterior elongation of the false palate.

While these atoposaurids are early enough to provide possible eusuchian ancestors, the members of the family so far discovered are perhaps too specialized in their small size, dentition, large orbits, and overgrown supratemporal fenestrae to be themselves wholly acceptable as such ancestors. If they do prove to be unrelated to the Eusuchia, the atoposaurids at least provide an interesting example of parallel evolution.

#### REMARKS ON THE CONCEPT OF DWARFISM

Dwarfism has two main connotations, the first of which may be dismissed for the purpose of this discussion, being a pathological term applied to individuals with specific genetic or physiological defects. The second meaning of the term is very widely used in biology to define small varieties of animal or plant closely related to other, larger varieties. It is possible to produce 'dwarf' varieties by controlled, selective breeding, and, of course, the same process can occur in nature. Far more commonly found in nature, however, is the opposite tendency, namely the tendency to grow larger, the reasons for which need not be discussed here. But to use the term 'dwarf' to describe an individual or species whose evolutionary history is unknown is to render meaningless the essence of the term 'dwarfism', inherent in which is the process of reduction from a previous larger size. Thus a small creature is not a dwarf *sensu stricto* unless it has evolved from a larger ancestor. When limited in this way, the definition naturally excludes most small members of the animal and plant kingdoms.

The suitability of the term 'dwarf' to describe Owen's small genera may finally be considered briefly. *Nannosuchus* is, of course, no longer a problem; as discussed previously, it is merely a juvenile. The position of *Theriosuchus*, however, has not been defined above. One may first note that the material of *Theriosuchus* belongs mainly to immature individuals (the isolated femur being perhaps an indication of the possible size of the adult). No known atoposaurid is longer than 90 cm., however, the American specimens (very probably members of the same family) being likewise of small individuals. There is no evidence that any larger atoposaurids or atoposaurid ancestor ever existed. The reasons for this small size are probably various; for example, it may be a result of the absence of larger predators, or of the presence of a supply of small food, etc. However, Owen's belief that they had actually reduced their size has no foundation on present evidence. It is therefore suggested that the 'stigma' of dwarfism should be removed from them and that they should henceforth be recognized for what they are, a group of small and extremely interesting mesosuchian crocodiles.

#### SUMMARY AND CONCLUSIONS

The purpose of this paper has been to re-examine Owen's so-called 'dwarf' crocodiles of the Purbecks. On detailed reinvestigation it was realized that the first of the two species, *Nannosuchus gracilidens*, was based on an immature individual of *Goniopholis*

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*simus* from the same horizon and locality. The second species, *Theriosuchus pusillus*, which was originally assigned to the family Goniopholidae, was removed from this family and placed in the Atoposauridae, a family of advanced and specialized mesosuchians, known hitherto only from the Kimmeridgian of the Rhône area and Bavaria. One of the interesting features of the atoposaurids is that they do indeed appear to have been all small forms; though, in the author's opinion, the term 'dwarf' cannot be applied to them in the strict sense, there being no evidence of size reduction from a larger ancestor. The advanced features of the family Atoposauridae include a palate more eusuchian than that of typical mesosuchians, and the earliest record of a procoelous vertebra in the Crocodylia. They are, however, too specialized to have been direct eusuchian ancestors, and must therefore be included among the several Upper Mesozoic mesosuchians which paralleled those features which later became characteristic of the successful Eusuchia.

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