THE CALLOVIAN (MIDDLE JURASSIC) TELEOSAURID MARINE CROCODILES FROM CENTRAL ENGLAND

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ABSTRACT. For many years the taxonomy of the Callovian marine crocodiles of the genera *Steneosaurus* and *Mycterosuchus* has been in a state of confusion. Bivariate and principal coordinate analyses are used in an attempt to identify cranial characters for discriminating species. Many of the characters used previously to define five species of *Steneosaurus* and one of *Mycterosuchus* are shown to be individually variable. Only two Callovian species can now be identified on the basis of their skull proportions and numbers and form of their teeth: *S. leedsi* incorporates specimens previously assigned to *S. leedsi* Andrews, 1909, and *Mycterosuchus nasutus* Andrews, 1913; *S. durobrivensis* includes *S. durobrivensis* Andrews, 1909, *S. obtusidens* Andrews, 1909, *S. hulkei* Andrews, 1913, and *S. depressus* Phizackerley, 1951.

THE current classification of the Callovian marine crocodiles of the genera *Steneosaurus* and *Mycterosuchus* was established largely by E. E. Deslongchamps (1863–1869) and Andrews (1909, 1913). Deslongchamps gave the first detailed descriptions and figures of *Steneosaurus*, emending Geoffroy Saint-Hilaire's (1825) generic description, creating many new species for the material collected around Caen in Normandy and emending other specific diagnoses. He established the type specimen of *Steneosaurus* as that figured by Cuvier (1824, pl. 8) and named *S. megistorhynchus* by Geoffroy Saint-Hilaire (1825); he also emended the diagnosis of the species (1869, p. 217, pl. 15).

Andrews (1909, 1913) worked with crocodilian material of the Leeds Collection housed in the British Museum (Natural History). These mesosuchian crocodiles occur in the *jason* and *coronatum* zones of the Oxford Clay, and were found close to Peterborough, Cambridgeshire. Andrews (1913) described a range of additional material, extended his earlier descriptions (Andrews, 1909), and erected a new species *S. hulkei*. He established the new genus *Mycterosuchus* in 1913 to accommodate the specimen described in 1909 as *S. nasutus*. In distinguishing between the genera *Steneosaurus* and *Mycterosuchus* Andrews (1913) used the following cranial characters possessed by *Mycterosuchus*:

(i) greatly elongated snout, sharply marked off from the cranial region of the skull;
(ii) slender teeth;
(iii) temporal fossae relatively smaller and shorter than in the typical steneosaur.

The characters he used to determine the four species of *Steneosaurus* from the Oxford Clay were as follows:

S. leedsi—great length and slenderness of rostrum (i.e. preorbital length 73 % of total skull length); mandibular symphysis 58 % of mandible length; great distance between nasals and premaxillae; number and form of teeth.

S. hulkei—short rostrum (preorbital length less than 60 % of total skull length); nasals separated from premaxillae by a shorter distance than in *S. durobrivensis*; anterior angle of frontal blunt and far behind anterior angle of prefrontals; mandibular symphysis 40 % of mandible length; large teeth; scutes shallow, transversely elongate and bearing widely separated pits.

S. durobrivensis—rostrum of moderate length (preorbital length 61 % of total skull length); very large temporal fenestrae; frontals terminate in very obtuse angle a little way in front of anterior rim of orbits; mandibular symphysis 44 % of mandible length; number and form of teeth; scutes large with shallow pits but no tendency of elongation.

S. obtusidens—short rostrum (preorbital length 52 % of total skull length); species distinguished mainly by form and number of teeth, and by relationship of frontal and prefrontal bones.

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Thus, in the division of this genus, Andrews used the following criteria:

A, length of preorbital region of skull and its percentage of the skull as a whole;
B, degree of robustness or massiveness of cranial features, particularly the snout;
C, form and relationship of frontal and prefrontal bones;
D, separation of premaxillae and nasals;
E, length of mandibular symphysis;
F, tooth form and number;
G, scute form.

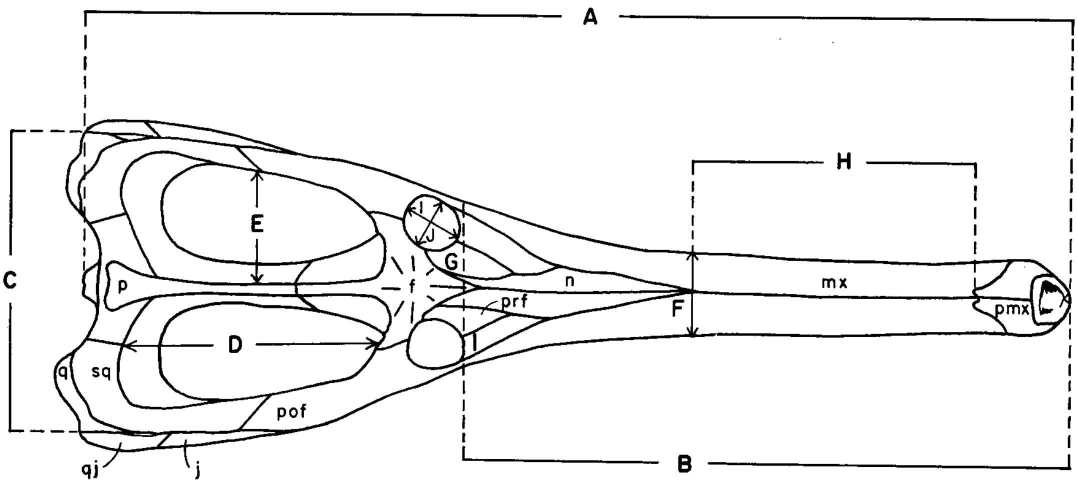
In 1951 Phizackerley diagnosed a further Callovian steneosaur species, *S. depressus*, on the basis of the 'delicate construction of the skull and narrow alveolar region', with rostrum 64 % of total skull length, and mandibular symphysis 48 % of mandible length.

These generic and specific diagnoses were all based on the typological species concept; each crocodile species was viewed as being virtually invariable, so that small morphological variations were considered to have specific significance. Most of the current taxonomic problems within Callovian steneosaurs have arisen from this methodology, which was applied uncritically by subsequent workers, such as Phizackerley (1951) and Mateer (1974).

MATERIAL AND METHODS

Mook (1921) was the first author to identify types of osteological variation seen in living crocodiles which had been previously interpreted as having taxonomic significance in fossil forms. Mook's study was an attempt to determine the 'value', in taxonomic terms, of the variations observed. He identified two sources of variation: age and individual—e.g. proportional relations of length and breadth of the skull, of preorbital and postorbital regions, shape of snout, size and number of teeth, variation in the form of certain sutures, and ornamentation of cranial bones.

A variety of cranial characters was measured, including those which had been used to diagnose species by



TEXT-FIG. 1. The pattern of dorsal cranial bones in *Steneosaurus*, defining the measurements taken during the morphological analysis (see Table 1). Abbreviations: f, frontal; j, jugal; l, lachrymal; mx, maxilla; n, nasals; p, parietal; pmx, premaxilla; pof, post frontal; prf, prefrontal; q, quadrate; qj, quadrato jugal; sq, squamosal; A, total length of skull (occipital condyle to tip of snout); B, preorbital length; C, width between outer angles of quadrates; D, length of supratemporal fenestra; E, width of supratemporal fenestra; F, width at anterior end of nasals; G, width at anterior rim of orbits; H, distance between nasals and premaxillae; I, long diameter of orbit; J, transverse diameter of orbit.

TABLE 1. Cranial measurements in *Steneosaurus* (see text-fig. 1). Abbreviations: BM(NH) British Museum (Natural History); CMP, City Museum, Peterborough; HM, Hunterian Museum, Glasgow; OUM, Oxford University Museum; SM Sedgwick Museum, Cambridge. OUM specimens J1401, J1403, J29850, J29851 are Bathonian steneosaurs which were not included in the computer analysis. Computer numbers were allocated to those specimens sufficiently complete for computer analysis. All measurements in millimetres (* denotes estimated value).

	BM(NH) R3320 *S. leedsi*	BM(NH) R3806 *S. leedsi*	BM(NH) R2619	BM(NH) R2074 *S. hulkei*	BM(NH) R3701 *S. durobrivensis*	BM(NH) R2865 *S. durobrivensis*	BM(NH) R3168 *S. obtusidens*	BM(NH) R2617 *M. nasutus*	OUM J1401 *S. boutilieri*	OUM J1403 *S. boutilieri*	OUM J29850 *S. meretrix*	OUM J29851 *S. meretrix*	OUM J1420 *S. depressus*	HM V1150 *S. leedsi*	CMP R179 *S. leedsi*	CMP R175 *S. durobrivensis*	CMP R178 *S. obtusidens*	SM 1 *M. nasutus*
computer number	**1**	**2**		**5**	**6**	**7**	**9**	**11**	—	—	—	—	**16**	**3**	**4**	**8**	**10**	**17**
A, total length of skull	810	853		600	740	935	1160	1000	768*	820*	746	731	792	744	598	1112	1030*	1003
B, preorbital length	590	613		350	450	589	710	730	474	508	474	464	509	533	378	686	635	752
C, width between outer angles of quadrates	180	204		220	240	312	375	250		264	232	240	212	181	175	312	348	234
D, length of supratemporal fenestrae	120	142		153	180	225	299	140		203	183	158	156	135	118*	249	255	140
E, width of supratemporal fenestrae	73	82		80	88	98	140	105		102	72	72*	71	63	49	118	119	96
F, width of snout at anterior end of nasals	43	59		54	64	82	90	63	58	66	53	51	48	48	43	82	81	58
G, width of skull at anterior rim of orbits	105	125		107	114		189	167	134*	153	104	119	113	112	92	156	192	134
H, distance between nasals and premaxillae	264	272		148	192	280		455		201	253	265	220	294	201	388	232	397
- mandible length	890	960	790	720	850		1370	1100			856							
- length of symphysis	520	508	431	289	375		580	620			407		418*		328	590*		
I, long diameter of orbits	55			53					70	72	60	68	60	44	35*	55	67	
J, transverse diameter of orbits	37			41					49	52	45	45	36	33	26	42	52	

Andrews, so that information about dissociated steneosaur material (belonging mainly to the Leeds Collection but including some important additional specimens) could be synthesized. In this way the sample size available for analysis was substantially increased (numbers in parentheses) beyond that analysed by Andrews: *S. leedsi*, 2 (5); *S. hulkei*, remains at 1; *S. durobrivensis*, 2 (6); *S. obtusidens*, 2 (4); and *M. nasutus*, 1 (2). The majority of the taxonomic criteria used in Andrews's species diagnoses were also quantified, thus facilitating both an objective critique of the existing taxonomy and an investigation into characters which may have taxonomic significance.

The cranial measurements taken on specimens of *Steneosaurus* and *Mycterosuchus* are shown in text-fig. 1. Mandible length and mandibular symphysis were also measured. The data obtained are shown in Table 1. Combinations of two or three measurements were plotted and their compatability with the present classification tested.

Ranked statistics derived from Table 1, a similarity matrix, and nearest neighbour scores have been tabulated for all specimens allocated a computer number; these tables have been deposited with the British Library as Supplementary Publication No. 14030 (5 pages). It may be purchased from the British Library, Lending Division, Boston Spa, Wetherby, Yorkshire LS23 7BQ, UK. Prepaid coupons for such purposes are held by many technical and university libraries throughout the world.

CHARACTER ANALYSES

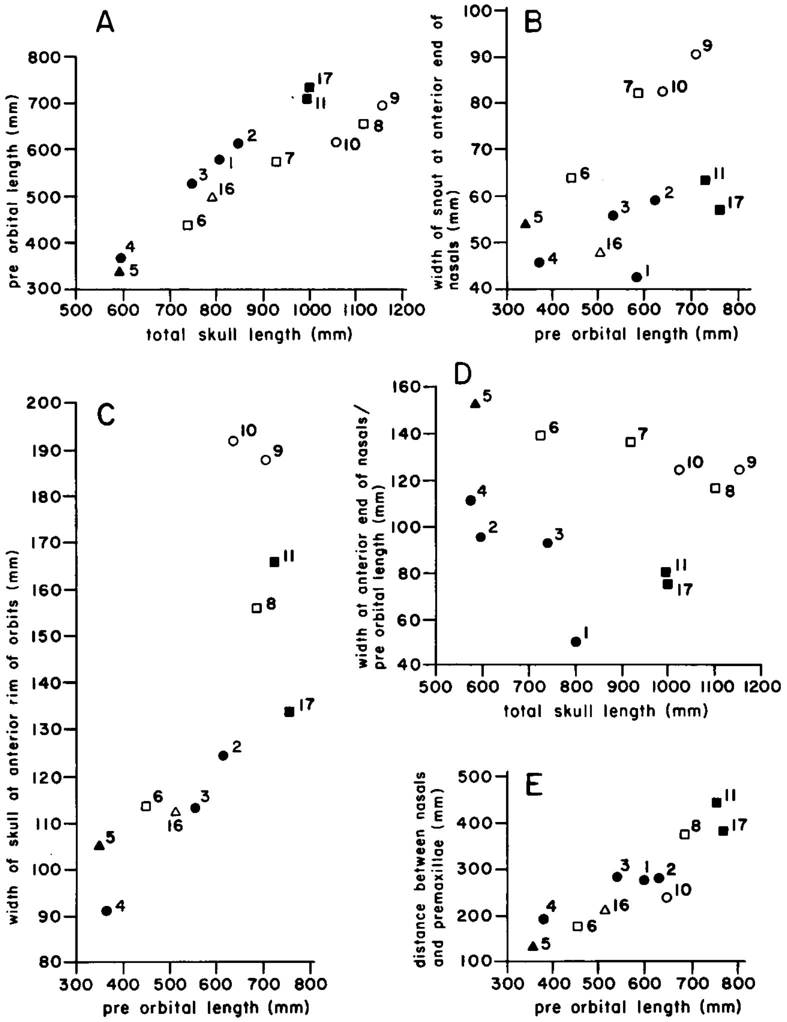
Bivariate plots

The length of the preorbital region of the skull, degree of robustness of the snout, and separation of nasals and premaxillae in both *Steneosaurus* and *Mycterosuchus* are quantified in text-fig. 2A–E. None of these plots shows groups that might imply the presence of two genera, with the possible exception of text-fig. 2D. It seems that differences can be detected in the length and robustness of the snout between specimens known at present as *S. leedsi* and *M. nasutus* (Group 1) and the remainder of the Callovian steneosaurs, *S. hulkei*, *S. durobrivensis*, *S. obtusidens*, and *S. depressus* (Group 2). But this is not compatible with the present recognition of two genera: *Mycterosuchus* (one species) and *Steneosaurus* (five species).

Some additional cranial measurements for the two groups suggested by text-fig. 2D were then examined by ranked ratio and percentage values as shown in Table 2. The data illustrate the wide range of overlap of values between species and a high level of individual variation within species. With the exception of character 1 (Table 2: preorbital region as a percentage of the total length of the skull), the variation within Groups 1 and 2 is greater than that which exists between them. The pattern shown in text-fig. 2D only becomes apparent when three, rather than two, cranial characters are compared simultaneously.

TABLE 2. Ranges in Groups 1 and 2 (see text-fig. 4) of ranked statistics derived from cranial measurements of *Steneosaurus*.

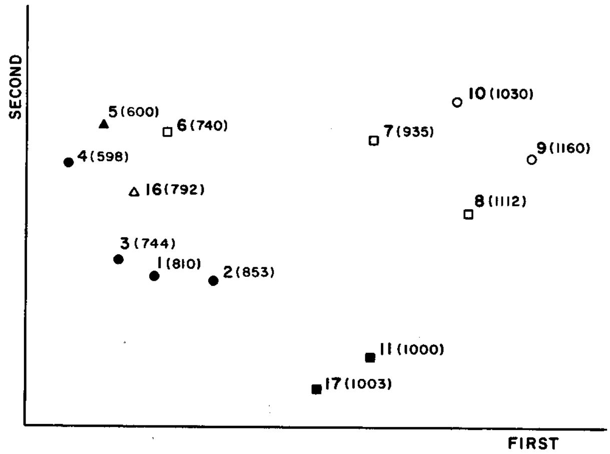
Character	Character number	Range in Group 1	Range in Group 2
Preorbital region as % of total length of skull	1	71·63–74·90 % (= 3·27 %)	58·33–64·26 % (= 5·93 %)
Ratio of width of skull (outer angles of quadrates) to length of skull	2	4·00–4·50:1	2·72–3·73:1
Length of supratemporal fenestrae as % of total length of skull	3	13·95–18·64 % (= 4·45 %)	19·69–25·70 % (= 6·01 %)
Length of supratemporal fenestrae as % of preorbital length	4	18·61–25·32 % (= 6·71 %)	30·64–46·47 % (= 15·83 %)
Width of supratemporal fenestrae as % of width between outer angles of quadrates	5	34·80–42·00 % (= 7·20 %)	33·49–37·82 % (= 4·33 %)
Width of snout at anterior end of nasals as % of preorbital length	6	7·28–9·62 % (= 2·34 %)	9·43–15·42 % (= 5·99 %)
Width of skull opposite anterior rim of orbits in relation to preorbital length	7	17·79–22·87 % (=5·08 %)	22·20–30·57 % (=8·37 %)
Distance between premaxillae and nasals as % of length of rostrum	8	Marked overlap between members of Groups 1 and 2	Marked overlap between members of Groups 1 and 2



TEXT-FIG. 2. Bivariate plots showing: A, relationship between preorbital length and total skull length; B, relationship between width of snout at anterior end of nasals and preorbital length; C, relationship between width of snout at anterior rim of orbits and preorbital length; D, relationship between width of snout at anterior end of nasals/preorbital length, and total skull length; and E, relationship between distance separating nasals and premaxillae, and preorbital length. Key to symbols used in text-figs. 2-4: ○ *Steneosaurus obtusidens*; □, *S. durobrivensis*; ●, *S. leedsi*; ▲, *S. hulkei*; △, *S. depressus*; ■ *Mycterosuchus nasutus*.

Principal coordinate analysis

A multivariate technique, principal coordinate analysis, was used in order to test further for differentiation of species. All of the measured cranial characters were analysed together, and the specimens (i.e. the vectors representing the specimens) represented by points in n-dimensional space, where n = number of crocodiles in the population minus 1, and the distance between any pair of



TEXT-FIG. 3. Principal coordinate analysis plot showing spatial relationships between members of the genera *Steneosaurus* and *Mycterosuchus* on the first and second axes. Specimens denoted by computer number (see Table 1); total skull length (mm) shown in parentheses alongside each computer number.

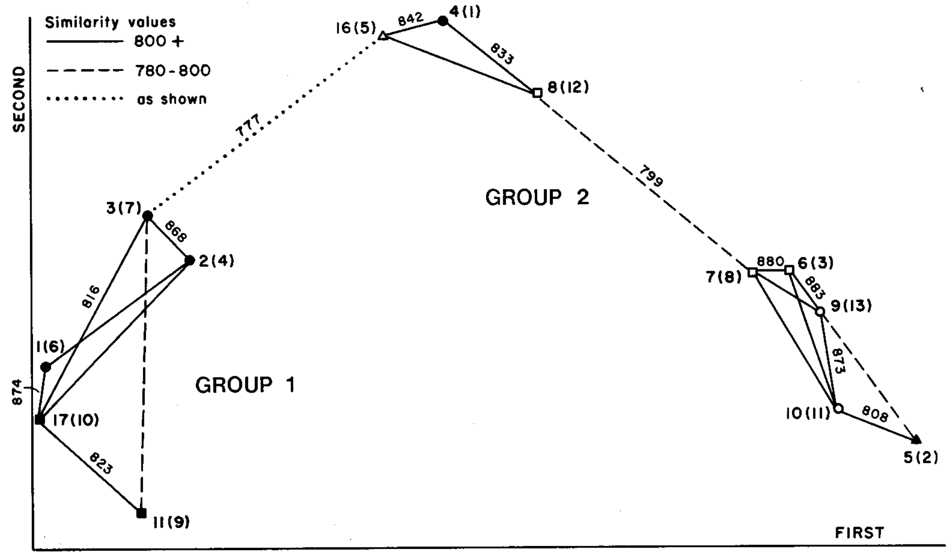
specimens is a measure of their overall similarity in terms of all the characters measured. Projecting the coordinates of the crocodiles along the first and second principal coordinate highlights the morphological differences that exist between members of the population because these axes are the two directions along which variance (of measured characters) is greatest. The results of the multivariate analysis are shown in text-fig. 3.

TAXONOMIC VALIDITY OF CHARACTERS

Cranial dimensions

The first axis in text-fig. 3 corresponds to measures of length or size. The spatial relationships between specimens illustrated in text-fig. 3 could, therefore, be explained by either a similar morphological form at different scales, or morphological differences which might be used to define species.

Using principal coordinate analysis the effect of size on the other measured characters can be eliminated. Size (defined here as total length in dorsal mid-line) is the first of ten variables measured, i.e. variable 1. This is divided into all the other variables and subsequently excluded from the analyses. The results of this procedure produced a similarity matrix and the new pattern in text-fig. 4. If the specimens in text-fig. 4 are ranked according to size, where 1 denotes the smallest specimen and 13 the largest (ranked numbers are shown in parentheses), no size trend is apparent—in contrast to text-fig. 3. The similarity values and spatial relationships between the specimens illustrated in text-fig. 4 must, therefore, depend on morphological characters that are not independent of size; the way in which they group together reinforces that seen already (text-fig. 2D; Character 1 of Table 2). Text-fig. 4 shows two groups linked internally by similarity values approaching, or in excess of, 80 %: Group 1 (on the left of the graph) includes all specimens of *S. leedsi* and *M. nasutus*; Group 2 contains the remaining Callovian steneosaur species. The value of the similarity coefficient linking the two 'most similar' end-members of these two groups reaches 77·7 %. The levels of similarity linking the end-members of these two groups can be seen clearly in text-fig. 4. Interestingly enough, the maximum value of 883 defines the morphological similarity between



TEXT-FIG. 4. Principal coordinate analysis plot showing similarity values between members of the genera *Steneosaurus* and *Mycterosuchus*. Rank values appear in parentheses alongside computer numbers.

specimens 6 and 9, which were previously defined as the type specimens of *S. durobrivensis* and *S. obtusidens* respectively.

The fact that it is so difficult to further subdivide these two groups of specimens is strong evidence that only two species exist.

Number of teeth

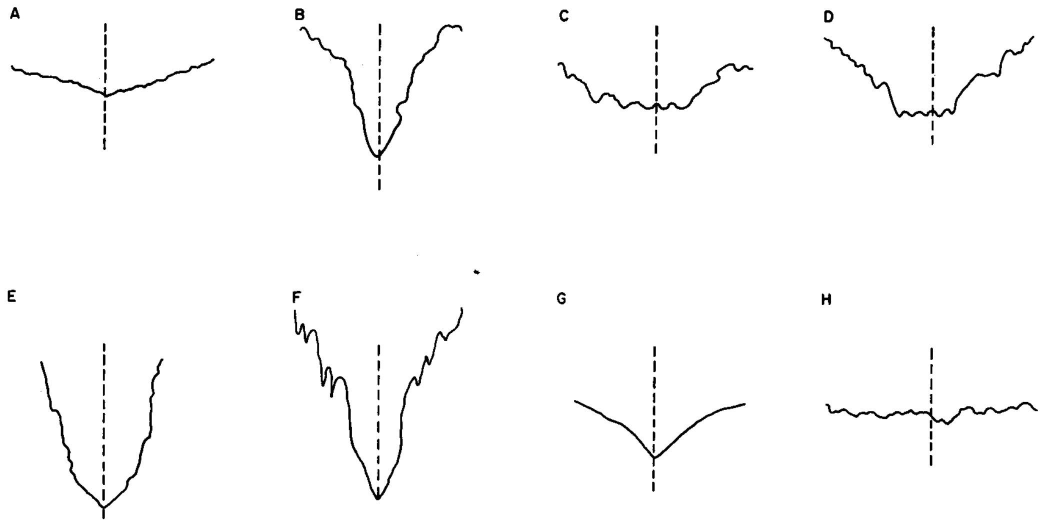
Specimens of *S. leedsi* are characterized by large numbers of teeth, *c.* 45–46 on each side of the upper jaw and 43–44 in the lower jaw. *M. nasutus* has c. 38–40 teeth in the upper jaw and 42 in the lower jaw. The remaining Callovian steneosaur species all have far fewer teeth: a minimum of 24 in the upper jaw and 26 in the lower jaw of *S. hulkei*; c. 28 in the lower jaw of *S. obtusidens*; and approximately 32 in the upper jaw and 30 in the lower jaw of *S. durobrivensis*.

If we assume that *S. leedsi* and *M. nasutus* belong to one species, and the other Callovian steneosaurs to another, then it must be acknowledged that this degree of variation exceeds, to some extent, the amount recorded by Kälin (1933) in his study of living crocodilians. It is clear from his study, however, that tooth numbers never provide the sole basis on which species are recognized, rather they occur together with clear morphological differences in the skull, and it is on the basis of the latter that different species are distinguished. No such differences in cranial morphology can be detected within the two groups of steneosaurs defined by the present study, and it would seem unwise to split them on the basis of Kälin's comments about tooth number in isolation from other aspects of cranial morphology.

Qualitative characters

Three of the criteria used by Andrews (1913) to distinguish species of *Steneosaurus* (and reiterated by Phizackerley 1951) are qualitative in nature—the form and relationship of the frontal and prefrontal bones, tooth form, and scute form:

1. *Frontal and prefrontal bones*. The range in form of the nasal/frontal suture and its relationship with the prefrontals is illustrated diagrammatically in text-fig. 5. The figure shows that this feature

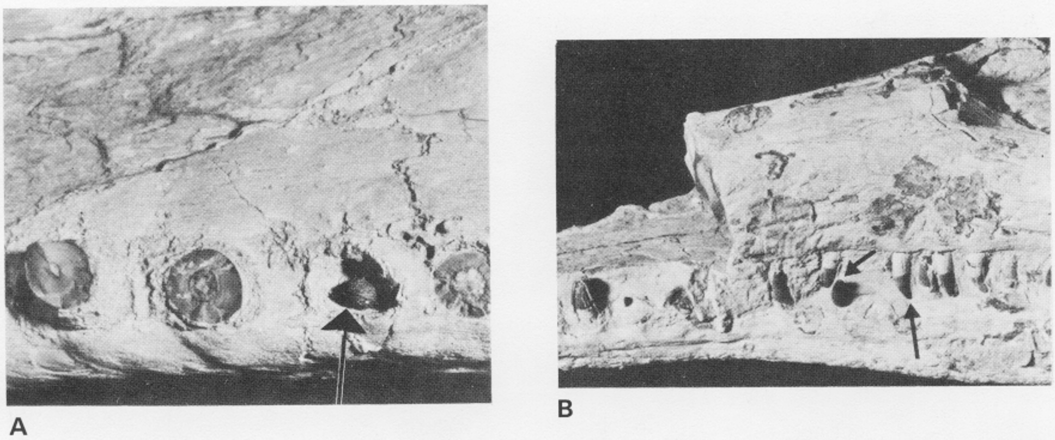


TEXT-FIG. 5. Variation in form of frontal/nasal suture in *Steneosaurus*. Distance separating the most anterior point of projection of frontal from prefrontals is indicated. A, *S. durobrivensis*, R3701 (30 mm); B, *S. durobrivensis*, R2073 (19 mm); C, *S. durobrivensis*, R2865 (27 mm); D, *S. hulkei*, R2074 (20 mm); E, *S. leedsi*, R3806 (4 mm); F, *S. leedsi*, R3320 (9 mm); G, *S. obtusidens*, R3168 (31 mm); H, *S. depressus*, OUM J1420 (32 mm). All R numbers are BM(NH) specimens.

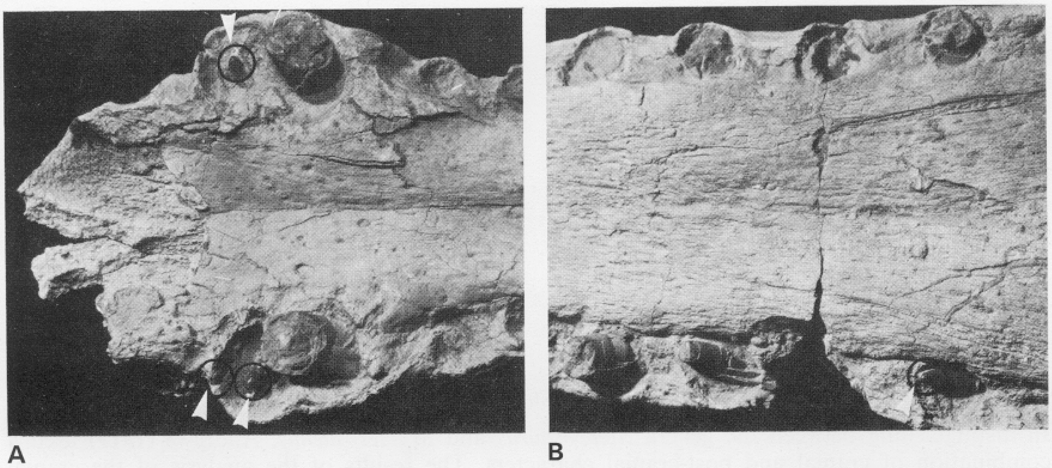
is highly variable in its intricacy and shape, in the length of the anterior projection of the frontal, and its level of termination relative to the most anterior point of the prefrontals. Andrews (1913, p. 122) attached great importance to the above character and at times used it as a major criterion by which species were distinguished, e.g. between *S. hulkei* and *S. durobrivensis* and between *S. edwardsi* and *S. hulkei*. The first example suggests that Andrews did not take account of the individual variation that occurs in this character in specimens of *S. durobrivensis*. The similarity in form of the frontal/nasal suture of *S. hulkei* and *S. durobrivensis*, BM(NH) R2865, in text-fig. 5 is notable, but if R2865 is compared with R3701 and R2073 (both *S. durobrivensis*) there are sharp contrasts between all specimens. Andrews, of course, would only have been able to compare *S. hulkei* with *S. edwardsi* by comparing the type of *S. hulkei* with a figure of the type of *S. edwardsi*. On the basis of the above evidence, the synonymy of *S. hulkei*, *S. edwardsi*, and *S. durobrivensis* seems probable.

2. *Form of teeth*. In *S. leedsi* and *M. nasutus* the teeth are slender with sharply pointed crowns and the enamel is sculptured into a series of very fine longitudinal ridges. The pattern of tooth development in the steneosaurs forming Group 2 shows a progressive change in crown form, i.e. teeth become increasingly blunt as the size of the snout increases. This trend is complicated by individual differences in tooth character between individuals with similar sized rostra (text-fig. 6). There are no differences in the sculpture of the enamel between these specimens and *S. leedsi* and *M. nasutus*.

Andrews (1913) diagnosed *S. obtusidens* mainly by the form of the teeth, which he stated were blunt and rounded at the tips. He noted (1913, pp. 130-131), however, 'that some of the replacing teeth in the type skull of *S. durobrivensis* [R3701] are somewhat similar in form [to *S. obtusidens*]... and although other differences between that species and the present one exist, the possibility that the specimens on which the latter is based may be very large and old individuals of *S. durobrivensis* cannot be ignored'. The two type specimens were widely separated in terms of 'massiveness of the rostra' (see text-fig. 2B) with an accompanying disparity in tooth crown form. BM(NH) R2075



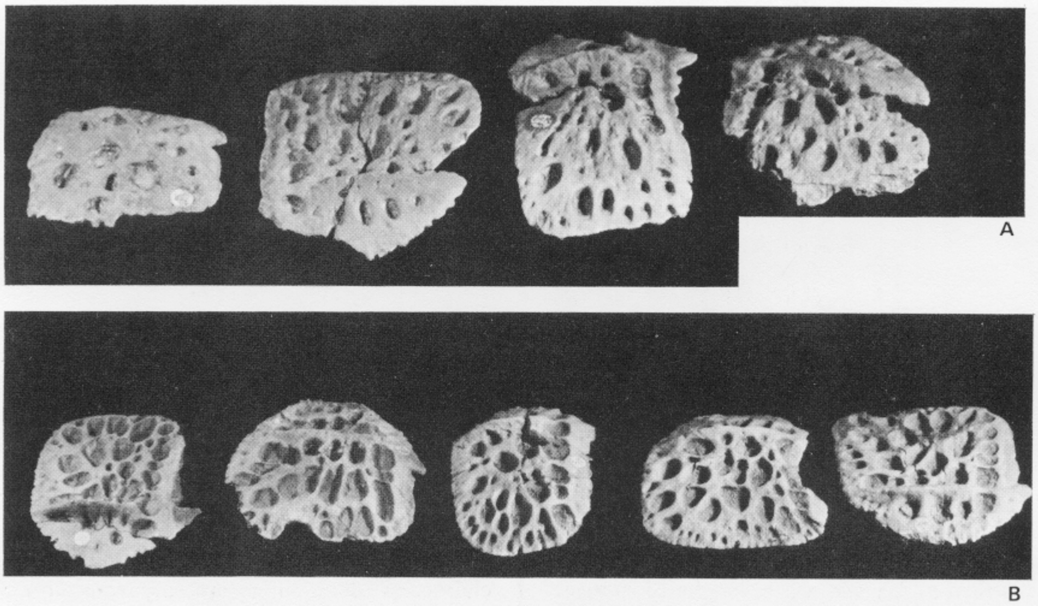
TEXT-FIG. 6. Variation in form of tooth crowns (arrowed) in *Steneosaurus obtusidens*. A, CMP R39; B, CMP R178.



TEXT-FIG. 7. A, B, form of tooth crowns (arrowed) in *Steneosaurus durobrivensis*, BM(NH) R2075.

(text-fig. 7) and some of the replacement teeth in BM(NH) R3701 indicate the change in tooth form. Also important in this context is the National Museum of Wales specimen 19 96 G12*a* showing tooth crowns intermediate in form between *S. durobrivensis* and *S. obtusidens*.

3. *Form of scutes*. Among the lines of evidence used by Andrews (1913) to distinguish *S. obtusidens* from *S. durobrivensis* (and the genera *Mycterosuchus* and *Steneosaurus*) is the form of the dorsal scutes. In *S. obtusidens* Andrews said these were shallow and elongated—arranged in lines radiating from the middle of the keel and sometimes almost running together to form shallow grooves. Few scutes are preserved in the type specimen of *S. obtusidens*, BM(NH) R3618 (Andrews figured only one), so reference was made to scutes of another specimen, BM(NH) R3169, labelled as *S. obtusidens* by Andrews, so that a more accurate assessment of their variance could be measured; both specimens were compared with the many scutes preserved in BM(NH) R3701 (the type of *S. durobrivensis*).



TEXT-FIG. 8. Variation in form of dorsal scutes. A, R3169 *Steneosaurus obtusidens*, BM(NH) R3169; B, *S. durobrivensis*, BM(NH) R2865. Both × 0·5.

The considerable amount of variation between individual scutes is illustrated by text-fig. 8 which shows that the elongate pits so characteristic and notable in the figured *S. obtusidens* scute (Andrews 1913, pl. 8, fig. 6) are neither universally present nor, indeed, representative of other *S. obtusidens* scutes. Examination of modern crocodilian scutes reveals a high degree of variation in form, dependent on the position of the scute on the body. The figured scute from the type specimen of *S. obtusidens* is an atypical representative of those available for analysis illustrating only one aspect of a highly variable feature and is, therefore, taxonomically invalid.

Additional characters used to establish Mycterosuchus

In distinguishing between the genera *Steneosaurus* and *Mycterosuchus*, Andrews (1913) used a combination of cranial and post-cranial characters. The results of the analysis of the cranial characters for the type specimen of *Mycterosuchus*, BM(NH) R2617 (specimen 11 on text-fig. 4) and another, SM1 (specimen 17), show that both exhibit high levels of similarity to specimens of *S. leedsi*. Four post-cranial characters were noted by Andrews (1913) as having taxonomic importance:

1. *Size of fore-limb*. Andrews described this as being less reduced than in *Steneosaurus*. There is a limited amount of material from which to derive relevant data (Table 3) but the measurements taken appear to indicate that fore-limb size in *Mycterosuchus* is broadly comparable with that of steneosaurs of similar size (e.g. CMP R178 in Table 3).

2. *Degree of development of fore-limb condyles*. Andrews described both distal condyles of the fore-limb as being well developed in *Mycterosuchus*. The nature of preservation of all Oxford Clay crocodiles renders this kind of evidence unreliable and of little importance.

3. *Form of caudal vertebrae*. Andrews noted that neural spines in the middle and posterior caudal regions were notched anteriorly and posteriorly in *Mycterosuchus*. Caudal notching was indeed found to be present in the specimens analysed. This feature was not seen in the steneosaur specimens examined in the course of this work.

TABLE 3. Forelimb measurements in *Steneosaurus* and *Mycterosuchus*. All measurements in millimetres (* denotes estimated value). Abbreviations: see Table 1; MB, private collection of M. Bishop.

Specimen number	Species	Humerus	Radius	Ulna
BM(NH) R3806	*S. leedsi*	128	67	88
BM(NH) R3701	*S. durobrivensis*	122	71	89
CMP R175	*S. durobrivensis*	186	101	99
CMP R178	*S. obtusidens*	197	94	125
SM 1	*M. nasutus*	188	102	116
BM(NH) R2617	*M. nasutus*	211	113	142
MB 1	*M. nasutus*	189*	106*	—

4. *Size of dorsal scutes*. Andrews concluded that the dorsal scutes were more massive than in *Steneosaurus*. The scutes from *S. leedsi* and *M. nasutus* show an increase in size which corresponds to the increase in the overall size of the specimens (analogous to that seen between *S. durobrivensis* and *S. obtusidens*).

The analysis of an albeit limited range of post-cranial characters exhibited by specimens currently classified as *Mycterosuchus* has failed to reveal any characters which differ markedly from those of Callovian steneosaurs (with the possible exception of the caudal vertebrae) and which could, by the nature of their variance, be considered taxonomically significant.

SYSTEMATIC PALAEONTOLOGY

Using the results of the analyses of the cranial dimensions of Callovian steneosaurs, two species are distinguished by the differences they show in the length and robustness of the rostral portions of the skull, and the type and number of teeth they possess.

Genus STENEOSAURUS Geoffroy Saint-Hilaire, 1825, emend. E. E. Deslongchamps, 1867

Type species. *Steneosaurus megistorhynchus* Geoffroy Saint-Hilaire, 1825.

Steneosaurus leedsi Andrews, 1909

1909 *Steneosaurus leedsi* Andrews, p. 300, pl. 8, fig. 1.
1909 *Steneosaurus nasutus* Andrews, pp. 308–309, pl. 9, fig. 1.
1913 *Mycterosuchus nasutus* Andrews, pp. 136–140, pl. 8, figs. 1–10; text-figs. 51–54.

Type data. Holotype, BM(NH) R3320.

Diagnosis. Elongated, slender rostrum; preorbital length 72 % or more of total length of skull. Considerable variation in degree of separation of nasals and premaxillae; this distance accounts for 45–62 % of length of rostrum. Teeth slender, with sharply pointed crowns, forty or more in each maxilla. Mandibular symphysis *c*. 58 % of length of jaw.

Steneosaurus durobrivensis Andrews, 1909

1867 *Steneosaurus edwardsi* E. E. Deslongchamps, p. 239, pl. 17, figs. 1–3.
1909 *Steneosaurus durobrivensis* Andrews, p. 304, pl. 8, fig. 2.
1909 *Steneosaurus obtusidens* Andrews, pp. 308–309, pl. 9, fig. 2.
1913 *Steneosaurus hulkei* Andrews, p. 122.
1951 *Steneosaurus depressus* Phizackerley, p. 1190, fig. 10A, B.

Type data. On the basis of the evidence presented here the synonymy of *S. edwardsi* is proposed. Characters isolated from E. E. Deslongchamps's (1867) original descriptions by Andrews (1913) as being taxonomically significant (i.e. those which could be used to distinguish between *S. edwardsi* and his Callovian species) have been shown to be invalid. Because of the destruction (during the Second World War) of material from which the diagnosis of *S. edwardsi* was made, it is not possible to make a direct comparison between the type specimen of *S. edwardsi* and the Callovian steneosaurs from England. There are no records of suitable material from similar stratigraphic horizons in France, which could be designated as lectotype, and one cannot, therefore, be absolutely certain that the proposed synonymy is correct. Although its relationship with the steneosaurs examined in this work remains problematical, it is important to record the existance of this senior Callovian steneosaur species *S. edwardsi.* The next available name is *S. durobrivensis* Andrews, 1909, whose holotype is BM(NH) R3701.

Diagnosis. Short rostrum; preorbital length *c.* 60 % or less of total length of skull. Nasals and premaxillae separated by 36–56 % of total length of rostrum. Teeth blunt, rounded at tips; crowns become increasingly blunt as size of skull increases; twenty-eight to thirty teeth in each maxilla. Mandibular symphysis *c.* 40 % of length of jaw.

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