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(Reptilia, Ichthyosauria)

C. McGowan





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# Differential Growth in Three Ichthyosaurs: *Ichthyosaurus communis*, *I. breviceps* and *Stenopterygius quadriscissus*

## Abstract

Changes in morphological proportions during growth were investigated in the Lower Jurassic ichthyosaurs, *Ichthyosaurus communis* Conybeare 1822, *I. breviceps* Owen 1881, and *Stenopterygius quadriscissus* (Quenstedt) 1858. The growth constants  $\alpha$  and  $b$  from the allometric equation  $y = bx^\alpha$  were evaluated using Bartlett's Model II regression method, and Kermack and Haldane's reduced major axis method.

Intracranial growth was mainly isometric in all three species. Growth of the orbit had a negative allometry in *I. communis* with some indication of positive allometry in *I. breviceps*. The external naris had a positive allometric growth in *I. communis*. There is some indication that maxillary growth had a negative allometry in *I. breviceps*, and a positive allometry in *Stenopterygius quadriscissus*. Independent evidence suggests that positive allometric growth in the maxilla was characteristic of the longipinnates.

Growth of the head relative to the body was negatively allometric in *I. communis* and *S. quadriscissus* while growth of the forefins was largely isometric. In *S. quadriscissus* the area of the tail and dorsal fin increased exponentially, and the dorsal fin came to lie proportionally further forward. There was a trend towards increasing the angle of the tail bend. The possible significance of these changes is discussed, together with the functional morphology of the tail.

## Introduction

In a systematic study of Lower Liassic latipinnate ichthyosaurs (McGowan, 1969), it was necessary to determine whether differential growth was responsible for some of the observed differences among taxa. *Ichthyosaurus intermedius* Conybeare and *I. communis* Conybeare were shown to represent respectively upper and lower parts of a growth series, but a critical evaluation of growth constants was not given. The present investigation reports on growth phenomena in three species: *I. communis*, *I. breviceps* (both Lower Liassic in age) and *Stenopterygius quadriscissus* (Upper Liassic).

Numerous allometric growth studies have been conducted on a variety of animals since the publication of Huxley's classic study (1932) on the subject (e.g. Mackay, 1943, on *Cancer*; Martin, 1949, on fishes; Olson, 1951, on the Permian amphibian *Diplocaulus*; Gould, 1966a, on Pleistocene snails). Allometric growth is expressed by the equation,  $y = bx^\alpha$ , where  $y$  = organ size,  $x$  = body size,  $\alpha$  = the allometric growth constant,  $b$  = a constant which is numerically equal to organ size when body size equals unity (see Huxley, 1932; Gould, 1966b). This exponential equation can be transformed into the linear logarithmic form,  $\log y = \log b + \alpha \log x$ . A serious criticism of most studies is the absence of significance tests of the results. Gould (1966b, p. 600) noted that even rather high values of  $\alpha$  may not necessarily differ significantly from unity and referred to the increase in thickness of the parietal bone relative to the skull length in *Diplocaulus magnicornis*. Although the value for  $\alpha$  was high (1.79) it was not significantly different from unity despite a high correlation coefficient ( $r = 0.88$ ). Sometimes departures from simple allometry have been made to "fit" the linear logarithmic transformation, with meaningless results (for an excellent review of the subject see Gould, 1966b). Investigations of allometry therefore must include significance tests on estimates of the growth constants.

In allometric studies,  $\alpha$  and  $b$  are frequently evaluated by least squares regression of the logarithmically transformed values of organ and body size. However, least squares is a Model I regression technique which assumes that the independent variable ( $x$ ) is measured without error (see Sokal and Rohlf, 1969). As both  $x$  and  $y$  are measured with error, a Model II regression technique must be used if significance tests are to be computed. Kermack and Haldane (1950) proposed the reduced major axis method for evaluating  $\alpha$  and  $b$ , a technique which fits the reduced major axis of the correlation ellipse and which is independent of the regression models. The reduced major axis may be calculated from raw or logarithmic data, using different equations which produce slightly different values for  $\alpha$  and  $b$  (Kermack and Haldane, 1950, p. 40). The reduced major axis technique has the advantage of being invariant with change of scale, but significance tests are not available. A Model II regression technique devised by Bartlett (1949) and advocated by Simpson et al. (1960) provides both confidence limits and significance tests of estimates of  $\alpha$  and  $b$  and is therefore preferable. Several other methods are available, and a useful evaluation of ten of these was given by Kidwell and Chase (1967) in a computer-simulation growth study. They found four methods to be most accurate: Kermack and Haldane's reduced major axis method calculated from logarithmic data, Bartlett's method calculated from logarithmic data, and two least squares regression methods.

Even though least squares is a Model I regression method it continues to be used, and Gould (1966b, p. 600) noted that when the correlation between the two variates ( $x$  and  $y$ ) is high, the least squares regression and the reduced major axis methods give almost identical results. Brown and Davies (1972), investigating allometric growth in the cockroach *Ectobius*, pointed out the inappropriateness of using least squares but



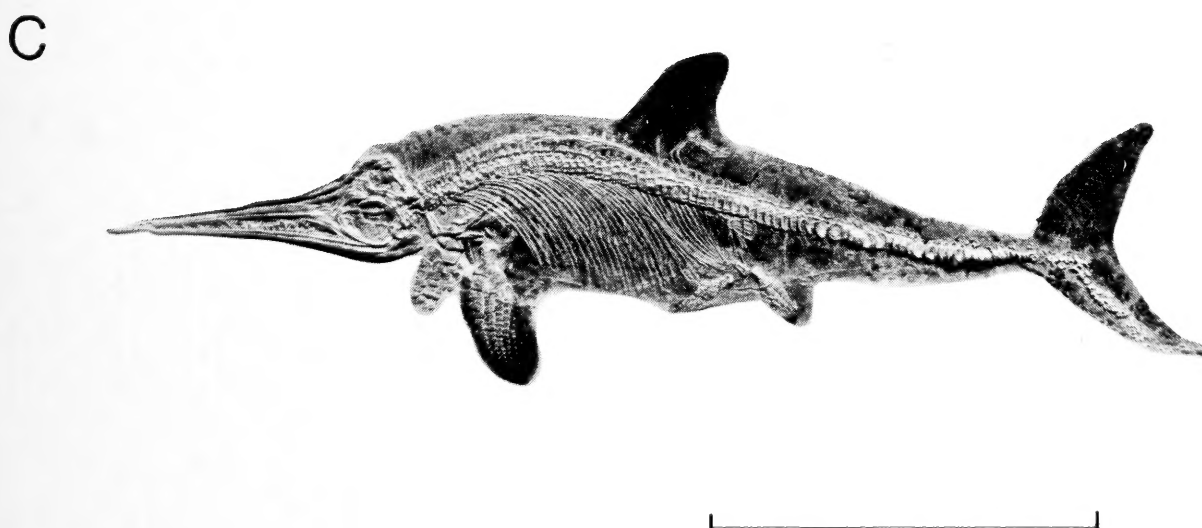
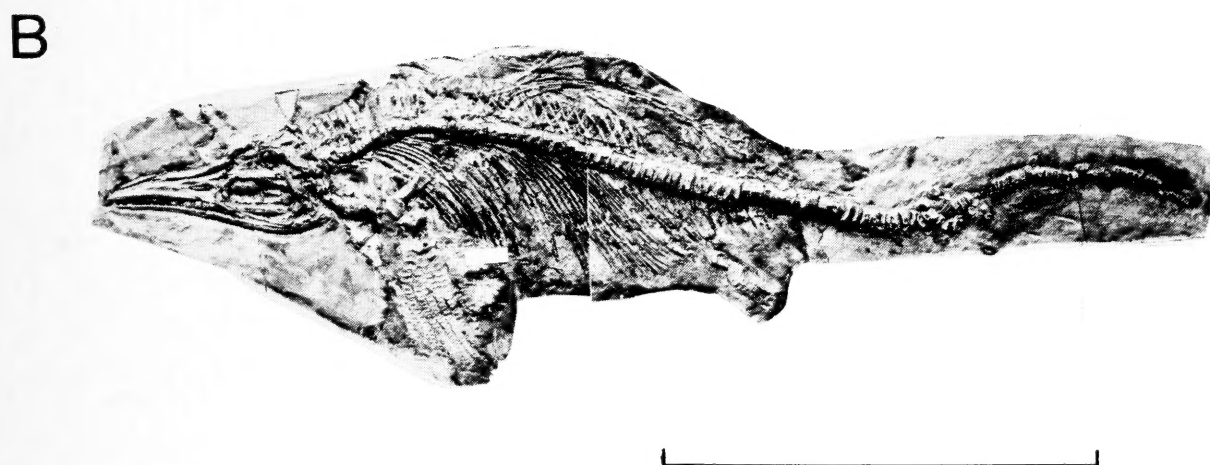
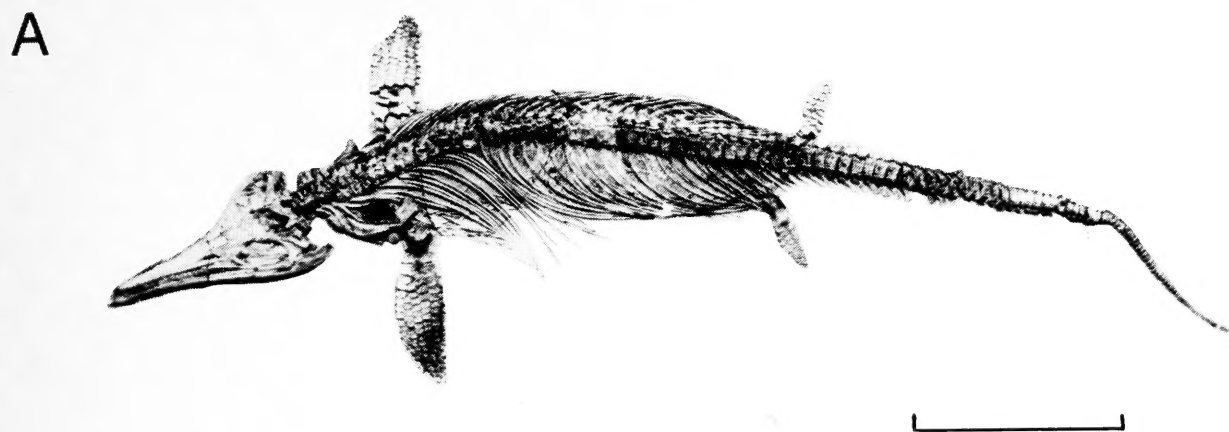


Fig. 1 Representative specimens of three ichthyosaur species (scale = 50 cm)  
A. *Ichthyosaurus communis* BMNH 2013.  
B. *I. breviceps* BMNH 43006.  
C. *Stenopterygius quadriscissus* BMNH R4086.

still included limits for  $\alpha$  and  $b$  and tests of significance derived from that method. However, they also used a Model II method (Bartlett's) and found the results compared closely. Of all methods outlined above, least squares tends to give the best fit for known data, producing values for  $\alpha$  and  $b$  which are more appropriate for predicting outside the range of the original data. It is therefore useful to include least squares estimates of  $\alpha$  and  $b$  along with those from Bartlett's method and Kermack and Haldane's method.

## Materials and Methods

Measurements were taken from: 35 specimens of *I. communis*, Lower Liassic (Hettangian and Sinemurian) of England; seven specimens of *I. breviceps*, Lower Liassic (Hettangian and Sinemurian) of England; and nine specimens of *S. quadriscissus*, Upper Liassic (Lower Toarcian) of Germany (Fig. 1). Additional data were obtained from photographs of five specimens of *S. quadriscissus* (Hauff, 1953), and data for five foetal specimens of this species were taken from Fraas (1891). The abbreviations used for collections examined are: BC, Bath Collection, at present located in the University of S. Wales and Mons., Cardiff; BMNH, British Museum (Natural History), London; CM, Carnegie Museum, Pittsburgh; GS, Geological Survey, London; LCM, Leicester County Museum; OUM, Oxford University Museum; ROM, Royal Ontario Museum; SMC, Sedgwick Museum, Cambridge University; SCC, Street Collection, in care of Clarks Shoe Company, Street, Somerset; USNM, United States National Museum, Washington.

All measurements (cm) were made with vernier calipers accurate to .01 cm, except those of body length which were taken with a tape, accurate to 0.1 cm.

### EVALUATION OF $\alpha$ AND $b$

Bartlett's method was used to evaluate  $\alpha$  and  $b$ , to set 95% confidence limits, and also to test the significance of the results. Kermack and Haldane's reduced major axis method (calculated from logarithmic data) and least squares were used to give comparative values for  $\alpha$  and  $b$ . All computations were performed on an IBM 370/165 computer at the University of Toronto Computer Centre, using the programs ALOMET, LINREG and BARTLT (available from author). The latter program was adapted from that in Davies (1971, p. 208). In the reduced major axis method, natural logarithms were used, whereas common logarithms were used in the other methods.

### CONFIDENCE LIMITS AND SIGNIFICANCE TESTS

Bartlett's method was used to calculate 95% confidence limits for  $\alpha$  and  $b$  and to compute three significance tests, each with  $(n-3)$  degrees of freedom, as follows: 1) to test whether  $\alpha$  differs significantly from zero, i.e. to test the significance of the regression; 2) to test whether  $\alpha$  differs



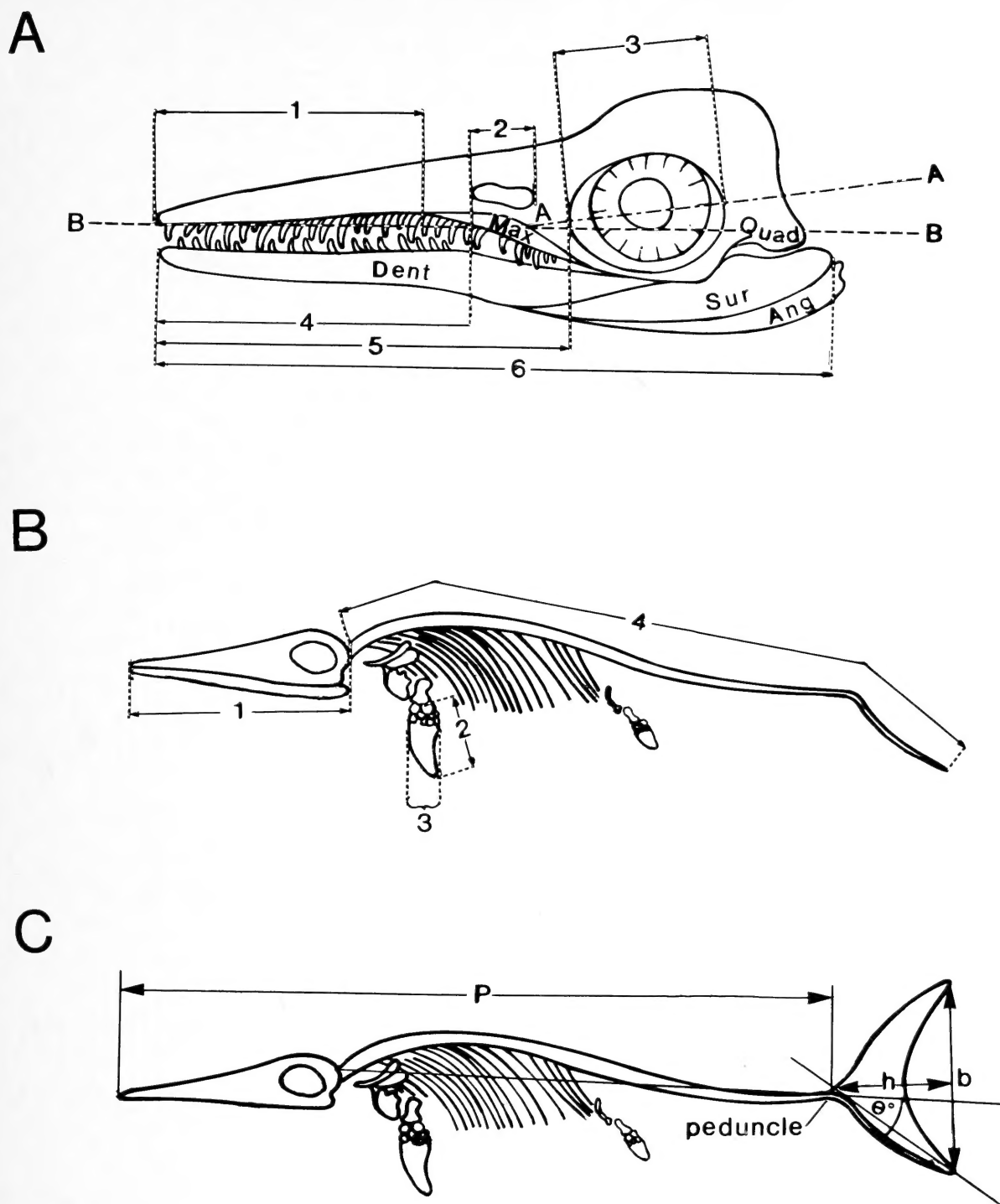


Fig. 2 Standard measurements for the ichthyosaurs studied.

- A. Diagram of skull showing cranial measurements: 1 — length of premaxillary segment, 2 — length of external naris, 3 — diameter of orbit, 4 — length of prenasal segment, 5 — length of snout, 6 — length of jaw; B-B — longitudinal axis of skull, A-A — longitudinal axis of orbit, Ang — angular, Dent — dentary, Quad — quadrate, Sur — surangular, Max — maxilla.
- B. Diagram showing body measurements: 1 — length of jaw, 2 — length of forefin, 3 — width of forefin, 4 — length of body (without the skull).
- C. Diagram showing characters measured in investigating growth of the tail: P — precaudal body length, b — base length of the triangle formed between tips of the tail fin and the peduncle, h — height of the triangle, measured at right angles to the base,  $\theta^\circ$  — angle of tail bend.

significantly from one, i.e. whether there is significant departure from isometric growth; 3) to test whether the relationship between  $x$  and  $y$  is linear, i.e. whether growth is simple with no changes in the allometric growth constant  $\alpha$ . These three test statistics are designated  $T_0$ ,  $T_1$ , and  $T_L$  respectively in the sections beyond. Probabilities are designated throughout accordingly:  $P < 0.001$  as \*\*\*,  $0.01 > P > 0.001$  as \*\*,  $0.05 > P > 0.01$  as \*,  $0.1 > P > 0.05$  as † (near-significant),  $P > 0.1$  as ns (not significant).

#### SIZE AND SIZE RANGES

In any allometric investigation a selected reference dimension serves as a general indicator of body size. For most of my analyses the length of the jaw is used in preference to body length as the reference because many skeletons were incomplete. Jaw length is used in preference to skull length because it can be measured more easily and more accurately (see McGowan, 1972a). Predicted size ranges were taken to be those within which 95% of the population would fall, i.e.  $\bar{x} \pm 1.96s$  where  $\bar{x}$  is the mean jaw length and  $s$  is the standard deviation.

#### PARAMETERS USED IN GROWTH INVESTIGATIONS

Intracranial growth was investigated by comparing cranial characters ("organs") with the length of the jaw ("body size"). The cranial characters used (Fig. 2A) are length of snout, diameter of orbit, length of external naris, length of premaxillary segment (distance between the tip of the snout and the anterior tip of the maxilla), and the length of prenarial segment (distance between the tip of the snout and the anterior margin of the external naris). Relative changes in body proportions were investigated by comparing body characters with the length of the body minus the skull. The body characters used (Fig. 2B) are length of jaw, length of forefin and width of forefin.

Changes in the shape of the tail in *S. quadriscissus* were evaluated by measuring the angle of the tail bend (Fig. 2c) and by comparing an estimate of the area of the caudal fin with the pre-caudal body length. The area of the caudal fin was estimated by approximating the tail to a triangle, and taking the product of half the base (Fig. 2c: b) and the height (Fig. 2c: h). Pre-caudal body length (Fig. 2c: p) was measured from the tip of the snout to the tail peduncle. Changes taking place in the dorsal fin were examined by measuring its area (approximated to a triangle, as in the tail), its shape, and its relative position. Because these data were all obtained from photographs and therefore subject to error (estimated empirically at 10%) it was not possible to evaluate any of the growth constants. However, the correlation coefficient was evaluated in each case, and the significance of the correlation ( $t$ ) tested in the usual manner (see Simpson et al., 1960, p. 242).

## Results

Bartlett's method, the reduced major axis and the least squares method give essentially similar estimates of  $\alpha$  and  $b$ , especially when the correlation coefficient ( $r$ ) is high (Table 1). With one possible exception (orbital growth in *I. breviceps*) growth was simple throughout with no changes occurring in the allometric growth constant  $\alpha$  during ontogeny.

## Discussion

### INTRACRANIAL GROWTH

Intracranial growth was mostly isometric (Table 1). In all three species the relative length of the snout remains constant throughout life, as does the relative length of the prenarial segment. In both *I. breviceps* and *S. quadriscissus* the values of  $\alpha$  for the length of the premaxillary segment deviate rather widely from unity, being 1.420 and 0.652 respectively. Because of the small sample sizes on which the estimates were based, however, the deviations are not statistically significant. Growth of the prenarial segment (which has similar dimensions to the premaxillary segment; see Fig. 2A) is isometric in *I. breviceps* and *S. quadriscissus*; thus it is evident that allometric growth occurs in the maxilla. There is therefore some indication that the growth of the maxilla is negatively allometric in *I. breviceps*, and positively allometric in *S. quadriscissus*. Positive allometric growth of the maxilla may have been a longipinnate character.

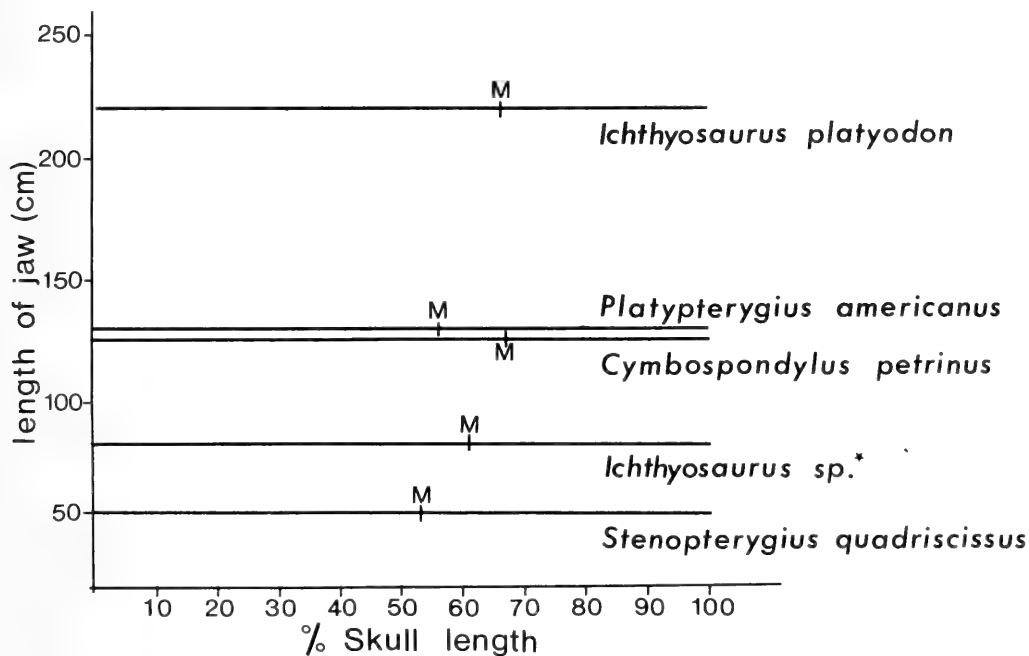


Fig. 3 Relative length of the maxilla in longipinnate ichthyosaurs; species are arranged in order of maximum skull length: M — position of anterior tip of the maxilla (tip of the snout at right). *Ichthyosaurus sp.\** is a new species of Lower Liassic longipinnate, not yet described (McGowan, in press).

TABLE 1

Estimated values of  $\alpha$  and  $b$  for cranial and body characters

CHARACTERS		BARTLETT'S					
y	x	n	r	$\alpha$	b	95% confidence limits for $\alpha$	95% confidence limits for b
<i>Ichthyosaurus communis</i>							
length of snout	} length of jaw	27	0.993	0.988	0.652	0.936 - 1.039	0.644 - 0.660
diameter of orbit		22	0.979	0.916	0.299	0.815 - 1.018	0.283 - 0.315
length of external naris		20	0.930	1.356	0.025	1.099 - 1.669	-0.016 - 0.666
length of prenarial segment		21	0.979	0.972	0.534	0.868 - 1.075	0.519 - 0.550
length of premaxillary segment		23	0.979	0.948	0.521	0.852 - 1.045	0.509 - 0.535
length of jaw	} length of body	18	0.980	0.753	0.921	0.676 - 0.855	0.903 - 0.939
length of forefin		16	0.970	1.007	0.115	0.870 - 1.176	0.083 - 0.147
width of forefin		18	0.966	0.977	0.059	0.834 - 1.125	0.030 - 0.088
<i>Stenopterygius quadriscissus</i>							
length of snout	} length of jaw	9	0.983	0.950	0.809	0.810 - 1.247	0.796 - 0.822
diameter of orbit		10	0.938	0.882	0.307	0.351 - 1.194	0.284 - 0.333
length of external naris		7	0.051	0.221	1.349	-1.199 - 4.156	1.250 - 1.444
length of prenarial segment	} length of jaw	6	0.980	0.894	0.831	-0.310 - 1.226	0.812 - 0.851
length of premaxillary segment		8	0.822	0.652	1.669	0.257 - 1.458	1.634 - 1.700
length of jaw	} length of body	9	0.926	0.357	7.085	0.152 - 0.498	7.058 - 7.111
length of forefin		9	0.950	1.023	0.099	0.627 - 1.353	0.042 - 0.155
width of forefin		9	0.954	0.754	0.163	0.468 - 0.980	0.123 - 0.200
<i>S. quadriscissus</i> (includes embryos)	} length of body						
length of jaw		13	0.970	0.507	3.363	0.428 - 0.601	3.340 - 3.380
<i>Ichthyosaurus breviceps</i>							
length of snout	} length of jaw	7	0.957	1.172	0.314	0.830 - 1.600	0.230 - 0.320
diameter of orbit		6	0.945	1.620	0.045	0.466 - 4.280	-0.002 - 0.002
length of external naris	} length of jaw	7	0.661	1.350	0.037	-2.768 - 3.411	-0.077 - 0.111
length of prenarial segment		6	0.809	1.134	0.247	0.270 - 1.413	0.230 - 0.270
length of premaxillary segment		7	0.969	1.420	0.107	0.700 - 2.008	0.082 - 0.111

*Ichthyosaurus communis*, *I. breviceps* and *Stenopterygius quadriscissus*

METHOD			REDUCED MAJOR AXIS METHOD CALCULATED FROM LOGARITHMIC DATA		LEAST SQUARES VALUES		INFERRED GROWTH PATTERNS
T <sub>0</sub>	T <sub>1</sub>	T <sub>L</sub>	α	b	α	b	
0.988***	0.490 ns	70.491***	0.998±0.022	0.630±0.074	0.992	0.644	simple isometry
9.068***	1.740†	6.096***	0.931±0.040	0.284±0.137	0.956	0.303	simple isometry
0.325***	2.985**	3.077**	1.363±0.112	0.025±0.386	1.268	0.034	simple, positive allometry
8.507***	0.583 ns	69.081***	1.007±0.044	0.475±0.151	0.986	0.501	simple isometry
0.724***	1.137 ns	24.782***	0.961±0.040	0.497±0.138	0.949	0.519	simple isometry
3.034***	4.174***	4.759***	0.734±0.034	1.007±0.157	0.731	1.025	simple, negative allometry
0.081***	0.110 ns	24.983***	0.992±0.060	0.124±0.278	0.930	0.163	simple isometry
8.681***	0.343 ns	30.436***	0.996±0.061	0.054±0.282	0.946	0.068	simple isometry
5.341***	0.631 ns	75.420***	0.913±0.054	0.928±0.203	0.898	0.980	simple isometry
3.047*	0.854 ns	31.523***	1.012±0.110	0.189±0.412	0.951	0.238	simple isometry
0.398 ns	1.104 ns	8.145***	1.044±0.394	0.065±0.455	0.059	3.779	simple, may have negative allometry but inconclusive
3.023*	1.203 ns	102.006***	0.936±0.074	0.711±0.275	0.919	0.752	simple isometry
4.403**	1.458 ns	17.580***	0.682±0.137	1.492±0.511	0.561	2.340	simple, some evidence of negative allometry
3.670*	12.370***	6.132 ns	0.416±0.052	5.311±0.255	0.385	6.163	simple negative allometry
4.967**	0.160 ns	7.073***	1.101±0.114	0.068±0.557	0.047	0.088	simple isometry
1.921**	2.682*	14.901***	0.812±0.081	0.123±0.398	0.775	0.147	simple negative allometry
2.312***	7.429***	36.365***	0.511±0.034	3.301±0.155	0.496	3.534	simple negative allometry
0.837**	1.507 ns	204.570***	1.177±0.129	0.310±0.395	1.127	0.361	simple isometry
0.789*	1.914 ns	0.555 ns	1.639±0.217	0.042±0.662	1.551	0.056	may not be simple, some evidence of positive allometry
0.293 ns	0.383 ns	10.160***	2.375±0.673	0.002±2.065	0.252	1.188	inconclusive
0.585*	0.884 ns	568.950***	1.345±0.322	0.129±0.997	1.089	0.285	simple isometry
0.867*	1.874 ns	10.118***	1.481±0.137	0.089±0.421	1.436	0.102	simple, some evidence of positive allometry

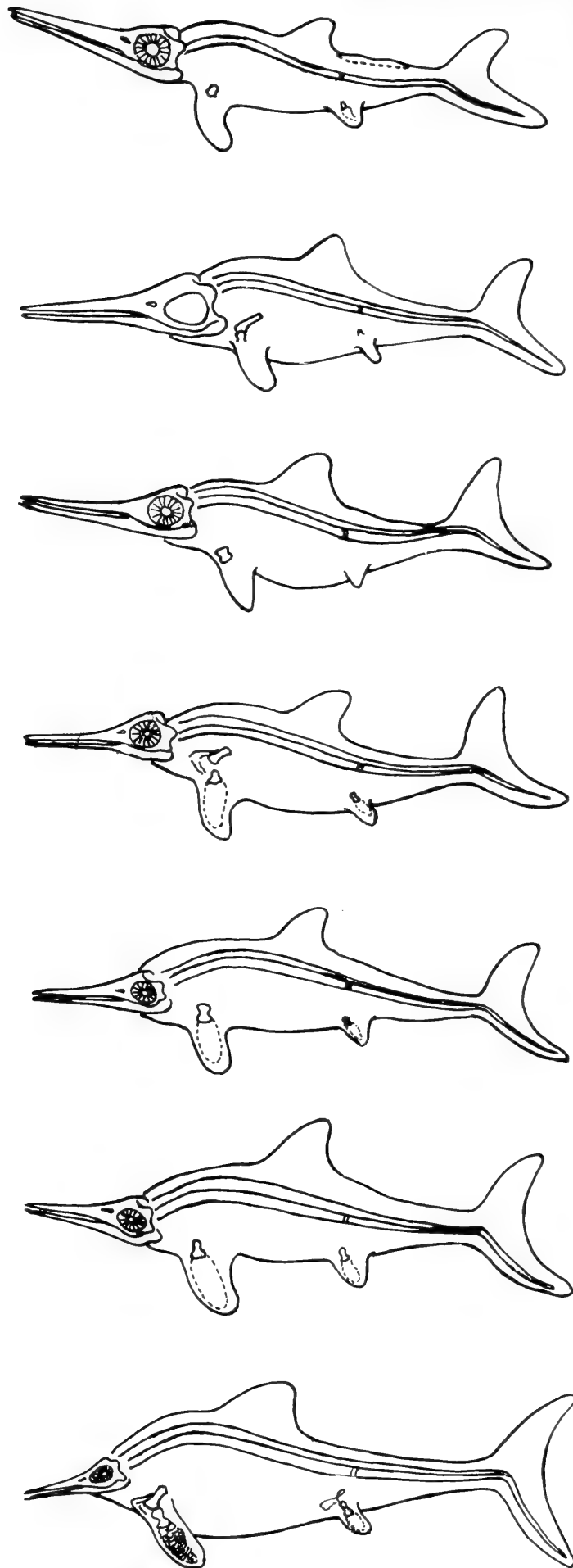


Fig. 4 Growth series for *Stenopterygius quadricissus* (after Von Huene, 1922, pl. 21). Starting at the top, the body lengths are 50.0, 62.5, 83.0, 112.0, 135.0, 213.0, and 255.0 cm.



During the evolution of the longipinnates there was a trend towards maxillary reduction, but this was reversed during post-Liassic times (McGowan, 1972b, fig. 6). If longipinnate species are arranged in order of adult skull length it is apparent that the larger species have relatively longer maxillae (Fig. 3). Therefore the maxillary trend seen during longipinnate evolution is explicable in terms of allometric growth.

Orbital growth is isometric in *S. quadriscissus* and in *I. communis* but may be positively allometric in *I. breviceps* ( $\alpha = 1.620$ ). Here non-significance is attributable to small sample size ( $n = 6$ ), because the correlation coefficient is high ( $r = 0.945$ ). Small sample size may also be responsible for the low  $T_L$  value, though there may also be departure from simple growth in this character. The growth of the external naris has a positive allometry in *I. communis* ( $\alpha = 1.356$ ), but results are inconclusive in the other two species where the correlation coefficients are low. It has been suggested that variations in narial size are probably correlated with olfaction rather than respiration (McGowan, 1972b) and it could be that olfactory acuity increased with age in *I. communis*. However, caution should be exercised in drawing conclusions from such evidence.

#### GROWTH OF THE HEAD AND FOREFINS

##### RELATIVE TO THE BODY IN *I. communis* AND *S. quadriscissus*

Two sets of values for  $\alpha$  and  $b$  were obtained for *S. quadriscissus* for the growth of the head relative to the body (Table 1); one set for post-natal individuals, mainly adults, ( $n = 9$ ), the other including additional data from four foetuses ( $n = 13$ ). Values for  $\alpha$  and  $b$  calculated by Bartlett's method for the two groups are 0.357 and 7.085, and 0.507 and 3.363 respectively; the correlation coefficient was higher for the larger grouping ( $r = 0.970$  compared with 0.926). When the two sets of values for  $\alpha$  and  $b$  were used to predict jaw length in a known specimen of *S. quadriscissus* (Hauff, 1953, pl. 9b, data not used in original calculation of  $\alpha$  and  $b$ ) the values from the smaller group gave an error of 7.7% whereas the error was only 0.30% in the group including foetuses. The most appropriate values for  $\alpha$  and  $b$  are therefore 0.507 and 3.363.

In common with most vertebrates, growth of the head relative to the body had a negative allometry in *I. communis* and *S. quadriscissus*. In mammals negative allometric growth of the head is probably correlated with very rapid growth of the brain during foetal life. However, in the blue whale (*Sibbaldus musculus*) the head has a positive allometry ( $\alpha = 1.55$ ) (Huxley, 1932, p. 137). (The blue whale is a filter-feeder and it seems that the increase in relative size of the head is correlated with this mode of feeding; the food requirement of the whale increases with the cube of the length, whereas the area of the filtering surfaces increases only with its square.) In ichthyosaurs, in which approximately 70% of length of skull is dentigerous, negative allometric growth of the head is far more likely correlated with development of the feeding apparatus than with brain growth. Presumably young animals required relatively more food than older individuals, and consequently had relatively larger heads. The very small value of  $\alpha$  for head growth in *S. quadriscissus* explains the

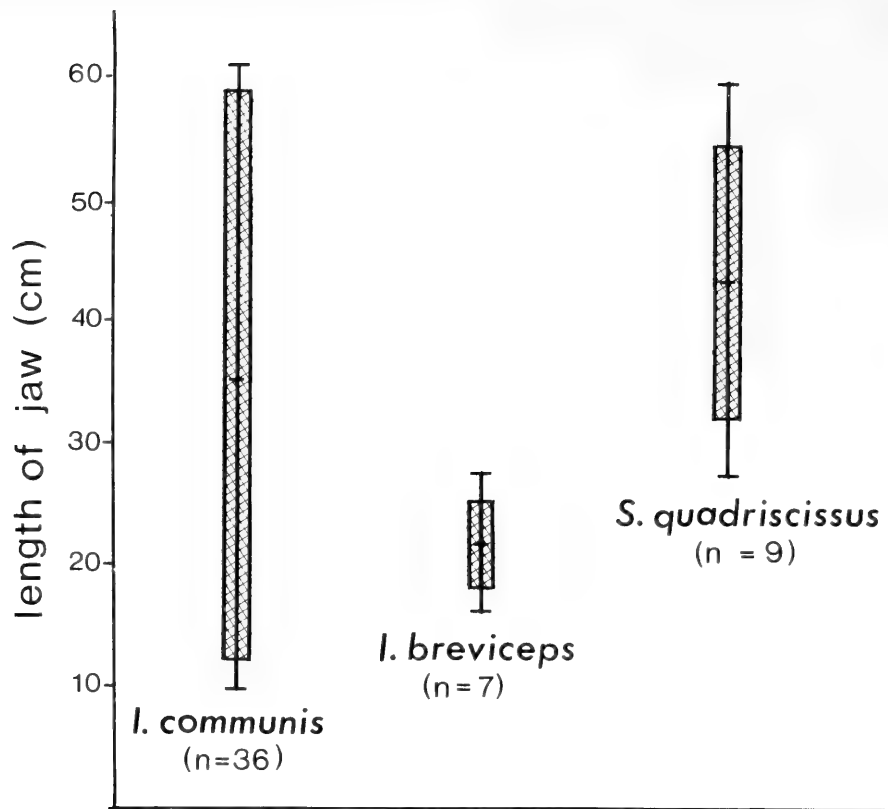


Fig. 5 Size ranges of *Ichthyosaurus communis*, *I. breviceps*, and *Stenopterygius quadriscissus*, based on 95% confidence limits of jaw length. Solid boxes — observed range.

great disparity in head proportions at the extreme ends of the growth series in this species as shown in Fig. 4 (redrawn from Von Huene, 1922, pl. 21).

Growth of the forefins is isometric in *I. communis* (Table 1), and in *S. quadriscissus* fin length increases isometrically, whereas fin width has a weak negative allometry ( $\alpha = 0.754$ ). The forefins were broad-based structures in both species, and were used as hydroplanes for adjusting the swimming level, and probably also as stabilizers. The force generated by a forefin at a given angle of attack is directly proportional to its area (see Alexander, 1969). As this area remains relatively constant during growth in *I. communis* and even undergoes a slight reduction in *S. quadriscissus*, it seems that there was no increase in the relative force produced by the fins during ontogeny.

#### SIZE RANGES

Size ranges are based on jaw lengths, and although these are directly proportional to body lengths the proportionality is not the same in all three species. Furthermore, because of the allometric growth of the head, the relationship between jaw length and body length is not constant throughout each size range. The size ranges given (Fig. 5) are therefore only an approximation to total body size. Although sample sizes are small in *I. breviceps* ( $n = 7$ ) and *S. quadriscissus* ( $n = 9$ ), the 95% confidence

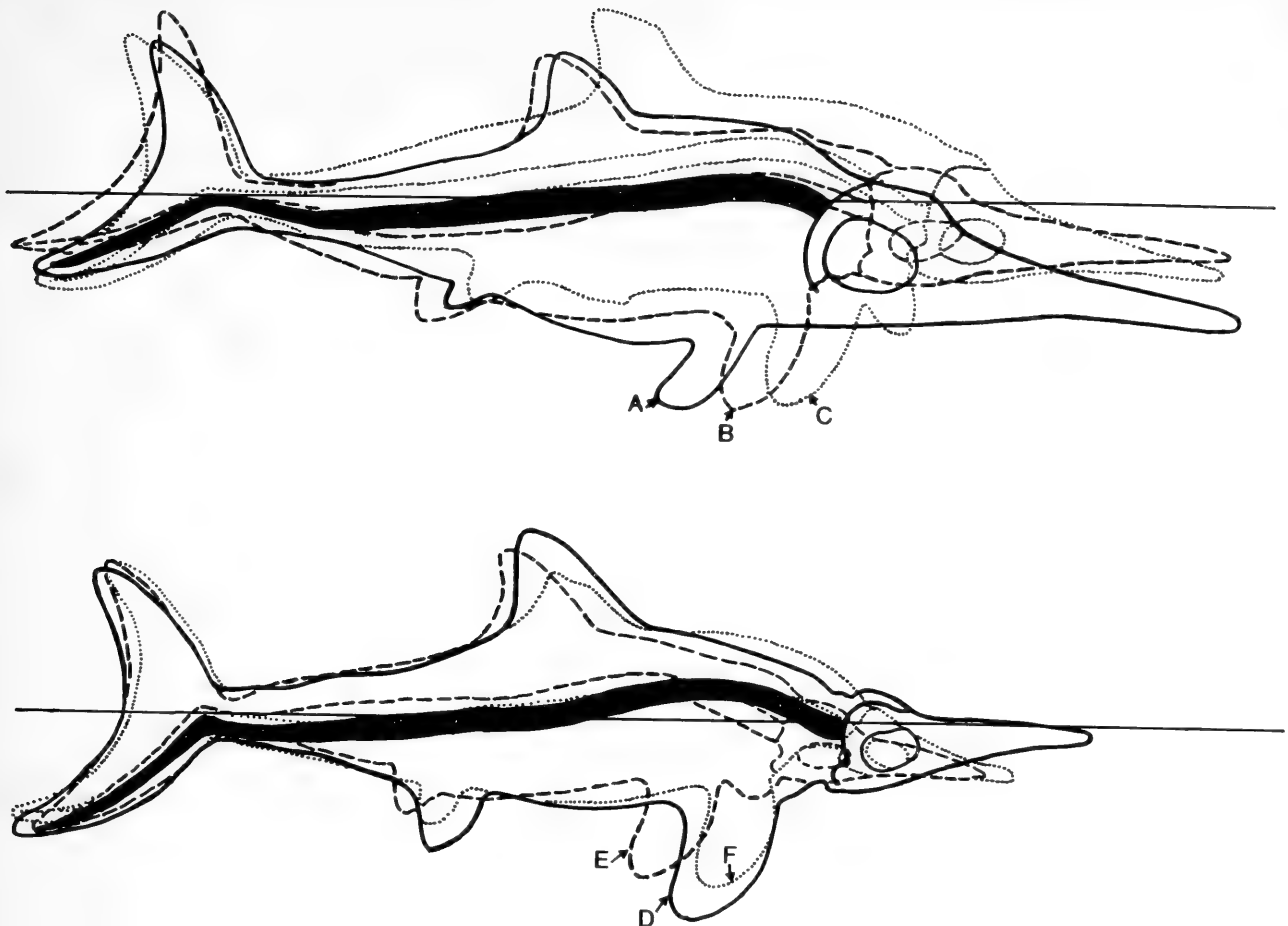


Fig. 6 Superimposed body outlines of specimens of *Stenopterygius quadriscissus* (drawn to same size), taken from extremes of the size range (smallest individuals at top). A. From Hauff (1953, pl. 9a), 62 cm long. B. From Hauff (1953, pl. 4c), 115 cm. C. BMNH R4086, 145 cm. D. From Hauff (1953, pl. 5), 200 cm. E. From Hauff (1953, pl. 7a), 230 cm. F. From Hauff (1953, pl. 9b), 304 cm.

limits (see p. 6) do not differ greatly from the observed ranges (Fig. 5). *I. breviceps* is smaller than its latipinnate contemporary *I. communis*, and also has a smaller size range. Longipinnates tended to be larger than latipinnates (McGowan, 1972b), and although the size range of *S. quadriscissus* falls within that of *I. communis* (Fig. 5), the mean value is higher in the former species ( $t = 2.592^*$ ).

#### CHANGES OCCURRING IN THE TAIL AND DORSAL FIN DURING ONTOGENY IN *S. quadriscissus*

The remarkable state of preservation of certain specimens of *S. quadriscissus* where the body outline is preserved as a thin carbonaceous film has facilitated observations of ontogenetic changes in the tail and dorsal fin. During development of the tail, the area relative to the precaudal body length increased, and there is some evidence that the angle of the tail bend increased (Table 2). Changes in tail bend angle, however, might simply reflect greater flexibility in younger individuals. Certainly the greatest variation in the angle of the tail bend is seen in the smaller individuals in

the growth series, and if body outlines of individuals from either end of the growth series are superimposed, it is apparent that the greatest variation in body posture occurs in the smaller individuals (Fig. 6). The dorsal fin retained the same general shape during ontogeny, but as with the caudal fin, its relative area increased with body size (Table 2). Furthermore, the position of the dorsal fin, seemingly shifted anteriorly during ontogeny (Fig. 7). Before examining the functional significance of the changes in the tail and dorsal fin, it is necessary to discuss the functional morphology of the ichthyosaur tail.

Fig. 7 Outlines of specimens of *Stenopterygius quadriscissus* (drawn to same size) illustrating the changing relative position of the dorsal fin during ontogeny. A. From Hauff (1953, pl. 9a), 62 cm. B. From Hauff (1953, pl. 7a), 230 cm.

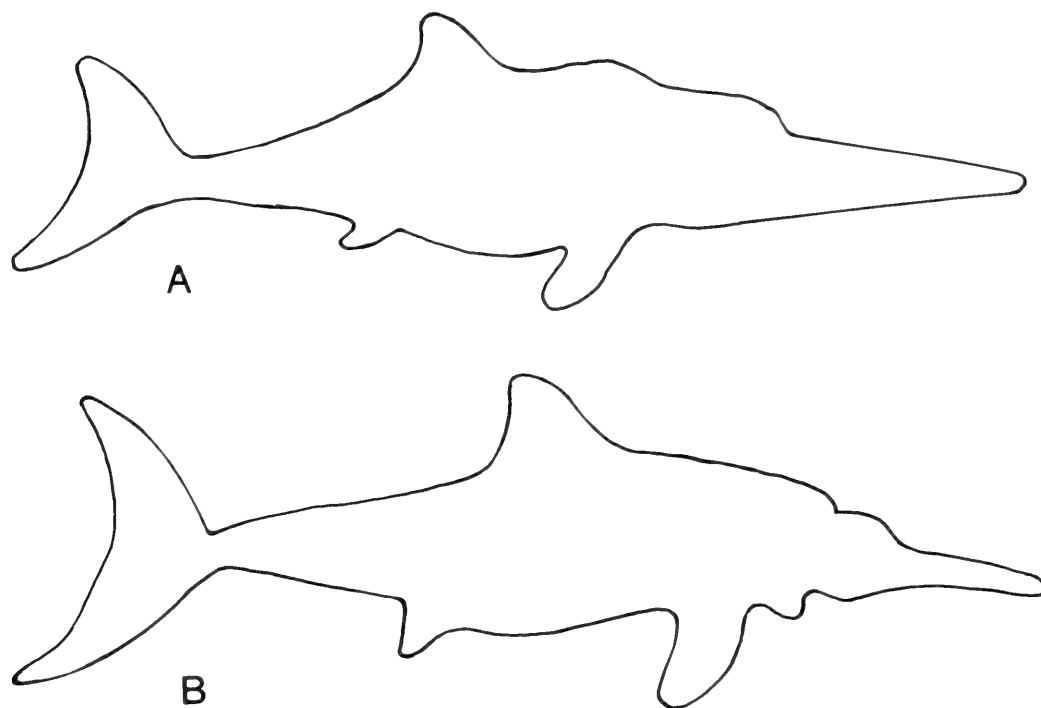


TABLE 2 Changes in the area of the tail and dorsal fin relative to the body size, and in angle of the tail bend during ontogeny in *Stenopterygius quadriscissus*

Specimen	Length of body (cm)	Ratio of tail area to precaudal body length	Ratio of dorsal fin area to precaudal body length	Angle of tail bend (degrees)
Hauff 1953, pl. 9a	62	1.28	0.58	22
ROM 1794	112	—	—	33
Hauff 1953, pl. 4	115	1.59	0.72	18
CM 6003	125	2.37	1.40	32
BMNH R4086	145	1.31	0.68	31
OUM JZ163	200	2.53	1.68	32
Hauff 1953, pl. 7a	230	3.88	1.59	35
ROM 3180	248	—	—	32
Hauff 1953, pl. 9b	304	2.80	—	33
Correlation coefficient		0.738†	0.802†	0.599†

## FUNCTIONAL MORPHOLOGY OF THE ICHTHYOSAUR TAIL

Although excellent accounts of tail function in fishes are already available (see Alexander, 1967, 1968), it would be useful to outline some important points. Most swimming problems can be resolved in terms of the properties of inclined planes. When a bony fish with a homocercal tail sweeps its tail from side to side the water resistance deflects the tail (Fig. 8A) about the peduncle, and the whole tail acts as an inclined plane moving at an acute angle of attack to the direction of motion of the tail (Fig. 8C), giving a resultant forward thrust (upthrust in Fig. 8D). Superimposed upon this

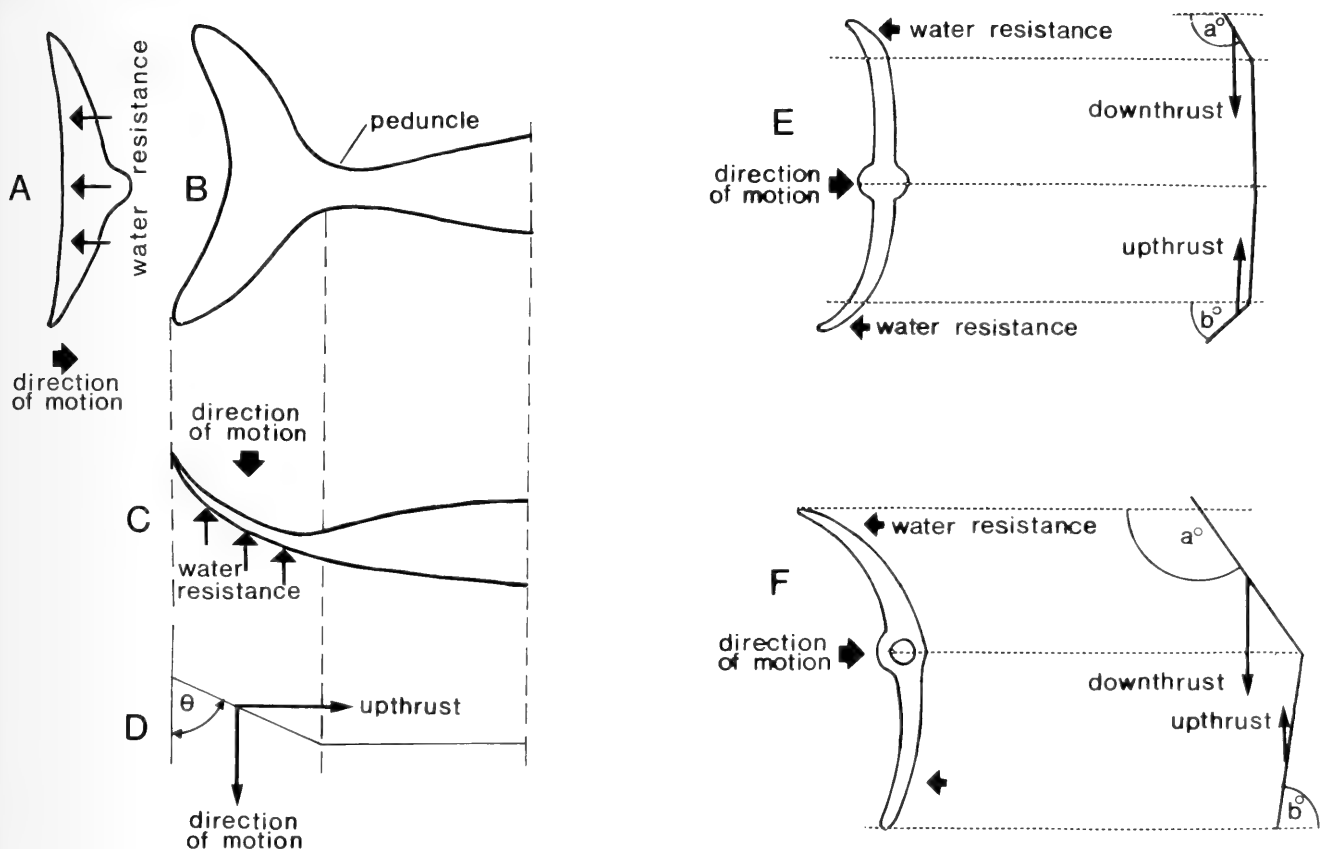


Fig. 8 Caudal mechanics.

- A-D. Diagrams showing the forces generated by a homocercal (teleost fish) tail moving from side to side in the water. A. Posterior view. B. Lateral view. C. Dorsal view. D. Dorsal view, resolving the motion of the tail into the motion of an inclined plane moving at an angle of attack,  $\theta^\circ$ .
- E. Diagram of a homocercal tail moving from side to side, showing how the deflections of the tips can be resolved into movements of inclined planes (posterior view); the downthrust produced by the epicaudal tip, moving at an obtuse angle of attack,  $a^\circ$ , is balanced by the upthrust produced by the hypocaudal tip, moving at an acute angle of attack,  $b^\circ$ .
- F. Diagram of an ichthyosaur tail moving from side to side, showing how deflections of the epicaudal and hypocaudal lobes can be resolved into the movements of two inclined planes (posterior view):  $a^\circ$  — angle of attack of epicaudal plane,  $b^\circ$  — angle of attack of hypocaudal plane.

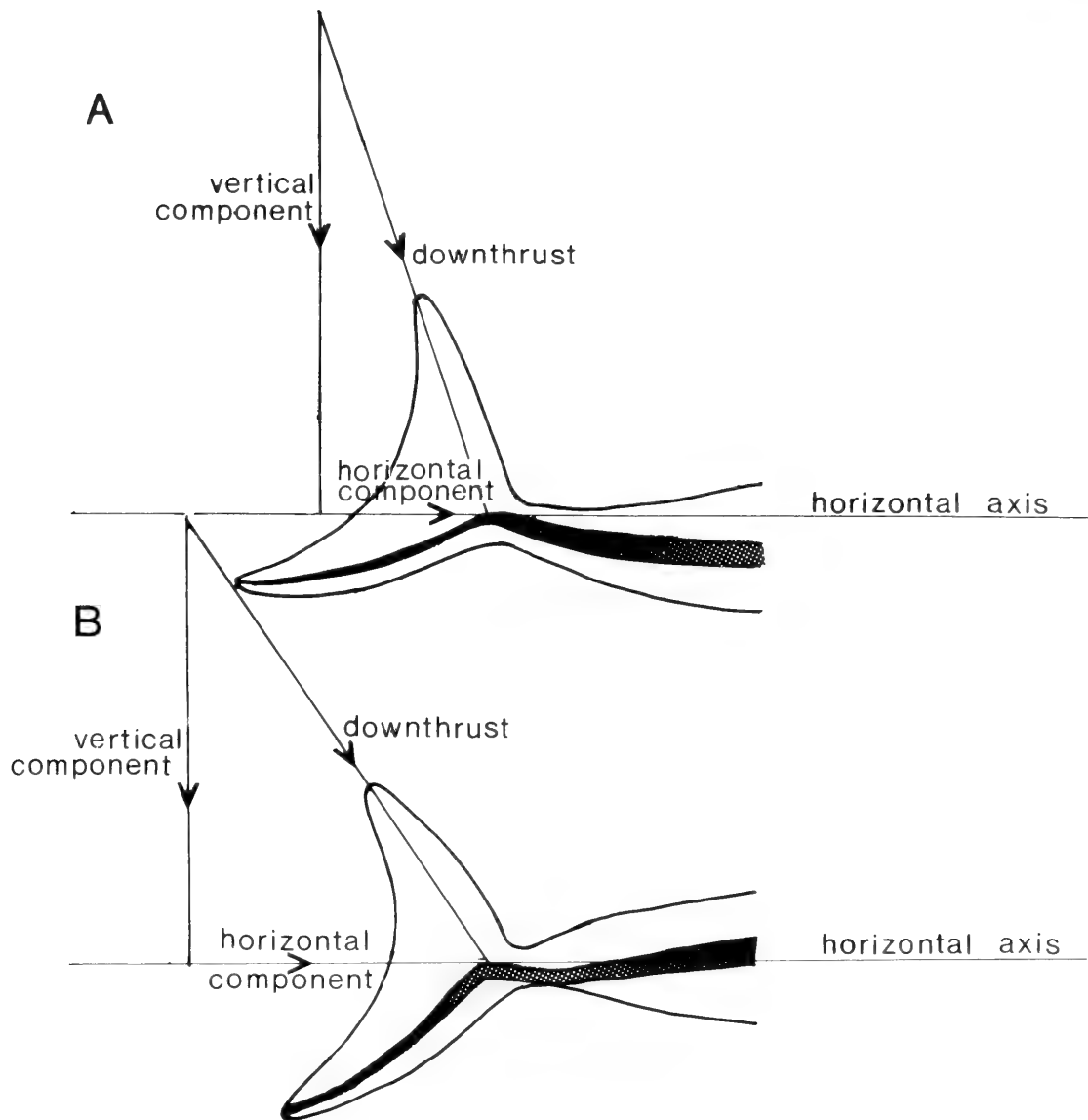


Fig. 9 Diagrams of an ichthyosaur tail showing how the downthrust produced by the epicaudal lobe can be resolved into vertical and horizontal components. A. Angle of tail bend is small. B. Angle is larger and the vertical component is correspondingly decreased.

system are two more inclined planes resulting from deflections of the epicaudal and hypocaudal lobes, particularly towards their tips which are more flexible (Fig. 8E). The epicaudal lobe moves at an obtuse angle of attack (Fig. 8E:  $a^\circ$ ) to the direction of motion of the tail giving a downthrust, which is compensated for by the upthrust given by the hypocaudal lobe moving at an acute angle of attack (Fig. 8E:  $b^\circ$ ) to the direction of motion. In the ichthyosaur, which had a reversed heterocercal tail, the hypocaudal lobe of the tail was more rigid than the epicaudal lobe because of the support afforded by the downturned vertebral column. Thus when the tail was moved from side to side, the epicaudal lobe was deflected more than the hypocaudal lobe (Fig. 8F), producing a greater thrust (down-



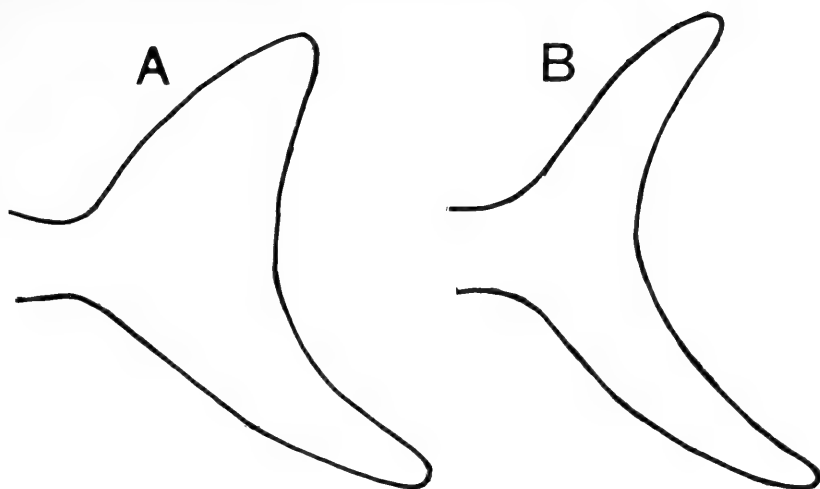


Fig. 10 Outline drawings of the tails of two specimens of *Stenopterygius quadriscissus* illustrating that the aspect ratio of the tail increases during ontogeny. A. Length of body 62 cm (from Hauff, 1953, pl. 9a). B. Length of body 304 cm (from Hauff, 1953, pl. 9b).

ward) than that of the lower lobe (upward). The forward propulsive thrust was therefore accompanied by a net downthrust. The line of action of the epicaudal downthrust was at right angles to the axis of the tail (i.e. the axis about which the upper lobe was deflected), and can be resolved into vertical and horizontal components (Fig. 9A). If the angle of the tail bend is increased the vertical component decreases (Fig. 9B). Thus the net downthrust of the ichthyosaur tail is inversely proportional to the angle of the tail bend.

The caudal downthrust, acting behind the centre of gravity, would be compensated by a downthrust in front of the centre of gravity produced by the pectoral fins. The attitude of the body could be adjusted by changing the angle of attack of the paired fins, and probably also by altering the force applied by the tail. Parenthetically it may be noted that while the animal was swimming on the surface the epicaudal lobe would be largely clear of the water so that the tail would not produce a downthrust. Diving could then be initiated by the negative inclination of the pectoral fins, and once the tail was again submerged the horizontal swimming attitude could be restored.

#### FUNCTIONAL SIGNIFICANCE OF THE TRENDS OCCURRING IN THE TAIL AND DORSAL FIN

Three trends occur during ontogeny: an increase in the relative areas of the caudal fin and dorsal fin, and a weak trend towards an increase in the angle of the tail bend. The exponential growth of the area of the tail can readily be explained in terms of power output and drag. In *S. quadriscissus* the forward propulsive thrust was derived solely from the tail, perhaps with a minor contribution from lateral undulations of the posterior body region (the broad-based paired fins functioned as hydrofoils and it is very doubtful that they could have functioned as paddles). The assumption can be made that swimming would take place at a high Reynold's

number, where

$$\text{Reynold's number} = \frac{\text{density of fluid} \times \text{velocity of object} \times \text{length of object}}{\text{viscosity of fluid}}$$

The Reynold's number for a 200 cm individual, moving at 10 miles per hour, at a sea temperature of 20° C is approximately  $1.1 \times 10^5$ . At high Reynold's numbers the drag force is directly proportional to the square of the body length (drag  $\propto$  length<sup>2</sup>  $\times$  velocity<sup>2</sup>  $\times$  density of fluid). Other things being equal (which is rarely the case) a doubling in body length would require an increase in caudal power-output in the order of four times. The power-output of the tail is proportional to its surface area, and therefore the significance of the exponential growth of the tail becomes obvious. The tail itself produces drag, and the ratio of the thrust produced to the drag generated increases with increased aspect ratio (aspect ratio =  $\frac{\text{vertical height of tail}}{\text{width of tail}}$ ).

Therefore it would be advantageous for the aspect ratio of the tail to increase with growth, and this indeed does happen (Fig. 10).

If the trend towards an increase in the angle of the tail bend is real, it could be explained in terms of relative buoyancy. Because of incomplete ossification and the accumulation of body fat, the specific gravity of juvenile animals is frequently less than that of adults; e.g. marine birds (pers. obs.), harbour porpoise (*Phocoena phocoena*, Gaskin, pers. comm.), elephant seal (*Mirounga leonina*), Bryden (1972). If this were true for ichthyosaurs, there would be an obvious adaptative advantage in having a low-pitched tail in early life as this produces a relatively greater downthrust.

The dorsal fin serves as a stabilizer, mainly to correct yaw, and also roll. The correction of yaw requires that the dorsal fin be placed behind the centre of gravity. Thus, as the body yaws (about an axis passing through the centre of gravity) the dorsal fin acts as an inclined plane giving a corrective thrust (Fig. 11) which brings the body back into line with the direction of motion. Because the corrective force generated by the dorsal fin has to act against the inertia of the body, which is directly proportional to body mass, it follows that the force must increase in proportion to the cube of the body length. Thus the positive allometry of the growth of the dorsal fin is a response to the need for maintaining hydrodynamic stability throughout ontogeny. The change in relative position of the fin during ontology probably reflects a forward shift of the centre of gravity.

### Summary of Conclusions

With some exceptions, intracranial growth in the ichthyosaurian species *Ichthyosaurus communis*, *I. breviceps* and *Stenopterygius quadriscissus* was mainly isometric. Whereas the maxilla appears to have grown with a negative allometry in *I. breviceps*, a latipinnate ichthyosaur, its growth was possibly positive in the longipinnate species *S. quadriscissus*. The suggestion

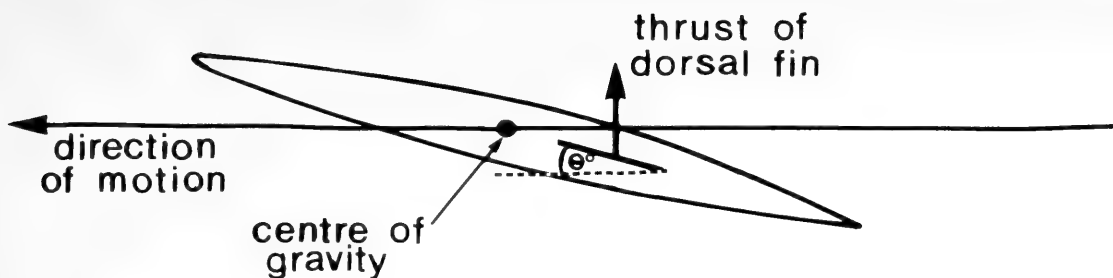


Fig. 11 Representation of an ichthyosaur body in yaw (dorsal view), and the corrective force generated by the dorsal fin. The dorsal fin acts as an inclined plane moving at an angle of attack  $\theta^\circ$  to the direction of motion.

that positive allometry in the maxilla was a longipinnate character is strengthened by the observation that longipinnate species with larger heads usually have relatively larger maxillae. Orbital growth was isometric in *I. communis* with some evidence of positive allometry in the other latipinnate species *I. breviceps*. Results pertaining to the growth of the external naris were inconclusive, except in *I. communis*, where growth of the naris had a positive allometry.

Changes in body proportions during ontogeny are generally more marked than those in the skull and are mainly correlated with hydrodynamics. The negative allometric growth of the head in *I. communis* and *S. quadriscissus* parallels that of most other vertebrates, but here is probably correlated with feeding; juveniles required relatively more food than adults and thus had relatively larger heads. Exponential growth of the tail in *S. quadriscissus* is explained by the need to increase the propulsive thrust to overcome increased drag forces in larger animals. Growth of the dorsal fin is also exponential in order to keep pace with the rapidly increasing inertia of the body.

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