# TWO TRIASSIC FISH FROM SOUTH AFRICA AND AUSTRALIA, WITH COMMENTS ON THE EVOLUTION OF THE CHONDROSTEI

*by* PETER HUTCHINSON

ABSTRACT. Two chondrostean fish from the Triassic are redescribed: *Dicellopyge* from Bekker's Kraal, South Africa; and *Belichthys* from Brookvale, New South Wales, Australia. Analysis of the dermal skull bones in early chondrosteans shows that three distinctive patterns occur, and that there is some evidence that there is a fundamental dichotomy within the Chondrostei.

TWO of the richest Triassic freshwater fish localities are those at Bekker's Kraal, South Africa, and Brookvale, New South Wales. Both faunas include members of the Palaeonisciformes (*sensu lato*), the Redfieldiiformes and the Perleidiformes. The members of the Redfieldiiformes and Perleidiformes have recently been reviewed (Hutchinson 1973) in a paper in which the age of both these localities was also discussed. Two further genera are now redescribed: *Dicellopyge* from Bekker's Kraal, first described by Brough (1931); and *Belichthys* from Brookvale, first described by Wade (1935).

## SYSTEMATIC DESCRIPTIONS

Subclass CHONDROSTEI
Family DICELLOPYGIDAE
DICELLOPYGE Brough, 1931

1931   *Dicellopygae* Brough, pp. 238–239.

*Emended diagnosis.* Skull short with well-developed rostrum. Frontal broad posteriorly, parietal small. Dermopterotic short antero-posteriorly, dermosphenotic crescent shaped, meeting the nasal, and almost entirely separated from the orbital edge by a narrow infraorbito-supraorbital. Infraorbito-supraorbital without posterior extension. Opercular series moderately oblique, including, sometimes, an accessory opercular. Posterior infraorbital extending along anterior edges of both suborbitals. Antorbital separated from upper jaw margin by a rostro-premaxilla. Dermal bones of skull ornamented with ridges and, in the case of the postrostral, with tubercles. Dentition consisting of teeth arranged in two series. Scales with pectinated posterior edges. Caudal fin deeply cleft, inequilobate. Posterior edge of body lobe with strongly developed S-shaped curve. Hinge line at base of body lobe not markedly developed, posterior end terminating at the posterior scale of the convex part of the S curve. Lateral line extending into body lobe and separated from its posterior edge by a row of antero-posteriorly directed scales.

*Type species. Dicellopyge macrodentata* Brough.

*Remarks.* The genus *Dicellopyge* was erected by Brough for the inclusion of two species from Bekker's Kraal, South Africa, *D. macrodentata* and *D. lissocephalus*.

### *Dicellopyge macrodentata* Brough

Plate 72, figs. 1–2; text-figs. 1–4, 6

1931   *Dicellopygae macrodentatus* Brough, pp. 239–242; text-fig. 1, pl. 1, fig. 2.

*Horizon and locality.* Lower Cynognathus Zone (Scythian) of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State, South Africa.

*Diagnosis.* Scale formula

$$\frac{25}{8 \quad 20 \quad 41} \, 47.$$

Angle between axis of body and axis of body lobe 40°. Caudal fin web composed of about 110 rays. About forty epaxial basal fulcra present. Lateral line extending halfway along body lobe.

*Holotype.* G.N. 306 and counterpart G.N. 322 (ex D. M. S. Watson Collection P. 8 and P. 27 together with P. 28).

*Material.* Holotype, P. 16081 and counterpart P. 16082, P. 16084A, and counterpart P. 16085.

*Description.* *D. macrodentata* is a fusiform fish attaining a length of 128 mm measured from snout tip to the posterior tip of the body lobe.

*Skull.* The restoration of the skull of *D. macrodentata* (text-fig. 1) is based mainly on G.N. 322 (Hutchinson 1973, text-fig. 53), P. 16084A, and P. 16085, while the restoration of the pattern of dermal bone ornament (text-fig. 2) is based on P. 16084A. The bones of the extrascapular series have pectinated posterior edges
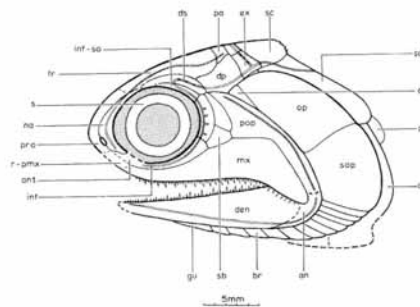


TEXT-FIG. 1. *Dicellopyge macrodentata* Brough. Restoration of skull and pectoral girdle in lateral view.
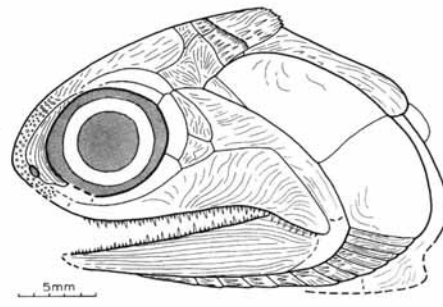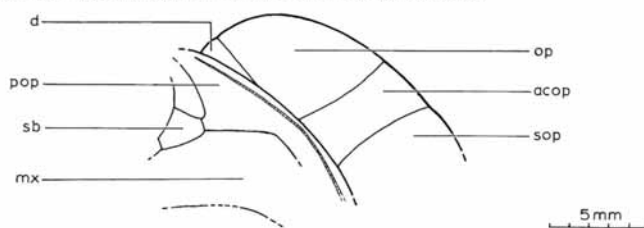
TEXT-FIG. 2. *Dicellopyge macrodentata* Brough. Restoration of skull and pectoral girdle in lateral view showing pattern of dermal bone ornament.

(P. 16084A). The antero-ventral corner of the extrascapular lies close to the antero-dorsal corner of the opercular (P. 16085); its more posterior position in G.N. 322 is due to displacement prior to fossilization. The frontal is broad, especially at the point dorsal to the junction between the dermopterotic and dermosphenotic, and the parietal is rectangular and small.

   The dermopterotic is short antero-posteriorly, and has a sinuous dorsal edge. The opercular series is oblique and is composed of an opercular and subopercular (P. 16084). In the counterpart of the holotype

G.N. 322 (restored in text-fig. 3, see also Hutchinson 1973, text-fig. 53), an accessory opercular is clearly present. The presence of an accessory opercular may indicate that more than one species of *Dicellopyge* are represented by the available specimens; alternatively, there may be variation with respect to this character within the species *D. macrodentata*. As there are no other visible differences between P. 16084A and G.N. 322, the latter hypothesis is assumed to be correct. Similar variation within the species *Perleidus madagascariensis* has previously been observed (Lehman 1952). The area occupied by the opercular in P. 16084A is identical to that occupied by the opercular and accessory opercular in G.N. 322. A dermohyal is present. The pre-opercular is boomerang-shaped and its anterior edge is excavated to receive the posterior edge of the dorsal suborbital and the posterior corner of the ventral suborbital. The dorsal end of the preopercular is not separated from the dermopterotic by several small elements as figured by Brough (1931, text-fig. 1). The area anterior to the dermopterotic is occupied by narrow, crescent-shaped dermosphenotic and infraorbito-supraorbital bones. The anterior ends of these bones are imperfectly preserved, but the dermosphenotic appears to extend anteriorly to meet the nasal, while the infraorbito-supraorbital tapers to a point just anterior to the midpoint of the dorsal orbital edge. The infraorbital sensory canal extends anteriorly along half of the length of the dermosphenotic (G.N. 322) before bending ventrally to enter the infraorbito-supraorbital. The posterior edge of the orbit is bordered by the posterior infraorbital which extends along the anterior edges of both suborbitals. The anterior part of the anterior infraorbital is not preserved. The orbit contains a sclerotic ring composed of an unknown number of elements.
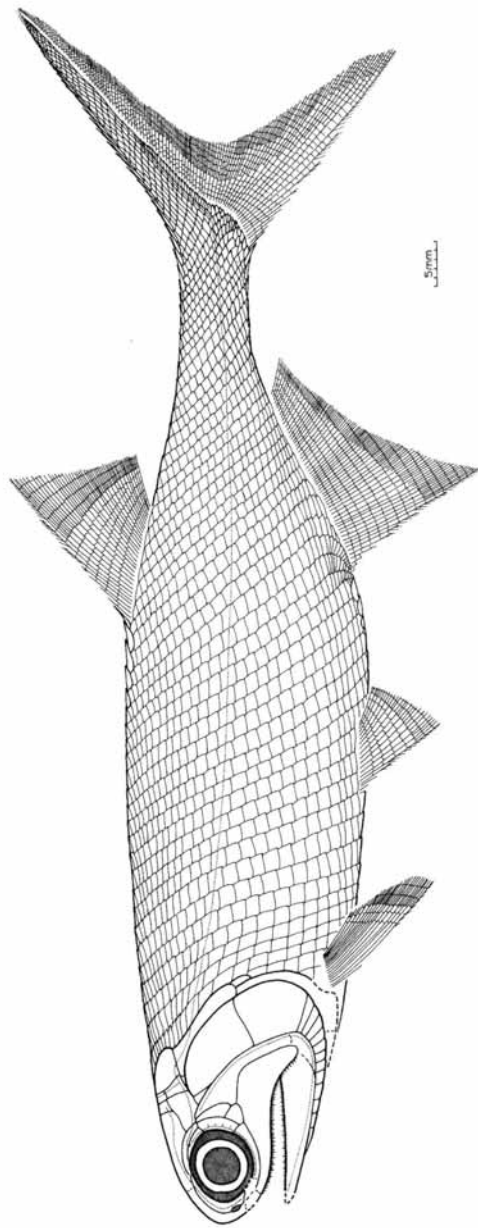


TEXT-FIG. 3. *Dicellopyge macrodentata* Brough. Restoration of cheek region in lateral view, based on specimen G.N. 322.

The pronounced rostrum is composed of a pair of sharply curved nasals separated by a postrostral. The posterior edge of the nasal is smooth, and it is therefore likely that the posterior nasal aperture was situated between the nasal and the sclerotic ring and enclosed by soft tissues. The ventral part of the snout is imperfectly preserved, but it appears likely that an antorbital bone was present, and that it was separated from the upper jaw margin by a rostro-premaxilla. The maxilla overlaps the posterior part of the lower jaw. The lower jaw tapers evenly to the symphysis. The teeth are composed of two series; large conical teeth that are up to 10 mm long, and more numerous teeth that are less than 5 mm long.

*Paired fins.* The paired fins are restored in text-fig. 4. The pectoral fin is composed of sixteen rays that are jointed so that the proximal lepidotrichia are eight times as long as the distal lepidotrichia. All the rays are bifurcated at their distal ends and the anterior ray bears fringing fulcra along its distal edge. The pectoral fin is preceded by a single basal fulcral scale. The pelvic fin lies midway between the pectoral and anal fins. It has fifteen rays that are evenly jointed and which are bifurcated at their distal ends. The anterior rays bear fringing fulcra.

*Unpaired fins.* The unpaired fins are restored in text-fig. 4. The rays of both the dorsal and anal fins are evenly jointed and bifurcated distally. The dorsal fin is composed of thirty-three rays, and the anal fin of fifty-eight rays. In both, the anterior rays bear fringing fulcra. The caudal fin is completely heterocercal and has a high aspect ratio, the angle between the axis of the body and the axis of the body lobe being 40°. The fin web is composed of about 110 rays, and is deeply cleft, while the dorsal lobe appears to extend a little further posteriorly than does the ventral lobe. The caudal fin of P. 16084A is well preserved (text-fig. 6; Pl. 72, fig. 1). The posterior edge of the body lobe is characterized by a well-developed S-shaped curve similar to that described in *Aeduella blainvillei* (Heyler 1969). The convex part of the S forms the posterior limit of the ventral half of the body.

TEXT-FIG. 4. *Dicellopyge macrodentata* Brough. Restoration of whole fish in lateral view. The squamation of the body lobe is somewhat diagrammatic, for details of the caudal fin see text-fig. 6.
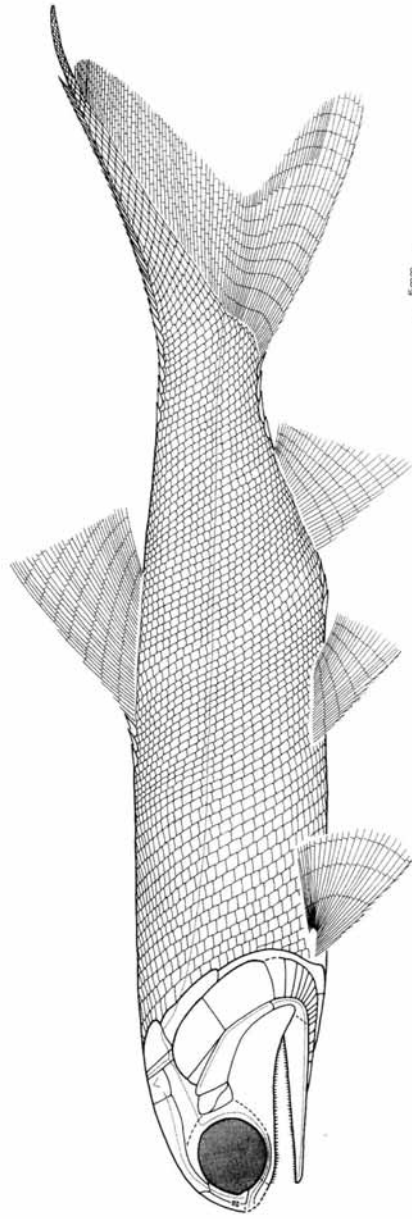
The hinge line between the body and body lobe squamation is not as marked as in some chondrosteans, but its position can be readily determined, its postero-ventral end forming the centre limb of the S-shaped curve (text-fig. 6). The scale rows that run posteriorly from the dorsal edge of the body lobe lie at an angle of between 18° and 60° with the axis of the body lobe. If lines along which these rows are aligned are projected anteriorly, they meet at a point on the dorsal side of the body where the hinge line terminates (this point, B in text-fig. 6 corresponds to the point F in Heyler 1969, p. 127, text-fig. e). There are about forty epaxial basal fulcra. There is no clear numerical relationship between these scales and the scale rows of the body lobe. The long axes of most of the scales of the body lobe are directed along the axis of the body lobe, the only exceptions being the series of nineteen scales which form the postero-ventral border of the body lobe. These scales have their long axes directed along the axes of the rays with which they are associated. The lateral line does not terminate at the posterior end of the body, but extends into the body lobe. It turns dorsally at the point where it crosses the hinge line and then passes along half the length of the body lobe. Its course is clearly visible through a series of twelve scales, it is seen again on the 19th scale, and appears to terminate on the 20th scale. The caudal fin rays can be divided into two groups comprising the ventral and dorsal lobes. The distal ends of the caudal fin rays are rarely preserved and, to facilitate comparison with other forms, the ventral lobe is here defined as being composed of rays which emanate from the body, and the dorsal lobe as being composed of rays which emanate from the body lobe. The junction between the dorsal and ventral lobes therefore coincides with the postero-ventral termination of the hinge line. The ventral lobe is composed of twenty rays, ten of which participate in the leading edge of the caudal fin web. They are stout, but become finer as one progresses dorsally. The degree to which these rays bifurcate is variable: the first nine rays do not bifurcate; while the 14th ray bifurcates as follows (the figures indicate the number of joints between each bifurcation):
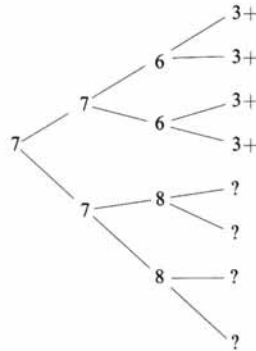


The first five rays to participate in the leading edge of the caudal fin web do not bear fringing fulcra, although their terminal joints each taper to a point. The posterior part of the leading edge is bordered by fringing fulcra that branch from rays 6–10. These fulcra are interspersed by the terminal joints of these five rays. There is no constant numerical relationship between the rays of the ventral lobe and the scales bordering the postero-ventral edge of the body. The dorsal lobe is composed of about ninety rays which are evenly jointed and bifurcate once. Those forming the central part of the fin web are extremely stout and contrast sharply with the adjoining rays of the ventral lobe. Further dorsally, the rays are finer and appear to occur in pairs, each pair being associated with a single scale of the row that forms the posterior border of the body lobe. This relationship is particularly clear in the series of rays labelled c–d in text-fig. 6.

*Squamation.* The scale formula of *D. macrodentata* is:

$$\frac{25}{8 \quad 20 \quad 41} 47.$$

The surfaces of the scales are smooth. On the anterior part of the body, the scales are rhombic with pectinated posterior edges. In the posterior part of the body they gradually attain a leaf-like shape and have smooth posterior edges. The ventral ends of the scale rows that adjoin the anterior end of the base of the anal fin curve antero-ventrally in a manner similar to that described in *Moythomasia nitida* (Jessen 1972).
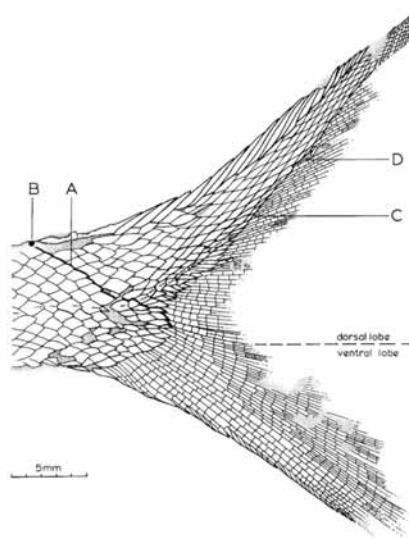


TEXT-FIG. 6. *Dicellopyge macrodentata* Brough. Left side of caudal fin of specimen P. 16084A. A, hinge line; B, point of intersection of lines projected along antero-posteriorly orientated body lobe scale rows; C–D, fin ray series in which pairs of rays are each associated with a single scale of the row bordering the body lobe.

## *Dicellopyge lissocephalus* Brough

Plate 72, fig. 2; text-fig. 7

1931    *Dicellopygae lissocephalus* Brough, pp. 242–244, text-fig. 2; pl. 1, fig. 3.

*Horizon and locality.* Lower Cynognathus Zone (Scythian) of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State, South Africa.

*Diagnosis.* Scale formula

$$\frac{24}{9 \quad 19 \quad 36}\, 42.$$

Angle between axis of body and axis of body lobe 32°. Caudal fin web composed of about eighty rays. About thirty epaxial basal fulcra present. Lateral line extending less than one-third of the way along body lobe.

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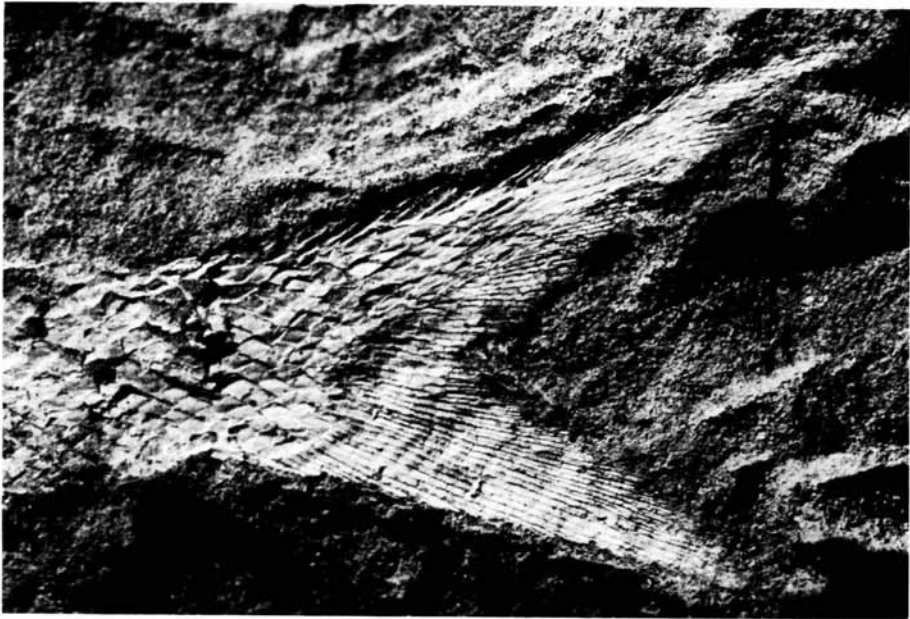
EXPLANATION OF PLATE 72

Fig. 1. *Dicellopyge macrodentata* Brough. Left side of caudal fin of specimen P. 16084A, from Rouxville, South Africa.

Fig. 2. *Dicellopyge lissocephalus* Brough. Left side of caudal fin of specimen P. 16084B, from Rouxville, South Africa.
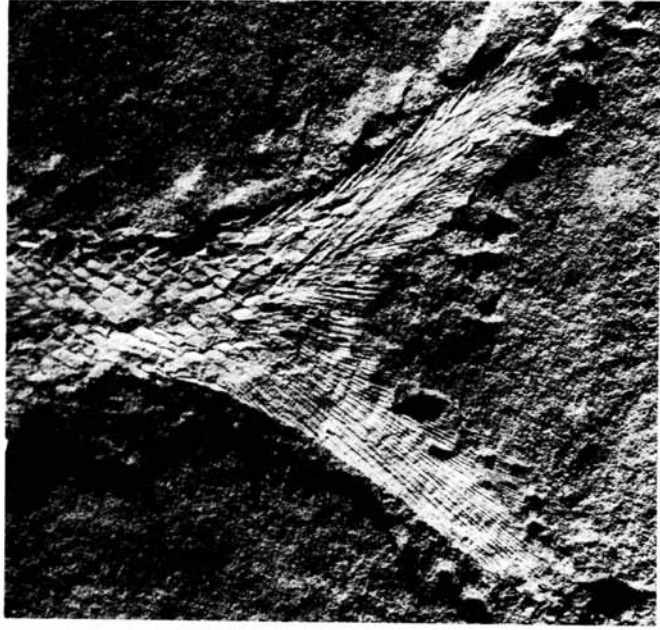
PLATE 72





HUTCHINSON, Triassic *Dicellopyge* from South Africa

*Holotype.* G.N. 949E. (ex D. M. S. Watson Collection P. 13E and counterpart P. 38E. Specimen P. 13E was housed for a period in the National Museum of Wales, where it received the catalogue number N.M.W. 70.2G.97E.)

*Material.* Holotype and P. 16084B. In his original description of *D. lissocephalus*, Brough (1931, p. 242) mentions only the holotype, P.13E. Examination of the posterior half of a body preserved with a specimen of *D. macrodentata* on block P. 16084 has revealed that the former is, in fact, *D. lissocephalus*. A distinction is therefore made between P. 16084A (*D. macrodentata*) and P. 16084B (*D. lissocephalus*).

*Description.* *D. lissocephalus* is a fusiform fish attaining an estimated length of about 110 mm.

*Skull.* The only known skull of *D. lissocephalus* (the holotype) is badly crushed. The orbit is large and anterior in position. The only dermal bones that are well preserved are the opercular, subopercular, pre-opercular, maxilla, and dentary: these are identical in shape with the corresponding bones in *D. macrodentata*.

*Paired fins.* The paired fins are incompletely preserved. Their rays are evenly jointed and the anterior rays of both pectoral and pelvic fins bear fringing fulcra. The pectoral fin is composed of at least seventeen rays, and the pelvic fin of thirteen rays.

*Unpaired fins.* The dorsal and anal fins are similar in size and shape to those of *D. macrodentata*. Their rays are evenly jointed and the anterior rays of both bear fringing fulcra. The dorsal fin is composed of twenty-nine or thirty rays and the anal fin of about forty rays. The anterior part of the anal fin of the holotype was obscured by matrix. Preparation has revealed that its anterior edge is more anterior in position than was suspected by Brough. In fact, the dorsal and anal fins are similarly positioned in both *D. macrodentata* and *D. lissocephalus* and the observation that the dorsal fin is 'almost completely in advance of the anal' (Brough 1931, p. 242), is incorrect. The realization that the anal fin is not as posterior in position as was previously suspected has made the identification of specimen P. 1608B as *D. lissocephalus* possible. The caudal fin of *D. lissocephalus* is best preserved in P. 1608B (text-fig. 7; Pl. 72, fig. 2), but almost all the details described here can be confirmed by examination of the holotype. The caudal fin is completely heterocercal, but has a low aspect ratio, the angle between the axis of the body and the axis of the body lobe being about 32°. Apart from this difference, the caudal fin of *D. lissocephalus* is remarkably similar to that of *D. macrodentata*, and the only other differences between the two species are as follows. There are about eighty rays in the caudal fin web, eighteen in the ventral lobe. The rays forming the central part of the fin web are each associated with a single scale. The rays occurring further dorsally do not have any constant numerical relationship with the scales bordering the posterior edge of the body lobe. There are about thirty epaxial basal fulcra. Finally, the lateral line canal extends posteriorly for less than one-third of the length of the body lobe, passing through a series of sixteen scales after crossing the hinge line.
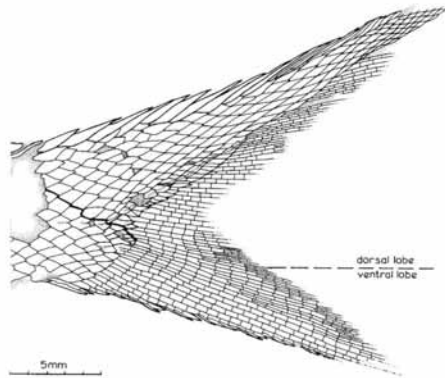


TEXT-FIG. 7. *Dicellopyge lissocephalus* Brough. Left side of caudal fin of specimen P. 16084B.

*Squamation.* The scale formula of *D. lissocephalus* is:

$$\frac{24}{9 \quad 19 \quad 36} 47.$$

Apart from the different scale formula, the squamation of *D. lissocephalus* is identical with that of *D. macro-dentata.*

## Family *incertae sedis*
## BELICHTHYS Wade, 1935

1935 *Belichthys* Wade, pp. 6-7.

*Diagnosis* (emended). Skull roof composed of narrow, extrascapulars, square parietals, and long frontals. Suspensorium oblique. Opercular and subopercular equal in size. Dermohyal elongate. Two suborbitals, together occupying a rectangular area immediately anterior to the antero-dorsal edge of the preopercular. Maxilla elongate posteriorly. Snout composed of paired nasals separated by a postrostral, paired premaxillae, and either paired rostro-antorbitals or separate rostrals and antorbitals. Teeth small, sharply conical. Dentary slender. Ornament of tubercles on the bones of the skull roof, and of concentric ridges on the postrostral. Fin rays not bifurcated except in the ventral caudal lobe. Fulcra few in number and absent from the dorsal and anal fins. Caudal fin inequilobate, body lobe extending posteriorly beyond the posterior ends of the caudal fin rays. Scales small, ornamented with rugae. No clear hinge line at base of body lobe.

*Type species. Belichthys minimus* Wade.

### *Belichthys minimus* Wade

Text-figs. 5, 8

1935 *Belichthys minimus* Wade, pp. 7-10, text-fig. 3; pl. 2, figs. 1-2.

*Horizon and locality.* Ladinian(?) 560 ft above the base of the Hawkesbury Sandstone, Beacon Hill, Brook-vale, N.S.W., Australia.

*Diagnosis.* Dorsal fin slightly larger than anal fin. Number of fin rays: pectoral 26; pelvic 25; anal 31; dorsal 38 and caudal about 80. Scale formula:

$$\frac{28}{12 \quad 32 \quad 59} 68.$$

*Holotype.* P. 16360.

*Material.* Holotype and P. 15812, P. 15857, P. 15864, P. 15866-15867, P. 15869-15870, P. 15873-15875, P. 15877, P. 15911-15913, P. 15950, P. 16210, P. 16213-16215, P. 24702-24705, P. 24706 and counterpart P. 24707, P. 24708 and counterpart P. 24709, P. 24736, F. 152, F. 451, F. 18649, L. 12142.

*Description. B. minimus* is a slender fusiform fish attaining a length of up to 60 mm measured from snout tip to the posterior tip of the body lobe.

*Skull.* The skull of *B. minimus* is restored in text-fig. 8. The parietal and frontal bones are ornamented with tubercles (P. 24706, P. 24707). The parietal bears the posterior part of the supraorbital sensory canal and also a pair of pit lines that meet to form an inverted V. There is some doubt as to the structure of the lateral part of the skull roof because the suture between the infraorbito-supraorbital and the dermopterotic
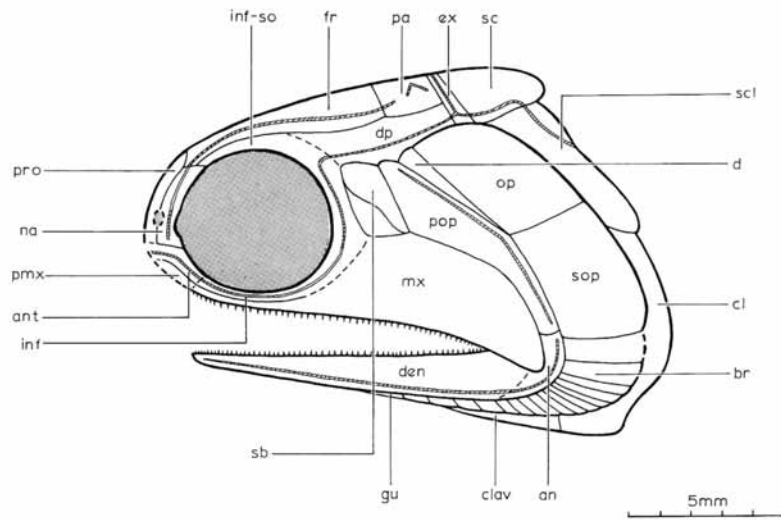
TEXT-FIG. 8. *Belichthys minimus* Wade. Restoration of skull and pectoral girdle in lateral view.

is never clearly preserved. Both bones bear an ornament of tubercles. The dermopterotic is narrow, and long antero-posteriorly. The infraorbito-supraorbital separates the frontal from the orbit edge and extends anteriorly to meet the nasal. The suture between the infraorbito-supraorbital and the infraorbital series is not preserved in any known specimen. The opercular series is oblique, and is composed of opercular and subopercular bones, and up to sixteen branchiostegal rays (P. 15866, P. 24706). The opercular and subopercular bones are equal in size and bear an ornament of low concentric ridges which follow the outline of the bones. The preopercular is boomerang-shaped and separated from the opercular by a long, narrow dermohyal. A pair of suborbitals occur between the dorsal part of the preopercular and the infraorbital series. Together they cover a rectangular area, and are divided by a sinuous suture (P. 15866). There does not appear to be any ornament on the surface of the cheek bones. The orbit is large. Its posterior and ventral edges are bordered by an unknown number of infraorbital elements. The dorsal part of the blunt snout is composed of nasals separated by a postrostral. The postrostral bears an ornament of five or six curved concentric rugae on its dorsal end. The ventral part of the snout is rarely preserved. A canal-bearing element, an antorbital, or a rostro-antorbital, appears to be separated from the edge of the snout by a premaxilla. The posterior part of the maxilla is long and moderately high, but below the orbit it becomes extremely narrow. There are estimated to be about fifty pointed maxillary teeth that are up to 0·4 mm high. It is not possible to determine with certainty whether the teeth are arranged in one or two series. The dentary is extremely slender and ornamented with ridges which, in some cases, run along the entire length of the bone (F. 451). There are about sixty teeth on the lower jaw.

*Pectoral girdle.* The suprascapular is ornamented with fine rugae. There is a marked dome close to its antero-ventral corner below which the infraorbital sensory canal bends (P. 24706). The supracleithrum bears an ornament of concentric rugae which follow the outline of that bone.

*Paired fins.* The paired fins are restored in text-fig. 5. The pectoral fin has twenty-six rays that are jointed so that the proximal lepidotrichia of the anterior rays are up to twice as long as the two distal lepidotrichia. The anterior rays of both paired fins bear fringing fulcra. The pelvic fin has twenty-five rays that are evenly jointed.

*Unpaired fins.* The unpaired fins are restored in text-fig. 5. The dorsal fin is slightly larger than the anal fin but is of similar shape. Fringing fulcra appear to be absent from both the dorsal and anal fins, and both are composed of evenly jointed rays. There are 38 rays in the dorsal fin and 31 in the anal fin. The caudal fin has about 80 rays, about 52 in the dorsal lobe and 27 in the ventral lobe. All the rays are evenly jointed, the anterior rays of the ventral lobe bear fringing fulcra, and the rays in the ventral lobe, except those occurring close to the ventral edge of the fin, are bifurcated.

*Squamation.* It is difficult to give a precise scale formula for *B. minimus,* but it appears to be:

$$\frac{28}{12 \quad 32 \quad 59} 68.$$

The scales are leaf-shaped near the dorsal and ventral parts of the body, but are rhombic in the region of the lateral line. Most scales, including those on the body lobe of the caudal fin, bear an ornament of a single horizontal ruga.


## DISCUSSION

*The caudal fin of* Dicellopyge. The caudal fin of *Dicellopyge* has been described in some detail in the hope that character states would be revealed that would help elucidate the phylogenetic position of the genus. In fact it is difficult to assess the significance of many features because the caudal fin has been described in so few other early chondrosteans, and comparisons are therefore not easy to make. However, comparison between the two closely related species, *D. macrodentata* and *D. lissocephalus*, does reveal character states that are constant within the genus and which may be shown by future research to be important indicators of phylogenetic position.

One such feature is the shape of the posterior edge of the body and body lobe. In primitive chondrosteans such as *Moythomasia* this edge is smoothly curved from the antero-ventral corner of the caudal fin web to the posterior tip of the body lobe (Jessen 1968, text-fig. 4). In *Dicellopyge* the posterior edge of the body lobe has a distinct S-shape that appears to be the result of reduction in the width of the body lobe. A similar S-shape is seen in *Aeduella* and *Bourbonella* (Heyler 1969) and in *Commentrya* (Blot 1966), but is only weakly developed in these genera. A second feature seen in both species of *Dicellopyge* is the extension of the lateral line into the body lobe. In *Cornuboniscus* (White 1939, text-fig. 9) the lateral line extends almost to the extreme tip of the body lobe, a condition which it is reasonable to assume is primitive for the Actinopterygii. Various degrees of reduction of the lateral line in the body lobe have been demonstrated by Westoll (1944) in closely related haplolepid genera, while in forms such as *Indaginilepis*, the lateral line terminates close to the base of the body lobe (Schultze 1970, text-fig. 1*d*). If it is correct to assume that a long extension of the lateral line in the body lobe is the primitive character state, *D. lisso-cephalus* is more advanced than *D. macrodentatus* with respect to this character. It is also very unlikely that *Dicellopyge* evolved from any form displaying the condition such as is seen in *Indaginilepis*.

*The phylogenetic position of the Dicellopygidae.* The family Dicellopygidae was erected by Romer (1945) for the inclusion of *Dicellopyge* and *Aneurolepis*. The latter genus, first described by Bellotti (1857) as *Urolepis*, is poorly known (Alessandri 1910) and there are no valid reasons why it should be classified in the same family as

*Dicellopyge.* The Dicellopygidae is, therefore, best regarded as a monogeneric family. Gardiner (1967a, p. 184) has suggested that the Dicellopygidae is descended from the Gonatodidae, but this opinion was based on an earlier description of *Dicellopyge* (Brough 1931) which differs in certain important respects from that given here.

One of the few known derived character states of *Dicellopyge* is the presence of a narrow, curved dermosphenotic which extends anteriorly to meet the nasal. This character state is also found in representatives of the following chondrostean families as listed by Gardiner (1967a) with an addition by Blot (1966): the Stegotrachelidae (*Stegotrachelus*, Gardiner 1963, and *Kentuckia*, Rayner 1951, but not *Moythomasia*, Jessen 1968); the Boreosomidae (*Boreosomus*, Nielsen 1942; Lehman 1952); the Palaeoniscidae (*Pteronisculus* [*Glaucolepis*], Nielsen 1942; Lehman 1952, and *Turseodus*, Schaeffer 1952, but not *Palaeoniscus*, Aldinger 1937); the Pygopteridae (*Nematoptychius*, Gardiner 1963, but not *Pygopterus*, Aldinger 1937); the Acro-lepididae (*Acrolepis* Aldinger 1937, but not *Mesonichthys*, Gardiner 1963); the Paramblypteridae (*Paramblypterus*, Blot 1966); the Cornuboniscidae (*Cornuboniscus*, White 1939); and the Platysomidae (*Paramesolepis*, Moy-Thomas and Dyne 1938, but not *Platysomus*, Moy-Thomas and Dyne 1938). These genera will hereafter be referred to as having the palaeonisciform type of dermal skull pattern.

To appreciate the significance of this dermal pattern, it is first necessary to examine the condition of the dermosphenotic, infraorbito-supraorbital complex in early chondrosteans. The skull roof is known in only five Devonian genera: *Cheirolepis* (Lehman 1947), *Moythomasia* (Jessen 1968), *Tegeolepis* (Dunkle and Schaeffer 1973), the 'Gogo Palaeoniscids' (Gardiner unpublished), and *Stegotrachelus* (Gardiner 1963). In all five, the lateral part of the skull roof is composed of two elements: a dorsal or posterior dermosphenotic, and a ventral or anterior infraorbito-supraorbital (supraorbito-postorbital of Jessen, supraorbital of Dunkle and Schaeffer). The infraorbito-supraorbital in each genus has a pronounced posterior prolongation that extends to a point lateral to the anterior half of the dermopterotic. The infraorbital sensory canal passes from the dermopterotic, on to the dermo-sphenotic, and then curves ventrally to cross the infraorbito-supraorbital before entering the infraorbital series. In one species of *Cheirolepis*, *C. trailli*, the dermo-sphenotic and infraorbito-supraorbital appear to have fused to form a single element (Gardiner 1963, p. 305). In *Moythomasia*, *Tegeolepis*, the 'Gogo Palaeoniscids', and *Cheirolepis*, the dermosphenotic is excluded from contact with the nasal by the infraorbito-supraorbital. In these genera and *Stegotrachelus*, the dermosphenotic is excluded from the dorsal orbital edge by the infraorbito-supraorbital. Except for the fact that in *Stegotrachelus* the dermosphenotic has contact with the nasal, the follow-ing character states are therefore found in all chondrostean genera from the Devonian in which the skull roof is preserved (text-fig. 9A): the anterior part of the lateral dermal roof is composed of two elements, the dermosphenotic and the infraorbito-supraorbital; the dermosphenotic is excluded from contact with the nasal by the infraorbito-supraorbital; the dermosphenotic is excluded from the orbital edge by the infraorbito-supraorbital; and the infraorbito-supraorbital has a pronounced posterior prolongation.

It is significant that this suite of character states is found in only one chondrostean

preserved in sediments that are younger than Devonian—*Elonichthys caudalis* from the Carboniferous of Fenton, Staffordshire, England (Watson 1928, text-fig. 9). Because, with one exception, the character states listed above are found in all known Devonian genera (which are otherwise very different from each other, and which occur in localities which, even during Devonian times, would have been widely separated), and because they are found together in only one post-Devonian chondrostean, it would appear extremely likely that they represent primitive character states for the Chondrostei. Unfortunately, the stratigraphic evidence is the only kind that can be brought to bear on this investigation, as comparison with members of the Dipnoi and Crossopterygii does not provide evidence either for or against the hypothesis outlined above.

A brief review of the literature shows that the lateral part of the skull roof in Lower Carboniferous chondrosteans differs from that of *Moythomasia*, and that two distinct types can be discerned. In one, the dermosphenotic is elongate and meets the posterior end of the nasal—the palaeonisciform pattern (text-fig. 9b). In chondrosteans with the second pattern, referred to here as the elonichthyiform type, the lateral part of the skull roof is formed by the dermopterotic which often extends anteriorly to meet the posterior part of the nasal, and a second element usually called the dermosphenotic (but see discussion below), through which the infraorbital sensory canal passes before it enters the infraorbital series (text-fig. 9c). This dermal
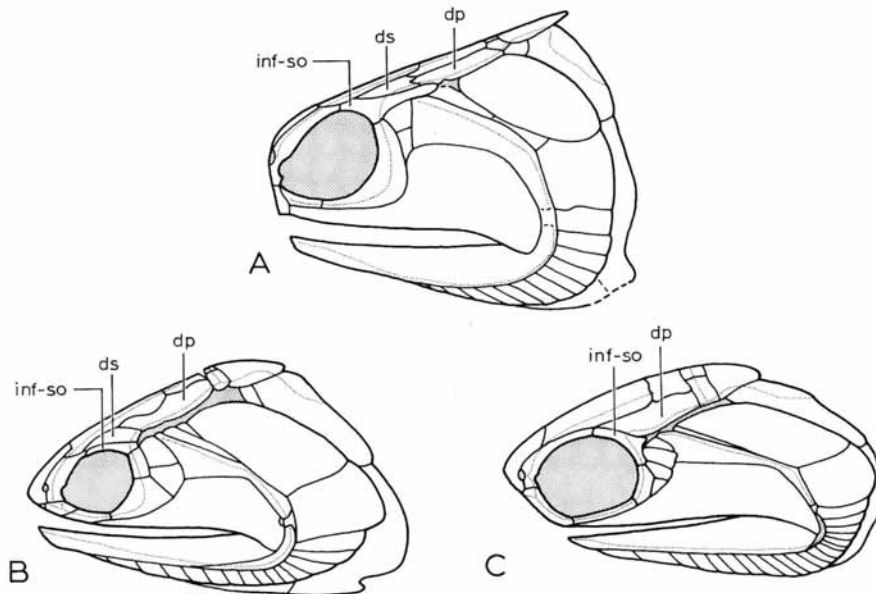


TEXT-FIG. 9. Three dermal bone patterns found in early chondrosteans. A, *Moythomasia nitida*, Jessen (1968, text-fig. 1); B, *Pteronisculus stensioi*, Nielsen (1942, text-fig. 27); C, *Namaichthys schroederi*, Gardiner (1962, text-fig. 1). Not drawn to same scale.

bone pattern is seen in members of the following families, again as defined by Gardiner (1967a) with an addition by Gardiner (1969): the Elonichthyidae (*Elonichthys*, Moy-Thomas and Dyne 1938, and *Namaichthys*, Gardiner 1962); the Cosmo-ptychiidae (*Watsonichthys* and *Cosmoptychius*, Gardiner 1963); the Rhadinichthyidae (*Rhadinichthys* and *Cycloptychius*, Moy-Thomas and Dyne 1938, and *Mentzichthys*, Gardiner 1969); the Canobiidae (*Canobius*, Moy-Thomas and Dyne 1938); the Holuridae (*Australichthys*, Gardiner 1969); the Willomorichthyidae (*Willomorichthys*, Gardiner 1969); the Platysomidae (*Platysomus*, Moy-Thomas and Dyne 1938, but not *Paramesolepis*, Moy-Thomas and Dyne 1938); the Amphicentridae (*Cheirodopsis*, Moy-Thomas and Dyne 1938); the Tarrasiidae (*Tarrasius*, Moy-Thomas and Dyne 1938); the Pygopteridae (*Pygopterus*, Aldinger 1937, but not *Nematoptychius*, Gardiner 1963); and the Acrolepididae (*Mesonichthys*, Gardiner 1963, but not *Acrolepis*, Aldinger 1937).

If the elonichthyiform and palaeonisciform patterns could be shown to be unique specializations, the consequences for chondrostean taxonomy would be far reaching as the presence of a fundamental dichotomy within the complex of Carboniferous families would have been demonstrated. This possibility will now be discussed.

The elonichthyiform pattern. In many genera of the elonichthyiform type; e.g. *Namaichthys* (Gardiner 1962); *Rhadinichthys* and *Cycloptychius* (Moy-Thomas and Dyne 1938); and *Mentzichthys* and *Australichthys* (Gardiner 1969); the bone that forms the postero-dorsal orbital edge (the dermosphenotic of Moy-Thomas and Dyne, Gardiner, and other authors, the postfrontal of Watson) bears a short posterior prolongation. This prolongation appears to be an abbreviated form of that seen in *Moythomasia* and suggests that the bone in question is, in fact, an infraorbito-supraorbital. The elonichthyiform pattern is therefore characterized by the absence of a dermosphenotic, an absence which may be due to the loss of the dermosphenotic, or to its fusion with either the infraorbito-supraorbital or the dermopterotic. Identi-fication of this derived character state does not constitute proof that genera with the elonichthyiform pattern form a monophyletic group. Some could have evolved from an ancestor of the palaeonisciform type while others could have evolved from an ancestor such as *Moythomasia*. The fact that there are several phylogenetic 'pathways' along which the elonichthyiform pattern could have been derived, means that testing of the hypothesis that the elonichthyiform genera constitute a monophyletic group must await detailed examination of other character states in these genera. Such examination is outside the scope of this paper, but will be carried out by the author at a future date. The problem of the monophyletic origin of the elonichthyiform genera therefore remains unresolved. There is, however, no evidence at the present time to suggest that they are not uniquely derived.

The palaeonisciform pattern. Because the dermosphenotic is retained in the palaeonisciform pattern, it follows that it could not have evolved from ancestors of the elonichthyiform type. Genera of the palaeonisciform type must have been derived from an ancestor such as *Moythomasia*, and all display an advanced character condition in that the dermosphenotic meets the nasal. It is therefore at least likely that they constitute a monophyletic group. Once again, further investigations must be made before the question as to whether genera of the palaeonisciform type are uniquely derived can be settled. If, at a later date, the presence of a dichotomy within

the Carboniferous chondrosteans can be demonstrated, the families Stegotrachelidae, Palaeoniscidae, Pygopteridae, Acrolepididae, and Platysomidae will require extensive revision, for all contain genera with different dermal bone patterns. It may be argued that this last fact constitutes evidence against the hypothesis of a dichotomy within early chondrosteans, but this is in fact not the case because these families, like many others, are founded on suites of character states which are primitive and which have no phylogenetic significance. For a discussion of this point, see Schaeffer (1973).

Returning now to *Dicellopyge*. The presence of a narrow curved dermosphenotic which extends anteriorly to meet the nasal, suggests that this genus is allied to forms such as *Boreosomus*, *Pteronisculus*, *Nematoptychius*, and *Acrolepis*, and that all may be members of a monophyletic group which has separate ancestry from that of the majority of other chondrosteans.

*The phylogenetic position of* Belichthys. The genus *Belichthys* was first described by Wade (1935, pp. 6–7), who recognized three species, *B. minimus*, *B. longicaudatus*, and *B. magnidorsalis*. The two latter species are very poorly preserved and represented by few specimens (four of *B. longicaudatus* and three of *B. magnidorsalis*). Their skull structure is unknown, but they differ from one another and from *B. minimus* in the size and position of the fins, in the number of fin rays present, and in the size of the scales (Wade 1935, pp. 10–11). There is, however, one feature of the anatomy of all three species that is a specialization rarely found in members of the Chondrostei, and which is reasonable evidence of close relationship between these species. In all three, the body lobe of the caudal fin extends posteriorly beyond the posterior limit of both the epaxial basal fulcra of the body lobe and the rays of the caudal fin (text-fig. 5). This feature justifies the inclusion by Wade of the species under discussion in a single genus.

Because *B. longicaudatus* and *B. magnidorsalis* are so poorly preserved, discussion of the phylogenetic position of *Belichthys* must depend on analysis of the anatomy of *B. minimus*. Most of the character states of *B. minimus* appear to be primitive, and the species may readily be compared with an ancestral chondrostean morphotype such as that described by Schaeffer (1973). The only known character states of *B. minimus* that are advanced with respect to this morphotype are as follows: fulcral scales are absent from the dorsal and anal fins; the rays of all fins, with the exception of those of the caudal fin, do not bifurcate; there is no well-developed hinge line at the base of the body lobe; the opercular is equal in size to the subopercular; and there is a long posterior extension of the body lobe. Unfortunately, all these character states are of little use in the determination of the phylogenetic position of *Belichthys* because they are states that could be derived from almost any known early chondrostean. *Belichthys*, then, presents a problem that is commonly posed by fish remains from the Palaeozoic and Mesozoic. Because our knowledge of these fish is often limited, there is no way in which phylogenetic relationships can be accurately assessed. It is therefore proposed that *Belichthys* be classified as Chondrostei *incertae sedis*.

## APPENDIX

The location of specimens cited in this paper is as follows: F. Sedgwick Museum, Cambridge. G.N. University Museum of Zoology, Cambridge. (Some specimens in this collection also bear the prefix P., indicating that they are derived from the collection of the late D. M. S. Watson. These specimens have been recatalogued and bear the prefix G.N., but the old numbers prefixed by P. are also given.) L. Manchester Museum. P. British Museum (Natural History). N.M.W. National Museum of Wales.

Abbreviations used in the figures:

| | | | | |
|---|---|---|---|---|
| acop | accessory opercular | | inf-so | infraorbito-supraorbital |
| an | angular | | mx | maxilla |
| ant | antorbital | | na | nasal |
| br | branchiostegal ray | | op | opercular |
| cl | cleithrum | | pa | parietal |
| clav | clavicle | | pcl | postcleithrum |
| d | dermohyal | | pop | preopercular |
| den | dentary | | pro | postrostral |
| dp | dermopterotic | | r-pmx | rostro-premaxillary |
| ds | dermosphenotic | | s | sclerotic ring |
| ex | extrascapular | | sb | suborbital |
| fr | frontal | | sc | suprascapula |
| gu | gular plate | | scl | supracleithrum |
| inf | infraorbital | | sop | subopercular |

In the skull restorations, sensory canals are represented by fine parallel lines. These are hatched if there is material evidence of their position, elsewhere, their presumed course is depicted without hatching.

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