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PSEUDOBEACONIA, A PERLEIDIFORM FISH FROM THE TRIASSIC SANTA CLARA FORMATION, ARGENTINA

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ABSTRACT. Two species of the genus *Pseudobeaconia*, *P. bracac*cinii and *P. elegans*, from the Santa Clara Formation, Argentina, are described. The genus is an advanced member of the family Colobodontidae (subclass Chondrostei, order Perleidiformes), and is closely related to *Mendocinia* from the same locality. It is suggested that the success of the Perleidiformes is due, in part, to the evolution of a crushing dentition. The detailed structure of the unpaired fin rays indicates that control of the fin web area was possible in *Pseudobeaconia*, and probably in all Perleidiformes. The identification of *Pseudobeaconia* does not help the determination of the age of the Santa Clara Formation.

ABSTRACTO. Se describen dos especies del género Pseudobeaconia, P. bracaccinii y P. elegans, de la Formación de Santa Clara, Argentina. El género es un miembro avanzado de la familia Colobodontidae (subclase Chondrostei, orden Perleidiformes), y está íntimamente relacionado con Mendocinia de la misma localidad. Se sugiere que el éxito de los Perleidiformes se debe, en parte, a la evolución de una dentición molar. La estructura detallada de los rayos de las aletas impares indica que el control del área de la membrana de las aletas era posible en Pseudobeaconia, y probablemente en todos los Perleidiformes. La identificación de Pseudobeaconia no facilita la determinación de la edad de la Formación de Santa Clara.

INTRODUCTION

In 1944 three genera of fossil fish were described from the Santa Clara Formation, a series of shales, mudstones, and sandstones that outcrop between the provinces of San Juan and Mendoza, western Argentina (Bordas, 1944). Two of these genera were new, *Mendocinia* and *Pseudobeaconia*, while the

^{&#}x27;Gothic House, Drayton, Berks, England.

third was doubtfully identified as *Cleithrolepis*. More recently Schaeffer (1955) has redescribed *Mendocinia* and has shown that it is a member of the Perleidiformes. *Pseudobeaconia* remained relatively unknown, although it appeared in most classifications as a member of the Redfieldiiformes (e.g., Gardiner, 1967a) because Bordas had described similarities between it and a redfieldiiform genus called *Beaconia* (= *Brookvalia*, Hutchinson, 1972) from the Triassic Hawkesbury Series of New South Wales (Wade, 1935).

The material described here was collected by an expedition from the Museo de La Plata and the Museum of Comparative Zoology, Harvard University, in 1964, and is derived from two localities in the Santa Clara Formation. The first is near the north end of the formation, near the Puesto of Santa Clara, at the east margin of the Precordillera in southern San Juan Province. This is the same locality that produced the fish described by Bordas in 1944. The second locality is north of the Quebrada de la Montaña, a short distance east of the boundary between the Santa Clara beds and the Villavicencio group (Romer, 1966).

There is little doubt that the specimens described here represent the two species of *Pseudobeaconia* described by Bordas in 1944. The reasons for this identification are given in the discussion below. *P. bracaccinii* occurs in both the localities mentioned above, while *P. elegans* occurs only in the former.

Pseudobeaconia is preserved in a matrix of dark mudstone or, more commonly, shale. The shales from the second locality usually contain bands of a light calcareous deposit. There may be up to ten such bands in a sample 10 mm thick. As well as fish, fragments of plant material are preserved in the shales. Preservation is extremely good and the fish have either been prepared with a fine needle or sometimes, when they occur in calcareous bands, dissolved in acetic acid to reveal natural moulds. All the specimens had been crushed to a thickness of, at most, 2 mm.

The Santa Clara Formation is difficult to date because it is limited to a block isolated by faulting during the Tertiary. Bordas (1944) is of the opinion that the Santa Clara Formation is contemporaneous with the Hawkesbury Sandstone of Brookvale, New South Wales. This conclusion is based on the supposed close relationship between *Pseudobeaconia* and *Beaconia*, a conclusion that is unfounded according to evidence presented here. Harrington (unpublished MS) notes that, near the locality described by Bordas, there are plant remains that include Glossopteris, Walkonia, Pecopteris, Gondwanidium, Cordaites, and Dicranophyllum, which are Permian in age. But, as noted above, the Santa Clara Formation is isolated from other sediments in the area, and there is no evidence that the flora listed by Harrington occurred within its boundaries. Schaeffer (1955: 3) has estimated the age of the beds of the Cacheuta basin (and by inference the Santa Clara Formation) to be Norian. This estimate is based on a similarity between floras of the Cacheuta and Upper Triassic sediments of the Northern Hemisphere. Lack of similar comparative data from the Middle Triassic means that this estimate can only be regarded as an indication of the youngest possible age of the Cacheuta beds.

A possible estimate of the age of the Santa Clara Formation depends on correlations made recently by Bonaparte and runs as follows. The Santa Clara Formation forms one of several outcrops that lie within the Cacheuta basin of deposition (Stipanicic, 1967: 3). Another of these outcrops contains the Potrerillos Formation from which a cynodont lower jaw, *Colbertosaurus*, has been recovered (Minoprio, 1954). *Colbertosaurus* is similar to *Pascualgnathus* from the Puesto Viejo Formation (Bonaparte, 1966a: 4–5). Thus the Potrerillos and Puesto Viejo formations can be considered to be very similar in age. The age of the Puesto Viejo formation is considered to be Scythian because it also contains a dicynodont *Kannemeyeria* (Bonaparte, 1966b: 266) and a cynodont *Cynognathus* (Bonaparte, 1969), both typical genera of the Lower Triassic South African fauna.

It should be emphasized that this estimate of Lower Triassic age for the Santa Clara Formation is tentative and open to two objections. Firstly, it is not certain that all the outcrops within the Cacheuta basin were once continuous. Secondly, the resemblance between *Colbertosaurus* and *Pascualgnathus* is not completely convincing, and has limited significance, according to Bonaparte (1966a: 5).

The identification of *Mendocinia* and *Pseudobeaconia* from Santa Clara adds nothing of significance to the debate on the possible age of the formation. Both genera are more advanced than *Perleidus* from the Lower Triassic of Madagascar, Greenland, and Spitsbergen but, because they are not directly descended from *Perleidus*, this does not necessarily indicate that the Santa Clara Formation is younger than Lower Triassic. Another member of the same perleidid radiation, *Meidiichthys*,

from the Cynognathus zone of South Africa, demonstrates that advanced features such as an anteriorly inclined suspensorium evolved extremely rapidly, and the presence of such characters in forms from Santa Clara does not exclude the possibility that the Santa Clara Formation is Lower Triassic in age.

DESCRIPTION

Order Perleidiformes Family COLOBODONTIDAE Stensio 1916 Pseudobeaconia Bordas 1944

Pseudobeaconia Bordas, 1944: 454. Type species. Pseudobeaconia bracaccinii Bordas 1944

Diagnosis (emended). Skull short anteroposteriorly. Skull roof evenly curved to snout tip, upper jaw steeply inclined. Skull roof composed of two extrascapulars, a parietal, and a frontal. Lateral walls of skull roof composed of a dermopterotic and an accessory dermopterotic. Ventral end of the suspensorium inclined anteriorly so that the jaw articulation lies vertically below the posterior orbital edge. Opercular series composed of opercular, subopercular, and three or four branchiostegal rays. Opercular anterior in position so that its anterior edge lies in advance of the level of the posterior edge of the parietal. Subopercular larger than opercular. Triangular dermohyal and suborbital elements. Dermohyal small, extending ventrally along half the anterior edge of the opercular. Dermosphenotic short anteroposteriorly, in contact dorsally with both the posterior supraorbital and the dermopterotic. Dorsal orbital edge bordered by two supraorbital elements. Maxilla not greatly expanded posteriorly. Snout composed of paired nasals, antorbitals and (probably paired) toothed premaxillae, and a medial rostral and postrostral. Nasal bordering anterior orbital edge. Rostral large, bordering the anterior edge of the nostril. Nostril elliptical. Marginal teeth on maxilla and dentary conical and pointed, palatal teeth low and rounded.

Body fusiform, attaining a total length of up to 120 mm. Dorsoventral length of scales in flank region up to three times their anteroposterior length. Scales in the transverse row immediately behind the pectoral girdle twice as long anteroposteriorly as succeeding body scales. Scale ornament of between two and six ridges running concentrically along posterior and ventral borders. Scales in lateral line series with an indentation in their posterior borders. No hinge line at base of caudal lobe of body. Ridge scales present anterior to unpaired fins and on the dorsal side of the body midway between the skull and dorsal fin. Dorsal and anal fins posterior in position. Caudal fin hemiheterocercal. All fin rays jointed and usually bifurcated. Basal fulcra present anterior to all fins. Paired fin rays apparently lacking fringing fulcra. Proximal lepidotrichia of all fins at least three times as long as distal lepidotrichia. Proximal lepidotrichia of unpaired fins equal in number to endoskeletal supports, and expanded proximally, with insertions for depressor and erector muscles.

Pseudobeaconia bracaccinii Bordas 1944 Figures 1–5

Pseudobeaconia bracaccinii Bordas, 1944: 454-455, pl. 1.

Diagnosis (emended). Parietal just under half the length of the frontal. Opercular plate roughly rectangular, its anteroposterior length being under half its dorsoventral length. Ventral edge of opercular deeply convex. Posterior edge of maxilla lying anterior to the level of the posterior orbital edge. Anterior supraorbital extending anteriorly as far as the anterior end of frontal. Suprascapulars separated at midline. Dorsoventral length of supracleithrum twice that of cleithrum.

Body fusiform. Body length, from snout tip to the posterior tip of the caudal lobe of the body, three times the greatest depth of the body. Scale formula:

$$\begin{array}{c} 25\\ 13 & 21 & 35 \end{array}$$

Length of the longest pectoral fin rays 1.5 times the length of the longest pelvic fin rays. Some paired fin rays bifurcated distally. Dorsal fin rays not bifurcated. Dorsal fin slightly in advance of anal fin. Dorsal lobe of caudal fin slightly longer than ventral lobe.

Holotype. Museo Argentino de Ciencias Naturales at Bernardino Rivadavia, Catalogue of Paleontology (Vertebrates) No. 14.868 (Bordas, 1944: pl. 1).

Additional material. Thirty-two specimens in the collection of the Museum of Comparative Zoology, Cambridge, Massachusetts.

Skull. The dermal bones of the skull are restored in Figure 1. The skull roof slopes evenly to the snout, and is composed of extrascapulars (which are divided [MCZ 12891]), parietals,



Figure 1. Pseudobeaconia bracaccinii Bordas. Restoration of skull and pectoral girdle, ornament omitted. \times 5 approx.



Figure 2. Pseudobeaconia bracaccinii Bordas. MCZ 12883. Left side of skull and pectoral girdle.

and frontals. The parietal is square; its anteroposterior length is just under half the length of the frontal. The frontal is deep and excavated above the orbit so that its widest part lies above the posterior edge of the orbit.

The lateral part of the skull roof is composed of two elements, a dermopterotic and an accessory dermopterotic, which are separated from one another by a vertical suture that runs from a point midway along the ventral margin of the parietal (Fig. 2). In MCZ 12883, the dermopterotic appears to be shallow, but this is because the preopercular has been displaced and overlaps its ventral part. The full depth of the dermopterotic is seen in MCZ 12894. The dermopterotic meets the posterodorsal border of the dermosphenotic, and may also have point contact with the posterior supraorbital element. A postspiracular lies posterior to the accessory dermopterotic and meets the ventral border of the extrascapular series. In lateral view the anterior part of the postspiracular is overlapped by the opercular, but in MCZ 12893 it is seen to extend anteriorly along the entire dorsal border of the opercular.

The opercular is circular, and the subopercular roughly oblong but with a curved posteroventral border. In most speciments the ventral part of the subopercular is crushed against the pectoral girdle, but its outline is clearly seen in MCZ 12898, where it has been slightly displaced. Its dorsoventral length is slightly longer than that of the opercular. There are only three or four rather broad branchiostegal rays. The preopercular is high, and meets the ventral edge of the dermopterotic. Its ventral part is inclined forwards so that the lower jaw articulation lies almost directly below the posterior edge of the orbit. The preopercular has a short infraorbital process. In MCZ 12883 (Fig. 2) an element lies between the posterior edge of the maxilla and the anteroventral corner of the subopercular. This is not a fragment of the preopercular, for in MCZ 12900 there is a notch on the median surface of the ventral end of the preopercular which indicates the position of a separate element (Fig. 1). It is likely, therefore, that a quadratojugal is present. There is no sign of any sensory canal on the quadratojugal. The dorsal end of the preopercular is constricted between triangular dermohyal (MCZ 12893, 12891) and suborbital elements (MCZ 12883). In MCZ 12893, which includes a natural mould of the median surface of the cheek, there is a small triangular accessory opercular at the anterodorsal corner of the subopercular. This element is not visible in lateral view, as it is completely overlain by the subopercular.

The dorsal orbital edge is bordered by two supraorbitals. There is some variation in the relative lengths of these elements; in MCZ 12898 and probably also in MCZ 12883 (Fig. 2) the posterior element is slightly longer than the anterior element, whereas in MCZ 12891 (Fig. 3A), the posterior element is slightly shorter than the anterior one. The posterior orbital edge is bordered by a narrow dermosphenotic, which has an expanded dorsal end, and the ventral orbital edge by two infraorbitals. The anterior infraorbital is expanded anteriorly, while the posterior infraorbital is expanded midway along its length.

In MCZ 12883 (Fig. 2), the maxilla has been displaced so that its posterior part is overlapped by the preopercular. The preopercular is so thin in this region, however, that the outline of the maxilla is clearly seen as a ridge. The upper jaw margin is steeply inclined, but lies at right angles to the anterior edge of the subopercular. The maxillary teeth are pointed (MCZ 12894, 12895, 12898, and 12901), and appear to be present only along the anterior half of the maxillary border. There are about 20 teeth in the upper jaw row.

The snout is best preserved in MCZ 12893, 12891 (Fig. 3A), and 12894 (Fig. 3B). The nasal borders the anterior orbital edge and is in contact dorsally with both the frontal and



Figure 3. *Pseudobeaconia bracaccinii* Bordas. A. MCZ 12891. Snout regon, right side unless otherwise indicated. B. MCZ 12894. Snout region, left side.

the anterior supraorbital. The ventral part of the snout is composed of paired antorbitals, which border the anteroventral corner of the orbit, and premaxillaries, which bear up to six teeth (MCZ 12894, Fig. 3B). It is not known for certain whether the premaxillaries are paired or fused. The anterior part of the snout is composed of medial rostral and postrostral elements. The rostral bears the ethmoid commissure and extends dorsally so that it borders the anterior margin of the nostril (Fig. 3), while the postrostral is a small bone which just borders the anterodorsal corner of the nostril. The suture between the rostral and postrostral elements is indistinct in MCZ 12891, but clearly seen in MCZ 12894 (Fig. 3B).

The lower jaw is best preserved in MCZ 12893.

Most of the dermal bones of the skull are smooth. Tubercles are present, however, on the anterior ends of the frontal and anterior supraorbital, on the nasal, and on the infraorbital part of the maxilla. Low ridges are seen on the opercular and subopercular elements and near the edges of the branchiostegal rays (Fig. 4).

The sensory canals of the head are enclosed in massive tubes which open to the surface through well-defined pores (MCZ 12883, Fig. 2). In addition, there is a vertical pit line on the ventral part of the preopercular, while short, curved, middle and posterior pit lines are present on the parietal.

All the skulls of *P. bracaccinii* are crushed and few details of the internal anatomy are displayed. In MCZ 12897, however, part of the palate is visible and about ten low and rounded palatal tusks can be seen. In MCZ 12897 two branchial arch elements are seen, lying against the anterior edge of the cleithrum; they are flattened and their posterior edges bear numerous toothlike projections that are less than 0.1 mm long.

Pectoral girdle. The suprascapulars are D-shaped and do not meet at the midline as they are separated by a pair of scales that meet the posterior edges of the dorsal extrascapular elements (MCZ 12883, Fig. 2; MCZ 12891). The infraorbital sensory canal crosses the anteroventral corner of the suprascapular (MCZ 12893). The supracleithrum, which extends ventrally to a point close to the ventral edge of the opercular, has an excavated dorsal end. This excavation does not appear to fit directly onto the ventral edge of the suprascapular, for in several specimens it terminates at a level nearer the midline than does the suprascapular edge (MCZ 12893, 12891, and 12894). It is possible, therefore, that the dorsal end of the pectoral girdle is buttressed, in part at least, against the posterolateral wall of the braincase. The dorsoventral length of the



 \times 2.5 approx.

cleithrum is twice as long as that of the supracleithrum. The cleithrum has a broad ventral plate, and its anterior border bears an ornament of sinuous rugae. Small clavicles are present (MCZ 12893, 12899, 12901).

Paired fins. The paired fins are restored in Figure 4. In both, the rays are jointed so that the proximal lepidotrichia are up to six times as long as the distal ones, while the longest rays are bifurcated at their extreme distal ends (MCZ 12893, 12906). Fringing fulcra were not observed and are probably absent, but in both fins a stout basal fulcral scale participates in the leading edge. The pectoral fin is composed of 13 rays, which have between 4 and 12 joints. In well-preserved specimens (for example MCZ 12883, Fig. 2), the bases of the anterior rays are inserted in a more dorsal position than are those of the posterior rays. The pelvic fin lies two-thirds of the way between the pectoral and anal fins. It is composed of seven rays, which have between four and eight joints.

Unpaired fins. The unpaired fins are restored in Figure 4. In all, the rays are jointed, so that the proximal lepidotrichia are from three to eight times as long as the distal ones. The rays of the anal and caudal fins are bifurcated, and in all the unpaired fins the leading rays bear fringing fulcra. The dorsal fin is composed of 16 rays, which have between three and nine joints, and is preceded by three basal fulcra. The anal fin is composed of 14 rays, which have between 9 and 22 joints, and is preceded by a single basal fulcral scale. The dorsal and anal fins are similar in shape, but the former is larger and is slightly more anterior in position than the anal fin. The caudal fin is hemiheterocercal and the rays of its dorsal lobe are slightly longer than those of its ventral lobe. It is composed of 21 rays, which have between 15 and 24 joints. The four rays, which have their origins on the dorsal side of the caudal lobe of the body, do not bifurcate. There are about six basal fulcral scales on the dorsal side of the caudal lobe of the body; their exact number is difficult to determine because anteriorly they become very similar in form to the ridge scales, which extend posteriorly from the posterior edge of the dorsal fin.

In MCZ 12892 and 12905 some details of the articulation of the anal fin rays are seen, and in MCZ 12912 (Fig. 5) similar details are seen in the dorsal fin. In both fins the number of radials equals the number of rays. In the dorsal fin the proximal lepidotrichia have expanded proximal ends but, whereas the posterior lepidotrichia are almost straight, the anterior ele-



Figure 5. *Pseudobeaconia bracaccinii* Bordas. MCZ 12912. Proximal lepidotrichia and distal radials of dorsal fin rays 7-10. Right side.

ments become progressively more curved. Two grooves extend along the entire length of each fin ray, running close to the anterior and posterior edges. At their proximal ends, these grooves open into broad depressions so that there is an anterior and a posterior depression on each side of the base of every fin ray. As one passes anteriorly along the dorsal fin ray series, the anterior depressions become progressively larger, while the posterior depressions become progressively smaller (Fig. 5). The probable significance of these features is discussed below.

Squamation. The scales are restored in Figure 4. There are 35 transverse scale rows between the anterior transverse scale row and the row in front of the anterior caudal fin ray. The positions of the pelvic, dorsal, and anal fins relative to the scale rows is given in the formula:



(See Westoll, 1944: 20. Note that, because there is no clear hinge line in *Pseudobeaconia*, the last figure given in Westoll's formula is not used here.) The scales in the transverse row immediately behind the pectoral girdle are considerably longer anteroposteriorly than are the scales in any other row. Each scale in the lateral line series has a slight indentation in its posterior border, coinciding with the lateral line canal. The outlines of all the other scales are smooth. There is no hinge line between the scales of the body and those of the caudal lobe. Ornament is limited to between 2 and 6 ridges that run concentrically along the posterior and ventral borders of each scale.

Ridge scales occur in front of the unpaired fins and also on the dorsal side of the body between the skull and the dorsal fin.

Pseudobeaconia elegans Bordas, 1944 Figures 6-8

Pseudobeaconia elegans Bordas, 1944: 456, pl. 1.

Diagnosis (emended). Parietal just over half the length of the frontal. Opercular plate D-shaped, its anteroposterior length being over half its dorsoventral length. Ventral edge of the opercular slightly convex. Posterior edge of the maxilla lying posterior to the level of the posterior orbital edge. Anterior supraorbital extending anteriorly beyond the anterior end of the frontal. Suprascapulars meeting in the midline. Dorsoventral length of supracleithrum equal to that of the cleithrum.

Body fusiform. Body length, from snout tip to the posterior tip of the caudal lobe of body, 3.5 times the greatest depth of the body. Scale formula:



Figure 6. *Pseudobeaconia elegans* Bordas. Restoration of skull and pectoral girdle, ornament omitted. \times 5 approx.



Figure 7. *Pseudobeaconia elegans* Bordas. MCZ 12892. Skull and pectoral girdle, right side unless otherwise indicated.

Length of the longest pectoral fin rays about 2.5 times the length of the longest pelvic fin rays. Paired fin rays probably not bifurcated. Dorsal fin rays bifurcated. Dorsal fin almost entirely in advance of anal fin. Caudal fin equilobate.

Holotype. Museo Argentino de Ciencias Naturales at Bernardino Rivadavia, Catalogue of Paleontology (Vertebrates) No. 14.689 (Bordas, 1944 : pl. 1).

Additional material. Four specimens in the collection of the Museum of Comparative Zoology, Cambridge, Massachusetts.

A full description of *P. elegans* is not necessary, as many of its features have already been observed in the type species *P. bracaccinii*.

Skull. The restoration of the dermal bones of the skull (Fig. 6) is based mainly on MCZ 12892 (Fig. 7). The anteroposterior length of the parietal is just over half the length of the frontal. The dermopterotic appears to be deeper than in *P. bracaccinii*, and the anterior supraorbital extends ante-

riorly beyond the anterior tip of the frontal. The opercular is less rounded than in *P. bracaccinii*, and has a straighter ventral edge, and the subopercular is relatively longer anteroposteriorly (MCZ 12893). As a result of these differences the opercular plate is D-shaped rather than rectangular, as in *P. bracaccinii*. The maxilla, although similar in shape to that of *P. bracaccinii*, extends posteriorly beyond the level of the posterior edge of the orbit.

Pectoral girdle. The suprascapulars are D-shaped and appear to meet in the midline. The supracleithrum extends ventrally beyond the ventral edge of the opercular. The dorsoventral length of the supracleithrum is the same as that of the cleithrum.

Paired fins. The paired fins are restored in Figure 8. Both are incompletely preserved. The rays are jointed so that the proximal lepidotrichia are up to eight times as long as the distal ones. Fringing fulcra are not preserved, and the rays appear not to be bifurcated. The pectoral fin is composed of at least seven rays that are extremely long, so that the fin is a fifth of the length of the entire fish (MCZ 12893). The pelvic fin is composed of at least seven rays that have up to four joints, and lies two-thirds of the way between the pectoral and anal fins.

Unpaired fins. The unpaired fins are restored in Figure 8. In all, the rays are jointed so that the proximal lepidotrichia are from five to eight times as long as the distal ones. The anterior rays of each fin bear fringing fulcra, and all the others are bifurcated. The dorsal fin is composed of 13 long rays that have between 11 and 14 joints, and is preceded by three basal fulcra. The anal fin is composed of 15 rays that have between 10 and 18 joints, and is preceded by two basal fulcra. The base of the dorsal fin lies almost entirely in advance of the level of the anterior end of the anal fin. The caudal fin is hemiheterocercal and equilobate. It is composed of 20 rays that have between 18 and 25 joints. There are about seven basal fulcral scales on the dorsal side of the caudal lobe of the body.

Squamation. The scales are restored in Figure 8. There are 34 transverse scale rows between the anterior transverse scale row and the row in front of the anterior caudal fin ray. The scale formula is:

$$\begin{array}{c} 23\\ \hline 11 & 20 & 34 \end{array}$$

The transverse scale rows are less steeply inclined than in P.





bracaccinii, a feature to be expected in the squamation of a more fusiform body.

DISCUSSION

THE SYSTEMATIC POSITION OF THE GENUS Pseudobeaconia

Before discussing the systematic position of *Pseudobeaconia*, it is necessary to state why the material described in this paper is considered to represent the genus described by Bordas in 1944. *Pseudobeaconia* is usually assigned to the order Redfieldiiformes (Gardiner, 1967b), whereas the specimens described here are clearly members of the Perleidiformes, as will be shown below.

The original diagnosis of Pseudobeaconia (Bordas, 1944: 454) is based on poorly preserved material and is therefore brief. The most important diagnostic features of the genus noted by him are: the absence of branchiostegal rays; the presence of a reduced tabular and postparietal; a dorsal fin divided into two parts, an anterior part near the head and a posterior part lying in the posterior part of the body; and finally, scales longer dorsoventrally than anteroposteriorly. These features are seen in the material described here, or can reasonably be considered as misinterpretations based on poorer material of the same taxa investigated in the present paper. The tabular and postparietal of Bordas correspond to the two extrascapular elements, and the anterior dorsal fin to the row of ridge scales that lie between the head and the dorsal fin. The supposed absence of branchiostegal rays is probably due to the poor preservation of Bordas' material. The similarities discussed so far would not allow certain identification of the present material with *Pseudobeaconia*. However, Bordas recognized two species of the genus: P. bracaccinii, which was characterized by a quadrangular opercular, a subopercular slightly longer dorsoventrally than anteroposteriorly, and a dorsal fin that was slightly anterior to the level of the anal fin; and P. elegans, which was characterized by a more delicate body shape, an opercular that was less quadrangular than in P. bracaccinii, and a dorsal fin that was more clearly anterior to the level of the anal fin (Bordas, 1944: 455, 456). These differences correspond exactly to the differences between the two species recognized in the present material (cf. Figs. 4 and 8), strongly suggesting that we are dealing with the same taxa. The material described here can therefore be ascribed to the genus Pseudobeaconia with a high degree of confidence. This conclusion is strongly supported by the fact that

Bordas' material and most of that described here have been collected from the same locality.

Returning to the systematic position of Pseudobeaconia, it is clear that the genus is not a redfieldiiform. Members of the Redfieldiiformes are characterized by a number of features, such as a dermosphenotic that borders the orbital edge, an R-shaped preopercular, an antorbital that borders the nostril edge, and an excess of rays over endoskeletal supports in the unpaired fins (Hutchinson, 1972), none of which are seen in Pseudobeaconia. On the contrary, consideration of the morphology of Pseudobeaconia leaves no doubt that it is a member of the Colobodontidae (= Perleididae), a perleidiform family well represented in both marine and freshwater Triassic deposits. With two exceptions, Pseudobeaconia has all the diagnostic characters of this family (cf. Schaeffer, 1955: 19). The exceptions are the presence of a suspensorium that slopes forwards, and a rostral that extends dorsally to take part in the nostril border. The first of these characters represents an advanced state of a trend well known in the family, while the second must be regarded as a specialization of the genus.

When compared to other members of the Colobodontidae, *Pseudobeaconia* appears to be similar to *Mendocinia* (Fig. 9B), which occurs in the same locality (Bordas, 1944; Schaeffer, 1955), but differs from that genus in having the following characteristics: subdivided extrascapulars; lateral part of skull roof composed of dermopterotic and accessory dermopterotic elements; ventral end of suspensorium inclined anteriorly; opercular anterior in position relative to skull roof elements; dermohyal small; two supraorbital elements; maxilla not greatly expanded posteriorly; rostral large and bordering anterior edge of nostril; scales with ornament of ridges; scales of lateral line series indented; unpaired fins with fringing fulcra.

Pseudobeaconia is also extremely similar to Praesemionotus from the Lower Triassic of Germany (Jörg, 1969). There are however, two characters mentioned in the diagnosis of Praesemionotus that do not appear in Pseudobeaconia. They are an interopercular and a narrow preopercular that separates the opercular series from the suborbital bones (Jörg, 1969: 89). The presence of these characters led to the classification of Praesemionotus in the order Parasemionotiformes. Jörg has recently revised this opinion (personal communication), and now believes that there is no interopercular, and that the preopercular extends over that part of the cheek previously described TRIASSIC FISH FROM ARGENTINA

as being composed of both preopercular and suborbital bones. There is little doubt that *Praesemionotus* is a perleidiform, and that it should be referred to the family Colobodontidae.

In conclusion, therefore, *Pseudobeaconia* is in no way related to the redfieldiiform *Beaconia*. It represents the termination (as far as is known at present) of a line of colobodontid perleidiforms. Although its immediate ancestors are not known, they are likely to have been those that also gave rise to *Mendocinia* and *Praesemionotus*.

The Evolution of the Skull in the Perleidiformes

The evolution of the holostean feeding mechanism from the palaeoniscoid type is well known. The functional advantages of the former have been discussed by Schaeffer and Rosen (1961) and by Gardiner (1967b), and reviewed recently by Olson (1971). As Schaeffer and Rosen have noted (1961: 203), the modifications that occurred during the palaeoniscoidholostean transition "permitted a considerable adaptive radiation in the feeding mechanism at the holostean level." However, during the Triassic period, two chondrostean orders, the Redfieldiiformes and the Perleidiformes, underwent a considerable adaptive radiation of their own, yet neither group achieved the holostean condition. The Redfieldiiformes owed their success in part to the evolution of a suctorial habit of feeding (Schaeffer. 1967; Hutchinson, 1972), and it remains to examine the Perleidiformes to see if there are equally obvious reasons for their success.

The skulls of four perleidiform genera are compared in Figure 9. They are not directly related to one another, but they are members of a radiation that must have had a beginning sometime during Upper Permian times. In an earlier radiation, haplolepid genera show parallel evolution of an almost vertical suspensorium from an oblique one (Westoll, 1944); in the perleidiforms the skull structure shows even more variation. Three main trends in their evolution can be traced: 1. The evolution of an anteroventrally inclined suspensorium from one that is posteroventrally inclined. 2. The shortening of the lower jaw from a length equal to 68 percent of the anteroposterior length of the skull (*Perleidus madagascariensis*) to one only 55 percent of the length of the skull (*Pseudobeaconia bracaccinii*). 3. The elevation of the anterior end of the upper jaw.

Associated with these changes are alterations in the shape of

the maxillary-preopercular complex, and a shift of the level of the jaw articulation from a point well behind the orbit to a point below the orbit.

The advantage of a suspensorium that is anteroventrally inclined has been demonstrated by Schaeffer and Rosen; it allows greater posterior and lateral expansion of the orobranchial chamber (1961: 191). However, evolution of such a suspensorium does not necessarily involve significant shortening of the lower jaw (See, for example, the haplolepids [Westoll, 1944: fig. 44]), and the latter phenomenon in perleidids cannot therefore be regarded simply as a corollary of the former.

The advantage of a short lower jaw over a longer one is







Figure 9. Restorations of the skulls and pectoral girdles of representatives of four perleidiform genera to show variation in shape of the preopercular, maxilla, and dentary. Ornament and sensory canals omitted. Not to scale.

- A. Perleidus madagascariensis. Lower Triassic, Madagascar. From Lehman, 1952, fig. 85.
- B. Mendocinia brevis. Lower Triassic, Argentina. From Schaeffer, 1955, fig. 4.
- C. Cleithrolepidina extoni. Lower Triassic, Orange Free State. From Hutchinson, 1972, fig. 41.
- D. Pseudobeaconia bracaccinii. Lower Triassic, Argentina.

that it can exert a greater force when adducted, assuming other factors such as the mass of the adductor muscle are constant. It may be concluded, therefore, that changes in the perleidid skull architecture are related, not only to the evolution of more efficient abduction of the orobranchial chamber, but also to the need to exert a powerful force on adduction of the lower jaw. It is not difficult to discover why this last requirement was of great adaptive significance to the perleidids. The group is characterized by the presence of low rounded teeth on the palate (*Perleidus*, *?Colobodus*, and *Pseudobeaconia*) and on the lower jaw (*Perleidus*, *Colobodus*, and *Meridensa*). These teeth suggest that an important element of the perleidid diet consisted of food that required crushing, such as small molluscs and crustaceans.

The third trend in perleidid evolution, the gradual elevation of the anterior end of the upper jaw, is probably related to the evolution of shorter jaws. The disadvantage of short jaws is that the gape is reduced, but this appears to have been compensated for by elevation of the anterior end of the maxilla.

This brief analysis suggests that an important reason for perleidid success is that the evolution of short jaws and crushing teeth enabled them to feed, in part, on prey not accessible to other forms. This interpretation is not complete, however, for it does not explain the success of the Cleithrolepididae, which have rather slender lower jaws and few teeth (Fig 9C). Members of this family, although early offshoots from perleidid stock (Hutchinson, 1972), have an advanced type of suspensorium and laterally flattened bodies, and must have occupied a somewhat different niche to that of other perleidids.

THE STRUCTURE OF THE UNPAIRED FINS IN THE PERLEIDIFORMES

The detailed structure of the unpaired fin rays in *Pseudobea*conia shows that control of the fin web area was possible.

The unpaired fins of modern selachians are similar to those of chondrosteans in that each radial is associated with a large number of ceratotrichia (lepidotrichia in chondrosteans). In selachians, lateral movement of the fin web is effected by contraction of radial muscles that originate on the radials and that have broad insertions on either side of the proximal ends of the ceratotrichia. The area of the fin web cannot, however, be altered, and the fins cause considerable drag even when not

being used to aid stability. The unpaired fins of *Acipenser* have essentially the same structure and restricted range of movements as have those of selachians (Alexander, 1967: 38), and the same is almost certainly true of the fossil chondrosteans in which the number of rays exceeds the number of radials.

In the unpaired fins of teleosts a discrete musculature, which originates on the radials, enables erection, depression, and lateral movement of each ray. Such a system is only possible because the numbers of rays and radials are equal.

Westoll (1944: 83) has suggested that control of the fin web area was possible in haplolepids because in the Haplolepididae the unpaired fin rays are small in number, stout, and beveled along their anterior edges to facilitate overlapping when the web is collapsed. In *Pseudobeaconia* there is even more evidence which suggests that in that genus, and possibly in all 'subholosteans' in which the unpaired fin rays and radials are equal in number, the fins were capable of almost as much mobility as is seen in teleosts.

The dorsal fin of P. bracaccinii has been described above (Fig. 5). The rays and radials are equal in number, a condition which suggests that a discrete musculature between the two was present. This is confirmed by the presence of an anterior and a posterior depression at the proximal end of each ray. The anterior depression is here interpreted as the point of insertion of an erector muscle, and the posterior depression as that of a depressor muscle. Anteriorly, the erector muscle insertions become progressively larger and the depressor insertions progressively smaller. Because of their position and greater length, the anterior rays are more affected by water forces that tend to collapse the fin. As a result, more effort is required to erect, and less to depress, these anterior rays, and these requirements are reflected by the variation in size of the erector and depressor muscle insertions. There is no sign of any depression which would indicate the presence of an inclinator muscle, but inclination of the fin is theoretically possible if the erector and depressor muscles of one side are contracted simultaneously. Such a mechanism does in fact occur in modern Siluriformes (Alexander, 1967: 40), but cannot be confirmed in Pseudobeaconia because the state of preservation of the joint between each lepidotrichium and radial does not allow an accurate assessment of the degrees of freedom of the ray.

The grooves that run along the anterior and posterior edges of the rays in P. bracaccinii (Fig. 5) probably helped to support the soft fin web tissues.

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ABREVIATIONS

| aop | accessory opercular |
|-------|-------------------------------|
| adp | accessory dermopterotic |
| an | angular |
| ant | antorbital |
| b | branchial arch element |
| br | branchiostegal ray |
| cl | cleithrum |
| clav | clavicle |
| d | dermohyal |
| de | insertion of depressor muscle |
| den | dentary |
| dp | dermopterotic |
| ds | dermosphenotic |
| ecomm | ethmoid commissure |
| er | insertion of erector muscle |
| ex | extrascapular |
| f | fulcral scale |
| fr | frontal |
| g | groove |
| inf | infraorbital |
| (1) | left side |
| mx | maxilla |
| na | nasal |
| no | nostril border |
| op | opercular |
| pa | parietal |
| par | parasphenoid |
| pmx | premaxilla |
| ро | postorbital |
| pop | preopercular |
| pro. | postrostral |
| pspi | postspiracular |
| q.j | quadratojugal |
| r | radial |
| ro | rostral |
| SD | suborbital |
| sc | suprascapular |
| sci | supracleithrum |
| SO | supraorbital |
| sop | subopercular |



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