ON *BIRGERIA ACUMINATA* AND THE ABSENCE OF LABYRINTHODONTS FROM THE RHAETIC

by R. J. G. SAVAGE and N. F. LARGE

ABSTRACT. A maxilla of *Birgeria acuminata* from the Rhaetic of the Bristol Channel is described. Previous records of labyrinthodonts from the British Rhaetic are shown to belong to this piscine genus.

VERTEBRATE remains from the Rhaetic Bone Bed around the Bristol Channel are well known. The great majority of the small specimens comprise fish teeth, scales, and spines while the larger specimens are attributable to reptiles, mainly plesiosaurs and ichthyosaurs. The fish remains usually figure under the names *Acrodus*, *Hybodus*, '*Saurichthys*', *Nemacanthus*, *Sargodon*, *Gyrolepis*, and *Ceratodus*. In addition to the marine reptiles, *Plesiosaurus* and *Ichthyosaurus*, occasional terrestrial reptiles have been found; these bones have been referred to dinosaurs but the material is not sufficiently diagnostic for more precise identification. From specimens which have been described and from material now in the University of Bristol Geology Museum, at least two species of terrestrial reptile are clearly represented, a large species and a small species about 2–3 ft. long. No pterosaurs or mammals are recorded from the Bone Bed, and there remains for consideration only one other vertebrate group, the amphibia.

Miall (1875) reported that *Metopias diagnosticus* von Meyer, a labyrinthodont from the Keuper of Germany, was present in the Aust Bone Bed and the statement has been often repeated in the literature. Reynolds (1946) stated that labyrinthodont remains were common at Aust, usually very fragmentary cranial bones with 'characteristic' pitted surface and rarely jaw fragments with teeth. Reynolds further noted that two types of teeth are found on these jaw fragments, and that some isolated teeth commonly attributed to *Saurichthys* may be labyrinthodont.

The true identity of these 'labyrinthodont' specimens has remained unresolved, due largely to lack of really good material. Reynolds illustrated a mandible fragment with five teeth, but the specimen is highly pyritized and impossible to prepare. In 1954 Professor C. F. A. Pantin found a dentary which he kindly donated to the University of Bristol Geology Museum (UBGM 19001); this specimen prepared well in acetic acid and has four teeth. More recently one of us (N.F.L.) found a maxilla at Westbury-on-Severn which contains seven major teeth and a labial row of smaller teeth. The specimen has been beautifully prepared by Mr. A. E. Rixon of the British Museum (Natural History) and is described in detail below; it is patently *Birgeria* and indistinguishable from other specimens previously referred to the labyrinthodonts, which can now be placed in this piscine genus.

Family BIRGERIIDAE Berg 1940

Diagnosis. Body almost naked, scales only present on dorsal half of caudal pedicle, on body axis of caudal fin, and anteriorly to the caudal pedicle in a single row along the main lateral line. As in the Palaeoniscidae, two nasal openings on each side, one anterior

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and one posterior to the postrostral. Sensory canal system differing from that in Palaeoniscidae mainly in the following respects: supraorbital sensory canal ending blindly in rostropremaxillary without communicating with ethmoidal commissure of infraorbital sensory canals; dorsal part of preopercular sensory canal extending from radiation centre of preoperculum in an almost anterior direction towards most dorsal part of postorbital vertical section of infraorbital sensory canal. Very large unpaired rostropremaxillary. Parietals (one or two on each side) separated by frontals. One (or two?) extrascapulars on each side. Supratemporal independent. Intertemporal fused with dermosphenotic and with a number of posterior supraorbitals. A larger or smaller number of free supraorbitals. Neural endocranium not ossified in a single piece but in separate bones (an unpaired occipital bone, a paired prootico-opistotic, a paired autosphenotic, an unpaired sphenoid, and a paired ethmoidal bone). Posterior myodome smaller than in Palaeoniscidae. Parasphenoid strong, extending backward below the whole neural endocranium, and with a strong paired processus ascendens. Mouth much larger than in Palaeoniscidae. Suspensorium very oblique. Teeth on jaws arranged in a labial and a lingual row. Labial teeth small, lingual teeth very large. Operculum small, suboperculum lobate much as in *Polyodon*. Spiracle present. Branchiostegal rays numerous. Fin rays jointed, devoid of ganoine. Pelvic fin large, with about fifty lepidotrichia. Dorsal and anal fins both situated far back, dorsal fin slightly anterior to anal fin, both fins large and with more than fifty lepidotrichia. Fulcra present only on the body axis of the caudal fin. Endoskeleton of dorsal fin represented by three series of radial ossifications; an axonost, a baseost, and a distal series. Endoskeleton of anal fin represented by two series of radial ossifications, probably an axonost and a baseost series; baseost series very short, supporting only posterior third of fin. Posterior elements of axonost series of endoskeleton of both dorsal and anal fins fused to a fairly extensive axonost plate. Notochord persistent. Axial skeleton with ossified dorsal and ventral arcuals, in abdominal region moreover with supraneurals, in part of caudal region possibly also with independent infrahaemals. Skeleton of pelvic fin consisting of an ossified pelvic plate and one or two rows of radial ossifications.

Remarks. The family name was erected by Aldinger (1937) but without a diagnosis. Nielson (1949) gave the above detailed amended diagnosis in the light of new Greenland Triassic material. Nielsen bases the family on *Birgeria* and does not definitely include in it any other genus.

Genus BIRGERIA Stensiö 1919

Diagnosis. Large or fairly large fishes. Trunk long and slender, oval in transverse section. Head rather large, with big eyes and extremely long jaws. Neural endocranium narrow both anteriorly and posteriorly, but very broad in its middle part and especially between its strong postorbital processes. Neural endocranium in both small and large specimens partly occupied by a number of independent bones. External dermal bones of the head relatively thick and mainly ornamented with tubercles, to a smaller extent, however, also with striae. Striae best developed on maxillary and dentalo-splenial, and on these bones to some extent covered by more superficially situated tubercles of varying shape. On the jaws a labial row of small, and a lingual row of large teeth. Parallel with these two rows, a third row consisting of small to medium-sized teeth on the ventral or ventro-

lateral part of the oral faces of the ectopterygoid and the dermopalatines. Moreover, large areas of oral faces of ectopterygoid, entopterygoid, dermopalatines, dermometapterygoid, and prearticular covered by very small teeth. Small teeth also present on ossifications of basibranchial series and branchial arches. Teeth of jaws and at least larger teeth on dermal bones of palate pointed and conical with a two-edged enamel cap, in the geologically older species on the whole smooth, in the geologically youngest species equipped with vertical, elevated, sharp striae; basally to enamel cap the teeth of all the species vertically striated, either with fine striae alone or with coarse striae which in their turn bear the fine striae; plicidentine not present. Teeth of branchial arches more slender than those of the jaws and with an enamel cap, which always seems to be smooth. [Abbreviated from Nielsen 1949, pp. 280–4.]

Type species. Birgeria mougeoti (Ag.) from the Triassic of Europe and Spitsbergen.

Species. In addition to the type species, the following species have been recognized by Nielsen as belonging to the genus:

Birgeria stensiöi Aldinger 1931	from Triassic of Europe
Birgeria groenlandica Stensiö 1932	from Triassic of Greenland
Birgeria velox (Jordan) 1907	from Triassic of California
Birgeria acuminata (Ag.) 1844	from Rhaetic of Europe
Birgeria costata (Münster) 1839	from Rhaetic of Europe
Birgeria annulata (Winkler) 1880	from Triassic of Europe
Birgeria nielseni Lehman 1948	from Triassic of Madagascar

Remarks. The diagnosis in Nielsen (1949, pp. 280–4) contains an account of the anatomy of the genus. It has been shortened here to the statements apposite to the present discussion. Lehman (1952) gives a full synonymy for the genus. Although eight species are listed, most are poorly known. They have a wide geographic distribution and relatively narrow stratigraphical range from the Lower Triassic to the Rhaetic.

Birgeria acuminata (Agassiz)

Plate 20

Abbreviated Synonymy.

1843 *Saurichthys apicalis*, J. E. Portlock (*errore*), p. 470, pl. 14, fig. 19.
1844 *Saurichthys acuminatus*, L. Agassiz, p. 86, pl. 55*a*, figs. 1–5.
1844 *Saurichthys longidens*, L. Agassiz, p. 87, pl. 55*a*, figs. 17, 18.
1921 *Birgeria acuminatus*, E. A. Stensiö, p. 150.

Remarks on the Synonymy. Without a detailed study of the German material it would be pointless and possibly confusing to list the twelve specific names sometimes ascribed to *Saurichthys*, among which some are probably synonymous with *B. acuminata*. Details of these are to be found in Woodward (1895, pp. 21–23) and Boni (1937).

Diagnosis. Large fish with robust dentition. Basal portion of teeth below enamel cap relatively shorter than in *B. mougeoti*. Enamel cap terminated proximally by prominent collar; teeth with fine vertical striations, best developed immediately proximal to collar.

Remarks on Diagnosis. Agassiz (1844) noted the dental characters which differentiate *B. mougeoti* from *B. acuminata*. Woodward (1895) restated some of these. Boni (1937, pp. 584–5) listed characters including table of jaw lengths, which he regarded as

differentiating *B. mougeoti*, *B. stensiöi*, *B. groenlandica*, and *B. acuminata*. Lehman (1952) stated that *B. groenlandica* had two forms, a large and a small, the latter being comparable with *B. nielseni*. Boni (1937, p. 596) in discussing *B. costata* from the Rhaetic of the Imagna Valley in Italy, suggested that presence or absence of a keel on the tooth crown is a variable which cannot be relied upon as a specific character. *B. costata* is very much larger than *B. acuminata*. Stratigraphically only *B. acuminata* and *B. costata* among *Birgeria* species have a Rhaetic range; whether these are merely stratigraphic species or represent biological differences must await better material. *B. acuminata* is common in the Rhaetic of north-west Europe and there are no known occurrences outside the Rhaetic.

Holotype. The teeth illustrated by L. Agassiz (1844) on Plate 55, figs. 1–5 were described by him as coming from the Muschelkalk of Aust Cliff. The specimens, then in the Bristol Institution Museum, were later incorporated in the Bristol City Museum collections and registered collectively under the catalogue number C 4578. Unfortunately all were destroyed when the Museum was bombed in 1941. The horizon is undoubtedly the Rhaetic Bone Bed at Aust Cliff, 10 miles on 6° west of north from Bristol (NGR 566898). The International Rules of Zoological Nomenclature do not encourage the creation of neotypes unless circumstances are exceptional and to conform to this ruling no new type is here established.

Description. The new specimen of *Birgeria acuminata*, BMNH P47287, is from the Westbury Shales of the Rhaetic at Westbury-on-Severn, 8 miles WSW. of Gloucester, (NGR 715132). The specimen comprises the middle portion of a left maxilla, and is broken both anteriorly and posteriorly while the dorsal ramus is largely missing. The external surface is completely covered with fine tubercles except along the antero-dorsal margin where the orbital bones overlapped. The tubercles are densest along the dental margin and near to the orbital region are extremely fine. The dorsal part of the bone is insufficiently preserved to detect any pattern in the arrangement of the tubercles. Internally the bone is smooth and extended along the ventral margin of the teeth.

Along the 12 cm. of tooth row preserved there are 14 alveoli for lingual teeth and in 8 of these the teeth are present. Lateral to these the maxilla margin carries a row of small labial teeth, of which some 8 remain intact. The lingual teeth are conical, lie close together in a row without any space between them at the level of the insertion into the maxillary bone. When a tooth is missing an ovoid pit remains which extends on either side to the base of the adjoining teeth. At the level of the ventro-lateral maxillary margin the lingual teeth appear more spaced due to the effect of the tapering cone and the distance between the teeth is about equal to the tooth diameter at this level. The ventro-lateral margin of the bone varies in thickness a little; is thickest between the lingual teeth and thinnest around them. The distribution of the labial teeth is slightly irregular, but the pattern is broadly a single row with on average 6 labial teeth to every one lingual tooth. In size the labial teeth tend to be slightly larger between the linguals and smallest when alongside the linguals. The lingual teeth also vary slightly in size, but without any observable pattern; their size may reflect more the time of eruption than their position in the jaw.

EXPLANATION OF PLATE 20

Birgeria acuminata (Agassiz), UBGM 19001, Rhaetic of Westbury-on-Severn, Gloucs. Left maxilla *a*, lateral aspect; *b*, occlusal aspect. ×1·5.

The lingual teeth are roughly conical in outline, the basal portion being flayed out for attachment to the bone. The conical axis of the teeth is curved slightly inward, but there is no detectable anterior or posterior curvature. Each tooth is terminated by an enamel cap, which in newly erupted teeth is pointed but becomes blunted with wear. The tooth cap is terminated proximally by a ring, collar, or cingulum. From this collar arise anterior and posterior keels which do not quite reach the summit. Fine striations also arise from the level of the collar, and extend both proximally and distally; they are densest on the medial side of the tooth and are few or lacking on the lateral side. Those rising on to the cap do not reach the summit and frequently unite. Those extending proximally also disappear before reaching the base. The labial teeth appear to have a similar build to the linguals though striations and keels are rarely detectable.

Remarks. The purpose of the present paper is to clear up some of the confusion prevailing with respect to labyrinthodonts in the Rhaetic and a detailed appraisal of *Birgeria* is not attempted. The Westbury beds of the Rhaetic yield vertebrates at several horizons, from the shales and limestones as well as from the basal bone conglomerate. The vertebrate fauna appears to be essentially the same at all levels though reptile bones are rare outside the basal bone bed. Isolated conical teeth are abundant in the Westbury beds and these can invariably be assigned to either *Birgeria* or *Ichthyosaurus*. The *Ichthyosaurus* teeth differ from those of *Birgeria* in being larger, less tapering and hence more nearly parallel sided, and in lacking a collar; keels on the caps are wanting and the proximal portion of the teeth is infolded to a greater or lesser extent. While most teeth are recognizable on external morphology, preliminary investigations suggest that histological structure can be used to distinguish reptile and fish, and possibly even to identify genera. Careful collecting from individual beds and use of histological techniques could considerably advance our knowledge of these faunas.

Several other maxillae and mandibles are known beside the specimen described above; though none is so well preserved they are all clearly *Birgeria* and not labyrinthodont. Reynolds (1946) described a mandible (UBGM 7976) as '*Metopias diagnosticus*'; the specimen is unfortunately highly pyritized and cannot be prepared with acid, but is undoubtedly *Birgeria acuminata*. Woodward (1889) described a left maxilla (BCM C4579) as *Saurichthys acuminatus*; the specimen is closely comparable with that described above, has two lingual teeth and the row of alveoli for the labial teeth is distinguishable. Numerous other smaller pieces of maxilla and mandible exist in collections. Another frequently found part is the symphysis of the mandible; this is very thick and heavy (e.g. UBGM 18038, i–iv). Comparison of *Birgeria* with the living *Lepidosteus* is particularly close on many anatomical features—the long jaws, the heavy mandibular symphysis, the external ornament, the arrangements of the lingual and labial teeth; striations and keel are present on the lingual teeth but differ in detail from those of *Birgeria*.

A search of the Rhaetic exposures around the Bristol Channel and museum collections has revealed no vertebrate material that cannot be assigned to either fish or reptile. The previous records of 'labyrinthodont' are shown to be misidentifications for large specimens of *Birgeria*. No evidence for amphibia remains. Stratigraphically this interpretation clarifies the position regarding the labyrinthodonts. It can now be stated that there are no known Rhaetic metaposaurid labyrinthodonts; their last appearance is in

the Upper Triassic beds of India and North America. Jain, Robinson, and Roy Chowdhury (1964) record metaposaurs from the Maleri beds of the Pranhita–Godavari valley, India, and these beds they equate with the Carnian to Middle Norian zones of the marine Upper Triassic.

Nilsson (1946) recorded the presence of a plagiosaur from the Rhaetic of Scania, Sweden; the material he identified as *Gerrothorax* and is well preserved in a coal-bearing deposit of Middle Rhaetic age. Nilsson considered the plagiosaurs to form the type family of an order of Triassic stegocephalians, distinct from labyrinthodonts. Panchen (1959) writing on plagiosaur affinities, excluded the brachyopids from his order Plagiosauria and placed the plagiosaurs within the superorder Labyrinthodontia. Hence the presence or absence of labyrinthodonts in deposits of post-Triassic age depends on (*a*) whether the definition of the Labyrinthodontia includes or excludes the Plagiosauria and (*b*) whether the definition of the Trias includes or excludes the Rhaetic. The Rhaetic of Britain has yielded no amphibia; the Rhaetic elsewhere contains amphibia which may be labyrinthodont.

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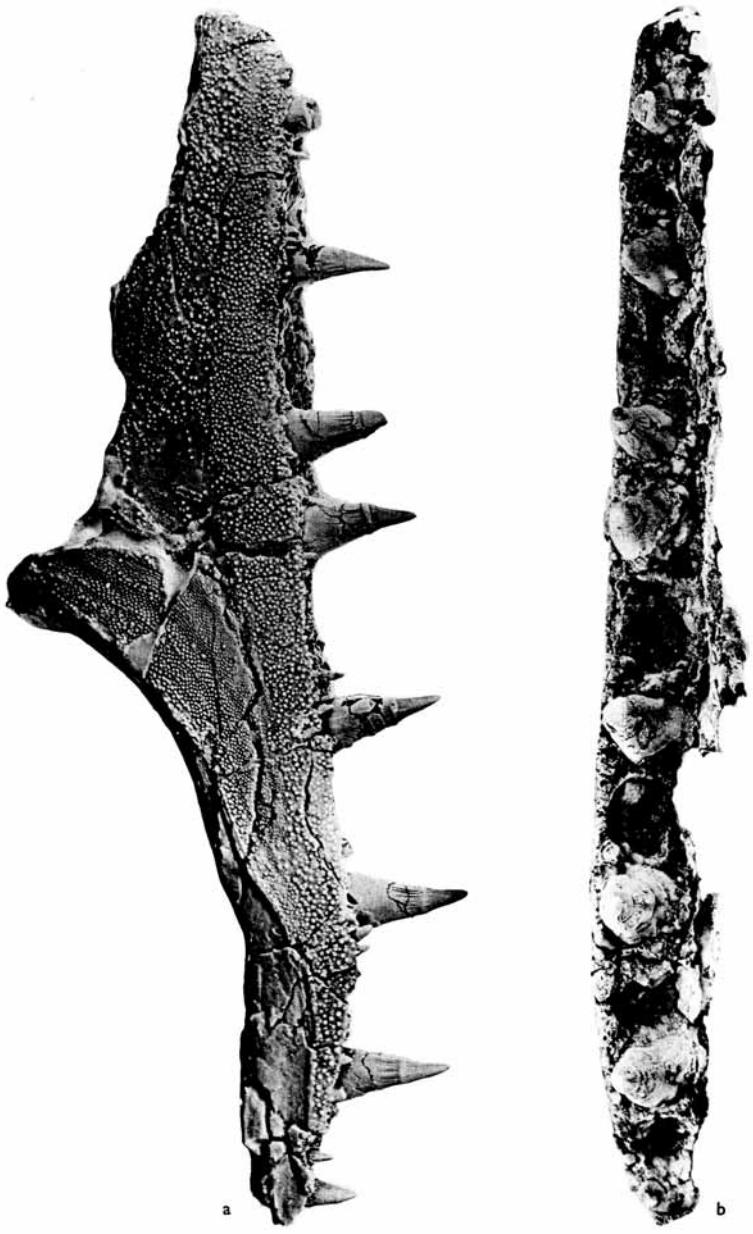

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