

THE PERMIAN LEOPTERIID *MERISMOPTERIA* AND THE ORIGIN OF THE PTERIIDAE

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ABSTRACT. The musculature and dentition of *Merismopteria* Etheridge jun. 1892 are described and illustrated. Muscles are present both in front and behind the 'clavicle' or buttress ridge. Lateral and cardinal teeth may be present. *Merismopteria* is closely related to and may be a synonym of *Leiopteria* Hall 1883. Modern pteriids are considered to be derived from the Palaeozoic leiopteriids which lack a chondrophore and have a flattish ligament area with chevron-shaped or parallel-longitudinal ligament grooves and it is concluded that the 'pteriid' type of ligament with a chondrophore is independently developed in the pteroids and the pectinoids.

IN describing a specimen from the Bowen River, Queensland, Etheridge jun. (1892, p. 271) proposed a new generic name *Merismopteria*, designating as type *Pterinea macroptera* Morris (1845, p. 276, pl. 13, fig. 2; 3). The characters of this genus, including the nature of the clavicle and the anterior musculature, and the relationship to other genera, especially *Leiopteria* Hall, have caused considerable speculation.

Under the heading 'Generic Characters' Etheridge gave the following diagnosis:

'Pteronitiform in appearance, the anterior end lobe-like and well developed; posterior end alate. Area excavated along the cardinal edge of both valves, and deeply ridged for the reception of a ligament; cardinal teeth wanting but a strong clavicle descends in each valve before the anterior adductor muscles; one or more lateral teeth in each valve. Anterior muscle scars double and strong, the superior scar situated towards the umbones. External ornament of concentric ridges.'

Etheridge states under the heading 'Observations', however, that there is 'one lateral tooth only, either oblique or horizontal'.

In order to clarify the characters of *Merismopteria* an attempt has been made to find the type specimen or specimens described by Morris and according to Morris collected by Strzelecki from Spring Hill, Van Diemen's Land (Tasmania). According to a letter from the British Museum (Natural History) the types are not in this institution where most of the Strzelecki Collection is housed, so that it appears that they are lost. Two specimens, however, from the Strzelecki Collection (PL2865-6) are housed in the British Museum. These have the locality label 'Carboniferous Australia'. These and other specimens have been kindly lent by the British Museum, and, together with specimens in the Australian Museum, Sydney, and in the Bureau of Mineral Resources, Canberra, afford considerable additional information on *Merismopteria*.

Type Specimens of Pterinea macroptera Morris. Although Morris's figured specimen (or specimens) from Spring Hill, Tasmania, appear to be lost it is not proposed to choose a neotype at present.

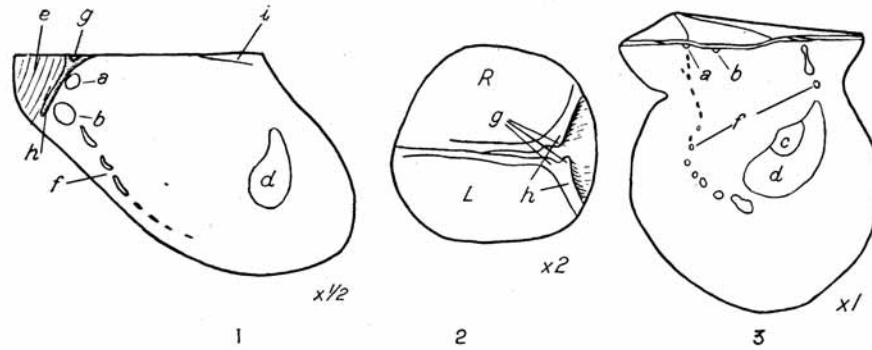
Mr. M. R. Banks, of the Geology Department of the University of Tasmania, in a letter of 19 November 1958, says: 'I have so far been unable to find the Permian rocks at Spring Hill. . . . Permian rocks occur a few miles to the east at Eastern Marshes and about ten or fifteen miles to the west near Waddamana.' He also says the University of Tasmania has no specimens from this area. Although it is possible that PL2865 and

PL2866 are from the type locality it appears better to defer choice of a neotype until the locality of the specimens can be confirmed or until suitable topotype material is available.

PL2865 and PL2866 are contained in a light buff to white (? leached) dense silt to fine sandstone with many quartz grains, some mica, and, apparently, a clay matrix.

Dimensions of British Museum Specimens

Locality	Number		Length	Height	Width
Carboniferous Australia	PL2865 (internal impression)	Left valve	38	19+	2.5
		Right valve	36	21+	2.0
	PL2866 (internal impression)	Left valve	36	23	3.0
		Right valve	32	21	2.5
McCallum's Block, Bowen Coal Field, about 4 miles south-west of Collinsville, probably above Big <i>Strophalosia</i> Bed and below <i>Derbyia</i> Bed.	PL541 (internal impression)	Left valve	103+	63	18.0
		Right valve	103+	60+	16.0
	PL540 (external impression)	Right valve	46	31	6.0



TEXT-FIG. 1. Composite internal impression of a left valve of *Merismopteria*. 2, Cardinal teeth or *Merismopteria*. 3, Musculature of a right valve of *Pinctada vulgaris* (based on Newell 1938). *a*, *b*, *c*, impressions of pedal muscles; *d*, impression of 'posterior' adductor; *e*, impression of 'anterior' adductor; *f*, pallial line; *g*, cardinal teeth or their impressions; *h*, 'clavicle' (anterior buttress ridge) of its impression; *i*, posterior lateral tooth; *L*, left valve; *R*, right valve.

Musculature. Etheridge considered that the anterior muscle scar was situated behind the clavicle, an observation which I have been able to confirm (Dickins 1957, p. 30). On the other hand, in apparently closely related leiopteriids, for example *Dozierella* Newell (1940, p. 284), the anterior muscle is found in front of the 'clavicle' which thus represents a buttress ridge. The two specimens from the Strzelecki Collection allow a resolution of this apparent contradiction. Muscles are present both in front of and behind the 'clavicle'. In front of the 'clavicle' in PL2865 the presence of a relatively large anterior adductor muscle is indicated by muscle growth lines (the muscle track). The anterior adductor muscle is bounded behind by the 'clavicle' which is thus a buttress ridge confirming the interpretation made by Newell (1940, p. 283).

In PL2866, however, two distinct muscles occur behind the buttress. The larger, which is not much smaller than the anterior adductor, is situated immediately behind the buttress and lies below the smaller. The smaller is placed on the anterior side of the internal impression of the beak. Although they are unusually large, it seems likely that these muscles are connected with the action of the foot (pedal muscles).

Further information is given on the musculature by PL541, from McCallum's Block, Bowen Coal Field. The posterior adductor scar is large and kidney-shaped, situated over the posterior umbonal ridge. The intermittent pits of the pallial line run from the base of the ventral pedal muscle along the anterior side of the umbonal ridge towards the posterior adductor. A number of small round pits occur on the surface of the shell within the pallial line, marking the mantle attachment to the shell.

The musculature is thus more primitive than that characteristically found in adult living pteriids, the anterior adductor and the pedal muscles being considerably more highly developed.

Hinge structure. Examination of specimens in the Australian Museum, Sydney, and in the Bureau of Mineral Resources, Canberra, confirms Etheridge's description of the ligament (1892, p. 271) and shows this structure is of the same type as that described for *Leiopteria? carrandibbiensis* Dickins (1957, p. 30, pl. 4, figs. 13-17, text-fig. 4). A specimen from the collections at Canberra is figured. The ligament is borne on an area which is elongated on either side of the umbo, and on which are a number of parallel-longitudinal ligament grooves. Recognition of a posterior lateral by Morris, de Koninck, and Etheridge is confirmed by the presence of a lateral tooth in PL2866 and in specimens in the Australian Museum. In PL2866 a lateral tooth is visible in the left valve towards the rear of the cardinal margin. By analogy with living pteriids at least a single tooth could be expected in the right valve, although such a tooth has not been visible in most of the specimens which I have examined. However, even though the lateral dentition is difficult to see in internal impressions, because it diverges only slightly from the cardinal plate, it does appear possible that in some specimens or species lateral teeth are absent. Living pteriids vary in this way.

In PL2865 the impressions of small cardinal teeth are visible immediately in front of the umbos. In the right valve these comprise a projection with a groove on either side and in the left valve a socket for the projection of the right valve with a clasping lamella on either side fitting in the sockets of the right valve. These are similar to those of living Pteriidae and by analogy, like the lateral teeth, may be variable. The details of the dentition would appear to be of doubtful value for generic separation.

Shell structure. The main shell layer is composed of prisms at right angles to the surface (specimens in the Australian Museum). The prisms are of a similar size to those recorded for *L.? carrandibbiensis*. Under the hand lens the structure appears the same as that found in *Atomodesma*. It may be assumed that during life a thin inner nacreous layer was present.

Relationship to Leiopteria Hall 1883. Amongst described genera *Merismopteria* appears to be closest to *Leiopteria*. On the basis of Hall's diagnosis (1884, p. xiii) there is little to choose between the two, but the detailed characters of Hall's species still remain obscure and until more is known about these species it is not possible to decide whether

Merismopteria is a synonym of *Leiopteria* or not. Meantime perhaps *L. ? carrandibbiensis* Dickins should be assigned to *Merismopteria* rather than *Leiopteria*. Such species as *Leiopteria ? dutoiti* Harrington (1955, p. 120, pl. 24, figs. 5, 11) and *Leiopteria bonaerensis* Harrington (1955, p. 120, pl. 24, fig. 10) may be more closely related to *Merismopteria* than is suggested by their generic assignment to *Leiopteria*. (According to Neave (1939, p. 960) *Leiopteria* is an emendment proposed by Fischer 1886 for *Leiopteria*.)

ORIGIN OF THE PTERIIDAE

In this paper the Pteriidae are restricted to those forms, characteristically with a well-developed prismatic shell layer, which possess the 'pteriid' type of hinge, that is with a single distinct ligament pit on the area. This does not include the Mesozoic forms such as *Meleagrinnella*, *Oxytoma*, and *Maccoyella* which properly belong to the Pectinacea (see Ichikawa 1958). Pteriidae in this restricted sense are at least very rare in Palaeozoic rocks, and I know of no definite occurrence. However, *Bakevellia* King from the Upper Permian has multiple ligament pits on the area like *Perna* and is thus apparently derived from a form with a single ligament pit. Most of the Palaeozoic forms which have been referred to the Pteriidae have areas with a number of parallel-longitudinal or chevron-shaped ligament grooves and are more satisfactorily referred to the Leiopteriidae or other families.

Although *Merismopteria* differs in some important characters from modern Pteriidae, it shows sufficient similarity to suggest that the Pteriidae were derived from leiopteriids or related shells. The general shape and shell structure of *Merismopteria* are similar to modern pteriids, and its dentition and posterior musculature to species of *Pinctada*. In all these respects it is significantly different from the pectinoid forms. It differs markedly from the pteriids only in the anterior musculature, which is apparently more primitive and in the ligament structure. The poor development of the subauricular notch in right valves in Palaeozoic forms appears to be of lesser importance. From these data it seems that the 'pteriid' type of hinge was developed independently in the Pteriacea and the Pectinacea, a suggestion which has already been made by Newell (1942, p. 26). Alternative explanations such as derivation of the pteriids from the aviculopectinids seem unlikely. Such a derivation would require modification of the shell in a great number of respects, including shell shape, shell structure, and musculature to produce a type of shell already in existence but requiring essentially only modification of the hinge.

Bernard (1895-7) observed that the ligament was internal when it first appeared in the young pelecypod and concluded this was the primitive condition of nuculoids. Newell (1942, p. 28), after referring to Bernard's observation, states that 'in some genera such as *Pecten*, *Nucula*, *Pteria*, *Lima*, and *Ostrea*, this condition apparently continues to maturity'. Newell thus suggests the early internal ligament corresponds to the adult resilifer.

However, the phylogeny of at least some of these forms suggests that the early ligament recorded by Bernard is unlikely to be analogous with the adult resilifer, and indeed Bernard's ontogenetic studies also seem to show this. If Bernard's and Newell's suggestion were correct this would seem to contradict the conclusion that the 'pteriid' ligament is derived independently in the Pectinacea and the Pteriacea.

There seems little doubt, however, that the ancestors of the pteriids in the restricted sense are represented in the Upper Palaeozoic mainly by forms which have parallel-

longitudinal or chevron-shaped grooves, and all these forms can be satisfactorily placed in the superfamily Pteriacea. Earlier in the Palaeozoic the superfamilies such as the Pteriacea, the Pectinacea, and the Mytilacea become less easy to distinguish as these groups converge but none of these earlier forms can be expected to possess the 'pteriid' type of ligament.

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