BRADYODONT SHARKS IN THE PERMIAN OF WESTERN AUSTRALIA.

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ABSTRACT. *Helodus* sp. and *Crassidonta subcrenulata*, n. sp., are described from Permian (Artinskian) beds in the North-West Division of Western Australia. *Crassidonta subcrenulata* is similar to *Crassidonta stuckenbergi* Branson from the Phosphoria formation of Wyoming.

REMAINS of bradyodont sharks are not very common in the Permian and, in particular, records of their occurrence in Australia are scanty. For Western Australia the first and so far only reference to the occurrence of a bradyodont is contained in an early report by E. T. Hardman (1884, p. 10) who conducted the first geological reconnaissance of the Kimberley District, in the north of Western Australia. He lists a species determined as "*Poecilodus jonesi*" from supposedly Carboniferous limestone of the "plains near Mount Percy", the only associated fossil from that locality being "*Fenestella antiqua*". It is now known that Hardmann's "Carboniferous" includes strata which are of Devonian and partly of Permian age, and the fossils mentioned above were probably Permian. According to Wade's geological map (1937), Mount Percy itself consists of Devonian limestone, but an outcrop of Lower Permian sandstone is shown less than a mile west of Mount Percy and the occurrence in the same region of Permian limestones from which Hardmann could have collected "*Fenestella*" and "*Poecilodus*" can be considered as possible.

Poecilodus jonesi is a Carboniferous species which has been well described by Portlock (1843, p. 468) and by Davis (1883, p. 442), but as far as I am aware no representative of that genus has ever been described from strata of Permian age. Unfortunately, it is now impossible to verify Hardmann's determination. After Hardmann's return from the Kimberleys his collections were dispersed, and while some specimens were sent to the British Museum, it is not known where the others, among them "*Poecilodus jonesi*", were deposited.

Another bradyodont has been described from the Permian of New South Wales as "*Tomodus convexus Agassiz?*" by de Koninck (1877, p. 354; 1898, p. 281). Unfortunately, neither can this identification be confirmed, because all collec-

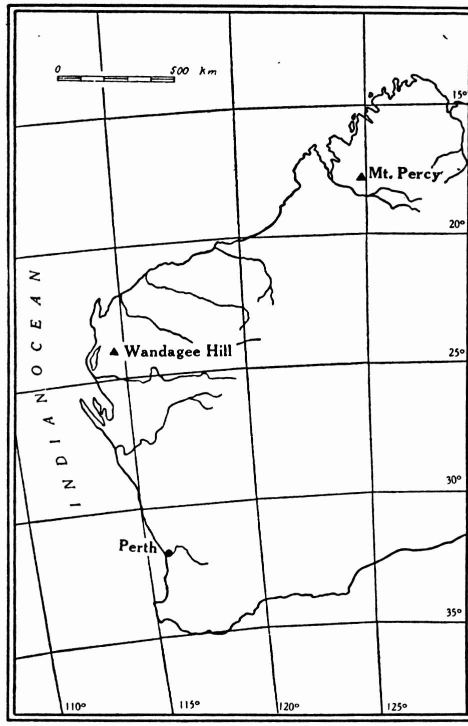


Fig. 1. Index map of Western Australia, showing localities mentioned in the text.

tions described by de Koninck were subsequently destroyed by fire.

Helicoprion, now known from several localities in Western Australia, would probably be included in the bradyodonts by some authors, but both Moy-Thomas (1939, p. 12) and the present writer (1940, p. 14) have independently questioned the affinities of that genus with the Bradyodonti.

In 1940 the writer discovered several specimens of bradyodont teeth in the higher parts of the Permian system of the North-West Division of Western Australia. One specimen belongs to the widely distributed group of teeth that is known under the name of *Helodus* and was found near the top of the Wandagee series in the highest ammonoid horizon of the *Linoproductus* zone, where it is associated with *Pseudogastrioceras goochi* (see Teichert, 1942, p. 223) and with *Agathiceras applanatum*. The specimen is not well enough preserved to be named specifically.

Another find was made in strata lower down in the Wandagee series, in the upper part of the *Calceolispongia* zone. A number of teeth were found in one locality within a few square yards so that it is believed that they form part of the dentition of one individual. These teeth must be referred to the rare genus *Crassidonta* Branson.

Crassidonta was established by E. B. Branson in 1916 on specimens from the "Embar formation" of Wyoming. Only one species was described, *Crassidonta stuckenbergi* Branson, which must be regarded as the genotype by monotypy. Also Branson discovered that his specimens of *C. stuckenbergi* were almost indistinguishable from teeth that Stuckenberg, in 1905, had figured, but not described or named, from strata in the region of the Samara Bend of the Volga in Russia which Branson stated were of Moscovian (Middle Carboniferous) age. The Embar formation was later discarded and the strata thus named were included in the basal part of the Phosphoria formation. Whereas Miller and Cline (1934) demonstrated that the cephalopods from the higher parts of the Phosphoria formation indicated an Artinskian age of that part of the succession, both C. C. Branson (1930) and Miller and Cline stressed the fact that the occurrence of *Crassidonta* in the lower part of the Phosphoria tied it up with the Moscovian of Russia.

However, since Stuckenberg published his description of the fossils from the Samara Bend it has been shown by Noinsky that no Moscovian is exposed anywhere in this vicinity.[1] It is true that in the Tsarev Kurgan, a hill to the north of Kuibyshev from which Stuckenberg's specimens of *Crassidonta* were obtained, the lowermost fossiliferous zones of the Samara Bend succession are exposed. A more detailed description of the section in this locality is given by Boutrov (1937, p. 58). But these strata belong to the *Triticites* zone (Upper Carboniferous), as has also been confirmed by Dunbar (1940, p. 245), and not to the Middle Carboniferous.

The difference between the Western Australian species here referred to *Crassidonta* and *Crassidonta stuckenbergi* from Wyoming and from the Samara Bend cannot at present be regarded as more than of specific rank, and since the Western Australian species is undoubtedly of Artinskian age, it may be expected that the time gap between the two species will, at some

[1] I have not had access to Noinsky's original publication in the Geological Studies of Kazan University (1915), but Forsch (1937) has given a summary of his results on which I have relied.

future date, be bridged by the discovery of additional species elsewhere.[2]

There are probably at present not sufficient facts known to assign *Crassidonta* to its correct taxonomic position within the Division Bradyodonti, other than that it obviously belongs to the Order Eubradyodonti of Moy-Thomas (1939). Although Hay (1929, p. 557) lists *Crassidonta* among the Cochliodontidae, the teeth are most similar in general shape to *Psammodus* of the Suborder Psammodonti, and *Crassidonta* may be a Permian descendant of this otherwise Carboniferous group. This suggestion is also supported by a study of the microstructure of the series which will be discussed more fully below.

PALAEONTOLOGICAL DESCRIPTIONS.

Genus *Helodus* Agassiz.

Helodus sp. ind.

Plate 1, Figs. 15, 16.

Only one poorly preserved fragment of a crown which is 18 mm. long and 6 mm. wide. In an undamaged condition, however, the crown must have been about 22 mm. long. Its surface was flattened at both ends with a strongly convex central part. The surface is smooth, though penetrated by numerous openings of the medullary canals.

Occurrence: In the upper part of the *Linoproductus* zone of the Wandagee series (uppermost zone with *Pseudogastrioceras goochi*), 300 yards east of mouth of southeastern gully of Wandagee Hill, Mungadan Paddock, Wandagee Station. No. 21400, Department of Geology, University of Western Australia.

Genus *Crassidonta* E. B. Branson.

Crassidonta subcrenulata Teichert, n. sp.

Plate 1, Figs. 1-14; Plate 2, Figs. 17, 18; Plate 3, Figs. 19, 20.

Nine teeth and some smaller fragments of teeth were found so close together that it is believed that they all belong to one

[2] In view of C. C. Branson's statement (1930, p. 20) that there is no stratigraphical break within the Phosphoria formation, a fact that Miller and Cline (1934, p. 286) found it hard to reconcile with the palaeontological evidence, it might be suggested that unless the identity of the Russian species with *Crassidonta stuckenbergi* is considered to have been established beyond possible doubt, the mere occurrence of the genus *Crassidonta* in the lower part of the Phosphoria formation ceases to be an obstacle to the inclusion of these strata in the equivalents of the Artinskian.

individual and since the specimens can be roughly grouped into pairs of about equal size, it may be that they belonged to one jaw only.

The teeth are elongated, somewhat obliquely rectangular in outline. Their main part is a symmetrical ridge which in the larger teeth is strongly rounded, almost semicircular in transverse section, whereas in the smaller teeth it is lower and somewhat flattened on top. In the longitudinal section the ridge is slightly and evenly arched. Its sides are steep and also slope steeply towards both ends of the teeth. The ridges are flanked on both sides by flattened extensions which thin towards the edges, but do not continue around the anterior and posterior ends. Unfortunately, these lateral rims are mostly broken off so that it is somewhat difficult to reconstruct the original outline of most of the teeth. The lower side of the teeth is concave, though less curved than the upper side, so that the thickness of the tooth is greatest along the middle line. The lower surfaces of the teeth are crenulated transversely, with the wrinkles about 2.5 to 3.5 mm. apart.

The following measurements, in millimeters, have been taken from the specimens:—

Specimen	Total[3] length	Width of central ridge	Width of rim	Maximum Thickness	
21401a	37	26	?	16	
21401b	?	30	?	14.5	
					First pair
21401c	32.5	26.5	7	14	
21401d	31.5	28	5.5	14	
					Second pair
21401e	27.5	25	3.5	12	
21401f	28.5	24	4	12	
					Third pair
21401g	29.5	22.5	?	10	
21401h	30 ?	?	5	9	
					Fourth pair
21401i	22	14 ?	?	8	
					Part of fifth pair ?

[3] Measured along the oblique longitudinal axis.

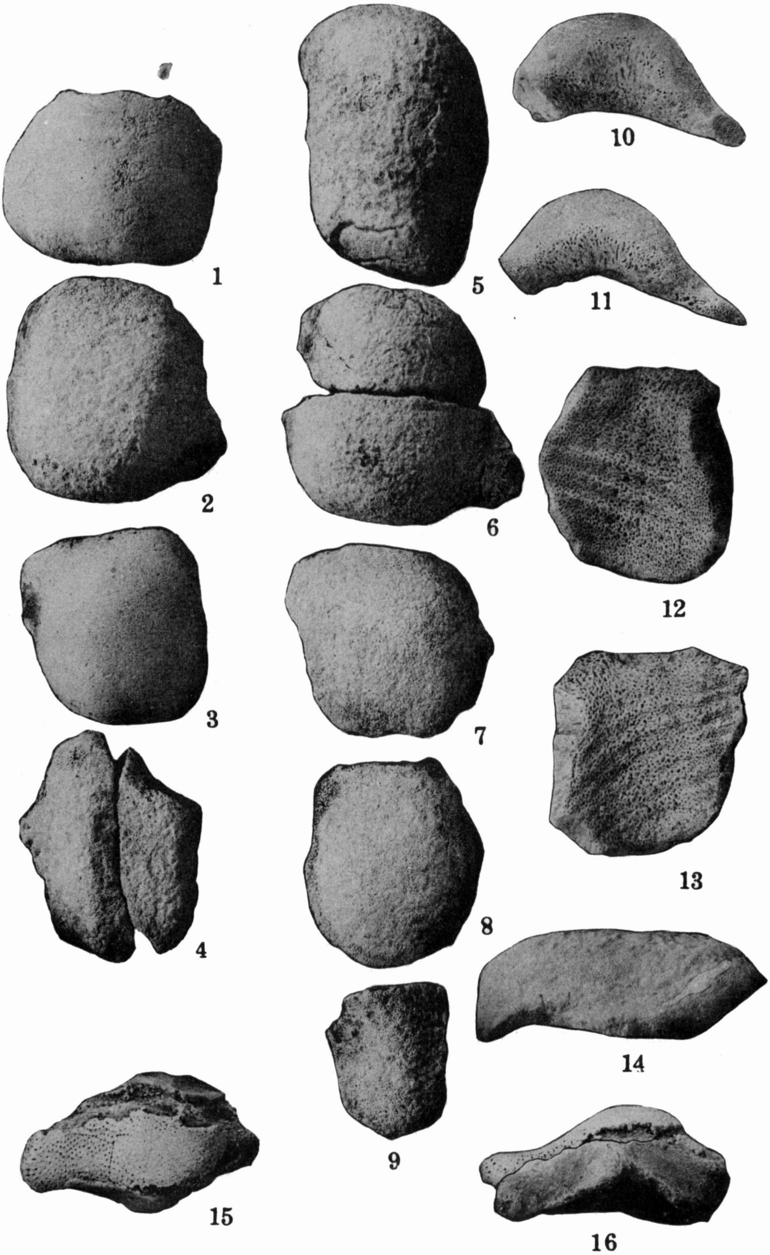
Structure of the teeth:—The roots of the teeth which could be expected to consist of vasodentine are not preserved and only the crowns are represented. These have the typical bradyodont structure with vertical, more or less parallel medullary canals, surrounded by dentine tubes which are embedded in a substance of somewhat doubtful derivation. The medullary canals are closely spaced, not more than about 0.5 mm. apart. They are fairly straight and apparently freely anastomosing so that even in a vertical section through the crown numerous cross-sections of medullary canals are seen. The canals are now filled with an opaque substance of unknown composition. They are surrounded by a layer of tubular dentine which is translucent in thin section and the dentine tubes are embedded in a yellowish-brown substance which makes up the main body of the crown.

From the medullary canals there issue at right angles great numbers of very fine dentinal canals which penetrate the tubular dentine and continue into the yellowish-brown substance beyond. These very fine canals do not anastomose, but are often ramified, although the individual branches are never very long. The canals penetrate into the yellowish-brown substance, but come to an end well before they reach the ends of the dentinal canals issuing from the neighbouring medullary canal so that between each two adjacent medullary canals and their surrounding dentinal tubes there is a narrow space which is not penetrated by dentinal canals. It is possible that the yellowish-brown substance in which the dentinal tubes are embedded can be regarded as enamel (see below).

Occurrence: 700 yards in the direction N 150° E from a very conspicuous, isolated "White Gum" tree in the northern half of Nalbia Paddock, Wandagee Station[4] (approximately 3320 yards in the direction N 63° E from the Trigonometrical Station on Wandagee Hill). Nos. 21401a to 21401i (Holotype 21401a), Department of Geology, University of Western Australia.

Comparisons:—*Crassidonta subcrenulata* differs from *Crassidonta stuckenbergi* Branson from the Phosphoria formation of Wyoming mainly in its transverse outline. In the American species the central ridge is higher and more strongly rounded, with almost vertical sides which are more sharply set off from the flattened flanks. In the Australian species the ridge is not quite as high proportionally, its sides are less steep, and the passage into the flattened flanks is more gradual. Another point of difference is the transverse wrinkling on the upper side of the crown of *C. stuckenbergi* which is particularly apparent

[4] It might seem unusual to fix the position of a fossil locality in relation to a tree, but this particular tree is the only one of its kind within many miles; it is an outstanding landmark in that extraordinarily flat country, and it is likely to stand there for some generations to come.



1-9 Coronal view of set of nine teeth of *Crassidonta subcrenulata* Teichert, n. sp. (Nos. 21401, b, d, f, h, a, c, e, g, i). Nat. size.
10, 11 End views of two of the teeth (Nos. 21401 d and c = figs. 2 and 6). Nat. size.
12, 13 Underside of two of the teeth (Nos. 21041 g and f = figs. 8 and 3). Nat. size.
14 Side view of holotype (No. 21401 a = fig. 5). Nat size.
15, 16 *Helodus* sp. Coronal and side views. No. 21400. 2 X.

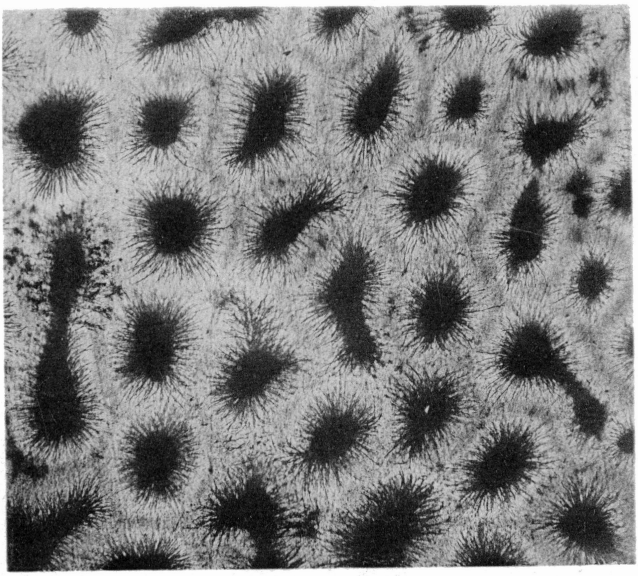


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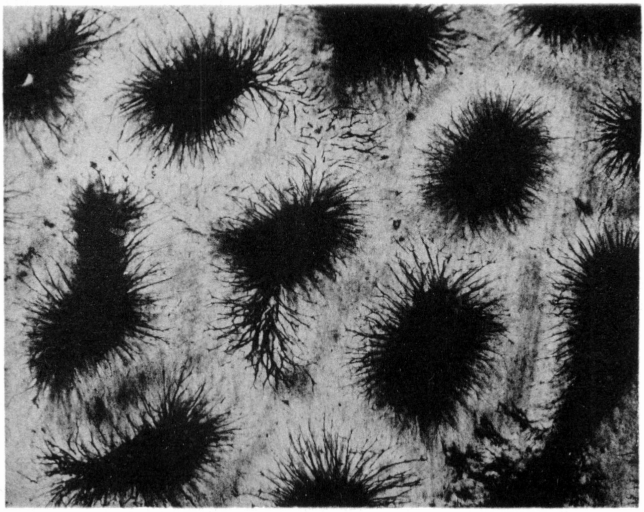
PLATE 2.

17 Portion of a transverse section of a tooth of *Crassidonta subcrenulata* Teichert, n. sp. No. 41175. 50 X.

18 Portion of longitudinal section of another tooth of the same species. No. 41176. 50 X.



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19 Same specimen as fig. 17 (No. 41175), but enlarged 85 X.

20 Same specimen as fig. 18 (No. 41176), another part of the slide enlarged 85 X. c = medullary canal, filled with opaque substance, d = translucent, tubular, dentine, surrounding the medullary canals.

on the flattened portions of the larger specimens. There is no clear evidence of the appearance of wrinkles on the upper side of the specimens of *C. subcrenulata.* Unfortunately, Branson does not describe the lower aspect of *Crassidonta stuckenbergi* so that the two species cannot be compared in this respect. The representatives of the two species seem to compare fairly well in size: The largest specimen of *C. stuckenbergi* is 34 mm. long, though the figures for width cannot be compared owing to the inferior state of preservation of the Australian specimens.

The Russian specimens from the Upper Carboniferous of the Samara Bend which Branson referred to *Crassidonta stuckenbergi* are more similar to the American species than to *C. subcrenulata.* They seem to differ mainly in that they apparently do not possess a crenulated surface; their upper surfaces seem to be entirely smooth like those of the Australian specimens.

In order to compare the micro-structure of *Crassidonta subcrenulata* with that of other bradyodonts, one has to refer to the classical monographs of Agassiz (1838) and Owen (1840), since no histological studies comparable to these have been published in the intervening century, with the exception of Nielsen's investigations (1932) on primitive Edestids which, however, are not strictly comparable with *Crassidonta.* Although Agassiz, in his first attempt at a classification of the "Cestraciontes," had placed equal importance on the outer shape and on the micro-structure of the teeth, later authors were as a rule satisfied to restrict their description to external features, when they established new genera or species. It might, therefore, be well to recall Agassiz's statement on the bearing of histological studies on the classification of that group.

"La structure microscopique des dents des Cestraciontes n'est pas moins caractéristique que leur forme extérieur; elle est si particulière qu'il suffit d'en connaître le type pour pouvoir dire du premier morceau détaché que l'on rencontre, non-seulement à quelle famille, mais même à quelle genre il appartient."

Agassiz compared in particular the micro-structure of *Cochliodus* and *Psammodus,* now regarded as representative of two important families of the bradyodonts. The micro-structure of *Crassidonta* is not very similar to that of *Chochliodus contortus*, the genotype of Cochliodus, as described by Agassiz (1838, p. 165 and Pl. L Fig. 3). Agassiz observed that the medullary canals of *Cochliodus* are larger than in any other genus, their diameter approximately equalling that of the substance that separates them. In this respect *Psammodus* seems to be much more similar to *Crassidonta* (Agassiz, 1838, Pl. L Fig. 4); it has much narrower medullary canals which have a diameter equalling one-fourth to one-sixth of the distance between them. However, the medullary canals seem to be straighter than in *Crassidonta subcrenulata* and although they frequently bifurcate, they do not seem to anastomose. Again, the arrangement of the dentinal canals in *Psammodus* is rather similar to that in *Crassidonta*; Agassiz calls special attention to the fact that they are less ramified than in Cochliodus.

Another genus that must be compared is *Psephodus*. Owen's illustration of "*Psammodus*" *magnus*, the genotype of that genus, (Owen, 1840, Pl. 20) suggests great similarity with *Psammodus contortus*, except for the fact that in *Psephodus* the medullary canals are probably still farther apart and branching less frequently than in *Psammodus*. Although apparently the micro-structures of *Psammodus*, *Psephodus*, and *Crassidonta* are quite closely related, the similarity seems to be greatest between *Crassidonta* and *Psammodus*. It should be noted that, if there is any real relationship between these two genera, the arrangement of the teeth in *Crassidonta* might have been quite different from the one suggested above, since Woodward (1921) has shown that the teeth of *Psammodus* were arranged in unsymmetrical paired series.

Branson did not describe the micro-structure of *Crassidonta stuckenbergi*, but merely stated that "the crown surface is closely and evenly punctate with subcircular punctations". The punctations are undoubtedly the openings of the medullary canals and there is at present no reason to assume that the structure of *C. stuckenbergi* differs essentially from that of *C. subcrenulata*. This structure is identical with that of typical Bradyodonti. Nielsen, in 1932, has figured a vertical section through a crown of the Carboniferous *Orodus ramosus* which differs from *Crassidonta subcrenulata* only in the greater distance between the dentinal tubes and in the fact that the fine dentinal canals are directed obliquely forward instead of at right angles to the medullary canals from which they issue. It appears, therefore that it is necessary to compare the structure of the teeth of genera from different families in much greater detail than can be attempted at the present moment.

Nielsen interpreted the substance between the dentinal tubes as enamel, stating that "the distribution of the medullary canals in this enamel may be due to the pulp cavity having .... been irregularly folded, so that each of the folds corresponds to one of the numerous medullary canals of the crown." Although the material of *Crassidonta subcrenulata* is not sufficient to allow me to form an independent opinion on this question, it can be stated that Nielsen's interpretation of the structure of bradyodont teeth can be applied to it.

REFERENCES.[5]

Agassiz, L.: 1838, *Recherches sur les poissons fossiles,* Vol. 3, Pt. 2, pp. 73-359. Neuchatel.

Boutrov, V.: 1937, The Oil Fields of the Samarskaya Luka (Samara Bend). *Int. Geol. Congr., XVII Sess., The Petrol. Excurs.,* Pt. 1, pp. 33-63.

Branson, C. C.: 1930, Palaeontology and stratigraphy of the Phosphoria formation. *Univ. Missouri Studies,* Vol. 5, No. 2, 66 pp., 16 pls.

Branson, E. B.: 1916, The Lower Embar of Wyoming and its fauna. *Jour. Geology,* Vol. 24, pp. 639-664, pls. 1-6.

Davis, J. W.: 1883, On the fossil fishes of the Carboniferous Series of Great Britain. *Sci. Trans. Roy. Soc. Dublin,* Vol. 1 (Ser. II), pp. 327-548, pls. 42-65.

Dunbar, C. O.: 1940, The Type Permian: Its classification and correlation. *Bull. Amer. Assoc. Petrol. Geol.,* Vol. 24, pp. 237-281.

Forsch, N. N.: 1937, Samarskaya Luka. *Intern. Geol. Congr., XVII Session, The Permian Excursion, Southern Part,* pp. 37-53.

Hardmann, E. T.: 1884, *Report on the geology of the Kimberley District, Western Australia,* 22 pp. Perth: By Authority.

Hay, O. P.: 1929, Second bibliography and catalogue of the fossil Vertebrata of North America; *Carnegie Inst. Washington,* Publ. No. 390, Vol. 1, viii + 915 pp.

De Koninck, L. G.: 1898, Descriptions of the Palaeozoic Fossils of New South Wales (Australia), *Geol. Survey New South Wales. Mem., Palaeont.,* No. 6, 298 pp., 24 pls.

Miller, A. K., and Cline, L. M.: 1934, The cephalopods of the Phosphoria formation of northwestern United States, *Jour. Palaeontology,* Vol. 8, pp. 281-302, pl. 39.

Moy-Thomas, J. A.: 1939, The early evolution and relationships of the Elasmobranchs, *Biol. Reviews,* Vol. 14, pp. 1-26.

Nielsen, E.: 1932, Permo-Carboniferous Fishes from East Greenland, *Meddelelser om Gronland,* Vol. 86, No. 3, 63 pp., 16 pls.

[5] Unfortunately, Moy-Thomas' book on "Palaeozoic Fishes" (1941) had not yet arrived in Western Australia, when this manuscript was completed in January, 1943, and therefore could not be consulted.

Owen, R.: 1840, *Odontography; or, a treatise on the comparative anatomy of the teeth, &c.*, pp. 1, pls. 1-93. (The rest of the volume appeared later.)

Portlock, J. E.: 1843, *Report on the geology of the County of Londonderry, and of parts of Tyrone and Fermanagh,* 784 pp., 38 pls., Dublin and London.

Stuckenberg, A.: 1905, Die Fauna der oberkarbonischen Suite des Wolgadurchbruches bei Samara. *Mém. Com. géol. St. Pétersbourg,* N. S., Livr. 23, 144 pp., 13 pls.

Teichert, C.: 1940, Helicoprion in the Permian of Western Australia. *Jour. Paleontology,* Vol. 14, pp. 140-149, pls. 22-23.

Wade, A.: 1937, *Geological map of part of the Kimberley Division, Western Australia.* Prepared on behalf of the Freney Oil Co., Department of the Interior, Canberra.

Woodward, A. S.: 1921, Observations on some extinct Elasmobranch fishes. *Proc. Linn. Soc. London,* 133rd sess., pp. 29-39.

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