OLDHAMINID BRACHIOPODS IN THE PERMIAN OF NORTHERN AUSTRALIA*

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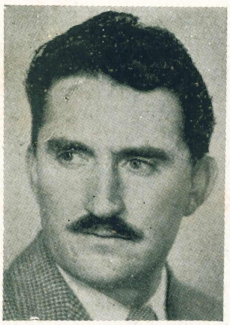
ABSTRACT—Oldhaminid brachiopods, not previously known in Australia, have been found in the Permian rocks of Port Keats, Northern Territory. One species is present and this is most closely related to *Leptodus nobilis* (Waagen), a species characteristic of the Upper Permian of the Tethys.

The Permian faunas and floras of the Port Keats Group are reviewed. The Port Keats Group is correlated with the Liveringa Formation of the Fitzroy Basin, Western Australia. Sediments of probable Triassic age overlie the Permian rocks.

INTRODUCTION

EVER since the masterly recognition in the Permian Salt Range faunas by W. Waagen in 1883, of the strange brachiopods *Lyttonia* and *Oldhamina*, these forms have aroused much interest and discussion.



These two genera and a number of later described ones are now known as the Oldhaminoidaea (Williams). The literature is now considerable but despite the attention given to them, their morphology and taxonomy are not yet completely elucidated. The most recent reviews by Williams (1953) and Stehli (1956) bring out contrasting views on the morphology of the dorsal valve and on the fundamental basis of their classification. The earliest known oldhaminoids are of late Carboniferous age and they flourished in the Permian, with a last and most interesting survivor, *Pterophloios*, in the Triassic of Austria. The group is a very good example of evolutionary development. At least thirteen genera are now distinguished. Although at first thought to be peculiar to Asia, the oldhaminoids are now known over a wide area which to a large extent represents the spread of the Tethyan sea in late Carboniferous and Permian times. Countries in which oldhaminoids are known include Sicily, South Tunis, Greece, Yugoslavia, Hungary, Armenia, North Caucasus, Urals, Salt Range (Pakistan) and Himalaya (India), Indo-China, China, Mongolia, Ussuriland in Eastern Russia, British Columbia, Kansas and Texas, Sumatra, Timor, and now Northern Australia.

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OLDHAMINOIDEA (WILLIAMS 1953)

It is not necessary to discuss here the full details of morphology and classification of the group. This can be obtained from the literature, especially the recent reviews of Williams (1953) and Stehli (1956). The species are all thought to be pseudopunctate, i.e., with taleolae (Williams, 1956) in the inner shell layer of the ventral valve, and throughout in the dorsal. Williams (1953) included in his sub-order the families Oldhaminidae Schuchert and Levene 1925, with genera of bilaterally symmetrical form, and the Poikilosakidae Williams with the asymmetric genera. In the same paper he argued that the peculiar lobate dorsal valve of the group is in reality an internal supporting plate for the lophophore, the brachial valve proper being a much reduced remnant at the posterior end. The articulatory apparatus was degenerate and the dorsal valve did not move.

Stehli (1956) from a study of West Texan silicified material regards the proposed classification as premature and suggests that asymmetry or symmetry of the muscles is an equally important basis of classification. This is a morphological feature which does not necessarily correspond to symmetry in the shell shape. He also argues that the lobate dorsal valve is a true functional valve, articulating like other brachiopods, and cites *Richthofenia* as another genus, pseudopunctate on inner and outer surfaces of the dorsal valve.

All the oldhaminoids are believed to be attached to foreign bodies at some stage of their ontogeny. The better known species commonly vary considerably in shape and dimensions and thus specific recognition of poorly known faunas is often difficult.

The Australian form was found at Port Keats, Northern Territory in October 1956. It is of interest in emphasising the known relationships of the west and north-west Australian faunas with those of India and the Tethyan Permian. The Port Keats specimens show closest relationships to *Leptodus nobilis* (Waagen) and the ensuing discussion is concentrated on *Leptodus* in general and *L. nobilis* in particular.

GENUS LEPTODUS (KAYSER)

The name *Leptodus* was proposed by Kayser (1883) with *L. richthofeni* from the Loping beds of China as type species. Kayser erroneously thought his fossils were fish remains. Waagen in the same year described the Salt Range genera *Oldhamina* and *Lyttonia* and clearly indicated the true affinity of these fossils. He thought his *Lyttonia* to be congeneric with *Leptodus* but incorrectly suppressed that name because of its mistaken derivation. Subsequent authors have often followed Waagen by using *Lyttonia* but others, e.g., Girty, Branson, Williams, have rightly recognised the priority of *Leptodus*.

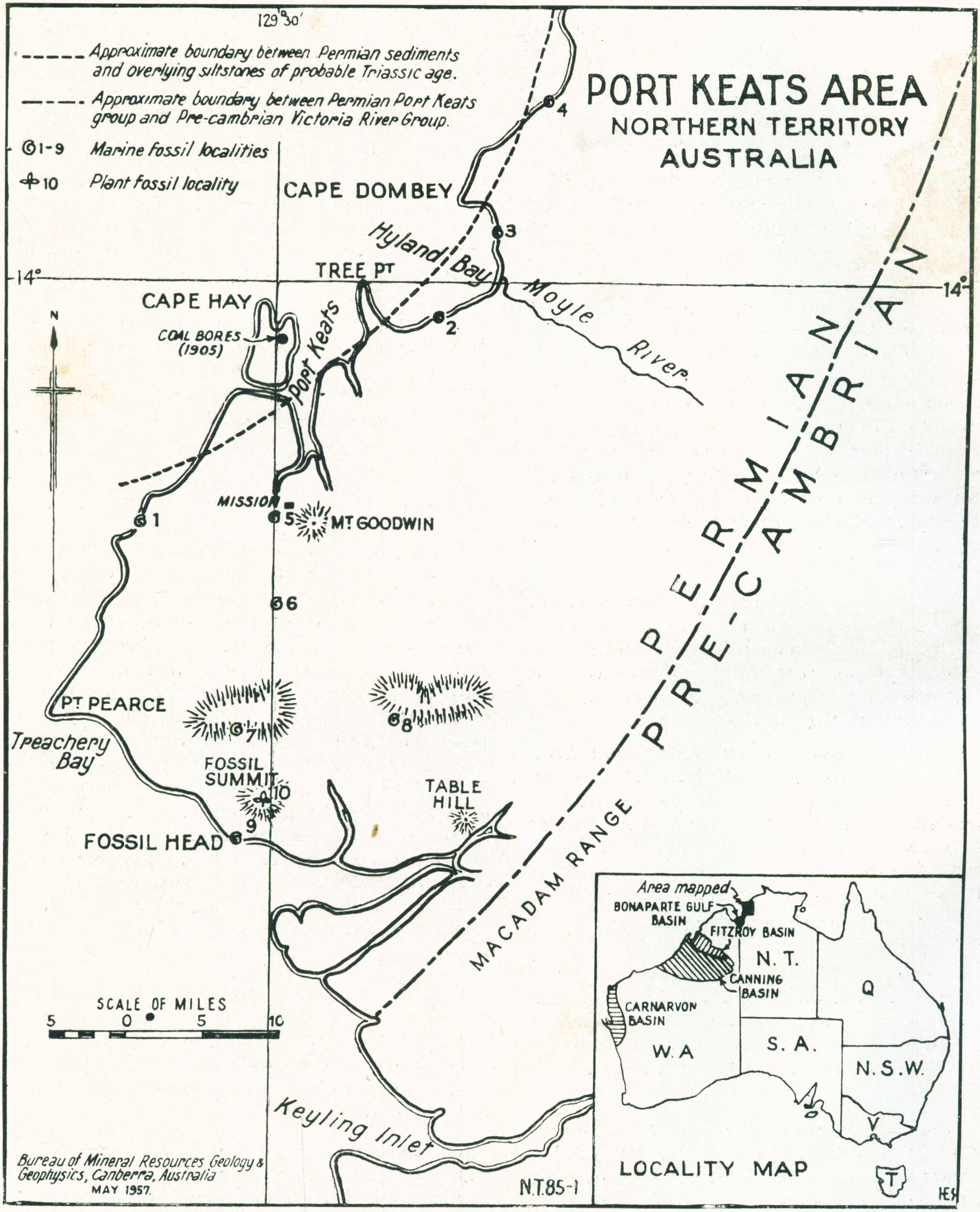
However, it is by no means certain that *Leptodus richthofeni* Kayser and *L. nobilis* Waagen are congeneric. The Chinese species is very inadequately known and as pointed out by Stehli (1954), its mode of growth has not been demonstrated and thereforeit may differ significantly from the much better known *L. nobilis*. For the purpose of this paper *Lyttonia nobilis* Waagen is included, with reservations, in the genus *Leptodus*.

LEPTODUS NOBILIS (WAAGEN)

The following description of this species is derived largely from the descriptions of the Salt Range forms by Waagen (1883) and Noetling (1905). The new Australian specimens are described separately below. It is the largest known species of oldhaminid, attaining dimensions of at least 150 mm. long and 100 mm. wide. The length always exceeds the width. The ventral valve is commonly more or less flat or gently convex and the main body of the shell is elongate-oval with irregular lateral and posterior extensions. The ventral exterior surface is not conspicuously folded or wrinkled and is fairly smooth, sometimes showing growth lines.

Internally the ventral valve possesses a median septum or ridge which extends nearly the length of the shell and in some specimens is less pronounced in the posterior part. On either side are rows of parallel septa or carinea (Licharev, 1932), which are inclined to the median septum. The angle of inclination varies in different parts of the shell and is commonly near a right angle about the mid-length. The carinae are convex towards the front and may curve back at their distal ends, especially in the hinder part of the shell, as in Plate 20, fig. 1. The angle of inclination is a variable feature. The carinae number up to about 40 on each side in large specimens and are spaced at intervals of about 14–16 in 5 cm. of shell length. In some Chinese examples, the carinae may be closer. Huang (1932) suggested that the difference might indicate sexual dimorphism.

In cross section the carinae are usually somewhat blunt with a broad base, and are either vertical to the floor or slope up to the front. They may display a notch or even appear to be divided on weathering (text figures 2c, d). Some of the carinae have a row of bead-like pustules, commonly on the



TEXT-FIG. 1—Geological sketch map of Port Keats area, Northern Territory, showing main fossil localities.

anterior side. The carinae are usually deeper nearer the midline of the shell; they do not touch the mid-septum. The floor of the valve between the carinae may be striated or slightly ridged. At their distal ends the carinae are sometimes connected to their neighbours by low looped ridges.

The hinge line is short. Small symmetrical muscle scars are present in front of the hinge line and extend on to the posterior two or three carinae (Waagen 1883, Plate 30, Figure 6).

Beyond the main body of the thick ventral valve are irregular extensions of the shell both at the sides and backwards. In *L. nobilis* the thin lateral extensions do not appear to arch upwards to any great extent and in Waagen's view they spread out on the substratal rock. The thicker backward extension or posterior flap also spreads out but may be somewhat coarsely and irregularly gnarled in appearance. It does not however seem to grow forward and arch over the dorsal valve.

The main body of the shell broadens out close to the hinge line and retains this width for much of the length and is rounded in front. The entire ventral inside surface is pustulose; the pustules are the surface expression of the taleolae.

The thin dorsal valve is pustulose on both surfaces. It has a small bilobed cardinal process and is pinnate or lobate with a median slit at the front and deep lateral incisions. The lateral incisions correspond exactly to the ventral carinae upon which the dorsal valve rests. A median internal ridge with a corresponding external groove is present.

Noetling (1905) thought that the dorsal valve was well-nigh fused to the ventral valve at the posterior end. The presence of muscles and a definite cardinal process indicate however that the valves were articulated.

Waggen considered that the entire ventral valve grew attached to the more or less flat substratum and the general form strongly supports this view. Noetling, however, thought that by analogy with *Oldhamina*, the shell was attached to a foreign body only in early life and was later free with the ventral valve lying upwards. Noetling refers to the absence of attachment scars. These would not be visible if much of the surface was attached and it is noteworthy that both Waagen's and Noetling's figures of ventral valves showing the external surface are exfoliated.

The high proportion, in the published figures of this species, of forms showing the interior posterior part of the ventral valve strongly suggests that at least the posterior ventral part of the shell was closely adpressed to the substratum. Other species such as *Leptodus richthofeni lopingensis* Licharev (1932) show the imprint of foreign bodies such as the shells of pelecypods upon which the brachiopod grew. Some of the smaller and more primitive genera, such as *Poikilosakos*, were attached by their entire ventral surface to crinoid stems or other shells.

LEPTODUS CF. NOBILIS (WAAGEN)

The Australian specimens were collected in 1956 at Tchindi Beach, from a bed about 3 feet thick, about 9 miles south of west of the Port Keats Mission, Northern Territory (Locality 1 in Text-figure 1). Twelve incomplete specimens are available, all ferruginized replacements with no shelly material preserved. In April, 1957, several dozen specimens were collected from locality 2, Hyland Bay. These specimens, from beds about 20 feet thick, though more complete, are mainly impressions in friable rock with the shelly material leached away. The illustrated specimens are all from Tchindi Beach. The enclosing rock is a fine sandstone, probably originally calcareous, and all the fossils are more or less embedded in the tough matrix.

The size and general form suggest that this species probably belongs to *L. nobilis*, but the incompleteness of the specimens and lack of certainty of the mode of growth of this species, induce some caution before complete identification is made.

All specimens are in the Commonwealth Palaeontological Collection, Canberra. Six of them are illustrated. One large ventral valve, not illustrated (CPC 1525), is incomplete but approaches the dimensions of *L. nobilis*. It is about 10 cm. wide and the incomplete length is 6 cm., with 15 carinae in that distance. The other specimens are smaller. CPC 1526, (Plate 20, figure 1) is the internal surface of the posterior part of a ventral valve. The floor is irregularly flat with gentle depressions. The median septum is low. The carinae number 8 in 2.7 cm. and are strongly convex to the front in plan. In cross section they vary as in text-figures 2a, b. This specimen shows a close resemblance to the Salt Range specimens of *L. nobilis* figured by Noetling 1905 (Plate 18, figs. 6 and 9) and to Wanner and Sievert's figure (1935, Plate 9, Fig. 28) of the Timor example. It also closely resembles in size and shape Diener's specimen from Chitichun (1897, Plate 1, fig. 5). CPC 1527 (Plate 20, figure 2) is a ventral exterior, much eroded. It is a front portion, nearly flat, with a round margin.

CPC 1528 (Plate 20, figure 3) is an incomplete ventral valve internal surface showing the cardinal region. The short hinge line is visible and in front of it the small median, oval nearly symmetrical muscle scars seem to extend across the proximal ends of the hindmost 2 or 3 pairs of carinae. The flat posterior flap can be seen in the upper right part of the figure. This specimen shows a very close resemblance to Waagen's (1883) plate 30, figure 6. Williams (1953) figured a *Leptodus* from the Word of Texas which shows a general similarity. The small dental areas illustrated by Williams at the ends of the hinge line are not evident in our form. Perhaps the first pair of very short carinae functioned as teeth, as suggested by Waagen.

Plate 20, figure 4, illustrates CPC 1529, the interior of a ventral valve partly obscured by another shell. This is probably from near the anterior end of the shell. The variable inclination of the carinae is evident. On the posterior side of some of the carinae a row or fringe of bead-like pustules can be seen. This is comparable with Plate 18, figure 4 of Noetling (1905); however, in his specimens the fringe is on the anterior side. In Chinese specimens of *L. nobilis* the fringe is on the posterior side (Huang 1932). In other species, e.g., *Leptodus americanus* Girty, the fringe may be present on either or both sides of the carinae, e.g., Licharev (1932) and King (1930).

Plate 20, figure 5 illustrates CPC 1530 which is largely embedded in tough pale-grey rock. It may be a dorsal valve but is probably an eroded ventral valve. A low median ridge is visible. Low ridges on each side are either dissected broad carinae or the lateral inter-pinnal incisions of a dorsal valve. If the specimen is a ventral valve, it must have been decorticated before incorporation in the rock. It appears to be in the same condition as Waagen's figure (Waagen, 1883, plate 30, figure 7). He considered this a ventral valve and referred it to his species *L. tenuis,* which Noetling regarded as a synonym of *L. nobilis.*

CPC 1531 is illustrated in Plate 20, figure 6. It is part of the interior of a ventral valve and shows a distinct ridge along some of the carinae. The fragment is flat.

The Port Keats specimens show a lesser resemblance to other described species of *Leptodus*. *L. richthofeni* Kayser is apparently a small form with a convex ventral valve. It is not sufficiently well known. *L. richthofeni lopingensis* Licharev from the Caucasus is also smaller and is concentrically wrinkled

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EXPLANATION OF PLATE 20

LEPTODUS cf. NOBILIS (Waagen)

FIG. 1—Interior of ventral valve, posterior part, showing carinae and median septum. CPC 1526.
2—Exterior of ventral valve, anterior part, much weathered. CPC 1527.
3—Interior of ventral valve, posterior part, showing portion of flat posterior and lateral flaps, and hinge line. CPC 1528.
4—Interior of ventral valve, middle to anterior part. CPC 1529.
5—Interior of ventral valve, (much weathered) or possibly interior of dorsal valve showing inter-pinnal incisions. CPC 1530.
6—Interior of ventral valve, middle to anterior portion. CPC 1531.
All specimens, excepting 5, are coated with ammonium chloride. All figures are at natural size and with posterior at the top.

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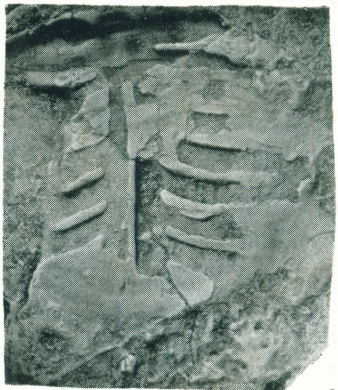

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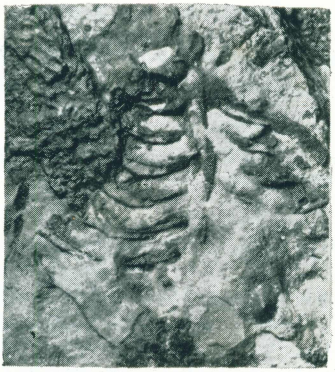

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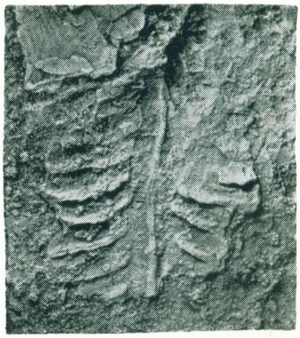

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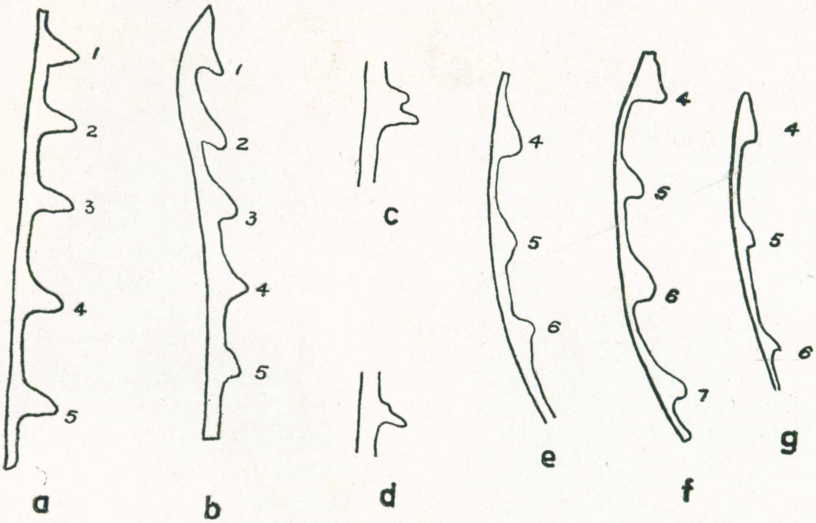
THOMAS : OLDHAMINID BRACHIOPODS, N. AUSTRALIA in the ventral valve and has posterior flaps which arch over on to the dorsal valve. *L. americanus* Girty is smaller and also has a forward growth of the posterior flap. *L. catenata* Wanner and Sieverts is a smaller flat form attached to a crinoid stem by growth of the posterior flap. Other known species show less resemblance.

(b) Amarassi beds of Timor—*Timorites* zone.
(c) Upper Permian Lopingian beds of China (Huang 1932).
(d) Chitichun beds of the Himalayas (*Cyclolobus* zone ammonites).
(e) Upper Permian Zewan beds of the Himalayas.



TEXT-FIG. 2—Profile views of carinae in longitudinal section. The thickness of shell is shown diagrammatically. The posterior is at the top of each profile.
a. *Leptodus* cf. *nobilis* (Waagen)—CPC 1925, on left side of median septum. x3.
b. Same specimen, on right side of median septum. x3.
c. *Leptodus* cf. *nobilis* (Waagen). Incomplete specimen showing carina with deep notch, possibly the result of weathering. x3.
d. Similar to c but not as deeply notched.
e. f. *Leptodus nobilis* (Waagen), from Amarassi beds, Timor. f. is nearer the median septum than e. x3.2. (After Wanner and Sieverts 1935, Fig. 17).
g. *Leptodus nobilis* (Waagen), from Virgal, Salt Range, Pakistan. x2.75. (After Wanner and Sieverts 1935, Fig. 18).

GEOGRAPHICAL DISTRIBUTION AND AGE

The advanced oldhaminid species which can be referred to *Leptodus* or *Lyttonia* are known only from Permian rocks. *L. nobilis* Waagen appears to be exclusively Upper Permian. The most adequately described occurrences are the following:

(a) Middle and Upper Products Limestones of the Salt Range of Pakistan (late Kazanian to Tartarian in age—see Ruzencev 1956; they contain *Timorites* and *Cyclolobus* zone ammonites).

(f) Upper Permian Jisu Honguer beds of Mongolia.

(g) Probable Upper Permian of Indo-China (Cambodia).

(h) Probable Upper Permian of Japan.

(i) Probable Upper Permian of the North Caucasus. The most recent Russian views on the age of these beds are unavailable to the writer.

Unfigured examples of *L. nobilis* are reported from the Upper Permian of Djebel Tebaga, Tunisia.

Leptodid species are reported also in rocks ranging from Lower Permian (Artinskian) to Upper Permian age in Greece, Yugoslavia, Sosio beds of Sicily, North Caucasus, Darvas, Djoulfa, in Armenia, Ussuriland in eastern Russia, China (Lopingian and older Permian beds), Sumatra, Timor, Texas (Leonardian and possibly Wolfcampian to Guadalupian) and from the Upper Permian of British Columbia.

GEOLOGY OF THE PORT KEATS AREA

Comparatively little geological work has been done in this area until recent years. It was first visited by Commander Lort Stokes in the survey ship H.M.S. Beagle in 1839. Stokes named Fossil Head and Fossil Summit. H.Y.L. Brown (1895 and 1906) made a geological reconnaissance along the coast and initiated drilling for coal. A number of holes were drilled on Cape Hay and further north at Cape Ford and Anson Bay. Etheridge (1907) described fossils from the Cape Hay bores and from Fossil Head (Locality 9, fig. 1) and one specimen (*Aulosteges*) from locality 4, (figure 1). Probably the next geologist to visit the area after Brown was H. J. Evans (in Reeves, 1948). Evans found a new fossil horizon at the Mission, which was also visited by H. O. Fletcher of the Australian Museum in 1952. In 1956 and early 1957 the writer collected fossils from numerous localities, mostly new, in collaboration with S. Derrington and J. Burbury, geologists of Associated Australian Oil Fields N.L.

The previously known geology was reviewed by Noakes, Öpik and Crespin (1952) and by Traves (1955). The bryozoa of the Cape Hay bore were redescribed by Joan Crockford (1943).

The outcropping Permian beds were named the Port Keats Group by Noakes 1949. They overlie unconformably the Proterozoic Victoria River Group in the east. To the south, they presumably overlie the Carboniferous Weaber Group, of the Bonaparte Gulf Basin, but the wide Victoria River and Fitzmaurice River estuaries effectively cover any outcrops; other formations not known in outcrop may be present. Outcrops consist mainly of medium to coarse grained sandstone and siltstone, commonly ferruginized and probably in part, calcareous originally. Outcrops total less than 1,000 feet, though a bore at Cape Ford, further north penetrated 1,500 feet of sediments. However, there is no fossil evidence available from this bore.

The beds have a gentle, prevailing west to north-westerly dip, very low on the eastern margin and reaching 4–5° on the west. They are gently folded in one or two places, notably near the Moyle River. The latest work shows the presence of four fossil assemblages which are arranged here in ascending order:

Assemblage A comprises marine fossils at localities 9, 7, 8 of Figure 1. Localities 7 and 8 represent numerous collecting spots in the general vicinity of the positions shown.

Assemblage B includes terrestrial plant fossils from localities 10 and above the marine beds at 8.

Assemblage C comprises marine fossils from localities 5 and 6.

Assemblage D grades into C and occurs at localities, 1, 2, 3 and 4.

Assemblage A includes the fossils described by Etheridge (1907) from Fossil Head, with some additional new forms. This fauna is dominantly molluscan and includes *Aviculopecten hardmani* Eth., *Nuculana basedowi* Eth., *Oriocrassatella stokesi* Eth., *Bellerophon pennatus* (Eth.), and in addition new species of *Stutchburia*, *Astartila*, *Schizodus*, *Pseudomyalina*, *Leiopteria?*, and other pectinids and bellerophontids. (The mollusca have been identified by J. M. Dickins of the Bureau of Mineral Resources, Canberra). Brachiopods include *Streptorhynchus perfidiabadensis* (Eth.), *Strophalosia* sp. and *Chonetes* sp.

This fauna is closely allied to that of the lower beds of the Liveringa Formation (the Lightjack Member) of the Fitzroy Basin. It is considered by Thomas and Dickins (1954) to be of late Artinskian to early Kungurian age.

Assemblage B comprises land plants which are provisionally referred to, *Glossopteris*, *Lepidodendron*, and *Gangamopteris?*

Assemblage C is again of marine fossils and is notably different from Assemblage A. Brachiopods are more numerous than molluscs. The molluscs (determined by J. M.

Dickins) include new species of pectinids, cf. *Sanguinolites* sp., *Astartila?* sp., and new pleurotomariid and bellerophontid gastropods. The brachiopods include *Neospirifer* sp. nov., a new large spiriferid genus *Martiniopsis* sp. nov., *Aulosteges* spp. (described by Coleman, 1957) and *Streptorhynchus* cf. *luluigui* Hosking. A large species of *Conularia* is also present. This fauna has very much in common with that of the Hardman Member of the Liveringa Group which was correlated with the Upper and Middle Productus Limestones by Thomas and Dickins (1954), and is consequently probably of late Upper Permian age.

Assemblage D is quite transitional with C. It contains some of the same species, but is less rich in mollusca and contains some additional elements. These include *Leptodus* cf. *nobilis* Waagen, *Derbyia* sp., *Dictyoclostus* sp., *Cleiothyridina* sp., *Dielasma* sp., *Hustedia* sp., *Camarophoria* sp., *Waagenoconcha imperfecta* Hosking and a problematic richthofenid, plus numerous fenestellid and other bryozoa. These faunas are now being studied and they strongly confirm a correlation with the Middle and Upper Productus Limestones, more particularly the latter. Direct comparison of specimens, especially types, would be of great value in these studies.

TRIASSIC SEDIMENTS

Overlying the fossiliferous Permian rocks at Hyland Bay, apparently conformably, is a sequence of thin-bedded grey and yellow to reddish mottled cross-bedded siltstone. It crops out at Cape Dombey, Tree Point and Cape Hay. No fossils were collected from the outcrops. However, in the Cape Hay No. 3 Bore, the top 550 feet is mainly siltstone and contains estheriids between 102 and 342 feet (Etheridge 1907). Brunnschweiler (1954) correlated this part of the bore with the Triassic Blina Shale of the Fitzroy Basin. The Blina Shale contains *Isaura* cf. *minuta* (Goldfuss) and other estheriids. The siltstones of Cape Hay, Tree Point and Cape Dombey are probably therefore of Triassic age.

In the Cape Hay Bore from 555 to 715 feet, fossils occur which (as figured by Etheridge) can be matched with fossils from Assemblages C and D of the outcropping Permian beds. From 724 to 730 feet he recorded land plants including *Glossopteris* which perhaps correspond to Assemblage B. No fossils are available from lower levels.

CONCLUSION

The fauna of the Permian rocks of the Port Keats area, especially *Leptodus* cf. *nobilis* (Waagen), confirms the presence of Upper Permian deposits in Western and Northern Australia.

It also emphasises the relationship between these Australian faunas and the Indian and other Tethyan Permian faunas. These affinities are becoming more evident as the result of recent palaeontological studies by Crockford (1957), (on bryozoa), Coleman (1957), (on productacean brachiopods), Dickins (1956, 1957), (on molluscs), Thomas (1957), (on orthotetacean brachiopods), and Dickins and Thomas (1957), (on the general affinities of early Permian faunas of the Carnarvon Basin).

ACKNOWLEDGMENTS

The help of Bureau colleagues and of Professor E. S. Hills of Melbourne University, is gratefully acknowledged. The author wishes to thank Mr. D. M. Traves, chief geologist, and Messrs. S. Derrington and J. Burbury, geologists of Mines Administration Pty. Ltd., for the opportunity to visit the Port Keats area and for collaboration in the field. He is very grateful for hospitality to Rev. Father Dockerty and his fellow missionaries of the Sacred Heart Mission, Port Keats. He also thanks the efficient aboriginal Australian fossil collectors at the mission.

The photographs were taken by Mr. G. T. Reid, photographer of the Bureau of Mineral Resources, Canberra.

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