

AN EVOLUTIONARY SEQUENCE IN *ARATRISPORITES* MIOSPORES FROM THE TRIASSIC OF QUEENSLAND, AUSTRALIA

by N. J. DE JERSEY

ABSTRACT. Specimens of *Aratrisporites*, a miospore genus of probable lycopsid affinity, are common in some palynofloral assemblages of Early Triassic age, from the Rewan Formation of the Bowen Basin, Queensland. Study of numerous specimens from a sequence about 1710 m. thick supports the view that *A. tenuispinosus* developed, by increase in spine dimensions, from *A. wollariensis*. The observed development of this evolutionary sequence favours quantum speciation, rather than a gradualistic process, as the change from one species to the other takes place over a relatively short stratigraphic interval. It is unusual, in the palynological record, for specimens, showing an evolutionary transition between species, to be observed; reasons for their occurrence in this case are suggested.

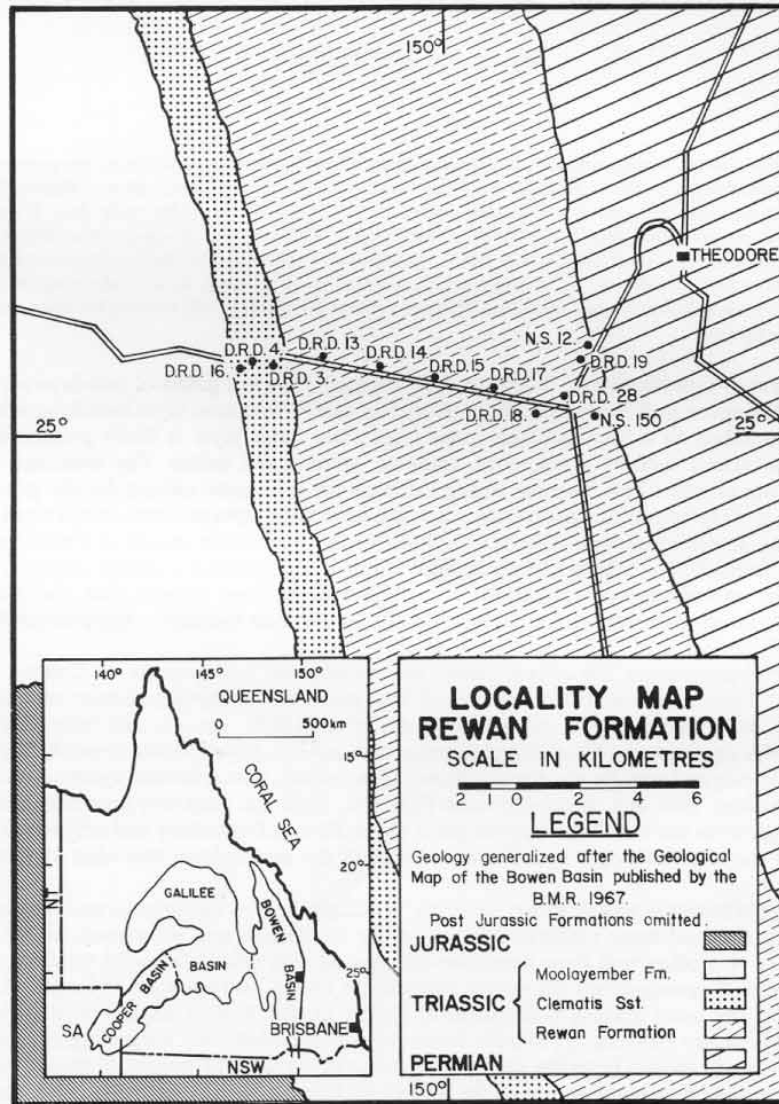
ARATRISPORITES Leschik emend. Playford & Dettmann, 1965 is a genus of two-layered, monolete miospores. The spore wall is cavate and consists of an outer structured layer loosely enveloping but proximally attached to a homogeneous inner layer. The outer layer is finely patterned and has sculptural elevations such as grana, coni, spinulae, spinae, and saetae. The monolete laesura is enclosed within elevated lips. There is strong evidence for a lycopsid affinity for the genus; Balme stated (1970, p. 351) 'spores of the *Aratrisporites* type have been reported from four Triassic lycopsid fructifications: *Lycostrobus scotti* (Nathorst), and recently from three species of *Cylostrobus* Helby and Martin, from the Narrabeen Group in New South Wales, Australia (Helby and Martin 1965). Such unusual morphological characters are combined in these spores that the presence of *Aratrisporites* in an assemblage may be confidently assumed to indicate a lycopsid element in its parent flora.'

Species of *Aratrisporites* are characteristic and widespread components of Triassic miospore assemblages. There are numerous records of the genus in European, Asian, and Australian palynofloras; both Balme (1970, p. 445) and de Jersey (1979, pp. 35, 36) have discussed the biostratigraphic significance of its first appearance. In Australia *Aratrisporites* is widely distributed in Early Triassic palynofloras. In the Bowen Basin, Queensland, two apiculate species, *Aratrisporites wollariensis* Helby, 1967 and *A. tenuispinosus* Playford, 1965, are relatively persistent components of assemblages from the middle and upper parts of the Rewan Formation and comprise from 20 to over 80% of the total miospore population in some of the assemblages recorded (de Jersey 1970, fig. 3).

As interpreted here (see also de Jersey 1970, pp. 11, 12, pls. 3, 4) *A. wollariensis* and *A. tenuispinosus* are similar in size and basic construction, but differ in the size and robustness of the apiculate projections. In *A. wollariensis* these comprise coni, grana, and spinae from 0.5 to about 2.0 μm in length, while in *A. tenuispinosus* the spinae range from about 2.0 to 6.0 μm in length. As the first appearance of the latter species is significantly higher in this Rewan succession than that of *A. wollariensis* (de Jersey 1970, fig. 3), there is biostratigraphic evidence for suggesting an evolutionary development of one species from the other, by increase in the size of the spinose projections. In this paper, the results of a re-examination of the Rewan material, undertaken, first, to reassess evidence for separating the two species and, secondly, to explore the possibility of an evolutionary relationship between them, are recorded.

STRATIGRAPHIC SETTING

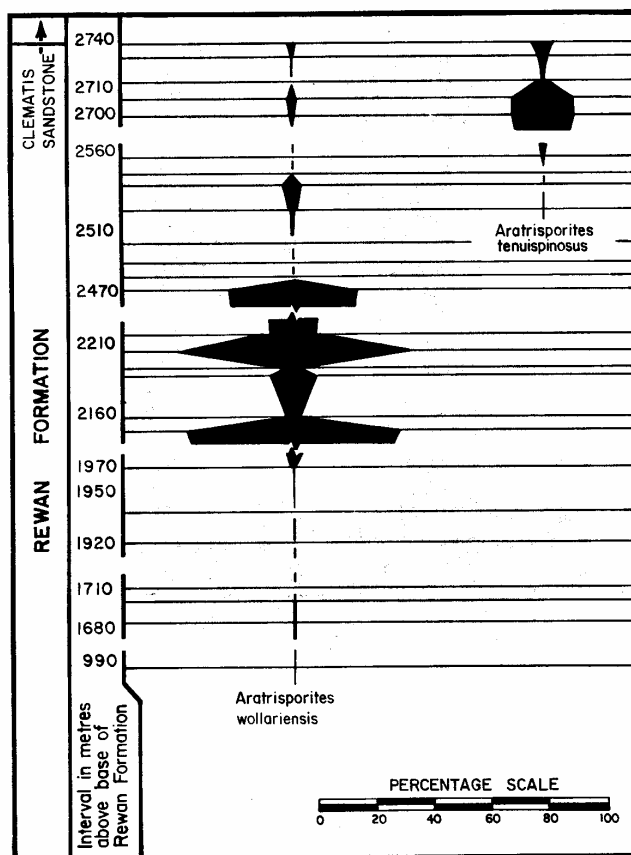
The material studied came from the eastern side of the Bowen Basin, one of three large basins of Permian and Triassic sediments in Queensland (text-fig. 1). The section sampled is located east of the axis of the Mimosa Syncline, where the Rewan Formation attains its thickest development, of approximately 2750 m (de Jersey 1970, pp. 1-3). The initial study of miospore distribution in this sequence (de Jersey 1970) was based on samples from a series of stratigraphic boreholes (text-fig. 1), sections from which were assembled to provide a composite stratigraphic section (de Jersey 1970, fig. 2). As the boreholes were relatively shallow (about 100 to 130 m) there



TEXT-FIG. 1. Map (based on de Jersey 1970, fig. 1), showing locations of stratigraphic boreholes in the eastern Bowen Basin of Queensland.

are gaps in the composite sequence, especially in the lower part of the Formation; there was, however, better coverage of the middle and upper parts of the sequence, which provided the material recorded in this paper.

The Rewan Formation is of continental origin; it consists dominantly of mudstone and siltstone, with minor sandstone and conglomerate beds and is virtually devoid of coal—a feature which differentiates it readily from the underlying Permian coal measures. A striking feature is the presence of 'red-beds', consisting dominantly of chocolate mudstone, which form a prominent part of the sections penetrated in D.R.D. 15, D.R.D. 17, D.R.D. 18, and D.R.D. 28 (text-fig. 1). Red-beds are absent, or of only minor significance in the other borehole sections. The effect of facies on the miospore assemblages has been demonstrated by comparison of palynofloras from sediments interbedded with red-beds, with those from sediments in sections devoid of red-beds. Marked differences in composition of the assemblages were observed (de Jersey 1970, pp. 22–24) with *Aratrisporites* present in only small proportions in the middle part of the sequence, in sediments interbedded with red-beds, but occurring in relatively high percentages, as shown above the 1950 m level in text-fig. 2, in the upper part of the Formation, which is devoid of red-beds.



TEXT-FIG. 2. Percentage distribution of *Aratrisporites wollariensis* and *Aratrisporites tenuispinosus* in miospore assemblages from the middle and upper Rewan Formation (based on de Jersey 1970, fig. 3). Horizontal lines represent sample levels; gaps in the chart represent gaps in coverage of borehole sections.

In a comprehensive account of lithostratigraphy and sedimentation in the Bowen Basin (Jensen 1975), two units of formational rank were distinguished in the Rewan succession of the central and western portions of the Basin and the Rewan Formation was raised to the status of a Group. However, those units are not recognized in subsurface sections in the south-eastern part of the Basin (Jensen 1975, p. 60), which includes the area considered in this paper and the designation Rewan Formation has therefore been retained for the sequence considered here.

The age of the Rewan Formation has been discussed by de Jersey (1970, pp. 26, 27; 1979, pp. 34–36) and Foster (1979, pp. 129–139) on the basis of comparison of palynofloras from that formation with others from Upper Permian–Lower Triassic successions, dated by marine faunas. There is some uncertainty where the Permian–Triassic boundary should be located, within the lower part of the Rewan Formation; however, there is strong evidence for regarding the middle and upper portions of the sequence (containing *Aratrisporites*) as Early Triassic in age.

SEQUENCE OF POPULATIONS INDICATING DEVELOPMENT OF
ARATRISPORITES TENUISPINOSUS FROM *ARATRISPORITES WOLLARIENSIS*

The percentage distribution of *A. wollariensis* and *A. tenuispinosus* in the Rewan Formation is shown in text-fig. 2 (after de Jersey 1970). Re-examination of this material has been carried out by morphological study of numerous specimens from various levels in the section covered by text-fig. 2, supplemented by quantitative studies of size distribution of the spines. Data from the quantitative studies are based on measurements of the maximum spine length at the equator of 100 well preserved, suitably oriented specimens, from four assemblages in which specimens of *Aratrisporites* are abundant and well preserved. The results of these quantitative studies are summarized in Table 1.

TABLE 1. Size distribution of spine lengths in specimens of *Aratrisporites* from the Rewan Formation

Sample (borehole, depth)	Approximate interval in metres above base of Rewan Formation	Size distribution of maximum spine lengths (in μm , based on 100 specimens)				Representative illustration in pl. 65
		<1	1–2	2–4	4–6	
D.R.D. 3, 34–57 m	2700		2	73	25	
D.R.D. 3, 38–89 m	2700	1	4	50	45	Figs. 1–3
D.R.D. 14, 44–35 m	2200		95	5		Fig. 7
D.R.D. 14, 89–79 m	2150	1	98	1		Figs. 6, 8

It is clear that over an interval of 550 m there is a marked change in the morphological distribution of the assemblages, indicated by an approximate doubling of the average maximum spine length. The differences between the lower and upper assemblages become even more apparent with detailed study

EXPLANATION OF PLATE 65

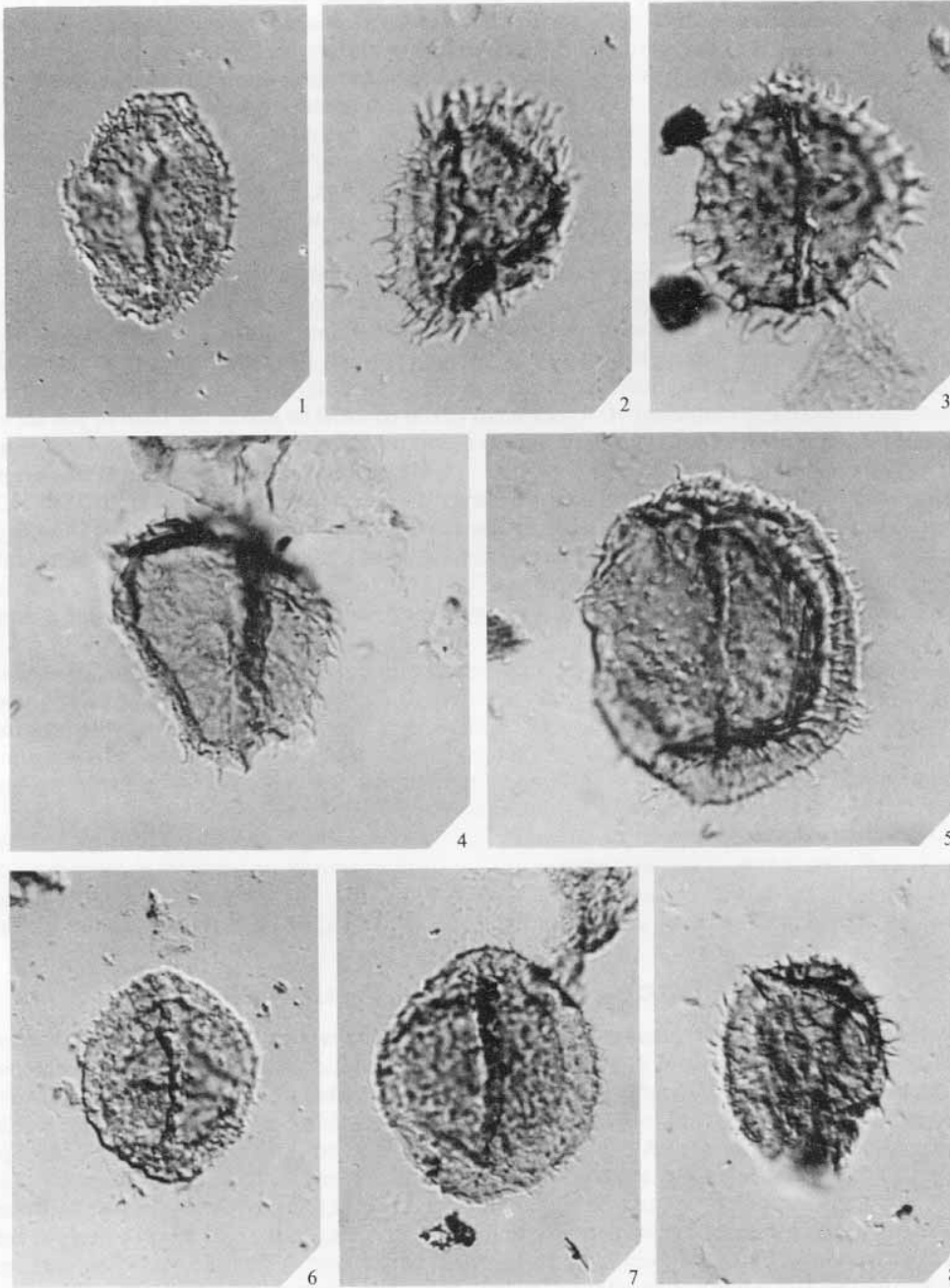
All specimens approximately $\times 1000$, equatorial focus, differential interference contrast; for details of the provenance of figured specimens see Appendix. The numbers in metres recorded after the species indicate the approximate interval above the base of the Rewan Formation, and are arranged on the plate in lines of similar depth.

Fig. 1. *Aratrisporites wollariensis* Helby, 1967, 2700 m.

Figs. 2, 3. *Aratrisporites tenuispinosus* Playford, 1965, 2700 m.

Figs. 4, 5. Specimens transitional between *A. wollariensis*, and *A. tenuispinosus*, 2520–2540 m.

Figs. 6–8. *Aratrisporites wollariensis* Helby, 1967, 2150–2200 m.



DE JERSEY, *Aratrisporites*

of the specimens, from which it is evident that in the two lower assemblages specimens with maximum spine lengths over 2 μm have only a small proportion of longer spines, and are regarded as extreme variants of *A. wollariensis*. In the two upper assemblages, in specimens with spines of maximum length greater than 2 μm , the spines tend to be uniformly longer.

Specimens representative of the populations used for these measurements are illustrated in Pl. 65 with the spine length increasing from left to right, for each of the stratigraphic levels considered. In terms of described species, specimens represented by fig. 1 and figs. 6–8 (Pl. 65) conform in all significant diagnostic features to the description and figures of *A. wollariensis* Helby, 1967 (Helby 1967, p. 67, pl. 1, figs. 17–19). Specimens represented by figs. 2 and 3 conform in all significant features to the description and figures of *A. tenuispinosus* Playford, 1965 (Playford 1965, pp. 196, 197, pl. 11, figs. 3–7).

The marked differences between the lower and upper populations support the view that *A. wollariensis* and *A. tenuispinosus* should be retained as separate species, and that the older assemblages (from 2150 to 2200 m above the base of the formation) containing only *A. wollariensis* are replaced by a mixed population, containing both species, in assemblages from about 2700 m above the base of the formation. In the intervening section, comprising the interval between assemblages containing abundant *A. wollariensis* (2150 to 2470 m above the base of the formation) and those containing abundant *A. tenuispinosus* (2700 to 2740 m above the base of the formation), quantitative studies of spine lengths have not been possible because of the relative scarcity of *Aratrisporites* in all the material examined. However, the combined population from 2520 to 2540 m above the base of the formation contains specimens which are intermediate in length and general robustness of the spines, between *A. wollariensis* and *A. tenuispinosus* (Pl. 65, figs. 4, 5). The transition between the species is evident in comparing figs. 7, 8 (2150 to 2200 m), figs. 4, 5 (2520 to 2540 m), and figs. 2, 3 (2700 m). It is concluded that *A. tenuispinosus* developed, by increase in spine dimensions, from *A. wollariensis*.

With regard to *in situ* *Aratrisporites* (from microsporangia), spores morphologically similar to *A. tenuispinosus* have been described from three species of *Cylostrobos*, a genus of lycopsid cones, by Helby and Martin (1965). The relatively close similarity in morphology of the microspores from the three species (*Cylostrobos sydneyensis*, *C. major*, and *C. grandis*) is indicative of conservatism in microspore characters, in contrast to differences in the other features of these species. The evidence, recorded above, for derivation of *A. tenuispinosus* from *A. wollariensis* is thus suggestive of the derivation of these three species of *Cylostrobos* from a lycopsid species which produced microspores of the *A. wollariensis* type. The three species of *Cylostrobos* were recorded from the upper part of the Narrabeen Group, in the Sydney Basin. This part of the Narrabeen Group is regarded, on palynological evidence, as being approximately equivalent in age to the upper Rewan Formation.

CONCLUSIONS: EVOLUTIONARY SIGNIFICANCE

The value of palynological evidence in interpreting the mechanism of evolution was discussed by Professor W. G. Chaloner in a lecture to the Fifth International Palynological Conference. His remarks are so relevant to the current study that they are quoted almost in their entirety. He stated (Chaloner 1980, p. 7): 'the fossil record of both plants and animals is singularly lacking in evidence of gradual evolutionary change. A statement from the first edition of "The Origin of Species" summarises the situation now as aptly as when Darwin published it: "Geological research, though it has added numerous species to existing and extinct genera, and has made the intervals between some few groups less wide than they otherwise would have been, yet has done scarcely anything in breaking down the distinction between species, by connecting them together by numerous fine, intermediate varieties, and this not having been effected, is probably the gravest and most obvious of all the many objections which may be urged against my views". Now, a hundred years later, this objection is still with us. Wherever we have long successions of plant-bearing deposits—the Coal Measures, the middle Jurassic of Yorkshire—there is a limited amount of change—of species and genera coming and going, but very little evidence of gradual change. In the current jargon of palaeontology the

evidence favours a punctuational process rather than a gradualistic one. The *incompleteness* of the macroplant record, which is, of course, what Darwin invoked for the lack of evidence of gradual change in the animal fossil record, was, I suppose, accepted by most palaeobotanists. But with the surge of palynology from the 1950's onwards, we came to have a much fuller and more continuous record of spores than we ever had from the more discontinuous occurrences of plant macrofossils. Many of us hoped that somehow we would see behind the scenes, and catch one species turning into another. And yet the record of evolutionary change remained as discontinuous as ever. Spore species through the Carboniferous Coal Measures show no more sign of evolutionary drift, of one species "turning into another" than do the macrofossils.

We have to conclude that the plant population which is involved in the process of relatively rapid change is very small, the "bottleneck" process of quantum speciation, so convincingly advocated by Steven Stanley.'

If the Rewan sequence recorded here is considered in relation to gradualistic and punctuational processes of evolution, it provides evidence favouring the latter. Over a relatively long interval, between 990 and 2470 metres above the base of the formation, populations of *A. wollariensis* do not show significant changes in spine morphology. The abundance of specimens of the species at some horizons within this interval enables this lack of change to be clearly demonstrated. Coincident with reduction of the species to low proportions in the assemblages, presumably as a result of adverse conditions, specimens with larger spines appear between 2520 and 2540 metres above the base of the formation. This relatively rapid change, at a time when the species is reduced to quite minor proportions of the assemblages, can be related to Mode D, or quantum speciation of Stanley (1979, pp. 26-28), whereby rapidly divergent speciation occurs by way of a very small population. Higher in the formation, between 2560 and 2740 metres above its base, there is a further increase in spine length which warrants differentiation of a separate species, *A. tenuispinosus*. Stanley (1979, figs. 2-8 (D)) indicated that the new and the pre-existing species would coexist, and both *Aratrisporites* species are found at the higher levels in the Rewan succession.

The question that remains to be answered is why an intermediate stage, of one species 'turning into another', has been observed in this particular case. It can only be suggested that conditions in this case are exceptionally favourable. A long, continuous succession, reasonably well sampled, is available. The samples have yielded abundant, well-preserved miospores, and the evolutionary change occurs in a morphological feature that is readily observed and easily measured. Perhaps the most important factor of all is that the two species are so abundant at lower and upper levels that the size of the 'bottleneck' between them may be appreciably greater than usual, so that indications of it are observed in this case.

Acknowledgements. The author expresses his appreciation of the helpful advice of Professor W. G. Chaloner, Dr. G. Playford, and Mr. J. F. Rigby, who have reviewed the manuscript. He also acknowledges the assistance of Mr. J. L. McKellar and Mr. M. W. Sayers, for photography and for preparation of the plate and text-figures.

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N. DE JERSEY

Geological Survey of Queensland
Mineral House
41 George Street
Brisbane, 4000
Australia

Typescript received 1 June 1981

Revised typescript received 11 August 1981

APPENDIX

Provenance of specimens figured in Pl. 65

Specimens listed below are all on microslides in the palynological collection of the Geological Survey of Queensland, Brisbane. Stage co-ordinates are those of a Carl Zeiss GFL Microscope; the reference point refers to the lower right-hand corner of the cover glass, when the slide is inserted with the label to the observer's left.

Figure no. in Pl. 65	Species	Slide no.	Stage co-ords.	Reference point co-ords.	Sample locality (borehole, depth)
1	<i>A. wollariensis</i>	S1558	12·7, 94·2	22·7, 85·0	D.R.D. 3, 38·89 m
2	<i>A. tenuispinosus</i>	S1559	11·7, 87·6	22·8, 84·3	D.R.D. 3, 38·89 m
3	<i>A. tenuispinosus</i>	S1559	9·3, 93·5	22·8, 84·3	D.R.D. 3, 38·89 m
4	Transitional between <i>A. wollariensis</i> and <i>A. tenuispinosus</i>	S1584	21·2, 95·2	22·7, 83·5	D.R.D. 13, 52·58 m
5	<i>A. tenuispinosus</i>	S1584	5·7, 84·4	22·7, 83·5	D.R.D. 13, 52·58 m
6	<i>A. wollariensis</i>	S1623	16·7, 89·4	22·5, 85·1	D.R.D. 14, 89·79 m
7	<i>A. wollariensis</i>	S1640	11·5, 100·0	22·8, 85·9	D.R.D. 14, 44·35 m
8	<i>A. wollariensis</i>	S1624	16·7, 90·0	22·1, 82·0	D.R.D. 14, 89·79 m