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A TAXONOMIC REVISION OF THE TERTIARY ECHINOID GENUS
MONOSTYCHIA

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ABSTRACT

For over 100 years the genus *Monostychia* (Echinoidea: Clypeasteroidea) and its type species *M. australis* Laube, 1869 have been a taxonomic home for a wide range of genera and species with the commonality of a rounded to pentagonal, discoidal test and a submarginal periproct. The specimens comprising this group are all extinct and from the Tertiary strata of southern Australia. While there have been a few minor species identified beyond *M. australis*, notably *M. etheridgei* Woods, 1877 and *P. loveni* (Duncan, 1877), it has been clear to many researchers that the variability remaining in *M. australis* was representative of numerous other taxa awaiting discovery.

Recent taxonomic works on the Clypeasteroidea suggested that the number of interambulacral plates on the oral surface of the test of some species was a useful diagnostic character. Of interest were the plates that first come into contact with the periproct. However, there appeared little evidence in the literature that it had been established that the number of such plates remained constant with test length and age, or that the variability in each taxon, of those plate numbers, has been determined. Without understanding those two issues the utility of plate numbers was questionable. This study set out to resolve some of those issues for *Monostychia* and its relatives. It was found that the number of interambulacral and ambulacral plates on the oral surface was fixed and did not change with increasing test length and therefore there was potential utility for plate numbers as a taxonomic tool. However, there was substantial variability in the numbers. As a result, the use of plate numbers in the paired interambulacra, paired ambulacra, and ambulacrum III on the oral surface appears to have limited utility at genus level. At the species level, however, such numbers can be quite useful diagnostically, particularly when paired interambulacral, paired ambulacral and ambulacrum III plate numbers are used in combination. The plates that first come into contact with the periproct was shown to

have little value taxonomically at the genus or species level within the monostychioids, largely because most species had the same plate number dominating, but also because of the variability. At subfamily level the taxonomic value of this feature is yet to be established.

A previously unreported structural feature was identified in many of the specimens. This was a thin circumferential wall of stereom present on the right-hand side of the test, lying half way between the marginal and central buttressing. It was a form of intestinal buttressing referred to hereafter as the intermulum. Its presence enabled the establishment of a new subfamily, Monostychinae in the family Arachnoididae. Four genera have been placed in the Monostychinae; *Monostychia* Laube, 1869, *Quinquestychia* gen. nov., *Rotundastychia* gen. nov. and *Deltoidstychia* gen. nov. A key to these genera is provided.

Several species have been established and others redescribed in this study. In *Monostychia* there are seven species; *M. australis* Laube, 1869, *M. macnamarai* Sadler *et al.* 2017, *M. alanruxi* Sadler *et al.* 2017, *M. merrimanensis* Sadler *et al.* 2019, *M. etheridgei* Woods, 1877, *M. glenelgensis* Sadler *et al.* 2019 and *M. robheathi* sp. nov. A new genus, *Quinquestychia* gen. nov., has also been established. It contains four species: *Q. mannumensis* sp. nov., *Q. gigas* sp. nov., *Q. berylmorrisae* sp. nov. and *Q. robertirwini* (Sadler *et al.* 2017). The last of these species was published as a *Monostychia* earlier in this study but reassigned later on the basis of further data. A second new genus, *Rotundastychia* gen. nov., has also been established. It contains three species: *R. pledgei* sp. nov., *R. aquilaensis* sp. nov. and *R. eyriei* sp. nov. A third new genus, *Deltoidstychia* gen. nov., has also been established. It currently contains a single species, *D. erioaster* sp. nov.

In addition to the above, two other new genera were established but they do not belong in the subfamily Monostychinae. Instead they are tentatively placed in the subfamily Ammotrophinae.

The first of these is *Obscurostychia* gen. nov. with two new species: *O. spirographica* sp. nov. and *O. curtus* sp. nov.

Keys to all the genera discussed above that contain more than one species have been provided.

DECLARATION

This is to certify that:

- i. this thesis comprises only my original work towards the PhD except where indicated in the preface;
- ii. due acknowledgement has been made in the text to all other material used; and
- iii. this thesis is fewer than 100,000 words in length, exclusive of tables, maps, bibliographies and appendices.

Tony Sadler

PREFACE

This thesis contains the product of work carried out by me in a part-time capacity over the period September 2012 to May 2020 inclusive of minor breaks agreed to by the University. The work includes several manuscripts that have been published or submitted for publication in collaboration with other researchers as outlined below. The project was conceived entirely by myself. Associate Professor Stephen Gallagher acted as Principal Supervisor throughout the study and contributed to the writing and editing of both the thesis and manuscripts for publication. A/Prof Gallagher also provided logistical and financial support through University channels together with discussion and interpretation of the work throughout.

The introduction to this thesis and the description of the genus *Monostychia* along with the species *M. australis*, *M. elongata* and part of *M. etheridgei* were published in Sadler, T., Kroh, A. & Gallagher, S.J., 2016, **A review of the taxonomy and systematics of the echinoid genus *Monostychia* Laube, 1869**. *Alcheringa* 40, 341-253. (Date accepted 12/01/2016.) Dr Andreas Kroh of the Department of Geology and Palaeontology, Naturhistorisches Museum Wien contributed to this publication by providing access to the type specimens of Laube, insightful discussions around taxonomy of echinoids, editing of the manuscript and suggestions with respect to analysis of CT scanning data, including defining intestinal buttressing in the specimens.

The description of *M. macnamara* and *M. alanrxi* were published in Sadler, T., Martin, S.K. & Gallagher, S.J., 2017, **Three new species of the echinoid genus *Monostychia* Laube, 1869 from Western Australia**. *Alcheringa* 41, 464–473. (Date accepted 11/11/2016.) A third species, *M. robertirwini* was also published in this paper but has been reassigned to *Quinquestychia* in this thesis. Dr Sarah Martin of the Geological Survey of Western Australia contributed to this publication by providing access to specimens held by the Geological Survey,

writing the initial draft of the section on stratigraphy, discussions about taxonomy of the various species involved and editing the manuscript.

The description of *M. merrimanesnis*, *M. glenelgensis* and a revised version of *M. etheridgei* were published in Sadler, T., Holmes, F.C. & Gallagher, S.J., 2019, **Two new species of the echinoid genus *Monostychia* from the Miocene of Victoria and a redescription of *M. etheridgei* Tenison-Woods, 1877**. *Alcheringa* 43, 279-290. (Date accepted 22/09/2018.) Frank Holmes, an Honorary at Museum Victoria, contributed to this publication by assisting with access to specimens held at Museum Victoria, intense discussions about the data collected, their interpretation and the taxonomy of echinoids, and editing the manuscript.

Several images used in this thesis are under copyright. Permission for use has been obtained from the National Library of Australia for images in Fig. 1.1.A. (permission number CD-6789738) and Fig. 1.1.B. (permission number CD-6802093). The image in Fig. 1.1.D. is provided by the courtesy of the University of Adelaide Archives. The image in Fig. 1.1.C. is from a photographer unknown first published over 100 years ago and is an orphan work. Several images have been used from the three publications identified above in *Alcheringa*. While copyright for these images was transferred to *Alcheringa* as part of the publishing agreement, a precondition of that transfer was that the images could be used in educational works such as this thesis.

ACKNOWLEDGEMENTS

Foremost I thank my supervisor, Stephen Gallagher. It was a leap of faith on his behalf to take on a student unknown to him with a project somewhat removed from his specialty. This was compounded by the fact I chose to enroll as a part-time external student. We managed to communicate regularly, succinctly and effectively throughout and the success of the project is in no small way a result of Stephen's management skills and good humour.

I also acknowledge the Australian Commonwealth Government for the financial support of my PhD program through the Australian Government Research Training Program Fee-Offset Scholarship.

I am grateful to The University of Melbourne for awarding me two scholarships. The Baragwanath Research Scholarship was used to travel to Vienna to access the type specimens for *Monostychia*. A separate Science Abroad Travelling Scholarship (SATS) was used to travel to London to access a range of specimens in the Natural History Museum.

I am indebted to Dr Rich Mooi of the California Academy of Sciences for providing me with the impetus to engage in this PhD. While I have never met or spoken to him, we did engage in several critical emails prior to my enrolment. He outlined the need for this work to be completed and urged me onward.

Such a study would never have been possible without access to museum specimens, equipment and services and I am pleased to acknowledge that I received positive support from all the museum and university staff from whom I sought such. Not in any specific order were Dr Tim Ewin, Senior Curator, Invertebrate Palaeontology, Department of Earth Science, The Natural History Museum London along with Nils Schluter, University of Gottingen who provided specimen photographs; Dr Ken MacNamara, now of Downing College Cambridge and Director of Sedgwick Museum, but formerly from the Western Australian Museum along with

his colleague Dr Mikael Siversson, Curator of Palaeontology, Department of Earth Sciences, Western Australian Museum and also Technical Officers Helen Ryan and Cassia Piper; Dr Mary-Anne Binnie, Collection Manager, Palaeontology, South Australian Museum along with Neville Pledge, former Curator of Paleontology and Ben McHenry, Senior Collections Manager; Dr David Holloway, Senior Curator, Invertebrate Palaeontology, Museum Victoria along with Dr Rolf Schmidt, Collections Manager; Dr Maria del Carmen Gomez Cabrera, School of Biological Sciences, The University of Queensland who provided access to and assistance with CT scanning equipment; and Irene Zorn, Geological Survey of Austria for information donated by Tate.

Separately but more importantly I am very thankful to the assistance of Dr Andreas Kroh of the Department of Geology and Palaeontology, Naturhistorisches Museum Wien. Apart from providing access to the type specimens of Laube, Andreas has been extremely generous with his time and his knowledge. He enabled me to bounce ideas on taxonomy that, at times, may have seemed simplistic and naïve, while enabling me to feel I was a valued member of the broad echinoid community.

Also of note is Dr Morana Mihaljevic, School of Earth Sciences, The University of Queensland with whom I had numerous in depth discussions about this work in the early stages that enabled me to clarify the direction of this study.

The co-authors of the published papers were most important to this study including Stephen Gallagher and Andreas Kroh, whom I have already mentioned. Dr Sarah Martin of the Geological Survey of Western Australia was very helpful with her time and access to specimens. She engaged in deep and thoughtful discussion and also provided some written material for inclusion in the publication. Finally, and yet very importantly is Frank Holmes. Apart from being an author of one of the papers, Frank was most useful in gaining access to

appropriate Museum Victoria collections. Frank has also been a close colleague and mentor in echinoid studies over many years and in no small way was responsible for me engaging in this study.

Finally, and most importantly I am beholden to my wife Beryl for the encouragement she has offered unconditionally throughout this study.

TABLE OF CONTENTS

ABSTRACT	ii
DECLARATION	v
PREFACE.....	vi
ACKNOWLEDGEMENTS.....	viii
LIST OF ILLUSTRATIONS	xiii
LIST OF TABLES.....	xx
LIST OF ACRONYMS, ABBREVIATIONS AND TERMINOLOGY	xxiii
Chapter 1. Introduction	1
Chapter 2. Materials and methods	37
Chapter 3. Systematics	41
Chapter 3.a. Subfamily Monostychinae	47
Chapter 3.b. Genus <i>Monostychia</i> Laube, 1869	50
Chapter 3.c. Genus <i>Quinquestychia</i> gen. nov.	93
Chapter 3.d. Genus <i>Rotundastychia</i> gen. nov.	120
Chapter 3.e. Genus <i>Deltoidstychia</i> gen. nov.	140
Chapter 3.f. Subfamily Ammotrophinae	146
Chapter 3.g. Genus <i>Obscurostychia</i> gen. nov.....	147
Chapter 3.h. Genus <i>Phalangistychia</i> gen. nov.....	163
Chapter 3.i. Key to genera	170
Chapter 4. Oral plate architecture and its implications for systematics	171

Chapter 4.a. Phylogenetic Systematics	215
Chapter 5. Conclusions	229
Chapter 5.a. Future avenues of investigation	233
Chapter 6. References.....	238
Appendices	255
Appendix 1. Raw linear data	256
Appendix 2. Raw plate data	271
Appendix 3. Diagrams for Chapter 4 (Plate architecture)	285
Appendix 4. Refereed publications	306

LIST OF ILLUSTRATIONS

Fig. 1.1. Historical actors in the <i>Monostychia</i> journey.	4
Fig. 1.2. Historical illustrations of <i>Monostychia australis</i>	5
Fig. 1.3. Map of the southern Australian localities from which specimens of <i>Monostychia</i> and related forms have been reported in the past.	7
Fig. 1.4. Type material of <i>Monostychia australis</i> Laube, 1869.	10
Fig. 2.1. Explanation of some measurements used in describing <i>Monostychia</i>	39
Fig. 2.2. Box plot of number of plates in the oral paired ambulacra of <i>Monostychia merrimanensis</i>	40
Fig. 3.1. CT scan of <i>Monostychia australis</i>	48
Fig. 3.b.1. Holotype of <i>Monostychia macnamarai</i> Sadler, Martin & Gallagher, 2017.	57
Fig. 3.b.2. Holotype of <i>Monostychia alanixi</i> Sadler, Martin & Gallagher, 2017.	62
Fig. 3.b.3. <i>Monostychia merrimanensis</i> Sadler, Holmes & Gallagher, 2019.	65
Fig. 3.b.4. Location map for three species of <i>Monostychia</i>	69
Fig. 3.b.5. <i>Monostychia etheridgei</i> Woods, 1877.	71
Fig. 3.b.6.. <i>Monostychia glenelgensis</i> Sadler, Holmes & Gallagher, 2019.	74
Fig. 3.b.7. Holotype of <i>Monostychia robheathi</i> sp. nov.	78
Fig. 3.b.8. Figured syntype of <i>Arachnoides elongata</i> Duncan, 1877.	82
Fig. 3.b.9. Box plot of width to length ratio of <i>Monostychia</i> species.	88
Fig. 3.b.10. Box plot of height to length ratio of <i>Monostychia</i> species.	88
Fig. 3.b.11. Box plot of number of pores per mm TL of <i>Monostychia</i> species.	89
Fig. 3.b.12. Box plot of the ratio of ambulacrum width at ambitus against interambulacrum width of <i>Monostychia</i> species.	89
Fig. 3.b.13. Box plot of the ratio of width of ambulacrum III at ambitus against test length (TL) of <i>Monostychia</i> species.	90
Fig. 3.b.14. Box plot of the number of plates in the paired interambulacra on the oral surface of <i>Monostychia</i> species.	90
Fig. 3.b.15. Box plot of the number of plates in the paired ambulacra on the oral surface of <i>Monostychia</i> species.	91

<i>Fig. 3.b.16. Box plot of the number of plates in the ambulacrum III on the oral surface of Monostychia species.</i>	91
<i>Fig. 3.c.1. Holotype of Quinquestychia mannumensis sp. nov.</i>	96
<i>Fig. 3.c.2. Holotype of Quinquestychia gigas sp. nov.</i>	99
<i>Fig. 3.c.3. Holotype of Quinquestychia berylmorrisae sp. nov.</i>	103
<i>Fig. 3.c.4. Holotype of Quinquestychia robertirwini (Sadler, et al. 2017.</i>	107
<i>Fig. 3.c.5. Box plot of width to length ratio of Quinquestychia species.</i>	114
<i>Fig. 3.c.6. Box plot of height to length ratio of Quinquestychia species.</i>	114
<i>Fig. 3.c.7. Box plot of the ratio of petal length to distance to margin for Quinquestychia species.</i>	115
<i>Fig. 3.c.8. Box plot of number of pores per mm TL of Quinquestychia species.</i>	115
<i>Fig. 3.c.9. Box plot of the ratio of ambulacrum width at ambitus against interambulacrum width of Quinquestychia species.</i>	116
<i>Fig. 3.c.10. Box plot of the ratio of width of ambulacrum III at ambitus against test length (TL) of Quinquestychia species.</i>	116
<i>Fig. 3.c.11. Box plot of the number of plates in the paired interambulacra on the oral surface of Quinquestychia species.</i>	117
<i>Fig. 3.c.12. Box plot of the number of plates in the paired ambulacra on the oral surface of Quinquestychia species.</i>	117
<i>Fig. 3.c.13. Box plot of the number of plates in the ambulacrum III on the oral surface of Quinquestychia species.</i>	118
<i>Fig. 3.d.1 Holotype of Rotundastychia pledgei sp. nov.</i>	122
<i>Fig. 3.d.2 Holotype of Rotundastychia aquilaensis sp. nov.</i>	126
<i>Fig. 3.d.3 Holotype of Rotundastychia eyriei sp. nov.</i>	129
<i>Fig. 3.d.4. Box plot of width to length ratio of Rotundastychia species.</i>	134
<i>Fig. 3.d.5. Box plot of height to length ratio of Rotundastychia species.</i>	134
<i>Fig. 3.d.6. Box plot of number of pores per mm TL of Rotundastychia species.</i>	135
<i>Fig. 3.d.7. Box plot of test length vs ambital thickness of Rotundastychia species.</i>	135
<i>Fig. 3.d.8. Box plot of the ratio of ambulacrum width at ambitus against interambulacrum width of Rotundastychia species.</i>	136

Fig. 3.d.9. Ambulacrum to interambulacrum ratio compared to TL in Rotundastychia species.	136
Fig. 3.d.10. Box plot of the ratio of width of ambulacrum III at ambitus against test length (TL) of Rotundastychia species.	137
Fig. 3.d.11. Box plot of the number of plates in the paired interambulacra on the oral surface of Rotundastychia species.	137
Fig. 3.d.12. Box plot of the number of plates in the paired ambulacra on the oral surface of Rotundastychia species.	138
Fig. 3.d.13. Box plot of the number of plates in the ambulacrum III on the oral surface of Rotundastychia species.	138
Fig. 3.e.1. Holotype of Deltoidstychia erioaster sp. nov.	142
Fig. 3.g.1. Holotype of Obscurostychia spirographica sp. nov.	149
Fig. 3.g.2. Holotype of Obscurostychia curtus sp. nov.	153
Fig. 3.g.3. Scatter plot of relative length of anterior petal in Obscurostychia species.	158
Fig. 3.g.4. Box plot of relative length of anterior petal in Obscurostychia species.	159
Fig. 3.g.5. Box plot of number of plates in the oral paired interambulacra of Obscurostychia species.	160
Fig. 3.g.6. Box plot of number of plates in the oral paired ambulacra of Obscurostychia species.	161
Fig. 3.g.7. Box plot of number of plates in the oral ambulacrum III of Obscurostychia species.	161
Fig. 3.h.1. Holotype of Phalangistychia loveni (Duncan, 1877).	165
Fig. 3.h.2. Historical illustrations of Phalangistychia loveni.	166
Fig. 4.1. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of all species of Monostychia.	178
Fig. 4.2. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of all species of Quinquestychia.	179
Fig. 4.3. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of all species of Rotundastychia.	179
Fig. 4.4. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of Deltoidstychia erioaster.	180
Fig. 4.5. Scatter plot of number of post-basiceoral ambulacral plates in each of the paired oral interambulacrum against TL for all species of Monostychia.	182

<i>Fig. 4.6. Scatter plot of number of post-basicoronal ambulacral plates in each of the paired oral interambulacrum against TL for all species of Quinquestychia.</i>	<i>182</i>
<i>Fig. 4.7. Scatter plot of number of post-basicoronal ambulacral plates in each of the paired oral interambulacrum against TL for all species of Rotundastychia.</i>	<i>183</i>
<i>Fig. 4.8. Scatter plot of number of post-basicoronal ambulacral plates in each of the paired oral interambulacrum against TL for Deltoidstychia erioaster.</i>	<i>183</i>
<i>Fig. 4.9. Scatter plot of number of post-basicoronal ambulacral plates in ambulacrum III against TL for all species of Monostychia.</i>	<i>185</i>
<i>Fig. 4.10. Scatter plot of number of post-basicoronal ambulacral plates in ambulacrum III against TL for all species of Quinquestychia.</i>	<i>186</i>
<i>Fig. 4.11. Scatter plot of number of post-basicoronal ambulacral plates in ambulacrum III against TL for all species of Rotundastychia.</i>	<i>186</i>
<i>Fig. 4.12. Scatter plot of number of post-basicoronal ambulacral plates in ambulacrum III against TL for Deltoidstychia erioaster.</i>	<i>187</i>
<i>Fig. 4.14. Box plot of number of plates in the oral paired interambulacra of Monostychia species.</i>	<i>190</i>
<i>Fig. 4.15. Box plot of number of plates in the oral paired interambulacra of Quinquestychia species.</i>	<i>191</i>
<i>Fig. 4.16. Box plot of number of plates in the oral paired interambulacra of Rotundastychia species.</i>	<i>191</i>
<i>Fig. 4.17. Box plot of number of plates in the oral paired ambulacra of Monostychia species.</i>	<i>193</i>
<i>Fig. 4.18. Box plot of number of plates in the oral paired ambulacra of Quinquestychia species.</i>	<i>194</i>
<i>Fig. 4.19. Box plot of number of plates in the oral paired ambulacra of Rotundastychia species.</i>	<i>194</i>
<i>Fig. 4.20. Box plot of number of plates in the oral ambulacrum III of Monostychia species.</i>	<i>196</i>
<i>Fig. 4.21. Box plot of number of plates in the oral ambulacrum III of Quinquestychia species.</i>	<i>197</i>
<i>Fig. 4.22. Box plot of number of plates in the oral ambulacrum III of Rotundastychia species.</i>	<i>197</i>
<i>Fig. 4.23. Box plot of number of plates in the oral paired interambulacra of Monostychinae genera.</i>	<i>199</i>

Fig. 4.24. Box plot of number of plates in the oral paired ambulacra of Monostychinae genera.	200
Fig. 4.25. Box plot of number of plates in the oral ambulacrum III of Monostychinae genera.	201
Fig. 4.26. Box plot of the first plate to contact the periproct in seven species of Monostychia.	203
Fig. 4.27. Box plot of the first plate to contact the periproct in four species of Quinquestychia.	204
Fig. 4.28. Box plot of the first plate to contact the periproct in three species of Rotundastychia.	204
Fig. 4.29. Box plot of the first plate to contact the periproct in four genera of Monostychinae.	205
Fig. 4.a.1. Strict consensus tree found from parsimony analysis of data in Table 4.a.2.	222
Fig. 4.a.2. Inferred phylogeny of the taxa in this study.	227
Appendix Fig.4.1. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of Monostychia australis.	285
Appendix Fig.4.2. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of Monostychia macnamarai.	285
Appendix Fig.4.3. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of Monostychia alanixi.	286
Appendix Fig.4.4. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of Monostychia merrimanensis.	286
Appendix Fig.4.5. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of Monostychia etheridgei.	287
Appendix Fig.4.6. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of Monostychia glenelgensis.	287
Appendix Fig.4.7. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of Monostychia robheathi.	288
Appendix Fig.4.8. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of Quinquestychia mannumensis.	288
Appendix Fig.4.9. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of Quinquestychia gigas.	289
Appendix Fig.4.10. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of Quinquestychia berylmoorisae.	289

Appendix Fig.4.11. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of <i>Quinquestychia robertirwini</i>	290
Appendix Fig.4.12. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of <i>Rotundastychia pledgei</i>	290
Appendix Fig.4.13. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of <i>Rotundastychia aquilaensis</i>	291
Appendix Fig.4.14. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of <i>Rotundastychia eyriei</i>	291
Appendix Fig.4.15. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of <i>Monostychia australis</i>	292
Appendix Fig.4.16. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of <i>Monostychia macnamarai</i>	292
Appendix Fig.4.17. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of <i>Monostychia alanrxi</i>	293
Appendix Fig.4.18. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of <i>Monostychia merrimanensis</i>	293
Appendix Fig.4.19. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of <i>Monostychia etheridgei</i>	294
Appendix Fig.4.20. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of <i>Monostychia glenelgensis</i>	294
Appendix Fig.4.21. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of <i>Monostychia robheathi</i>	295
Appendix Fig.4.22. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of <i>Quinquestychia mannumensis</i>	295
Appendix Fig.4.23. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of <i>Quinquestychia gigas</i>	296
Appendix Fig.4.24. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of <i>Quinquestychia berylmorrisae</i>	296
Appendix Fig.4.25. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of <i>Quinquestychia robertirwini</i>	297
Appendix Fig.4.26. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of <i>Rotundastychia pledgei</i>	297
Appendix Fig.4.27. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of <i>Rotundastychia aquilaensis</i>	298

<i>Appendix Fig.4.28. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of Rotundastychia eyriei.</i>	<i>298</i>
<i>Appendix Fig.4.29. Scatter plot of number plates in ambulacrum III against TL of Monostychia australis.</i>	<i>299</i>
<i>Appendix Fig.4.30. Scatter plot of number plates in ambulacrum III against TL of Monostychia macnamarai.</i>	<i>299</i>
<i>Appendix Fig.4.31. Scatter plot of number plates in ambulacrum III against TL of Monostychia alanrxi.</i>	<i>300</i>
<i>Appendix Fig.4.32. Scatter plot of number plates in ambulacrum III against TL of Monostychia merrimanensis.</i>	<i>300</i>
<i>Appendix Fig.4.33. Scatter plot of number plates in ambulacrum III against TL of Monostychia etheridgei.</i>	<i>301</i>
<i>Appendix Fig.4.34. Scatter plot of number plates in ambulacrum III against TL of Monostychia glenelgensis.</i>	<i>301</i>
<i>Appendix Fig.4.35. Scatter plot of number plates in ambulacrum III against TL of Monostychia robheathi.</i>	<i>302</i>
<i>Appendix Fig.4.36. Scatter plot of number plates in ambulacrum III against TL of Quinquestychia mannumensis.</i>	<i>302</i>
<i>Appendix Fig.4.37. Scatter plot of number plates in ambulacrum III against TL of Quinquestychia gigas.</i>	<i>303</i>
<i>Appendix Fig.4.38. Scatter plot of number plates in ambulacrum III against TL of Quinquestychia berylmorrisae.</i>	<i>303</i>
<i>Appendix Fig.4.39. Scatter plot of number plates in ambulacrum III against TL of Quinquestychia robertirwini.</i>	<i>304</i>
<i>Appendix Fig.4.40. Scatter plot of number plates in ambulacrum III against TL of Rotundastychia pledgei.</i>	<i>304</i>
<i>Appendix Fig.4.41. Scatter plot of number plates in ambulacrum III against TL of Rotundastychia aquilaensis.</i>	<i>305</i>
<i>Appendix Fig.4.42. Scatter plot of number plates in ambulacrum III against TL of Rotundastychia eyriei.</i>	<i>305</i>

LIST OF TABLES

<i>Table 1.1. Age of Exploration.</i>	31
<i>Table 1.2. Age of Collection.</i>	33
<i>Table 1.3. Age of Orderliness.</i>	34
<i>Table 1.4. Age of Research.</i>	36
<i>Table 3.1. Classification of Clark (1946).</i>	41
<i>Table 3.2. Classification of Durham et al. (1966).</i>	42
<i>Table 3.3. Classification of Mooi (1989).</i>	42
<i>Table 3.4. Classification of Kroh & Smith (2011).</i>	43
<i>Table 3.5. Classification of Byrne & O'Hara (2017).</i>	44
<i>Table 3.6. Classification of The Echinoid Directory (Smith & Kroh, 2011).</i>	44
<i>Table 3.b.1. Comparison of diagnostic features of the seven species of Monostychia.</i>	87
<i>Table 3.b.2. Key to species of Monostychia.</i>	92
<i>Table 3.c.1. Comparison of diagnostic features of the four species of Quinquestychia.</i>	113
<i>Table 3.c.2. Key to species of Quinquestychia.</i>	119
<i>Table 3.d.1. Comparison of diagnostic features of the three species of Rotundastychia.</i>	133
<i>Table 3.d.2. Key to species of Rotundastychia.</i>	139
<i>Table 3.e.1. Comparison of diagnostic features of Deltoidstychia.</i>	145
<i>Table 3.g.1. Comparison of diagnostic features of the four species of Obscurostychia.</i>	158
<i>Table 3.g.2. Key to species of Obscurostychia.</i>	162
<i>Table 3.h.1. Diagnostic features of Phalangistychia.</i>	169
<i>Table 3.i.1. Key to the genera of Monostychinae.</i>	170
<i>Table 3.i.2 Key to the genera of Ammotrophinae described in this thesis.</i>	170
<i>Table. 4.1. Mean TL (SD) of the number of plates first in contact with periproct.</i>	188
<i>Table. 4.2. The percentage (and sample size) of plates of each oral interambulacra series that start from the peristome on the left, or 'a' side, species by species for Monostychinae.</i>	207
<i>Table 4.3. The percentage (and sample size) of plates of each oral ambulacra series that start from the peristome on the left, or 'a' side, species by species for Monostychinae.</i>	209

Table 4.4. The percentage (and sample size) of plates of each oral interambulacra series that start from the peristome on the left, or 'a' side, by genera for Monostychinae.	210
Table 4.5. The percentage (and sample size) of plates of each oral ambulacra series that start from the peristome on the left, or 'a' side, by genera for Monostychinae.	211
Table 4.a.1. List of morphological characters scored and data matrix used in the cladistic analysis. ..	220
Table 4.a.2. Character data matrix of the 20 species used in this study.	220
Table 5.1. A list of the species and genera identified in this study.	232
Table 5.a.1. Potential species and genera yet to be described from Cainozoic strata of southern Australia.	234
Appendix Table 1. Abbreviations for linear data tables. All measurements in mm.	255
Appendix table 2. Abbreviations for plate data tables. All measurements in whole numbers.....	255
Appendix 1.1. Raw linear data for <i>M. australis</i>	258
Appendix 1.2. Raw linear data for <i>M. macnamarai</i>	259
Appendix 1.3. Raw linear data for <i>M. alanruxi</i>	259
Appendix 1.4. Raw linear data for <i>M. merrimanensis</i>	261
Appendix 1.5. Raw linear data for <i>M. etheridgei</i>	261
Appendix 1.6. Raw linear data for <i>M. glenelgensis</i>	262
Appendix 1.7. Raw linear data for <i>M. robheathi</i>	263
Appendix 1.8. Raw linear data for <i>Q. mannumensis</i>	264
Appendix 1.9. Raw linear data for <i>Q. gigas</i>	264
Appendix 1.10. Raw linear data for <i>Q. berylmoorissae</i>	265
Appendix 1.11. Raw linear data for <i>Q. robertirwini</i>	265
Appendix 1.12. Raw linear data for <i>R. pledgei</i>	266
Appendix 1.13. Raw linear data for <i>R. aquilaensis</i>	267
Appendix 1.14. Raw linear data for <i>R. eyriei</i>	267
Appendix 1.15. Raw linear data for <i>D. erioaster</i>	268
Appendix 1.16. Raw linear data for <i>O. spirographica</i>	269
Appendix 1.17. Raw linear data for <i>O. curtus</i>	269
Appendix 1.18. Raw linear data for <i>P. loveni</i>	270
Appendix 2.1. Raw plate numbers count for <i>M. australis</i>	273
Appendix 2.2. Raw plate numbers count for <i>M. macnamarai</i>	274
Appendix 2.3. Raw plate numbers count for <i>M. alanruxi</i>	274

<i>Appendix 2.4. Raw plate numbers count for M. merrimanensis.</i>	276
<i>Appendix 2.5. Raw plate numbers count for M. etheridgei.</i>	276
<i>Appendix 2.6. Raw plate numbers count for M. glenelgensis.</i>	277
<i>Appendix 2.7. Raw plate numbers count for M. robheathi.</i>	278
<i>Appendix 2.8. Raw plate numbers count for Q. mannumensis.</i>	278
<i>Appendix 2.9. Raw plate numbers count for Q. gigas.</i>	279
<i>Appendix 2.10. Raw plate numbers count for Q. berylmoorisae.</i>	279
<i>Appendix 2.11. Raw plate numbers count for Q. robertirwini.</i>	280
<i>Appendix 2.12. Raw plate numbers count for R. pledgei.</i>	281
<i>Appendix 2.13. Raw plate numbers count for R. aquilaensis.</i>	281
<i>Appendix 2.14. Raw plate numbers count for R. eyriei.</i>	282
<i>Appendix 2.15. Raw plate numbers count for D. erioaster.</i>	283
<i>Appendix 2.16. Raw plate numbers count for O. spirographica.</i>	283
<i>Appendix 2.17. Raw plate numbers count for O. curtus.</i>	284
<i>Appendix 2.18. Raw plate numbers count for P. loveni.</i>	284

LIST OF ACRONYMS, ABBREVIATIONS AND TERMINOLOGY

Abbreviation	Meaning
Amb.	Ambulacrum
CT	Computed tomography
ICZN	International Commission on Zoological nomenclature
Interamb.	Interambulacrum
MV	Museum Victoria
N	Sample size
NHML	Natural History Museum London
NHMW	Naturhistorisches Museum Wien (Natural History Museum of Vienna)
SAM	South Australian Museum
SD	Standard deviation
TL	Test length
TMAG	Tasmanian Museum & Art Gallery
WAM	Western Australian Museum

When comparing the test size of the species, five test sizes are used. These sizes refer to the length of test as shown in the following Table.

Size	Length in mm
Very small	Less than 10
Small	10 to 22
Medium	23 to 44
Large	45 to 60
Very large	Greater than 60

In this thesis reference is made to plates numbers in contact with the periproct. While the terminology for identifying plate numbers under the Lovenian system usually requires the identification of the ambulacral or interambulacral segment of the test to be included, all of the plate numbers used in this these refer to interambulacrum 5 and specifically to the numbering of the plates that first come into contact with the periproct as reading out from the peristome. Hence, while identifying the plates as 5.a.3 and 5.b.3 (or similar) is more accurate, this has been simplified to 3a/3b.

Chapter 1. Introduction

Monostychia and its type species, *M. australis*, hold a unique and fascinating place in Australian palaeontology. First recorded in the journals of Sturt's epic journey down the River Murray in South Australia in 1829-31 (Sturt 1832), it is the first fossil echinoid to be recorded from Australia. Two other Australian echinoid species, *Echinodiscus orbicularis* (Leske 1778) and *Echinus* [= *Echinometra*] *mathaei* (Blainville 1825), were described as new species prior to Sturt's exploration, but the descriptions were of extant species that were not recognised as fossils until Foster and Philip (1980) and McNamara (1992) redescribed these species.

Monostychia has been recorded from the Jurassic (White 1999) through to Pleistocene (Tate 1895). This long stratigraphic range is not supported by museum specimens and is certainly erroneous.

In the 188 years since the first record of the genus, *Monostychia* has undergone a remarkable journey of misplaced identification that stems from numerous factors. Among these are insufficient collection data for museum specimens that has resulted in confusion over locations and stratigraphic distributions of specimens. In addition, a range of species and genera appear to have been lumped together in this genus. In particular, one species, *M. australis*, has been described by successive authors (Laube 1869, Woods 1876, McCoy 1879, Pomel 1883, Duncan 1887, Gregory 1890, Bittner 1892) without comparison to the full range of specimens available, including the types in many cases.

Using the literature relating to the clypeasteroids and specifically *Monostychia*, the history of fossil echinoid collecting and research in Australia can be grouped into four distinct 'ages'.

The first, from 1832-1868, was characterised by exploration of the continent and opportunistic collecting; the second, from 1869-1945, by the deliberate collection of fossils for the purpose of determining the extent of variation; the third, from 1946-1969, by the ordering of specimens collected and publication of papers on the suite of fossil echinoids known from various locations; and finally, the fourth era, from 1970 to the present, when data from the fossil record are being integrated with that collected from disparate sciences to shed light on wider questions so that new interpretations of the history of life can be written.

The age of exploration

The first ‘age’ of exploration began with the epic journey of Sturt down the Murray River in 1829-31 and the publication of the first fossil echinoid (Sturt 1832), later to be known as *Monostychia australis*. This age, which lasted for 37 years, was characterised principally by visitors to the largely undiscovered Australian continent and by those academics, mainly back in Europe, who received and commented upon the antipodean discoveries of amateur collectors. The focus of this era was on the exploration of a new land while the collection of fossils and other natural history specimens was secondary and the resulting analysis and publication of interpretations reflected a strong European-centric bias, or ‘localism’ (Le Grand 1988, Oreskes 1999, Donovan 2013).

However, the exploration was not limited to the people and specimens, it was also intellectual. For the naturalists and academics, it was a time when those involved were starting to grapple with the exploration of new salient diagnostic characters and even the relatively recent concepts of classification to reflect apparent relatedness. Publications by prominent scholars of the time included Forbes (1852), Woods (1860) and Duncan (1864). Toward the end of this first age Darwin published his *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. (Darwin 1859)

and although the new concept of systematically describing the living world had existed for some time previous to Darwin's seminal publication, such systems, including hierarchical ones, were based on commonality of morphological characters. The concept of phylogeny was just beginning to emerge.

A military man, Captain Charles Sturt (Fig. 1.1.A) commanded the first European exploration of a large tract of Australia. Although observant, he was not a scientist and it is understandable, indeed quite remarkable, that he attached the genus name *Scutella* to his echinoid fossil find. Such naming was presumably a result of its close resemblance to a sand dollar genus described some years before in Europe (Lamarck 1816) but also a casual assumption that discoveries from the antipodes must be mere extensions of European fauna. The criteria upon which he relied in this identification are not given and appear to be little more than a superficial appearance of a rounded, flat test. The specimen pictured by Sturt (Fig. 1.2.A) is unmistakably what we now acknowledge as *M. australis* despite the relatively simplistic line drawing. Notably, Sturt partnered this specimen with *Lovenia forbesi* (as *Spatangus hoffmanni*) and *Psammechinus* (as *Echinus*). As will be discussed later, *M. australis* is restricted to the Glenforslan Formation of the Murray River cliffs (Fig. 1.3) whereas the other two species are found immediately below in the Mannum Formation (Gallagher and Gourley 2007).



Fig. 1.1. Historical actors in the Monostychia journey. A.: Captain Charles Sturt (<http://nla.gov.au/nla.pic-an9941030>); B: Reverend Julian Edmund (Tenison) Woods (<http://nla.gov.au/nla.pic-an23530162>); C: Professor Gustav Carl Laube (http://www.mackovo.nazory.cz/dejepisny_projekt/rodaci/kglaube/laube.jpg); D: Professor Ralph Tate (<http://hdl.handle.net/2440/50055>).

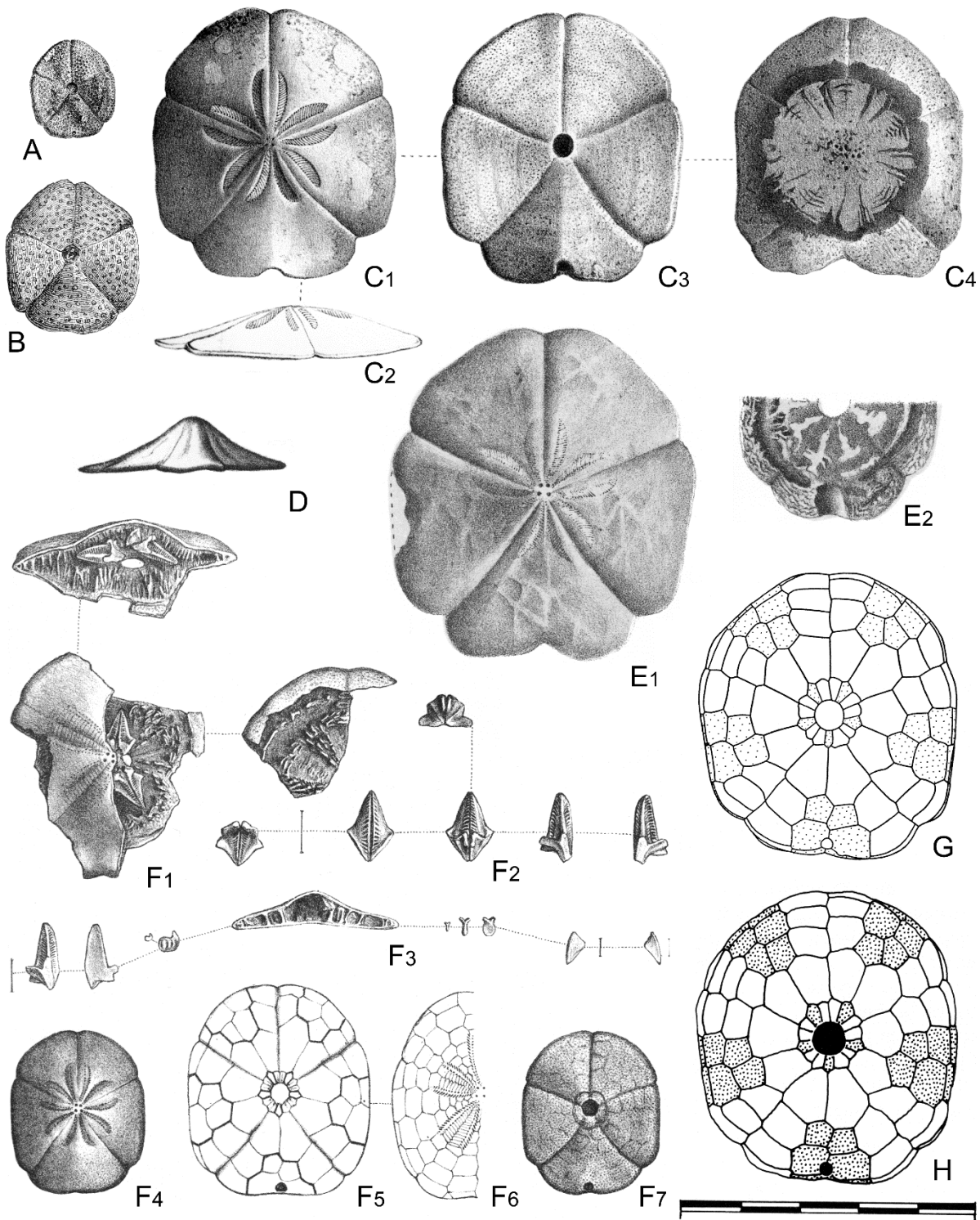


Fig. 1.2. Historical illustrations of *Monostychia australis*. A: oral view of corona from Sturt (1832): (pl. 3: fig. 9); B: oral view of corona Woods (1862), (text-fig. on p. 77); C1-C4: aboral (C1, C4), oral (C3) and lateral (C2) views from Laube (1869): (fig. 3, 3a-c); D: lateral view of “*Monostychia australis elongata*” from Duncan (1877): (pl. 3: fig. 8); E1-E2: aboral view (E1) and horizontal section through corona (E2) from McCoy (1879): (pl. 60: figs 5, 7); F1-F7: various views of the corona (F1, F4-F7), vertical section through corona (F3) and lantern elements (F2, F3) from Bittner (1892), (pl. 2: figs 5-9; F4 also reproduced in Durham, et al. 1966): (fig. 359.1a); G: oral plating from Durham (1955): (fig. 29d; also

used in Durham, et al.1966), (fig. 359.1b); H: oral plating from Mooi (1989), (fig. 5b; redrawn from Durham (1955)). Reproduced at original printing size.

Professor Edward Forbes (1852), a prominent British naturalist, commented on Sturt's observations and also mentioned a range of sea-urchins brought to him from Melbourne (although their appearance suggests an origin from the Murray River Cliffs in South Australia; Fig. 1.3). These included the genera *Echinolampas*, *Brissus*, *Spatangus* (the picture provided by Forbes is clearly that of *Lovenia forbesi*), *Echinus* and *Scutella* (most likely *Monostychia*). The use of the name *Scutella* was probably drawn from Sturt's paper. These genera are all common in the Murray River cliffs of the lower Murray River in South Australia. Additionally, with the exception of Sturt's *Scutella*, all are from the Mannum Formation although similar, yet to be described, *Monostychia*-like forms are also common in the Mannum Formation. Forbes was the first of a series of researchers who worked with *Monostychia* specimens delivered to them from the other side of the world with little accurate data attached and with no context in relation to stratigraphy or associated fauna.

The Reverend Julian Edmund Tenison-Woods (generally referred to as Woods); (Fig. 1.1.B) was a Catholic preacher who spent many years wandering southeast South Australia and western Victoria. He had a keen interest in natural history and was an avid collector. In one of his earlier works (1860) he mentioned the presence of fossil echinoderms in the Cainozoic rocks of south-eastern South Australia, in the area near Mt Gambier (Fig. 1.3), and specified *Lovenia (Spatangus) forbesi*. In a footnote, he further recorded *Eupatagus*, *Echinolampas* and *Clypeaster*. He made no mention of the diagnostic characters used in his identifications. Without further description and no diagrams it is difficult to identify with certainty, however, his *Clypeaster* is possibly identical with what was in time erroneously called *Clypeaster folium* (a European form), later to be equated to *M. australis* (Etheridge, 1875), although as the specimen was from south-eastern South Australia it may be a species

described by Sadler *et al.* (2019) and confused with *Monostychia elongata* rather than *M. australis*.

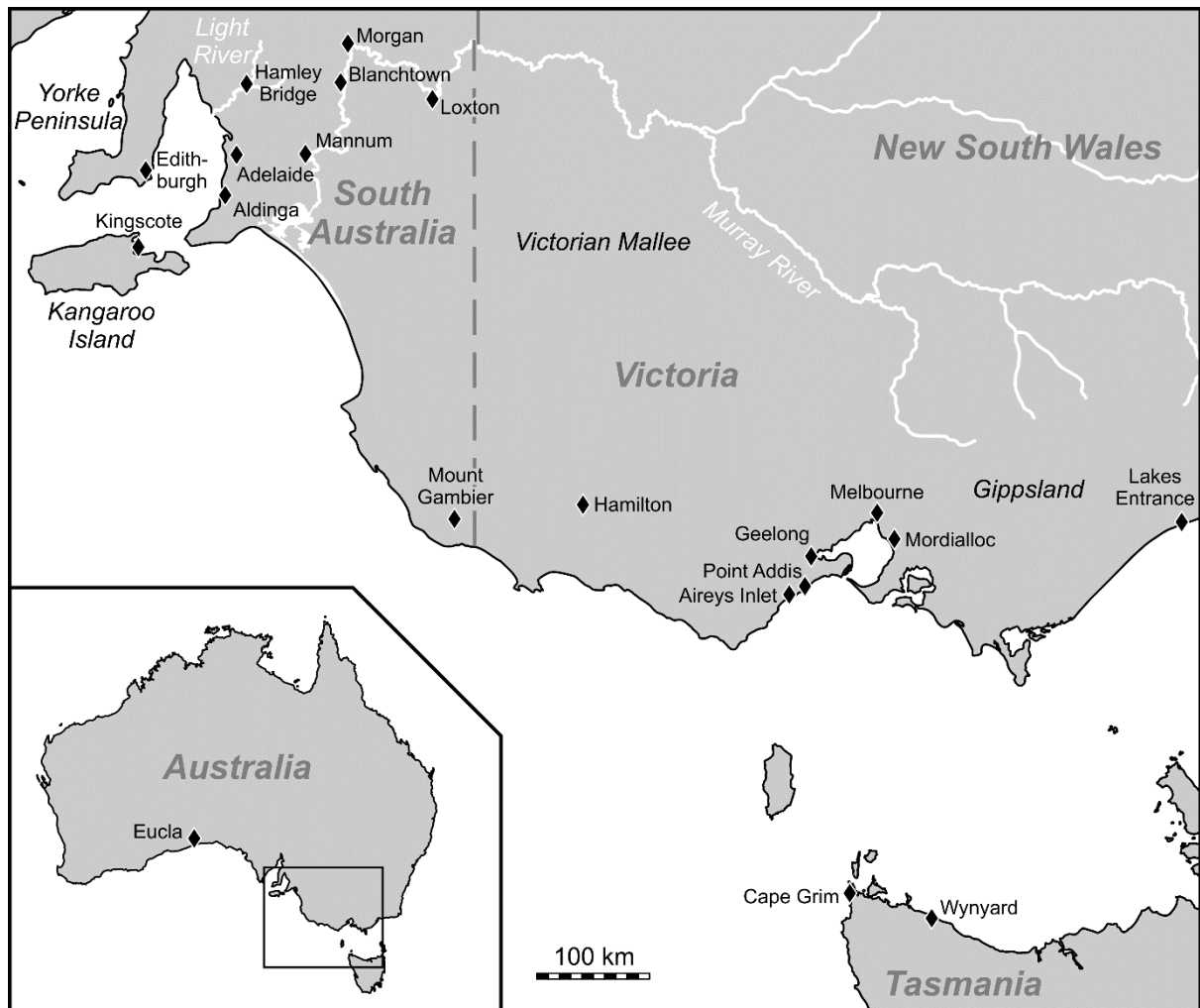


Fig. 1.3. Map of the southern Australian localities from which specimens of *Monostychia* and related forms have been reported in the past. Inset shows position of study area. Locality Eucla lies outside of the map area and is indicated in the inset.

In a later list of genera, Woods (1862) observed that *Clypeaster*, *Lovenia* (*Spatangus*) *forbesi* and “*Echinolampus*” [sic] (a misspelling for *Echinolampas*; the illustrated specimen, moreover, is misidentified, representing a species of the spatangoid echinoid *Cyclaster* instead) are present in the strata of Mt Gambier (Fig. 1.3). He illustrated *Lovenia forbesi* and the *Echinolampas* from the Mannum Formation in the western part of the Murray Basin (Fig. 1.3). The *Clypeaster* he identified (Fig. 2B) had food grooves extending to the ambitus.

However, many *Clypeaster* species have this feature and it is not particularly diagnostic. The indentations of the ambitus at the extent of the food grooves on his illustrated specimen suggest this is a species of *Monostychia* or a closely related genus and not a species of *Clypeaster*.

Professor Peter Martin Duncan was a British palaeontologist, a one-time President of the Royal Society and another prolific author. Duncan (1864) referred to *Clypeaster folium* (Agassiz & Desor, 1847) from “*Muddy Creek, the Murray, South Australia*” although the location of Muddy Creek most likely refers to Muddy Creek near Hamilton, Victoria (Fig. 1.3) and not the River Murray, some 400 km away. He commented that this appears to be a variety of *C. folium* with a marginal periproct, thus providing the first example of a useful diagnostic feature (the marginal periproct), but he continued to rely more upon a general resemblance for identification. His specimen was most probably one of the *Monostychia*-like fossils, but the limited description and lack of a diagram makes it difficult to assign it either to the genus or species level. Woods (1865) briefly commented on *Scutella* the following year when he mentioned that *Scutella* “*is, according to Dr Duncan, identical with an urchin found in the Miocene beds of Malta*”.

The age of collection

The second ‘age’, termed here ‘the age of collection’ because of the apparent emphasis on trying to collect every specimen of fossil echinoid, witnessed the incorporation into the proponents’ thinking of much of Darwin’s new paradigm. Researchers showed attention to the meaning of the characters they chose to use as they endeavoured to place the specimens into a classification system reflecting consideration of both space and time. It was, however, a time of confusion brought about by the lack of specimens, which undoubtedly prompted the focus on the rapid acquisition of more and more, and the proliferation of descriptions of new

species. The age was heralded by Laube's description of the genus *Monostychia* (Laube 1869), but dominated by Tate (1885), Etheridge (1878), McCoy (1879) and Johnston (1877).

Professor Gustav Carl Laube (Fig. 1.1.C) specialised in echinoid palaeontology at the Natural History Museum Vienna and the Geological Survey of Austria (Wähner 1924). He erected a new genus (1869), *Monostychia*, with the type species *M. australis* (Fig. 1.2.C), from the River Murray cliffs in South Australia. In his description of *M. australis*, Laube stated, “*Woods obviously refers to this species when he mentions Scutella sp. on p. 105 (Woods 1862) of his list of species from the Murray Cliffs. In another reference on p. 77 (Woods 1862) he pictures the backside (aboral) of an echinoid from Mount Gambier as Clypeaster. It seems to me however it is also Monostychia australis since as far as is discernible from the woodcut, its form is quite similar and since Hemipatagus forbesi Woods is also found, it appears to represent the same formation as is present in the Murray Cliffs*”.

Laube examined eight specimens that had been sent to him from Australia (Fig. 1.4). They comprised a size range from 10–44 mm that Laube used to suggest the smaller ones were juveniles and from which he drew the conclusion that the lack of certain features was due to their age. Upon comparison by the current author with specimens of known provenance it is apparent that two of his specimens belong to one of the Mannum Formation *Monostychia*-like forms that are yet to be described and another two lack the features to place them accurately at genus level. Consequently, any conclusions Laube made in relation to ontogeny are not supported by the small dataset he studied.

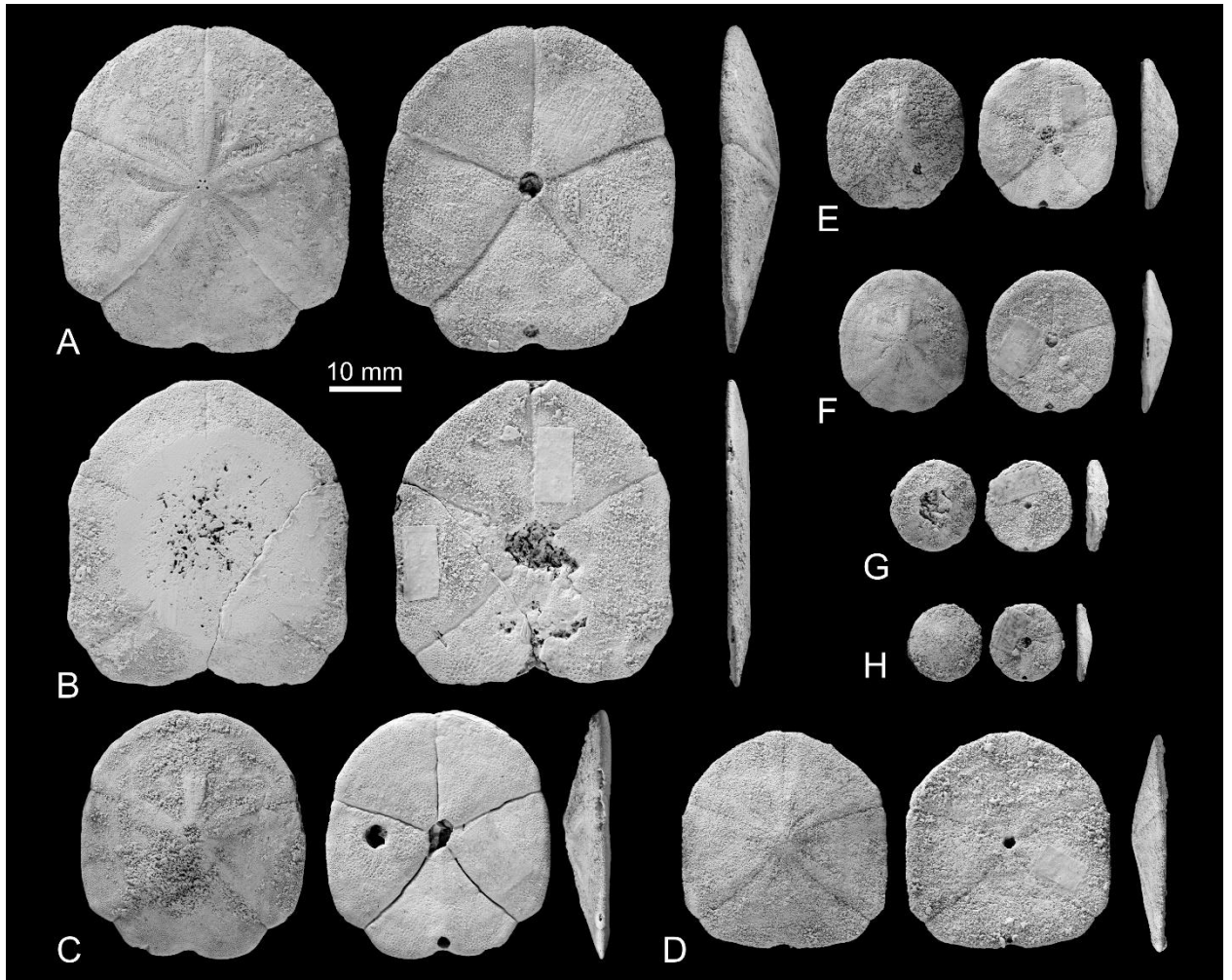


Fig. 1.4. Type material of *Monostychia australis* Laube, 1869. **A**, lectotype NHMW 2000z0068/0001; **B**, paralectotype NHMW 2000z0068/0002 (here excluded from *M. australis*); **C**, paralectotype NHMW 1864/0001/0065a; **D**, paralectotype NHMW 1864/0001/0065b (here excluded from *M. australis*); **E**, paralectotype NHMW 1864/0001/0065c; **F**, paralectotype NHMW 1864/0001/0065d; **G**, paralectotype NHMW 1864/0001/0065e (here excluded from *M. australis*); **H**, paralectotype NHMW 1864/0001/0065f. All in aboral (left), oral (middle) and left lateral (right) view, except for C and D in which the lateral view is from the right-hand side. All specimens coated with ammonium chloride.

Notwithstanding the problems with his sample dataset, Laube first defined a range of diagnostic characters for *Monostychia*. These are as follows: body flat, shield-shaped, longer than wide; margin notched opposite each petaloid; apical side of the test slightly arched, less so at the rear, almost flat and steeper at the front falling off in somewhat of a curve; apex lies front of centre; four genital pores with the front pair closer together than the rear pair; petals extend beyond 50% to ambitus and are wide open at front; the ambulacral zone has obliquely

paired pores joined by sharp furrows with the outer pore slit-like, the inner rounded; the interpore zone nearly double the width of one pore zone, is smooth and sharply triangular with barely curved edges, the tip toward the apex; interambulacral fields between the petaloids narrow, becoming broader beneath and somewhat wider than the ambulacral fields at the edges; adapical surface quite flat, in some specimens slightly hollowed toward the centre; peristome central, circular to pentagonal in shape; five simple deep ambulacral furrows run from the peristome to the ambitus – the unpaired ones straight and the paired ones weakly curved away from each other; ambulacral furrows run into the notch in the sides then extend to the apical surface, over the ambulacral field and up to the interpore zone and continue on to disappear at the apex; periproct lies close to, but under the rear edge; and a weak but noticeable elevation or keel runs from the peristome to the periproct.

Laube outlined in detail why *Monostychia* does not belong with the Scutellidae. He also identified several differences between this genus and the closely related *Arachnoides*, including shape, strong combing, position of periproct and number of gonopores. This detailed description provided a range of comparative features with other irregular echinoids.

Mr Robert Etheridge was a palaeontologist with the Geological Survey Museum, London, and spent time at the British Museum (Natural History). He noted (1875) Laube's new species and stated that on examination of material held by the Geological Society, *Clypeaster folium* Duncan (*non* Agassiz) from Mt Gambier should be referred to Laube's species.

Duncan (1877) declined to recognise the genus *Monostychia* and transferred Laube's species to *Arachnoides*, then considered a member of the family Scutellidae. Duncan did not use objective diagnostic features and instead used the general resemblance of the species as is exemplified by his statement, "*Laube distinguishes Arachnoides from his genus because the first has five, and the latter only four genital pores; but this is an error; and he makes the*

position of the periproct of genetic importance in spite of all the other great resemblances, this being an insufficient generic differentiation.” Duncan did, however, accept Etheridge’s reassignment of *Clypeaster folium* to *Arachnoides australis* (Laube). He described two new species, *Arachnoides loveni* from Mordialloc (Fig. 1.3) and *A. elongatus* (Fig. 1.2.D.) from Mt Gambier. The Mordialloc locality probably refers to the upper Miocene Black Rock Formation at Beaumaris on Port Phillip Bay, Victoria (Holdgate and Gallagher 2003). The Gambier Limestone is Oligocene-Miocene, but mostly lowermost Miocene in outcrop (Gallagher and Holdgate 2000).

In 1875 Ralph Tate (Fig. 1.1.D.) was appointed Professor of Natural Science at the University of Adelaide, and shortly after entered the discussion surrounding *Monostychia* and continued to have influence for many years. His principal interests before migrating to Australia were in botany, non-marine conchology and geology. Tate (1877) included *Arachnoides* in a list of genera found at Aldinga, South Australia (Fig. 1.3). Other echinoids included were *Fibularia*, *Laganum*, *Brissus*, *Cardiaster*, *Cidaris*, *Hemiaster*, *Echinobrissus* and *Meoma*. The *Arachnoides* specimen to which he referred is a species yet to be described; however, it is possibly referable to *Monostychia*.

Woods (1876) briefly described, without measurement or illustration, a new species of small, flat echinoid under the name *Micraster etheridgei* from the lower Miocene strata of Table Cape near Wynyard on the north coast of Tasmania (Fig. 1.3). Significantly, Woods has clearly advanced his understanding of nomenclature moving to a series of objective diagnostic features and away from general appearance. However, his description has been incorrectly assigned to Johnston by all subsequent authors, including both Woods and Johnston. This confusion seems to have originated from the fact that Woods (1876, p. 116) began his discussion with the words, “*The following notes on the Echinodermata have been made by Mr Johnston, some of which I have examined and compared the species, and added*

the specific names, with a few verbal alterations.” To compound the confusion of this statement the preceding paper in the Proceedings of the Royal Society of Tasmania was by Johnston (1877). According to the Code (ICZN 1999, Article 50.1.), “*The author of a name or nomenclatural act is the person who first publishes it ... in a way that satisfies the criteria of availability ...*” and since the name *Micraster etheridgei* according to the above cited statement was coined by Woods, who also is the sole author of the paper containing the name, it is he who is to be considered the correct author according to the Code.

Why Woods placed his new species into this genus is not clear. He assigned it to *Micraster* despite the fact that *Micraster* is a spatangoid and not a clypeasteroid. Yet, the preceding description in his paper was of a different form of *Micraster brevistella* (Laube, 1869) described in the same publication that introduced the genus *Monostychia*. In addition, *Monostychia australis* and *Micraster brevistella* are illustrated on the same plate. It is difficult to understand how this new species of *Monostychia* could be mistaken at order level. The currently accepted name of *Micraster brevistella* is *Cyclaster archeri* (Woods, 1867) (McNamara *et al.* 1986) from his own previous description (Woods 1867).

Woods continued his criticism of the validity of the genus *Monostychia* when he stated (1878) “*Monostychia australis is another of the forms closely allied to the existing Arachnoides, of which two other species are described by Professor Duncan. The genus Monostychia must be abandoned, according to the same author, because it is founded on a mistaken appreciation of the reproductive system and on the position of the periproct. With regard to this, I may say that since seeing Professor Laube’s monograph I have examined forty or fifty specimens of Arachnoides placenta from various localities. I find it a very variable species. The position of the periproct is the most uncertain feature. It is very infra-marginal and marginal.*” It is not his reluctance to accept the validity of the new genus name that is of issue since *Arachnoides* and *Monostychia* are closely related. The issue is that in his

analyses he abandons measurable features (such as the number of gonopores and position of the periproct) in favour of qualitative features.

Following the taxonomic interpretations of Duncan and Woods, Etheridge (1878) identified three species: *Arachnoides australis*, *A. elongatus* and *A. loveni*. However, he continued to assign one species, *M. australis*, to the genus *Monostychia*.

McCoy (1879) accepted the new genus *Monostychia* and redescribed *M. australis*. He reassigned the *A. loveni* specimens from Mordialloc as a variety of *M. australis*. McCoy suggested that Duncan's species are varieties of *M. australis*, and did not use *A. elongatus*. In his redescription of *M. australis*, McCoy (1879) emphasised how *Monostychia* differs from *Scutella* in its simple unbranched ambulacral furrows from the peristome, and how it differs from *Arachnoides* in being longer than wide and having the periproct positioned submarginally. One of McCoy's figures (Fig. 1.2.E. herein) appears to be *Monostychia australis*, but the two neighbouring images with the side view appear to be *Monostychia loveni*.

Pomel (1883) provided a brief redescription of the genus *Monostychia* and concluded that there are four species: "*M. australis* Laube, *M. Laubei*, *M. Loveni* and *M. elongatus* (Duncan sub *Arachnoides*)". He transferred *Arachnoides elongatus* to *Monostychia* creating a *nomen imperfectum* due to the mismatch of gender endings. This was remedied later by Gregory (1890). *Monostychia laubei* has no description and hence is unavailable, that is, it is a *nomen nudum* (ICZN 1999: Article 12.1). The genus *Monostychia* was included with the Laganids.

Tate (1885) commented on Sturt's work that "*Most of those of the first three classes [corals, echinoderms and bivalves] are referred to by specific names employed for European tertiary fossils. Of those figured a shrewd guess can be made at the species referred to, but in no case can Captain Sturt's determination [e.g., attribution to *Scutella*] be accepted*". Under

Echinodermata, Tate (1885) listed eight new species identified by Laube (1869). This included *Arachnoides australis* (*Monostychia*). Unfortunately, the Tate collection, now held at the South Australian Museum (SAM), has no *Monostychia*-like specimens except for the type of *Fellaster incisa* and so it is assumed that those upon which Tate commented are lost to science. This is especially so as the material donated by Tate to the Geological Survey of Austria (Bittner 1892), which did contain specimens of *Monostychia* cannot be located anymore at this institution and presumably was destroyed during the second world war (pers. comm. Irene Zorn, Nov. 2014).

Johnston (1887) listed in his “Reference list of the Tertiary fossils of Tasmania” *Micraster etheridgei*, Johnston. This is *Monostychia etheridgei*. Murray (1887) included in his list of Victorian fossils of the “Upper Tertiary” (Pliocene) *Monostychia australis* associated with *Lovenia forbesi*. It is not clear to which species Murray referred. It is possible that Murray misinterpreted the age because the presence of *Lovenia forbesi* suggests Miocene.

Duncan (1887) confirmed his determination of *Clypeaster folium* in Australia for a specimen from Geelong, Victoria (Fig. 1.3.), naming it a variety *C. folium elongata* without saying whether it has any association with his former *Arachnoides elongatus*. Subsequently, in the same paper, he withdrew his previous referral of *Monostychia* to *Arachnoides* and made it a subgenus of *Clypeaster*. He suggested *M. elongatus* is a synonym of *M. australis* yet assigned *M. loveni* as a synonym and a separate species.

Duncan (1887) stated, “*Having had the opportunity of examining very much better specimens than those which I studied formerly, and having seen a fortunate fracture of a specimen of Monostychia australis Laube, I still find myself in the difficulty of not being able to agree with my fellow-workers. My reading of the nature of the internal part of the test does not agree at all with that of my predecessors. But it is necessary that I should state that, had I*

seen the specimen I now allude to, I should not have placed the specimens in relation to Arachnoides. The new specimens have enabled me to make out the distribution of the pores beyond the petaloid parts of the ambulacra, and to describe the nature of the plating of the actinal surface, and the nature of the plates which enter the peristomial margin. It now appears to me that the alliance is with Clypeaster, a notion which, so far as I am concerned, dates back to 1864." Laube (1869) and McCoy (1879) observed no internal structures near the edge of the test. Duncan identified such structures and argued that "*the presence of upright and small needle-shaped pillars become evident, and this Clypeasteroid character became still more pronounced on studying one of the specimens which had been fractured across.*" Therefore, the internal structure became the main diagnostic character that Duncan used to identify *Clypeaster* in the absence of his identification of ambulacral grooves that go all the way from the apical disc to the peristome, that there are four and not five gonopores and other characters that indicate this was not *Clypeaster*. Duncan also noted the fact that, "*The groove is not a simple depression of the test along the median line of the ambulacrum, for close to the peristome there is a slight median ridge, which is also seen on the little projection which each groove makes into the peristome and beyond the rest of its plates. In one specimen, pores are seen on either side of the ridge, and connected with it by indistinct grooves.*" He argued that in clypeasteroids it was common for young specimens to show diversity of shape and that this might be one reason why a separate genus had been erected. However, there is no evidence to suggest that the specimens Duncan examined were juvenile. This may be a similar error to that of Laube in his original description. Nevertheless, Duncan (1887) was the first reference to the use of plates as a diagnostic tool and to focus on the peristomial point at the entrance of the food groove into the peristome.

Johnston (1888) reassigned *Micraster etheridgei* to *Monostychia*. Despite an apparent acceptance of the genus, he listed the type species of *Monostychia* as *Arachnoides australis* Laube (p. 168).

Tate (1888), in his “Census of the Older Tertiary fauna of Australia”, listed two species of *Clypeaster* and three species of *Arachnoides*. In this list it is possible that his *Arachnoides* taxa are *Monostychia*, and he also recognised *M. australis* Laube, 1869, *M. loveni* Duncan, 1877, and *M. elongatus* Duncan, 1877. The deletion of *M. etheridgei* (Woods, 1877) was not explained in this work.

Duncan (1889) looked at the revised classification system of cosmopolitan genera. Similar to Duncan (1887), he treated *Monostychia* as a subgenus of *Clypeaster*. He redescribed the subgenus *Monostychia* as having: “*Apical system small; madreporite button-shaped; four genital pores; margin notched when young decidedly, and the peristomial ambulacral grooves straight and continued abactinally*”. Again there was a reference to juvenile specimens that commented on a notched margin; however, there is no evidence his specimens were juvenile. Laube (1869), who made a similar assumption, came to the opposite conclusion – that the margin lacked a notch in juveniles.

Gregory (1890) described a collection of echinoids from the late lower Miocene Morgan Limestone, now Glenforslan Formation (Gallagher and Gourley 2007), and identified *Clypeaster (Monostychia) australis* and *C. australis* var. *elongata* (the correction of the *nomen imperfectum*). *Monostychia* was seen as a subgenus. Gregory stated that the specimens came from “*the uppermost beds of the South Australian...series*” in the Murray River cliffs at Morgan, South Australia (Fig. 1.3.): from this, one might conclude that the material derives from the Glenforslan Formation. However, he also claimed that one specimen was clearly that of *C. australis* var. *elongata*.

Tate (1891) provided a bibliography and revised list of echinoids, and included an Eocene *Monostychia*, accepting it as a separate genus in the absence of *Arachnoides* even though he had previously commented on its discovery. He also stated that, “*it will serve no useful purpose to retain Mr. Johnston’s species, Monostychia etheridgei.*”

Dennant (1891a) listed *Arachnoides* sp. nov. from the ‘Miocene’ strata at Jemmy’s Point, Lakes Entrance, Victoria (Fig. 1.3.). A few months later Dennant (1891b) listed *Monostychia australis* from the Mitchell River “*a few miles higher up the stream*” than the fossils collected at Jemmy’s Point and that the age was more likely Eocene. Although it is likely that in both cases *Arachnoides* and *Monostychia* refer to the same species, it is likely to be *Fellaster incisa* (Tate, 1893). This is because the strata are more likely to be from the Pliocene Jemmy’s Point Formation since Eocene marine strata do not crop out in the region (Holdgate and Gallagher 2003).

Gregory (1892) transferred *Sismondia marginalis* and *S. plana* to *Monostychia*. Clark and Twitchell (1915) rejected this and listed *Monostychia marginalis* in synonymy with *Scutella ? conradi* and *Monostychia plana* in synonymy with *Sismondia ? plana*.

Pritchard (1892a) listed *Monostychia deltoidalis* Tate, m.s., from the Yorke Peninsula in South Australia (Fig. 1.3.). In another paper of the same year he again listed *Monostychia deltoidalis* Tate, along with *Monostychia patellus* Tate (Pritchard 1892b). These species erected by Tate are likely to be those from Wool Bay, north of Edithburgh (Fig. 1.3.), and are unavailable *nomina nuda* because these names were published without description or illustration.

Bittner (1892) described and figured *Monostychia australis* and its variety *elongata* (Fig. 1.2.F.), probably from the Glenforslan Formation (Gallagher and Gourley 2007) of the River Murray. For this he used six specimens of *M. australis* and four specimens of *M. elongata*.

The latter seemed to differ from *M. australis* more than *M. loveni* (Duncan), although these differences were not specified, and Bittner again combined *M. loveni* with *M. australis*. Since no illustration of the narrower form existed, Bittner considered that one such well-preserved specimen should be added (illustrated in Pl. 2, fig. 9). It is noteworthy that Bittner's diagram (Fig. 1.2.F.) shows four interambulacral plates in the paired interambulacra and a periproct that is bounded first by plates 3a/3b (using Loven's system) in interambulacrum 5.

Bittner (1892) commented that Laube suggested *Arachnoides* as the most closely related genus, where the periproct is situated supramarginally and that Duncan, in 1877, suggested the Australian form be placed in *Arachnoides*. However, in 1887, Duncan subsequently created *Monostychia* as a subgenus of *Clypeaster*. He also noted that Duncan later redescribed *M. australis* more precisely and gave his reasons for making it a subgenus of *Clypeaster*. Bittner provided a detailed commentary on these positions and determined *Monostychia* should stand as a genus.

Tate (1892) reinstated Johnston's *Monostychia etheridgei* on the basis of a single specimen collected from Table Cape, near Wynyard, Tasmania (Fig. 1.3.). In doing so, he provided a further description of the species, observing that it is only half the size of full grown *Monostychia australis* from the River Murray, which usually reach 45 mm. Hall and Pritchard (1892) registered *Monostychia australis* and *Clypeaster* as being present in the Cainozoic of the Geelong area (Fig. 3).

Tate (1893) said of the genus *Monostychia*, "*Laube's genus should be restored; whilst Arachnoides can be still retained, as a representative of this more modern genus has occurred in the Miocene of the Gippsland Lakes, which I describe as follows.*" He then described a new species *Arachnoides incisa*, from Pliocene strata at Red Bluff near Lakes

Entrance, Victoria (Fig. 1.3.). *Arachnoides incisa* was later reassigned to *Fellaster* by Foster & Philip (1980).

Mulder (1893) reported on a new species, *Monostychia woodsianna*, from Airey's Inlet in Victoria (Fig. 1.3.). Lacking a description or illustration, according to the Code, this species is a *nomen nudum*.

Tate (1895) suggested *Arachnoides conica* Hutton, 1873 was a *Monostychia*, probably *M. australis* var. *loveni*, reducing *M. loveni* to a variety of *M. australis*. Hutton (1873) described *A. conica*, but without illustration. Its description was similar to *A. zealandae* and *F. incisa*. No mention was made of the position of the periproct, but its raised ambulacral areas and combing, along with its Pleistocene age and presence in New Zealand, suggest it is possibly not *Monostychia*.

Kitson (1902) listed *Monostychia australis* among the echinoids at Flinders south of Mordialloc, Victoria (Fig. 1.3.). Dennant and Clark (1903) reported *Monostychia australis* co-occurs with *Clypeaster gippslandicus*, *Eupatagus murrayensis* and “*Echinolampus*” [sic] on the Lower Mitchell River near Lakes Entrance (Fig. 1.3.). Howchin (1912), in the absence of a description of their diagnostic features, identified *Monostychia australis* in Cainozoic deposits on the Light River near Hamley Bridge north of Adelaide, South Australia (Fig. 1.3.), and in the presence of *Lovenia forbesi*. Gregory (1914) noted *Monostychia australis* co-occurs with *Lovenia forbesi* in Australian marine Kainzoic [sic] deposits. Chapman (1916) referred to “*Arachnoides (Monostychia) australis*” from a bore and “*Arachnoides (Monostychia) cf. australis*” from bores in the Victorian Mallee (Fig. 1.3.), linked with *Lovenia forbesi*.

Lambert and Thiéry (1914) recognised the genus *Monostychia* but made *M. loveni* and *M. elongatus* synonyms of *M. australis*. Lambert and Thiéry (1925) accepted *M. etheridgei* as a

valid species and referred it to the genus *Monostychia*, and also *Scutella mississippiensis* [sic] Twitchell, Clark & Twitchell, (1915) (later made the type species of *Protoscutella*).

Howchin (1918) listed *Monostychia* as a genus found in the sedimentary rocks at Kingscote, Kangaroo Island, South Australia (Fig. 1.3.). Later (1928), he commented on its presence in the Janjukian beds of South Australia and stated that “*Monostychia is thin and discoidal with its under and upper surfaces almost parallel. It is exclusively Australian in its occurrence, and is closely related to Arachnoides; there are two species, of which M. australis, Laube, is the more important, and is very common in some localities; occurs in the Murray cliffs, also at Mt Gambier and in many places in Victoria.*” Howchin also documented *M. australis* in lower Pliocene (Kalinman) strata with *Echinus* (*Psammechinus*) *woodsii* Laube 1869, *Clypeaster gippslandicus* McCoy 1879, and *Lovenia forbesi* Woods 1862, without specifying a location. However, he did comment that *Fellaster incisa* is present in similar-aged strata in Victoria. In this work, there is subjective and superficial reference to shape in the absence of reference to key diagnostic features.

Chapman (1926) listed *Arachnoides (Monostychia) australis* along with *A. australis* var. *elongata* Duncan among the echinoids in the Orbost region north of Lakes Entrance, Victoria (Fig. 1.3.). Colliver (1937) noted the presence of *Monostychia australis* along with *Lovenia forbesi* and *Clypeaster gippslandicus* at or near Mordialloc, Victoria (Fig. 1.3.). The identification of *L. forbesi* is likely an error with *L. woodsii* being the species present. Crespin (1943) recorded *Arachnoides (Monostychia) australis* from Le Grand’s quarry north of Lakes Entrance (Fig. 1.3.).

The age of orderliness

In the third ‘age’, the age of orderliness, the argument moved from one characterised by whether or not *Monostychia* can be justified as a separate genus and by what criteria, to

determining where *Monostychia* belongs within the broader systematic hierarchy. The focus transferred away from the specimens and species to the genus, family and higher levels of classification. It was an era of understanding phylogenetic relationships. With the mounting number of collected specimens, derivation of advanced levels of knowledge were possible, resulting in publication of major treatises emphasising the story of higher levels of classification with less and less emphasis on the individual specimen or species. There was a move away from the geographical quaintness of the new worlds and a focus on taxonomy. Systematics had integrated the theories of Darwin and defined phylogenetic relationships were becoming the norm. The age begins with the influential work of Clark (1946), incorporates the monograph by Mortensen (1948) and closes with the ‘Treatise of Invertebrate Paleontology’ by Durham *et al.* (1966).

Clark (1946) accepted the conclusions of Lambert and Thiéry (1914). In the hierarchy Order Exocycloida, suborder Clypeasterina, family Clypeastridae, he identified six genera; *Anomalanthus*, *Clypeaster*, *Monostychia*, *Arachnoides*, *Hesperaster* and *Ammotrophus*, and provided a key. Within the key *Monostychia* was characterised as having a test that was more or less discoidal or flat with four gonopores. In addition, the test was longer than wide, the petals small, sharply defined, slightly narrowed and rounded distally, and the periproct inframarginal. In comparison, the same key characterised *Arachnoides* as having a periproct that is marginal or supramarginal. Clark recognised *Monostychia australis* and commented, “*The fossils on which this genus is based seem to be rather common, and show enough variety of structure to make it doubtful how many species there are and in how many genera they belong*”. He recognised the confusion and difference of opinion of Duncan, McCoy, Johnston and Tate, but concluded “*there is no reason to question Laube’s account or figures given in 1869*”. Clark concluded that *Monostychia* had only two species (*M. australis* and *M. etheridgei*), “*so diverse in form that several varietal names, already proposed, might be used*

if only the forms showed sufficient constancy to permit definition". He provided a key to those two species.

Mortensen (1948) introduced the family Arachnoididae into the suborder Clypeasterina and confirmed *Monostychia* as one of three genera in the family with *Arachnoides* and *Ammotrophus*. He was critical of Pomel (1883) for including it in the laganids stating, "*with its deep ambulacral furrows continuing to the apical system and its open petals, [it]differs so widely from typical Laganids that it is out of the question that it could have anything to do with Laganids. Its double auricles and the presence of "combed" areas prove that it belongs to Arachnoidids*". Mortensen did not attempt to clarify the validity of the various species beyond suggesting that *M. loveni* and *M. elongata* of Duncan "may only be varieties of *australis*", and that the form *M. etheridgei* was unknown to him. Mortensen was also critical of Lambert & Thiéry (1914) for suggesting the inclusion into *Monostychia* of *Scutella mississippiensis* based on the five gonopores when the lack of resemblance should have been enough to prevent such a referral. Had this conclusion been accepted, the result would have extended *Monostychia* as a genus beyond Australia and into the Eocene of North America.

Mortensen's (1948) diagrams did not enhance taxonomic resolution. He placed *Monostychia loveni* as a variety of *M. australis*. His description of 'combed' areas in *M. loveni* (and not *M. australis*) specimens, led him to suggest that it was more closely related to *Ammotrophus* than *Arachnoides*. His diagrams of *M. australis* var. *elongata* copied from Bittner (1892) repeated the presentation of four interambulacral plates and a periproct that is bounded first by plates 3a/3b in interambulacrum 5.

Piveteau (1953) treated *Monostychia* and *Arachnoides* as the only two members of Arachnoidides. That family, together with 'Clypeastrides' made up the order Clypeastroidea

in his paper. His description of *Monostychia* was brief, stating that it has short petals, a lobed contour and a sub-central mouth.

Fell (1953) used the *nom. null.* spelling *Monostichia* when trying to explain the origins of the echinoderm fauna. Those origins, Fell suggested, are Australasian and although the parentage of *Monostychia* is unknown, *Arachnoides* is from *Monostychia* stock.

Durham (1955) included the family Arachnoididae in the suborder Clypeasterina and he recognised several subfamilies including the new Ammotrophinae. It is here that Durham placed *Monostychia* with the genera *Ammotrophus* and added the new genus *Scutellinoides*. He stated that Arachnoididae was easily recognisable because of its striking ambulacral combed areas both in and beyond the petals, although in *Monostychia* he acknowledged that “*only occasionally are the secondary tube feet pores and the tubercles as perfectly aligned as they are in the younger species. In the Miocene species, the most distinct areas of recognized alignment are on the oral surface just inside the ambitus*”. Such comments were probably drawn from observations of *M. loveni* and to a lesser extent the Mannum Formation *Monostychia*-like form, which remains of questionable affiliation. Durham also suggested that *Fellaster incisa* could be a *Monostychia*.

Durham’s (1955) figure (Fig. 1.2.G.) showed six interambulacral plates, compared to Bittner’s four. In interambulacrum 5, the periproct was bounded first by plates 3a/3b. Of *Monostychia*, Durham defined a “*test somewhat similar to that of Ammotrophus, either polygonal or oblong; ambitus with prominent ambulacral indentations; apical system slightly elevated; ambulacral food grooves extending to apical system, with adjacent areas of test also depressed; no groove from periproct to peristome; combed areas present on ambulacral plates, relatively small and often poorly defined; petals short and open; periproct immediately submarginal; only one pair of ambulacral plates meeting across*

interambulacral suture; two post-basicoronal plates in each interambulacral column on oral surface; periproct between second pair of post-basicoronal interambulacral plates; basicoronal interambulacral plates about same size as adjacent ambulacral plates; internal supports concentric in marginal areas and radial toward centre of test as in Ammotrophus". Durham focused on plate architecture as diagnostic at genus level.

Ludbrook (1958) listed *Monostychia australis* from both the Gambier Limestone and the Mannum Formation. In both strata it is linked to *Eupatagus murrayensis* and *Lovenia forbesi*. Ludbrook (1961) listed *M. australis* from both the upper and lower members of the Mannum Formation. For the Morgan Limestone she indicated in her list the absence of *M. australis* in the lower reaches of the Murray River near Mannum but included it in the area around Morgan (Fig. 1.3.). She included a plate of a deformed example from the Morgan Limestone.

Durham *et al.* (1966) continued this classification with three genera in the subfamily Ammotrophinae: *Ammotrophus*, *Monostychia* and *Scutellinoides*. The authors separated the subfamilies using four main characters: position of periproct (supramarginal in Arachnoidinae and "usually" submarginal in Ammotrophinae); combed areas (large in Arachnoidinae and small in Ammotrophinae); internal supports (in outer margin only in Arachnoidinae, and marginal and around peristome in Ammotrophinae, where they are also concentric peripherally); and petals raised above interambulacral in Arachnoidinae but no comment in Ammotrophinae. *Monostychia* was said to have two coronal interambulacral plates on the oral surface. Also, the periproct is "*just submarginal, between 2nd pair of coronal plates*". Durham *et al.* provided a photograph and line drawing. The photographed specimen appears an elongate form whereas the line drawing, which is a reproduction of the drawing by Durham (1955), showing six interambulacral plates, is more the typical *M. australis*.

Kenley (1967) referred to *Monostychia* cf. *australis* and *Lovenia* from the Black Rock Sandstone near Mordialloc, Victoria (Fig. 1.3.). Singleton (1968) also commented on the presence of *M. australis* with *L. forbesi* in the upper Oligocene Point Addis Limestone (McLaren *et al.* 2009) at Point Addis, Victoria (Fig. 1.3.). The Point Addis Limestone was noted as passing into the Jan Juc Marl in a “*lateral change of facies*” and the echinoid fauna changes: *Monostychia* becomes extinct, *L. forbesi* persists and *Eupatagus murrayensis* occurs for the first time. In the Murray Cliffs *L. forbesi* and *E. murrayensis* occur in the Mannum Formation with the Mannum *Monostychia*-like form, although it remains unlikely this is the species mentioned here.

The age of research

The final ‘age’, the age of research, began with a move away from the broader treatises and their way of viewing the world, and returned to a more detailed ‘collecting’ phase where a wider range of undescribed species that might impact upon the systematics is being uncovered. Combined with this local increase in understanding, there is a return to a focus on diagnostic features largely driven by a cladistic systematics approach from abroad, concentrating on the lower levels of classification, particularly genus and subfamily. There is a ‘sense of science’, and a preparedness to develop and use new instrumentation from other fields to provide utility to the specimens in hand. It was a new age when the theory of plate tectonics was starting to impact on the meaning of information, where exploration for commercial resources, such as oil and gas was driving fossil analyses, and where the specimens themselves were enhancing understanding of the world in which we live, not simply taxonomy. Those worlds include a broader history of life on our planet and an understanding of climate change, as well as trying to understand our place in the cosmos.

Philip (1970) commented on the presence of two species of *Monostychia* from the Eucla Basin, north of Eucla in Western Australia (Fig. 1.3.). One specimen he noted as *Monostychia* cf. *australis* from the lower Miocene Colville Sandstone (Lowry 1970) and included a photograph. The other he simply suggested is a new species from the lower Miocene Nullarbor Limestone (Lowry 1970). Philip and Foster (1970) commented on the occurrence of “*Monostychia*” *loveni* in the late Miocene Cheltenhamian (Holdgate and Gallagher 2003) of southeast Australia. Their use of quotes implies a questionable level of acceptance that *M. loveni* belongs to *Monostychia*. In their list, they did not comment upon the occurrence of *Monostychia australis* or any other *Monostychia*-like forms. Quilty (1972) noted the presence of *M. australis* with *Scutellinoides patellus* at Cape Grim in Tasmania (Fig. 1.3.). Playford *et al.* (1975) observed *M. australis* in the Colville Sandstone (Lowry 1970) of Western Australia.

Milnes *et al.* (1983) reported *M. australis* in the Oligocene strata of Kangaroo Island (Fig. 1.3.). They suggested that the Eocene age of previous records of echinoids from the Kingscote Limestone should be treated with caution due to the presence of unconformities.

Sadler *et al.* (1983) pictured both *M. australis* and the Mannum Formation *Monostychia*-like form. Their description characterised *Monostychia* as having: four gonopores; a size and shape that is variable, but the shape being roundly pentagonal; thin, flat below and conical on top; the apical system is centrally placed on the highest point; the peristome is centrally placed beneath; and the periproct is submarginal.

Pledge (1985) recorded *Monostychia* sp. indet., with *Lovenia woodsi* from the Sunlands fossil assemblage, lower Pliocene Loxton Sands near Loxton, South Australia (Fig. 1.3.). Holmes (1987) provided line drawings of *M. australis* in a brief discussion of Laube’s

contribution to echinoid work in Australia and separated the *M. australis* form from the Mannum *Monostychia*-like form without names or descriptions.

Mooi (1989) did not attempt to “*follow any particular family level of classification*” arguing the clypeasteroid group is in need of phylogenetic revision. He accepted the Suborder Clypeasterina A. Agassiz, 1872, as the appropriate place for *Monostychia*. In his key to the genera, Mooi identified the important characters of *Monostychia* as: having two enclosed sphaeridia in each ambulacrum near the peristome; a submarginal periproct; food grooves continuing from the peristome around the ambitus and onto the aboral surface toward the apical system; combing in the ambulacra adjacent to the food grooves and provided a diagram in support; four gonopores; and six plates in each paired interambulacrum on the oral surface (Fig 1.2.H.).

Holmes (1989) discussed some of the earlier issues about the work of Woods, Duncan, McCoy and Etheridge in relation to the lack of consistent discrimination between the taxa *Clypeaster*, *Scutella* and *Monostychia*, and emphasised the difficulties arising from poor geographical data collection. White (1999) illustrated an unnamed “*sand dollar echinoderm from South Australia*” and suggested it is of Jurassic age. This is clearly an error; the specimen is most likely *Monostychia australis* and the age Miocene. The error appears to be a misplacement of a photo in a manuscript.

Torres *et al.* (2002) examined the use of the mathematics of a eutactic star to define a morphospace for irregular echinoids and as a potential tool in taxonomy. *Monostychia australis* was analysed with other echinoids sourced from the Natural History Museum London (NHML). It is likely that this sample of *Monostychia* extended beyond *M. australis* and into related taxa. As a result, until it can be established whether the Mannum Formation form belongs to *Monostychia*, the conclusions may not be valid. This work is an attempt to

bring algebraic mathematics to solve taxonomic problems of fossil echinoids. However, it assumes a two-dimensional test, which may lead to the results having less relevance as height increases in proportion to the other dimensions. In addition, as it was a preliminary work, it will need to be established whether in a given species, and then in a given genus, the variability of features measured remains consistent.

Holmes (2004) listed two undescribed species of *Monostychia* from Kingscote, Kangaroo Island (Fig. 1.3.), and described *Rhynchopygus janchrisorum*, a new species of cassiduloid. Holmes *et al.* (2005) noted *Monostychia australis* and another undescribed species of *Monostychia* with the spatangoids *Murraypneustes biannulatus* and *Spatagobrissus dermodyorum* in the Glenforslan Formation in the River Murray Cliffs.

Kroh & Smith (2010) presented a cladistic phylogenetic analysis of echinoids. This work separated various features so they can be computationally analysed. These features are primarily objective diagnostics. Included in this key are features such as test shape, plate architecture, buttressing, position and organisation of periproct, petal arrangement, food grooves, tuberculation and sphaeridia. As their study included extant species it also included features relating to feeding apparatus and external appendages. Although these may be important across the group, unfortunately, they rarely fossilise. Using their key derived from extant and fossil characters, Kroh & Smith placed *Monostychia* in the subfamily Ammotrophinae from the early Miocene.

Mihaljevic *et al.* (2011) included *Monostychia* with *Scutellinoides*, *Philipaster*, *Arachnoides*, *Ammotrophus* and *Fellaster* in the family Arachnoididae. No details of the *Monostychia* material are provided, hence it is uncertain which of the various forms in the genus were included.

This review has identified the need for a new taxonomic key to identify irregular fossil echinoids that is based upon observable and consistent morphological features. The broad group of specimens currently labelled as *Monostychia* has a variety of distinct morphologies, some of which have been interpreted as species and others that may be so construed, although other researchers to date have deduced some of those morphologies as intraspecific variation (Duncan 1877, Tate 1877, Woods 1876, Bittner 1892). When it comes to fossils where a reproductive community or species is impossible to confirm, it is commonly a problem to differentiate between intraspecific variation resulting from ontological change or ecophenotypic plasticity and interspecific variation that allows delimitation of different species. However, before embarking on a major morphometric study of *Monostychia*-related taxa it is necessary to establish a firm foundation for the breadth of species and genera that are represented in the fossil record and this needs to begin with a revision of *Monostychia* and its currently accepted species.

A summary of the taxonomic treatment of *Monostychia* is presented in Tables 1.1.-4.

Reference	Taxonomic treatment of <i>Monostychia</i> and/or <i>M. australis</i>	Comment	<i>Monostychia</i> sp. locality
Sturt, 1932	Named as <i>Scutella</i> sp	Collection and publication of the first fossil echinoid from Australia	River Murray cliffs, South Australia
Forbes, 1852	Maintained as <i>Scutella</i> sp	Working from the UK, identified echinoderm fossils sent from SE Australia, generally without the aid of provenance and stratigraphy data	SE Australia, presumably the lower Murray River in South Australia
Woods, 1860	Named what is possibly <i>M. australis</i> (Etheridge, 1875) as <i>Clypeaster</i> . As the specimen was from south-eastern South Australia, it may be the <i>Monostychia elongata</i> form rather than <i>M. australis</i>	Collection of specimens over a large range of southern Australia	SE Australia and western Victoria
Duncan, 1864	Named what was most likely one of the <i>Monostychia</i> -like	First to use a diagnostic feature (the marginal periproct) to separate specimens sent to the UK	River Murray Cliffs, South Australia

	fossils as <i>Clypeaster folium</i>		
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Table 1.1. Age of Exploration.

Reference	Taxonomic treatment of <i>Monostychia</i> and/or <i>M. australis</i>	Comment	<i>Monostychia</i> sp. locality
Laube, 1869	Created the type species <i>M. australis</i>	Erected a new genus (1869), <i>Monostychia</i> , and defined diagnostic characters	River Murray cliffs, South Australia
Duncan, 1877	Transferred Laube's species to <i>Arachnoides</i> , (then a member of the family Scutellidae)	Declined to recognise the genus <i>Monostychia</i>	
Etheridge, 1878	<i>M. australis</i>	Determined that Duncan's <i>Clypeaster folium</i> in the British Geological Society collection was <i>M. australia</i> ; used the genus <i>Monostychia</i> in his own identifications	
Woods, 1878		Highlighted the variability within <i>Arachnoides</i> and suggested the possibility that " <i>Monostychia</i> " is a variant of <i>Arachnoides</i>	
McCoy, 1879	<i>M. australis</i>	Redescribed <i>M. australis</i> and provided characteristics to distinguish it from <i>Arachnoides</i> and <i>Scutella</i>	Mordialloc, Victoria
Pomel, 1883	<i>M. australis</i>	Identified four species within <i>Monostychia</i> : <i>M. australis</i> Laube, <i>M. Laubei</i> , <i>M. Loveni</i> and <i>M. elongatus</i> (Duncan sub <i>Arachnoides</i>)	
Tate, 1885	Identified specimens as <i>Arachnoides australis</i> (<i>Monostychia</i>)	Collected and published in South Australia over an extended period but little remains in world collections of the echinoderm specimens	Aldinga, South Australia
Johnston, 1886	<i>Monostychia etheridgei</i> , Woods listed as <i>Micraster etheridgei</i> , Johnston	Published a reference list of the Cainozoic fossils of Tasmania.	Tasmania
Murray, 1887	<i>M. australis</i>	Published a list of Upper Cainozoic fossils of Victoria.	Victoria
Duncan, 1887	<i>Monostychia</i> relegated to subgenus level under <i>Clypeaster</i> .	First reference to the use of plates as a diagnostic tool along with the peristomial point at the entrance of the food groove into the peristome	Geelong, Victoria
Johnston, 1888	Listed the type species of <i>Monostychia</i> as <i>Arachnoides australis</i> Laube	Reassigned <i>Micraster etheridgei</i> to <i>Monostychia</i>	
Tate, 1888	Recognised <i>M. australis</i> Laube, 1869, <i>M. loveni</i> Duncan, 1877, and <i>M. elongatus</i> Duncan, 1877	Published the <i>Census of the Older Tertiary fauna of Australia</i>	
Duncan, 1889		Redescribed the <i>Clypeaster</i> subgenus <i>Monostychia</i>	
Gregory, 1890	<i>Clypeaster</i> (<i>Monostychia</i>) <i>australis</i>	Late early Miocene echinoids described	Morgan, South Australia

	and the variety <i>C. australis</i> var. <i>elongate</i>		
Tate, 1891	Raised <i>Monostychia</i> to genus level		
Dennant, 1891a., 1891b	Listed <i>Arachnoides</i> sp. nov. and <i>M. australis</i> (potentially both <i>Fellaster incisa</i>)	Collected along the Mitchell River, potentially misidentifying strata and genera	Lakes Entrance, Victoria
Gregory, 1892		Transferred <i>Sismondia marginalis</i> and <i>S. plana</i> into the genus <i>Monostychia</i>	
Pritchard, 1892a	<i>Monostychia deltoidalis</i> Tate, m.s.	Catalogued South Australian Cainozoic species	Yorke Peninsula, SA
Pritchard 1892b	<i>Monostychia deltoidalis</i> Tate <i>Monostychia patellus</i> Tate	These species of Tate (Fig. 3) are unavailable <i>nomina nuda</i> since the names were published without description or illustration	Wool Bay, north of Edithburgh, South Australia
Bittner. 1892	Determined <i>Monostychia</i> should stand as a genus	Described and figured <i>Monostychia australis</i> and its variety <i>elongata</i> (Fig. 2F).	Glenforslan Formation, River Murray, South Australia
Tate, 1892	Reinstated Johnston's <i>Monostychia etheridgei</i> on the basis of a single specimen	Described <i>Monostychia etheridgei</i> , providing comparative notes between it and <i>M. australis</i>	Table Cape, near Wynyard, Tasmania (Fig. 3)
Hall & Pritchard, 1892	List both <i>Monstychia</i> and <i>Clypeaster</i>	Collected Victorian Cainozoic echnoids	Geelong, Victoria
Tate, 1893	<i>Monstychia</i>	Endorsed restoration of Laube's genus <i>Monstychia</i> , recognising it as distinguishable from <i>Arachnoides</i> , of which he described <i>Arachnoides incisa</i> sp. nov.	Red Bluff near Lakes Entrance, Victoria, Pliocene strata (Fig. 3)
Mulder, 1893	<i>Monstychia woodsiana</i> which is a <i>nomen nudum</i>	Described a new Cainozoic echinoid species but without illustration or description	Aireys Inlet, Victoria (Fig. 3)
Tate, 1895		Suggested <i>Arachnoides conica</i> Hutton, 1873 was a <i>Monostychia</i> , probably <i>M. australis</i> var. <i>loveni</i> reducing <i>M. loveni</i> to a variety of <i>M. australis</i> .	
Kitson, 1902	<i>Monostychia australis</i>		Flinders south of Mordialloc, Victoria(Fig. 3).
Dennant and Clark, 1903	<i>M. australis</i>	Co-occurs with <i>Clypeaster gippslandicus</i> , <i>Eupatagus murrayensis</i> and " <i>Echinolampus</i> " [sic!].	Lower Mitchell River near Lakes Entrance, Victoria (Fig. 3).
Howchin, 1912	<i>M. australis</i>	In the presence of <i>Lovenia forbesii</i> .	Light River near Hamley Bridge north of Adelaide, South Australia (Fig. 3) in a Cainozoic outcrop
Gregory, 1914	<i>M. australis</i>	Co-occurs with <i>Lovenia forbesii</i>	Australian marine Kainzoic [sic!] deposits.

Lambert & Thiéry, 1914	<i>Monostychia loveni</i> and <i>elongatus</i> in synonymy with Laube's <i>M. australis</i> <i>M. etheridgei</i>	In the presence of <i>Lovenia forbesii</i>	
Howchin, 1918	<i>Monostychia australis</i>		Kingscote, Kangaroo Island, South Australia (Fig. 3)
Clark & Twitchell, 1915	<i>Monostychia marginalis</i> listed in synonymy with <i>Scutella ? conradi</i> and <i>Monostychia plana</i> in synonymy with <i>Sismondia ? plana</i>	Catalogued Mesozoic and Caenozoic echinodermata of the US	
Chapman, 1916	<i>Arachnoides (Monostychia) australis</i> Laube and var. <i>elongata</i> Duncan <i>Arachnoides (Monostychia) australis</i> <i>Arachnoides (Monostychia) cf. australis</i>	Linked with <i>Lovenia forbesii</i>	Orbost region north of Lakes Entrance, Victoria (Fig. 3) A bore, Victoria Bores in the Victorian Mallee (Fig. 3)
Howchin, 1928	<i>Monostychia</i>	Describes <i>Monostychia</i> as exclusively Australian, thin and discoidal with its under and upper surfaces almost parallel. <i>M. australis</i> , Laube is listed as very common in some localities, occurring in the Murray cliffs, Mt Gambier, many places in Victoria and the lower Pliocene (Kallimnan) strata.	Janjukian beds of South Australia
Colliver, 1937	<i>Monostychia australis</i> Laube	Associated with <i>Lovenia forbesii</i> and <i>Clypeaster gippslandicus</i> at near. The identification of <i>L. forbesii</i> is likely an error with <i>L. woodsii</i> being the species present.	Mordialloc, Victoria (Fig. 3)
Crespin, 1943	<i>Arachnoides (Monostychia) australis</i>		Le Grand's quarry north of Lakes Entrance, Victoria (Fig. 3)

Table 1.2. Age of Collection.

Reference	Taxonomic treatment of <i>Monostychia</i> and/or <i>M. australis</i>	Comment	<i>Monostychia</i> sp. locality
Clark, 1946	<i>Monostychia australis</i> Laube	<i>Monostychia</i> one of six genera keyed from Clypeastridae by recognising a more or less discoidal or flat test longer than wide, four gonopores petals small, sharply defined, slightly narrowed and rounded distally and the periproct inframarginal. Key lists only two species, (<i>australis</i> and <i>etheridgei</i>).	

Mortensen, 1948		Introduced Arachnoididae into the Suborder Clypeasterina and confirmed <i>Monostychia</i> as one of three genera in the Family with <i>Arachnoides</i> and <i>Ammotrophus</i> . Suggested <i>loveni</i> and <i>elongata</i> of Duncan may only be varieties of <i>australis</i> and that the form <i>etheridgei</i> Woods was unknown to him.	
Piveteau, 1953		Treated <i>Monostychia</i> and <i>Arachnoides</i> as the only two members of the family Arachnoidides. <i>Monostychia</i> diagnostics were short petals, a lobed contour and a sub-central mouth.	
Fell, 1953		Used the nom. null. spelling <i>Monostichia</i> when defining echinoderm fauna origins as Australasian. Claimed <i>Arachnoides</i> is from <i>Monostychia</i> stock and parentage of <i>Monostychia</i> was unknown.	
Durham, 1955		Using plate architecture as a diagnostic at genus level, placed <i>Monostychia</i> , <i>Ammotrophus</i> and <i>Scutellinoides</i> in the new subfamily Ammotrophinae under family Arachnoididae. Suggested <i>Fellaster incisa</i> could be a <i>Monostychia</i> .	
Ludbrook, 1958	<i>Monostychia australis</i>	Linked to <i>Eupatagus murrayensis</i> and <i>Lovenia forbesii</i> .	Gambier Limestone and the Mannum Formation
Ludbrook, 1961	<i>Monostychia australis</i>		upper and lower members of the Mannum Formation and Morgan, South Australia(Fig. 3).
Durham <i>et al.</i> , 1966		Placed three genera in the subfamily Ammotrophinae: <i>Ammotrophus</i> , <i>Monostychia</i> and <i>Scutellinoides</i> using four main characters: position of periproct; combed areas; internal supports; and petal elevation.	
Kenley, 1967	<i>Monostychia</i> cf. <i>australis</i>	With <i>Lovenia</i>	Black Rock Sandstone near Mordialloc, Victoria. (Fig. 3)
Singleton, 1968	<i>M. australis</i>	Located with <i>L. forbesii</i> .	Point Addis, Victoria (Fig. 3), upper Oligocene Point Addis Limestone (McLaren <i>et al.</i> 2009)

Table 1.3. Age of Orderliness.

Reference	Taxonomic treatment of <i>Monostychia</i> and/or <i>M. australis</i>	Comment	<i>Monostychia</i> sp. locality
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Philip, 1970	<i>Monostychia</i> cf. <i>australis</i> and a new <i>Monostychia</i> species		Eucla, Western Australia (Fig. 3) from the lower Miocene Colville Sandstone and Nullarbor Limestone respectively (Lowry 1970)
Philip & Foster, 1970	" <i>Monostychia</i> " <i>loveni</i>	The use of quotes and lack of further reference to <i>Monostychia australis</i> or any other <i>Monostychia</i> -like fauna suggests a low confidence that <i>M. loveni</i> is of the genus <i>Monostychia</i> .	Southeast Australia in the late Miocene Cheltenhamian (Holdgate and Gallagher 2003)
Quilty, 1972	<i>M. australis</i>		Cape Grim, Tasmania (Fig. 3)
Playford <i>et al.</i> , 1975	<i>M. australis</i>		Colville Sandstone (Lowry 1970), Western Australia
Milnes <i>et al.</i> , 1983	<i>M. australis</i>	Suggested the Eocene age of previous records of echinoids from the Kingscote Limestone should be treated with caution due to the presence of unconformities.	Oligocene strata, Kangaroo Island, South Australia (Fig. 3)
Sadler <i>et al.</i> , 1983	<i>M. australis</i> and the Mannum Formation <i>Monostychia</i> -like form	<i>Monostychia</i> described as having: 4 gonopores, a size and shape that is variable but the shape being roundly pentagonal, thin, flat below and conical on top; the apical system is centrally placed on the highest point; the peristome is centrally placed beneath; and the periproct is submarginal.	Murray River cliffs, South Australia
Pledge, 1985	<i>Monostychia</i> sp. indet.	Recorded with <i>Lovenia woodsi</i>	Sunlands fossil assemblage, lower Pliocene Loxton Sands near Loxton, South Australia (Fig. 3)
Holmes, 1987	Separated the <i>australis</i> form from the Mannum <i>Monostychia</i> -like form without names or descriptions.	Provided line drawings of <i>M. australis</i> in a brief discussion of Laube's contribution to echinoid work in Australia.	
Mooi, 1989	accepted the Suborder Clypeasterina A. Agassiz, 1872 as the appropriate place for <i>Monostychia</i>	Identified the important characters for <i>Monostychia</i> as: having two enclosed sphaeridia in each ambulacrum near the peristome; a submarginal periproct; food grooves continuing from the peristome around the ambitus and onto the aboral surface toward the apical system; combing in the ambulacra adjacent to the food grooves and provided a diagram in support; four gonopores; and six plates in each paired interambulacrum on the oral surface (Fig 2H).	
Holmes, 1989		Discussed work of Woods, Duncan, McCoy and Etheridge and lack of consistent discrimination of the taxa <i>Clypeaster</i> , <i>Scutella</i> and <i>Monostychia</i> . Comments on the taxonomic	

		difficulties arising out of poor geographical data collection.	
White, 1999		An unnamed “sand dollar” echinoderm captioned as Jurassic age. The specimen is most likely a Miocene <i>Monostychia australis</i> .	South Australia
Torres <i>et al.</i> , 2002	<i>Monostychia australis</i>	Examined the use of the mathematics of a eutactic star to define a morphospace for irregular echinoids and as a potential tool in taxonomy.	
Holmes, 2004	Listed two undescribed species of <i>Monostychia</i> (Fig. 3)		Kingscote, Kangaroo Island, South Australia
Holmes <i>et al.</i> , 2005	Noted <i>Monostychia australis</i> and another undescribed species of <i>Monostychia</i>		Glenforslan Formation in the River Murray Cliffs, South Australia
Kroh & Smith, 2010	Placed <i>Monostychia</i> in the subfamily Ammotrophinae	Test shape, plate architecture, buttressing, position and organisation of periproct, petal arrangement, food grooves, tuberculation and sphaeridia of fossil specimens were combined in a cladistics study along with eating apparatus and external appendages of extant species.	
Mihaljevic <i>et al.</i> , 2011	Included <i>Monostychia</i> in the Family Arachnoididae.		

Table 1.4. Age of Research.

Chapter 2. Materials and methods

Materials

Laube's (1869) type specimens (Fig. 1.4), housed at the Naturhistorisches Museum Wien (NHMW) were examined (Fig. 1.4.). Also examined were the type specimen of *M. loveni* residing at the Natural History Museum London (NHML) as specimen NHM E42444; the type specimen for *M. elongata* also residing at the Natural History Museum London (NHML) as specimen NHM E42457 and the type specimen for *M. etheridgei* at the Tasmanian Museum and Art Gallery (TMAG) as specimen Z504. Other specimens were sourced from the Invertebrate Palaeontology collections of Museum Victoria (MV), the South Australian Museum (SAM), and the Western Australian Museum (WAM) or collected from the field. A number of the specimens already in these Australian museums or collected from the field have been raised to type status as detailed later in this thesis. Of specific note are 73 specimens of *M. australis* that were collected from the field and chosen according to the quality of preservation (in that they showed most of the characters used in past studies) and size (to provide a size range). All 73 specimens came from the Glenforslan Formation in the Murray River cliffs between Morgan and Blanchetown, South Australia, although most were collected within a few kilometres of the type section south of Morgan. This collection has been accessioned by the South Australian Museum as SAM P29608–1 to –73.

The collection of 73 specimens identified above, along with some specimens from other localities were stained using a range of procedures depending upon the need to highlight plate boundaries. These specimens have since been accessioned at museums. This was often determined by the substrate in which the fossils were derived. One procedure involved soaking in undiluted vinegar for 12 hours followed by neutralizing in bleach for 12 hours and then two washes in water. After air drying, the oral surface was painted with a water-based

black poster paint (*Craft Works*). The paint was left to dry for 12 hours then the specimen placed in water and as much paint as possible was removed using a camel-hair brush.

Measurements

Measurements were made using a digital calliper accurate to 0.1 mm. Many of the measurements related to counting of pores and plates were made using a light microscope.

Measurements made included length, width, height, anterior to line of maximum width, anterior to centre of apical disc, anterior to centre of peristome, distance from posterior to posterior edge of periproct; distance from the centre of the apical disc in ambulacra I and II, to the most distal pore of the anterior poriferous zone, and to the ambitus (Fig. 2.1.), and a count of the number of respiratory pore pairs in a single poriferous zone. Where damage prevented these latter measurements being taken, measurements from similar areas in ambulacra IV and V were substituted. The ratios between most measurements were calculated and expressed as a percentage of test length (TL). In addition, the widths of interambulacrum 1 and ambulacrum II were measured where they intersect the ambitus (Fig. 2.1.) and the ratio of interambulacrum I to ambulacrum II made along with the width of ambulacrum III and TL. The means, standard deviation (SD) and sample size (n) for all measurements was made calculated. In all cases the sample size was limited to the number of specimens in which the character was able to be measured or calculated.

The number of post-basiconial plates in each interambulacrum and ambulacrum region on the oral surface was counted, with reference noted of the number of interambulacral plates between the peristome and periproct. An ANOVA test using the Paleontological Statistics (PAST) software program (Hammer *et al.* 2001) was performed using a significance level of $p < 0.001$.

The raw data is presented in the Appendix.

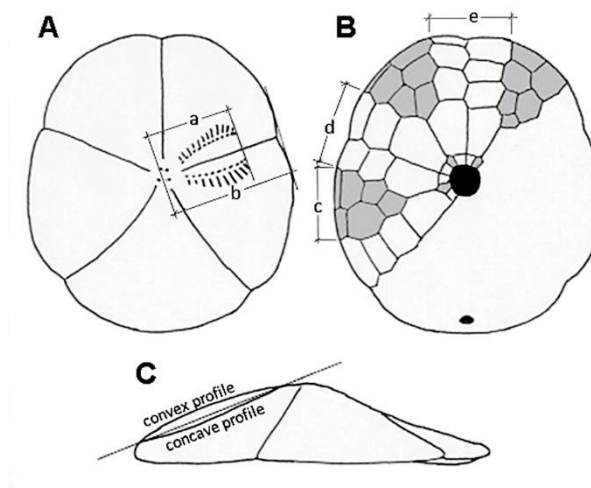


Fig. 2.1. Explanation of some measurements used in describing Monostychia. (a), distance from the centre of the apical disc in ambulacrum II, to the most distal pore of the anterior poriferous zone; (b) distance from the centre of the apical disc in ambulacrum II, to the ambitus; (c) width of interambulacrum 1 at the ambitus; (d) width of ambulacrum II at the ambitus; (e) width of ambulacrum III at the ambitus.

Some of the data on oral surface plate numbers were analysed using the EXCEL box-and-whisker chart. Technically, EXCEL does not have a formal box-and-whisker chart with their version being a five-number summary of the data. As such, some of the analyses will appear in the form of Fig. 2.2. The box plot comprises several points in need of clarification. The upper and lower horizontal bars (in this case nine and twelve plates) indicate the minimum and maximum number of plates in the sample once outliers are excluded. The coloured box in the centre is bounded on the lower side by the median of the lower 50% of data and hence equates to the 1st quartile (ten plates) and on the upper side by the median of the upper 50% of data and hence equates to the 3rd quartile (12 plates). If the data comprises an odd number of observations the median number of the total data is removed from calculations of the 1st and 3rd quartiles. The space between the 1st and 3rd quartiles is the interquartile range.

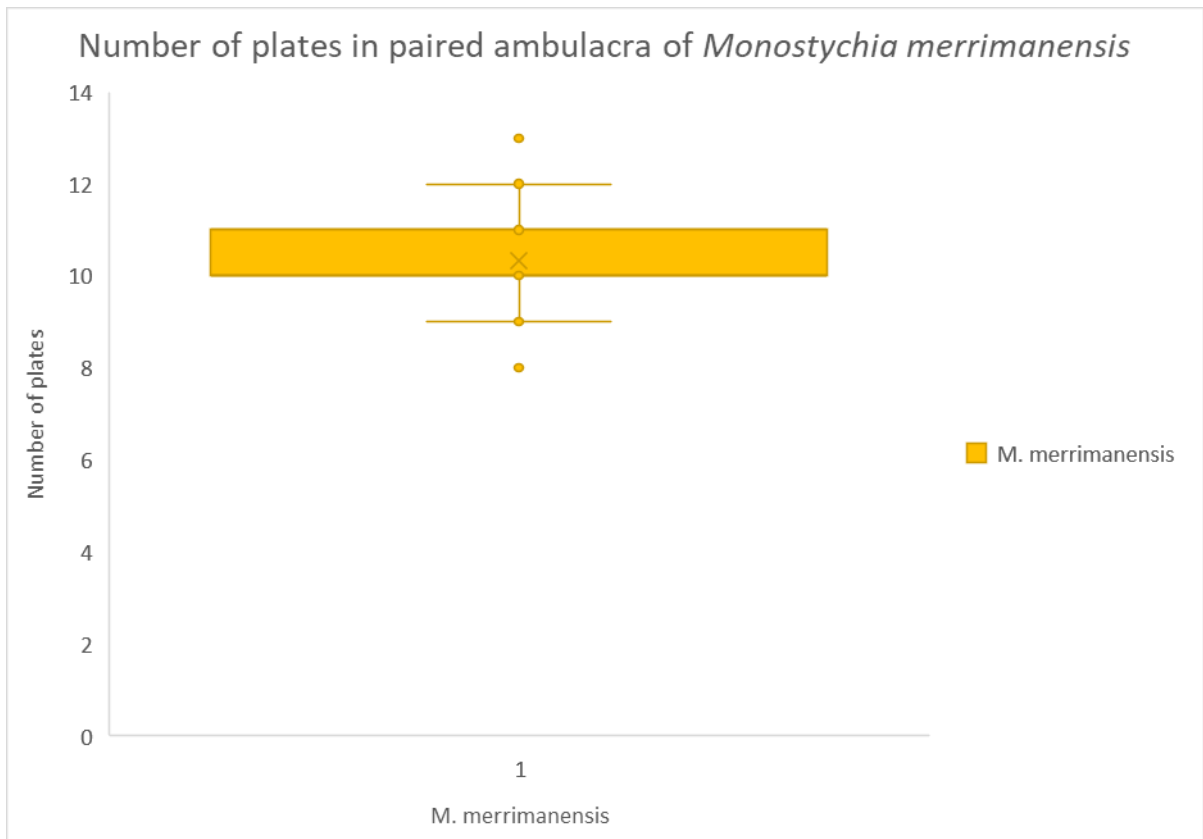


Fig. 2.2. Box plot of number of plates in the oral paired ambulacra of *Monostychia merrimanensis*.

The isolated dots above the maximum number and below the minimum number are outliers. An outlier is herein defined as exceeding 1.5 times the interquartile range. In this example plate numbers eight and 13 are considered outliers.

Within the interquartile range an 'X' marks the mean of the data excluding outliers. In this example the mean is 10.34. The median of the data excluding outliers is marked by a horizontal bar within the interquartile range. In this example the median is 10 and coincides with the 1st quartile at the bottom of the box.

Chapter 3. Systematics

Introduction

The focus of this thesis is on the systematics of *Monostychia* and their close relatives from the Cainozoic strata of southern Australia. *Monostychia* and its relatives belong to the Order Clypeasteroida Agassiz, 1872. They comprise echinoids with tests ovoid to flattened with the petaloid ambulacra as wide or wider than the interambulacra; primary tube feet restricted to the petals; accessory tube feet extending outside the petals and sometimes into the interambulacra; small peristome; test usually has internal supports; spines small and short (Durham *et al.* (1966)). Recent and relatively frequent updates on levels at and above Order level can be sourced online from The Echinoid Directory (Smith & Kroh, 2011) or the World Echinoidea Database (Kroh & Mooi, 2020). While there appears to be no controversy that the specimens referred to in this thesis belong in the order Clypeasteroida, at the suborder, family and subfamily level uncertainty still abounds.

Clark (1946) recognized in the then order Exocycloida, the suborder Clypeasterina in which was placed four families (Table 3.1.). While Clark lumped the genera of interest in this discussion under the one family, the genera *Clypeaster* and *Anomalanthus* were separated from the rest principally by the number of genital pores (five versus four).

Order	Suborder	Family	Subfamily	Genus
Exocycloida	Clypeasterina	Clypeasteridae		<i>Anomalanthus</i>
				<i>Clypeaster</i>
				<i>Monostychia</i>
				<i>Arachnoides</i>
				<i>Hesperaster</i>
				<i>Ammotrophus</i>
		Laganidae		
		Fibulariidae		
		Scutellidae		

Table 3.1. Classification of Clark (1946). Genera in families beyond Clypeasteridae have been purposely excluded.

Durham *et al.* (1966) placed four suborders under the order Clypeasteroida. Within the suborder Clypeasterina two family levels of classification were used along with a subfamily level. (Table 3.2.). At the family level, Durham followed Clark in using the presence of five genital pores to separate out the Clypeasteridae from the Arachnoididae. At the subfamily level, Arachnoidinae were identified principally in having a supramarginal periproct and internal supports restricted to the margins of the test while the Ammotrophinae having the periproct usually submarginal and the internal supports both marginal and around the peristome.

Order	Suborder	Family	Subfamily	Genus
Clypeasteroida	Clypeasterina	Clypeasteridae		<i>Clypeaster</i>
		Arachnoididae	Arachnoidinae	<i>Arachnoides</i>
				<i>Fellaster</i>
			Ammotrophinae	<i>Ammotrophus</i>
				<i>Monostychia</i>
				<i>Scutellinoides</i>
			uncertain	<i>Fossulaster</i>
	Laganina			
	Scutellina			
	Rotulina			

Table 3.2. Classification of Durham *et al.* (1966). Genera in suborders beyond Clypeasterina have been purposely excluded.

Mooi (1989) chose to ignore the family level of classification indicating ongoing uncertainty at that level. Within the order Clypeasteroida was placed three suborders and then genera directly under those (Table 3.3.).

Order	Suborder	Family	Subfamily	Genus
Clypeasteroida	Clypeasterina			<i>Clypeaster</i>
				<i>Ammotrophus</i>
				<i>Monostychia</i>
				<i>Arachnoides</i>
				<i>Fellaster</i>
				<i>Scutellinoides</i>
				<i>Fossulaster</i>
				<i>Willungaster</i>
	Laganina			
	Scutellina			

Table 3.3. Classification of Mooi (1989). Genera in suborders beyond Clypeasterina have been purposely excluded.

Kroh & Smith (2010) did an extensive reorganization of the classification system based on cladistics. Within the Clypeasteroida they assigned two suborders and within one of those (Clypeasterina) they had two families (Fig. 3.4.). Their study brought Clypeasterinae, Arachnoidinae and Ammotrophinae within the family Clypeasteridae but it was not clear whether they were prepared to accept a subfamily level of classification, or if they did, which genera belonged in which. It is notable that their analysis did not include the genus *Monostychia* possibly because the genus lacks the ‘spine-based’ data which was important to their analysis. This lack of *Monostychia* increases the uncertainty as to whether the genus might belong with Arachnoidinae or Ammotrophinae if those subfamily names remain acceptable.

Order	Suborder	Family	Subfamily	Genus
Clypeasteroida	Clypeasterina	Clypeasteridae	Clypeasterinae?	<i>Clypeaster</i>
			Ammotrophinae?	<i>Ammotrophus</i>
			Arachnoidinae	<i>Arachnoides</i>
		Fossulasterinae	<i>Fossulaster</i>	
			<i>Scutellinoides</i>	
	Scutellina			

Table 3.4. Classification of Kroh & Smith (2011). Genera in family beyond Clypeasteridae have been purposely excluded.

Byrne & O’Hara (2017) do not use the suborder level of classification but do identify six families within the order Clypeasteroida (Table 3.5.) in their overview of echinoids in Australian waters. It should be assumed that this classification system ignores non-Australian genera and therefore may not be complete.

Order	Suborder	Family	Subfamily	Genus
Clypeasteroida		Clypeasteridae	Clypeaster	
		Arachnoididae	Arachnoides	
			Ammotrophus	
			Monostychia	
			Fellaster	
		Fibulariidae		
		Echinocyamidae		
		Laganidae		
		Astriclypeidae		

Table 3.5. Classification of Byrne & O'Hara (2017). Genera in families beyond Clypeasteridae and Arachnoididae have been purposely excluded.

The Echinoid Directory hosted by the NHML (Smith & Kroh 2011, as updated 2020) accepts a two-family classification albeit different from Durham *et al.* (1966), within the suborder Clypeasterina (Table 3.6.). However, searching within the Directory provides different alternatives. This is possibly a result of the difficulties in keeping all areas of an active online database current but may also reflect a level of uncertainty at family and subfamily level. As Smith & Kroh (2011) reunite *Clypeaster* with *Arachnoides* and *Ammotrophus* in the one family in line with Clark (1946) it suggests that there is uncertainty over whether the number of genital pores is an adequate distinguishing feature at this level. Similarly, the lack of subfamilies as introduced by Durham *et al.* (1966) suggests concern over the value of the positioning of the periproct (supra- versus sub-marginal) and the simple versus more complex internal buttressing are useful at these levels.

Order	Suborder	Family	Subfamily	Genus
Clypeasteroida	Clypeasterina	Clypeasteridae		<i>Clypeaster</i>
				<i>Alexandria</i>
				<i>Arachnoides</i>
				<i>Willungaster</i>
				<i>Prowillungaster</i>
				<i>Ammotrophus</i>
				<i>Monostychia</i>
				<i>Fossulaster</i>
				<i>Scutellinoides</i>
				<i>Fellaster</i>

Table 3.6. Classification of The Echinoid Directory (Smith & Kroh, 2011). Genera in suborders beyond Clypeasterina have been purposely excluded.

Since Durham *et al.* (1966) there have been several changes to the classification system below order level. However, none are convincing or accompanied by detailed descriptions or reasons for the change. The exception is Kroh & Smith (2010), but as commented, they failed to make clear the situation below family level. As a result, for the purposes of this thesis the system of Durham *et al.* (1966) is accepted. In this system the genus *Monostychia* is classified thus:

Class Echinoidea Leske, 1778

Crown group Neognathastomata Smith, 1981

Order Clypeasteroida L. Agassiz, 1872

Suborder Clypeasterina L. Agassiz, 1872

Family Arachnoididae Duncan, 1889

Subfamily Ammotrophinae Durham, 1955

Genus *Monostychia* Laube, 1869

A diagnosis for the Order Clypeasteroida Agassiz, 1872 has been provided at the beginning of this Chapter.

The Suborder Clypeasterina Agassiz, 1872 is diagnosed as having a test with internal supports; petals with pseudocompound plates; discontinuous interambulacra terminated apically by a pair of plates; an apical system that is pentagonal or stellate; and separate auricles (Durham *et al.* (1966)).

The Family Arachnoididae Duncan, 1889 is diagnosed as having a flattened test with an outline that is generally rounded; thin ambitus; open petals; simple, well-defined food grooves; lacking secondary tube feet in grooves; accessory tube feet outside of the petals

usually in dense obliques series (called combs); four genital pores; peristome not sunken; and primordial interambulacral plates externally larger than the ambulacral plates (Durham *et al.* (1966)).

Chapter 3.a. Subfamily Monostychinae

Introduction

In the previous Chapter 3. Systematics, it was concluded that the best taxonomic position for the genus *Monostychia* prior to this study was in the subfamily Ammotrophinae. It shares with *Ammotrophus* the features of a sub-marginal periproct and internal supports both marginal and around the peristome. Unlike *Arachnoides* which has a supramarginal periproct and internal supports restricted to the margins. The use of the periproct position is emphasized by Mooi (1989) who separated *Arachnoides* from *Clypeaster*, *Ammotrophus* and *Monostychia* using the supra- versus sub-marginal periproct position. However, as will be demonstrated later in this thesis, there appears to be variability in the position of the periproct in *Monostychia* and its close relatives whereby the periproct can vary from being up to one periproct diameter distance from the margin to clearly touching the margin.

Mooi (1989) further suggests that the plate number in which the periproct first comes into contact with might be diagnostic and shows *Ammotrophus* as having the periproct first in contact with plates 2a/2b while *Monostychia* has the periproct first in contact with plates 3a/3b. The plate contact of *Arachnoides* is not shown but Durham *et al.* (1966) suggest it may be 2a/3b (3a/2b). Mooi (1989) also suggests that the number of paired interambulacral plates on the oral surface distinguished between the three species with *Ammotrophus* having seven, *Monostychia* having six and *Arachnoides* having two. Again, as will be demonstrated later in this thesis, there is substantial variability in the plate numbers in *Monostychia* and its relatives.

There appears to be doubt about the accuracy and hence validity of some of the characters used by previous researchers to place these genera at subfamily level. If another character

that displayed greater objectivity than plate counts or periproct position was available, it could provide utility at subfamily level.

An alternate character

During this investigation it was noted that there was a previously undiscovered structural feature in many of the specimens. This was a thin circumferential wall of stereom present on the right-hand side of the test, lying half way between the marginal and central buttressing. This wall originally separated the proximal and distal tracts of the intestine (Fig. 3.a.1.). This form of intestinal buttressing has been given the name “intermurum” (Latin for wall in-between). The intermurum is not apparent on the exterior of the test. On three specimens (two different species) its presence was determined by a CT scan. With other selected specimens the test was dissected either transversely or laterally. The presence or absence, as well as shape and extent, of an intermurum was noted for a limited number of the specimens in this study, with at least one representative from each of the proposed species.

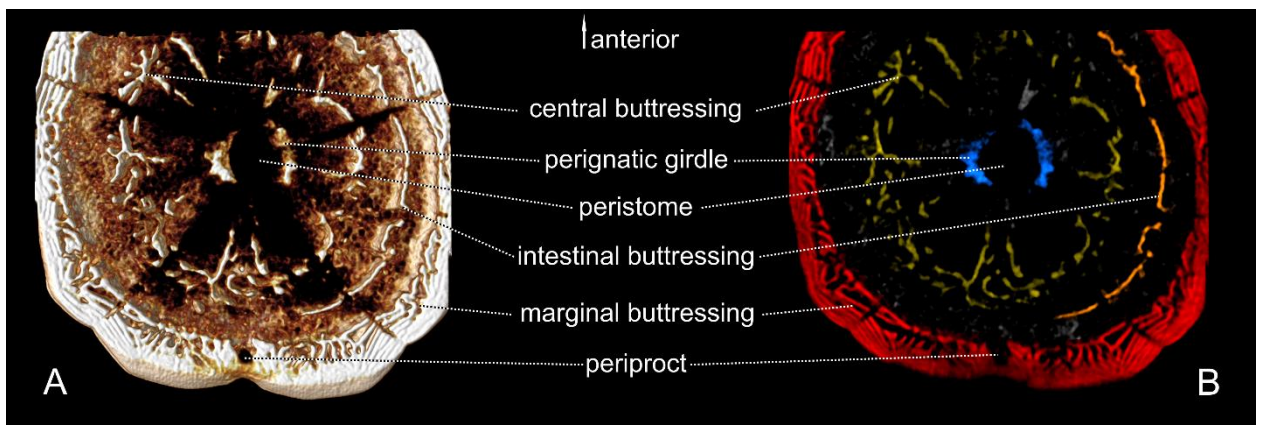


Fig. 3.1. CT scan of Monostychia australis. (A) cut volume rendering and (B) single slice of specimen SAM P33712 showing internal buttressing. Different buttressing types and the perignathic girdle are highlighted in different colors in B. Width of specimen 33.1 mm.

During this thesis, and as will be described in the following chapters, the intermurum has been identified in four different genera: *Monostychia* Laube, 1869, *Quinquestychia* gen. nov.,

Rotundastychia gen. nov., and *Deltoidstychia* gen. nov. It has not been referenced before in *Clypeaster*, *Arachnoides* or *Ammotrophus*. As a result it is proposed to use the presence or absence of this feature in defining a new subfamily, Monostychinae.

Subfamily Monostychinae

Diagnosis. Arachnoidid echinoid with an intermulum or intestinal buttressing running either unbroken or in a series of smaller segments or needles parallel to the margin from about interambulacrum 2 to interambulacrum 5; internal supports beyond the intermulum are both marginal and around the peristome; periproct oral but close to or touching the margin.

Chapter 3.b. Genus *Monostychia* Laube, 1869

Abstract

The genus *Monostychia* Laube, 1869 is redescribed along with the species *M. australis* Laube, 1869 and *M. etheridgei* Woods, 1877. *M. elongata* (Duncan, 1877) is declared a junior synonym of *M. australis*. *M. macnamarai* Sadler *et al.* 2017, *M. alanrxi* Sadler *et al.* 2017, *M. merrimanensis* Sadler *et al.* 2019 and *M. glenelgensis* Sadler *et al.* 2019 are re-presented from their recent publications. *M. robheathi* is described as a new species. A key to the seven species is included.

Systematic palaeontology

Order Clypeasteroida A. Agassiz, 1872

Suborder Clypeasterina A. Agassiz, 1872

Family Arachnoididae Duncan, 1889

Subfamily Monostychinae sub.fam. nov.

***Monostychia* Laube, 1869.** Sitzungsber. Kais. Akad. Wissensch. Wien, vol. 69, p. 188.

Type species. *Monostychia australis* Laube, 1869, by monotypy. (Fig. 1.4.A.)

Etymology. Laube (1869) omitted the explanation for the derivation of the name *Monostychia*. Although the prefix “mono” almost certainly means ‘single’ or ‘sole’ (Greek), the root for ‘stychia’ is more problematic. It is used in recent medical texts to mean a ‘row’. Laube’s (1869) diagrams of *Monostychia* highlighted five simple, deep ambulacral furrows and one might conclude that the meaning of the name *Monostychia* derives from the ‘single row’ and refers to the simple ambulacral furrows that are so characteristic (Sadler *et al.* 2016).

Emended diagnosis. Monostychioid echinoid with test longer than wide, a reuleaux pentagonal to oval shape in plan and a tumid ambitus; A keel, more prominent toward the periproct, gives a concave lateral profile orally and the lateral appearance of a drooping tail; Combing is present but weak or indistinct; Petals relatively long and distinctly arced with the distal ends of each pair essentially parallel; Periproct within one periproct diameter of and often touching the ambitus and bounded by the second pair of post-basical plates (3a/3b).

Description. The tests of species within this genus generally range in size from very small to medium (range less than 10–40 mm.). While some of the species are somewhat oval, they are generally reuleaux pentagonal in shape depending on how deeply indented the food grooves are at the margin. The ambitus is tumid to very tumid ranging from an average of 9–11%TL in thickness. The lateral profile of the oral surface is concave due the presence of a keel, or drooping tail, between the peristome and periproct, more prominent nearest the periproct. The lateral profile of the aboral surface in some species is slightly concave but most are generally to distinctly convex. Apical disc monobasal with four gonopores; anterior pair more closely spaced than posterior pair. Madreporite dotted with numerous hydropores. Tubercles are rarely observed on apical disc.

The petals are distinctively arced in shape and inflated above the test. The mean length of petals, measured as a percentage of the distance to the ambitus in the line of each pore zone, for the anterior pair range from 52–67% and the posterior pair from 48–60% with the anterior pair always longer than the posterior pair. The inner line of pores forms a distinct arc and the outer line distinctly more so giving an impression that the two halves of the petal are lyrate. This, however, is not so. For the last 25–40% of the petal length they remain almost parallel. In the immature members of some of the species and also in the small species, this distinct curvature appears not to be so well developed. The tips of the petals end abruptly in a point as the lines of the pore pairs converge. The inner pore is almost always round or nearly so. The

outer pore ranges in the various species from lacrimiform through oval to a distinct elongated furrow more than twice the length of the inner pore diameter.

The periproct is always submarginal. In most species, the periproct may be one-half to a full diameter of the periproct from the margin. In others it is touching the margin.

The intermural ranges from an almost uninterrupted thin wall of stereom to a minor and discontinuous wall comprised of a small series of needles.

***Monostychia australis* Laube, 1869.**

1832 *Scutella*; Sturt, pl. 3, fig. 9.

1869 *Monostychia australis* Laube, p. 190, fig. 3, 3a–c.

1877 *Arachnoides australis*, Laube; Duncan, p. 48.

1879 *Monostychia australis*; McCoy, pp. 40–42, pl. 60, figs 5, 7.

1883 *Monostychia australis* Laube; Pomel, p. 70.

1887 *Clypeaster (Monostychia) australis*, Laube; Duncan, p. 420.

1892 *Monostychia australis* Laube; Bittner, pp. 345–347, pl. 2, figs 5–8.

1946 *Monostychia australis*; Clark, p. 338.

1948 *Monostychia australis* Laube; Mortensen, pp. 154–155, figs 91a, 92b.

1955 *Monostychia australis* Laube; Durham, p. 128.

1966 *Monostychia australis*; Durham *et al.*, p. U468, fig. 359.1a–b.

1989 *Monostychia australis* Laube, 1869; Mooi, p. 35, figs. 1b, 5b.

Type material. The syntypes of Laube are stored at the Natural History Museum Vienna (eight specimens; NHMW1864/0001/0065a to f, 2000z0068/0001, .../0002); (Fig. 1.4.). Because the type-series contains at least two species [NHMW 2000z0068/0002 (Laube 1869: fig. 3c) and 1864/0001/0065b differ from the others but are both too incompletely preserved to serve as a type for a new species], plus two juveniles indeterminable at species level (NHMW 1864/0001/0065e, .../0065f), it is necessary to designate a lectotype in order to provide stability to the nomenclature for *Monostychia*.

Lectotype. Specimen NHMW 2000z0068/0001, designated herein. This is the specimen figured by Laube (1869) as fig. 3, 3a and 3b (Fig. 1.4.A. herein). It is consistent with the forms that occur only in the Glenforslan Formation.

Paralectotypes. NHMW 1864/0001/0065a to f, 2000z0068/0002 (Fig. 1.4.). Note that specimens 2000z0068/0002, 1864/0001/0065b, 1864/0001/0065e and 1864/0001/0065f are herein excluded from *Monostychia australis*.

Type locality. Murray Cliffs, South Australia. Comparison with material of known provenance suggests that the lectotype came from the area of Swan Reach, South Australia.

Type-stratum. Uppermost lower Miocene Glenforslan Formation, Morgan Subgroup, Murray Group (Gallagher & Gourley 2007).

Additional material. A further group of 73 specimens, numbered SAM P29608–1 to –73, is housed at the South Australian Museum.

Etymology. Laube (1869) omitted a derivation of the epithet *australis*. However, it is commonly used as a descriptor for Australian or southern species.

Diagnosis: *Monostychia* species characterised by a reuleaux pentagonal to oval test; low, slightly concave to domed profile in lateral profile; ratio of width of ambulacrum to interambulacrum at ambitus <140%; apex greater than 45% TL from anterior margin; length of ambulacral basicoronal plates greater than 170% of their width; barely inflated petals.

Description: Remarkably consistent in form. Test small to medium in size, variable in shape from a reuleaux pentagonal to oval in plan and slightly concave to domed in profile. Specimens range in length from 11.7–43.9 mm; maximum width 86–96% TL (mean = 91%, SD = 2%, n = 73) occurring generally at the centre, but in the range 41–66% TL from anterior ambitus (mean = 49%, SD = 5%, n = 73). Test 18–29% TL high (mean = 22%, SD =

3%, n = 72); apex 42–54%TL from anterior ambitus (mean = 50%, SD = 2%, n = 72); apical disc 46–54%TL from anterior ambitus (mean = 51%, SD = 2%, n = 73).

Orally, test generally flat with a slightly sunken peristome and indented food grooves. An indistinct keel runs from the periproct forward towards the peristome. The apical surface of the test is slightly concave in transverse profile but in longitudinal profile, is slightly convex anteriorly but tapers posteriorly in a straight line. Ambitus tumid. The anal notch is shallow. Minor ambulacral notches although slightly deeper in ambulacra I and V than elsewhere. While combing has been observed in several specimens it is always weak or indistinct and often requires careful preparation of the specimen to be observed.

Of the 72 specimens for which plates could be observed in paired post-basicoronal interambulacra, plate counts were obtained in 282 of the possible 288 regions. 64% of regions had six plates, 28% seven, 6% eight, 1% had five, 1% had nine. One region also recorded 10 plates but as a percentage this recorded as 0%. For the paired post-basicoronal ambulacra, post-basicoronal plate counts were obtained in 278 of a potential maximum of 284 regions; 55% had eight plates, 33% nine, 8% had 10, 2% had seven and 2% had 11. In the 71 specimens where unpaired post-basicoronal ambulacrum III plates could be counted, 35% had nine plates, 30% eight, 25% had 10, 7% had 11, 1% had seven and 1% had 12.

Petals are barely raised or inflated above test surface in most specimens. The mean length of petals measured as a percentage of the distance to the ambitus in the line of each pore zone is for the anterior pair 52% (SD = 6%, n = 71) and posterior pair 48% (SD = 4%, n = 69). Poriferous zones curved, open distally, with outer pore rows distinctly more arcuate than inner ones. Petals almost parallel distally for the final 40% or so of their length. Petal interporiferous zones widest at their distal end. Distally, petals end abruptly, trailing podia not developed. Ambulacral pores are oblique elongate anisopores with round inner and elongate, slit-like outer pores that are often in excess of twice the diameter of the inner pores.

Tubercles not observed between pores. The anterior poriferous zone in the ambulacrum II has 15–37 pore pairs; slightly more in ambulacrum I (17–40). The number of pore pairs in the anterior zone per mm of TL is 0.87 (SD = 0.1, n = 68). Mean width of ambulacrum II at ambitus is 128% of the mean width of interambulacrum 1 (SD = 12%, n = 73). Mean width of ambulacrum III 33%TL (SD = 2%, n = 73).

Peristome medium in size. Five deep, simple, unbranched and narrow food grooves extend from the peristome around the ambitus to the apical disc, becoming less prominent apically. The three anterior grooves are almost straight, whereas the two posterior ones are arched slightly laterally. The peristome is circular to subpentagonal. Each food groove becomes wider and displays distinctive crenulations upon reaching the basicoronals and ends in a broad and flat peristomial region that borders the opening. It is these five flat edges of the grooves facing the peristome that give the appearance that the peristome is pentagonal. The adoral edge of each groove has a pair of prominent buccal podial pores, one on the outer edge (i.e. adradial) each side of the groove. These pores emerge perpendicular to the test, but positioned slightly internal to the peristomal edge, such that it is best viewed at an angle. Basicoronal plates longer than wide, outer margin flat; the interambulacral plates are distinctly narrower than the ambulacral ones and narrow markedly toward the peristome. They are about 10% longer than the ambulacral ones and end distally with a slightly obtuse angled projection.

Periproct is medium size. Distance between posterior edge and ambitus is 30–50% of periproct's longitudinal diameter. It comes into contact aborally with interambulacral plates 3a/3b. Although rare, contact with 2a/3b and 4a/3b have also been observed.

A well-developed, complex system of peripheral pillars and buttresses occurs around the test (Fig. 2.2.). Radiating interambulacral pillars or walls are not apparent. Central pillars are present, but poorly developed. In addition, an intermulum is present on the right-hand side of

the test, lying half way between the marginal and central buttressing and comprised of an almost uninterrupted but relatively thin and simple wall of stereom.

The tract of the digestive system leaves the peristome left of centre (in aboral view), curves outward along ambulacrum IV, follow the ambitus posteriorly (but within the peripheral pillar system) and then continues anteriorly on the right side to beyond ambulacrum II where it curves aborally to proceed posteriorly to the periproct.

Stratigraphy and age. *M. australis* is restricted to the Glenforslan Formation in the Morgan Subgroup of the Murray Group in South Australia. This is equivalent to the (former) lower Morgan Limestone. There is ongoing debate concerning the exact limitations and extent of some of these stratigraphic units (Lukasik & James 1998, Cowley & Barnett 2007, Gallagher & Gourley 2007), but current estimates for the strata from which these specimens were collected suggests they are latest early Miocene in age. Along the Murray River cliffs, the Glenforslan Formation is up to 15 m thick, and thins markedly toward the south due to uplift and erosion. It comprises partially sublithified to lithified calcarenite and calcisiltite interbedded with marl, weathering to a whitish-cream colour in outcrop (Lukasik & James 1998). The middle Glenforslan Formation has been interpreted as being deposited in shallow marine conditions, possibly in depths less than 10 m (Holmes *et al.* 2005).

***Monostychia macnamarai* Sadler, Martin & Gallagher, 2017 (Fig. 3.b.1.)**

Holotype. WAM 16.18.

Type stratum and locality. Colville Sandstone (middle Miocene), near track at grid reference 413293, Jubilee 1:250 000 map sheet.

Additional material. WAM 67.337, 89.35a, b, 89.37b, d, e, g, 91.15.1, 91.17a –c, 16.1–4, 16.11–24.

Etymology. The species is named after Dr Ken McNamara, University of Western Australia and Western Australian Museum, former Director of the Sedgwick Museum, University of Cambridge and Fellow Downing College, Cambridge. Over a long and distinguished career, Ken has contributed significantly to the field of fossil echinoid research, particularly in Western Australia.

Diagnosis. *Monostychia* species characterized by elongate oval test; significantly domed profile in lateral view; ratio of width of ambulacrum to interambulacrum at ambitus >140%; very tumid margin; apex less than 41% TL from anterior margin; periproct not in touch with margin; length of ambulacral basicoronal plates greater than 170% of their width; inflated petals.



Fig. 3.b.1. Holotype of *Monostychia macnamarai* Sadler, Martin & Gallagher, 2017. (WAM 16.18), aboral (A) and oral (B) view; TL = 34.90 mm.

Description: Medium, elongate oval test with sides between anterior and posterior food grooves almost parallel. Specimens range in length from 29.0–42.1 mm; maximum width 73–87% TL (mean = 78%, SD = 3%, n = 26) occurring generally forward of centre, but in the range 35–73% TL from anterior ambitus (mean = 45%, SD = 8%, n = 26). Test 20–27% TL high (mean = 22%, SD = 2%, n = 18); apex 26–42% TL from anterior ambitus (mean = 34%,

SD = 4%, n = 19); apical disc 48–52% TL from anterior ambitus (mean = 49%, SD = 1%, n = 23).

Orally, test is generally flat with a sunken peristome; deep food grooves give the oral interambulacra a slightly bulbous appearance. An indistinct keel running forwards from the periproct towards the peristome gives the appearance of a drooping tail and hence, a longitudinal concavity when viewed in profile. Test distinctly convex in both lateral and longitudinal profile; ambitus very tumid. Ambital notches minor, slightly deeper in ambulacra I and V than elsewhere. Anal notch absent in most specimens, although in some examples the test becomes a little squarer with a hint of an indentation. Indistinct combing observed in only two specimens; although absences in other specimens may be the result of inadequate preservation.

Of the 11 specimens for which plates could be observed in paired post-basicoronal interambulacra, plate counts were obtained in 31 of the possible 44 regions. 55% of regions had eight plates, 35% seven, 6% had nine and 3% six. For the paired post-basicoronal ambulacra plates could be counted in 12 specimens where counts were obtained in 21 of a potential maximum of 48 regions; 48% had 12 plates, 29% 10, and 24% had 11. In the 8 specimens where unpaired post-basicoronal ambulacrum III plates could be counted, 50% had 12 plates, 25% had 11 and 25% had 13.

Petals are noticeably raised or inflated above test surface. The mean length of petals measured as a percentage of the distance to the ambitus in the line of each pore zone is for the anterior pair 65% (SD = 9%, n = 18) and posterior pair 60% (SD = 4%, n = 18). Poriferous zones curved, open distally, with outer pore rows distinctly more arcuate than inner ones. Petals almost parallel distally for the final 25% or so of their length. Petal interporiferous zones widest at their distal end. Distally, petals end abruptly, trailing podia not developed. Ambulacral pores are oblique elongate anisopores with round inner and elongate, slit-like

outer pores. Tubercles not observed between pores. The anterior poriferous zone in ambulacrum II has 18–40 pore pairs; more in ambulacrum I (28–41). The number of pore pairs in the anterior zone per mm of TL is 0.87 (SD = 0.1, n = 19). Mean width of ambulacrum II at ambitus is 150% of the mean width of interambulacrum 1 (SD = 13%, n = 15). Mean width of ambulacrum III 32%TL (SD = 2%, n = 16).

Peristome large and circular. Five very deep, simple, unbranched, narrow food grooves extend from peristome around ambitus to apical disc, becoming less prominent apically. Three anterior grooves are almost straight; two posterior grooves arc laterally to a slight extent. Each food groove becomes wider upon reaching the basicoronal plates, ending in a broad and flat region bordering the peristomial opening. Food grooves are not crenulate as observed in the type species *M. australis*; adoral edge of each groove with a pair of small buccal podial pores, one on each of the outer edges of the groove (i.e., adradial). Basicoronal plates twice as long as wide, outer margin flat; interambulacral basicoronal plates are about 30% longer than the basicoronals, with an equilateral triangular projection.

Periproct submarginal, medium to large, circular to oval in shape. Distance between periproct edge and ambitus is 10–20% of periproct's longitudinal diameter. In interambulacrum 5, periproct comes into contact adorally with plates 3a/3b although contact with 2a/3b was observed in one specimen.

Internally, a complex system of peripheral pillars and buttresses is developed around the test, although these are less well developed than in *M. australis*. Radiating interambulacral pillars or walls are not apparent. Central pillars are present and well developed, and a substantial and continuous intermuralum is present on the right-hand side of the test, half way between the marginal and central buttressing.

Stratigraphy and age: Onshore, the Eucla Basin successions in Western Australia represent four separate depositional pulses—in the middle to upper Eocene (Hampton

Sandstone, Wilson Bluff Limestone, Eundynie Group and Plantagenet Group), upper Oligocene to lower Miocene (Abrakurrie Limestone), middle Miocene (Colville Sandstone, Nullarbor Limestone, Plumridge Formation), and upper Pliocene to lower Pleistocene (Roe Calcarenite) (Lowry 1970, James & Bone 1991, Clarke *et al.* 2003, Li *et al.* 2004); however, in the broader depositional setting of the Australian southern margin, the Oligo–Miocene and middle Miocene strata are considered part of the same stratigraphic package (McGowran *et al.* 1997, 2004). The sediments in the basin are predominantly undeformed and flat lying, with only a slight west-side up-tilting caused by the far-field effects of continental collision between Asia and Australia during the Miocene (Dickinson *et al.* 2001, 2002, Sandiford 2007, Hou *et al.* 2008).

Despite cropping out extensively across the Bunda Plateau, the middle Miocene units are in general poorly studied; the Colville Sandstone has not been reviewed or studied in depth since Lowry’s (1970) seminal review of the onshore basin, whereas aspects of the Nullarbor Limestone have recently been studied by O’Connell (2011) and O’Connell *et al.* (2012).

The Nullarbor Limestone is a fine- to medium-grained, in many areas strongly indurated, calcarenite, apart from a basal rhodolith rudstone–floatstone facies named the Mullamullang Member (Lowry 1970, O’Connell 2011, O’Connell *et al.* 2012). The unit is almost entirely biogenic, with minor clastic input; coralline algae and foraminifera are the dominant components, with bryozoan, echinoid, and mollusc (bivalve and gastropod) fragments also common (Lowry 1970, O’Connell 2011, O’Connell *et al.* 2012). Corals are also found in this unit, and this, plus the presence of large foraminifera and tropical mollusc species, suggests deposition during the subtropical middle Miocene Climatic Optimum (O’Connell 2011, O’Connell *et al.* 2012).

The Colville Sandstone is far more restricted in outcrop area than the Nullarbor Limestone, being found predominantly along the northern edge of the basin (Lowry 1970).

Basally, the unit consists of fine- to coarse-grained sandstone, overlain by sandy calcarenites, reflecting reduced siliciclastic input into the area with time. Lowry (1970) noted that thick-shelled bivalves are common in this unit, with rare echinoids, bryozoans and gastropods. The molluscs are larger and more common in the sandstone compared to the calcarenite lithologies, suggesting that the distribution of thick-shelled taxa reflects relatively high energy conditions.

Although the boundary is difficult to map due to a lack of outcrop, observed interbedding of Nullarbor Limestone and Colville Sandstone lithologies has led researchers to consider the units as lateral equivalents (Lowry 1970, O'Connell *et al.* 2012). Therefore, the units represent different sedimentological environments on the same Cenozoic shoreline, deposited along the inner margin of a wide continental shelf (Lowry 1970). The Colville Sandstone represents a beach or shallow marginal marine succession, whereas the Nullarbor Limestone represents lower energy epeiric platform conditions at water depths up to 30 m (Lowry 1970, O'Connell 2011, O'Connell *et al.* 2012). Both units have been dated using planktonic foraminiferal biostratigraphy and extend across zones N8 to N10. This corresponds to the Batesfordian to Balcombian Australian regional stages (= Langhian) (McGowran *et al.* 1997).

***Monostychia alanrixi* Sadler, Martin & Gallagher, 2017 (Fig. 3.b.2.)**

1970 *Monostychia australis* Laube; Philip, p. 186, fig. 59.

Holotype. WAM 91.15-2.

Type stratum and locality. Colville Sandstone (middle Miocene), approximately 40 km WSW of Lake Colville, WA.

Additional material. WAM 88.925a–c, 16.5–6, 16.25–28.

Etymology. The species is named after Professor Alan Rix, Pro-Vice-Chancellor of The University of Queensland.

Diagnosis. *Monostychia* species characterised by a reuleaux pentagonal to oval test, low and slightly domed in lateral profile; ratio of width of ambulacrum to interambulacrum at ambitus >140%; apex less than 45% TL from anterior margin; length of ambulacral basicoronal plates less than 160% of their width; inflated petals.



Fig. 3.b.2. Holotype of *Monostychia alanrxi* Sadler, Martin & Gallagher, 2017. (WAM 91–15–2), aboral (A) and oral (B) view; TL = 33.13 mm.

Description: Medium test broadly oval to reuleaux pentagonal in shape. Specimens range in length from 26.5–41.3 mm; maximum width 81–88% TL (mean = 85%, SD = 2%, n = 7) occurring anterior of centre in the range 40–52% TL from anterior ambitus (mean = 45%, SD = 4%, n = 7). Test 16–21% TL high (mean = 19%, SD = 2%, n = 6); apex 32–47% TL from anterior ambitus (mean = 40%, SD = 6%, n = 5); apical disc 46–52% TL from anterior ambitus (mean = 48%, SD = 2%, n = 7).

Test generally flat orally with slightly sunken peristome and deep food grooves. Indistinct keel running forwards from periproct towards peristome gives the appearance of a drooping tail and hence a longitudinal concavity when viewed in profile. In plan view, test shape is oval to elongate pentagonal, rounded anteriorly but squarish posteriorly. In both lateral and longitudinal profile, test above the ambitus begins with a distinct convexity, becoming slightly concave approaching apical disc and apex. Ambitus is tumid, less so than in *M.*

macnamarai but more than in *M. australis*. Ambital notches are minor, being slightly deeper in ambulacra I and V than elsewhere. Anal notch generally lacking, but shallow and broad when present. Indistinct combing evident in two specimens only.

Of the 6 specimens for which plates could be observed in paired post-basicoronal interambulacra, plate counts were obtained in 23 of the possible 24 regions. 39% of regions had seven plates, 30% eight, 22% six, 4% had nine and 4% had 10. For the paired post-basicoronal ambulacra, post-basicoronal plate counts were obtained in 23 of a potential maximum of 24 regions; 35% had 10 plates, 30% nine, 22% had 11 and 13% had 12. In the 6 specimens where unpaired post-basicoronal ambulacrum III plates could be counted, counts of 10, 11 and 12 were seen in equal proportion.

Petals noticeably raised or inflated above test surface. The mean length of petals measured as a percentage of the distance to the ambitus in the line of each pore zone is for the anterior pair 58% (SD = 2%, n = 6) and posterior pair 54% (SD = 4%, n = 6). Poriferous zones curved, open distally, with outer pore rows more arcuate than inner ones. Petals almost parallel distally for the final 25% or so of their length. Petal interporiferous zones widest at their distal end. Distally, petals end abruptly, trailing podia not developed. Ambulacral pores are oblique elongate anisopores with round inner and slightly elongate outer pores. Tubercles not observed between pores. The anterior poriferous zone in ambulacrum II has 21–35 pore pairs; slightly more in ambulacrum I (24–36). The number of pore pairs in the anterior zone per mm of TL is 0.84 (SD = 0.1, n = 7). Mean width of ambulacrum II at ambitus is 133% of the mean width of interambulacrum 1 (SD = 14%, n = 5). Mean width of ambulacrum III 33%TL (SD = 2%, n = 6).

Peristome medium to large and longitudinally elongate. Food deep grooves extend from peristome around ambitus to apical disc, becoming less prominent apically. Three anterior grooves are almost straight; two posterior grooves arced very slightly laterally, each food

groove becoming wider upon reaching basicoronal plates and ending in a broad and flat region bordering the peristomial opening. Immediately adjacent to the peristome, small buccal pores occur at the side of the groove. Food grooves do not display crenulations as observed in the type species *M. australis*. Basicoronal plates twice as long as wide, outer margin slightly convex; the interambulacral plates are slightly longer than the ambulacral ones and end distally with an obtuse angled triangular projection.

Periproct submarginal, medium to large and circular lying within 10% of periproct's longitudinal diameter. It comes into contact aborally with interambulacral plates 3a/3b in 40% of specimens and 2a/3b in 60% of specimens (n=5).

Internally, a complex system of peripheral pillars and buttresses is developed around the test, although these are less well developed than in *M. australis* or *M. macnamarai*. Radiating interambulacral pillars or walls are not apparent. Central pillars are present and well developed. An intermurum is present on right hand side of the test, half way between marginal and central buttressing and comprising of intermittent group of columns.

Stratigraphy and age: As for *M. macnamarai*.

***Monostychia merrimanensis* Sadler, Holmes & Gallagher, 2019 (Fig. 3.b.3.)**

Type material: Holotype MV P332691, Paratypes MV P327753, 327754

Additional material: SAM P33713.1–53

Type locality: Former Merriman Creek Limestone Quarry, south-east of Rosedale, Victoria.

Type stratum: Interbedded limestones and marls of the lower Miocene Gippsland Limestone.

Etymology: ‘merrimanensis’, for the former quarry on Merriman Creek from where most specimens were sourced.

Diagnosis: *Monostychia* species characterised by an oval test, low domed profile ratio of width of ambulacrum to interambulacrum at ambitus >140%; slightly inflated petals; food grooves gently indented at margin; combing absent.

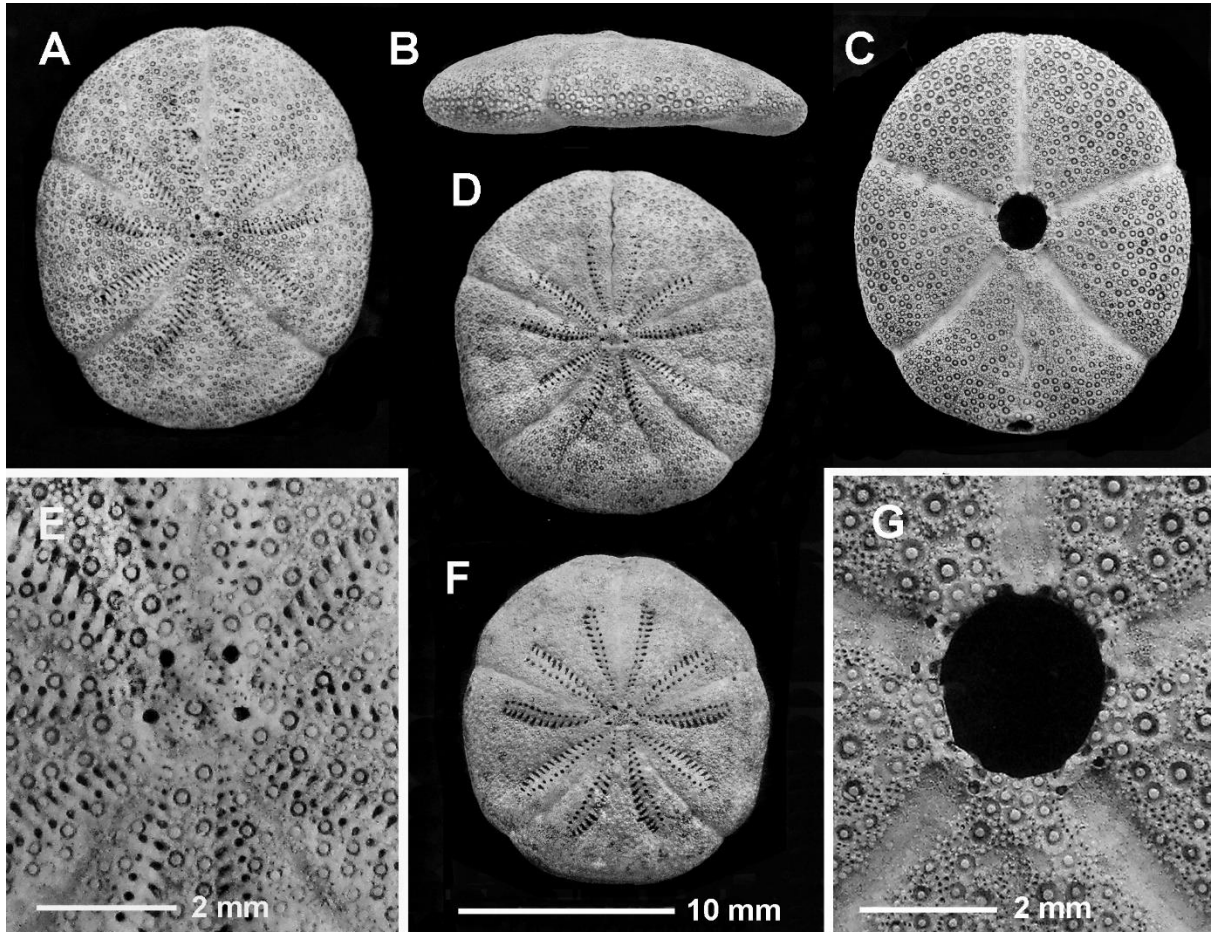


Fig. 3.b.3. *Monostychia merrimanensis* Sadler, Holmes & Gallagher, 2019. A–C, aboral, left lateral, and oral views, E & F, apical disc and peristome details of holotype MV P332691; D, aboral view of paratype MV P327754; F, aboral view of paratype MV P327753. All specimens from the lower Miocene Gippsland Limestone, S.E. of Rosedale, Victoria.

Description: Small oval test ranging in length from 5.9–21.4 mm; maximum width 78–93% TL (mean = 86%, SD = 3%, n = 101), occurring generally at the centre, but in the range 43–70% TL from anterior ambitus (mean = 50%, SD = 6%, n = 53). Height 20–34% TL

(mean = 26%, SD = 3%, n = 90); apex forward of the apical disc 33–48% TL from anterior ambitus (mean = 40%, SD = 3%, n = 82); apical disc 43–53% TL from anterior ambitus (mean = 49%, SD = 2%, n = 78).

Orally, test has a sunken peristome and slightly indented food grooves (Fig. 3.b.3.C). An indistinct keel runs from the periproct forward toward to the peristome. The apical surface of the test is slightly convex in both transverse and longitudinal profile; ambitus very tumid. Ambital notches minor, slightly deeper in ambulacra I and V than elsewhere. Anal notch lacking. Combing not apparent.

Of the 43 specimens for which plates could be observed in paired oral post-basicoronal interambulacra, plate counts were obtained in 136 of the possible 172 regions. 43% of the regions preserved had seven plates, 29% eight, 25% six, and the balance five or nine. For the paired ambulacra, post-basicoronal plate counts were obtained in 150 of a potential maximum of 188 regions; 42% of regions preserved had 10 plates. 26% had 11, 15% had nine, 11% had 12 and 3% had eight. Four specimens recorded 13 plates but at the first approximation this registers 0%. In the 39 specimens where post-basicoronal ambulacrum III plates were counted, 31% had 13 plates, 28% had ten, 21% had 12, 15% had 11 and 3% had nine

Petals slightly raised or inflated above test surface in most specimens. The mean length of petals, measured as a percentage of the distance to the ambitus in the line of each pore zone, is for the anterior pair 59% (SD = 6%, n = 41) and the posterior pair 56% (SD = 5%, n = 41). Poriferous zones slightly curved, open distally, with outer pore rows more arcuate than inner ones. Petals almost parallel distally for the final 25% or so of their length. Petal interporiferous zones widest at their distal end; mean distance between inner pores at the end of the anterior zone is 92% the mean distance between inner pores at the end of the posterior zone (SD = 10%, n = 47). Distally, petals end abruptly, trailing podia are not developed. Ambulacral pores are oblique elongate anisopores with round inner and oval outer pores. The

anterior poriferous zone in ambulacrum II has 9–18 pore pairs; slightly more in ambulacrum I (10–23). The number of pore pairs in the anterior zone per mm of TL is 0.92 (SD = 0.1, n = 39). Mean width of ambulacrum II at ambitus 147% mean width of interambulacrum 1 (SD = 20%, n = 52). Mean width of ambulacrum III 29% TL (SD = 3%, n = 51).

Peristome large and circular. Food grooves extend from peristome around the ambitus becoming less prominent towards the apical disc, Adorally, the three anterior grooves are straight and the two posterior grooves very slightly arced laterally. Grooves becomes wider upon reaching basicoronal plates and end in a broad, flat region bordering the peristomial opening. Immediately adjacent to the peristome, small buccal podial pores occur at the side of the groove, one on each side (Fig. 3.b.3.G.). These grooves do not display crenulations as observed in the type species *M. australis*. Basicoronal plates longer than wide, radial margins straight; interambulacral basicoronal plates end with an equilateral triangular projection and are about 10% longer than their ambulacral counterparts.

Periproct submarginal, medium size, oval in shape, angled posteriorly with edge touching the ambitus. In interambulacrum 5, periproct comes into contact adorally with plates 3a/3b but contact with plates 2a/2b, 2a/3b and 3a/4b also observed.

Internally, a complex system of peripheral pillars and buttresses is developed around the test, although these are less well developed than in *M. australis*. Radiating interambulacral pillars or walls are not apparent. Central pillars are present but sparse and not well developed. A minor and discontinuous circumferential wall of stereom is present on right hand side of the test, half way between marginal and central buttressing. This wall is interpreted as having segregated the proximal and distal tracts of the intestine.

Remarks: The key diagnostic features are summarised in Table 1. Unlike other described *Monostychia* species, with the exception of *M. etheridgei*, *M. merrimanensis* is oval in shape,

significantly smaller and has the periproct in touch with the margin. It has the greatest mean height and along with *M. macnamarai* (Sadler *et al.*, 2017), the most tumid margin.

Stratigraphy and age: Most of the specimens used in this study are from the former Gippsland Cement Quarry adjacent to Merriman Creek, south east of Rosedale, Victoria (Fig. 3.b.4., locality 1). They were found in the Gippsland Limestone, generally from 3–10m above the base of the quarry's south-western slope. The strata are largely cemented and contain numerous macrofauna including bivalves, bryozoans, brachiopods, gastropods as well as an echinoid fauna (Gallagher & Holdgate, 1996). The quarry has recently been filled and revegetated. Other specimens are recorded from both Dowd's Quarry and Brock's Quarry, close to Longford and on the opposite side of the Baragwanath Anticline to the Merriman Creek site.

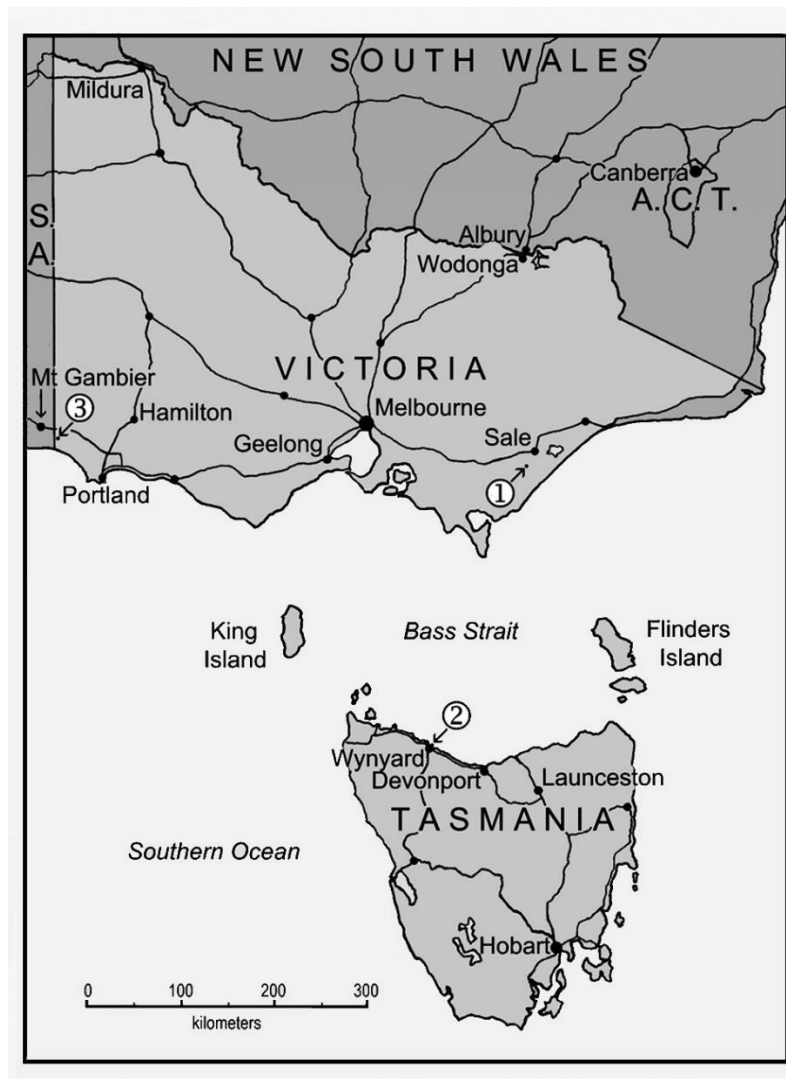


Fig. 3.b.4. Location map for three species of *Monostychia*. *M. merrimanensis* sp. nov. (1), *M. etheridgei* Woods, 1877 (2) and *M. glenelgensis* sp. nov. (3).

The Gippsland Limestone Formation conformably overlies the Lakes Entrance Formation, is of early Miocene, Longfordian [Burdigalian], age and consists of a thick sequence of marls and limestones with a higher carbonate content than the Lakes Entrance Formation (Gallagher *et al.*, 2001; Holdgate and Gallagher, 1997, 2003).

***Monostychia etheridgei* Woods, 1877 (Fig. 3.b.5.)**

1877 *Micraster etheridgei* n.s., Woods, p. 116.

1887 *Micraster Etheridgei* Johnston; Johnston, p.130.

1888 *Monostychia Etheridgei* (*Micraster Eth.*) Johnston; Johnston p.169.

1892 *Monostychia Etheridgei* Johnston; Tate, p. 192.

1925 *Monostychia Etheridgei* Johnston (*Micraster*); Lambert & Thiéry, p. 583.

1946 *Monostychia etheridgei* Johnston; Clark, p. 338.

2012 *Monostychia etheridgei* Woods; Squires, p.49.

2016 *Monostychia etheridgei* Woods; Sadler *et al.*, p. 350.

Type material: Holotype Z504, Tasmanian Museum and Art Gallery.

Additional material: MV P27351–54, P27358, P82434–35, P128077-8, P135101, P320411,

Type locality: Fossil Bluff, Wynyard, Tasmania.

Type stratum: The lower Miocene Fossil Bluff Sandstone.

Diagnosis: *Monostychia* species characterised by a flattened oval to pentagonal test, domed profile, ratio of width of ambulacrum to interambulacrum at ambitus >140%; food grooves strongly indented at margin; combing present.

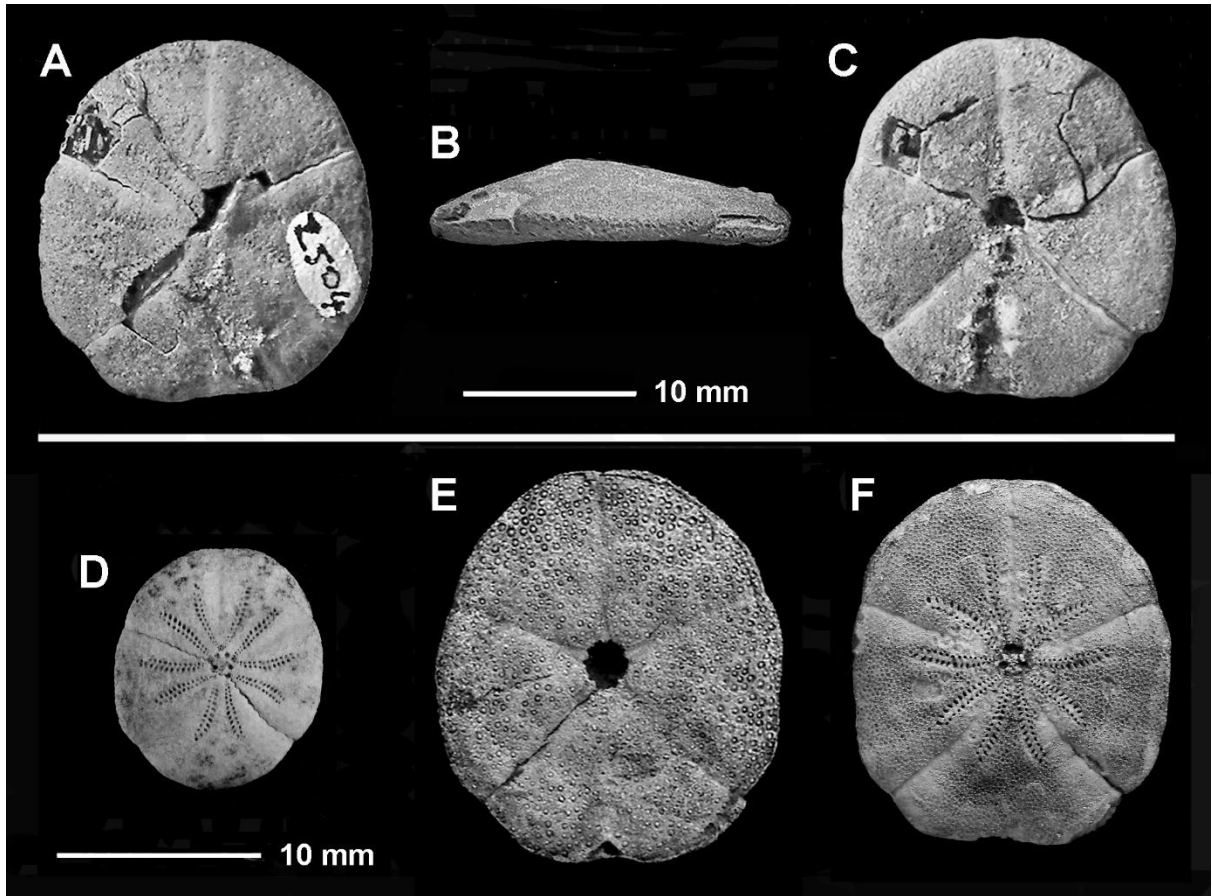


Fig. 3.b.5. *Monostychia etheridgei* Woods, 1877. A–C, aboral, left lateral, and oral views of holotype Z504; D, aboral view of MV P27375; E, oral view of MV P128077; F, aboral view of MV P 128078. All specimens from the lower Miocene Fossil Buff Limestone, Wynyard, Tasmania.

Description: The species was redescribed in the revision of *Monostychia* by Sadler *et al.* (2016) based solely on the damaged type specimen. The additional specimens now available for study are highly variable, particularly in relation to the size, test and petal shape. This suggests there may be more than one species represented, but the lack of comparable material and exact information of the bed from which specimens were found within the formation makes this difficult to determine.

Test very small to small, ranging from oval to pentagonal in shape; length 7.3–19.0 mm; maximum width 81–95% TL (mean = 88%, SD = 4%, n = 13), occurring generally at the centre, but in the range 44–70% TL from anterior ambitus (mean = 54%, SD = 8%, n = 13); height 16–30% TL (mean = 22%, SD = 4%, n = 11); apex 49–52% TL from anterior ambitus

(mean = 51%, SD = 3%, n = 2); apical disc 47–52% TL from anterior ambitus (mean = 49%, SD = 2%, n = 12).

Orally, test has a sunken peristome and strongly indented food grooves. An indistinct keel runs from the periproct forward toward to the peristome. The apical surface of the test is convex in both transverse and longitudinal profile; ambitus tumid; ambital notches minor, slightly deeper in ambulacra I and V than elsewhere; anal notch lacking; indistinct combing noted on one specimen only.

Of the 4 specimens for which plates could be observed in paired oral post-basicoronal interambulacra plate counts, were obtained in 15 of the possible 16 regions. Of these, 93% of the regions preserved had six plates, and 7% seven. For the paired post-basicoronal ambulacra plate counts were obtained in 14 of a potential maximum of 16 regions; 50% of regions preserved had eight plates, 29% 10, and 21% nine. Where post-basicoronal ambulacrum III plates could be counted, 50% had 10 plates, 25% nine, and 25% eight.

Petals are slightly raised or inflated above test surface in most specimens. The mean length of petals, measured as a percentage of the distance to the ambitus in the line of each pore zone, is for the anterior pair 67% (SD = 9%, n = 9) and posterior pair 60% (SD = 8%, n = 9). Poriferous zones straight to slightly curved, open distally, with outer pore rows more arcuate than inner ones and with interporiferous zones widest at their distal end. Petals almost parallel distally for the final 35% or so of their length. Ambulacral pores are oblique elongate anisopores with round inner and rounded to elongate outer pores. Tubercles not observed between pores. The anterior poriferous zone in ambulacrum II has 10–17 pore pairs; slightly more in ambulacrum I (12–18). The number of pore pairs in the anterior zone per mm of TL is 0.97 (SD = 0.2, n = 8). At the ambitus the mean width of ambulacrum II is 193% mean width of interambulacrum 1 (SD = 39%, n = 2). Mean width of ambulacrum III 37% TL (SD = 3%, n = 2).

Peristome large and circular. Food grooves extend from peristome around ambitus, becoming less prominent towards the apical disc. All grooves are straight, each one becoming wider upon reaching basicoronal plates and ending in a broad and flat region bordering the peristomial opening. Immediately adjacent to the peristome, small buccal podial pores occur at the edge of the groove, one on each side. Food grooves do not display crenulations as observed in the type species *M. australis*. Basicoronal plates longer than wide, radial margin slightly rounded; ambulacral and interambulacral basicoronal plates are the same length, the latter with an obtuse angular projection.

Periproct submarginal, large and circular in shape, angled posteriorly with the edge touching the ambitus and usually in contact with interambulacrum 5 plates 3a/3b adorally, but sometimes with plates 2a/2b and 2a/3b.

Internal buttressing has not been observed.

Stratigraphy and age: The specimens used in this study are from the early Miocene, Longfordian [Burdigalian], Fossil Bluff Sandstone near Fossil Bluff near Wynyard, Tasmania (Fig. 3.b.4., locality 2). The Table Cape Group which comprises the Freestone Cove Sandstone overlain by the Fossil Bluff Sandstone (Gee, 1971) disconformably overlies the Permian Wynyard Tillite. The late Oligocene Freestone Cove Sandstone is a ferruginous coarse sandstone less than 1.2m thick, interpreted as being deposited in very shallow water, possibly intertidal, at the beginning of a transgression and is equivalent to the Jan Juc Marl in Torquay, Victoria (Quilty, 1972, McLaren *et al.*, 2009). However, The Fossil Bluff Sandstone is up to 24m thick and interpreted as being deposited in deeper water, possibly later in the same transgression that deposited the Freestone Cove Sandstone. It has a variety of lithologies from a friable yellow glauconitic sandstone to fine siltstones, calcareous sandstones and calcarenites (Quilty, 1972).

***Monostychia glenelgensis* Sadler, Holmes & Gallagher, 2019 (Fig. 3.7.)**

Holotype. MV P27375 from the Upper Gambier Limestone.

Additional material: MV P27376–82, P27384–85, P305221, P305223–28, P305244A, P305245–46, P306714, P317117.

Type locality: Banks of the Glenelg River upstream of Nelson, Victoria.

Type stratum: Lower Miocene Upper Gambier Limestone.

Etymology: ‘*glenelgensis*’, refers to the Glenelg River in western Victoria, the area from which specimens were sourced.

Diagnosis: *Monostychia* species characterized by pentagonal to oval test; domed profile in lateral view; ratio of width of ambulacrum to interambulacrum at ambitus >140%; tumid margin; apex greater than 41% TL from anterior margin; periproct not in touch with margin; length of ambulacral basicoronal plates less than 160% of their width; inflated petals.

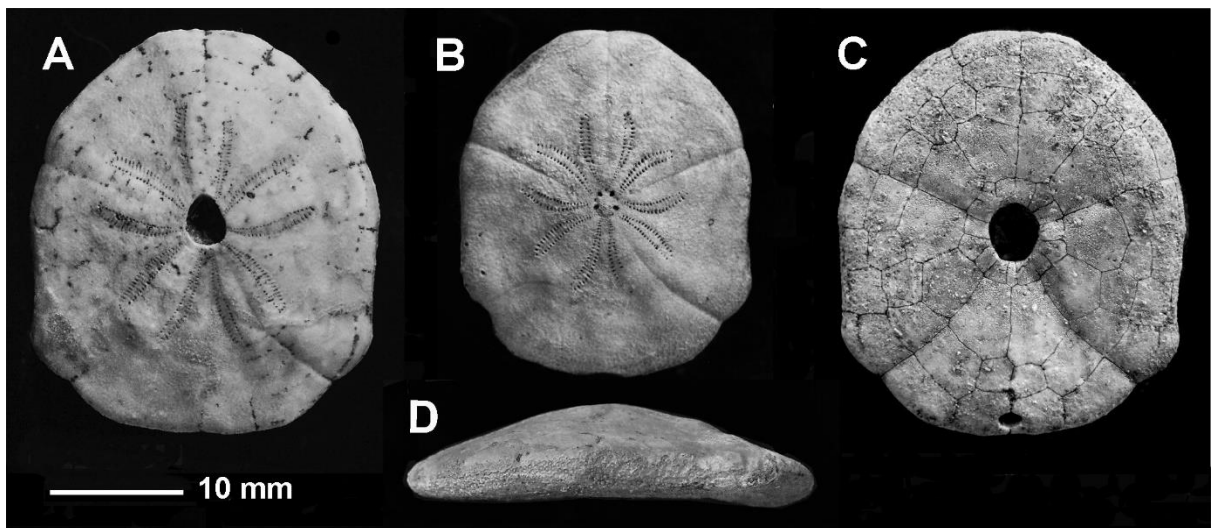


Fig. 3.b.6.. *Monostychia glenelgensis* Sadler, Holmes & Gallagher, 2019. A, C & D, aboral, oral, and left lateral, views of holotype MV P27375; B, aboral view of paratype MV P305224. Both specimens from the lower Miocene upper Gambier Limestone, north of Nelson, Victoria.

Description: Test small to medium in size, variable in shape from pentagonal to oval in plan and flattened to distinctly domed in profile. Specimens range in length from 17.2–34.1 mm; maximum width 78–91% TL (mean = 84%, SD = 4%, n = 31) occurring generally at the centre, but in the range 41–74% TL from anterior ambitus (mean = 54%, SD = 13%, n = 30). Test 17–26% TL high (mean = 22%, SD = 2%, n = 31); apex 41–50% TL from anterior ambitus (mean = 47%, SD = 2%, n = 28); apical disc 48–52% TL from anterior ambitus (mean = 50%, SD = 1%, n = 28).

Orally, test has a slightly sunken peristome and indented food grooves. An indistinct keel runs from the periproct forward toward to the peristome. The apical surface of the test ranges from distinctly convex to slightly concave in both transverse and longitudinal profile, a feature that may reflect ontogeny. Ambitus tumid, no anal notch but minor ambulacral notches, slightly deeper in ambulacra I and V than elsewhere. Indistinct combing has been observed in only one specimen.

Of the 23 specimens for which plates could be observed in paired post-basicoronal interambulacra, plate counts were obtained in 50 of the possible 92 regions. 54% of regions had seven plates, 28% eight and 14% six; regions with nine plates were also observed, but more rarely. For the paired post-basicoronal ambulacra, post-basicoronal plate counts were obtained in 61 of a potential maximum of 84 regions; 54% had 10 plates, 36% nine, 8% had eight and 2% had 11. In the 18 specimens where unpaired post-basicoronal ambulacrum III plates could be counted, 44% had 11 plates, 33% had 10, 17% had 12 and 6% had 13.

Petals are noticeably raised or inflated above test surface in most specimens. The mean length of petals measured as a percentage of the distance to the ambitus in the line of each pore zone is for the anterior pair 56% (SD = 5%, n = 28) and posterior pair 52% (SD = 5%, n = 27). Poriferous zones slightly curved, open distally, with outer pore rows more arcuate than inner ones. Petals almost parallel distally for the final 40% or so of their length. Distally,

petals end abruptly, trailing podia not developed. Ambulacral pores are oblique elongate anisopores with round inner and elongate, slit-like outer pores. Tubercles not observed between pores. The anterior poriferous zone in ambulacrum II has 17–30 pore pairs; slightly more in ambulacrum I (21–31). The number of pore pairs in the anterior zone per mm of TL is 0.84 (SD = 0.1, n = 25). Mean width of ambulacrum II at ambitus is 152% of the mean width of interambulacrum 1 (SD = 19%, n = 31). Mean width of ambulacrum III 32% TL (SD = 2%, n = 31).

Peristome large and circular to oval. Food grooves extend from peristome around ambitus to apical disc, becoming less prominent apically. Three anterior grooves are almost straight; two posterior grooves arced very slightly laterally, each food groove becoming wider upon reaching basicoronal plates and ending in a broad and flat region bordering the peristomial opening. Immediately adjacent to the peristome, small buccal pores occur at the side of the groove, one on each side angled at 45°. Food grooves do not display crenulations as observed in the type species *M. australis*. Basicoronal plates longer than wide, outer margin flat; the interambulacral plates narrow markedly toward the peristome, are about 20–30% longer than the ambulacral ones and end distally with an obtuse angled projection.

Periproct submarginal, medium size, oval in shape. Distance between posterior edge and ambitus is 30–70% of periproct's longitudinal diameter. It comes into contact adorally with interambulacral plates 3a/3b.

Internally, a complex system of peripheral pillars and buttresses is developed around the test, although these are less well developed than in *M. australis*. Radiating interambulacral pillars or walls are not apparent. Central pillars are present but sparse and not well developed. A wall of stereom is present on right hand side of the test, half way between marginal and central buttressing. This wall is interpreted to have segregated the proximal and distal tracts of the intestine.

Stratigraphy and age: The specimens used in this study derive from outcrops of the Upper Gambier Limestone along the banks of the Glenelg River in both South Australia and Victoria and from the nearby Princess Margaret Rose Cave area (Fig. 3.b.4., locality 3). The Upper Gambier Limestone forms part of the Gellibrand Marl Formation of the Heytesbury Group (Gallagher *et al.*, 1999; Gallagher and Holdgate, 2000). While the Group extends from late Oligocene to early Miocene in the western end of the Otway Basin, the Glenelg River area, where the specimens occur, is early Miocene in age (Holdgate and Gallagher, 2003).

***Monostychia robheathi* sp. nov.** (Fig. 3.b.7.)

Type material: Holotype SAM P33717, Paratype SAM P33718

Additional material: SAM P33719–28

Type locality: Steinfeld (formerly Stonefield), South Australia (34.3266S, 139.3000E).

Type stratum: Mannum Formation.

Etymology: The species is named after Dr Rob Heath, petroleum geologist and palaeontologist, formerly of Santos Limited and Woodside Limited.

Diagnosis: *Monostychia* species characterised by an elongate test; domed aboral profile; ratio of width of ambulacrum to interambulacrum at ambitus >140%; slightly inflated petals; periproct in touch with margin.

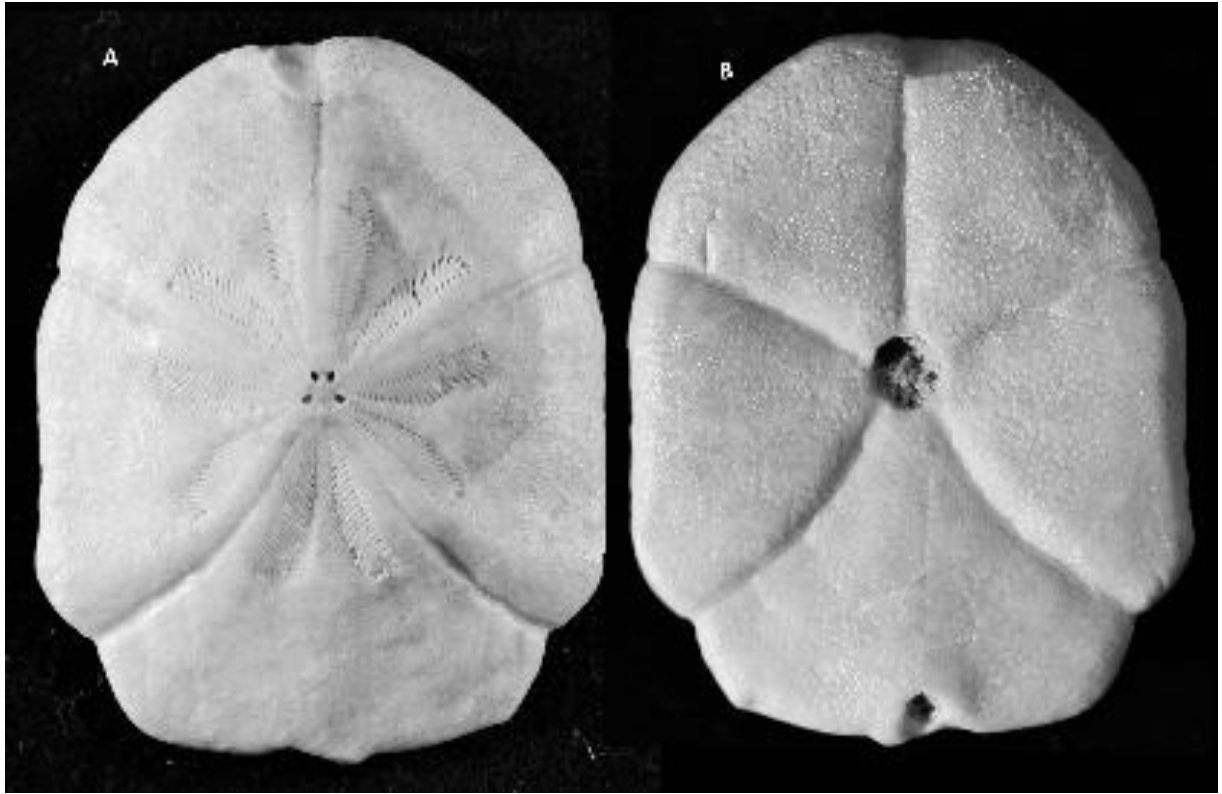


Fig. 3.b.7. Holotype of *Monostychia robheathi* sp. nov. (SAM P33717), aboral (A) and oral (B) view; TL = 33.80 mm.

Description: Small to medium test elongate in shape, ranging in length from 14.0–36.0 mm; maximum width 75–89% TL (mean = 83%, SD = 4%, n = 12), occurring generally at the centre, but in the range 43–75% TL from anterior ambitus (mean = 54%, SD = 11%, n = 12). Height 17–23% TL (mean = 21%, SD = 2%, n = 12); apex forward of the apical disc 37–49% TL from anterior ambitus (mean = 45%, SD = 4%, n = 12); apical disc 47–52% TL from anterior ambitus (mean = 49%, SD = 1%, n = 12).

Orally, test has a sunken peristome and distinctly indented food grooves. A distinct keel runs from the periproct forward toward to the peristome. The apical surface of the test is convex in both transverse and longitudinal profile; ambitus very tumid. Ambital notches minor, slightly deeper in ambulacra I and V than elsewhere. Anal notch lacking. Combing present in some specimens but muted.

Of the eight specimens for which plates could be observed in paired oral post-basicoronal interambulacra, plate counts were obtained in 23 of the possible 32 regions, 57% of the regions preserved had seven plates, 39% eight, and 4% had nine. For the paired ambulacra, post-basicoronal plate counts were obtained in 18 of a potential maximum of 32 regions; 56% of regions preserved had 10 plates and 44% nine. In the five specimens where post-basicoronal ambulacrum III plates were counted, 60% had 12 plates with 20% in each of ten and 11.

Petals raised or inflated above test surface. The mean length of petals, measured as a percentage of the distance to the ambitus in the line of each pore zone, is for the anterior pair 56% (SD = 5%, n = 12) and the posterior pair 50% (SD = 5%, n = 12). Poriferous zones distinctly curved particularly toward the tip, open distally, with outer pore rows more arcuate than inner ones. Petals almost parallel distally for the final 40% or so of their length. Distally, petals end abruptly, trailing podia are not developed. Ambulacral pores are oblique elongate with inner pores about twice as long as wide and outer pores much more elongate. A furrow connects the two. The anterior poriferous zone in ambulacrum II has 15–30 pore pairs; slightly more in ambulacrum I (14–35). The number of pore pairs in the anterior zone per mm of TL is 0.93 (SD = 0.1, n = 12). Mean width of ambulacrum II at ambitus 162% mean width of interambulacrum 1 (SD = 24%, n = 11). Mean width of ambulacrum III 33% TL (SD = 2%, n = 11).

Peristome large and round to pentagonal. Food grooves extend from peristome around the ambitus and remain prominent towards the apical disc, Adorally, the three anterior grooves are straight and the two posterior grooves very slightly arced laterally. Grooves becomes wider upon reaching basicoronal plates and end in a broad, flat region bordering the peristomial opening. Immediately adjacent to the peristome, small buccal podial pores occur at the side of the groove, one on each side. These grooves do not display crenulations as

observed in the type species *M. australis*. Basicoronal plates are slightly longer than wide becoming distinctly wider toward their end, radial margins straight; interambulacral basicoronal plates end with an equilateral triangular projection and are about 20% longer than their ambulacral counterparts.

Periproct submarginal, medium size, circular, angled posteriorly with edge about 10% periproct diameter from margin. In interambulacrum 5, periproct comes into contact adorally with plates 3a/3b but contact with plates 2a/2b, 2a/3b also occurs.

A well-developed, complex system of peripheral pillars and buttresses occurs around the test. Radiating interambulacral pillars or walls are not apparent. Central pillars are present, but poorly developed. In addition, an intermulum is present on the right-hand side of the test, lying half way between the marginal and central buttressing and comprised of an uninterrupted thick wall of stereom.

Stratigraphy and age: Specimens P33717–18, P33720 and P33725–28 are from the type locality at Steinfeld, the remaining specimens are from the cliffs of the Murray River near Blanchetown (34.3601S, 139.6309E). In both cases they are from the Mannum Formation. The Mannum Formation ranges in age from late Oligocene to early Miocene (Gallagher & Gourley, 2007) but these specimens come from the upper member and should be considered early Miocene. Lithologically it is a calcareous sandstone with clayey pockets that tends to weather to a “raggy” limestone (Ludbrook, 1961). In both the Steinfeld and Blanchetown localities the specimens are found in association with *Lovenia forbesi* (Woods 1862), *Eupatagus murrayensis* Laube 1869 and *Ortholophus woodsi* (Laube 1869).

***Monostychia elongata* (Duncan, 1877) (Fig. 3.b.8.) (= *M. australis*)**

1877 *Arachnoides elongatus*, sp. nov., Duncan, p. 48, pl. 3, fig. 8.

1883 *M. elongatus* (Duncan sub *Arachnoïdes*); Pomel, p. 70.

1890 *Clypeaster (Monostychia) australis* var. *elongata*; Gregory, p. 487.

1948 *Monostychia australis*, var. *elongata*; Mortensen, pp. 154–155, fig. 93a–d.

Diagnosis. As for *M. australis*.

Material. The type is lodged at the Natural History Museum London (E42457). Based on the specimens examined in the South Australian Museum, Museum Victoria and the type, along with the description of *M. glenelgensis* Sadler *et al.*, 2019, *M. elongata* is not a unique species or should be placed into synonymy with *M. australis*.

Remarks. Duncan (1877) did not discuss how this species can be distinguished from *M. australis* and provided only a lateral view (Fig. 1D). Although his description mentions no features that are not present in *M. australis*, Duncan (1877) commented that “*The test slopes very gradually upwards from the ambitus for a little distance, and then suddenly forms a sharp curve...*”. This, combined with only the lateral view being presented in the original figures infers that *M. elongata* differs from *M. australis* in height or the manner in which the slope of the test changes. Neither of these appear correct although the posterior apical surface is concave compared to *M. australis* in which it is straight. In terms of height, the type specimen (E42457) has a height/length ratio of 25%; *M. australis* has a maximum of 29%, minimum of 18% and mean of 22% (Fig. 4B). The shape shown by Duncan (1887) lies within the range encompassed by *M. australis*. Duncan (1887) did not explain the etymology of ‘*elongata(us)*’. One could interpret it to mean the test is comparatively elongate compared to *M. australis*. Durham *et al.* (1966) included a distinctly elongate form in their description of *Monostychia*, although a length/width ratio was not included in the original description. Specimen P22618 in the South Australian Museum, which comprises five individuals labelled as *M. elongata*, was examined in this work. It was concluded they were all *M. australis* and not from the type stratum of *M. elongata* (Gambier Limestone) as labelled, but

from the Glenforslan Formation. Several specimens labelled as *M. elongata* in Museum Victoria do not match either the description or the features of the type specimen and are not here considered *M. elongata* and have since been assigned to *M. glenelgensis* Sadler *et al.*, 2019. Sadler *et al.* (2016) assigned *M. elongata* Duncan 1877 to a junior synonym of *M. australis* based primarily on it being described as having a convex upper test profile that curved sharply upward in a tall, tent-like manner; this is not the case with *M. glenelgensis*. As these are the only specimens of *Monostychia* known from the Gambier Limestone this data further supports synonymising *M. elongata* with *M. australis*.

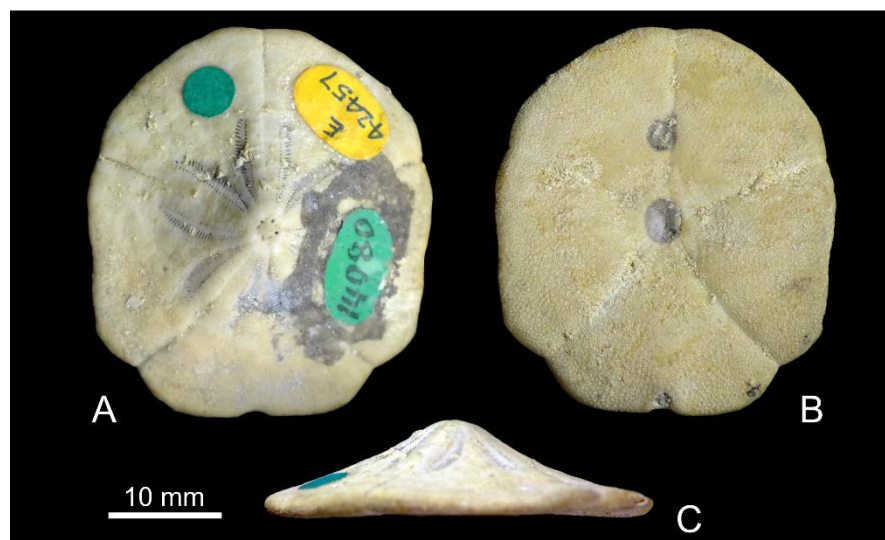


Fig. 3.b.8. Figured syntype of *Arachnoides elongata* Duncan, 1877. (NHML E42451) from Mt Gambier, Victoria; **A**, aboral, **B**, oral, and **C**, left lateral views.

Remarks on the species of *Monostychia*

The key diagnostic features of the type and six other species allocated to this genus are summarised in Table 3.b.1. In addition, a box plot of the seven species is presented in Figs 3.b.9–16. with each figure representing a different diagnostic feature. *M. alanrivi* is similar to *M. australis* in size and shape, although these two species differ in the nature of the lateral

profile and periproct position. In addition, *M. australis* has a greater width to length ratio (Fig. 3.b.9.), lower ratio of ambulacral to interambulacral width at the ambitus (Fig. 3.b.12.) and a smaller number of plates in each of the paired interambulacra (Fig. 3.b.14.), paired ambulacra (Fig. 3.b.15.) and ambulacrum III (Fig. 3.b.16.).

M. glenelgensis is also similar to *M. australis* in size and general shape, however, unlike the latter it has a test profile that is strongly convex in larger specimens and possesses inflated petals. Compared to *M. glenelgensis*, *M. australis* has a greater width to length ratio (Fig. 3.b.9.), lower ratio of ambulacral to interambulacral width at the ambitus (Fig. 3.b.12.) and a smaller number of plates in each of the paired interambulacra (Fig. 3.b.14.), paired ambulacra (Fig. 3.b.15.) and ambulacrum III (Fig. 3.b.16.).

M. macnamarai approaches *M. glenelgensis* in size, shape and profile, but can be separated by the distinctly narrower test compared to its length (Fig. 3.b.9.), the larger number of plates in the paired ambulacra (Fig. 3.b.15.) and ambulacrum III (Fig. 3.b.16.), distinctly longer petals and increased pore numbers.

M. robheathi is similar to *M. australis* but can be separated on the very thick ambitus with the strongly convex profile and position of the periproct. In addition, *M. australis* has a greater width to length ratio (Fig. 3.b.9.), greater height to length ratio (Fig. 3.b.10.), lower ratio of ambulacral to interambulacral width at the ambitus (Fig. 3.b.12.) and a smaller number of plates in each of the paired interambulacra (Fig. 3.b.14.), paired ambulacra (Fig. 3.b.15.) and ambulacrum III (Fig. 3.b.16.).

M. robheathi is also similar to *M. macnamarai* but can be separated by the shorter petals, smaller number of pore pairs and position of the periproct. In addition, *M. robheathi* has a greater width to length ratio (Fig. 3.b.9.), lesser height to length ratio (Fig. 3.b.10.) and a smaller number of plates in each of the paired ambulacra (Fig. 3.b.15.) and ambulacrum III (Fig. 3. b.16.).

The two very small to small species, *M. etheridgei* and *M. merrimanensis* are easily distinguished from the other five species, however, they are quite similar to one another. They can be separated based on relative petal length and, to a lesser extent, the shape of the interambulacral basicoronal plates. In addition, *M. etheridgei* has a greater width to length ratio (Fig. 3.b.9.), lesser height to length ratio (Fig. 3.b.10.), higher number of pores pairs per mm TL (Fig. 3.b.11.), higher ratio of ambulacral to interambulacral width at the ambitus (Fig. 3.b.12.) (indeed, the highest of all *Monostychia* species), a higher ratio of width of ambulacrum III at the margin versus TL (Fig. 3.b.13.) and a smaller number of plates in each of the paired interambulacra (Fig. 3.b.14.), paired ambulacra (Fig. 3.b.15.) and ambulacrum III (Fig. 3.b.16.).

A key to the species is provided (Table 3.b.2.).

Diagnostic feature	<i>M. australis</i> Laube, 1869	<i>M. macnamarai</i> Sadler, Martin & Gallagher, 2017	<i>M. alanruxi</i> Sadler, Martin & Gallagher, 2017	<i>M. merrimanensis</i> Sadler, Holmes & Gallagher, 2019	<i>M. etheridgei</i> Woods, 1877	<i>M. glenelgensis</i> Sadler, Holmes & Gallagher, 2019	<i>M. robheathi</i> sp. nov.
Test plan outline	Reuleaux pentagonal to oval	Elongate oval	Reuleaux pentagonal to oval	Oval	Oval to pentagonal	Oval to pentagonal	Elongate oval
Test length	Small to medium	Medium	Medium	Small	Very small to small	Small to medium	Small to medium
Test lateral profile, apical surface	Slightly concave to apex	Strongly convex	Convex from ambitus becoming slightly concave near apex	Slightly convex	Convex	Flat to distinctly convex	Strongly convex
Oral surface profile	Flat orally except for drooping tail	Peristome and food grooves deeply indented; drooping tail	Flat with slightly sunken peristome; drooping tail	Sunken peristome; slightly indented food grooves; drooping tail	Sunken peristome; strongly indented food grooves; drooping tail	Slightly sunken peristome; strongly indented food grooves; drooping tail	Sunken peristome; strongly indented food grooves; drooping tail
Mean height	22% TL	22% TL	19% TL	26% TL	22% TL	22% TL	21% TL
Distance of apex from anterior (mean)	50% TL	34% TL	40% TL	40% TL	51% TL	47% TL	45% TL
Ambitus	Tumid	Very tumid	Tumid	Very tumid	Tumid	Tumid	Very tumid

Diagnostic feature	<i>M. australis</i> Laube, 1869	<i>M. macnamarai</i> Sadler, Martin & Gallagher, 2017	<i>M. alanrxi</i> Sadler, Martin & Gallagher, 2017	<i>M. merrimanensis</i> Sadler, Holmes & Gallagher, 2019	<i>M. etheridgei</i> Woods, 1877	<i>M. glenelgensis</i> Sadler, Holmes & Gallagher, 2019	<i>M. robheathi</i> sp. nov.
Interambulacral plates in oral paired interambulacra	6-7	7-8	7-8	6-8	6	7-8	7-8
Post-basicoronal amb. plates in oral paired amb.	8-9	10-12	9-11	10-11	8-10	9-10	9-10
Post-basicoronal plates in anterior oral ambulacra III	8-10	11-13	10-12	10-13	8-10	10-11	11-12
Anterior petal to ambitus (mean)	52%	65%	58%	59%	67%	56%	56%
Posterior petal to ambitus (mean)	48%	60%	54%	56%	60%	52%	50%
Number of pore pairs	Ant. 15–37 Post. 17–40	Ant. 18–40 Post. 28–41	Ant. 21–35 Post. 24–36	Ant. 9–18 Post. 10–23	Ant. 10–17 Post. 12–18	Ant. 17–30 Post. 21–31	Ant. 15–30 Post. 14–35

Diagnostic feature	<i>M. australis</i> Laube, 1869	<i>M. macnamarai</i> Sadler, Martin & Gallagher, 2017	<i>M. alanrxi</i> Sadler, Martin & Gallagher, 2017	<i>M. merrimanensis</i> Sadler, Holmes & Gallagher, 2019	<i>M. etheridgei</i> Woods, 1877	<i>M. glenelgensis</i> Sadler, Holmes & Gallagher, 2019	<i>M. robheathi</i> sp. nov.
Number pore pairs per mm TL (mean)	0.87	0.87	0.90	0.92	0.97	0.84	0.93
Petals inflated	Barely	Noticeably	Noticeably	Slightly	Slightly	Noticeably	Noticeably
Amb. width at ambitus as a % of interamb. width (mean)	128%	150%	133%	147%	193%	152%	162%
Width ambulacrum III at ambitus as percentage TL	33%	32%	33%	29%	37%	32%	33%
Submarginal periproct	Lacriform with about 30% to ambitus	Circular to oval with 10–20% to ambitus	Circular, 0% – 10% of the ambitus	Oval, touching ambitus	Circular, touching ambitus	Oval, 30% –70% of the ambitus	Circular, touching ambitus
Contact plates with periproct (principal)	3a/3b	3a/3b	2a/3b	3a/3b	3a/3b	3a/3b	3a/3b
Interambulacral basicoronal plates	10% longer than basicoronal plates; obtuse angled triangular projection	30% longer than basicoronal plates; equilateral triangular projection	Slightly longer than basicoronal plates; obtuse angled triangular projection	10% longer than basicoronal plates; equilateral triangular projection	Same length as basicoronal plates; obtuse angled triangular projection	20% –30% longer than basicoronal plates; obtuse angled triangular projection	20% longer than basicoronal plates; equilateral triangular projection

Table 3.b.1. Comparison of diagnostic features of the seven species of Monostychia.

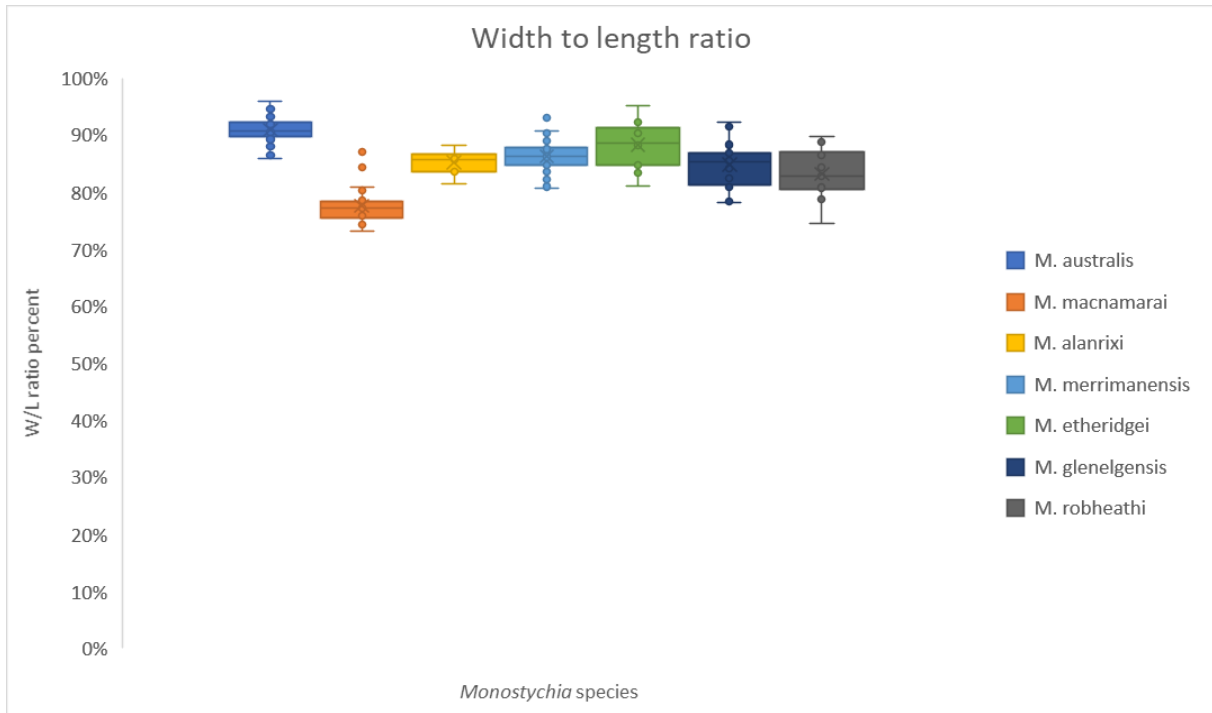


Fig. 3.b.9. Box plot of width to length ratio of *Monostychia* species.

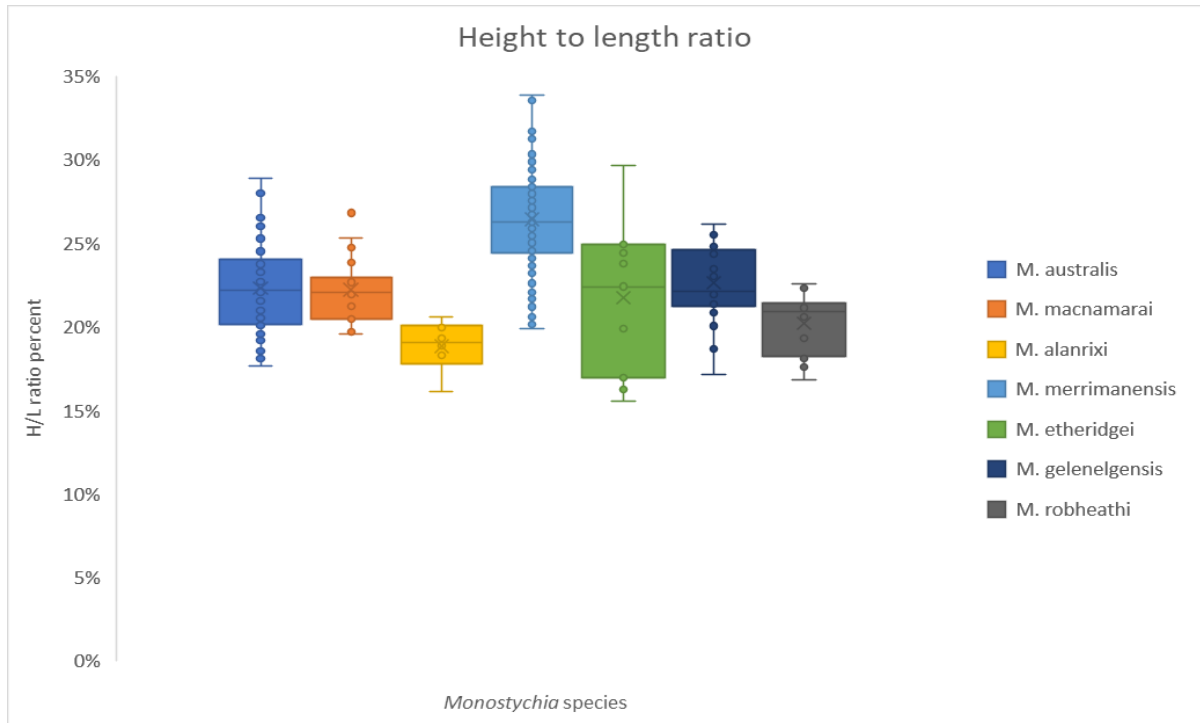


Fig. 3.b.10. Box plot of height to length ratio of *Monostychia* species.

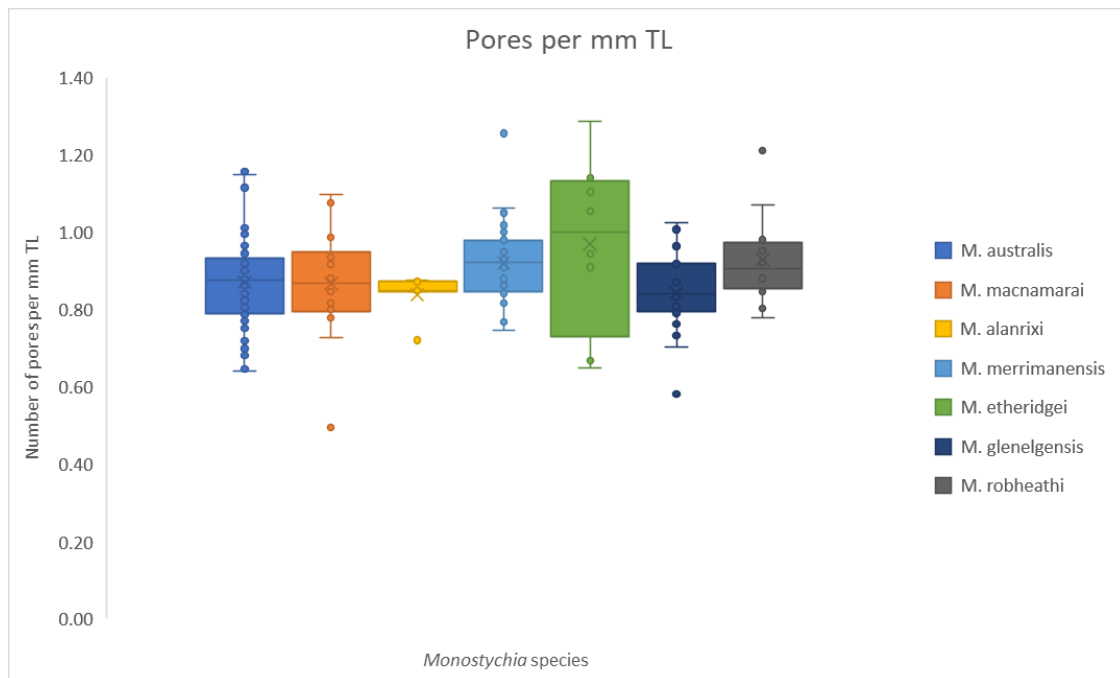


Fig. 3.b.11. Box plot of number of pores per mm TL of *Monostychia* species.

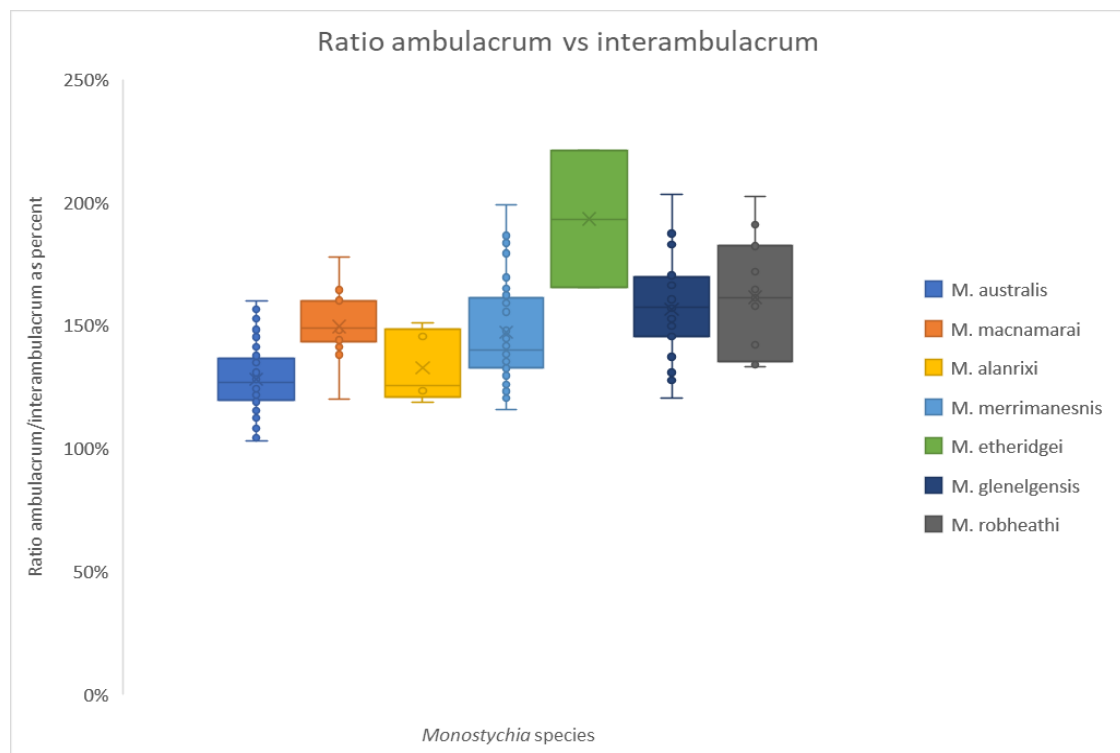


Fig. 3.b.12. Box plot of the ratio of ambulacrum width at ambitus against interambulacrum width of *Monostychia* species.

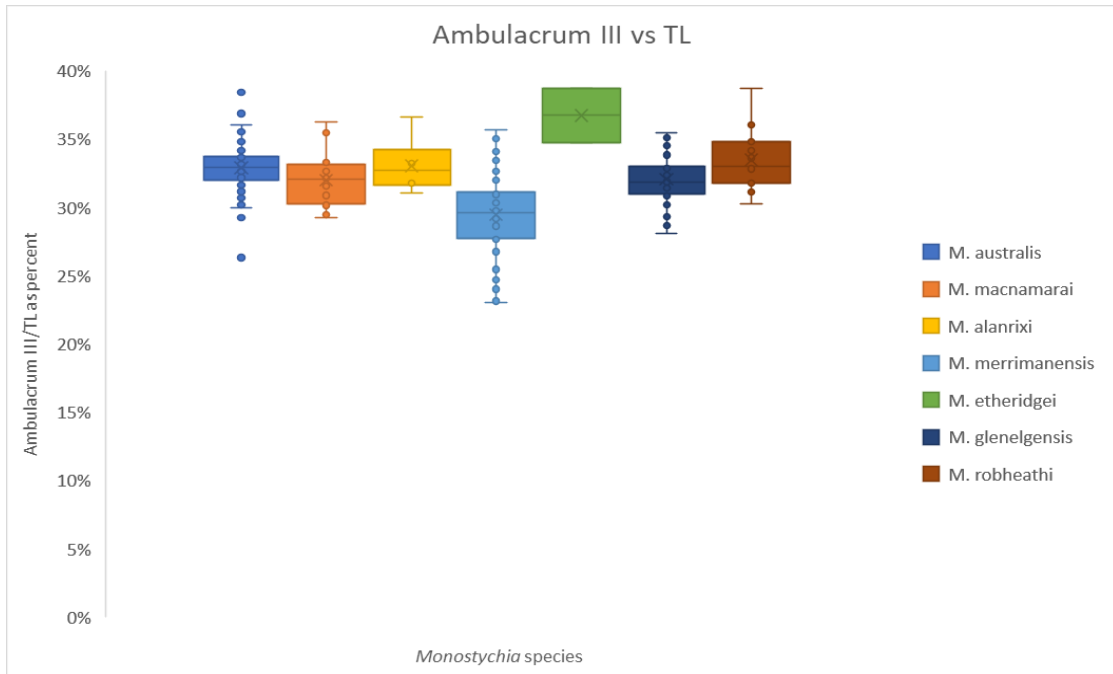


Fig. 3.b.13. Box plot of the ratio of width of ambulacrum III at ambitus against test length (TL) of *Monostychia* species.

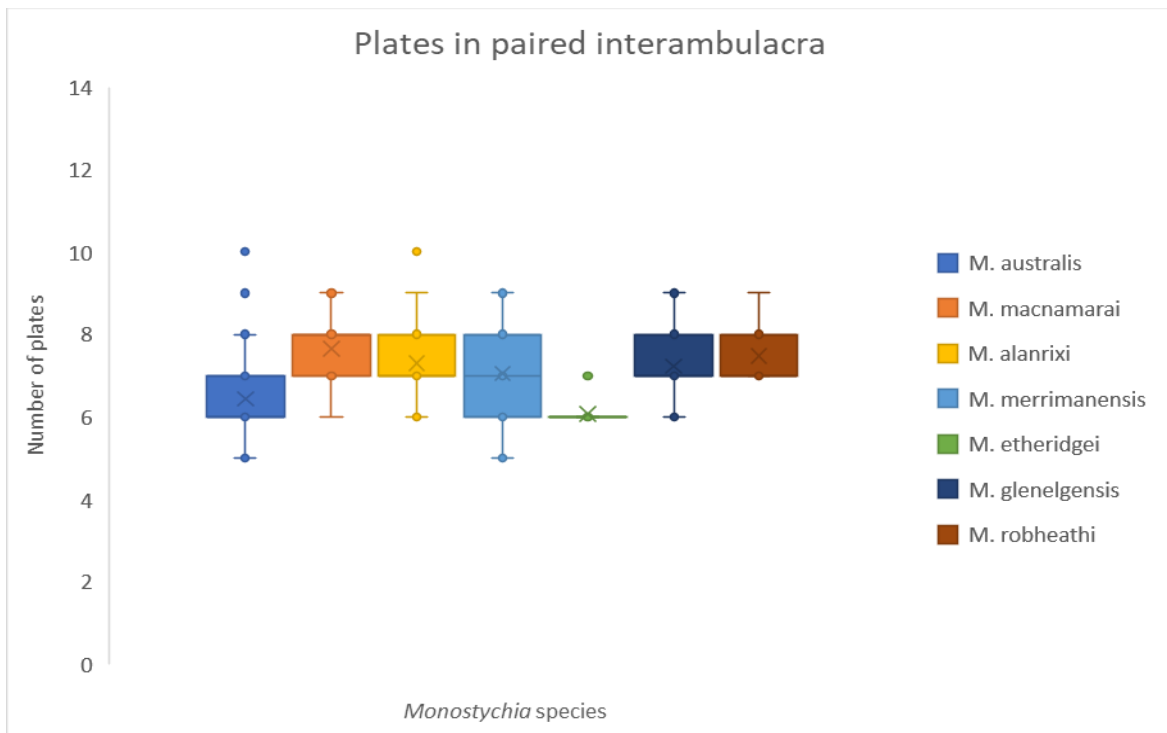


Fig. 3.b.14. Box plot of the number of plates in the paired interambulacra on the oral surface of *Monostychia* species.

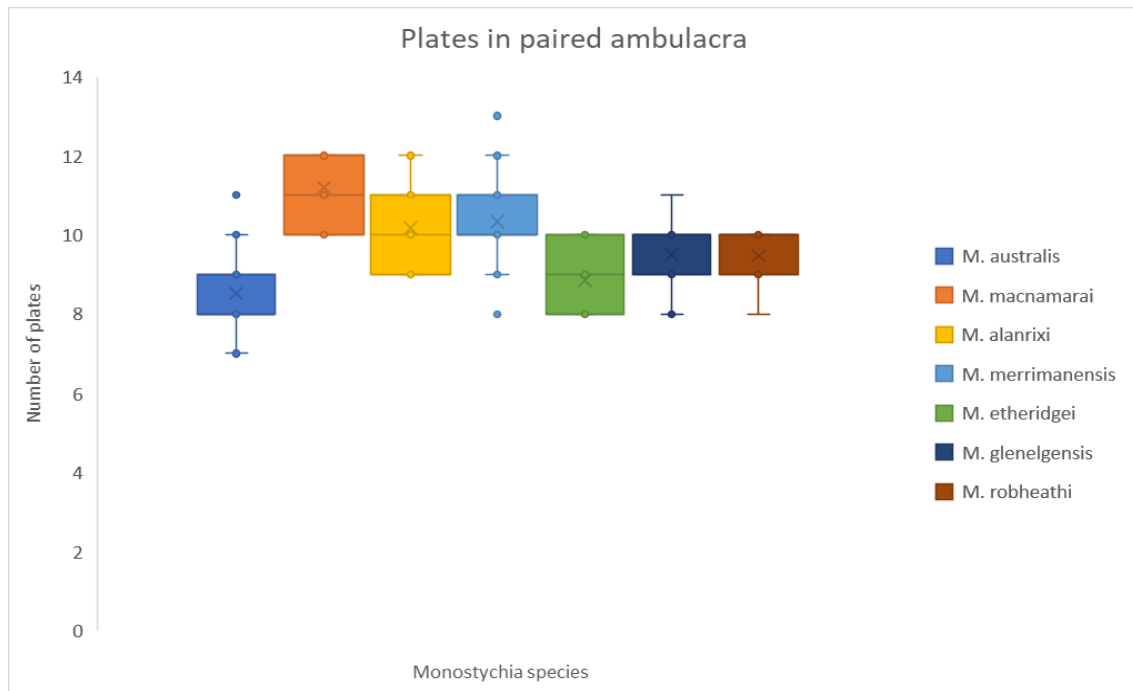


Fig. 3.b.15. Box plot of the number of plates in the paired ambulacra on the oral surface of *Monostychia* species.

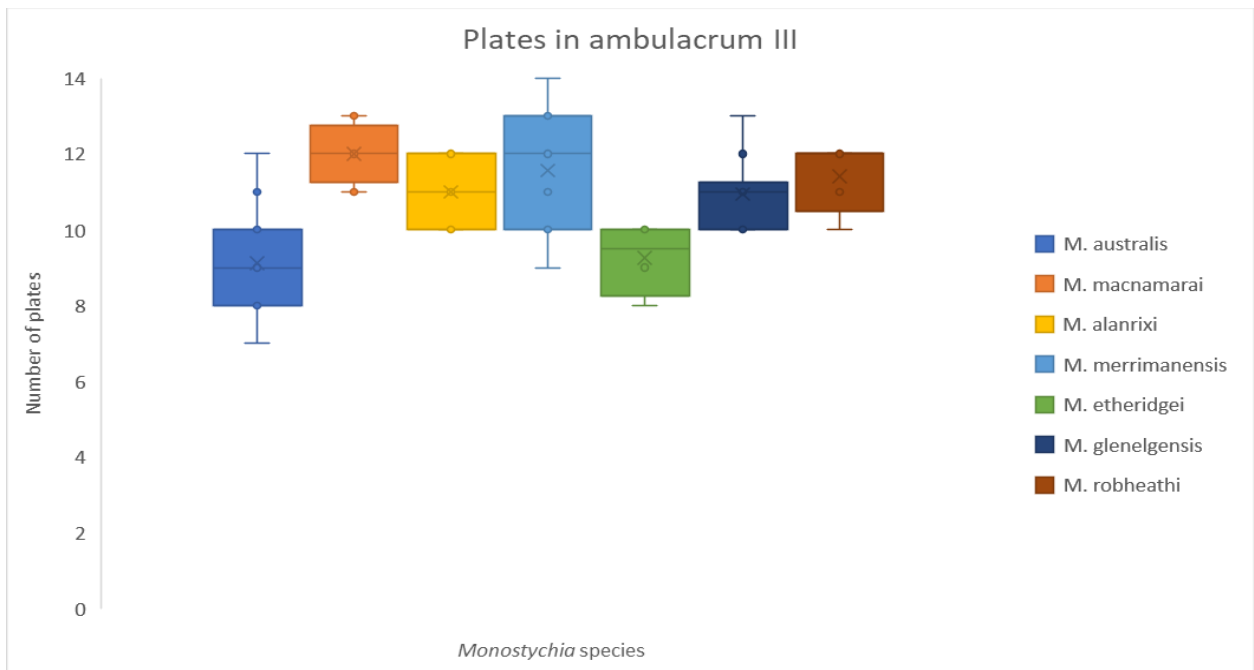


Fig. 3.b.16. Box plot of the number of plates in the ambulacrum III on the oral surface of *Monostychia* species.

1a. Aboral lateral profile of test concave; mean interamb/amb ratio <140%.....	2
1b. Aboral lateral profile of test concave; mean interamb/amb ratio >140%	3
2a. Width to TL ratio >87%; height to TL ratio >20%; apex to TL ratio >45%; length ambulacral basicoronal plates >170% width	<i>australis</i>
2b. Width to TL ratio <87%; height to TL ratio <20%; apex to TL ratio <45%; length ambulacral basicoronal plates <160% width	<i>alanrivi</i>
3a. Periproct not in touch with margin	4
3b. Periproct in touch with margin.....	5
4a. Very tumid margin (>10%TL mean); shallow anal notch; position of apex as %TL <41; length ambulacral coronal plates >170% width	<i>macnamarai</i>
4b. Tumid margin (<10%TL mean); anal notch lacking; position of apex as %TL >41; length ambulacral coronal plates <160% width	<i>glenelgensis</i>
5a. Small test (max < 21); very tumid margin (>10%TL mean); keel indistinct; interambulacral basicoronal plates <15% longer than ambulacral basicoronal plates	6
5b. Medium test (max 28); tumid margin (<10%TL mean); keel distinct; interambulacral basicoronal plates >15% longer than ambulacral basicoronal plates	<i>robheathi</i>
6a. Mean width Amb III as %TL <35; combing absent; food grooves indented but not strongly; predominant number of interambulacral plates in a single segment of paired oral interambulacrum 6-8; predominant number of plates in oral ambulacrum III 10-13.....	<i>merrimanensis</i>
6b. Mean width Amb III as %TL >35; combing present (muted); food grooves strongly indented; predominant number of interambulacral plates in a single segment of paired oral interambulacrum 6; predominant number of plates in oral ambulacrum III 8-10.....	<i>etheridgei</i>

Table 3.b.2. Key to species of Monostychia.

Chapter 3.c. Genus *Quinquestychia* gen. nov.

Abstract

The genus *Quinquestychia* gen. nov. is described along with four species. Three of these species are new; *Q. mannumensis*, *Q. gigas* and *Q. berylmorrisae*. The fourth, *Q. robertirwini* (Sadler *et al.* 2017) has been moved into this genus from *Monostychia* and re-presented from a recent publication. A key to the four species is included.

Systematic palaeontology

Order Clypeasteroida A. Agassiz, 1872

Suborder Clypeasterina A. Agassiz, 1872

Family Arachnoididae Duncan, 1889

Subfamily Monostychinae sub.fam. nov.

***Quinquestychia* gen. nov.**

Type species: Quinquestychia mannumensis sp. nov.

Etymology: The genus name, *Quinquestychia*, derives from the Latin ‘quinqui’ meaning five and referring to the angular pentamerous shape of the test. While five-sided tests are the norm within the Family, members of this genus display this with greater angularity. ‘Stychia’ means row (Sadler *et al.* 2016) and refers to the food grooves but here it is used to provide a link back to *Monostychia* from whence the genus has been historically divided.

Diagnosis: Monostychioid echinoid with test longer than wide, an angular pentamerous shape in plan and with a concave profile aborally; lacking a keel or drooping tail; sharp to weakly tumid

ambitus; Petals medium in length and straight to slightly arced with the distal ends of each pair divergent; marginal periproct first bounded generally by the first or second pair of post-basicoronal plates.

Description: The tests of species within this genus generally range in size from medium to very large (23–87 mm.). The test outline is generally an angular pentagon. The ambitus sharp, generally between 3-8% TL. The lateral profile of the test on the oral surface is flat and the aboral surface slightly to very strongly concave.

The petals are slightly arced to almost straight and continue to diverge toward their tips. Inflated in some species. The mean length of petals, measured as a percentage of the distance to the ambitus in the line of each pore zone, for the anterior pair range from 52% to 61% and the posterior pair from 44% to 65% with the anterior pair always longer than the posterior pair. In the pore pairs, the outer pore is frequently much greater than twice the diameter of the inner pore.

The periproct is sub-marginal and generally distinctly removed from the margin. In the one species where it appears to be touching, it does so via a very distinct anal notch.

The intermulum is a solid unbroken wall sometimes very thick and comprised of a complex microcanal system.

Quinquestychia mannumensis sp. nov. (Fig. 3.c.1.)

1961 *Monostychia australis* Laube, 1869; Ludbrook, p. 44–45.

1983 *Monostychia australis* Laube, 1869; Sadler *et al.*, P. 12.

2011 *Monostychia australis* Laube, 1869; Mihaljevic *et al.*, P. 23, 35, 38.

2017 *Monostychia australis* Laube, 1869; Byrne & O'Hara, P. 362.

Type material: Holotype SAM P22600-1, Paratype SAM P4776.

Additional material: SAM P 22600-2, P 29665, P29667, P29672-1,2, P29883, P4776-1, NHML EE1146, EE1153.

Type locality: Cliffs of the River Murray south of Blanchetown, South Australia.

Type stratum: Mannum Formation.

Etymology: 'mannumensis', for the Mannum Formation from which these specimens were derived.

Diagnosis: *Quinquestychia* species having an ambulacral to interambulacral ratio less than 120%; outer pores being greater than twice the size of the inner pores and a distinct anal notch.

Description: Medium to very large pentamerous test with sides generally parallel or slightly concave, ranging in length from 39.8–73.7 mm; maximum width 86–96% TL (mean = 90%, SD = 2%, n = 15), occurring posterior of centre, but in the range 42–79% TL from anterior ambitus (mean = 51%, SD = 9%, n = 15). Height 12–21% TL (mean = 15%, SD = 3%, n = 10); apex slightly forward of the apical disc 48–50% TL from anterior ambitus (mean = 49%, SD = 2%, n = 2); apical disc 49–53% TL from anterior ambitus (mean = 51%, SD = 1%, n = 9).

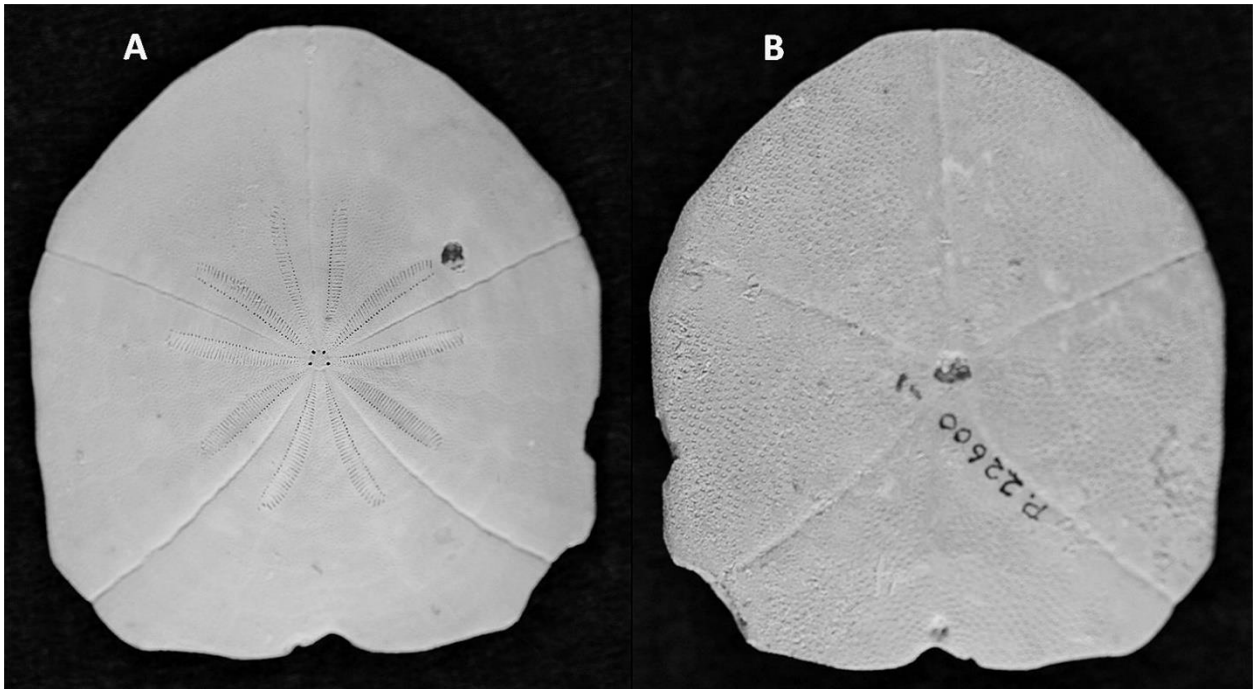


Fig. 3.c.1. Holotype of *Quinquestychia mannumensis* sp. nov. (SAM P22600-1), aboral (A) and oral (B) view; TL = 67.27 mm.

Orally, test very flat except for slightly indented food grooves. Keel from the periproct forward toward to the peristome lacking. The apical surface of the test rises in a slight concave from ambitus to apical disc; ambitus sharp. Ambital notches very minor to non-existent in the anterior three perradial sutures and little more than a bevel in the posterior pair. Anal notch distinct. Combing strong.

Of the 2 specimens for which plates could be observed in paired post-basicoronal interambulacra, plate counts were obtained in 5 of the possible 8 regions. 60% of regions had seven plates, and 40% had eight. For the paired post-basicoronal ambulacra, post-basicoronal plate counts were obtained in 5 of a potential maximum of 8 regions; 100% had ten plates. In the 4 specimens where unpaired post-basicoronal ambulacrum III plates could be counted, 50% had 11 plates, 25% ten and 25% had 12.

Petals very slightly raised or inflated above test surface in most specimens. The mean length of petals, measured as a percentage of the distance from the apical disc to the ambitus in the line of each pore zone, is for the anterior pair 52% (SD = 4%, n = 10) and the posterior pair 44% (SD = 3%, n = 8). Poriferous zones are thin, almost straight and open distally.

Distally, petals end abruptly, trailing podia are not developed. Inner are round and outer pores elongate and significantly more than twice the size of the inner pore. The anterior poriferous zone in ambulacrum II has 28–41 pore pairs; slightly more in ambulacrum I (32–46). The number of pore pairs in the anterior zone per mm of TL is 0.56 (SD = 0.1, n = 6). Mean width of ambulacrum II at ambitus 114% mean width of interambulacrum 1 (SD = 1%, n = 9). Mean width of ambulacrum III 28%TL (SD = 3%, n = 7).

Peristome moderate in size and circular to pentagonal. Food grooves extend from peristome around the ambitus becoming and remain prominent to the apical disc. Aborally, the three anterior grooves are straight, and the two posterior grooves arced laterally. Grooves become wider upon reaching basicoronal plates and end in a broad, flat region bordering the peristomial opening; peristomial point present in some specimens. These grooves do not display crenulations as observed in *M. australis*. Immediately adjacent to the peristome, small buccal podial pores occur at the side of the groove, one on each side and widely spaced. Basicoronal plates twice as long as wide, radial margins straight; interambulacral basicoronal plates narrow markedly toward the peristome, end with an obtuse triangular projection and are about 10% longer than their ambulacral counterparts.

Periproct submarginal, medium size, round to laterally oval, angled slightly posteriorly but with edge up to 20% the periproct diameter from the ambitus. A minor furrow sometimes extends to the ambitus. In interambulacrum 5, the plates first in contact with the periproct have

only been observed in three specimens. In all cases the periproct comes into contact with plates 3a/3b.

The internal buttressing has been observed by cross section. A complex system of peripheral pillars and buttresses is developed around the test, similar to those in *M. australis* and extending between 5-10% the test diameter from the margin. An intermurum is present and presents as a solid wall although its extent and continuity have not been determined.

Stratigraphy and age: These specimens are from the Mannum Formation which ranges in age from late Oligocene to early Miocene (Gallagher & Gourley, 2007). The lower beds of the Formation are dominantly medium- to coarse-grained light-cream to yellow-brown fossiliferous calcareous sandstones rich in limonite and with abundant echinoid tests of various forms. Towards the upper beds the strata become a calcareous sandstone with clayey pockets that tends to weather to a “raggy” limestone (Ludbrook, 1961). Numerous hard grounds exist throughout the Formation. Specimens of *Q. mannumensis* can be found throughout the Formation.

Quinquestychia gigas sp. nov. (Fig. 3.c.2.)

Type material: Holotype SAM P29623, Paratype SAM P29624.

Additional material: SAM P29625–9.

Type locality: Cliffs of the River Murray, Devlins Pound, South Australia (34.1556S, 140.1637E).

Type stratum: Mannum Formation.

Etymology: ‘*gigas*’, from the Latin *gigantum* meaning giant and reflecting the size of this species relative to other monostychioids.

Diagnosis: *Quinquestychia* species having an ambulacral to interambulacral ratio greater than 120%; outer pores being more than twice the size of the inner pores; number of pores per TL less than 0.60; and having a very prominent anal notch.

Description: Very large pentamerous test with sides parallel, ranging in length from 67.3–86.8 mm; maximum width 88–90% TL (mean = 89%, SD = 1%, n = 7), occurring anterior of centre, but in the range 43–54% TL from anterior ambitus (mean = 46%, SD = 4%, n = 7). Height 13–22% TL (mean = 19%, SD = 3%, n = 7); apex and apical disc roughly coincide with apex 44–57% TL from anterior ambitus (mean = 50%, SD = 4%, n = 7); apical disc 49–53% TL from anterior ambitus (mean = 51%, SD = 1%, n = 7).

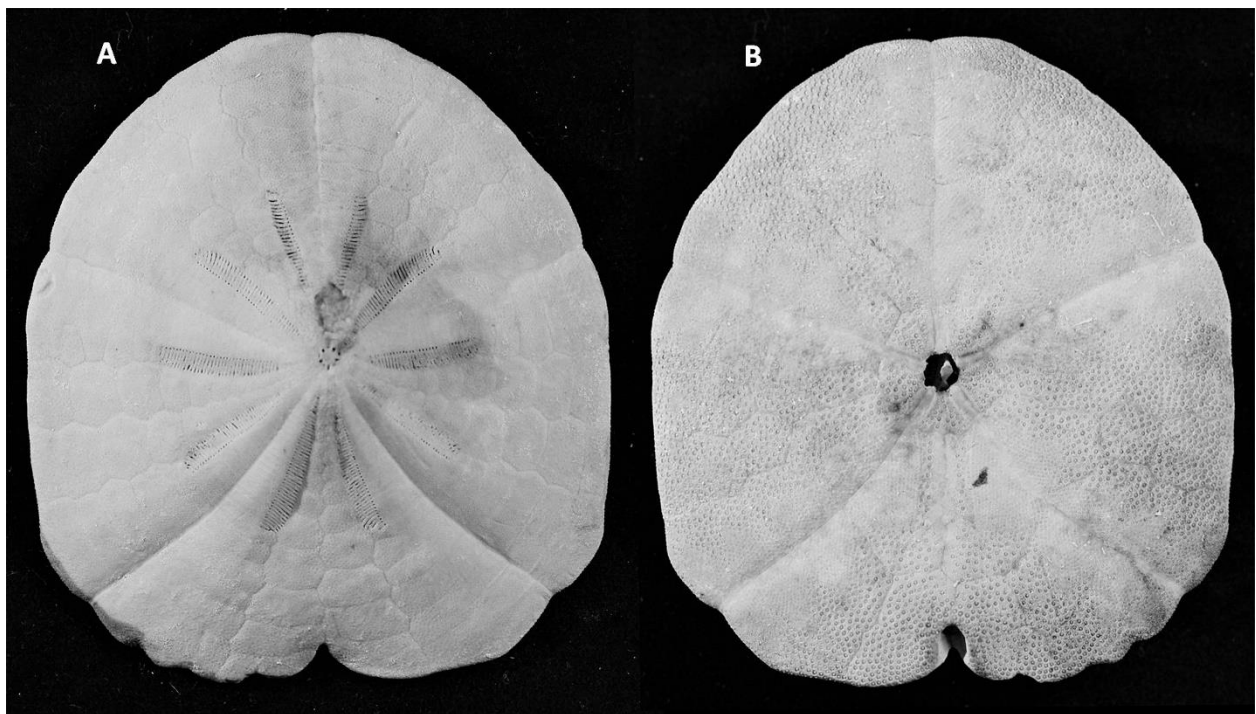


Fig. 3.c.2. Holotype of *Quinquestychia gigas* sp. nov. (SAM P29623), aboral (A) and oral (B) view; TL = 85.33 mm.

Orally, test very flat except for slightly indented food grooves. Keel from the periproct forward toward to the peristome lacking. The aboral surface of the test is distinctly concave from ambitus to apical disc, the latter being relatively flat, forming a flat-topped tent structure; ambitus sharp. Ambital notches very minor to non-existent in the anterior three perradial sutures and little more than a bevel in the posterior pair. Anal notch deep and distinct. Combing strong.

Of the four specimens for which plates could be observed in paired oral post-basicoronal interambulacra plates counts were obtained in 14 of the possible 16 regions. 86% of the regions preserved had seven plates, 7% had six and 7% had eight. For the paired ambulacra, four specimens had observable post-basicoronal plates and counts were obtained in all 16 of the potential regions; 50% of regions preserved had 11 plates, 31% ten, 13% had 12 and 6% had nine. In the five specimens where post-basicoronal ambulacrum III plates were counted, 40% had 10 plates, 20% had 11, 20% had 12 and 20% had 13.

Petals inflated. The mean length of petals, measured as a percentage of the distance from the apical disc to the ambitus in the line of each pore zone, is for the anterior pair 52% (SD = 4%, n = 7) and the posterior pair 46% (SD = 2%, n = 7). Poriferous zones are almost straight and open distally.

Distally, petals end abruptly. Trailing podia are not developed. Inner are round to slightly lacriiform and outer pores are very elongate and significantly more than twice the width of the inner pores. The anterior poriferous zone in ambulacrum II has 32–46 pore pairs; slightly more in ambulacrum I (37–52). The number of pore pairs in the anterior zone per mm of TL is 0.52 (SD = 0.04, n = 7). Mean width of ambulacrum II at ambitus 128% mean width of interambulacrum 1 (SD = 7%, n = 7). Mean width of ambulacrum III 32% TL (SD = 1%, n = 6).

Peristome large and pentamerous. Food grooves extend from peristome around the ambitus becoming and remain prominent to the apical disc. Aborally, the three anterior grooves are straight and the two posterior grooves arced laterally. Grooves become significantly wider upon reaching basicoronal plates and end in a broad, flat region bordering the peristomial opening; peristomial point present. These grooves do not display crenulations as observed in *M. australis*. Immediately adjacent to the peristome, large buccal podial pores occur at the side of the groove, one on each side and widely spaced. Sphaeridea can also be observed. Basicoronal plates more than twice as long as wide, radial margins distinctly curved; interambulacral basicoronal plates narrow markedly toward the peristome, end with an obtuse triangular projection and are no longer than their ambulacral counterparts. Of note is that each of the basicoronal plates is unsymmetrical with the highest point of the rounded basicoronal plates favouring the side toward the interambulacral basicoronal plates. The tip of the triangular projection of the interambulacral plates is also distinctly offset but without a consistent direction of bias. The exception is the plate in interambulacrum 5 which is not only symmetrical but very thin compared to its ambulacral counterparts.

Periproct submarginal, round with edge touching the ambitus although this is usually via a very distinct furrow. This furrow is much more pronounced than in the type species *Q. mannumensis*. In interambulacrum 5, the plates first in contact with the periproct have only been observed in three specimens. In two the plates were 2a/3b and the other 2a/2b.

The internal buttressing has been observed by both a transverse and cross section. Internally, a complex system of peripheral pillars and buttresses is developed around the test, although these are significantly more developed than in *M. australis*. Radiating interambulacral pillars or walls are apparent but limited. Around the margins there is a complex network of structures that extend

from the ambitus about 5–10% the distance to the centre of the test. An intermurum is present and presents as a very thick almost continuous wall from within interambulacrum 5 through to interambulacrum III broken only at the perradial sutures. An intermurum is present and presents as a thick, solid almost continuous wall from within interambulacrum 5 through to interambulacrum III and comprising a complex microcanal system with solid elements parallel to the line of the wall.

Stratigraphy and age: Specimens of *Q. gigas* are relatively rare and appear restricted toward the top of the Mannum Formation and as such their age should be considered early Miocene. The lithology is as described for *M. robheathi* and *Q. mannumensis*.

Quinquestychia berylmorrisae sp. nov. (Fig. 3.c.3.)

2017 *Monostychia australis* Laube, 1869; Byrne & O'Hara, P. 167.

Type material: Holotype SAM P29621, Paratype SAM P29622.

Additional material: SAM P29609–20.

Type locality: Cliffs of the River Murray north of Blanchetown, South Australia (32.2932S, 139.6464E).

Type stratum: Glenforslan Limestone.

Etymology: ‘*berylmorisae*’, for Dr Beryl Morris currently of the University of Queensland but previously the Curator of Information and Publicity for the South Australian Museum. Dr Morris has co-authored a field guide on echinoid fossils of the River Murry Cliffs (Sadler *et al.*

1983) and has contributed significantly on numerous field trips including the ones where this species was found.

Diagnosis: *Quinquestychia* species having an ambulacral to interambulacral ratio less than 124%; outer pores being less than twice the size of the inner pores; number of pores per TL less than 0.7; and either lacking an anal notch or, if present, is a minor indent.

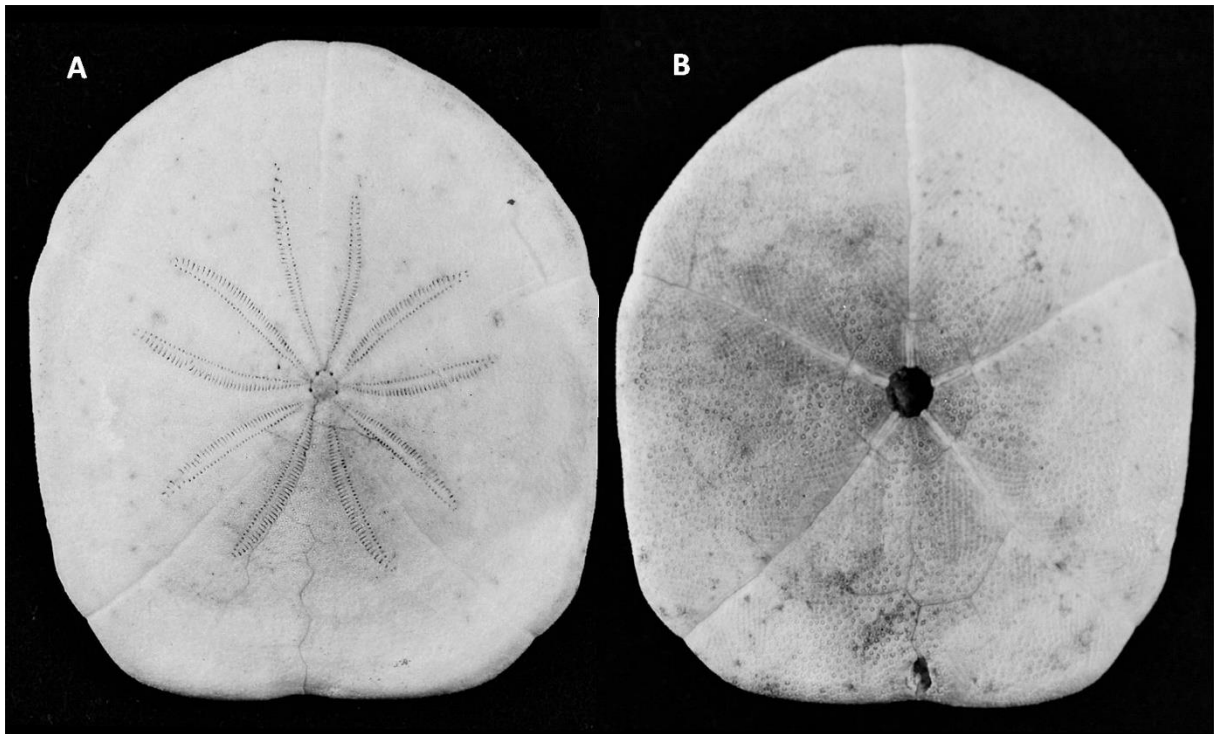


Fig. 3.c.3. Holotype of Quinquestychia berylmorrisae sp. nov. (SAM P29621), aboral (A) and oral (B) view; TL = 58.91 mm.

Description: The test shape of this species is highly variable. Large to very large pentamerous test with sides generally converging posteriorly, ranging in length from 51.0–81.3 mm; maximum width 81–89% TL (mean = 84%, SD = 2%, n = 14), occurring anterior of centre, but in the range 43–46% TL from anterior ambitus (mean = 44%, SD = 11%, n = 14). Height 12–27% TL (mean = 18%, SD = 4%, n = 13); apex slightly forward of the apical disc 41–55% TL

from anterior ambitus (mean = 50%, SD = 3%, n = 13); apical disc 50–53% TL from anterior ambitus (mean = 51%, SD = 1%, n = 13).

Orally, test very flat except for slightly indented food grooves. Keel from the periproct forward toward to the peristome lacking. The apical surface of the test is distinctly concave from ambitus to apical disc; ambitus relatively sharp. Ambital notches very minor to non-existent in the anterior three perradial sutures and little more than a bevel in the posterior pair. Anal notch either lacking or if present is little more than a minor indent. Combing strong.

Of the seven specimens for which plates could be observed in paired oral post-basicoronal interambulacra plates counts were obtained in 25 of the possible 28 regions. 56% of the regions preserved had eight plates, 28% had nine and 16% had seven. For the paired ambulacra, eight specimens had observable post-basicoronal plate and counts were obtained in all 32 of the potential regions; 41% of regions preserved had 11 plates, 28% had 12, 28% had ten and 3% had 13. In the seven specimens where post-basicoronal ambulacrum III plates were counted, 86% had 12 plates and 14% 11.

Petals not inflated. The mean length of petals, measured as a percentage of the distance from the apical disc to the ambitus in the line of each pore zone, is for the anterior pair 60% (SD = 5%, n = 13) and the posterior pair 53% (SD = 4%, n = 13). Poriferous zones are thin, almost straight and open distally although the pair in each of the three anterior petals do parallel each other for the outer 50% or so of their length.

Distally, petals end in a point. Trailing podia are not developed. Inner are round and outer pores elongate and more than twice the diameter of the inner pores. The anterior poriferous zone in ambulacrum II has 32–48 pore pairs; slightly more in ambulacrum I (35–51). The number of pore pairs in the anterior zone per mm of TL is 0.62 (SD = 0.1, n = 12). Mean width of

ambulacrum II at ambitus 116% mean width of interambulacrum 1 (SD = 6%, n = 10). Mean width of ambulacrum III 30% TL (SD = 2%, n = 8).

Peristome large and circular to pentamorous. Food grooves extend from peristome around the ambitus becoming and remain prominent to the apical disc. Aborally, the three anterior grooves are straight and the two posterior grooves arced laterally. Grooves become slightly wider upon reaching basicoronal plates and end in a broad, flat region bordering the peristomial opening; peristomial point present in most specimens. These grooves do display crenulations as observed in *M. australis* on each side of the groove. Immediately adjacent to the peristome, moderately large buccal podial pores occur at the side of the groove, one on each side and widely spaced. Sphaeridea can also be observed. Basicoronal plates more than twice as long as wide, radial margins slightly curved; interambulacral basicoronal plates narrow markedly toward the peristome, end with an obtuse triangular projection and are less than 10% longer than their ambulacral counterparts.

Periproct submarginal, lacrimiform in shape, with edge up to 20–40% the periproct diameter from the ambitus. There is no furrow between the periproct and margin as in the type species *Q. mannumensis*. In interambulacrum 5, periproct generally comes into contact with plates 3a/3b but contact with plates 2a/3b has been observed in two specimens.

The internal buttressing has been observed by both a transverse and cross section. Internally, a complex system of peripheral pillars and buttresses is developed around the test, although these are significantly more developed than in *M. australis*. Radiating interambulacral pillars or walls are apparent but limited. Around the margins there is a complex network of structures that extend from the ambitus about 5–10% the distance to the centre of the test. An intermulum is present and presents as a very thick solid continuous wall from within interambulacrum 5 through to

interambulacrum III and comprising a complex microcanal system with solid elements at a distinct angle to the line of the wall.

Stratigraphy and age: *Q. berylmorrisae* are restricted to a two-metre section near the centre of the Glenforslan Formation. This stratum was described in Chapter 3.a. being the type stratum of *M. australis*. The two-metre section containing *Q. berylmorrisae* is situated about two metres above the *Lepidocyclina* ingress layer identified as early Miocene in the planktonic foraminiferal standard zone M5a (Gallagher & Gourley, 2007).

Quinquestychia robertirwini (Sadler, *et al.*, 2017) (Fig. 3.c.4.)

2017 *Monostychia robertirwini* Sadler *et al.*, P. 6–7

Type material: Holotype WAM 91.15–3

Additional material: WAM 89.37a, c, f, l 16.7–10, 16.29–42.

Type locality: Approximately 40 km WSW of Lake Colville, Western Australia.

Type stratum: Colville Sandstone (middle Miocene).

Etymology: The species is named after Mr Robert Irwin of Australia Zoo. Robert has contributed to palaeontology with the discovery of a jaw of an Ichthyodectiformes fish previously unknown in Australia, along with authoring a series of books on dinosaurs.

Diagnosis: *Quinquestychia* species having an ambulacral to interambulacral ratio greater than 124%; outer pores being less than twice the size of the inner pores; number of pores per TL greater than 0.70; and lacking an anal notch or having a very minor indentation in the margin of the test in that area.



Fig. 3.c.4. Holotype of *Quinquestychia robertirwini* (Sadler, et al. 2017). (WAM 91-15-3), aboral (A) and oral (B) view; TL = 42.36 mm.

Description: Medium to large pentamerous shield-shaped test with sides parallel, ranging in length from 28.8–52.7 mm; maximum width 80–92% TL (mean = 85%, SD = 3%, n = 19), occurring anterior of centre, but in the range 39–48% TL from anterior ambitus (mean = 42%, SD = 2%, n = 19). Height 13–19% TL (mean = 16%, SD = 2%, n = 17); apex anterior of apical disc and 32–49% TL from anterior ambitus (mean = 40%, SD = 4%, n = 18); apical disc 45–52% TL from anterior ambitus (mean = 49%, SD = 2%, n = 18).

Orally, test very flat except for slightly indented food grooves. Keel from the periproct forward toward to the peristome lacking. The apical surface of the test is distinctly concave from ambitus to apical disc; ambitus relatively sharp. Ambital notches very minor to non-existent in the anterior three perradial sutures and little more than a bevel in the posterior pair. Anal notch either lacking or if present is little more than a minor indent. Combing has been observed in only four specimens.

Of the nine specimens for which plates could be observed in paired oral post-basicoronal interambulacra plates counts were obtained in 23 of the possible 36 regions. 43% of the regions preserved had eight plates, 35% had seven, 17% had nine and 4% had 10. For the paired ambulacra, post-basicoronal plate counts were obtained in 23 of the potential 36 regions; 52% of regions preserved had 11 plates, 26% had 10, 22% had 12. In the nine specimens where post-basicoronal ambulacrum III plates were counted, 33% had 10 plates, 33% had 12, 22% had 13 and 11% had 11.

Petals not inflated. The mean length of petals, measured as a percentage of the distance from the apical disc to the ambitus in the line of each pore zone, is for the anterior pair 61% (SD = 5%, n = 18) and the posterior pair 55% (SD = 6%, n = 17). Poriferous zones are almost straight and open distally.

Distally, petals end abruptly. Trailing podia are not developed. Inner are round and outer pores are very elongate and significantly more than twice the width of the inner pores. The anterior poriferous zone in ambulacrum II has 28–42 pore pairs; slightly more in ambulacrum I (29–48). The number of pore pairs in the anterior zone per mm of TL is 0.9 (SD = 0.1, n = 13). Mean width of ambulacrum II at ambitus 142% mean width of interambulacrum 1 (SD = 16%, n = 17). Mean width of ambulacrum III 32% TL (SD = 3%, n = 17).

Peristome medium in size and circular to pentamerous. Food grooves extend from peristome around the ambitus becoming and become less prominent toward the apical disc. Aborally, the paired grooves arc slightly. Grooves become slightly wider upon reaching basicoronal plates and end in a broad, flat region bordering the peristomial opening. These grooves do display crenulations as observed in *M. australis*. Immediately adjacent to the peristome, small buccal podial pores occur at the side of the groove, one on each side and widely spaced. Basicoronal

plates more than twice as long as wide; interambulacral basicoronal plates end with an obtuse triangular projection and about 10% than their ambulacral counterparts.

Periproct just submarginal, circular within about 10% periproct longitudinal diameter of the margin. In interambulacrum 5, the plates first in contact with the periproct have only been observed in two specimens. In one the plates contact was 3a/3b while the other was 2a/3b.

The internal buttressing has been observed by cross section. Internally, test contains a complex system of peripheral pillars and buttresses, although this develops as many fine needles. No apparent radiating interambulacral pillars or walls; central pillars present and well developed. An intermurmum is present and presents as a wall.

Stratigraphy and age: As for *M. macnamarai*.

Remarks (for this species): This species was originally described as belonging to the genus *Monostychia* (Sadler *et al.*, 2017). However, its shape, including the ambital thickness, the almost absence of a keel between the peristome and periproct, and the shape of the petals suggest it belongs in this genus instead. Strong combing is a characteristic of members of the genus *Quinquestychia* and yet *Q. robertirwini* displays combing in only four of the 23 specimens studied. While most specimens were of relatively poor quality, the fact that oral plates were counted in many of the specimens indicates that if combing was a feature it would have been observed.

Remarks on the species of *Quinquestychia*

The key diagnostic features of the type and six other species allocated to this genus are summarised in Table 3.c.1. In addition, a box plot of the seven species is presented in Figs 3.b.5–13 with each figure representing a different diagnostic feature.

The width to length ratio clearly separates *Q. mannumensis* and *Q. gigas* from *Q. berylmorrisae* and *Q. robertirwini* with the latter two having a distinctly lower ratio than the first two (Fig. 3.b.5.). The height to length ratio is useful in separating *Q. mannumensis* from *Q. gigas* with the former having a lower ratio although this is not conclusive (Fig. 3.c.6.).

The ratio of petal length to distance to margin (Fig. 3.c.7.) is useful in separating *Q. mannumensis* and *Q. gigas* from *Q. berylmorrisae* and *Q. robertirwini* with the latter pair having a distinctly higher ratio. The number of pore pairs in the petal as a percentage of TL is useful in separating *Q. robertirwini* from the other three species (Fig. 3.c.8.). The mean number of 0.90 is significantly higher than *Q. mannumensis* at 0.56, *Q. gigas* at 0.52 and, to a lesser extent, *Q. berylmorrisae* at 0.62 (Table 3.c.1.).

The ratio of interambulacrum width at the margin to ambulacrum width is also useful in separating *Q. robertirwini* from the other three species (Fig. 3.c.9.). The ratio of the width of ambulacrum III at the margin as a ratio of TL clearly separates *Q. gigas* from *Q. mannumensis* with the latter having a lower ratio (Fig. 3.c.10.). Similarly, although not as clearly defined, *Q. robertirwini* can be separated from *Q. mannumensis* with the latter having the lower ratio, and *Q. gigas* can be separated from *Q. berylmorrisae* with the latter having the lower ratio.

A count of the number of plates in the paired interambulacra, paired ambulacra and ambulacrum III (Figs 3.c.11–13) have the potential to prove useful in separating the four species but the overlap of numbers is such that a reasonable population of specimens will be required. *Q. berylmorrisae* appears to stand out as the species with the higher number of each of the three regions.

Other features that are useful in separating the species include the thickness of the margin. For *Q. mannumensis* and *Q. gigas* the anterior margin is 4% TL while for *Q. berylmorrisae* it is 6% TL and for *Q. robertirwini* 7% TL. While the plan shape of the test is rather subjective, it is worth noting that even though *Q. berylmorrisae* is possibly the most variable of all species within the subfamily Monostychinae, it frequently displays a shape that narrows between the anterior and posterior food grooves thus giving it a true pentagonal shape. This compares to most other species within the subfamily where the sides tend to be parallel even when considering the rounded nature of the test in some species.

Table 3.c.2. provides a key to the species of *Quinquestychia*.

Diagnostic feature	<i>Q. mannumensis</i> sp. nov.	<i>Q. gigas</i> sp. nov.	<i>Q. berylmorrisae</i> sp. nov.	<i>Q. robertirwini</i> (Sadler, <i>et al.</i>, 2017)
Test plan outline	Pentamerous with parallel sides	Pentamerous with parallel sides	Highly variable pentamerous with side converging posteriorly	Pentamerous with parallel sides
Test length	Medium to very large	Very large	Large to very large	Medium to large
Test lateral profile, apical surface	Slightly concave	Distinctly concave	Distinctly concave	Distinctly concave
Oral surface profile	Very flat	Very flat	Very flat	Very flat
Mean height	15% TL	19% TL	18% TL	16% TL
Distance of apex from anterior (mean)	49% TL	50% TL	50% TL	40% TL
Ambitus	Sharp	Relatively sharp	Relatively sharp	Relatively sharp
Interambulacral plates in oral paired interambulacra	7–8	7	8–9	7–8
Post-basicoronal amb. plates in oral paired amb.	10	10–11	10–12	10–11
Post-basicoronal plates in anterior oral ambulacra III	10–12	10–13	12	10–13
Anterior petal to ambitus (mean)	52%	52%	59%	61%
Posterior petal to ambitus (mean)	44%	46%	54%	55%
Number of pore pairs	Ant. 15–37 Post. 17–21	Ant. 32–46 Post. 37–52	Ant. 32–48 Post. 35–51	Ant. 28–42 Post. 29–48

Number pore pairs per mm TL (mean)	0.56	0.52	0.62	0.90
Petals inflated	Very slightly	Inflated	No	No
Amb. width at ambitus as a % of interamb. width (mean)	114%	128%	115%	142%
Width ambulacrum III at ambitus as percentage TL	28%	32%	29%	32%
Submarginal periproct	Circular to oval; up to 20% to margin	Circular; touching margin with distinct furrow	Lacriform; 30% to margin	Circular; 10% to margin
Contact plates with periproct (principal)	3a/3b	2a/3b	3a/3b	3a/3b
Interambulacral basicoronal plates	Twice as long as wide; obtuse triangular projection	Unsymmetrical	Twice as long as wide; obtuse triangular projection	Twice as long as wide; obtuse triangular projection

Table 3.c.1. Comparison of diagnostic features of the four species of Quinquestychia.

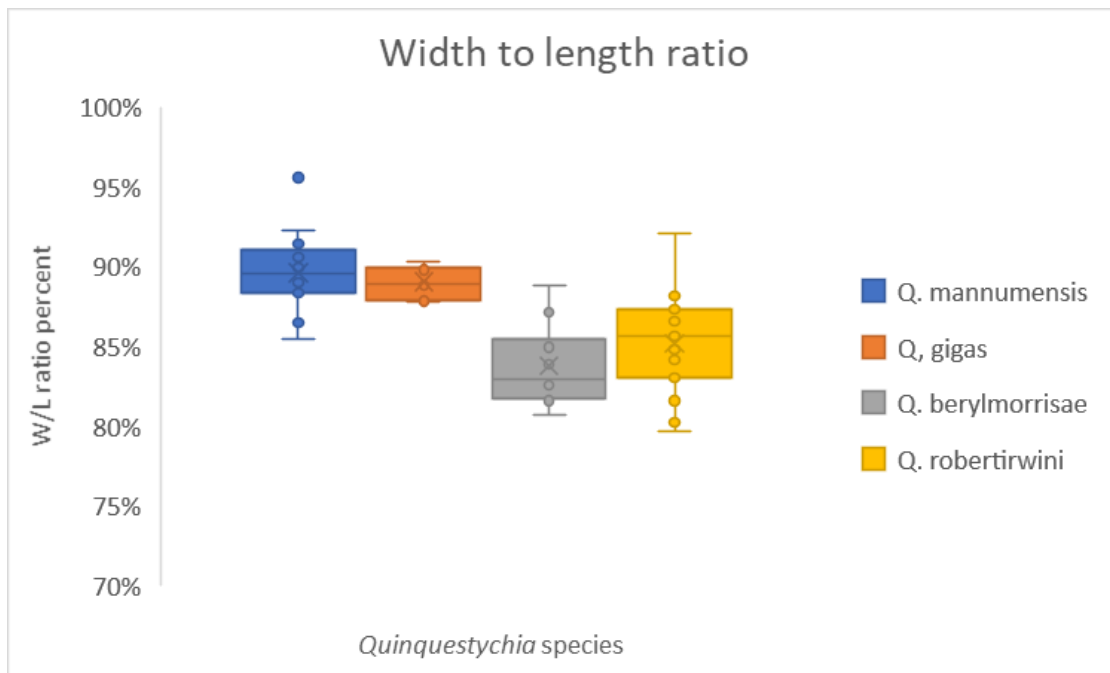


Fig. 3.c.5. Box plot of width to length ratio of *Quinquestychia* species.

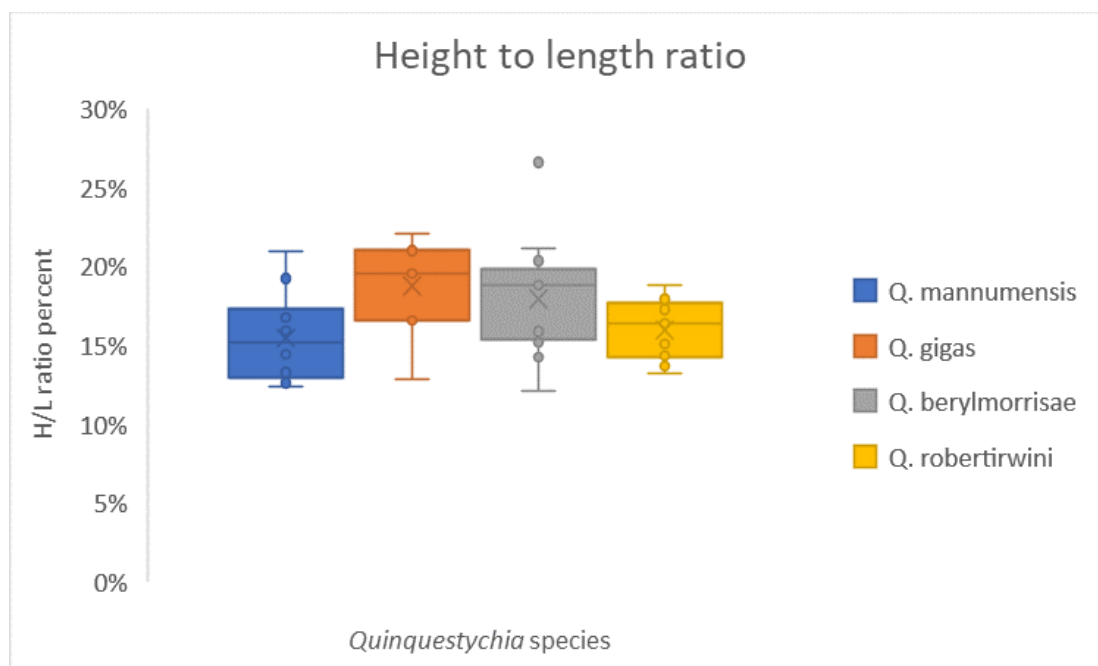


Fig. 3.c.6. Box plot of height to length ratio of *Quinquestychia* species.

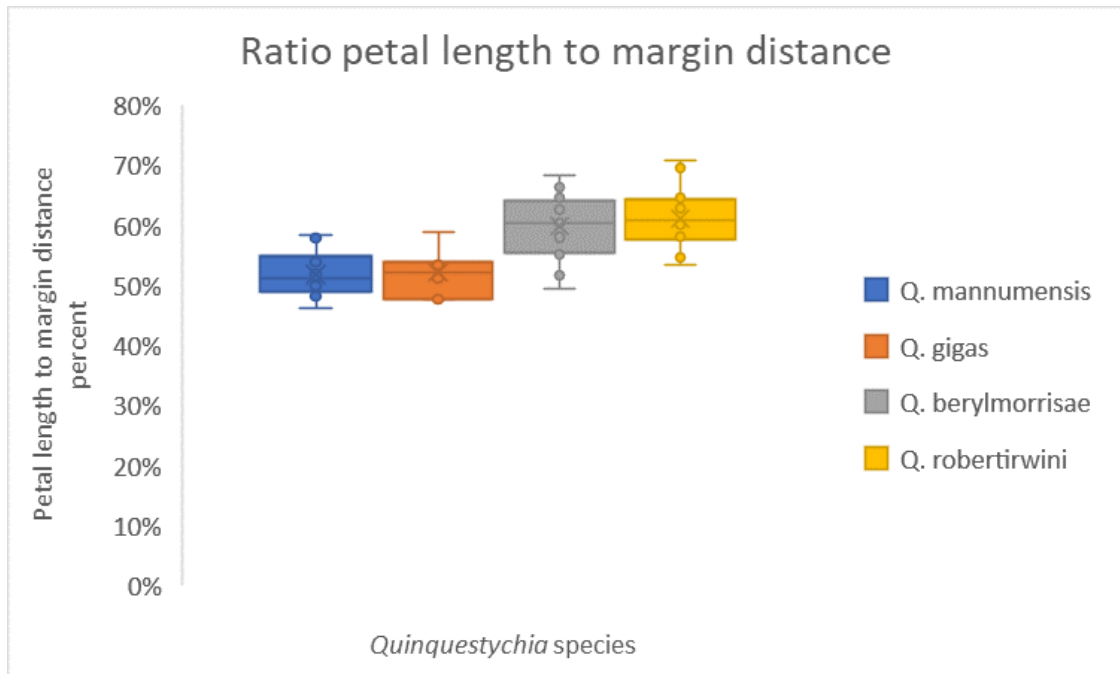


Fig. 3.c.7. Box plot of the ratio of petal length to distance to margin for Quinquostychia species.

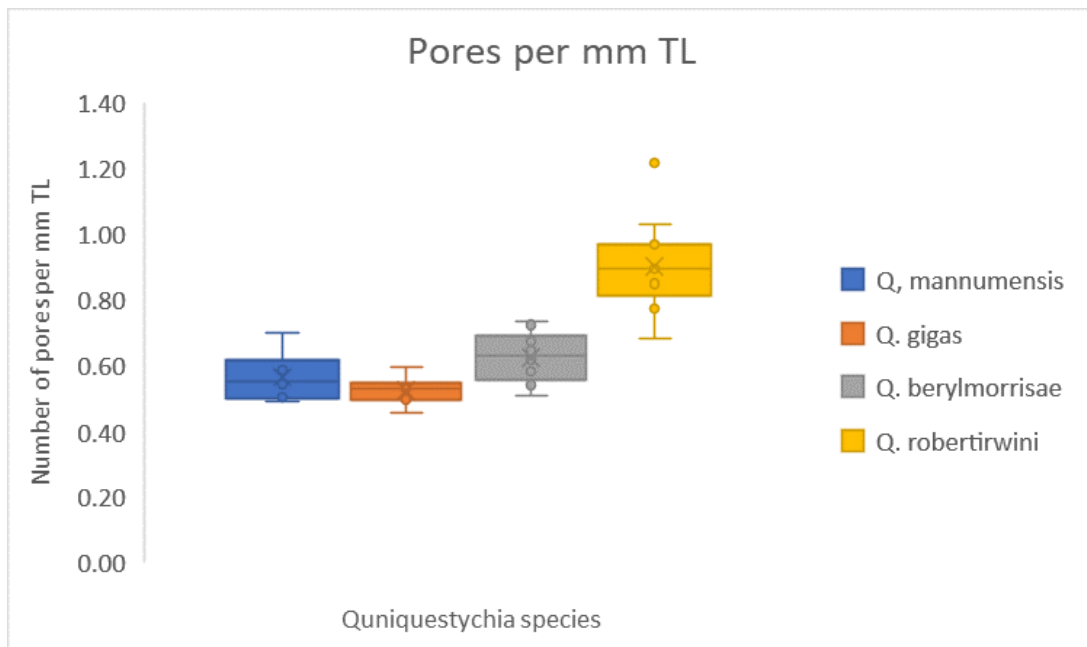


Fig. 3.c.8. Box plot of number of pores per mm TL of Quinquostychia species.

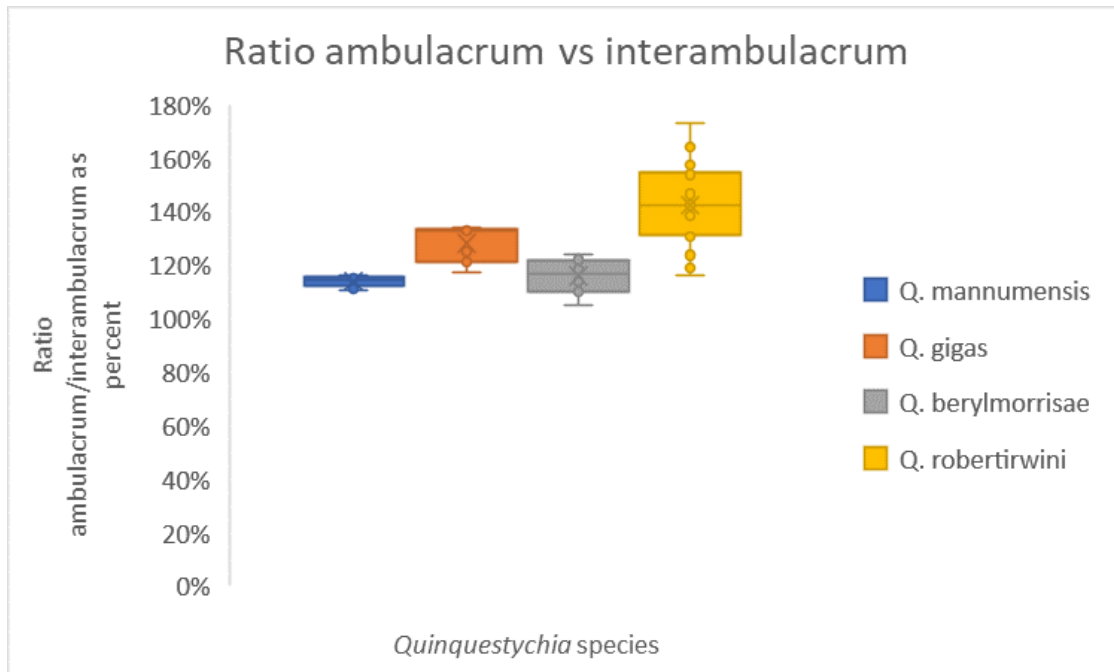


Fig. 3.c.9. Box plot of the ratio of ambulacrum width at ambitus against interambulacrum width of Quinquestychia species.

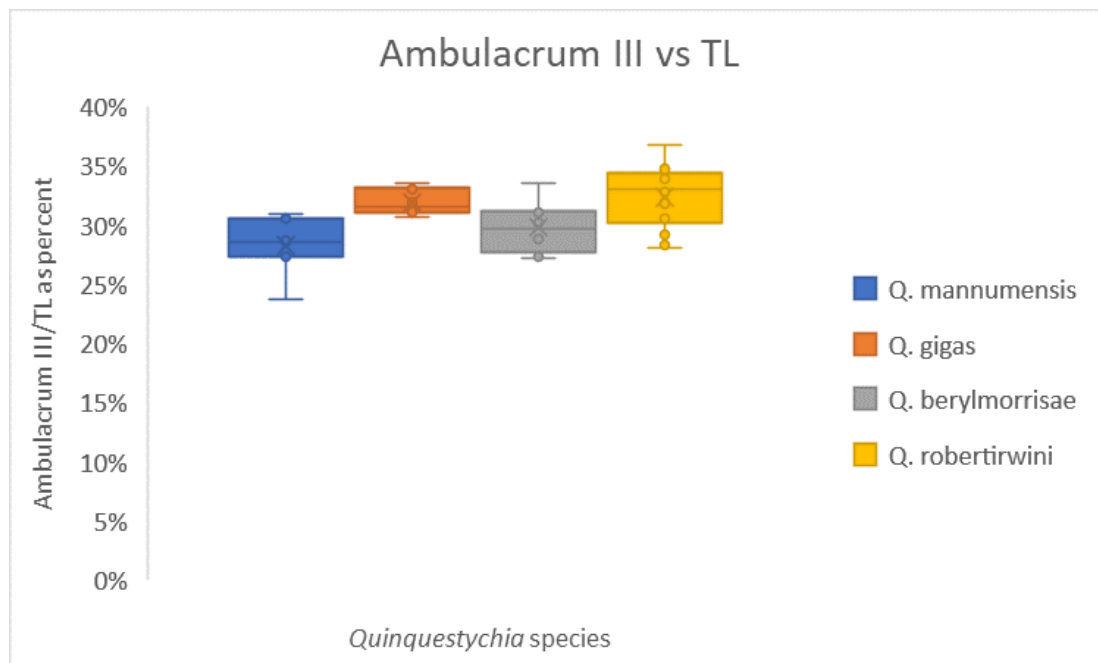


Fig. 3.c.10. Box plot of the ratio of width of ambulacrum III at ambitus against test length (TL) of Quinquestychia species.

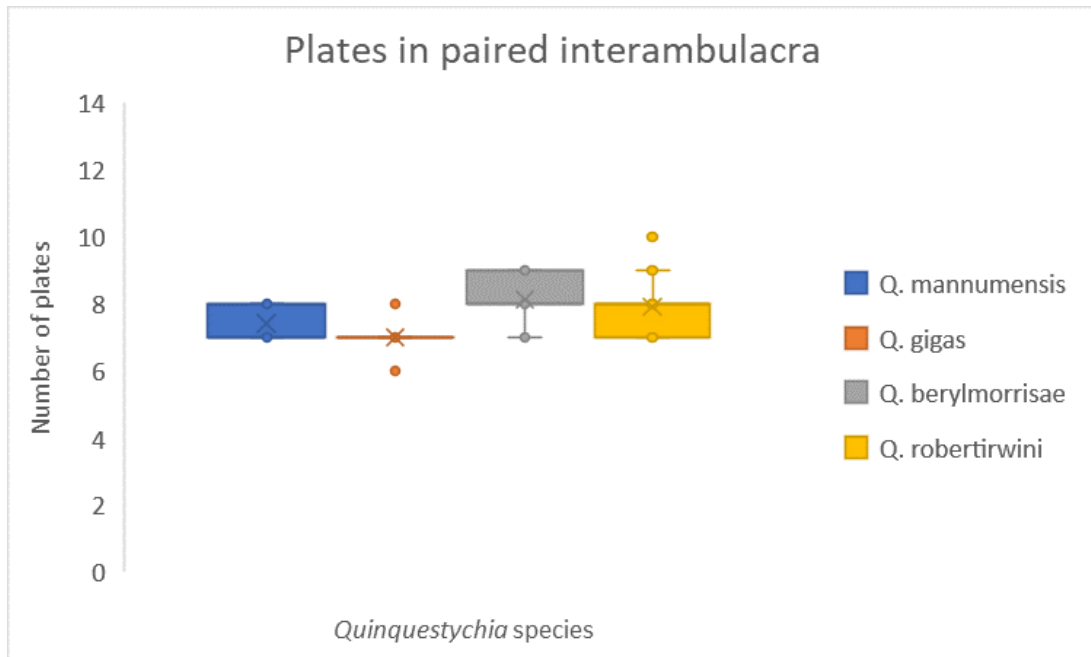


Fig. 3.c.11. Box plot of the number of plates in the paired interambulacra on the oral surface of Quinquestychia species.

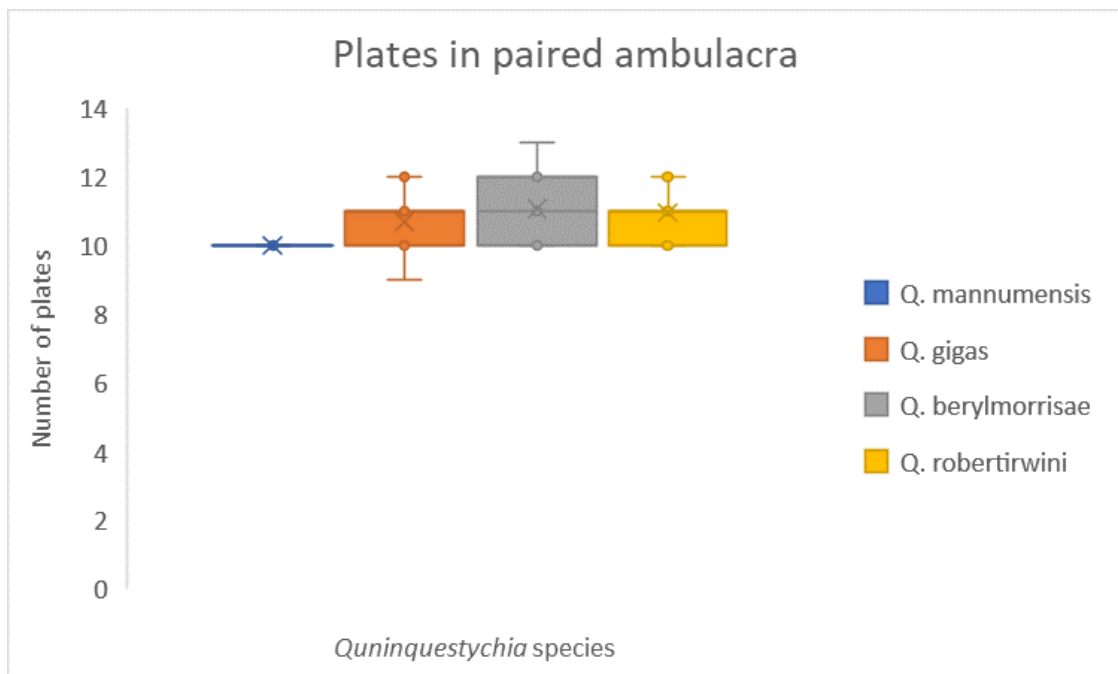


Fig. 3.c.12. Box plot of the number of plates in the paired ambulacra on the oral surface of Quinquestychia species.

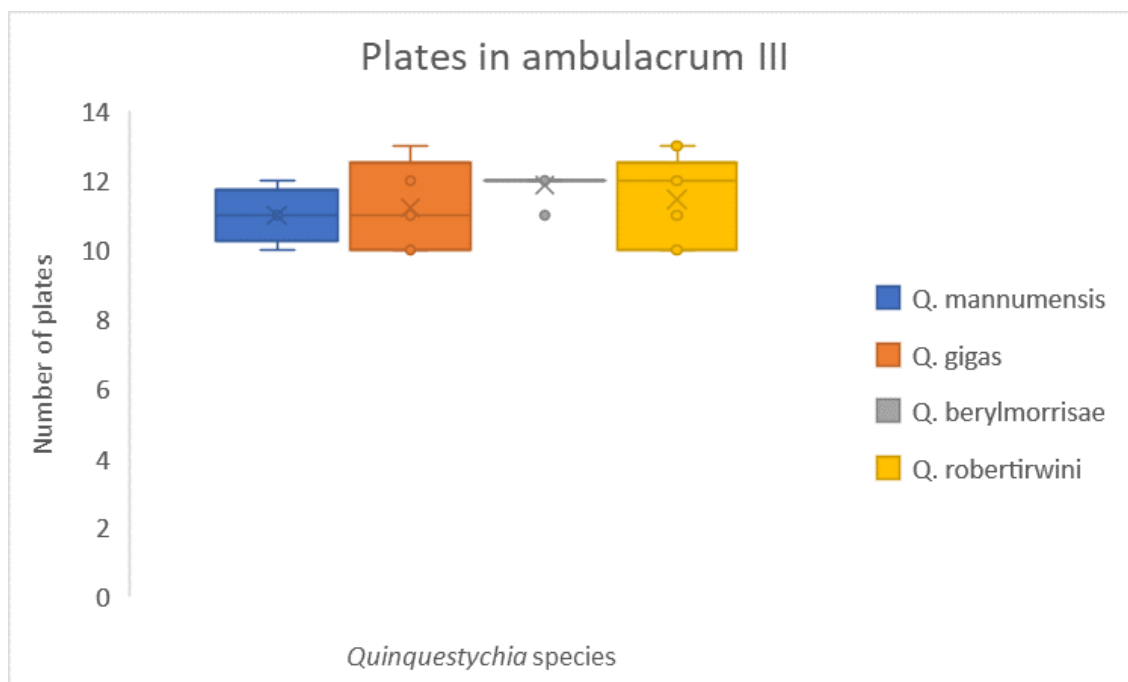


Fig. 3.c.13. Box plot of the number of plates in the ambulacrum III on the oral surface of *Quinquestychia* species.

1a. Pores per mm TL<0.6; distinct anal notch; outer pore of pore pair>twice the diameter of inner pore; anterior petal length<55% distance to margin.....	2
1b. Pores per mm TL>0.6; minor or no indentation for anal notch; outer pore of pore pair<twice the diameter of inner pore; anterior petal length>55% distance to margin.....	3
2a. Test aboral profile flat to gently tented; ambulacrum/interambulacrum ratio<116%; width of ambulacrum III 31% and less.....	<i>mannumensis</i>
2b. Test aboral profile strongly tented; ambulacrum/interambulacrum ratio>115%; width of ambulacrum III 31% and more	<i>gigas</i>
3a. Marginal buttressing comprised of complex microcanal system covering 5% test width; ambulacrum/interambulacrum ratio<124%; pores per mm TL<0.7	<i>berylmorrisae</i>
3b. Marginal buttressing comprised of independent needles; ambulacrum/interambulacrum ratio>124%; pores per mm TL>0.7	<i>robertirwini</i>

Table 3.c.2. Key to species of Quinquestychia.

Chapter 3.d. Genus *Rotundastychia* gen. nov.

Abstract

The genus *Rotundastychia* gen. nov. is described along with three new species; *R. pledgei* sp. nov. from the upper Oligocene-lower Miocene Mannum Formation and Port Vincent Formation, South Australia, along with *R. aquilaensis* sp. nov. and *R. eyriei* sp. nov. both from the upper Oligocene Point Addis Limestone in Victoria. A key to the species is included.

Systematic palaeontology

Order Clypeasteroida A. Agassiz, 1872

Suborder Clypeasterina A. Agassiz, 1872

Family Arachnoididae Duncan, 1889

Subfamily Monostychinae sub.fam. nov.

***Rotundastychia* gen. nov.**

Type species: *Rotundastychia pledgei* sp. nov.

Etymology: The genus name, *Rotundastychia*, derives from the Latin ‘rotundus’ meaning round or circular and referring the shape of the test. ‘Stychia’ means row (Sadler *et al.* 2016) and refers to the food grooves but here it is used to provide a link back to *Monostychia* from whence the genus has been historically divided.

Diagnosis: Monostychioid echinoid with very flat, generally circular test and very sharp ambitus; Petals short and straight to slightly arced with the distal ends of each pair divergent;

submarginal periproct first bounded generally by the first or second pair of post-basical plates.

Description: *The tests of species within this genus generally range in size from small to very large (10–>60 mm.). All species are almost circular in shape with a slight tendency to a pentagon with square sides and rear margin. The ambitus is sharp to very sharp averaging of 3–6%TL in thickness. The lateral profile of the oral surface is very flat. The lateral profile of the aboral surface in some species is straight to slightly convex. Apical disc monobasal with four gonopores; anterior pair more closely spaced than posterior pair. Madreporite dotted with numerous hydropores. Tubercles rarely observed on apical disc.*

The petals are slightly arched to almost straight and continue to diverge toward their tips; slightly inflated in one species. The mean length of petals, measured as a percentage of the distance to the ambitus in the line of each pore zone, is short. For the anterior pair range from 42% to 44% and the posterior pair from 37% to 40% with the anterior pair always longer than the posterior pair. *The petals continue to diverge toward their tips. The inner of the pore pairs is almost always round or nearly so. The outer pore of the pair is generally more than twice the length of the inner pore diameter.*

The periproct is always submarginal. In most species, the periproct may be one-half to a full diameter of the periproct from the margin. In others it is touching the margin.

The intermural is a continuous wall of stereom.

Rotundastychia pledgei sp. nov. (Fig. 3.d.1.)

Type material: Holotype SAM P29630, Paratype SAM P29631

Additional material: SAM P29632–41, NHML EE2112–4, MV P18294, MV P33721.

Type locality: Cliffs at the junction of the River Murray and River Marne, South Australia (34.6986S, 139.5771E).

Type stratum: Mannum Formation.

Etymology: ‘pledgei’, for Mr Neville Pledge, the former Curator of Fossils at the South Australian Museum.

Diagnosis: *Rotundastychia* species characterised by a low, flat test, fewer than 0.73 pores per mm TL in petals and an ambulacral to interambulacral ratio less than 140%.

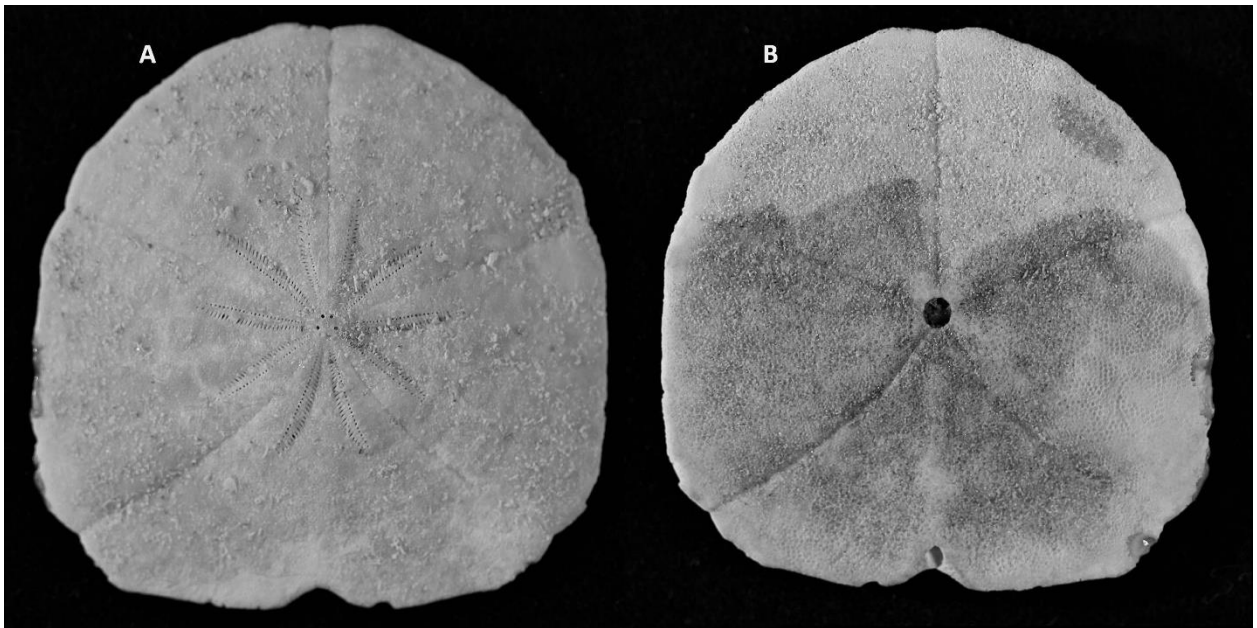


Fig. 3.d.1 Holotype of *Rotundastychia pledgei* sp. nov. (SAM P29630), aboral (A) and oral (B) view; TL = 50.53 mm.

Description: Test medium to very large, tending to circular in shape in shape with squarish sides and posterior, ranging in length from 30.6–66.1 mm; maximum width 96–103% TL (mean = 99%, SD = 2%, n = 18), occurring posterior of centre, but in the range 46–81% TL from

anterior ambitus (mean = 62%, SD = 10%, n = 18). Height 10–16% TL (mean = 13%, SD = 2%, n = 10); apex slightly forward of the apical disc 40–53% TL from anterior ambitus (mean = 48%, SD = 4%, n = 13); apical disc 48–53% TL from anterior ambitus (mean = 51%, SD = 1%, n = 13).

Orally, test very flat except for slightly indented food grooves. Keel from the periproct forward toward to the peristome lacking. The apical surface of the test rises in a straight line from ambitus to apical disc; ambitus very sharp. Ambital notches very minor to non-existent in the anterior three perradial sutures and little more than a bevel in the posterior pair. Anal notch present. Combing weak and seen in only a few specimens.

Of the three specimens for which plates could be observed in paired oral post-basicoronal interambulacra, plate counts were obtained in 10 of the possible 12 regions. 80% of the regions preserved had seven plates and 20% had six. For the paired ambulacra, four specimens had observable post-basicoronal plate and counts were obtained in 14 of a potential maximum of 16 regions; 70% of regions preserved had 10 plates, 20% 11 and 10% had nine. In the three specimens where post-basicoronal ambulacrum III plates were counted, 33% had 10 plates, 33% 11 and 33% 12.

Petals very slightly raised or inflated above test surface in most specimens. The mean length of petals, measured as a percentage of the distance from the apical disc to the ambitus in the line of each pore zone, is for the anterior pair 44% (SD = 3%, n = 10) and the posterior pair 40% (SD = 3%, n = 8). Poriferous zones are thin, almost straight and open distally.

Distally, petals end in a point, trailing podia are not developed. Inner are round and outer pores elongate. The anterior poriferous zone in ambulacrum II has 23–36 pore pairs; slightly more in ambulacrum I (23–38). The number of pore pairs in the anterior zone per mm of TL is

0.63 (SD = 0.1, n = 8). Mean width of ambulacrum II at ambitus 113% mean width of interambulacrum 1 (SD = 8%, n = 10). Mean width of ambulacrum II at ambitus 112% mean width of interambulacrum 1 (SD = 8%, n = 12). Mean width of ambulacrum III 28% TL (SD = 3%, n = 9).

Peristome small and circular. Food grooves extend from peristome around the ambitus and remain prominent to the apical disc. Aborally, the three anterior grooves are straight and the two posterior grooves arced laterally. Grooves becomes wider upon reaching basicoronal plates and end in a broad, flat region bordering the peristomial opening; peristomial point present in some specimens. Immediately adjacent to the peristome, small buccal podial pores occur at the side of the groove, one on each side and widely spaced. These grooves do not display crenulations as observed in the type species *M. australis*. Basicoronal plates twice as long as wide, radial margins straight; interambulacral basicoronal plates narrow markedly toward the peristome, end with an acute triangular projection and are about 20% longer than their ambulacral counterparts.

Periproct submarginal, medium size, round to lacrimiform in shape, angled posteriorly but with edge up to 30% the periproct diameter from the ambitus. In interambulacrum 5, periproct comes into contact with plates 3a/3b (20% of specimens), plates 2a/3b (20%), and 3a/2b (10%).

Internally, a complex system of peripheral pillars and buttresses is developed around the test, although these are significantly more developed than in *M. australis*. An intermuralum is present and presents as a solid unbroken wall from within interambulacrum 5 through to interambulacrum III. Radiating interambulacral pillars or walls are apparent. Around the margins there is a complex network of structures that extend from the ambitus about 30% the distance to the centre of the test. This network comprises a series of short walls that align perpendicular to

the margin in the paired interambulacral areas and parallel to the margin in the ambulacral areas and interambulacrum 5.

Stratigraphy and age: Most of the specimens used in this study are from the lower Mannum Formation. The strata are dominantly medium- to coarse-grained light-cream to yellow-brown fossiliferous calcareous sandstones rich in limonite and with abundant echinoid tests of various forms and range in age from late Oligocene to early Miocene (Gallagher & Gourley, 2007). Other specimens are from the sea cliffs of Wool Bay, Yorke Peninsular, South Australia. They are from the upper Oligocene-lower Miocene Port Vincent Limestone. This Limestone is a friable, highly porous sandy, bryozoan calcarenite (Schubber, 1996) and is transitional to the eastern part of St. Vincent Gulf with the Port Willunga Limestone (Zang, 2003).

***Rotundastychia aquilaensis* sp. nov.** (Fig. 3.d.2.)

Type material: Holotype SAM P33729, Paratype SAM P33730

Additional material: SAM P33731–38

Type locality: Sea cliffs at Aireys inlet, Victoria (38.4685S, 144.03994E).

Type stratum: Point Addis Limestone.

Etymology: ‘*aquilaensis*’, for the sea cliff tidal island of Eagle Rock near Aireys Inlet.

Diagnosis: *Rotundastychia* species characterised by a low, flat test, more than 0.72 pores per mm TL in petals and an ambulacral to interambulacral ratio less than 140%.

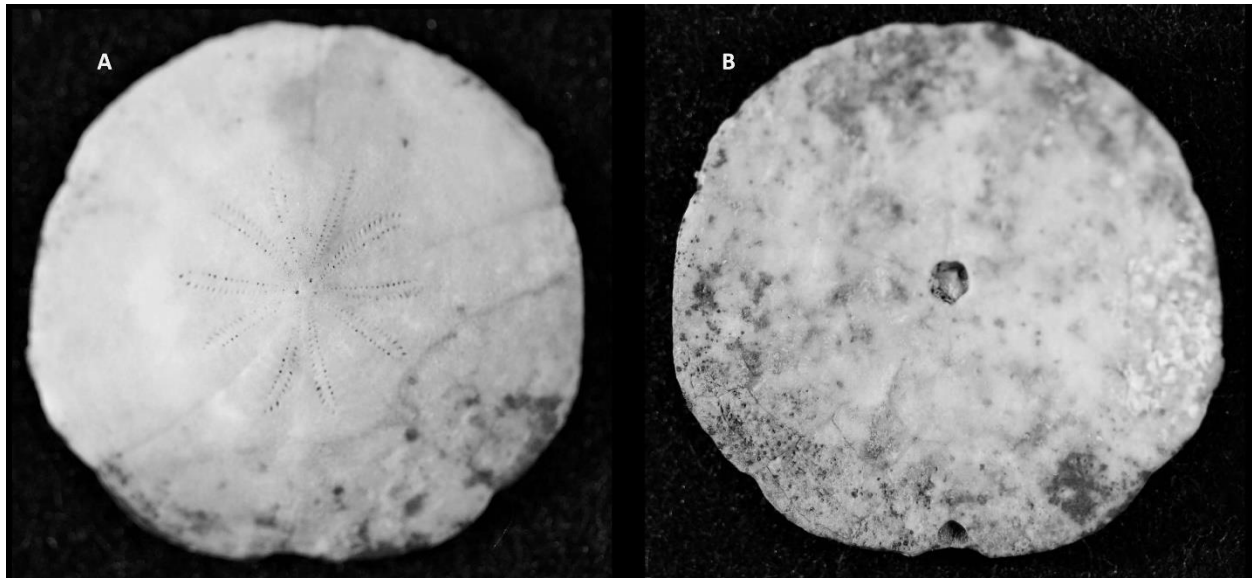


Fig. 3.d.2 Holotype of *Rotundastychia aquilaensis* sp. nov. (SAM P33729), aboral (A) and oral (B) view; TL = 20.79 mm.

Description: Test medium to large, generally circular or nearly so in outline, ranging in length from 11.2–30.0 mm; maximum width 98–106% TL (mean = 101%, SD = 3%, n = 10), occurring rear of centre, but in the range 43–71% TL from anterior ambitus (mean = 54%, SD = 9%, n = 10). Height 11–15% TL (mean = 13%, SD = 1%, n = 10); apex forward of the apical disc 42–49% TL from anterior ambitus (mean = 46%, SD = 2%, n = 8); apical disc 47–51% TL from anterior ambitus (mean = 49%, SD = 1%, n = 8).

Orally, test very flat except for slightly indented food grooves. Keel from the periproct forward toward to the peristome lacking. The apical surface of the test rises in a straight line from ambitus to apical disc; ambitus very sharp. Ambital notches very minor to non-existent in the anterior three perradial sutures and little more than a bevel in the posterior pair. Anal notch minimal. Combing weak and seen in only a few specimens.

Of the 2 specimens for which plates could be observed in paired oral post-basicoronal interambulacra, plate counts were obtained in 7 of the possible 8 regions. 71% of the regions

preserved had seven plates and 29% had six. For the paired ambulacra, four specimens had observable post-basicoronal plate and counts were obtained in 8 of a potential maximum of 16 regions; 63% of regions preserved had 10 plates and 13% having each of eight, nine and 11 respectively. In the two specimens where post-basicoronal ambulacrum III plates were counted, both had 10 plates.

Petals not raised or inflated above test. The mean length of petals, measured as a percentage of the distance from the apical disc to the ambitus in the line of each pore zone, is for the anterior pair 44% (SD = 9%, n = 8) and the posterior pair 39% (SD = 8%, n = 8). Poriferous zones are almost straight and open distally.

Distally, petals end in a point, trailing podia are not developed. Inner are round and outer pores slightly elongate. The anterior poriferous zone in ambulacrum II has 12–25 pore pairs; slightly more in ambulacrum I (16–26). The number of pore pairs in the anterior zone per mm of TL is 0.80 (SD = 0.1, n = 7). Mean width of ambulacrum II at ambitus 113% mean width of interambulacrum 1 (SD = 12%, n = 10). Mean width of ambulacrum III 31% TL (SD = 4%, n = 9).

Peristome small and circular. Indistinct food grooves extend from peristome around the ambitus and can be traced to the apical disc. Aborally, the three anterior grooves are straight and the two posterior grooves arced laterally. Grooves becomes wider upon reaching basicoronal plates and end in a broad, flat region bordering the peristomial opening; peristomial point present in some specimens. Immediately adjacent to the peristome, small buccal podial pores occur at the side of the groove and angled inward toward the peristome. These grooves do not display crenulations as observed in the type species *M. australis*. Basicoronal plates twice as long as wide, radial margins straight; interambulacral basicoronal plates narrow markedly toward the

peristome, end with an obtuse triangular projection and are about 10% longer than their ambulacral counterparts giving the combined basicoranal plates a neat pentagonal shape.

Periproct submarginal, small size, round to lacrimiform in shape, angled posteriorly but with edge up to 20% the periproct diameter from the ambitus. In interambulacrum 5, periproct comes into contact with plates 3a/3b.

The internal structure of *R. aquilaensis* has not been observed.

Stratigraphy and age: The Point Addis Limestone is a shelly bryozoal calcarenite with burrowed sandy marl and calcirudites and is believed to be deposited in a near-shore, high-energy environment (Holdgate & Gallagher, 2003). It onlaps the Angahook Formation at the type section and transitions into the Jan Jac Marl towards the north-east. The age is considered late Oligocene (Holdgate & Gallagher, 2003).

***Rotundastychia eyriei* sp. nov.** (Fig. 3.d.3.)

Type material: Holotype SAM P33739, Holotype SAM P33740

Additional material: SAM P33741–50??, MV P18762-1, MV P18768-1, MV P18769-1, MV P20157-1, MV P20159-1.

Type locality: Sea cliffs at Aireys inlet, Victoria (38.4605S, 144.1107E).

Type stratum: Point Addis Limestone.

Etymology: ‘eyriei’, for Mr John Moore Eyrie who was granted a pastoral lease in the area in 1842. The spelling of his name was changed to Airey at some point in historical texts and the town of Aireys Inlet with that revised spelling was named after him.

Diagnosis: *Rotundastychia* species characterised by a relatively high, flat test, up to 1.3 pores per mm TL in petals and an ambulacral to interambulacral ratio more than 140%.

Description: Test small to medium, circular in shape in shape, ranging in length from 10.7–37.0 mm; maximum width 93–105% TL (mean = 100%, SD = 3%, n = 16), occurring posterior of centre, but in the range 45–70% TL from anterior ambitus (mean = 57%, SD = 8%, n = 16). Height 13–18% TL (mean = 15%, SD = 1%, n = 16); apex slightly forward of the apical disc 40–51% TL from anterior ambitus (mean = 46%, SD = 3%, n = 12); apical disc 46–50% TL from anterior ambitus (mean = 48%, SD = 2%, n = 12).

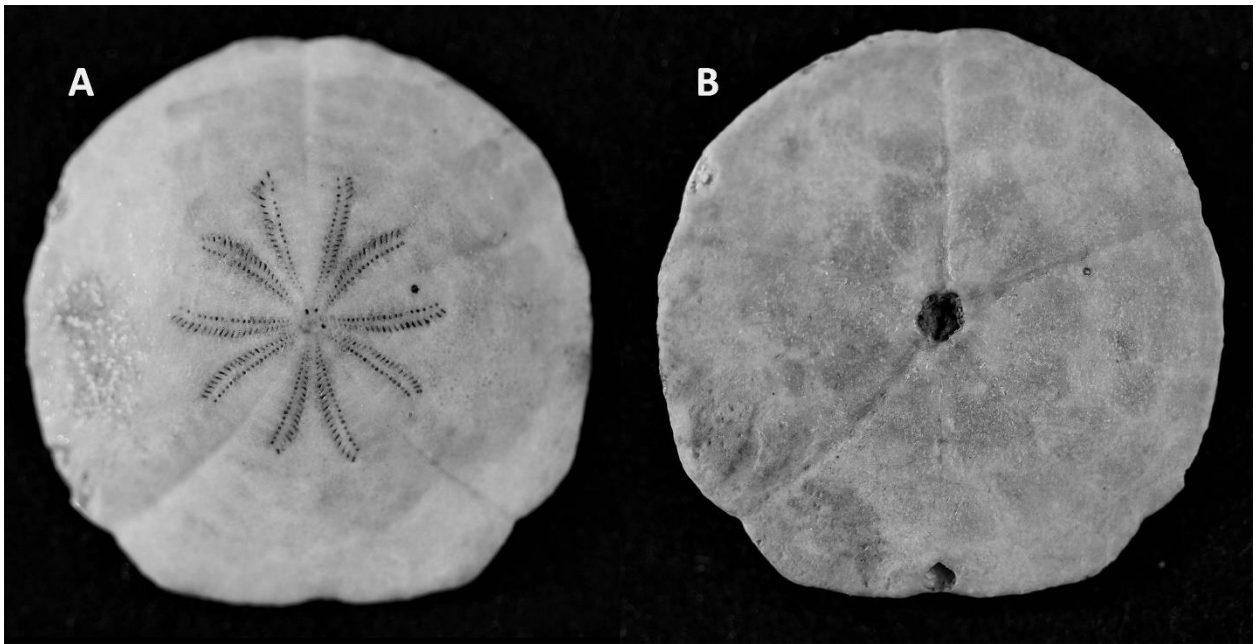


Fig. 3.d.3 Holotype of *Rotundastychia eyriei* sp. nov. (SAM P33739), aboral (A) and oral (B) view; TL = 22.15 mm.

Orally, test very flat except for slightly indented food grooves. Keel from the periproct forward toward to the peristome lacking. The apical surface of the test rises in a slight convex line from ambitus to apical disc; ambitus very sharp. Ambital notches very minor to non-existent

in the anterior three perradial sutures and little more than a bevel in the posterior pair. Anal notch present in some specimens but minor. Combing weak and seen in only a few specimens.

Of the nine specimens for which plates could be observed in paired oral post-basicoronal interambulacra, plate counts were obtained in 25 of the possible 36 regions. 76% of the regions preserved had seven plates and 24% had six. For the paired ambulacra, 12 specimens had observable post-basicoronal plate and counts were obtained in 23 of a potential maximum of 48 regions; 52% of regions preserved had nine plates, 26% had 10 and 22% had eight. In the 10 specimens where post-basicoronal ambulacrum III plates were counted, 40% had nine plates, 40% had 10 plates, 10% 11 and 10% 12.

Petals not raised or inflated above test surface. The mean length of petals, measured as a percentage of the distance from the apical disc to the ambitus in the line of each pore zone, is for the anterior pair 42% (SD = 4%, n = 12) and the posterior pair 37% (SD = 3%, n = 12).

Poriferous zones are thin, almost straight and open distally.

Distally, petals end abruptly, trailing podia are not developed. Inner are round and outer pores elongate. The anterior poriferous zone in ambulacrum II has 10–24 pore pairs; slightly more in ambulacrum I (10–25). The number of pore pairs in the anterior zone per mm of TL is 1.00 (SD = 0.2, n = 12). Mean width of ambulacrum II at ambitus 165% mean width of interambulacrum 1 (SD = 20%, n = 15). Mean width of ambulacrum III 33% TL (SD = 3%, n = 14).

Peristome small and pentagonal. Food grooves extend from peristome around the ambitus and can be traced to the apical disc. Aborally, the three anterior grooves are straight and the two posterior grooves arced laterally. Grooves becomes wider upon reaching basicoronal plates and end in a broad, flat region bordering the peristomial opening; peristomial point present. Immediately adjacent to the peristome, small buccal podial pores occur at the side of the groove,

one on each side and widely spaced. A pair of sphaeridia is prominent. These grooves do not display crenulations as observed in the type species *M. australis*. Basicoronal plates twice as long as wide, radial margins straight; interambulacral basicoronal plates narrow markedly toward the peristome, end with an acute triangular projection and are about 20% longer than their ambulacral counterparts.

Periproct submarginal, medium size, round, angled posteriorly but with edge touching the ambitus. In interambulacrum 5, periproct comes into contact principally with plates 3a/3b but contact with plates 2a/3b also observed in one specimen.

Internally, a complex system of peripheral pillars and buttresses is developed around the test, similar to *R. pledgei*. An intermulum is present and presents as a solid but thin, almost unbroken wall from within interambulacrum 5 but stopping short of interambulacrum III. Radiating interambulacral pillars or walls are apparent. Around the margins there is a complex network of structures that extend from the ambitus about 30% the distance to the centre of the test. This network comprises a series of short walls that align parallel to the margin.

Stratigraphy and age: As for *R. aquilaensis*.

Remarks on the species of *Rotundastychia*.

The key diagnostic features of the type and six other species allocated to this genus are summarised in Table 3.d.1. In addition, a box plot of the seven species is presented in Figs 3.d.4–13 with each figure representing a different diagnostic feature. *R. pledgei* is the largest of the three species and has a shape that while tending to circular still has the pentagonal features of almost straight sides and posterior. *R. aquilaensis* and *R. eyriei* are both almost circular (Table 3.d.1.).

While the width to length ratio of the species is inconclusive (Fig. 3.d.4.), *R. aquilaensis* has the highest such ratio. In the case of height to length ratio (Fig. 3.d.5.) *R. eyriei* has the highest ratio and it does appear significant. *R. pledgei* clearly has a significantly lower number of pore pairs per mm TL (Fig.3.d.6.) than *R. aquilaensis* although the difference with *R. eyriei* appears less significant.

R. pledgei has sharper margins than the other two species (Fig.3.d.7.) at 3% TL compared to *R. aquilaensis* at 4–6% TL and *R. eyriei* at 5–7% TL.

The ratio of the width at the margin of the interambulacrum to ambulacrum clearly separates *R. eyriei* from the other two species (Fig.3.d.8.). While the ratio for *R. eyriei* has a mean of 165% the ratio for both *R. pledgei* and *R. aquilaensis* is 113% (Table 3.d.1.). While this ratio may be impacted by TL Fig. 3.d.9. clearly shows that the measurements for *R. eyriei* appear mutually exclusive to those of the other two species indicating TL is not a factor in the conclusion that *R. eyriei* could be separated from the other two species on this criterion alone. However, the width of ambulacrum III at the margin as a percentage of TL is not at all inclusive even though *R. pledgei* has the lowest ratio and *R. eyriei* the highest (Fig. 3.d.10.).

The number of plates on the oral surface might be useful criteria in separating the species although populations will be needed as the number of plates overlap between the species. *R. pledgei* has 7 paired interambulacrum plates, 10–11 paired ambulacrum plates and 10–12 plates in ambulacrum III while *R. aquilaensis* has 6–7, 9–10 and 10 respectively and *R. eyriei* 7, 9–10 and 9–10 plates respectively (Table 3.d.1, Figs 3.d.11–13.).

A key to the three species is provided (Table 3.d.2.).

Diagnostic feature	<i>R. pledgei</i> sp. nov.	<i>R. aquilaensis</i> sp. nov.	<i>R. eyriei</i> sp. nov.
Test plan outline	Tending to circular	Circular	Circular
Test length	Medium to very large	Medium to large	Small to medium
Test lateral profile, apical surface	Straight	Straight	Slightly convex
Oral surface profile	Very flat	Very flat	Very flat
Mean height	13% TL	13% TL	15% TL
Distance of apex from anterior (mean)	51% TL	46% TL	46% TL
Ambitus	Very sharp	Sharp	Sharp
Interambulacral plates in oral paired interambulacra	7	6–7	7
Post-basicoronal amb. plates in oral paired amb.	10–11	9–10	9–10
Post-basicoronal plates in anterior oral ambulacra III	10–12	10	9–10
Anterior petal to ambitus (mean)	44%	44%	42%
Posterior petal to ambitus (mean)	40%	39%	37%
Number of pore pairs	Ant. 23–36 Post. 23–38	Ant. 12–25 Post. 16–26	Ant. 10–24 Post. 10–25
Number pore pairs per mm TL (mean)	0.63	0.88	1.00
Petals inflated	Very slightly	No	No
Amb. width at ambitus as a % of interamb. width (mean)	113%	113%	165%
Width ambulacrum III at ambitus as percentage TL	28%	31%	33%
Submarginal periproct	Circular to lacrimiform; 30% to margin	Circular; 20% to margin	Circular; touching margin
Contact plates with periproct (principal)	3a/3b	3a/3b	3a/3b
Interambulacral basicoronal plates	20% longer than basicoronal plates; narrow markedly; acute triangular projection	10% longer than basicoronal plates; narrow markedly; obtuse triangular projection	20% longer than basicoronal plates; narrow markedly; acute triangular projection

Table 3.d.1. Comparison of diagnostic features of the three species of *Rotundastychia*.

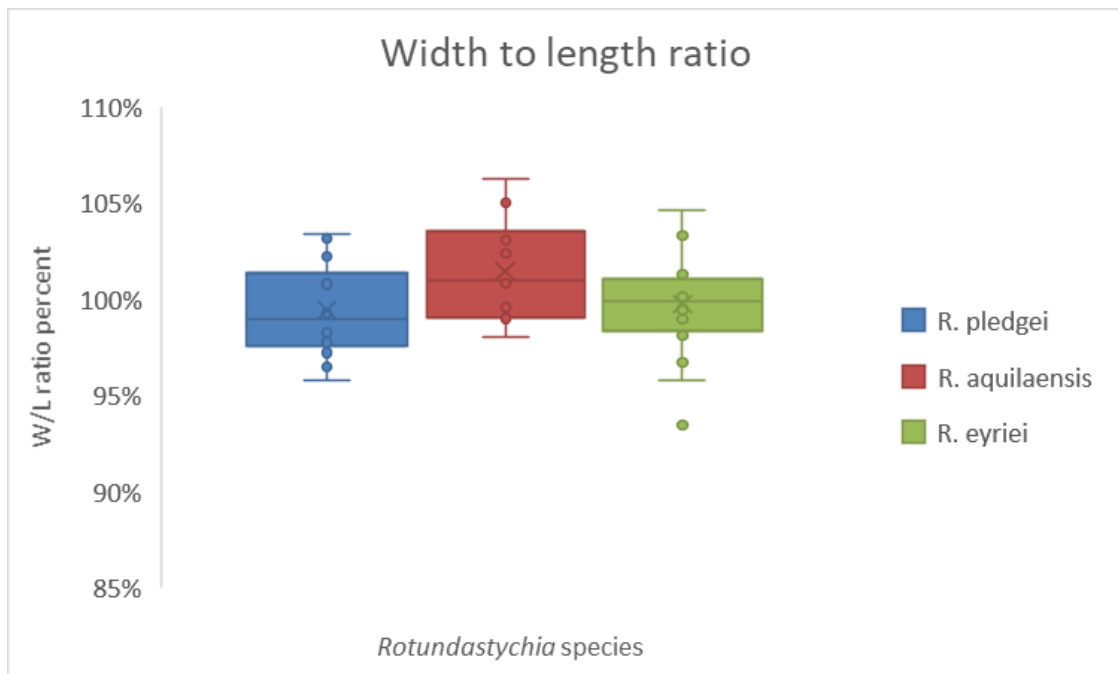


Fig. 3.d.4. Box plot of width to length ratio of *Rotundastychia* species.

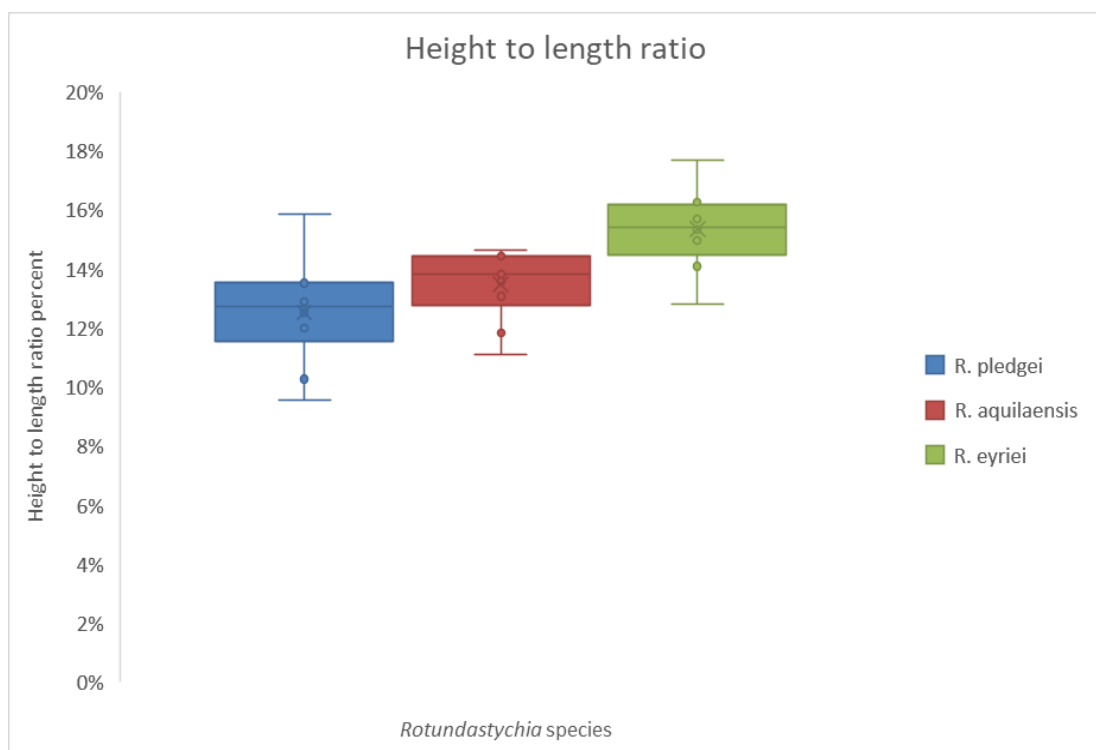


Fig. 3.d.5. Box plot of height to length ratio of *Rotundastychia* species.

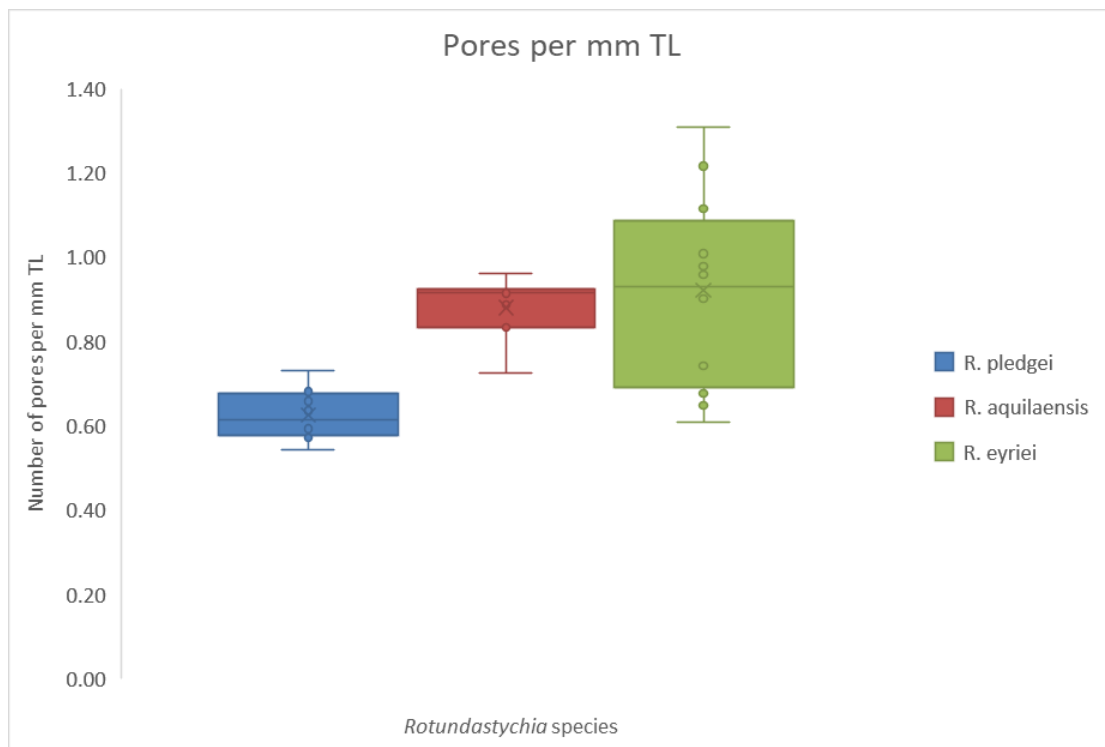


Fig. 3.d.6. Box plot of number of pores per mm TL of Rotundastychia species.

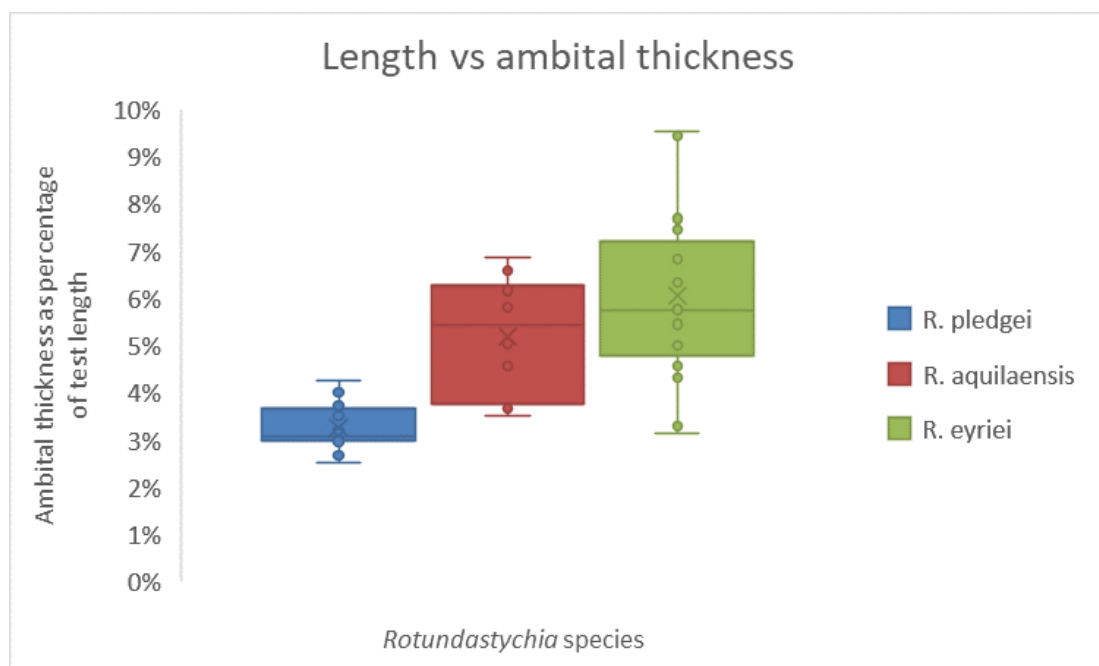


Fig. 3.d.7. Box plot of test length vs ambital thickness of Rotundastychia species.

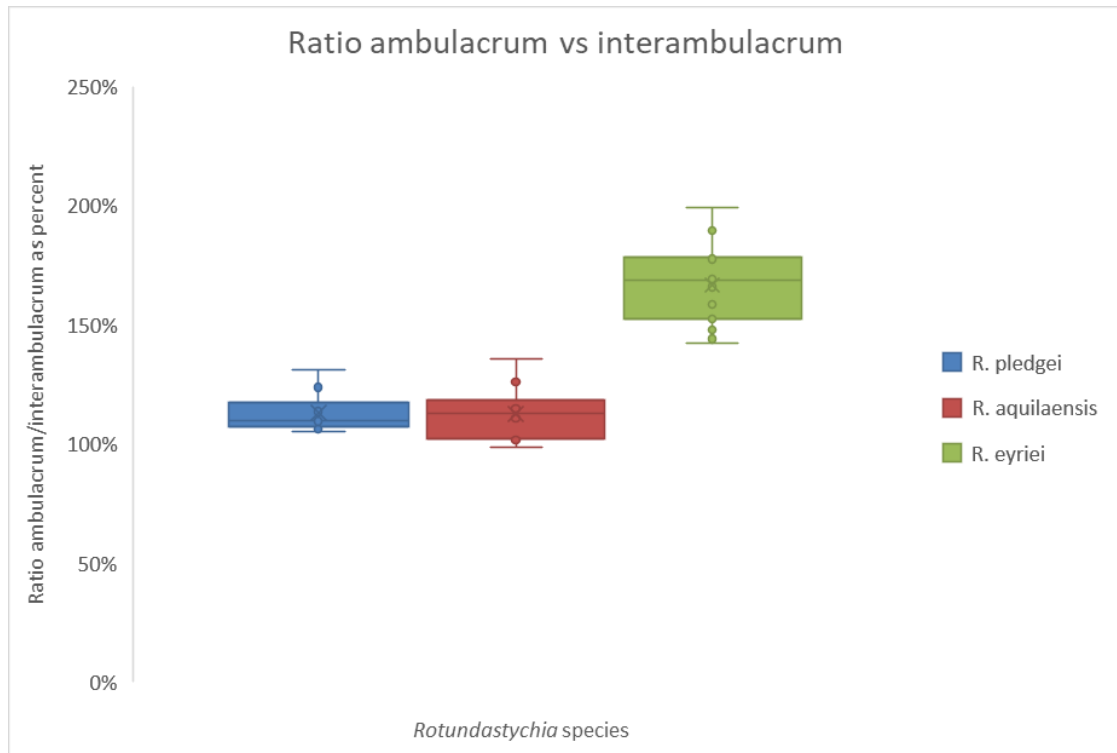


Fig. 3.d.8. Box plot of the ratio of ambulacrum width at ambitus against interambulacrum width of *Rotundastychia* species.

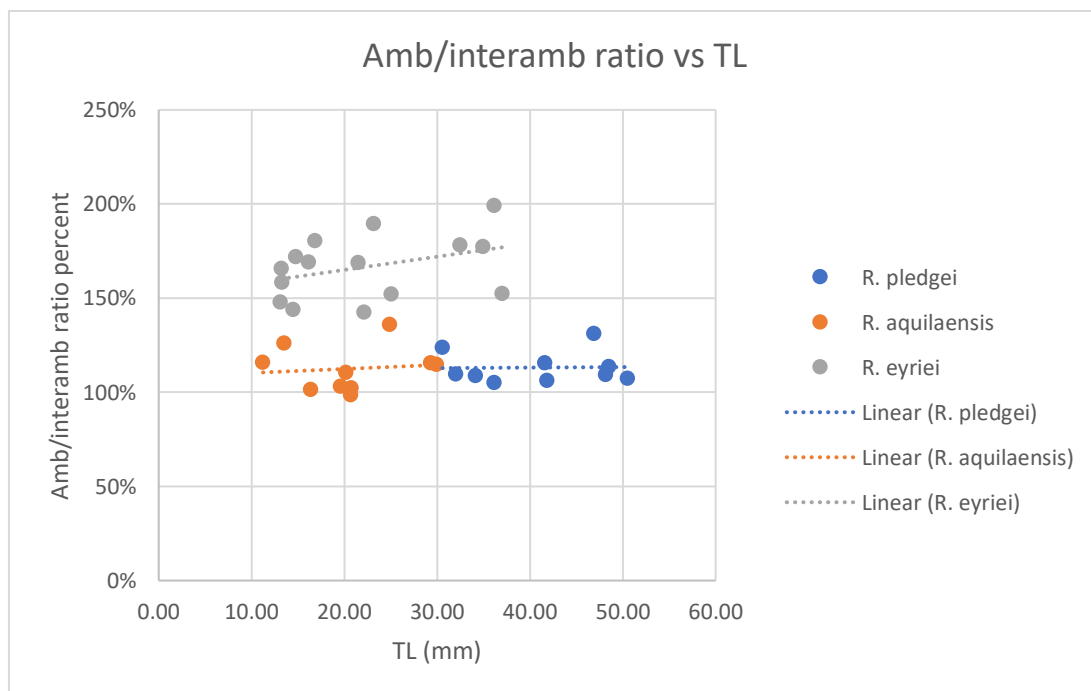


Fig. 3.d.9. Ambulacrum to interambulacrum ratio compared to TL in *Rotundastychia* species.

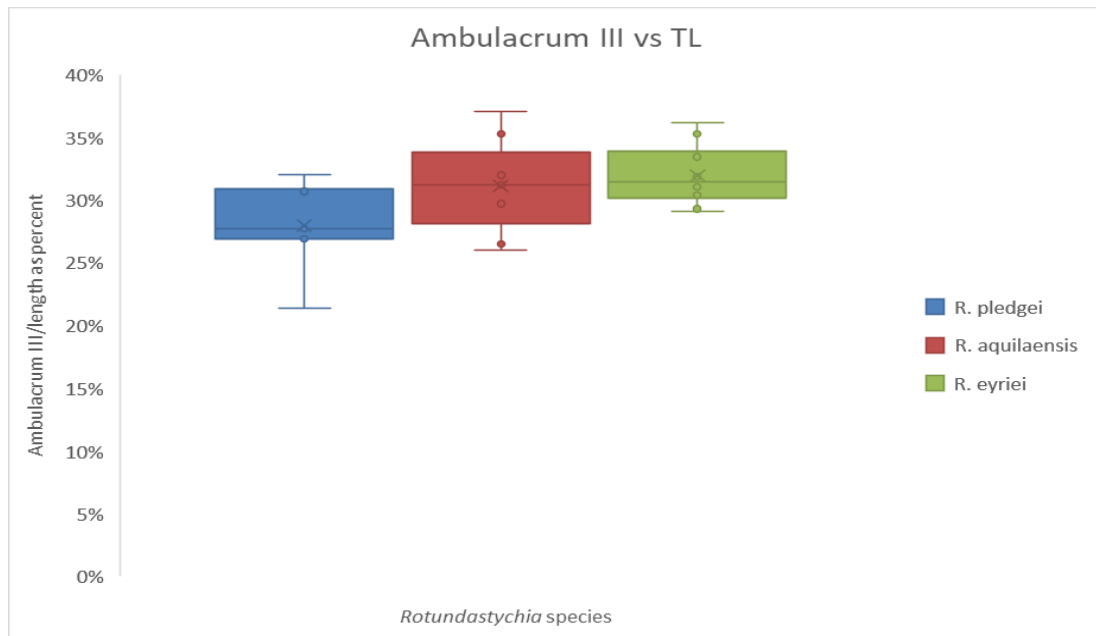


Fig. 3.d.10. Box plot of the ratio of width of ambulacrum III at ambitus against test length (TL) of *Rotundastychia* species.

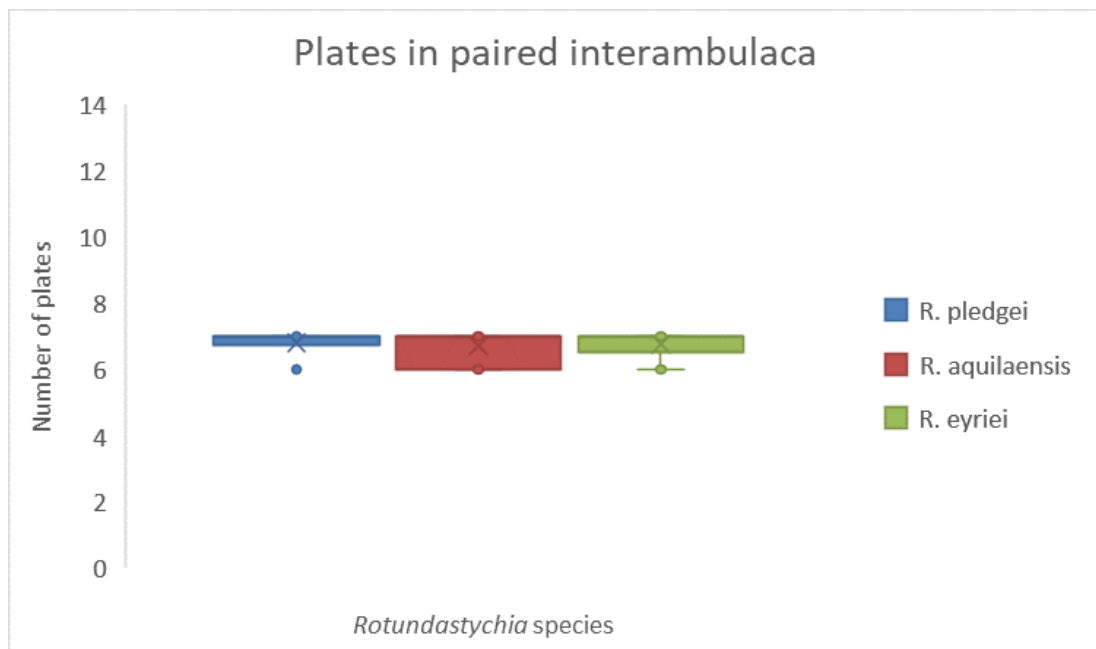


Fig. 3.d.11. Box plot of the number of plates in the paired interambulacra on the oral surface of *Rotundastychia* species.

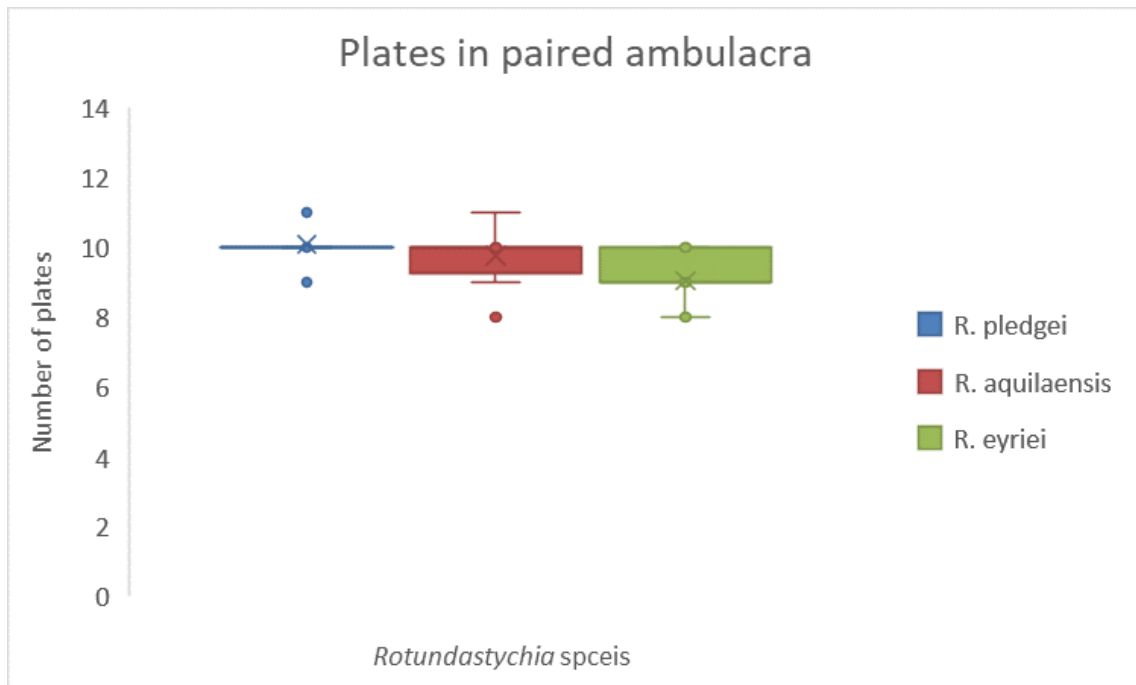


Fig. 3.d.12. Box plot of the number of plates in the paired ambulacra on the oral surface of *Rotundastychia* species.

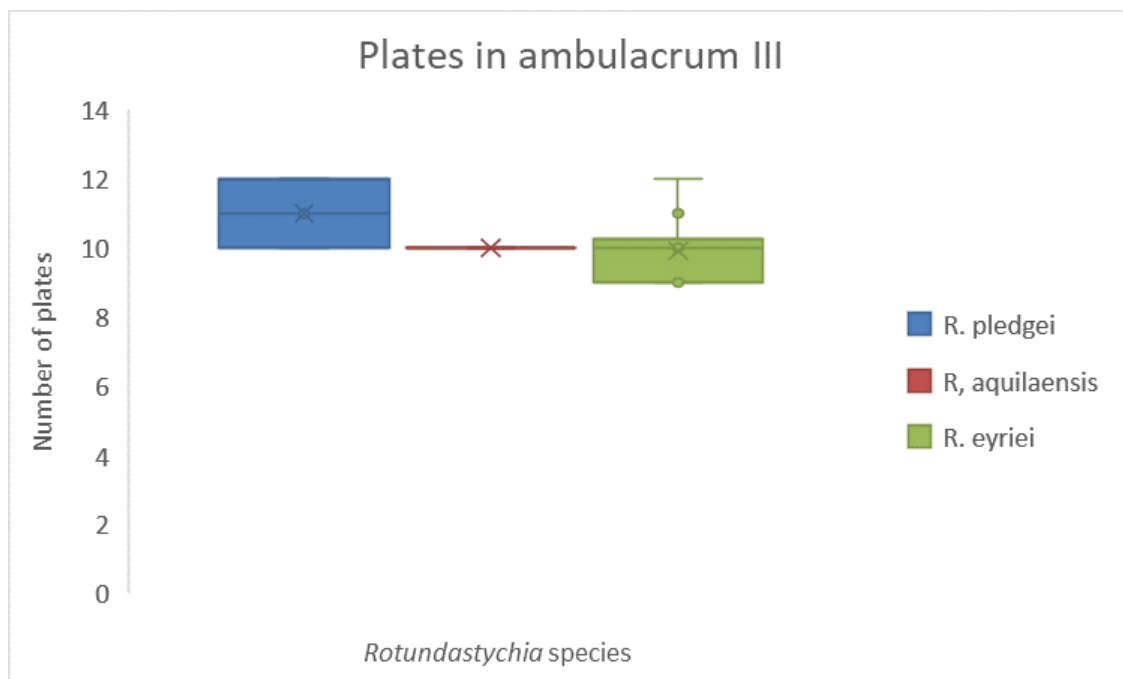


Fig. 3.d.13. Box plot of the number of plates in the ambulacrum III on the oral surface of *Rotundastychia* species.

1a. Mean interamb/amb ratio <140%; number of pores per mm TL>0.92; periproct not touching margin	2
1b. Mean interamb/amb ratio >140%; number of pores per TL<0.92; periproct touching margin.....	<i>eyriei</i>
2a. Petals inflated; Number of pores per mm TL<0.73	<i>pledgei</i>
2b. Petals not inflated; number of pores per mm TL>0.73.....	<i>aquilaensis</i>

Table 3.d.2. Key to species of Rotundastychia.

Chapter 3.e. Genus *Deltoidstychia* gen. nov.

Abstract

The genus *Deltoidstychia* gen. nov. is described along with one species, *D. erioaster* sp. nov. from upper Oligocene-lower Miocene Port Vincent Limestone, South Australia. The fundamental difference that sets this genus apart from *Monostychia* and *Quinquestychia* is a test whose width equals its length. It differs from *Rotundastychia* in having its maximum width toward the posterior making it deltoid in shape rather than circular.

Systematic palaeontology

Order Clypeasteroida A. Agassiz, 1872

Suborder Clypeasterina A. Agassiz, 1872

Family Arachnoididae Duncan, 1889

Subfamily Monostychinae sub.fam. nov.

***Deltoidstychia* gen. nov.**

Type species: Deltoidstychia erioaster sp. nov.

Etymology: The genus name, *Deltoidstychia*, derives from the Greek ‘delta’ referring to the broad triangularity shape of the test outline. It has been chosen to maintain a link with the work of Pritchard (1892b) who lists *Monostychia deltoidalis* Tate *m.s.* as a species from the western shores of St. Vincent’s Gulf. He refers the species to Tate *m.s.* however no Tate publication comments on this species. There was no description and no figure. As a result the name is

considered *nomen nudum*. ‘Stychia’ means row (Sadler *et al.* 2016) and refers to the food grooves but it is used here to provide a link back to *Monostychia* from whence the genus has been divided.

Diagnosis: Monostychioid echinoid with test width equal to its length, delta-shaped in plan; prominent protuberances (or wings) on posterior margin; sharp ambitus; petals short to medium and straight to slightly arched with the distal ends of each pair divergent; periproct submarginal, generally touching ambitus; keel lacking between peristome and periproct; flat oral surface.

Description: as for the type species.

***Deltoidstychia erioaster* sp. nov.** (Fig. 3.e.1.)

1892b *Monostychia deltoidalis* Tate *ms*; Pritchard, P. 180.

Type material: Holotype SAM P29660, Paratype SAM P29661.

Additional material: SAM P29662–1 to –10, P29663–1 to –10, P29664–1 to –9.

Type locality: Sea cliffs of Wool Bay, Yorke Peninsular, South Australia.

Type stratum: Port Vincent Limestone.

Etymology: ‘*erioaster*’, derives from ‘erio’ (Greek) for ‘wool’ and ‘aster’ (Latin) meaning ‘star’. The name refers to the sea star from Wool Bay.

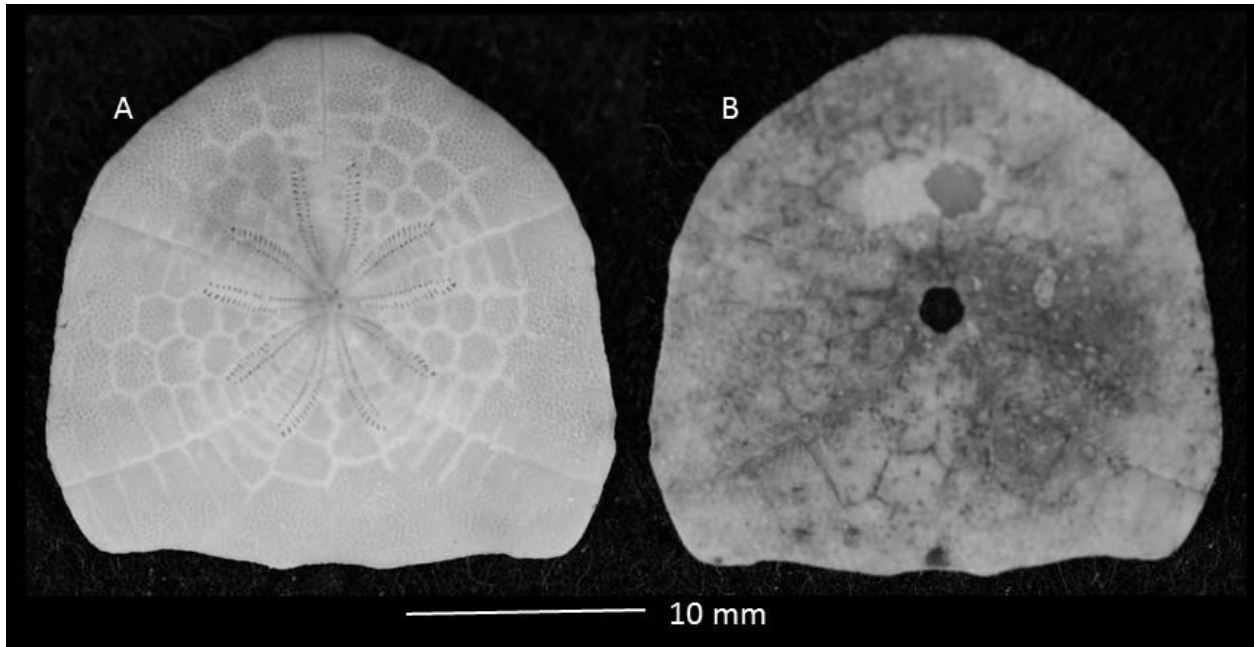


Fig. 3.e.1. Holotype of *Deltoidstychia erioaster* sp. nov. (SAM P29660), aboral (A) and oral (B) view; TL = 23.19 mm.

Description: Small to medium test in which width equals length; anterior rounded to slightly pointed with the test continuing to widen posteriorly to a delta shape in mature specimens; the posterior margin is straight and generally at right angles to the anterior-posterior axis except for two pair of prominent protuberances (or wing-like structures), one pair immediately adjacent to the periproct and the second at the end of the bevel of the posterior perradial sutures; both the deltoid shape and the size of protuberances become more pronounced with test size and are assumed to be ontogenetic. Test ranging in length from 10.6–32.2 mm; maximum width 91–110% TL (mean = 100%, SD = 5%, n = 31), occurring significantly posterior of centre, but in the range 51–83% TL from anterior ambitus (mean = 74%, SD = 7%, n = 31). Height 15–21% TL (mean = 18%, SD = 2%, n = 26); apex forward of the apical disc 34–55% TL from anterior ambitus (mean = 43%, SD = 5%, n = 21); apical disc 47–55% TL from anterior ambitus (mean = 51%, SD = 2%, n = 23).

Orally, test flat; food grooves do not indent the oral part of the test in most specimens except for immediately adjacent to the peristome although they are more obvious on the aboral surface. Lacking keel from the periproct forward toward to the peristome. The aboral surface of the test rises in a slight concave from ambitus to apical disc; ambitus sharp. Ambital notches are absent in the anterior three perradial sutures and a minor bevel in the posterior pair. At the posterior end of the bevel is a distinct projection formed by the test margin scalloping in on itself leading into a second projection prior to the margin reaching the periproct. Combing has not been observed.

Of the 27 specimens for which plates could be observed in paired oral post-basicoronal interambulacra plates counts were obtained in 96 of the possible 108 regions. 38% of the regions preserved had eight plates, 38% had nine and 18% had 10, 4% had seven and 3% had 11. For the paired ambulacra, post-basicoronal plate and counts were obtained in 93 of a potential maximum of 108 regions; 34% of regions preserved had 11 plates, 24% had 12, 18% had 10, 13% had nine, 6% had 13, 2% had eight, 1% had seven and 1% had 14. In the 21 specimens where post-basicoronal ambulacrum III plates were counted, 38% had 10 plates, 24% had 12, 14% had 11, 14% had nine, 5% had 13 and 5% had 14.

Petals not inflated. The mean length of petals, measured as a percentage of the distance from the apical disc to the ambitus in the line of each pore zone, is for the anterior pair 47% (SD = 5%, n = 24) and the posterior pair 41% (SD = 4%, n = 24). Poriferous zones are thin, almost straight and open and continuing to widen distally.

Distally, petal ends are truncated, trailing podia are not developed. Inner are round and outer pores elongate and less than twice the size of the inner pore. The anterior poriferous zone in ambulacrum II has 12–22 pore pairs; slightly more in ambulacrum I (12–23). The number of pore pairs in the anterior zone per mm of TL is 0.98 (SD = 0.2, n = 21). Mean width of

ambulacrum II at ambitus 133% mean width of interambulacrum 1 (SD = 16%, n = 29). Mean width of ambulacrum III 27% TL (SD = 3%, n = 28).

Peristome small and circular. While the perradial sutures are relatively easy to follow, the food grooves are difficult to discern. Grooves become a little more distinct and slightly wider upon reaching basicoronal plates. Aborally, the three anterior grooves are straight, and the two posterior grooves arced laterally. Immediately adjacent to the peristome, small buccal podial pores occur at the side of the groove, one on each side and relatively closely spaced. Basicoronal plates barely twice as long as wide, radial margins straight to slightly convoluted; interambulacral basicoronal plates comparatively narrow with almost parallel sides and end with an acute triangular projection and are about 20% longer than their ambulacral counterparts.

Periproct submarginal, small, round, angled distinctly posteriorly and in touch with the ambitus. In interambulacrum 5, periproct comes into contact with plates 3a/3b with the exception of two specimens in which it was 2a/3b and 3a/4b.

The internal buttressing has been observed in cross section. A complex system of peripheral pillars and buttresses is developed around the test and extending less than 5% the test diameter from the margin. An intermurum is present and presents as a series of columns and broad pillars.

Stratigraphy and age: Specimens are from the sea cliffs of Wool Bay, Yorke Peninsular, South Australia. They are from the upper Oligocene-lower Miocene Port Vincent Limestone. This Limestone is a friable, highly porous sandy, bryozoan calcarenite (Schubber, 1996) and is transitional to the eastern part of St. Vincent Gulf with the Port Willunga Limestone (Zang, 2003).

Diagnostic feature	<i>D. erioaster</i> sp. nov.
Test plan outline	Delta shaped
Test length	Small to medium
Test lateral profile, apical surface	Slightly concave
Oral surface profile	Very flat
Mean height	18% TL
Distance of apex from anterior (mean)	43% TL
Ambitus	Sharp
Interambulacral plates in oral paired interambulacra	8–9
Post-basicoronal amb. plates in oral paired amb.	10–12
Post-basicoronal plates in anterior oral ambulacra III	10–12
Anterior petal to ambitus (mean)	47%
Posterior petal to ambitus (mean)	41%
Number of pore pairs	Ant. 12–22 Post. 12–23
Number pore pairs per mm TL (mean)	0.98
Petals inflated	No
Amb. width at ambitus as a % of interamb. width (mean)	133%
Width ambulacrum III at ambitus as percentage TL	27%
Submarginal periproct	Circular, angled and touching margin
Contact plates with periproct (principal	3a/3b
Interambulacral basicoronal plates	Twice as long as wide; acute triangular projection

Table 3.e.1. Comparison of diagnostic features of *Deltoidstychia*.

Chapter 3.f. Subfamily Ammotrophinae

Introduction

In Chapter 3. Systematics, it was concluded that the best taxonomic position for the genus *Monostychia* prior to this study was in the subfamily Ammotrophinae. In this study *Monostychia* and its closest relatives have been moved to the subfamily Monostychinae. Two other new genera, both lacking the intermulum of monostychioids, need to be placed in a subfamily. In both cases the choice appears to be between Ammotrophinae and Arachnoidinae. As they both have the ammotrophinoid characters of the more complex internal supports and a periproct that is not supra-marginal, it appears they should be assigned to the subfamily Ammotrophinae.

Subfamily Ammotrophinae

Diagnosis. Clypeasteroid echinoid lacking an intermulum or intestinal buttressing; internal supports both marginal and around the peristome; periproct generally oral but close to or touching the margin; five genital pores.

Chapter 3.g. Genus *Obscurostychia* gen. nov.

Abstract

The genus *Obscurostychia* gen. nov. is described along with two species, *O. spirographica* sp. nov. and *O. curtus* sp. nov., all from the late Eocene–early Oligocene Kingscote Limestone of Kangaroo Island, South Australia. Members of the genus lack an intermulum or intestinal buttressing and hence cannot be placed in the subfamily Monostychinae. Instead the genus is tentatively placed in the subfamily Arachnoidinae Duncan, 1889. The genus differs from *Arachnoides* in that the periproct is terminal and not oral, the food grooves are faint or absent, combing is also absent and there are trailing podia in ambulacrum III. The two species of *Obscurostychia* are separated primarily by the length and shape of the petals.

Introduction

Howchin, 1918 first commented on a species of clypeasteroid from Kingscote and placed it within *Monostychia* Laube, 1869 stating that it “*is thin and discoidal with its under and upper surfaces almost parallel*”. Milnes *et al.* (1983) reported *M. australis* in Oligocene strata of Kangaroo Island. They suggested that the Eocene age of previous records of echinoids from the Kingscote Limestone should be treated with caution due to the presence of unconformities. Holmes (2004) listed two undescribed species of *Monostychia* from Kingscote, Kangaroo Island and describes *Rhynchopygus janchrisorum*, a new species of cassiduloid. While there can be no certainty that the specimens referred to by these researchers are the herein described *Obscurostychia*, the two species described appear to be the most common of the *Monostychia*-like fossils in the lowest strata of the Kingscote Limestone and is therefore likely to be the same.

Materials

Twenty specimens collected from the sea cliffs of Kingscote, Kangaroo Island were used in this study. The specimens have been lodged at the South Australian Museum and numbered P29642–P29660 and P29665–6.

Systematic palaeontology

Order Clypeasteroida A. Agassiz, 1872

Suborder Clypeasterina A. Agassiz, 1872

Family Arachnoididae Duncan, 1889

Subfamily Ammotrophinae Durham, 1955

***Obscurostychia* gen. nov.**

Type species: Obscurostychia spirographica sp. nov.

Etymology: The genus name, *Obscurostychia*, derives from the Latin ‘obscurus’ meaning to be hidden or concealed and referring the apparent absence of food grooves. ‘Stychia’ means row (Sadler *et al.* 2016) and refers to the food grooves. It is also used here to provide a link back to *Monostychia* from whence the genus has been historically classified.

Diagnosis: Ammotrophid echinoid with sharp ambitus, four gonopores, marginal or terminal periproct first bounded by the third or fourth pair of post-basicoronal plates (plates 3a/3b, 4a/4b or a combination of third and fourth pair); seven to ten post-basicoronal plates on the oral surface in the paired interambulacra, ten to 13 plates on the oral surface in the paired ambulacra and 11 to 14 plates on the oral surface in ambulacrum III; food grooves faint or may be absent; lacks combing; trailing podia on the petals in ambulacrum III; intermulum (intestinal buttressing) absent.

Description: Test rounded, almost circular to slightly elongate and pentagonal, flat on the oral surface and barely rising on the aboral surface to the apex which is forward of the apical disc; food grooves are faint or absent; ambitus is sharp; four gonopores with the posterior pair more widely spaced than the anterior pair; seven to ten post-basicoronal plates on the oral surface in the paired interambulacra, ten to 13 plates on the oral surface in the paired ambulacra and 11 to 14 plates on the oral surface in ambulacrum III; combing absent; petals remain wide open distally; trailing podia in ambulacrum III; the ambulacral zone has conjugate pores with a weak furrow between, the inner pore rounded and the outer pore tear-drop in shape; the periproct is terminal.

***Obscurostychia spirographica* sp. nov.** (Fig. 3.g.1.)

Type material: Holotype is SAM P29642, Paratype SAM P29643

Additional material: SAM P 29644–52

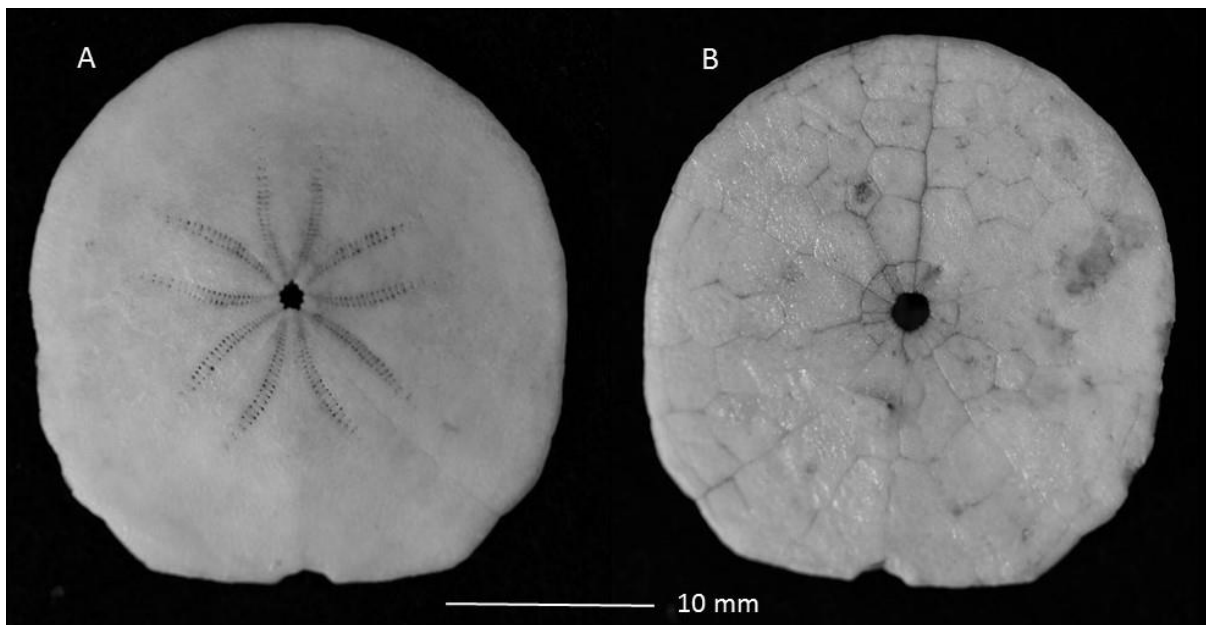


Fig. 3.g.1. Holotype of *Obscurostychia spirographica* sp. nov. (SAM P29642), aboral (A) and oral (B) view; TL = 26.60 mm.

Type-locality: Type section of the Kingscote Limestone in the cliffs below the Ozone Hotel, Kingscote, Kangaroo Island, South Australia (35.6563S 137.6402E).

Type stratum: Kingscote Limestone.

Etymology: ‘*spiro*’, derives from the Latin for ‘spiral’ and Greek for ‘coil’ and ‘graphic’ from Latin meaning ‘writing or drawing’. The name refers to the shape of the petals that form such a perfect spiral shape one to another as though produced by a spirograph machine.

Diagnosis: *Obscurostychia* species with marginal periproct sometimes favouring the oral side, generally first bounded by plates 3a/3b, 3a/4b, 4a/3b or 3a/4b; eight to nine plates on the oral surface in the paired interambulacra, ten to 12 plates on the oral surface in the paired ambulacra and 11 to 12 plates (generally 12) on the oral surface in ambulacrum III; long thin petals generally extending more than 50% to the ambitus.

Description: Test circular to slightly elongate, small to medium in size ranging in length from 10.1–31.3 mm.; maximum width 84–100% TL (mean = 95%, SD = 5%, n = 11), occurring generally slightly posterior of centre, but in the range 42–67% TL from anterior ambitus (mean = 51%, SD = 7%, n = 11). Height 11–22% TL (mean = 16%, SD = 3%, n = 10); apex forward of the apical disc 37–50% TL from anterior ambitus (mean = 44%, SD = 4%, n = 10); apical disc 48–52% TL from anterior ambitus (mean = 50%, SD = 1%, n = 10).

Orally, test is flat. There is no keel or drooping tail between the periproct and peristome. The apical surface rises from the ambitus to the apical disc in an almost straight line; ambitus sharp. Ambital notches are absent in the anterior three ambulacra and are only a minor bevel in ambulacra I and V. Anal notch is present. Combing is absent.

Of the eight specimens for which plates could be observed in paired oral post-basicoronal interambulacra, plate counts were obtained in 29 of the possible 32 regions. 55% of the regions preserved had eight plates, 31% nine, 7% ten, and 7% had seven. For the paired ambulacra where nine specimens had plates that could be counted, post-basicoronal plate counts were obtained in 28 of a potential maximum of 36 regions; 43% of regions preserved had 12 plates, 32% 11 and 25% had ten. In the eight specimens where post-basicoronal ambulacrum III plates were counted, 63% had 12 plates, 25% 11 and 13% 13.

Petals not raised or inflated above test surface. The mean length of petals, measured as a percentage of the distance to the ambitus in the line of each pore zone, is for the anterior pair 51% (SD = 3%, n = 10) and the posterior pair 49% (SD = 6%, n = 10). Poriferous zones are long, thin and slightly curved, open distally, with outer pore rows slightly more arcuate than inner ones. The zones of one petal appear to extend in an unbroken arc into the zone of the adjacent petal.

Petal interporiferous zones widest at their distal end. Distally, petals end in a fine point, trailing podia (generally three) are developed in ambulacrum III. The pores are conjugate with the inner pore of each pair are round and the outer pore oval to elongate often with a small furrow joining them. The anterior poriferous zone in ambulacrum II has 12–25 pore pairs; slightly more in ambulacrum I (14–26). Number of pores per mm TL is 0.88 (SD = 0.01, n = 6). Mean width of ambulacrum II at ambitus 128% mean width of interambulacrum 1 (SD = 13%, n = 11). Mean width of ambulacrum III 32% TL (SD = 3%, n = 11).

Peristome small and circular to slightly elongate and pentagonal. While the perradial sutures are clear, food grooves appear absent except immediately adjacent to the peristome where they are relatively wide. Basicoronal plates distinctly longer than wide, radial margins straight;

interambulacral basicoronal plates are thin and end with an obtuse triangular projection and are about 5% longer than their ambulacral counterparts.

Periproct terminal, sometimes favouring the oral side (20%), small and tear-dropped in shape. In interambulacrum 5, periproct first comes into contact orally with a variety of plate combinations. Of the nine specimens observed, three had 3a/3b, two had 3a/4b, one had 4a/3b and three had 4a/4b.

Internally, a complex system of peripheral pillars and buttresses is developed around the test, although these are less well developed than in *M. australis*. Radiating interambulacral pillars or walls are not present. Central pillars are present but rare and not well developed. Complex marginal buttressing is apparent around the edges of the test. Strong and complex central buttressing is present. The test lacks an intermurum.

Stratigraphy and age: The Kingscote Limestone is a 41 m thick, richly fossiliferous yellow to buff limestones exposed along the cliffs at Kingscote, Kangaroo Island, South Australia. The sequence has four units: the lowest consisting of echinoid-rich grainy calcarenites capped by a rubbly mollusc-rich conglomerate of late Eocene age; two early Oligocene units, the first fossiliferous quartzose grainstones and rudstones and the second bryozoan grainstones and rudstones; and an upper unit of cross-bedded and burrows bryozoal limestones of early to late Oligocene age (James, *et.al.*, 2016).

Despite the uncertainty expressed by previous researchers as the age of the various strata, the presence *Maslinella chapmani* (Glaessner & Wade, 1959) in samples associated with this species suggest they are late Eocene (James, *et.al.*, 2016).

***Obscurostychia curtus* sp. nov.** (Fig. 3.g.2.)

Type material: Holotype is SAM P29653, Paratype SAM P29654

Additional material: SAM P 29655–9, SAM P29665–6

Type-locality: Type section of the Kingscote Limestone in the cliffs below the Ozone Hotel, Kingscote, Kangaroo Island, South Australia (35.6563S 137.6402E).

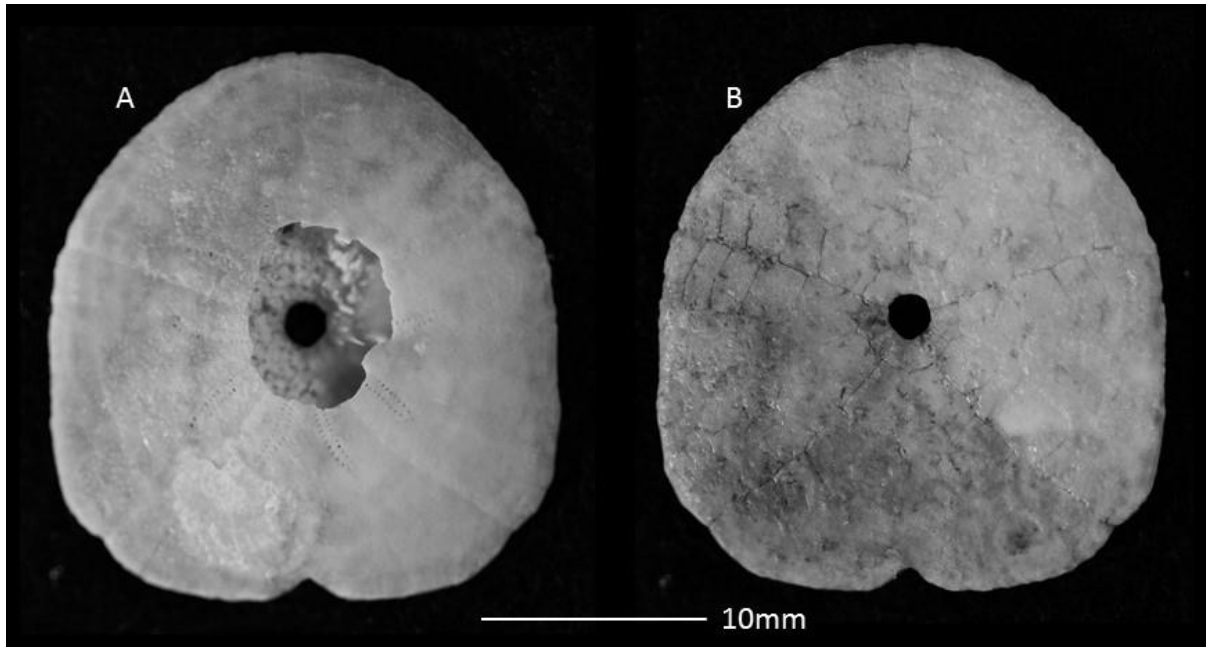


Fig. 3.g.2. Holotype of *Obscurostychia curtus* sp. nov. (SAM P29653), aboral (A) and oral (B) view; TL = 22.68 mm.

Type stratum: Kingscote Limestone.

Etymology: ‘*curtus*’, derives from the Latin for short or incomplete and this refers to the shape of the petals which are short and stubby in comparison to *O. spirographica*.

Diagnosis: *Obscurostychia* species with marginal periproct generally sometimes the aboral side, first bounded by plates 3a/4b or 4a/4b; eight to ten plates on the oral surface in the paired interambulacra, 12 to 13 plates on the oral surface in the paired ambulacra and 13 to 14 plates

(generally 13) on the oral surface in ambulacrum III; short stubby petals extending less than 50% to the ambitus.

Description: Test slightly elongate and pentagonal, very small to small in size ranging in length from 8.2–22.7 mm; maximum width 91–98% TL (mean = 94%, SD = 3%, n = 10), occurring generally posterior of centre, but in the range 48–67% TL from anterior ambitus (mean = 59%, SD = 8%, n = 10). Height 13–22% TL (mean = 18%, SD = 3%, n = 9); apex forward of the apical disc 36–55% TL from anterior ambitus (mean = 45%, SD = 6%, n = 9); apical disc 47–55% TL from anterior ambitus (mean = 50%, SD = 2%, n = 9).

Orally, test is flat. There is no keel or drooping tail between the periproct and peristome. The apical surface rises from the ambitus to the apical disc in a slightly curved line; ambitus sharp. Ambital notches are absent in the anterior three ambulacra and are only a minor bevel in ambulacra I and V. Anal notch is present. Combing is absent.

Of the four specimens for which plates could be observed in paired oral post-basicoronal interambulacra, plate counts were obtained in 14 of the possible 16 regions. 43% of the regions preserved had nine plates, 29% eight and 29% had ten. For the paired ambulacra, where four specimens had observable plates, post-basicoronal plate counts were obtained in 14 of a potential maximum of 16 regions; 50% of regions preserved had 12 plates and 50% had 13. In the four specimens where post-basicoronal ambulacrum III plates were counted, 75% had 13 plates and 25% 14.

Petals not raised or inflated above test surface. The mean length of petals, measured as a percentage of the distance to the ambitus in the line of each pore zone, is for the anterior pair 43% (SD = 5%, n = 6) and the posterior pair 37% (SD = 5%, n = 6). Poriferous zones are short,

stubby and barely curved, open distally, with outer pore rows slightly more arcuate than inner ones.

Petal interporiferous zones widest at their distal end. Distally, petals end abruptly, trailing podia are developed in ambulacrum III. The pores are conjugate with the inner pore of each pair are round and the outer pore oval to slightly elongate often with a furrow joining them. The anterior poriferous zone in ambulacrum II has 11–16 pore pairs; slightly more in ambulacrum I (13–17). Number of pores per mm TL is 1.10 (SD = 0.01, n = 5). Mean width of ambulacrum II at ambitus 129% mean width of interambulacrum 1 (SD = 11%, n = 8). Mean width of ambulacrum III 29% TL (SD = 2%, n = 7).

Peristome small and circular to slightly pentagonal. While the perradial sutures are clear, food grooves are absent. Basicoronal plates distinctly longer than wide, radial margins straight to slightly curved; interambulacral basicoronal plates slightly thinner and end with an obtuse triangular projection and are barely longer than their ambulacral counterparts.

Periproct terminal, sometimes favouring the aboral side (30%), small and tear-dropped in shape. In interambulacrum 5, periproct first comes into contact orally with two plate combinations. Of the four specimens documented, two had 3a/4b and two had 4a/4b.

Internally, a complex system of peripheral pillars and buttresses is developed around the test, although these are less well developed than in *M. australis*. Radiating interambulacral pillars or walls are not present. Central pillars are present but rare and not well developed. Complex marginal buttressing is apparent around the edges of the test. Strong and complex central buttressing is present. The test lacks an intermurum.

Stratigraphy and age: As for *O. spirographica*.

Remarks: *Obscurostychia* lacks an intermulum and therefore is not in the subfamily Monostychinae subfam. nov., precluding it from being aligned to *Monostychia*. However, *Obscurostychia* does not belong in *Ammotrophus* either because in *Ammotrophus* the periproct is on the oral surface and situated distant from the ambitus whereas in *Obscurostychia* it is at the ambitus and terminal. While the actual position of the periproct in relation to the ambitus might not be as important as the interambulacral plates that first come into contact with the periproct, in *Ammotrophus* that number appears to be 2a/2b (Mooi, 1989) while in *Obscurostychia* it is 3a/3b to 4a/4b. Other features that separate *Obscurostychia* from *Ammotrophus* are its small size, circular or discoidal shape compared to *Ammotrophus* with an oval outline, sharp ambitus, faint or apparent lack of food grooves and lack of combing.

Obscurostychia has several features in common with *Arachnoides*. It is flat, discoidal and with a sharp ambitus. Neither have the periproct on the oral surface, however, *Obscurostychia* differs in that the periproct is not on the aboral surface either. *Arachnoides* has a single plate in each column of the oral interambulacra while *Obscurostychia* has many. Other differences include the lack of combing and the presence of trailing podia in *Obscurostychia*.

Obscurostychia also shares some features in common with *Fellaster*. As with *Arachnoides*, the basic flat, discoidal shape with sharp margins appear the same. In addition, there are multiple plates in the columns of the oral interambulacra. However, differences include the position of the periproct (aboral in *Fellaster*), combing (present in *Fellaster*) and trailing podia (lacking in *Fellaster*).

In summary, *Obscurostychia* is a genus separate to those currently described and is placed tentatively with *Arachnoides* in the Subfamily Arachnoidinae based principally on its superficial

appearance of a flat, discoidal test and a periproct that is not oral. This placement acknowledges the fact that the systematic taxonomy at this level is in a state of flux.

The two species, *O. spirographica* and *O. curtus* were present in the same strata but differ in a number of ways. A summary of the diagnostic features of the two species is presented in Table 3.g.1.

In *O. spirographica* the relative length of the anterior petal in relation to the distance to the ambitus is distinctly longer than in *O. curtus* (Fig. 3.g.3. –4.). In addition, the shape of the petals differs with *O. spirographica* having thin petals compared to *O. curtus* with thick ones.

Diagnostic feature	<i>O. spirographica</i> sp. nov.	<i>O. curtus</i> sp. nov.
Test plan outline	Circular to slightly elongate	Slightly elongate to pentagonal
Test length	Small to medium	Very small to small
Test lateral profile, apical surface	Straight	Straight
Oral surface profile	Flat	Flat
Mean height	16% TL	18% TL
Distance apex from anterior (% TL)	44% TL	45% TL
Ambitus	Sharp	Sharp
Interambulacral plates in oral paired interambulacra	8–9	8–10
Post-basicoronal amb. plates in oral paired amb.	10–12	12–13
Post-basicoronal plates in anterior oral ambulacra III	11–12	13–14
Anterior petal to ambitus (mean)	51%	43%
Posterior petal to ambitus (mean)	49%	37%
Number of pore pairs	Ant. 12–25 Post. 14–26	Ant. 11–16 Post. 13–17
Number pore pairs per mm TL (mean)	0.88	1.10
Petals inflated	No	No
Amb. width at ambitus as a % of interamb. width (mean)	128%	129%
Width ambulacrum III at ambitus as percentage TL	32%	29%
Periproct	Terminal, sometimes favouring oral surface	Terminal, sometimes favouring aboral surface

Contact plates with periproct (principal	3a/3b to 4a.4b	3a/4b and 4a/4b
Interambulacral basicoronal plates	Long and thin; obtuse triangular projection	Longer than wide; obtuse triangular projection

Table 3.g.1. Comparison of diagnostic features of the four species of *Obscurostychia*.

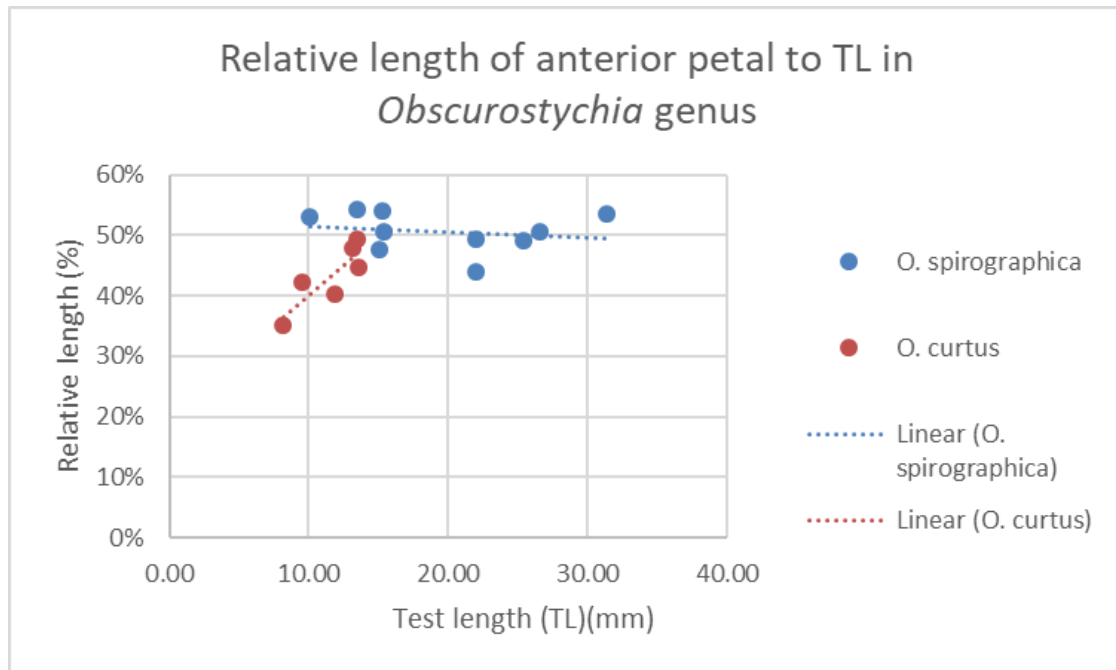


Fig. 3.g.3. Scatter plot of relative length of anterior petal in *Obscurostychia* species.

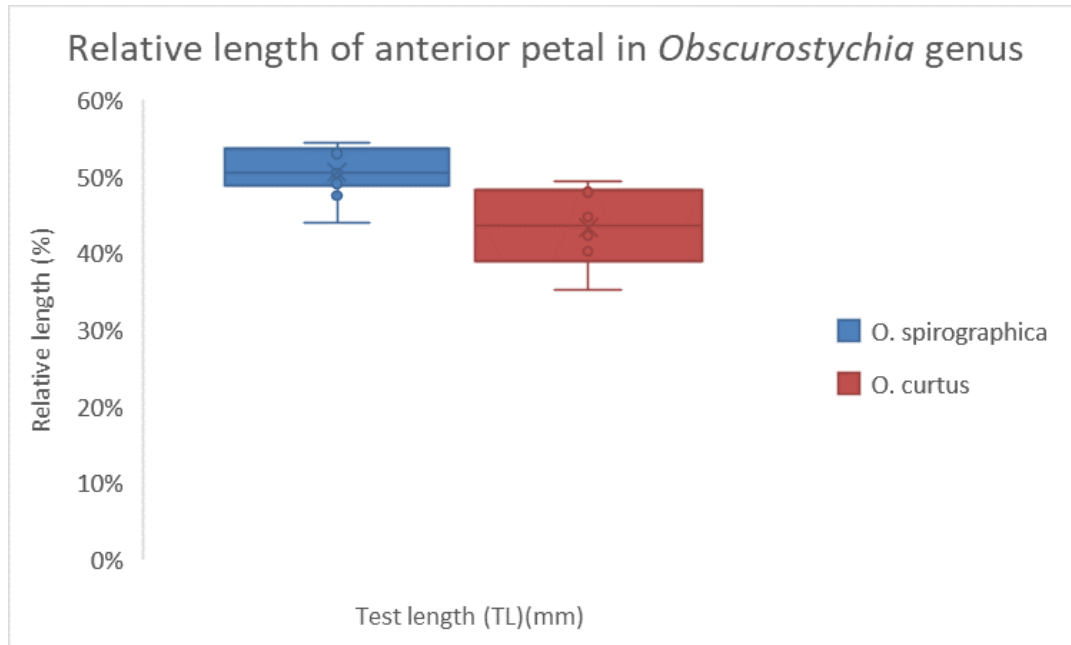


Fig. 3.g.4. Box plot of relative length of anterior petal in *Obscurostychia* species.

The number of plates in each of the paired interambulacra, paired ambulacra and ambulacrum III on the oral surface also differs. (Fig. 3.g.5. –7.). For the paired interambulacra (Fig. 3.g.5.), while the numbers significantly overlap, the median of the counts is eight for *O. spirographica* and nine for *O. curtus*. In addition, the median of the third quartile is nine for *O. spirographica* and ten for *O. curtus*.

The differences are more significant for the paired ambulacra (Fig. 3.g.6.). The mean and the median for the number counts are 11.2 and 11 respectively for *O. spirographica* and 12.5 and 12.5 respectively for *O. curtus*. The first and third quartile medians also differ markedly being ten and 12 respectively for *O. spirographica* and 12 and 13 respectively for *O. curtus*.

In addition, differences are significant in ambulacrum III (Fig. 3.g.7.) although limited by the smaller sample size. The mean and the median for the number counts are 11.9 and 12

respectively for *O. spirographica* and 13.25 and 13 respectively for *O. curtus*. The first and third quartile medians also differ markedly being 11 and 12.5 respectively for *O. spirographica* and 13 and 14 respectively for *O. curtus*.

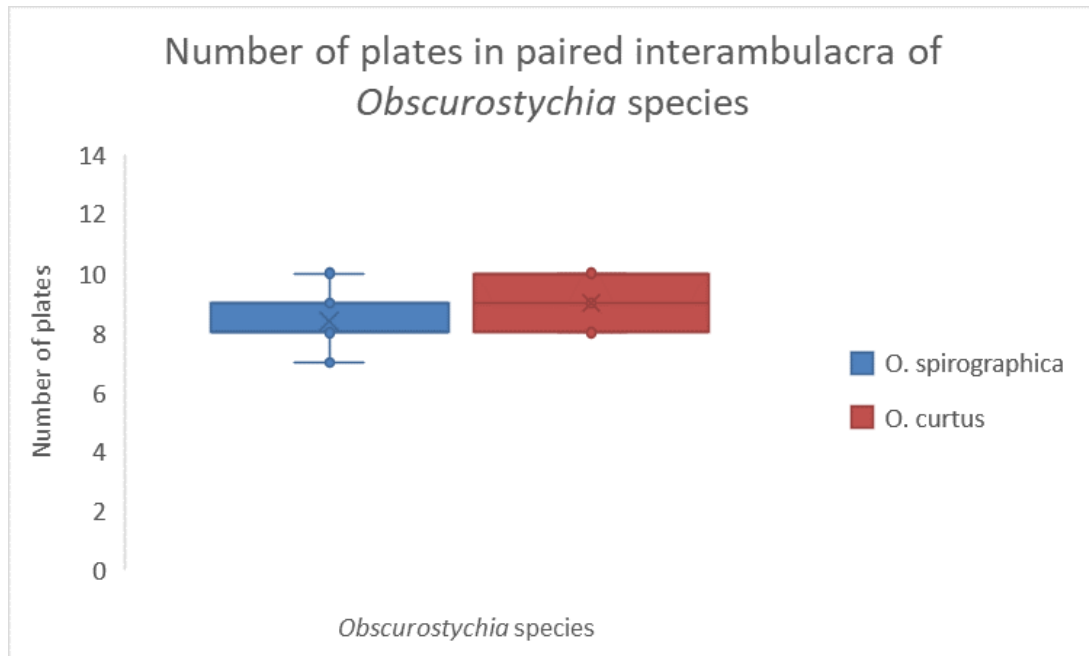


Fig. 3.g.5. Box plot of number of plates in the oral paired interambulacra of *Obscurostychia* species.

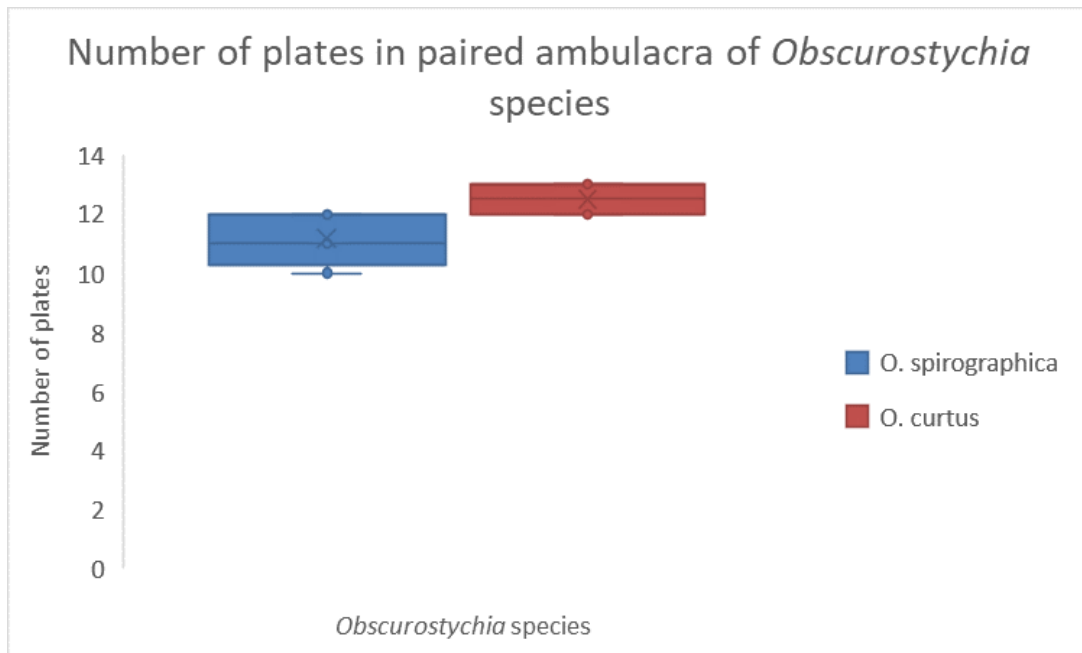


Fig. 3.g.6. Box plot of number of plates in the oral paired ambulacra of *Obscurostychia* species.

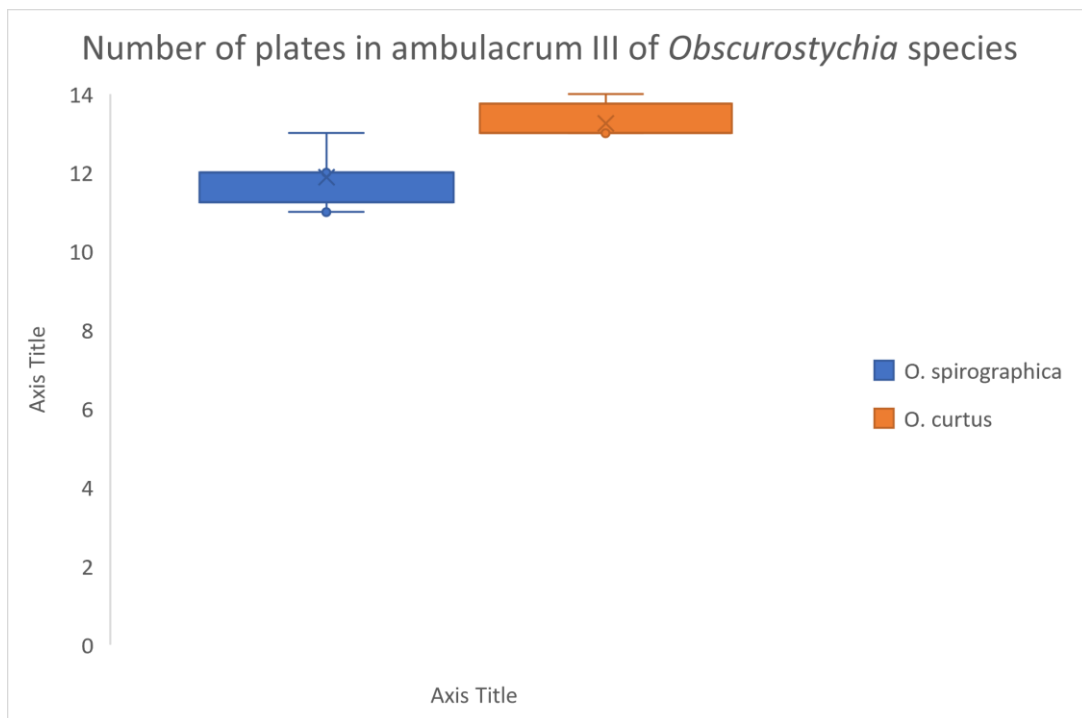


Fig. 3.g.7. Box plot of number of plates in the oral ambulacrum III of *Obscurostychia* species.

A key to species of *Obscurostychia* is presented in Table 3.g.2.

- | | |
|--|----------------------|
| 1a. Length of anterior petal >48% distance to ambitus; petals thin | spirographica |
| 1b. Length of anterior petal <48% distance to ambitus; petals stubby | curtus |

Table 3.g.2. Key to species of Obscurostychia.

Chapter 3.h. Genus *Phalangistychia* gen. nov.

Abstract

The genus *Phalangistychia* gen. nov. is described along with its only known species *P. loveni* (Duncan, 1877). The lack of an intermurum, or intestinal buttressing, precludes it from inclusion in the Subfamily Monostychinae and hence from its previous affiliation with the genus *Monostychia* Laube, 1869. The genus is tentatively placed in the Subfamily Arachnoidinae. It has many similarities to *Arachnoides* Leske, 1778 but differs in having a submarginal periproct and significantly more aboral interambulacral plates.

Systematic palaeontology

Order Clypeasteroida A. Agassiz, 1872

Suborder Clypeasterina A. Agassiz, 1872

Family Arachnoididae Duncan, 1889

Subfamily Ammotrophinae Durham, 1955

***Phalangistychia* gen. nov.**

Type species: Phalangistychia loveni (Duncan, 1877)

Etymology: The genus name, *Phalangistychia*, derives from the Greek ‘phalangium’ for a kind of venomous spider. The choice of the name relates to the external appearance of the test being similar to that of *Arachnoides*. ‘Stychia’ means row (Sadler *et al.* 2016) and while it refers to the food grooves it is used here to provide a link back to *Monostychia* from whence the genus has been divided.

Diagnosis: Large Ammotrophid echinoid, circular except for deep perradial notches, very sharp ambitus, sub-marginal periproct adorally bounded by the first pair of post-basicoronal plates (plates 2a/2b).

Description: as for the type species.

Remarks. This species has a distinctive shape making it easily recognizable, even in literature descriptions. The type is housed at the NHML as E42444. The absence of an intermural precludes it from inclusion in the Subfamily Monostychinae and therefore it cannot be in the genus *Monostychia*. The sharp ambitus, circular shape and strong combing are also not consistent with *Monostychia*. Plating architecture has been examined in only two specimens in which the periproct is framed by plates 2a/2b aborally, which is consistent with the situation in the holotype. The only feature currently available that links it to *Monostychia* is its submarginal periproct. This is at odds with that of *Arachnoides* and yet it has been chosen to place this new genus into the Subfamily Arachnoidinae, although it is acknowledged that this placement is tentative. The placement of the periproct between interambulacral plates 2a/2b is a factor in that decision considering that the periproct may be more variable in relation to the ambitus than previously considered and therefore the placement in relation to plates might be more important. It has deep perradial notches that are much more defined than either *Monostychia* or *Arachnoides*. There is a minor anal notch. The paired oral interambulacra have seven to eight plates, paired oral ambulacra have eight plates and ambulacrum III has nine plates.

***Phalangistychia loveni* (Duncan, 1877) (Fig. 3.h.1. –2.)**

1877 *Arachnoides Loveni*, sp. nov., Duncan, p. 47, pl. 3, figs 6, 7.

1879 *Monostychia australis* Var. *loveni* (Dunc.); McCoy, p. 42, pl. 60, fig. 6, 6a–b.

1883 *M. Loveni*; Pomel, p. 70.

1887 *Clypeaster* (*Monostychia*) *loveni*, Laube; Duncan, p. 420.

1948 *Monostychia australis* var. *Lovéni* Duncan; Mortensen, pp. 154–155, figs. 91b–c, 92a.

Type material: Holotype NHM E42444.

Additional material: MV P17599, P17604, P27365, P142063, P302897–900, P317123–4, SAM P33751.

Type locality: Beaumaris on Port Phillip Bay, Victoria.

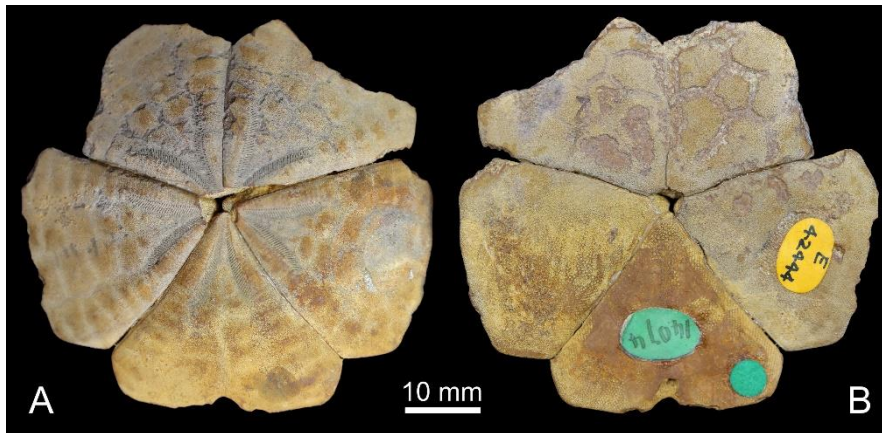


Fig. 3.h.1. Holotype of *Phalangistychia loveni* (Duncan, 1877). (NHML P4244).

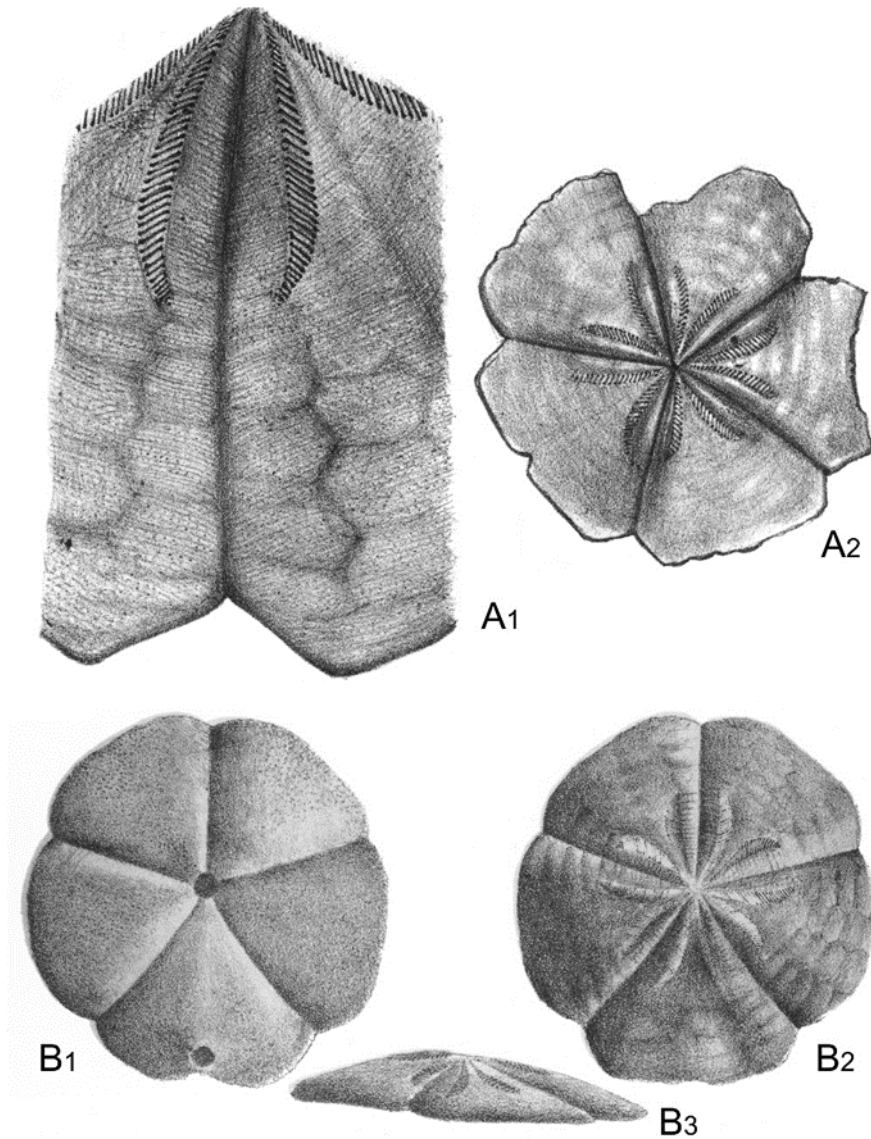


Fig. 3.h.2. Historical illustrations of Phalangistychia loveni: A1–A2 petal (A1) and aboral view (A2) from Duncan (1877), pl. 3, figs 6, 7); B1–B3 oral (B1), aboral (B2) and lateral (B3) views from McCoy (1879, pl. 60, figs 6, 6a–b). Reproduced at original printing size.

Type stratum: Black Rock Formation (late Miocene) (Holdgate & Gallagher 2003).

Etymology: Duncan, 1877 did not explain the etymology of the species in the original description. It is assumed that ‘loveni’ derives from the Swedish marine zoologist Sven Ludvig Loven (1809-1895) who in 1874 established the Lovenian numbering system for echinoids in

which ambulacral and interambulacral areas of the test are designated Roman and Arabic numerals respectively.

Diagnosis: As for the genus.

Description: Test circular, medium to very large ranging in length from 35.6–63.6 mm.; maximum width 93–104% TL (mean = 99%, SD = 3%, n = 11), occurring slightly anterior of centre, but in the range 44–60% TL from anterior ambitus (mean = 49%, SD = 5%, n = 11). Height 11–15% TL (mean = 13%, SD = 1%, n = 8); apex slightly forward of the apical disc 49–53% TL from anterior ambitus (mean = 51%, SD = 2%, n = 6); apical disc 47–53% TL from anterior ambitus (mean = 52%, SD = 2%, n = 6).

Orally, test very flat. Food grooves strongly indented on the aboral surface of the test but less so on the oral surface. No keel from the periproct forward toward to the peristome. The aboral surface of the test rises in a slight concave from ambitus to apical disc; ambitus very sharp. Ambital notches distinct. Anal notch present. Combing distinct.

Paired oral post-basicoronal interambulacra plate counts were obtained in all four of the regions of the only specimen for which plates could be seen. 75% of the regions preserved had seven plates and 25% had eight. For the paired ambulacra, post-basicoronal plate and counts were obtained in all four regions of only one specimen; 100% of regions preserved had eight plates. In the one specimen where post-basicoronal ambulacrum III plates were sighted there was nine plates.

Petals inflated. The mean length of petals, measured as a percentage of the distance from the apical disc to the ambitus in the line of each pore zone, is for the anterior pair 48% (SD = 3%, n = 4) and the posterior pair 44% (SD = 4%, n = 3). Poriferous zones are thin, almost straight to

slightly curved for most of their distance but curve more distinctly inward toward their tip producing a lyrate shape.

Distally, petal ends are pointed, trailing podia are not developed. Inner are round and outer pores elongate being significantly more than twice the size of the inner pore. The anterior poriferous zone in ambulacrum II has 25–44 pore pairs; slightly more in ambulacrum I (30–43). The number of pore pairs in the anterior zone per mm of TL is 2.77 (SD = 0.5, n = 3). Mean width of ambulacrum III at ambitus 169% mean width of interambulacrum 1 (SD = 18%, n = 2). Mean width of ambulacrum III 41% TL (SD = 6%, n = 2).

Peristome small and circular. Aborally, the three anterior grooves are straight, and the two posterior grooves arced slightly laterally. Basicoronal plates significantly longer than wide, radial margins strongly curved outward and sometimes angular; interambulacral basicoronal plates similar in size, end with a triangular projection and are about 10% longer than their ambulacral counterparts.

Periproct submarginal, small, round and about 20% periproct diameter removed from the ambitus. In interambulacrum 5, periproct comes into contact with plates 2a/2b in the two specimens in which the plates were counted.

The internal buttressing has been observed by cross section. A complex system of peripheral pillars and buttresses is developed around the test and extending more than 30% the test diameter from the margin. An intermulum is not present.

The diagnostic features are summarised in Table 3.h.1.

Stratigraphy and age. *P. loveni* appears to be restricted to the upper Miocene Black Rock Formation at Beaumaris on Port Phillip Bay, Victoria (Holdgate & Gallagher 2003).

Diagnostic feature	<i>P. loveni</i> (Duncan, 1877)
Test plan outline	Circular
Test length	Medium to very large
Test lateral profile, apical surface	Slightly convex
Oral surface profile	Very flat
Mean height	13% TL
Distance of apex from anterior (% TL)	49% TL
Ambitus	Very sharp
Interambulacral plates in oral paired interambulacra	7
Post-basicoronal amb. plates in oral paired amb.	8
Post-basicoronal plates in anterior oral ambulacra III	9
Anterior petal to ambitus (mean)	48%
Posterior petal to ambitus (mean)	44%
Number of pore pairs	Ant. 25–44 Post. 30–43
Number pore pairs per mm TL (mean)	2.77
Petals inflated	Slightly
Amb. width at ambitus as a % of interamb. width (mean)	169%
Width ambulacrum III at ambitus as percentage TL	41%
Submarginal periproct	Circular, 20% from margin
Contact plates with periproct (principal)	2a/2b
Interambulacral basicoronal plates	Longer than wide; triangular projection

Table 3.h.1. Diagnostic features of Phalangistychia.

Chapter 3.i. Key to genera

Keys of provided for the four genera of Monostychinae (Table 3.i.1.) and for the two genera of Ammotrophinae described in this thesis (Table 3.i.2).

1a. Test length greater than width	2
1b. Test length equal to width	3
2a. Reuleaux pentagonal test plan; keel or drooping tail between peristome and periproct; combing weak; strongly arced petals that become parallel towards tips	<i>Monostychia</i>
2b. Angular pentagonal test plan; no keel or drooping tail between peristome and periproct; weakly arced to straight petals that continue to diverge toward tips; combing strong	<i>Quinquestychia</i>
3a. Test circular or nearly so; combing present.....	<i>Rotundastychia</i> m,
3b. Delta shape with wings on rear edge; combing lacking	<i>Deltoidstychia</i>

Table 3.i.1. Key to the genera of Monostychinae

1a. Periproct terminal and bounded by plates 3a/3b or 4a/4b; perradial notches lacking	<i>Obscurostychia</i>
1b. Periproct submarginal and bounded by plates 2a/2b; Perradial notches deep.....	<i>Phalangistychia</i>

Table 3.i.2 Key to the genera of Ammotrophinae described in this thesis.

Chapter 4. Oral plate architecture and its implications for systematics

4.1. Abstract

Counting the number of plates on the oral surface of monostychioids (and possibly other related clypeasteroids) has the potential of providing useful characters for taxonomy at both species and genus level. Data on the numbers of plates on the oral surface of 15 species across four genera of Monostychinae were examined. It was established that the number of plates appears independent of TL and therefore remains essentially static through the life of the test.

The potential useful plates include the paired interambulacra, the paired ambulacra, ambulacrum III and the plates first in contact with the periproct in interambulacrum 5. At both the species and genus level the first three of these options provide taxonomic utility. However, due to the variation of plate numbers they cannot be relied upon as the only taxonomic character although combined their utility increases. Ambulacrum III is of least value.

The plates first in contact with the periproct appear of no utility at either species or genus level. While it has been established that the plate numbers first in contact does not decrease with increasing TL and therefore the periproct does not appear to be mobile during ontogeny, the plate number 3a/3b appears so dominant that other options (of which there appear many) are best treated as outliers.

In echinoids the pairs of plates in a series alternate. When measuring plates on the oral surface in broken specimens of monostychioids, whether a plate series starts on the left ('a') side or right ('b') side is not a particularly useful tool in determining which test segment is being measured and therefore the results of such plate counts should be treated with caution taxonomically.

4.2. Introduction

Vertebrate taxonomists long ago developed a system of skeletal homologues to act as first-order morphologies to aid their work. The presence of a backbone, skull features, pelvic and limb features in vertebrates rise in importance above other lesser features in developing a taxonomical hierarchy. In echinoderm taxonomy, attempts have been made to develop such homologues, for example, the Extra axial/axial Theory (Mooi & David 1996).

However, plate architecture is possibly similar to the vertebrate skeleton as a morphometric variable. It is a fundamental aspect of the echinoid body plan and as such, powerfully prefigured by phylogeny. Fortunately, work has been done on modern echinoderms relating genetic make-up and resulting architectural organisation thus providing valuable insights as to whether plate architecture is a morphology of use in classification. For example, the AV and DV genes control the development of the oral-aboral axis (Hinman & Jarvela 2014), the *veg2* gene has function in determining left-right symmetry (Luo & Su 2012) and the *tbrain* gene is involved in expression of skeletogenic structural genes (Hinman *et al.* 2003). This work is principally at embryonic level, however the principle is likely applicable during further ontogenetic development although a study of schizasterids noted that some morphological features such as fascioles change markedly during ontogenesis and that the overall shape was not enough to accurately determine a species (Madon-Senez 1999). However, on the oral side of the test the first three plates of interambulacrum 5 show a consistent difference between species within a genus although not between genera. Mooi & David (1996) suggested the holasteroids show a similar predisposition. Such features occur along the axis of bilateral symmetry.

There is no doubt that an understanding of past echinoderms and their phylogeny can be derived from living species. Indeed, if we wish to understand the form and function of extinct

groups such as *Monostychia* and its relatives, it is important to base that understanding on phylogenetic relationships of known extant groups. In echinoids any change in external morphological features comes about as a result of changes in a reorganisation of the plate architecture of the test and that in turn must be due to modifications of the genetic pattern within the organism as it evolves – the development of apomorphic characters. The implication of this of course is that a stable form or test over time is the result of stability in the genes.

The fact that such structural genes occur across a wide range of echinoderms and that they result in predetermined morphologies means that we can infer the presence of these genes in *Monostychia* and its relatives despite our inability to directly test their genetic make-up. Further, we can say with reasonable confidence that the resulting plate architecture is likely to be of greater importance in the development of shape and form than other characters commonly used in taxonomy such as the shape of the eating apparatus or the shape and variety of spination, both of which are difficult to determine from fossils.

In studying shape and form, the development of anterior-posterior asymmetry of clypeasteroid tests has been matched in some species by a similar asymmetry in the development of the eating apparatus (Lawrence & Pomory 1999). Asymmetry in bilaterally symmetrical echinoids is common. For example, the gut path is asymmetrical. The overall bilateral symmetry is likely a result of basically unidirectional movement.

The monostychioid group has a variety of distinct morphologies, some of which have been interpreted as species and others that may be so interpreted, although other researchers to date have interpreted some of those morphologies as intraspecific variation (Woods 1876, Duncan 1877, Tate 1877, Bittner 1892). When it comes to fossil species where a reproductive community or species is impossible to confirm by reproductive means, it is often a problem to differentiate

between intraspecific variation resulting from ontological change or ecophenotypic plasticity and intraspecific variation that will enable the definition of a new species.

Generally, the echinoid test increases in size during growth by the addition of new plates adjacent to the ocular plate in the apical disc. The process is known as the ‘ocular plate rule’ (Mooi *et al.* 1994). This takes place in a pre-determined sequence in each of the twenty columns, ambulacral and interambulacral, that make up the test. In addition, plates increase in size by growth around their margins and it has been shown that the adoral plates of clypeasteroids can undergo increased allometric growth and result in peramorphosis, an expression of heterochrony (McNamara 1988). During ontogeny in *Dendraster* the ambulacral plates show positive allometry compared with adjacent interambulacral plates and translocate equatorially between the first and second interambulacral plates in each column. The Arachnoididae and Clypeasteridae also display equatorial ambulacral/interambulacral plate translocation. In this regards all these families are peramorphic (McNamara 1988). The increase in adoral surface area of the ambulacra in many clypeasteroids has also been accompanied by the evolution of extensive food grooves (McNamara 1988).

The ocular plate rule states that during ontogeny there is an increasing number of plates in a column which may lead to an assumption that the number of plates below the ‘equator’ continues to increase (Mooi *et al.* 1994). In regular echinoids and irregular echinoids which have a rounded ambitus, this is likely to be true. However, in echinoids with a particularly sharp ambitus, such as *Monostychia* and *Arachnoides*, it remains uncertain how the test grows and the implication it has on the number of plates on the oral surface. One possibility is that the plates migrate around the ambitus, possibly due to growth on one margin and decay on another (McNamara 1989). However, another possibility is that the plates on the oral surface remain constant in number, or

nearly so. If this is the case, such plate architecture may provide a useful diagnostic character at species and genus level. The number of plates on the oral surface of such genera has not been determined in any extensive analysis (Mooi, pers. comm. October 2012), and until that is done the current keys relying on such features remain questionable.

The periproct lies in the line of bilateral symmetry in irregular echinoids. The position of the periproct along that line is a frequently used diagnostic feature to define genera (Mooi 1989). For example, *Arachnoides* has the periproct on the aboral surface, *Monostychia* has the periproct orally, but submarginal, and *Ammotrophus* has the periproct orally but well removed from the ambitus (Kroh & Smith 2010). But the periproct position may be more flexible than currently acknowledged. In a study of holasteroids (Mooi & David 1996) the focus moved from the periproct position *per se* to the number of plates between the peristome and periproct. To date few studies have looked at a significant number of specimens in relation to this architectural feature (Mooi, pers. comm. October 2012). It appears that in many clypeasteroids the position of the periproct moves to lower plate numbers as the animal grows and TL increases.

From the preliminary literature review, it is seen that there is no robust set of primary characters for use in fossil echinoderm systematics. This study aims to critically assess a range of candidate characters for application to range of species and genera. This will allow development of cladistic hypotheses relating to the place within phylogeny for the monostychioid group. To achieve this aim, several hypotheses will be tested.

First, it needs to be established whether the number of plates on the oral surface of species and genera within the monostychioid group change with increasing TL or remain fixed. This will be done by examining the number of plates in the paired oral interambulacra, the paired ambulacra and the unpaired ambulacrum III. In addition, the Lovenian number of the plates to

first touch the periproct in interambulacrum V will be compared to TL to determine if there is ontogenetic movement of the periproct relative to the plates.

Second, and assuming the first question determines that the number of plates is not related to TL, the interambulacral and ambulacral plate numbers on the oral surface of various species and genera of Monostychinae will be compared to determine if they offer a robust method of separating the species and genera.

Third, the various species and genera of Monostychinae will be compared in relation to the Lovenian number of the plates to first touch the periproct in interambulacrum V. to determine if they offer a robust method of separating the species and genera.

Finally, an analysis of the left- and right-handedness of the plates in a series of both interambulacral and interambulacral regions will be made to determine if they offer an acceptable a method of distinguishing species and genera. In addition, the left-handedness and right-handedness of the plates can be useful in determining which test segment of a broken specimen is in-hand that might enable plate counts for taxonomic purposes.

4.3. Results

Hypothesis 1: Within the subfamily Monostychinae the number of post-basicoronal interambulacral plates in the paired interambulacra on the oral surface of increase as TL increases.

H₀: In each of a range of species within the genera *Monostychia*, *Quinquestychia*, *Rotundastychia*, and *Deltoidstychia* the number of post-basicoronal interambulacral plates on the oral surface in each of the four paired segments increases with TL.

H₁: In each of a range of species within the genera *Monostychia*, *Quinquestychia*, *Rotundastychia*, and *Deltoidstychia* the number of post-basicoronal interambulacral plates on the oral surface in each of the four paired segments does not increase with TL.

The results of the seven species of *Monostychia* show variability in the relationship between plates and TL (Fig. 4.1., Appendix Figs 4.1–7.). For all data across the species of the genus the number decreases with TL ($y = -0.0044x + 6.885$). The individual species show greater variability with *M. australis*, *M. robheathi* and *M. etheridgei* having an increasing plate number with TL while *M. merrimanensis*, *M. macnamarai* and *M. etheridgei* having a decreasing number. For *M. glenelgensis* the number does not change with TL.

The results for the four species of *Quinquestychia* also show variability (Fig. 4.2., Appendix Figs 4.8–11.). For all data across the species of the genus the number decreases with TL ($y = -0.0107x + 8.3556$). For the individual species *Q. mannumensis*, *Q. gigas* and *Q. robertirwini* the number of plates increases with TL but for *Q. berylmorrisae* the number decreases. It is notable that for *Q. mannumensis* the sample size is only five measurements.

The results for the three species of *Rotundastychia* again show variability (Fig. 4.3., Appendix Figs 4.12–14). For all data across the species of the genus the number increases with TL ($y = 0.0035x + 6.6729$). For the individual species *R. pledgei* and *R. aquilaensis* the number increases with TL while for *R. eyriei* the number decreases.

The result for the single species of *Deltoidstychia* (Fig. 4.4) shows that for *D. erioaster* the number decreases with TL ($y = -0.0138x + 9.1322$).

Across the 15 species and four genera, eight species show an increase with TL, six a decrease and one remains unchanged while two genera show an increase and two genera a decrease. Data for the subfamily Monostychinae show a slight decrease in number with TL ($y = -0.0027x + 7.1712$). The null hypothesis is rejected.

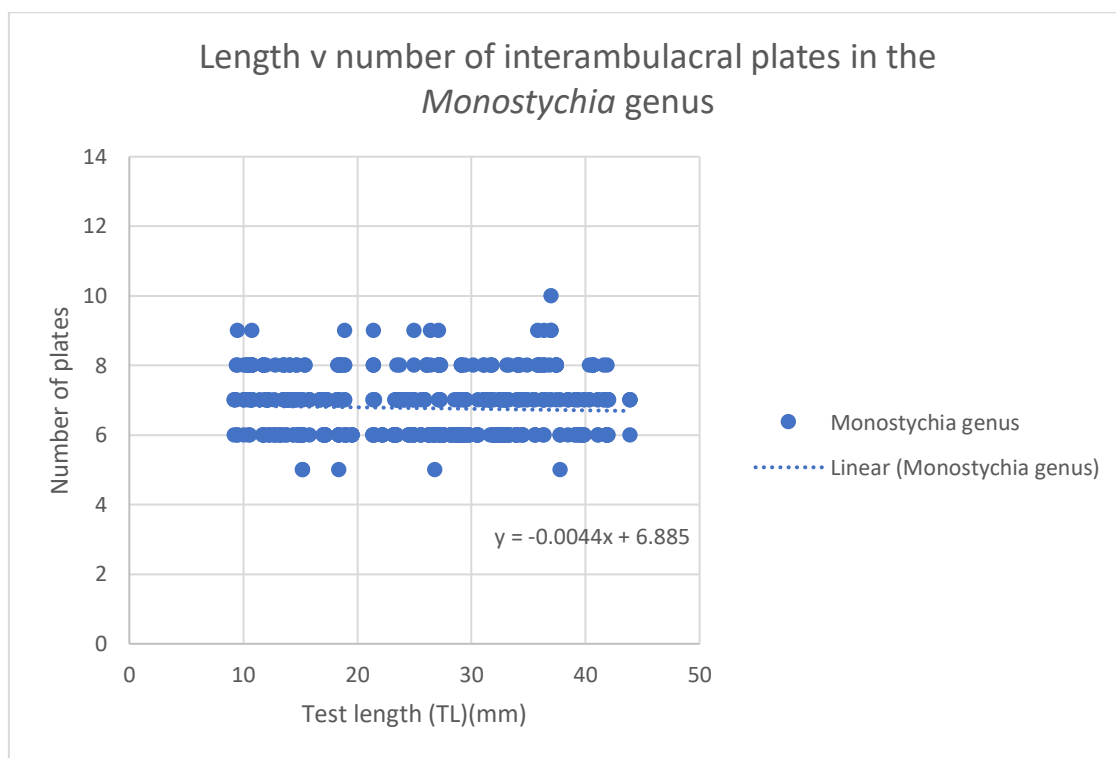


Fig. 4.1. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of all species of Monostychia.

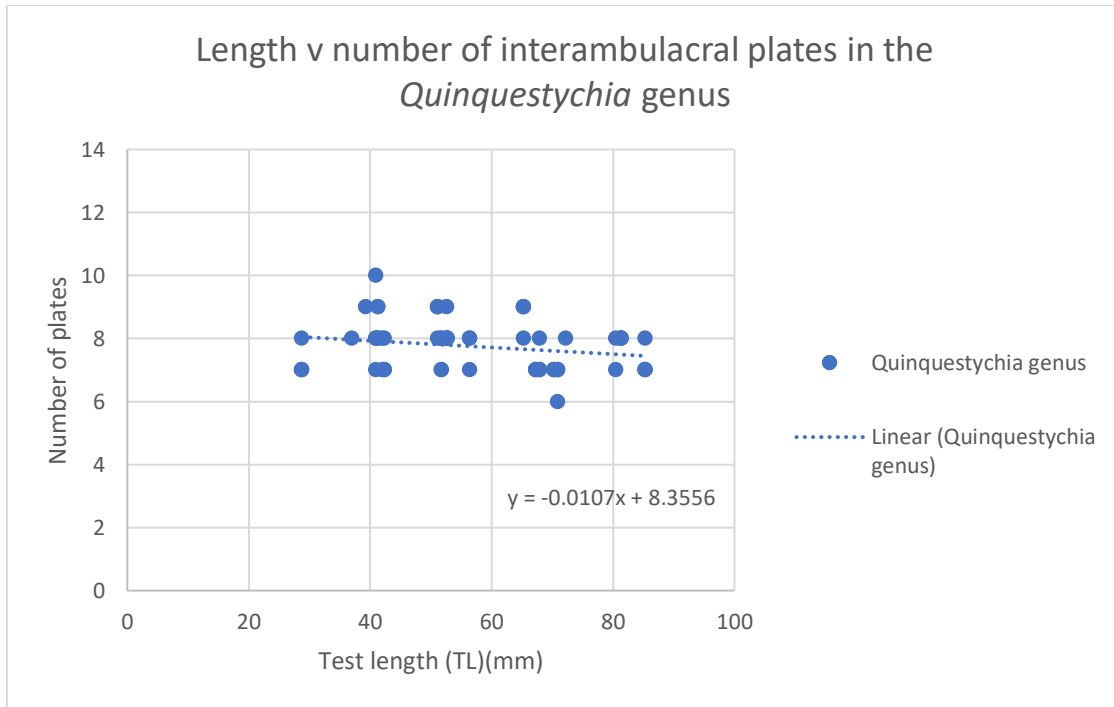


Fig. 4.2. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of all species of *Quinquestychia*.

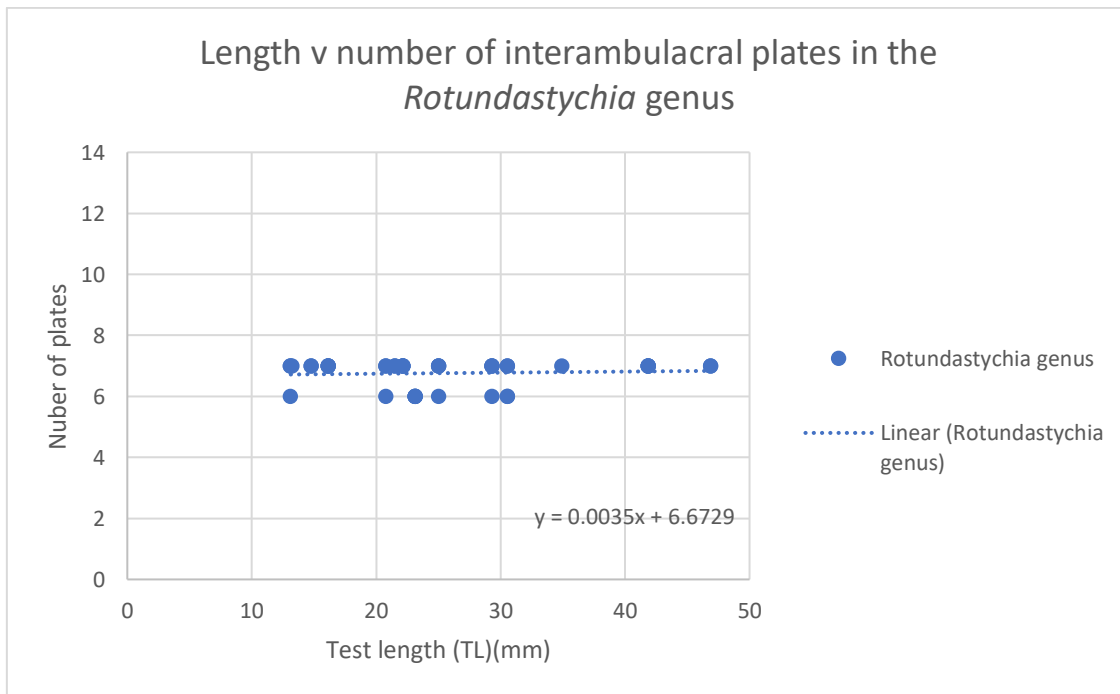


Fig. 4.3. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of all species of *Rotundastychia*.

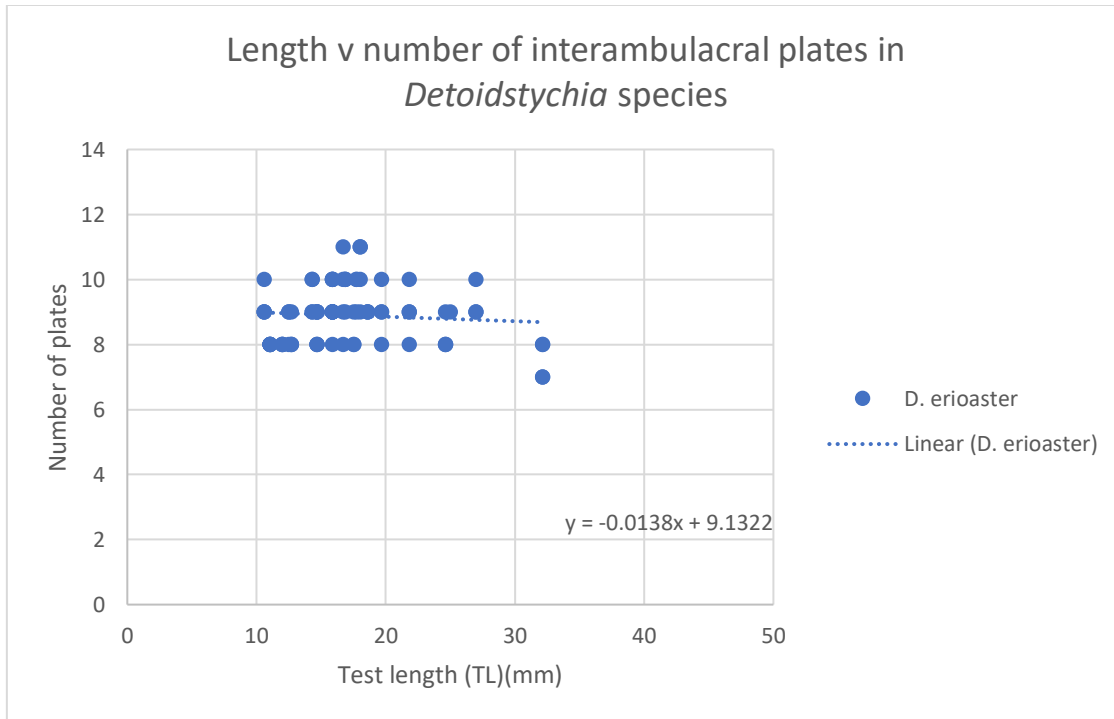


Fig. 4.4. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of *Deltoidstychia erioaster*.

Hypothesis 2: Within the subfamily Monostychinae the number of post-basicoronal ambulacral plates in the paired ambulacra on the oral surface increase as TL increases.

H₀: In each of a range of species within the genera Monostychia, Quinquestychia, Rotundastychia, and Deltoidstychia the number of post-basicoronal ambulacral plates on the oral surface in each of the four paired segments increases with TL.

H₁: In each of a range of species within the genera Monostychia, Quinquestychia, Rotundastychia, and Deltoidstychia the number of post-basicoronal ambulacral plates on the oral surface in each of the four paired segments does not increase with TL.

The results of the seven species of *Monostychia* show variability in the relationship between plates and TL (Fig. 4.5., Appendix Figs 4.15–21.). For all data across the species of the genus the

number decreases with TL ($y = -0.0392x + 10.301$). For the individual species, *M. australis*, *M. merrimanensis*, *M. etheridgei* have increasing numbers with TL but for *M. macnamarai*, *M. alanixi*, *M. glenelgensis* and *M. robheathi* the number decreases.

The results for the four species of *Quinquestychia* also show variability (Fig. 4.6., Appendix Figs 4.22–25.). The data across the species in the genus shows the number of plates increasing with TL ($y = 0.0019x + 10.753$). For *Q. berylmorrisae* the number of plates increases with TL but for *Q. gigas* and *Q. robertirwini* the number decreases. For *Q. mannumensis* the number is not changed. It is notable that for *Q. mannumensis* the sample size is only three measurements.

The results for the three species of *Rotundastychia* again show variability (Fig. 4.7., Appendix Figs 4.26–28.). The data across the species in the genus shows the number of plates increasing with TL ($y = 0.0367x + 8.506$). For *R. pledgei* and *R. aquilaensis* the number increases with TL while for *R. eyriei* the number decreases.

The result for the single species of *Deltoidstychia* (Fig. 4.8) shows that for *D. erioaster* the number increases with TL ($y = 0.0195x + 10.384$).

Across the 15 species and four genera, seven species show an increase with TL, seven a decrease and one remains unchanged while three genera show an increase and one genus a decrease. Data for the subfamily Monostychinae show a slight decrease in number with TL ($y = -0.0034x + 9.5212$). The null hypothesis is rejected.

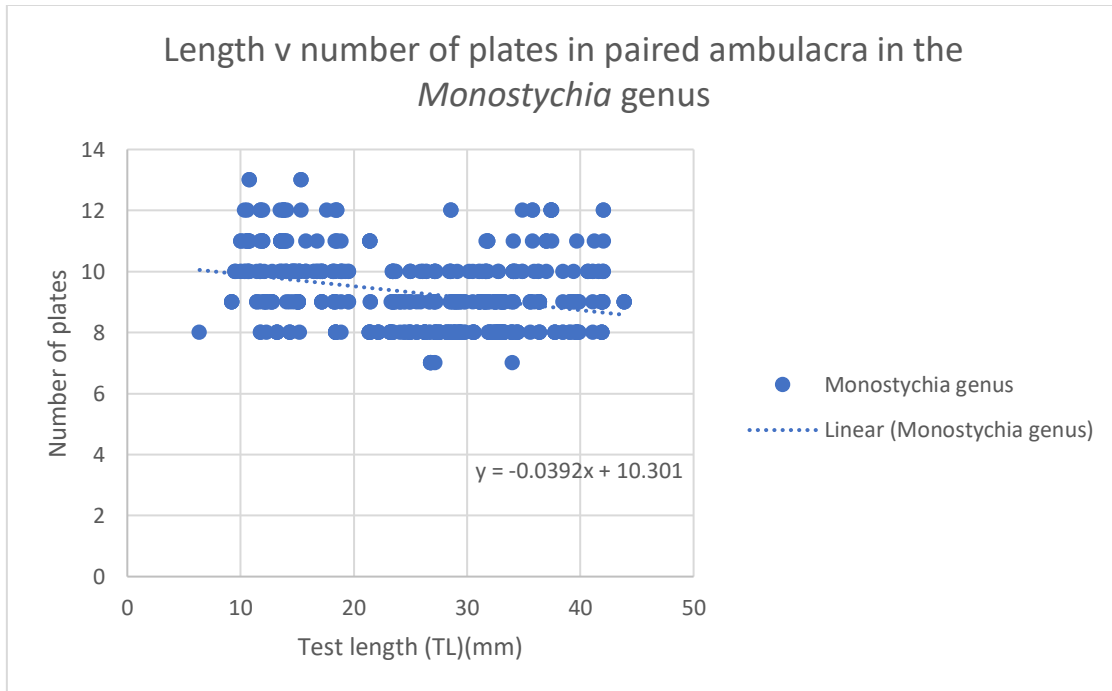


Fig. 4.5. Scatter plot of number of post-basical coronal ambulacral plates in each of the paired oral interambulacrum against TL for all species of *Monostychia*.

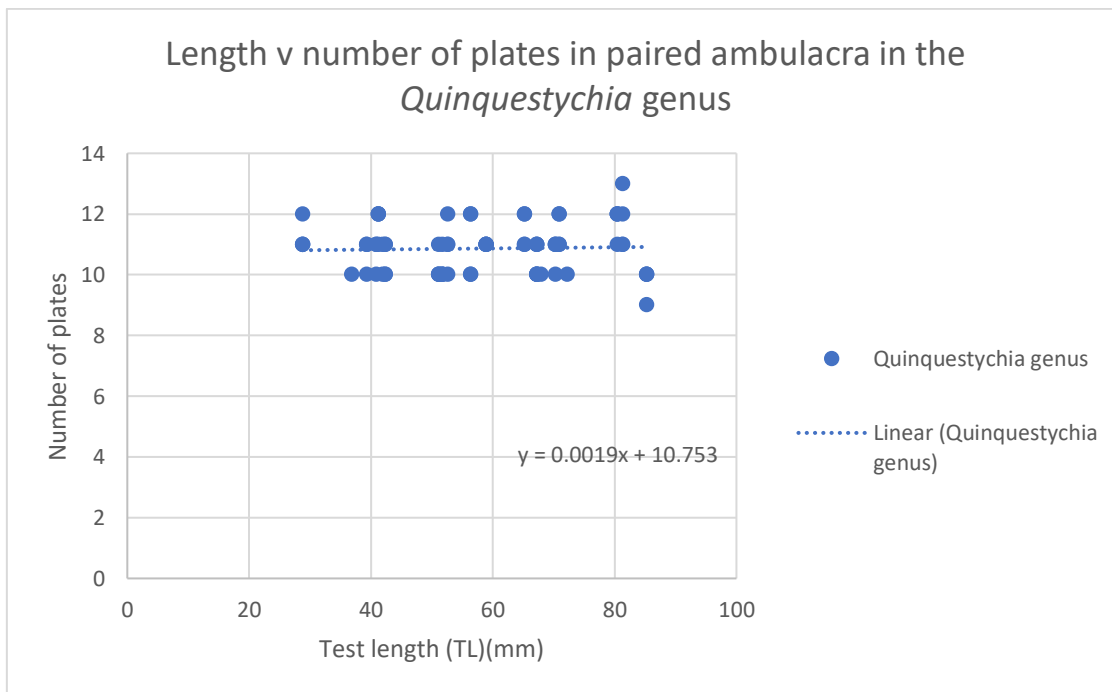


Fig. 4.6. Scatter plot of number of post-basical coronal ambulacral plates in each of the paired oral interambulacrum against TL for all species of *Quinquestychia*.

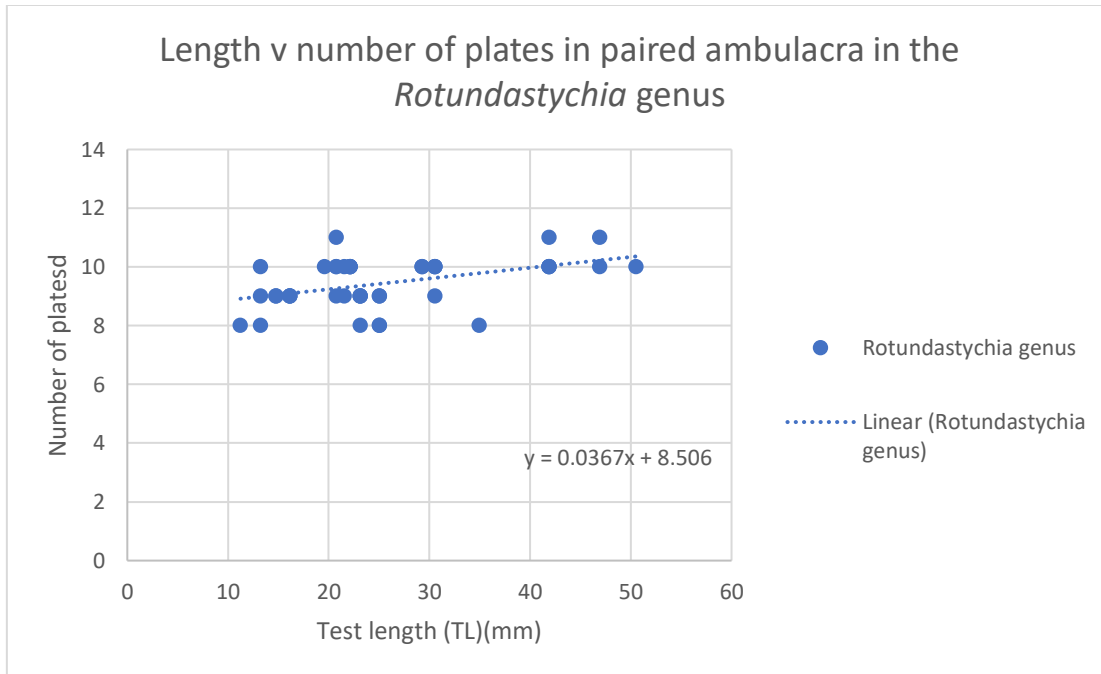


Fig. 4.7. Scatter plot of number of post-basicoronal ambulacral plates in each of the paired oral interambulacrum against TL for all species of *Rotundastychia*.

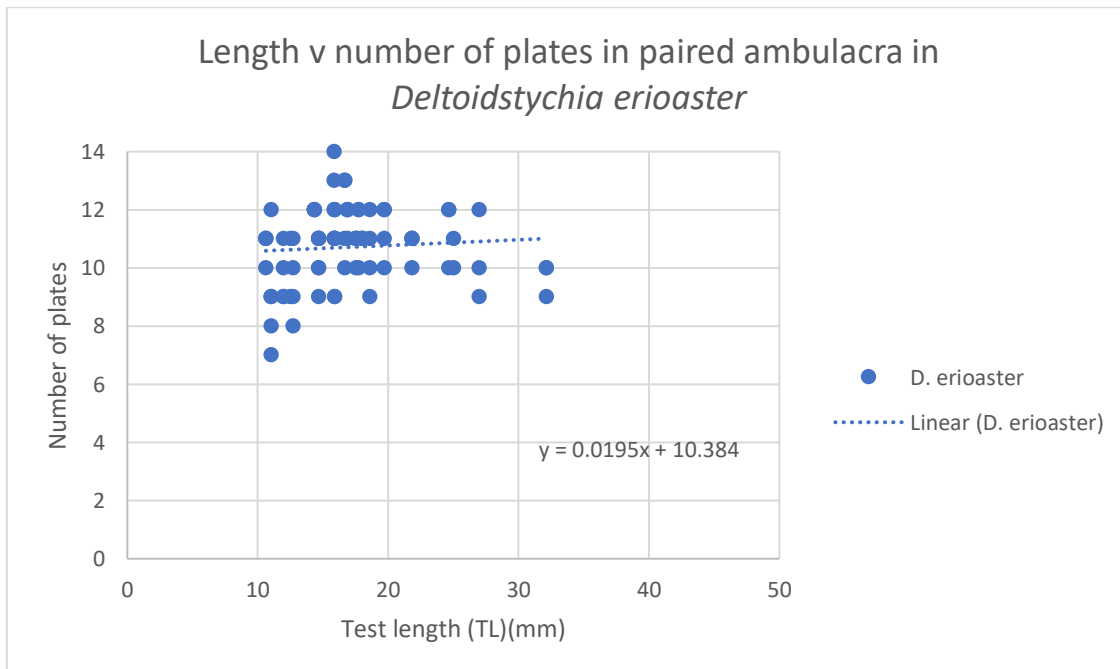


Fig. 4.8. Scatter plot of number of post-basicoronal ambulacral plates in each of the paired oral interambulacrum against TL for *Deltoidstychia erioaster*.

Hypothesis 3: Within the subfamily Monostychinae the number of post-basicoronal ambulacral plates in ambulacrum III on the oral surface increase as TL increases.

H₀: In each of a range of species within the genera Monostychia, Quinquestychia, Rotundastychia, and Deltoidstychia the number of post-basicoronal ambulacral plates on the oral surface in ambulacrum III increases with TL.

H₁: In each of a range of species within the genera Monostychia, Quinquestychia, Rotundastychia, and Deltoidstychia the number of post-basicoronal ambulacral plates on the oral surface in ambulacrum III does not increase with TL.

The results of the seven species of *Monostychia* show variability in the relationship between plates and TL (Fig. 4.9., Appendix Figs 4.29–35.). For all data across the species of the genus the number decreases with TL ($y = -0.0524x + 11.597$). For the individual species, *M. australis*, *M. macnamarai*, *M. alanrixi*, *M. merrimanensis*, *M. glenelgensis* and *M. etheridgei* the number increases with TL and for *M. robheathi* the number decreases. It is notable that for *M. etheridgei* the sample size is only four counts.

The results for the four species of *Quinquestychia* also show variability (Fig. 4.10., Appendix Figs 4.36–39.). For all data across the species of the genus the number decreases with TL ($y = -0.0036x + 11.585$). For the individual species, *Q. mannumensis* and *Q. berylmorrisae* the number of plates increases with TL but for *Q. gigas* and *Q. robertirwini* the number decreases. It is notable that for *Q. mannumensis* the sample size is only four measurements.

The results for the three species of *Rotundastychia* again show variability (Fig. 4.11., Appendix Figs 4.40–42). For all data across the species of the genus the number decreases with

TL ($y = -0.04x + 9.1552$). For *R. pledgei* and *R. eyriei* the number increases with TL, while for *R. aquilaensis* the number remains unchanged. It is notable that for *R. pledgei* the sample size is only three measurements and for *R. aquilaensis* only two measurements.

The result for the single species of *Deltoidstychia* (Fig. 12.) shows that for *D. erioaster* the number increases with TL ($y = -0.0053x + 10.72$).

Across the 15 species and four genera 11 show an increase with TL, three a decrease and one remains unchanged. Data for the subfamily Monostychinae show a slight decrease in number with TL ($y = -0.0004x + 10.442$). The null hypothesis is rejected.

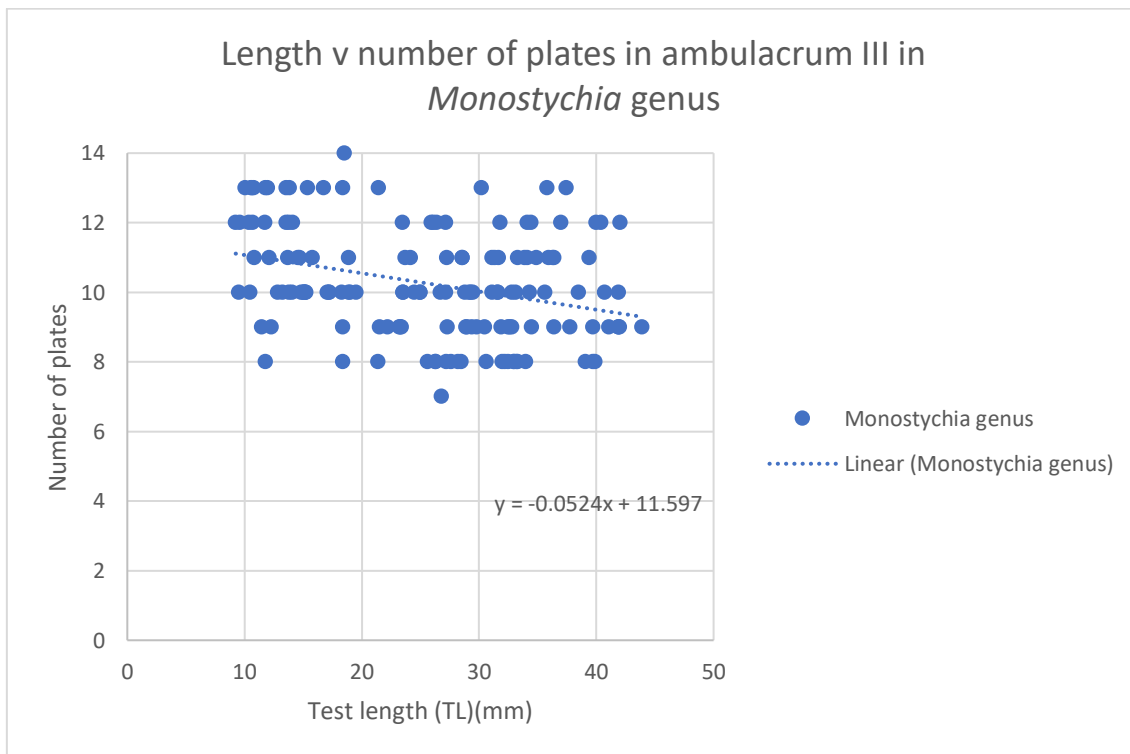


Fig. 4.9. Scatter plot of number of post-basicoronal ambulacral plates in ambulacrum III against TL for all species of Monostychia.

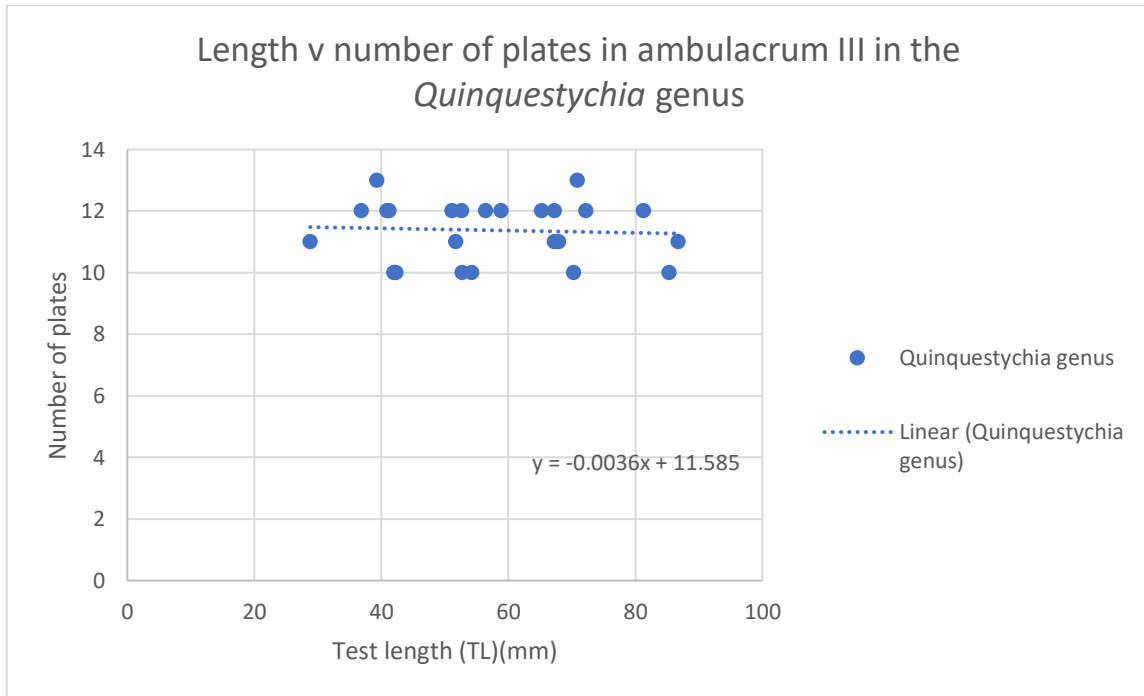


Fig. 4.10. Scatter plot of number of post-basicoronal ambulacral plates in ambulacrum III against TL for all species of *Quinquestychia*.

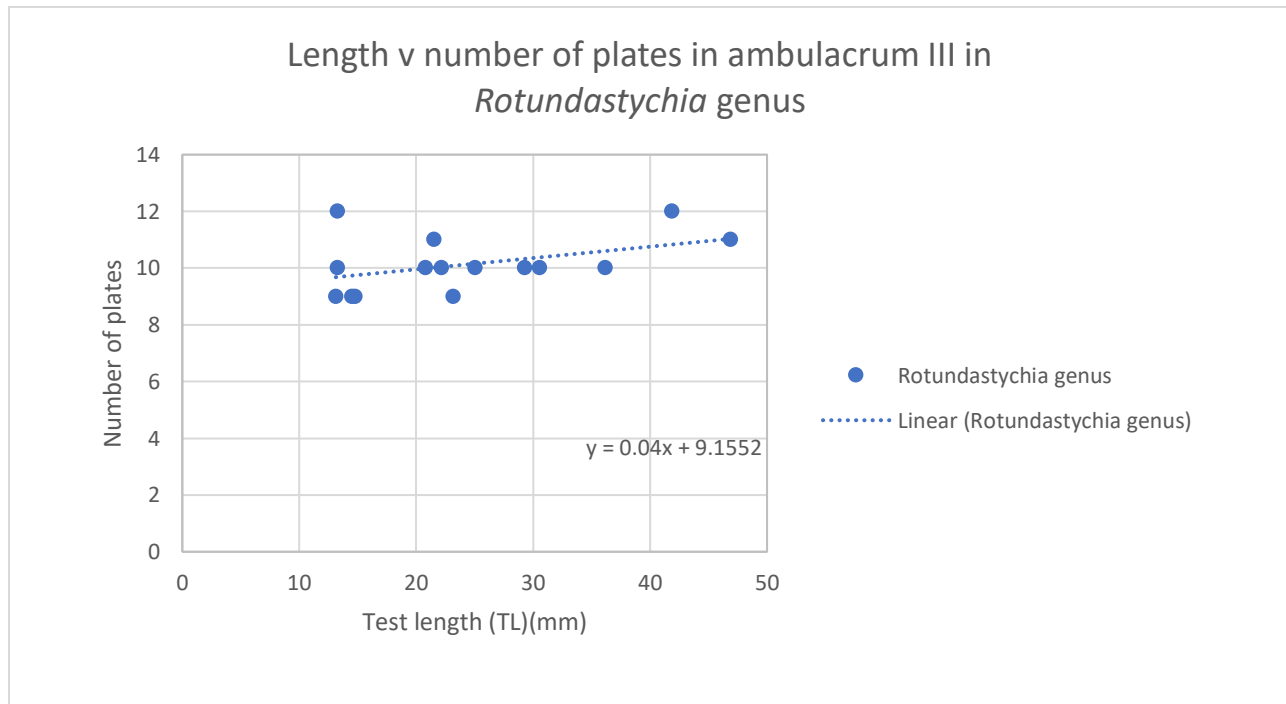


Fig. 4.11. Scatter plot of number of post-basicoronal ambulacral plates in ambulacrum III against TL for all species of *Rotundastychia*.

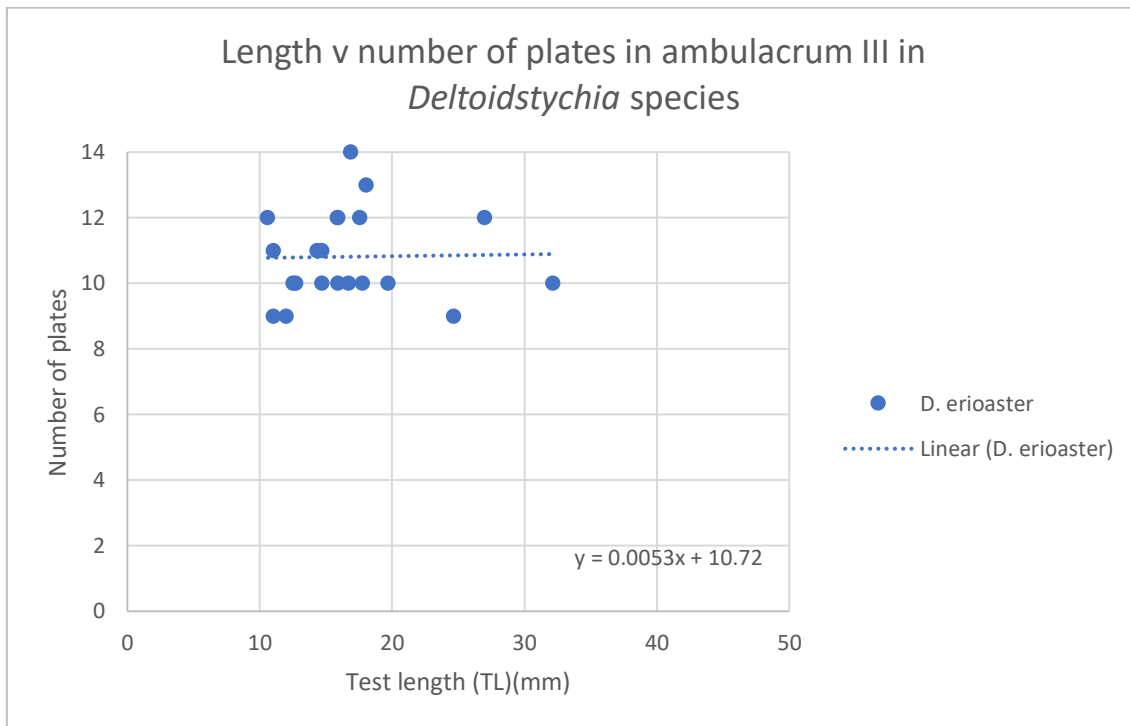


Fig. 4.12. Scatter plot of number of post-basicoronal ambulacral plates in ambulacrum III against TL for *Deltoidstychia erioaster*.

Hypothesis 4: Within the subfamily Monostychinae the first plates in touch with the periproct decrease in number as TL increases.

H₀: In each of a range of species within the genera Monostychia, Quinquestychia, Rotundastychia, and Deltoidstychia the first plates in touch with the periproct decrease in number as TL increases.

H₁: In each of a range of species within the genera Monostychia, Quinquestychia, Rotundastychia, and Deltoidstychia the first plates in touch with the periproct do not decrease in number as TL increases.

Table 4.1. displays the mean TL of the number of plates first in contact with the periproct. Care needs to be taken in interpreting this data for two reasons. First, the sample sizes can be small in many instances (refer to Figs 4.26–29. for further clarification). Second, the change from one to another is not necessarily sequential. Numbers 2a/3b and 3a/2b have the same number of plates, just a different orientation. So too with 3a/4b and 4a/3b. As most data falls in 3a/3b followed by 2a/3b a comparison of just these two columns may be appropriate.

In most species the mean decreases as the number increases. The null hypothesis is rejected.

Species	n	2a/2b	2a/3b	3a/2b	3a/3b	3a/4b	4a/3b
<i>M. australis</i>	71		22.6 (5.9)		31.0 (6.9)	23.2 (0)	43.9 (0)
<i>M. macnamarai</i>	6		29.2 (0)		37.3 (2.0)		
<i>M. alanrxi</i>	5		30.7 (1.8)		31.1 (2.8)		
<i>M. merrimanensis</i>	43	11.8 (4.7)	13.5 (1.6)		14.0 (3.5)	15.5 (3.9)	
<i>M. etheridgei</i>	5	13.2 (0)	17.6 (0)		14.4 (4.0)		
<i>M. glenelgensis</i>	20		18.9 (0)		26.7 (4.5)		
<i>M. robheathi</i>	8	29.3 (0)	30.6 (4.9)		24.7 (9.1)		
<i>Q. mannumensis</i>	3				64.8 (9.4)		
<i>Q. gigas</i>	3	85.3 (0)	68.8 (2.1)				
<i>Q. berylmorrisae</i>	10		57.9 (1.4)		63.2 (12.4)		
<i>Q. robertirwini</i>	4		40.9 (0)		37.5 (7.5)		
<i>R. pledgei</i>	6		36.2 (8)	46.9 (0)	42.6 (1.1)		
<i>R. aquilaensis</i>	6				19.4 (6.6)		
<i>R. eyriei</i>	9				54.7 (0)		
<i>D. erioaster</i>	24		21.9 (0)		17.7 (5.2)	12.5 (0)	

Table 4.1. Mean TL (SD) of the number of plates first in contact with periproct. (When SD = (0) indicates single sample for which no SD is measurable.)

Hypothesis 5: The number of paired interambulacral plates on the oral surface can be used to separate the species within a genus within the subfamily Monostychinae.

H₀: In each of a range of species within the genera Monostychia, Quinquestychia, and Rotundastychia, the number of paired interambulacral plates on the oral surface is not a useful guide to separating the species.

H₁: In each of a range of species within the genera Monostychia, Quinquestychia, and Rotundastychia, the number of paired interambulacral plates on the oral surface is a useful guide to separating the species.

In relation to the genus *Monostychia* (Fig. 4.14.), and leaving aside outliers, the data for the interquartile range shows a clear separation of *M. australis* from *M. macnamarai*, *M. alanixi*, *M. glenelgensis* and *M. robheathi* but a considerable overlap with *M. merrimanensis* and *M. etheridgei*. The closely related pair of *M. merrimanensis* and *M. etheridgei* do show a significant difference in mean and median plate numbers although there remains a complete overlap of the plate numbers. *M. macnamarai*, *M. alanixi*, *M. glenelgensis* and *M. robheathi* cannot be separated using these plates alone. In summary each of the species can be defined as having the following number of plates in the interquartile range (and the maximum and minimum range): *M. australis* 6–7 (5–8); *M. macnamarai* 7–8 (6–9); *M. alanixi* 7–8 (6–9); *M. merrimanensis* 6–8 (5–9); *M. etheridgei* 7 (7); *M. glenelgensis* 7–8 (6–9) and *M. robheathi* 7–8 (7–9).

For the genus *Quinquestychia* (Fig. 4.15.), *Q. berylmorrisae* stands out with significantly higher plate numbers than the others. *Q. gigas* is notable because its lack of variability and while

its numbers overlap those of *Q. mannumensis* and *Q. robertirwini* its mean and median differ substantially (12.0 compared to 7.4 and 7.8 respectively).

The genus *Rotundastychia* (Fig. 4.16.) shows remarkable consistency in plate numbers both within each species and between the species compared to the data of *Monostychia* and *Quinquestychia*. While it may appear that *R. aquilaensis* is different to the other two species, the small number of observations (seven) suggests the difference may not be reliable.

Collectively the results suggest that the number of plates in the oral paired interambulacra can be used as a character to separate species within the genera on the Monostychinae, although not as a metric that can stand alone. The null hypothesis is rejected.

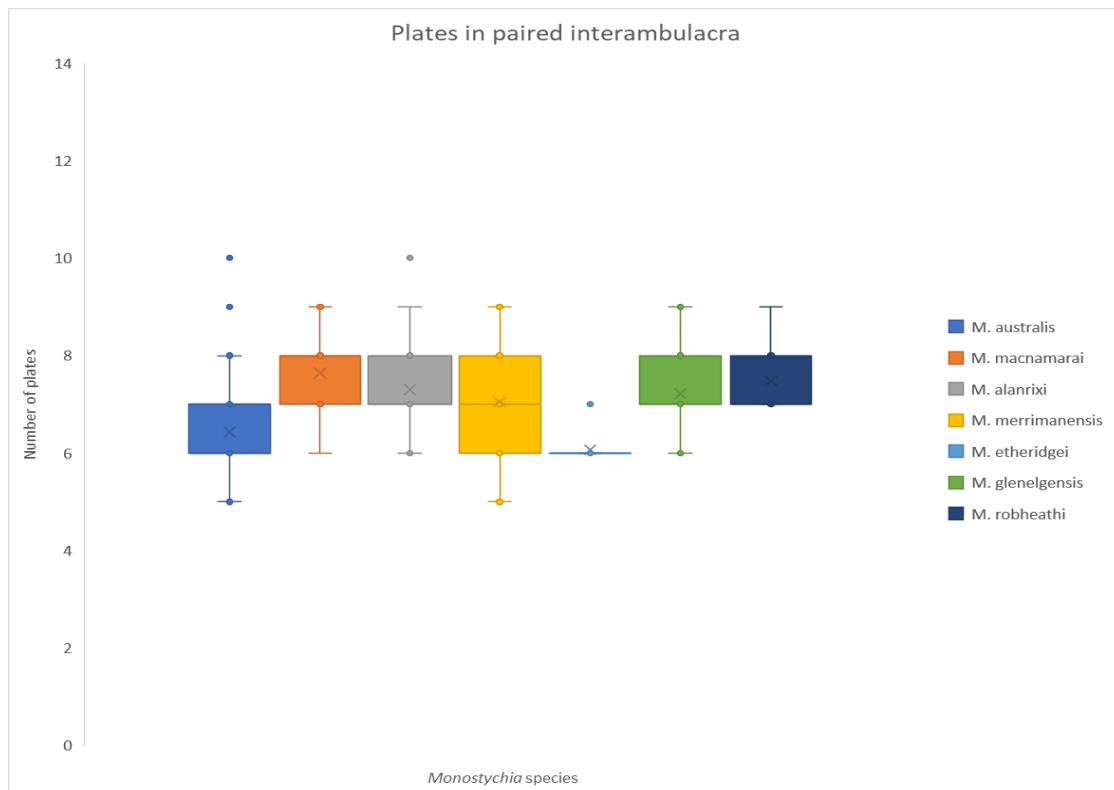


Fig. 4.14. Box plot of number of plates in the oral paired interambulacra of *Monostychia* species.

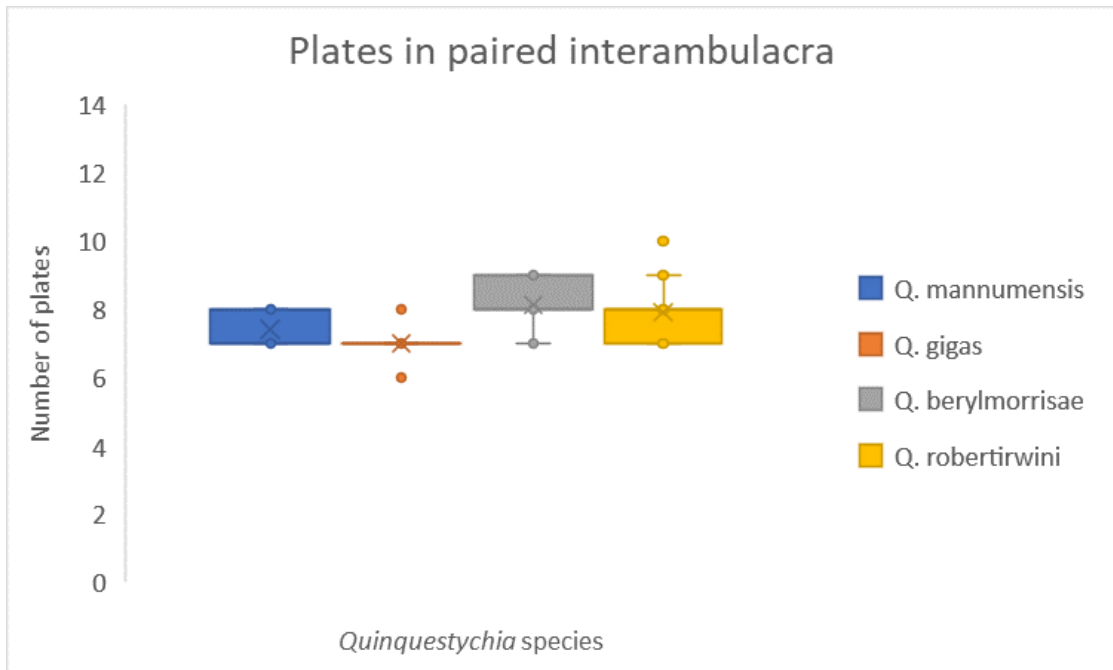


Fig. 4.15. Box plot of number of plates in the oral paired interambulacra of *Quinquestychia* species.

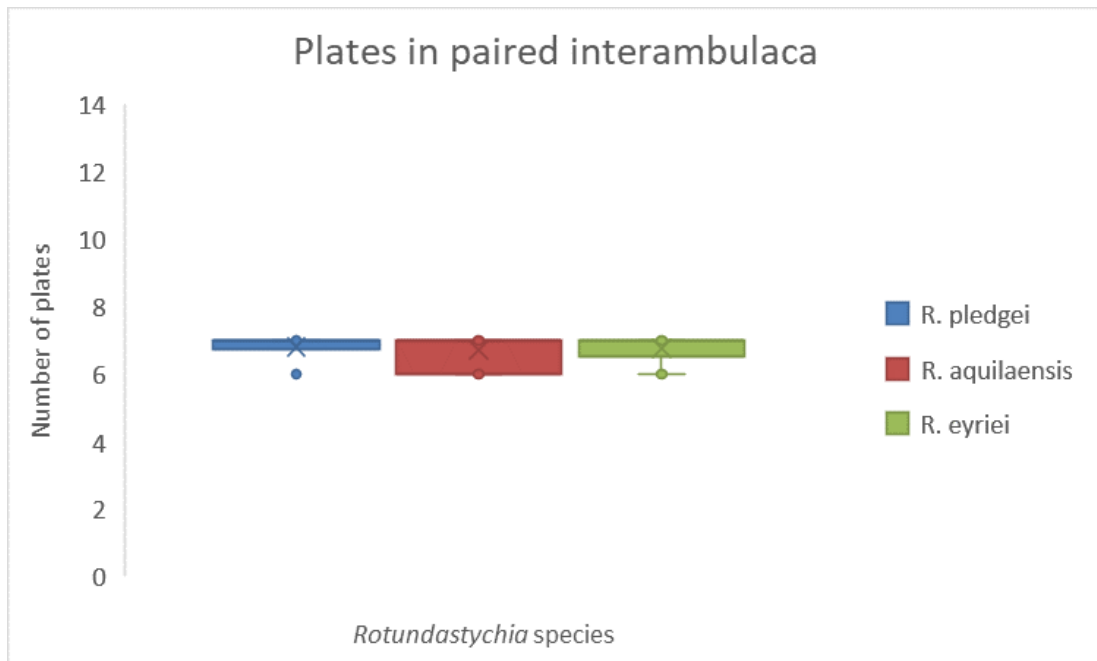


Fig. 4.16. Box plot of number of plates in the oral paired interambulacra of *Rotundastychia* species.

Hypothesis 6: The number of paired ambulacral plates on the oral surface can be used to separate the species within a genus within the subfamily Monostychinae.

H₀: In each of a range of species within the genera Monostychia, Quinquestychia, and Rotundastychia, the number of paired ambulacral plates on the oral surface is not a useful guide to separating the species.

H₁: In each of a range of species within the genera Monostychia, Quinquestychia, and Rotundastychia, the number of paired ambulacral plates on the oral surface is a useful guide to separating the species.

In relation to the genus *Monostychia* (Fig. 4.17.), the bulk of the data suggests there appears a clear separation of *M. australis* from all the other species except *M. etheridgei* where there is substantial overlap. *M. macnamarai*, *M. alanrxi* and *M. merrimanensis* have distinctly greater plate numbers than the rest and these three can be separated using mean (11.2, 9.9 and 10.3 respectively) or median (11, 10 and 10 respectively) of plate numbers. While *M. glenelgensis* and *M. robheathi* cannot be separated from each other with this character they can be clearly separated from *M. australis*, *M. macnamarai* and *M. merrimanensis* and potentially from *M. alanrxi* and *M. etheridgei* using means or medians.

For the genus *Quinquestychia* (Fig. 4.18), the four species share having 10 plates in the paired ambulacra. However, *Q. mannumensis* only has ten while the other three species have greater numbers in addition. Considering *Q. mannumensis* has limited data (five observations) available for this character, this separation is not considered significant. On the other hand, *Q. berylmoorise* does have up to 13 plates and its mean (11.1) appears significantly greater than the other three species (10.0, 10.5 and 11.0 respectively).

A similar argument can be presented for the three species of *Rotundastychia* (Fig. 4.19). *R. eyriei* has more data than either of the other two species and shows fewer plates. Its mean (9.0) is less than the other two species (both 10.0) however the significance of the difference is questionable.

Collectively the results suggest that the number of plates in the oral paired interambulacra can be used as a character to separate species within the genera on the Monostychinae, although not as a metric that can stand alone. The null hypothesis is rejected.

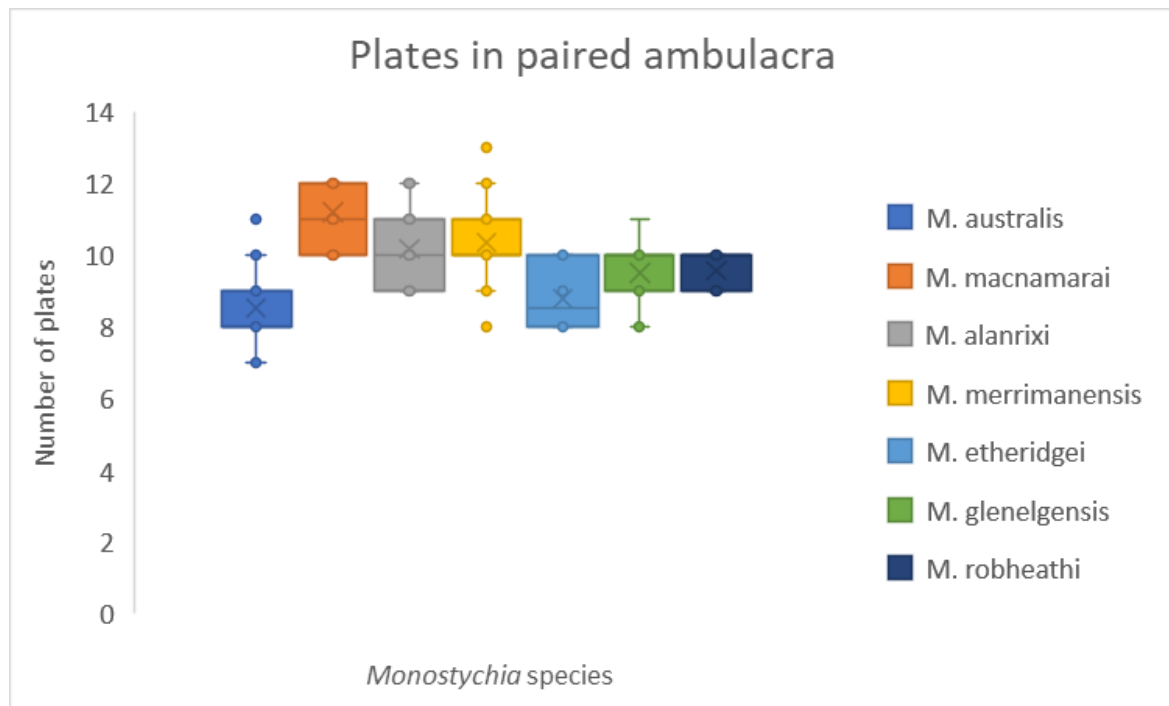


Fig. 4.17. Box plot of number of plates in the oral paired ambulacra of *Monostychia* species.

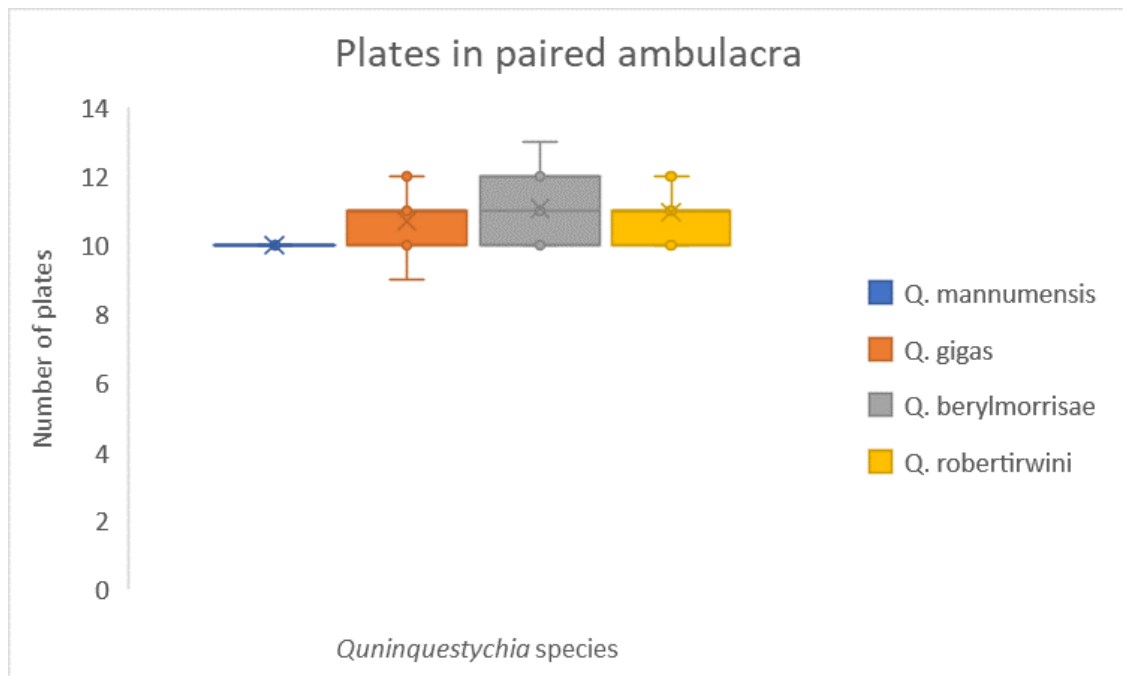


Fig. 4.18. Box plot of number of plates in the oral paired ambulacra of *Quinquostychia* species.

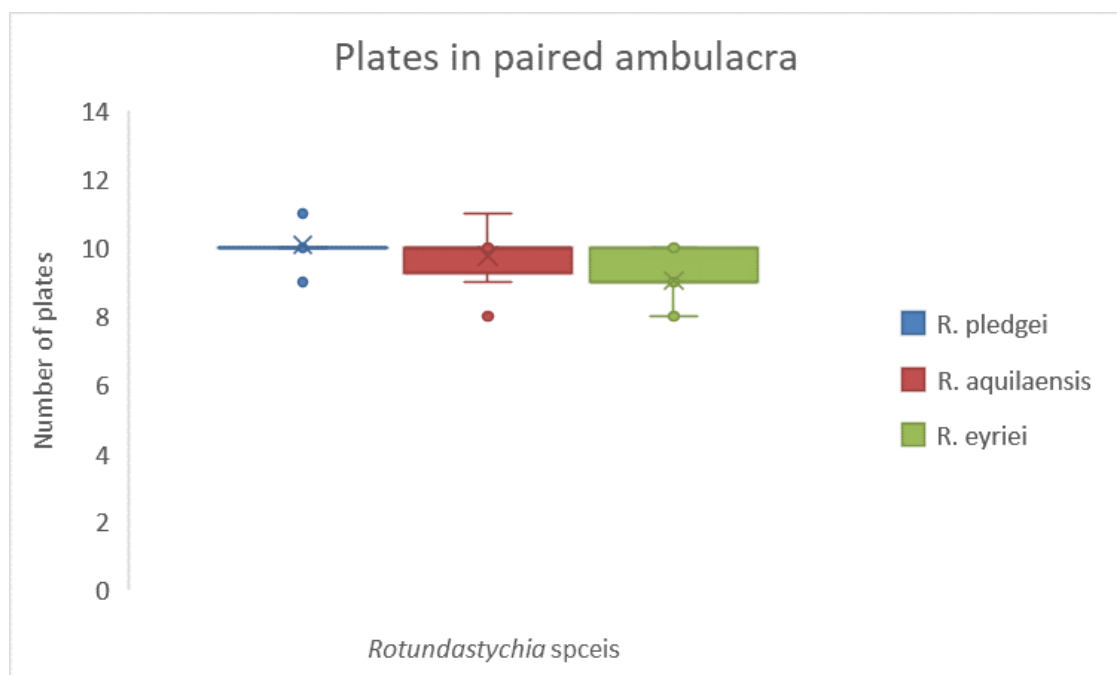


Fig. 4.19. Box plot of number of plates in the oral paired ambulacra of *Rotundastychia* species.

Hypothesis 7: The number of plates in ambulacrum III on the oral surface can be used to separate the species within a genus within the subfamily Monostychinae.

H₀: In each of a range of species within the genera Monostychia, Quinquestychia, and Rotundastychia, the number of plates in ambulacrum III on the oral surface is not a useful guide to separating the species.

H₁: In each of a range of species within the genera Monostychia, Quinquestychia, and Rotundastychia, the number of plates in ambulacrum III on the oral surface is a useful guide to separating the species.

In relation to the genus *Monostychia* (Fig. 4.20.), *M. australis* and *M. etheridgei* can be separated from the other five species although not from each other using this character. *M. macnamarai* and *M. glenelgensis* can also be separated from each other but not from the remaining three species.

For the genus *Quinquestychia* (Fig. 4.21.), the overlaps of the data make it difficult to use this character to separate any of the species. *Q. mannumensis* and *Q. gigas* have a median number of 11 while *Q. berylmorrisae* and *Q. robertirwini* have a median of 12. *Q. mannumensis* and *Q. berylmorrisae* might be separated from each other using both the median and the mean (11.0 and 12.0 respectively). However, such a determination cannot be made with the current limited data.

For the genus *Rotundastychia* (Fig. 4.22.), *R. pledgei* and *R. eyriei* are potentially separable from each other using the means (11.0 and 12.0 respectively) and medians (11 and 12 respectively). The data for both *R. pledgei* and *R. aquilaensis* is lacking (three and two observations respectively) and hence little weight should be placed on this character at present.

Collectively the results suggest that the number of plates in ambulacrum III can be used as a character to separate species within the genera on the Monostychinae, although not as a metric that can stand alone. The null hypothesis is rejected.

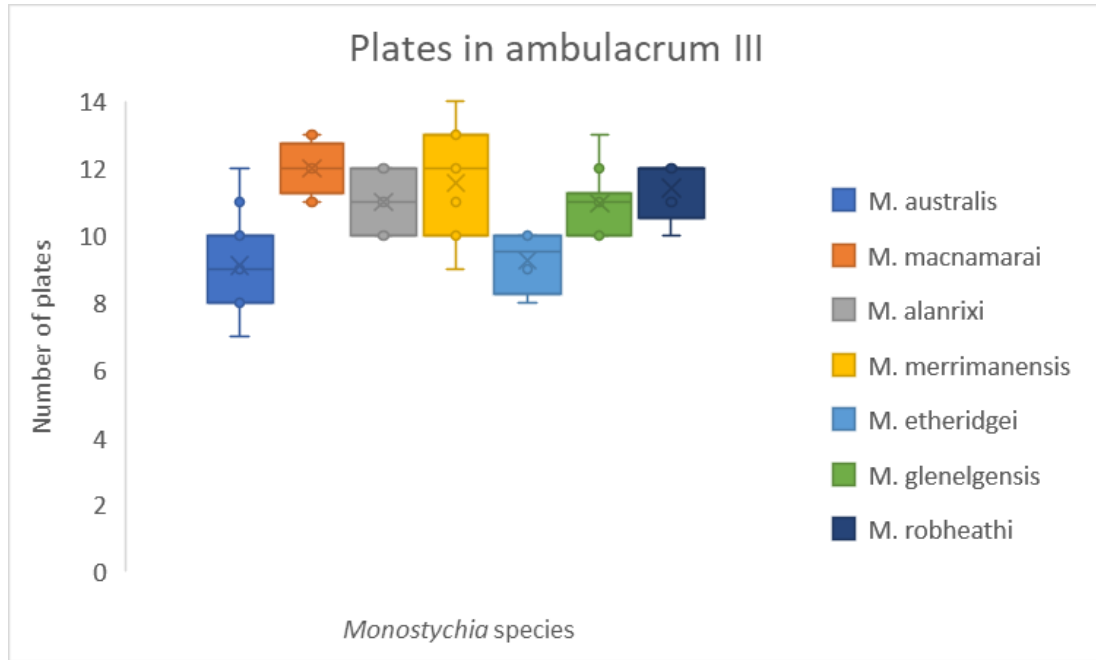


Fig. 4.20. Box plot of number of plates in the oral ambulacrum III of *Monostychia* species.

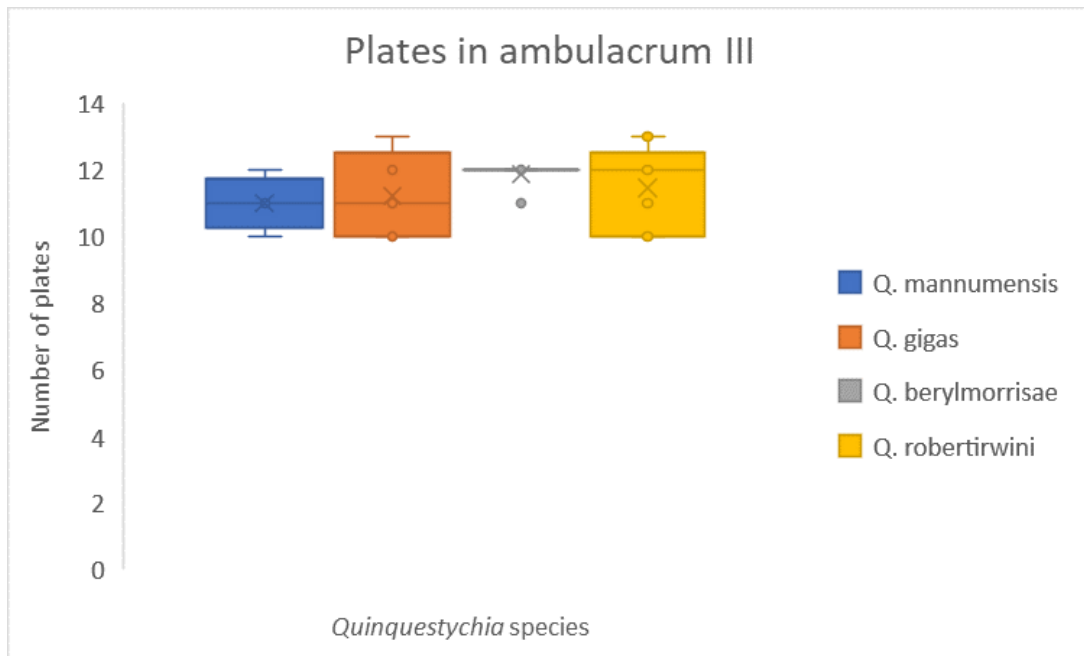


Fig. 4.21. Box plot of number of plates in the oral ambulacrum III of *Quinquestychia* species.

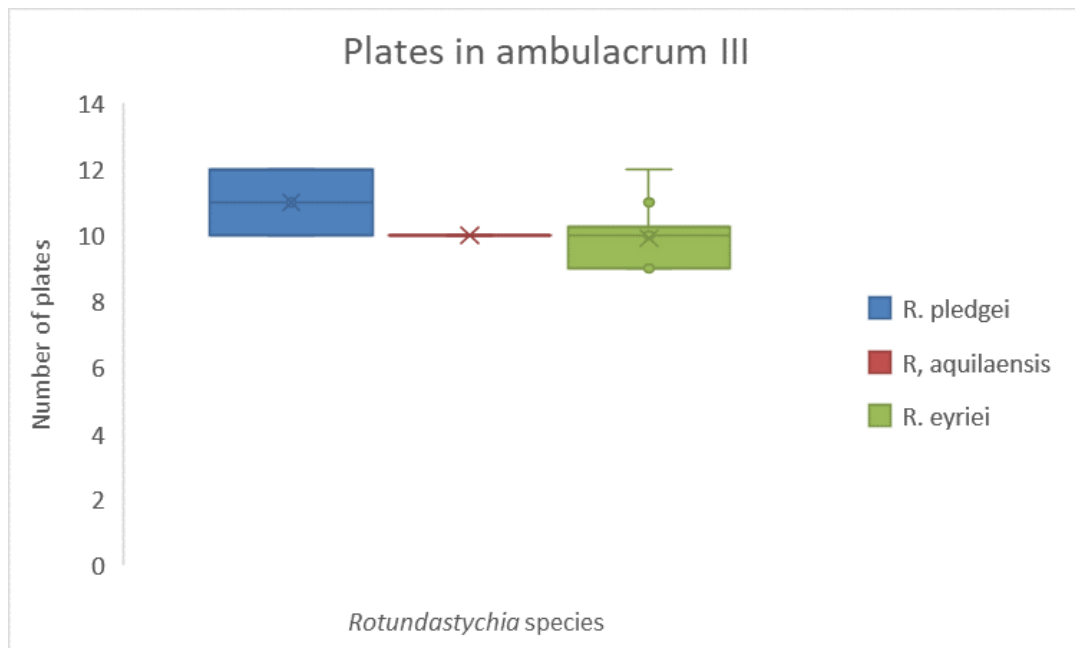


Fig. 4.22. Box plot of number of plates in the oral ambulacrum III of *Rotundastychia* species.

Hypothesis 8: In the subfamily Monostychinae the number of paired interambulacral plates on the oral surface is a useful guide to separate the four genera.

H₀: In the subfamily Monostychinae the number of paired interambulacral plates on the oral surface is not a useful guide to separating the genera.

H₁: In the subfamily Monostychinae the number of paired interambulacral plates on the oral surface is a useful guide to separating the genera.

Data from the four genera are presented in Fig. 4.23. Leaving aside the outliers, the medians for *Monostychia* and *Rotundastychia* are the same (seven) while their means differ slightly, being 6.7 and 7.0 respectively. The range from first to third quartile medians differ, being six to seven for *Monostychia* and seven for *Rotundastychia*. The medians for *Quinquestychia* and *Deltoidstychia* differ markedly from each other (eight and nine respectively) and from *Monostychia* and *Rotundastychia*. Their means also differ markedly (7.7 and 8.7 respectively). The range from first to third quartile medians differ, being seven to eight for *Quinquestychia* and eight to nine for *Rotundastychia*.

The maximum and minimum plate numbers (and first and third quartile medians) for each of the genera are: *Monostychia* has 5–8 (6–7), *Quinquestychia* has 6–9 (7–8), *Rotundastychia* 7 (7), and *Deltoidstychia* 7–10 (8–9). The null hypothesis is rejected however the utility of this character has limitations.

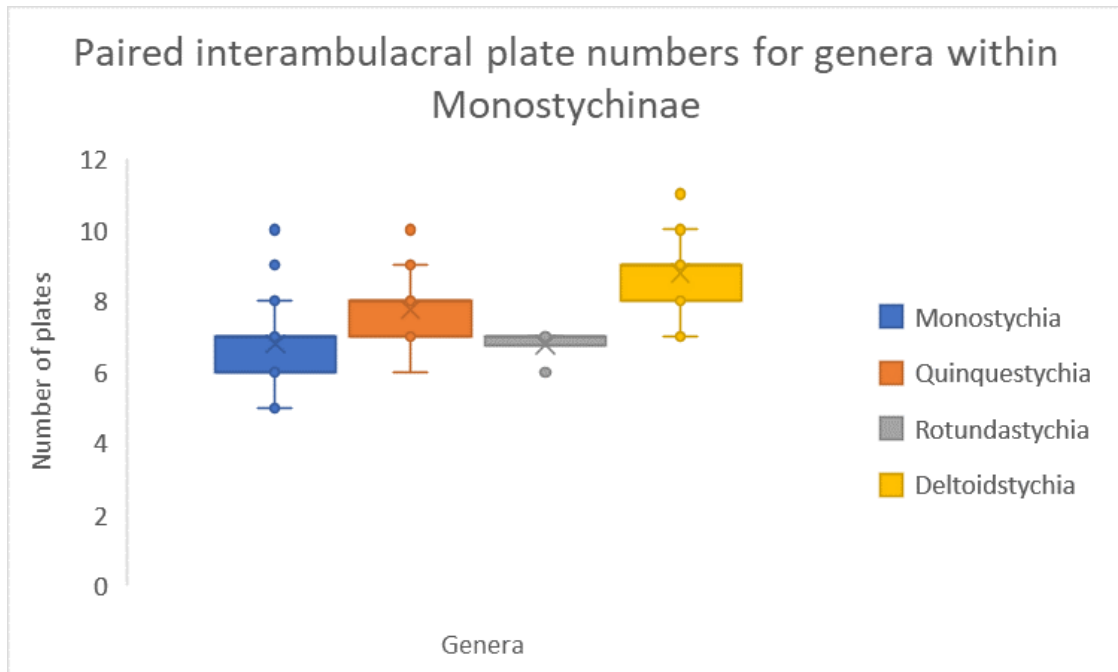


Fig. 4.23. Box plot of number of plates in the oral paired interambulacra of Monostychinae genera.

Hypothesis 9: In the subfamily Monostychinae the number of paired ambulacral plates on the oral surface is a useful guide to separate the four genera.

H₀: In the subfamily Monostychinae the number of paired ambulacral plates on the oral surface is not a useful guide to separating the genera.

H₁: In the subfamily Monostychinae the number of paired ambulacral plates on the oral surface is a useful guide to separating the genera.

Data from the four genera are presented in Fig. 4.24. *Monostychia* and *Rotundastychia*, while difficult to separate do have different medians (nine and ten respectively). The pair of *Quinquestychia* and *Deltoidstychia* cannot be separated. However, the pair of *Monostychia* and *Rotundastychia* are relatively easily separated from the pair of *Quinquestychia* and

Deltoidstychia using means (8.9 and 9.4 respectively for the first pair and 10.9 and 10.9 respectively for the second pair) and medians nine and ten respectively for the first pair and eleven for each of the second pair). The null hypothesis is rejected however the utility of this character has limitations.

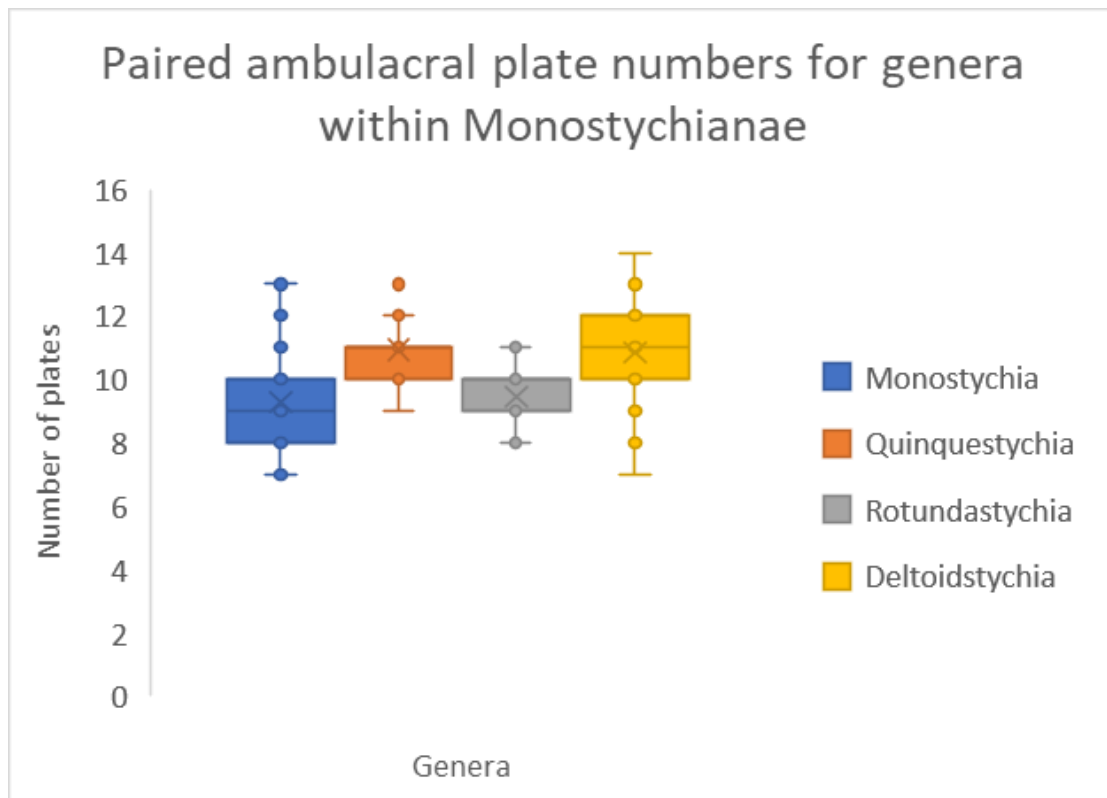


Fig. 4.24. Box plot of number of plates in the oral paired ambulacra of Monostychinae genera.

Hypothesis 10: In the subfamily Monostychinae the number of plates in ambulacrum III on the oral surface is a useful guide to separate the four genera.

H₀: In the subfamily Monostychinae the number of plates in ambulacrum III on the oral surface is a not useful guide to separating the genera.

H₁: In the subfamily Monostychinae the number of plates in ambulacrum III on the oral surface is a useful guide to separating the genera.

Data from the four genera are presented in Fig. 4.25. *Quinquestychia* can be separated from the other three genera in that it has a median number of 12 compared to ten for the others. It also has the highest mean of 11.5. *Monostychia* and *Rotundastychia* cannot be separated having the same median overall and for the 1st and 3rd quartiles (nine and 11 respectively). The difference in their means (10.3 and 10.1) are not considered significant. *Deltoidstychia* has a slightly higher 1st and 3rd quartile reading (ten and 12) than *Monostychia* and *Rotundastychia*, however, its usefulness taxonomically is doubtful. The null hypothesis is rejected however the utility of this character has limitations.

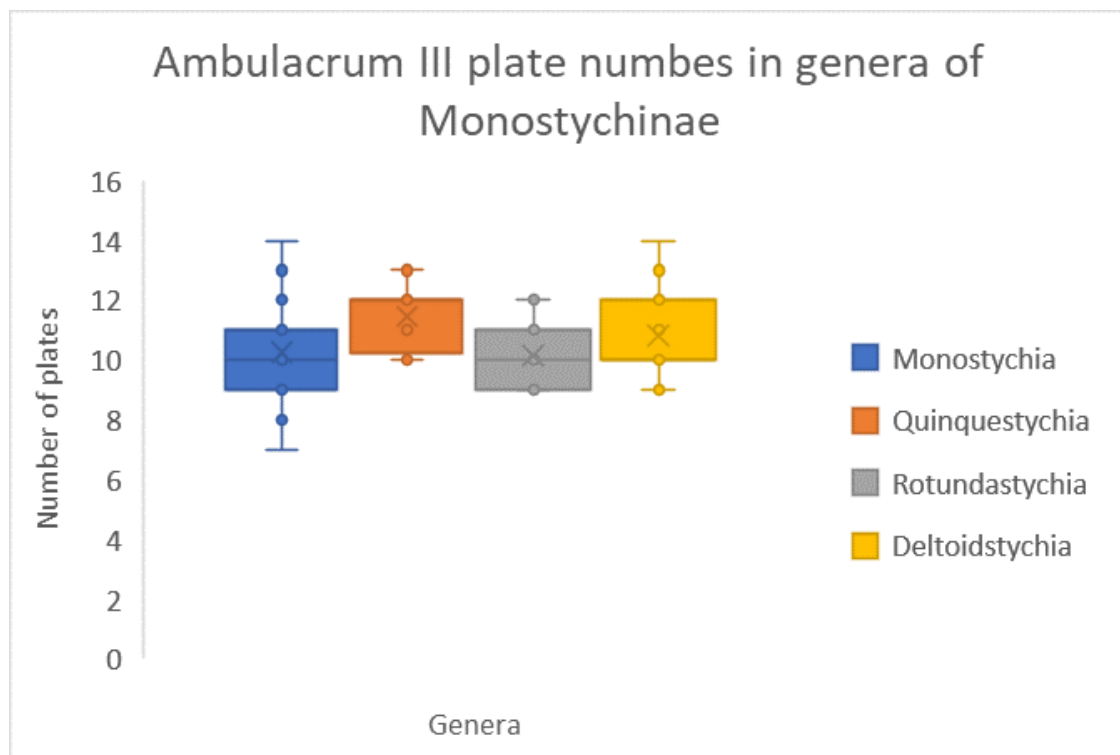


Fig. 4.25. Box plot of number of plates in the oral ambulacrum III of Monostychinae genera.

Hypothesis 11: The first plates in interambulacrum 5 to contact the periproct can be used to separate the species within a genus within the subfamily Monostychinae.

H₀: In each of a range of species within the genera Monostychia, Quinquestychia, and Rotundastychia, the first plate in interambulacrum 5 to contact the periproct is not a useful guide to separating the species.

H₁: In each of a range of species within the genera Monostychia, Quinquestychia, and Rotundastychia, the first plate in interambulacrum 5 to contact the periproct is a useful guide to separating the species.

Data from the seven species of *Monostychia* is presented in Fig. 4.26. Along the x-axis the numbers refer in order to *M. australis*, *M. macnamarai*, *M. alanrxi*, *M. merrimanensis*, *M. etheridgei*, *M. glenelgensis* and *M. robheathi*. In all species except for *M. alanrxi* the dominant plate to first contact the periproct is 3a/3b. For *M. alanrxi* the number of observations is very low (five) and therefore the results presented should be treated with caution. In all species the second most frequent plate is 2a/3b. Notably, the plate 3a/2b has not been observed in any specimen and the plate 4a/3b observed in only one specimen of *M. australis*.

Data from the four species of *Quinquestychia* is presented in Fig. 4.27. Along the x-axis the numbers refer in order to *Q. mannumensis*, *Q. gigas*, *Q. berylmoorisae* and *Q. robertirwini*. In three of the species plate 3a/3b is dominant. Interestingly, in *Q. gigas* this number and greater numbers were not observed. The very low observation number of three for each of *Q. mannumensis* and *Q. gigas* suggest this result cannot be relied upon to persist in this species.

Data from the three species of *Rotundastychia* is presented in Fig. 4.28. Along the x-axis the numbers refer in order to *R. pledgei*, *R. aquilaensis* and *R. eyriei*. For all three species the dominant plate first in contact with the periproct is 3a/3b.

In none of the three genera can individual species be separated with confidence using the first plate to contact the periproct. The null hypothesis cannot be rejected.

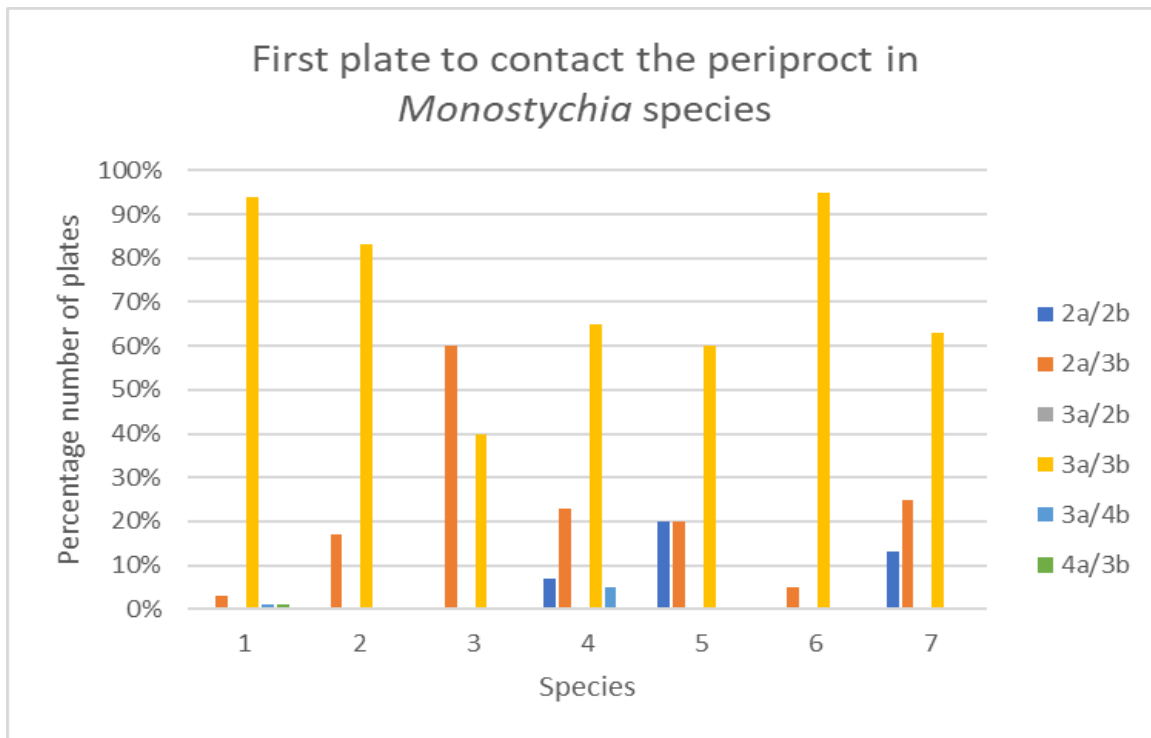


Fig. 4.26. Box plot of the first plate to contact the periproct in seven species of *Monostychia*. (1 = *M. australis* ($n = 71$); 2 = *M. macnamarai* ($n=6$); 3 = *M. alanrxi* ($n=5$); 4 = *M. merrimanensis* ($n = 43$); 5 = *M. etheridgei* ($n = 5$); 6 = *M. glenelgensis* ($n = 20$); 7 = *M. robheathi* ($n = 8$).)

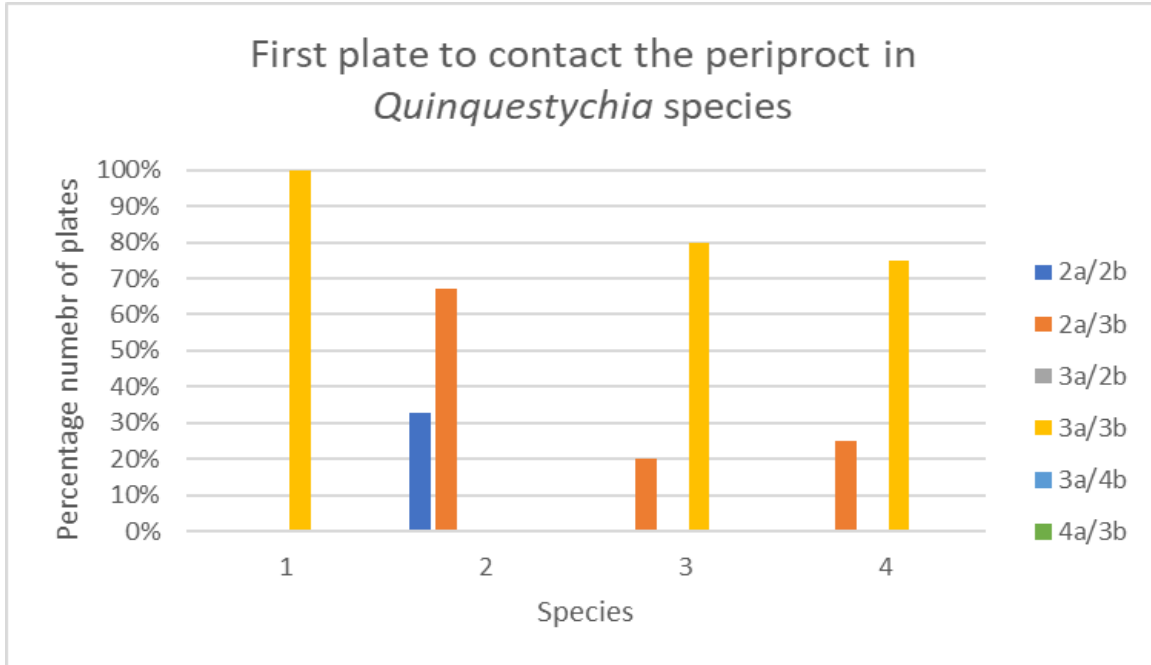


Fig. 4.27. Box plot of the first plate to contact the periproct in four species of *Quinquestychia*. (1 = *Q. mannumensis* (n = 3); 2 = *Q. gigas* (n = 3); 3 = *Q. berylmorrisae* (n = 10); 4 = *Q. robertirwini* (n = 4).)

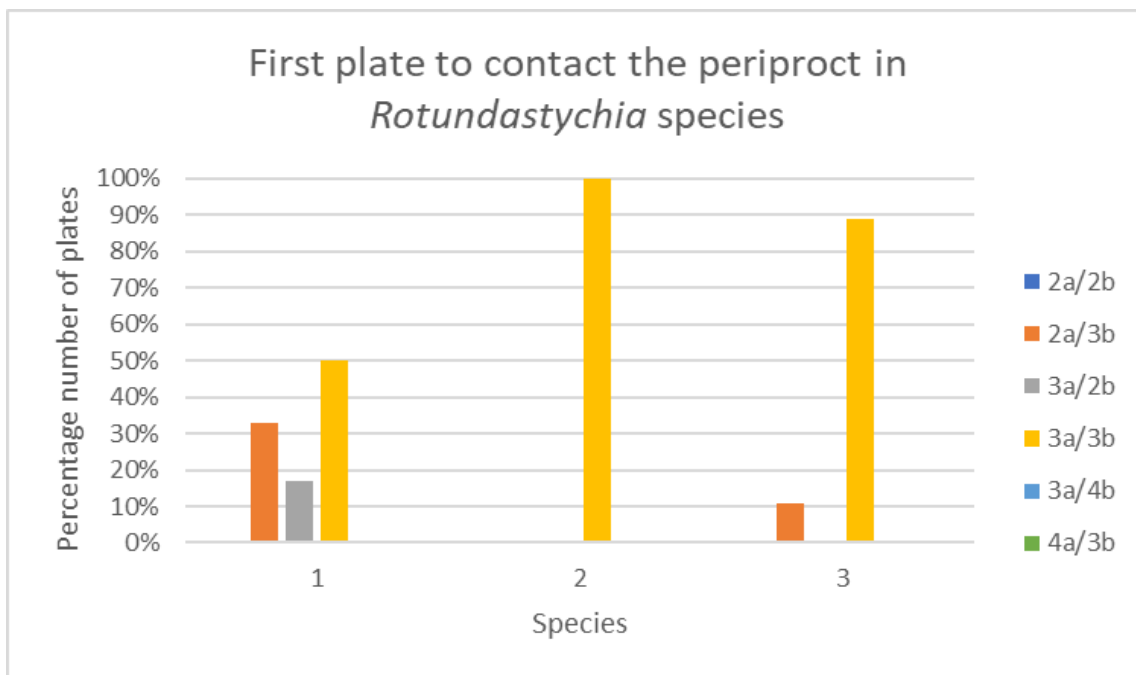


Fig. 4.28. Box plot of the first plate to contact the periproct in three species of *Rotundastychia*. (1 = *R. pledgei* (n = 6); 2 = *R. aquilaensis* (n = 6); 3 = *R. eyriei* (n = 9).)

Hypothesis 12: In the subfamily Monostychinae the first plate in interambulacrum 5 to contact the periproct is a useful guide to separate the four genera.

H₀: In the subfamily Monostychinae the first plate in interambulacrum 5 to contact the periproct is not a useful guide to separating the genera.

H₁: In the subfamily Monostychinae the first plate in interambulacrum 5 to contact the periproct is a useful guide to separating the genera.

Data from the four genera of Monostychinae is presented in Fig. 4.29. Along the x-axis the numbers refer in order to *Monostychia*, *Quinquestychia*, *Rotundastychia* and *Deltoidstychia*. The first plate to contact the periproct appears consistent between the genera with 3a/3b clearly dominant and 2a/3b the next dominant. The null hypothesis cannot be rejected.

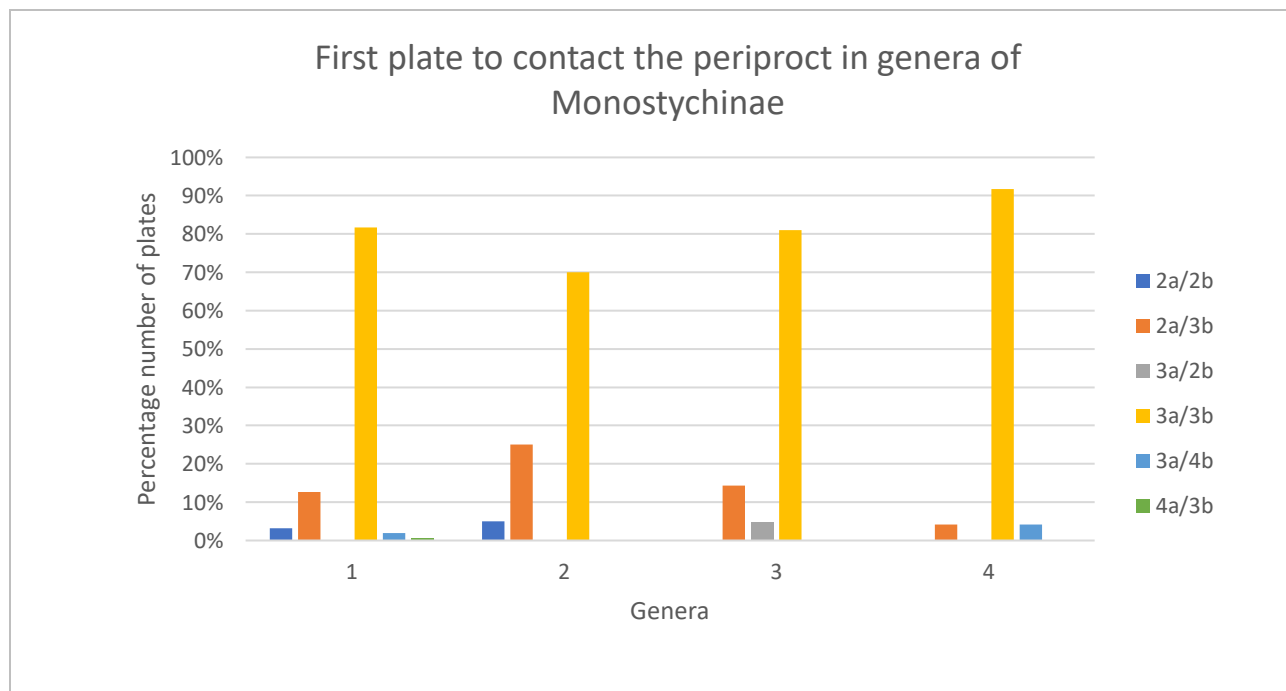


Fig. 4.29. Box plot of the first plate to contact the periproct in four genera of Monostychinae. (1 = *Monostychia* (n = 158); 2 = *Quinquestychia* (n = 20); 3 = *Rotundastychia* (n = 24); 4 = *Deltoidstychia* (n = 24).)

Hypothesis 13: Within the subfamily Monostychinae the left-handedness and right-handedness of a plate series in the interambulacral oral plates is consistent across a range of species.

H₀: In each of a range of species within the genera Monostychia, Quinquestychia, Rotundastychia and Deltoidstychia the series of oral plates in each of the interambulacra does not consistently begin with either a left-hand or right-hand bias.

H₁: In each of a range of species within the genera Monostychia, Quinquestychia, Rotundastychia and Deltoidstychia the series of oral plates in each of the interambulacra consistently begins with either a left-hand or right-hand bias.

The data is presented in Table 4.2. The series of plates start from the peristome in interambulacrum 1 on the left or ‘a’ side. In 10 of the 15 species 100% of the plates start with this orientation. *R. aquilaensis* has only 50% start this way, however, with a sample size of two this data is insignificant. *M. glenelgensis* has 93% start in this orientation and while the sample size of 15 is still small this does indicate inconsistency. Similar, although smaller inconsistencies are displayed by *M. australis* (99%), *M. merrimanensis* (95%) and *D. erioaster* (96%).

The plate series for interambulacrum 3 also starts on the left or ‘a’ side. The consistency however is significantly less than for interambulacrum 1. While eight of the 15 species have 100% starting with this orientation, in every case the sample size is low. The two species with the largest sample sizes (*M. australis* and *M. merrimanensis*) display a significant decrease in consistency compared to interambulacrum 1. *D. erioaster*, also with a reasonably large sample size shows the same percentage orientation as interambulacrum 1.

For interambulacra 2, 4 and 5, the data shows the plates series starts on the right or ‘b’ side. There is a similar level of inconsistency for this starting orientation as for interambulacrum 3 in relation to interambulacra 2 and 5. However, with interambulacrum 4, there appears a significantly higher level of consistency. Twelve of the 15 species show 100% consistency, including *M. australis* and *D. erioaster* both with large sample sizes.

The null hypothesis cannot be rejected for interambulacra 1, 2, 3 and 5. However, for interambulacrum 4 the null hypothesis is rejected.

Species	Intamb 1	Intamb 2	Intamb 3	Intamb 4	Intamb 5
<i>M. australis</i>	99% (70)	17% (71)	87% (71)	0% (70)	13% (71)
<i>M. macnamarai</i>	100% (10)	0% (7)	100% (7)	14% (7)	0% (7)
<i>M. alanrxi</i>	100% (5)	0% (6)	100% (6)	0% (6)	40% (5)
<i>M. merrimanensis</i>	95% (39)	29% (31)	56% (32)	6% (34)	2% (44)
<i>M. etheridgei</i>	100% (3)	75% (4)	50% (4)	0% (4)	20% (5)
<i>M. glenelgensis</i>	93% (15)	7% (14)	88% (17)	6% (16)	20% (20)
<i>M. robheathi</i>	100% (7)	0% (4)	100% (6)	0% (6)	25% (8)
<i>Q. mannumensis</i>	100% (1)	0% (1)	100% (2)	0% (1)	100% (2)
<i>Q. gigas</i>	100% (4)	0% (3)	100% (3)	0% (4)	0% (3)
<i>Q. berylmorrisae</i>	100% (8)	0% (6)	71% (7)	0% (8)	0% (10)
<i>Q. robertirwini</i>	100% (5)	0% (7)	86% (7)	0% (4)	0% (4)
<i>R. pledgei</i>	100% (2)	0% (4)	100% (4)	0% (3)	40% (5)
<i>R. aquilaensis</i>	50% (2)	50% (2)	100% (2)	0% (1)	40% (5)
<i>R. eyriei</i>	100% (6)	0% (7)	100% (6)	0% (6)	44% (9)
<i>D. erioaster</i>	96% (24)	4% (25)	96% (26)	0% (23)	18% (28)

Table 4.2. The percentage (and sample size) of plates of each oral interambulacra series that start from the peristome on the left, or ‘a’ side, species by species for Monostychinae.

Hypothesis 14: Within the subfamily Monostychinae the left-handedness and right-handedness of a plate series in the ambulacral oral plates is consistent across a range of species.

H₀: In each of a range of species within the genera Monostychia, Quinquestychia, Rotundastychia and Deltoidstychia the series of oral plates in each of the ambulacra does not consistently begin with either a left-hand or right-hand bias.

H₁: In each of a range of species within the genera Monostychia, Quinquestychia, Rotundastychia and Deltoidstychia the series of oral plates in each of the ambulacra consistently begins with either a left-hand or right-hand bias.

The data is presented in Table 4.3. The series of plates start from the peristome in ambulacrum I on the left or ‘a’ side. In nine of the 15 species 100% of the plates start with this orientation. For the other species a significant number start from the right or ‘b’ side. For example, in the three species with the highest sample size, *M. australis*, *M. merrimanensis* and *D. erioaster*, the orientation is only 93%, 97% and 96% respectively.

The series of plates in ambulacrum III also start on the left or ‘a’ side and with a similar level of consistency to ambulacrum I.

Ambulacra II, IV and V start on the right or ‘b’ side. However, for ambulacrum II a significant number start on the left or ‘a’ side (in one case 50%). For example, *R. aquilaensis*, *M. etheridgei* and *R. pledgei*, all of which have high percentages. However, each of these also have

low sample sizes and so it is questionable as to their real significance. *M. australis*, with the highest sample size also has 7% starting on the left or ‘a’ side, as does *D. erioaster* with 8%.

In ambulacrum V all but two species have 100% of their measurements starting on the right or ‘b’ side. However, those two are *M. australis* and *D. erioaster* both with large sample sizes albeit relatively small percentages 7% and 4% respectively.

The null hypothesis cannot be rejected for ambulacra I, II, III and IV. However, for ambulacrum V the null hypothesis is rejected.

Species	Amb I	Amb II	Amb III	Amb IV	Amb V
<i>M. australis</i>	93% (69)	7% (71)	97% (71)	3% (70)	7% (68)
<i>M. macnamarai</i>	100% (2)	0% (7)	100% (8)	0% (7)	0% (5)
<i>M. alanrxi</i>	100% (6)	0% (6)	100% (6)	0% (6)	0% (5)
<i>M. merrimanensis</i>	97% (39)	0% (35)	87% (39)	3% (36)	0% (42)
<i>M. etheridgei</i>	75% (4)	33% (3)	67% (3)	0% (4)	0% (3)
<i>M. glenelgensis</i>	100% (16)	0% (14)	89% (18)	19% (16)	0% (14)
<i>M. robheathi</i>	80% (5)	25% (4)	100% (5)	0% (4)	0% (5)
<i>Q. mannumensis</i>	100% (1)	0% (1)	100% (4)	0% (2)	0% (1)
<i>Q. gigas</i>	100% (4)	0% (4)	100% (5)	0% (4)	0% (4)
<i>Q. berylmorrisae</i>	100% (9)	0% (9)	100% (8)	0% (9)	0% (9)
<i>Q. robertirwini</i>	100% (5)	0% (8)	100% (9)	0% (6)	0% (4)
<i>R. pledgei</i>	75% (4)	25% (4)	100% (4)	0% (4)	0% (2)
<i>R. aquilaensis</i>	100% (3)	50% (2)	100% (2)	0% (1)	0% (1)
<i>R. eyriei</i>	100% (5)	0% (6)	100% (10)	0% (7)	0% (5)
<i>D. erioaster</i>	96% (24)	8% (24)	96% (23)	0% (24)	4% (25)

Table 4.3. The percentage (and sample size) of plates of each oral ambulacra series that start from the peristome on the left, or ‘a’ side, species by species for Monostychinae.

Hypothesis 15: Within the subfamily Monostychinae the left-handedness and right-handedness of a plate series in the interambulacral oral plates is consistent across a range of genera.

H₀: In each of a range of genera within the genera Monostychia, Quinquestychia, Rotundastychia and Deltoidstychia the series of oral plates in each of the interambulacra does not consistently begin with either a left-hand or right-hand bias.

H₁: In each of a range of genera within the genera Monostychia, Quinquestychia, Rotundastychia and Deltoidstychia the series of oral plates in each of the interambulacra consistently begins with either a left-hand or right-hand bias.

The data is presented in Table 4.4. As with Hypothesis 13 the general orientation of the first plates from the peristome is left or ‘a’ for interambulacra 1 and 3 and the right or ‘b’ side for interambulacra 2, 4 and 5. Only interambulacra 4 has that orientation with such consistency that the null hypothesis can be rejected.

Genus	Intamb 1	Intamb 2	Intamb 3	Intamb 4	Intamb 5
<i>Monostychia</i>	97% (149)	18% (137)	81% (143)	3% (143)	12% (160)
<i>Quinquestychia</i>	100% (18)	0% (17)	84% (19)	0% (17)	11% (19)
<i>Rotundastychia</i>	90% (10)	8% (13)	100% (12)	0% (10)	42% (19)
<i>Deltoidstychia</i>	96% (24)	4% (25)	96% (26)	0% (23)	18% (28)

Table 4.4. The percentage (and sample size) of plates of each oral interambulacra series that start from the peristome on the left, or ‘a’ side, by genera for Monostychinae.

Hypothesis 16: Within the subfamily Monostychinae the left-handedness and right-handedness of a plate series in the ambulacral oral plates is consistent across a range of genera.

H₀: In each of a range of genera within the genera Monostychia, Quinquestychia, Rotundastychia and Deltoidstychia the series of oral plates in each of the ambulacra does not consistently begin with either a left-hand or right-hand bias.

H₁: In each of a range of genera within the genera Monostychia, Quinquestychia, Rotundastychia and Deltoidstychia the series of oral plates in each of the ambulacra consistently begins with either a left-hand or right-hand bias.

The data is presented in Table 4.5. As with Hypothesis 14 the general orientation of the first plates from the peristome is left or ‘a’ for interambulacra I and III and the right or ‘b’ side for interambulacra II, IV and V. The interambulacra IV and V both have that orientation with such consistency that the null hypothesis can be rejected.

Genus	Amb I	Amb II	Amb III	Amb IV	Amb V
<i>Monostychia</i>	94% (141)	5% (140)	93% (150)	4% (143)	4% (142)
<i>Quinquestychia</i>	100% (19)	0% (22)	100% (26)	0% (21)	0% (18)
<i>Rotundastychia</i>	92% (12)	17% (12)	100% (16)	0% (12)	0% (8)
<i>Deltoidstychia</i>	96% (24)	8% (24)	96% (23)	0% (24)	4% (25)

Table 4.5. The percentage (and sample size) of plates of each oral ambulacra series that start from the peristome on the left, or ‘a’ side, by genera for Monostychinae.

Conclusions

Hypotheses 1–3 relate to the consistency of the number of plates on the oral surface of monostychioids relative to TL. It is assumed that TL increases with age and with age the total number of plates in the test increases according to the ocular plate rule (Mooi et al. 1994). From a taxonomic perspective, if the plates migrate around the ambitus and therefore increase in number on the oral surface with increasing TL then this character will be of no use. The data relating to these three hypotheses clearly rejected the notion that the plate numbers increase with size. Until further data casts doubt on this conclusion the number of plates on the oral surface have the potential to be useful taxonomically.

Hypothesis 4 also relates to the number of plates on the oral surface in relation to TL but instead of the quantum of plates it tested at which plates were first to contact the periproct. Mooi (pers. comm. October 2012) suggested that as TL increases the periproct appears to move to be in contact with a lower plate number in clypeasteroids. This study did not find this to be the case in monostychioids. Indeed, the data suggests the opposite. In five of the seven species of *Monostychia* the mean TL was larger when 3a/3b was in first touch with the periproct than when 2a/2b was in touch. In the other two species the number decreased. In *Quinquestychia*, two species showed a decrease in number, one an increase and the fourth, no change. In *Rotundastychia* one species showed an increase and the other two no change while in *Deltoidstychia* there was a decrease in number with increasing TL. Overall, seven species showed an increase, five had a decrease and three species had no change. Many of these species and plate numbers had low sample sizes which prevents a positive conclusion but of the five species with the largest sample size only one shows a decrease with TL.

Hypotheses 5–7 related to whether the plate count on the oral surface for the paired interambulacra, paired ambulacra and ambulacrum III could provide any utility for distinguishing species within the genera of the monostychioids. It seems reasonable to conclude that, despite the variation recorded, in all plate series considered the plate number count is useful although it is only in the case of *Q. berylmorrisae* that the number of interambulacral plates might be used definitively. In numerous cases pairs or small groups of species can be separated from other species using these numbers. Mooi (1989) only referred to

the interambulacral plates as a taxonomic tool. Sadler *et al.* (2016, 2017, 2019) suggested that in addition to interambulacral plates the ambulacral plates, both paired and unpaired might be useful, indeed that the ambulacral plates might have more utility than the interambulacral plates. The data here suggests that while all three (paired interambulacra, paired ambulacra and ambulacrum III) all have some utility, none of them can be used with confidence as a single definitive character to separate species within these genera. The data further indicates that of the three, the paired ambulacral plates are possibly better than the paired interambulacral plates. The plates of ambulacrum III appear to have least utility, since there are comparatively fewer of them in any population study. Using a combination of the plate series considered in combination may be useful in separating species within these genera, although additional characters will always be required.

Hypotheses 8–10 related to whether the plate count on the oral surface for the paired interambulacra, paired ambulacra and ambulacrum III could provide any utility for separating genera within the subfamily Monostychinae. It seems reasonable to conclude that, despite the variation recorded, in all plate series considered, the plate number count is useful. Using the paired interambulacral plates *Monostychia* could be separated from *Deltoidstychia*. The pair of *Monostychia* and *Rotundastychia* could be separate from the pair of *Quinquestychia* and *Deltoidstychia* using the paired ambulacral plates. Ambulacrum III plate counts appeared least useful. Using a combination of the three plate series in combination may be useful in separating species within these genera, although additional characters will always be required.

Hypotheses 11 and 12 explored the utility of using the Lovenian plate number of the plate first to contact the periproct. It can be concluded that across the species and genera plate number 3a/3b is typical. While other plate numbers were observed they did provide any evidence of utility as a taxonomic tool at either the species or genus level within the subfamily Monostychinae and are best treated as outliers.

Hypotheses 13–16 related to the left- or right-handedness of the start of a series of plates as read from the peristome. While there was no intention or expectation that such a feature might be a direct taxonomic character, its potential utility arises from the ability to determine which segments are which in broken

specimens. If that were possible then other counting techniques described above may be useful. At species level, interambulacrum 4 is almost always right-handed to start with. Interambulacra 1 and 3 are generally left-handed but occasionally right-handed. Interambulacra 2 and 5 are generally right-handed but occasionally left-handed. At species level, ambulacrum V is almost always right-handed to start with. Ambulacra I and III are generally left-handed but occasionally right-handed. Ambulacra II and IV are generally right-handed but occasionally left-handed. At genus level the interambulacra left- and right-handedness is the same as for the species while ambulacra IV and V appear consistent (orientation the same as for the species) and I, II and III generally consistent but occasionally otherwise. This lack of consistency suggests that left- or right-handedness alone does not indicate which test segment one may have and therefore its use in degerming a test segment for the purpose of plate counts with a taxonomic outcome in mind is not recommended.

In summary, this study set out to determine if the number of plates on the oral surface of monostychioid echinoids could be useful as a taxonomic character. It determined that the number of plates, while variable, was essentially fixed ontologically and therefore did have that potential. It further determined that for the paired interambulacra the number of plates was useful although not to the point they could be used without other characters. This character has been used previously but without an extensive analysis of data and so this outcome is particularly important. It further determined that the number of plates in the paired interambulacra and ambulacrum III were also of use but again not without the assistance of other characters. Finally, the study found that the first plates in touch with the periproct are 3a/3b but that this was not of taxonomic use within the subfamily Monostychinae.

Chapter 4.a. Phylogenetic Systematics

Abstract

Prior to this study the genus *Monostychia* comprised three species although it was generally recognized that the great diversity within the genus suggested the possibility of other taxa. In addition, *Monostychia* was tentatively placed within the subfamily Arachnoidinae (or Ammotrophinae). This analysis introduces several new characters such as internal buttressing and plate architecture to support the establishment of a new subfamily Monostychinae, five new genera and 15 new species. A cladistic analysis allows the testing of the validity of these new taxa and confirms that the subfamily Monostychinae is monophyletic and the four genera are placed within a new subfamily as separate clades.

Introduction

Systematics existed well before Darwin's *Theory of Natural Selection*. It was based on the principle that various organisms had a range of morphological characters in common (Hughes & Chapman 2001). Attempts were made at the time to organise the results into hierarchical groups. While some still see systematics as little more than classifying the surfeit of species according to morphological resemblances, since Darwin, there has been greater emphasis and need to use the commonality of characters to develop various hypotheses that ultimately express the phylogenetic relationship of various member species (McLennan & Brooks 2001). These two systems – morphological and phylogenetic – are fundamentally different in their purpose and each requires a clear understanding at the outset of how the information derived is to be used or else erroneous interpretations about relatedness and classification may result.

Phylogenetic systematics is based on the methodology of Hennig(1966) who argues that from analysis of the shared characters of a range of specimens, relationship patterns may be distinguished among the taxa. Using this methodology, a null hypothesis can be enunciated in which one assumes that as more and more characters are sampled, no consistent pattern of relationships will emerge. When such a pattern emerges the null hypothesis can be rejected in favour of the pattern (Funk & Brooks 1990).

An appraisal of the Hennig (1966) system suggests difficulties in applying phylogenetic systematics to the fossil record. Theoretically, the first principle of phylogenetic analysis states that there is only one true phylogeny (Adrain *et al.* 2001). Due chiefly to the gaps in the fossils record, it is impossible to accurately support this principle. There is also the issue that fossils rarely preserve the full range of characters (e.g., soft parts are absent and specifically in the case of Monostychioid echinoids, mouthparts and spines, which are important in the taxonomy of modern species). This poses a challenge when applying the method of phylogenetic reconstruction, which is an open-ended process where one can never have sufficient characters. Systematists using cladistics suggest that all characters should be treated with equal value, however, this seems untenable (Hughes & Chapman 2001).

The lack of completeness of the fossil record is a further test for applying a phylogenetic system since the latter requires that it contain only monophyletic groups (ancestral species and all their descendants) with every group formation established by demonstration of distinguishing (apomorphic) characters. However, there is no reliance on the degree of morphological resemblance as this is not equated to the phylogenetic relationship (Adrain *et al.* 2001). There are morphological variations within every species, or communities of reproduction. In

palaeontology, however, reproduction or genetics is not available for establishing species designation, leaving morphology to distinguish each species.

Some have suggested that morphological change within a species is more or less continuous and normally distributed (Nichols 1959). However, studies of modern sea urchins of the genus *Echinocardium* show that two seemingly discrete species from widely separated regions may have that morphological discrepancy obscured (David, *et al.* 1999). Further, the morphospace data in that study suggests that shape can be controlled more by geography than by species. As such, ecophenotypic plasticity is common and it is likely that many palaeontological taxonomists have confused it with speciation. In addition, some characters have remained unchanged through repeated speciation.

Finally, the possession of plesiomorphic (conserved) characters by different groups is not evidence of a close relationship. This is exemplified in the *Sea Urchin Genome Sequencing Project* (SUGSP) based in Houston, USA. The outcome of sequencing of a regular sea urchin, *Strongylocentrotus purpuratus* suggests a common ancestor with humans, albeit about 540My. Over 23,000 genes were identified, including 10-20 times the number of genes relating to innate immunity than the human genome (National Science Foundation 2006).

Materials and methods

Taxa. Eighteen species representing the six genera described in this thesis were included for detailed analysis. Except for *Monostychia australis* and *Phalangistychia loveni* the specimens used were the holotype for the species. With those two exceptions, individuals were chosen as they appeared to be representative of that species. In addition, *Ammotrophus cyclius* and

Arachnoides placenta were included as outgroups to establish character polarity. In both cases data for inclusion was gleaned from literature descriptions and not individual specimens.

Morphological characters used in analysis. Twenty-nine phylogenetically informative morphological characters were identified (Table 4.a.1.) to construct a character matrix (Table 4.a.2.). The methodology of taking measurements along with the description of some of the features has been described in Chapter 2. The choice of characters was based initially on the matrixes of both Kroh & Smith (2010) and Mihaljevic, *et al.* (2011) and augmented with data from this thesis. While most of the morphological characters were measured from holotypes or selected representatives as above, some characters required semi-destructive techniques (characters 1 and 2 in Table 4.a.1) and hence an alternative specimen was used. In addition, some characters required population data for maximum size (characters 4 and 21 in Table 4.a.1.) or means (character 28 in Table 4.a.1.).

Cladistic methods. A parsimony analysis of the taxon-character matrix was performed using PAUP V4.0a166 (Swofford & Bell 2017). Multistate characters based on linear or continuous characters were treated as ordered and these have been identified in Table 4.a.1. Initially all characters were given equal weight. The most parsimonious trees were found using a heuristic search algorithm with 1,000 random addition replicates to ensure the most parsimonious trees were identified. After this initial run, characters were reweighted. Additional replicate analyses were performed, and bootstrap and Bremer support values calculated.

Buttressing

1. Intermurum: Present (0); Absent (1).
2. Marginal buttressing: Absent (0); Simple second wall parallel to test margin with no significant interconnection (1); Complex microcanal system but limited to marginal 10% or less the width of test (2); Complex microcanal system extending beyond 10% width of test (3). [O].

Test Shape

3. Width to length ratio of test: Longer than wide (<93%) (0); Width equal to length (94%+) (1).
4. Maximum length of test: <10 mm (0); 10–24.9 mm (1); 25–39.9 mm (2); 40–59.9 mm (3); 60mm+ (4). [O].
5. Thickness of ambitus: Very tumid (rounded) (0); Tumid (1); Sharp (2); Very sharp (3). [O].
6. Oral surface of test: Completely flat from ambitus to ambitus (0); Generally flat but with rounded edges and slightly sunken near peristome (1); Distinctly sunken peristome and deep food grooves or broad concavity (2), [O].
7. Anterior of aboral surface of test between ambitus and apical disc: Convex (0); Flat (1); Concave (2). [O].
8. Ambital notch in posterior interambulacra (anal notch): Present (0); Absent (1).
9. Notch in ambitus at anterior perradial suture: Absent (0), Bevel only (1); Bevel and/or minor indentation (2); Distinct and deep (3). [O].
10. Notch in posterior perradial suture: Absent (0), Bevel only (1); Bevel and/or minor indentation (2); Distinct and deep (3). [O].
11. Ambulacral projection into peristome at perradius (peristomal point): No (0); Yes (1).
12. Keel between peristome and periproct (drooping tail): Absent (0); Present but indistinct, noticeable only adjacent to periproct (1); Present and distinct, extending at least 50% toward peristome (2). [O].
13. Wing-like projections of test at the posterior side of rear ambulacra: Present (0); Absent (1).
14. Wing-like projections at the boundary of rear ambulacra and interambulacrum 5: Present (0); Absent (1).

Petals

15. Petals inflated: Not inflated (0); Inflated (1).
16. Length of petal in ambulacrum II as a percentage of the distance from the apical disc to the margin: <50% (0); 50%–60% (1); 61%–70% (2); >70% (3). [O].
17. Openness of petal end in ambulacrum II: Lyrate (0); Petal ends are essentially parallel for the last 20–40% of their length (1); Petal ends continue to diverge (2). [O].
18. Shape of individual petal part: Strongly curved (0); Weakly curved to almost straight (1).
19. Pore pairs in lateral ambulacra appear to form a continuous arc: No (0); Yes (1).
20. Size of pores in a pair in comparison to each other: Outer pore no more than twice the width of the inner pore (0); Outer pore significantly wider and more slit-like (1).
21. Maximum number of pore pairs in petal (ambulacrum II): <10 (0); 10–19 (1); 20–29 (2); 30–39 (3); 40+ (4). [O].
22. Mean number of pores per mm of TL (measured from centre of apical disc to petal tip): <1.2 (0); >1.2 (1).
23. Trailing podia in anterior petal: Absent (0); Present (1).

Food grooves

24. Food grooves in ambulacra: Appear absent (0); Faint (1); Distinct (2); Very distinct (3). [O].
25. Food grooves extend aborally: No (0); Yes (1).
26. Combing: Absent (0); Present but muted or not always present (1); Strong and distinct (2). [O].

Plate architecture

27. Interambulacral plates first in contact with periproct: 2a/2b (0); 2a/3b or 3a/2b (1); 3a/3b (2); greater than 3 in either (3). [O].
 28. Width of ambulacrum II at ambitus as a percentage of the width of interambulacrum 1: <130% (0); 130–150%; >150% (2). [O].
 29. Position of periproct: oral and distant from margin (at least two times periproct diameter) (0); oral and not touching margin (but within two times periproct diameter) (1); inframarginal (but touching margin) (2); marginal (terminal) (3); aboral and not touching margin (4). [O].
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Table 4.a.1. List of morphological characters scored and data matrix used in the cladistic analysis. [O] = ordered state. Character numbers 1, 4, 9, 11, 12, 13, 14, 15, 19, 20, 21, 22, 23, 26 and 28 are novel to this study. Other characters are modified from those of Kroh & Smith (2010) and Mihaljevic, et al. (2011).

<i>Arachnoides placenta</i>	131?3	0?011	?0110	?2???	???11	21?4
<i>Ammotrophus cyclius</i>	131?1	0?122	?011?	?2???	???21	10?0
<i>Monostychia australis</i>	02031	12022	11111	11001	30021	1201
<i>Monostychia macnamarai</i>	02030	20122	11111	21001	40031	1211
<i>Monostychia alanrxi</i>	01031	10022	11111	11001	30031	1111
<i>Monostychia merrimanensis</i>	02010	10122	11111	11001	10021	0212
<i>Monostychia etheridgei</i>	??011	10022	11111	21001	10031	1222
<i>Monostychia glenelgensis</i>	02021	10122	01111	11001	30021	1221
<i>Monostychia robheathi</i>	02020	20122	12111	11001	30031	1222
<i>Quinquestychia mannumensis</i>	02042	00011	10111	12101	40021	2201
<i>Quinquestychia gigas</i>	02042	00011	10111	12101	40021	2101
<i>Quinquestychia berylmorrisae</i>	02042	00011	10110	22101	40021	2201
<i>Quinquestychia robertirwini</i>	02032	00011	10110	22101	40021	1211
<i>Rotundastychia pledgei</i>	03133	00001	10111	02101	30021	1201
<i>Rotundastychia aquilaensis</i>	03133	00001	10110	02100	20011	1201
<i>Rotundastychia eyriei</i>	03143	01001	10110	02101	20011	1222
<i>Deltoidstychia erioaster</i>	02123	02101	10000	02100	20011	0212
<i>Obscurostychia spirographica</i>	12123	01001	10110	12110	20100	0303
<i>Obscurostychia curtus</i>	12113	01001	00110	02100	10100	0303
<i>Phalangistychia loveni</i>	13143	02033	00111	00101	41031	2021

Table 4.a.2. Character data matrix of the 20 species used in this study.

Results

Phylogenetic results. The heuristic analysis of the data matrix generated 100 most parsimonious trees of 197 steps length, a consistency index of 0.513, a homoplasy index of 0.487, and a retention index of 0.715. Ten characters of greater weight. Sixteen characters were ordered and 13 unordered. A strict consensus tree (Fig. 4.a.1.) is taken as the best hypothesis. The consensus tree is presented as a cladogram rather than a phylogram to emphasise that it shows differences between species rather than representing their phylogeny. However, several tentative conclusions might be drawn.

The youngest species on the tree is *P. loveni*, (late Miocene). Prior to this study it was considered one of the three species of *Monostychia*. However, this cladogram suggests its affiliation is closer to *Arachnoides* than the Monostychinae. This may suggest that the position of the periproct in relation to the ambitus is not as phylogenetically significant as previously thought and not as significant as the plates first in contact with the periproct.

The oldest species grouping on the tree are the Eocene *O. spirographica* and *O. curtus*. These taxa are unlikely to have evolved from *Arachnoides* (Oligocene and younger), although Mihaljevic, *et al.* (2011) suggest from their study of *Clypeaster* that “the earliest fossil record of arachnoids must be missing”.

Within the Monostychinae, the oldest species are the late Oligocene/early Miocene *D. erioaster* and *R. pledgei* which coexist in the strata. The youngest species are the middle Miocene *M. macnamarai*, *M. alanrxi* and *Q. robertirwini*, all from the Nullarbor Limestone.

The monophyly of the Monostychinae is supported. Within the subfamily each of the genera are also monophyletic.

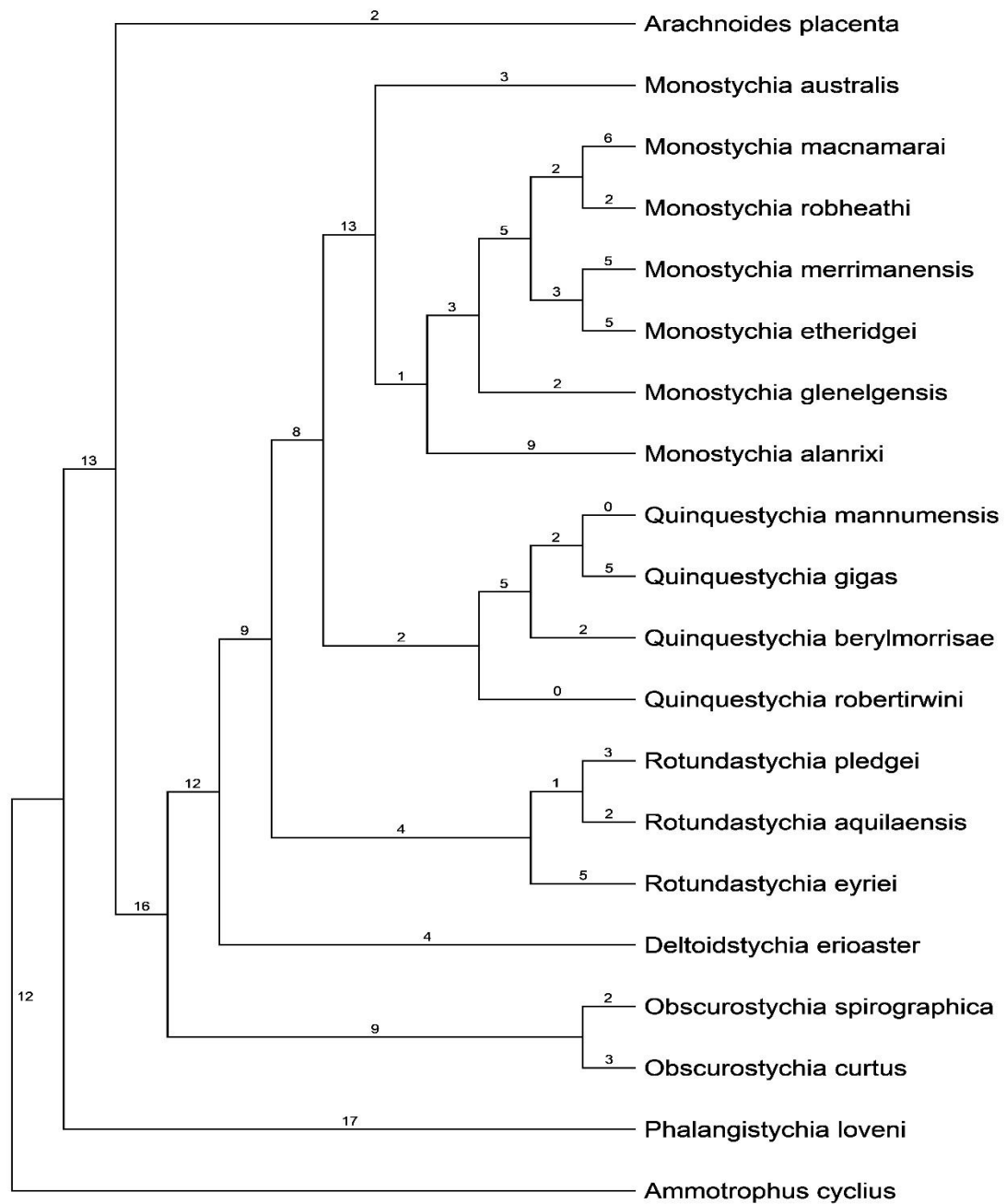


Fig. 4.a.1. Strict consensus tree found from parsimony analysis of data in Table 4.a.2. Trees have a length of 197 steps, a consistency index of 0.513 and a retention index of 0.715. Numbers next to nodes are the node at which the diversion occurred.

Internal buttressing. An intermurum, or intestinal buttressing, is present in all members of the subfamily Monostychinae but not in the *Arachnoides*, *Ammotrophus*, *Obscurostychia* or *Phalangistychia* and it is this feature that has been used to define the subfamily. Its presence has been established using a CT scan in *M. australis* and *D. erioaster*. In the other species of the subfamily its presence has been established using cross and transverse sections. The exception has been *M. etheridgei* where its presence has not been confirmed. Specimens of this species are rare, meaning that a destructive technique such as sectioning cannot be justified. It is very similar to *M. merrimanensis* in which the intermurum is reduced to three or four fine and fragile pillars. This, combined with the fact that many *M. etheridgei* specimens appear filled with a fine to coarse sand, suggests that the use of a CT scan is unlikely to prove useful.

Marginal buttressing is variable and its measurement more subjective. Except for *M. alanrivi* in which the buttressing is minimal, members of *Monostychia*, *Quinquestychia* *Deltoidstychia* and *Obscurostychia* possess a complex microcanal system that extends 5–10% from the margin. *Arachnoides*, *Ammotrophus*, *Rotundastychia* and *Phalangistychia* also possess a complex system but it extends further from the margin. The subjectivity of this feature is twofold. First, the buttressing varies considerably in each individual depending on where it is measured. It tends to be thinner anteriorly and thicker posteriorly. The measurements made in this study were at the midway point. Second, the choice of cut-off points of 5% and 10% are arbitrary. The buttressing in *Phalangistychia* extends substantially further than in the other species studied (up to 30%).

Test shape. Several separate features that jointly define test shape have been used. *Monostychia* and *Quinquestychia* are both longer than wide. *Rotundastychia*, *Deltoidstychia*, *Obscurostychia* and *Phalangistychia* all have a length essentially the same as the width.

The thickness of the ambitus also showed distinct differences between the genera. Although this feature has here been presented as a subjective comparison ranging from very tumid to very sharp, the thickness of each specimen was measured and compared to TL. *Monostychia* and *Ammotrophus* are both tumid to varying degrees while *Quinquestychia*, *Rotundastychia*, *Deltoidstychia*, *Obscurostychia*, *Phalangistychia* and *Arachnoides* have a sharp ambitus (to varying degrees).

The oral surfaces of *Quinquestychia*, *Rotundastychia*, *Deltoidstychia*, *Obscurostychia* and *Phalangistychia* are flat whereas in *Monostychia* the peristome and food grooves indent to varying degrees and the edge rounds toward the margin.

The curvature of the aboral surface differs only in a few species. In most cases the surface is convex but in *Rotundastychia eyriei* and the two *Obscurostychia* species, it is flat while in *Monostychia australis*, *Deltoidstychia erioaster* and *Phalangistychia loveni* it is concave.

The presence of a keel between the periproct and peristome appears to be restricted to the genus *Monostychia* while the presence of wings at both the posterior side of the rear ambulacra and between the rear ambulacra and interambulacrum 5 is restricted to the genus *Deltoidstychia*.

Petals. The shape of the petals is distinctive for the various groups. *P. loveni* is the only species in which the petals are lyrate. Species of *Monostychia* have petals that often have the outward appearance of being lyrate, however the inner line of pores tends to run parallel to each other for the distal 20% or more and the outer line of pores are often strongly curved leading to this false lyrate appearance. All the other genera in this study have petals that continue to diverge towards their ends.

The number of pores in the petal of ambulacrum II per mm of TL appears significant only for *P. loveni*. In that species the pores are large in number and packed closely together compared to the other species.

Trailing podia are present only in the genus *Obscurostychia*.

Food grooves. The major feature relating to the food grooves is the associated combing. In *Arachnoides*, *Phalangistychia* and *Quinquestychia* combing is strong and distinct (except for *Q. robertirwini* where it is muted). Combing is absent in *Obscurostychia* and *Deltoidstychia*. In *Ammotrophus*, *Monostychia* and *Rotundastychia* combing is present but always muted, indistinct or hard to find (although in *M. merrimanensis* it is not present).

Plating architecture. The basic test construction of all genera in this study, including *Ammotrophus* and *Arachnoides*, appears highly conserved with all species showing a similar basic plating arrangement. The interambulacral zones are disjunct from the basicoronal plate by a single pair of enlarged ambulacral plates. This basic structure is also common with *Clypeaster* (Mihaljevic, *et al.*, 2011) although the single ambulacral plate within the basicoronal ring is often much reduced in size. The plating architectural features that appear more phylogenetically significant are the positioning of the periproct and the total number of plates on the oral surface.

The periproct always opens on the oral surface in the four genera within the subfamily Monostychinae. This is also the case in *Ammotrophus* and *Phalangistychia*. In *Obscurostychia* the periproct is marginal and in *Arachnoides* it is aboral. For those genera in which the periproct is oral, the exact positioning varies. In *Ammotrophus* it is clear of the ambitus but for the other taxa it is always within one periproct diameter of the ambitus and often touching it. Within the Monostychinae, *Monostychia* and *Rotundastychia* have some species in which the periproct is

clear of the ambitus and some that touch the ambitus while no *Quinquestychia* species have the periproct touching the ambitus and in the only species of *Deltoidstychia* it touches the ambitus.

The positioning of the periproct in relation to the interambulacral plates that first come in contact with it may also be phylogenetically significant. For *Ammotrophus* and *Phalangistychia* these plates are 2a/2b. In *Obscurostychia* the plates are combinations of 4 (4a/3b, 3a/4b, 4a/4b) or more. The common plates within the Monostychinae are 3a/3b, however, in both *M. alanrxi* and *Q. gigas* the plates are recorded as 2a/3b. It is noteworthy that in all the species of this study there are substantial variations in plate numbers that first contact the periproct.

The total number of plates on the oral surface has been documented in detail in Chapter 4. However, this potentially diagnostic feature was not included in this cladistical analysis because of the variability and considerable overlap within and between species and genera. Scoring any one individual, or even all individuals studied, was likely to lead to having the feature rejected from the analysis as being of little use. One of the major issues with this feature is that there are potentially four paired interambulacra and four paired ambulacra that need to be counted on each specimen. It is common for plates to be counted only on a limited number of such segments in each individual meaning that a combination of numbers or even an average is of little value. Each plate number could, and frequently does differ, resulting in a combination of plate numbers for a given individual. While it is possible to see each of the nine plate regions (four for each of the paired interambulacra and ambulacra along with ambulacrum III) as separate features and record them accordingly, variation, particularly from one of the paired regions to another on the one individual, is more than diagnostically significant. As discussed previously, looking at a population and using a combination of the count of the paired interambulacral plates, paired

ambulacral plates and plates in ambulacrum III on the oral surface for a population may be quite useful taxonomically but does not neatly fit the methodology of cladistical analysis.

An inferred phylogeny of the taxa in this study is presented in Fig. 4.a.2.

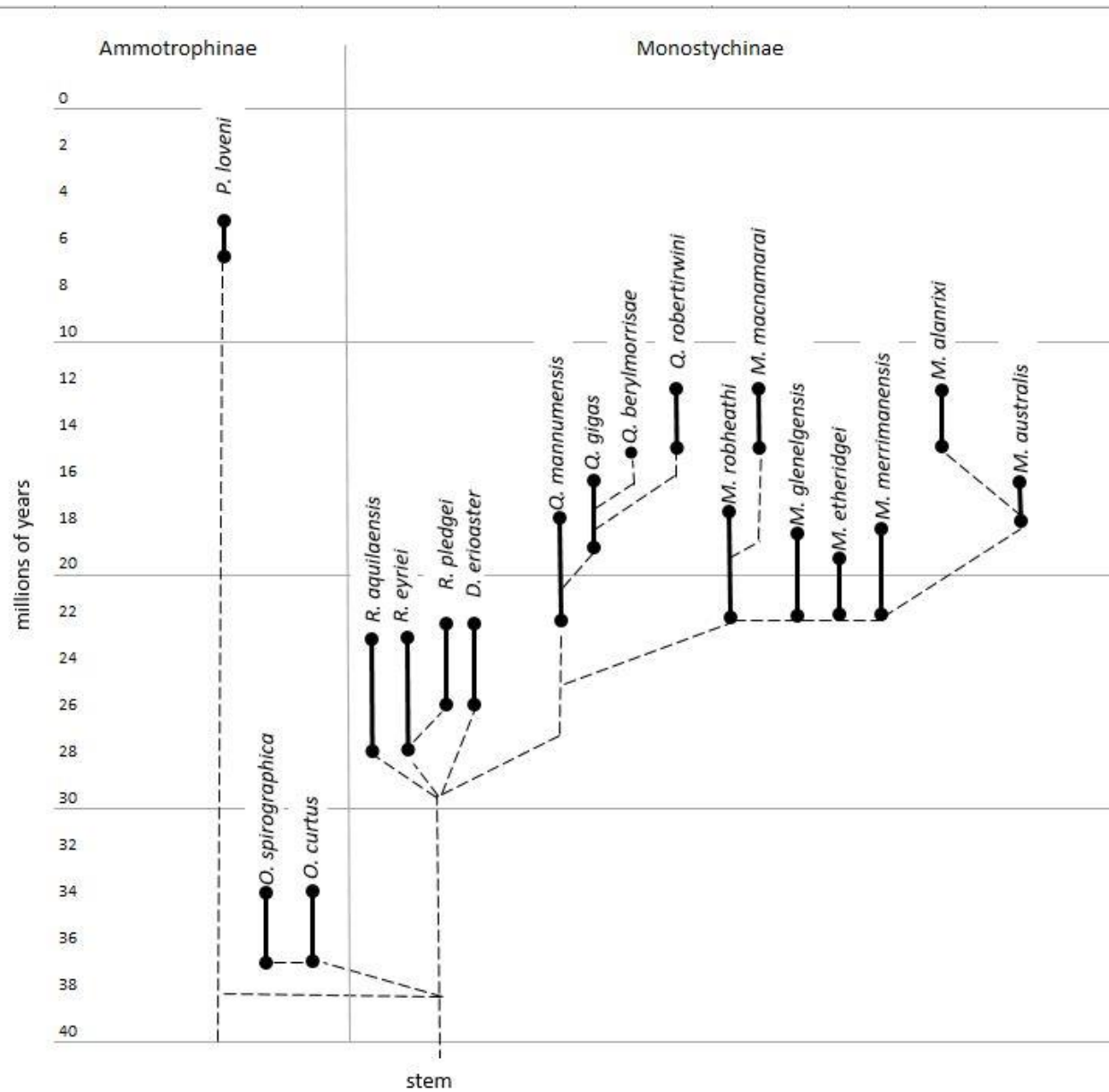


Fig. 4.a.2. Inferred phylogeny of the taxa in this study.

Conclusions

This systematics analysis has indicated strong support for the establishment of a new subfamily Monostychinae and for the four genera placed within. There is also support for the establishment of the genus *Obscurostychia*. The surprising result is the placement of *P. loveni*. For a species that has, until now, been placed within *Monostychia*, the magnitude of differences from *Monostychia* is noteworthy. This analysis only considered 29 morphological features and when several more subjective features are considered it is not surprising to see *P. loveni* close to *Arachnoides*. In relation to subfamilies, there is support to place *Obscurostychia* and *Phalangistychia* into the subfamily Arachnoidinae.

Chapter 5. Conclusions

The genus *Monostychia* was established by Laube in 1869. For most of the last 140 or so years it has been a genus of one major and two minor species. The major one, *M. australis* was an omnibus species: a taxonomic home for a wide range of genera and species with the commonality of a rounded to pentagonal, discoidal test and a submarginal periproct. The material comprising the type consists of six specimens. On close examination it was found that only two of those specimens could be confirmed as *M. australis*. Two others belong to the new genus and species *Q. mannumensis*. While Laube assumed the final two were simply juvenile forms of *M. australis*, the specimens are so lacking in diagnostic features they cannot be accurately placed taxonomically (although they are most likely juvenile forms of either *M. australis* or *Q. mannumensis* because of the location in which they were found).

The taxonomic hierarchy of *Monostychia* and its relatives appears clear cut in that they all reside within the order Clypeasteroida, family Arachnoididae. However, prior to this study, there remained substantial uncertainty over the subfamily and genus level of classification. Indeed, the uncertainty at subfamily level remains for genera such as *Arachnoides* and *Ammotrophus*. This study provided a resolution for *Monostychia* and its closest relatives by establishing a new subfamily - Monostychinae. During investigations of the internal structure of the tests it was discovered that a new structural feature, intestinal buttressing, was present. This feature was given the name 'intermurum'. It provides a wall between the proximal and distal segments of the gut and exists only on one side of the test. While its function is uncertain, it may provide stability for the gut in a high energy environment. The intermurum has not to date been found in specimens of *Clypeaster*, *Arachnoides* and *Ammotrophus* and is thus considered new to science.

In addition to this new feature, the former features separating subfamilies of Arachnoididae remain. For Monostychinae these features are: a) internal supports beyond the intermurum that are both marginal and around the peristome; and b) the periproct is submarginal but close to or touching the margin.

Prior to this study there was uncertainty as to whether the plates that make up the test were of taxonomic utility. Mooi (1989) had used the number of paired interambulacral plates on the oral surface to differentiate between *Monostychia* and *Ammotrophus*. Plate diagrams of the oral surface were also shown for a range of other genera. Durham *et al.* (1966) had also shown these plate diagrams and diagnostically used the interambulacral plates that first came into contact with the periproct. In both cases there was an assumption that the number of plates on the oral surface was fixed in number and did not change with ontogeny. This was seemingly at odds with the ocular plate rule, which describes how new plates are formed during growth and how they migrate down the test and beyond the 'equator'. It further assumed that there was no significant variation in plate numbers between species of the same genus or, by extension, between individual specimens of the same species. No studies had been done to substantiate these assumptions.

This study measured those plates across many individuals for the purpose of determining if such assumptions were correct. It found that the data did support the assumption that the number of plates (both interambulacral and ambulacral) did not change with increasing test size in *Monostychia* and its relatives that have been included in the Monostychinae. As a result, it was possible that counting plates had the potential to be useful diagnostically. It is likely that the sharp margin to the test makes migration around the margin too difficult. While it has not been established for other genera with sharp margins such as other members of the family Arachnoididae (and possibly of the order Clypeasteroida), it is likely to be the case.

However, the data did not support the assumption that within a given taxon (genus or species) a simple number of plates could separate groups within that taxon. *Monostychia* could not be separated from *Ammotrophus* in having six paired interambulacral plates on the oral surface versus seven. Instead, it was found to have between five and ten plates, although six to seven plates were the mode. Plate groupings could, however, provide some utility. Species within *Monostychia*, for example, could be separated

utilising a combination of the number of paired interambulacral plates, paired ambulacral plates and the number of plates in ambulacrum III, although rarely using plates alone.

The data collected from the numerous specimens that geographically ranged from the Eucla Basin of Western Australia to the Gippsland Basin of Victoria and temporally from the late Eocene of the Kingscote Limestone of Kangaroo Island to the late Miocene of the Black Rock Formation near Melbourne, showed that they could be readily divided into taxonomic groups well beyond the genus *Monostychia*. Five new genera were established. Two of those, *Obscurostychia* and *Phalangistychia*, lacked the intermulum that defined the subfamily Monostychinae and so have been left in the subfamily Ammotrophiae. The other three genera, *Quinquestychia*, *Rotundastychia* and *Deltoidstychia* all possessed the intermulum and so joined *Monostychia* in the subfamily Monostychinae.

Of the 18 species identified in this study 15 are new (Table 5.1.). *M. australis* and *M. etheridgei* along with *P. loveni* (formerly *M. loveni*) have been kept as original species. Of the others, five have been published during this study (*Q. robertirwini* was published as *M. robertirwini* and modified following further data collection from other species) and the remainder are yet to be published.

Name	Subfamily
<i>Monostychia australis</i>, Laube 1869	Monostychinae
<i>Monostychia macnamarai</i>, Sadler, Martin, & Gallagher, 2017	Monostychinae
<i>Monostychia alanruxi</i>, Sadler, Martin, & Gallagher, 2017	Monostychinae
<i>Monostychia merrimanensis</i>, Sadler, Holmes & Gallagher, 2019	Monostychinae
<i>Monostychia etheridgei</i>, Woods, 1877	Monostychinae
<i>Monostychia glenelgensis</i>, Sadler, Holmes & Gallagher, 2019	Monostychinae
<i>Monostychia robheathi</i>, sp. nov.	Monostychinae
<i>Quinquestychia mannumensis</i>, sp. nov.	Monostychinae
<i>Quinquestychia gigas</i>, sp. nov.	Monostychinae
<i>Quinquestychia berylmorrisae</i>, sp. nov.	Monostychinae

<i>Quinquestychia robertirwini</i>, (Sadler, Martin, & Gallagher, 2017)	Monostychinae
<i>Rotundastychia pledgei</i>, sp. nov.	Monostychinae
<i>Rotundastychia aquilaensis</i>, sp. nov.	Monostychinae
<i>Rotundastychia eyriei</i>, sp. nov.	Monostychinae
<i>Deltoidstychia erioaster</i>, sp. nov.	Monostychinae
<i>Obscurostychia spirographica</i> sp. nov.	Ammotrophinae
<i>Obscurostychia curtus</i>, sp. nov.	Ammotrophinae
<i>Phalangistychia loveni</i>, (Duncan, 1877)	Ammotrophinae

Table 5.1. A list of the species and genera identified in this study.

Finally, this study has demonstrated that, not surprisingly, substantial variation exists within any taxonomic group, particularly so in species. While at times it may be necessary due to lack of material to describe species from only one or two specimens, large numbers of specimens are usually required to establish robust diagnostic tools for identification. In the case of *Monostychia* and its relatives there have always been ample specimens available both in Australian museums and easily accessible from the field.

Chapter 5.a. Future avenues of investigation

Much progress has been made during this study in the understanding of the taxonomic breadth of *Monostychia* and its relatives in the Cainozoic strata of southern Australia. However, there is still more to be done. While this study established that in members of the subfamily Monostychinae the number of plates on the oral surface does not change with test size, that finding alone suggests two further questions.

First, in relation to the Monostychinae, at what point in the ontological development do the plates become fixed? Little work has been done on the ontology of these species and although little or no comment has been made in this thesis, it does appear that there is much to be learnt, even beyond the time at which plates become fixed. For example, in *Monostychia*, the TL of the test at sexual maturity appears to be in the range of 9–13 mm and after sexual maturity the shape of the adoral section of the test begins to rise and change from concave to flat and often slightly convex. These and other ontological observations could be substantiated for *Monostychia* and the other genera in the subfamily.

Second, while the fixing of the plates has been established for Monostychinae it also needs to be established for other members of the family Arachnoididae, and indeed order Clypeasteroida. If the plates are fixed in those taxa the plates and the plate relationship with the periproct needs to also be established as there is the potential that these are diagnostically important.

While this study used a parsimony analysis using PAUP V40a166 it would be interesting to re-analyse the data using Bayesian analysis. In addition, a re-analysis of the data using a multivariate approach to the determination of the character variance would be interesting. As this study used 29 informative characters, the support values recorded were low. A re-analysis of the

specimens using other techniques, including extending CT scanning, may provide additional characters that could improve those support values and hence consolidate the taxa discussed.

During this study many specimens were amassed from the field or located in the reference collections of various museums. There are numerous examples of specimens that did not fit neatly into the various taxa under study. Some of these are identified in Table 5.a.1. In most cases the potential new taxa are represented by too few specimens to provide certainty in a new description or the specimens are of poor quality and do not show enough of the characters needed for identification. However, in some, there are large numbers of reasonable quality that show such variability that it will require more time than was available in this study to establish new taxa. Working through that list one species at a time may help future researchers in completing the task.

Suggested genus	Subfamily	Formation	Location
Species A (<i>Quinquestychia</i>?)	Monostychinae	Nullarbor Limestone	Eucla, WA
Species B (new genus A)	Ammotrophinae?	Kingscote Limestone	Kingscote, SA
Species C (new genus B)	Ammotrophinae?	Kingscote Limestone	Kingscote, SA
Species D (<i>Monostychia</i>?)	Monostychinae		Muddy Creek, Vic
Species E (<i>Monostychia</i>?)	Monostychinae	Black Rock Formation	Mordialloc, Vic
Species F (<i>Monostychia</i>?)	Monostychinae		Melton, Vic
Species G (<i>Monostychia</i>?)	Monostychinae	Fossil Bluff Limestone	Wynyard, Tas
Species H (<i>Monostychia</i>?)	Monostychinae		Flinders, Vic
Species I (new genus C)	Ammotrophinae?	Port Vincent Limestone	Wool Bay, SA
Species J (new genus C)	Ammotrophinae?	Port Vincent Limestone	Wool Bay, SA
Species K (<i>Monostychia</i>?)	Monostychinae		Orbost, Vic

Table 5.a.1. Potential species and genera yet to be described from Cainozoic strata of southern Australia.

Species A is a small flat test from the Nullarbor Limestone of the Nullarbor Plain. Fewer than 10 specimens are held at the Geological Survey of Western Australia and they are of poor quality. The specimens have been labelled as *M. australis* but differ in their petal shape and may belong to *Quinquestychia*. The specimens are difficult to find and extract with most coming from various caves or road cuttings across the Plain.

Species B and C are from the same or adjacent strata as *Obscurostychia* at the type locality of the Kingscote Limestone, Kingscote, Kangaroo Island. One is very large and although frequently found in transverse section, the specimens are always badly fractured and to date it has proven impossible to extract a whole specimen. Even though sections have been found it remains uncertain as to whether an intermulum is present. The other is much smaller and while around the size of *Obscurostychia*, it has a submarginal periproct, not circular in shape and has a different petal shape.

Species D has been reported as *M. australis* from Muddy Creek, Victoria. Only small numbers of poor specimens have been available to date.

Species E is from the same strata as *P. loveni* (Black Rock Formation, Mordialloc, Victoria) however it is much smaller, lacks the deep indentations of *P. loveni*. Its shape is more akin to *Monostychia* or *Quinquestychia*. Only one specimen has been sited.

Species F is from Melton, Victoria. Substantial numbers are available for study in Museum Victoria. They are small, rounded and poorly preserved, lacking most surface features required for taxonomy.

Species G is from Fossil Bluff, Tasmania, the same strata as *M etheridgei*. However, its features are more like *M. australis* than *M. etheridgei*. Only a single specimen appears in collections.

Species H is from Flinders, Victoria. Only a single specimen is available although it is in good condition. It appears to be clearly a *Monostychia* but does not belong to any of the currently named species. The locality from which it originated was due to become a housing estate and so acquiring additional specimens may be problematic.

Species I and J are from the Port Vincent Limestone of Wool Bay, South Australia. The cliffs of Wool Bay contain very large numbers of easily accessed specimens. While one new genus and species was identified in this study it is apparent that there are other genera and species to be described from this site. Most specimens are small with structural and surface detail often difficult to ascertain. A full understanding of the echinoids of this site is possibly worthy of a separate research higher degree study.

Species K is from Orbost, Victoria. As with species H it is represented by a single specimen but one of good quality.

Finally, while this study did include a minor foray into CT scanning, that technology has advanced markedly and continues to do so. With so many undescribed species lacking surface features or difficult to extract, CT scanning should be utilised more in future studies. The internal structure of the intermural, peripheral buttressing and around the peristome appear to be important in the taxonomy of this group and such features will become more accessible using CT scanning. In addition, the classification of extant species appears heavily reliant upon features of the eating apparatus which to date has been limited with extinct species. It is probable that the

eating apparatus is present in many of these fossils but difficult to see or extract without damage. CT scanning could be used to add details of this feature and reduce the gap that currently exists between the taxonomy of extant and extinct species.

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Appendices

Appendix abbreviations

Lgth	Length of specimen
Wdth	Width of specimen
A/wp	Distance from the anterior to the widest point
Hght	Height of specimen
A/ad	Distance from anterior to apical disc
A/apex	Distance from anterior to highest point
A/ps	Distance from anterior to peristome
L/petal amb II	Length of petal in ambulacrum II
Dist margin amb II	Distance from apical disc to margin at ambulacrum II
L/petal amb I	Length of petal in ambulacrum I
Dist margin amb I	Distance from apical disc to margin at ambulacrum I
P amb II	Number of pore pairs in one petal segment of ambulacrum II
P amb I	Number of pore pairs in one petal segment of ambulacrum I
ThAm	Thickness of anterior margin
ThPm	Thickness of posterior margin
Amb ambit	Width of ambulacrum I at ambitus
IntAmb ambit	Width of interambulacrum 1 at ambitus
Width amb III at ambit	Width of ambulacrum III at ambitus

Appendix Table 1. Abbreviations for linear data tables. All measurements in mm. (except pore numbers which are whole numbers).

IntAmb 5	Plates in contact with periproct excluding plate in contact with peristome
IntAmb 2	Number of post-basicoronal plates in interambulacrum 2
IntAmb 3	Number of post-basicoronal plates in interambulacrum 3
IntAmb 4	Number of post-basicoronal plates in interambulacrum 4
IntAmb 1	Number of post-basicoronal plates in interambulacrum 1
Amb III	Number of post-basicoronal plates in ambulacrum III
Amb II	Number of post-basicoronal plates in ambulacrum II
Amb IV	Number of post-basicoronal plates in ambulacrum IV
Amb V	Number of post-basicoronal plates in ambulacrum V
Amb I	Number of post-basicoronal plates in ambulacrum I

Appendix table 2. Abbreviations for plate data tables. All measurements in whole numbers.

Appendix 1. Raw linear data

Number (SAM)	Lgth	Wdth	A/wp	Hght	A/ad	A/apx	A/ps	L/petal amb II	Dist margin amb II	L/petal amb I	Dist margin amb I	P amb II	P amb I	ThAm	ThPm	Amb ambit	IntAm ambit	Width amb III ambit
29608-1	43.9	41.2	21.0	8.8	22.34	22.34	22.5	10.93	22.40	10.80	24.06	33	34	3.0	1.5	12.79	12.26	14.25
29608-2	41.9	38.8	18.4	9.6	21.87	20.33	21.4	8.85	21.94	11.03	22.76	32	36	2.8	1.7	12.73	10.79	14.58
29608-3	41.9	37.9	18.8	8.1	21.84	20.27	20.9	11.40	21.00	10.21	22.35	29	38	2.9	1.8	11.70	10.76	13.11
29608-4	42.0	37.2	25.2	9.3	21.18	21.18	20.4	11.34	20.56	11.14	22.41	33	36	2.8	1.9	12.53	10.92	13.96
29608-5	41.1	38.4	18.0	11.6	21.31	21.31	20.0	12.15	21.53	12.94	23.46	28	28	3.2	1.9	12.48	8.59	13.72
29608-6	41.9	38.0	18.8	11.0	21.47	21.47	20.3	12.09	21.44	11.71	23.09	37	40	2.6	1.5	13.78	8.62	14.48
29608-7	40.7	36.6	19.3	8.6	21.15	21.15	20.5	10.00	20.11	10.70	21.41	32	35	2.6	1.8	13.70	10.15	13.94
29608-8	39.7	35.6	18.0	8.4	19.98	19.98	19.6	9.56	19.45	10.92	21.89	31	34	2.7	1.4	12.54	9.61	13.44
29608-9	39.1	37.0	19.5	8.3	20.63	20.63	19.9	8.45	20.05	9.76	21.62	31	32	2.5	1.8	12.25	10.05	13.34
29608-10	39.4	35.4	23.2	8.0	20.26	20.26	19.9	9.54	19.52	9.85	21.40	31	35	3.0	2.1	12.58	9.25	12.31
29608-11	37.2	34.6	20.0	8.3	18.08	18.08	17.9	8.98	18.65	9.60	21.45	24	29	2.6	1.6	10.87	9.52	11.77
29608-12	34.3	30.5	17.9	7.3	17.86	17.86	16.1	8.45	16.74	8.82	18.31	30	33	2.3	1.4	10.26	8.19	10.90
29608-13	36.3	32.7	19.5	9.0	19.04	19.04	17.5	11.24	18.33	9.02	19.33	30	25	2.5	1.9	10.78	8.40	11.94
29608-14	32.8	31.0	15.2	7.5	17.20	17.20	16.2	9.59	16.51	8.19	17.91	21	29	2.8	1.6	10.52	8.34	10.68
29608-15	36.4	33.0	16.2	8.1	18.07	18.07	17.4	8.51	17.64	9.56	19.84	30	33	2.8	1.8	11.41	8.75	12.24
29608-16	39.9	35.5	21.7	7.4	19.96	19.96	18.6	10.18	18.49	9.70	20.53	33	38	3.0	1.6	11.88	10.28	12.73
29608-17	33.9	31.7	14.7	7.8	18.09	18.09	17.9	9.72	17.54	8.47	18.20			2.5	1.9	10.45	8.10	12.21
29608-18	32.5	29.0	14.0	7.8	17.20	16.46	15.9	7.59	16.15	8.62	17.40	29	32	2.8	2.0	10.73	7.84	10.94
29608-19	38.5	34.9	17.1	10.0	20.65	20.65	18.2	9.20	18.73	10.60	21.18	34	33	3.0	2.0	12.47	9.57	12.67
29608-20	33.2	30.0	16.0	7.6	16.87	16.87	16.1	7.50	16.08	8.86	17.52	31	31	2.8	1.7	10.36	8.26	10.74
29608-21	35.6	32.2	16.0	7.3	18.75	18.75	17.3	9.24	17.46	9.46	19.14	32	35	2.8	1.8	10.74	8.83	11.99
29608-22	37.0	33.3	23.4	6.7	18.86	18.86	18.5	9.44	18.18	9.06	20.06	34	38	2.4	1.6	11.26	7.62	12.47
29608-23	36.4	33.5	17.9	7.9	18.14	18.14	17.7	7.80	17.77	9.79	18.77	28	29	2.8	2.0	11.99	8.15	12.40
29608-24	28.5	26.5	13.0	7.0	14.56	14.56	14.0	7.48	13.43	6.95	14.95	26	27	2.8	2.1	10.26	6.56	9.70
29608-25	37.8	32.7	20.1	8.4	18.55	18.55	18.1	8.43	17.71	11.05	20.00	31	35	3.0	1.9	11.61	9.56	11.32
29608-26	31.1	29.0	14.2	6.4	15.75	15.75	15.2	8.64	15.54	7.44	16.88	31	31	2.3	1.5	9.22	7.81	10.69
29608-27	32.8	30.9	17.3	6.4	17.47	17.47	16.6	8.14	16.22	8.69	16.99	27	37	2.1	1.6	9.95	8.79	10.40
29608-28	39.7	36.9	18.4	8.7	20.63	20.58	20.0	10.03	19.53	10.74	20.61	36	39	2.8	1.8	12.28	9.94	13.18

29608-29	29.4	27.1	15.0	7.8	15.54	15.54	14.1	7.47	15.21	7.42	16.03	24	27	2.2	1.6	9.38	7.05	9.52
29608-30	34.0	30.3	16.5	8.6	18.04	18.04	16.2	7.13	17.10	8.65	18.28	31	31	2.3	1.9	10.61	8.11	11.10
29608-31	34.1	30.9	14.3	6.4	17.41	17.41	16.8	9.09	16.47	7.90	17.41	26	26	2.6	1.9	10.29	8.17	11.33
29608-32	32.6	29.5	14.5	6.1	16.83	16.83	15.9	8.25	16.31	8.70		32	33	2.1	1.5	9.17	8.49	10.48
29608-33	32.5	29.6	18.4	6.1	16.68	16.68	16.6	8.51	15.43	7.31	17.17	28	30	2.8	1.7	9.65	8.36	10.62
29608-34	34.5	31.6	16.6	7.3	17.77	17.77	17.2	8.90	16.67	8.43	18.30	28	31	2.5	1.7	10.74	8.62	11.05
29608-35	33.0	29.9	16.9	6.5	16.37	16.37	16.0	10.62	16.24	9.14	17.68	29	31	2.7	1.7	10.80	7.65	11.21
29608-36	29.8	26.0	13.5	7.3	15.59	15.59	14.9	7.23	14.10	8.10	15.78	27	29	2.7	1.8	9.25	6.24	9.99
29608-37	32.0	28.9	14.6	6.7	16.45	16.45	16.2	7.84	15.35	7.73	17.22	26	27	2.6	1.9	10.47	7.76	10.81
29608-38	33.3	30.0	14.4	7.9	17.53	17.53	16.9	7.20	15.50	8.48	17.38	32	32	2.8	1.6	9.99	7.54	11.46
29608-39	28.8	26.2	14.0	6.4	14.87	13.75	14.8	7.00	13.76	6.10	14.99	24	27	2.2	1.6	7.90	7.04	9.09
29608-40	29.3	26.9	12.1	8.2	14.82	15.20	14.3		15.02	8.79	16.67	28	30	2.6	1.5	8.93	7.18	9.32
29608-41	28.9	26.4	13.0	7.3	14.74	14.74	14.6	5.92	14.19	7.22	15.20	26	29	2.2	1.5	8.89	7.26	9.54
29608-42	32.2	29.1	14.0	9.3	16.48	16.48	15.5	8.92	15.08	9.85	16.99	30	33	3.0	1.9	8.54	7.76	10.55
29608-43	29.0	27.8	15.0	6.4	14.70	14.70	14.3	8.55	14.33	7.05	15.54	28	28	2.3	2.1	9.26	7.21	9.41
29608-44	30.5	27.2	15.0	7.5	14.30		14.3	8.11	14.12		15.34	34	36	2.8	1.9	8.30	6.79	10.03
29608-45	33.0	30.3	15.7	8.2	17.73	17.73	16.9	7.60	15.56	8.27	16.92	30	32	3.2	2.0	10.77	7.75	12.16
29608-46	27.2	24.3	13.0	4.8	13.23	13.23	13.0	6.67	12.53	5.76	14.02	19	21	2.0	1.4	7.86	6.68	8.76
29608-47	26.8	24.2	12.8	5.3	13.57	13.57	13.3	8.25	12.06	6.40	12.64	31	29	2.0	1.4	8.07	6.66	8.96
29608-48	27.6	23.7	14.0	5.4	14.06	14.06	13.3	6.67	12.29	7.01	13.73	27	31	2.5	1.6	8.13	6.84	8.47
29608-49	26.3	24.1	11.9	6.0	13.61	13.61	13.1	6.96	12.45	7.00	13.47	25		2.3	1.7	9.21	6.60	8.77
29608-50	28.2	26.3	15.9	5.4	14.15	14.15	13.4	7.49	13.50	6.85	15.24	23	20	2.4	1.6	8.24	7.47	8.85
29608-51	26.3	24.5	12.1	6.3	13.16	13.16	12.9	6.03	12.49	6.81	13.40	27	30	2.0	1.4	7.70	6.79	8.69
29608-52	27.3	23.7	13.4	6.2	13.27	13.27	13.8	7.00	12.22	6.73	13.72	22	24	2.8	2.1	8.05	6.49	8.44
29608-53	31.9	29.3	15.1	6.4	16.26	16.26	15.5	7.48	14.81	8.70	16.89	28	32	2.4	1.5	9.58	7.86	10.94
29608-54	26.7	23.5	17.6	5.3	12.86	12.86	13.0	5.04	12.12	5.87	14.46	27	27	2.5	1.6	8.08	6.09	8.36
29608-55	29.5	26.9	14.3	6.1	15.48	15.48	14.9	9.50	14.54	6.45	15.63	23	23	2.3	1.8	9.43	7.00	10.05
29608-56	25.0	22.6	12.4	6.5	12.63	12.63	12.3	5.93	12.27	5.92	13.07	19	21	2.3	1.5	7.94	5.55	8.31
29608-57	25.6	23.0	13.6	5.8	12.74	12.74	12.5	6.37	12.70	6.21	13.40	21	22	2.6	1.7	6.70	6.50	8.57
29608-58	23.2	20.5	13.9	5.0	11.29	11.29	10.9	5.70	10.57	6.02	11.77	20	19	2.8	1.8	6.72	4.86	7.00
29608-59	24.5	22.3	11.1	4.8	12.28	12.28	12.0	4.93	12.15	5.61	13.17	19	23	2.0	1.2	7.46	5.78	8.01
29608-60	23.5	21.1	12.6	5.8	11.73	11.73	11.3	6.37	11.39	6.08	12.51	24	24	2.3	1.5	6.82	5.24	7.68
29608-61	30.6	27.4	16.8	6.7	15.75	15.75	14.7	6.90	14.73	6.79	15.91	22	23	2.8	1.9	9.34	7.14	9.71
29608-62	23.4	22.0	12.0	*	11.64	11.64	11.7	6.56	12.11	6.00	12.52			2.4	1.9	7.85	5.14	7.87
29608-63	23.3	21.9	11.0	5.3	11.83	11.83	11.3	6.62	11.29	5.13	12.44	22	25	2.2	1.6	7.04	5.66	8.28
29608-64	21.4	19.0	10.1	4.5	9.95	9.95	9.9	5.79	9.51	4.80	10.75	18	18	2.7	2.0	6.93	5.07	6.95
29608-65	22.2	19.2	13.9	4.6	10.45	10.45	10.5	4.61	9.03	5.12	10.20			2.3	1.5	6.63	5.87	7.35
29608-66	21.5	19.6	10.6	5.0	10.41	10.41	10.7	5.13	10.18	5.33	10.95	22		2.4	2.1	6.59	5.24	6.29
29608-67	18.3	16.4	9.7	4.4	9.26	9.26	8.3	3.88	8.81	4.68	9.92	21	20	2.6	2.0	5.78	3.79	5.98

29608-68	18.4	17.2	9.2	3.4	8.74	8.74	8.7	4.83	8.77	3.81	8.77	17	18	1.8	1.5	5.71	4.15	4.84
29608-69	18.4	16.9	10.4	3.7	8.74	8.74	8.8	3.99	8.36	4.20	9.10	17	18	2.3	1.6	5.09	4.02	5.73
29608-70	15.1	13.7	8.2	4.0	7.32	7.32	7.3	4.45	6.88		6.92			1.7	1.6	4.18	3.47	4.96
29608-71	17.2	15.2	7.3	3.9	7.86	7.86	8.1	4.35	7.75	4.81	8.82	16	20	1.9	1.5	5.38	3.90	5.60
29608-72	15.1	13.9	7.0	3.6	7.12	7.12	7.6	3.53	7.06	3.90	7.48	15	17	1.7	1.5	4.54	3.55	5.25
29608-73	11.7	10.8	6.1	2.9	5.62	4.90	5.8							1.4	1.4	3.68	2.60	4.49

Appendix 1.1. Raw linear data for *M. australis*.

Number (WAM)	Lgth	Wdth	A/wp	Hght	A/ad	A/apx	A/ps	L/petal I amb II	Dist margin amb II	L/petal I amb I	Dist margin amb I	P amb II	P amb I	ThA m	ThP m	Amb ambit	IntA m ambit	Width amb III ambit
16.1	36.43	27.33	12.89	7.45	17.41	11.87		8.57	17.85			18						
16.11	42.05	31.27	17.88	9.34	21.00	10.80	20.29			11.43	20.03		34	6.61	4.55	13.67	9.09	13.76
16.12	33.67	26.13	13.94					9.39	13.31	9.17	14.09			4.76	4.20			
16.13	28.97	22.39	11.56		14.69	10.41				8.45	13.50			3.83	2.93	9.16	6.16	8.73
16.14	41.64	32.28	19.6	8.28	21.13	12.54	20.24	11.59	18.46	11.87	19.32	34	34	5.53	4.69	13.25	7.45	15.10
16.15	40.01	29.97	17.76	9.07	19.56	14.00		10.93	16.63	10.82	20.09	32	34	5.05	3.75	11.84	7.97	12.78
16.16	33.39	26.81	24.43	6.57	16.56	10.16	16.03	9.23	15.64	9.48	16.24	26	33	4.51	3.55	9.94	6.05	11.84
16.17	31.61	24.14	12.75	8.47	15.57	11.58		8.63	13.97	9.27	14.46	28	29	4.32		9.11	6.60	10.15
16.18	34.90	26.35	14.35	7.53	17.29	11.93	17.80	8.84	14.82	10.57	17.25	32	36	4.92	2.75	10.63	6.64	11.01
16.19	35.81	27.18	25.27	7.59	18.20	12.53	17.12	10.50	14.19	10.28	17.43	28	38	4.07	2.85	10.94	7.36	11.05
16.2	39.00	30.08	15.68	8.62		12.31	19.10							4.87	3.10			
16.20	41.28	31.65	18.25	9.35	20.23	17.18	20.92	12.56	18.12	12.32	20.86	33	37	4.62	3.85	11.15	7.90	12.60
16.21	40.38			9.62	21.06	15.19	19.72							5.56	3.41	12.05	7.52	12.97
16.22	37.46	28.05	15.66	7.66	18.93	12.32	18.60	11.08	17.01	9.70	17.30	33	29	4.58	2.59	11.66	8.10	11.06
16.23	38.52	29.98	15.71	9.75	19.37	13.46		10.58	17.00	11.06	19.54	28	35	5.14	2.92	12.02	8.38	12.57
16.24	34.46	26.57	14.69	8.52	16.39	11.73	17.31	9.95	14.86	11.24	16.78	34	35	4.81	2.98			11.47
16.3				7.97	18.33	13.71	17.41	10.57	15.90			30		4.97				
16.4	37.47	29.22	15.89	8.22	18.37	14.30	19.14	10.99	16.01	11.14	17.95	35	37	4.77	3.93	10.49	8.74	
67.337	33.13	26.78	15.71		16.21			9.14		10.01		28	28	2.32				
89.35a	36.84	28.94	18.31		18.56		18.58							4.15	3.09			
89.35b	34.39	29.95	14.59															11.54
89.37b	38.69	29.43	16.8	7.57	19.03	11.41		11.30	16.08	10.77	18.10	33	36	4.52	3.45	11.65	7.87	
89.37d	36.77	28.37	15.18	8.05	18.23	12.64	18.67	10.81	14.51	9.40	17.24			5.04	3.18	11.35	7.56	10.83
89.37e		27.64	14.9	7.49	16.41	11.14	16.93	10.55	14.28	10.09	16.72	32	35	4.39				

89.37g	36.97	27.05	15.16	8.37	18.14	10.89		11.12	14.92	10.67	16.94	37	36	5.01	3.49			10.80
91.15.1	29.17	24.58	12.52		14.19		13.47	9.19		8.66		32	32	2.27	1.59			
91.17a	35.78	28.00	16.51		17.00		17.61	10.76		10.43			35	3.75	2.42			
91.17b	35.59	26.83	16.1		17.06		16.89	11.51		12.08		33	34					
91.17c	37.18	29.48	14.87					11.56		11.49		40	41					

Appendix 1.2. Raw linear data for *M. macnamarai*.

Number (WAM)	L gth	W dth	A/ wp	H ght	A /ad	A/ apx	A /ps	L/p etal amb II	D ist marg in amb II	L/p etal amb I	D ist marg in amb I	P am b II	P am b I	Th Am	Th Pm	A mb ambit	Int Am ambit	Wi dth amb III ambit
16.25	28.59	24.76	14.96	5.23	13.51	10.40	13.02	7.84	12.85	8.42	14.96	25	28	3.23	2.81	8.33	6.75	9.21
16.26	29.15	24.37	12.83	5.62	13.70	11.77	14.36	7.52	13.00	7.97	15.12	21	24	2.36	2.09	7.90	6.66	9.04
16.27	31.82	25.90	13.37	5.13	16.52	10.32	15.84	8.57	14.58	7.76	15.31	27	26	3.09	2.25	9.84	6.76	10.56
16.28	31.68	27.96	13.57	6.51	15.97	13.75	15.50	8.58	15.06	8.86	16.96	27	30	2.74	2.41	9.19	7.32	10.60
16.5	30.69																	9.75
16.6		24.48	19.93	5.45	14.59	11.83	13.97	7.57	13.38	8.39	14.05	24	27	2.49				
88.925a	27.53	23.61	12.93		12.60			7.79		8.21		24	25	3.25	2.14			
88.925b	41.27							11.62		13.74		35	36	5.33	3.71			
88.925c	26.51	22.34	12.95	5.00	12.42		12.55							2.49	1.80			
91-15-2	33.13	28.72	13.37	6.60	16.05	15.42	16.09	9.46	16.23	9.09	17.92	28	30	3.70	3.17	10.73	7.11	12.12

Appendix 1.3. Raw linear data for *M. alanrxi*.

Number (SAM)	Lgth	Wdt h	A/wp	Hght	A/ad	A/apx	A/ps	L/petal amb II	Dist margi n amb II	L/petal amb I	Dist margi n amb I	P am b II	P am b I	ThAm	ThPm	Amb ambit	IntAm ambit	Width amb III ambit
P33713-1	19.53	16.69	9.52	4.80	10.30	7.19	9.57	6.14	9.05	6.13	9.84	18	23	2.94	2.21	6.09	4.34	5.93
P33713-2	15.24	13.04	7.25	4.28	7.33	7.31	7.33	4.93	6.57	4.78	8.96	16	18	3.01	2.58	4.49	3.60	4.55
P33713-3	17.05	14.60	8.16	4.08	8.30	5.84	7.86	4.92	7.50	4.92	8.66	15	16	3.12	2.12	4.97	3.44	4.88
P33713-4	13.54	11.53	7.09	3.32	6.66	5.33	6.66	3.67	5.56	3.84	6.53	14	15	2.48	1.85	4.05	2.74	4.24

P33713-5	15.21	12.97	9.50	3.90			7.01							2.35	1.98	5.03	2.67	3.91
P33713-6	14.56	12.35	6.91	3.47	6.65	6.00	6.74	3.53	6.47	3.51	7.00	13	13	2.39	2.10	4.21	3.04	4.42
P33713-7	13.80	11.79	6.50	3.52	6.55	5.92	6.74	3.81	6.20	3.89	6.59	13	14	2.77	1.99	4.04	2.72	4.70
P33713-8	13.72	12.28	6.73	3.40	6.89	5.59	6.82	4.14	6.55	4.24	6.39	13	14	2.33	1.94	4.96	2.66	4.89
P33713-9	13.85	11.85	7.22	3.87	7.30	5.81	6.88	3.50	6.58	3.45	6.47	13	14	2.15	1.84	4.44	2.42	4.85
P33713-10	13.78	11.83	6.52	3.91	6.95	5.56	6.47	4.19	6.39	4.07	6.76	13	15	2.79	2.12	3.72	2.73	4.83
P33713-11	13.58	12.08	7.36	3.21	6.97	6.04		3.96	6.13	3.21	6.97	13	13	1.89	1.62	4.06	2.81	4.26
P33713-12	10.12	8.64	5.39	2.58	4.69	4.17	4.90	2.30	4.48	2.77	4.68	9	10	1.59	1.41	3.39	2.65	2.99
P33713-13	15.38	13.07	7.33	4.34	7.44	6.43	7.16	4.73	7.55	4.83	8.19	13	17	2.31	1.86	4.29	2.60	5.14
P33713-14	14.10	11.92	6.85	4.14	7.04	5.35	6.57	4.22	6.26	4.57	6.91	13	13	2.61	2.37	4.43	3.27	4.57
P33713-15	11.96	10.40	5.77	2.88	6.01	5.02	6.19	3.06	5.22	2.78	5.88	12	11	1.98	1.41	3.47	2.85	3.54
P33713-16	11.79	10.23	6.04	2.93	6.28	4.74	5.94	2.96	5.76	3.36	5.79	12	13	1.78	1.47	3.76	2.39	3.38
P33713-17	10.36	8.96	5.32	3.01	5.23	3.87	4.78	2.90	4.97	2.96	5.51	13	13	1.79	1.50	2.98	2.35	2.87
P33713-18	10.58	8.98	5.11	2.29			5.04							1.75	1.20	3.26	2.19	3.21
P33713-19	10.77	9.28	5.59	2.81	5.69	4.47	5.11	2.80	5.17	2.50	5.35	10	10	1.85	1.55	3.22	2.02	2.74
P33713-20	17.62	14.73	8.21	4.67	8.77	7.85	8.37	4.86	8.43	5.05	8.66	16	20	2.45	2.15	5.32	3.76	5.25
P33713-21	18.37	16.15	9.71	4.26	9.36	7.19		5.19	8.13	5.10	9.22	15	16	2.31	2.13	5.83	4.27	5.11
P33713-22	15.79	12.96	7.37	4.05	8.14	6.56	7.38	4.18	6.98	4.13	8.46	13	13	2.55	1.78	4.53	3.16	4.72
P33713-23	18.20	15.24	8.37	4.64	8.83	6.64	8.75	5.45	8.88	5.21	8.58	15	15	3.07	2.00	5.10	3.01	5.94
P33713-24	12.82	10.87	5.83	4.00	6.60	5.29	6.48	3.91	5.97	4.05	6.42	13	14	2.48	1.67	3.96	2.21	3.79
P33713-25	14.39	12.64	6.76				6.68							2.54	2.22	5.05	2.70	
P33713-26	6.38	5.78	3.30	1.94														
P33713-27	9.42	8.12	4.07	2.93	4.40	3.87	4.47	2.42	4.06	2.52	4.59	10	10	2.13	1.77	3.08	2.56	2.18
P33713-28	9.24	8.32	4.72				4.71							1.46	1.25	2.95	1.72	2.76
P33713-29	9.51	8.46	5.29				4.86							1.72	1.62	3.38	1.70	3.08
P33713-30	10.46	9.22	6.77											1.66	1.21	3.36	2.67	3.27
P33713-31	12.74	10.47	5.61				5.85							1.95	1.25	3.68	2.66	3.76
P33713-32	16.76	14.38	9.46	3.79	8.34	6.64		4.44	7.69	4.41	8.47	15	17	2.27	1.71	5.23	2.91	4.82
P33713-33	15.00	13.39	6.76	4.21	7.53	5.65	7.15	4.62	7.51	4.87	7.93	15	16	2.51	1.96	4.45	3.29	4.80
P33713-34	18.55	16.11	8.75	4.09	9.30	7.05	9.31	5.42	8.72	5.26	9.90	16	17	2.56	1.90	5.25	3.79	5.41
P33713-35	14.69	12.63	7.70	3.91	7.37	6.47	6.82	4.09	7.28	4.10	7.48	13	14	2.41	1.69	4.07	3.29	4.50
P33713-36	10.81	9.05	5.17	2.83	5.37	3.98	5.37	3.05	5.22	2.70	5.15	11	10	1.71	1.51	2.98	2.26	3.22
P33713-37	15.44	13.04	8.60	3.07	7.86			3.81	7.33	3.43	7.56	13	13	2.20	1.50	4.70	3.39	4.15
P33713-38	16.48	13.96	8.11	4.28	8.26	6.91	7.90	4.16	7.43	4.68	8.42	15	17	2.67	2.01	4.91	2.94	4.88
P33713-39	10.04	8.26	4.32	2.52	5.13	4.28	4.69	2.60	4.86	2.64	5.08			1.73	1.60	2.55	2.07	2.31
P33713-40	10.21	8.32	5.26	3.27	5.36	4.33		3.00	4.59	3.04	4.96	10	12	1.89	2.00	2.44	1.90	2.94
P33713-41	10.63	8.73	4.80	2.84	4.82	5.10	5.29	2.27	4.46	3.25	5.89	9	10	1.81	1.57	3.13	2.70	2.86
P33713-42	19.26	16.85	9.17	5.26	9.21	8.50	9.64	5.17	9.09	5.58	9.16	15	17	2.69	2.11	5.64	4.12	4.76
P33713-43	12.61	11.26	8.86				6.09							1.98	1.55	4.21	3.25	3.75

P33713-44	11.45	10.12	7.06				5.78	2.76	5.06	2.78	5.30			1.32	1.28	3.35	2.51	3.11
P33713-45	9.61	8.10	5.27	2.53	4.85	3.95	4.91	2.25	4.13	2.42	4.69	9	10	1.59	1.22	2.58	1.88	2.68
P33713-46	11.74	9.86	5.14	2.86	5.80	4.42	5.44	3.06	4.90	2.93	5.10	9	12	1.77	1.30	3.99	2.47	3.63
P33713-47	12.12	9.44	6.40	2.98	5.56	4.82	5.66	2.24	4.78	3.28	5.36	10	12	2.21	1.58	3.66	2.30	2.91
P33713-48	10.71	8.95	4.88	2.83	5.17	3.76	5.24	2.58	4.40	2.50	4.66	10	11	1.86	1.27	3.10	2.34	3.17
P33713-49	21.43	18.29	9.33	4.84	10.95	8.53	10.17	6.09	10.36	5.58	10.54	16	16	2.80	2.01	6.39	4.11	6.67
P33713-50	18.52	16.16	9.60				9.00							2.29	1.80	5.67	4.06	5.31
P33713-51	15.03	12.65	7.47	3.61	7.45	5.61	7.26	3.85	7.03	3.38	6.69	13	14	2.11	1.91	5.16	3.18	4.02
P33713-52	14.82	12.80	6.78	3.14	6.91	6.07	7.18							1.86	1.42	4.50	3.27	4.10
P33713-53	14.06	11.33	6.06	3.44			6.53							2.02	1.70	4.16	2.89	3.80

Appendix 1.4. Raw linear data for *M. merrimanensis*.

Number	Lgth	Wdth	A/wp	Hght	A/ad	A/apx	A/ps	L/petal amb II	Dist margin amb II	L/petal amb I	Dist margin amb I	P amb II	P amb I	ThAm	ThPm	Amb ambit	IntAm ambit	Width amb III ambit
TMAG Z504	21.0	19.3	15.2	5.3		8.19												
MV P128077	19.03	17.18	12.72				9.54											
MV P128078	17.95	15.83	8.58	3.04	8.48			4.71	8.08	4.92	8.5	12	15	2.14	1.51			
MV P135101	15.39	13.6	7.52	3.06	7.42			4.13	6.82	4.13	7.05	10	12	1.75	1.57			
MV P27351	13.29	11.07	6.78	2.16	6.69		6.8	3.82	5.05	3.97	6.9	14	17	1.24	1.25			
MV P27352	15.9	14.44	7.7	3.56	8.28		8.02	5.86	7.53	5.48	7.44	15	17	2.2	1.55			
MV P27353	8.21	7.3	5	2.43	3.97		4.35							1.5	1.55			
MV P27354	14.57	11.81	7.34		6.94													
MV P27358	12.28	10.41	6.32	3.09	6.07		5.6	3.72	6.04	3.34	5.52	14	16	1.78	1.95			
MV P320411	17.6	16.42	11.03	2.74	8.87		8.78	5.18	8.17	4.44	9.16	16	18	1.82	1.59			
MV P82434	11.21	9.46	5.61	2.79	5.29		5.86	3.06	4.49	3.06	5.55			1.96	1.48			
MV P82435	13.02	11.61	5.78	2.6	6.47		6.45											
SAM P33715	11.78	11.21	8.24	2.8	5.86	5.75	5.82	3.19	5.79	3.25	6.06	13	13	1.62	1.23	3.95	2.39	4.56
SAM P33716	13.23	11.31	7.26	3.23	6.94	6.94	6.64	4.74	5.89	4.77	6.68	17	18	2.24	1.66	4.62	2.09	4.59

Appendix 1.5. Raw linear data for *M. etheridgei*.

Number	Lgth	Wdth	A/wp	Hght	A/ad	A/apx	A/ps	L/petal amb II	Dist margin amb II	L/petal amb I	Dist margin amb I	P amb II	P amb I	ThAm	ThPm	Amb ambit	IntAm ambit	Width amb III ambit
SAM P33714-1	24.14	19.11	10.78	5.90	12.34	10.89	11.46	5.96	11.00	6.24	12.05	21	25	2.90	1.96	8.13	4.00	7.39
SAM P33714-2	31.14	24.41	13.23	6.85	15.93	12.76	15.36	8.14	13.93	8.25	15.56	30	31	2.83	2.41	10.38	6.61	8.75
SAM P33714-3	17.34	15.49	10.23	3.83	8.77	7.28	8.57	3.94	8.39	4.13	8.90	16	19	1.65	1.25	5.51	3.79	5.87
SAM P33714-4	34.11	29.56	15.83	8.00	17.79	15.12	15.89	9.70	15.69	9.72	17.62	26	27	3.62	2.59	9.97	7.62	10.74
SAM P33714-5	24.41	19.76	18.37	5.09	12.35	11.62	11.97	6.08	10.90	5.73	12.34	25	24	2.11	1.59	8.23	4.95	7.78
SAM P33714-6	26.41	22.83	16.66	5.63	12.85	12.10	12.96	7.18	12.41	6.71	13.51	22	26	2.79	1.92	8.29	5.67	8.72
MV P147941	23.52	20.49	12.82	4.96	11.99	11.30	10.90	6.04	11.07	6.12	12.33	19	20	2.22	1.74	7.69	4.18	7.48
MV P27030A	31.35	25.85	14.11	7.31	15.21	14.64	15.08	7.42	14.62	8.51	16.24	22	30	3.24	2.48	10.38	6.06	9.84
MV P27030B	24.99	21.03	16.93	6.19	12.29	12.11	12.22	6.12	11.66	6.28	13.65	21	21	2.59	2.08	7.61	5.50	7.33
MV P27375	31.64	27.11	13.56	7.70	15.43	15.43	16.05	8.61	14.21	8.49	16.65	25	27	3.26	2.47	10.47	6.51	10.70
MV P27376	18.88	15.33	13.52	4.14	8.95	8.26	9.09	4.78	7.82	5.07	9.60	19	22	2.25	1.57	6.12	3.64	5.87
MV P27377	30.19	25.76	13.16	7.88	15.71	14.99	14.90	8.26	14.54	8.84	15.91	24	28	3.27	2.26	9.30	5.77	9.60
MV P27378	28.46	22.26	20.54	6.28			13.43									8.71	4.65	8.16
MV P27379	28.55	23.21	20.81	6.05	14.25	12.50	13.72	6.78	12.70	7.39	13.86	24	26	2.76	2.40	7.46	5.44	9.33
MV P27384	27.31			6.28	13.25	13.25	13.29	7.03	12.18	7.22	13.38	20	24	2.73	2.41	9.19	5.71	8.83
MV P27385								8.46	15.41	7.31	15.00	17	21	2.60		9.30	5.38	
MV P305221	27.17	23.56	17.48	5.68	13.65	12.72	12.95	6.99	12.70	6.95	14.05	25	28	2.07	1.71	7.98	6.20	8.80
MV P305223		24.20	14.96	6.13	15.32	13.20	14.75	7.08	12.86									
MV P305224	26.11	22.33	19.40	5.23	12.61	12.90	12.84	5.73	12.20	5.83	13.43	21	22	2.25	1.62	7.56	5.19	9.24
MV P305225	33.31	26.94	15.69	8.37	17.38	15.39	15.93	10.22	15.45	11.68	17.16	29	31	3.23	2.78	10.98	6.84	10.52
MV P305226	25.93	21.99	15.94	6.02	13.23	12.26	12.96	6.89	12.17	6.97	13.01	22	26	2.50	1.97	7.07	5.87	8.52
MV P305227	24.85	20.30	12.34	6.14	12.68	11.16	12.47	6.72	11.83	7.55	12.63	22	26	2.96	2.04	7.33	4.64	7.50
MV P305228	23.71	20.58	9.78	5.08	12.51	11.16	11.81	5.53	11.13	5.44	12.16	19	21	1.99	1.38	6.88	4.60	8.40
MV P305244A	21.47	19.72	12.65	4.73	10.81	9.98	10.02							2.46	2.09	9.70	6.36	7.53
MV P305245	27.26	23.56	11.18	6.99	14.11	13.19	13.65	7.53	13.18	7.17	13.96	25	27	3.18	2.41	9.23	5.42	8.40
MV P305246	17.24	15.22	7.74	3.79	8.48	7.87	7.90	3.74	8.20	4.24	8.64	16	17	1.70	1.36	5.15	3.50	5.65
MV P306714A	32.64	27.65	14.49	5.60	16.40	15.68	16.09	7.32	15.18	8.07	16.93	19		2.65	1.91			10.11
MV P306714B	29.15	26.66	13.75	5.44	14.55	14.55	14.08							1.98	1.83	7.82	6.13	9.25
MV P306714C	23.54	19.57	15.08	5.80	11.81	10.48	11.04	5.77	11.04	5.52	12.23	19	19	2.43	1.70	6.99	4.74	
MV P317117	18.88	17.42	9.00	4.81	9.74	9.23	9.00	4.03	9.45	4.23	10.42	15	16	2.15	1.58	7.02	3.84	6.51

Appendix 1.6. Raw linear data for *M. glenelgensis*.

Number (SAM)	Lgth	Wdth	A/wp	Hght	A/ad	A/apx	A/ps	L/petal amb II	Dist margin amb II	L/petal amb I	Dist margin amb I	P amb II	P amb I	ThAm	ThPm	Amb ambit	IntAm ambit	Width amb III ambit
P33717	33.8	26.6	25.32	7.14	16.63	13.24	16.15	8.74	14.71	7.86	16.43	30	30	4.46	2.26			
P33718	32.07	23.92	13.86	5.8	15.49	13.46	15.57	8.13	13.11	7.96	15.12	30	32	3.31	2.59	9.93	5.2	9.97
P33719	29.3	24.26	19.55	5.66	13.85	13.66	14.6	6.42	12.74	6.52	15.49	26	26	3.63	1.64	9.82	5.97	9.66
P33720	27.15	22.19	11.81	6.06	13.54	12.2	13.24	7.21	12.29	7.1	13.03	25	25	2.18	1.11	8.88	5.51	8.71
P33721	23.48	20.31	13.42	4.83	11.77	11.11	11.08	6.08	10.97	5.47	12.05	23	26	2.37	1.74	7.31	5.15	8.46
P33722	23.69	21.17	10.9	5.04	12.11	11.46	11.22	6.01	13.20	5.59	11.65	19	19	1.82	1.65	7.81	4.95	7.77
P33723	18.19	16.16	12.45	3.88	8.65	8.21	8.82	4.41	8.51	4.39	9.40	22	22	1.61	1.1	5.58	4.16	6.21
P33724	14.03	11.61	7.45	3.16	6.81	6.03	6.5	3.47	6.34	3.44	6.89	15	14	1.47	1.08	4.56	3.33	4.24
P33725	31.57	25.68	13.77	6.76	15.41	11.8	15.73	8.41	14.34	8.46	15.46	30	29	3.69	1.99	11.04	6.06	10.99
P33726	34.1	28.76	15.66	7.03	17.59	15.43	16.51	9.26	15.75	10.34	17.34	30	35	3.24	1.93	12.12	5.99	13.18
P33727	35.96	28.54	15.32	6.04	18.38	16.67	17.25	9.66	16.41	9.13	17.28	28	28	2.73	2.25	11.93	6.94	12.08
P33728	35.46	28.64	20.22	7.6	17.21	17.52	17.47	9.04	15.57	8.45	17.32	30	33	2.96	1.89	11.51	8.52	11.26

Appendix 1.7. Raw linear data for *M. robheathi*.

Number	Lgth	Wdth	A/wp	Hght	A/ad	A/apx	A/ps	L/petal amb II	Dist margin amb II	L/petal amb I	Dist margin amb I	P amb II	P amb I	ThAm	ThPm	Amb ambit	IntAm ambit	Width amb III ambit
SAM P22600-1	67.27	60.93	28.97	10.79	35.67		35.34	15.94	32.50	15.82	36.80	38	38			19.88	17.07	20.77
SAM P22600-2	69.78	63.52	30.23	14.65	36.59		35.01	20.41	34.95	18.51	38.17	41	42			20.06	17.65	16.54
SAM P22638																		
SAM P29665	42.67	37.71	18.18	5.66	21.77		21.95	9.64	20.01									
SAM P29667	47.25	41	20.57	6.81	23.32		23.83											
SAM P29672-1	55.67	50.05	23.88	7.03	28.65		28.00	14.03	26.04	13.55	29.41	28	32			15.88	13.7	15.93
SAM P29672-2	66.45	59.15	30.95					14.44	31.32	14.49	35.52							
SAM P29883	42.28	37.87	17.8	5.23				9.97	19.76	9.59	23.05					11.75	10.28	11.62
SAM P4776	71.46	63.24	31.83		37.28			16.88	32.60	16.92	38.05	35	36			19.33	17.12	
SAM P4776-1	39.81	35.31	17.86	6.33	20.76			9.23	18.50	9.77	20.09							
NHML EE1146	54.28	50.06	38.29	10.44	26.95	25.88	26.07	14.85	25.66			38		2.88	1.87			
NHML EE1153	52.96	47.7	32.11	8.86			26.92							3.09	2.1			
Qm P1001	71.77	68.58	31.06	9.4	35.32	36.12		17.75	33.90	17.08	40.48	39	46	1.98	0.99	20.92	18.06	21.92

Qm P1002	2	62.5	57.39				37.23									18.96	17.03	
Qm P1003	67.95	58.1	52.75				31.37							2.63	1.42	19.07	16.54	18.54
Qm P1004	73.74	67.41	33.37				38.23									21.83	19.74	21.46

Appendix 1.8. Raw linear data for *Q. mannumensis*.

Number (SAM)	Lgth	Wdth	A/wp	Hght	A/ad	A/apx	A/ps	L/petal amb II	Dist margi n amb II	L/petal amb I	Dist margi n amb I	P am b II	P am b I	ThAm	ThPm	Amb ambit	IntAm ambit	Width amb III ambit
P29623	85.33	76.62	45.71	16.71	41.67	48.59	44.24	21.31	39.86	21.62	45.72	43	48	4.01	2.32	26.88	22.15	28.6
P29624	70.29	63.49	30.75	13.87	36.74	35.29	37.05	17.26	33.71	17.57	37.61	32	38	3.38	1.99	22.44	16.87	21.85
P29625	71.34	63.35	36.92	15.74	36.20	31.57	35.49	18.41	31.27	19.68	40.06	39		2.37	1.32	21.06	15.86	22.26
P29626	86.76	76.21	38.26	18.22	44.28	41.00	43.96	21.81	41.74	22.49	47.36	46	52	4.09	1.92	26.66	19.99	28.68
P29627	70.89	63.02	30.62	11.77	37.48	35.60	36.45	18.11	33.61	16.76	36.27	38	37	2.9	1.29	20.94	15.63	22.64
P29628	86.45	75.87	38.66	11.08	44.37	44.37	43.93	18.58	38.98	19.91	46.64	43	51	2.28	1.28	25.99	20.78	
P29629	67.26	60.51	29.75	13.14	35.60	35.12	34.13	15.96	33.51	15.6	35.07	40	44	2.74	1.28	19.63	16.73	20.65

Appendix 1.9. Raw linear data for *Q. gigas*.

Number (SAM)	Lgth	Wdth	A/wp	Hght	A/ad	A/apx	A/ps	L/petal amb II	Dist margi n amb II	L/petal amb I	Dist margi n amb I	P am b II	P am b I	ThAm	ThPm	Amb ambit	IntAm ambit	Width amb III ambit
P29609	81.32	67.59	35.00	17.20	40.95	45.00	41.57	21.4	36.91	23.25	41.60	45	51	4.06	2.38	22.93	19.39	23.39
P29610	80.46	68.35	35.08	9.72	41.33	40.07	41.24	20.01	35.83	20.77	39.84	45	48	3.84	2.74	22.34	21.23	24.24
P29611	72.04	59.47	31.24	11.44	37.45	29.51		20.65	30.23	18.88	35.40	39	35	4.82	2.81			
P29612	68.25	55.81	29.83											4.51	2.83			
P29613	56.4	46.7	26.00	10.90	29.53	30.53	28.71	16.3	25.24	14.97	28.58	38	42	3.74	2.59	16.54	15.05	15.34
P29614	52.64	42.95	23.45	8.20	26.73	24.57	26.34	13.31	24.16	14.36	27.93	34	35	2.41	1.8	15.66	12.89	16.33
P29615	51.16	42.91	22.14	13.60	26.56	27.12	26.63	15.73	23.74	15.58	27.33	37	44	4.31	3.41	15.73	12.89	17.17
P29616	51.02	41.2	21.99	7.96	26.00	25.87	25.81	13.63	21.64	13.41	24.98							
P29617	56.92	49.61	24.64	10.92	28.37	28.22	27.32	13.08	26.53	13.8	30.06	37	36	2.6	1.52	16.74	15.17	
P29618	51.75	43.67	22.04	9.74	27.05	26.04	26.31	14.89	23.78	16.13	26.20	32	38	3.21	1.93	15.33	12.92	
P29619	66.89	59.42	29.12	10.16	34.01	33.82	34.06	16.27	31.46	15.69	35.27	34	35	3.73	1.81	19.47	15.72	20.84

P29620	77.27	63.13	33.25	11.01	39.28	39.68	38.83	19.3	32.68	18.81	37.60	45	41	4.11	2.47			
P29621	58.91	51.52	25.67	11.98	31.46	29.56	31.02	17.46	27.55	17.26	30.70	41	45	3.41	2.7	17.18	14.87	17.27
P29622	65.25	53.61	28.51	12.43	34.26	35.00	33.33	17.7	29.33	17.49	32.64	48	50	3.68	2.83	18.69	16.42	17.82

Appendix 1.10. Raw linear data for *Q. berylmorrisae*.

Number (WAM)	Lgth	Wdth	A/wp	Hght	A/ad	A/apx	A/ps	L/petal amb II	Dist margin amb II	L/petal amb I	Dist margin amb I	P amb II	P amb I	ThAm	ThPm	Amb ambit	IntAm ambit	Width amb III ambit
16.1	41.20	37.94	16.88	5.90	20.58	16.61	19.46	10.39	19.44	11.06	22.26	32	34	2.63	1.98			
16.3	41.98	33.47	18.23	7.53	20.67	15.88	20.98	13.34	19.18	13.95	22.16	38	40	3.54	2.21	13.65	9.80	13.88
16.4	39.30	32.07	17.38	5.38	20.29									2.27	1.75	11.94	8.37	11.48
16.8	52.72	43.77	23.29	8.65	26.91	20.50	26.38	16.63	23.50	16.75	26.54			4.26	3.12	16.70	12.07	18.01
16.9	37.03	32.91	16.34	5.85	18.89	14.69		10.93	18.00	10.97	19.62	36	36	2.32	1.61			11.79
16.29	38.57	30.96	14.97	6.87	18.16	15.32		9.70	16.44	11.40	18.41		42	2.98	1.51	11.28	7.80	11.52
16.31	40.92	34.71	16.93	7.18	20.07	15.42	20.24	10.66	18.32	10.91	21.12	28	34	2.75	1.99	13.21	8.38	13.55
16.32	35.36	30.32	15.14	6.66	18.11	13.37		10.51	16.47	10.59	17.95	31	37	3.18	2.98	12.16	7.90	10.87
16.33	37.48	32.72	16.53	6.68		12.97								3.21	2.75	11.55	8.11	13.11
16.34	28.78	25.37	12.09	3.80	13.68	11.78	14.20	8.38	13.35	7.29	14.87	35	31	1.92	1.19	9.45	6.67	9.76
16.35	46.38	39.02	19.4		23.42	16.71	23.37							2.92	1.84	15.41	11.78	14.16
16.36	41.27	35.73	17.3	7.22	20.23	19.19	21.26	11.97	19.45	12.36	22.03	37	41	2.77	1.51	13.61	8.29	15.16
16.37	36.90	31.62	15.58	5.46	17.95	18.00	18.48	11.37	17.60	10.14	18.69	38	33	2.32	1.31	12.77	7.37	12.80
16.38	40.00	34.06	17.65	6.03	19.04	15.23		10.84	17.75	10.65	20.39	36	41	2.88	1.92	11.71	10.10	13.90
16.39	46.59	39.57	19.15	6.59	22.16	14.86	22.06	13.48	20.55	14.40	22.27	36	41	2.84	2.04	12.26	9.32	13.17
16.41	29.96	26.32	14.24	4.95	14.88	13.42		7.36	13.35	7.39	15.9	29	29	1.57	1.25	11.11	7.13	8.41
16.42		38.57	18.59	6.14	21.82	15.91	22.10	10.95	20.05	11.28		38	38	2.05		12.72	10.28	13.13
89.37a	48.23	39.51	18.71	6.93	21.92	21.51	22.40	13.20	20.58	12.61	24.33	42	46	2.75	2.08	14.41	12.09	15.96
89.37c		42.31	21.64	5.70	24.25	17.08	23.40	11.71	21.14			42		2.24				14.45
89.37f	44.46	38.09	18.4	6.22	21.48	15.50	21.82	11.92	19.82	14.68	24.65			2.84	1.99			
89.37-l	51.11	44.66	21.92		25.32	20.74				15.21	29.21		48	3.01	2.00			
91.15.3	42.36	36.67	17.73	7.32	21.29	17.00	21.73	11.31	19.32	10.26	21.71	36	33	2.63	1.85	14.02	9.56	13.90

Appendix 1.11. Raw linear data for *Q. robertirwini*.

Number	Lgth	Wdth	A/wp	Hght	A/ad	A/apx	A/ps	L/petal amb II	Dist margin amb II	L/petal amb I	Dist margin amb I	P amb II	P amb I	ThAm	ThPm	Amb ambit	IntAm ambit	Width amb III ambit
SAM P 29637	41.88	42.82	31.95				21.54											
SAM P 29638	32.03	32.87	25.89	3.84	16.18	14.91	16.74							1.36	0.84	9.10	8.29	8.61
SAM P29630	50.53	49.83	30.12	5.19	25.76	23.87	25.47	10.92	25.35	11.04	27.47	30	30	1.53	0.96	14.42	13.41	10.80
SAM P29631	46.91	46.11	30.25	6.06	23.54	23.54	23.23	10.35	22.98	10.3	25.68	32	31	1.43	1.11	14.05	10.71	14.61
SAM P29632	48.20	46.69	29.18	6.56	24.14	23.12	24.99							1.54	1.78	14.56	13.29	13.08
SAM P29633	36.14	36.53	17.24	4.35	17.97	14.28	18.44	7.54	18.58	7.63	19.93	23	23	1.13	1.15	9.73	9.26	10.10
SAM P29634	48.54	48.99	29.92	7.7	24.55	24.55	24.44	11.84	24.15	11.04	26.50	32	35	1.3	1.33	13.53	11.90	15.53
SAM P29635	32.39	31.67	19.67	4.06	16.66	16.37	16.47	7	16.02	7.18	18.34			1.14	0.87			
SAM P29636	30.57	30.13	16.63				14.61									8.42	6.80	9.38
SAM P29639	43.80	44.15	31.59		21.46	20.27		8.82	20.66	10	24.81	26	29					
SAM P29640	43.37	43.10	33.96											1.74	1.12			
SAM P29641	41.60	41.30	26.12		20.93	20.69		9.16	20.91						1.00	11.40	9.86	
SAM P33729	42.07	43.48	25.4				21.17											
NHML EE 2112	50.26	51.85	33.65	6.48	26.50	26.5	26.28							1.49	1.19			
NHML EE 2113	66.06	64.52	30.71	6.31	34.12	32.52	34.26	13.56	32.34	16.94	36.86	36	38	1.67	1.39			
NHML EE 2114	60.19	58.09	28.46				30.31											
MV P18294	34.16	33.21	18.17		17.43	15.1		7.37	16.88	6.86	18.56	25	25	1.02	0.92	9.88	9.07	9.47
MV P33721	41.87	40.10	26.23	5.66	20.26	18.23	20.39	9.52	19.81			24		1.56	0.86	10.58	9.96	11.29

Appendix 1.12. Raw linear data for R. pledgei.

Number (SAM)	Lgth	Wdth	A/wp	Hght	A/ad	A/apx	A/ps	L/petal amb II	Dist margi n amb II	L/petal amb I	Dist margi n amb I	P am b II	P am b I	ThAm	ThPm	Amb ambit	IntAm ambit	Width amb III ambit
P33733	19.61	19.53	8.9	2.3	9.2	8.94	9.2	3.65	9.68	3.5	10.46	18	18	0.99	0.72	5.14	4.98	5.20
P33734	20.68	20.49	11.98	2.86	10.04	9.16	9.79	3.97	9.98	4.22	10.90	15	16	1.2	0.83	5.77	5.84	6.23
P33735	20.20	20.44	11.57	2.74			9.05	5.37	9.58	5.25	10.83			0.92	0.77	5.19	4.69	5.26
P33736	16.39	16.53	8.14	2.27	7.83	7.97	7.64	3.11	8.34	3.16	8.91	15	16	1.01	0.78	4.34	4.27	
P33737	13.51	14.19	9.56	1.5	6.91	6.09	6.71	2.36	7.32	2.05	7.66	12		0.8	0.77	3.56	2.82	4.22
P33738	11.24	11.94	6.2	1.58			5.59							0.77	0.71	3.55	3.06	3.34
P33729	20.79	21.43	10.21	3.04	10.41	9.69	10.18	4.42	10.70	4.5	11.11	20	20	1.37	0.85	5.90	5.76	6.65

P33730	24.89	25.48	16.63	3.59	11.88	11.32	11.97	6.00	12.58	5.49	14.08	23	23	0.91	0.82	7.41	5.45	8.78
P33731	29.30	28.73	12.68	3.83	14.39	12.31	14.77							1.03	0.89	7.76	6.71	10.85
P33732	29.97	29.67	14.66	4.32	14.63	14.21	15.57	8.45	14.69	8.14	16.21	25	26	1.14	1.08	9.54	8.31	9.70

Appendix 1.13. Raw linear data for *R. aquilaensis*.

Number	Lgth	Wdth	A/wp	Hght	A/ad	A/apx	A/ps	L/petal amb II	Dist margin amb II	L/petal amb I	Dist margin amb I	P amb II	P amb I	ThAm	ThPm	Amb ambit	IntAm ambit	Width amb III ambit
SAM P33739	22.15	22.23	10.95	3.6	11.03	10.52	11.26	4.57	11.16	5.01	11.78	20	23	1.01	0.86	7.27	5.10	7.10
SAM P33740	16.15	16.08	10.23	2.66	7.94	7.44	7.77	3.6	8.27	3.28	8.89	18	20	0.88	0.87	5.09	3.01	4.70
SAM P33741	23.17	23.05	13.23	3.81			11.91							1.78	1.21	7.68	4.05	6.79
SAM P33742	14.53	14.26	8.73	1.86	7.12	6.21	6.92	3.04	7.24	2.86	7.15	19	17	0.81	0.57	3.76	2.61	5.19
SAM P33743	36.18	36.31	16.29	5.11	17.33	17.33	17.73	8.28	18.27	8.15	20.52	22	24	1.13	1.20	12.78	6.41	11.52
SAM P33744	10.69	10.34	6.08	1.89	4.92	4.88	5.21	2.12	5.28	1.94	5.75	13	12	1.02	0.75			
SAM P33745	25.05	25.99	12.71	3.75	12.62	11.67	12.47	6.37	12.88	5.3	13.95	24	19	1.25	1.15	8.70	5.71	8.38
SAM P33746	13.28	13.72	7.03	1.87	6.44	6.78	6.62	2.71	6.54	2.67	7.24	13	13	0.84	0.74	4.31	2.72	4.05
SAM P33747	13.26	13.87	8.85	2.05	6.10	5.86	6.49	2.39	6.91	2.47	7.39	12	13	0.92	0.83	4.33	2.61	4.68
SAM P33748	13.13	12.27	9.23	2.09			6.54							1.24	1.06	3.92	2.65	4.23
SAM P33749	10.99	10.53	6.63	1.73			5.27							0.75	0.55			
SAM P33750	14.78			2.21	7.00	7	7.00	2.49	6.70	2.6	7.17	10	10	1.1	0.88	4.85	2.82	4.49
MV P18762-1	37.01	36.89	16.99	5.81	17.80	16.49		8.44	19.23	8.82	20.75	24	25	1.6	1.07	12.94	8.48	11.50
MV P18768-1	16.85	16.87	7.68	2.56	7.85	6.81	8.46	3.9	8.72	3.3	9.26	17	17	0.97	0.87	5.40	2.99	6.10
MV P18769-1	34.95	35.03	17.92	5.01			17.04							1.15	0.87	12.02	6.77	10.36
MV P20157-1	21.54	21.82	12.44	3.3	10.43	10.08	10.53	4.66	10.89	4.16	10.84	16	18	1.28	1.10	7.94	4.70	6.55
MV P20159-1	32.46	32.13	19.46				15.94							1.83	1.50	11.43	6.41	

Appendix 1.14. Raw linear data for *R. eyriei*.

Number (SAM)	Lgth	Wdth	A/wp	Hght	A/ad	A/apx	A/ps	L/petal amb II	Dist margi n amb II	L/petal amb I	Dist margi n amb I	P am b II	P am b I	ThAm	ThPm	Amb ambit	IntAm ambit	Width amb III ambit
P29660	23.19	24.75	18.67	4.32	12	11.67	11.75	5.64	11.66	5.62	13.77	22	22	1.4	0.96	6.70	5.24	6.25
P29661	15.88	15.96	12.36	3.39	7.75	6.27	7.75	3.89	7.61	3.59	9.37	15	16	1.68	0.87	4.46	3.48	4.52
P29662-1	24.66	26.98	20.32	4.1	12.84	11.96	12.14	6.76	12.78	7.35	15.85	19	22	1.62	0.86	7.19	6.08	6.81
P29662-2	15.91	16.38	11.59	3.22	8.32	7.54	8.07	3.29	8.01	2.93	9.03	15	13	1.32	1.02	4.78	2.90	4.44
P29662-3	12	12.12	9.92	2.31		5.45	6.07	2.57	6.16	2.81	6.71			1.33	1.14	3.46	2.53	3.38
P29662-4	12.73	11.61	10.24	2.3	6.11	4.39	6.11	2.62	5.85	3.23	6.82	15	17	1.04	0.85	3.53	2.69	3.08
P29662-5	11.06	10.61	8.17	2.36	5.32	4.06	5.53	2.32	5.00	2.24	5.71	12	12	1.19	0.92	2.77	2.02	2.88
P29662-6	19.7	19.92	14.23	3.23	10.21	9.09	9.84	4.74	9.52	4.44	11.09	17	19	1.28	0.87	5.68	4.04	5.59
P29662-7	17.55	16.35	13.03	2.78	9.29	7.52	9.09	4.06	8.36	3.9	9.84	14	16	1.6	1.00	4.29	3.33	3.45
P29662-8	14.34	13.54	11.45	2.65	7.29	5.39	7.17	3.31	6.81	3.37	7.96	13	13	1.43	0.92	3.91	2.88	3.85
P29662-9	16.71	17.08	13.11	2.75	8.11	6.73	8.41	4.6	8.26	4.05	10.3	18	20	1.15	0.86	4.61	3.77	5.08
P29662-10	18.61	18.94	14.96				8.9									5.09	4.50	5.42
P29663-1	12.52	11.63	9.89	2.32	6.52	4.92	6.33	3.39	6.18	2.65	6.63	18	17	1.05	0.74	3.48	2.22	3.46
P29663-2	17.76	17.12	13.93	2.89	8.5	8.15	8.97	3.53	8.18	4.29	10.26	16	22	1.46	1.02	4.30	3.58	5.03
P29663-3	11.34	11.25	8.95	2.15	6.13	4.06	5.42	2.12	5.64	2.14	5.85	13	14	1.17	1.06	2.92	2.60	3.19
P29663-4	14.7	13.94	11.13	2.76	7.01	5.99	6.94	3.05	7.07	3.54	7.69	14	15	1.35	0.91	3.89	3.37	4.05
P29663-5	15.91	15.58	12.32	2.41	7.52	7.14	7.52	3.55	7.91	3.37	9.64	18	20	1.52	1.43	5.37	3.22	5.04
P29663-6	18.05	17.66	12.35	2.95	8.98	7.43	9.19	4.3	8.66	4.08	9.69	17	17	1.4	1.07	5.05	4.12	4.19
P29663-7	16.89	16.66	10.31				8.14							1.3	1.11	4.72	3.27	5.03
P29663-8	10.62	10.39	7.56				5.4							0.95	0.74	2.96	1.93	2.91
P29663-9	25.02	26.39	19.64	3.91			12.46							1.52	1.61			
P29663-10	21.86	22.43	16.82				11.72									6.21	4.53	
P29664-1	14.69	13.83	9.96	2.79	8.05		7.46	3.78	7.06	3.39	8.03	17	16	1.39	0.95	3.91	2.83	3.66
P29664-2	19.21	21.1	13.88	3.15	9.82	8.13	10.08	4.01	9.85	5.87	11.58			1.81	1.48	5.56	4.59	5.03
P29664-3	32.15	33.28	19.32	4.96	16.76	17.63	15.58	6.58	15.86	6.37	18.64					9.87	8.46	9.00
P29664-4	11.05	10.34	5.62													2.98	1.89	2.38
P29664-5	26.99	28.16	22	4.26	13.81		13.43	7.13	13.22	7	16.15	20	23	1.87	1.13			
P29664-6	21.82	21.71	16.11	4.16	11.69		10.73	4.3	10.91	4.41	12.78	14	16	1.31	0.82	6.27	4.34	5.59
P29664-7	23.06	24.22	18.52	3.35	12.32	11.45	11.99	4.69	10.69	6.19	14.44	16	20	1.6	1.02	6.28	5.13	6.03
P29664-8	20.29	20.94	13.32				10.06							1.1	0.70	5.67	5.02	5.32
P29664-9	12.96	12.66	9.53	2.55	6.27	4.83	6.09	2.91	5.86	2.59	7	16	14	1.05	0.94	3.35	2.49	3.24

Appendix 1.15. Raw linear data for *D. erioaster*.

Number (SAM)	Lgth	Wdth	A/wp	Hght	A/ad	A/apx	A/ps	L/petal amb II	Dist margi n amb II	L/petal amb I	Dist margi n amb I	P am b II	P am b I	ThAm	ThPm	Amb ambit	IntAm ambit	Width amb III ambit
P29651	10.09	8.46	4.58	2.2	4.94	3.96	4.76	2.41	4.55	2.29	4.74	12	14	1.07	1.05	2.80	2.23	2.71
P29650	13.41	12.62	7.49	2.41	6.83	4.96	6.96	3.38	6.22	4.12	6.62	17	17	1.37	1.04	4.33	2.94	4.39
P29647	15.03	14.45	7.4	2.63	7.34	6.95	7.38	3.49	7.34	4.06	7.89	16	18	1.09	0.80	4.50	3.31	4.85
P29649	15.24	14.19	8.6	2.77	7.88	6.95	7.61	4.11	7.60	3.7	7.78	14	16	1.28	1.09	4.52	3.38	4.64
P29648	15.35	13.94	7.41	2.64	7.91	6.53	8.35	3.57	7.06	3.25	7.90	19	17	1.2	0.83	4.82	3.53	5.05
P29646	21.92	21.69	10.12	2.89	11.14	10.12	10.53	5.45	11.04	5.61	11.88	17	19	1.03	0.89	6.22	5.38	7.94
P29652	21.98	21.09	9.86	3.59	10.86	10.91	11.53	4.41	9.89	4.9	11.19	20	22			6.56	5.44	6.17
P29643	25.37	25.45	14.39	4.19	13.18	11.55	12.86	6.45	13.14	6.84	14.45	22	21	1.57	1.17	7.36	7.30	7.82
P29642	26.60	25.46	11.11	3.56	12.80	11.92	13.24	6.69	13.24	7.73	14.75	23	25	1.34	0.94	8.16	6.92	8.38
P29644	29.30	29.30	14.45				15.00							1.42	0.95	9.62	6.91	9.85
P29645	31.32	29.41	21.1	3.45	15.54	14.15	15.24	8.06	15.07	8.22	16.58	25	26	1.44	0.98	8.38	6.38	9.99

Appendix 1.16. Raw linear data for *O. spirographica*.

Number (SAM)	Lgth	Wdth	A/wp	Hght	A/ad	A/apx	A/ps	L/petal amb II	Dist margi n amb II	L/petal amb I	Dist margi n amb I	P am b II	P am b I	ThAm	ThPm	Amb ambit	IntAm ambit	Width amb III ambit
P29653	22.68	21.15	15.11				11.06							1.55	1.15			
P29654	16.44	15.06	8.5	2.43	8.34	7.96	8.19							1.05	0.95	4.72	3.90	4.66
P29655	9.50	8.60	5.8	1.86	4.46	3.46	4.79	1.84	4.35	1.66	5.00	12	13	1.19	0.85	2.60	2.19	2.55
P29656	13.54	13.23	8.92	2.47	6.64	5.69	7.22	2.75	6.15	2.98	7.63	13	13	1.33	0.95	3.82	3.26	4.00
P29657	11.86	11.03	5.72	2.36	5.8	4.26	6.13	2.28	5.66	2.35	6.26	11	14	1.6	1.18	3.65	2.59	
P29658	13.10	12.27	6.8	2.05	6.55	5.82	6.19	2.95	6.15	2.92	6.93	15	17	1.47	1.05	3.64	2.81	3.69
P29659	13.46	13.12	8.95	2.35	6.72	6.21	6.55	3.09	6.26	3.03	7.05	16	15	1.09	0.99	3.87	3.03	4.30
P29665	8.16	7.92	5.41	1.76	4.45	4.45	4.27	1.44	4.10	1.25	4.17							
P29666	21.01	19.80	11.48	2.82	10.05	9.43	10.41							1.41	0.97	6.17	4.23	5.99

Appendix 1.17. Raw linear data for *O. curtus*.

Number	Lgth	Wdth	A/wp	Hght	A/ad	A/apx	A/ps	L/petal amb II	Dist margin amb II	L/petal amb I	Dist margin amb I	P amb II	P amb I	ThAm	ThPm	Amb ambit	IntAm ambit	Width amb III ambit
SAM P33751	61.84	59.86	26.94		30.3			14.44	30.56	14.69	31.42			1.34	1.25	23.56	12.96	28.35
MV P17599	58.54	60.94	28.84															
MV P17604	61.83	57.6	27.3	6.96	29.15		30.16	15.62	30.69	14.42	30.02	44	43	1.46	1.08	20.42	13.10	22.73
MV P27365	63.64	66.24	38.3															
MV P142063	43.35	44.13	21.47	5.35	21.37		21.24	11.13	22.32	9.84	21.14	25	30	1.38	1.15			
MV P302897	59.34	59.42	30.3	7.63	31.52		30.62											
MV P302898	51.11	49.42	22.37	7.76	26.35		26.55			11.51	26.51							
MV P302899	44.07	44.11	22.23	6.09	23.26		22.42											
MV P302900	35.56	34.11	17.5	4.84	19		17.52											
MV P317123	49.59	49.66	25.01	5.6	25.01		26.17	11.09	24.68	10.73	26.91	36	37	1.35	0.87			
MV P317124	52.23	51.25	25.23	7.42	27.01													

Appendix 1.18. Raw linear data for *P. loveni*.

Appendix 2. Raw plate data

Number	IntAmb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
SAM 29608-1	4a/3b	7	6	7	7	9	9	9	9	9
SAM 29608-2	3a/3b	6	6		6	9	9	8	9	9
SAM 29608-3	3a/3b	6	6	7	7	9	8	8		8
SAM 29608-4	3a/3b	6	7	7	7	9	9	9	10	10
SAM 29608-5	3a/3b	7	6	6	7	9	9	8	10	10
SAM 29608-6	3a/3b	6	6	6	8	10	9	9	9	9
SAM 29608-7	3a/3b	8	8	8	8	10	10	10		10
SAM 29608-8	3a/3b	6	6	6	6	9	8	8	8	8
SAM 29608-9	3a/3b	6	7	6	7	8	8	9	8	9
SAM 29608-10	3a/3b	6	6	7	7	11	9	8	9	10
SAM 29608-11										
SAM 29608-12	3a/3b	6	8	7	7	10	10	10	10	8
SAM 29608-13	3a/3b	6	7	7	7	11		9	10	10
SAM 29608-14	3a/3b	7	7	6	6	9	8	10	10	9
SAM 29608-15	3a/3b	7	7	7	6	11	9	9	9	9
SAM 29608-16	3a/3b	6	6	7	7	8	8	8	9	9
SAM 29608-17	3a/3b	6	6	6		11	8	8	9	
SAM 29608-18	3a/3b	6	7	7	7	9	9	9	9	9
SAM 29608-19	3a/3b	7	7	6	7	10	10	9	8	8
SAM 29608-20	3a/3b	6	6	7	6	8	8	9	9	8
SAM 29608-21	3a/3b	7	6	6	6	10	8	9	9	9
SAM 29608-22	3a/3b	9	10	9	7	12	10	11	11	11
SAM 29608-23	3a/3b	8	9	8	8	9	8	9	8	8
SAM 29608-24	3a/3b	6	7	6	6	8	8	8	8	8
SAM 29608-25	3a/3b	6	6	7	5	9	8	8	8	8
SAM 29608-26	3a/3b	8	8	7	7	10	9	10	9	10
SAM 29608-27	3a/3b	7	7	6	6	10	8	8	8	8
SAM 29608-28	3a/3b	6	6	6	6	8	8	9	11	8

SAM 29608-29	3a/3b	8	7	6	6	9	9	8	8	9
SAM 29608-30	3a/3b	6	6	6	7	8	7	8	8	8
SAM 29608-31	3a/3b	8	8	7	7	11	10	11	9	9
SAM 29608-32	3a/3b	6	6	6	6	9	8	9	8	8
SAM 29608-33	3a/3b	6	7	6	6	8	8	9	8	8
SAM 29608-34	3a/3b	7	6	6	6	9	8	8	8	8
SAM 29608-35	3a/3b	6	7	6	6	8	8	8	8	8
SAM 29608-36	3a/3b	6	6	6	6	9	8	9	9	8
SAM 29608-37	3a/3b	6	7	6	6	8	8	8	8	8
SAM 29608-38	3a/3b	6	7	6	6	8	8	8	8	8
SAM 29608-39	3a/3b	6	6	6	7	10	9	8	8	9
SAM 29608-40	3a/3b	6	6	7	6	10	8	8	8	8
SAM 29608-41	3a/3b	7	7	7	6	9	8	9	8	8
SAM 29608-42	3a/3b	6	6	6	6	8	8	9	8	8
SAM 29608-43	3a/3b	6	6	6	6	9	8	8	9	9
SAM 29608-44	3a/3b	6	6	6	6	9	10	9	8	8
SAM 29608-45	3a/3b	7	7	6	7	8	9	9	8	8
SAM 29608-46	3a/3b	6	6	6	6	8	7	8	8	8
SAM 29608-47	2a/3b	6	6	5	6	7	7	7	7	7
SAM 29608-48	3a/3b	6	6	6	6	8	8	8	8	8
SAM 29608-49	3a/3b	6	6	6	6	8	8	8	8	8
SAM 29608-50	3a/3b	6	6	6	6	8	8	8	8	8
SAM 29608-51	3a/3b	6	6	6	6	8	8	8	8	8
SAM 29608-52	3a/3b	6	6	6	6	9	8	8	8	8
SAM 29608-53	3a/3b	6	6	6	6	9	9	9	9	8
SAM 29608-54	3a/3b	6	6	6	6	10	8	8	9	9
SAM 29608-55	3a/3b	7	7	7	6	10	9	8	8	8
SAM 29608-56	3a/3b	6	7	6	6	10	8	8	9	8
SAM 29608-57	3a/3b	7	6	6	6	8	8	9	8	8
SAM 29608-58	3a/4b	6	6	6	6	9	8	8	8	8
SAM 29608-59	3a/3b	6	6	7	6	10	8	9	9	8
SAM 29608-60	3a/3b	7	7	7	6	10	8	9	9	9
SAM 29608-61	3a/3b	6	6	7	6	8	8	8	8	8
SAM 29608-62	3a/3b	6	6	6	6	9	9	8	10	9
SAM 29608-63	3a/3b	6	7	6	6	9	8	8	9	8
SAM 29608-64	3a/3b	6	6	6	7	8	8	8	8	8
SAM 29608-65	3a/3b	6	6	6	6	9	8	8	8	8
SAM 29608-66	3a/3b	6	6	7	7	9	9	8	8	9
SAM 29608-67	3a/3b	8	7	7	7	10	9	10	9	9

SAM 29608-68	2a/3b	8	7	7	6	9	9	9	8	8
SAM 29608-69	3a/3b	6	5	6	6	8	8	8	8	8
SAM 29608-70	3a/3b	6	6	6	6	10	9	9	9	9
SAM 29608-71	3a/3b	6	6	6	6	10	9	9	9	9
SAM 29608-72		7	6	7		10	9	9		
SAM 29608-73	3a/3b				6					

Appendix 2.1. Raw plate numbers count for *M. australis*.

Number	IntA mb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
WAM 16.1										
WAM 16.11			7			12	11	10	12	12
WAM 16.12										
WAM 16.13										
WAM 16.14		8	7	7	7		10	10		
WAM 16.15						12				
WAM 16.16				6						
WAM 16.17										
WAM 16.18	3a/3b	8		7	7	11	10	10	12	
WAM 16.19		8	9	8		13	12	12	11	
WAM 16.2										
WAM 16.20							11			
WAM 16.21	3a/3b	7		8	7	12				
WAM 16.22	3a/3b	8	8	7	8	13	12	12	12	12
WAM 16.23										
WAM 16.24						12				
WAM 16.3		8	8	7	8		10			
WAM 16.4			8	8				12	11	
WAM 67.337										
WAM 89.35a	3a/3b			7	8					
WAM 89.35b										
WAM 89.37b										
WAM 89.37d	3a/3b									
WAM 89.37e		8	8	8	9	11		11		
WAM 89.37g										
WAM 91.15.1	2a/3b									

WAM 91.17a										
WAM 91.17b										
WAM 91.17c										

Appendix 2.2. Raw plate numbers count for M. macnamarai.

Number	IntAmb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
WAM 16.25	2a/3b	6	6	6	6	11	10	10	12	12
WAM 16.26	3a/3b	8	8	8	7	10	9	10	9	9
WAM 16.27	2a/3b	8	8	7	7	12	11	11	10	11
WAM 16.28	2a/3b	7	7	6	7	11	10	11	10	10
WAM 16.5										
WAM 16.6		10	9		8	12	10	12		11
WAM 88.925a										
WAM 88.925b										
WAM 88.925c										
WAM 91-15-2	3a/3b	7	8	7	7	10	9	9	9	9

Appendix 2.3. Raw plate numbers count for M. alanixi.

Number	IntAmb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
SAM P33713-1	3a/3b	6	6	6	6	10	9	9	10	10
SAM P33713-2	2a/3b	6	6	7	6	10	10	10		10
SAM P33713-3	3a/3b	6		6	6	10	10	10		10
SAM P33713-4	2a/3b	7	8	6	7	13	12	10	10	10
SAM P33713-5	2a/2b	6	6	5	5	10	10	10	8	
SAM P33713-6	3a/3b	7	7	7	7	11	10	10	10	10
SAM P33713-7	3a/3b	7	7	7	6	10	12	12	11	11
SAM P33713-8	2a/3b			7		11		11	11	11
SAM P33713-9	2a/3b	7	7	7	7	13	11	11	12	12
SAM P33713-10	2a/2b	6	7	7	7	12	10	11	10	11
SAM P33713-11	3a/3b	8	8	7	7	12	11	11	11	11
SAM P33713-12										

SAM P33713-13			8			13	12	13	13	
SAM P33713-14	3a/3b	8	8	7	7	12	9	11	10	12
SAM P33713-15	3a/3b	8	7	7	7	13	11	11	11	12
SAM P33713-16	3a/3b	8	8	8	8	13	12	12	11	11
SAM P33713-17	3a/3b	8	8	8	7	12	12	10	11	10
SAM P33713-18	3a/3b	6	7	8	7	13	10	12	11	11
SAM P33713-19		8	8	8	9	13	13		13	
SAM P33713-20	3a/3b								12	
SAM P33713-21	3a/3b	8		8		13	10		12	11
SAM P33713-22	3a/3b	6	7	7	7	11	10	11	10	10
SAM P33713-23	3a/4b						10		10	10
SAM P33713-24	2a/3b	6	8	6	6	10	10	9	9	9
SAM P33713-25	2a/3b			6	6		8	8	8	9
SAM P33713-26	2a/2b									8
SAM P33713-27		7		8						
SAM P33713-28	3a/3b	6		7	7	12	9	9	9	9
SAM P33713-29	3a/3b	6	6	9	8	10			10	10
SAM P33713-30	3a/3b		6			10				10
SAM P33713-31	3a/4b			7					9	
SAM P33713-32	3a/3b	7	7	7	7	13	10	10	10	11
SAM P33713-33										
SAM P33713-34										
SAM P33713-35	2a/3b	8	8	7	7	11	9	10	10	10
SAM P33713-36	3a/3b	7	8	8	7	11	11	11	10	10
SAM P33713-37	3a/3b			8						
SAM P33713-38									10	10
SAM P33713-39	2a/3b	6	7	8	7	13	10	11	11	10
SAM P33713-40										
SAM P33713-41	3a/3b			8		13		11	11	
SAM P33713-42	3a/3b							10		
SAM P33713-43					6					9
SAM P33713-44	2a/3b			7		9	9	9	10	
SAM P33713-45	3a/3b					12				10
SAM P33713-46					8	12	10		9	10
SAM P33713-47	3a/3b	7	7	7	7	11	9	9	10	9
SAM P33713-48	3a/3b	7	7	7	8	12	10	10	10	11
SAM P33713-49	3a/3b	9	8	8	8	13	11	11	11	11
SAM P33713-50	3a/3b	8	8	8	8	14	12	12	11	11
SAM P33713-51	2a/3b	6	7	6	7	10	10	9	9	9

SAM P33713-52	3a/3b	6	6	6	6	10	10	10	10	10
SAM P33713-53	3a/3b		7	7	7	10	10	11	10	10

Appendix 2.4. Raw plate numbers count for M. merrimanensis.

Number	IntAmb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
TMAG Z504										
MV P128077	3a/3b	6	6		6	10	10			10
MV P128078										
MV P135101										
MV P27351										
MV P27352										
MV P27353										
MV P27354										
MV P27358	3a/3b	7	6	6	6	9	8	9	9	9
MV P320411	2a/3b									
MV P82434										
MV P82435										
SAM 33715	3a/3b	6	6	6	6	8	8	8	10	10
SAM 33716	2a/2b	6	6	6	6	10	8	8	8	8

Appendix 2.5. Raw plate numbers count for M. etheridgei.

Number	IntAmb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
SAM P33714-1	3a/3b	7	7	7	7	11	8	9	9	9
SAM P33714-2	3a/3b	7	7	7	7	11	9	9	9	9
SAM P33714-3	3a/3b			7	7					
SAM P33714-4										
SAM P33714-5										
SAM P33714-6			9	8		12		10	10	
MV P147941	3a/3b	7	7	7	7	10	8	9	10	10
MV P27030A	3a/3b	7				11	10			
MV P27030B	3a/3b	7	9	7	8	10	10	9	10	10

MV P27375	3a/3b	7	8	7	7	10	9	9	10	10
MV P27376		8	9		8	11	10	10		11
MV P27377		8				13	10			
MV P27378										10
MV P27379	3a/3b				7	11	9	9	10	10
MV P27384	3a/3b				8					
MV P27385										
MV P305221	3a/3b	8	8	7		10	10	10	10	10
MV P305223										
MV P305224	3a/3b	8	8		8	12	10		10	
MV P305225	3a/3b			8		11	9	9		9
MV P305226	3a/3b		7	7	7	12		10		9
MV P305227	3a/3b	6		7	6		8		9	8
MV P305228	3a/3b	7	8	7		11	9	10	10	9
MV P305244A										
MV P305245	3a/3b	7	8	7	7	11			10	9
MV P305246	3a/3b	7	7		7	10	10	10	10	10
MV P306714A	3a/3b	6			7					
MV P306714B	3a/3b	6		6						
MV P306714C										
MV P317117	2a/3b	7	6	7	6	10	9	8	10	10

Appendix 2.6. Raw plate numbers count for *M. glenelgensis*.

Number	5 IntAmb	2 IntAmb	3 IntAmb	4 IntAmb	1 IntAmb	III Amb	II Amb	IV Amb	V Amb	Amb I
SAM P33717										
SAM P33718										
SAM P33719	2a/2b									
SAM P33720	2a/3b	8	9	8	7	12	9	9	9	10
SAM P33721		7		8	7	12	10	10	10	10
SAM P33722	3a/3b			7						
SAM P33723	3a/3b			7						
SAM P33724	3a/3b									

SAM P33725	3a/3b	7	7	7	7	10	9	9	9	9
SAM P33726	2a/2b	8	8	7	7	12	10	10	10	10
SAM P33727	3a/3b	8	8	8	8	11			10	9
SAM P33728		7			7					

Appendix 2.7. Raw plate numbers count for M. robheathi.

Number	IntAmb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
SAM P22600-1						11	10	10	10	
SAM P22600-2										
SAM P22638										
SAM P29665										
SAM P29667										
SAM P29672-1										
SAM P29672-2										
SAM P29883										
SAM P4776										
SAM P4776-1										
NHML EE1146	3a/3b					10				
NHML EE1153										
Qm P1001										
Qm P1002	3a/3b	8				12				10
Qm P1003	3a/3b	7	7	7	8	11	10			
Qm P1004										

Appendix 2.8. Raw plate numbers count for Q. mannumensis.

Number	IntAmb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
SAM P29623	2a/2b	7	8	7	7	10	9	10	10	10
SAM P29624	2a/3b		7	7	7	10	10	11	11	11

SAM P29625										
SAM P29626						11				
SAM P29627		7	7	6	7	13	11	11	12	12
SAM P29628										
SAM P29629	2a/3b	7		7	7	12	10	11	11	11

Appendix 2.9. Raw plate numbers count for Q. gigas.

Number	IntAmb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
SAM P29609	3a/3b	8	8	8	8	12	12	11	11	13
SAM P29610	3a/3b			8	7		11	12	12	12
SAM P29611										
SAM P29612										
SAM P29613	3a/3b	8		8	7	12	10	10	12	12
SAM P29614	3a/3b	8	9	8	8	12	10	12	11	11
SAM P29615	3a/3b	8	9	9	9	12	10	11	10	10
SAM P29616										
SAM P29617	2a/3b									
SAM P29618	3a/3b	8	8	7	7	11	10	11	10	10
SAM P29619	3a/3b									
SAM P29620										
SAM P29621	2a/3b					12	11	11	11	11
SAM P29622	3a/3b	8	9	9	9	12	11	12	12	11

Appendix 2.10. Raw plate numbers count for Q. berylmorrisae.

Number	IntAmb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
WAM 16.1										
WAM 16.3			8	7		10		11	10	
WAM 16.4		9				13	10	11		11
WAM 16.8		8	8			10				
WAM 16.9			8							
WAM 16.29										

WAM 16.31	2a/3b	8	10	8	7	12	10	11		11
WAM 16.32										
WAM 16.33										
WAM 16.34	3a/3b	7	7	8	7	11	12	11	11	11
WAM 16.35										
WAM 16.36	3a/3b	9	8	9	8	12	12	11	12	12
WAM 16.37						12		10		
WAM 16.38										
WAM 16.39										
WAM 16.41										
WAM 16.42		9				13	12	11		
WAM 89.37a										
WAM 89.37c										
WAM 89.37f										
WAM 89.37-1										
WAM 91.15.3	3a/3b	7	7	8	7	10	10	11	11	10

Appendix 2.11. Raw plate numbers count for Q. robertirwini.

Number	IntAmb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
SAM P 29637	3a/3b	7	7	7	7	12	10	11	10	10
SAM P 29638										
SAM P29630										10
SAM P29631	3a/2b	7	7			11	10	11		
SAM P29632										
SAM P29633										
SAM P29634										
SAM P29635										
SAM P29636	2a/3b	7	7	6	6	10	9	10	10	10
SAM P29639										
SAM P29640	3a/3b									
SAM P29641										
SAM P33729										

NHML EE 2112										
NHML EE 2113										
NHML EE 2114										
MV P18294										
MV P33721	2a/3b									

Appendix 2.12. Raw plate numbers count for R. pledgei.

Number	IntAmb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
SAM P33733	3a/3b									10
SAM P33734										
SAM P33735										
SAM P33736	3a/3b									
SAM P33737										
SAM P33738	3a/3b									8
SAM P33729	3a/3b	7	7	6		10	9	11	10	10
SAM P33730										
SAM P33731	3a/3b	6	7	7	7	10		10	10	
SAM P33732										

Appendix 2.13. Raw plate numbers count for R. aquilaensis.

Number	IntAmb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
SAM P33739	3a/3b	7	7	7	7	10	10	10	10	10
SAM P33740	3a/3b	7	7	7	7		9	9		9
SAM P33741	3a/3b	6	6	6	6	9	9	8	9	9
SAM P33742						9				
SAM P33743						10				
SAM P33744										
SAM P33745	2a/3b	6	7	7	7	10	8	9	9	8
SAM P33746						12				
SAM P33747	3a/3b				7	10	8		10	9
SAM P33748	3a/3b	6	7	7		9				

SAM P33749	3a/3b									
SAM P33750	3a/3b		7	7		9		9	9	
MV P18762-1										
MV P18768-1										
MV P18769-1					7		8			
MV P20157-1	3a/3b	7	7			11	9	10		
MV P20159-1										

Appendix 2.14. Raw plate numbers count for R. eyriei.

Number	IntAmb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
SAM P29660	3a/3b	8	8	9	8	13	12	11	13	13
SAM P29661	3a/3b	10	10	10	10	12	12	11	13	14
SAM P29662-1	3a/3b	8	9	8	8	9		10	12	12
SAM P29662-2	3a/3b	8	9	9	9	10	9	9	12	11
SAM P29662-3	3a/3b	8	8	8	8	9	9	9	10	11
SAM P29662-4	3a/3b	8	8	9	8	10	8	9	11	10
SAM P29662-5	3a/3b	8	8		8	11	9			12
SAM P29662-6	3a/3b	8	9	9	10	10	10	11	12	12
SAM P29662-7	3a/3b	9		8	8	12	10	11	11	11
SAM P29662-8	3a/3b	10	10	9	9	11	12	12	12	
SAM P29662-9	3a/3b	8	9	11	10	10	10	11	13	13
SAM P29662-10	3a/3b		9	9	9		9	10	11	12
SAM P29663-1	3a/4b	9	9		8	10	9			11
SAM P29663-2	3a/3b	9	10	10		10		10	12	12
SAM P29663-3										
SAM P29663-4	3a/3b	8	8	9	8	11	10	9	11	11
SAM P29663-5	3a/3b	9	9	9	9	12	11	11	12	11
SAM P29663-6	3a/3b	11	11	10	9	13		11	11	11
SAM P29663-7	3a/3b	10	10	10	9	14	12	11	12	12
SAM P29663-8	3a/3b	9	10	9	9	12	10	11	11	11
SAM P29663-9	3a/3b			9					10	11
SAM P29663-10	2a/3b	9	10	8	9		10	11	11	11
SAM P29664-1		9		9	9	10	10		11	11
SAM P29664-2	3a/3b									
SAM P29664-3	3a/3b	8	8	7	7	10	9	10	10	

SAM P29664-4	3a/3b	8	8	8		9	7	8	9	
SAM P29664-5		9	10	9		12	9	10	12	
SAM P29664-6	3a/3b	7	8	8	7		11	11	12	13
SAM P29664-7	3a/3b									
SAM P29664-8										
SAM P29664-9	3a/3b	8	8		8	13	10	12		12

Appendix 2.15. Raw plate numbers count for *D. erioaster*.

Number	IntAmb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
SAM P29651	4a/4b	8	9	9	9	12	10		11	11
SAM P29650	3a/4b								10	
SAM P29647	4a/4b	7	8		8	12	10			12
SAM P29649										
SAM P29648	3a/3b	8	8	8	8	12	10	10	11	11
SAM P29646	4a/4b	8	9		8	12	12	12	12	12
SAM P29652										
SAM P29643	4a/3b	9		10	9	11			12	12
SAM P29642	3a/3b	9	10	9	9	13	10	11	11	12
SAM P29644	3a/3b	8	8	8	8	11	10	11	12	12
SAM P29645	3a/4b	7	8	8	8	12	11	11	12	12

Appendix 2.16. Raw plate numbers count for *O. spirographica*.

Number	IntAmb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
SAM P29653	3a/4b	9	9	9	10	13	12	12	13	13
SAM P29654	3a/4b	9	10	9	9	13	13	13	13	13
SAM P29655										
SAM P29656										
SAM P29657										

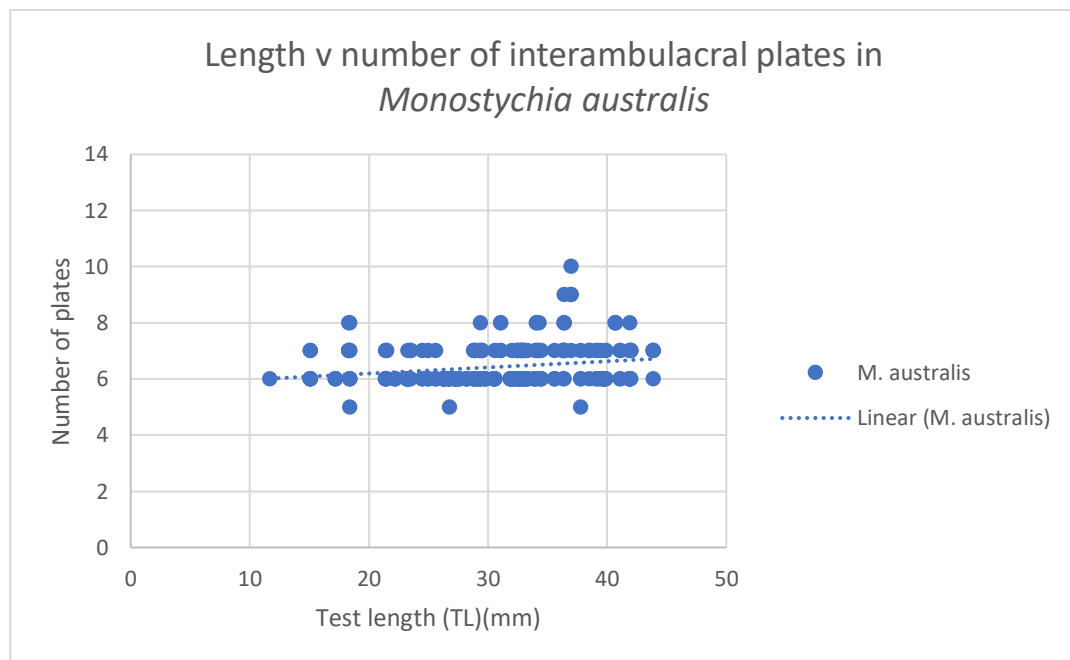
SAM P29658	4a/4b	8	10	8	8	14	12	12	13	12
SAM P29659										
SAM P29665										
SAM P29666	4a/4b		10	8		13		12	12	

Appendix 2.17. Raw plate numbers count for O. curtus.

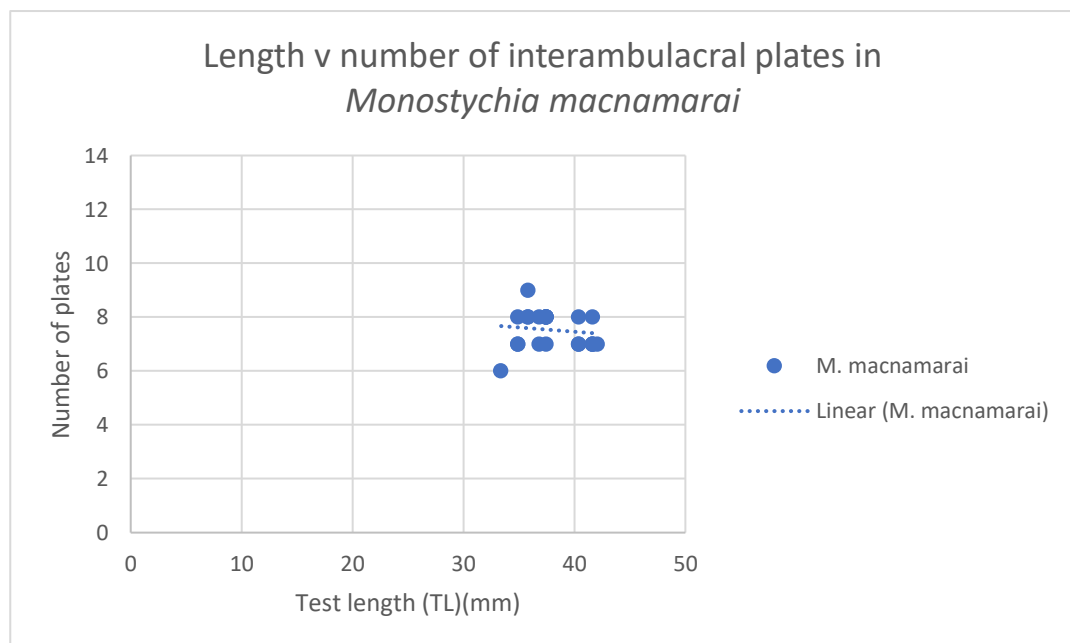
Number	IntAmb 5	IntAmb 2	IntAmb 3	IntAmb 4	IntAmb 1	Amb III	Amb II	Amb IV	Amb V	Amb I
SAM P33751										
MV P17599										
MV P17604	2a/2b	7	7	8	7	9	8	8	8	8
MV P27365										
MV P142063										
MV P302897										
MV P302898										
MV P302899										
MV P302900										
MV P317123	2a/2b									
MV P317124										

Appendix 2.18. Raw plate numbers count for P. loveni.

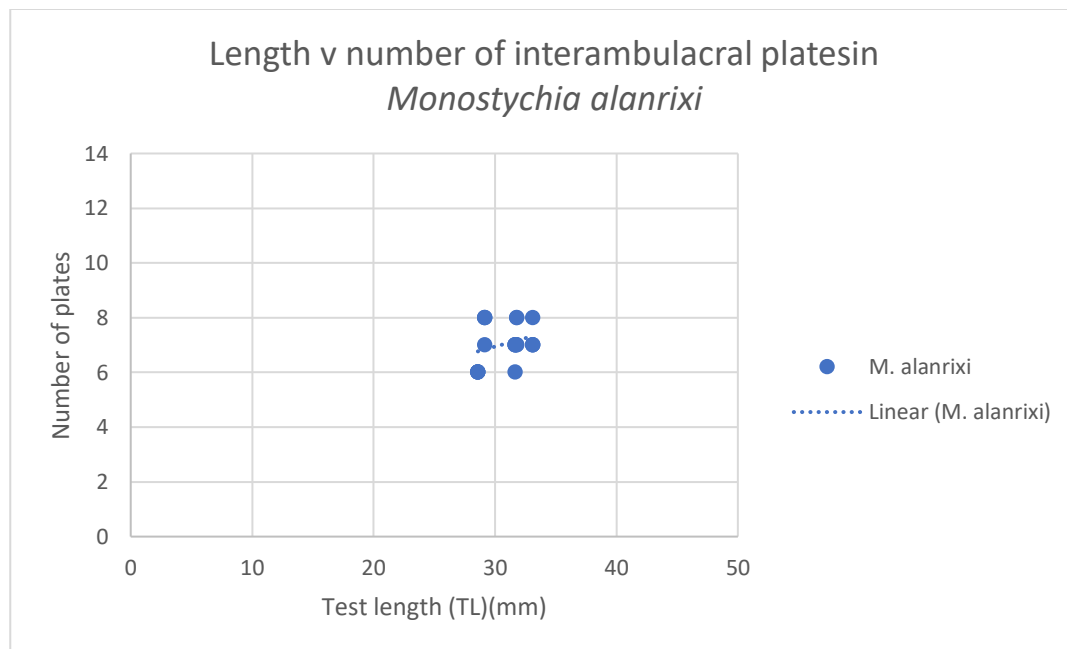
Appendix 3. Diagrams for Chapter 4 (Plate architecture)



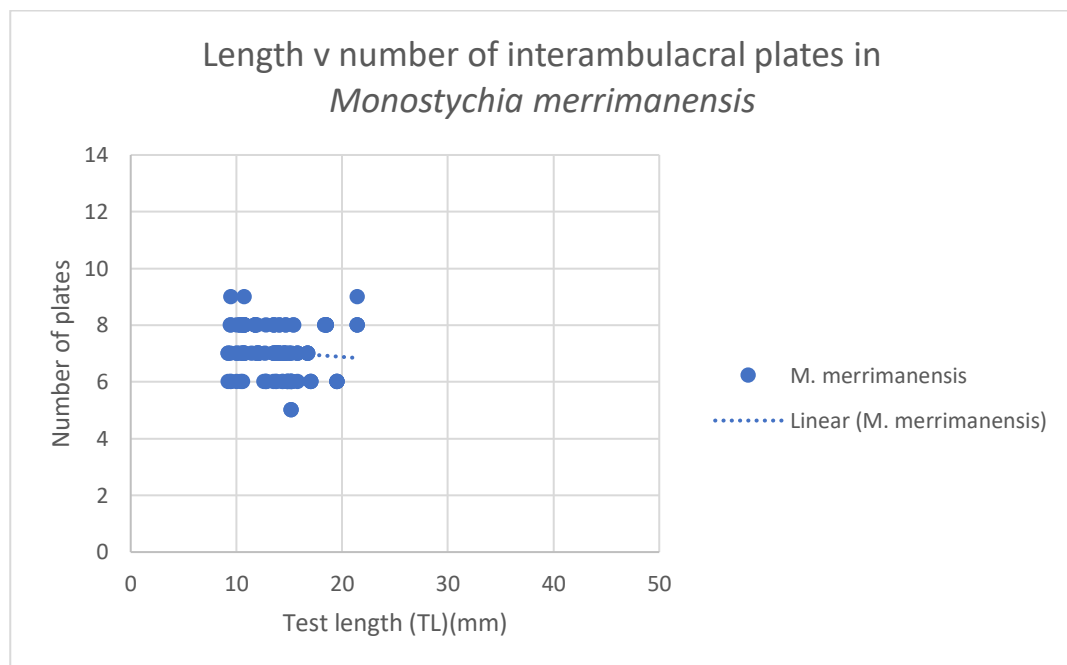
Appendix Fig.4.1. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of *Monostychia australis*.



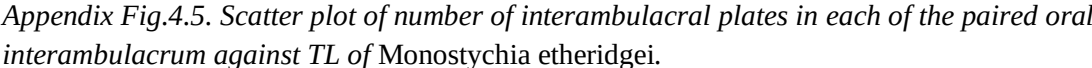
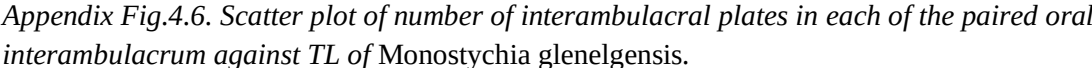
Appendix Fig.4.2. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of *Monostychia macnamarai*.

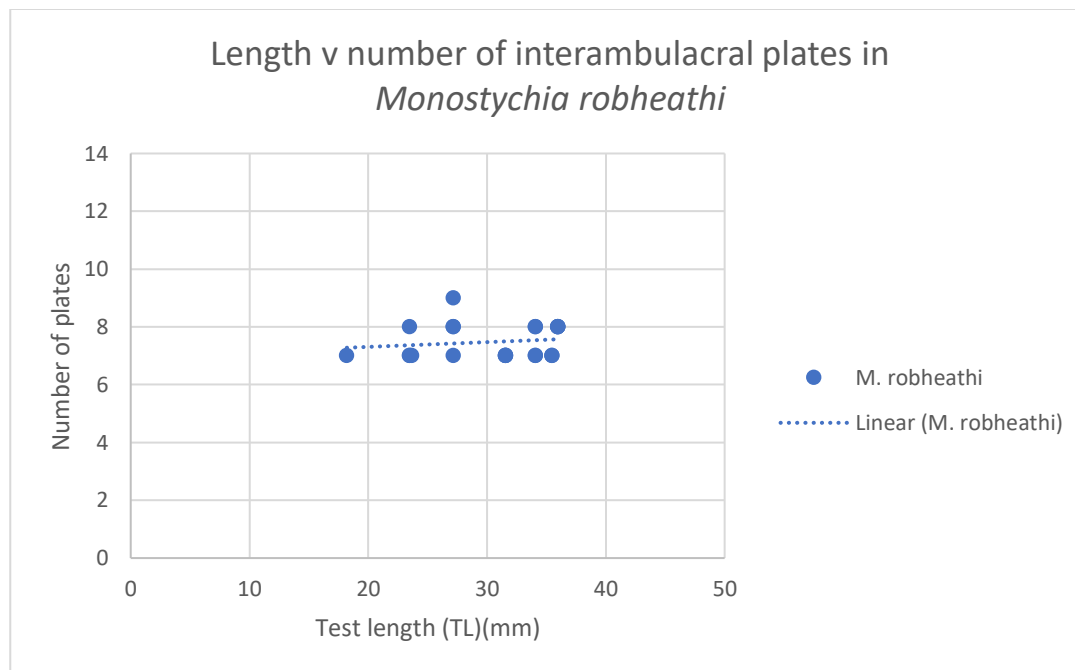


Appendix Fig.4.3. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of *Monostychia alanrxi*.

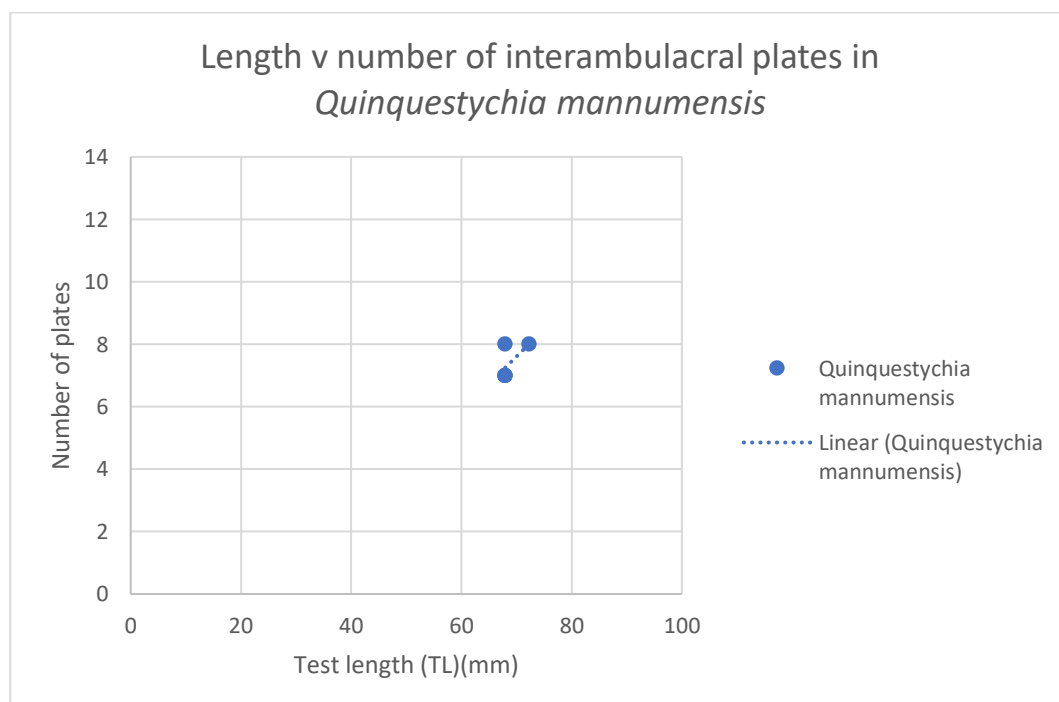


Appendix Fig.4.4. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of *Monostychia merrimanensis*.

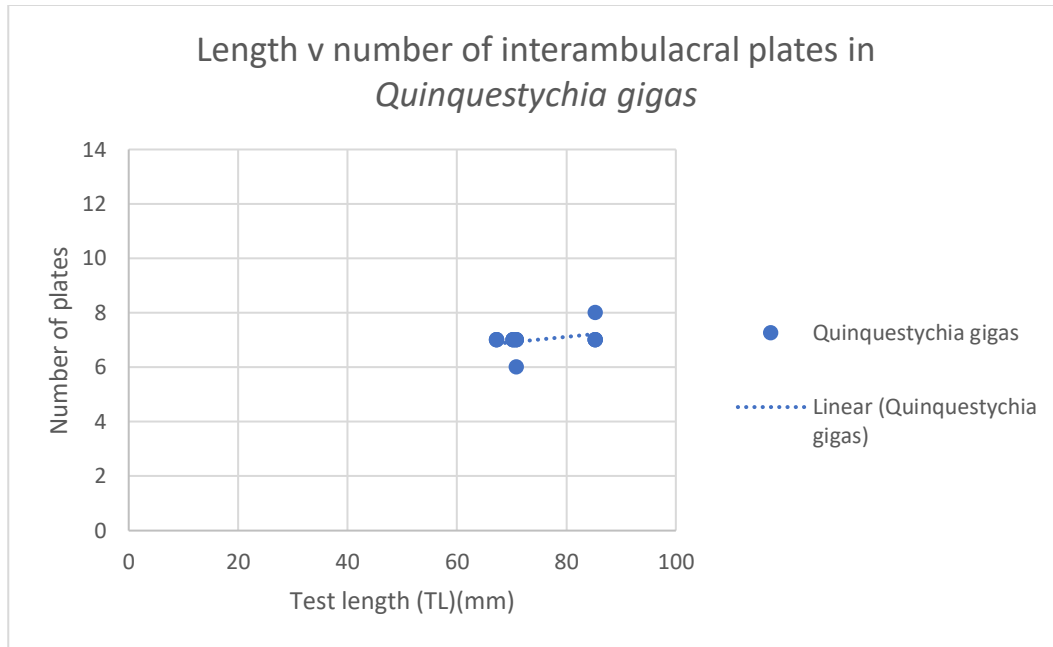




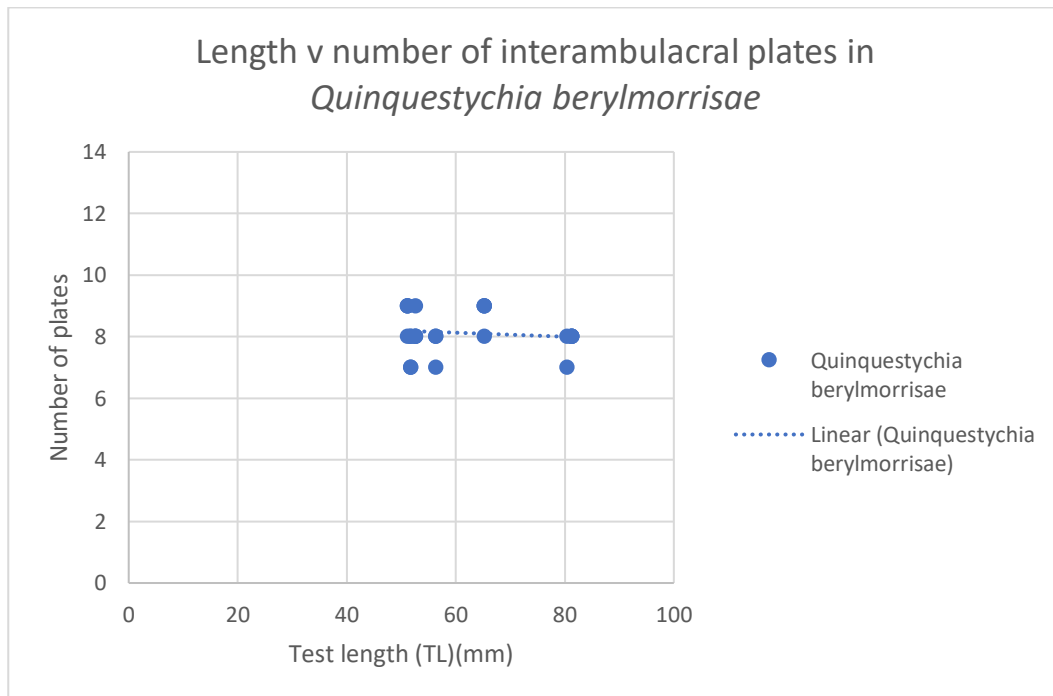
Appendix Fig.4.7. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of *Monostychia robheathi*.



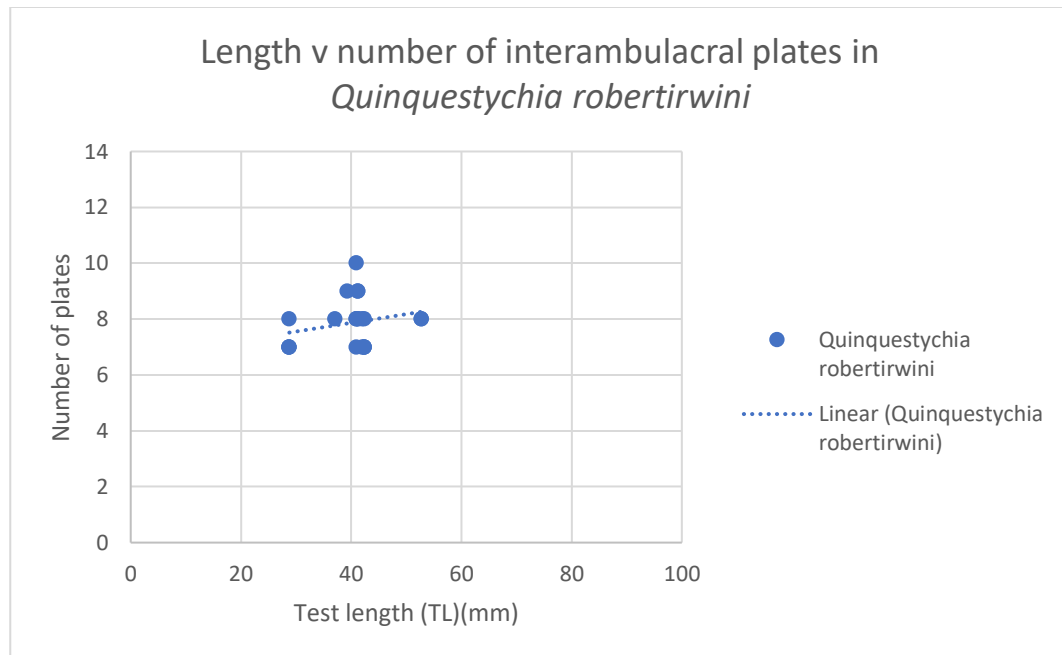
Appendix Fig.4.8. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of *Quinquestychia mannumensis*.



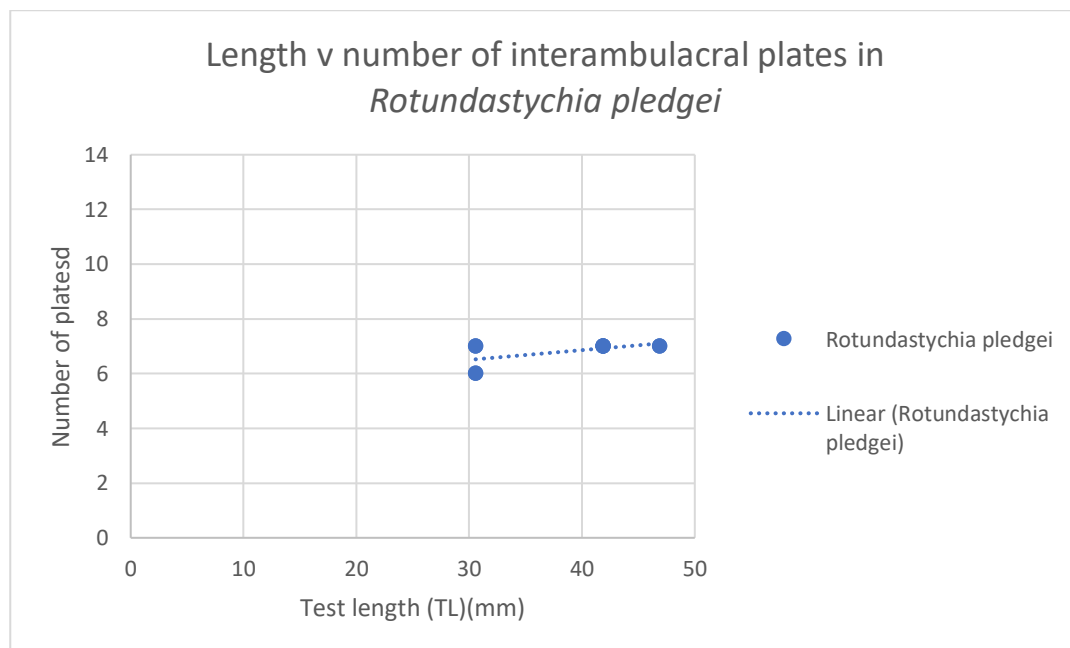
Appendix Fig.4.9. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of *Quinquestychia gigas*.



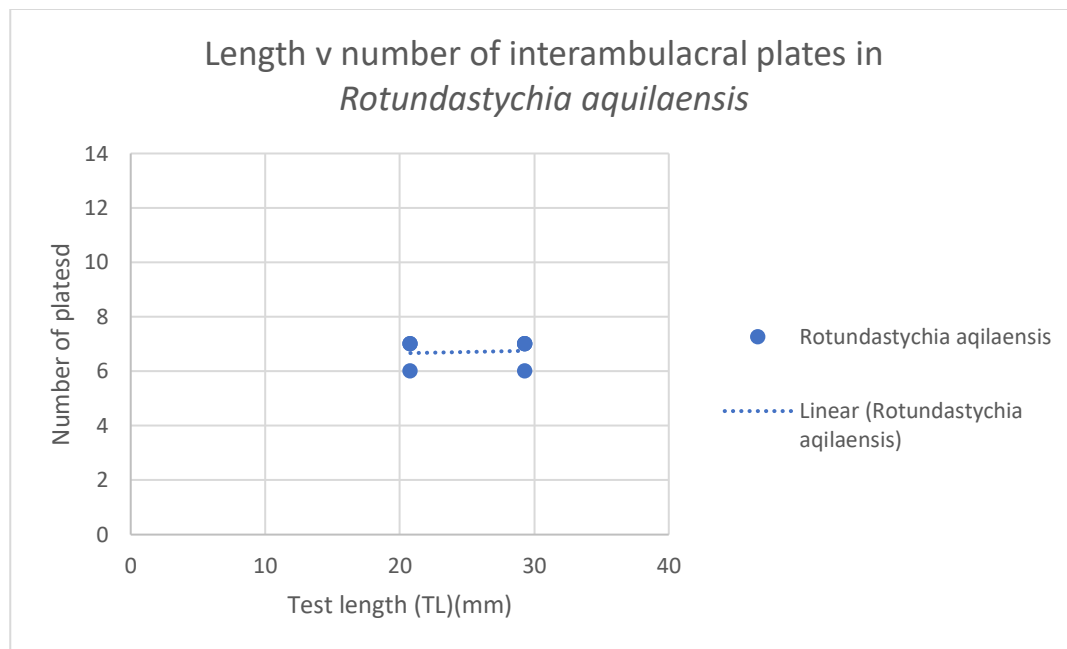
Appendix Fig.4.10. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of *Quinquestychia berylmorrisae*.



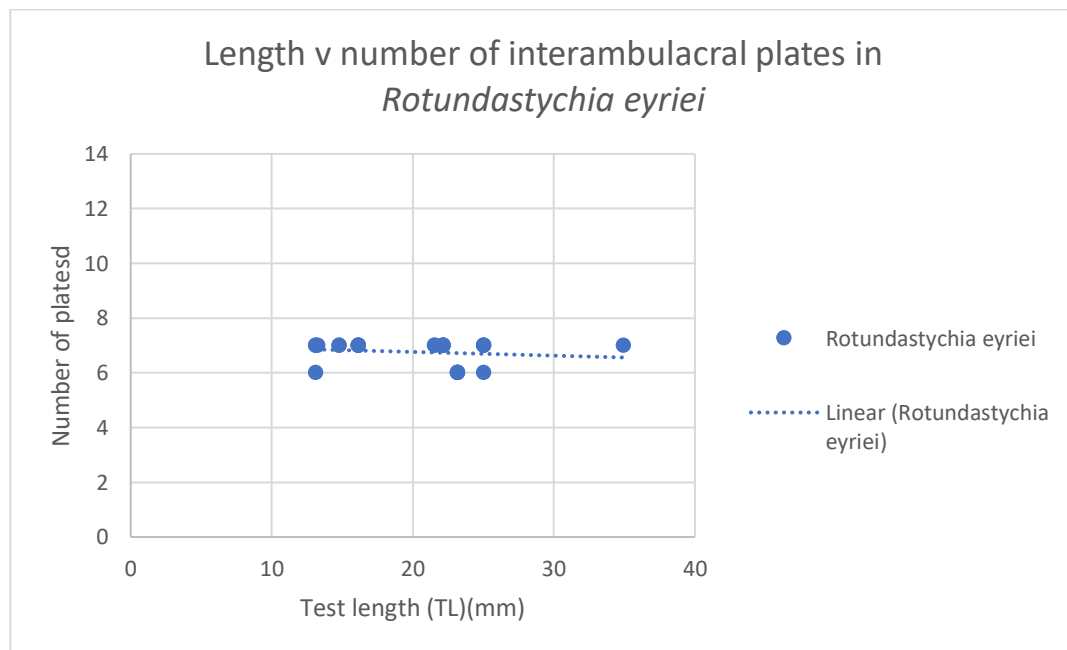
Appendix Fig.4.11. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of *Quinquestychia robertirwini*.



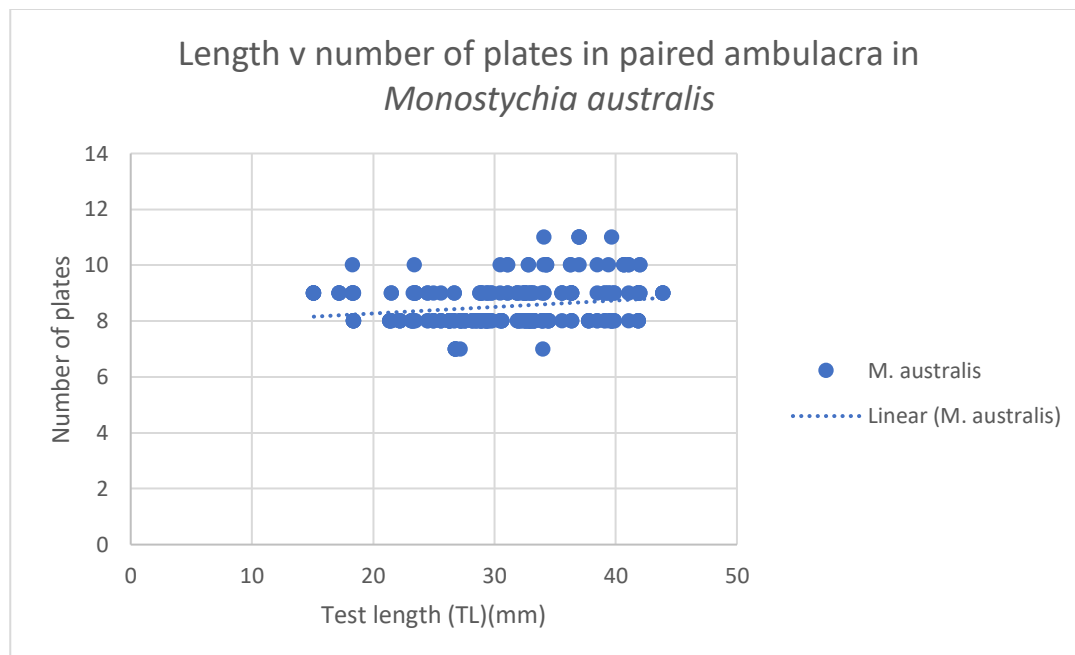
Appendix Fig.4.12. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of *Rotundastychia pledgei*.



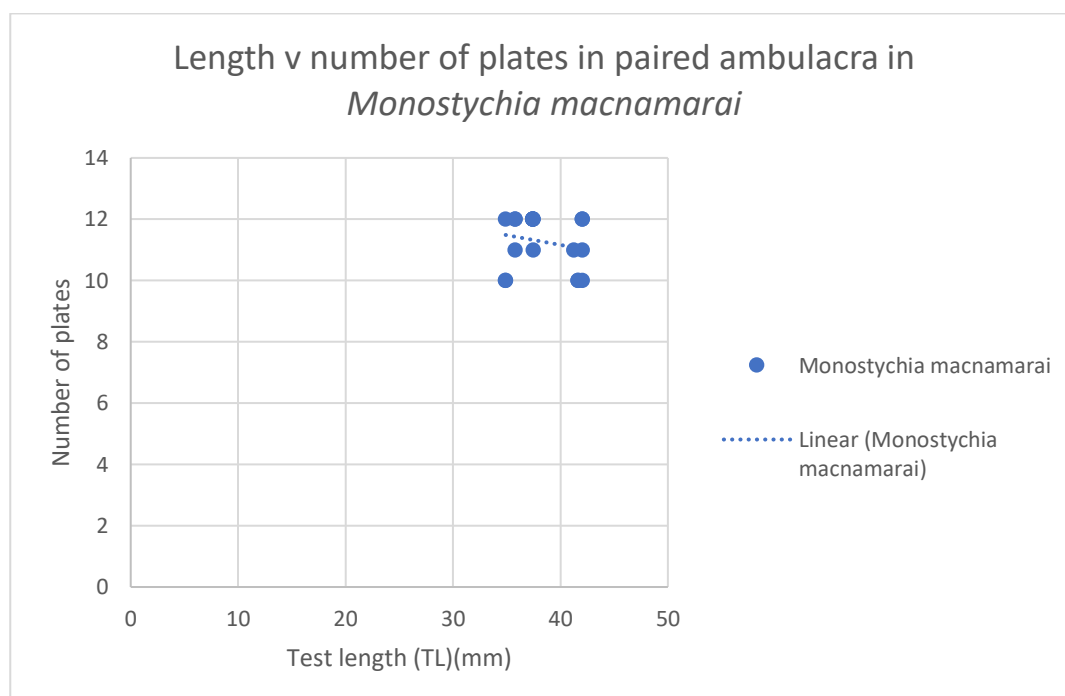
Appendix Fig.4.13. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of *Rotundastychia aquilaensis*.



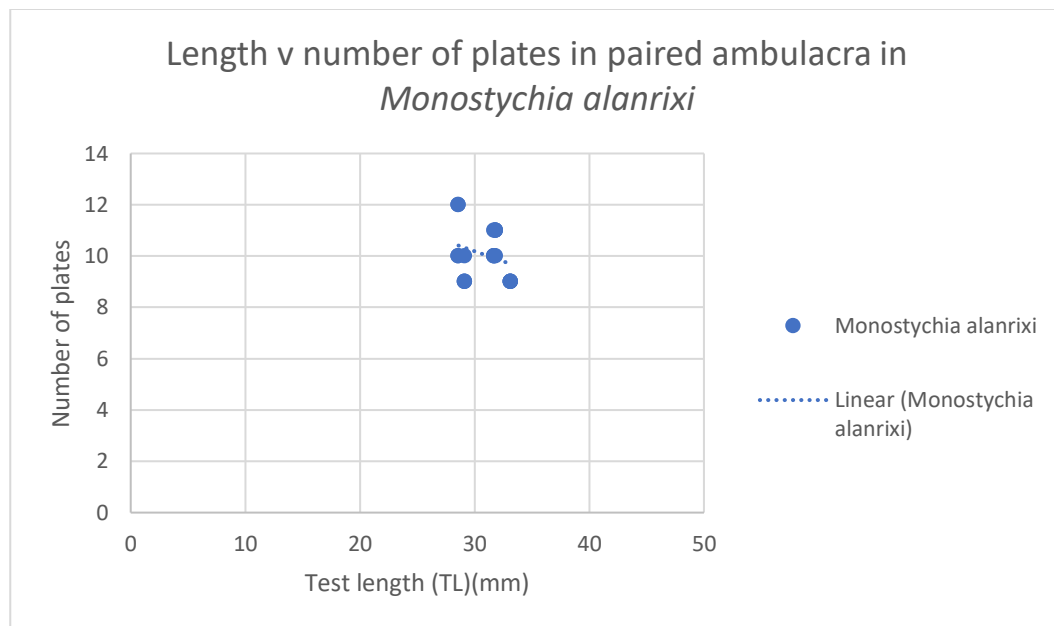
Appendix Fig.4.14. Scatter plot of number of interambulacral plates in each of the paired oral interambulacrum against TL of *Rotundastychia eyriei*.



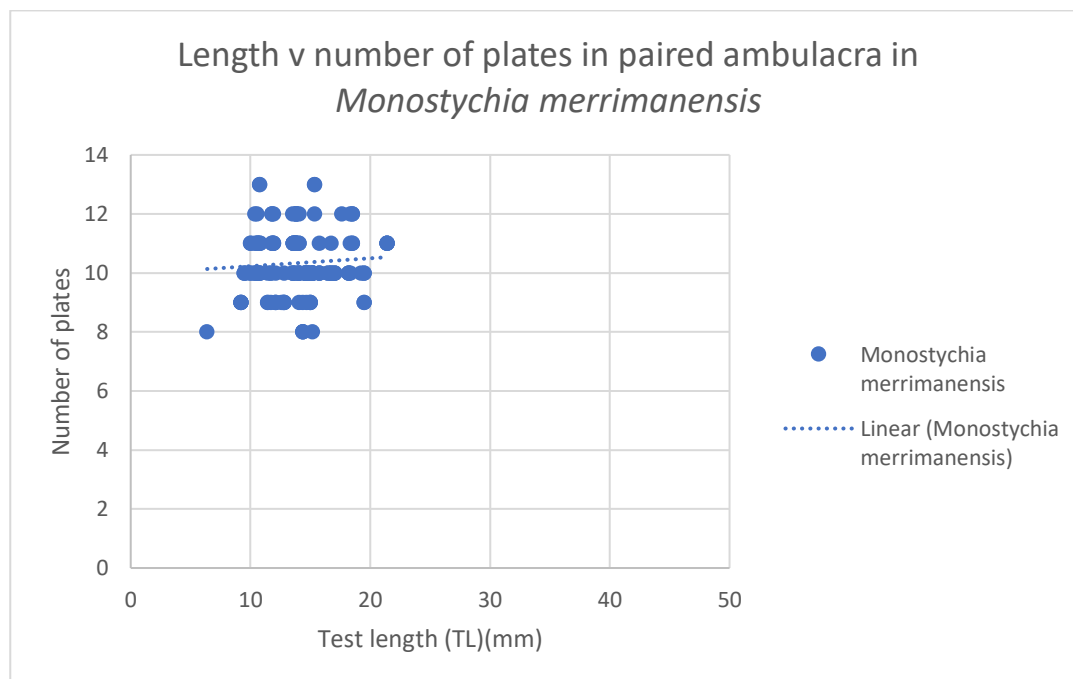
Appendix Fig.4.15. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of *Monostychia australis*.



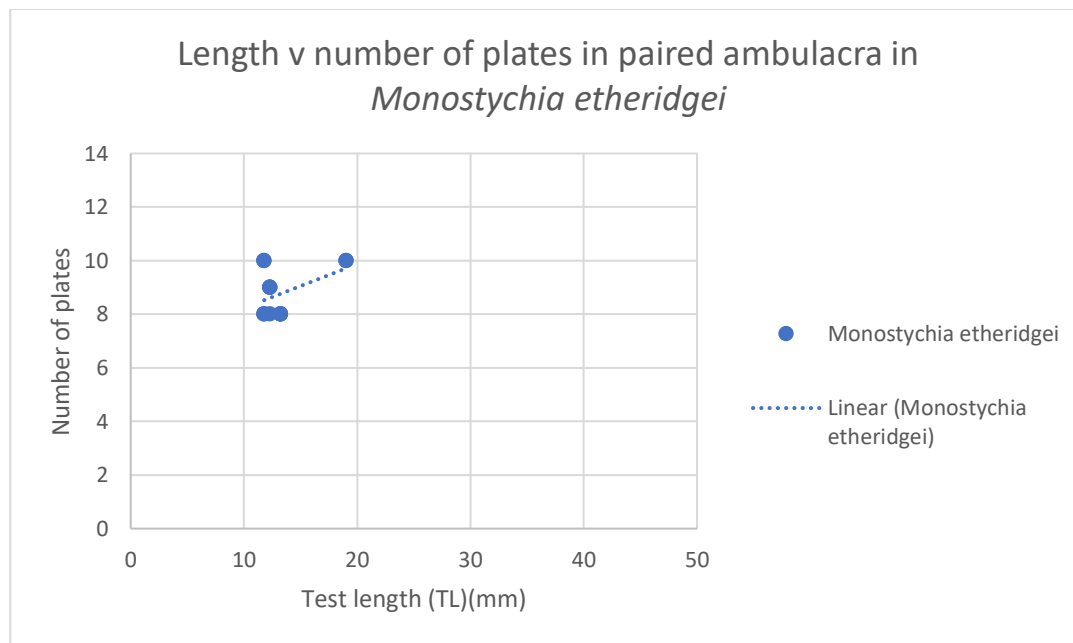
Appendix Fig.4.16. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of *Monostychia macnamarai*.



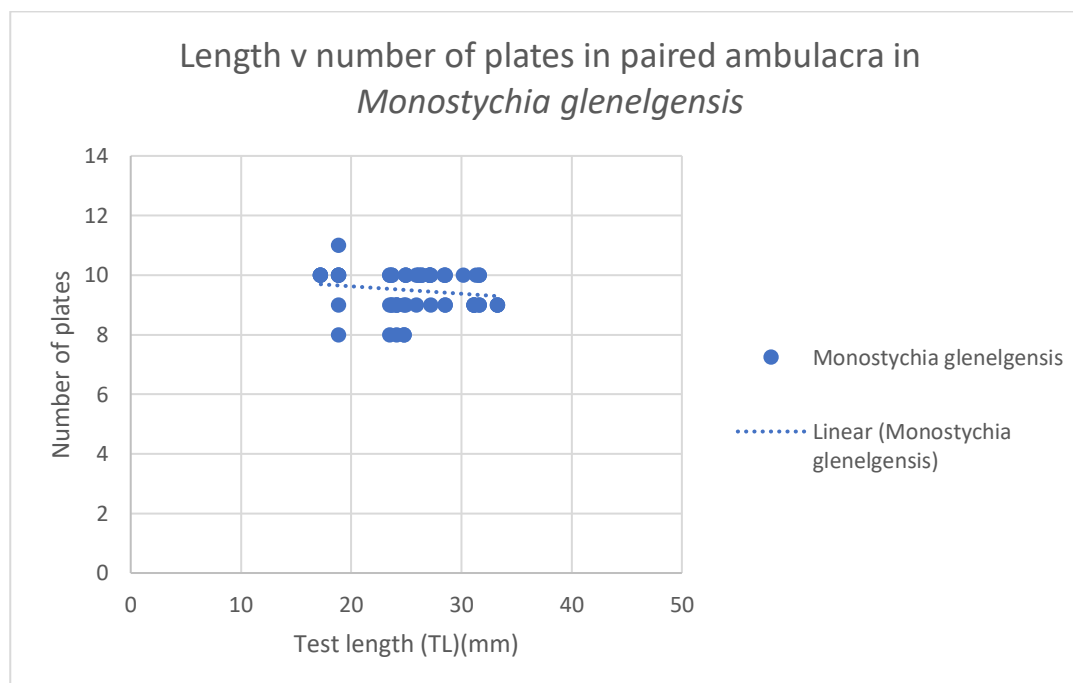
Appendix Fig.4.17. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of *Monostychia alanixi*.



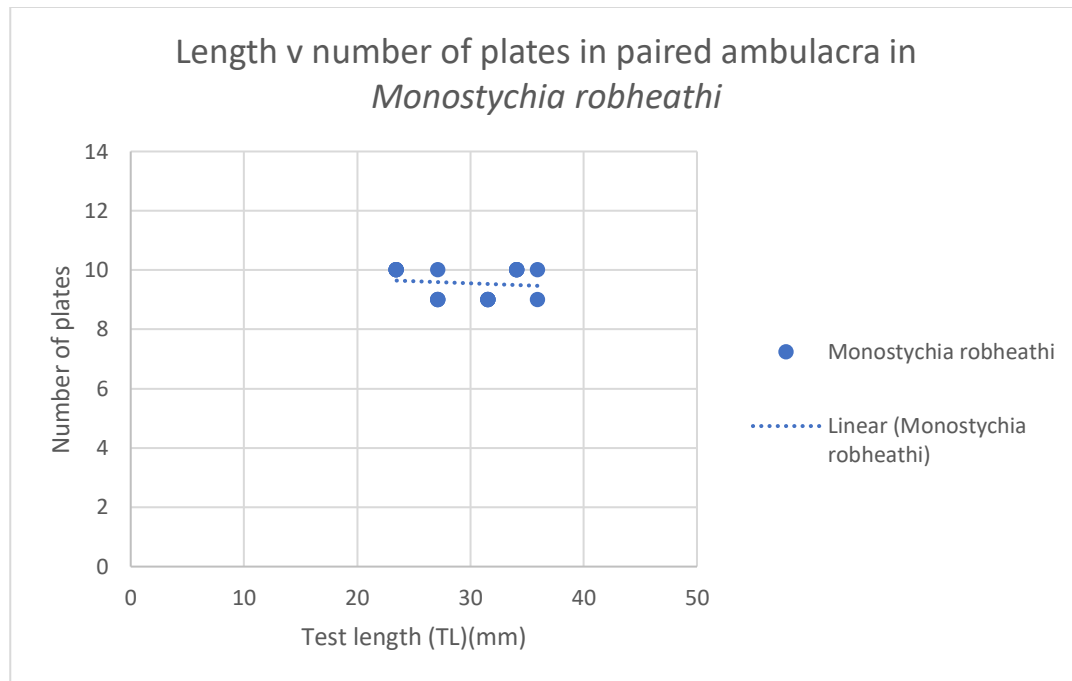
Appendix Fig.4.18. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of *Monostychia merrimanensis*.



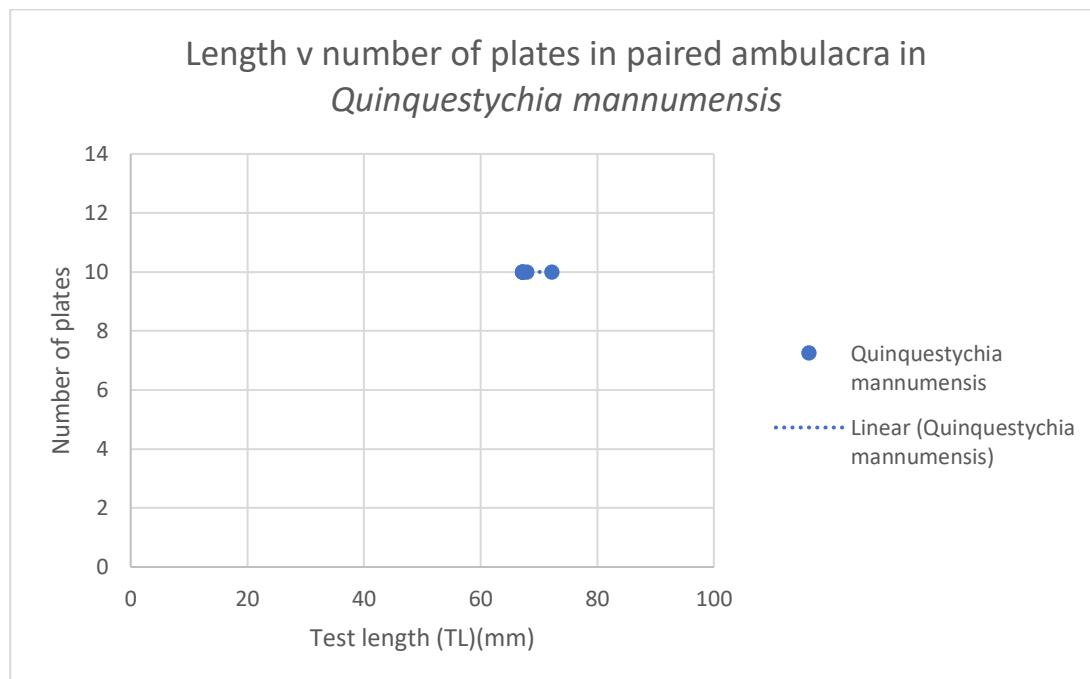
Appendix Fig.4.19. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of *Monostychia etheridgei*.



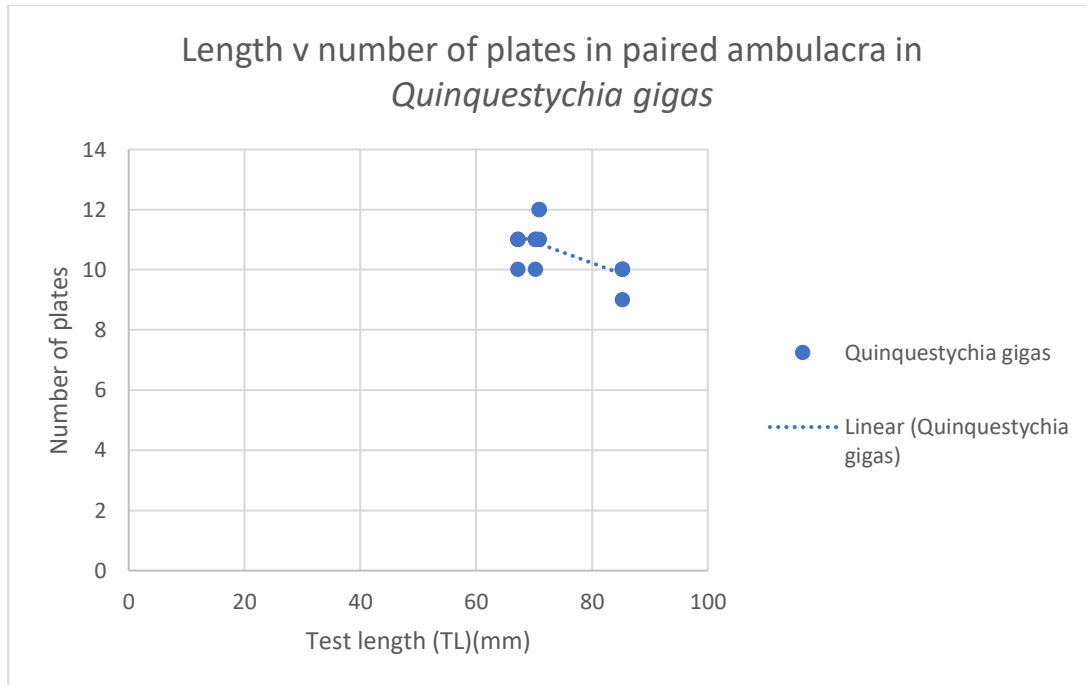
Appendix Fig.4.20. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of *Monostychia glenelgensis*.



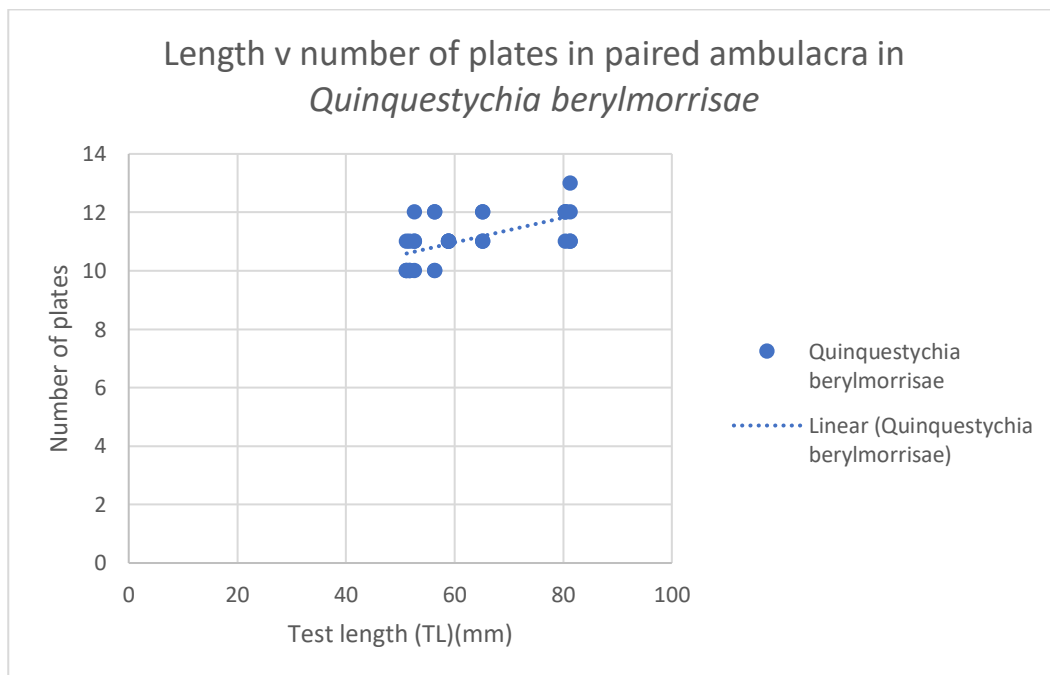
Appendix Fig.4.21. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of *Monostychia robheathi*.



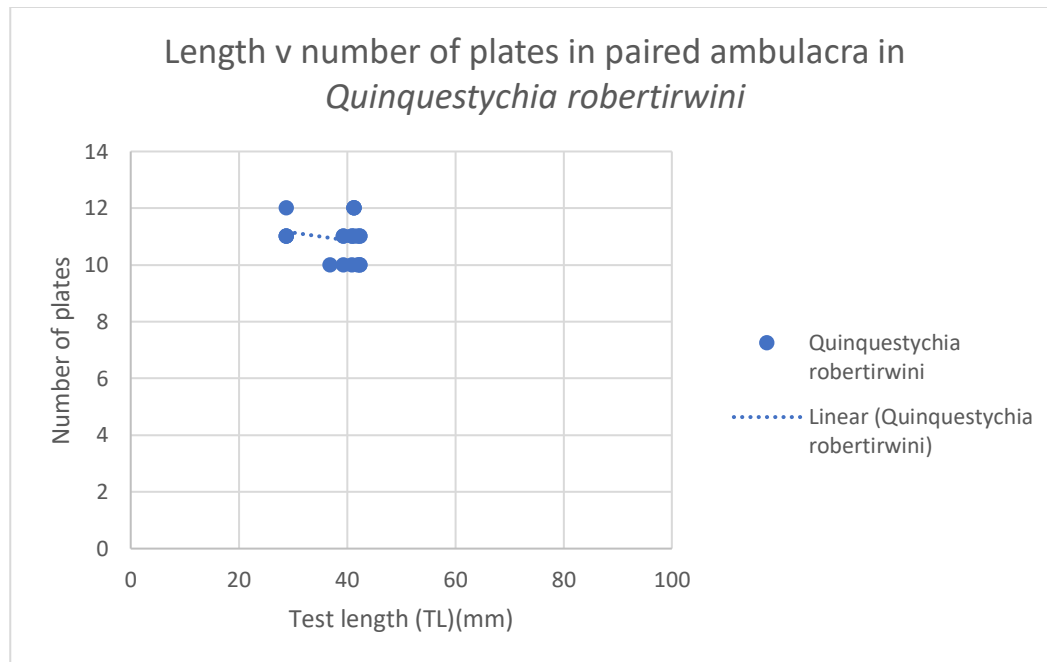
Appendix Fig.4.22. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of *Quinquestychia mannumensis*.



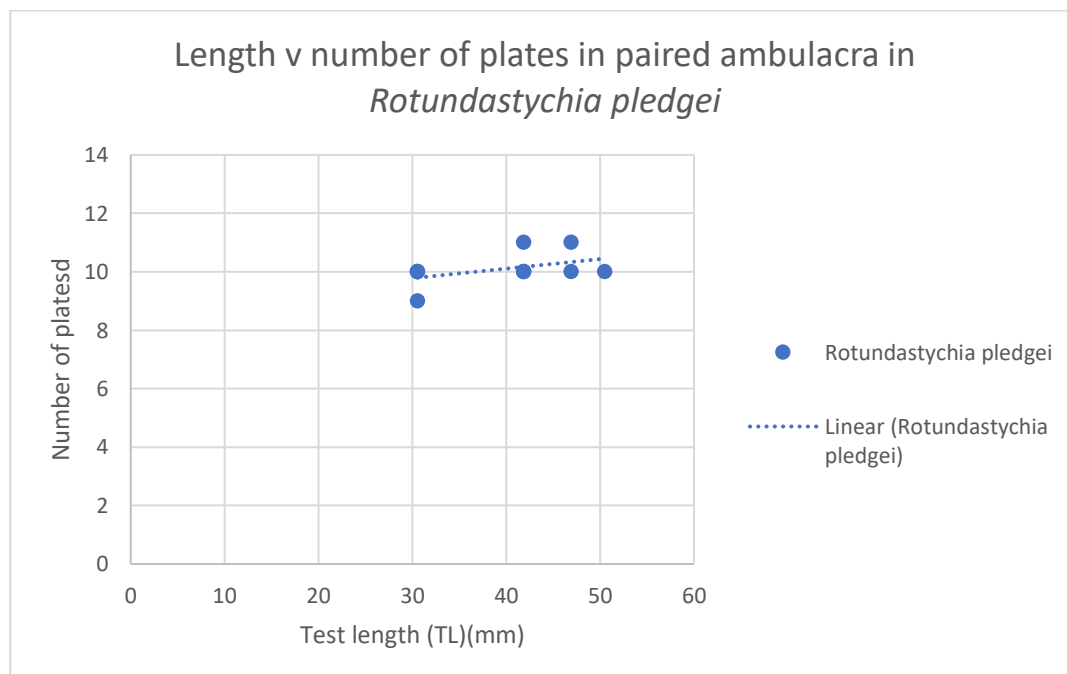
Appendix Fig.4.23. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of *Quinquestychia gigas*.



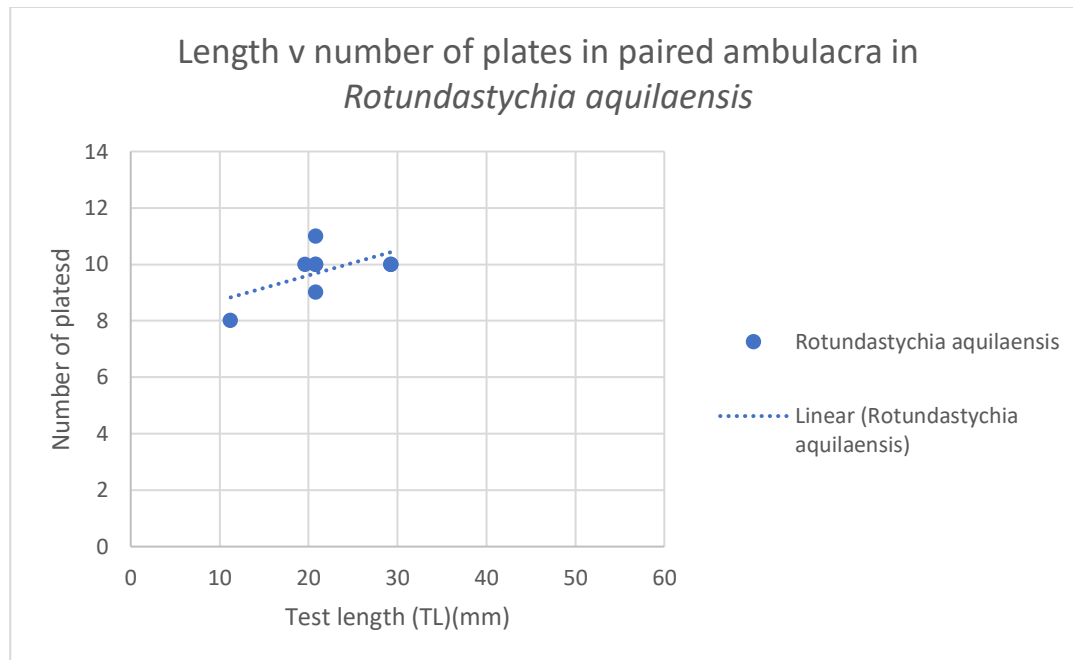
Appendix Fig.4.24. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of *Quinquestychia berylморrisae*.



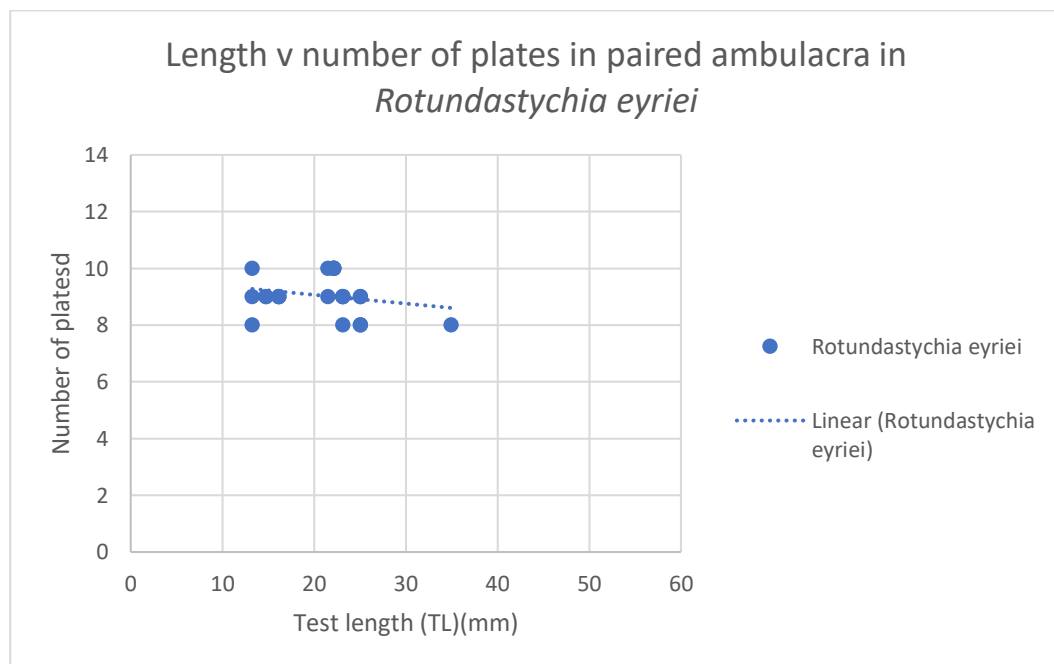
Appendix Fig.4.25. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of *Quinquestychia robertirwini*.



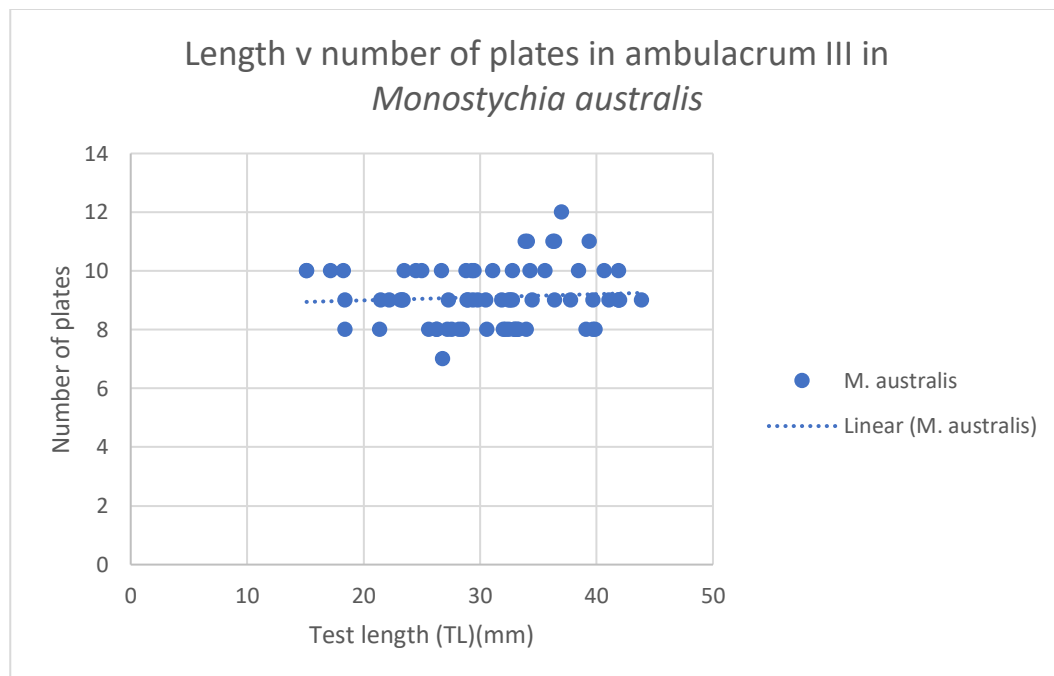
Appendix Fig.4.26. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of *Rotundastychia pledgei*.



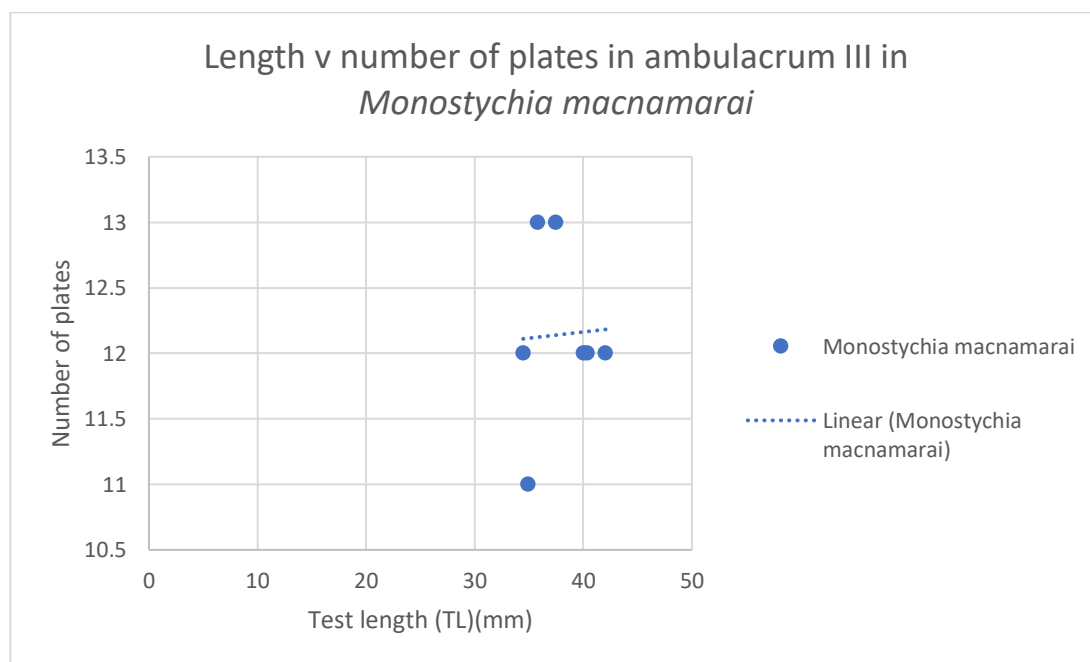
Appendix Fig.4.27. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of *Rotundastychia aquilaensis*.



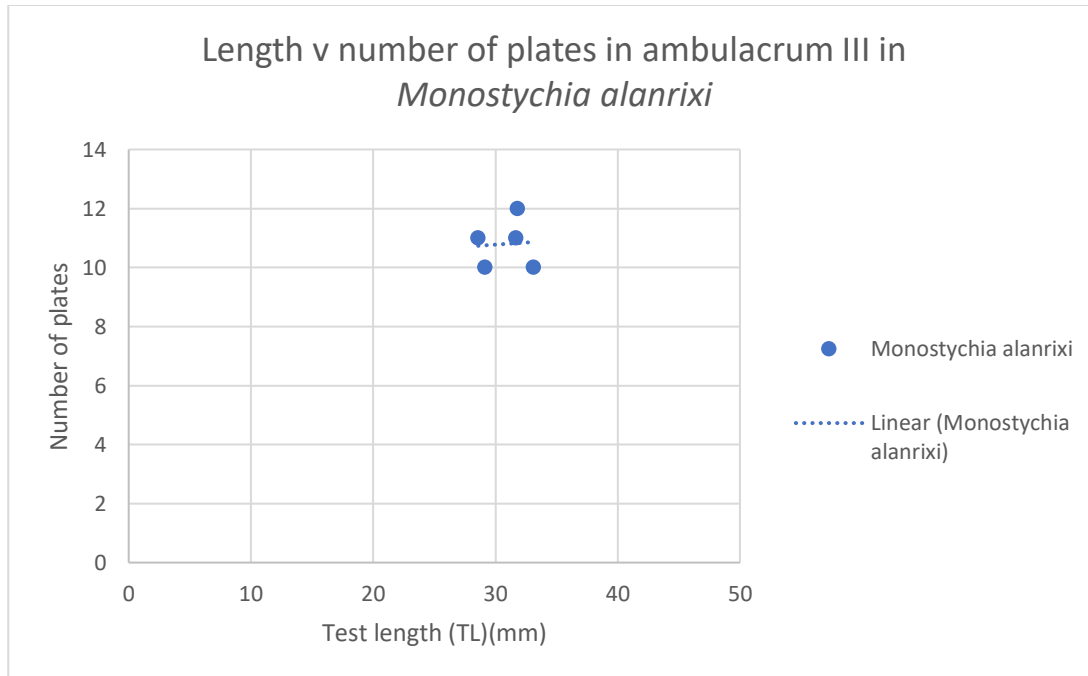
Appendix Fig.4.28. Scatter plot of number of ambulacral plates in each of the paired oral ambulacrum against TL of *Rotundastychia eyriei*.



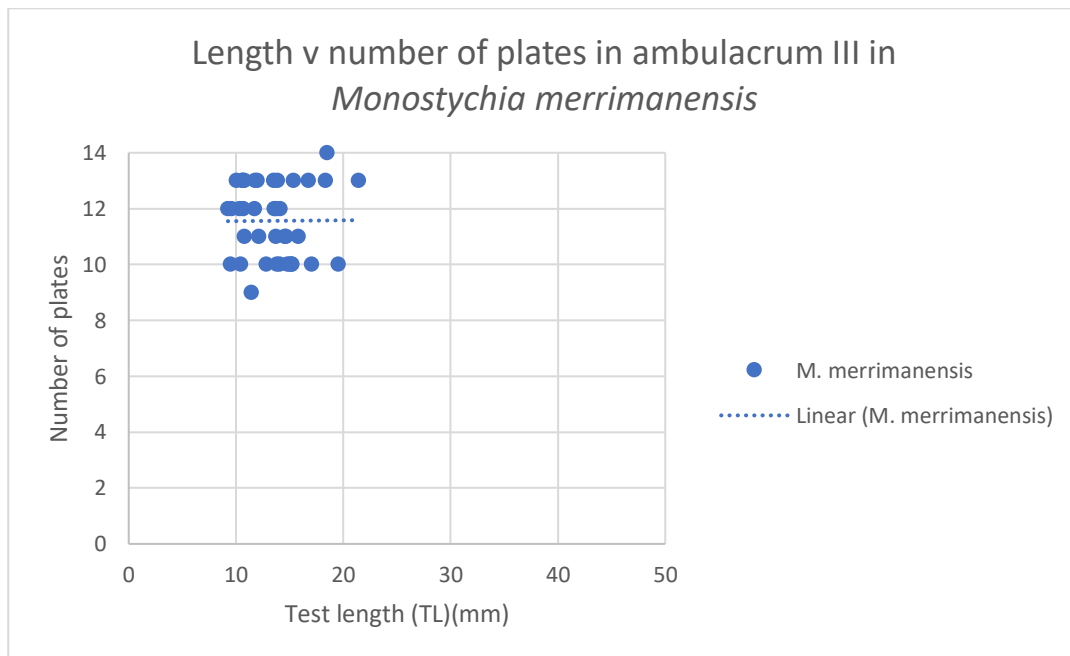
Appendix Fig.4.29. Scatter plot of number plates in ambulacrum III against TL of *Monostychia australis*.



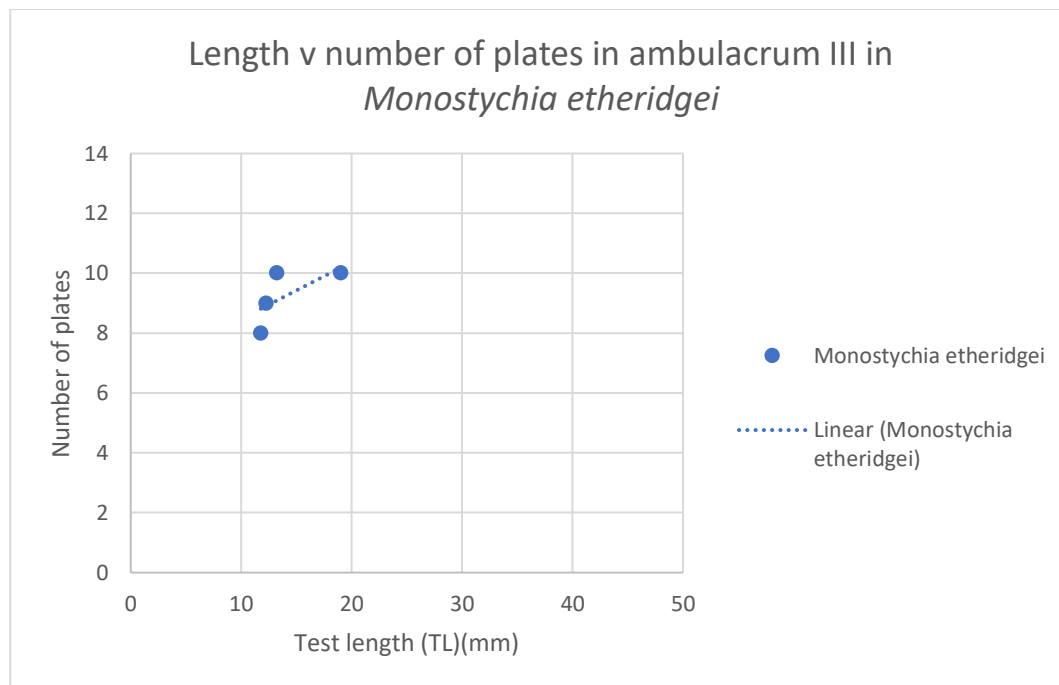
Appendix Fig.4.30. Scatter plot of number plates in ambulacrum III against TL of *Monostychia macnamarai*.



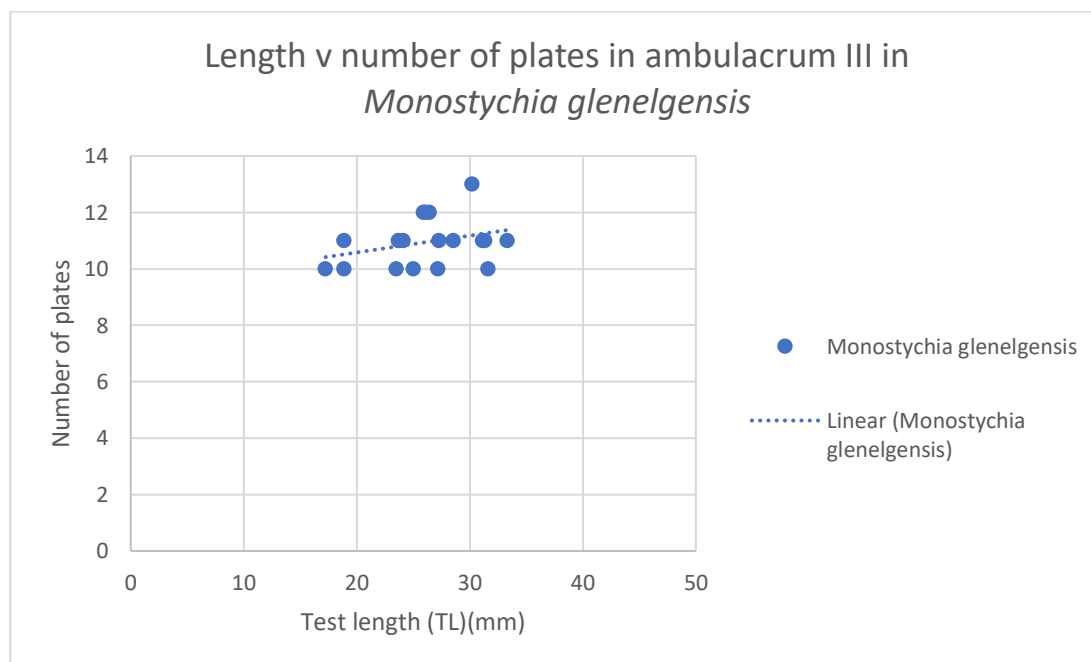
Appendix Fig.4.31. Scatter plot of number plates in ambulacrum III against TL of *Monostychia alanrxi*.



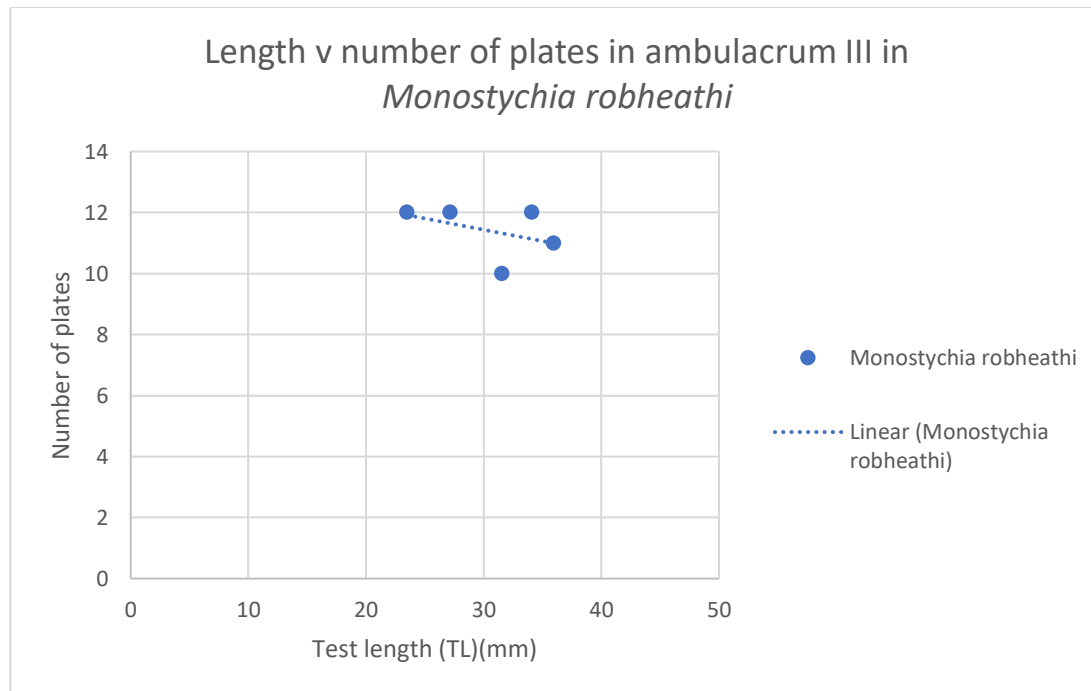
Appendix Fig.4.32. Scatter plot of number plates in ambulacrum III against TL of *Monostychia merrimanensis*.



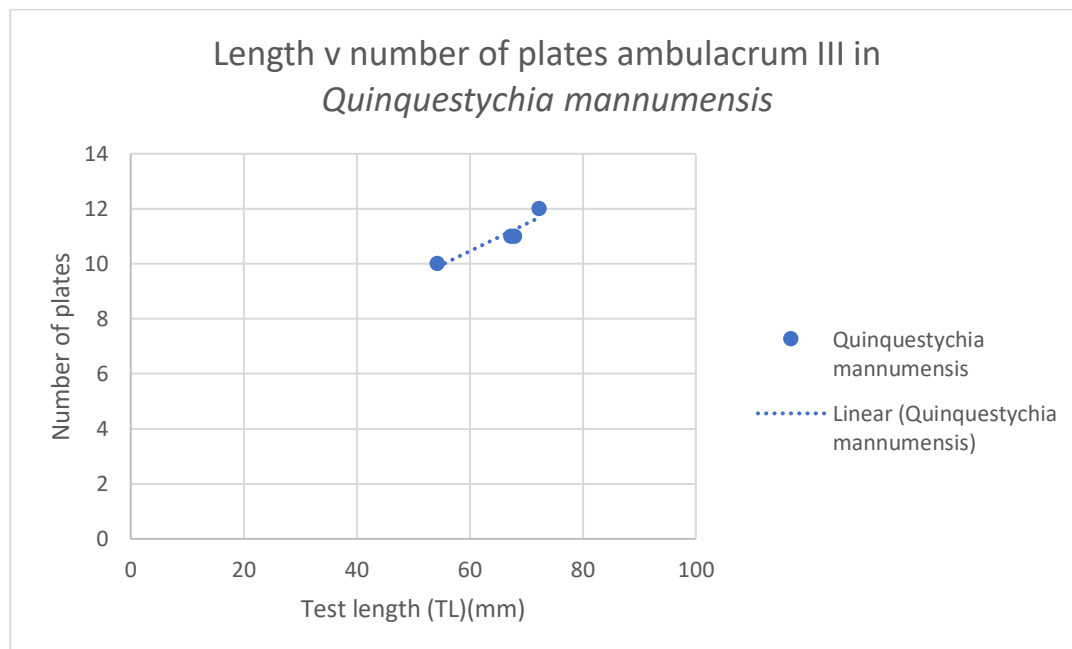
Appendix Fig.4.33. Scatter plot of number plates in ambulacrum III against TL of *Monostychia etheridgei*.



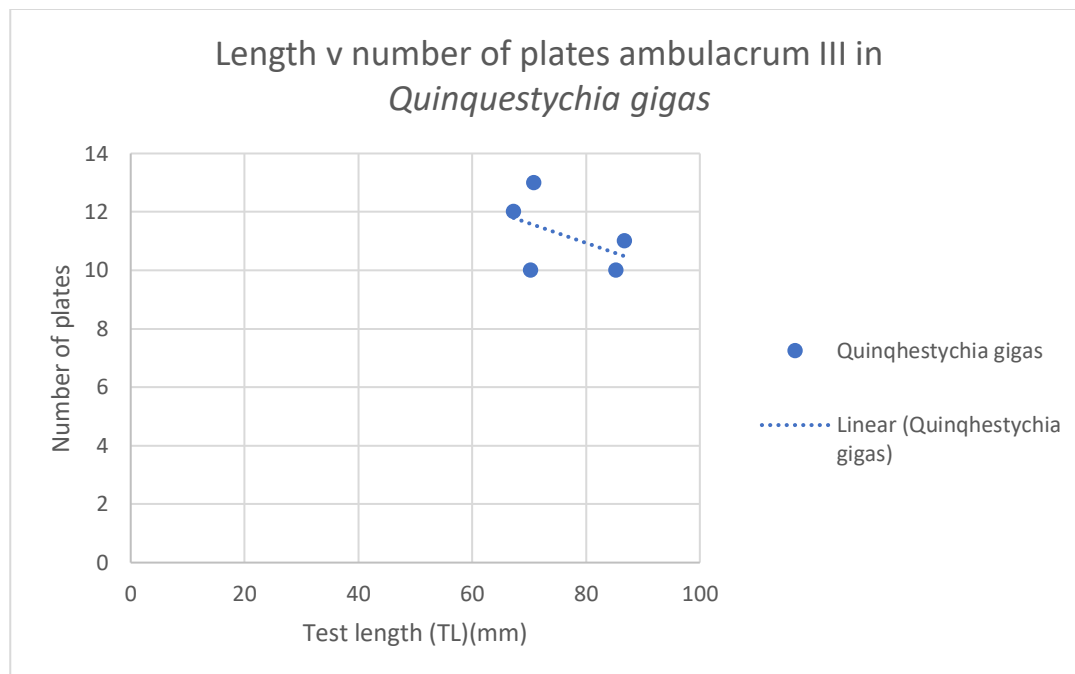
Appendix Fig.4.34. Scatter plot of number plates in ambulacrum III against TL of *Monostychia glenelgensis*.



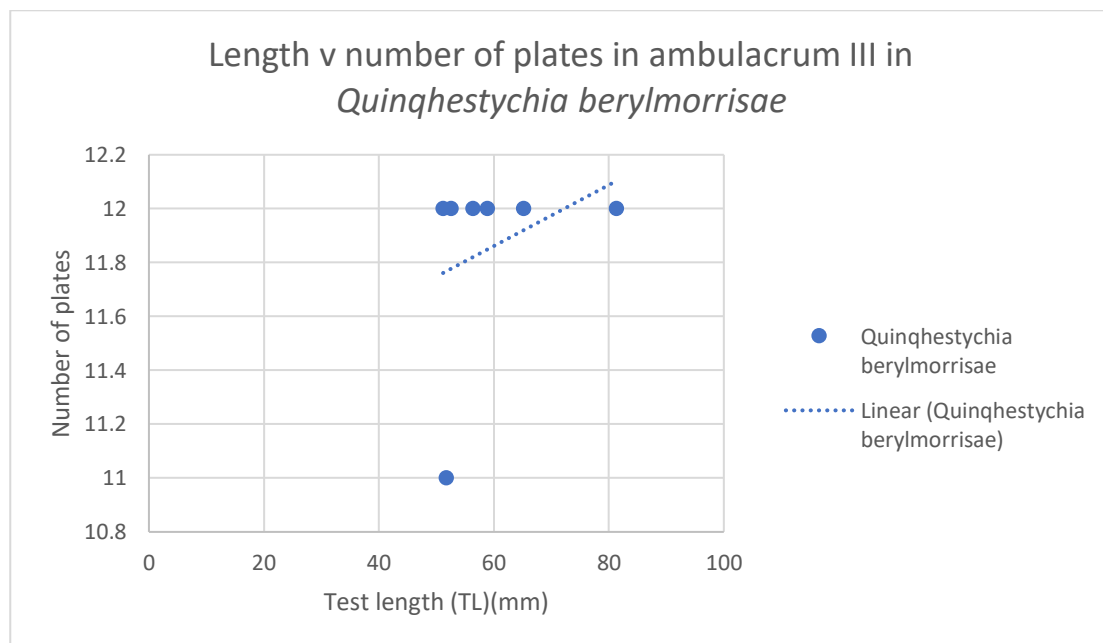
Appendix Fig.4.35. Scatter plot of number plates in ambulacrum III against TL of *Monostychia robheathi*.



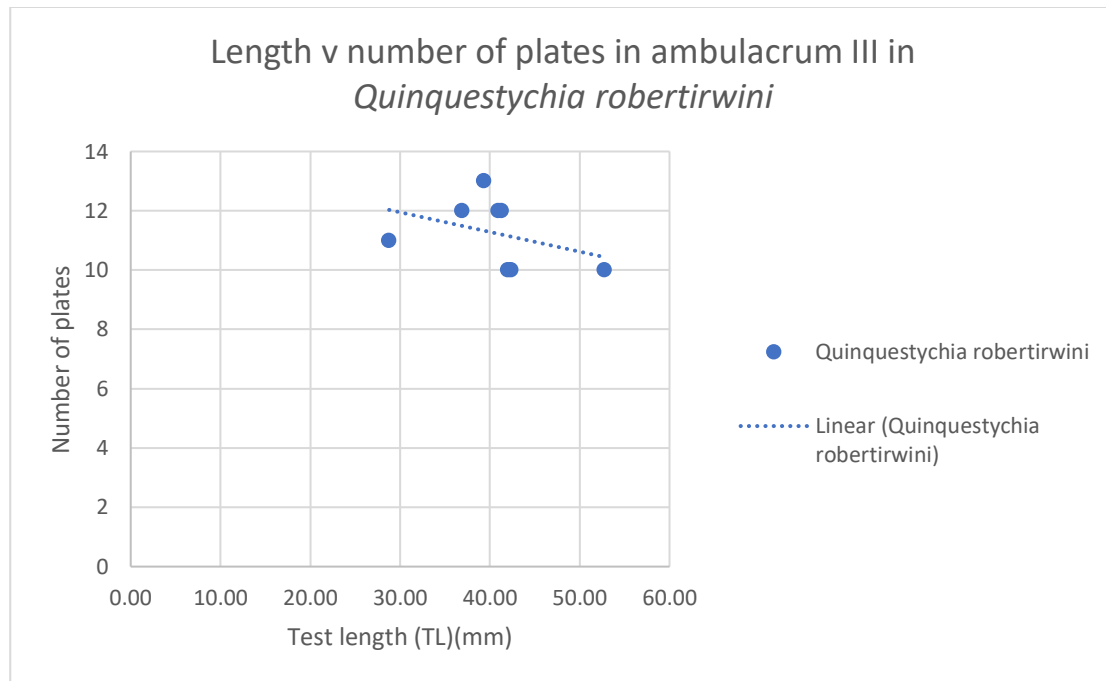
Appendix Fig.4.36. Scatter plot of number plates in ambulacrum III against TL of *Quinquestychia mannumensis*.



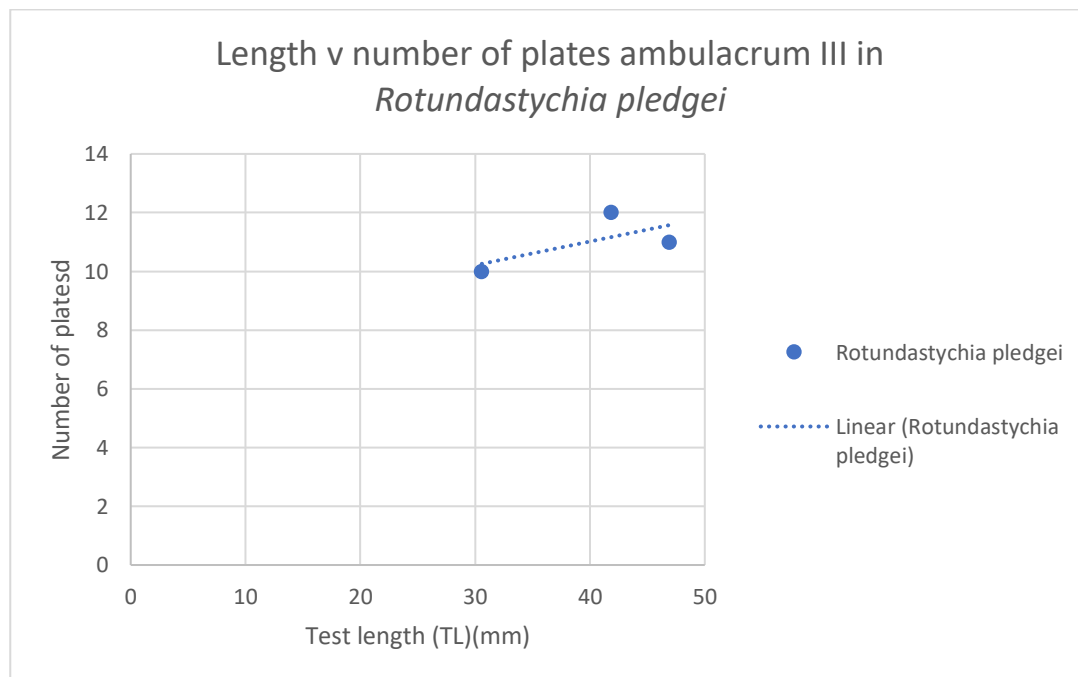
Appendix Fig.4.37. Scatter plot of number plates in ambulacrum III against TL of *Quinquestychia gigas*.



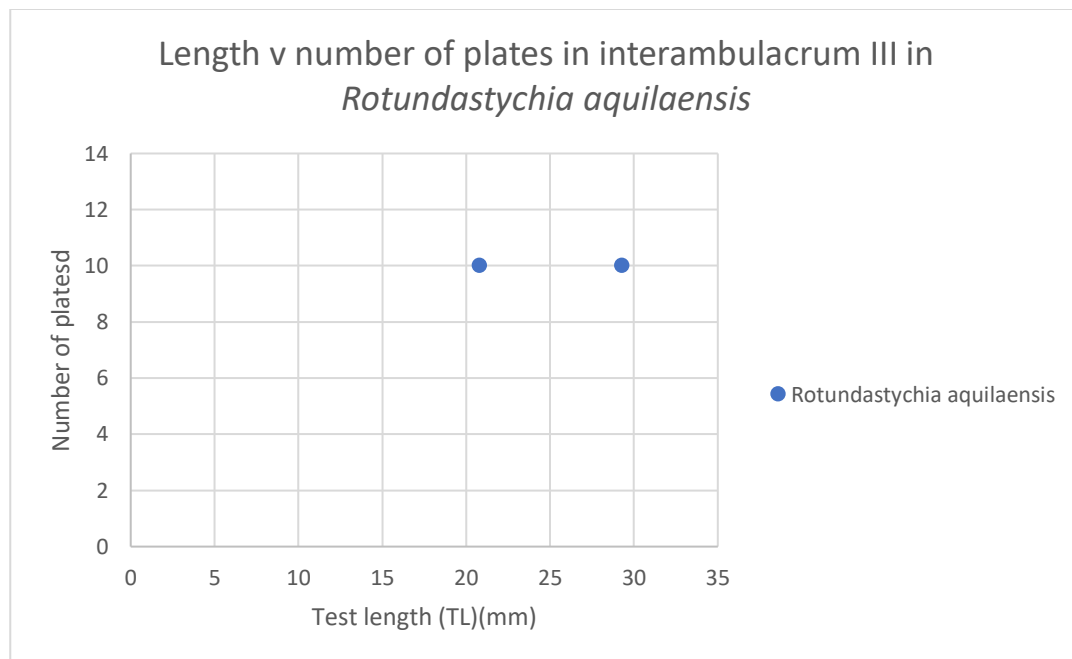
Appendix Fig.4.38. Scatter plot of number plates in ambulacrum III against TL of *Quinquestychia berylmorrisae*.



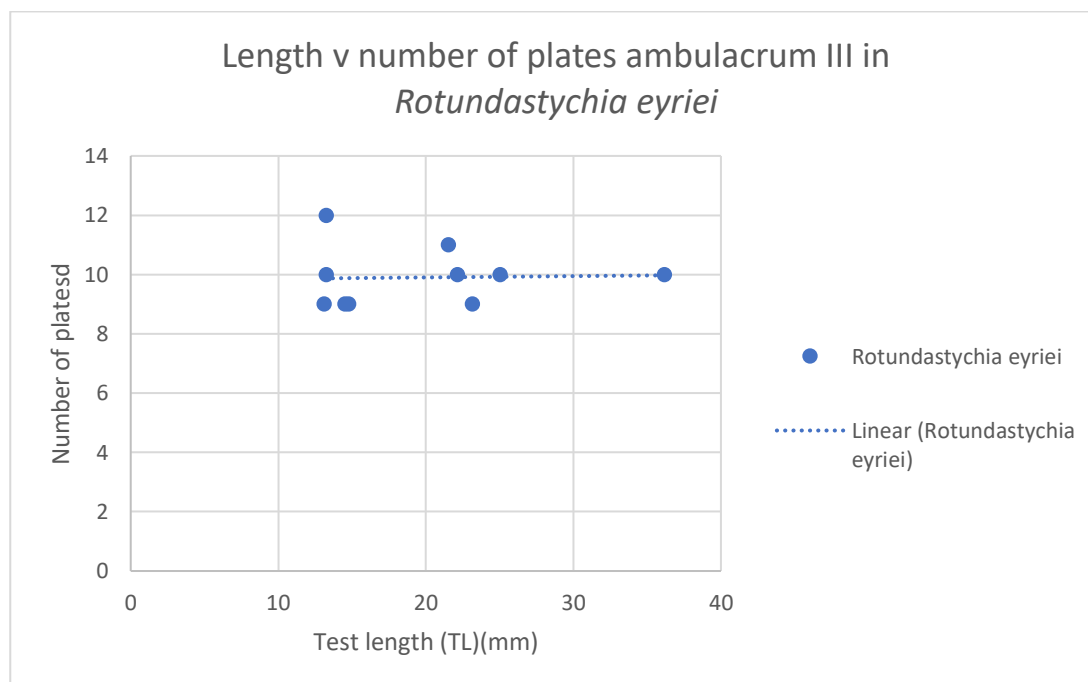
Appendix Fig.4.39. Scatter plot of number plates in ambulacrum III against TL of *Quinquestychia robertirwini*.



Appendix Fig.4.40. Scatter plot of number plates in ambulacrum III against TL of *Rotundastychia pledgei*.



Appendix Fig.4.41. Scatter plot of number plates in ambulacrum III against TL of *Rotundastychia aquilaensis*.



Appendix Fig.4.42. Scatter plot of number plates in ambulacrum III against TL of *Rotundastychia eyriei*.

Appendix 4. Refereed publications

Some of the findings of this research have been published. While none of these publications have been used in their entirety as chapters of this thesis, several chapters have significant overlap with the publications. The three publications listed below have been provided in their entirety in this appendix.

Sadler, T., Kroh, A. & Gallagher, S.J., 2016, **A review of the taxonomy and systematics of the echinoid genus *Monostychia* Laube, 1869**. *Alcheringa* 40, 341-253. (Date accepted 12/01/2016.)

Sadler, T., Martin, S.K. & Gallagher, S.J., 2017, **Three new species of the echinoid genus *Monostychia* Laube, 1869 from Western Australia**. *Alcheringa* 41, 464–473. (Date accepted 11/11/2016.)

Sadler, T., Holmes, F.C. & Gallagher, S.J., 2019, **Two new species of the echinoid genus *Monostychia* from the Miocene of Victoria and a redescription of *M. etheridgei* Tenison-Woods, 1877**. *Alcheringa* 43, 279-290. (Date accepted 22/09/2018.)