CHAPTER 4. RESULTS - PHYLOGENY AND BIOGEOGRAPHY OF THE ANASPIDACEA

Introduction

The current phylogenetic position of the Syncarida and its three orders, the Anaspidacea, Palaeocaridacea and Bathynellacea, has been generally accepted as being one of the basal groups with the Malacostraca although the exact position still seems to be a matter of some debate. The relationships within the Syncarida are historically accepted as monophyletic (Schram 1984, Jenner 2009, Coineau & Camacho 2013) although there has again been recent debate about the inclusion of the Bathynellacea and whether this Order should be placed in its own Superorder Podophallocarida (Serban 1972, Tabacaru & Danielopol 2011, Coineau & Camacho 2013). This monophyletic concept of the relationships of the taxa within the Anaspidacea is tested against a more detailed morphological examination of all previously described species and new taxa. The phylogeny of the Anaspidacea is determined by cladistic analysis of morphological characters and character states. The analysis includes 65 taxa with the Anaspidacea and Palaeocaridacea included within the ingroup and the two families of Bathynellacea, the Parabathynellidae and Bathynellidae as the outgroup. A revised classification of the Anaspidacea and Palaeocaridacea is provided and new higher level diagnoses are provided for the Suborders.

In order to investigate the evolutionary pathways and changes in morphology of the Anaspidacea, it is also necessary to include in this examination, the extinct group of Syncarida, the Palaeocaridacea as the possible ancestral lineage of the Anaspidacea. This group illustrates the diversity in form and it is necessary to test this diversity in relation to the Anaspidacea in order to determine the most likely evolutionary pathways. Indeed, *Gampsonyx fimbriatus* Jordan (later to renamed by Roemer; (1856) *Uronectes fimbriatus* (Jordan 1847)) was the first described species of what came to be acknowledged as a diverse radiation of 'palaeocaridaceans' in the Palaeozoic. However, previous cladistic analyses (Schram 1984) reveal that the so-called 'Order' Palaeocaridacea constitutes a paraphyletic series of stem families that lead to the crown group Anaspidacea. This analysis will also examine the possible paraphyletic relationship within the Palaeocaridacea and with the Anaspidacea. The cladistic analysis is followed by an examination of the implications of the results in terms of the biogeography and evolutionary pathways of the Anaspidacea.

Materials and Methods

The character matrix for the cladistic analysis was developed from the detailed examination of the three Orders of the Syncarida with a particular focus on the Anaspidacea in Chapter 3, and the Palaeocaridacea in Appendix 7.3. In total there are 65 species analysed including 40 species from the Anaspidacea, 23 Palaeocaridacea and 2 species of Bathynellacea. The Bathynellacea were used as the outgroup, as all previous studies described earlier indicated were coded using a combination of the examination of one

species from each of the two families and the general characteristics of each family as described in McLaughlin 1980. The two species included *Bathynella natans* Vejdovsky 1882 for the Bathynellidae, and *Kimberleybathynella gigantea* Cho *et al.* 2005, for the Parabathynellidae. The investigation accumulated 130 characters which were assembled in a DELTA (Description language for Taxonomy; (Dallwitz et al. 1980, 2005) database. Of the 130 characters initially coded, 126 were used in the analysis with four excluded as they are extrinsic characters which include habitat salinity (marine/freshwater), habitus (surface water/hyporheic or phreatic), family distribution (global to localised), and the age of existence (extant or age of fossils in million years).

The phylogenetic reconstruction analysis was performed with MESQUITE Version 2.75 (build 564) (Maddison & Maddison 2011) and (PAUP version 4.0b8a (Swofford 2003) using heuristic searches and the maximum parsimony (MP) approaches. 2000 different replications were performed, with each having a different random swap sequence of taxa to form the Wagner tree with subsequent TBR branch swapping for each replication. To examine relationships between species of Anaspidacea, the Palaeocaridacea was included in the ingroup with no inference was made regarding the age of the fossils. Two outgroups were used (No. 64-65). All characters were equally weighted. A nonparametric bootstrapping was used with 1000 replicates to assess the stability of internal branches in the resulting topologies (Felsenstein 1985; Felsenstein & Kishino 1993). Heuristic search settings: Optimality criterion = parsimony. 126 total characters were used. All characters are of type 'ord' (Wagner). All characters have equal weight. 2 characters are constant and 3 variable characters are parsimony-uninformative. There were 121 parsimony-informative characters = 121 with gaps are treated as "missing". Multistate taxa interpreted as uncertainty. Starting tree(s) were obtained via stepwise addition with a random addition sequence. 2000 replicates were performed with a starting seed = 265301734. Number of trees held at each step during stepwise addition = 1. Branch-swapping algorithm was tree-bisection-reconnection (TBR). Steepest descent option was not in effect. No more than 100 trees of score (length) greater than or equal to 1 were saved in each replicate. 'MaxTrees' setting = 1000 (will not be increased). Branches collapsed (creating polytomies) if maximum branch length is zero. 'MulTrees' option in effect. The Heuristic search completed a total number of rearrangements tried = 5.9991e+009. Score of best tree(s) found = 900. Number of trees retained = 625

Morphological Analysis

The variability in morphology of the Anaspidacea has been as a result of being an ancient lineage that has occupied a range of habitats from surface water lakes, rivers, wetlands, deltas, estuaries and even inshore marine environments. The complexity of their morphology was additional complicated by have genetically conservative genes that genetic change has not been reflected in morphological change for example within *Anaspides tasmaniae* (Jarman & Elliot, 2000) and the Bathynellacea (Coineau & Camacho 2013) as well as having a number of families colonizing and progressively adapting to subterranean interstitial life. The adaption to this environment within the Syncaridan has involved morphological convergence with its

progressive loss of articulation, segmentation, sense organs as well as the development of specialised structures (Coineau & Camacho 2013). Another phenomenon exhibited by the Syncarida is progenesis which has retention of larval characteristics in adult groundwater fauna. This has resulted in a diverse and intrinsically difficult group from which to determine useful diagnostic characters for analyzing phylogenetic relationships. The characters sequences used in the analysis follow the general concept that body structures such as body segmentation and limb articulation, particularly for species that migrate from the surface into subterranean environments will change from multisegmented states to reduced states to total absence via a reduction in segmentation. The analysis has included all taxa listed except for the fossil syncarid, *Brooksyncaris canadensis*, which was not included due to the poor preservation and therefore a lack of features. Each character below has been assigned a number of states representing the changes in that state across the taxa. Each state is numbered representing the ordering of the states is from state 0 to state 1, state 2 … etc., where the states progress from a considered plesiomorphic to apomorphy state. For example the first character, the carapace, contain two states that indicate a taxa may either not possess a carapace (state 0) or possess a carapace (state 1) with the assumption that the plesiomorphic state is the absence of a carapace. Each state is represented by a number that is coded into the Character Matrix in Appendix 7.3.

Body

1- Carapace: state 0- absent, state 1- present.

2- Body Shape: state 0- straight, state 1- slight dorsal flexure, state 2- prominent dorsal flexure between per 7-8 and expanded per 6.

3- Body Size (maximum length in mm): state 0- 40-60, state 1- 20-39, state 2- 10-19, state 3- 4-9, state 4- 0-5-3.

4- Number of free pereonites: state 0- 8, state 1- 7.

5- Number of free pleonites: state 0- 6, state 1- 5.

6- Colouration: state 0- externally pigmented with spots, state 1- non-pigmented.

7- Dorsal body surface structure: state 0- smooth, state 1- setose, state 2- crenulated, state 3- transverse striations, state 4- dorsal midline ridges and spines , state 5- pereonites with anterior row of tubercles, state 6- long spines on somite margins.

Thoracomeres

8- Thoracomere 1 connection with cephalon: state 0- unfused, state 1- partly fused, prominent mandibular groove present, state 2- fused, no groove present.

9- Thoracomere 1 length relative to pereonite 2: state 0- subequal, state 1- shorter = 50%, state 2- shorter =30%, state 3- absent.

10- Thoracomere 1 fenestra dorsalis: state 0- absent, state 1- broad, oval plate, state 2- narrow, bright red, cylindrical plate.

11- Thoracomere 2 length relative to pereonite 3: state 0- subequal, state 1- shorter.

12- Thoracomere 2-8 length to pleonites length: state 0- all uniform, state 1- pereonites shorter, state 2- pereonites longer, state 3- pleonites progressively longer.

13- Thoracomere 8 with lateral semi-circular ridges: state 0- absent, state 1- present.

Pleonites

14- Pleonite 5 posterior margin: state 0- smooth or with small simple setae, state 1- short robust setae, state 2- serrate.

15- Pleonite 5 lateral posterior margin shape: state 0- straight, state 1- indented, state 2- extended.

16- Pleonite 6 posterior margin shape: state 0- straight, state 1- indented, state 2- extended.

17- Pleonite 6 posterior margin: state 0- smooth, state 1- short robust setae, state 2- long, robust, articulated spines, state 3- serrate - short cuticular spines.

18- Pleonite 6 length to Pleopod 5 length: state 0- subequal, state 1- longer, state 2- shorter.

19- Pleonite 6 length to width ratio: state 0- subequal, state 1- longer than wide, state 2- shorter than wide.

20- Pleonite 6 (No of articulated spines on posterodorsal margin): state 0- 0, state 1- 2, state 2- 3, state 3- 4, state 4- 5, state 5- >5.

21- Pleonite 6 length of posterior margin spines to telson length ratio: state 0- < 0-1, state 1- 0-5, state 2- 1-0 <.

22- Pleonite pleura shape: state 0- straight or extended posteriorly, state 1- rounded, state 2- triangular, state 3- spiny or serrate, state 4- single, elongate spine, state 5- pl 1-4 large rounded lappets.

Cephalon

23- Cephalon length to height: state 0- length < height, state 1- length = height, state 2- length > height.

24- Cephalon mandibular groove: state 0- absent, state 1- present.

25- Cephalon cervical grooves: state 0- 0 grooves, state 1- 1 groove dorsal, state 2- 1 groove lateral.

26- Cephalon dorsal lobes: state 0- absent, state 1- single cross shaped medial endite covering rostrum and nuccal organ, state 2- present as 2 large lateral and 1 smaller anteromedial dorsal lobes.

27- Cephalon anteromedial shape: state 0- broad rounded, state 1- broad triangular, state 2- elongate rounded, state 3- elongate triangular, state 4- elongate rectangular, state 5- anteromedial notch.

28- Nuccal organ: state 0- absent, state 1- present.

29- Optic notch: state 0- absent, state 1- small semicircular concavity on anterolateral corner of cephalon state 2- anterior margin of cephalon strongly concave with no defined notch.

Eyes

30- Eye Structure: state 0- stalked, state 1- sessile, state 2- absent.

31- Eye stalk direction: state 0- anteriorly, state 1- directed laterally.

32- Eye-stalk tubercle: state 0- absent, state 1- present.

33- Ocelli Occurrence: state 0- present, state 1- reduced, state 2- absent.

34- Eye position: state 0- distal, state 1- distolateral, state 2- lateral.

Rostrum

35- Rostrum formation: state 0- anterior margin of cephalon dorsal plate, state 1- anterior articulated plate separate from cephalon dorsal plate.

36- Rostrum - number of terminal points: state 0- 0, state 1- 1, state 2- triangular, distally bilobed, state 3- triangular bilobed separate by diastema, state 4- 3.

37- Rostrum seta - number of pairs: state 0- 0, state 1- 1, state 2- 2, state 3- >2.

38- Rostrum setal position: state 0- distal, state 1- lateral.

Antennule

39- Peduncle segment 2 - Length to width ratio: state 0- length > width, state 1- length subequal width.

40- Peduncle segment 3 - Length to width ratio: state 0- length > width, state 1- length = width, state 2- length < width.

41- Antennal lobe on basal segment of flagellum in the males: state 0- absent, state 1- present.

42- Lateral antennular flagellum length to body length ratio: state 0- 100% or <, state 1- 50-40%, state 2- 40-30%, state 3- <30%.

43- Medial antennular flagellum length to lateral flagellum length ratio: state 0- <50%, state 1- 50-70%, state 2- >70%.

Antenna

44- Antenna peduncle - No- of segments: state 1- 4, state 2- 3.

45- Antenna length to body length ratio: state 0- greater than 1 body length, state 1- 80-100% body length , state 2- 50-80%, state 3- < 50%.

46- Antenna length to antennule length: state 0- shorter, state 1- equal.

47- Antenna peduncle segment 1 length to width ratio: state 0- length > width, state 1- length = width, state 2- length < width.

Scaphocerite

48- Scaphocerite structure: state 0- absent, state 1- oval distally pointed, state 2- oval distally rounded, state 3- oval distally rounded with distomedial spine, state 4- oval distally pointed with distomedial spine, state 5- diamond shaped with distomedial spine.

Labrum

49- Labrum ventral margin: state 0- round, state 1- small medial notch, state 2- large medial concavity.

Mandible

50- Mandible left incisor process (pars incisiva) - denticle structure: state 0- 5-6 subequal denticles, state 1- 1 large bicuspid, 5 subequal smaller denticles, state 2- 1 large bicuspid, 5 smaller, subequal denticles, and row of minute denticles, state 3- 1 large bicuspid, 4 smaller denticles separate from 1-2 larger, pointed, medial denticles, state 4- 1 large bicuspid, 4 smaller denticles, 1 larger medial denticle, not separate, state 5- large bicuspid, 3 smaller denticles, row 2-4 very small, 1 small medial denticle.

51- Mandible spine row (processus incisivus accessorius): state 0- row of 10-11 small simple setae, state 1- row of 3-4 large penicillate setae, state 2- row of 2 large penicillate setae , state 3- 1 large penicillate setae, state 4- absent.

52- Mandible diastema between incisor and molar processes: state 0- broad, state 1- narrow v-shaped.

53- Mandible molar process (pars molaris) terminal surface: state 0- bristle-like short stout setae covering surface, state 1- tuberculate triturating surface, state 2- large, cuticular, spinose denticles.

54- Mandibular palp - No of segment: state 0- 3, state 1- 1 reduced, state 2- 0.

Paragnath

55- Paragnath shape: state 0- oval, state 1- spatulate lobes with straight medial margin, state 2- spatulate lobes with notch in medial margin, state 3- spatulate lobes with notch and v-shaped diastema, state 4- spatulate lobes with a distally directed, medial, triangular extension.

56- Paragnath medial lobe: state 0- absent, state 1- small triangle, state 2- large pointed, mediodistal projection.

57- Paragnath segment No-: state 0- 2, state 1- 1.

Maxillula

58- Maxillula palp - No- of segments: state 0- 1 segment with terminal plumose setae, state 1- 1 segment with no setae, state 2- 0 segments with lateral extension, state 3- no segments and no extension.

59- Maxillula - No- of lobes: state 0- 2 without medial endite, state 1- 2 with medial endite.

60- Maxillula lateral lobe spine row: state 0- > 12 comb setae of equal length to spine, state 1- 12-8 comb setae of equal length to spine, state 2- 7 or > comb setae of equal length to spine, state 3- 7 or > comb setae of shorter than spine.

61- Maxillula spine row structure: state 0- 1 straight tier, state 1- 2 tiers - upper lateral and lower medial.

62- Maxillula lateral lobe spine row angle to length of lobe: state 0- near horizontal, state 1- diagonal, state 2- near vertical.

63- Maxillula medial endite - No- of pectinate spines: state 0- >11 uniform spines, state 1- 5 uniform spines, state 2- 5 with 1 large spine, state 3- 4 uniform spines, state 4- 4 variable size spines, state 5- 3 .

Maxilla

64- Maxilla No- of lobes: state 0- 4 subequal, state 1- 3 subequal with 1 medial endite reduced, state 2- 3 subequal with 2 medial endites reduced, state 3- 2 subequal with 2 endites reduced endites, state 4- 1 large and 2 reduced endites.

65- Medial endite medial margin spine row: state 0- large spine row, state 1- small row with 1-3 spines, state 2- absent.

Maxilliped

66- Maxilliped function/relative size to other thoracopods: state 0- ambulatory, similar to other thoracopods, state 1- raptorial, enlarged, state 2- raptorial with chelae-like propodus and dactylus, state 3- reduced.

67- Maxilliped - No- of coxal epipodites: state 0- 2 large, round lobes, state 1- 2 lobes, 1 large round, 1 narrow, spatulate, state 2- 2 small, subequal, state 3- 2 small lobes, unequal in size, state 4- 1 narrow, spatulate, state 5- 0.

68- Maxilliped coxa endites or medial lobes: state 0- 0, state 1- 1, state 2- 3.

69- Maxilliped basis exopodite shape: state 0- multisegmented, state 1- tubular, elongate apically rounded, state 2- tubular, apically pointed, state 3- absent.

70- Maxilliped basis mediodistal extension or lobe: state 0- absent, state 1- present.

71- Maxilliped propodus terminal setae: state 0- unmodified, simple setae, state 1- modified terminal claw forming a chelate structure with dactylus.

Thorcapods

72- Thoracopod 2 function: state 0- ambulatory, similar to other thoracopods, state 1- raptorial, enlarged, state 2- raptorial with chelae-like propodus and dactylus.

73- Thoracopod 2 - coxa endites or medial lobes state 0- absent, state 1- present.

74- Thoracopod 2 coxa - No- of epipodites state 0- 2 large, round lobes, state 1- 2 lobes - 1 large, round and 1 narrow, spatulate, state 2- 1 narrow, spatulate, state 3- 0.

75- Thoracopod 2 basis exopodite - No of segments: state 0- multisegmented, state 1- tubular, single segment with terminal setae, state 2- 0.

76- Thoracopod 3 function: state 0- ambulatory, similar to other thoracopods, state 1- raptorial, enlarged.

77- Thoracopod 3, Thoracopod - coxa endites or medial lobes: state 0- absent, state 1- present.

78- Thoracopod 3 coxa - No- of epipodites state 0- 2 large, round lobes, state 1- 2 lobes - 1 large round, 1 narrow, spatulate, state 2- 1 narrow, spatulate, state 3- 0.

79- Thoracopod 3 basis exopodite - No of segments: state 0- multisegmented, state 1- tubular, single segment with terminal setae, state 2- tubular, single segment, state 3- 0.

80- Thoracopod 7 - coxa endites or medial lobes: state 0- absent, state 1- present.

81- Thoracopod 7 coxa - No- of epipodites: state 0- 2 large, round lobes, state 1- 2 lobes - 1 large round and 1 narrow, spatulate, state 2- 1 narrow, spatulate.

82- Thoracopod 7 basis exopodite - No of segments: state 0- multisegmented, state 1- tubular, single segment with terminal setae, state 2- tubular, single segment, state 3- 0.

83- Thoracopod 8 - coxa endites or medial lobes: state 1- absent, state 2- present.

Pleopod 1 female

84- Pleopod function: state 0- natatory, multisegmented, state 1- swimming, single segment paddle shapes on peduncle, state 2- reduced, state 3- absent.

85- Pleopod 1 coxa endites or medial lobes: state 0- absent, state 1- present.

86- Pleopod 1 exopodites - No of segments: state 0- multisegmented, state 1- 1-2, state 2- 1 plumose seta, state 3- 0.

87- Pleopod 1 female endopodites - No of segments: state 0- multisegmented, state 1- 1-2, state 2- plumose seta, state 3- 0.

Pleopod 1 Male
88- Pleopod 1 - No- of segments: state 0- 2, state 1- 1.

89- Pleopod 1 distal segment structure: state 0- flat, state 1- moderate medial ridges, state 2- medial ridges form extended/folded to forming distal hood, state 3- medial ridges extended to form ventral and dorsal lobes, state 4- medial ridges extended to form horizontal, lateral and medial digitate lobes.

90- Pleopod 1 distal segment shape: state 0- oblong, state 1- triangular, distally blunt or round, state 2- triangular, distally pointed, state 3- rectangular.

91- Pleopod 1 Coupling hooks: state 0- present, state 1- absent.

92- Pleopod 1 Coupling Hooks position: state 0- distal,   state 1- central, state 2- proximal.

93- Pleonite 1 ventral keel on ventral margin: state 0- absent, state 1- small semi-circular lobe, state 2- tongue shaped lobe, state 3- rectangular lobe.

94- Pleonite 1 ventral keel posterior projection: state 0- absent, state 1- short, round, state 2- elongate spike.

Pleopod 2 Male
95- Pleopod 2 exopodites - No of segments: state 0- multisegmented, state 1- 1-2 segments, state 2- 1-2 seta.

96- Pleopod 2 proximal segment length to distal segment length: state 0- proximal > distal, state 1- proximal = distal, state 2- proximal < distal.

97- Pleopod 2 endopodite shape of distal segment: state 0- stylet, state 1- forming cup shape, state 2- truncate with 3-4 distal lobes.

98- Pleopod 2 endopodite position: state 0- lateral, state 1- medial.

99- Pleopod 2 coupling hooks position on proximal segment: state 0- absent, state 1- proximal, state 2- central, state 3- distal.

Pleopod 3

100- Pleopod 3 coxa endites or medial lobes: state 0- absent, state 1- present.

101- Pleopod 3 exopodite - No of segments: state 0- multisegmented, state 1- 1-2 segments, state 2- 1-2 seta.

102- Pleopod 3 endopod - No of segments: state 0- multisegmented, state 1- 1-2 segments, state 2- 1-2 seta.

Pleopod 4

103- Pleopod 4 coxa endites or medial lobes: state 0- absent, state 1- present.

104- Pleopod 4 exopod - No of segments: state 0- multisegmented, state 1- 1-2 segments state 2- 1-2 seta.

105- Pleopod 4 endopodite - No of segments: state 0- multisegmented, state 1- 1-2 segments, state 2- 1-2 seta.

Pleopod 5

106- Pleopod 5 coxa endites or medial lobes: state 0- absent, state 1- present.

107- Pleopod 5 exopodite (No of segments): state 0- multisegmented, state 1- 1-2 segments, state 2- 1-2 seta, state 3- 0.

108- Pleopod 5 endopod (No of segments): state 0- multisegmented, state 1- 1-2 segments, state 2- 1-2 seta.

Telson

109- Telson distal margin shape: state 0- round, state 1- round with flat distal tip, state 2- square, state 3- triangular, state 4- triangular, spear shaped, state 5- bifid or with medial groove, state 6- sinuous, state 7- absent.

110- Telson - separation of distal and lateral margin: state 0- no delineation, round, state 1- distinct separation with distolateral corner.

111- Telson lateral margin shape: state 0- straight, state 1- convex, state 2- concave.

112- Telson length to uropod length: state 0- 100%, state 1- 70-90%, state 2- 50%, state 3- <35%, state 4- 0.

113- Telson with medial longitudinal ridge: state 0- absent, state 1- round, state 2- sharp.

114- Telson with lateral flange state 0- absent, state 1- present.

115- Telson dorsal surface submarginal setae - No- of setae: state 0- 0, state 1- 2, state 2- 4 or <.

116- Telson posterior ventral margin setae: state 0- absence, state 1- presence.

117- Telson posterior margin with two large distolateral spines (one on each lateral corner): state 0- absent, state 1- present.

118- Telson lateral margin setation coverage: state 0- complete, state 1- distal 2/3, state 2- distal 1/3, state 3- distal tip only, state 4- no setae.

119- Telson lateral margin setae types: state 0- no setae, state 1- thin simple setae, state 2- robust simple spines, state 3- complex serrate spines, state 4- cuticular spines.

Uropod

120- Uropod shape: state 0- tubular, state 1- narrow, flat paddle shaped, distally rounded, state 2- narrow, flat spatulate shaped, distally pointed, state 3- broad, flat paddle shaped, state 4- spear shaped.

121- Protopod length to width: state 0- shorter, state 1- subequal, state 2- longer.

122- Rami reinforced with lateral rib: state 0- absent, state 1- present.

123- Medial ramus - no- of segments: state 0- 2, state 1- 1, state 2- 0.

124- Lateral ramus No- of segments: state 0- 2, state 1- 1 with straight diastema, state 2- 1 with curved or circular diastema, state 3- 1 with reduced, round diastema, state 4- 1 with medial and lateral subdistal notch, state 5- 1 with laterodistal notch , state 6- 1 with no articulation or lateral notch.

125- Lateral rami posterolateral margin: state 0- smooth, state 1- fine simple setae, state 2- robust simple spines, state 3- cuticular spines.

126- Furca: state 0- elongate, state 1- subequal in length, state 2- small, flat lobe, state- absent.

Results

Tree Descriptions

The results of the phylogenetic analyses produced three trees in which all species of both Anaspidacea and Palaeocaridacea are clearly separated from the two Bathynellacea outgroup taxa. Three cladograms are presented below that present an increasing degree of resolution of relationships within the Anaspidacea. They including the boot strapped tree, the consensus tree and the maximum parsimony tree (No. of steps = 625). The phylogenetic reconstruction revealed that the each of the trees presented are well resolved into four Orders: the Bathynellacea, Stygocaridacea, Palaeocaridacea and the Anaspidacea. The Order Stygocaridacea Noodt 1965 is re-instated in order to accommodate the taxa that are now clearly divergent from the Anaspididae based on this analysis.

Bootstrap Tree

The bootstrap tree clearly delineates the six families previously identified under the Order Anaspidacea, however, it also sharply separates the Anaspididae from the remaining five families and joins it as a sister group to the Palaeocaridacea. The Patagonaspididae has also been distinctly separated from both the Stygocarididae and the Psammaspididae although it now forms a group incorporating the Stygocarididae, that represent a sister group to the Psammaspididae, Raptornungidae, Palaeocaridacea and the Anaspidacea. All major anaspidacean families remain consistent across each of the trees except for the Palaeocaridacea in which the resolution and delineation collapses in both the Bootstrap and Consensus trees indicating substantial variability in branch swapping. The same applies to the Koonungidae genera *Pholeteronunga*, *Drummonunga* and *Boolarrunga* although each of these genera are represented by one species and in this case it is the resolution of the matrix under bootstrapping and consensus that is insufficient to adequately define the evolutionary pathways for the genus *Koonunga*, as well as the genera of the Raptornungidae and Psammaspididae.

The genera that show distinct separation with boot strapping (and therefore retaining their designation) include all of the genera within the Stygocarididae except for *Tasmanocaris* and *Stygocarella* that have formed a close association. In the Koonungidae, all genera are easily delineated from *Koonung*a with *Neonunga* and

Micraspides forming a significant association. Within the Palaeocaridacea only two families standout as having distinct alignment of the taxa. These are Acanthotelsonidae and the Palaeocarididae. The two families Psammaspididae and the Raptornungidae while distinct and separate, have a close association although contain sufficient apomorphies to separate into them into distinct units. The Anaspididae form a distinct clade that is retained throughout the analyses with *Allanaspides* and *Paranaspides* diverging from the Palaeocaridacea stock at an early age. *Paranaspides* is indicated to be the sister group of the remaining '*Anaspides'*-like genera. Each of the three '*Anaspides'*-like genera show distinct autapomorphies that clearly separate them and the two *Occidentaspides* species form a coherent genus.

Consensus Tree

The Consensus tree is similar to the Bootstrap tree in that it still constrains the trees resolution, particular within the Palaeocaridacea. The major difference is the separation of the Psammaspididae and Koonungidae from the Palaeocaridacea and the Anaspididae. The Syncarida now form a clear monophyletic group that includes the Anaspididae and Palaeocaridacea. The Superorder Syncarida is now defined by the presence of a petasma in the males and excludes the Bathynellacea. The Stygocarididae now form the basal family within Syncarida followed by the Patagonaspididae, the Psammaspididae/Raptornungidae, the Koonungidae and the Anaspididae and Palaeocaridacea clade. Within the Koonungidae the only genera to have diverged in this tree is *Drummonunga* that is now forming the basal component of the clade. The Palaeocaridacea are still largely unresolved although Squillitidae is defined by the genera *Squillites* and *Praenaspides*. Another set of genera that were previous unassigned and placed within the Uncertain family of Palaeocaridacea now form a distinct South American/Australian clade that is distinctly separate from the northern hemisphere fossil Syncarida and is now a sister clade to the Palaeocaridacea. These genera include *Anaspidites* as the basal taxa with *Clarkecaris* and *Koonaspide*s forming a close association. The Anaspididae has also become disassociated with the Palaeocaridacea.

The Stygocarididae have now become quite delineated and form a monophyletic family commencing with the mid-South American genus *Parastygocaris* forming the basal clade followed by the eastern (Argentinian) South American genus *Argentocaris* and *Oncostygocaris*. The western (Chilean) South American genus *Stygocaris* and the New Zealand genus *Zealandacaris* diverge followed by the Australian *Tasmanocaris* and New Zealand *Stygocarella* forming the terminal clade.

Maximum Parsimony Tree

The analysis presented in this tree retains the base monophyletic structure of the Syncarida and within the Anaspidacea as previously described however, the maximum parsimony tree provides significantly more detailed resolution of most of the taxa and now provides indications of possible evolutionary pathways for the Syncarida at the family and genus levels. The Anaspididae form a distinct clade from the fossil Palaeocaridacea, however, the closest association is with the clade formed by the clade formed *by Clarkecaris*, *Koonaspides* and *Anaspidites*. This association is based primarily on the shortened length of the pereonites, telson and uropod

structures. The Anaspididae displays a south western origin with the genera *Allanaspides* and *Paranaspides* representing the basal groups from which the *Septentrionaspides* and *Anaspides* diverge in central Tasmania. The final two genera originate from *Anaspides* stock and separate with *Occidentaspides* migrating to the central south and *Spinaspides* separating and forming a distinct clade along the south western margin of Tasmania. The large divergences genera within the Anaspididae particularly within the *Allanaspides*, *Paranaspides* and *Septentionaspides* clades may be sufficient to elevate these clades to subfamily status.

The Palaeocaridacea is an unstable group containing the highest degree of branch swapping within the Syncarida. The families that have retained the distinctness include the Palaeocaridae and Squillitidae. The most significant change is the family Acanthotelsonidae which has increased its coverage and subsumed the Minicaridae although it is still present as a distinct smaller clade. It has however, lost *Palaeosyncaris dakotensis* to a more basal position without other affinities. The other major change as mentioned previously is the new familial association of *Clarkecaris*, *Koonaspides* and *Anaspidites*.

The Koonungidae remain largely unchanged except for delineation of the genera *Drummonunga*, *Pholeteronunga*, *Boolarrunga* forming the more basal taxa supporting the two divergent clades *Koonunga* and the *Zeidlerunga/Micraspides/Neonunga* clade.

The consistency of the Psammaspididae/Raptornungidae clade gives support for a subfamilial grouping to accommodate the two. The only difference in this tree is that genera of Psammaspididae has diverged with the Tasmanian *Eucrenonaspides* becoming basal followed by the more north eastern *Psammapides* and terminating with *Cavernaspides* in the western regions of NSW thus indicating a northern coastal and then western dispersal of the family. The analysis did not have sufficient resolution to delineate genera or species of Raptornungidae. The relationships within the Stygocaridae have remained unchanged.
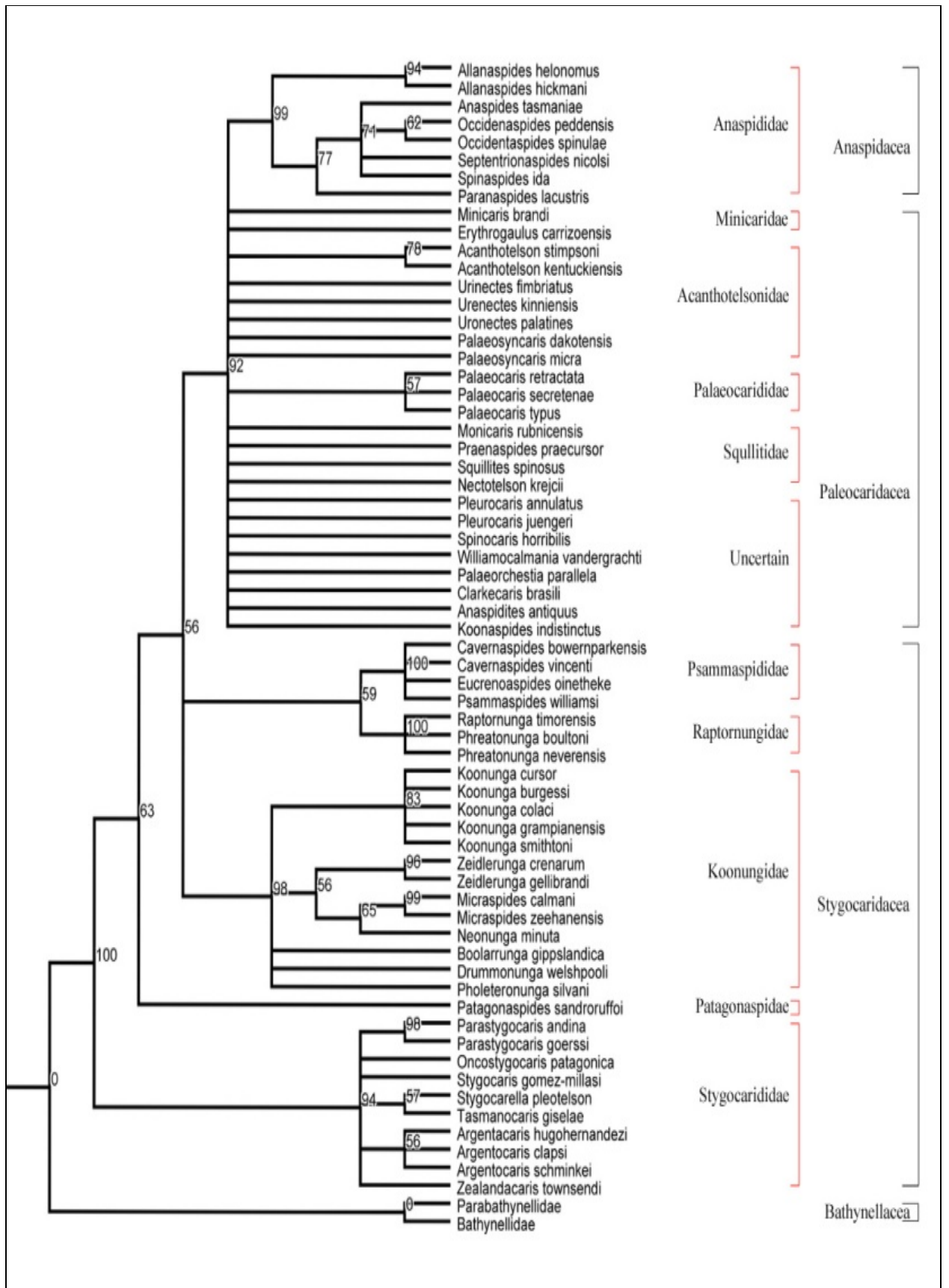
Figure 4.1. Bootstrap tree for the phylogeny of the Syncarida based on morphological data with confidence indices over 50%.
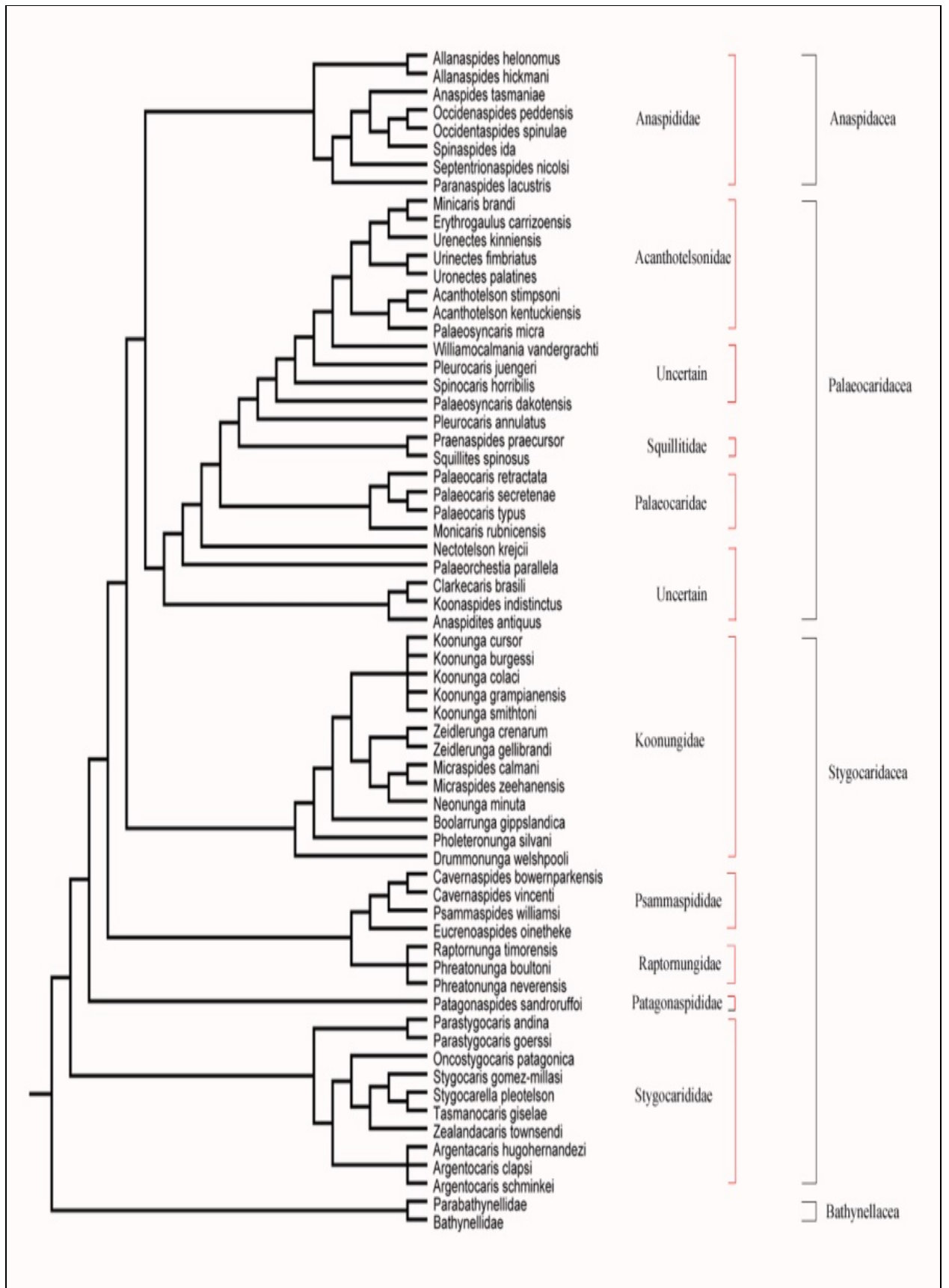
Figure 4.2. Consensus tree for the phylogeny of the Syncarida based on morphological data.

Figure 4.3. Maximum parsimony tree for the phylogeny of the Syncarida based on morphological data.

CHAPTER 5. GENERAL DISCUSSION

Scientists have long described the Anaspidacea as the most interesting group of freshwater crustaceans (Schram 1984, Williams 1980), as they possess a unique combination of morphological (Calman 1896; Smith 1908; 1965a; Schminke 1982), distributional (Schminke 1982) and physiological (Wallis & Macmillan 1998) characteristics that places them in a singularly significant position, both within the Syncarida and in the evolution of the Malacostraca as a whole. They are an intriguing group of small to tiny crustaceans that have, since their discovery in Tasmania in 1893, tantalised scientists by their uncanny resemblance to the extinct and primitive Carboniferous to Permian fossil Syncarida, the Palaeocaridacea of North America and Europe. For this reason the order and the Family Anaspididae particularly, has been described as classic 'living fossils' (Smith 1909a, Drummond 1959, Schram and Hessler 1984, Schram 1984) that has supposedly remained unchanged morphologically for over 300 million years, and in so doing have thus retained the unmodified, archetypal body form from which all advanced crustaceans have evolved. The term was originally coined by Smith in 1909 for *Anaspides tasmaniae* from Mount Wellington, Tasmania. The term was later defined by Stanley (1979) as "long lineages that persist as restricted bradyletic lines". The other families of the Anaspidacea, particularly the Psammaspididae and Stygocarididae, also suggest linkages with the cosmopolitan, and possibly oldest order of Syncarida, the Bathynellacea.

This interest however, has not translated into comprehensive and detailed research to understand the species diversity, species distribution, detailed morphology, physiology, life history, environmental requirements or the evolutionary relationships of the species or higher taxonomic levels. Instead, most of what is known is based on limited descriptions and ecological studies of a very small number of species and from limited localities. This knowledge has then been extrapolated to cover all other taxa within the order. This study provides a morphological analysis of all species of the Anaspidacea and the Palaeocaridacea using phylogenetic analysis to infer a greater understanding of the relationships within the Anaspidacea. The Palaeocaridacea have been included in the analysis in order to more fully understand the history of the morphology and the evolutionary pathways.

The structural morphology of the Anaspidacea appears to reflect the habitats in which they occur, the niches within those habitats and the food they consumed. The changes in morphology may also indicate the climatic conditions that have occurred during their evolution. The structure of the Palaeocaridacea indicate that they were open water benthic organisms who were quite good swimmers. The paddle shaped pleopods, the large scaphocerite and elongated antennae, fan shaped uropods and large leaf shaped respiratory endopods on the thoracopods closely resemble those of *Anaspides* except for the multisegmented pleopods. Instead of paddle shaped pleopods of the Palaeocaridacea, *Anaspides* has lateral rows of setae which function predominantly as water circulators rather than as swimming legs although they do perform this function. The development of the

paddle shaped pleopods are analogous to the pleopods of the decapods shrimps and would indicate that they were far better swimmers that the present day Anaspides. This is an adaptation that would have suited them better in the very large deltas, swamps and lakes that covered much of North America and Europe during the Mesozoic. The ability to be good swimmers and prevalence of such large water bodies with large transition zones between fresh, brackish and marine environments would have significantly aided in the dispersal of the Palaeocaridacea and is suggested as the reason why they have been found across large areas of the northern hemisphere. With the absence of frozen polar areas the climate is suggested to be relatively consistent across large areas, which would have produced organisms with narrow environmental tolerances.

The large leaf shaped endopods on the thoracopods of the Palaeocaridacea and Anaspididae are indicators of a high oxygen demand presumably from high activity or higher activity in habitats with low oxygen levels. The production of higher oxygen levels during the Mesozoic caused by the extensive swamps and woodlands would have produced larger species particularly in surface waters however, with the large input of allochthonous material into the swamps and lakes there would have also been large areas of low DO particularly within the standing pools and lakes. As the Syncarids of then and now are predominantly benthic the development of strategies for inhabiting these would have occurred and would have started the development of a group of crustaceans that could inhabit the benthic and soft interstitial sediments. The evolution of this trait would be the savior of the group over millennia as they progressively evolved to inhabit environments that would not change dramatically over time and would protect them from the numerous cataclysmic extinction events. The demise of the Northern hemispheres Palaeocaridacea occurred at the end the Mesozoic at the time of the massive Permian extinction event that wiped out about 90% of life on earth. This is speculated to have been a combination of a meteor strike and extensive volcanisms centering on the Siberia steps. This volcanism extended over much or North America and Europe and would have resulted in the wiping out of the vegetation through fires and dust clouds. This in turn would have produced extensive sedimentation of the waterways. Most pelagic aquatic species would have perished as the clean, vegetated streams, lakes and swamps were filled with fine, possibly acidic, low oxygenated sediments that would have smothered the benthos and eradicated most aquatic life in these systems. The only groups that would have survived these conditions would have been those that already pre-adapted to living in these environments.

The common fauna groups found in similar environments today included aquatic oligochaetes and crustaceans such as the benthic syncarids and some of the isopods such the Phreatoicoidea. It is suggested that although the Palaeocaridacea were wiped out in Europe, North America and Northern South America they had already dispersed south by this time along the western margin of Gondwanaland that included southern South America, Western Antarctica and south Eastern Australia and that they were sufficiently far enough away from the epicenter of the Northern Hemisphere extinction events that they were able to survive. Evidence of this is the presence of *Anaspidites antiquus* in the rivers and deltas of the Sydney sandstone formation 240 million ago and *Koonaspides* within the Cretaceous Murray Basin in Victoria as well as the fact that the

Stygocarididae had dispersed from South America to New Zealand prior to the separation of Gondwanaland. The preadaptation to living in interstitial environments would have also later aided in the survival during the frequent climate changes that occurred following the Mesozoic including the ice ages and increases in aridity. These climatic changes would have encouraged the continued adaptation from a benthic interstitial to phreatic interstitial.

The morphological changes necessary to make this transition from an open water pelagic organism to an underground interstitial organism can be clearly correlated to the changes in the morphologies within the Anaspidacea. These changes include size (related to the size of the water body or void in which they live – the smallest species occur in the finer sediments and the largest species occur in large water bodies or caves with large voids.). These changes in habitat or adaptation to specific habitats are reflected size and shape of the respiratory epipods, the rate of oxygen consumption, the length of the antennae, the length to width ration of the body and body segments, the design and length of the uropods and telson. The reduction and loss in the size and projection of appendages such as the loss or lack of development of the antennal scaphocerite is another adaptation to a more interstitial existence. The width and length of the uropods and telson is correlated to the size of the water body and the need to swim whereas the shorter the telson and the rounder the uropods correlated to the smaller the void or finer the sediments that they live in. The size and number of spines on the telson is indicative of the fineness of the pore spaces or sediments in which they live. For examples, the setation of the a) Anaspididae is generally small and plumose and are designed to aid the hydrodynamics of the body shape for swimming, b) the setae on the pleonite 6, the uropods and the telson of both Psammaspides and Raptornungidae (both exclusive benthic interstitial organisms that occupy larger voids such as caves and course sediments with larger voids such as sand and gravel bars in rivers or alluvial /fractured rock aquifers) are designed as defensive mechanisms to protect the rear part of the animal from predation in restricted environments where it cannot turn around and face a predator. The reduction in the size of the telson and the size and number of robust setae or spines from the Raptornungids/Psammaspid clade to the koonungids and finally to the Stygocarids represent a transition from habitats with structure such as coarse grain sediments and fractures of caves and alluvial aquifers of 1st to 3rd order streams to the finer sediments of deltas of larger 4th to 6th order rivers.

It is clear that the Anaspididae are direct offshoot and last surviving members of the ancient Palaeocaridacea although the cladograms indicates they are a sister clade the Palaeocaridacea. The Anaspididae and the other families diverged at an early stage most likely before the Mesozoic and dispersed and evolved alongside each other. They however inhabited different environments and therefore had differing survival abilities. The fact that Anaspides now only occurs in Tasmania is related to the survival of the habitats and the climate in this region is a testament to the changing global environments around the globe.

The Stygocarididae have also demonstrate clear evolutionary pathways starting with the separation of the *Stygocaris* and *Argentacaris* geographically when considered with the morphological differences has significant implications for estimates of the age of separation and speciation as well as the possible direction of the evolutionary pathyways. The *Argentocaris* species all occur on the eastern side the Andes in Argentina and *Stygocaris* occurs to the west on the western side of the Andes. The similarities between the species of the two genera, in overall morphology indicates that they were once part of the same group and probably within the same catchment system. The rise of the Andes Mountain chain divided the catchment and isolated the species. It is suggested that as *Stygocaris* has developed more apomorphic features such as the fusion of the lateral rami, the development of the male antennule and the changes to the male petasma, that the divergence between *Stygocaris* and *Argentocaris* was at a far earlier period than the divergence between the species of *Argentocaris*. It is also suggested that the evolutionary pathway has been from the east to the west and that there has been a change in the habitat structure such as sediment size on the western side of the Andes in Chile that has necessitated the change in morphology. This is opposed to the continuation of previous habitat conditions on the eastern side that has mean there has been little change and there a retention of the more plesiomorphic morphology.

This includes the two to three segments of the male pleopod 1 and the three segments and stylet form of the male pleopod 2 as well as the extension of the telson, the shapes of the paragnath and maxillula. There is, however significant variation between the two including the bilobed rostrum in the Tasmanocaris that is more akin to either Psammaspididae or *Oncostygocaris* from Patagonia, whereas the rostrum of *Stygocarella* has similarities to the rostrums in taxa such as the South America *Parastygocaris goerssi* or *Argentocaris schminkei*. Other features that separate the two genera is the reduced nature of the New Zealand genus compared with the Australian genus as can be seen on the reduction of segments on the male pleopod 1 and the maxilla. The differences between the two genera clearly delineate the two, while still demonstrating a close relationship.

The Order Anaspidacea is currently divided into two Suborders, the Anaspidinea and the Stygocaridinea by Knott and Lake (1980). The first suborder the Anaspidinea was erected by Calman in 1904 to accommodate the newly discovered *Anaspides tasmaniae* and later the new genus Paranaspides, Smith in 1908. In 1965 Noodt erected a new order, the Stygocaridacea, initially to accommodate the Stygocarididae. The Order Stygocaridacea was later subverted to a subordinal status to Stygocaridinea by Knott & Lake in 1980 and placed within the Order Anaspidacea. The family Psammaspididae was also included within the Stygocaridinea by Knott & Lake (1980). The concept that the stygocarids should not be an order was also suggested by Schminke in 1975 where he treated Stygocarididae as belonging to the Anaspidacea as well, although he did not qualify the reasoning behind the placement. The original diagnosis for the order included: Mesopsammale Syncarida; thoracomere 1 fused with cephalon; 6 pleonites; mandible with

penicillate setae between the molar and incisor processes; furcal rudiments on telson; petasma of the male; antennula with statocyst.

A majority of these features however, are also found within the other Anaspidacea and are already covered in the ordinal diagnosis. The delineation of the suborders by Knott & Lake (1980) however, cannot be supported by the current analysis and is therefore abolished. As is the grouping of the Koonungidae with the Anaspididae as it was based on a misinterpretation of characters, particular the structure of the telson and uropods and an insufficiently detailed examination of more diagnostic characters such as the male genitalia.

After the re-examination and analysis of all anaspidacean and Palaeocaridacea taxa with a far more comprehensive dataset that also incorporates the fossil taxa it is recognised that the significant differences in overall body form and habitus between the Stygocaridacea and the Anaspidacea. The results also demonstrate the close relationship between Anaspididae and the Palaeocaridacea and that the reinstatement of the Stygocaridacea is necessary to accommodate the extant Syncarida that were previous assigned to just the Anaspidacea. This results in three Orders within the Syncarida, and refinement of the diagnosis of the Syncarida to exclude the Bathynellacea, where the Anaspidacea and the Palaeocaridacea would form sister Orders separate from the Stygocaridacea. The Bathynellacea is separated into its own Superorder (Superorder Podophallocarida) which has previously been suggested by Serban (1972), Tabacaru & Danielopol (2011) and Coineau & Camacho 2013. This discussion however is outside the parameters of this study and will be left to another time. This study therefore presents new diagnoses and new familial compositions below. The Stygocaridacea encapsulates all anaspidacean families except the Anaspididae. The Order Anaspidacea, which was originally designated by Calman in 1904, now reduced to only contain the Anaspididae. The diagnoses for the two Orders are presented below.

Revised Diagnoses of the Anaspidacea

Order STYGOCARIDACEA NOODT 1965a

Diagnosis. Modified from Noodt 1965 and Knott & Lake 1980.
Minute to moderate sized Anaspidacea (0.5-15mm); eyes absent or sessile and incorporated into the distolateral margin of cephalic shield and no eyestalk; antenna without a scaphocerite on the second segment; cephalon frontal margin round or broadly triangular with no anteromedial extensions; rostrum formed by extension of vertex which can be a single or bilobed; mandible consisting of a incisor process with a large terminal denticle not separated by a large gap or diastema; male pleopod 1 with single or multiple subdistal hooks; male pleopod 2 distal segment of endopodite ≥ to the proximal segment; male pleopod 2 proximal segment stylet shaped tapering to a point; uropods round or slightly flattened and

distally rounded; telson and uropods not forming a flattened fan, uropodal rami with 1 to 2 segments; telson with 2-3 lateral spine rows

Family Composition

Psammaspididae

Raptornungidae

Koonungidae

Patagonaspididae

Stygocarididae

Order ANASPIDACEA Calman 1904

Diagnosis. Modified from Thomson 1893, Calman 1904 and Knott & Lake 1980.

Moderate to large anaspidaceans; eyes pedunculate on an articulated eyestalk and separate from the cephalic shield; cephalon and all body segments distinct rostrum formed by an anteromedial extension of the cephalic plate consisting of an elongate rounded or triangular lobe; antenna with an oval scaphocerite on the second segment with a round distal margin; mandible consisting of a incisor process with a medial accessory incisor lobe or terminal denticle with or without setae, separated by a large gap or diastema; maxilla with two broad, setose lobes and a palp, maxilla with four short, broad setose lobes without a palp, maxillipeds with lamellar epipodites and endopodites on the coxa, basis with a tubular elongate exopodite and ischium distolaterally expanded; succeeding seven pairs of legs nearly uniform in structure, adapted for walking; thoracopod epipodites lamellar, broad, leaf or oval shaped; thoracopod exopodites, natatory and multisegmented; pleopoda with well-developed natatory, multisegmented exopodites; male pleopod 1 without subdistal hooks; male pleopod 2 distal segment distinctly shorter than proximal segment; male pleopod 2 proximal segment paddle shaped, distally rounded or folded and not tapering to a point; pleonite 6 posterior margin with a row or short simple setae or spines; telson short, distally triangular or rounded with a row of short setae or spines on posterior margin only; uropods flattened and broad, single segmented with no diastema, spatulate or leaf shaped and distally truncated; telson and uropods forming a flattened fan; telson with only one lateral spine row

Family Composition

Anaspididae

Revised Classification of the Syncarida

A new classification of the Orders Anaspidacea and Palaeocaridacea is presented below based a detailed re-examination of morphology. The Bathynellacea families are included for completeness..

Table 4.1. Revised checklist of Species

Superorder SYNCARIDA Packard 1885
Order ANASPIDACEA Calman 1904
Family ANASPIDIDAE Thomson 1893
Genus *Allanaspides* Swain, Wilson, Hickman & Ong 1970
Allanaspides helonomus Swain, Wilson, Hickman & Ong 1970
Allanaspides hickmani Swain, Wilson & Ong 1971
Genus *Anaspides* Thomson 1894
Anaspides tasmaniae (Thomson 1893)
Genus *Occidentaspides* n. gen
Occidentaspides pedderensis n. sp.
Occidentaspides spinulae Williams 1965(= *Anaspides* Thomson 1893)
Genus *Paranaspides* Smith 1908
Paranaspides lacustris Smith 1908
Genus *Septentrionaspides* n. gen
Septentrionaspides nicholsi n. sp.
Genus *Spinaspides* n. gen
Spinaspides ida n. sp.
Order STYGOCARIDACEA NOODT 1965
Family PATAGONASPIDIDAE Grosso & Peralto 2002
Genus *Patagonaspides* Grosso & Peralto 2002
Patagonaspides sandroruffoi Grosso & Peralto 2002
Family PSAMMASPIDIDAE Schminke 1974
Genus *Cavernaspides* n. gen
Cavernaspides bowenparkensis n. sp.
Cavernaspides vincenti n. sp.
Genus *Eucrenonaspides* Knott & Lake 1980
Eucrenonaspides oinotheke Knott & Lake 1980
Genus *Psammaspides* Schminke 1974a
Psammaspides williamsi Schminke 1974a
Family RAPTORNUNGIDAE n.fam. (= Family A Serov 2002)
Genus *Raptornunga* n. gen.
Raptornunga timorensis n. sp.

Genus *Phreatonunga* n. gen

    Phreatonunga boultoni n. sp.

    Phreatonunga neverensis n. sp.

Family KOONUNGIDAE Sayce 1908

Subfamily Koonunginae n.subfam.

Genus *Koonunga* Sayce 1907

    Koonunga cursor Sayce 1907

    Koonunga burgessi n. sp.

    Koonunga colaci n. sp.

    Koonunga grampianensiss n. sp.

    Koonunga smithtoni n. sp.

Genus *Zeidlerunga crenarum* n. gen (= *Koonunga* Sayce 1908)

    Zeidlerunga gellibrandi n. sp.

Subfamily Micraspidinae n.subfam.

Genus *Micraspides* Nicholls 1931

    Micraspides calmani Nicholls 1931

    Micraspides zeehanensis n. sp.

Subfamily Drummonunginae n.subfam.

Genus *Boolarrunga* n. gen

    Boolarrunga gippslandica n. sp.

Genus *Drummonunga* n. gen

    Drummonunga welshpooli n. sp

Genus *Neonunga minuta* n. gen

    Neonunga minuta n. sp.

Genus *Pholeteronunga* n. gen

    Pholeteronunga silvani n. sp

Family STYGOCARIDIDAE Noodt 1963

Genus *Parastygocaris* Noodt 1963

    Parastygocaris andina Noodt 1963

    Parastygocaris goerssi Noodt 1963

Genus *Oncostygocaris* Schminke 1980

    Oncostygocaris patagonica Schminke 1980

Genus *Stygocaris* Noodt 1963

    Stygocaris gomez-millasi Noodt 1963

Genus *Stygocarella* Schminke 1980

    Stygocarella pleotelson Schminke 1980

Genus *Argentacaris* n. gen

Argentacaris hugofernandezi Grosso & Peralto 1997 (= Stygocaris Schminke 1980)

Argentacaris clapsi Grosso & Peralto 1997 (= Stygocaris Schminke, 1980)

Argentacaris schminkei Grosso & Peralto 1997 (= Stygocaris Schminke 1980)

Genus *Tasmanocaris* n. gen

Tasmanocaris giselae (= Stygocaris Schminke 1980)

Genus Zealandacaris n. gen

Zealandacaris townsendi Morimoto 1977 (= *Stygocaris* Schminke, 1980)

*Order PALAEOCARIDACEA Brooks 1962

*Family MINICARIDAE Schram 1984

*Genus *Minicaris* Schram 1979

*Minicaris brandi Schram 1979

*Genus *Erythrogaulus* Schram 1984

**Erythrogaulus carrizoensis* Schram 1984

*Family ACANTHOTELSONIDAE Meek and Worthen 1865

*Genus *Acanthotelson* Meek and Worthen 1865

*Acanthotelson stimpsoni Meek and Worthen 1865

**Acanthotelson kentuckiensis* Schram 1984

*Genus *Uronectes* Bronn, 1850 (= *Gampsonychus* Burmeister 1855)

**Uronectes fimbriatus* Jordan 1847

**Uronectes kinniensis* Schram & Schram 1979

**Uronectes palatinus Uhl and Raisch 1999 (See Uhl 1999)*

*Genus *Palaeosyncaris* Brooks 1969

**Palaeosyncaris dakotensis* Brooks 1969

**Palaeosyncaris micra* Schram 1984

*Family PALAEOCARIDIDAE Meek and Worthen 1865

*Genus *Palaeocaris* Meek and Worthen 1865

**Palaeocaris typus* Meek and Worthen 1865

**Palaeocaris secretanae* Schram 1984

**Palaeocaris retractata* Calman 1932

*Genus *Monicaris* Stamberg 2000

**Monicaris rubnicensis* Stamberg 2000

*Family SQUILLITIDAE Schram and Schram 1974

*Genus *Squillites* Scott 1938

Squillites spinosus Scott 1938x

*Genus *Praenaspides* Woodward 1908

Praenaspides praecursor Woodward 1908

*Family PALAEOANASPIDIDAE n.fam.

*Genus *Anaspidites* Brooks 1962

Anaspidites antiquus Chilton 1929

*Genus *Clarkecaris* Messalira 1952

Clarkecaris brasili Messalira 1952

*Family PALAEOKOONASPIDIDAE n.fam.

*Genus *Koonaspides* Jell & Duncan 1986

Koonaspides indistinctus Jell & Duncan 1986

*Family UNCERTAIN Schram 1984

*Genus *Nectotelson* Brocchi 1880

Nectotelson krejcii Brocchi 1880

*Genus *Pleurocaris* Calman 1911a

Pleurocaris annulatus Calman 1911a

Pleurocaris juengeri Schöllman 1999

Genus Spinocaris Uhl 1999

Spinocaris horribilis Uhl 1999

*Genus *Williamocalmania* Schram 1984

Williamocalmania vandergrachti (Pruvost) 1912

*Genus *Brooksyncaris* Schram 1984a

Brooksyncari canadanensis (Brooks) 1969

*Genus *Palaeorchestia* Zittel 1885

Palaeorchestia parallela (Fritsch) 1876

Superorder PODOPHALLOCARIDA

**Order BATHYNELLACEA Chappuis 1915

**Family Bathynellidae

**Family Parabathynellidae

* Indicates that these taxa are extinct and represented in the fossil record.

** Group not examined in this study.

Conclusion

Historically the Anaspidacea only contained five families. This study presents eight families: the

Anaspididae, Koonungidae, Psammaspididae, Stygocarididae, Patagonaspididae and one new family the

Raptornungidae, and two Australian fossil families, the Palaeoanaspididae and Palaeokoonaspidae. The Syncarida is now divided into three Orders in which the Stygocaridacea is reinstated to accommodate five of the extant families and the Anaspidacea is reduced to contain only the Anaspididae and the Bathynellacea is separated into its own Superorder. In total the extant Syncarida contains 28 genera and 40 species exhibiting a broad array of morphologies, behaviour, ecology, habitats and distributions. The Palaeocaridacea contribute five families, 16 genera and 23 species to the analysis.

The morphological analysis of the structure of the Anaspidacea has resulted in the need to redefine our concepts of the relationships within the Anaspidacea and the degree of change necessary to separate species, genera and the higher classifications. The very conservative rates of morphological variation as indicated by Jarman and Elliot (2000) on *Anaspides* in Tasmania and the retention of consistent gross morphology over millions of years, dictate that instead of using major morphological differences to delineate specie and genera we should refine our examinations to much smaller differences. Historically, all previous classifications have been focused on the large obvious features of the group, which has resulted in. for example, single species with no arboreal method of dispersal, apparently occurring across a state with catchments that have been isolated for millions of years and even apparent genera of groundwater organisms that occur on separate continents that have been separated for tens or hundreds of millions of years. Therefore, it is necessary to refine our paradigm for separating species to much smaller units and shift all of the current classifications, except for the Ordinal level up a level. The overall biogeography of the Superorder is one that originated in the Northern Hemisphere alongside the evolution of the Palaeocaridacea and dispersed south along the coastline of Laurasia and Gondwanaland during and possibly prior to the Mesozoic. The dispersal continued South through South America and the western margin of Antarctica to occupy New Zealand and the South of Australia by the Triassic.

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