A Higher Systematic Revision of the trilobite family Phillipsiidae Oehlert, 1886 and a Historical and Theoretical Critique of Systematics and Biostratigraphy

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The separation of comparative morphology from the palaeontological methods heralded the rise of phylogenetic systematics or cladistics, namely to find monophyletic taxa. While cladistics has been embraced by comparative biologists, it has been long shunned in the invertebrate palaeontology community. Cladistics seeks to find natural classifications independently of geography and time, however conventional palaeontological classification techniques include both stratigraphic and morphological data, which may lead to non-monophyletic (aphyletic) taxa. In palaeontology, aphyletic taxa are often used in biostratigraphic correlations, which have led to erroneous results. One fossil taxon, the Late Palaeozoic trilobite family Philippsidae, is an example of an aphyletic taxon that is defined using stratigraphic and morphological characteristics. The Philippsidae are reappraised herein using cladistics.

The validity of monophyletic marker taxa is demonstrated using a hypothetical and real example. The foraminifera Praemurica and the bryozoan Peroncopora are examples of marker taxa that have been shown through cladistic analysis to be aphyletic. Using the cladogram all the genera are re-classified, and the stratigraphy revised, which has been termed herein Systematic Biostratigraphy. The monophyly of Philippsidae is tested by performing two high-level systematic analyses at the sub-family and genus level, using 21 characters derived from previously published systematic analyses. The results do not support a monophyletic Philippsidae, however the sub-familial level analysis may reveal a separate family consisting of Philippsinae and Linguaphilippinae.

The first complete review of the Australian Carboniferous and Permian, (Lower Tournaisian to Westphalian; 358.9 Ma to 304 Ma), trilobite species is presented. The species are classified in accordance with the results in the systematic analysis of Philippsidae. The review consists of 4 families, 22 genera and 54 species. Emended diagnoses are provided for 7 genera and 33 species.

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Chapter 1. General Introduction

This thesis aims to use the Carboniferous and Permian trilobites of Australia as an example of a poorly classified fossil group to demonstrate the need for natural classifications systems in both palaeontological systematics and biostratigraphy. The thesis is in three sections:

1. A history and critique of important concepts in systematics, focusing on the development of cladistics and the definition of a monophyletic group.
2. The demonstration of a systematic method for a better defined biostratigraphy.
3. The systematic revision of the Phillipsiidae family, with a taxonomic revision of Carboniferous and Permian trilobites found in Australia.

The past two centuries have seen a revolution in the theoretical understanding of systematic classification. The introduction of evolutionary theory saw a radiation of taxonomists wanting to discover “true” classifications in nature, those that occur naturally, rather than the artificial system that was in place since Linnaeus (1758).
Natural classifications are seen as those that exist in nature. Many fields within palaeontology, such as biostratigraphy and phylogenetics, rely on accurate classification systems as a precursor to their studies. Unfortunately there has been an increase in the number of palaeontologists who fail to accurately identify the groups that they work on. The natural classification of fossil taxa should be the first step in any study that requires their taxonomic rank, yet there is rarely an emphasis on accurate classifications. Poorly classified taxa will ultimately produce inaccurate results for these studies.

From the time of Haeckel, various methodologies were established with the aim to propose natural classifications. A radiation of methods and theories during the 20th century brought about a sort of minefield of systematic theory and practice. For every theory there were two or more methods and, where there were different methodologies and opinions there were arguments. One of the more popular, and most highly debated methods of systematics was called phylogenetic systematics or cladistics.

Chapter 2 aims to highlight the important events leading up to the development of cladistics, and the reasons why cladistics has become so heavily debated. Debates within cladistics have been centred not only on theory, but methodology as well. There has also been a recent push by some cladists to move away from phylogenetic aims (i.e., transformation series or ancestor-
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descendant lineages), and focus solely on accurate classification systems, known as pattern cladists.

Chapter 2 also explores the reasons why palaeontologists did not accept cladistics as a reasonable systematic method when it was first introduced. Australian palaeontologists in particular did not use cladistic methods until the 1980s and 1990s, three decades after cladistics was introduced into biological classification. Moreover, it hasn’t been until the 2000s that cladistic methods have been seen more widely within Australian paleontological literature.

Discovering a monophyletic group is considered to be one of the prime reasons for a systematic study (Hennig 1950; 1966). The definition of a monophyletic group is also one of the most hotly debated concepts in recent years. Chapter 3 focuses on the debate arising in the early 1970s between evolutionary biologists such as Ashlock (1971, 1972) and Mayr (1974), and the cladists, such as Nelson (1972, 1974) and Farris (1974). There is also a focus on the theoretical differences between cladist’s definitions that make them unique, dividing the cladistic definition of monophyly into two terms.

A monophyletic group, whichever definition is being used, is always considered to indicate a natural classification system. When aphyletic groups (i.e., paraphyletic, polyphyletic, monotypic and unresolved clades; Ebach & Williams 2010) are used in biostratigraphic studies, problems have been shown
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to arise. Chapter 4 looks at four case studies where inaccurate classification has negatively affected biostratigraphic studies. The case studies highlight why it is essential for biostratigraphic studies to use monophyletic groups as marker taxa. To remedy this a method labelled Systematic Biostratigraphy is developed, giving biostratigraphers a way in which to reevaluate their studies if the marker taxon is considered artificial.

Carboniferous trilobites can be a useful group of fossils for localised biostratigraphic reconstructions (Engel & Morris 1990, Brauckmann & Hahn 1984). The family Phillipsiidae, the most prolific of the Carboniferous trilobites, has had its monophyletic designation called into question (Owens 1994; Jell & Adrain 2003). Chapter 5 aims to answer the question of whether or not Phillipsiidae is a monophyletic group. This is done through a systematic reappraisal of the subfamilies within Phillipsiidae, compared with subfamilies from the closely related Proetidae, as well as a systematic reappraisal of the genera within Phillipsiidae. The systematic reappraisals are achieved through the cladistic methods of parsimony and three-item analysis. A new classification system is also suggested in Chapter 5, to incorporate the findings of the cladistic analysis.

There has never been a taxonomic revision of Carboniferous and Permian trilobites from Australia. Engel & Morris (1997) counted 62 Carboniferous species, while 4 Permian species have been described (Teichert 1944; Wass &
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Banks 1971; Engel & Laurie 1978). Another Carboniferous species was recently described by Galtier et al. (2007). Chapter 6 revises the 67 original species, and places their genera and subfamilies into the appropriate classification based on the findings in Chapter 5.
Chapter 2. The Development of Cladistics: 19th Century Natural Classification to the late 20th Century Cladistic War

2.1 Introduction

Throughout the 19th century there were a number of important advancements to natural classification systems, not only the methods of obtaining them, but the theory which formed them. These included the development of homology as a concept, the introduction of evolution and phylogenetics, and the combination of the homology concept with the theory of evolution.

Cladistics, defined herein as the study of natural relationships amongst taxa (Williams & Ebach 2008), developed from the fusion of phylogenetics, popularised by Walter Zimmermann and Adolf Rename, with traditional biological systematics, most notably championed by the German speaking comparative biologists Adolf Naef, Joseph Kälin and Rainer Zangerl and later by the pattern cladists of the later 20th and early 21st centuries. The fusion of phylogenetics with systematics was first proposed by Ernst Haeckel (1894), and was called Die systematische Phylogenie, namely an attempt to combine “the theory of descent to create a common field of ontogeny [organische Formenlehre] systematics” (Haeckel 1894: v).
The opposition to this combination of the theory of descent and systematics was voiced most strongly by the morphological systematists (idealistic morphologists) in the early 20th century (Naef 1919; 1927; 1931; Zangerl 1948). Largely ignored by English speaking comparative biologists, *Idealistic Morphology* (Naef 1919), *Holistic Morphology and Homology* (Kälin 1941) and *Comparative Morphology* (Zangerl 1948), fell on deaf ears (Zangerl 1948; Ebach & Williams 2006). The criticisms, mainly that phylogenetics was dependent upon systematics, was continually challenged by Ernst Mayr and the bastions of the Modern Synthesis (Zangerl 1948; Simpson 1961; Mayr 1963). While the systematic morphologists posed a credible threat in the early 20th century, the post-WWII German literature finally laid their criticisms to rest. The appearance of *Grundzüge einer theorie der phylogenetischen systematik*, by German entomologist Willi Hennig (1950), once again embraced the fusion of phylogenetics and systematics with comparative biology. This time, however, the melding of two caused greater division among comparative biologists, one that with the addition of numerical methods lead to an outright “war” by the 1980s between the pheneticists and the cladists, and within the ranks of the cladists themselves (Hull 1988). Palaeontologists too had entered the debate, mostly siding with the Modern Synthesists (e.g., Simpson 1961), only to adopt cladistics at a much later date (late 1990s), particularly in Australian invertebrate palaeontology.
2.2 The History of Systematics

The history of systematics, the search for a natural classification system, stretches back to the late 18th/ early 19th centuries, from the works of Antoine Laurent de Jussieu (1789) and Augustin Pyramus de Candolle (1813). Systematics is the study of natural classification, formerly the domain of taxonomy and comparative biology, it is seemingly equated with evolutionary biology and the Modern Synthesis (Haas & Simpson 1946; Nelson & Platnick 1981). While there were numerous influences on the development of the field of systematics, several stand out. The development of the concept of homology, the introduction of evolution, the introduction of phylogenetics and the combination of all three have shaped systematics considerably.

2.2.1 The Development of the Homology Concept

One of the most important concepts in the field of systematics is that of homology (Patterson 1982; Brigandt 2003; Williams 2004). It is defined as the relationship of similar parts in different organisms through common ancestry (Haas & Simpson 1946). Homologies are currently seen as the evidence for evolution, providing evidence for evolution that similar structures are seen in different organisms as they had evolved from a common organism (Brigandt 2003; Hossfeld & Olsson 2005; Williams & Ebach 2008). The development of the concept of homology has been addressed from a wide variety of biological and
palaeontological fields (Haas & Simpson 1946; Hall 1994; Nelson 1994; Laubichler 2000; Brigandt 2003), though is recognised to begin with Owen’s (1843) comparative biology. The development of homology started with the recognition of the similar parts between organisms, homologs:

‘...For what the feather is in the bird, the scale is in the fish.’ (Aristotle, *Historia Animalium*, Lib I., Ch. 1, Sect. 4)

Owen (1843) however more decisively defined what a homolog was:

“The same organ in different animals under every variety of form and function” (Owen, 1843, glossary).

Since the term homolog was defined, the term homology has had greater meaning. Even though the term homology had already been in use well before Owen’s definition of a homolog, being seen in 18th century German literature (Appel 1987), the precise definition was unclear (Williams 2004). Although three concepts of homology were discussed by Owen (1848: 7–8), special homology, serial homology was originally proposed by French anatomist Felix Vicq D’Azyr (1774) and, general homology was originally proposed by Étienne Geoffroy Saint-Hiliare (Appel 1987). Owen defined repeating parts, within an individual organism (serial), between groups of organisms (general), and among all organisms said to be constructed on a common archetype (special).
Owen’s definitions were in line with the field of comparative morphology (or comparative biology) (Nelson 1994; Panchen 1994; Brigandt 2003). He did not, as we now understand homology, base his definitions on evolutionary theory or common ancestry (Szarski 1949; Hall 1994; Panchen 1994).

The systematic definition of homology was achieved through the addition of the theory of evolution, or that of common descent (Rieppel 1994). The first person to include any sort of concept we now associate with evolution was Agassiz (1857) who, whether deliberately or not, implied a relationship between those sharing a homology:

“Such an agreement in the structure of animals is called their homology and is more or less close in proportion as the animals in which it is traced are more less nearly related” (Agassiz 1857: 21)

Just two years later Darwin (1859) used the concept of homologous organs as one of the most important arguments for his theory of evolution (see Darwin, 1859: 198). Owen’s archetype was viewed by Darwin not as just an idea but as a real entity, turning the archetype into a common ancestor (Amundson 2007; Richards 2008).
2.2.2 The Introduction of Evolutionary Theory

Darwin’s (1859) *On The Origin of Species* had a significant impact for the field of systematic classification. Common descent was introduced by Darwin (1859) after recognising similar groups of taxa held similar characteristics. A common ancestor was used as an explanation for the patterns within and between biological taxa. Common descent implied that closely similar species are related genealogically, not just through a created archetype, as was Owen’s understanding (Phillips 1984; Panchen 1994; Edwards 2004; Richards 2008). When Darwin related homologous organs to common descent he provided an explanation that was more logical to those who did not consider Owen’s archetype adequate (Williams 2004). Systematists were now able to explain the hierarchical nature of biological taxa found from homologies (Phillips 1984). As well as an explanatory tool, Darwin’s (1859) *On the Origin of Species* largely used Owen’s definitions of homologs and homologies as a basis for his theory of evolution. So, in turn, early systematic theory helped to shape evolutionary theory as well.

The introduction of evolution then went on to influence other notable systematics works, including Haeckel (1866), who introduced phylogenetics, and Lankester (1870), who shaped the concept of homology into what we now recognise it as today, by combining it with evolutionary theory.
2.2.3 Haeckel and Phylogenetics

Ernst Haeckel considered Darwin’s (1859) *On the Origin of Species* to be one of the most important advancements in comparative biology (Haeckel 1866; Williams & Ebach 2008). The theory of common descent influenced his understanding of comparative biology by providing an explanation for natural groups. While Haeckel is considered to have influenced the field of systematics in numerous ways, there are three concepts he developed that have been reported widely. These include the creation of terms such as *phylogeny* and *monophyletic* (Dayrat 2003; Rieppel 2011), the promotion of trees as an illustrative depiction of classification systems (Breidbach 2003; Williams & Ebach 2008; Williams *et al.* 2010), and the creation the biogenetic law (Nelson 1978; Richards 2008).

The development of the term monophyly and its definition is discussed in Chapter 3. Phylogeny is currently considered to mean:

‘...a process of branching diversification of taxa...’ (Schuh & Brower 2009)

The concept of a phylogeny was first created by Haeckel as a term for the processes in the genealogical trees he was creating to explain the entire evolution of animal life (Breidbach 2003; Williams *et al.* 2010). A phylogeny was defined as the palaeontological history of evolution, or tribal history, with
Haeckel attempting to transform natural classifications into phylogenies (Williams & Ebach 2008). This idea was picked up by systematists, some of which would go on to consider phylogenies as the most important aim of systematics (Zimmermann 1931; Simpson 1961; Hennig 1966).

The “tree” Haeckel created has been one of the most influential ideas in modern systematics, particularly for phylogeneticists. Darwin’s classification tree was turned into a tree denoting the evolutionary steps taken by taxa (Williams et al. 2010). The trees depicted in Haeckel were used in Zimmermann (1931), whose work went on to influence Hennig (Hennig 1966; Williams & Ebach 2008; Schmitt 2013). These trees would eventually come to be termed cladograms, phenograms, evolutionary trees or phylogenetic trees (Breidbach 2003).

Haeckel’s main goal was to discover the phylogenies of all life on Earth, both as individual groups, and combining these as a whole. The tree was a way to demonstrate these phylogenies illustratively. The creation of these trees saw a need for an explanation of evolutionary processes. Haeckel came up with the biogenetic law, that ontogeny recapitulates phylogeny (Haeckel 1866; Nelson 1978; Hossfeld & Olsson 2005). The concept Haeckel developed went on to significantly influence systematists of the 20th century, the phylogeneticists, by putting an emphasis on phylogenies.
Lankester (1870) is not heralded in systematic literature as much as Darwin or Haeckel. However, he did provide an important link between Darwin’s theory of evolution and Owen’s concept of homology (Williams 2004). Lankester (1870) discussed the concept of homology for the “new biologists”, those who were not following the “Platonic” theory of comparative biology. The platonic theory was the theory followed by taxonomists, such as Owen, who believed in an archetype created by a creator, (Lankester 1870; Williams 2004).

Lankester recognised that many taxonomists were not satisfied with the platonic theory, and had begun using an embryological approach to explain homologs. These taxonomists were already open to new possibilities, and therefore readily took on common descent as a plausible explanation for homologies (Lankester 1870: 35). Lankester felt that he first had to differentiate between Owen’s original concepts of homology, and the one being used by those following Darwin’s theory. To do this he created the term “homogeny”:

“Structures which are genetically related, in so far as they have a single representative in a common ancestor, may be called homogenous” (Lankester 1870: 36).
While the term homogeny never actually caught on (Williams 2004), what Lankester did achieve for systematic theory was to successfully incorporate the theory of a common ancestor as an explanation for homology in nature. Haeckel’s and Lankester’s involvement of Darwin’s theory with the important systematic ideas of homology and phylogeny greatly influenced the systematists in the 20th century up until the 1960s.

2.3 Natural Classifications: Early 20th Century Systematists

The emphasis of finding phylogenies since Haeckel caused concern to some early 20th century systematists. Systematics had become the discovery of phylogenies, rather than the discovery of natural classifications. Two systematists who were vocal about the combination of phylogenetics with natural classifications were the German systematists Adolf Naef and Rainer Zangerl. Their work focussed on the importance of accurate classification methods in order to find phylogenies, but were dismissed by some as “anti-evolutionary” or “pre-evolutionary” (Naef 1919; 1927; 1931; Haas & Simpson 1946; Zangerl 1948; Hull 1989).

2.3.1 Naef and Systematic Morphology

Naef (1919) was the first to voice his concerns over the reigning trend in early 20th century systematic work to focus on phylogenies. Much of Naef’s (1919;
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1927; 1931) work was centred on what he termed idealistic or systematic morphology, which he used to determine natural classifications (Rieppel 2012). His idealistic morphology was based on the idea that there was a “type” or bauplan that would form a hierarchy. This was the idea that had him labelled pre-evolutionary by Haas & Simpson (1946) who considered the type idea to be directly from Owen’s archetype. Naef was however insistent that the type concept was from evolutionary origins (Naef 1931; Rieppel 2006), and that to discover natural classifications through systematic morphology was a precursor to discovering phylogenies (Naef 1919).

2.3.2 Zangerl and Comparative Morphology

Haas & Simpson (1946) saw Naef’s ideas as anti-evolutionary in nature, as he did not stress a purely phylogenetic method for systematists. The ideas of Naef were defended by Zangerl (1948), who discussed at length the morphological method, the method of Comparative Morphology. Zangerl (1948) was particularly adamant that homology should be removed from a phylogenetic context, as he felt that homology was not a functional concept. The difference Zangerl saw between comparative morphology, and phylogenetics, was that morphology and homology were based on facts, while phylogenies were based on human interpretations (Zangerl 1948; Rieppel 2006). While Zangerl’s discussion did not stress phylogenetic methods as had Haas & Simpson, he still considered them important. Zangerl was one of the translators of Hennig’s (1966) Phylogenetic
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Systematics, a revised english version of Hennig (1950), *Grundzüge einer Theorie der phylogenetischen Systematik*.

2.4 Fields of Systematics During the 1960s

Systematics was divided into three broad fields during the 1960s, evolutionary biology, phenetics and cladistics (Smith 1994; Williams & Ebach 2008). The division of these fields was based on two competing theories, two competing aims, and a multitude of competing methods. The two theories were broadly “phenetic theory” versus “cladistic theory”. Phenetic theory considered presence and absence of homologs to be useful, and cladistic theory considered only presence of homologs to be useful (Smith 1994). The competing aims were those that felt phylogenies to be the end goal versus those that felt it was only a part of the picture (Simpson 1961; Mayr 1942; Hennig 1966; Sneath & Sokal 1973). Evolutionary biology and cladistics preferred the former, while phenetics regarded the latter. Finally, the competing methods were dependent on the combination of theory and aims of the individual systematist.

Pheneticists were adamant that phylogenetics could not show a true classification system, and that overall similarity was able to achieve this. Cladists, on the other hand, felt homology to be the only way to address classification, and that phylogenetics was the end goal. The third group, the evolutionary biologists, seemed to follow a combination of the two. While
phylogenetic classification was deemed the ultimate goal of systematists (Mayr 1942; Simpson 1961), the use of only cladogenesis to establish a classification was frowned upon. Mayr (1965) even went so far as to praise the "numerical taxonomists" (i.e., pheneticists) for their inclusion of cladogenesis and anagenesis. Yet, pheneticists, such as Sneath & Sokal (1973), were highly critical of evolutionary biologists for considering phylogenetics to be the only useful aim of systematic studies.

2.4.1 Phenetics

Phenetics is the study of the overall similarity of taxa (Cain & Harrison 1960). Theoretically, phenetics holds to the opinion that all characters should be equally weighted \textit{a priori}, to avoid subjective "authoritarian" classification systems that were currently in place (Sneath & Sokal 1973; Wheeler 2012). The aim of phenetics is to produce an objective classification system with reference to the similarity of taxa (Sneath & Sokal 1973). Methodological application of phenetic theory is called numerical taxonomy (Sneath & Sokal 1973; Sneath 1995). Numerical taxonomy creates phenograms, branching diagrams constructed from the overall similarity of taxa through data matrices (Scotland 1992). The theory also includes the basic premise that the more data included in a systematic study, the better the classification. During the 1960s phenetic classification was preferred by some systematists over phylogenetic classification as it was considered to be applied to all taxa, even when fossil
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evidence was scarce. This was an element that was felt to be important to some phylogeneticists as well, the evolutionary biologists (Simpson 1961; Sneath & Sokal 1973).

Evolutionary biologists were part of a revolution in biology called the Modern Synthesis (Huxley 1942). The Synthesis was the combination of biological methods focussed on evolutionary theory. These included palaeontology, ecology, population genetics and zoogeography (Rieppel 2006). The Synthesis was developed from Huxley by the likes of Simpson and Mayr, who described the Modern Synthesis as evolutionary processes understood through the species concept (Mayr 1963). Simpson and Mayr encouraged a completely phylogenetic view within the Modern Synthesis, to the exclusion of comparative morphology and cladistics (Simpson 1961; Mayr 1963; Hull 1988; Rieppel 2006).

There were several major criticisms of phenetic theory and methodology at the time. One of those was that recognising only degrees of similarity, rather than degrees of homology, would produce non-monophyletic, or *aphyletic*, groups. Aphyly incorporates all notions of non-monophyly, that is, when monophyly is unknown (i.e., paraphyly, polyphyly and monotypy) (Ebach and Williams 2010). The basic theoretical concept of phenetics was to equally weight all characters (Sneath & Sokal 1973), rather than identify homologs, which would mean homoplasy could not be detected (Wheeler 2012). Systematists were also
critical of numerical taxonomy. Scotland (1992) discussed three major flaws in phenetic methodology, firstly that many topologies could be found from the same data matrices, depending upon choice of computer algorithm. Secondly, that terminal taxa cluster at different hierarchies in a phenogram, meaning that relationships of individual characters are not known. And thirdly, that the phenetic clustering algorithms used would group on both absence and presence of characters (first mentioned by Patterson 1982).

The recognition of aphyletic groups being included erroneously in classification systems of pheneticists and some evolutionary biologists was first addressed by Hennig (1950, 1965, 1966). His response was to introduce the “new” theory of phylogenetic systematics. This new phylogenetic method and theory was quickly condemned as *cladism* (Mayr 1965).

### 2.4.2 Cladistics

Cladistics was first coined as a new method of phylogenetics by Mayr (1965), and included those phylogeneticists (e.g., Hennig, Copeland and Dillon) who considered only cladogenesis as important for the discovering classifications. Two principles of phylogenetics were recognised by Mayr, the branching of lineages and the divergent evolution of daughter lineages. The former was what Mayr determined as the “cladistic approach”, 
“Phylogeny is characterized by two basic evolutionary processes, the branching of lineages (cladogenesis) and the subsequent divergent evolution of daughter lines...To prevent further confusion, I shall call this the cladistic approach, in conformance with the terminology proposed by Rensch (1960) (cladogenesis) and by Cain and Harrison (1960)” (Mayr 1965: 78).

The recognition of a cladogenetic approach is often attributed to Hennig, who focussed on the branching diagrams of taxa as a representation of their phylogenetic classification. Phylogenetic systematics was first introduced by Hennig (1950), and again reiterated Hennig (1965). Mayr (1965) responded to Hennig’s theory (as well as others who followed suit) by dismissing it as too restrictive for current classification systems. In an attack on cladistics and Hennig, Mayr (1974) claimed that cladistic analysis and cladistic classification were not necessarily the same thing. Two points were agreed upon by Mayr (1974), that taxa should form monophyletic groups, and that those groups must consist of a common ancestor. Mayr’s main criticism was that a cladistic analysis was turned directly into a classification, using tree-branching as an elucidation of categorical rank. These categorical ranks were felt by Mayr to be all important in classification systems. Mayr (1974) used the specific example of grouping birds with crocodilians as sister groups, as they had previously been contained in different ranks (e.g., birds within Class Aves, Crocodilians within Order Crocodylia). If Hennig’s cladogenetic theory was to be followed, many of
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the known groups would not be monophyletic, such as the Reptilia, containing the crocodilians.

Hennig’s (1966) argument was that monophyletic groups should contain all known taxa within a group, that descended from a common ancestor (See Chapter 3 for a full discussion of the concept of monophyly). This was probably Mayr’s biggest criticism. However, there were many systematists who did not agree with Mayr’s point of view, and felt his classifications were now artificial, rather than natural as he had hoped. The cladistic movement had begun, but along with it came two very different interpretations of Hennig’s (1966) initial arguments (Charig 1982; de Quieroz & Donoghue 1990; Williams & Ebach 2008).

2.5 Cladistic Theory

2.5.1 The Two Cladistics

Cladistics was originally named by Mayr (1965) for the Hennigian phylogenetic method. But Hennig’s method was interpreted in two ways by its supporters (Nelson & Platnick 1981; Eldredge & Cracraft 1980; Wiley 1981), and the difference in interpretation created a split between cladists (see Hull 1988; Ebach & Williams, 2008). This split was only noticed by a few cladists early on (Brady 1982; Patterson 1982; Platnick 1982; Nelson 1985), with Charig (1982)
defining two types of cladist, the Hennigian-cladists and the transformation or “Nelsonian” cladists, now commonly called “pattern cladists” (Brady 1982; Williams & Ebach 2008). Charig’s (1982) distinction was based on the aim of the cladist, Hennigian cladists centred their work on discovering phylogenies only, while pattern cladists centred their work on using classification to order nature, with phylogeny being inferred from the result. Those who were not considered Hennigian by Charig included Colin Patterson, Gareth Nelson and Norman Platnick (Charig 1982). Transformed or pattern cladists had gained notoriety, particularly among non-cladists (Beatty 1982; Ridley 1983).

The \textit{a priori} assumptions of phylogeny were not deemed necessary to pattern cladists for cladistic analyses, requiring only a recognition of homologies to discover natural classification systems (Patterson 1982; Scotland 1992). The main criticism of more traditional Hennigian cladists at the time was that pattern cladistics ignored time, which in turn they equated to evolution (Charig 1982). At a more methodological level, Hennigian cladists did not agree with Nelson’s (1989a) argument that cladistics could not discover ancestor-descendant relationships (de Queiroz & Donoghue 1990). These views contradicted the basic premise of phylogenetic systematics, that of discovering the processes for evolution, which required a real, or at least hypothetical, ancestor. Nelson was adamant in his view that Hennig did not intend ancestors to be considered real entities (Nelson 1972a, 1974) (though this can be disputed. See Chapter 3).
Despite the different aims of these cladists, their methodology remained the same. The reigning methodology of the time was parsimony, which could be used for both phylogenetic purposes, and discovering the homologies for classification systems (Charig 1982). The theoretical divide came to light to the multitude of others cladists in the 1990s when Nelson & Platnick (1991) published a method for determining cladistic classifications called three-item analysis. The methodology required the users to follow the pattern cladist theory, that cladism should focus on finding classifications, and that the common ancestor first developed by Darwin should be considered theoretical for methodological practices (Nelson 1972a; Platnick 1977; Charig 1982; de Queiroz & Donoghue 1990).

2.5.2 The Influence of Numerical Methods

The application of numerical methods (i.e., computer programs) to systematics allowed an increasingly large number of data sets to be computed in a relatively short space of time. When computers were first being used as a tool in systematics, they were often lauded as the way forward for the field (Mayr 1965; Edwards 2004). The ability to compute large amounts of data was only seen as a positive step forward (Arnold & Duncan 1984). This brought about the question of how to properly implement a computer program in systematics, with respect to the theoretical basis of the method.
At the time there was a rush to create computer programs for systematic analyses. Numerical taxonomy was the domain of pheneticists, but was quickly being claimed by evolutionary taxonomists (Mayr 1965; Sneath & Sokal 1973). Cladistics and cladists were also creating their own programs, starting with Wagner Parsimony (Farris 1970). Each field was eager to prove that their ultimate systematic aims, for example phylogenetic inference in cladistics, could be calculated by a computer.

2.5.2.1 Parsimony

It has been said that the creation of the method Wagner Parsimony by Farris (1970) was what catapulted Hennig’s phylogenetic systematics into mainstream phylogenetics (Farris 1983; Kluge 1984). Parsimony was first used in the context of systematics by Camin & Sokal (Camin & Sokal 1965; Edwards 2004), stating that classification should follow the “principle of evolutionary parsimony” (Camin & Sokal 1965). The parsimony method of cladistics sees synapomorphies arranged into a nested hierarchy based on the greatest number of characters, in the shortest number of steps (Kitching et al. 1998). Farris (1970) came up with a statistical method combining the theory of parsimony with computer algorithms, so that a parsimonious cladistic analysis could be achieved computationally. The method was picked up by cladists, who needed a means to compute their enlarging data sets (Arnold & Duncan 1984; Edwards
2004). The method was quickly replacing the theory, with parsimony considered synonymous with phylogenetic systematics, and therefore cladistics (Farris 1983; Williams et al. 2010):

“Most phylogeneticists recognize that inferring genealogy rests on the principle of parsimony, that is, choosing genealogical hypotheses so as to minimize requirements for ad hoc hypotheses of homoplasy” (Farris 1983: 7).

That a method had such a large influence over a theory was hardly surprising. While Hennig created a theory many wanted to follow, he did not create a means to achieve the phylogenetic reconstructions that he recommended.

2.5.2.2 Three-Item Analysis

The introduction of three-item analysis by Nelson and Platnick (1991) as a new method of parsimony finally triggered the acknowledgement of other cladists that there were two competing theories. Three-item analysis methods use three-taxon statements of data sets as the simplest way of showing a relationship between taxa. These statements are then added together to find the most parsimonious fit of all the relationships that existed between taxa within the data (Nelson & Platnick 1991; Kitching et al. 1998). The method does not automatically presume an ancestor-descendant relationship between the taxa, nor does it require any a priori assumptions of an evolutionary process (Kitching
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et al. 1998). Three-item methods (known originally as three-taxon statement analysis) have also been dubbed taxic homology, as they focus on taxon relationships rather than evolutionary relationships (de Pinna 1991; Kitching et al. 1998; Scotland 2000).

By removing a need for a priori assumptions of evolutionary processes, including ancestor-descendant relationships, Nelson & Platnick (1991) considered they had improved up Wagner Parsimony for cladists. The assumption was however that all cladists followed their theoretical understanding of cladistics, which was not the case. Three-item analysis went directly against the original cladistic (i.e., phylogenetic systematics) hypothesis that true phylogenies could be discovered through an analysis of homologies. Couple this with the increasing view that Wagner Parsimony equated to cladistics, and the method was received very negatively (Kluge 1993).

2.6 Systematics versus Phylogenetics

The general reception to the three-item analysis method saw an obvious split in what are still termed cladists. Those who followed both the methodology and theory of Nelson & Platnick began to distance themselves from the more traditional Hennigians. The pattern cladists saw systematics as the ultimate goal of an analysis, the process cladists, a phylogeny. Pattern cladists felt that
the combination of phylogenetics with systematics by Hennig had clouded the importance of classification (Ebach & Williams 2008; Wheeler 2010).

Separation of systematics from phylogenetics was actually first proposed by Naef (1919). Haeckel developed genealogical trees as a symbol of the phylogeny of taxa, and in so doing argued that phylogenies were the most important aims of a systematist. Naef disagreed with Haeckel’s interpretation, that phylogenetics was equivalent with systematics. Instead, Naef argued that systematic classification was a forerunner to phylogenetic inference, and that recognition of the two as separate enterprises ensured correct classification systems were maintained (Naef 1919).

Pattern cladists use the relationships of taxa obtained through recognition of homologies to create natural classification systems. Process cladists use relationships of taxa obtained through homologies to create phylogenies. While the two areas have similar methodologies (parsimony computer programs) they have inherently different aims. They are in effect, two different fields. Pattern cladistics should probably be called systematics, while process cladistics or phylogenetic systematics should probably be called cladistic phylogenetics.
2.7 Cladistics in Palaeontology: More Misunderstandings?

Palaeontologists did not have a significant impact on the development of natural classification methods (Cracraft 1981). Despite Haeckel’s (1866) belief that palaeontology and fossils held the key to phylogenetic reconstructions, few palaeontologists were aligned with systematics in the mid 20th century. One of the few was George Gaylord Simpson, who advocated phylogenetic reconstructions, yet was an “anti-cladist” (Simpson 1975) along with most other palaeontologists at the time:

“A SPECTRE is haunting palaeontology — the spectre of cladism” (Campbell 1975: 87, original emphasis).

The opinion of Simpson (1961) was that fossils were the real ancestors of modern taxa, and as such were necessary for phylogenetic reconstructions. Nelson (1972b) refuted this theory, and suggested that fossils could not be used as ancestors for phylogenetic analyses. This tied in with his view that ancestor-descendant relationships could not be deduced from a phylogenetic system (Nelson 1972b).

The reaction by palaeontologists to Nelson’s point of view was to discredit cladistics as a method of classification. Campbell’s (1975) publication mentioned above was in retaliation to Nelson (1972b). Some palaeontologists
even went so far as to suggest phenetics was the only reasonable method of
classification, so as not to include fossil taxa in a cladistic approach (Gingerich
1979). It had been a long held view by palaeontologists that fossil taxa were the
real ancestors of modern taxa, and that they were all important for phylogenetic
analyses (Simpson 1961; Gingerich 1979). When cladistics was introduced it
removed the need for fossil taxa in phylogenies, as it provided a method for
natural classifications without ancestors (Nelson 1972b). Nelson’s removal of
ancestors was also the removal of fossils as necessary to phylogenies,
undermining the importance of palaeontologists to systematics (Patterson 1981;
Smith 1998).

Since the illusion of fossil taxa representing ancestral taxa was extinguished,
palaeontologists needed to focus on what fossil taxa could tell them (Smith
1998). Patterson (1981) viewed fossils as a means of supporting or refuting
current hypotheses of homologous characters, giving ages of groups plus
providing palaeobiogeographic data. Palaeontologists felt that cladists thought
of fossils as useless in systematics (Campbell 1975; Eldredge 1979; Lazarus &
Prothero 1984). Cladistics had been misread. What cladists were really trying to
say was that fossils are a source of data, nothing more or less, and can be used
in the same way as modern taxa for systematic studies (Schaeffer et al. 1972;
Williams & Ebach 2004). Surprisingly, the cladistic revolution had started in
palaeontology, in the works of Colin Patterson, and in doing so had removed
the mystique of palaeontology and the fossil record (Williams & Ebach 2008).
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Evolutionary relationships, once confined to the fossil record, were now discoverable by all comparative biologists, even those who work on taxa without a fossil record.

2.8 Cladistics in Australian Palaeontology

Cladistics in Australian palaeontological studies came much later than in palaeontological studies from other countries such as the United States (Eldredge 1972; 1973; Cracraft 1981). One reason why Australians were late adopters of cladistics may be because of the publication by Kenneth Campbell (1975), who openly dismissed cladistics as worthless for palaeontology, especially invertebrate studies. Campbell was an important and well respected palaeontologist in Australia at the time, working on groups from both the vertebrates and invertebrates. Campbell’s rejection of cladistics may have been the precursor to the lack of cladistic studies from Australia until the late 1990’s.

2.8.1 A Spectre is Haunting Palaeontology

Campbell worked on both fossil fishes, and invertebrates, having produced several seminal works on trilobites (Campbell 1967; 1973; 1977; Chatterton & Campbell 1979). In 1975 Campbell published a paper titled “Cladism and Phacopid trilobites”, in which he seemingly demonises cladistics:
“The manifesto is out (Hennig, 1950, 1966), the commentaries are coming thick and fast as each volume of Systematic Zoology attests, and with some workers being accorded the accolade ‘progressive’ (Nelson 1972b: 372), can the derogation ‘reactionary’ be far behind? As with the original spectre there may be something to be said in its favour, from a theoretical point of view at least, and no doubt it will be in the haunting business for many years to come. Whether it is allowed to take up a permanent post of spirit-in-residence, however, will depend not so much on the frequency of its visitations or the sophistication of the guises it adopts, as on the benefits we derive from having it around the ancestral home” (Campbell 1975: 88)

The paper published in the first volume of *Alcheringa*, the newly founded journal of the *Association of Australasian Palaeontologists*, criticised the cladistic analysis of phacopids by Niles Eldredge, a palaeontologist and cladist (see Nelson & Ladiges 2011). Eldredge (1972; 1973) attempted to re-analyse North American *Phacops* taxa that were diagnosed by Campbell (1967). The re-analysis led Eldredge (1973) to conclude that Campbell’s stratigraphical zonation of taxa to form genera, “creates a hodge-podge of paraphyletic and polyphyletic taxa” (Eldredge 1973: 292), thereby dismissing Campbell’s horizontal zonation of taxa and seemingly the use of stratigraphy in determining genera.
Campbell’s reaction was striking. What should have been a reply to Eldredge (1973), and his opposition to Eldredge’s method, turned out to be a full scale attack against an entire field. Campbell (1975) defends the palaeontological and stratigraphical method by opposing the use of morphology independently of stratigraphy in making claims about classification — a claim championed by the cladists (Schaeffer et al. 1973; Lazarus & Prothero 1984; see also Williams & Ebach 2004). Secondly, Campbell makes a claim that has been long accepted by invertebrate palaeontologists:

“For various reasons vertebrate fossils lend themselves more readily to cladistic analysis than do invertebrates” (Campbell 1975: 89).

The notion that invertebrate fossils alone cannot contribute meaningfully to a classification or phylogeny, gives greater support for the use of stratigraphy in determining monophyletic taxa. Clearly modern cladistic analyses have overturned these two old chestnuts (see below). In Chapter 4 it is clearly demonstrated that genera determined using stratigraphy have resulted in highly unstable and aphyletic groups. Moreover, as will be shown in Chapter 5, cladistic analysis is possible on even the most poorly preserved taxa (i.e., Permo-Carboniferous trilobites), using a small number of characters. Chapter 4 will also show how morphology and cladistics can be beneficial to refining biostratigraphical hypotheses, rather than being dependent on them.
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Campbell (1975) seemingly raises these two points to discredit Eldredge’s findings. According to Campbell, *Acernaspis, Ananaspis* and *Paciphacops* were phylogenetically “entangled” and paraphyletic. Only a method that uses both stratigraphy and morphology (outlined in Campbell 1977) can be used to find monophyletic genera.

“And if it has not proved possible to define monophyletic taxa at the generic level, is there any point in attempting to use cladistic methods for the definition of higher taxa?” (Campbell 1975: 95)

Campbell only had to wait. *Acernaspis, Ananaspis* and *Paciphacops* were found to be monophyletic using cladistic analysis (Ramskold & Werdelin 1991). Since 1991, there have been an increasing number of cladistic analyses in invertebrate palaeontology, which show highly resolved monophyletic groups, independently of stratigraphy (see below).

Viewed historically, Campbell (1975) was clearly wrong about the influence of cladism. Cladistics was slowly adopted by palaeontologists. But what effect, if any, did Campbell’s paper have on the Australian invertebrate palaeontological community?
2.8.2 Australian Palaeontology after Campbell (1975)

In the years following Campbell (1975), cladistics was seemingly rejected or ignored by all but a few palaeontologists working in Australia. Evidence for this is the total lack of published cladistic analysis in the invertebrate community before 1999. The earliest acknowledgement of its applications was by Young (1981) who used Platnick & Nelson’s (1978) cladistic biogeographical-vicariance method on major vertebrate groups from the Early Devonian. Following this study Young (1986; 1990; 1995a; 1995b) also discussed the use of cladistic methods for palaeogeographical and geological data.


Invertebrate studies involving cladistic analyses in the 1990s only involved one Australian palaeontologist, Gregory D. Edgecombe (a former Ph.D student of
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Eldredge). These studies included collaborations such as Edgecombe & Ramskold (1996; 1999) Edgecombe et al. (1997), Chatterton et al. (1998), Edgecombe et al. (1998) and Ebach & Edgecombe (1999). The 2000’s saw an increase in interest in invertebrate palaeontological cladistic analyses. Some of the studies included Ebach & Edgecombe (2001), Ebach & Humphries (2002), Paterson & Edgecombe (2006), Paterson et al. (2010) and Edgecombe et al. (2011), to name a few (both Ebach and Paterson were students of Edgecombe). Vertebrate palaeontology underwent the same trend (Ahlberg & Johanson 1997; Long 1989). The rise in cladistics among palaeontologists trained in Australia was mostly due to the arrival of overseas trained Ph.Ds (e.g., Gregory D. Edgecombe, Michael Lee and Zerina Johanson) or Australian postdoctorates working overseas (e.g., John A. Long) supervising students of their own, as well as international journals adopting cladistics as a standard for systematic analysis.

2.8.3 The Legacy of Cladistics in Australian Palaeontology

Cladistic biogeography is perhaps one the most popular uses of cladistics outside of systematics (see Parenti & Ebach 2009). The theory associated with cladistic biogeography, rather than the method itself, had by 1981 become the mainstay of biogeography. Vicariance, the concept that geographical isolation responsible for speciation is driven by Earth processes, was the basis for cladistic biogeography. The theory of vicarance is the basis for terrane analysis.
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(Young 1987; 1990; 1995), namely the use of geological terranes to define areas over time. The method is used to reconstruct the geological and biotic histories by comparing hypothetical geological areagrams against areagrams. Terrane analysis forms the basis for area cladistics (Ebach 1999; Ebach & Humphries 2002), in which areagrams can be used to retrodict the positions of former terranes based on the assumption that biotic relationship is equivalent to geographical proximity. Both these methods developed in Australia by Australian palaeontologists have had a large effect on both palaeobiographical and modern biogeographical studies worldwide (see Morrone 2009). The use of vicariance in Australian biogeography was also championed in the early 1980s by vertebrate palaeontologists such as Michael Archer (Archer & Clayton 1984), well before the cladistic biogeographical movement in Australian phytogeography (Ladiges et al. 1991; Weston & Crisp 1994; Crisp et al. 1995) and Australian zoogeography (Cracraft 1991).

2.9 Conclusion

The development of systematics as the field of natural classification was strongly influenced originally by comparative biologists. From the time of Owen (1848) decisively defining a homology, taxonomists sought to develop classification systems that reflected nature. The introduction of evolution saw an explanation developed for natural classification systems, especially for those who did not follow Owen’s archetype theory. Although Darwin came up with
the theory of evolution, he felt it was impossible to come up with one entire classification system for all taxa. Haeckel (1866; 1876) took the theory of evolution and the natural classification of all taxa as a puzzle, one which he wanted to solve. Haeckel used Darwin’s metaphorical “tree” of classification, and turned the steps into real events, creating a genealogical tree (Haeckel 1866; Williams & Ebach 2008). Those events and the path in which they created was termed a phylogeny by Haeckel. A few short years after Haeckel’s (1866) first introduction of a genealogical tree and a phylogeny, Lankester (1870) included a common ancestor as the explanation for Owen’s homology, the relationships of homologs between taxa. The combination of evolution with homology saw a proliferation of taxonomists, now deemed systematists, using these theories to create Haeckel’s phylogenies.

The expansion of phylogenetic studies in systematics ultimately saw the demise of an emphasis on classification. This was discussed at length by the German systematists Naef (1919; 1931) and Zangerl (1948). Naef was the first to advocate the separation of phylogenetics from systematics, and pointed out that while phylogenetics relied on systematic classifications, classifications did not rely on phylogenetics (Naef 1919). Zangerl (1948) also emphasised a need for accurate classifications first and foremost in systematics, and lamented the trend of focussing solely on finding phylogenies. Despite these concerns being raised in the early 20th century, systematists still went on to argue over systematic methods involving phylogenetics.
During the 1960’s a surge in phylogenetic theoretical publications (Simpson 1961; Mayr 1965; Hennig 1965; 1966) and a preference for phylogenetic classification systems saw a debate arise between phenetic and phylogenetic theories. Pheneticists were sure phylogeneticists were not producing objective classification systems (Sokal & Sneath 1963), and that by including all data, including absence and presence of characters, they were addressing natural classification as thoroughly as possible. Unfortunately, the rise of phylogenetics since Haeckel had seen numerous publications on the pitfalls of homoplasy in classification (Patterson 1982; Farris 1983; Rieppel 1988). Without reference to homologies in classification systems, convergence and parallelism of characters could not be detected. This meant that a phenetic classification system could produce aphyletic groups (Scotland 1992; Wheeler 2012). Hennig (1950; 1965; 1966) stressed the importance of only using what he termed synapomorphies, homologous characters, to produce classifications. Hennig was also very adamant about the definition of a monophyletic group, and insisted all groups to be considered natural, should contain all taxa belonging to it. These strict demands of phylogenetic systems saw some phylogeneticists term the users “cladists” to denote their belief that cladogenesis was the only important evolutionary process (Mayr 1965).

Cladistics developed fast, beginning the Hennig’s (1966) Phylogenetic Systematics. During the 1970’s two cladistic theories were emerging. One which
stated that Hennig meant to denote common ancestors as theoretical (Nelson 1972a; Platnick 1977), and the other that believed Hennig meant ancestors to be real (Charig 1982). This simple theoretical difference caused a rift between systematists who called themselves cladists, one group known as pattern cladists, the others process cladists. Process cladists used Hennig’s (1966) phylogenetic theories in conjunction with the method Parsimony to deduce phylogenies. Pattern cladists also originally used parsimony methods (although this changed to three-item methods) to deduce classification systems using homologies to develop monophyletic groups, and then in turn would infer a phylogeny from their results (Platnick 1977). The main difference between the two groups of cladists? The aim of their analysis. Process cladism required only a phylogeny to be found, pattern cladism a hierarchical classification. Both groups claimed their aim was more likely to be the evidence for evolution, that was the ultimate goal.

Pattern cladists had begun to distance themselves from Hennig’s phylogenetic teachings. Hennig compounded the muddying of systematics and phylogenetics, to a point that phylogeneticists following the cladistic theory considered the two words to be synonymous. The pattern cladistic theory had aims more inline with the original field of systematics, to formally identify classifications that occurred in nature. A phylogeny could then be deduced, if that were the aim of the study. The idea that systematics could be removed from phylogenetics was first mentioned by Naef (1919; 1931), who suggested while
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phylogeny relied on accurate systematic classifications, systematic classifications did not rely on phylogeny. Pattern cladists took up this idea by focussing on accurate classification systems alone (Williams & Ebach 2008).

The development of pattern cladistics saw the alienation of palaeontologists to the field. This was because pattern cladistics did not require a real ancestor, removing the reliance on fossil taxa (Nelson 1972b; Patterson 1981). Indeed, palaeontologists shunned cladistics as a whole, as neither pattern nor process methods actually required fossil taxa. The palaeontological community saw this as cladists saying fossils were useless. Rather, cladists were trying to emphasise that fossils could be viewed at the same level of extant taxa. Invertebrate palaeontology in Australia has really only seen cladistic methods accepted in the past 15 years. This late acceptance of cladistics, possibly delayed by the call to arms by Campbell (1975), has drastically improved our understanding of natural groups in Australian invertebrate palaeontology as well as going some way to introducing a method in Australian palaeobiogeography (Young 1990; 2011; Ebach & Edgecombe 2001).

The importance of an accurate classification system is the main focus of Chapters 4, 5 and 6. Even though phylogenies have been the driving force behind many systematic studies in recent years, classification was, and still should be the driving force behind phylogenies. Without accurate classification, phylogenetics will not prosper. Cladistic methodology signified the removal of
stratigraphy from classifications in palaeontology, and made morphology independent. This removed the need for the palaeontological method, which used both stratigraphy and morphology to propose phylogenies. The independence of morphology from stratigraphy meant that monophyletic groups could be discovered without a complete knowledge of a fossil group’s stratigraphy. More to the point, monophyletic fossil groups can now be used to influence biostratigraphic studies by ensuring a natural marker taxon. Artificial classification systems, such as those used in invertebrate palaeontology involving both biostratigraphy and morphology, only seem to produce aphyletic groups. Natural classification systems, on the other hand, hold a vast influence over palaeontological fields. This is the reason why natural classification is the main theme to this thesis.
Chapter 3. Defining and Redefining Monophyly

(Manuscript currently ‘in press’ in Australian Systematic Botany)

3.1 Introduction

A history of systematic development in Chapter 2 has demonstrated the need for adequately defined nomenclature in the field. Many terms in systematics are re-defined over time. Homology is shown to have developed over a 50 year time span, from Owen (1843) to Lankester (1870), and is still understood as the most important concept for systematics. On the other hand newer terms, such as monophyly and its definition, are still being debated, despite being considered as a very important concept for cladistics.

*Citius emergit veritas ex errore quam ex confusione* (Hennig 1950).

“The general confusion as to the interpretation of the concept phylogenetic relationship can be characterized as the dilemma of systematics” (Brundin 1966: 16).

Throughout the late nineteenth and early twentieth centuries the term monophyly, a neologism coined by Haeckel (1866), was used in a very loose
way meaning either all organisms originate from just a single stem form (Stamm-form) (Rieppel 2011; Richards 2008) or a single origin of the animal kingdom (Ashlock 1984). Biologists Ernst Mayr (1942), Robert Sidney Bigelow (1956) and George Gaylord Simpson (1961) redefined the term to be more specific, to include a species concept (Mayr and Simpson), and a time concept (Bigelow). German entomologist Willi Hennig took up these ideas in his 1966 revision of Hennig (1950), changing his original definition to include the species and time concepts of Mayr and Bigelow (1956), while incorporating his original ideas on phylogeny. At the same time Brundin (1966) had used Hennig’s original (1950) definition of monophyly to propose his own definition.

Regardless, Mayr, Simpson and in particular Peter Ashlock, found Hennig’s now more widely read definitions to be far too restrictive. Rather, it was the exclusion of paraphyletic taxa from a monophyletic group sensu Hennig that began the modern debate on the meaning of monophyly (Hennig 1965).

When Hennig defined monophyly as a concept separate from paraphyly, it invoked a responses from Ashlock and like-minded evolutionary biologists. A debate ensued from the newly emerging “cladists”, followers of Hennig’s theoretical work that he referred to as Phylogenetic Systematics, and the more traditional evolutionary biologists. The debates centered around the definition of monophyly touch on two important issues, but were not appreciated at the time. The first of these issues was whether the definition was based on a genealogical-phylogenetic inference, or a concept about kinship, that is
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topological relationship. These issues have been the driving force behind the prolonged debate, which in recent times has devolved into three distinct positions: 1. those that consider monophyly to be a stem group, which include aphyly and holophyly; 2. those that consider monophyly to include the most recent common ancestor, and; 3. those that consider monophyly to be topographical relations, namely when two taxa are more closely related to each other than they are to a third.

3.2 Hennig and Brundin: A new definition of monophyly

Hennig (1965, 1966), as well as the theoretical parts of Brundin (1966), are derived from Hennig (1950) (See also Schmitt 2013: 94-95 for a summary on the Brundin - Hennig correspondence). These publications discuss the merits of phylogenetic systematics, such as the use of synapomorphy to make statements about monophyly.

3.2.1 The evolution of Hennig’s monophyly

The first definition Hennig gave of monophyly was,

“... monophyletic groups of species - and these are all groups of higher rank - are referred to as those that ultimately can be traced back to a common
ancestral species [...] must be added that a monophyletic group must not only include species that are derived from a common ancestral species, rather that they must include in addition, all the species that come from this ancestral species” (translated from Hennig 1950: 307-308).

In his following publications Hennig’s definitions were consistent with that given in 1950, though the wording changed considerably. Hennig defined a monophyletic group as,

“Monophyletic groups” are small or large species-groups whose member species can be considered to be more closely related to one another than to species which stand outside these groups” (Hennig 1965: 98).

He later goes on to write,

“The supposition that two or more species are more closely related to one another than to any other species, and that, together they form a monophyletic group, can only be confirmed by demonstrating their common possession of derivative characters ("synapomorphy"). When such characters have been demonstrated, then the supposition has been confirmed that they have been inherited from an ancestral species common only to the species showing these characters” (Hennig 1965: 104).
A year later, the first definition is given as,

“...A monophyletic group is a group of species descended from a single ("stem") species, and which includes all species descended from this stem species. Briefly, a monophyletic group comprises all descendants of a group of individuals that at their time belonged to a (potential) reproductive community, i.e., to a single species” (Hennig 1966: 73).

Hennig (1966) claimed to have developed this definition from two authors, Mayr (1942) and Bigelow (1956). Mayr (1942) is attributed by Hennig as representing the commonly used definition of monophyly,

“The definition of Mayr (1942) probably represents a widely held view: ‘We employ the term monophyletic as meaning descendants of a single interbreeding group of populations, in other words, descendants of a single species’” (Hennig 1966: 72).

This lacked the important dimension of time for Hennig, so he then added Bigelow’s (1956) definition,

“...Unless the time element is introduced, say, as follows: ‘the members of a monophyletic group share a more recent common ancestry with one
another than with any member of any other such group of equal
categorical rank,’ the term ‘monophyletic’ is meaningless. The time
element is the very essence of monophyletic classification” (Hennig 1966: 145).

Hennig’s first definition appears to be extremely similar to Mayr’s, even though he claims Mayr’s definition is incomplete. Though Hennig cites Bigelow as a source of a time aspect, this concept is extremely vague in Hennig (1966). So much so, it would be forgiven if a third party read both definitions and did not see a difference.

The placement of Hennig’s (1966) first definition is not consistent with the placement of Hennig’s (1950) definition. Monophyly is first defined by Hennig (1966: 72), and includes the now widely-used diagrams depicting monophyly versus paraphyly and polyphyly (Hennig 1966: fig 45). Compare this to the definition of monophyly and polyphyly in Hennig (1950) and one can see it occurs much later in the book (page 307).

Hennig’s 1950 book did not incur the reaction from evolutionary taxonomists in regards to the definition of monophyly that his 1966 book received. Mayr (1965) did criticise his use of a purely “cladistic” view, especially in regards to monophyly. After the 1966 book was published there were a much greater number of criticisms on his theories on phylogenetic systematics (Bock 1968,
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1973; Mayr 1969, 1974; Ashlock 1971, 1972, 1974; Colless 1967; Darlington 1970, 1972 to name a few). Time and time again authors such as Mayr, Bock and Ashlock took offense to Hennig’s redefinition of monophyly,

“...controversies have arisen over the past decade largely because of redefinition of long established terms such as monophyly by “cladists” (Bock 1973: 383)

As shown above, Hennig did not redefine monophyly in his 1966 book, but did so as far back as his first book (Hennig 1950). One possible explanation is that his latter papers and his 1966 book were much more widely available to audiences as they were written in English (Schmitt 2013). Although this was true to an extent, his 1950 book was cited by Borgmeier (1957), Mayr (1965), Sokal and Camin (1965), Sattler (1964) and Kiriakoff (1959), proving that it had been read before his 1966 book was published. Why then was his definition of monophyly not criticised as much as after his 1966 book was published? The placement of the definition of monophyly lends a clue: in his 1950 book it was on page 307, whereas his 1966 book it was on page 73. The change between Hennig’s books can be seen as a change in focus on concepts. It would appear monophyly was not as important to him as the concept of “phylogenetic relationship”, which is discussed throughout the beginning, middle and end of his 1950 book (with monophyly almost as an afterthought). The 1966 book, however, dramatically changes focus from phylogenetic relationships to
monophyletic groups. It could be suggested that Hennig was now using the term monophyly as a replacement for phylogenetic relationships. The definition of monophyly in 1950 did not come under fire like the definition in 1966, and it may be that this sudden focus on monophyly, and its very rigid definition, was a source of concern for those who did not agree.

3.2.2 Hennig’s Second Definition and Brundin

The second definition Hennig gave was,

“Another definition is: A monophyletic group is a group of species in which every species is more closely related to every other species than to any species that is classified outside this group” (Hennig 1966: 73).

This definition was connected to the idea of kinship, a concept Hennig disliked. He felt it was interchangeable with affinity, defined by Cain and Harrison (1958) on overall similarity. The second definition could in fact be attributed to Cain and Harrison,

“Whenever a taxonomist (or anyone else) says of three things that on their “overall resemblance” or “general likeness” or some such property, two of them are more closely related to each other than is either to a
third, he is making a judgement of affinity of an extremely familiar sort.” (Cain & Harrison 1958: 85; italics in original)

Hennig preferred the word relationship to affinity, which he defined as,

“A species x is more closely related to another species y than it is to a third species z if, and only if, it has at least one stem species in common with species y that is not also a stem species of z” (Hennig 1966: 74).

This definition of relationship was created by Hennig to include the stem species, or a notion of genealogy, rather than overall similarity. It was derived from Zimmermann (1931), who stated:

“The relative age relationship of ancestors X₁ and X₂ is the only direct measure of phylogenetic relationship” (Zimmermann 1931: 989-990).

Genealogy was supported by Hennig over kinship (i.e., the concepts of age and ancestors over overall similarity). Hennig also states that in all definitions of a monophyletic group (presumably he was referring to Mayr’s, Bigelow’s and his own, though he does not state this) that it must include all species or individuals descended from the stem species, and that none of the derived species be allocated outside the group (Hennig 1966: 73).
The next definition was supplied by Brundin,

“...The definition of a monophyletic group is a direct consequence of the definition of phylogenetic relationship: Monophyletic is every group of the system fulfilling the demand that any species belonging to it is more closely related to any other species likewise belonging to the group than to any species which does not belong to it” (Brundin 1966: 17 original emphasis).

And he goes on to add,

“...It is important to note not only that a monophyletic group may comprise species which are derivable from a common ancestral species, but, what is the more, that it must comprise all species derivable from that ancestral species” (Brundin 1966: 17).

Brundin’s definition includes both of Hennig’s (1966) definitions, by including both the kinship and genealogical concepts. Brundin also makes the particular point that all species must be included in the group to be monophyletic, which was taken from Hennig (1953). Hennig is very clear about this (Hennig 1966: 73). It is interesting to note that at this point Brundin does not include the “stem” species discussed in detail in Hennig’s (1966) definition.
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Monophyly was defined by Hennig to support his overall theory that classification should be based on phylogenetic principles, not overall similarity (Richter & Meier 1994). The concept of time was important to Hennig, as it encompassed his ideas of phylogeny based on Zimmermann’s definition. Brundin (1966), on the other hand, gave a definition of monophyly that was based on Hennig’s (1953) original definitions. Monophyly was defined by Brundin on Hennig’s principles, but was intended to be applied to biogeographical concepts (Brundin 1966). A number of early publications on the use of phylogeny in systematics referred to both Hennig (1966) and Brundin (1966) as their source of theoretical work (Nelson 1969, 1972, 1974; Darlington 1970; Mayr 1969). It was the reading and understanding of these two authors that sparked the beginning of the debate over the definition of monophyly.

3.3 The beginning of the debate: Ashlock versus Nelson

Heteropterist Peter D. Ashlock, from the United States, was an early adopter of phylogenetic systematics, having been introduced to Hennig (1950) by fellow entomologist Pedro Wygodzinsky in 1961 (Slater and Polhemus 1990: 115). While learning Hennig’s approach, Ashlock published a definition of monophyly that he felt would encompass both the traditional definition of monophyly and Hennig’s (1966) newer definition. Ashlock did not find fault with Hennig’s version of monophyly, rather he found it far too restrictive, “...since it is more restricted in meaning than that generally held, it probably...
should be renamed. I proposed the word holophyly, a tribe of all, for the concept that Hennig calls monophyly. Holophyly and paraphyly, then, become two aspects of the more general concept, monophyly (Ashlock 1971: 65). The exclusion of paraphyletic taxa went against Ashlock’s views of “traditional” monophyletic groups. It was this exclusion of paraphyly from monophyly that led Ashlock (1971) to formally redefine monophyly, holophyly and paraphyly,

“A **monophyletic** group is one whose most recent common ancestor is cladistically a member of that group.

A **holophyletic** group is a monophyletic group that contains all of the descendants of the most recent common ancestor of that group (monophyly of Hennig).

A **paraphyletic** group is a monophyletic group that does not contain all of the descendants of the most recent common ancestor of that group” (Ashlock 1971: 68-69, original emphasis).

Why would Ashlock wish to redefine monophyly? Ashlock’s definition of monophyly deliberately included paraphyly. Given that many recognised groups, such as Reptilia for example, were paraphyletic, Ashlock believed that they should be retained as monophyletic, despite Hennig’s (1966) views. The redefinition preserved all names and recognised all definitions as useful to classification. Ashlock was considered an early proponent of the cladistic method, and his views along with that of Wygodzinsky, resounded
more with evolutionary biologists such as Mayr, particularly in the adoption of Hennig’s monophyly in biological classification (Slater and Polhemus 1990). Then why is Ashlock seen as detrimental to the development of cladistics? Slater and Polhemus believe it is “Ashlock’s defense of paraphyly lost him much of his standing in the coterie of the new cladists” (Slater and Polhemus 1990: 116). Why this might be true for some debates (Nelson 1974), it does not necessary ring true for others (Ashlock 1971) as I will show below.

Ashlock introduced a new term to distinguish one type of “monophyly” from another, thereby unwittingly reducing the ambiguity of the term “monophyly”. Interestingly, while Ashlock ascribes the term holophyly to Hennig’s definition, he does not cite a source for the original term,

“Systematists have long used the term monophyly and have felt sure they knew what was meant when they used it” (Ashlock 1971: 63).

While the ambiguity of terms is presently seen as an issue, it was not as problematic as the defense of paraphyly and paraphyletic groups.

Nelson (1971) responded to Ashlock’s (1971) paper with his own definitions. But, these were definitions for paraphyly and polyphyley, not monophyly, as Nelson found Hennig’s (1966) definition of monophyly adequate.
“Hennig’s concept of monophyly seems adequately defined. I would propose to redefine the concepts of paraphyly and polyphyly with reference to a sister-group system:

Monophyly: a quality of a group including all species, or groups of species, assumed to be descendants of a hypothetical ancestral species. The members of such a group are all interrelated, for a sister-group system, and include all species of that system. Such groups may be considered complete sister-group systems” (Nelson 1971: 471-472).

The argument Nelson made was that Ashlock did not fully grasp Hennig’s (1966) definition of monophyly. He disagreed with Ashlock’s views on systematic biology, and argued for the newer “Hennigian” school of thought. One point that was agreed upon by Nelson was that Hennig had left the terms paraphyly and polyphyly poorly defined. Definitions for these terms were constructed by Nelson on his interpretation of Hennig’s meaning, namely that a paraphyletic group was one that was missing one taxon, and a polyphyletic group was one that was missing multiple taxa (Nelson 1971).

Nelson’s response to Ashlock seemed to be derived from Ashlock’s statement that he could appease both schools of thought (i.e., evolutionary biology and cladistics) with his new definitions. His disagreement on the position of paraphyly was what spurred Nelson’s dislike of Ashlock’s definition. By
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placing paraphyly within the definition of monophyly, Ashlock (1971) had obviously changed Hennig’s (1966) more specific definition of monophyly. This went against the grain of the cladists. Ashlock (1972) replied to Nelson’s response, pointing out that he had no desire to accept the cladistic point of view of systematic biology. Ashlock’s definitions were purely for nomenclatorial purposes, so that the proponents of both schools would be able to argue their points of view without getting confused by different definitions of the same word.

Ashlock (1972) felt that cladists did not understand the meaning of paraphyletic because it hadn’t been adequately defined by Hennig (1966). He also claimed that Hennig’s (1966) definition of monophyly was ambiguous, as it did not include the common ancestor in its wording, which he felt was a source of confusion for cladists. Coupling these points of view with the fact that Ashlock agreed with all current biological classifications, it was clear Ashlock had no intention of agreeing with not only Hennig’s (1966) definition of monophyly, but his theoretical position on systematic biology as well.

It is unclear whether Ashlock’s opinion of monophyly and cladistics was properly understood by cladists. A second response by Nelson (1974) to Ashlock stated that his concepts were inadequate because he failed to include the concept of relationships (or kinship) in his definitions, meaning that they did not fulfill the requirements of a cladistic definition. The discussion between
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Ashlock and Nelson was purely about defining monophyly *sensu stricto*. That there was both a phylogenetic and cladistic definition did not help matters, particular when both conflicted. By adopting holophyly as a new term, Ashlock had provided a partial solution. The problem of two conflicting definitions of monophyly was and still is an endless source of confusion for evolutionary taxonomists, phylogeneticists and cladists.

“Finally, unless we develop a precise definition of monophyly, evolutionary and theoretical systematics will always remain more ‘art’ than ‘science’” (Ashlock 1972: 438).

3.4 Ancestors

Another source of confusion, not only for the cladists, as stated by Ashlock (1972), but seemingly for the evolutionary biologists as well, was role of the common ancestor. Ashlock believed Hennig (1966) had left out the crucial information of whether or not the common ancestor be included in a monophyletic group, which confused cladists (Ashlock 1972). But Nelson (1974) stated that both he and Hennig’s understanding was that the common ancestor was not actually a real entity, so the inclusion of it into a monophyletic group was redundant. Nelson (1974) felt this was the basis for Hennig’s *Phylogenetic Systematics*. However, Hennig never talked about hypothetical ancestors or of excluding ancestors from his definition of monophyly. Rather, the source for
Nelson’s new definition of monophyly, and his views on the artificial ancestor, may have stemmed from Brundin’s (1966) definition. Hennig (1965) was actually very clear in his views,

“In morphological systems, the “beginner” which belongs to each group is a formal idealistic standard (“Archetype”) whose connections with the other members of the group are likewise purely formal and idealistic. But, in a phylogenetic system, the “beginner” to which each group formation relates is a real reproductive community which has at some time in the past really existed as the ancestral species of the group in question, independently of the mind which conceives it, and which is linked by genealogical connections with the other members of the group and only with these” (Hennig 1965: 99, my emphasis).

The debate over the definition of monophyly therefore appears to have started with Ashlock and Nelson arguing from a mixture of the definitions supplied in Hennig (1965, 1966) and Brundin (1966). Ashlock, representing the evolutionary biologists, found Hennig’s views on the definition of monophyly simultaneously restrictive and ambiguous. Nelson, representing the cladists, stated that he agreed with Hennig’s definition of monophyly, even though it is clear he is not actually agreeing with Hennig’s stance on the common ancestor, and is probably using the first part of Brundin’s definition, namely,
“[A] monophyletic group (?) is every group of the system fulfilling the demand that any species belonging to it is more closely related to any other species likewise belonging to the group than to any species which does not belong to it” (Brundin 1966: 17)

It is not surprising that Nelson would refer to Brundin rather than Hennig. Most early cladists in Europe were exposed to Hennig via Brundin’s 1966 monograph, but not Ashlock, who would have read straight from Hennig (1950).

Ashlock (1972) was concerned that there were two concepts being argued as the same term, namely monophyly. One concept is that the common ancestor plays a pivotal role in the definition of a monophyletic group (i.e. the time concept), as initially introduced by Bigelow (1956) and defined by Hennig (1966, first definition). The other concept is that a common ancestor is not necessary as the definition should only relate to relationships (i.e. the concept of kinship), as mentioned by Brundin (1966) in the first part of his definition, in Hennig’s second definition (1966) and Nelson (1971, 1974).

3.5 Diamonophyly and Synmonophyly
The monophyly debate did not only result in three distinct definitions of monophyly, but also in two very distinct interpretations of a branching diagram.

Figure 3.1 shows that birds are monophyletic and reptiles are aphytic. Three sides of the debate will identify the grouping of birds as monophyletic, with the exception of Ashlock, who would see both reptiles and birds as conditions of monophyly, that is, paraphyly and holophyly respectively. All parties would consider reptiles and birds together as monophyletic. While all three parties will identify the branching structure as monophyletic or holophyletic, they would however define it differently. The differences in definition is based on what assumptions or inferences are made. Those that see the birds as being more closely related to one another than they are to reptiles are making a
statement of classification, which is based on shared derived characters (synapomorphies). Those that make the inference that the relationship involves a most recent common ancestor, are making a claim about phylogeny, that is synapomorphies and symplesiomorphies (see Nixon and Carpenter 2011). The most recent common ancestor and plesiomorphies are inferred from synapomorphy. The differences between the two definitions may appear to be trivial, however they differ greatly at the level of interpretation and theory.

The first group, who define relationship as requiring an ancestor, or ancestral state, are making a claim about inference, namely ancestral-descendant relationships. Notions of ancestry, however, require a concept of time (i.e., complete chronology or a literal unbroken ancestor-descent lineage), the Greek prefix *dia-* (complete or through) is used to distinguish a chronological or inferential monophyly. Ashlock’s and Hennig’s definitions are *diamonophyletic* definitions.

The second group do not require notions of ancestry to justify claims of relationship. Rather a monophyletic taxon is based only on evidence, and not inference. Given that such evidence identifies which two taxa are more closely related together than to a third, the prefix *syn* (together) is used. Nelson’s definition of monophyly is thus a *synmonophyly* definition.
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The two definitions of diamonophyly and synmonophyly can separate the two interpretations of monophyly used in the literature: taxa which require some form of explanation in order to make a claim about relationship, with taxa that are defined based on evidence alone. These definitions become vital when distinguishing monophyly within systematics.

3.5.1 Practical uses and impact of synmonophyly and diamonophyly

For practical identification purposes, a taxon or group, such as the birds in Figure 3.1, can be said to be monophyletic. Monophyly as an identifiable structure within a branching diagram that can be identified without a definition. Perhaps this is why there are no precise definitions given by Haeckel, who clearly uses the term to identify one type of branching diagram from another. The problem with monophyly begins when systematists and phylogeneticists attempt to define it in terms of classification and evolutionary biology respectively.

The two terms syn- and diamonophyly are practical when interpreting branching diagrams and discussing theory. While two practitioners may identify a monophyletic taxon within a branching diagram, a pattern cladist, for instance, will see a cladogram, while a process cladist will see a phylogenetic tree. Given that the branching diagram has exactly the same structure and contains the same evidence (i.e., synapomorphies), two practitioners may
interpret the same structure in two entirely different ways. At this point, distinguishing between these two contrasting views become important to avoid confusion. While the term monophyly was useful in identification, syn- and diamonophyly are essential in discussing theory and interpretation, as the next example demonstrates.

3.6 Farris (1974) and the methodological application of monophyly

In 1974 Farris published updated definitions of paraphyly and polyphyly, primarily for a methodological application of the terms. The reason for this was so that systematists were able to use his definitions to discover whether or not their groups were monophyletic with respect to a given tree (cladogram), the chief goal of phylogenetic systematics (Farris 1974). Farris was discussing the term (dia)monophyly in reference to Hennig’s (1966) first definition.

The definition by Farris (1974) was proposed not only for a methodological application, but also because Farris did not agree with Nelson’s (1971) interpretation of Hennig’s paraphyly and polyphyly. Farris claimed that Hennig’s definitions specify whether the most recent common ancestor of a group belongs to that group, and Nelson’s specify membership only for known species (Farris 1974: 550). He wanted to specify in his definitions that polyphyletic groups were defined by convergent characters, whereas paraphyletic groups were defined by plesiomorphic characters (both
unobserved and inferred *a posteriori* to analysis). This, claimed Farris, was more in line with Hennig’s (1966) original views,

“The group is said to be monophyletic if its group membership character appears uniquely derived and unreversed. The group is said to be paraphyletic if its group membership character appears uniquely derived, but reversed. The group is said to be polyphyletic if its group membership character appears non-uniquely derived.” (Farris 1974:554).

The definitions, and subsequent usage of them, were strongly supported by Platnick (1977). Platnick (1977), while commending both Hennig’s (1966) and Nelson’s (1971) definitions of the terms paraphyly and polyphyly, was concerned about the position of monotypic genera. He claimed that Hennig’s (1966) definitions were too ambiguous, as he distinguished between (dia)monophyletic groups and non-(dia)monophyletic (paraphyletic and polyphyletic) groups by genealogical relationships existing within these groups, and not on the ability to recognise the relationships. This was a problem for Platnick, as he felt Hennig was inconsistent between his theoretical definitions and his belief in their purpose. That is to say, while Hennig could define paraphyly and polyphyly, the definitions in themselves were unable to be used to discover paraphyly and polyphyly (Platnick 1977). This was the reason for Platnick (1977) supporting Farris’s (1974) updated definitions of the terms paraphyly and polyphyly, and subsequently diamonophyly.
3.6.1 Farris versus Hull

The publication of Hull’s (1988) *Science as a Process* caused a brief dispute on the history of the definition of monophyly between himself and Farris (Farris 1990, 2007, Hull 1990). The dispute arose from the fact that Hull (1988) claimed the debate (between Ashlock and “the cladists”) was based on each side attributing their version to Haeckel’s definition. This caused further response from Farris (1990).

Farris (1990) raised issues with Hull’s book, in response to the claim that Haeckel was being used by both sides of the debate. The first point Farris chose to make focused on the mistake Hull made of attributing Nelson and Platnick to ridiculing Ashlock at a systematics conference in 1980. According to Hull (1988: 191-192),

> “Nelson and Platnick had obviously done their homework. They came primed with historical references designed to show that the term “monophyly” went back to Haeckel and that Haeckel had used it in Hennig’s sense. They celebrated their defeat of Ashlock by raising a toast to the great Haeckel” (Hull 1988: 192).
This was denied by Farris on behalf of Nelson and Platnick (Farris 1990), claiming it was he who spoke to Ashlock,

“Ashlock could hardly have been surprised in 1980 by the news of Haeckel’s authorship of the term, for he had earlier (Ashlock, 1979: 441) discussed it himself. Nor did Nelson (pers. comm.) take part in such an encounter. Platnick (pers. comm.) discussed monophyly with Ashlock at that social, but not Haeckel’s definition....It was I who discussed Haeckel’s work with Ashlock.” (Farris 1990: 81-82)

Hull’s defense was that he made an error in his notes, but did not believe Farris had merely discussed Haeckel’s terms for a “historical reference”, and that rather, it was probably Farris who ridiculed Ashlock (Hull 1990). This was responded to again by Farris (2007) by calling Hull a liar,

“No, Hull’s point in that anecdote was to cover for Ashlock and to lie about Haeckel’s tree. And it wasn’t “another” and it wasn’t an “error” [ ...] And they were not “errors” at all, but consisted of Hull changing history to support Mayr’s preposterous claims” (Farris 2007: 8).

Probably the more plausible point made by Farris (1990) was that neither the evolutionary biologists nor the cladists originally attributed their definitions of monophyly to Haeckel. Haeckel was not mentioned in terms of definitions of
monophyly by Hennig (1966), Ashlock (1971; 1972), Nelson (1971) or even by Farris himself (Farris 1974). Nor did Ashlock ever attribute his “traditional”
definition to Haeckel in his early papers (1971; 1972). Simpson’s definition, used
by Mayr and Ashlock, did not make reference to the original author of the term
(Simpson 1961; Farris 1990). The first mention of Haeckel’s use of monophyly
was in Mayr (1974), although it was not until 1979 when Ashlock discussed
Haeckel’s original meaning (Ashlock 1979; 1984). This was the fatal flaw in
Hull’s (1988) argument that both sides (evolutionary biologists and cladists)
were using Haeckel as a sort of poster child for monophyly.

Hull defended his position on the use of Haeckel in the definition’s debate as he
wanted to express how scientists use historical citations to defend their work
(Hull 1990). At a later point in his response, though, Hull claimed that the
historical accuracy of Haeckel’s definition of monophyly was irrelevant to
today’s use,

“The point I attempted to make, however, is that historical accuracy is not
all that important in such endeavors...Farris and I agree that Haeckel’s use
of the term “monophyly” is fundamentally irrelevant to the issue of which
usage contemporary systematists should adopt.” (Hull 1990: 398)

In turn, he defended the fact that the authors did not originally use Haeckel in
this way. Unfortunately, the contradiction that authors used Haeckel as a
historical figure for the definition, then the view that Haeckel’s definition was irrelevant for current use of the term monophyly leant no credibility to Hull’s (1988) stance. It appears that Hull (1990) realized his mistake in Hull (1988) too late, and was backtracking. Farris (2007) claimed Hull twisted the truth of history to support his agreement with the evolutionary biologists Mayr, Simpson and Ashlock (Farris 2007: 8). It certainly appears Hull was unable to get his story straight in regards to Haeckel. The debate and Hull’s (1988) claim, however, stirred up the question, about Haeckel and his influence on the current definition, if there ever was any.

3.7 What about Haeckel?

Haeckel was the first to use the term *monophyly* within a figure caption (Haeckel 1866, vol. II, Plate I). Haeckel defined monophyly several years later,

“... a monophyletic concept of the animal kingdom as a single root-form and all of its descendants.” (Ashlock 1984: 42, translated from Haeckel 1874)

Definitions of monophyly during the 1940 to the 1960s were not actually attributed to Haeckel directly. Neither Mayr’s (1942) nor Bigelow’s (1956) definition of monophyly, used by Hennig (1966) to create his first definition, included a citation to Haeckel. Neither did Hennig (1966). Brundin (1966) use
Chapter 3. Defining and Redefining Monophyly

Hennig’s (1950) original definition, while Ashlock (1971) cited Simpson (1961), whose definition did not refer to Haeckel. Finally, Nelson (1971) and Farris (1974) cited Hennig (1966) as their main source, whereas the earliest definitions by Mayr (1942), Bigelow (1956) and Simpson (1961) were not cited.

Ashlock first cited Haeckel in his 1979 paper. He states that Haeckel (1874) originally coined the term monophyly, and that it was used by Haeckel to support Darwin’s *Origin of Species* claim that groups of similar organisms existed due to descent from a common ancestor. This, Ashlock states, shows that Haeckel’s (1874) use of the term (dia)monophyly includes paraphyletic taxa (Ashlock 1979). In 1984 Ashlock argued that his use of the term (dia)monophyly was in accordance with Haeckel’s (1874) definition as meaning from a single origin.

In 1990, Farris discussed Ashlock’s use of Haeckel for his definition of (dia)monophyly, and stated that Ashlock did not in fact agree with Haeckel. This was because, Farris (1990) stated, Ashlock had acknowledged Hennig’s (1966) definition was in accordance with Haeckel’s (1874) definition. Ashlock (1979) did state that Hennig’s definition was in essence the same as Haeckel’s, if, and only if, it was taken as meaning Haeckel’s thoughts on the entire (dia)monophyly of life, that is that all organisms descend from one ancestor. The belief by Ashlock that his definition was more closely related to Haeckel’s
definition was based on Haeckel’s use of paraphyletic taxa in classifications, and that it upheld the traditional views of polyphyly.

The confusion between Ashlock (1979; 1984) and Farris (1990) probably stems from Haeckel using the term monophyly for several meanings. Uses by Haeckel for (dia)monophyly included the derivation of a species from an ancestral form, the phylogenetic differentiation of organisms’ forms from a primitive form, and the origin of anatomical structures, which did not have to be related to the monophyly of the taxon it was within (Rieppel 2011). In fact, Rieppel discusses in detail Haeckel’s use of the term monophyly, and how its meaning cannot be determined from his publications. Given this information it is not surprising the redefinitions of monophyly were hindered rather than helped by the re-introduction of Haeckel in the literature.

Those who consider themselves to be “using” Haeckel’s definition are most likely to be using a diamonophyletic definition. Haeckel’s numerous definitions all included a notion of genealogy, a derivation of species from an ancestor or primitive form (see Richards 2008). Hennig also favoured a diamonophyletic definition in his later publications (Hennig 1966; 1975). However, as Haeckel did not use the term for one specific purpose, Hennig’s explicit definition of (dia)monophyly was more highly favoured, and cited, in recent literature. The diamonophyletic definition has spawned a debate on its use in population level studies. These studies have focused on the fiercely debated species concept.
Two types of monophyly are used in the literature, *reciprocal monophyly* in molecular systematics, and less commonly *oligophyly*, in population level studies on fossils. The both refer to monophyly as a process rather than a concept.

3.8 A concept or a process?

The term *reciprocal monophyly* is a concept used in molecular systematics to define a group of individuals labelled as a species who are more closely related genetically to one another than to individuals labelled as other species, in regards to their maternally transmitted mitochondrial DNA (Kizirian & Donnelly 2004; Neigel & Avise 1986). The term was differentiated by molecular systematists from the traditional term monophyly when it was found that mitochondrial DNA of populations within a species were not more closely related to one another than any other population outside of the species (Avise *et al.* 1983; Neigel & Avise 1986). This apparent paraphyly was explained in a phylogenetic context by Neigel & Avise by suggesting that populations needed a certain number of generations to “become monophyletic” genetically. They suggest that mitochondrial DNA will transform from polyphyletic to paraphyletic to monophyletic (though sometimes polyphyly and/or paraphyly may not happen). By using the term monophyly in this way they have taken a concept of relatedness and turned have turned it into a mechanism. Reciprocal monophyly does not in fact have much to do with the original monophyly
debate, instead it has more to do with the tokogenetics versus phylogenetics debate over the inclusiveness of species. This has recently been discussed in the literature (see Assis 2013; Rieppel 2009, 2010, 2011; Assis & Rieppel 2011; Nixon & Wheeler 1990; Wheeler & Meier 2000).

Like monophyly terms, reciprocal monophyly has also changed definition over time. In population genetics, reciprocal monophyly “is central to the genealogical species concept. According to this concept, two groups come from different species if they form distinct monophyletic groups” (Zhu et al. 2011: 220). In this sense reciprocal monophyly is linked to the genealogical species concept (see de Querioz 2007) and departs significantly from all other definitions of monophyly. However, others claim that reciprocal monophyly occurs when “most common recent ancestor (MRCA) of all individuals in each species is more recent than the global MRCA” (Austerliz et al. 2009: 2), harking back to Hennig’s nearest “stem species”. In any case, definitions for reciprocal monophyly fall squarely within the diamonophyletic definition as it requires an ancestor or lineage.

Similar to reciprocal monophyly, oligophyly was defined as being derived from few ancestral forms, and the opposite of monophyletic in the 1960 dictionary of scientific terms (Kenneth 1960: 367). Urbanek (1998) calls oligophyly “near monophyly” or “strongly restricted polyphyly”, and refers to it as a scanty ancestry. It was defined by Urbanek as,
“... a restrictive factor in evolution leading to minimization of the number of phyletic lines owing to an occasional reduction by means of mass extinction as well as to their recovery from scanty survivors” (Urbanek 1998: 549).

Oligophyly is used by Urbanek as a process or explanation of the concept monophyly, rather than a concept in itself,

“... the paucity of ancestry (oligophyly) explains why both the monophyletic origin and evolutionary parallelism are such common features of the phylogeny in most fossil groups ” (Urbanek 1998: 549).

According to Urbanek, the term refers to individuals or populations that have evolved from only a few ancestors, a phenomenon existing after mass extinctions. It is used as an explanation of a process, rather than a concept, as with reciprocal monophyly. Both oligophyly and reciprocal monophyly are diamonophyletic definitions that are used at a sub-species or population level to explain the process of individuals “becoming monophyletic”.
3.9 Conclusion

The debate on the definition of monophyly has stemmed from a misconception that the term was applied in the same way methodologically and theoretically. Monophyly itself was never used by Haeckel, the original author, for one concept. Throughout the 1960s and 1970s a debate began on what the definition should be, centering around Hennig’s proposal to exclude paraphyly. In actuality the debate stemmed from a miscommunication on the importance of the inclusion or exclusion of the common ancestor. Authors such as Hennig argued for a genealogical concept to be included in the definition, termed here as diamonophyly. Authors such as Nelson argued for a kinship concept to be included, termed here as synmonophyly. This, however, was not recognised at the time, to the confusion of other authors, in particular Ashlock, who recognised the original problem. If monophyly is split into two meanings, a debate would not be needed as to its definition, and it could be used for the appropriate situation. For example, phylogeneticists would say their group was diamonophyletic if its taxa all stemmed from one common ancestor, including a notion of genealogy, whereas systematists would say their group was synmonophyletic if all of their taxa were more closely related to one another than to any outside taxa, including a notion of kinship without genealogy.
Chapter 4. Systematic Biostratigraphy: A Solution to Problematic Classification Systems in Biostratigraphy

(Currently submitted to Palaeoworld)

4.1 Introduction

“To date, evolutionary theory owes more to biostratigraphy than vice versa. Perhaps in the future evolutionary theory can begin to repay its debt” (Eldredge and Gould 1977, p. 40).

Chapters 2 and 3 explore the history and theory that have created debates within systematics. Without an understanding of general systematic methodological practices, and how these may differ from field to field, or even person to person, it is often difficult to understand discrepancies between similar systematic studies. Once these differences are recognised, the goal of the systematist, whether it be classification or phylogenetics, can be communicated clearly.

The goal of this thesis is to understand and communicate the classification of taxa, that is systematics and its methodology. The field of biostratigraphy has
yet to properly implement systematic methodological practices for classification purposes. Chapter 4 will show how a lack of continuity between biostratigraphic studies with regards to classification can affect stratigraphies. The combining of the two fields, systematics and biostratigraphy, will be discussed as a new methodology, herein termed Systematic Biostratigraphy.

Systematic biostratigraphy is a stratigraphic column that is based on monophyletic marker taxa. Non-monophyletic or artificial marker taxa have been shown to change biostratigraphic correlations, which can be rectified by using systematics to ensure marker taxa are monophyletic or natural. A hypothetical and real example are used to demonstrate the validity of monophyletic taxa. Using systematic biostratigraphy will ensure marker taxa are monophyletic, artificial classifications do not hinder stratigraphic correlations and stratigraphic columns are more accurate.

Biostratigraphy is the recognition and correlation of strata based on the particular fossils it contains (Teichert 1958; Hancock 1977; Ludvigsen et al. 1986). Biostratigraphy can also be used to create the most accurate division of a stratigraphic column (Young 1960; Kauffman 1977). The fossils on which biostratigraphy depends are often known as marker fossils (herein marker taxa). As the marker taxa are being used to determine stratigraphic correlation it is reasonable to suppose that they must be well defined taxonomically prior to a biostratigraphic study (Jenkins 1995).
Biological systematics is the field of science that aims to find natural classifications of taxa (Smith 1994; Williams & Ebach 2008). Natural classifications are used within many fields of science, the main contenders being cladistics, phenetics and evolutionary biology. Smith (1994) recognised systematics as a useful tool for palaeontologists to use, in particular cladistic analysis, and discussed some of the problems faced by biostratigraphers (Smith 1994, pp. 107–124). Unfortunately the arguments raised by Smith for natural classification systems within palaeontology have not been widely acknowledged within biostratigraphy. Marker taxa are still classified without reference to systematic biology.

German-American palaeontologist Curt Teichert (1958) stated that,

“[i]nsufficient knowledge of paleontologic facts and incorrect interpretation of the paleontologic record have led to, and are still responsible for, grave errors in the interpretation of historical succession”

Teichert (1958, p. 102).

In short, marker taxa are only as good as the taxonomies into which they are classified. But what if these classifications are artificial? What impact will they have on biostratigraphy? I aim to answer these concerns by demonstrating the
problem of traditional biostratigraphic uses of classification. I also suggest an easily applied method to increase validity of biostratigraphic studies.

4.2 Species concepts and taxa

The natural classification of marker fossils is closely related to species concepts within biostratigraphy. This “problem” is found in most areas of biological science. Marker “species”, or the groups of organisms being used for a biostratigraphic study, are deemed to be useful if they evolve quickly and have a widespread distribution (Kauffman 1977). A “species” being used as a marker could bring inherent problems to a biostratigraphic study. Young (1960) recognised the changing definitions of species within biology and palaeontology. He was referring to the difference between a palaeontological and biological definition of species. When an individual fossil, or a number of very similar fossils, are referred to as a species, it invokes a different understanding to many individuals within science. The most well known and one of the most popular species concepts is the “biological species” concept, which defines species as,

“... interbreeding natural populations that are reproductively isolated from other such populations” (Noor 2002, p. 153, discussed by Mayr 1992 and Sokal & Crovello 1970 among many others).
Another highly popular concept is the phylogenetic species concept, which often refers to organisms with a shared history, or genealogical relationships (Hennig 1966; Nelson & Platnick 1981; Nixon & Wheeler 1990; Baum & Donoghue 1995). Wilkins (2009) identified twenty-two different species concepts. One of those concepts was the “successional species” concept, that which identifies species based on their stratigraphic and geographical location (Wilkins 2009). The successional species is also known as a paleospecies and a chronospecies, and is described by Wilkins (2009) as arbitrary anagenetic stages, mainly from the palaeontological record. However, Young (1960) suggested the only precaution biostratigraphers take is to “realize that he is not working with species, but is working and correlating with samples” (Young 1960: 356).

The comment by Young (1960) was in reference to the fact that palaeontologists of the time were not defining species on the above mentioned biological species concept, the preferred species concept of the age. They were instead using the successional species concept, as Young recognises, the species being used were artificial. In order to avoid the species concept debate, it may be advisable to take Young’s advice, and forego a species identification altogether. This is not to say the taxa being used should not be naturally classified, as is discussed above, and will be shown below, artificial classification has an impact on biostratigraphy too. Instead we follow Nelson (1989) in referring to (and treating) marker fossils as taxa, rather than as species. A taxon is defined in the glossary of the ICZN as:
“A taxonomic unit, whether named or not: i.e. a population, or group of populations of organisms which are usually inferred to be phylogenetically related and which have characters in common which differentiate (q.v.) the unit (e.g. a geographic population, a genus, a family, an order) from other such units. A taxon encompasses all included taxa of lower rank (q.v.) and individual organisms” (ICZN Glossary, http://www.nhm.ac.uk/hosted-sites/iczn/code/index.jsp?booksection=glossary&nfv=true).

If the term species is to be used, a species concept will first need to be defined, whereas if a the term taxon is used the definition is universal (and is not highly debated) (Nelson 1989).

The use of a taxon instead of a species brings us back to classification. If a taxon is indeed required for a biostratigraphic study, according to the above definition, it needs to belong to a natural classification, in which individuals of the taxon are considered to be related. Taxa that are more closely related to each other than they are to any other taxon, are considered to be monophyletic, that is, part of a natural classification.
4.3 The problem of using poorly classified marker taxa in biostratigraphy

4.3.1 Classifying marker taxa

The field of biostratigraphy has existed since the early 19th century beginning, with William Smith (Smith 1815). He had discovered and discussed the uses of fossils around Bath by 1796, with his observations being first published in 1815 (Smith 1815; Hancock 1977). By 1817 Smith stated:

“The organized Fossils which may be found, will enable him to identify the Strata of his own estate with those of others...” (Smith 1817: v).

The “organized Fossils”, or marker taxa, were the most significant component of his discovery. The same can be said with marker taxa used in modern day biostratigraphy.

Classification of marker taxa is currently left to the discretion of the individual biostratigrapher. The classification of an already widely accepted marker taxon is rarely questioned, yet there are increasing examples where this has either hindered an ongoing biostratigraphic study, or has required a complete reassessment of an already produced study (Patterson & Smith 1989; Berggren
& Norris 1997; Pachut & Anstey 2002; Angielczyk & Kurkin 2003; Adrain & Westrop 2005; Lee et al. 2008). Minimal knowledge of the taxa being used in a study, poorly preserved specimens, or inadequate descriptions from previous authors will contribute to incorrect classifications. These classification systems will often result in the artificial classification of a taxon.

The artificial or non-monophyletic (aphyletic, Ebach & Williams 2010) classification of marker taxa could pose problems for biostratigraphers. Whereas artificially classified groups will change with additional taxa and characteristics, naturally classified groups will be stable. An artificially classified group causes problems if the group is an important biostratigraphic marker, as any additional taxa found may group together or split up the already established marker. A change in the marker fossil group will ultimately change any biostratigraphic correlation in place.

Natural classification systems are also considered to be superior by just about all fields of biological and palaeontological sciences (Simpson 1961; Mayr 1969; Schuh & Brower 2009; Wheeler 2012). It stands to reason that if biostratigraphers are to use a classification system, that the classification is natural and not artificial. In order to consider biostratigraphic marker fossils as suitably classified into natural taxa, a systematic study would be required.
4.3.2 Case studies

There are few current studies that combine systematics with biostratigraphy. Those that do usually use biostratigraphic units as a form of evidence for phylogenetic studies, for example strato-phenetics (Gingerich 1979) and strato-cladistics (Fox et al. 1999; Fisher 2008) or, use hierarchical patterns in cladograms to ordinate fossil assemblages, namely phylogenetic biochronology (Fara & Langer 2004). Neither of these methods are what we are suggesting to do. A systematic study involves a taxonomic revision, based on a detailed analysis in which natural groups are identified and taxonomies revised in order to reflect these natural classifications. Three case studies by Lee et al. (2008), Angielczyk & Kurkin (2003) and, Smith & Patterson (1988) involve the use of a systematic method, namely cladistics, which points out flaws in previous biostratigraphic studies due to the artificial classification of marker taxa. An additional case study by Pachut & Anstey (2002) does in fact use a cladogram to re-classify and then review stratigraphy based on these classifications, but highlights the misuse of species concepts.
4.3.2i Case Study 1: Missisquoiidae trilobites

In 2008 Lee et al. published a paper discussing the Missisquoiidae family of trilobites. The type genus of Missisquoiidae, Missisquoia Shaw, 1951 was indicated to be an important marker taxon for defining the base of the Ordovician (Lee et al. 2008). Originally confined to Laurentia, Missisquoia was discovered in North China and Korea, part of the Gondwanan supercontinent. As an important marker taxon for the base of the Ordovician Missisquoia’s original classification had been accepted by previous studies to Lee et al. (Geyer & Shergold 2000; Choi et al. 2003). The discovery of Missisquoia on both Laurentia and Gondwana allowed better correlations between the two supercontinents. After better preserved specimens were found and described from North China, the specimens classified as Missisquoia from eastern Gondwana were re-defined as Pseudokoldinioidia Endo 1944, not Missisquoia. Inter-continental correlations already in place based on the Missisquoiids now lack credibility. To rectify this situation Lee et al. (2008) suggested a complete phylogenetic analysis of species and genera from the group. A cladistic analysis was performed on 22 species, which showed that the Missisquoia was aphyletic, as many of the species are more closely related to other taxa than to each other (see Lee et al. 2008: 322—323, Fig. 5). Missisquoia was subsequently treated as a junior synonym of Parakoldinioidia Endo, 1937. While the aphyly of Missisquoia was confirmed, Lee et al. (2008) proceeded to address the palaeogeographic
history of the group, rather than change the stratigraphic correlations to coincide with the natural classification.

4.3.2ii Case Study 2: Therapsid mammal *Dicynodon*

Angielczyk & Kurkin (2003) discussed the therapsid genus *Dicynodon* Owen, 1845 used for biostratigraphic correlations of the Permian-Triassic boundary. *Dicynodon* has been particularly used for the correlation of the Upper Permian between South Africa and Russia (Angielczyk & Kurkin 2003). Cladistic analyses showed *Dicynodon* to be aphyletic, with some species of the genus more closely related to species from other genera (Angielczyk & Kurkin 2003: 365). The results also suggest that the genus *Dicynodon* does not occur in Russia, which would impact the correlations made between Russia and South Africa during the Permian using this genus. Angielczyk & Kurkin to raise the question whether *Dicynodon* should be used as a marker taxon at all given that, in their terms, it was not “a biologically real entity” (i.e., aphyletic) (Angielczyk & Kurkin 2003).

4.3.2iii Case Study 3: Periodicity in extinction theory

The periodicity in extinction theory was a large scale study based on patterns seen from worldwide extinction data. The theory suggested that mass
extinction could be periodical (Raup & Sepkoski 1984; 1986; Sepkoski 1986). In 1988, Smith and Patterson suggested Raup & Sepkoski’s theory was based in part on data from aphyletic groups. Data was cladistically analysed in Patterson & Smith (1987), using the fish and echinoderm families of Sepkoski’s (1982) data, and discovered that only 25% of taxa were in fact monophyletic. The other 75% were termed “noise” by Smith & Patterson (1988), which included “spurious data”. The findings by Smith & Patterson cast serious doubt on Raup & Sepkoski’s theory as it has long been recognised that aphyletic taxa could not in fact become extinct, as they are not biologically real entities (Patterson & Smith 1989).

4.3.2iv Case Study 4: Aphyly in the bryozoan genus *Peronopora*

Pachut & Anstey (2002) performed a phylogenetic, systematic and biostratigraphic study of the bryozoan genus *Peronopora* from the Ordovician. The study consisted of 211 specimens using 31 characters. Pachut & Anstey (2002) state that the taxa *P. decipiens*, *P. milleri* and *P. vera* have the “poorest records” in previous taxonomic studies, which is attributed to the fact that they were previously identified based on their stratigraphic position (i.e. the successional species concept). The cladogram was used by Pachut & Anstey (2002) to re-classify *Peronopora* into 8 species, *P. dubia*, *P. sparsa*, *P. vera*, *P. horowitzi*, *P. milleri*, *P. pauca*, *P. compressa* and *P. decipiens*. These re-classifications were used to review the biostratigraphic range of each species and was changed
Accordingly (see Pachut & Anstey 2002, Figures 3.1 and 3.2). However, according to the cladogram there is only one monophyletic species, *Peronopora dubia*. All of the crown groups are within monophyletic clades, but the stem groups are not. Pachut & Anstey attribute their classification system to a misinterpretation of the phylogenetic species concept (see Wilkins 2009). Seven of the 8 species described in Pachut & Anstey (2002) are aphyletic and require further revision in order to represent monophyletic species groups.

Case studies 1-3 show how problems can arise when aphyletic taxa are used in biostratigraphy. Despite the obviously artificial classification of important marker taxa, there is still no revision of biostratigraphy. The fourth case study by Pachut & Anstey (2002), highlights how misuse of species concepts will also impact the legitimacy of re-classified taxa and ultimately and revised stratigraphies. We propose a series of protocols, using cladistic methodology, in order to use identify aphyletic groups within biostratigraphy, and the removal of species concepts in favour of taxa (see Nelson 1989).
4.4 Systematic biostratigraphy

4.4.1 Outline

The above case studies suggest that classification systems based on artificial taxa will often require a biostratigraphic correlation or study to be revised. To reduce this prospect it has already been proposed above to re-analyse the classification of marker taxa. The concept of using a systematic method for classification purposes in biostratigraphy is not new (see Padian et al. 1994; Smith 1994; Pachut & Anstey 2002), but appears to be largely unused. The following protocol for a systematic biostratigraphy, that is, *a stratigraphy based on monophyletic marker taxa*, includes both a hypothetical and a real example. Each step within the protocol are highlighted throughout the systematic biostratigraphical process, which are listed as follows:

1. Identify the marker taxon
2. Perform a cladistic analysis
3. Identify aphyletic taxa
4. Re-classify the marker taxon
5. Revise biostratigraphy
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The first two steps are largely performed by most palaeontologists, while the
second two are often overlooked, and the fifth rarely implemented (and the
purpose of this discussion). The following hypothetical example shows how the
identification of aphyletic taxa and their reclassification help improve a
biostratigraphic column.

4.4.2 Hypothetical example

A diagrammatic example of a biostratigraphic column and a cladogram is
shown below (Figures 4.1A and 4.1B).
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**FIGURE 4.1A.** Hypothetical range chart showing three zones A, B and C. Zone A is based on stratigraphy of Taxa A1 and A2, Zone B is based on stratigraphy of Taxa B1 and B2 and Zone C is based on stratigraphy of Taxa C1 and C2.

**FIGURE 4.1B.** Hypothetical cladogram demonstrating the classification of taxa A1, A2, B1, B2, C1 and C2. The cladogram shows the aphyly of taxa B1 and B2, and the monophyly of A1 and A2, and C1 and C2.
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Identify the marker taxa

The range chart has been divided into three distinct zones A, B and C. These zones are based on the taxa A1, A2, B1, B2, C1 and C2. These are the marker taxa used to subdivide the column.

Cladistic analysis

The cladogram (Figure 4.1B) is based on the cladistic analysis of the taxa A1, A2, B1, B2, C1 and C2.

Identify aphyletic taxa

The original range chart is classified using a traditional biostratigraphic classification (Figure 4.1A). The cladogram (Figure 4.1B), resulting from a cladistic analysis on the taxa, uses a classification based on biological systematics. The cladogram highlights that one zone has been subdivided based on the artificial clade of B1 and B2. That is, the taxa of zone B, taxa B1 and B2, are not more closely related to one another than any other taxa. Taxon B1 is more closely related to the taxa A1 and A2 than it is to the other taxon B2.
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Re-classify marker taxa

The information in the cladogram (Figure 4.1B) shows that the taxa holding together Zone B are non-monophyletic. The taxa can however be divided into their own clades.

Revise biostratigraphy

As the taxa B1 and B2 are now considered distinct from one another they can be used to re-define the biostratigraphic column, so that it uses naturally classified taxa, rather than artificial. The resulting biostratigraphic column is now divided into four distinct zones, rather than three (Figure 4.1C).
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FIGURE 4.1C. Hypothetical stratigraphic column showing a revised stratigraphy using classification provided by the cladogram (Figure 4.1B.). Taxa B1 and B2 are aphyletic, so must be revised into two distinct zones. The stratigraphic column is then divided into four zones, A, B1, B2 and C.

To show how a cladogram may be used with real data to improve classification and ultimately change a biostratigraphic column, two examples are taken from the literature which perform both a cladistic and biostratigraphic study.

4.4.3 Real example

Paleocene trochospiral foraminifera
Identify the marker taxon or taxa

Berggren and Norris (1997) present a biostratigraphic and systematic study of Paleocene trochospiral foraminifera. A number of taxa are analysed in the study including, *Praemurica*, *Acarinina*, *Morozovella*, *Parvularugoglobigerina*, *Subbotina*, *Eoglobigerina* and *Parasubbotina*.

Cladistic analysis

The phylogenetic analysis performed used 42 taxa and 73 characters (Berggren and Norris, 1997, table 1, pp. 18—19), and was based on cladistic methodology (Berggren and Norris, 1997, p. 20). A full description of the characters used can be found in the appendix. The cladistic analyses performed involved numerous outgroups (Text-fig 8, p. 21). By looking at the figures A, B, C and D in text-figures 8, 10 and 12 it is clear different outgroups had no effect on overall tree topology.

Identify aphyletic taxa

The cladogram produced by Berggren and Norris (1997), Figure 4.2B, shows two aphyletic taxa, *Praemurica* (Pr.) and *Parvularugoglobigerina* (P.). *Praemurica* has four species, none of which are within the same clade. Two are found
within the *Morozovella* clade, one with *Acarinina* and the other with the taxa *Parvularugoglobigerina, Subbotina, Eoglobigerina* and *Parasubbotina*.

*Parvularugoglobigerina* has two species, one of which is grouped with the *Parasubbotina* clade, and one which is not.

**Re-classification of marker taxa**

The cladogram shows that the species *Pr. inconstans* and *Pr. uncinata* are within the *Morozovella* clade, suggesting they should be classified under *Morozovella*. In fact the synonymy list within the systematic palaeontology section shows that they have previously been classified as *Morozovella* species (*Pr. inconstans* Berggren, 1992, p. 56 and *Pr. uncinata* Berggren, 1977, p. 57). By re-classifying these taxa as *Morozovella* their monophyletic classification is ensured and their extensive synonymies are resolved.
FIGURE 4.2A. Revised stratigraphic column based on original stratigraphic ranges of foraminifera genera (from Berggren and Norris, 1997, Text-Figure 17, p. 35).

FIGURE 4.2B. Revised cladogram of foraminifera genera showing the aphyly of Praemurica and Parvularugoglobigerina (from Berggren and Norris, 1997, Text-Figure 12, p. 25).
Stratigraphic ranges of all taxa found within Berggren & Norris (1997) can be seen in Figure 4.2A. Original *Morozovella* taxa are shown to range from midway through P2 to the end of P6. The re-classification of *Pr. inconstans* and *Pr. uncinata* into the genus *Morozovella* would see that the *Morozovella* range extends to the start of P1b. This effectively changes the stratigraphic range of *Morozovella*, requiring the revision of the original biostratigraphic chart, which can be seen in Figure 4.2C.
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FIGURE 4.2C. Revised stratigraphic column based on the re-classification of Praemurica taxa into Morozovella. Demonstrates the lengthening of Morozovella’s stratigraphic range from P2–P6 to P1–P6. (From Berggren and Norris, 1997, Text-Figure 17, p. 35).

4.5 Conclusion

Padian et al. (1994) has shown how a systematic study using cladistics could be beneficial for stratigraphy. Many workers now recognise the need for taxa to be monophyletic if their data and assumptions are to be trusted. Not only are monophyletic taxa important, but examples of how aphylectic taxa can hinder
studies has also been shown (Patterson & Smith 1989). The emphasis of monophyletic taxa, rather than monophyletic species, genera etc. treats the marker taxa at equal ranks, so that species concepts can be avoided. A taxon is a unit of classification, regardless of its Linnaean ranking (e.g., species, families, orders, etc.). Berggren & Norris’s (1997) study highlights the problem of using previously accepted rankings for a biostratigraphic study. *Praemurica* is aphylectic when analysed cladistically, yet is being used to define a biostratigraphic section. When the entire monophyletic taxon is considered, the biostratigraphy changes. The rank of *Praemurica* is at a generic level, yet the taxa affecting the biostratigraphy are at a specific level. When the two are considered separately the results are skewed. This is an example of a monophyletic taxon changing the stratigraphy based on formerly phyletic taxa.

A systematic study of marker taxa could potentially be very useful for biostratigraphers. If the aim of biostratigraphy is to create the most well defined stratigraphic sections using fossil taxa, then their taxonomic identification should be key. Many studies have already commented on the usefulness of this technique for biostratigraphers (Lee *et al.*, 2008, Adrain & Westrop 2005, Angielczyk & Kurkin 2003, Padian *et al.* 1994 and Patterson & Smith 1989). By using an already established monophyletic taxon, or identifying and/or revising marker taxa as monophyletic, biostratigraphers could create more accurate stratigraphic columns and hence intercontinental correlations.
5.1 Introduction

The trilobite family Phillipsiidae Oehlert, 1886 is classified as the group of proetid trilobites spanning from the Late Devonian to Permian (Hahn et al. 1980). Oehlert (1886) originally diagnosed the Phillipsiidae based on a carapace with an oval shape and:

"a thorax of 6 to 10 rings, one end of the facial suture terminates obliquely at the edge of the posterior cheek, roughly below the eye. The eyes are rather developed, always close to the glabella and posterior border. The glabella has two conditions in the anterior area; one which matches genera with a conical glabella, as seen in the Proetidae and, the other, characterized by genera with an enlarged forward glabella for which we propose the name Phillipsidae [sic]" (Oehlert 1886: 126–127).
In 1963, Hessler declared the Phillipsiidae a paraphyletic group, herein *aphyletic* (see Ebach & Williams 2010), stating that the three basic members, *Phillipsia*, *Cummingella* and *Griffithides* showed closer affinities to members belonging to the Proetidae than to each other. Hessler also suggested that the lumping of most Carboniferous taxa within these three genera obscures interesting phylogenetic relationships. Only Weller (1936) and Reed (1943) had begun the task of separating the proetid taxa into more stable classifications (Hessler 1963). Hahn & Hahn (1967) followed suit, and treated the sub-families of the Phillipsiidae (Linguaphillipsiinae, Phillipsiinae, Cummingellinae, Griffithidinae and Ditomopyginae) as part of the Proetidae, referring to the former family as the “Carbon-Permian proetid trilobites”.

Hahn *et al.* (1980) re-erected the Phillipsiidae based on two factors, stratigraphy and ancestry. Prior to the re-erection of Phillipsiidae, all subfamilies were placed within the Proetidae. Since Hessler (1963) raised his concerns of proetid lumping, the Proetidae expanded substantially, with large quantities of species, genera and even subfamilies now identified (Hahn & Hahn 1969; 1970; 1972). Hahn *et al.* (1980) felt the Proetidae had become unmanageable, and could not be properly diagnosed. A proposed solution was to separate the subfamilies based on stratigraphy, those subfamilies from the latest Devonian through to the Permian were now part of their own family, the Phillipsiidae (Hahn *et al.* 1980: 174). The membership of the families Cyrtosymbolidae and Phillipsiidae in the *Treatise on Invertebrate Paleontology* (Weller in Moore 1959) were
considered to be incorrect by Hahn et al. (1980), as it was hypothesised that taxa of the original Phillipsiidae had developed from the subfamily Cyrtosymbolinae. If the subfamilies of the Phillipsiidae, which included Linguaphillipsiinae, Phillipsiinae, Cummingellinae, Griffithidinae and Ditomopyginae (coincidentally all from the Carboniferous and Permian), evolved from the Cyrtosymbolinae then the inclusion of the cyrtosymbolids with the phillipsiids would create a monophyletic group. Hahn et al. (1980) resurrected the family Phillipsiidae, as conceived by Oehlert (1886), taking precedence over Cyrtosymbolidae Hupé 1953. According to Hahn et al. (1980), the division of the Phillipsiidae based on stratigraphy could now be justified using ancestry:

“The Phillipsiidae, conceived herein, are monophyletic, when the Cyrtosymbolinae is considered to be the stem group and the subfamilies [Linguaphillipsiinae, Phillipsiinae, Cummingellinae, Griffithidinae and Ditomopyginae] are considered their descendants” (Hahn et al. 1980: 174).

The justification by Hahn et al. (1980) would suggest that the aphyletic Cyrtosymbolinae is monophyletic when grouped with the above five subfamilies, in the same way Dinosauria are monophyletic when grouped with birds (see de Querioz & Gauthier, 1990). The justification of common ancestry for a Phillipsiidae grouping by Hahn et al. (1980) was upheld in a series of publications on the phylogeny of each subfamily, including Linguaphillipsiinae
Prior to the re-erection of Phillipsiidae, Hahn & Hahn (1967) discussed the characteristic traits of proetid trilobites from the Carboniferous and Permian, which are highlighted as important for phylogenetic reconstruction. Despite the broad range of phylogenetic discussions of the Phillipsiidae and its subfamilies, the only publications with an actual cladistic analysis of the Phillipsiidae are by Brezinski (2003; 2005; 2008). Brezinski’s publications, however, are solely species level analyses of the North American genera *Paladin, Kaskia* and *Weberides*.

Since the erection of the Phillipsiidae there has been little debate as to what exactly constitutes the characteristics of the group. The characters proposed by Hahn & Hahn (1967) represent the first in-depth analysis of phillipsiid
characters and an attempt at a phylogenetic reconstruction. However, many species, genus and sub-familial level classifications within the Phillipsiidae are based primarily on biostratigraphy (Figure 5.1), but more emphasis is needed on actual morphological homologs. Hahn and Hahn (1967) attempted to outline a series of characters for use in a high level phylogenetic analysis within the Phillipsiidae, however, many of these, such as a vaulted unincised glabella, are also characteristic of the Proetidae. Owens (1994) also suggested that some of the genera within Phillipsiidae are more closely related to genera within Proetidae, thereby raising the issue of the validity of the Phillipsiidae as a monophyletic taxon. Jell and Adrian (2003) place the Phillipsiidae within the Proetidae, however without explanation. We recognise the current uncertainties about the phylogenetic relationships of Permo-Carboniferous trilobites, especially the conflicting classification schemes regarding the Proetidae and Phillipsiidae, and stress that a review of their morphological characters and associated cladistic analyses are needed to resolve these relationships.

The aim of this study is to use the characters described by Hahn & Hahn (1967) in order to find a cladistic signal within separate sub-family and genus level analyses. The analyses will provide a basic framework for the classification of the family Phillipsiidae, and test for its monophyly. Moreover, the results can be used to either justify the retention or removal of the Phillipsiidae as a valid monophyletic group, using synapomorphies of the sub-families as potential diagnostic features of the family.
FIGURE 5.1. Biostratigraphic ranges of currently classified Phillipsiidae genera.
5.2 Methodology

Three cladistic programs used to analyse the data were TNT v1.1 (Goloboff et al. 2008), NONA v2.0 (Goloboff 1999) using the WinClada v.1.00.08 (Nixon 2002) graphical interface, and LisBeth v 1.3 (Zaragüeta-Bagils et al. 2012). TNT was used to perform a parsimony analysis of subfamilies. NONA was used to perform a parsimony analysis of genera plus separate cephalic and pygidial analyses of subfamilies, while LisBeth was used to perform a three–item analysis of the subfamilies and genera, the latter analysis using the heuristic search function within TNT. A three–item analysis was used in conjunction with the parsimony analyses to find a more resolved pattern in the small data sets.

Cladistic analyses were performed on exemplar taxa from each of the nine currently classified subfamilies within Phillipsiidae, two Proetidae subfamilies and the outgroup Brachymetopinae. Exemplar taxa were used as the monophyly of genera and subfamilies cannot be guaranteed, with the exception of Paladin, Kaskia and Weberiides (see Brezinski 2003, 2005, 2008). The exemplar taxa include Brachymetopus (Brachymetopinae), Pudoproetus (Proetinae), Crassiproetus (Crassiproetinae), Phillipsia (Phillipsiinae), Archegonus (Archegoninae), Bollandia (Bollandiinae), Spinibole (Cystispininae), Cummingella (Cummingellinae), Ditomopyge (Ditomopyginae), Griffithides (Griffithidinae), Linguaphillipsia (Linguaphillipsiinae) and Weania (Weaniinae). The two Proetidae subfamilies were chosen as they have had the Carboniferous/
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Permian genera *Pudoproetus* and *Conophillipsia* classified within them respectively. The analysis contains 21 characters (discussed below).

An analysis was also run separating the cephalic characters from the pygidial characters. This was done for two reasons. Firstly, previous systematic treatments of Phillipsiidae taxa by Weller (1937) emphasised the pygidial characters as being the most important for Phillipsiidae phylogeny. Secondly, the separate analyses were used as a way to recognise conflicting taxa.

Cladistic analyses were performed on exemplar taxa from 82 genera currently classified within the subfamilies of Phillipsiidae (Table 5.1), five genera classified within Proetidae and the outgroup *Brachymetopus* using 21 characters. The five Proetidae genera include *Pudoproetus, Crassiproetus, Conophillipsia, Dechenella* and *Monodechenella*.

*Table 5.1. (Below) List of all genera included in the cladistic analyses. 42 Phillipsiidae genera have been excluded from the analysis due to poor preservation. Those with an asterisk (*) are used as exemplar taxa for the subfamily analysis.*
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| Acanthophillipsia gulyangensis | AA | Gapeevella gapeevi | BE | Planokasia gibsoni | CI |
| Ameropiltonia perplexa | AB | Gitarra pupuloides | BF | Pseudocyrtosymbole acutangularis | CJ |
| Ameura missouriensis | AC | Globusia differtigena | BG | Pseudophillipsia (Nodiphillipsia) aff. obtusicauda | CK |
| Anisoppyge perannulata | AD | Gracemerea archeri | BH | Pseudowaribole (P.) quaesita | CL |
| *Archegonus (Philibole) habena | AE | *Griffithidella caballieroensis | BI | *Pudoproetus fernensis | CM |
| Australokaskia collina | AF | Griffithides claviger halnae | BJ | Reediella echniata | CN |
| Bedicella palentina | AG | Hentigia bulbops | BK | Richterella snakedenensis | CO |
| Belgibole elektra | AH | Hesslerides arcentensis | BL | Schizophillipsia irvingi | CP |
| *Bollandia globiceps | AI | Hunanoproetus brevicus | BM | Sduyaspis sduyi | CQ |
| Breviphillipsia sampsoni | AJ | Kaskia chesterensis | BN | Sevillia sevillensis | CR |
| *Brachymetopus (Br.) maccoyi | AK | Kathwaia capitorosa | BO | Sinosymbole guanxiensis | CS |
| Carbonocoryphe (Winterbergia) australis | AL | Kollarcephalus granatali | BP | Spatulata diversa | CT |
| Carbonoproetus calvus | AM | Kulmiella leei | BQ | Spergenasps boonensis | CU |
| Comptonaspis swallowi | AN | Lichanocoryphe cephalispa | BR | *Spinibole olgae | CV |
| Conophillipsia breviceps | AO | *Linguaphillipsia elongata | BS | Thalabaria plana | CW |
| *Crassiproetus traversensis | AP | Liobole glabra proxima | BT | Thigriffides triangulatus | CX |
| *Cummingella jaroszi jaroszi | AQ | Malchi magnificus | BU | Timoraspis breviceps | CY |
| Cyphinioides limbatus | AR | Menorcasps tiedti | BV | Triproetus angustus | CZ |
| Dayinaspis dayinensis | AS | Monodechenella macrocephala | BW | Vandergrachtia vandergrachtii | DA |
| Dechenella (D.) alpenensis | AT | Nipponaspis? lapemienisis | BX | Wagnerispina wagneri | DB |
| Dechenelloides angustigenatus | AU | Novoameura mckeei | BY | Waideggula (W.) cantabrica | DC |
| Delaria antiqua | AV | Nunnaspis stitti | BZ | Waribole conifera | DD |
| Diacoryphe pfeifferi pygmaea | AW | Paladin morrowensis | CA | *Weania goldringi | DE |
| *Ditomopyge scitula | AX | Palaeophilpsia sp. | CB | Weberides chamberlaii | DF |
| Doulatia inflata | AY | Parangustibole sinensis | CC | Weberihillipsia girvanensis | DG |
| Dudu blodgetti | AZ | Perexigupyge hodgesi | CD | Witryides rosmerta | DH |
| Dushania heisingi | BA | Persia praecox | CE | Xenoboloides peregrina | DI |
| Elliptophilpsia ellipticus | BB | Philiboloides cornicangulus | CF | Yishanaspis xiaouensis | DJ |
| Eocyphium seminiferum | BC | *Philippia gemmulifera | CG | |

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5.3 Character Analysis

Hahn & Hahn (1967) (herein H&H) set out 18 morphological traits that they felt were important for classification of Carboniferous and Permian proetid trilobites. In their descriptions they indicated the characteristics that are important for phylogenetic reconstructions of the group (see Figure 5.2). Each of the 18 traits are considered individually below.
The systematic significance of the characters discussed by H&H are given at the sub-family and genus level respectively. The familial-level characters assigned
by H&H largely overlap with the genus-level assigned by Weller (1937: 338–346) and Hessler (1963: Table 1). The characters assigned by Brezinski (2003, 2005, 2008) group both closely related species and genera. Given that the characters of Weller, Hessler and Brezinski are based on North American genera, they may be representative of Carbon-Permian trilobites as a whole. Even so, these characters are considered with those of H&H. We also attribute equal weight to all characters, despite Weller’s insistence that pygidia (particularly of the North American Carboniferous species) “present a more complex and convincing example of evolutionary advancement than any other part of these fossils” (Weller 1937: 339). In fact, Weller (1937) has dedicated a large part of his character descriptions to quantifying pygidial ratios and determining the structure of pygidial segmentation in cross-section. While we appraise several of Weller’s characters below, we refrain from using continuous characters (e.g., arbitrary percentages and ratios), as they are unlikely to represent homologous states (see Pimentel & Riggins 1987).

5.3.1 Character descriptions

Glabellar shape. H&H divide the glabellar shape, first proposed by Oehlert (1886) into four “types”: Proetus–type, Ungiloproetus–type, Cornuproetus–type and Griffithides–type. The first, the Proetus–type, was limited by H&H to the Devonian sub-family Proetinae. The latter three types were included in the Carboniferous and Permian genera and subfamilies. The Ungiloproetus–type is
typically conical in outline with no constriction. The *Cornuproetus*-type has a cylindrical or box-shape, and when constricted forms an hourglass shape, or is sub-cylindrical (cf. Brezinski 2008). The *Griffithides*-type is seen in later Permo-Carboniferous genera and have an anteriorly expanding shape, which is also constricted, akin to the forward expanded shape referred to by Oelhert (1866) and the pyriform shape noted by Brezinski (2008). Glabellar shape is not used in either analysis by Weller or Hessler. Character 1. Constriction of the glabella — Not constricted (0), or constricted (1). Character 2. Glabellar shape — *Proetus*-type (0), *Ungiloproetus*-type (1), *Cornuproetus*-type (2), or *Griffithides*-type (3).

**Glabellar furrows.** The maximum number of glabellar furrows in the proetids is four. S1 is the most strongly developed, and can often completely separate L1 from the rest of the glabella. S3 and S4 are considered plesiomorphic characters by H&H. Hessler assigned three characters, the autapomorphic “1p furrows” (“curved”) and “basal lobes” (“convex” or “flat”) as well as “2p–4p furrows” as being “well separated”. Both Weller (1937) and Brezinski (2005, 2008) emphasised the degree of curvature in the basal furrow (S1), which we consider to be vague and possibly non-homologous. Neither of these characters is considered. Our coding is based on Brezinski (2008) “presence/absence of “L2 and L3 glabellar furrows [sic]”. H&H considered having only S1 and S2, or just S1, as the apomorphic state, as such a presence of S2 to S4 is coded as 0 to reflect the plesiomorphic state. Character 3. Glabellar furrows — S1–S4 present
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(0), or S1–S2 only (1). Character 4. S2 — present (0), or absent (1). Character 5. S3 — present (0), or absent (1). Character 6. S4 — present (0), or absent (1).

Median pre-occipital lobe. The median pre-occipital lobe occurs in two states, the first is the development of bifurcated branch furrows running adaxially from S1, the second a full furrow creating a distinct lobe above the occipital ring, between L1. According to H&H, the branch furrows evolved several times throughout Carboniferous and Permian proetids (e.g., Griffithidinae). The median pre-occipital furrow, however, only occurs in the Griffithidinae and Ditomopyginae. The median pre-occipital lobe is considered an apomorphic character by H&H. Weller considers the pre-occipital lobe to be non-homologous between Ditomopyge and Sevillia, while Hessler and Brezinski omit the character completely. Character 7. Median pre-occipital lobe — Absent (0), branch furrows bifurcated (1), or fully developed median pre-occipital furrow (2).

Occipital ring (LO). Four different features of the occipital ring are described by H&H, namely, a curved median area, absence of an occipital node, lateral narrowing of the ring and, the formation of lateral occipital nodes. The first two are dismissed here as uninformative as they occur throughout the genera of many subfamilies. The lateral narrowing of the occipital ring is considered to be an apomorphic character. Lateral occipital lobes also occur throughout different subfamilies, so are considered here to be uninformative (although H&H state
that this feature arises independently in Carboniferous and Permian genera, there is no evidence for this). The lateral narrowing of the occipital ring could also be considered as the inflation of the medial region (extremely similar to the first trait). Neither Weller, Hessler or Brezinski use LO. Character 8. Occipital ring — Not inflated medially (0), or inflated medially (1).

**Anterior border.** In the Devonian and early Carboniferous trilobites the glabella does not reach the anterior border furrow. Subfamilies including Phillipsiinae, Cummingellinae and Griffithidinae (all Carboniferous and Permian subfamilies) have glabellae that reach, and often cover, the anterior border furrow and margin. There also appears to be a split between taxa that have glabella which covers or only reach the anterior border furrow. Hessler (1963) and Brezinski (2005, 2008) use qualitative characters such as thickness/width of the anterior border. However, in many distorted specimens this character trait is impossible to ascertain even when the anterior border is preserved. In order to code potential homologous information about the anterior border, we choose to use the relative positions of the anterior border and border furrow in relation to the glabella, which is obvious in most distorted specimens. Character 9. Extent of glabella relative to anterior border furrow — Glabella does not reach anterior border furrow (0), glabella touches anterior border furrow (1), or the glabella covers anterior border furrow (2).
**Eyes.** The change in eye shape and size is considered by H&H to be highly important phylogenetically within the Carboniferous and Permian proetids. However, as Clarkson (1979) had shown change in eye shape to be ecophenotypic, Brezinski, Weller and Hessler use only eye size to distinguish between taxa. In our view, there are two forms of eye reduction: in length and in width, with some genera eventually becoming blind. The type of reduction (i.e., in length or width), is herein considered to be independent of one another. The presence of eyes is considered the plesiomorphic state, and as such has been coded as 0. Those with character 10 state 1 have been coded as inapplicable for characters 11 and 12. **Character 10. Eyes — Present (0), Absent (1).**

**Character 11. Eye Width — Wide, width ≥ 56% length (0), narrow, width ≤ 50% length (1).**

**Character 12. Eye Length — Long, eye length ≥ 30% cephalic length (0); short, eye length ≤ 25% cephalic length (1).**

**Facial suture.** The facial suture is observed in post–larval ontogeny and is considered by H&H to be useful for phylogenetic relationships between genera and species. H&H consider the suture line between ε and ζ (epsilon and zeta, see Figure 5.2) of particular importance, with the section between the two either being short and curved, or long and straight. Oehlert (1886) also considered the posterior termination of the facial sutures diagnostic for the Phillispsiidae. Brezinski (2005, 2008) considers short and long posterior facial sutures, similar to that of H&H. **Character 13. Facial suture length — ε – ζ short (0), or ε – ζ long (1).**
Fixigena. The fixigenal width is proportional to the size of the glabella, however, H&H state that ontogenetic studies show an increase in width from wide to very narrow. This can also be observed from older to younger genera, making it a useful character for phylogenetic studies. Neither studies by Weller, Hessler or Brezinski consider fixigenal width. Character 14. Fixigenal width — Wide fixigena, width ≥ 60% length (0), or narrow fixigena, width ≤ 50% length (1).

Librigena. H&H note that the librigenae are completely dependent on other characteristics. These include the size of the eyes, curvature of the cephalon, course of the facial suture and the genal spine. Weller, Hessler and Brezinski also omit the librigena.

Genal spines. The genal spines are not considered useful for phylogenetic studies by H&H. They note that species with both long spines and spineless occur in the same genera. H&H also remark that while it appears spineless forms are derived from spiny forms, there have not been enough ontogenetic studies to clarify this. They are therefore not useful for phylogenetic studies. However, Weller (1937) and Brezinski (2008) consider the presence/absence of spines and spine length respectively, despite Weller’s insistence that “no progressive changes of the genal spines have been noted among the
Carboniferous trilobites as a whole [with the exception of Ditomopyge]” (Weller 1937: 346).

**Ventral side of cephalon.** The ventral side of the cephalon includes the rostrum, hypostome, sub-cranial furrow and cephalic doublure. These traits were not considered useful by H&H as there have been too little studies comparing their differences within the Carboniferous and Permian proetids. For these reasons, they have not been used as characters in the present study.

**Thorax.** H&H note that the thorax has not been well described or illustrated in older literature. They state that usual thoracic segment counts amount to 10 in the Devonian proetids, and nine in Carboniferous and Permian taxa. This however has been contradicted in more recent literature, with Hahn & Brauckmann (1993) placing the Conophillipsia within the Phillipsiidae subfamily Conophillipsiinae (considered here as defunct), which contains 10 thoracic segments. It is not considered a useful character due to the general lack of articulated material or contradictory segment counts.

**Pygidial shape.** In general, the pygidial shape changes from short with few segments in the Devonian to long with many segments in the Carboniferous and Permian. Length and shape are considered important. Three shapes are observed by H&H, bluntly rounded, semi-circular and oblong or triangular, and two lengths, long and short. Brezinski (2005, 2008) uses pygidial outline in
both analyses (parabolic and semielliptical). Character 15. Pygidial length — Short, length is ≤ 74% of width (0), or long, length is ≥ 77% width (1). Character 16. Pygidial shape — Rounded (0), semi–circular (1), or oblong/triangular (2).

**Number of pygidial segments.** Weller and H&H consider the increasing number of axial rings to rib pairs to be important in Carboniferous and Permian proetids. However, not all of these proetids show the change in ring/rib count. For instance, *Bollandia* has a low number of ring and rib segments. Permian genera such as *Neoproetus, Permoproetus* and *Kathwaia* also show an almost equal number of rings to ribs (minimum of 5 rings and ribs). The variations amongst genera mean that pygidial segment number is not a useful phylogenetic character.

**Pleural ribs.** The pleural ribs often have inter-pleural furrows in the Carboniferous and Permian proetids. Four traits have been recognised by H&H in regards to the inter-pleural furrows. These include: an absence of inter-pleural furrows, the inter-pleural furrow is placed at an uneven distance between the anterior and posterior pleural furrows, the inter-pleural furrow widens abaxially, the inter-pleural furrows are very predominant and wide. H&H consider the inter-pleural furrows to be very important phylogenetically, but note that they are often overlooked. Three of these characters, the presence or absence of the furrows, an abaxial widening of the furrows and width of the rib pairs are considered useful. Hessler’s “normally developed” versus
“unusually suppressed” “posterior half-ribs” may be better coded as the presence/absence of inter-pleural furrows. Brezinski (2005, 2008) uses a similar character to define the presence of inter-pleural furrows. The presence of inter-pleural furrows is considered the plesiomorphic state, following H&H, and as such have been coded as character state 0. Taxa that have been coded as absent for character 17 are inapplicable for characters 18 and 19. **Character 17. Inter-pleural furrows** — Present (0), or absent (1). **Character 18. Inter-pleural furrow width** — Equal width (0), or widening abaxially (1). **Character 19. Pleural rib width** — Anterior ribs wider than posterior (0) or, anterior ribs about equal width to posterior ribs (1).

**Pygidial border.** Pygidial borders are often present in Carboniferous and Permian proetid genera. They do not however occur in specific subfamilies, with a number of younger genera lacking the pygidial border (e.g., some of the Phillipsiinae). The pleural ribs are shown to terminate in two different ways when a border is present, at a distinct furrow, or fade abaxially toward the border. The character proposed by Hessler, pygidial border absent/present, is adopted. Taxa that have been coded as absent for character 20 are inapplicable for character 21. **Character 20. Pygidial border** — Absent (0), or present (1). **Character 21. Pygidial border termination** — Pleural furrows fade abaxially towards pygidial border (0), or furrows terminate at pygidial border furrow (1).
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**Exoskeletal relief and sculpture.** H&H state that many Carboniferous and Permian proetids have a strong relief, with distinct furrows. Weller provides multiple transverse profiles of pygidial relief, showing different types of vaulting within North American Carboniferous trilobite genera. Hessler too has a character concerning the “vaulting of carapace”. Some genera, however, show a decrease in relief posteriorly on the glabella. H&H also state that these same genera show a decrease in relief anteriorly on the cephalon, though this cannot be seen in any known genera. Sculpture (or ornamentation) is also said to be degraded in particular genera, for example *Liobole* and *Diacoryphe*. These characters discussed by H&H, Weller and Hessler do not appear to be contained within particular subfamilies or even genera, and can also reflect taphonomic variation (e.g., degree of compaction), so are not considered phylogenetically useful in this study.

**Spines.** H&H refer to spines as the spinose ornament on the dorsal shield or margins, not including the genal spines. There are very few known spines (excepting the genal spines) occurring in the Carboniferous and Permian proetid genera. Only two genera in the meraspid stage show pygidial margin spines, *Ditomopyge* and *Vidria*. Otherwise no other genera haves spines (excepting genal spines). The trait is therefore not useful for a phylogenetic study.

5.4 Results
5.4.1 Sub-Family analysis

Figures 5.3A and 5.3B are a comparison of the cladograms produced by TNT and LisBeth respectively. All zero length branches and homoplastic nodes have been collapsed, with only homologous nodes shown. Figure 5.3A shows a small clade containing Archegonus and Spinibole, grouped on 10:1. There is also a larger clade grouped on 1:1, 2:2, 8:1 and 20:1 containing Phillipsia, Linguaphillipsia, Pudoproetus, Weania, Cummingella, Griffithides, Ditomopyge and Bollandia, while character 16:2 groups Phillipsia and Linguaphillipsia.
FIGURE 5.3A. Single most parsimonious cladogram produced from the subfamily level TNT parsimony analysis (branch length = 62, consistency index (C.I.) = 0.41 and retention index (R.I.) = 0.93). B. Single most compatible cladogram produced from the subfamily level LisBeth three-item analysis (R.I. = 0.633, compliancy 97.7%). C. Strict consensus of cephalic characters based on 16 most parsimonious cladograms (length = 50, C.I. = 0.36, R.I. = 0.91). D. Strict consensus of pygidial characters based on 10 most parsimonious cladograms (length = 13, C.I. = 0.61, R.I. = 0.96). Note: All zero length branches and homoplastic nodes have been collapsed, with only homologous nodes shown.

Figure 5.3B contains the same Archegonus-Spinibole clade, on the same character as Figure 5.3A. There is a larger clade containing Phillipsia, Linguaphillipsia, Pudoproetus, Weania, Cummingella, Griffithides, Ditomopyge and Bollandia, grouped on character 1:1. The large clade consists of two smaller clades. One contains Griffithides, Ditomopyge and Bollandia, which are grouped on character
2:3, and the other *Phillipsia, Pudoproetus* and *Linguaphillipsia* grouped on character 6:1.

Figures 5.3C and 5.3D represent a partitioned analysis of cephalic and pygidial characters respectively. Figure 5.3C consists of one clade containing *Phillipsia, Linguaphillipsia, Pudoproetus, Weania, Cummingella, Griffithides, Ditomopyge* and *Bollandia*, grouped on characters 1:1, 2:2 and 9:2. Figure 5.3D contains one large clade containing *Phillipsia, Linguaphillipsia, Pudoproetus, Crassiproetus, Cummingella, Griffithides, Ditomopyge* and *Bollandia*, grouped on characters 16:1 and 20:1. *Ditomopyge, Linguaphillipsia* and *Phillipsia* group on character 17:1, with *Phillipsia* and *Linguaphillipsia* grouping on characters 16:2.

There are two conflicting taxa, *Crassiproetus* and *Weania*. In the cephalic analysis, *Crassiproetus* falls outside of the large clade mentioned above. In the pygidial analysis, *Weania* falls outside of the large clade.

### 5.4.2 Genus analysis

Figure 5.4 is the single cladogram produced by *LisBeth*. All zero length branches and homoplastic nodes have been collapsed, with only the homologous nodes shown. Figure 5.4 shows two supported polytomies (Group 1 and 3). Group 1 contains *Acanthophillipsia, Ameropiltonia, Anisopyge, Cyphinioides, Delaria, Ditomopyge, Dudu, Hentigia, Novoameura, Pseudophillipsia* and *Sevillia*, and are
grouped on character 7:1. Group 3 contains *Archegonus*, *Dayinaspis*, *Diacoryphe*, *Lichanocoryphe*, *Liobole*, *Menorcapsis*, *Spatulata*, *Spinibole* and *Vandergrachtia*, and are grouped on character 10:1. The remaining genera are not grouped on homologous characters.

**FIGURE 5.4.** Single most compatible cladogram produced from the genus level LisBeth three-item analysis + NONA (R.I. = 0.574, compliancy 95%). For Group codes see Table 5.1. Group 1: AA, AB, AD, AR, AV, AX, AZ, BK, BY, CK, CR; Group 2: AC, AF-AQ, AT, AU, AY, BA-BJ, BL-BQ, BS, BU, BW, BX, BZ, CA-CJ, CL-CQ, CS, CU, CW-CZ, DB-DJ; Group 3: AE, AS, AW, BR, BT, BV, CT, CV, DA. Note: All zero length branches and homoplastic nodes have been collapsed, with only homologous nodes shown.
5.5 Discussion

5.5.1 Exemplar taxa

The use of exemplar taxa has meant that the analysis is focused on character states that are potentially informative at the generic or subfamilial level. In doing so, this has eliminated any problems concerning the monophyly of representative genera within the analysis.

5.5.2 Monophyly of Phillipsiidae

The characters proposed by H&H have recovered an aphyletic Phillipsiidae at both the subfamilial and genus level. When looking at the subfamily analyses there is no clear distinction between the subfamilies of Phillipsiidae and the subfamilies of Proetidae. In fact, two of the Phillipsiidae subfamilies Archegoniinae and Cystispininae (represented by *Archegonus* and *Spinibole*, respectively), consistently group separately from all the other subfamilies (see Figures 5.3A and 5.3B). The genus level parsimony analysis resulted in an unresolved cladogram. The 3IA analysis shows some resolution (see Figure 5.4), but there is also no clear distinction between those genera classified under Phillipsiidae and those found in Proetidae.
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The analysis of exemplar taxa of subfamilies upholds two relationships suggested by H&H (1967, figs. 1 – 5), an *Archegonus-Spinibole* relationship (consistently), and a *Phillipsia-Linguaphillipsia* relationship (not upheld in the cephalic character analysis). A computational analysis of genera upholds one of the generic relationships proposed by H&H. *Archegonus, Diacoryphe, Liobole, Spatulata,* and *Spinibole* are found within both the genus level clade and H&H’s first phyletic tree. However, a number of genera within their tree are not grouped in the genus level clade. Those include *Weania, Belgibole* (both *Archegonus* subgenera in H&H) and *Carbonocoryphe.* If the characters proposed by H&H are to be used to elucidate their phyletic trees, then the relationships of the genera should form at some level. Our analyses show only one small *Archegonus-Spinibole* relationship is able to be upheld.

5.5.3 High level versus low level character states

The higher resolution in the sub-family level analysis may be a result of double the number of characters versus taxa, as well as representing a broad spectrum of the family as a whole, i.e., greater disparity. The characters proposed by H&H are aimed at a high-level family analysis, as shown in their subfamilial-level analyses (Hahn and Hahn 1967, figs. 1 – 5). The genus-level analysis suffered both from a far greater number of taxa (88) versus characters (21). The characters may also have been too general to address any specific genus or species level characteristics (Figure 5.5, compare A with C).
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FIGURE 5.5. Types of topographical resolution based on character-states. A. Unresolved trees are a result of general or unspecialised character-states (i.e., using the “presence of vertebrae” to distinguish between different species of mammals). B. Specialised character-states, which may group a larger clade (i.e., “presence of wings in mammals”). C. Highly specialised character-states, which may group individual taxa, such as species. However, in larger analyses, highly specialised character-states may be too specific and result in homoplasy, such as the presence of an opposable thumb in vertebrates, which would group primates and the frog genus Phyllomedusa. D. A combination of general, specialized and highly specialised character-states are ideal in most large analyses.

Ideally, a distribution of both high, medium and low level characters are needed to find resolution throughout the cladogram (Figure 5.5D). Given that the genus-level analysis also had a broad spectrum of representative species, the characters were not sufficient to group the taxa into distinct morphotypes, suggesting that the characters are too broad for such an analysis (Figure 5.5A). Even so, informative characters within a monophyletic taxon would group
clusters of taxa as polytomies. The genus-level result suggests that not all genera and subfamilies are monophyletic.

The claim by Weller (1937) that pygidia are significant in classifying North American Carboniferous and Permian trilobites only partially holds in the subfamily-level analysis. The pygidial characters group *Linguaphillipsia* and *Phillipsia*, based on the notable oblong/triangular pygidial shape, however, that relationship is not recovered in the cephalic characters. Overall, the pygidial and cephalic characters overlap, with the exception of *Crassiproetus* and *Weania*. Cephalic characters such as *Cornuproetus*-type glabellar shape, the glabella covering the anterior border and a constricted glabella group *Weania* within the larger clade containing *Phillipsia*. However, pygidial characters such as a semi-circular pygidium and a pygidial border group *Crassiproetus* within the larger clade, to the exclusion of *Weania*.

The overlap between the pygidial and cephalic characters in the subfamily analysis does show an overall pattern between two sets of morphological structures. The pygidial characters appear to be at the species or genus-level (Figure 5.3D; See Figure 5.5C), while the cephalic characters are placed more basally (Figure 5.3C; see Figure 5.5B). Given this, it is not surprising that Weller suggested that pygidia are ideal for grouping North American genera.

### 5.6 Conclusion
The family Phillipsiidae (*sensu* Hahn *et al.* 1980) most likely represents an aphyletic group. A revision could restrict the family to Phillipsiinae and Linguaphillipsiinae as shown in the subfamily analysis. While this may seem reasonable at the subfamily level, there is however, no evidence for this grouping in the genus-level analysis. The characters suggested by Hahn and Hahn (1967) are too broad and too few to resolve genus-level monophyly, while the characters proposed by Weller (1937), Hessler (1963) and Bresinski (2003, 2005, 2008) are too specific and restricted to North American species to be useful for any higher level analysis. We strongly suggest that the Phillipsiidae should be treated as possibly aphyletic, thereby following the recent re-designation by Jell and Adrain (2003).
Chapter 6. A Taxonomic Revision of the Carboniferous and Permian trilobites of Australia

6.1 Introduction

The first major publication documenting and describing Australian Carboniferous species was written by Mitchell (1918) in which he described 17 new species, and evaluated the other Carboniferous trilobite species already described from Australia by M’Coy (1847), Etheridge Snr. (1872), de Koninck (1877) and Etheridge Jr. (1892). Mitchell’s (1918) species were described from the three genera, Phillipsia Portlock 1843, Griffithides Portlock 1843 and Brachymetopus M’Coy 1847. Mitchell (1922) described a new species from the genus Cordania Clarke 1892 (see Ebach & Edgecombe 1999), and re-described specimens from his own species Griffithides convexicaudatus Mitchell 1918. In fact, Mitchell (1918) was the first author to publish photographs of Australian Carboniferous trilobite specimens, and discussed the inaccuracy of previous authors’ drawn figures that had been published.

The next few decades consisted of a limited number of mentions of Australian Carboniferous trilobites. Stubblefield (1948) suggested the species P. collinsi Mitchell 1918 could be ?Linguaphillipsia collinsi (Mitchell 1918) and Cvancara
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(1958) described the new species *Linguaphillipsia divergens* Cvancara 1958. Some new genera were also diagnosed on Australian specimens, including *Australosutura* Amos et al. 1960, *Conophillipsia* Roberts 1963 (to encompass trilobites with a proetid-like cephalon and phillipsid-like pygidium), *Weania* Campbell & Engel (1963), and *Pudoproetus (Megaproetus)* Jell 1977. The bulk of Carboniferous trilobite literature, however, was undertaken by Engel & Morris between 1975 and 1997.

The first study by Engel & Morris (1975) focused on the genus *Linguaphillipsia* Stubblefield 1948. This was the first publication in almost 60 years that focussed solely on Carboniferous trilobites of Australia. Over the next two decades Brian Engel and Noreen Morris proceeded to publish a vast literature on Carboniferous trilobites (1975; 1980; 1983; 1984; 1989; 1991; 1992; 1994; 1995; 1996; 1997). The publications were focussed on a specific genera and sub-families. They also had a number of publications highlighting the use of these trilobites for biostratigraphic studies in Australia (Engel & Morris 1985; 1990; 1997). Engel & Morris described more than 40 new species from Australia in this time, and re-described most of Mitchell’s (1918; 1922) taxa. They also added a large amount of specimens to already existing Carboniferous trilobite collections.

Since their last publication (Engel & Morris 1997), only one new Carboniferous trilobite species has been described from Australia, *Linguaphillipsia engeli* Galtier
et al. 2007. Until now, none of Engel & Morris’s species, genus, subfamily or even family placements have been re-assessed, however, several genera have been disputed in published literature (see *Conophillipsia* Roberts 1963; *Pudoproetus* Hessler 1963; Owens 1994; Feist & Petersen 1995; and in remarks below). There have also been a large number of publications on Carboniferous trilobites from Europe and America in this time (Hahn et al. 2001; 2003; 2007; Lerosey-Aubril & Feist 2005; 2006), which have re-diagnosed genera found in Australia.

A taxonomic review has been conducted for a number of reasons. Genus level classifications that have been called into question by Owens (1994), Feist & Petersen (1995), G. Hahn (pers. comm. 2011) and Brezinski (pers. comm. 2012) are addressed. The subfamily and family level placements of the Australian species within the genera *Conophillipsia* Roberts 1963, *Pudoproetus* Hessler 1963, *Carbonocoryphe* (Winterbergia) Hahn & Brauckmann 1975 and *Carbonocoryphe* (Aprathia) Hahn & Brauckmann 1975 have been reconsidered. In addition, in light of newer literature and data published over the last 15–18 years, the re-diagnoses of genera and species seems appropriate as well as reassessing species and genera that are based on poorly preserved specimens.

Only four Permian trilobite species are known from Australia. *Ditmopyge meridionalis* Teichart 1944 from northwestern Western Australia, *Doublata inflata* Wass & Banks 1971 from the Hunter Valley in New South Wales, *D. matheri*
Engel & Laurie 1978 from Wingham, New South Wales, and *D. pyriforme* Wass & Banks 1971 from eastern Tasmania. No further revision of either of these taxa has been made since their original designations.

### 6.2 Localities

The material used for this study comes from the Carboniferous and Permian of Australia, specifically from Queensland, New South Wales, Tasmania and Western Australia (Figure 6.1). Carboniferous material is found in the Manning district, otherwise known as the Hunter Valley and New England regions of New South Wales, Mount Morgan-Rockhampton district in Queensland, and the Burdekin Shelf near Townsville in Queensland (Engel & Morris 1997). Permian material is found in the Lower Hunter Valley and Manning River Districts of New South Wales, Elephant’s Pass and Ray’s Hill in North-East Tasmania and, Wandagee in the North-West division of Western Australia (Engel & Morris 1997; Teichert 1944). The specific localities have been listed in Table 1.

All but one of the Carboniferous species were collected from the Early Carboniferous, namely the lower Tournaisian to the late Viséan (358.9Ma to 330.9Ma). The remaining Carboniferous species, *Australosutura gardneri* (Mitchell 1922) was collected from the Westphalian, during the Mid-Late
Carboniferous (~ 313Ma to 304Ma). The Permian species were collected from the Sakmarian to Wordian, in the Early to Middle Permian (295Ma to 265Ma).

6.3 Biostratigraphy

Trilobites have not been found in the Devonian-Carboniferous boundary in Australia. Five brachiopod zones have been identified by Engel & Morris (1997) that correlate with the Carboniferous trilobites (Figure 6.2). The *Spirifer sol* Zone, during the early Tournaisian (labelled as Tn2a/b to Tn2c), the *Schellwienella burlingtonensis* Zone, from the early to latest Tournaisian labelled as (Tn3a to Tn3c), the *Orthotetes australis* Zone, the very earliest Viséan (labelled as V1a to V1b), the *Delepinea aspinosa* Zone, early to late Viséan (labelled as V1c to V2b) and the *Rhipidomella fortimuscula* Zone, the very latest Viséan (labelled as V3a/b). The oldest brachiopod zone in the Carboniferous, the *Tulcumbella tenuistriata* Zone (labelled as Tn1), does not contain any trilobite taxa.

The first appearance of Australian Carboniferous trilobites was *Linguaphillipsia stanwellensis* (Mitchell 1918) at the Tournaisian 2a/b level in Queensland in the *Spirifer sol* Zone (Engel & Morris 1997). The majority of species (29 known so far) have been found in the *Schellwienella burlingtonensis* Zone, followed by 21 species in the *Delepinea aspinosa* Zone, 8 species in the *Orthotetes australis* Zone, 7 species in the *Spirifer sol* Zone and 6 species in the *Rhipidomella fortimuscula* Zone. *Australosutura gardneri* (Mitchell 1922) was found in the *Levipustula levis* Zone from Westphalian (the zone is from the Namurian to the Westphalian
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Roberts et al. (1993), and is the youngest known species of Carboniferous trilobite in Australia.

The Tournaisian saw a change in shorelines throughout the New England and Yarrol Orogens, and the North Queensland Basins. The development of the Currabubula Volcanic Arc caused a regression event in the New England Orogen, which resulted in shallow water forearc basin marine environments (Engel & Morris 1997; Roberts et al. 2006). This allowed the deposition of highly abundant invertebrate faunas, including the majority of the Carboniferous trilobites (Engel & Morris 1997).

Trilobites from the Permian of Australia are very rare. Only four known species have been found throughout Australia, from the Sakmarian to the Wordian. The oldest species, Doublatia matheri is from the Colraine Mudstone, part of the Manning Group in the southern section of the New England Orogen (Engel & Laurie 1978). The Colraine Mudstone is the youngest fossiliferous section of the Manning group, found in the early Sakmarian (Jenkins & Offler 1996). Doublatia pyriforme is found only in Tasmania, in the Berridale Limestone and Enstone Park Limestone near St Mary’s, which are thought to be comparable in stratigraphic age to one another (Wass & Banks 1971). The Berridale and Enstone Park Limestones are of Artinskian age (Rao 1988). Ditomopyge meridionalis is also from the Artinskian, but is found only in Western Australia, in the Wandagee Formation, Wandagee Station (Teichert 1944). The youngest
trilobite from Australia is *Doublatia inflata* Wass & Banks 1971, which is found in the Branxton Formation, Mulbring in New South Wales. The Branxton Formation is the oldest section of the Maitland Group, found in the Lower Hunter Valley, New South Wales. It has recently been determined to be very Early Wordian in age from the Middle Permian (Percival *et al.* 2012).
# Chapter 6: A Taxonomic Revision

## Carboniferous

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FIGURE 6.2. Stratigraphical column of the Carboniferous and Permian in Australia, showing the distribution of trilobite species. All species have been updated in the following systematic palaeontology section. Stratigraphic names have been taken from the 2013 International Commission on Stratigraphy International Chronostratigraphic Chart (http://www.stratigraphy.org/ICSchart/ChronostratChart2013-01.pdf). West European time periods of the Carboniferous have also been included as they were originally used for dating in Australian Carboniferous trilobite literature. Brachiopod zones indicated for the Carboniferous were also taken from Engel and Morris (1997). Emended from Engel & Morris (1997, text-figure 2). ICS = International Chronostratigraphic Chart, BZ = Brachiopod Zone, B = Brachymetopidae, A = Aulacopleuridae, TZ = Tulcumbella enustriata Zone, OAZ = Orthotetes australis Zone, RFZ = Rhipidomella fortimuscula Zone, MZ = Marginirugus barringtonensis Zone.

6.4 Anatomical nomenclature

The following morphological terms are taken from the Treatise on Invertebrate Paleontology Part O (revised) (Whittington et al. 1997). A number of terms used by Engel & Morris have been updated to correspond to recent literature. The terms used within the taxonomic review are in italics, while any terms that are different in the treatise to what is used in this study are shown in brackets before the description.

The term *axial furrow* has been used by Engel & Morris (1975 – 1997) to represent what is known as an *inter-ring furrow* in Whittington et al. (1997). The *dorsal furrow* is used by Engel & Morris to describe what is known as an *axial furrow* in Whittington et al. (1997). Given that the same term is being used for a different feature by Engel & Morris, term *axial furrow* has been changed to the term *inter-ring furrow*. The *axial furrow*, as described by Whittington et al. (1997), will remain as the *dorsal furrow*, (sensu Engel & Morris), so as to not cause any confusion.
The terms free cheek and fixed cheek have been changed to librigena and fixigena respectively. Rib furrow has been changed to interpleural furrow as well. These changes correspond to newer Carboniferous trilobite studies using these terms (Lerosey-Aubril & Feist 2005; 2006; Lerosey-Aubril 2012), as they are more commonly used for trilobite morphology.

Several terms used by Engel & Morris are not described in Whittington et al. (1997), namely the anterior margin and genal furrow, are indicated in bold and described below. The terms, labelled on Figure 5.2, show the corresponding morphology. Terms shown in square brackets after the description are the terms used by Engel & Morris (1975 – 1997) that have been changed in this study.

1. Cephalon

1.1 Occipital Ring: Axial region of most posterior segment of cephalon, bounded at sides by axial furrows, at front by occipital furrow, and at back by posterior margin. Posterior part of the glabella.

1.2 Occipital Furrow: Transverse furrow that isolates occipital ring from remainder of glabella.

1.3 Posterior Border Furrow: Portion of border furrow bounding posterior border.

1.4 Occipital Lobe: [Lateral Occipital Lobe] Lateral or anterolateral portion of occipital ring.
1.5 **Preoccipital Lobe**: [Lateral Preoccipital Lobe] Lobe L1; lateral portion of glabellar region directly in front of preoccipital ring.

1.6 **Border Furrow**: Furrow defining adaxially border of cephalon.

1.7 **Antennal Pore**: [Fossula] Small, circular or oval depression that may occur in axial furrow at or near anterolateral edge of glabella and that lies at junction with anterior edge of eye ridge.

1.8 **Anterior Margin**: The margin of the anterior portion of the cephalon.

1.9 **Anterior Border**: Portion of cephalic border between anterior branches of facial sutures, when anterior branches of suture cross border.

1.10 **Preglabellar Field**: Portion of cranidium lying between front of glabella and anterior border furrow.

1.11 **Preglabellar Furrow**: Portion of axial furrow outlining front of glabella.

1.12 **Facial Suture**: Suture bounding adaxial margin of eye surface, which has anterior and posterior branches, each of which may extend over the border and on to the doublure; suture separates librigena from fixigena.

1.13 **Dorsal Furrow**: [Axial Furrow] Groove on external surface formed by fold in exoskeleton that outlines axial region of the cephalon.

1.14 **Palpebral Lobe**: Protruding subsemicircular flange of fixigena bounded distally by palpebral suture.

1.15 **Posterior Border**: Portion of cephalic border between genal angle and occipital ring.
Chapter 6. A Taxonomic Revision

1.16 Occipital Node: Median pointed structure projecting from exterior of occipital ring.

1.17 Genal Furrow: Groove on the external surface of the genal spine.

1.18 Genal Spine: General term for hollow, posteriorly directed extension of border and doublure at genal angle forming pointed projection.

2. Thorax

2.1 Dorsal Furrow: [Axial Furrow] Groove on external surface formed by fold in exoskeleton that outlines axial region of the thorax.

2.2 Pleural Furrow: Groove in external surface of pleural region of thoracic pleura, formed by fold in exoskeleton.

3. Pygidium

3.1 Dorsal Furrow: [Axial Furrow] Groove on external surface formed by fold in exoskeleton that outlines axial region of the pygidium.

3.2 Interpleural Furrow: Transverse groove extending from axial furrow across pleural region of pygidium, indicating boundary of fused pleurae (ribs). [Rib Furrow]

3.3 Pleural Furrow: Groove in external surface of pleural region of pygidium, formed by fold in exoskeleton.

3.4 Inter-Ring Furrow: Groove bounding successive axial rings of pygidium. [Axial Furrow]
Chapter 6. A Taxonomic Revision

3.5 Pleural Rib: [Rib] Portion of pygidial pleural region bounded by two successive pleural furrows.

3.6 Border Furrow: Furrow defining adaxially border of pygidium.

3.7 Border: Outer dorsal portion of pygidium, usually bounded by border furrow.

6.5 Open Nomenclature

There are inconsistencies in the Carboniferous and Permian trilobite literature with regards to synonymy lists. Little of the literature before 1990 has agreement on their open nomenclature. To correct for this the recommendation by Bengston (1988) has been followed.

6.6 Repositories

AMF, Earth Science Collections [Department of Paleontology], Australian Museum, Sydney, Australia; ANU, Australian National University, ANU Palaeontology Collection, Canberra, Australia; NGS, Geological Survey of New South Wales, Londonderry, Australia; QM, Queensland Museum, Brisbane, Australia; QGS, Geological Survey of Queensland, Brisbane, Australia; SMF,
6.7 Systematic Palaeontology

6.8 Class TRILOBITA Walch 1771

6.9 Order PROETIDA Fortey & Owens 1975

*Diagnosis.* See Fortey & Owens (1975).

*Remarks.* Much debate has ensued since Fortey & Owens (1975) original diagnosis (Fortey & Owens 1979; Hahn & Hahn 1975b), including whether the order is in fact monophyletic (Bergstrom 1977; Fortey & Owens 1979). Fortey (2001) agreed that most of the characters used to originally diagnosis the order were plesiomorphic and apomorphic. The single shared character that seemed to unite the families was the adult morphology of the protaspids (Fortey 2001). Lerosey-Aubril and Feist (2005) however, described the first post Devonian protaspid fossils from the superfamily Proetoidea Hawle & Corda 1847. The difference in protaspid ontogeny to other superfamilies of the order was suggested to separate them into two separate clades, the Proetoidea and the Aulacopleuroidea/Bathyuroidea group (Lerosey-Aubril & Feist 2005; Adrain in
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Zhang 2011). Due to a lack of protaspid fossils from the post Devonian era it is difficult to confirm this point of view.

The following taxonomy has been divided into sections based on family assignment. Families include Proetidae Salter 1864, Phillipsiidae (Oehlert 1886), Brachymetopidae Prantl & Pribyl 1950 and Aulacopleuridae Angelin 1854. Originally the bulk of Australian Carboniferous trilobites were assigned to the subfamily Phillipsiidae by Engel & Morris (1997), but after a revised analysis of recent literature, as well as the Australian specimens, a number of the Phillipsiidae genera have been moved to Proetidae.

Superfamilies Included. Proetoidea Hawle & Corda 1847, Aulacopleuroidea Angelin 1854, Bathyuroidea Walcott 1886.

Age and range. Mid-Ordovician to Late Permian, worldwide (Hahn & Hahn 1969).

6.10 Superfamily AULACOPLEUROIDEA Angelin 1854

6.11 Family AULACOPLEURIDAE Angelin 1854

6.11.1 Subfamily OTARIONINAE Richter & Richter 1926

6.11.1.1 Genus Namuropyge Richter & Richter 1939

1939 Namuropyge Richter & Richter: 2–7
Chapter 6. A Taxonomic Revision

1943  *Brachymetopus (Coignouina)* Reed: 64–65

1969  *Coignouina* Hahn & Hahn: 46–47

1969  *Namurophyge* Hahn & Hahn: 48

1977  *Namurophyge* Tilsley: 160

1977  *Namurophyge* Thomas & Owens: 73

1980  *Namurophyge* Hahn *et al.*: 354–360

1986  *Namurophyge* Owens: 4–6

1989  *Namurophyge* Hahn *et al.*: 120

1991  *Namurophyge* Engel & Morris: 124

1996  *Namurophyge (Namurophyge)* Hahn & Hahn: 169

*Type species.* *Namurophyge demaneti* Richter & Richter 1939.


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between the genera (Lerosey-Aubril et al. 2008). The classification of Adrain & Chatterton (1994) has been retained here.


**6.11.1.1i Namuropyge australis** Engel & Morris 1991

1991 Namuropyge australis Engel & Morris: 127–128, Pl. 2 Figs. 8–11, Text Figs. 3–4

Holotype material. AMF81904 (external cephalic mold).
Paratype material. AMF81905a/b (external/internal cephalon), AMF81906 (external pygidium), AMF81907 (external pygidium), AMF81908 (external pygidium), AMF81909a/b (external/internal pygidium).

Locality. NU L1049.


Remarks. See below.

6.11.1.1ii Namuropyge uniserialis Engel & Morris 1991

Figure 6.3

1991 Namuropyge uniserialis Engel & Morris: 124–127, Pl. 1 Figs. 1–8, Pl. 2 Figs. 1–4; Text Figs. 1–2

Holotype material. AMF81889 (external cephalic mold).

Paratype material. AMF81878 (external cephalon), AMF81879a/b (external/internal cranidium), AMF81880 (external librigena), AMF81881a/b (external/internal cephalon), AMF81882 (external cranidium), AMF81883 (external cranidium), AMF81884 (partial external cephalon), AMF81885 (external librigena), AMF81886 (external cephalon), AMF81887 (partial external cephalon).
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cephalon), AMF81888 (internal cephalon), AMF81890 (internal cephalon), AMF81891 (external librigena), AMF81892 (internal cephalon), AMF81893 (internal cephalon), AMF81894 (internal cephalon), AMF81895 (internal cephalon), AMF81896 (internal cephalon), AMF81899 (external pygidium), AMF81898a/b (internal/external pygidium), AMF81899 (external pygidium), AMF81900a/b (external/internal pygidium), AMF81901 (internal pygidium), AMF81902 (internal pygidium), AMF81903 (internal cephalon).

Locality. NU L8.


Remarks. The two Australian species of Namuropyge differ from other species of the genus in that they do not possess two rows of marginal cephalic spines, where the vertical row of spines is missing. They differ from one another in that N. australis has longer, wider and higher eyes, and longer cephalic spines. The marginal pygidial spines of N. australis are horizontal, whereas they are vertical in N. uniserialis (Engel & Morris 1991).
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FIGURE 6.3. Representative Australian genera of the Order Proetida. 1. Namuropyge uniserialis external cranidium Holotype, AMF81889, 5x. Australosutura campbelli, 2. external cephalon Holotype, AMF84389a, dorsal view, 7x, 3. external deformed pygidium Paratype, AMF85454, dorsal view, 6.5x. Xenoboloides peregrina, 4. internal cephalon Holotype, AMF80812, dorsal view, 4.5x, 5. external pygidium Paratype, AMF80797, dorsal view, 9.1x. 6. Brachymetopus (Spinimetopus) subtilis external cranidium Holotype, AMF81910, dorsal view, 15x. Conophillipsia breviceps, 7. external cephalon Paratype, AMF85468, dorsal view, 8x, 8. external pygidium Paratype, AMF80473a, dorsal view, 5.2x. 9. external librigena, AMF85425, dorsal view, 7.9x. Phillipsia squamata, 10. external cephalon Holotype, AMF80267, dorsal view, 7x, 11. external pygidium Paratype, AMF80269, dorsal view, 11x. 12. Brachymetopus (Brachymetopus) mccoyi regularis external cephalon Paratype, AMF84295, dorsal view, 7x.
6.12 Family BRACHYMETOPIDAE Prantl & Pribyl 1950

6.12.1 Subfamily BRACHYMETOPINAE Prantl & Pribyl 1950

6.12.1.1 Genus Brachymetopus M’Coy 1847

6.12.1.1(a) Subgenus Brachymetopus M’Coy 1847

1847 Brachymetopus (Brachymetopus) M’Coy 1847: 230

1985 Brachymetopus (Brachymetopus) Hahn & Hahn: 456–461

1989 Brachymetopus (Brachymetopus) Hahn et al.: 121–122

Type species. Phillipsia maccoyi Portlock 1843.


Remarks. Brachymetopus (Brachymetopus) M’Coy 1847 was re-diagnosed by Hahn & Hahn (1985). A full discussion of the subgenus compared to other the other subgenera of Brachymetopus M’Coy 1847 can also be found there. The following species list includes species originally diagnosed under the subgenus Brachymetopus (Brachymetopina) Reed 1903 as it is a junior synonym of Br. (Brachymetopus) M’Coy 1847 (see Goldring & Stubblefield 1957). The species list also includes species not originally assigned to a subgenus, designated by Gandl (2011). The species listed in Gandl (2011) for Brachymetopus does not include some of the Chinese species by Kobayashi & Hamada (1980), though no reason is given for this.

*Age and range.* Upper Devonian to Upper Carboniferous, in Germany, Spain, China, Australia and North America (Gandl 2011).

6.12.1.1(a).i *Brachymetopus* (*Brachymetopus*) *maccoyi* (Portlock 1843)

1843 *Phillipsia maccoyi* Portlock: 309, Pl. 11 Fig. 6a–b
1969 *Brachymetopus maccoyi* Hahn & Hahn: 24–25
1982 *Brachymetopus maccoyi* Hahn & Hahn: 97–98
1986 *Brachymetopus maccoyi* Owens: 15
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1992  \textit{Brachymetopus (Brachymetopus) maccoyi} Engel & Morris: 74–75


\textbf{Remarks.} \textit{Brachymetopus (Brachymetopus) maccoyi} (Portlock 1843) is a very common species found throughout the world during the Carboniferous (Engel & Morris 1992). A large number of sub-species have been described by Engel & Morris (1992; 1996) from eastern Australia, all showing similar features to the type species. These include a rounded cephalon, distinct anterior border with at least one row of nodes, concave to flat wide anterior border furrow and highly nodose cephalic ornament.

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Age and range. Upper Tournaisian to Viséan in Europe, Australia and China (Engel & Morris 1992).

6.12.1.1(a).i(a) Brachymetopus (Brachymetopus) maccoyi gloriosus Engel & Morris 1996

1996 Brachymetopus (Brachymetopus) maccoyi gloriosus Engel & Morris: 134–136, Pl. 11 Figs. 21–22

Holotype material. AMF96995a (external cephalon lacking right librigena and gena).

Paratype material. AMF96995b (external pygidium), AMF96995c (external pygidium).

Locality. NU L546.

Emended diagnosis. Small nodes in the preglabellar furrow; nodes on librigena, fixigena and glabella are large. Pygidium with 17(18?) axial rings, 7 pleural ribs; juvenile pygidium with marginal spines.

Remarks. Even though only one specimen has been found, it has characteristics making it distinguishable from other subspecies of Brachymetopus.
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(\textit{Brachymetopus}) maccoyi (Portlock 1843). These include small nodes on the preglabellar furrow, other subspecies only have a smooth furrow, and a much longer pygidium with a greater number of axial rings.

6.12.1.1(a).i(b) \textit{Brachymetopus} (\textit{Brachymetopus}) maccoyi \textit{intermedius} Engel & Morris 1992

1918 \textit{Brachymetopus dunstani} Mitchell: Pl. 49 Fig. 1, Pl. 52 Fig. 1
1918 \textit{Brachymetopus} sp. indet. Mitchell: 488
1992 \textit{Brachymetopus} (\textit{Brachymetopus}) \textit{maccoyi intermedius} Engel & Morris: 78–80, Pl. 1 Figs. 10–15, Text Figs. 3–4

\textit{Type material}. QGSF1011 (external cephalon lacking one librigena and genal spines).

\textit{Paratype material}. From NU L1049: AMF84316a/b (external/internal cephalon), AMF84317a/b (external/internal cephalon), AMF84318 (external pygidium), AMF84319 (external pygidium), From QGS L3004: QMF2839(2) (4 partial internal pygidia).

\textit{Locality}. Type - QGS L3004. Other - NU L 1049.
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*Emended diagnosis.* Glabella just over half cephalic length, tapers anteriorly; coarse nodular ornament, two rows of nodes on the cephalic border; anterior border furrow distinct and wide. Pygidium with 12 axial rings, 7 pleural ribs; marginal spines developed onto pygidial border.

*Remarks.* The above diagnosis has been emended to exclude much of Engel & Morris’s (1992) discussion of ornament, as the nodular ornament is slightly variable between specimens of the species. There does however appear to be a second row of nodes on the cephalic border which distinguishes this species from the similar looking species *Brachymetopus (Brachymetopus) maccoyi ararat.*

6.12.1.1(a).i(c) *Brachymetopus (Brachymetopus) maccoyi medinodulosus* Engel & Morris 1992

1992 *Brachymetopus (Brachymetopus) maccoyi medinodulosus* Engel & Morris: 82–84, Pl. 2 Figs. 8–15, Text Figs. 8–10

*Type material.* AMF84332 (external cephalon).

*Paratype material.* AMF84333a/b (external/internal cephalon), AMF84334 (external cephalon), AMF84335 (external pygidium), AMF84336 (external pygidium), AMF84337 (external pygidium), AMF84338 (external pygidium),
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AMF84339 (external pygidium), AMF84340 (internal pygidium), AMF84341 (internal pygidium).

Locality. NU L890.


Remarks. Brachymetopus (Brachymetopus) maccoyi medinodulosus closely resembles the species Br. (Brachymetopus) maccoyi spinimarginatus in that they both have very similar proportioned pygidia and cephalic features. Differences between the two species include much smaller eyes, a narrower glabella and pygidial spines only developed in small specimens (less than 2mm) of Br. (Brachymetopus) maccoyi medinodulosus. Brachymetopus (Brachymetopus) maccoyi medinodulosus also closely resembles the species Br. (Brachymetopus) maccoyi cathayensis in its ratio of glabella to cephalon length and eye length. They differ in that Br. (Brachymetopus) maccoyi cathayensis has nodular ornament developed on the cephalic border furrow, and much narrower genal spines.

6.12.1.1(a).i(d) Brachymetopus (Brachymetopus) maccoyi ararat Engel & Morris 1992

1992 Brachymetopus (Brachymetopus) maccoyi ararat Engel & Morris: 80–82, Pl. 2 Figs. 1–7, Text Figs. 5–7
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Type material. AMF84320a (external cephalon lacking genal spines).

Paratype material. From NU L375: AMF84320b (internal cephalon), AMF84321a/b (external/internal cephalon), AMF84322a/b (external/internal pygidium), AMF84323 (external pygidium), AMF84324 (internal pygidium), AMF84325 (internal cephalon and pygidium), AMF84326 (external cephalon). From NU L740: AMF84327 (external cephalon), AMF84328 (external cephalon), AMF84329 (external pygidium), AMF84330 (internal pygidium), AMF84331 (external pygidium).

Locality. Type - NU L375. Other - NU L740.

Emended diagnosis. Cephalic and glabella shape slightly triangular anteriorly; glabella under half cephalic length; eye length almost half glabellar length; cephalon inflate, preglabellar field steep (50–60°); strong flattened nodular ornament, tending to become obsolete on the occipital ring and posterior border; 2 large nodes in front of the eyes appear to constrict the glabella; single row of nodes around inner margin of the cephalic border. Pygidium with 11–15 axial rings, 7–8 pleural ribs; posterior ribs not incurved.

Remarks. The above diagnosis has been emended from Engel & Morris (1992) to remove some of the descriptive text of the nodose prosopon. Br. (Brachymetopus)
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*maccyi ararat* is obviously different from other subspecies in that it has a slightly triangular cephalon and two distinct nodes above the eyes.

6.12.1.1(a).i(e) *Brachymetopus (Brachymetopus) maccyi regularis* Engel & Morris 1992

Figure 6.3

1992 *Brachymetopus (Brachymetopus) maccyi regularis* Engel & Morris: 75–77, Pl. 1 Figs. 1–9, Text Figs. 1, 2.

**Holotype material.** AMF84292 (external cephalon).

**Paratype material.** From NU L39: AMF84293 (external cephalon), AMF84294 (external cephalon), AMF84295 (external cephalon), AMF84296 (external cephalon), AMF84297 (external cephalon), AMF84298 (external cephalon), AMF84299 (external cephalon), AMF84300 (external cephalon), AMF84301 (external cephalon), AMF84302 (external cephalon), AMF84303 (external cephalon), AMF84304 (external cephalon), AMF84305a–c (2 internal cephalas and external pygidium), AMF84306 (internal cephalon), AMF84307 (internal cephalon), AMF84308 (external pygidium), AMF84309 (external pygidium), AMF84310 (external pygidium), AMF84311 (external pygidium), AMF84312 (external pygidium), AMF84313 (internal pygidium), AMF84314 (internal pygidium), AMF84315 (internal pygidium). From AGS L3004: QGSF1007(3)
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(partial external pygidium), QGSF1007(4) (2 partial cranidia), QGSF1007(5) (partial internal preglabellar field).

Locality. Type - NU L39. Other - QGS L3004.

Emended diagnosis. Glabella about half the cephalic length; preglabellar field sloping at 35–40°; smooth furrow inside cephalic border. Coarse nodular ornament of variable size. Eyes at least half glabellar length, up to three quarters; nodes around inner edge of cephalic border with parallel row of nodes around outer edge. Pygidium with 11–12 axial rings; 7 pleural ribs; marginal spines present; posterior ribs not incurved.

Remarks. The above diagnosis has been emended from Engel & Morris (1992) with minimal changes. One notable exception is the length of the eyes, which appear to be much greater than the one third to half glabellar length originally stated by Engel & Morris (1992) (upwards of three quarters of the glabellar length).

6.12.1(a).ii Brachymetopus (Brachymetopus) strzeleckii M’Coy 1847

1847 Brachymetopus strzeleckii M’Coy: 231, Pl. 12 Fig. 1a, b
1987 Brachymetopus (Brachymetopella) strzeleckii strzeleckii Gandl: 50
1992 Brachymetopus (Brachymetopus) strzeleckii strzeleckii Engel & Morris: 84

Remarks. Brachymetopus strzeleckii was first placed within the subgenus Br. (Brachymetopella) Kobayashi & Hamada 1978 by Gandl (1987) after Hahn & Hahn’s (1985) subgenus classification. The subgenus Br. (Brachymetopella) was originally erected on the absence of basal glabella lobes. Engel & Morris (1992) state that basal lobes are found on juveniles of Kobayashi & Hamada’s (1978) type species Br. (Brachymetopella) akiyoshiensis Kobayashi & Hamada 1978 and are obscured by strong nodular ornament in adults. Due to this the subgenus is synonymised and Engel & Morris (1992) chose to place Br. strzeleckii within the subgenus Br. (Brachymetopus) M’Coy 1847.

Included Sub-species. Brachymetopus (Brachymetopus) strzeleckii strzeleckii M’Coy 1847, Brachymetopus (Brachymetopus) strzeleckii dunstani Mitchell 1918, Brachymetopus (Brachymetopus) strzeleckii akiyoshiensis Kobayashi & Hamada 1978.

Age and range. Late Tournaisian to mid Viséan, in Australia and Japan (Engel & Morris 1992).
1847  *Brachymetopus strzeleckii* M'Coy: 231, Pl.12 Figs. 1a, b

1876/77 *Brachymetopus strzeleckii* de Koninck: 352–353, Pl.24 Figs. 10a–c

1898  *Brachymetopus strzeleckii* de Koninck: 280–281, Pl.24 Figs. 10a–c

1903  *Brachymetopus strzeleckii* Reed: 193–196, Figs. 1–2

1918 *Brachymetopus strzeleckii* Mitchell: 483–486, Pl.53 Figs. 3–6

1969 *Brachymetopus strzeleckii* Hahn & Hahn: 36–37

1987 *Brachymetopus (Brachymetopella) strzeleckii strzeleckii* Gandl: 50

1992 *Brachymetopus (Brachymetopus) strzeleckii strzeleckii* Engel & Morris: 84–86, Pl. 3 Figs. 9–17, Text Figs. 9–11

*Type material.* CSME10583 on 1803 (external cephalon lacking genal spines).

*Paratype material.* CSME10577 on 1718 (external cephalon), CSME10585b (external cephalon), CSM(C) on 1747 (external cephalon), CSME10579 on 1718 (internal cephalon), CSME10581 on 1686 (internal cephalon), CSME10585a on 432 (internal cephalon), CSM(A) on 1686 (internal cephalon), CSM(D) on 1747 (internal cephalon), CSME10580b on 1747 (external pygidium), CSME10584 on 1803 (external pygidium), CSME10578 on 1718 (internal pygidium), CSME10580a on 1718 (internal pygidium), CSME10582 on 686 (internal pygidium), CSM(B) on 1686 (internal pygidium).

*Locality.* DV1.
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Remarks. Brachymetopus (Brachymetopus) strzeleckii strzeleckii M’Coy 1847 differs from the other Australian subspecies, Br.(Brachymetopus) strzeleckii dunstani Mitchell 1918, by its arrangement of the cephalic nodose ornament. The ornament of Br. (Brachymetopus) strzeleckii strzeleckii is much smaller but much less sparse from Br. (Brachymetopus) strzeleckii dunstani (see below for a discussion of separating the species into two subspecies).

6.12.1(a).ii(b) Brachymetopus (Brachymetopus) strzeleckii dunstani Mitchell 1918

1918 Brachymetopus dunstani Mitchell: 486–488, Pl. 49 Fig. 15, Pl. 52 Fig. 2
1969 Brachymetopus dunstani Hahn & Hahn: 20–21
1987 Brachymetopus (Brachymetopella) strzeleckii? dunstani Gandl: 50
1992 Brachymetopus (Brachymetopus) strzeleckii dunstani Engel & Morris: 86–87, Pl. 3 Figs. 7–8, Text Fig. 14

Type material. QGSF1031C (external cephalon lacking genal spines, damaged occipital ring).

Locality. QGS L3004.

Remarks. Only one external cephalon has been allocated to this subspecies. The cephalon is reasonably well preserved but it lacks genal spines and has a damaged occipital ring. The specimen resembles the species *Brachymetopus (Brachymetopus) strzeleckii strzeleckii* M’Coy 1847. They both have a long glabella (in comparison to other species of the subgenus, such as *Br. (Brachymetopus) maccoyi*, small eyes and a rounded anterior cephalic margin. Engel & Morris (1992) created the new subspecies based on the differences in cephalic nodular ornament from other *Br. (Brachymetopus) strzeleckii* specimens. *Brachymetopus (Brachymetopus) strzeleckii dunstani* has fewer larger nodes on the librigena, fixigena and preglabellar fields, and lacks two large nodes in the midline of the glabella. Due to the difference in ornament the specimen has been left as separate subspecies.

6.12.1.1(b) Subgenus *Brachymetopus (Spinimetopus)* Hahn & Hahn 1985

1985  *Brachymetopus (Spinimetopus)* Hahn & Hahn: 463
1991  *Brachymetopus (Spinimetopus)* Engel & Morris: 129

Type species. *Brachymetopus coignouides* Hahn & Hahn 1981.
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Remarks. Brachymetopus (Spinimetopus) is different from other Brachymetopus subgenera in that it is the only subgenus to possess cephalic marginal spines. This makes the assignment of species into this subgenus relatively easy, and at this time there are only two known species.


Age and range. Tournaisian to Viséan, in Germany and Australia (Engel & Morris 1991).

6.12.1.1(b).i Brachymetopus (Spinimetopus) subtilis Engel & Morris 1991

Figure 6.3

1991 Brachymetopus (Spinimetopus) subtilis Engel & Morris: 129–130, Pl. 2 Figs. 5–7, Text Fig. 5

Type material. AMF81910a (external cephalon lacking eyes).

Paratype material. From FB: AMF81910b–d (external cephalon), AMF81910e (internal librigena). From ST: QMF15180a/b (external/internal cephalon).
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Locality. Type - FB. Other - ST.


Remarks. Brachymetopus (Spinimetopus) subtilis resembles other species of Br. (Brachymetopus) by a smooth band inside the cephalic margin and shape of the glabella. Brachymetopus (Spinimetopus) subtilis differs from the other species of Br. (Spinimetopus), Br. (Spinimetopus) coignouides by the rounded glabella outline, the longer genal spines, the smooth band inside the cephalic margin and the large spines around the glabella.

6.12.1.2 Genus Australosutura Campbell & Goldring 1960

1960 Australosutura Campbell & Goldring: 229–230
1969 Australosutura Hahn & Hahn: 14
1992 Australosutura Engel & Morris: 88

Type species. Cordania gardneri Mitchell 1922.

Emended diagnosis. Glabella nodose, subcylindrical with prominent basal lobes; S1 and S2 distinct, anteriorly placed. Preglabellar field very steep close to the glabella, with nodular ornamentation; Eyes short, sublunate, strongly convex.
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Genal spines long with median channel; Facial suture curves strongly away from eye; $\beta$ and $\omega$ considerable distance from dorsal furrow; anterior and posterior fixigenae long and wide; 9 thoracic segments; up to 16 axial rings, 9 pleural ribs; segment bands with a row of nodes.

Remarks. The diagnosis in Engel & Morris (1992) describes in detail ornamentation of the cephalon. The above diagnosis is a shorter summarised version. Australosutura was first erected by Campbell & Goldring 1960 to encompass material described by Mitchell (1922; 1924), and newly found material from Argentina. Since then a number of species have been assigned to this genus, from North America, Europe and China (Brezinski 1998; Yuan & Xiang 1998). Specimens appear to be from the Tournaisian to Viséan, however, ages of both the Argentinian and Australian material are not certain (Amos et al. 1960). Australosutura is most similar to the genera Cordania and Brachymetopus but differs from Cordania by having a longer glabella, with a shorter, steeper pre-glabella field, as well as a much longer pygidium. Australosutura differs from Brachymetopus in that it has facial sutures, and a longer glabella (Amos et al. 1960).

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*Age and range*. Famennian to Viséan in Australia, North America, South America and China (Amos *et al.* 1960, Ormiston 1966, Yuan & Xiang 1998).

### 6.12.1.2.i *Australosutura campbelli* Engel & Morris 1992

#### Figure 6.3

1963 *Australosutura* sp. Campbell & Engel: 110–112, Pl. 3 Figs. 3–9

1992 *Australosutura campbelli* Engel & Morris: 88–89, Pl. 3 Figs. 1–6, Text Figs. 15–16

*Holotype material*. AMF84389a (external cranidium).

*Paratype material*. From NU L740: AMF84389b (internal cranidium), AMF84390 (external librigena). From NU L366: AMF84391 (external librigena), AMF85454 (external pygidium), AMF85456 (external pygidium).

*Locality*. Type - NU L740. Other - NU L366.
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Diagram. Very wide preglabellar field; short glabella, only half the cephalic
length; both the glabella and preglabellar field are highly nodose; anterior
border is upturned with two strong terrace lines; eyes are small, narrow and
steep; short pointed genal spines. Pygidium with 10–12 axial rings; rings with
large central node, smaller nodes at sides; pygidium highly nodose.

Remarks. A diagnosis is not provided in Engel & Morris (1992), only a
morphological description. The above serves as a diagnosis for the species.

6.12.1.2.ii Australosutura gardneri (Mitchell 1922)

1922 Cordania gardneri Mitchell: 535–540, Pl. 54
1924 Cordania gardneri Mitchell: 53, Pl.10 Fig. 15
1960 Australosutura gardneri Campbell & Goldring: 229–230, Pl. 40

Lectotype material. AMF26974 (internal cephalon).

Paralectotype material. AMF27345 (internal cephalon).

Locality. Brambles Farm, Myall Lakes, Eurenderee, Gloucester NSW (Amos et al.
1960).
Emended diagnosis. Cephalon and glabella strongly inflated; glabella sub-cylindrical with prominent subtriangular basal lobes and deeply incised S1 furrows; S2 present; preglabellar field short and high; border furrow very broad, concave and pitted preceded by a short convex border; strongly convex eyes; long genal spines; facial suture curves strongly away from the eye; surface of librigena, fixigena, preglabellar field, glabella and occipital ring with numerous tubercles. 9 thoracic segments. Pygidium with 15 axial rings, 8 or more pleural ribs; rings strongly arched and tuberculate, with a prominent median row of tubercles; ribs also tuberculate.

Remarks. The original diagnosis of Australosutura gardneri (Mitchell 1922) is also the same for the genus, but unfortunately only the lectotype and one paralectotype specimen could be located in the Australian Museum where the specimens are held, which are both internal cephalic molds. According to Amos et al. (1960) a number of the figured specimens are said to have been lost in a fire. Amos et al. (1960) also do not provide the corresponding Australian Museum numbers to the numbers on the plate. It is difficult to use the figured specimens in Amos et al. (1960) as the plates do not provide much detail. The diagnosis above has been emended to reflect the specimens now available for classification. Nevertheless, Australosutura gardneri can be distinguished from the other Australian species A. campbelli in having a shorter glabellar field and a strongly convex glabella (Engel & Morris 1992).
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6.13 Superfamily PROETOIDEA Hawle & Corda 1847

6.14 Family PROETIDAE Salter 1864

6.14.1 Subfamily PROETINAE Salter 1864

6.14.1.1 Genus Pudoproetus Hessler 1963


Type species. Proetus fernglenensis Weller 1909.


Remarks. Pudoproetus was first assigned as a subgenus to Proetus by Hessler (1963). The subgenus classification was based on North American taxa of Mississippian age that shared characteristics with Devonian proetids (Feist & Petersen 1995; Hessler 1963). Hahn & Brauckmann (1988) elevated it into a monotypic genus within the Bollandiinae Hahn & Brauckmann 1988 due to it being much younger age than other proetine taxa. This classification is questioned by Feist & Petersen (1995) due to a typical proetine glabella outline, an absence of a frontal lobe and the presence of 10 thoracic segments. They also noted that the absence of taxa between the last proetine and Pudoproetus is not cause to remove it from the Proetinae subfamily entirely (Feist & Petersen 1995). The original designation of Pudoproetus in the family Proetidae is upheld herein.
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Age and range. Late Devonian to Viséan, in North America, China, Europe, Australia and Russia (Hessler 1963; Feist & Petersen 1995; Owens 1994).

6.14.1.1.i *Pudoproetus woodwardi* (Etheridge Jr. 1892b)

1892 *Phillipsia woodwardi* Etheridge Jr. in Jack & Etheridge: 215, Pl. 7 Fig. 11
1996 *Pudoproetus woodwardi* Engel & Morris: 124–125, Pl. 2 Fig. 20
**Type material.** QGSF966 (internal cranidium lacking palpebral lobes and most of occipital ring).

**Locality.** Not known, possibly from Early to Mid Tournaisian (Engel & Morris 1996).

**Diagnosis.** See Engel & Morris (1996).

**Remarks.** One internal cranidium originally classified as *Phillipsia woodwardi* by Etheridge (1892b) was re-diagnosed by Engel & Morris (1996) as *Pudoproetus*. The cranidium was found with specimens of *Conophillipsia* Roberts 1963, but as Mitchell (1918) remarked was not the same genus due to differences in length/width ratios of the glabella to cephalon (Engel & Morris 1996). The cranidium does look similar to other species of *Pudoproetus*, such as *P. priscus* in dorsal view, but appears to have a wider and convex anterior border as opposed to the narrow almost concave border of *P. priscus*. The cranidium also has a similar glabella to the other Australian *Pudoproetus* species, such as *P. cambrertus*, but it does not overhang the anterior margin. The classification of *P. woodwardi* (Etheridge Jr. 1892b) remains provisional due to the lack of specimens.

**6.14.1.1.ii Pudoproetus cambrertus** (Jell 1977)
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1977  

*Megaproetus cambretus* Jell: 173–175, Pl. 1 Figs. 1–7

**Type material.** ANU36849 (enrolled external dorsal shield).

**Paratype material.** ANU36850 (enrolled external dorsal shield).

**Locality.** Mundubbera Sandstone in Queensland, from the Late Viséan (Jell 1977).

**Emended diagnosis.** Highly vaulted cephalon; glabella overhangs anterior margin, S1 well incised, widest at L1; deep preglabellar furrow; terrace lines on cephalic border; anterior facial sutures almost parallel to glabella; eye socle high; wide eye platform, slightly concave. Occipital ring with median node; genal spines absent. 9 thoracic segments. Pygidium with 5 clearly defined axial rings, up to 3 indistinct; 6–7 pleural ribs; pygidial border, no border furrow (defined by change in slope); broad pygidial axis

**Remarks.** Owens (1994) states that differences noted by Jell between *P. (Megaproetus)* and *Pudoproetus* could be variable between species and, so did not distinguish *Megaproetus* as a new subgenus. Owens (1994) designated *P. (Megaproetus)* a junior synonym of *Pudoproetus*, which has been retained here.

The above diagnosis is an abbreviated version of the original diagnosis of Jell (1977).
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6.14.2 Subfamily CRASSITPROETINAE Osmolska 1970

6.14.2.1 Genus Conophillipsia Roberts 1963

1963 Conophillipsia Roberts: 25
1967 Conophillipsia Hahn & Hahn: 327
1970 Conophillipsia Osmolska: 13–25
1972 Conophillipsia Hahn & Hahn: 382
1978 Conophillipsia Kobayashi and Tachibana: 262
1984 Conophillipsia Engel & Morris: 23–64
1990 Conophillipsia Schraut: 36
1993 Conophillipsia Hahn & Hahn: 16–21, Tab. 2–3
1994 Conophillipsia Owens: 214–216
1996 Conophillipsia Schraut: 21

Type species. Conophillipsia brevicaudata Roberts 1963


Remarks. The genus Conophillipsia has posed a taxonomic problem since it was first diagnosed. It appears to have a proetid-like cephalon with a phillipsiid-like pygidium (Owens 1994). Various authors have suggested different subfamily and family placement for the genus. Those arguing for a proetid placement do
so due to the strongly similar cephalic features, including a broad flat tapering glabella, impressed L1, occipital ring with distinct lateral lobes, and, though not a cephalic feature, 10 thoracic segments (Owens 1994; Schraut 1996; Osmolska 1970). Those arguing for a placement within the Phillipsiidae do so due to the multi-segmented pygidia, and the much later occurrence of Conophillipsia (Tournaisian to Late Viséan) than other similar proetids (e.g., Mid-Devonian Crassiproetus) (Hahn & Hahn 1993; Hahn & Brauckmann 1993; Engel & Morris 1997). Conophillipsia has been placed within Proetidae here as it strongly resembles the genera Monodechenella Stumm 1953 and Crassiproetus Stumm 1953, two proetids with similar cephalic features, as well as the multi-segmented pygidium of Crassiproetus (Owens 1994; Osmolska 1970). Its placement within Phillipsiidae based on biostratigraphic occurrence is also rejected (see Owens 1994 for a discussion of pseudo-extinctions in genera of proetids in the Late Devonian).

Conophillipsia is one of the most abundant genera of Carboniferous trilobites in Australia and is also found in Japan and China. The Australian species are all large (compared to the other Carboniferous trilobites from Australia), many have a nodose ornament of some description, and similar glabellar shapes. Differences are unique, Conophillipsia subtriangularis Engel & Morris 1984 and Conophillipsia speciosa Engel & Morris 1984 both have a triangular pygidial profile, Conophillipsia grandis (Etheridge Jr. 1892a) and Conophillipsia subquadrata Engel & Morris 1984 have very convex profiles compared to the rest, and C.
grandis, Conophillipsia subquadrata Engel & Morris 1984 and Conophillipsia morganensis (Mitchell 1918) all have a convex pygidial border while the other species have slightly concave pygidial borders.


Age and range. Early Tournaisian to Late Viséan in Australia, Russia, Japan and Austria (Engel & Morris 1984; Schraut 1996).

6.14.2.1.i Conophillipsia breviceps (Mitchell 1918)

Figure 6.3

1892a Phillipsia sp. indet.(b) Etheridge Jr.: 129, Pl. 22 Fig. 14
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1918  *Phillipsia dungogensis* Mitchell: 474, Pl. 47 Figs. 6–7

1918  *Phillipsia breviceps* Mitchell: 449, Pl. 46, Figs. 11–12 Pl. 51, Figs. 2–3

1963  *Conophilipisa brevicaudata* Roberts: 25, Pl. 6 Figs. 13–20

1965  *P. cf. Phillipsia dungogensis* Roberts: 56

1965  *Conophilipisa brevicaudata* Roberts: 57

1967  *Conophilipisa brevicaudata* Hahn & Hahn: 327, Text Fig. 2e

1969  *Proetus (Pudoproetus) breviceps* Hahn & Hahn: 60

1970  *Conophilipisa brevicaudata* Osmolska: 26, Tab. 1

1972  *Phillipsia? (Phillipsia?) dungogensis* Hahn & Hahn: 392

1972  *Conophilipisa brevicaudata* Hahn & Hahn: 382

1984  *Conophilipisa breviceps breviceps* Engel & Morris: 31–35, Figs. 4–5

1984  *Conophilipisa breviceps dungogensis* Engel & Morris: 35–36, Figs. 6–7

**Holotype material.** AMF28383 (part external cranidium).

**Paratype material.** Unknown locality: AMF28371 (internal pygidium). From NU L372: AMF35851a/b (external/internal pygidium).

**Locality.** Type - unknown. Others - NU L372.

**Emended diagnosis.** Dorsal shield flat with a semicircular outline; glabella tapers anteriorly; S1 very distinct, S2 less so. Anterior border concave, glabella just
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touches border furrow; genal spines short. Pygidial border concave; pygidium with 11+ pleural ribs, 12+ axial rings.

Remarks. Engel & Morris (1984) separate Conophillipsia breviceps into two sub-species based on the larger number of ribs and rings in C. breviceps dungogensis. However, there are few preserved cranial features for this second sub-species, and the pygidia are almost identical. It is also apparent that not all rings in many of the C. breviceps breviceps specimens are preserved, so they may in fact consist of more. The specimens identified as C. breviceps dungogensis have therefore been synonymised with C. breviceps breviceps, removing the need for the subspecies name. The pygidial axial ring and rib pair counts in the above emended diagnosis has been changed to reflect this.

6.14.2.1.ii Conophillipsia speciosa Engel & Morris 1984

1984 Conophillipsia speciosa Engel & Morris: 41–47, Figs. 12–13

Holotype material. AMF80538 (internal cranidium and partial external glabella and anterior border).

Paratype material. From NU L427: AMF80523 (internal pygidium), AMF80524 (internal pygidium). From NU L894: AMF80525a/b (external/internal pygidium), AMF80526 (external pygidium), AMF80527 (external pygidium),
AMF80528 (partial external pygidium), AMF80529 (external pygidium), AMF80530 (external librigena), AMF80531a/b (external/internal pygidium), AMF80532 (external pygidium), AMF80533 (internal pygidium), AMF80534 (internal pygidium), AMF80535 (internal pygidium), AMF80536a/b (external/internal pygidium), AMF80537 (external hypostome), AMF80539 (external cranidium), AMF80540 (internal librigena), AMF80541a/b (external/internal cranidium), AMF80542 (external cranidium), AMF80543 (external cranidium), AMF80544 (internal librigena), AMF80545 (internal cranidium), AMF80546 (internal pygidium), AMF80547 (internal pygidium), AMF80549 (partial external cranidium), AMF80550 (external cranidium), AMF80551 (internal cranidium), AMF80552 (internal cranidium), AMF80553 (partial external pygidium), AMF80554 (external pygidium), AMF80555 (internal pygidium), AMF80556 (internal pygidium), AMF80557a/b (external/internal cranidium), AMF80558 (external cranidium), AMF80559 (external cranidium), AMF80560 (external cranidium), AMF80561 (external cranidium), AMF80562 (external cranidium), AMF80563 (external cranidium), AMF80564 (external cranidium), AMF80565 (external pygidium), AMF80566 (partial external cranidium). From NU L652: AMF80548 (partial external pygidium), AMF80567 (external cranidium), AMF80568 (external pygidium), AMF80569a/b (external/internal pygidium), AMF80570a/b (external/internal pygidium), AMF80571a/b (external/internal pygidium).

 Locality. Type - NU L894. Others - NU L427, NU L652.
**Emended diagnosis.** Dorsal shield flat, coarsely punctate with strong nodular ornament; glabellar length equal to width, extends over preglabellar furrow, but does not touch anterior border. Pygidial axis triangular in section, created by median node down axis, flanked by smaller nodes; distinct extra axial furrows create distinct lateral lobes; pygidium with 12–15 axial rings, 11–13 pleural ribs.

**Remarks.** The above diagnosis was emended to change glabellar length. Moreover, the glabella does not touch the anterior border in available specimens. There is also a furrow running laterally on either side of the pygidial axis, which created the lateral lobes described by Engel & Morris (1984). The size of the eyes is also questioned as they have not been preserved in any of the available specimens. *Conophillipsia speciosa* is similar to *C. subtriangularis* other than the nodose ornament and a smaller number or rings and ribs. *Conophillipsia speciosa* also resembles *C. decisegmenta* other than its small, has relatively high eyes and a triangular pygidial axis (Engel & Morris 1984).

6.14.2.1.iii *Conophillipsia subtriangularis* Engel & Morris 1984

1847  *Phillipsia* cf. *gemmulifera* McCoy: 231
1984  *Conophillipsia subtriangularis* Engel & Morris: 39–41, Figs. 10–11

*Holotype material.* AMF80518 (internal cranidium).
Paratype material. From NU L353: AMF80519 (internal pygidium), AMF80520 (external pygidium), AMF80522 (external pygidium). From MUM: AMF80521 (internal pygidium). From DV: CSMF10586a/b (internal/external pygidium).

Locality. Type - NU L353. Others - DV, MUM.

Emended diagnosis. Glabella tapers anteriorly; slightly incised at $\gamma$; S1 very distinct, S2 less distinct; comparatively convex (to other Conophillipsia species). Triangularly transverse pygidium; concave pygidial border; pygidium with 12+ pleural ribs and 14+ axial rings.

Remarks. There are few specimens of Conophillipsia subtriangularis available for comparison, but they seem to closely resemble Conophillipsia speciosa. Some of the distinguishing features between the two species noted by Engel & Morris (1984) appear to be dubious, for instance there are a greater number of rings and ribs in C. subtriangularis. The other distinguishing characters between C. subtriangularis and C. speciosa seem more valid, that is the highly nodose ornament of C. speciosa, the different convexities of the pygidial borders and the more convex axis of the glabella in C. subtriangularis. Given these differences the species will remain separate.

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1918 *Phillipsia woodwardi* Mitchell: Pl. 51 Fig. 13, Pl. 52 Fig. 2

1918 *Phillipsia woodwardi?* Mitchell: Pl. 51 Fig. 14, Pl. 52 Fig. 1

1984 *Conophillipisa subquadrata* Engel & Morris: 50–53, Figs. 16–17

**Holotype material.** AMF80575 (external cranidium).

**Paratype material.** From NSW 58–12: AMF80574 (partial internal pygidium), AMF80576a/b (external/internal pygidium), AMF80577a/b (external/internal pygidium). From NU L39: AMF80572 (external pygidium), AMF80573 (external pygidium), AMF80578 (internal pygidium), AMF80579 (internal librigena), AMF80580 (internal pygidium), AMF80581 (internal cranidium), AMF80582 (internal pygidium), AMF80583 (external pygidium), AMF80584 (internal pygidium), AMF80585 (internal pygidium), AMF80586 (internal pygidium), AMF80587 (partial internal thorax), AMF80588a/b (external/internal pygidium), AMF80589 (external pygidium), AMF80590a/b (external/internal pygidium), AMF80593 (external pygidium), AMF80594 (external pygidium), AMF80595 (internal pygidium), AMF80596 (external librigena), AMF80597 (internal pygidium), AMF80598 (external pygidium). From NSW 112–6: AMF80591 (internal pygidium), AMF80592 (internal pygidium). From QGS L3004: QGSF1017 (external cranidium), QGSF1031 (external pygidium), QMF2839 (external pygidium).
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Emended diagnosis. Rounded genal angles; glabellar length equal to width, moderately convex. Pygidial border convex; pygidium broadly parabolic, convex axis; pygidium with 13+ axial rings, 10–11 pleural ribs; ring furrows straight; extra axial furrow present creating lateral lobes on the axis.

Remarks. The diagnosis is emended to remove the length of the glabella, as where it reaches the anterior of the cephalon has not been preserved. An extra axial furrow can also be seen on the pygidium, which has been included in the emended diagnosis. Conophillipsia subquadrata appears to be most similar to Conophillipsia grandis (Etheridge Jr. 1892a) (see C. grandis remarks for a detailed comparison).

6.14.2.1.v Conophillipsia magna (Hahn & Hahn 1972)

1892a Phillipsia grandis Etheridge Jr.: 128, Pl. 21 Fig. 5
1892b Phillipsia sp. indet Etheridge Jr.: 215
1917 Phillipsia grandis Etheridge Jr.: 11, Pl. 3 Fig. 3
1918 Phillipsia grandis Mitchell: 463, Pl. 47 Fig. 2, Pl. 50 Figs. 1–3
1972 Linguaphillipsia? magna Hahn & Hahn: 369, 372
1984 Conophillipsia magna Engel & Morris: 36–39
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Holotype material. AMF35852 (part internal pygidium).

Paratype material. From NU L400: AMF80500a/b (external/internal pygidium). From CN: QGSF927 (external pygidium and external librigena).

Locality. Type - CN. Other - NU L400.

Emended diagnosis. Concave pygidial border; pygidium with 17+ axial rings, 15+ pleural ribs; pygidial axis rounded in section, with a shallow lateral furrow on either side, creating small lateral lobes.

Remarks. The diagnosis of Engel & Morris (1984) is emended. Axial ring count is 17 or above, but due to preservation it is unclear if there are exactly 19 as originally stated by Engel & Morris (1984). They also state that the species is moderately convex, though the specimens used for identification appear flat. There are also shallow lateral furrows on the axial region, creating the small lateral lobes mentioned by Engel & Morris (1984).

6.14.2.1.vi Conophillipsia grandis (Etheridge Jr 1892a)

1892 Phillipsia grandis Etheridge Jr.: 128, Text Fig. 5
1892a Griffithides sweeti Etheridge Jr.: 125
1892b Phillipsia woodwardi Jack and Etheridge Jr.: 215, Pl. 7 Fig. 13
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1892b *Phillipsia dubia* Jack and Etheridge Jr.: 214, Pl. 8 Fig. 6

1892b *Phillipsia? sp. indet. (grandis)* Jack and Etheridge Jr.: 215

1894 *Griffithides sweeti* Etheridge Jr.: 528, Pl. 39 Fig. 3

1918 *Phillipsia? robusta* Mitchell: 441, 451, Pl. 47 Figs. 1–8

1918 *Phillipsia grandis* Mitchell: 463, Pl. 47 Fig. 2, Pl. 50 Figs. 1–3

1918 *Phillipsia woodwardi* Mitchell: 465, Pl. 49 Figs. 1, 5–8

1918 *Griffithides sweeti* Mitchell: 479, Pl. 53 Figs. 1–2

1969 *Cyrtoproetus sweeti* Hahn & Hahn: 371

1970 *Linguaphillipsia grandis* Osmolska: 48, Tab. 1

1972 *Linguaphillipsia? grandis* Hahn & Hahn: 371

1972 *Conophillipsia woodwardi* Hahn & Hahn: 387

1984 *Conophillipsia grandis* Engel & Morris: 53–58

*Holotype material.* AMF35853 (internal pygidium).

*Locality.* Type - location unknown.

*Emended diagnosis.* Highly convex glabella which overhangs the anterior border furrow; glabellar width greater than length. 10 thoracic segments. Pygidium semi-elliptical and convex; pygidial axis of equal heights anteriorly to posteriorly; pygidial axial ring furrows undulating; pygidium with 11–12 pleural ribs; pygidial border convex.
Remarks. *Conophillipsia grandis* (Etheridge Jr. 1892a) closely resembles *C. subquadrata* in that they both have thin convex pygidal borders, a convex axis, sub-cylindrical shaped pygidia and a highly nodose glabella. They can be differentiated by the distinct shape of the cephalon of *C. grandis*, distinct S2 and S3 on *C. subquadrata*, and curving ribs of *C. subquadrata*. The diagnosis in Engel & Morris (1984) has been emended to include the thoracic segment count, and remove the shape of the genal angles, as preservation of the specimens do not allow this characteristic to be seen.

6.14.2.1.vii *Conophillipsia morganensis* (Mitchell 1918)

1918 *Phillipsia morganensis* Mitchell: 471, Pl. 49 Figs. 11–12, Pl. 51 Fig. 1
1969 *Cyrtoproetus morganensis* Hahn & Hahn: 56
1984 *Conophillipsia morganensis* Engel & Morris: 47

*Holotype material.* QGSF1000 (internal cranidium).

*Locality.* Type - QGS L3004.

*Emended diagnosis.* Glabella touches anterior border furrow; glabellar length slightly longer than width, gently convex. Pygidium outline parabolic, border convex; axis slopes posteriorly; pygidium with 12+ axial rings, ring furrows
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straight or gently curving posteriorly; 9+ pygidial pleural ribs; low rounded
nodular ornament.

Remarks. Originally *Conophillipsia morganensis* was described from a single
specimen QGSF1000 (Engel & Morris 1984). A number of other specimens were
assigned to *C. ?morganensis* as though the specimens were remarkably similar to
the type specimen of *C. morganensis*, they had more axial rings and pleural ribs
(Engel & Morris 1984). The pygidial features the original type specimen are not
fully preserved.

6.14.3 Subfamily ARCHEGONINAE Hahn & Brauckmann 1984

6.14.3.1 Genus *Xenoboloides* Brauckmann 1987

1987 *Xenoboloides* Brauckmann: 106–107, Text Figs. 3a,b

*Type species. Xenoboloides peregrina* (Engel & Morris 1980).

*Emended diagnosis.* Glabella tapering anteriorly, slightly incised at \( \gamma \); \( \varepsilon - \zeta \) is
parallel to dorsal furrow; S1 distinct; anterior border wide and flat; eyes and
palpebral lobes large, posteriorly placed. Pygidial border moderately wide.

Remarks. Engel & Morris (1980) initially described specimens of *Xenoboloides
peregrina* as belonging to the genus *Liobole* Richter & Richter 1949. Brauckmann
(1987) erected a new monotypic genus for the Australian specimens due to a lack of an “occipital solution” (a characteristic of Liobole, described as a special differentiation of the occipital region of the glabella in Hahn & Hahn 2005; Groning 1986), and an inflated area between the glabella furrows S1. Brauckmann (1987) states that the new genus is similar to Liobole and Philliboloides Gandl 1969 other than these features, as well as a lack of a very wide pygidial border (found in Philliboloides). Australian specimens show very little distinguishing characteristics due to poor preservation. Brauckmann (1987) created a new genus due to a lack of characters, rather than distinguishing ones. The genus Xenoboloides may become obsolete if new better preserved specimens are found. The above diagnosis has been emended to include more definitive characters for the new genus.

*Species included.* Xenoboloides peregrina (Engel & Morris 1980).

*Age and range.* Mid Viséan, in Australia (Engel & Morris 1980).

6.14.3.1.i *Xenoboloides peregrina* (Engel & Morris 1980)

**Figure 6.3**

1980 *Liobole peregrina* Engel & Morris: 268–274, Pl. 1 Figs. 1–12, Text Figs. 2–6

1987 *Xenoboloides peregrina* Brauckmann: 106–107, Text Figs. 3a–b
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*Type material.* AMF80812 (internal cranidium).

*Paratype material.* From NU L492: AMF80785 (internal pygidium), AMF80786 (internal pygidium), AMF80788 (external pygidium), AMF80791 (internal pygidium), AMF80793 (external pygidium), AMF80794 (external pygidium), AMF80795 (internal pygidium), AMF80796 (internal cranidium), AMF80806 (internal cranidium), AMF80811 (external cranidium), AMF80813 (partial internal pygidium), AMF80817 (internal pygidium), AMF80818 (partial external pygidium), AMF80819 (internal pygidium), AMF80820 (internal cranidium), AMF80823 (external librigena), AMF80827 (partial internal pygidium), AMF80830 (internal pygidium), AMF80831 (internal pygidium), AMF80832 (external pygidium), AMF80833 (partial external pygidium), AMF80834 (internal cranidium), SMF28830, SMF28831, SMF28832, SMF28833. From NU L522: AMF80784 (internal librigena), AMF80787 (external pygidium), AMF80789 (external pygidium), AMF80790 (external pygidium), AMF80792 (external pygidium), AMF80797 (external pygidium), AMF80798 (external pygidium), AMF80799 (internal pygidium), AMF80800 (internal pygidium), AMF80801 (internal pygidium), AMF80802 (internal pygidium), AMF80803 (internal pygidium), AMF80804 (internal cranidium), AMF80805 (external pygidium), AMF80807 (internal pygidium), AMF80808 (internal pygidium), AMF80809 (internal thorax), AMF80810 (internal cranidium), AMF80816 (internal cranidium), AMF80821 (internal cranidium), AMF80822 (internal pygidium), ...
librigena), AMF80824 (external cranidium), AMF80826 (partial external cranidium), AMF80828 (partial external hypostome), AMF80829 (partial internal hypostome), SMF28824, SMF28825, SMF28826, SMF28827, SMF28828, SMF28829. From NU L412: AMF80814 (enrolled internal dorsal shield), AMF80815 (external pygidium). From NU L8: AMF80825 (internal pygidium).

Localities. Type - NU L492. Others - NU L522, NU L412, NU L8.

Emended diagnosis. As for genus.

6.14.4 Subfamily BOLLANDIINAE Hahn & Brauckmann 1988

6.14.4.1 Genus Bollandia Reed 1943

1943 Bollandia Reed: 62–63.

Type species. Asaphus globiceps Phillips 1836.

Remarks. The monotypic subgenus *Capricornia* was erected by Engel & Morris (1996) for the genus *Bollandia* Reed, 1943. Ozdikman (2009) stated that *Bollandia (Capricornia)* is a junior homonym of *Capricornia* Obraztsov 1960, and proposed a new subgenus name *Bollandia (Engelmorriisia)* (Ozdikman 2009). However, the subgenus *B. (Capricornia)* is synonymized within *Bollandia*, *B. (Capricornia) queenslandia*, thereby remaining in the genus *Bollandia*. The synonymy is justified as neither of the defining characteristics, namely four glabella lobes, and a highly nodular ornament on the glabella, appear in the sole species *B. (Capricornia) queenslandia*.


Age and range. Tournaisian to Viséan in Ireland, Great Britain, Germany, Poland, Central Asia and Australia (Osmolska 1970; Engel & Morris 1996).
6.14.4.1.i *Bollandia queenslandica* (Engel & Morris 1996)

**Figure 6.4**

1996  *Bollandia (Capricornia) queenslandica* Engel & Morris: 126–127, Pl. 3 Figs. 20–27, Text Fig. 4

*Holotype material.* AMF96996 (external cranidium).

*Paratype material.* AMF96997 (partial internal cephalon), AMF96998 (internal cranidium), AMF96999 (internal cranidium), AMF97000a/b (external/internal pygidium), AMF97001 (internal pygidium), AMF97002 (internal pygidium).

*Locality:* NU L1047.

*Emended diagnosis.* Glabella highly convex, parallel sided; median anterior border inflated; glabella touches border; S1–S3 developed (possibly S4?); L1–L3 developed (possibly L4?); S1 and S2 deep, almost parallel to one another; L1 short; S3 (S4?) short. Pygidium with 11 axial rings, 5–6 pleural ribs; nodular ornament on pygidal axis.

*Remarks.* The species is kept within the genus *Bollandia* Reed 1943 due to a highly arched glabella, a vertical anterior border, and strongly arched pygidium (based on the diagnosis by Hahn *et al.* 1984).
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FIGURE 6.4. Representative Australian genera of the Order Proetida. Australokaskia corrugata, 1. external cephalon Paratype, AMF90256, dorsal view, 11.5x, 2. external pygidium Paratype, AMF90266, dorsal view, 12x, 3. external librigena Paratype, AMF90249a, dorsal view, 8.1x. Bollandia queenslandica, 4. external cephalon Holotype, AMF96996, dorsal view, 16.8x. 5. external pygidium Paratype, 97000a, dorsal view, 8x. Malchi magnificus, 6. external cranidium Holotype, AMF90331a(1), lateral view, 11.7x, 7. external cranidium Holotype, AMF90331a(1), dorsal view, 9.1x, 8. external pygidium and part thorax Holotype, AMF90331a (2), dorsal view, 4.6x. Planokaskia gibsoni, 9. external cephalon Holotype, AMF90314a, dorsal view, 8.8x, 10. external pygidium Paratype, AMF90321a, dorsal view, 9x, 11. external librigena Paratype, AMF90322, dorsal view, 12.9x.

6.14.5 Subfamily DITOMOPYGINAE

6.14.5.1 Genus Australokaskia Engel & Morris 1994

1994 Australokaskia Engel & Morris: 82–83

1995 Australokaskia Engel & Morris: 194

Type species. Australokaskia (Australokaskia) corrugata Engel & Morris 1994.

Emended diagnosis. Cephalic margin up to 10 terrace lines; glabella steep, constricted at γ, rather flat to strongly convex; eyes large. Pygidium with up to 12 axial rings, 8 pleural ribs; wide pygidial border; ornament of concentric ridges.

Remarks. Engel & Morris (1994; 1995) described a large number of specimens from the Viséan of Australia as a new genus, Australokaskia. The genus is similar to both Witryides Hahn & Brauckmann 1986 and Kaskia Weller 1936 (Engel & Morris 1994). Australokaskia is distinct in that it has a convex dorsal shield (at
varying convexities), upwards of 10 terrace lines on a distinct cephalic border, glabella which are often highly convex and expanding anteriorly and pygidia which always have wide borders.

The genus was originally divided into three subgenera, *Australokaskia* (*Australokaskia*), *Australokaskia* (*Longilobus*) and *Australokaskia* (*Planilobus*), none of which are retained herein. The subgenera were erected on the premise of a difference in shape of the basal lobes (L1), and their anterior position in relation to γ (Engel & Morris 1994). The diagnoses for *Australokaskia* (*Longilobus*) Engel & Morris 1995 and *Australokaskia* (*Planilobus*) Engel & Morris 1995 indicate relatively long basal lobes exsagitally, almost extending to γ (Engel & Morris 1995 pp. 194, 199), in contrast to the moderately inflated basal lobes in *A.* (*Longilobus*), and flat basal lobes *A.* (*Planilobus*). L1 convexity differs in each of the diagnoses. Specimens diagnosed under both *A.* (*Australokaskia*) and *A.* (*Longilobus*) show no difference in either length or shape. The basal lobe length and shape used by Engel & Morris (1994) to define the subgenera is not significant enough to establish new subgenera. Due to these factors the subgenera have been synonymised within *Australokaskia*.

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noorooensis (Engel & Morris 1995), Australokaskaia constricta (Engel & Morris 1995), Australokaskaia soldevilae (Hahn et al. 1996)

Age and range. Upper Tournaisian to Viséan, in Australia, Spain and Belgium (Engel & Morris 1994; 1995; Hahn et al. 1996).

6.14.5.1.i Australokaskaia corrugata (Engel & Morris 1994)

Figure 6.4

1994 Australokaskaia (Australokaskaia) corrugata Engel & Morris: 82–84, Pl. 1 Figs. 1–9

Holotype material. AMF90247a/b (external cranidium/librigena).

Paratype material. From NU L484: AMF90248 (internal cephalon and part thorax), AMF90249 (external dorsal shield), AMF90250 (external librigena), AMF90251 (external librigena), AMF90252 (external pygidium), AMF90253 (external pygidium), AMF90254 (internal pygidium). From NU L890: AMF90255a/b (internal cranidium/pygidium), AMF90256 (external cranidium), AMF90257 (partial external cephalon), AMF90258 (internal cranidium), AMF90259 (external pygidium), AMF90260 (external pygidium), AMF90261 (internal librigena), AMF90262 (internal librigena), AMF90263 (external pygidium), AMF90264 (external pygidium), AMF90265 (external
pygidium), AMF90266 (external pygidium), AMF90267 (external pygidium), AMF90268 (external pygidium), AMF90269 (internal pygidium), AMF90270 (internal pygidium), AMF90271 (internal pygidium), AMF90272 (internal pygidium), AMF90273 (internal pygidium). From NU L353: AMF90274 (internal pygidium).

Locality. Type - NU L484. Other - NU L890, NU L353.

Emended diagnosis. Glabella not reaching anterior margin, separated by very narrow furrow; anterior border with terrace lines; glabella widest at $\delta$; L1 small, rounded; S2 & S3 distinct but short; $\beta$ – $\beta$ wider than $\delta$ – $\delta$; eyes long, moderately wide; lateral borders inclined steeply inwards; Short genal spines. Pygidium with 11 axial rings, 7 pleural ribs; wide pygidial border with distinct border furrow.

Remarks. Two characteristics of the original diagnosis (Engel & Morris 1994) are not visible on the external molds. These include an antennal pore, and a detailed description of nodular ornament on the pygidial rings and ribs. They are not included in the emended diagnosis.

6.14.5.1.ii Australokaska collina (Engel & Morris 1994)
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1994 Australokaska (Australokaska) collina Engel & Morris: 86–88, Pl. 2 Figs. 1–19

Holotype material. AMF90295 (external dorsal shield).

Paratype material. AMF90296a/b (external/ internal dorsal shield), AMF90297 (internal dorsal shield), AMF90298 (external cranidium), AMF90299 (external librigena and cranidium), AMF90300 (external cranidium), AMF90301 (internal cranidium), AMF90302 (internal cranidium and thorax), AMF90303 (partial internal cranidium), AMF90304 (internal cranidium), AMF90305 (external cranidium), AMF90306a/b (external glabella, hypostome, librigena and pygidium), AMF90307a/b (external/ internal dorsal shield), AMF90308 (external pygidium), AMF90309 (external pygidium), AMF90310 (external hypostome), AMF90311 (external pygidium), AMF90312 (internal pygidium), AMF90313 (internal pygidium).

Locality. NU L8.

Emended diagnosis. Glabella reaches anterior margin, expands anteriorly, widest at β; S1 distinct, L1 small, rounded; S2 and S3 distinct but short. Eyes long; lateral border flat, with marginal terrace lines; genal angles pointed to slightly rounded. Pygidium with 12 axial rings, 8 pleural ribs; wide pygidial border with distinct furrow; 9 thoracic segments.
Remarks. Engel & Morris (1994) describe the pygidium as having rows of very small nodes on the rings and ribs. These structures are not visible on external molds. The diagnosis has been emended to omit this characteristic.

6.14.5.1.iii Australokaska coulteri (Mitchell 1918)

1918  
Phillipsia coulteri Mitchell: 448–449, Pl. 46 Figs. 6–10

1984  
Paladin (Kaskia) cf. arduennensis Engel & Morris: 33

1986  
Paladin (Kaskia) cf. arduennensis Hahn et al.: 99

1994  
Australokaska (Australokaska) coulteri Engel & Morris: 84–86, Pl. 1 Figs. 10–23

Holotype material. AMF28627 (internal dorsal shield).

Paratype material. From NU L456: AMF85469 (internal cranidium), AMF85473 (partial librigena and partial external pygidium), AMF85474 (internal cranidium), AMF85476 (internal librigena), AMF85481 (internal pygidium), AMF90275 (external cranidium), AMF90276a/b (external/internal cephalon), AMF90277 (external cranidium), AMF90278 (internal cranidium), AMF90279 (internal cranidium), AMF90280a/b (external/internal cranidium, librigena and pygidium), AMF90281 (internal librigena), AMF90282 (external pygidium), AMF90283 (external pygidium), AMF90284a/b (external/internal pygidium),
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AMF90285 (internal pygidium), AMF90286 (external hypostome), From NU L359: AMF90287 (internal cranidium), AMF90288 (external pygidium), AMF90289 (internal cranidium), AMF90338 (external pygidium), - From NU L375, AMF90290 (internal cranidium), AMF90291 (external pygidium, cranidium and hypostome), AMF90292 (internal pygidium). From NU L672: AMF90293 (internal librigena). From NU L740: AMF90294 (internal pygidium).

Locality. Type - NU L404. Other - NU L740, NU L456, NU L375, NU L359, NU L672.

Emended diagnosis. Moderately convex; $\beta - \beta$ approximate to $\delta - \delta$ and occipital furrow; long eyes, about half glabellar length, narrow. Pygidium with 10–11 axial rings, 6–7 pleural ribs; wide pygidial border with distinct furrow.

Remarks. Engel & Morris (1994) described in detail distinct pygidial ornament in their original diagnosis, which is not visible on external molds. The diagnosis has been emended to allow for this fact.

6.14.5.1.iv Australokaskaia convexicaudata (Mitchell 1918)

1918 | Griffithides convexicaudatus Mitchell: 475–479, Pl. 46 Fig. 13, Pl. 48 Figs. 1–2

non 1922 Phillipsia convexicaudata Mitchell: 535–536, Pl. 54 Figs. 8–10
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non 1963 Griffithides? convexicaudatus Campbell & Engel: 112–113, Pl. 8 Figs. 5–10

1972 Cummingella convexicaudata Hahn & Hahn: 346

1985 Cummingella (Cummingella) convexicaudata Hahn et al.: 54

1995 Australokaskia (Longilobus) convexicaudata Engel & Morris: 196–198, Pl. 1 Figs. 10–27

Holotype material. AMF28626 (external dorsal shield missing half the cephalon).

Paratype material. AMF90346 (external cephalon), AMF90443a/b (external/internal cephalon), AMF90444a/b (external/internal cranidium), AMF90445 (internal cranidium), AMF90446 (internal cranidium), AMF90447 (internal cranidium), AMF90448a/b (external/internal librigena), AMF90449 (internal librigena), AMF90450a/b (external/internal pygidium), AMF90451 (internal pygidium), AMF90452 (internal pygidium).

Locality. NU L1039.

Emended diagnosis. Convex, glabella widest near $\beta$, covers anterior margin; L1 short, more or less triangular. Pygidium convex, with 11 axial rings, up to 6 pleural ribs; pleurae become obsolete posteriorly.

Remarks. The specimens originally described by Mitchell (1918) as Griffithides convexicaudatus have undergone considerable synonymies over the past 100
years. The introduction of the new genus *Australokaskia* by Engel & Morris (1994) has meant that specimens originally attributed to *G. convexicaudatus* can be definitively identified. The above diagnosis was emended as the antennal pores, described as being present by Engel & Morris (1995), were not seen when assessing the external mold specimens.

### 6.14.5.1.v *Australokaskia similis* (Engel & Morris 1995)

1995 *Australokaskia (Longilobus) similis* Engel & Morris: 194–196, Pl. 1 Figs. 1–9

*Holotype material.* AMF90339a/b (external/internal cephalon missing one librigena).

*Paratype material.* AMF80340a/b (external/internal dorsal shield), AMF80340c/d (external/internal librigena), AMF90340e/f (external/internal partial cranidium), AMF90340g/h (external/internal dorsal shield), AMF90341a/b (external/internal dorsal shield), AMF90342a/b (external/internal pygidium and thorax), AMF90343 (internal pygidium and external librigena), AMF90344 (external pygidium), AMF90345 (external pygidium).

*Locality.* Type - NU L448.
Emended Description. Moderately convex, glabella slightly narrows anteriorly, extends to anterior margin; L1 long, triangular; Eyes long; lateral border dips steeply inwards; Genal angles rounded or with very short genal spines. Pygidium with 11 axial rings, 7 pleural ribs; ribs equal width; single row of nodes along rings.

Remarks. Engel & Morris (1995) remark in their original diagnosis that S2 and S3 are present, though weak. However, neither S2 or S3 are present on external specimens and so have been omitted from the diagnosis. An antennal pore was also included in the original diagnosis but has been removed as it also cannot be seen in external specimens.

6.14.5.1.vi Australokaskia noorooensis (Engel & Morris 1995)

1995 Australokaskia (Planilobus) noorooensis Engel & Morris: 199–201, Pl. 2 Figs. 1–8

Holotype material. AMF90458a/b (partial external/ internal dorsal shield).

Paratype material. From NU L404: AMF90458c/d (external/ internal pygidium and thorax), AMF90458e (external dorsal shield), AMF90458f (external pygidium). From NU L8: AMF90459a (external dorsal shield), AMF90459b/c (internal dorsal shield/ partial external pygidium and thorax), AMF90459d
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(external pygidium), AMF90460 (internal cranidium and pygidium), AMF90461
(external cranidium and hypostome), AMF90462 (external cranidium and
internal pygidium), AMF90463 (external cranidium and pygidium), AMF90464
(external cranidium), AMF90465 (external cranidium), AMF90466 (internal
cranidium), AMF90467 (internal cranidium), AMF90468 (internal cranidium
and pygidium), AMF90469 (external pygidium), AMF90470 (internal
cranidium), AMF90471 (external librigena), AMF90472 (internal librigena),
AMF90473 (external pygidium), AMF90474 (external pygidium), AMF90475
(external pygidium), AMF90476 (external pygidium), AMF90477 (internal
pygidium and thorax), AMF90478 (internal pygidium), AMF90479 (internal
pygidium).

Locality. Type - NU L404. Other - NU L8.

Diagnosis. See Engel & Morris 1995.

Remarks. Australokaskia (Planilobus) nooroensis strongly resembles Australokaskia
(Planilobus) constricta Engel & Morris 1995 (see below). L1 and the glabella in
both species are similar in convexity and shape. The difference between the two
species can be seen in the pygidia. A. (Planilobus) constricta has a distinctive
constriction on its axial region in all specimens, only a faint constriction can be
seen in some of the specimens of A. (Planilobus) nooroensis. A. constricta is also
longer in proportion, with more axial rings and pleural ribs than \textit{A. (Planilobus) noorooensis}.

6.14.5.1.vii \textit{Australokaskia constricta} (Engel & Morris 1995)

1995 \textit{Australokaskia (Planilobus) constricta} Engel & Morris: 201–202, Pl. 2 Figs. 9–17

\textit{Type material.} AMF90490 (external dorsal shield lacking anterior cephalon and part thorax).

\textit{Paratype material.} From NU L620: AMF90480a/b (external/internal pygidium and thorax), AMF90481 (external cranidium), AMF90482 (external hypostome), AMF90483 (external pygidium), AMF90484 (external pygidium), AMF90485 (external pygidium), AMF90486 (external pygidium), AMF90487 (external pygidium), AMF90488 (external pygidium and internal hypostome). From NU L652: AMF90489 (external librigena), AMF90491 (external pygidium), AMF90492 (external pygidium). From NU L871: AMF90493 (external pygidium and thorax).

\textit{Locality.} Type - NU L652. Others - NU L620, NU L871.

Remarks. *Australokaskia* (Planilobus) *constricta* is easily distinguished from other *Australokaskia* species due to a distinct constriction on the sides of the axial rings. A single pygidium designated as *Australokaskia* sp. also has this distinct constriction, but its posterior pleural furrows are obsolete. The pygidial border is narrow, and there are a number of nodes on the axial rings. *A. (Planilobus) constricta* however has a wide pygidial border, all of its pleurae are distinct, and there is only one row of nodes on the axial rings (Engel & Morris 1995).

6.14.5.2 Genus *Ditomopyge* Newell 1931

*Type species. Phillipsia (Griffithides) scitula* Meek & Worthen 1865.

*Diagnosis. See Newell (1931; 1935).*

Remarks. *Ditomopyge* was a cosmopolitan genus that persisted from the Late Carboniferous to Late Permian. It was one of the few trilobites to have survived into the Late Permian (Owens & Hahn 1994). *Ditomopyge* was originally placed within the family Phacopidae by Newell (1931), but was moved to Proetidae when new specimens were found to be comparable to what Weller (1935) described as the *Griffithides scitula* series. *Ditomopyge* was placed within the subfamily Ditomopyginae by Hupé (1953).
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Age and range. Westphalian (Late Carboniferous) to Wuchiapingian (Late Permian) in North America, Australia, Central Asia, Western Europe and Eastern Europe (Owens & Hahn 1993, Owens 2004).
6.14.5.2.i *Ditomopyge meridionalis* Teichert 1944

1944 *Ditomopyge meridionalis* Teichert: 458–461, Pl. 77 Figs. 1–5, 7–12

*Type material.* UWA 21331 (external cephalon and thorax).

*Paratype material.* UWA 21332 (internal pygidium), UWA 21333 (internal pygidium), UWA 21334 (internal cephalon), UWA 21335 (internal pygidium).

*Locality.* North-West Division of Western Australia, upper Wandagee series, *Helicoprion-Paragastrioceras* Zone (Teichert 1944).

*Diagnosis.* See Teichert (1944).

*Remarks.* *Ditomopyge meridionalis* is the only species of trilobite known from either the Carboniferous or Permian in Western Australia. *Ditomopyge meridionalis* is Artinskian (Early Permian) in age (Teichert 1944), and is the youngest known trilobite species from Australia.

6.14.5.3 Genus *Malchi* Engel & Morris 1994

1994 *Malchi* Engel & Morris: 90

Emended diagnosis. Glabella just narrower anteriorly, not reaching the margin, very highly convex; terrace lines on cephalic border. Lateral borders flat; L1 triangular shape; S1 very distinct. Pygidium with up to 11 axial rings, 5 pleural ribs, which become indistinct to the posterior of the pygidium.

Remarks. Engel & Morris (1994) erected the genus Malchi to include specimens considered similar to species of Australokaskia Engel & Morris 1994 and Planokaskia Engel & Morris 1994 in Australia. Malchi is more similar to Planokaskia Engel & Morris 1994 as they have a similar glabella in shape and length. Malchi can be distinguished from both genera by its very long genal spines, reaching midway down the thorax, and a vaulted glabella. The above diagnosis was emended to remove descriptions of ornament by Engel & Morris (1994) on the juvenile cephala. The diagnosis also includes the highly distinct S1 characteristic.


Age and range. Tournaisian, in Australia (Engel & Morris 1994).

6.14.5.3.i Malchi magnificus Engel & Morris 1994
1994 *Malchi magnificus* Engel & Morris: 91–93, Pl. 3 Figs. 14–27, Text Figs. 5A–C, 6E

_Type material._ AMF90331a1/a2 (external glabella and part pygidium).

_Paratype material._ From NU L1049: AMF90331b (internal dorsal shield), AMF90332a/b (internal pygidium and thorax), AMF90333 (partial internal cephalon), AMF90334 (external cranidium), AMF90335a (external cranidium), AMF90336 (internal pygidium). From QM L508: AMF90337 (external pygidium). From ST: QMF18142 (external pygidium), QMF18143 (external pygidium), QMF18144 (internal pygidium).

_Localities._ Type - NU L1049. Others - QM L508, ST.

_Diagnosis._ As for genus. Engel & Morris (1994) included a diagnosis in their description of the species, but as this is a monotypic genus the species diagnosis is herein considered to be the genus diagnosis.

6.14.5.4 Genus *Planokaskia* Engel & Morris 1994

1994 *Planokaskia* Engel & Morris: 88
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Diagnosis. See Engel & Morris (1994).

Remarks. Engel & Morris (1994) assigned specimens similar to Australokaskia species in Australia to a new genus Planokaskia due to their low profile, short genal spines, wide flat pygidial border and less ornamented hypostome, compared with species of Australokaskia. Only one species, Planokaskia gibsoni Engel & Morris 1994, has been assigned to this genus.


Age and range. Viséan, in Australia (Engel & Morris 1994).

6.14.5.4.i Planokaskia gibsoni Engel & Morris 1994

Figure 6.4

1994 Planokaskia gibsoni Engel & Morris: 88–90, Pl. 3 Figs. 1–13, Text Figs. 4A–C, 6D

Type material. AMF90314a/b (external/ internal cranidium, hypostome, pygidium and thorax).
Paratype material. AMF27815 (internal pygidium), AMF28381 (internal pygidium), AMF28382 (internal pygidium), AMF28383 (internal pygidium), AMF28384 (internal pygidium and external librigena), AMF28385 (external pygidium), AMF90315a/b (external/internal cranidium), AMF90316 (external cranidium), AMF90317 (external cranidium), AMF90318 (external cranidium), AMF90319 (partial internal cephalon), AMF90320 (internal cranidium), AMF90321 (internal cranidium), AMF90322 (external librigena), AMF90323 (internal librigena), AMF90324 (internal librigena), AMF90325 (internal librigena), AMF90326 (external pygidium), AMF90327 (external pygidium), AMF90328 (external pygidium), AMF90329 (external pygidium), AMF90330 (internal pygidium).

Locality. NU L1039.

Diagnosis. As for genus.

6.14.6 Subfamily WEANIINAE Owens 1983

6.14.6.1 Genus Carbonocoryphe Richter & Richter 1950

1950 Carbonocoryphe Richter & Richter: 278.
1951 Carbonocoryphe Richter & Richter: 221, 251.
1953 Carbonocoryphe Hupé: 217.
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1955  *Carbonocoryphe* Hupé: 203.

1959  *Carbonocoryphe* Richter *et al.*: 394.


1962  *Carbonocoryphe* Osmolska: 69.


1966  *Carbonocoryphe* Chlupáč: 93-94

1966  *Carbonocoryphe* Erben: 175.


1969  *Carbonocoryphe* Hahn & Hahn: 121-122.


Type species. *Carbonocoryphe bindemanni* Richter & Richter 1950

Diagnosis. See Hahn & Brauckmann 1975.

Remarks. Engel & Morris (1980; 1989) assigned a number of Australian trilobites to the *Carbonocoryphe* subgenera *C. (Aprathia)* and *C. (Winterbergia)*. Three of these species have been placed within *nomen dubium* (see below). Two species, *C.? (A.?) rockhamptonensis* and *C.? (W.?) waterhousei* have been left within the genus. This classification has been thought to be suspect by Hahn (*pers. comm.*
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2011). See below for remarks on the classification of these species within *Carbonocoryphe*.


Age and range. Tournaisian to Viséan in North America, Europe and Australia (?) (Brezinski 1998; Hahn & Hahn 1969; Engel & Morris 1980).

6.14.6.1.i *Carbonocoryphe? (Aprathia?) rockhamptonensis* (Mitchell 1918)

Figure 6.5

1892  *Phillipsia dubia* Etheridge Jr.: 214–215, Pl. 44 Fig. 4
1892  *Phillipsia woodwardi* Etheridge Jr.: 215, Pl. 44 Fig. 6
1918  *Phillipsia rockhamptonensis* Mitchell: 495–461, Pl. 49 Figs. 9–10, Pl. 50 Fig. 8
1963  *Conophilipsia?* sp. Campbell & Engel: Pl. 8 Figs. 1–2
1972  *Phillipsia (Phillipsia?) rockhamptonensis* Hahn & Hahn: 400
1989  *Aprathia rockhamptonensis* Engel & Morris: 327–332, Figs. 11–12

Type material. QMF17–1234a/b (half internal/external dorsal shield).
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*Paratype material. QMF17–1233 (external pygidium).*

*Locality. NU L1064.*

*Emended diagnosis. Glabella conical, widest close to occipital furrow, distinct S1–S3; eyes long and wide; long genal spines. Pygidial pleural grooves extend to margin (faint at posterior); 11–12 pygidial axial rings; sub-cylindrical shape.*

*Remarks. The specimens of *Carbonocoryphe? (Aprathia?) rockhamptonensis* were placed within the subgenus *C. (Aprathia)* by Engel & Morris (1989) who originally described this species as *Aprathia rockhamptonensis* (Mitchell 1918) after elevating the subgenus to generic level. *Aprathia* is still considered a subgenus of *Carbonocoryphe* after Hahn et al. 1980. The placement of the species within this genus is thought to be suspect (G. Hahn, *pers. comm.* 2011). *Carbonocoryphe? (Aprathia?) rockhamptonensis* however does not resemble any other genus found within Australia during the Carboniferous, or in fact other phillipsiid genera. *Carbonocoryphe? (Aprathia?) rockhamptonensis* has not been described as a new genus as the specimens that have been found are not distinctive enough. *Carbonocoryphe? (Aprathia?) rockhamptonensis* has been given a question mark to reflect these findings. Once new specimens are found it is possible C.? (Aprathia?) rockhamptonensis could be placed within a new genus.*
FIGURE 6.5. Representative Australian genera of the Order Proetida. 1. Linguaphillipsia elongata external dorsal shield Holotype, NGSF1500b, dorsal view, 2.2x. Carbonocoryphe? (Aprathia) rockhamptonensis, 2. external cranidium Paratype, AMF80712, dorsal view, 7x, 3. external pygidium Paratype, AMF80714, dorsal view, 6.5x, 4. external cranidium Paratype, AMF80712, lateral view, 8.3x. 5. cf. Gitarra semicircularis external dorsal shield, AMF27749, dorsal view, 6.5x. 6. Dechenelloides? peoui internal cephalon Holotype, AMF96983, dorsal view, 7x. Weberiphillipsia collinsi, 7. external cephalon Paratype, 80349a, dorsal view, 8x, 10. external pygidium, thorax and part librigena, AMF83638, dorsal view, 4x. Gracemerea archeri, 8. external cephalon Holotype, AMF80721, dorsal view, 12x, 11. external pygidium Paratype, AMF80724, dorsal view, 11.1x. 9. Doublatia inflata external dorsal shield Holotype, AMF69779a, dorsal view, 3x.

6.14.6.1.ii Carbonocoryphe? (Winterbergia?) waterhousei (Mitchell 1918)

1989 Winterbergia? waterhousei Engel & Morris: 341–343, Fig. 18A–B

Lectotype material. NGSF15451 (external dorsal shield).

Locality. Unknown, possibly Dungog district, New South Wales (Engel & Morris 1989).

Diagnosis. See Engel & Morris (1989).

Remarks. Only two specimens of Carbonocoryphe? (Winterbergia?) waterhousei (Mitchell 1918), one complete external dorsal shield, and one internal dorsal shield, exist. The specimens are said to be from the “late meraspid” stage of growth by Engel & Morris (1989). The specimens were tentatively placed within the subgenus C. (Winterbergia) by Engel & Morris (1989) who originally described this species as Winterbergia? waterhousei (Mitchell 1918) after elevating the subgenus to generic level. Hahn et al. (1998; 2003; 2007) do not recognized
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Winterbergia as a valid genus. Due to a lack of specimens the species is kept under C.? (Winterbergia?) waterhousei. Only a single lectotype was designated by Mitchell (1918) for the original species Phillipsia? waterhousei, the name however is valid under ICZN article 74 stating that lectotypes before 2000 can be named in place of holotype if a holotype has not been designated in the original publication.


1968 Dechenelloides Gandl: 47
1975 Dechenelloides Hahn & Hahn: 31
1978 Dechenelloides Brauckmann: 2
1980 Dechenelloides Kobayashi & Hamada: 84
1984 Dechenelloides Yuan: 630–631
1987 Dechenelloides Brauckmann and Tilsley: 145
1988 Dechenelloides Hahn & Brauckmann: 99
1989 Dechenelloides Hahn et al.: 189
1996 Dechenelloides Engel & Morris: 120

Type species. Proetus angustigenatus Leyh 1897

Remarks. *Dechenelloides* are characterised by a very wide anterior border, wide palpebral lobes, and $\beta - \beta$ shorter than $\delta - \delta$. Only one internal cranidium has been found from Australia, making the occurrence of *Dechenelloides* in Australia somewhat dubious (see below).


*Age and range.* Tournaisian to Late Viséan, in Australia, China, Japan and Europe (Osmolska 1970; Engel & Morris 1996).


**Figure 6.5**

1996 *Dechenelloides peoui* Engel & Morris: 120, Pl. 2 Fig. 19, Text Fig. 1

*Holotype material.* AMF96983 (internal cranidium).

*Locality.* NU L861.

Remarks. Whilst assigning *Dechenelloides? peoui* to the genus *Dechenelloides*, Engel & Morris (1996) remarked that it must remain provisional due to the lack of pygidial and thoracic detail. There are some similarities between a number of the species assigned to the genus, such as *Dechenelloides shanlingoensis* (Sheng 1974), *Dechenelloides angustigenatus* (Leyh 1897) and *Dechenelloides hofensis* (Leyh 1897), but there are also major differences, such as the very wide anterior border and deeply incised glabellar furrows (Engel & Morris 1996). The assignment of *D.? peoui* to *Dechenelloides* will remain provisional, as no other specimens have been found.


1971 *Doublatia* Wass & Banks: 227

1978 *Doublatia* Engel & Laurie: 51

*Type species.* *Doublatia inflata* Wass & Banks 1971.

*Emended diagnosis.* Cephalon semicircular to parabolic in outline with narrow border; glabellar furrows S2 and S3 weakly developed; lateral preoccipital lobes and occipital ring strongly developed; palpebral region opposite posterior half
of the glabella; short genal spines. Nine thoracic segments. Pygidium with axis only two-thirds of the pygidial length; pygidium with 8–9 axial rings, fewer pleural ribs than axial rings; no pygidial border; wide pygidial doublure. Surface finely granulose.

Remarks. *Doublatia* was diagnosed as having a strongly inflated glabella with a median preoccipital lobe. Newer specimens have been located since this original publication indicating the type species of the genus, *D. inflata*, does not have a vaulted glabella or a median preoccipital lobe. The diagnosis of *Doublatia* has been emended to take this into account.

*Doublatia* was originally placed within the subfamily Griffithidinae by Wass & Banks (1971) but was moved to Ditomopyginae by Engel & Laurie (1978) based on *Doublatia*’s similarities to *Ditomopyge*, and the fact that it lacks a highly vaulted glabella characteristic of Griffithidinae. Engel & Morris (1989) moved the genus to the subfamily Weaniinae (though there is no explanation for this).


Age and range. Sakmarian to Wordian (Early to Middle Permian) in Australia (Wass & Banks 1971; Engel & Laurie 1978; Percival *et al.* 2012).
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6.14.6.3.i **Doublatia inflata** Wass & Banks 1971

**Figure 6.5**

1971 **Doublatia inflata** Wass & Banks: 227–229, Pl. 36 Figs. 1–4

*Type material.* AMF69779a (external dorsal shield).

*Other Material.* AMF117831 (external pygidium), AMF117832 (external librigena), AMF117833 (external librigena and pygidium).

*Locality.* Mulbring Quarry, Mulbring, New South Wales.

*Diagnosis.* See Wass & Banks (1971).

*Remarks.* The species *Doublatia inflata* was described from early Permian material in New South Wales. The type specimen was the only known material when *D. inflata* was first described. Since then more material has been found at the location of the original specimen. Other specimens have also been located by the *Fossil Club of New South Wales*, which have been figured in Percival *et al.* (2012). The new specimens have allowed the diagnosis for the genus *Doublatia* to be emended. The diagnosis for *D. inflata* remains the same.

6.14.6.3.ii **Doublatia matheri** Engel & Laurie 1978
1978  *Doublatia matheri* Engel & Laurie: 51–54, Figs. 2–3

*Type material.* NUF2600a/b (internal/external dorsal shield).

*Locality.* NU L925.

*Diagnosis.* See Engel & Laurie (1978).

*Remarks.* *Doublatia matheri* was collected from Early Permian (Artinskian) material near Manning River in New South Wales. *Doublatia matheri* most closely resembles the type species *D. inflata* in that they both have semi-circular shaped cephalas. *Doublatia matheri* differs from *D. inflata* by a glabella that reaches the anterior margin, which is also less incised, and a pygidial axis that is longer compared with the total pygidial length (Engel & Laurie 1978).

**6.14.6.3.iii *Doublatia pyriforme* Wass & Banks 1971**

1971  *Doublatia pyriforme* Wass & Banks: 229–233, Pl. 37 Figs. 1–12, 14, 15, Text Fig. 2

*Type material.* UT90142  (cranidium).
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Paratype material. UT90113 (librigena), UT90144 (librigena), UT90155 (librigena), UT90094a,b (pygidium), UT90115 (pygidium), UT90121 (pygidium).

Locality. Ray’s Hill, St. Mary’s, Tasmania.

Emended diagnosis. Species of Doublatia with a median preoccipital lobe and parabolic shaped cephalon. Pygidium with eight axial rings and seven pleural ribs.

Remarks. Doublatia pyriforme differs from the type species D. inflata in that it has an obvious preoccipital median lobe, and a parabolic shaped cephalon. Doublatia pyriforme also has triangular L1, whereas the L1 in D. inflata are much more rounded. Doublatia pyriforme is similar in age to the species D. matheri, buts D. pyriforme’s glabellar length, cephalic shape and median preoccipital lobe differentiate it from D. matheri. Specimens of D. pyriforme are only found in Tasmania. The above diagnosis of Doublatia has been emended to include the median preoccipital lobe, which was excluded on account of new material that had been found.


1968 Gitarra Gandl: 89
1970 Gitarra Hahn & Hahn: 195
Type species. Griffithides pupuloides Leyh 1897

Diagnosis. See Engel & Morris (1989).

Remarks. Gitarra was diagnosed on its distinctive bell-shaped glabella and resembles the genera Linguaphillipsia and Paladin. Gitarra, however, can be distinguished from them by its much flatter overall convexity of the dorsal shield. There are also significant differences in the pygidia, in Gitarra the pleural ribs correspond to the axial rings plus they have well defined pleural furrows, unlike the other two genera (Engel & Morris 1989).


Age and range. Late Tournaisian to mid Viséan (Engel & Morris 1989).

6.14.6.4.i Gitarra cf. semicircularis (Engel & Morris 1996)

Figure 6.5

1922 Phillipsia convexicaudata Mitchell: 535–536, Pl. 54 Figs. 8–10
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1996  \textit{Aprathia semicircularis} Engel & Morris: 121–124, Pl. 1 Figs. 1–20, Text

Fig. 2

\textit{Type material.} AMF27747 / AMF28010 (external dorsal shield / internal counterpart).

\textit{Paratype material.} AMF27449 (external dorsal shield), AMF96984a/b (external cranidium, internal/external librigena and internal/external pygidium), AMF96985a/b (2 internal/external cranidia), AMF96986 (external cranidium), AMF96987 (internal cranidium), AMF96988a/b (2 external pygidia and internal librigena), AMF96989a (2 external pygidium and glabella), AMF96990a/b (internal/external pygidium), AMF96991a/b (external/internal pygidium), AMF96992 (external pygidium), AMF96993 (external pygidium), AMF96994 (internal pygidium).

\textit{Locality.} NU L1039.

\textit{Emended diagnosis.} Cephalon semicircular, lacking genal spines. Glabella touching anterior border, well constricted, at $\gamma$. Nine thoracic segments with wide axis. Pygidium with 9–10 axial rings, 8 pleural ribs; pleural furrows long, extend almost to margin; inter-pleural furrows broad and shallow, do not reach the pygidial margin; no border furrow.
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Remarks. G. cf. semicircularis was assigned to the genus Aprathia based on the similarities to the pygidium of cf. Weania (Weania) applanata (Engel & Morris 1980), as well as a lack of a defined pygidial border or border furrow. As the pygidium of W. cf. (Weania) applanata was not thought to be Carbonocoryphe (Aprathia), the validity of this diagnosis is also questioned. After examination of the specimens assigned to Aprathia semicircularis by Engel & Morris (1996) it appears it is most like the genus Gitarra. Due to a lack of well preserved specimens it cannot be placed within this genus with confidence. Similarities include a very well incised glabella, posteriorly placed palpebral lobes, few axial rings and pleural ribs and strongly developed pleural furrows. The species has been tentatively placed within this genus because of these features.

6.14.6.5 Genus Gracemerea Engel & Morris 1989

1989 Gracemerea Engel & Morris: 324


Diagnosis. See Engel & Morris (1989).

Remarks. Gracemerea is a monotypic genus found only in Australia.

Characteristics used to identify the genus include a wide occipital ring, flat profile, long genal spines and a short pygidium with obsolete posterior pleural
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segments. The wide occipital ring, short pygidium and an inflated border is also found in Weania, however Gracemerea lacks a strong constriction at γ and has much longer genal spines and also resembles species of Carbonocoryphe (Winterbergia) by its genal spines and glabella shape. However, ornament is lacking on the glabella and L2 is missing in Gracemerea. Similarities between Gracemerea and other Weaniinae genera place it within the subfamily Weaniinae, but its distinct combination of characters distinguish it from other genera.


Age and range. Late Tournaisian to Early Viséan, in Australia (Engel & Morris 1989).

6.14.6.5.i Gracemerea archeri Engel & Morris 1989

Figure 6.5

1989 Gracemerea archeri Engel & Morris: 325–327, Figs. 9–10

Type material. AMF80721 (partial external cranidium).

Paratype material. AMF80722 (internal cranidium), AMF80723 (external cranidium), AMF80724 (external pygidium), AMF80725 (external cranidium), AMF80726 (external cranidium), AMF80727 (internal pygidium), AMF80728
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(internal pygidium), AMF80729 (internal pygidium), AMF80730 (external librigena), AMF80731 (internal librigena), AMF80732 (partial external pygidium).

Locality. NU L1049.

Diagnosis. As for genus.


1980 Schizophillipsia Kobayashi & Hamada: 86
1989 Schizophillipsia Engel & Morris: 316

Type species. Schizophillipsia yukisawensis Kobayashi & Hamada 1980.

Diagnosis. See Engel & Morris (1989).

Remarks. The genus was originally diagnosed based on a tropidium (Kobayashi & Hamada 1980). The tropidium, however, is not unique to Schizophillipsia, being found in most weaniinid genera and Linguaphillipsia species. Instead the very distinctive bell-shaped glabella is diagnostic of the genus.
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Age and range. Middle Tournaisian to late Viséan, in Japan and Australia (Engel & Morris 1989).

6.14.6.6.i *Schizophillipsia irvingi* Engel & Morris 1989

Figure 6.6

1989 *Schizophillipsia irvingi* Engel & Morris: 316–319, Figs. 5–6

Type material. AMF59518 (internal dorsal shield).

Locality. BBS.

Diagnosis. See Engel & Morris (1989).

Remarks. *Schizophillipsia irvingi* is based on a single specimen, in which the glabella shape and width of the thorax places it within *Schizophillipsia*. *Schizophillipsia irvingi* is similar to both *S. yukisawensis* and *S. otsuboensis*, but differs in it’s slightly longer glabella, shorter genal spines and narrower pygidium (Engel & Morris 1989).
6.14.6.7 Genus *Thalabaria* Engel & Morris 1989

1989 *Thalabaria* Engel & Morris: 343–344, Fig. 19.

*Type species.* *Cyrtoproetus planus* Engel & Morris 1980.
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Diagnosis. See Engel & Morris (1989).

Remarks. Engel & Morris (1989) designated the new genus Thalabaria for the originally described Cyrtoproetus planus specimens and is to date being the only species described for the genus. The specimens closely resemble Weania specimens, however have a flatter profile, shallow glabellar furrows and longer pygidia (Engel & Morris 1989). They were provisionally placed within Dechenelloides by Brauckmann and Tilsley (1987), though this was rejected by Engel & Morris (1989) due to the differently shaped glabella and smaller eyes. Due to the inability to place this species within any known genus it will be left as Thalabaria.

Species included. Thalabaria plana (Engel & Morris 1980).

Age and range. Early Viséan in Australia (Engel & Morris 1989).

6.14.6.7.i Thalabaria plana (Engel & Morris 1980)

Figure 6.6

1980 Cyrtoproetus planus Engel & Morris: 277–281, Pl. 2 Figs. 16–22, Text Fig.

10

1989 Thalabaria plana Engel & Morris: 344, Fig. 19.
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Type material. AMF80781 (external dorsal shield).

Paratype material. AMF80748 (internal cranidium), AMF80749 (internal cranidium), AMF80750 (internal cranidium), AMF80751 (internal cranidium), AMF80752 (internal pygidium), AMF80753 (partial internal pygidium), AMF80754 (partial internal pygidium), AMF80755 (external cranidium), AMF80756 (internal cranidium), AMF80757 (external pygidium), AMF80758 (partial internal pygidium), AMF80759 (internal pygidium), AMF80760 (internal cranidium), AMF80761 (internal pygidium), AMF80762 (internal pygidium), AMF80763 (partial internal pygidium), AMF80764 (partial internal cranidium), AMF80765 (external dorsal shield), AMF80766 (external pygidium), AMF80767 (external dorsal shield), AMF80768 (internal pygidium), AMF80769, AMF80770 (external librigena), AMF80771 (internal hypostome), AMF80772 (partial internal pygidium), AMF80773 (internal cranidium), AMF80774 (partial external pygidium), AMF80775 (internal pygidium and partial thorax), AMF80776 (external pygidium), AMF80777 (internal pygidium), AMF80778 (external glabella), AMF80779 (internal librigena), AMF80780 (external cranidium), AMF80782 (external cranidium), AMF80783 (partial internal cranidium).

Locality. NU L356.
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Diagnosis. See Engel & Morris (1989).

6.14.6.8 Genus *Weania* Campbell & Engel 1963

1963 *Weania* Campbell & Engel: 107–108

1969 *Archeogonus (Weania)* Hahn & Hahn: 118–119

1970 *Weania* Osmolska: 117–118

1988 *Weania* Hahn & Brauckmann: 100, Text Fig. 1

1989 *Weania* Hahn *et al.*: 149

1989 *Weania* Engel & Morris: 310

*Type species.* *Weania goldringi* Campbell & Engel, 1963.


Remarks. The genus is typical of the subfamily Weaniinae, and is very similar to *Belgibole* Hahn 1963. The two genera are separated based on the presence of occipital lobes in *Weania* and species previously defined within *Weania* have consequently been moved to *Belgibole* by Hahn *et al.* (1989). Engel & Morris (1989) and Hahn *et al.* (1989) redescribed the genus, the latter of which has been used as a reference here as it is more succinct.
Species included. Weania anglica (Osmolska 1970), Weania brewi Hahn & Hahn 1992, Weania goldringi (Campbell & Engel 1963), Weania librovitchi (Weber 1937), Weania neso (Fey 1985), Weania persistens Hahn et al. 1989, Weania superba (Mitchell 1918), Weania zarecznyi (Jarosz 1913)

Age and range. Tournaisian to Westphalian in Australia, Europe, Central Asia and China (Hahn et al. 1989, Engel & Morris 1989).


1989 Weania berricoensis Engel & Morris: 314–316, Figs. 3–4

Type material. AMF80612 (external pygidium).

Paratype material. AMF80613 (internal pygidium), AMF80614a/b (external/internal pygidium), AMF80615a/b (external/internal pygidium), AMF80616a/b (external/internal pygidium), AMF80617 (external pygidium), AMF80618 (internal librigena), AMF80619 (partial external cranidium).

Locality. NU L446.

Diagnosis. See Engel & Morris (1989).
Remarks. Engel & Morris (1989) distinguished a number of specimens of *Weania* into the new species *Weania (Weania) berricoensis* based on a larger pygidium. The specimens are diagnosed purely on pygidial characters, as only fragments of *W. (Weania) berricoensis* cranidia have been found. The pygida of these specimens resemble other species of *Weania* in their broadly semicircular shape and pleural ribs becoming obsolete posteriorly. Their size and number of axial rings and pleural ribs separate them from *W. (Weania) goldringi* (Campbell & Engel 1963).

6.14.6.8(a).ii *Weania (Weania) goldringi* Campbell & Engel 1963

**Figure 6.6**

1963 *Weania goldringi* Campbell & Engel: 107–110, Pl. 6 Figs. 1–9, 11–14, Text Fig. 11

1969 *Archegonus (Weania) goldringi* Hahn & Hahn: 119

1989 *Weania goldringi* Engel & Morris: 310–314, Figs. 1–2

*Type material.* AMF85439 (external cranidium).

*Paratype material.* AMF85443 (external pygidium), AMF85444 (internal pygidium), AMF85445 (external librigena), AMF85446 (external librigena), AMF85447 (external pygidium), AMF85448 (external pygidium), AMF85449
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(internal pygidium), AMF85450 (internal pygidium), AMF8545 (internal pygidium), AMF85452 (internal pygidium), AMF85453 (external librigena).

Locality. NU L366.

Diagnosis. See Engel & Morris (1989).

Remarks. Weania goldringi is similar to Weania anglica, but has a wider glabella base and longer pygidium (Engel & Morris 1989). Weania librovitchi also resembles W. goldringi, but has more axial rings and pleural ribs (Engel & Morris 1989).

6.14.6.8(b) Subgenus Weania (Rosehillia) Engel & Morris 1997


Type species. Phillipsia superba Mitchell 1918

Diagnosis. See Engel & Morris 1997.

Remarks. Weania (Rosehillia) superba was originally placed within the genus Gitarra due to its highly distinct bell-shaped glabella, and flat profile. W. (Rosehillia) superba was moved to Weania as a separate subgenus by Engel &
Morris (1997) as its flatter profile fit with newer species assigned to *Weania*, and their pygidial features were the same. A new subgenus was erected within *Weania* due to its very distinctly shaped glabella.

Species included. *Weania (Rosehillia) superba* (Mitchell 1918).

Age and range. Mid Viséan in Australia (Engel & Morris 1997).

6.14.6.8(b).i *Weania (Rosehillia) superba* (Mitchell 1918)

Figure 6.6

1918  *Phillipsia superba* Mitchell: 454–455, Pl. 48 Fig. 15, Pl. 52 Fig. 3
1922  *Phillipsia convexicaudata* Mitchell: 535–536, Pl. 54 Figs. 8–10
1972  *Cummingella? superba* Hahn & Hahn: 355
1989  *Gitarra superba* Engel & Morris: 320–324, Figs. 7–8
1997  *Weania (Rosehillia) superba* Engel & Morris: 69, 79, 92 & 94

Holotype material. NGSF15453 (internal cranidium and librigena).

Locality. Type - unknown.

Emended diagnosis. Dorsal shield barely convex; strongly incised glabella at $\gamma$, creating a bell-shape; eyes large; palpebral lobes large, posteriorly placed;
convex librigenae; short genal spines; occipital ring broader than glabella base. Strong relief on pygidium; 10–11 pygidial axial rings, 8–9 pygidial pleural ribs.

Remarks. Weania (Rosehillia) superba shares similar pygidial characteristics to Weania (Weania) goldringi and Weania (Weania) berricoensis. Cephalic characteristics can only be compared to W. (Weania) goldringi. Weania (Rosehillia) superba shares a similar shape and relative size to the body, but its glabella is much more incised, creating its very distinct shape and also has more rings and ribs than W. (Weania) goldringi, as well as has a flatter axis. The emended diagnosis above includes both the original diagnosis by Engel & Morris (1989), and the updated diagnosis by Engel & Morris (1997) as the updated diagnosis did not include specific pygidial features.

6.15 Family PHILLPSIIIDAE (Oehlert 1886)

6.15.1 Subfamily PHILLPSIIINAE (Oehlert 1886)

6.15.1.1 Genus Phillipsia Portlock 1843

1843 Phillipsia Portlock: 305
1883 Phillipsia Woodward: 11
1936 Phillipsia Weller: 704
1943 Phillipsia Reed: 55–57
1963 Phillipsia Hessler: 551–552
1970 Phillipsia Osmolska: 78–80
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1975b  *Phillipsia* Hahn & Hahn

1983  *Phillipsia* Engel & Morris: 228

Type species. *Phillipsia kellyi* Portlock 1843.

Diagnosis. See Engel & Morris (1983).

Remarks. The Australian Carboniferous *Phillipsia* species have been called into question by Owens (1990) and G. Hahn (pers. comm. 2011). Same conclusions were drawn from careful examination of the Australian specimens diagnosed as *Phillipsia squamata* Engel & Morris 1983 (see below). *Phillipsia squamata* specimens include the diagnostic characteristics attributed to the *Phillipsia* species in the most recent diagnosis of the genus by Engel & Morris (1983). The specimens most resemble *Phillipsia moelleri* Osmolska 1970, they both have inflated anterior cephalic borders that wrap around the front of the glabella (Engel & Morris 1983; Osmolska 1970). Differences include longer palpebral lobes in *P. squamata* and a longer pygidium in *P. moelleri*. Due to the similarities between the Australian species, *P. squamata* has been left as *Phillipsia* Portlock.


6.15.1.1.i *Phillipsia squamata* Engel & Morris 1983

**Figure 6.3**

1983 *Phillipsia squamata* Engel & Morris: 228–231, Figs. 1A, 3, 4A–C

*Type material.* AMF80267 (external cranidium).

*Paratype material.* From NU L484: AMF80258 (external pygidium), AMF80259 (partial external pygidium), AMF80260 (internal pygidium), AMF80261 (internal pygidium), AMF80262 (external pygidium), AMF80263 (external pygidium), AMF80264 (external pygidium), AMF80265 (external pygidium), AMF80266 (internal pygidium), AMF80268 (internal cranidium), AMF80269 (external pygidium), AMF80272 (internal pygidium). From NU L890: AMF80270 (external cranidium), AMF80271 (external librigena), AMF80273 (external pygidium), AMF80274 (external pygidium), AMF80275 (internal pygidium), AMF80276 (internal cranidium).

*Locality.* Type - NU L890. Other - NU L484.
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Diagnosis. See Engel & Morris (1983).

Remarks. *Phillipsia squamata*, as first described by Engel & Morris (1983), is the only species of *Phillipsia* described from Australia. Engel & Morris (1983) use the *P. moelleri* group to justify the placement of this species in the genus, citing the distinctive change of slope in the anterior border furrow as a telling feature.

*Phillipsia squamata* shares similarities with the cephalic features found in Australian species of *Weberiphillipsia* Osmolska 1970, but is distinguished from this genus by a lack of a distinctive pygidial border and furrow, and border ornament.

Age and range. Late Tournaisian to early Viséan in New South Wales, Australia (Engel & Morris 1983).

6.15.2 Subfamily LINGUAPHILLIPSIINAE Hahn & Hahn 1972

6.15.2.1 Genus *Linguaphillipsia* Stubblefield 1948

1948 *Linguaphillipsia* Stubblefield: 97–99
1951 *Linguaphillipsia* Richter & Richter: 245
1958 *Linguaphillipsia* Cvancara: 883
1959 *Linguaphillipsia* Weller: 401
1967 *Linguaphillipsia* Hahn & Hahn: 325–327
1970 *Linguaphillipsia* Osmolska: 13, 48–50
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1972  *Linguaphillipsia* Hahn & Hahn: 369

1973  *Linguaphillipsia* Hahn & Hahn: 481


1980  *Linguaphillipsia* Kobayashi & Hamada: 76

1987  *Linguaphillipsia* Hahn et al.: 152

1988  *Linguaphillipsia* Tilsley: 157

1995  *Linguaphillipsia* Yuan & Li: 22–23

Type species. *Linguaphillipsia terapaiensis* Stubblefield 1948

Emended diagnosis. Glabella slim, bell-shaped, elongated constricted at γ; weakly to moderately inflated; length variable, reaching or extending over the anterior border, not reaching the margin; S1–S3 well developed, S4 only in some species. Anterior border of variable width, generally broad; anterior furrow present; border concave with distinct terrace lines; eyes large; facial suture lacking a straight ε – ζ section; long to short genal spines. Pygidium with 12–20 axial rings, 9–15 pleural ribs; pleural furrows clearly developed; border wide to moderately narrow, sharply set off from pleurae with or with a furrow; ribs stop short of border.

Remarks. The genus was first described by Stubblefield (1948), and was updated by Hahn & Hahn (1972; 1973). The emended diagnosis is taken from Engel & Morris (1975) with some of the anterior border descriptions removed. This is
because Engel & Morris (1975) described all possible variable border structures with the addition of the Australian species, which was not deemed necessary for the diagnosis. *Linguaphillipsia* is a common species in Australia, as well as throughout the world.

Age and range. Tournaisian to Viséan (Engel & Morris 1975), in Australia, Europe, South-east Asia, Japan and China (Engel & Morris 1975; Hahn & Hahn 1972; Yuan & Li 1995; Kobayashi & Hamada 1980).

6.15.2.1.i Linguaphillipsia cangonensis Engel & Morris 1975

1975 Linguaphillipsia cangonensis Engel & Morris: 160–164, Pl. 1 Figs. 5–8

Holotype material. AMF80211 (external pygidium).

Paratype material. From NU L415: AMF80205 (internal librigena), AMF80206 (external librigena), AMF80207 (external pygidium), AMF80208 (internal pygidium). From NU L506: AMF80209 (external cranidium), AMF80210 (external pygidium), AMF80212 (external pygidium), AMF80213 (external cephalon), AMF80214 (internal pygidium), SMF27575, SMF27576, SMF27577.

Locality. Type - NU L506. Other - NU L415.

Emended diagnosis. Glabella low and broad, extending onto the wide anterior border; central section of glabella vaulted, moderately constricted at γ; palpebral lobes long, posteriorly placed; short divergent ε – ζ section; eyes large. Pygidium parabolic to sub-circular, with 17 axial rings and 12–13 pleural ribs; wide pygidial border, flat to gently convex; weak border furrow.
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Remarks. The above diagnosis was emended to remove descriptions of juvenile facial sutures, and the description that the mid-section of the glabella expands forward, which cannot be seen on the specimens available. *Linguaphillipsia cangonensis* shares a short, straight, divergent $\varepsilon$ – $\zeta$ section and eye platform characters with other Australian species of *Linguaphillipsia*. However, it can be readily distinguished as a separate species due to its very broad anterior border and glabella (Engel & Morris 1975).

6.15.2.1.ii *Linguaphillipsia divergens* Cvancara 1958

1918 *Phillipsia proxima* Mitchell: 451, Pl. 46 Figs. 15–16

1958 *Linguaphillipsia divergens* Cvancara: 883–886, Pl. 113 Figs. 18–25

1972 *Linguaphillipsia divergens* Hahn & Hahn: 370


Holotype material. AMF78030 (internal part cephalon and thorax).

Paratype material. AMF78028a/b (external/internal pygidium), AMF78029 (external pygidium), AMF78031 (external pygidium), AMF70832A (internal cephalon), AMF70832B (external librigena), AMF70832C (internal cranidium),
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AMF70832D (internal cranidium), AMF70832E (internal librigena), AMF70832F (internal hypostome).

Locality. NU L258.

Emended diagnosis. Glabella long, tapering anteriorly, almost reaching the anterior margin; moderately constricted at $\gamma$; anterior sections of facial suture highly divergent resulting in broad fixigenae; $\beta - \beta$ equal or greater than $\delta - \delta$; long palpebral lobes; short straight $\varepsilon - \zeta$ section; large crescentic eyes, on eye platform with marginal rim. Parabolic pygidium, with 19–20 axial rings, 11–13 pleural ribs; ribs becoming reduced posteriorly; wide flat to gently concave pygidial border.

Remarks. Linguaphillipsia divergens was first described by Cvancara (1958), with an emended diagnosis by Engel & Morris (1975). The emended diagnosis of Engel & Morris (1975) has been updated to reflect new terminology in the recent literature.

6.15.2.1.iii Linguaphillipsia elongata (Mitchell 1918)

Figure 6.5

1892a  Phillipsia dubia Etheridge Jr.: 126–128, Pl. 21 Figs. 3–4
1892a  Phillipsia sp. indet. Etheridge Jr.: 129, Pl. 21 Figs. 6–7

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1918  *Phillipsia elongata* Mitchell: 456–458, Pl. 47 Figs. 3–5, Pl. 48 Fig. 14, Pl. 50 Figs. 4–7

1918  *Phillipsia stroudensis* Mitchell: 453–454, Pl. 46 Fig. 14, Pl. 51 Fig. 11

1918  *Phillipsia rouchelensis* Mitchell: 473, Pl. 48 Figs. 4–7

1971  *Phillipsia elongata* Fletcher: 117

1971  *Phillipsia? stroudensis* Fletcher: 116


1972  *Conophillipsia? rouchelensis* Hahn & Hahn: 386–387

1972  *Conophillipsia? stroudensis* Hahn & Hahn: 387

1975  *Linguaphillipsia elongata elongata* Engel & Morris: 166–170, Pl. 1 Figs. 9–11, Pl. 2 Figs. 12–16, Text Fig. 13

*Lectotype Material.* NGSF1500a/b (external/internal dorsal shield).

*Paralectotype Material.* AMF35697 (internal cranidium and partial thorax), AMF35846 (partial internal pygidium), NGSF1498 (internal dorsal shield), NGSF1506 (internal pygidium and glabella).

*Locality.* Type - Given only as Binge Berry, Rouchel Brook NSW in Engel & Morris (1975).
Emended diagnosis. Glabella constricted, weakly tapering anteriorly, ending prior to the anterior margin; anterior border narrow, rolled; fixigenae broad, $\beta - \beta$ sub–equal to $\delta - \delta$; palpebral lobes broad, with a straight $\varepsilon - \zeta$ section; eyes large, mounted on eye platform delineated by an elevated crescentic ridge. 9 thoracic segments. Pygidium with 18 – 20 axial rings, 13 – 15 pleural ribs; border slightly convex, without distinct furrow, separated by changed of slope from pleura; dorsal surface granulose.

Remarks. Linguaphillipsia elongata (Mitchell 1918) was separated by Engel & Morris (1975) into two sub-species, Linguaphillipsia elongata elongata (Mitchell 1918) and Linguaphillipsia elongata rouchelensis (Mitchell 1918). Specimens of L. elongata rouchelensis are only known from pygidia. These pygidia differ from L. elongata elongata specimens in that they have a flatter profile and the slope of the pygidial border to pleurae is indistinct, unlike L. elongata elongata where it is distinct. The pygidia are distinctive enough to be from different species, with the subspecies now divided into L. elongata and L. rouchelensis.

The above diagnosis was taken from Engel & Morris’s (1975) diagnosis for Linguaphillipsia elongata (Mitchell 1918), but changed to remove the differences in border convexities that was included when L. rouchelensis was a subspecies.

6.15.2.1.iv Linguaphillipsia engeli Galtier et al. 2007
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2007 Linguaphillipsia engeli Galtier et al.: 237–238, Pl. 4 Figs. 9–14

Holotype material. AMF125013 (external cephalon).

Paratype material. AMF125010 (external librigena), AMF125011 (external pygidium), AMF125012 (external cranidium).

Locality. Section RUR (Mawson & Talent 1999), gully parallel to Blue Range-Ewan Road, Ruxton, northern Queensland (Galtier et al. 2007).

Diagnosis. See Galtier et al. (2007).

Remarks. Linguaphillipsia engeli differs from most of the other Australian species of Linguaphillipsia by the length of the glabella, as it does not go beyond on the anterior border furrow. This can be seen in one other species, Linguaphillipsia parvula Engel & Morris 1996, but they differ as L. engeli has a more semi-circular cephalon, and L. parvula has a distinctively triangular pygidium (Galtier et al. 2007).

6.15.2.1.v Linguaphillipsia parvula Engel & Morris 1996

1996 Linguaphillipsia parvula Engel & Morris: 129–130, Pl. 2 Figs. 9–18, Text Fig. 6
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Holotype material. AMF97019a/b (external/internal cranidium).

Paratype material. From NU L39: AMF97020 (external librigena), AMF97021 (external librigena), AMF97022a/b (external/internal pygidium), AMF97023 (external pygidium and librigena), AMF97024 (external pygidium), AMF98025 (internal pygidium), AMF97026 (external pygidium), AMF97027 (external pygidium), AMF97028 (external pygidium), AMF97029 (internal pygidium).

From NU L1054: AMF97030 (internal librigena), AMF97031a/b (external/internal pygidium), AMF97032 (external pygidium).

Locality. Type - NU L39. Other - NU L1054.

Emended diagnosis. Eyes long, posteriorly placed; S1 distinct, obliquely placed; L1 short and wide. Pygidium triangular, with 11–13 axial rings, 7 pleural ribs; posterior rings and ribs poorly defined.

Remarks. Specimens of Linguaphillipsia parvula are very small compared to other Australian Linguaphillipsia species. Engel & Morris include this in their diagnosis, and claim they are distinguished from other species by their size, but as size should not be used as defining characteristic it has been removed from the diagnosis. The triangular pygidium and short glabella however make it distinguishable from other Linguaphillipsia species in Australia.
6.15.2.1.vi Linguaphillipsia raglanensis Engel & Morris 1975

1975 Linguaphillipsia raglanensis Engel & Morris: 157–160, Pl. 1 Figs. 1–4, Text Figs. 3–6
1996 Linguaphillipsia raglanensis Engel & Morris: 127–129, Pl. 2 Figs. 1–8, Text Fig. 5

Holotype material. AMF80202a/b (external/internal pygidium).

Paratype material. AMF80200a/b (partial external/internal cephalon), AMF80201 (external pygidium), AMF80203a/b (external/internal pygidium), AMF80204 (internal pygidium), SMF27569 (external pygidium), SMF27570 (external pygidium).

Locality. NU L448.


Discussion. Linguaphillipsia raglanensis was first described by Engel & Morris (1975), using only poor preserved cephalic specimens. Due to this an external pygidium was chosen as the type specimen. In 1996 Engel & Morris found a
well preserved and complete specimen, allowing an emended diagnosis of the original species.

6.15.2.1.vii *Linguaphillipsia rouchelensis* (Mitchell 1918)

1892a *Phillipsia* sp. indet. Etheridge Jr.: 129, Pl. 21 Figs. 6–7

1918 *Phillipsia rouchelensis* Mitchell: 473, Pl. 48 Figs. 4–7

1971 *Phillipsia rouchelensis* Fletcher: 116

1972 *Conophillipsia? rouchelensis* Hahn & Hahn: 386–387

1975 *Linguaphillipsia elongata rouchelensis* Engel & Morris: 170–173, Pl. 2 Figs. 17–21

*Lectotype material.* AMF35855 (internal pygidium).

*Paralectotype material.* AMF35696 (internal pygidium), AMF35747 (internal pygidium), AMF35850 (internal pygidium).

*Locality.* Type - Given only as Binge Berry Rouchel Brook NSW in Engel & Morris (1975).

*Emended Diagnosis.* Pygidium with 18–19 axial rings, 14 pleural ribs; convex pygidial border; elongated semi-circular shape.
Remarks. Engel & Morris (1975) re-diagnosed the species *Phillipsia rouchelensis* Mitchell 1918 as a subspecies of *Linguaphillipsia elongata*, *Linguaphillipsia elongata rouchelensis*. No cephalas were ever found for *L. elongata rouchelensis* so the comparisons have been limited. The species described by Engel & Morris as *L. elongata rouchelensis* has a much more semi-circular shaped pygidium, less pygidial axial rings and pleural ribs, and a wider more convex pygidial border, compared with the species *L. elongata elongata*. As there are these differences in the pygidia between the two subspecies, they have been separated into two species, *L. elongata* and *L. rouchelensis*.

6.15.2.1.viii *Linguaphillipsia stanvellensis* (Mitchell 1918)

1892 *Phillipsia dubia* Etheridge Jr.: 214–215, Pl. 8 Fig. 5

1918 *Phillipsia stanvellensis* Mitchell: 461–463, Pl. 48 Figs. 10–12, 13, Pl. 51 Figs. 8–10

1964 *Phillipsia? stanvellensis* Hill & Woods: Pl. C14 Fig. 10

1972 *Phillipsia? stanvellensis* Hahn & Hahn: 420

1996 *Linguaphillipsia stanvellensis* Engel & Morris: 130–133, Pl. 3 Figs. 1–19

Holotype material. QGSF969 (internal dorsal shield).

Paratype material. QGSF980 (external glabella, hypostome and pygidium), QGSF977 (external pygidium).
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Locality. NU L1064.


Remarks. The distinct bell-shaped glabella of *L. stanvellensis* sets apart from other *Linguaphillipsia* species in Australia. *Linguaphillipsia stanvellensis* has a similar glabella shape to *L. elongata*, but can be distinguished from it as the glabella is wider posteriorly and more highly constricted.

6.15.2.2 Genus *Weberiphillipsia* Osmolska 1970

1970 *Weberiphillipsia* Osmolska: 13, 75–77
1972 *Weberiphillipsia* Hahn & Hahn: 378–379
1973 *Weberiphillipsia* Hahn & Hahn: 508–509
1978 *Weberiphillipsia* Yin: 443
1982 *Spinolimbella* Liu: 343
1983 *Weberiphillipsia* Engel & Morris: 232
1989 *Weberiphillipsia* Xiang: 122
1990 *Weberiphillipsia* Engel & Morris: 190–192
1995 *Weberiphillipsia* Yuan & Li: 8–9

Type species. *Phillipsia kirgisica* Weber 1932
Emended diagnosis. Convex anterior border in front of glabella; glabella just touches anterior border; weakly constricted at $\gamma$; 3–4 pairs of glabella furrows; eyes long, crescentic; strong pustulose ornament on glabella, librigenae, eyes and occipital ring. Pygidium same length as cephalon; 12–16 axial rings, 7–12 pleural ribs; border well defined with border furrow; ribs extend onto border as ornament, usually one or two nodes; nodular ornament on rings and ribs, well developed.

Remarks. The diagnosis of Weberiphillipsia by Engel & Morris (1983) stays relatively the same, with a few modifications. The pygidia of all specimens are not short or broad compared to the cephalon, and the glabella is not narrower towards the anterior in all specimens. Species of Weberiphillipsia from Australia have been reduced from five to four, after careful examination of all the specimens. Weberiphillipsia girvanensis Engel & Morris 1983 has been synonymised with Weberiphillipsia collinsi (Mitchell 1918) (see W. collinsi remarks for justification). The species Weberiphillipsia inostranzewi (Tolmachov 1924) and Weberiphillipsia kuzneciana (Weber 1937) included in the genus by Osmolska (1970) are considered dubious (Engel & Morris 1983; Brezinski 1988).

Weberiphillipsia was assigned to the subfamily Cummingellinae due to similar pygidial ornament in the genus Cummingella Reed 1942. Hahn & Hahn (1972) placed the genus within Linguaphillipsiinae Hahn & Hahn 1972 due to
similarities of the cephalon, as they argued the pygidial features are not
diagnostic, and are found in genera outside Cummingellinae Hahn & Hahn
1967. Engel & Morris (1983) created a new sub-family following the discovery
of a number of specimens in Australia. Engel & Morris (1983) argue that the
Weberiphillipsia species are derived from Phillipsia species, and developed
parallel to Linguaphillipsiinae genera during the Carboniferous (Engel &
Morris 1983). Brezinski (pers. com. 2011) has suggested that Weberiphillipsia is a
junior synonym of Palaeophillipsia Sugiyama and Okano 1944, though this is
difficult to assess as very few specimens of Palaeophillipsia exist, as well as good
quality photographs. The genus is upheld here until it can be proven it is a
junior synonym of Palaeophillipsia.

Species included. Weberiphillipsia angustilimbata Yuan & Li 1995, Weberiphillipsia
kirgisica (Weber 1932), ?Weberiphillipsia kuzneciana (Weber 1937), ?Weberiphillipsia
inostranzewi (Tolmatchoff 1924), Weberiphillipsia collinsi (Mitchell 1918),
Weberiphillipsia altoculata Engel & Morris 1983, Weberiphillipsia linguiformis Yuan
& Li 1995, Weberiphillipsia osmolskae Engel & Morris 1983, Weberiphillipsia robertsi
Engel & Morris 1983

Age and range. Late Touraisian to late Viséan in Asia and Australia (Engel &

6.15.2.2.i Weberiphillipsia altoculata Engel & Morris 1983
1983  *Weberiphillipsia altoculata* Engel & Morris: 244–246, Figs. 1F, 15, 16A–L

*Holotype material.* AMF80417 (external cephalon).

*Paratype material.* From NU L546: AMF80398 (partial internal pygidium). From NU L495: AMF80399 (external pygidium), AMF80400 (internal pygidium), AMF80401 (partial internal pygidium). From NU L652: AMF80402a/b (external/internal pygidium), AMF80403 (internal pygidium), AMF80404 (external pygidium), AMF80405 (external pygidium), AMF80406 (partial external cephalon), AMF80407 (internal cranidium), AMF80408 (external cranidium), AMF80409 (external cranidium), AMF80410 (external cranidium), AMF80411 (internal librigena), AMF80412 (two external pyidia), AMF80413 (external pygidium), AMF80414 (external pygidium), AMF80415 (external pygidium), AMF80423 (external pygidium), AMF80424a/b (external/internal librigena), AMF80425 (internal pygidium), AMF80426 (internal pygidium), AMF80427a/b (external/internal cranidium), AMF80428 (external cranidium), AMF80429 (external cranidium). From NU L701: AMF80416 (external pygidium), AMF80418 (external thorax and pygidium), AMF80419 (external pygidium), AMF80420 (external cranidium), AMF80421 (partial external pygidium), AMF80422 (external cranidium).

*Localities.* Type - NU L701. Others - NU L546, NU L495, NU L652.
Emended diagnosis. Cephalon parabolic; glabella long, nodose, gently expanded to maximum width posteriorly; greatest height anteriorly; palpebral lobes very large, steep, rising vertically to maximum height of cephalon, adjacent to large crescentic eyes; genal spines small, pointed. Pygidium with 13–14 axial rings, 7–9 pleural ribs; axial rings ornamented with large posteriorly inclined tubercles; ribs with two to four large tubercles; border wide with weak furrow; ribs extend onto border as low ridges, bearing a tubercle; outer border flat and smooth.

Remarks. The above diagnosis has been emended slightly from Engel & Morris (1983). The size of the genal spines has been changed from very small to small, and the second pygidial border furrow described by Engel & Morris (1983) is not visible on any of the external mold specimens examined herein.

6.15.2.2.ii Weberiphillipsia collinsi (Mitchell 1918)

Figure 6.5

1878  Phillipsia seminifera de Koninck: 210, Pl. 24 Fig. 9
1878  Phillipsia seminifera Etheridge: 42
1892  Phillipsia seminifera Etheridge Jr.: 124, 131
1892  Griffithides? sp. Etheridge Jr.: 130, Pl. 22 Figs. 15–16
1898  Phillipsia seminifer de Koninck: 276, Pl. 24 Figs. 9–9a
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1918  *Phillipsia collinsi* Mitchell: 444, Pl. 46 Figs. 1–5, Pl. 48 Figs. 8–9, Pl. 52

Fig. 4

1937  *Phillipsia* sp. 9 (cf. *Phillipsia collinsi* Mitchell); Weber: 59, Pl. 6 Fig. 43

1948  *Linguaphillipsia? collinsi* Stubblefield: 98, 100

1970  *Weberiphillispia (Linguaphillipsia?) collinsi* Osmolska: 48–49, 75

1972  *Weberiphillispia collinsi* Hahn & Hahn: 378

1978  *Weberiphillispia (Linguaphillipsia?) collinsi* Kobayashi & Hamada: 96, tab.1

1983  *Weberiphillispia collinsi* Engel & Morris: 238–241, Figs. 1D, 11, 12A–N

1983  *Weberiphillispia girvanensis* Engel & Morris: 241–244, Figs. 1E, 13, 14A–E

*Type material.* AMF28373 (internal cranidium).

*Paratype material.* From NU L361: AMF27748 (external pygidium), AMF28374 (internal pygidium), AMF28375 (internal pygidium), AMF28376 (internal pygidium), AMF28382 (internal dorsal shield). From NU L8: AMF80367 (internal dorsal shield), AMF80368 (external dorsal shield), AMF80369 (external pygidium), AMF80370 (external pygidium), AMF80371 (internal cranidium), AMF80372b (external cranidium), AMF80373 (internal pygidium), AMF80374 (internal pygidium), AMF80395 (external pygidium), AMF80396 (external pygidium), AMF80397 (partial external pygidium). From NU L538: AMF80375 (external pygidium), AMF80376 (internal pygidium), AMF80377 (internal
cranidium), AMF80378 (external pygidium), AMF80379 (internal pygidium),
AMF80380 (external cranidium), AMF80382 (external pygidium), AMF80383
(external cranidium), AMF80384 (partial external cranidium), AMF80385
(partial external pygidium), AMF80386 (external cranidium), AMF80387 (partial
external pygidium). From NU L585: AMF80388 (external pygidium), AMF80389
(external pygidium), AMF80390 (partial external pygidium), AMF80391 (partial
internal pygidium), AMF80392 (internal pygidium), AMF80393 (external
pygidium). From NU L404: AMF80394 (partial internal pygidium).

Localities. Type - NU L361. Others - NU L8, NU L404, NU L538, NU L585.

Emended diagnosis. Cephalon parabolic; glabella long, densely nodose,
considerably wider posteriorly to the medial constriction; greatest height in the
centre of the glabella; palpebral lobes wide, raised laterally; genal spines short
and pointed. Pygidium with 13–14 axial rings, 9–10 pleural ribs; border wide
with distinct furrow; anterior ribs pass onto border as one or two nodes or
spines; alignment of nodes with ribs diminishes posteriorly; outer area of
border smooth; axial rings and ribs highly nodose.

Remarks. *Weberiphillipsia girvanensis* Engel & Morris 1983 has been synonymised
with *W. collinsi*. The specimens of *W. girvanensis* show a highly nodose
pygidium and cephalon, a very wide posterior section of the glabella, a row,
sometimes two, of nodes on the pygidial border, with an outer smooth margin,
and parabolic cephalas. These characteristics are identical to specimens of *W. collinsi*. There does not appear to be any difference between the two original species as separated by Engel & Morris. The above diagnosis has been emended to include some variations within the newly synonymised species.

### 6.15.2.2.iii Weberiphillipsia osmolskae Engel & Morris 1983

1983 *Weberiphillipsia osmolskae* Engel & Morris: 232–235, Figs. 1B, 6, 7A–G

**Type material.** AMF80293 (external pygidium).

**Paratype material.** From NU L353: AMF80277 (external pygidium), AMF80278 (internal pygidium), AMF80279 (internal pygidium), AMF80280 (partial internal pygidium), AMF80281 (external cephalon), AMF80282 (external librigena), AMF80283 (external cranidium), AMF80284 (internal cephalon), AMF80285 (internal pygidium), AMF80286 (partial internal pygidium), AMF80287 (external pygidium and thorax), AMF80288 (external pygidium), AMF80289 (partial external cranidium), AMF80290 (external cranidium), AMF80291 (external librigena), AMF80292 (internal librigena). From NU L336: AMF80294 (external pygidium), AMF80295 (external pygidium), AMF80296 (external cranidium). From NU L984: AMF80297a/b (external/internal pygidium), AMF80298 (external pygidium), AMF80299 (external glabella), AMF80300 (partial external pygidium), AMF80301 (internal hypostome).
**Locality.** Type - NU L25. Others - NU L336, NU L353, NU L984.

**Emended diagnosis.** Cephalon semicircular; glabella nodose, weakly constricted medially, greatest height and width to the posterior; wide palpebral lobes elevated laterally; genal spines medium length. Pygidium with 14–15 axial rings, 11–12 pleural ribs; border wide, convex to flat with weakly impressed border furrow; ribs intersect border as elongate spinose ridges, extend to outer margin; axial rings nodose.

**Remarks.** The above diagnosis has been emended from Engel & Morris (1983). Pleural rib ornament is not visible in specimens, and the length of the glabella described in Engel & Morris (1983) has been removed. Weberiphillipsia osmolskae has a semi-circular cephalon and pygidium, a unique pygidial border ornament, long ridges continuing to the margin of border. All other species of Weberiphillipsia have nodes or spines.

**6.15.2.2.iv Weberiphillipsia robertsi Engel & Morris 1983**

1983  
*Weberiphillipsia robertsi* Engel & Morris: 235–238, Figs. 1C, 8, 9, 10A–H

**Type material.** AMF80320 (external thorax and pygidium).
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Paratype material. From NSW 17/7: AMF80302 (partial external pygidium), AMF80303 (internal librigena), AMF80304 (partial external pygidium), AMF80314 (partial external pygidium), AMF80315 (external pygidium), AMF80316 (external librigena and hypostome). From NU L979: AMF80318 (external pygidium), AMF80319 (internal cranidium), AMF80321 (external thorax and pygidium), AMF80322 (external pygidium), AMF80323 (internal pygidium), AMF80324 (external cranidium), AMF80325 (external librigena), AMF80326 (external hypostome), AMF80330a/b (external/internal pygidium), AMF80331 (external pygidium), AMF80332 (external pygidium), AMF80333 (external pygidium), AMF80334 (internal pygidium). From NU L396: AMF80317 (external pygidium). From NU L262: AMF80329 (partial internal pygidium), AMF80335 (internal glabella), AMF80336a/b (external/internal librigena). From NU L263: AMF80327 (partial external pygidium), AMF80328 (external pygidium). From NU L264: AMF80305 (half internal cephalon), AMF80306 (internal pygidium), AMF80307 (partial external cephalon), AMF80308 (partial external pygidium), AMF80309 (external pygidium), AMF80310 (external pygidium), AMF80311 (external pygidium), AMF80312 (internal pygidium), AMF80313 (half internal cephalon).

Locality. Type - NU L979. Others - NU L262, NU L263, NU L264, NU L396, NU L979, NSW17/7.

Diagnosis. See Engel & Morris (1983).
Remarks. *Weberiphillipsia robertsi* is easily distinguishable from other species of *Weberiphillipsia* in that it has a triangular shaped cephalon and, a particularly spinose pygidium, with 2 to 3 nodes on the pygidial border, not seen in other species. The diagnosis in Engel & Morris (1983) is sufficient, other than the length of the genal spines, which appear to be a medium pointed length, not short.

6.16 Nomen Dubia

Cladistics began to develop long before the term was coined. With homology formalised by Owen (1843) and evolutionary theory proposed as a mechanism by Darwin (1859), systematists such as Haeckel and Lankester were able to develop theories such as phylogeny (Haeckel 1966) and, a common ancestor as an explanation for homology (Lankester 1870). These added to the natural classification of taxa by providing a source of evidence (homology) and explanation (phylogeny) of their hierarchical nature.

Cladistics had many proponents who synthesized the ideas of Willi Hennig differently, creating an epistemological split in the theoretical underpinnings of homology and monophyly. On one side, there are the process cladists, those who considered ancestors to be real entities and who created phylogenies as their ultimate goal. On the other side, are the pattern cladists, those who considered ancestors to be theoretical and unnecessary in discovering natural classifications. The pattern cladists eventually distanced themselves from the numerical or process oriented discussions, and focussed more on the role of natural classification for systematics and taxonomy, rather than phylogenetic reconstruction (i.e., character transformations).
Chapter 7. General Conclusion

As with differences in theory and aims of cladistics, so too have their been differences in understanding of the definition of monophyly. The concept of a monophyletic group was first proposed by Haeckel (1866) who considered life to have evolved from one source. The concept grew from there, with the definition of a monophyletic group radically changing throughout the 20th century. The evolutionary biologists Simpson (1961), Mayr (1965) and Ashlock (1971, 1972) considered a monophyletic group to consist of taxa descended from a common ancestor. Hennig (1950, 1965, 1966) insisted that a monophyletic group should be considered as a group containing all taxa descended from a common ancestor. A debate ensued as to how monophyly should be defined.

An analysis of the historical development of the definition found there were two interpretations behind the theory of the concept of monophyly. As such, monophyly can actually be divided into two distinct definitions. The first, \textit{diamonophyly}, is defined as a group of taxa requiring an ancestor, and is considered an inference of the relationships between ancestors and descendants. The second, \textit{synmonophyly}, is based on evidence of relationship only, by not considering an ancestral taxon. The difference is evidence versus inference, and is considered here to explain the debate on the definition of monophyly.

The reason for such a heated debate on monophyly is that it is considered to be the ultimate goal for a systematic study. A monophyletic group represents natural and not \textit{artificial} relationships. Despite this, biostratigraphers using
existing classifications have not ensured their groups are monophyletic. The biggest problem with not considering a monophyletic group for biostratigraphy is that the marker taxa used for the study may be artificial. Artificial or aphyletic taxa are often re-classified when more taxa are found, which leads to a need for re-evaluation of any biostratigraphic work that has been done. The role of cladistics is to separate natural classification of fossil groups from spatio-temporal studies in geology, in effect making systematics independent of biostratigraphy (contra Campbell 1975).

In order to embrace this new position, it is suggested that biostratigraphers take advantage of the modern systematic method of cladistics to ensure a monophyletic group is being used. By ensuring marker taxa are naturally occurring the group in question will not need to be re-classified. Any biostratigraphic study resulting from those marker taxa can then be considered to be more accurate, as the groups truly existed in nature.

Unfortunately, biostratigraphers do not use monophyletic groups as marker taxa and often taxa are classified based on biostratigraphy. The classification of taxa based on stratigraphy is known as the successional species concept (Wilkins 2009). One such group that appears to be based on this concept is the Phillipsiidae, a family of trilobites specifically classified as the proetids from the Late Devonian to the Permian (Hahn et al. 1980). The consequences of using
stratigraphy for classification purposes may not be apparent at first, but an analysis of the family Phillipsiidae has shown that the family is aphyletic.

When the genera and subfamilies currently considered belonging to Phillipsiidae had their important characters assessed, using cladistic analysis, they fail to form a monophyletic group. While there could well be a Phillipsiidae family, consisting of the subfamilies Linguaphillipsiinae and Phillipsiinae, at this stage it is only conjecture. The other subfamilies currently considered part of the Phillipsiidae including Archegoninae, Bollandiinae, Cummingellinae, Cystispininae, Ditomopyginae, Griffithidinae and Weaniinae are considered to belong to the larger family Proetidae.

With the new Phillipsiidae classification in mind, the Carboniferous and Permian trilobites of Australia have been revised. Many of the species and genera were originally classified on the successional species concept. Of the 63 originally classified species, only 54 are maintained. Emended diagnoses for 33 of those species plus 7 of the 22 genera have also been completed. This is the first complete review of the Carboniferous and Permian trilobites of Australia. The taxa now included in the Phillipsiidae family are Phillipsia, Linguaphillipsia and Weberiphillipsia. All other proetid genera and species are considered to be from the family Proetidae.


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<td>Flagstaff Formation, Middle-Upper Viséan</td>
<td></td>
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<tr>
<td>NU L415</td>
<td>Cangon, west of Dungog - Clarence Town, near Dungog, NSW</td>
<td>Flagstaff Formation, Middle-Upper Viséan</td>
<td></td>
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<tr>
<td>NU L427</td>
<td>Berrico Station, Gloucester, NSW</td>
<td>Wootton Beds, Middle-Upper Viséan</td>
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<tr>
<td>NU L446</td>
<td>Gloucester Tops Road, Berrico, NSW</td>
<td>Wootton Beds, Middle-Upper Viséan</td>
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<tr>
<td>NU L448</td>
<td>Raglan Station, near Dungog, NSW</td>
<td>Ararat Formation, Lower-Upper Tournaisian</td>
<td></td>
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<tr>
<td>NU L456</td>
<td>Lewinsbrook, NSW</td>
<td>Bonnington Siltstone, Lower Viséan</td>
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<tr>
<td>NU L484</td>
<td>Oaky Creek, east of Dungog, NSW</td>
<td>Ararat Formation equivalent, Lower-Upper Tournaisian</td>
<td></td>
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<tr>
<td>NU L492</td>
<td>Salisbury area, northwest of Dungog, NSW</td>
<td>Flagstaff Formation, Middle-Upper Viséan</td>
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<tr>
<td>NU L506</td>
<td>Road cutting south of Raglan Station towards Booral, near Dungog, NSW</td>
<td>Wootton Beds, Middle-Upper Viséan</td>
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<tr>
<td>NU L522</td>
<td>Salisbury area, northwest of Dungog, NSW</td>
<td>Flagstaff Formation, Middle-Upper Viséan</td>
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<tr>
<td>NU L546</td>
<td>Quartpot Creek, Brownmore, NSW</td>
<td>Flagstaff Formation, Middle-Upper Viséan</td>
<td></td>
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<tr>
<td>NU L620</td>
<td>Southwest Rawdon Vale, near Gloucester Tops, NSW</td>
<td>Berrico Creek Formation, Upper Viséan</td>
<td></td>
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<tr>
<td>NU L652</td>
<td>North Rawdon Vale, near Cobark, NSW</td>
<td>Berrico Creek Formation, Upper Viséan</td>
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<tr>
<td>NU L672</td>
<td>Clarencetown, NSW</td>
<td>Bonnington Siltstone, Lower Viséan</td>
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<tr>
<td>NU L701</td>
<td>North Rawdon Vale, near Cobark NSW</td>
<td>Wootton Beds, Middle-Upper Viséan</td>
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<tr>
<td>NU L740</td>
<td>South of Pindimar Turnoff, Tea Gardens, NSW</td>
<td>Wootton Beds, Lower-Upper Tournaïsan</td>
<td></td>
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<tr>
<td>NU L861</td>
<td>In creek, Berrico Station, Gloucester, NSW</td>
<td>Berrico Creek Formation, Upper Viséan</td>
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<tr>
<td>NU L871</td>
<td>Arundel Station, Rawdon Vale, NSW</td>
<td>Berrico Creek Formation, Upper Viséan</td>
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<tr>
<td>NU L890</td>
<td>Nugra Road, south of Girvan, NSW</td>
<td>Wootton Beds, Lower-Upper Tournaïsan</td>
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<tr>
<td>NU L894</td>
<td>Branch Creek Road, northwest of Gloucester, NSW</td>
<td>Conger Formation, Middle-Upper Viséan</td>
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<tr>
<td>NU L925</td>
<td>South bank of the Manning River, near Wingham, NSW</td>
<td>Colhaine Mudstone, Lower Permian</td>
<td></td>
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<tr>
<td>NU L979</td>
<td>Back Creek, Rouchel Brook, NSW</td>
<td>Woolooma Formation, Lower Viséan</td>
<td></td>
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<tr>
<td>NU L984</td>
<td>Mt. Richardson road cuttings, Mt. Richardson, near Dungog, NSW</td>
<td>Bonnington Siltstone, Lower Viséan</td>
<td></td>
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<tr>
<td>NU L1039</td>
<td>Glen William Road, 3km north of Clarence Town, NSW</td>
<td>Flagstaff Formation, Middle-Upper Viséan</td>
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<tr>
<td>NU L1047</td>
<td>Boulder Creek, near Mt. Morgan, Queensland</td>
<td>Neils Creek Clastics, Lower-Upper Tournaïsan</td>
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<tr>
<td>NU L1049</td>
<td>Malchi Creek, Malchi, near Gracemere, Queensland</td>
<td>Malchi Creek Formation, Lower-Upper Tournaïsan</td>
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<tr>
<td>NU L1054</td>
<td>Creek on the west bank of Lake Keept, near Manilla, NSW</td>
<td>Namoi Formation, Lower-Upper Tournaïsan</td>
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<tr>
<td>NU L1064</td>
<td>Corner creek and Star River, near Paluma, Queensland</td>
<td>Hardwick Formation, Tournaïsan</td>
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<tr>
<td>QGS L3004</td>
<td>Trilobite Ridge, Mt. Morgan, Queensland (Mitchell 1918)</td>
<td>Crow’s Nest area, Tournaïsan</td>
<td></td>
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<tr>
<td>QM L508</td>
<td>Mrs Harding’s Property on low hills, 1km southeast of homestead, above limestone hard ground, Queensland</td>
<td>Lower Carboniferous (exact formation/age unknown)</td>
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<tr>
<td>NSW L58-12</td>
<td>Northeast of Glenhawn Dam, Rouchel district, NSW</td>
<td>Waverley Formation, Lower-Upper Tournaïsan</td>
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<tr>
<td>NSW L112-6</td>
<td>Swain’s Gully, southwest of Somerton, NSW</td>
<td>Namoi Formation, Lower-Upper Tournaïsan</td>
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<tr>
<td>NSW17/7</td>
<td>Back Creek, Rouchel Brook area, NSW</td>
<td>Woolooma Formation, early Viséan</td>
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<tr>
<td>MUM</td>
<td>Near Alison, Dungog district, NSW</td>
<td>Ararat Formation, Lower-Upper Tournaïsan</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Location Description</td>
<td>Formation &amp; Age</td>
<td></td>
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<td>---------------------------------------------</td>
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<tr>
<td>BBS</td>
<td>Bury Bury Station, southwest of Barraba, NSW</td>
<td>Namoi Formation, Lower-Upper Tournaisian</td>
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<tr>
<td>CN</td>
<td>Mt. Morgan, Queensland (Mitchell 1918); exact location unknown</td>
<td>Unknown</td>
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<tr>
<td>DV</td>
<td>Unknown locality in Gresford district NSW; Description by M’Coy 1847</td>
<td>Unknown</td>
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<tr>
<td>FB</td>
<td>Fairy Bower, west of Rockhampton, Queensland</td>
<td>Ponds Formation equivalent, age unknown</td>
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<tr>
<td>MULBRING QUARRY</td>
<td>Mulbring Quarry, Mulbring, NSW</td>
<td>Branxton Formation, Middle Permian</td>
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<tr>
<td>RAY’S HILL</td>
<td>Ray’s Hill, St. Mary’s, Tasmania</td>
<td>Enstone Park Limestone, Lower Permian</td>
<td></td>
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<tr>
<td>ST</td>
<td>Stanwell, west of Rockhampton, Queensland</td>
<td>Unknown</td>
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